The Future of High-Elevation, Five-Needle White Pines in Western North America

Proceedings of the High Five Symposium

28-30 June 2010; Missoula, Montana

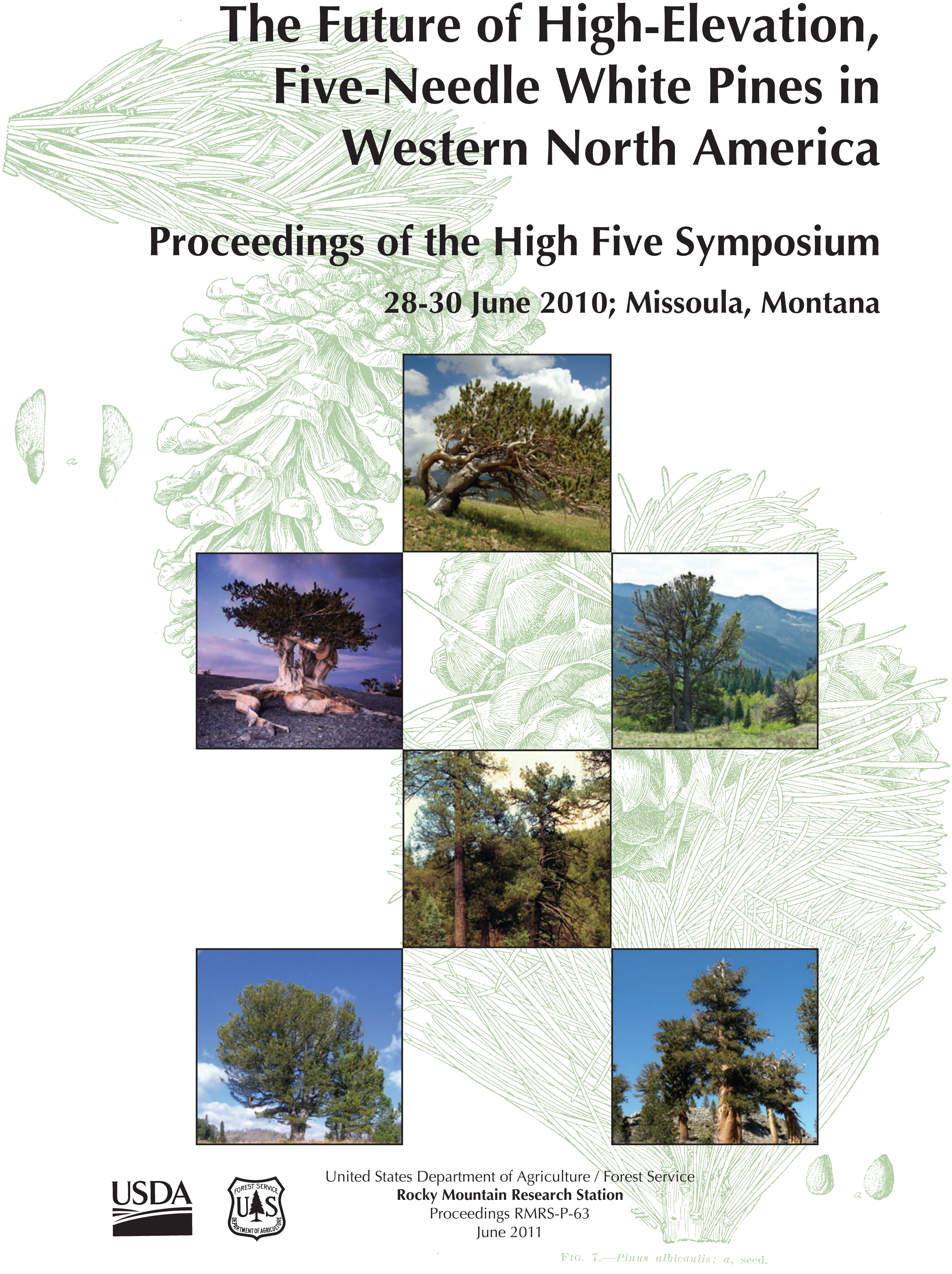

FIG. 7.—*Pinus albicaulis: a*, seed.

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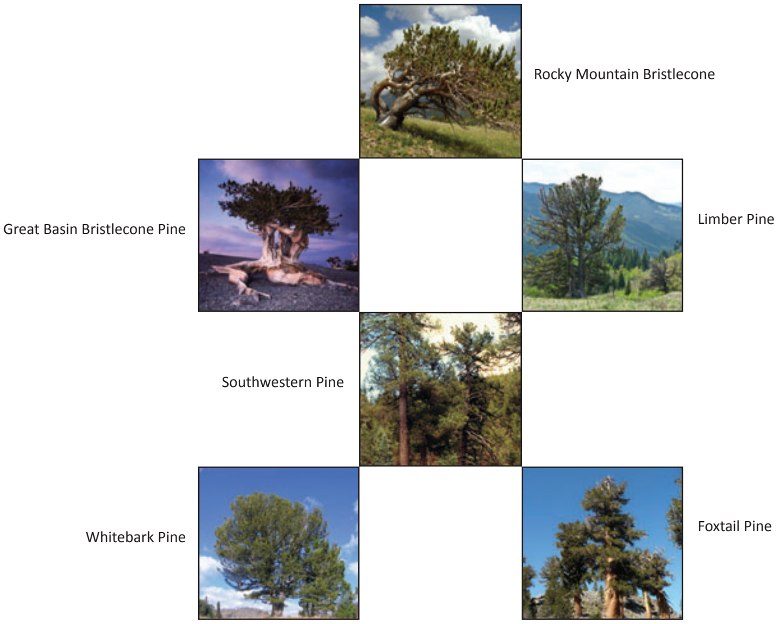
Abstract

High elevation five-needle pines are rapidly declining throughout North America. The six species, whitebark (*Pinus albicaulis* Engelm.), limber (*P. flexilis* James), southwestern white (*P. strobiformis* Engelm.), foxtail (*P. balfouriana* Grev. & Balf.), Great Basin bristlecone (*P. longaeva* D.K. Bailey), and Rocky Mountain bristlecone pine (*P. aristata* Engelm.), have limited timber value but are of great ecological and symbolic importance to both the U.S. and Canadian West. A comprehensive International symposium, called the High Five symposium, was held June 28-30, 2010, in Missoula, Montana to: (1) bring together scientists, managers, and concerned citizens to exchange information on the ecology, threats, and management of these pines; (2) learn about the threats and current status of pine populations; (3) describe efforts to mitigate threats through restoration techniques and action plans; and, (4) build a foundation for the synthesis of research efforts and management approaches. These proceedings present reports of some of the presentations given at the conference in the form of abstracts, extended abstracts, papers, and plenary papers in the areas of ecology, disturbance dynamics, genetics, climate change, and restoration techniques.



Cover photos: High-elevation, five-needle white pines of North America.

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The Future of High-Elevation, Five-Needle White Pines in Western North America:

Proceedings of the High Five Symposium

28-30 June 2010; Missoula, Montana

Editors:

Robert E. Keane
Diana F. Tomback
Michael P. Murray
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Preface

The High Five Symposium (*The Future of High-Elevation, Five-Needle White Pines in Western North America*) was the first major conference to focus on a group of high elevation white pines of limited timber value but of great ecological and symbolic importance to both the United States and the Canadian West. The six species, whitebark (*Pinus albicaulis* Engelm.), limber (*P. flexilis* James), southwestern white (*P. strobiformis* Engelm.), foxtail (*P. balfouriana* Grev. & Balf.), Great Basin bristlecone (*P. longaeva* D. K. Bailey), and Rocky Mountain bristlecone pine (*P. aristata* Engelm.), are confronted with a number of threats to their existence. As these pines decline, North America faces a significant loss in biodiversity—not only in habitat but in the many species that depend on these species (see plenary paper by Tomback and others, these proceedings).

The high-elevation five-needle white pines ("High Five") play important functional roles in high-mountain ecosystems, acting as keystone and foundation species by providing ecosystem stability, wildlife habitat and food, and forest biodiversity. At least one High Five pine species is found in every high mountain region of the western United States and Canada, occurring in association with many other forest trees and understory species, and thus collectively contributing a diversity of forest cover types.

The High Five pines vary both successionally and geographically from minor to major forest and treeline components. As a group, they are also moderately to strongly shade intolerant and dependent on disturbance, particularly fire, on productive sites for forest renewal. The high elevation pines tolerate cold, arid sites with poor soils. On exposed sites with infrequent disturbance, these trees can live for 1000 to 4500 years, depending on the species. Whitebark, limber, and southwestern white pine produce large, wingless seeds that are eaten by a diversity of wildlife. Clark's nutcrackers (*Nucifraga columbiana* [Wilson]) are important seed dispersers for whitebark and limber pine, for southwestern white pine in its northern range, and to a lesser extent for the bristlecone pines. Furthermore, the High Five pines provide important ecosystem services directly benefiting humans—for example, the use by Native Americans of seeds, needles, and resin and other tree parts as food or medicine, the regulation of downstream flow and the prevention of soil erosion by treeline forests, and the aesthetic and spiritual values often associated with high elevation forests.

In fact, the High Five pines contribute unique aesthetics to high elevation forest ecosystems in their varied forms. They may occur in multi-layered forests of old growth trees, as rare millennium-aged stalwart individuals growing solitarily or in small stands on remote slopes, as wind-battered, strip-barked survivors on harsh upper subalpine sites, or as mat-like, creeping krummholz growth forms under the harshest conditions at the highest treeline elevations.

The future survival of the High Five pines is threatened by the exotic blister rust pathogen *Cronartium ribicola* JC. Fisch. in Rabh., current mountain pine beetle (*Dendroctonus ponderosae* Hopkins) outbreaks, successional replacement from fire exclusion, and climate change. These multiple challenges to the persistence of the High Five pines on the Western landscape are the direct or indirect consequence of human activities, complicated by the unique ecology of the pines. In effect, the vulnerabilities of the high elevation pines reflect the challenges faced by natural communities in today's rapidly changing world. The most pervasive and widespread threat is the invasive fungal pathogen *Cronartium ribicola*, which causes the disease white pine blister rust in five-needle white pines. From the time of its introduction to the West more than a century ago, this destructive and fatal fungal pathogen has spread to all five-needle white pine hosts except Great Basin bristlecone pine, from montane to treeline elevations, into cold and arid climatic regimes, and even to the northernmost populations of pines. Most infected trees lose their cone-producing capacity years before succumbing to blister rust, resulting in diminished natural regeneration. In the late 1990s, mountain pine beetle outbreaks, a natural, recurrent disturbance in the West, again moved into high elevation white pine forests throughout the western United States and Canada. These outbreaks have achieved an unprecedented geographic scale and incidence of white pine mortality. Reduction in the frequency and size of fires by effective and extensive fire suppression programs and fire exclusion policies has led to the successional replacement of the high-elevation five-needle white pines growing on productive sites, given their shade-intolerance. Because fire-return intervals are so long in upper subalpine ecosystems, the effects of fire exclusion are most apparent at the landscape scale rather than the stand scale, with an increasing proportion of successionally advanced communities over time. Finally, we know that we need healthy white pine populations to meet the challenges posed by changing climatic regimes in order to effect range shifts and create new forest community assemblages.

The High Five symposium was organized to achieve several objectives in relation to the high-elevation white pines: (1) bring together scientists, managers, and concerned citizens to exchange information on the ecology, threats, and management of these pines; (2) learn about the threats and current status of pine populations; (3) describe efforts to combat the threats through research and restoration techniques and plans; and (4) build the foundation for a synthesis of research efforts and management approaches. Working together to realize these objectives, contributors from the United States and Canada, across the distributions of all the High Five pines, have brought the wisdom of their own observations, research, and perspectives.

This symposium has been a major collaborative project of the Whitebark Pine Ecosystem Foundation for two years. It would not have been possible without the commitment of Carl Fiedler, chief organizer, who has worked on the symposium since its inception with our conference liaison Debbra Graham and her staff at University of Montana Continuing Education. Bob Keane organized an excellent program as well as the preliminary editing and assembly of the proceedings volume. Michael Murray, Cyndi Smith, and I helped with the editorial responsibilities. Dan Reinhart organized the poster session, and Bryan Donner orchestrated a tremendously enjoyable and highly educational field trip to Montana Snow Bowl, accommodating all attendees, as well as guided post-conference fieldtrips. We are truly grateful to our trans-boundary High Five Steering Committee, who provided advice on plenary session speakers and helped with organizational decisions, often on short notice (see below).

Finally, we would like to thank our federal agency and NGO sponsors who have helped fund this symposium, enabling us to keep down registration costs and provide travel and registration fellowships to several deserving attendees. They include the Crater Lake Institute, Crater Lake National History Association, Greater Yellowstone Park Inventory and Monitoring Network, National Park Service, Natural Resources Defense Council, Parks Canada, Rocky Mountains Cooperative Ecosystem Studies Unit, Sierra Nevada Inventory and Monitoring Network, The Nature Conservancy, Upper Columbia Basin Inventory and Monitoring Network, University of Montana College of Forestry and Conservation, U.S. Forest Service Northern Region, and U.S. Forest Service Rocky Mountain Research Station.

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Whitebark Pine Ecosystem Foundation

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The Magnificent High-Elevation Five-Needle White Pines: Ecological Roles and Future Outlook

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Abstract—The High Five symposium is devoted to exchanging information about a small group of pines with little commercial value but great importance to the ecology of high-mountain ecosystems of the West. These High Five pines include the subalpine and treeline species—whitebark (*Pinus albicaulis*), Rocky Mountain bristlecone (*P. aristata*), Great Basin bristlecone (*P. longaeva*), and foxtail (*P. balfouriana*)—the montane to subalpine pine, southwestern white (*P. strobiformis*), and the lower treeline to upper treeline pine, limber (*P. flexilis*). Here, we discuss the taxonomy, distribution, ecology, and Native American use of these pines, as well as current threats and conservation status. Traditional classification places the bristlecones and foxtail pine together in Subsection Balfourianae, limber and southwestern white pine in Subsection Strobi, and whitebark pine in Subsection Cembrae. Whitebark pine has the largest range and most northerly occurrence. The distribution of limber pine is also large, with a wide elevational range. Southwestern white pine occurs from the southwestern U.S. through northern Mexico; foxtail pine is found in two widely-separated regions in California; and, Rocky Mountain bristlecone pine occurs in northern Arizona and the southern Rocky Mountains. Great Basin bristlecone pine is restricted to the high desert ranges of eastern California, Utah, and Nevada. The High Five pines vary successionally and geographically from minor to major forest and treeline components. As a group, they are also moderately to strongly shade intolerant, and dependent on disturbance, particularly fire, on productive sites for forest renewal. The high elevation pines tolerate cold, arid sites with poor soils. On exposed sites with infrequent disturbance, these trees can live for 1000 to 4500 years, depending on the species. Thus, these pines together comprise geographically extensive and ecologically diverse forest habitat types. Whitebark, limber, and southwestern white pine produce large, wingless seeds that are eaten by a diversity of wildlife. Clark's nutcrackers (*Nucifraga columbiana*) are important seed dispersers for whitebark and limber pine, for southwestern white pine in its northern range, and to a lesser extent for the bristlecone pines. Furthermore, the High Five pines provide important ecosystem services directly benefiting humans, including the use of the seeds and other parts of pines as food and medicines by Native Americans, the regulation of downstream flow and the prevention of soil erosion by treeline forests, and the aesthetic and spiritual values often associated with high elevation forests. The future survival of the High Five pines is threatened by the exotic blister rust pathogen *Cronartium ribicola*, current mountain pine beetle (*Dendroctonus ponderosae*) outbreaks, successional replacement from fire suppression, and climate change. Whitebark pine has been assigned special status in Washington and British Columbia, and endangered status along with limber pine in Alberta. A petition to list whitebark pine as an endangered or threatened species is currently being evaluated by the U.S. Fish and Wildlife Service. In Canada, whitebark pine has been assessed federally as Endangered and is expected to be legally listed soon under the Species at Risk Act.

Why the High Five Pines?

The High Five Symposium was precedent-setting in that it focused on a group of pines comprising six high-elevation five-needle white pines (Family Pinaceae, Genus *Pinus*, Subgenus *Strobus*) with little to no timber value but with considerable ecological importance. These pines include whitebark (*Pinus albicaulis*), limber (*P. flexilis*), southwestern white (*P. strobiformis*), foxtail (*P. balfouriana*), Rocky Mountain bristlecone (*P. aristata*), and Great Basin bristlecone (*P. longaeva*) (Figure 1). Although not a treeline species, southwestern white pine is included within the "High Five" because it is a subalpine forest species that tolerates harsh, wind-swept sites. In the southwestern U.S. and Mexico, southwestern white pine is an important component of high elevation forests.

Research on the High Five pines during the past decade has provided new information on their ecology and distribution, threats to their survival, and changing population status. It also spurred the development of management tools such as survey and monitoring protocols and potential restoration strategies. The High Five symposium, hosted by the Whitebark Pine Ecosystem Foundation in collaboration with various federal resource agency and non-profit sponsors, provided a forum for information exchange, with the ultimate goal of achieving effective long-term management and restoration plans, and speeding their implementation.

The High Five pines play important functional roles in high-mountain ecosystems, with several acting as keystone and foundation species (Tomback and others 2001a; Schoettle 2004; Tomback and Achuff 2010) and thus providing both stability to ecosystems and fostering biodiversity (Mills and others 1993; Ellison and others 2005). At least one High Five pine species is found in every high mountain region of the western U.S. and Canada, contributing a diversity of forest cover types (Eyre 1980; Tomback and Achuff 2010). These pines are functional components of high-elevation ecosystems and provide ecosystem services directly benefitting humans (Tomback and others 2001; Tomback and Achuff 2010). Collectively, they represent a large array of community types because they occur in association with many other forest trees and understory species (for example, see Tables 3a, 3b in Tomback and Achuff 2010). In addition, these pines contribute a unique aesthetic to high elevation forest ecosystems whether as multi-layered forests of tall, old growth trees, through the rare presence of millennium-aged

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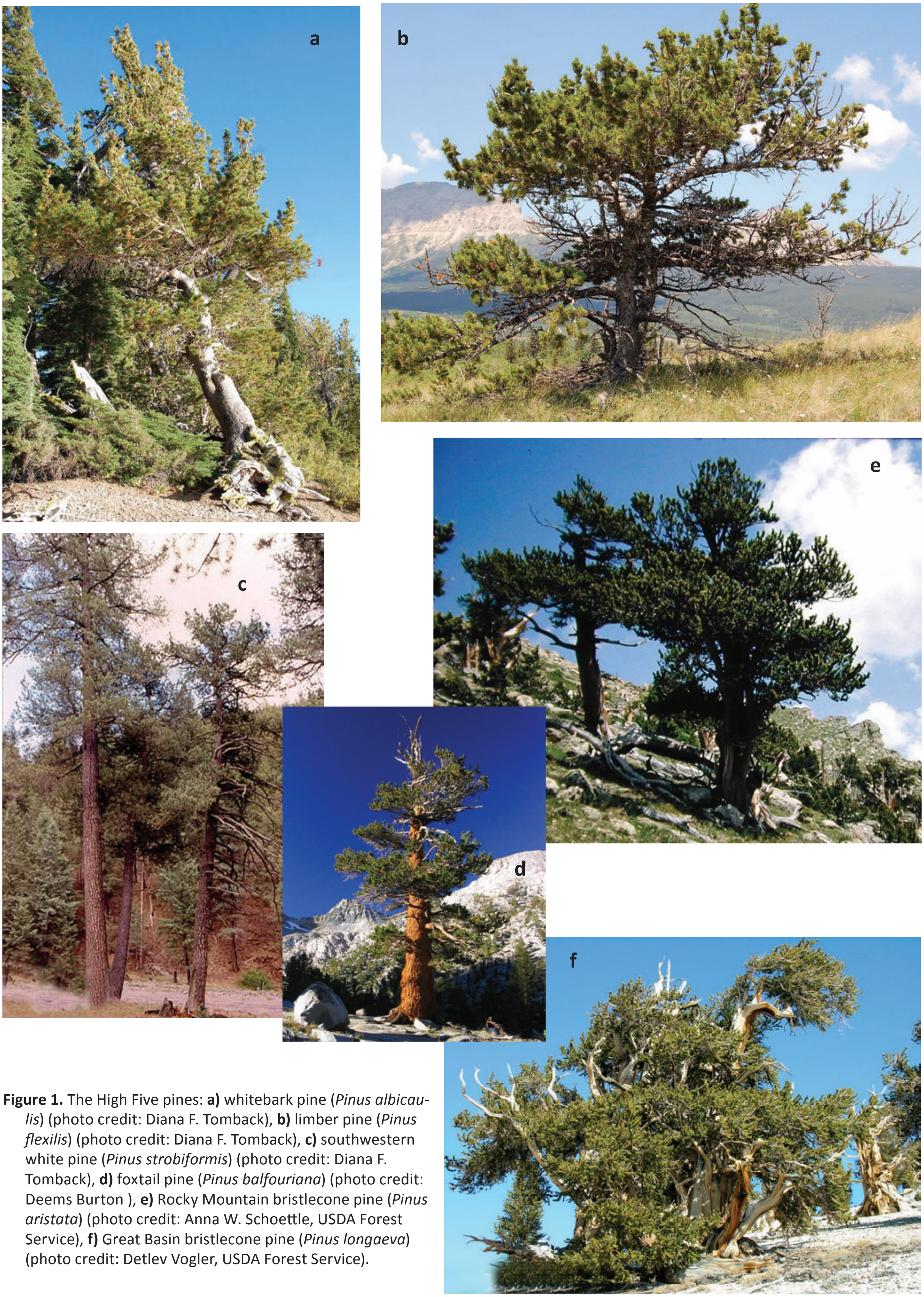


Figure 1. The High Five pines: **a)** whitebark pine (*Pinus albicaulis*) (photo credit: Diana F. Tomback), **b)** limber pine (*Pinus flexilis*) (photo credit: Diana F. Tomback), **c)** southwestern white pine (*Pinus strobiformis*) (photo credit: Diana F. Tomback), **d)** foxtail pine (*Pinus balfouriana*) (photo credit: Deems Burton), **e)** Rocky Mountain bristlecone pine (*Pinus aristata*) (photo credit: Anna W. Schoettle, USDA Forest Service), **f)** Great Basin bristlecone pine (*Pinus longaeva*) (photo credit: Detlev Vogler, USDA Forest Service).

trees growing solitarily or in small stands on remote slopes, as wind-battered, strip-barked survivors on harsh upper subalpine sites, or as mat-like, creeping krummholz growth forms under the harshest conditions at the highest treeline elevations (Figure 1).

In this paper, we present basic information on the High Five pines concerning the taxonomy, distribution, community ecology, seed dispersal ecology, and Native American use of these pines, as well as current threats and conservation status. We intend this overview to provide background for the other papers in these proceedings, as well as to highlight some of the issues of concern.

Taxonomy and Distribution

According to traditional classification, the High Five pines are taxonomically diverse species within subgenus *Strobus* (also known as the soft or haploxylon pines) and have distinct evolutionary and biogeographic histories. These different histories have resulted in different patterns of geographic distribution. The High Five pines, however, are similar ecologically and in having needles in fascicles of five as well as sharing susceptibility to infection by *Cronartium ribicola*, the exotic pathogen that causes white pine blister rust.

Taxonomy

The traditional classification of the High Five pines places whitebark pine in Section *Strobus*, Subsection *Cembrae*, as the only North American member of a taxon that otherwise comprises European and Asian species (Table 1). The *Cembrae* pines or stone pines were traditionally considered a monophyletic group with derived traits adapted to avian seed dispersal by the nutcrackers, Clark's (*Nucifraga columbiana*) and the Eurasian or Spotted nutcracker (*N. caryocatactes*). Among these derived traits are indehiscent (non-opening) cones and relatively large, wingless seeds (Lanner 1990; Tomback and Linhart 1990; Price and others 1998). Limber and southwestern white pine, also traditionally classified in Section *Strobus* but in Subsection *Strobi*, are closely related species (Andresen and Steinhoff 1971). Both species have large, wingless seeds but cones that open when seeds have matured. The three "foxtail" pines, the Rocky Mountain and Great Basin bristlecones and foxtail, are considered distant relatives of the other pines and placed in Section Parrya, Subsection *Balfourianae*. The seeds of these species are small and winged and the cones open when seeds ripen—traits common for seed and cone morphology within the genus *Pinus* (Tomback and Linhart 1990).

The traditional classification of the *Strobi* and *Cembrae* pines has been challenged by studies of gene sequences of nuclear and chloroplast DNA. Sequence analyses of *Cembrae* pines do not support a common ancestor (a monophyletic origin) for these pines and indicate close affinity to the *Strobi* pines (Liston and others 1999; Gernandt and others 2005; Syring and others 2007). Gernandt and others (2005) recommended that *Strobi* and *Cembrae* be merged into the single subsection *Strobus*, and that subsection *Strobus* and two other five-needle white pine subsections (*Gerardianae* and *Krempfianae*) together comprise a new section *Quinquefoliae*.

Distribution

Although the pines that are the focus of the High Five symposium generally occur at the highest forest elevations of our western mountains, their different distributions reflect their unique species-specific histories of origin and spread. Distributions of the western high elevation five-needle white pines vary from curiously disjunct and regionally restricted to wide-ranging, and the elevational ranges vary from broad to narrow (Figure 2, Table 2).

Table 1. Traditional classification of North American five-needle white pines, based on Price et al. (1998) but with southwestern white pine as a species distinct from Mexican white pine (Kral 1993; Farjon and Styles 1997).

Genus *Pinus* L.
Subgenus *Strobus* Lemmon

- Section *Parrya* Mayr (foxtail pines)
  - Subsection *Balfourianae* Engelm.
    - **Rocky Mountain bristlecone pine, *P. aristata* Engelm.**
    - **Foxtail pine, *P. balfouriana* Grev. & Balf.**
    - **Great Basin bristlecone pine, *P. longaeva* D.K. Bailey**
- Section *Strobus* (white pines)
  - Subsection *Strobi* Loudon
    - Mexican white pine, *P. ayacahuite* Ehrenb. ex Schltdl.
    - **Southwestern white pine, *P. strobiformis* Engelm.**
    - Chiapas white pine, *P. chiapensis* (Martínez) Andresen
    - **Limber pine, *P. flexilis* James**
    - Sugar pine, *P. lambertiana* Dougl.
    - Western white pine, *P. monticola* Dougl. ex D. Don
    - Eastern white pine, *P. strobus* L.
  - Subsection *Cembrae* Loudon (stone pines)
    - **Whitebark pine, *P. albicaulis* Engelm.**

Whitebark pine has the largest geographic distribution of all U.S. and Canadian white pines, but the narrowest elevational limits, inhabiting only the upper subalpine forest zone up to the limits of treeline (Figure 2A, Table 2) (Arno and Hoff 1990; Tomback and Achuff 2010). Reflecting its tolerance of harsh conditions, the range of whitebark pine extends farther north than any other North American white pine. Its distribution consists of a western portion, which includes the Sierra Nevada, Cascade, and Coastal Ranges north to central British Columbia, and an eastern portion, which ranges from the Greater Yellowstone region of the central Rocky Mountains north through the Canadian Rocky Mountains and beyond Willmore Wilderness Park, Alberta, to nearly 54° latitude in east-central British Columbia and west-central Alberta (Olgivie 1990; McCaughey and Schmidt 2001).

Limber pine is nearly as broadly distributed as whitebark pine, but occurs at lower latitudes and over more arid regions, including the southern Sierra Nevada, southern California, the U.S. Southwest, the southern Rocky Mountains, and many Great Basin mountain ranges, occurring as far east as the Black Hills, South Dakota (Thilenius 1970; Steele 1990) (Figure 2C, Table 2). Farjon and Styles (1997) note that it has been collected in several locations in northern Mexico as well. Particularly noteworthy about limber pine is its broad elevational tolerance—broader perhaps than any other species within the Pinaceae. Within a given region, limber pine may occur at both lower and upper treeline and in patchy stands at all elevations in between (Steele 1990; Schoettle 2004; Tomback and Achuff 2010). For example, on the eastern plains of southern Wyoming and northern Colorado, limber pine occurs as isolated populations on rocky escarpments at elevations of 1600 m or lower, and in the Front Range of Colorado from the lower montane forest zone up to treeline to 3300 m (Schuster and others 1995; Schoettle and Rochelle 2000). Throughout western Wyoming and along the eastern Rocky Mountain Front of Montana and southern Alberta, limber pine forms woodlands on arid foothills, ridges, and escarpments, but also occurs at subalpine and treeline elevations (Knight 1994; Achuff and others 2002; Resler and Tomback 2008).

Southwestern white pine is restricted in distribution to the southwestern U.S., but ranges more widely in northern Mexico (Figure 2C, Table 2). It overlaps and appears to hybridize with limber pine in northern Arizona and New Mexico and in southern Utah and Colorado (Steinhoff and Andresen 1971). Because southwestern white pine occurs at high elevations, but not at treeline, it principally inhabits the "sky-island" forests near the top of high desert mountain ranges, which are surrounded by desert vegetation at lower elevations (Steinhoff and Andresen 1971; Perry 1991; Farjon and Styles 1997).

The three "foxtail pines" have the most restricted geographic distributions of all the high-elevation white pines (Bailey 1970; Mastrogiuseppe and Mastrogiuseppe 1980; Kral 1993; Eckert and Sawyer 2002) (Figure 2B; Table 2). Bailey (1970) describes these pines as "...closely related

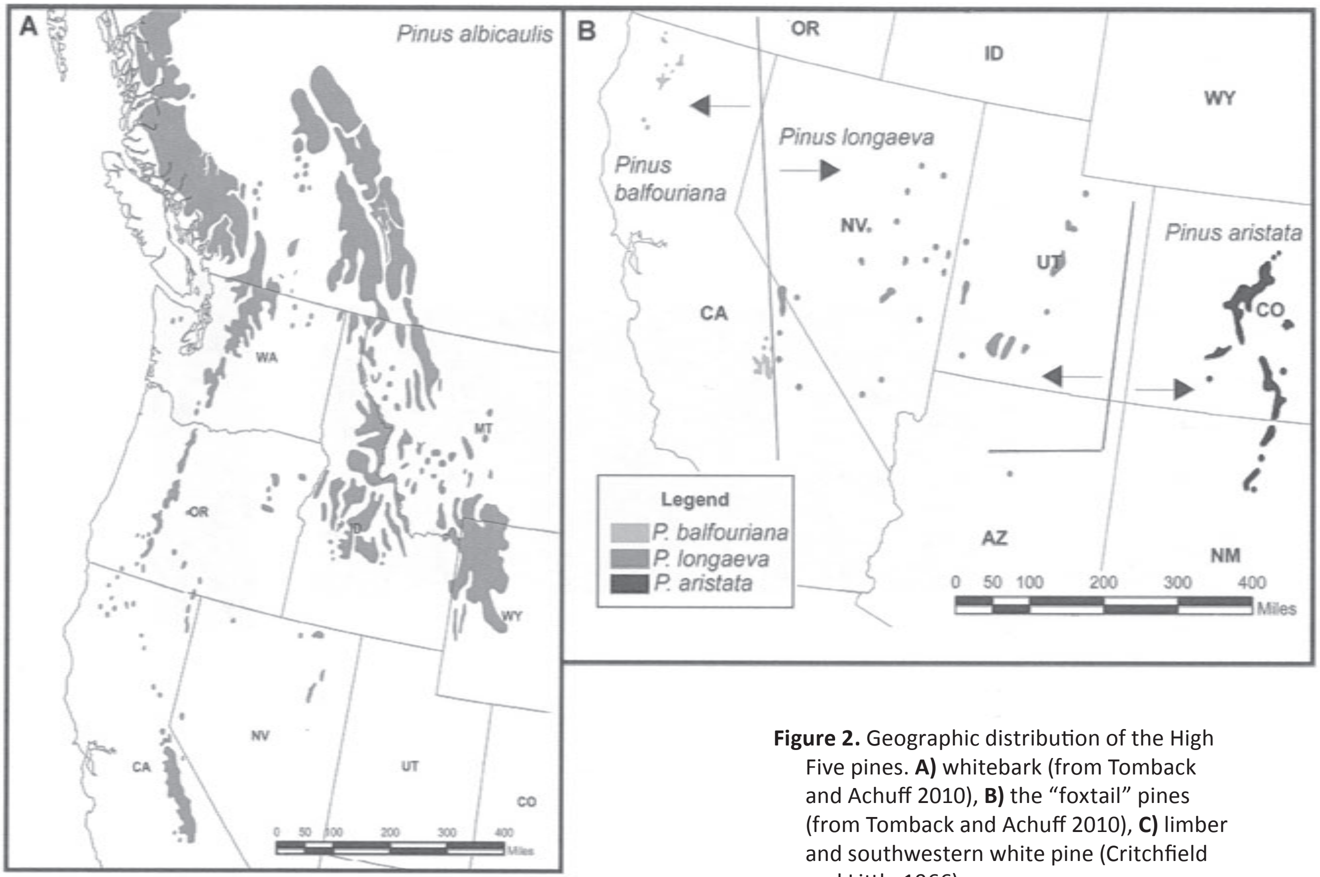
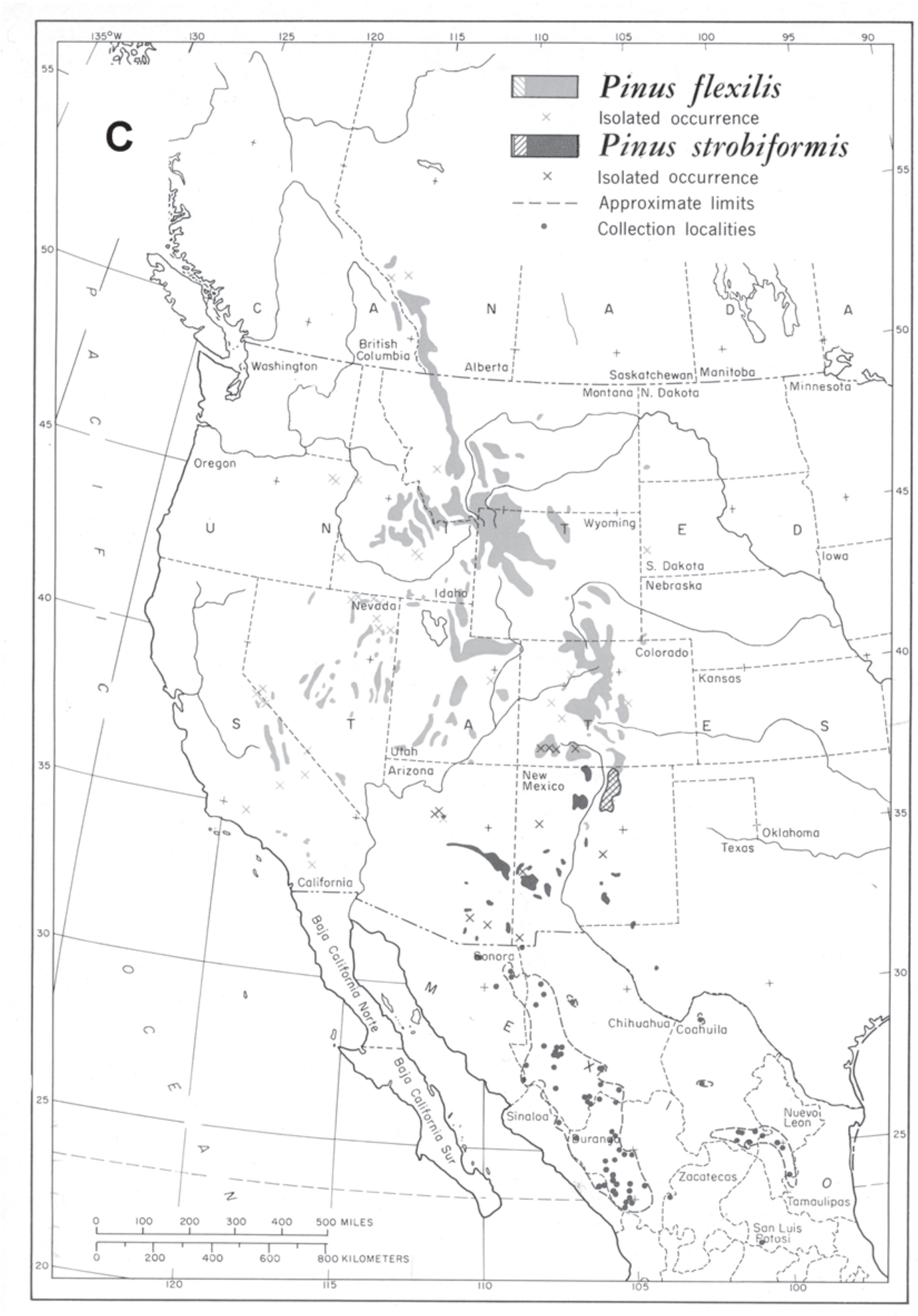


Figure 2. Geographic distribution of the High Five pines. **A)** whitebark (from Tomback and Achuff 2010), **B)** the "foxtail" pines (from Tomback and Achuff 2010), **C)** limber and southwestern white pine (Critchfield and Little 1966).



Tertiary relics confined to high elevations," and notes their extreme tolerance of low moisture and prolonged drought. Both foxtail pine and Rocky Mountain bristlecone pine have disjunct distributions. Foxtail pine occurs at subalpine and treeline elevations in the vicinity of Sequoia and Kings Canyon National Park and south to Olanche Peak in the southern Sierra Nevada but also in the Klamath Mountains of northern California (ca. 1700 to 2500 m elevation) (Mastrogiussepe 1972; Eckert and Sawyer 2002). Both bristlecone pines have a wider elevational tolerance than foxtail pine. Rocky Mountain bristlecone pine occurs throughout much of Colorado and northern New Mexico, but a small population also occurs in northern Arizona; elevations range from about 2800 to 3600 m (Hawksworth and Bailey 1980). Great Basin bristlecone pine has the greatest elevational range, occurring from subalpine to treeline elevations (about 2300 to 3500 m) throughout the higher desert mountain ranges of the Great Basin.

Table 2. Distributions, forest zones, and elevational limits for western high elevation white pines (modified from Table 2 in Tomback and Achuff 2010). Also see Figs. 1 and 2.

Pine species	General distribution	Forest zone	Elevation m	References
Whitebark	Rocky Mountains from western WY north and Sierra Nevada, Cascades, and Coastal ranges north to about 55˚ in Alberta and B.C.	Upper subalpine to upper treeline	900 to 3660	Arno and Hoff 1990; Olgivie 1990; McCaughey and Schmidt 2001
Limber	Southern Rocky Mountains to southern Alberta, east to ND, SD, and NE; southern CA; Great Basin ranges	Lower treeline to upper treeline	850 to 3810	Barney 1980; Steele 1990
Southwestern white	Southwest U.S. (southern UT & CO, AZ, NM), south through northern Mexico	Montane to subalpine	1900 to 3000	Kral 1993; Steinhoff and Andresen 1971; Farjon and Styles 1997
Foxtail	Southern Sierra Nevada and Klamath Mountains of CA	Subalpine to treeline	1500 to 3500	Bailey 1970; Mastrogiuseppe and Mastrogiuseppe 1980; Kral 1993
Rocky Mountain bristlecone	Southern and central Rocky Mountains (CO, northern NM & AZ)	Montane to treeline	2500 to 3670	Bailey 1970; Kral 1993; Baker 1992
Great Basin bristlecone	Great Basin (eastern CA, NV, western UT)	Subalpine to treeline	1700 to 3400	Bailey 1970; Kral 1993

Community Ecology

The High Five pines are similar in many aspects of their community ecology (for overview, see Tomback and Achuff 2010 and Table 3a and 3b therein). These pines comprise minor to major components of forest communities, depending on site productivity, proximity to seed sources, time since last disturbance, and successional stage. On productive sites, where closed canopy forests form, white pines tend to be early seral species, which are replaced over time by more shade-tolerant species. Thus, these high elevation white pines are moderately to strongly shade intolerant and dependent on fire or other disturbance for renewal of early seral communities. However, some white pines established early in succession may persist into late seral communities.

The High five pines are generally poor competitors, and survive best where better competitors are disadvantaged—such as on harsh, cold sites. Under these conditions, including strong winds, intense solar radiation, aridity, and nutrient-poor soils, most of the white pines form climax or self-replacing forest communities through sparse but continuous regeneration (for example, Bailey 1970; Arno 2001; Schoettle 2004; Brown and Schoettle 2008). In fact, all the High Five pines except southwestern white pine occur at treeline as isolated trees or within tree islands. Some of the key features of the community ecology of each pine are reviewed in the following sections.

Whitebark Pine

Despite occurring within only a narrow elevational range, whitebark pine is found in a diversity of community types, and varies greatly within and across its range in prevalence, species composition, elevation, and successional status (Arno 2001 and references therein; Tomback and Kendall 2001). These different community types form in relation to climate at a regional scale, but also in response to local factors, such as soil depth and bedrock type, or topography (Daubenmire 1968; Franklin and Dyrness 1973). Arno and Weaver (1990) note that "whitebark pine is abundant in regions having humid, snowy winters and long, dry periods in summer…." They further note that as summers become wetter at more northerly latitudes, whitebark pine abundance decreases.

Climax whitebark pine communities are the most widespread (Arno and Weaver 1990; Arno 2001). Whitebark pine's moderate tolerance of cold, dry conditions enables it to persist at the highest forest elevations and to form dwarf or krummholz growth forms near and at treeline. Whitebark pine abundance, however, diminishes as the annual period of drought increases or as precipitation and humidity increase (Arno and Weaver 1990; Weaver 2001). Seral whitebark pine communities occur over the greatest area in the continental climates of the central and northern Rocky Mountains of the U.S., but also occur in the more maritime-influenced climates from eastern Oregon to western Montana (Arno 2001). There appear to be two general successional pathways for seral whitebark pine communities: one pathway that is dominated by whitebark pine and lodgepole pine early in succession, and the other pathway with some whitebark pine but dominated by more shade-tolerant conifers early in succession, especially subalpine fir (*Abies lasiocarpa*) (Keane 2001; Campbell and Antos 2003). In both situations, some whitebark pine may persist into advanced seral stages.

Fire is the primary disturbance factor that renews seral whitebark pine communities. Fire regimes in whitebark pine communities are complex, and range from small, localized fires and low intensity burns caused by lightning strikes in treeline and extremely harsh upper subalpine sites to mixed-severity burns to stand-replacing fires (Tomback 1986; Arno 2001; Keane 2001; Walsh 2005). Fire return-intervals vary with a number of factors, including ignition frequency, drought frequency, local topography, forest structure, and forest composition. Steep terrain with heterogeneous forest structure and available fuels tend to support mixed-severity burns, and large expanses of continuous subalpine forest tend to support stand-replacing burns (Arno 2001). Overall, the mean fire return intervals for whitebark pine communities range from about 30 to 400 years (Table 4-5 in Arno 2001). Regeneration of recently burned areas may occur fairly rapidly as a result of seed dispersal by Clark's nutcracker, depending on proximity and health of seed sources, local snow depth, and moisture availability (Tomback and others 1990; Tomback and others 1993; Tomback and others 2001b).

Limber Pine

Broadly distributed both geographically and in elevation, limber pine occurs with diverse forest associates, such as aspen (*Populus tremuloides*), ponderosa pine (*Pinus ponderosa*), and the bristlecone pines, thus comprising a variety of community types (Tomback and Achuff 2010). For example, limber pine forms woodland communities at lower treeline elevations throughout much of its distribution in the Central and Northern Rocky Mountains, but also may be found in montane and subalpine zone communities in mixed coniferous forests (for example, Peet 1978; Knight 1994; Schoettle and Rochelle 2000). Limber pine competes poorly on productive sites, but tolerates highly xeric environments, including steep slopes, shallow, rocky soils, and windy, arid sites (Peet 1978; Veblen 1986; Schoettle 2004). Like whitebark pine, it occurs in early successional communities on favorable sites and self-regenerating climax communities on harsh sites (Rebertus and others 1991). Unlike whitebark pine, it may occupy harsh sites at all elevations. However, Peet (1978) suggests that the presence of whitebark pine or Rocky Mountain bristlecone pine at high elevations restricts limber pine to lower elevations or rocky substrates. Limber pine also forms krummholz forest communities at treeline.

After disturbance such as fire, limber pine is a colonizing pioneer on many sites, primarily the result of both its hardy, drought-tolerant seedlings together with long distance seed dispersal by Clark's nutcracker (Lanner and Vander Wall 1980; Robertus and others 1991; Donnegan and Rebertus 1999; Coop and Schoettle 2009). Seedling recruitment continues for over 30 years post-disturbance in both small and large burned areas, and is facilitated by nurse objects, such as rocks and standing snags (Coop and Schoettle 2009). On all but the harshest montane and subalpine sites, limber pine is replaced over time by shade-tolerant conifers (Veblen 1986). The rate of replacement is faster on more mesic sites, but can take up to a century on the most xeric sites (Veblen 1986; Rebertus and others 1991). This process of disturbance and recolonization results in a patchy distribution of limber pine stands of different ages across the landscape (Webster and Johnson 2000). However, the maximum ages attained by limber pine appear to vary with elevation, possibly related to fire frequency (Schuster and others 1995). The oldest trees sampled from the eastern plains of Colorado achieved maximum ages of less than 200 years, whereas the oldest trees from upper treeline had ages greater than 1500 years.

Southwestern White Pine

In the southwestern U.S., southwestern white pine forms pure stands or mixed conifer associations primarily with ponderosa pine (or Arizona pine, *Pinus arizonica*), white fir (*Abies concolor*), and Douglas-fir (*Pseudotsuga menziesii*) (Tomback and Achuff 2010). Like limber pine, southwestern white pine has a patchy distribution, reflecting past disturbance history of forest communities. On productive sites, the pine may become tall, straight, old growth trees with high canopies; on harsher sites, such as wind-or sun-exposed slopes, they assume a shorter and more irregular growth form.

In northern Arizona, southwestern white pine forms unique communities with Rocky Mountain bristlecone pine and limber pine; and, in southern Colorado and northern New Mexico, southwestern white pine may co-occur with limber pine (Benkman and others 1984; Samano and Tomback 2003). It is prevalent on steep, rocky terraces and slopes, especially on more arid exposures in moister regions, such as the San Juan Mountains of Colorado. In drier regions, such as the Guadalupe Mountains of west Texas, southwestern white pine inhabits north-facing slopes (Sakulich and Taylor 2007). Southwestern white pine occurs in a number of community types as a minor and major seral component in southern New Mexico and Texas. It is successionally replaced by white fir and Douglas-fir, but persists late in succession in some communities and may co-dominate with Douglas-fir, or form even-aged old growth forests (Alexander and others 1984; Samano and Tomback 2003; Sakulich and Taylor 2007). Mean fire return intervals for open, mixed conifer forests with southwestern white pine were found to be very short—about 2 to 4 years—in the pre-settlement period, resulting from rapid fuel accumulation (Grissino-Mayer and others 1995; Sakulich and Taylor 2007).

Foxtail Pine

Foxtail pine, which has a disjunct distribution in California, comprises a minor to major species in upper subalpine and treeline communities of both its northern and southern populations (for overviews, see Bailey 1970; Mastrogiuseppe and Mastrogiuseppe 1980; Eckert and Sawyer 2002; Tomback and Achuff 2010). Although all three pines in the *Balfourianae* tolerate poorly developed soils, wind, and prolonged drought, foxtail pine grows under the most mesic conditions. Foxtail pine appears to be shade-intolerant at all life stages, occurs on a variety of substrates, and grows at high elevations on slopes and ridges. In the Klamath Mountains, which experience a maritime climate, foxtail pine occurs on all slope aspects, principally in mixed conifer forests on south- and west-facing slopes. The pine dominates west-facing slopes and commonly associates with red fir (*Abies magnifica*), Jeffrey (*Pinus jeffreyi*), lodgepole (*Pinus contorta*), and whitebark pine. On ridgetops, it associates with mountain hemlock (*Tsuga mertensiana*), western white pine (*Pinus monticola*), and red fir, which are all restricted to the northern and eastern aspects with deeper soils and snowpack (Mastrogiuseppe 1972). Foxtail pine communities in more northern stands include montane zone conifers such as Douglas-fir, white fir, and incense cedar (*Calocedrus decurrens*) (Mastrogiuseppe 1972; Mastrogiuseppe and Mastrogiuseppe 1980; Eckert and Sawyer 2002).

Frequent fire enables foxtail pine to recolonize forest communities on more productive sites. Foxtail pine is self-replacing in more open communities and on some substrates, but surface fires may kill old foxtail pine (Mastrogiuseppe 1972). In the Klamath Mountains, there is evidence that foxtail pine may be expanding its range both to the north and to the south. At Lake Mountain, the northern-most stand known, foxtail pine has established on the northeastern slope during drought years with less snowpack and longer growing seasons. Within the South Yolla Bolly Mountains, the southern-most population in the Klamath Mountains, foxtail pine also has abundant regeneration.

In the southern Sierra Nevada, conditions are more severe: the weather is extreme with high winds and stronger insolation, and the coarse substrates have little water-holding capacity. There, foxtail pine forms self-replacing communities with lodgepole, limber, whitebark, and western white pine, as well as red fir and western juniper (*Juniperus occidentalis*), with the highest densities on north-facing slopes (Ryerson 1983 cited in Eckert and Sawyer 2002). Near the eastern crest of the Sierra Nevada, foxtail pine occurs in open, nearly pure stands intermixed with a small number of lodgepole and whitebark pines.

Foxtail pine does not assume krummholz growth forms at the upper limits of tree growth, and tree occurrence abruptly ends at treeline (Bunn and others 2005). Trees in the southern population are known to reach ages as great as 1200 to 2000 years, whereas trees in the Klamath Mountains attain maximum ages of 800 to 1000 years. Survival in the latter population appears limited by frequent fires and by widespread heart rot (Mastrogiuseppe 1972; Eckert and Sawyer 2002 and references therein; Bunn and others 2005). Further information on the community dynamics of this pine for both northern and southern populations is needed.

Rocky Mountain Bristlecone Pine

Despite a restricted geographic distribution, Rocky Mountain bristlecone pine forms communities that vary in composition and structure in response to a latitudinal gradient in climate and elevation in the southern Rocky Mountains, but also in relation to geological substrate and aspect (Peet 1978; Ranne and others 1997; Coop and others 2010).

Within the southern Rocky Mountains, bristlecone pine typically grows on igneous and volcanic soils on steep, south-facing slopes at elevations between 2,750 and 3,670 m (Hawksworth and Bailey 1980; Baker 1992). The maximum ages attained are about 2,400 years (Brunstein and Yamaguchi 1992). Ancient trees are found on extremely arid sites, such as bedrock, talus slopes, south-facing slopes, and in small stands separated from larger forested areas. These individuals are protected from fire by isolation and sparse fuels.

Baker (1992) found that Rocky Mountain bristlecone pine is an early seral, shade intolerant species, regenerating primarily on burned terrain. Because successional replacement may be extremely slow on harsh sites, Baker (1992) refers to the bristlecone pine as "a long-lived pioneer species." Recent studies suggest that a mixed fire regime is common in communities occupied by Rocky Mountain bristlecone pine (Brown and Schoettle 2008). Rocky Mountain bristlecone pine seedlings tend to concentrate along the forest-disturbance interface near nurse objects. Greater densities of seedlings occur in small, patchy burns than in more extensive burns (Coop and Schoettle 2008). Furthermore, regeneration occurs over a protracted timeframe; for example, 30 years after a severe burn, Rocky Mountain bristlecone pine densities were not comparable to those in adjacent, unburned stands.

Throughout much of its distribution, Rocky Mountain bristlecone pine grows in association with limber pine. In the Spanish Peaks and in South Park, bristlecone pine occurs as low as 2,775 m in association with ponderosa pine and Gambel oak (*Quercus gambelii*). Above about 3,200 m elevation, it is the principal tree on most xeric sites. In this region, krummholz communities are not widespread (Peet 1978). Farther north in the Front Range of Colorado, bristlecone pine dominates on open, south-facing slopes and may form krummholz communities at treeline, whereas limber pine grows on ridge tops.

In the disjunct population in northern Arizona in the San Francisco Peaks, bristlecone pine forms a unique open white pine community with limber and southwestern white pine as associates at the higher elevations, and Engelmann spruce (*Picea engelmannii*), subalpine fir (corkbark fir, var. *arizonica*) (*Abies lasiocarpa*), southwestern white pine, and ponderosa pine at lower elevations (Hawksworth and Bailey 1980; Benkman and others 1984).

Great Basin Bristlecone Pine

Great Basin bristlecone pine grows on the most arid sites of all the High Five pines, and of all the North American five-needle white pines (Tomback and Achuff 2010). It is usually found on the most nutrient-deficient, well-drained soils, and is the dominant conifer in treeline communities. Bailey (1970) noted its restriction primarily to limestone and dolomite soils, with few trees growing on other substrate types evidently because they are competitively disadvantaged. The light colors of limestone and dolomite apparently result in lower soil temperatures and thus more soil water (Wright and Mooney 1965 cited in Bailey 1970). The other two "foxtail" species readily grow on other substrates.

Despite restricted substrates, this pine forms a wider diversity of forest community types than does Rocky Mountain bristlecone pine (Tomback and Achuff 2010;

see also Table 2 in Lanner 1988). For example, in eastern California at its lower elevational limits, it associates with singleleaf pinyon (*Pinus monophylla*); at the mid-elevations, it forms mixed stands with limber pine, and at the highest elevations, it occurs in pure stands, growing only on dolomite substrate (Billings and Thompson 1957; Vasek and Thorne 1977). Billings and Thompson (1957) found no seedlings or small trees in the stands they sampled—only mature pines, suggesting limited reproduction. In more mesic regions of the Great Basin, such as eastern Nevada, Great Basin bristlecone pine forms subalpine and treeline communities primarily with limber pine and Engelmann spruce; in northern Nevada, it associates with whitebark pine (Currey 1965; LaMarche and Mooney 1972; Vasek and Thorne 1977; Beasley and Klemmedson 1980; Hawksworth and Bailey 1980). In eastern Nevada where Great Basin bristlecone pine occurs in mixed subalpine conifer associations, it tends to be a minority species. Under these conditions, it shows faster growth and better crown and bole development, but a shorter life span, which may result from its poor competitive ability and shade intolerance (Beasley and Klemmedson 1980).

Great Basin bristlecone pine reaches the highest elevations of treeline, but varies in stature and growth form at these elevations. For example, at the highest treeline elevations on Mt. Washington (ca 3,500 m) in the Snake Range of east-central Nevada, bristlecone pine assumes a krummholz growth form, whereas in the White Mountains of east-central California, bristlecone pine maintains an erect growth form up to treeline (Currey 1965; LaMarche and Mooney 1972; Beasley and Klemmedson 1980). LaMarche and Mooney (1972) attribute the differences in Great Basin bristlecone pine growth form at treeline to differences in precipitation between the two ranges: the White Mountains receive less than half the annual precipitation of the Snake Range, and experience extreme summer drought. Reduced snowpack in the White Mountains and in other very arid mountain ranges may preclude the formation of krummholz growth forms, which depend on snow cover for protection (Arno and Hammerly 1984).

Harsh conditions, including low annual precipitation and well-drained dolomite substrates, result in extremely slow growth. These conditions as well as sparse ground litter, which prevents low intensity fires, may account for the extreme ages attained by Great Basin bristlecone pine at high elevations. As reviewed by Currey (1965) and Ferguson (1969), maximum ages for these pines vary geographically from between 1,500 and 4,900 years, with many ancient trees between 3000 and 4000 years of age. Thus, the Great Basin bristlecone pines are the oldest trees known.

Seed Disperal

Within the genus *Pinus* there is much variation in seed size, seed and wing morphology, cone size, and cone morphology. Seed size alone varies by two orders of magnitude—for example, the differences in seed mass averages of 0.0035 g for jack pine (*Pinus banksiana*) and 0.9072 g for Torrey pine (*Pinus torreyana*) (Table 3 in Tomback and Linhart 1990). The various morphologies of cone and seed traits are assumed to be the product of selection for effective seed dispersal, given the constraints of taxonomy, life history, and environmental conditions (Tomback and Linhart 1990; Keeley and Zedler 1998; Lanner 1998). However, seed dispersal from cones by wind appears to be the ancestral condition within the genus *Pinus*, and among species of the Pinaceae in general (for example, Lanner 1980).

For subgenus *Strobus* (the white pines) alone, there is variation in seed size and seed wing lengths as well as cone morphologies, but the seed sizes of white pines, expressed as seed mass, vary only about tenfold (Table 3 in Tomback and Linhart 1990). The white pines in general have significantly larger seed sizes than do the subgenus *Pinus* (the yellow pines) species (average of 0.212 g vs. 0.094 g, respectively, Tomback and Linhart 1990). The greater seed size in many *Strobus* and some *Pinus* pines may be an adaptation to comparatively harsh environments, including both xeric and high elevation environments, potentially resulting in greater seedling survival (Lanner 1980; Tomback and Linhart 1990). Also, within the white pines there is a preponderance of species with relatively large, wingless seeds. Seed masses for *Strobus* pines are significantly larger for wingless seeds than for winged seeds (average of 0.279 g vs. 0.057 g, respectively, Table 3 in Tomback and Linhart 1990). The wingless condition appears to facilitate seed dispersal from cones by nutcrackers and jays and, through seed fall, by small mammals (Tomback and Linhart 1990; Vander Wall 1997).

The high-elevation white pines demonstrate an array of cone and seed traits and seed dispersal modes (Table 3). For pines, there can be two different phases to seed dispersal: Phase I or primary seed dispersal, which is the means by which seeds are removed from cones; and Phase II or secondary seed dispersal, which is the means by which seeds move from the ground substrate, or even animal seed caches, to a final caching site ("safe site") (Chambers and MacMahon 1994; Vander Wall and Longland 2004).

Pines Dependent on Nutcrackers for Primary Seed Dispersal

Whitebark pine

Whitebark pine is an obligate, co-evolved mutualist of Clark's nutcracker, depending almost exclusively on nutcrackers for Phase I seed dispersal (Figure 3a) (Lanner 1980; Tomback and Linhart 1990). The interaction with nutcrackers may have influenced the evolution of whitebark pine morphology (Lanner 1980; Lanner 1982). Whitebark pine has large, wingless seeds and cones that do not open when seeds are ripe, traits characteristic of the pines traditionally classified within subsection *Cembrae* (Lanner 1990; Price and others 1998) (Table 3, Figure 4). In addition, whitebark pine has a canopy with upswept branches (referred to as "lyrate" or "candelabra-shaped"). The purple-brown cones of whitebark pine grow in horizontally-oriented whorls at the tips of vertically-oriented branches, increasing visibility from above

Table 3. Seed weights, seed and cone traits, and seed dispersal mechanisms in the high-elevation five-needle white pines. See text for references and discussion. Seed masses from Table 3 in Tomback and Linhart (1990) which are based on data primarily from Krugman and Jenkinson (1974).[a] Seed mass data from the Sierra Nevada, California, and Wind River Range, Wyoming, illustrating variation (Tomback 1982, Tomback 1988).[b] Data calculated from 10 seed means from two populations for Great Basin bristlecone pine reported from two populations by Connor and Lanner (1991).[c] Data from Baud (1993) from the Front Range, Colorado.[d]

Species	Mean seed mass (g)	Seed wing	Cones open	Phase I seed dispersal[1]	Phase II seed dispersal[2]
Whitebark	0.157[b]				
	0.099[b]	No[3]	No	Nutcrackers	Rodents, jays?
Limber	0.093[a]				
	0.085[d]	No[3]	Yes	Nutcrackers, jays, seed fall	Rodents, jays
Southwestern white	0.168[a]	No[3]	Yes	Nutcrackers, jays, seed fall	Rodents, jays
Foxtail	0.027[a]	Yes	Yes	Wind, nutcrackers, jays?	Rodents, jays?
Rocky Mountain bristlecone	0.025[a4]				
	0.016[d]	Yes	Yes	Wind, nutcrackers, jays	Rodents, jays?
Great Basin bristlecone	0.010[c]	Yes	Yes	Wind, nutcrackers, jays	Rodents, jays?

[1] Phase I seed dispersal refers to mode of dispersal of seeds from cones.

[2] Phase II seed dispersal refers to mode of seed movement from substrate or cache to final "safe site."

[3] For a small proportion of trees, seeds bear short seed wing remnants.

[4] This mass appears to be based on collections that predate the recognition of two bristlecone pine species (Bailey 1970) and may be unreliable.

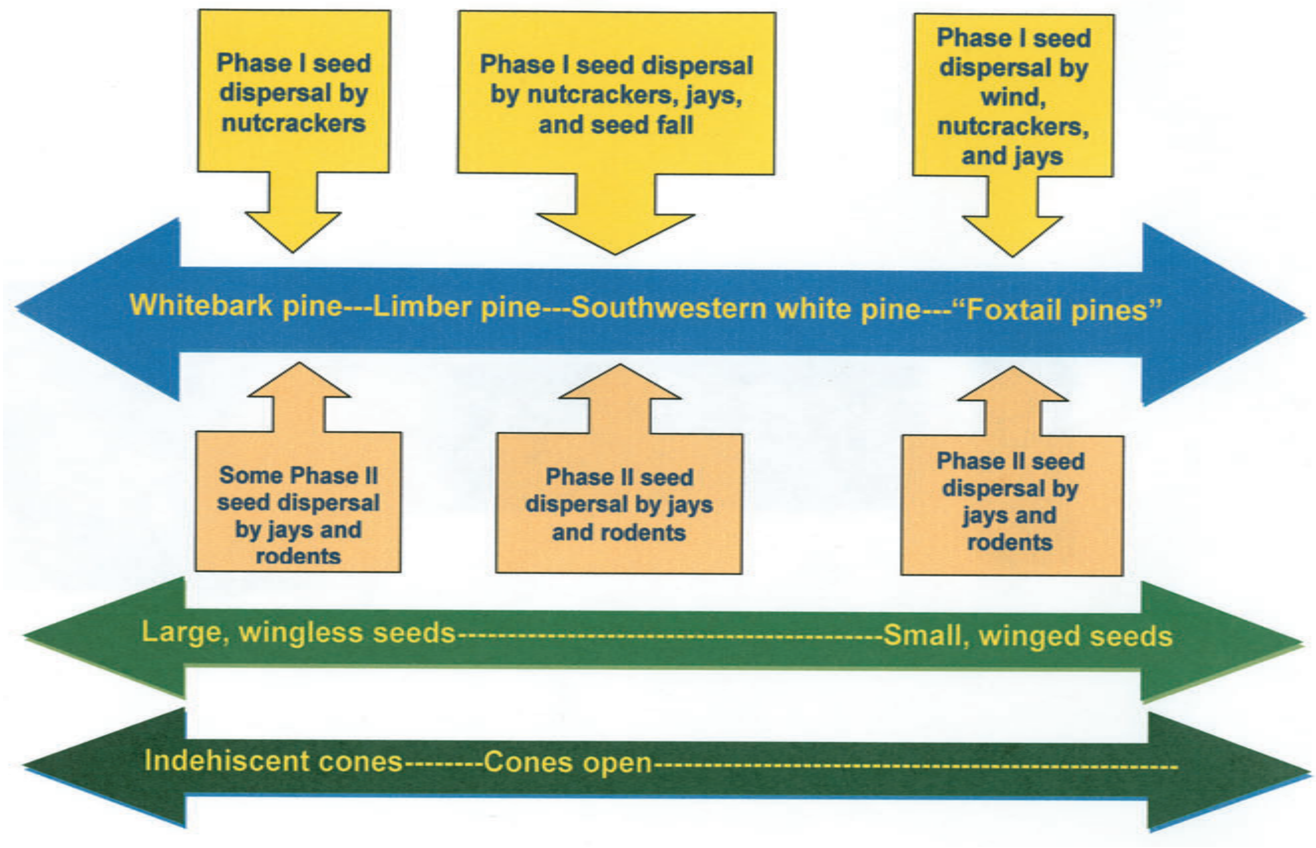


Figure 3. Seed dispersal in High Five pines. Cone and seed morphology vary along a continuum from the large, wingless seeds and non-opening (indehiscent) cones of whitebark pine to the small, winged seed, and dehiscent cones of the "foxtail pines," which include foxtail, Rocky Mountain bristlecone, and Great Basin bristlecone pine. Whitebark pine cones are adapted for seed dispersal by Clark's nutcrackers, whereas at the other end of the continuum, wind is the primary means by which seeds are dispersed from cones. Phase I or primary seed dispersal: removal of seeds from cones; Phase II or secondary seed dispersal: removal of seeds from substrate or caches and redispersal (see text for further explanation).

Figure 4. a) Clark's nutcracker harvesting whitebark pine seeds. **b)** Clark's nutcracker harvesting limber pine seeds. Photo credits: Diana F. Tomback

and providing access for nutcrackers (Tomback 1978; Lanner 1982). The cones are considered indehiscent rather than serotinous. Although cone scales may separate slightly from the cone axis, non-opening results from the absence in the cones of *Cembrae* pines of hygroscopic cellulose microfibrils that shrink as they dry (Harlow and others 1964; Lanner 1982). The ripe but closed cones retain the large seeds, which provide a high energy reward for nutcrackers; and the wingless seeds increase foraging efficiency (Tomback and Linhart 1990). Nutcrackers break into ripe cones using their long, sharp beaks, and rapidly remove seeds (Tomback 1978; Hutchins and Lanner 1982) (Figure 4a). In contrast, when harvesting winged conifer seeds from cones, nutcrackers pause to remove the wing before each seed is pouched, slowing harvesting rates. Tomback (2001, 2005) provide detailed overviews of the interaction between Clark's nutcracker and whitebark pine, whereas Tomback (1998) reviews the life history of Clark's nutcracker.

Whitebark pine cones vary in timing of ripening, particularly with topography, and nutcrackers are selective, taking seeds from the riper cones (Tomback 1978). Seed mass appears to peak in early September (Hutchins and Lanner 1982). Nutcrackers are able to remove entire whitebark pine seeds with dark seed coats from cones by mid to late August, begin caching seeds at this time, and continue caching throughout fall, until the cone crop is depleted. They transport harvested seeds within their sublingual pouch, which may hold more than 100 whitebark pine seeds, to seed caching sites or to feed dependent but fledged young (Vander Wall and Balda 1977; Tomback 1978; Hutchins and Lanner 1982).

Pine squirrels compete with nutcrackers for pine seeds. In mid-summer, they efficiently cut down the cones of nearly all the high-elevation white pines for storage in middens, often taking a high proportion of the cones produced (Benkman and others 1984; Samano and Tomback 2003; McKinney and others 2009). Nutcrackers will take whitebark pine cones from red squirrel (*Tamiasciurus hudsonicus*) middens, even with squirrels present; they fly in, quickly find a cone, and fly off holding the cone in their beak (Tomback 1989).

Nutcrackers may store whitebark pine seeds in the vicinity of source trees or fly to more distant cache sites. They frequently store their seeds on steep, south-facing slopes, which are within a few kilometers of source trees and tend to accumulate minimal snowpack. In the eastern Sierra Nevada, they have been observed to fly 12 km or farther from source trees to lower elevations to store seeds, where whitebark pine does not grow (Tomback 1978). In addition, they cache seeds at treeline and in alpine tundra (Tomback 1986; Baud 1993). In the Cascade Range, Lorenz and Sullivan (2009) used radio-telemetry to determine that nutcrackers transported whitebark pine seeds an average of 10.6 km and a maximum of about 29 km.

Nutcrackers place whitebark pine seeds in caches of 1 to 15 or more seeds, with means ranging from 3 to 5 seeds per cache (Tomback 1978; Tomback 1982; Hutchins and Lanner 1982; Tomback 1986; Tomback and others 2001b; Wells 2011). The seeds are buried under 1 to 3 cm of substrate, such as mineral soil, gravel, pumice, or forest litter. Caches are placed next to trees, rocks, plants, logs, and other objects; under closed canopy forest and in open terrain; at treeline among krummholz tree islands; in recent clearcuts and burned soil soon after fire; and high in trees and logs in cracks, holes, fissures, and under bark. The morphology of whitebark seeds differs from other conifer seeds; the differences appear to be adaptive for maintaining viability in buried caches (Tillman-Sutela and others 2008). Buried seeds may be stimulated to germinate by snowmelt and summer precipitation, leading to regeneration (Sidebar) (Tomback 1982; McCaughey 1990).

Steller's jays (*Cyanocitta stelleri*) harvest and cache whitebark pine seeds to a limited extent: they cannot open closed cones, and have not been observed caching seeds in the ground in whitebark pine communities (Hutchins and Lanner 1982). At this time, it is not known to what extent cached nutcracker seeds might be pilfered by mice and squirrels and either consumed or re-cached, which would constitute Phase II seed dispersal (Figure 4). Caches are likely to be less prone to discovery if well-dispersed and in harsh, wind-swept sites, open terrain, rocky ledges, and in volcanic substrates, where rodent populations may be sparse, and where many whitebark pine communities grow. Regardless, nutcrackers as dispersers determine where and how far seeds are moved from source trees; secondary dispersers move seeds locally.

Sidebar: What Is A Nutcracker Worth—In Dollars?

Ecosystem services are the conditions, processes, and functions provided by ecological communities that benefit humans (Daily 1997). The economic valuation of ecosystem services is based on the cost of replacing natural ecosystem processes (for example, Costanza and others 1997). Seed dispersal by animals is viewed as an ecosystem service, critical to initiating, developing, and regenerating forests and other plant communities. Clark's nutcrackers provide important ecosystem services by sowing whitebark pine seeds.

Restoration practice involves planting seedlings in whitebark pine communities or large burns, where high proportions of trees or nearby seed sources are damaged or killed by white pine blister rust. Where whitebark pine populations are declining, cone production is greatly reduced, and nutcrackers may not disperse seeds reliably (McKinney and Tomback 2007; McKinney and others 2009). The restoration strategy involves planting seedlings with genetic resistance to the blister rust pathogen, thus speeding up the effects of natural selection and improving tree survival. This effort requires that planting stock be grown from parent trees known to have rust resistance (see Sniezko and others, these proceedings). Although these restoration practices replace nutcrackers in planting efforts, one important difference is that nutcrackers would cache seeds from trees with anywhere from no resistance to strong genetic resistance to *Cronartium ribicola*.

National Forests plant whitebark pine seedlings at a density of 175 seedlings/acre, or about 440 seedlings/hectare. The costs for planting whitebark pine seedlings in one hectare of forest (2.47 acres) are calculated below from Tomback (unpublished data), based on information contributed from Bridger-Teton National Forest, Wyoming, and Flathead National Forest, Montana. An abbreviated version of this cost estimate appears in Wenny and others (2011). The following are conservative assumptions used in calculations:

1) Although multiple seed sources are used to maintain genetic diversity, here we base the costs on obtaining seeds from one tree only. It is typical to place 30 cone cages per tree, each cage protecting a whorl of cones. One tree would thus produce an excess of the seeds needed to plant 440 seedlings.

2) Maturing cones require protection from foraging nutcrackers and pine squirrels. These calculations assume that cages for protecting cones are already available.

3) Parent trees known to be genetically resistant or potentially resistant to the blister rust pathogen are protected from mountain pine beetle with applications of verbenone or carbaryl, but this is not included in cost calculations.

4) Also, costs of identifying and screening parent trees, travel and transportation, and cone storage are not included.

Estimated costs:

- Climb and cage cones: $250 to $375 per tree.
- Climb and collect ripe cones: $250 to $425 per tree.
- Administrative oversight: $100 per tree.
- Growing seedlings: 440 seedlings @ $2/ seedling = $880
- Planting 1 hectare: $250 to $375
- Planting layout, administration: $250/ha

Estimated costs of replacing one nutcracker for one hectare of forest: $1980 to $2405.

The time frame of natural regeneration will be longer than planting all seedlings within one field season. Tomback (unpublished data) used weighted means for new seedlings produced each year across different study sites after the 1988 Yellowstone fires to calculate the number of new whitebark pine seedlings that germinated per hectare from natural seed caches (Tomback and others 2001). Results indicated that it would take a minimum of 5 to 6 years for nutcrackers to produce 440 whitebark pine seedlings per hectare. Spreading regeneration over time may actually reduce risk, since conditions for seedling survival may vary from year to year.

Limber pine

Limber pine has moderately large, wingless seeds, but cones that open when ripe (Table 3, Figure 3, Figure 4b). Tree form is similar to that of whitebark pine, with upswept branches forming a lyrate canopy with horizontally-oriented cones borne in whorls around branch tips. In the core range of limber pine, Clark's nutcracker is probably the most important Phase I seed disperser for limber pine (Figure 3b) (Vander Wall and Balda 1981; Lanner and Vander Wall 1980; Tomback and Kramer 1980; Vander Wall 1988). Nutcracker seed harvest and caching behaviors for limber pine are very similar to those reported for whitebark pine with an important difference: as limber pine cones open, seeds begin to fall from cones. The cones are resinous, retaining some seeds (for example, Tomback and Kramer 1980), but seeds may be dislodged by branch movement from wind and animals.

The cones of limber pine ripen asynchronously both within and among trees, slowly turning from green to pale brown as scales open (Tomback and Kramer 1980; Vander Wall 1988). In regions where whitebark pine is sympatric with limber pine, and a whitebark pine cone crop is produced, nutcrackers will first harvest whitebark pine seeds. Then, nutcrackers will move into limber pine stands later in summer, taking seeds from partly open or open limber pine cones (Tomback and Kramer 1980; Tomback 1998). Otherwise, nutcrackers first harvest and cache seeds from closed, green cones in late August (Vander Wall and Balda 1977; Tomback and Taylor 1987; Vander Wall 1988). Frequently, nutcrackers detach closed limber pine cones from trees and wedge them into a branch fork or carry them to an "anvil"—a stump, rock, or log—to support the cone while digging into and loosening cone scales (Tomback and Taylor 1987; Torick 1995). Also, nutcrackers will take limber pine cones from red squirrel middens (Torick 1995).

Steller's jays may serve as Phase I seed dispersers for limber pine (Table 3). They have been observed harvesting seeds directly from open limber pine cones in the Colorado Front Range (Breindel 2000). In general, they harvest pine seeds from the cones of many conifers, but only from open cones (Hutchins and Lanner 1982; Samano and Tomback 2003; Vander Wall 2008). They make caches of one to three seeds in soil or other substrate within their territories in forested communities (Vander Wall and Balda 1981). Chipmunks (*Tamias* spp.) are known to harvest seeds from cones in several pines, removing cone scales and leaving behind characteristic spiky cores. We lack information as to whether chipmunks transport and cache these seeds or consume them as they are harvested (Tomback 1978; Samano and Tomback 2003). Seed fall, which occurs when seeds are dislodged from open cones and accumulate beneath trees, comprises another Phase I mechanism of seed dispersal.

Seed fall leads to Phase II or secondary seed dispersal in limber pine. The population genetic structure of limber pine, discussed below, provides evidence that Phase I seed dispersal by nutcrackers is more important in core populations than gravity dispersal. Although not studied specifically for limber pine seeds within the core range, diurnal secondary dispersers, including Steller's jays, chipmunks, and golden-mantled ground squirrels (*Spermophilus lateralis*), forage on the forest floor for conifer seeds and then distribute the seeds within caches, which may lead to seedling production (Breindel 2000; Samano and Tomback 2003; Vander Wall 1992). Nocturnal seed dispersers, especially deer mice (*Peromyscus maniculatus*) harvest and cache pine seeds as well, including large, wingless seeds (Vander Wall 1997; Vander Wall 2003). Because larger pine seeds are preferred by rodents, it is likely that limber pine seeds are harvested and cached by secondary dispersers (Vander Wall 2008). Secondary seed dispersal tends to be over much shorter distances than nutcracker seed dispersal—for example, within about 60 m of seed sources (Vander Wall 1992).

Limber pine occurs in a number of isolated populations at some distance from core populations (for example, Potter and Green 1964; Thilenius 1970; Schuster and Mitton 1991). Some of these isolates may be outside the typical range of Clark's nutcrackers. For example, within the Pawnee National Grasslands, seed fall and Phase II seed dispersal by rodents, especially deer mice and Ord's kangaroo rats (*Dipodomys ordii*) appear to be the main mechanisms for seed dispersal (Tomback and others 2005). This has produced a population genetic structure that is substructured (varies over short distances) compared to the core populations of limber pine (Schuster and Mitton 2000).

Rodents are known to raid the caches made by other animals, including nutcrackers (Vander Wall and Longland 2004). Baud (1993) examined rodent predation on simulated caches of limber pine and Rocky Mountain bristlecone pine placed at alpine, subalpine, and montane elevations. She found an inverse relationship between elevation and predation, with only 13 percent loss of caches to rodents in the alpine zone. Using a 100 trap grid at each location, she determined the density of rodents during spring and summer and found the lowest densities in the alpine and subalpine zones.

How seed dispersal by nutcrackers impacts pine ecology and population biology

Seed dispersal by Clark's nutcrackers has profoundly influenced the ecology, population genetic structure, and distribution of both whitebark and limber pine (for overview for whitebark pine, see Tomback 2005): 1) Nutcracker selection of topography and location for seed caching, coupled with the environmental requirements of whitebark and limber pine seeds for germination and seedling survival, determine where trees grow (Lanner 1980; Tomback 1982; Tomback and Linhart 1990). 2) After fire or other disturbance, nutcrackers will cache seeds in open terrain, leading to the pioneering status of both whitebark and limber pine (Lanner and Vander Wall 1980; Tomback and others 2001b). 3) Seedlings originating within a whitebark or limber pine seed cache may produce a "tree cluster" growth form—a multi-genet cluster of trunks, often composed of siblings, contiguous or fused at the base (Linhart and Tomback 1985; Carsey and Tomback 1994; Rogers and others 1999). This is a common growth form in both whitebark and limber pine on harsher sites, and represents a highly "clumped" population dispersion pattern. 4) Long distance seed dispersal by nutcrackers results in lower than expected genetic differentiation among neighboring and regional populations (Schuster and others 1989; Jorgensen and Hamrick 1997; Rogers and others 1999; Bruederle and others 2001). 5) Seed dispersal by nutcrackers enabled whitebark and limber pine to migrate out of refugia following the retreat of Pleistocene glaciers. Nutcracker seed dispersal along mountain corridors, and limits to dispersal, may explain current range-wide population structure of mitochondrial DNA haplotypes (Mitton and others 2000; Richardson and others 2002a,b).

Pines With Mixed Seed Dispersal Strategies

Southwestern white pine

Southwestern white pine has the largest seeds of the high-elevation white pines, and the seeds are wingless (Table 3, Figure 3). The trees vary in branch morphology, with a mixture of upswept branches around the crown and more horizontally-directed branches lower in the canopy. The cones are the longest of the high-elevation white pines and range in orientation within a tree from upward-pointing to horizontally-oriented to pendulous. A large proportion of the cones have reflexed basal scales, which may deter pine squirrels (Samano and Tomback 2003). As in limber pine, southwestern white pine cones open when ripe, changing in color from green to light brown; cone opening is asynchronous both within and among trees.

For populations at the edge of the northern range of southwestern white pine, such as in the San Francisco Mountains of northern Arizona and San Juan Mountains of southern Colorado, Clark's nutcracker is a dependable primary seed disperser (Benkman and others 1984; Samano and Tomback 2003). In the San Juan Mountains, nutcrackers begin harvesting and caching seeds from closed southwestern white pine in late August. In the northern range, nutcrackers least prefer pendulous cones and most prefer horizontally-oriented cones for seed harvest. All cones do not fully open until early October. Samano and Tomback (2003) report that as nutcrackers forage, they drop seeds, and seeds are also dislodged by the movement of branches. By the time all cones opened, seed fall was common during strong winds. Colorado chipmunks (*Tamias quadrivitatus*) were observed foraging for seeds in the canopies of southwestern white pine trees, but also under canopies. Steller's jays removed seeds from cones frayed by nutcrackers and from open cones, but also harvested seeds from the ground.

To the south, in the core region of sky island forests, southwestern white pine has a different seed dispersal biology. In this region, nutcrackers are neither resident nor reliable dispersers (Tomback 1998). In the Chiricahua Mountains of southeastern Arizona, seed harvesting from cones by Steller's jays and seed fall are probably the major primary dispersal modes; and, harvest and dispersal of fallen seeds by nocturnal rodents comprised an important secondary dispersal mechanism (Pruett 2007; Tomback and others, these proceedings). Furthermore, Tomback and others (these proceedings) determined that cones in the Chiricahua Mountains were more frequently pendulous in orientation than in the San Juan Mountains, and had larger seeds.

The "foxtail pines"

The three pines in subsection *Balfourianae* have relatively small, winged seeds and cones that open (Table 3, Figure 3). The small seeds and well-developed seed wings suggest that Phase I seed dispersal by wind is important for all three species. There is some anecdotal evidence that Clark's nutcrackers also serve as primary seed dispersers in some years for the "foxtail" pines. For example, Baud (1993) reported that nutcrackers first harvested seeds in mid-October from open cones of Rocky Mountain bristlecone pine on Mt. Evans, Colorado Front Range, after a cone crop of limber pine seeds had been depleted. The nutcrackers removed the seed wings before pouching the seeds. She observed nutcrackers transporting these seeds to alpine areas, presumably for caching. Torick and others (1996) found that 20 percent of multi-stemmed Rocky Mountain bristlecone pine of a small sample from the Colorado Front Range were multi-genet tree clusters, which indicates an origin from caches.

Lanner (1988) noted that unripe cones of Great Basin bristlecone pine in two stands in the White Mountains of eastern California were shredded in the manner typical of nutcrackers. He noted the presence of nutcrackers in the vicinity, but never observed nutcrackers harvesting or caching the seeds. He also recorded infrequent visits to bristlecone pine stands by Western Scrub-jays (*Aphelocoma californica*) and Pinyon jays (*Gymnorhinus cyanocephalus*) (Lanner and others 1984); these birds are known to cache pine seeds (Vander Wall and Balda 1981). Although the growth forms of many Great Basin bristlecone pines appear to be composed of multiple stems, which would imply multiple genotypes—a common growth form in whitebark and limber pine as a result of nutcracker seed dispersal—genetic analysis indicates only a single genotype per tree (Lee and others 2002). Thus, most seeds in both bristlecone pine species are likely to be dispersed from cones by wind, but jays and especially rodents may act as secondary seed dispersers. This conclusion may apply to foxtail pine as well. Northern foxtail pine populations are more genetically differentiated than southern populations (Oline and others 2000). This could conceivably result from more frequent seed dispersal by nutcrackers in the southern range.

Ecological Importance

Foundation and Keystone Functions

A foundation species is viewed as "A single species that defines much of the structure of a community by creating locally stable conditions for other species, and by modulating and stabilizing fundamental ecosystem processes" (Dayton 1972 cited in Ellison and others 2005). Keystone species influence community diversity to a greater extent than predicted by their abundance or through their interactions with other species (for example, Mills and others 1993; Soulé and others 2003). Whitebark pine has been regarded as both a foundation and keystone species in subalpine and treeline ecosystems with influences on biodiversity that transcend its elevational range (Tomback and others 2001a; Ellison and others 2005; Tomback and Achuff 2010). These ecological roles result primarily from four characteristics of whitebark pine: large, nutritious seeds; seed dispersal by nutcrackers; hardy, robust seedlings; and high tolerance for cold and extremely windy sites (McKinney and Tomback 2011). The other high-elevation five-needle white pines share some or all of these traits and thus serve to varying degrees as foundation and keystone species.

The high-elevation five-needle white pines contribute to community biodiversity, providing large seeds as wildlife food. The seeds of whitebark pine are the largest among its conifer associates at high elevations, and are eaten by a number of granivorous birds, squirrels, and mice, as well as by grizzly (*Ursus arctos*) and black bears (*U. americanus*), which raid squirrel cone middens (Kendall 1983; Table 12-1 in Tomback and Kendall 2001). Limber pine seeds are eaten by black bears (McCutchen 1996). The smaller seeds of the "foxtail" pines are also potentially a food resource for granivorous birds and small mammals.

The large latitudinal and longitudinal distributions of whitebark and limber pine, combined with their various community types—treeline, climax, and successional—and mosaics of seral stages, result in considerable geographic variation in forest structure and understory diversity (Arno 2001; Tomback and Kendall 2001; Schoettle 2004; Tomback and Achuff 2010). Collectively, the high-elevation white pines occur within a number of different forest communities and cover types across the western U.S. and Canada, representing considerable forest biodiversity (Tomback and Achuff 2010). Furthermore, many plant species are unique to whitebark pine communities (for example, see Tomback and Kendall 2001); other high elevation white pine communities may have unique plants as well.

The high-elevation, five-needle white pines contribute to community development and stability after disturbance with respect to their pioneering status and tolerance of harsh sites and poor seedbeds both as seedlings and later as mature trees (for example, Beasley and Klemmedson 1980; Baker 1992). Nutcrackers frequently cache whitebark and limber pine seeds in newly burned terrain, typically enabling both pines to establish after fire, although delay may occur under extremely droughty conditions (Lanner and Vander Wall 1980; Veblen 1986; Tomback 1986; Tomback and others 1990; Rebertus and others 1991; Tomback and others 1993; Webster and Johnson 2000; Tomback and others 2001b; Coop and Schoettle 2009). In the Rocky Mountains on particularly harsh sites, whitebark pine often acts as a "nurse" tree to spruce and fir regeneration by protecting seedlings from high winds and ice particles (Callaway 1998). On dry, lower treeline sites, limber pine protects wax currant (*Ribes cereum*) shrubs and Douglas-fir seedlings from high winds, facilitating their survival (Baumeister and Callaway 2006).

Treeline conditions in the Rocky Mountain Front of Montana, which is east of the Continental Divide, include strong winds and extreme temperatures. There, whitebark pine functions as the most frequent tree to initiate krummholz tree islands (Resler 2004; Resler and Tomback 2008). Whitebark pine becomes established and mitigates the force of the wind to its leeward side, where other trees then become established. Apparently, the hardiness of whitebark pine seedlings, possibly combined with selection of sheltered sites by nutcrackers for whitebark pine seed caches, enables whitebark pine to survive these conditions. Similarly, Rocky Mountain bristlecone pine at treeline facilitates the establishment of Engelmann spruce and subalpine fir (Schoettle 2004).

All of the high-elevation five-needle white pines, with the exception of southwestern white pine, grow on harsh sites at treeline and in the subalpine zone, and they often occur at the highest elevations where other conifers are absent (LaMarche and Mooney 1972; Arno and Hammerly 1984; Bunn and others 2005). In these upper-watersheds, these trees stabilize snowpack, and the shade and shelter provided by their tree canopies and by krummholz tree islands delay snow melt and thus protract downstream flow. Also, their root systems stabilize the loose, shallow, rocky substrates, reducing erosion (for example, Arno and Hammerly 1984; Farnes 1990).

Ecosystem Services

The keystone and foundation processes and functions provided by the High Five pines provide direct or indirect ecosystem services to humans. Ecosystem services have been generally defined, and economic valuation tentatively assigned to some broad categories of services (Dailey 1997; Costanza and others 1997). Several ecosystem services provided to humans by the high-elevation white pines stand out in particular: the use of the seeds, needles, resins, and inner bark as food and for medicinal purposes by humans (see below; food production services); the regulation of downstream water supply through snowpack protection, snow stabilization, and the prevention of soil erosion by treeline communities (water regulation); and, the aesthetic and spiritual values often associated with high elevation forests (see below; cultural services). From this perspective, it is theoretically possible to place an economic valuation on these pines in different geographic regions—to estimate their monetary contribution to human welfare, both past and present. Similarly, it is possible to estimate the economic value of nutcrackers for their seed dispersal services (see Sidebar).

Native American Use of the High Five Pines

The ethnobotany literature includes records of Native American use of different pines for food and for ceremonial or medicinal purposes. In the compendiums of Moerman (1998, 2009), the uses of several high-elevation white pines are described (Table 4), but may be under-reported. The more widely distributed five-needle white pines, such as western white pine (*Pinus monticola*) and eastern white

Table 4. Native American use of the high-elevation white pines for food, medicinal, or ceremonial purposes (Moerman 1998, 2009).

Food

Whitebark pine

- Seeds generally used as food, eaten raw or roasted.
- Seeds cooked in hot ashes.
- Seeds stored for winter use.
- Dried or cooked and crushed seeds mixed with dried service berries (*Amelanchier alnifolia*) and stored.
- Seeds ground into flour and water added to make mush.
- Inner bark used as food.

Limber pine

- Seeds important as a food source.
- Seeds roasted and eaten whole or ground up either after hulling or with hulls (seed coats).

Medicinal uses

Limber pine

- Ceremonial emetic.*
- Cough medicine.*
- Reduce fever.*

Rocky Mountain bristlecone pine

- Heated pine pitch applied to sores and boils as a poultice.

Ceremonial uses

Limber pine

- Smoked before hunting for "good luck."
- Wood used to make a small bow and arrow for ceremonial chants.

* Reports for other pine species indicate that various decoctions of needles were used for making medicines and emetics. Both pine needles and resin (pitch) were used to make cough medicine.

pine (*Pinus strobus*) served many more purposes, providing a greater variety of medicines and also construction materials (Moerman 1998).

In particular, the large seeds of whitebark pine were an important food source for a number of Northwestern tribes, and records for limber pine seed consumption come from Montana as well as the Southwest (Moerman 1998). (Some of these latter records may confuse southwestern white pine with limber pine.) Consumption of the inner bark (bark-peeling) of the high-elevation white pines may also be under-reported, although it is noted for whitebark pine (Table 4). This food source is listed for several more accessible pines (Moerman 1998). Östlund and others (2009) report on the traditional use of the inner bark of pines by indigenous people in northern Scandinavia and in North America. Bark was stripped from the trees only in spring or in early summer when the sap contains high levels of sugars and other nutrients.

Aesthetics: the High-Mountain Experience

All the high-elevation white pines may be found on extremely harsh sites—on steep, rocky slopes, ridges, and canyon walls—with wind-sculpted irregular or flagged crowns. But, southwestern white pine may also grow as a magnificent, tall and full-crowned old-growth tree on favorable sites. Under the harshest conditions, whitebark, limber, and the foxtail pines assume massive, gnarled, bark-stripped forms with twisted wood—forms that are the product of a millennium or more of survival under adverse conditions (Tomback and Achuff 2010). The progressive loss of bark on the stout trunks, known as cambial die-back, eventually leaves isolated strips of live bark surrounded by exposed, weathered wood, supporting remnant canopies (Tang and others 1999; Schauer and others 2001; Bunn and others 2003). Visitors to high elevations may perceive these trees as 'survivors' and symbolic of perpetual struggle. The snags of the dead "warriors" are frequently photographed by hikers.

McCool and Freimund (2001) discuss the symbolism of trees—how trees assume the role of "…gatekeeper between what is civilized and what is wild." Tomback and Achuff (2010, p. 201) write, "Lofty and majestic or ancient and wind-sculpted, the white pines of the western forests are important symbols of the primeval forest, the wilderness, and the forces of nature. Their rugged forms speak of endurance, stoicism and timelessness to the many tens of thousands of skiers, hikers, backpackers, climbers and mountain visitors. For these admirers, our natural world would be spiritually impoverished without the white pine gate-keepers of forests and treelines."

Threats

There are multiple challenges to the persistence of the High Five pines on the Western landscape, and some of these challenges are the direct or indirect consequence of human activities, complicated by the unique ecology of the pines. Despite the fact these pines inhabit remote locations, it is remarkable that they have been so severely impacted by anthropogenic events. In effect, the vulnerabilities of the high elevation pines reflect the challenges faced by natural communities in today's rapidly changing world.

White Pine Blister Rust

The most pervasive and widespread threat is the invasive fungal pathogen *Cronartium ribicola*, which causes the disease white pine blister rust in five-needle white pines. The blister rust pathogen, which is native to Asia and alternates between pines and other hosts within its life cycle, was inadvertently introduced to the Pacific Northwest around 1910 (McDonald and Hoff 2001; Geils and others 2010; Geils and Vogler, these proceedings). The cool, humid northwest climate coupled with an abundance of white pines and alternate hosts, especially currants and gooseberries (*Ribe*s spp.), created a highly favorable environment for the spread of the disease.

Although the rust fungus infects pines through the stomates of needles, it rapidly grows from the needles into the branches and the stem of trees, girdling and killing tissues as it advances. When infections start in the tree canopy, the girdling process kills cone-bearing branches and weakens the tree by reducing photosynthetic biomass (McDonald and Hoff 2001; Geils and others 2010). If the infection reaches the main stem, it girdles the tree, resulting in top kill or mortality. However, infections in small trees and seedlings results in rapid mortality. As a result, in seral communities, blister rust may hasten the replacement of high elevation white pines by more shade-tolerant conifers (Keane and others 1990; Keane and Arno 1993).

In the century since its introduction to the West, *Cronartium ribicola* has spread nearly throughout the collective ranges of five-needle white pines in the western United States and Canada, including the high elevation white pines (Schwandt and others 2010; Tomback and Achuff 2010). At this time, there is no record of blister rust in the interior ranges of the Great Basin; and, the only western five-needle white pine not yet infected is Great Basin bristlecone pine, which is known to be susceptible (Hoff and others 1980). Although the blister rust pathogen is now widely distributed, the incidence of infection varies by species and by region (Schwandt and others 2010). Differences in infection levels even within a region may depend on host abundance and distribution and microclimate (for example, Kearns and Jacobi 2007; GYWPMWG 2010).

Whitebark pine is infested by blister rust to varying degrees throughout its distribution in both the U.S. and Canada, up to the pine's northern limits, again with the exception of interior Great Basin ranges (Tomback and Achuff 2010; Schwandt and others 2010). The highest incidence of blister rust infection is in the northern U.S. and southern Canadian Rocky Mountains, and particularly in the Northern Continental Divide Ecosystem (Northern Divide), which includes the Bob Marshall Wilderness Area, and Glacier and Waterton Lakes National Parks (for example, Kendall and Keane 2001; Smith and others 2008). Throughout the Northwestern U.S. and Northern Divide, infection levels in some stands may range as high as 90 to 100 percent. Even within the more xeric regions, such as the Greater Yellowstone, incidence of blister rust appears to be increasing during this past decade (GYWPMWG 2010). As whitebark pine experiences more damage and mortality, cone production declines within stands. In the Northern Divide, the extensive and widespread loss of whitebark pine has greatly diminished the functional roles and ecosystem services provided by the pine. With reduced cone production, red squirrels harvest most available cones, and Clark's nutcrackers may not reliably visit stands to harvest and cache seeds (Smith and others 2008; McKinney and Tomback 2007; McKinney and others 2009). Thus, whitebark pine regeneration may be greatly reduced.

White pine blister rust occurs throughout all but the southernmost populations of limber pine, with infection levels varying among stands and regions, but reaching as high as 100 percent in some stands (Kliejunas and Dunlap 2007; Kearns and Jacobi 2007; Schwandt and others 2010 and references therein). In Alberta, the pine is heavily infested throughout its range (Langor 2007). Southwestern white pine is infested in the Sacramento Mountains of southern New Mexico, and in adjacent ranges—a region with large populations of pines and alternate hosts and suitable moisture conditions from a summer monsoon season that coincides with *Cronartium ribicola* spore production (Geils 2000; Schwandt and others 2010). In recent years, blister rust has been discovered on southwestern white pines in northern and western New Mexico and in western Arizona.

Foxtail pine is infested with blister rust in the Klamath Mountains but not in its Sierra Nevada populations (Kliejunas and Dunlap 2007). The occurrence of blister rust in Rocky Mountain bristlecone pine currently appears to be primarily in the vicinity of Mosca Pass in the Sangre de Cristo Mountains and in the Wet Mountains (Blodgett and Sullivan 2004).

Mountain Pine Beetle

Mountain pine beetle (*Dendroctonus ponderosae*, Family Curculionidae) is a native western insect that requires pines for its life cycle. Although all western pines may serve as hosts, lodgepole and ponderosa pine, which comprise major forest types, have been the primary hosts. The adult females typically attack pines in late spring by burrowing into the phloem, where they feed and lay their eggs. Attacking beetles also deposit spores of mutualistic fungi. As the larvae develop and feed on phloem and sapwood and the fungi spread, together they disrupt the flow of nutrients and water, killing their hosts (Gibson and others 2009; Bentz and others, these proceedings).

Mountain pine beetle outbreaks have historically produced episodic, natural disturbances in western forests (Romme and others 1986; Perkins and Swetnam 1996; Lynch and others 2006). Beetle outbreaks, which occur on a regional scale and often last a decade or more, may result in forest openings and initiate successional communities. During severe outbreaks, mountain pine beetles may move from lodgepole pine into adjacent higher elevation white pine forest communities. For example, outbreaks in whitebark pine forests have been dated to more than 8,000 years ago as well as the 18th and 19th centuries (Perkins and

Swetnam 1996; Brunelle and others 2008). During last century, widespread outbreaks occurred between 1909 and 1940 and from the 1970s to the 1980s, creating the still-standing "ghost forests" of the central and northern U.S. Rocky Mountains (Perkins and Swetnam 1996; Kendall and Keane 2001; Logan and Powell 2001).

In the late 1990s, mountain pine beetle outbreaks again moved into high elevation white pine forests throughout the western U.S. and Canada. These outbreaks have achieved an unprecedented geographic scale and incidence of white pine mortality (Taylor and Carroll 2004; Gibson and others 2008). The expanses of mature lodgepole pine forests throughout the West, coupled with a decade of drought and warmer than average temperatures, may explain the extent and intensity of the current outbreaks. Warmer temperatures have facilitated beetle survival and population growth, made possible by the widespread occurrence of mature stands of hosts (Logan and Powell 2001; Logan and others 2003; Taylor and Carroll 2004). Several authors attribute the warmer temperatures to a global warming trend (Logan and Powell 2001; Logan and others 2003; Raffa and others 2008; Bentz and others, these proceedings). The magnitude of whitebark pine losses in the Greater Yellowstone Ecosystem, in particular, has been considered historically unprecedented, and a threat to the persistence of functional whitebark pine communities (Logan and others 2010).

Fire Exclusion

Reduction in the frequency and size of fires eventually leads to successional replacement of the high-elevation five-needle white pines growing on productive sites, given their shade-intolerance. Because fire-return intervals are so long in upper subalpine ecosystems, the effects of fire exclusion are most apparent at the landscape scale rather than the stand scale, with an increasing proportion of successionally-advanced communities over time (Keane 2001).This results in a reduction in landscape diversity as well as biodiversity.

National programs in the U.S. and Canada to eliminate fire in western forests had achieved a large degree of success by the 1920s, and these programs achieved even greater success by the mid-twentieth century (Arno and Allison-Bunnell 2002; Taylor and Carroll 2004). By the late 20th century, the effects of exclusion were evident from a number of studies: longer mean fire return intervals and reduction in annual forest area burned (Brown and others 1994; Van Wagner and others 2006; Keane and others 2002). By the late 1970s, the annual area burned by wildfires began to increase again, but it still falls far short of historic (pre-1900) burning rates (Arno and Allison-Bunnell 2002).

Whitebark pine has experienced altered fire frequencies since the late 1800s, particularly in some areas of the central and northern Rocky Mountains (Morgan and Bunting 1990; Keane and Arno 1993; Murray and others 2000; Murray 1998; for overview, see Tomback and Achuff 2010). However, Walsh (2005) found no evidence for suppression after compiling fire histories from stands from multiple locations in the Greater Yellowstone Area. It is also likely that subalpine forests with long fire return intervals may not yet be outside their historical range of variability (Agee 1993; Chappell and Agee 1996).

Similarly, in some areas limber pine communities are showing evidence of changing fire regimes: Kipfmueller and Baker (2000) found evidence of lengthened fire return intervals in subalpine forests in southeastern Wyoming. Along the Rocky Mountain Front, Montana, limber pine is expanding its distribution at lower elevations, apparently because of the reduction in fire frequency (Gruell 1983). A fire history study of two Rocky Mountain bristlecone pine and limber pine mixed forest communities in Colorado indicated an alteration of fire regime in the mid-1800s, which may be attributed to intense cattle-grazing (Brown and Schoettle 2008). Both human settlement and grazing practices have resulted in altered fire regimes in the Southwest, resulting in advancing succession and changing composition in southwestern white pine communities (Alexander and others 1984; Grissino-Mayer and others 1995; Danzer and others 1996; Sakulich and Taylor 2007.)

Climate Change

The Intergovernmental Panel on Climate Change (IPCC) (2007) identified a global warming trend of ~0.1°C per decade over the past 50 years, which they attributed to increasing greenhouse gas emissions since 1850. Using several different general circulation models in conjunction with different greenhouse gas emission scenarios, the IPCC projects temperature increases from 1 to 6°C by the year 2100. Given these predictions, the distributions of many forest trees are expected to shift, but independently, potentially resulting in new forest communities; and, fire frequencies and severities are expected to increase (Swetnam and Betancourt 1990; Heyerdahl and others 2008). This past decade, higher temperatures and associated water-stress, regional drought, and bark beetle outbreaks have resulted in broad-scale tree mortality in the Southwest, as well as tree mortality in forests of the western U.S. and southern Canada (Breshears and others 2005; van Mantgem and others 2009).

A number of bioclimatic models, also referred to as "niche-based" models have recently been used to predict the distribution of white pine species under different temperature scenarios (Hamann and Wang 2006; McKenny and others 2007; Warwell and others 2007; Schrag and others 2008). In general, these models predict shifts to higher elevations and more northern latitudes, with losses of lower elevation and more southern populations (Tomback and Achuff 2010). According to interpretation of these models, forest tree species have the option of three responses, or possibly a combination within a species, to rapidly changing climate: migration to track their niches, adaptation in current distributions to changing conditions, or population extirpation (Aitken and others 2008). However, niche-based models produce coarse-scale predictions, not incorporating information on topographic variation within regions, potentially leading to persistence, or species-specific ecological or phenological processes that affect survival, such as timing of bud-break or flowering or the requirements for seedling germination and survival or mediation of response to climate through other processes or interactions, such as damage and mortality from blister rust and fire (Tomback and Resler 2007; Keane and others 2008; Morin and Thuiller 2009; Chuine 2010; Loehman and Keane, these proceedings). The high elevation white pines are among the most vulnerable species to climate change, because of little area to support these pines above current treeline, patchy and isolated "sky island" populations without 'migration corridors,' stressed southern populations, and, especially, current forest health challenges from the blister rust pathogen, mountain pine beetle outbreaks, and advancing succession from fire suppression. The velocity of climate change within montane landscapes, however, is predicted to be comparatively slow because of steep and complex topography. Plants may be able to keep pace with change based on historic rates of migration (Loarie and others 2009).

Some high elevation white pines may have moderate to high levels of genetic diversity within populations, but they show fewer differences among populations (Jorgensen and Hamrick 1997; Bruederle and others 2001). In whitebark pine, for example, there appears to be only modest geographic variation in phenotypic traits (Mahalovich and others 2006; Bower and Aitken 2008), which may limit the ability of local populations to migrate or adapt quickly enough to changing climate regimes. Regardless, healthy populations at the treeline elevation and northern latitude migration fronts are critical to facilitate species' responses.

Conservation Status of the High Five Pines

The conservation status of these pines has been assessed by the International Union for Conservation of Nature (IUCN 2007) and NatureServe (2010) at the global, national (Canada and USA), and state/provincial levels (Table 5a and 5b). Globally, whitebark pine is ranked as *Vulnerable* by the IUCN Red List; it is ranked by NatureServe as *Vulnerable* in Canada and *Vulnerable-Secure* in the U.S. At the state or provincial level, whitebark pine is ranked as *Imperiled* to *Vulnerabl*e; but, in three states it is unranked, and in Washington state it is considered a *Species of Concern* by the U.S. Fish and Wildlife Service (2009).

These varying classifications are highly questionable, given that whitebark pine is now recommended for listing as *Endangered* under the federal Species at Risk Act in Canada and is now listed in Alberta under the Wildlife Act. Furthermore, last July, 2010, a review of whitebark pine under the Endangered Species Act by the U.S. Fish and Wildlife Service concluded that "substantial" information supported the petition for federal listing of whitebark pine, and that listing "throughout all or a significant portion of its range may be warranted" (U.S. Fish and Wildlife Service 2010). This finding has prompted a full status evaluation by the U.S. Fish and Wildlife Service for possible listing of whitebark pine as *Threatened* or *Endangered*. In general, there appear to be time lags and inadequate information disseminated for the international conservation ranking processes,

Table 5a. Conservation status of whitebark and limber pine in Canada and the U.S.

Jurisdiction	Whitebark pine	Limber pine
International Union for Conservation of Nature (IUCN)	Vulnerable	Least concern
NatureServe		
Global	Vulnerable-Secure	Secure
Canada	Vulnerable	Vulnerable
Provincial	Imperiled-Vulnerable	Imperiled-Vulnerable
U.S.A.	Vulnerable-Secure	Secure
State	Vulnerable-Secure	Critically imperilled-Secure
Not ranked	Three states	Six states
Canada: Species at Risk Act (SARA)	Proposed as Endangered	Not assessed
Alberta: Wildlife Act	Endangered	Endangered
U.S.A.: Endangered Species Act	Under review	
Washington state: U.S. Fish & Wildlife	Species of concern	

Table 5b. Conservation status of southwestern white pine, the bristlecone pines, and foxtail pine in the U.S.

Jurisdiction	Southwestern white pine	Foxtail pine	Rocky Mountain bristlecone pine	Great Basin bristlecone pine
IUCN	Least concern	Conservation dependent	Not threatened	Vulnerable
NatureServe				
Global	Secure	Secure	Vulnerable	Secure
U.S.A.	Secure	Secure	Vulnerable-Secure	Secure
State	Not ranked	Apparently secure	Imperiled-Not ranked	Vulnerable-Not ranked

as well as for regional authorities. The recent federal listing processes in Canada and the U.S. appear to have compiled more current information, which indicates that the status of whitebark pine is precarious throughout its range.

Similar conflicts in ranking apply to limber pine. Limber pine is considered of *Least Concern* by the IUCN and as *Secure* globally and in the U.S. by NatureServe, but as *Vulnerable* in Canada. However, limber pine has been listed as *Endangered* in Alberta, and will undergo federal review in Canada. It is ranked as *Critically Imperiled* in three states and as *Imperiled* in one province; *Secure* in three states and *Vulnerable* in one province, and it is *Not Ranked* in six states. Time lags, inattention, and differing information may be affecting some of these assessments. There is, however, significant geographic variation in the incidence of white pine blister rust and mountain pine beetle outbreaks.

Southwestern white pine is considered to be of *Least Concern* by IUCN and to be *Secure* globally and nationally in the USA by NatureServe. It is *Not Ranked* in the four states in which it occurs. Foxtail pine is considered *Conservation Dependent* by the IUCN and *Secure* both globally and in the U.S. by NatureServe. Globally and nationally, Rocky Mountain bristlecone pine is considered *Not Threatened* by the IUCN but *Vulnerable* to *Secure* by NatureServe. It is designated as *Imperiled* in Arizona and *Not Ranked* in two other states. Great Basin bristlecone pine is ranked as *Vulnerable* by the IUCN but *Secure* both globally and nationally in the U.S. by NatureServe. Two states rank this pine as *Vulnerable* and it is *Not Ranked* in one state.

The Future of the High Five: Challenges to Maintaining Viable Populations

Maintaining healthy populations of the high-elevation white pines depends on a favorable climatic regime, cycles of disturbance and successional renewal, good seed production, successful regeneration, and sufficient genetic variation to provide resilience to stress and adaptation to environmental change (Figure 5). However, the high-elevation white pines are facing an unprecedented combination of challenges which, by interaction and synergism, create a downward spiral of population health.

There is every indication that the blister rust pathogen *Cronartium ribicola* will ultimately spread throughout the ranges of all six high-elevation white pine species. Blister rust kills trees and branches, reducing seed production as well as natural regeneration (Figure 5). Mountain pine beetle outbreaks result in further losses of trees and seed production. With reduced seed production, Clark's nutcrackers may

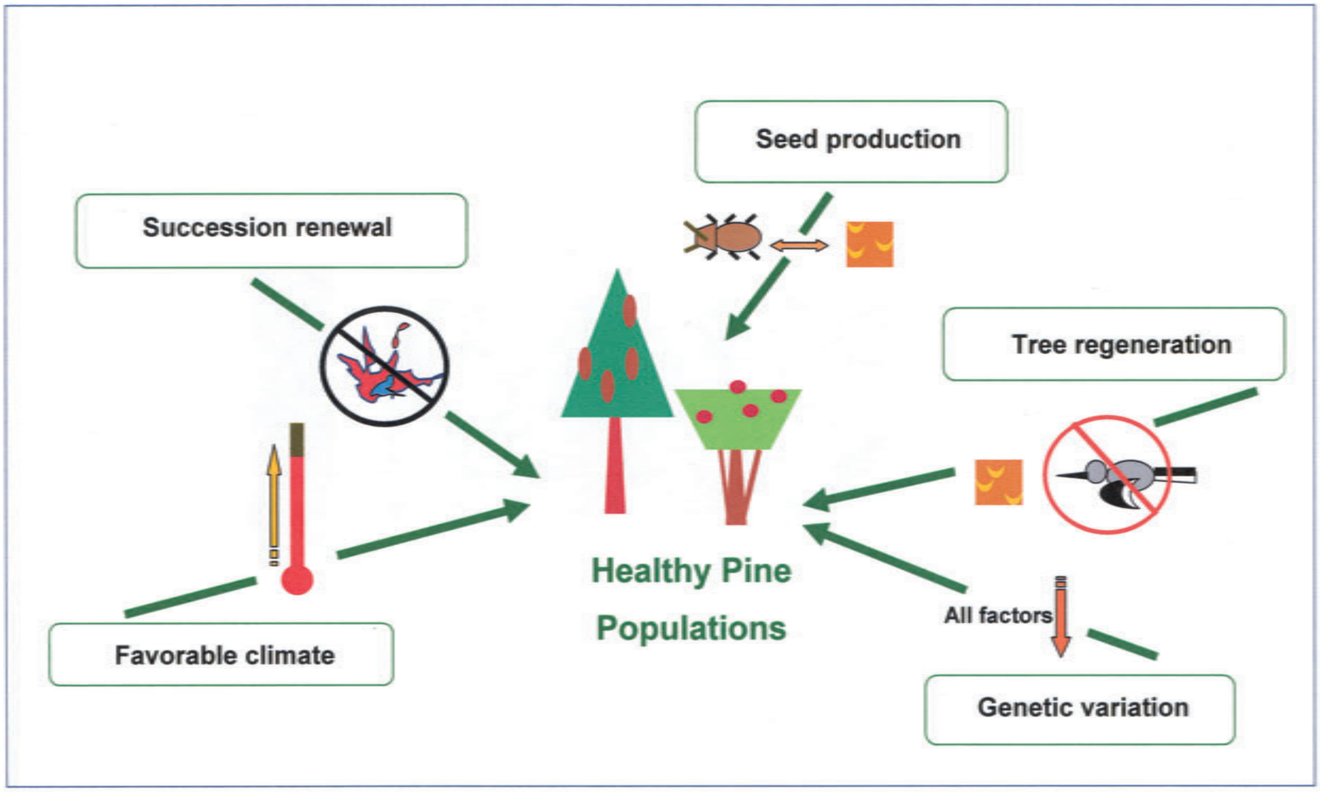


Figure 5. Challenges to maintaining viable populations of the High Five pines. The processes required to maintain healthy populations of the high-elevation white pines include: Seed production, tree regeneration, renewal of successional communities, a favorable climate, and sufficient genetic variation to enable adaptation to the changing biotic and abiotic environment. These processes are being disrupted by the spread of the white pine blister rust pathogen, outbreaks of mountain pine beetles, and the decline of seed dispersal services by Clark's nutcrackers where cone production is reduced; and, by fire suppression and advancing succession in some regions, and by warming trends in climate. (See text for discussion.)

be less reliable as a seed disperser, which may in turn reduce regeneration and alter population structure for at least five of the six High Five pines (McKinney and others 2009). Fewer seeds will be available for dispersal by wind for three of the pines. This sequence of events progressively erodes genetic variation and potentially fragments populations (Schoettle and Sniezko 2007). With a loss of genetic variation and decrease in effective population sizes, pine populations are less able to adapt to changing and stressful conditions (for example, Aitken and others 2008). With a reduction in seed production and dispersal, populations become severely constrained in their abilities to shift their ranges in response to changing climate.

This scenario is similar to the four "extinction vortices" of Gilpin and Soulé (1986), which are driven by inbreeding depression, genetic drift, fragmentation, and demographic variation. Each process by itself results in an ever-faster spiral to species extinction. All four processes working alone or together may reduce population size rapidly. Tomback and Kendall (2001), suggested that whitebark pine in some regions has already entered the spiral, propelled by demographic variation from the reduction in population size by blister rust and mountain pine beetles, and reduction in seed dispersal services, and thus potential regeneration, by Clark's nutcrackers (McKinney and others 2009). The loss of trees leads to fragmentation, which potentially increases the chances of extirpation in local populations with the highest whitebark pine mortality. The reduction in effective population size results in inbreeding depression and further loss of genetic variation through genetic drift, thus impacting the ability of populations to adapt to change. At the same time, the decline of whitebark pine and the resulting fragmentation of populations lead to the loss of ecosystem services and functions, as well as declines in regional biodiversity, changes in forest composition and fire regimes, loss of ecological processes, and declines in forest resilience.

Maintaining the magnificent High Five on the Western landscape will require a long-term commitment to strategic management of these species (Keane and Schoettle, these proceedings). Whitebark pine requires immediate restoration intervention in much of its range to counteract the downward spiral. For the other high-elevation white pines, we may have time to enact proactive management strategies (Schoettle and Sniezko 2007) in the hope of avoiding the extinction vortices altogether.

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References

Achuff, P. L.; McNeil, R. L.; Coleman, M. L.; Wallis, C.; Wershler, C. 2002. Ecological land classification of Waterton Lakes National Park, Alberta. Volume I: Integrated Resource Description. Waterton Park, Alberta: Parks Canada, Waterton Lakes National Park.

Agee, James K. 1993. Fire ecology of Pacific Northwest forests. Washington, DC: Island Press. 493 p.

Aitken, Sally N.; Yeaman, Sam; Holliday, Jason A.; Wang, Tongli; Curtis-McLane, Sierra. 2008. Adaptation, migration or extirpation: climate change outcomes for tree populations. Evolutionary Applications. 1: 95-111.

Alexander, Jr., Billy. G.; Ronco, Jr., Frank.; Fitzhugh, E. Lee; Ludwig, John A. 1984. A classification of forest habitat types of the Lincoln National Forest, New Mexico. Gen. Tech. Rep. RM-104. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station. 29 p.

Andresen, John W.; Steinhoff, Raphael J. 1971. The taxonomy of *Pinus flexilis* and *Pinus strobiformis*. Phytologia. 22(2): 57-70.

Arno, Stephen F. 2001. Community types and natural disturbance processes. In: Tomback, Diana F.; Arno, Stephen F.; Keane, Robert E., eds. Whitebark pine communities: ecology and restoration. Washington, DC: Island Press: 74-88.

Arno, Stephen F.; Hammerly, Ramona P. 1984. Timberline: mountain and arctic forest frontiers. Seattle, WA: The Mountaineers. 304 p.

Arno, Stephen F.; Weaver, T. 1990. Whitebark pine community types and their patterns on the landscape. In: Schmidt, Wyman C.; McDonald, Kathy J., comps. Proceedings—Symposium on whitebark pine ecosystems; 1989 March 29-31; Bozeman, MT. Gen. Tech. Rep. INT-270. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station: 97-105.

Arno, Stephen F.; Hoff, Raymond J. 1990. *Pinus albicaulis* Engelm. Whitebark pine. In: Burns, Russell M.; Honkala, Barbara H., technical coordinators. Silvics of North America, Volume 1, Conifers. Washington, DC: U.S. Department of Agriculture, Forest Service, Agriculture Handbook 654: 268-279.

Arno, Stephen F.; Allison-Bunnell, Steven. 2002. Flames in our forest: disaster or renewal? Washington, DC, USA: Island Press. 227 p.

Bailey, D. K. 1970. Phytogeography and taxonomy of *Pinus* Subsection *Balfourianae*. Annals of the Missouri Botanical Garden. 57: 210-249.

Baker, William L. 1992. Structure, disturbance, and change in the bristlecone pine forests of Colorado, U.S.A. Arctic and Alpine Research. 24(1): 17-26.

Barney, C. W. 1980. Limber pine. In: Eyre, F. H., ed. Forest Cover Types of the United States and Canada. Washington, DC: Society of American Foresters: 98-99.

Baud, Karen S. 1993. Simulating Clark's Nutcracker caching behavior: germination and predation of seed caches. Denver, CO: University of Colorado Denver. 67 p. Thesis.

Baumeister, Dayna; Callaway, Ragan M. 2006. Facilitation by *Pinus flexilis* during succession: A hierarchy of mechanisms benefits other plant species. Ecology. 87(7): 1816-1830.

Beasley, R. S.; Klemmedson, J. O. 1980. Ecological relationships of bristlecone pine. American Midland Naturalist. 104(2): 242-252.

Benkman, Craig W.; Balda, Russell P.; Smith, Christopher C. 1984. Adaptations for seed dispersal and the compromises due to seed predation in limber pine. Ecology. 65(2): 632-642.

Bentz, Barbara and others, these proceedings

Billings, W. D., Thompson, J. H. 1957. Composition of a stand of old bristlecone pines in the White Mountains of California. Ecology. 38(1): 158-160.

Blodgett, J. T.; Sullivan, K. F. 2004. First report of white pine blister rust on Rocky Mountain bristlecone pine. Plant Disease. 88: 311.

Bower, Andrew D.; Aitken, Sally N. 2008. Ecological genetics and seed transfer guidelines for *Pinus albicaulis* (Pinaceae). American Journal of Botany. 95: 66-76.

Breindel, Sara. 2000. Seasonal foraging dynamics and the importance of pine seeds in the diet of Steller's Jays (*Cyanocitta stelleri*). Denver, CO: Department of Biology, University of Colorado at Denver. 39 p. Thesis.

Breshears, David D.; Cobb, Neil S.; Rich, Paul M.; Price, Kevin P.; Allen, Craig D.; Balice, Randy G.; Romme, William H.; Kastens, Jude H.; Floyd, M. Lisa; Belnap, Jayne; Anderson, Jesse J.; Myers, Orrin B.; Meyer, Clifton W. 2005. Regional vegetation die-off in response to global-change-type drought. Proceedings of the National Academy of Sciences. 102(42): 15144-15148.

Brown, Peter M.; Anna W. Schoettle. 2008. Fire and stand history in two limber pine (*Pinus flexilis*) and Rocky Mountain bristlecone pine (*Pinus aristata*) stands in Colorado. International Journal of Wildland Fire. 17: 339-347.

Brown, James K.; Arno, Stephen F.; Barrett, Stephen W.; Menakis, James P. 1994. Comparing the prescribed natural fire program with presettlement fires in the Selway-Bitterroot Wilderness. International Journal of Wildland Fire. 4(3): 157-168.

Bruederle, L. P.; Rogers, D. L.; Krutovskii, K. V.; Politov, D. V. 2001. Population genetics and evolutionary implications. In: Tomback, Diana F.; Arno, Stephen F.; Keane, Robert E., eds. Whitebark pine communities: ecology and restoration. Washington, DC: Island Press: 137-153.

Brunelle, Andrea; Rehfeldt, Gerald E.; Bentz, Barbara; Munson, A. Steven. 2008. Holocene records of *Dendroctonus* bark beetles in high elevation forests of Idaho and Montana, USA. Forest Ecology and Management. 255: 836-846.

Brunstein, F. Craig; Yamaguchi, David K. 1992. The oldest known Rocky Mountain bristlecone pines (*Pinus aristata* Engelm.). Arctic and Alpine Research. 24(3): 253-256.

Bunn, Andrew G.; Lawrence, Rick L.; Bellante, Gabriel J.; Waggoner, Lindsey A.; Graumlich, Lisa J. 2003. Spatial variation in distribution and growth patterns of old growth strip-bark pines. Arctic and Alpine Research. 35(3): 323-330.

Bunn, Andrew G.; Waggoner, Lindsey A.; Graumlich, Lisa J. 2005. Topographic mediation of growth in high elevation foxtail pine (*Pinus balfouriana* Grev. et Balf.) forests in the Sierra Nevada, USA. Global Ecology and Biogeography. 14: 103-114.

Callaway, Ragan M. 1998. Competition and facilitation on elevation gradients in subalpine forests of the northern Rocky Mountains, USA. Oikos. 82: 561-573.

Campbell, Elizabeth M.; Antos, Joseph A. 2003. Postfire succession in *Pinus albicaulis—Abies lasiocarpa* forests of southern British Columbia. Canadian Journal of Botany. 82: 383-397.

Carsey, Katherine, S.; Tomback, Diana F. 1994. Growth form distribution and genetic relationships in tree clusters of *Pinus flexilis*, a bird-dispersed pine. Oecologia. 98: 402-411.

Chambers, Jeanne C.; MacMahon, James A. 1994. A day in the life of a seed: movements and fates of seeds and their implications for natural and managed systems. Annual Review of Ecology and Systematics. 25: 263-292.

Chappell, Christopher B.; Agee, James K. 1996. Fire severity and tree seedling establishment in *Abies magnifica* forests, southern Cascades, Oregon. Ecological Applications. 6: 628-640.

Chuine, I. 2010. Why does phenology drive species distribution? Philosophical Transactions of the Royal Society B. 365: 3149-3160.

Connor, Kristina F.; Lanner, Ronald M. 1991. Effects of tree age on pollen, seed, and seedling characteristics in Great Basin bristlecone pine. Botanical Gazette. 152(1): 107-113.

Coop, Jonathan D.; Schoettle, Anna W. 2009. Regeneration of Rocky Mountain bristlecone pine (*Pinus aristata*) and limber pine (*Pinus flexilis*) three decades after stand-replacing fires. Forest Ecology and Management. 257: 893-903.

Coop, Jonathan D.; Massattii, Robert T.; Schoettle, Anna W. 2010. Subalpine vegetation pattern three decades after stand-replacing fire: effects of landscape context and topography on plant community composition, tree regeneration, and diversity. Journal of Vegetation Science. 21: 472-487.

Costanza, Robert; d'Arge, Ralph; de Groot, Rudolf; Farber, Stephen; Grasso, Monica; Hannon, Bruce; Limburg, Karin; Naeem, Shahid; O'Neill, Robert V.; Paruelo, Jose; Raskin, Robert G.; Sutton, P.; van den Belt, Marjan. 1997. The value of the world's ecosystem services and natural capital. Nature. 387: 253-260.

Critchfield, William B.; Little, Jr., Elbert L. 1966. Geographic distribution of the pines of the world. Miscellaneous Publication 991. Washington, DC: U.S. Department of Agriculture Forest Service. 97 p.

Currey, Donald R. 1965. An ancient bristlecone pine stand in eastern Nevada. Ecology. 46(4): 564-566.

Daily, Gretchen. 1997. Nature's services: Societal dependence on natural ecosystems. Washington, DC: Island Press. 412 p.

Danzer, S. R.; Baisan, C. H.; Swetnam, T. W. 1996. The influence of fire and land-use history on stand dynamics in the Huachuca Mountains of southeastern Arizona. In: Ffolliott, P. F.; DeBano, L. F.; Baker, Jr., M. B.; Gottfried, G. J.; Solis-Garza, G.; Ednimster, C. B.; Neary, D. G.; Allen, L. S.; Hamre, R. H. Effects of fire on Madrean Province Ecosystems—A symposium proceedings;1996 March 11-15; Tucson, AZ. RM-GTR 289. Ft. Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station: 265-270.

Daubenmire, Rexford F. 1968. Plant communities. New York, NY: Harper and Ross. 300 p.

Donnegan, J. A.; Rebertus, A. J. 1999. Rates and mechanisms of subalpine forest succession along an environmental gradient. Ecology. 80: 1370-1384.

Eckert, Andrew J.; Sawyer, John O. 2002. Foxtail pine importance and conifer diversity in the Klamath Mountains and southern Sierra Nevada, California. Madroño. 49(1): 33-45.

Ellison, A. M.; Bank, M. S.; Clinton, B. D.; Colburn, E. A.; Elliott, K.; Ford, C. R.; Foster, D. R.; Kloeppel, B. D.; Knoepp, J. D; Lovett, G. M.; Mohan, J.; Orwig, D. A.; Rodenhouse, N. L.; Sobczak, W.V.; Stinson, K. A.; Stone, J. K.; Swan, C. M.; Thompson, J.; Von Holle, B.; Webster, J. R. 2005. Loss of foundation species: consequences for the structure and dynamics of forested ecosystems. Frontiers in Ecology and the Environment. 3: 479-486.

Eyre, F. H., ed.1980. Forest cover types of the United States and Canada. Washington, DC: Society of American Foresters: 148 p.

Farjon, Aljos; Styles, Brian T. 1997: *Pinus* (Pinaceae). Flora Neotropica, Monograph 75. New York, NY: Organization for Flora Neotropica, The New York Botanical Garden. 293 p.

Farnes, Phillip E. 1990. SNOTEL and snow course data: describing the hydrology of whitebark pine ecosystems. In: Schmidt, Wyman C.; McDonald, Kathy J., comps. Proceedings—Symposium on whitebark pine ecosystems; 1989 March 29-31; Bozeman, MT. Gen. Tech. Rep. INT-270. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station: 302-304.

Ferguson, C. W. 1969. A 7104-year annual tree-ring chronology for bristlecone pine, *Pinus aristata*, from the White Mountains, California. Tree-ring Bulletin. 29(3-4): 3-17.

Franklin, Jerry R.; Dyrness, C. T. 1973. Natural vegetation of Oregon and Washington. General Technical Report PNW-8. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Forest and Range Experiment Station: 417 p.

Geils, Brian W. 2000. Establishment of white pine blister rust in New Mexico. HorTechnology. 10(3): 528-529.

Geils, Brian W.; Hummer, Kim E.; Hunt, Richard S. 2010. White pines, *Ribes*, and blister rust: a review and synthesis. Forest Pathology. 40: 147-185.

Gernandt, David S.; Geada Lopez, Gretel G.; Ortiz Garcia, Sol; Liston, Aaron. 2005. Phylogeny and classification of *Pinus*. Taxon. 54(1): 29-42.

Gibson, Ken; Kegley, Sandy; Bentz, Barbara. 2009. Mountain pine beetle. Forest Insect and Disease Leaflet 2. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Region (R6): 12 p.

Gibson, Ken; Skov, Kjerstin; Kegley, Sandy; Jorgensen, Carl; Smith, Sheri; Witcosky, Jeff. 2008. Mountain pine beetle impacts in high-elevation five-needle pines: Current trends and challenges. Forest Health Protection R1-08-020. Missoula, MT: U.S. Department of Agriculture, Forest Service: 32 p.

Gilpin, Michael E.; Soulé, Michael E. 1986. Minimum viable populations: Processes of species extinction. In: M. E. Soulé, editor. Conservation biology: The science of scarcity and diversity. Sunderland, MA: Sinauer Associates: 19-34.

Greater Yellowstone Whitebark Pine Monitoring Working Group (GYWPMWG). 2010. Monitoring whitebark pine in the Greater Yellowstone Ecosystem: 2009 annual report. In: Schwartz, C. C.; Haroldson, M. A.; West, K., eds. Yellowstone grizzly bear investigations: annual report of the Interagency Grizzly Bear Study Team, 2009. Bozeman, MT: U.S. Geological Survey: 63-71.

Grissino-Mayer, Henri D.; Baisan, Christopher H.; Swetnam, Thomas W. 1995. Fire history in the Pinaleño Mountains of southeastern Arizona: Effects of human-related disturbances. In: Debano, L. F.; Gottfried, G. J.; Hamre, R. H.; Edminster, C. B.; Ffolliott, P. F.; Ortega-Rubio, A., editors. Biodiversity and management of the Madrean Archipelago: The sky islands of the southwestern United States and northwestern Mexico; 1994 Sept. 19-23; Tucson, AZ. Gen. Tech. Rep. RM-GTR-264. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station: 399-407.

Gruell, George E. 1983. Fire and vegetative trends in the Northern Rockies: Interpretations from 1871-1982 photographs. Gen. Tech. Rep. INT-GTR 158. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station: 117 p.

Hamann, Andreas; Wang, Tongli. 2006. Potential effects of climate change on ecosystem and tree species distribution in British Columbia. Ecology. 87(11): 2773-2786.

Harlow, W. M., W. A. Côté, Jr., and A. C. Day. 1964. The opening mechanism of pine cone scales. Journal of Forestry. 62: 538-540.

Hawksworth, Frank G.; Bailey, D. K. 1980. Bristlecone pine. In: Eyre, F. H., ed. Forest Cover Types of the United States and Canada. Washington, DC: Society of American Foresters: 90-91.

Heyerdahl, Emily K., Morgan, Penelope; Riser II, James P. 2008. Multi-season climate synchronized historical fires in dry forests (1650-1900), Northern Rockies, USA. Ecology. 89(3): 705-716.

Hoff, R.; Bingham, R. T.; McDonald, G. I. 1980. Relative blister rust resistance of white pines. European Journal of Forest Pathology. 10(5): 307-316.

Hutchins, H. E.; Lanner, R. M. 1982. The central role of Clark's nutcracker in the dispersal and establishment of whitebark pine. Oecologia. 55: 192-210.

Intergovernmental Panel on Climate Change (IPCC). 2007. Summary for policy makers. In: Solomon, S.; Qin, D.; Manning, M.; Chen, Z.; Marquis, M.; Averyt, K. B.; Tignor, M.; Miller, H. L., eds. The physical science basis. Contributions of Working Group 1 to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge, United Kingdom and New York, New York: Cambridge University Press. Available: http://www.ipcc.ch/publications_and_data/ [last accessed 2011 February 17].

International Union for Conservation of Nature (IUCN). 2007. IUCN Red List of Threatened Species. [Online]. Available: http://www.redlist.org [2010 June 15].

Jorgensen, Stacey M.; Hamrick, J. L. 1997. Biogeography and population genetics of whitebark pine, *Pinus albicaulis*. Canadian Journal of Forest Research. 27: 1574-1585.

Keane, Robert E. 2001. Successional dynamics: modelling an anthropogenic threat. In: Tomback, Diana F.; Arno, Stephen F.; Keane, Robert E., eds. Whitebark pine communities: ecology and restoration. Washington, DC: Island Press: 159-192.

Keane, Robert E.; Arno, Stephen F. 1993. Rapid decline of whitebark pine in western Montana: evidence from 20-year remeasurements. Western Journal of Applied Forestry. 8(2): 44-47.

Keane, Robert E.; Arno, Stephen F.; Brown, James K.; Tomback, Diana F. 1990. Modelling stand dynamics in whitebark pine (*Pinus albicaulis*) forests. Ecological Modelling. 51(1-2): 73-95.

Keane, Robert E.; Holsinger, Lisa M.; Parsons, Russell A.; Gray, Kathy. 2008. Climate change effects on historical range and variability of two large landscapes in western Montana, USA. Forest Ecology and Management. 254: 375-389.

Keane, Robert E.; Ryan, Kevin C.; Veblen, Thomas T.; Allen, Craig D.; Logan, Jesse A.; Hawkes, Brad. 2002. Cascading effects of fire exclusion in Rocky Mountain ecosystems. In: Baron, J. S., ed. Rocky Mountain Futures: An Ecological Perspective. Washington, DC: Island Press: 133-152.

Kearns, Holly S. J.; Jacobi, William R. 2007. The distribution and incidence of white pine blister rust in central and southeastern Wyoming and northern Colorado. Canadian Journal of Forest Research. 37: 462-472.

Keeley, Jon E.; Zedler, Paul H.1998. Evolution of life histories in *Pinus*. In: Richardson, David M. Ecology and biogeography of Pinus. Cambridge, United Kingdom, and New York, NY: Cambridge University Press: 219-249.

Kendall, Katherine C. 1983. Use of pine nuts by grizzly and black bears in the Yellowstone area. International Conference on Bear Research and Management. 5: 166-173.

Kendall, Katherine C.; Keane, Robert E. 2001. Whitebark pine decline: infection, mortality, and population trends. In: Tomback, Diana F.; Arno, Stephen F.; Keane, Robert E., eds. Whitebark pine communities: ecology and restoration. Washington, DC: Island Press: 221-242.

Kipfmueller, Kurt F.; Baker, William L. 2000. A fire history of a subalpine forest in south-eastern Wyoming, USA. Journal of Biogeography. 27: 71-85.

Kliejunas, John T.; Dunlap, Joan. 2007. Status of whitebark pine and other high-elevation five-needle pines with emphasis on Pacific Coast ecosystems; what are the issues and concerns? Perspective from California. In: Goheen, Ellen M.; Sniezko, Richard A., coords. Proceedings of the conference Whitebark pine: a Pacific Coast perspective; 2006 August 27-31; Ashland, OR. R6-NR-FHP-2007-01. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Region: 29-35.

Knight, Dennis H. 1994. Mountains and Plains: the Ecology of Wyoming Landscapes. New Haven, CT: Yale University Press. 338 p.

Kral, Robert. 1993. *Pinus*. In: Flora of North America Editorial Committee, eds. Flora of North America North of Mexico, Vol. 2. Oxford University Press.

Krugman, Stanley L.; Jenkinson, James L. 1974. *Pinus* L. Pine. In: Schopmeyer, C. S., tech. coord. Seeds of woody plants in the United States. Agriculture Handbook No. 450. Washington, DC: U.S. Department of Agriculture: 598-638.

LaMarche, Valmore C., Jr.; Mooney, Harold A. 1972. Recent climatic change and development of the bristlecone pine (*P. longaeva* Bailey) krummholz zone, Mt. Washington, Nevada. Arctic and Alpine Research. 4(1): 61-72.

Langor, David W. 2007. Status of the limber pine (*Pinus flexilis*) in Alberta. Alberta Wildlife Status Report No. 62. Edmonton, Alberta, Canada: Sustainable Resource Development, Alberta Conservation Association: 17 p.

Lanner, Ronald M. 1980. Avian seed dispersal as a factor in the ecology and evolution of limber and whitebark pines. Proceedings of Sixth North American Forest Biology Workshop; 1980 August 11-13; Edmonton, Alberta, Canada: 15-48.

Lanner, Ronald M. 1982. Adaptations of whitebark pine for seed dispersal by Clark's Nutcracker. Canadian Journal of Forest Research. 12(2): 391-402.

Lanner, Ronald M. 1988. Dependence of Great Basin bristlecone pine on Clark's nutcracker for regeneration at high elevations. Arctic and Alpine Research. 20(3): 358-362.

Lanner, Ronald M. 1990. Biology, taxonomy, evolution, and geography of stone pines of the world. In: Schmidt, Wyman C.; McDonald, Kathy J., comps. Proceedings—Symposium on whitebark pine ecosystems; 1989 March 29-31; Bozeman, MT. Gen. Tech. Rep. INT-270. Ogden, Utah: U.S. Department of Agriculture, Forest Service, Intermountain Research Station: 14-24.

Lanner, Ronald M. 1998. Seed dispersal in *Pinus*. In: Richardson, David M. Ecology and biogeography of *Pinus*. Cambridge, United Kingdom, and New York, NY: Cambridge University Press: 281-295.

Lanner, Ronald M.; Vander Wall, Stephen B. 1980. Dispersal of limber pine seed by Clark's Nutcracker. Journal of Forestry. 78 (October): 637-639.

Lanner, Ronald M.; Harry E. Hutchins, and Harriette A. Lanner. 1984. Bristlecone pine and Clark's Nutcracker: probable interaction in the White Mountains, California. Great Basin Naturalist. 44(2): 357-360.

Lee, Seok-Woo; Ledig, F. Thomas; Johnson, D. R. 2002. Genetic variation at allozyme and RAPD markers in *Pinus longaeva* (Pinaceae) of the White Mountains, California. American Journal of Botany. 89: 566-577.

Linhart, Yan B.; Tomback, D. F. 1985. Seed dispersal by nutcrackers causes multi-trunk growth form in pines. Oecologia. 67: 107-110.

Liston, Aaron; Robinson, William A.; Piñero, Daniel; Alvarez-Buylla, Elena R. 1999. Phylogenetics of *Pinus* (Pinaceae) based on nuclear ribosomal DNA internal transcribed spacer region sequences. Molecular Phylogenetics and Evolution. 11(1): 95-109.

Loarie, Scott R.; Duffy, Philip B.; Hamilton, Healy; Asner, Gregory P.; Field, Christopher B.; Ackerly, David. D. 2009. The velocity of climate change. Nature. 462: 1052-1055.

Logan, Jesse A.; Powell, James A. 2001. Ghost forests, global warming, and the mountain pine beetle (Coleoptera: Scolytidae). American Entomologist. 47(3): 160-172.

Logan, Jesse A.; Régnière, Jacques; Powell, James A. 2003. Assessing the impacts of global warming on forest pest dynamics. Frontiers in Ecology and the Environment. 1(3): 130-137.

Logan, Jesse A.; MacFarlane, William, W.; Willcox, Louisa. 2010. Whitebark pine vulnerability to climate-driver mountain pine beetle disturbance in the Greater Yellowstone Ecosystem. Ecological Applications. 20(4): 895-902.

Lorenz, Teresa J.; Sullivan, Kimberly, A. 2009. Seasonal differences in space use by Clark's nutcrackers in the Cascade Range. The Condor. 11(2): 326-340.

Lynch, Heather J.; Renkin, Roy A.; Crabtree, Robert L.; Moorcraft, Paul R. 2006. The influence of previous mountain pine beetle (*Dendroctonus ponderosae*) activity on the 1988 Yellowstone fires. Ecosystems. 9: 1318-1327.

Mahalovich, M. F.; Burr, K. E.; and Foushee, D. L. 2006. Whitebark pine germination, rust resistance, and cold hardiness among seed sources in the Inland Northwest: Planting strategies for restoration. In: Riley, L. E.; Dumroese, R. K.; Landis, T. D., tech. coord. National Proceedings: Forest and Conservation Nursery Associations—2005. Proc. RMRS-P-43, Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station: 91-101.

Mastrogiuseppe, Ronald J. 1972. Geographic variation in foxtail pine, *Pinus balfouriana* Grev. & Balf. Arcata, CA: Humboldt State University. 98 p. Thesis.

Mastrogiuseppe, R. J.; Mastrogiuseppe, J. D. 1980. A study of *Pinus balfouriana* Grev. & Balf. (Pinaceae). Systematic Botany. 5(1): 86-104.

McCaughey, Ward W.1990. Biotic and microsite factors affecting whitebark pine establishment. In: Schmidt, Wyman C.; McDonald, Kathy J., comps. Proceedings—Symposium on whitebark pine ecosystems; 1989 March 29-31; Bozeman, MT. Gen. Tech. Rep. INT-270. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station: 140-150.

McCaughey, Ward W.; Schmidt, Wyman C. 2001. In: Tomback, Diana F.; Arno, Stephen F.; Keane, Robert E., eds. Whitebark pine communities: ecology and restoration. Washington, DC: Island Press: 29-40.

McCool, Stephen F.; Freimund, Wayne A. 2001. Threatened landscapes and fragile experiences: Conflict in whitebark pine restoration. In: Tomback, Diana F.; Arno, Stephen F.; Keane, Robert E., eds. Whitebark pine communities: ecology and restoration. Washington, DC: Island Press: 263-284.

McCutchen, Henry E. 1996. Limber pine and bears. Great Basin Naturalist. 56(1): 90-92.

McDonald; Geral I.; Hoff, Raymond J. 2001. Blister rust: an introduced plague. In: Tomback, Diana F.; Arno, Stephen F.; Keane, Robert E., eds. Whitebark pine communities: ecology and restoration. Washington, DC: Island Press: 193-220.

McKenny, Daniel W.; Pedlar, John H.; Lawrence, Kevin; Campbell, Kathy; Hutchinson, Michael F. 2007. Potential impacts of climate change on the distribution of North American trees.

BioScience. 57(11): 939-948. Supplementary material accessed from http://planthardiness.gc.ca/ 5 July 2008.

McKinney, Shawn T.; Tomback, Diana F. 2007. The influence of white pine blister rust on seed dispersal in whitebark pine. Canadian Journal of Forest Research. 37: 1044-1057.

McKinney, Shawn T.; Fiedler, Carl E.; Tomback, Diana F. 2009. Invasive pathogen threatens bird-pine mutualism: implications for sustaining a high-elevation ecosystem. Ecological Applications. 19(3): 597-607.

McKinney, Shawn T.; Tomback, Diana F. 2011. Altered community dynamics in Rocky Mountain whitebark pine forests and the potential for accelerating declines. In: Richards, K. E., ed. Mountain ecosystems: dynamics, management and conservation. Hauppauge, NY: Nova Science Publishers: In press.

Mills, L. Scott; Soulé, Michael E.; Doak, Daniel F. 1993. The keystone-species concept in ecology and conservation. BioScience. 43(4): 219-224.

Mitton, J. B.; Kreiser, B. R.; Latta, R. G. 2000. Glacial refugia of limber pine (*Pinus flexilis* James) inferred from the population structure of mitochondrial DNA. Molecular Ecology. 9: 91-97.

Moerman, Daniel E. 1998. Native American ethnobotany. Portland, OR: Timber Press. 927 p.

Moerman, Daniel E. 2009. Native American medicinal plants: An ethnobotany dictionary. Portland, OR: Timber Press. 800 p.

Morgan, Penny; Bunting, Stephen C. 1990. Fire effects in whitebark pine forests. In: Schmidt, Wyman C.; McDonald, Kathy J., comps. Proceedings—Symposium on whitebark pine ecosystems; 1989 March 29-31; Bozeman, MT. Gen. Tech. Rep. INT-270. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station: 166-170.

Morin, Xavier; Thuiller, Wilfried. 2009. Comparing niche- and process-based models to reduce prediction uncertainty in species range shifts under climate change. Ecology. 90 (50): 1301-1313.

Murray, Michael P.; Bunting, Stephen C., Morgan, Penny. 1998. Fire history of an isolated subalpine mountain range of the Intermountain Region, United States. Journal of Biogeography. 25: 1071-1080.

Murray, Michael P.; Bunting, Stephen C.; Morgan, Penny. 2000. Landscape trends (1753-1993) of whitebark pine (*Pinus albicaulis*) forests in the West Big Hole Range of Idaho/Montana, U.S.A. Arctic, Antarctic, and Alpine Research. 32(4): 412-418.

NatureServe. 2010. Home page of NatureServe Explorer (Version 7.1). [Online]. Available: http://www.natureserve.org/explorer [2010 June 15].

Ogilvie, R. T. 1990. Distribution and ecology of whitebark pine in western Canada. In: Schmidt, Wyman C.; McDonald, Kathy J., comps. Proceedings—Symposium on whitebark pine ecosystems; 1989 March 29-31; Bozeman, MT. Gen. Tech. Rep. INT-270. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station: 54-60.

Oline, David K.; Mitton, Jeffrey B.; Grant, Michael C. 2000. Population and subspecific genetic differentiation in the foxtail pine (*Pinus balfouriana*). Evolution. 54(5): 1813-1819.

Östlund, Lars; Ahlberg, Lisa; Zackrisson, Olle; Bergman, Ingela; Arno, Stephen F. 2009. Bark-peeling, food stress and tree spirits—the use of pine inner bark for food in Scandinavia and North America. Journal of Ethnobiology. 29(1): 94-112.

Peet, Robert K. 1978. Latitudinal variation in southern Rocky Mountain forests. Journal of Biogeography. 5: 275-289.

Perkins, Dana L.; Swetnam, Thomas W. 1996. A dendroecological assessment of whitebark pine in the Sawtooth-Salmon River region Idaho. Canadian Journal of Forest Research. 26: 2123-2133.

Perry, Jr., Jessee P. 1991. The pines of Mexico and Central America. Portland, OR: Timber Press. 231 p.

Potter, Loren D.; Green, Duane L. 1964. Ecology of a northeastern outlying stand of *Pinus flexilis*. Ecology. 45: 866-868.

Price, Robert A.; Liston, Aaron; Strauss, Steven H. 1998. Phylogeny and systematics of *Pinus*. In: Richardson, David M., ed. Ecology and Biogeography of *Pinus*. Cambridge, UK: Cambridge University Press: 49-68.

Pruett, Elizabeth L. 2007. The role of nocturnal rodents in dispersal of southwestern white pine seeds. Denver, CO: University of Colorado Denver. 48 p. Thesis.

Raffa, Kenneth F.; Aukema, Brian H.; Bentz, Barbara J.; Carroll, Allan L.; Hicke, Jeffrey A.; Turner, Monica G.; Romme, William H. 2008. Cross-scale drivers of natural disturbances prone to anthropogenic amplification: the dynamics of bark beetle eruptions. BioScience. 58(6): 501-517.

Ranne, Brigitte M.; Baker, William L.; Andrews, Tom; Ryan, Michael G. 1997. Natural variability of vegetation, soils, and physiography in the bristlecone pine forests of the Rocky Mountains. Great Basin Naturalist. 57(1): 21-37.

Rebertus, A. J.; Burns, B. R.; Veblen, T. T. 1991. Stand dynamics of *Pinus flexilis*-dominated subalpine forests in the Colorado Front Range. Journal of Vegetation Science. 2: 445-458.

Resler, Lynn M. 2004. Conifer establishment sites on a periglacial landscape, Glacier National Park, Montana. San Marcos, TX: State University-San Marcos. 186 p. Dissertation.

Resler, Lynn M.; Tomback, Diana F. 2008. Blister rust prevalence in krummholz whitebark pine: Implications for treeline dynamics. Arctic, Antarctic, and Alpine Research. 40(1): 161-170.

Richardson, B. A.; Brunsfeld, S. J.; Klopfenstein, N. B. 2002a. DNA from bird-dispersed seed and wind-disseminated pollen provides insights into postglacial colonization and population genetic structure of whitebark pine (*Pinus albicaulis*). Molecular Ecology. 11: 215-227.

Richardson, Bryce A.; Klopfenstein, Ned B.; Brunsfeld, Steven J. 2002b. Assessing Clark's nutcracker seed-caching flights using maternally inherited mitochondrial DNA of whitebark pine. Canadian Journal of Forest Research. 32: 1103-1107.

Rogers, Deborah L.; Millar, Constance I.; Westfall, Robert D. 1999. Fine-scale genetic structure of whitebark pine (*Pinus albicaulis*): Associations with watershed and growth form. Evolution. 53(1): 74-90.

Romme, William H.; Knight, Dennis H.; Yavitt, Joseph B. 1986. Mountain pine beetle outbreaks in the Rocky Mountains: regulators of primary productivity? American Naturalist. 4: 484-494.

Sakulich, John; Taylor, Alan H. 2007. Fire regimes and forest structure in a sky island mixed conifer forest, Guadalupe Mountains National Park, Texas, USA. Forest Ecology and Management. 241: 62-73.

Samano, Sheridan; Tomback, Diana F. 2003. Cone opening phenology, seed dispersal, and seed predation in southwestern white pine (*Pinus strobiformis*) in southern Colorado. Écoscience. 10(3): 319-326.

Schauer, Andrew J.; Schoettle, Anna W.; Boyce, Richard L. 2001. Partial cambial mortality in high-elevation *Pinus aristata* (Pinaceae). American Journal of Botany. 88(4): 646-652.

Schoettle, Anna W. 2004. Ecological roles of five-needle pines in Colorado: Potential consequences of their loss. In: Sniezko, Richard A.; Samman, Safiya; Schlarbaum, Scott E.; Kriebel, Howard B., eds. Breeding and genetic resources of five-needle pines: growth, adaptability, and pest resistance, IUFRO Working Party 2.02.15.; 2001 23-27 July, Medford, OR. Proc.

RMRS-P-32, Fort Collins, CO: U.S Department of Agriculture, Forest Service, Rocky Mountain Research Station: 124-135.

Schoettle, A. W.; Rochelle, S. G. 2000. Morphological variation of *Pinus flexilis* (Pinaceae), a bird-dispersed pine, across a range of elevations. American Journal of Botany. 87(12): 1797-1806.

Schoettle, Anna W.; Sniezko, Richard A. 2007. Proactive intervention to sustain high elevation pine ecosystems threatened by white pine blister rust. Journal of Forest Research. 12: 327-336.

Schrag, Anne M.; Bunn, Andrew G.; Graumlich, Lisa J. 2008. Influence of bioclimatic variables on treeline conifer distribution in the Greater Yellowstone Ecosystem: implications for species of conservation concern. Journal of Biogeography. 35: 698-710.

Schuster, William S. F.; Mitton, Jeffry B. 1991. Relatedness within clusters of a bird-dispersed pine and the potential for kin interactions. Heredity. 67: 41-48.

Schuster, William S. F.; Mitton, Jeffrey B. 2000. Paternity and gene dispersal in limber pine (*Pinus flexilis* James). Heredity. 84: 348-361.

Schuster, William S. F.; Alles, David L.; Mitton, Jeffry B. 1989. Gene flow in limber pine: evidence from pollination phenology and genetic differentiation along an elevational transect. American Journal of Botany. 76(9): 1395-1403.

Schuster, William S. F.; Mitton, Jeffry B.; Yamaguchi, David K.; Woodhouse, C. A. 1995. A comparison of limber pine (*Pinus flexilis*) ages at lower and upper treeline sites east of the Continental Divide in Colorado. American Midland Naturalist. 133: 101-111.

Schwandt , J. W; Lockman, I. B.; Kliejunas, J. T.; Muir, J. A. 2010. Current health issues and management strategies for white pines in the western United States and Canada. Forest Pathology. 40: 226-250.

Smith, Cyndi M.; Wilson, Brendan; Rasheed, Salman; Walker, Robert C.; Carolin, Tara; Sheppard, Brenda. 2008. Whitebark pine and white pine blister rust in the Rocky Mountains of Canada and northern Montana. Canadian Journal of Forest Research. 38: 982-995.

Soulé, Michael E.; Estes, James A.; Berger, Joel; Martinez del Rio, Carlos. 2003. Ecological effectiveness: conservation goals for interactive species. Conservation Biology. 17: 1238-1250.

Steele, Robert. 1990. *Pinus flexilis* James, Limber pine. In: Burns, Russell P., Honkala, Barbara H., eds. Silvics of North America, Volume 1, Conifers, Agriculture Handbook 654. Washington, DC, USA: USDA Forest Service: 348-354.

Steinhoff, R. J.; Andresen, J. W. 1971. Geographic variation in *Pinus flexilis* and *Pinus strobiformis* and its bearing on their taxonomic status. Silvae Genetica. 20: 159-167.

Swetnam, Thomas W.; Betancourt, Julio L.1990. Fire-southern oscillation relations in the Southwestern United States. Science. 249: 1017-1020.

Syring, John; Farrell, Kathleen; Businsky, Roman; Cronn, Richard; Liston Aaron. 2007. Widespread genealogical nonmonophyly in species of Pinus subgenus Strobus. Systematic Biology. 56(2): 163-181.

Tang, Kulian; Feng, Xiahong; Funkhouser, Gary. 1999: The δ13 C of tree rings in full-bark and strip-bark bristlecone pine trees in the White Mountains of California. Global Change Biology. 5(1): 33-40.

Taylor, S. W.; Carroll, A. L. 2004. Disturbance, forest age, and mountain pine beetle outbreak dynamics in BC: A historical perspective. In: Shore, T. L.; Brooks, J. E.; Stone, J. E., eds. Proceedings of the Mountain Pine Beetle Symposium: Challenges and Solutions; 2003 October 30-31; Kelowna, British Columbia. Information Report BC-X-399. Victoria, British Columbia, Canada: Natural Resources Canada, Canadian Forest Service, Pacific Forestry Centre: 41-56.

Thilenius, John F. 1970. An isolated occurrence of limber pine (*Pinus flexilis* James) in the Black Hills of South Dakota. American Midland Naturalist. 84: 411-417.

Tillman-Sutela, Eila; Kauppi, Anneli; Karppinen, Katja; Tomback, Diana F. 2008. Variant maturity in seed structures of *Pinus albicaulis* (Engelm.) and *Pinus sibirica* (Du Tour): key to a soil seed bank, unusual among conifers? Trees. 22: 225-236.

Tomback, Diana F. 1978. Foraging strategies of Clark's nutcracker. Living Bird. 16: 123-161.

Tomback, Diana F. 1982. Dispersal of whitebark pine seeds by Clark's nutcracker: A mutualism hypothesis. Journal of Animal Ecology. 51: 451-467.

Tomback, Diana F. 1986. Post-fire regeneration of krummholz whitebark pine: a consequence of nutcracker seed caching. Madroño. 33(2): 100-110.

Tomback, Diana F. 1988. Nutcracker-pine mutualisms: Multi-trunk trees and seed size. In: Oellet, Henri,ed. Acta XIX Congressus Internationalis Ornithologici, Vol. 1, Ottawa, Canada, 22-29 June 1986. Ottawa, Canada: National Museum of Natural Sciences, University of Ottawa Press.

Tomback, Diana F. 1989. Observations of Clark's nutcrackers harvesting and caching whitebark pine seeds on Palmer Mountain, north of Yellowstone National Park, Gallatin National Forest. Unpublished data on file, Department of Integrative Biology, University of Colorado Denver.

Tomback, Diana F. 1998. Clark's nutcracker (*Nucifraga columbiana*). In: Poole, A.; Gill, F., eds. The birds of North America, No. 331. Philadelphia, PA: The Birds of North America: No. 331: 24 p.

Tomback, Diana F. 2001. Clark's nutcracker: Agent of regeneration. In: Tomback, Diana F.; Arno, Stephen F.; Keane, Robert E., eds. Whitebark Pine Communities: Ecology and Restoration. Washington, DC: Island Press: 89-104.

Tomback, Diana F. 2005. The impact of seed dispersal by Clark's nutcracker on whitebark pine: Multi-scale perspective on a high mountain mutualism. In: Broll, Gabriele; Keplin, Beate, eds. Mountain Ecosystems: Studies in Treeline Ecology. Germany: Springer: 181-201.

Tomback, Diana F. 2010. Calculations of yearly mean rate of whitebark pine seed germination after the Yellowstone fires. Unpublished data on file in Department of Integrative Biology, University of Colorado Denver.

Tomback, Diana F.; Kramer, Kathryn A. 1980. Limber pine seed harvest by Clark's Nutcracker in the Sierra Nevada: Timing and foraging behavior. Condor. 82: 467-468.

Tomback, Diana F.; Taylor, Cheryl L. 1987. Tourist impact on Clark's Nutcracker foraging activities in Rocky Mountain National Park. In: Singer, Francis J., ed. Toward the year 2000—Conference on science in the National Parks; Vol. 2 Wildlife management and habitats. Fort Collins, CO: George Wright Society and the U.S. National Park Service: 158-172.

Tomback, Diana F.; Linhart, Yan B. 1990. The evolution of bird-dispersed pines. Evolutionary Ecology. 4: 185-219.

Tomback, Diana F.; Kendall, Katherine C. 2001. Biodiversity losses: The downward spiral. In: Tomback, Diana F.; Arno, Stephen F.; Keane, Robert E., eds. Whitebark Pine Communities: Ecology and Restoration. Whitebark Pine Communities: Ecology and Restoration. Washington, DC: Island Press: 243-262.

Tomback, Diana F.; Resler, Lynn M. 2007. Invasive pathogens at alpine treeline: consequences for treeline dynamics. Physical Geography. 28(5): 397-418.

Tomback, D. F.; Achuff, P. 2010. Blister rust and western forest biodiversity: ecology, values and outlook for white pines. Forest Pathology. 40: 186-225.

Tomback, Diana F.; Hoffmann, Lyn A.; Sund, Sharren K. 1990. Coevolution of whitebark pine and nutcrackers: implications for forest regeneration. In: Schmidt, Wyman C.; McDonald, Kathy J., comps. Proceedings—Symposium on whitebark pine ecosystems; 1989 March 29-31; Bozeman, MT. Gen. Tech. Rep. INT-270. Ogden, Utah: U.S. Department of Agriculture, Forest Service, Intermountain Research Station: 118-129.

Tomback, Diana F.; Sund, Sharren K.; Hoffmann, Lyn A. 1993. Post-fire regeneration of *Pinus albicaulis*: height-age relationships, age structure, and microsite characteristics. Canadian Journal of Forest Research. 23: 113-119.

Tomback, Diana F.; Arno, Stephen F.; Keane, Robert E. 2001a. The compelling case for management intervention. In: Tomback, Diana F.; Arno, Stephen F.; Keane, Robert E., eds. Whitebark Pine Communities: Ecology and Restoration. Washington, DC: Island Press: 3-25.

Tomback, Diana F.; Anderies, Angela J.; Carsey, Katherine S.; Powell, Mary L.; Mellmann-Brown, Sabine. 2001b. Delayed seed germination in whitebark pine and regeneration patterns following the Yellowstone fires. Ecology. 82(9): 2587-2600.

Tomback, Diana F.; Schoettle, Anna W.; Chevalier, Kristen E.; and Jones, Cheri A. 2005. Life on the edge for limber pine: Seed dispersal within a peripheral population. Écoscience. 12(4): 519-529.

Torick, Lisa L.1995. The interaction between Clark's Nutcrackers and ponderosa pine, a "wind-dispersed" pine; Energy efficiency and multi-genet growth forms. Denver, CO: University of Colorado Denver. 44 p. Thesis.

Torick, Lisa L.; Tomback, Diana F.; Espinoza, Ronald. 1996. Occurrence of multi-genet tree clusters in "wind-dispersed" pines. American Midland Naturalist. 136: 262-266.

U.S. Fish and Wildlife Service. 2009. Endangered, Threatened, Proposed, Candidate, and Species of Concern, and Designated Critical Habitat [in Washington State]. [Online]. Available: http://www.pws.gov/endangered/ [2010 June 15].

U.S. Fish and Wildlife Service. 2010. Endangered and threatened wildlife and plants; 90-day finding on a petition to list *Pinus albicaulis* (whitebark pine) as endangered or threatened with critical habitat. Federal Register. 75(138), July 20: 42033-42040.

Vander Wall, Stephen B. 1988. Foraging of Clark's Nutcrackers on rapidly changing pine seed resources. The Condor. 90: 621-631.

Vander Wall, Stephen B. 1992. The role of animals in dispersing a "wind-dispersed" pine. Ecology. 73(2): 614-621.

Vander Wall, Stephen B. 1997. Dispersal of singleleaf piñon pine (*Pinus monophylla*) by seed-caching rodents. Journal of Mammalogy. 78(1): 181-191.

Vander Wall, Stephen B. 2003. Effects of seed size of wind-dispersed pines (*Pinus*) on secondary seed dispersal and the caching behavior of rodents. Oikos. 100: 25-34.

Vander Wall, Stephen B. 2008. On the relative contributions of wind vs. animals to seed dispersal of four Sierra Nevada pines. Ecology. 89(7): 1837-1849.

Vander Wall, Stephen B.; Balda, Russell P. 1977. Coadaptations of the Clark's nutcracker and piñon pine for efficient seed harvest and dispersal. Ecological Monographs. 47(1): 89-111.

Vander Wall, Stephen B.; Balda, Russell P. 1981. Ecology and evolution of food-storage behavior in conifer-seed-caching corvids. Zeitschrift für Tier psychologie. 56:217-242.

Vander Wall, Stephen B.; Longland, W. S. 2004. Diplochory: are two seed dispersers better than one? Trends in Ecology and Evolution. 19(3): 156-161.

Van Mantgem, Phillip J.; Stephenson, Nathan L.; Byrne, John C.; Daniels, Lori D.; Franklin, Jerry F.; Fulé, Peter Z.; Harmon, Mark E.; Larson, Andrew J.; Smith, Jeremy M.; Taylor, Alan H.; Veblen, Thomas T., 2009: Widespread increase of tree mortality rates in the western United States. Science. 323: 521-524.

Van Wagner , Charles E.; Finney, Mark A.; Heathcott, M. 2006. Historical fire cycles in the Canadian Rocky Mountain parks. Forest Science. 52(6): 704-717.

Vasek, F. C.; Thorne, R. F. 1977. Transmontane coniferous vegetation. In: Barbour, M. G.; Major, J. Terrestrial Vegetation of California. New York, NY: John Wiley and Sons: 797-832.

Veblen, Thomas T. 1986. Age and size structure of subalpine forests in the Colorado Front Range. Bulletin of the Torrey Botanical Club .113: 225-240.

Walsh, James R. 2005. Fire regimes and stand dynamics of whitebark pine (*Pinus albicaulis*) communities in the Greater Yellowstone Ecosystem. Fort Collins, CO: Colorado State University. 72 p. Thesis.

Warwell, Marcus V.; Rehfeldt, Gerald E.; Crookston, Nicholas L. 2007. Modeling contemporary climate profiles and predicting their response to global warming for whitebark pine (*Pinus albicaulis*). In: Goheen, Ellen M.; Sniezko, Richard A., cords. Proceedings of the conference Whitebark pine: a Pacific Coast perspective; 2006 August 27-31; Ashland, OR. R6-NR-FHP-2007-01. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Region: 139-142.

Weaver, Tad. 2001. Whitebark pine and its environment. In: Tomback, Diana F.; Arno, Stephen F.; Keane, Robert E., eds. Whitebark Pine Communities: Ecology and Restoration. Washington, DC: Island Press: 41-73.

Webster, Kara L.; Johnson, Edward A. 2000. The importance of regional dynamics in local populations of limber pine (*Pinus flexilis*). Écoscience. 7: 175-182.

Wells, Gail. 2011. Clark's nutcracker and whitebark pine: Can the birds help the embattled high-country pine survive? Pacific Northwest Science Findings. 130: 6 p.

Wenny, Daniel G.; DeVault, Travis L.; Johnson, Matthew D.; Kelly, Dave; Sekercioglu, Cagan; Tomback, Diana F.; Whelan, Christopher, J. 2011. On the need to quantify ecosystem services provided by birds. The Auk. 128: 1-14.

Synthesis of Lower Treeline Limber Pine (*Pinus flexilis*) Woodland Knowledge, Research Needs, and Management Considerations

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Abstract—Lower treeline limber pine woodlands have received little attention in peer-reviewed literature and in management strategies. These ecologically distinct systems are thought to be seed repositories between discontinuous populations in the northern and central Rocky Mountains, serving as seed sources for bird dispersal between distinct mountain ranges. Their position on the lower treeline and foothills in semi-arid climate systems is predicted to be particularly vulnerable to climate change. The genetic variation within these stands is viewed as important to conservation geneticists in developing seed sources resistant to blister rust.

The isolated locations and different climatic conditions of these woodlands may have provided them some protection in the past from the mountain pine beetle (*Dendroctonus ponderosae*) and white pine blister rust (*Cronartium ribicola*) that are threatening upper treeline limber pine forests region-wide. But, recent studies show that the lower treeline woodlands are just as, or more, susceptible to white pine blister rust infections and mountain pine beetle infestations.

Lower treeline woodlands are often thought to be "invading" more desirable sagebrush and grass vegetation types, so eradication via chaining, mastication, and burning have been accepted practices to limit woodland growth or "encroachment." The lack of economic value has led to the common perception that these lower treeline woodlands are "weeds" which need to be controlled to prevent their expansion into more economically valuable grazing lands. The common perception of these woodlands is that they should be maintained only on steep rocky slopes that will not support other vegetative types. Their expansion into grass and shrublands is thought to be from wildland fire suppression and other management actions such as livestock grazing. This view does not account for the dynamic relationships among vegetation, climate and wildland fire. It also does not take into account that these are ecotones between biomes that move elevationally, based on the above conditions. The conditions and characteristics that are used for baseline vegetation developed during the Little Ice Age conditions from approximately 1300 to 1900; a climatic period that was both wetter and cooler than present conditions. Many of the current models for the areas encompassing the lower treeline limber pine woodlands predict an increase in temperature of between 1° to 7° F in the summer and from 1° to 6° F in the winter, which may increase the growing season evapo-transpiration rates. For much of the area, seasonal changes in precipitation are also predicted, including a summer precipitation decrease from 10 to 50 percent and winter precipitation increase from 10 to 25 percent.

Not enough is known ecologically about the lower treeline limber pine and its relationship to upper treeline populations and the biotic communities dependent upon them, to assume "business as usual" activities and management. In order to change the management paradigms that exist for the lower treeline woodlands, a series of carefully delineated basic and applied research questions need to be formulated for these stands. Answering these questions will provide managers with a fuller understanding of the ecological role(s) of the lower treeline limber pine woodlands, resulting in more informed management decisions on the ground.

Introduction

Limber pine grows across the widest elevational range of any conifer in the Rocky Mountains, ranging from approximately 5,250 feet (1,600 m) to almost 11,000 feet (3,300 m) (Schoettle and Rochelle 2000). This elevational range increases when the isolate found in North Dakota at 2,850 feet (869 m) is considered. The mean daily temperature in areas where limber pine grows also varies considerably (from 22.8° C to 12.6° C) and is linearly related to elevation (Schoettle and Rochelle 2000). Schoettle and Rochelle (2000) concluded that limber pine has a high degree of physiological plasticity in that the fundamental niche, where the tree can grow, and the realized niche, where it competes the best, are very broad.

The limber pine woodlands under discussion in this paper are those woodlands that occupy the lower slopes of the mountains and foothills, and the ecotones bordering the sagebrush/grass biome in Montana, Wyoming and northern Colorado. Defining the actual elevational range for these lower treeline populations is challenging because the limber pine has such a large elevational gradient and a wide latitudinal range. For the purposes of this paper, the lower treeline limber pine woodland is defined as outside the alpine vegetative community and below 8,500 feet (2,580 M) in elevation (Kearns and Jacobi 2007). It also includes the isolated stands (isolates) that occur within the Western Great Plains biome in Colorado, Nebraska, Wyoming, South Dakota, North Dakota and Montana.

A current literature search finds a paucity of information on the lower treeline limber pine (*Pinus flexilis*) woodlands compared to the upper treeline (above 8,500 feet) whitebark (*Pinus albicaulis*) and limber pine woodlands. The majority of research that has been done is on the isolates in the Western Great Plains, not on the lower treeline and isolated mountains that form the bulk of the lower treeline limber pine woodlands which serve as ecotones between the sage/grass and forest/woodlands biomes.

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Figure 1. Lower treeline limber pine woodland, Beaver Divide, WY. Elevation is 6,560 ft. (2000 m).

The lower treeline limber pine woodlands have a different set of management pressures than the upper treeline limber and whitebark pines. At the higher elevations, insect and disease, fire exclusion, visual resources, wildlife habitat, and climate change issues are at the forefront. The lower treeline woodlands not only have these issues, but also have issues related to livestock grazing, fuels management and energy development. They also entail management of a different set of wildlife species.

These low elevation woodlands are often characterized as "invading" more desirable vegetation types, so eradication *via* chaining, mastication, and burning have been accepted practices to limit woodland growth or "encroachment", particularly in the ecotone adjacent to the sagebrush/grassland biome. These low elevation woodlands, because of their position on the landscape as transitional areas between biomes, have a history of movement both up and down the elevational gradient. The limber pine woodland can be considered a functional ecological replacement of the pinyon pine (*Pinus monophylla/edulis*) woodland. It waxes and wanes with climate and fire, facilitated by the Clark's nutcracker (*Nucifraga columbiana)* (Tomback, personal communication) (figure 1).

These are ecologically distinct systems that serve as seed repositories between the upper treeline populations in the northern and central Rocky Mountains. They serve as a seed source for bird dispersal between mountain ranges (Perkins and DeArmond 2009). These lower treeline/foothills systems are thought to be particularly vulnerable to climate change (Aiken and others 2008; Romme and Turner 1991). Additionally, limber pine has been designated a "Regional Plant Species" by the National Phenology Network. Species placed with this designation are considered important in a locale or region of the nation in terms of ecological processes, biological diversity, or conservation (USA National Phenology Network 2010).

Current State of Knowledge

Wildlife Usage

Schoettle (2004) notes that "The role of limber pine forests as habitat for wildlife species is unknown." Although many authors (Latta and Minton 1997; Schoettle 2004; Tomback 2009) have tied some specific species to limber pine usage such as the Clark's nutcracker, grizzly and black bears (*Ursus* spp.), red squirrels (*Tamaisciurus hudsonicus*), and other small rodents. But overall, this lack of knowledge remains an important gap in information needed to develop multi-resource management strategies for the lower treeline limber pine.

Tree Longevity

Upper treeline limber pine is a very long-lived species with documented reports of live trees ranging from 1,500 to more than 1,600 years of age (Brown 2009; Schuster and others 1995). Studies located in the isolates of Pawnee Buttes/Pine Bluff (Schuster and others 1995), Black Hills (Thilenius 1970) and North Dakota (Potter and Green 1964) found no trees older than 238 years. Goodding (1923) did find three "old" limber pines at the Pine Bluffs site in Nebraska. Millar and others (2007b) found episodic Little Ice Age (from approximately 1300 to 1900) establishment of lower elevation limber pine stands in the eastern Sierra Nevada escarpment, with stands ranging in age from 90 to 200 years old.

The reasons for the difference in oldest age within these isolate woodlands compared to the upper treeline woodlands are not clear. Schuster and others (1995) suggest that it may be due to a more frequent wildland fire disturbance regime in the plains compared with those of the upper treeline woodlands. Other potential reasons include:

- The stands are composed of recent migrants (Latta and Mitton 1997; Millar and others 2007b; Schuster and others 1995).
- Anthropogenic movement of limber pine seeds by the Native Americans that used the seeds as a food source (Potter and Green 1964; Schuster and others 1995).

To date, there have been no studies looking at the age classes and structure of the lower treeline woodlands that occur primarily on Bureau of Land Management (BLM) and private lands in Wyoming, Montana and Colorado.

Importance to Watershed and as a Nurse Plant

Upper treeline limber pine woodlands are valued for watershed protection. They provide shade that delays snowmelt, which causes the retention of snowdrifts until early to mid-summer. At the lower treeline, limber pine woodlands influence snow retention and available soil moisture (Perkins and DeArmond 2009). The growth form of the tree with upswept branches provides shade and a windbreak that holds snow on the lee side of the trees. Baumeister and Callaway (2006) found higher soil moistures on the leeward side of the trees compared with the windward side. Beauvais (personal communication) and the author have observed the extended period of vegetative green-up on the lee side of limber pine.

Baumeister and Callaway (2006), Rebertus and others (1991) and Tomback (2009) have found that limber pine serves as a nurse tree facilitating tree and shrub growth underneath as well as on the lee side for multiple species including: fir (*Abies* spp.*)*, spruce (*Picea* spp.), Douglas fir *(Pseudotsuga menziesii),* and currant (*Ribes* spp.). This nurse tree function also is true for other species such as ponderosa pine (*Pinus ponderosa*) and curl leaf mountain mahogany (*Cercocarpus ledifolius*).

Genetics

There has been a limited amount of work on the genetics of the isolates included within the lower treeline limber pine woodlands. Latta and Mitton (1997) compared the genetic variation in the Pawnee Buttes isolate in Northeastern Colorado (including the Pine Bluffs isolate in Wyoming/Nebraska) to upper treeline limber pine stands found on the eastern slopes of the Rocky Mountain National Park (RMNP). Their analysis noted little genetic difference between the isolate and the RMNP stands. Only the southern-most stand located several hundred kilometers away outside of Fairplay, CO, was significantly differentiated.

The USDA Forest Service (1999) performed a similar study comparing the North Dakota isolate with other isolated stands in Montana (proximate to Terry) and South Dakota (Black Hills) as well as with two upper treeline alpine limber pine stands in south central Montana (Crazy and Pryor mountains) samples which are located within the contiguous range of limber pine in Montana. Their data suggested that the North Dakota stand has a closer relationship to the Montana stands than the geographically closer Black Hills stand. All three of the isolates exhibited less genetic variation than the Pryor and Crazy mountains. Latta and Mitton (1997) also noted the same lack of genetic variation in the Pawnee Buttes stand as compared to the more contiguous RMNP stands. These findings suggest a recent genetic bottleneck or a recent founding event.

Schoettle and Rochelle (2000) noted that different molecular genetic analyses produce different answers on estimates of limber pine gene flow between the upper treeline and the lower treeline/isolate populations. No common method has yet been used with which one may compare results among the different studies.

To date, reciprocal transplant studies (common garden) to examine the potential differing genetics of different elevational zones have not been conducted. Schoettle and Rochelle (2000) performed on-site measurements of limber pine to approximate this method. Because current genetic testing methods only analyze neutral variation, the common garden experiments are needed to evaluate the adaptive genetic traits of varying populations.

Insects and Disease

Many authors have documented the three primary insect and disease agents acting on limber pine: white pine blister rust (WPBR; *Cronartium ribicola*), mountain pine beetle (MPB; *Dendroctonus ponderosae*), and limber pine dwarf mistletoe (*Arceuthobium cyanocarpum*) (Kearns and Jacobi 2007; Millar and others 2007b; Schoettle 2004). Although these are the most important, other recognized insects include the ponderosa pine cone worm (*Dioryctria auranticella*) (Potter and Greene 1964; Schoettle and Negron 2001), the western conifer seed bug (*Leptoglossus occidentalis*), and the cone beetle *Conophthorus contortae* (Schoettle and Negron 2001).

To date, Hoff and McDonald (1993) has conducted the only known greenhouse trial of seedling susceptibility to WPBR. In that study, limber pine appears to have less resistance to blister rust than the other North American white pines. Limber pine had infection levels as high as 98 to 100 percent. In the three years of the study, limber pine mortality due to WPBR was 75 percent. In comparison, mortality in whitebark pine was 33 percent.

Since limber pine grows in very dry areas, ecologists hoped that WPBR would not be able to substantially spread into limber pine stands. It is now apparent that it may be just a matter of time before the necessary climatic conditions combine to produce a large wave of infection, even in the southern dry climates within the limber pine range (Kinloch and Dulitz 1990).

Kearns and Jacobi (2007) confirmed this with their study of 13 areas in Wyoming and Colorado. They found that the lower treeline limber pine has a significantly greater incidence of WPBR than the upper treeline limber pine. They found that plots at elevations of less than 8,500 ft (2,590 m) had an infection rate of 82 percent while those above 8,500 ft (2,590 m) had an infection rate of 30 percent. They also found that plots located at the bottom of slopes had higher incidences of WPBR infection than midslope,

Figure 2. Mountain pine beetle-caused mortality, Pole Mountain, WY. Elevation is 8,200 ft (2500 m).

summit or slope shoulder plot locations. When populations are lost due to WPBR infections, the limber pine becomes functionally extinct in the local area for hundreds of years until rust-resistant types emerge (Kendall 1997).

Unlike some pine species such as lodgepole (*Pinus contorta*), limber pine did not co-evolve a normative relationship with the mountain pine beetle (Logan and Powell 2001). The upper treeline five-needle pines evolved at higher elevations that did not support consistent MPB presence that is an important disturbance component of the ecology of other pine species. Consequently, the limber pine has limited or no resistance to the MPB. Of the 13 tree species attacked by MPB, limber pine shows some of the least resistance (Six 2010). Widespread MPB infestations in the upper treeline limber/whitebark pine communities have occurred previously. For example, above average temperatures in the 1930's led to widespread MPB infestations and mortality in the upper treeline woodlands in Idaho (Logan and Powell 2001; Perkins and Swetnam 1996). This susceptibility to MPB along with the potential of limber pine shifting its species range to lower elevations where there is a higher potential for contact with MPB may lead to significant MPB outbreaks in the lower treeline limber pine woodlands, impacting the specie's distribution and abundance on the landscape.

In addition to the above factors, because the lower treeline limber pine woodlands tend to be younger and more densely stocked than the upper treeline alpine woodlands, their susceptibility to MPB is increased. Perkins and Roberts' (2001) work in whitebark pine stands as well as Millar and others' (2007b) work in limber pine stands provide evidence that younger and denser limber pine stands exhibit increased susceptibility to MPB. The author has observed MPB-caused mortality in the lower treeline limber pine stands in Wyoming (figure 2).

Ecotonal Dynamics

Ecotones are the boundaries between ecosystems and/or biomes (Allen and Breshears 1998). They are subject to movement dependent upon many local and regional factors, including drought, changing climate and management practices. The semiarid ecotones (where the lower treeline limber pine is located) are considered to be among the most sensitive to change (Intergovernmental Panel on Climate Change 1996). The low elevation woodland ecotones have moved both up- and down-slope throughout the Holocene (approximately 11,500 years BP to present) driven by changes in the above factors.

Allen and Breshears (1998) have documented rapid ecotone woodland/forest movement on the Frijolito Mesa in the Jemez Mountains of New Mexico. They documented a drought-induced shift over a five-year period of more than two kilometers, which has persisted over the last 40 years. They attributed this rapid movement and resulting persistence on the landscape to climate, primarily through drought. They also noted that management activities such as fire suppression had amplified this climate-induced ecotone shift by modifying the disturbance intervals.

Millar and others (2007b) studied limber pine sites on the eastern escarpment of the Sierra Nevada. Their work indicates that the upper treeline woodlands vary considerably in age and structure from the lower treeline woodlands. The lower elevational woodlands were established during the Little Ice Age and are much denser than the upper treeline stands. Eckert and Eckert's (2007) research on another five-needle pine, foxtail (*Pinus balfouriana*), in the Klamath Mountains of California, has also shown downhill expansion (using diameter class as a surrogate for age).

Recent droughts, temperature increases, and the attendant increase in insect and disease mortality have thinned the Sierra Nevada stands and have had the net effect of increasing their health and resistance to drought while maintaining them on the landscape. Although Eckert and Eckert (2007) did not specifically look at climate in their analysis, they conclude that although historic climate change could be a driver, habitat heterogeneity and ecological context are critical factors. Millar's (2007b) conclusion that that these stands may retreat downslope into new microsites, in effect shifting the species range downslope, on the landscape in response to a series of complex climatic, environmental and disturbance variables is important and reinforces the diversity of change agents involved in species range movement (figure 3).

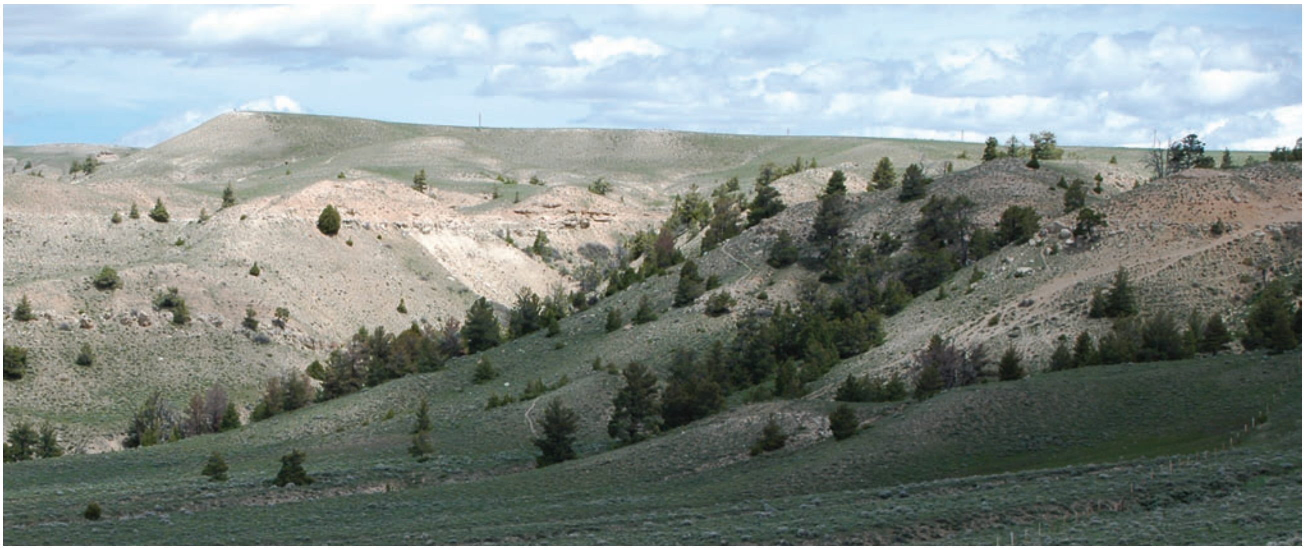

Figure 3. Limber pine downhill movement in drainages, Beaver Divide, WY. Elevation is 6,360 ft (1940 m).

Climate change modeling and field observations indicate that these downslope microsites and their microclimates may well become wetter and cooler than the upslope sites, creating the conditions for a downward shift in limber pine species range (Millar, personal communication). Recent work by Daly and others (2009) shows a de-coupling of nocturnal cold air drainage from normal synoptic patterns in complex topography and shows that the temperature changes due to this may well be less that those changes predicted by regional and global climate models. They suggested that these cold air drainages may act as refugia in times of changing climatic conditions. McLachlan and others' (2005) and Pearson's (2006) analyses show that tree species movements in periods of rapid climate change are closely tied to spread from refugia throughout the range of the species.

Conifer movement downslope is also supported the with long term "common garden" ponderosa pine experiments at the Fort Valley Experimental Station (DeWald and Mahalovich 2008) showing that ponderosa pine from higher elevations grew well at lower elevations but not vice versa.

Allen and Breshears (1998) propose that the unprecedented rapid change in climatic conditions will produce rapid and extensive shifts in the woodland's associated ecotones. The range of the lower treeline limber pine in Montana, Wyoming and Colorado is within the area forecasted by Rehfeldt and others (2006) to be extramural climates, i.e. "having no contemporary analogs among the communities of today," within the next 80 years. These extramural climates may change not only the distribution of genetic variability across the landscape, but also invoke evolutionary processes related to migration, selection and recombination (Rehfeldt and others 2006).

In the past, ecotone movement has been connected to changing climatic conditions. The current period promises change at a more rapid rate than what has been seen in the past. Recurring droughts in the west have synchronized forest composition, structure and the associated functions across broad landscapes, which then become vulnerable to climate shifts (Millar and others 2007a). The shifting ecotones may well provide important refugia for species such as the limber pine, maintaining population levels to survive rapid change.

We may be able to adapt to present and future conditions by promoting diversity within and across the landscapes and managing the ecotones in their early successional movement. The proactive approach of modifying the ecological trajectories of the ecotones is preferential to overreacting to change based on past conditions.

Wildland Fire

There is a lack of research targeting wildland fire disturbances in limber pine. Much of the information must be derived from similar whitebark pine studies. The fire regimes in limber pine are highly variable (Tomback 2009), ranging from low severity surface fire to high severity crown fires depending on elevation and stand structure. At the upper treeline, disturbance by fire was rare and not an important ecological driver in the high elevation old-growth stands (Millar and others 2007b). On more mesic sites where limber pine stands were intermingled with other tree species, the mixed severity to high severity fires probably occurred much like the fire histories of whitebark pine in similar locations (Keane 2010). The lower treeline woodlands and isolates are thought to have a more frequent disturbance regime (Schuster and others 1995). Changing Fire Return Intervals (FRI) in low elevation limber pine may be assisting their survival and expansion by reducing the frequency of disturbance (Tomback 2009).

Information from LANDFIRE (2007) in zones 21, 22, and 29, where most of the lower treeline limber pine occurs, has FRI that vary widely depending on where the limber pine is found. FRI ranges from 100 to 1000+ years, with the shortest being 100-200 years in Wyoming big sagebrush (*Artemesia tridentata* ssp. *wyomingensis*) and up to

1,000 years in Rocky Mountain (*Juniperus scopulorum*) and Utah (*Juniperus osteosperma*) juniper with discontinuous fuels.

While LANDFIRE and the Fire Regime and Condition Class (FRCC) have provided important new information about vegetation and its potential relationship with wildland fire disturbance regimes, this information is limiting in two respects:

- Many field personnel use this as static information, which fixes the disturbance return interval and does not allow for the movement of vegetation, especially ecotones on the landscape.
- LANDFIRE was developed using historic conditions as the desired reference point and does not include changing climate and its effect on the vegetation in its modeling.

Recent research shows that while understanding the relatively recent past provides important insights, the paleoecological record shows that the fire frequency has changed continually over the Holocene in response to changes in the climate (Whitlock and others 2003). The variability in the record of fire history is important because it contradicts the idea of a static fire return interval (Whitlock and others 2003). As Littell (2010) noted, fire frequency and the area burned are controlled by climate more so than by weather and fuels. Also, fire regimes are not static, but dynamic, changing over time and space.

The conditions that we generally use for baseline vegetation and fire—were developed under the Little Ice Age conditions, a period of wetter and cooler conditions. These conditions are something we will probably never see again. The present communities are relatively young having only developed over the last few millennia with shifts in species distribution and characterized by both range contraction and expansion (Whitlock and others 2003).

The terms that we have traditionally used to describe fire and vegetation relationships as being in equilibria are inconsistent with our current understanding of the nature of the relationships among fire, climate, vegetation and fuels, which are highly dynamic and very transient in time. Current research suggests that ecosystems are non-equilibrium systems subject to driving factors at multiple scales (Littell 2010).

Management Issues

The lower treeline limber pine woodlands have a different set of use and management pressures than the upper treeline limber pine and other five-needle pine species. Because of the ecotone fluctuations, these woodlands are often thought to be "invading" more desirable sagebrush and grass vegetation types, so eradication *via* chaining, mastication, and burning have been accepted practices to limit woodland growth or "encroachment."

The common perception, reinforced in part by the static nature of commonly used planning tools, is that limber pine woodlands should be maintained only on steep rocky slopes that will not support other vegetative types. Their expansion into grasslands and shrublands is viewed as a result of management activities such as grazing and wildland fire suppression, not as a natural movement up- and downslope based on a much more complex set of factors.

As an example, during a recent presentation to a group of resource management specialists, describing the rationale behind the decision to place limber and whitebark pine on the BLM sensitive species list there was much discussion and some resistance to this idea. The response of one resource specialist was telling: "I've got 1940's aerial photos showing that the area was a grass/sagebrush stand and I'm going to burn all the limber pine to return it to that condition, and I'm doing a presentation tomorrow on how to burn limber pine that way."

Appropriate management strategies, including maintenance of forest and woodland structure and function as well as restoration, require an understanding of the structural and ecological conditions in order to adequately determine and prioritize management actions. Additional management actions must be based on the appropriate historical and potential future contexts when the objectives include maintenance of "natural" conditions. There is a need to perform assessments of the actual distribution of the lower treeline limber pine, insect and disease levels, population levels, genetic variability, wildlife habitat provided by limber pine, and potential range shifts among species.

Research Needs

Sound resource management on public lands depends upon a solid understanding of the ecological context on which to base decisions. In order to develop management strategies for the lower treeline limber pine woodlands, the scientific and land management communities must develop, prioritize and address research questions for these woodlands. Among the suggested research topics are the following:

- Perform common garden studies to evaluate the genetic basis of limber pine distribution and the potential of the *ex situ* movement of lower treeline stock to upper treeline woodlands. Elevationally-derived experiments such as Rehfeldt (1990) are needed to quantitatively measure the genetic differences in the limber pine elevational gradient.
- Measure the gene flow between the upper and lower treeline limber pine communities.
- Develop limber pine seed zone maps based on common garden and genetic studies.
- Document vegetative composition changes in the Great Plains isolated stands that were initially surveyed from 1923 to 1970 in Colorado, Nebraska, South Dakota and North Dakota.
- Determine the ecological role of lower treeline limber pine woodlands with respect to wildlife habitat, and watershed and hydrologic function
- Define the spatial distribution of the lower treeline limber pine woodlands and determine the extent of insect infestations and disease infections in these stands.

- Develop predictive models of the potential movement of lower treeline limber pine woodlands in response to changing climatic conditions.

Conclusions

Until some of these critical research needs are filled, it will be difficult for land managers to recognize lower treeline limber pine woodlands as a valuable, unique ecosystem that requires management to maintain its long term viability across the landscape.

We must emphasize to land managers the suggestions of Millar and others (2007a) that we cannot reply on past forest conditions to provide us with the information to maintain forests sustainably into the future. The complexities of changing climate, insect and disease, changing land use patterns, etc. will create new unique environmental conditions. Our incomplete understanding of the ecology and adaptive genetic traits of lower treeline limber pine woodlands greatly constrain our ability to manage and conserve this ecosystem in a changing world.

Managing these unique woodlands in the face of uncertainty requires a non-deterministic management strategy which emphasizes vegetative diversity and multiple successional pathways leading to multiple outcomes. Adoption of options that accommodate change rather than holding woodlands to a previously accepted norm will ultimately reduce costs. Most importantly it will improve the land managers' chances of successfully facilitating these systems adaptive response to environmental change.

Literature Cited

Aitken, S. N.; Yeaman, S.; Holliday, J. A.; Wang, T.; Curtis-McLane, S. 2008. Adaptation, migration or extirpation: climate change outcomes for tree populations. Evolutionary Applications. 1: 95-111.

Allen, Craig D.; Breshears, David D. 1998. Drought induced shift of a forest-woodland ecotone: rapid landscape response to climatic variation. Proc. Natl. Acad. Sci. 95: 14839-14842. December.

Baumeister, Danya; Callaway, Ragan M. 2006. Facilitation by *Pinus flexilis* during succession: a hierarchy of mechanisms benefits other plant species. Ecology. 87(7): 1816-1830.

Beauvais, Gary. 2010. [Personal communication]. March 10, 2010. Laramie, WY: University of Wyoming, Wyoming Natural Diversity Database.

Brown, Peter M. (Ed.) (2009, November-last update). OLDLIST. [Homepage of Rocky Mountain Tree-Ring Research], [Online]. Available: http://www.rmtrr.org/ [November 2009].

Daly, Christopher; Conklin, David R.; Unsworth, Michael H. 2009. Local atmospheric decoupling in complex topography alters climate change impacts. International Journal of Climatology. DOI: 10.1002/joc. P.1-8.

DeWald, Laura; Mahalovich, Mary Frances. 2008. Historical and contemporary lessons from ponderosa pine genetic studies at the Fort Valley experimental forest, Arizona. In: Olberding, Susan D.; Moore, Margaret M., tech coords. 2008. Fort Valley Experimental Forest—A Century of Research 1908-2008. Proceedings RMRS-P-53CD. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station. 204-213.

Eckert, Andrew J.; Eckert, Melissa L. 2007. Environmental and ecological effects on size class distributions of foxtail pine (*Pinus balfouriana*) in the Klamath Mountains, California. Madroño. 45(2): 117-125.

Goodding, L. N. 1923. An interesting area of limber pine extending into southwestern Nebraska. Journal of Forestry. 21(2): 175-176.

Hoff, R. J.; McDonald, G. I. 1993. Variation of virulence of white pine blister rust. European Journal of Forest Pathology. 23: 103-109.

Intergovernmental Panel on Climate Change. 1996. Climate change 1995, impacts, adaptations and mitigation of climate change: scientific-technical analyses. Cambridge University Press. p. 171-189.

Keane, Robert. 2010. U.S. Forest Service, Missoula Fire Sciences Laboratory, Rocky Mountain Research Station, Missoula, MT. Presentation at: US Forest Service, National Advanced Silviculture Program, Module 3. Missoula, MT. January 8, 2010.

Kearns, Holly S. J.; Jacobi, William R. 2007. The distribution and incidence of white pine blister rust in central and southeastern Wyoming and Colorado. Canadian Journal of Forest Research. 37: 462-472; May.

Kendall, K. 1997. Limber Pine Communities [Homepage of High Elevation White Pines]. [Online]. US Forest Service. Available: http://www.fs.fed.us/rm/highelevationwhitepines/index.htm

Kinloch, Bohun B., Jr.; Dulitz, David. 1990. White pine blister rust at Mountain Home Demonstration State Forest: a case study of the epidemic and prospects for genetic control. Res. Pap. PSW-204. Berkeley, CA: Pacific Southwest Research Station, Forest Service, U.S. Department of Agriculture. 7 p.

LANDFIRE. (February 8, 2007). [Homepage of the LANDFIRE Project, U.S. Department of Agriculture, Forest Service; U.S. Department of Interior], [Online]. Available: http://www.landfire.gov/index.php [2007, February 8].

Latta, R. G., Minton, J. B. 1997. A comparison of population differentiation across four classes of gene marker in limber pine (*Pinus flexilis* James). Genetics 146: 1153-1163; June.

Littell, Jeremy, S. 2010. JISAO CSES Climate Impacts Group, University of Washington. Fire, climate, fuels: climate change and fire in western forests. Presentation at: U.S. Forest Service, National Advanced Silviculture Program, Module 3. Missoula, MT. January 11, 2010.

Logan, Jesse A.; Powell, James A. 2001. Ghost forests, global warming, and the mountain pine beetle (*Coleoptra: Scolytidae*). American Entomologist. 47(3): 160-172; Fall.

McLachlan, Jason S.; Clark, James S.; Manos, Paul S. 2005. Molecular indicators of tree migration capacity under rapid climate change. Ecology. 86(6): 2008-2098.

Millar, Constance. 2010. (Personal Communication). March 26, 2010. Albany, CA: U.S. Forest Service, Sierra Nevada Research Center, Southwest Experimental Station.

Millar, Constance I.; Stephenson, Nathan L.; Stephens, Scott L. 2007a. Climate change and forests of the future: managing in the face of uncertainty. Ecological Applications. 17(8): 2145-2151.

Millar, Constance I.; Westfall, Robert D.; Delany, Diane L. 2007b. Response of high-elevation limber pine (*Pinus flexilis*) to multiyear droughts and 20th-century warming, Sierra Nevada, California, USA. Canadian Journal of Forest Research. 37: 2508-2520; December.

Pearson, Richard G. 2006. Climate change and the migration capacity of species. Trends in Ecology and Evolution. 21(3): 111-113

Perkins, Dana; DeArmond, Mike. 2009. Limber pine and whitebark pine on BLM lands: a need for action. Unpublished paper on file at: U.S. Department of the interior, Bureau of Land Management, Idaho State Office, Boise, ID. 14 p.

Perkins, Dana L.; Roberts, David W. 2003. Predictive models of whitebark mortality from mountain pine beetle. Forest Ecology and Management. 174: 495-510.

Perkins, Dana L.; Swetnam, Thomas W. 1996. A dendroecological assessment of whitebark pine in the Sawtooth-Salmon River region, Idaho. Canadian Journal of Forest Resources. 26: 2123-2133.

Potter, Loren D.; Green, Duane L. 1964. Ecology of a northeastern outlying stand of *Pinus flexilus*. Ecology. 45(4): 866-868.

Rebertus, A. J.; Burns, B. R.; Veblen T. T. 1991. Stand dynamics of *Pinus flexilis* dominated subalpine forests in the Colorado Front Range. Journal of Vegetation Science. 2(4): 445-458.

Rehfeldt, G. E. 1990. Genetic differentiation among populations of *Pinus ponderosa* from the Upper Colorado River Basin. Bot. Gaz. 151(1): 125-137.

Rehfeldt, Gerald E.; Crookston, Nicholas L.; Warwell, Marcus V.; Evans, Jeffrey S. 2006. Empirical analyses of plant-climate relationships for the Western United States. International Journal of Plant Science. 167(6): 1123-1150.

Romme, W. H; Turner, M. G. 1991. Implications of global climate change for biogeographic patterns in the Greater Yellowstone Ecosystem. Conservation Biology. 5(3): 373-386.

Schoettle, A. W. 2004. Developing proactive management options to sustain bristlecone and limber pine ecosystems in the presence of a non-native pathogen. In: Shepperd, Wayne D.; Eskew, Lane G. 2004. Silviculture in special places: proceedings of the 2003 National Silviculture Workshop. Proceedings RMRS-P-34. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station. 255 p.

Schoettle, A. W.; Negron, J. F. 2001. First report of two cone and seed insect on *Pinus flexilis*. Western North American Naturalist. 61(2): 252-254.

Schoettle, A. W.; Rochelle, S. G. 2000. Morphological variation of *Pinus flexilis* (Pinaceae), a bird dispersed pine, across a range of elevations. American Journal of Botany. 87(12): 1797-1806.

Schuster, William S. F.; Mitton, Jeffrey B.; Yamaguchi, David K.; Woodhouse, Connie A. 1995. A comparison of limber pine (*Pinus flexilis*) at lower and upper treeline sites east of the Continental Divide in Colorado. American Midland Naturalist. 133(1): 101-111.

Six, Diana. 2010. University of Montana, Missoula, MT. Managing for healthy forests: biological disturbance agents. Presentation at: U.S. Forest Service, National Advanced Silviculture Program, Module 3. Missoula, MT. January 9, 2010.

Thilenius, John E. 1970. An isolated occurrence of limber pine (*Pinus flexilus*, James) in the Black Hills of South Dakota. American Midland Naturalist. 84(2): 411-417.

Tomback, Diana F. 2009. Whitebark and limber pine: ecology and status in the Rockies. [Online]. National Park Service. RM-CESU. Available: http://www.cfc.umt.edu/CESU/NEWCESU/Assets/Partner%20Activities/FY09%20Activities/Cluster%20Meeting%202009/Tomback_Whitebark%20pine%20and%20limber%20pine.pdf [April, 2010].

Tomback, Diana F. 2010. [Electronic communication to Robert Means]. February 17. Denver, CO: University of Colorado, Denver.

USA National Phenology Network. (2010, March 19) Homepage of USA National Phenology Network, [Online]. Available: http://www.usanpn.org/ [2010, March 19].

U.S. Department of Agriculture, Forest Service. 1999. Annual Report 1998-1999 (FY99), National Forest Genetics Electrophoresis Laboratory. [Online]. Camino, CA. 39p. Available: http://www.fs.fed.us/psw/programs/nfgel/annualreports/fy99.pdf

Whitlock, Cathy; Shafer, Sarah L.; Marlon, Jennifer. 2003. The role of climate and vegetation change in shaping past and future fire regimes in the northwestern U.S. and the implications for ecosystem management. Forest Ecology and Management. 178: 5-21.

Native Ectomycorrhizal Fungi of Limber and Whitebark Pine: Necessary for Forest Sustainability?

Paper

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Abstract—Ectomycorrhizal fungi are an important component of northern coniferous forests, including those of *Pinus flexilis* (limber pine) and *P. albicaulis* (whitebark pine) which are being decimated by white pine blister rust and mountain pine beetles. Ectomycorrhizal fungi are known to promote seedling establishment, tree health, and may play a role in forest sustainability. The goal of this research is to discover the native ectomycorrhizal fungi associated with these two pines in the Rocky Mountain region. Here we report 32 species of ectomycorrhizal fungi associated with whitebark pine, 26 with limber pine, with an overlap of 14 species (primarily suilloids). The ectomycorrhizal fungi can be grouped into 1. generalists, 2. western conifer associates, 3. calcareous species (limber pine) and 4. specialists for five-needle pine or stone pines (primarily suilloids). Some of the *Suillus* species occur with stone pines globally, suggesting a long co-evolutionary history and important ecological roles. Their association with limber pines is newly reported. These five-needle pine specialists could confer a competitive advantage over spruce and fir when present. A preliminary study of the physiology of the suilloid fungi reveals intra- and inter-specific variation in pH preference/tolerance *in vitro*. Strains with limber pines from calcareous sites exhibit a broader pH tolerance than those found with whitebark pine which is restricted to high elevations. It is hoped that these efforts contribute to an understanding of the native ectomycorrhizal fungi with whitebark and limber pine and provide information useful towards sustaining these tree species, including strain selection for inoculation of nursery seedlings.

Introduction

Ectomycorrhizal fungi are an important component of northern coniferous forests (Smith and Read 1997), including those of limber (*Pinus flexilis*) and whitebark pine (*P. albicaulis*) (Mohatt and others 2008). These two pine species are currently being seriously impacted by white pine blister rust and mountain pine beetles in much of their range (Schwandt 2006). Pines are highly dependent on ectomycorrhizal fungi for establishment (Hasselquist and others 2005) and growth (Smith and Read 1997). Ectomycorrhizal fungi are assumed to play a strong role in forest sustainability. It is acknowledged that a successful reforestation strategy for whitebark pine will need to incorporate information on links between seed/seedling performance and various biotic and abiotic factors (Bower and Aitken 2008). One factor that has not been addressed previous to our research is the beneficial association between ectomycorrhizal fungi and whitebark and limber pines (Mohatt and others 2008).

There are 7,000-10,000 species of ectomycorrhizal fungi (Taylor and Alexander 2005) associated with trees and woody shrubs. Each tree species hosts a particular subset of these fungi. Some, such as Douglas fir are capable of hosting over 2,000 species of ectomycorrhizal fungi (Trappe 1962) while others such as alder host only a few (Brunner and others 1992; Hirose and others 2010). Fungal associations are further restricted by soil type, climate, tree age and other factors (Cripps 2003). As five-needle pines, both whitebark and limber pine are likely to host a fairly limited set of ectomycorrhizal fungi further restricted by the harsh nature of growing sites (Mohatt and others 2008).

Ectomycorrhizal fungi (as species or strains) vary in host specificity, soil preference, host age requirements, dispersal strategies, ability to enhance nitrogen (N) or phosphorus (P) uptake, types of N and P accessed and in protective abilities against pathogens, drought, heavy metals, and soil grazers (Smith and Read 1997). The more we learn, the less functional redundancy appears to be the rule with each species/ecotype filling a unique niche (Tedersoo and others 2009). Therefore, the set of benefits provided to hosts depends on the specific community of fungi present on a root system or in a forest. Diversity of ectomycorrhizal fungi in a community can range from a few species on stressed or disturbed sites to hundreds in mature forests (Tedersoo and others 2009).

The goal of this research is to discover the native ectomycorrhizal fungi associated with limber and whitebark pine. Prompt attention is necessary as host-specific fungi and certain ecotypes could disappear along with specific pine populations. Here we report the ecological (not applied) aspects of this research focused on the Rocky Mountain region. We compare the ectomycorrhizal fungi found with whitebark pine (Mohatt and others 2008) to our new findings on the ectomycorrhizal fungi associated with limber pine. This is of interest for restoration purposes and because evolutionary histories of the two pine species differ, but they can co-occur. We do not know if they host the same ectomycorrhizal species. Also, in order to begin to understand the physiological diversity of ectomycorrhizal fungi associated with these pines, we examined pH preferences of various strains of suilloid fungi (of high importance to pines) to see if this links with host (limber/whitebark) or original soil type (calcareous/not). Here we report preliminary results. It is hoped that these efforts contribute to a greater understanding of the ectomycorrhizal fungi with whitebark and

In: Keane, Robert E.; Tomback, Diana F.; Murray, Michael P.; and Smith, Cyndi M., eds. 2011. **The future of high-elevation, five-needle white pines in Western North America: Proceedings of the High Five Symposium.** 28-30 June 2010; Missoula, MT. Proceedings RMRS-P-63. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station. 376 p. Online at http://www.fs.fed.us/rm/pubs/rmrs_p063.html

limber pine and provide information useful towards sustaining these tree species.

Methods

Fruiting bodies of ectomycorrhizal fungi were collected from various sites in the north-central Rocky Mountains, primarily in the Greater Yellowstone Area (GYA), mountain ranges in southwest Montana, and Waterton Lakes National Park from 2001 to 2010. Sporocarps were collected, described, photographed, dried and tissue-cultured when possible. Voucher specimens are in the MONT Herbarium at Montana State University. The description of sites A-K is as follows:

- *Site A. Greater Yellowstone Area* (largest site) includes *a*) New World district: approximately 2590- 3105 m a.s.l. (8497-10187 ft), Fisher and Miller Creek drainages, Gallatin National Forest, Beartooth/Absaroka Mountains, Park County, Montana b) Dunraven Pass, approximately 2682 m a.s.l. (8800 ft), northeast side of Yellowstone National Park and c) Beartooth Pass, approximately 2890 m a.s.l. (9480 ft), east side of pass, Beartooth/Absaroka Mountains, Custer National Forest, Carbon County, Montana. Predominately whitebark pine with some scattered spruce and *Vaccinium* understory present. Mineral soil has a pH of 5.8 on Beartooth Pass area.
- *Site B. Sacajawea Saddle,* approximately 2700 m a.s.l (8860 ft), Bridger Mountains, Gallatin National Forest, Gallatin County, Montana. Predominately limber pine with occasional whitebark pine at lower elevations and a pure stand across the saddle. Mineral soil has a pH of 6.3 at lower elevations.
- *Site C. Golden Trout Lake,* approximately 2590 m a.s.l. (8497 ft), across Gallatin Canyon from Big Sky, Gallatin County, Montana. Predominantly in whitebark pine with a *Vaccinium* understory. Soil pH was not tested.
- *Site D. Gravelly Mountain Range,* approximately 2500-2630 m a.s.l. (8202-8628 ft), Gravelly Mountains, Madison County, Montana. Limber pine at lower elevations and whitebark pine at higher elevations. Soil pH is 5.5 in whitebark pine area.
- *Site E. Waterton Lakes-Glacier International Peace Park, and Crow's Nest pass,* approximately 1524-1890 m a.s.l. (5000-6200 ft), southern Alberta, Canada. Limber pine at Horseshoe Basin, whitebark pine at Cameron Trail, mixed at Lineham Trail, and limber pine on Crow's Nest Pass. Soil pH was not tested.
- *Site F. Lewis and Clark State Park,* approximately 1675 m a.s.l. (5500 ft), above trail from Visitor Center, Lewis and Clark State Park, Jefferson County, Montana. Pure stand of limber pine with grass and forbs understory. Soil has a pH of 6.9.
- *Site G. Red Lodge,* approximately 2300 m a.s.l. (7600 ft), on ridge opposite Red Lodge Ski area, Custer National Forest, Carbon County, Montana. Predominately limber pine of mixed ages with Douglas fir at lower elevations. Mineral soil has a pH of 7.2.
- *Site H. Crown Mountain*, approximately 2011 m a.s.l. (6600 ft), upper Whitewater Creek drainage, Front Range/Lewis Mountains, Lewis and Clark National Forest, Lewis and Clark County, Montana. Predominately limber pine with occasional Douglas fir at lower elevations. Mineral soil has a pH of 7.6.
- *Site I. Storm Lake,* approximately 2511 m a.s.l. (8238 ft), west of Anaconda, Deer Lodge Forest, Deer Lodge County, Montana. Primarily in whitebark pine. Soil pH not tested.
- *Site J. Red Mountain*, approximately 2347 m a.s.l. (7770 ft), upper Alice Creek drainage, Helena National Forest, Lewis and Clark County, Montana. Predominately limber pine with mixed Douglas fir and lodgepole pine at lower elevations. Soil pH is 6.31.
- *Site K. Avalanche Lake*, approximately 2473 m a.s.l. (9000 ft), Madison Range, Lee Metcalf Wilderness, Gallatin National Forest, Madison County, Montana. Predominately whitebark pine with some scattered spruce and *Vaccinium* understory present. Soil pH was not tested.

Tissue Culture of Fungi and Method for pH Study

Isolations of fungi into pure culture were generally attempted within 24 hours of fruiting body collection. Tissue was removed aseptically from the context of mushroom caps and placed on sterile Modified Melin Norkran's agar (Molina and Palmer 1982) supplemented with 50 mg l^{-1} each of ampicillin and tetracycline. Duplicate tissue samples were placed in vials of 2 percent CTAB (buffer) and frozen for subsequent DNA analysis. Parafilm-sealed petri dishes were incubated at room temperature (22-25°C) until visible signs of growth appeared at which point they were subcultured on a modified MMN medium that lacked malt extract and contained biotin at 1.0 g per liter and a trace element solution. Stock cultures were maintained on slants of the latter medium at 4°C.

Three hypogeous (subterranean) suilloid fungi were examined including isolates of *Rhizopogon roseolus* (Corda) Th. Fr. from Avalanche Lake (CLC 2489), Beartooth site (CLC 2469) and Crown Mountain (CLC 2475). The first two isolates were associated with whitebark pine whereas the last was associated with limber pine. Four isolates of epigeous suilloid fungi were examined including: *Suillus sibericus* Singer from the Beartooth site (CLC 2472) and New World site (CLC 2345); both with whitebark pine. Two limber pine associates were studied including *Suillus tomentosus* var. *discolor* Smith, Thiers, Miller (CLC 2422) from Sacajawea and *Suillus cf placidus* (Bon.) Singer (CLC 2473) from Crown Mountain. It should be noted that associates from sites with limber pine generally have higher pH soils.

For pH work, the base medium was MMN salts (Molina and Palmer 1982) lacking malt extract and with glucose reduced to 5 g l^{-1} giving a final C:N ratio of approximately 30:1. As malt extract was removed the base medium was supplemented with biotin 1.0 g l^{-1} and a trace elements solution (Dickie 1998). Media were buffered with MES buffer according to Hilger et al. (1986) and others adjusted to pHs of 4.0, 5.5 and 7.0 with either HCl or NaOH prior to autoclaving (20 min at 121°C). Gellan (Phytagel, Sigma Life Sciences, St Louis, USA) was used at 6.5 g l^{-1} as a solidifying agent following (Dickie and others 1998). The pH of each treatment was verified after autoclaving.

Fungi to be used as inoculum were grown on plates with 20 ml MNN agar medium lacking malt extract at 22°C for at least 21 days. Plates were aseptically center-inoculated with one disk obtained from the active colony margin with a sterile 6 mm cork borer and sealed with parafilm. Three replicate plates were established for each treatment. Twenty disks were placed on pre-dried and weighed filter paper and dried overnight at 60°C. The average dry weights of these disks were used to remove the contribution of agar plugs from final mycelial dry weights. Plates were subsequently incubated at 22-25°C. Plates were examined weekly and radial growth measurements were obtained in two directions at right angles. Data were recorded on colony morphology and pigment production as described by (Keller 1996). At the end of the growing period plates were photographed under ambient natural light with lids removed on a Dreadnaught gray (# 6099 Daler-Rowney, Berkshire, UK) background for subsequent area and color analysis.

Dry weights for use in density calculations were collected when the fastest growing treatment had covered approximately two-thirds of the plate surface (90 X 15 mm dishes), for our isolates this ranged from 21 to 42 days. Colonies were removed by cutting around the margins with a scalpel and transferring this to a weighing dish to obtain a fresh weight. Colonies were then cut into pie-shaped wedges and placed in plastic drink cups. Citrate buffer pH 6.0 was then added to give a solution volume to mycelium-gel weight ratio of 10:1; the covered cups then stood 24 to 72 h prior to filtration and rinsing (Dickie and others 1998). Mycelium on pre-dried filter paper was weighed after 24 h at 60°C.

Results

Forty-five species of ectomycorrhizal fungi were collected from whitebark and limber pine forests (Table 1) and are considered putative associates of these tree species. Most species in the important suilloid group have been confirmed molecularly on roots and by mycorrhizal synthesis with seedlings in the greenhouse (Cripps and others 2008; Mohatt and others 2008). Other species await molecular or synthesis confirmation. Of these, 32 species of ectomycorrhizal fungi are reported for whitebark pine (Table 1, column 2), 26 species for limber pine (Table 1, column 3) with an overlap of approximately 14 species at this point in time. Examples of ectomycorrhizal species are shown in Figure 1.

The small pH study tested the growth of ectomycorrhizal fungi *in vitro* at pH 4, 5.5 and 7 (Figure 2). The two strains of *Suillus* from whitebark pine forests (CLC 2422, CLC 2345) grew similarly at pH 4 and pH 5.5, but growth was significantly reduced at pH 7. The two *Suillus* strains from limber pine forests (CLC 2472, CLC 2473) grew comparably at all three pH levels, thus spanning a pH range of 1000x. Similarly, the two *Rhizopogon* strains from whitebark pine forests grew at pH 4 and pH 5.5, but growth was significantly reduced at pH 7. The *Rhizopogon* strain from the limber pine forest grew at all three pH levels, but there was a lag phase at pH 7 (data not shown). In general, limber pine occurs on higher pH soils than whitebark pine.

Discussion

Overall, the diversity of species of ectomycorrhizal fungi in whitebark and limber pine forests in the north-central Rocky Mountain region appears relatively limited in comparison to other tree species (Mohatt and others 2008). This could reflect dry, cold conditions at these high elevations which are not conducive to fungal fruiting. Alternatively, results might mean that these pines are dependent on a rather limited set of ectomycorrhizal fungi. For the studied area, the ectomycorrhizal fungi in whitebark pine forests consist of 33 percent in Boletales (primarily suilloids), 21 percent in Cortinariales, 12 percent in Russulales, with 33 percent as other types (mostly *Hygrophorus* and *Tricholoma* species). For limber pine the numbers are 20 percent in Boletales (suilloids), 16 percent in Cortinariales, 28 percent in Inocybaceae (mostly *Inocybe* from one site), 16 percent in Russulales and 16 percent as miscellaneous types. This is in line with results from a study of ectomycorrhizal fungi with the European stone pine (*Pinus cembra*) done by Keller (1997) who found 44 percent in Boletales, 32 percent in Cortinariales, 6 percent in Inocybaceae, 11 percent in Russulales and 7 percent from other groups. This suggests that these limber and whitebark pine forests host a Boletales-Cortinariales type of ectomycorrhizal community as reflected by aboveground sporocarps. Fungi not, or rarely, represented by sporocarps such as thelephoroids, *Cenococcum, Amphinema,* and *Piloderma* have been confirmed on roots of whitebark pine seedlings (Mohatt and others 2008), but roots of limber pine have not yet been analyzed and so these fungi are not included in Table 1. However, whitebark pine seedlings from a belowground ectomycorrhizal perspective were found to be dominated by *Cenococcum,* suilloids and Cortinariales (Mohatt and others 2008). However, proportions of these species are known to change on seedling roots after severe fire (Trusty and Cripps, these proceedings).

Ecologically, the ectomycorrhizal fungi reported can be grouped into a) generalists known to associate with many tree species under a variety of conditions (*Amphinema, Cenococcum, Piloderma, thelephoroid fungi*), b) high-elevation western conifer associates including species of *Cortinarius, Russula, Lactarius, Tricholoma* and *Hygrophorus,* c) fungi with a preference for calcareous and/or sandy soil (i.e. *Inocybe* species found on one limber pine site), and d) those specific for pines, five-needle pines or stone pines (*Suillus, Rhizopogon,*

Table 1. Fruiting ectomycorrhizal species collected in whitebark (*Pinus albicaulis,* PA) and limber pine (*P. flexilis,* PF) forests in the Greater Yellowstone Area and north to Waterton Lakes National Park. Sites are: A= New World Mine district and YNP (PA), B= Sacagawea Saddle (PA, PF), C= Golden Trout Lake (PA), D= Gravelly Range (PA, PF), E= Waterton Lakes and Glacier Parks (PA, PF), F= Lewis and Clark State Park (PF), G= Red Lodge (PF), H= Crown Mt. (PF), I= Storm Mt (PA), J= Red Mt. (PF), and K= Avalanche Lake (PA). na = not checked.

Species	***P. albicaulis***	***P. flexilis***	**Both PA & PF**
BASIDIOMYCOTA - AGARICALES			
AMANITACEAE			
Amanita "alpina" A.H. Smith nom. prov.	A, B, C		
Amanita muscaria sl (Fr.) Gray	A		
HYGROPHORACEAE			
Hygrophorus gliocyclus Fr.	A, B, D, E	G, E	yes
Hygrophorus marzuolus (Fr.) Bres.	A, C		
Hygrophorus olivaceoalbus (Fr.:Fr.) Fr.	A		
Hygrophorus subalpinus A. H. Smith	A,C		
Hygrophorus sp. (aff. *H. piceae*)	B		
TRICHOLOMATACEAE			
Leucopaxillus paradoxis (Cost. & Durfour) Boursier	D		
Leucopaxillus gentianus (Quél.) Kotl.		G	
Tricholoma argyraceum (Bull.) Sacc.		F, D	
Tricholoma moseri Singer	A ,B, C, D	D, F	yes
CORTINARIACEAE			
Cortinarius cf *clandestinus* A.H. Smith	A, D		
Cortinarius duracinus Fr.	A, B, E	E?	
Cortinarius "flavobasalis" McKnight & Moser	A, D		
Cortinarius flavoroseus nom. prov.	A, D		
Cortinarius aff. *fulminoides* (Moser) Moser	B, D		
Cortinarius cf *subolivescens* A.H. Smith	A, D	C? B?	yes?
Cortinarius cf *evernius* Fr.		D	
Hebeloma sp.		G, J	
INOCYBACEAE			
Inocybe aff. *arenicola* (Heim) Bon		F	
Inocybe dulcamara (Alb. & Schw.) Kummer		F	
Inocybe cf. *fraudens* (Britz.) Sacc.		F	
Inocybe nitidiuscula (Britz.) Sacc.		F	
Inocybe aff. *rufuloides* Bon		F	
Inocybe sororia group Stuntz	A	B, D, F	yes
Inocybe splendens group Heim		F	
RUSSULALES			
Lactarius cf. *deterrimus* Gröger	A, B, D	D	yes
Russula albonigra (Krombh.) Fr.	E?	E?	yes?
Russula brevipes Peck	A	E?	yes?
Russula torulosa /queletii group	A, D, E	G, E?	yes
BOLETALES			
SUILLOIDS			
Chroogomphus sp. nov. (secotioid)	A		
Rhizopogon evadens A.H. Smith	A, D, I?	B, D	yes
Rhizopogon milleri A.H. Smith	A, D	D	yes
Rhizopogon molligleba	A		
Rhizopogon roseolus group	A	B, H, J	yes
Rhizopogon olivaceofuscus	A		
Suillus cf *placidus/plorans group*		H	
Suillus sibiricus (Singer) Singer	A, C, D, E	B, D, E, G	yes
Suillus subalpinus M.M. Moser	A, C, I?		
Suillus tomentosus var. *discolor* (bluing)	A, C, D, I	B, D, E?	yes
Suillus sp. (veil)		B, E, H, J	yes
THELEPHORALES			
Pseudotomentella sp.	A	na	
Tomentellopsis sp.	A	na	
Thelephora caryophylla		E	
ASCOMYCOTA			
Cenococcum geophilum Fr.	A, B, C, D, E	na	yes?
Total Species	**32**	**26**	**14**

Figure 1. Ectomycorrhizal fruiting bodies of fungi associated with whitebark pine. a. *Rhizopogon* species ("pogies") and b. *Suillus sibiricus*. *Photos by C. Cripps*.

Chroogomphus). The latter group is termed suilloid fungi (Bruns et al., 2002).

Limber pine is thought to have a southwestern history with possible Mexican pine relatives while whitebark pine appears historically related to Eurasian stone pines (Richardson 1998). However, relationships may be rearranged as suggested by new molecular data (Gernandt and others 2005; Tomback and Linhart 1990; Tsutsui and others 2009). These different histories combined with preferences for different soil types (more calcareous in general for limber pine) might lead to the conclusion that this should be reflected in differences in ectomycorrhizal communities. However, on some study sites, the pines co-occur, and have the potential to host the same ectomycorrhizal fungi. There appears to be only a 25 percent overlap in ectomycorrhizal fungi species for the two pines, although examination of roots is likely to increase the overlap of generalist fungi. Species that separate the two are limber pine associates with a strong preference for calcareous or sandy soil. Interestingly, many of the shared species are suilloid fungi i.e. *Suillus* and *Rhizopogon* species. These fungi are specialists and some occur only with pines in the Section *Strobus* (Grubisha and others 2002; Hirose and others 2010; Kretzer and others 1996). Other suilloid species are further restricted to five-needle or stone pines (Moser 2004).

Suillus sibiricus is known to be restricted to five-needle pines and occurs with stone pines world wide in Europe and Asia (Moser 2004) and it is now recorded with both whitebark and limber pine in the Rocky Mountains. *Suillus tomentosus* var. *discolor* also appears restricted to five-needle pines, but more information is needed to determine its molecular relationship to *S. tomentosus*, a three-needle associate. *Suillus subalpinus* is known only with whitebark pine in the north-central Rocky Mountains (Moser 2004). Other suilloids known to occur with stone pines worldwide are *Suillus plorans* and *S. placidus*, neither of which has been recorded on our sites. Keller (1997) reports *Suillus placidus, S. plorans* and *S. sibiricus* with the stone pines in Europe. Only a few of the hundreds of *Rhizopogon* species have been recorded with limber and whitebark pines on our sites, primarily *Rhizopogon evadens, R. milleri*, and a species in the *roseolus* group also found with three-needle lodgepole pine (Dowie and others, in prep.). A few other species have been reported with *P. albicaulis* but are not confirmed (Molina and Trappe 1992). A new secotioid species of *Chroogomphus* species is recorded with whitebark pine from our study sites. The *Suillus* species appear to be those restricted to five-needle pines or stone pines (Grubisha and others 2002). This host restriction is less clear for the *Rhizopogon* species however, *R. evadens* is both common and widespread with whitebark pine on many of our sites.

Rhizopogon and *Suillus* species (suilloids) are multi-age fungi that occur on both young seedlings and mature trees (Tedersoo and others 2009). They grow well in culture and have been used successfully for restoration purposes. While selected *Rhizopogon* species are used commercially as an inoculum for pine seedlings in North America, it is primarily the *Suillus* species that have been used to regenerate stone pines in Europe for 50 years (Weisleitner, personal communication). The use of ECM fungi restricted to five-needle pines in restoration practices is more likely to give these pines a competitive advantage; typical commercial inoculum generally contains fungi that favor other tree species. *Rhizopogon* is more dependent on mammals (squirrels, deer, etc.) for their spore dispersal, while *Suillus* spores are also dispersed by wind (Ashkannejhad and Horton 2006).

Soil conditions are known to further restrict the set of ECM fungi that can occur with a single host. Cripps (2003) found acidic conditions to restrict the ECM soil community for aspen (*Populus tremuloides*). Our early results demonstrate both strong intraspecific (ecotypes) and interspecific differences in pH growth responses for isolates of five-needle pine suilloid fungi; these results appear linked to the original soil pH and host plant. A wider pH tolerance was exhibited (in terms of growth) in isolates obtained from sites with higher soil pH that were generally associated with limber pine. Earlier work has shown strain and species variation in tolerance to soil acidification *in vitro* (Willenberg and others 1990), but little has been done to try to link original soil properties with pH responses (Smith and Read 1997). Earlier work on pH effects with pure cultures has been summarized by Hung and Trappe (1983). Much more work will

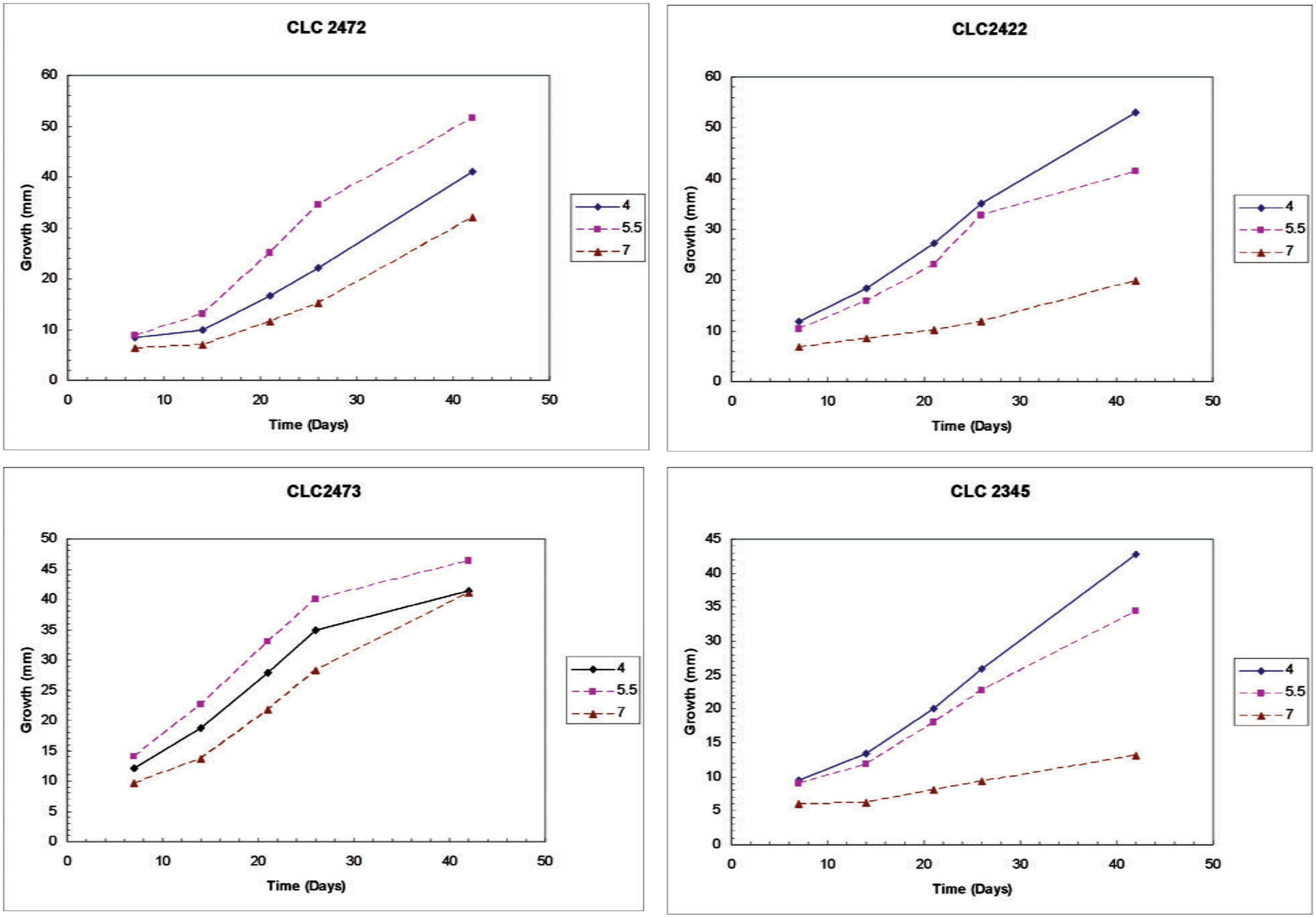

Figure 2. Growth of ectomycorrhizal fungi *in vitro* at pH 4, 5.5 and 7. The two strains of *Suillus* from whitebark pine forests (CLC 2345, CLC 2422) grew comparably at pH 4 and pH 5.5, but growth was reduced at pH 7. The two strains of *Suillus* from limber pine forests (CLC 2472, CLC 2473) grew comparably at all three pH levels, with a slight lag at pH 7. In general, limber pine occurs on higher pH soils than whitebark pine.

be needed to determine if our *in vitro* results translate to differences in mycorrhizal formation and function under greenhouse or field conditions (Dunabitia and others 2004; Ek and others 1994). It should be noted that these are only preliminary results, but limber pine occurs from the plains to timberline, and isolates from this pine, had a wider pH tolerance that those from whitebark pine forests more restricted to high elevations.

It has been suggested that ectomycorrhizal fungi have the ability to alter the course of plant establishment and succession through control of tree nitrogen uptake (Kronzucker and others 1997). Generally these fungi absorb a range of nitrogen sources not necessarily available to non-mycorrhizal pine roots; an important consideration given the potential effects of soil pH (as observed herein) on the nitrogen cycle. These fungi are also prolific producers of protease and phosphatase enzymes that mineralize soil organic compounds; again little is known about the pH response of these enzymes and whether site adaptation occurs (Antibus and others 1986). The current study also reveals differences in pigment production by different fungi in response to pH (results not shown). The production of pigments and low molecular weight organic compounds potentially add carbon sources to soil that could influence the size and structure of the rhizosphere community and be important in the release of essential elements from soil minerals (Rosling 2009). Our plans for future work include an examination of a wider range of ectomycorrhizal fungal species for their ability to use a variety of inorganic and organic nitrogen sources *in vitro*. In addition we are working with greenhouse inoculations and ^{15}N stable isotope analyses to better understand the range of physiological variation found in fungi associated with whitebark and limber pine. Applications from this type of research might include: assessment for the presence of appropriate native fungi in restoration, selection of species/ecotypes for nursery inoculation of seedlings, and monitoring out-planted seedlings for mycorrhizal colonization on various pH soils. Applied research on this topic is reported in Cripps and Grimme (these proceedings).

Whitebark and limber pines are involved in complex plant-fungus coevolutionary interactions under different abiotic conditions across the landscape (Hoeksema 2010). The suilloid fungi are an important group of mycorrhizal symbionts with pines and five-needle pines globally and should be considered as an important aspect of their ecology, distribution and sustainability (Wu and others 2000). It should also be considered that host-specific fungi and particular ecotypes could disappear along with specific pine forests.

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References

Antibus, R. K.; Kroehler, C. J.; Linkins, A. E. 1986. The effects of external pH, temperature and substrate concentrations on the acid phosphatase activity of ectomycorrhizal fungi. Canadian Journal of Botany. 64: 2383-2387.

Ashkannejhad, S.; Horton, T. 2006. Ectomycorrhizal ecology under primary succession on coastal sand dunes: interactions involving *Pinus contorta*, suilloid fungi and deer. New Phytologist. 169: 345-354.

Bower, A. D.; Aitken, S. N. 2008. Ecological genetics and seed transfer guidelines for *Pinus albicaulis* (Pinaceae). American Journal of Botany. 95: 66-76.

Brunner, I.; Brunner, F.; Laursen, G. A. 1992. Characterization and comparison of macrofungal communities in an *Alnus tenuifoilia* and an *Alnus crispa* forest in Alaska. Canadian Journal of Botany. 70: 1247-1258.

Bruns, T.; Bidartondo, M.; Taylor. L. 2002. Host specificity in ectomycorrhizal communities: what do the exceptions tell us? Integrative and Comparative Biology. 42: 352-359.

Cripps, C. L. 2003. Native mycorrhizal fungi with aspen on smelter-impacted sites in the Northern Rocky Mountains: occurrence and potential use in reclamation. Pgs. 193-208. In: National Billings Reclamation Publication, June 2003, Billings, MT. Published by the American Society of Mined Land Reclamation, Lexington, KY.

Cripps, C. L.; Grimme, E. 2010. Inoculation and successful colonization of whitebark pine seedlings with native mycorrhizal fungi under greenhouse conditions. Proceedings of the Hi-Five Symposium, Missoula, MT, June 28-30.

Cripps, C. L.; Smith, C.; Lapp, J.; Carolin, T. 2008. Assessment of Ectomycorrhizal Fungi with Whitebark Pine: Waterton-Glacier International Peace Park. Nutcracker Notes. 14: 12-14.

Dickie, I. A.; Koide, R. T.; Stevens, C. M. 1998. Tissue density and growth response of ectomycorrhizal fungi to nitrogen source and concentration. Mycorrhiza. 8: 145-148.

Dowie, N.; Hemenway, J.; Miller, S. L. (in prep.). A fourth *Rhizopogon* of *Pterospora andromedea* found in the Greater Yellowstone Area.

Dunabeitia, M. K.; Hormilla, S.; Garcia-Plazaola, J. I.; Txarterina, K.; Arteche, U.; Becerril, J. M. 2004. Differential responses of three fungal species to environmental factors and their role in mycorrhization of *Pinus radiata* D. Don. Mycorrhiza. 14: 11-18.

Ek, H.; Andersson, S.; Arnebrant, K.; Soderstom, B. 1994. Growth and assimilation of NH^+ and NO_3^- by *Paxillus involutus* in association with *Betula pendula* and *Picea abies* as affected by substrate pH. New Phytologist. 128: 629-637.

Gernandt, D. S.; López, G. G.; García, S. O.; Liston, A. 2005. Phylogeny and classification of *Pinus*. Taxon. 54(1): 29-42.

Grubisha, L.; Trappe, J. M.; Molina, R.; Spatafora, J. 2002. Biology of the ectomycorrhizal genus *Rhizopogon*. VI. Re-examination of infrageneric relationships inferred from phylogenetic analyses of ITS sequences. Mycologia. 94: 607-619.

Hasselquist, N.; Germino, M. J.; McGonigle, T.; Smith, W. K. 2005. Variability of *Cenococcum* colonization and it ecophysiological significance to young conifers. New Phytologist. 165: 867-873.

Hilger, A. B.; Thomas, K. I.; Krause, H. H. 1986. The effects of several buffers on growth and phosphorus nutrition of selected ectomycorrhizal fungi. Soil Biology and Biochemistry. 18: 61-67.

Hirose, D.; Shirouzu, T.; Tokumasu, S. 2010. Host range and potential distribution of ectomycorrhizal baidiomycete *Suillus pictus* in Japan. Fungal Ecology. 3: 255-260.

Hoeksema, J. D. 2010. Ongoing coevolution in mycorrhizal interactions. New Phytologist. 187: 286-300.

Hung, L. L.; Trappe, J. M. 1983. Growth variation between and within species of ectomycorrhizal fungi in response to pH *in vitro.* Mycologia. 75: 234-241.

Keller, G. 1996. Utilization of inorganic and organic nitrogen sources by high-subalpine ectomycorrhizal fungi of *Pinus cembra* in pure culture. Mycological Research. 100: 989-998.

Keller, G. 1997. Mykosocoziologische Studie über die Mykorrhizapilze der Zirbe [Mycosociological study on mycorrhizal fungi of stone pine]. FBVA-Berichte, Schriftenreihe der Forstlichen Bundesversuchsanstalt, Wein, Austria. Pp. 74.

Kretzer, A.; Li, V.; Szaro, T.; Bruns, T. 1996. Internal transcribed spacer sequences from 38 recognized species of *Suillus* sensu lato: Phylogenetic and taxonomic implications. Mycologia. 88: 776-785.

Kronzucker, H. J.; Siddiqi, M. Y.; Glass, A. D. M. 1997. Conifer root discrimination against soil nitrate and the ecology of forest succession. Nature. 385: 59-61.

Molina, R.; Palmer, J. G. 1982. Isolation, maintenance, and pure culture manipulation of ectomycorrhizal fungi. Pp. 115-129. In: N. C. Schenck (ed.), Methods and principles of mycorrhizal research, The American Phytopathological Society, St. Paul, MN.

Molina, R.; Trappe, J. M. 1994. Biology of the ectomycorrhizal genus *Rhizopogon.* I. Host associations, host-specificity and pure culture syntheses. New Phytologist. 125: 653–675.

Mohatt, K. R.; Cripps, C. L.; Lavin, M. 2008. Ectomycorrhizal fungi of whitebark pine (a tree in peril) revealed by sporocarps and molecular analysis of mycorrhizae of treeline forests in the Greater Yellowstone Ecosystem. Botany. 86: 14-25.

Moser, M. 2004. Subalpine conifer forests in the Alps, the Altai, and the Rocky Mountains: a comparison of their fungal populations. Pp. 151-158. In: Cripps, C. L. (ed.), Fungi in Forest Ecosystems: systematics, diversity and ecology. New York Botanical Garden Press, NY.

Richardson, D. 1998. Ecology and Biogeography of *Pinus.* Cambridge University Press, U.K. Pp. 527.

Rosling, A. 2009. Trees, mycorrhizae and minerals—field relevance of *in vitro* experiments. Geomicrobiology Journal 26: 389-401.

Schwandt, J. 2006. Whitebark pine in peril: A case for restoration. USDA Forest Service Report R1-06-28.

Smith, S. E.; Read, D. J. 1997. Mycorrhizal symbiosis. Academic Press, San Diego, CA.

Taylor, A. F. S.; Alexander, I. 2005. The ectomycorrhizal symbiosis: life in the real world. Mycologist. 19: 102-112.

Tedersoo, L.; May, T. W.; Smith, M. E. 2009. Ectomycorrhizal lifestyle in fungi: global diversity, distribution, and evolution of phylogenetic lineages. Mycorrhiza. 20: 217-263.

Tomback, D.; Linhart, Y. 1990. The evolution of bird-dispersed pines. Evolutionary Ecology. 4: 185-219.

Trappe, J. M. 1962. Fungus associates of ectotrophic mycorrhizae. Botanical Review. 38: 538-606.

Trusty, P.; Cripps, C. L. 2010. Impact of fire on the mycorrhizal community with planted and natural seedlings (Fridley Burn, Montana). Hi-Five Symposium, Missoula, MT, June 28-30, 2010.

Tsutsui, K.; Suwa, A.; Sawada, K.; Kato, T.; Ohsawa, T.; Watano, Y. 2009. Incongruence among mitochondrial, chloroplast and nuclear gene trees in *Pinus* subgenus *Strobus* (Pinaceae). Journal of Plant Research. 122: 509-521.

Weisleitner, H. 2008. [Personal communication]. Federal Nursery of Austria, Innsbruck, Austria.

Willenborg, A.; Schmitz, D.; Lelley, J. 1990. Effects of environmental stress factors on ectomycorrhizal fungi *in vitro.* Canadian Journal of Botany. 68: 1741-1746.

Wu, Q.-X.; Mueller, G.; Lutzoni, F.; Huang, Y.-Q.; Guo, S.-Y. 2000. Phylogenetic and biogeographic relationships of eastern Asian and eastern North American disjunct *Suillus* species (fungi) as inferred from nuclear ribosomal RNA ITS sequences. Molecular Phylogenetics and Evolution. 17: 37-47.

The Relationship Between Whitebark Pine Health, Cone Production, and Nutcracker Occurrence Across Four National Parks

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Background

Whitebark pine (*Pinus albicaulis*) is declining in the central and northern Rocky Mountains from infection by the exotic pathogen *Cronartium ribicola*, which causes white pine blister rust, and from outbreaks of mountain pine beetle (*Dendroctonus ponderosae*). White pine blister rust has been present in Glacier and Waterton Lakes National Parks (NP) about two decades longer than in the Greater Yellowstone Area, but both Grand Teton and Yellowstone NP are currently experiencing major outbreaks of mountain pine beetle. McKinney and Tomback (2007) and McKinney and others (2009) demonstrated that as whitebark pine stands are progressively damaged by blister rust or trees are killed, Clark's nutcrackers (*Nucifraga columbiana*) make fewer stand visits when seeds are ripe. Our goals were to determine what variables best predict the occurrence of nutcrackers in whitebark pine stands in Grand Teton, Yellowstone, Glacier, and Waterton Lakes NP, and to compare the relationship we determine between cone production and nutcracker occurrence to that determined by McKinney and others (2009).

Experimental Design

In 2008, we established ten 30 m x 1000 m (1 km) transects for nutcracker point counts and two 10 m x 50 m plots per transect to examine forest health and cone production in Yellowstone, Grand Teton, Glacier, and Waterton Lakes National Parks (NP). In July and again in late August and early September in 2008 and 2009, we gathered data from these transects and plots to determine whitebark pine infection levels and canopy damage from blister rust; recent mortality from mountain pine beetle; living basal area; cone production; and, Clark's nutcracker occurrence and seed foraging activities through point counts. One-way MANOVA was used to examine differences in forest health variables, cone production, and nutcracker occurrence among parks. We used simple linear regression and correlation analysis to examine relationships between the number of cones and number of nutcrackers observed per year. Logistic regression analyses were used to look at the relationship between the multiple response variables, described above, and the dependent variable nutcracker presence and absence. For each explanatory variable in turn, we summed the AIC (Akaike's Information Criterion) scores of every model in which it appeared and normalized these sums to determine the relative importance weight for each variable. To compare our data to the linear regression model of nutcracker occurrence and cone production of McKinney and others (2009), we transformed our data from the number of nutcracker observations per point count to the proportion of total point count observation hours with at least one nutcracker observed.

Health Variables

Whitebark pine health differed greatly between the southern parks (Yellowstone and Grand Teton) and northern parks (Glacier and Waterton Lakes). No recently dead trees from blister rust infection were found on our health plots in Yellowstone and Grand Teton NP. These two parks had the lowest blister rust infection levels (1.4 and 20% overall, respectively). However, mountain pine beetle infestation levels were moderate to high in Yellowstone and Grand Teton NP (17.9 and 48.1%, respectively). Glacier and Waterton Lakes NP had more whitebark pine dying from blister rust (4.3 and 8.3%, respectively), and high levels of blister rust infection (32.5 and 70%, respectively). Pine beetle infestation was much lower in Glacier and Waterton Lakes National Parks (0 and 15.5%, respectively). MANOVA indicated that *park* was a significant predictor of variation in stand health; each park had a unique set of whitebark pine forest conditions.

Cone Production and Nutcracker Sightings

Cone production was low in all parks in 2008. In Yellowstone and Grand Teton, cone production rose dramatically in 2009, but not in Glacier and Waterton Lake NP. Nutcracker sightings were highest in Yellowstone and Grand Teton National Parks where whitebark pine was healthiest and cones were most abundant. Nutcrackers were observed breaking into cones and actively caching whitebark seeds on one Yellowstone transect. The fewest nutcrackers were observed in Glacier and Waterton Lakes NP. We obtained significant correlations between numbers of nutcrackers observed and cones counted (per year) for both 2008 and 2009. MANOVA indicated that *park* was a significant predictor of variation in nutcracker occurrence. However, AIC analysis failed to isolate a single variable or multivariate model responsible for nutcracker occurrence. All models included

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most of the following variables: total healthy trees, total trees infected with blister rust, total infested with mountain pine beetle, total dead trees, total cones, live basal area, and total squirrels. Whereas McKinney and others (2009) found that nutcrackers occurred reliably with cone production above ~130 cones/ha, our study found nutcrackers occurring reliably above the lower value of ~70 cones/ha.

Management Implications

The lower number of cones per hectare (cone threshold) corresponding to reliable nutcracker occurrence that we found offers more potential for nutcracker visitation in whitebark pine communities with fewer living trees or heavily damaged trees. However, if nutcrackers stop visiting whitebark pine stands with high mortality, natural regeneration will diminish greatly. This has particular relevance to stands near areas burned by wildfire. If nutcrackers are not dispersing seeds from damaged stands, then planting may be a highly appropriate management strategy for these areas.

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References

McKinney, Shawn T.; Tomback, Diana F. 2007. The influence of white pine blister rust on seed dispersal in whitebark pine. Canadian Journal of Forest Research. 37: 1044-1057.

McKinney, Shawn T.; Fiedler, Carl E.; Tomback, Diana F. 2009. Invasive pathogen threatens bird-pine mutualism: implications for sustaining a high-elevation ecosystem. Ecological Applications. 19(3): 597-607.

Monitoring Limber Pine Health in the Rocky Mountains and North Dakota

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Abstract—Ecological impacts are occurring as white pine blister rust spreads and intensifies through ecologically and culturally important limber pine ecosystems of the Rocky Mountains and surrounding areas. The imminent threat of mountain pine beetle has heightened concerns. Therefore, information on the health status of limber pine is needed to facilitate management and restoration efforts. The objectives of this study were to: (1) evaluate the health of limber pine in Colorado, Wyoming, Montana, and North Dakota, (2) establish monitoring plots to assess cumulative ecological impacts of blister rust and other damaging agents over time, and (3) gather baseline information needed to sustain, protect, and restore impacted stands. Eighty-three long-term monitoring plots were established in limber pine stands in 2006 and 2007. Most surveyed limber pines were classified as healthy (74 percent), while 19 percent were declining or dying, and 7 percent were dead. White pine blister rust and twig beetles were the most common damages observed. Evidence of recent mountain pine beetle activity was observed in 19 percent of all plots but mortality levels were low. Average plot incidence of white pine blister rust was greatest in the north and decreased southward except in ND where the disease was not detected. Limber pine regeneration was present in most plots but levels of blister rust infection on regeneration were fairly low. Mountain pine beetle populations have increased substantially since this study was initiated. Since blister rust rapidly kills young trees and bark beetles kill mature trees, their combined impacts could be significant.

Introduction

Limber pine (*Pinus flexilis* James) is an ecologically and culturally important, yet little studied, tree species within the western United States. Its distribution extends from Alberta and southeastern British Columbia to New Mexico, Arizona, and southeastern California with isolated populations in North Dakota, South Dakota, Nebraska, eastern Oregon, and southwestern California (Burns and Honkala 1990). Limber pine has a very wide elevational distribution, ranging from 2,850 feet in North Dakota to 12,500 feet in Colorado (Burns and Honkala 1990). Limber pines serve many important ecological functions such as providing food for wildlife, stabilizing slopes, regulating snow retention and runoff, and maintaining cover on harsh, rugged sites where little else can grow (Schoettle 2004). However, recent reports suggest significant ecological impacts to the species as the result of white pine blister rust (*Cronartium ribicola* J. C. Fisch. ex Rabenh.), mountain pine beetle (*Dendroctonus ponderosae* Hopkins), and other damaging agents (Blodgett and others 2005, Gibson and others 2008, Kearns and Jacobi 2007). Information on the status of limber pine and the long-term ecological impacts of this disease is needed to facilitate management and restoration efforts. The objectives of this study were to (1) assess the current ecological impacts of white pine blister rust on limber pine, (2) establish plots for future re-measurement to assess long-term and cumulative ecological impacts, and (3) gather baseline information needed to sustain, protect, and restore impacted stands.

Methods

Long-term monitoring plots were established in 2006 and 2007 in four study areas (1) northern Colorado and southern Wyoming (COWY), (2) northern Wyoming (NWY), (3) central Montana (MT), and (4) southwestern North Dakota (ND) (fig. 1). Plots were located by systematically selecting stands with a high limber pine component (20 percent or greater) based on vegetation layers, previous surveys, and suggestions from local land managers. Survey methods were adapted from the Whitebark Pine Ecosystem Foundation (Tomback and others 2004). Plots were 200 feet by 50 feet and were divided into three sections with a fixed area circular regeneration and understory vegetation subplot (1/100 acre, 11.8-foot radius) at the center point of each section.

Plot data collected included elevation, slope, aspect, slope position, stand structure, predominant understory species, and disturbance history. Tree data recorded for all trees greater than 4.5 feet tall included species, health status (healthy, less than 5% of crown damaged; declining 6 percent to 50 percent of crown dead or exhibiting symptoms indicating it is dying; dying, >50 percent of crown dead or dying; recent dead, some red needles and fine twigs intact; old dead, no needles or fine twigs intact), diameter at breast (d.b.h.), height, and size class (small: >0-2 in d.b.h.; medium >2-8 in d.b.h.; large: >8 in d.b.h.). Additionally, crown class, crown ratio, percent canopy kill (topkill), and damages and their severities were recorded for all white pines with the exception of those classified as old dead.

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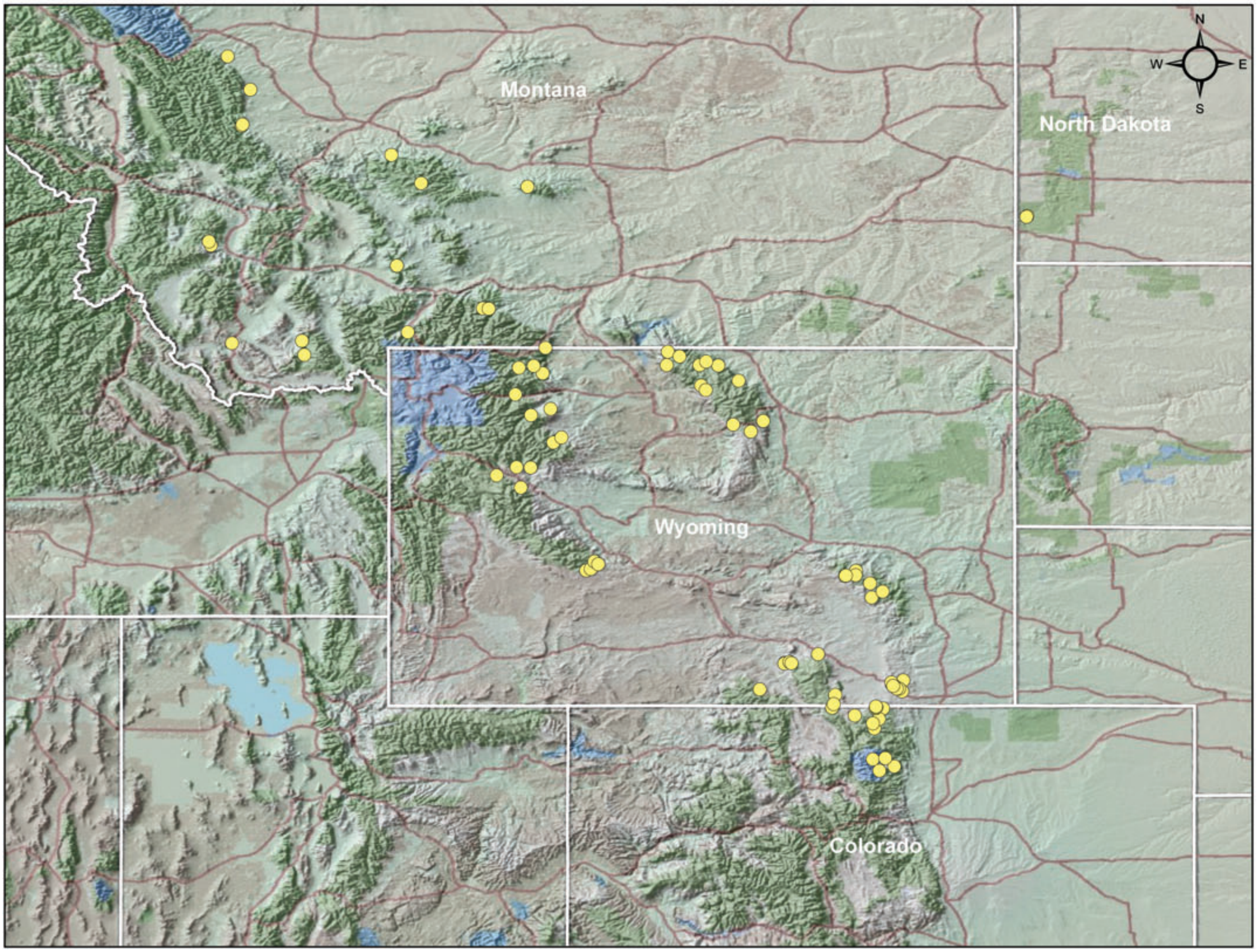

Figure 1. Limber pine monitoring plots (yellow dots) in Colorado, Wyoming, Montana, and North Dakota.

Blister rust disease severity was calculated for all white pines based on cumulative crown and stem damage (Six and Newcomb 2005). This included recording the number of branch cankers per crown third and stem cankers per stem third, and canker lengths. The total score for a tree can range from 0 (no infection) to 18 (all branches and stem infected), with scores from 1 to 4 associated with low severity, 5 to 8 with moderate severity, and over 8 with severe damage.

In subplots, all regeneration (trees less than 4.5 ft tall) was tallied and blister rust infection was recorded for white pine species. Percent and type of ground cover and *Ribes* species was estimated within each subplot.

Results and Discussion

Eighty-three long-term monitoring plots were established (36 in COWY, 29 in NWY, 16 in MT, and 2 in ND) (figure 1). Monitoring plots ranged in elevation from 2,900 to 10,243 feet and were located on a variety of aspects, slopes, and slope positions. On average, 40 limber pines were sampled per plot (range 9 – 180). Across all plots, limber pine density ranged from 39 to 783 trees per acre.

A total of 6,533 trees greater than 4.5 feet tall were assessed in all study areas combined. This included 3,296 limber pine and 22 whitebark pine. Most of the limber pines surveyed were classified as healthy (74 percent), 15 percent were declining, 4 percent were dying, 2 percent were recently killed, and 5 percent were old dead (table 1). White pine blister rust and twig beetles were the most common damages observed, although twig beetle damage severity was generally low. Fifty-three percent of declining and dying trees were infected with white pine blister rust and 51 percent had twig beetle damage. Evidence of bark beetles, including mountain pine beetle, *Ips* engravers, and others was identified on 43 percent of all recently killed trees but this represented only 2 percent of all white pines surveyed. Other less common damages included limber pine dwarf mistletoe (*Arceuthobium cyanocarpum* (A. Nels. ex Rydb.) A. Nels.), other canker diseases, and porcupine damage.

The average incidence of white pine blister rust over all plots was 29 percent (30 percent in COWY, 38 percent in NWY, 49 percent in MT, and 0 percent in ND plots). Based on Six and Newcomb (2005), disease severity is currently low in all areas (table 2). Average disease severity for all plots with

Table 1. Limber pine by health status and percent impacted by white pine blister rust (WPBR), twig beetles, and bark beetles in northern Colorado and southern Wyoming (COWY), northern Wyoming (NWY), Montana (MT), and North Dakota (ND) study areas.

		Healthy[a]			Declining/dying[b]			Recent dead[c]			Old dead[d]
Study Area	Total N	Count	WPBR %	Twig beetles %	Count	WPBR %	Twig beetles %	Count	WPBR %	Bark beetles[e] %	Count
COWY	1434	1217	24	12	155	56	21	32	3	19	30
NWY	1081	884	33	61	84	39	76	17	0	71	96
MT	661	303	36	49	312	69	63	23	57	57	23
ND	120	17	0	6	77	0	38	0	na	na	26
Total/means	3296	2421	29	34	628	53	51	72	19	43	175

[a] <5 % visual damage to crown or stem.

[b] 6-50 % (declining) or >50 % (dying) of the crown showing symptoms that indicated it is dead or will be.

[c] No green needles, red needles and fine twigs present.

[d] Damages were not recorded on the 175 trees classified as old dead.

Table 2. Mean incidence and severity of white pine blister rust in northern Colorado and southern Wyoming (COWY), northern Wyoming (NWY), Montana (MT), and North Dakota (ND) study areas.

	All plots			Plots with WPBR				
Study Area	N	Incidence[a]	S.D.[b]	N	Incidence	S.D.	Severity[c]	S.D.
COWY	36	30	28	29	37	27	1.1	1.1
NWY	29	38	30	25	44	28	1.1	1.1
MT	16	49	35	13	61	27	2.3	1.2
ND	2	0	0	0	*na*	*na*	*na*	*na*
Total/means	83	29	21	67	47	12	1.3	1.2

[a] The number of infected limber pines / the number of evaluated limber pines. Living trees only.

[b] Standard deviation.

[c] White pine blister rust (WPBR) disease severity was calculated for all white pines based on cumulative crown and stem damage (Six and Newcomb 2005). The total score for a tree can range from 0 (no infection) to 18 (total infection), with scores from 1 to 4 associated with low severity, 5 to 8 with moderate severity, and over 8 with severe damage.

infected trees was 1.3 and ranged from 0.1 to 3.9 (SD: 1.2; 95% CI: 1.0-1.6).

White pine blister rust occurred more frequently on medium and large trees than on small trees (table 3). Large trees had a greater number of total infections, but the incidence of stem cankers was highest (66 percent) in small trees and lowest (25 percent) in large trees. Fourteen percent of all infected trees had stem cankers in the bottom third of the crown, 22 percent had stem cankers in the middle third of the crown, and 26 percent had stem cankers in the top third of the crown. The incidence of basal stem cankers was greatest (24 percent) in small trees and least (2 percent) in large trees. Branch cankers occurred throughout the crown in all size classes in all areas.

Limber pine regeneration (trees < 4.5 ft tall) was present in 60 percent of all plots with an average density of 95 trees per acre (range 0-1000 trees per acre). White pine blister rust was detected on regeneration in 7 percent of all plots. The average incidence of white pine blister rust in regeneration plots where limber pine occurred was 3 percent (range 0-75 percent).

Table 3. Proportion of living limber pine trees infected with white pine blister rust (WPBR), mean number of WPBR cankers per infected limber pine, and proportion of infected trees with stem cankers by size class.

			Total Cankers[a]				
Size class	Total N	WPBR Count	%	Mean	Range	S.D.	Proportion of infected trees with stem cankers
Small[a]	830	201	24	2.6	1-13	2.2	66
Medium[b]	1630	617	38	3.9	1-43	4.4	47
Large[c]	589	211	36	7.0	1-48	8.6	25

[a] Mean number of branch and stem cankers per infected limber pine.

[b] >0-2 in d.b.h.

[c] >2-8 in d.b.h.

[d] > 8 in d.b.h.

Conclusions

White pine blister rust is well established in all of the study areas except North Dakota, and results suggest the disease is a major damaging agent in limber pine of the Rocky Mountains. This study provides baseline information on limber pine health. Long-term monitoring of these sites will provide critical information to guide future management and restoration. Although blister rust severity was low in all study areas based on the Six and Newcomb (2005) rating system, our results suggest that ecological impacts are occurring. Blister rust damage was observed on most declining and dying trees, and small trees had a higher frequency of severe infections, suggesting that mortality of small trees is occurring and can be expected to continue. Impacts to medium and large trees are evident as well. Unlike western white (*Pinus monticola* Dougl. ex D. Don) and sugar pine (*Pinus lambertiana* Dougl.), which are infected near the ground where the microclimate is more favorable for infection, infections in limber pine occur throughout the crown (Kearns 2005). Although medium and large trees have fewer severe infections, they have more total infections; this may eventually impact cone production and regeneration potential.

The incidence of blister rust on regeneration (trees < 4.5 ft tall) was low, but it is possible that very small trees are quickly killed and therefore not adequately represented in surveys of this kind. A more thorough examination of limber pine regeneration and the implications of blister rust is warranted.

Mountain pine beetle was present in all study areas except ND but at the time of the survey mortality was minimal. Beetle activity has increased substantially and it is predicted that most mature limber pines are threatened. The combined impacts of mountain pine beetle and white pine blister rust could be devastating in some areas since mountain pine beetles kill mature trees and young trees are especially susceptible to rust. Continued monitoring of limber pine health in the Rocky Mountains will be critical for assessing impacts of these two threats.

Acknowledgments

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Literature Cited

Blodgett, J.T.; Schaupp, W.C.; Long, D.F.; Cross, F. 2005. Evaluation of white pine blister rust and mountain pine beetle on limber pine in the Bighorn National Forest. Biological Evaluation. R2-05-08. Colorado: U.S. Department of Agriculture Forest Service, Rocky Mountain Region, Renewable Resources. 19 p.

Burns, R.M.; Honkala, B.H., tech. coords. 1990. Silvics of North America: 1. conifers; 2. hardwoods. Agriculture Handbook 654. Washington, DC. U.S. Department of Agriculture, Forest Service. 877 p.

Gibson K.; Skov, K.; Kegley, S.; Jorgensen, C.; Smith, C.; Witcosky, J. 2008. Mountain pine beetle impacts in high elevation five-needle pines: current trends and challenges. R1-08-020. Missoula, Montana. U.S. Department of Agriculture, Forest Service, Forest Health Protection.

Kearns, H.S.J. 2005. White pine blister rust in the central Rocky Mountains: modeling current status and potential impacts. Fort Collins, CO: Colorado State University. 243 p. Dissertation.

Kearns, H.S.J.; Jacobi, W.R. 2007. The distribution and incidence of white pine blister rust in central and southeastern Wyoming and northern Colorado. Can. J. For. Res. 37: 1-11.

Schoettle, A.W. 2004. Ecological roles of five-needle pine in Colorado: potential consequences of their loss. In: Sniezko, R.; Samman, S.; Schlarbaum, S; Kriebel, H.; Eds. Breeding and genetic resources of five-needle pines: growth adaptability and pest resistance. 2001 July 24-25; Medford, OR. IUFRO Working Party 2.02.15. Proceedings RMRS-P-32. Ogden, UT: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station: 124-135.

Six, D.L.; Newcomb, M. 2005. A rapid system for rating white pine blister rust incidence, severity, and within-tree distribution in whitebark pine. Northwest Science. 79(2&3): 189-193.

Tomback, D.F.; Keane, R.E.; McCaughey, W.W.; Smith, C. 2004. Methods for surveying and monitoring whitebark pine for blister rust infection and damage. Missoula, MT. Whitebark Pine Ecosystem Foundation. 28 p.

Long-Term Monitoring of High-Elevation White Pine Communities in Pacific West Region National Parks

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Background

National Park Service Inventory and Monitoring (I&M) networks conduct long-term monitoring to provide park managers information on the status and trends in key biological and environmental attributes (Vital Signs). Here we present an overview of a collaborative approach to long-term monitoring of high-elevation white pine forest dynamics among three Pacific West Region I&M networks: Klamath (KLMN), Sierra Nevada (SIEN), and Upper Columbia Basin (UCBN). Whitebark pine (*Pinus albicaulis*) is monitored in five national parks: Lassen Volcanic and Crater Lake in the KLMN, and Yosemite, Sequoia, and Kings Canyon in the SIEN. Foxtail pine (*P. balfouriana*) is monitored in Sequoia and Kings Canyon, and limber pine (*P. flexilis*) is monitored in Craters of the Moon in the UCBN (Figure 1).

Previous but limited sampling efforts report relatively low levels of infection by the non-native pathogen, *Cronartium ribicola* (white pine blister rust). In the KLMN, up to 20 percent of whitebark pine trees were found to be rust infected during a 2000 survey (Murray and Rasmussen 2003). In 2009, the same general areas were surveyed again, and 25 percent of whitebark pine trees were rust infected; however 18 percent of the trees had cankers that were inactive, complicating current estimates of impact (KLMN unpublished report). Mountain pine beetle were largely responsible for a 5.4 percent decrease in whitebark pine since 2003 in the KLMN (Murray 2010). Several surveys report that less than 1 percent of sampled whitebark pine are rust infected in SIEN parks (Duriscoe and Duriscoe 2002; Maloney and others 2008; Das and Stephenson unpublished data). Rust was not found on foxtail or limber pine within plots in our parks; however, one infected foxtail pine was identified in Sequoia in 1995, and several infected limber pine trees were found in Craters of the Moon in 2006 (Duriscoe and Duriscoe 2002; McKinney and others submitted).

Long-Term Monitoring Objectives

Determine the status and trends in the following:

- Tree species composition and structure.
- Tree species birth, death, and growth rates.
- Incidence of white pine blister rust and level of crown kill.
- Incidence of mountain pine beetle (*Dendroctonus ponderosae*).
- Incidence of dwarf mistletoe (*Arceuthobium* spp).
- Cone production of white pine species.

Approach

Permanent macroplots are allocated to random locations using an equal-probability spatially-balanced approach by means of the Generalized Random Tessellation Stratified (GRTS) algorithm (Stevens and Olsen 2004). Two different macroplot sizes are employed in our protocol. KLMN uses a 20 m x 50 m macroplot (0.1 ha or 1,000 m^2) and SIEN and UCBN use a 50 m x 50 m macroplot (0.25 ha or 2,500 m^2) (Figure 2). The KLMN macroplot size was chosen to accommodate additional objectives related to other vegetation monitoring efforts. The SIEN and UCBN macroplot size choice was based on analysis results of pilot data collected in Network parks (Craters of the Moon, Yosemite, and Sequoia) in 2009 and 2010 that showed the lowest variation, and therefore greatest efficiency, in plots of 2,500 m^2 to 3,000 m^2 (Figure 3). Macroplots in all three networks are comprised of multiple 10 m x 50 m subplots, and data are collected by subplot to allow for comparisons among networks and with other white pine monitoring efforts. For example, the Greater Yellowstone I&M Network's whitebark pine protocol (GYWPMWG 2007) and the Whitebark Pine Ecosystem Foundation's monitoring methods (Tomback and others 2005) employ a 10 m x 50 m plot design. Hence the KLMN design incorporates two parallel 10 m x 50 m subplots and the SIEN and UCBN design incorporates five parallel 10 m x 50 m subplots.

A serially alternating panel design is used with a three-year rotation for re-surveying permanent plots (Table 1). Plot-level data are collected on slope, elevation, and aspect. Tree-level data are collected on status (live or dead), species name, diameter, height, cone production, rust infection (active cankers and indicators), crown kill, pine beetle infestation, and presence/absence of mistletoe infection. In the SIEN and UCBN, nine 3 m x 3 m regeneration plots are located within macroplots and data are collected on seedling

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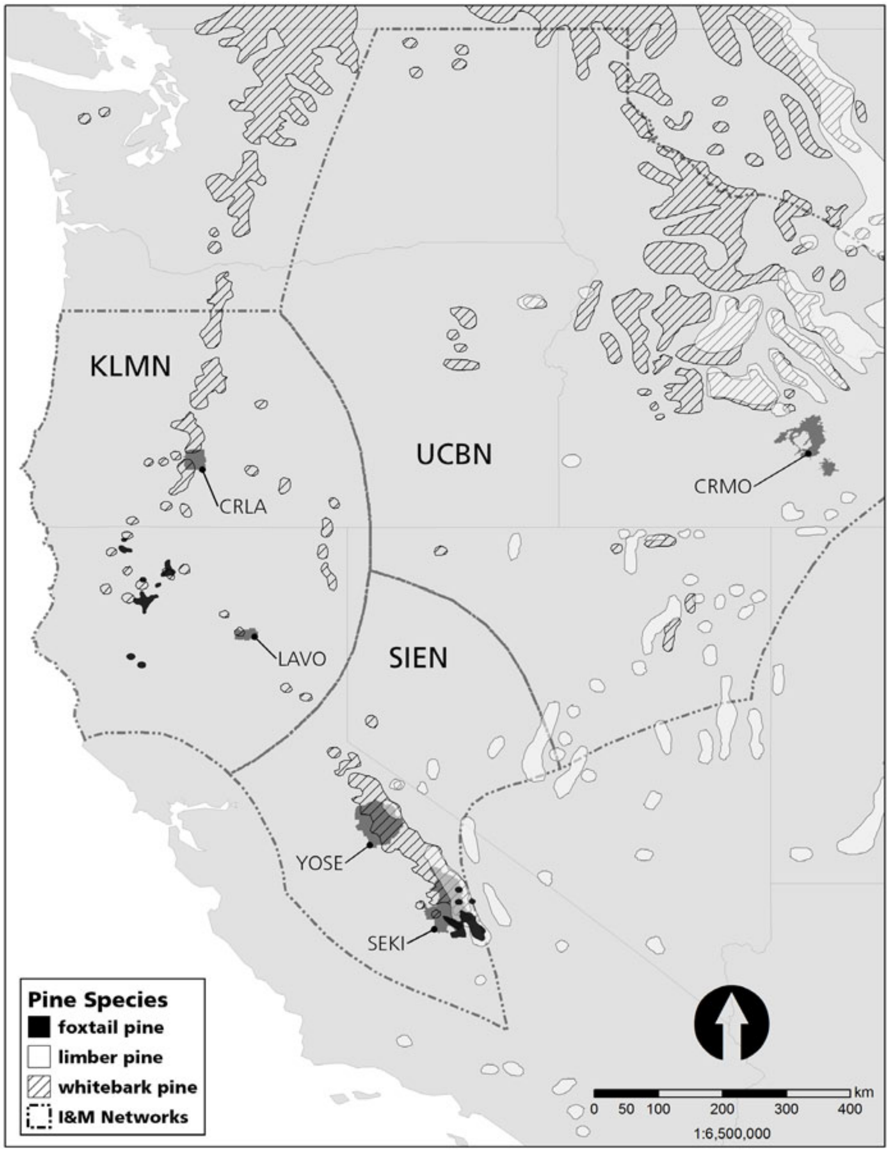

Figure 1. Distribution of whitebark pine, limber pine, and foxtail pine (from Little 1971), boundaries of the three Pacific West Region Networks, and National Park locations where the protocol is implemented. Network abbreviations: KLMN=Klamath, SIEN=Sierra Nevada, UCBN=Upper Columbia Basin. National Park unit abbreviations: CRLA=Crater Lake, LAVO=Lassen Volcanic, YOSE=Yosemite, SEKI=Sequoia and Kings Canyon, CRMO=Craters of the Moon.

counts by species and height class (20 to < 50 cm; 50 to < 100 cm; and 100 to < 137 cm) and averaged for plot-level values. By using a three-year rotation design, the project achieves a greater sample size with broader spatial extent for a given level of funding. The trade-offs are not knowing cone production, and year of seedling emergence, tree death, rust infection, beetle attack, and mistletoe infection during the two-year rest period.

Analysis Methods

Descriptive

Descriptive statistics include estimates of the proportion of trees and plots affected by blister rust, pine beetle, and mistletoe; the density of seedlings by height class; and the proportion and number of white pine trees producing cones. Stand tables are constructed displaying combinations of species composition, diameter class, height class, tree status, and health status.

Trend modeling

Within each network, temporal trends are analyzed in demographic (birth and death), reproductive (regeneration and cone production), growth (diameter and height), and infection (rust, beetle, mistletoe) rates. A linear mixed model developed by VanLeeuwen et al. (1999) and Piepho and Ogutu (2002) for correlated data is used to test the null hypothesis that the trend coefficient β_1 is equal to zero (H_0: $\beta_1 = 0$), with type I error (α) = 0.1. The model (equation 1) includes fixed effects, which contribute to the mean of the outcome of interest (park unit for example), and random effects, which contribute to the variance. Random effects estimate variation that can affect the ability to detect trend, such as site-to-site and year-to-year variation.

$$y_{ijk} = \mu + w_j \beta_i + a_{k(i)} + b_{j(ik)} + \gamma_i + w_j t_{k(i)} + e_{j(ik)} \qquad (1)$$

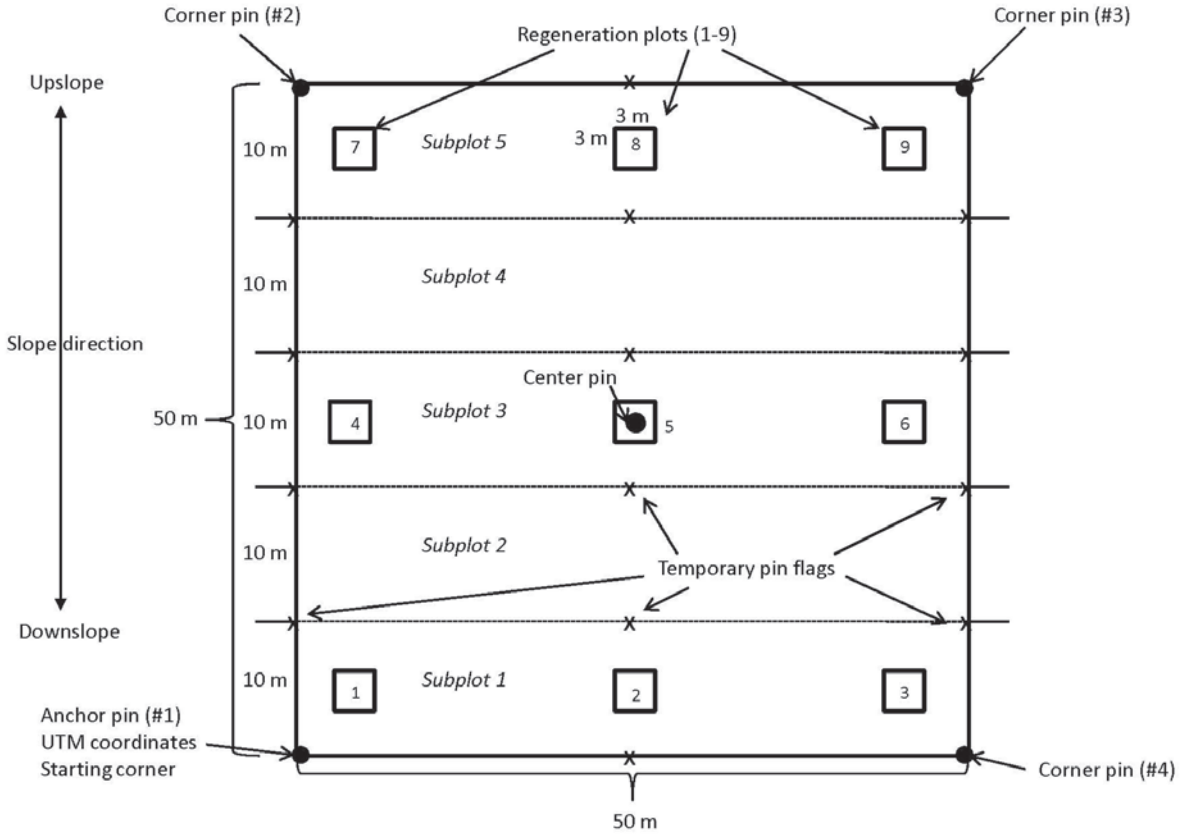

Figure 2. Layout of the 50 m x 50 m macroplot containing five 10 m x 50 m subplots, and nine 3 m x 3 m regeneration plots used in the Sierra Nevada and Upper Columbia Basin Networks. Regeneration plots are not permanently marked and are located 3 m in from the macroplot boundary lines.

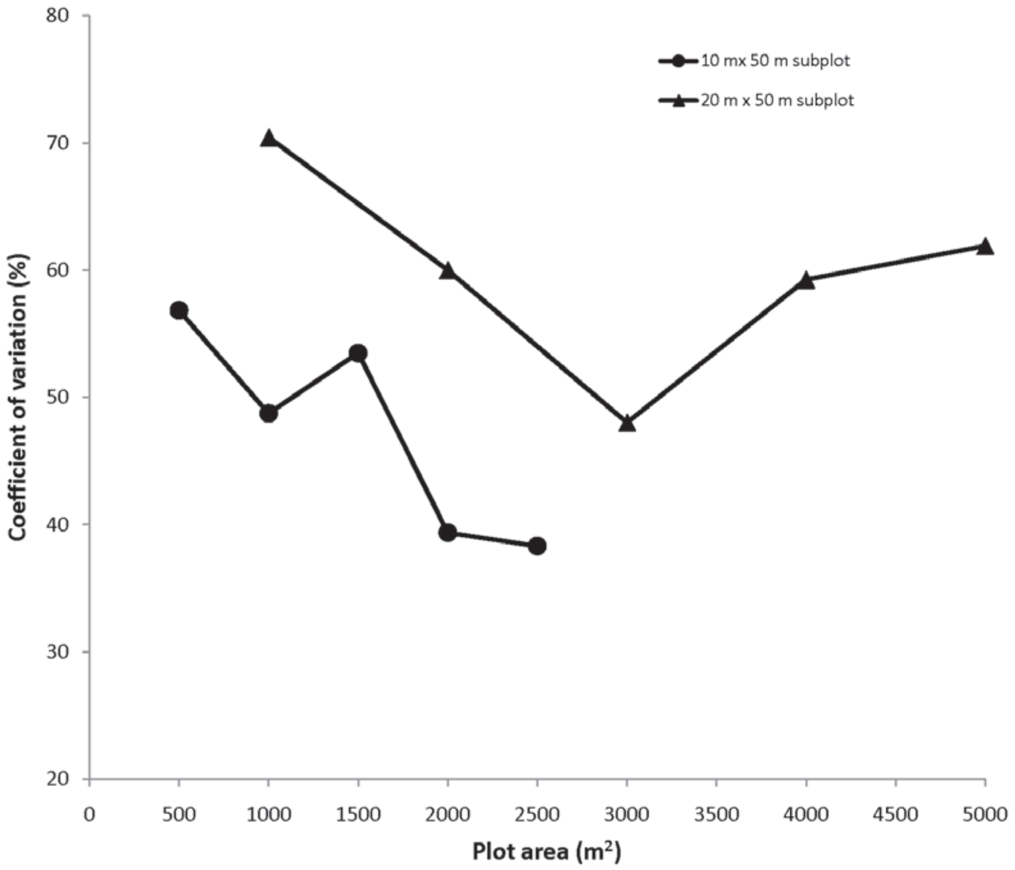

Figure 3. Variation in the total number of trees ≥ 1.37 m height as a function of plot area for two subplot sizes. The coefficient of variation is calculated as the sample standard deviation divided by the sample mean, multiplied by 100. Data were collected by laying out five consecutive subplots for each size. The 10 m x 50 m subplot (total area = 2,500 m^2) was used in Yosemite National Park in whitebark pine habitat (n = 4), and the 20 m x 50 m subplot (total area = 5,000 m^2) was used in Craters of the Moon National Monument in limber pine habitat and in the Inyo National Forest in foxtail pine habitat (n = 9).

where:

$m_{a(i)}$ = the number of sites sampled in the i^{th} park;

$m_{b(i)}$ = the number of years sampled in the i^{th} park;

m = the number of parks;

$i = 1, \ldots, 5$ indexes the five parks;

$k = 1, \ldots, m_i$ indexes the k^{th} site within the i^{th} park;

$j = 1, \ldots, m_{b(ki)}$ indexes the j^{th} survey year of the k^{th} site in the i^{th} park;

μ = fixed intercept of the linear time trend;

w_j = is a constant representing the j^{th} year (covariate) which is centered such that the year of least variation occurs at $w_j = 0$;

β_i = fixed linear slope of the i^{th} park;

$a_{k(i)}$ = the random intercept of the k^{th} site in the i^{th} park, assumed independent and identically distributed as $N(0, \sigma^2_{a(i)})$;

$b_{j(i)}$ = random effect of the j^{th} year in the i^{th} park, assumed independent and identically distributed as $N(0, \sigma^2_{b(i)})$;

γ_i = fixed effect of the i^{th} park;

$t_{k(i)}$ = random slope of the l^{th} site in the k^{th} park in the i^{th} network, assumed independent and identically distributed as $N(0, \sigma^2_{t(ik)})$; and

$e_{j(ik)}$ = unexplained error, assumed independent and identically distributed as $N(0, \sigma^2_{e(ij)})$.

Regional analyses

Mixed linear models are used to estimate trends in the response variables across the three networks. Comparisons of rates of change among the networks are made using F-tests to test for differences in slope and intercept coefficients. Descriptive statistics are compared among the networks using standard uni- and mulitvariate approaches.

Application

Blister rust and mountain pine beetle occurrence within several of the network parks, coupled with projections of increased temperature and decreased precipitation in the region, portend future declines in white pine communities, underscoring the need for broad-scale collaborative monitoring. Our joint efforts will provide comparable data on rust infection rates and tree damage, pine beetle outbreaks, and tree mortality across a large region with diverse forest types. Collaborative monitoring will also create opportunities to share information to better understand the effects of modern stressors on the dynamics of high-elevation forest ecosystems, and add to our knowledge of blister rust spread and epidemiology. This information can help park managers adapt to anticipated short- and long-term changes in ecosystem structure and function. Annual reports will be published through the NPS Natural Resources Technical Report series and served through NPS websites. Resource briefs will be produced and updated each year to provide a quick overview on the status of high-elevation white pine communities in each park. The first trend analyses will occur at the end of nine years (three panel rotations), and subsequently after each three-year panel rotation, ultimately resulting in more in-depth reports for the NPS technical report series and manuscripts for peer-reviewed publication.

Table 1. Revisit design for monitoring white pine species in a) the Klamath Network, b) the Sierra Nevada Network, and c) the Upper Columbia Basin Network. LAVO=Lassen Volcanic, CRLA=Crater Lake.

a. This panel design is followed for whitebark pine in the Klamath Network. Each third year is an off (or rest) year yielding a total $n = 50$ unique plots.

	Year												
	2011	**2012**	**2013**	**2014**	**2015**	**2016**	**2017**	**2018**	**2019**	**2020**	**2021**	**2022**	**2023**
LAVO (n = 25)	x			x			x			x			x
CRLA (n = 25)		x			x			x			x		

b. This panel design is followed for whitebark pine in Yosemite and for whitebark and foxtail pine each in Sequoia-Kings Canyon for a total SIEN $n = 144$ unique plots.

Panel	**Year**												
	2011	**2012**	**2013**	**2014**	**2015**	**2016**	**2017**	**2018**	**2019**	**2020**	**2021**	**2022**	**2023**
1 (n = 16)	x			x			x			x			x
2 (n = 16)		x			x			x			x		
3 (n = 16)			x			x			x			x	

c. This panel design is followed for limber pine in Craters of the Moon for a total UCBN $n = 90$ unique plots.

Panel	**Year**												
	2011	**2012**	**2013**	**2014**	**2015**	**2016**	**2017**	**2018**	**2019**	**2020**	**2021**	**2022**	**2023**
1 (n = 30)	x			x			x			x			x
2 (n = 30)		x			x			x			x		
3 (n = 30)			x			x			x			x	

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Literature Cited

Duriscoe, D. M., and C. S. Duriscoe. 2002. Survey and monitoring of white pine blister rust in Sequoia and Kings Canyon National Parks: Final report on 1995-1999 survey and monitoring plot network. Science and Natural Resources Management Division Sequoia and Kings Canyon National Parks, Three Rivers, CA.

Greater Yellowstone Whitebark Pine Monitoring Working Group (GYWPMWG). 2007. Interagency whitebark pine monitoring protocol for the Greater Yellowstone Ecosystem, v 1.00. Greater Yellowstone Coordinating Committee, Bozeman, MT.

Little, E. L., Jr. 1971. Conifers and important hardwoods. Volume 1 of Atlas of United States trees. U.S. Department of Agriculture Miscellaneous Publication 1146.

Maloney, P., J. Dunlap, D. Burton, D. Davis, D. Duriscoe, J. Pickett, R. Smith, and J. Kliejunas. 2008. White Pine Blister Rust in the High Elevation White Pines of California: A Forest Health Assessment for Long-Term Monitoring. USDA Forest Service, Forest Health Protection. Internal Draft Report. Pages 64.

McKinney, S. T., T. Rodhouse, L. Chow, G. Dicus, L. Garrett, K. Irvine, D. Sarr, and L. A. H. Starcevich. [Submitted September 2010]. Monitoring white pine (*Pinus albicaulis*, *P. balfouriana*, *P. flexilis*) community dynamics in the Pacific West Region: Klamath, Sierra Nevada, and Upper Columbia Basin Networks. Natural Resource Report NPS/PWR/NRR-2011/XXX. National Park Service, Fort Collins, CO.

Murray, M. P.; Rasmussen, M. C. 2003. Non-native blister rust disease on whitebark pine at Crater Lake National Park. Northwest Science. 77: 87-91.

Murray, M. P. 2010. Will whitebark pine not fade away? Insight from Crater Lake National Park (2003-2009). Park Science. 27(2): 64-67.

Piepho, H. P.; Ogutu, J. O. 2002. A simple mixed model for trend analysis in wildlife populations. Journal of Agricultural, Biological, and Environmental Statistics. 7(3): 350-360.

Stevens, D. L.; Olsen, A. R. 2004. Spatially balanced sampling of natural resources. Journal of the American Statistical Association. 99: 262-278.

Tomback, D. F.; Keane, R. E.; McCaughey, W. W.; Smith, C. 2005. Methods for surveying and monitoring whitebark pine for blister rust infection and damage. Whitebark Pine Ecosystem Foundation, Missoula, MT.

VanLeeuwen, D. M.; Birkes, D. S.; Seely, J. F. 1999. Balance and orthogonality in designs for mixed classification models. The Annals of Statistics. 27(6): 1927-1947.

Altered Species Interactions and Implications for Natural Regeneration in Whitebark Pine Communities

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Background

Whitebark pine (*Pinus albicaulis*) decline has altered trophic interactions and led to changes in community dynamics in many Rocky Mountain subalpine forests (McKinney and Tomback 2007). Here we discuss how altered species interactions, driven by disproportionate whitebark pine mortality, constrain the capability of whitebark pine forests to contribute genetic material to subsequent generations. The degree to which whitebark pine forests are reproductively limited, however, depends in large part on tree species composition and forest structure. The results of these changed dynamics have several important implications for restoration decisions.

Seed Production

Whitebark pine cone production was positively correlated with live whitebark pine basal area (BA) and negatively correlated with whitebark pine tree mortality at the site-level in the U.S. Rocky Mountains (McKinney and others 2009; Table 1). White pine blister rust (*Cronartium ribicola*) damages and kills whitebark pine trees by girdling branches and trunks (McDonald and Hoff 2001), and therefore reduces seed production within trees and forest stands. Thus, blister rust directly constrains the ability of individual trees and forest stands to contribute propagules, and hence genetic material, to subsequent generations. This reduction in regeneration potential is further aggravated by altered interactions between whitebark pine and two key vertebrate species resulting from disproportionate whitebark pine mortality.

Table 1. Pearson's correlation coefficients of whitebark pine forest characteristics from 24 sites in the central and northern Rocky Mountains, USA. Correlations are based on site-level mean values and are all significant at $\alpha = 0.01$.

Site variable	Cone production ($\ln[\text{no./ha.}]^2$)	Tree mortality (%)
Basal area ($\ln m^2/ha$)	0.81	-0.78
Cone production ($\ln[\text{no./ha.}]^2$)		-0.71

Predispersal Seed Predation

The North American red squirrel (*Tamiasciurus hudsonicus*) is a highly efficient, voracious consumer of conifer seeds. Squirrels cut down conifer cones and store them in large, conspicuous piles, called middens. Red squirrels preferentially select tree species based on cone energy content, foraging first on the highest energy species before moving on to the next highest energy species (Smith 1970, Hutchins and Lanner 1982). This adaptation is significant to the fate of whitebark pine because it has the greatest cone energy content of all sympatric species in U.S. Rocky Mountain upper subalpine forests (McKinney and others 2009). Due to their high foraging efficiency and central-place foraging lifestyle, red squirrels can greatly diminish cone crops at a local level. Indeed red squirrels are the primary predispersal seed predator of whitebark pine in the Rocky Mountains, taking more than 80 percent of the cone crop (Hutchins and Lanner 1982, McKinney and Tomback 2007).

Predispersal cone predation within a given forest is directly associated with red squirrel residential status. Squirrels remove proportionately more cones in forests where they reside (mixed conifer stands) versus whitebark pine-dominated stands where they simply feed and move on. In U.S. central and northern Rocky Mountain forests, the proportion of total squirrel detections comprised of active middens was significantly correlated with whitebark pine predispersal cone predation ($r = 0.65$, $P < 0.05$) (McKinney and Fiedler 2010). As cone production increases, squirrel predation increases at both tree- and stand-levels; however, the strength of the relationship between production and consumption is dependent on whitebark pine relative abundance (McKinney and Tomback 2007, McKinney and Fiedler 2010) (Figure 1). Predispersal cone predation decreases linearly with increasing proportion of total stand basal area comprised of whitebark pine (Figure 2). Therefore as whitebark pine becomes an increasingly dominant structural component, conditions for squirrel residence become less favorable, and cone predation declines.

Whitebark pine dominant forests provide suboptimal red squirrel habitat; conversely, squirrels thrive in mixed conifer forests containing whitebark pine. The reason for the disparity between the two forest types in squirrel residential status appears due to a higher degree of uncertainty in annual cone crops (Reinhart and Mattson 1990), and uncertainty appears

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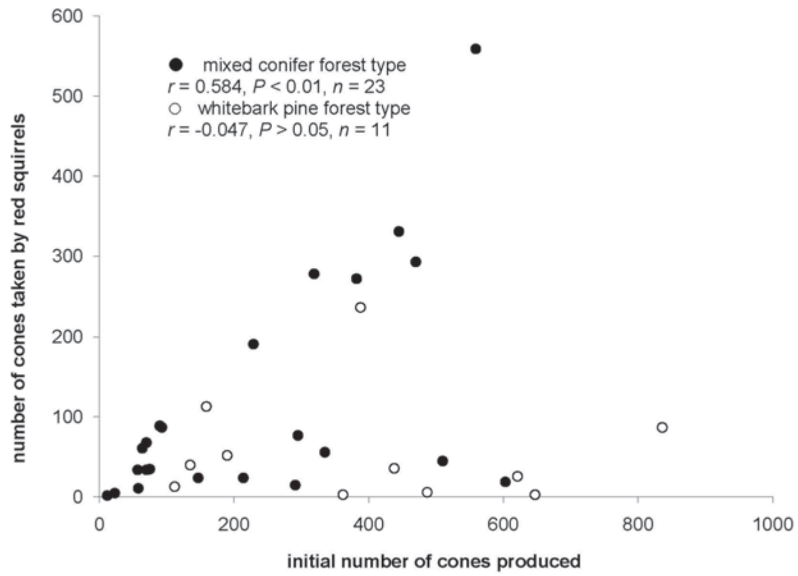

Figure 1. Correlation between red squirrel predispersal cone predation and whitebark pine cone production in two forest types (mixed conifer and whitebark pine dominant) in the Rocky Mountains, USA. Forest type defined by whether whitebark pine comprised > 50 per cent of total basal area; sites were classified as mixed conifer if condition was not met. Number of initial cones (*x*-axis) is the number of cones counted in late June to early July (McKinney and Fiedler 2010).

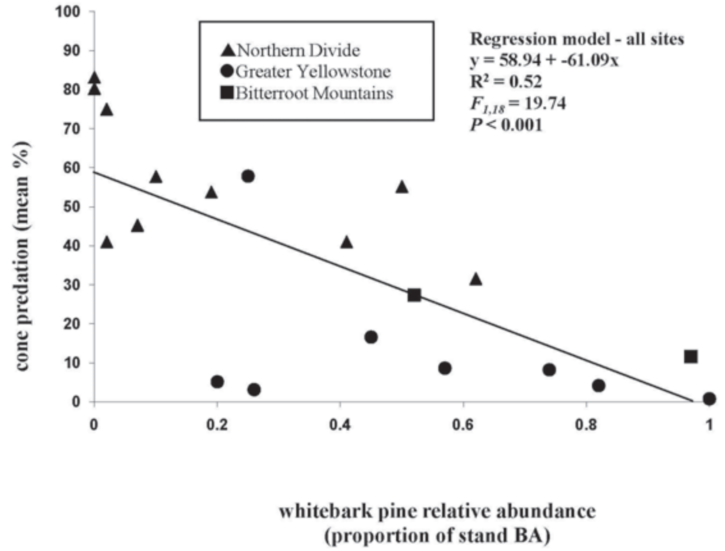

Figure 2. Simple linear regression analysis of the relationship between red squirrel mean predispersal cone predation (percentage of initial cone crop lost) and the relative abundance of whitebark pine at 20 subalpine forest sites in the Rocky Mountains, USA (McKinney and Fiedler 2010).

to be inversely related to tree species diversity. Squirrels, however, still prefer whitebark pine cones to sympatric conifers and will disperse into whitebark pine dominant forests to harvest cones, especially after disturbances such as wildfire (McKinney and Tomback 2007, McKinney and Fiedler 2010). However, because squirrel residence is low and ephemeral in whitebark pine dominant forests, overall cone consumption is low compared to mixed conifer forests containing whitebark pine. Hence whitebark pine dominant forests will likely have a larger proportion of their annual initial cone crop available for seed dispersal relative to mixed conifer forests.

Although squirrels appear to favor whitebark pine seeds, their residential status is dependent on forest structure and tree species composition (Mattson and Reinhart 1997, Fisher and Bradbury 2006). Squirrels need enough cones to store in order to survive long boreal winters (Steele 1998), and over time this requirement is best met in mature mixed conifer forests; those with high basal area and tree species diversity. These conditions are rarely met in forests where whitebark pine makes up greater than 50 per cent of stand basal area (McKinney and Fiedler 2010). Indeed, red squirrel occurrence in whitebark-dominated stands is often transient, with a higher degree of cones eaten *in situ* and a lower degree of active middens relative to mixed conifer forests (McKinney and Fiedler 2010).

Seed Dispersal

Clark's nutcracker (*Nucifraga columbiana*) and whitebark pine are coevolved mutualists (Tomback 1982), whereby the pine is obligately dependent upon the bird for dispersal of its large, wingless seeds. In late summer and early fall, nutcrackers extract ripe whitebark pine seeds from cones, transport seeds in a specialized sublingual pouch, and cache them in the ground at an average depth of 2.5 cm (Tomback 1982). In early summer, nutcrackers forage in subalpine forests and assess the developing cone crop (Vander Wall 1988). This behavior presumably alerts birds to imminent seed shortages

(Vander Wall and others 1981). Depending on the severity of cone crop failure, nutcrackers either emigrate regionally or from large geographic areas in search of food (Davis and Williams 1957, 1964, Bock and Lepthien 1976).

The frequency of nutcracker occurrence in a whitebark pine forest is strongly associated with the number of available cones. The proportion of total observation hours with at least one Clark's nutcracker sighting increased linearly with increasing whitebark pine cone production across 24 research sites in the U.S. Rocky Mountains (Figure 3). Furthermore, because nutcracker occurrence is strongly associated with cone production, it is also positively correlated with live whitebark pine basal area and negatively correlated with whitebark pine tree mortality (Table 1). This suggests that these measurable site variables (BA and mortality) can be important indicators of cone production, and thus, bird occurrence.

Cone production is also a strong predictor of the probability of nutcracker seed dispersal (Figure 4). It appears that by the time seed dispersal behavior initiates (late summer to early fall), nutcrackers have decided whether or not to settle in an area, and this decision is largely determined by the size of the existing cone crop. Moreover, the combined results indicate that there is a threshold of whitebark pine cone production below which there is a rapid decline in both the frequency of nutcracker occurrence (Figure 3) and probability of seed dispersal (Figure 4).

Continued degradation of cone production capacity within whitebark pine forests coupled with the tendency of nutcrackers to emigrate when cone crops are small, could result in fewer seed dispersal events in many whitebark pine forests. This outcome is especially troubling because high-mortality stands have lower cone abundance (McKinney and Tomback 2007); yet harbor a higher relative frequency of rust-resistant trees than similar stands with low mortality simply because most non-resistant tees in high-mortality stands have succumbed to blister rust (Hoff and others 1994). If nutcrackers are rare or absent in high-mortality stands, the putative resistance in the surviving trees would have little chance to be passed on to the next generation. Thus, identifying whether a threshold exists in whitebark pine cone production necessary to elicit seed dispersal by nutcrackers is an important question for restoration planning.

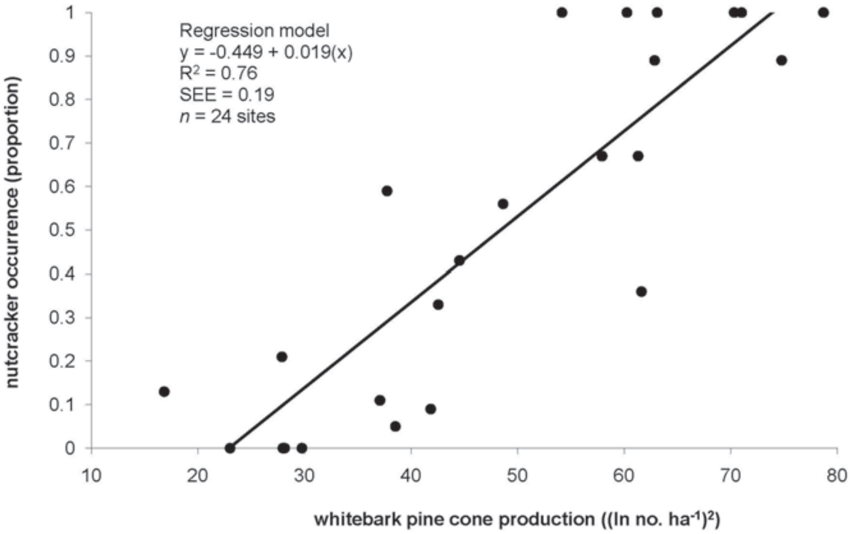

Figure 3–Simple linear regression analysis of the proportion of total observation hours (all years combined) with ≥ 1 Clark's nutcracker present as a function of mean, transformed whitebark pine cone production in Rocky Mountain forest sites, USA. SEE indicates the standard error of the estimate (proportion) (McKinney and others 2009).

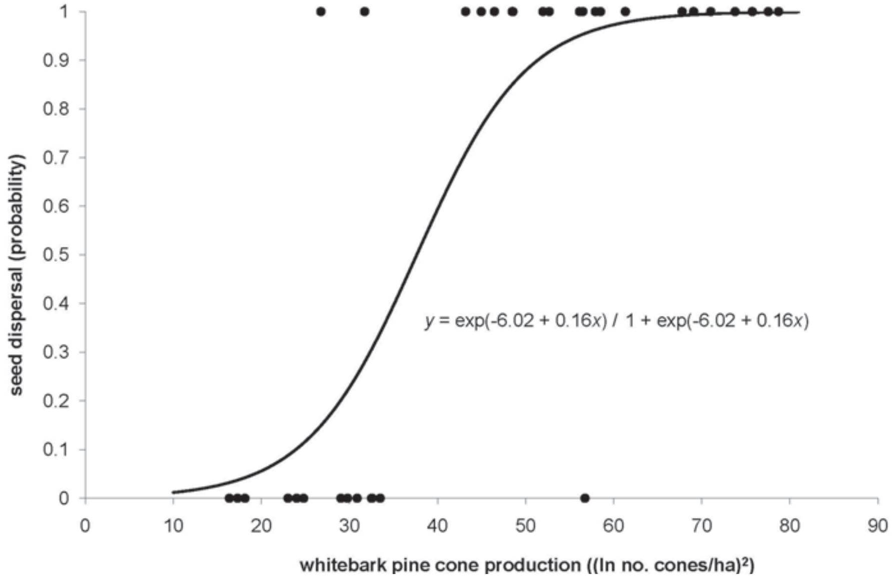

Figure 4–Binary logistic regression analysis of Clark's nutcracker seed dispersal (1 = dispersed, 0 = not dispersed) as a function of mean annual whitebark pine cone production in Rocky Mountain forest sites, USA (*n* = 34). The solid line represents the probability function derived from the prediction equation. A solid circle along the *y*-axis "1" indicates that a site had a seed-dispersal event recorded and a circle along the "0" line indicates that none was recorded (McKinney and others 2009).

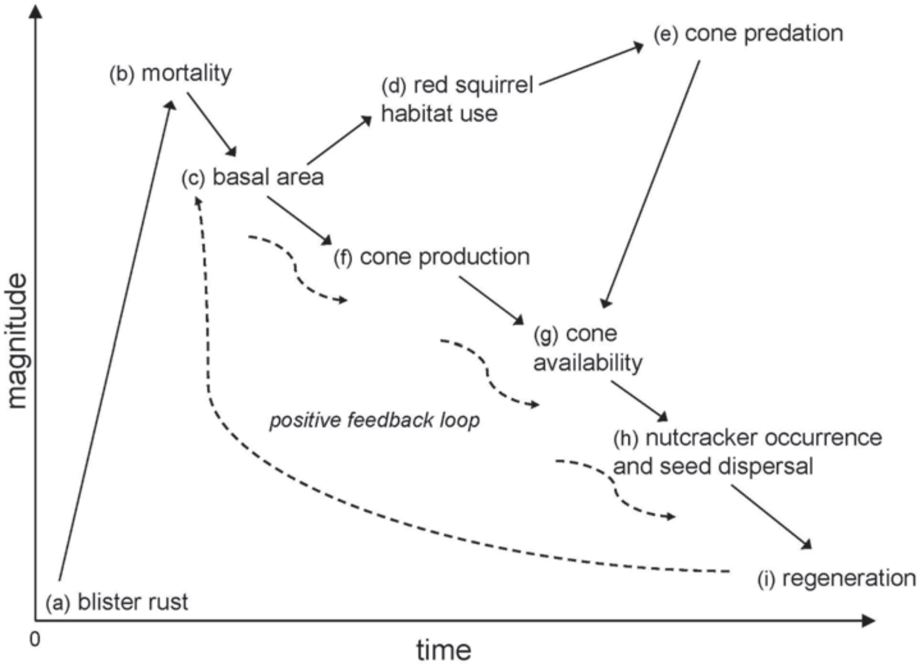

Figure 5–Analytically-based model depicting the series of processes between blister rust invasion of a whitebark pine forest and the creation of a positive feedback loop hastening the decline of whitebark pine within the forest. The arrow preceding a component represents the direction of influence of its associated component. For example, basal area (c) declines with increasing tree mortality (b). All components except (d) and (h) refer specifically to whitebark pine. For example, basal area (c) indicates resulting effects of whitebark pine basal area declining. Data are from 24 forest sites ranging in size from two to seven ha located in the central and northern Rocky Mountains, USA (2001-2006).

Management Implications

An analytically-based model is presented in Figure 5 that depicts the series of processes that occur following the arrival of blister rust within a whitebark pine stand. These processes erode community composition and function, culminating in the creation of a positive feedback cycle. It is difficult to identify exactly where in the cycle active management intervention is needed. Uncertainty is due to differing management goals and priorities between jurisdictions, and to the complexities inherent in the habitat and landscape context of the forest in question. We can, however, point to empirical data that may indicate a particular forest has entered this cycle. The seed dispersal model (Figure 4) can be used to estimate the level of cone production where seed dispersal can be expected. Decisions regarding an acceptable level of uncertainty need to be made first, however. For example, if we set a cutoff probability of seed dispersal to 0.70 (we want to be 70 percent sure some seeds will be dispersed), 94.7 percent (18/19) of all the dispersed sites were correctly classified by the model and predicted to have seed dispersal. Based on the logistic equation, a whitebark pine forest has a predicted seed dispersal probability ≥ 0.70 when average cone production ≥ 700 cones ha^{-1} ((ln cones $ha^{-1})^2$ ≥ 42.9: Figure 4).

We have shown that specific habitat conditions of a forest are crucial elements in predicting the number of cones available for nutcrackers, nutcracker seed dispersal probability, and thus, the potential to contribute genetic material to future generations through natural regeneration. We propose that altered interspecific interactions result in a positive feedback mechanism whereby increased whitebark pine mortality leads to higher rates of predispersal seed predation, fewer seed dispersal events, and reduced regeneration. Without management intervention, these trends portend accelerated decline and possible extinctions of some whitebark pine populations.

Acknowledgments

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Literature Cited

Bock, C. E.; L. W. Lepthien. 1976. Synchronous eruptions of boreal seed-eating birds. The American Naturalist. 110: 559-571.

Davis, J.; L. Williams. 1957. Irruption of the Clark Nutcracker in California. The Condor. 59: 297-307.

Davis, J.; L. Williams. 1964. The 1961 Irruption of the Clark's Nutcracker in California. The Wilson Bulletin 76: 10-18.

Fisher, J. T.; S. M. Bradbury. 2006. Understory protection harvest expedites recolonisation of boreal forest stands by North American red squirrels. Forest Ecology and Management. 234: 40-47.

Hoff, R. J.; S. K. Hagle; R. G. Krebill. 1994. Genetic consequences and research challenges of blister rust in whitebark pine forests. Pages 118-126 *in* W. C. Schmidt and F. K. Holtmeier, editors. Proceedings—International Workshop on Subalpine Stone Pines and Their Environment: the Status of Our Knowledge. General Technical Report INT-GTR-309. U.S. Department of Agriculture, Rocky Mountain Research Station, Ogden, UT, USA.

Hutchins, H. E.; R. M. Lanner. 1982. The central role of Clark's Nutcracker in the dispersal and establishment of whitebark pine. Oecologia. 55: 192-201.

Mattson, D. J.; D. P. Reinhart. 1997. Excavation of red squirrel middens by grizzly bears in the whitebark pine zone. Journal of Applied Ecology. 34: 926-940

McDonald, G. I.; R. J. Hoff. 2001. Blister rust: an introduced plague. Pages 193-220 *in* D. F. Tomback, S. F. Arno, and R. E. Keane, editors. Whitebark pine communities: ecology and restoration. Island Press, Washington, DC.

McKinney, S. T., and D. F. Tomback. 2007. The influence of white pine blister rust on seed dispersal in whitebark pine. Canadian Journal of Forest Research. 37: 1044-1057.

McKinney, S. T.; C. E. Fiedler; D. F. Tomback. 2009. Invasive pathogen threatens bird-pine mutualism: implications for sustaining a high-elevation ecosystem. Ecological Applications. 19: 597-607.

McKinney, S. T.; C. E. Fiedler. 2010. Tree squirrel habitat selection and predispersal seed predation in a declining subalpine conifer. Oecologia. 162: 697-707.

Reinhart, D. P.; D. J. Mattson. 1990. Red squirrels in the whitebark zone. In Schmidt, W.C.; McDonald, K.J., eds. Proceedings–Symposium on whitebark pine ecosystems: Ecology and management of a high-mountain resource. Gen. Tech. Rep. INT-270, U.S. Dept. Agric.

Smith, C. C. 1970. The coevolution of pine squirrels (*Tamiasciurus*) and conifers. Ecological Monographs. 40: 349-371.

Steele, M. A. 1998. *Tamiasciurus hudsonicus*. Mammalian Species. 586: 1-9.

Tomback, D. F. 1982. Dispersal of whitebark pine seeds by Clark's nutcracker: A mutualism hypothesis. Journal of Animal Ecology. 51: 451-467.

Vander Wall, S. B. 1988. Foraging of Clark's Nutcrackers on rapidly changing pine seed resources. The Condor. 90: 621-631.

Vander Wall, S. B.; S. W. Hoffman; W. K. Potts. 1981. Emigration behavior of Clark's Nutcracker. The Condor. 83: 162-170.

Determining Clark's Nutcracker Use of Whitebark Pine Communities in Regard to Stand Health in Waterton-Glacier International Peace Park

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Introduction

Whitebark pine (*Pinus albicaulis*), one of five stone pines worldwide, is found at treeline and subalpine elevations in the mountains of western North America (McCaughey and Schmidt 2001). Considered a keystone species, it helps maintain subalpine biodiversity, protects watersheds and promotes post-fire regeneration (Tomback and others 2001).

The Clark's nutcracker (*Nucifraga columbiana*) and whitebark pine are co-evolved mutualists (Tomback 1982). Nutcrackers remove seeds from whitebark pine cones and cache them in high- and low-elevation forests and terrain, returning to feed on the seeds for up to a year. Nutcrackers are the principal mode of seed dispersal for whitebark pine, and unretrieved seeds are the primary source for regeneration (Hutchins and Lanner 1982; Tomback 1982, 2001).

White pine blister rust, caused by the exotic fungus *Cronartium ribicola,* has damaged whitebark pine communities throughout most of their range. Whitebark pine has been hit especially hard in the Crown of the Continent Ecosystem, an area of approximately 41,439 square kilometers, where Alberta, British Columbia, and Montana meet. This ecosystem includes Waterton-Glacier International Peace Park, and the Bob Marshall Wilderness Complex in Montana (Thompson 2009). Blister rust was found in Glacier National Park in 1938 (Mielke 1943). Today, approximately 50 percent of the whitebark pine in Waterton-Glacier International Peace Park are dead, with 70 percent infected. There is an estimated 5 percent per year increase in mortality in Waterton Lakes National Park (Smith and others 2008).

By killing the upper canopy—the cone producing branches of whitebark pine—blister rust reduces or ends cone production (McDonald and Hoff 2001). Previously, McKinney and Tomback (2007) found, in their study in the Bitterroot and Salmon national forests, that whitebark pine stands with higher levels of blister rust infection and damage had lower cone densities than those stands with lower levels of blister rust infection and damage. They also found that stands with lower cone densities had a lower proportion of cones surviving to time of seed dispersal, and thus stands with a lower proportion of cones surviving were less likely to have seeds dispersed by nutcrackers. McKinney and Tomback (2007) and McKinney and others (2009) suggest that loss of whitebark pine cone production due to tree damage and mortality caused by blister rust and mountain pine beetle (*Dendroctonus ponderosae*) will likely lead to a decline in nutcracker visits over time, and thus a reduction in future whitebark pine regeneration. With continued losses of whitebark pine, it is likely that nutcrackers will no longer be attracted to whitebark pine communities and thus the potential for regeneration will be lost (Tomback and others 2001).

There is concern over potentially declining numbers of nutcrackers in the Crown of the Continent Ecosystem. Given the extent of blister rust infection, canopy kill, and tree mortality, it is unknown whether nutcrackers will appear and harvest seeds during years of cone production. Nutcracker numbers, distribution, and use of their habitat within the Crown of the Continent Ecosystem require further study.

Objectives

Our objectives in this study are to determine: 1) health status and cone production in whitebark pine, 2) the density of nutcrackers in whitebark pine communities in selected study areas when seeds are available, and 3) whether the nutcrackers are harvesting and potentially storing seeds from the remaining productive whitebark pine within the park.

Methods

In July 2009, we selected four whitebark pine study areas in Glacier National Park: Numa Ridge, Preston Park, White Calf Mountain, and Two Medicine. One study area was selected in Waterton Lakes National Park: Summit Lake. Within each study area we set up one to three transects ranging from 0.5 to 1.0 km in length for the purpose of using transect distance sampling to determine nutcracker densities. For each transect, we established two 10 x 50 m plots to determine whitebark pine health status and cone production. Stand health was assessed once, in July 2009. We visited each transect three times between 28 July and 16 September, 2009, to conduct nutcracker surveys, and to count cones.

Results

Thirty-five nutcrackers were observed over the 2009 field season, with the majority observed at Numa Ridge

In: Keane, Robert E.; Tomback, Diana F.; Murray, Michael P.; and Smith, Cyndi M., eds. 2011. **The future of high-elevation, five-needle white pines in Western North America: Proceedings of the High Five Symposium.** 28-30 June 2010; Missoula, MT. Proceedings RMRS-P-63. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station. 376 p. Online at http://www.fs.fed.us/rm/pubs/rmrs_p063.html

and Summit Lake. We found a blister rust infection level of 72 percent to 97 percent across study areas, with no sign of recent pine beetle infestation. Seventy-seven of 170 whitebark pine trees evaluated (45 percent) were dead from previous mountain pine beetle infestations. Only two out of 93 live trees within our 20 health plots were cone-bearing, producing a total of 11 cones. There seemed to be a greater number of nutcrackers in areas with a greater number of living whitebark pine, although nutcrackers and numbers of cones did not appear to be correlated. However, sample sizes for 2009 cone data are too small to be statistically analyzed at this time. Canopy kill was greatest at Numa Ridge and Preston Park, where about half the trees evaluated had canopy kill greater than 50 percent.

Discussion

The results reported here for the 2009 field season must be considered preliminary. Nutcrackers were sighted more often in whitebark pine stands which had a higher number of live trees. However, this generalization did not apply to Preston Park, where no nutcrackers were observed during surveys, despite an extensive stand of mature whitebark pine. In addition, the preliminary data suggest little relationship between numbers of cones and nutcrackers. Tree damage from a high rate of blister rust infection has led to low cone production, which in turn may reduce the number of nutcrackers that forage in these areas. One sampling issue with the 2009 data was that nutcrackers were observed over long transects but cone counts were restricted to two health plots; data were not entirely comparable. We altered our methodology for the 2010 field season in the following ways to collect more data: 1) nutcracker surveys were increased to seven per transect over the summer, with two counts per survey per day, one in the morning and one in the afternoon, and 2) we surveyed for cones using the same distance sampling method in order to better evaluate cone production surrounding our transects. Results for the 2010 field season are pending.

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Literature Cited

Hutchins, Harry E.; Lanner, Ronald M. 1982. The central role of Clark's nutcracker in the dispersal and establishment of whitebark pine. Oecologia. 55: 192-201.

McCaughey, Ward W.; Schmidt, Wyman C. 2001. Taxonomy, distribution and history. In: Tomback, D. F.; Arno, S. F.; Keane, R. E., eds. Whitebark pine communities: ecology and restoration. Island Press.Washington, DC: Island Press, 29-34.

McDonald, Geral I.; Hoff, Raymond J. 2001. Blister rust: an introduced plague. In: Tomback, D. F.; Arno, S. F.; Keane, R. E., eds. Whitebark pine communities: ecology and restoration. Island Press.Washington, DC: Island Press, 193-220.

McKinney, Shawn T.; Tomback Diana F. 2007. The influence of white pine blister rust on seed dispersal in whitebark pine. Canadian Journal of Forest Research. 37: 1044-1057.

McKinney, Shawn T.; Fiedler, Carl E.; Tomback, Diana F. 2009. Invasive pathogen threatens bird-pine mutualism: implications for sustaining a high-elevation ecosystem. Ecological Applications. 19: 597-607.

Mielke, J. L. 1943. White pine blister rust in western North America. Yale University, School of Forestry. 5: 155.

Smith, Cyndi M.; Wilson, Brendan; Rasheed, Sal; Walker, Robert C.; Carolin, Tara; Shepherd, Brenda. 2008. Whitebark pine and white pine blister rust in the Rocky Mountains of Canada and northern Montana. Canadian Journal of Forest Research. 38: 982-995.

Thompson, Steve. (2009, 3 May—last update). *About the Crown of the Continent.* Homepage of National Parks Conservation Association. [Online]. Available: http://www.crownofthecontinent.net/about_crown_of_continent.php. [20 November 2009].

Tomback, Diana F. 1982. Dispersal of whitebark pine seeds by Clark's nutcracker: a mutualism hypothesis. Journal of Animal Ecology. 51: 451-467.

Tomback, Diana F. 2001. Clark's nutcracker: agent of regeneration. In: Tomback, D. F.; Arno, S. F.; Keane, R. E., eds. Whitebark pine communities: ecology and restoration. Island Press.Washington, DC: Island Press, 89-104.

Tomback, Diana F.; Arno, Steve F.; Keane, Robert E. 2001. The Compelling Case for Management Intervention. In: Tomback, D. F.; Arno, S. F.; Keane, R. E., eds. Whitebark pine communities: ecology and restoration. Island Press.Washington, DC: Island Press, 3-11.

Limber Pine Health in the Canadian Rockies

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Limber pine (*Pinus flexilis*) reaches the northern limit of its range at about 52 degrees latitude in Alberta (AB) and 51 degrees latitude in British Columbia (BC). Most populations are found on the eastern slopes of the Rocky Mountains, with a few disjunct populations west of the Continental Divide in southeastern BC. Limber pine commonly grows in montane and lower subalpine regions on xeric to sub-xeric, exposed and wind-swept sites (ASRD & ACA 2007).

Limber pine plays an important role in the harsh environments in which it lives, providing ecological services including retention and slow release of moisture, shade for other species (Baumeister and Callaway 2006), and large seeds that serve as a high energy food source for many animals, such as Clark's nutcracker (*Nucifraga columbiana*) (Benkman and others 1984) and black bear (*Ursus americana*) (McCutchen 1996). Limber pine populations in Canada are threatened by a combination of white pine blister rust (WPBR; *Cronartium ribicola*), mountain pine beetle (*Dendroctonus ponderosae*), drought and fire suppression (Achuff 1997, Kendall and others 1996, ASRD & ACA 2007). As a consequence, limber pine was listed as Endangered under *The Wildlife Act* in Alberta in 2008 (Government of Alberta 2010).

WPBR was first identified on limber pine in Canada in 1952 in southwestern Alberta, and within a decade had caused heavy infection (average 79-100 percent) and mortality (29-83 percent) in an unspecified number of sample plots in three general areas (Gautreau 1963). In 1996, Kendall and others (1996) reported average infection levels of 84 percent and 52 percent, and average mortality from all causes of 40 percent and 15 percent, in Waterton Lakes National Park (WLNP) and Whaleback, respectively (Table 1).

In this study, our objective was to quantify the incidence of WPBR and mortality of limber pine in the Canadian Rockies, and compare these to previous studies.

In 2003 and 2004, we re-established 12 plots that Kendall had measured in 1996, and established 73 new plots; 83 of these plots are in AB and two are in BC (Figure 1). In 2009, we re-measured all 85 plots. Methods for establishing plots and assessing health were adapted from those recommended by Tomback and others (2005) for whitebark pine. All trees on public land plots were marked with numbered aluminum tags, while most on private land were not. Although Kendall's original plots were not permanently marked nor were the trees tagged, we were able to resample within the original stands by using geographical coordinates, plot photographs and azimuths (Kendall 2003). Plot size averaged 683 m^2 (range 125-3000 m^2). Tomback and others (2005) recommend a fixed transect length of 50 m, but these surveys were started in 2003, using a draft of the methodology which recommended a minimum number of live and dead trees rather than a fixed length, which resulted in large plot sizes where mortality was very high.

Table 1. Incidence of white pine blister rust and limber pine mortality in the Canadian Rockies.

Zone and location	Year	No. of plots	Mean mortality % (range) [a]	Mean infection % (range)
Northern				
Bow Valley to Kootenay Plains	2003-04	28	12 (0-67)	2 (0-27)
Bow Valley to Kootenay Plains	2009	28	13 (0-62)	11 (0-85)
Central				
Hwy 3 to Bow Valley	2003-04	34	32 (0-60)	54 (0-96)
Hwy 3 to Bow Valley	2009	34	37 (0-80)	59 (2-97)
Whaleback	1996[b]	4	15 (5-24)	52 (43-60)
Whaleback	2003-04	4	43 (37-50)	40 (18-69)
Whaleback	2009	4	32 (28-38)	64 (43-79)
Southern				
Hwy 3 to WLNP	2003-04	23	45 (24-87)	55 (20-79)
Hwy 3 to WLNP	2009	23	52 (24-69)	77 (26-100)
WLNP	1996[b]	8	40 (22-57)	84 (65-96)
WLNP	2003-04	8	56 (39-87)	61 (44-79)
WLNP	2009	8	52 (24-66)	67 (26-93)

[a] Includes mortality from all causes.

[b] Kendall et al. 1996 and Kendall, unpublished data.

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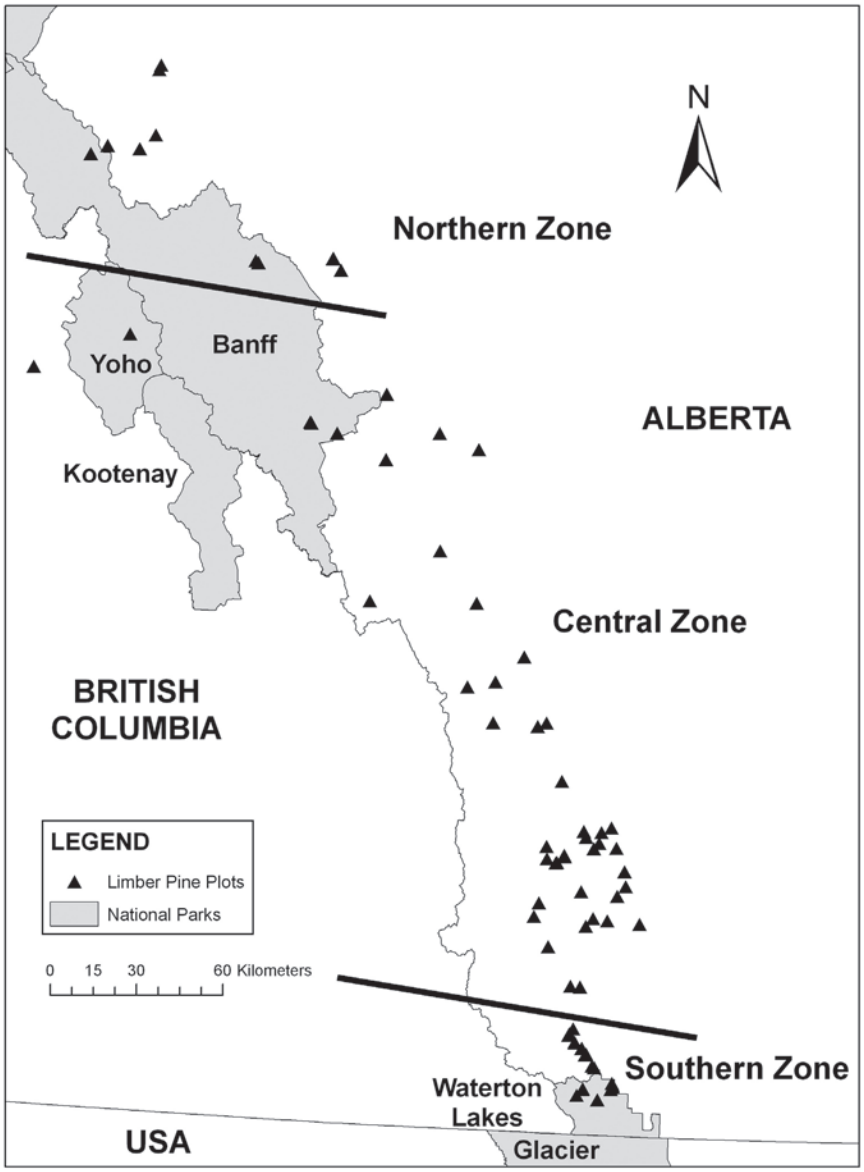

Figure 1. Study area showing three zones in the Canadian Rockies range of limber pine.

Incidence of infection by blister rust was reported as proportion of live trees (tree growth form > 1.3 m tall and krummholz growth form of reproductive age) that were infected at the time of each survey. Mortality was from all causes and reported as proportion of dead standing trees at the time of each survey. Some dead trees may be decades old, while others were recently dead (still had red needles).

We assessed 4,676 trees and 623 seedlings (< 1.3 m, separated from krummholz) in 2003-04 and 4,566 trees and 900 seedlings in 2009. The decrease in number of trees assessed is an artifact of standardising the size of many plots in 2009.

Over all 85 plots, WPBR infection increased from 33 percent in 2003-04 to 43 percent in 2009, while mortality increased from 32 percent to 35 percent. Infection and mortality is highest in southern Alberta and decreases near the northern limit of its range, but is present in all areas. Infection of seedlings (two size classes) was low, at 7 percent in 2003-04 and 4 percent in 2009, mostly in the 50-130 cm height class. This decrease in infection in seedlings may account for the 30 percent increase in number of seedlings between the two time periods. Infected seedlings are known to have high mortality in other five-needled pines, such as whitebark pine (Hoff and Hagle 1990).

In the 12 plots that were established by Kendall and others (1996), WPBR infection varied from an average of 73 percent, 46 percent and 66 percent in 1996, 2003-04 and 2009, respectively, while mortality increased from 30 percent to 50 percent between 1996 and 2003-04, then dropped to 46 percent in 2009 (Table 1). Differences in infection levels between years might be due to 1) different trees being measured between the first two time periods, as Kendall's plots were not re-located exactly, but were within the same stand, 2) difficulty of field teams in identifying WPBR cankers due to limber pine's naturally rough bark, and the destruction of old cankers by wind, 3) incidence dropping after the most susceptible individuals die, and/or 4) a true change in infection levels. The apparent drop in mortality in 2009 is most likely a function of standardising plot sizes.

While WPBR infection levels may have stabilized during the last decade, the high levels in the very southwestern corner of Alberta will lead to additional mortality of limber pine. It is conceivable that there may be local extirpations of limber pine in the most heavily impacted areas, which could affect wildlife habitat, the distribution of forested land, the rate and possible fate of forest succession, and reforestation dynamics after fire (Schoettle 2004).

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Literature Cited

Achuff, Peter L. 1997. Special plant and landscape features of Waterton Lakes National Park, Alberta. Unpublished Technical Report. Waterton Park, AB: Parks Canada, Waterton Lakes National Park. 51 p.

ASRD & ACA (Alberta Sustainable Resource Development and Alberta Conservation Association). 2007. Status of the limber pine (*Pinus flexilis*) in Alberta. Wildlife Status Report No. 62. Edmonton, AB: Alberta Sustainable Resource Development. 17 p.

Baumeister, D.; Callaway, R.M. 2006. Facilitation by *Pinus flexilis* during succession: a hierarchy of mechanisms benefits other plant species. Ecology. 87: 1816-1830.

Benkman, C.W.; Balda, R.P.; Smith, C.C. 1984. Adaptations for seed dispersal and the compromises due to seed predation in limber pine. Ecology. 65: 632-642.

Gautreau, E. 1963. Effects of white pine blister rust in limber pine stands of Alberta. 1963. Canada Department of Forestry: Forest Entomology and Pathology Branch. Ottawa, ON. Bi-monthly Progress Report. 19(4): 3.

Government of Alberta. 2010. Species assessed by Alberta's Endangered Species Conservation Committee: short list. [Online]. Available: http://www.srd.alberta.ca/BioDiversityStewardship/SpeciesAtRisk/SpeciesSummaries/SpeciesAtRiskFactSheets.aspx [July 30, 2010].

Hoff, R.J.; Hagle, S. 1990. Diseases of whitebark pine with special emphasis on white pine blister rust. Pp 179-190 *in* Proceedings of a symposium on whitebark pine ecosystems: ecology and management of a high-mountain resource. INT-GTR-270. Fort Collins, CO; USDA Forest Service, Rocky Mountain Research Station.

Kendall, Katherine C. 2003. Whitebark pine study master database. West Glacier, MT: U.S. Geological Survey, Northern Rocky Mountain Science Center.

Kendall, Katherine C.; Ayers, Dayna; Schirokauer, David. 1996. Limber pine status from Alberta to Wyoming. Nutcracker Notes. 7:16-18.

McCutchen, H.E. 1996. Limber pine and bears. Great Basin Naturalist. 56(1): 90-92.

Schoettle, Anna W. 2004. Ecological roles of five-needle pines in Colorado: potential consequences of their loss. Pp 124-135 *in* Breeding and genetic resources of five-needle pines: growth, adaptability, and pest resistance. Proceedings RMRS-P-32. Fort Collins, CO: USDA Forest Service, Rocky Mountain Research Station.

Tomback, Diana F.; Keane, Robert E.; McCaughey, Ward W.; Smith, Cyndi M. 2005. Methods for surveying and monitoring whitebark pine for blister rust infection and damage. Missoula, MT: Whitebark Pine Ecosystem Foundation.

Regeneration and Survival of Whitebark Pine After the 1988 Yellowstone Fires

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Introduction

Successional whitebark pine (*Pinus albicaulis*) communities are dependent on fire and other disturbances for renewal (Arno 2001). Where whitebark pine regenerates results from cache site selection by Clark's nutcrackers (*Nucifraga columbiana*) in relation to the environmental tolerances of seeds and seedlings (Tomback 2001). After the 1988 Yellowstone fires, we studied the development of upper subalpine forest communities with particular focus on the regeneration of whitebark pine in two study areas—Mt. Washburn in Yellowstone National Park, and Henderson Mtn. in Gallatin National Forest. Fire history and patterns of community regeneration of the predominantly seral lodgepole pine forests in the southcentral and southwestern regions of Yellowstone National Park have been well studied (e.g., Romme 1982; Turner and others 1997), whereas whitebark pine communities have been less studied.

We examined the following hypotheses: (1) the density of whitebark pine regeneration surpasses the density of the late successional pre-fire canopy forest by 13 years post-fire; (2) growth rates for whitebark pine regeneration are reduced under closed canopies in mid to late-seral forests; and, (3) seedling survival is better correlated with some micro-site attributes than others.

Study Areas and Methods

Both study areas included xeric and mesic study sites with stand-replacing burns, and ranged in elevation from 2560 to 2745 m (for details, see Tomback and others 2001). On Henderson Mtn., we also included unburned study sites and, on Mt. Washburn, a mesic site with mixed severity burn (Table 1). Data were collected at both sites from 1990 to 1995, in every year but 1993, and in 2001 (i.e., up to 13 years post-fire), and also on Henderson Mtn. in 2004 and 2005. A whitebark pine regeneration micro-site was defined as either supporting a solitary seedling or a seedling cluster.

To evaluate study hypotheses, we reconstructed the pre-fire forest from intact tree skeletons on 30 x 30 m quadrats, tracked individual post-fire whitebark pine seedlings on a total of 275 permanent plots, each 20 m^2 in area, and gathered data on seedling micro-sites throughout the study. Data comparing seedling growth rates under open vs. closed canopy conditions were based on comparisons of seedling height growth from regeneration on the Henderson Mtn. burned and unburned study sites. Information on whitebark pine regeneration micro-sites came from a combination of description at the initial time seedlings were surveyed and also from information in subsequent years. The position of seedlings in relation to objects, such as rocks and standing trees, and plot aspect, were used to estimate whether shade was present in the morning or afternoon.

Stepwise Poisson Log-linear Regression Analyses were performed to determine the best models predicting whitebark pine occurrence among the study sites, with the response variable comprising the number of whitebark pine regeneration sites per plot. Altogether, 25 different models were examined. Multivariate Logistic Regression and Proportional Hazards Models were used to identify micro-site variables facilitating seedling survival. All statistical analyses were performed using SAS (SAS Institute Inc., 2004). For the Proportional Hazards Model, the known or estimated year of death for each seedling regeneration site was related to the micro-site variables retained in the Multivariate Logistic Regression Model.

Results

The pre-fire forest on Mt. Washburn was dominated by Engelmann spruce (*Picea engelmannii*) and lodgepole pine (*Pinus contorta*), and the pre-fire forest on Henderson Mtn. by subalpine fir (*Abies lasiocarpa*), with whitebark pine a minor pre-fire overstory component in both areas. The density of whitebark pine in the pre-fire forest ranged from 0 stems/m^2 on the Henderson Mtn. mesic, burned study site to

Table 1. Study sites, ecological conditions, and numbers of plots. Each plot is circular and 20 m^2 in area.

Study site conditions	Number of plots
Henderson Mountain, Gallatin National Forest: 2680-2745 m elevation	
Xeric burned	50
Mesic burned	50
Xeric unburned	25
Mesic unburned	25
Mt. Washburn, Yellowstone National Park: 2560-2745 m elevation	
Xeric burned	50
Mesic burned	50
Mesic mixed severity burn	25

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Table 2. Density (stems/m^2) of whitebark pine in the pre-fire forest and density (regeneration sites/m^2) of post-fire regeneration as of 2001, 13 years after the 1988 Yellowstone fires.

Study area	Pre-fire density	Post-fire density
Henderson Mountain		**Mean (S.D.)**
Xeric burned	0.002	0.039 (0.150)
Mesic burned	0	0.020 (0.038)
Xeric unburned	0.009	0.038 (0.044)
Mesic unburned	0.002	0.022 (0.043)
Mt. Washburn		
Xeric burned	0.016	0.026 (0.049)
Mesic burned	0.0005	0.092 (0.110)
Mesic mixed severity burn	0.0055	0.044 (0.055)

0.016 stems/m^2 on the Mt. Washburn xeric, burned study site (Table 2). Whitebark pine cotyledon seedlings first appeared in all burned study sites in 1991, three years after fire. Combining all seedlings across study sites to generate cumulative numbers over time, there was an exponential increase in seedlings from 1989 to 10 years post-fire, followed by some fluctuation in numbers, possibly drought-related. By 1995, the highest whitebark pine regeneration density was on the Mt. Washburn mesic, burned study site that had experienced stand-replacing fire. By 2001, whitebark pine regeneration density was the lowest on the Henderson Mtn. mesic, burned study site (0.020 regeneration sites/m^2) and the highest on the Mt. Washburn mesic, burned study site (0.092 sites/m^2). This latter result sharply contrasts with the very low density of whitebark pine in the pre-fire overstory in the mesic, burned study site. The best Stepwise Poisson Regression model predicting whitebark pine distribution was the additive combination of variables: Study area, Burn (unburned, burned, mixed severity burn), and Moisture level (xeric, mesic). Whitebark pine seedling growth rates in the Henderson Mtn. study sites ranged from 0.62 to 2.19 cm/year. The highest whitebark pine seedling growth rates occurred on the two burned Henderson Mtn. study sites.

From the Logistic Regression Model and Proportional Hazards Model, statistically significant positive predictors of seedling survival on Henderson Mtn. included presence of undergrowth vegetation, wood debris, and standing dead trees, whereas survival was reduced by grazing on seedlings. Using these variables to test the performance of the model, 67% of the seedlings were correctly classified as alive or dead. For Mt. Washburn, significant predictors of seedling survival included presence of wood debris, standing dead trees, gopher soil disturbance, and shade; and, survival was reduced by deeper char depth and the presence of duff. In this analysis, 83% of the seedlings were correctly classified as alive or dead. Differences in predictors between the two study areas probably related to different environmental characteristics. For example, Henderson Mtn. is south-facing, and undergrowth vegetation may provide consistent shade and retain moisture. Char depth was much lower on Henderson Mtn., which may explain its lack of significance for that study area.

Discussion

We address each hypothesis, with the following results:

(1) Whitebark pine regeneration density increased throughout the study, without indication of plateau; by 2001, whitebark pine regeneration densities greatly exceeded those of the pre-fire canopy. These results are in sharp contrast with the pattern of lodgepole pine regeneration after the Yellowstone fires (Turner and others 1997). The numbers of new lodgepole pine seedlings declined from 1990 to 1993, and lodgepole pine regeneration density (seedlings/m^2) declined after it peaked in 1992. The seedling recruitment primarily came from 1989 and 1990 cohorts.

(2) Thirteen years after fire, whitebark pine regeneration densities were similar between the burned and unburned study sites on Henderson Mountain, but seedling growth increments as of 2005 were 2.6 times greater in the burned treatments, indicating seedling suppression in the unburned closed canopy study sites. Thus, fire or other disturbances, which provide canopy openings, appear required for healthy whitebark pine growth in mid to late successional communities.

(3) The presence of wood debris and standing dead trees predicted seedling survival for both study areas. For Henderson Mtn. other predictors of survival included presence of undergrowth vegetation. For Mt. Washburn, seedling survival was also favored by shade and gopher soil disturbance.

This unique 15 year dataset of repeat observations on post-fire regeneration of whitebark pine provides information on the timeframe and dynamics of seedling establishment and on micro-site correlates of seedling survival, which may be used for restoration planning and the refinement of planting protocols.

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References

Arno, Stephen F. 2001. Community types and natural disturbance processes. In: Tomback, Diana F.; Arno, Stephen F.; Keane, Robert E., eds. Whitebark pine communities: ecology and restoration. Washington, DC: Island Press: 74-88.

Romme, William H. 1982. Fires and landscape diversity in subalpine forests of Yellowstone National Park. Ecological Monographs. 52(2): 199-221.

Tomback, Diana F. 2001. Clark's nutcracker: agent of regeneration. In: Tomback, D. F.; Arno, S. F.; Keane, R. E., eds. Whitebark pine communities: ecology and restoration. Washington, DC: Island Press: 89-104.

Tomback, Diana F.; Anderies, Angela J.; Carsey, Katherine S.; Powell, Mary L.; Mellmann-Brown, Sabine. 2001. Delayed seed germination in whitebark pine and regeneration patterns following the Yellowstone fires. Ecology. 82(9): 2587-2600.

Turner, Monica G.; Romme, William H.; Gardner, Robert H.; Hargrove, William W. 1997. Effects of fire size and pattern on early succession in Yellowstone National Park. Ecological Monographs. 67(4): 411-433.

Seed Dispersal in Limber and Southwestern White Pine: Comparing Core and Peripheral Populations

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Introduction

According to the geographic mosaic theory of coevolution (Thompson 2005), the potential for coevolutionary relationships between interacting species varies with the presence of other species within a community. This implies that the strength of coevolution between two species may vary geographically. In this study, we ask whether there is a shift in vertebrate seed dispersers between core range and peripheral populations in two related five-needle white pines, limber (*Pinus flexilis*) and southwestern white (*P. strobiformis*). In the Rocky Mountains, limber pine ranges from southern British Columbia and Alberta south to New Mexico. Southwestern white pine ranges through the higher mountains of northern Mexico north to southern Colorado and Utah, and northern Arizona. The pines overlap in southern Colorado, southern Utah, northern New Mexico, and northern Arizona (Fig. 2a in Tomback and Achuff 2010).

The seeds of both limber and southwestern white pine are essentially wingless, lacking all or most of the thin, woody seed wing that enables dispersal by wind for species in Family Pinaceae. The seeds are also moderately large to large: the average masses of limber and southwestern white pine seeds are 0.093 mg and 0.168 mg, respectively (Tomback and Linhart 1990). The syndrome of large, wingless seeds typically corresponds to seed dissemination by vertebrates—either birds of the family Corvidae or rodents (Tomback and Achuff 2010).

Limber Pine in a Peripheral Population

Throughout the core range of limber pine, Clark's nutcracker (*Nucifraga columbiana*) is the primary seed disperser, influencing growth form and population structure (Lanner and Vander Wall 1980; Schuster and others 1989; Carsey and Tomback 1994). On the eastern plains in northern Colorado and southern Wyoming, limber pine forms isolated, peripheral populations on rocky escarpments, 100 km east of the core Rocky Mountain populations. We (DFT, AWS) studied limber pine seed dispersal at Dave's Draw, Pawnee National Grasslands, Colorado, between 1600 and 1690 m elevation (Tomback and others 2005). Nutcrackers are rare visitors to this region, and none were observed by researchers over several years. Previous studies indicated that the limber pine population at Dave's Draw is highly genetically substructured, unlike limber pine within core populations, suggesting differences in seed dispersal distances despite long-distance pollen flow (Schuster and Mitton 2000). We hypothesized that seed-caching rodents were the primary seed dispersers at Dave's Draw. Chipmunks and squirrels, however, are absent in this region, so nocturnal rodents were the candidate dispersers.

Methods

Research methods included fluorescent pigment tracking of seed dispersers for 6 nights to determine dispersal distances, cache type, and cache location. This entailed setting out 1 to 4 seed stations each night, each station comprising a glass dish containing limber pine seeds on a sandpaper tray. Both the seeds and sandpaper were covered with a different fluorescent pigment color at each seed station, and seed stations were placed under limber pine canopies, 30 to 40 m apart. Each night beginning at 03:00, we used a powerful UV light to follow the fluorescent tracks created by small mammals after they had removed seeds from seed stations, dispersed, and cached them. Small mammal trapping was also conducted for 3 nights, using 106 Sherman traps in two traplines to determine the identity of potential seed cachers. Furthermore, we constructed an experiment using replicated simulated seed caches based on observed rodent cache types in order to test for seed germination. We had observed rodents store two-seed caches on substrate surfaces, and bury larger numbers of seeds under plants and soil. Each replicate of simulated seed caches consisted of 5 five-seed caches buried under plants and 5 two-seed caches placed on the soil surface, for a total of 5 replicates; and three additional replicates of 5 two-seed caches placed on duff and protected by hardware cloth. Simulated caches were examined for germination during the following summer.

Results

The results are summarized from Tomback and others (2005). Using fluorescent pigment tracking, we found a total of 36 seed caches: 20 buried, with a mean of 4.4 seeds per cache, dispersed a mean of 8.2 m from a seed station; and 16 surface caches, with a mean of 1.6 seeds, dispersed a mean of 5.5 m from a seed station. We left caches in place and revisited them over several weeks. Our traplines caught 73 animals consisting mostly of deer mice, but also western

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harvest mice (which do not store seeds), and Ord's kangaroo rats. Simulated caches buried under plants and soil had higher germination success than caches on the soil or litter surface.

Conclusions

These results indicated that nocturnal rodents, especially deer mice and kangaroo rats, may be the major dispersers of limber pine seeds in the Dave's Draw population, and potentially in other peripheral populations (Tomback and others 2005). Repeated visits to natural caches revealed that not all seeds were removed over time, and thus seeds could potentially germinate. Rodents moved seeds relatively short distances from seed stations to cache sites, thus potentially creating much greater population substructure than observed for core populations.

Southwestern White Pine in Core and Peripheral Populations

We (DFT, SS, EP) studied southwestern white pine seed dispersal within a peripheral population, the San Juan Mountains, Colorado, and within a core population, the Chiricahua Mountains, Arizona (Samano and Tomback 2003; Pruett 2007; Tomback and Samano, unpublished data). The latter population is part of the "sky island" forests of southwest desert ranges, which are typical habitat of southwestern white pine. We asked whether there were differences in seed dispersers or seed predators between the two populations. We also looked for differences in cones and seeds that might correspond to differences in seed dispersers and seed predators.

Methods

In both study areas during September, we monitored cone opening phenology and quantified differences in cone orientation on tree branches. We identified potential diurnal seed dispersers and seed predators by observing diurnal birds and mammals foraging for seeds; we used fluorescent pigment tracking in both study areas during good cone years to determine if nocturnal rodents were dispersing seeds, and if so, how far seeds were dispersed and where they were cached. In the Chiricahua Mountains, we set up two traplines consisting of 100 Sherman traps for three nights in order to identify potential nocturnal seed cachers.

Results

Cone opening among southwestern white pine in the San Juan Mountains occurred from late August through late September, and in the Chiricahua Mountains from early September through early October (Samano and Tomback 2003; Pruett 2007). Cone opening in both areas was asynchronous both within and among trees, a trait associated with seed dispersal by vertebrates. In the San Juan Mountains in September, we routinely observed nutcrackers disperse southwestern white pine seeds, but never observed nutcrackers in the Chiricahuas: their dependable range ended farther north. Nocturnal rodents were not attracted to our seed stations in the San Juan Mountains, but we documented rodents making 28 caches over 6 nights of fluorescent pigment tracking in the Chiricahua Mountains (Pruett 2007). The 11 buried caches contained a mean of 2.5 seeds per cache and were on average 8.7 m from a seed station; and, the 17 surface caches contained a mean of 1.7 seeds and were on average 7.2 m from a seed station. Only deer mice were trapped in the Chiricahua Mountains. The red squirrels in the San Juan Mountains were highly efficient seed predators that cut down cones for winter stores; the Chiricahua fox squirrels were less efficient at pine seed removal and did not store cones (Samano and Tomback 2003; Tomback and Samano, unpublished data).

Southwestern white pine differed morphologically between the two study areas: the cones on southwestern white pine in the San Juan Mountains were most frequently horizontally-directed, whereas the cones in the Chiricahua Mountains were most frequently pendulous, a morphology avoided by nutcrackers in the San Juan Mountains (Samano and Tomback 2003; Pruett 2007). Seed dimensions (length, width, and depth) and mass from the Chiricahua Mountains were significantly greater than those of seeds from the San Juan Mountains. In fact, seed dimensions taken from the Santa Catalina and Huachuca Mountains, neighboring ranges to the Chiricahua Mountains, had similarly larger seed dimensions (Tomback and Samano, unpublished data).

Conclusions

Primary seed dispersers differed between core and peripheral populations of southwestern white pine, with Clark's nutcrackers dispersing seeds in the San Juan Mountains, and nocturnal rodents dispersing seeds in the Chiricahua Mountains. Seed predators, cone orientation, and seed morphology also differed between these populations. The predominantly horizontal cone orientation in the San Juan Mountains was also the orientation preferred by Clark's nutcrackers.

Questions raised by our results: Are the morphological differences between southwestern white pine in the San Juan Mountains (peripheral population) compared to the Chiricahua Mountains (core range) the result of selection by nutcrackers or by red squirrels, or both? Or, alternatively, could morphological differences result from gene flow from limber pine to southwestern white pine in the San Juan Mountains (an area of overlap), reducing seed size and altering cone orientation? Are nocturnal rodents the primary seed dispersers for southwestern white pine throughout its core range?

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References

Carsey, Katherine, S.; Tomback, Diana F. 1994. Growth form distribution and genetic relationships in tree clusters of *Pinus flexilis*, a bird-dispersed pine. Oecologia. 98: 402-411.

Lanner, Ronald M.; Vander Wall, Stephen B. 1980. Dispersal of limber pine seed by Clark's Nutcracker. Journal of Forestry. 78 (October): 637-639.

Pruett, Elizabeth L. 2007. The role of nocturnal rodents in dispersal of southwestern white pine seeds. M.S. Thesis, Department of Biology, University of Colorado Denver, Denver, CO.

Samano, Sheridan: Tomback, Diana F. 2003. Cone opening phenology, seed dispersal, and seed predation in southwestern white pine (*Pinus strobiformis*) in southern Colorado. Écoscience. 10, 319-326.

Schuster, William S.; Alles, David L.; Mitton, Jeffry B. 1989. Gene flow in limber pine: evidence from pollination phenology and genetic differentiation along an elevational transect. American Journal of Botany. 76(9): 1395-1403.

Schuster, William S.; Mitton, Jeffry B. 2000. Paternity and gene dispersal in limber pine (*Pinus flexilis* James). Heredity. 84: 348-361.

Thompson, John N. 2005. The geographic mosaic of coevolution. Chicago, IL: The University of Chicago Press.

Tomback, Diana F.; Linhart, Yan B. 1990. The evolution of bird-dispersed pines. Evolutionary Ecology. 4: 185-219.

Tomback, Diana F.; Achuff, Peter. 2010. Blister rust and western forest biodiversity: ecology, values and outlook for white pines. Forest Pathology. 40: 186-225.

Tomback, Diana F.; Samano, Sheridan. Southwestern white pine seed size variation by region, an observations of seed predators. Unpublished data: 2000-2010. On file in the Forest Ecology Laboratory, Department of Integrative Biology, University of Colorado Denver, Denver, CO.

Tomback, Diana F.; Schoettle, Anna W.; Chevalier, Kristen E.; Jones, Cheri A., 2005: Life on the edge for limber pine: Seed dispersal within a peripheral population. Écoscience. 12(4): 519-529.

Sugar Pine Seed Harvest by Clark's Nutcracker: Annual Use of a Transient Resource in Crater Lake National Park, Oregon

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Introduction

Clark's nutcrackers (*Nucifraga columbiana*) are well known for using conifer seeds as their principal nutriment source. Seeds are primarily harvested from whitebark (*Pinus albicaulis*), piñon (*P. edulis*), limber (*P. flexilis*), southwestern white (*P. strobiformis*), Jeffrey (*P. jeffreyi*), and ponderosa (*P. ponderosa*) pine as well as Douglas-fir (*Pseudotsuga menziesii*) (Tomback 1998). However, prior to our studies, sugar pine (*Pinus lambertiana*) seed harvest by Clark's nutcrackers was not documented. Sugar pine seeds, which bear long seed wings, are among the largest of pine seeds (average of 0.216 g; Tomback and Linhart 1990) and the cones are the longest among all pines (up to 66 cm, Kinloch and Scheuner 1990). Observations over several years in Crater Lake National Park (CLNP), Oregon, indicate that Clark's nutcrackers harvest sugar pine seeds, but only for about a week in late September when most cones open. The first observations of nutcrackers using sugar pine seeds in CLNP were made by Michael Murray from 2004 to 2006, and then more detailed studies were conducted by Taylor Turner, Brad Van Anderson, and Diana F. Tomback in 2008 and 2009, working in the old-growth sugar pine forest.

We predicted that the timing of use of sugar pine seeds by nutcrackers coincided with rapid cone opening. We also predicted that the use of sugar pine seeds varies with the availability of other pine seed resources. In Crater Lake National Park, the sugar pine stand under study is located at 1375 m elevation and about 14 km straight-line distance from the rim of the crater, which supports extensive whitebark pine communities.

Here, we describe the behavior used by nutcrackers while harvesting seeds from sugar pine cones, the timing of cone opening, stage of cone opening preferred by nutcrackers for seed harvest, and seed harvest rates by nutcrackers.

Methods

Our study area was located in the southern panhandle of CLNP, and covered about 50 hectares. Study dates were 21 to 26 September, 2008, and 20 to 25 September, 2009. We patrolled this section of forest everyday from 08:00 to 15:00 in search of nutcrackers by listening for vocalizations and watching the treetops; observations were made with binoculars. The forest was comprised primarily of sugar pine, ponderosa pine, and occasional lodgepole pine (*P. contorta*), red cedar (*Thuja plicata*), white fir (*Abies concolor*), and Douglas-fir. The height of the old growth sugar pines surpassed the surrounding canopy, and most sugar pines had a minimum diameter of one meter. Upon seeing a nutcracker land on a sugar pine cone, we would observe its behavior for the duration of each cone visit. This included the position the bird assumed while harvesting, the number of seeds extracted, and the amount of time spent harvesting. We observed whether each seed was swallowed or placed in the sublingual pouch of each nutcracker, and any post-harvest activity was subsequently observed. In addition, the cone opening stage (scales separating, partially open, or open) was recorded for each cone visited. Seed extraction rates were examined by cone opening stage in order to determine if there was any correlation. In 2009 we recorded the total number of cones as well as distribution of cone opening stages for each of 13 sugar pines in addition to every sugar pine visited by a nutcracker.

Results

Nutcrackers assumed an inverted position for harvesting sugar pine seeds, requiring that they swing forward and hang upside-down parallel to the cone. They then removed one or more seeds from the cone while maintaining this upside down posture before returning to the upright. The seed wing was always removed prior to the nutcracker either consuming or pouching the wingless seed, often while still in the inverted position. Oftentimes, nutcrackers harvested seeds while in groups of three to six, which may have represented family units consisting of parents and juveniles. After harvesting, the group would leave simultaneously and fly in the same direction to cache seeds.

Steller's jays (*Cyanocitta stelleri*) were also observed taking sugar pine seeds. However, in contrast to nutcrackers, they utilized a "smash and grab" method in which they collided with a cone feet-first, and then gathered the dislodged seeds mid-air or on the ground.

At the start of the study week in 2009, sugar pine cones in all opening stages were observed on each tree, demonstrating asynchronous cone ripening. The cones opened rapidly during the five-day period that we were present, and nearly all cones that were counted and classified by phenology opened by September 25. Furthermore, the distribution of

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cone opening stages on September 20 was significantly different than on September 25, illustrating the speed at which cones progressed to the open stage.

In 2008, we recorded 316 total sugar pine cone visits by nutcrackers with an average overall seed extraction rate of 6.5 sec per seed. Open cones (O) were most frequently visited, followed by partially open cones (PO), with the fewest visits to cones with scales separating (SS). O cones had an average extraction rate of 6.5 sec per seed, but nutcrackers harvested seeds from PO cones most rapidly at 5.8 sec per seed, and pouched the most seeds per cone visit. In 2009, we recorded only 35 total cone visits, all to O cones, also with an average seed extraction rate of 6.5 sec per seed. Extraction rates for O cones in 2009 were not statistically different from those in 2008. On average more seeds were harvested per cone visit in 2009 even though fewer birds were visiting cones.

On one occasion in 2009, we observed a nutcracker burying three caches. Each cache consisted of 7 to 10 sugar pine seeds and was placed in soil and duff among woody debris within 35 meters of the sugar pine from which the seeds originated. In addition, nutcrackers routinely flew off to unknown caching locations with full throat pouches in both 2008 and 2009. There were sufficient sugar pine cone crops in both 2008 and 2009, but the birds were more numerous and easy to locate within the study site in 2008. In contrast, whitebark pine cone production in CLNP was extremely high in 2009, and we observed many more nutcrackers harvesting whitebark pine seeds at the higher elevations around the crater rim than sugar pine seeds.

Discussion

Clark's nutcrackers harvest sugar pine seeds directly from the cone during the week when the cones open rapidly, in late September. Nutcrackers collect seeds using an inverted, or downward pointing body position, while perched atop the cone. Completely open cones represent the most commonly visited cone opening stage, while partially open cones offer the most efficient seed extraction rates and highest number of seeds per cone visit.

The high availability of whitebark and sugar pine cones, and the low number of nutcrackers observed in the sugar pine forest in 2009 suggests that nutcrackers supplement their diets with sugar pine seeds, although whitebark pine seeds are preferred. Hundreds of nutcrackers were observed harvesting, eating, and caching whitebark pine seeds around the rim of the crater, which was in stark contrast to the few sightings of nutcrackers in the sugar pine forest below. The relatively long flight distance and substantial elevation change required to access sugar pine stands may not represent an energetically optimal foraging technique for most birds. However, in the event of an inadequate whitebark pine cone crop the sugar pine may become an important alternative seed source for the CLNP nutcracker population.

Pouched seeds and the caching observation suggest nutcrackers are caching the seeds within and possibly outside the sugar pine forest. Furthermore, numerous sugar pine seedling clusters were seen growing throughout the study area, although all cannot be attributed to nutcracker caches, since some rodents may cache sugar pine seeds as well (Vander Wall 2008). Nutcrackers generally bury 1-15 seeds per cache site, placing seeds 1-3 cm deep in forest litter, mineral soil, gravelly soil, or volcanic pumice sometimes near the parent tree (Tomback 1998). In accordance with this description, the clusters observed in the sugar pine stand were most often in small clearings surrounded by sugar pines with up to nine seedlings emerging from the forest litter. These observations together suggest that nutcrackers may at least disperse some seeds of sugar pine.

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References

Kinloch, Bohun B., Jr.; Scheuner, William H. 1990. Sugar pine (*Pinus lambertiana*). In: Burns, Russell P.; Honkala, Barbara H., eds. Silvics of north america. Volume 1. Conifers. Agricultural Handbook 654, Washington, DC. U.S. Department of Agriculture, Forest Service: 370-379. [13194]

Tomback, Diana F. 1998. Clark's nutcracker (*Nucifraga columbiana*). In: Poole, A. Gill, F., eds. The birds of North America, No. 331. Philadelphia, PA. The Birds of North America.

Tomback, Diana F.; Linhart, Yan B. 1990. The evolution of bird-dispersed pines. Evolutionary Ecology. 4: 185-219.

Vander Wall, Stephen B. 2008. On the relative contributions of wind vs. animals to seed dispersal of four Sierra Nevada pines. Ecology. 89: 1837-1849.

Pre-Dispersal Seed Predator Dynamics at the Northern Limits of Limber Pine Distribution

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Abstract—Limber pine (*Pinus flexilis*) is listed provincially as endangered in the northern part of its geographic range (Alberta) due to the high mortality caused by white pine blister rust (WPBR) (*Cronartium ribicola*) and mountain pine beetle (*Dendroctonus ponderosae*), and limited regeneration opportunities due to fire exclusion. In the case of an endangered species, seed predators may accelerate this decline, particularly when their populations are regulated by more factors than the abundance of the declining species. Red squirrels (*Tamiasciurus hudsonicus*) are a major cause of pre-dispersal seed loss in many species of conifers. Stands with varying combinations of conifer species that have different reproductive strategies (i.e., masting or persistent aerial seed sources) may experience different amounts of cone predation by squirrels. With no prior studies on cone predation in the northern part of the species' range, we investigated whether: 1) squirrel cone predation differs in areas with low versus high WPBR infection rates, and 2) cone predation differs in limber pine-dominated versus mixed-conifer stands containing limber pine.

Limber pine populations in Alberta occur in the southern foothills of the Rocky Mountains at elevations typically ranging from 1300 to 1900 m. Our low WPBR study area (one percent live tree infestation in 2003; lat. 52.00°, long. -116.50°) contained nine stands ranging from pure limber pine, to limber pine mixed with Douglas-fir (*Pseudotsuga menziesii*), white spruce (*Picea glauca*), or lodgepole pine (*Pinus contorta*). Our high WPBR study area (38 percent live tree infestation in 2003; lat. 49.60°, long -114.20°) contained stands of either pure limber pine or limber pine–Douglas-fir mixtures. All species except lodgepole pine masted in 2007 and had low cone production in 2008 and 2009. We assumed that one active midden equals one squirrel, based on previous research. Preliminary results suggest that large differences in squirrel abundance in low vs. high WPBR study areas (1.6 vs. 0.4 active middens/ha, respectively) did not affect the proportion of cones removed. On average, red squirrels removed 85 percent of cones in low WPBR landscapes and 81 percent of cones in high WPBR landscapes. Additionally, fewer squirrels (0.25 as many) harvested the much greater cone production in high WPBR study areas (15.3. vs. 5.9 cones produced per live tree, in high vs. low WPBR areas). Cone predation was highly variable amongst all 17 stands, ranging from 0 to 100 percent. Cone predation varied less than one percent between 2008 and 2009 (averaged across all 17 stands), despite a two-fold increase in cone production in 2009.

More limber pine cones were removed in stands where lodgepole pine was present (93 percent) versus pure limber pine (77 percent). Mixed-limber and lodgepole pine stands generally supported higher squirrel populations, suggesting stands with lodgepole pine (i.e., a persistent aerial seed source) provide a more stable cone supply than stands with one or more masting species (limber-fir or limber-spruce mixtures). Preliminary analyses suggest cone predation and active midden abundance increases as tree basal area increases; however, species composition, and midden proximity were not significant predictors of cone predation amongst trees within each stand. These findings suggest that limber pine may frequently escape seed predation by squirrels, by virtue of it preference for open and exposed habitats, which have fewer trees of other species and lower basal area overall.

Our results suggest that red squirrels are capable of removing most of the cones in non-mast years, even when squirrels are present in low numbers. Seed predators may accelerate the decline of an endangered species if it is preferentially selected over other abundant species. Conserving limber pine will require rapidly identifying populations that are most subject to seed limitation and in need of mitigation.

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Clark's Nutcracker Demography and Habitat Use in Bridger-Teton National Forest—Preliminary Analyses

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Abstract—The population status of and habitat use by Clark's nutcrackers (*Nucifraga columbiana*) has rarely been studied and remains poorly understood, in part due to the previous lack of a reliable method of surveying nutcracker populations. Anecdotal evidence suggests that Clark's nutcrackers have recently declined precipitously throughout large parts of their range. A likely factor causing these declines is their mutualism with whitebark pine (*Pinus albicaulis*), which has suffered massive die-offs due to the recent mountain pine beetle (*Dendroctonus ponderosae*) epidemic and white pine blister rust (*Cronartium ribicola*) infections. Because nutcrackers enable whitebark pine regeneration through their caching behavior, ongoing whitebark pine restoration efforts will not be sustainable if nutcracker populations decline or their habitat use changes to a degree that they are not available to carry out seed dispersal. Reliable long-term monitoring of nutcrackers is necessary to assess their population trends, to determine conservation priorities and to assess effectiveness of management activities. Because data quality determines validity of managers' decisions, it is critical that monitoring programs obtain results that are statistically robust. Previous research has shown that nutcrackers are difficult to monitor accurately with common songbird survey techniques including point counts, playback point counts, line transects, and Breeding Bird Survey routes. My study is based on the predictions that nutcracker detectability differs seasonally and in different habitats, and sampling bias occurs when detection probability is not taken into account. I am studying a population of Clark's nutcrackers in Bridger-Teton National Forest, in the Greater Yellowstone Ecosystem, where the birds are still relatively abundant. In 2009, I carried out occupancy surveys to determine which covariates influenced changes in detectability of nutcrackers. My initial objectives were to determine if: (1) season and habitat are significant causes of heterogeneity of detectability of nutcrackers, (2) occupancy probabilities corrected for detectability improve occupancy estimates, and (3) occupancy surveys are a reliable, cost-effective means to survey nutcrackers. Using the likelihood-based method in the program PRESENCE (ver. 2.3), I calculated nutcracker detectability and occupancy as a function of season and within differing habitats. In my preliminary analyses, I concluded that nutcracker detectability varies with season and habitat composition, corrected occupancy probabilities are essential for accurate nutcracker occupancy estimates, and occupancy surveys are an effective method to use to monitor nutcracker population trends. Complete results will be forthcoming in a separate paper. When developing Clark's nutcracker monitoring programs, it is important to take variation in detectability into account, in order to determine accurate occupancy and abundance estimates. By incorporating detectability into monitoring designs, we can implement management interventions that will successfully facilitate the persistence of the nutcracker populations. This will enable effective restoration of the whitebark pine communities and will help maintain a healthy ecosystem.

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Mountain Pine Beetle Dynamics

Mountain Pine Beetle in High-Elevation Five-Needle White Pine Ecosystems

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Abstract—Across western North America mountain pine beetle, *Dendroctonus ponderosae* (Coleoptera: Curculionidae, Scolytinae), populations are growing at exponential rates in pine ecosystems that span a wide range of elevations. As temperature increased over the past several decades, the flexible, thermally-regulated life-history strategies of mountain pine beetle have allowed for increased population success in numerous habitats. Of particular concern are the high-elevation five-needle white pines that are currently being infested. In a recent study of high-elevation whitebark pine forests, mountain pine beetles from multiple generations were found killing pines within a single summer. These generations included parent beetles that overwintered and emerged to attack new host trees, adult beetles that developed in a single year (univoltine), and adult beetles that required two years for life-cycle completion (semivoltine). The occurrence of univoltine brood emerging from host trees at elevations above 2600 m is potentially due to warming temperatures in recent years. To test if warming temperatures are a contributing factor, mountain pine beetle thermal suitability was simulated using historical temperatures estimated for a single high-elevation whitebark pine site in Wyoming. Although there was substantial variability among years, model predictions for this high-elevation site suggest that thermal conditions in the late 20th and early 21st century have been increasingly conducive to mountain pine beetle univoltine lifecycles, and well within the species cold tolerance limits. Predictions also suggest that in the late 1920s and early 1930s conditions were thermally suitable for mountain pine beetle univoltine lifecycle timing, although extreme cold temperatures in the early 1930s may have resulted in high mountain pine beetle larval mortality. We briefly discuss the implications of these results to past trends in high-elevation white pine mortality. The role of temperature in mountain pine beetle population success, genetic variability among populations, fungal associates, and management implications for high elevation white pine forests are also discussed.

Introduction

The mountain pine beetle, *Dendroctonus ponderosae* Hopkins (Coleoptera: Curculionidae, Scolytinae), is a phytophagous insect with eruptive population dynamics and an expansive geographic range, extending from southern California USA, north to central British Columbia and recently into eastern Alberta, Canada (Safranyik and others 2010). Mountain pine beetle can attack and successfully reproduce in all *Pinus* species within their geographic range, except Jeffrey pine (*P. jeffreyi*), and larval feeding within the phloem typically results in death of the host tree. In central British Columbia, more than 14 million hectares of lodgepole pine (*P. contorta*), a principle host of mountain pine beetle, were killed during a decade-long population outbreak that is considered the largest in recorded history (Safranyik and others 2010). In the western United States, more than 12 million hectares of multiple pine species have been affected by the mountain pine beetle in the past decade (figure 1). The fact that suitable pine hosts extend to the north and south of the current geographic range of mountain pine beetle, suggests that climate has historically constrained the geographic distribution of this insect. In the early 21st century, as a result of rising temperatures, there was a significant extension of the mountain pine beetle geographic range in Canada, and populations are now established in lodgepole pine stands that were previously climatically unsuitable (Safranyik and others 2010). Notably, in western Alberta, mountain pine beetle is established in lodgepole pine stands that are close to the boreal zone where jack pine (*P. banksiana*) occurs. The suitability of jack pine for beetle population persistence is unknown, and there is concern that mountain pine beetle range expansion may continue east across the continent.

In addition to geographic range expansion, mountain pine beetle population activity within its historical range has increased in recent years, and outbreaks are currently found in areas where they either were not recorded or were

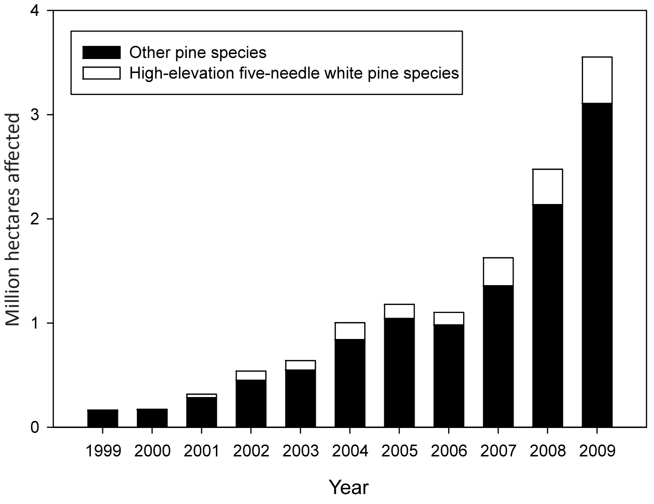

Figure 1. Million hectares of high-elevation five-needle white pine species, and all other pine species, affected by mountain pine beetle from 1999 to 2009 in the western United States. Data from USDA Forest Service, Forest Health Protection.

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recorded infrequently (Gibson and others 2008). In particular, mountain pine beetle populations are currently affecting high-elevation five-needle white pine species including whitebark pine (*Pinus albicaulis*), limber pine (*P. flexilis*), foxtail pine (*P. balfouriana*), western white pine (*P. monticola*), Rocky Mountain bristlecone pine (*P. aristata*), Great Basin bristlecone pine (*P. longaeva*), and southwestern white pine (*P. strobiformis*). Mountain pine beetle macrofossils were found in lake sediment cores in Montana at time periods during the Holocene when whitebark pine was also predominate suggesting a long association of bark beetles and high-elevation white pines, although the frequency and intensity of historical outbreaks can not be inferred from these data (Brunelle and others 2008). While tree death associated with mountain pine beetle was observed in some whitebark pine ecosystems during intermittent warm periods in the 20th century (Arno 1986; Kipfmueller and others 2002; Perkins and Swetnam 1996), population activity at high elevations was not typically sustained due to a lack of seasonal thermal input that is required for population growth (Amman 1973).

Increasing temperature and shifts in precipitation patterns associated with climate change are likely contributing to the recent widespread death of five-needle white pines, which perform critical keystone functions in high-elevation ecosystems (Logan and Powell 2001). Temperature directly influences mountain pine beetle development and survival (Bentz and others 1991; Régnière and Bentz 2007), and shifts in precipitation can affect host tree vigor and defense mechanisms (Raffa and others 2008), the principle determinates of beetle attack success. Other factors that are contributing to high-elevation white pine decline include replacement by, and competition with, other tree species often following fire exclusion (Keane and Parsons 2010) and the exotic disease white pine blister rust caused by *Cronartium ribicola* (Schwandt and others 2010).

In this paper, we focus our discussion on mountain pine beetle, exploring the influence of temperature on beetle population dynamics and potential outbreak activity in high-elevation white pine forests. Using established models of thermally-dependent beetle physiological processes and current and historical temperatures, we provide predictions of mountain pine beetle population success over the last century at a single high-elevation whitebark pine site. We also present a brief overview of fungal species that are closely associated with the beetle (in other words, symbionts) and can influence mountain pine beetle population dynamics, genetic variability among mountain pine beetle populations, and management options for protection of high-elevation five-needle white pines against mountain pine beetle attack.

Temperature Affects Mountain Pine Beetle Population Success

Mountain pine beetle adults attack host trees in the summer, mate, and oviposit eggs under the bark. After the eggs hatch, individuals develop through four larval instars as they feed through the phloem and then pupate to become an adult beetle that emerges from the tree to attack a new pine host. Like all insects, mountain pine beetle developmental timing is greatly affected by temperature and each life-stage has specific thermal requirements (Bentz and others 1991). The timing of tree attack and length of a generation are both dependent on annual temperature patterns as they influence life-stage specific developmental thresholds and ultimately the synchronicity of adult emergence (Logan and Bentz 1999). Emergence timing is a critical determinant of whether the number of adults attacking individual trees are sufficient to overcome host defenses, thereby allowing for successful host colonization and reproduction (Powell and Bentz 2009). A one-year (univoltine) generation time, which reduces the time individuals spend exposed to mortality factors, is considered optimal for mountain pine beetle population growth (Safranyik 1978). Annual thermal patterns can also influence mountain pine beetle survival through control of metabolites that are important for tolerating cold temperatures (Bentz and Mullins 1999; Safranyik and Linton 1998).

In mid-elevation lodgepole pine forests, the mountain pine beetle life-cycle is consistently univoltine, which means that a single generation is completed within one year (Amman and Cole 1983; Safranyik and Carroll 2006). The timing of beetle emergence from hosts in these forests can also be remarkably synchronous. For example, in a lodgepole pine forest at 2042 m, greater than 90 percent of adults emerged during a period of 15 days in each of the three years that emergence was monitored (2001, 2002, and 2003) (Bentz 2006). In contrast, at several high elevation whitebark pine sites (2652 to 2926 m) in 2004 and 2005, mountain pine beetle emerged at each site over a period greater than 60 days (Bentz and Schen-Langenheim 2007). Moreover, mountain pine beetle life-cycle timing in the individual whitebark pine trees monitored at the high-elevation sites was both univoltine and semivoltine (in other words, one generation of beetles develops every two years). At both the high-elevation whitebark pine site and the mid-elevation lodgepole pine site, at least some proportion of parent adults survived the winter and emerged in early summer (Bentz, unpublished data). Although the ability of these parents to oviposit additional eggs has not been fully investigated, it is known that they can attack live host trees (DeLeon and others 1934). Collectively, these data suggest that mountain pine beetle has a flexible life-history, and that beetles from multiple generations may be killing pines within a single summer. At high elevations, parent beetles that overwintered in hosts, adults produced from a univoltine life-cycle (eggs laid the previous summer), and adults produced from semivoltine life-cycles (eggs laid two summers ago) emerged within the same summer to attack whitebark pines. A mixture of adults produced from univoltine life-cycles and parent beetles that overwintered attacked lower elevation lodgepole pines. Because mountain pine beetle populations were at outbreak levels in both the mid-elevation lodgepole pine and high elevation whitebark pine sites, these data also suggest that a strictly univoltine life-cycle is not necessary for population

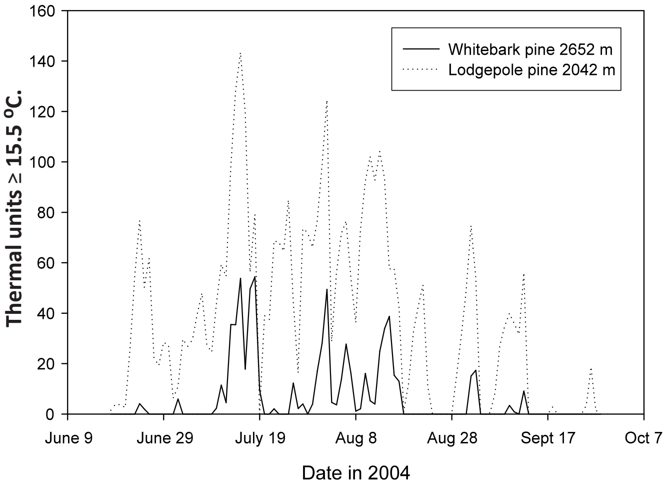

Figure 2. Air temperature recorded in a mountain pine beetle-infested lodgepole pine forest at 2042 m (Sawtooth National Recreation Area, ID) and an infested whitebark pine forest at 2652 m (Targhee National Forest, ID). Shown are daily thermal units ≥ 15.5°C during the summer of 2004.

outbreaks. Thermal patterns that differ between the elevations (figure 2) undoubtedly influence mountain pine beetle life-cycle and emergence timing.

With the exception of warm periods during the 20th century (Perkins and Swetnam 1996), high-elevation white pine ecosystems were considered thermally unsuitable for mountain pine beetle population growth. Low temperatures at the high-elevation sites resulted in beetle life-cycles that historically required two or even three years for completion resulting in poor survival and low population growth (Amman 1973). However, our data suggests that at least some proportion of mountain pine beetle populations were able to complete a univoltine life-cycle in recent years at elevations above 2600 m (Bentz and Schen-Langenheim 2007). Amman (1973) observed that five-needle white pine forests at these elevations produced only semivoltine life-cycles in the early 1970's. Increasing temperature associated with climate change may have been a positive influence on mountain pine beetle population activity in high-elevation white pine forests in the early 21st century. We used mechanistic models that describe the relationship between temperature and mountain pine beetle development time (Bentz and others 1991; Gilbert and others 2004; Logan and Amman 1986) and cold-induced mortality (Régnière and Bentz 2007) to investigate this hypothesis.

These mechanistic models describe ecologically important and thermally-regulated traits that underlie population success (for example, development time and cold-temperature survival), and use hourly records of temperature from multiple years as input. We used these models to investigate trends in mountain pine beetle population success at a single high-elevation site over the past century. Hourly temperature for the years 1920 to 2008 were estimated using daily air temperature data collected in one mountain pine beetle-infested whitebark pine site near Togwotee Pass, WY (2950 m) from 2003 to 2005, and daily temperature data from a nearby site (Moran, WY, 2072 m) that is part of the Historical Climatology Network (HCN). Two years of daily maximum and minimum temperature from the whitebark pine site were regressed against daily maximum and minimum temperature data from the HCN site for the same time period (Proc Mixed, SAS Institute) (daily maximum R^2 = 0.9090; daily minimum R^2 = 0.6970; df = 754). The resulting regression parameters were then applied to historical daily temperature recorded at the HCN site between 1920 and 2008 to estimate daily maximum and minimum temperature at the high-elevation whitebark pine site. Hourly temperatures were estimated from the daily maximum and minimum temperatures using a sine wave function. Estimated hourly temperatures were then used to drive a mountain pine beetle phenology model (Gilbert and others 2004) and mountain pine beetle cold tolerance model (Régnière and Bentz 2007). The annual proportion of univoltine mountain pine beetle and annual probability of cold temperature-related survival from 1920 to 2008 were predicted. A LOESS curve was fit to the annual predictions to approximate trends throughout the modeled time period.

Model results over the 78 year period indicated substantial variability in annual probability of beetle survival among years, which is likely the result of variability in the annual temperature pattern that drives accumulation of polyols responsible for larval cold tolerance (Bentz and Mullins 1999). We also predicted annual peaks in population univoltinism that were separated by years dominated by a semivoltine life-cycle. One hundred percent univoltinism was not predicted for any of the simulated years. Model results suggest that during the late 1920s and early 1930s thermal regimes at the high-elevation whitebark pine site were particularly favorable for univoltine mountain pine beetle life-cycle development (figure 3). A high proportion of individuals with a univoltine life-cycle, relative to a semivoltine life-cycle, can result in increased mountain pine beetle population success (Amman 1973). These findings are supported by tree-ring studies indicating mountain pine beetle killed whitebark pine during this same time period at several locations in the northern Rocky Mountains (Kipfmueller and others 2002; Perkins and Swetnam 1996) (figure 4), and also in southern mountain ranges of British Columbia and Alberta (Jackson and Campbell 2008; Wong and others, submitted).

Cold tolerance model predictions suggest that winter temperatures in 1933 may have caused significant mountain pine beetle mortality at the high-elevation whitebark pine site near Togwotee Pass, WY. Tree-ring data also suggest a reduction in mountain pine beetle-caused whitebark pine deaths in MT and ID following 1933 (figure 4). Although temperatures during the growing season were favorable for univoltine life-cycle development and mountain pine beetle population growth from the late-1920s into the late-1930s, extreme cold temperatures probably resulted in high levels of larval mortality during this time period.

Considering the more recent weather record, model predictions suggest a generally increasing trend during the late 20th and early 21st century (in other words, from around 1990 to 2008) in thermal regimes conducive to univoltine

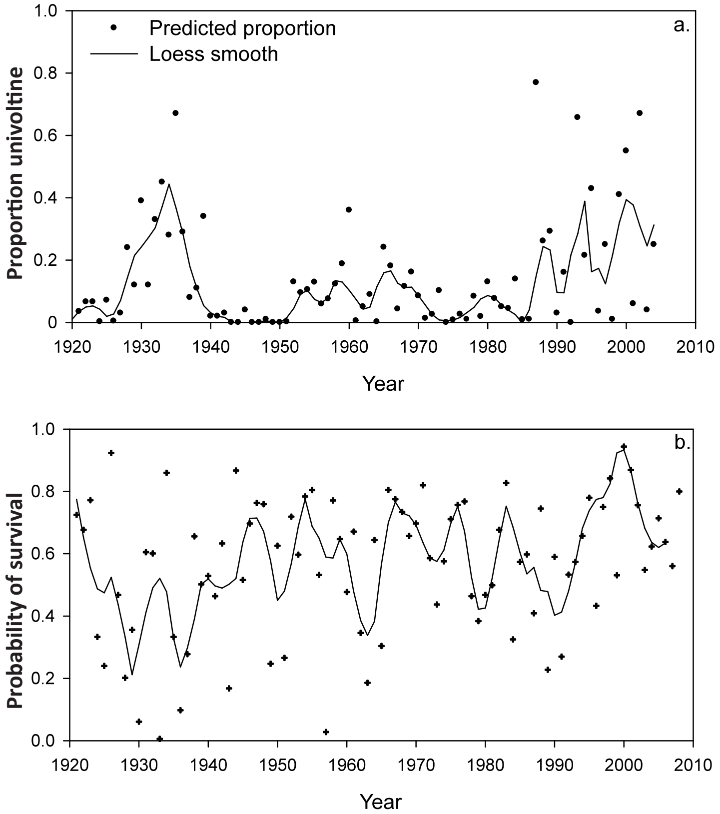

Figure 3. Predicted annual (a) proportion univoltine mountain pine beetle and (b) probability of mountain pine beetle cold temperature-related survival from 1920 through 2008 for a whitebark pine site near Togwotee Pass, WY (2950 m). The solid line is a LOESS smooth approximation to the annual model predictions.

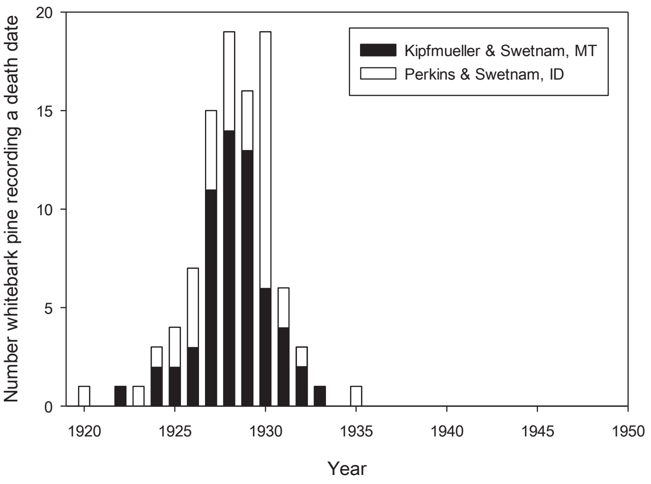

Figure 4. Number of whitebark pine recording a death date due to mountain pine beetle at several high elevation sites in Montana (Kipfmueller and others 2002) and Idaho (Perkins and Swetnam 1996). Death dates were determined using dedrochronology, and gallery patterns on the exposed tree bole were used to assign mountain pine beetle as the mortality agent.

life-cycles *and* cold temperature-related beetle survival at our high-elevation whitebark pine site. Mechanistic model projections of mountain pine beetle population success in whitebark pine habitats of British Columbia produced similar results—the percentage of whitebark pine's range highly susceptible to beetle outbreaks was projected to double, increasing to 20 percent over the next century (Campbell and Carroll 2007). Projections of future warming suggest this increasing trend in thermal suitability for mountain pine beetle will continue throughout this century in high-elevation five-needle white pine forests (Bentz and others 2010; Hicke and others 2006).

Genetic Variability Among Mountain Pine Beetle Populations

The geographic distribution of mountain pine beetle extends across pronounced latitudinal temperature gradients. One result of this widespread distribution is phenotypic and genetic variability in thermally-regulated traits such as beetle developmental timing (Bentz and others 2001; Bentz and others 2011). In replicated common garden rearing experiments using mountain pine beetle populations from multiple latitudes reared at multiple temperatures, temperature contributed to substantial variation among populations in development time suggesting a role for phenotypic plasticity. Source population (in other words, the geographic location where the population was collected) was also significant in explaining differences in development time, an indication of genetic variation among latitudinally-separated populations that have adapted to local thermal regimes (Bentz and others 2011). An interesting result from these common garden experiments was that mountain pine beetle from Idaho developed faster, at a common optimal temperature, than mountain pine beetle from a either a high-elevation southwestern white pine forest in Arizona (Bentz, unpublished data) or a pinyon pine (*P. monophylla*) forest in southern California (Bentz and other 2011). If we assume the univoltine life-cycle is optimal for beetle population growth (Logan and Bentz 1999), results from these studies suggest that time constraints in growth season have selected for fast development rates of one or more life-stages in more northern latitudes and for slow rates or different developmental thresholds in southern latitudes. Thus, a generation would be completed annually in both climates, with synchronous brood adult emergence at a suitable time of year. The optimal genotypes and phenotypes, however, will depend on the thermal habitat occupied, and could vary substantially across the elevational and latitudinal range of the species.

Plasticity in mountain pine beetle thermal response has allowed for close tracking of changing environmental conditions, thereby providing avenues for mountain pine beetle range expansion in Canada, and population eruptions in mid-elevation forests of multiple pine species (for example, lodgepole pine and ponderosa pine) and high-elevation five-needle white pine forests including whitebark pine and limber pine among others. As the climate continues to change, however, populations at all elevations may be increasingly exposed to conditions that exceed the capacity of existing phenotypic plasticity to maintain synchrony with environmental conditions. The limits within which mountain pine beetle can maintain its capacity to adapt to continued climate warming across all elevations is currently unknown. Moreover, evidence of adaptation in thermally-regulated life-history traits to local climates (Bentz and others 2011) suggests that mountain pine beetle response to a changing climate will differ across the geographic range of this insect.

Mountain Pine Beetle Fungal Associates

Mountain pine beetle population dynamics are influenced by a close association with several fungal species that are introduced into a tree upon beetle colonization (Klepzig and Six 2004; Lee and others 2006). The relationship between mountain pine beetles and their fungal associates is often described as symbiotic, as they have evolved morphological adaptations to assist in the transport of specific associates, derive nutritional and defensive benefits from them, or both (Klepzig and Six 2004). The association of mountain pine beetle with various fungal species is integral to their survival. For example, developing mountain pine beetle larvae acquire vital nutrients (for example, nitrogen and ergosterol), which are not found in host tree tissue, by feeding on at least two fungi, *Grosmannia clavigera* and *Ophiostoma montium*, the hyphae of which spread throughout the phloem and sapwood following inoculation into the tree by attacking beetles (Adams and Six 2006). Although both fungi are important, one species (*G. clavigera*) supports faster brood development, larger body size, and higher brood production than does the other (Bleiker and Six 2007). Each fungus possesses different thermal ranges for optimal growth and survival, and seasonal temperature can dictate which fungal species is ultimately vectored by dispersing beetles (Six and Bentz 2007). *Grosmannia clavigera* can survive colder temperatures than *O. montium*, and *O. montium* grows better than *G. clavigera* at warmer temperatures (Rice and others 2008). Based on the observed thermal tolerances of each fungal species, we would expect to find a higher proportion of beetles carrying *G. clavigera* at high-elevation sites although this relationship has not been investigated. Because benefits to mountain pine beetle are not the same for each fungal species, ongoing temperature changes in high-elevation pine forests could indirectly affect mountain pine beetle population success through direct effects on their fungal symbionts.

Management Implications

Lodgepole pine is often considered the main host of mountain pine beetle (Safranyik and Carroll 2006). Baker and others (1971) found that mountain pine beetle attacked proportionately more lodgepole pine than whitebark pine in mixed high-elevation stands of Wyoming, although Waring and Six (2005) found that mountain pine beetle appeared to prefer whitebark pine to lodgepole pine at a site in Montana. Reduced precipitation and increased temperature associated with climate change may differentially affect host tree species. Little is known about responses of pine trees at any elevation to changing environmental conditions and how this may influence defensive response to mountain pine beetle attack. Future management and restoration of high-elevation pine forests would benefit from a better understanding of how geographic location, site condition, host tree species, and differential host tree defensive response to changing abiotic conditions influence mountain pine beetle attack success and brood production in high-elevation pine forests.

Widespread deaths of high-elevation five-needle white pine due to a combination of mountain pine beetle and the exotic disease white pine blister rust, caused by *Cronartium ribicola* (Geils and Volger, these Proceedings; Tomback and others, these Proceedings), is threatening the existence of these species in many parts of their range. Protection of blister rust resistant trees from mountain pine beetle attack is crucial for continued collection of genetic material for development of rust-resistant strains, in addition to out-planting in heavily-affected areas. Although protection of high-elevation five-needle pines against mountain pine beetle attacks is difficult, in part due to the isolated location of high elevation ecosystems, there are options for protection of individual trees and stands. In particular, properly applied insecticide, applied annually, on the bole of living trees can provide protection (Hastings and others 2001). Semiochemical treatment using verbenone in stands (Perkins and others, these Proceedings) and on individual trees (Kegley and Gibson 2009) can also reduce high-elevation five-needle pine mortality due to mountain pine beetle. Aerial application of verbenone flakes in whitebark pine stands has also shown efficacy in reducing mountain pine beetle attacks over large areas (Gillette and others, unpublished data). Research on removing currently infested brood trees along with verbenone flake application to improve residual whitebark pine protection is on-going. These and other management options are described in detail in other sections of these Proceedings. In addition to stand and tree-level tactics for protection of high-elevation pines, population monitoring is a crucial aspect of restoration and conservation of high-elevation ecosystems (Macfarlane and others 2010).

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Literature Cited

Adams, A. S.; Six, D. L. 2006. Temporal variation in mycophagy and prevalence of fungi associated with developmental stages of the mountain pine beetle, *Dendroctonus ponderosae* (Coleoptera: Scolytinae, Curculionidae). Environmental Entomology. 36: 64-72.

Amman, G. D. 1973. Population changes of the mountain pine beetle in relation to elevation. Environmental Entomology. 2: 541-547.

Amman, G. D.; Cole, W. E. 1983. Mountain pine beetle dynamics in lodgepole pine forests. Part II: population dynamics. USDA Forest Service, Intermountain Forest and Range Experiment Station, General Technical Report INT-145. 59 p.

Arno, S. F. 1986. Whitebark pine cone crops a diminishing source of wildlife food. Western Journal of Applied Forestry. 9: 92-94.

Baker, B. H.; Amman, G. D.; Trostle, G. C. 1971. Does the mountain pine beetle change hosts in mixed lodgepole and whitebark pine stands? USDA Forest Service, Research Note. INT-151.

Bentz, B. J.; Logan, J. A.; Amman, G. D. 1991. Temperature dependent development of the mountain pine beetle (Coleoptera: Scolytidae), and simulation of its phenology. Canadian Entomologist. 123: 1083-1094.

Bentz, B. J.; Mullins, D. E. 1999. Ecology of mountain pine beetle cold hardening in the Intermountain West. Environmental Entomology. 28: 577-587.

Bentz, B. J.; Logan, J. A.; Vandygriff, J. C. 2001. Latitudinal variation in *Dendroctonus ponderosae* (Coleoptera: Scolytidae) development time and adult size. The Canadian Entomologist. 133: 375-387.

Bentz, B. J. 2006. Mountain pine beetle population sampling: Inferences from Lindgren pheromone traps and tree emergence cages. Canadian Journal of Forest Research. 36(2): 351-360.

Bentz, B. J.; Six, D. L. 2006. Ergosterol content of three fungal species associated with *Dendroctonus ponderosae* and *D. rufipennis* (Coleoptera: Curculionidae, Scolytinae). Annals of the Entomological Society of America. 99: 189-194.

Bentz, B.; Schen-Langenheim, G. 2007. The mountain pine beetle and whitebark pine waltz: has the music changed? In: Goheen, comps. Proceedings of the Conference Whitebark Pine: A Pacific Coast Perspective. www.fs.fed.us/r6/nr/fid/wbpine/papers/2007-wbp-impacts-bentz.pdf

Bentz, B. J.; Régnière, J.; Fettig, C. J.; Hansen, E. M.; Hicke, J.; Hayes, J. L.; Kelsey, R.; Negrón, J.; Seybold, S. 2010. Climate change and bark beetles of the western US and Canada: Direct and indirect effects. BioScience. 60: 602-613.

Bentz, B.; Bracewell, R.; Mock, K.; Pfrender, M. 2011. Genetic architecture and phenotypic plasticity of thermally-regulated traits in an eruptive species, *Dendroctonus ponderosae*. Evolutionary Ecology, Accepted March 13.

Bleiker, K. P.; Six, D. L. 2007. Dietary benefits of 497 fungal associates to an eruptive herbivore: potential implications of multiple associates on host population dynamics. Environmental Entomology. 36: 1384-1396.

Brunelle, A.; Rehfeldt, G.; Bentz, B.; Munson, S. 2008. Holocene records of *Dendroctonus* bark beetles in high elevation pine forests of Idaho and Montana, USA. Forest Ecology and Management. 255: 836-846.

Campbell, E.; Carroll, A. 2007. Climate-related changes in the vulnerability of whitebark pine to mountain pine beetle outbreaks in British Columbia. Nutcracker Notes. 12: 13-15.

DeLeon, D.; Bedard, W. D.; Terrell, T. T. 1934. Recent discoveries concerning the biology of the mountain pine beetle and their effect on control in western white pine stands. Journal of Forestry. 32: 430-436.

Gilbert, E; Powell, J. A.; Logan, J. A.; Bentz, B. J. 2004. Comparison of three models predicting developmental milestones given environmental and individual variation. Bulletin of Mathematical Biology. 66: 1821-1850.

Hastings, F. L.; Holsten, E. H.; Shea, P. J.; Werner, R. A. 2001. Carbaryl: A review of its use against bark beetles in coniferous forests of North America. Environmental Entomology. 30: 803-810.

Hicke, J. A.; Logan, J. A.; Powell, J.; Ojima, D. S. 2006. Changing temperatures influence suitability for modeled mountain pine beetle (*Dendroctonus ponderosae*) outbreaks in the western United States. Journal of Geophysical Research. 111: G02019.

Historical Climatology Network. (cdiac.orni.gov/epubs/ndp/ushcn).

Jackson, S.; Campbell, E. 2008. Assessing the threat of mountain pine beetle to whitebark pine in British Columbia. Project Report, FIA-FSP Project #M07-5048. BC Ministry of Forests and Range.

Kegley, S.; Gibson, K. 2009. Individual-tree tests of verbenone and green-leaf volatiles to protect lodgepole, whitebark and ponderosa pines, 2004-2007. USDA Forest Service, Forest Health Protection Report. 09-03.

Kipfmueller, K. F.; Swetnam, T. W.; Morgan, P. 2002. Climate and mountain pine beetle-induced tree mortality in the Selway-Bitterroot Wilderness Area. Final Report, RMRS-99611-RJVA.

Klepzig, K. D.; Six, D. L. 2004. Bark beetle fungal symbiosis: Context dependency in complex interactions. Symbiosis. 37: 189-206.

Lee, S.; Kim, J-J.; Breuil, C. 2006. Diversity of fungi associated with the mountain pine beetle, *Dendroctonus ponderosae* and infested lodgepole pines in British Columbia. Fungal Diversity. 22: 91-105.

Logan, J. A.; Bentz, B. J. 1999. Model analysis of mountain pine beetle (Coleoptera: Scolytidae) seasonality. Environmental Entomology. 28(6): 924-934.

Logan, J. A.; Amman, G. D. 1986. A distribution model for egg development in mountain pine beetle. Canadian Entomologist. 118: 361-372.

Macfarlane, W. W.; Logan, J. A.; Kern, W. R. 2010. Using the landscape assessment system to assess mountain pine beetle-caused mortality of whitebark pine, Greater Yellowstone Ecosystem, 2009: Project Report, 69 pages. http://docs.nrdc.org/land/files/lan_10072101a.pdf.

Perkins, D. L.; T. W. Swetnam. 1996. A dendroecological assessment of whitebark pine in the Sawtooth-Salmon River region, Idaho. Canadian Journal of Forest Research. 26: 2123-2133.

Rice, A. V.; Thormann, M. N.; Langor, D. W. 2008. Mountain pine beetle-associated blue-stain fungi are differentially adapted to boreal temperatures. Forest Pathology. 38: 113-123.

Raffa, K. F.; Aukema, B.H.; Bentz, B. J.; Carroll, A. L.; Hicke, J. A.; Turner, M. G.; Romme, W. H. 2008. Cross-scale drivers of natural disturbances prone to anthropogenic amplification: Dynamics of biome-wide bark beetle eruptions. BioScience. 58: 501-518.

Safranyik, L.; Carroll, A. L. 2006. The biology and epidemiology of the mountain pine beetle in lodgepole pine forests. In The mountain pine beetle: a synthesis of its biology, management and impacts on lodgepole pine. Edited by L.Safranyik and B. Wilson. Pacific Forestry Centre, Canadian Forest Service, Natural Resources Canada, Victoria, British Columbia. pp. 3-66.

Safranyik, L.; Carroll, A. L.; Regniere, J.; Langor, D. W.; Riel, W. G.; Shore, T. L.; Peter, B.; Cooke, B. J.; Nealis, V. G.; Taylor, S. W. 2010. Potential for range expansion of mountain pine beetle into the boreal forest of North America. Canadian Entomologist. 142: 415-442.

Safranyik, L.; Linton, D. A. 1998. Mortality of mountain pine beetle larvae, *Dendroctonus ponderosae* (Coleoptera: Scolytidae) in logs of lodgepole pine (*Pinus contorta* var. *latifolia*) at constant low temperatures. Journal of the Entomological Society of British Columbia. 95: 81-87.

Six, D. L.; Bentz, B. J. 2007. Temperature determines symbiont abundance in a multipartite bark beetle-fungus ectosymbiosis. Microbial Ecology. 54: 112-118.

Stahl, K.; Moore, R. D.; McKendry, I. G. 2006. Climatology of winter cold spells in relations to mountain pine beetle in British Columbia, Canada. Climate Research. 32: 13-23.

Waring, K. M.; Six, D. L. 2005. Distribution of bark beetle attacks after whitebark pine restoration treatments: a case study. Western Journal Applied Forestry. 20(2): 110-116.

Wong, C. M.; Daniels, L. D.; LeMay, V. [Submitted]. A triple whammy disturbance: conservation implications of bottom-up controls on and responses to blister rust and two bark beetles in whitebark pine forests.

Health of Whitebark Pine Forests After Mountain Pine Beetle Outbreaks

Extended Abstract

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Abstract—Whitebark pine (*Pinus albicaulis*), a keystone high-elevation species, is currently at risk due to a combination of white pine blister rust (WPBR) (*Cronartium ribicola*), forest succession, and outbreaks of mountain pine beetle (MPB) (*Dendroctonus ponderosae)*. While recent mortality is often quantified by aerial detection surveys (ADS) or ground surveys, little information is presented to describe what stands look like following MPB outbreaks. This information may help prioritize areas for restoration. In 2008 and 2009, the severity of MPB impacts was measured in 42 whitebark pine stands in Idaho, Montana, and Wyoming. WPBR was recorded on remaining live, mature whitebark pine and whitebark pine regeneration. Probable stand trajectory was determined by comparing abundance and health of remaining whitebark pine with other competing tree species. During the recent outbreak, 30 to 97 percent of whitebark pine basal area tallied within each stand was killed by MPB. The density of live whitebark pine dropped by more than 80 percent on over half of areas surveyed. WPBR infection levels on remaining live, mature whitebark pine averaged 64 percent in northern Idaho, western Montana, and the Greater Yellowstone Area (GYA) (southwestern Montana, eastern Idaho, and northwest Wyoming) but only 4 percent in drier central Idaho. Infection levels on whitebark pine regeneration ranged from 0 to 81 percent. Regeneration of other tree species, primarily subalpine fir (*Abies lasiocarpa*), outnumbered whitebark pine in 69 percent of areas. Based on WPBR and MPB impacts on whitebark pine and abundance of other tree species, at least 57 percent of sites surveyed will likely convert from whitebark pine to other cover types without restoration efforts or wildfire. In central Idaho, current outbreak losses were compared to losses from an outbreak that occurred circa the 1930s. In four of six stands attacked in both periods, more whitebark pine basal area was killed in the 1930s.

Introduction

Whitebark pine (*Pinus albicaulis*) is a keystone species of high elevation ecosystems throughout western North America. It is often the only tree species capable of surviving in harsh subalpine areas, and is crucial in watershed stabilization and creating habitats that support a wide diversity of plants and animals. Old gnarled relics in remote timberline areas provide important aesthetic values by creating high elevation vistas and providing much of the character of the alpine experience (Schwandt 2006, Tomback and others 2001).

Whitebark pine is currently at risk in much of its natural range due to a combination of white pine blister rust (WPBR, *Cronartium ribicola*) (an introduced disease) (fig. 1); successional replacement by shade tolerant species (fig. 2), and recent outbreaks of mountain pine beetle (MPB, *Dendroctonus ponderosae*) (Keane and others 2002, Gibson and others 2008). Although MPB outbreaks have occurred historically in whitebark pine causing huge losses of mature trees, the additional impacts of WPBR on regeneration and cone production have caused population declines far exceeding previous levels resulting in local extirpation of some populations and threatened extinction of others (Schwandt 2006).

Aerial detection surveys (ADS) have documented recent increases in MPB activity in the Northern Rockies (Gibson 2004), but coverage has not always been complete or

Figure 1. Whitebark pine regeneration infected with white pine blister rust.

In: Keane, Robert E.; Tomback, Diana F.; Murray, Michael P.; and Smith, Cyndi M., eds. 2011. **The future of high-elevation, five-needle white pines in Western North America: Proceedings of the High Five Symposium.** 28-30 June 2010; Missoula, MT. Proceedings RMRS-P-63. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station. 376 p. Online at http://www.fs.fed.us/rm/pubs/rmrs_p063.html

Figure 2. Subalpine fir becoming dominant cover type as whitebark pine is killed by mountain pine beetle at Kings Hill, Lewis & Clark National Forest, Montana.

consistent. In addition, surveys only record recent mortality, so cumulative mortality is not known if areas are not flown annually. Even where annual mortality levels have been reported, ADS does not document WPBR infection levels or the amount of live whitebark pine remaining to provide regeneration. Since whitebark pine depends almost exclusively on the Clark's nutcracker for natural regeneration (Tomback and Linhart 1990), the loss of most mature whitebark pines in a stand may result in little to no regeneration if there are too few cone-bearing trees to support a nutcracker population (McKinney and others 2009).

There have been several reports documenting MPB mortality in lodgepole and whitebark pine stands during MPB outbreaks (Kegley and others 2001, 2004; Gibson 2004, 2005, 2007; Gibson and Aquino 2006; Gibson and others 2008), but these have usually been limited in scope, conducted before the outbreak has run its course, or have not always looked at competing vegetation or regeneration. Recent MPB outbreaks have received a great deal of attention (Gibson 2004, Logan and Powell 2001) and have been prevalent across much of the whitebark pine range – especially in the Northern Rockies. However, little information is presented to describe what the stands look like following MPB outbreaks except to claim the future prognosis for whitebark pine is bleak (Tomback and others 2001).

We investigated this information gap by documenting the condition of regeneration and remaining live, mature trees in various stand types following MPB outbreaks (fig. 3). We hope this information will help resource managers better understand losses from a combination of insect and disease agents and provide information that will assist in developing and prioritizing restoration activities.

The primary goal of this project was to obtain information that could be used to make recommendations and set priorities regarding restoration of whitebark pine in the Northern Rockies. Specific objectives to meet this goal were to:

1. determine the severity of MPB impacts in whitebark pine stands following outbreaks and to quantify both dead and remaining live, mature whitebark pine

Figure 3. Stand evaluated near Avalanche Peak in Yellowstone National Park with 93% whitebark pine mortality following a recent mountain pine beetle outbreak.

Figure 4. Current mountain pine beetle killed trees with red needles (circle) compared to trees killed during the 1930s outbreak (pentagon) on Poverty Flat near Clayton in central Idaho. Trees killed during the 1930s outbreak are visible throughout the photo as gray snags with no fine limbs.

2. determine WPBR status of remaining mature, live whitebark pine
3. determine WPBR infection levels in whitebark pine regeneration
4. determine probable stand trajectory by recording health and abundance of other tree species in mixed stands

In semiarid central Idaho, there were several stands where skeletal trees killed by MPB in an outbreak circa the 1930s remained on site and were quantified and aged by tree ring analysis in 1998 (Perkins and Roberts 2003). This presented an opportunity to compare current outbreak losses with losses from the earlier outbreak (fig. 4).

Methods

Forests in Idaho, Montana, and Yellowstone National Park (YNP) in Wyoming where recent MPB outbreaks have occurred in whitebark pine were identified from past ADS, local specialists, or other surveys. Within these forests, we selected 42 stands on National Forest, Bureau of Land Management, YNP, and private lands. These stands were accessible by road or within reasonable hiking distance and had several years of MPB-caused tree mortality (fig. 5). Stands were sampled using variable-radius plots for large trees and fixed-radius plots for regeneration. Plots were taken at a frequency that adequately sampled selected stands. From plot center, a 10 or 20 basal-area-factor (BAF) prism was used to select sample trees greater than 5 inches diameter at breast height (dbh). BAF was chosen to get an average of 8 to 10 trees per plot. The same BAF was used for all plots in a given stand. Data collected for each tree included tree species, dbh, condition, and damage code (mortality causes and blister WPBR severity levels for live trees). Stand information included GPS coordinates, slope, aspect, elevation, and slope position. All trees less than five inches dbh and greater than six inches in height were tallied in a 1/300th acre regeneration subplot (radius = 6.8') at plot center of each variable-radius plot. Regeneration includes seedlings and saplings from six inches tall to 4.9 inches dbh.

Survey data were entered into a spreadsheet and analyzed using the **F**orest **In**sect and **Di**sease **T**ally (FINDIT) program (Bentz 2000). The following statistics were calculated for each stand:

1. Total trees/acre (TPA) by species
2. Total live and dead basal area (BA ft^2/ac)
3. Quadratic mean diameter (QMD) of live trees by species
4. Live stand density index (SDI)
5. Number of dead and live trees
6. Percentage TPA of each tree species
7. Percentage BA of each tree species
8. Percentage of BA killed by damaging agents in 2009, 2008, and mortality older than 2008
9. TPA by species in 1/300th acre regeneration plots

Multiple linear regression analysis and ANOVA was used to examine relationships between slope, elevation, and aspect with basal area killed by MPB and amount of WPBR infection. We also analyzed differences in MPB and WPBR impacts and tree composition by geographical locations.

In central Idaho, whitebark pine BA lost in the current MPB outbreak was compared to BA lost in the 1930s outbreak.

Results

Mountain Pine Beetle Mortality

Mortality from MPB in the 42 stands surveyed ranged from 30 to 97 percent (mean 72 percent) of whitebark pine BA (fig. 6). Over 90 percent mortality occurred in eight stands in the following locations: Sawtooth National Recreation Area (SNRA) in central Idaho, Beaverhead-Deerlodge National Forest in the Tobacco Roots and Gravelly Ranges, Helena

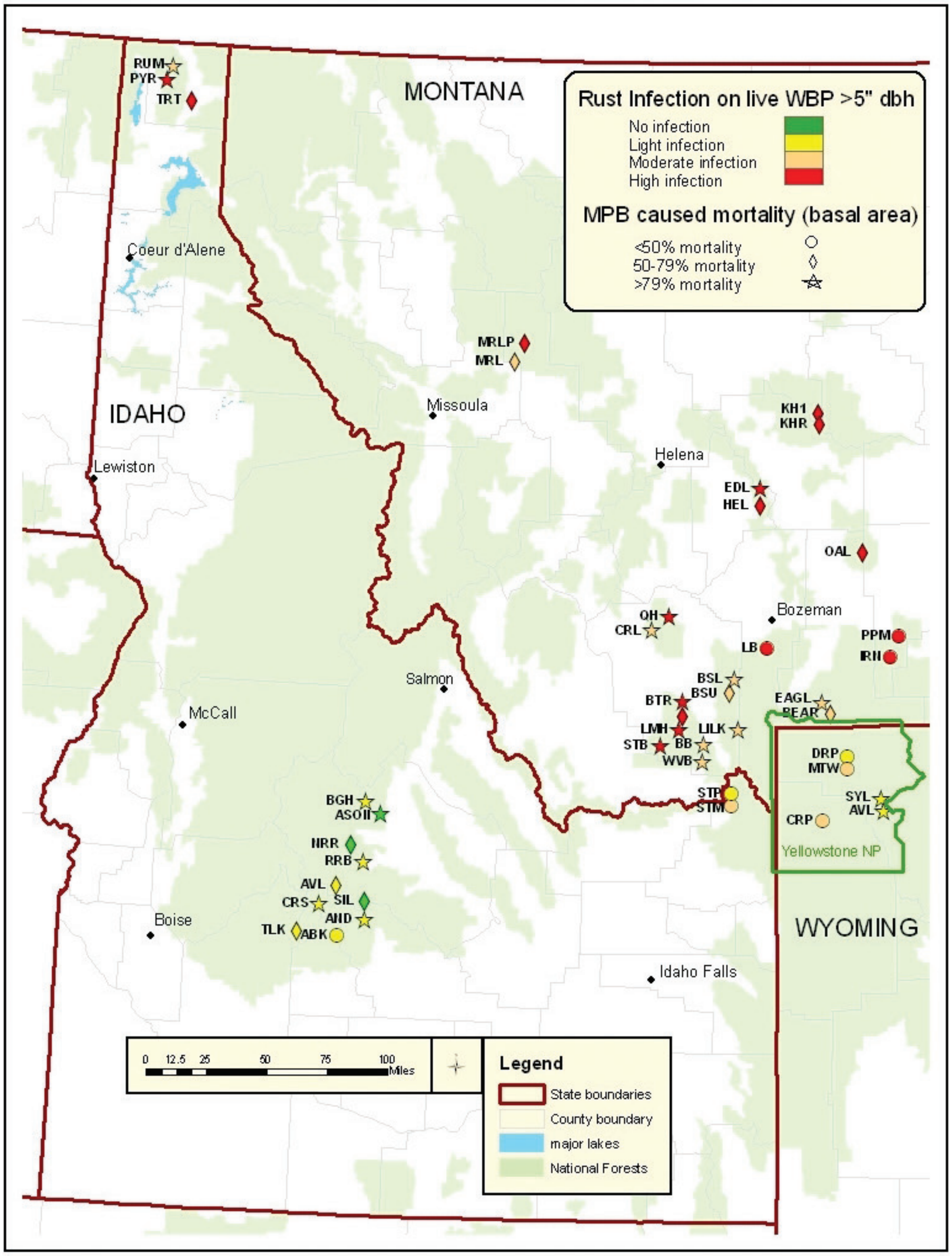

Figure 5. Locations of 42 whitebark pine (WBP) stands surveyed in Idaho, Montana, and Wyoming with white pine blister rust infection levels and mountain pine beetle (MPB) caused mortality.

National Forest in western Montana, Idaho Panhandle National Forests in northern Idaho, and YNP in Wyoming (table 1).

Whitebark pine density (BA) was reduced by more than 80 percent on over half of stands surveyed. Over 50 percent of whitebark pine BA was lost on 81 percent of stands and 76 percent of sites currently have less than 50 ft^2/acre of live whitebark pine BA remaining. Although stands were purposely selected where the MPB outbreak had peaked, a few stands contained current beetle attacks so losses in these stands are likely to increase.

We found no statistically significant relationships between geographic area, slope, elevation, or aspect and basal area killed by MPB.

1930s outbreak compared to current outbreak

Of six stands in central Idaho where MPB outbreaks occurred in both the 1930s and 2000s time periods, three had significantly more BA killed in the 1930s, two had approximately the same amount of BA killed during both periods, and one had more BA killed in the current outbreak (fig. 7). For *some* susceptible stands in central Idaho, this provides

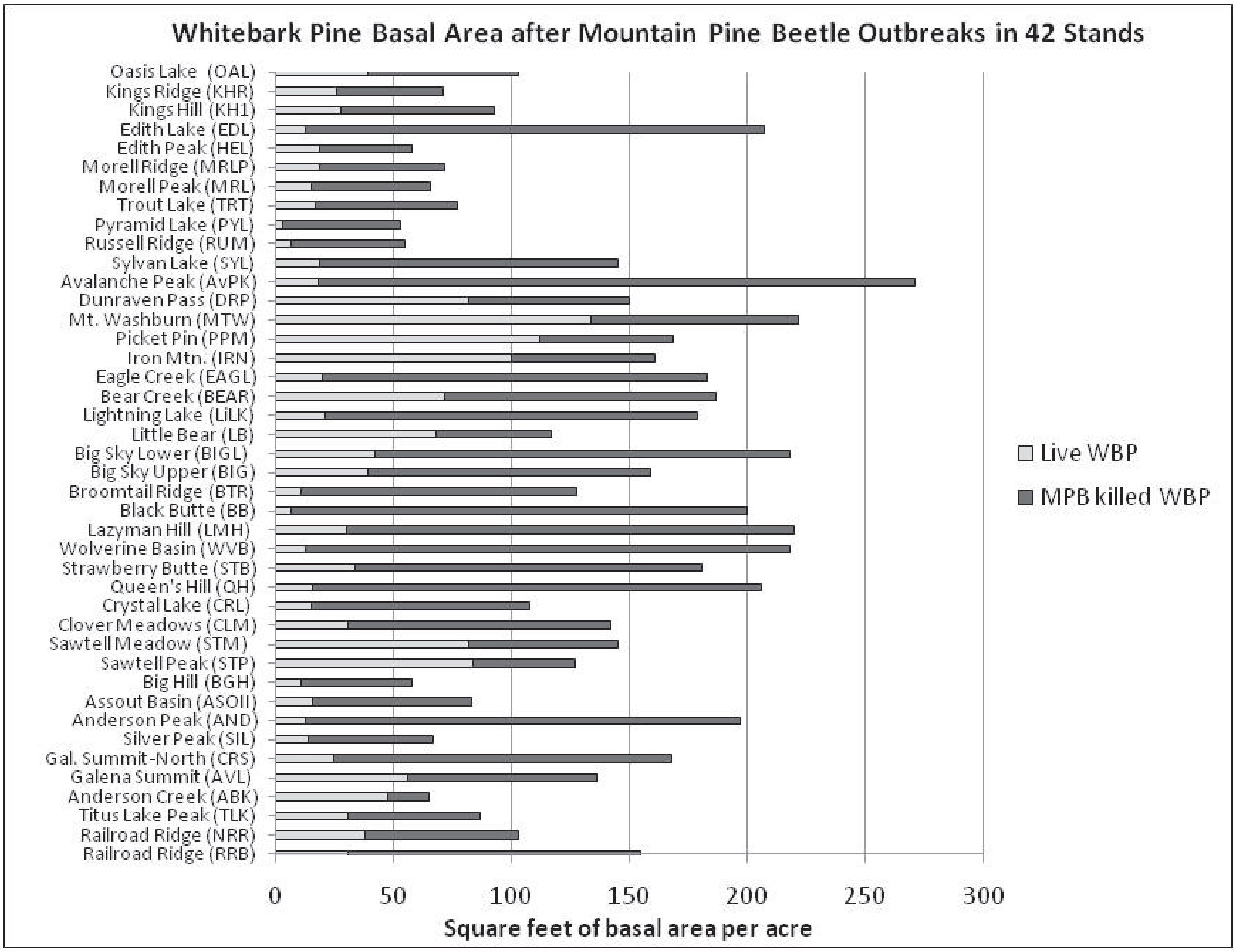

Figure 6. Basal area of live and mountain pine beetle killed whitebark pine by stand.

evidence that whitebark pine mortality during the 1930s MPB outbreak was as great as, or greater than, current mortality levels.

White Pine Blister Rust

Infection on live, mature whitebark pine

WPBR infection levels on remaining live, mature trees ranged from 0 to 100 percent (Table 1). Stands were grouped into 12 general locations based on proximity (fig. 8). The average WPBR infection levels on remaining live, mature whitebark pines in the Helena and Lewis & Clark locations in Montana was over 80 percent, and in four other locations the average rust infection was over 60 percent. The Sawtooth and Salmon stands in central Idaho consistently had low average rust infections (0 to16 percent), while infection levels in other areas varied widely. For example, three of four sites in YNP in Wyoming varied from 12 percent to 28 percent while the Mt. Washburn site had an infection level of nearly 43 percent. Similarly, three of four West Gallatin Montana sites had infection levels from 60 to78 percent, but Lightning Lake was only 37 percent. We found statistically significant differences (p<.01) between both Sawtooth and Salmon blister rust infection levels and most other locations. Blister rust levels at YNP were not statistically different than Salmon or Targhee but significantly different than all other locations (p<.05).

There were a total of 2,473 whitebark pine tallied, and slightly more than half were infected with WPBR. However, only 10 percent of all trees had severe infections with top kill that would affect cone production. Most infections (54 percent) tallied were branch cankers, and severity was light.

There was a significant inverse correlation between percent of trees infected with WPBR and elevation (p<.001); infection levels increased as elevation declined. There were no statistically significant relationships between WPBR infection level and either slope or aspect.

Infection on live whitebark regeneration

Only 26 of 42 sites tallied sufficient numbers of whitebark pine regeneration to get an estimate of WPBR infection. (Only five sites tallied enough regeneration on the 1/300 ac. subplots, the rest were determined by off-plot tallies). Average infection level on these 26 sites was 23 percent and ranged from 0 percent to over 80 percent. The lowest average rust infection levels were in central Idaho (0 to 5.3 percent). Infection levels of regeneration in northern Idaho varied from 15 percent to 23 percent. Those in western Montana

Table 1. Whitebark pine (WBP) stand characteristics used to predict cover type conversion risk with critical levels highlighted. These characteristics include WBP BA killed by mountain pine beetle (WBP BA dead, % WBP BA killed) and white pine blister rust (WPBR) infection levels on live, mature WBP and WBP < 5 inches dbh.

Region/Area	Stand/Year surveyed	WBP BA Live (ft^2/acre)	WBP BA dead	Other spp. BA	% WBP BA killed	% WBP after outbreak	% WPBR on live mature WBP	WBP <5 inch % of total TPA	% WPBR on WBP <5 inch	High Risk convert to other cover type	
Central ID/ Sawtooth NRA	Railroad Ridge *2008*	31	124	3	80%	91%	6%	100%			
	Railroad Ridge *2008*	38	65	9	63%	81%	0%	15%	5%		
	Titus Lake Peak *2008*	31	56	26	64%	54%	5%	34%			
	Anderson Creek *2008*	48	17	14	26%	77%	1%	71%	0%		
	Galena Summit *2008*	56	80	30	59%	65%	3%	44%			
	Galena Sum-North *2008*	25	143	6	85%	81%	3%	32%	0%		
	Silver Peak 2008	**14**	53	20	79%	41%	0%	72%			
	Anderson Peak *2008*	13	184	14	93%	48%	10%	21%		yes	
Central ID/ Salmon Challis NF	Assout Basin *2008*	16	67	2	81%	89%	0%	70%	2%		
	Big Hill *2008*	11	47	2	81%	85%	16%	89%			
GYA/ Targhee NF	Sawtell Peak *2008*	84	43	51	34%	62%	29%	27%			
	Sawtell Meadow *2008*	82	63	41	43%	67%	53%	14%			
GYA/ BVDR-Tobacco Roots	Clover Meadows *2008*	31	111	4	78%	89%	84%	48%	27%	yes	
	Crystal Lake *2009*	15	93	48	86%	24%	65%	13%		yes	
	Queen's Hill *2009*	16	190	12	92%	57%	76%	74%	55%	yes	
GYA/ BVRD-Gravelly Range	Strawberry Butte *2009*	34	147	17	81%	67%	77%	100%	61%	yes	
	Wolverine Basin *2009*	13	205	34	94%	28%	55%	20%		yes	
	Lazyman Hill *2009*	30	190	7	86%	81%	72%	66%	16%		
	Black Butte *2009*	7	193	10	97%	41%	58%	68%	21%	yes	
	Broomtail Ridge *2009*	11	117	36	91%	23%	94%	3%	81%	yes	
GYA/ Yellowstone Club	Big Sky Upper *2009*	39	120	19	75%	67%	41%	29%			
	Big Sky Lower 2009	42	176	16	81%	72%	53%	8%		yes	
GYA/ Gallatin -West	Little Bear *2009*	68	49	33	42%	67%	78%	36%	33%	yes	
	Lightning Lake *2009*	21	158	40	88%	34%	38%	8%	21%	yes	
	Bear Creek *2009*	72	115	15	61%	83%	60%	24%	21%		
	Eagle Creek *2009*	20	163	66	89%	23%	64%	14%	27%	yes	
GYA/ Gallatin-Beartooth	Iron Mtn. *2009*	100	61	63	38%	61%	71%	7%			
	Picket Pin *2009*	112	57	24	34%	82%	73%	95%	11%		
GYA/ Yellowstone NP	Mt. Washburn *2008*	134	88	38	40%	78%	43%	26%			
	Dunraven Pass *2008*	82	68	8	45%	91%	28%	40%			
	Avalanche Peak *2009*	18	253	8	93%	69%	13%	81%	4%	yes	
	Sylvan Lake *2009*	19	126	26	87%	42%	19%	0%	24%	yes	
North ID/ IPNF	Russell Ridge *2008*	7	48	43	87%	14%	60%	14%	15%	yes	
	Pyramid Lake *2008-09*	3	50	121	94%	2%	77%	2%	23%	yes	
	Trout Lake *2009*	17	60	64	78%	21%	89%	19%	23%	yes	
Western MT/ Lolo NF	Morell Peak *2008*	15	51	23	77%	39%	54%	18%	6%	yes	
	Morell Ridge *2008*	19	53	36	74%	35%	79%	5%		yes	
W MT/ Helena NF	Edith Peak *2008*	19	39	103	67%	16%	75%	45%	31%	yes	
	Edith Lake *2008*	13	194	30	94%	30%	100%	88%	16%	yes	
W MT/ Lewis & Clark NF	Kings Hill *2008*	28	65	20	70%	58%	89%	57%	22%	yes	
	Kings Ridge *2008*	26	45	47	63%	36%	90%	21%	68%	yes	
W MT/ Gallatin	Crazy Mtns										
	Oasis Lake *2009*	39	64	110	62%	26%	97%	7%	27%	yes	

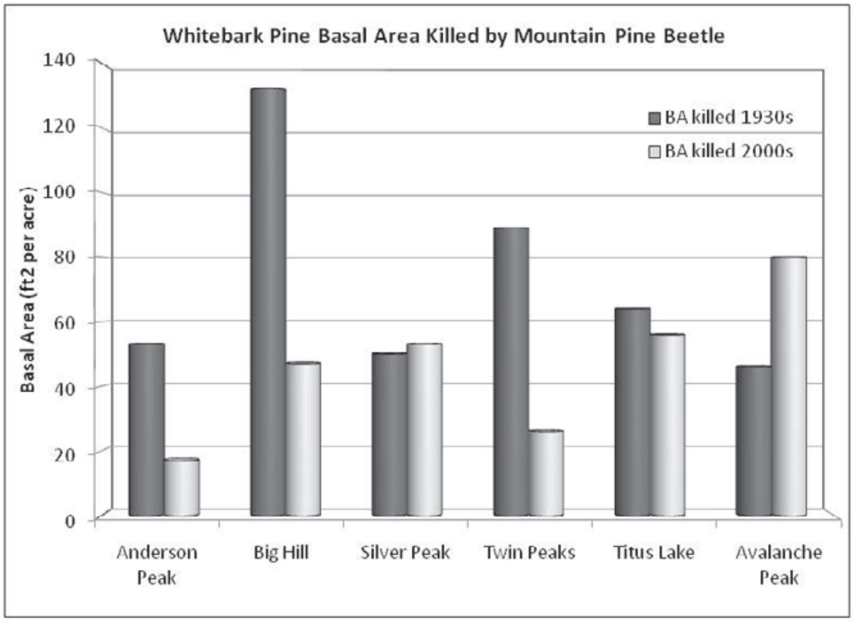

Figure 7. Whitebark pine basal area killed in current and historic outbreaks in 6 stands in central Idaho.

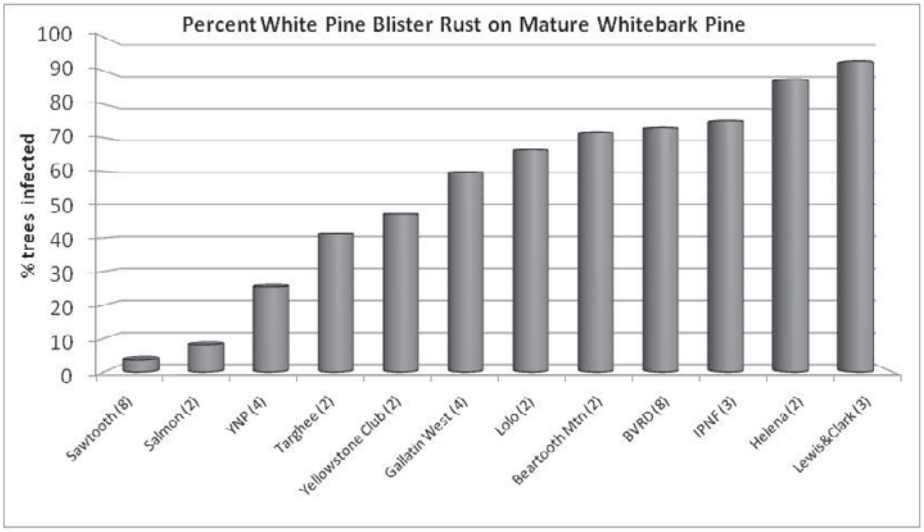

Figure 8. Percent of mature trees infected with white pine blister rust on 12 forests or areas. Number of stands sampled in each area is in parentheses.

ranged from 6.1 percent to 67.9 percent, and those in the GYA varied from 4.2 percent to 80.8 percent.

Competing Vegetation

Mature tree species abundance

The abundance of other mature tree species outnumbered live, mature whitebark pine after MPB outbreaks in 18 of the 42 stands surveyed. This represented 90 percent of sites in northern Idaho and western Montana, 32 percent of sites in the GYA, and 20 percent of sites in central Idaho. Subalpine fir (*Abies lasiocarpa*) was the most abundant mature tree species on 71 percent of sites surveyed followed by lodgepole pine (*Pinus contorta*), Engelmann spruce (*Picea engelmannii*), and Douglas-fir (*Pseudotsuga menziesii*).

Regeneration

Tree species other than whitebark pine less than five inches in diameter were more prevalent on 28 (69 percent) of the 42 areas surveyed (fig. 9). By far, the most abundant other species was subalpine fir (nearly 97 percent of all other species tallied). Other species recorded were Englemann spruce, Douglas-fir, and lodgepole pine. Regeneration per acre of other species varied from 0 percent at Railroad Ridge in the SNRA to 100 percent at Sylvan Lake in YNP. Twenty-three sites had more than 500 TPA of other species, and 13 of these sites had over 1000 TPA of other species. There were 18 stands with more than 500 whitebark pine regeneration TPA, and four of these had more than 1000 TPA. The maximum TPA (3,000) of whitebark pine regeneration was recorded at Edith Lake in western Montana.

Discussion

In order to determine the probable stand-composition trajectory for these whitebark pine sites, we looked at WPBR infection levels, whitebark pine basal area reduction due to

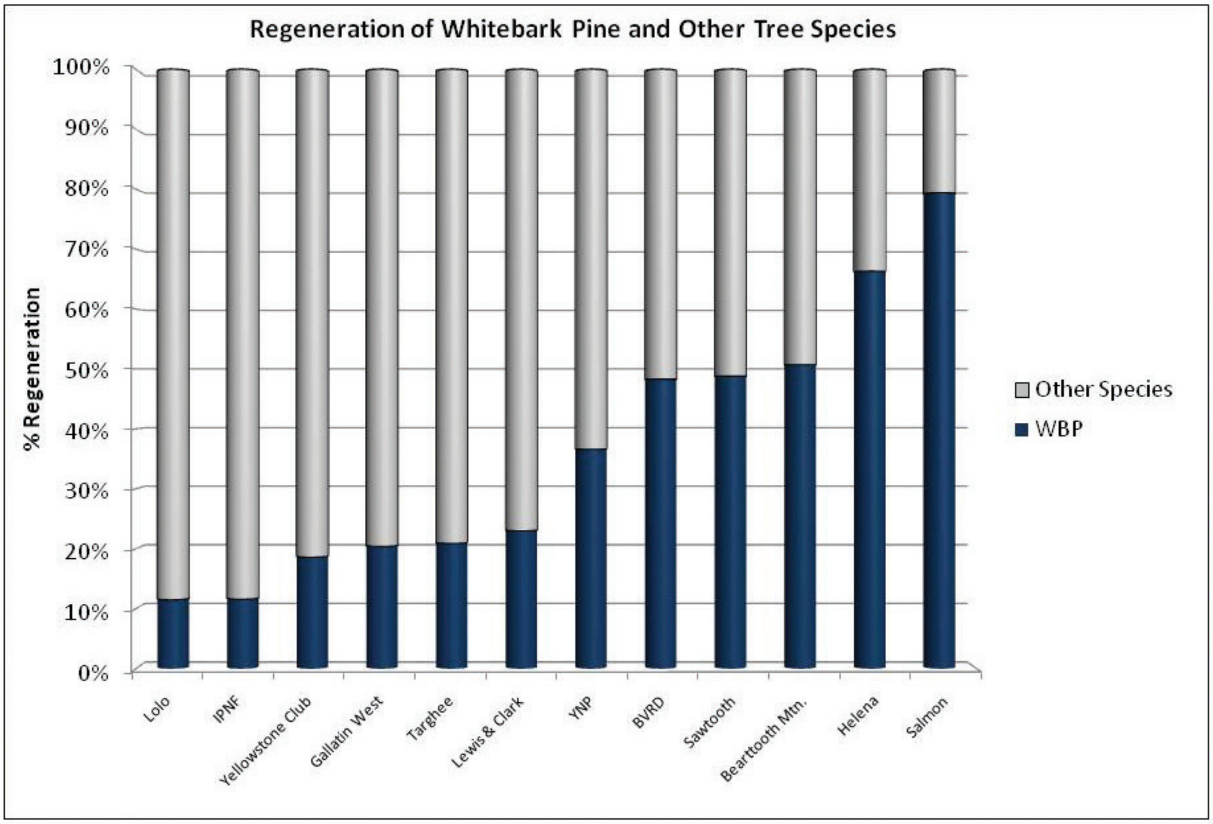

Figure 9. Percent whitebark pine and other tree species regeneration.

MPB, live whitebark pine BA and percent of stand composition, abundance of other mature species, and the abundance and health of all regeneration. Live whitebark pine BA is important for cone production levels needed for seed dispersal by Clark's Nutcracker. Below a threshold level of 22 ft^2 per acre (equivalent to 5 m^2/ha as per McKinney and others 2009) seed dispersal by the bird is disrupted. We defined critical levels based on logical assumptions for the following characteristics:

- whitebark pine BA reduction due to MPB > 90 percent
- live whitebark pine basal area remaining < 22 ft^2/acre
- remaining live, mature whitebark pine <50 percent of stand composition
- percent whitebark pine regeneration minus percent infection of regeneration <50 percent
- percent WPBR in remaining live mature trees >50 percent
- percent WPBR in whitebark pine regeneration >50 percent

Based on these criteria, we found that 24 of 42 of stands surveyed (57 percent) met at least two of these criteria and will likely convert from whitebark pine to other cover types without restoration efforts or wildfire (table 1). Stands that fall into this category should be considered higher priority for active management alternatives that would assist in enhancing whitebark pine restoration.

Restoration activities

Natural regeneration is closely related to fires that historically removed competing vegetation and created seed beds for nutcracker seed caching activities. Aggressive fire control activities may be impacting these opportunities and prescribed fire may be necessary to replace the role of historical wildfires (Keane and Arno 2001).

In many areas, whitebark pine has already been extirpated or nearly so due to MPB, WPBR, and competing vegetation. If these isolated areas are more than a few miles from existing seed sources, it is unlikely that whitebark pine will ever be restored naturally (Schwandt, 2006; McKinney and others 2009). The Forest Service, Bureau of Land Management, and National Park Service are actively collecting cones for restoration and screening for blister rust resistance.

Unfortunately, planting seedlings in remote areas is expensive. Current tests using direct seeding to restore whitebark populations are showing promise, but more information is needed to determine the impact of various seed treatments on seed germination. Even if methods to enhance seed germination are developed, there is a critical need to increase survival of young seedlings. Over 200,000 whitebark pine seedlings grown in nurseries have been recently planted in the western United States. However, survival rates are low in some areas. One possibility for enhancing seedling survival is the application of beneficial mycorrhizal fungi.

These fungi enhance survival by providing nutritional benefits, imparting drought tolerance, and offering protection from pathogens and soil grazers (Cripps 2002, 2004, Cripps and Antibus, these proceedings). Recent studies in northern Montana and Wyoming have identified over 40 fungi in whitebark pine sites and several promising candidates are currently being tested (Cripps and others 2008, Mohatt and others 2008).

In some areas, competing vegetation is being reduced mechanically by thinning or girdling over story species. The success of these treatments is not well known at this time although monitoring plots have been established at some sites.

Verbenone, an anti-aggregation pheromone of MPB, and carbaryl, a contact insecticide, are being used to protect high-value, cone bearing, and potentially WPBR resistant whitebark pine from beetle attack. Verbenone does not offer complete protection but can be a useful tool in reducing beetle-caused mortality in the short term (Kegley and Gibson 2009, Kegley and Gibson, these proceedings). Carbaryl, which is sprayed on tree boles, offers 100 percent tree protection for two years when properly applied (Fettig and others 2006) and should be considered where whitebark pine stands are accessible to spray equipment.

It is critical that restoration efforts, including cone collections and protection of cone bearing trees, be planned for isolated whitebark pine populations, especially if they are threatened by MPB and WPBR. The results of this study should help prioritize restoration efforts in whitebark pine stands in Idaho, Montana, and Wyoming that are at greatest risk.

Literature Cited

Bentz, Barbara J. 2000. Forest insect and disease tally system (FINDIT) user manual. General Technical Report RMRS-GTR-49. Logan, UT: USDA Forest Service, Rocky Mountain Research Station. 12 p.

Cripps, C. L. 2002. Mycorrhiza. In: Pscheidt J. W. and Ocamb, C. M., eds. Pacific Northwest Plant Disease Management Handbook. Oregon State University Press, Corvallis, OR: 21-23.

Cripps, C. L. (editor) 2004. *Fungi in Forest Ecosystems: Systematics, Diversity and Ecology*. New York Botanical Garden Press, NY. 363 p.

Cripps, C. L.; Smith, C.; Lapp, J.; Carolin, T. 2008. Assessment of Ectomycorrhizal Fungi with Whitebark Pine: Waterton-Glacier International Peace Park. Nutcracker Notes. 14: 12-14.

Fettig, C. J.; Allen, K. K., Borys, R. R.; Christopherson, J.; Dabney, C. P.; Eager, T. J.; Gibson, K. E.; Hebertson, E. G.; Long, D. F.; Munson, A. S.; Shea, P. J.; Smith, S. L.; Haverty, M. I. 2006, Effectiveness of bifenthrin (onyx) and carbaryl (SevinSL) for protecting individual, high-value conifers from bark beetle attack (Coleoptera: Curculionidae: Scolytinae) in the western United States. J. Econ. Entomol. 99: 1691-1698.

Gibson, K. E. 2004. Bark Beetle Conditions Northern Region. USDA Forest Service, Northern Region, Forest Health Protection, Missoula Field Office. 47 p.

Gibson, K. E. 2005. Bark Beetle Conditions Northern Region. USDA Forest Service, Northern Region, Forest Health Protection, Missoula Field Office. 46 p.

Gibson, K. E. 2006. Mountain pine beetle conditions in the Greater Yellowstone Ecosystem, 2006. USDA Forest Service, Northern Region, Forest Health Protection, Missoula Field Office. FHP Rpt. 06-03. 7 p.

Gibson, K. E. 2007. Bark Beetle Conditions Northern Region. USDA Forest Service, Northern Region, Forest Health Protection, Missoula Field Office. 55 p.

Gibson, K. E.; Aquino, L. 2006. Bark Beetle Conditions Northern Region. USDA Forest Service, Northern Region, Forest Health Protection, Missoula Field Office. 52 p.

Gibson, K.; Skov, K.; Kegley, S.; Jorgensen, C.; Smith, S.; Witcosky, J. 2008. Mountain pine beetle impacts in high–elevation five-needle pines: current trends and challenges. USDA Forest Service, Forest Health Protection, FHP report R1-08-020. 32 p.

Gibson, K. E.; Steed, B.; Sturdevant, N. 2008. Mountain pine beetle-caused mortality in whitebark pine stands, Northern Region, 2001-2007. USDA Forest Service, Northern Region, Forest Health Protection, Missoula Field Office. 5 p.

Keane, R. E.; Arno, S. F. 2001. Restoration concepts and techniques In: Tomback, D. F., Arno, S. F., Keane, R. E. (Eds.), Whitebark Pine Communities: Ecology and Restoration. Island Press, Washington, D.C., USA. pp. 367-400.

Keane, R. E.; Ryan, K. C.; Veblen, T. T.; Allen, C. D.; Logan, J. A.; Hawkes, B. 2002. Cascading effects of fire exclusion in Rocky Mountain ecosystems. In: Baron, J. S. (Ed.), Rocky Mountain Futures: An Ecological Perspective. Island Press, Washington, DC, USA. pp. 133-152.

Kegley, S.; Gibson, K. 2009. Individual-tree tests of verbenone and green-leaf volatiles to protect lodgepole, whitebark and ponderosa pines, 2004-2007. USDA Forest Service, Northern Region Forest Health Protection, FHP Report 09-03. 12 p.

Kegley, S.; Schwandt, J. W.; Gibson, K. 2001. Forest health assessment of whitebark pine on Pyramid Pass, Russell Mountain, and Burton Ridge in the Selkirk Mountains on the Idaho Panhandle National Forests. USDA Forest Service, Northern Region Forest Health Protection, FHP Report 01-8. 11 p.

Kegley, S.; Schwandt, J. W.; Gibson, K. 2004. Forest health assessment of whitebark pine in selected stands in the Selkirk Mountains of Northern Idaho. USDA Forest Service, Northern Region Forest Health Protection, FHP Report 04-5. 8 p.

Logan, J. A.; Powell, J. A. 2001. Ghost Forests, Global Warming, and the Mountain Pine Beetle (Coleoptera: Scolytidae). American Entomologist. 47(3): 160-172.

McKinney, S. T.; Fiedler, C. E; Tomback, D. F. 2009. Invasive pathogen threatens bird-pine mutualism: implications for sustaining a high-elevation ecosystem. Ecological Applications 19(3): 597-607.

Mohatt, K. R.; Cripps, C. L.; Lavin, M. 2008. Ectomycorrhizal fungi of whitebark pine (a tree in peril) revealed by sporocarps and molecular analysis of mycorrhizae from treeline forests in the Greater Yellowstone Ecosystem. Botany. 86: 14-25.

Perkins, D. L.; Roberts, D. W. 2003. Predictive models of whitebark pine mortality from mountain pine beetle. Forest Ecology and Management. 174: 495-510.

Schwandt, J. W. 2006. Whitebark Pine in Peril: A case for restoration. USDA Forest Service, Report R1-06-28, Missoula, MT.

Tomback, D. F.; Linhart, Y. B. 1990. The evolution of bird-dispersed pines. Evolutionary Ecology. 4: 185-219.

Protecting Whitebark Pines Through a Mountain Pine Beetle Epidemic With Verbenone—Is It Working?

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We initiated a multi-year project to protect individual cone-bearing whitebark pines (*Pinus albicaulis*) from mountain pine beetle (MPB), *Dendroctonus ponderosae* (Hopkins), attack with the anti-aggregating pheromone, verbenone (4,5,5-trimethylbicyclo [3.1.1] hept-3-en-2-one). Our objective was to protect trees through the course of the epidemic that began ca. 2000 in central Idaho. The study population was a subalpine stand of whitebark pine at 9,400 feet elevation near Clayton, ID. Associated conifer species included lodgepole pine, Douglas-fir and subalpine fir.

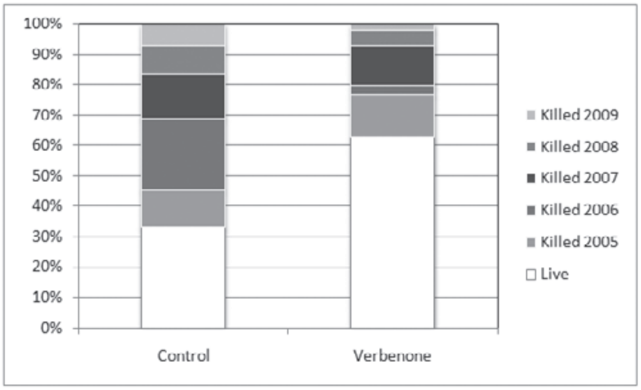

Figure 1. Percent of trees killed by year in control and verbenone treatments for 2005-2009. In 2009, trees treated with verbenone had a 66% survivorship as compared with control trees with 34% survivorship.

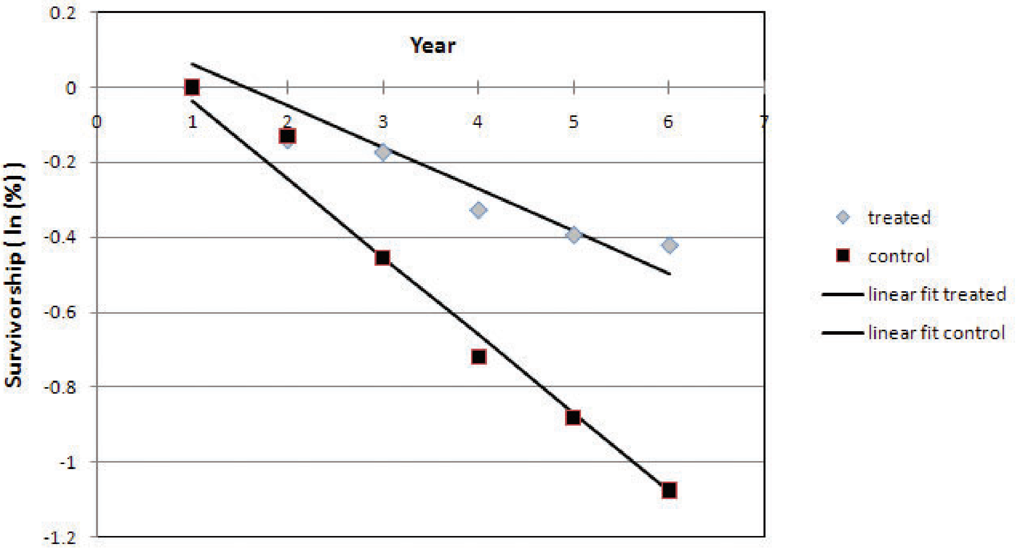

Figure 2. A linear model fit to the natural log of the survivorship proportions beginning in 2005 (year 1). Verbenone treatment: y = 0.172233-0.1115x (slope SE = 0.013); control treatment: y = 0.172233-0.2086x (slope SE = 0.013). Verbenone treated trees had a higher rate of survivorship.

Initially, we followed the methods of Kegley and others (2003) and Kegley and Gibson (2004). These studies had shown effective individual tree protection from mountain pine beetle using verbenone over one season. However, unlike Kegley and others (2003) we monitored the trees for consecutive years and did not use beetle attractants to provide beetle pressure. We identified 149 trees, greater than 8” diameter at breast height, spaced at least 130 feet apart and randomly assigned one of three treatments: (1) a control - no verbenone pouches; (2) two pouches or “low” dose (5 g verbenone/pouch) applied early summer; and (3) two pouches or “high” dose applied early summer and replaced in August. These three treatments were implemented in 2005 and 2006. Our methods were altered in 2007 when the manufacturers of verbenone stopped producing 5-g pouches and increased the pouch dose to 7.5 g of verbenone. Therefore, in 2007 we replaced the “high” dose treatment with two pouches of 7.5 g of verbenone applied once in early summer. And in 2008 and 2009, all previously verbenone treated study trees received one treatment of two pouches of 7.5 g of verbenone applied in early summer. As a result of the industry standard changing from year to year, all levels of verbenone treatments were combined to one treatment, “verbenone,” for the analysis. Verbenone pouches were stapled approximately 6-8 feet above the ground on the northwest and northeast sides to the bole of each selected tree. On multiple stemmed tree clumps, the pouches were stapled to the largest stem in the cluster. Trees were evaluated each fall after peak MPB flight for their condition or MPB-attack status (live, partial attack,

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pitchout or mass attack/dead). Partial attacks and pitchouts were grouped with live trees in this analysis.

Results from 2005 through 2009 indicate whitebark pines treated with verbenone had a 66% survival compared to 34% survival of untreated trees and that the MPB-caused mortality varied from year to year (Fig. 1). A linear model fit to the natural log of the survivorship proportions showed the mortality rate was greater in control than treated trees (Fig. 2). The 95% CI on the mortality rate for control (0.20 ± 0.03) and treated (0.11± 0.03) trees do not overlap and so provides evidence that verbenone conferred some protection. According to the point estimates from these CIs, on average, 20% of control trees died each year while only 11% of treated trees died each year.

We plan to continue this verbenone treatment and monitoring until MPB-caused mortality subsides at the study site.

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References

Kegley, Sandra; Gibson, Ken; Schwandt, John; Marsden, Michael. 2003. A test of verbenone to protect individual whitebark pine from mountain pine beetle attack. FHP Report 03-9. U.S. Department of Agriculture, Forest Service, Forest Health Protection, Northern Region. 6 p.

Kegley, Sandra; Gibson, Ken. 2004. Protecting whitebark pine trees from mountain pine beetle attack using verbenone. FHP Report 04-8. U.S. Department of Agriculture, Forest Service, Forest Health Protection, Northern Region. 4 p.

The Use of Verbenone to Protect Whitebark Pine From Mountain Pine Beetle

Sandra Kegley and **Ken Gibson**

Abstract—Verbenone is a known anti-aggregation pheromone of mountain pine beetle (MPB), *Dendroctonus ponderosae* Hopkins, and has been tested in protecting susceptible host trees from attack since 1988. Inconsistent performance of verbenone during field trials caused formulations and release devices to change through time, resulting in three products currently registered with the Environmental Protection Agency—two pouch formulations containing 7 grams of verbenone that are stapled to tree boles (available from Synergy Semiochemicals Corp. and Contech Enterprises, Inc.), and a flake formulation (available from Hercon Environmental) that can be aerially applied or applied on the ground using fertilizer spreaders.

For several years we tested currently registered 7-gram verbenone pouches by placing two per tree on whitebark pine in northern Idaho and western Montana. At least 80 percent protection of treated trees was consistently achieved, even when using tree baits to ensure beetle pressure. Test plots were located in areas with high MPB populations. More recently, the addition of non-host green leaf volatiles (a hexenol/hexanol blend present in many broadleaf plants), has shown promising results in protecting whitebark, lodgepole and ponderosa pine from beetle attack. Although not yet registered, non-host green leaf volatiles have the potential to enhance treatment effectiveness and decrease the cost of verbenone treatments.

Verbenone-releasing laminated flake formulations aerially applied to lodgepole and whitebark pine stands have shown efficacy in reducing MPB attack over large areas. Tests of flakes applied directly to tree boles have shown similar efficacy to pouches in protecting individual lodgepole pine from beetle attack and are currently being tested on whitebark and limber pines.

Verbenone has been used operationally in many areas to protect high-value, cone-bearing, phenotypically blister-rust-resistant whitebark pine. However, there have been disappointing results in some areas with extreme MPB populations. Unusually warm years may require replacing pouches at mid-season and the clumpy nature of whitebark pine may necessitate using additional pouches per tree or clump of trees. Surrounding clumps of whitebark pine with verbenone pouches has successfully protected trees in some areas. Tree protection in lodgepole pine may be improved by removing currently infested trees in areas of concern and a similar strategy might be considered for protecting whitebark pine in accessible high elevation forests. Ongoing research studies in whitebark pine will determine the efficacy of this treatment tactic.

Verbenone is not the long-sought "silver bullet" and has never protected 100 percent of individual trees or areas of susceptible hosts where it was applied. It should be recognized as another tool useful in reducing beetle-caused mortality (particularly with developing populations) in the short term, with the understanding that environmental conditions and extreme beetle populations may decrease its effectiveness.

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Genetics

Conservation Genetics of High Elevation Five-Needle White Pines

Plenary Paper

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Abstract—Conservation genetics examines the biophysical factors influencing genetic processes and uses that information to conserve and maintain the evolutionary potential of species and populations. Here we review published and unpublished literature on the conservation genetics of seven North American high-elevation five-needle pines. Although these species are widely distributed across much of western North America, many face considerable conservation challenges: they are not valued for timber, yet they have high ecological value; they are susceptible to the introduced disease white pine blister rust (caused by the fungus *Cronartium ribicola*) and endemic-turned-epidemic pests; and some are affected by habitat fragmentation and successional replacement by other species. Potential range shifts resulting from global climate change pose additional threats to these high-elevation species, as suitable climates may no longer exist on the mountains where they grow. The combined impacts of these threats have necessitated active management and conservation activities. While several high-elevation five-needle pines have been well studied, large information gaps exist regarding the genetic diversity and population structure of others. This information is crucial for the development of conservation management strategies. In this report, information on genetic diversity, population structure, and strategies for gene conservation is presented and information gaps identified for North America's high-elevation five-needle pines.

Introduction

What Is Conservation Genetics?

Conservation genetics is "the application of genetics to preserve species as dynamic entities capable of coping with environmental change. It encompasses genetic management of small populations, resolution of taxonomic uncertainties, defining management units within species and the use of molecular genetic analyses in forensics and understanding species' biology" (Frankham and others, 2002: p1). Every species, and each population within species, is the product of a unique evolutionary lineage. The genetic diversity within and among populations and individuals is influenced by the dynamics of past, present and future genetic processes. The objective of conservation genetics is to shed light on these factors to develop strategies to conserve and maintain the evolutionary potential of species. Genetic management in biodiversity conservation also aims to maintain sufficient population sizes to avoid inbreeding, and reducing anthropogenic effects on evolutionary processes. This involves investigating current levels of genetic diversity and population structure using molecular markers and quantitative traits and assessing how these measures are affected by ecological changes. Genetic diversity is influenced by the evolutionary forces of mutation, selection, migration, and drift, which impact within- and among-population genetic diversity in differing ways. Discussions of how these forces impact genetic diversity can be found in many genetics texts (for example Frankham and others 2002; Hartl and Clark 1989) and will not be discussed here.

Why Is Genetic Diversity Important?

Genetic diversity and its conservation have become a priority for many taxa. Genetic diversity can be used to identify unique species or populations. For example, these may be populations that have been geographically isolated for a long time and have diverged from each other by adapting to their local environments. Genetic diversity provides the raw materials for adaptation to changing environments. Conserving genetic diversity protects a population's evolutionary potential, which may be especially important given climate change and increasing disease pressures. Maintaining high levels of genetic diversity is also important because it helps offset the generally deleterious fitness effects of inbreeding depression. There is a growing body of evidence that inbred individuals may be more susceptible to diseases (Frankham and others 2002; Altizer and others 2003; Spielman and others 2004), so preventing inbreeding may help reduce the probability of disease epidemics. Maintenance of genetic diversity and knowledge of the distribution of genetic variation in adaptive traits is important in developing guidelines for the movement of seed in reforestation or restoration projects via developing appropriate seed transfer guidelines and will be especially important in predicting the potential effects of climate change.

How Is Genetic Diversity Assessed?

Genetic diversity is generally assessed using molecular markers and/or phenotypic traits measured on individual seedlings or trees growing in the field or in a common garden. Molecular markers include different enzyme products (proteins) resulting in alternate forms of a gene (isozymes and allozymes), or differences in the DNA sequence of the gene itself. Molecular markers in non-coding regions of the DNA sequence are likely to be selectively neutral, reflecting only

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the effects of demographic and historical processes and not natural selection, while those within coding sequence may not be. There is a growing body of evidence indicating that these markers may not truly be immune to selection, since they may be very close to or linked to adjacent segments of DNA which are impacted by selection (Hahn 2008). A relatively new branch of genomics research, association genetics, specifically investigates the differences found between single nucleotide polymorphisms, called SNPs, which, when assessed in combination with phenotypic information, can reflect local or lineage-wide adaptation (Eckert and others 2009; Eckert and others 2010; Gonzalez-Martinez and others 2007; Gonzalez-Martinez and others 2008; Hall and others 2010; Holliday and others 2008; Manel and others 2010; Neale and Savolainen 2004).

Any physical trait that can be measured on a plant is a quantitative trait. Examples include height, diameter, leaf area, volume, root:shoot ratio, biomass, stress tolerance (e.g., cold or drought), and phenology (e.g., timing of flowering, growth initiation and cessation). If a trait is associated with an environmental gradient, such as temperature or precipitation, then it may reasonably be inferred that the trait has been affected by natural selection and is considered to be adaptive (Endler 1977). Assessing quantitative traits, whether they are adaptive or not, requires measurement of the traits on individuals from a wide variety of geographic origins that are all growing in a common environment to eliminate differing environmental influences on genotypic expression. The physical expression of a plant's genetic makeup, its phenotype, is a product of its genotype and the environment where it is growing. Mature trees in field test sites or seedlings growing in a common garden study are examples (for example Bower and Aitken 2008; Schoettle and Rochelle 2002; Steinhoff and Andresen 1971; and Wright and others 1971). Both of these tests involve collecting seeds or cuttings from a wide geographic range and growing individual trees. Field test sites are often long term, while common gardens usually only last for a few years.

Conservation Challenges

High elevation five-needle white pines are widely distributed across much of western North and Central America and all face conservation challenges: for example habitat fragmentation, introduced disease and insect pests (for example mountain pine beetle *Dendroctonus ponderosae*), advanced succession and climate change (Gibson and others, 2008b, Tomback and Achuff, 2010) as well as harvesting for firewood and incidental cutting during harvest of other co-occurring species. They have low timber value, yet they have high ecological value; and they are all susceptible to the introduced disease white pine blister rust (caused by the fungus *Cronartium ribicola*) (Schoettle and Sniezko 2007). Potential range shifts resulting from global climate change pose an additional threat to these high elevation species, as suitable climates may only occur above the mountaintops where they are often found (Rehfeldt and others 2006; Warwell and others 2007; Wang and others in preparation). The impacts of rust differ by species and also within the geographic range of each species (Schoettle and Sniezko 2007). The combined impacts of these threats have necessitated active management and conservation activities for all of these species.

Genetic conservation approaches may be categorized as either *in situ* or *ex situ*. *In situ* conservation means that genetic resources are protected within a species' natural habitat. This type of conservation is relatively inexpensive and simple, and includes areas such as federally designated wildernesses, National Parks, Research Natural Areas, and other parks and preserves where management activities are limited serve to protect standing genetic diversity. The network of currently existing reserves serve *in situ* conservation purposes well; however, there are risks associated with this conservation strategy. Large-scale disturbances, such as fires, disease, and insect outbreaks, could potentially wipe out large areas of protected habitat. In *ex situ* gene conservation, the resources are protected outside their natural environment. This includes seed orchards, clone banks, long-term seed storage, and cryopreservation. While more secure in some respects, *ex situ* gene conservation can be costly and requires sampling, preferably range-wide, in order to capture as much of the standing genetic diversity as possible. This method focuses on long-term storage and contingency usage of the germplasm, and does not explicitly accommodate the ecological processes or linkages among species inherent with *in situ* conservation approaches.

Taxonomy

The high elevation five-needle pines are all in the group of soft or white pines called haploxylon pines. Taxonomically they are all classified as *Pinus* subgenus *Strobus*, which is split into the sections *Parrya* and *Quinquefoliae* (Gernandt and others 2005; Little and Critchfield 1969; Price and others 1998). Within section *Parrya*, Rocky Mountain bristlecone pine (*Pinus aristata*), foxtail pine (*P. balfouriana*), and Great Basin bristlecone pine (*P. longaeva*) are classified in subsection *Balfourianae* (Bailey 1970). Rocky Mountain and Great Basin bristlecone pine were considered a single species (*P. aristata*) until 1970 (Bailey 1970). Within section *Quinquefoliae* (formerly section *Strobus,* Little and Critchfield 1969), limber pine (*P. flexilis*), southwestern white pine (*P. strobiformis*), and Mexican white pine (*P. ayacahuite*) are classified in subsection *Strobus* (formerly subsection *Strobi*, Little and Critchfield 1969; Price and others 1998). While Mexican white pine is not a North American high-elevation five-needle white pine, we have included it here for completeness because of its inclusion in subsection *Strobus* and its close affinity with southwestern white and limber pine. Whitebark pine (*P. albicaulis*) has traditionally been classified in subsection *Cembrae* (Little and Critchfield 1969; Mirov 1967; Price and others 1998; Shaw 1914), the stone pines, which contains four other Eurasian species distinguished by wingless seeds and indehiscent cones (Shaw 1914; Lanner 1982), a character that appears to be an adaptation to seed dispersal by nutcrackers (genus *Nucifraga*, family Corvidae) (Lanner 1982; Tomback and Linhart 1990). However, a recent treatment by Gernandt and others (2005) using chloroplast DNA sequences collapsed the subsection *Cembrae* into subsection *Strobus*, supporting earlier results that failed to find differences between subsections *Cembrae* and *Strobus* (Strauss and Doerksen 1990; Liston and others 1999; Tomback and others, these proceedings).

Mexican white pine and foxtail pine are the only species with recognized varieties. *P. ayacahuite* var. *veitchii* is found primarily in the northern part of the species' range while var. *ayacahuite* which is found in the southern part of its range (Farjon and Styles 1997). Perry (1991) also recognized var. *brachyptera* which often is synonymous with southwestern white pine in accordance with Farjon and Styles (1997). We have, therefore, included southwestern white pine as a distinct species. Foxtail pine also has two subspecies, defined by their geographic distributions with subspecies delineated by several quantitative, needle, cone and bark characteristics. Subspecies *austrina* is found in the southern Sierra Nevada and subspecies *balfouriana* is found in the Klamath Mountains of northern California (Bailey 1970; Mastrogiuseppe and Mastrogiuseppe 1980). Indirect estimates of divergence times between northern and southern populations are ~10^6 years ago (Eckert and others 2008).

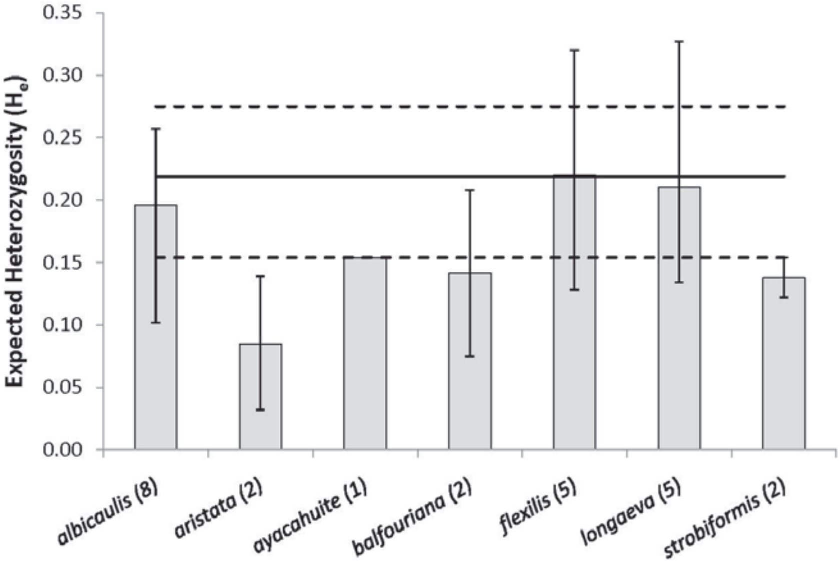

Figure 1. Expected heterozygosity (H_e) for seven species of high elevation five-needle pines. Bars indicate range of reported values[a]. Lines are the mean (solid) and range (dashed) for pines in the subgenus *Strobus* summarized from Ledig (1998). Error bars are the range of values given in Table 1, numbers in parentheses are the number of values reflected in chart.

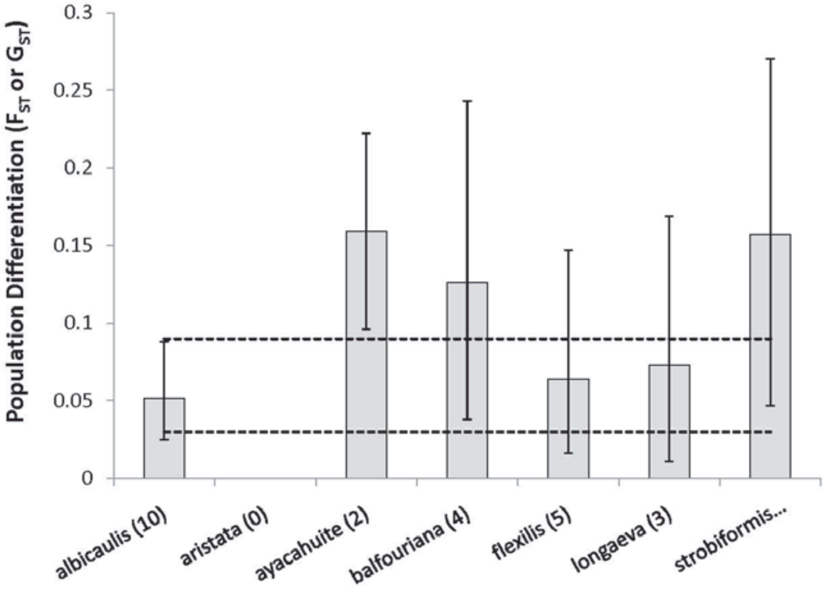

Figure 2. Population differentiation (F_{ST} or G_{ST}) for seven species of high-elevation five-needle pines[a]. Bars indicate the range of reported values. Dashed lines are means for samples of pines with wind- or seed-dispersed seed from (Bruederle et al. 1998). Error bars are the range of values given in Table 1, numbers in parentheses are the number of values reflected in chart

Genetic Diversity and Population Structure

While the genetics of some of these species have been well studied, large information gaps remain regarding the genetic diversity and population structure of others. This information is crucial for the development of management strategies designed to conserve genetic diversity. To date, most molecular assessments of genetic diversity have used isozymes, although the number of DNA marker studies is increasing. Diversity statistics from DNA studies vary depending on marker type and the number of loci assessed. For consistency we have focused on studies using isozymes, as these values are generally comparable across species. We have included results from DNA studies when this is the only information currently available. Genetic diversity (expected heterozygosity, H_e) for these species is generally at or below the mean relative to other widespread western North American conifers (figure 1). However, there is a great deal of variation among species, both in the number and the range of published values. For instance, a value reported (0.327) for Great Basin bristlecone pine is one of the highest observed in any conifer, while reports for its closest relative, Rocky Mountain bristlecone pine, have been low (figure 1). Population differentiation (F_{ST} or G_{ST}) also varies considerably among species (figure 2). Pines with bird-dispersed seed on average exhibit levels of population differentiation only one third of those with wind-dispersed seed (figure 2), due to the more efficient mechanism of seed dispersal leading to population homogenization (Bruederle and others 1998; Bruederle and others 2001; Tomback and others, these proceedings). Whitebark and limber pine both rely on the Clark's Nutcracker for seed dispersal, and have relatively low levels of population differentiation. The other species have average or above levels of population differentiation, possibly due to their patchy and discontinuous distributions on mountaintops across large areas. Only a single report of heterozygosity from two populations is available for southwestern white pine, c.f. unpublished data in Ledig (1998).

Genetic Management

Gene conservation strategies have been developed and implemented for whitebark and Rocky Mountain bristlecone pine. The Pacific Northwest Region of the USDA Forest Service developed a restoration strategy for whitebark pine in Oregon and Washington (Aubry and others 2008) and an *ex situ* gene conservation plan (Bower and Aubry 2009), and a range wide restoration strategy is in development (Keane and others in preparation). As noted above, all of these high-elevation five-needle white pine species face a variety of threats. In some instances, the threats are acute (for example, mountain pine beetle, or white pine blister rust), while other threats are more slow acting (for example climate change, habitat fragmentation, land use conversion). Regardless of the threat(s) faced, all of these species are vulnerable to population declines, and active management is necessary to preserve the existing genetic resources and restore degraded populations. Extensive gene conservation efforts are under way for most high elevation five-needle pine species. Development of blister rust resistant planting stock is a crucial part of a restoration plan for any of these species: rust resistance trials are under way for whitebark pine (Mahalovich and Dickerson 2004; Mahalovich and others 2006; Sniezko and others 2007; R. Sniezko personal communication), southwestern white pine (R. Sniezko, personal communication), Great Basin bristlecone pine (D. Vogler, personal communication), limber pine, and Rocky Mountain bristlecone pine (A. Schoettle, personal communication). Blister rust resistance screening has identified some resistance in all of these species (Sniezko and others, these proceedings), including a hypersensitive reaction type of resistance in several species (Kinloch and Dupper 2002).

Whitebark Pine (*Pinus albicaulis* Engelm.)

Occurrence

Whitebark pine occurs in high-elevation treeline ecotones throughout much of northwestern United States and southwestern Canada. The species' range is comprised of two major components: the Sierra Nevada, Cascades, and coastal ranges of British Columbia, Canada, to the west; and the Rocky Mountain ranges to the east, with scattered patches of habitat in between (Arno and Hoff 1989, Tomback and Achuff 2010, Tomback and others, these proceedings). The breadth of temperatures experienced by whitebark pine is relatively consistent throughout its range (Weaver 2001), while the elevation at which it grows drops from 3,600 m in the Sierra Nevada to 900 m in central British Columbia. Whitebark pine is unique among North American pines in that the cones remain closed and affixed to the tree at maturity. The species is almost entirely dependent on Clark's Nutcrackers (*Nucifraga columbiana*) for seed dispersal (Tomback 2001).

Genetic Diversity

Range-wide and regional studies have yielded a range of genetic-diversity estimates for whitebark pine (table 1). In an allozyme study using populations from throughout the species range, Jorgensen and Hamrick (1997) found whitebark pine to have lower within (H_e = 0.092) and among (H_e = 0.102) population genetic diversity than most pines. Bruederle and others (1998) found similar patterns (H_e = 0.152) among whitebark pine populations in the Greater Yellowstone Ecosystem. In a regional study within British Columbia, expected heterozygosity levels were higher (H_e = 0.262), perhaps as a result of founding events from multiple populations within the region (Krakowski and others 2003). There is some evidence of higher genetic diversity in the eastern portion of the species' range than in the west (Jorgensen and Hamrick 1997), and there appears to be lower genetic diversity in the Olympic Peninsula populations than in the Oregon and Washington Cascades (Bower and others unpublished data). Whitebark pine harbors similar levels of genetic diversity relative to other widespread, wind-dispersed pines based on the aggregate of published data (figure 1) (Bruederle and others 1998; Hamrick and others 1992).

Population-level genetic variation and differentiation have been assessed for whitebark pine using both molecular markers (table 1) and quantitative traits (Bower and Aitken 2006; 2008). Neutral marker studies generally reveal little genetic structure among broadly distributed populations (F_{ST} or G_{ST} < 0.09) (table 1 and figure 2). On average, over 95 percent of genetic variation was distributed within populations, and less than 5 percent was among populations.

In a broad-ranging study using microsatellite data from both pollen and seeds, Richardson and others (2002) found relatively homogeneous mtDNA haplotype distributions at both coarse and fine scales within populations, but considerable genetic divergence among populations separated by over 20 km. Pollen-dispersal distances, by contrast, appeared much higher (F_{ST} < 0.007 for cpDNA markers) (Richardson and others 2002). These results concur with expectations of high pollen-mediated gene flow due to wind distribution, but restricted seed-mediated gene flow due to the Clark's Nutcracker, which cache most seeds relatively close to the parent tree, but can fly over a dozen kilometers, thereby mediating long-distance dispersal of genetic material (Tomback 2001). While average genetic diversity is similar among

Table 1. Population genetic information for seven high-elevation five-needle pine species. Data are for isozymes except where noted.

Species	**Sample Distribution**	**# populations**	**He**[a]	**Fst or Gst**[b]	**F**[c]	**Reference**
albicaulis	BC, ID, MT, WY	14		0.075		Bower and others *in press*
	USA range wide and northern AB	30	0.102	0.034	0.084	Jorgensen and Hamrick 1997
	USA Great Basin	14	0.204	0.088	0.06	Yandell 1992
	Canadian Rockies	29	0.224	0.062		Stuart-Smith 1998
	British Columbia	17	0.257	0.061	0.345	Krakowski and others 2003
	range wide	18		0.046[d]		Richardson and others 2002b
	Greater Yellowstone	9	0.152	0.025	0.016	Bruederle and others 1998
	range wide	85	0.194	0.038	0.111	Bower and others these proceedings
	Olympic Peninsula	9	0.163	0.059	0.131	Bower and others these proceedings
	Inland NW	117	0.271	0.026	-0.016	Mahalovich these proceedings
	OR, No. CA, No. NV	13		0.058[e]		Oline unpublished data
flexilis	USA range wide and southern AB	30	0.186	0.101	0.193	Jorgensen and others 2002
	CO	5	0.3	0.035	0.007	Schuster and Mitton 2000
	CO	2	0.32	0.022		Schuster and others 1989
	CO	7		0.016		Latta and Mitton 1997
	n/a[f]	5	0.165	0.147		Hipkins unpublished data
	n/a		0.128			Politov and Krutovsky 2004
strobiformis	Nuevo Leon, MX	2	0.154	0.047		Ledig 1998
	MX	23		0.27[g]		Moreno-Letelier and Pinero 2009
	n/a		0.122			Politov and Krutovsky 2004
ayacahuite	range wide	14	0.154	0.222		Ledig 1998
	MX	7		0.096[h]		Moreno-Letelier and Pinero 2009
balfouriana	range wide	4	0.208			Hiebert and Hamrick unpublished data
	species	16	0.075	0.038	0.267	Oline and others 2000
	subsp. *balfouriana*	5		0.242	0.203	Oline and others 2000
	subsp. *austrina*	11		0.075	0.443	Oline and others 2000
	species	20		0.15[i]		Eckert and others 2008
	between N & S	20		0.17[j]		Eckert and others 2008
aristata	range wide	5	0.139			Hamrick and others 1981
	range wide	4	0.032			Oline unpublished data
longaeva	UT NV	5	0.327	0.0378	0.103	Hiebert and Hamrick 1983
	White Mountains	3	0.134	0.011	0.078	Lee and others 2002
	Great Basin		0.218	0.169		Hamrick and others 1994
	UT		0.237			Hamrick and others 1994
	White Mountains		0.135			Hamrick (cited in Lee and others 2002)

[a] H_e = expected heterozygosity – a measure of genetic diversity;
[b] F_{ST} and G_{ST} are measures of population differentiation;
[c] F is a measure of inbreeding
[d] $\boldsymbol{\Phi}_{\mathbf{ST}}$ from chloroplast DNA microsatellite data
[e] F_{ST} from chloroplast DNA microsatellite data
[f] n/a = information not available
[g] R_{ST} from chloroplast DNA microsatellite data
[h] R_{ST} from chlorplast DNA microsatellite data
[i] $\boldsymbol{\Phi}_{\mathbf{SC}}$ from nuclear DNA sequences
[j] $\boldsymbol{\Phi}_{\mathbf{CT}}$ from nuclear DNA sequences

pines with bird-dispersed and wind-dispersed seed, population differentiation is considerably lower for bird-dispersed species because of the homogenizing effect of birds moving seed among populations (Bruederle and others 1998).

Stand-scale genetic structure is strong for whitebark pine. Stems comprising a "tree cluster" are often half or full-sib relationships, while neighboring clusters in close proximity have the same family structure as those located farther apart (Furnier and others 1987). This was demonstrated by Rogers and others (1999), who found negligible genetic structure among watersheds (F_{ST} = 0.004), but strong differentiation among tree clumps within sites (F_{ST} = 0.334). Again, these trends are directly linked to Clark's Nutcracker seed-caching habits as they can harvest up to 150 seeds at a time, often from a single parent tree, then fly to a caching site and deposit numerous seeds in each cache (Tomback 1982).

Quantitative trait analyses for 48 whitebark pine populations from throughout the species range revealed higher population differentiation (Q_{ST}) for many quantitative traits compared to the differentiation estimates using neutral markers (F_{ST} and G_{ST}) (Bower and Aitken 2006, 2008). Cold adaptation (date of needle flush and fall cold injury) traits showed the strongest geographic differentiation (Q_{ST} = 0.36 – 0.47), while height and biomass growth showed low to moderate differentiation (Q_{ST} = 0.07 – 0.14). In a study using populations from Idaho, Montana and Washington, Mahalovich and others (2006) also found populations differentiated by latitude and climate, with seedlings from milder provenances growing taller but having lower freezing tolerances than those from harsher locations. Using populations from the same region, Warwell (In preparation) found similar trends, with populations from lower elevations and higher latitudes having higher growth potential than their conspecifics. Together, these findings suggest that selection pressures, particularly temperature, are driving local population adaptation.

Mating Systems and Inbreeding Depression

In whitebark pine, high inbreeding rates are attributed to the clustered growth of half and full-sibling individuals caused by Clark's Nutcrackers seed-caching habits (Jorgensen and Hamrick 1997). Numerous studies have quantified inbreeding in whitebark pine at local and regional scales (table 1), indicated by a deficiency of heterozygotes ($F_{IS} > 0$). In populations from Oregon, Montana and British Columbia, Bower and Aitken (2007) found that outcrossing rates varied among families, with the multilocus outcrossing rate (t_m) averaging 0.86 (range: 0.73 to 0.93). Krakowski and others (2003) found very high inbreeding levels (F_{IS} = 0.345) and outcrossing rates below average for conifers (t_m = 0.73), although only two populations separated by ~100 km were used for these estimates.

Conservation Status and Action

Whitebark pine is declining throughout its range, primarily due to white pine blister rust and secondarily due to mountain pine beetle and fire suppression (Tomback and others, these proceedings). Climate change is also predicted to have devastating effects for whitebark populations, particularly throughout southern and central portions of the species' range, where forecasted 21st century temperatures are too warm for whitebark pine to retain a competitive advantage (Warwell and others 2007; Wang and others in preparation). Recognizing that Canada's whitebark pine population is expected to decline by over 50 percent due to all these factors within the next 100 years, Canada's Committee on the Status of Endangered Wildlife in Canada (COSEWIC) formally recommended that whitebark pine be classified as endangered in April, 2010 (Tomback and others, these proceedings). Once it is classified as endangered, the Canadian federal government will be responsible for ensuring that a conservation strategy is put in place for the species. In the United States, the Fish and Wildlife Service is currently conducting a status review for whitebark pine in light of its decline (Tomback and others, these proceedings). Whitebark pine is classified as "vulnerable" according to the IUCN, due to declines attributed to 1) white pine blister rust, 2) mountain pine beetle, and 3) successional replacement by shade tolerant species as a result of fire exclusion (Reuling 2008).

In response to its rapid and widespread decline, numerous governmental and non-governmental organizations are drafting conservation strategies at various scales for whitebark pine. The Pacific Northwest region of the USDA Forest Service has drafted a comprehensive, regional conservation strategy for the species focusing on research, restoration, genetic conservation, and blister rust resistance screening (Aubry and others 2008). Over 500 tagged permanent monitoring plots have been installed at nearly 100 locations in Oregon and Washington to monitor health and status over time. A range-wide conservation strategy is also being developed, focused on providing land management agencies with tools to plan, design and implement fine-scale restoration activities (Keane and others in preparation)

Gene conservation

Much of the range of whitebark pine in the United States is located within protected areas on public lands. In Oregon and Washington, 60 percent of the species' habitat is in congressionally-designated wilderness areas (Aubry and others 2008). Whitebark pine is also found in several national parks, including North Cascades, Mount Rainier, Olympic, Crater Lake, Lassen Volcanic, Yosemite, Glacier, Yellowstone, and Grand Teton in the U.S. and seven National Parks in Canada, including Mount Revelstoke, Glacier, Jasper, Banff, Kootenay, Yoho, and Waterton Lakes. There are also extensive populations in provincial parks and other protected areas throughout southern British Columbia and western Alberta. These lands provide an extensive *in situ* gene conservation resource; however, the integrity of this resource is seriously threatened in many areas by white pine blister rust and mountain pine beetle. Range-wide cone collections have been made for *ex situ* gene conservation, blister rust resistance screening, and restoration (see Sniezko and others these proceedings; Bower and Aubry 2009; Bower and others 2009). To date, seed has been collected from approximately 700 individuals in the United States for long term *ex situ* gene conservation.

White pine blister rust resistance

White pine blister rust resistance screening initiated at USDA forest genetics centers (Dorena Genetic Resource Center in Cottage Grove, OR; Pacific Southwest Research Station in Placerville, CA; Coeur d'Alene Nursery in Coeur d'Alene, ID) have reported low to moderate levels of natural rust resistance in some populations, as evidenced by the ability of seedlings to survive multiple spore inoculations (Mahalovich and others 2006; Vogler and others 2006; Sniezko and others 2008; Sniezko and others these proceedings). Resistance varies along a geographic cline within the intermountain western U.S., increasing from southeast to northwest (Mahalovich and others 2006). Resistance also appears to be higher among populations from milder climates (Mahalovich these proceedings). In Oregon and Washington, early results show that approximately 25 percent of families field selected for possibly resistance and tested had some level of resistance (R. Sniezko, personal communication). Resistant seedlings have been recommended for immediate use in restoration planting as well as in breeding programs. However, it will be critical to account for other factors—particularly temperature and day length—that may affect survival of planting seedlings. Seed transfer guidelines have been developed based on adaptive traits, in an attempt to minimize maladaptation risks at an acceptable level (Aubry and others 2008; Bower and Aitken 2008; Mahalovich and Dickerson 2004). Exceeding these transfer distances increases the risk of maladaptation under current conditions, and should only be done after weighing this risk against the need for restoration. In the case of white pine blister rust, the risk of disease infection may outweigh the risk of maladaptation, and it may be desirable to move resistant seedlings beyond the recommended limits.

Predicted climate change impacts

Whitebark pine is expected to fare poorly as the climate warms (see also Tomback and others, these proceedings). Within its current range, models predict that faster-growing species such as subalpine fir and Engelmann spruce will encroach from lower elevations (Schrag and others 2008), while ecologically and climatically suitable habitat may not open at higher elevations due to the slow development of adequate soils in alpine environments. Results from growth chamber experiments similarly indicate that lodgepole pine dominates whitebark pine in height growth at virtually all growing season temperatures predicted to occur within whitebark pine's current range within the 21st century (McLane and Aitken in preparation). Moving seed only from south to north has been recommended, as these populations may be "pre-adapted" to a warmer climate. Mixing seed from different populations within the acceptable transfer range would likewise facilitate natural selection among a wider range of genotypes (Bower and Aitken 2008).

Whitebark pine is expected to lose up to 90 percent of its climatic range within Canada by the end of the 21st century (Warwell and others 2007, Wang and others in prep.). However, a large area of northwestern British Columbia that does not currently support this species may be climatically suitable for the species at present, and remain so as the climate warms (Wang and others in preparation). McLane and Aitken (in preparation) established common garden trials at multiple latitudes within the predicted climatic range to assess how climatic and environmental factors impact whitebark pine germination and survival in these areas, and whether populations respond differently across the range of growing conditions. In the first three growing seasons, germination, survival and growth were positively influenced by early-melting snow packs and warmer growing conditions, while population differences were negligible. The common gardens will continue to be monitored at least until the 2030s. McLane and Aitken are also initiating an experiment to evaluate growth and survival of seedlings planted along an altitudinal transect representing a ~3 °C temperature gradient in Whistler, BC. The seedlings were planted in August, 2010, and will be monitored for survival and growth.

Limber Pine (*Pinus flexilis* James)

Occurrence

Occurring from southern Canada to northern New Mexico, limber pine is one of the most widely distributed five-needle pines in North America (Tomback and Achuff 2010; Tomback and others, these proceedings). Mostly occurring in the Rocky Mountain and the Basin and Range regions, populations are also found in the White and Sierra Nevada ranges of California, the Black Hills of South Dakota and as isolates in the Great Plains. Limber pine has a wider elevation al distribution than any of its co-occurring conifers; it grows on sites from 870 m in North Dakota to over 3400 m in Colorado (Steele 1990). While primarily an upper timberline species in relatively dry locations, limber pine is also found at lower timberline in locations such as along the Rocky Mountain Front and in the Great Plains and Black Hills (Steele 1990). Substantial fossil evidence suggests the Pleistocene distribution of the species extended into the Great Plains, Texas and northern Mexico (Wells 1983; Betancourt 1990).

Like whitebark pine, limber pine is partially dependent on Clark's Nutcracker for long distance seed dispersal (Tomback 1978; Tomback and Linhart 1990). Morphologically, it is difficult to distinguish the two species without cones, but the dehiscent and slightly longer and slimmer cones readily identify limber pine, and limber pine usually grows at lower, climatically milder elevations. Despite the similar morphology and reliance on the Clark's Nutcracker for dispersal, limber pine is most closely related to southwestern white pine (*P. strobiformis*) of the southwestern U.S. and northern Mexico, and Mexican white pine (*P. ayacahuite*), which extends into southern Mexico. This group of three species, which form a seed dispersal cline from wind-dependent in the south to Nutcracker-dependent in the north, has been described as the "world's greatest north-south chain of pine populations…" (Lanner 1996, p. 111). *Pinus flexilis* var. *reflexa* or *P. reflexa* is a taxon of apparently hybrid origin between *P. flexilis* and *P. strobiformis* (Farjon and Styles 1997). There has been speculation that the origin of the hybrid zone is ancient, with most current individuals being later generation backcrosses to *P. strobiformis* (Perry 1991).

Genetic Diversity and Structure

Compared to other North American high elevation five-needle pines, limber pine has relatively high levels of allozyme diversity (table 1 and figure 1). However, there is substantial variation in the amount and distribution of genetic diversity over the species' range (Jorgensen and others 2002). In general, populations from the Basin and Range and central Rocky Mountain regions exhibit higher levels of genetic diversity than northern Rocky Mountain or peripheral isolated populations (Jorgensen and others 2002; Schuster and Mitton 2000).

Genetic variation in quantitative traits has been found among populations and among families within populations. Differences among populations exhibited a gradation with cone size, seed weight, and seedling growth slightly increasing and leaf color darkening from north to south (Steinhoff and Andresen 1971; Wright and others 1971). Quantitative genetic variation in limber pine has been characterized as low (Steinhoff and Andresen 1971).

Contemporary gene flow among populations appears to occur mainly via pollen flow (Latta and Mitton 1997; Schuster and Mitton 2000), despite the Clark's Nutcracker's ability to disperse seeds long distances. Latta and Mitton (1997) examined seven populations of limber pine from Colorado using chloroplast (cpDNA) and mitochondrial (mtDNA) DNA, which are paternally and maternally inherited, respectively. There was virtually no genetic structure among cpDNA haplotypes, representing both pollen and subsequent seed dispersal (F_{ST} = 0.013). In contrast, strong genetic structure was detected among the mtDNA haplotypes, which are dispersed via seeds only (F_{ST} = 0.679). Because of substantial pollen flow, genetic neighborhoods of limber pine populations are quite large (Schuster and Mitton 2000).

Substantial amounts of local pollen flow have not translated to broad-scale patterns of homogeneity, however. Mitochondrial DNA indicates that the current distribution of limber pine was derived from several Pleistocene-era refugial populations (Mitton and others 2000). These ancestral populations, combined with low recent historical seed flow, have resulted in contemporary populations that are substantially differentiated. These patterns are not uniform over the species' range, however. For example, genetic structure among populations in the Basin and Range region, which harbored Pleistocene populations, is substantially higher than among populations from the relatively recently colonized northern Rocky Mountains (G_{ST} of 0.084 and 0.038, respectively). Studies with a more limited range tended to reveal lower geographic structure than a range-wide study (table 1). Across all of these studies, population differentiation is intermediate between mean values for pines with bird-dispersed and wind-dispersed seed, although there is a substantial range in these values (figure 2).

As a result of the seed foraging and caching behavior of the Clark's nutcracker, limber pine can be found growing as single stems, single genet multi-stemmed trees, and as clusters of genetically distinct individuals. Genetic analysis has shown that approximately 20 percent of these tree groups contain more than one distinct individual. Furthermore, individual stems in these clusters are often related at the level of half to full siblings but were unrelated to stems in nearby clusters (Carsey and Tomback 1994; Schuster and Mitton 1991).

Mating System and Inbreeding Depression

Inbreeding within populations appears to be quite variable over the species' range. The mean F_{IS} for 12 polymorphic allozyme loci analyzed in five populations sampled from northern Colorado was 0.007 (Schuster and Mitton 2000). In contrast, a range-wide survey of 30 populations found a mean F_{IS} = 0.108 using 18 polymorphic allozyme loci (Jorgensen and others 2002). However, there was significant regional variation in the levels of inbreeding within populations, with those from the Basin and Range having significantly more inbreeding on average (F= 0.127) than those from the northern Rocky Mountains (F= 0.025). Given the highly isolated nature of populations in the Basin and Range region, inbreeding there may be of conservation concern, especially since these populations may represent remnants of Pleistocene populations that may harbor genetic diversity or unique alleles not present in other locations within limber pine's range (Jorgensen and others 2002; Mitton and others 2000).

Conservation Status and Action

Populations of limber pine have been severely impacted by pathogens such as white pine blister rust and mountain pine beetle infestations. Among populations in Wyoming and northern Colorado, the mean number of trees infected with blister rust within populations is about 14 percent, although some populations have more than 50 percent rust incidence (Kearns and Jacobi 2007). While the mean infection incidence is lower (5-8 percent) in southern Colorado, local infection pockets also exceed 50 percent rust incidence (Burns 2006). Mountain pine beetle infestations have caused high mortality in limber pine populations. For example, large numbers were killed in the early 1980s in Alberta (Langor 1989). More recently, significant mortality has occurred the northern Rocky Mountains, particularly in the Yellowstone plateau region (Gibson and others 2008) and the southern Rockies (Schoettle and others 2008). As current beetle outbreaks are sustained, increased mortality in limber pine is expected. Other pathogens that have inflicted substantial mortality in limber pine populations include limber pine dwarf mistletoe (*Arceuthobium cyanocarpum*) (Hawksworth and others 2002). In Canada, *C. ribicola* is known to hybridize with comandra blister rust (*Cronartium comandrae*), a native rust of hard pines, and hybrids have been documented to occur on limber pine (Hamelin and others 2005; Joly and others 2006). What effect this may have on the rust's pathogenicity is currently unknown.

Gene conservation

As a result of its wide distribution, limber pine is protected *in situ* in a number of designated wilderness areas, research natural areas, state and provincial parks and preserves, and national parks, including Waterton Lakes, Glacier, Yellowstone, Grand Teton, Rocky Mountain, Great Sand Dunes, Great Basin, Bryce Canyon, Cedar Breaks, and Death Valley National Parks. These lands provide an extensive *in situ* gene conservation resource; however, the value of this resource is seriously threatened in many areas by white pine blister rust and mountain pine beetle. Seed collections have been made for gene conservation, rust resistance screening and research for limber pine in the Rocky Mountains (Schoettle and others these proceedings); more are planned (see Sniezko and others these proceedings). The range of limber pine covers areas where blister rust has been present for almost 100 years to areas where blister rust is not present. This presents a unique opportunity to sample areas for *ex situ* gene conservation both with and without the impacts of blister rust. In 2009 limber pine was recognized as a provincial Endangered Species under the Alberta Wildlife Act.

White pine blister rust resistance

Rust resistance testing for partial and complete resistance mechanisms are underway (Sniezko and others 2008). Early results showed a wide range in rust susceptibility with several families having a large proportion of seedlings developing no stem symptoms following artificial inoculation (Sniezko and others 2008), and final results of this screening are forthcoming. A complete disease resistance phenotype consistent with that found in western white and sugar pines has been detected in a bulk sample from Colorado (Kinloch and Dupper 2002). This resistance mechanism was not found in single bulk populations sampled from Arizona, California or Montana; however, at these locations, seeds were assessed from only a single tree (Kinloch and Dupper 2002). The geographic distribution of this trait will be further defined with more extensive sampling and testing. Preliminary results from ongoing studies suggest evidence for partial resistance mechanisms in limber pine, but results are not yet available (Schoettle and others 2010).

Predicted climate change impacts

Limber pine has broad environmental tolerances (Schoettle and Rochelle 2000); and, because of its adaptation to dry sites, limber pine may be less affected by climate change than other high elevation five-needle pines (Letts and others 2009; Millar and others 2007). It may adjust to changing climatic conditions via migration or adaption within populations (Schoettle and others 2009). Some climate modeling scenarios have predicted potential range expansion for this species (McKenney and others 2007). For example, an increase in the incidence of fire could benefit limber pine; most populations are sparse with little ground cover, fires typically do not cause extirpation. Furthermore, sites are rapidly re-colonized via seed dispersal by the Clark's Nutcracker (Webster and Johnson 2000). Fire and climate change can also halt or slow succession, which can increase the longevity of limber pine on sites, particularly those at lower timberline and more xeric habitats (Coop and Schoettle 2009; Donnegan and Rebertus 1999; Rebertus and others 1991).

Interactions among threat vectors & other factors

It has been hypothesized that trees weakened by white pine blister rust may be more susceptible to mountain pine beetle attack (Gibson and others 2008). As limber pine is dependent on Clark's Nutcracker for long distance seed dispersal, the status of the two species are interlinked. In 2005, the conservation status of the Clark's Nutcracker was listed as 'sensitive' in Alberta (changed from 'secure') because of its reliance on declining species such as whitebark pine and limber pine. Additionally, the Clark's Nutcracker may also be susceptible to West Nile virus (Blouin 2004).

Southwestern White Pine (*Pinus strobiformis* Engelm.)

Occurrence

Southwestern white pine has a wide but scattered distribution, restricted to very specific environments in high-elevation mixed conifer forests in temperate and humid areas of northern Mexico and the southwestern states of Arizona, New Mexico and a few scattered populations in southwestern Texas (Farjon and Styles 1997; Perry 1991; Tomback and Achuff 2010; Tomback and others, these proceedngs). The taxonomic status of southwestern white pine is ambiguous and it has been classified as a variety of Mexican white pine (var. *brachyptera*, var. *reflexa*, and var. *strobiformis*), as a variety or possibly a hybrid with limber pine (var. *reflexa*); and as distinct species *P. reflexa* and *P. strobiformis* (Andresen and Steinhoff 1971). There is speculation that trees that are morphologically intermediate between limber and southwestern white pine are hybrids between these species (*P. flexilis* var. *reflexa*). These putative hybrids generally occur in the contact zone between these species in Arizona and New Mexico, and possibly on the top of Cerro Potosi in Nuevo Leon, Mexico (Farjon and Styles 1997). The taxonomic ambiguity of southwestern white pine as a possible intermediate between limber pine to the north and Mexican white pine to the south illustrates the hypothesis that these three species are actually a complex of closely related species following a north-south cline of seed wing size, with near-wingless limber pine in the north, to fully winged Mexican white pine in the south (Farjon and Styles 1997; Lanner 1996).

Genetic Diversity

Southwestern white pine is perhaps the least studied of the high elevation five-needle pines in North America. Published population genetic statistics are sparse and of limited use in comparing genetic diversity and population structure of this species to other high elevation five-needle pines. Ledig (1998) presents the only published heterozygosity estimate for the species, but it is based on only two populations (table 1). A more extensive population genetic study covering much of the range of the species is under way but results are not yet available (T. Ledig, personal communication). Moreno-Letelier and Pinero (2009) found significant genetic structure in southwestern white pine; however, their results are not directly comparable with results from other species because they used a different type of genetic marker (chloroplast microsatellite). They reported that genetic diversity was high, especially in western populations, while diversity was less variable in eastern populations and more similar to *P. ayacahuite* of central Mexico.

Genetic variation in quantitative traits has been assessed on a limited number of geographic sources. Seedling traits differed among populations, with populations from northern New Mexico and Arizona generally being shorter, with shorter needles and a shorter period of growth than populations from central and southern Arizona. Seedlings from southern New Mexico and Texas were similar to seedlings from southern Arizona. The differences between northern and southern sources were more pronounced, with a steeper gradient than in limber pine (Steinhoff and Andresen 1971). Compared with limber pine in the same plantings, growth of southwestern white pine was three to four times greater at age two, and was southwestern white pine was five to six times taller at age nine, but was relatively uniform across population sources (Wright and others 1971).

Mating Systems and Inbreeding Depression

No information on mating system or inbreeding depression is currently available for this species.

Conservation Status and Action

Like all five-needle pines, southwestern white pine is susceptible to white pine blister rust. Blister rust was first observed in southwestern white pine in the wild in the Sacramento Mountains in southern New Mexico in 1990 (Hawksworth 1990) and was subsequently traced back to 1970 (Geils and others 1999). Subsequently, blister rust has been found at several sites in northern and western New Mexico and western Arizona (Schwandt 2010 and references therein; Tomback and others, these proceedings) and there is a high risk of the infection spreading to surrounding mountain ranges (Geils and others 1999). In addition to white pine blister rust, this species is the primary host for the dwarf mistletoe *Arceuthobium blumeri*, which extends from southern Arizona south through Durango and east to Cerro Potosí in Nuevo León (Hawksworth and Wiens 1996).

Gene conservation

Seed collections of southwestern white pine have predominantly been made for research purposes; however, this seed may be useful for *ex situ* gene conservation. Recently, seed has been collected specifically for rust testing and gene conservation purposes (see Sniezko and others these proceedings), and further *ex situ* gene conservation collections are planned.

White pine blister rust resistance

Screening for blister rust resistance in southwestern white pine has been limited until recently. The hypersensitive reaction type resistance has been observed in this species (Kinloch and Dupper 2002; Sniezko and others 2008), as have some types of partial resistance in the limited number of families tested (Sniezko and others 2008). Screening of additional families is currently underway (R. Sniezko, personal communication).

Predicted climate change impacts

Climate modeling has not specifically addressed southwestern white pine; however, as in other areas, predictions of future climates under the most common global circulation models and emission scenarios generally predict increased temperatures and aridity (Saenz-Romero and others 2009). This is predicted to lead to a decrease in suitable habitat for other high elevation tree species with which it grows, such as *P. hartwegii* (Saenz-Romero and others 2009) and several Mexican spruces (Ledig and others 2010). It can be inferred that if suitable habitat for sympatric species is predicted to decrease, it is likely that suitable habitat for southwestern white pine therefore may also decrease under predicted global warming scenarios.

Mexican White Pine (*Pinus ayacahuite* Ehren. Ex. Schlecht.)

Occurrence

Mexican white pine is found at 1500-3500 m from central Mexico south to Guatemala, El Salvador, and Honduras, often in mixed conifer stands with other pines, fir, and oak species. It forms a large tree to 45 m tall and 200 cm DBH, with a straight round trunk, conical crown, and regular branch whorls. It is one of the most important and sought-after softwoods native to Central America and Mexico (Farjon and Styles 1997; Wright and others 1996). It has been harvested for use in furniture and finishing carpentry as well as for firewood, leading to depletion of many previously extensive and mature stands (Farjon and Styles 1997). It also occurs in a number of areas where human pressure to expand agricultural land has resulted in a reduction of forest cover (Dvorak and Donahue 1992).

There are three named varieties within this species; however, var. *brachyptera* recognized by Perry (1991), found in central and northern Mexico, is often considered synonymous with southwestern white pine in accordance with Farjon and Styles (1997). Var. *veitchii* is distributed in central

Mexico and is distinguished by its larger cones which are 15-50 cm long with elongated and thickened scales, giving the cone a woody appearance more similar to a hard (diploxylon) pine than a typical five-needle pine (Farjon and Styles 1997) and larger seed size. Var. *ayacahuite* is distributed in the states of southern Mexico as well as Guatemala, El Salvador, and Honduras.

Genetic Diversity

The only published value for genetic diversity indicates that it is about average relative to other pines (table 1 and figure 1). Allozyme studies indicate population differentiation is high (table 1 and figure 2), probably as a result of the patchy, disjunct nature of the distribution. Population differentiation in the central portion of the species' range was lower based on DNA markers (Moreno-Letelier and Pinero 2009).

Studies of genetic variation of adaptive traits are also limited for this species. A provenance test including sources from Honduras, Guatemala, and southern Mexico (Chiapas), areas that ranged in rainfall from 868 to 2367 mm, revealed significant differences in volume per tree, but height growth was relatively low relative to other local pine species (Wright and others 1996).

Mating Systems and Inbreeding Depression

No information on mating system or inbreeding depression is currently available for this species.

Conservation Status and Action

P. ayacahuite var. *ayacahuite* is classified as "least concern" by the IUCN, but var. *veitchii* is classified as "near threatened". The threats identified are pressure from urban development and harvesting for timber. The area where it was formerly described in El Salvador has been intensively exploited for firewood and Mexican white pine may have now been extirpated from El Salvador (Perry 1991).

Gene conservation

In 1983, CAMCORE (Central America and Mexico Coniferous Forest Resources Cooperative) collected seed from 365 trees in 15 provenances in the native range of *P. ayacahuite* for *ex situ* gene conservation and to evaluate its commercial potential. Initial efforts at *ex situ* conservation through plantings in Columbia showed promise (Wright and others 1996). Isolation of many stands makes *in situ* conservation difficult, although it is present in Los Altos de San Miguel Totonicapán Park, Guatemala (ParksWatch 2004). In Mexico the pine is represented in most high elevation national parks within its distribution (for example Parque Nacional Tztacchuatl Popocatepetl, Parque Natural Lagunas de Zempoala, and Parque Natural del Tado de Guerro) (D. Tomback, personal observation)

White pine blister rust resistance

No information on white pine blister rust resistance is currently available for this species. It was ranked last or second to last of 16 North American and Eurasian white pine species for six resistance mechanisms (Hoff and others 1980). The hypersensitive reaction was not observed in a limited sample of 506 seedlings from four populations (Kinloch and Dupper 2002).

Predicted climate change impacts

Climate modeling for Mexico has not specifically addressed Mexican white pine; however, as in other areas, predictions of future climates under the most common global circulation models and emission scenarios (Hadley, Canadian Centre for Climate Modeling and Analysis, Geophysical Fluid Dynamics Laboratory A2 and B1 scenarios) generally indicate increased temperatures and aridity (Saenz-Romero and others 2009). These will also lead to a decrease in suitable habitat for other pine species such as *P. hartwegii* and *P. pseudostrobus,* (Saenz-Romero and others 2009) which grow with Mexican white pine (Farjon and Styles 1997), and several Mexican spruces (Ledig and others 2010). Suitable habitat for Mexican white pine therefore is also likely to decrease under predicted global warming scenarios.

Foxtail Pine (*Pinus balfouriana* Grev. & Balf.)

Occurrence

Foxtail pine (*Pinus balfouriana* Grev. & Balf.) is distributed within the mountains of California and is divided into two disjunct populations separated by 500 km—the Klamath mountains of northern California and the Sierra Nevada of southern California (Tomback and Achuff 2010; Tomback and others, these proceedings). These regional populations experience dramatically different climate and environmental regimes, as well as ecological conditions (Eckert and Sawyer 2002). Stands in the north are relatively diverse, dense and are located along mountaintops and ridgelines. Within these stands, foxtail pine forms a minor to major ecological component depending on microsite and soil type (Eckert 2006a; Eckert 2006b). Foxtail pine stands in the south form extensive, typically single species subalpine communities throughout most of the southern Sierra Nevada. They are geographically extensive and relatively less diverse and (Rourke 1988; Ryerson 1983). These regional populations have been divided into two subspecies based on needle, cone and bark morphology (Bailey 1970; Mastrogiuseppe 1980)—*P. balfouriana* subsp. *balfouriana* in the north and *P. balfouriana* subsp. *austrina* in the south. Priority was given to the northern population due to John Jeffrey's collection of the first foxtail pine specimen in the Scott Mountains of northern California in 1852 (Colville 1897). The first taxonomic treatment, however, was provided by R. K. Greville and J. Balfour in 1853 (Murray 1853).

Genetic Diversity

Genetic differentiation has been assessed for foxtail pine primarily through molecular markers (Eckert and others 2008; Eckert and others 2010; Hamrick and others 1981;

Oline and others 2000). Although needle, cone and bark morphologies were used to define subspecies (Mastrogiuseppe and Mastrogiuseppe 1980), there has been no published analysis of quantitative characters. Genetic diversity within this species has been assessed with allozymes (Hamrick and others 1981; Oline and others 2000), as well as DNA sequences and nuclear SSRs (Eckert and others 2008; Eckert and others 2010). In general, genetic diversity is low to moderate (table 1). Estimates of F_{ST} between regional populations vary depending on marker type, with allozymes giving the lowest value of 0.038 and mitochondrial DNA sequences (mtDNA) giving the highest value of 0.476 (table 1 and figure 2), both indicating that population structure is greater among stands in the northern population relative to the southern population (allozymes: F_{ST} = 0.242 [north] vs. 0.075 [south]; mtDNA: F_{ST} = 0.321 [north] vs. 0.174 [south]).

There is no information on genetic variation of adaptive traits for this species.

Mating Systems and Inbreeding Depression

Breeding structure and inbreeding depression have not fully been assessed for foxtail pine across its natural range. The allozymes used by Oline and others (2000) tended to have significantly positive values of F_{IS} across various population-level comparisons, which is consistent with substructuring, possibly due to inbreeding. This effect was greater among northern stands. There are, however, pronounced effects of ecological conditions on marker diversities at small spatial scales in the Klamath Mountains. In a study using five nuclear microsatellites, F_{IS} was significantly positive for two stands characterized by high species diversities with low foxtail pine density, and zero for two stands with the opposite patterns (Eckert and others 2010). This pattern was attributed to population bottlenecks followed by spatial expansion within ecologically disparate stand types

Conservation Status and Action

Analysis of size class distributions for foxtail pine in the Klamath region suggests that most stands are stable or growing (Eckert 2006; Eckert and Eckert 2007). This was also confirmed recently for stands located in both regions, with the southern Sierra Nevada having somewhat lower growth rates data (Maloney, unpublished data). These results were attributed to high recruitment in some stands and high survival in most stands, consistent with the pines long lifespan. Downslope expansion within stands in the Klamath Mountains has also been shown by Eckert and Eckert (2007). The magnitude of expansion was correlated to several ecological and environmental variables suggesting that response to climate change in this region will be complex, especially since current estimates of demographic stability or growth are correlated far more with survivorship than recruitment (Maloney, unpublished data).

Gene conservation

Up to 70-90 percent of the range of foxtail pine is protected in federally designated wilderness areas, Research Natural Areas, and in Sequoia-Kings Canyon National Park, providing *in situ* genetic conservation. Cone collections have been made from several stands in both the northern and southern portions of the species distribution (see also Sniezko and others, these proceedings). A portion of these seed will be used for long term *ex situ* gene conservation, and additional cone collections are planned to adequately sample the genetic diversity of the species.

White pine blister rust resistance

Little is known about pathogenic threats to foxtail pine. The hypersensitive response (HR) locus, which confers immunity to white pine blister rust, has not been detected in foxtail pine (Kinloch and Dupper 2002). A recent survey of foxtail pine stands demonstrated that white pine blister rust is present in northern stands but not in southern stands, with considerable variation in frequency among stands (Maloney, unpublished data; see also Duriscoe and Duriscoe 2002; Kliejunas and J. 2007). An opposite pattern was observed for mountain pine beetle, with higher prevalence in the southern Sierra Nevada. A limited blister rust inoculation test (13 families) has been established to adjust the protocols for rust resistance screening at the USDA Forest Service Institute of Forest Genetics in Placerville, CA. Early observations show very high susceptibility to rust infection (A. Delfino-Mix, personal communication).

Predicted climate change impacts

Climate models predict that the distributions of high elevation species will decrease under a variety of climate change scenarios (Parmesan 2006; Rehfeldt and others 2006), therefore foxtail pine is expected to be highly sensitive to climate change. Dendrochronological data and climate modeling, however, suggest that drought stress has been a historical driver of local distribution patterns for many subalpine forest trees, including this species (Bunn and others 2005; Millar and others 2004; Millar and others 2006; Millar and others 2007). Indeed, Maloney (personal communication) postulated that drought stress in combination with mountain pine beetle-induced mortality were the drivers behind low population growth rates in two marginal stands of foxtail pine. Response to climate by this species will be complex, because the effect of climate change on realized drought stress has strong environmental and geographical components, and interactions of climate change with various pathogens affecting this species are unknown.

Rocky Mountain Bristlecone Pine (*Pinus aristata* Engelm.)

Occurrence

Rocky Mountain bristlecone pine is found in montane and subalpine habitats in the Southern Rocky Mountains (Tomback and Achuff 2010; Tomback and others, these proceedings). The core of its range is in south central Colorado, east of the continental divide. The range extends south into New Mexico along the Sangre de Cristo Mountains and north to just south of Rocky Mountain National Park in northern Colorado. A disjunct population occurs on the San Francisco Peaks in Central Arizona. Rocky Mountain bristlecone pine is a high elevation species occupying dry sites from 2750 to 3670 m elevation (Baker, 1992). Though not common, this species occasionally grows in multi-genet tree clumps. At least 20-25 percent of these clumps are made up of more than one genetically distinct individual (Torick and others 1996; Oline unpublished data). Great Basin bristlecone pine (*Pinus longaeva*) was split from Rocky Mountain bristlecone pine in 1970 by Bailey based on anatomical differences (Bailey 1970).

Genetic Variation

This species contains low levels of genetic variation (expected heterozygosity) as measured by isozymes. Genetic diversity in this species is lower than other high elevation five-needle pine species, and is considerably lower than other pines (Hamrick and others 1992; Ledig 1998; Schoettle and others, these proceedings) (table 1 and figure 1). However, Ledig (1998) cites unpublished data by Hiebert and Hamrick who found much higher than expected heterozygosity compared to the studies mentioned above. Conversely, population differentiation in Rocky Mountain bristlecone pine is much higher than in other pines (Hamrick and others 1992; Schoettle et al, these proceedings) (table 1 and figure 2). Studies of genetic variation in adaptive traits are complete with results forthcoming.

Mating System and Inbreeding Depression

High fixation index (F) values have been observed in Rocky Mountain bristlecone pine, indicating the likely presence of both population substructure and inbreeding. Oline (unpublished data) showed that stands as close as 11 km from one another near the northern extreme of the species range differed from one another in the distribution and presence of certain alleles, suggesting a strong founder effect.

Conservation Status and Action

White pine blister rust was first found on Rocky Mountain bristlecone pine in 2003 in south-central Colorado, and rust incidence is still low (Blodgett and Sullivan 2004). The species is experiencing endemic mountain pine beetle impacts; but, now beetle populations are building and mortality in bristlecone stands in increasing (A. Schoettle and others these proceedings). Several studies have assessed the condition and habitat associations of Rocky Mountain bristlecone pine (Baker 1992; Burns 2006; Cocke and others 2005; Coop and Schoettle 2009; Coop and others 2010; Moir and Ludwig 1979). Evidence of increased stand densities due to fire exclusion is suspected in Arizona (Cocke and others 2005).

Gene conservation

The Rocky Mountain Research Station (RMRS) and Forest Health Protection high elevation five-needle pine program focuses on selection, rust resistance, climate change interactions, and neutral and adaptive genetic variation of Rocky Mountain bristlecone and limber pine (Burns and others 2010; Schoettle and others these proceedings). *Ex situ* gene conservation activities such as long-term performance tests, clone banks, and seed orchards have not yet been established; however, seed collections have been made since 2001 by RMRS and over 340 individual tree collections have been made from over 30 sites thus far (see Schoettle and others, these proceedings). Completion of range wide collections are underway, a portion of which will be archived for long term gene conservation (Sniezko et al, these proceedings). Rocky Mountain bristlecone pine *in situ* genetic resources include several Research Natural Areas as well as national parks and preserves.

White pine blister rust resistance

The distribution of white pine blister rust on bristlecone pine is concentrated within the Mosca Creek drainage in the southern portion of the Sangre de Cristo Mountains within the Great Sand Dunes National Park (Burns 2006). Symptoms of white pine blister rust were more inconspicuous on the bristlecone pines observed in this study than on infected limber pines, making the disease much harder to identify, particularly in the early stages of infection. The latent period between infection and sporulation may be longer on Rocky Mountain bristlecone pine than on other species, possibly as long as 8-16 years (A. Schoettle, this proceedings). Permanent plots have been installed in and around the infection center to provide valuable information on the rate of spread of the rust, disease progression, and mortality on Rocky Mountain bristlecone pine (Burns 2006). A risk analysis showed that 50 percent of the five-needle pine habitat in Colorado has an average climate suitable for white pine blister rust (Kearns 2005; Howell and others 2006). Therefore, we expect the continued spread of blister rust in Rocky Mountain bristlecone pine. Proactive resistance trials of Rocky Mountain bristlecone pine families from the core portion of its range are currently under way (Sniezko and others 2008; Schoettle and others 2010).

Predicted climate change impacts

Maps of predicted future climates show a significant decrease in habitat in the U.S. climatically suitable for Rocky Mountain bristlecone pine under future climate warming scenarios (USDA Forest Service). A related species, Great Basin Bristlecone pine, has shown an increase in radial growth at treeline due to increased temperature in recent years (Salzer and others 2009). Rocky Mountain bristlecone pine may respond similarly. Climate change may also result in range shifts in the frequency of and expansions for mountain pine beetle epidemics, possibly resulting in them becoming more prevalent due to higher survival, or the possibility of supporting a 1-year as opposed to its temperature-restricted 2-year reproductive cycle in the higher elevation forests (Gibson and others 2008; Cudmore and others 2010; Bentz et al these proceedings).

Great Basin Bristelcone Pine (*Pinus longaeva* Bailey)

Occurrence

Based on morphology, bristlecone pine was split in 1970 into two species, Great Basin and Rocky Mountain bristlecone pines (Bailey 1970). Great Basin bristlecone pine occurs at high altitudes in Utah, Nevada, and in the White Mountains of California (Tomback and Achuff 2010, Tomback and others, these proceedings). In the Great Basin it is found on isolated mountain ranges separated by xeric valleys. It usually inhabits sites with poor soils, but can form extensive stands. It has small, winged seeds typical of wind-dispersed conifers, but on harsh sites at high elevation it regenerates more frequently from seed caches of Clark's Nutcracker (Lanner 1988; Tomback and others, these proceedings). On more mesic sites it has an upright growth form, instead of the twisted, gnarled growth form found on the poorest sites (Hiebert and Hamrick 1984). It is most famous for its extreme longevity, reaching ages of nearly 5000 years (Currey 1965; Schulman 1958).

Genetic Diversity

Across the range of the species, the genetic diversity of *P. longaeva* is about average to above average for pines (figure 1). There is a range of values that have been reported for the species (table 1 and figure 1), and it appears that genetic diversity is highest in the eastern Great Basin (Hiebert and Hamrick 1983) and lower in the White Mountains of California (Hamrick personal communication cited in Lee and others 2002; Lee and others 2002); the reason for the difference is unknown. Expected heterozygosity in the eastern Great Basin is one of the highest ever reported for a conifer (Hiebert and Hamrick 1983).

Population differentiation for *P. longaeva* is slightly lower than for other wind-dispersed pines (table 1 and figure 2). This may be due to dispersal of the seed by birds (Lanner 1988) or may also be explained by continuity among stands during the Pleistocene glacial periods (Hiebert and Hamrick 1983). However, all of the studies have been confined to within one mountain range.

Mating Systems and Inbreeding Depression

Mating system and inbreeding depression in this species have not been explicitly studied, but positive fixation index values (F) indicate a lower level of heterozygosity than would be expected based on allele frequencies, most likely due to some degree of inbreeding (table 1).

Conservation Status and Action

Great Basin bristlecone pine is classified as "vulnerable" by the IUCN. The main threat identified is that it is doubtful whether present rates of regeneration are sufficient to replace the population under present climatic and environmental conditions.

Gene conservation

Portions of Great Basin bristlecone pine's range are protected *in situ* in national parks, including Death Valley, Great Basin, Bryce Canyon, and Cedar Breaks National Parks. Other *in situ* resources include wilderness areas and research natural areas. In 2009, seed was collected from 300 individuals in three widely separated areas of Nevada for *ex situ* gene conservation and rust resistance screening (see Sniezko and others these proceedings), and additional collections are planned from areas in northern Nevada where the range of Great Basin bristlecone pine overlaps with either whitebark or limber pine (D. Vogler, personal communication).

White pine blister rust resistance

Since 2005, 37 families of Great Basin bristlecone pine from groves in the White Mountains have been inoculated with blister rust to screen for resistance at the USDA Forest Service Institute of Forest Genetics in Placerville, CA. These families have shown some resistance in stems, which is being further investigated (D. Vogler, personal communication). Recent collections from the Great Basin and planned collections in northern Nevada will be screened for resistance in the future.

Predicted climate change impacts

Climate change is predicted to have a significant impact on higher elevation ecosystems, resulting in a drastic reduction of suitable habitat for many high elevation plant species (Ledig and others 2010; Tomback and Achuff 2010; Tomback and others, this proceedings; Warwell and others 2007;). Predictions of climate change impacts have not been developed for Great Basin bristlecone pine specifically, but increased radial growth in upper treeline stands of Great Basin bristlecone pine has been linked to warmer temperatures in the last ~50 years (Kipfmueller and Salzer 2010; Salzer and others 2009). Trees at upper treeline sites appear to be sensitive recorders of temperature for several five-needle white pine species, while trees at high elevation sites below treeline appear to be more sensitive to precipitation (Kipfmueller and Salzer 2010). In the Patriarch Grove in the White Mountains of California, anecdotal observations of higher survival of seedlings may be due to warmer temperatures (R. Lanner, personal communication), and while slightly warmer temperature may result in increased radial growth at treeline, the impacts of further warming, especially if there is no increase in moisture, are unknown and may impact survival negatively (Lanner 2007).

Knowledge Gaps

We have identified the following knowledge gaps regarding the conservation genetics of these high elevation five-needle white pine species

- Range wide genetic diversity and population structure of *P. longaeva, P. strobiformis*, and *P. ayacahuite*.
- Quantitative trait variation of all species except *P. albicaulis* (results of several species are forthcoming).
- Potential impacts of climate change.
- Levels, types, durability of white pine blister rust resistance.

Future Research Needs

Understanding the genetics of these species will be helpful in developing and implementing strategies for the conservation and/or restoration of these species to minimize the negative consequences of white pine blister rust and climate change, in particular. The following research and conservation needs have been identified:

- Further investigate the ability of different populations to withstand warming temperatures using *in situ* and *ex situ* common garden experiments
- Continue screening for rust-resistant individuals and/or populations that can be used for restoration planting
- Establish policy frameworks regarding whether and how to assist the migration of species threatened to be extirpated within their current ranges, as may be the case for whitebark pine
- Establish conservation strategies for species where such strategies are not already in place
- Acknowledgements

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References

Altizer, Sonia; Harvell, Drew; Friedle, Elizabeth. 2003. Rapid evolutionary dynamics and disease threats to biodiversity. Trends in Ecology & Evolution. 18(11): 589-596.

Andresen, J. W.; Steinhoff, R. J. 1971. The taxonomy of *Pinus flexilis* and *P. strobiformis*. Phytologia. 22: 57-70.

Arno, Stephen F.; Hoff, Raymond J. 1989. Silvics of whitebark pine (*Pinus albicaulis*). Gen.Tech. Rep. INT-GTR-253. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station. 11 p.

Aubry, Carol; Goheen, Don; Shoal, Robin; Ohlson, Therese; Lorenz, Teresa; Bower, Andrew; Mehmel, Connie; Sniezko, Richard. 2008. Whitebark pine restoration strategy for the Pacific Northwest Region, 2009-2013. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Region. 212 p.

Bailey, D. K. 1970. Phytogeography and taxonomy of *pinus* subsection Balfourianae. Annals of the Missouri Botanical Garden. 57(2): 210-249.

Baker, W. L. 1992. Structure, disturbance, and change in the bristlecone-pine forests of Colorado, U.S.A. Arctic and Alpine Research. 24(1): 17-26.

Betancourt, Julio L. 1990. Late quaternary biogeography of the Colorado Plateau. In: Betancourt, Julio L.; Van Devender, Thomas R.; Martin, Paul S., eds. Packrat middens: the last 40,000 years of biotic change. Tucson, AZ: University of Arizona Press: 259-293.

Blodgett, J. T.; Sullivan, K. F. 2004. First report of white pine blister rust on Rocky Mountain bristlecone pine. Plant Disease. 88(3): 311.

Blouin, François. 2004. Clark's nutcracker (*Nucifraga columbiana*). In: Blouin, François; Taylor, Brad N.; Quinlan, Richard W., eds. The southern headwaters at risk project: a multi-species conservation strategy for the headwaters of the Oldman River. Volume 2: species selection and habitat suitability models. Edmonton, AB: Alberta Sustainable Resource Development, Fish and Wildlife Division; Alberta Species at Risk Report No. 90: 73-81.

Bower, Andrew D.; Aitken, Sally N. 2006. Geographic and seasonal variation in cold hardiness of whitebark pine. Canadian Journal of Forest Research. 36(7): 1842-1850.

Bower, Andrew D.; Aitken, Sally N. 2007. Mating system and inbreeding depression in whitebark pine (*Pinus albicaulis* Engelm.). Tree Genetics & Genomes. 3(4): 379-388.

Bower, Andrew D.; Aitken, Sally N. 2008. Ecological genetics and seed transfer guidelines for *Pinus albicaulis* (Pinaceae). American Journal of Botany. 95(1): 66-76.

Bower, Andrew D.; Aitken, Sally N. [In press]. Changes in genetic diversity of whitebark pine (*Pinus albicaulis* Engelm.) associated with inbreeding and white pine blister rust. Silvae Genetica.

Bower, Andrew D.; Aubry, Carol. 2009. Whitebark pine *ex situ* gene conservation strategy for the Pacific Northwest Region. [Online]. Available: http://fsweb.f9.r6.fs.fed.us/eco/whitebark/index.html

Bower, Andrew D.; Ohlson, Therese; Aubry, Carol. 2009. Whitebark pine restoration program 2009 annual progress report, USDA Forest Service Pacific Northwest Region. [Online]. Available: http://fsweb.f9.r6.fs.fed.us/eco/whitebark/index.html

Bower, Andrew D.; Richardson, Bryce A.; Hipkins, Valerie; Rochefort, Regina; Aubry, Carol. 2008. Unpublished data on file at: U.S. Department of Agriculture, Forest Service, Olympic National Forest, Olympia, WA.

Bruederle, Leo P.; Rogers, Deborah L.; Krutovskii, Konstantin V.; Politov, Dmitri V. 2001. Population genetics and evolutionary implications. In: Tomback, Diana F.; Arno, Stephen F.; Keane, Robert E., eds. Whitebark pine communities: ecology and restoration. Washington, DC: Island Press: 137-153.

Bruederle, Leo P.; Tomback, Diana F.; Kelly, Kathleen K.; Hardwick, Renea C. 1998. Population genetic structure in a bird-dispersed pine, P*inus albicaulis* (Pinaceae). Canadian Journal of Botany. 76(1): 83-90.

Bunn, Andrew G.; Waggoner, Lindsey A.; Graumlich, Lisa J. 2005. Topographic mediation of growth in high elevation foxtail pine (P*inus balfouriana* Grev. et Balf.) forests in the Sierra Nevada, U.S.A. Global Ecology and Biogeography. 14(2): 103-114.

Burns, Kelly; Blodgett, Jim; Conklin, David; Fairweather, Mary Lou; Geils, Brian; Guyon, John; Hoffman, Jim; Jackson, M.; Jacobi, William; Kearns, Holly; Schoettle, Anna. 2010. White pine blister rust in the Interior Mountain West. In: Adams, J. comp. 2010. Proceedings of the 57th Western International Forest Disease Work Conference; 2009 July 20-24; Durango, CO. Fort Collins, CO: Forest Health Technology Enterprise Team: 57-65. [Online]. Available: http://www.cnr.usu.edu/quinney/files/uploads/wifdwc2009.pdf

Burns, Kelly S. 2006. White pine blister rust surveys in the Sangre de Cristo and Wet Mountains of southern Colorado. Biol. Evaluation. R2-06-05. Denver, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Region. 22 p.

Carsey, Katherine S.; Tomback, Diana F. 1994. Growth form distribution and genetic relationships in tree cluster of *Pinus flexilis*, a bird-dispersed pine. Oecologia. 98: 402-411.

Cocke, Allison E.; Fule, Peter Z.; Crouse, Joseph E. 2005. Forest change on a steep mountain gradient after extended fire exclusion: San Francisco Peaks, Arizona, U.S.A. Journal of Applied Ecology. 42(5): 814-823.

Colville, Frederick V. 1897. The itinerary of John Jeffrey, an early botanical explorer of western North America. Proceedings of the Biological Society of Washington. 11: 57-60.

Coop, Jonathan D.; Schoettle, Anna W. 2009. Regeneration of Rocky Mountain bristlecone pine (*Pinus aristata*) and limber pine (*Pinus flexilis*) three decades after stand-replacing fires. Forest Ecology and Management. 257: 893-903.

Coop, Jonathan D.; Massatti, Robert T.; Schoettle, Anna W. 2010. Subalpine vegetation pattern three decades after stand-replacing fire: effects of landscape context and topography on plant community composition, tree regeneration, and diversity. Journal of Vegetation Science. 21(3): 472-487.

Cudmore, Timothy J.; Björklund, Niklas; Carroll, Allan L.; Lindgren, B. Staffan. 2010. Climate change and range expansion of an aggressive bark beetle: evidence of higher beetle reproduction in naive host tree populations. Journal of Applied Ecology. 47(5): 1036-1043.

Currey, Donald R. 1965. An ancient bristlecone pine stand in eastern Nevada. Ecology. 46: 564-566.

Delfino-Mix, Annette. 2010 [Personal communication]. Placerville, CA: U.S. Department of Agriculture, Forest Service, Institute of Forest Genetics.

Donnegan, Joseph A.; Rebertus, Alan J. 1999. Rates and mechanisms of subalpine forest succession along an environmental gradient. Ecology. 80: 1370-1384.

Duriscoe, Dan M.; Duriscoe, Cindy S. 2002. Survey and monitoring of white pine blister rust in Sequoia and Kings Canyon National Parks—final report of 1995-1999 survey and monitoring plot network. Science and natural resources management division, Sequoia and Kings Canyon National Parks.

Dvorak, W. S.; Donahue, J. K. 1992. The Central America and Mexico Coniferous Resources Cooperative (CAMCORE) research review, 1980-1992. Raleigh, NC: College of Forest Resources, North Carolina State University. 93 p.

Eckert, Andrew J. 2006a. Influence of substrate type and microsite availability on the persistence of foxtail pine (*Pinus balfouriana*, Pinaceae) in the Klamath Mountains, California. American Journal of Botany. 93(11): 1615-1624.

Eckert, Andrew J. 2006b. The phylogenetic position, historical phylogeographical and population genetics of foxtail pine (*Pinus balfouriana* Grev. & Balf.). Seattle, WA: University of Washington. Dissertation.

Eckert, Andrew J.; Bower, Andrew D.; Gonzalez-Martinez, Santiago C.; Wegrzyn, Jill L.; Coop, Graham; Neale, David B. 2010. Back to nature: ecological genomics of loblolly pine (*Pinus taeda*, Pinaceae). Molecular Ecology. 19(17): 3789-3805.

Eckert, Andrew J.; Bower, Andrew D.; Wegrzyn, Jill L.; Pande, Barnaly; Jermstad, Kathleen D.; Krutovsky, Konstantin V.; St. Clair, J. Bradley; Neale, David B. 2009. Asssociation genetics of coastal Douglas-fir (*Pseudotsuga menziesii* var. *menziesii*, Pinaceae). I. Cold-hardiness related traits. Genetics. 182(4): 1289-1302.

Eckert, Andrew J.; Eckert, Melissa L. 2007. Environmental and ecological effects of size class distributions of foxtail pine (*Pinus balfouriana*, Pinaceae) in the Klamath Mountains, California. Madroño. 54: 117-125.

Eckert, Andrew J.; Eckert, Melissa L.; Hall, Benjamin D. 2010. Effects of historical demography and ecological context on spatial patterns of genetic diversity within foxtail pine (*Pinus balfouriana*; Pinaceae) stands located in the Klamath Mountains, California. American Journal of Botany. 97(4): 650-659.

Eckert, Andrew J.; Sawyer, John O. 2002. Foxtail pine importance and conifer diversity in the Klamath Mountains and southern Sierra Nevada, California. Madroño. 49: 33-45.

Eckert, Andrew J.; Tearse, Brandon R.; Hall, Benjamin D. 2008. A phylogeographical analysis of the range disjunction for foxtail pine (*Pinus balfouriana*, Pinaceae): the role of Pleistocene glaciation. Molecular Ecology. 17(8): 1983-1997.

Endler, John A. 1977. Genetic variation, speciation, and clines. Princeton, NJ: Princeton University Press.

Farjon, A.; Styles, B. T. 1997. *Pinus* (Pinaceae). Flora Neotropica Monograph 75. New York: The New York Botanical Garden.

Frankham, Richard; Ballou, Jonathan D.; Briscoe, David A. 2002. Introduction to conservation genetics. New York: Cambridge University Press.

Furnier, Glenn R.; Knowles, Peggy; Clyde, Merlise A.; Dancik, Bruce P. 1987. Effects of avian seed dispersal on the genetic-structure of whitebark-pine populations. Evolution. 41(3): 607-612.

Geils, Brian W.; Conklin, David A.; van Ardsel, Eugene P. 1999. A preliminary hazard model of white pine blister rust for the Sacramento Ranger District, Lincoln National Forest. Res. Note. RMRS-RN-6. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station. 6 p.

Gernandt, David S.; Lopez, Gretel Geada; Garcia, Sol Ortiz; Liston, Aaron. 2005. Phylogeny and classification of *Pinus*. Taxon. 54(1): 29-42.

Gibson, K.; Skov, K.; Kegley, S.; Jorgensen, C.; Smith, S.; Witcosky, J. 2008. Mountain pine beetle impacts in high-elevation five-needle pines: current trends and challenges. R1-08-020. Missoula, MT: U.S. Department of Agriculture, Forest Service, Forest Health Protection. 32 p.

Gonzalez-Martinez, S. C.; Huber, D.; Ersoz, E.; Davis, J. M.; Neale, D. B. 2008. Association genetics in *Pinus taeda* L. II. Carbon isotope discrimination. Heredity. 101(1): 19-26.

Gonzalez-Martinez, S. C.; Wheeler, N. C.; Ersoz, E.; Nelson, C. D.; Neale, D. B. 2007. Association genetics in *Pinus taeda* l. I. Wood property traits. Genetics. 175(1): 399-409.

Hahn, Matthew W. 2008. Toward a selection theory of molecular evolution. Evolution. 62(2): 255-265.

Hall, David; Tegström, Carolina; Ingvarsson, Pär K. 2010. Using association mapping to dissect the genetic basis of complex traits in plants. Briefings in Functional Genomics. 9(2): 157-165.

Hamelin, R.; Joly, D.; Langor, D. 2005. A hybrid between white pine blister rust and comandra blister rust on limber pine. Phytopathology. 95(6): S39-S40.

Hamrick, James L.; Godt, Mary Jo W.; Sherman-Broyles, Susan L. 1992. Factors influencing levels of genetic diversity in woody plant species. New Forests. 6: 95-124.

Hamrick, James L.; Mitton, Jeffry B.; Linhart, Yan B. 1981. Levels of genetic variation in trees: influence of life history characteristics. In: Conkle, M. Thomas., ed. Proceedings of a symposium on Isozymes of North American Forest Trees and Forest Insects;1979 July 27; Berkeley, CA. Gen. Tech. Rep. PSW-GTR-48. Berkeley,CA: U.S. Department of Agriculture, Forest Service, Pacific Southwest Forest and Range Experiment Station: 35-41.

Hamrick, James L.; Schnabel, A. F.; Wells, P. V. 1994. Distribution of genetic diversity within and among populations of Great Basin conifers. In: Harper., K. T.; St. Clair, L. L.; Thorne, K.H.; Hess, W.W., eds. Natural history of the Colorado Plateau and Great Basin. Niwot, CO: University Press of Colorado: 147-161.

Hartl, Daniel L.; Clark, Andrew G. 1989. Principles of population genetics. 2d ed. Sunderland, MA: Sinauer Associates, Inc. 682 p.

Hawksworth, Frank G. 1990. White-pine blister rust in southern New Mexico. Plant Disease. 74(11): 938-938.

Hawksworth, Frank G.; Wiens, Delbert. 1996. Dwarf mistletoes: Biology, pathology and systematics. Agriculture Handbook 709. Washington, DC: U.S. Department of Agriculture, Forest Service. [Online]. Available: http://www.rmrs.nau.edu/publications/ah_709/index.html [2010, September 2].

Hawksworth, Frank G.; Wiens, Delbert; Geils, Brian W. 2002. *Arceuthobium* in North America. In: Geils, Brian W.; Cibrián Tovar, Jose; Moody, Benjamin, tech. coords. Mistletoes of North American conifers. Gen.Tech. Rep. RMRS-GTR-98. Ogden, Utah: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station: 29-56.

Hiebert, Ronald D.; Hamrick, James L. 1983. Patterns and levels of genetic-variation in Great-Basin bristlecone pine, *Pinus longaeva*. Evolution. 37(2): 302-310.

Hiebert, Ronald D.; Hamrick, James L. 1984. An ecological study of bristlecone pine (*Pinus longaeva*) in Utah and eastern Nevada. Great Basin Naturalist. 44: 487-494.

Hipkins, Valerie. Unpublished data on file at: U.S. Department of Agriculture, Forest Service, National Forest Genetic Electrophoresis Laboratory, Placerville, CA.

Hoff, R.; Bingham, R. T.; McDonald, G. I. 1980. Relative blister rust resistance of white pines. European Journal of Forest Pathology. 10(5): 307-316.

Holliday, Jason A.; Ralph, Steven G.; White, Richard; Bohlmann, Jörg; Aitken, Sally N. 2008. Global monitoring of autumn gene expression within and among phenotypically divergent populations of Sitka spruce (P*icea sitchensis*). New Phytologist. 178(1): 103-122.

Howell, B. E.; Burns, K. S.; Kearns, H. S. J. 2006. Biological evaluation of a model for predicting presence of white pine blister rust in Colorado based on climatic variables and susceptible white pine species distribution. Biol. Eval. R2-06-04. U.S. Department of Agriculture, Forest Service, Rocky Mountain Region, Renewable Resources. 15 p. [Online]. Available: http://www.fs.fed.us/r2/fhm/ [2006, March 21].

Joly, D. L.; Langor, D. W.; Hamelin, R. C. 2006. Molecular and morphological evidence for interspecific hybridization between *Cronartium ribicola* and *C. comandrae* on *Pinus flexilis* in southwestern Alberta. Plant Disease. 90: 1552.

Jorgensen, Stacy; Hamrick, James; Wells, P. V. 2002. Regional patterns of genetic diversity in *Pinus flexilis* (Pinaceae) reveal complex species history. American Journal of Botany. 89: 792-800.

Jorgensen, Stacy M.; Hamrick, James L. 1997. Biogeography and population genetics of whitebark pine, *Pinus albicaulis*. Canadian Journal of Forest Research. 27(10): 1574-1585.

Keane, Robert E.; Tomback, Diana; Aubry, Carol; Bower, Andrew; Campbell, Elizabeth; Jenkins, Melissa; Manning, Mary; McKinney, Shawn; Murray, Michael; Perkins, Dana; Reinhart, Dan; Ryan, Chris; Schoettle, Anna; Smith, Cyndi. [In preparation]. A range-wide restoration strategy for whitebark pine (*Pinus albicaulis*). Gen. Tech. Rep. RMRS-GTR-xxx. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station. 183 p.

Kearns, Holly S. J. 2005. White pine blister rust in the central Rocky Mountains: modeling current status and potential impacts. Fort Collins, CO: Colorado State University. 243 p. Dissertation.

Kearns, Holly S. J.; Jacobi, William R. 2007. The distribution and incidence of white pine blister rust in central and southeastern Wyoming and northern Colorado. Canadian Journal of Forest Research. 37(2): 462-472.

Kinloch, Bohun B.; Dupper, Gayle E. 2002. Genetic specificity in the white pine-blister rust pathosystem. Phytopathology. 92(3): 278-280.

Kipfmueller, Kurt F.; Salzer, Matthew W. 2010. Linear trend and climate response of five-needle pines in the western United States related to treeline proximity. Canadian Journal of Forest Research. 40(1): 134-142.

Kliejunas, John; Dunlap, Joan. 2007. Status of whitebark pine and other high-elevation five-needle pines with emphasis on Pacific Coast ecosystems: What are the issues and concerns? Perspectives from California. In: Goheen, Ellen M.; Sniezko, Richard A., tech. coords. Proceedings of the conference: whitebark pine: a Pacific Coast perspective. 2006 August 27-37; Ashland, OR. R6-NR-FHP-2007-01. Portland, OR: Pacific Northwest Region, Forest Service, U.S. Department of Agriculture: 29-35.

Krakowski, J.; Aitken, S. N.; El-Kassaby, Y. A. 2003. Inbreeding and conservation genetics in whitebark pine. Conservation Genetics. 4(5): 581-593.

Langor, D. W. 1989. Host effects on the phenology, development, and mortality of field populations of the mountain pine beetle, *Dendroctonus ponderosae* Hopkins (Coleoptera: Scolytidae). Canadian Entomologist. 121: 149-157.

Lanner, R. M. 1982. Adaptations of whitebark pine for seed dispersal by Clark's nutcracker. Canadian Journal of Forest Research. 12(2): 391-402.

Lanner, Ronald M. 1988. Dependence of Great Basin bristlecone pine on Clark's nutcracker for regeneration at high elevations. Arctic and Alpine Research. 20(3): 358-362.

Lanner, Ronald M. 1996. Made for each other: a symbiosis of birds and pines. New York: Oxford University Press. 176 p.

Lanner, R. M. 2007. The bristlecone book: a natural history of the world's oldest trees, Missoula, MT: Mountain Press Publishing Company. 128 p.

Lanner, Ronald M. 2010. [Personal communication]. Placerville, CA: U.S. Department of Agriculture, Forest Service, Institute of Forest Genetics.

Latta, Robert G.; Mitton, Jeffry B. 1997. A comparison of population differentiation across four classes of gene marker in limber pine (*Pinus flexilis* James). Genetics. 146(3): 1153-1163.

Ledig, F. Thomas. 1998. Genetic variation in *Pinus*. In: Richardson, D. M., ed. Ecology and Biogeography of *Pinus*. Cambridge: Cambridge University Press. p. 251-280.

Ledig, F. Thomas; Rehfeldt, Gerald E.; Saenz-Romero, Cuauhtémoc; Flores-Lopez, Celestino. 2010. Projections of suitable habitat for rare species under global warming scenarios. American Journal of Botany. 97(6): 970-987.

Lee, Seok-Woo; Ledig, F. Thomas; Johnson, David R. 2002. Genetic variation at allozyme and RAPD markers in *Pinus longaeva* (Pinaceae) of the White Mountains, California. American Journal of Botany. 89(4): 566-577.

Letts, Matthew G.; Nakonechny, Kevin N.; Van Gaalen, K. Eric; Smith, Cyndi M. 2009. Physiological acclimation of *Pinus flexilis* to drought stress on contrasting slope aspects in Waterton Lakes National Park, Alberta, Canada. Canadian Journal of Forest Research. 39(3): 629-641.

Liston, Aaron; Robinson, William A.; Piñero, Daniel; Alvarez-Buylla, Elena R. 1999. Phylogenetics of *Pinus* (Pinaceae) based on nuclear ribosomal DNA internal transcribed spacer region sequences. Molecular Phylogenetics and Evolution. 11(1): 95-109.

Little, Elbert L., Jr.; Critchfield, William B. 1969. Subdivisions of the genus *Pinus* (pines). Misc. Publ. No. 1144. Washington, DC: U.S. Department of Agriculture, Forest Service.

Mahalovich, Mary F.; Burr, Karen E.; Foushee, David L. 2006. Whitebark pine germination, rust resistance, and cold hardiness among seed sources in the Inland Northwest: planting strategies for restoration. In: Riley, L. E.; Dumroese, R. K.; Landis, T. D., tech. coords. National Proceedings: Forest and Conservation Nursery Association—2005. Proc. RMRS-P-43. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station: 91-101.

Mahalovich, M. F.; Dickerson, G. A. 2004. Whitebark pine genetic restoration program for the Intermountain West (U.S.A.). In: Sniezko, Richard; Samman, Safiya; Schlarbaum, Scott E.; Kriebel, Howard B., eds. Breeding and genetic resources of five-needle pines: growth, adaptability and pest resistance; 2001 July 23-27; Medford, OR, USA. IUFRO Working Party 2.02.15. Proc. RMRS-P-32. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station.

Maloney, Patricia E. 2010. [Personal communication]. Davis, CA: University of California.

Maloney, Patricia E. Unpublished data on file at: University of California, Davis, CA.

Manel, Stéphanie; Joost, Stéphane; Epperson, Brian K.; Holderegger, Rolf; Storfer, Andrew; Rosenberg, Michael S.; Scribner, Kim T.; Bonin, Aurélie; Fortin, Marie-Josée. 2010. Perspectives on the use of landscape genetics to detect genetic adaptive variation in the field. Molecular Ecology. 19(17): 3760-3772.

Mastrogiuseppe, R. J.; Mastrogiuseppe, J. D. 1980. A study of *Pinus balfouriana* Grev. and Balf. (Pinaceae). Systematic Botany. 5(1): 86-104.

McKenney, Daniel W.; Pedlar, John H.; Lawrence, Kevin; Campbell, Kathy; Hutchinson, Michael F. 2007. Potential impacts of climate change on the distribution of North American trees. Bioscience. 57(11): 939-948.

McLane, Sierra; Aitken, Sally N. [In preparation]. Whitebark pine assisted migration trial. Centre for Forest Conservation Genetics, University of British Columbia, Vancouver, B.C., Canada.

McLane, Sierra; Aitken, Sally N. [In preparation]. Whitebark pine germination and growth at extreme temperatures. Centre for Forest Conservation Genetics, University of British Columbia, Vancouver, B.C., Canada.

Millar, Constance I.; Westfall, Robert D.; Delaney, Diane L. 2006. Elevational gradients and differential recruitment of limber pine (*Pinus flexilis*) and bristlecone pine (*Pinus longaeva*); White Mountains, California, USA. American Geophysical Union, Fall Meeting, 2006. Poster: C33C-1289. Berkeley, CA: U.S. Department of Agriculture, Forest Service, Sierra Nevada Research Center.

Millar, Constance I.; Westfall, Robert D.; Delany, Diane L. 2007. Response of high-elevation limber pine (*Pinus flexilis*) to multiyear droughts and 20th-century warming, Sierra Nevada, California, USA. Canadian Journal of Forest Research. 37(12): 2508-2520.

Millar, Constance I.; Westfall, Robert D.; Delany, Diane L.; King, John C.; Graumlich, Lisa J. 2004. Response of subalpine conifers in the Sierra Nevada, California, USA, to 20th-century warming and decadal climate variability. Arctic, Antarctic, and Alpine Research. 36(2): 181-200.

Mirov, Nicholas T. 1967. The genus *Pinus*. New York: The Ronald Press Company.

Mitton, J. B.; Kreiser, B. R.; Latta, R. G. 2000. Glacial refugia of limber pine (*Pinus flexilis* James) inferred from the population structure of mitochondrial DNA. Molecular Ecology. 9(1): 91-97.

Moir, W. H.; Ludwig, J. A. 1979. A classification of spruce-fir and mixed conifer habitat types of Arizona and New Mexico. Res. Pap. RM-207. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station. 47 p.

Moreno-Letelier, Alejandra; Piñero, Daniel. 2009. Phylogeographic structure of *Pinus strobiformis* Engelm. across the Chihuahuan Desert filter-barrier. Journal of Biogeography. 36(1): 121-131.

Murray, Andrew. 1853. Botanical expedition to Oregon. Report No. 8. Edinburgh, UK: Scottish Oregon Association.

Neale, David B.; Savolainen, Outi. 2004. Association genetics of complex traits in conifers. Trends in Plant Science. 9(7): 325-330.

Oline, David K. 2001. Unpublished data on file at: Southern Oregon University, Ashland, OR.

Oline, David K.; Mitton, Jeffry B.; Grant, Michael C. 2000. Population and subspecific genetic differentiation in the foxtail pine (*Pinus balfouriana*). Evolution. 54(5): 1813-1819.

ParksWatch. 2004. Los Altos de San Miguel Totonicapán Regional Park - Park Profile – Biodiversity. [Online]. Available: http://www.parkswatch.org/parkprofile.php?l=eng&country=gua&park=torf&page=bio [2010, August 26].

Parmesan, Camille. 2006. Ecological and evolutionary responses to recent climate change. Annual Review of Ecology, Evolution, and Systematics. 37: 637-669.

Perry, Jesse P. 1991. The pines of Mexico and Central America. Portland, OR: Timber Press.

Politov, D. V.; Krutovsky, K. V. 2004. Phylogenetics, genogeography and hybridization of five-needle pines in Russia and neighboring countries. In: Sniezko, Richard; Samman, Safiya; Schlarbaum, Scott E.; Kriebel, Howard B., eds. Breeding and genetic resources of five-needle pines: growth, adaptability and pest resistance; 2001 July 23-27; Medford, OR, USA. IUFRO Working Party 2.02.15. Proc. RMRS-P-32. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station.

Price, R. A.; Liston, A.; Strauss, S. H. 1998. Phylogeny and systematics of *Pinus*. In: Richardson, D. M., ed. Ecology and biogeography of *Pinus*. Cambridge, UK: Cambridge University Press: 49-68.

Rebertus, A. J.; Burns, B. R.; Veblen, T. T. 1991. Stand dynamics of *Pinus flexilis*-dominated subalpine forests in the Colorado Front Range. Journal of Vegetation Science. 2: 445-458.

Rehfeldt, Gerald E.; Crookston, Nicholas L.; Warwell, Marcus V.; Evans, Jeffrey S. 2006. Empirical analyses of plant-climate relationships for the western United States. International Journal of Plant Sciences. 167(6): 1123-1150.

Reuling, M. 2008. *Pinus albicaulis*. In: IUCN 2010. IUCN Red List of Threatened Species. Version 2010.2. [Online]. Available: www.iucnredlist.org [2010, August 17].

Richardson, B. A.; Brunsfeld, J.; Klopfenstein, N. B. 2002. DNA from bird-dispersed seed and wind-disseminated pollen provides insights into postglacial colonization and population genetic structure of whitebark pine (*Pinus albicaulis*). Molecular Ecology. 11(2): 215-227.

Richardson, Bryce A.; Klopfenstein, Ned B.; Brunsfeld, Steven J. 2002b. Assessing Clark's nutcracker seed-caching flights using maternally inherited mitochondrial DNA of whitebark pine. Canadian Journal of Forest Research. 32(6): 1103-1107.

Rogers, Deborah L.; Millar, Constance I.; Westfall, Robert D. 1999. Fine-scale genetic structure of whitebark pine (*Pinus albicaulis*): associations with watershed and growth form. Evolution. 53(1): 74-90.

Rourke, M. D. 1988. The biogeography and ecology of *Pinus balfouriana* Grev. & Balf. in the Sierra Nevada of California. Tucson, AZ: University of Arizona. 225 p. Dissertation.

Ryerson, Diane 1983. Population structure of *Pinus balfouriana* Grev. & Balf. Along the margins of its distribution area in the Sierran and Klamath regions of California. Sacramento, CA: Sacramento State University. 198 p. Thesis.

Saenz-Romero, Cuauhtémoc; Rehfeldt, Gerald E.; Crookston, Nicholas L.; Duval, Pierre; St.-Amant, Rémi; Beaulieu, Jean; Richardson, Bryce A. 2009. Spline models of contemporary, 2030, 2060, and 2090 climates for Mexico and their use in understanding climate-change impacts on the vegetation. Climatic Change. 102(3-4): 595-623.

Salzer, Matthew W.; Hughes, Malcolm K.; Bunn, Andrew G.; Kipfmueller, Kurt F. 2009. Recent unprecedented tree-ring growth in bristlecone pine at the highest elevations and possible causes. Proceedings of the National Academy of Sciences of the United States of America. 106(48): 20348-20353.

Schoettle, Anna. 2010. Unpublished data on file at: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Fort Collins, CO.

Schoettle, A. W.; Burns, K. S.; Costello, S.; Witcosky, J.; Howell, B.; Connor, J. 2008. A race against beetles: conservation of limber pine. Nutcracker Notes. 14: 11-12.

Schoettle, A. W.; Rochelle, S. G. 2000. Morphological variation of *Pinus flexilis* (Pinaceae), a bird-dispersed pine, across a range of elevations. American Journal of Botany. 87(12): 1797-1806.

Schoettle, Anna W.; Sniezko, Richard A. 2007. Proactive intervention to sustain high-elevation pine ecosystems threatened by white pine blister rust. Journal of Forest Research. 12(5): 327-336.

Schoettle, Anna W.; Sniezko, Richard A.; Burns, Kelly S. 2009. Sustaining *Pinus flexilis* ecosystems of the Southern Rocky Mountains (USA) in the presence of *Cronartium ribicola* and *Dendroctonus ponderosae* in a changing climate. In: Noshad, David; Noh, Eun Woon; King, John; Sniezko, Richard A. eds. Breeding and genetic resources of five-needle pines; Proceedings of the Conference; IUFRO Working Party 2.02.15; 2008 September 22-26; Yangyang, Korea. Seoul: Korea Forest Research Institute: 63-65.

Schoettle, Anna W.; Sniezko, Richard A.; Kegley, Angelia; Hill, Jerry; Burns, Kelly S. 2010. Resistance to white pine blister rust in *Pinus flexilis* and *Pinus aristata* of the Southern Rockies—initial findings. In: Adams, Judy; Jamieson, Carrie; Palacios, Patsy, comps. 2010. Proceedings of the 57th Western International Forest Disease Work Conference; 2009 July 20-24; Durango, CO. Fort Collins, CO: Forest Health Technology Enterprise Team: 109-110. [Online]. Available: http://www.cnr.usu.edu/quinney/files/uploads/WIFDWC2009.pdf

Schrag, Anne M.; Bunn, Andrew G.; Graumlich, Lisa J. 2008. Influence of bioclimatic variables on tree-line conifer distribution in the Greater Yellowstone Ecosystem: implications for species of conservation concern. Journal of Biogeography. 35(4): 698-710.

Schulman, E. 1958. Bristlecone pine, oldest known living thing. National Geographic. 113: 355-372.

Schuster, William S.; Alles, David L.; Mitton, Jeffry B. 1989. Gene flow in limber pine: evidence from pollination phenology and genetic differentiation along an elevational transect. American Journal of Botany. 76(9): 1395-1403.

Schuster, William S. F.; Mitton, Jeffry B. 1991. Relatedness within clusters of a bird-dispersed pine and the potential for kin interactions. Heredity. 67:41-48.

Schuster, William S. F.; Mitton, Jeffry B. 2000. Paternity and gene dispersal in limber pine (*Pinus flexilis* James). Heredity. 84(3): 348-361.

Schwandt, J. W.; Lockman, I. B.; Kliejunas, J. T.; Muir, J. A. 2010. Current health issues and management strategies for white pines in the western United States and Canada. Forest Pathology. 40: 226-250.

Shaw, George Russell. 1914. The genus *Pinus*. Cambridge: Riverside Press.

Sniezko, Richard. 2010. [Personal communication]. Cottage Grove, OR: U.S. Department of Agriculture, Forest Service.

Sniezko, Richard A.; Kegley, Angelia; Danchok, Robert; Long, Sally. 2007. Variation in resistance to white pine blister rust in 43 whitebark pine families from Oregon and Washington—early results and implications for conservation. In: Goheen, Ellen M.; Sniezko, Richard A., tech. coords. Proceedings of the conference: whitebark pine: a Pacific Coast perspective. 2006 August 27-37; Ashland, OR. R6-NR-FHP-2007-01. Portland, OR: Pacific Northwest Region, Forest Service, U.S. Department of Agriculture: 24-27.

Sniezko, Richard A.; Kegley, Angelia; Danchok, Robert; Schoettle, Anna W.; Burns, Kelly S.; Conklin, Dave. 2008. *Cronartium ribicola* resistance in whitebark pine, southwestern white pine, limber pine and Rocky Mountain bristlecone pine—preliminary screening results from first tests at Dorena GRC. In: McWilliams, Michael; Palacios, Patsy, comps. Proceedings of the 55th Annual Western International Forest Disease Work Conference; 2007 October 15-19; Sedona, AZ. Logan: Utah State University: 84-86.

Spielman, Derek; Brook, Barry W.; Briscoe, David A.; Frankham, Richard. 2004. Does inbreeding and loss of genetic diversity decrease disease resistance? Conservation Genetics. 5(4): 439-448.

Steele, Robert. 1990. *Pinus flexilis* James, limber pine. In: Burns, Russell M.; Honkala, Barbara H., tech. coords. Silvics of North America, Vol. 1, Conifers. Agriculture Handbook 654. Washington, DC: U.S. Department of Agriculture, Forest Service.

Steinhoff, R. J.; Andresen, J. W. 1971. Geographic variation in *Pinus flexilis* and *Pinus strobiformis* and its bearing on their taxonomic status. Silvae Genetica. 20: 159-167.

Strauss, Steven H.; Doerksen, Allan H. 1990. Restriction fragment analysis of pine phylogeny. Evolution. 44(4): 1081-1096.

Stuart-Smith, G. J. 1998. Conservation of whitebark pine in the Canadian Rockies: blister rust and population genetics. Edmonton, Alberta: University of Alberta. Thesis.

Tomback, D. F. 1978. Foraging strategies of Clark's nutcracker. Living Bird. 16: 123-161.

Tomback, Diana F. 1982. Dispersal of whitebark pine seeds by Clark's nutcracker: a mutualism hypothesis. Journal of Animal Ecology. 51(2): 451-467.

Tomback, D. F. 2001. Clark's nutcracker: agents of regeneration. In: Tomback, Diana F.; Arno, Stephen F.; Keane, Robert E., eds. Whitebark pine communities: ecology and restoration. Washington, DC: Island Press: 89-104.

Tomback, Diana F.; Linhart, Yan B. 1990. The evolution of bird-dispersed pines. Evolutionary Ecology. 4(3): 185-219.

Tomback, D. F.; Achuff, P. 2010. Blister rust and western forest biodiversity: ecology, values, and outlook for white pines. Forest Pathology. 40: 186-225.

Torick, Lisa L.; Tomaback, Diana F.; Espinoza, Ronald. 1996. Occurrence of multi-genet tree clusters in "wind-dispersed" pines. American Midland Naturalist. 136(2): 262-266.

U.S. Department of Agriculture, Forest Service. 2010. Plant species and climate profile predictions. U.S. Department of Agriculture, Rocky Mountain Research Station, Moscow Forestry Sciences Center. [Online]. Available: http://forest.moscowfsl.wsu.edu/climate/species/ [2010 September].

Vogler, Detlev. 2010. [Personal communication]. Placerville, CA: U.S. Department of Agriculture, Forest Service, Pacific Southwest Research Station.

Vogler, Detlev R.; Delfino-Mix, Annette; Schoettle, Anna W. 2006. White pine blister rust in high-elevation white pines: screening for simply-inherited, hypersensitive resistance. In: Guyon, J. C., comp. Proceedings of the 53rd Western International Forest Disease Work Conference; 2005 September 26-30; Jackson, WY. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Region: 73-82.

Wang, T. L.; McLane, S. C.; Campbell, E.; Schroeder, T. A. [In preparation]. Whitebark pine may not survive climate change.

Warwell, M. V. [In preparation]. Adaptive variation among whitebark pine populations in the Intermountain West.

Warwell, Marcus V.; Rehfeldt, Gerald E.; Crookston, Nicholas L. 2007. Modeling contemporary climate profiles of whitebark pine (*Pinus albicaulis*) and predicting responses to global warming. In: Goheen, Ellen M.; Sniezko, Richard A., tech. coords. Proceedings of the conference: whitebark pine: a Pacific Coast perspective. 2006 August 27-37; Ashland, OR. R6-NR-FHP-2007-01. Portland, OR: Pacific Northwest Region, Forest Service, U.S. Department of Agriculture: 139-142.

Weaver, T. 2001. Whitebark pine and its environment. In: Tomback, Diana F.; Arno, Stephen F.; Keane, Robert E., eds. Whitebark pine communities: ecology and restoration. Washington, DC: Island Press: 41-73.

Webster, Kara L.; Johnson, Edward A. 2000. The importance of regional dynamics in local populations of limber pine (*Pinus flexilis*). Ecoscience. 7(2): 175-182.

Wells, Phillip V. 1983. Paleobiogeography of montane islands in the Great Basin since the last glaciopluvial. Ecological Monographs. 53(4): 341-382.

Wright, J. A.; Marin, A.; Dvorak, W. 1996. *Ex situ* gene conservation of *Pinus ayacahuite*. FAO Forest Genetic Resources. 24: 48-51.

Wright, J. W.; Kung, F. H.; Read, R. A.; Steinhoff, R. J.; Andresen, J. W. 1971. Nine-year performance of *Pinus flexilis* and *P. strobiformis* progenies in Michigan and Nebraska. Silvae Genetica. 20: 211-214.

Yandell, U. G. 1992. An allozyme analysis of whitebark pine (*Pinus albicaulis* Engelm.). Reno, NV: University of Nevada. Thesis.

Molecular Genetic Variation in Whitebark Pine (*Pinus albicaulis* Engelm.) in the Inland West

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Abstract—Levels of genetic variation within and among 163 individual-tree collections and one bulk lot of whitebark pine were estimated using isozymes, mitochondrial DNA and chloroplast DNA; 79 of the samples are also part of a common garden study evaluating survival, rust resistance, late winter cold hardiness, and early height-growth. Within the species, 100 percent of the isozyme loci are polymorphic, with the number of alleles per locus (Na) equal to 4.0. Genetic diversity is high (H_e = 0.271) relative to other conifers in the same forest cover type and is comparable to quaking aspen (*Populus tremuloides* Michx) and limber pine (*Pinus flexilis* James), two of the most geographically widespread tree species in North America. Fixation values indicate general random mating with no marked excess of heterozygosity or inbreeding. Poor genetic differentiation among zones (F_{ST} = 0.026), low F_{IS} (-0.016) and F_{IT} (0.011) values, and a high number of migrants (N_m = 9.354) also indicate a lack of inbreeding. The oldest known whitebark pine specimen on the Sawtooth National Forest is homozygous for 13 loci (12 for common alleles and one for a rare allele). Of the 164 samples grouped into 117 collection sites, 108 of the *nad5a* intron of the mitochondrial genome contained haplotype 1 present in Idaho, Montana, eastern Washington, and Wyoming, while nine contained haplotype 2 from eastern California and Nevada. This mitochondrial marker, along with high pairwise F_{ST} values, underscores the uniqueness of the Nevada zone. High levels of diversity (H_e = 0.481, Na = 4.2) measured by three, chloroplast simple sequence repeat (SSR) markers indicate the Bitterroots-Idaho Plateau zone has the largest amount of diversity, while the Selkirk-Cabinet zone has the lowest diversity among zones. Similar relationships occur among the Selkirk-Cabinets, Clark Fork-Lolo Pass, and Missions-Glacier Park zones as a group and the Bitterroots-Idaho Plateau and Central Montana zones as another distinct group. Until further sources can be evaluated south of 44.5° N latitude for key adaptive traits, a conservative approach maintains the Bitterroots-Idaho Plateau and Central Montana groups as distinct zones. The four adaptive traits from the common garden study, isozyme data and three chloroplast SSR markers support the Greater Yellowstone-Grand Teton zone remaining a distinct zone. Taken collectively there is sufficient genetic diversity and genetic variation to support the continuation of a rust resistance screening and genetic restoration program for this species.

Introduction

Evolutionary forces of gene mutation, gene flow, random drift, and selection shape the genetic structure of a species. Examples of contemporary forces shaping whitebark pine include wildland fire, fire suppression and exclusion, blister rust (*Cronartium ribicola* A. Dietr.), and mountain pine beetle (*Dendroctonus ponderosae* Hopkins). Uncontrolled wildfire can kill young whitebark pine regeneration or trees of cone-bearing age, which will limit the food supply for dependent wildlife and cause loss of future seed sources for restoration purposes. Wildfires during the 2000 fire season burned 929.2 thousand hectares on USDA National Forest System lands in Idaho and Montana. Much of the fire occurred in higher elevation populations resulting in the reduction of both diseased and healthy whitebark pine trees (Mahalovich and Dickerson 2004). Wildfire aids in the preparation of a seedbed for natural regeneration. Fire suppression and the policy of fire exclusion has reduced the role of fire in regeneration of pure whitebark pine stands and has allowed successional replacement in mixed-conifer stands to subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.), lodgepole pine (*Pinus contorta* Douglas ex Louden) and Engelmann spruce (*Picea engelmannii* Parry ex Engelm.). The frequency and magnitude of these evolutionary forces has the potential to reduce or eliminate available seed sources and advanced reproduction. Even with the recent introduction of a non-native rust pathogen, blister rust resistance is present in the Northern Rockies (Mahalovich and others 2006). Local adaptation is sustainable relative to blister rust resistance, owing to whitebark pine having a generalist adaptive strategy, where the largest proportion of genetic variation is within seed sources (Mahalovich submitted).

A successful genetic restoration program depends on understanding a species' genetic structure. Obtaining basic genetic information facilitates the development of seed transfer guidelines, operational cone collection protocols, selective breeding and gene conservation strategies, and priority setting of high risk areas in need of management intervention through site-specific prescriptions. The first whitebark pine cone collections began in 1991, with a combination of 26 individual-tree and bulked collections in Montana on the Bitterroot, Custer, Gallatin, and Lewis and Clark National Forests. By 1998, the importance of conserving whitebark pine became critical due to the combination of blister rust infection, mountain pine beetle, wildland fire in high elevation ecosystems, and emerging concerns over seed viability in long-term storage. Proactive restoration efforts with a genetic component began in earnest in 1999 (Mahalovich and Dickerson 2004).

Successful tree planting has improved since the earliest efforts in 1991 due to the selection of planting sites best suited for whitebark pine, the application of appropriate seed transfer guidelines, and the development of blister rust resistant

In: Keane, Robert E.; Tomback, Diana F.; Murray, Michael P.; and Smith, Cyndi M., eds. 2011. **The future of high-elevation, five-needle white pines in Western North America: Proceedings of the High Five Symposium.** 28-30 June 2010; Missoula, MT. Proceedings RMRS-P-63. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station. 376 p. Online at http://www.fs.fed.us/rm/pubs/rmrs_p063.html

planting stock. The presence of genetic differentiation in whitebark pine due to directional selection and adaptation to local environments has managerial implications with respect to the control of seed movement in the form of zoning or expert systems.

Seed zones are geographic subdivisions within a region encompassing areas of similar environmental conditions with possible altitudinal limits within zones. When boundaries among subdivisions do not reflect patterns of genetic variation in traits inferring adaptive value, these subdivisions are referred to as provisional seed zones. Provisional seed zones in the Inland West were delineated based on early rust screening trials, the orientation of mountain ranges, and blister rust hazard ratings over large geographic areas (Mahalovich 2000, Mahalovich and Dickerson 2004). Hazard rating systems measure the susceptibility of forested areas to a particular disease by evaluating its impact in a specific host species (for example, percent of trees from an area infected with blister rust and the average number of cankers per tree from that location). These zonal boundaries were conservative in scope (Mahalovich and Dickerson 2004) until genetic data for adaptive traits became available (Mahalovich submitted).

While common garden studies provide essential information regarding the genetic structure in adaptive traits, population genetic studies are also necessary to define genetic structure, genetic diversity, and levels of inbreeding in neutral markers (for example, isozymes or allozymes, mitochondrial DNA (mtDNA), and chloroplast DNA (cpDNA) (Mitton 1995)). Both types of studies share a critical role in determining the effectiveness of a genetic restoration program. Population genetics research using allozymes show little population structure in a range-wide study (F_{ST} = 0.034, Jørgensen and Hamrick 1997), and moderate differentiation in regional (F_{ST} = 0.025, Bruerderle and others 1998) or isolated population studies (F_{ST} = 0.088, Yandell 1993). Fine-scale genetic structure of whitebark pine in the eastern Sierra Nevada Range of California also reveal negligible genetic differentiation among three watersheds (F_{ST} = 0.004) and strong family structure (growth form) due to the seed-caching behavior of Clark's nutcracker (*Nucifraga columbiana* Wilson) (Rogers and others 1999).

Mitochondrial markers track seed movement since mtDNA is maternally inherited in the Pinaceae. Richardson and others (2002) identified variation in the *nad5a* intron of the mitochondrial genome in whitebark pine. This variation was found to occur in a sequence recognized by the restriction endonuclease *Mse*I, resulting in two haplotypes at that locus. After amplifying the *nad5a* intron, one haplotype is cut by *Mse*I, and can be identified by the presence of two bands, while the other haplotype does not contain a restriction site and produces a single band. Evaluation of seed movement in this broader sampling of whitebark pine seed lots, as compared to Richardson and others (2002) is highly desirable.

Isozyme analyses are well established and a cost-effective approach for estimating measures of genetic structure (amount and pattern of variation among and within seed zones), genetic diversity (heterozygosity) and mating systems (outcrossing rate) (USDA Forest Service 2003). These quantitative measures are also comparable to upwards of 3,000 whitebark pine samples submitted to the National Genetic Laboratory in Placerville, CA (USDA Forest Service 2009).

Chloroplast markers track pollen movement since cpDNA is paternally inherited in the Pinaceae. Three cpDNA SSR markers, Pt15169, Pt30204, and Pt71936 (Vendramin and others 1996), are another useful tool to characterize patterns of geographic variation in whitebark pine from the perspective of pollen movement.

The research presented here investigates genetic diversity using isozyme and molecular data, and relates those findings to patterns of genetic variation in key adaptive traits in an earlier seed source study (Mahalovich submitted, Mahalovich and others 2006). Since the majority of the adaptive trait variation occurs within seed sources and the provisional seed zones are conservative in scale, rather than evaluating genetic diversity among and within populations, this study focuses on the amount of genetic diversity among and within seed zones. Project objectives include:

- Determining the genetic structure, genetic diversity, and level of inbreeding among a number of cone collections and branch samples collected from across the Northern Rockies, California, and Nevada;
- Determining whether there is correspondence among provisional seed zone boundaries (Figure 1) using isozyme and molecular data; and
- Developing a comprehensive genetics profile to identify seed sources that are most at risk for being lost due to their apparent uniqueness.

Material and Methods

Material Collection

Low seed yields and a limited geographic representation of bulk seed in inventory narrowed seed lot selection to individual-tree cone collections to achieve a broad geographic sample from eastern California, Idaho, Montana, Nevada, eastern Washington, and Wyoming. A total of 163 individual-tree collections and one bulk lot representing 117 seed source groupings (as determined using common area name and geographic coordinates) are included in this study (Table 1). The bulk lot represents the easternmost population in this collection and is of special interest because of its widespread use for restoration from 2002 to the present, with the last planting of seed from this source anticipated in 2011 (McLaughlin, personal communication). There is no indication from the records that cones were collected from trees of the krummholz growth form.

All seed lots used in Mahalovich and others (2006) were desirable to develop a comprehensive genetics profile of adaptive trait, isozyme and molecular data for each seed source; 79 of the original 110 lots had sufficient seed for this study. When seed quantities were too low or geographic areas were not well represented from the 1991-1997 collections (for example, central ID, NV, northwestern WY), additional seed lots from the

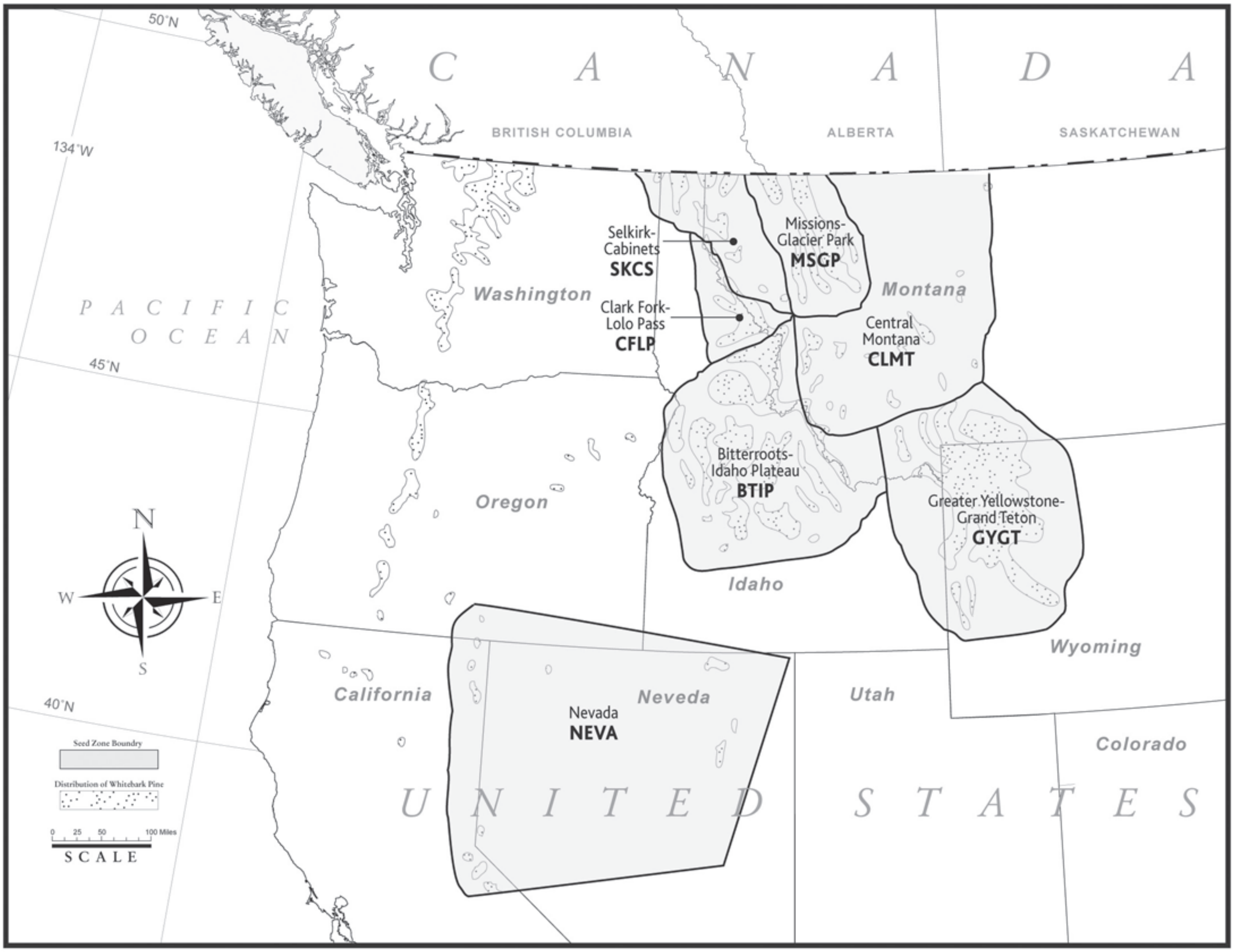

Figure 1. Provisional whitebark pine seed zones in the Inland West overlaying current species distribution (Little 1971).

2001-2006 collections (6000-series plus trees) and 16 vegetative samples from previous research in the Northern Rockies (Richardson 2001) were included. One branch tip and a cone containing five seeds from the oldest known living whitebark pine specimen (1,285 years) located at Railroad Ridge on the Sawtooth National Forest (Perkins and Swetnam 1996) were also included. The authors acknowledge that a representative sample of bulked collections may have better served the parameter estimates for isozyme and molecular data (this paper); however, resources were not available to collect additional bulked collections.

Seed Preparation and Germination

Seed samples were stratified and germinated following Mahalovich and others (2006) and Burr and others (2001). For each germinated seed (10 seeds per collection): (1) the embryo was dissected from the megagametophyte tissue, placed in a microfuge tube, and frozen at -80°C for future analyses, (2) a portion of each of the 10 megagametophytes per collection were placed in a collection tube to achieve a single DNA extraction per collection, effectively genotyping the mother tree through DNA analysis (White and others 2007), and (3) the remaining megagametophyte tissue was placed in an individual well into a microtiter plate for isozyme analysis.

Mitochondrial DNA (mtDNA) Analysis

Amplification of the *nad5a* intron in these samples was completed using primers designed by Wu and others (1998). For each sample, 2.0 ng of mtDNA was amplified following the reaction conditions described by Richardson and others (2002). Amplification was carried out on a MJ Research® PTC-200 thermalcycler (MJ Research, Watertown, Massachusetts, USA). Following amplification the product was purified using the Qiagen™ Qiaquick PCR Purification Kit following the recommended protocols (Qiagen Corp., Valencia, California, USA). Samples were then restricted with *Mse*I. Restriction products were separated via electrophoresis on a 1% agarose gel using 1X TBE buffer (0.045 M Tris-borate, 0.001 M EDTA pH 8) and visualized using ethidium bromide under UV light.

Table 1. Comprehensive genetics profile for the Inland West Whitebark Genetic Restoration Program (percent of blister rust resistance individuals[1], rust resistance family index, late winter cold hardiness and 6-year height ranks described in Mahalovich and others (2006)); by latitude.

National Forest or National Park (NP)	Latitude °N	Longitude °W	Elevation (ft)	Seed Zone[2]	Area	Seed Source Group Number[3]	Proportion Observed Polymorphic Loci[4]	Number of Unique Alleles[4]	No-Spot (%)[5]	Needle Shed (%)	Short Shoot (%)	Bark Reaction (%)	Susceptible (%)	Resistant (%)	Rust Resistance Famil Index Rank	7th-yr Late Winter Cold Hardiness Rank	6-yr Height Rank
Humboldt-Toiyabe	38.08	-119.24	9,146	NEVA	Virginia Lakes	71	0.25	20									
Humboldt-Toiyabe	38.08	-119.24	9,677	NEVA	Dunderberg	72	0.188	19									
Humboldt-Toiyabe	38.08	-119.24	9,745	NEVA	Dunderberg	72	0.313	20									
Humboldt-Toiyabe	38.08	-119.24	9,848	NEVA	Dunderberg	72	0.25	20									
Humboldt-Toiyabe	38.08	-119.24	9,883	NEVA	Virginia Lakes	73	0.25	20									
Humboldt-Toiyabe	38.08	-119.24	9,894	NEVA	Virginia Lakes	73	0.25	20									
Humboldt-Toiyabe	38.08	-119.24	10,117	NEVA	Dunderberg Top	74	0.25	20									
Humboldt-Toiyabe	38.08	-119.24	10,184	NEVA	Dunderberg Top	74	0.188	19									
Humboldt-Toiyabe	38.34	-119.58	9,112	NEVA	Sonora Pass	75	0.313	21									
Humboldt-Toiyabe	38.34	-119.58	9,300	NEVA	Sonora Pass	75	0.375	22									
Humboldt-Toiyabe	38.34	-119.6	9,464	NEVA	Sonora Pass	76	0.125	18									
Humboldt-Toiyabe	38.34	-119.6	9,509	NEVA	Sonora Pass	76	0.375	22									
Humboldt-Toiyabe	38.34	-119.62	9,327	NEVA	Sonora Pass	76	0.125	18									
Humboldt-Toiyabe	39.31	-119.89	8,930	NEVA	Mt. Rose-Tahoe Meadows	77	0.188	19									
Humboldt-Toiyabe	39.31	-119.91	8,677	NEVA	Mt. Rose-Tahoe Meadows	77	0.438	23									
Humboldt-Toiyabe	39.31	-119.91	8,968	NEVA	Mt. Rose Trailhead	78	0.188	19									
Humboldt-Toiyabe	39.31	-119.91	8,968	NEVA	Mt. Rose Trailhead	78	0	16									
Humboldt-Toiyabe	39.32	-119.91	8,587	NEVA	Mt. Rose-Tamarack Lake	79	0.25	20									
Humboldt-Toiyabe	39.32	-119.91	8,640	NEVA	Mt. Rose-Tamarack Lake	79	0.375	22									
Humboldt-Toiyabe	39.44	-119.96	8,560	NEVA	Garson Road	80	0.375	22									
Humboldt-Toiyabe	39.44	-119.96	8,596	NEVA	Garson Road	80	0.25	20									
Shoshone	42.64	-109.7	10,200	GYGT	Blue Ridge	81	0.375	22									
Bridger-Teton	43.48	-109.94	8,680	GYGT	Jackson Hole Mountain Resort	82	0.125	18									
Shoshone	43.5	-109.86	9,590	GYGT	Union Pass	83	0.188	19									
Shoshone	43.51	-109.84	9,800	GYGT	Wind River Ranger District	70	0.375	22	0.112	0.045	0.119	0.097	0.627	0.373	57.5	16	58
Bridger-Teton	43.61	-110.26	9,400	GYGT	Gunsight Pass	84	n/a	n/a									
Bridger-Teton	43.61	-110.26	9,400	GYGT	Gunsight Pass #1	84	n/a	n/a									
Bridger-Teton	43.61	-110.86	9,085	GYGT	Labarge Creek	85	0.25	20									
Boise	43.61	-115.45	8,300	BTIP	Trinity	86	0.188	19									
Grand Teton NP	43.68	-110.8	9,080	GYGT	Stewarts Draw	87	0.313	21									
Shoshone	43.73	-109.6	9,512	GYGT	Bog Lakes	88	0.313	21									
Caribou-Targhee	43.78	-110.95	9,000	GYGT	Grand Targhee Ski Resort	89	n/a	n/a									
Caribou-Targhee	43.79	-110.93	8,000	GYGT	East Dry Creek	90	0.063	17									
Caribou-Targhee	43.79	-110.93	9,530	GYGT	Grand Targhee	91	0.125	18									
Bridger-Teton	43.82	-110.21	8,520	GYGT	Togwater Lodge #1	92	n/a	n/a									
Sawtooth	43.88	-114.72	8,880	BTIP	Galena Summit	93	0.313	21									
Sawtooth	44.05	-114.66	9,520	BTIP	4th of July	94	0.125	18									
Sawtooth	44.1	-114.6	9,440	BTIP	Railroad Ridge	95	0	13									
Boise	44.19	-115.76	7,830	BTIP	Scott Mountain	96	0.188	19									
Caribou-Targhee	44.53	-111.69	8,100	GYGT	Boatman Springs	97	0.25	20									
Caribou-Targhee	44.54	-111.61	8,100	BTIP	Keg Springs	98	0.188	19									
Caribou-Targhee	44.54	-111.43	8,200	GYGT	Mt. Sawtelle #1	99	n/a	n/a									
Caribou-Targhee	44.54	-111.43	8,200	GYGT	Mt. Sawtelle #2	99	n/a	n/a									
Caribou-Targhee	44.54	-111.41	8,350	GYGT	Sawtel Peak	1	0.25	20	0.129	0.007	0.107	0.021	0.736	0.264	95.5	20	78
Caribou-Targhee	44.55	-111.43	8,600	BTIP	Sawtell Mountain	1	0.25	20									
Yellowstone NP	44.81	-110.44	8,936	GYGT	Washburn	100	0.375	22									
Beaverhead-Deerlodge	44.82	-111.87	8,800	GYGT	W.F. Cabin	2	0.188	19	0.167	0.08	0.167	0.029	0.558	0.442	74		56
Beaverhead-Deerlodge	44.82	-111.87	8,800	GYGT	W.F. Cabin	2	0.313	21	0.186	0.062	0.142	0.062	0.549	0.451	46		76
Shoshone	44.95	-109.47	10,000	GYGT	Beartooth Pass #1	101	n/a	n/a									
Shoshone	44.95	-109.47	10,000	GYGT	Beartooth Pass #2	101	n/a	n/a									
Payette	45	-116.14	7,200	BTIP	Brundage Mountain	102	0.188	19									
Gallatin	45.03	-109.95	9,018	CLMT	Miller Trail	103	0.313	21									
Custer	45.04	-109.43	8,900	GYGT	Hellroaring I	4	0.375	23	0.087	0.022	0.043	0.065	0.783	0.217	81	33	104
Custer	45.04	-109.45	9,200	GYGT	Hellroaring II	5	0	14	0.07	0.023	0.047	0.093	0.767	0.233	87		91
Custer	45.04	-109.56	8,900	GYGT	Hellroaring I	4	0.313	21	0.064	0	0.064	0.043	0.83	0.17	110	43	68
Gallatin	45.05	-109.95	9,600	GYGT	Daisy Pass	6	0.313	21	0.087	0	0	0.043	0.87	0.13	95.5		100
Beaverhead-Deerlodge	45.15	-113.55	8,400	CLMT	Goldstone Pass	7	0.25	20	0.068	0	0.136	0	0.795	0.205	106	28	97
Beaverhead-Deerlodge	45.15	-113.55	8,400	CLMT	Goldstone Pass	7	0.313	21	0.113	0.05	0.149	0.035	0.652	0.348	44.5		19
Beaverhead-Deerlodge	45.15	-113.55	8,400	CLMT	Goldstone Pass	7	0.313	21	0.021	0.021	0.104	0.021	0.833	0.167	85		83

Table 1. *Continued.*

National Forest or National Park (NP)	Latitude °N	Longitude °W	Elevation (ft)	Seed Zone[2]	Area	Seed Source Group Number[3]	Proportion Observed Polymorphic Loci[4]	Number of Unique Alleles[4]	No-Spot (%)[5]	Needle Shed (%)	Short Shoot (%)	Bark Reaction (%)	Susceptible (%)	Resistant (%)	Rust Resistance Famil Index Rank	7th-yr Late Winter Cold Hardiness Rank	6-yr Height Rank
Beaverhead-Deerlodge	45.15	-113.55	8,400	CLMT	Goldstone Pass	7	0.25	20	0.149	0	0.064	0.064	0.723	0.277	29		30
Beaverhead-Deerlodge	45.15	-113.55	8,400	CLMT	Goldstone Pass	7	0.375	22	0.183	0.12	0.204	0.042	0.451	0.549	17		49
Payette	45.22	-116.12	7,800	BTIP	Lava Ridge	104	0.438	23									
Gallatin	45.27	-111.42	9,000	GYGT	Lone Mountain	8	0.25	20	0.125	0.014	0.063	0.083	0.715	0.285	86	11	64
Nez Perce	45.36	-116.51	8,000	BTIP	Riggins	10	0.438	23	0.182	0.015	0.106	0.061	0.636	0.364	25		72
Nez Perce	45.38	-116.48	8,000	BTIP	Heavens Gate	11	0.313	21	0.182	0.045	0.227	0.045	0.5	0.5	41		101
Gallatin	45.4	-111.28	8,600	GYGT	Little Bear	14	0.313	21	0.225	0.099	0.12	0.035	0.521	0.479	67	13	60
Salmon-Challis	45.47	-114.29	7,860	BTIP	Tin Cup	16	0.188	19	0.191	0.085	0.227	0.085	0.411	0.589	20	35	16
Salmon-Challis	45.47	-114.29	7,860	BTIP	Tin Cup	16	0.188	19	0.237	0.017	0.186	0.051	0.508	0.492	77.5		103
Nez Perce	45.63	-115.95	8,200	BTIP	Gospel Peak	17	0.125	18	0.064	0.05	0.329	0.071	0.486	0.514	36.5		33.5
Beaverhead-Deerlodge	45.71	-112.93	8,000	CLMT	Quartz Hill	18	0.375	22	0.05	0.014	0.05	0.029	0.856	0.144	104	4	85
Nez Perce	45.71	-115	8,200	BTIP	Burnt Knob	19	0.188	19	0.133	0.119	0.315	0.056	0.378	0.622	42	41	25
Bitterroot	45.72	-113.99	8,270	CLMT	Saddle Mountain	20	0.188	19	0.263	0.113	0.165	0.023	0.436	0.564	59		38
Bitterroot	45.72	-113.99	8,270	CLMT	Saddle Mountain	20	0.375	22	0.133	0.035	0.077	0.021	0.734	0.266	91	19	24
Gallatin	45.89	-110.96	8,861	CLMT	Corbly Gulch	105	0.5	24									
Nez Perce	45.91	-115.71	7,140	BTIP	Pilot Knob	22	0.438	23	0.22	0.073	0.165	0.147	0.394	0.606	10	40	42
Nez Perce	45.91	-115.71	7,140	BTIP	Pilot Knob	22	0.125	18	0.141	0.049	0.366	0.141	0.303	0.697	2	5	80
Nez Perce	45.91	-115.07	6,940	BTIP	Elk Mountain	106	0.125	18									
Beaverhead-Deerlodge	45.94	-113.51	7,900	CLMT	Mudd Ridge	23	0.25	20	0.104	0.042	0.042	0.042	0.771	0.229	72		2
Bitterroot	46.07	-113.8	8,040	CLMT	Coyote Meadows	24	0.375	22	0.161	0.073	0.095	0.036	0.635	0.365	73	17	61
Bitterroot	46.07	-113.8	8,040	CLMT	Coyote Meadows	24	0.188	19	0.118	0.022	0.074	0.022	0.765	0.235	83	26	75
Bitterroot	46.07	-113.8	8,040	CLMT	Coyote Meadows	24	0.438	23	0.117	0.146	0.08	0.051	0.606	0.394	57.5	17	35
Clearwater	46.3	-114.61	7,400	BTIP	Diablo Mountain	26	0.438	23	0.156	0.067	0.356	0.067	0.356	0.644	12		32
Beaverhead-Deerlodge	46.39	-112.19	7,600	CLMT	Occidental Plateau	28	0.125	18	0.294	0.118	0.059	0.059	0.471	0.529	15		63
Helena	46.4	-111.17	7,500	CLMT	Mt. Edith	107	0.313	21									
Clearwater	46.45	-114.73	6,895	BTIP	Tom Beal Park	108	0.188	19									
Bitterroot	46.51	-114.22	6,470	CLMT	St. Mary's Peak	30	0.125	18	0.134	0.045	0.08	0.018	0.723	0.277	101	18	59
Bitterroot	46.51	-114.22	6,470	CLMT	St. Mary's Peak	30	0.375	22	0.117	0.058	0.109	0.058	0.657	0.343	66		18
Clearwater	46.53	-115	7,000	CFLP	Indian Post Off.	31	0.25	20	0.2	0.096	0.207	0.104	0.393	0.607	34		77
Clearwater	46.55	-114.5	6,970	BTIP	Beaver Meadows	109	0.313	21									
Clearwater	46.56	-114.44	7,300	CFLP	Beaver Ridge	32	0.25	20	0.134	0.071	0.17	0.116	0.509	0.491	44.5		40
Clearwater	46.56	-114.44	7,300	CFLP	Beaver Ridge	32	0.438	23	0.125	0.059	0.272	0.007	0.537	0.463	103	38	28
Clearwater	46.56	-114.44	7,300	CFLP	Beaver Ridge	32	0.313	20	0.174	0.094	0.377	0.022	0.333	0.667	30.5	10	13
Clearwater	46.56	-114.44	7,300	CFLP	Beaver Ridge	32	0.25	20	0.022	0.058	0.18	0.101	0.64	0.36	79		73
Clearwater	46.61	-114.78	6,970	CFLP	Lost Lake Trail #3	110	0.188	19									
Clearwater	46.64	-114.86	7,200	CFLP	Blacklead Mountain	34	0.438	23	0.336	0.044	0.239	0.097	0.283	0.717	3	3	81
Clearwater	46.64	-114.86	7,200	CFLP	Blacklead Mountain	34	0	15	0.261	0.085	0.183	0.127	0.345	0.655	4	15	51
Lewis & Clark	46.77	-110.6	8,068	CLMT	Ant Park	111	0.375	22									
Lewis & Clark	46.77	-110.62	8,073	CLMT	Higgins Park	112	0.375	22									
Clearwater	46.87	-115.25	6,200	CFLP	Indian Henry Ridge	113	0.125	18									
Bridger-Teton	46.97	-107.09	9,028	GYGT	Fish Creek	114	0.375	22									
Clearwater	46.99	-115.06	6,556	CFLP	Long Creek Ridge	115	0.188	19									
Idaho Panhandle	47.	-116.03	5,800	CFLP	Freezeout	36	0.25	20	0.429	0	0.429	0	0.143	0.857	61.5		79
Idaho Panhandle	47.	-116.03	5,940	CFLP	Freezeout	36	0.313	21	0.415	0.128	0.16	0.043	0.255	0.745	13	21	107
Idaho Panhandle	47.01	-116.07	5,600	CFLP	Marks Butte	116	n/a	n/a									
Lolo	47.01	-114.01	7,860	MSGP	Snow Bowl	37	0.125	18	0.087	0.007	0.181	0.08	0.645	0.355	76	39	43
Idaho Panhandle	47.01	-116.03	5,920	CFLP	Freezeout	38	0.25	20	0.208	0.042	0.375	0.083	0.292	0.708	26		11
Idaho Panhandle	47.01	-116.03	5,920	CFLP	Freezeout	38	0.375	22	0.081	0.067	0.422	0.089	0.341	0.659	64	52	95
Lolo	47.03	-113.99	7,284	SKCS	Point Six	39	0.25	20	0.321	0.122	0.374	0.046	0.137	0.863	9	25	65
Idaho Panhandle	47.09	-115.27	6,707	CFLP	Simmons Peak Look Out	117	0.188	19									
Lolo	47.09	-114.57	7,420	SKCS	Stark Mountain	42	0.188	19	0.278	0.083	0.226	0.098	0.316	0.684	16		105
Helena	47.11	-112.73	8,400	CLMT	Red Mountain	118	0.188	19									
Lolo	47.15	-115.25	6,972	SKCS	Little Joe Mountain	43	0.375	22	0.076	0.069	0.313	0.097	0.444	0.556	33		9
Lolo	47.15	-115.25	6,925	BTIP	Stark Mountain	119	0.25	20									
Lolo	47.16	-114.37	6,960	SKCS	Squaw Peak	44	0.25	20	0.093	0.047	0.163	0.116	0.581	0.419	47		87
Lolo	47.16	-115.25	7,050	SKCS	Little Joe Mountain	43	0.25	20	0.095	0.048	0.286	0.095	0.476	0.524	11		1
Idaho Panhandle	47.19	-116.05	5,880	CFLP	Freezeout	46	0.125	18	0.196	0.174	0.116	0.058	0.457	0.543	19		54
Lolo	47.19	-113.34	7,275	MSGP	Morrell Look Out	120	0.188	19									
Lolo	47.19	-113.34	7,300	MSGP	Morrell Look Out	120	0.25	20									

Table 1. *Continued.*

National Forest or National Park (NP)	Latitude °N	Longitude °W	Elevation (ft)	Seed Zone[2]	Area	Seed Source Group Number[3]	Proportion Observed Polymorphic Loci[4]	Number of Unique Alleles[4]	No-Spot (%)[5]	Needle Shed (%)	Short Shoot (%)	Bark Reaction (%)	Susceptible (%)	Resistant (%)	Rust Resistance Famil Index Rank	7th-yr Late Winter Cold Hardiness Rank	6-yr Height Rank
Lolo	47.19	-113.37	7,670	MSGP	Morrell Look Out	121	0.125	18									
Lolo	47.19	-113.37	7,796	MSGP	Morrell Lookout	121	n/a	n/a									
Idaho Panhandle	47.27	-115.49	6,150	CFLP	Craddock	122	0.25	20									
Idaho Panhandle	47.29	-115.53	6,414	CFLP	Quarrles Peak	123	0.125	18									
Lewis & Clark	47.37	-112.75	6,724	MSGP	Crown Mtn	124	0.375	22									
Lewis & Clark	47.39	-112.75	6,859	MSGP	Crown Mtn	124	0.25	20									
Lolo	47.52	-115.71	6,405	SKCS	Burke Summit	47	0.25	20	0.268	0.042	0.394	0.042	0.254	0.746	27	49	29
Lewis & Clark	47.52	-112.8	7,600	MSGP	Sheep Shed Mountain	48	0.313	21	0.077	0.07	0.317	0.021	0.514	0.486	75		14
Lolo	47.52	-115.7	6,150	SKCS	Burke Summit	49	0.25	20	0.229	0.063	0.333	0.042	0.333	0.667	43		5
Kootenai	47.65	-115.74	5,650	CFLP	Beaver Creek	50	0.125	18	0.113	0.057	0.284	0.135	0.411	0.589	8	47	27
Kootenai	47.65	-115.74	5,650	CFLP	Beaver Creek	50	0.188	18	0.238	0.033	0.082	0.082	0.566	0.434	32		48
Kootenai	47.65	-115.74	5,650	CFLP	Beaver Creek	50	0.125	20	0.188	0.104	0.229	0.083	0.396	0.604	6.5	42	57
Lolo	47.75	-114.85	6,140	SKCS	Thompson Peak	51	0.063	17	0.161	0.07	0.308	0.021	0.441	0.559	63	36	10
Lolo	47.77	-115.32	6,200	SKCS	Vermillion Pass #1	125	n/a	n/a									
Flathead	47.78	-113.72	6,550	MSGP	Napa Point #2	126	n/a	n/a									
Kootenai	47.83	-115.39	5,928	SKCS	7-Point Mountain	52	0.25	20	0.167	0.014	0.181	0.069	0.569	0.431	35		8
Lewis & Clark	47.84	-112.81	7,500	MSGP	Our Lake	53	0.313	21	0	0	0.4	0	0.6	0.4	94		98
Kootenai	47.95	-115.56	6,000	SKCS	Baree Mountain	55	0.313	21	0.194	0.032	0.226	0.032	0.516	0.484	68.5	30	7
Flathead	48.19	-113.35	6,480	MSGP	25-Mile	56	0.25	20									
Flathead	48.19	-113.35	6,600	MSGP	25-Mile	56	0.25	20									
Idaho Panhandle	48.35	-116.75	5,430	SKCS	Gisborne	57	n/a	n/a	0.167	0	0.583	0.083	0.167	0.833	14		23
Idaho Panhandle	48.37	-116.2	6,370	SKCS	Lunch Peak	58	0.188	19	0.228	0.162	0.309	0.066	0.235	0.765	24		71
Idaho Panhandle	48.38	-116.19	6,200	SKCS	Lunch Peak	58	n/a	n/a									
Flathead	48.44	-113.97	6,200	MSGP	Desert Mountain	127	0.313	21									
Flathead	48.49	-114.34	6,000	MSGP	Big Mountain	60	0.313	21	0.185	0.054	0.3	0.077	0.385	0.615	22		31
Flathead	48.49	-114.34	6,500	MSGP	Big Mountain	61	0.188	19	0.135	0.027	0.162	0.027	0.649	0.351	70.5	29	67
Flathead	48.49	-114.34	6,000	MSGP	Big Mountain	60	0.438	23	0.132	0.081	0.184	0.081	0.522	0.478			41
Flathead	48.49	-114.34	6,000	MSGP	Big Mountain #2	60	n/a	n/a									
Flathead	48.49	-114.34	6,810	MSGP	Big Mountain #1	61	n/a	n/a									
Flathead	48.54	-114.14	5,400	MSGP	Nicola	128	0.188	19									
Flathead	48.55	-114.23	6,200	MSGP	Standard	129	0.125	18									
Kootenai	48.57	-115.72	5,700	SKCS	Huson Peak	130	0.125	18									
Colville	48.71	-118.47	7,135	SKCS	Copper Butte	61	0.313	21	0.087	0.065	0.217	0.022	0.609	0.391	97	50	106
Colville	48.71	-118.47	7,137	SKCS	Copper Butte	61	0.188	19	0.158	0	0.158	0	0.684	0.316	105		108
Idaho Panhandle	48.83	-116.6	6,800	SKCS	Pyramid Pass	62	0.375	22	0.304	0.13	0	0.043	0.522	0.478	28		17
Idaho Panhandle	48.84	-116.51	6,700	SKCS	Farnham Ridge	63	0.125	18	0.092	0.042	0.155	0.028	0.683	0.317	82	42	33.5
Idaho Panhandle	48.86	-116.47	5,820	SKCS	Farnham Peak	64	0.25	20	0.12	0.174	0.283	0.12	0.304	0.696	38		82
Colville	48.88	-117.24	6,480	SKCS	Sullivan Look Out	65	0.25	20	0.182	0.091	0.205	0.091	0.432	0.568	6.5	46	66
Glacier NP	48.88	-114.49	6,000	MSGP	Siyeh Bend	131	0.25	20									
Flathead	48.88	-114.49	6,450	MSGP	Big Mountain	66	0.375	22	0.056	0.028	0.141	0.056	0.718	0.282	88		15
Flathead	48.88	-114.51	6,000	MSGP	Hornet Mountain	67	0.563	25	0.022	0.043	0.087	0.022	0.826	0.174	70.5	22	46
Kootenai	48.93	-114.79	5,800	MSGP	Foundation Creek	132	0.313	21									
Colville	48.97	-117.11	6,800	SKCS	Salmo Lookout	68	0.375	22	0.34	0.064	0.128	0.255	0.213	0.787	1	7	102
Kootenai	48.97	-115.84	7,200	SKCS	NW Peaks	69	0.438	23	0.174	0.13	0.13	0	0.565	0.435	52	48	21
Kootenai	48.98	-114.7	5,400	MSGP	Frozen Lake	133	0.25	20									

[1] No-spot (%) = no spot symptoms on needles, no canker development, only trait to infer immunity; Needle shed (%) = seedlings drop their infected (spotted) needles less than 12 months after inoculation and before the mycelium reaches the stem; Short shoot (%) = seedlings retain their infected (spotted) needles beyond 12 months after inoculation, but never develop a canker; mycelium do not enter woodier bark tissue at the base of the needle fascicle or junction of the short shoot and needle fascicle bundle; Bark reactions (%) = increased number of callus formation on branches and stems, walling off cankers, and thereby preventing further infection.

[2] Seed zone designations: BTIP=Bitterroots-Idaho Plateau, CFLP=Clark Fork-Lolo Pass, CLMT=Central Montana, GYGT=Greater Yellowstone-Grand Teton, MSGP=Missions-Glacier Park, NEVA=Nevada, SKCS=Selkirk-Cabinets.

[3] Seed source group number determined using common area name and geographic coordinates.

[4] Isozyme data not available from branch samples.

[5] Blister rust resistence, late winter cold hardiness or height data added at the conmpletion of each rust screening.

Isozymes

Megagametophyte tissue was homogenized in phosphate buffer and absorbed onto 2 mm wide paper wicks. Starch gel (11% w/v) electrophoresis revealed 16 loci in three buffer systems that resolved strong enzyme activity in all tissue analyzed (USDA Forest Service 2003). Four loci were resolved in a lithium borate electrode buffer-tris citrate gel buffer combination (system LB): leucine aminopeptidase (LAP1 and LAP2; EC 3.4.11.1), phosphoglucomutase (PGM; EC 5.4.22), and phosphoglucose isomerase (PGI2; EC 5.3.1.9). Five loci were resolved in a sodium borate electrode buffer-tris citrate gel buffer combination (system SB): aspartate aminotransferase (AAT1, AAT2 and AAT3; EC 2.6.1.1), uridine diphosphoglucose pyrophosphorylase (UGPP; EC 2.7.7.9), and triose-phosphate isomerase (TPI; EC 5.3.1.1). Seven loci were resolved in a morpholine citrate electrode and gel buffer, pH 8 (system MC8): phosphogluconate dehydrogenase (6PGD; EC 1.1.1.44), isocitrate dehydrogenase (IDH; EC 1.1.1.42), shikimic acid dehydrogenase (SKD1 and SKD2; EC 1.1.1.25), and malate dehydrogenase (MDH1, MDH2 and MDH3; EC 1.1.1.37). Following incubation in ten substrate specific stains, genotypic data were collected for 16 loci (PGM, LAP-1 and 2, PGI-2, AAT-1, 2, and 3, UGPP, TPI, SKD-1 and 2, IDH, 6PGD, MDH-1, 2, and 3). Because of the condition of the 16 samples of branch tissue upon arrival at the lab, no isozyme activity was present in these tissues.

The presence of seed from at least two trees in one sample was detected in four collections (three samples from 'Coyote Meadows' and one from 'Blue Ridge'). These seed lots could be the result of seed contamination from the point of field collections to seed processing. When more than two alleles were detected for a sample at a locus, the least common allele at each three-allele score was discarded so that the samples could be used in the analysis. Of the 147 multilocus isozyme genotypes generated, no two samples matched (resulting in 147 unique genotypes).

DNA Extraction and Amplification

DNA was extracted from each sample using the Qiagen DNEasy 96-well format protocol. Tissue was first homogenized in a collection tube, AP1 buffer added, the sample re-homogenized on the MixerMill, then an aliquot of slurry transferred to a new collection tube for extraction. The remaining slurry was frozen for additional extractions if needed. DNA concentrations were quantified using fluorometry with pico-green.

Though isozyme activity was not present in the 16 samples of branch tissue, it was still possible to extract DNA from each sample using the Qiagen DNEasy-Mini protocol. Approximately 150 mg of needle tissue per sample was ground by hand under liquid nitrogen in a mortar and pestle and DNA extracted following Qiagen DNEasy kit instructions. DNA concentrations were quantified using fluorometry with pico-green. DNA quality was further checked by electrophoresing each sample on a 0.8% agarose gel (1X TBE), staining with ethidium bromide and visualizing under UV light.

Chloroplast DNA (cpDNA) Analysis

Polymerase chain reaction (PCR) amplification was performed simultaneously for three loci: Pt15169, Pt30204, and Pt71936 (Vendramin and others 1996) in 25-µl reaction volumes containing 10 ng cpDNA, 0.2 µM of each primer, and 12.5 ul of the Qiagen multiplex PCR mix including *Taq* DNA polymerase. The PCRs were completed using the following protocol on PTC-200 thermal cyclers: 15 minutes at 95 °C; 30 cycles of 30 seconds at 94 °C, one minute 30 seconds at 57 °C, and one minute at 72 °C; 30 minutes at 60 °C; followed by an indefinite hold at 4 °C. The resulting PCR products were separated on an ABI Prism 3130xl Genetic Analyzer (Applied Biosystems, Foster City, CA, USA), as recommended by the manufacturer. Peaks were sized and binned, with alleles called using GeneMarker 1.51 (SoftGenetics, State College, PA, USA), with GS (500-250) ROX as an internal size standard for each sample.

Three cpDNA SSR markers characterize 164 samples. The three Coyote Meadows samples were removed from the analysis because they show the presence of seed from at least two trees in each collection. The bulk collection from Wind River was removed because this sample could not be analyzed within this dataset. The Blue Ridge sample also shows evidence of containing seed from at least two trees; but instead of discarding this sample, it was possible to artificially double the information because only one SSR locus shows the presence of the alternate tree.

Data Analysis

Analysis of mtDNA data was completed by assigning a haplotype to each individual, based on the presence of a single band (haplotype 1) or two bands (haplotype 2). Descriptive statistics for isozyme and cpDNA data were estimated with the GDA program (Lewis and Zaykin 2001), GenAlEx-6 (Peakall and Smouse 2005), and Popgene (Yeh and others 1997). The following parameters were estimated to describe the observed genetic diversity: percent polymorphic loci (P), number of alleles per locus (Na), number of alleles per locus with a frequency greater than 5 percent (Na Freq > 5 percent), effective number of alleles (N_e), information index (equivalent to the Shannon-Weaver Index, I), number of alleles unique to a seed zone (number of private alleles), unbiased expected heterozygosity (H_e), observed heterozygosity (H_o), number of migrants (N_m), fixation index (F), and outcrossing rate (t).

Pairwise measures of the fixation index (F_{ST}) quantify the distribution of genetic diversity among seed zones. Nei's genetic distance (1972) was estimated for all pairs of zones using the program GenAlEx-6 (Peakall and Smouse 2005). GenAlEx-6's test of isolation by distance was employed using the pairwise F_{ST} values (based on isozyme data), with significance determined using the Mantel test. Genetic differentiation among seed sources for survival, rust resistance, late winter cold hardiness and early height-growth was estimated for all traits (Mahalovich submitted) by calculating the index $Q_{ST} = \sigma^2_p / (\sigma^2_p + 2\,\sigma^2_a)$, where σ^2_p is the among seed source variance and σ^2_a is the within-population additive genetic variance (Spitze 1993). The F_{ST} values among seven seed zones were then compared to the Q_{ST} indices to examine which evolutionary forces may be operating in the Inland West.

Principal component analysis, cluster analysis and discriminant analysis of the continuous variables (chloroplast (cpDNA) SSR markers and geographic variables) were performed using the statistical program R (R Foundation http://www.r-project.org).

Population phenograms (Figure 3) were constructed to describe the ancestral relationship among samples, using predefined seed zone assignments (Figure 1). Phenograms were built separately from Nei's genetic distance (1972) estimated from the isozyme and cpDNA data sets, using Neighbor-Joining methods; significance of branches was determined over 1,000 bootstrap replicates using the majority rule extended method to build the consensus tree, as employed by the package PHYLIP (Felsenstein 2005). Principal Coordinate Analysis (GenAlEx-6; Peakall and Smouse 2005) was used to find and plot the major patterns among predefined zones.

Results

Mitochondrial DNA (mtDNA) Variation

Variation identified in the *nad5a* intron of the mitochondrial genome in whitebark pine results in two haplotypes or genetic variants (Richardson and others 2002). Of the 117 collection sites represented, 108 of them contain haplotype 1, while the remaining nine contain haplotype 2. Haplotype 1 is present in the Idaho, Montana, eastern Washington and Wyoming collections. Haplotype 2 is characteristic of the eastern California and Nevada collections. Based on these two haplotypes, the Nevada zone is genetically differentiated (separated) from the remaining zones in the Northern Rockies.

Isozyme Variation

Genetic Diversity: Isozyme data from 16 loci were generated from 147 samples. Levels of genetic diversity are high within these whitebark samples: percent polymorphic loci or P = 100%; number of alleles or Na = 4.0; and expected heterozygosity or H_e = 0.271 (Table 2). Similar levels of diversity occur within each zone, where zone means are also high: P = 88.4%; Na = 2.5; H_e = 0.263. Mean fixation index (F) is 0.01, and for all trees within a zone range from -0.059 to 0.076, indicating general random mating with no marked excess of heterozygosity or inbreeding. Mean outcrossing rate (t) is 0.98, and for trees within a zone range from 0.858 to 1.125, indicating a lack of inbreeding.

Genetic Structure: Of the total variation measured, very little is among zones, indicating zones share a large degree of genetic similarity. Analysis of Molecular Variance (AMOVA) indicates that 99 percent of the variation measured is within zones (only 1 percent is among zones). Wright's (1951) inbreeding coefficient within individuals relative to zones (F_{IS}) = -0.016 and the inbreeding coefficient within individuals relative to the total (F_{IT}) = 0.011. F_{ST} (genetic differentiation among populations, or in this study, the proportion of the total diversity that separates the zones) is only 2.6 percent. Low F_{IS} (-0.016) and F_{IT} (0.011) values and a high number of migrants per generation (N_m = 9.354) also indicate a lack of inbreeding. Nei's (1972) genetic identity (I) in this study is a measure of genetic similarity between zones, with a value of 100 percent meaning that two zones share the same alleles in the same frequencies, and a value of 0 meaning that two zones have no allele in common. Identity values range from 97.7 to 99.4 percent (Table 3 lower triangle) confirming high genetic similarity among zones. Although all zones are very similar to one other, the Clark Fork-Lolo Pass and Missions-Glacier Park

Table 2. Genetic diversity statistics for Inland West whitebark pine samples based on 16 isozyme loci. N = sample size; P = percent polymorphic loci; Na = number of alleles; N_e = effective number of alleles; I = information index; H_e = expected heterozygosity; H_o = observed heterozygosity; F = fixation index; t = outcrossing rate.

Zone (Standard Errors)	Bitterroots-Idaho Plateau		Clark Fork-Lolo Pass		Central Montana		Greater Yellow-stone-Grand Teton		Missions-Glacier Park		Nevada		Selkirk-Cabinets		Zone Mean		All Samples	
N	20.9	(0.781)	20.6	(0.176)	20.5	(0.195)	20.5	(0.176)	20.8	(0.127)	21	(0)	19.8	(0.127)	20.5	(0.398)	147	(0.532)
P	100	——-	93.8	——-	93.8	——-	75	——-	87.5	——-	81.3	——-	87.5	——-	88.4	——-	100	——-
Na	2.7	(0.270)	2.4	(0.180)	2.8	(0.262)	2.5	(0.316)	2.5	(0.258)	2.4	(0.258)	2.4	(0.203)	2.5	(0.160)	4	(0.400)
Na Freq. >= 5%	21.9	(0.180)	1.9	(0.180)	1.9	(0.202)	1.8	(0.209)	1.9	(0.202)	1.9	(0.180)	2.1	(0.193)	1.9	(0.090)	1.9	(0.180)
N_e	1.5	(0.112)	1.4	(0.135)	1.6	(0.136)	1.5	(0.125)	1.5	(0.131)	1.4	(0.121)	1.4	(0.103)	1.5	(0.076)	1.5	(0.119)
I	0.495	(0.076)	0.416	(0.078)	0.508	(0.086)	0.447	(0.092)	0.464	(0.086)	0.441	(0.083)	0.457	(0.073)	0.461	(0.032)	0.496	(0.078)
Number of Private Alleles	0.25	(0.112)	0.063	(0.063)	0.125	(0.085)	0.188	(0.136)	0.063	(0.063)	0.313	(0.151)	0.125	(0.085)	0.152	(0.094)	4	(0.428)
H_e	0.283	(0.048)	0.238	(0.051)	0.287	(0.054)	0.254	(0.055)	0.264	(0.053)	0.25	(0.049)	0.263	(0.046)	0.263	(0.018)	0.271	(0.049)
H_o	0.251	(0.049)	0.234	(0.048)	0.309	(0.074)	0.266	(0.064)	0.28	(0.058)	0.253	(0.050)	0.257	(0.047)	0.264	(0.024)	0.264	(0.052)
F	0.076	(0.062)	-0.025	(0.022)	-0.049	(0.044)	-0.051	(0.014)	-0.059	(0.029)	-0.013	(0.029)	-0.008	(0.044)	-0.018	(0.046)	0.01	(0.019)
t	0.858	(0.091)	1.051	(0.077)	1.103	(0.082)	1.107	(0.064)	1.125	(0.084)	1.026	(0.072)	1.016	(0.063)	1.036	(0.069)	0.98	(0.045)

Table 3. Pairwise zone matrix of Nei's genetic identity (lower triangle) and FST (upper triangle) for Inland West whitebark pine samples based on 16 isozyme loci.

Zone	Bitterroots-Idaho Plateau	Clark Fork-Lolo Pass	Central Montana	Greater Yellowstone-Grand Teton	Missions-Glacier Park	Nevada	Selkirk-Cabinets
Bitterroots-Idaho Plateau		0.017	0.011	0.016	0.013	0.013	0.018
Clark Fork-Lolo Pass	0.986		0.016	0.020	0.010	0.022	0.012
Central Montana	0.992	0.988		0.011	0.012	0.011	0.017
Greater Yellowstone-Grand Teton	0.988	0.986	0.991		0.015	0.019	0.019
Missions-Glacier Park	0.988	0.994	0.990	0.990		*0.025	0.011
Nevada	0.990	0.982	0.991	0.985	0.977		*0.026
Selkirk-Cabinets	0.987	0.992	0.985	0.989	0.992	0.978	

* = significance at the 5% level of probability.

are most similar. The two least similar zones are Selkirk-Cabinets and Nevada, followed closely by Missions-Glacier Park and Nevada. F_{ST} values show similar trends of high genetic similarity and weak differentiation between zones, with estimates ranging from 1.0 to 2.6 percent (Table 3 upper triangle).

Principal Coordinate Analysis of the isozyme data shows that the Missions-Glacier Park, Selkirk-Cabinets, and Clark Fork-Lolo Pass zones cluster somewhat together and the Central Montana and Bitterroots-Idaho Plateau zones cluster (Figure 2a). The Greater Yellowstone-Grand Teton and Nevada zones occur by themselves. The percentage of variation explained by the first two principal coordinates is 62.8 percent (the first three, principal coordinates explain 77.0 percent of the total variation). Mid-point phenograms (Figure 3a) show similar zonal relationships (cluster Bitterroots-Idaho Plateau, Nevada and Central Montana; cluster Clark Fork-Lolo Pass, Selkirk-Cabinets, and Missions-Glacier Park; and Greater Yellowstone-Grand Teton by itself). There is no evidence for isolation by distance following a geographic pattern based on latitude and longitude ($R^2 = 0.0001$; $P = 0.45$). These results indicate that neighboring trees are as similar genetically as trees separated by large geographic distances.

Summarizing these data by seed source for the comprehensive genetics profile, the number of unique alleles among 16 loci, range from eight to 32, assuming two alleles present per locus. Among the top 10 rust-resistance entries the proportion of observed polymorphic loci P = 0.238 and the average number of alleles is 20 (Table 1). Among all samples P = 0.258 and the average number of alleles is also 20. The oldest known living whitebark pine specimen located at Railroad Ridge is homozygous for 13 of the loci scored (no detectable protein activity at the remaining three loci): 12 loci are homozygous for common alleles and one locus is homozygous for a rare allele.

Chloroplast DNA (cpDNA) Variation

Among 160 samples, 34 unique multilocus SSR genotypes were generated. High levels of genetic diversity are found in all samples (expected heterozygosity (H_e) = 0.516 and number of alleles (Na) = 6.7, Table 4). Zone means are less diverse though still high (H_e = 0.481, Na = 4.2). The zones containing the largest amount of diversity are Bitterroots-Idaho Plateau then Clark Fork-Lolo Pass. The Selkirk-Cabinets zone contains the lowest level of diversity compared to the other zones.

Of the total variation measured, very little is found among zones, indicating that the zones share a large degree of genetic similarity and genetic structure (as did the isozyme data). Analysis of Molecular Variance calculations show 97 percent of the total variation is within zones, while only 3 percent among zones. Genetic identity also indicates high degrees of similarity among zones (Table 5). Zones are differentiated more by the cpDNA SSR data than with the isozyme data. Similarity among zone pairs ranges from 81.6 percent (Nevada and Selkirk-Cabinets zones) to 98.4 percent (Clark Fork-Lolo Pass and Selkirk-Cabinets zones). A graphical representation of the similarity among zones using Principal Component Analysis highlights that the Nevada zone is strongly separated from the other zones, whereas the Central Montana and Bitterroots-Idaho Plateau zones share proximity (Figure 2b). The Selkirk-Cabinets zone is closest to Clark Fork-Lolo Pass, followed by Missions-Glacier Park, Central Montana and Bitterroots-Idaho Plateau, then the Greater-Yellowstone-Grand Teton zone. The percentage of variation explained by the first two coordinates is 77.0 percent (87.9 percent by the first three coordinates). A mid-point phenogram (Figure 3b) shows similar zonal relationships: the Selkirk-Cabinets, Clark Fork-Lolo Pass, and Missions-Glacier Park zones form a group; followed by Central Montana and Bitterroots-Idaho Plateau, Greater-Yellowstone-Grand Teton, then the Nevada zone.

When removing the *a priori* defined zone designations from the samples, Principal Component Analysis using all continuous variables (cpDNA SSR markers, latitude, longitude, and elevation) indicates that each principal component is explaining different characteristics of the structure of the data. Cluster analysis using these variables shows that there are some imperfect groupings by zone, with individuals from the Nevada zone being strongly associated as a group. Discriminant analysis has a 44 percent mean correct classification rate for zone designations when using the cpDNA SSR markers. By adding latitude, longitude, and elevation to the analysis, the mean correct classification rate increases to 84 percent, showing that cpDNA variation alone does not recreate *a priori* zone designations well.

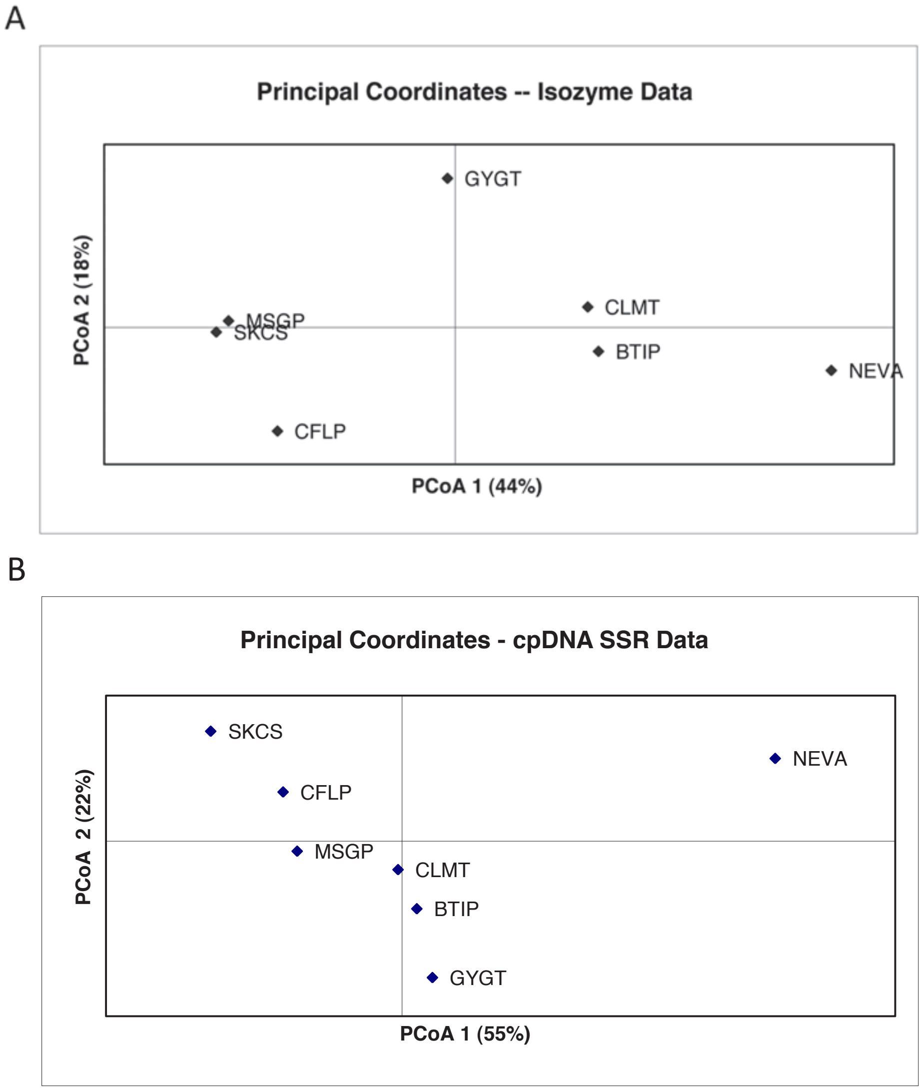

Figure 2. Principal Coordinate Analysis of seven zones of whitebark pine based on isozyme (A) and chloroplast (cpDNA) SSR markers (B). Zone designations as follows: BTIP=Bitterroots-Idaho Plateau, CFLP=Clark Fork-Lolo Pass, CLMT=Central Montana, GYGT=Greater Yellowstone-Grand Teton, MSGP=Missions-Glacier Park, NEVA=Nevada, SKCS=Selkirk-Cabinets.

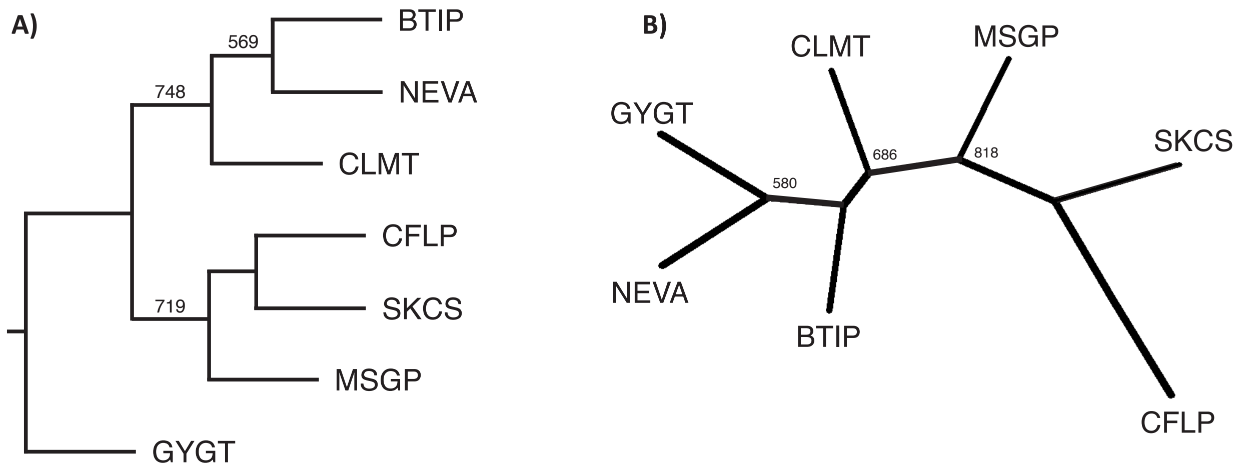

Figure 3. Mid-point phenograms of seven seed zones of whitebark pine from pairwise genetic distances using Neighbor-joining methods based on isozyme (A) and chloroplast (cpDNA) SSR markers (B). Significance of branches determined from 1,000 bootstrap replicates, resolved using Majority Rule extended method in Phylip v 3.68. Numbers at nodes represent the number of replicates out of 1,000 where the branch pattern occurred (>500). Zone designations as follows: BTIP=Bitterroots-Idaho Plateau, CFLP=Clark Fork-Lolo Pass, CLMT=Central Montana, GYGT=Greater Yellowstone-Grand Teton, MSGP=Missions-Glacier Park, NEVA=Nevada, SKCS=Selkirk-Cabinets.

Table 4. Genetic diversity statistics for Inland West whitebark pine samples based on three chloroplast (cpDNA) SSR markers. N = sample size; N_a = number of alleles; N_e = effective number of alleles; I = information index; H_e = expected heterozygosity.

Zone (Standard Errors)	Bitterroots-Idaho Plateau		Clark Fork-Lolo Pass		Central Montana		Greater Yellow-stone-Grand Teton		Missions-Glacier Park		Nevada		Selkirk-Cabinets		Zone Mean		All Samples	
N	22	(0.000)	22	(0.000)	18	(0.000)	29	(0.000)	25	(0.000)	21	(0.000)	23	(0.000)	22.9	(3.400)	160	(0.000)
Na	5	(1.155)	4.333	(1.333)	4.333	(2.333)	4.000	(1.000)	4.333	(1.453)	3.667	(0.882)	4.000	(1.528)	4.238	(0.480)	6.667	(1.764)
Na Freq. >= 5%	3.333	(0.667)	3.333	(0.882)	4.333	(2.333)	3.000	(1.000)	3.000	(1.000)	2.667	(0.333)	2.000	(0.577)	3.095	(0.648)	4.000	(1.528)
N_e	2.927	(1.025)	2.68	(0.997)	2.991	(1.745)	2.386	(0.841)	2.527	(0.960)	2.116	(0.431)	2.174	(0.807)	2.543	(0.395)	3.059	(1.460)
I	1.169	(0.310)	1.042	(0.341)	0.904	(0.555)	0.901	(0.400)	0.978	(0.367)	0.889	(0.249)	0.805	(0.399)	0.955	(0.096)	1.116	(0.434)
Number of Private Alleles	0.333	(0.333)	0.000	(0.000)	0.000	(0.000)	0.333	(0.333)	0.000	(0.000)	0.333	(0.333)	0.000	(0.000)	0.143	(0.178)	6.667	(1.764)
H_e	0.574	(0.124)	0.526	(0.139)	0.414	(0.216)	0.472	(0.162)	0.494	(0.149)	0.479	(0.120)	0.407	(0.188)	0.481	(0.035)	0.516	(0.172)

Table 5. Pairwise zone matrix of Nei's genetic identity for Inland West whitebark pine samples using three chloroplast (cpDNA) SSR markers.

Zone	Bitterroots-Idaho Plateau	Clark Fork-Lolo Pass	Central Montana	Greater Yellowstone-Grand Teton	Missions-Glacier Park	Nevada	Selkirk-Cabinets
Bitterroots-Idaho Plateau	1.000						
Clark Fork-Lolo Pass	0.958	1.000					
Central Montana	0.969	0.961	1.000				
Greater Yellowstone-Grand Teton	0.955	0.937	0.950	1.000			
Missions-Glacier Park	0.956	0.980	0.964	0.957	1.000		
Nevada	0.883	0.854	0.884	0.873	0.852	1.000	
Selkirk-Cabinets	0.921	0.984	0.937	0.899	0.966	0.816	1.000

Discussion

High levels of genetic diversity over all samples and within zones are found in whitebark pine when measured with isozymes. These measures of genetic diversity correspond to the species distribution occurring in eastern California, Idaho, Montana, Nevada, eastern Washington, and Wyoming (Figure 1, Table 1). Compared to whitebark pine from Oregon and Washington (USDA Forest Service 2009, unpublished report) these samples had higher mean expected heterozygosity (H_e = 0.271 vs. 0.194), more alleles per locus (Na = 4.0 vs. 1.9), and higher percent polymorphic loci (P = 100 vs. 65.0 percent). However, levels of diversity detected with chloroplast SSR variation in these two studies are similar for expected heterozygosity (H_e = 0.516 vs. 0.568) and effective number of alleles (Na = 3.1 in both studies).

Species with an outcrossing breeding system, large geographic range, long-life span, high fecundity, and wind-dispersed pollen and seeds, often have high levels of genetic diversity; though seed dispersal in whitebark pine is largely attributed to seed caching by Clark's nutcracker. Diversity levels in these collections of whitebark pine are similar to or greater than levels found in other conifers (Hamrick and others 1994, Steinhoff and others 1983, Wheeler and Guries 1982, Yang and Yeh 1993, Yeh and Layton 1979) that occupy the same forest cover type (Table 6). Expected heterozygosity is also greater, though similar in level to some other studies of whitebark pine (Bruederle and others 1998, Jørgensen and Hamrick 1997, Krakowski and others 2003, Rogers and others 1999, Yandell (1992) and limber pine (Hamrick and others 1994, Jørgensen and others 2002, Schuster and others 1989, Schuster and Mitton 2000) and similar to quaking aspen (H_e = 0.271), historically regarded as the most genetically diverse tree species (Cheliak and Dancik 1982). The degree of expected heterozygosity may be confounded due to the large geographic scale represented among the samples included in this study (38.08^0 to 48.98^{0}N latitude and -107.09^0 to -119.96^{0}W longitude).

Overall zones share a high degree of genetic similarity; however, some relationships appear to exist. The Nevada zone is differentiated from the other zones as seen by the unique maternal haplotype, high pairwise F_{ST} values, low overall genetic similarity values, and placement in the principal component plots, cluster diagrams, and phenograms. Though the three-year bumper cone crop cycle is predictable for members of the subgenus *Strobus*, another unique feature of whitebark pine from the Nevada zone is the timing of the three-year cycle; for example, recent bumper cone crops in the Northern Rockies were in 2003 and 2006, whereas bumper cone crops in Nevada followed in 2004 and 2007. The Greater Yellowstone-Grand Teton zone also shows a larger degree of differentiation from the other zones. The Selkirk-Cabinets, Clark Fork-Lolo Pass, and Missions-Glacier Park zones share similarity and cluster together in the principal component plots and phenograms, regardless of the genetic marker used for the analysis. The Central Montana and Bitterroots-Idaho Plateau zones also share similarity and cluster together in the principal component plots and cpDNA phenogram.

Table 6. Contrast of genetic diversity and *F*-statistics from isozyme date for selected members of the subgenus *Strobus* and associated species in the subalpine, mixed-conifer forest cover type. N = sample size (population or individuals); P = percent polymorphic loci; Na = number of alleles; H_e = expected heterozygosity; F_{ST}/ G_{ST} = genetic structure among populations or seed zones.

Species	# Loci	N	P	Na	H_e	F_{ST}/ G_{ST}	Citation
Strobus							
Pinus albicaulis	16	147	100	4	0.271	0.026	This study
	13	14	48.8	1.6	0.204	0.088	Yandell (1992)
	20	30	85	3	0.102	0.034	Jørgensen and Hamrick 1997
	19	9	79	2.1	0.154	0.025	Bruederle and others 1998
	21	80	54.5	-	-	0.004	Rogers and others 1999
	10	~510	70	2.0	0.262	0.061	Krakowski and others 2003
Pinus aristata	21	597	76	2.1	0.070	0.220	NFGEL, unpublished data
Pinus flexilis	12	5	93.3	2.4	0.295	0.035	Schuster and Mitton 2000
	20	30	95	3.7	0.186	0.101	Jørgensen and others 2002
	27	16	65.1	2.4	0.223	0.149	Hamrick and others 1994
	10	2	-	-	0.320	0.022	Schuster and others 1989
	23	550	59	2	0.165	0.147	NFGEL, unpublished data
Pinus monticola	12	28	92	2	0.191	0.148	Steinhoff and others 1983
Associated species in mixed-conifer type							
Abies lasiocarpa	25	10	56.5	2.49	0.181	0.109	Hamrick and others 1994
Picea engelmannii	26	19	63.5	2.53	0.182	0.101	Hamrick and others 1994
Pinus contorta ssp. *contorta*	21	66	12	-	0.180	0.076	Yang and Yeh 1993
	42	5	65	1.81	0.126	0.032	Wheeler and Guries 1982
	25	135	59	1.9	0.167	0.041	Yeh and Layton 1979

Gene flow in whitebark pine involves the movement of pollen and seed. Pollen dispersal (as elucidated by the cp-DNA data) is not sufficient to swamp the genetic structure resulting from seed dispersal among seed zones (Figure 3a, 3b). Moreover, with such a small proportion of the variability found among seed zones, substituting bulked cone collections for individual-tree cone collections in the sampling scheme would likely not have shown any additional genetic structure. As with limber pine (Latta and Mitton 1997), the large difference between cpDNA and mtDNA data indicates pollen rather than seed movement is contributing to the bulk of gene flow in whitebark pine.

Whitebark pine is hypothesized to have inbred populations due to its discontinuous distribution, with isolated populations occurring at high elevations, and its seed dispersal by Clark's nutcracker. Supporting this, Jørgensen and Hamrick (1997) found a higher degree of inbreeding in whitebark pine than in other conifers, which they attributed to pollination within tree clusters. Here, mean outbreeding rates among seed sources within a zone as measured by isozymes indicate a lack of inbreeding, confirmed by neutral fixation index values (*F*), low inbreeding coefficient values (F_{IS} and F_{IT}), and high numbers of migrants (N_m = 9.354). Typical for conifers, N_m ranges from 5 to 20 (Ledig and others 1997, Mitton and Williams 2006). Limited pollen flow or seed dispersal near tree line, due to a climatic warming trend, might lead to subpopulation structuring, increases in inbreeding, or a reduction in genetic variation (Rogers and others 1999). Genetic structure (F_{ST}=0.026) among these 144 samples and 16 isozyme loci show a 6.5-fold increase in the fixation index as compared to three watersheds and 21 loci (F_{ST} = 0.004) sampled by Rogers and others (1999) in the eastern Sierra Nevada, but comparable in genetic structure (F_{ST} =0.025) among nine populations sampled in the Greater Yellowstone area (Bruederle and others 1998). Wind-pollination and seed caching by Clark's nutcrackers promotes a high degree of within-population variation in whitebark pine. Practical applications of these findings ratify existing management direction for cone collections used in restoration planting, where an operational lot of a wind-pollinated tree species contains seed from no fewer than 20 cone-bearing trees separated by 200 ft (61 m) in distance to minimize inbreeding depression in the subsequent progeny (USDA Forest Service 2010). Maintenance of three, bulked seed lots in inventory, for each seed zone and 400-foot (122 m) elevation band, satisfies the requirement of genetic sampling in space to maintain an effective population size of 60 individuals. Effective population size is defined as the number of breeding individuals in an idealized population that show the same amount of dispersion of allele frequencies under random genetic drift or the same amount of inbreeding as the population under consideration. Moreover, there is no need for additional seed orchard design considerations to maintain a suitable effective population size (spatially separating ramets of the same genotype by more than 80 feet (24 m)).

An opportunity to correlate these molecular data (F_{ST}) with quantitative trait data indices (Q_{ST}) observed in a common garden study (Mahalovich submitted), provides additional insights into the evolutionary forces operating in whitebark pine. The relative magnitude of these indices is informative regarding the role of natural selection and genetic drift as a causal agent of the observed degree of seed source differentiation in quantitative (adaptive) traits. Genetic drift involves random fluctuations in the frequency of alleles that can lead to allele loss in isolated or small populations. Genetic drift can also occur when the size of a population is reduced through a genetic bottleneck. Present-day examples of potential bottlenecks affecting whitebark pine include mortality due to mountain pine beetle, uncontrolled fire, or blister rust. Omitting the Nevada samples, which were not available in the common garden study, F_{ST} is equal to 0.025. Q_{ST} in the control (uninoculated) seedlings for six-year height (0.12) and late winter cold hardiness (0.11) indicate differentiation due to directional selection and adaptation to local environments ($Q_{ST} > F_{ST}$), whereas survival (0.25) indicates differentiation due to genetic drift ($Q_{ST} = F_{ST}$). Q_{ST} in the treatment (inoculated) seedlings for spot symptoms per meter (0), no spotting symptoms (<0.01), shedding of infected needles (<0.01), and canker tolerance (0.02) indicate convergent selection favoring the same genotype in different environments. These traits however, are highly sensitive to the deliverable basidiospore load and could be more indicative of lighter spotting (the first observable symptom in needle tissue) in an artificial inoculation. Q_{ST} in the remaining treatment seedlings for survival (0.07), six-year height (0.19), late winter cold hardiness (0.10), percent rust resistance (0.14), and the individual, rust-resistance traits of early stem symptoms (0.03), fungicidal short shoot (0.17), and bark reaction (0.37) favor differentiation due to directional selection and adaptation to local environments. Where $Q_{ST} > F_{ST}$ and the average observed heterozygosity in the top 10 rust resistant selections is less than all samples ($0.238 < H_o < 0.258$, Table 1), the introduction of blister rust around 1925 in whitebark pine cover types (McDonald and Hoff 2001) appears to be exerting selection pressure and adaptation to local environments in the last two generations. The blister rust introduction site corresponds to the geographic location of the Selkirk-Cabinet zone, which also exhibits the lowest level of genetic diversity ($H_e = 0.407$, Table 4). These data however, do not indicate there is a strong enough selection pressure to begin to identify unusual genes limited in their geographic distribution.

Mahalovich (submitted) supports the consolidation of six seed zones to four in the Northern Rockies. The current study evaluating neutral markers is largely in agreement with those findings and further supports consolidation of six seed zones to *three* in the Northern Rockies, while maintaining the uniqueness of the Nevada zone. Nei's genetic identity supports combining the Clark Fork-Lolo Pass and Missions-Glacier Park zones. The Principal Component Analysis (PCA) for the isozyme data extends the similarity among the Clark Fork-Lolo Pass, Missions-Glacier Park and Selkirk-Cabinets zones. Though the PCA shows similarity among the Bitterroots-Idaho Plateau, Central Montana and Nevada zones, samples from Nevada zone were not available for the common garden study. The Nevada samples reported here all contain maternal haplotype 2; therefore, the Nevada zone will remain a distinct seed zone. Isozyme data would then support combining the Bitterroots and Central Montana zones. Owing that more samples were not available south of 44.5° N latitude (from central and southern Idaho) and that the common garden study emphasizes traits with adaptive value, these two zones will remain distinct. Genetic diversity statistics using the three chloroplast SSR markers also show the Bitterroots-Idaho Plateau zone to be distinct with the highest level of genetic diversity. Lastly, the four adaptive traits from the common garden study, isozyme data and three chloroplast SSR markers reported here, all support the Greater Yellowstone-Grand Teton zone remaining a distinct zone. Taken collectively, the Bitterroots-Idaho Plateau, Central Montana, and Greater Yellowstone-Grand Teton zone boundaries remain as originally defined (Mahalovich submitted); however, the Selkirk-Cabinets, Clark Fork-Lolo Pass and Missions-Glacier Park zones show sufficient overlap to support consolidation into one zone, renamed the 'Inland Northwest'. This consolidated zone is approximate to Bailey's M333 Northern Rocky Mountain Forest-Steppe—Coniferous Forest—Alpine Meadow Province (Bailey 1995). The geographic areas defined by the three remaining Northern Rockies zones show little congruence to other mountain province boundaries in the temperate steppe division.

Since both studies incorporate genetic data, these realigned seed zones will also serve as breeding zones or geographic areas based on the anticipated adaptability of an improved population of trees in the genetic restoration program for the Inland West (Mahalovich and Dickerson 2004). These five breeding zones are already in effect for seed procurement planning, genetic testing and seed orchard establishment. Field data (10 years from seed) on control (uninoculated) and treatment (inoculated) seedlings planted in a long-term field test are being evaluated in combination with climatic data to reconfirm the veracity of the zone boundaries.

The development of a comprehensive genetic profile (Table 1) to determine those seed sources at risk for being lost due to their apparent uniqueness will facilitate gene conservation in whitebark pine. *Ex situ* conservation activities in the Inland West Genetic Restoration Program (Mahalovich 2000, Mahalovich and Dickerson 2004) include establishing seed orchards, clone banks, and long-term genetic tests, while building long-term seed and pollen banks. *In situ* conservation is being met by: (1) federal lands classified in wilderness areas, (2) Research Natural Areas (RNAs) specific to the USDA Forest Service (Evenden and others 2001), and (3) the network of plus trees designated and protected against mountain pine beetle across multiple federal ownerships (USDA Forest Service, USDI-Bureau of Land Management and USDI-National Park Service). Upwards of 950 plus trees are designated in the program. A recent assessment shows 21 percent of those plus trees have been lost to mountain pine beetle, fire, and blister rust in descending order.

For the USDA Forest Service Northern Region there are 25 RNAs with a whitebark pine component covering 53,771 acres, and 23 RNAs covering 34,416 acres in the Intermountain Region (Evenden and others 2001). Identification of potential candidate areas involves the selection of seed sources utilizing the available genetic statistics

(Table 1). Among the 48 RNAs there is little geographic representation from the Clark Fork-Lolo Pass and Missions-Glacier Park zones. Using the Missions-Glacier Park zone as an example, the sample with the highest number of alleles (n=25) and proportion of polymorphic loci (P = 0.563) is Hornet Mountain (Flathead National Forest), whereas Big Mountain from the same zone qualifies as a candidate area because it has the highest percent rust resistance. Blacklead Mountain (Clearwater National Forest) from the Clark Fork-Lolo Pass zone qualifies as a candidate area with high proportion of polymorphic loci (P = 0.438) and a highly desirable combination of blister rust resistance *and* late winter cold hardiness. Mahalovich (submitted) characterized blister rust resistance in whitebark pine from the Northern Rockies as having an unfavorable correlation to late winter cold hardiness. The sample with the lowest number of unique alleles (n=13) is from Railroad Ridge (Bitterroots-Idaho Plateau zone), with no polymorphic loci (P = 0). Railroad Ridge at first glance may not receive additional consideration; however, other factors such as containing a rare allele and supporting the oldest specimen of whitebark pine may elevate it as a candidate area for further evaluation. Where RNAs embody preservation, other areas (for example, Corbly Gulch, Gallatin National Forest, Central Montana zone, P = 0.5 and n=24,) may facilitate active management favoring silvicultural prescriptions to minimize species encroachment or to prepare seedbeds for natural regeneration.

Collectively these data show complementary relationships between molecular markers and adaptive traits in a common garden study. Continued analysis of long-term field data, incorporating climatic variables, and artificial inoculations of additional cone collections will facilitate the identification of neutral markers influenced by selection and genetic drift, particularly those genotypes demonstrating resistance to blister rust and tolerance to mountain pine beetle. A comprehensive genetics profile will also benefit future research addressing the molecular basis of blister rust resistance by facilitating the identification of seed sources with both blister rust resistance and non-segregating isozyme loci. Moreover, there is sufficient genetic diversity and genetic variation to support the continuation of a rust resistance screening and genetic restoration program for this species.

Management Implications (USDA Forest Service 2010)

Operational cone collections in the field shall be comprised of no fewer than 20 cone-bearing trees separated by 200 ft (61 m) in distance.

For each seed zone and 400-foot (122 m) elevation band, a minimum of three, bulked seedlots shall be maintained to achieve an effective population size of 60 individuals at any given time.

Seed zones in the Whitebark Pine Inland West Genetic Restoration Program have been consolidated from seven to five geographic areas. The revised seed zones shall be used for seed procurement planning and seed transfer.

These five seed zones also serve as breeding zones for seed orchard design, future genetic testing and breeding orchard establishment.

Seed orchard design will adhere to considerations for wind-pollinated conifer species with no increase in spatially separating ramets of a genotype by more than 80 feet (24 m)).

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References

Bailey, Robert G. 1995. Description of the ecoregions of the United States. 2d ed. rev. and expanded (1st ed. 1980) Misc. Publ. No. 1391 (rev.), Washington, DC: USDA Forest Service. 108 p. with separate map at 1:7,500,000.

Bruederle, Leo P.; Tomback, Diana F.; Kelly, Kathleen K.; Hardwick, Renea C. 1998. Population genetic structure in a bird-dispersed pine, *Pinus albicaulis* (Pinaceae). Canadian Journal of Botany. 76: 83-90.

Burr, Karen E.; Eramian, Aram; Eggleston, Kent. 2001. Growing whitebark pine seedlings for restoration. In: Tomback, Diana F.; Arno, Steven F.; Keane, Robert E., eds. Whitebark pine communities: ecology and restoration. Washington, DC: Island Press. 325-345.

Cheliak, William M.; Dancik, Bruce P. 1982. Genic diversity of natural populations of a clone forming tree *Populus tremuloides*. Canadian Journal of Genetics and Cytology. 24: 611-616.

Evenden, Angela G.; Moeur, Melinda; Shelly, J. Stephen; Kimball, Shannon F.; Wellner, Charles A. 2001. Research natural areas on National Forest System lands in Idaho, Montana, Nevada, Utah, and western Wyoming: A guidebook for scientists, managers, and educators. General Technical Report RMRS-GTR-69. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station. 84 p.

Felsenstein, Joseph. 2005. PHYLIP (Phylogeny Inference Package) version 3.6. Distributed by the author. Department of Genome Sciences, University of Washington, Seattle.

Hamrick, James L.; Schnabel, Andrew F.; Wells, Pat V. 1994. Distribution of genetic diversity within and among populations of Great Basin Conifers. In Natural History of the Colorado Plateau and Great Basin, K. T. Harper, L. L. St. Clair, K.H. Thorne, and W.M. Hess (eds). University of Colorado Press, p 147-161.

Jørgensen, Stacy M.; Hamrick, James L.; Wells, P. V. 2002. Regional patterns of genetic diversity in *Pinus flexilis* (Pinaceae) reveal complex species history. American Journal of Botany. 89(5): 792-800.

Jørgensen, Stacy M.; Hamrick, James L. 1997. Biogeography and population genetics of whitebark pine, *Pinus albicaulis*. Canadian Journal of Forest Research. 27: 1574-1585.

Krakowski, Jodie; Aitken, Sally N.; El-Kassaby, Yousry A. 2003. Inbreeding and conservation genetics in whitebark pine. Conservation Genetics. 4: 581-593.

Latta, Robert G.; Mitton, Jeffrey B. 1997. A comparison of population differentiation across four classes of gene marker in limber pine (*Pinus flexilis* James). Genetics. 146: 1153-1163.

Ledig, F. Thomas; Jacob-Cervantes, Virginia; Hodgskiss, Paul D.; Eguiluz-Piedra, Teobaldo. 1997. Recent evolution and divergence among populations of a rare Mexican endemic, Chihuahua spruce, following Holocene climatic warming. Evolution. 51(6): 1815-1827.

Lewis, Paul O.; Zaykin, Dmitri. 2001. Genetic Data Analysis: Computer program for the analysis of allelic data. Version 1.0(d16c). Free program distributed by the authors over the internet from http://lewis.eeb.uconn.edu/lewishome/software.html.

Little, Elbert L. 1971. Atlas of the United States Trees. Volume 1 Conifers and important hardwoods. USDA Forest Service, Miscellaneous Publication No. 1146.

Mahalovich, Mary F. [Submitted May 2009]. Genetic differentiation of *Pinus albicaulis* Engelm. populations from the Northern Rocky Mountains. The Americas Journal of Plant Science and Biotechnology.

Mahalovich, Mary F.; Burr, Karen E.; Foushee, David L. 2006. Whitebark pine germination, rust resistance and cold hardiness among seed sources in the Inland Northwest: Planting Strategies for Restoration. In: National Proceedings: Forest and Conservation Nursery Association; 2005 July 18-20; Park City, UT, USA. Proceedings RMRS-P-43. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station: 91-101.

Mahalovich, Mary F.; Dickerson, Gary A. 2004. Whitebark pine genetic restoration program for the Intermountain West (United States). In: Sniezko, R. A., Samman, S.; Schlarbaum, S. E.; Scott, E.; Kriebel, H. B., eds. Breeding and genetic resources of five-needle pines: growth, adaptability and pest resistance. 2001 July 23-27; Medford, OR, USA. IUFRO Working Party 2.02.15 Proceedings RMRS-P-32. Fort Collins, CO: USDA Forest Service, Rocky Mountain Research Station: 181-187.

Mahalovich, Mary F. 2000. Whitebark Pine Restoration Strategy—Some genetic considerations. In: Nutcracker Notes, January 1, 2000. Number 11. USDA Forest Service, Rocky Mountain Research Station, Fire Sciences Laboratory. Missoula, MT. 4 p.

McDonald, Geral I.; Hoff, Raymond. 2001. Blister rust: an introduced plague. In: Whitebark pine communities, ecology and restoration. Tomback, Diana F.; Arno, Steve F.; Keane, Robert E. (eds.). Island Press, Washington, DC. 193-220.

McLaughlin, Marie. 2010. [Personal communication]. June 15, Coeur d'Alene, ID: U.S. Department of Agriculture, Forest Service, Northern Region, Coeur d'Alene Nursery.

Mitton, Jeffrey B.; Williams, Claire G. 2006. Geneflow in conifers. In: Landscapes, Genomics, and Transgenic Conifers (Claire G. Williams, ed). Springer. 147-168.

Mitton, Jeffrey B. 1995. Genetics and physiological ecology. In: Smith, William K.; Hinckley, Thomas M., eds. Ecophysiology of coniferous forests. San Diego, CA: Academic Press, Inc.: 1-36.

Nei, Masatoshi. 1972. Genetic distance between populations. American Naturalist. 106: 283-292.

Peakall, Rodney; Smouse, Peter E. 2005. GENALEX 6: genetic analysis in Excel. Population genetic software for teaching and research. Molecular Ecology Notes. 6: 288-295.

Perkins, Dana L.; Swetnam, Thomas W. 1996. A dendroecological assessment of whitebark pine in the Sawtooth-Salmon River region, Idaho. Canadian Journal Forest Research. 26: 2123-2133.

Richardson, Bryce A. 2001. Gene flow and genetic structure of whitebark pine (*Pinus albicaulis*): Inferences into bird-dispersed seed movement and biogeography. Unpublished Master Thesis. University of Idaho. 55 p.

Richardson, Bryce A.; Klopfenstein, Ned B.; Brunsfeld, Steven J. 2002. Assessing Clark's nutcracker seed-caching flights using maternally inherited mitochondrial DNA of whitebark pine. Canadian Journal of Forest Research. 32: 1103-1107.

Rogers, Deborah L.; Millar, Constance I.; Westfall, Robert D. 1999. Fine-scale genetic structure of whitebark pine (*Pinus albicaulis*): assocations with watershed and growth form. Evolution. 53(1): 74-90.

Schuster, William S. F.; Mitton, Jeffrey B. 2000. Paternity and gene dispersal in limber pine (*Pinus flexilis* James). Heredity. 84: 348–361.

Schuster, William S. F.; Alles, David L., Mitton, Jeffrey B. 1989. Gene flow in limber pine: evidence from pollination phenology and genetic differentiation along an elevational transect. American Journal of Botany. 76(9): 1395-1403.

Spitze, Ken. 1993. Population structure in *Daphnia obtuse*: Quantitative genetic and allozymic variation. Genetics 135: 367-374.

Steinhoff, Raymond J.; Joyce, Dennis G.; Fins, Lauren. 1983. Isozyme variation in *Pinus monticola*. Canadian Journal of Forest Research. 13: 1122-1131.

USDA Forest Service. 2010. Combined Seed Handbook FSH 2409.26f, Northern, Rocky Mountain, Southwestern and Intermoutain Regions. Missoula, MT, Lakewood, CO, Albuquerque, NM and Ogden, UT.

USDA Forest Service. 2009. Assessment of Genetic Diversity of Whitebark Pine in Washington and Oregon. National Forest Genetics Laboratory Lab Report #156, 157, and 221. NFGEL, Placerville, CA.

USDA Forest Service. 2003. National Forest Genetic Electrophoresis Laboratory Standard Operating Procedures. NFGEL, Placerville, CA.

Vendramin, Giovanni G.; Lelle, L.; Rossi, P.; Morgante, Michele. 1996. A set of primers for the amplification of 20 chloroplast microsatellites in Pinaceae. Molecular Ecology. 5: 595-598.

Wheeler, Nicholas C.; Guries, Raymond P. 1982. Population structure, genetic diversity and morphological variation in *Pinus contorta* Dougl. Canadian Journal of Forest Research. 12: 595-606.

White, Tim L.; Adams, W. Thomas; Neale, David B. 2007. Forest Genetics. CABI Publishing, Cambridge, MA. 682 p.

Wright, Sewell. 1951. The genetical structure of populations. Annals of Eugenics. 15: 323-354.

Wu, Junyuan; Krutovskii, Konstantin V.; Strauss, Steven H. 1998. Abundant mitochondrial genome diversity, population differentiation and convergent evolution in Pines. Genetics. 150: 1605-1614.

Yandell, Ulla G. 1992. An allozyme anlayis of whitebark pine (*Pinus albicaulis* Engelm). Unpublished master's thesis. University of Nevada, Reno. 64 p.

Yang, Rong-Cai; Yeh, Francis C. 1993. Multilocus structure in *Pinus contorta* Dougl. Theoretical and Applied Genetics. 87: 568-576.

Yeh, Francis C.; Yang, Rong-Cai; Boyle, Timothy. 1997. Popgene Version 1.32. University of Alberta, Edmonton, Alberta.

Genetic Variation of Whitebark Pine (*Pinus albicaulis*) Provenances and Families From Oregon and Washington in Juvenile Height Growth and Needle Color

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Abstract—A three year common garden study was conducted on whitebark pine (*Pinus albicaulis)* which included 215 families from the eight provenances or seed zones in Oregon and Washington. Total height and needle color were assessed. Height differed significantly among provenances and families, and was primarily associated with source elevation, longitude, and precipitation. A moderate to high heritability was estimated for total height. Seedling needle color differed among provenances and was associated with temperature:moisture indexes and source elevation. Height growth along the Cascade mountain range (USA), representing four adjoining provenances or seed zones, appeared to be similar and clinal in nature. The four remaining provenances, representing seed zones from a more moderate or extreme environmental settings, differed significantly from the Cascade provenances for one or more traits that were examined. It would seem prudent to restrict seed transfers to within each of these four seed zones respectively. This study also supports the need to plan gene conservation collections within each seed zone for whitebark pine in the Pacific Northwest region.

Introduction

Understanding geographic patterns of genetic variability in adaptive traits will be a key to successful restoration and genetic conservation of whitebark pine (*Pinus albicaulis*). A large common garden study was conducted with seedlings at the Dorena Genetic Resource Center (DGRC) and used to assess family and provenance variation in height growth, foliage color, and resistance to white pine blister rust (the assessment of blister rust is still in progress). This summary reports on data from collections in Oregon and Washington, and complements the few other studies that have been reported to-date for this species.

Materials and Methods

The study included 215 families from eight provenances in Oregon and Washington. The eight provenances represent the current seed zones (geographic subdivisions) associated with whitebark pine in the Pacific Northwest region (Figure 1; Aubry and others 2008); the number of parents (seedling families) varied from seven to 51 per provenance (Table 1). Wind-pollinated seeds collected in natural stands were stratified in November 2006. Germination occurred in a germination chamber, and emerging seedlings were transplanted into 164 cm^3 tubes and placed in a greenhouse at DGRC (Cottage Grove, Oregon) in March 2007. The seedlings were randomized into complete blocks in August 2007. They were inoculated with blister rust in fall 2008, and then transplanted to a common garden raised bed (in the same complete block randomization) for future assessment of disease resistance and other traits (Figure 2).

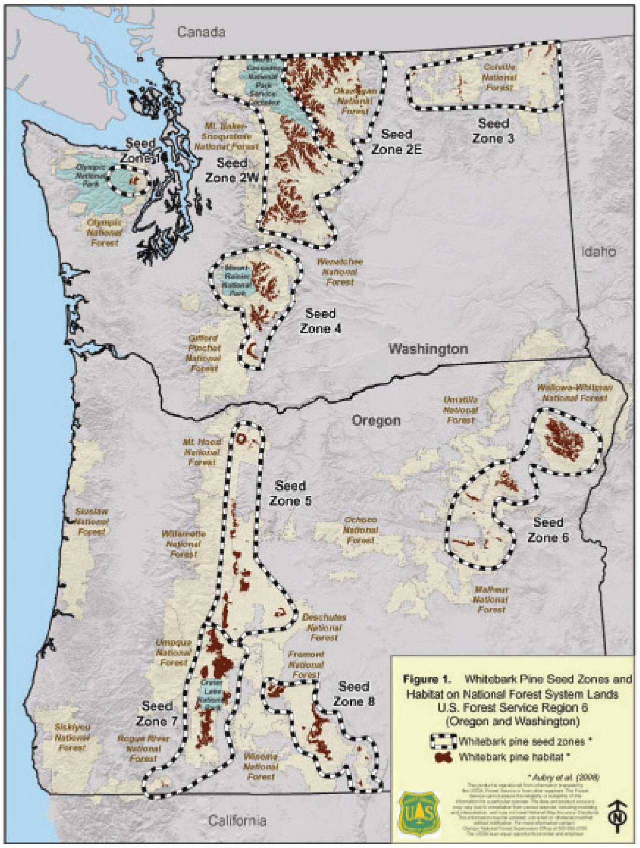


Figure 1. Whitebark pine seed zones and habitat on National Forest system lands in U.S. Forest Service Region 6 (Oregon and Washington). See Table 1 for listing of provenances.

The experimental design was a randomized complete block with six blocks. For the blister rust inoculation, the experiment was divided into two separate trials; where each trial was inoculated with a different geographic source of blister rust spore inoculums in early fall 2008. Each of the six blocks consisted of 215 families planted in row-plots (up to 10 trees/family/plot).

In: Keane, Robert E.; Tomback, Diana F.; Murray, Michael P.; and Smith, Cyndi M., eds. 2011. **The future of high-elevation, five-needle white pines in Western North America: Proceedings of the High Five Symposium.** 28-30 June 2010; Missoula, MT. Proceedings RMRS-P-63. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station. 376 p. Online at http://www.fs.fed.us/rm/pubs/rmrs_p063.html

Table 1. Provenance locations and sample size (number of parent trees) in the common garden study[a].

Provenance	Latitude (°N)	Longitude (°W)	Elevation (m)	Sample Size (N)
Washington				
1. Olympic	47.8	123.1	1792-1981	7
2. N. Cascades	46.9	121.2	1792-2084	51
3. Northeastern	49.0	117.1	1755-2072	9
4. S. Cascades	46.2	121.5	1896-2118	16
Oregon				
5. N. Cascades	44.0	121.7	1676-2457	56
6. Blue Mountains	44.8	118.2	2219-2469	22
7. S. Cascades	43.4	122.1	2011-2446	33
8. Southeastern	42.5	122.1	2286-2535	20

[a] The common garden locale was located near Cottage Grove, Oregon; 43.7° N latitude, 122.9° W longitude, 128 m in elevation.

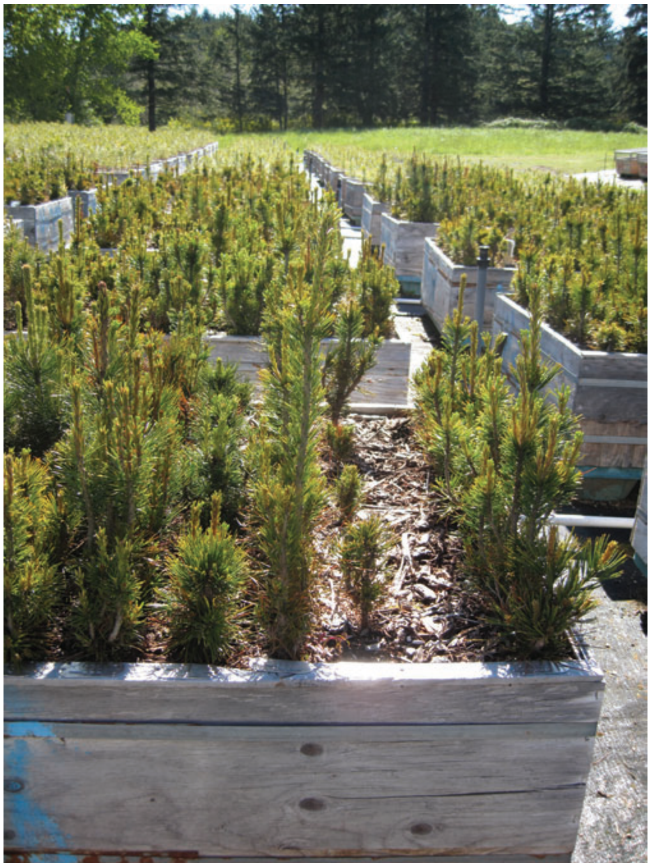


Figure 2. Family row plots of whitebark pine in common garden study. Note variation in height.

Figure 3. Variation in foliage color; some individuals and families are 'blue' and others are 'green'.

Total height after the second (prior to spore inoculation in 2008) and third growing season (fall 2009) were recorded for all seedlings. The correlation between the two measurements was 0.97 (family mean basis) and only total height after the third growing season is reported in this paper. The affect of inoculating seedlings with blister rust in 2008 on the third year height growth (2009) and color assessment (2010) is assumed to be indeterminate (with unknown bias) and negligible. Color of the 2009 foliage was assessed in 2010; five seedlings per family row-plot were assessed for color. One person performed the color assessments to minimize the variation, where the color categories were based on a subjective assessment of color differences. Four initial color categories were assessed : green, intermediate green, intermediate blue, and blue color. After an initial look at frequencies, the colors were combined to form two classes (Figure 3): green (green + intermediate green) and blue (blue + intermediate blue).

The ClimateWNA v4.60 program (Wang and Hamann 2010) was used to derive climate variables on the basis of each parent tree's source location (latitude, longitude, elevation).

The mean, minimum, and maximum temperatures on an annual, seasonal, and monthly basis were obtained in addition to the annual, seasonal and monthly precipitation data. Various indexes were also utilized from the ClimateWNA program. The annual heat:moisture index is defined as the (mean annual temperature (degrees C) + 10) / (mean annual precipitation (mm)/1000)). The summer heat:moisture index is defined as the ((mean warmest month temperature (degrees C)) / (mean annual summer (May to Sept.) precipitation (mm))/1000)). These climate variables and source location variables were used in the regression on height and color frequency data.

Statistical analysis procedures were conducted using SAS (SAS Institute Inc. 2008). The analysis of variance (ANOVA) of height was based on family-plot means using Proc Glimmix. Provenance was considered as a fixed effect, while trial, block within trial, family within provenance, and associated interactions were considered as random effects in the generalized linear mixed model. Proc Glimmix was used to estimate variance components for use in the estimation of individual tree heritability for selected provenances where individual tree data was used. Individual tree heritability was estimated as: $3\ (\sigma^2_f)\ /\ (\sigma^2_f + \sigma^2_{fr} + \sigma^2_w)$ where σ^2_f, σ^2_{fr}, σ^2_w are the components of variance for family (f), plot (fr), and within-plot (w) respectively. The value of $3\ (\sigma^2_f)$, used in the numerator to estimate the additive genetic variance, reflects the likelihood that offspring from an open-pollinated parent are related to a greater degree than half-sibs (Campbell 1986). Standard errors of heritability were calculated according to Becker (1984). Proc Reg (selection = stepwise with default probability settings) was used in the regression of height and foliage color on source location and environmental variables. Proc Surveyfreq was used to summarize the color frequency data (green-blue distribution per provenance) and to determine if a significant association exists between the provenances and color frequency distribution.

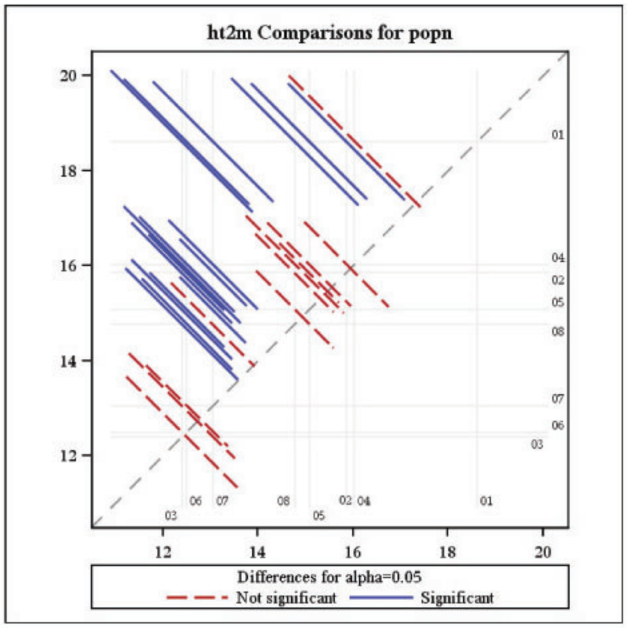


Figure 4. Statistical significance (P < .05) among provenance means for total height. Height shown on vertical and horizontal axis (cm.). See Table 1 for listing of provenances (popn).

Results

Height

Significant differences among provenances were observed in the ANOVA (F = 9.6, P < .004) and the pair-wise provenance contrasts are exhibited in Figure 4. There was substantial variation among families within provenances (Z = 8.7, P < .0001) as well (Figure 5), with family means varying from 6.2 to 21.3 cm across provenances. The range of family means within provenances is striking with mean height ratios (largest family mean/smallest family mean) ranging from 1.5 to 2.9. If provenance had been considered as a random variable along with the remaining variables, it would have accounted for 20 percent of the total observed variation with family within provenance accounting for an additional 31 percent. The variation accounted for by family within provenance is a high value for a biometric trait in conifers. Provenance mean heights ranged from 12.4 to 18.6 cm. Height differences were significant among geographic areas as shown in the following selected contrasts. The Olympic provenance (# 1; mean = 18.6 cm) differed significantly (P < .05) from six of the seven provenances in the pair-wise contrasts (Figure 4). It was not, however, significantly different than the Washington – S. Cascades provenance (# 4; mean = 16.0 cm). The Cascade region provenances (combined # 2, 4, 5, 7, 8; mean = 15.0 cm) differed significantly from the northeastern Washington and Blue Mountains region (combined # 3, 6; mean = 12.5 cm). In addition, the Oregon - S. Cascades provenance (# 7; mean = 13.1 cm) differed significantly from the rest of the combined Cascade provenances (combined # 2, 4, 5, 8; mean = 15.4 cm).

Elevation, longitude, temperature, and precipitation explained only 35 percent of the variation in height (regression model df = 182). The final set of variables in the regression model were: elevation, longitude, temperature difference between mean warmest and coldest monthly temperature, October precipitation, June precipitation, May precipitation, and mean annual precipitation. Elevation, as a singular variable, was associated with height to the greatest extent (r = - 0.41, Figure 6). A subset of the data was also analyzed in a separate regression analysis; where the subset designates the higher elevation sources that are greater than 2286 m. Longitude and precipitation in the month of June explained 50% of the variation (regression model df = 35). Elevation was not a significant variable in the regression model for this subset.

Individual tree heritability was estimated for three of the eight provenances (# 2, 5, 7) where sample sizes (n = 51, 56, 33) were deemed sufficient. Heritability (and standard errors) estimates were 0.57 (0.10), 0.56 (0.10), and 0.83 (0.16) for the respective provenances. Thus, height appears to possess a moderate to high degree of heritability even after considering the high standard errors and single common garden test site.

Foliage Color

There was a significant association between the eight provenances and green-blue frequency distribution (Rao-Scott chi-square, P < .0001). The percentage of green seedlings ranged from 64 to 99 percent (Figure 7). The two lowest percentages (64 and 76) were associated with the provenances from sources representing the highest elevations in Oregon

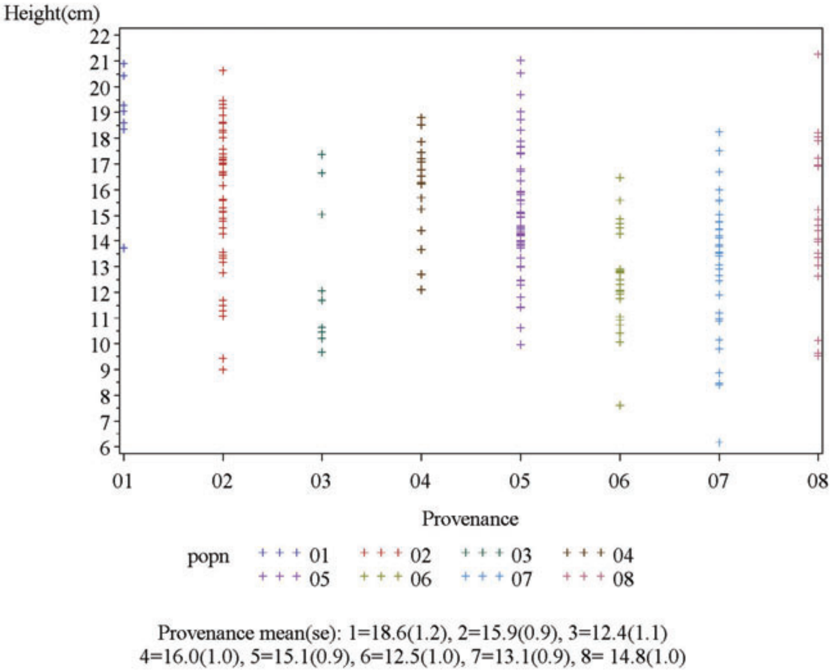


Figure 5. Family mean heights by provenance. See Table 1 for listing of provenances.

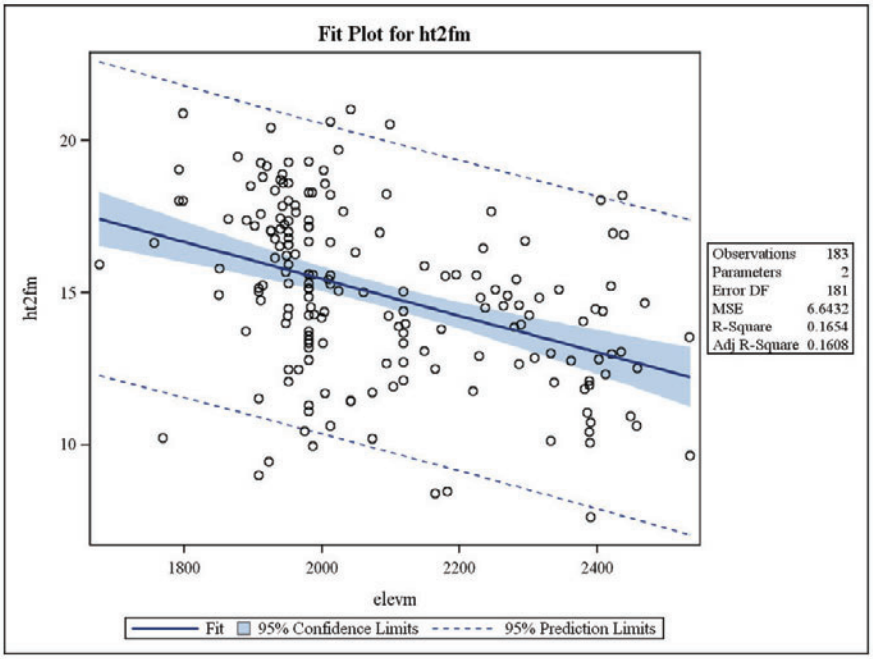


Figure 6. Family mean heights (cm) by elevation (m) across provenances.

(# 6, 8), while the two highest percentages (98 and 99) were associated with provenances from two lower elevation sources in Washington (#1, 3).

A total of 132 families were 100 percent green while one family was 100 percent blue. The remaining 82 families segregated into blue and green seedlings. The frequency of color segregation among families varied considerably among provenances. Only one seedling scored as blue in the Olympic provenance where one family out of seven segregated into green and blue seedlings. In stark contrast, 36 percent of the seedlings scored as blue in the southeastern Oregon provenance (# 8) where 13 of the 20 families segregated into green and blue seedlings and one family was 100 percent blue. The vast majority (83 percent) of blue seedlings in the four lower elevation provenances (# 2, 3, 4, and 5) occurred in families where the parent tree source elevation was equal to or greater than 1981 m. The individual family segregation proportions (expressed as the proportion of blue seedlings) were wide ranging within the respective provenances; where proportion of blue seedlings in a family ranged from 0 to 100 percent. Figure 8 displays the segregation proportions for those families (82 in total) which segregated into blue and green seedlings in addition to the single family that was 100 percent blue.

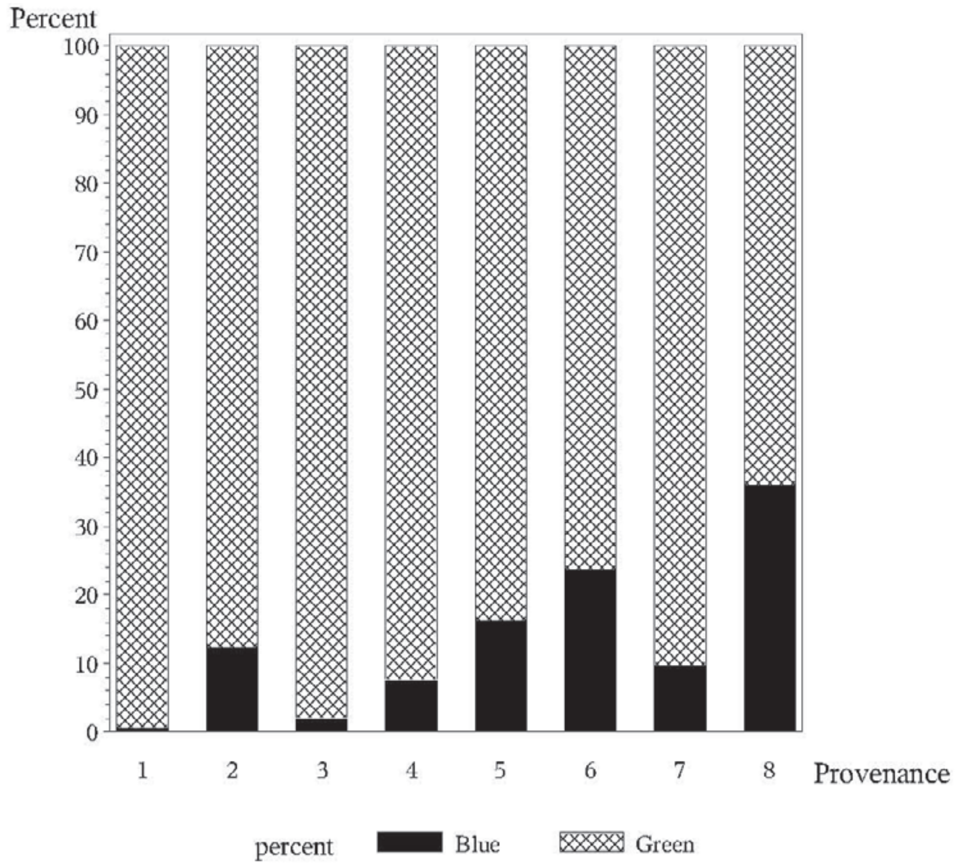
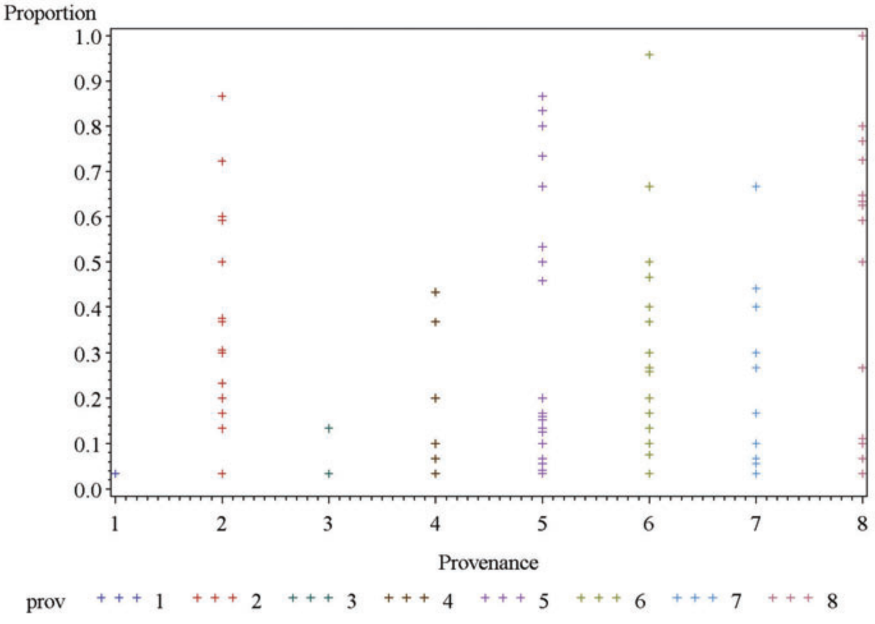


Figure 7. Percent of green/blue needle color by provenance (see Table 1).



For the 83 of 215 families that segregated into blue/green or 100 % blue color.

Figure 8. Proportion of blue seedlings per family that segregated into blue and green seedlings. See Table 1 for listing of provenances.

A suite of 14 environmental and location variables explained 57 percent of the variation in color frequency (family mean basis, regression model df = 188). The first three variables entered into the model explained the majority of the variation (38 percent): annual heat:moisture index, elevation, and summer heat:moisture index. The remaining variables (eight of which related to monthly or seasonal precipitation values) explained a relatively low percentage of the variation as they entered the model. A higher annual heat:moisture index, higher elevation, and lower summer heat:moisture index were associated with a relatively higher percentage of blue seedlings.

Discussion

The results from this study confirm some of the general trends that were found in an earlier study which summarized the third year growth increment of seedlings for four of the sampled provenances in this study (# 4, 5, 6, 7; Hamlin and others 2008). The families and sampled geographic areas differed in the two studies, but both studies sampled within the four respective provenances. Similar height growth trends were depicted for provenance differences and tier rankings. In the earlier study, provenances representing the Washington - S. Cascades (# 4) and Oregon - N. Cascades (#5) were the tallest (top tier group) and differed significantly from the Blue Mountains (#6) and Oregon - S. Cascade (#7) provenances (shorter, lower tier group). A similar general trend of declining height increment with increased elevation was evident. Precipitation amounts explained 34 percent of the variation in height increment in the earlier study. Height increment also exhibited a moderate degree of heritability (0.27) in the earlier study. Thus, the two studies exhibit a repeatable difference (relative tier ranking) among the sampled provenances and a measureable degree of genetic adaptation across the region for height growth.

In the earlier study (Hamlin and others 2008), growth initiation and completion were estimated for provenances (# 4,5,6,7) on the basis of one season's growth. The results indicated a difference in phenology among the provenances where the Blue Mountains provenance (# 6) initiated growth at the earliest date in the spring and completed growth at an earlier date. The remaining provenances (# 4, 5, 7) were more similar in their phenology pattern, although a low elevation subset (1676 m) within provenance # 5 exhibited later dates for growth initiation and growth cessation. This additional trait suggests a difference between the higher elevation eastside provenance (# 6) and the relatively lower elevation (with warmer temperature and higher precipitation) Cascade provenances. Such differences in phenology can affect the hardiness and potential for cold injury when moving sources to more extreme environments (Bower and Aitken 2006).

The results from this study indicate an association between the provenances and foliage color (green-blue frequency distribution) which in turn are associated to a degree with source elevation and temperature to moisture ratios. The color differences (green to blue) in a myriad of other studies of conifers have been attributed to differences in surface wax on the needles (Hanover and Reicosky 1971), and there has been speculation that this may be a physiological response to certain ecological habitats; example, as an adaptive character response to higher UV irradiation levels (Clark and Lister 1975). UV radiation increases with elevation, and decreases with cloud cover (Noaa/National Weather Service 2006). The Blue Mountains (#6) and southeastern Oregon (#8) provenances represent the two higher elevation ranges within the study, and the higher source elevations (with correspondingly higher UV irradiation levels) represent a logical causal factor for the higher blue frequency distribution in these two provenances.

The Blue Mountains and southeastern Oregon provenances also experience the larger annual heat to moisture ratios which would affect the basic physiological response to moisture deficits.

Hanover and Reicosky (1971) suggested that these waxes represent an additional resistance to the diffusion of water, while Clark and Lister (1971) have also suggested the importance of waxes in relative reflectance of UV light which may aid in dealing with high irradiation levels, lower relative humidities, and low soil moisture levels.

A few general observations in reference to the current seed zones might be garnered from this small study and previous studies. Variation patterns among the eight provenances (current seed zones) differ, depending on the trait studied. A previous wide ranging study of whitebark pine (Bower and Aitken 2008) noted the importance of date of needle flush in seed transfer. They also noted the clinal nature for height growth within the study area and correlation to length of growing season. In addition, previous and current studies at DGRC suggest there may be geographic trends such as higher rust resistance in the northern areas or hotspots for rust resistance in the region (Sniezko and others 2007; and Sniezko, personal communication). Height growth along four of the Cascade provenances (# 2, 4, 5, 8) appear to be more similar and clinal in nature; where growth appears to be associated to an extent with elevation, temperature, and precipitation gradients. Therefore, one should be cognizant of the differences in the respective environmental gradients prior to determining a seed transfer within or among these four provenances. The remaining four provenances (# 1, 3, 6, 7) differ significantly from the aforementioned Cascade provenances for one or more traits that were examined in either this or the previous study (Hamlin and others 2008). The Olympic provenance (#1) differs in growth rate from the majority of provenances and is located in a more moderate climate. The annual rainfall (mean = 2621 mm in the provenance sample area) is approximately two to three times that of the other provenances and relatively lower summer temperatures exist within the Olympic provenance. The northeastern Washington provenance (# 3) differs in growth rate from the Olympic (# 1) and Cascades (# 2, 4, 5, 8), and is separated a great distance from the Blue Mountains provenance (#6). The phenology of the Blue Mountains provenance (# 6) differs substantially from the Cascades and height growth is substantially slower than the Cascades (#2, 4, 5, 8). The Oregon - S. Cascades provenance (#7) was unique in that growth rates were similar to the eastside provenances (# 3, 6) while phenology and foliage color were similar to the northern Cascade provenances (# 2, 4, 5). Thus, on the basis of these few studies and traits examined, it would seem prudent to restrict seed transfers to within each of these four provenances (# 1, 3, 6, 7) and seed zones respectively.

This short term study suggests the need to utilize seed zone delineations to an extent when considering seed deployment. This study also suggests that there exists a large amount of genetic variation among families within any single provenance. This large amount of genetic variation would be desirable when deploying seed/seedlings into a planned restoration effort, and may serve as a desirable buffering in future climate change scenarios. Additional short or long-term studies of additional fitness traits are still desirable and would be useful in furthering knowledge of the species genecology. Any additional studies should also try to increase the sampling of parent trees where sample sizes have been less than desirable (for example, provenance # 1 and # 3 in this study).

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References

Aubry, C. A.; Goheen, D.; Shoal, R.; Ohlson, T.; Lorenz, T.; Bower, A.; Mehmel, C.; Sniezko, R. 2008. Whitebark pine restoration strategy for the Pacific Northwest. Olympia, WA: U.S. Forest Service, Pacific Northwest Region.

Becker, W. A. 1984. Manual of quantitative genetics. 4th edition, Academic Enterprises, Pullman, WA. 186 p.

Bower, A. D.; Aitken, S. N. 2006. Geographic and seasonal variation in cold hardiness of whitebark pine. Can. J. For. Res. 36: 1842-1850.

Bower, A. D.; Aitken, S. N. 2008. Ecological genetics and seed transfer guidelines for *Pinus alicaulis* (Pinaceau). Am. J. Bot. 95(1): 66-76.

Campbell, R. K. 1986. Mapped genetic variation of Douglas-fir to guide seed transfer in southwest Oregon. Silvae Genet. 35: 85-95.

Clark, J. B.; Lister, G. R. 1975. Photosynthetic action spectra of trees. II. The relationship of cuticle structure to the visible and ultraviolet spectral properties of needles from four coniferous species. Plant Physiol. 55: 407-413.

Hamlin, J.; Doede, D.; Kegley, A.; Sniezko, R. 2008. An assessment of genetic variation of *Pinus albicaulis* populations from Oregon and Washington in relation to height increment, phenology, and form. In: Noshad, D.; Noh, E.W.; King, J.; Sniezko, R., Eds. 2009. Breeding and genetic resources of five-needle pines; Ecophysiology, disease resistance and developmental biology, Proceedings of the conference 2008, Yangyang, Korea, Korea Forest Research Institute, Seoul 104p. ISBN 978-89-8176-605-4: 24-26.

Hanover, J. W.; Reicosky, D. A. 1971. Surface wax deposits on foliage of *Picea pungens* and other conifers. Am. J. Bot. 58(7): 681-687.

Noaa/National Weather Service 2006. UV index:Information, National Oceanic and Atmospheric Administration, National Weather Service, Climate Prediction Center; http://www.cpc.ncep.noaa.gov/products/stratosphere/uv_index/uv_clouds.shtml SAS Institute Inc. 2008. SAS/STAT 9.2 user's guide. Cary, NC, SAS Institute Inc.

Sniezko, R. A.; Kegley, A.; Danchok, R.; Long, S. 2007. Variation in resistance to white pine blister rust among whitebark pine families from Oregon and Washington—early results and implications for conservation. In: Goheen,E.M.; Sniezko, R.A., tech. cords. Proceedings of the conference whitebark pine: A Pacific Coast perspective. 2006 August 27-31. Ashland, OR. R6-NR-FHP-2007-01. Portland, Or: Pacific Northwest Region, Forest Service, U.S. Department of Agriculture; p. 82-97.

Sniezko, R. A. 2010. [Personal communication]. September, 2010. Cottage Grove, OR: U.S. Department of Agriculture, Forest Service, Dorena Genetic Resource Center.

Wang, T.; Hamann, A. 2010. ClimateWNA v4.60. A program to generate climate normal, annual, and monthly data for genecology and climate change studies in western North America (WNA) region. Centre for Forest Conservation Genetics, Dept. of Forest Sciences, U. of British Columbia, Vancouver B.C., Canada; available online at: http://www.genetics.forestry.ubc.ca/cfcg/ClimateWNA/ClimateWNA.html

A Sugar Pine Consensus Map: Comparative Mapping Between the *Pinus* Subgenus *Pinus* and the Subgenus *Strobus*

Extended Abstract

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Abstract—We have constructed a consensus genetic linkage map for sugar pine using three mapping populations that segregate for resistance to white pine blister rust, a disease caused by the fungal pathogen *Cronartium ribicola*. The major gene of resistance, *Cr1*, was mapped in two of the populations and included in the consensus map, which contains 400 markers organized into 19 linkage groups. All 19 linkage groups align with the 12 linkage groups of the loblolly pine reference map. This work provides the foundation for comparative genomics and mapping within the *Pinus* subgenus *Strobus*.

Genetic Mapping in Sugar Pine

Genetic maps are useful integrative tools in genomic research in many crop species (Kole 2007) and have also been constructed for several species within the *Pinus* subgenus *Pinus* and within other genera of the Pinaceae family. The majority of genetic maps constructed in pines thus far have been to species belonging to the *Pinus* sub-genus *Pinus* (commonly referred to as hard pines; Table 1) because of their wide economic importance, with relatively little progress being made in species from the subgenus *Strobus* (commonly referred to as soft pines). A genetic map was constructed in eastern white pine (*P. strobus* L., Echt and others 1997) using random amplified polymorphic DNA (RAPD) markers. Some progress has been made in western white pine (*P. monticola* Dougl. ex D. Don) and in sugar pine (*P. lambertiana* Dougl.) for mapping the major gene of resistance (MGR) to *Cronartium ribicola*, the fungal pathogen that causes white pine blister rust (Liu and others 2006; Devey et al. 1995; Harkins et al. 1998). In Harkins et al. (1998), *Cr1* (the MGR) was positioned on a linkage group in five sugar pine trees with RAPD (OPG_16_950) markers that were segregating for the hypersensitive response. A RAPD marker that was positioned at 1.2 cM from *Cr1* was converted to a sequence characterized amplified region (SCAR) marker for use in constructing a full genome consensus map (Jermstad et al. 2010). In the mapping study presented here, three sugar pine mapping populations were used for constructing individual and consensus maps with single nucleotide polymorphisms (SNPs) derived from genes that were originally amplified and sequenced in loblolly pine. The amplicons represent annotated genes that 1) are related

Table 1. Genetic maps constructed in hard pines and other genera of the Pinaceae. A comprehensive list of maps in conifers can be viewed at http://www.pierroton.inra.fr/genetics/labo/mapreview.html

Common Name	Taxonomic Name	Map Publication
—Subgenus *Pinus*		
Loblolly pine	*Pinus taeda* L	Devey et al. (1994) Theor Appl Genet 83:238-242
Longleaf pine	*Pinus elliotti* Engel	Nelson et al. (1994) J Hered 85: 433-439
Slash pine	*Pinus palustris* Mill	Nelson et al. (1993) Theor Appl Genet 87: 145-151
Monterey pine	*Pinus radiata* L	Devey et al. (1996) Theor Appl Genet 99 : 656-662
Turkish red pine	*Pinus brutia* Ten	Kaya and Neale (1995) Silvae Genet 44: 110-116
Maritime pine	*Pinus pinaster* Aiton	Plomion et al. (1995) Heredity 74:661-668
Japanese black pine	*Pinus thunbergii* Parl	Hayashi et al. (2001) Theor Appl Genet 102: 871-875
Scots pine	*Pinus sylvestris* L	Lerceteau et al. (2000) Mol Breeding 6: 451-458
Japanese red pine	*Pinus densiflora* Sieb. et Zucc.	Yong-Yul Kim et al. (2005) Mol Cells 20: 201-209
—Other genera		
Douglas fir	*Pseudotsuga menziesii* [Mirb.] Franco	Jermstad et al. (1998) Theor Appl Genet 97:762-770
Norway spruce	*Picea abies* [L] Karst	Binelli and Bucci (1994) Theor Appl Genet 88: 283-288
White spruce	*Picea glauca* Moench	Tulsieram et al. (1992) BioTechnology 10: 686-690
Japanese Cedar (Sugi)	*Cryptomeria japonica* D. Don	Mukai et al. (1995) Theor Appl Genet 90: 835-840

In: Keane, Robert E.; Tomback, Diana F.; Murray, Michael P.; and Smith, Cyndi M., eds. 2011. **The future of high-elevation, five-needle white pines in Western North America: Proceedings of the High Five Symposium.** 28-30 June 2010; Missoula, MT. Proceedings RMRS-P-63. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station. 376 p. Online at http://www.fs.fed.us/rm/pubs/rmrs_p063.html

Table 2. A summary of sugar pine linkage analyses. Maps 5701 and 6000 were derived from megagametophytes (n=95) from adult open-pollinated trees that are heterozygous for *Cr1*. Maps 5038 and 5500 are derived from the parents of the QTL population, while the sex-averaged map is derived from the progeny (n=94) and the two parents of the QTL population. The consensus map is derived from the four adult trees.

	Tree 5701 (TG101)	Tree 6000 (TG102)	Tree 5038 (♀) (TG103)	Tree 5500 (♂) (TG104)	QTL sex-averaged (TG105)	Consensus (TG106)
No. markers in JM input file	192	190	165	165	282[a]	457[b]
No. markers unmapped[c]	9	4	43	48	69	57
No. markers mapped	183	186	122	117	213	400
No. LGs	16	17	19	19	23	19
Map length (cM)	822.1	849.1	642.8	883.8	1142.7	1230.9
Cr1 mapped	√	√	-	-	-	√
*scar*OPG_16	√	√	-	√	√	√

[a] 165 markers segregated in the maternal parent and 165 markers segregated in the paternal parent. Forty-eight of these markers were in the intercross configuration and should only be counted once in the sex-averaged linkage analysis because the marker data merge and map to a single position. [165+165 = 330 - 48 (IC) = 282]

[b] Although the sum of segregating markers for the individual adult trees = 712, the number of markers recognized and analyzed by JoinMap = 457. Similar to the way JoinMap analyzed IC loci in the sex-averaged linkage analysis, TYPE II COS marker data found in > one tree were merged and analyzed as a single locus, and thus, counted only once. Among the four trees, there were 255 TYPE II COS markers (712-255= 457)

[c] these are markers that linked to ≤ 1 marker (s)

to stress responses, 2) are transcription factors. Two of the populations consist of megagametophytes from open-pollinated trees (5701 and 6000) that are heterozygous for *Cr1*. A third mapping population (*QTL*) consists of progeny (needle tissue) from a controlled-cross that is segregating for partial resistance to white pine blister rust. JoinMap v. 1.4 software (Stam 1993) was used for linkage analysis with the following parameters: LinkLOD 4.0, MapLOD 0.1, and Kosambi mapping function. *Cr1* was positioned in the 5701 and 6000 maps, and the SCAR linked to *Cr1* was positioned in 5701, 6000 and 5500 (the male parent of the QTL population). Segregation data from the parents of the QTL population (5038 and 5500) and from trees 5701 and 6000 were combined in order to construct a consensus map for sugar pine (Jermstad et al. 2010). The consensus map consisted of 400 markers organized into 19 linkage groups (Table 2), which is seven more linkage groups than what is expected for pine (n=12). In total, six maps were constructed: 1) 5701, 2) 6000, 3) 5038, 4) 5500, 5) a sex-averaged map (5038 x 5500), and 6) a consensus map (5701, 6000, 5038 and 5500) (Table 2). These genetic linkage maps (TG101-106) are recorded in the TreeGenes Comparative Mapping Database (Wegrzyn et al. 2008) and can be viewed at http://dendrome.ucdavis.edu/cmap/. The amplicons used for mapping in sugar pine were developed in the ADEPT2 project (http://dendrome.ucdavis.edu/NealeLab/adept2/overview.php/).

Comparative Mapping

Several comparative mapping studies have reported syntenic relationships among the subgenus *Pinus* (Devey et al. 1999; Brown et al. 2001; Chagne et al. 2003; Komulainen et al. 2003). Synteny has also been observed between loblolly pine and conifers from other genera of the Pinaceae, i.e., *Pseudotsuga* (Krutovsky et al. 2004) and *Picea* (Neale and Krutovsky 2004). Therefore, we hypothesized that synteny would be found not only between the novel sugar pine maps, but, also observed between loblolly pine (subgenus *Pinus*) and sugar pine (subgenus *Strobus*).

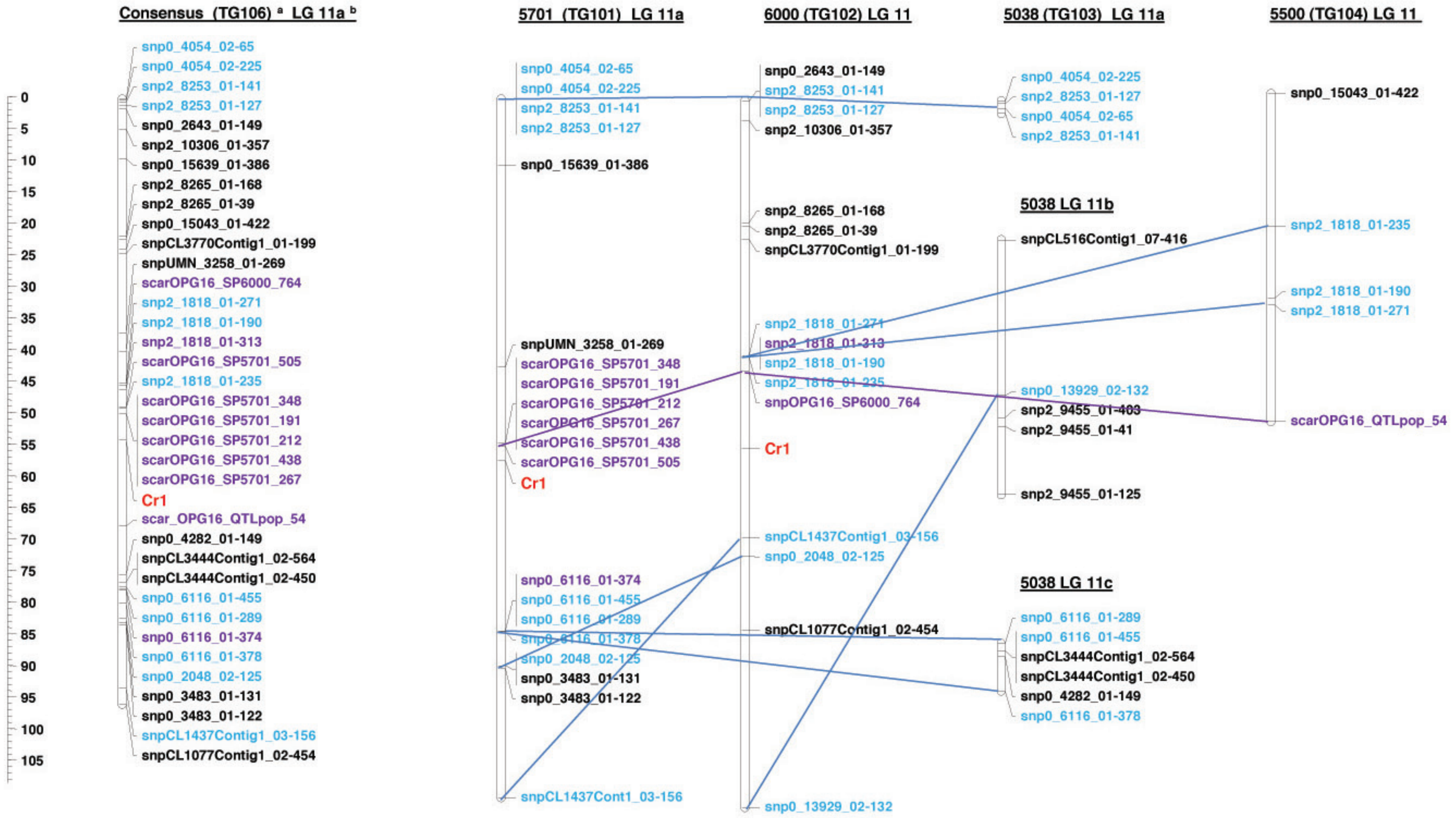
In our mapping study, two types of conserved orthologous sequence (COS) markers are observed: 1) TYPE I = the same amplicon but different SNPs within the amplicon, and 2) TYPE II = precise SNP location within the amplicon. When making intra-specific comparisons, both types of COS markers were available. However, in inter-specific comparative mapping, TYPE II COS markers are rare, as SNPs are usually not conserved across species. We first aligned the consensus map (TG106) with the four maps constructed for the individual trees 5701 (TG101), 6000 (TG102), 5038 (TG103), and 5500 (TG105). Subsequently, we aligned the consensus map with the loblolly pine reference map (TG091).

Intra-specific

Through comparative mapping within species, the integrity of the map can be determined by examination of marker groups and positions. Also, through comparative mapping, the position of genes/loci can be inferred from one map to another when orthologous markers align. For example, the hypersensitive response (i.e. *Cr1*) is not expressed in the parents of the *QTL* population (5038 x 5500) that is segregating for partial resistance. However, by aligning markers that are in common among the various trees (including the SCAR marker linked to *Cr1*), the mapped position of *Cr1* in trees 5701 and 6000 is inferred upon the maps constructed from the *QTL* population, even though *Cr1* is not expressed in this population (Fig. 1).

Inter-specific

We identified 60 TYPE I COS markers (amplicons) between sugar pine and loblolly pine, with 56 of them (93 percent) showing alignment to the loblolly pine map. Four of the markers were not collinear. A plausible explanation for this is that these markers are paralogs (alternate member



[a] Accession number assigned to maps in the TreeGenes Comparative Mapping Database (http://dendrome.ucdavis.edu/cmap/)

[b] Maps with > 1 linkage group aligning with the *P. taeda* map are given letter suffixes, such as “a”, “b”, etc.

Figure 1. Linkage group 11a of the sugar pine consensus map (TG106) aligned with the same linkage group from the four individual tree maps derived from three mapping populations. TYPE I COS markers (amplicons) that coaligned among two or three trees are shown in blue font. TYPE II COS markers (SNP) that coaligned among two or three trees are shown in purple font. The major gene for resistance to white pine blister rust (*Cr1)* is shown in red font.

Table 3. Summary of 56 collinear Type I COS markers in loblolly and sugar pine maps (Jermstad et al. 2010). Annotations are derived from BLAST queries of non-redundant (nr) plant protein sequences (BLASTx; http://www.ncbi.nlm.nih.gov).

***Pt* LG**	**Type i COS**	***Pl* LG**	**GenBank GI**	**Annotation**
1	*snp*CL3036Contig1_01	1a	255547830	Signal recognition particle subunit srp72, putative *[Ricinus communis]*
	*snp*UMN-1609-01	1a	N/A	-
	*snp*0-7471-01	1b	N/A	-
	*snp*0-18587-01	1b	115450977	Conserved hypothetical protein *[Oryza sativa]*
	*snp*0-18261-01	1b	18394104	Oxireductase *[Arabidopsis thaliana]*
2	*snp*2-374-01	2	N/A	-
	*snp*0-18470-01	2	N/A	-
	*snp*0-13565-01	2	255585824	small heat-shock protein *[Ricinus communis]*
	*snp*0-1453-01	2	255538284	fms interacting protein *[Ricinus communis]*
	*snp*UMN-915-01	2	42562204	senescence-associated E3 unbiquitin ligase 1 *[Arabidopsis thaliana]*
	*snp*CL572Contig1-04	2	255585914	alcohol dehydrogenase *[Ricinus communis]*
3	*snp*CL1530Contig1-04	3a	15237148	HTB2; DNA-binding; histone H2b *[Arabidopsis ricinus]*
	*snp*0-9922-01	3a	30689298	UBX domain-containing protein *[Arabidopsis thaliana]*
	*snp*CL1209Contig1-02	3b	15240918	transferase family protein *[Arabidopsis thaliana]*
4	*snp*0-5204-01	4	255570480	sec15, putative *[Ricinus communis]*
	*snp*0-17247-02	4	115459326	Armadillo-like helical domain containing protein *[Oryza sativa]*
	*snp*2-4011-03	4	15234240	HSP21 heat shock protein 21 *[Arabidopsis thaliana]*
	*snp*2-7808—01	4	115483694	Conserved hypothetical protein *[oryza sativa]*
	*snp*0-11649-03	4	224104341	beta tubulin *[Populus trichocarpa]*
5	*snp*CL4432Contig-04	5	42570490	AFC1 (ARABIDOPSIS FUS3-COMPLEMENTING GENE 1)
	*snp*CL544Contig1-03	5	15235213	Caffeoyl-CoA-O-methyltransferase *[Arabidopsis thaliana]*
	*snp*0-744-01	5	255550431	Xylem seine proteinase 1 precursor *[Ricinus communis]*
	*snp*2-5064-01	5	255551501	Big map kinase/bmk *[Ricinus commnunis]*
	*snp*0-12929-02	5	255551669	Receptor serine/threonine protein kinase *[Ricinus commnunis]*
6	*snp*0-806-01	6	115447491	GRAM domain contining protein *[Oryza sativa]*
7	*snp5488-02*	7a	255569410	Peroxidase 44 precursor *[Ricinus communis]*
	*snp*CL3162Contig1-02	7b	15238392	AtRAB4A GTP-binding protein *[Arabidopsis thaliana]*
	*snp*CL1698Contig1-01	7b	N/A	-
8	*snp*CL3037Contig1-06	8a	115455427	Similar to 60s ribosomal protein L13a-4 *[Oryza sativa]*
	*snp*CL3758Contig1-05	8a	115462873	Similar to TGF-beta receptor-interacting protein 1 [*Oryza sativa]*
	*snp*2-5724-02	8b	115472857	Homeodomain-related containing protein *[Oryza sativa]*
	*snp*CL363Contig1-04	8b	255564363	Rhicadhesin receptor precursor *[Ricinus communis]*
	*snp*2-5962-01	8b	30689268	PFT1 (PHYTOCHROM AND FLOWERING TIME 1) *[Arabidopsis thaliana]*
	*snp*CL2117Contig1-03	8b	255553619	Receptor protein kinase CLAVATA1 precursor *[Ricinus communis]*
9	*snp*0-12156-02	9	255543198	ATP binding protein *[Ricinus communis]*
	*snp*2-6541-01	9	N/A	-
10	*snp*CL1694Contig1-04	10a	115468878	Similar to Small nuclear ribonucleoprot4ein component [*Oryza sativa]*
	*snp*0-7321-01	10b	226531267	LOC100286137 *[Zea mays]*
	*snp*2-684-01	10b	168023746	LRR receptor-like protein [*Physcomitrella patens*]
	*snp*UMN-CL228Contig1-03	10b	255558550	40s ribosomal protein S26 *[Ricinus communis]*
	*snp*CL3116Contig1-03	10b	255548998	ran-family (Ras-related nuclear proteins) small gtpase *[Ricinus communis]*
	*snp*2-7852-01	10b	N/A	-
	*snp*2-8491-01	10b	25587817	acyl-CoA thioeserasse *[Ricinus communis]*
	*snp*CL305Contig1-05	10b	255556504	dihydrolipoamide dehydrogenase *[Ricinus communis]*
11	*snp*2-10306-01	11a	159469223	hydroxyproline-rich glycoprotein *[Chlamydomonas reinhardtii]*
	*snp*UMN-3258-01	11a	N/A	-
	*snp*0-13929-02	11b	115466184	GAGA binding- like family protein *[Oryza sativa]*
	*snp*2-9455-01	11b	190612857	pentatricopeptide repeat protein *[Picea abies]*
	*snp*2-3141-01	11c	15240885	disease resistsance protein (TIR-NBS-LRR class) *[Arabidopsis thaliana]*
12	*snp*0-17197-01	12	115474617	slu7a_arath pre-mRNA splicing Prp18-interacting factor [*Arabidosis thaliana*]
	*snp*0-16860-01	12	115436956	Armadillo-like helical domain containing protein *[Oryza sativa]*
	*snp*0-13058-01	12	255550387	polygalacturonase *[Ricinus communis]*
	snp0-489-01	12	N/A	-
	*snp*2-4724-01	12	115447049	Similar to protein kinase ATN1 *[Oryza sativa]*
	*snp*UMN-5833-01	12	255585558	S-adenosylmethionine-dependent methyltransferase *[Ricinus communis]*
	*snp*CL1052Contig-03	12	115443669	YqeH GTP-binding protein; nitric oxide synthase

of the same gene-family). All 19 linkage groups of the consensus sugar pine map found alignment with the 12 linkage groups of the loblolly pine reference map (Table 3). In some cases, multiple sugar pine linkage groups aligned to a single loblolly pine linkage group due to gaps in the sugar pine map. Where gaps exist in the map, a well-defined pine reference map can serve as a scaffold onto which other pine maps can align and be ordered. The sugar pine linkage group containing *Cr1,* aligned to linkage group 11 in loblolly pine (Table 3). Although loblolly pine is not susceptible to white pine blister rust and *Cr1* expression is not observed, a locus resembling *Cr1* might be present in all pines at this location, perhaps in a cluster of *R* genes, a phenomenon commonly observed in plants (Michelmore and Meyers 1998). It will be interesting to see what genes reside on this linkage group when the loblolly pine genome sequence becomes available.

Summary

We present the first genome-scale genetic map for sugar pine using several populations, two of which are segregating for the major gene resistance conferred by the *Cr1* locus. Because of marker collinearity and successful RAPD-to-SCAR conversion, we were able to infer the position of *Cr1* on the consensus map. We also present here the first comparative mapping study to show syntenic relationships between hard pines (subgenus *Pinus*) and soft pines (subgenus *Strobus*). Because we observe synteny between subgenus *Pinus* and subgenus *Strobus*, we anticipate an even greater degree of synteny among the members of the subgenus *Strobus*. The ability to transfer information regarding gene sequence (amplicon) and function across taxonomic boundaries will be invaluable, saving time and effort for future studies in the soft pines. This becomes particularly relevant as forests and landscapes are challenged by rapidly changing climate.

Literature Cited

Brown, G.R.; Kadel III, E.E.; Bassoni, D.L.; Kiehne, K.L.; Temesgen, B.; van Buijtenen, J.P.; Sewell, M.M.; Marshall, K.A.; Neale, D.B. 2001 Anchored reference loci in loblolly pine (*Pinus taeda* L.) for integrating pine genomics. Genetics. 159: 799–809.

Chagne, D.; Brown, G.R.; Lalanne, C.; Madur, D.; Pot, D.; Neale, D.B.; Plomion, C. 2003. Comparative genome and QTL mapping between maritime and loblolly pines. Mol Breed. 12:185-195.

Devey, M.E.; Delfino-Mix, A.; Kinloch, B.B. Jr.; Neale, D.B. 1995. Random amplified polymorphic DNA markers tightly linked to a gene for resistance to white pine blister rust in sugar pine. Proc Natl Acad Sci. 92:2066-2070.

Devey, M.E.; Sewell, M.M.; Uren, T.L.; Neale, D. B. 1999. Comparative mapping in loblolly and radiata pine using RFLP and microsatellite markers. Theor Appl Genet. 99:656-662.

Echt, C.S.; Nelson, C.D. 1997. Linkage mapping and genome length in eastern white pine (*Pinus strobus* L.). Theor Appl Genet. 94:1031-1037.

Harkins, D.M.; Johnson, G.; Skaggs, A.P.; Mix, A.; Dupper, G.; Devey, M.; Kinloch, B. Jr.; Neale, D. 1998. Saturation mapping of a major gene for resistance to white pine blister rust in sugar pine. Theor Appl Genet. 97:1355-1360.

Jermstad, K.D.; Eckert, A.J.; Wegrzyn J.L.; Kinloch, B.B.; Mix, A.D.; Davis, D.A.; Burton, D.C.; Neale, D.B. 2010. Comparative Mapping in *Pinus*: Sugar Pine (*Pinus lambertiana* Dougl.) and Loblolly Pine (*Pinus taeda* L.). Tree Genetics and Genomes DOI 10.1007/s11295-010-0347-1.

Liu J.J.; Ekramoddoullah, A.K.M.; Hunt, R.S; Zamani A. 2006. Identification and characterization of random amplified polymorphic DNA markers linked to a major gene (*Cr2*) for resistance to *Cronartium ribicola* in *Pinus monticola.* Phytopath. 96:395-399.

Kole, C, ed. 2007. Genome Mapping and Molecular Breeding in Plants, Volume 7, Forest Trees. Springer Berlin Heidelberg.

Komulainen, P.; Brown, G.R.; Mikkonen, M.; Karhu, A.; Garcia-Gil, M.R.; O'Malley, D.; Lee B.; Neale, D.B.; Savolainen, O. 2003. Comparing EST-based genetic maps between *Pinus sylvestris* and *P. taeda*. Theor Appl Genet. 107:667-678.

Krutovsky, K.V.; Troggio, M.; Brown, G.R.; Jermstad, K.D.; Neale, D.B. 2004. Comparative mapping in the Pinaceae. Genetics. 168:447-461.

Liu, J.J.; Ekramoddoullah, A.K.M.; Hunt, R.S.; Zamani, A. 2006. Identification and characterization of random amplified polymorphic DNA markers linked to a major gene (Cr2) for resistance to *Cronartium ribicola* in *Pinus monticola*. Phytopath. 96:395-399.

Michelmore, R.W.; Meyers, B.C. 1998. Clusters of Resistance Genes in Plants Evolve by Divergent Selection and a Birth-and-Death Process. Genome Res. 1998 8:1113-1130.

Neale, D.; Krutovsky, K. 2004. Comparative genetic mapping in trees: the group of conifers. In: Biotechnology in Agriculture and Forestry, Vol. 55:267-277, Molecular Marker Systems in Plant Breeding and Crop Improvement. (Eds., H. Lörz and G. Wenzel) Springer-Verlag Berlin Heidelberg.

Stam, P. 1993. Construction of integrated genetic linkage maps by means of a new computer package. Plant J. 6:739-744.

Wegrzyn, J.L.; Lee, J.M.; Tearse, B.R.; Neale, D.B. 2008. TreeGenes: A Forest Tree Genome Database. International Journal of Plant Genomics. 2008:1-7.

A Population Genetic Model for High-Elevation Five-Needle Pines: Projecting Population Outcomes in the Presence of White Pine Blister Rust

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The slow growth and long generation time of the five-needle pines have historically enabled these trees to persist on the landscape for centuries, but without sufficient regeneration opportunities these same traits hinder the species' ability to adapt to novel stresses such as the non-native disease white pine blister rust (WPBR). Increasing the frequency of resistance to WPBR is the foundation for options to sustain five-needle pine species in the presence of the pathogen. Depending on the condition of the ecosystems, increasing resistance can be achieved via outplanting resistant seedling stock and/or stimulating natural regeneration (Schoettle and Sniezko 2007). As the objective of management intervention in the high elevation ecosystems is often to promote multiple generations of sustainability, greater understanding of the regeneration cycle and the potential for increasing the frequency of resistance are needed. This is especially critical for the WPBR pathosystem as WPBR kills trees of all ages and therefore impacts multiple stages of the regeneration cycle of five-needle pines.

We are developing a population genetic model, parameterized for high elevation five-needle pines, to improve our understanding of pine population dynamics in the presence of WPBR and to identify key processes that could be manipulated with management to sustain high elevation pines over multiple generations. This model allows us to address questions such as: (1) What frequency of resistance to WPBR is enough to sustain a population? (2) What regeneration densities will be sufficient to promote increased frequency of resistance over time? (3) During what state of infestation and impact by WPBR is intervention most effective? The matrix model includes 6 age classes (cohorts): seeds, primary seedlings (1-4 yrs old), secondary seedlings (5-20 yrs), saplings (21-40 yrs), young adults (41-90 yrs), and mature adults (>90 yrs) (Fig. 1). The model includes non-linear functions for the effects of competition (leaf area index) on germination and cone production. Population size, incidence of infection by WPBR and frequency of a simply inherited dominant WPBR resistance gene by age class over time are all included in the model output. This model can examine the interactions between regeneration and resistance under different WPBR infection probabilities and their effects on population dynamics and changes in the frequency of the resistant allele over time.

Early evaluations of the population genetic model reveal realistic disease incidence and demographic dynamics (Field and others, submitted). The model predicted a similar pattern of disease incidence among the age classes that is commonly observed in the field (i.e., higher disease incidence in the older cohorts than the younger cohorts). One interpretation of this pattern is that the young seedlings present such a small target for infection that they escape infection resulting in the low observed rust infection incidence. However, our model output revealed the same pattern even when a uniform probability of infection was applied across all cohorts. Since young trees die rapidly after infection and new uninfected germinants are added yearly, disease incidence remained low in the young cohorts. The cost of infection is lower for the older larger trees, thus the infected individuals can persist and accumulate over time and therefore the incidence of rust infection in the older cohorts was greater. The model confirmed that a low incidence of rust infection in live young cohorts can be consistent with high infection in the young cohorts and does not necessitate the interpretation that the young cohorts are 'escaping' infection relative to the older cohorts (Field and others, submitted). The model suggests that infection and subsequent mortality, and therefore natural selection for resistance, efficiently occurs in the young age classes. Therefore stimulating regeneration to promote selection may be a viable management option to accelerate natural selection and increase the frequency of rust resistance in a population (Schoettle and Sniezko 2007). Further application of the model to examine the selection process and the accumulation of resistance in the population and each age class over time is underway.

Understanding these interactions will facilitate evaluation of the ecological efficacy of management options to sustain high elevation pines over multiple generations and help inform proactive or restoration planning. This research is one aspect of an interdisciplinary project. It will be integrated with epidemiology, social preferences, non-market valuation and economic theory into a dynamic economic model to examine the economic trade-offs of different WPBR management options in high elevation pine ecosystems (see Bond and others this proceedings; Meldrum and others this proceedings; Jacobi and others this proceedings; Nelson and others this proceedings).

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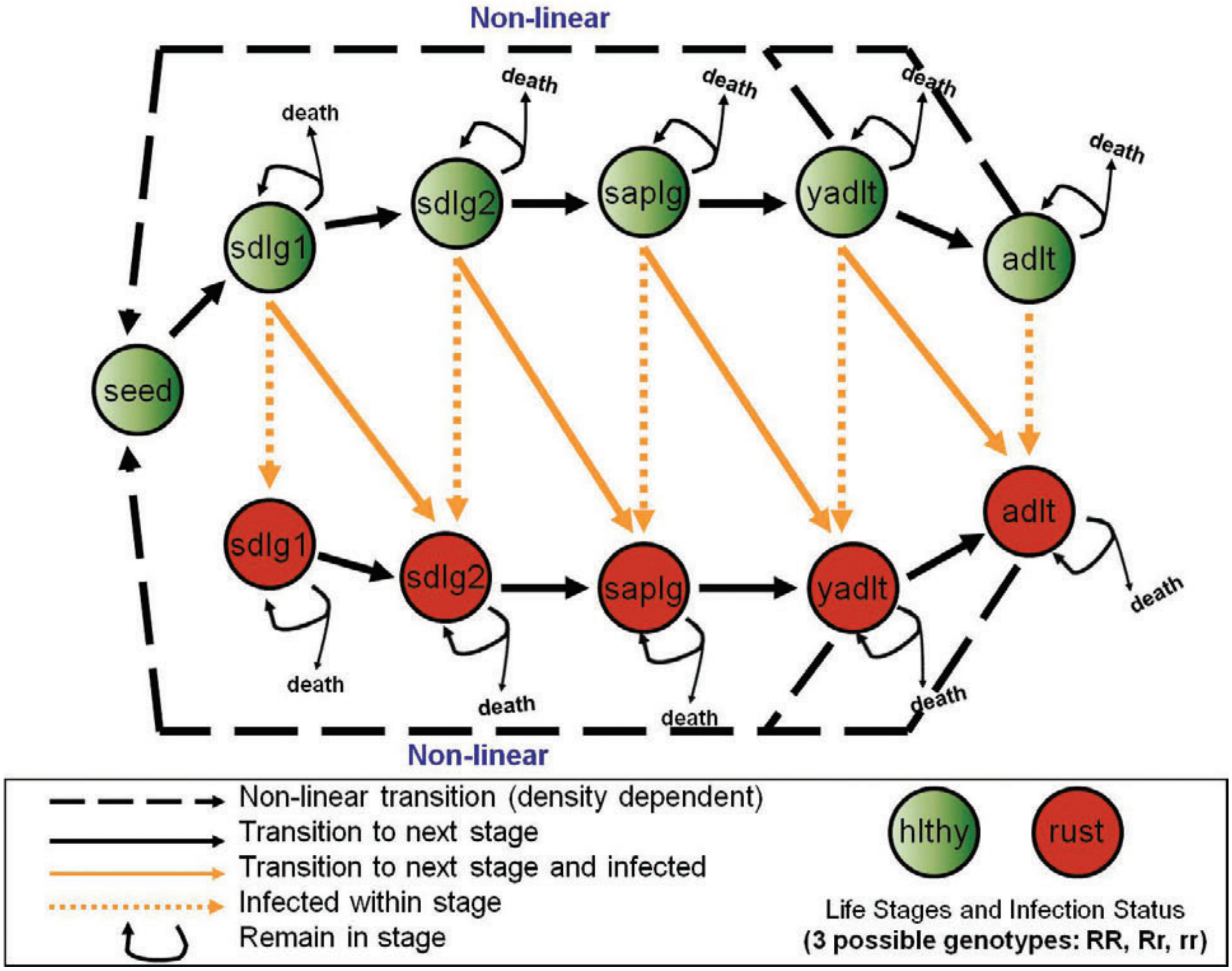

Figure 1. Schematic of the six age class population genetic model (adapted from Field and others, submitted). The six age classes (cohorts) are seeds, primary seedlings (sdlg1), secondary seedlings (sdlg2), saplings (saplg), young adults (yadlt) and mature adults (adlt). All age classes, except seeds, can become infected and transition into an infected class. Resistance is modeled for a simply inherited single dominant gene (R). The healthy cohorts (green) can be any of 3 genotypes (RR, Rr, rr) while only the susceptible genotype (rr) can be in the infected age classes (red).

that highlighted the interdisciplinary project to develop a dynamic economic model to evaluate efficient management of WPBR in high elevation ecosystems. Partial funding for this project was provided by USDA Economic Research Service Program of Research on the Economics of Invasive Species Management (PREISM; Award No. 58-7000-8-0096) and USDA Forest Service Rocky Mountain Research Station (Award No. 07-RJVA-11221616-252). We thank the PREISM Project team: Craig Bond, Patty Champ, Bill Jacobi, Cara Nelson and Richard Sniezko as well as Simon Tavener for helpful suggestions and discussions.

References

Schoettle, Anna W.; Sniezko, Richard A. 2007. Proactive intervention to sustain high elevation pine ecosystems threatened by white pine blister rust. Journal of Forest Research. 12 (5): 327-336.

Field, Stuart G.; Schoettle, Anna W.; Klutsch, Jennifer G.; Tavener, Simon J.; Antolin, Michael F. *Submitted.* Demograpic projection of high-elevation white pines infected with white pine blister rust: sensitivity analysis of a nonlnear disease model. Ecological Applications.

Ex Situ Gene Conservation in High Elevation White Pine Species in the United States—A Beginning

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Overview

The eight white pine species native to the western United States face an array of biotic and abiotic challenges that impact the viability of populations or the species themselves. Well-established programs are already in place to conserve and restore *Pinus monticola* Dougl. ex D. Don and *P. lambertiana* Dougl. throughout significant portions of their geographic ranges. More recently, programs have been initiated for the other six species: *P. albicaulis* Engelm., *P. aristata* Engelm., *P. balfouriana* Grev. & Balf., *P. flexilis* James, *P. longaeva* D.K. Bailey, and, *P. strobiformis* Engelm. In December 2008, concerns about the future of one of these species, *P. albicaulis* (whitebark pine), led one group to propose 'Listing' of this species under the Endangered Species Act (Natural Resource Defense Council 2008); a status review of the species is now underway, and a 12-month petition finding is expected in July 2011 (U.S. Fish and Wildlife Service 2010).

Gene conservation activities provide a conduit to help ensure the genetic variation within a species is potentially available for future utilization. Preserving genetic variation is important because it provides the foundation for species to evolve and respond to challenges such as white pine blister rust (caused by the non-native, invasive fungal pathogen *Cronartium ribicola* J.C. Fisch.), mountain pine beetle (*Dendroctonus ponderosae* Hopkins), and a changing environment (including climate change). Until relatively recently, few seed collections had been made for the six high elevation white pine species, with only a limited number available for *ex situ* gene conservation. Seed collections are also required for studying neutral and adaptive genetic variation, including blister rust resistance. High mortality of *P. albicaulis* and *P. flexilis* from mountain pine beetle attack is occurring in several geographic areas (Schoettle and others 2008), and some *P. albicaulis* trees exhibiting rust resistance have already been lost in southern Oregon (Stubbs, personal communication; Jensen, personal communication). Seed collections or clone banking of these relatively rare parents can help preserve valuable material for future use.

Since 2000, interest in the high elevation species has increased and the USDA Forest Service successfully organized many additional seed collections for whitebark pine (coordinated by National Forest Systems & Forest Health Protection), limber pine (*P. flexilis*) and Rocky Mountain bristlecone pine (*P. aristata*) (coordinated by Rocky Mountain Research Station). In 2007 a USDA Forest Service national workshop on genetic conservation identified the nine white pine species native to the United States as a focal point for genetic conservation. Subsequent funding in 2008 and 2009 from Forest Health Protection and in-kind support from other branches of the Forest Service facilitated and accelerated several gene conservation activities, including individual tree seed collections of *Pinus albicaulis*, *P. aristata*, *P. balfouriana*, *P. flexilis*, *P. longaeva*, and *P. strobiformis* (table 1) and

Table 1. Individual tree and bulked seedlots collected in 2008 or 2009 as part of national gene conservation efforts for six high elevation white pine species.

Species		Area	Year	# Individual Tree Collections	# Bulked collections	# Sites
P. albicaulis	Whitebark pine	CA	2009	23	0	1
P. albicaulis	Whitebark pine	OR/WA	2009	276	0	33
P. aristata	Rocky Mountain bristlecone pine	CO	2008	95	9	9
P. aristata	Rocky Mountain bristlecone pine	CO	2009	79	5	5
P. balfouriana	Foxtail pine	CA	2009	44	0	2
P. flexilis	Limber pine	CA/NV	2009	46	0	2
P. flexilis	Limber pine	CO/WY	2008	44	6	7
P. flexilis	Limber pine	CO/WY/MT	2009	149	16	15
P. longaeva	Great Basin bristlecone pine	CA	2009	22	0	1
P. longaeva	Great Basin bristlecone pine	NV	2009	300	0	3
P. strobiformis	Southwestern white pine	NM	2008	54	0	3

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maintenance of small clone banks for *ex situ* conservation for *P. albicaulis* and *P. flexilis*. For several of these species, these were the first or among the first-ever substantial collections of seedlots from individual trees.

Additional and higher levels of support for gene conservation in 2010 has significantly increased the total number of collections as well as the extent of the range of these species for which seed collections are available for *ex situ* conservation. For some species such as *P. aristata*, collections are now available for much of its range, while for *P. flexilis* and *P. albicaulis* (with much larger geographic ranges) there are more gaps. Two of these six species are also of concern in Canada and one of them in Mexico (Tomback and Achuff 2010), so information exchanges between the U.S., Canada and Mexico will help strengthen the gene conservation efforts. Such seed collections will provide long-term archiving of the genetic diversity of these white pine species and provide opportunities for new and continuing studies that will expand our understanding of the patterns of genetic variation in adaptive traits, including resistance to *C. ribicola*. Some larger bulked collections for restoration efforts have also been made.

Summary of 2008 & 2009 Gene Conservation Activities

The USDA Forest Service national gene conservation workshop in 2007 'Genetic Conservation of US Forest Trees Threatened by Invasive Insects and Pathogens' provided the impetus for a coordinated national gene conservation effort for the white pine species. Since the Workshop, Species Profile Sheets (Genetics and Gene Conservation) have been completed for several of the white pine species and a range of activities have begun. These species profiles will be posted at one or more websites, including http://www.fs.fed.us/rm/highelevationwhitepines/ and www.fs.fed.us/r6/dorena. These profiles are compiled by a number of different people and are intended to be dynamic documents that will be updated as new information becomes available. Contact Richard Sniezko (rsniezko@fs.fed.us) or Anna Schoettle (aschoettle@fs.fed.us) for more information or updated information for the species profiles.

The 'seed money' (~$50,000/year) for gene conservation work in 2008 and 2009 was provided by Forest Health Protection (FHP). Most recipients were also able to leverage the FHP funds with other monetary and in-kind contributions. The gene conservation activities of 2008 and 2009 covered a range of species and locations (table 1). All groups submitting projects received at least partial funding in one or both years (including some work with eastern white pine, *P. strobus L*). The primary activity funded was cone collection, but clone bank maintenance and grafting tests were also included. Most collections were on Forest Service lands, but the Bureau of Land Management (BLM) has also chosen to participate and contribute seeds collected from their land. Additional seed collection efforts for these species or other white pines, funded through other avenues, are ongoing or have been started by the Forest Service, National Park Service, and Indian Nations. These efforts have primarily centered on evaluating white pine blister rust resistance or examining genetic variation in the species (table 2). It was fortunate that the species had a good cone crop in one or both years, greatly facilitating the collection of seed. The

Table 2. Current inventory of seedlots for six high elevation white pine species[a].

Species	Region or Province	# Individual Tree Collections	# Bulked Collections	TOTAL # indiv tree collections
P. albicaulis	Alberta	163	10	2457
	British Columbia	263	5	
	Interior West-NFS	1,020	51	
	Pacific SW-NFS	201	2	
	Pacific NW-NFS	810	30	
P. aristata	Interior West-RMRS	341	29	341
	Interior West-NFS	0	2	
P. balfouriana	Pacific SW-NFS	166	-	166
P. flexilis	Alberta	180	28	1034
	British Columbia	0	3	
	Interior West-RMRS	786	44	
	InteriorWest-NFS	1	11	
	Pacific SW-NFS	67	2	
P. longaeva	Pacific SW-NFS	22	0	337
	Pacific SW-PSW	315	0	
P. strobiformis	Interior West-FHP	88	3	88

[a] Numbers cited for each species represent information available via phone and email survey of programs, summer 2010. The amount of seed per seedlot varies and significant numbers of new collections are expected in 2010 or 2011 for several species. U.S. collections include seedlots from cooperators (Forest Service, National Parks, BLM, Tribes).

seed collections, to date, are an excellent beginning to the first nation-wide *ex situ* conservation program to safeguard the genetic resources of high elevation white pine species. The collections also provide an opportunity to learn more about adaptive genetic variation and blister rust resistance in these species. Some studies have already begun utilizing these collections (e.g., screening of *P. strobiformis* and *P. flexilis* families for resistance to blister rust); others are planned or awaiting funding. These collections will complement other seedlots collected on National Forest and other lands (BLM, National Park Service and Indian Nations).

The current plans for these collections include long-term gene conservation storage at the USDA's Agricultural Research Service National Center for Genetic Resources Preservation (ARS-NCGRP). Back-up and working Forest Service collection(s) will be retained by the collecting National Forest (usually at their regional forest genetics facility) or Research Station involved in the collection. Working collections may be used for gene conservation, blister rust resistance screening, and studies to examine genetic variation and the potential impacts of climate change, etc. Information on the collections will be entered into a central database.

The small prototype clone banks/orchards, such as the whitebark pine clone bank at Dorena GRC, will serve as an *ex situ* conservation resource as well as provide an area to more easily study the biology of the species, do control pollinations, and provide demonstration/education to schools and other groups interested in learning more about this species.

The extraordinary efforts put forth in the gene conservation work in just two years (2008 and 2009) have helped garner support for a significant increase in funds for gene conservation in 2010. These funds will bring about a significant increase in seed collections for several of the white pine species. There is potential for further funding in 2011. In addition to the U.S. efforts, additional collections of limber pine and whitebark pine are underway in 2010 in British Columbia and Alberta by government agencies there. Individual tree cone collections for gene conservation are anticipated for many areas in 2010 or 2011, including (partial listing): *P. albicaulis* (California, Oregon, Idaho, Montana, Wyoming, Washington, British Columbia, Alberta), *P. aristata* (Arizona, New Mexico, Colorado), *P. balfouriana* (California), *P. flexilis* (California, British Columbia, Alberta), and *P. longaeva* (California).

Acknowledgements

Cone collections and other gene conservation related activities can only be successful with planning and execution by numerous people. The assistance of numerous Forest Service personnel and contractors for help in cone collections is gratefully acknowledged. Information provided by a number of people in Canada and the U.S., including Tom Blush, Dave Kolotelo, Donna Palamarek, Cyndi Smith, John King, Mary Frances Mahalovich, Jodie Krakowski, Don Pigot, Jude Danielson, Jerry Hill, Annie Mix and Dana Perkins was used for table 2 and for projections of new seed collections for 2010. Angelia Kegley provided assistance with manuscript preparation and reviewed an earlier version of the document. We also thank Vicky Erickson and Tom Blush for their review of an earlier version of this paper.

References

Dorena Genetic Resource Center. (2010, July 26—last update). [Homepage of Dorena Genetic Resource Center, Forest Service, U.S. Department of Agriculture], [Online]. Available: http://www.fs.fed.us/r6/dorena/ [2010, September 30].

High elevation white pines. [Homepage of High elevation white pines], [Online]. Available: http://www.fs.fed.us/rm/highelevationwhitepines/index.htm [2010, September 30].

Jensen, Chris. 2010. [Email to Richard Sniezko]. September 15. USDA Forest Service, Deschutes and Ochoco National Forests.

Natural Resources Defense Council (2008, December 8—last update). A petition to list the whitebark pine as an endangered species [Homepage of Natural Resources Defense Council], [Online]. Available: http://docs.nrdc.org/legislation/leg_08120801.asp [2010, September 30].

Schoettle, A.W.; Burns, K. S.; Costello, S.; Witcosky, J.; Howell, B; Connor, J. 2008. A race against beetles: conservation of limber pine. Nutcracker Notes. 14: 11-12.

Stubbs, Donna. 2010. [Email to Richard Sniezko]. September 16. USDA Forest Service, Fremont-Winema National Forests.

Tomback, D.F.; Achuff P. 2010. Blister rust and western forest biodiversity: ecology, values and outlook for white pines. Forest Pathology. 40: 186-225.

U.S. Fish & Wildlife Service, Wyoming Ecological Services Field Office. 2010. 50 CFR Part 17 [Docket No. FWS–R6–ES–2010–0047] [MO 92210–0–0008] Endangered and threatened wildlife and plants; 90–day finding on a petition to list *Pinus albicaulis* (whitebark pine) as endangered or threatened with critical habitat. Federal Register 75(138):42033-42040, [Online]. Available: http://edocket.access.gpo.gov/2010/pdf/2010-17650.pdf [2010, September 30].

Comparison of Genetic Diversity and Population Structure of Pacific Coast Whitebark Pine Across Multiple Markers

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Abstract—Analysis of "neutral" molecular markers and "adaptive" quantitative traits are common methods of assessing genetic diversity and population structure. Molecular markers typically reflect the effects of demographic and stochastic processes but are generally assumed to not reflect natural selection. Conversely, quantitative (or "adaptive") traits can be associated with climatic or other environmental variables that drive natural selection, but may not reflect the past demographic processes, such as bottlenecks, post-glacial recolonization, and population isolation. The genetics of whitebark pine has been studied using both molecular markers and adaptive traits, but never from a common set of samples so that the results could be directly compared. In addition, previous studies have not included samples from the Olympic Mountains in northwestern Washington, the westernmost distribution of whitebark pine that is geographically isolated from the rest of the species range.

We have analyzed genetic diversity and population structure using isozymes (88 populations ~30 individuals/population), organelle DNA (88 populations, ~30 individuals/population for chloroplast DNA [cpDNA] and ~8 individuals/population for mitochondrial DNA [mtDNA]), and genomic DNA (13 populations that were a subset of the 88, 22-28 individuals/population). Seedling quantitative traits were assessed in a common garden (92 families from 50 locations), mostly in Oregon and Washington, including the Olympic Mountains. Genomic DNA was analyzed with amplified fragment length polymorphisms (AFLPs) from 13 locations which also were analyzed with isozymes and organelle DNA (cpDNA and mtDNA), and 10 of which also had seedling traits measured. Twenty-five sites had assessments of isozymes, organelle DNA and measurements on seedling traits.

The Olympic Mountain populations had lower genetic diversity and were differentiated from all other populations by isozymes, nuclear and organelle DNA. Genetic diversity varied by marker type but among non-Olympic populations was generally within the ranges reported in other studies. Among non-Olympic populations, there was only weak genetic structure based on isozymes separating the Oregon and Washington populations. Isozyme analysis distinguished two population "groups": the Olympics and everything else. Analysis of organelle and nuclear DNA showed more distinct population separation, with three "groups": the Olympics, Oregon and southwestern Washington, and northern and eastern Washington, although the locations of the boundaries among haplotypes varied by marker type. Populations also differed significantly based on seedling traits. Mean date of needle flush was more than 3 weeks later in southern Oregon populations than populations from northern Washington and British Columbia. Date of needle flush was strongly associated with several winter and spring temperature variables, growth was associated with winter temperature and fall and winter precipitation, and needle length was associated with spring and summer maximum temperature. The Olympic populations were not differentiated from other populations based on these quantitative traits. This result illustrates that information from neutral molecular markers and adaptive traits is complimentary but completely independent based different ecological and evolutionary processes. These results also show that Olympic peninsula populations are genetically distinct and warrant conservation. In combination, the results across multiple genetic markers indicate that seed can be moved within the northern and eastern parts of Washington, and within southwestern Washington and Oregon, but should not be moved between these regions. In addition, seed should not be moved into or out of the Olympic peninsula populations.

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The U.S. Forest Service's Renewed Focus on Gene Conservation of Five-Needle Pine Species

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Abstract—The U.S. Forest Service (FS) has been actively working with five-needle pine species for decades. The main focus of this interest has been in restoration efforts involving disease-resistance screening activities in western white (*Pinus monticola*), sugar (*Pinus lambertiana*), and eastern white (*Pinus strobus*) pines in the face of white pine blister rust (WPBR), caused by the non-native invasive pathogen, *Cronartium ribicola*. There has also been some effort in whitebark pine (*Pinus albicaulis*) and limber pine *(Pinus flexilis)* disease-resistance work, but to a lesser degree. Recently the FS has been actively pursuing a gene conservation effort in whitebark, Rocky Mountain (RM) bristlecone (*Pinus aristata*), southwestern white (*Pinus strobiformis*), foxtail (*Pinus balfouriana*) and limber pines to conserve germplasm as a result of increased mortality from WPBR, mountain pine beetle (*Dendrotonus ponderosae*) (MPB) and the warming effects of climate change. This paper will describe the renewed focus of gene conservation of these iconic species.

Currently, we are experiencing the worst epidemic in recorded history of MPB, a native insect. About 8.8 million acres had some level of mortality in 2009. Part of this current epidemic is the result of large, relatively even-aged homogeneous forests of susceptible lodgepole pine (*Pinus contorta*) that are mature and have thus become beetle-prone. In addition, the warming effects of a changing climate have resulted in MPB being able to survive winters that aren't as cold as they used to be. This warming effect has allowed beetles to attack high elevation tree species that normally were not affected. The combined effects of WPBR, MPB and the effects of climate change have resulted in many high-elevation five-needle pine forests of whitebark, limber, foxtail and RM bristlecone pine being heavily impacted.

In 2007, the Forest Health Protection (FHP) Program developed a framework for gene conservation to save seed of these important species for later replanting. The "Forest Service General Framework for Genetic Conservation of US Forest Tree Species" is a multi-step plan that includes assessment and planning activities, as well as outlining pertinent actions that need to occur to conduct proper gene conservation efforts. We used the Framework for four species or groups of species that were at risk from various pests or climate change. These include ash (*Fraxinus* sp.) (at risk from emerald ash borer), butternut (*Juglans cinerea*) (at risk from butternut canker), eastern hemlock (*Tsuga canadensis*) and Carolina hemlock (*Tsuga caroliniana*) (at risk from hemlock woolly adelgid, *Adelges tsugae*) and the five-needle pine species group. In this paper I focus strictly on the activities concerning the five-needle pine group.

A group of specialists assembled a plan for gene conservation of four species of five-needle pine (whitebark, limber, foxtail and RM bristlecone pine). Using existing seed zones and expert judgment about ecological and genetic differentiation, a target of about 2830 individual trees was established to cover these four species. With good cone crops in 2008 and 2009 and acceptable cone crops in 2010, extensive collections were made and are discussed elsewhere in this proceedings. At this juncture, we have collected about 1350 trees (families). We are storing the seed in FS facilities, as well as establishing back-up collections at the Agricultural Research Service National Center for Genetic Resources Preservation (ARS-NCGRP) facility in Fort Collins, CO.

This stored seed will allow for the re-establishment of populations of these species, as needed, in the future. This seed provides a representative sample of conserved material tied to current seed zones of each species. Conceivably, in the future we will need/want to use the seed to re-establish plantations or seed orchards through seedlings or vegetative propagation of the material.

We are linking these *ex situ* gene conservation efforts with ongoing restoration efforts taking place within the FS. These restoration efforts include screening trees for resistance to WPBR, reforestation efforts planted with WPBR-resistant seedlings, pruning western white pine plantations, prescribed burning of sites to promote regeneration of whitebark pine, etc.

We will continue to collect seed, as cone crops permit, of the four species of five-needle pines in order to meet our initial goal of 2830 families. Afterward, other activities will be contemplated. These might include collecting more seed of these species or collecting other at-risk tree species.

Our hope is that we will never really need this collected material because we hope the existing populations are resilient enough to adapt and survive long into the future. However, it's a good policy to hedge our bets in these uncertain times and have at least *ex situ* genetic resources available for future reforestation needs if needed.

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Geographic Patterns of Genetic Variation, Population Structure and Adaptive Traits in *Pinus aristata*, Rocky Mountain Bristlecone Pine

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Abstract—*Pinus aristata* Engelm., Rocky Mountain bristlecone pine, has a narrow geographic and elevational distribution and occurs in disjunct mountain-top populations throughout Colorado and New Mexico in its core range. The species' unique aesthetic and ecological traits combined with the threats of the exotic disease white pine blister rust (WPBR), climate change in high elevation systems, and an outbreak of a native bark beetle make *P. aristata* of conservation interest, however, little is known about the species genetic structure or adaptive capabilities. Genetic diversity is the foundation for a population's adaptive capacity and knowledge of genetic diversity, population structure and geographic distribution of quantitative traits for this species will help guide gene conservation strategies and evaluation of risk among geographic regions. *Pinus aristata* seeds were collected in 2001 from 200 individual trees from 11 sites throughout Colorado; growth and phenology were measured in 2004 on two-year-old seedlings in a common garden setting. Genetic differentiation among sites was high for growth phenology but weak for duration of growth. Some growth traits were correlated with latitude of the source material yet elevation did not explain significant variation. Source elevation was not a strong correlate with growth traits yet did explain variation in mid-winter cold hardiness. Genetic diversity was further assessed using 21 isozyme loci from 615 samples from 16 sites across 4 mountain ranges in the core distribution of *P. aristata*. The genetic diversity of *P. aristata* was generally lower than measurements of other long-lived woody perennials or other five-needle pine species, while among-population genetic variation was comparatively higher. Genetic diversity was not randomly distributed across the landscape and both sites and mountain ranges showed evidence of sub-structuring, isolation and inbreeding. The combination of low genetic diversity, high population isolation and a very protracted regeneration dynamic for *P. aristata* puts populations at risk for extirpation by novel stresses. We recommend that gene conservation strategies for *P. aristata* include sampling the full range along the latitudinal gradient, with more intensive sampling focused in areas with higher genetic diversity. Following these recommendations, a rangewide seed and tissue conservation effort for *P. aristata* is nearly complete and is expected to have captured the genetic diversity of the species before it has been constrained by WPBR invasion and the recent climatic warming trends.

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Disturbance Ecology & Climate Change

Disturbance Ecology of High-Elevation Five-Needle Pine Ecosystems in Western North America

Plenary Paper

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Abstract—This paper synthesizes existing information about the disturbance ecology of high-elevation five-needle pine ecosystems, describing disturbances regimes, how they are changing or are expected to change, and the implications for ecosystem persistence. As it provides the context for ecosystem conservation/restoration programs, we devote particular attention to wildfire and its interactions with mountain pine beetle (*Dendroctonus ponderosae* Hopkins) outbreaks and white pine blister rust (*Cronartium ribicola* J.C. Fisch.).

Patterns of fire disturbance and post-fire regeneration in high-elevation five-needle pine ecosystems are highly variable over space and time. While stand-replacing fires predominate in some regions, mixed severity fire regimes that include low intensity surface fires and crown fire components, appear most common. Fire disturbance provides critical regeneration opportunities for most high-elevation five-needle pines but fire exclusion over the last century is having some impacts—such as major declines of whitebark pine (*Pinus albicaulis* Englem). Historic mountain pine beetle outbreaks caused episodes of mature high-elevation five-needle pine death over large regions. While these pines have adapted to this historic pattern of disturbance, global climate change is causing the geographic expansion of beetle outbreaks that are killing high-elevation pines in places with no history of major impacts. Expanding beetle outbreaks and exotic blister rust infections, which continue to intensify and spread into the southernmost geographic range of high-elevation five-needle pines, reduce the density of seed bearing trees and hasten succession. Global climate change may also generate more frequent severe fires. This may pose a threat to some pines and generate regeneration opportunities for others, provided beetle outbreaks and blister rust have not reduced the density of seed-bearing trees below critical thresholds.

High-elevation five-needle pine ecosystem responses to disturbance are complex and while there is still much to learn, management efforts are moving forward to conserve and restore these critical components of mountain landscapes. Given the complexity and uncertainty of ecosystem response to disturbance, a cautious yet proactive approach to management will be necessary to build ecosystem resilience to future disturbances, whether natural or human-caused.

Introduction

Disturbances are key natural components of forest ecosystems. Variation in the type, timing and severity of disturbances generate forest heterogeneity, which is linked to biodiversity and ecosystem resilience to subsequent perturbations and environmental change (Gunderson and others 2009). However, substantial alterations to historical disturbance regimes—the type, timing and severity of disturbances—can compromise the capacity of ecosystems to recover from disturbance and persist on landscapes. Human interactions with ecosystems are the primary cause of recent major changes in disturbance regimes.

In western North America, land use activities (including wildland fire management, livestock grazing, logging and planting patterns), global climate change caused by increased greenhouse gas emissions, and introduction of the Eurasian white pine blister rust fungus (*Cronartium ribicola* J.C. Fisch.) are altering historical disturbance regimes and threatening the persistence of high-elevation five-needle (high-five) pine ecosystems dominated by whitebark pine (*Pinus albicaulis* Englem.), limber pine (*P. flexilis* James), Rocky Mountain bristlecone pine (*P. aristata* Engelm.), Great Basin bristlecone pine (*P. longaeva* D.K. Bailey), foxtail pine (*P. balfouriana* Grev. & Balf.), and southwestern white pine (*P. strobiformis* Engelm.) (Campbell and Carroll 2007; Keane 2001; Tomback and Achuff 2010). In this paper, we synthesize existing information about the disturbance regimes of high-five pine ecosystems and describe how they are changing or are expected to change. We devote particular attention to the importance of wildfire and its interactions with other major disturbances—mountain pine beetle (*Dendroctonus ponderosae* Hopkins) outbreaks and the white pine blister rust epidemic—since this provides most of the context for interpreting threats to high-five pine decline and the design of ecosystem conservation and/or restoration programs.

Fire Disturbance

Fire is a component of the disturbance regimes of most high-five pine ecosystems. We currently know the most about fire disturbance in the whitebark pine ecosystem, which is more widely distributed than any of the other high-five pine ecosystems. The presence of charcoal in lake sediment cores from the northern U.S. Rocky Mountains indicates that fires burned in areas supporting whitebark pine for at least the past 14,000 years (Brunelle and Whitlock 2003; Minckley and others 2007). Tree-ring studies, which provide more temporally precise information about fires over the last several hundred years, indicate complex and highly variable fire regimes in space and time. Severe stand-replacing,

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Figure 1. Evidence for past fires in whitebark pine forests including a) fire-scarred whitebark pine trees indicative of surface fires, b) charred remnant wood, and c) dense, post-fire cohorts of whitebark pine indicative of stand-replacing fires. Photos by E. Larson.

partial-stand replacing and low-severity surface fires all occur in whitebark pine ecosystems with mean fire-return intervals ranging from 13 to 400+ years (figure 1, table 1). Mixed-severity fire regimes, which are very common in whitebark pine ecosystems, include low intensity surface fire and crown fire components that typically create complex patterns of tree death and survival in stands and over landscapes (Murray and others 1998; Romme and Knight 1981). Burned patches typically range from 1 to 30 ha in size, depending on weather, topography and fuel connectivity (Norment 1991; Tomback and others 1993). Large stand-replacement fires occur within mixed-severity fire regimes but as infrequent events that often originate in lower elevation forests and move to whitebark ecosystems when weather conditions facilitate fire spread (Morgan and Bunting 1990; Murray and others 1998). In dense mixed-conifer subalpine forests, which are most extensive in the U.S. Rocky Mountains and in mountain ranges of British Columbia, whitebark pine fire regimes are often characterized by large stand-replacement fires occurring over long time intervals (250+ years) (Campbell and Antos 2003; Romme 1980).

With somewhat thicker bark, higher and thinner crowns, and deeper roots, whitebark pine is better adapted to survive low intensity surface fires than its shade-tolerant competitors (Morgan and others 1994). When surface fires are relatively frequent, mature cone-bearing whitebark pine survive fires that generally kill competing species, such as subalpine fir (*Abies lasiocarpa* [Hook.] Nutt.) and Engelmann spruce (*Picea engelmannii* Parry ex. Engelm.), which have denser canopies that typically extend to the ground. Such disturbances delay the successional process (Keane 2001) typically producing stands with fire-scarred whitebark pine and multiple post-fire cohorts of this species (figure 2). Whitebark pine is also well adapted to severe, large stand-replacing fires because the Clark's nutcracker (*Nucifraga columbiana* Wilson) can disperse whitebark pine seeds up to 100 times farther (over 10 km) than wind can disperse the seeds of its major competitors (Tomback 2005). As such, the species can more readily colonize large burned areas and seedlings can grow without competition for some time unless lodgepole pine—with predominantly serotinous cones—were a significant component of the pre-burned stand (Campbell and

Table 1. Tree-ring studies reporting fire-return intervals for whitebark pine forests (modified from Arno 2001).

Fire-free interval (yrs)	Methods	Geographic area	Source
13–46	Fire-scar and age-structure analyses	Russell Peak, Wyoming	Morgan and Bunting 1990
19–350+	Fire-scar and age-structure analyses	Lolo National Forest, Montana	Larson and others 2009
20–173	Fire-scar and age-structure analyses	Selway-Bitterroot Wilderness, Montana/Idaho	Kipfmueller 2003
57–94	Fire-scar and age-structure analyses	Bitterroot Valley, West Montana	Arno 1980; Arno and Petersen 1983
50–119	Fire-scar and age-structure analyses	Big Hole Range, Montana/Idaho	Murray and others 1998
47–250+	Fire-scar and age-structure analyses	Cascade Range, Oregon/Washington	Siderius and Murray 2005
55–304	Fire-scar and age-structure analyses	Bob Marshall Wilderness, NW Montana	Keane and others 1994
80–300	Age-structure analysis	Yellowstone National Park, Wyoming	Mattson and Reinhardt 1990
66–>350	Fire-scar and age-structure analyses	Yellowstone National Park, Wyoming	Barrett 1994
300–400	Fire-scar and age-structure analyses	Yellowstone National Park, Wyoming	Romme 1982

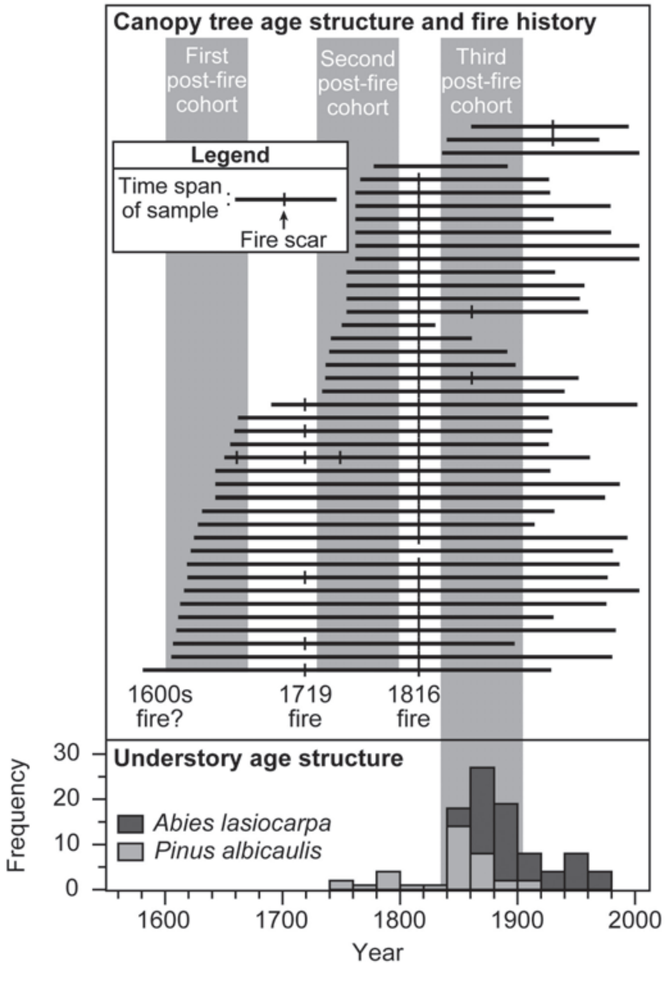

Figure 2. Age structure and fire history of a whitebark pine forest on Point Six, near Missoula Montana. The lack of fire since the widespread 1816 fire event likely reflects the effects of fire suppression on this forest. Also note that subalpine fir was establishing in this forest within one decade of the most recent widespread fire. Restoration plans have been developed for the whitebark pine forests on Point Six. For more detail about fire on this site, see Larson and others 2009.

Antos 2003; Kipfmueller and Kupfer 2005). However, in the upper subalpine zone, generally beyond the altitudinal limits of lodgepole pine, crown fires commonly leave scattered unburned patches that serve as important biological legacies, resulting in subalpine fir and Engelmann spruce colonizing burns synchronously with whitebark pine (Campbell and Antos 2003). Fire disturbance is less important near the timberline or on dry sites where whitebark pine's tolerance to harsh environments permits it to thrive in places other subalpine tree species cannot. Much of what we know about the fire ecology of whitebark pine ecosystems comes from research in the U.S. and southern Canada. Information from the northern part of the range, in Canada, is sparse; however preliminary data (Haeussler and others 2009; Clason and others 2010) suggest that patterns of whitebark pine response to fire disturbance are broadly similar to the patterns described above.

Our knowledge about the fire ecology of other North American high-five pine ecosystems is limited and needs further study. A few studies report mixed-severity fires regimes for high-five pine ecosystems dominated by limber pine, Rocky Mountain bristlecone pine and Great Basin bristlecone pine in Colorado, Nevada and Utah, with mean fire return intervals ranging from 11 to 129 years (Brown and Schoettle 2008; Coop and Schoettle 2009; Kitchen 2010). On an isolated desert mountain range in Arizona, frequent low-intensity surface burns dominate a mixed-severity fire regime in southwestern white pine ecosystems—mean fire return intervals range from 4 to 22 years (Iniguez and others 2009). Fire disturbance is considered rare in the driest southern U.S. landscapes where Great Basin bristlecone pine, foxtail pine and limber pine dominate dry, rocky ridges; and, when fires do occur, they are usually small and of low severity due to sparse fuels. Caprio and Lineback (2002) report mean and maximum fire-return intervals in foxtail pine ecosystems as 187 and 580 years, respectively. Like whitebark pine, fires scars have been found on all other high-five pine species, indicating that they can also survive low-intensity surface fires (Iniguez and others 2009; Brown and Schoettle 2008; Kitchen 2010; Ryerson 1983).

Mounting evidence suggests temporal variations in fire activity are linked to natural global ocean-atmospheric processes. The El Niño/Southern Oscillation (ENSO), the Pacific Decadal Oscillation (PDO), and the Atlantic Multidecadal Oscillation (AMO) may influence patterns of drought occurrence from regional to continental spatial scales, and from seasonal to multidecadal temporal scales, synchronizing fire activity over large areas (McCabe and others 2004; Skinner and others 2006). Recent studies report more frequent severe fires in subalpine forests in western Colorado during cool phases of the PDO and ENSO and warm phases of the AMO (Schoennagel and others 2007). However, the relative influence of these natural phenomena may vary spatially and even reduce fire activity in subalpine forests of other regions. The influence of ocean-atmospheric oscillations on regional climate and linkages to fire activity remains an active area of research.

Human land use activities can also influence temporal patterns of fire activity. Since the early 1930s, fire suppression programs in the U.S. have successfully limited the extent of wildland fire in many western North American ecosystems (Keane and others 2002). Information about the effects of fire exclusion policies on high-five pine ecosystems come from two different kinds of studies in the U.S.: stand-level tree-ring analyses and landscape-level assessments. Using fire scar and tree age data, some stand-level tree-ring studies readily detect a reduction in fire activity that could be attributed to fire suppression management (Brown and Schoettle 2008; Buechling and Baker 2004; Kitchen 2010; Larson and others 2009; Murray and others 1998; Sherriff and others 2001). However, because tree-ring studies are labour intensive work, many are based on too few samples (that is, stands) to make definitive conclusions about the effects of fires suppression across landscapes. Moreover, while they can detect the effects of fire suppression in regions where frequent surface fires were historically common, in moist/cool regions where fire return intervals are longer, the effects of fire suppression are not yet manifest at the stand-level and generally not yet detectable. In these regions, the effects of fire suppression can be examined at the landscape-level by assessing areal extent of early to mid-seral pine stands and increases in late-seral stands in high-elevation landscapes (Keane and others 1994). Using this approach, Keane (2001) reported that a major reduction in high-elevation fires since about 1929 has led to the successional replacement of whitebark pine by subalpine fir on the most productive sites in parts of its range. Although subalpine fir communities currently comprise about 12-22 per cent of the landscapes in the Bob Marshall Wilderness Complex (Keane and others 1994), modelling efforts estimated that historical landscapes in this area had 3-13 per cent late-seral subalpine fir stands. Similarly, Murray and others (2000) show that nearly 50 percent of the landscape has shifted to late successional stands over the last 250 years in the Big Hole Range of Idaho and Montana.

In Canada, fire suppression programs have been effective reducing the extent of forest area burned since the late 1950s (Cumming 2002). However, very little information is available about the effects of fire exclusion policies on high-five pine ecosystems. While there has been a tendency to let fire burn in remote locations of Canada, this is most common in boreal forest zones north of the geographic range of high-five pines. A summary of fire data for British Columbia, indicated a clear decrease in the extent of fire in subalpine zones where whitebark pine occurs (Campbell, unpublished data). Given these data, we expect fire exclusion policies are having the same impacts on high-five pines in Canada as they are in the U.S.

There is much yet to learn about the fire ecology of high-elevation five-needle pine ecosystems and the effects of fire suppression. Some analogies can be drawn from high-elevation pine ecosystems of Eurasia. For example, Cembran pine (*Pinus cembrae* L.), which shares many life-history traits with the taxonomically similar North America high-elevation pines, currently occurs as fragmented populations in mountain landscapes where fire has been suppressed for centuries. During the Holocene, when the climate was warmer and fire disturbance was more frequent, Cembran pine was much more abundant, even in valleys and above the current timberline (Ali and others 2005). Moderately frequent surface fires, which promote Cembran pine regeneration (Genries and others 2009a), resulted in the expansion of Cembran pine forests, while very frequent fires occurred to the detriment of the species (Genries and others 2009b).

Other Disturbances and Interactions With Fire

High-elevation pines are subject to damaging agents other than fire—such as localized insect infestations of *Ips* spp. bark beetles (Campbell, unpublished data) or the pine leaf adelgid (*Pineus pinifolia*, Fitch) (Woods, unpublished data) and dwarf mistletoe infections (Mathiasen and Daugherty 2001; Mathiasen and Hawksworth 1988)—but mountain pine beetle (MPB) outbreaks and the introduced white pine blister rust (WBPR) fungus are the only other major disturbances. All high-five pines are currently being attacked by MPB (see Bentz and others, this proceedings) with the most beetle-caused deaths during this outbreak occurring among whitebark, limber and Rocky Mountain bristlecone pines (Gibson and others 2008). Over the last several decades, WPBR has caused widespread pine decline and death throughout most of the geographic range of whitebark pine and limber pine, and in all but the western extent of southwestern white pine's range (Campbell and Antos 2000; Schoettle and Sniezko 2007; Smith and others 2006). WPBR is currently limited to a small portion of Rocky Mountain bristlecone pine's range and it has yet to be found on Great Basin bristlecone pine (see Tomback and others, this proceedings), presumably because the arid climate of these regions slows infection. However, the disease continues to spread and it is expected to intensify wherever five-needle pines occur (Schoettle and Sniezko 2007). Most of the context for interpreting high-elevation five-needle pine ecosystem decline, and its conservation, come from understanding the interactions among these three major disturbances: fire, MPB, and WPBR.

In many areas, whitebark pine deaths caused by MPB outbreaks and concurring WPBR hasten forest succession, converting pine stands to forests dominated by the shade-tolerant conifers, such as subalpine fir, Engelmann spruce (Jackson and Campbell 2008; Keane 2001; Kipfmuller and Kupfer 2005). This, in turn, increases the potential for high-severity crown fires because of greater canopy bulk densities and multi-layered canopy of spruce-fir forests (Reinhardt and others 2006). These high severity fires then kill most of the whitebark pine that survived past MPB outbreaks and were potentially blister rust-resistant trees. Continued rigorous management to suppress wildland fire may result in the same cycle of spruce-fir dominance fostering large, crown fires, particularly in mesic forests where severe fires were more common historically (Keane and others 2002). While not well studied, the same interactions among fire, MPB and WPBR might be expected in mesic forests where other high-five pines occur as seral species in mixed forests, particularly among the high-five pines that depend almost entirely on nutcracker to disperse seed. In northern British Columbia, however, where MPB have killed whitebark pine and balsam bark beetle (*Dryocoetes confusus*, Swaine) infestations that have killed subalpine fir, stands are succeeding to shade-tolerant mountain hemlock (*Tsuga mertensiana*, [Bong.] Carr.) (Clason and others 2010), which would generate stands with similar canopy fuels a tendency for crown fires.

Wildland fire disturbance is pivotal to the persistence of some high-five pine ecosystems. Newly burned patches provide regeneration opportunities for these shade-intolerant species. Burns can be colonized by seed from putatively blister rust-resistant pines in nearby maturing forests where pines are at increasing risk of loss due to other pests and pathogens, wildfire or successional replacement. When seed sources are plentiful in the landscape, due to high rust resistance or low rust incidence, wildfire disturbance stimulates regeneration and efficient natural selection for rust resistance (Hoff and others 1976; Schoettle and Sniezko 2007). However, if the density of seed-bearing trees is low (that is, tree basal area < 5 m^2/ha), due to blister rust, successive MPB outbreaks and decades of fire suppression, colonization of open habitat may be limited by inadequate seed, limited nutcracker dispersal, and a relative increase in the rate of seed predation by nutcrackers and squirrels (Haeussler 2010; Larson 2009; McKinney and others 2009). By generating a forest landscape mosaic with diverse age class and patch structures, fires also facilitate ecosystem resistance to subsequent disturbances. For example, given that the beetle rarely attacks small pine trees, young, fire-originated pine stands generally persist in landscapes during beetle population outbreaks and a sufficient proportion of young stands in landscapes could prevent catastrophic losses of pine during MPB outbreaks (Li and others 2005). Some forest patches created by previous fires could also act as fire-breaks and reduce the likelihood of the severity of future fire impacts.

It is often presumed that MPB outbreaks increase the likelihood and intensity of crown fire disturbances because they increase forest fuels. However, studies about the interaction between MPB outbreaks and fire have yielded mixed results. Jenkins and others (2008) report an increase in surface fire intensity due to an increase in fine surface fuels (for example, pine needles). However, these studies could not determine if increased surface fire intensity would lead to more severe crown fires. Some argue that the increased risk of intense fires following MPB outbreaks is short-lived (as fine fuels quickly decompose) and fire risk decreases again until later successional stages when shade-tolerant species, such as spruce and subalpine fir, grow to fill the gaps left by dead pines and increase crown fire risk (Lynch and others 2006). Most recently, Simard and others (2011) found that the interaction between fire and MPB outbreaks is the opposite of what is widely presumed; rather than increase the probability high intensity crown fires, outbreaks decrease crown fire risk in the short term by thinning pine forests. Studies conducted following the last MPB outbreak report similar findings (Despain 1990; Schmid and Amman 1992). While these studies focus predominantly on lodgepole pine (*Pinus contorta,* Dougl.) forests, we expect they can be applied similarly to subalpine forests containing high-elevation five-needle pines. In fact, many sites dominated by high-elevation pines are probably at even lower risk of crown fires following MPB outbreaks because of their more open canopies.

In regions where fire disturbance is infrequent, bark beetle outbreaks may play a more important role in high-elevation pine regeneration dynamics. For example, in southern Alberta, MPB and *Ips* spp. outbreaks create forest gaps that facilitate self-perpetuation of whitebark pine in subalpine forests (Wong and others, submitted). This historic role for bark beetle outbreaks has also been suggested for whitebark pine forests in Montana (Larson and others 2009; Larson and Kipfmueller 2010) and for lodgepole pine forests in Oregon (Stuart and others 1989). Similar to wildfire disturbance, MPB outbreaks may provide regeneration opportunities that facilitate natural selection of blister rust-resistant whitebark pine (Larson, in press).

High-elevation pines are often considered more susceptible to attack by MPB when they are stressed by WPBR infections. However, while WPBR infections appear to make pines more susceptible to attack by MPB when beetles are at endemic population levels (Six and Adams 2007), during population outbreaks, there is no correlation between WPBR infection and susceptibility to beetle infestation. During outbreaks, beetles kill mature pines regardless of vigor or health (Bockino 2008; Jackson and Campbell 2008).

Global Climate Change

Global warming has the potential to significantly impact high-elevation pine ecosystems. Like all species, high-five pines respond to environmental changes by adapting *in situ* or by migrating to more suitable habitat. Despite moderate levels of genetic diversity, many wonder if temperate trees species can rapidly adapt—given their long generation times—or migrate at a sufficient pace to keep up with rapid climate change (Aitken and others 2008).

Bioclimatic envelope models, which quantify relationships between climate and a species occurrences, project dramatic reductions in the geographic distribution of climatically suitable habitat for whitebark pine over the next century (Hamman and Wang 2006; Warwell and others 2007) and similar results could be expected for other high-five pines. Warwell and others (2007) speculate that increasing temperatures could "push" whitebark pine off mountains by moving its lower elevational limits above the tallest peak. Conventional wisdom suggests that this would occur because less cold-hardy, shade-tolerant conifer species would establish more abundantly and out-compete whitebark pine at high elevations where it currently dominates (Koteen 1999).

Interpretations about the persistence of high-five pines from bioclimate envelope models, however, are not simple because climate influences a complex array of multi-scaled, interacting ecological processes that determine species ranges, not all of which are captured with these modelling techniques (Araujo and Guisan 2006). More information about the constraining effects of local topoedaphic conditions on climate change impacts will be important to high-five pine conservation efforts in a changing climate (Lafleur et al. 2010; Mbogga and others 2010; Hof and others 2011). For example, we may expect high-elevation five-needle pines to remain free of competition and persist on sites with shallow soils (including rock outcrops) despite climate change. In addition, a greater understanding of the potential effects of climate change on growth, regeneration processes, and dispersal rates, which may come from mechanistic models, can also provide insights into the management of high-five pines in a changing climate. For example, recent mechanistic modelling work in British Columbia, which considers frost and drought thresholds, suggests decreased whitebark pine seedling survivorship could contribute to range reductions (Nitschke and Campbell, in prep.).

Most major ecosystem changes caused by global climate change will likely be precipitated by shifts in disturbance regimes (Dale and others 2001). Such shifts have already been observed in high-five pine ecosystems. For example, current mountain pine beetle outbreaks are killing more whitebark pine, and probably other high-five pines, than at any time in the historical record, and this trend is expected to continue to the end of the century as warmer winter temperatures facilitate the survival and reproduction of beetles in high-elevation zones (Bentz and others, this proceedings; Campbell and Carroll 2007; Logan and Powell 2001) (figure 3). Although many suggest that a warmer climate would accelerate the spread of blister rust where temperature is limiting (Koteen 1999), increased aridity in other regions may retard the spread and intensification of WPBR infections (Boland and others 2004).

A warmer climate may also increase in frequency and size of wildfires (Keeton and others 2007; Ryan 1991; Running

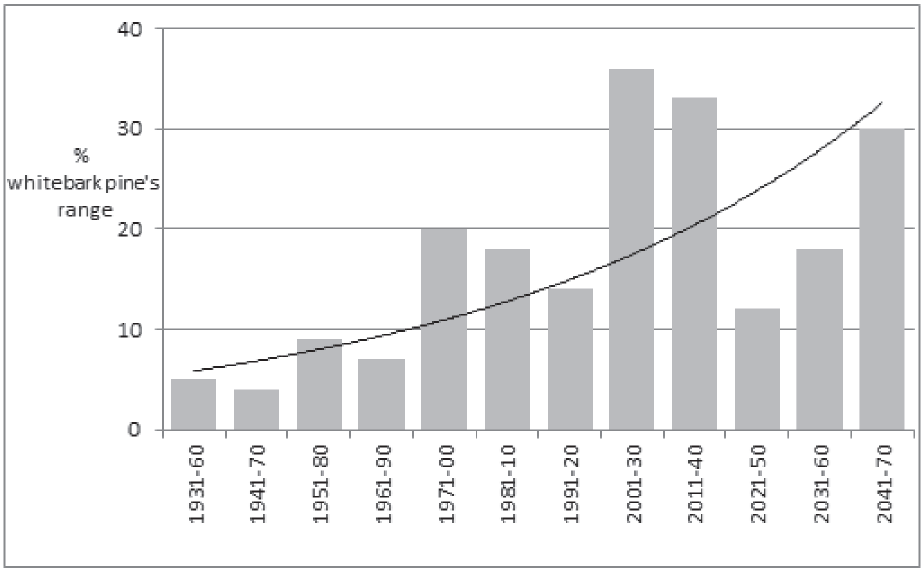

Figure 3. Historical and future projections indicating the percentage of whitebark pine's range in British Columbia that is climatically suitable habitat for mountain pine beetle. Beetle outbreak risk is high in these areas. Indices of climatically suitable habitat were calculated for each map pixel based on climate threshold values for critical beetle life-stages (see Carroll and others 2006). Weather station data were used to calculate historical climate suitability indices and the Canadian Global Climate Model (CGCM), for a mid-range climate change scenario (A2), was used to project indices of climate suitability into the future. Indices were calculated for 30-year normal periods. Classes of climatically suitable habitat were derived from indices and mapped. The range of whitebark pine was then overlayed on these maps to calculate percentage of the range where outbreak risk is high.

2006). While an increase in fire size frequency and size may pose a threat to southern high-five pines with limited and isolated geographic ranges, it may benefit other pines, for example, whitebark pine (Loehman and Keane, in prep). Provided that sufficient seed sources remain on the landscape, and that microsites favouring establishment exist (Moody 2006), whitebark pine populations could increase as a result of increased fire activity. Coincidently, increased fire activity that generates more young pine stands on landscapes could reduce the impact of future MPB outbreaks.

While disturbance rates are expected to increase with climate change, high-five pines may possess some capacity to adapt to changed disturbance regimes and persist in landscapes as the climate changes, particularly with some proactive management. Variability in high-five pine responses to current disturbance agents—including variability in responses to MPB outbreaks due to site, stand age, and genetics, or variability in the incidence and timing of blister rust deaths due to genetic resistance and tree size (Jackson and Campbell, 2008; Hof and others 2011; Jewett 2009; Schoettle and Sniezko 2007; Wong and others, submitted; Yanchuk and others 2008)—can provide insights and guide management actions to minimize disturbance impacts in a rapidly changing climate. High-five pine species with limited geographic ranges are likely most vulnerable to the increased frequency and extent of disturbances expected to accompany global climate change.

The effects of global climate change could be severe for high-five pine ecosystems. However, not only is the degree of future climate change uncertain, the response of high-five pine ecosystems to climate change are complex and difficult to predict. As such, the potential for major climate change effects should not be used as an excuse for not implementing restoration projects (Hobbs and Cramer 2008), but it could guide the choice of restoration activities used over the range of high-five pines, with differing activities occurring in some climatic regions or on some sites.

Management

The exotic white pine blister rust, wildfire suppression, MPB outbreaks, and global climate change are causing a rapid decline of whitebark pine and posing serious threats to other high-five pines. Management to stem the threats to high-five pine ecosystems is essential and described in greater detail throughout this proceedings (for example, see Schoettle and others, and references therein). Management can take two complementary approaches: targeted actions to minimize the impacts of on-going disturbances, and proactive management that enhances ecosystem resilience to future disturbances, natural or human-caused.

In the short term, targeted efforts could be used to protect highly-valued trees, or small groups of trees during a disturbance. If pines are not resistant to blister rust, pruning blister rust cankers from individual trees can prolong their life (Burns and others 2008). During MPB outbreaks, applying insecticides or treating putatively blister-rust resistant trees with verbenone will protect seed sources and the genetic material needed to develop rust-resistance strains of high-five pines (see Bentz and others, this proceedings). During slow moving lightning-ignited fires, actions can also be taken to protect pine seed sources from the fire. In 2006, during the Bybee fire at Crater Lake National park (OR), crews removed flammable debris and installed fire lines at the base of putatively rust-resistant whitebark pine to improve their chance of survival (Murray 2007).

Over the longer-term, proactive management that builds high-five pine ecosystem resilience to future disturbances should be a key aspect of conservation strategies. Understanding, and harnessing, high-five pine response diversity to disturbance and environmental change can help achieve this goal. For example, selection, breeding, and future out-planting of high-five pines with a range of rust-resistance mechanisms will help to minimize the impact of the exotic blister rust fungus. Also, because forests of various ages, and on various sites, exhibit differential responses to blister rust infection, MPB outbreaks, fire, and probably even global climate change, diversifying forest age class structure across site types and over subalpine landscapes can help to build high-five pine ecosystem resilience to future disturbance (Schoettle and Sniezko 2007). Fire management can play a central role in achieving this goal by maintaining, or increasing, the proportion of pine-dominated forests in subalpine landscapes. This may include actions that decrease fuel loads to reduce the risk of severe crown fires and protect mature seed-bearing pines. It may also include controlled management of lightning-ignited burns or prescribed burns that reintroduce fire.

Fire has been reintroduced in subalpine landscapes of the Rocky Mountains of Alberta, Idaho, and Montana to promote whitebark pine regeneration. These prescribed fires had mixed results. In Montana, despite pre-fire thinning treatments to control the spread of fire and protect mature, cone-bearing and putatively blister rust-resistant trees, many overstory whitebark pines died on most burns. While competing spruce and fir regeneration were often markedly reduced and the numbers of nutcrackers caching seed in the post-burn environment increased, five years after the burn, whitebark pine regeneration was insignificant at most sites (Haeussler 2010; Keane and Parsons 2010). A better understanding of whitebark pine regeneration dynamics in areas without severe blister rust will provide valuable baselines for evaluating management in areas with severe infections and help assess the needs for out-planting seedlings. Also, detailed guidelines to identify high-priority target stands (*sensu* Shoal and others 2008), including stands where introducing fire poses too large a risk, should be developed for prescribed burning.

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References

Aitken, S. N.; Yeaman, S.; Holliday, J. A.; Wang, T.; Curtis-McLane, S. 2008. Adaptation, migration or extirpation: Climate change outcomes for tree populations. Evolutionary Applications. 1: 95-111.

Ali, A.; Carcaillet, C; Talon, B.; Roiron, R.; Terral, J.-F. 2009. *Pinus cembra* (arolla), a common tree in the inner French Alps since the early Holocene and above the present tree line: a synthesis based on charcoal data from soils and travertines. Journal of Biogeography. 32: 1659-1669.

Araujo, M. B.; Guisan, A. 2006. Five (or so) challenges for species distribution modelling. Journal of Biogeography. 33: 1677-1688.

Arno, S. F.; Hoff, R. 1990. *Pinus albicaulis* Engelm. Whitebark Pine. Pages 268-279 *in* Silvics of North America. Vol. I. Conifers. Agr. Handbook. U.S. Department of Agriculture, Forest Service.

Arno, S. F.; Petersen, T. D. 1983. Variation in estimates of fire intervals: A closer look at fire history on the Bitterroot National Forest. General Technical Report GTR-INT-301, Ogden, UT: U.S. Department of Agriculture, Forest Service Intermountain Forest and Range Experiment Station.

Barrett, S. W. 1994. Fire regimes on andesitic mountain terrain in northeastern Yellowstone National Park, Wyoming. International Journal of Wildland Fire. 4: 65-76.

Bockino, N. K. 2008. Interactions of white pine blister rust, host species, and mountain pine beetle in whitebark pine ecosystems in the Greater Yellowstone. M.S. Thesis. University of Wyoming, Laramie, WY.

Boland, G. J.; Melzer, M. S.; Hopkin, A.; Higgins, V.; Nassuth, A. 2004. Climate change and plant diseases in Ontario. Canadian Journal of Plant Pathology. 26: 335-350.

Brown, P. M.; Schoettle, A. W. 2008. Fire and stand history in limber pine (*Pinus flexilis*) and Rocky Mountain bristlecone (*Pinus aristata*) stands in Colorado. International Journal of Wildland Fire. 17: 339-347.

Brunelle, A.; Whitlock, C. 2003. Postglacial fire, vegetation, and climate history in the Clearwater Range, Northern Idaho, USA. Quaternary Research. 60: 307-318.

Buechling, A.; Baker, W. L. 2004. A fire history from tree rings in a high-elevation forest of Rocky Mountain National Park. Canadian Journal of Forest Research. 34: 1259-1273.

Burns, K. S.; Schoettle, A. W.; Jacobi, William R.; Mahalovich, M. F. 2008. Options for the management of white pine blister rust in the Rocky Mountain Region. Gen. Tech. Rep. RMRS-GTR-206. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station. 26 p.

Campbell, E.; Carroll, A. 2007. Climate-related changes in the vulnerability of whitebark pine to mountain pine beetle outbreaks in British Columbia. Nutcracker Notes. 12: 13-15.

Campbell, E.; Antos, J. 2000. Distribution and severity of white pine blister rust and mountain pine beetle on whitebark pine in British Columbia. Canadian Journal of Forest Research. 30: 1051-1059.

Campbell, E.; Antos, J. 2003. Postfire succession in *Pinus albicaulis-Abies lasiocarpa* forests of southern British Columbia. Canadian Journal of Botany. 81: 383-397.

Caprio, A. C.; Lineback, P. 2002. Pre-twentieth century fire history of Sequoia and Kings Canyons National Park: a review and evaluation of our knowledge. Pages 180-199 *in* Proceedings—Symposium on Fire in California ecosystems: integrating ecology, prevention and management: November. Association for Fire ecology. [Place of publication unknown].

Carroll, A. L.; Régnière, J.; Logan, J.; Taylor, S.; Bentz, B.; Powell, J. P. 2006. Impacts of climate change on range expansion by mountain pine beetle. Mountain Pine Beetle Initiative Working Paper. 2006-14. Ottawa, ON: Canadian Forest Service.

Clason, A.; MacDonald, E., Haeussler, S. 2010. Ecosystem change at Whitebark Pine's northern limit. Nutcracker Notes. 18: 12-13.

Coop, J. C.; Schoettle, A.W. 2009. Regeneration of Rocky Mountain bristlecone pine (*Pinus aristata*) and limber pine (*Pinus flexilis*) three decades after stand-replacing fires. Forest Ecology and Management. 257: 893-903.

Cumming, S. G. 2002. Effective fire suppression in boreal forests. Canadian Journal of Forest Research. 35: 772-786.

Dale, V. H.; Joyce, L. A.; McNulty, S.; Neilson, R. R.; Ayres, M. P.; Flannigan, M. D.; Hanson, P. J.; Irland, L. C.; Lugo, A. E.; Peterson, J.; Simberloff, D.; Swanson, F. J.; Stocks, B. J.; Wotton, B. M. 2001 Climate change and forest disturbances. BioScience. 51: 723-734.

Despain, D. G. 1990. Yellowstone vegetation. Consequences of environment and history in a natural setting. Roberts Rinehart Publishers, Boulder, Colorado.

Genries, A.; Mercier, L.; Lavoie, M.; Muller, D.; Radakovitch, O.; Carcaillet, C. 2009a. The effect of fire frequency on local cembra pine populations. Ecology. 476-476.

Genries, A.; Morin, X.; Chauchard, S.; Carcaillet, C. 2009b. The function of surface fires in the dynamics of formerly grazed old subalpine forest. Journal of Ecology. 97: 728-741.

Gibson, K.; Skov, K.; Kegley, S.; Jorgensen, C.; Smith, S.; Witcosky, J. 2008. Mountain pine beetle impacts in high-elevation white pines: current trends and challenges. Report # R1-08-020 Missoula, MT. U.S. Department of Agriculture, Forest Service. 32 p.

Gunderson, L.; Allen, C. R.; Holling, C. S. 2009. Foundations of Ecological Resilience. Washington: Island Press. 466 p.

Haeussler, S. 2010. Exploring whitebark pine at it northern limits. Nutcracker Notes: 18:11-22

Haeussler, S; Woods, A.; White, K; Campbell, E.; LePage, P. 2009. Do whitebark pine—lichen ecosystems of west central British Columbia display tipping point behaviour in response to cumulative stress? Bulkley Valley Centre for Natural Resources Research & Management. Research Report. Smithers, BC. 23 p.

Hamann, A.; Wang, T. 2006. Potential effects of climate change on ecosystem and tree species distribution in British Columbia. Ecology, 87: 2773-2786.

Hobbs, R. J.; Cramer, V. A. 2008. Restoration ecology: Interventionist approaches for restoring and maintaining ecosystem function in the face of rapid environmental change. Annual Review Environmental Resources. 33: 39-61.

Hof, C.; Levinsky, I.; Araújo, M. B.; Rahbek, C. 2011. Rethinking species' ability to cope with climate change. Global Change Biology. Accepted Article doi: 10.111/j.1365-2486.2011.02418.x.

Hoff, R. J.; McDonald, G. I.; Bingham, R. T. 1976. Mass Selection for blister rust resistance: A method for natural regeneration of western white pine. Research Note INT-202, Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station. 11 p.

Iniguez, J. M.; Swetnam, T. W.; Baisan, C. H. 2009. Spatially and temporally variable fire regime on Rincon Peak, Arizona, USA. Fire Ecology. 5: 3-21

Jackson, S.; Campbell, E. 2008. Assessing the threat of mountain pine beetle to whitebark pine in British Columbia. Project Report, FIA-FSP Project #M07-5048. BC Ministry of Forests and Range, Victoria, BC.

Jenkins, M. J.; Hebertson, E.; Page, W.; Jorgensen, C. A. 2008. Bark beetles, fires, and implications for forest management in the Intermountain West. Forest Ecology and Management. 16-34.

Jewett, J. T. 2009. Spatiotemporal relationships between climate and whitebark pine mortality in the Greater Yellowstone Ecosystem. Thesis. Montana State University, Bozeman, MT, USA.

Keane, R. E. 2001. Successional dynamics: modeling an anthropogenic threat. Pages 159-192. *in* Whitebark pine communities: ecology and restoration. Washington: Island Press.

Keane, R. E.; Veblen, T.; Ryan, K. C.; Logan, J.; Allen, C.; Hawkes, B. 2002. The cascading effects of fire exclusion in the Rocky Mountains. Pages 133-153 in Rocky Mountain Futures: An Ecological Perspective. Washington: Island Press.

Keane, R. E.; Parsons, R. A. 2010. A management guide to ecosystem restoration treatments: Whitebark pine forests of the Northern Rocky Mountains. General Technical Report RMRS-GTR-232, U.S. Department of Agriculture, Forest Service Rocky Mountain Research Station, Fort Collins, CO.

Keane, R.; Morgan, P.; Menakis, J. 1994. Landscape assessment of the decline of whitebark pine (*Pinus albicaulis*) in the Bob Marshall Wilderness Complex, Montana, USA. Northwest Science. 68: 213-229.

Keeton, W. S.; Mote, P. W.; Franklin, J. F. 2007. Climate variability, climate change, and western wildfire with implications for the urban-wildland interface. Advances in the Economics of Environmental Resources. 6: 225-253.

Kitchen, S. 2010. Historic Fire Regimes of Eastern Great Basin Mountains Reconstructed from Tree Rings. Ph.D. Dissertation. Brigham Young University. Provo, UT. 166 p.

Kipfmueller, K. F. 2003. Fire-climate-vegetation interactions in subalpine forests of the Selway-Bitterroot Wilderness Area, Idaho and Montana, USA. Ph.D. Dissertation. The University of Arizona, Tucson, AZ, USA. 322 p.

Kipfmueller, K. F.; Kupfer, J. A. 2005. Complexity of successional pathways in subalpine forests of the Selway-Bitterroot Wilderness Area. Annuals of the Association of American Geographers. 95: 495-510.

Koteen, L. 1999. Climate change, whitebark pine, and grizzly bears in the greater Yellowstone ecosystem. Pages 343-364 *in* S. H. Wildlife responses to climate change. Washington: Island Press.

Lafleur, B.; Paré, D.; Munson, A. D.; Bergeron, Y. 2010. Response of northeastern North American forests to climate change: Will soil conditions constrain tree species migration? Environmental Reviews. 18: 279-289.

Larson, E. R. 2009. Status and dynamics of whitebark pine (*Pinus albicaulis* Engelm.) forests in southwest Montana, central Idaho, and Oregon, U.S.A. Ph.D. Dissertation. University of Minnesota, Minneapolis, MN, USA. 176 p.

Larson, E. R. (In press) Influences of the biophysical environment on blister rust and mountain pine beetle, and their interactions, in whitebark pine forests. Journal of Biogeography.

Larson, E. R.; Kipfmueller, K. F. 2010. Patterns in whitebark pine regeneration and their relationships to biophysical site characteristics in southwest Montana, central Idaho, and Oregon, USA. Canadian Journal of Forest Research. 40: 476-487.

Larson, E. R.; van de Gevel, S. L.; Grissino-Mayer, H. D. 2009. Variability in fire regimes of high-elevation whitebark pine communities, western Montana, USA. Ecoscience. 16: 282-298.

Li, C.; Barkley, H.; Hawkes, B.; Taylor, S. 2005. Lodgepole pine forest age class dynamics and susceptibility to mountain pine beetle outbreaks. Ecological Complexity. 3: 232-239.

Logan, J. A.; Powell, J.A. 2001. Ghost forests, global warming, and the mountain pine beetle (Coleoptera: Scolytidae). American Entomologist. 47: 160-173.

Lynch, H. J.; Renkin, R. A.; Crabtree, R. L.; Moorcroft, P. R. 2006. The influence of previous mountain pine beetle (*Dendroctonus ponderosae*) activity on the 1988 Yellowstone fires. Ecosystems. 9: 1318-1327.

Mathiasen, R. L.; Daugherty, C. M. 2001. Susceptibility of foxtail pine and western white pine to limber pine dwarf mistletoe in northern California. Western Journal of Applied Forestry. 16: 58-60.

Mathiasen, R. L.; Hawksworth, F. J. 1988. Dwarf mistletoes on western white pine and whitebark pine in northern California and southern Oregon. Forest Science. 34: 429-440.

Mattson, D. J.; Reinhart, D. P. 1990. Whitebark pine on the Mount Washburn Massif, Yellowstone National Park. Pages 106-117 *in* Proceedings—Symposium on whitebark pine ecosystems: Ecology and management of a high-mountain resource. Bozeman, MT: U.S. Department Agriculture, Forest Service.

Mbogga, M. S; Wang, X. L.; Hamann, A. 2010. Bioclimate envelope model predictions for natural resource management: dealing with uncertainty. Journal of Applied Ecology. 47: 731-740.

McCabe, G. J.; Palecki, M. A.; Betancourt, J. L. 2004. Pacific and Atlantic Ocean influences on multidecadal drought frequency in the United States. Proceedings of the National Academy of Sciences. 101: 4136-4141.

McKinney, S. T.; Fiedler, C. E.; Tomback, D. F. 2009. Invasive pathogen threatens bird-pine mutualism: implications for sustaining a high-elevation ecosystem. Ecological Applications. 19: 597-607.

Minckley, T. A.; Whitlock, C.; Bartlein, P. J. 2007. Vegetation, fire, and climate history of the northwestern Great Basin during the last 14,000 years. Quaternary Science Reviews. 26: 2167-2184.

Moody, R. 2006. Post-fire regeneration and survival of whitebark pine (*Pinus albicaulis* Engelm.). M.Sc. Thesis. University of British Columbia, Vancouver, BC. 108 p.

Morgan, P.; Bunting, S. C. 1990. Fire effects in whitebark pine forests. Pages 166-170 *in* Symposium on Whitebark Pine Ecosystems: Ecology and Management of a High-Mountain Resource. General Technical Report GTR-INT-270. Ogden, UT: U.S. Department of Agriculture, Forest Service Intermountain Forest and Range Research Station.

Morgan, P.; Bunting, S. C.; Keane, R. E.; Arno, S. F. 1994. Fire ecology of whitebark pine (*Pinus albicaulis*) forests in the Rocky Mountains, USA. Pages 136-142 in Proceedings—Symposium on subalpine stone pines and their environment: The status of our knowledge. General Technical Report GTR-INT-309. Ogden, UT: U.S. Department of Agriculture, Forest Service Intermountain Research Station.

Murray, M. 2007. Fire and Pacific Coast whitebark pine. Pages 51-60 in: Whitebark pine: a Pacific Coast perspective. R6-NR-FHP-2007-01. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Region.

Murray, M. P.; Bunting, S. C.; Morgan, P. 1998. Fire history of an isolated subalpine mountain range of the intermountain region, United States. Journal of Biogeography. 25: 1071-1080.

Murray, M. P.; Bunting, S. C.; Morgan, P. C. 2000. Landscape trends (1753-1993) of whitebark pine (*Pinus albicaulis*) forests in the West Big Hole Range, Idaho/Montana, U.S.A. Arctic, Antarctic, and Alpine Research. 32: 412-418.

Norment, C. J. 1991. Bird use of forest patches in the subalpine forest-alpine tundra ecotone of the Beartooth Mountains, Wyoming. Northwest Science. 65: 1-10.

Reinhardt, E. J.; Scott, H.; Gray, K. L.; Keane, R. E. 2006. Estimating canopy fuel characteristics in five conifer stands in the western United States using tree and stand measurements. Canadian Journal Forest Research. 36: 1-12.

Romme, W. H. 1980. Fire frequency in subalpine forests of Yellowstone National Park. Pages 27-30 in Proceedings of the fire history workshop. Tucson, AZ: U.S. Department of Agriculture, Forest Service Rocky Mountain Forest and Range Experiment Station.

Romme, W. H. 1982. Fire and landscape diversity in subalpine forests of Yellowstone National Park, Wyoming. Ecological Monographs. 52: 199-221.

Romme, W. H.; Knight, D. H. 1981. Fire frequency and subalpine forest succession along a topographic gradient in Wyoming. Ecology. 62: 319-326.

Running, S. W. 2006. Is global warming causing more, larger wildfires. Science. 313: 927-928.

Ryan, K. C. 1991. Vegetation and wildland fire: implications of global climate change. Environment International. 17: 169-178.

Ryerson, D. 1983. Population structure of *Pinus balfouriana* Grev. & Balf. along the margins of its distribution area in the Sierran and Klamath regions of California. Thesis. Sacramento, CA: California State University. 197 p.

Schmid, J. M.; Amman, G. D. 1992. *Dendroctonus* beetles and old-growth forests in the Rockies. Pages 51-59 in Proceedings of the workshp on: Old growth forests in the Southwest and Rocky Mountain region. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station. Gen. Tech. Rep. RM-213.

Schoettle, A. W.; Sniezko, R. A. 2007. Proactive intervention to sustain high-elevation pine ecosystems threatened by white pine blister rust. Journal of Forest Restoration. 12: 327-336.

Sherriff, R.; Veblen, T. T.; Sibold, J. S. 2001. Fire history in high elevation subalpine forests in the Colorado Front Range. Ecoscience. 8: 369-380.

Shoal, R. Z.; Lorenz, T.; Aubry, C. 2008. Land managers guide to whitebark pine restoration techniques. USDA Forest Service Pacific Southwest Region, Olympia, WA.

Siderius, J.; Murray, M. 2005. Fire knowledge for managing Cascadian whitebark pine ecosystems. Final report to the Interagency Joint Fire Sciences Program, (#01B-3-3-26). 44 p.

Skinner, W. R.; Shabbar, E.; Flannigan, M. D.; Logan, K. 2006. The association between circulation anomalies in the mid-trophosphere and area burned by wildland fire in Canada. Journal of Geophysical Research. 111, D14106, doi:10.1029/2005JD006738.

Simard, M.; Romme, W. H.; Griffin, J. M.; Turner, M. 2011. Do mountain pine beetle outbreaks change the probability of active crown fire in lodgepole pine forests? Ecological Monographs. 81:3-24.

Smith, C.; Wilson, B.; Rasheed, S.; Walker, R.; Carolin, T.; Sheperd, B. 2008. Whitebark pine and blister rust in the Rocky Mountains of Canada and northern Montana. Canadian Journal of Forest Research. 38: 982-995.

Six, D. L.; Adams, J. 2007. White pine blister rust severity and selection of individual whitebark pine by the mountain pine beetle (Coleoptera: Curculionidae, Scolytinae). Journal of Entomological Science. 42: 345-353.

Stuart, J. D.; Agee, J. K.; Gara, R. I. 1989. Lodgepole pine regeneration in an old, self-perpetuating forest in south central Oregon. Canadian Journal of Forest Research. 19: 1096-1104.

Tomback, D. F. 2005. The impact of seed dispersal by the Clark's Nutcracker on whitebark pine: Multi-scale perspective on a high mountain mutualism. Pages 181-201 in Mountain Ecosystems: Studies in treeline ecology. New York, NY: Springer.

Tomback, D.; Achuff, P. 2010. Blister rust and western forest biodiversity: ecology, values, and outlook for white pines. Forest Pathology. 40: 186-225.

Tomback, D. F.; Sund, S. K.; Hoffman, L. A. 1993. Post-fire regeneration of *Pinus albicaulis*: height-age relationships, age structure, and microsite characteristics. Canadian Journal of Forest Research. 23: 113-119.

Warwell, M. V.; Rehfeldt, G.; Crookston, N. 2007. Modeling contemporary climate profiles of whitebark pine (*Pinus albicaulis*) and predicting responses to global warming. Pages 139-142 *in* Proceedings of the conference whitebark pine: a Pacific Coast perspective. Ashland, OR. Ashland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Region.

Yanchuk, A.; Murphy, J.; Wallin, K. 2008. Evaluation of genetic variation of attack and resistence in lodgpole pine in the early stages of a mountain pine beetle outbreak. Tree Genetics Genomes. 4: 171-180.

Fire and High-Elevation, Five-Needle Pine (*Pinus aristata* & *P. flexilis*) Ecosystems in the Southern Rocky Mountains: What Do We Know?

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Abstract—Rocky Mountain bristlecone pine (*Pinus aristata* Engelm) and limber pine (*P. flexilis* James) are high-elevation, five-needle pines of the southern Rocky Mountains. The pre-settlement role of fire in bristlecone and limber pine forests remains the subject of considerable uncertainty; both species likely experienced a wide range of fire regimes across gradients of site productivity and connectivity of fuels and flammable landscapes. In dense stands and more continuous forests, stand history reconstructions provide evidence for infrequent, high-severity fires. Limber pine can be dispersed long distances by Clark's nutcrackers (*Nucifraga columbiana*), and in the high-elevation subalpine forests of the northern Colorado Front Range, it is an early colonist of extensive, high-severity burns. However, this relationship with fire may not be general to the southern Rockies. The degree to which high-severity fire was typical of bristlecone pine, and the spatial extent of such fires, is uncertain. Following fire, bristlecone pine regeneration tends to be constrained to burn edges or beneath surviving trees. In both five-needle pines, regeneration dynamics take decades to centuries. Where open stands border grassy openings both species frequently exhibit fire scars indicative of fairly frequent but low-intensity fire; because of the great ages attained by both species, they offer potentially very long fire history reconstructions in such settings. Whether or not fire suppression has led to declines in either species—through successional shifts to shade-tolerant competitors or by shifts to a stand replacing fire-regime—remains an open question that deserves further inquiry. In any case, re-establishing pre-settlement fire regimes, whatever they were, may not be as important as determining appropriate disturbance regimes given current conditions and management objectives. Both species are highly susceptible to rapid declines caused by white pine blister rust (*Cronartium ribicola*) and mountain pine beetles (*Dendroctonus ponderosae*). In the face of these threats, and uncertain consequences of climate change, fire management (both prevention and application) can be a tool to promote resilient landscapes. Appropriate fire management may be used to conserve valuable stands, promote regeneration and diversify age class structures, and/or alter the balance between these species and their competitors. Many of these themes and questions indicate the need for further basic and applied research.

Introduction

Rocky Mountain bristlecone pine (*Pinus aristata*) and limber pine (*P. flexilis*) are high-elevation, five-needle pines of the southern Rocky Mountains. These tree species frequently occur at the high-elevation and xeric margins of the arborescent life form, and as such they form biological communities and provide ecological services that cannot be replaced. However, both species are highly vulnerable to large scale changes caused by white pine blister rust (*Cronartium ribicola*) and mountain pine beetle (*Dendroctonus ponderosae*). Considerable uncertainty remains surrounding the role of fire in southern Rocky Mountain five-needle pine ecosystems. First, few quantitative studies have explicitly addressed this theme. Secondly, both species can occupy a diversity of ecological settings, and nearly the entire spectrum of fire regimes and their effects probably occurred within their ranges. For this reason, generalizations from any given line of evidence are likely to be inaccurate. For example, based on ordinations of morphological traits, McCune (1988) and Keeley and Zedler (1998) concluded that fire is essentially absent or unimportant for bristlecone and limber pine. While fire may be inconsequential in some settings, there is clear evidence for abundant fire, a diversity of fire regimes, and a significant role of fire in many bristlecone and limber pine ecosystems, as discussed below.

The purpose of this review is to summarize what we do know about fire ecology of the high-elevation, five-needle pine forests of the southern Rocky Mountains, including both published and unpublished data, anecdotal information, and the observations of ourselves and others. The geographic scope of this review is limited to the southern Rocky Mountains, extending from southern Wyoming south through the major ranges of Colorado into northern New Mexico. At the southern end of this region, there appears to be a broad, unresolved transition zone between limber pine and southwestern white pine (*P. strobiformis; P. flexilis* var. *reflexa*), which we also discuss briefly, though little work has been done on the fire ecology of these transitional populations. We also include some discussion of the disjunct Rocky Mountain bristlecone pine population in the San Francisco Peaks of northern Arizona. Our primary goals are to review what we know generally about the ecology of these species, fire regimes, effects of fire on stand dynamics, and possible human and climatic influences on fire in these systems. Throughout, we point out deficiencies in our understanding of these systems and suggest possible research directions. Lastly, we consider how the management of fire may be used to promote resilient southern Rocky Mountain five-needle pine ecosystems in a future of certain change of uncertain direction and magnitude.

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Overview of Bristlecone and Limber Pine Ecology

Rocky Mountain bristlecone pine (henceforth, bristlecone pine) and limber pine are five-needle pines of *Pinus* subgenus *Strobus*. Within this large group they are not particularly closely related, bristlecone pine is classified in section *Parrya* and limber pine in section *Quinquefoliae* (Gernandt and others 2005). However, they share many morphological and ecological characteristics: both are short-statured, slow-growing, drought- and cold-tolerant tree species that may be very long-lived, and frequently occupy xeric and high-elevation sites where conditions for arborescent growth are marginal and competitors are few. Bristlecone and limber pines rarely achieve heights greater than 15 m or bole diameters greater than 1 m. For both species, radial growth rates of <0.01 mm/year are common on dry, high-elevation sites and rarely exceed 3 mm/year on more mesic or lower-elevation sites (J.D. Coop, unpublished data). Where bristlecone and limber pine co-occur, limber pine typically exhibits greater rates of radial growth with greater variance (J.D. Coop, unpublished data). Both bristlecone and limber pine are well-known for their extreme longevity. The oldest known Rocky Mountain bristlecone pine, found in Colorado, is nearly 2500 years (Brunstein & Yamaguchi 1992), and the oldest known limber pine, found in northern New Mexico, exceeds 1600 years in age (Swetnam & Brown 1992).

An important difference between bristlecone and limber pine is seed morphology and dispersal mode. Bristlecone seeds are small (ca. 20 mg) and winged, typical of wind-dispersal; the large (ca. 100 mg), wingless (or near-wingless) seeds of limber pine are dispersed primarily by Clark's nutcrackers (Woodmansee 1977; Lanner & Vander Wall 1980). Because nutcrackers often deposit numerous seeds in each cache, limber pine seedlings arising from caches often occur as multi-stem clusters (Woodmansee 1977; Lanner & Vander Wall 1980; Carsey & Tomback 1994). Based on frequent stem-clusters and observations of nutcrackers, Lanner (1988) concluded that Great Basin bristlecone pine (*Pinus longaeva*; which produces small, winged seeds similar to those of Rocky Mountain bristlecone pine) is often nutcracker-dispersed, particularly at high elevations. Multi-stemmed Rocky Mountain bristlecone pines also occur occasionally, although whether these trees usually represent single, multi-stemmed individuals or separate individuals arising from a seed caches is not known. However, it is likely that nutcrackers occasionally serve as the dispersal agents for this species as well, though their importance relative to wind has not been studied.

In general, both bristlecone and limber pine are found on xeric sites at moderate to high elevations where competition from other tree species is limited, and are replaced on mesic sites by more rapidly growing competitors—often Engelmann spruce (*Picea engelmannii* var. *engelmannii*). South-facing slopes dominated by five-needle pines usually give way to mixed conifer or spruce-fir forests on north aspects. Both species can form krummholtz at alpine treeline. Although both five-needle pines are often associated with subalpine and alpine timberline environments (3100-3650 m), both species also commonly occur at lower (2650-3100 m) elevations, often on montane rocky outcrops, or bordering valley- bottom montane and subalpine grasslands. At such lower sites, five-needle pine communities often give way to mixed conifer or spruce-fir forests above. Both species can also be found co-occurring with nearly every other tree species in the region, including piñon pine (*Pinus edulis*), ponderosa pine (*Pinus ponderosa* var. *scopulorum*), lodgepole pine (*Pinus contorta* var. *latifolia*), Douglas fir (*Pseudotsuga menziesii* var. *glauca*), aspen (*Populus tremuloides*), Colorado blue spruce (*Picea pungens*), Engelmann spruce, and subalpine and corkbark fir (*Abies lasiocarpa* var. *lasiocarpa* & var. *arizonica*).

Geographic Distributions and Environmental Settings

Rocky Mountain bristlecone pine is restricted to the southern Rocky Mountains between central Colorado and northern New Mexico, and a small disjunct population on the San Francisco Peaks of north-central Arizona (Fig. 1). Farther west it is replaced by Great Basin bristlecone pine (*Pinus longaeva*), which ranges from the central plateaus of Utah to eastern California. Other than geography, the two species were separated by Bailey (1970) by longer bristles on the cones of Rocky Mountain bristlecone, and the abaxial groove and resin-dotted needles of Rocky Mountain bristlecone which are not present in Great Basin bristlecone pine. While macrofossils preserved in packrat middens indicate that Great Basin bristlecone pine was widespread at low elevations across its range during the last glacial period (Betancourt and others 1990), the Pleistocene distribution of Rocky Mountain bristlecone pine is not documented. Bailey (1970) hypothesized that Rocky Mountain bristlecone pine was distributed across the Mogollon Rim from the San Francisco Peaks through west-central New Mexico during the glacial maximum.

Limber pine is widespread throughout western North America, between the Pacific crest and the Rockies, from British Columbia and Alberta south through at least as far south as the southern Rockies, with several outlier populations east of the Rockies (Fig. 1). At the southern end of its range in the southern Rockies there is a broad transition zone with southwestern white pine, a taller, straight-boled, thick-barked tree that is an important component of southwestern montane mixed-conifer forests. Many populations within this region appear intermediate in ecology and the morphological characteristics used to separate the two species (longer needles and cones, and reflexed cone scales in *P. strobiformis*, stomata present on all leaf surfaces in *P. flexilis* but absent from the abaxial surface in *P. strobiformis*). Limber pine is well-known to have occupied an extensive range during the last Pleistocene glaciation at lower elevations now occupied by piñon pines (*P. edulis* and *P. monophyla*) across the Great Basin (Betancourt and others 1990), along the

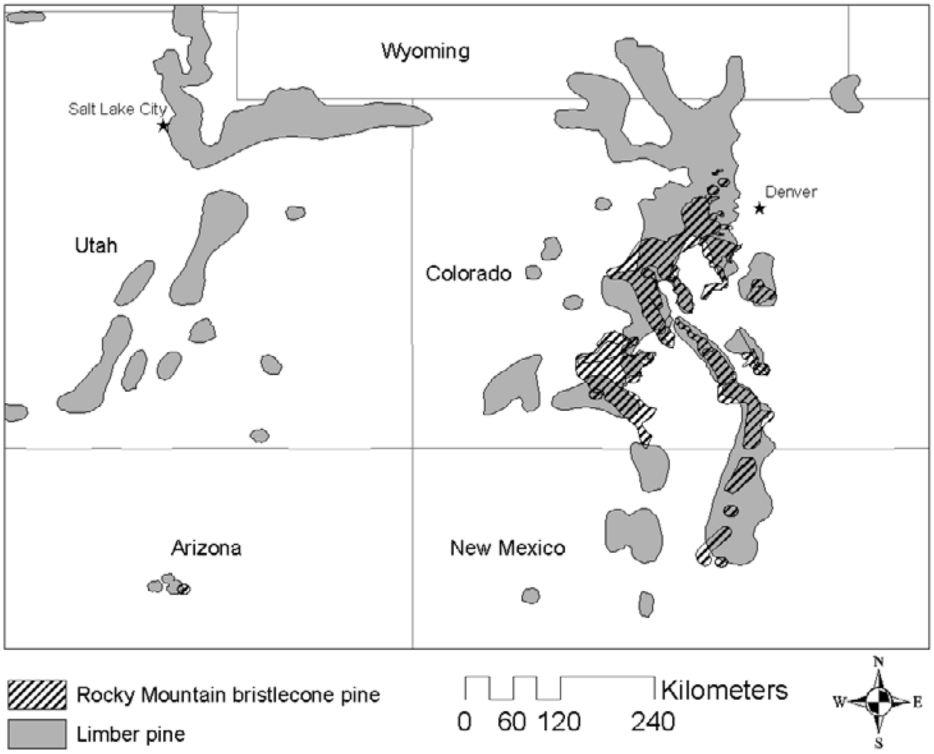

Figure 1. Map showing the ranges of Rocky Mountain bristlecone pine (*P. aristata*) and limber pine (*P. flexilis*) in the southern Rocky Mountains, modified from Little (1971), with several additions by the authors.

eastern Great Plains (Wells & Stewart 1987) and possibly areas in southern New Mexico, central Colorado, Wyoming, and California (Mitton and others 2000).

Across the southern Rockies, bristlecone pine and limber pine exhibit a latitudinal and elevational shift in dominance (Peet 1978): in the north, limber pine is more abundant and occupies a very wide elevational range, but is gradually replaced by bristlecone pine, at first only at high elevations, but at progressively lower elevations as bristlecone pine increases in importance to the south. The extent to which this apparent displacement is driven by variation in competitive ability, shifting physiological limits by either species along the climatic gradient over which they both occur, or other factors altogether, is unknown.

In southern Wyoming and northern Colorado, north of the range limits of bristlecone pine, limber pine occupies one of the largest elevational ranges of any species in the Rockies (from 1660 to 3300 m; Schoettle & Rochelle 2000), including dry sites at alpine treeline in Rocky Mountain National Park, extensive stands on xeric subalpine slopes and montane ridges across the northern Front Range, foothill sites in intermountain valleys such as North Park and the Great Divide Basin of Wyoming, and even topographic breaks in Great Plains east of the Rockies. At the northern end of the range of bristlecone pine (the Front Range south of Rocky Mountain National Park), bristlecone pine occupies only xeric alpine treeline sites just above stands of limber pine. As one progresses south along the Front Range, bristlecone pine appears to gradually displace limber pine entirely from alpine treeline sites; limber pine is increasingly restricted to south-facing subalpine and montane slopes. In the southern Front Range and throughout much of the Mosquito and Sawatch Range, bristlecone pine forms extensive subalpine stands and limber pine is mostly confined to lower elevations, being more or less restricted to dry upper montane ridges.

Bristlecone pine is particularly abundant around South Park and along the Cochetopa Hills where it also forms extensive lower treeline stands abutting Arizona or Thurber's fescue (*Festuca arizonica* & *F. thurberi*) grasslands (Ranne and others 1997) of parks and valleys. Other tree species may be excluded from these valley-bottom grassland margins in the southern Rockies by fine-textured soils with extremely low moisture potential during dry periods and frequent temperature inversions causing frost damage to tree seedlings (Coop & Givnish 2008). Frequently, bristlecone pine at these lower-treeline settings gives way to species with more mesic affiliations at higher elevations. Along the eastern margins of South Park, bristlecone pine occasionally exhibits a bimodal distribution, coexisting with ponderosa pine at low elevations, absent from the montane lodgepole pine zone, then reappearing at high elevations with spruce. Some bristlecone pine stands reach essentially unbroken from lower treeline up to alpine treeline. Limber pine is much less frequent in these areas, and may be limited to unusual topo-edaphic conditions such as limestone ridges. Throughout its range in the Wet Mountains, the Sangre de Cristos, and the eastern San Juans in Colorado, bristlecone pine may occur in patches at alpine treeline, in extensive subalpine forests, at the margins of subalpine grasslands, and isolated stands in dry, rocky sites at lower elevations. In northern New Mexico, bristlecone pine extends along the length of the Sangre de Cristo range, but does not occur farther west in the San Juan or Jemez Mountains. Around the Valle Vidal in northern New Mexico, bristlecone pine is particularly abundant, reaching from montane grasslands to alpine treeline. Bristlecone pine decreases in abundance toward the southern terminus of the Sangres, where it is more often associated with montane and subalpine grasslands, and occurs only rarely at alpine treeline.

At the approximate location of a SW-NE trending diagonal line through the southern San Juans, the northern Sangre de Cristo range, and the Wet Mountains, there is an apparent transition zone from limber pine to southwestern white pine, with morphologically and taxonomically variable populations. Interestingly, the region of this transition also represents the southern range limit of lodgepole pine and the approximate location of the shift from subalpine fir (*Abies lasiocarpa* var. *lasiocarpa*) to corkbark fir (*Abies lasiocarpa* var. *arizonica*). The apparent *P. flexilis/P. strobiformis* intermediates in this region occur in both dry montane mixed-conifer forests, often associated with Douglas fir, and also occasionally form small, monodominant stands on exposed settings such as low summits, ridges, and rocky outcrops. Taxonomic affinities to southwestern white pine increase to the south (J.D. Coop, personal observation). In some areas, such as the Jemez Mountains, more limber pine-like trees can be found on exposed sites, and more southwestern white pine-like trees occur in mixed conifer forests.

Bristlecone Pine Fire Regimes and Stand Dynamics

The most geographically extensive characterization of bristlecone pine stands was carried out by Baker (1992), who collected size-class data and dated the oldest trees in 65 stands dominated by bristlecone pine between 2700 and 3700 m elevation across Colorado and concluded that many of these stands were initiated following stand-replacing fire. Two stands had burned recently and contained many seedlings and saplings. In nineteen stands the oldest trees were dated to 1900-1925 or 1625-1700, which Baker inferred were periods of stand-initiating wildfire activity. The abundance of aspen in some of these stands may also be indicative of an infrequent, stand-replacing disturbance regime. However, direct evidence for wildfire was not presented in this research, and other stand-initiating disturbance and/or climatic drivers may also be important. Baker concluded that stand-replacing fire was the primary disturbance regime for bristlecone pine, with a fire rotation interval of approximately 300 years. Though this estimate undoubtedly masks considerable variation, it is apparent many stands can reach canopy densities sufficient to support crown fire, particularly on relatively mesic settings where bristlecone co-occurs with other conifer species. In these settings, an important unanswered question is what spatial scale typified such burns.

While stand-replacing fire may have been prevalent in some settings, at least some stands may be best characterized by a low-severity fire regime. Fire-scarred bristlecone pines in open, low-density stands with grassy understories occur nearly throughout the range of the species, particularly where stands abut montane and subalpine grasslands, such as around South Park, in the Cochetopa Hills, the Wet Mountains, and the Sangre de Cristo range (J.C. Coop, personal observation; Fig. 2), and numerous fire histories have been reconstructed from bristlecone pines scarred by low-severity fires (Table 1). Donnegan and others (2001) collected fire scar data from several stands dominated by bristlecone pine around South Park, Colorado between 2865-3108 m elevation. These authors reported mean fire intervals (MFIs) in some bristlecone pine stands < 20 years, similar to fire frequencies from lower elevation (1996-2865 m) stands of ponderosa pine reported in the same study. Sherriff and others (2001) also relied on several primarily bristlecone pine sites to reconstruct fire history from high-elevations (>3100 m) in the Colorado Front Range. These sites, representing some of the northernmost locations of bristlecone pine, also showed abundant, low severity fires, two with MFIs of 13 and 15 years. In the southern Sangre de Cristo range in New Mexico, a fire-scarred bristlecone pine stand bordering subalpine grasslands in the Pecos Wilderness yielded a reconstructed MFI of 59 years (C.D. Allen, unpublished data). In the disjunct bristlecone pine population of the San Francisco Peaks of northern Arizona, Cocke and others (2005) noted large, old trees with multiple fire scars, and cited unpublished data indicative of both low-severity fire and small patches of high-severity fire.

Figure 2. Fire-scarred bristlecone pines near Bobcat Pass in the Sangre de Cristo range, northern New Mexico.

Bristlecone pine stands exhibit substantial variation in composition and structure and occur across a wide range of ecological conditions, so a variety of disturbance regimes is not unexpected. Large gradients in stand conditions can occur over short distances. For example, open bristlecone pine stands bordering montane grasslands that likely experienced a frequent, low-severity fire regime can give way abruptly to dense, mixed species forests above that would be more likely to experience stand-replacing fire (Fig. 3). Stand conditions and fire regimes may also change over time, as at Packer Gulch, a bristlecone site in the Puma Hills bordering South

Table 1. Low-severity fire sites in bristlecone and limber pine stands that have been used to reconstruct fire histories, from north to south across the southern Rocky Mountains, and mean fire intervals (MFI).

Site	Region	Authors	Species	Trees*	Period	MFI†
Lake John	Northern CO	Brown & Schoettle 2008	*Pinus flexilis*	6	1464-1832	41
Wild Basin	Northern CO	Sherriff and others 2001	*Pinus flexilis, Pinus contorta, Picea engelmannii, Abies lasiocarpa*	74	1559-1996	7
Hidden Valley	Northern CO	Sherriff and others 2001	*Pinus flexilis*	31	1298-1988	23
Arapaho NF	Northern CO	Sherriff and others 2001	*Pinus aristata, Pinus flexilis, Picea engelmannii*	48	1288-1986	15
Mt. Evans	Northern CO	Sherriff and others 2001	*Pinus aristata, Pinus flexilis, Picea engelmannii*	33	1266-1986	13
Packer Gulch	Central CO	Brown & Schoettle 2008	*Pinus aristata, Pinus flexilis, Picea engelmanii, Pseudotsuga menziesii*	26	1106-1824	103
Badger Mtn.	Central CO	Donnegan and others 2001	*Pinus aristata, Pinus flexilis, Pinus ponderosa, Pseudotsuga menziesii*	58	1456–1920	67
BSA Shortcut	Central CO	Donnegan and others 2001	*Pinus flexilis, Pinus ponderosa*	15	1727–1920	33
Crooked Cr.	Central CO	Donnegan and others 2001	*Pinus aristata*	12	1532–1920	56
39 Mile Mtn.	Central CO	Donnegan and others 2001	*Pinus aristata*	13	1622–1920	19
Round Mtn.	Northern NM	C.D. Allen unpubl.	*Pinus aristata*	19	1580-1923	59

* Total number of fire-scarred trees sampled.

† Number of trees used for calculation of MFIs as follows: Allen, ≥ 2; Brown and Schoettle, not provided; Donnegan and others, ≥ 2; Sherriff and others, >2.

Park, used to reconstruct fire history and stand dynamics over the last ca. 1000 years by Brown & Schoettle (2008). This site experienced low-severity fire, apparently maintaining an open canopy, at intervals of 5-155 years from 1106 to 1824. However, fire frequency decreased and tree recruitment of both bristlecone pine and other species increased from the 1600s-1800s, leading to stand density sufficient to support a high-severity fire in 1978 that was outside the range of variation of at least the ca. 1000 years (Brown & Schoettle 2008).

In addition to the high-severity Packer Gulch fire, several other recent historic fires also attest to variability in bristlecone pine fire regimes in the southern Rocky Mountains. The Badger Mountain (near South Park) and Maes Creek (in the Wet Mountains) fires, also occurring following extremely dry conditions in 1978, led to near-complete mortality in many bristlecone pine stands (Coop & Schoettle 2009). In 2000, the 11760-ha Viveash Fire was primarily a moderate- or high-severity fire in ponderosa pine, mixed conifer, and spruce-fir forests in the southern Sangres. However, the fire was less severe where it entered bristlecone pine stands in the headwaters of Cow Creek. Many of these stands are very open and intermixed with subalpine *Festuca thurberi* grasslands on steep, south-facing slopes. Only scattered

Figure 3. High variation in bristlecone pine stand structure and recent disturbance over short spatial distances in the Cochetopa hills of southern Colorado. This small drainage contains isolated fire-scarred bristlecone pines bordering montane grasslands, a recent (2007) 21-ha., mixed-severity burn and evidence of small patches of historic stand-replacing fire in mixed bristlecone pine, Douglas fir, and spruce stands on more densely forested summits.

individuals and patches of bristlecone pine were killed, leaving most trees undamaged or with scorch marks and/or fire scars (J.D. Coop, personal observation). In the Cochetopa Hills of Colorado, the 21-ha Lujan Ridge fire in 2007 was a mixed-severity burn that appeared to preferentially kill spruce and aspen in a mixed bristlecone pine stand (J.D. Coop, personal observation).

The regeneration response of bristlecone pine to fire also appears to be the subject of some uncertainty. While Baker (1992) concluded that bristlecone pine is a "long-lived pioneer that regenerates primarily after fire", Brown and Schoettle (2008) found regeneration to be associated with long fire-free intervals, and Cocke and others (2005) reported nearly continuous regeneration over ca. 400 years. It may be these apparent contradictions can be reconciled when the very gradual tempo of regeneration dynamics of this species is considered, particularly at the least productive sites. Open conditions that favor five-needle pine seedling establishment may persist for decades to centuries after disturbance in xeric, high-elevation settings in the southern Rockies (Shankman & Daly 1988; Coop and others 2010). Coop & Schoettle (2009) examined patterns of bristlecone pine regeneration three decades after the stand-replacing fires at Badger Mountain and Maes Creek. Regeneration in these burns was generally poor, and bristlecone pine populations were substantially depressed in burn interiors relative to unburned stands. However, relative to both unburned stands and burn interiors, seedling numbers were elevated near or beneath surviving trees, and total density (of all size classes) was increased in these partially burned patches. This is likely due to propagule limitations related to wind-dispersal, and suggests that mixed-severity or small (≤ 15 m) patches of high-severity fire would be most likely to promote bristlecone pine regeneration. Seedlings also showed strong affinities to "nurse objects" (rocks, fallen logs, live or dead standing boles) that may provide sheltered microenvironments for establishment.

Limber Pine Fire Regimes and Stand Dynamics

The role of fire in limber pine ecosystems in the southern Rockies is perhaps even less well understood than that of bristlecone pine, with the important exception of its ecology in dry subalpine forests of the northern Front Range of northern Colorado. In the Front Range, limber pine is well-known to be an early colonist of high-severity burns, where it forms stable, self-replacing stands on xeric sites and successional stands that over time give way to spruce and fir on more mesic sites (Peet 1981; Veblen 1986; Rebertus and others 1991; Donnegan & Rebertus 1999). Limber pine appears to require a mosaic of successional stages across the landscape generated by infrequent, stand-replacing fir. This ecological role of limber pine is analogous to that described for whitebark pine (*Pinus albicaulis*) in northern Rockies of the continental U.S and southern Canada (Arno 2001). Both species are dispersed by Clark's nutcrackers, who may preferentially cache seeds in open sites such as the exposed interiors of large burns (Tomback 2001 and references cited therein). Limber pine stands in this setting display metapopulation dynamics, with patches constantly undergoing episodes of colonization, contraction, extinction, and recolonization (Webster and Johnson 2000, Antolin and Schoettle 2001).

Veblen (1986) reconstructed forest development from age cores from several subalpine stands recovering from high-severity fire in the northern Front Range of Colorado. In the two most xeric stands, limber pine was the first post-fire colonist, and dominated recruitment for up to a century before substantial establishment next by lodgepole pine, then Engelmann spruce, and later, subalpine fir. As these other tree species became abundant, limber pine recruitment ceased, probably due to dense shading by competitors. Rebertus and others (1991) also reconstructed temporal and spatial patterns of stand development in ca. 100- and 250-year old burns in the northern Front Range, and found that colonization by limber pine began very soon after fire and continued for at least a century; spruce and fir recruitment lagged behind by several decades. Two old-growth limber pine stands did not show any evidence of stand-replacing disturbance, and showed essentially continuous, albeit limited recruitment, throughout the ca. 400-1000 years for which stand history could be reconstructed. Finally, Donnegan & Rebertus (1999) mapped and collected nearly two thousand increment cores from 25 subalpine forest plots in two watersheds in the northern Front Range to reconstruct spatial and temporal patterns of stand development, and found limber pine was the initial colonist following an extensive (at least ca. 1000 ha.) stand replacing fire that occurred over their entire study area around 1700. Succession to spruce and fir was most rapid on more mesic sites, decreasing with site aridity. Spruce and fir seedlings became preferentially established beneath limber pine trees. Successional rates peaked with high limber pine mortality around 200 years post-fire, which was highest for multi-stemmed limber pine clusters and limber pines that had high spruce and fir establishment in close spatial proximity (Donnegan & Rebertus 1999).

Extensive subalpine stands dominated by limber pine or mixed limber pine/spruce/fir are less common out of the northern Front Range, and it seems unlikely this successional sequence is general of limber pine elsewhere in the southern Rocky Mountains. However, only one other limber pine stand history has been developed anywhere else in this region. Brown & Schoettle (2008) reconstructed nearly 600 years of stand development and fire history of isolated limber pine woodland bordering sagebrush-bunchgrass steppe in North Park. The early part of record shows numerous low-severity fires with a gradual decrease in the 1600's and 1700's (MFI = 41 years). The last fire in this stand occurred in 1832, apparently following an episode of mortality caused by bark beetles. Abundant recruitment occurred through the 1800s and early 1900s, stand density increased dramatically, and no further fire in occurred in this stand through the period of settlement, livestock grazing, and fire suppression (Brown & Schoettle 2008).

Frequent, low-severity fires in limber pine stands were also recorded in mixed, high-elevation bristlecone and limber pine stands around South Park by Donnegan and others (2001), and several limber pine-dominated subalpine stands in the Front Range by Sherriff and others (2001; Table 1). As with the bristlecone pine fire chronologies discussed previously, these stands were subjectively chosen for sampling based on the presence of fire scars, and the extent to which any of these are representative of limber pine disturbance regimes across the southern Rockies cannot be determined without substantially more research. Few fire history reconstructions have focused specifically on intermediate *P. flexilis-strobiformis* populations occurring within the broad transition zone between limber pine and southwestern white pine in the San Juans, the Sangres, and the Jemez Mountains. These populations frequently occur as a component of mixed-conifer forests also including ponderosa pine, Douglas fir, and white fir. There is strong evidence for a low-severity, high-frequency fire regime in such forests in the Jemez Mountains, where many fire history reconstructions have included fire-scarred *P. flexilis/strobiformis* intermediates, and indicate a return interval of ca. 4-12 years (Allen, 1989). These ranges are similar to those reported from mixed-conifer stands farther south in Arizona that include a substantial component of *P. strobiformis*. In the Rincon Mountains, MFI's for "open pine forests" (including ponderosa and southwestern white pine) ranged from 6.7-7.3 years and were 9.9 years in mixed conifer forests containing southwestern white pine (Baisan & Swetnam 1990); mixed conifer forests with a southwestern white pine component in the Pinaleño Mountains had an MFI of 6.24 years (Grissino-Mayer and others 1995).

The 1978 Ouzel fire caused stand-replacing tree mortality across a broad swath of Rocky Mountain National Park east of the continental divide, including many areas dominated by limber pine. Consistent with stand reconstructions from the northern Front Range described above, limber pine regeneration has been extensive and ongoing on dry slopes and high elevations in the burn interior, even hundreds of meters from possible seed sources (Coop & Schoettle 2009; Fig. 4). Within thirty years post-fire, limber pine population density in the high-severity burn interior exceeded that in either adjacent or unburned or incompletely burned stands. However, in the 1978 Badger Mountain and Maes Creek burns (near South Park and in the Wet Mountains, respectively, discussed previously) limber pine regeneration in burn interiors was far lower (Coop & Schoettle 2009). At Badger Mountain, where limber pine is mixed with bristlecone pine and Engelmann spruce, recent limber pine regeneration and total population were greatest in burn margins. Limber pine forms monotypic stands on rocky outcrops at moderate elevations at the Maes Creek burn; at this site regeneration was greater outside of the burn perimeter than within. This apparent shift in limber pine regeneration pattern from north to south was not associated with any changes in the frequency of multi-stem clusters and distance from probable seed sources, but was accompanied by a decrease in limber pine seedling height growth (J. D. Coop, unpublished data). Thus, rather than any change in dispersal mechanism, variation in post-fire regeneration pattern across these three burns appears more likely related to some fundamental shift in limber pine physiological performance that may be also correspond with the elevational shift across the southern Rockies described by Peet (1978).

Figure 4. Recent post-fire limber pine seedling establishment in the interior of the 1978, stand-replacing Ouzel burn, Rocky Mountain National Park, northern Colorado.

Anthropogenic and Climatic Influences on Fire in Bristlecone and Limber Pine Ecosystems

Have recent changes in human land use, including fire suppression, driven changes in stand conditions and fire regimes in southern Rocky Mountain five-needle pine ecosystems? Based on the few fire- and stand-history reconstructions that have been completed, no clear trends emerge, and any effects appear to be variable and context-specific. Where bristlecone and limber pine stands typically experienced infrequent, high-severity fire (such as bristlecone stands characterized by the 300-year rotation interval estimated by Baker 1992 and successional limber pine forests of the northern Front Range), direct fire suppression over the last century is unlikely to have led to stand-level shifts in structure and composition outside of historic ranges of variation. However, the extent to which fire suppression has driven landscape-level changes in the distribution of mosaics of different successional stages remains an open question. In forest types that experienced infrequent stand-replacing fire, suppression may have reduced the proportion of early-successional landscapes that promoted five-needle pines, leading to decreases in the proportion of five-needle pines across the landscape. This is an important topic in need of further inquiry.

Stands that experienced more frequent, low-severity or mixed-severity fires are more likely to have experienced structural or compositional changes in the absence of recent fire. However, the extent to which such changes have occurred is unknown. In bristlecone, limber, and ponderosa pine stands that recorded many low-severity fires around South Park, Colorado, Donnegan and others (2001) noted increases in fire frequency that began with the large influx of settlers into the region in the mid-late 1800s, followed by a pronounced decline in fire frequency contemporaneous with the onset of fire suppression in the 1900's. However, reductions in fire in the 1900's also correspond with a period of reduced climatic variability (Donnegan and others 2001), and the relative importance of these two factors cannot be determined. Contrasting these findings, subalpine stands that recorded frequent fire in the Front Range (primarily composed of limber pine, but also some bristlecone pine and other tree species, see Table 1) generally showed increased fire in the 1900s compared with the 1800s (Sherriff and others 2001). Only one limber pine stand showed 20th century reductions in fire frequency consistent with anthropogenic fire suppression.

The best documentation of changes in bristlecone and limber pine stand structure attributable to fire suppression is the work done by Cocke and others (2005) in the San Francisco Peaks of northern Arizona. These authors compared modern stand structure (2000) with a dendroecological reconstruction of historic stand structure (1876) along a gradient from low to high elevation to assess the effects of over a century of livestock grazing, timber harvest, and fire suppression. The high-elevation bristlecone pine stands they assessed were the least-changed of any forest type, but the changes were not insubstantial. Bristlecone-dominated forests showed a 92 percent increase in density (from 282.9 to 546.2 trees/ha). These changes were driven primarily by increased abundance of Engelmann spruce which expanded from 19.3 to 169.5 trees/ha; bristlecone density increased from 258.7 to 342.6 trees/ha. Tree density in mixed-conifer forests composed of limber pine (noted to be possible limber-southwestern white pine hybrids) and Douglas fir also showed large increases. All these changes were attributed in large part to fire suppression over the last century (Cocke and others 2005).

Brown and Schoettle (2008) provide clear evidence of gradual infilling of both a bristlecone and limber pine stand following reductions in fire severity. At the Lake John limber pine site, frequent, low-severity fires ended and increases in stand density began in the mid-1800s and may have been reinforced by livestock grazing and direct fire suppression in the 1900s (Brown & Schoettle 2008). At Packer Gulch, gradual reductions in fire frequency coupled with increased tree recruitment appear to have led to stand conditions conducive to the 1978 high-severity wildfire. These changes began in the 1600s—probably associated with cooler and wetter climatic conditions—and effects of modern fire suppression appear inconsequential at this site (Brown & Schoettle 2008).

The longevity of both bristlecone and limber pine and the presence of fire-scarred trees across the region suggest considerable potential to reconstruct southern Rocky Mountain fire chronologies and assess both human and climatic influences over multi-century time scales. Comparisons of the handful of fire chronologies that have been developed from these species (included Table 1) hint at some regional synchronicity in periods of reduced fire (ca. 1780-1830) and increased fire activity (late 1800's-ca. 1900). However, no fire years appear common to all studies, though samples within particular regions indicate some shared fire years. Donnegan and others (1991) found only three years that showed fire across multiple sites: 1748, 1851, and 1871. However, Sherriff and others (1991) found many years in which fire was recorded across > 20 percent of their sites, including one year (1880) that was recorded by trees in seven of 13 sites. Both of these authors noted that fires occurred primarily in years of decreased precipitation (typically La Niña years), particularly those that followed years of enhanced precipitation (typically, El Niño). Several of these authors also reported fire scars found in latewood or dormancy, suggesting late summer or fall burns. It would undoubtedly be interesting to develop additional chronologies from elsewhere within these species' ranges in the southern Rocky Mountains.

Fire and Management for Resilient Southern Rocky Mountain High-Five Ecosystems

Our knowledge of the role of fire in bristlecone and limber pine ecosystems is substantially incomplete, and further research is necessarily for more informed management. Significant questions remain as to what kinds of pre-settlement fire regimes best characterized these ecosystems generally, how these have changed, and what kinds of fire regimes are most likely to promote these ecosystems. High variability in historic and current stand conditions and characteristic disturbance regimes also suggests there is no "one-size-fits all" prescription for suitable burning regimes in these ecosystems, which may be highly localized and context-dependent.

Regardless of any anthropogenic changes to fire in these systems, re-establishing or maintaining pre-settlement fire regimes may not be as important as determining appropriate disturbance regimes to meet management and conservation objectives given current and projected changes to these systems. Both bristlecone and limber pine are highly susceptible to declines caused by white pine blister rust and mountain pine beetles (Schoettle 2004; Schoettle and others 2008), as with the rapidly collapsing whitebark pine ecosystems farther north (e.g., Keane & Arno 1993; Logan & Powell 2001). Southern Rocky Mountain five-needle pines are beginning to display the consequences of this vulnerability: by 2010, blister rust had been recorded in both species in Colorado, and limber pine stands across northern Colorado were experiencing high rates of mortality from mountain pine beetles (Burns, personal communication). There appears to be little reason to expect either five-needle pine not to decline substantially across the entire region. Under this scenario, combined with probable warming and drying conditions projected under anthropogenic climate change, there are pressing needs to develop management strategies for resilient bristlecone and limber pine ecosystems. Resilience is the ability of a system, such as a forest ecosystem, to absorb change and persist (e.g., Holling 1973). The appropriate application and prevention of fire may be important tools to promote regeneration, diversify age class structures, alter the balance between these species and their competitors, and conserve valuable stands and seed sources.

In areas currently affected by mountain pine beetle and/or blister rust, there appear to be few management options other than 1) retaining any surviving five-needle pines as seed sources for post-disturbance regeneration and/or 2) replanting five-needle pines where feasible. Mortality from disease and insects may in fact generate suitable habitat for five needle pine regeneration—ranging from small canopy openings to entire beetle-killed landscapes—however, subsequent recolonization is likely to be severely constrained by propagule availability and/or blister rust-induced seedling mortality. Conserving seed sources may require active management to prevent crown fire; reintroducing fire into already heavily impacted systems could be harmful. For example, high-severity fire in areas that have been decimated by beetles or rust might kill surviving seed sources, impeding regeneration, and worse, eliminating valuable genotypes with proven survival capacity. Particularly in areas impacted by white pine blister rust, any surviving trees are likely to have genetic resistance to the pathogen, and their conservation should be a priority. Strategies to protect stands containing valuable seed sources from high-severity fire may include reducing surface fuels and crown density, increasing the height to living branches, and retaining large, fire-resistant trees (e.g., Agee & Skinner 2005). Individual disease-resistant trees can also be protected by removing fuels in their immediate vicinity, water dropping, wet lining, or foil wraps (Murray 2007). As an example, possible disease-resistant whitebark pine trees were identified by field surveys in advance of the Bybee Complex Fire in Oregon; 26 trees were protected by the removal of dead and down fuel and the establishment of hand lines at each tree crown's drip line (Murray 2007). Surviving trees in areas impacted by white pine blister rust may not only benefit from reduced fire risk but also protection from other hazards—such as mountain pine beetle, for example, through the use of verbenone (e.g., Bentz and others 2005).

Reforestation may also be a useful and/or necessary option to restore southern Rocky Mountain five-needle pine stands in landscapes heavily impacted by insects and disease. Further work identifying and protecting rust-resistant individuals, collecting seeds, developing rust-resistant stock, and outplanting seedlings appear essential. Guidelines for bristlecone and limber pine planting—as have been advanced for whitebark pine (Scott & McCaughey 2006)—may also require development and testing. Spatial associations in recent burns suggest seedlings of both bristlecone and limber pine will benefit when planted adjacent to objects, especially in areas affording shelter by several objects (Coop & Schoettle 2009). In some cases, light burning may be useful to prepare sites for outplanting, though further research specific to bristlecone and limber pine planting is needed.

In stands not yet affected by mountain pine beetle or white pine blister rust, management must balance current concerns with the forecast for significant future declines in five-needle pines due to beetles and/or rust. Proactive management strategies can be developed to mitigate some of the dramatic changes these agents are likely to produce (Schoettle & Sniezko 2007). Rust-resistance screening, protection of rust-resistant populations, and outplanting can be carried out before blister rust arrives at a site. Diversifying age-class structure, particularly through increased abundance of younger cohorts, may serve the twin purposes of 1) facilitating more rapid selection for rust resistance (Schoettle & Sniezko 2007), and 2) ensuring the presence of many small-diameter individuals likely to survive mountain pine beetle attack. The abundant post-fire limber pine regeneration present in the three-decade-old Ouzel burn in Rocky Mountain National Park will represent one of the largest populations of this species remaining at high elevations in the Front Range if current rates of mountain pine beetle mortality in mature trees continue. As such, the appropriate use of burning or mechanical treatments may be useful in boosting regeneration and populations of both five-needle pines prior to the arrival of insects or disease. Treatments that disproportionately remove competing tree species from stands will be most beneficial for five-needle pines. Small openings (< 15 m diameter) are likely to be most effective for promoting bristlecone pine regeneration; much larger openings may be more beneficial for limber pine (Coop & Schoettle 2009). However, the protracted regeneration response to disturbance suggests positive responses of either species may require decades or centuries to be realized. While the current mountain pine beetle outbreak is likely to have played itself out long before then, management to increase regeneration may still mitigate some of the projected consequences of white pine blister rust, which is a longer-term threat. Conversely, in some settings, ongoing, gradual increases in stand density in the absence of fire may best serve the purpose of augmenting five-needle pine populations in advance of projected disease- or insect-caused mortality. Equally as important, settings that currently hold high densities of younger age classes may prove valuable in the context of mountain pine beetle and blister rust even if they represent recent regeneration that would historically have been constrained by fire. For example, recent and ongoing expansion of bristlecone pine into subalpine grasslands in northern New Mexico is widely held to be a symptom of a collapsed low-severity fire regime, and it may be desirable from a management perspective to return more frequent fire into these systems to conserve these ecologically (and economically) valuable grasslands. However, these populations of bristlecone pine seedlings and saplings may also be considered as a potential buffer against future mountain pine beetle or blister rust mortality.

Concluding Thoughts

Our knowledge of the role of fire in southern Rocky Mountain bristlecone and limber pine ecosystems is substantially incomplete, revealing many directions and opportunities for further research. Bristlecone pine stands appear to have experienced a range of low- to high-severity fire. What proportion of the bristlecone pine ecosystem could be best characterized by any of these regimes, their spatial extent, and how they may have been affected by fire suppression, remain open questions. In some settings, open stands bordering grassy valley bottoms and experiencing one fire regime can give way over short distances (and also over time) to dense, mixed-dominance stands that experienced another. Post-fire regeneration responses tend to be concentrated beneath or near seed sources, and may be protracted over decades. In the absence of fire, stands are likely to exhibit gradual infilling by five-needle pines and more shade-tolerant tree species. Many of these same questions and themes apply to limber pine. While the role of fire in promoting successional stands of limber pine is well known in the Colorado Front Range, this role is unlikely characteristic of the species elsewhere in the southern Rocky Mountains, where limber pine occurs in quite different ecological settings, and very little quantitative research has been conducted. As with bristlecone pine, post-wildfire regeneration dynamics of limber pine also take place on the time scale of decades to centuries.

Management in response to current threats to high-elevation five-needle pines in the southern Rocky Mountains, particularly white pine blister rust and mountain pine beetles, will need to balance a range of concerns and may include both the application and prevention of fire. Restoring pre-settlement fire regimes where they have been altered may be less important than determining the appropriate use of fire in response to current concerns. These concerns also suggest the need for further research. Under the scenario of continued expansion and intensification of white pine blister rust, what would be an optimal age-class distribution for mitigating severe losses in these communities and the services they provide during selection for rust resistance? How should this distribution be spread across the landscape—diversity at the stand level or in a mosaic of different patches each of uniform age distribution? How would this ideal be different under the scenario of mountain pine beetle attack and/or climate change? Finally, how might management tools, including fire (or the lack thereof), be best used to encourage such conditions? Applied research is needed to gain insight into these questions.

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References Cited

Allen, C. D. 1989. Changes in the landscape of the Jemez Mountains, New Mexico. Dissertation. University of California, Berkeley, CA, USA.

Antolin, M. F.; Schoettle, A. W. 2001. Fragments, extinction, and recolonization: the genetics of metapopulations. In: Joyce, D.; Simpson, J. D., eds. Part 2. Genetic Resource Management: Building Strategies for the New Millennium. Proceedings of the 27th Biennial Conference of the Canadian Tree Improvement Association. Pp 37-46.

Arno, S. E. 2001. Community types and natural disturbance processes. In: Tomback, D. F.; Arno, S. E.; Kearne, R. E., eds. Whitebark Pine Communities. Island Press, Washington, DC. Pp. 74-88.

Bailey, D. K. 1970. Phytogeography and taxonomy of *Pinus* subsection *balfourianae*. Annals of the Missouri Botanical Garden. 57: 210-249.

Baisan, C. H.; Swetnam, T. W. 1990. Fire history on a desert mountain range: Rincon Mountain Wilderness, Arizona, U.S.A. Canadian Journal of Forest Research. 20: 1559-1569.

Baker, W. L. 1992. Structure, disturbance, and change in the bristlecone pine forests of Colorado, U.S.A. Arctic and Alpine Research. 24: 17-26.

Bentz, B. J.; Kegley, S.; Gibson, K.; Their, B. 2005. A test of high-dose verbenone for stand-level protection of lodgepole and whitebark pine from mountain pine beetle (Coleoptera: Curculionidae: Scolytinae) attacks. Journal of Economic Entolomolgy. 98: 1614-1621.

Betancourt, J. L.; Van Devender, T. R.; Martin, P. S. 1990. Packrat Middens: the Last 40,000 Years of Biotic Change. The University of Arizona Press, Tucson. 467 p.

Brown, P. M.; Schoettle, A. W. 2008. Fire and stand history in limber pine (*Pinus flexilis*) and Rocky Mountian bristlecone (*Pinus aristata*) stands in Colorado. International Journal of Wildland Fire. 17: 339-347.

Burns, K. S. 2011. [Personal communication]. January 21. Lakewood, CO: U.S. Department of Agriculture, Forest Service, Forest Health Protection Region 2.

Brunstein, F. C.; Yamaguchi, D. K. 1992. The oldest known Rocky Mountain bristlecone pines (*Pinus aristata* Engelm.) Arctic and Alpine Research. 24: 253-256.

Carsey, K. S.; Tomback, D. F. 1994. Growth form distribution and genetic relationships in tree clusters of *Pinus flexilis*, a bird-dispersed pine. Oecologia. 98: 402-411.

Cocke, A. E.; Fule, P. Z.; Crouse, J. E. 2005. Forest change on a steep mountain gradient after extended fire exclusion: San Francisco Peaks, Arizona, USA. Journal of Applied Ecology. 42: 814-823.

Coop, J. D. 2011. Unpublished data. Western State College of Colorado, Gunnison, CO.

Coop, J. D.; Givnish, T. J. 2008. Constraints on tree seedling establishment in montane grasslands of the Valles Caldera, New Mexico. Ecology. 89: 1101-1111.

Coop, J. D.; Massatti, R. T.; Schoettle, A. W. 2010. Subalpine vegetation three decades after stand-replacing fire: effects of landscape context and topography on plant community composition, tree regeneration, and diversity. Journal of Vegetation Science. 21: 472-487.

Coop, J. D.; Schoettle, A. W. 2009. Regeneration of Rocky Mountain bristlecone pine (*Pinus aristata*) and limber pine (*Pinus flexilis*) three decades after stand-replacing fires. Forest Ecology & Management. 257: 893-903.

Donnegan, J. A.; Veblen, T. T.; Sibold, J. S. 2001. Climate and human influences on fire history in the Pike National Forest, central Colorado. Canadian Journal of Forest Research. 31: 1526-1539.

Donnegan, J. A.; Rebertus, J. 1999. Rates and mechanisms of subalpine forest succession along an environmental gradient. Ecology. 80: 1370-1384.

Gernandt, D. S.; Lopez, G. G.; Garcia, S. O.; Liston, A. 2005. Phylogeny and classification of *Pinus*. Taxon. 54: 29-45.

Grissino-Mayer, H. D.; Baisan, C. H.; Swetnam, T. W. 1995. Fire history in the Pinaleño Mountains of southeastern Arizona: effects of human-related disturbances. In: DeBano, L. F.; Ffolliott; P. F. (tech. coords.). Biodiversity and management of the Madrean Archipelago: The Sky Islands of Southwestern United States and Northwestern Mexico. September, 19-23, 1994, Tucson, AZ. USDA Forest Service General Technical Report RM-GTR-264, Rocky Mountain Forest and Range Experiment Station. Fort Collins, CO. Pp. 399-407.

Holling, C. S. 1973. Resilience and stability of ecological systems. Annual Review of Ecology and Systematics. 4: 1-23.

Keane, R. E.; Arno, S. F. 1993. Rapid decline of whitebark pine in western Montana: evidence from 20-year remeasurements. Western Journal of Applied Forestry. 8: 44-47.

Keeley, J. E.; Zedler, P. H. 1998. Evolution of life histories in pines. In: Richardson, D.; Cowling, R., eds. Ecology and Biogeography of *Pinus*. Cambridge University Press, Cambridge, UK. Pp. 220-248.

Lanner, R. M. 1988. Dependence of Great Basin bristlecone pine on Clark's Nutcracker for regeneration at high elevations. Arctic and Alpine Research. 20: 358-362.

Lanner, R. M. 1996. Made for Each Other: A Symbiosis of Birds and Pines. Oxford University Press, NY. 162 p.

Lanner, R. M.; Vander Wall, S. B. 1980. Dispersal of limber pine seed by Clark's Nutcracker. Journal of Forestry. 78: 637-639.

Little, E. L., Jr. 1971. Atlas of United States Trees. USDA Forest Service. Washington, DC: 1146 p.

Logan, J. A.; Powell, J. A. 2001. Ghost forests, global warming, and the mountain pine beetle (Coleoptera: Scolytidae). American Entomologist. Fall 2001: 160-172.

McCaughey, W. W.; Schmidt, W. C.; Shearer, R. C. 1986. Seed dispersal characteristics of conifers of the intermountain West. In: Shearer, R. C., compiler. Proceedings-conifer tree seed in the Inland Mountain West symposium, August 5-6 1985, Missoula, MT. USDA Forest Service General Technical Report INT-203. Intermountain Research Station, Ogden, UT. Pp. 50-62.

McCune, B. 1988. Ecological diversity in North American pines. American Journal of Botany. 75: 353-368.

Mitton, J. B.; Kreiser, B. R.; Latta, R. G. 2000. Glacial refugia of limber pine (*Pinus flexilis* James) inferred from the population structure of mitochondrial DNA. Molecular Ecology. 9: 91-97.

Murray, M. P. 2007. Fire and Pacific coast whitebark pine. In: Goheen, E. M.; Sniezko, R. A., eds. Proceedings of the conference: Whitebark Pine: a Pacific Coast perspective. August 27-31 2006, Ashland, OR. USDA Forest Service, Pacific Northwest Region R6-NR-FHP-2007-01. Ashland, OR. Pp. 51-60.

Peet, R. K. 1981. Forest vegetation of the Colorado Front Range: composition and dynamics. Vegetatio. 43: 3-75.

Peet, R. K. 1978. Latitudinal variation in southern Rocky Mountain forests. Journal of Biogeography. 5: 275-289.

Ranne, B. M.; Baker, W. L.; Andrews, T.; Ryan, M. G. 1997. Natural variability of vegetation, soils and physiography in the bristlecone pine forests of the Rocky Mountains. Great Basin Naturalist. 57: 21-37.

Rebertus, A. J.; Burns, B. R.; Veblen, T. T. 1991. Stand-dynamics of *Pinus flexilis*-dominated subalpine forests in the Colorado Front Range. Journal of Vegetation Science. 2: 445-458.

Schoettle, A. W. 2004. Ecological roles of five-needle pines in Colorado: potential consequences of their loss. In: Sniezko, R. A.; Samman, S.; Schlarbaum, S. E.; Howard, B. E., eds. Breeding and genetic resources of five-needle pines: growth, adaptability and pest resistance. USDA Forest Service Proceedings RMRS-P-32. Rocky Mountain Forest and Range Experimental Station, Fort Collins, CO. Pp. 124-135.

Schoettle, A. W.; Burns, K. S.; Costello, S.; Witcosky, J.; Howell, B.; Connor, J. 2008. A race against beetles: Conservation of limber pine. Nutcracker Notes. 14:11-12.

Schoettle, A. W.; Rochelle, S. G. 2000. Morphological variation of *Pinus flexilis* (Pinaceae), a bird-dispersed pine, across a range of elevation. American Journal of Botany. 87: 1797-1806.

Schoettle, A. W.; Sniezko, R. A. 2007. Proactive intervention to sustain high elevation pine ecosystems threatened by white pine blister rust. Journal of Forest Research. 12: 327-336.

Scott, G. L.; McCaughey, W. W. 2006. Whitebark pine guidelines for planting prescriptions. In: Riley, L. E.; Dumroese, R. K.; Landis, T. D. (tech. coords). National Proceedings: Forest and Conservation Nursery Associations—2005. USDA Forest Service Proceedings RMRS-P-43. Rocky Mountain Research Station, Fort Collins, CO. Pp. 84-90.

Shankman, D.; Daly, C. 1988. Forest regeneration above tree limit depressed by fire in the Colorado Front Range. Bulletin of the Torrey Botanical Club. 115: 272-279.

Sherriff, R. L.; Veblen, T. T.; Sibold, J. S. 2001. Fire history in high elevation subalpine forests in the Colorado Front Range. Ecoscience. 8: 369-380.

Swetnam, T. W.; Brown, P. M. 1992. Oldest known conifers in the southwestern United States: temporal and spatial patterns of maximum age. In: Kaufman, M. R.; Moir, W. H.; Bassett, R. L., eds. Old-Growth Forests in the Southwest and Rocky Mountain Regions: Proceedings of a Workshop. Rocky Mountain Forest and Range Experiment Station General Technical Report RM-213. Fort Collins, CO. Pp. 24-38.

Tomback, D. F. 2001. Clark's nutcracker: an agent of regeneration. In: Tomback, D. F.; Arno, S. E.; Kearne, R. E., eds. Whitebark Pine Communities. Island Press, Washington, DC. Pp. 89-104.

Tomback, D. F. 1982. Dispersal of whitebark pine seeds by Clark's Nutcracker: a mutualism hypothesis. Journal of Animal Ecology. 51: 451-467.

Veblen, T. T. 1986. Age and size structure of subalpine forests in the Colorado Front Range. Bulletin of the Torrey Botanical Club. 113: 225-240.

Webster, K. L.; Johnson, E. A. 2000. The importance of regional dynamics in local populations of limber pine (*Pinus flexilis*). Ecoscience. 7: 175-182.

Wells, P. V.; Stewart, J. D. 1987. Cordilleran-boreal taiga and fauna on the central Great Plains of North America, 14,000-18,000 years ago. American Midland Naturalist. 118: 94-106.

Woodmansee, R. G. 1977. Clusters of limber pine trees: a hypothesis of plant-animal coaction. Southwestern Naturalist. 21: 511-517.

Modeling Climate Changes and Wildfire Interactions: Effects on Whitebark Pine (*Pinus albicaulis*) and Implications for Restoration, Glacier National Park, Montana, USA

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Abstract—Climate changes are projected to profoundly influence vegetation patterns and community compositions, either directly through increased species mortality and shifts in species distributions, or indirectly through disturbance dynamics such as increased wildfire activity and extent, shifting fire regimes, and pathogenesis. High-elevation landscapes have been shown to be particularly sensitive to climatic change and are likely to experience significant impacts under predicted future climate change conditions. Whitebark pine (*Pinus albicaulis*), a keystone and foundation five-needle pine species, is vulnerable to multiple and interacting disturbances that have already caused major changes in species distribution and abundance. We used the mechanistic simulation model FireBGCv2 to assess potential interacting effects of future climate changes and wildfire patterns on the presence and persistence of whitebark pine in a high-elevation watershed in Glacier National Park, Montana, USA. We did not include white pine blister rust and mountain pine beetles as disturbance factors in our simulation so that we could isolate climate-fire impacts, and because these disturbance factors have already so severely reduced whitebark pine populations in the area that few live trees remain. Hence, our results presume the establishment of initial populations of live, rust-resistant trees on the MD-GNP landscape through successful restoration efforts. Our results indicate that climate changes may significantly impact whitebark pines in this region through indirect mechanisms including altered distributions of competing tree species and increased fire frequency and fire size. The sensitivity of the species to a complex suite of interacting disturbance agents suggests that conservation efforts must address and mitigate these multiple threats through a suite of restoration treatments including planting of rust-resistant stock, fuels treatments, and prescribed burning to restore whitebark pine to its current range. In addition, additional simulation modeling experiments should be developed to identify areas suitable for restoration under potential future climate regimes and test efficacy of restoration strategies under these new climate conditions.

Introduction

Climate changes are projected to profoundly influence landscape patterns and biotic community compositions either directly through increased species mortality and shifts in species distributions, or indirectly from factors such as increased wildfire activity and extent, shifting fire regimes, and pathogenesis (Bentz and others 2010; Dale and others 2001; Flannigan and others 2000; Lenihan and others 2003; McKenzie and others 2004). High-elevation landscapes have been shown to be particularly sensitive to climatic change and are likely to experience significant impacts under predicted future climate change conditions (Fagre and Peterson 2000). Whitebark pine (*Pinus albicaulis*), an important high-elevation five-needle pine that is both a keystone and foundation species (Logan and others 2010), is particularly sensitive to a complex set of interacting disturbances—climatic change, anthropogenic fire exclusion, white pine blister rust (*Cronartium ribicola*), and mountain pine beetles (*Dendroctonus ponderosae*)—that have already caused major changes in species distribution and density (Keane and Parsons 2010). Further changes in abiotic and biotic conditions will likely pose additional threats to the success of this treeline species, with likely negative consequences for snowpack accumulation and retention, timing and amount of surface water runoff, wildlife habitat and food availability, and forest succession and structure in subalpine environments in the northern Rocky Mountains (Keane and Parsons 2010; Klasner and Fagre 2002; Tomback and others 2001).

We developed a simulation modeling experiment using the mechanistic ecosystem process model FireBGCv2 (Keane and others 2011) to assess the effects of predicted future climate changes and wildfire patterns on whitebark pines in the Northern Rocky Mountains. Our objective was to test whether different trajectories of climate change would result in markedly different wildfire patterns and abundance and persistence of whitebark pine-dominated stands within the study landscape. We incorporated two climate change scenarios designed to span a range of potential regional climate futures from warmer and wetter to hotter, drier conditions. Differences in these climate projections result from alternate trajectories of global anthropogenic drivers and associated greenhouse gas emissions (IPCC 2007). We hypothesized that warming temperatures would negatively affect whitebark pine stands at lower elevations within their current range as the result of species thermal limits and competitive replacement by lower-elevation conifers; but

In: Keane, Robert E.; Tomback, Diana F.; Murray, Michael P.; and Smith, Cyndi M., eds. 2011. **The future of high-elevation, five-needle white pines in Western North America: Proceedings of the High Five Symposium.** 28-30 June 2010; Missoula, MT. Proceedings RMRS-P-63. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station. 376 p. Online at http://www.fs.fed.us/rm/pubs/rmrs_p063.html

that habitat areas for whitebark pine would increase at the upper margins of subalpine niches as temperature isotherms shifted upslope. Such upward and latitudinal migration of high-elevation forests has been previously noted in response to long-term climate trends (IPCC 2007; Millar and others 2004). Ecological niche shifts may be further complicated by altered fire regimes, which have been associated with observed and predicted changes in temperature and moisture regimes at multiple temporal and spatial scales (Heyerdahl and others 2008; Littell and others 2009; Schoennagel and others 2004; Westerling and others 2006). For example, climate changes may increase fire frequencies in high-elevation forests that historically experienced stand-replacement wildfires at long fire return intervals, as warmer temperatures and altered moisture patterns contribute to changes in fuel availability and fuel moisture. Although the important role of climate as a driver of wildfires (Heyerdahl and others 2008; Kitzberger and others 2007; Morgan and others 2008) together with the dominant role of wildfires in shaping vegetation composition and structure (Flannigan and others 2000) suggests that predictive modeling approaches for species distributions must incorporate wildfire-climate dynamics, few models are capable of integrating these complex dynamics. For example, correlative species distribution or bioclimatic envelope models are commonly used to assess climate change effects on species ranges, but are widely criticized for failing to take complex ecological interactions and species life histories into account (Hampe 2004; Heikkinen and others 2006; Sinclair and others 2010). In contrast, FireBGCv2 provides a method for mechanistically modeling the interactive effects of climate changes and wildfires on vegetation dynamics.

The FireBGCv2 modeling platform combines a mechanistic, individual tree succession model with a spatially explicit fire model incorporating ignition, spread, and effects on ecosystem components, all with stochastic properties implemented in a spatial domain (Keane and others 2011; Keane and others 1999; Keane and others 1998; Keane and others 1996). The model is designed around five hierarchical levels of spatial organization from coarse, fixed-boundary sites defined on the basis of similar topography, weather, soils, and potential vegetation; to dynamically-created stands that differ by existing vegetation composition and structure; to simulation plots on which ecosystem processes are modeled for computational efficiency; to species with well-defined physiological parameters; to individual trees, each of which is explicitly represented with attributes such as age, height, diameter at breast height, and height to live crown (Figure 1).

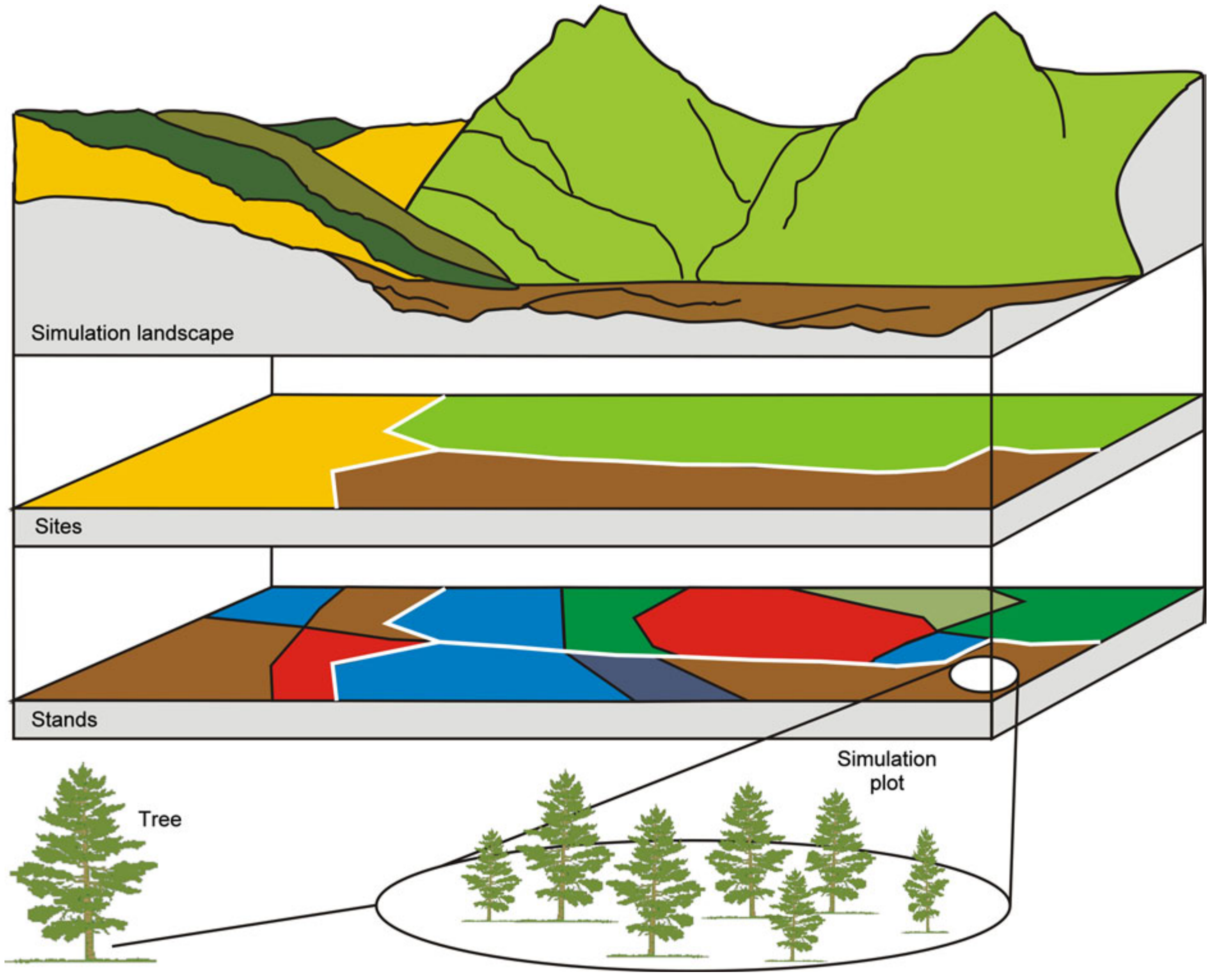


Figure 1. Hierarchical levels of spatial organization in the FireBGCv2 simulation modeling platform.

Weather and climate are important inputs to FireBGCv2 because they drive the primary canopy processes of transpiration, photosynthesis and respiration. Potential climate change effects on ecosystems are incorporated into the simulation through a series of parameters that alter daily observed (instrumental) weather streams along user-defined climate pathways including projected offsets of seasonal precipitation and temperature and annual offsets of atmospheric CO_2. Weather and climate also dynamically affect the simulation of wildfires through stand-level effects on fuel availability and fuel moisture.

Tree growth, regeneration, organic matter decomposition, litterfall and other ecological processes are simulated using detailed physical biogeochemical relationships for individual tree species. Tree establishment and mortality are modeled using probability functions with ecologically-derived parameters. Annual carbon and nitrogen gains computed daily for each stand are allocated to each tree in the stand at the end of each year and then apportioned to the stem, roots and leaves. Carbon allocation to the stem of a tree is used to calculate a corresponding diameter and height growth. Material from trees (fallen needles, leaves, and branches) is added to the fuelbed and eventually decomposes based on available water, nitrogen, and light. Whitebark pine regeneration is accomplished through a species-specific module that simulates the effects of seed crop, seed dispersal by the Clark's nutcracker, and light on whitebark tree sapling establishment (Keane and others 1990). Although FireBGCv2 can also be used to simulate effects of additional mortality factors such as white pine blister rust and mountain pine beetles, these factors were not included in the current simulation experiment.

Methods

Study Area

We simulated climate-disturbance interactions on the McDonald drainage of Glacier National Park, Montana, USA (MD-GNP, Figure 2). The MD-GNP watershed is a long, narrow, glaciated valley approximately 45,000 ha in area that contains a large lake at its base and is surrounded by rugged mountains. Elevations range from approximately 830 to 2,900 meters above sea level (masl), and the watershed is characterized by diverse and complex topography, climate, vegetation, and fire regimes. Climate within the MD-GNP watershed is mainly inland-maritime with cool, wet winters and short, warm-dry summers (Finklin 1986). Average annual precipitation ranges from 760 millimeters at West Glacier to over 1,980 millimeters at Flattop Mountain, and the majority of annual precipitation occurs as snow (Finklin 1986). Maximum July daily temperatures range from 26 °C in the lower valleys to 18 °C at 2,000 masl.

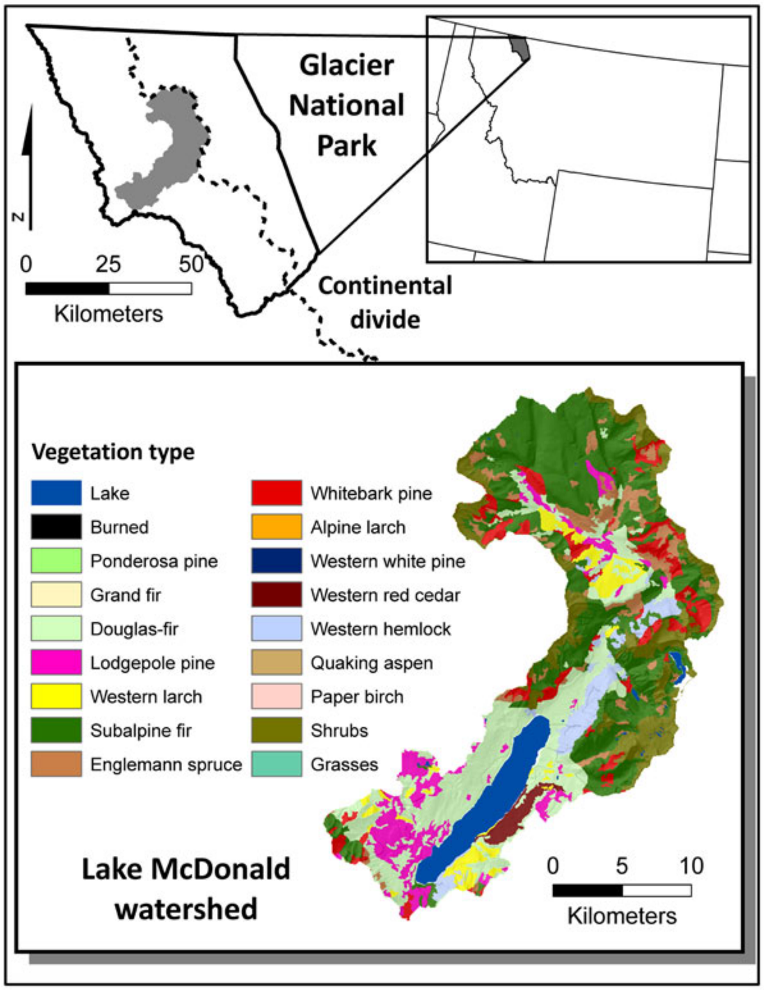


Figure 2. McDonald drainage of Glacier National Park, Montana, USA (MD-GNP).

Vegetation in the MD-GNP watershed consists of low-elevation forests of western hemlock (*Tsuga heterophylla*) and western red cedar (*Thuja plicata*) in relatively, warm, moist lakeside environments, and western larch (*Larix occidentalis*), western white pine (*Pinus monticola*), interior Douglas-fir (*Pseudotsuga menziesii* var *glauca*), and lodgepole pine (*Pinus contorta* var. *contorta*) in drier low-elevation areas (Habeck 1970a; Kessell 1979). Upper subalpine forests consist primarily of subalpine fir (*Abies lasiocarpa*), Engelmann spruce (*Picea engelmannii*), and whitebark pine (*Pinus albicaulis*) (Habeck 1970a). Alpine environments (2,200 masl and above) support Krummholz conifer and forb meadow communities (Habeck and Choate 1963). Although historically whitebark pine communities were a significant component on up to 20 percent of forested lands in Glacier National Park, currently an estimated 44 to 90 percent of these trees are dead and more than 75 percent of remaining trees are lethally infected with white pine blister rust and likely to die within the next 20 years (Graumlich 2006; Kendall and Keane 2001). Additional threats to whitebark pine persistence in Glacier National Park and elsewhere include mountain pine beetle outbreaks that have killed larger, cone-bearing trees and fire exclusion practices that have allowed for the incursion of shade tolerant tree species (notably subalpine fir) into whitebark pine forests (Keane and Parsons 2010). Although our field data indicated that whitebark pines were present as a stand-level dominant tree species on approximately seven percent of the MD-GNP watershed, the presence of stumps and snags within study plots suggests that combined biotic and abiotic disturbances had already significantly reduced the abundance of the tree species at the time of data collection (Keane and others 1999).

Two distinct fire regimes are historically evident on the MD-GNP landscape: large, stand-replacement fires at return intervals of 120 to 350 years on moist sites and mixed-severity surface fires with approximately the same return intervals on drier areas of the watershed (Barrett 1986; Barrett and others 1991; Habeck 1970b) (Table 1). This mixed fire regime features a combination of fires that kill all trees in some areas and nonlethal underburns that kill only small trees and fire-intolerant species in other areas (Habeck 1970a). The complex topography of MD-GNP has considerable influence on fire behavior and effects via the spatial arrangement of fuels on the landscape. Rocky areas with low accumulation of woody fuels impede fire spread across and within the watershed, and moist conditions on north-facing slopes often prevent spread of fire from the drier south-facing slopes (Habeck 1970a).

Table 1. Biophysical characteristics and historical fire frequency for the McDonald drainage of Glacier National Park, Montana, USA.

Site ID	Site Potential Vegetation	Average elevation (m)	Historical Fire Frequency (yrs)
1	Subalpine fir (low/wet)	1334	300
2	Subalpine fir (upper/dry)	1954	250
3	Subalpine fir (middle/dry)	1682	250
4	Subalpine fir (upper/wet)	1850	350
5	Subalpine fir (low/dry)	1288	250
6	Subalpine fir (middle/wet)	1513	300
7	Western hemlock (wet)	1086	350
8	Western hemlock (dry)	1006	300
9	Barren/Low vegetation	2180	450

Simulation Methods

We implemented three climate scenarios on the MD-GNP landscape over a 350-year simulation period. Detailed simulation methods are given in Keane and others (1996); briefly, site, stand and tree input spatial data layers and data files needed to parameterize and initialize the MD-GNP simulation landscape were quantified from field data, the literature, existing spatial data layers, and satellite imagery. Parameters that describe various site-level ecological processes and conditions across the simulation landscape were quantified from summaries of the field data, as were stand-level input parameters for fuels and tree and understory species. We modeled multiple climate regimes because although, as mentioned above, anthropogenic climate changes are projected to significantly alter ecosystem processes and patterns, few modeling studies examine potential future terrestrial landscape changes in the context of restoration (but see Covington and others 2001; Diggins and others 2010; Ravenscroft and others 2010). We suggest that simulation models provide one of the best vehicles to investigate the dynamic interactions among climate, fire, vegetation, and management, and can provide useful assessment tools for land managers designing restoration efforts under conditions of rapid ecological change, particularly where multiple trajectories of future climate regimes may exist.

Climate

We tested the effects of three climate regimes (historical conditions and two climate change scenarios) on landscape and fire dynamics. Historical conditions were derived from a 44-year (1950-1994) daily instrumental weather stream from the West Glacier weather station located within the McDonald watershed (NCDC 2011). We further used the Mountain Climate Simulator (MT-CLIM) (Hungerford and others 1989; Running and others 1987) to extrapolate the historical weather stream to sites on the simulation landscape with different elevations, slopes, and aspects. To simulate an historical climate regime the model cycled through this 44-year weather record in sequence for the duration of the simulation period. Warmer-wetter and hotter-drier climate regimes represent potential future climate trajectories for the northern Rocky Mountain region in the coming centuries, and provide insight into the conditions under which whitebark pine restoration may be implemented in the future. Both climate change scenarios used the West Glacier historical weather data set as a baseline, adjusted by modifying seasonal temperature and precipitation and starting and ending atmospheric CO_2

Table 2. Temperature (ΔT, °C) and precipitation (ΔP, cm) offsets and starting and ending atmospheric CO_2 concentrations (ppmv) for historical, A2, and B2 climate scenarios. Offsets are implemented seasonally, where Winter = January/February, Spring = March/April/May, Summer = June/July/August, and Fall = September/October/November/December.

	Element	HIST	B2	A2
Winter	ΔT	0.00	1.80	2.50
	ΔP	0.00	0.99	1.11
Spring	ΔT	0.00	1.00	3.00
	ΔP	0.00	1.17	1.02
Summer	ΔT	0.00	2.10	6.70
	ΔP	0.00	1.24	0.66
Fall	ΔT	0.00	1.60	4.60
	ΔP	0.00	1.05	0.93
	start CO_2	287	369	369
	end CO_2	287	621	856

levels (Table 2). Values for these offsets were derived relative to a 1950-1999 base period from the Hadley Centre (UK) HadCM3 general circulation model (GCM), using an average of grid points corresponding to the Pacific northwest region (Mote 2003) for Intergovernmental Panel on Climate Change (IPCC) Special Report on Emission Scenarios (SRES) A2 and B2 emissions scenarios (Nakicenovic and others 2000). The A2 scenario describes a heterogeneous world with high population growth, slow economic development and slow technological changes and is associated with significant changes in regional climatology; specifically hotter-drier summers (+6.7 ˚C, -34 percent precipitation) and warmer-wetter winters (+2.5 ˚C, -11 percent precipitation) as compared with current conditions. The B2 scenario describes a world with intermediate population and economic growth, emphasizing local solutions to economic, social, and environmental sustainability, and is projected to result in warmer- wetter summer conditions (+2.1 ˚C, +24 percent precipitation) and warmer but slightly drier winters (+1.8 ˚C, -1.0 percent precipitation) across the study region. Temperature and precipitation offsets and CO_2 levels were ramped up in even annual increments for the first 100 years of the simulation and then held at those levels for the following 250 simulation years.

Whitebark pine

Although none of the whitebark pines present in the input tree list for MD-GNP were live at the time of field data recording due to high mortality from white pine blister rust as described above, we recoded them as live trees to produce a viable parent population. Even so, this tree list describes a relatively low initial proportion of whitebark pine-dominated stands on the simulation landscape (approximately seven percent), likely because of long-term competitive exclusion from subalpine fir. We further did not include white pine blister rust as a disturbance factor in the simulations because it is likely that few whitebark pines would have persisted long enough for seed dispersal to occur, as when white pine blister rust is specified as a factor a 99 percent rust mortality probability is imposed on all five-needle pines. Mountain pine beetle mortality can be selected as an additional simulated disturbance type, but this mortality factor was not included in this experiment so that we could isolate climate-fire impacts. Thus our experimental results assume an initial population of live, rust-resistant, reproductively mature whitebark pines on the MD-GNP landscape such as would result from the implementation of a successful integrated restoration program.

Wildfire

All simulations were performed under natural fire regime conditions in which all fires simulated on the study area were allowed to burn without enacting fire suppression factors. We defined historical fire return intervals using fire chronologies, fire history data, and fire atlases for Glacier National Park and elsewhere (Keane and others 1999). The frequency of ignition and points of origin of simulated fires were stochastically predicted at a yearly time step across the simulation landscape and climate, fuels and fire management were mechanistically linked such that the stand-level probability of fire occurrence was scaled to the size of the stand, level of fire management, and climate. The potential for a stand to experience ignition (burnability) was determined by the amount and type of fuel in the stand (Keane and others 2011).

Analysis

Our simulation experiment produced both non-spatial and spatial output files. Non-spatial, stand-level output contained an array of variables aggregated by simulation year; we summarized stand area and dominant tree species per stand based on basal area using data management and analysis tools in the R and MATLAB software packages (MATLAB 1984-2009; R Development Core Team 2010). Non-spatial, landscape-level output included cumulative number of wildfires, average and maximum fire size, and cumulative area burned during each simulation year. We produced spatial output in the form of thematic map layers for specific annual stand-level variables including dominant species by basal area and cumulative number of fires. ESRI ArcMap software was used to display and analyze spatial data layers (ESRI 1999-2009).

Results

We observed significant changes in abundance and persistence of whitebark pine on the MD-GNP simulation landscape across the 350-year simulation period (Figure 3). The proportion of the landscape dominated by whitebark pine decreased sharply during the first 100 years of the simulation for all modeled climate scenarios, consistent with an increase in wildfires under our modeled natural fire regime. Subsequently, under historical climate conditions the proportion of whitebark pine increased as newly germinated trees reached minimum reproductive age (60 years) and produced seed. Thus, by simulation year 190 whitebark

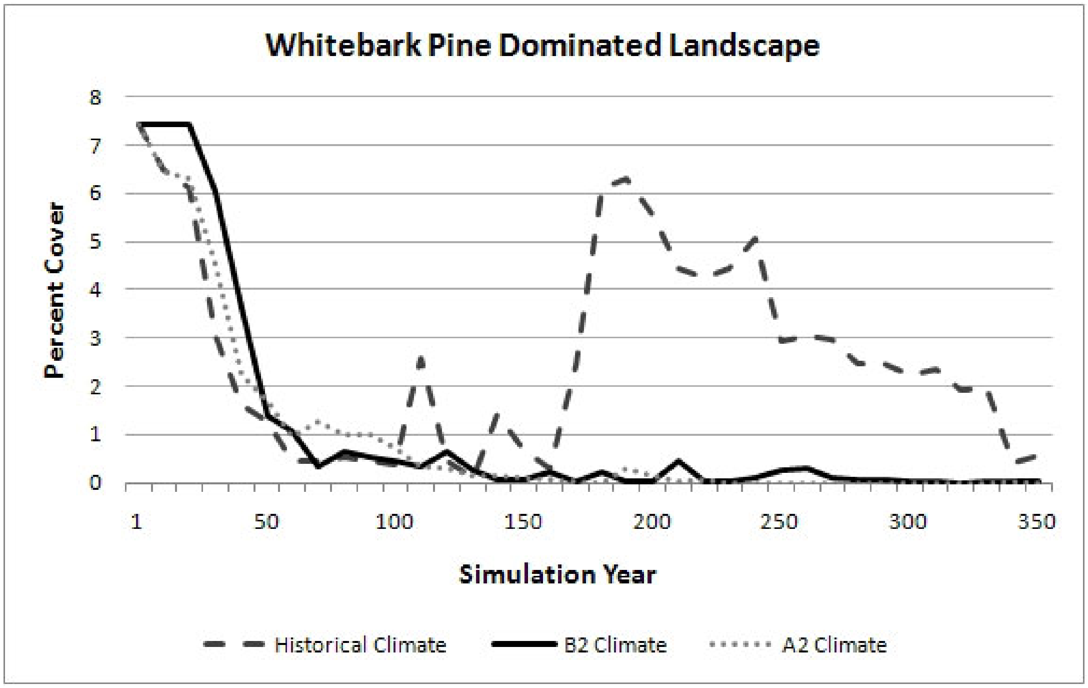


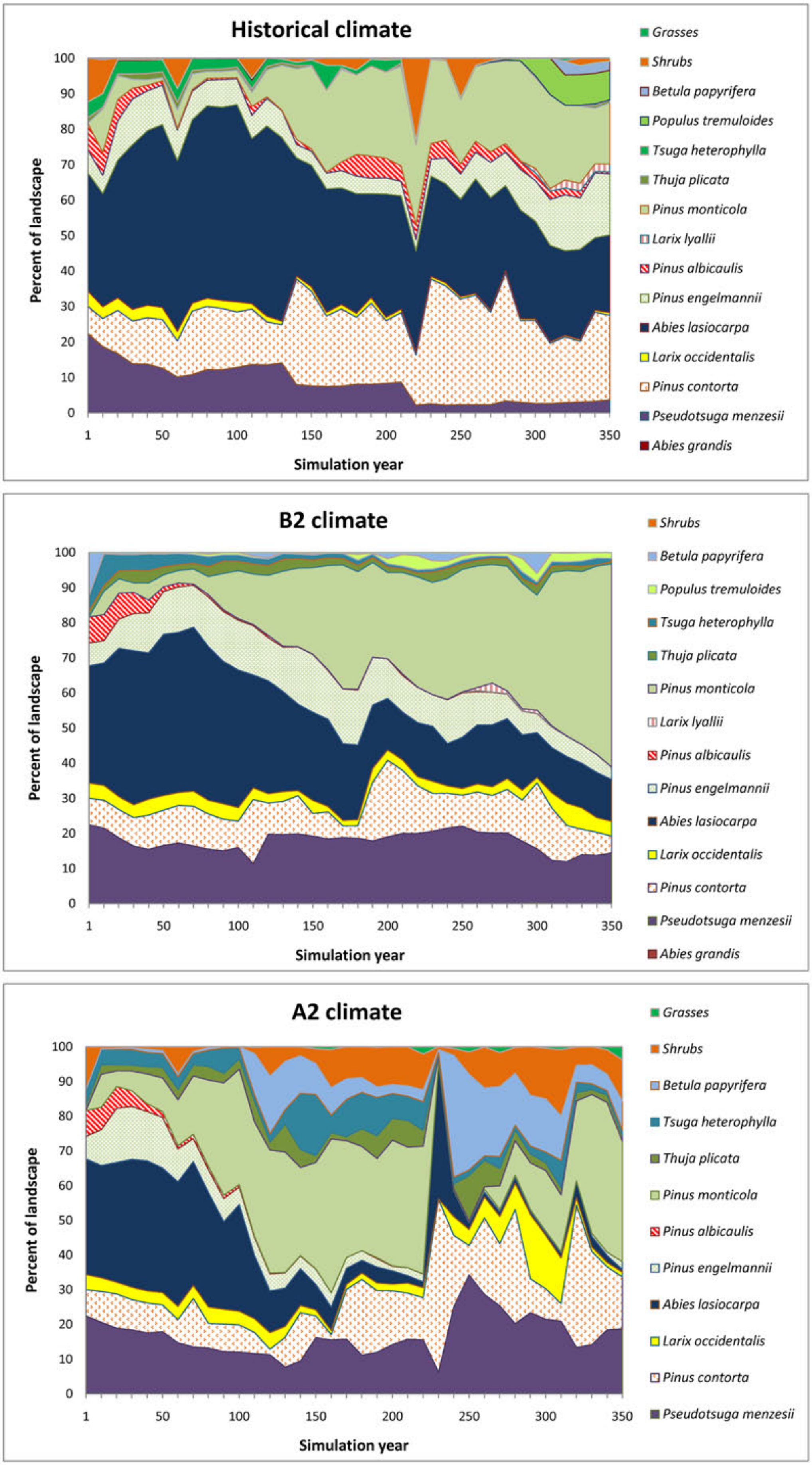
Figure 3. Changes in abundance and persistence of whitebark pine on the MD-GNP simulation landscape across the 350-year simulation period for historical (solid line), B2 (dash) and A2 (dot) climate scenarios.

pines were dominant in over six percent of the MD-GNP landscape, nearly to the level described by our input data. For the A2 and B2 climate scenarios less than one percent of the landscape retained whitebark pines as a dominant overstory component from simulation years 60 onward, and no whitebark-pine dominated stands existed under A2 climate conditions beyond simulation year 230.

Simulated historical climate conditions resulted in temporal variation in the proportion of the MD-GNP watershed occupied by subalpine fir, Douglas-fir, lodgepole pine, and western white pine (Figure 4). The abundance of western white pines was facilitated by the exclusion of blister rust and mountain pine beetles as disturbance factors in the simulation experiment; although these trees were historically a major constituent of landscapes in the inland northwest before the 20th century, they have declined greatly in both distribution and extent (Tomback and Achuff 2010).

The percent of the MD-GNP landscape dominated by shade tolerant tree species decreased across the simulation period for all climate scenarios (Figure 5), likely as the result of our imposed natural fire management scenario and its effect on reducing overstory biomass developed during the 20th century period of fire exclusion in the northern Rocky Mountains. Increases in shade tolerant species within scenarios occurred during periods of decreased wildfire activity, as expected in forested landscapes where shade-tolerant species usually dominate later stages of succession (Keane and others 1998). In addition, the spatial arrangement of vegetation types differed among scenarios and as simulations progressed as the result of climate-fire interactions. Under historical climate conditions some upper elevation areas of the watershed initially dominated by subalpine fir were replaced by Englemann spruce and, to a lesser extent, subalpine larch and aspen-dominated stands, while lodgepole pine and western white pine increased in lower elevation areas (Figure 6). For the B2 and A2 scenarios upper elevation subalpine fir stands were almost completely replaced by western white pine and Douglas-fir dominated stands, with an additional component of lodgepole pine and paper birch *(Betula papyrifera)*. The dominant role of wildfires in shaping landscape vegetation is evident in thematic maps of overstory structural stage showing the decrease in mature trees with increasing fire activity on the landscape (Figure 7).

Wildfire patterns differed across historical and climate change scenarios. The model simulated 251 wildfires in 170 fire years for the historical climate scenario, as compared with 304 wildfires in 180 fire years for the B2 scenario and 536 fires in 253 fire years for the A2 scenario (Table 3). Maximum and average wildfire size were larger for the A2 climate than simulated historical or B2 climates, and over the 350 years of the simulation two and a half times more area burned under the A2 scenario than under simulated historical conditions (Figure 8, Table 3). Fires burned a majority of the landscape area under all simulated climate conditions, and only a very small proportion of the landscape was left unburned under A2 climate conditions (0.03 percent). Warmer-wetter conditions associated with the B2 climate scenario decreased average and maximum wildfire size and cumulative area burned and increased the proportion of unburned landscape as compared with the historical climate scenario. Repeat fires (reburns) occurred across much of the simulation landscape for all modeled climate regimes. Approximately 78 percent of the simulation landscape reburned under the modeled historical climate regime as compared with 85 percent for the B2 scenario and 95 percent for the A2 scenario (Figure 9). Shifts in temperature and precipitation associated with the A2 and B2 scenarios did not markedly alter the distribution



Figures 4a-4c. Percent of the MD-GNP simulation landscape occupied by tree species, shrubs, and grasses for the 350-year simulation period, where colored bands represent individual cover types and the width of the area fill at each timestep represents the percentage of the landscape occupied by that cover type.

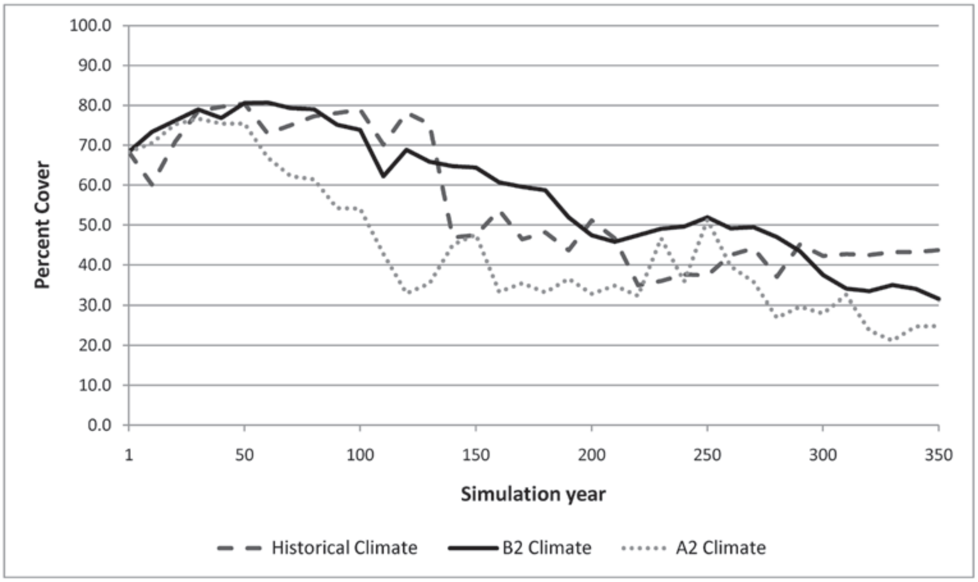


Figure 5. Temporal changes in the percent of the MD-GNP landscape dominated by shade tolerant tree species for historical, A2, and B2 climate scenarios. Shade tolerant tree species are grand fir, Douglas-fir, subalpine fir, Englemann spruce, western red cedar, and western hemlock.

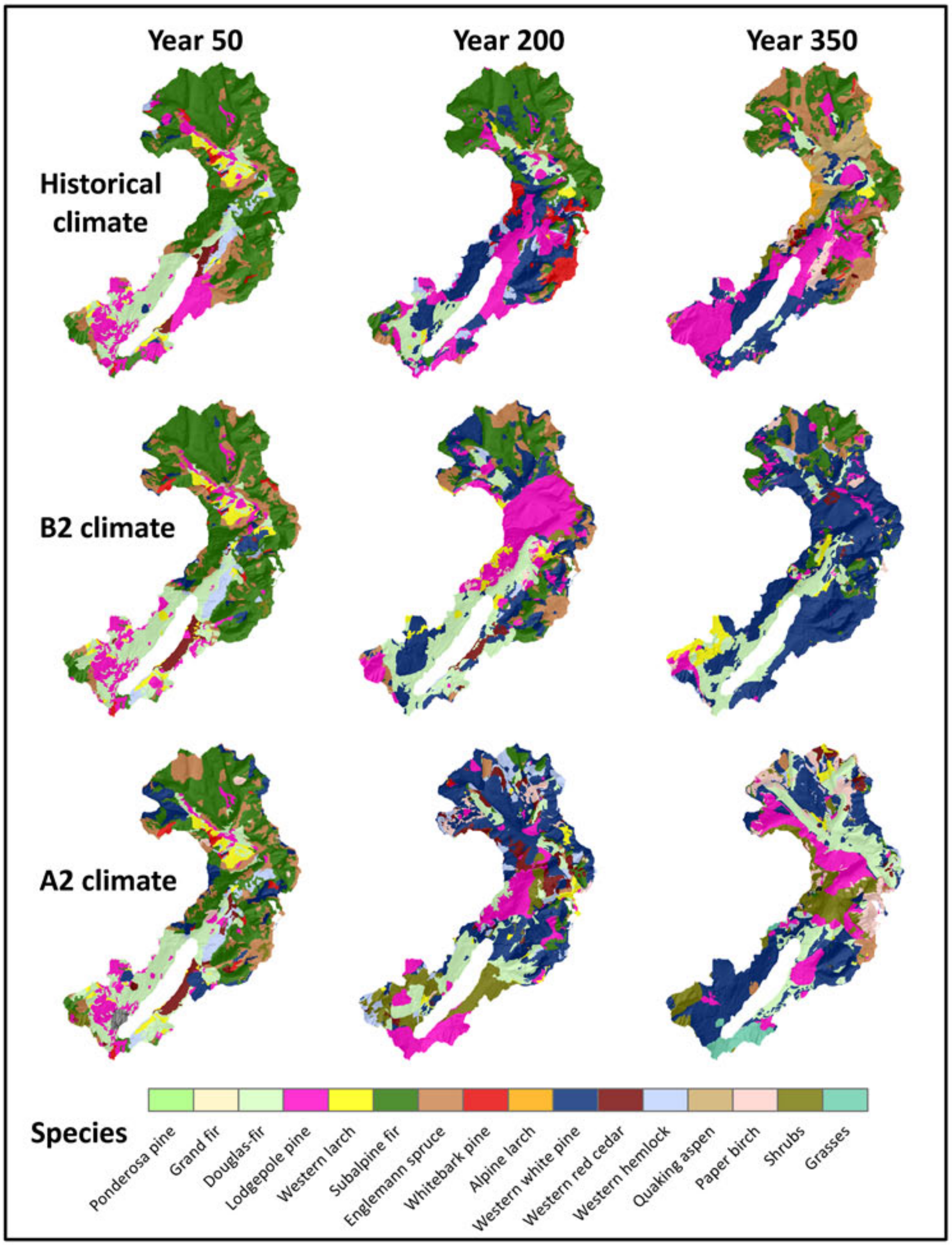


Figure 6. Dominant species by basal area on the MD-GNP simulation landscape for historical, B2, and A2 climate scenarios, simulation years 50, 200, and 350.

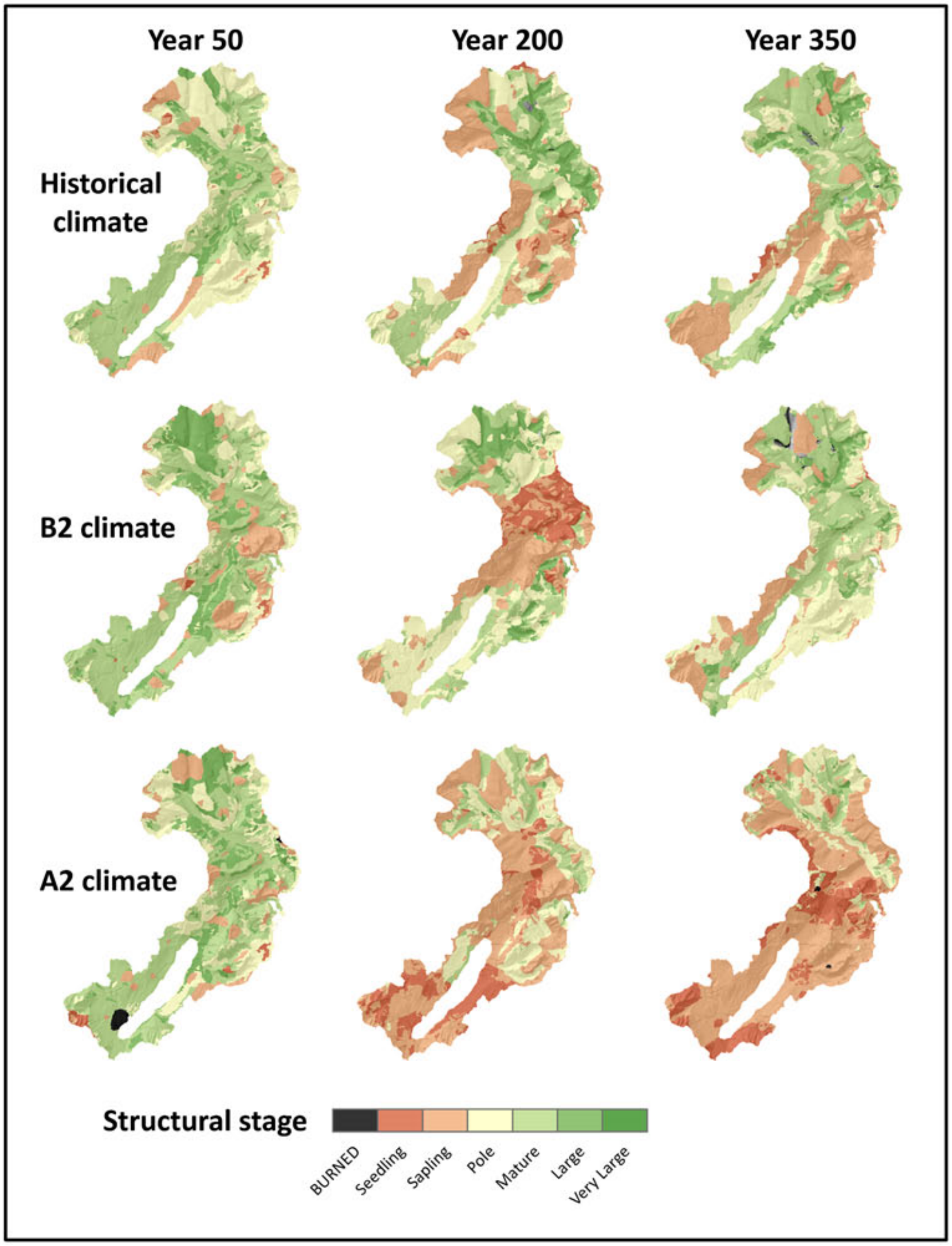


Figure 7. Overstory structural stage on the MD-GNP simulation landscape for historical, B2, and A2 climate scenarios, simulation years 50, 200, and 350.

Table 3. Simulated wildfire dynamics for the McDonald drainage of Glacier National Park, Montana, USA under historical, B2, and A2 climate scenarios for a 350-year simulation period.

Parameter	Historical climate	B2 climate scenario	A2 climate scenario
Cumulative number of wildfires	251	304	536
Cumulative number of wildfire years (yrs)	170	180	253
Cumulative area burned (ha)	126774.72	112406.94	314900.37
Landscape burned area multiplier	2.94	2.61	7.31
Percent of landscape unburned (%)	8.77	10.29	0.03
Average fire size (ha)	505.10	369.76	587.50
Maximum fire size (ha)	14233.33	7281.63	27383.4

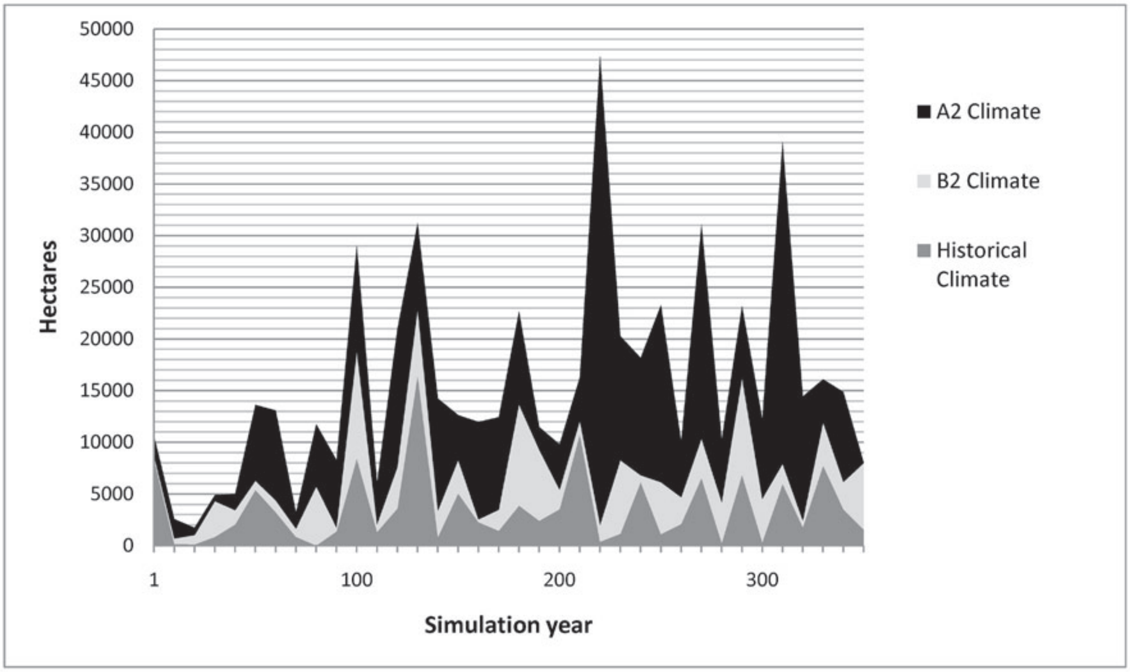


Figure 8. Annual burned area on the MD-GNP simulation landscape for historical, B2, and A2 climate scenarios for a 350-year simulation period.

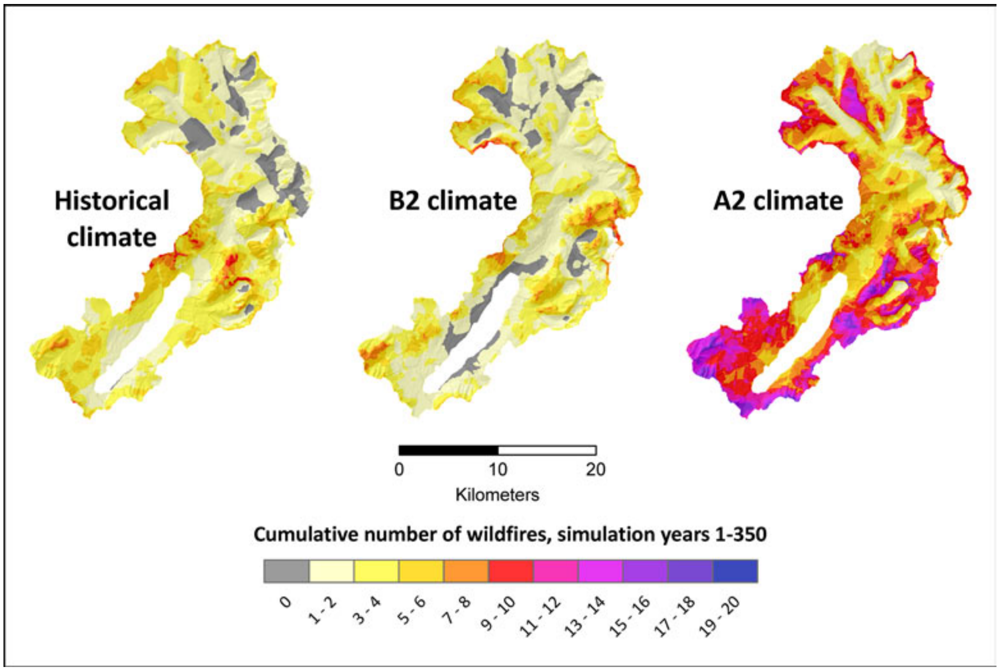
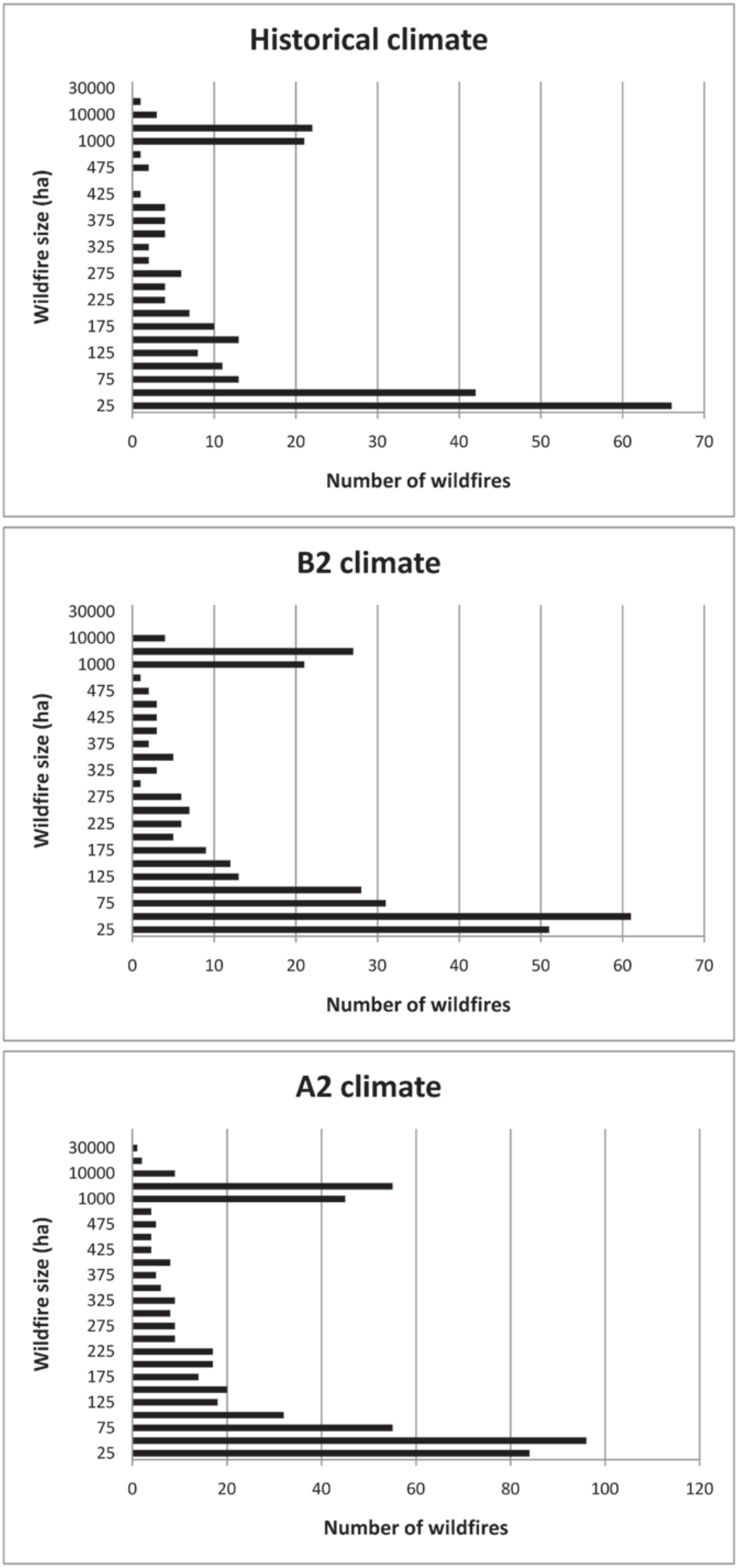


Figure 9. Cumulative number of wildfires on the MD-GNP simulation landscape for historical, B2, and A2 climate scenarios for a 350-year simulation period.

of fire sizes across the simulation period as compared with the historical simulation, but instead influenced the overall number of fires burning within coarse fire size classes (Figure 10).

Discussion

Our objective was to test whether climate and disturbance interactions influenced abundance and persistence of whitebark pine-dominated stands within the MD-GNP watershed. The study location provided an ideal context within which to perform this simulation experiment because it is a landscape where whitebark pine was an historically significant component but has declined severely in recent decades as the result of the combined effects of white pine blister rust, mountain pine beetles, and fire exclusion. Recent attention has been focused on restoring whitebark pines to this region (Keane and Parsons 2010), but current recommendations do not incorporate potential effects of climatic change as a factor in long-range management plans although shifts in climate are predicted to further reduce



Figures 10a-10c. Distribution of fire sizes simulated under historical, B2, and A2 climate scenarios.

whitebark pine populations either directly through increased climate-related mortality or indirectly through increased activity of pests and pathogens and competition from lower-elevation conifer species (Koteen 2002; Logan and others 2010; Logan and Powell 2001; McKenney and others 2007).

We hypothesized that climate changes, and in particular warming temperatures, would shift the whitebark pine distribution in GNP-MD upward in elevation via expansion of suitable habitat in upper subalpine zones and competitive replacement from lower elevation tree species in response to warming temperatures in the subalpine zone. We further posited potential synergistic interactions of climate changes and wildfires in which increased fuel loading in upper, previously lightly vegetated zones might result in an increase in wildfire frequencies and extents within those zones. Although our results suggest that hotter-drier conditions associated with the A2 climate scenario increased wildfire frequency and the number of large fires in GNP-MD, we did not observe shifts in whitebark pine distribution or increased abundance for either of the climate change scenarios. In fact, whitebark pine decreased in abundance by the end of the 350-year simulation period for the three climate scenarios. For the historical climate scenario we attribute this decline to competitive exclusion by shade-tolerant Englemann spruce and subalpine fir that dominated in the absence of few repeat fires. Given the historical (pre-fire exclusion) fire rotation of 250 years or more in areas of the simulation landscape suitable for whitebark pine establishment, it is likely that the abundance of whitebark pine would peak again were the simulation period extended for additional centuries. Keane and Parsons (2010) note that it may take 50 to 250 years for shade-tolerant trees to replace whitebark pine in the overstory, a period that matches the temporal dynamics of our simulation. Specifically, whitebark pine abundance peaked at about year 200 in the simulation, but decreased over the following 150 years as shade-tolerant species readily colonized recently-burned stands.

We attribute the rapid decline of whitebark pine in the B2 scenario to increasing abundance of western white pines within subalpine habitats (Figure 4). Western white pine has the least restricted distribution of all white pine types, and exists within elevations of 0-3,350 masl and a geographic range that spans 17 degrees of latitude and 13 degrees of longitude (Tomback and Achuff 2010). Characteristics of western white pine that enable its success under warmer-wetter climate conditions as compared with whitebark pine include its increased heat tolerance and faster reproductive maturity. The extirpation of whitebark pine from GNP-MD under the A2 climate regime was caused by the combined effects of climate-mediated vegetation shifts in stands that were initially dominated by whitebark pines, especially in higher elevation areas of the simulation landscape; and by the marked increase in wildfire activity. The two and a half times increase in area burned under A2 climate conditions coupled with the increase in number of repeat fires over the simulation period resulted in the entrainment of much of the landscape in early seral stage, immature forests. Because the cone-bearing age for whitebark pine is 60 to 100 years on most sites (Arno and Hoff 1989), trees that germinated post-fire likely did not reach either cone-producing age or grow taller than a lethal scorch height before the next wildfire occurred.

Changes in vegetation observed under climate change scenarios result from the interaction of temperature and precipitation-driven changes in species habitats and wildfire dynamics. Wildland fire was historically an important component of many forests in the western U.S., as evidenced by many resident species that exhibit morphological and physiological adaptations that provide survival advantages during fire events (Agee 1996; Habeck and Mutch 1973). It is believed that past uncontrolled fires did not, at any one point in time, completely burn over a given landscape, because many stages of successional development are usually present (Habeck and Mutch 1973). Although historical and B2 climate conditions do not seem to violate this description of fire-adapted landscapes, the wildfire and vegetation patterns resulting from our A2 climate simulations do. This drastic change in vegetation composition and structure, and its attendant shift in wildfire regimes, suggests that future forests within the northern Rocky Mountain region may appear and function very differently than the forests of the past.

Management Implications

Our results demonstrate that potential future regional climatic changes described by the SRES B2 and A2 emissions scenarios will likely have significant impacts on the abundance and persistence of whitebark pines in the MD-GNP watershed, and perhaps within other high-elevation areas with similar biotic and abiotic characteristics. Our modeling results indicate that the mechanisms influencing whitebark pine success are different for each of our simulated climate regimes, suggesting that each of these climate trajectories may require different management strategies to maintain the tree species on the landscape. Keane and Parsons (2010) recommended restoration treatments for whitebark pine forests that include emulation of historical fire regimes through prescribed burning and wildland fire management and manual planting of whitebark pine seedlings. Although these treatments may be effective under current climate conditions, the results of our experiment indicate that these strategies may not be appropriate given potential future climate changes.

Our recommendations for restoring whitebark pines to treeline environments in the northern Rocky Mountains include the following: first and foremost, augment existing populations through intensive outplanting of proven rust resistant stock. This activity should be initiated immediately so that trees reach cone-bearing age under climate conditions as close to the historical range as possible. Second, identify areas where whitebark pine establishment and growth are viable under both current and future conditions, and proactively restore these areas. Restoration treatments should include rust-resistant planting, fuels treatments to reduce shade-tolerant competitors, insect protection strategies such as verbenone, and prescribed burning to emulate historical fire regimes. Third, anticipate effects of hotter, drier future climate conditions on increasing wildfire frequency and size and design a program of fuels treatments and prescribed burning to reduce fuel loading in areas of historically mixed-severity fire regimes. Finally, implement additional research projects that (1) include the synergistic effects of white pine blister rust, mountain pine beetles, and climate changes on whitebark pine populations; (2) identify levels of rust resistance necessary for successful establishment and persistence of whitebark pine forests; and (3) use simulation modeling experiments to test the efficacy of alternative suites of management activities in the context of multiple disturbances.

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References

Agee, J. 1996. Fire ecology of Pacific Northwest forests. Washington, DC, USA: Island Press. 493 p.

Arno, S.; Hoff, R. 1989. Silvics of whitebark pine (*Pinus albicaulis*). Gen. Tech. Rep. INT-253. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station. 11 p.

Barrett, S. W. 1986. Fire history of Glacier National Park: Middle Fork Flathead River drainage. Final Report Supplement 22034. Missoula, MT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station.

Barrett, S. W.; Arno, S. F.; Key, C. H. 1991. Fire regimes of western larch-lodgepole pine forests in Glacier National Park, Montana. Canadian Journal of Forest Research. 21(12): 1711-1720.

Bentz, B.; Régnière, J.; Fettig, C.; Hansen, E.; Hayes, J.; Hicke, J.; Kelsey, R.; Negrón, J.; Seybold, S. 2010. Climate change and bark beetles of the western United States and Canada: Direct and indirect effects. BioScience. 60(8): 602-613.

Covington, W.; Fulé, P.; Hart, S.; Weaver, R. 2001. Modeling ecological restoration effects on ponderosa pine forest structure. Restoration Ecology. 9(4): 421-431.

Dale, V. H.; Joyce, L. A.; McNulty, S.; Neilson, R. P.; Ayres, M. P.; Flannigan, M. D.; Hanson, P. J.; Irland, L. C.; Lugo, A. E.; Peterson, C. J.; Simberloff, D.; Swanson, F. J.; Stocks, B. J.; Wotton, B. M. 2001. Climate change and forest disturbances. BioScience. 51(9): 723-734.

Diggins, C.; Fulé, P.; Kaye, J.; Covington, W. 2010. Future climate affects management strategies for maintaining forest restoration treatments. International Journal of Wildland Fire. 19(7): 903-913.

ESRI. 1999-2009. ArcMap 9.2. ESRI, Inc.

Fagre, D. B.; Peterson, D. L. 2000. Ecosystem dynamics and disturbance in mountain wildernesses: Assessing vulnerability of natural resources to change. In: McCool, S. F.; Cole, D. N.; Borrie, W. T.; O'Loughlin, J., eds. Wilderness Science in a Time of Change, Vol. 3: Wilderness as a Place for Scientific Inquiry. Ogden, UT: Rocky Mountain Research Station, USDA Forest Service: 74-81.

Finklin, A. I. 1986. A climatic handbook for Glacier National Park: With data for Waterton Lakes National Park. Gen. Tech. Rep. INT-204. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station. 55 p.

Flannigan, M.; Stocks, B.; Wotton, B. 2000. Climate change and forest fires. The Science of the Total Environment. 262(3): 221-229.

Graumlich, L. J. 2006. Interpretive Resource Bulletin Series: Whitebark Pine. West Glacier, MT: National Park Service, Crown of the Continent Research Learning Center. 2 p.

Habeck, J.; Mutch, R. 1973. Fire-dependent forests in the northern Rocky Mountains. Quaternary Research. 3(3): 408-424.

Habeck, J. R.; Choate, C. M. 1963. An analysis of Krummholz Communities at Logan Pass, Glacier National Park. Northwest Science. 37(4): 165-166.

Habeck, J. R. 1970a. The vegetation of Glacier National Park, Montana. U.S. Department of Interior National Park Service Final Report on file at Glacier National Park, West Glacier, Montana. 132 p.

Habeck, J. R. 1970b. Fire ecology investigations in Glacier National Park—Historical considerations and current observations. U.S. Department of Interior National Park Service Final Report on file at Glacier National Park, West Glacier, Montana. 80 p.

Hampe, A. 2004. Bioclimate envelope models: what they detect and what they hide. Global Ecology and Biogeography. 13(5): 469-471.

Heikkinen, R.; Luoto, M.; Araújo, M.; Virkkala, R.; Thuiller, W.; Sykes, M. 2006. Methods and uncertainties in bioclimatic envelope modelling under climate change. Progress in Physical Geography. 30(6): 751.

Heyerdahl, E. K.; McKenzie, D.; Daniels, L. D.; Hessl, A. E.; Littell, J. S.; Mantua, N. J. 2008. Climate drivers of regionally synchronous fires in the inland Northwest (1651-1900). International Journal of Wildland Fire. 17(1): 40-49.

Hungerford, R. D.; Nemani, R. R.; Running, S. W.; Coughlan, J. C. 1989. MTCLIM: A mountain microclimate simulation model. Gen. Tech. Rep. INT-414. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station. 52 p.

IPCC. 2007. Climate Change 2007: Synthesis Report. Contribution of Working Groups I, II, and III to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change. Geneva, Switzerland: IPCC. 104 p.

Keane, R.; Arno, S. F.; Brown, J. K.; Tomback, D. F. 1990. Modelling stand dynamics in whitebark pine (*Pinus albicaulis*) forests. Ecological Modelling. 51: 73-95.

Keane, R.; Parsons, R. 2010. Restoring whitebark pine forests of the northern Rocky Mountains, USA. Ecological Restoration. 28(1): 56-70.

Keane, R. E.; Ryan, K. C.; Running, S. W. 1996. Simulating effects of fire on northern Rocky Mountain landscapes with the ecological process model FIRE-BGC. Tree Physiology. 16(3): 319-331.

Keane, R. E.; Ryan, K.; Finney, M. 1998. Simulating the consequences of fire and climate regimes on a complex landscape in Glacier National Park, USA. Tall Timbers. 20: 310-324.

Keane, R. E.; Morgan, P.; White, J. D. 1999. Temporal patterns of ecosystem processes on simulated landscapes in Glacier National Park, Montana, USA. Landscape Ecology. 14(3): 311-329.

Keane, R. E.; Loehman, R. A.; Holsinger, L. M. 2011. A research simulation platform for exploring fire and vegetation dynamics: The FireBGCv2 landscape fire succession model. Gen. Tech. Rep. RMRS-GTR-255. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station. 200 p.

Kendall, K.; Keane, R. 2001. Whitebark pine decline: infection, mortality, and population trends. In: Tomback, D. F.; Arno, S. F.; Keane, R. E., eds. Whitebark pine communities: Ecology and restoration. Washington, DC: Island Press: 221–242.

Kessell, S. R. 1979. Gradient modeling: resource and fire management. New York: Springer-Verlag. 432 p.

Kitzberger, T.; Brown, P.; Heyerdahl, E.; Swetnam, T.; Veblen, T. 2007. Contingent Pacific–Atlantic Ocean influence on multicentury wildfire synchrony over western North America. Proceedings of the National Academy of Sciences. 104(2): 543.

Klasner, F. L.; Fagre, D. B. 2002. A half century of change in alpine treeline patterns at Glacier National Park, Montana, USA. Arctic, Antarctic, and Alpine Research. 34(1): 49-56.

Koteen, L. 2002. Climate Change, whitebark pine, and grizzly bears in the Greater Yellowstone Ecosystem. In: Schneider, S. H.; Root, T. L., eds. Wildlife responses to climate change: North American case studies. Washington, DC: Island Press.

Lenihan, J.; Drapek, R.; Bachelet, D.; Neilson, R. 2003. Climate change effects on vegetation distribution, carbon, and fire in California. Ecological Applications. 13(6): 1667-1681.

Littell, J.; McKenzie, D.; Peterson, D.; Westerling, A. 2009. Climate and wildfire area burned in western US ecoprovinces, 1916-2003. Ecological Applications. 19(4): 1003-1021.

Logan, J.; Macfarlane, W.; Willcox, L. 2010. Whitebark pine vulnerability to climate-driven mountain pine beetle disturbance in the Greater Yellowstone Ecosystem. Ecological Applications. 20(4): 895-902.

Logan, J. A.; Powell, J. A. 2001. Ghost forests, global warming, and the mountain pine beetle (Coleoptera: Scolytidae). American Entomologist. 47(3): 160-173.

MATLAB. 1984-2009. MATLAB: The Language of Technical Computing. The MathWorks.

McKenney, D.; Pedlar, J.; Lawrence, K.; Campbell, K.; Hutchinson, M. 2007. Potential impacts of climate change on the distribution of North American trees. BioScience. 57(11): 939-948.

McKenzie, D.; ZE'EV, G.; Peterson, D.; Mote, P. 2004. Climatic change, wildfire, and conservation. Conservation Biology. 18(4): 890-902.

Millar, C. I.; Westfall, R. D.; Delany, D. L.; King, J. C.; Graumlich, L. J. 2004. Response of subalpine conifers in the Sierra Nevada, California, USA, to 20th-century warming and decadal climate variability. Arctic, Antarctic, and Alpine Research. 36(2): 181-200.

Morgan, P.; Heyerdahl, E.; Gibson, C. 2008. Multi-season climate synchronized forest fires throughout the 20th century, northern Rockies, USA. Ecology. 89(3): 717-728.

Mote, P. 2003. CLIMET downscaled HadCM3 model output, SRES A2 and B2, northern Rocky Mountain region. Unpublished data supplied to authors by Phillip Mote.

Nakicenovic, N.; Alcamo, J.; Davis, G.; de Vries, B.; Fenhann, J.; Gaffin, S.; Gregory, K.; Grubler, A.; Jung, T. Y.; Kram, T.; La Rovere, E. L.; Michaelis, L.; Mori, S.; Morita, T.; Pepper, W.; Pitcher, H. M.; Price, L.; Riahi, K.; Roehrl, A.; Rogner, H.-H.; Sankovski, A.; Schlesinger, M.; Shukla, P.; Smith, S. J.; Swart, R.; van Rooijen, S.; Victor, N.; Dadi, Z. 2000. Special Report on Emissions Scenarios : A special report of Working Group III of the Intergovernmental Panel on Climate Change. Cambridge, UK: Cambridge University Press. 612 p.

NCDC. 2011. Daily surface data. U.S. Department of Commerce National Climatic Data Center [Accessed 2008].

R Development Core Team. 2010. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing.

Ravenscroft, C.; Scheller, R.; Mladenoff, D.; White, M. 2010. Forest restoration in a mixed-ownership landscape under climate change. Ecological Applications. 20(2): 327-346.

Running, S. W.; Nemani, R. R.; Hungerford, R. D. 1987. Extrapolation of synoptic meteorological data in mountainous terrain and its use for simulating forest evapotranspiration and photosynthesis. Canadian Journal of Forest Research. 17(6): 472-483.

Schoennagel, T.; Veblen, T. T.; Romme, W. H. 2004. The interaction of fire, fuels, and climate across Rocky Mountain forests. BioScience. 54(7): 661-676.

Sinclair, S. J.; White, M. D.; Newell, G. R. 2010. How Useful Are Species Distribution Models for Managing Biodiversity under Future Climates? Ecology and Society. 15(1): 8.

Tomback, D.; Stephen F. Arno; Keane, R. E. 2001. Whitebark pine communities: Ecology and Restoration. Washington DC, USA: Island Press. 440 p.

Tomback, D.; Achuff, P. 2010. Blister rust and western forest biodiversity: ecology, values and outlook for white pines. Forest Pathology. 40(3-4): 186-225.

Westerling, A. L.; Hidalgo, H. G.; Cayan, D. R.; Swetnam, T. W. 2006. Warming and Earlier Spring Increase Western U.S. Forest Wildfire Activity. Science. 313: 940-943.

Fuel and Fire Behavior in High-Elevation Five-Needle Pines Affected by Mountain Pine Beetle

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Abstract—Bark beetle-caused tree mortality in conifer forests affects the quantity and quality of forest fuels and has long been assumed to increase fire hazard and potential fire behavior. In reality, bark beetles and their effects on fuel accumulation and subsequent fire hazard have only recently been described. We have extensively sampled fuels in three conifer forest types (lodgepole pine, Engelmann spruce and Douglas-fir) and described bark beetle/fuels/fire interactions within the context of intermountain disturbance regimes. Our data sets were developed by measuring the forest biomass in stands with endemic, epidemic and post-epidemic bark beetle populations and comparing the quantity and quality of fuels present within each beetle population phase. Surface and canopy fuels data were used to create fuel models that are customized to represent the actual fuel conditions created by the bark beetles. Fire behavior predictions based on these custom fuel models showed that surface fire rate of spread and fireline intensities were higher in the current epidemic stands than in the endemic stands due to increased litter and fine fuel in all three forest types. Bark beetles selectively remove large diameter trees altering stand level canopy fuels and promoting release of herbaceous and shrub species which further affects fire potential. Bark beetle-caused tree mortality decreases vegetative sheltering which affects mid-flame wind speed and increases rate of fire spread. Passive crown fires are more likely in post-epidemic stands, but active crown fires are less likely due to decreased aerial fuel continuity. Intense surface fires are possible in post epidemic stands, but they are very much dependent on the rate at which dead trees fall.

Our present research will utilize this information in addition to spatial data to describe the influence of mountain pine beetle (MPB) on fuels and fire behavior in stands of high-elevation five-needle pines, including whitebark, limber, foxtail, Rocky Mountain bristlecone, and Great Basin bristlecone pine.

Introduction

Bark beetles in the genus *Dendroctonus* (Coleoptera: Curculionidae, Scolytinae) are native insects that play an important role in western North American coniferous forest ecosystems. At low population levels bark beetles infest large, old, often injured trees, thus recycling nutrients and creating openings for regeneration. When landscapes are composed of many susceptible host trees eruptive outbreaks are possible, especially during warm, dry periods which weaken otherwise vigorous trees and decrease bark beetle development time. Episodic bark beetle outbreaks have been a common feature of coniferous forests at least since the last glacial retreat about 13,000 years ago. New evidence, however, supports the hypothesis that anthropogenic forcing of global temperatures has increased the vulnerability of whitebark pine to mountain pine beetle MPB (*D. ponderosae* Hopkins) attack and bark beetle population potential (Logan, these proceedings).

It is equally important to note, however, that bark beetle outbreaks are not possible without susceptible stands which are usually dense stands comprised of a large percentage (>60%) of mature, large diameter host trees. Changes to fuels complexes and fire behavior due to 20th century fire suppression and exclusion policies, livestock grazing and a more recent decrease in active timber management has created an abundance of large, old conifers in western North America. Baker (2009) suggested that the rash of large, human-caused wildfires in the late 1800s may have also contributed to susceptible landscapes. As a result, dramatic bark beetle outbreaks have occurred during the last 20-30 years involving spruce beetle (*D. rufipennis* Kirby) in Engelmann spruce, Douglas-fir beetle (*D. pseudotsugae* Hopkins) in Douglas-fir and mountain pine beetle in lodgepole pine (USDA 2009). Since about 2000 mountain pine beetle-caused tree mortality has increased in whitebark and limber pines and it is reasonable to assume that susceptible stands of other high-elevation, five-needle white pines are also at risk.

The scientific community, land managers, and the public at large have expressed concern that the widespread conifer mortality could increase wildfire occurrence and severity. Jenkins and others (2008) reviewed available literature on bark beetles, fuels and fires and described the changes to fuel bed characteristics and predicted fire behavior resulting from bark beetle activity. Other studies have elaborated the relationships for specific bark beetle/host systems including Douglas-fir in Utah (Hill and Jenkins, *in review*), lodgepole pine in Utah, southern Idaho (Page and Jenkins 2007a and b), Colorado (Klutsch and others 2009) and Wyoming (Simard and others 2011) and Engelmann spruce in Utah (Jorgensen and Jenkins 2011, Jorgensen and Jenkins, *in review*). From these papers it is possible to provide a general description of the effect of bark beetle activity on conifer fuels and the influence that an altered fuel complex has on fire

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hazard and potential fire behavior. However, little research has been conducted to describe the relationship between bark beetle-caused tree mortality and wildfire in other forest systems, particularly for high-elevation five-needled pine species.

The purpose of this paper is to describe our current understanding of the influence of bark beetles on fuels and fire behavior in the conifers studied and how this may be related to high-elevation five-needle pine species and ecosystems.

Bark Beetle Effects on Fuel Bed Characteristics

The general changes in seven fuel bed characteristics over the course of a bark beetle rotation were described by Jenkins and others (2008). The bark beetle rotation begins when a stand becomes susceptible to bark beetle infestation and is capable of supporting an outbreak or epidemic. This bark beetle condition class is referred to as endemic and tree mortality is restricted to a few, weakened, or overmature individuals. During the endemic phase generally only one to several trees are attacked per hectare (Bentz and Munson 2000). Epidemics occur when otherwise healthy, but susceptible stands, are subjected to a period of short-term stress, such as drought. Under stressful conditions, aggressive bark beetle species, like MPB, can overcome host tree resistance resulting in rapidly increasing population numbers. During the epidemic phase 80 percent or more of susceptible trees are killed. The length of the epidemic phase varies with conifer species, but generally lasts 5 to 10 years and ending when most large diameter trees have been killed and bark beetle population levels decline. At this time, stands enter the post-epidemic phase which lasts for decades to centuries until small surviving or newly regenerated host trees again reach susceptible age and size.

Litter and Fine Woody Fuels

Significant increases in needle litter amount and depth, and increases in woody fuels less than 0.64 cm occur between the endemic and epidemic MPB phase in lodgepole pine (Page and Jenkins 2007a, Klutsch and others 2009). Figures 1a and 1b show similar changes in whitebark pine fuels in Wyoming. During outbreaks, the accumulation of these fuels occurs in pulses beneath the crowns of individual attacked trees. We expect that needle accumulation under high-elevation five-needle pines, especially foxtail and bristlecone species, will be greater than described for lodgepole pine since these species tend to retain a greater proportion of older needles. Increased duration of needle retention will also result in lesser litter amounts deposited in endemic stands of high-elevation five-needle pines, than in stands of lodgepole pine, or other pine species.

The rate of accumulation and spatial distribution of these fuels is dependent upon the arrangement of individual attacked trees within the stand and the number of trees attacked each year. The rate of litter and fine woody fuel accumulation under an individual tree is also affected by crown condition as described later. Litter decomposes to duff within one to two years and results in a balance between litter accumulation and decomposition. Litter accumulation ceases when all needles have fallen off an individual attacked tree. Duff depth and amount increases to a maximum the year following the end of needle fall. Fine woody fuels will continue to accumulate as snow and wind break small twigs off standing snags. There is considerable variability in the accumulation of larger woody fuel and may continue for several decades into the post-epidemic phase. By the end of the epidemic phase, litter, fine woody fuel, and duff accumulations decrease and quickly return to endemic background levels.

Herbaceous and Shrub Fuels

The death of an overstory tree allows more available moisture and sunlight to reach both live and dead herbaceous and shrub fuels. The relative abundance and composition of herbaceous and shrub fuels very much depends on the biophysical environment and moisture regime, and spatial distribution and density of overstory trees. In general however, both fuel types increase dramatically in height and aerial coverage immediately following the death of the overstory tree (Figure 1c). Initially herbaceous fuels are most abundant, but are replaced by woody shrubs which will dominate well into the post-epidemic phase. Shrub abundance will begin to decrease as conifer cover increases reducing available moisture and sunlight beneath the developing canopy.

Coarse Woody Fuel and Fuel Bed Depth

Woody fuels larger than 0.64 cm in diameter do not increase significantly until well into the post-epidemic phase as large branches from standing snags fall to the forest floor. The fall rate for trees killed by bark beetles is not well known and varies considerably with topography (slope steepness, position, and aspect for example), soils, decay pathogens and exposure of the stand to wind. The accumulation of larger fuels increases woody fuel bed depth (Page and Jenkins 2007a, Jorgensen and Jenkins 2010). During the post-epidemic phase a balance between accumulation and decay is achieved as coarse woody debris decomposes. Deep winter snowpacks characteristic of high elevation pine sites mechanically compact fuels which decreases fuel bed depth during the post-epidemic phase.

Bark Beetle-Affected Surface and Canopy Fuel Matrices in High-Elevation, Five-Needle Pine Systems

Figure 2 describes the bark beetle-affected surface and canopy fuel matrices and the important variables affecting crown fire initiation and spread during the course of the bark beetle rotation in high-elevation five-needle pine species.

Figure 1. Bark beetle-affected crown and surface fuels characteristics of the endemic condition and green crown class (Fig. 1a), epidemic and green-infested and red crown classes (Fig. 1b) and post-epidemic and gray crown class (Fig. 1c) in whitebark pine in west-central Wyoming.

Surface Fuel Descriptors

Pine fuel zone (P_z)

P_z is best visualized as a circle of fuels lying under the drip line of an attacked tree. During the endemic phase fuel loads under high-elevation, five-needle pines are low (Figure 1a). During the time a tree is colonized by beetles there will be an increase in litter and fine woody fuel increasing for 1 to 4 years (Figure 1b). These fuels will then give way to forbs and shrubs (Figure 1c) into the post-epidemic phase. P_z will see an increase in coarse woody debris during the decades following tree death. The extent of stand or landscape level P_z will increase as slope angle increases which effectively decreases the distance between adjacent tree crowns.

Non-pine fuel matrix (NP_z)

NP_z is the area between the drip lines of adjacent trees and consists of dead and living shrubs, forbs, grasses, non-host trees and small host and the litter and down woody fuel they produce. The specific composition of the NP_z is highly variable with pine species, geographic location, elevation and plant community type.

Canopy Fuel Descriptors

Canopy fuel descriptors as used by Page and Jenkins (2007 a and b) and Scott and Reinhardt (2001) are based on stand characteristics, not individual trees. For purpose of illustration the following discussion describes canopy fuels based on individual tree crowns.

Crown width (CW)

CW is the greatest distance from one edge of the crown to the other. CW affects the size of P_z and the potential for adjacent trees to have overlapping P_z. CW also affects the potential for crown fire spread from tree to tree. The broad open crowns characteristic of high-elevation five-needle pines may increase the potential for active crown fire in high tree density stands.

Inter-crown Distance (ICD)

ICD is the distance from one tree crown to an adjacent tree crown. On average, ICD may be less in high-elevation five-needle pine stands when compared to stands of other pine species with similar basal areas due to the relatively broad architecture of trees.

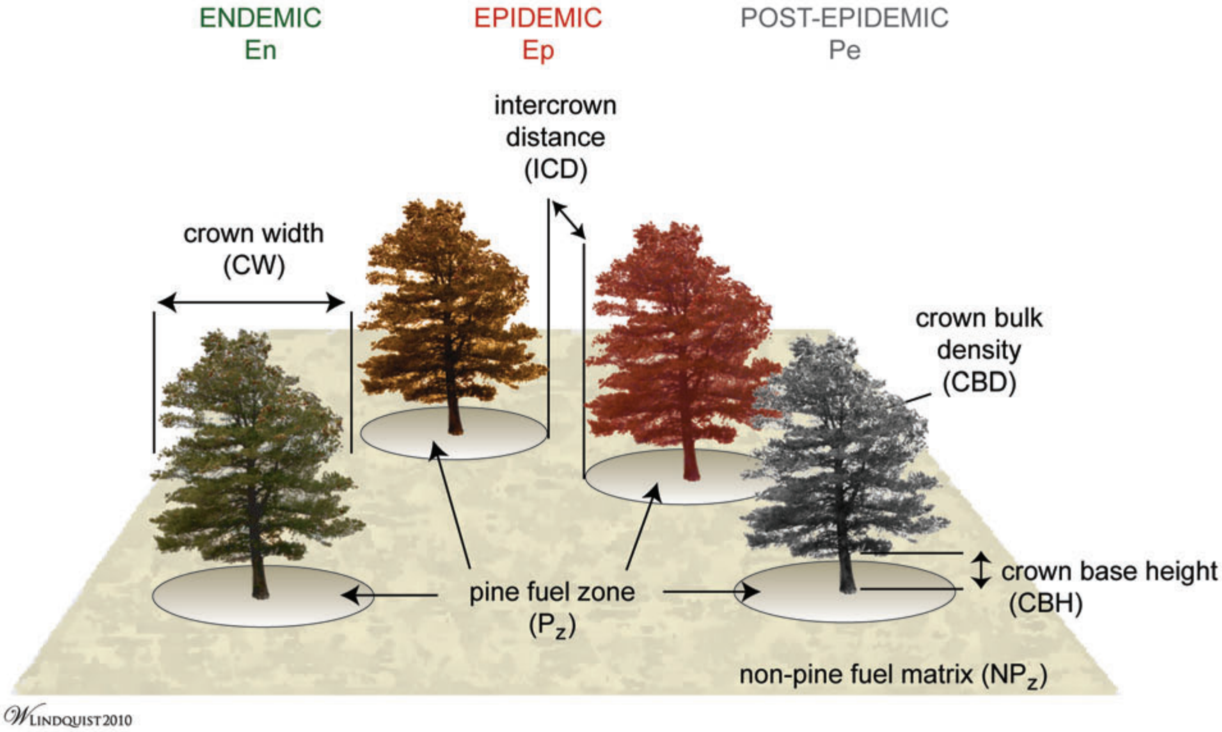

Figure 2. Bark beetle-affected surface and canopy fuel matrix and the important variables affecting crown fire initiation and spread during the course of the bark beetle rotation.

Crown base height (CBH)

CBH is the lowest live crown height in a stand at which there is a sufficient amount of forest canopy fuel to propagate fire vertically into the canopy (Scott and Reinhardt 2001). Bark beetles effectively increase CBH by causing needles to die and fall to the ground. As needles in the lower crown fall there is a substantial reduction in the potential for crown fire initiation. The presence of advanced regeneration, especially shade tolerant conifers, may lower average stand CBH.

Canopy bulk density (CBD)

CBD is the biomass of available canopy fuel per canopy unit volume. Available canopy fuel load (ACFL) is that which is consumed in the short duration flaming front of a crown fire and consists of live and dead foliage, 0 to 3 mm live branchwood, and 0 to 6 mm dead branchwood, plus any lichen and moss (Scott and Reinhardt 2001). Beginning the first season following bark beetle colonization, CBD and ACFL begins to decrease as needles die and fall to the forest floor. There is, in essence, a transfer of CBD to litter and fine woody fuel beneath the tree crown over the course of two to four years following colonization. CBD and ACFL values approach zero after all the needles have fallen from the tree.

Potential Changes to Bark Beetle-Affected Tree Crowns and Fuel Descriptors in High-Elevation, Five-Needle Pines

The characteristics of the crowns of individual attacked trees change during the period of bark beetle colonization, brood development, and adult emergence (Figures 1 a-c). For purposes of the following discussion, consider an otherwise healthy, susceptible pine host with a normal green crown (G). G will have typical CBD, ACFL and FMC_n (foliar moisture content). This tree is mass attacked by MPB at time zero during the flight period (July to August). It is assumed that this MPB population matures from eggs to adults in one year (although this may not be the case at high elevations and/or north latitudes). Eggs deposited by female beetles hatch and larvae develop to the overwintering stage (fourth instar) during the first season at zero plus four months (0 + 4). During the first season, the crown of the infested tree remains visibly green (G_i) with the only outward signs of successful attack being pitch tubes and boring dust present on the tree bole (Figure 1a). It is during this first season of beetle colonization that the development of the blue stain fungus also begins.

Blue stain is caused by a complex of fungi that are carried by bark beetles in their mycangia (specialized mouthpart

Figure 3. Bolts of mountain pine beetle-infested lodgepole pine in southwestern Montana showing characteristics of blue stain fungus infection in sapwood.

structures) and inoculated onto the sapwood surface (Figure 3). The fungi spread in the sapwood through living parenchyma cells and bordered pit pairs of dead, water conducting tracheid elements. The degree of blue stain development is dependent upon degree of host colonization, fungal pathogenicity, host resistance and the ability of the tree to compartmentalize the fungi. The amount of sapwood affected thus varies considerably, but in any case, the fungi will reduce water flow to the crown resulting in a net reduction in FMC_n. G_i will have normal CBD, ACFL, but may have lowering FMC_n due to initial blue stain development.

At the beginning of the second season (0+12 months), overwintering larvae resume development, pupate and new adults emerge from the brood tree to colonize another susceptible host. The tree crown will begin to fade from green to yellow (Y) (Figure 1b). Y trees have been infested for 12 months and will begin to show crown symptoms indicative of attack. FMC_n has been greatly reduced due to maximum blue stain development. CBD and ACFL remain normal.

By 0 + 16 months the crown will begin to turn red (R) (Figure 1b). Our preliminary observations of whitebark pine in Wyoming suggest that the R crown class can last up to 0 + 48 months. R needles begin to drop until all needles have fallen from the crown to the forest floor and the gray (GR) stage appears (Figure 1c). CBD and ACFL of R trees will decrease and approach, or become zero when the GR stage is entered.

Foliar Fuel Moisture Relationships

Live and dead FMC_n is an important parameter in crown fire initiation and spread. FMC_n is the amount of water in needles and very fine twigs on a dry weight basis. Figure 4 shows FMC_n relationships for G, Gi, Y, and R needles during the growing season. No specific FMC_n relationships have been established for high-elevation, five-needle pines. Figure 4 displays the FMC_n live, currently infested, and older needles for eastern white pine (*P. strobus*) based on data reviewed by Keyes (2006). Fuel moisture values for R needles which follow trends of dead fuel moisture are also shown in Figure 4. FMC_n for R needles is affected by diurnal fluctuations in weather variables including precipitation, cloudiness, temperature, relative humidity and dew point. During wet conditions, R needle FMC_n values will approach 30%, but equilibrate within 0-2 hours when conditions become dry. We assume that the diurnal and seasonal weather-affected fluctuations will be at a greater range of moisture content during the cool, wet conditions of spring than the hot, dry summer months. Also displayed in Figure 4 is a hypothetical range of FMC_n for Y crown classes which we assume to lie between G and R crown classes. The actual values of FMC_n for Y crown classes will depend upon blue stain development, and is likely affected by diurnal and seasonal weather fluctuations especially as Y goes to R.

Volatile Compounds in Foliage

Plant terpenes are assumed to increase flammability of forest fuels, however, few studies have documented the effect in pine species (Ormeño and others 2008). It is unknown how much influence, if any, these compounds have on flammability. No previous work has been done on the possible changes to pine terpenes that may occur during the course of changes in pine foliage resulting from MPB activity as described above. We conducted very preliminary experiments collecting whitebark pine volatiles in situ from G, G_i, Y, and R-needled trees. The most common pine terpenes found in preliminary gas chromatograph analyses were alpha-pinene, beta-pinene, beta-myrcene, beta-phellandrene and 3-carene. The level of all compounds decreased from G to G_i to Y, but was elevated in R needles. An increase in flammable terpenes in R needles would be expected to increase surface rate of spread and crown fire potential. Ormeño and others

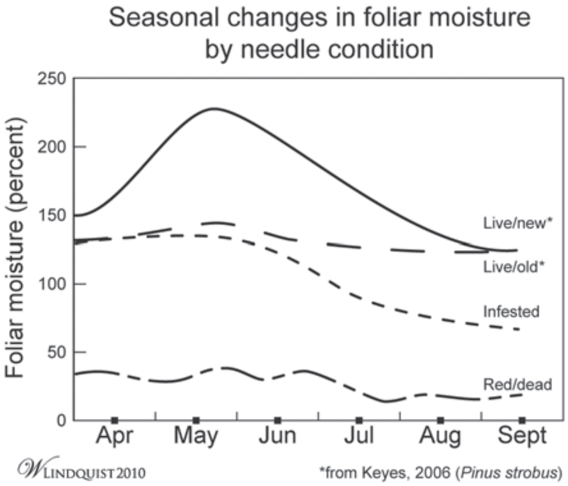

Figure 4. Seasonal changes in foliar moisture by needle condition. Live/new and live/old data are from Keyes (2006). Infested and red/dead needle condition represent suggested hypothetical values.

(2009) found increased terpene concentration and flammability in the litter of Mediterranean *Pinus* spp. studied. Mutch (1970) speculated that natural selection might favor increased flammability in certain fire regimes.

Effect of Bark Beetle-Altered Fuels on Fire Hazard and Potential Fire Behavior

Bark beetles are one of few native agents in nature capable of rapidly altering the quality of coniferous forest vegetation over large spatial scales. The effect of the altered fuel complex on the principle fire behavior descriptors including rate of spread, fireline intensity and flame length over the course of a bark beetle rotation was described by Jenkins and others (2008). There is also a dramatic increase in probability of ignition and potential for crown fire initiation and spread.

Surface Fire Ignition and Spread

The most important influence of bark beetle-caused tree mortality on fire behavior is the reduction in sheltering that occurs as crown bulk density decreases. The opened canopy allows for greater solar insolation and dryer fuels, and increased midflame wind speeds (Page and Jenkins 2007b). The combined effect of increased fine fuels with reduced FMC_n and increased windspeed during the epidemic phase is an increase in fireline intensity under moderate fire weather conditions (Page and Jenkins 2007b). The increase in the amount and depth of litter and fine woody fuel increases the probability of ignition under bark beetle-killed trees.

Coarse woody fuel accumulation and the increase in fuel bed depth that occur during the post-epidemic phase does not influence fire ignition or spread, but may add to surface fire energy release especially during periods of drought. The coarse woody fuel contained in standing snags may contribute to an increased period of flammability and fireline intensity when the site is shared with advanced regeneration in the decades following the outbreak.

In high elevation, five-needle pine stands, we expect that the fuel influence on surface fire behavior will be a function of the relative distribution of P_z and NP_z for a given species, plant community type and location. P_z will increase as pine species stand density increases and may compose 100% of the surface fuel matrix in very dense stands where P_z circles overlap.

Crown Fire Initiation and Spread

Factors affecting crown fire dynamics that are altered by bark beetle-caused tree mortality include CBH, ACFL, FMC_n and ICD. Crown fires are most dependent upon fire weather factors especially relative humidity, windspeed and weather influences on FMC_n. Crown fires are possible when CBH is sufficiently low for a surface fire of given intensity to ignite the foliage. Vertical fire spread within a tree crown is affected by CBD, ACFL and FMC_n. The initial process of crown fire initiation is also called passive crown fire. Active crown fires occur when effective canopy windspeeds are sufficient to move the fire from one tree crown to another. Active crown fires can occur in connection with an intense surface fire (dependent) or rarely without interacting with the surface fire (independent). Active crown fires are affected by FMC_n, the presence of flammable volatile foliage organic compounds and ICD. The transition from R to GR trees early in the post-epidemic period may result in a short term reduction in the probability of active crown fire due to canopy thinning (Simard and others 2011).

Herbaceous and Shrub Fuels

The dramatic increase in shrubs and forbs during the epidemic and post-epidemic bark beetle phases was discussed above. Fire behavior prediction systems do not accurately handle inputs of live shrubs and forbs which occur under bark beetle-killed conifer stands. Intuition suggests that the shrub and forb layer acts as a "wet blanket" over the litter and fine woody fuels that accumulated prior to shrub and forb release. The high live fuel moisture contents of many shrubs and forbs functions as a heat sink tending to reduce the probability of ignition and surface fire spread rates expected from a "typical" conifer litter understory fuel model. The fact that this fuel bed is difficult to model is further complicated by the considerable variability in herbaceous plant and shrub composition and flammability.

Fire Behavior in High-Elevation, Five-Needle Pine Systems

High intensity, stand-replacing crown fires are a common feature of conifer forests in western North America, with or without bark beetle-altered canopy fuels. Real-time fire weather characterized by low relative humidity, high wind speeds, and low fuel moisture across live and dead fuel classes will dominate fire behavior regardless of fuel bed characteristics (Bessie and Johnson 1995). However, bark beetle-affected fuels may create conditions capable of producing high-intensity surface fires with the ability to transition to crown fires across a wider range of fire weather conditions. This is particularly true at higher elevations where narrow fire weather conditions exist due to a shorter snow free period, higher relative humidities, and lower temperatures.

The infinite array and complex assemblages of coniferous species, bark beetle-altered fuels condition classes, and the activity of other biotic and abiotic disturbance agents over complex terrain and large spatial and long temporal landscape scales also complicates potential fire behavior (Figure 5). Disturbance agents alter the landscape-scale fuel complex which may affect actual fire spread, severity and intensity within the affected landscape. The specific pattern and size of the affected area also has the ability to alter fire intensity and severity beyond the affected area.

The potential for crown fire in high-elevation, five-needle pines is greatest in mixed, transitional forests at lower elevations where they are a minor seral species in stands composed

Figure 5. Landscape view of a mixed conifer forest showing canopy fuels altered by mountain pine beetle and western spruce budworm near Butte, Montana.

of lodgepole pine, Douglas-fir and/or true firs (*Abies* spp.) and Engelmann spruce. In these forests, hazardous fuel pathways may have resulted from; 1) the suppression and exclusion of fire; 2) recent mountain pine beetle outbreaks that developed in pine types at lower elevations and spread up into pure five-needle pine stands; 3) bark beetle outbreaks triggered by drought in the numerous susceptible stands of Douglas-fir and Engelmann spruce; 4) vertical fuel ladders resulting from cyclic western spruce budworm, *Choristoneura occidentalis* Freeman (Lepidoptera: Tortricidae), outbreaks affecting true firs and Douglas-fir; and 5) other agents of disturbance including dwarf mistletoes (*Arceuthobium* spp.), root pathogens and rust fungi that are increasingly common in overmature conifer forests characteristic of the fire suppression era. The net result is a variably flammable, disturbance-altered complex of surface, ladder, and canopy fuels that may extend up in elevation to stands where high-elevation five-needle pines are a major seral or climax species.

In climax high-elevation, five-needle pine stands, surface and crown fire flammability are probably more closely governed by the mountain pine beetle-induced surface and canopy fuel changes described in this paper. Climax stands are generally fire-prone only during the period in the bark beetle rotation when green-infested, yellow and red crown classes share the canopy with green trees. As gray trees become dominant, shrubs and forbs increase, CBH increases in the absence of conifer reproduction, ACFL and CBD decrease and fire potential is reduced. Climax high-elevation, five-needle pine stands are most vulnerable to high intensity, high severity fires where extensive landscapes of disturbance-altered, mixed conifer fuels exist at lower elevations.

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Literature Cited

Baker, W. L. 2009. Fire ecology in Rocky Mountain Landscapes. Island Press. 605 p.

Bentz, B. J.; Munson, A. S. 2000. Spruce beetle population suppression in northern Utah. West. J. Appl. For. 15: 122-128.

Bessie, W. C. and E. A. Johnson. 1995. The relative importance of fuels and weather of fire behavior in subalpine forests. Ecol. 76:747-762.

Hill, T. and M. J. Jenkins. The changing fuel and fire behavior mosaic in Douglas-fir beetle (*Dendroctonus pseudotsugae*)-affected Douglas-fir forests in the Intermountain West (in preparation).

Jenkins, M. J.; Hebertson, E.; Page, W.; Jorgensen, C. A. 2008. Bark beetles, fuels, fires and implications for forest management in the Intermountain West. Forest Ecol. Manage. 254: 16-34.

Jorgensen, C. A. and M. J. Jenkins. 2011. Fuel complex alterations associated with spruce beetle-induced tree mortality in Intermountain spruce-fir forests, USA. For. Sci. 57(3).

Jorgensen, C. A. and M. J. Jenkins. Potential fire behavior in spruce beetle (*Dendroctonus rufipennis)* induced stand mortality in Intermountain spruce-fir forests. Forest Ecol. Manage. (*in review).*

Keyes, C. R. 2006. Foliar moisture contents of North American conifers. Pp. 395-399 in *Fuels Management—How to Measure Success: Proceedings of the 1st Fire Behavior and Fuels Conference*. USDA Forest Service Proceedings RMRS-P-41.

Klutsch, J. G.; Negron, J. F.; Costello, S. L.; Rhoades, C. R.; West, D. R.; Popp, J.; Caissie, R. 2009. Stand characteristics and downed woody debris accumulations associated with a mountain pine beetle (*Dendroctonus ponderosae* Hopkins) outbreak in Colorado. Forest Ecol. and Manage. 258: 641-649.

Mutch, R. W. 1970. Wildland fires and ecosystems—a hypothesis. Ecol. 51: 1046-1051.

Ormeño, E. B. Céspedes, I.A. Sanchez, A. Velasco-García, J.M. Moreno, C. Fernandez, V. Baldy. 2009. The relationship between terpenes and flammability of leaf litter. For. Ecol. Manage. 257: 471-482.

Page, W. G.; Jenkins, M. J. 2007a. Mountain pine beetle induced changes to selected lodgepole pine fuel complexes within the Intermountain region. For. Sci. 53(4), 507-518.

Page, W. G.; Jenkins, M. J. 2007b. Predicted fire behavior in selected mountain pine beetle infested lodgepole pine stands within the Intermountain region. For. Sci. 53(6), 662-674.

Scott, Joe H.; Reinhardt, Elizabeth D. 2001Assessing crown fire potential by linking models of surface and crown fire behavior. Res. Pap. RMRS-RP-29. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station. 59 p.

Simard, M., W. H. Romme, J. M. Griffin and M. G. Turner. 2011. Do mountain pine beetle outbreaks change the probability of active crown fire in lodgepole pine forests? Ecological Society of America, *Ecological Monographs,* 81(1), pp.3-24.

USDA Forest Service. 2009. Major forest insect and disease conditions in the United States 2008 update. FS 933. 27 p.

Influence of Fire on Mycorrhizal Colonization of Planted and Natural Whitebark Pine Seedlings: Ecology and Management Implications

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Introduction

Whitebark pine (*Pinus albicaulis*) is a threatened keystone species in subalpine zones of Western North America that plays a role in watershed dynamics and maintenance of high elevation biodiversity (Schwandt, 2006). Whitebark pine has experienced significant mortality due to white pine blister rust, mountain pine beetle outbreaks and successional replacement possibly due to fire suppression (Schwandt 2006; Smith and others 2008). Current management strategies include letting lightning fires burn or applying prescribed fire to provide habitat for natural seedling establishment or the planting of rust resistant seedlings (Keane and Parsons 2010a, 2010b). However survival rates after fire are variable and can be low (Izlar 2007; Keane and Parsons 2010a; Perkins 2004; Tomback and others 2001).

All pines in nature require ectomycorrhizal (ECM) fungi for establishment, growth, health and sustainability (Read, 1998). ECM fungi enhance nutrient uptake and offer protection against drought, pathogens, soil grazers and heavy metals (Smith and Read 1997). Fire can affect ECM communities in soil but impacts are unpredictable and depend on the intensity of the fire, forest type and other factors (Cairney and Bastias 2007). Intense fire has the potential to detrimentally impact ECM communities because of the deep penetration of lethal soil temperatures, the complete loss of the original tree host, and changes in abiotic conditions, including an increase soil surface temperature (Neary and others 1999; Wiensczyk and others 2002). When tree hosts are lost or removed, studies show that ECM fungal viability in the soil declines rapidly after two or three years (Haggerman and others, 1999) and recovery of ECM communities from burning and cutting can take decades (Visser 1995). It is unknown how long ECM fungi, and particularly those specific to whitebark pine, can remain in the soil of ghost forests without presence of a living host.

Fire is historically linked to whitebark pine ecology (Keane and Arno 1993). Fire has the potential to reduce shade-tolerant understory species such as fir; remove canopy for shade-intolerant whitebark pine seedlings; provide openings for nutcrackers to plant seed; reduce rust and beetle infested older trees, and facilitate plantings of rust resistant seedlings (Keane and Parsons 2010a). However, little is known of how fire affects the beneficial fungi on roots of this tree species. This study evaluated the impact of fire on the mycorrhizal communities on planted and naturally occurring whitebark pine seedlings from an ecological perspective and to address management concerns.

Methods

The 2001 Fridley fire (SW Montana) burned a portion of a mature whitebark pine forest; the burn was considered severe and killed many trees (Fridley Fire BAER Team 2001). A year later 20,000 (non-inoculated) rust-resistant seedlings were planted in the burned areas (Trusty 2009). After four years, natural and planted seedlings on the burn and natural seedlings in the adjacent unburned forest were assessed for mycorrhizal colonization levels and diversity of ECM fungi. Root samples were taken along transects in a non-destructive manner and ectomycorrhizae were sorted and counted by species/morphotype for samples in each treatment. Morphotypes were defined by mantle color, presence or absence of rhizomorphs, and other unique characteristics (Trusty 2009). DNA was extracted from samples and identified by matching ITS sequences to reference species in Genbank or UNITE (Trusty 2009). A total of 21,971 root tips from 144 seedlings were assessed and 21 fungal taxa were identified. The relative abundance and frequency for the most encountered ectomycorrhizal fungal taxa (morphotypes) were also determined and summed for importance values (Horton and Bruns 2001). Data from the two different sampling times were pooled after it was determined that there were no statistical differences between them. Shannon's diversity index compared diversity (number and evenness of morphotypes) among groups (done in Program R). Principal Component analysis (PCA) was used to examine the structure of ectomycorrhizal fungal communities based on whitebark pine seedling groupings. PCA of the log-transformed abundances was plotted for the ectomycorrhizal fungal communities and includes loading vectors for taxa that have an absolute value loading score of at least 0.1. This allows for easy interpretation of which taxa are driving sample distances.

Results

All whitebark pine seedlings sampled were well-colonized by ECM fungi (over 90 percent for all treatments) although a portion may be residual E-strain fungi for those from the

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nursery. Seedlings on the burn (both planted and natural) supported a lower diversity of ECM fungi (0.21 and 0.32, respectively) compared to those in the unburned area (0.56) according to the Shannon diversity index. This reduction in 40-60 percent of the ECM fungal diversity was assessed 5 years after the fire. There was a dramatic shift (change) in the dominant fungal species between those establishing in the adjacent unburned forest and those in the burn (Fig. 1). There were smaller differences in the ECM community between planted and natural seedlings within the burn (Fig. 1, Band C).

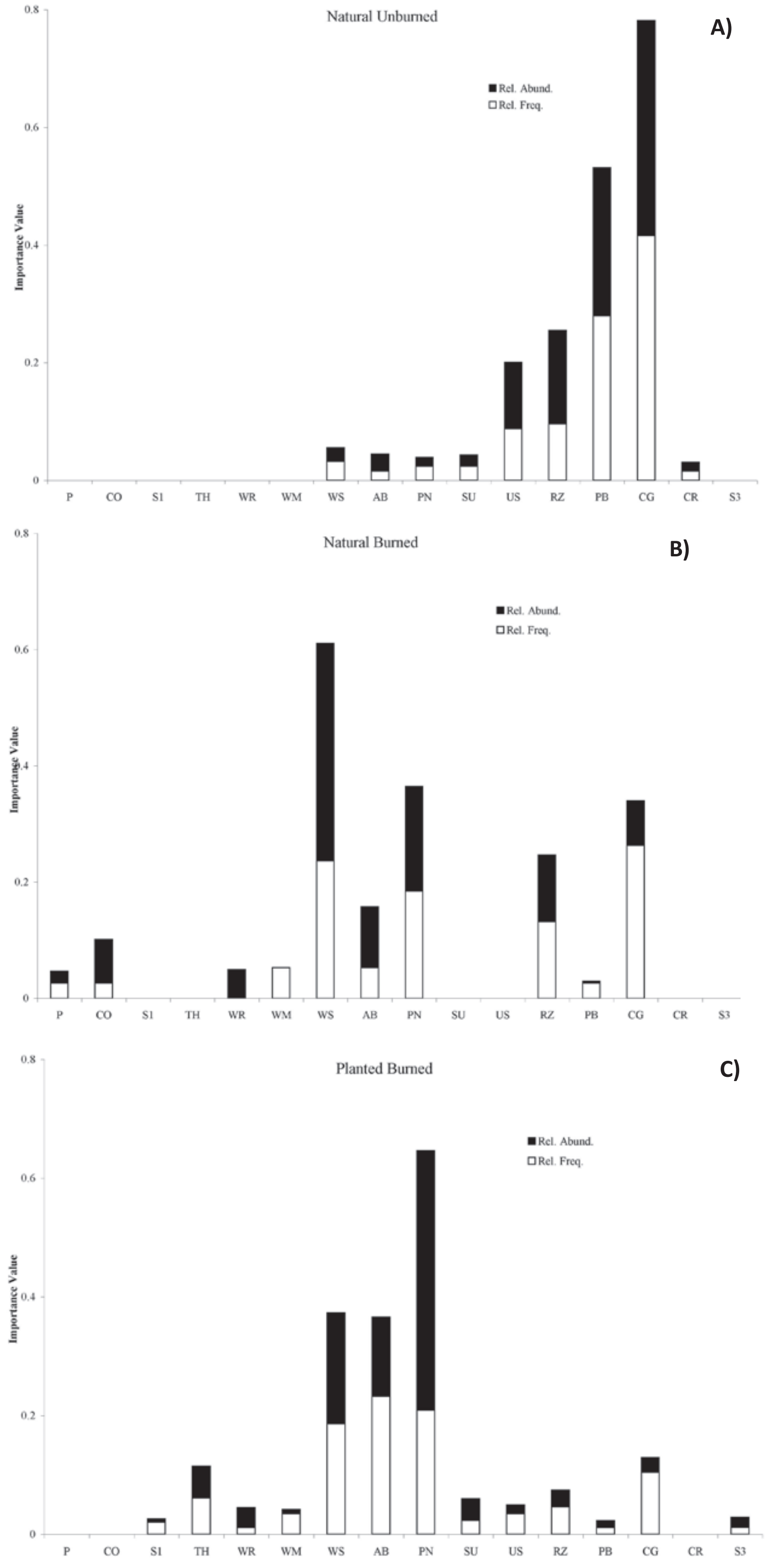

Figure 1. Importance values (frequency + abundance) for 10 most common taxa of ectomycorrhizal fungi on whitebark pine seedlings. A. regenerating naturally in the unburned forest, B. regenerating naturally in burned area, C. planted in burned area. Abbreviations: P-*Phialocephala fortinii*, S1-Species 1, CO- *Coltricia* sp., TH-Thelephoroid spp., WM- *Wilcoxina mikolae*, WR- *Wilcoxina rhemii*, WS- *Wilcoxina* spp., AB- *Amphinema byssoides*, PN- *Pseudotomentella nigra*, SU- *Suillus* spp., US- Unknown suilloids, RZ -*Rhizopogon* spp., PB- *Piloderma byssinum*, CG- *Cenococcum geophilum*, CR- *Cortinarius* spp., S3- Species 3.

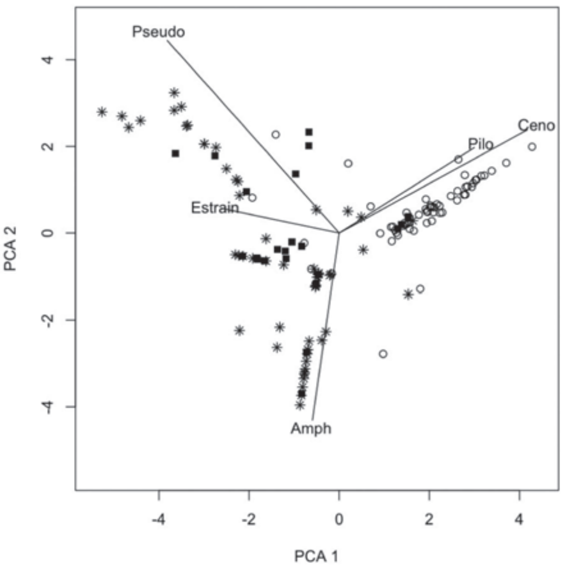

Figure 2. Principal components analysis plot of abundances of ectomycorrhizal fungal species according to group status: circles (0) = natural unburned, squares (■) = natural burned, stars (*) = planted burned. Pseudo= *Pseudotomentella,* E-strain= *Wilcoxina*, Amph= *Amphenima*, Pilo= *Piloderma,* Ceno= *Cenococcum*. Loading vectors are for taxa with loading values greater than 0.1.

Natural seedlings in the unburned forest hosted mainly *Cenococcum geophilum*, *Piloderma byssinum* and suilloid fungi. *Cenococcum* does not produce spores and *Piloderma* species are often associated with woody organic matter in mature forests, thus their dispersal potential into the burn is limited. The suilloids are specific for 5-needle pines and important associates of whitebark pine (Cripps and others 2008; Cripps and Antibus 2011; Mohatt and others 2008). Seedlings in the burn (both natural and planted) were dominated by *Wilcoxina* species (E-strain), *Amphinema byssoides* and *Pseudotomentella nigra*. The latter was more dominant on planted seedlings and there is some historical question as to its pathogenicity. E-strain is common on nursery seedlings but was also found on naturally establishing seedlings. All are considered non-host specific fungi known to occur on burned soil. Suilloid fungi (*Rhizopogon, Suillus*), known to be important in pine establishment, were found on seedlings in all treatments, although colonization rates were lower in the burn. Suilloids were less frequent (10-13 percent) on seedlings in the burn compared to those establishing in the mature unburned forest (25 percent). Spores of suilloids are imported into burns by wind and animal vectors via fecal pellets from nearby inoculum sources (Ashkannejhad and Horton 2005). An important note is that roots of planted seedlings sampled still retained the shape of containers after four years and roots had not yet spread out into the soil.

Over 60 percent of the variation in abundances of ECM fungi can be accounted for by the variable *burning* according to Principal Component Analysis (Fig. 2). This is primarily driven by larger abundance of *Pseudotomentella*, E-strain and *Amphinema* in the burn (for both planted and natural seedlings) and by large abundance of *Cenococcum* and *Piloderma* in the unburned area. Differences between communities of fungi on planted and natural seedlings within the burn were not well defined as data points from planted seedlings were scattered within those for the natural seedlings (Fig. 2).

Discussion

The functional significance of the shift (change) in ECM fungal species after fire in terms of seedling survival is not yet known. However, it is assumed to have physiological implications since fungi vary in benefits to seedlings and as a community (Tedersoo 2009). Five years after the fire, planted and natural seedlings in the burn were partially colonized by suilloids likely due to the availability of a nearby inoculum source (the adjacent unburned forest), the presence of vectors (deer, small mammals) that import inoculum and a management plan that included planting one year after the burn (Trusty 2009). These factors should be considered when planting in severe burns (Wiensczyk and others 2002). While some fungal species can survive and rapidly re-colonize after fire, removal of the duff layer can be problematic for other ECM fungi (Smith and others 2005).

Mycorrhizal colonization was high for seedlings planted on the burn, but seedling survival was still low, assessed at 42 percent during the study (Izlar, 2007). This suggests that other factors (biotic and abiotic) might be involved in seedling mortality or that the timing and type of mycorrhizal colonization might be problematic. A lag time before colonization and lack of appropriate fungi could still be factors. Soil temperatures were about 8^{o}C higher at sampling dates during the study, and this in itself can affect ECM fungal communities (Wiensczyk and others 2002).

Fire is historically important in whitebark pine forests (Keane and Arno 1993), and it is often assumed that the ECM system is also adapted to this disturbance. However, the time and space scales needed for recovery without the loss of fungi specific to whitebark pine are not known. One concern is to determine if intense fires on a large scale coupled with losses from white pine blister rust and mountain pine beetles contribute to irretrievable losses of ECM fungi specific to whitebark pine. These fungi have a co-evolutionary history with stone pines spanning thousands of years which suggests their importance in the system.

Ponderosa pine seedlings inoculated with suilloid fungi (for 2-3 needle pines) showed an increase in survival rate of 40 percent on harsh, dry sites compared to controls (Steinfeld and others, 2003). European stone pines (*Pinus cembra*) have been inoculated with suilloids specific to 5-needle pines for over 50 years and coupled with improved planting techniques, survival has increased from 50 to 90 percent (Weisleitner, personal communication). Whitebark pine seedlings have been successfully inoculated with native fungi (Cripps and Grimme 2011), but out-plantings have not yet been assessed.

Management Implications

In general, the overall benefits of fire in whitebark pine systems need to be weighed against potential microbial impacts. When planting whitebark pine in severe burns, managers should consider planting as soon as possible (within a year) before ECM fungi decline further in the soil, minimizing distances to an inoculum source (living whitebark pine) for prescribed burns, and promoting animal vectors that import inoculum (unless seedling damage is problematic). Monitoring ECM colonization in risky situations and inoculation of planted seedlings with native fungi are management strategies that can be used on severe burns where appropriate fungi do not exist (Brundrett and others 1996; Cripps and Grimme 2011). Inoculation and soil transfer can be considered when plantings are in areas not previously in whitebark pine. There is no information on the persistence of the suilloid fungi in ghost forests but we are working to answer this question. Preservation of the ECM fungi specific to whitebark pine should be considered in management strategies as well.

There is no evidence to date that light burns affect ECM fungi in whitebark pine forests and results reported here are for one fire, thus implications are limited. The impact of the shift of ECM fungal *species* reported in this study on seedling survival is not known particularly since overall mycorrhizal colonization levels were high on seedlings in the burn five years after the fire.

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References

Ashkannejhad, S.; Horton, T. R. 2005. Ectomycorrhizal ecology under primary succession on coastal sand dunes: interactions involving *Pinus contorta*, suilloid fungi and deer. New Phytologist. 169: 345-354.

Brundrett, M.; Boucher, N.; Dell, B.; Grove, T.; Malajczuk, N. 1996. Working with Mycorrhizas in Forestry and Agriculture. ACIAR Monograph. 32. 374 p.

Cairney, J. W.; Bastias, B. A. 2007. Influences of fire on forest soil fungal communities. Canadian Journal of Forest Research. 37: 207-215.

Cripps, C. L.; Antibus, R. K. 2011. Native Ectomycorrhizal Fungi of Limber and Whitebark pine: necessary for Forest Sustainability? Proceedings of the Hi-Five Symposium, Missoula, MT. June 28-30.

Cripps, C. L.; Grimme, E. 2011. Inoculation and successful colonization of whitebark pine seedlings with *native* mycorrhizal fungi under greenhouse conditions. Proceedings of the Hi-Five Symposium, Missoula, MT. June 28-30.

Cripps, C. L.; Smith, C.; Lapp, J.; Carolin, T. 2008. Assessment of Ectomycorrhizal Fungi with Whitebark Pine: Waterton-Glacier International Peace Park. Nutcracker Notes. 14: 12-14.

Fridley Fire BAER Team. 2001. Map of the Fridley Fire burn intensity/severity map, September 2008. Fridley Fire burn area emergency rehabilitation team, Gallatin National Forest, Bozeman, MT.

Haggerman, S.; Jones, M.; Gillespie, M.; Bradfield, G.; Durall, D. 1999. Effects of clear-cut logging on the diversity and persistence of ectomycorrhizae at a subalpine forest. Canadian Journal of Forest Research. 29: 1856-1870.

Horton, T. R.; Bruns, T. D. 2001. The molecular revolution in ectomycorrhizal ecology: peeking into the black-box. Molecular Ecology. 10: 1855-1871.

Izlar, D. K. 2007. Assessment of whitebark pine seedling survival for Rocky Mountain plantings. M.Sc. Thesis, University of Montana, Missoula.

Keane, R. E.; Arno, S. F. 1993. Rapid decline of whitebark pine in western Montana: evidence from 20-year remeasurements. Western Journal of Applied Forestry. 8: 44-47.

Keane, R. E.; Parsons, R. A. 2010a. Management guide to ecosystem restoration treatments: Whitebark pine forests of the northern Rocky Mountains, U.S.A. General Technical Report RMRS-GTR-232. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station. 133 p.

Keane, R. E.; Parsons, R. A. 2010b. Restoring whitebark pine Forests of the Northern Rocky Mountains, U.S.A. Ecological Restoration. 28(1): 1543-4060.

Mohatt, K. R.; Cripps, C. L.; Lavin, M. 2008. Ectomycorrhizal fungi of whitebark pine (a tree in peril) revealed by sporocarps and molecular analysis of mycorrhizae from treeline forests in the Greater Yellowstone Ecosystem. Botany. 86: 14-25.

Neary, D. G.; Klopatek, C. C.; DeBano, L. F.; Folliott, P. F. 1999. Fire effects on belowground sustainability: A review and synthesis. Forest Ecology and Management. 122: 51-71.

Perkins, J. L. 2004. *Pinus albicaulis* seedling regeneration after fire. Ph.D. Dissertation, University of Montana, Missoula, MT. 123 p.

Read, D. J. 1998. The mycorrhizal status of *Pinus*. Pgs. 324-340. In: Richardson, D. M. (ed.), Ecology and Biogeography of *Pinus*, Cambridge University Press, Cambridge, U.K.

Schwandt, J. 2006. Whitebark pine in peril: A case for restoration. USDA Forest Service, Northern Region, Forest Health Protection Report R1-06-28.

Smith, S. E.; Read, D. J. 1997. Mycorrhizal Symbiosis, 2nd edition. Academic Press, San Diego, CA.

Smith, C.; Wilson, M. B.; Rasheed, S.; Walker, R. C.; Carolin, T.; Shepherd, B. 2008. Whitebark pine and white pine blister rust in the Rocky Mountains of Canada and northern Montana. Canadian Journal of Forestry Research. 38(5): 982-995.

Smith, J. E.; McKay, D., Brenner, G., McIver, J., Spatafora, J. 2005. Early impacts of forest restoration treatments on the ectomycorrhizal fungal community and fine root biomass in a mixed conifer forest. Journal of Applied Ecology. 42: 526-535.

Steinfeld, D.; Amaranthus, M.; Cazares, E. 2003. Survival of Ponderosa pine (*Pinus ponderosa*) Dougl. Ex Laws.) seedlings outplanted with *Rhizopogon* mycorrhizae inoculated with spores at the nursery. Journal of Arboriculture. 29(4): 197-208.

Tedersoo, L.; May, T. W.; Smith, M. E. 2009. Ectomycorrhizal lifestyle in fungi: global diversity, distribution, and evolution of phylogenetic lineages. Mycorrhiza. 20: 217-263.

Tomback, D. F.; Sund, S. K.; Hoffman, L. A. 1993. Post-fire regeneration of *Pinus albicaulis*; height-age relationships, age structures, and microsite characteristics. Canadian Journal of Forest Research. 23: 113-119.

Trusty, P. 2009. Impact of severe fire on ectomycorrhizal fungi of whitebark pine seedlings. M.Sc. Thesis, Montana State University, Bozeman, MT.

Visser, S. 1995. Ectomycorrhizal fungal succession in Jack pine stands following wildfire. New Phytologist 129: 389-401.

Weisleitner, H. 2008. [Personal communication]. Federal Nursery of Austria, Innsbruck, Austria.

Wiensczyk, G.; Durall, D.; Jones, M.; Simard, S. 2002. Ectomycorrhizae and forestry in British Columbia: A summary of current research and conservation strategies. B. C. Journal of Ecosystems and Management. 2(1): 1-20.

Climate Change Response of Great Basin Bristlecone Pine in the Nevada NSF-EPSCoR Project (www.nvclimatechange.org)

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Abstract—Predicting the future of high-elevation pine populations is closely linked to correctly interpreting their past responses to climatic variability. As a proxy index of climate, dendrochronological records have the advantage of seasonal to annual resolution over multiple centuries to millennia (Bradley 1999). All climate reconstructions rely on the 'uniformity principle' (Camardi 1999), which assumes that modern natural processes have acted similarly in the past, and is used to calibrate proxy records of climate against instrumental observations (National Research Council 2006). The possibility has recently been raised that long proxy records of climate could be biased by the presence of periods during which relationships inferred from the instrumental period no longer hold, an issue that can potentially transform the entire discipline of paleoclimatology. One of the best known cases involves high-latitude tree-ring parameters (width and maximum latewood density) that used to correlate closely with air temperature, but have shown a 'divergence' from instrumental temperature data during the late 20th century (Jacoby and D'Arrigo 1995; Briffa et al. 1998). While multiple explanations have been provided for this phenomenon, they differ between regions and species, and have mostly been based on observational and correlation studies (e.g., Vaganov et al. 1999; Biondi 2000).

Especially for treeline environments in the western USA, the interpretation of tree-ring records has been severely limited by the lack of in-situ observations on hydroclimatic variables, and has had to rely on instrumental records interpolated from much lower elevations, often without the ability to correct for potential bias due to recent urbanization and land use changes. High-elevation Great Basin conifers, such as bristlecone pine, have provided some of the longest annually resolved and continuous records of air temperature (LaMarche Jr. 1978). Individual bristlecone trees growing within about 150 m of the upper treeline limit have reached unprecedented growth peaks in the last few decades (Salzer et al. 2009). This trend is matched by increased air temperature in PRISM data (Daly et al. 1994), which are generated by combining records from stations far away from treeline and potentially affected by various instrumental biases. Recently, a number of NSF-supported environmental observing projects have generated exciting opportunities to improve our understanding of the climatic sensitivity of these pine species.

The Nevada system of Higher Education, including the University of Nevada, Las Vegas, the University of Nevada, Reno, the Desert Research Institute, and Nevada State College have begun a five year research and infrastructure building program, funded by NSF Experimental Program to Stimulate Competitive Research (EPSCoR) with six major components: Climate Modeling, Ecological Change, Water Resources, Cyberinfrastructure, Education, and Policy, Decision-Making, and Outreach. As part of the new infrastructure, two observational transects are going to be established across Great Basin Ranges, one in the Sheep Range (southern Nevada), and the other in the Snake Range (eastern Nevada), which will both encompass bristlecone pine (*Pinus longaeva* D.K.Bailey) treeline stands. A number of environmental parameters will be monitored at the transect locations, including atmospheric (barometric pressure, air temperature, relative humidity, wind speed and direction, precipitation, insolation, net radiation, snow accumulation, etc.), pedologic (soil moisture, soil temperature, hydraulic head, etc.), and vegetational (stem increment, sap flow, NDVI, phenological changes, etc.) ones.

Specific hypotheses can be tested at the sites, for example on how wood formation responds to climate. Some of the bristlecone pines used by Salzer et al. (2009) are found within the Nevada EPSCoR transects in the Snake Range. We will test the hypothesis that bristlecone growth is a record of mean air temperature by first using detailed field data on soil moisture, sap flow, and stem size to determine what controls the length of the growing season. Radial changes will be measured using point dendrometers to the nearest μm at half-hour intervals (Deslauriers et al. 2003; Biondi and Hartsough 2010). In addition, repeated microcore sampling can be combined with histological analysis to determine the timing of cambium activity, subdivision, elongation, and lignification of new xylem cells during the season (Rossi et al. 2006). Finally, field experiments could be set up using rainfall simulators (Mutchler and Moldenhauer 1963; Munn and Huntington 1976) to determine how bristlecone pine rings may reflect changes in, for instance, increased summertime precipitation compared to reduced snow cover. The combination of long-term monitoring sites with targeted field investigations is a powerful tool to achieve transformative scientific results in environmental science.

References

Biondi, F. 2000. Are climate-tree growth relationships changing in north-central Idaho? Arctic, Antarctic, and Alpine Research. 32, 111-116.

Biondi, F., and P. C. Hartsough. 2010. Using automated point dendrometers to analyze tropical treeline stem growth at Nevado de Colima, Mexico. Sensors. 10, 5827-5844.

Bradley, R. S. 1999. Paleoclimatology. 2nd ed. Academic Press, San Diego, CA.

Briffa, K. R.; F. H. Schweingruber; P. D. Jones; T. J. Osborn; S. G. Shiyatov, et al. 1998. Reduced sensitivity of recent tree-growth to temperature at high northern latitudes. Nature. 391, 678-682.

Camardi, G. 1999. Charles Lyell and the Uniformity Principle. Biology and Philosophy. 14, 537-560.

In: Keane, Robert E.; Tomback, Diana F.; Murray, Michael P.; and Smith, Cyndi M., eds. 2011. **The future of high-elevation, five-needle white pines in Western North America: Proceedings of the High Five Symposium.** 28-30 June 2010; Missoula, MT. Proceedings RMRS-P-63. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station. 376 p. Online at http://www.fs.fed.us/rm/pubs/rmrs_p063.html

Daly, C.; R. P. Neilson; and D. L. Phillips. 1994. A statistical-topographic model for mapping climatological precipitation over mountainous terrain. Journal of Applied Meteorology. 33, 140-158.

Deslauriers, A.; H. Morin; C. Urbinati; and M. Carrer. 2003. Daily weather response of balsam fir (*Abies balsamea* (L.) Mill.) stem radius increment from dendrometer analysis in the boreal forests of Québec (Canada). Trees. 17, 477-484.

Jacoby, G. C.; and R. D. D'Arrigo. 1995. Tree-ring width and density evidence of climatic and potential forest change in Alaska. Global Biogeochemical Cycles. 9, 227-234.

LaMarche Jr., V. C. 1978. Tree-ring evidence of past climatic variability. Nature. 276, 334-338.

Munn, J. R.; and G. L. Huntington. 1976. A portable rainfall simulator for erodibility and infiltration measurements in rugged terrain. Soil Science Society of America Journal. 40, 622-624.

Mutchler, C. K.; and W. C. Moldenhauer. 1963. Applicator for laboratory rainfall simulator. Transactions of the ASAE. 6, 220-222.

National Research Council. 2006. Surface Temperature Reconstructions for the Last 2,000 Years. The National Academies Press, Committee on Surface Temperature Reconstructions for the Last 2,000 Years. Washington, DC. 196 p.

Rossi, S.; A. Deslauriers; T. Anfodillo; H. Morin; A. Saracino, et al. 2006. Conifers in cold environments synchronize maximum growth rate of tree-ring formation with day length. New Phytologist. 170, 301-310.

Salzer, M. W.; M. K. Hughes; A. G. Bunn; and K. F. Kipfmueller. 2009. Recent unprecedented tree-ring growth in bristlecone pine at the highest elevations and possible causes. Proc. Nat. Acad. Sci. USA 106, 20348-20353.

Vaganov, E. A.; M. K. Hughes; A. V. Kirdyanov; F. H. Schweingruber, and P. P. Silkin. 1999. Influence of snowfall and melt timing on tree growth in subarctic Eurasia. Nature. 400, 149-151.

Whitebark Pine (*Pinus albicaulis*) Assisted Migration Trial

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Abstract—Assisted migration—the translocation of a species into a climatically-suitable location outside of its current range—has been proposed as a means of saving vulnerable species from extinction as temperatures rise due to climate change. We explore this controversial technique using the keystone wildlife symbiote and ecosystem engineer, whitebark pine (*Pinus albicaulis*). Species distribution models (SDMs) predict that whitebark pine will be extirpated from most of its current range over the next 70 years. However, the same models indicate that a large quadrant of northwestern British Columbia is climatically suitable for the species under current conditions, and will remain so beyond the 21st century. To test the accuracy of this model, as well as the capacity of treated (x-rayed, stratified and nicked) and untreated whitebark pine seeds to germinate, survive and grow relative to geographic, climatic, microsite and genetic factors, we planted seeds from seven populations in eight trial locations ranging from 600 km southeast to 800 km northwest of the northern boundary of the species range. During the first two growing seasons, germination occurred in all locations, with treated seeds germinating at three times the rate and a year earlier, relative to untreated seeds. Seed weights and x-ray-based viability estimates helped predict germination rates among populations for both seed treatments. Earlier snowmelt dates and corresponding warmer early-growing-season temperatures positively influenced untreated, but barely affected treated, seed germination. Seedling survival, health and growth were also positively influenced by earlier snowmelt dates, with better-developed seed stocks performing best. Our experiment provides initial verification of SDM predictions for whitebark pine, and informs the creation of scientific and ethical guidelines for assisted migration prior to a time of critical need.

Keywords: climate change, common garden, quantitative genetics, species distribution models, species range, genecology

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Whitebark Pine (*Pinus albicaulis*) In Cascadia: A Climate Change Prognosis

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Abstract—Species distribution models (SDMs) predict that whitebark pine (*Pinus albicaulis*) will lose much of its current climatic range in Cascadia (the Pacific Northwest in the United States plus British Columbia, Canada) by the 2080s as the climate warms. However, the same models indicate that the species will simultaneously gain a large, climatically-favorable habitat expanse northwest of its current northern range limit. While SDMs are one of the best tools available for predicting range shifts under climate change, their shortcomings, particularly for threatened species like whitebark pine, must be tested and accounted for prior to their use in conservation planning. The potential for whitebark pine to independently migrate northward, and the management option of assisting its migration should natural dispersal not suffice, must also be assessed. I examine these questions using existing literature and new experimental data. Problems associated with whitebark pine distribution modeling include the existence of large differences between the fundamental and realized niche of the species, a lack of knowledge regarding the species distribution at high elevations, and a current lack of accounting for snow accumulation and persistence. These issues must be addressed, but they do not nullify the overall prediction that whitebark pine will lose a substantial portion of its current climatically-suitable range by the 2080s, while gaining new habitat in northwestern British Columbia. Predicting the rate of natural range expansion into newly habitable areas under climate change is challenging for whitebark pine because of its dependency on Clark's nutcrackers (*Nucifraga columbiana*) for seed dispersal. However, based on past seed-dispersal observations, it seems unlikely that the species will naturally disperse into a significant portion of its future climatic range within the century. Pests, pathogens and warming-induced vegetative competition are predicted to kill the majority of reproductively-viable whitebark pines in current populations by then, potentially leaving assisted migration as the only viable strategy for protecting the species from extinction. Results from an assisted migration common garden trials in western British Columbia confirm whitebark pine's ability to germinate and survive in climatically-favorable areas north of the species range, while growth chamber data confirm that whitebark pine is a poor height competitor at all but the coldest growing-season temperatures. These findings suggest three critical future research needs: 1) further refinement of SDMs, particularly for threatened and high-elevation species, 2) evaluation of Clark's nutcracker and whitebark pine dynamics at the northern edge of the species range to determine the pine's natural migration potential, and 3) continued development of ecological and ethical decision-making frameworks for assisted migration, using whitebark pine as a test case because of its threatened status and favorable life history attributes.

Keywords: species distribution model, climate envelope, range expansion, population differentiation

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Establishment Patterns of Whitebark Pine Following Fire in the Canadian Rockies

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Abstract—I examined the regeneration of whitebark pine (*Pinus albicaulis*) and four other high elevation conifers in young subalpine forest following two stand replacing fires in the Canadian Rockies. These were the Vermilion Pass fire of 1968, located in Kootenay and Banff national parks, and the Rock Canyon Creek fire of 1960, located approximately 125 km further southeast in the Invermere Forest District of British Columbia. I surveyed 103 100-m^2 plots in total, with roughly equal sampling intensity across the environmental gradients of altitude, aspect, and distance to the mature forest edge. I measured stand structural variables within each plot, including vegetation species cover and tree species seedling and sapling density. Both landscape and microsite scales of environmental variables were measured at each plot. Regeneration niches for whitebark pine and other conifers present were identified by classifying the post-disturbance plant community data into groups associated with the regenerating conifers. The analysis of the data using canonical correspondence analysis indicated that whitebark pine seedlings (< 30 cm in height) and saplings (≥ 30 cm in height) were associated with a distinct, but broadly ordinated group of plant species which occurred in the higher, drier, and more open regions of the burn areas. Alpine larch (*Larix lyallii*) had a relatively compact regeneration niche, sharing the similar higher, but moist, north-facing environmental space with the niches of subalpine fir (*Abies lasiocarpa*) and Engelmann spruce (*Picea engelmannii*). For spruce and larch seedlings, intermediate levels of low shrub cover appeared beneficial. The lodgepole pine (*Pinus contorta*) regeneration niche occupied a similar environmental space, except at lower elevations where the taller, denser cover associated with this species largely excluded the other tree species' establishment. Distance to seed source was also important in this multi-species regeneration model, as it showed that whitebark pine, alpine larch, and subalpine fir seedlings and saplings were all more likely found closer to perimeter adult trees. Engelmann spruce, and the relatively well dispersed lodgepole pine recruits, were less affected by that distance. Overall, the study showed that niche partitioning among subalpine tree species appears to occur relatively rapidly following large scale, stand replacing disturbance, as a function of both landscape and microsite factors.

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Blister Rust: Ecology & Assessment

A Natural History of *Cronartium ribicola*

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Abstract–*Cronartium ribicola* is a fungal pathogen that causes a blister rust disease of white pines, *Ribes,* and other hosts in the genera *Castilleja* and *Pedicularis.* Although blister rust can damage white pine trees and stands, the severity and significance of these impacts vary with time, place, and management. We use a natural history approach to describe the history, biology, and management of *C. ribicola.* We review its status as a non-native pathogen, likely ecological and evolutionary behavior, and implications for management.

Introduction

The history of white pine blister rust is little more than 100 years old. European interest first began in response to an epidemic that devastated plantations of introduced North American white pines. Then shortly after 1900, concern developed in the United States and Canada due to multiple rust introductions and severe commercial losses. Although *Cronartium ribicola* is native to Asia, brief local epidemics have occurred there. In North America, the pathogen has recently spread into the Southwest and intensified in high-elevation stands of the Pacific and Rocky Mountain regions. A typical pattern for blister rust epidemics has three phases—latent establishment, exponential growth, and endemic persistence. Demographic, ecological, and genetic factors determine the duration and severity of these phases. In the past, managers have used quarantine, eradication, sanitation, and genetics with variable success in controlling the rust. The present management strategy is to protect and sustain white pines through silviculture and genetics.

Similar to most pine stem rusts, *C. ribicola* is an obligate parasite of living hosts and has a complex life cycle comprising multiple spore stages for reproduction, dispersal, and perennial survival. *Cronartium ribicola* and related taxa are distributed across temperate Asia, Europe, and North America almost everywhere susceptible hosts occur. Most species of North American white pines have naturally infested populations, but disease severity ranges widely by location because of differences in site hazard and stand history. Most white pines and *Ribes* escape infection by geographic isolation or other environmental factors. Disease in susceptible white pines can result in death of individual branches, the upper crown, or an entire tree. Resistant white pines recognize pathogen presence and respond with physiological defenses that confer immunity if the pathogen is eliminated or tolerance if both survive. Subject to multiple, complex, ecological interactions, the long-term course of an epidemic and its effects on pathogen and host populations depend on their fitness in passing genes to the next generation.

Managers have historically considered *C. ribicola* as an introduced invasive pathogen causing unacceptable losses that can be reduced by silvicultural and genetic intervention. Economic rust control in commercial timber stands has often been difficult to achieve. Rust control to protect ecological values in natural high-elevation forests presents even greater difficulties. Important questions include the dispersive capability of the pathogen, distribution of hazardous sites, vulnerability of susceptible populations, rate of co-evolutionary adaption, resilience of affected ecosystems, and criteria for assessing values and risk. We agree with those who believe that management should be based on real understanding, support healthy ecosystems, and value life.

A Natural History Perspective

> *It seems to me that the natural world is the greatest source of excitement; the greatest source of visual beauty; the greatest source of intellectual interest. It is the greatest source of so much in life that makes life worth living.*
>
> —*Sir David Attenborough, 2006*

Many people might profess that an alpine meadow of white pines makes life worth living (Figure 1). Few, however, would see *Cronartium ribicola,* the disease agent causing white pine blister rust, as interesting and anything but a pest. We view the *Cronartia* (pine stem rust fungi) as organisms with value in themselves. They exercise a creative role in the evolution and dynamics of biotic communities. They form enduring, intimate associations with their hosts and co-evolve with these and other dependent species. In contrast to native stem rusts, however, *C. ribicola* is often perceived only as an introduced, invasive pathogen that can and should be controlled to reduce loss of ecological values. Although there are scientific and philosophical bases for this perception, our consideration of an alternative perspective leads to several questions with different implications for management. Is *C. ribicola* naturalizing? Can affected ecosystems remain diverse, productive, and attractive? Are the dynamics of the white pine blister rust pathosystem significantly different

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Figure 1. A high-elevation meadow of whitebark (*Pinus albicaulis*) and limber pine (*P. flexilis*), upper Lamoille Canyon, Ruby Mountains, NV. Photo by B. Geils.

from those of native blister rust pathosystems? What are the ethical responsibilities for preserving existing biotic entities such as populations, species, and communities? In wildlands, should maintaining natural ecological and evolutionary processes have precedence over management intervention? How do we ensure that management in the long-run does not cause more harm than good?

Our objective in raising these questions is not to dispute *what* to think about these issues but to encourage deeper reflection on *how* to think about them. Conservation biologists are motivated to act, but selection among strategies from a single-species focus to ecosystem management is problematic and fraught with ambiguity and contradiction (Simberloff 1998). Reiners and Lockwood (2010) provided a philosophical framework for examining how ecologists select and interpret facts according to their perceptions of what is relevant, attractive, and ethical. A thorough presentation of the history, biology, and management of blister rust and application of the Reiners and Lockwood model would require an entire monograph. For a comprehensive review of white pine blister rust, we refer the reader to the synthesis by Geils and others (2010) and to additional reviews in the same issue of Forest Pathology (Shaw and Geils 2010). Here, we only briefly describe several observations from the natural history of *C. ribicola,* offer our interpretations, and urge serious scientific investigation and philosophical discussion of the goals and means for stewardship of the natural world.

The term *history* in natural history derives from the Greek for *inquiry* or *knowing*. A natural history is a description of one kind of organism in its natural environment. It is a narrative on the development, behavior, relationships, evolution, and significance of a subject organism. We are inspired by Charles Darwin and E. O. Wilson. Their work demonstrates that natural history is not just for charismatic species, but also for 'lowly' barnacles and ants. Natural history unites biology and philosophy. What we perceive depends on how we observe and integrate that observation into an operational model of reality (see Hawking and Mlodinow 2010). What we perceive determines what we accept as true, beautiful, and right—therefore, what motivates our action.

Our own perceptions emerge from the sciences of biogeography and genetics. We have studied rust distribution and epidemiology to investigate how the pathogen finds its host or, conversely, how the host escapes infection. We have studied the pathology and genetics of rust–pine interactions to learn how the rust evades host defenses and how the host resists or tolerates the pathogen[1]. The scientific and historical literature provides a wealth of observation and interpretation on the white pine blister rust pathosystem. The articles in Shaw and Geils (2010) serve as a synthesis and guide to original references and additional scholarly reviews.

Diverse scientists, managers, and other concerned individuals hold various perspectives on blister rust. A widely held perspective in the mode of *command-and-control* (Holling and Meffe 1996) considers blister rust as a forest health problem that can and should be solved through management intervention. This perspective emphasizes blister rust as: 1) a recently introduced disease; 2) caused by an aggressively invasive non-native pathogen; 3) infecting highly susceptible host species; and 4) causing dire economic and ecological impacts. Along with fire, succession, bark beetles, and climate change, blister rust contributes to the decline

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[1] Use of active verbs such as *find* do not imply purposeful intent by the pathogen or host. The statement *the pathogen finds* is a contraction for "the fungus produces and releases myriad spores, diffusion and mass transport widely disperse these spores, and some spores randomly impact and adhere to the leaf surfaces of potential hosts."

of white pine populations and loss of biodiversity (Tomback and others, The Magnificent High-Elevation Five-Needle White Pines: Ecological Roles and Future Outlook these proceedings). Therefore, damaged ecosystems ought to be restored and maintained to historical conditions by management intervention using silviculture and genetics to control pests and to mitigate losses (Schwandt and others 2010).

Our alternative perspective highlights other aspects of the blister rust pathosystem. Fungi are living organisms that participate in ecological and evolutionary processes. Fungi have intrinsic biotic value regardless of their nutritional strategy as saprophytes or parasites and distribution as endemic or cosmopolitan. Our natural history perspective views the organism called *Cronartium ribicola* as comprising diverse genetic lineages and interbreeding populations. Their interactions with hosts and other organisms develop from the processes of speciation, migration, extirpation, reproduction, dispersal, parasitism, co-evolution, and ecosystem dynamics. *Cronartium ribicola* itself is a keystone species for communities of fungi, insects, and other animals which depend on blister rust cankers for food and habitat (Furniss and others 1972; Stillinger 1944).

Because *C. ribicola* is an introduced invasive exotic, blister rust could be seen as a novel challenge requiring intervention to protect threatened white pine species. But, the biological behavior of the organism is wholly analogous with that of blister rust fungi native to North America. The presence of both genetic resistance and ecological tolerance in its hosts indicates that they are not defenseless to the pathogen. Our perspective is not meant to justify selection of the "do nothing" management option. It is intended to provide a useful and realistic contrast for assessing the costs and long-term results of intervention to manage complex natural systems.

We value natural ecosystems as vital to human welfare, but so complex as to require an adaptive approach such as that first described by Holling (1978). We recognize biotic systems as *complex*—exhibiting non-linear behavior, embedded in hierarchical structures, and affected by various, often obscure contingencies. We consider *change* as the most common attribute of biotic systems. Resilient systems persist; adaptable systems evolve. Prudent stewardship requires adaptive learning that strives for desired results within a context of social and economic constraints, an appreciation of beauty, and regard, if not fondness, for all living organisms.

The reason for our caution with management intervention is that forest ecosystems are sufficiently complex that either treatment or neglect can produce unexpected or unwanted results. Therefore, a pragmatic strategy should be based on an understanding of ecosystem dynamics and biotic evolution and should recognize the limits of our knowledge and ability. We do not judge the sincerity of others. Rather, we urge use of observations from history and long-term monitoring for adapting management practice to changing environments and goals. For example, the history of blister rust includes many cases where control failed, was inappropriate, or ill-applied (Van Arsdel 2011). Early in the epidemic of eastern North America, losses were so severe that warnings of the blister rust threat and declarations of need for control were strongly voiced (e.g., Detwiler 1918). When managers realized that they could not readily eliminate blister rust, they abandoned white pine silviculture (Van Arsdel 2011). This fear of blister rust, however, was unjustified—eventually, white pines displayed their great reproductive potential and the epidemic progressed into an endemic phase. Even within a region of high rust hazard, a dedicated and knowledgeable land manager can produce white pine timber along with wildlife dependent on white pine snags and *Ribes* (Van Arsdel 2011).

Several concepts are especially useful for developing that understanding which can serve as a basis for management. Gunderson and Holling (2002) described a conceptual model of the creative renewal of ecosystems that incorporates resilience as a fundamental dimension of change. Their approach of adaptive management is derived from studies of complex natural and human systems and serves as an alternative to the command-and-control approach appropriate to definable engineering projects. Thompson (2005) offered hypotheses on the geographic mosaic of co-evolution between parasites and hosts that integrate both spatial and temporial aspects of genetic interactions. The specifics of co-evolutionary patterns vary with the life histories of parasite–host systems, but one generality is that significant genetic changes occur at a local scale from one generation to the next. To move from hypothesis to theory, however, studies have to be installed and monitored. Keane and Arno (2001) identified seven steps for developing and executing whitebark pine restoration projects that could be extended to other white pine species. These steps are: 1) multiscale inventory of existing conditions; 2) identification of key natural processes; 3) ranking landscapes and stands for treatment priority; 4) selection of sites potentially benefiting from treatment; 5) design of treatments specific to individual sites; 6) efficient implementation; and 7) response monitoring.

The importance Keane and Arno (2001) placed on monitoring is consistent with the Gunderson and Holling (2002) approach of adaptive management. Monitoring is an opportunity for learning how stands and landscapes change over time and for testing hypotheses of co-evolution. For example, rust incidence and host mortality can be high early in a regional epidemic or in a young stand (Zambino 2010; Tomback and others 1995). These early trends, however, may not extend into later epidemic stages or to older stands. Ostrofsky and others (1988) re-assessed the regional incidence of blister rust after 70 years of *Ribes* eradication in Maine. They learned that incidence was only 3.8% in treated areas and less than 10% in areas not treated.

Paleobiology

The evolution and biogeographical history of stem rust fungi can be inferred from life-cycles, morphologies, host ranges, extant distributions, disease symptoms, and phylogenetic relationships. Although fungi are mostly absent from the geological record, the pines are well represented as fossils and pollen. Millar and Kinloch (1991) used a phylogenetic tree indicating evolutionary relationships among the pine hosts to hypothesize about former hosts and the distributions of stem rusts. A similar study with the non-pine hosts would likely also be instructive. Richardson and others (2010) reviewed molecular approaches for producing gene-based phylogenetic trees of stem rusts and *Cronartium ribicola*.

Evidence from diverse sources (above, and review by Van Arsdel 2011) suggests that the association of an ancestral *C. ribicola* with *Strobus* pines dates to the Cretaceous Period before Laurasia broke into Eurasia and North America (about 65 million years ago). In the warm Tertiary epochs, pines in North America retreated to refugia too cold for blister rust while hosts and pathogens in Eurasia survived in more diverse refugia. During the Pleistocene, distributions of stem rusts, white pines, and other hosts shuffled across the northern continents repeatedly for several million years in response to the advances and retreats of glaciers. By the Holocene, only a few species of white pines remained in isolated alpine locations in Europe; but a diversity of white pines persisted in Asia along with their stem rusts (Kim and others 2010). The white pines in North America consisted of one species widely distributed in the East and representatives of the stone pines, foxtail pines, other five-needle pines, and pinyon pines in the West. The only stem rust on any of these species was *C. occidentale* on pinyon pines (Kinloch and others 2003).

Several ideas emerge from considering paleobiology in light of recent history. White pines and stem rusts have long shared a co-evolutionary history characterized by co-incidence, migration over continental distances, separation, and reunion. *Cronartium ribicola* and *C. occidentale* share common hosts in the genus *Ribes* and, though long separated, are closely related genetically (Vogler and Bruns 1998). Kinloch and others (2003) observed that the distribution of resistance in sugar pine (*P. lambertiana*) to *C. ribicola* correlates with the distribution of pinyon pines and surmised that, before the recent introduction of *C. ribicola* to North America, natural selection for blister rust resistance in sugar pine may have been induced by prior challenge from *C. occidentale*. For *C. ribicola*, the distinction between native and non-native may be less relevant than for other introduced plant pathogens.

Past Management

Literature on blister rust reveals that divergent epidemiological and management histories have unfolded in geographic regions with different environments and different host–pathogen combinations (Geils and others 2010). In the 1800s, foresters planted *Pinus strobus*, a valuable North American timber species, across northern and central Europe to western Russia (Gäumann 1950). Once introduced into Russia, *P. strobus* was exposed to *Cronartium ribicola* alternating between *Ribes* and the native Siberian white pine (*P. sibirica*). The combination of a favorable climate and close proximity of susceptible white pines and European black currants (*R. nigrum*) permitted rapid development of a severe epidemic in Europe. Although the silviculture of *P. strobus* was mostly abandoned in Europe by the early 1900s, European nurseries continued to ship inexpensive white pine seedlings to North America. Since blister rust infection can be latent in young seedlings, the rust was carried in cryptically-infected white pines that were planted at many locations across eastern North America. The pathogen was soon introduced as well to western North America. Inspection, quarantine, seedling destruction, and other early control responses failed to prevent widespread establishment of *C. ribicola*.

Foresters had been unable to stop the rapid and nearly complete destruction of American chestnut (*Castanea dentata*) from an introduced blight (Anagnostakis 1987), raising concern that the white pine blister rust might be similarly intractable and potentially disastrous. But, *C. ribicola* was more vulnerable to control because its life cycle required alternation between pines and *Ribes* (see historical reviews in Geils and others 2010 and Zambino 2010). Government-managed and publicly-supported blister rust control programs focused on eradicating cultivated European black currant first and then wild native *Ribes*. Eradication was easier and relatively more effective in eastern North America than in western regions because of differences in labor costs and *Ribes* biology. The impact of eradication on the blister rust epidemics varied greatly, and its long-term consequences are still unresolved. Perhaps eradication's most important contributions were employment and fire protection. The experience of working in the woods exposed many young men (and some women) to the beauty, challenge, and reality of forestry in North America (Shaw 2010).

Besides eradication, silvicultural methods have been used to regenerate and tend white pine stands and have reduced blister rust damage (Ostry and others 2010; Zeglen and others 2010). Direct control of the disease on pine was attempted for a brief time; but antibiotics, biocontrol, and pine-removal ultimately proved impractical in North America. Sites differ in the expected severity of rust damage because of variations in climate and spatial distributions of hosts. Rating and mapping site hazard have been used to select favorable sites for regenerating white pines and determining appropriate treatments for site preparation, thinning, and sanitation. Stand treatments include pruning branches to remove infections or reduce the risk of future infections that would be lethal to the host. Although these methods impose additional costs with uncertain benefits, they remain important management tools in North America (Schwandt and others 2010).

In North America, genetic resistance programs have provided planting stock selected for improved performance in response to *C. ribicola* (King and others 2010). Improved stock is available for western white pine (*P. monticola*) and sugar pine, and it is being developed for high-elevation white pines (Sniezko and others, Past and Current Investigations of the Genetic Resistance to *Cronartium ribicola* in High-elevation Five-needle Pines these proceedings). Although increasing genetic resistance through artificial or natural regeneration is an important component along with silviculture in sustaining white pine populations, this approach faces several challenges. Schwandt and others (2010) cited a lack of planting opportunities as fewer sites are managed intensively and poor long-term field performance resulting from interactions of complex environmental and genetic factors. Restoration programs involving thinning and controlled burning can increase planting opportunities. Sniezko and others (Past and Current Investigations of the Genetic Resistance to *Cronartium ribicola* in High-elevation Five-needle Pines these proceedings) provide a realistic appraisal of the potential for developing durable resistance in high-elevation white pines and identify additional needs in methods and monitoring for successful deployment.

Life History and Parasitism

Cronartium ribicola is a fungus comprised of a thallus (or body) of filamentous and often multinucleate hyphae and reproducing sexually by spores borne on a basidium (a club-like structure). Common to the Pucciniales or rust fungi, *C. ribicola* is an obligate parasite of vascular plants. That is, the fungus requires a live host to grow and regenerate—when the host tissue dies, the fungus dies. Typical of parasites, its life cycle has multiple spore stages (it is macrocyclic) and alternates between phylogenetically unrelated hosts (it is heteroecious).

The distinguishing visible signs of *C. ribicola* become apparent on infected white pine and *Ribes* (see Geils and others 2010). The first signs on a pine are the darkening spermogonia, which produce sweetish exudates, microscopic non-infective spores (spermatia), and receptive hyphae. Next produced are the blister-like aecia with powdery, bright orange aeciospores erupting through a white peridium. Since infection is perennial on pine, spermogonia and aecia from present and past years may be found on an infected pine stem. Uredinia form as pustules on the undersides of leaves of the annual host, usually a *Ribes*. Several cycles of urediniospores from the uredinia may be produced in a season. The fungus produces brown, hair-like masses of telia visible in late summer or early fall on leaves of the non-pine host.

Colley (1918) described the cytology and parasitism of *C. ribicola*. Spermatia and receptive hyphae provide for genetic outcrossing. Aeciospores effect long-distance dispersal from pine and infection of a telial host. Urediniospores spread and intensify the fungus on the telial host within a season. Teliospores aggregated into telia germinate *in situ* and produce basidia, from which basidiospores are discharged to infect nearby pines.

Cummings and Hiratsuka (2003) conceptualized the nuclear cycle of a heteroecious *Cronartium* rust. The strategy of the rust is a combination of: 1) sexual reproduction and outcrossing for genetic diversity; 2) short- and long-distance dispersal for spatial diversity; 3) persistence on a perennial host for longevity; and 4) intensification on an annual host for amplification.

There are several oddities in the life history of *C. ribicola*. A form of rust on Asian white pines appears to have a simplified, autoecious or pine-to-pine life cycle that bypasses an alternate host (Kaneko and Harada 1995; Zhang and others 2010). Rust collections by Joly and others (2006) at a few sites in southern Alberta indicate that spermatia of *C. comandrae* from lodgepole pine (*P. contorta*) can fertilize the receptive hyphae of *C. ribicola* on limber pine (*P. flexilis*). The hybrid aeciospores produced are not known to be infective.

Combes (1995) reviewed the very successful strategy of parasitism in diverse groups of organisms, including intricate modes of dispersal and reproduction as well as multiple evolutionary pathways. Parasites are wholly dependent upon their hosts except during periods of spore dispersal. Although a parasite can damage a host and reduce its fitness, natural selection upon a biotrophic parasite favors host fitness, not lethality. Rapid, local, cell death in the host (hypersensitivity) is a common defense. Typical of parasites, *C. ribicola* obtains from its host protection from the external environment, an elevated position from which to launch its propagules, and the nutrition necessary for growth and reproduction. *Cronartium ribicola* infects its host by means of hyphae entering host stomates, ramifying between host cells, and extracting nutrition from host cells with a specialized structure called an haustorium (Colley 1918).

Hosts and Distribution

The most common telial hosts of *Cronartium ribicola* in North America are plants in the genus *Ribes* (Grossulariaceae), but several species of *Pedicularis* and *Castilleja* (Orobanchaceae) are also infected and can support telial production and subsequent infection of pine (Zambino 2010). In eastern Asia, hosts occur in all three genera, but the genus-host range is reported to vary by location (Kim and others 2010).

In North America, most species of *Ribes* appear to be compatible hosts; but species, populations, and individual plants vary in susceptibility and tolerance because of genetic and ecological factors (Zambino 2010). Although resistance is found among the cultivated black currants, they are often the most contagious hosts. The spiny alpine gooseberry, *R. montigenum,* often occurs under whitebark pine (*P. albicaulis*) in high-elevation meadows, but becomes infected in summer from urediniospores produced on western black currants (*R. hudsonianum*) that are restricted to riparian zones in lower-elevation forests. The widely distributed wax currant (*R. cereum*) is susceptible to *C. ribicola* and contagious in some regions. But in the American Southwest, the currant referred to as *R. cereum* is commonly infected by a leaf rust of pinyon (*Coleosporium ribicola*), but not by *Cronartium ribicola* even where other *Ribes* species are severely infested.

Judging from natural and artificial inoculations, all species of five-needle white pines (subgenus *Strobus,* section Quinquefoliae) can serve as aecial hosts (Tomback and Achuff 2010). Extraordinarily, other pines such as *P. radiata* in subgenus *Pinus* may be infected, and the infections endure without producing spores (D. Vogler, personal observation). Typically infected pines are the white pines related to *P. strobus*, the stone pines (e.g., *P. albicaulis*) and the foxtail-bristlecone pines (e.g., *P. aristata*). *Pinus pumila* is a high-latitude pine of eastern Asia related to whitebark pine and with a similar low, bushy form. This native pine is susceptible to white pine blister rust but co-exists well with the parasite.

Some susceptible species of white pines in North America are not known to be naturally infected. The white pines such as *P. ayacahuite* of Mexico and central America occur with *Ribes* in habitats that appear to be environmentally suitable for rust infection. But their geographic isolation from rust-infested regions in the United States may have allowed them to escape infection (so far). In contrast, *P. longaeva* (Great Basin bristlecone pine) and associated *Ribes* appear to be within the dispersal range of *C. ribicola* aeciospores (Frank and others 2008). The environment of the Great Basin may be so unfavorable for rust infection that these susceptible hosts have also escaped infection.

Biotic Interactions

Each white pine blister rust pathosystem is nested within a larger ecosystem and network of biotic interactions including competition, herbivory, predation, and various forms of symbiosis. The best recognized of these interactions is between host and pathogen—expressed at the organism level as a physiological disease and at the population level as an epidemic with ecological and genetic dimensions.

The symptoms of blister rust result from the altered physiological responses of a host to the presence and action of a pathogen and secondary agents (Geils and others 2010). Pathogenesis in an aecial host proceeds from needle spots to shoot, branch, and stem reactions including localized necrosis, resinosis, and altered cell growth and division. As a consequence of rust sporulation, desiccation, and attack by insects and other fungi, the inner bark within a branch or bole canker is killed. After a stem is girdled, distal portions die, producing either a branch flag or top-kill; mortality results from crown decline and/or insect attack. Growth of an infection may be slowed or halted before or after the rust sporulates as result of a hypersensitive host reaction in the needle or bark or from external processes such as rodent feeding. The likelihood and impact of infection varies with host age. Disease is more damaging on seedlings, but more infections are likely found on large trees because of their size, exposure, and retention of infected branches. Infection in a telial host is usually limited to deciduous leaves. Symptoms of infection are necrotic spots; signs of the fungus are uredinia and telia. Damage results from early defoliation. For each aecial or telial host, environmental and genetic factors affect the severity and outcome of pathogenic interactions.

Although hosts are often ranked on a scale from susceptible to resistant, the pathogen–host interaction may be better characterized by the four modes of escape, susceptibility, resistance, and tolerance (Vogler and Delfino Mix 2010). A plant *escapes* if geographic isolation or other external, environmental factors prevent challenge by the rust. Most host plants remain uninfected because of escape. A plant is *susceptible* to infection if the pathogen can establish an intimate and enduring presence in the host to meet its nutritional and reproductive requirements. A plant demonstrates host *resistance* when it recognizes an invading pathogen and responds with active defensive mechanisms. *Virulent* genotypes of the pathogen can evade detection in an infected host and thus are capable of causing disease in a plant that would otherwise be characterized as resistant. A *tolerant* host can survive and reproduce in spite of established infection. Because susceptible and tolerant plants allow the pathogen to reproduce, they are contagious.

Years of research have unraveled some of the biochemical mechanisms behind pathogenesis and the modes of pathogen–host interactions (see reviews in Shaw and Geils 2010). Observations in genetics have increased our knowledge of the inheritance of specific traits associated with resistance. However, we are only beginning to understand the population genetic consequences of artificial selection in natural white pine ecosystems. New introductions and gene movement at larger scales of landscapes to regions are infrequent and subject to random effects. Because of heterogeneity in effective population size, outcrossing, dispersal, extirpation, and other metapopulation dynamics, co-evolution of rust and host may occur rapidly at the fine scale of individual stands. Many epidemics have demonstrated a common temporal pattern in the frequency of infected trees (discussed in Zambino 2010). In the latent period, infections are too uncommon to be detected; then the number of infections seems to explode among highly vulnerable young trees. Later in an epidemic and in older stands, the infection rate and percentage of diseased trees appears to decline or fluctuate at a low level. This pattern could result from demographic and ecological processes such as host maturation and aging, succession and reduction in *Ribes* density, or population genetic processes (naturalization).

Management using silvicultural and genetic approaches has focused on young stands and plantation forestry. If we are to sustain natural stands of white pine in high-elevation forests, we need to better understand disease processes at the pathogen-host level and epidemiological processes over generations of trees. Both ecological and evolutionary processes are critical.

Human Relations

In this review of the natural history of *Cronartium ribicola*, we have identified several instructive features of its biology and management. We have also described our perspective on the blister rust pathosystem and implications for white pine management. Science provides a method for assessing the likelihood an intervention would be cost-effective and reliable for achieving a specified objective. Ethics provides a frame for discussing whether a manager ought to act, given the costs, risks, tradeoffs, and consequences of intervention. Ethics also describes the utilitarian or intrinsic values implicit in human relations to other humans and other beings that determine what are right and good objectives.

In *A Sand County Almanac*, Aldo Leopold (1949), father of wildlife conservation, introduced the concept of a *land ethic*. Leopold recounted Odysseus's return to Ithaca and discovery that his palace was occupied by suitors seeking to take his wife and kingdom. Odysseus slew not only the suitors but also his unfaithful servants. He was considered justified by the ethics of the age in disposing of the servants because they were his property. Today's ethics require that servants be treated as persons with human rights not as property. Leopold thought of the 'land' as more than property, but as the soil, water, and whole biotic community upon which life depends. By a land ethic, we do not have a right to abuse the land; rather we have a responsibility to care for it.

Human self-interest leads to valuing plants, animals, and nature for their utility in providing food, shelter, comfort, and pleasure. Formerly, predators such as wolves were hunted for bounty because they destroyed game and livestock. Although some Americans still view wolves as varmints, others esteem wolves as aesthetic symbols of wild nature and agents for maintaining healthy wildlife herds. Charismatic predators such as wolves have worthy qualities of personality and behavior that humans view as intelligent and beautiful. White pines are still harvested for timber and other products, but their stature and grace have earned them aesthetic value and protection (Tomback and Achuff 2010). Mistletoes are parasites of forest trees that foresters have long considered a scourge because they reduce timber yield. But, the Druids considered them a symbol of the divine. Artists are inspired by them, and biologists protect them for wildlife habitat. A forest wildfire can be threatening and destructive. Many older foresters thought fire had no place in managed stands. But, fire displays an awesome beauty if viewed from a safe vantage. At the urging of a new generation of fire ecologists, land managers now use fire to renew forest stands.

We suggest that *Cronartium ribicola* is worthy of thoughtful and creative consideration. Darwin found grandeur in that "endless forms most beautiful" could evolve from fixed laws. So simple a thing as the blister rust fungus has survived with its hosts for millions of years; it can find its hosts a thousand kilometers from its origin, and adapt to and create new environments in which to thrive. *Cronartium ribicola* is now a permanent resident of the white pine ecosystems of North America. In response, we suggest that pragmatic, science-based management of these ecosystems consider three principles:

- Management based on an informed and deep understanding will be met with positive reinforcement from nature;
- The health of an ecosystem is best judged by its beauty of form and function;
- Good management respects both the utility and intrinsic value of all living organisms.

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References

Anagnostakis, S. L. 1987. Chestnut blight: the classical problem of an introduced pathogen. Mycologia. 79(1): 23-37.

Colley, R. H. 1918. Parasitism, morphology, and cytology of *Cronartium ribicola*. Journal of Agricultural Research. 15: 619-659.

Combes, C. 1995. Parasitism, the Ecology and Evolution of Intimate Interactions. Chicago, IL: University of Chicago Press. 728 p.

Cummins, G. B.; Hiratsuka, Y. 2003. Illustrated Genera of Rust Fungi. St. Paul, MN: American Phytopathological Society Press. 225 p.

Detwiler, S. B. 1918. Battling the pine blister rust. American Forestry. 24 (296): 451-457.

Frank, K. L.; Geils, B. W.; Kalkstein, L. S.; Thistle, H. W., Jr. 2008. Synoptic climatology of the long distance dispersal of white pine blister rust. II. Combination of surface and upper-level conditions. International Journal of Biometeorology. 52: 653-666. [Online]. doi: 10.1007/s00484-008-0158-3

Furniss, M. M.; Hungerford, R. D.; Wicker, E. F. 1972. Insects and mites associated with western white pine blister rust cankers in Idaho. Canadian Entomologist. 104: 1713-1715.

Gäumann, E. 1950. Principles of plant infection, a text-book of general plant pathology for biologists, agriculturists, foresters, and plant breeders. In: Brierley, W.B. [English ed.] New York: Hafner Publishing. 543 p.

Geils, B. W.; Hummer, K. E.; Hunt, R. S. 2010. White pines, *Ribes*, and blister rust: a review and synthesis. Forest Pathology. 40: 147-185. [Online]. doi: 10.1111/j.1439-0329.2010.00654.x Available: http://www.treesearch.fs.fed.us/pubs/36222

Gunderson, L. H.; Holling, C. S., eds. 2002. Panarchy, Understanding Transformations in Human and Natural Systems. Washington, DC: Island Press. 507 p.

Hawking, S.; Mlodinow, L. 2010. The Grand Design. New York: Bantam Books. 198 p.

Holling, C. S., ed. 1978. Adaptive Environmental Assessment and Management. Caldwell, NJ: Blackburn Press. 377 p.

Holling, C. S.; Meffe, G. K. 1996. Command and control and the pathology of natural resource management. Conservation Biology. 10: 328-337. [Online]. doi: 10.1046/j.1523-1739.1996.10020328.x

Joly, D. L.; Langor, D. W.; Hamelin, R. C. 2006. Molecular and morphological evidence for interspecific hybridization between *Cronartium ribicola* and *C. comandrae* on *Pinus flexilis* in southwestern Alberta. Plant Disease. 90: 1552. [Online]. doi: 10.1094/PD-90-1552A

Kaneko, S.; Harada, Y. 1995. Life cycle of *Endocronartium sahoanum* and its nuclear condition in axenic culture. In: Kaneko, S.; Katsuya, K.; Kakishima, M.; Ono, Y.; 4th IUFRO Rusts of Pines Working Party Conference; 1994 October 2-7; Tsukuba, Japan. Kukizaki, Japan: Forestry and Forest Products Research Institute, Forest Microbiology Section: 95-100.

Keane, R. E.; Arno, S. F. 2001. Restoration concepts and techniques. In: Tomback, D. F.; Arno, S. F.; Keane, R. E. Whitebark pine communities: Ecology and restoration. Washington, DC: Island Press: 367-400.

Kim, M.-S.; Klopfenstein, N. B.; Ota, Y.; Lee, S. K.; Woo, K. S.; Kaneko, S. 2010. White pine blister rust in Korea, Japan and other Asian regions: Comparisons and implications for North America. Forest Pathology. 40: 382-401. [Online]. doi: 10.1111/j.1439-0329.2010.00664.x

King, J. N.; David, A.; Noshad, D.; Smith, J. 2010. A review of genetic approaches to the management of blister rust in white pines. Forest Pathology. 40: 292-313. [Online]. doi: 10.1111/j.1439-0329.2010.00659.x

Kinloch, B. B., Jr.; Sniezko, R. A.; Dupper, G. E. 2003. Origin and distribution of *Cr*2, a gene for resistance to white pine blister rust in natural populations of western white pine. Phytopathology. 93: 691-694. [Online]. doi: 10.1094/PHYTO.2003.93.6.691

Leopold, A. 1949. A Sand County Almanac and Sketches Here and There. New York: Oxford University Press. 228 p.

Millar, C. I.; Kinloch, B. B. 1991. Taxonomy, phylogeny, and coevolution of pines and their stem rusts. In: 3rd IUFRO Rusts of Pine Working Party Conference, Banff, AB, 1989 September 18-22. Ed. By Hiratsuka, Y.; Samoil, J. K.; Blenis, P. V.; Crane, P. E.; Laishley, B. L. Info. Rep. NOR-X-317. Edmonton, AB: Forestry Canada, Northern Forestry Centre. pp. 1-38.

Ostrofsky, W. D.; Rumpf, T.; Struble, D.; Bradbury, R. 1988. Incidence of white pine blister rust in Maine after 70 years of a *Ribes* eradication program. Plant Disease. 72(11): 967-970. [Online]. doi: 10.1094/PD-72-0967

Ostry, M. E.; Laflamme, G.; Katovich, S.A. 2010. Silvicultural approaches for management of eastern white pine to minimize impacts of damaging agents. Forest Pathology. 40: 332–346. [Online]. doi: 10.1111/j.1439-0329.2010.00661.x

Reiners, W.A.; Lockwood, J. A. 2010. Philosophical Foundations for the Practice of Ecology. New York: Cambridge University Press. 212 p.

Richardson, B. A.; Ekramoddoullah, A. K. M.; Liu, J.-J.; Kim, M.-S.; Klopfenstein, N. B. 2010. Current and future molecular approaches to investigate the white pine blister rust pathosystem. Forest Pathology. 40: 314-331. [Online]. doi: 10.1111/j.1439-0329.2010.00660.x

Schwandt, J. W.; Lockman, I. B.; Kliejunas, J. T.; Muir, J. A. 2010. Current health issues and management strategies for white pines in the western United States and Canada. Forest Pathology. 40: 226-250. [Online]. doi: 10.1111/j.1439-0329.2010.00656.x

Shaw, C. G. 2010: Foreword [to Special Issue. White Pines, *Ribes*, and Blister Rust]. Forest Pathology. 40: 145-146. [Online]. doi: 10.1111/j.1439-0329.2010.00653.x

Shaw, C. G.; Geils, B. W., guest eds. 2010. Special Issue: White Pines, *Ribes* and Blister Rust. Forest Pathology. 40: 145-417. Woodward, S., editor-in-Chief. Berlin, Germany: Blackwell Verlag GmbH.

Simberloff, D. 1998. Flagships, umbrellas, and keystones: Is single-species management passé in the landscape era? Biological Conservation. 83: 247-257.

Stillinger, C. R. 1944. Damage to conifers in northern Idaho by the Richardson red squirrel. Journal of Forestry. 42(2): 143-144.

Thompson, J. N. 2005. The Geographic Mosaic of Coevolution. Chicago, IL: University of Chicago Press. 443 p.

Tomback, D. F.; Achuff, P. 2010. Blister rust and western forest biodiversity: ecology, values and outlook for white pines. Forest Pathology. 40(3/4): 186-225. [Online]. doi: 10.1111/j.1439-0329.2010.00655.x

Van Arsdel, E. P. 2011. Blister Rust in North America: What We Have Not Learned in the Past 100 Years. In: Fairweather, M. Comp. 2011. Proceedings of the 58th Annual Western International Forest Disease Work Conference; 2010 October 4-8; Valemount, BC. U.S. Forest Service, AZ Zone Forest Health, Flagstaff, AZ: in press.

Vogler, D. R.; Bruns, T. D. 1998. Phylogenetic relationships among the pine stem rust fungi (*Cronartium* and *Peridermium* spp.). Mycologia. 90: 244-257. [Online]. Available: http://www.jstor.org/stable/3761300

Vogler, D. R.; Delfino Mix, A. 2010. Resistance: What is it? In: Cleary, M.; 3rd Western White Pine Management Conference; 2008 June 17-18; Vernon, BC. Kamloops, BC: BC Ministry of Forests and Range: 24-30.

Zambino, P. J. 2010. Biology and pathology of *Ribes* and their implications for management of white pine blister rust. Forest Pathology. 40: 264-291. [Online]. doi: 10.1111/j.1439-0329.2010.00658.x

Zeglen, S.; Pronos, J.; Merler, H. 2010. Silvicultural management of white pines in western North America. Forest Pathology. 40: 347-368. [Online]. doi: 10.1111/j.1439-0329.2010.00662.x

Zhang, X. Y.; Lu, Q.; Sniezko, R. A.; Song, R. Q.; Man, G. 2010. Blister rusts in China: hosts, pathogens, and management. Forest Pathology. 40: 369-381. [Online]. doi: 10.1111/j.1439-0329.2010.00663.x

Monitoring White Pine Blister Rust Infection and Mortality in Whitebark Pine in the Greater Yellowstone Ecosystem

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Background

There is a critical need for information on the status and trend of whitebark pine (*Pinus albicaulis*) in the Greater Yellowstone Ecosystem (GYE). Concerns over the combined effects of white pine blister rust (WPBR, *Cronartium ribicola*), mountain pine beetle (MPB, *Dendroctonus ponderosae*), and climate change prompted an interagency working group to design and implement a long-term monitoring program in the GYE. Our primary objective was to determine the status and trends in the proportion of trees >1.4 m tall infected with WPBR and to provide information to federal managers, at a regional scale, on estimates of tree survival, taking into account the presence of WPBR and MPB. Long-term monitoring of whitebark pine in the GYE and across its range is vital to understanding the ecological impact of forest insect and disease pathogens on this important high elevation species.

Methods

Details of our sampling design and field methodology can be found in the Interagency Whitebark Pine Monitoring Protocol for the GYE (GYWPMWG 2007). The target population addressed by this protocol includes whitebark pine growing in pure whitebark pine or mixed conifer stands on six national forests and two national parks (figure 1). In the GYE, whitebark pine grows on over 1 million ha (GYCCWPS 2010) of public land in Wyoming, Montana, and Idaho.

The sample frame for our monitoring program was stratified by the U.S. Fish and Wildlife Service Grizzly Bear Recovery Zone (RZ) boundary using two Geographic Information System (GIS) sources: inside the RZ the GIS vegetation layer used in the grizzly bear cumulative effects model (Dixon 1997) was used while outside the RZ, stands of whitebark pine mapped by the U.S. Forest Service were used. Forest stands that burned in the 1988 wildfires or later were excluded from the sample frame as these stands were considered too young to have whitebark pine trees >1.4 m tall.

We selected our sampling units using a 2-staged, probability based sampling design. Our primary sampling units are randomly selected forest stands approximately 2.5 ha in size or larger that have a component of whitebark pine in the species composition. Our secondary sampling units are 10 by 50 m transects randomly selected from each stand. At least one whitebark pine tree >1.4 m tall was required for a permanent transect to be established.

Transects were established in the RZ in 2004 and expanded to the surroundings forests the following years. After completing transect establishment in 2007, we adopted a "rotating panel" with a 4-year schedule as our default resurvey design. A panel is a subset of the total sample size that is visited within a given year. Transects were randomly assigned to one of four panels; each panel consists of approximately 44 transects which is the number that can be realistically visited in a given field season by one, two-person field crew.

The resurvey design ensures that the sampling units are revisited on the same time frame and facilitates useful statistical comparisons (Tomback and others 2005) of our monitoring data in the future. Based on the history of when transects were initially established, the interval between the first and second survey for WPBR will vary until 2011 when all the transects will have been surveyed twice for WPBR infection. After 2011, the time interval between resurveys will be 4 years unless a resurvey cannot take place due to fire, weather, wildlife encounters, etc. In these situations, the transect will be resurveyed the following year.

The 4-year resurvey schedule was chosen because WPBR spread is a slow process and the detection of annual change would not be effective or practical (GYWPWG 2008). MPB infestation is much more rapid and can causes mortality quicker than WPBR. In response to the current MPB outbreak we temporarily adopted a two-year resurvey design to report MPB infestation and whitebark pine mortality during the current epidemic. With this approach, two of the four panels are surveyed annually; one panel is subject to the full survey for WPBR infection, MPB infestation and tree mortality and the second panel is subject to a partial survey focused on MPB infestation and tree mortality.

Within the 5 by 10 m wide belt transect, we measured diameter breast height (DBH) and permanently marked live

In: Keane, Robert E.; Tomback, Diana F.; Murray, Michael P.; and Smith, Cyndi M., eds. 2011. **The future of high-elevation, five-needle white pines in Western North America: Proceedings of the High Five Symposium.** 28-30 June 2010; Missoula, MT. Proceedings RMRS-P-63. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station. 376 p. Online at http://www.fs.fed.us/rm/pubs/rmrs_p063.html

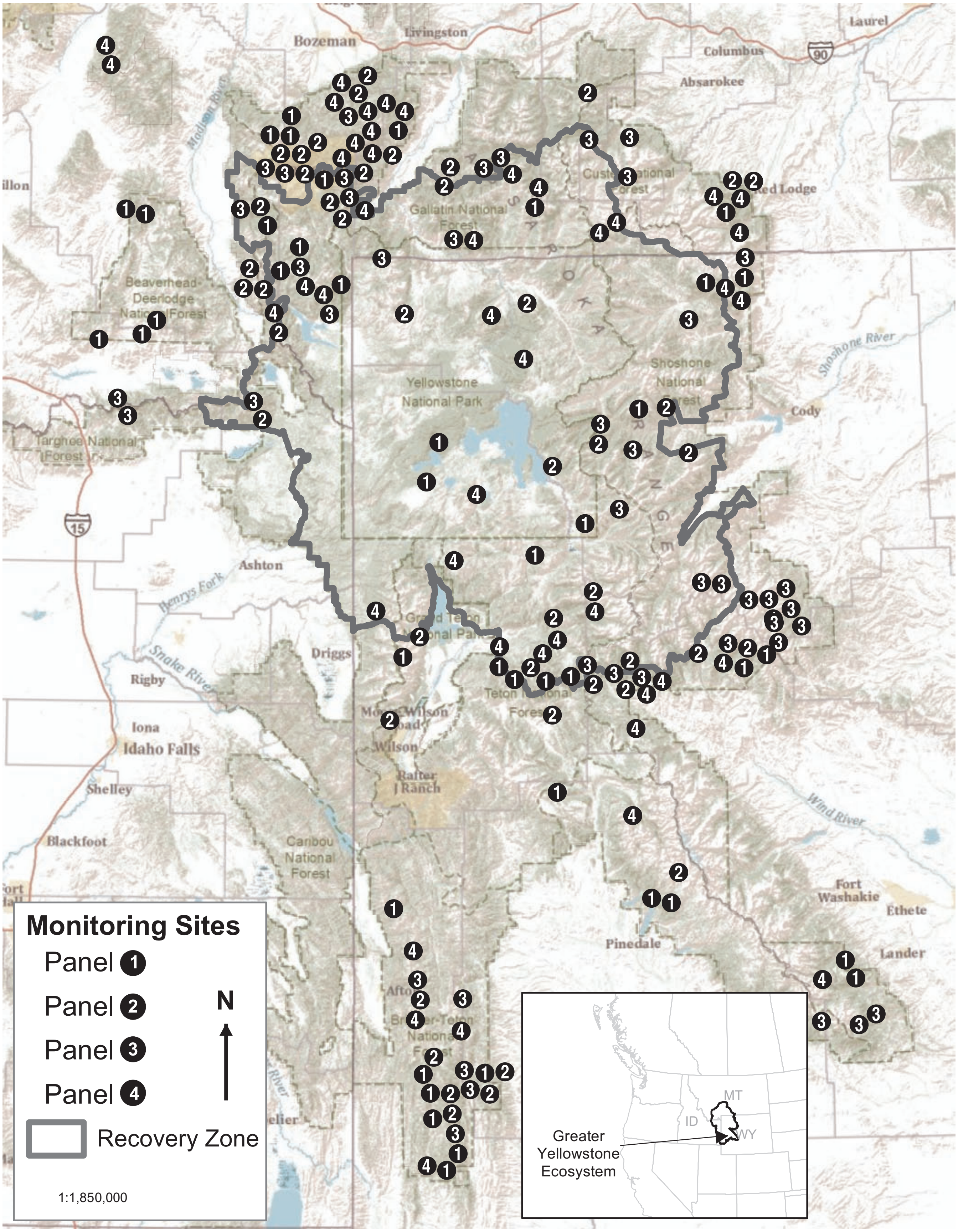

Figure 1. Location of whitebark pine survey transects (n=176) in the Greater Yellowstone Ecosystem in Idaho, Montana, and Wyoming, USA. In 2008 and 2009, 175 transects were surveyed for tree status and indicators of mountain pine beetle infestation.

Table 1. Design based ratio estimates for the proportion of live whitebark pine trees > 1.4 m tall infected with white pine blister rust in the Greater Yellowstone Ecosystem (GYE), 2004-2007, within and outside the grizzly bear recovery zone (RZ).

	Within RZ	Outside RZ	Total for GYE
Total number of mapped stands	2362	8408	10770
Number of stands sampled	64	86	150
Number of transects	66	110	176
Number of trees sampled	1307	3467	4774
Proportion of transects infected	0.79	0.86	0.84
Proportion of live trees infected	0.14	0.217	0.20
Proportion of live trees infected standard error	0.044	0.035	0.037

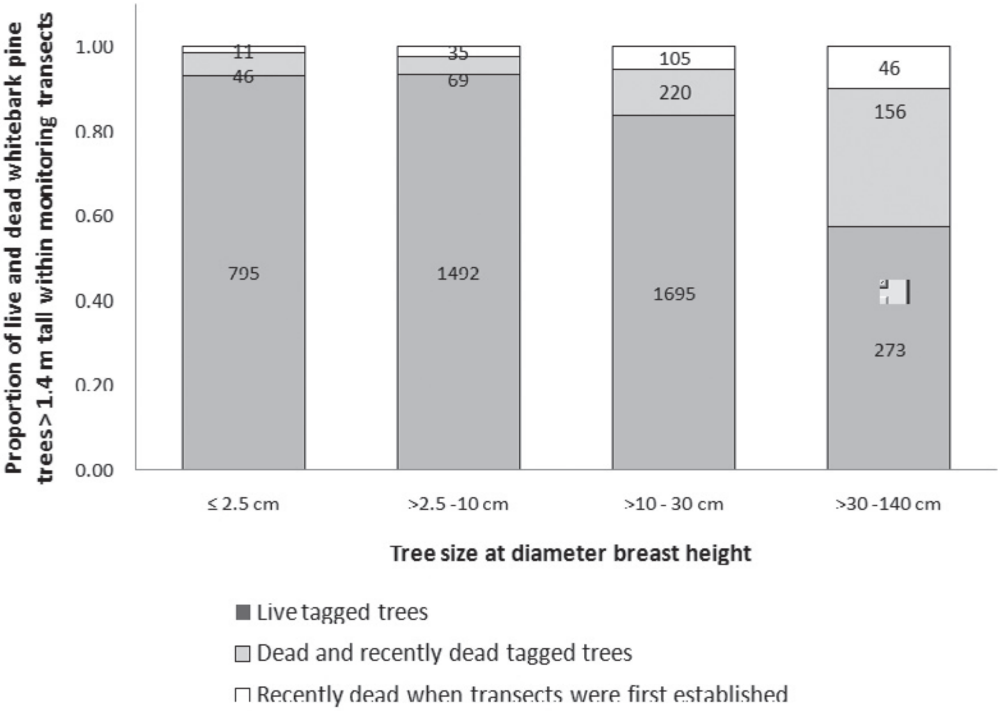

Figure 2. Proportion of live, dead and recently dead tagged and untagged whitebark pine >1.4 m tall within the monitoring transects by size class. Categories show the 2009 status of trees that were alive and permanently tagged and also trees that were recently dead but not tagged when transects were first established between 2004 and 2007. A recently dead tree has persistent non-green needles and a dead tree has shed all its needles. Numeric values on the bars represent the numbers of trees in each category.

whitebark pine trees >1.4 m tall with an aluminum tag so that we can follow the incidence of WPBR and survivorship of individual trees over time. We also measured the DBH of standing dead and recently dead whitebark pine trees >1.4 m tall within the transect but did not permanently tag these trees.

Each live whitebark pine tree >1.4 m tall was surveyed for WPBR cankers based on aecia (the active, fruiting body of the canker) which is the definitive symptom of WPBR (Tomback and others 2005) and also for auxiliary signs of WPBR infection. These signs include: rodent chewing, branch flagging, swelling, roughened bark and oozing sap (Hoff 1992). If three of the five auxiliary signs occurred in the same spot on a tree, that location was noted as having WPBR infection based on the auxiliary signs rather than the active canker. The numbers of branch and trunk cankers were recorded for each of the tree sections. For analysis purposes, we considered an individual whitebark pine tree infected with WPBR if one canker (aecia or three auxiliary signs) on either the tree bole or branch was observed.

We also surveyed trees for evidence of MPB infestation based on the presence of pitch tubes and boring dust in live trees and the presence of J-shaped galleries beneath the bark of dead trees. Pitch tubes are small, popcorn-shaped resin masses produced by a tree at the beetle entry hole as a means to stave off a MPB attack. Boring dust is created during a mountain pine beetle mass attack and can be found in bark crevices and around the base of an infested tree. J-shaped galleries are created by adult MPB and are used by adults to live and feed.

During resurveys, each permanently tagged tree was evaluated for its status as live (green needles present), recently dead (having non-green needles present) or dead (needles are absent). Live trees with a fading crown were noted in the tree comment field.

The proportion of trees infected with WPBR was calculated using a design-based ratio estimator that accounts for the total number of mapped stands within the sample frame and stratified by within and outside the RZ (GYWPMWG 2007). We used data from repeat surveys to document rates of tree mortality. Tree mortality, expressed as a percent, was calculated by dividing the total number of tagged dead and recently dead trees observed between 2007 and 2009 by the total number of live trees tagged between 2004 and 2007 and multiplied by 100.

Results

Between 2004 and 2007, we established 176 permanent transects in 150 randomly selected whitebark pine stands, and permanently marked 4,774 individual live trees >1.4 m tall. Following transect establishment we calculated the baseline estimate for WPBR infection rate within the GYE as 20 percent (±4 percent) (table 1). In the GYE, we found WPBR to be widespread and highly variable in intensity and severity (GYWPMWB 2008).

Beginning with our first resurvey and continuing through 2009 we observed mortality of whitebark pine within our monitoring transects. Mortality at the end of 2009 among trees that were tagged during transect establishment and resurveyed (n = 4748) was 10 percent (n=491) with 62 percent of dead trees containing J-shaped galleries consistent with MPB attack. Mortality was greater in the larger size classes where 36 percent of trees >30 cm DBH had died.

The MPB epidemic was well underway when we began establishing permanent monitoring transects in 2004. To illustrate cumulative mortality within our monitoring transects, we added the standing dead trees that still had persistent non-green needles at the time of transect establishment to calculate the proportion of live and dead trees (>1.4 m tall) by size class (figure 2). This dataset was used to recalculate the percent of dead trees >30 cm DBH that died over approximately the last 10 years. Cumulatively, 52 percent (n = 291) of the trees >30 cm DBH within our monitoring transects were dead. Field crews also recorded fading crowns, pitch tubes, and boring dust, as indicators of MPB attack on at least 8 percent of the live trees. Based on tree size alone, 38 percent of the remaining live whitebark pine trees in the monitoring sample were in the size class (≥12 cm DBH) that is most susceptible (Furniss and Carolin 1977) to MPB attack.

Conclusion

Whitebark pine health in the GYE is currently affected by WPBR and MPB as well as other stressors such as fire management and climate change conditions. Long-term monitoring of whitebark pine in the GYE and across its range is vital to understanding the ecological impact these stressors have on this highly important high elevation species. Initial results from our project provide a baseline of current infection and distribution of WPBR and will allow us to continue to document changes in WPBR and mortality rates in whitebark pine during the current and future outbreaks of MPB.

Whitebark pine trees surviving the current MPB outbreak will continue to be stressed by WPBR, which can affect all aspects of forest regeneration and could impair ecosystem recovery long after the current MPB epidemic retreats to endemic levels (Schoettle and Sniezko 2007). The whitebark pine monitoring program provides valuable information to help guide management strategies, restoration planning, and application of scarce funding and other resources (Schwandt 2006, GYWPWG 2007). Moreover, the collaborative, interagency approach of monitoring and management of whitebark pine in the GYE and in other regional ecosystems will be the best strategy to allow this important high elevation species to persist across the landscape and maintain its ecological function.

Literature Cited

Dixon, Beverly Gail. 1997. Cumulative effects modeling for grizzly bears in the Greater Yellowstone Ecosystem. Bozeman, MT: Montana State University. 143 p. Thesis.

Furniss, R. L.; Carolin, V. M. 1977. Western forest insects. Misc. Publ. 1339. Washington, DC: U.S. Department of Agriculture, Forest Service. 654 p.

GYWPMWG (Greater Yellowstone Whitebark Pine Monitoring Working Group). 2007. Interagency whitebark pine monitoring protocol for the Greater Yellowstone Ecosystem, version 1.00. Unpublished protocol on file at: U.S. Department of Interior, National Park Service, Greater Yellowstone Network, Bozeman, MT. 95 p.

GYWPMWG (Greater Yellowstone Whitebark Pine Monitoring Working Group). 2008 Monitoring Whitebark Pine in the Greater Yellowstone Ecosystem: 2007 Annual Report. Pages 50-56 in C. C. Schwartz, M. A. Haroldson, and K. West, editors. Yellowstone grizzly bear investigations: annual report of the Interagency Grizzly Bear Study Team, 2007. U.S. Geological Survey, Bozeman, Montana, USA.

GYCCWPS (Greater Yellowstone Coordinating Committee Whitebark Pine Subcommittee). 2010. Draft whitebark pine strategy for the Greater Yellowstone Ecosystem. Unpublished paper on file at: U.S. Department of Interior, National Park Service, Grand Teton National Park, Moose, WY. 21 p.

Hoff, R. J. 1992. How to recognize blister rust infection on whitebark pine. Research Note INT-406. Ogden, UT. USDA Forest Service, Intermountain Research Station.

Schwandt, John W. 2006. Whitebark pine in peril: a case for restoration. Forest Health Protection R1-06-28. USDA Forest Service.

Schoettle, Anna W.; Sniezko, Richard A. 2007. Proactive intervention to sustain high-elevation pine ecosystems threatened by white pine blister rust. Journal of Forest Research. 12: 327-336.

Tomback, Diana F.; Keane, Robert E.; McCaughey, Ward W.; Smith Cyndi. 2005. Methods for surveying and monitoring whitebark pine for blister rust infection and damage. Whitebark Pine Ecosystem Foundation, Missoula, MT, USA. 26 p.

Limber Pine Forests on the Leading Edge of White Pine Blister Rust Distribution in Northern Colorado

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Introduction

The combined threats of the current mountain pine beetle (*Dendroctonus ponderosae*, MPB) epidemic with the imminent invasion of white pine blister rust (caused by the non-native fungus *Cronartium ribicola*, WPBR) in limber pine (*Pinus flexilis*) forests in northern Colorado threatens the limber pine's regeneration cycle and ecosystem function. Over one million hectares of Colorado forests have been infested by MPB between 1996 and 2008 (U.S. Department of Agriculture 2010). Limber pine makes up only approximately 3 percent of this infested area (U.S. Department of Agriculture, unpublished data), but is a disproportionately important component of forested ecosystems for recreation, biodiversity, and watershed protection (Schoettle 2004). White pine blister rust was first detected in northern Colorado in 1998 on limber pine and continues to spread (Johnson and Jacobi 2000; Blodgett and Sullivan 2004; Kearns and Jacobi 2007).

Proactive strategies to sustain limber pine in the southern Rocky Mountains are focused at the forefront of WPBR invasion in Colorado and include disease monitoring plots, tree seed collections, protection of seedtrees from MPB, and WPBR resistance screening trials (Schoettle and Sniezko 2007; Burns and others, submitted; Schoettle and others, The Proactive Strategy for Sustaining Five-Needle Pine Populations, this proceedings). This study is adding information on disturbance and stand characteristics to compliment these ongoing efforts and improve land manager's abilities to assess the risks and better evaluate proactive management options to sustain limber pine in northern Colorado. Objectives of this survey in limber pine seed collection sites throughout northern Colorado are to: 1) quantify the amount of understory (height<137 cm), intermediate (diameter at breast height [dbh] >0 and <10 cm), and overstory (dbh ≥10 cm) limber pine and other tree species, 2) identify site, stand, and climate characteristics related to limber pine advanced regeneration densities, 3) determine stand resilience to MPB and predict potential post-MPB stand structure and species composition, and 4) examine age, height, growth, microsite, and stand relationships of understory trees to evaluate whether limber pine advanced regeneration will release with overstory tree removal due to MPB-caused mortality. In this paper, we will report some preliminary findings for objective one and discuss the implications of the other objectives.

Methods

In 2009, a network of 29 sites in limber pine forest (2450-3420 m in elevation, 9-12 hectares per site) was surveyed for site and stand characteristics and disturbances (Fig. 1). Seventeen of the sites were in Rocky Mountain National Park and 12 were in the Roosevelt and Pike National Forests. These locations are also limber pine seed collection sites from which seeds are being tested for resistance to WPBR (Schoettle and others 2009; Schoettle and others, Preliminary Overview of the First Extensive Rust Resistance Screening Tests of *Pinus flexilis* and *Pinus aristata*, this proceedings). At each site, 10 plots (0.02 ha each) spaced 50 m apart over two transects were assessed. Overstory, intermediate, and understory tree density, tree health, crown class, and biotic damage were recorded. Information recorded specifically on limber pine included: microsite, tree age estimate, vigor assessments for understory trees, and reproductive effort for all tree sizes. Percent ground cover and canopy cover were also estimated.

Results and Discussion

Applying the major habitat types defined by Peet (1981), the habitat types of our 29 sites were montane limber pine forests (12 sites), limber pine forest type with Engelmann spruce (*Picea engelmannii*) and subalpine fir (*Abies lasiocarpa*) (limber pine forest type) (9 sites), and subalpine limber pine forests (8 sites). Sites in the montane limber pine forest type were less than 3100 m in elevation and had highly variable limber pine understory density with an average of 347.7/ha (standard error [SE]=134.2) (Table 1). Ponderosa pine (*Pinus ponderosa*) and Douglas-fir (*Pseudotsuga menziesii*) were significant portions of the understory, intermediate, and overstory trees in montane limber pine forest types. The density of understory limber pine in the limber pine forest type was also variable and averaged 491.8/ha (SE=201.0) (Table 1). Engelmann spruce and subalpine fir were large components of the understory, intermediate, and overstory trees in both the limber pine forest type and subalpine limber pine forest type. Lodgepole pine (*Pinus contorta*) occurred throughout the elevational range of the sites except at two treeline krummholz sites and the lowest elevation site.

The relationship between limber pine intermediate and understory density with the density of overstory limber pine

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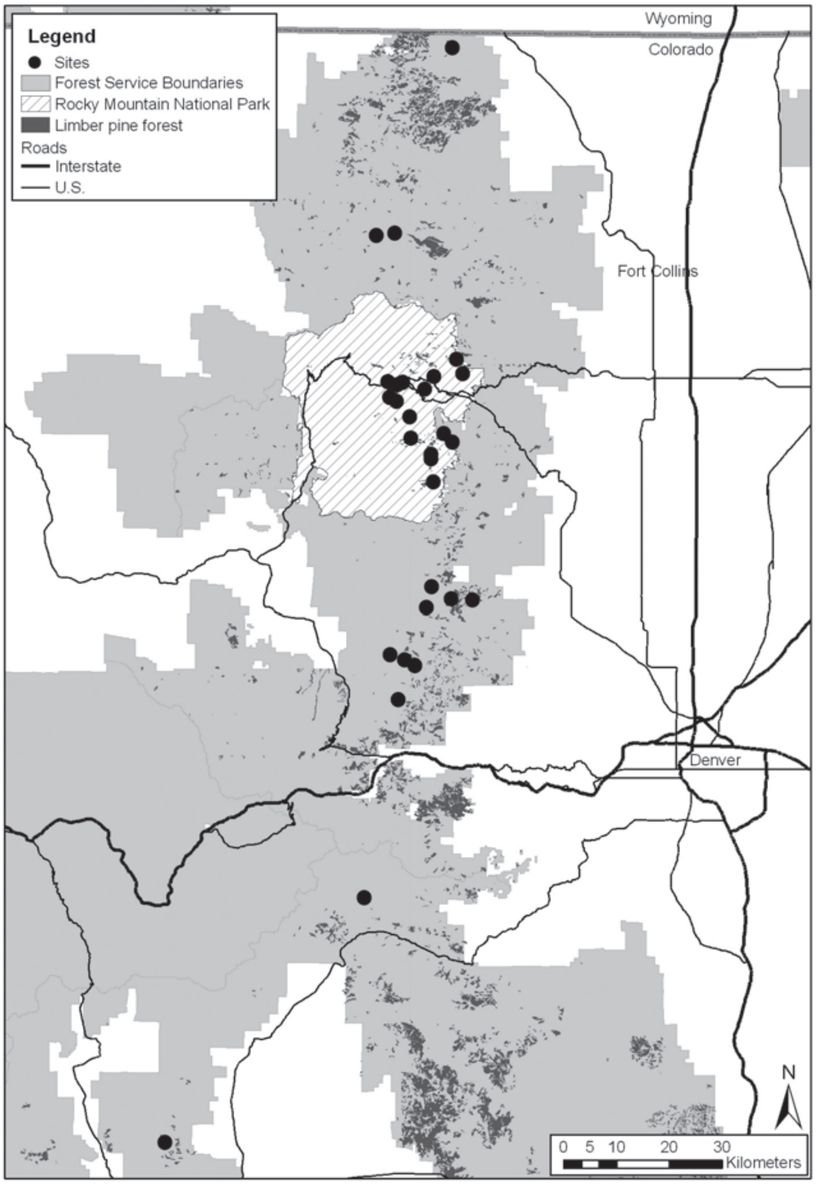

Figure 1. Map of study area with limber pine sample sites in the Arapaho-Roosevelt and Pike-San Isabel National Forests and Rocky Mountain National Park, Colorado.

Table 1. Mean (standard error) density of elevation, live limber pine, and percent of limber pine killed by mountain pine beetle from 2005 to 2009 by habitat type as defined by Peet (1981)[a] in the Roosevelt and Pike National Forests and Rocky Mountain National Park, Colorado.

	Habitat type[a]		
	Montane limber pine (n=12)	**Limber pine with spruce and fir (n=9)**	**Subalpine limber pine (n=8)**
Elevation (m)	2803 (56)	3098 (52)	3286 (36)
Overstory limber pine/ha	186.1 (52.6)	354.2 (57.2)	286.0 (60.9)
Intermediate limber pine/ha	179.9 (40.7)	262.5 (117.3)	238.7 (71.8)
Understory limber pine/ha	347.7 (134.2)	491.8 (201.0)	399.1 (61.4)
Percent overstory limber pine killed by MPB	2% (1)	6% (2)	7% (3)

[a] Overstory, intermediate, and understory trees are defined as: dbh ≥ 10 cm, dbh between 0 and 10 cm, and height < 137 cm, respectively

will be important in understanding the regeneration dynamics of our study area. Analyses to define significant site and stand characteristics associated with greater understory limber pine densities are ongoing.

Mountain pine beetle-caused mortality has the potential to significantly alter the species composition and stand characteristics of northern Colorado limber pine forests. Limber pine and other MPB-host trees (ponderosa, lodgepole, and Rocky Mountain bristlecone (*Pinus aristata*) pine) comprised over 50 percent of overstory trees at all sites and all host species were being infested by mountain pine beetle. As of 2009, limber pine mortality caused by MPB was present at 15 of the 29 sites in all forest types except at treeline krummholz. The average percent of overstory limber pine killed by MPB were 2 percent, 6 percent, and 7 percent in the montane, limber pine, and subalpine forest types, respectively (Table 1). The proportion of limber pine being infested by MPB on these sites is similar to the proportion of other MPB-host trees being infested. The MPB epidemic is continuing to build in this region as indicated in Aerial Survey data from 2009 and 2010 (U.S. Department of Agriculture 2010). The MPB-caused mortality of limber pine seedtrees necessitates the urgency for genetic conservation of limber pine to provide material for assessing the frequency of resistance to WPBR in these populations (Schoettle and others 2009; Schoettle and others, The Proactive Strategy for Sustaining Five-Needle Pine Populations, this proceedings).

Following the current MPB outbreak, both competition from other tree species and the likelihood of the remaining live limber pine component to release will determine whether sites will continue to sustain limber pine. The MPB outbreak may result in an acceleration of succession from MPB-host trees to more shade tolerant non-MPB-host tree species in some forest types (Hawkes and others 2003; Sibold and others 2007). However, the MPB outbreak may also act as a thinning event that could promote resilience and short-term health of the remaining live limber pine (Millar and others 2007). Due to the long maturation time for limber pine to be reproductive, it could take up to 50 years for young limber pine to produce seed cones (McCaughey and Schmidt 1990). The reduction of overstory limber pine density across the landscape and its delayed maturation may leave limber pine in northern Colorado susceptible to stresses, such as WPBR, competition, and climate change (Millar and others 2007). A proactive strategy to sustain limber pine in Colorado provides integrating information on the frequency of genetic resistance to WPBR, the potential density of live limber pine component after the MPB outbreak, reproductive potential of seedtrees that escape MPB infestation, and the site characteristics associated with limber pine advanced regeneration density (Schoettle and Sneizko 2007; Schoettle and others, The Proactive Strategy for Sustaining Five-Needle Pine Populations, this proceedings). When complete, this study will contribute key information to assist managers in developing and prioritizing management options for limber pine in the southern Rocky Mountains.

References

Blodgett, James T.; Sullivan, Kelly F. 2004. First report of white pine blister rust on Rocky Mountain bristlecone pine. Plant Disease. 88: 311.

Burns, Kelly S.; Blodgett, James.; Jackson, Marcus; Howell, Brian; Jacobi, William R.; Schoettle, Anna W.; Casper, Anne Marie; Klutsch, Jennifer G. *Submitted*. Monitoring limber pine health in the Rocky Mountains and North Dakota. Chapter 18 In: Potter, K. M.; Conkling, B. L., eds. In review. Forest health monitoring 2009 national technical report. Gen Tech. Rep. SRS-xx. Asheville, NC: U.S. Department of Agriculture, Forest Service, Southern Research Station.

Hawkes, B.; Taylor, S. W.; Stockdale, C.; Shore, T. L.; Alfaro, R. I.; Campbell, R.; Vera, P. 2003. Impact of mountain pine beetle on stand dynamics in British Columbia. In: Shore, T. L.; Brooks, J. E.; Stone, J. E., eds. Mountain pine beetle symposium: challenges and solutions; 2003 October 30-31; Kelowna, BC, Canada. Information Report BC-X-399.Victoria, BC, Canada: Natural Resources Canada, Canadian Forest Service, Pacific Forestry Center: 177-199.

Johnson, D. W.; Jacobi, William R. 2000. First report of white pine blister rust in Colorado. Plant Disease. 84(5): 595.

Kearns, Holly S. J.; Jacobi, William R. 2007. The distribution and incidence of white pine blister rust in central and southeastern Wyoming and northern Colorado. Canadian Journal of Forest Research. 37: 462-472.

McCaughey, W. W.; Schmidt, W. C. 1990. Autecology of whitebark pine. In: Schmidt, W. C.; McDonald, K. J., eds. Proceedings—Symposium on whitebark pine ecosystems: Ecology and management of a high-mountain resource. Gen. Tech. Rep. INT-270. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station: 85-96.

Millar, Constance I.; Westfall, Robert D.; Delany, Diane L. 2007. Response of high-elevation limber pine (*Pinus flexilis*) to multiyear droughts and 20th-century warming, Sierra Nevada, California, USA. Canadian Journal of Forest Research. 37: 2508-2520.

Peet, Robert K. 1981. Forest vegetation of the Colorado Front Range: composition and dynamics. Vegetatio. 43: 3-75.

Schoettle, Anna W. 2004. Ecological roles of five-needle pines in Colorado: Potential consequences of their loss. In: Sniezko, R. A.; Samman, S.; Schlarbaum, S. E.; Kriebel, H. B., eds. Breeding and genetic resources of five-needle pines: growth, adaptability, and pest resistance. Proc. RMRS-P-32. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station: 124-135. http://www.fs.fed.us/rm/pubs/rmrs_p032/rmrs_p032_124_135.pdf

Schoettle, Anna W.; Sniezko, Richard A. 2007. Proactive intervention to sustain high-elevation pine ecosystems threatened by white pine blister rust. Journal of Forest Research. 12: 327-336.

Schoettle, Anna W.; Sniezko, Richard A.; Burns, Kelly S. 2009. Sustaining *Pinus flexilis* ecosystems of the southern Rocky Mountains (USA) in the presence of *Cronartium ribicola* and *Dendrotonus ponderosae* in a changing climate. In: Noshad, D.; Woon, N. W.; King, J.; Sniezko, R. A., eds. Breeding and genetic resources of five-needle pines. Proceedings of the IUFRO Conference; 2008; Yangyang, Korea. Korea Forest Research Institute, Seoul: Pp. 63-65.

Sibold, Jason S.; Veblen, Thomas T.; Chipko, Kathryn; Lawson, Lauren; Mathis, Emily; Scott, Jared. 2007. Influences of secondary disturbances on lodgepole pine stand development in Rocky Mountain National Park. Ecological Applications. 17(6): 1638-1655.

U.S. Department of Agriculture, Forest Service, Forest Health Management. 2010. Rocky Mountain Region, Forest Insect & Disease Aerial Survey [Online]. Available: http://www.fs.fed.us/r2/resources/fhm/aerialsurvey/ [2010, 19 May].

U.S. Department of Agriculture, Forest Service, Forest Health Management, Forest Health Technology Enterprise Team. 2009. Unpublished data supplied to J. Klutsch by Forest Health Technology Enterprise Team.

Valuing the Forest for the Trees: Willingness to Pay for White Pine Blister Rust Management

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Abstract—The nearly two million acres of high elevation forests in the Western United States are not an important source of timber or any other market products. However, that does not mean that the forests are not highly valuable. Visitors and non-visitors alike value the unique five-needle pine trees found in these high elevation ecosystems. In this study, we estimate the nonmarket benefits of preserving high elevation forests in the Western United States from the threat of white pine blister rust (WPBR), a non-native pathogen. A contingent valuation survey collected information about attitudes, behaviors, and economic preferences related to high elevation forests and the threat posed by WPBR. The estimated values suggest high-elevation forests in the Western United States provide the public with significant nonmarket benefits. The magnitude of the estimated nonmarket benefits and responses to attitudinal measures reflect survey respondents' concern about the continued existence of healthy high-elevation forests. Attitude and behavior data demonstrate varied motivations for nonmarket values. The majority of the survey respondents had visited a high-elevation forest in the past, yet recreation was rated the least important feature of high elevation forests. Results of this study can be used in benefit-cost or other types of analysis to improve management efficiency of high elevation white pine ecosystems.

Introduction

High-elevation forests are home to native five-needle pine species including foxtail pine (*Pinus balfourniana* Grev. and Balf.), Great Basin bristlecone pine (*P. longaeva* Bailey), limber pine (*P. flexilis* James), Rocky Mountain bristlecone pine (*P. aristata* Engelm.), and whitebark pine (*P. albicaulis* Engelm.). Most of the high-elevation forests are found on public lands where they are valued for their beauty, uniqueness, or role in recreation (Burns and others 2008; Logan and Powell 2001; Samman and others 2003). However, these forests are threatened by the invasive disease white pine blister rust (WPBR). Caused by the non-native fungus *Cronartium ribicola*, WPBR first invaded the high-elevation forests of North America in the early 20th century and has slowly, but continually, spread across much of their range (Burns and others 2008; Liebhold and others 1995). This fungus threatens the sustainability of these forests by causing mortality at all stages of the trees' lifecycles, disrupting the forests' regeneration cycle (Burns and others 2008). In addition, the fungus's complex lifecycle, which involves multiple hosts and an airborne spread, makes either eradication or containment of the disease difficult, if not impossible (Burns and others 2008; Liebhold and others 1995; Maloy 1997).

Typical strategies for managing invasive species in forests involve a combination of prevention, eradication, and containment as a first stage, followed by mitigation of impacts and restoration of degraded areas if that first stage proves unsuccessful (Liebhold and others 1995; Schoettle and Sniezko 2007). Historically, widespread attempts at controlling WPBR may have slowed the spread but have not successfully eradicated the disease (Maloy 1997). Therefore, current research suggests the most viable approach to managing WPBR is to increase the frequency of the genetic resistance to rust naturally occurring at low levels across the range of the forests. This can be done either by planting seedlings screened for genetic resistance or by encouraging more seedlings than would be established naturally, through techniques such as prescribed burning and thinning of competitor species (Burns and others 2008; Samman and others 2003; Schoettle and Sniezko 2007; Schwandt 2006). Although invasive species management often occurs only after the infection of an area, this disease has not yet spread throughout the entire range of the high-elevation forests in the Western United States. This presents a potential for proactive management, which refers to the application of these treatments prior to an area's infection, to lessen the impacts of future WPBR invasions (Schoettle and Sniezko 2007).

While proactive treatment of WPBR seems promising, it is not clear whether the public will support intervening in forests that are not yet infested, as proactive treatments would lead to a potentially costly loss of benefits through the disturbance of healthy forests, referred to as "management externalities" (Bond and others 2010). A study of public attitudes toward managing the mountain pine beetle infestation in Canada found support for management, but not when measures were proactive (McFarlane and others 2006). In addition, proactive management techniques might prove quite costly in terms of management expenditures (Burns and others 2008; Schoettle and Sniezko 2007). When timber values are high, the economic rationale for management can be self-apparent despite the possibility of management externalities. However, where there are few if any market benefits, as with high-elevation forests, the optimal approach to management often is less straightforward (Holmes and others 2009). In such cases, the associated nonmarket benefits for the protection of a resource can be elicited through a variety of techniques, including the contingent valuation

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method (Carson and others 2001). To date, these methods have not been utilized to elicit the nonmarket benefits associated with treating high-elevation forests for WPBR.

Past studies on the native bark beetle epidemics highlight the subtleties involved in public preferences and attitudes regarding intervention in forests. Although residents living near Canadian national parks favored control of the beetles on average, respondents with more ecologically-oriented attitudes and greater knowledge of the beetles were less in favor of intervening with the natural processes driving the epidemics (McFarlane and others 2006). In contrast, tourists to a German national park favored non-intervention against that park's bark beetle infestation, with a suggested explanation of the difference being that the tourists accepted the German epidemic as more of a natural process (Muller and Job 2009). These studies suggest the importance of valuation that accommodates the different perspectives of respondents, as well as the distinction between natural ecological processes and disruptions caused by invasive species.

The present paper contributes to this general line of inquiry into attitudes and preferences for environmental benefits related to the protection of forests in two new directions. First, this research focuses on public preferences regarding a specific threat; namely, the fungus that causes WPBR. The invasive nature of this threat, and the novel proactive opportunities available for addressing it, make this application a unique case study, as well as one pertinent to contemporary policy decisions. Second, this research reports on a survey of a representative sample of the population of the entire Western United States. The survey elicited a variety of attitudes and preferences related to management of high-elevation forests. As such, it allows estimation of the benefits of managing high-elevation forests in response to the threat posed by white pine blister rust. Specifically, this paper addresses the following questions:

a) What attitudes do the public hold that might influence opinions of WPBR management?

b) What attributes of high-elevation forests are important to the public?

c) Does the public support the management of WPBR in high-elevation forests, and if so, what economic benefits are associated with this management?

Literature Review

There are many reasons to expect significant nonmarket benefits from the high-elevation five-needle pine forests. Bristlecone pines rank among the oldest living species on earth, sometimes exceeding 2500 years of life. All the five-needle pines are notable for contributing to the rugged natural beauty and scenic grandeur of important natural landmarks (Burns and others 2008; Logan and Powell 2001; Samman and others 2003; Schoettle and Sniezko 2007). Nonmarket valuation research on other tree species has used travel cost analysis to show that some recreationists value forests more highly as trees in the forests age, with upper range benefits of $152 and $478 per additional trail-mile through old-growth spruce/fir forests and lodgepole pine forests, respectively (Englin and others 2006). A contingent valuation study demonstrated high values for the high-elevation experience on Colorado's "14ers" (mountains with summits over 14,000 feet high) relative to those for other outdoor recreation, estimating average consumer surplus from a single 14er trip to be between $67, for respondents more willing to substitute to different mountains, and $397, for less flexible individuals (Loomis and Keske 2009). This result demonstrated a recreational preference for the type of terrain that often includes high-elevation forests.

Recreational use is just one of many possible sources of value related to support for protection-oriented management of forests. For decades, resource economists have recognized the benefits provided to the public through so-called "nonuse values" of resources, which cover demands for the option for future use, for the opportunity to offer resources as a bequest to future generations, and for the pure existence of the resource (Krutilla 1967; Walsh and others 1984). These benefits can be quite significant for the general population. For example, based on a contingent valuation study, Walsh and others (1990) estimated that nonuse values account for roughly three-quarters of the total value for protecting forest quality in public forests across Colorado, which averaged $47 per household per year. More recently, Kramer and others (2003) used follow-up questions to a contingent valuation exercise to decompose a total estimated per household willingness to pay (WTP) of $28.49 per year for protecting the high-elevation spruce-fir forest ecosystem in the Southern Appalachian Mountains into $16.24 for existence value, $8.55 for bequest, and $3.70 for use. More directly assessing existence value, Amirnejad and others (2006)'s contingent valuation study estimated a mean WTP for the existence of Iranian forests of $30.12 (in U.S. dollars) per Iranian household per year, even though most of the respondents do not visit the forests. Other contingent valuation studies about protecting large public forests from a variety of hazards found values for protection in the range of about $20 to $100 per household per year (Kramer and others 2003).

Additional indirect benefits contributing to these values for protection might relate to the ecological importance of forests. In the case of high-elevation forests, the five-needle pines occupy harsh habitats and facilitate the establishment of other high-elevation species, often defining treelines, initiating reforestation after large fires, and playing an important role in maintaining snowpack and protecting against soil erosion (Ellison and others 2005; Kearns and Jacobi 2007; Schoettle 2004). They provide habitat and an important dietary component for other species, including the Clark's nutcracker (*Nucifraga columbiana* Wilson), red squirrels (*Tamiasciurus hudsonicus* Ercleben), and grizzly bears (*Ursus arctos* L.) (Burns and others 2008; Logan and Powell 2001; Schoettle 2004).

Approach

The field of nonmarket valuation is well established, and it is often possible to transfer estimated values from one study to another if the goods being valued across studies are similar. However, in this study, it was necessary to develop a survey instrument and collect the requisite data, as no previous studies have estimated the benefits of managing high elevation forests for the threat of WPBR. This required ascertaining the general population's baseline knowledge of high-elevation forests, five-needle pine trees, and WPBR. The final survey instrument was developed through an iterative process over a two-year period. To ensure adequate treatment of the complex interdisciplinary issues of the project, nearly constant communication about the questionnaire was maintained with researchers specializing in natural sciences including plant ecophysiology, forest genetics, plant epidemiology, and restoration ecology. Four focus groups with the public offered insight into the relevance of information provided and questions asked, helping redirect the survey from a focus on recreational values of high-elevation forests to a broader focus on total value, which is largely comprised of nonuse values. In addition, a pilot survey tested the questionnaire and survey design with 29 randomly chosen respondents before finalizing the design.

The survey was administered online to a representative sample of households in the U.S. Census Bureau's Mountain and Pacific divisions (excluding Alaska and Hawaii). Knowledge Networks (KN), a private online research firm[1], recruited a panel through a combination of random-digit dialing and address-based sampling, which accounts for the large number of contemporary households without landline telephones. This panel consists of potential respondents for KN surveys. Panelists typically respond to approximately one survey per week in exchange for modest incentives, such as entrance into raffles and special sweepstakes. For this survey, KN selected 895 active panelists through random stratified sampling, oversampling in the Mountain division to assure adequate coverage. Over 11 days in June 2010, 542 of the selected sample completed the survey, for a completion rate of 61%.

The questionnaire, developed according to recommendations on nonmarket valuation survey design by Boyle (2003), Carson and others (2001), and Champ (2003), provided respondents with relevant background information on high-elevation forests, WPBR, and management options.[2] The background information included pictures of the five-needle pine species and WPBR, maps of the species' distributions, and descriptions of distinctive features of healthy high-elevation forests. A healthy high-elevation forest was defined as one in which all functional stages of the tree lifecycle occur simultaneously. To establish the plausibility of protecting the high-elevation forests despite the lack of options for abating the spread of WPBR, the questionnaire provided information on treatment options (which could be implemented either proactively or reactively) and typical short-term and long-term effects of these treatments on forests and related services.

The survey asked about experiences and knowledge related to high-elevation forests and WPBR. Numerous questions measuring attitudes toward the environment, both specific to this issue and in general, were included. General attitudinal questions included a subset of the New Ecological Paradigm scale items, which are widely implemented measures that have been used to explain nonuse values (Dunlap and others 2000; Kotchen and Reiling 2000). Other questions addressed relevant attitudes toward taxes, government agencies, and scientific research, as these might influence both the responses to the valuation questions and public acceptance of various management actions. The attitudinal questions asked for responses on a 5-point Likert scale for each statement, ranging from "Strongly Disagree" to "Strongly Agree" with the statement. One last set of general questions asked respondents to rate how important the various described features of high-elevation forests are to them, offering insight into the benefits provided to respondents by the resource. In addition, detailed information was obtained about each survey respondent from KN's panelist database.

After a description of management options for WPBR, survey respondents were asked about their willingness to pay for a program to manage all high-elevation forests in the Western United States for the threat of WPBR with a dichotomous-choice contingent valuation question. Respondents were told the management would be funded through a combination of individual donations, increased visitor fees, and tax increases[3]. Specifically, respondents were asked:

> *Suppose managers treat [quantity]% of the high-elevation forests in the Western United States. As a result, these acres will be healthy in 100 years from now. The remainder of the acreage would not be treated. Would your household be willing to pay a one-time cost of $[bid] to fund this program?*

Each respondent was given a randomly selected quantity level of 30%, 50%, or 70% and a randomly selected bid amount of $10, $25, $50, $100, $250, $500, or $1000. The set of possible bid values was constructed to cover and transcend the range of plausible values suggested by focus group results. Respondents indicated a "Yes" or "No" response to the contingent valuation question. Asking respondents about varying bid amounts allows estimation of the probability

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[1] For more information on the Knowledge Networks panel and methodology, contact the authors for supporting documentation and a list of published research utilizing the KN service, or visit www.knowledgenetworks.com.

[2] Copies of the questionnaire in its entirety are available from the authors upon request.

[3] Immediately before answering the contingent valuation questions, respondents were reminded about budget constraints and of possible reasons why they might not support the program.

that the average respondent would support the program under a given bid level by fitting responses to a logit model[4].

Results

Sample Demographics

Table 1 shows descriptive statistics of select demographic variables for the 542 respondents completing the survey. As reflected in the raw sample column, the mountain division was oversampled to assure regional coverage. To adjust for non-response, non-coverage, and the stratification by region, Knowledge Networks provided probability weights that match the data to benchmark distributions derived from the most recent Current Population Survey.[5] These benchmark distributions match the distributions of gender, age, race/ethnicity, categorical educational attainment, Census Region, residence within a metropolitan area, and internet access. Most of the raw sample demographics statistically differ from population statistics, although the most dramatic difference is in the Census divisions. As expected, the weighted sample demographics, with the exception of internet access rates, are statistically indistinguishable from those for the population, which consists of 27,115,377 individual households (U.S. Census Bureau 2009). Thus, the weighted sample is demographically representative of the population of the Western United States (excluding Hawaii and Alaska). All subsequent results are reported for this weighted sample.

Experiences and Knowledge

Respondents were asked about their past and expected future visitation to high-elevation forests in the Western United States, as well as some more specific locations within this area. Table 2 summarizes the responses to these questions. In general, respondents from the Mountain States differ significantly from Pacific State respondents in terms of prior recreational experience, with individuals from the Mountain States more likely to have visited one or more of

Table 1. Demographics of raw sample, weighted sample, and study population.

Variable	Raw Sample	Weighted Sample	Population[a]
Census Division			
Mountain (MT, ID, WY, CO, NM, AZ, UT, NV)	71%	32%	34%
Pacific (WA, OR, CA)	29%	68%	66%
Gender			
Male	47%	49%	50%
Female	53%	51%	50%
Age			
18-29	16%	23%	24%
30-44	22%	28%	28%
45-59	30%	26%	27%
60+	31%	22%	22%
Educational Attainment			
Less than High School	10%	15%	16%
High School	23%	25%	27%
Some College	35%	31%	31%
Bachelor and beyond	32%	29%	26%
Race / Ethnicity			
White, Non-Hispanic	75%	59%	55%
Black, Non-Hispanic	2%	2%	5%
Other, Non-Hispanic	6%	10%	10%
Hispanic	14%	25%	29%
2+ Races, Non-Hispanic	2%	4%	2%
Other Criteria			
In a Metropolitan Statistical Area	86%	91%	91%
Household Internet Access	76%	68%	76%
Number of Respondents / Housing Units	542	542	27,115,377

[a] Statistics derived from U.S. Census Bureau, Current Population Survey, 2007, U.S. Census Bureau, Population Estimates Program, 2009, and 2006-2008 American Community Survey 3-Year Estimates.

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[4] We calculate mean WTP with Hanemann (1989)'s equation, mean WTP= $-\alpha/\beta$, 95% confidence intervals calculated via the delta method.

[5] Household Internet Access differs in that that benchmark was derived from KN's panel recruitment data, which dates back to 1999, rather than the Current Population Survey.

Table 2. Percentage of respondents reporting relevant experiences, plans, and knowledge.

	Mountain	Pacific	Regional Difference[a]	Combined
Have you ever visited…				
high-elevation forests in Western U.S.	59	47	*	51
Central Colorado's mountains	53	27	***	36
Rocky Mountain National Park	43	23	***	30
Glacier National Park	26	21	-	23
Yellowstone National Park	48	32	***	37
at least one of the above places	*81*	*64*	***	*69*
Do you expect to ever visit…				
Central Colorado's mountains	64	51	**	55
Rocky Mountain National Park	70	62	-	64
Glacier National Park	61	60	-	60
Yellowstone National Park	71	66	-	67
at least one of these places	*84*	*70*	**	*74*
Have you ever…				
heard of any of the 5-needle pines	39	35	-	36
heard of a high-elevation forest	55	47	-	50
heard of white pine blister rust	9	13	-	12
seen white pine blister rust	18	18	-	18

[a] Outcome of Wald test of significance of percentage point difference between regions:
*** significantly different at $p < 0.01$; ** - significantly different at $p < 0.05$;
* significantly different at $p < 0.10$.

the locations, presumably because all locations asked about are within the Mountain States region. Notably, more than two-thirds have visited at least one of the listed sites, and roughly half have visited a high-elevation forest specifically. More respondents expect to visit the listed locations in the future than have visited in the past. Nearly three-quarters of the respondents expect to visit at least one of the listed sites in the future, suggesting that the opportunity to experience the forests and the areas surrounding them is important to a large proportion of the population of the Western U.S. For comparison, a nationwide, 1983 survey of the general population found that 15% had been to Yellowstone National Park, 15% to Rocky Mountain National Park, and 6% to Glacier National Park (U.S. Department of Interior 1983), and a later report cites double-digit growth rates in visitation in the late 1980's and 1990's (Cole 1996). In addition, a recent non-scientific survey of U.S. travelers found that 73% plan to visit a national park in 2009 (TripAdvisor 2008).

The respondents from the Mountain States and those from the Pacific States did not exhibit any significant differences in response to questions about familiarity with five-needled pines, high-elevation forests, and white pine blister rust. Half of the respondents had heard of a high-elevation forest, while only about one-third had heard of the specific trees described as inhabiting the forests. Familiarity with the disease WPBR was low. More respondents reported seeing WPBR than hearing about it, suggesting that they have seen the symptoms without knowing their causes. One might worry also that respondents are conflating the effects of WPBR with other threats to the trees in high-elevation forests, such as mountain pine beetles. However, this question followed text in the questionnaire that explicitly differentiated WPBR from these threats. Regardless, experiences with WPBR are significantly less prevalent than with the high-elevation forests that the disease threatens.

Attitudes

Respondents were also asked about their level of agreement with statements about the environment and governance. The responses to these statements are shown in table 3. The statements are ordered by how strongly respondents agreed with the statements on average. A few general patterns stand out among these results, including a story of the importance of the existence of the forests themselves. Statements 1, 3, and 4, receiving relatively strong support, speak to the long-term protection of the forests. The low level of support for the statements at positions 12 and 13 corroborates this, because, taken together, the inverse of these statements says that people should intervene in the forests but not for the purpose of fulfilling human needs. Similarly, recreation and other direct uses of the forests receive only moderate support in positions 8, 9, and 11. The support for statement 2 reflects an understanding of the dominance of natural processes, whereas most other general perspectives pertaining to the relationship between humans and the environment receive relatively moderate support. In a final note on the attitudes, despite aggregate neutrality for statement 16, which describes opposition to new taxes in general, the statement that tax money is often spent ineffectively (14) received high support, while low support for statement 17 demonstrates a general lack of trust in government agencies or, at least, that they could improve their public relations.

Respondents were also asked about the importance of some of the features of high-elevation forests. Table 4 summarizes the responses to these statements. Again, direct

Table 3. Respondent attitudes.

	Mean[a]	Agree[b]
Environmental Attitudes		
1. It is important that high-elevation forests exist for future generations.	4.2	76%
2. Despite our special abilities humans are still subject to the laws of nature.	4.1	72%
3. Protecting five-needled pines from the threat of extinction is important.	4.0	68%
4. Humans have the responsibility to protect ecosystems from pests or diseases that humans introduced.	4.0	66%
5. All environmental issues are important.	3.8	56%
6. When humans interfere with nature it often produces disastrous consequences.	3.5	48%
7. The earth has plenty of natural resources if we just learn how to develop them.	3.5	50%
8. It is important that high-elevation forests provide recreation activities, such as hiking or camping.	3.4	47%
9. It is important that forests I am personally attached to are treated for WPBR.	3.4	41%
10. It is important that I pay my fair share for the environment.	3.4	44%
11. Tourism related to high-elevation forests is important.	3.1	29%
12. People should not intervene in high-elevation forests.	2.7	22%
13. Humans have the right to modify the natural environment to suit their needs.	2.6	21%
Governance Attitudes		
14. Tax money is often wasted or applied to unimportant purposes.	3.9	59%
15. Scientific research provides an important service to society.	3.8	65%
16. I oppose all new taxes.	3.0	23%
17. U.S. government agencies typically act in the best interests of U.S. citizens.	2.7	25%

[a] Responses range from Strongly Disagree = 1 through Neutral = 3 to Strongly Agree = 5.
[b] Percentage of respondents responding > 3, expressing agreement at some level.

use ranked lowest in importance, with the least supported features being recreation opportunities and unique appearance, the latter of which relates directly to the experience of visiting the forests. In contrast, the top three rated features, water provision, protection of soil, and habitat for wildlife, all link to the importance of the role of high-elevation forests in providing broader ecosystem services. Each of these favored features emphasizes the function of the forests rather than the value of the individual trees as trees.

Economic Preferences

In addition to exploring the public's attitudes toward high-elevation forests and the threat of WPBR, we measured economic preferences, and thus the value of the benefits provided by the forests, with a contingent valuation question. Table 5 summarizes responses to this question by bid value, and table 6 reports five models based on these responses. Because the dependent variable in each model is dichotomous (i.e., yes/no), logistic regressions are estimated. Table 5 shows that each successively higher bid value corresponds to a smaller proportion of respondents choosing "yes." Similarly, the coefficient on Bid is negative and significant at $p < 0.01$ in each of the models reported in table 6. This demonstrates the effect predicted by economic theory that, all else equal, as the cost of a treatment plan increased, respondents were less likely to respond "yes."

Models 1, 2, and 3 in table 6 explore the effect of the quantity of forest treated on the probability of a respondent choosing yes. Attitude and demographic variables that plausibly could relate to specific motivations for nonmarket values are included in models 1, 2, and 3, including living in a metropolitan area, which is often assumed to relate to environmental attitudes in general, Census region, which is shown in table 2 to correlate with visitation and plans, and presence of children, which could be expected to relate to a certain type of concern for future generations[6]. Model 1 tests for a linear quantity effect on this probability by including the percentage of all high-elevation forests in the Western U.S. treated for WPBR as an independent variable.

Table 4. Ratings of the importance of features of high-elevation forests.

Forest Feature	Mean[a]
Water Provision	4.3
Protection of Soil	4.3
Habitat for Wildlife	4.3
Very Old Trees	4.2
Scientific Value	3.9
Unique Appearance	3.7
Recreation Opportunities	3.6

[a] Responses range from Not at all Important = 1 to Very Important = 5.

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[6] Although one might speculate that income would influence respondents' choices over the dependent variable, economic theory predicts that income is not part of the data generating process estimated here (Hanemann 1998).

Table 5. Percentage of respondents choosing "yes" or "no" at each bid amount.

	Bid Amount							
Choice	**$10**	**$25**	**$50**	**$100**	**$250**	**$500**	**$1,000**	**Overall**
No	12%	32%	46%	48%	65%	71%	91%	52%
Yes	88%	68%	54%	52%	35%	29%	9%	48%

Table 6. Logit equation coefficients for dichotomous-choice responses.

	Model 1	**Model 2**	**Model 3**	**Model 4**	**Model 5**
Constant[a]	-1.0647 (.8304)	-.8704 (.7150)	-.8465 (.6234)	-1.1368** (.5138)	.7280*** (.2049)
Bid	-.0047*** (.0006)	-.0047*** (.0006)	-.0047*** (.0006)	-.0047*** (.0006)	-.0041*** (.0006)
Quantity	.0046 (.0098)	-	-	-	-
Quantity 50% (Dummy)	-	-.0108 (.4073)	-	-	-
Quantity 70% (Dummy)	-	.1829 (.3915)	-	-	-
Existence for future generations matters[b]	1.2277*** (.4497)	1.2303*** (.4494)	1.2302*** (.4507)	1.1949** (.4638)	-
Recreation activities are important[b]	.6038* (.3469)	.6052* (.3462)	.6048* (.3467)	.6617* (.3513)	-
Opposition to all new taxes[b]	-1.4541*** (.3975)	-1.4663*** (.3997)	-1.4621*** (.3965)	-1.4464*** (.4018)	-
Have visited areas with high-elevation forests	1.1254*** (.3819)	1.1101*** (.3870)	1.1162*** (.3812)	1.0852*** (.3621)	-
Plan to visit areas with high-elevation forests	.5290 (.4275)	.5398 (.4305)	.5502 (.4317)	.4097 (.4247)	-
Metropolitan region (Dummy)	-.1898 (.3664)	-.2031 (.3722)	-.1948 (.3640)	-	-
Mountain Census division (Dummy)	-.3505 (.3056)	-.3553 (.3051)	-.3558 (.3059)	-	-
Presence of Any Children in Household (Dummy)	-.3447 (.3304)	-.3476 (.3322)	-.3367 (.3304)	-	-
Log likelihood	-283.759	-283.497	-283.823	-284.464	-324.366
Likelihood ratio statistic[c] (deg. of f.)	181.93 (10)	182.45 (11)	181.80 (9)	180.52 (6)	100.72 (1)

[a] The dependent variable is set to 1 if the respondent chose "yes," and 0 for "no."

[b] Attitude represented by dummy variable corresponding to response > 3, expressing some level of agreement with statement.

[c] Statistic compares fit of each model against restricted model of only a constant.

Linearized standard errors in parentheses, omitted coefficients signify variables not included in model; *** - significant at $p < 0.01$; * - significant at $p < 0.10$.

This effect is not found; the coefficient on Quantity is insignificant (a Wald test fails to reject null hypothesis that the coefficient is equal to zero, $p = 0.480$). Model 2 loosens the restriction of linearity, but the lack of significance on the two quantity dummy variables signifies that the response to neither the 50% quantity (a Wald test rejects a test of difference from 0 at $p = 0.552$) nor the 70% quantity (rejected at $p = 0.481$) differs from the response to 30% quantity. Further, the coefficients on the two dummy variables are statistically indistinguishable (Wald test rejects difference at $p = 0.849$). Likelihood ratio tests verify that neither model 1 nor model 2 statistically improves upon the fit of model 3, which pools responses across Quantity levels (with likelihood ratio test statistics 0.13 and 0.65, 1 and 2 degrees of freedom, and $p = 0.719$ and $p = 0.722$, respectively), demonstrating that choices were not responsive to differences in the quantity of acreage protected.

Comparison of models 3 and 4 demonstrates a lack of influence of the included demographic variables upon a respondent's predicted choice. Not only are the coefficients on each of the demographic variables in model 3 insignificant, but also the fit of the restricted model (model 4) is statistically identical to that of the extended model (with likelihood ratio test statistic 1.28, with 3 degrees of freedom, failing to reject the null that the coefficients on excluded variables are 0 at p = 0.734). Thus, neither the presence of children in the household, residence within a metropolitan area, nor living in the Mountain States influenced responses to the contingent valuation question.

In contrast, inclusion of responses to attitude and visitation questions improves model 4's fit over the restricted model 5 (with likelihood ratio test statistic 79.80 for 5 degrees of freedom, rejecting the null hypothesis at $p < 0.01$). Not surprisingly, respondents opposed to taxes in general had a lower probability of positive response than those more accepting of new taxes (significant by Wald test at $p < 0.01$). While those who have visited areas with high-elevation forests had a higher probability of positive response than those who have not (significant by Wald test at $p < 0.01$), the smaller coefficient, with a weaker significance, on the importance of recreational opportunities in the forests (significant by Wald test at $p < 0.1$) suggests that users' positive responses were driven by other motivations, in addition to their ability to enjoy use of the forests. The "option" motivation for nonuse valuation is not demonstrated, as plans for future visitation fail to significantly predict response (Wald test failed at p = 0.335), whereas the "bequest" motivation, which holds that the existence of high-elevation forests for future generations matters, is supported by the significance of the corresponding attitude (significant by Wald test at p = 0.010).

Given these tests, model 4 provides the most robust and parsimonious specification. Using this model and the percentages of respondents supporting attitudes presented in table 3, mean per household willingness to pay for a program to treat high-elevation forests for WPBR is estimated to be \$172.55 (statistically different from 0 at $p < 0.01$), with a 95% confidence interval ranging from \$104.06 to \$241.04. If we extrapolate this estimate to the population of the Western United States, an aggregate value of treating high-elevation forests for WPBR is estimated to be between \$2.8 billion and \$6.5 billion, with a point estimate of \$4.7 billion.

Discussion

The most obvious conclusion of this study, reflected in the large and significant aggregate values reported above, is that an informed, general population of the Western United States cares about the problem of WPBR in their high-elevation forests and is willing to trade off household income in order to manage the threat. Despite expressing a lack of trust in the beneficence of government agencies and the efficiency of spending of public tax dollars, people exhibited an average willingness to pay a substantial amount into what, in all likelihood, would be a government-implemented program for protecting high-elevation forests. The large confidence interval reflects a large variance associated with this estimate. Nonetheless, the estimated lower bound of aggregate benefits to the Western U.S. of \$2.8 billion demonstrates that the public strongly supports the allocation of substantial funding toward addressing the threat of WPBR in high-elevation forests.

The lack of sensitivity to the quantity of forest protected in the contingent valuation question, paired with the direct evidence of the effect of attitudes upon responses, highlights that existence values dominate in terms of what matters to the population. Given that the valuation question asked about a program aimed at forest health 100 years from now despite being implemented today, this result reflects that, though respondents recognize that a lot might change over the next century, they assert that the sustained existence of at least some of the high-elevation forests will remain important. Supporting this interpretation, responses to the attitudinal questions demonstrate an understanding of the importance of benefits derived from the natural services provided by these forests and a recognition of the role that natural processes play in determining changes in resources such as forests.

Not only indirect uses, such as the enjoyment of ecosystem services supported by the high-elevation forests, but also values related to nonuse contribute substantially to the public benefit provided by the continued existence of the forests. Indirect uses, such as the services of water provision and soil retention, tend to be produced by disperse, interrelated ecological systems not conducive to meaningful valuation of their individual, essential parts through valuation of the end uses. In addition, responses to attitudinal questions tend to de-emphasize the importance of direct uses, such as recreation and tourism, even though large proportions of the population have visited areas with high-elevation forests in the past. Instead, the importance of protecting some of the forests for the future is emphasized, and the proportion of the population intending to visit the areas at some undetermined point in the future matches or exceeds the proportion already visiting them, suggesting a combination of bequest and option motivations for nonuse values. In sum, our findings support the argument that adequate valuation of natural resources for public decision-making must accommodate nonmarket values, and that in some cases, such as the presently examined issue of protecting high-elevation forests from white pine blister rust, these values are quite substantial.

References

Amirnejad, Hamid; Sadegh Khalilian; Mohammad H. Assareh; and Majid Ahmadian. 2006. Estimating the existence value of north forests of Iran by using a contingent valuation method. Ecological Economics. 58(4): 665-675.

Bond, Craig A.; Patricia Champ; James Meldrum; and Anna Schoettle. 2010. Proactive or reactive? Optimal management of an invasive forest pest in a spatial framework. Agricultural and Applied Economics Association, 2010 Annual Meeting, Selected Paper. 11633.

Boyle, Kevin J. 2003. Contingent valuation in practice. In A Primer on Nonmarket Valuation, Patricia A. Champ, Kevin J. Boyle, and Thomas C. Brown, 111-170. Boston: Kluwer Academic Publishers.

U.S. Census Bureau. 2009. 2009 Population Estimates.

Burns, Kelly S.; Anna W. Schoettle; William R. Jacobi; and Mary F. Mahalovich. 2008. Options for the management of white pine blister rust in the Rocky Mountain Region. RMRS-GTR-2. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station.

Carson, Richard T.; Nicholas E. Flores;, and Norman F. Meade. 2001. Contingent valuation: Controversies and evidence. Environmental and Resource Economics. 19: 173-210.

Champ, Patricia A. 2003. Collecting survey data for nonmarket valuation. In: A Primer on Nonmarket Valuation, Patricia A. Champ, Kevin J. Boyle, and Thomas C. Brown, 59-98. Boston: Kluwer Academic Publishers.

Cole, David N. 1996. Wilderness recreation use trends, 1965 through 1994. INT-RP-488. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station.

Dunlap, Riley E.; Kent D. Van Liere; Angela G. Mertig; and Robert Emmet Jones. 2000. Measuring endorsement of the New Ecological Paradigm: A revised NEP scale. Journal of Social Issues. 56(3): 425-442.

Ellison, Aaron M.; Michael S. Bank; Barton D. Clinton; Elizabeth A. Colburn; Katherine Elliott; Chelcy R. Ford; David R. Foster; et al. 2005. Loss of foundation species: Consequences for the structure and dynamics of forested ecosystems. Frontiers in Ecology and the Environment. 3(9): 479-486.

Englin, Jeffrey E.; Jered M. McDonald; Klaus Moeltner. 2006. Valuing ancient forest ecosystems: An analysis of backcountry hiking in Jasper National Park. Ecological Economics. 57(4): 665-678.

Hanemann, W. Michael. 1989. Welfare evaluations in contingent valuation experiments with discrete response data: Reply. American Journal of Agricultural Economics. 71(4): 1057-1061.

Hanemann, W. Michael. 1998. The statistical analysis of discrete-response CV data. Working Paper 798. Berkeley, CA: University of California, California Agricultural Experiment Station, Giannini Foundation of Agricultural Economics.

Holmes, Thomas P.; Juliann E. Aukema; Betsy Von Holle; Andrew Liebhold; Erin Sills. 2009. Economic impacts of invasive species in forests: past, present, and future. Annals of the New York Academy of Sciences. 1162: 18-38.

Kearns, Holly S. J.; William R. Jacobi. 2007. The distribution and incidence of white pine blister rust in central and southeastern Wyoming and northern Colorado. Canadian Journal of Forest Resources. 37: 462-472.

Kotchen, Matthew J.; Stephen D. Reiling. 2000. Environmental attitudes, motivations, and contingent valuation of nonuse values: a case study involving endangered species. Ecological Economics. 32: 93-107.

Kramer, Randall A.; Thomas P. Holmes; Michelle Haefele. 2003. Contingent valuation of forest ecosystem protection. In Forests in a Market Economy, Erin O. Sills and Karen Lee Abt, 303-320. Boston: Kluwer Academic Publishers.

Krutilla, John V. 1967. Conservation reconsidered. The American Economic Review. 57(4): 777-786.

Liebhold, Andrew M.; William L. MacDonald; Dale Bergdahl; Victor C. Mastro. 1995. Invasion by exotic forest pests: a threat to forest ecosystems. Forest Science Monograph 30. Society of American Foresters.

Logan, Jesse A.; James A. Powell. 2001. Ghost forests, global warming, and the mountain pine beetle (Coleoptera: Scolytidae). American Entomologist. 47(3): 160-173.

Loomis, John B.; Catherine M. Keske. 2009. Mountain substitutability and peak load pricing of high alpine peaks as a management tool to reduce environmental damage: a contingent valuation study. Journal of Environmental Management. 90(5): 1751-60.

Maloy, O. C. 1997. White pine blister rust control in North America: a case history. Annual Review of Phytopathology. 35: 87-109.

McFarlane, Bonita L.; R. Craig; G. Stumpf-Allen; David O. Watson. 2006. Public perceptions of natural disturbance in Canada's national parks: The case of the mountain pine beetle (Dendroctonus ponderosae Hopkins). Biological Conservation. 130(3): 340-348.

Muller, Martin; Hubert Job. 2009. Managing natural disturbance in protected areas: Tourists' attitude towards the bark beetle in a German national park. Biological Conservation. 142(2): 375-383.

Samman, Safiya; J. W. Schwandt; J. L. Wilson. 2003. Managing for healthy white pine ecosystems in the United States to reduce the impacts of white pine blister rust. R1-03-118. Missoula, MT: U.S. Department of Agriculture, Forest Service, Northern Region.

Schoettle, Anna W.; Richard A. Sniezko. 2007. Proactive intervention to sustain high elevation pine ecosystems threatened by white pine blister rust. Journal of Forest Research. 12: 327-336.

Schoettle, Anna W. 2004. Ecological roles of five-needle pines in Colorado: Potential consequences of their loss. In: Breeding and Genetic Resources of Five-Needle Pines: Growth, Adaptability and Pest Resistance, Richard A. Sniezko; Safiya Samman; S. E. Schlarbaum; H. B. Kriebel, 124-135. RMRS-P-32. Fort Collins, CO: USDA Forest Service, Rocky Mountain Research Station.

Schwandt, John W. 2006. Whitebark pine in peril: A case for restoration. R1-06-28. Coeur d'Alene, ID: U.S. Department of Agriculture, Forest Service, Forest Health Protection.

TripAdvisor. 2008. TripAdvisor travelers offer glimpse into 2009 trends. http://multivu.prnewswire.com/mnr/tripadvisor/35236/

U.S. Department of Interior. 1983. Americans and their National Parks. In: 1982-1983 Nationwide Recreation Survey, 41-45. U.S. Department of Interior, National Park Service.

Walsh, R.; R. Bjonback; R. Aiken; D. Rosenthal. 1990. Estimating the public benefits of protecting forest quality. Journal of Environmental Management. 30(2): 175-189.

Walsh, Richard G.; John B. Loomis; Richard A. Gillman. 1984. Valuing option, existence, and bequest demands for wilderness. Land Economics. 60(1): 14-29.

Annual Observations of Conspicuous Canker Activity on Whitebark Pine (2003 to 2007)

Extended Abstract

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Introduction

Whitebark pine's (*Pinus albicaulis*) notable ecological values, combined with its precarious state, underscore the need for monitoring its health and dynamics. Populations of whitebark pine are in decline throughout most of its range. White pine blister rust, caused by the fungus *Cronartium ribicola*, has denuded stands since introduction during the early 1900s (Tomback and Achuff 2010). The exclusion of fire, which historically promoted whitebark pine over its competitors, has further lessened its proportional abundance with competitors (Murray 2007; Murray and others 2000). Mountain pine beetle epidemics have killed vast acreages since 2003 (Haeussler 2008; Kegley and others, these proceedings; Logan and others 2010). Due to one or more of these threats, whitebark pine has declined in areal cover up to 98 percent in places (Schwandt 2006).

Rust-induced mortality is becoming well-documented across the natural range of whitebark pine (Schwandt and others 2010). However, at a finer scale (i.e., individual tree), the biological interactions taking place between the infected host (whitebark pine) and disease are not well-studied. Understanding dynamics pertaining to natural inactivation of cankers may improve our ability to model death rates, monitor virulence, and develop measures for blister rust control (Kimmey 1969). Natural inactivation of blister rust cankers on western white pine has been described on young trees (Hungerford 1977; Kimmey 1969). Knowledge of canker activity from mature western white pine (*Pinus monticola*), or whitebark pine of any age, appear absent from the literature.

The objective of this study was to track the most apparent signs of canker activity on a sample of whitebark pine over a five-year period. The magnitude and duration of inactive periods were documented. Further insight regarding possible differences between canker locations (branch vs. stem, location on Cascade Crest) was also sought.

Methods

The study location is centered around Crater Lake, Oregon, located on the crest of the southern Cascade Mountain Range. Whitebark pine achieves co-dominance from 2,080 m to the highest elevation in the study area (2,722 m). Mountain hemlock (*Tsuga mertensiana*) and lodgepole pine (*Pinus contorta* var. *murrayana*) are common co-dominants. Shasta red fir (*Abies × shastensis*), western white pine, and ponderosa pine (*P. ponderosa*) are occasional associates. Common understory flora include California needlegrass (*Achnatherum occidentale),* squirreltail (*Elymus elymoides*), *Ross' sedge (Carex rossii*), Davidson's penstemon (*Penstemon davidsonii* var. *davidsonii), knotweed (Polygonum davisiae*), buckwheat (*Eriogonum umbellatum*), woodrush (*Luzula hitchcockii*), and spreading phlox (*Phlox diffusa*). Soils are relatively young, having been derived from the volcanic eruption of Mt. Mazama about 7,700 years ago. Composition is pumice-ash with varying amounts of cobble-size cinder stone, resulting in rapid permeability and loose structure. The climate is typified by heavy snowfall (average = 12.2 m/year) with depths commonly peaking at about 4.5 meters in April (Crater Lake National Park, unpublished data). Winter temperatures are somewhat mild (average = -3.0 ˚C (26.6 ˚F)) with summer days averaging 11.0 ˚C (52.0 ˚F). Because the study area straddles the crest of the southern Cascade Range, a climate gradient occurs between the east and west portion of the study area. The east side receives less precipitation and has cooler temperatures.

All monitored trees were associated with a set of seven permanent sampling plots established in 2003. The vicinity of each plot was pre-determined to represent the whitebark pine communities present in the study area. Next, each plot was placed within each vicinity based on field reconnaissance of the area, then choosing a plot center location that appeared typical for the vicinity and community (Mueller-Dombois and Ellenberg 1974). Plots were circular, encompassing 300 square meters. Within each plot, all trees were mapped for ease in relocating each subsequent year. In many instances, labelled aluminum tags were affixed to trees to provide additional reference. The following information was recorded for all live and dead standing trees: a unique alphanumeric identifier, species, diameter at breast height (dbh), and overall status (healthy, sick, recently dead, and dead). Trees classified as sick were infected by one or more biotic agents. Also included were instances of mechanical damage that caused foliage-kill. Where white pine blister rust was identified, the following data were recorded: status (active or inactive) and location (distance from ground and main stem) of each canker, plus percent of crown killed. Cankers were noted as occurring on either live branches or stems, but those that grew on both were classified as stem cankers. Blister rust cankers were noted as active when one

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Figure 1. Active canker with fruiting structures, resinosus, orange-tinted bark, and rodent gnawing.

or more of the following symptoms were present: resin on surface, fungal fruiting structures, or yellow to orange coloured bark (figure 1). Rodent gnawing deemed to occur during the current year's sampling season was also indicative of an active canker.

Results were tabulated and tested for statistical significance. Specifically, annual tallies of active cankers were tested with X^2 (chi-square) to determine potential differences in activity according to each year (Fowler and Cohen 1990). The number of active vs. inactive cankers were also compared across location in the study area (east vs. west sides) and position on the tree (branch vs. stem) using the Mann-Whitney *U*-test (Fowler and Cohen 1990). The magnitude of inactivity (percentage of years inactive) was also tested to see if cankers tended to be significantly inactive over their entire span of observations. For this, the randomization goodness-of-fit test was applied (McDonald 2009).

Results

A total of 52 cankers from 46 trees were tracked but tallies varied in any given year due to new infections detected or tree mortality. Trees varied in height from 0.19 m to 7 m (0 to 28.7 cm dbh). Overall, 42 percent of cankers changed their status (active vs. inactive) at least once. Active cankers were more numerous than inactive cankers in every year except 2004 (table 1). Cankers were significantly more active in 2003 and 2006 (X^2, Yates correction, $P < 0.05$). The east side tended to have lower activity, however, the disparity between sides was not significant ($U = 8$, $P < 0.05$). Branch cankers were observed to be more active than stem cankers in all years except 2003, although not with significance.

The degree of inactivity for each canker was examined (table 2). Seven cankers showed no activity during the study period and may be devoid of the *C. ribicola* inoculum. For those cankers that had activity, years of idleness tended to be skewed low. For example, 32 of 52 cankers were inactive for less than 50 percent of annual observations. Correspondingly, in comparing inactivity among all percentage classes (table 2), both stem and branch cankers were more likely to be active than inactive ($P = 0.005$ and $P = 0.000$ respectively). A subset of cankers went inactive, and then returned to activity. For these re-activated cankers, eight were latent for only a single year. Another five cankers were inactive two consecutive years. None were found to re-activate after three years. Half of all inactive cankers (at any time during the study) failed to re-activate.

Discussion and Conclusions

This study presents the first published account of annual canker activity of white pine blister rust on whitebark pine. Based on these observations, canker activity appears to vary each year. Activity was significantly higher in 2003 and 2006, but a cause was not investigated. Hungerford (1977) found activity for branch cankers to decrease consistently every year—possibly due to aging trees and/or aging cankers. That result was not observed in this study. Also in contrast, Kimmey (1969) and Hungerford (1977) observed more activity among stem cankers. Because they did not define a classification for individual cankers occurring on both the stem and adjoining branch, these comparisons are of limited merit. While Hungerford (1977) found that 78 percent of inactive cankers failed to re-activate, in this study half of inactive cankers re-activated. During his most active two years, 60 and 72 percent of all cankers were active. Similarly, 67 and 83 percent were active during peaks in my observations.

The reliability of outward signs of activity closely reflecting fungal virulence is not well-documented in literature. The disease may continue to thrive, and possibly spread beneath the bark without conspicuous resin, sporulation, rodent-gnawing, or bark discoloration. Notwithstanding, no cankers appeared to re-activate after three years of inactivity.

Table 1. Percentage of individual blister rust cankers found active.

	2003	2004	2005	2006	2007
All Cankers	83.3	45.2	59.5	66.7	59.5
West-Side Plots	77.3	56.7	71.0	66.7	68.8
East-Side Plots	87.5	22.2	40.0	70.0	45.5
Branch Cankers	80.0	62.5	66.7	75.0	66.7
Stem Cankers	83.3	25.0	56.3	57.9	55.0

Table 2. Proportion of inactivity for individual blister rust cankers (2003-2007).

	Percentage of Years Canker Found Inactive										
	0%	20%	25%	33%	40%	50%	60%	66%	75%	80%	100%
No. Stem Cankers	8	1	0	1	2	3	2	1	0	2	2
No. Branch Cankers	14	2	0	0	4	3	0	1	0	1	5

Additional studies could explore the utility of this potential threshold in determining when a canker is no longer infected with inoculum. Also, half of inactive cankers failed to re-activate. Thus, classifying a tree as having blister rust based on the existence of a single canker, which appears inactive, would risk over-estimating disease incidence.

References

Crater Lake National Park. 2008. Headquarters weather station raw unpublished data. U.S. Department of Interior, National Park Service, Crater Lake, OR.

Fowler, J.; Cohen, L. 1990. Practical statistics for field biology. Bristol, PA: Open University Press. 227 p.

Haeussler, S. 2008. Threatened whitebark ecosystems at their northern limits in B.C. Nutcracker Notes. 14: 17-18.

Hungerford, R. D. 1977. Natural inactivation of blister rust cankers on western white pine. Forest Science. 23(3): 343-350.

Kimmey, J. W. 1969. Inactivation of lethal-type blister rust cankers on western white pine. Journal of Forestry. 67: 296-299.

Logan, J. A.; MacFarlane, W. W.; Willcox, L. 2010. Whitebark pine vulnerability to climate-driven mountain pine beetle disturbance in the Greater Yellowstone Ecosystem. Ecological Applications. 20(4): 895-902.

McDonald, J. H. 2009. Handbook of Biological Statistics. 2nd ed. Baltimore, MD: Sparky House Publishing. 293 p.

Mueller-Dombois, D.; Ellenberg, H. 1974. Aims and methods of vegetation ecology. New York: J. Wiley & Sons. 547 p.

Murray, M. 2007. Fire and Pacific Coast whitebark pine. In: Goheen, E. M.; Sniezko, R. A., tech. coords. Whitebark pine: a Pacific Coast perspective; 2006 August 27-31; Ashland, OR. R6-NR-FHP-2007-01. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Region: 51-60.

Murray, M. P.; Bunting, S. C.; Morgan, P. C. 2000. Landscape trends (1753-1993) of whitebark pine (*Pinus albicaulis*) forests in the West Big Hole Range, Idaho/Montana, U.S.A. Arctic, Antarctic, and Alpine Research. 32(4): 412-418.

Schwandt, J. 2006. Whitebark pine in peril. Rep. R1-06-28. U.S. Department of Agriculture, Forest Service, Forest Health Protection. 18 p.

Schwandt, J. W.; Lockman, I. B.; Kliejunas, J. T.; Muir, J. A. 2010. Current health issues and management strategies for white pines in the western United States and Canada. Forest Pathology. 40(3-4): 226-250.

Tomback , D. F.; Achuff, P. 2010. Blister rust and western forest biodiversity: ecology, values and outlook for white pines. Forest Pathology. 40(3-4): 186-225.

Re-measurement of Whitebark Pine Infection and Mortality in the Canadian Rockies

Extended Abstract

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Whitebark pine (*Pinus albicaulis*) populations are under threat across the species' range from white pine blister rust (*Cronartium ribicola*), mountain pine beetle (*Dendroctonus ponderosae*), fire exclusion and climate change (Tomback and Achuff 2010). Loss of whitebark pine is predicted to have cascading effects on the following ecological services: provision of high-energy food for wildlife (Tomback and Kendall 2001), facilitation of succession (Callaway 1998) and retention of snowpack (Tomback and others 2001).

While numerous studies have reported on the incidence of white pine blister rust on whitebark pine and subsequent mortality (see Kendall and Keane 2001 and Smith and others (2008) for examples), only a few have reported on rates of change in these variables (Keane and Arno 1993, Smith and others (2008), GYWPMWG 2010). We report here on the change in blister rust incidence and mortality of whitebark pine, over two and three time periods, in the Canadian Rockies from Waterton Lakes National Park (WLNP) on the international boundary (49°N), north to McBride, British Columbia (53°N).

In 2003 and 2004, we re-established eight plots that Kendall and others (1996) had measured in 1996 in WLNP, and established 107 new plots; 71 of the total 115 plots are east of the Continental Divide in Alberta and 44 are west of the Divide in British Columbia (Figure 1). Although Kendall's original plots were not permanently marked nor were the trees tagged, we were able to resample within the original stands by using geographical coordinates, plot photographs and azimuths from plot center along transect (Kendall 2003).

Methods for establishing plots (10 m x 5 m) and assessing health were those recommended by Tomback and others (2005). All trees (≥ 1.3 m) were marked with numbered aluminum tags. Both single seedlings and clumps of seedlings were counted as only one seedling site, and classified by two size classes (< 50 cm or ≥ 50 cm). Incidence of infection by blister rust was reported as proportion of live trees that were infected at the time of each survey. Mortality was from all causes and reported as proportion of dead trees at the time of each survey. Some dead trees may be decades old, while others were recently dead (still had red needles).

In 2009, we re-measured 114 plots, as we were unable to re-locate one. We assessed a total of 5,865 trees (≥ 1.3 m) and 2,874 seedling clumps (< 1.3 m) in 2003-04, and 5,896 trees and 3,645 seedling clumps in 2009. The increase in the number of trees was because some seedlings grew above 1.3 m in height during the interval.

In all 114 plots, the rust infection increased from 42 percent in 2003-04 to 52 percent in 2009, while mortality increased from 18 percent to 28 percent (Figure 2), or about 2 percent yr^{-1} over the 6 to 7 year interval. Of the recently dead trees white pine blister rust was the dominant cause of death. Levels of infection continue to show a latitudinal gradient of highest infection in the southern zone of the study area, lowest in the central zone and rising again in the northern zone (Figure 2).

Infection level for seedlings was virtually unchanged, averaging 17 percent in 2003-04 and 15 percent in 2009, but again, levels were highest in the southern zone at 30 percent compared to 6 percent in the central zone and 2 percent in the northern zone. The mean density of the combined size classes was 0.04 seedling clumps per m^2 (±0.06 seedling clumps per m^2 one standard deviation from the mean).

In the eight plots that have been measured three times, infection increased from 43 percent of live trees in 1996, to 70 percent in 2003 and 78 percent in 2009 (Figure 3). The highest increase in mortality occurred between 1996 to 2003-04, (from 26 percent to 61 percent) then rose slightly to 65 percent in 2009. Infection levels increased 4 percent yr^{-1} in the first seven years (Smith and others 2008), but only 1.3 percent yr^{-1} in the six years of the second remeasurement interval—the combined total was an increase of 3 percent yr^{-1} over the 13 years from 1996 to 2009. Mortality levels increased 5 percent yr^{-1} in the first seven years (Smith and others 2008), but less than 1 percent yr^{-1} during the second interval, for a combined increase of 3 percent yr^{-1} over 13 years.

While it appears that the rates of increase in infection and mortality have decreased in the last six years, rust is still killing many whitebark pine trees and this is cause for concern. Infection and mortality from white pine blister rust are present in all plots, but the highest levels were in southwestern Alberta and southeastern British Columbia. This area also had the highest levels of infection of seedlings, and canopy kill (Smith and others 2008).

The decline in whitebark pine populations has led to this species being listed as Endangered under *The Wildlife Act* in the Province of Alberta in 2008 (Government of Alberta 2010), and a recovery strategy is in preparation. Nationally, whitebark pine has been assessed as Endangered (COSEWIC 2010), public consultations have been completed, and legal

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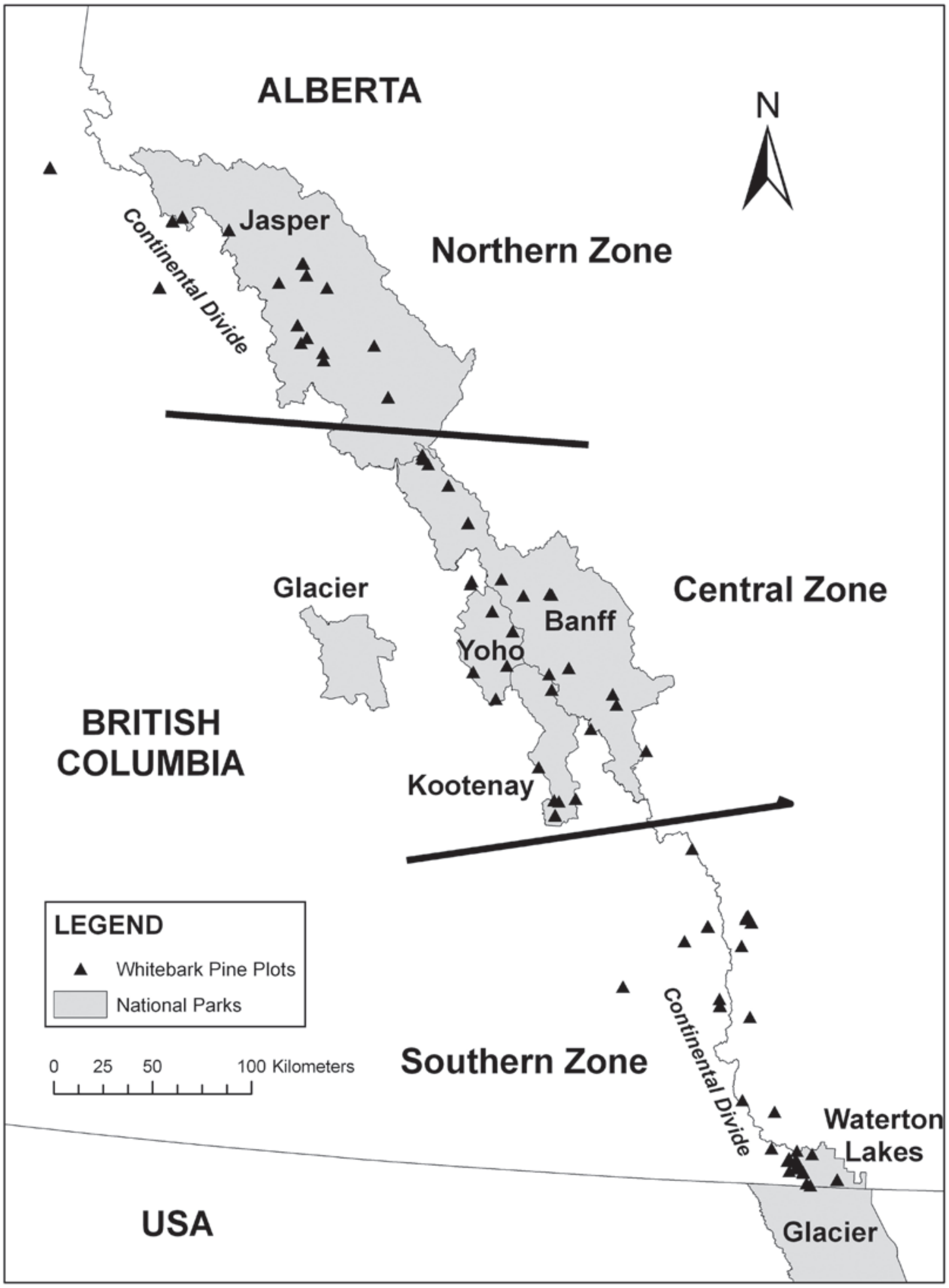

Figure 1. Study area showing three zones in the Canadian Rockies range of whitebark pine.

listing is pending. In WLNP, restoration activities underway include caging and collecting cones from putatively resistant whitebark pine trees and planting seedlings.

Acknowledgements

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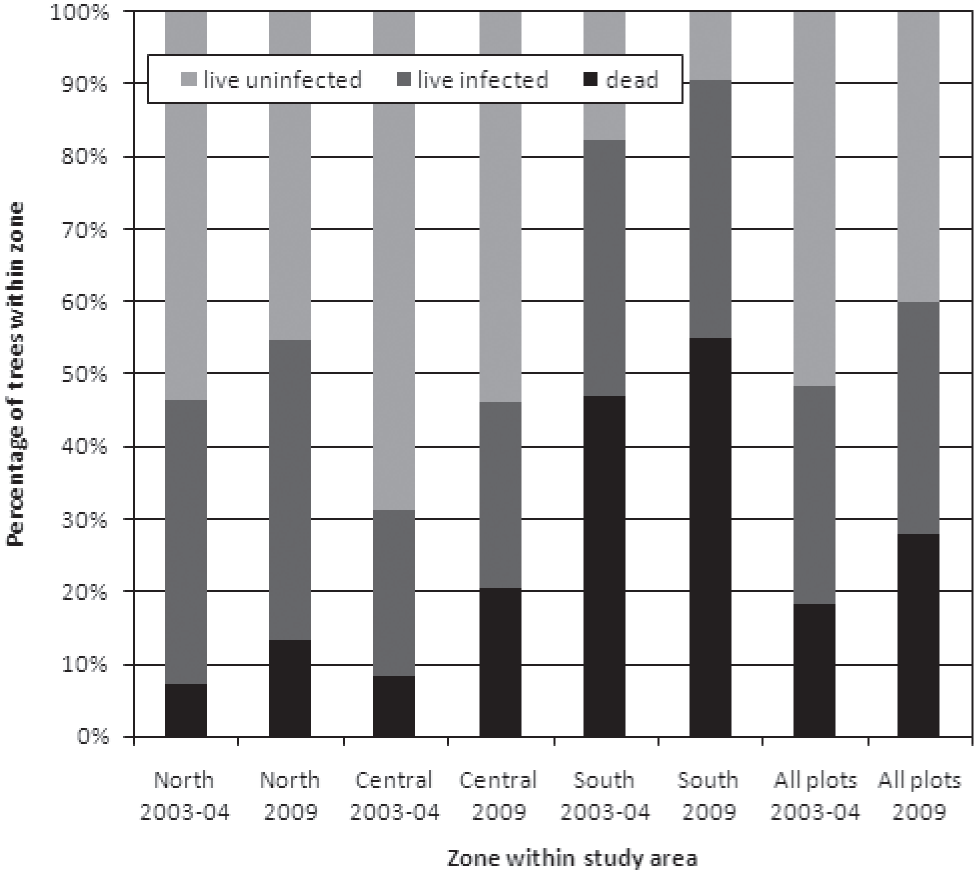

Figure 2. Incidence of white pine blister rust and whitebark pine mortality in the Canadian Rockies by latitude and study area.

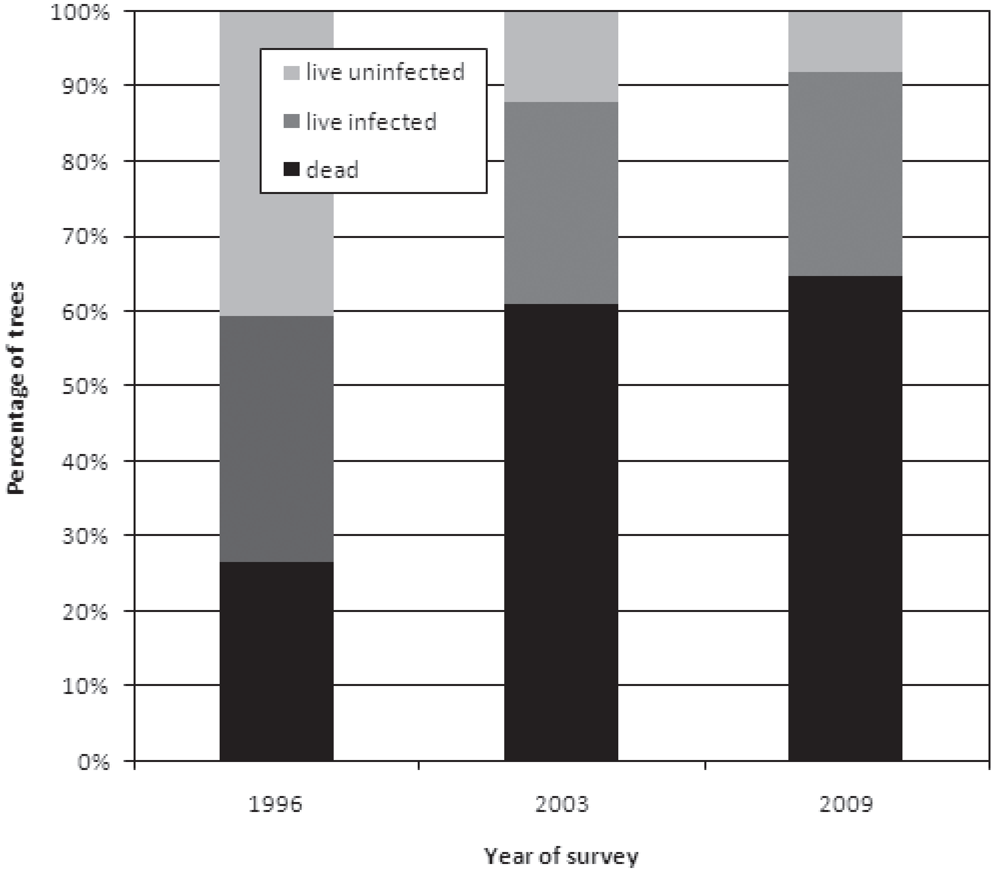

Figure 3. Incidence of white pine blister rust and whitebark pine mortality for eight plots over three time periods in Waterton Lakes National Park, Alberta.

Literature Cited

Callaway, R. M. 1998. Competition and facilitation on elevation gradients in subalpine forests of the northern Rocky Mountains. Oikos. 82: 561-573.

COSEWIC. 2010. Species at risk increase in 2010—the international year of biodiversity. Committee on the Status of Endangered Wildlife in Canada. [Online]. http://cosewic.gc.ca/eng/scf7/scf7_3_15_e.cfm [September 7, 2010].

Government of Alberta. 2010. Species assessed by Alberta's Endangered Species Conservation Committee: short list. [Online]. Available: http://www.srd.alberta.ca/BioDiversityStewardship/SpeciesAtRisk/SpeciesSummaries/ [July 30, 2010].

GYWPMWG (Greater Yellowstone Whitebark Pine Monitoring Working Group. 2010. Monitoring whitebark pine in the Greater Yellowstone Ecosystem: 2009 annual report. Pp 63-71. In: Yellowstone grizzly bear investigations: annual report of the Interagency Grizzly Bear Study Team, 2009. Bozeman, MT: U.S. Geological Survey.

Keane, R. E.; Arno, S. F. 1993. Rapid decline of whitebark pine in western Montana: evidence from 20-year remeasurements. Western Journal of Applied Forestry. 8(2): 44-47.

Kendall, Katherine C. 2003. Whitebark pine study master database. West Glacier, MT: U.S. Geological Survey, Northern Rocky Mountain Science Center.

Kendall, K. C.; Keane, R. E. 2001. Whitebark pine decline: infection, mortality, and population trends. Pp 221-242. In: Whitebark pine communities: ecology and restoration. Washington, DC: Island Press.

Kendall, K. C.; Schirokauer, D.; Shanahan, E.; Watt, R.; Reinhart, D.; Renkin, R.; Cain, S.; Green, G. 1996. Whitebark pine health in northern Rockies national park ecosystems. Nutcracker Notes. 7: 16-16.

Smith, C. M.; Wilson, B.; Rasheed, S.; Walker, R. C.; Carolin, T.; Shepherd, B. 2008. Whitebark pine and white pine blister rust in the Rocky Mountains of Canada and northern Montana. Canadian Journal of Forest Research. 38: 982-995.

Tomback, D. F.; Achuff, P. 2010. Blister rust and western forest biodiversity: ecology, values and outlook for white pines. Forest Pathology. 40: 186-225.

Tomback, D. F.; Kendall, K. C. 2001. Biodiversity losses: the downward spiral. Pp 243-262. In: Whitebark pine communities: ecology and restoration. Washington, DC: Island Press.

Tomback, D. F.; Arno, S. F.; Keane, R. E. 2001. The compelling case for management intervention. Pp 3-25. In: Whitebark pine communities: ecology and restoration. Washington, DC: Island Press.

Tomback, Diana F.; Keane, Robert E.; McCaughey, Ward W.; Smith, Cyndi M. 2005. Methods for surveying and monitoring whitebark pine for blister rust infection and damage. Missoula, MT: Whitebark Pine Ecosystem Foundation.

Can Microscale Meteorological Conditions Predict the Impact of White Pine Blister Rust in Colorado and Wyoming?

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Abstract—White pine blister rust occurs when there are compatible interactions between susceptible hosts (white pines and *Ribes* spp.), inoculum (*Cronartium ribicola* spores), and local weather conditions during infection. The five spore stages of the white pine blister rust (WPBR) fungus have specific temperature and moisture conditions necessary for production, germination, and dissemination of spores. Local meteorological conditions may be important factors in infection success, infection periodicity and disease intensification over time.

Predictions of white pine blister rust occurrence and severity depend on various tree, secondary host, site and environmental factors. Recent predictions have also used spatial climate data of 30-year monthly averages (which are available for a matrix of points over large geographic areas) and concluded that meteorological conditions are dynamic forces determining successful infestation. Hourly temperature and relative humidity data at the local, microsite level (in white pine stands) allow specific temporal resolution not offered by spatial climate datasets. The objectives of this study were to determine: 1) if short-term, microsite weather data could be used to adjust longer-term, regional data to accurately represent conditions within white pine stands; 2) suitable infection periods for WPBR at sites with host and disease information; and 3) if modified regional data is useful in explaining variability in WPBR occurrence, severity, periodicity or impact on host health.

Nine to 21 years of data from 27 long-term, regional stations were adjusted to microsite white pine stand meteorological conditions by 48 short-term, local station data from corresponding white pine stands in Colorado and Wyoming. Paired site equations (from 1 to 4 microsite data sources per site) were averaged by site and used to adjust regional station data. Adjusted hourly data were used to determine suitable infection periods (relative humidity >90% and air temperature within 0-23.8 °C for periods of at least 6 or 12 hours) for study sites with information on WPBR occurrence and site factors.

Canker size and canker growth rate estimation data recently collected in limber pine stands throughout Colorado and Wyoming were extrapolated to explain periodicity of WPBR infection and temporal estimations of infestation length and disease intensification. We are attempting to combine various aspects of disease occurrence, severity and intensification with host responses (dieback or mortality due to WPBR) to categorize sites as high- or low-impact over time and use this information in site-specific hazard predictions. Preliminary models indicate that predictions of WPBR hazard still rely on the knowledge of important site factors such as *Ribes* presence and density; however, local relative humidity, temperature fluctuations and suitable infection periods are also important variables that can help forecast how rust will intensify once it establishes on a site.

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Histological Observations on Needle Colonization by *Cronartium ribicola* in Susceptible and Resistant Seedlings of Whitebark Pine and Limber Pine

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Abstract—Resistance to white pine blister rust based on a hypersensitive response (HR) that is conferred by a dominant gene has been identified as functioning in needles of blister rust-resistant families of sugar pine, western white pine and southwestern white pine. The typical HR response displays a characteristic local necrosis at the site of infection in the needles during the early stages of needle colonization by *Cronartium ribicola*. The localized host cell death early in the infection process is thought to prevent the pathogen from reaching the shoot tissue, thereby preventing further disease development. However, variation in macroscopic symptoms of needle reactions has been observed within and between different pine species and families. Blister rust resistance and variation in needle reactions to infection by *C. ribicola* have been observed in families of whitebark pine and limber pine, but it is not known whether HR type resistance functions in these species. Furthermore, it is not known whether the variation observed in macroscopic needle reactions reflects intra- and interspecific variation in the HR type reaction, or if different cellular resistance mechanisms are expressed during needle colonization by *C. ribicola*. This study was undertaken to compare the histological details of needle colonization by *C. ribicola* in whitebark pine and limber pine seedlings with those of susceptible and HR reactions in western white pine seedlings. Histological observations and comparisons of needle colonization by *C. ribicola* in blister rust susceptible and resistant limber pine, whitebark pine and western white pine individuals suggests that substantial colonization of resistant phenotype needles occurs, despite the presence of a HR-like response. The presence of large amounts of *C. ribicola* hyphae observed in western white pine individuals displaying HR-like needle reactions was unexpected, and suggests that mechanisms other than HR responses in needles may be involved in blister rust resistance. Further examinations are underway.

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Genetic Resistance to Blister Rust

Past and Current Investigations of the Genetic Resistance to *Cronartium ribicola* in High-elevation Five-needle Pines

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Abstract—All nine species of white pines native to the U.S. or Canada are susceptible to the introduced pathogen *Cronartium ribicola*. Of the six high elevation white pine species, the severe infection and mortality levels of *Pinus albicaulis* have been the most documented, but blister rust also impacts *P. aristata*, *P. balfouriana*, *P. flexilis* and *P. strobiformis*; only *P. longaeva* has not been documented to be infected in its natural range. Early evaluations of resistance included relatively few seedlots and demonstrated that these species have some genetic resistance to blister rust but generally less than their Eurasian relatives. Recently, more extensive evaluations of these six species have begun. These recent rust tests capitalize on the methods developed from decades of prior experience by the USDA Forest Service in testing *P. monticola* and *P. lambertiana*. Following artificial inoculation, seedlings are evaluated for up to five years for an array of putative resistant responses including reduced number of needle spots, needle spot color, hypersensitive reaction in the needles, shedding of infected needles, presence or absence of stem infections, number of stem infections, latency of infection, severity of infection, bark reactions, and survival with stem infections. *P. albicaulis* has undergone the most extensive testing, with 650 families inoculated as of 2010. Seedling families of *P. albicaulis* have been tested under several inoculum densities and with different geographic sources of blister rust. Extensive work is also underway for *P. aristata* and *P. flexilis* and significant efforts have begun with *P. balfouriana*, *P. longaeva* and *P. strobiformis*. Initial results indicate that common resistance responses appear to be present in most species, that geographic variation in some types of resistance are present, and that some types of resistance may not be present in some species. Many more field selections are needed to build sufficient genetic diversity among resistant selections for each species within a breeding zone. A few field trials have been established for *P. albicaulis*, but additional trials for long-term verification of rust resistance from seedling screenings should be established to examine durability of rust resistance, correlated response with other adaptive traits, and response to climate change. Further examination of the many *P. monticola* field trials, some more than 30 years old, will help provide data on durability and stability of resistance in this species and give possible insights for examining the six high elevation white pine species. Regional programs can use resistance information to designate additional parent trees for seed collection, establish seed orchards to produce greater levels of rust resistance, and provide *ex situ* conservation of resistant individuals. The USDA Forest Service's Inland West program for *P. albicaulis* was the first to begin, but most regions are now active to varying extents. Based on results of seedling tests, the first resistant seedlings have been planted in several regions. Continued research on underlying resistance mechanisms and their inheritance, potential for greater virulence/aggressiveness in the pathogen, and molecular tools to facilitate more efficient resistant selections are needed. Recent discussions of high levels of infection in the native ranges of some Asian species in China and South Korea suggest that a more virulent/aggressive race of *C. ribicola* may be present, and that a second species may exist; if so, then added precautions are needed to prevent importation of these pathogenic variants or other species.

Introduction

The nine white pine species native to the United States or Canada are highly susceptible to white pine blister rust, caused by the invasive pathogen *Cronartium ribicola* J.C. Fisch. in Rabh. *C. ribicola* is currently present in the native ranges of eight of these white pine species, and it has already produced severe mortality and ecosystem disruption in some (Tomback and Achuff 2010). The focus in this paper is on continuing efforts to evaluate the genetic resistance of the six high elevation species present in the U.S. and Canada: *P. albicaulis* Engelm. (whitebark pine), *P. aristata* Engelm. (Rocky Mountain bristlecone pine), *P. balfouriana* Grev. & Balf. (foxtail pine), *P. flexilis* James (limber pine), *P. longaeva* D.K. Bailey (Great Basin bristlecone pine), and, *P. strobiformis* Engelm. (southwestern white pine). Eradication of *C. ribicola* is not feasible, and it is now a permanent resident of most of our white pine ecosystems. Genetic resistance to white pine blister rust will be a key to retaining or restoring populations of these species in areas that have been heavily impacted by the rust. Proactive measures to alleviate future impacts of rust will also require knowledge of the frequency of genetic resistance (Schoettle and Sniezko 2007).

Increasing concerns about the impact of the blister rust on natural populations of the high elevation white pine species has given impetus to make extensive seed collections for gene conservation (Sniezko and others, *Ex situ* gene conservation in high elevation white pine species in the United States—a beginning, this proceedings) and to undertake blister rust resistance testing of these species. The early work examining blister rust resistance with these white pine species used relatively few seedlots but indicated that some degree of genetic resistance was present in at least some of them (Delatour and Birot 1982; Hoff and others 1980; Stephan 1986). Additional

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work is needed to elucidate the frequency and types of resistance present in each species in order to provide land managers with options to utilize this resistance.

In this paper, we summarize efforts underway to evaluate genetic resistance to white pine blister rust for these six species and prospects for the future. For most of the six species, resistance screening trials have only recently begun, and many of the specific results await summary and publication in the next few years. Key questions include: What types of resistance, if any, are present? What is the frequency and geographic distribution of the various resistance mechanisms for each species? What is the mode of inheritance for these mechanisms? How is resistance screening done and what are its limitations? What is the capacity to screen more progenies of more parent trees? How do we utilize the resistance? Will the resistance be 'durable'? How will climate change affect resistance? How soon can we utilize resistance for restoration?

Past and Current Resistance Screening

The USDA Forest Service has over 65 years of experience in screening trees for resistance to blister rust, most of it involving *P. monticola* Douglas ex D. Don and *P. lambertiana* Douglas (McDonald and others 2004). A series of international trials involving inoculation of seedlings, proposed by Bingham and Gremmen (1971), and implemented in Idaho, France, Germany and Japan, provides most of the pre-2000 data on resistance for some of the high elevation white pines and racial variation in virulence in the pathogen (see Hoff and McDonald 1993; Stephan 1986 for summaries).

The USDA Forest Service is the principal organization investigating blister rust resistance in these six species. Screening facilities at three Forest Service locations (see below) are currently utilized among five groups examining genetic resistance to blister rust. Testing of the six high elevation species uses protocols similar to those in the long-standing Pacific Northwest and Interior West programs for *P. monticola* and *P. lambertiana*. Forest Service programs in the Interior West and the Pacific Northwest regions have begun screening the progenies of hundreds of parent trees of *P. albicaulis* for resistance; in addition, the Rocky Mountain Research Station has led the effort to collect seed and evaluate large numbers of seedlots of *P. aristata* and *P. flexilis* for resistance to blister rust (Table 1) (Schoettle and others, Preliminary overview of the first extensive rust resistance screening tests of *Pinus flexilis* and *Pinus aristata*, this proceedings). The Institute of Forest Genetics (IFG) at the Pacific Southwest Research Station is evaluating resistance in all six species (Vogler and others 2006), and the Southwestern Region (Region 3) has expanded the testing of *P. strobiformis* at Dorena Genetic Resource Center (DRGC; Table 1). Cooperators from several other organizations in the United States and Canada have provided some seedlots and/or funding to assist with efforts.

Table 1. Number of seedlots of six high elevation white pine species in white pine blister rust resistance testing (inoculated with rust as of fall 2010) by test location[a].

		# Individual Tree seedlots			**# Bulked seedlots**		
Species	**Test location**	**Long duration test[b]**	**Short duration test[c]**	**Total**	**Long duration test**	**Short duration test**	**Total**
P. albicaulis	CDA	200	0	200	3	0	3
	DGRC	380	0	380	1	0	1
	IFG	0	70	70	0	0	0
P. aristata	DGRC	189	0	189	11	11	11
	IFG	0	108	108	0	0	0
P. balfouriana	IFG	0	14	14	0	0	0
P. flexilis	DGRC	70	271	341	0	32	32
	IFG	0	33	33	0	2	0
P. longaeva	IFG	0	84	84	0	0	0
P. strobiformis	CDA	0	0	0	3	0	3
	DGRC	51	1	52	0	0	0
	IFG	0	76	76	0	0	0

[a] Number of unique lots within a test location; if a seedlot was tested for both short- and long-duration testing the seedlot was listed only in the long-duration test. Some seedlots have been tested across test facilities (see text for details). See paper for estimate of number of additional seedlots for inoculation in 2011 and 2012.

[b] Long-duration testing is focused on identifying multiple resistance mechanisms. In general the seedlings are 2 or more years old at the time of rust inoculation, the seedlings are planted outdoors and disease symptom development and mortality are followed for up to 5 years. The outdoor planting environment allows vigorous tree growth.

[c] Short-duration testing is focused on identifying complete resistance mechanisms including the HR needle reaction; some other resistance types may also be identified. Seedlings for these tests are in small containers which allow for limited seedling growth. Disease symptoms and mortality are generally followed for 2 years or more, depending on the facility and species.

Blister Rust Resistance Screening

Blister rust resistance screening, using artificial inoculation, for one or more of the six white pine species discussed here is currently underway at three regional locations: Coeur d'Alene Nursery (CDA) in Idaho and Dorena Genetic Resource Center in Oregon for *P. albicaulis*, *P. aristata*, *P. flexilis*, and *P. strobiformis*; and Institute of Forest Genetics (IFG) in California for all six species (Table 1). The CDA and DGRC programs use protocols that evolved from their long-existing operational resistance screening programs of *P. monticola* (western white pine) and *P. lambertiana* (sugar pine) in which seedlings are evaluated for 3 to 5 years after inoculation for a range of resistance types (Mahalovich 2010; Mahalovich submitted; McDonald and others 2004; Kegley and Sniezko 2004). For the high elevation white pine species, the IFG program had previously focused on short-term testing of young seedlings for one type of resistance, a hypersensitive response (HR) in the needles (Kinloch and Dupper 2002); however, IFG has recently expanded its protocols to evaluate other types of resistance in these species (Vogler and others 2006). A fourth rust resistance program in the western United States at Placerville, California, has focused on *P. lambertiana* (McDonald and others 2004), and more recently, *P. monticola.*

The basic procedure for screening parent trees for genetic resistance to white pine blister rust is to obtain wind-pollinated seed from field selections in natural stands, grow seedlings for one to three years, and then inoculate them with blister rust by suspending infected (with telial stage of *C. ribicola*) *Ribes* leaves over them under conditions of high humidity. Bulk seedlots from populations of trees are used on occasion to examine some broad trends in resistance among populations. After inoculation, resistance responses are observed for one to five years or longer to categorize these seedling families (and their parents) in a gradient from highly susceptible to varying degrees and types of resistance. Based on resistance screening results, frequencies of various resistance types and their geographic distribution can be discerned for each species. This information can then be used to designate parent trees from which to collect seed for restoration, to select trees to put into seed orchards for future seed production, or to perform repeat inoculations to verify resistance phenotypes and to begin to ascertain their inheritance and robustness.

Artificial inoculation of seedlings under controlled environmental conditions (figures 1 and 2) helps ensure uniform infection of seedlings of the various families in trials. Subsequent resistance rating of parent trees can be done in a relatively short time period (1 to 5 years or more after inoculation, depending on the type of information desired). Each facility fine tunes its operation to help ensure that 100 percent of the seedlings are exposed to sufficient density of rust spores to infect seedlings and minimize escapes. The use of known highly susceptible and resistant checklots is essential to establish the relative effectiveness of artificial inoculation. Susceptible checklots usually show 100 percent needle and stem infection. The source of rust inoculum used by each of the three facilities generally represents that found in the regional areas in which they are located, and may come from *Ribes* gardens and/or field collections of infected *Ribes* (the main alternate host for the blister rust fungus). Little information is available on any differences in pathogenicity of these rust sources on various white pine species. The 'Champion Mine' race (Kinloch and others 2004; McDonald and others 1984), which is more virulent (to HR resistance in *P. monticola*) and possibly more aggressive than some other races of blister rust in western North America, is one of the geographic sources of rust used in inoculation trials at DGRC (Sniezko and others 2007).

Details of artificial inoculation using infected *Ribes* leaves are summarized elsewhere (Kegley and Sniezko 2004, Mahalovich and others 2006, Sniezko and others 2007, Vogler and others 2006). Very high levels of seedling

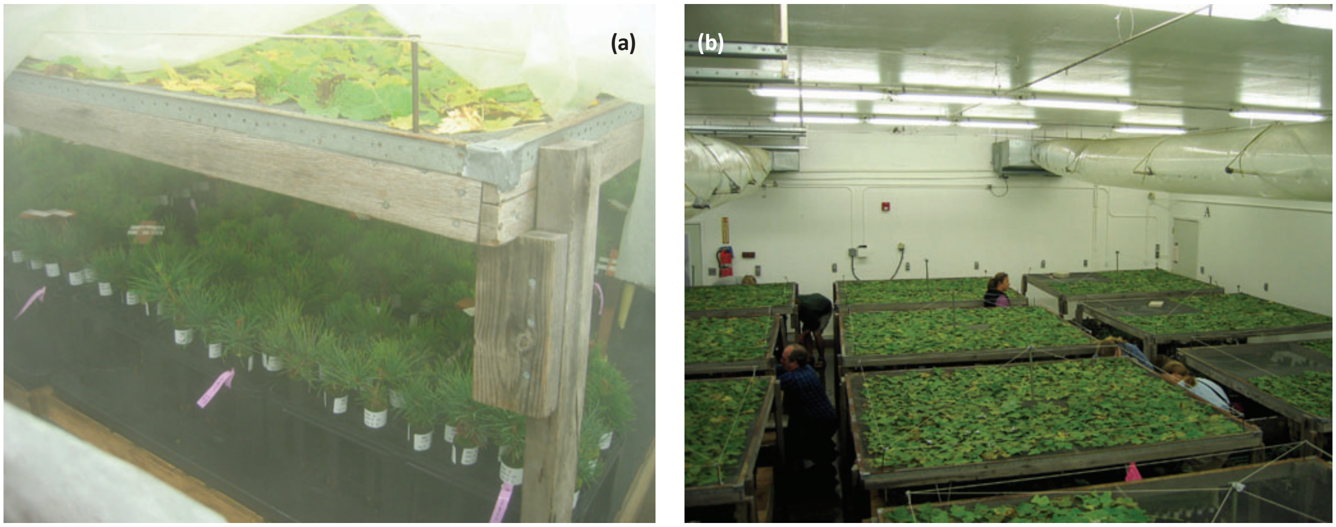

Figure 1. Blister rust inoculation setup at Dorena Genetic Resource Center: (a) *P. albicaulis* seedlings in 'fog' chamber for blister rust inoculation; (b) infected *Ribes* leaves over white pine seedlings in inoculation chamber.

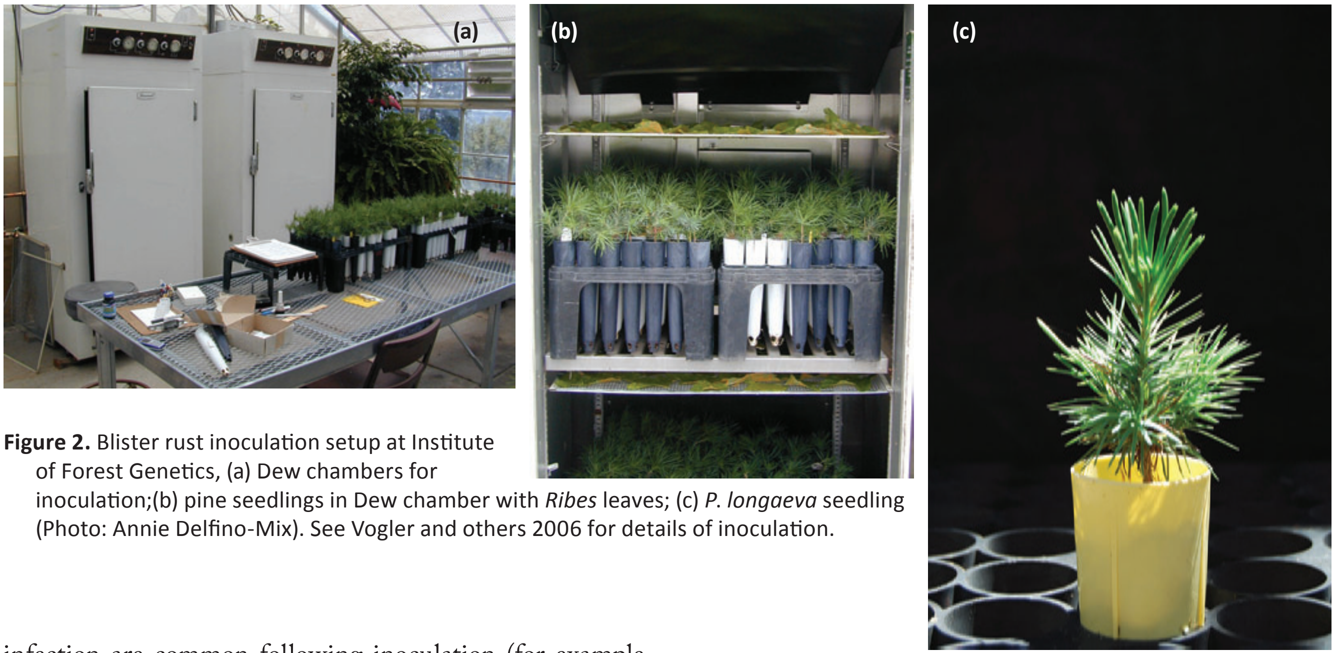

Figure 2. Blister rust inoculation setup at Institute of Forest Genetics, (a) Dew chambers for inoculation;(b) pine seedlings in Dew chamber with *Ribes* leaves; (c) *P. longaeva* seedling (Photo: Annie Delfino-Mix). See Vogler and others 2006 for details of inoculation.

infection are common following inoculation (for example, in trials at DGRC, >99 percent of seedlings of *P. albicaulis* and *P. flexilis* typically show needle infections). IFG strives for 100 percent "challenge", identifies "escapes", and removes them from the test-population (but they continue to be observed for latent infection or cryptic responses that may be signs of resistance). However, in some species, such as *P. monticola*, artificial inoculation under lower inoculum density can result in some families with less than 100 percent of seedlings with needle spots (Sniezko and Kegley, unpublished data). Families with only this type of resistance (a higher percentage of seedlings with no needle spots and no cankers after artificial inoculation) may be useful in the field under moderate rust hazards. However, field validation is needed to confirm that these "no-needle-spot" individuals or families are not escapes.

After inoculation, test seedlings are placed in a greenhouse (IFG and DGRC) or outside (CDA and DGRC) for assessments (figure 3). The greenhouse tests are usually short duration (1 to 2 years after inoculation), while the logistics

Figure 3. Field layout of seedlings following blister rust inoculation at (a) Dorena Genetic Resource Center; the seedlings of the five species shown here (*P. albicaulis*, *P. flexilis*, *P. lambertiana*, *P. monticola* and *P. strobiformis*) will be examined for five years post-inoculation for resistance responses; (b) Coeur d'Alene Nursery; Cycle 20 *P. monticola* and *P. albicaulis* trials (Photo: D. Foushee).

permit the outdoor tests to proceed for 3 to 5 years and longer. At various periods after artificial inoculation (at a minimum, once annually), individual seedlings are assessed for phenotypic responses. Needle lesions (or 'spots') are the first trait assessed, usually within 6 to 12 months following artificial inoculation (figure 4a). At IFG, the younger seedlings are scored for needle infection within 3 to 4 weeks or sooner, depending upon the onset and frequency of needle spots. At IFG or in the DGRC greenhouse tests, seedlings are examined early to classify spots as either susceptible or resistant hypersensitive reactions. However, in these tests, all seedlings are assessed for disease symptoms for 2 years post-inoculation to confirm and characterize associate traits for the complete resistance phenotype and gain insights into other possible resistance mechanisms. Depending on the trial and test facility, presence or absence of needle spots, number of needle spots, and color of needle spots may be noted.

Stem infections usually appear on some seedlings within 3 to 9 months and are abundant on many seedlings within 12 to 20 months (figures 4b, 4c). The timing of the appearance of needle spots and stem infections may vary by testing location or seedling, with later appearance on a seedling being a potential expression of resistance. Recently, two new traits for assessment have been added at DGRC: the number of stem infections and their overall severity. The number of stem infections on individual seedlings can vary from 0 to 50 or more. The severity code (0 to 9) denotes the extent of damage from all stem infections (cankers and bark reactions) on the seedling, from none (0) to very extensive (6, 7, 8) to dead from rust (9). This rating changes over time as the stem infection progresses or is inactivated. Timing of mortality following inoculation can vary by trial, by species and by seedling family (note: a family is defined as the seedling progeny of a seed tree (maternal parent) that has been wind-pollinated by several pollen parents). In some cases, the most significant mortality occurs two to four years after inoculation, and even earlier on the smaller, younger seedlings at IFG and in the DGRC greenhouse trials. Terminating a trial too early can lead to over-estimating the level of survival from the rust inoculation.

Data collected are used to compile family means and summaries in order to rate each parent tree for types and levels of resistance. These data provide baseline information on the degree of rust resistance in different populations and different families for each species. This information can be used to designate specific parent trees for further seed collection in restoration efforts, for scion collection and grafting of the top-ranking trees or progeny into orchards or clone banks, and to determine the contribution to that resistance of the known maternal parent. The data also provide information on the possible inheritance of the resistance types and their geographic distribution. Information on specific protocols and summaries to date from the first *P. albicaulis* trials at CDA and DGRC is available (Mahalovich submitted; Mahalovich and others 2006; Sniezko and others 2007, 2008).

The general goal of the National Forest System genetics programs is to maintain genetic variation and adaptability of populations of trees while increasing genetic resistance to a level higher than is present in current populations. For the Forest Service research groups (IFG and RMRS), more focus is on describing the resistance/tolerance mechanisms in white pines, and on uncovering their modes of inheritance. Resistance in trees needs to be long-lasting, that is, 'durable', to be of most utility in restoration. The resistant trees need to survive to sexual maturity and produce cones. At least some of the resistances (or combinations thereof) need to last over generations to help ensure continued ecological functioning of these white pines. The resistance screening effort is complicated, because it aims to uncover an array of resistance types available in each species. Some resistance types are known to be controlled by a single gene, while others are thought to be controlled by several to many genes (Kinloch 1982). Some resistance types may be 'complete' and prevent needle and/or stem infections, while 'incomplete' or partial resistance may mean fewer infections or slower growth of the pathogen in the host tissues. Frequencies of the various resistances are low in natural populations for at least some of these species (since the North America white pines did not co-evolve with the recently introduced blister rust fungus); therefore, testing many seedling families will be necessary to maintain genetic diversity and adaptability. Fortunately, the CDA and DGRC screening facilities have capacity to undertake the screening of large numbers of seedlings as funding becomes available.

Knowledge of the types of resistance mechanisms to blister rust infection and information about their inheritance in North American white pines has been studied mostly in other white pines such as *P. monticola* and *P. lambertiana* (Hoff 1986; Hoff and others 1980; Kegley and Sniezko 2004; Kinloch 1982; Kinloch and Davis 1996; Kinloch and others 2003; Sniezko and Kegley 2003a,b), but similar resistance phenotypes appear to be present in the six high elevation white pines (Hoff 1994; Hoff and others 1980; Kinloch and Dupper 2002; Mahalovich submitted; Mahalovich and others 2006; Sniezko and others 2007, 2008; Sniezko and Kegley, unpublished data). Following artificial inoculation, seedlings are evaluated for an array of resistant types including presence and number of needle spots, needle spot color, hypersensitive reaction in the needles, shedding of infected

Figure 4. Seedlings after inoculation at Dorena Genetic Resource Center: **(a)** 100's of needle lesions ('spots') on a *P. albicaulis* seedling nine months after inoculation; **(b)** within-family variation in cankering in 2 *P. flexilis* seedlings, 13 cankers on seedling on left, no cankers on seedling on right, 21 months after inoculation; **(c)** many incipient stem infections on a *P. albicaulis* seedling, 13 months post-inoculation; **(d)** putative 'needle shed' mechanism on a *P. albicaulis* seedling, nine months after inoculation, seedling had 50 needle spots at 1st assessment in 2009, but is still canker-free in winter 2010; **(e)** bark reaction on main stem of a *P. albicaulis* pine seedling, 23 months after inoculation; **(f)** large bark reaction or 'inactive' canker on *P. strobiformis* seedling, 7 years after inoculation.

→


(a)
(d)
(b)
(e)
(c)
(f)

needles (NS), presence or absence of stem infections, number of stem infections, latency of stem infection, severity of infection, bark reactions (BR), and survival with stem infections. The array of resistant types evaluated varies somewhat by facility (for example, CDA does not evaluate for HR at this point in time). Some of these resistance types, such as HR and NS (figure 4d), prevent the rust fungus from progressing to a stem infection (McDonald and Hoff 1970; Kinloch and others 2003), while others such as BR curtail or greatly slow the progress of the fungus in the stem (figures 4e and 4f) (Hoff 1986). Needle shed can occur over different time periods and can be complete (all needles with spots are shed), or partial (Sniezko and Kegley, unpublished data). Some trees with needle shed exhibit stem cankers. However, operationally, seedlings are rated as NS only if they drop all needles with spots and do not develop stem infections. More work is needed to confirm the underlying resistance mechanisms of canker-free seedlings (other than HR) and how much they are impacted by different environmental conditions and spore densities.

Because of extensive work in *P. lambertiana* and *P. monticola*, HR is the most well documented resistance mechanism in white pines (Kinloch and Dupper 2002; Kinloch and others 1999, 2003). Vogler and others (2006) provide a useful overview of HR in white pines. HR has also been found in *P. strobiformis* and *P. flexilis.* The inheritance of HR has been found to be conditioned by different single dominant genes in three of these species (Kinloch and Dupper 2002). Work on the inheritance in a fourth species, *P. flexilis*, is underway (Schoettle and others, Preliminary overview of the first extensive rust resistance screening tests of *Pinus flexilis* and *Pinus aristata*, this proceedings). HR is very effective initially, but in at least some cases, it may not be durable over the life of the tree if virulence arises in the rust population. Unfortunately, in *P. monticola* and *P. lambertiana*, virulent strains of the rust are now known to exist in some parts of the range of these species, limiting effectiveness of HR resistance (Kinloch and others 2004). Where possible, HR resistance should be used in conjunction with other resistances, as is being done for *P. monticola* in Oregon and British Columbia, and *P. lambertiana* resistance programs in California and Oregon.

Progeny of resistant parent trees will generally be a mixture of resistant and susceptible seedlings, and 100 percent survival from natural regeneration or restoration plantings is not expected in the presence of blister rust. The level of survival in progeny of resistant parents will depend upon an array of factors, including frequency of resistance genes, type(s) of resistance and their modes of inheritance, resistance of parent trees contributing pollen, site rust hazard, virulence/aggressiveness of the rust, the age and physiological condition of hosts at time of exposure to infection in the field, and the overall environmental conditions on the site. All of this should be taken into account in planning restoration efforts. Young seedlings exposed to high levels of rust will show the fastest and highest levels of mortality. Some outstanding parents may yield progeny that show 25 to 50 percent survival or higher following inoculation testing, but survival of plantings using seedling progeny of many parents will be reduced due to lower overall selection intensity (many resistant selections will be included, not only the very top ones). In general, extreme caution should be practiced in extrapolating the level of resistance in seedling tests to predicting field performance. Multiple tests of some seedlots are needed to confirm potential levels of resistance. Seed from seed orchards would be expected to yield the highest levels of survival, since all pollen contributions would be from presumably resistant parent trees, but large quantities of seed from orchards may not be available for a decade or more

Blister Rust Resistance

Species

Pinus albicaulis: The small, early artificial inoculation trials in Idaho and France indicated that genetic resistance to blister rust was present in *P. albicaulis* (Delatour and Birot 1982; Hoff and others 1980). A small trial in 1992 showed large differences among stands and among families in the percentage of trees canker-free (Hoff 1994; Hoff and others 2001). The resistance mechanisms observed included: 'needle shed' (NS), 'short-shoot' (SS) and 'bark reaction' (BR) (Hoff 1994; Hoff and others 1980, 2001). Two of these, NS and SS, prevent stem infection, while BR essentially walls off the rust fungus in the stem (Hoff 1986). Families from stands experiencing high prior rust mortality had a much higher percentage of moderate to high levels of canker-free seedlings than did families from stands with low or moderate levels of rust mortality, indicating that some natural selection for resistance had occurred (Hoff 1994). Recent work at CDA and DGRC, using hundreds of families of *P. albicaulis,* has confirmed the presence of resistance in whitebark pine (Mahalovich submitted; Mahalovich and others 2006; Sniezko and others 2007, 2009; Sniezko and Kegley, unpublished data).

Of the six high elevation species, whitebark pine has the most parent trees currently in rust resistance testing (table 1; figure 5a). Although larger-scale testing of whitebark pine began nearly a decade ago (Mahalovich and others 2006; Sniezko and others 2007), the number of seedlots in testing has greatly increased since 2007 (figure 5a). Most of the seedlots currently in testing are from Pacific Northwest and Interior West U.S. (table 1), but 15 families from Alberta are included in 2010 testing at CDA, and 5 families from British Columbia and three from California were included in the 2008 inoculation trials at DGRC (figure 5a). Testing of *P. albicaulis* families from California is now underway at IFG. There have been only a few common seedlots tested at more than one facility: two seedlots tested previously at CDA were inoculated in 2008 at DGRC (DGRC trial is still underway), one additional family tested at CDA was inoculated at DGRC in 2004, and one bulk seedlot from WY has also been tested at both facilities.

Seed from over 2,400 parent trees, covering much of the range of the species, are potentially available as of 2009

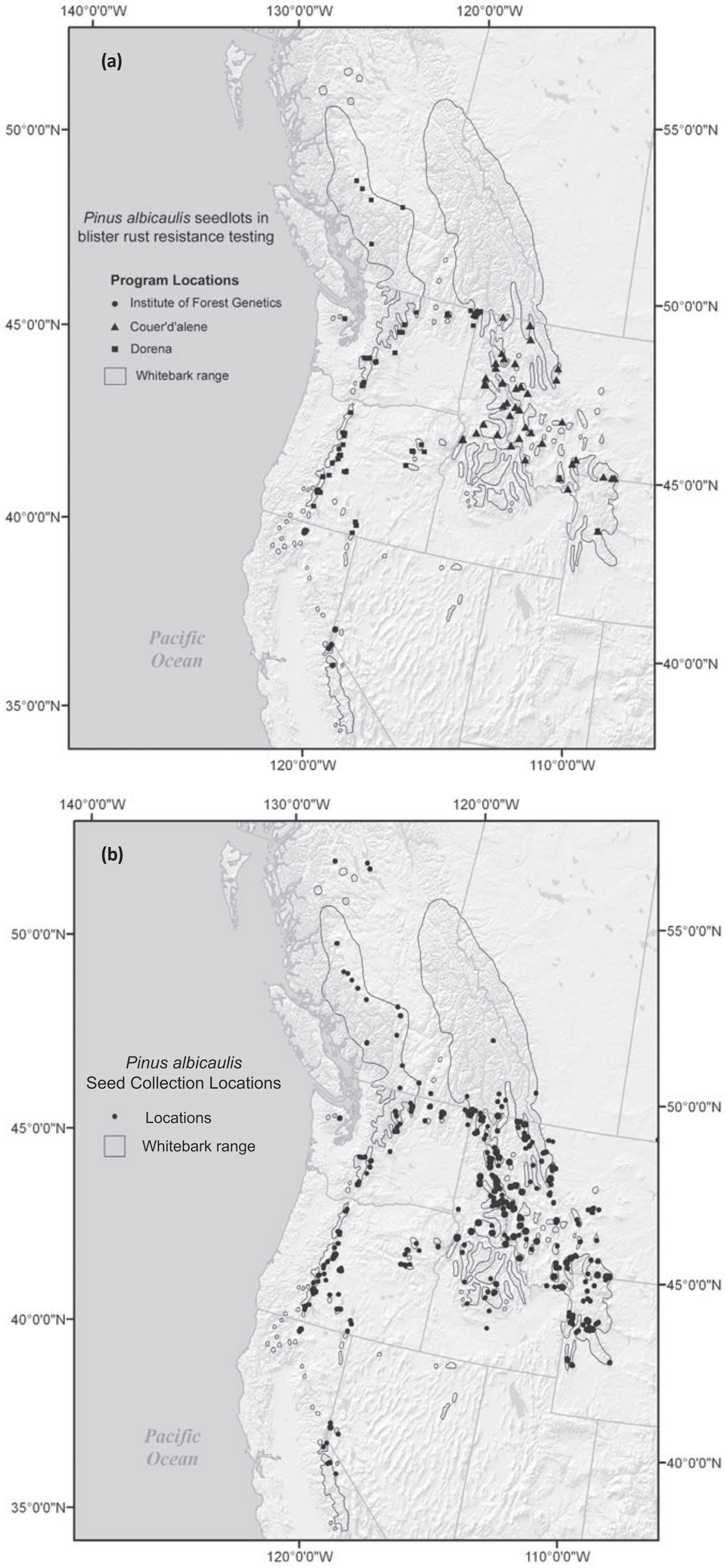

Figure 5. (a) Geographic distribution of parent trees of *P. albicaulis* families in blister rust testing (inoculated as of 2010); **(b)** Geographic sources of *P. albicaulis* with seed collected as of 2009 (*P. albicaulis* range from Little 1971).

for rust testing and gene conservation (figure 5b; Sniezko and others, *Ex situ* gene conservation in high elevation white pine species in the United States—a beginning, this proceedings), with additional collections underway in many areas. Through fall 2010, trials have been completed or started for 650 individual tree seed collections (table 1; figure 5a). Assessments of most of these trials are still underway. At DGRC, sowing of an additional 180 seedlots from throughout Oregon & Washington is planned for March 2011; inoculation will be in September 2012. CDA sowed 248 seedlots in 2010 for fall 2011 inoculation, and 195 seedlots in 2011 for fall 2012 inoculation. IFG sowed 70 families of California whitebark in 2007, and inoculated one set of all 70 families in September 2009 and a second set of the same families in December 2010. At IFG, replicate inoculations at different seedling ages are designed to compare host responses (for example, needle symptoms, stem reactions, pathogen establishment, and host mortality) to refine differentiation and characterization of prospective resistance mechanisms. Thirty-six families of whitebark from the Lake Tahoe region of California were sown for resistance testing in 2010, and another 100 families will be sown in 2011 for phenology assessments and for characterization for future inoculation tests.

Results from the first large-scale tests are encouraging, indicating that whitebark pine has several types of resistance and that there may be geographic trends in resistance (Mahalovich submitted; Mahalovich and others 2006; Sniezko and others 2007; Sniezko and Kegley, unpublished data). For many *P. albicaulis* families, over 90 percent of the seedlings develop stem infections, but some families in these trials and the earlier Hoff (1994) trial show much lower levels of stem infection (figures 6a, 6b, 6c; Sniezko and others 2007). Seed can now be collected from a limited number of confirmed rust-resistant parent trees for restoration, and the first re-collections have been made. Many additional seedlots need to be evaluated for each breeding zone to develop a list of parent trees that will supply rust resistance while maintaining the genetic diversity of the species. Three common families (Sources 78, 252 and 289) that ranked high in the CDA 110 seed source study (Mahalovich and others 2006) have also been tested at DGRC. At CDA, families #78 and #252 had 39 and 64 percent of seedlings with no stem infections (Mahalovich, unpublished data), while early results from the 2008 inoculation trials at DGRC showed 100 percent of the seedlings for both families had stem infections (and show >75 percent mortality two years after inoculation, additional mortality is expected). These two families ranked near the bottom for all geographic sources for rust resistance in the DGRC trial (Sniezko and Kegley, unpublished data). The third family, #289, in the CDA trial had 53 percent canker-free seedlings; in four 2004 inoculation trials at DGRC this family had 3.3 to 38.9 percent canker-free seedlings, depending upon inoculum density. Even with the higher stem infection levels at DGRC, this family showed good survival levels (30 to 68.5 percent versus the overall trial means at DGRC of 7.7 to 17.1 percent) four years after inoculation. These differences are intriguing and could be due to several factors, including higher effective inoculation levels at DGRC, differences in geographic sources of rust, or physiological differences in seedlings from the Interior West when grown in Oregon. Further investigations are needed.

No evidence of HR resistance has been found in the seedlots of *P. albicaulis* tested so far at IFG and DGRC (Kinloch and Dupper 2002; Sniezko and others 2008; Sniezko and Kegley, unpublished data; Vogler and others 2006). Results from the current screening of hundreds of additional families of whitebark pine will greatly increase our knowledge of the frequencies of resistance types in the Pacific Northwest and Interior West portions of this species' geographic range. More extensive inoculation trials are needed for western Canada and the Pacific Southwest portions of the whitebark pine range to develop a fuller understanding of resistance mechanisms and frequency of resistance in this species and to maximize its utility to land managers.

Pinus aristata: The earlier international trials indicated that *P. aristata* had a surprising level of resistance and probably the highest level of rust resistance of any North American white pine species (Delatour and Birot 1982; Hoff and others 1980; Stephan 1986, 2004). However, these early trials tested few seedlots, so additional work is needed and some is underway.

The Rocky Mountain Research Station (RMRS) has been the principal coordinator of recent seed collections and rust resistance testing of *P. aristata* (Schoettle and others, Preliminary overview of the first extensive rust resistance screening tests of *Pinus flexilis* and *Pinus aristata*, this proceedings; Sniezko and others, *Ex situ* gene conservation in high elevation white pine species in the United States—a beginning, this proceedings). RMRS currently has seedlots in resistance testing at both IFG and DGRC. In the first trials at both facilities, many of the individual parent seedlots are in common, with the 109 individual tree seedlots at IFG being a subset of the 189 in testing at DGRC.

Originally, the shorter term test at IFG was designed to find HR, a hypersensitive type response in needles, which in sugar pine, western white pine, and southwestern white pine is indicative of a simply-inherited genetic mechanism for resistance in needles. However, in the test at IFG no HR was found for *P. aristata*, and many of the seedlings are now being evaluated for other resistance responses (Vogler and others 2006). The subset of families in common between IFG and DGRC will provide a comparison of resistance among families under different nursery/greenhouse cultural regimes and using different geographic sources of rust.

In the initial *P. aristata* trial at DGRC a small number of *P. monticola* and *P. lambertiana* seedlings were included as controls with the 189 *P. aristata* families. Due to the suspected higher level of resistance in *P. aristata*, the inoculum density used for inoculation in this trial was four times that typically used for *P. monticola* at DGRC. This first set of trials at IFG and DGRC are nearly complete and the data analysis is underway. Initial examination of the data indicates large differences among families in resistance (Schoettle and others, Preliminary overview of the first extensive rust

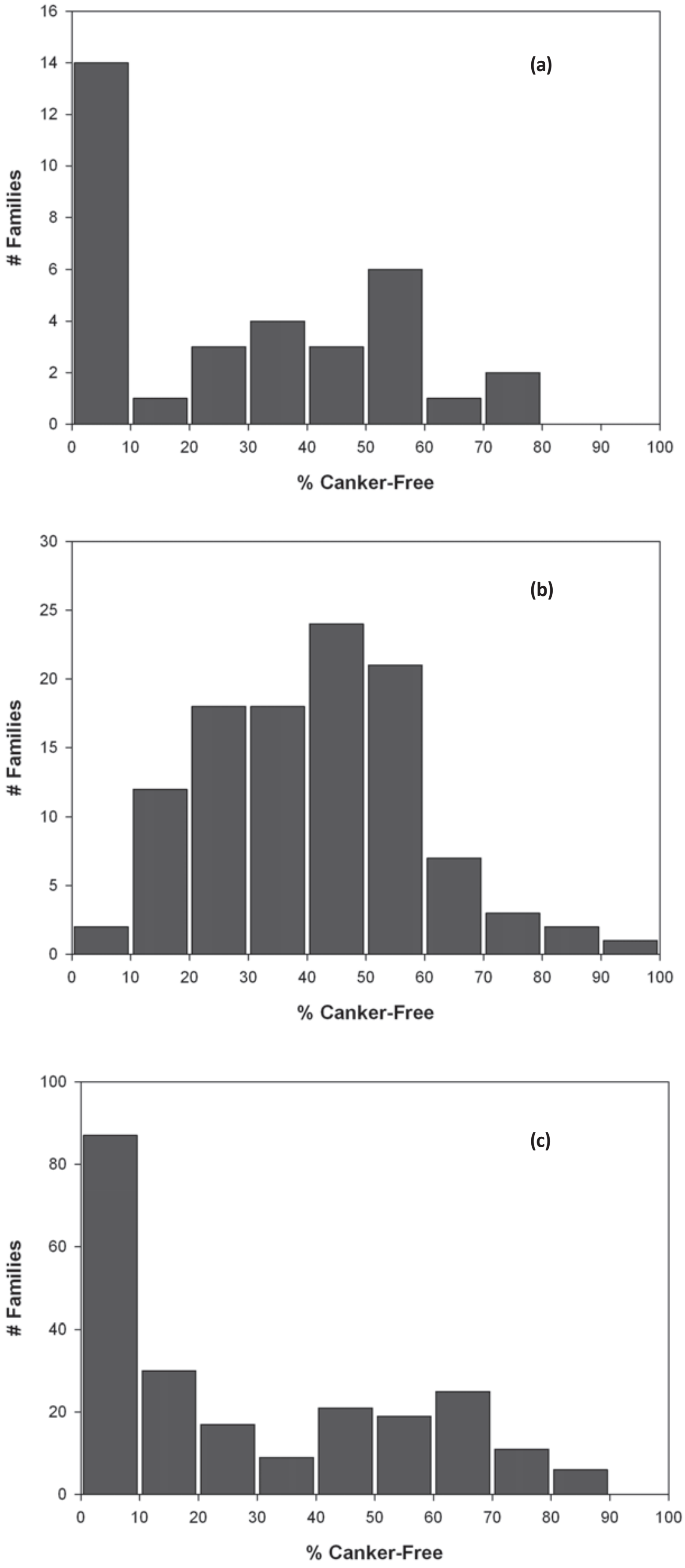

Figure 6. Histograms of family mean variation in percentage of canker-free seedlings for 3 trials **(a)** RMRS test of 34 Interior West families (adapted from Hoff 1994); **(b)** 108 families from Interior West 110 seed source trial at Coeur d'Alene Nursery (Mahalovich and others 2006); **(c)** early data (13 months after inoculation) for 225 families for Run 3 at Dorena Genetic Resource Center (inoculated in 2008 using AVCr2 source of rust). Note: histograms display family variation in separate trials at different facilities with generally different families and different inoculation levels (e.g., percent of seedlings with needle spots) which generally precludes direct comparisons across trials and regions. See paper for summary of three families in common between two of the testing facilities.

resistance screening tests of *Pinus flexilis* and *Pinus aristata*, this proceedings; Vogler and others 2006).

Additional testing of *P. aristata* at DGRC is underway and another 36 families will be sown in 2011. Overall, families from across the full geographic distribution of *P. aristata* are now in testing; however, more intensive and comprehensive testing throughout the range is still needed. More research on the association of resistance with other adaptive traits is also ongoing (Schoettle, unpublished data). Hundreds of additional seedlots collected throughout the range of *P. aristata* are available for testing, but funding is currently not available. Four lots from Rocky Mountain Region are being screened at CDA.

Pinus balfouriana: Previous tests in Idaho and Germany included very few seedlots; in these tests, *P. balfouriana* showed relatively little rust resistance (Hoff and others 1980; Stephan 1986, 2004) and no evidence of HR resistance was found in a test of six seedlots (Kinloch and Dupper 2002). IFG has recently begun testing of 14 seedlots of this species; results are pending. Many additional seedlots are potentially available for testing (Sniezko and others, *Ex situ* gene conservation in high elevation white pine species in the United States – a beginning, this proceedings).

Pinus flexilis: In the international trial series, a small number of seedlots of *P. flexilis* were tested for rust resistance in Idaho, France and Germany, and the level of resistance appeared to be relatively low, although at least one seedlot in the French trial showed a high level of resistance (Delatour and Birot 1982; Hoff and others 1980; Stephan 2004). In a separate test of five seedlots, a bulk seedlot of *P. flexilis* showed 19% incidence of HR phenotypes (Kinloch and Dupper 2002).

Beginning in 2006, RMRS began a series of resistance trials at DGRC, using seedlots from the Southern Rockies. In some of these trials, HR resistance, primarily, is being examined in individual seedling families, while in other trials families are being examined for additional resistance types over a more extended period of time. In another trial, 30 bulked seedlots are being evaluated for differences in the frequency of HR among populations. As of 2010, RMRS had 341 seedlots in testing at DGRC (table 1); additional lots will be sown in 2011. At IFG, 33 seedlots were sown in 2010; these are currently undergoing evaluation for symptom development and potential resistance mechanisms, including both HR and stem reactions.

P. flexilis has a very large geographic range, and seed collections have recently become available for some other portions of the range in the U.S. and Canada. However, no individual seedlots from Canada have been tested yet, but twelve families from Alberta sown in January 2011 will be inoculated fall 2012 at CDA. Four bulks lots from Utah will be inoculated in fall 2011 at CDA and 30 families from Montana will be inoculated in 2011 at DGRC.

Early results from the RMRS tests show that some families have moderate to high levels of resistance, but most trials are still ongoing and interpretation of the types of resistances is still underway (Schoettle, unpublished data). These trials should help delineate resistance types and their frequency in some portions of the species' range. Many additional seedlots are available for rust testing (Sniezko and others, *Ex situ* gene conservation in high elevation white pine species in the United States—a beginning, this proceedings). Collections are still needed, particularly for Arizona, Idaho, Utah, Nevada, New Mexico, Montana, and northern Wyoming.

Pinus longaeva: When the earlier testing of many of the North American species was done for the international trial, *P. aristata* and *P. longaeva* were both still considered as one species, *P. aristata*, so no separate summary of rust resistance is readily available (see section above for early results from *P. aristata* testing). In a more recent trial, two seedlots tested at IFG showed no evidence of the HR resistance (Kinloch and Dupper 2002). Twenty-three California families were inoculated at IFG in 2005. Early results (4 months post-inoculation) showed that 30 percent of the seedlings were canker-free (Vogler and others 2006); a summary of final assessments is underway. IFG has recently inoculated 16 additional seedlots, and results are pending. Seventy-five seedlots from three locations in west-central, east-central, and southern Nevada are currently in stratification at IFG for inoculation in 2 or 3 years, depending upon seedling development. Hundreds of additional seedlots are potentially available for testing (Sniezko and others, *Ex situ* gene conservation in high elevation white pine species in the United States – a beginning, this proceedings), but lack of funding may limit the amount of testing for the present.

Pinus strobiformis: Early work with a small number of seedlots indicated that genetic resistance to the blister rust fungus is present in *P. strobiformis* (Delatour and Birot 1982; Hoff and McDonald 1980; Hoff and others 1993; Stephan 2004), and one of the resistance types is due to a simply-inherited hypersensitive response (HR) in needles (Kinloch and Dupper 2002; Vogler and others 2006). Since 1996, progeny of many more parent trees (91) have been tested or are currently under evaluation for rust resistance, with 78 and 53 families being evaluated at IFG and DGRC, respectively. Data from the 49 of the 78 parents with IFG evaluations for the HR resistance, finalized as of 2007, indicate 6 of these parents are heterozygotes for *Cr3*, the putative single dominant gene conditioning the hypersensitive response in the needles (HR) of this species. The six confirmed *Cr3* heterozygotes are from the Bradford Canyon area on the Lincoln National Forest in New Mexico, an area with a high incidence (>80%) of rust infection. These six selections were all from canker-free parent trees, and the parent trees have remained canker-free through the last field assessment in 2008. Unlike the *Cr1* and *Cr2* genes for HR in *P. lambertiana* and *P. monticola*, no strain of the rust virulent to *Cr3* in *P. strobiformis* has been documented to date. A number of the other seedlots from the other 43 parents from the Bradford Canyon area showed a low frequency of HR in the IFG testing, indicating that they were likely pollen receptors for this resistance.

Testing of progeny of 10 of the Bradford Canyon parents has been completed at DGRC (a subset of the same seedlots tested at IFG for HR). DGRC results confirmed two *Cr3* heterozygotes. In another test that included 7 of the

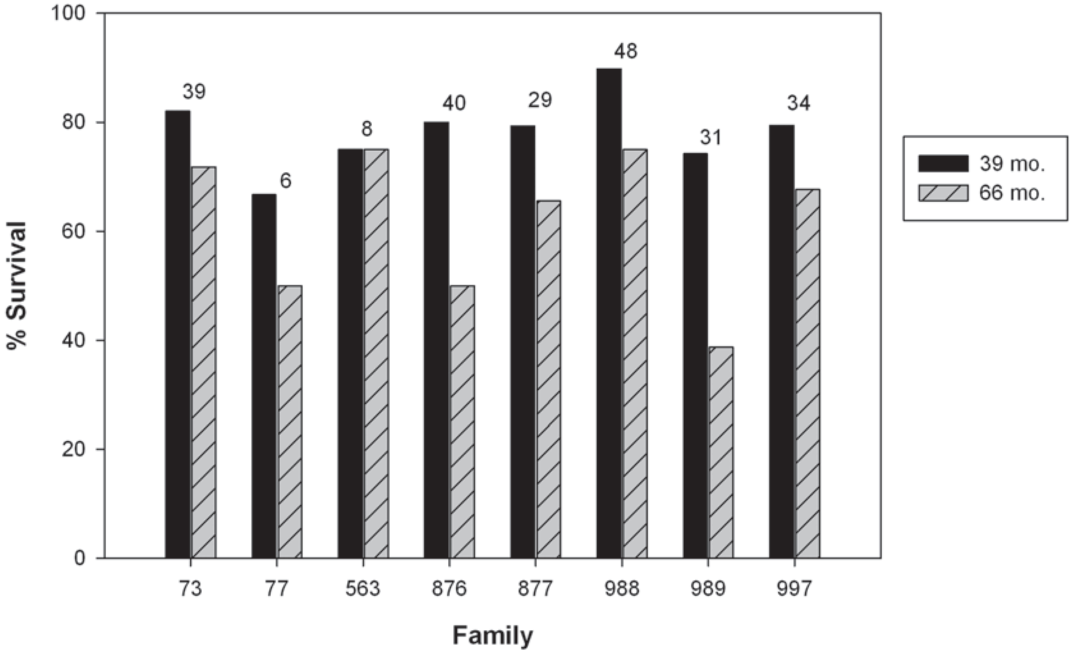

Figure 7. Percent survival at 39 and 66 months after inoculation in 8 *P. strobiformis* families inoculated at Dorena Genetic Resource Center (see Sniezko and others 2008 for trial background). Number of trees in family is noted above each bar.

non-HR parents, progeny of those 7 parents demonstrated other types of resistance, including bark reaction and very high survival (figure 7) (Sniezko and others 2008). Similar observations were made in Fall 2006 on the same families of *P. strobiformis*, inoculated at IFG in Fall 2005 (Delfino-Mix and Vogler, unpublished). For the DGRC trial at both 39 and 66 months after inoculation, all 8 of these families showed much higher survival than *P. lambertiana* and *P. monticola* controls included in the trial (Sniezko and others 2008; Sniezko and Kegley, unpublished data). The increase in mortality from 39 months to 66 months after inoculation in some families emphasizes the potential need to follow seedling trials over more than a few years. All 10 of these trees are from canker-free parent trees in a heavily cankered stand, and all were still canker-free in 2008. The relatively high level of resistance in the 7 families that are not from HR parents is encouraging. It is notable that, for this species, both HR resistance and other strong resistances are documented among progeny of parents from the same stand, and thus it is likely that some seedlings will have HR plus other types of resistance, effectively pyramiding the resistances. This may be the first documentation of this combination of resistances in a stand for any white pine species. The large bark reaction type response in some of the *P. strobiformis* families (figure 4f) appears similar to that in a *P. peuce* seedlot tested at DGRC (R. Sniezko, personal observation in rust resistant screening trials at DGRC, May 2010). This is also one of the first reports in a white pine species of non-HR type resistance in common seedlots from two screening facilities using different protocols and different geographic sources of the rust. Further discussion of the specific results at DGRC and IFG of these common seedlots (and additonal ones now in testing) is planned.

Forty-three additional seedlots, encompassing three National Forests in New Mexico, were inoculated at DGRC in September 2010 and will be evaluated for a range of resistant types. Some of these have been previously tested at IFG and been confirmed as non-*Cr3* parents (non-HR). Progenies of 30 parent trees, including some also in testing at DGRC, are still in rust testing at IFG. The subset of seedlots represented at both DGRC and IFG will help facilitate some comparisons of resistance under different nursery/greenhouse conditions and geographic sources of rust. One lot from the Coronado NF (AZ) and one from the Lincoln NF (NM) were inoculated in fall 2009 at CDA; percent needle spotting for both lots (58.2) was below the F_2 rust-resistant *P. monticola* orchard lot (67.4). A bulk seedlot from the Nebraska Forest Service was sown at CDA in January 2011 and will be inoculated in fall 2012.

Rust Resistance Under Field Conditions

Short-term seedling tests for rust resistance are useful if they are representative of results that occur in the field. It is possible that the high spore densities used in inoculation trials on young seedlings may make it more difficult to discern some types of partial resistance that may be more effective on many field sites, where exposures to lower spore densities are prevalent. Trees in the field will often be exposed to multiple infection events over a longer time period, compared with the usually one-time inoculation of seedlings in nursery or greenhouse trials. Field trials of the six species of focus here are lacking or only recently established. For *P. albicaulis*, the first long-term field trial was established in 2006 at Lone Mountain in northern Idaho (using survivors from the 110-seed source study); data 10-years from seed are being evaluated for stability of rust resistance along with key climatic variables. Field trials of *P. albicaulis* using families with a range of rust resistance have recently been established at Crater Lake and Mount Rainier National Parks and on the Deschutes NF, and these seedling families will be monitored for seedling survival and rust resistance. The inclusion of families that are highly susceptible to blister rust, as controls, will provide an important monitor to gauge the first exposure and extent of rust challenge under field conditions. Additional trials with whitebark pine are planned in the Pacific Northwest. Some small plantings of *P. albicaulis* and other white pine species have been planted in northern CA and southern OR. Six long-term field trials of *P. albicaulis* will be established in Idaho and Montana following completion of the artificial inoculation trials at CDA. At least a subset of the trials needs to be followed for decades to examine what types of resistance are durable.

Until more data on field rust resistance in these six species are available, some insights can be drawn from much older and more extensive trials involving *P. monticola* and *P. lambertiana* that were established by regional resistance programs in the U.S. and Canada. The general results from the oldest trials are encouraging regarding durability of resistance (Kinloch and others 2008; Lupo 2004; Sniezko and others 2004b), but more information is needed such as the types of resistance that are effective and the level of survival to expect on higher hazard sites. For *P. monticola*, a large number of field trials have been established in the Pacific Northwest since 1996 specifically to examine family variation in field resistance. Early results are encouraging (Kolpak and others 2008; Sniezko and others 2000, 2004a, 2010), but more time is needed to follow the impacts of exposure to rust in the field on specific families and resistance types. One series of trials, replicated at six sites in Washington, includes *P. monticola* resistant seedlots from the three regional resistance programs based in Idaho, Oregon and British Columbia. In the future, these *P. monticola* trials should provide much more information on the effectiveness and durability of different resistances as well as the correspondence between short-term seedling tests and field performance for rust resistance. Although the data on *P. monticola* will be useful in making initial inferences about stability and durability of resistance in this species, data are also needed for the six high elevation species discussed here.

A second method that may be useful to examine durability of resistance is to monitor parent trees in the field. In areas where rust is present and susceptible parents succumb, what happens over time to the trees designated as resistant based upon their progeny in the seedling screening trials? The good news is that in some areas, such as Mount Rainier National Park, the surviving trees have endured the onslaught of the blister rust pathogen for decades. Early results from progeny of the first trees tested from parents from this location rated very high for resistance (Sniezko and Kegley, unpublished data). Continued monitoring of these trees for resistance is warranted and would provide much needed data on its durability.

Operational Programs—Utilizing Resistance

Some resistant parent trees have been identified from rust screening trials using their progeny over the last decade. With the levels of resistance found to date in *P. albicaulis*, *P. flexilis* and *P. strobiformis*, immediate utilization of resistance can be made by collecting seed from resistant parent trees and using it for reforestation or restoration, especially in areas where blister rust is a damaging agent. To minimize the chance of losing the high-resistant parent trees to other causes (fire, bark beetles, climate change, etc.) scion collection, grafting, and archiving of grafts in clone banks or orchards is of paramount importance (DeSpain, personal communication). These grafts should be preserved in areas that are likely to ensure their long-term survival. Some grafting has been done in both the Interior West and Pacific Northwest programs. Guiding documents for management of these species in several regions are now available and managers can now utilize rust resistance in some of the species (Aubry and others 2008; Burns and others 2008; Conklin and others 2009; Mahalovich submitted; Mahalovich and Hipkins, this proceedings; Mahalovich and Dickerson 2004; Mahalovich and others 2006). These documents can be updated as new data necessitate. Substantial additional rust screening is needed to increase the number of resistant parents available in all seed zones and to help provide greater genetic diversity in the resistant seedlots.

One example of an active program is in the Interior West for *P. albicaulis* (Mahalovich and Dickerson 2004). This program has targeted 650 selections, 100 in each breeding zone within ID, MT, and WY, and 50 for Nevada. This goal has already been exceeded with 983 selections made to date. Three short-term rust resistance screening tests have been started, and two additional tests are scheduled. The first restoration plantings began in 1996. Approximately 1,989 acres of rust-resistant seedlings have been planted to-date (1996-2010) in Idaho, Montana and Wyoming (Mahalovich, personal communication). One field test has been established (in 2006), and seven more are planned. Two seed orchards (each with 30 parents) have been established, and two additional orchards will be planted in fall 2011 (figure 8).

Pathogen Evolution and Durability of Blister Rust Resistance

The rust pathogen is genetically variable and has shown the capacity to evolve more virulent strains, at least to HR type resistance (Kinloch and others 2004). Less is known for most pathogens, including *C. ribicola*, about the evolution of aggressiveness, the quantitative component of pathogenicity (Pariaud and others 2009). Long-term success in restoring areas with moderate and higher rust hazards will likely depend upon developing populations of white pines with several types of resistance. In addition, silvicultural tools

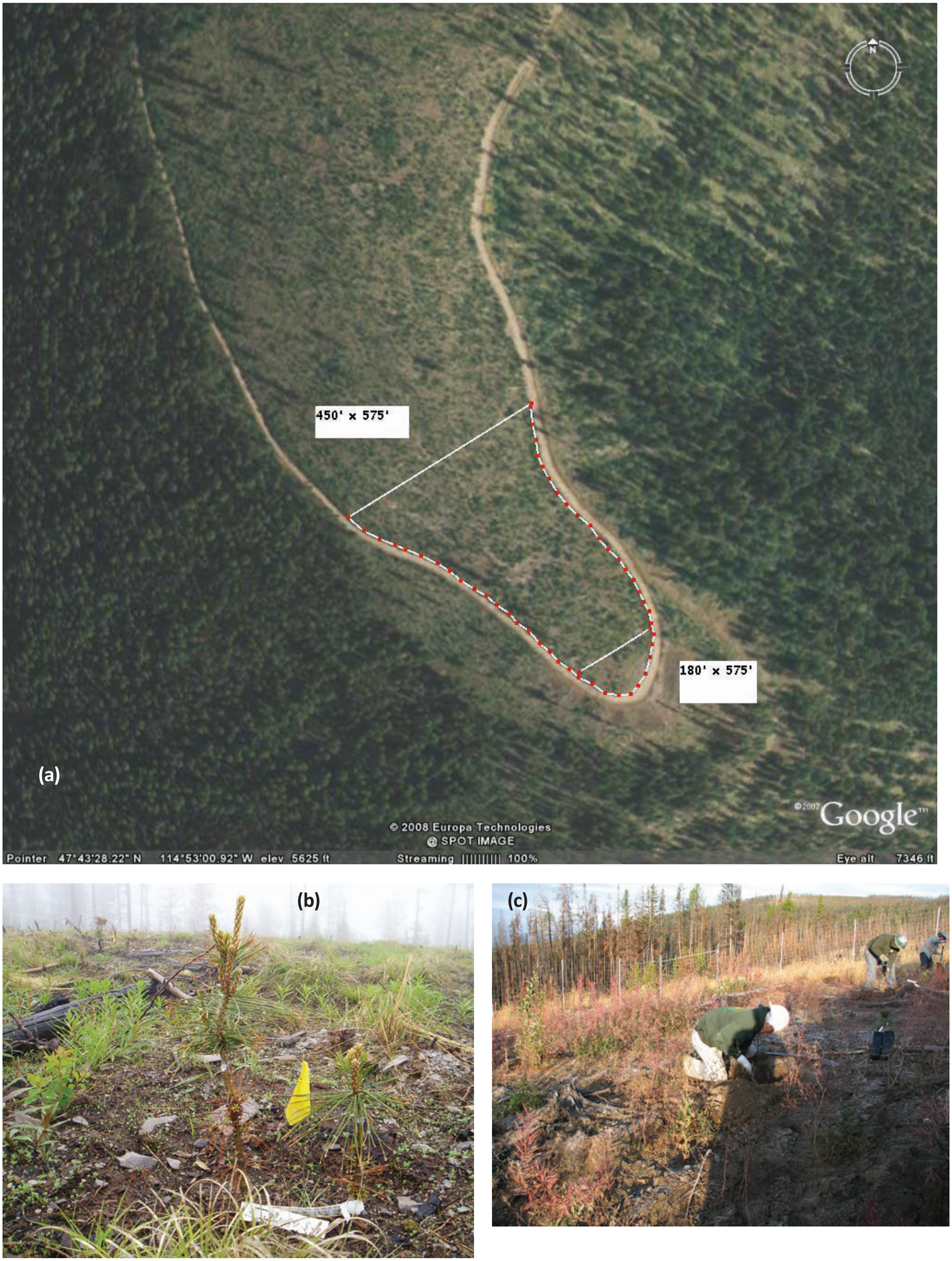

Figure 8. *P. albicaulis* orchard planted on Lolo National Forest, Montana, at 5650ft (1722 m): **(a)** aerial view of orchard; **(b)** close-up view of grafted tree; **(c)** planting grafts. First grafts planted Oct 2009. Grafted from parent trees in March 2008.

such as pruning, and measures to reduce rust hazard, such as *Ribes* removal, may aid the efforts in some areas. Avoidance of sites with extreme rust hazards may be necessary, except for small field tests to determine the effectiveness of genetic resistance under those conditions.

In resistance screening to evaluate host parents for restoration, heterogeneous mixtures of rust genotypes from *Ribes* plants in one or more geographic areas of a region are used to inoculate the seedlings in the trials. Even in the paired trials at DGRC with different geographic sources of the rust, including the 'Champion Mine' strain, it is encouraging to see some seedling families of *P. albicaulis* and *P. flexilis* consistently showing resistance (Sniezko and others 2007; Sniezko, unpublished data; Schoettle, unpublished data). The testing of common seedlots of *P. aristata* and *P. strobiformis* underway at DGRC and IFG will provide information on the effectiveness of resistance in this species to different sources of rust and host condition.

Fortunately, the white pine species of the United States and Canada appear to have one or more types of resistance to white pine blister rust. In some species such as *P. strobiformis*, there appears to be both HR resistance as well as other types of resistance. In other species such as *P. albicaulis*, no HR resistance has been found to date. From experience with the *P. monticola* and *P. lambertiana* programs, HR resistance, conditioned by a single major gene, is assumed to be the least durable, but even this will depend on the dynamics of the pathosystem (Kinloch and others 2004). Although there have been reports of some geographic sources of rust in the western United States being somewhat more virulent or aggressive than others on pines with non-HR types of resistance (Hoff and McDonald 1993; McDonald and others 1984), multiple tests at DGRC with *P. monticola, P. albicaulis* and *P. flexilis* (Schoettle unpublished data; Sniezko and others 2007; Sniezko and Kegley, unpublished data) have indicated that families resistant to one source of the rust are generally resistant to other sources of the rust, including the 'Champion Mine' source reported on by McDonald and others (1984). However, more work is needed on this topic.

In several previous seedling screening trials, the Eurasian species of white pines have generally shown higher levels of resistance than their North American relatives (Delatour and Birot 1982; Hoff and others 1980; Hoff and McDonald 1993; Sniezko and others 2008; Stephan 2004). This higher level of resistance to blister rust may be due to co-evolution of these pines and the rust. However, recent reviews of the status of some white pine species in China and South Korea indicate that rust levels in plantations of *P. koraiensis* Siebold & Zucc. and *P. armandii Franch.* can reach relatively high levels (La 2009; Zhang and others 2010). The reasons for the higher level of infections in these pathosystems are unknown. It may be due to increased rust hazard from major changes in forest management and/or evolution of a more virulent race or aggressive genotypes of the rust pathogen. In the case of *P. armandii*, it may also be due to the presence of a second species of white pine blister rust (Zhang and others 2010). In general, the impact of different Eurasian races or putative species of blister rust on resistant white pine genotypes of North American species is unknown. Further examination of the rust-pine pathosystem in Asia could be helpful in understanding possible future outcomes in our own forests.

The virulence of *vcr1* and *vcr2* genotypes of *C. ribicola* to HR resistance in *P. lambertiana* and *P. monticola*, respectively, is well documented (Kinloch and others 2004). Some evidence for additional racial variation and increased pathogenicity in the blister rust pathogen comes from an international trial series. In France, Germany and Japan, some resistant seedlots of *P. monticola* and *P. lambertiana* from the U.S. programs showed a much higher percentage of seedlings with cankering than in the Idaho trial (Hoff and McDonald 1993; Stephan 1986). Bulked seedlots of the high elevation white pines from the United States generally showed low to moderate levels of resistance in these trials. In the trial in Japan with resistant seedlots of *P. monticola* (from the Idaho program), little or no resistance was found in this species, while the Asian and European white pines showed high resistance (Yokota 1983). In general, the Eurasian species of pines in these trials displayed much higher levels of resistance (lower percentage of cankering) at all trial locations. In the German trial, a few F_1 and F_2 seedlots of *P. monticola* showed some resistance three years after inoculation, but much less after six years (Stephan 1986). These trials suggest evidence of virulence or increased aggressiveness of the rust in Europe and Asia to at least some sources of resistance in U.S. species, but further investigations are needed to confirm possible differences in the pathogen in Europe, Asia and North America. Hoff and McDonald (1993) suggested the need for strong quarantines on hosts of blister rust to prevent importation of spores from outside North America.

Impacts of Climate Change

Changing climatic conditions may potentially alter dynamics of the blister rust-white pine pathosystem by influencing the geographic occurrence and intensity as well as the annual timing and duration of spread of the rust fungus. Differential changes in aggressiveness with different temperatures have been noted in various pathogens (Pariaud and others 2009). The spread of the rust to new locations may impact additional forest ecosystems where susceptible trees are present, but the spread of current local genotypes of rust is less likely to impact resistant trees. A significant increase in spore density in an area could conceivably impact some types of resistance, leading to higher frequency of stem infections, more cankers per tree, or mortality. However, the levels of rust spores used in the seedling resistance screening trials probably represent a high to extremely high level, and trees found to be resistant in these tests would likely be resistant in the field.

The timing and duration of rust infection events in the field could also be affected by changing climate, and trees (as well as their alternate hosts, such as *Ribes* spp.) could be infected at earlier or later times in the season than currently occurs. The physiology of the trees would be different during these different months, and conceivably some resistances might become less or more effective during different stages of a tree's seasonal growth or under different temperatures. Current rust resistance screening occurs at locations with generally much milder temperatures than the natural habitat of these six high elevation species, so the trees selected as resistant in these tests should have a good chance of being resistant under the relatively more modest climatic changes expected to occur in their natural habitat.

Monitoring genetically-identified parent trees in the field for changes in resistance will help confirm changes in resistance due to changing climate or evolution of increased virulence of the rust. Changes in resistance over time in the field trials will also serve a similar function.

Movement of seed sources to different environments may influence the efficacy of resistance. The most notable example is the apparent reduced rust resistance of *P. monticola* from interior sites in Idaho planted in low elevation coastal British Columbia sites (Hunt 2004). This may indicate that moving seedlings from 'harsher' to 'milder' climates may change the efficacy of response. If so, seedling testing in a milder climate may be advantageous. Two *P. albicaulis* seedlots (from ID and MT) from the 110 seed source study showed moderately high resistance in that test at CDA, but are highly susceptible in a test at DGRC. More work is needed to examine the stability of resistance in various seed sources over a range of environments.

The presumed impact of change in environmental conditions may be seen in some inoculation trials. Among other things, the year to year fluctuation in climate may alter the physiological state of the seedling pre- or post-inoculation as well as the activity of the rust fungus post-inoculation. This may be responsible for some substantial variation observed in whitebark pine trials inoculated in different years. In inoculation trials of whitebark pine at DGRC using similar spore densities, 99.9 percent of the seedlings have needle spots; yet, the number of needle spots per seedling averaged 14.9 & 18.9 in two trials inoculated in 2004, 6.3 for the trial inoculated in 2005, and 71.3 and 126.4 in the two trials inoculated in 2008. This represents more than a ten-fold difference of needle spots among the trials. Even with this large difference in the quantity of needle spots, the preliminary results indicate that resistant families tested are consistent across trials, but ongoing study will reveal if this consistency holds for different types of resistance and whether overall survival is affected. A few families are common in these trials, so these will be examined for differences in subsequent levels of resistance.

Summary and Information Needs

For all of these high-elevation species, we are in the relatively early stages of examining rust resistance. A compilation of screening results over the next five years should provide significant increases in knowledge about the level and geographic pattern of rust resistance in several of these white pine species. This information will be of immediate use to land managers wishing to restore populations in the face of blister rust.

The procedures to screen for rust resistance are relatively well established, and if funding permits, thousands of additional seedlots could easily be evaluated over the next decade. Current rust resistance screening technology could be easily extended to evaluating *P. ayacahuite* Ehrenb. ex. Schltdl. and *P. chiapensis* (Martinez) Andresen from Mexico.

With only a few exceptions, no common set of seedlots have been tested among all the programs. To enable comparisions over different resistance screening programs and different test years, a set of checklots for each species would be very helpful. These checklots should span the range from highly susceptible to highly resistant, and should have large amounts of seed available. A common trial among screening facilities would allow for comparisons of results under different screening conditions and geographic sources of rust and would aid in the development of common terminology. Such a trial was proposed by all groups more than a decade ago (at a 'Rustbusters' meeting) for *P. monticola*, but did not occur due to some personnel changing careers or retiring.

Basic research is still needed to complement the more applied development of resistant populations. Relatively little is known about the impressive resistance of the Eurasian white pine species and how it may differ from that of North American species. In general, these species showed good to excellent resistance in the international trial series, while the North American species showed dramatically less resistance. The high level of resistance in these pines to races of rust present in Idaho, Oregon, France, Germany and Japan is intriguing and worth further study. What resistance mechanisms are involved and how many genes? Understanding more about the underlying nature of the resistances in these species would give us more clues on our path to augmenting resistance in North American species. Also needing study is the reported breakdown in resistance in some Asian species in China and South Korea. Was this due to an increase in virulence or aggressiveness, an increase in rust hazard, changing climate, or other factors?

More information on variability in virulence and aggressiveness in blister rust races from throughout the world would also be of interest. Now that we have identified resistance in most of the white pine species, these resistant seedlots could be tested against races of rust from the eastern U.S., Europe, and Asia. More locally, a greater understanding of the differences in virulence and aggressiveness of the geographic sources of rust currently in western North America would be useful.

A greater understanding of resistance mechanisms, their underlying inheritance, and their efficacy under different environmental conditions would also be useful. Most of the work with blister rust resistance has been conducted using bulk collections of blister rust. Although this may serve the operational programs, research using single spore isolates of the rust fungus might help increase our understanding of resistance, as would testing of more uniform seedling materials (selfs and full-sib crosses). Also needed is more information on the association of resistance traits with other adaptive traits. The development of molecular markers for resistance could potentially expedite many aspects of the screening and research resistance programs.

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References

Aubry, C.; Goheen, D.; Shoal, R.; Ohlson, T.; Lorenz, T.; Bower, A.; Mehmel, C.; Sniezko, R. 2008. Whitebark pine restoration strategy for the Pacific Northwest Region 2009-2013. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Region. 212 p.

Bingham, R. T.; Gremmen, J. 1971. A proposed international program for testing white pine blister rust resistance. European Journal of Forest Pathology. 1: 93-100.

Burns, K. S.; Schoettle, A. W.; Jacobi, W. R.; Mahalovich, M. F. 2008. Options for the management of white pine blister rust in the Rocky Mountain Region. Gen. Tech. Rep. RMRS-GTR-206. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station. 26 p.

Conklin, D. A.; Fairweather, M. L.; Ryerson, D. E.; Geils, B. W.; Vogler, D. R. 2009. White pines, blister rust, and management in the Southwest. R3-FH-09-01. [Place of publication unknown]: USDA Forest Service, Southwestern Region. 16 p.

Delfino-Mix, A.; Vogler, D. R. 2010. White pine blister rust research at the Institute of Forest Genetics after major-gene resistance. Unpublished electronic presentation dated November 16, 2010, on file at: U.S. Department of Agriculture, Forest Service, Pacific Southwest Research Station, Institute of Forest Genetics, Placerville, CA. 23 p.

Delatour, C.; Birot, Y. 1982. The international IUFRO experiment on resistance of white pines to blister rust (*Cronartium ribicola*): the French trial. In: Heybroek, H. M.; Stephan, B. R.; Von Weissenberg, K., eds. Resistance to diseases and pests in forest trees: 3rd International Workshop on Genetics of Host–Parasite Interactions in Forestry; 1980 September 14-21; Wageningen, the Netherlands. Wageningen, the Netherlands: Centre for Agricultural Publishing and Documentation: 412-414.

DeSpain, Tom. 2011. [Email to Richard Sniezko]. January 31, 2011. U.S. Department of Agriculture, Forest Service, Dorena Genetic Resource Center, Cottage Grove, OR.

Hoff, R.; Bingham, R. T.; McDonald, G. I. 1980. Relative blister rust resistance of white pines. European Journal of Forest Pathology. 10: 307-316.

Hoff, R. J. 1986. Inheritance of the bark reaction resistance mechanism in *Pinus monticola* infected by *Cronartium ribicola*. Research Note INT-361. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station. 8 p.

Hoff, R. J. 1994. Artificial rust inoculation of whitebark pine seedlings—rust resistance across several populations. Nutcracker Notes. [Online]. Issue 4. Available: http://www.whitebarkfound.org/Nutcracker-Notes/number4.htm [10 January 2011].

Hoff, R. J.; Ferguson, D. E.; McDonald, G. I.; Keane, R. E. 2001. Strategies for managing whitebark pine in the presence of white pine blister rust. In: Tomback, D. F.; Arno, S. F.; Keane, R. E., eds. Whitebark pine communities: ecology and restoration. Washington, DC: Island Press: 346-366.

Hoff, R. J.; McDonald, G. I. 1993. Variation of virulence of white pine blister rust. European Journal of Forest Pathology. 23: 103-109.

Hunt, R. S. 2004. Environmental and inoculum-source effects on resistance of Idaho F_2 western white pine in British Columbia. Canadian Journal of Plant Pathology. 26: 351-357.

Kegley, A. J.; Sniezko, R. A. 2004. Variation in blister rust resistance among 226 *Pinus monticola* and 217 *P. lambertiana* seedling families in the Pacific Northwest. In: Sniezko, R. A.; Samman, S.; Schlarbaum, S. E.; Kriebel, H. B., eds. Breeding and genetic resources of five-needle pines: Genetics, breeding, and adaptability, Proceedings of the IUFRO 2.02.15 Working Party Conference; 2001 July 23-27; Medford, OR. Proceedings RMRS-P-32. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station: 209-225.

Kinloch, B. B., Jr. 1982. Mechanisms and inheritance of rust resistance in conifers. In: Heybroek, H. M.; Stephan, B. R.; Von Weissenberg, K., eds. Resistance to diseases and pests in forest trees: 3rd International Workshop on Genetics of Host–Parasite Interactions in Forestry; 1980 September 14-21; Wageningen, the Netherlands. Wageningen, the Netherlands: Centre for Agricultural Publishing and Documentation: 119-129.

Kinloch, B. B., Jr.; Davis, D. 1996. Mechanisms and inheritance of resistance to blister rust in sugar pine. In: Kinloch, B. B., Jr; Marosy, M.; Huddleston, M. E., eds. Sugar pine: Status, values, and roles in ecosystems: Proceedings of a symposium presented by the California sugar pine management committee; 1992 March 30-April 1; University of California, Davis. Publication 3362. Oakland, CA: University of California Division of Agriculture and Natural Resources: 125-132.

Kinloch, B. B., Jr.; Davis, D. A.; Burton, D. C. 2008. Resistance and virulence interactions between two white pine species and blister rust in a 30-year field trial. Tree Genetics and Genomes. 4: 65-74.

Kinloch, B. B., Jr.; Dupper, G. E. 2002. Genetic specificity in the white pine-blister rust pathosystem. Phytopathology. 92(3): 278-280.

Kinloch, B. B.; Sniezko, R. A.; Barnes, G. D.; Greathouse, T. E. 1999. A major gene for resistance to white pine blister rust in western white pine from the western Cascade Range. Phytopathology. 89(10): 861-867.

Kinloch, B. B., Jr.; Sniezko, R. A.; Dupper, G. E. 2003. Origin and distribution of Cr2, a gene for resistance to white pine blister rust in natural populations of western white pine. Phytopathology. 93(6): 691-694.

Kinloch, B. B.; Sniezko, R. A.; Dupper, G. E. 2004. Virulence gene distribution and dynamics of the white pine blister rust pathogen in western North America. Phytopathology. 94(7): 751-758.

Kolpak, S. E.; Sniezko, R. A.; Kegley, A. J. 2008. Rust infection and survival of 49 *Pinus monticola* families at a field site six years after planting. Annals of Forest Research. 51: 67-80.

La, Y. J. 2009. Korean successes in controlling blister rust of Korean pine. In: Noshad, D.; Noh, E.; King, J.; Sniezko, R., eds. Proceedings: Breeding and genetic resources of five-needle pines: Ecophysiology, disease resistance, and developmental biology; 2008 September 22-26; Yangyang, Republic of Korea. Seoul: Korea Forest Research Institute: 1-9.

Little, E. L., Jr. 1971. Atlas of United States Trees, Volume 1, Conifers and Important hardwoods: U.S. Department of Agriculture Miscellaneous Publication 1146, 9 p., 200 maps.

Lupo, P. 2004. Stability and expectations of blister rust resistance traits in F_2 western white pine. Moscow, ID: University of Idaho. 131p. Thesis.

Mahalovich, M. F. [Submitted May 2009]. Genetic differentiation of *Pinus albicaulis* Engelm. populations from the Northern Rocky Mountains. The Americas Journal of Plant Science and Biotechnology.

Mahalovich, M. F. 2010. U.S.A. Inland Northwest western white pine breeding and restoration program: history, current and future directions. In: Cleary, M. R., ed. Proceedings of the 3rd Western White Pine Management Conference; 2008 June 17-18; Vernon, BC. Kamloops, BC: BC Ministry of Forests and Range, Southern Interior Forest Region: 50-74.

Mahalovich, M. F.; Burr, K. E.; Foushee, D. L. 2006. Whitebark pine germination, rust resistance, and cold hardiness among seed sources in the Inland Northwest: planting strategies for restoration. In: Riley, L. E.; Dumroese, R. K.; Landis, T. D., tech. coords. National Proceedings: Forest and Conservation Nursery Associations—2005. Proceedings RMRS-P-43. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station: 91-101.

Mahalovich, M. F.; Dickerson, G. A. 2004. Whitebark pine genetic restoration program for the intermountain west (United States). In: Sniezko, R. A.; Samman, S.; Schlarbaum, S. E.; Kriebel, H. B., eds. Breeding and genetic resources of five-needle pines: Genetics, breeding, and adaptability, Proceedings of the IUFRO 2.02.15 Working Party Conference; 2001 July 23-27; Medford, OR. Proceedings RMRS-P-32. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station: 181-187.

McDonald, G. I.; Hansen, E. M.; Osterhaus, C. A.; Samman, S. 1984. Initial characterization of a new strain of *Cronartium ribicola* from the Cascade Mountains of Oregon. Plant Disease. 68: 800-804.

McDonald, G. I.; Hoff, R. J. 1970. Resistance to *Cronartium ribicola* in *Pinus monticola*: early shedding of infected needles. Research Note INT-124. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station. 8 p.

McDonald, G. I.; Zambino, P. J.; Sniezko, R. A. 2004. Breeding rust-resistant five-needle pines in the western United States: lessons from the past and a look to the future. In: Sniezko, R. A.; Samman, S.; Schlarbaum, S. E.; Kriebel, H. B., eds. Breeding and genetic resources of five-needle pines: Genetics, breeding, and adaptability, Proceedings of the IUFRO 2.02.15 Working Party Conference; 2001 July 23-27; Medford, OR. Proceedings RMRS-P-32. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station: 28-50.

Pariaud, B.; Ravigne, V.; Halkett, F.; Goyeau, H.; Carlier, J.; Lannou, C. 2009. Aggressiveness and its role in the adaptation of plant pathogens. Plant Pathology. 58: 409-424.

Schoettle, A.; Sniezko, R. A. 2007. Proactive intervention to sustain high-elevation pine ecosystems threatened by white pine blister rust. Journal of Forest Research. 12: 327-336.

Schoettle, A. 2010. Rust resistance screening of *P. aristata* and *P. flexilis*—trials in progress. Unpublished data on file at: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station.

Sniezko, R. A.; Bower, A.; Danielson, J. 2000. A comparison of early field results of white pine blister rust resistance in sugar pine and western white pine. HortTechnology. 10: 519-522.

Sniezko, R. A.; Bower, A. D.; Kegley, A. J. 2004a. Variation in *Cronartium ribicola* field resistance among 13 *Pinus monticola* and 12 *P. lambertiana* families: early results from Happy Camp. In: Sniezko, R. A.; Samman, S.; Schlarbaum, S. E.; Kriebel, H. B., eds. Breeding and genetic resources of five-needle pines: Genetics, breeding, and adaptability, Proceedings of the IUFRO 2.02.15 Working Party Conference; 2001 July 23-27; Medford, OR. Proceedings RMRS-P-32. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station: 203-208.

Sniezko, R. A.; Hill, J.; Danchok, R. S.; Kegley, A. J.; Long, S.; Mayo, J. B.; Smith, A. J. 2010. White pine blister rust resistance in a seven year old field trial of 28 western white pine (*Pinus monticola*) families in the Coast Range of Oregon. Phytopathology 100:S120. Abstract.

Sniezko, R. A.; Kegley A. 2003a. Blister rust resistance experiences in Oregon and Washington: evolving perspectives. In: Stone, J.; Maffei, H., eds. Proceedings of the 50th Western International Forest Disease Work Conference; 2000 October 7-11; Powell River, BC, Canada. Bend, OR: USDA Forest Service, Central Oregon Forest Insect and Disease Service Center: 111-117.

Sniezko, R. A.; Kegley, A. 2003b. Blister rust resistance of five-needle pines in Oregon and Washington. In: Proceedings of the Second IUFRO Rusts of Forest Trees Working Party Conference; 2002 August 19-23; Yangling, China. Forest Research. 16 (Suppl.): 101-112.

Sniezko, R. A.; Kegley A. 2010. Rust resistance screening of high elevation pines—trials in progress. Unpublished data on file at: U.S. Department of Agriculture, Forest Service, Dorena Genetic Resource Center.

Sniezko, R. A.; Kegley, A. J.; Danchok, R. 2008. White pine blister rust resistance in North American, Asian and European species—results from artificial inoculation trials in Oregon. Annals of Forest Research. 51: 53-66.

Sniezko, R. A.; Kegley, A. J.; Danchok, R. S.; Long, S. 2007. Variation in resistance to white pine blister rust among 43 whitebark pine families from Oregon and Washington—early results and implications for conservation. In: Goheen, E. M.; Sniezko, R. A., tech. coords. Whitebark pine: a Pacific Coast perspective; 2006 August 27-31; Ashland, OR. R6-NR-FHP-2007-01. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Region: 82-97.

Sniezko, R. A.; Kegley, A.; Danchok, R.; Hamlin, J.; Long, S. 2009. Resistance to *Cronartium ribicola* in whitebark pine—family variation and effect of inoculum density. Phytopathology. 99: S122. Abstract.

Sniezko, R. A.; Kinloch, B. B., Jr.; Bower, A. D.; Danchok, R. S.; Linn, J. M.; Kegley, A. J. 2004b: Field resistance to *Cronartium ribicola* in full-sib families of *Pinus monticola* in Oregon. In: Sniezko, R. A.; Samman, S.; Schlarbaum, S. E.; Kriebel, H. B., eds. Breeding and genetic resources of five-needle pines: Genetics, breeding, and adaptability, Proceedings of the IUFRO 2.02.15 Working Party Conference; 2001 July 23-27; Medford, OR. Proceedings RMRS-P-32. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station: 243-249.

Stephan, B.R. 1986. The IUFRO experiment on resistance of white pines to blister rust (*Cronartium ribicola*) in northern Germany. In: Proceedings 18th IUFRO World Congress; 1986 September 7-21; Ljubljana, Yugoslavia. Division II, Vol. I: 80-89.

Stephan, B. R. 2004. Studies of genetic variation with five-needle pines in Germany. In: Sniezko, R. A.; Samman, S.; Schlarbaum, S. E.; Kriebel, H. B., eds. Breeding and genetic resources of five-needle pines: Genetics, breeding, and adaptability, Proceedings of the IUFRO 2.02.15 Working Party Conference; 2001 July 23-27; Medford, OR. Proceedings RMRS-P-32. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station: 98-102.

Tomback, D. F.; Achuff, P. 2010. Blister rust and western forest biodiversity: ecology, values and outlook for white pines. Forest Pathology. 40(3-4): 186-225.

Vogler, D. R.; Delfino-Mix, A.; Schoettle, A. W. 2006. White pine blister rust in high-elevation white pines: screening for simply-inherited, hypersensitive resistance. In: Guyon, J. C., comp. Proceedings of the 53rd Western International Forest Disease Work Conference; 2005 September 26-30; Jackson, WY. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Region: 73-82.

Yokota, S. 1983. Resistance of improved *Pinus monticola* and some other white pines to the blister rust fungus, *Cronartium ribicola* of Hokkaido, Japan. European Journal of Forest Pathology. 13: 389-402.

Zhang, X. Y.; Lu, Q.; Sniezko, R. A.; Song, R. Q.; Man, G. 2010. Blister rusts in China: hosts, pathogens, and management. Forest Pathology. 40(3-4): 369-381.

Preliminary Overview of the First Extensive Rust Resistance Screening Tests of *Pinus flexilis* and *Pinus aristata*

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Limber pine (*Pinus flexilis* James) and Rocky Mountain bristlecone pine (*P. aristata* Engelm.; hereafter referred to as bristlecone pine) are the dominant pines that occupy high elevation habitats of the southern Rockies. Bristlecone pine is primarily a subalpine and tree-line species while limber pine in the southern Rocky Mountains grows from 1600 m in the short grass steppe to over 3300 m elevation near the continental divide (see Schoettle 2004). These trees provide many ecosystem services including food for corvids, bears and squirrels, watershed protection, and picturesque gnarled tree forms on exposed sites. Both species are susceptible to infection by *Cronartium ribicola* J. C. Fisch., the non-native fungal pathogen that causes the lethal disease white pine blister rust (WPBR). WPBR has been present on limber pine since the 1970's in southern Wyoming and was first detected in northern Colorado in 1998 (Johnson and Jacobi 2000) and was discovered in southern Colorado infecting limber pine and bristlecone pine in 2003 (Blodgett and Sullivan 2004). The origin of the inoculum for the southern Colorado infection center is unclear, as it is over 200 km from the nearest known WPBR infections. Long distance transport of spores from California is possible (Frank and others 2008) and may be responsible for initiating this southern Colorado infection center.

Early WPBR resistance testing by Hoff and others (1980) confirmed the occurrence of resistance in both limber and bristlecone pines. Kinloch and Dupper (2002) reported the occurrence of an apparent hypersensitive (HR) needle-based reaction to WPBR in limber pine, similar in gross phenotype to a resistance controlled by a single dominate gene in western white pine (*P. monticola* Douglas ex D. Don) and sugar pine (*P. lambertiana* Douglas). However, Kinloch and Dupper (2002) were unable to confirm inheritance of the complete resistance trait in limber pine as their sample was a bulk seed collection from several trees.

After making seed collections, we initiated the first extensive studies of resistance to WPBR in limber pine and bristlecone pine in family structures (table 1). Our studies are quantifying the frequency of resistances within and among families and populations throughout the southern Rockies. In collaboration with Dorena Genetic Resource Center (DGRC; Cottage Grove, OR) and Institute of Forest

Table 1. Rust resistance studies ongoing for southern Rocky Mountain sources of limber pine and bristlecone pine.

Species	Exploring Resistance Type	Families in Testing (number)	Rust Inoculum Sources	Sow Year	Inoculation Year
P. flexilis	Complete	113[a]	1	2006, 2007	2006, 2007
		153[a]	1	2010	2010
		31 (bulk lots)[a]	1	2009, 2010	2009, 2010
	Partial	74[a]	2[b]	2007	2008
P. aristata	Complete	4[a]	1	2009	2009
	Partial	189[a]	1	2002	2005, 2009
		109[c]	1	2002	2004

[a] Studies lead by Rocky Mountain Research Station (RMRS, Fort Collins, CO) in collaboration with Dorena Genetic Resources Center (DGRC; Cottage Grove, OR).

[b] Inoculum from wild-type eastern Oregon sources was used in each study at DGRC. In addition, for the partial resistant test of limber pine, two trials were inoculated with different geographic sources of rust: a full set of replicates were inoculated with wild-type *C. ribicola* from eastern Oregon and a second set of replicates were inoculated with *C. ribicola* from western Oregon that contained the Champion Mine (vcr2) strain that is virulent to the HR-type simply inherited complete resistance in western white pine.

[c] Study initiated by RMRS (Fort Collins, CO) and lead by Pacific Southwest Station Institute of Forest Genetics (Placerville, CA). The families in this study are a subset of those included in the 189-family test at DGRC.

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Figure 1. Post-inoculation disease phenology on limber pine seedlings inoculated at 5-months old at Dorena Genetic Resource center. **A.** Needle lesions (spots) visible at 3 months; **B.** incipient cankers beginning to show by 4 to 6 months; **C.** *spermatia* (pyncia) evident at 10 months; **D.** aecia present at 18 months.

Genetics (Placerville, CA), we are conducting short- and long-duration tests to explore complete and partial resistance mechanisms (Table 1). Results presented here examine some preliminary findings for those trials conducted at DGRC.

Consistent seedling culture and effective seedling inoculation of both species with *C. ribicola* has been achieved. At DGRC, inoculation densities of 3,500 to 9,500 basidiospores/cm^2 produce very high infection frequencies (>99% of seedlings with needle infections) for 3-, 5- and 17-month-old seedlings of limber pine. Five-month-old bristlecone pine responded similarly. In 2005, for the large trial at DGRC of older, 36-month old bristlecone pine seedlings an inoculum density of approximately 14,000 basidiospores/cm^2 was used. Quantifying infection frequencies for bristlecone pine is more complex as needle lesions are less obvious on this species (see below).

A diversity of needle lesions (infection spots) develop on limber pine; they range in color from golden to deep red with some lesions expanding over time while others remaining more discrete. In the greenhouse environment, needle lesions become easily visible in as little as 3 months after inoculation for the young material and reliably by 4-8 months after inoculation for the older material. In the outdoor environment, the appearance of needle lesions was generally slightly later, similar to western white pine and whitebark pine (*P. albicaulis* Engelm.) at DGRC. The phenology of cankering on limber pine seedlings was also typical (fig. 1). In the greenhouse environment, stem symptoms (lesions) became visible on the younger limber pine seedlings within 4 months following inoculations and continued to appear and develop over the next 18 months. *C. ribicola* spermatia and aecia developed on both younger and older inoculated limber pine seedlings.

Complete resistance to WPBR in limber pine has been evaluated in progeny of 113 limber pine seedtrees (families) from 13 populations across the Southern Rockies. The frequency of resistance varied among populations from 1 to 29 percent and among families from 0 to 100 percent (Schoettle, Sniezko, and Burns, unpublished data). Assessment of the frequency of the partial resistance mechanisms in limber pine is underway at DGRC (Schoettle, Sniezko, Pineda-Bovin and Burns, in progress). The partial resistance testing utilizes two inoculum sources: a full set of replicates were inoculated with wild-type *C. ribicola* from eastern Oregon and a second set of replicates were inoculated with *C. ribicola* from western Oregon that contained the Champion Mine (vcr2) strain that is virulent to the HR-type simply inherited complete resistance in western white pine. Early results suggest that needle lesions and cankering develop earlier when the trees are exposed to the vcr2 strain of *C. ribicola* yet over time the families appear to be responding similarly to both inoculums (Schoettle, Sniezko, Pineda-Bovin and Burns, unpublished data). Two years after inoculations, many susceptible seedlings have died yet some evidence of tolerance to cankering has been observed suggesting the presence of at least one partial resistance mechanisms in limber pine.

An inoculation trial of young bristlecone pine seedlings (5-months old) revealed an abundance of needle lesions and a similar phenology of disease symptom development as limber pine and other species. However, needle lesions on the older 36-month-old bristlecone pines in the 2005 inoculation trial were less obvious. Needle lesions on the primary needles of bristlecone (usually near the lower portions of the stem) were easily visible nine months after inoculation but needle lesions on secondary needles were less clear than on the control seedlings (fig. 2). The control seedlings of susceptible sugar pine and western white pine, which were dispersed throughout the bristlecone trial, displayed numerous needle lesions and the expected phenology of disease expression verifying that the inoculation was successful in challenging all the seedlings with the pathogen. Stem symptoms, spermatia and aecia, developed on the susceptible older bristlecone pine seedlings even though macroscopic needle lesions were not always apparent as has been observed on other species. These seedlings were grown outdoors for two years prior to inoculation so the secondary needles were quite tough, which may have contributed to masking hyphal growth under the epidermis.

Stem lesions (cankers) developed later in bristlecone pine than the control seedlings of western white pine and sugar pine in the screening test in the DGRC test. This is consistent with field observations of latent periods as long as 8 to 14 years (see fig 3) or longer between needle infection and aecia production on some bristlecone pine trees compared to the more typical 1 to 3 year period for other species.

Preliminary assessments suggest that three years after rust inoculation the frequency of disease-free progeny from 189 bristlecone pine seedtrees from 11 populations in Colorado varies among populations from 17 to 60% and among families from 0 to 92 percent (Schoettle, Sniezko, Kegley, and Burns, in progress) with an overall frequency of 37 percent. Assessments of these seedlings continue at DGRC and frequencies of partial resistances are being estimated. The screening trial at the Institute of Forest Genetics (Placerville, CA) used younger seedlings grown in a greenhouse and early results (one year post-inoculation with rust) suggest 22 percent of the inoculated seedlings showed no symptoms of disease (Vogler and others 2006). Even with the difference in seedling culture and inoculums source, preliminary results between the two studies appear consistent and correlated. Further comparison of family performance differences is ongoing.

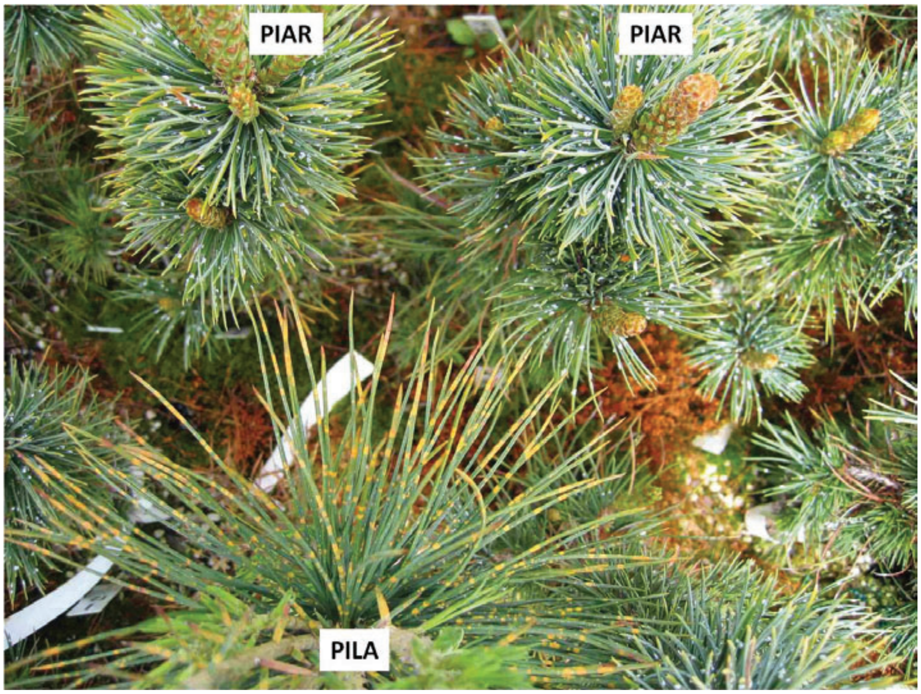

Figure 2. Comparison of bristlecone (PIAR) with a sugar pine (PILA; *Pinus lambertiana*) control seedling nine months post-inoculation; both seedlings were inoculated at the same time under the same conditions at Dorena Genetic Resource Center. Note the abundant visible needle lesions on the sugar pine seedling and the absence of obvious needle lesions on the bristlecone pine. The white dots on the bristlecone needles are resin and typical for this species; they are not a symptom of stress or *C. ribicola* infection.

Figure 3. *Pinus aristata* branch from a mature tree on Mosca Pass collected in 2004. The pins are placed at the bud scale scars which denote the end/beginning of each annual branch growth segment. The year listed is the year that the branch segment (and any attached needles for the foliated portion) was formed. This is not a particularly vigorous branch and its annual extension growth has decreased since 1990. Current year needles plus six previous years of needles are retained on this branch. The first year that *C. ribicola* aecia formed on the growth segment formed in 1990 was 2004, the year the shoot was collected. If we assume that needle retention is consistent from year to year (and the infection occurred through the needles as it typically does), and we assume the branch was infected in 1996, at which time the needles formed in 1990 were 6 years old, the latent period between infection and aecia formation would be 8 years. Alternatively, if the year of needle infection was earlier than 1996, when the needles formed in 1990 were younger, the latent period could be up to 14 years for this branch. Therefore, the latent period for this shoot is 8 to 14 years. However, without understanding the susceptibility of different needle age classes to infection or the length of the latent period, we are unable to determine which year between 1990 and 1996 rust infected the branch.

In summary, preliminary results confirm the occurrence of family-based resistances in both limber pine and bristlecone pine from the southern Rockies. Further examination of the infection at the needle level, using histological techniques, is ongoing in collaboration with Oregon State University to determine if the reaction in limber pine is similar to the HR-type in western white pine. No evidence of HR-type complete resistance was observed in the bristlecone pine trial at the Institute of Forest Genetics (Vogler and others 2006) or in the small 2009 greenhouse trial at DGRC. Preliminary results from the partial resistance tests suggest multiple resistance mechanisms are present in limber pine and bristlecone pine. These data also suggest geographic variation in the distribution of resistances and on-going studies are exploring these relationships further in both species.

Results from this research are being integrated with ecological and gene conservation efforts to develop proactive interventions to sustain limber pine and Rocky Mountain bristlecone pine populations into the future (Schoettle and Sniezko 2007; Schoettle and others, The Proactive Strategy for Sustaining Five-Needle Pine Populations, this proceedings; Keane and Schoettle this proceedings). The rust resistance studies provide baseline information on the resistance mechanisms and frequencies of WPBR resistances for populations of limber pine and bristlecone pine in the Southern Rockies before they are invaded or severely impacted by WPBR. Several detailed syntheses of results for the different trials are underway and other trials are ongoing. These first studies serve to refine the screening methodologies for limber and Rocky Mountain bristlecone pines and provide the first family-based estimates of the frequencies of resistances for these species.

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References

Blodgett, J. T.; Sullivan, K. F. 2004. First report of white pine blister rust on Rocky Mountain Bristlecone pine. Plant Dis. 88: 311.

Frank, K. L.; Geils, B. W.; Kalkstein, L. S.; Thistle Jr., H. W. 2008. Synoptic climatology of the long-distance dispersal of white pine blister rust II. Combination of surface and upper-level conditions. Int. J. Biometeorol. 52: 653–666.

Hoff, R. J.; Bingham, R. T.; McDonald, G. I. 1980. Relative blister rust resistance of white pines. European Journal of Forest Pathology. 10: 307-316.

Johnson, D. W.; Jacobi, W. R. 2000. First report of white pine blister rust in Colorado. Plant Disease. 84: 595.

Kinloch, B. B., Jr.; Dupper, G. E. 2002. Genetic specificity in the white pine/blister rust pathosystem. Phytopathology. 92: 278-280.

Schoettle, A. W. 2004. Ecological roles of five-needle pines in Colorado: Potential consequences of their loss. In: Sniezko, R.; Samman, S.; Schlarbaum, S.; Kriebel, H. Eds. Breeding and genetic resources of five-needle pines: growth adaptability and pest resistance. 2001 July 24-25; Medford, OR. IUFRO Working Party 2.02.15. Proceedings RMRS-P-32. Ogden, UT: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station. Pp. 124-135.

Schoettle, A. W.; Sniezko, R. A. 2007. Proactive intervention to sustain high elevation pine ecosystems threatened by white pine blister rust. Journal of Forest Research. 12(5): 327-336. http://www.springerlink.com/content/9v91t44278w74430/fulltext.pdf

Vogler, D. R.; Delfino-Mix, A.; Schoettle, A. W. 2006. White pine blister rust in high-elevation white pines: screening for simply-inherited, hypersensitive resistance. In: Guyon, J. C., compiler. Proceedings of the 53th Western International Forest Disease Work Conference; 2005 September 26-30; Jackson, WY. Ogden UT: USDA Forest Service, Intermountain Region. Pp 73-82.

Status of White Pine Blister Rust and Seed Collections in California's High-Elevation White Pine Species

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Abstract—White pine blister rust (caused by the non-native pathogen *Cronartium ribicola*) reached northern California about 80 years ago. Over the years its spread southward had been primarily recorded on sugar pine. However, observations on its occurrence had also been reported in several of the higher elevation five-needled white pine species in California. Since the late 1990s, field surveys have substantiated that rust is present in several of these higher elevation species. The combined results of three local surveys in the Sierra Nevada and Warner mountains documented the occurrence of rust in western white and whitebark pines, but not in southern Sierra foxtail or limber pine. A 2004-2006 Statewide survey, funded by the USDA Forest Service (USDA-FS) Forest Health Monitoring Program, showed that the incidence of rust varied considerably within and between regions. For western white pine, mean rust incidence (percentage of infected trees with aecial evidence in a plot), was highest in the North Coast region (42 percent), and averaged substantially less in other areas such as the Klamath, southern Cascades, and northern and southern Sierra Nevada of California (18, 14, 8, and 1 percent, respectively). For whitebark pine, rust incidence averaged 24 percent in the northern Sierra Nevada (plots were as far south as Yosemite), but means were much lower, up to 2 percent, in the other areas. It was recorded on both species, east of the Sierra crest in the Lake Tahoe area, and as high as 3443 m elevation in a southern Sierra whitebark plot. For the more geographically-limited foxtail pine, rust was confirmed in five of six plots of the northern subspecies (mean of six plots: 12 percent). Since the survey was completed, several plots have been added in foxtail stands to further examine rust occurrence and the population structure of this species, an endemic to California. In this survey, no rust was found on southern foxtail, limber, or Great Basin bristlecone pine, all located in southern mountain ranges. General plot mortality averaged 0 to 7 percent, depending on the species and regions.

The collection and storage of seed is a simple strategy for ex situ genetic conservation. In California, seed from high-elevation white pines is banked as conservation collections by the USDA-FS Region 5 Genetics group and as research collections by the USDA-FS Pacific Southwest Research Station's Institute of Forest Genetics (IFG). The Region's genetic seed inventory contains limited collections from foxtail and whitebark trees collected as early as 1994. In the mid-2000s, funds became available for cone collections of limber pine from southern California. In 2009, when the cone crop was very good and funding was available through the USDA Forest Service Forest Health Protection (FHP), cones were collected from trees at six new sites of whitebark, northern and southern foxtail, limber, and Great Basin bristlecone pine. In the last two years, separate research collections have been made at 28 sites of sugar, western white, and whitebark pine in the Lake Tahoe Basin and three sites of Great Basin bristlecone pine in Nevada, using funds from several grants (Sniezko and others, these proceedings). Collaboration between Region 5, IFG, and FHP is facilitating additional cone collections and seed banking. A national effort, led by FHP, has resulted in financial support for more California collections which will fill in geographic gaps where cone collections have not yet been made from these species.

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Polymerase Chain Reaction (PCR) Applications in White Pine Blister Rust Resistance Screening

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Abstract—A goal of breeding programs for resistance to white pine blister rust is the development of multigenic resistance, even if the genetics and mechanisms of resistance may be imperfectly understood. The goal of multigenic resistance has prompted efforts to categorize host resistance reactions at increasingly finer scales, to identify heritable traits that may confer quantitative resistance. PCR amplification of *Cronartium ribicola* DNA presents a sensitive and highly specific method for detection of *C. ribicola* in host tissues, and is well suited to screening of large numbers of samples for which other methods of pathogen detection (e.g., microscopy) may be unsuitable. PCR amplification can be used to detect presence of the pathogen in different host tissues, and so can provide useful information on putatative resistance responses that may be localized in specific tissue types. We report development of a PCR based assay for detection of *C. ribicola* in pine needle tissue and the results of PCR screening for *C. ribicola* in limber pine and whitebark pine individuals that have been identified as having as yet uncharcterized resistance responses that prevent or impair colonization in needle, shoot, root and bark tissues, and discuss the advantages of this method in operational breeding programs. PCR amplification detected *C. ribicola* in symptomatic regions of western white pine, whitebark pine and limber pine needles at 6 months after inoculation; *C. ribicola* was detected in the nonsymptomatic region of only one of six infected needles tested. Work is continuing to improve the sensitivity of the technique.

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Molecular Dissection of White Pine Genetic Resistance to *Cronartium ribicola*

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Abstract—*Pinus monticola* (Dougl. ex D. Don.) maintains a complex defence system that detects white pine blister rust pathogen (*Cronartium ribicola* J.C.Fisch.) and activates resistance responses. A thorough understanding of how it functions at the molecular level would provide us new strategies for creating forest trees with durable disease resistance. Our research focuses on molecular dissection of *P. monticola* major gene (Cr2) resistance and quantitative partial resistance. To characterize the Cr2 gene, resistance gene family encoding proteins with nucleotide-binding-site and leucine-rich- repeat (NBS-LRR) was identified and used to search for DNA polymorphisms by genotyping with a modified approach of amplified fragment length polymorphism (AFLP). Multiple DNA markers for NBS-AFLPs and LRR-AFLPs were mapped on the Cr2 linkage, potentially useful for marker-assisted selection (MAS) in breeding programs. A fine Cr2 genetic mapping is in progress for a final positional cloning of this R gene. The Cr2-triggered defence response was investigated by both genomic and proteomic strategies. A cDNA library was constructed from needles of a Cr2 family at early stages (at time 0-control to 96 hrs) post *C. ribicola* infection. From 5,000 clones randomly sequenced, 3,034 unique expressed sequence tags (ESTs) were identified, including 31 signal transduction genes, 47 transcription factor genes, and 326 down-stream stress-responsive genes. A case study of the thaumatin-like protein (PmTLP) family using quantitative reverse transcription-polymerase chain reaction (RT-qPCR) revealed that a coordinated up-regulation of multiple PmTLP genes was involved in *P. monticola* Cr2 resistance. A further analysis of changes in global gene expression patterns will allow us to identify candidate genes of other types that are involved in compatible and incompatible white pine-*Cronartium* interactions. In the *P. monticola* proteome, we sequenced 105 proteins that were differentially expressed between early stages post infection on resistant and susceptible seedlings. Among those identified proteins, the 14-3-3 proteins are significant in that they bind a number of functionally diverse signalling proteins such as kinases, phosphatases and transmembrane receptors. Multiple families of pathogenesis-related (PR) proteins are believed to contribute to plant quantitative resistance to various pathogens. Along with other host PR proteins, PR3 chitinase (PmCh4) and anti-microbial peptide (PmAMP1) are protein components participating in western white pine partial resistance to *Cronartium*. These researches on gene expression profiling have resulted in identifying different resistance mechanisms in western white pine. We also investigated single nucleotide polymorphisms (SNPs) of the PmCh4 gene family and protein accumulation of PmAMP1 in seed families, their partial resistance phenotypes were quantitatively assessed in USDA-FS trials using a series of parameters, including presence of aecia, canker damage and severity, number of stem symptoms by type (normal canker, partial bark reaction, complete bark reaction), or 'clean'/stem symptom free. A low level of PmCh4 intragenic linkage disequilibrium (LD), but most of them with statistic significance, was found within a distance of ~800 bp. The PmCh4 SNP data also revealed moderate to high levels of genetic structure among these seven seed families (average Fst = 0.163, $p < 0.001$). Our findings suggest that LD-based association analysis is as effective strategy to dissect genetic mechanisms underlying partial resistance phenotypes in conifers. Our studies using molecular genetic, genomic, and proteomic approaches are yielding a detailed understanding of how *P. monticola* confers resistance to *Cronartium*. We believe that similar approaches are feasible to investigate rust resistance in *P. albicaulis* and other white pines.

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Rust Resistance in Seedling Families of *Pinus albicaulis* and *Pinus strobiformis* and Implications for Restoration

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Abstract—Infection and mortality levels from *Cronartium ribicola*, the fungus causing white pine blister rust, are very high in parts of the geographic range of *Pinus albicaulis* (whitebark pine) and *P. strobiformis* (Southwestern white pine). Genetic resistance to this non-native fungus will be one of the key factors in maintaining or restoring populations of these species in areas of high blister rust incidence. Trials at Dorena Genetic Resource Center (Dorena GRC), OR, for blister rust resistance evaluation of seedling progenies of *P. albicaulis* from Oregon and Washington populations began in 2001; the first seedling rust resistance trial of *P. strobiformis* from New Mexico selections have been underway since 2002. Over 350 seedlots of whitebark pine have been inoculated with rust, and hundreds more are available for testing in the future. Ten seedlots of *P. strobiformis* have been tested to date at Dorena GRC, and the level of resistance in all 10 of these canker-free phenotypic selections from a highly infected stand is very encouraging. Forty-three additional *P. strobiformis* seedlots, from three national forests in New Mexico, were inoculated in September 2010, and will be evaluated over the next five years. In both species, seedling screening has identified several types of resistant responses, including a hypersensitive type needle spot that results in canker-free seedlings in several *P. strobiformis* families and bark reactions in other *P. strobiformis* families. Compared to *P. monticola* and *P. lambertiana* controls, *P. strobiformis* had a higher percent of seedlings with no needle spots, fewer needle spots per seedling, fewer seedlings with stem infections, fewer stem infections per tree, a higher percentage of seedlings alive with stem infections and higher overall survival. In some tests, the canker-free proportion in *P. albicaulis* has ranged from 0 to >80 percent for the different seedling families. The first tests suggest a possible geographic trend in rust resistance in *P. albicaulis* in Oregon and Washington, with lower frequency of resistance in southern populations. If the current tests confirm this trend, it would suggest that more trees would need to be tested in some parts of the species range than in others to provide a diverse genetic base within each breeding zone. Current results also suggest that the resistance in *P. albicaulis* is effective at both low and higher inoculum densities and to several geographic sources of blister rust. Monitoring of parent trees identified as resistant (based on rust testing of their progeny) will be useful in helping to detect potential changes in pathogen virulence or aggressiveness. Collection of cones from parent trees identified as resistant can be used immediately to facilitate restoration efforts. For greater levels of resistance, seed orchards can be established, but seed would not likely be available for a decade or more.

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Restoration & Management

Strategies, Tools, and Challenges for Sustaining and Restoring High Elevation Five-Needle White Pine Forests in Western North America

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Abstract—Many ecologically important, five-needle white pine forests that historically dominated the high elevation landscapes of western North America are now being heavily impacted by mountain pine beetle (*Dendroctonus* spp.) outbreaks, the exotic disease white pine blister rust (WPBR), and altered high elevation fire regimes. Management intervention using specially designed strategic treatments will be needed to conserve these keystone species. The goal of this intervention is to promote self-sustaining five-needle white pine ecosystems that have both resilience to disturbances and genetic resistance to white pine blister rust. Many tools and methods are available for land managers. In this paper we outline important steps for implementation of restoration treatments in declining high elevation white pine stands and discuss a number of proactive treatments in threatened ecosystems to mitigate adverse impacts of rust, beetles, and lack of fire. These steps for restoration include (1) create a strategy for restoration across multiple scales, (2) develop materials and techniques for conducting restoration treatments, such as seed collections and rust resistance assessments of the genetic material, (3) prioritize stands or landscapes by integrating the strategy with other management issues, administrative barriers, climate change mitigation, and other local concerns, (4) implement silvicultural cuttings and prescribed fire according to landscape and stand level strategies, (5) conduct activities and assessments to enhance and ensure restoration treatments are effective including planting rust-resistant pine seedlings and protecting valuable seed-sources, and finally (6) monitor treated landscape and stands for effects and adjust and modify future treatment designs accordingly. Examples from whitebark pine ecosystems in the northern Rocky Mountains will be presented to demonstrate this process. For those high elevation white pine ecosystems that are threatened by white pine blister rust or mountain pine beetle, there are actions that can be taken proactively to gain necessary information to evaluate risk and prepare landscapes for invasion to mitigate future impacts. The proactive strategy includes: (1) educate and engage the public and managers to shift from crisis management to management for resiliency, (2) conserve genetic diversity from native populations before they are impacted by WPBR or other stresses, (3) conduct research on patterns, processes and responses of native ecosystems to provide process level understanding of ecosystem behavior and (4) develop and conduct appropriate management activities to increase the resiliency of high elevation five-needle pine ecosystems to prepare them for change. Whether it is restoring impacted landscapes or interventions to mitigate the development of impacts on threatened landscapes, there are two important factors that will govern the success of these species even with comprehensive and effective rangewide strategies: (1) the magnitude of resources available over time to conduct restoration efforts, and (2) the commitment of natural resource agencies to conduct restoration activities over the long term, most likely for many decades to centuries.

Introduction

Many high elevation five-needle pines (HEFNP) forests in western North America are declining because of complex interactions across multiple factors. Whitebark pine (*Pinus albicaulis*) and limber pine (*Pinus flexilis*) are declining across many parts of their range in the United States and Canada because of the infestations of the exotic white pine blister rust (WPBR; *Cronartium ribicola*) and outbreaks of the native mountain pine beetle (*Dendroctonus ponderosae*), which are further exacerbated by the continued policies of fire exclusion and emerging changes in climate (Arno 1986; Koteen 1999; Kendall and Keane 2001; McKenney and others 2007). The other HEFNPs—foxtail pine (*P. balfouriana*), great basin bristlecone pine (*P. longaeva*), southwestern white pine (*P. strobiformis*), and Rocky Mountain (RM) bristlecone pine (*P. aristata*)—have not yet experienced the major declines observed in northern distributions of limber and whitebark pines, but they are also in imminent danger from blister rust and beetles (see Tomback and others, this proceedings, The Magnificent High-Elevation Five-Needle White Pines). These HEFNP upper subalpine and treeline forests are ecologically invaluable to landscape dynamics and biodiversity so restoring these ecosystems is important for ecological sustainability and society (Tomback and others 2001a; Tomback and others, this proceedings, The Magnificent High-Elevation Five-Needle White Pines). Management intervention is urgently needed in some cases to restore the declining keystone species (Schwandt 2006; Aubry and others 2008) and sustain the remaining healthy ones (Schoettle and Sniezko 2007).

In this paper we will present two separate but overlapping approaches for guiding restoration in HEFNP landscapes: (1) important steps for implementation of restoration activities in declining landscapes and stands, and (2) steps for implementing proactive intervention to provide opportunities for early treatments in threatened ecosystems to mitigate future impacts. The goal of both approaches is to promote self-sustaining five-needle pine ecosystems in the presence of the WPBR using those strategies, tools and methods that are available for land managers.

The steps for implementation of successful restoration in declining HEFNP ecosystems are:

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- *Develop a strategy*. Craft a comprehensive strategy for restoring HEFNP that spans multiple scales of time, space, and organizational structure;
- *Develop resources for restoration*. The success of a coordinated restoration effort will depend on diverse sets of materials and methods for conducting restoration treatments, such as seed collections, rust resistance assessments of the genetic material, development of planting guidelines, and cone collection techniques;
- *Prioritize areas for restoration*. A multi-scale prioritization scheme must be devised so that regions, landscapes, and stands can be identified for restoration by integrating the strategy mentioned above with management conflicts and issues, administrative barriers, climate change impacts, and the myriad of local to national issues;
- *Implement restorative treatments*. Passive and active treatments, such as wildland fire use, silvicultural cuttings and prescribed fire, must be implemented across the landscape following the strategy mentioned above;
- *Conduct restoration enhancement activities*. There are many management activities that can be conducted to ensure effective restoration treatments, including planting rust-resistant pine seedlings and protecting valuable seedsources; and finally
- *Monitor treatments*. Since research funds for studying these important HEFNP ecosystems are scarce, it is incumbent on forest managers, with extensive help from the research community, to monitor treated stands and landscapes for adverse effects so that future activities can be adjusted and modified to improve overall efficacy.

We will use examples from whitebark pine and limber pine ecosystems in the northern Rocky Mountains to demonstrate this process.

Activities in the HEFNP ecosystems that have not yet been impacted can be used to promote resiliency and sustainability. These steps include:

- *Educate and engage*. Increase awareness of the threats to the HEFNP ecosystems and facilitate a shift from crisis management to managing for sustained resilience.
- *Gene conservation*. Take advantage of the intact healthy ecosystems to assess and capture the genetic diversity for gene conservation, research and future management activities.
- *Research patterns, processes and responses*. Gain information on natural disturbances and management responses to provide valuable process-level information to evaluate future impacts and treatment effectiveness as well as parameterize predictive models. Assess geographic patterns of natural frequencies of resistance mechanisms to white pine blister rust.
- *Prepare the landscape for change*. Develop and implement interventions to increase adaptive capacity, mitigate ecosystem impacts of tree mortality, and accelerate the increase in frequency of rust resistance.

The proactive strategy will be outlined with examples from the southern Rockies.

There are two important factors that will govern the success of restoring HEFNP forests: (1) the magnitude and dependability of resources available over time to conduct restoration efforts, and (2) the commitment of natural resource agencies to conduct restoration activities over the long term, most likely for many decades to centuries. These resources can be in the form of funding, personnel, collaborative planning efforts, or public support. Because HEFNP ecosystems have little value as timber species, it is doubtful that any restoration treatment or activity will generate appreciable incomes, so the success of any restoration strategy depends on the effective and strategic allocation of limited government resources across multiple spatial scales. Government agencies must have a long-term commitment to HEFNP restoration because it takes a long time for high elevation ecosystems to respond to the effects of most restoration treatments so it may take decades to evaluate treatment success or failure (Agee and Smith 1984). Moreover, climate change may prolong and exacerbate fire, WPBR, and mountain pine beetle effects for many years so it is important that agencies commit to long-term restoration strategies now to prevent local extirpation later.

Restoration Strategy for Declining Ecosystems

Design a Strategy

The success of HEFNP restoration attempts will be greatly enhanced if a coordinated strategy is developed that integrates the latest scientific findings into a comprehensive plan for species conservation across multiple scales of time, space, and organization. Since more than 90 percent of whitebark pine forests, and most other HEFNP forests, exist on public lands managed by the U.S. Forest Service and National Park Service in the U.S. and by provincial and federal agencies in Canada (Keane 2000; Tomback and Achuff 2010), government land management agencies play key roles in ensuring the survival of these ecologically valuable tree species. It is important that these government agencies employ a coordinated plan for species restoration to ensure that there are no conflicting actions that could result in further declines of HEFNP species. An inter-agency, and even trans-boundary restoration strategy, must be crafted to emphasize infrastructure, expertise, and agency strengths for implementation, and to make efficient use of scarce resources in these under-funded HEFNP ecosystems. This integrated strategy can result in successful, cost-effective efforts for restoring declining pine species across its entire range.

Several U.S. Forest Service Regions have developed various management options and strategies for HEFNPs (Mahalovich and Dickerson 2004; Burns and others 2008; Aubry and others 2008; Conklin and others 2009), and a general range-wide strategy is being developed for whitebark pine (Keane and others 2012 [in press]) . The rangewide

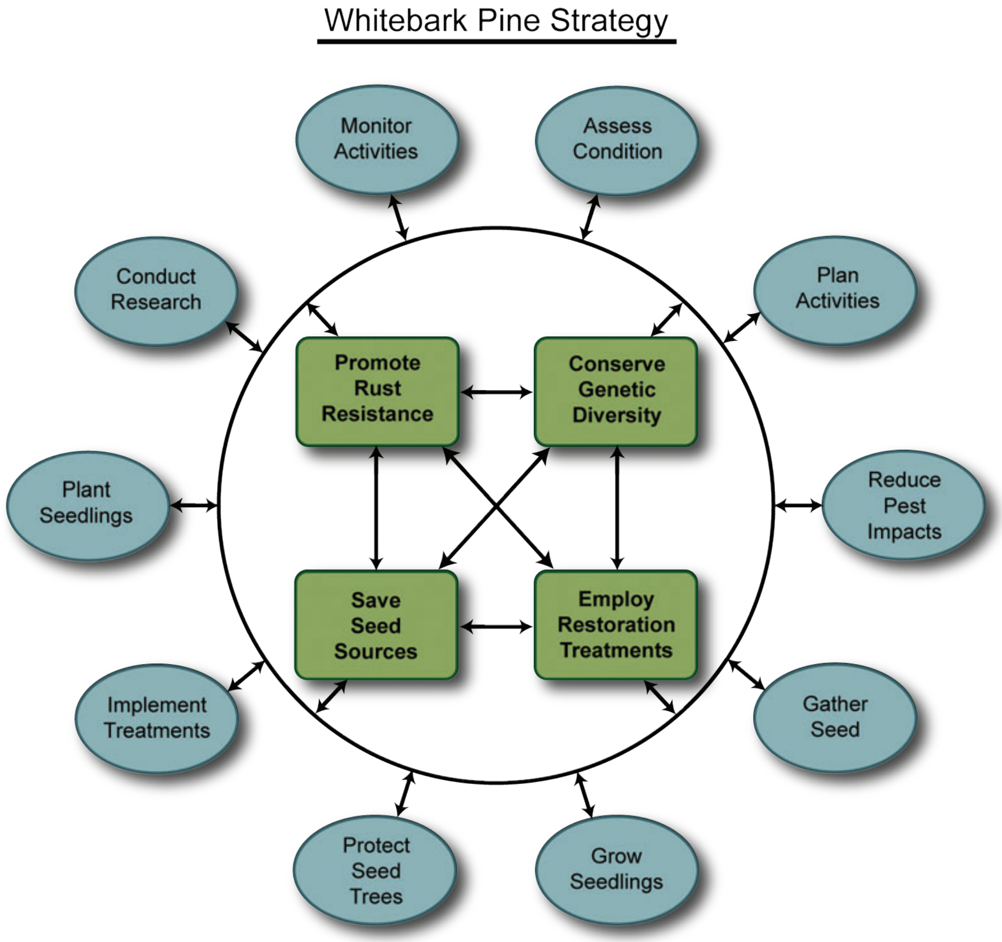

Figure 1. Important elements of the rangewide restoration strategy developed by Keane and others (2012[in press]).

restoration strategy for whitebark pine features coordinated efforts between agencies in both the U.S. and Canada and consists of a general set of four principles to guide the design, planning, and implementation of restoration activities (fig. 1): (1) promote rust resistance, (2) conserve genetic diversity, (3) save seed sources, and (4) employ restoration treatments. These guiding principles form the foundation for implementing the restoration strategy using a set of possible actions which include assess condition, gather seed, test the seed for genetic rust resistance, grow seedlings, protect seed sources, implement restoration treatments, plant rust-resistant seedlings, monitor activities, and support research. The strategy is organized by six spatial scales of analysis and organization: (1) rangewide, (2) regional (National Forests or Provincial Regions, for example), (3) forest (National Forest, National Park, and Canadian Forest District), (4) landscape (watershed, landform), (5) stand, and (6) tree. This general strategy can be used as a template for crafting strategies for all HEFNP species.

An effective strategy must be (1) implemented across all levels of organization, (2) fully integrated in planning, protection, and treatment activities across many land management agencies at various scales of management, (3) focused on specific local areas rather than implemented at low intensity across the entire species range, and (4) based on the best scientific information available to better predict and evaluate intervention outcomes. Thus, restoration efforts for high elevation pine forests need not be implemented across an entire National Forest or National Park; the most successful programs are probably those that concentrate limited restoration resources on high priority sites where potential restoration success is high.

Develop Resources for Restoration

There are a number of activities that can be done locally, regionally, or rangewide to provide the materials and methods needed to properly initiate and implement restoration treatments. Developing, collecting, and maintaining the comprehensive data that provide context for restoration actions is an important task so that the necessary information can be used to evaluate risk and prepare landscapes for invasion so future adverse impacts will be mitigated (Schoettle and Sniezko 2007). Mapping the distribution of the species, threats to the species, spatial context (land ownership, wilderness, and roads, for example), forest structure and developmental stages, and forest condition (level of mortality and their causes) at multiple scales is an important first step (Aubry and others 2008; Burns and others 2008; Keane and others 2012[in press]). Standard GIS spatial analysis techniques can be used on available digital maps describing HEFNP ecology and management issues to provide the

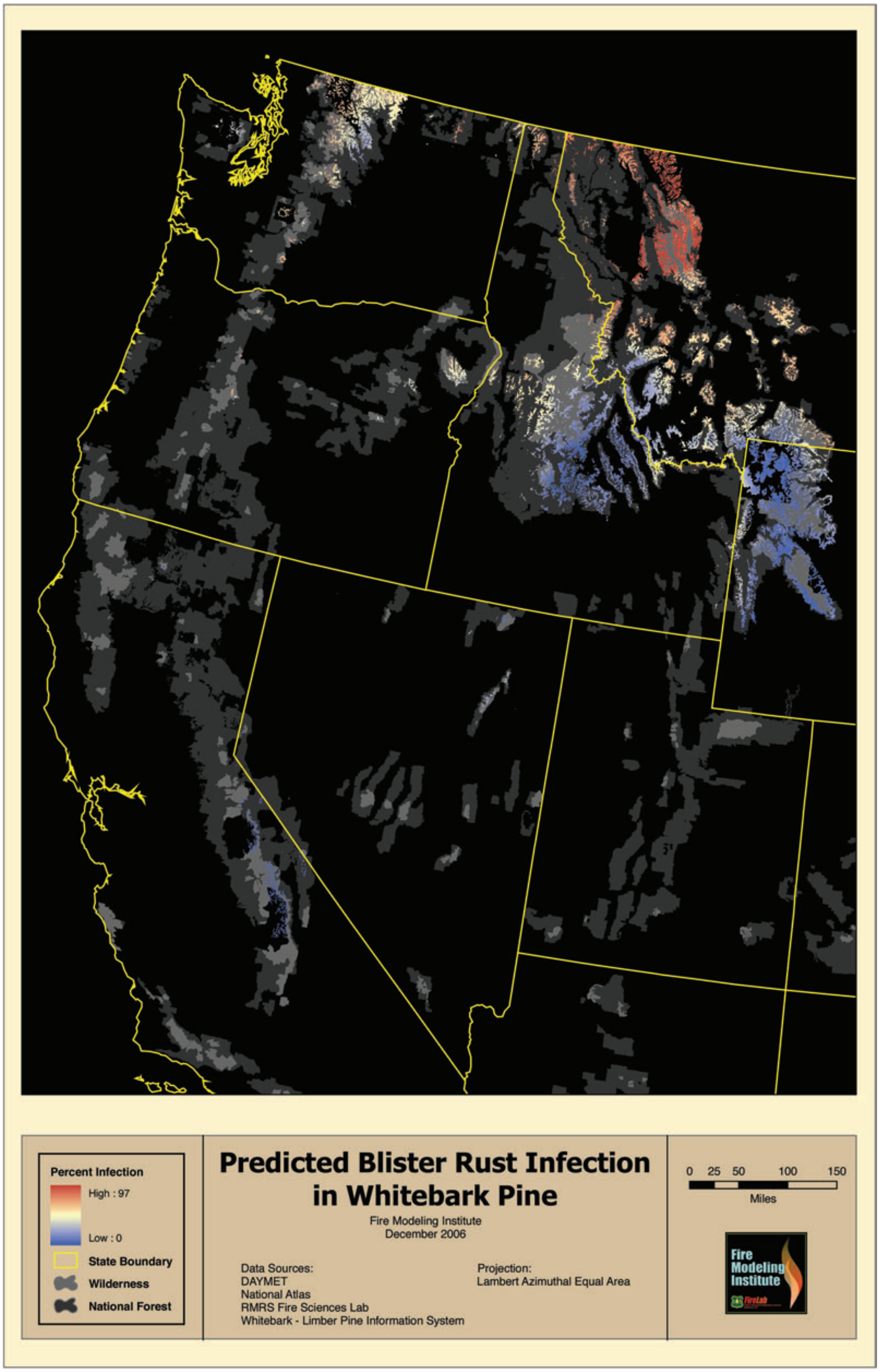

Figure 2. Digital GIS map showing modeled rust infection rates in whitebark pine across its range in the United States created using bioclimatic modeling.

critical spatial information needed for many restoration efforts. For example, gene conservation and seed collection guidelines can be geographically stratified by species distribution, biophysical settings, and ecological conditions. Risk maps of WPBR infection levels are useful to identify areas to monitor, collect seeds, and assess for intervention prioritization (fig. 2). Integrated research projects should address restoration effects and consequences such as assessing regeneration requirements and capabilities, testing silvicultural treatments to promote regeneration, and characterizing WPBR resistance frequencies, mechanisms and distributions across the landscapes.

The design of both a seed conservation plan and a blister rust screening process for creating rust resistent seeds and seedlings for restoration efforts are perhaps the two most important resources that can improve success and efficacy of restoration activities. Assessing the natural frequency of rust resistance in populations that are under consideration for treatment and developing a gene conservation plan to capture this resistance are essential for accurate predictions of restoration outcomes. Development of a regional cone collection program represents a significant step to ensure sufficient seeds are available for the growing and planting of rust-resistant seedlings in post-burn or post-treatment areas (Mahalovich 2000). U.S. Forest Service Regions 1, 2, 4 and 6 have developed an extensive whitebark pine program that includes collecting seed, screening rust resistance, initiating common gardens studies, and modifying seed zones (Mahalovich 2000, Aubry and others 2008). Stands with high infection levels are a high priority for cone collections from phenotypically resistant trees (Hoff and others 2001). Trees that appear healthy in high infection level areas are more likely to have genetic, and therefore heritable, rust-resistances and are less likely to be "escapes". However, rust-resistant seed trees can also be indentified in stands not yet infected by the WPBR (Schoettle and others 2009), so restricting collections to high WPBR hazard locations is probably not desirable if the goal is to capture high genetic diversity (Schoettle and Sniezko 2007). Since it is important to maintain genetic diversity in HEFNP ecosystems across their entire range, seeds should be collected from a variety of sources instead of continually harvesting cones from the same trees each year. It is also critical that the seeds harvested from HEFNP species be screened for blister rust-resistance to identify the level of blister rust resistance in the parent trees and estimate the frequency of resistance in the populations.

Developing techniques and approaches that will assist or enhance restoration efforts are also critical for improving restoration efficiency of HEFNP ecosystems. One essential task is collecting cones for seed for artificial regeneration. The cost of collecting whitebark pine seed is high because cones must be caged to prevent squirrels and nutcrackers from harvesting the seed, which requires climbing trees in the early summer to install the cages, and then climbing the trees again in late summer to harvest the caged cones. Comprehensive cone caging and collection techniques, such as the use of tree tongs (Ward and others 2006; Murray 2007), are greatly needed to reduce collection costs on the bird-dispersed HEFNPs (fig. 3). Tree climbing damages valuable rust-resistant trees so the development of any technique that reduces branch and bole damage, while also being cost effective, would ensure continued survival of the collection trees.

Figure 3. Tree tongs used to put cages on whitebark pine cones to protect against Clark's nutcracker and rodent damage

There also needs to be continued improvements in nursery techniques to reduce the cost of growing seedlings. There have been impressive gains in techniques for growing seedlings that have improved survival, reduced costs, and conserved valuable seed. However, the cost of growing whitebark pine seedlings is still high, making effective large-scale restoration plantings difficult with limited funding. Nursery techniques for growing whitebark, limber and RM bristlecone pines have been established, but there needs to be more work for the other HEFNPs. Progress has been made for planting guidelines for whitebark pine (Scott and McCaughey 2006; Izlar 2007; McCaughey and others 2009) and studies are underway for limber pine (Casper and others, these proceedings). The new guidelines have resulted in great improvements in whitebark pine seeding survival (Izlar 2007). However, planting techniques for the other HEFNPs are still needed.

Education and training programs for both the public and government agency personnel are critical for planning and implementing successful HEFNP restoration programs. Current scientific knowledge and research findings must be synthesized into formats that are easily understood by both agency staff and the public at large. Overview documents, such as Samman and others (2003) and Schwandt (2006) are useful, as are regional management plans (Aubry and others 2008; Burns and others 2008; Conklin and others 2009; Mahalovich and Dickerson 2004). The more the public and agency people know about HEFNP ecology and restoration, the easier it will be to establish a multi-scale restoration plan across the entire range of a species.

Prioritize Areas for Restoration

A first step towards implementing a comprehensive range-wide restoration effort is to identify those areas that, with management, have the greatest likelihood of success to support sustainable HEFNP populations and provide ecosystem services at the stand, landscapes, and regional levels Even in regions where pine losses are not yet great, such as the southern Rocky Mountains, the Sierra Nevada and interior Great Basin ranges, proactive strategies (see Schoettle and Sniezko 2007) may help prevent the severe declines experienced elsewhere (see proactive strategy section below).

Prioritizing landscapes for restoration requires comprehensive assessments of those factors that influence the decline of high elevation pines and those that function as barriers or facilitators of restoration activities. Assessments performed at this scale may be for several purposes: (1) to determine overall health and condition of the landscape or stand, (2) to inform design of restoration treatments, (3) to provide a context for assessing restoration goals (land ownership, accessibility for example), (4) to identify issues that could influence restoration efforts (grizzly bears, wilderness, for example), (5) to describe disturbance regimes that can be used to guide restoration design, and (6) to identify areas that provide ecosystems services (watershed protection, recreation). Collectively, these factors and others can be used to rank areas for restoration priority. For example, landscapes with stands that are experiencing high levels of pine mortality due to WPBR, beetles or succession and that are greater than 12-15 km (mean distance to expect nutcrackers to reestablish a whitebark stand) from a rust-resistant pine seed source might be a high priority for treatment when further decline of the stand might result in local extirpation.

Assessments at the stand level almost always involve some inventory or monitoring to provide the data that guides restoration planning, design, and implementation. There are many inventory and monitoring systems that can be used to sample stand attributes including FIREMON (Lutes and others 2006), FSVEG, and FFI (Benson and others 2005). It is critical that any inventory or monitoring effort include an assessment of those factors that are contributing to HEFNP decline or that are putting the populations at risk , such as rust infection incidence, rust-caused canopy kill, mountain pine beetle-caused mortality, pine regeneration potential, shade tolerant tree species density, and ground cover. The Whitebark Pine Ecosystem Foundation (www.whitebarkfound.org) methods for surveying whitebark pine are focused on health assessment of stands and they implicitly allow for comparisons among stands and areas. These methods are being adapted for use in limber pine stands (C. Smith, personal communications) and have already been modified for use in other HEFNP stands (for example, Burns 2006). For whitebark pine and limber pine, a database of forest health assessments has been established to facilitate the use of existing data and assessing changes in condition over time (WLIS; Lockman and Denitto 2007).

There are a multitude of variables that can be used to describe stand conditions for assessing restoration concerns and designing appropriate management treatments. Disturbance history can provide guidance to determine the frequency, intensity, and severity of restoration treatments that emulate historical disturbance regimes. Fire history can be assessed by visual evidence within the stand, such as fire scars on trees, age class structure of the stand, and charcoal in the soil. Successional status and current stand condition can be determined from the tree density by size class and species. Has the time since last fire has been excessively long (greater than one fire rotation) or past the historical fire-free interval, especially on seral whitebark pine sites? Wildfires can be used as restoration tools. If the stand burned within the last century, then the use of fire as a restoration tool would not be an option, but planting of resistant seedlings may be recommended if the post-fire recovery was hampered by blister rust or limited by inadequate seed supply and dispersal. Although mountain pine beetles are endemic to many HEFNP ecosystems, it is important that their outbreak levels be quantified to maximize the success of restoration treatments; many treatments can be rendered ineffective if they are followed by mountain pine beetle infestations. Some treatments, such as thinning, actually attract mountain pine beetles, which can then kill the pine that has been favored by treatments (Baker and Six 2001).

The degree of successional advancement is also an important prioritization criterion for some of the HEFNPs, and since successional dynamics differ by biophysical environment, it is important that successional condition be stratified by site type (Keane 2001). Succession is one of the three major factors causing the reduced whitebark pine prevalence throughout its range (Tomback and others 2001; Tomback and others, these proceedings, The Magnificent High-Elevation Five-Needle white Pines). For example, whitebark pine occurs on two general community types: climax and seral types. Climax whitebark pine stands are mostly dominated by whitebark pine, depending on the harshness of the site, and whitebark pine is the indicated climax species, so succession to more shade tolerant tree species is not a concern. In stands where whitebark is seral to more shade tolerant conifers (seral site types), the absence of disturbance often leads to a loss of HEFNP seral communities. Treating stands earlier in the successional process would reduce loss of the whitebark pine component, possibly increase cone production, and decrease the likelihood that the stand will support a crown fire that would kill cone-bearing whitebark. For whitebark pine, any stand with greater than 50 percent basal area in subalpine fir and Engelmann spruce might have a high priority for treatment, especially if the landscape is composed of greater than 20 percent subalpine fir dominated stands by area (Keane and others 2012[in press]). Stands with high densities of subalpine fir in the understory (greater than 1,000 trees acre-1) should also be prioritized for treatment.

Other management issues could be included as criteria for prioritization. The grizzly bear is a politically important species that takes whitebark seeds from squirrel middens. In general, squirrels and their middens are more abundant in stands with high numbers of mixed conifer species that produce more constant supplies of squirrel food compared to pure whitebark stands that produce highly variable seed crops (McKinney and Fiedler 2010). Midden size and probability of occupancy decrease with increasing elevation. Grizzly bears suffer from anything that removes cone-producing whitebark pine, reduces squirrel densities, or reduces the size of squirrel middens (Mattson and others 2001). Restoration prioritization for whitebark should emphasize data layers that integrate grizzly population levels and squirrel habitat (mixed conifer stands). Bears also avoid areas with on-going human activity, such as stand preparation for restoration activities. Management of whitebark pine forests for grizzly bears could emphasize maintaining large secure areas of diverse habitat types supporting stable numbers of whitebark pine trees and squirrels.

Areas that have high value for cultural, historic, recreational, and ecosystem services reasons may also be emphasized for restoration or intervention. Headwaters for many watersheds are stabilized by HEFNP forests; these areas could be prioritized for treatment if a change in hydrology could threaten water yield, water quality, geomorphology, aquatic organisms, or slope stability. Areas where the HEFNP forests are an integral aspect of Native American cultures should also be high priority as well as those areas of high esthetic value for recreation. Key ecological areas that connect other areas via gene flow or that may encompass a large isolated population may also be prioritized for intervention to help conserve the species' genetic structure.

Implement Restoration Treatments

The primary goal of most restorations treatments is to promote regeneration and establishment of the HEFNPs, and because these species are early seral, it is important to understand the disturbance ecology of the landscapes prioritized for treatment. Wildland fire is the keystone disturbance that shaped many HEFNP landscapes, so most cases, restoration treatments can be designed at the landscape- and stand-level to emulate fire's effects (Keane and Arno 2001; Perera and others 2004). While prescribed fire seems the obvious tool for mimicking historical fire effects at the stand level, mechanical cutting treatments can also be effective in accessible areas; properly designed silvicultural thinnings can be designed to emulate the effect of stand-replacement, mixed severity and non-lethal surface fires in whitebark stands (Keane and Arno 2001; Keane and Parsons 2010b). Treatment unit sizes and shapes should be similar to the patterns left by past fires and need to reflect the amount of available pine seed source in surrounding stands and the mode of seed dispersal for the target HEFNP (Coop and Schoettle 2009; Keane and Parsons 2010a). Burn patches of 5 to 50 acres were found to be attractive to Clark's nutcrackers for whitebark pine establishment (Norment 1991). Treatments that create large areas for whitebark pine regeneration should be avoided if there is little seed available for caching unless the planting rust-resistant seedlings is planned (McKinney 2004).

The efficacy of the treatment to stimulate natural HEFNP regeneration will also depend on local climatic, topography and biotic factors. Whitebark pine and limber pine are regenerated almost exclusively from Clark's nutcracker seed caches, so treatments should be designed to emphasize those site conditions that attract Clark's nutcrackers to cache their seed so unclaimed seed can germinate and grow into viable seed-producing trees. Caching habitat for the Clark's nutcracker is likely recently burned areas because it appears that the birds readily cache in recent burns, but research here is incomplete. What is more important is that the seedlings germinated from unclaimed cached seed can grow in the absence of competition which ensures the continued survival and growth of whitebark pine seedlings. Whitebark pine and limber pine seedling survival depends on many factors but the lack of competition, exposure to open sky, and protected microsite conditions that nutcrackers select appear to be the most important (Coop and Schoettle 2009; Izlar 2007; McCaughey and others 2009).

For whitebark pine forests, perhaps the most efficient tool for landscape level restoration efforts are planned wildfires (wildland fire use or prescribed natural fires: lightning-started fires that are allowed to burn under acceptable weather and site conditions as specified in a fire plan) and unplanned wildfires (Black 2004), assuming sufficient seed sources remain unburned. The aggressive use of planned wildfires has the potential to be an efficient, economical, and ecologically viable method of restoring whitebark pine in many areas, especially wilderness. Landscapes where wildfires might be contra-indicated are those with few whitebark pine seed sources both near and distant, and low frequency of rust resistance in the populations. In these places, we recommend the protection of mature, cone-producing trees and augmenting the population and the frequency of resistance with planting rust-resistant seedlings (see next section). Otherwise, most wildfires will probably improve whitebark pine's status and health if the fires are carefully monitored to minimize fire-caused mortality of potentially rust-resistant trees. However, it is highly recommend that burned areas in landscapes with high blister rust infection (greater than 50 percent) and mortality (greater than 20 percent) be planted with apparent rust resistance pine seedlings (Keane and Parsons 2010a; Keane and Parsons 2010b).

Large wildfires may be important for HEFNP restoration in those areas of their range that historically experienced extensive fires in a given year, such as the northern Rocky Mountains of the U.S. Conventional wisdom is that wildfires today may burn larger areas more severely than the past because of the buildup of fuel from fire suppression efforts (Van Wagtendonk 1985, Ferry and others 1995), but recent research has found that these large fires actually leave a mosaic of intensities and severities that are similar to historical conditions (Keane and others 2008). Land and fire managers should view wildfires as a possible mechanism for restoring high elevation systems and use ecologically based decision support tools to decide whether or not to let wildfires create potential restoration sites for HEFNPs. Moreover, wildfire rehabilitation teams should evaluate the levels of cone production, WPBR infection, and beetle mortality, along with levels of rust resistance on these landscapes to assess if planting putative rust-resistant whitebark pine is needed.

There are basically two major types of stand-level restoration treatments: prescribed burning and mechanical cuttings. Other treatments can be used to augment or complement the two major treatment types. Most restoration treatments are designed to reduce or eliminate competing species and increase the regeneration opportunities for blister rust-resistant HEFNP seedlings. Again, the primary objectives of these treatments are to promote self-sustaining five-needle pine ecosystems that have resilience to disturbances and genetic resistance to white pine blister rust. It is also important to emulate some historical disturbance process, mainly wildland fire, and to facilitate whitebark regeneration and cone production by creating optimum nutcracker caching habitat, protecting seed sources, and planting rust-resistant seedlings (see next section). Keane and Parsons (2010a; 2010b) summarized results of a 15 year whitebark pine restoration study by treatment across five diverse sites that can be use for evaluating, designing, and implementing HEFNP treatments.

Mechanical cuttings

Mechanical cuttings include treatments that manipulate the stand by cutting trees (fig. 4). Traditional silviculture may have limited effectiveness in these high mountain stands because of the severity of the site, the unique autecology of HEFNPs, and bird-mediated seed dispersal of some of the HEFNPs (Keane and Arno 2000). Silvicultural strategies that are specifically tailored to individual stands are needed to address restoration concerns in high elevation pine forests (Waring and O'Hara 2005). In general, most cuttings should attempt to eliminate shade-tolerant tree competitors while enhancing pine regeneration and vigor. Thinnings can be used to improve the health of potential cone-producing pine, while other cuttings can be used to create fuelbeds to support prescribed burning activities. Usually, mechanical cuttings are only effective when treated stands are in close proximity to roads and are easily to work in (gentle slopes, few rocks, few wet areas, for example).

Figure 4. Cutting subalpine fir trees in a mechanical restoration treatment in a whitebark pine forest.

Six types of mechanical cuttings are currently being used in restoration treatments for whitebark pine. Keane and Parsons (2010a) created nutcracker openings in successionally advanced subalpine fir stands containing healthy and dying, WPBR infected whitebark pine. These nutcracker openings were near-circular areas within which all trees except whitebark pine were cut. The size of these areas may vary, but they can be anywhere from 1-30 acres based on a study by Norment (1991). The nutcracker openings treatment also attempts to mimic patchy, mixed severity wildfires. Other cutting treatments include group selection cuts where all trees except whitebark pine are sawn down, and thinnings where all non-whitebark pine trees below a threshold diameter are cut (Chew 1990; Eggers 1990). Girdling subalpine fir trees has also been attempted on some restoration efforts because it is a cheap, rapid means of killing competing subalpine fir (Jenkins 2005). However, to be effective, the girdling has to be done below the lowest live branches or those branches can form new boles. Girdling also leaves a large portion of the fuel on the site which could foster high severity wildfires that could kill those pine trees being restored. Daylighting (cutting of shade-tolerant competing species in a circle around whitebark pine trees) has been gaining favor among managers because it is cheap and easy, but there is little research on its effectiveness. One last cutting is a fuel augmentation or fuel enhancement treatment where subalpine fir trees are directionally felled to increase fuel loadings and fuelbed contagion (Keane and Arno 1996; Keane and Arno 2001). Keane and Parsons (2010a) found this treatment highly effective for facilitating prescribed burning. It is important to reduce or remove the cutting slash from a treated site to (1) allow nutcrackers full access to the ground for caching (Keane and Parsons 2010b), (2) reduce potential mortality from *Ips* spp. beetles (Baker and Six 2001), and (3) reduce the severity of future unplanned wildfires (Keane and Arno 2000). This can be done by piling the slash and then burning the piles, whole tree skidding to a landing which removes the branches from the site, or augmenting the cutting with a prescribed fire.

To shift the advantage to shade-intolerant HEFNPs, elimination of the shade-tolerant competitors is the most important requirement of any cutting prescription, and the competing cone-bearing trees should be eliminated first. In whitebark pine forests, subalpine fir has frequent large cone crops with numerous seeds that can often create dense stands. The most effective cutting treatments will be those that eliminate the most subalpine fir trees, starting with the cone-bearing trees. The presence of residual seedling and sapling subalpine fir after a cutting treatment can shorten the life span of that treatment and render it ineffective after a short time. The implementation of a prescribed burn after a cutting treatment can kill the understory subalpine fir and make the treatment effective for longer.

Prescribed burning

Prescribed burning may be the most desirable treatment because it best emulates wildland fire regimes (fig. 5), but it is also the most difficult and riskiest treatment to implement. Prescribed burns can be implemented at three intensities to mimic the three types of fire regimes common in whitebark pine and other HEFNPs forests: non-lethal surface fires, mixed severity burns, and stand-replacement fires (Brown and Schoettle 2009; Murray and others 1995; Siderius and Murray 2005; Walsh 2005). The primary objective of low intensity prescribed fires is to kill competing overstory and perhaps understory, and to preserve the HEFNP component. Moderate intensity prescribed burns can be used to mimic mixed severity fires where passive crown fire behavior is common in dense thickets which burn patches of variable size depending on wind, canopy contagion, and fuel moisture conditions. A high intensity prescribed burn, while difficult to apply and control is important for the bird-dispersed HEFNP species because it creates patches that are so large that seeds from competitors are unable to disperse into the center of the burn, allowing HEFNP regeneration decades of competition-free growth after germinated seeds are cached by nutcrackers.

A fuel enhancement cutting implemented one year prior to a prescribed burn is a good way to ensure that burn objectives are fully realized (Keane and Parsons 2010a). The addition of cured slash to discontinuous fuelbeds improves burn effectivness by providing additional fine fuel to (1) aid fire spread into all areas of the stand and (2) augment quickly drying fine fuel loadings so the burn can be implemented under moist conditions. Prescribed burns have a greater coverage and higher severity in stands where the fuels were enhanced (Keane and Arno 2001). Fuel enhancement is somewhat easy, cheap, and relatively quick, and it can be done by timber crews, fire crews or contractors. Keane and Parsons (2010b) also found that shrub and herbaceous fuels were much drier after the first hard frost in late summer or early autumn. This frost kills the aboveground foliage that allows the plants to take water from the soil so the entire plant structure can dry sufficiently for burning.

Conduct Restoration Enhancement Activities

There are several activities that can be implemented before or after major treatments to ensure that the restoration is successful. These activities are usually done to enhance the continued survival of seed-producing individuals within the treated area, and also to facilitate the successful regeneration of high elevation pines in disturbed areas. These activities fall into two classes: planting and protection.

Planting

As HEFNP communities continues to decline across their range, there will be fewer seeds produced and fewer still available for pine regeneration (fig. 6). Furthermore, those seeds produced in damaged stands are highly sought after by pre-dispersal seed predators, especially pine squirrels but other birds, leaving few seeds for nutcracker caching (McKinney and Tomback 2007; McKinney and others 2009). For this reason, in high rust mortality or mountain pine beetle impacted areas, there may not be sufficient seed to naturally regenerate the HEFNPs and planting rust-resistant seedlings may be the only option to regenerate the species (Keane and Parsons 2010a). In addition, if the local seed sources contain little or no heritable resistance to white pine blister rust, artificial regeneration with rust-resistant seedlings will not only increase the population size, but also augment resistance in the future pine populations (Schoettle and Sniezko 2007). If there is higher than 50 percent HEFNP mortality, it is essential that the treated areas be planted with putatively rust-resistant pine seedlings (Keane and Parsons 2010b).

It may be beneficial to plant HEFNP seedlings on a variety of site conditions with a variety of methods to refine planting guidelines to optimize survival and growth of future plantings. Some general planting guidelines were developed by the various agencies and researchers for whitebark pine (Greater Yellowstone Coordinating Committee Whitebark Pine Committee 2001; McCaughey and others 2009; Scott and McCaughey 2006) and are in development for limber pine (Casper and others, this proceedings). On the broad scale, planting should be done on a variety of sites,

Figure 5. Prescribed burning in a whitebark pine forest as part of a restoration treatment to kill competing subalpine fir trees

Figure 6. Planting whitebark pine seedlings in area burned by a fire that was allowed to burn under prescribed conditions in Glacier National Park, Montana, USA (Photo from Kate Kendall).

including the more productive seral sites. When practical, planting crews should attempt to remove non-HEFNP conifers to make planting effective in the long-term. Reduce overstory, understory, and undergrowth (grasses and shrubs) competition to increase light and improve the effective growing season and increase available moisture. Avoid planting whitebark pine in swales or frost pockets and provide shade and protection for newly planted trees to improve water utilization and to reduce light intensity and stem heating (plant by stumps or other stationary shade-providing objects). Planting sites should have some protection from heavy snow loads and drifting snow and planted trees should be widely spaced to avoid long-term inter-tree competition. Summer and fall outplanting have been successful, thereby avoiding the need for expensive snow plowing and delayed entry due to heavy spring snow loads. Whitebark pine seedlings take five to seven years before they become fully established and start significant height growth.

Direct sowing of HEFNP seed instead of planting seedlings could significantly reduce the cost and effort of regenerating sites if technologies improve. Broadcast seeding results in nearly 100 percent consumption of whitebark pine seed by rodents (McCaughey and Weaver 1990), so these seeds must be sown to reduce predation. A potential tactic may be to plant two to four seeds about 2 to 3 cm deep in one planting site with a specially designed dibble. The seeding approaches are being investigated (Smith and others, these proceedings; Schwandt, personal communication) and if successful, they will provide cost-effective methods for regenerating large high elevation burns in a short time.

Protection

Protection is an activity ensuring high value mature, cone-producing, rust-resistant HEFNP trees remain on the landscape so that seeds are available for natural regeneration and collection by managers for rust screening and restoration plantings. A common tree-level restoration activity is to protect trees from a wide variety of disturbance agents, primarily fire, beetles, and rusts. These protection activities can be done prior to treatment and just after the treatment to ensure continued pine seed production. The best trees to protect from these agents are those that have been identified as important sources for genetic and phenotypic rust-resistant seeds (aka "plus" trees) (Mahalovich and Dickerson 2004). Protection of trees from damage from wildland fire (prescribed, wildland fire use, or wildfire) is difficult and costly, yet it can be successful (Keane and Parsons 2010a; Murray 2007c). Mechanical manipulation of fuel surrounding the trees by (1) raking or blowing (via leaf blower) litter and duff away from tree bases, (2) cutting competing fir and spruce, and (3) manual removal of downed woody, shrub, and herbaceous fuels has been attempted in other ecosystems with mixed success. Fire crews have wrapped large whitebark pine with fire shelters to protect against fire mortality with mixed results (Keane and Parsons 2010a). There are also anecdotal stories of marginal successes by foaming trees to lessen fire damage. Modification of ignition patterns by controlling burn severity using strip head fires ignited in thin strips may be the most successful way to minimize fire-caused pine mortality in prescribed burning or back-burning in wildfires.

All HEFNP trees greater than 4.0 inches DBH appear to be susceptible to mountain pine beetle mortality (Gibson and others 2008; Logan and Powell 2001; Logan and others 2003). Most HEFNP species often avoid contact with mountain pine beetle by living in cold, inhospitable mountaintop environments where mountain pine beetles can't complete their life cycle. However, the recent winter-time warming trend has facilitated successful mountain pine beetle outbreaks in HEFNP forests across North America (Bentz and others 2010, Bentz and others, this proceedings). Improving tree vigor by removing competing trees probably won't increase the pine's ability to ward off beetle outbreaks, and it may cause additional stress that makes trees more susceptible to mountain pine beetle attack (Baker and Six 2001). Managers can protect valuable rust-resistant trees from mountain pine beetle using either pesticides or pheromone treatments. Carbaryl is probably the most effective pesticide treatment, especially when beetles are below outbreak levels. Carbaryl has been shown to provide greater than 90 percent protection for 2 years (Gibson and Bennett 1985). The anti-aggregation pheromone Verbenone is currently being used to protect whitebark and limber pine trees during beetle epidemics (Bentz and others 2005; Burns and others 2010; Kegley and Gibson 2004). Even when mountain pine beetle populations are at epidemic levels, managers should also consider using Verbenone or spraying Carbaryl on high value trees within the stands where restoration treatments are implemented (Baker and Six 2001), even though there are some circumstance where Verbenone may have mixed effectiveness.

The proximity of the alternate host in WPBR life cycle, mostly Ribes species, to HEFNPs is a poor predictor of rust incidence (Newcomb 2003), therefore removal of Ribes does not offer an effective method of controlling blister rust in these mountain ecosystems. Pruning rust-infected branches from HEFNP pines might delay the spread of rust in the early stages of invasion, but this also delays the selection against susceptible pines and therefore delays the selection for rust resistance (Schoettle and Sniezko 2007). Sanitation pruning of infected limbs may be effective for extending survival of high value trees, but is not suitable for application on a forest scale. The use of fungicides to battle rust epidemics is costly and ineffective and not practical because of the sheer number of trees to be protected. The best approach is to promote natural regeneration and diverse age class structures to maintain ecosystem function and provide large populations for selection for rust resistance (Schoettle and Sniezko 2007).

Monitor Treatments

The success of future HEFNP restoration efforts will be greatly dependent on the lessons learned in current and past attempts (Keane and Parsons 2010a). Managers and scientists will both benefit by the detailed documentation of the effects, successes, and failures of restoration attempts—no matter the scale, intensity, and extent of treatment implementation. Allocating resources for monitoring restoration treatments using statistically credible sampling designs is critical for providing the essential information needed to fine tune this restoration strategy to local areas and adjust treatment recommendations to improve efficacy. The first need for monitoring efforts is a comprehensive system of protocols, databases, and sampling methods for implementing a monitoring project. There are several monitoring systems available including FIREMON (Lutes and others 2006), the FIREMON-FEAT Integration, the Forest Service's FSVEG, and the National Park Service's Fire Montoring Handbook (USDI 2001).

The next need is for the collection of all monitoring data for analysis at various time intervals. These data then need to be analyzed at the local, regional, and national scales to document ecosystem responses and timing of response to restoration treatments for modifying restoration designs. Next, results from these monitoring efforts need to be published so they are readily available. Last, these monitoring efforts need to be maintained well into the future because of the long response times in HEFNP ecosystems. There is a role for both management and research in restoration monitoring—management could collect the data while research could analyze and report the data, for example. However, the primary role of research should be to explore new aspects of HEFNP ecology, genetics and restoration so management can adapt their methods to respond to these rapidly changing times.

Proactive Strategy for Threatened Ecosystems

Not all HEFNP ecosystems have been invaded by white pine blister rust, though all are vulnerable to impacts. There is an opportunity with proactive management to enhance currently healthy HEFNP ecosystems to retain ecosystem function during the naturalization of the rust (fig. 7). The Proactive Strategy articulates the goals, identifies the critical information needs, and outlines how to develop a management plan for early intervention (Schoettle 2004b; Schoettle and Sniezko 2007; Schoettle and others, The Proactive Strategy for Sustaining Five-Needle Pine Populations, this proceedings).

The goal of proactive intervention in these ecosystems is to increase resiliency and sustainability of ecosystem functions in the presence of the spreading rust and other threats such that ecosystem impairment in the future is mitigated (Schoettle and Sniezko 2007). Healthy, functional ecosystems are better able to respond to management than heavily impacted ecosystems. Therefore, there are more management options available and the potential for a successful outcome is improved. We know that WPBR can kill trees of all ages and disease impacts the regeneration capacity of pine populations (Schoettle and Sniezko 2007). As a result, efforts to stimulate regeneration after the population is heavily impacted may be compromised due to seed and disperser limitations (McKinney and others 2010; Keane and Parson 2010b). Interventions in healthy ecosystems can avoid possible regeneration failure that constrain management options and affect outcomes. Our experience with WPBR impacts in whitebark pine ecosystems (Tomback and others 2001b and papers within), suggests that waiting for populations to be impacted before acting isn't advisable.

Promoting early selection and establishment of resistant genotypes provides time for the resistant seedlings to mature to seed-bearing age before high mortality in the mature susceptible trees, thereby reducing the window of time when the ecosystem's recovery capacity is compromised. Three approaches, two at the stand scale and one at the landscape scale, to proactively facilitate an increase in rust resistance and mitigate the impact of the mortality of rust-susceptible trees have been developed (Schoettle and Sniezko 2007). Stimulating natural regeneration can increase population size, multiplies genetic combinations, and promotes efficient selection for resistance in the younger cohorts when rust arrives. Additionally, planting rust-resistant seedlings before rust has impacted an area can directly introduce

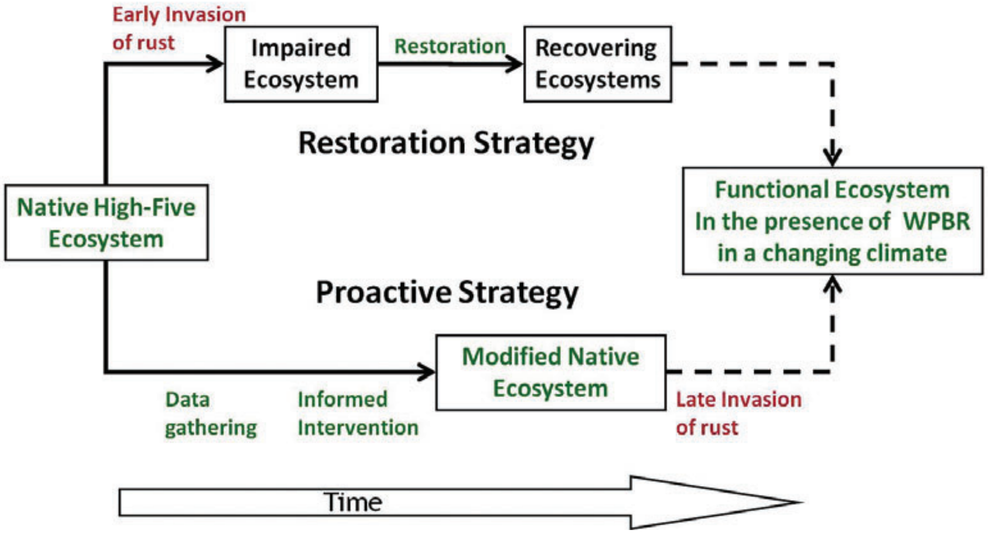

Figure 7. Schematic of the pathways to facilitating the transition of high elevation five-needle pine ecosystems threatened by white pine blister rust to functional ecosystems in the presence of white pine blister rust. If ecosystems have been invaded and are currently heavily impacted by white pine blister rust, the Restoration Strategy pathway would be followed (upper pathway) to restore ecosystem function. In ecosystems threatened but not yet heavily impacted by white pine blister rust, the Proactive Strategy would be followed (lower pathway) to sustain ecosystem function.

rust-resistant genotypes to the population. Diversifying the age class structure across the landscape will also result in rust-resistance selection (mortality of susceptible pines) proceeding at different rates in different patches that ultimately reduces the impact of mortality in any one cohort on ecosystem services. A mosaic of stand structures and ages positions the ecosystem for rapid and efficient natural selection for resistance in the younger cohort while the older cohort sustains ecosystem function (Schoettle 2004b). A structurally diverse landscape is also more resilient to mountain pine beetle impacts and has greater adaptive capacity to climate change. To conduct these interventions requires resources and process-level information on how these little-studied ecosystems respond to perturbation.

Efforts to prepare for the invasion of WPBR into the southern Rockies started in the late 1990's with the discovery by a graduate student of white pine blister rust on limber pine in Colorado (Johnson and Jacobi 2000). This event, while predictable, served as a wake-up call that the HEFNPs of the southern Rockies were at risk. Other isolated infection centers in central and southern Colorado, New Mexico, and Arizona have also been found (for example, Blodgett and Burns 2004, Kearns and Jacobi 2007) and demonstrate that blister rust continues to spread. WPBR was confirmed for the first time on RM bristlecone pine in 2003 in south-central Colorado (Blodgett and Sullivan 2004); this location is over 200 km from the nearest known inoculum source emphasizing the urgency for action because it is difficult to predict the epidemiology of the disease in these new habitats. Most southern Rocky Mountain HEFNP ecosystems are not yet impacted and this area is still considered the leading edge of WPBR spread.

The proactive approach was introduced in 2004 (Schoettle 2004), developed in 2007 (Schoettle and Sniezko 2007), integrated into a management framework for the HEFNPs in the central Rocky Mountain region in 2008 (Burns and others 2008), and currently implemented in the southern Rocky Mountains (Schoettle and others this proceedings, The Proactive Strategy for Sustaining Five-Needle Pine Populations). The combination of the mountain pine beetle outbreaks with the spreading WPBR is particularly threatening to the high elevation ecosystems in the southern Rocky Mountains because of their disjunct patchy distribution.

Unique opportunities and challenges face researchers and land managers interested in proactively increasing the resiliency of HEFNP ecosystems. These include: (1) educate and engage the public and managers to manage for resiliency, (2) conserve genetic diversity from native populations before they are impacted by WPBR and other stresses, (3) research patterns, processes and responses of native ecosystems to provide process level understanding of ecosystem behavior and (4) develop and implement management actions that increase the resiliency of HEFNP ecosystems to prepare them for change. Each are discussed below with examples from the southern Rockies.

Educate and Engage

Preparing to perform interventions in the traditionally unmanaged HEFNP ecosystems requires acceptance and engagement of land managers and the public. The long lifespan of the trees conveys a sense of perseverance that encourages the misconception that the species are invincible. While processes are slow at the higher elevations, so will be restoration and ecosystem response to intervention. The absence of dead trees on the landscape requires additional evidence of the validity of the threat for it to be competitive for management resources. Because this strategy requires engagement of land managers, public, research, and agencies, education is essential to reveal the vulnerabilities of these ecosystems.

Increasing awareness of the threats to the HEFNP ecosystems will facilitate a shift from crisis management to managing for sustained resilience. Most managers thought the southern Rocky Mountains and the Great Basin HEFNP ecosystems were too dry to support the disease. Quantitative estimates of the risk of rust impacts to HEFNP ecosystems are a critical first step to raise awareness of the threat to these ecosystems. Utilizing meteorological conditions to predict rust incidence, a risk analysis reveals that approximately 50 percent of the white pine ecosystems in Colorado have conditions on average that will support the disease (Howell and others 2006; Kearns 2005). Those sites without the appropriate conditions annually may also be vulnerable to infection intermittently.

Mapping spatial distribution and locations of the HEFNPs, WPBR, and other damage agents (mountain pine beetle, dwarf mistletoe) is also essential for elevating awareness of the threat to regional forest health and ecosystems services. In the southern Rocky Mountain HEFNP forests, field assessments began in the late 1990's (Harris and others 1999) and installation of additional monitoring plots continue. Plots from both extensive monitoring and intensive epidemiological studies are installed in both limber pine and RM bristlecone pine stands (Burns 2006; Kearns and Jacobi 2007). Permanent plots to assess the spread of rust from the new disjunction infection center in southern Colorado were installed in 2004 (Burns 2006).

Providing a forum for information exchange and dialogue among the diverse interest groups is critical. Establishment of the Central Rockies White Pine Health Working Group has served this purpose in the Southern Rockies. This group's annual meetings are open to all and often include presentations, discussions, and training sessions for forest health professionals, government and university researchers, land manager and resource professionals from multiple county, state and federal agencies, agency administrators, regulators, students, and other interested people. The meetings and follow-up interactions greatly increase awareness of the vulnerability of HEFNP resources in the central and southern Rockies and promote engagement and partnerships.

Management of federal lands includes extensive public involvement and therefore also requires public education. Recent research has revealed that people value HEFNPs for recreation and tourism; however, the primary reason for public support for managing forests under threat of WPBR is the continued existence of the forest for future generations (Meldrum and others, this proceedings). This indicates that with education and engagement, public support for proactive management is likely.

An educational website that serves as a primer on high elevation white pines, their ecosystems and the factors that threaten them provides easily accessible information for managers, teachers and the public (Schoettle and Laskowski 2006). Extensive seminars and training sessions to environmental, native plant and botanic garden interest groups also increase awareness. Coordination with local chapters of the Society of American Foresters has led to field tours in Colorado and Wyoming and their volunteer assistance with cone collections on the Medicine Bow NF. News media also helps increase awareness through targeted outlets such as newspapers, newsletters and public radio.

Gene Conservation

Blister rust can reduce genetic diversity (Kim and others 2003) and population size of the HEFNP hosts. Before rust affects the population, there is opportunity to capture the native species' genetic diversity for gene conservation, research and future management activities. Seed collections began in 2001 for RM bristlecone pine and in 2003 for limber pine in the Southern Rocky Mountains (Schoettle 2004b). Extensive collections are being made before the occurrence of high mortality caused by mountain pine beetle or blister rust, enabling research on adaptive traits, genetic structure and rust resistance screening to proceed (see below). Range-wide Rocky Mountain bristlecone pine collections, accompanied by stand condition plot information for each sampling location, will be complete soon. Contrary to past accounts of extremely infrequent seed crops in RM bristlecone pine, first year conelets occur most years on at least on some trees in every stand and some seeds mature each year. Bumper crops appear to occur every two to four years although synchrony of cone production is not tight among mountain ranges or sites within a range (Schoettle, unpublished data). Limber pine cone crops are less reliable with bumper crops every four to five years with smaller crops in intervening years and minimal to no production in some years in some populations. Seed and cone insects reduce seed yields in both species but are especially detrimental in limber pine following mast years at lower elevations (Schoettle and Negron 2001). The effect of warming in the treeline habitats on the distribution of seed and cone insects warrants research attention.

Research Patterns, Processes and Responses

Ecological and genetic information is scarce for HEFNPs compared to commercial tree species, and even the most basic information may be unavailable (Schoettle 2004a). Getting started early to fill the scientific knowledge gaps facilitates development of effective management resources and treatments. This information can best be gathered in healthy ecosystems to provide essential baseline information from which evaluation of disturbance (disease, insect outbreaks, climate change) and management outcomes can be compared. In addition, process-level understanding of natural disturbances and management responses enable models to be parameterized specifically for HEFNPs (Schoettle and others, this proceedings, A Population Genetic Model for High-Elevation Five-Needle Pines).

Studies of the disturbance ecology and colonization dynamics of southern Rocky Mountain HEFNPs can help develop silvicultural prescriptions that utilize natural processes to stimulate regeneration and diversify the age class structure of the pines. Stand-replacing fires were thought to be the primary disturbance regime (Baker 1992), although more recent studies suggest a mixed fire regime is also common (Brown and Schoettle 2008). Analyses of the spatial colonization of recent burns reveals that small patch burns are effective for regenerating RM bristlecone pine and limber pine in southern Colorado, while larger burned areas support greater limber pine regeneration in northern portion of the state (Coop and Schoettle 2009). This study also revealed that the temporal dynamic of regeneration for the HEFNPs in the southern Rockies is very protracted after disturbance. These patterns are being used to develop prescriptions to stimulate regeneration and evaluate future treatment effectiveness.

The concern that the use of fire as a silvicultural tool in high elevation pine ecosystems could increase the spread of invasive weed species is currently not founded in the southern Rocky Mountains (Coop and others 2010). *Ribes* cover was greater following fire (Coop and others 2010, Schoettle and others 2003), although the dominant *Ribes* species is a poor host for WPBR. The effect of this increase in *Ribes* cover on rust hazard is unknown and deserves further study. The benefits of increased regeneration with these treatments to the sustainability of the population will likely outweigh the marginal increase in rust hazard.

Microtopographic structure (nurse objects such as boulders, cobble, logs, and tree trunks) are important for successful establishment of both wind and bird-dispersed HEFNPs species (Coop and Schoettle 2009). Management focused toward promoting regeneration should ensure a high density of such objects. These patterns and microsites observed for natural regeneration help guide artificial planting guidelines (Casper and others this proceeding) and other silvicultural prescriptions.

Healthy ecosystems provide opportunities to gain information on the genetic structure of the pine host and population vulnerabilities to WPBR and other novel stresses, such as climate change. Seed zones were established for limber pine in 2006 (Maholovich 2006) and are in the process of being defined for RM bristlecone pine. The first adaptive traits study for RM bristlecone was initiated in 2002, and results will be used to aid in defining seed transfer guidelines. To further refine seed zones and guide gene conservation collections the genetic structure of RM bristlecone pine in the core portion of its range was studied using isozyme analyses in collaboration with the U.S. Forest Service's National Forest Gel Electrophoresis Lab (Schoettle and others, these proceedings Geographic patterns of genetic variation and population structure in *Pinus aristata*, Rocky Mountain bristlecone pine). Rust resistance testing of RM bristlecone began in 2004 and 2005 at Institute of Forest Genetics and Dorena Genetic Resource Center, respectively (Vogler and other 2006, Schoettle and others, Preliminary Overview of the First Extensive Rust Resistance Screening Tests of *Pinus flexilis* and *Pinus aristata*, this proceedings). The first extensive family-based rust resistance testing for limber pine began in 2006 (Schoettle and others 2010). Resistance is confirmed and the frequencies of those resistances vary geographically in both species.

Preparing the Landscape for Change

The proactive strategy focuses management on maintaining genetic diversity, facilitating the functional regeneration cycle, and promoting sustained adaptive capacity and ecosystems resiliency to novel stresses such as WPBR and climate change. We are just at the beginning of the implementation of treatments to work toward these goals. Specific proactive management plans have been prepared for Bureau of Land Management land in Wyoming (Means 2010) and are in preparation for Rocky Mountain National Park and Forest Service lands in northern Colorado; others are being considered.

Geographic variation in rust resistance and regeneration for HEFNPs as well as the coincidence of these factors with other stressors provide critical information to prioritize areas for seed collections and artificial regeneration or silvicultural treatments to stimulate natural regeneration (Schoettle and others, this proceedings, The Proactive Strategy for Sustaining Five-Needle Pine Populations). Populations with low frequencies of resistance are candidates for artificial regeneration with rust-resistant stock while those populations with higher frequencies are prioritized for seed collections and treatments that stimulate natural regeneration. Populations imminently threatened by disturbance are also a high priority for seed collections and protection.

The southern Rockies are poised to have the seed and technology to support artificial regeneration projects for limber pine and RM bristlecone pine. Extensive seed collections have been made and seed sources shown to have rust resistance are being protected from mountain pine beetle for both limber pine and RM bristlecone pine. Limber pine and RM bristlecone pine have been added to several National Forest seed procurement plans, and operational collections have begun on National Forest, National Park Service, Bureau of Land Management and county lands.

Any early establishment of rust-resistant seedlings will benefit the ecosystems over the long run. The high elevation five-needle pines are slow growing and require 30-50 years to produce their first seeds and much longer to reach full reproductive maturity (Schoettle 2004a). Proactive establishment of resistant seedlings would close the gap in time, upon invasion, between rust-impaired seed production of the susceptible older cohort and seed production of the resistant younger cohort (Schoettle and Sniezko 2007). Guidelines for planting limber pine in the southern Rockies are being developed (Casper and others, these proceedings).

Utilizing the information gained by ongoing and previous research, silvicultural prescriptions to stimulate high elevation five-needle pine regeneration have been prepared and are being implemented on the Pike and San Isabel National Forests in Central Colorado (Floyd Freeman, Salida RD, San Isabel NF, unpublished reports). Treatments use mechanical thinning and group selection; conditions have not yet been conducive for the use of prescribed fire. Pre- and post-treatment monitoring plots have been installed to assess new regeneration, release of advanced five-needle pine regeneration and mountain pine beetle impacts. Because of the protracted regeneration dynamics for HEFNP species (Coop and Schoettle 2009), the effectiveness of the treatments can't be fully evaluated for at least 10 years. As more treatments are installed, the more structurally diverse landscape should mitigate the impacts of mortality in any one cohort on ecosystem services and provide greater adaptive capacity to climate change. Silvicultural prescriptions to manage limber pine at the lower elevations have also been prepared for Bureau of Land Management lands in Wyoming (Means 2010).

The implementation of the Proactive Strategy in the southern Rockies has yielded vital information to sustain these valued ecosystems before white pine blister rust and mountain pine beetle caused extensive mortality of HEFNPs. Extensive outreach and education has engaged committed and diverse groups of managers, forest health professionals, researchers and local citizen groups. Management options for sustaining HEFNP in the southern Rockies and the Southwest have been prepared and intensive management plans are in preparation for northern Colorado. We have gained resources and knowledge that would not have been possible if had we waited until white pine blister rust had affected the populations and ecosystem functions. Active partners have been engaged to conserve the resource and gain critical information needed to take action before the ecosystems are heavily impacted. With early and committed management, we are optimistic that the HEFNP ecosystems will be sustainable in the presence of the rust and have improved resiliency to adapt to the changing climate.

Discussion

We have outline two strategies for the management of HEFNP ecosystems: the Restoration Strategy for restore ecosystem function in declining systems and the Proactive Strategy to sustain ecosystem function in threatened systems. The goal of both strategies is to promote self-sustaining five-needle pine ecosystems that have resilience to disturbances and genetic resistance to white pine blister rust. The strategies take different approaches based on the initial condition of the ecosystem. On landscapes currently impacted and degraded by WPBR and other stresses, the Restoration Strategy restores ecosystem function by reconstructing pine populations and reinstates disturbance regimes. Alternatively, in HEFNP ecosystems threatened by WPBR but not yet affected, the Proactive Strategy increases ecosystem resiliency to maintain ecosystem function throughout the naturalization of the rust. Many of the genetic and silvicultural tools are similar yet their applications differ among the two approaches. We have outlined the approaches for both strategies and presented examples of their implementation in declining and threatened HEFNP ecosystems. Sharing knowledge gained by the execution of either approach will provide valuable information to improve management of HEFNP ecosystems throughout western North America.

There is concern among some scientists and managers that treating declining or healthy HEFNP ecosystems during a time when mountain pine beetle outbreaks are rampant, extensive blister rust infection looms large, and the climate is rapidly changing might be fruitless and counterproductive by adversely impacting pine seed sources and by being an inefficient use of restoration funding. However, we feel these factors only further highlight the pressing need for immediate action and they provide a rational for strategic research and management planning for these slow-growing species. Sustaining ecosystem function on these valued landscapes requires understanding the ecosystems. The devastating impacts of the combination of white pine blister rust and mountain pine beetle and the unknown outcomes of climate change suggest that time for understanding these ecosystems cannot be delayed.

Allowing wildland fires to burn or lighting prescribed fire could kill cone bearing HEFNP trees and some feel that this may be counterproductive to restoration efforts. These concerns seem valid, but perhaps we should consider the alternative. Wildfires will happen regardless of our best suppression efforts, especially in these high elevation ecosystems that sit on the tops of mountains where most fires originating from dry forests below will eventually spread, and these unplanned wildfires might have a greater chance of killing valuable rust-resistant individuals than managed fires because uncontrolled wildfires tend to burn under drier, hotter, and windier conditions (Black 2004). Moreover, the seeds from these surviving, stressed trees would have a lesser chance of being sown in favorable sites free of competition because there could be fewer burned areas on the landscape due to reduced fires. Mountain pine beetle impacts on pine are devastating, but these impacts are no reason to suspend restoration activities, but rather they serve as a reason to accelerate seed collections for rust resistance testing, restoration plantings, and gene conservation. In fact, this might be the most important time to initiate management actions on the landscape to ensure HEFNP species will continue to inhabit high elevation forests into the future.

Restoring high elevation pine ecosystems is further complicated by other political and administrative barriers (Salwasser and Huff 2001). Since most HEFNPs are on public lands and they have little commercial potential for timber, agency funding and support is not as strong as for other timber species. Social acceptance of management in these high elevation ecosystems may be less of an obstacle. Initial surveys document that people value HEFNP forests and may support management to sustain their existence for future generations (Meldrum and others, this proceedings). Integration of public preferences with economic and ecological trade-offs will provide further insights into potential optimal management strategies (Bond and others, this proceeding). The U.S. Forest Service policy of not planting rust-resistant pine seedlings in Wilderness Areas is somewhat concerning since many high elevation ecosystems in the western U.S. are within designated Wilderness Areas (Keane 2000). The potential listing of whitebark pine as a threatened species under the Endangered Species Act may also pose both administrative challenges and opportunities. And the linkage of grizzly bear politics with whitebark pine may add an additional layer of complexity to the management of the HEFNP. All of these barriers can be overcome if comprehensive strategies can demonstrate the value of these ecosystems, provide a viable process for restoring and sustaining these forests, and show the dire consequences if these species are lost from the high elevation landscape through inaction. The crisis for whitebark pine has brought increased awareness to the severity of the combined threats of white pine blister rust, mountain pine beetle, and climate change to the other HEFNPs that have not yet been impacted as severely. A shift is beginning toward managing these still healthy ecosystems for resilience to these novel stresses to position them on a different trajectory from that followed by whitebark pine. HEFNP restoration management will take centuries and we must commit to a strategy for the "long haul". While it may seem that restoring high elevation pine forests is a monumental task with questionable outcomes, we believe that sustaining and restoring these forests is not only achievable, but essential for the long term sustainability of high mountain landscapes.

The key to successful restoration is facilitating the increase in rust resistance on the landscape, whether it is through natural selection or planting of rust-resistant pine seedlings after disturbance. Wildland fires, whether these fires are wildfires, controlled wildfires, or prescribed fires, are important disturbances for whitebark pine restoration and may also serve as an important component of management plans for the other HEFNP species. It is also vital that the genetic diversity of planted seedlings be maximized while also including rust resistance traits, to ensure HEFNPs forests remain on the landscape as the changes in climate alter landscape processes. The free flow of genetic material across the landscape using natural wind and bird-assisted seeding, along with human-assisted planting, may be our best strategy for sustaining pines on the high elevation landscape.

Management to sustain HEFNP populations in the presence of white pine blister rust, mountain pine beetle, and climate change has never been more important. The threats and their impacts are clear and are playing out on the landscape right now. Whitebark pine and some populations of limber pine are the harbingers of what is to come for the other HEFNP populations if no action is taken. Restoration of these hard hit areas are needed and it is time to act to prepare to sustain the other species as they are increasingly challenged by these inescapable threats. Early information gathering, planning and intervention will mitigate development of impacts in currently healthy populations and immediate action is required to restore function to those stands already impacted. Whether it is restoring impacts landscapes or interventions to mitigate the development of impacts on threatened landscapes, there are two important factors that will govern the success of HEFNP species even with comprehensive and effective rangewide strategies: (1) the amount of resources available over time to conduct restoration efforts, and 2) the commitment of natural resource agencies to conduct restoration activities over the long term, most likely for many decades to centuries.

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References

Agee, J. K.; Smith, L. 1984. Subalpine tree reestablishment after fire in the Olympic Mountains, Washington. Ecology. 65: 810-819.

Arno, S. F. 1986. Whitebark pine cone crops—A diminishing source of wildlife foods? Western Journal of Applied Forestry. 1: 92-94.

Aubry, C.; Goheen, D.; Shoal, R.; Ohlson, T.; Lorenz, T.; Bower, A.; Mehmel, C.; Sniezko, R. A. 2008. Whitebark pine restoration strategy for the Pacific Northwest 2009-2013. Region 6 Report, U.S. Department of Agriculture, Forest Service, Pacific Northwest Region, Portland, OR.

Baker, K. M.; Six, D. L. 2001. Restoring whitebark pine (*Pinus albicaulis*) ecosystems: a look at endemic bark beetle distribution. Pages 501-502. In: Society of American Foresters 2000 National Convention. Society of American Foresters, Bethesda, MD, Washington, DC, USA.

Baker, W. L. 1992. Structure, disturbance, and change in the bristlecone pine forests of Colorado, USA. Arctic and Alpine Research 24, 17-26.

Bentz, B. J.; S. Kegley; K. Gibson; R. Thier. 2005. A test of high-dose verbenone for stand-level protection of lodgepole and whitebark pine from mountain pine beetle (Coleoptera: Curculionidae: Scolytinae) attacks. Journal of Economic Entomology. 98: 1614-1621.

Bentz, Barbara J.; Regniere, Jacques; Fettig, Christopher J.; Hansen, E. Matthew; Hayes, Jane L.; Hicke, Jeffrey A.; Kelsey, Rick G.; Negron, Jose F.; Seybold, Steven J. 2010. Climate change and bark beetles of the western United States and Canada: Direct and indirect effects. BioScience. 60(8): 602-613.

Black, A. 2004. Wildland Fire Use: The "Other" Treatment Option. USDA Forest Service Rocky Mountain Research Station, Research Note RMRS-RN-23-6-WWW, Fort Collins, CO. p. 2.

Brown, P. M.; Schoettle, A. W. 2008. Fire and stand history in two limber pine (*Pinus flexilis*) and Rocky Mountain bristlecone pine (*Pinus aristata*) stands in Colorado. International Journal of Wildland Fire. 17: 339-347.

Burns, K. S. 2006. White pine blister rust in the Sangre de Cristo and Wet Mountains of southern Colorado. U.S. Department of Agriculture, Forest Service, Rocky Mountain Region, Renewable Resources. Biological Evaluation R2-06-05. 22 p. Available: http://www.fs.fed.us/r2/fhm/.

Burns, Kelly S.; Blodgett, James T.; Conklin, David; Fairweather, MaryLou; Geils, Brian; Guyon, John; Hoffman, James; Jackson, Marcus; Jacobi, William R.; Kearns, Holly S. J.; Schoettle, Anna W. 2010. White Pine Blister Rust in the Interior Mountain West. In: Adams, J. comp. 2010. Proceedings of the 57th Western International Forest Disease Work Conference; 2009 July 20-24; Durango, CO. Forest Health Technology Enterprise Team, Fort Collins, CO. Pp 57-65.

Burns, Kelly S.; Schoettle, Anna W.; Jacobi, William R.; Mahalovich, Mary F. 2008. Options for the management of white pine blister rust in the Rocky Mountain Region. Gen. Tech. Rep. RMRS-GTR-206. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station. 26 p.

Chew, J. D. 1990. Timber management and target stands in the whitebark pine zone. General Technical Report INT-270, USDA Forest Service, Intermountain Research Station, Ogden, UT, USA.

Conklin, D. A.; Fairweather, M. L.; Ryerson, D. E.; Geils, B. W.; Vogler, D. R. 2009. White pines, blister rust, and management in the Southwest. USDA Forest Service, Southwestern Region, R3-FH-09-01. 16 p. http://www.fs.fed.us/r3/resources/health.

Coop, Jonathon C.; Schoettle, Anna W. 2009. Regeneration of Rocky Mountain bristlecone pine (*Pinus aristata*) and limber pine (*Pinus flexilis*) three decades after stand-replacing fires. Forest Ecology and Management. 257: 893-903.

Coop, J. D.; Massatti, R. T.; Schoettle, A. W. 2010. Subalpine vegetation pattern three decades after stand-replacing fire: effects of landscape context and topography on plant community composition, tree regeneration, and diversity. Journal of Vegetation Science. 21: 472-487.

Dumroese, R. K. 2008. Observations on root disease of container whitebark pine seedlings treated with biological controls. Native Plants. 9: 93-103.

Eggers, D. E. 1990. Silvicultural management alternatives for whitebark pine. Pages 324-328. In: Symposium on whitebark pine ecosystems: Ecology and management of a high-mountain resource. USDA Forest Service, Intermountain Research Station, Ogden, UT, USA.

Ferry, G. W.; R. G. Clark; R. E. Montgomery; R. W. Mutch; W. P. Leenhouts; G. T. Zimmerman. 1995. Altered fire regimes within fire-adapted ecosystems. U.S. Department of the Interior—National Biological Service, Washington, DC.

Gibson, Ken; Skov, Kjerstin; Kegley, Sandy; Jorgensen, Carl; Smith, Sheri; Witcosky, Jeff. 2008. Mountain pine beetle impacts in high elevation five needle pines: current trends and challenges. Forest Health Protection Report R1-08-020. U.S. Department of Agriculture, Forest Service. 32 p.

Harris, J. L. 1999. White pine blister rust disease of limber pine in the Bighorn and Medicine Bow National Forests. USDA For. Serv., Rocky Mountain Region, Renewable Resources. Biol. Eval. R2-00-02. 8 p.

Howell, B.; Burns, K.; Kearns, H. 2006. Biological Evaluation of a Model for Predicting Presence of White Pine Blister Rust in Colorado Based on Climatic Variables and Susceptible White Pine Species Distribution USDA For. Serv., Rocky Mountain Region, Renewable Resources. Biol. Eval. R2-06-04. 15 p.

Izlar, D. K. 2007. Assessment of whitebark pine seedling survival for Rocky Mountain plantings. MS. University of Montana, Missoula.

Jenkins, M. M. 2005. Greater Yellowstone area decision guidelines for whitebark pine restoration. Silvicultural Report on file at the Caribou Targhee National Forest Island Park Ranger District, USDA Forest Service Caribou-Targhee National Forest, Island Park, ID.

Keane, R. E. 2000. The importance of wilderness to whitebark pine research and management. Pages 84-93. In: Proceedings of the symposium: Wilderness Science: In a time for change. Volume 3: Wilderness as a Place for Scientific Inquiry. USDA Forest Service General Technical Report RMRS-P-15-VOL-3, Missoula, MT, USA.

Keane, R. E. 2001. Successional dynamics : modeling an anthropogenic threat. Pages 159-192. In: D. Tomback, S. Arno, and R. Keane, editors. Whitebark pine communities: ecology and restoration. Island Press, Washington, DC, USA.

Keane, R. E.; J. Agee; P. Fule; J. Keely; C. Key; S. Kitchen; R. Miller; L. Schulte. 2008. Ecological effects of large fires in the United States: benefit or catastrophe. International Journal of Wildland Fire. 17: 696-712.

Keane, R. E.; S. Arno. 2000. Restoration of whitebark pine ecosystems in western Montana and central Idaho. Pages 324-330. In: Society of American Foresters 1999 National Convention. Society of American Foresters, Portland, OR.

Keane, R. E.; S. F. Arno. 1996. Whitebark pine (*Pinus albicaulis*) ecosystem restoration in western Montana. Pages 51-54. In: The use of fire in forest restoration—a general session at the annual meeting of the Society of Ecosystem Restoration "Taking a broader view". USDA Forest Service General Technical Report INT-GTR-341, Seattle, WA, USA.

Keane, R. E.; S. F. Arno. 2001. Restoration concepts and techniques. Pages 367-400. Whitebark pine communities: ecology and restoration. Washington, DC: Island Press c2001.

Keane, R. E.; James P. Menakis; W. J. Hann. 1996. Coarse scale restoration planning and design in Interior Columbia River Basin Ecosystems—An example using Whitebark Pine (*Pinus albicaulis*) forests. Pages 14-20. In: The use of fire in forest restoration—a general session at the annual meeting of the Society of Ecosystem Restoration "Taking a broader view". USDA Forest Service General Technical Report INT-GTR-341, Seattle, WA, USA.

Keane, R. E.; R. Parsons. 2010a. Restoring whitebark pine forests of the northern Rocky Mountains, USA. Ecological Restoration. 28: 56-70.

Keane, R. E.; R. A. Parsons. 2010b. A management guide to ecosystem restoration treatments: the whitebark pine forests of the Northern Rocky Mountains. General Technical Report RMRS-GTR-232, USDA Forest Service Rocky Mountain Research Station, Fort Collins, CO.

Keane, Robert E.; Aubry, C.; Bower, A.; Campbell, E.; Jenkins, M.; Manning, M.; McKinney, S.; Murray, M.; Perkins, D.; Reinhart, D.; Ryan, A.; Schoettle, C.; Smith, C.; Tomback D. 2012[in prep]. A range-wide restoration strategy for whitebark pine (*Pinus albicaulis*). General Technical Report. U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station.

Kearns, H. S. J. 2005. White pine blister rust in the central Rocky Mountains: modeling current status and potential impacts. Ph.D. Dissertation. Colorado State University, Fort Collins, CO.

Kearns, Holly S. J.; Jacobi, William R. 2007. The distribution and incidence of white pine blister rust in central and southeastern Wyoming and northern Colorado. Canadian Journal of Forest Research. 37: 462-472.

Kegley, S.; K. Gibson. 2004. Protecting whitebark pine trees from mountain pine beetle attack using verbenone. Forest Health

Protection Report 04-8, USDA Forest Service Northern Region, Missoula, MT, USA.

Kendall, K.; R. E. Keane. 2001. The decline of whitebark pine. Pages 123-145. In: D. Tomback, S. F. Arno, and R. E. Keane, editors. Whitebark pine communities: Ecology and Restoration. Island Press, Washington, DC, USA.

Koteen, L. 1999. Climate change, whitebark pine, and grizzly bears in the greater Yellowstone ecosystem. Pages 343-364. In: S. H. Schneider and T. L. Root, editors. Wildlife responses to climate change. Island Press, Washington, DC, USA.

Lockman, I. Blakey; Denitto, Gregg A. 2007. WLIS: The Whitebark-Limber Pine Information System and What It Can Do for You. USDA Forest Service R6-NR-FHP-2007-01. 146 p.

Logan, J. A.; W. W. Macfarlane; L. Willcox. 2008. Effective monitoring as a basis for adaptive management: a case history of mountain pine beetle in Greater Yellowstone Ecosystem whitebark pine. iForest. 2: 19-22.

Logan, J. A.; J. A. Powell. 2001. Ghost forests, global warming, and the mountain pine beetle (Coleoptera: Scolytidae). American Entomologist. 47: 160-173.

Logan, J. A.; J. Regniere; J. A. Powell. 2003. Assessing the impacts of global warming on forest pest dynamics. Frontiers in Ecology and the Environment. 1: 130-137.

Lorenz, T. J.; C. Aubry; R. Shoal. 2008. A review of the literature on seed fate in whitebark pine and the life history traits of Clark's Nutcracker and pine squirrels. General Technical Report PNW-GTR-742, USDA Forest Service Pacific Northwest Research Station, Portland, OR.

Lutes, D. C.; R. E. Keane; J. F. Caratti; C. H. Key; N. C. Benson; S. Sutherland; L. J. Gangi. 2006. FIREMON: Fire effects monitoring and inventory system. General Technical Report RMRS-GTR-164-CD, USDA Forest Service Rocky Mountain Research Station, Fort Collins, CO, USA.

Mahalovich, Mary F. 2006. Limber pine seed transfer guidelines. U.S. Department of Agriculture Forest Service Regions 1-4. Internal Report, 4 p. Prepared February 27, 2006.

Mahalovich, M. F.; Dickerson, G. A. 2004. Whitebark pine genetic restoration program for the Intermountain West (United States). In: Sniezko, R. A.; Samman, S.; Schlarbaum, S. E.; Kriebel, H. B., eds. Breeding and genetic resources of five-needle pines: growth, adaptability and pest resistance. Proc RMRS-P-32, USDA For. Serv., Rocky Mountain Res. Sta., Fort Collins, CO. pp 181-187.

McCaughey, W.; G. L. Scott; K. L. Izlar. 2009. Whitebark pine planting guidelines. Western Journal of Applied Forestry. 24: 163-166.

McCaughey, W. W.; T. Weaver. 1990. Biotic and microsite factors affecting whitebark pine establishment. General Technical Report INT-270, USDA For. Serv., Bozeman, MT, USA.

McKenney, D.W.; J. H. Pedlar; K. Lawrence; K. Campbell; M. F. Hutchinson. 2007. Potential impacts of climate change on the distribution of North American trees. BioScience. 57: 939-948.

McKinney, S. T. 2004. Evaluating natural selection as a management strategy for restoring whitebark pine. Master of Science. University of Colorado, Denver, CO.

McKinney, S. T.; C. E. Fiedler. 2010. Tree squirrel habitat selection and predispersal seed predation in a declining subalpine conifer. Oecologia. 162: 697-707.

Means, Robert. 2010. Whitebark and Limber Pine (Five Needle Pine) Management Guidelines for Wyoming BLM. Internal Report Wyoming Bureau of Land Management, Cheyenne, WY. 10 p.

Murray, M. P. 2007. Cone collecting techniques for whitebark pine. Western Journal of Applied Forestry. 22: 153-155.

Murray, M. P.; S. C. Bunting; P. Morgan. 1995. Subalpine ecosystems: The roles of whitebark pine and fire. Pages 295-299. In: Fire Effects on Rare and Endangered Species and Habitats Conference, Coeur d'Alene, ID.

Newcomb, M. 2003. White pine blister rust, whitebark pine, and Ribes species in the Greater Yellowstone Area. Masters of Sciences thesis. University of Montana.

Norment, C. J. 1991. Bird use of forest patches in the subalpine forest-alpine tundra ecotone of the Beartooth Mountains, Wyoming. Northwest Science. 65: 1-10.

Perera, A. H., L. J. Buse; M. G. Weber, editors. 2004. Emulating natural forest landscape disturbances: concepts and applications. Columbia University Press, New York, NY, USA.

Salwasser, H.; D. E. Huff. 2001. Social and environmental challenges to restoring whitebark pine. Pages 401-432. In: D. Tomback, Stephen F. Arno; R. E. Keane, editors. Whitebark pine communities: Ecology and Restoration. Island Press, Washington, DC, USA.

Samman S.; Schwandt, J. W.; Wilson, J. L. 2003. Managing for healthy white pine ecosystems in the United States to reduce the impacts of white pine blister rust. USDA For. Serv. Rep. R1-03-118. Missoula, MT.

Schoettle, A. W.; Berger, C. A.; Bonnet, V. H. 2003. Proactive conservation options for bristlecone pine forests in the presence of an exotic pathogen—use of fire? In: Abstracts—The Ecological Society of America 88th Annual Meeting, August 3-8, 2003, Savannah, GA. Washington, DC: The Ecological Society of America. 301.

Schoettle, A. W.; Negron, J. F. 2001. First report of two cone and seed insects on *Pinus flexilis*. Western North American Naturalist. 61: 252-254.

Schoettle, A. W. 2004a. Ecological roles of five-needle pines in Colorado: Potential consequences of their loss. In: Sniezko, R. A., S. Samman, S. E. Schlarbaum, H. B. Kriebel, eds. Breeding and genetic resources of five-needle pines: growth, adaptability, and pest resistance; 2001 July 23-27; Medford, OR, USA. IUFRO Working Party 2.02.15. Proceedings RMRS-P-32. Fort Collins, CO: USDA Forest Service, Rocky MountainResearch Station. Pp 124-135. Available at: http://www.fs.fed.us/rm/pubs/rmrs_p032/rmrs_p032_124_135.pdf.

Schoettle, A. W. 2004b. Developing proactive management options to sustain bristlecone and limber pine ecosystems in the presence of a non-native pathogen. In: Shepperd, W. D.; L. G. Eskew, compilers. Silviculture in special places: Proceedings of the National Silviculture Workshop; 2003 September 8-11; Granby, CO. Proceedings RMRS-P-34. Fort Collins, CO: USDA Forest Service, Rocky Mountain Research Station. Pp 146-155. Available at: http://www.fs.fed.us/rm/pubs/rmrs_p034/rmrs_p034_146_155.pdf.

Schoettle, A. W., Laskowski, M. 2006. Educational high elevation white pines website. http://www.fs.fed.us/rm/highelevationwhitepines/.

Schoettle, A. W.; R. A. Sniezko. 2007. Proactive intervention to sustain high-elevation pine ecosystems threatened by white pine blister rust. Journal of Forest Research. 12: 327-336.

Schoettle, A. W.; R. A. Sniezko; K. S. Burns; F. Freeman. 2007. Preparing the landscape for invasion—Early intervention approaches for threatened high elevation white pine ecosystems. In: Goheen, E. M.; R. A. Sniezko, tech. coords. Proceedings of the conference Whitebark Pine: a Pacific Coast Perspective. 2006 Aug 27-31, Ashland OR. R6-NR-FHP-2007-01. Portland, OR: Pacific Northwest Region, Forest Service, U.S. Department of Agriculture; pp 72-75. Available on-line at: http://www.fs.fed.us/r6/nr/fid/wbpine/proc.shtml

Schoettle, A. W.; Sniezko, R. A.; Burns, K. S. 2009. Sustaining *Pinus flexilis* ecosystems of the Southern Rocky Mountains (USA) in the presence of *Cronartium ribicola* and *Dendroctonus ponderosae* in a changing climate. In: Breeding and Genetic Resources of Five-Needle Pines Conference, IUFRO Working Party 2.02.15, Yangyang, Republic of Korea, 2008 September 22-26. Ed. By Noshad, D.; Noh, E.; King, J.; Sniezko, R. Yangyang: Korea Forest Research Institute. Pp. 63-65. http://www.iufro.org/download/file/4989/1191/20215-yangyang08-proceedings.pdf/

Schoettle, A. W.; Sniezko. R. A.; Kegley, A.; Hill, J.; Burns, K. S. 2010. Resistance to white pine blister rust in *Pinus flexilis* and *Pinus aristata* of the Southern Rockies—initial findings. In: Adams, J. comp. 2010. Proceedings of the 57th Western International Forest Disease Work Conference; 2009 July 20-24; Durango, CO. Forest Health Technology Enterprise Team, Fort Collins, CO. Pp. 109-110. Available at: http://www.cnr.usu.edu/quinney/files/uploads/WIFDWC2009.pdf

Schwandt, J. W. 2006. Whitebark pine in peril: a case for restoration. U.S. Forest Service Forest Health and Protection Report R1-06-28, U.S. Forest Service, Missoula, MT.

Scott, G. L.; W. W. McCaughey. 2006. Whitebark pine guidelines for planting prescriptions. Pages 84-90. In: National proceedings: Forest and Conservation Nursery Associations—2005. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station.

Siderius, J.; M. P. Murray. 2005. Fire knowledge for managing Cascadian whitebark pine ecosystems. Interagency Joint Fire Sciences Program.

Tomback, D. F.; Achuff, P. 2010. Blister rust and western forest biodiversity: ecology, values and outlook for white pines. Forest Pathology. 40: 186-225.

Tomback, D.; S. F. Arno; R. E. Keane. 2001a. The compelling case for management intervention. Pages 3-28. In: D. Tomback; Stephen F. Arno; R. E. Keane, editors. Whitebark pine communities: Ecology and Restoration. Island Press, Washington, DC, USA.

Tomback, D.; Stephen F. Arno; R. E. Keane. 2001b. Whitebark pine communities: Ecology and Restoration. Island Press, Washington, DC, USA.

USDI, N. P. S. 2001. Fire Monitoring Handbook., National Interagency Fire Center., Boise, ID.

Van Wagtendonk, J. W. 1985. Fire suppression effects on fuels and succession in short-fire-interval wilderness ecosystems. Pages 119-126. Proceedings, Symposium and Workshop on Wilderness Fire, Missoula, MT, November 15-18, 1983: proceedings of a symposium. Ogden, UT: U.S. Dept. of Agriculture Forest Service Intermountain Forest and Range Experiment Station 1985.

Walsh, J. R. 2005. Fire regimes and stand dynamics of whitebark pine (*Pinus albicaulis*) communities in the Greater Yellowstone Ecosystem. Colorado State University, Fort Collins, CO.

Ward, K.; R. Shoal; C. Aubry. 2006. Whitebark pine cone collection manual. Report March 2006, USDA Forest Service Pacific Northwest Region, Portland, OR.

Waring, K. M.; K. L. O'Hara. 2005. Silvicultural strategies in forest ecosystems affected by introduced pests. Forest Ecology and Management. 209: 27-41.

Waring, K. M.; D. L. Six. 2005. Distribution of bark beetle attacks after whitebark pine restoration treatments: a case study. Western Journal of Applied Forestry. 20: 110-116.

Investigating the Optimality of Proactive Management of an Invasive Forest Pest

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Abstract—This paper offers a preliminary investigation into the conditions under which it might be optimal to engage in proactive management of a non-timber forest resource in the presence of an invasive species whose spread is unaffected by management action. Proactive management is defined as treating an uninfected area to encourage healthy ecosystem function, given that the arrival of the invasive is inevitable. Inspired by the problem of white pine blister rust in the Rocky Mountain west of the United States, the model was solved under varying assumptions concerning the scale of management action, benefit and costs, discount rate, and uncertainty of spread. Results showed that proactive strategies tended to be optimal when, all else equal, a) more resources are available for treatment; b) the costs of treatment are rapidly increasing in forest health, or conversely, the benefits of healthy and unhealthy stands are relatively similar; and c) the discount rate is low. The introduction of uncertainty did not significantly affect the likelihood of a proactive management strategy being optimal, but it did show that the conditional probabilities of infection play important role in the decision of which uninfected stand should be treated if a choice is available to the manager.

Introduction

The emergence of a global economy, associated in large part with increased movement of goods and services, has also increased the probability of non-marketable organisms establishing themselves in areas outside of their native habitat (Mack and others 2000, Mack and Lonsdale 2001). In some cases, economic damages associated with such movement and establishment will be minimal.[1] In others, however, conditions such as a lack of natural enemies for the non-native species and/or a lack of resistance in native organisms to the new species may be sufficient to render significant damages, and earn the label of invasive pest (Schoettle and Sniezko 2007).

Forests are among the ecosystems being impacted by non-native pests and pathogens. Numerous pathogens, non-native arthropod pests and non-native plant species have already disrupted many forest ecosystems throughout North America. Examples include *Cryphonectria parasitica* (Murrill) Barr, the fungal pathogen responsible for chestnut blight of American chestnut trees; *Ophiostoma novo-ulmi* Brasier, the fungal pathogen responsible for the Dutch elm disease of American elm and other native elm species; and *Cronartium ribicola* J.C. Fisch., the fungal pathogen that causes white pine blister rust (WPBR) and cycles between native 5-needle white pines, currants, and gooseberries. Non-native pathogens have severely reduced some forest species populations, altered forest composition, and threatened the habitats of endangered animals (Liebold and others 1995).

Most invasive species management strategies focus on (1) prevention, (2) early detection and eradication, (3) containment and control, and when those efforts are unsuccessful, (4) mitigation of impacts and (5) restoration of the degraded forest (Schoettle and Sniezko 2007). However, in some cases (such as with WPBR), (1)-(3) have proven challenging, with no effective strategies identified. As such, there is a growing interest in preemptively managing ecosystems to mitigate the potential negative impacts of invasives before significant damage occurs, but without preventing the spread of the pest (usually due to technological or cost reasons). However, only recently have the physical outcomes of these forest management techniques been explored, and the economic conditions under which such "proactive management" is optimal have not been analyzed (Schoettle and Sniezko 2007).

This paper provides a preliminary model that can be used to analyze the conditions under which it might be optimal to pursue a proactive, as opposed to reactive, management strategy in the case of an invasive forest pathogen whose spread cannot be contained. A spatially-explicit stochastic dynamic programming model is developed that tracks the state of each of N number of stands of a host tree species potentially infected by a damaging invasive species. Subject to the expected evolution of the forest, a manager is assumed to allocate (finite) resources to treat the forest, and can treat any stand in either a proactive (prior to arrival of the invasive) or reactive (after invasive establishment) manner. Results highlight the circumstances under which proactive management is favored, including the physical structure of the forest, stand/forest benefits, management costs, and the probabilities of pathogen spread.

We contribute to the literature in the following ways. First, to our knowledge, there are no published articles in the economics or forestry literature that utilize a dynamic programming methodology to evaluate forest management strategies in the presence of an invasive species. There are, however, a few examples of using these techniques for timber management, including Spring and Kennedy (2005), who examined optimal harvest on multiple stands in the presence of stochastic fire risk and an endangered species in Australia, and Moore and Conroy (2006), who examined silviculture practices for management of old growth forests for habitat purposes in a wildlife refuge in Georgia. Second,

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there is little in the economics literature regarding proactive management, perhaps because these strategies are contrary to current conservation approaches that would advocate preservation of so-called "natural" systems, and thus hostile to human intervention into reasonably undisturbed systems. However, proactive management may enable naturalization of the non-native organism while sustaining host populations and ecosystem function (Kilpatrick 2006). Finally, this study contributes to the literature on spatial process in the environmental and resource literature through the incorporation of an explicit spatial structure in the representation of the forest through which an invasive organism moves. In the presence of budget constraints, decisions regarding which stands to manage (either proactively or reactively) will inevitably involve tradeoffs over space as well as time.

Rationale of Proactive Mangement: The Case of White Pine Blister Rust (WPBR)

Cronartium ribicola, the fungus that causes WPBR, is among the invasive species introductions into North America where containment and eradication efforts have failed (Maloy 1997). It was introduced on the northwest coast of North America from Europe in the early twentieth century, and has since caused a variety of damage to the various species (some keystone) of noncommercial five-needle pines in high elevation North American ecosystems, including foxtail, limber, Rocky Mountain bristlecone, southwestern white, and whitebark pines. WPBR is a lethal disease that causes tree mortality at all life stages, disrupting the regeneration cycle with potentially severe effects on white pine forests.[2] Damages as a result of WPBR infection and tree mortality include effects on various ecosystem components and services such as animal populations (such as Clark's nutcracker birds, grizzly bears, and red squirrels), watershed production through snow capture, biodiversity and degradation of high-quality recreation opportunities (Petit 2007; Samman and others 2003; Tomback and Kendell 2001; Tomback and others 1995; Mattson 1992; McKinney 2004; Kendell and Arno 1990; McDonald and Hoff 2001). In fact, forests of these types are among the most visited in the country, including those found in the Western region of the National Park system (e.g., Glacier, Yellowstone, and Rocky Mountain National Parks).

The nature of five-needle pine forests suggests that natural evolution of resistance to WBPR is unlikely without intervention[3], though some natural genetic resistance has been identified in some stands (Sniezko and others 2008; Schoettle and others, Preliminary Overview of the First Extensive Rust Resistance Screening Tests of *Pinus flexilis* and *Pinus aristata*, this proceedings). As such, breeding programs may help to preserve naturally resistant seed stock in high-elevation species, as is being done for commercial species of white pines (McDonald and others 2004). The potential may soon exist for proactive management in which genetically-resistant trees are either directly planted or indirectly encouraged through alternative management actions (stimulating natural regeneration of resistant trees) *prior to* infection (Schoettle 2004a, 2004b; Schoettle and Sniezko 2007). The rationale behind proactive management, then, is essentially one of "preparing the battlefield" for a transition from an uninfected to infected state. Acting prior to invasion would presumably increase the proportion of genetically resistant trees, thereby reducing impacts on various ecosystem services due to mortality, increasing the probability of a healthy, regenerative system in the long run, and reducing or eliminate the need for reactive management post-invasion. Of course, such management might also be not only directly costly (through management expenditures), but also generate costs (to, say, recreationalists or naturalists) from the disturbance of a previously undisturbed forest. We term such costs "management externalities".

To date, there has been little information provided to potential forest managers regarding the circumstances under which proactive management might be preferred to the more common reactive strategies (Burns and others 2008). In the following sections, we provide a preliminary model that helps to shed light on these issues. Future research will refine the model using data on non-market benefits of high-elevation forests and the epidemiology of WPBR in the Rocky Mountain region.

The Dynamic Management Model

General Description

We assume that a resource manager has responsibility over a forest threatened by a non-native species whose spread cannot be arrested through any management action (a circumstance such as WPBR). As in Spring and Kennedy (2005), the forest is composed of N stands, with the state of each stand in time period t represented by one of a countable number of states representing a) the health of the stand (or level of ecosystem services provided by the stand) and b) the status of the stand as "treated" or "untreated". An untreated stand, once infected by the invasive pest and left untreated, will dynamically evolve such that mortality increases (ecosystem services decrease) until a terminal level is reached and maintained throughout the infinite time horizon of the problem. Once treated, perhaps by either planting resistant seedlings or otherwise encouraging reproduction of resistant biomass, a stand recovers until it reaches a relatively healthy terminal state, where it remains for the remainder of the problem. Treatment thus does not eliminate invasive spread, but minimizes long-run impact through the addition of resistant trees in the spirit of Kilpatrick (2006). Treatment of an uninfected stand results in a transition to a healthy state with probability one, in accordance with the rest of the forest dynamics detailed below.

Managers may treat any stand at any time, but are subject to a budget constraint that limits the number of stands treated in any one decision period. For simplicity, we assume only one treatment alternative whose success is certain (though this is fairly easily relaxed), and per-stand treatment costs are assumed to decrease with tree mortality (increase with ecosystem service provision). As noted above, spread of the invasive species is assumed not to depend on management actions, and is directional and potentially probabilistic in its spread (as in the case of WPBR). Ecosystem service benefits from the physical state of each stand are assumed to be homogeneous and decreasing in stand mortality, and total net benefits from the forest are additive across stands. The manager is assumed to maximize the net present value of the expected net benefits from stand treatment over an infinite time horizon, subject to the spread and damage caused by the invasive species and the budget constraint.

Forest Dynamics

The model of the forest is cellular and spatial in nature, with N=4 stands. At any time t, each stand χ_i, $i = 1,\dots,N$, is assumed to be in one of $S = 7$ discrete states representing the overall health of the stand and the treatment status of it. Overall, there are three health states corresponding to ecosystem service provision (healthy, moderately healthy, and not healthy) and two treatment states (treated and untreated) for stands that have been infected by the invasive, plus one more state representing a healthy stand that has not yet been exposed to the non-native pathogen. The total number of potential states of the forest is thus $S^N = 7^4 = 2{,}401$, which illustrates the necessity of restricting attention to four stands using standard discrete-space numeric dynamic programming techniques.[4]

The states of each stand are defined categorically, where $\chi_i = 0$ implies lack of invasive establishment on an untreated stand. Let τ_i be an indicator variable that signifies if stand i has ever been treated, and restrict attention to stands where the invasive has been established. As such, untreated stands can take on states

$$\chi_i = \begin{cases} 1 \text{ if } \tau_i = 0 \text{ and stand } i \text{ is healthy} \\ 2 \text{ if } \tau_i = 0 \text{ and stand } i \text{ is moderately healthy} \\ 3 \text{ if } \tau_i = 0 \text{ and stand } i \text{ is not healthy} \end{cases} \quad (1)$$

Once treatment has occurred, the three potential states are

$$\chi_i = \begin{cases} 4 \text{ if } \tau_i = 1 \text{ and stand } i \text{ is healthy} \\ 5 \text{ if } \tau_i = 1 \text{ and stand } i \text{ is moderately healthy} \\ 6 \text{ if } \tau_i = 1 \text{ and stand } i \text{ is not healthy} \end{cases} \quad (2)$$

Note that by assumption, an uninfected or "just infected" stand (states 0 and 1) immediately transitions to the terminal healthy state (state 4) if treated.

State transitions in time t+1 depend on the initial state of the stand at time t (namely x_{it}), the value of the treatment control variable for that stand ($u_{it} = 1$ if treated), and in the case of an uninfected stand, the event of stand infection and establishment, denoted by the event indicator $\phi_i = 1$. The state transitions are thus defined as

$$x_{it+1}(x_{it}, \phi_{it}, u_{it}) = \begin{cases} 0 \text{ if } x_{it} = 0 \text{ and } \phi_{it} = 0 \text{ and } u_{it} = 0 \\ 1 \text{ if } x_{it} = 0 \text{ and } \phi_{it} = 1 \text{ and } u_{it} = 0 \\ 4 \text{ if } x_{it} = 0 \text{ and } \phi_{it} = 0 \text{ and } u_{it} = 1 \\ x_{it} + 1 \textit{ if } 0 < x_{it} < 3 \text{ and } u_{it} = 0 \\ x_{it} + 4 \textit{ if } 0 < x_{it} < 3 \text{ and } u_{it} = 1 \\ x_{it} - 1 \text{ if } 4 < x_{it} \le 6 \\ 3 \text{ if } x_{it} = 3 \text{ and } u_{it} = 0 \\ 6 \text{ if } x_{it} = 3 \text{ and } u_{it} = 1 \\ 4 \text{ if } x_{it} = 4 \end{cases} \quad (3)$$

Note that state 3 (unhealthy stand) is a terminal state for untreated regions, while state 4 (healthy stand) is a terminal state for treated regions. Assuming that the effects of treatment are certain and there are no other exogenous threats to the forest (for example, fire, climate change …), the only stochastic element in the model is the infection and establishment event $\varnothing_{it} = 1$. We turn to considerations of this variable in the next subsection.

Probabilities of Stand Infection and Spatial Forest Structure

The spatial configuration of the forest is represented by a NxNmatrix **z** with elements $z_{ij} = (0,1)$. For row i, a non-zero element in position j indicates that an infected neighbor j increases the probability of infection of stand i in the following period. Similarly, for column j, a non-zero element in row i indicates that stand i is more at risk once j is infected. As such, through specification of this matrix, a "directionality" of spread can be modeled. For example, suppose that spread is deterministic in a southeast direction (including due east and due south), in the sense that once a neighbor to the north or west of stand i is infected in time t, then stand i will become infected in time t+1 with a probability of one, and otherwise will not be infected. Further assume that are stands arranged in a rectangular formulation such that stand 1 is to the northwest, stand 2 is northeast, stand 3 is in the southwest, and stand 4 is in the southeast. The matrix **z** is thus defined as

$$\mathrm{z} = \begin{bmatrix} 0 & 0 & 0 & 0 \\ 1 & 0 & 0 & 0 \\ 1 & 0 & 0 & 0 \\ 1 & 1 & 1 & 0 \end{bmatrix}, \quad (4)$$

so that, for example, stand 4 will be infected in t+1 if any of stands 1, 2, or 3 are infected in time t (row 4), but the infection status of stand 2 only affects the probabilities associated with stand 4 (2nd column).

In general, we assume that the probabilities associated with establishment of the invasive on a given stand are a function of the number of infected neighboring stands as defined by the matrix **z**. Let $s_{ij} = 1$ if $x_j > 0$, 0 otherwise, and define the number of infected neighboring stands for stand i as $\overline{n_i} = \sum_i z_{ij} \cdot s_{ij}$, with $0 \le \overline{n_i} \le 3$. The infection and establishment event, then, is a function of the spatial structure of the

Table 1. Stand infection probabilities as a function of number of infected neighbors, deterministic and stochastic cases.

# of infected neighboring stands ($\bar{\boldsymbol{n}}_i$)	$\Pr(\varnothing_i \mid \bar{n}_i\ (\mathbf{x},\mathbf{z}))$ Deterministic	Stochastic
0	0.0	0.1
1	1.0	0.6
2	1.0	0.8
3	1.0	0.9

forest and the states of the surrounding stand, and the associated probabilities, namely $\Pr(\varnothing_i \mid \bar{n}_i\ (\mathbf{x,z}))$ are given in Table 1. Note that for this paper, the probabilities are illustrative, and not empirically based.

Using these probabilities, we define $\Pr(x_{ij}^{+} \mid x_i, \bar{n}_i(\mathbf{x},\mathbf{z}), u_i$) to be the probability of a stand transitioning from state x_i to state x_{ij}^{+} conditional on the state of the forest and the control chosen. Of the S^N potential states in the model, then, the transitions associated with $(S\text{-}1)^N$ are deterministic. In the case presented here, this is approximately 54 percent of all possible starting states.

Economic Parameters

Table 2 reports information about the benefits and costs associated with forest management. We assume that in each (multi-year) period, benefits from the forest are the net present value of the sum of stand-level ecosystem service benefits, which are increasing with the health of each stand. We denote these as $f(x_i)$. Treatment costs $c(u_i,x_i)$ are incurred only in the current period, and are decreasing with the health of each stand due to ease of management and the potential for management externalities.

The manager is assumed to be constrained in action due to budget, and as such can only treat a limited number of stands per period.[5] As such, the control set U is defined directly from this constraint. For example, if the budget is one stand per year, then the number of elements in U is five, corresponding to treating each individual stand plus not treating any. If, however, two stands may be treated in the same time period, then the control set is augmented to include eleven possible stand combinations.

Table 2. Net present value of benefits and costs for forest stand states per time period, baseline scenario.

State of stand x_i	Description	Per-stand benefits $f(x_i)$	Per-stand treatment costs $c(u_i, x_i)$
	Uninfected and not established		
0	Uninfected, healthy	10	7
	Infected and established		
1	Infected and healthy	10	7
2	Infected and moderately healthy	5	5
3	Infected and not healthy	0	2
4	Treated and healthy	10	7
5	Treated and moderately healthy	5	5
6	Treated and not healthy	0	2

Collecting these assumptions and placing them in the framework of a dynamic programming problem, the discrete-time Bellman equation characterizing the problem is

$$V(\mathbf{x}) = \max_{\mathbf{u}\epsilon U},\{\sum_i [f(x_{i)} - c(u_i,x_i)] + \beta E[V(\mathbf{x}^{+}(\mathbf{x},\boldsymbol{\varphi},\mathbf{u}))]\}$$

$$= \max_{\mathbf{u}\epsilon U}\{\sum_i [f(x_i) - c(u_i,x_i)]$$

$$+\beta \sum_{j=1}^{S^N} [\Pr(\mathbf{x}_j^{+} \mid \mathbf{x}, \bar{\mathbf{n}}(\mathbf{x},\mathbf{z}),\mathbf{u}) V(\mathbf{x}_j^{+}(\mathbf{x},\boldsymbol{\varphi},\mathbf{u}))]\}, \tag{5}$$

where $\mathbf{x}^{+}(\mathbf{x},\ \phi\ ,\mathbf{u})$ is the vector of state transition equations defined in (3), $\Pr(\mathbf{x}_j^{+} \mid \mathbf{x}, \bar{\mathbf{n}}(\mathbf{x},\mathbf{z}),\mathbf{u})$ is the probability of transition from state $\mathbf{x}$ to $\mathbf{x}_j^{+}$, defined as the product of the stand level probabilities $\Pr(x_{ij}^{+} \mid x_i, \bar{n}_i(\mathbf{x},\mathbf{z}), u_i)$, and β is the discount factor, suitably defined to reflect the number of years assumed between each time period.

The model was coded and solved numerically in MATLAB using the default policy iteration method of the CompEcon toolbox in Miranda and Fackler (2002). Given a particular parameterization of the model (including the probabilities, benefits and costs of each stand in each state, and the discount factor), the solution to (5) allows for recovery of the optimal management plan that maximizes the net present value of the entire forest (four stands) over an infinite time horizon using standard dynamic programming techniques (see Miranda and Fackler 2002). These optimal strategies are functions of the states of the system (defined as the health of all four stands), and take the form of a four by one vector that indicates treatment or non-treatment of each stand in each state. For the purposes of this study, treatment of a stand before infection is termed proactive.

Results

Optimal Deterministic Policies

Optimal policies for a sample of starting states under two budget constraints (a maximum of one stand treated per decision period and a maximum of two stands treated per decision period) are presented in Table 3, assuming deterministic invasive species spread in the southeast direction with stands one and two to the north and stands three and four to the south arranged in a rectangular fashion (see Figure 1). The discount factor is assumed to be 0.9. Note that "do nothing" is an admissible management strategy in all cases; as such, the optimal results reported below are superior to this option.

Under the baseline parameterization, and considering the case of a maximum of one treated stand per period, there are 1,105 forest configurations in which proactive management, defined relatively strictly as treating an uninfected, previously untreated stand, is feasible.[6] Of this set, approximately 13 percent (145) of the optimal management strategies could be classified as proactive. The large majority of these occur when the infection threat is immediate (i.e., a stand to the northwest of an uninfected stand is infected), and the other

Table 3. Optimal policies for selected starting states and budget constraints, deterministic model.

Starting States				Optimal Treated Stands and Proactive Indicator			
				max 1 treated		max 2 treated	
Stand 1	**Stand 2**	**Stand 3**	**Stand 4**	**Treated Stand**	**Proactive?**	**Treated Stands**	**Proactive?**
0	0	0	0	none	no	none	no
1	0	0	0	1	no	1,2	yes
1	1	0	0	1	no	1,2	no
1	4	0	0	1	no	1,3	yes
2	0	0	0	2	yes	1,2	yes
2	4	4	1	3	n/a	3,4	n/a
5	4	4	1	4	n/a	4	n/a
6	4	4	5	none	n/a	none	n/a
4	4	4	4	none	n/a	none	n/a

stands are either uninfected or have already been treated, and thus are in states 0 or 4 through 6. Intuitively, this makes sense as the opportunity costs of treating a stand proactively in this case are small, given that the remainder of the forest is relatively protected and increasing in health. If, however, at least one stand is actively degrading or degraded (states 1-3), it is generally optimal to treat one of these stands in a reactive fashion (though the specifics depend on the relative states of each degrading stand and the potential for damage through spread). One exception to this prescription is if exactly one of the stands is only moderately healthy (state = 2) and the only other infected stand has been treated. In this case, the optimal strategy is to proactively treat the northeast-most uninfected stand. Presumably, this result occurs as a result of the interaction between the opportunity costs of treatment and the fact that treatment costs for the moderately infected stand will fall enough such that it pays to wait to treat. We further explain the incentives below.

If the budget constraint is relaxed to accommodate treatment of up to two stands per time period, then the percentage of times it is optimal to pursue proactive strategies increases to 41%, more than three times the one-stand per time period number. This set of proactive strategies generally includes cases where if there are two or more stands infected, at least one has already been treated. Given the flexibility inherent in this parameterization of the problem, the spatial dimension is more apparent as well. For example, a manager will generally treat degrading cells to the northwest, ceteris paribus, through s/he still must trade off the potential for spread and increased future damage with the cost decrease (and own-stand damage increase) if treatment does not occur. As such, we conclude that proactive management under this deterministic directional spread scenario is generally favored as resource constraints are relaxed, but not at the expense of reactive management when multiple stands are degrading. However, this is but one set of benefit and cost schedules, suggesting an analysis of the effects of these measures at the margin is appropriate.

Effects of Benefits and Costs

Of course, the tradeoffs involved in dynamic forest management in the presence of an invasive species are in large part determined by the marginal benefits and costs of treatment, which in turn depend on both spatial and temporal features. We now turn to the effects of shifting the relative benefit and cost schedules associated with forest stands in order to determine their effects, and thus provide some sensitivity analysis of the results.

To illustrate, we run an experiment which doubles the cost of treatment in healthy stands and cuts the cost of treatment in unhealthy stands by half (the "high cost" scenario), while keeping costs for the moderately healthy stands the same in the two-stand constrained deterministic spread model. Thus, we have increased the marginal costs of treating a healthy forest, perhaps mirroring a case of relatively severe management externalities.

Following our earlier analysis, proactive strategies are now optimal for almost 57% (626/1105) of possible cases, despite the increase in treatment costs for uninfected and healthy stands. Part of the reason can be seen in from the difference in strategies from case (a) when $\mathbf{x}_a = [1\ \ 0\ \ 0\ \ 0]'$ and case (b) where $\mathbf{x}_b = [1\ \ 1\ \ 0\ \ 0]'$, as seen in Table 4. When the cost of treatment for healthy stands is relatively low, initial optimal treatment $u_a^{low}=[\textit{treat}\ 1\&2]$, but when it is relatively high, initial optimal treatment changes to $u_a^{high}=[\textit{treat}\ 2\&3]$. Similarly, for $\mathbf{x}_b$, $u_a^{low}=[\textit{treat}\ 1\&2]$ and $u_a^{high}=[\textit{treat}\ 3\&4]$. Note that in case *a*, both scenarios involve proactive management, while in case *b*, only u_a^{high} treats (both) uninfected stands.

This result cannot simply be explained by a change in the relative costs across cells, as treatment costs are homogeneous across all four stands. As such, the answer must lie with the opportunity costs of treatment. Advancing the system in case (a) according to the optimal policy, $\mathbf{x}_a^{+low}=[5\ \ 4\ \ 1\ \ 1]'$ and $\mathbf{x}_a^{+high}=[2\ \ 4\ \ 4\ \ 1]'$, with corresponding policies at these new states defined by $u_a^{+low}=[\textit{treat}\ 3\&4]$ and $u_a^{+high}=[\textit{treat}\ 1\&4]$. Following the paths to their terminal states of $\mathbf{x}^{\infty}=[4\ \ 4\ \ 4\ \ 4]'$, as in Table 4, it is clear that the *low* takes three decision periods to reach $\mathbf{x}^{\infty}$, while the *high* case takes four. The reason is that in the *high* case, the marginal benefit from the treatment cost reduction outweighs the discounted marginal reduction in benefits from allowing stand 1 to devolve into an unhealthy state, and then recovering once treated. Thus, the manager prefers what we might call a "purely" proactive strategy in

Table 4. Sample simulations under alterative treatment cost assumptions, deterministic, two-stand constraint model.

	Low Cost Scenario				Case *a* High Cost Scenario				High Cost Scenario Using Low-Cost Policy			
Time Period	Forest State	Treated Stands	Benefits - Costs	NPV	Forest State	Treated Stands	Benefits - Costs	NPV	Forest State	Treated Stands	Benefits - Costs	NPV
0	[1 0 0 0]	1,2	26	26.00	[1 0 0 0]	2,3	12	12.00	[1 0 0 0]	1,2	12	12.00
1	[5 4 1 1]	3,4	21	18.90	[2 4 4 1]	1,4	16	14.40	[5 4 1 1]	3,4	7	6.30
2	[4 4 5 5]	n/a	30	24.30	[6 4 4 5]	n/a	25	20.25	[4 4 5 5]	n/a	30	24.30
3	[4 4 4 4]	n/a	40	29.16	[5 4 4 4]	n/a	35	25.52	[4 4 4 4]	n/a	40	29.16
4	[4 4 4 4]	n/a	40	26.24	[4 4 4 4]	n/a	40	26.24	[4 4 4 4]	n/a	40	26.24
			Total	124.60			Total	98.41			Total	98.00

	Low Cost Scenario				Case *b* High Cost Scenario				High Cost Scenario Using Low-Cost Policy			
0	[1 1 0 0]	1,2	26	26.00	[1 1 0 0]	3,4	12	12.00	[1 1 0 0]	1,2	12	12.00
1	[5 5 1 1]	3,4	16	14.40	[2 2 4 4]	1,2	20	18.00	[5 5 1 1]	3,4	2	1.80
2	[4 4 5 5]	n/a	30	24.30	[6 6 4 4]	n/a	20	16.20	[4 4 5 5]	n/a	30	24.30
3	[4 4 4 4]	n/a	40	29.16	[5 5 4 4]	n/a	30	21.87	[4 4 4 4]	n/a	40	29.16
4	[4 4 4 4]	n/a	40	26.24	[4 4 4 4]	n/a	40	26.24	[4 4 4 4]	n/a	40	26.24
			Total	120.10			Total	94.31			Total	93.50

Low cost scenario: Treatment costs = $7 for healthy, $5 for moderately healthy, $2 for unhealthy
High cost scenario: Treatment costs = $14 for healthy, $5 for moderately healthy, $1 for unhealthy
Discount factor = 0.90

period one, but does so, perhaps counter intuitively, to capture the "benefits" of stand degradation.

Turning to case *b*, we see a very similar result, as the manager prefers to engage in a proactive strategy to protect stands 3 and 4 in the first period, while allowing for stands 1 and 2 to degrade in order to take advantage of the relative cost savings offered by treating partially healthy forests. These savings dominate the decision despite the additional expense of losing benefits in period two (after the second control decision), relative to the *low* case, as a result of two unhealthy treated stands that take an extra period to return to health.

We have thus illustrated that proactive strategies tend to be favored when the costs of stand treatment are increasing relatively rapidly in stand health, and conversely, then, when the benefits of stand health are relatively unresponsive to degradation. Put another way, the greater the change in net benefits as forest health changes, the more likely is proactive management to be optimal in a dynamic spatial setting, as the presence of "substitute" stands allows managers to take advantage of the cost savings resultant from degradation. Given the role that future damages play in the analysis, however, we now turn to the effect of the discount rate on the solution to the problem.

Effect of Discount Rate

The discount factor provides a relative weighting between the (unspecified) time period between which decisions regarding treatment are made and the forest stands evolve. The discount factor is defined as $\beta = \frac{1}{(1+r)}$ where *r* is the discount rate that represents the opportunity cost of capital, or conversely, the rate at which the next best alternative asset appreciates. In economic theory, the discount rate is used to represent the idea that one dollar of benefits today is preferred to one dollar of benefits in a future time period, as there is an intertemporal opportunity cost to waiting.

The baseline analysis assumed a discount factor of β=0.9. Without greater biological detail, it is hard to determine if such a weighting is appropriate for all scenarios. On the one hand, the length of time it takes species such as five-needle pines to grow and evolve might suggest that the discount factor should be lower; on the other hand, intergenerational equity and other concerns provide an argument that the discount factor should be relatively close to one (Spring and Kennedy 2005; Weitzman 2001). In order to investigate the effects of the discount rate, additional scenarios were analyzed as the discount factor decreased (less weight on the future). One would suspect that as the present was favored, the incentives for proactive management would decrease as the marginal benefits of treating an individual stand would decrease. In fact, this is exactly the case, and in some cases, is quite dramatic. For example, if the discount factor is 0.5 under the two-stand constraint, then the optimal strategy is to treat only completely degraded stands once that state is reached, and do nothing to any other stand in any other state. As such, the percentage of potential proactive management occasions that are optimal is zero. At β=0.65, this percentage increases to a very small one half of one percent (all cases where stand 1, which is positioned to spread the invasive to all other stands, is infected), and when β=0.70 and higher, the result is identical to the baseline scenario.

As such, so long as the discount rate (factor) is sufficiently low (high), proactive management strategies are part of the optimal forest management plan. In the cases considered here, there is a fairly narrow range with $.60<\beta<.70$ over which the optimal policies are affected, and tend to favor proactive strategies only when the spread potential for the invasive species is high and the forest is generally healthy. This corresponds to a situation in which a low weight placed on future outcomes is outweighed by the damage caused from increased invasive spread.

Effects of Uncertainty

In addition to the deterministic scenarios analyzed above, the model was also solved taking into account a probabilistic establishment regime for the invasive (see Table 1), but maintaining all other baseline scenario parameters for the two-stand constrained problem. In general, this scenario assumes that the threat of the invasive to an uninfected stand is increasing in the number of infected stands that have the ability to threaten it (in the sense of the matrix **z)**. In addition, there is an external threat in that the forest in the state [0 0 0 0] can become infected (in this case, with a probability of .4). For simplicity, the manager is assumed to maximize the expected net present value of profits, and thus is risk neutral in preferences.

Results of this exercise reveal that only small changes in optimal policy rules occur as a result of the uncertainty over spread.[7] In each case, it involves two infected stands with one treated, but the other two are undisturbed and must include stand 4 (the most threatened due to the directional nature of the spread). As direct result of the differential in probabilities of potential spread between the two stands, it is always optimal in the stochastic case to treat the "more threatened" stand 4, primarily as a direct result of the differential in probabilities of potential spread between the two stands. In the deterministic case, given the **z** matrix, the manager is indifferent between which stands to treat, as the probabilities related to spread are identical. As a result, there is no effect in the frequency of optimal proactive management over the deterministic case; rather, this result serves to guide the choice of stands to proactively manage, if there is indeed such a choice.

Discussion and Conclusions

This paper offers a preliminary investigation into the conditions under which it might be optimal to engage in proactive management of a non-timber forest resource in the presence of an invasive species whose spread is unaffected by management action. Although contrary to current practice, proactive management is defined as treating an uninfected area to encourage healthy ecosystem function, given that the arrival of the invasive is inevitable. The model is inspired by the problem of white pine blister rust (WPBR) in Whitebark Pine in the Rocky Mountain west of the United States, which has severely impacted Glacier National Park, and is currently threatening Yellowstone and Rocky Mountain National Park, among other public lands.

The model was solved under varying assumptions concerning the potential scale of management action (through the budget constraint), the benefit and cost schedules associated with the forest resource, the discount rate, and the level of uncertainty of spread. The primary management implications are that, all else equal, proactive management strategies are preferred when: a) more resources are available for treatment (a greater number of stands can be treated in any one decision period); b) the costs of treatment are rapidly increasing in forest health, or conversely, the benefits of healthy and unhealthy stands are relatively similar; and c) the discount factor (rate) is high (low), implying a relatively high weight on the future.

Additionally, although the introduction of uncertainty did not significantly affect the likelihood of a proactive management strategy being optimal, it did show that the conditional probabilities of infection play important role in the decision of which uninfected stand should be treated if a choice is available to the manager. At a more basic level, the results of the exercise can aid in developing optimal management plans so long as the model can be parameterized.

Although relatively simple, the model presented here should help managers understand the incentives related to non-timber forest management in the presence of an unavoidable and unalterable threat from an invasive species. Given a parameterization based in empirical data, this framework can be used to define optimal management plans given the state of a particular set of stands, and when and where proactive (and, indeed, reactive) management is preferred. Furthermore, it could also be used to evaluate the differences in discounted net benefits between treatment plans, though this is not explored in the current paper.

That said, future research can do much to clarify and augment the conclusions reported here. For example, improved parameterizations for a given circumstance, including the economic and biological/epidemiological representations of the system based on collected data, could assuage concerns about arbitrary assumptions. This includes not only state-space representation of the forest, but the number of potential management units as well. Similarly, managers have multiple treatment strategies available (planting, burning, both…), with outcomes of any strategy likely uncertain, with potentially varying streams of benefits and costs over time. As the modeling effort becomes more complex and thus more reflective of the system it represents, the results presented here can be used to verify and validate future results, help managers draw conclusions about the general conditions under which proactive and reactive management strategies are optimal, and inform about other similar processes and problems, such as the spread of infectious disease.

References

Bertsekas, D. P.; Tsitsiklis, J. N. 1996. Neuro-Dynamic Programming. Belmont, MA: Athena Scientific.

Brustein, F. C.; Yamaguchi, D. K. 1992. The oldest known Rocky Mountain bristlecone pines (Engelm.) Arctic and Alpine Research. 24(3): 253-256.

Burns, K. S., A. W. Schoettle, W. R. Jacobi, and M. F. Mahalovich. 2010. White pine blister rust in the Rocky Mountain Region and options for management. USDA Forest Service RMRS-GTR 206. 26p. Available at: http://www.fs.fed.us/rm/pubs/rmrs_gtr206.html.

Curry, D. R. 1965. An ancient bristlecone pine stand in eastern Nevada. Ecology. 46: 564-566.

Kendell, K. C.; S. F. Arno. 1990. Whitebark pine—an important but endangered wildlife resource. In: Schmidt W. C. and K. J. McDonald (eds). Proceedings—Symposium on whitebark pine ecosystems: Ecology and management of a high-mountain resource. General Technical Report INT-270, Ogden, UT: USDA Forest Service, Intermountain Research Station. pp 264-273.

Kilpatrick, A. M. 2006. Facilitating the evolution of resistance to avian malaria in Hawaiian birds. Biological Conservation. 128: 475-485.

Liebold, A. M., W. L. MacDonald, D. Bergdahl, and V. C. Mastro. 1995. Invasion by exotic forest pests: A threat to forest ecosystems. Forest Science. 41(2): 1-49.

Mack, R. N., D. Simberloff, W. M. Lonsdale, H. Evans, M. Clout, and F. A. Bazzaz. 2000. Biotic invasions: causes, epidemiology, global consequences, and control. Ecological Applications. 10: 689-710.

Mack, R. N.; W. M. Lonsdale. 2001. Humans as global plant dispersers: getting more than we bargained for. BioScience. 51: 95-102.

Maloy, O. C. 1997. White pine blister rust in North America: a case history. Annual Review of Phytopathology. 35: 87-109.

Mattson, D. J. 1992. Yellowstone grizzly bear mortality, human habituation and whitebark pine seed crop. Journal of Wildlife Management. 56: 432-442.

McDonald, G. I.; R. J. Hoff. 2001. Blister rust: an introduced plague. In: Tomback D. F., S. F. Arno, and R. E. Keane, eds. Whitebark Pine Communities. Washington, DC: Island Press. Pp. 193-220.

McDonald, G., P. Zambino, and R. Sniezko. 2004. Breeding rust-resistant five-needle pines in the western United States: lessons from the past and a look to the future. In: Sniezko, R. A., S. Samman, S. E. Schlarbaum, and H. B. Kriebel, eds. Breeding and genetic resources of five-needle pines: growth, adaptability, and pest resistance; 2001 July 23-27; Medford, OR, USA.

Miranda, M. J.; P. L. Fackler. 2002. Applied Computational Economics and Finance. Cambridge, MA: MIT Press.

Party 2.02.15. Proceedings RMRS-P-32. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station. Pp 28-50.

McKinney, S. T. 2004. Evaluating natural selection as a management strategy for restoring whitebark pine. Master of Arts Thesis, University of Colorado: Denver, CO.

Moore, C. T.; M. Conroy. 2006. Optimal regeneration planning for old-growth forest: addressing scientific uncertainty in endangered species recovery through adaptive management. Forest Science. 52(2): 155-172.

Petit, C. (Jan 30 2007) In the Rockies, pines die and bears feel it. New York Times. Available at: http://www.nytimes.com/2007/01/30/science/30bear.html?ex=1327813200en=9ba8339901252668ei=5088partner=rssnytemc=rss#.

Samman S., J. W. Schwandt, and J. L. Wilson. 2003. Managing for healthy white pine ecosystems in the United States to reduce the impacts of white pine blister rust. Forest Service Report R1-03-118. Missoula, MT: USDA, Forest Service. 10 p.

Schauer, A.J., A.W. Schoettle, and R.L. Boyce. 2001. Partial cambial mortality in high-elevation *Pinus aristata* (Pinaceae). American Journal of Botany. 88: 646-652.

Schoettle, A. W. 1994. Influence of tree size on shoot structure and physiology of *Pinus contorta* and *Pinus aristata*. Tree Physiololgy. 14: 1055-1068.

Schoettle, A. W. 2004a. Ecological roles of five-needle pine in Colorado: Potential consequences of their loss. In: Sniezko, R. A., S. Samman, S. E. Schlarbaum, and H. B. Kriebel, eds. Breeding and genetic resources of five-needle pines: growth, adaptability, and pest resistance; 2001 July 23-27; Medford, OR, USA. IUFRO Working Party 2.02.15. Proceedings RMRS-P-32. Fort Collins, CO: USDA Forest Service, Rocky Mountain Research Station. Pp 124-135. Available at: http://www.fs.fed.us/rm/pubs/rmrs_p032/rmrs_p032_124_135.pdf.

Schoettle, A. W. 2004b. Developing proactive management options to sustain bristlecone and limber pine ecosystems in the presence of a non-native pathogen. In: Shepperd, W. D., L. G. Eskew, compilers. Silviculture in special places: Proceedings of the National Silviculture Workshop; 2003 September 8-11; Granby, CO. Proceedings RMRS-P-34. Fort Collins, CO: USDA Forest Service, Rocky Mountain Research Station. Pp 46-155. Available at: http://www.fs.fed.us/rm/pubs/rmrs_p034/rmrs_p034_146_155.pdf.

Schoettle, A. W.; R. A. Sniezko. 2007. Proactive intervention to sustain high elevation pine ecosystems threatened by white pine blister rust. Journal of Forest Research. 12: 327-336.

Schulman, E. 1958. Bristlecone pine, oldest known living thing. Nattional Geographic Magazine. 113: 355-372.

Sniezko, R. A.; A. Kegley, R. Danchok, A. W. Schoettle, K. S. Burns, and D. Conklin. 2008. *Cronartium ribicola* resistance in whitebark pine, southwestern white pine, limber pine and Rocky Mountain bristlecone pine—preliminary screening results from first tests at Dorena GRC. In: McWilliams, Michael; Palacios, Patsy, comps. Proceedings of the 55th Annual Western International Forest Disease Work Conference; October 15-19, 2007; Sedona, AZ. Logan: Utah State University: 84-86. http://www.fs.fed.us/foresthealth/technology/wif/proceedings/WIFDWC2007.pdf

Spring, D. A.; J. O. S. Kennedy. 2005. Existence value and optimal timber-wildlife management in a flammable multistand forest. Ecological Economics. 55: 365-379.

Tomback, D. F.; K. C. Kendell. 2001. Biodiversity losses: the downward spiral. In: Tomback, D. F., S. F. Arno, and R. E. Keane (eds). Whitebark Pine Communities. Washington, DC: Island Press. Pp 243-262.

Tomback, D. F., J. K. Clary, J. Koehler, R. J. Hoff, and S. F. Arno. 1995. The effects of blister rust on post-fire regeneration of whitebark pine: the Sundance burn of Northern Idaho (USA). Conservation Biology. 9: 654-664.

Weitzman, M. L. 2001. Gamma discounting. American Economic Review. 91(1): 260-271.

ENDNOTES

[1] Such damages can be to marketable and/or non-marketable ecosystem services.

[2] Some infected areas in the American West have seen mortality of up to 90%.

[3] Individuals within these species can live for 1,000-4,500 years, can thrive in harsh environments, and are not frequently disturbed through stochastic events such as fire (Schoettle 1994; Schoettle and Rochelle 2000; Schauer et al. 2001; Schulman 1958; Curry 1965; Brustein and Yamaguchi 1992).

[4] For larger state spaces, more advanced techniques (rollout strategies, temporal difference learning, etc.) can be used to approximate the optimal solution. See, e.g., Bertsekas and Tsitsiklis (1996).

[5] Given this assumption, the interpretation of the budget constraint should not be strictly monetary. Rather, one might interpret it as a binding constraint on additional resources, such as labor or capital.

[6] Given the state transition structure assumed here, it might be logical to term treatment of infected, healthy stands (state 1) as proactive; but we choose not to in order to shed light on primarily “preventative” management options.

[7] We expect no difference in policy rules where proactive management is not possible, as these transitions are deterministic by assumption.

Exploring Whitebark Pine Resilience in the Crown of the Continent

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Abstract—Whitebark pine (*Pinus albicaulis*) populations are declining across western North America due to synergies of disturbances, both natural and anthropogenic. Losses at treeline may result in significant changes to the upper subalpine zone, which may result in a regime shift, thus affecting the ecological goods and services whitebark pine systems provide for other species, including humans. Management and restoration should acknowledge the coupled social-ecological dynamics of high-elevation forest systems. Resilience is proposed as an appropriate framework for understanding social-ecological systems because it acknowledges complexity and uncertainty in a changing world. Mismatches of scale (spatial, temporal and functional) are increasingly problematic in management, and can lead to a loss of resilience in connected systems, often years or decades after management strategies have been implemented. Identifying mismatches in whitebark pine systems may inform long-term restoration strategies across jurisdictional boundaries. This paper reviews resilience concepts, with an emphasis on scalar mismatches and the problem of 'fit'. A conceptual framework is proposed to measure the functional fit between institutions in a jurisdictionally diverse, transboundary region and the capacity to manage high-elevation whitebark pine systems.

Introduction

The boundaries of ecosystems are hard to define and rarely, if ever, match the socio-political boundaries that are imposed upon them. Yet the imposition of these boundaries, and how we manage within them, has led to the loss of ecological goods and services from local to global scales (Folke 2006). In addition, conventional natural resource management (NRM) often proceeds under the assumption that we can manage complex systems to yield the most benefits for humans (Walker and Salt 2006). However, this has resulted in ecological surprises that may not be seen or understood until decades later (e.g. loss of biodiversity, changes to biogeochemical cycles, and climate change) (Vitousek and others 1997). In fact, the anthropogenic effects on our natural systems are so pronounced that many researchers have suggested that we have entered a new era called the Anthropocene (Allenby 2004; Kotchen and Young 2007; Steffen and others 2007). Environmental degradation can also adversely affect our social systems through the loss of ecological goods and services that ecosystems provide making both social and ecological systems less resilient, or more vulnerable to disturbance. Therefore, acknowledgement of our world as a complex amalgam of coupled social-ecological systems is essential to maintain the resilience of these systems.

Land managers and scientists are moving away from traditional NRM paradigms and are beginning to adopt ecosystem-based approaches to management (EBM) that includes goals to maintain *ecosystem health and integrity*. However, defining such goals in explicit terms has proven elusive and makes the measurement of success problematic. The inherent complexity and uncertainty of ecosystems further complicates our ability to implement EBM effectively. Therefore, managers typically choose to manage for certain species, or indicators, that are representative of an ecosystem (Simberloff 1997).

However, the single-species approach mirrors traditional NRM paradigms by assuming that if particular species are present in an ecosystem, then a desired level of ecological health and function will be achieved. Managing under this paradigm may have negative impacts on other parts of the system, or at different spatial or temporal scales than were considered for managing indicator species. Although conservation efforts to protect species in decline are important, the single-species approach to conservation may not be sufficient over the long term.

Ecosystem-based management considers a wider context than a single-species approach by acknowledging that structure and function are both essential to maintain ecosystem integrity. It also acknowledges that human values influence what and how we manage our landscapes and resources. We suggest that EBM must also include a resilience approach that explicitly acknowledges the social-ecological connectedness of our resource and environmental systems. In such an approach, consideration of particular a species is made with a much stronger reference to its overall context. The re-framing of issues can be useful for eliciting new directions in management (Brugnach and others 2008). We suggest shifting our perspective from a single-species to a species-in context approach will result in strategies that better maintain or improve system resilience.

Whitebark pine (*Pinus albicaulis*) is one species that exemplifies how our past management regimes can result in ecological surprises at spatial and temporal scales well beyond what could have been predicted. Whitebark pine (WBP) is considered a foundation and keystone species in upper subalpine regions throughout its range, often growing in harsh windswept sites with poor soil quality (Resler and Tomback 2008; Smith and others 2008). WBP provides the conditions necessary for the succession of other species, and also regulates snowmelt, contributing to watershed dynamics (Ludwig

In: Keane, Robert E.; Tomback, Diana F.; Murray, Michael P.; and Smith, Cyndi M., eds. 2011. **The future of high-elevation, five-needle white pines in Western North America: Proceedings of the High Five Symposium.** 28-30 June 2010; Missoula, MT. Proceedings RMRS-P-63. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station. 376 p. Online at http://www.fs.fed.us/rm/pubs/rmrs_p063.html

and Smith 2005; Smith and others 2008; Tomback and others 1995). WBP produces large, high fat content seeds that are consumed by a variety of wildlife species, and has an obligate mutualistic relationship with Clark's nutcracker (*Nucifraga columbiana*), the primary seed dispersal agent for WBP (Logan and others 2010; Tomback 1982; Tomback and Resler 2007). Life history traits, ecological function, multiple stressors and system complexity, all combine to create a 'wicked problem' (Geist and Galatowitsch 1999; Rauscher 1999) for scientists and managers trying to restore WBP populations. Although ecologically important for the maintenance of high-elevation forests, WBP is only part of a larger social-ecological WBP system that includes its interconnectedness with other species, including humans, and processes. Without human intervention, this system may be lost (Keane 2000). Since WBP is not valued commercially (Tomback and others 1995), it creates an interesting case to examine from a resilience perspective because the values and drivers in this system are different than in a directly exploited system.

This paper will explore high-elevation WBP systems from a resilience perspective in a social-ecological context. We begin by outlining some of the major concepts of resilience theory that we think are pertinent to WBP systems and their decline. We conclude by proposing a framework to assess the capacity of the environmental regimes to maintain WBP across multiple scales in a transboundary region.

Resilience Overview

Ecological vs. Engineering Resilience

There are two ways in which resilience has been used in the literature. The distinction was first explored in the seminal paper "Resilience and Stability of Ecological Systems" (Holling 1973). The use of the term *stability* in ecosystems describes the amount of time it takes for a system to return to a state of equilibrium after a disturbance. This is central to the concept of *engineering resilience*, which assumes that ecosystems fluctuate around a single equilibrium or domain of attraction (Gunderson 2000). *Ecological resilience*, however, views ecosystems as having multiple state domains, in which different feedbacks and structures exist (Gunderson 2000). If a system threshold is exceeded, the system will move from one domain of attraction to another. This process is referred to as a regime shift (Folke and others 2004; Gunderson 2000). A classic example of a regime shift is the transformation of kelp forests to sea urchin barrens in the Pacific Northwest (Estes and Duggins 1995). Despite the focus on ecological systems, these concepts apply to complex, self-organizing social, ecological and social-ecological systems.

Social-Ecological Systems (SES)

People rely on ecological goods and services for survival, but the policies we create to manage them can cause environmental degradation and inhibit our capacity to react to environmental change. Thus, in order to manage for resilience, it is essential to consider social and ecological connections (Westley and others 2002; Zurlini and others 2006). The attributes of social-ecological systems are *resilience, adaptability* and *transformability*. As described above, resilience is defined as the ability of a system to absorb disturbance and still maintain essentially the same structure and feedbacks, or remain in the same domain of attraction as before a disturbance occurs (Holling and Gunderson 2002; Peterson and others 1998). The capacity to manage resilience reflects adaptability in the system, which is shaped by the systems of governance and the abundance of social, natural and other forms of capital available to maintain a system in a stability domain (Lebel and others 2006). This requires institutions and actors to self organize to learn and adapt to surprises that emerge from nonlinear behaviour (Lebel and others 2006). Transformability is the capacity to introduce new state variables into a system in order to transform it after a regime shift from one domain of attraction to another (Walker and others 2006; Walker and others 2004; Walker and Salt 2006) . This is necessary when a SES can no longer maintain itself, as seen in regions of Africa where villages shifted livelihoods to an ecotourism-based economy after resource depletion of lands rendered the agricultural systems untenable (Walker and others 2004).

Diversity plays an integral role in determining the resilience of social and ecological systems. In ecosystems, species that provide services, such as pollinators or grazers, belong to the same functional groups. The greater the number of functional groups, or *functional diversity*, the better a system will perform (Folke and others 2004; Walker and others 2006). The number of species that provide similar services acts as insurance for disturbance, so if one member of the group is affected, another can provide services to maintain ecosystem function. This *functional redundancy* is important for system resilience, and is enhanced if members within functional groups have a diverse set of responses to disturbances, called *response diversity* (Folke and others 2004; Walker and others 2006). Diversity in social systems is not as clear, but is intuitive that overlapping governance structures may be useful in event of the institutional collapse, and contribute to the resilience of adaptive governance structures (Walker and others 2006). However, NRM paradigms aim to reduce redundancies for efficiency in production (Walker and others 2006), where resilience recognizes that overlapping structures increases the ability of SES's to reorganize after disturbance.

The Adaptive Cycle and Panarchy Concepts

The core concept of how complex adaptive systems behave is illustrated in the adaptive cycle model (Figure 1) which shows how systems change over time. There are three components to the adaptive cycle; potential, connectedness and resilience (Holling 2001). The first two components are most commonly used to understand how a self-organizing system may undergo four phases in an adaptive cycle: growth, conservation, release and reorganization (Holling 2001; Holling and Gunderson 2002). The front-loop of the system is characterized by rapid growth or exploitation (r-phase) to a slower, more connected and rigid conservation phase (K-phase). The latter phase of the front-loop in resource-based SES's might be characterized by resource domination by a few species, high

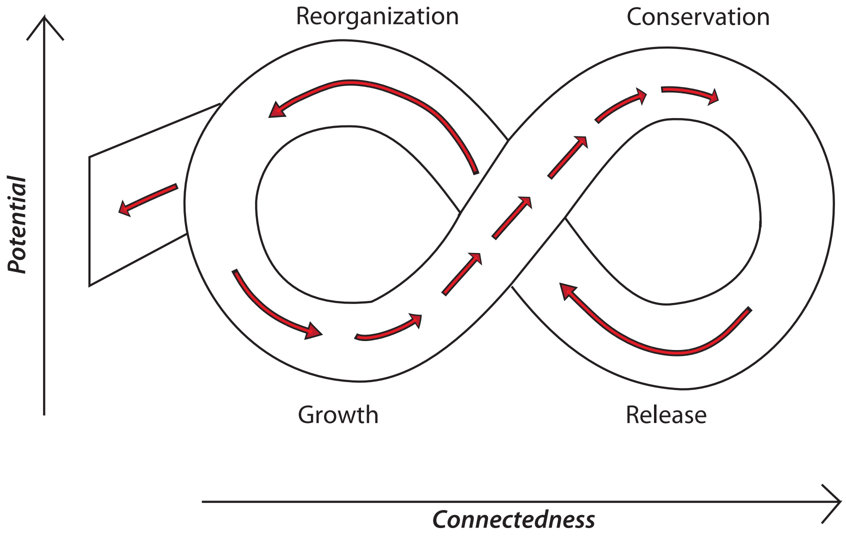

Figure 1. The adaptive cycle—A heuristic four-phase model of complex system behaviour. Arrows show that time in the foreloop (growth -conservation) is typically slow while the back-loop (release-reorganization) is fast. The X and Y-axis show how the connectedness and potential for change fluctuate through the cycle, demonstrating resilience as a dynamic trait of complex systems.

political influence by a few interest groups or even a lack of cultural diversity or innovative ideas (McAllister and others 2006). The growth and conservation phase is generally slow, where as the release and reorganization phase, also known as the back-loop of the adaptive cycle, is fast. The release phase (Ω-phase) is often caused by a trigger or disturbance that releases built up resources in the system which then reorganizes (α-phase), this is the part of the cycle where innovation and opportunity are generated (Holling and others 2002). If the system is reorganized in a manner that is recognizable, in terms of structure and function, it is thought to be in the same domain of attraction. However, if the resilience of a system is eroded, a disturbance may shift the system beyond a threshold into a new regime with new state variables and feedbacks dominating (Holling and Gunderson 2002; Holling and others 2002; Peterson and others 1998). How this plays out can either be a slow, gradual shift, such as with climate change, or fast, as seen with the eutrophication of lakes (Folke and others 2004). Returning to the previous system may be difficult or even impossible because the new system can also be resilient. Although the adaptive cycle model provides a useful heuristic for understanding complex system changes, not all systems will complete a full cycle of the model; a release event may occur when the system is still in a growth phase. The intention is not to use the model to explain what is happening, but to give a sense what might be (Walker and others 2006).

This model is used to describe dynamics at one scale of interest, but stability and function at one scale of influence is not easily generalized to larger scales (Peterson and others 1998). Resilience researchers also developed a conceptual model called *panarchy* (Figure 2) consisting of a nested set of interacting adaptive cycles (Holling and others 2002; Peterson and others 1998). Within this model, cross-scale interactions are identified to explain how bottom-up and top-down dynamics can influence the scale above or below. The panarchy model identifies two cross-scale processes that are essential for system sustainability; *revolt* and *remember* (Holling and others 2002).The *revolt* dynamic demonstrates when a system has become rigid at multiple scales, a small disturbance can trigger a release event that crosses scales, such as a fire moving from a stand to the landscape level. The *remember* dynamic is the source of renewal for a smaller system that is undergoing reorganization and helps regulate patterns across landscapes (Holling and others 2002; Peterson 2002). For example, surrounding mature forests can provide seed sources for stands after a fire event. Memory in social systems can come in the form of trust or cooperation after years of collaboration, or in financial assistance from higher levels of organizations. Panarchy does not assume only three levels of influence, but illustrates that research interests should consider at least one scale above and below when investigating a phenomena. Applying the adaptive cycle and panarchy for resource management appears highly promising. In the context of WBP systems, this approach has the potential to address transboundary problems by nesting the systems and acknowledging that ecosystems operate across scales.

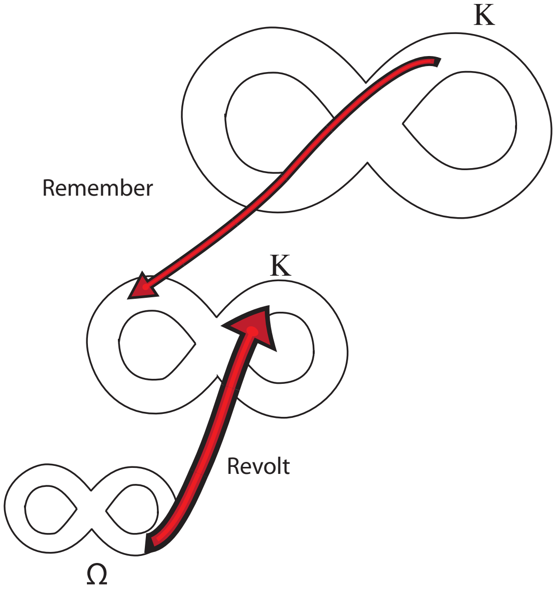

Figure 2. Panarchy—A set of nested adaptive cycles. Complex, self-organizing systems operate at multiple scales and across scales. Pattern and processes in ecosystems arise from the interplay of dynamics across scales.

Scale and Cross-scale Interactions

Scale is extremely important to consider in the natural world. Patterns and processes across a landscape arise from interplay among different spatial and temporal scales (Levin 2000). In the panarchy model, smaller and faster scales tend to induce change to the system above while larger and slower scales tend to constrain or conserve behaviour below (Carpenter and Turner 2000; Drever and others 2006; Peters and others 2007; Peterson and others 1998). Despite the apparent stability in this model, there is also danger that if a system is strongly connected across many scales, small disturbances at one scale can cascade through the system, which may have detrimental consequences (Drever and others 2006; Holling and others 2002; Raffa and others 2008). Cascading effects can flow from larger to smaller scales, and vice versa, as well as through the alteration of disturbance regimes (Folke and others 2004).

There are differences between scales of ecological systems and social systems. Social systems tend to be representative, including the actors and networks that make up the formal and informal mechanisms of governance (Cumming and others 2006). This is largely due to the fact that humans have foresight and act with intention; a quality not found in natural systems. Understanding scale presents new issues and uncertainty into the system when making decisions based in ecological research. Empirical data are difficult to measure across scales and management is often founded upon data collected at a restricted scale of interest (Cumming and others 2006). The subjectivity of the observer and organizational representation often contributes to a mismatch of scale between institutions and ecosystems.

Scale Mismatches and the Problem of Fit

Understanding how systems interact across scales is extremely important for understanding emergent behaviour that cannot be understood or predicted by focusing on one scale of interest (Peters and others 2007). However, these dynamics are not always as clear in social systems and mismatches between social and natural systems can become problematic (Levin 2000). Identifying mismatches may be crucial to develop strategies to maintain resilience. When the scale of social institutions that manage ecosystems and the scale of environmental variation of those ecosystems do not align, inefficiencies and disruptions of the social-ecological system, or important components are lost. This is what is termed a scale *mismatch* or *misfit* (Cumming and others 2006; Galaz and others 2008). Typically, there are three types of mismatches that are acknowledged in the literature; spatial, temporal and functional (Cumming and others 2006; Ekstrom and Young 2009; Young 2002)

Spatial mismatches are common. They can occur when the jurisdictional boundaries do not align with the ecological system boundaries. Some collaborative agency approaches have emerged to deal with landscape connectivity issues as a result of this. However, this does not ensure that a mismatch will be resolved. Another form of spatial mismatch can occur when centralized decisions are employed homogenously across landscapes without considering local biophysical differences (Galaz and others 2008).

Temporal mismatches can occur in a number of ways. For example, political cycles of planners and decision-makers may follow shorter cycles, perhaps every four years, but are making decisions on ecosystems that have evolved over hundreds or thousands of years. Inversely, environmental crises or surprise typically occur quickly by ecological standards, yet social responses to environmental change are slow (MacMynowski 2007).

Functional mismatches occur when institutions are unable to respond to the functionality and dynamics of the ecosystems they are managing (Ekstrom and Young 2009). A major source of misfit arises from a lack of knowledge, formal or informal, of ecological systems (Young 2002). Understanding when a threshold is being approached, or the consequences of management actions on other parts of the system, is highly uncertain. Often thresholds are only understood once they have been surpassed.

Ecosystem complexity and dynamics have inherent uncertainty which can make decision-making difficult, particularly when there are trade-offs to consider (Brown 2003). Misfits can arise from changes in variability of social or ecological systems, or dynamics from social-ecological interactions (Cumming and others 2006; Young 2002). However, the source of misfits may not be easy to identify and even more difficult to resolve. Due to the complexity of interactions within and across scales of social and ecological systems, a resolution to scalar mismatches will likely not occur at one scale, but require restructuring at multiple levels (Cumming and others 2006).

Whitebark Pine Resilience

Whitebark pine ecosystems are declining largely because of the mismatches we have created in our management regimes over the last 100 years. Despite the fact that much of WBP range is in wilderness areas and remote access areas (Keane 2000), anthropogenic stressors still negatively affect WBP populations. The levels of mortality through human drivers of change have threatened the very survival of this species in the long-term (Logan and others 2010). If whitebark pine were extirpated from these high-elevation regions, downstream hydrological impacts are likely, and the flashiness of run-off in spring may alter watershed dynamics (Ellison and others 2005; Yarnell and others 2010). Further potential consequences of loss over the long term could alter successional dynamics and further losses of biodiversity (Ellison and others 2005). Time lags, synergies and institutional/social barriers all have contributed to the current status of whitebark pine health. The implications for management are uncertain, particularly with potential climate change impacts for high-elevation forest dynamics.

Endogenous and Exogenous Stressors

Disturbance is a natural agent of renewal in social-ecological systems. Stressors can be endogenous or internal to system dynamics (such as fire regimes in WBP forests or staffing changes in an institution) or they can be exogenous, to the system (such as climate change or lack of funding).

Whitebark pine has a number of endogenous stressors that are natural sources of renewal. Fire regimes have been identified as a key ecological process that drives the structure and function of high-elevation forests. Mixed severity fires are most common in WBP stands, but large stand-replacing fires with a return interval of over 250 years tend to drive how it's distributed across the landscape (Keane 2000). Low severity fires, which WBP bark is adapted to resist, creates conditions favourable for seed dispersal by Clark's nutcrackers (Keane 2000; Resler and Tomback 2008). Avalanches also contribute to landscape patterns in high-elevation forests and are regulated by topography, snowpack and forest structure (Bebi and others 2009).

Mountain pine beetle have also played a role historically, with large outbreaks in the 1930's and 40's, and again in the 1970's (Brunelle and others 2008; Keane 2000; Logan and others 2010). They act as important sources of renewal by increasing the amount of woody debris on the forest floor, increasing streamflow in watersheds, and driving landscape heterogeneity (Raffa and others 2008). These disturbances act synergistically over space and time to drive the structure of WBP systems. For example, drought conditions may lead to larger stand-replacing fires, which reduces the amount of mature stands in an area, reducing the availability and suitability of host species for bark beetle outbreaks (Raffa and others 2008). Because these dynamics are internal to the system, the outcomes may be predictable when considering landscapes over longer time frames.

Exogenous stressors, on the other hand, are unpredictable and can alter dynamics across all scales of interest. Stressors outside the system tend to be anthropogenic. Climate change is a good example, and perhaps one of the greatest concerns for all social-ecological systems because changes are at the global scale. Scientists and managers are faced with the enormous challenge of managing ecosystems that may not behave as they have historically. Many researchers have asked the question whether studying historical ranges of variability will be useful for the future. Predictions of ecosystems shifting to higher elevations or latitudinal gradients could make it difficult for WBP to persist on the landscape (Logan and others 2010).

Another exogenous stressor for high-elevation WBP systems is white pine blister rust (WPBR) which has devastating effects over much of WBP range (Smith and others 2008). Introduced via infected white pine nursery trees in 1910, WPBR rapidly spread through much of the lower elevations of the white pine range by 1923 (Tomback and others 1995). Despite a complex life cycle that requires an alternate host (*Ribes*) to spread, this pathogen has been extremely successful in high-elevation WBP ecosystems where resistance to the rust has been estimated to occur in only 1 percent to 5 percent of the population (Tomback and others 1995). Elimination of the rust from the system is not considered an effective or possible strategy. Naturalization, which would shift WPBR from an external to internal stressor of the system through evolutionary adaptation is most desirable, assuming that management interventions of today will keep whitebark pine persisting on the landscape in the future.

Fire suppression is another exogenous stressor and a unique type of anthropogenic disturbance because it derives from the alteration of natural regimes, allowing less fire resistant species, subalpine fir and Engelmann spruce, to outcompete WBP and reduce the availability of microsite locations for natural regeneration processes (Keane 2000).

Threats to WBP are not homogenous; different regions are affected by a different set of stressors. For example, the Greater Yellowstone Ecosystem is primarily affected by an unprecedented level of mountain pine beetle infestations, while the Glacier-Waterton International Peace Park has high infection and mortality rates of WPBR (Berringer and others these proceedings, Logan and others 2010; Smith and others 2008). In most cases, it is the interaction of multiple disturbances that are responsible for WBP decline. Typically, WPBR does not kill a mature tree it infects for many years, but will kill cone-bearing branches, thus reducing the potential for regeneration and increases the ability for successional replacement of spruce and fir (Keane 2000). At some point, if cone production in a stand it too low, Clark's nutcrackers will begin to seek alternate food sources which may isolate stands, and thus reduce genetic diversity (McKinney and others 2009). Infected whitebark pine seedlings, on the other hand, will die within a couple years (Smith and others 2008). Moreover, blister rust weakens the tree, increasing its susceptibility to beetle attack or other agents.

Historically, bark beetles were constrained by cold winters, taking nearly three years to complete their life cycle in high-elevations. Increasing temperature from climate change has reduced that cycle to only one year, explaining why the current outbreak is considered to be outside the range of historical variation (Logan and others 2010).

Fire suppression has also contributed to unprecedented pine beetle outbreaks by creating the conditions that allow them to flourish (Raffa and others 2008). Looking at the adaptive cycle from the resilience literature, a mature forest is representative of the conservation phase (K-phase). By suppressing the natural agents for renewal, we allowed for the system to become too rigid and overconnected, thus increasing the potential for a larger disturbance event that may compromise the ability of the forest to regenerate within the same state domain. Since fire suppression was utilized over large landscapes and over long periods of time, the forest was too homogenous, and the MPB outbreak propagated across multiple scales, decimating the forest resources and the communities and institutions reliant upon them (Raffa and others 2008). Understanding interactions across space and time will be essential for increasing and maintaining resilience in WBP systems over the long term.

Conceptual Framework

Bounding the System—Study Site

The aim of this research is to identify mismatches of scale between institutions and ecosystems in WBP systems. We have chosen to bound our study in a regional transboundary context that reflects a diverse set of institutional scales. We have chosen to focus on the Crown of the Continent transboundary region for a number of reasons. First, it is considered to be a jurisdictionally fragmented region, representing institutions that range from federal levels of governance to individual households. Second, collaborative governance structures have begun to emerge from a desire to manage across scales by integrating EBM principles into management goals. Third, the geographic location of this area is centered between the northern and southern ranges of WBP ecosystems, and has the potential to serve as a core area for WBP regeneration in the face of climate change. Fourth, the region contains the Continental Divide, and is the source of water for many watersheds and agricultural regions downstream. Given the ecological role of WBP in watershed function, it provides an interesting social-ecological context for consideration. Finally, we are choosing to focus on WBP systems in the upper subalpine areas near treeline, where the role of WBP as a keystone species is most pronounced.

Proposed Framework and Methods

The theory and practice of understanding SES dynamics is still in its infancy, thus researchers are exploring new approaches to address the capacity of social systems to deal with uncertainty and change in managing natural systems over time (Folke 2006). A quantitative framework was recently suggested by Ekstrom & Young (2009) to assess the functional fit of institutions and ecosystems. The techniques described in their paper are intended to identify gaps in governance. The framework begins by creating an ecosystem model or matrix representing the system. The "ecosystem model" is generated around the ecosystem being managed or maintained, but includes identifying the key ecological and social components at multiple scales of the system in question. Then institutional data, which can be in the form of laws, management plans, meeting transcriptions or research, are collected and compared against the ecosystem model. Gaps are determined by the presence and absence of links acknowledged in the institutional data as compared with the ecosystem model, and a measurement of fit is produced for one or more regions.

We have adapted this model to determine the functional fit of institutions responsible for the recovery of WBP systems in the Crown of the Continent. To create the ecosystem model, we began by constructing a framework around conservation regimes for WBP recovery at multiple scales (Figure 3). The ecological components reflect the species-in-context approach by looking at specific species as well as more ecosystem-based dynamics. We began by considering genetic factors as well as other species connected to whitebark pine dynamics or its decline. Ecosystem functions are those processes that WBP systems provide as ecological goods and services. Ecosystem processes are those that are a source of renewal in the system, or are endogenous stressors. Only key components, derived mainly from literature on WBP research, are included in this representation of the ecosystem.

The social components focus on the management activities recommended for the recovery of WBP systems. Not all restoration tools are listed in this section, but multiple activities are considered under a single management action. For example, "cone caging" will also include cone collection for genetic seed bank storage and seedling production as that is the intention of the management action. We also included human values as a separate category because they can be a driver for conservation or may constrain the capacity of managers to act if not aligned with management goals. Anthropogenic stressors, despite being ecological in effect, are driven by human activity, thus are considered a social component in this framework. Furthermore, these exogenous stressors contribute high levels of uncertainty in the system, often without historical precedents that scientists and managers can draw upon to make better decisions. The WBP ecosystem model is then translated into matrix format by listing all the key ecological and social components identified in the conceptual framework along each axis (Table 1), then links between these components are identified.

The next phase of this research will be to collect the data to populate the framework. Institutional data will be collected through semi-structured interviews rather than through document review for two reasons. First, we have assumed that because the issue of whitebark pine decline is relatively new as a conservation priority, it is unlikely that ecosystem links are being acknowledged in documentation or that such documentation has been fully developed. Second, management prescriptions on paper may not get implemented on the ground (Ekstrom and Young 2009). Therefore, interviews will be used to collect the most accurate, current data for WBP systems, however an analysis of documentation may be considered later if additional data is required. The analysis of the data will also use a weighted representation of the ecosystem model to include priorities of concern for whitebark pine recovery.

Institutional mechanisms, such as learning, trust, and co-operation across jurisdictions, will not be included in the matrix, although it is our intention to address them in the semi-structured interviews. Recommendations to improve resilience will be made to improve transboundary management of WBP ecosystems. This research may further provide a framework for researchers working on other five-needled pine species, where the social-ecological context may have different feedbacks and structures to consider.

Conclusion

Whitebark pine systems are losing resilience, and adaptive approaches that try to cope with surprise may be insufficient without considering the social-ecological context. By gaining a better understanding of the capacity of institutions in managing ecosystem dynamics across scales, and where mismatches between them occur, we may be able to craft a better strategy to manage resilience in high-elevation ecosystems. With increased uncertainty due to climate change threats, adaptation will be essential for humans to cope with environmental change. How information is shared, learned and trusted across social-political boundaries will influence resilience, particularly in transboundary nations embodying multiple levels of governance.

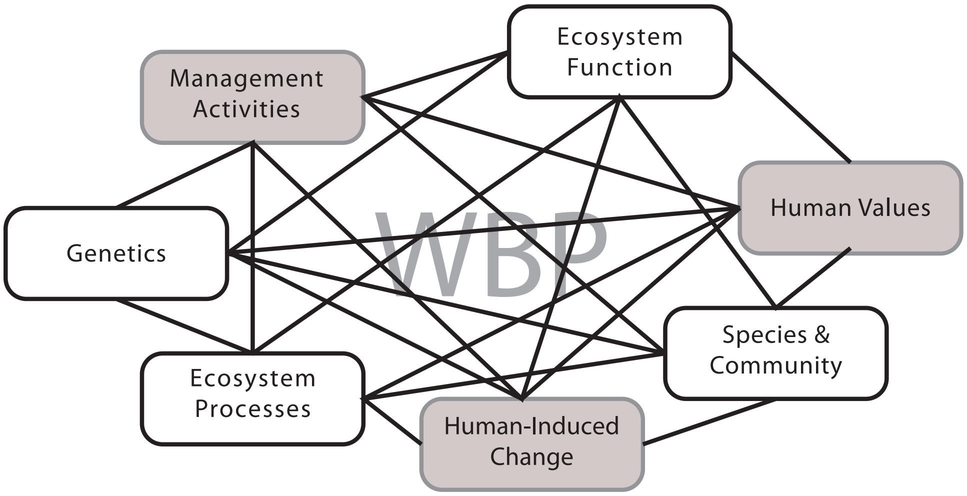

Figure 3. Conceptual framework—Component of whitebark pine restoration as a social-ecological system. Connections at the genetic, species and community levels are considered within high-elevation forests. Also, important functions and processes are included to capture cross-scale interactions that are essential to maintaining and restoring WBP populations. Social components consist of anthropogenic stressors, management activities and human values.

Table 1 - Proposed ecosystem matrix [a] - key ecological and social components at multiple scales as adapted from literature and relationships between variables are identified.

			rust resistance	whitebark pine	Clark's Nutcracker	squirrel/bear	mychorrizal fungi	*Ribes*	snow	slope stability	dispersal	establishment	competition	pine beetle	fire	white pine blister rust	fire suppression	climate change	cone caging	planting	pheremone	site alteration	aesthetic	recreation
ECOLOGICAL	**Genetic**	rust resistance	-	1	0	0	0	0	0	0	1	0	0	0	0	1	?	0	1	1	0	0	0	0
	Species & Community	whitebark pine	-	-	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
		Clark's Nutcracker	-	-	-	0	0	0	0	0	1	1	0	0	1	0	0	0	1	0	0	1	1	1
		squirrel/bear	-	-	-	-	0	?	0	0	0	0	0	0	0	0	0	0	?	0	0	0	1	1
		mychorrizal fungi	-	-	-	-	-	0	0	0	0	1	0	0	?	0	0	?	0	1	0	?	0	0
		Ribes	-	-	-	-	-	-	0	0	0	0	0	0	0	1	?	?	0	0	0	1	0	0
	Processes & Ecosystem Function	snow	-	-	-	-	-	-	-	1	0	1	0	0	0	0	0	1	0	1	0	0	1	1
		slope stability	-	-	-	-	-	-	-	-	0	0	0	0	1	0	0	0	0	0	0	0	0	0
		dispersal	-	-	-	-	-	-	-	-	-	1	0	0	1	1	1	?	0	1	0	1	0	0
		establishment	-	-	-	-	-	-	-	-	-	-	?	0	1	1	?	1	0	1	0	1	0	0
		competition	-	-	-	-	-	-	-	-	-	-	-	?	1	?	1	1	0	0	0	1	0	0
		pine beetle	-	-	-	-	-	-	-	-	-	-	-	-	1	1	1	1	0	0	1	1	1	?
		fire	-	-	-	-	-	-	-	-	-	-	-	-	-	?	1	1	0	0	0	1	1	1
SOCIAL	**Human-Induced Change**	white pine blister rust	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	1	1	1	0	0	1	0
		fire suppression	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	0	0	0	1	?	0
		climate change	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0	0	0	0	0	0
	Management Activities	cone caging	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	1	0	?	0
		planting	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0	1	0	0
		pheremone	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0	0	0
		site alteration	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	1
	Human Values	aesthetic	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1
		recreation	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-

1	connected
0	not connected
?	uncertain/ may be connected

.[a] matrix to be further developed and clarified through key-informant interviews

References

Allenby, B. 2004. Managing Earth Systems In the Anthropocene. Environmental Forum. 21(6): 42-43.

Bebi, P., D. Kulakowski, and C. Rixen. 2009. Snow Avalanche Disturbances in Forest Ecosystems—State of Research and Implications for Management. Forest Ecology and Management. 257(9): 1883-1892.

Brown, K. 2003. Integrating Conservation and Development: A Case of Institutional Misfit. Frontiers in Ecology and the Environment. 1(9): 479-487.

Brugnach, M., A. Dewulf, C. Pahl-Wostl, and T. Taillieu. 2008. Toward a Relational Concept of Uncertainty: about Knowing Too

Little, Knowing Too Differently, amd Accepting Not to Know. Ecology and Society. 13(2): 1-16.

Brunelle, A., G. E. Rehfeldt, B. Bentz, and A. S. Munson. 2008. Holocene Records of Dendroctonus Bark Beetles in High Elevation Pine Forests of Idaho and Montana, USA. Forest Ecology and Management. 255(3/4): 836-846.

Carpenter, S. R., and M. G. Turner. 2000. Hares and Tortoises: Interactions of Fast and Slow Variables in Ecosystems. Ecosystems. 3(6): 495-497.

Cumming, G. S., D. H. M. Cumming, and C. L. Redman. 2006. Scale Mismatches in Social-Ecological Systems: Causes, Consequences, and Solutions. Ecology & Society. 11(1): 164-183.

Drever, C. R., G. Peterson, C. Messier, Y. Bergeron, and M. Flannigan. 2006. Can Forest Management Based on Natural Disturbances Maintain Ecological Resilience? Canadian Journal of Forest Research. 36(9): 2285-2299.

Ekstrom, J. A., and O. R. Young. 2009. Evaluating Functional Fit between a Set of Institutions and an Ecosystem. Ecology & Society. 14(2): 1-18.

Ellison, A. M., M. S. Bank, D. C. Barton, E. A. Colburn, K. Elliott, C. R. Ford, D. R. Foster et al. 2005. Loss of Foundation Species: Consequences for the Structure and Dynamics of Forested Ecosystems. Frontiers in Ecology and the Environment. 3(9): 479-489.

Estes, J. A., and D. O. Duggins. 1995. Sea Otters and Kelp Forests in Alaska: Generality and Variation in a Community Ecological Paradigm. Ecological Monographs. 65(1): 75-100.

Folke, C. 2006. Resilience: The Emergence of a Perspective for Social-ecological Systems Analyses. Global Environmental Change Part A: Human & Policy Dimensions. 16(3): 253-267.

Folke, C., S. Carpenter, B. Walker, M. Scheffer, T. Elmqvist, L. H. Gunderson, and C. S. Holling. 2004. Regime Shifts, Resilience, and Biodiversity in Ecosystem Management. Annual Review of Ecology, Evolution & Systematics. 35(1): 557-581.

Galaz, V., T. Hahn, P. Olsson, C. Folke, and U. Svedin. 2008. The Problem of Fit between Ecosystems and Governance Systems: Insights and Emerging Challenges *in* O. R. Young, L. A. King, and H. Schroeder, eds. The Institutional Dimensions of Environmantal Change: Principle Findings and Future Directions. Boston, MA, USA, MIT Press.

Geist, C., and S. M. Galatowitsch. 1999. Reciprocal Model for Meeting Ecological and Human Needs in Restoration Projects. Conservation Biology. 13(5): 970-979.

Gunderson, L. H. 2000. Ecological Resilience—In Theory and Application. Annual Review of Ecology and Systematics. 31: 425-439.

Holling, C. S. 1973. Resilience and Stability of Ecological Systems. Annual Review of Ecology and Systematics. 4: 1-23.

Holling, C. S. 2001. Understanding the Complexity of Economic, Ecological, and Social Systems. Ecosystems. 4(5): 390-405.

Holling, C. S., and L. Gunderson. 2002. Resilience and Adaptive Cycles, Pages 25-62 *in* L. Gunderson, and C. S. Holling, eds., Panarchy: Understanding Transformations in Human and Natural Systems. Washington DC, USA, Island Press.

Holling, C. S., L. H. Gunderson, and G. D. Peterson. 2002. Sustainaibilty and Panarchies, Pages 63-102 *in* L. H. Gunderson, and C. S. Holling, eds., Panarchy: Understanding Transformations in Human and Natural Systems. Washington DC, USA, Island Press.

Keane, R. E. 2000. The Importance of Wilderness to Whitebark Pine Research and Management, Pages 9 *in* S. F. McCool, D. N. Cole, W. T. Borrie, and J. O'Laughlin, eds., Wilderness Science in a Time Of Change. Missoula, MT, USDA, Forest Service Proceedings.

Kotchen, M. J., and O. R. Young. 2007. Meeting the Challenges of the Anthropocene: Towards a Science of Coupled Human-biophysical Systems. Global Environmental Change Part A: Human & Policy Dimensions. 17(2): 149-151.

Lebel, L., J. M. Anderies, B. Campbell, C. Folke, S. Hatfield-Dodds, T. P. Hughes, and J. Wilson. 2006. Governance and the Capacity to Manager Resilience in Regional Social and Ecological Systems. Ecology and Society. 11(1): 230-250.

Levin, S. A. 2000. Multiple Scales and the Maintenance of Biodiversity. Ecosystems. 3(6): 498-506.

Logan, J. A., W. W. MacFarlane, and L. Willcox. 2010. Whitebark Pine Vulnerability to Climate-driven Mountain Pine Beetle Disturbance in the Greater Yellowstone Ecosystem. Ecological Applications. 20(4): 895-902.

Ludwig, J. A., and M. D. S. Smith. 2005. Interpreting and Correcting Cross-scale Mismatches in Resilience Analysis: A Procedure and Examples from Australia's Rangelands. Ecology & Society. 10(2): 353-359.

MacMynowski, D. 2007. Across Space and Time: Social Responses to Large-Scale Biophysical Systems. Environmental Management. 39(6): 831-842.

McAllister, R. R. J., N. Abel, C. J. Stokes, and I. J. Gordon. 2006. Australian Pastoralists in Time and Space: The Evolution of a Complex Adaptive System. Ecology & Society. 11(2): 687-702.

McKinney, S. T., C. E. Fiedler, and D. F. Tomback. 2009. Invasive Pathogen Threatens Bird-pine Mutualism: Implications for Sustaining a High-elevation Ecosystem. Ecological Applications. 19(3): 597-607.

Peters, D. P. C., B. T. Bestelmeyer, and M. G. Turner. 2007. Cross-Scale Interactions and Changing Pattern-Process Relationships: Consequences for System Dynamics. Ecosystems. 10(5): 790-796.

Peterson, G., C. R. Allen, and C. S. Holling. 1998. Ecological Resilience, Biodiversity, and Scale. Ecosystems. 1(1): 6-18.

Peterson, G. D. 2002. Contagious Disturbance, Ecological Memory, and the Emergence of Landscape Pattern. Ecosystems. 5(4): 329-338.

Raffa, K. F., B. H. Aukema, B. J. Bentz, A. L. Carroll, J. A. Hicke, M. G. Turner, and W. H. Romme. 2008. Cross-scale Drivers of Natural Disturbances Prone to Anthropogenic Amplification: The Dynamics of Bark Beetle Eruptions. BioScience. 58: 501-517.

Rauscher, H. M. 1999. Ecosystem Management Decision Support for Federal Forests in the United States: A Review. Forest Ecology & Management. 114(2/3): 173-197.

Resler, L. M., and D. F. Tomback. 2008. Blister Rust Prevalence in Krummholz Whitebark Pine: Implications for Treeline Dynamics, Northern Rocky Mountains, Montana, U.S.A. Arctic, Antarctic & Alpine Research. 40(1): 161-170.

Simberloff, D. 1997. Flagships, Umbrellas, and Keystones: Is Single-species Management Passe in the Landscape Era. Biological Conservation. 83(3): 247-257.

Smith, C. M., B. Wilson, S. Rasheed, R. C. Walker, T. Carolin, and B. Shepherd. 2008. Whitebark Pine and White pine Blister Rust in the Rocky Mountains of Canada and Northern Montana. Canadian Journal of Forest Research. 38(5): 982-995.

Steffen, W., P. J. Crutzen, and J. R. McNeill. 2007. The Anthropocene: Are Humans Now Overwhelming the Great Forces of Nature? AMBIO—A Journal of the Human Environment. 36(8): 614-621.

Tomback, D. F. 1982. Dispersal of Whitebark Pine Seeds by Clark's Nutcracker: A Mutualism Hypothesis. Journal of Animal Ecology. 51(2): 451-467.

Tomback, D. F., J. K. Clary, J. Koehler, R. J. Hoff, and S. F. Arno. 1995. The Effects of Blister Rust on Post-Fire Regeneration of Whitebark Pine: The Sundance Burn of Northern Idaho (U.S.A.). Conservation Biology. 9(3): 654-664.

Tomback, D. F., and L. M. Resler. 2007. Invasive Pathogens at Alpine Treeline: Consequences for Treeline Dynamics. Physical Geography. 2(5)8: 397-418.

Vitousek, P. M., H. A. Mooney, J. Lubchenco, and J. M. Melillo. 1997. Human Domination of Earth's Ecosystems. Science. 277(5325): 494-499.

Walker, B., L. Gunderson, A. Kinzig, C. Folke, S. Carpenter, and L. Schultz. 2006. A Handful of Heuristics and Some Propositions for Understanding resilience in Social-Ecological Systems. Ecology & Society. 11(2): 80-94.

Walker, B., C. S. Holling, S. R. Carpenter, and A. P. Kinzig. 2004. Resilience, Adaptability and Transformability in Social-ecological Systems. Ecology and Society 9:9pp [online] http://www.ecologyandsociety.org/vol9/iss2/art5/.

Walker, B., and D. Salt. 2006, Resilience Thinking: Sustaining Ecosystems and People in a Changing World. Washington, DC, Island Press.

Westley, F., S. Carpenter, W. A. Brock, C. S. Holling, and L. Gunderson. 2002. Why Systems of People and Nature Are Not Just Social and Ecological Systems, Pages 103-120 *in* L. H. Gunderson, and C. S. Holling, eds., Panarchy: Understanding Transformations in Human and Natural Systems. Washington DC, USA, Island Press.

Yarnell, S. M., J. H. Viers, and J. F. Mount. 2010. Ecology and Management of the Spring Snowmelt Recession. BioScience. 60(2): 114-127.

Young, O. R. 2002, The Institutional Dimensions of Environmental Change: Fit, Interplay, and Scale. Cambridge, Cambridge University Press, UK.

Zurlini, G., K. Riitters, N. Zaccarelli, I. Petrosillo, K. B. Jones, and R. L. 2006. Disturbance Patterns in a Socio-ecological System at Multiple Scales. Ecological Complexity. 3(2): 119-128.

Inoculation and Successful Colonization of Whitebark Pine Seedlings With Native Mycorrhizal Fungi Under Greenhouse Conditions

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Abstract—Efforts to maintain and restore whitebark pine (*Pinus albicaulis*) forests in western North America have increased dramatically over the last two decades and now include the planting of nursery-grown rust resistant seedlings in openings and burned areas. Over 200,000 nursery seedlings have been planted in the western U.S. but survival rates are low and in many areas approach zero. One possibility for enhancing seedling survival is application of mycorrhizal fungi in the greenhouse before out-planting. All pines require ectomycorrhizal fungi (ECM) to survive in nature, including whitebark pine. Non-mycorrhizal seedlings are at risk of dying when planted in soil lacking appropriate mycorrhizal fungi; this might include ghost forests, severe burns, dry habitats and areas not previously in pine. This study screened 25 isolates of native ECM fungi (primarily suilloids) from whitebark pine forests in the Greater Yellowstone Area as a preliminary step in development of an effective inoculum for whitebark pine seedlings grown in forest nurseries. Most are 'suilloid' fungi specific for 5-needle pines. A majority grew well *in vitro* and selected strains were then used to develop various types of mycorrhizal inoculum. Four basic inoculation methods were tested under greenhouse conditions using spore slurries and soil inocula. Spore slurries added to soil produced the highest rate of mycorrhizal colonization (100 per cent frequency) in the shortest time (3-5 months), but colonization also occurred with soil inoculum (mycelium). Fertilization was found to suppress mycorrhizal colonization at least at the high levels tested. Soil substrate was found to be an important factor in ECM colonization and some soil mixes suppressed or prevented colonization. Commercial inoculum is not recommended since it risks introduction of alien fungi, it may not favor 5-needle pines, and therefore has the potential to disturb sensitive whitebark pine systems. Here we report results from preliminary trials and discuss on-going research to provide up-to-date information.

Introduction

Whitebark pine (*Pinus albicaulis* Engelm.) forests are in serious decline due to blister rust, mountain pine beetles, fire suppression and possibly climate change (Schwandt 2006, Smith et al. 2008, Logan and others 2010). In some areas of the western U.S. forests have been reduced 90 percent or more. Restoration efforts have been on-going for over 15 years (Schwandt 2006; Tomback and others 2001) and this includes development of seed germination methods (Burr and others 2001), nursery production of whitebark pine seedlings (Burr and others 2001; Riley and others 2007), selection of rust resistant strains (Mahalovich and Dickerson 2004), research on seedling diseases (Dumroese 2008), development of cone collection techniques, improvement of planting methods (McCaughey and others 2010) and use of burned sites for out-plantings (Keane and Arno 2001; Keane and Parsons 2010). Over 200,000 nursery seedlings have been planted in the western U.S. and survival rates are low in many areas. Izlar (2007) found a 42 percent overall survival rate for the 100,000 seedlings assessed; in some areas survival approached zero. One neglected area of vital research which has the possibility of enhancing seedling survival on out-planting is inoculation of nursery seedlings with mycorrhizal fungi.

All pines, including whitebark pine, require ectomycorrhizal (ECM) fungi to survive in nature (Smith and Read 1997). These fungi enhance pine survival by providing nutritional benefits, imparting drought tolerance and offering protection from pathogens and soil grazers (Cripps 2002, 2004; Molina and Trappe 1984). In nature, non-mycorrhizal seedlings are at risk in soil lacking appropriate mycorrhizal fungi. Therefore mycorrhizal fungi should be considered in nursery or silvicultural methods and in monitoring out-planted seedling performance (Landis and others 1990, Khasa and others 2009). For nursery methods, the USFS handbook (Landis and others 1990) and 'Advances in Mycorrhizal Science and Technology' (Khasa and others 2009) both recommend that mycorrhizal inoculation be tested on a small scale before applying to an entire nursery. While mycorrhizal inoculation is routinely used in reforestation efforts (Khasa and others 2009), inoculation methods vary and need to be developed for *each* tree species. This is primarily because it is necessary to match greenhouse regimes required for a particular tree species with those conducive to mycorrhizal colonization by the appropriate fungi. While commercial inoculum is often used, the most effective inoculum is naturally associated with the tree species being inoculated (Davey and others 1990). Therefore, inoculation of whitebark pine seedlings should be with *native* mycorrhizal fungi adapted to local conditions and those known to be important in whitebark pine seedling survival in nature (Mohatt and others 2008). Use of commercial inoculum runs the risk of introducing alien fungi and those not appropriate for whitebark pine.

Inoculation of seedlings can also benefit the nursery as a 'green technology' that reduces fertilizer and irrigation as well as pesticide use, and protects against some pathogens (Whipps 2004). Colonized root systems are often 'bushier' with more secondary roots that are pre-conditioned to exploit soil resources when planted (Khasa and others 2009).

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In the field, inoculation can enhance seedling survival with the correct combination of host, fungus, soil/substrate and abiotic conditions; results can be dramatic in areas lacking appropriate fungi in the soil (Parlade 2004; Steinfield and others 2003; Stenströme and Ek 1990). Inoculation has been calculated to be cost effective when survival increases at least 5 percent (Parlade 2004).

'Host-specific' native mycorrhizal fungi can also be adapted to particular soil and climatic conditions. At the Federal Forest Nursery in Austria, European stone pines (*Pinus cembra* L.) have been inoculated for over 50 years with native suilloid fungi adapted to high elevation conditions. This has dramatically increased the out-planting success rate in these habitats (Moser 1956, Weisleitner, personal communication 2008). A multi-level approach using a combination of intensive silvicultural methods has increased survival of planted *P. cembra* seedlings from ca. 50 to 90 percent and these methods are still employed today (Weisleitner, personal communication 2008). We were able to visit this nursery for direct transfer of information on inoculation and planting techniques for stone pines.

Over 40 species of ectomycorrhizal fungi have been confirmed with whitebark pine on our sites in the Greater Yellowstone Ecosystem (GYE) which contain some of the last remaining intact forests (Cripps and Mohatt 2005; Cripps and others 2008; Mohatt 2006; Mohatt and others 2008). Many are suilloid fungi host-specific on some level (Bruns and others 2002). Individual species are restricted to pine, 5-needle pine, or stone pine; some appear to be strictly associated with whitebark pine. Amazingly, we have found *Suillus sibiricus* and other suilloids also known to occur with stone pines in Europe and Asia which suggests a long co-evolutionary history (Moser 2004). The suilloids (*Suillus* and *Rhizopogon* species) are also of interest because they are known to be important in the establishment of pine seedlings and have been used successfully in nurseries to this effect (Castellano and others 1985; Parladé and others 2004; Rincon and others 2005; Steinfeld and others 2003).

The challenges of using native fungi include 1) selecting native fungi for the nursery that ultimately enhance survival in the field, 2) determining which soil substrates are conducive to mycorrhizal colonization in the nursery, 3) finding fertilizer regimes that do not interfere with mycorrhizal colonization, and 4) avoiding chemicals for pest control (especially fungicides). There are economic challenges as well, but once mycorrhizal inoculation is integrated into normal nursery operations (hopefully with minor adjustments), studies have shown the economic benefits to nurseries can be positive as studies have shown (Davis and others 2009; Parladé and others 2004).

The main goal of the present research is to develop methods for inoculation of whitebark pine seedlings with native ectomycorrhizal fungi under nursery conditions that ultimately improves survival in the field. We have made significant progress in capturing native fungi from whitebark pine forests in the GYE for this project. Here we report initial screening data on 25 strains of native mycorrhizal fungi collected from whitebark pine forests for their potential as inoculum. We also report results of an early trial (Experiment 1) that tested various inoculation methods for efficacy of mycorrhizal colonization in the nursery. Experiments 2 and 3 examined the effects of fertilizer and various soil substrates on mycorrhizal colonization (Table 1). Assessment for these trials is percent colonization of root systems and not increased seedling size in the nursery. Results are discussed in context with our current research to provide as up-to-date information as possible. Goals outside the scope of this report are determining when inoculation is necessary and if inoculation enhances the survival of whitebark pine seedlings in the field.

Methods

Screening of Native Ectomycorrhizal Fungi

Ectomycorrhizal fungi were collected from whitebark pine forests in the Greater Yellowstone Ecosystem and ecological parameters recorded. Details of locations are in the MSU database of fungal collections (MONT Herbarium and Mohatt and others 2008). A majority are suilloid fungi, *Suillus* and *Rhizopogon*. *Cortinarius*, *Hygrophorus*, *Lactarius*

Table 1. Components of various soil media types used in various experimental Trials.

Soil Media	By Volume	pH	Origin	Used in
Soil Mix 1: Sunshine mix #1[a], MSU mix[b] & Vermiculite[c]	1Sm:1M:1V	6.5	Mixed at MSU Plant Growth Center	Experiment 1
Soil Mix 2: Sphagnum Peat Moss, MSU mix & Vermiculite	1P:1M:1V	5.0	Mixed at MSU Plant Growth Center	Experiments 1, 2, 3
Canadian sphagnum Peat Moss & Sawdust	8P: 2S	5.2	Original media from USDA nursery[d] in Styrofoam blocks	Experiments 1 & 2
Canadian sphagnum Peat Moss & Vermiculite	1P: 1V	7.0	Mixed at MSU Plant Growth Center	Experiment 3
Canadian Sphagnum Peat Moss and Bark (not composted)	1P: 1B	7.3	Original media from USDA nursery[d] in Styrofoam blocks	Experiment 3

[a] SunGrow, Bellevue, WA.

[b] Loam soil, Canadian Sphagnum peat moss, and washed concrete sand are blended in a 1:1:1 by volume ratio, including AquaGro 2000 G wetting agent at one lb./cubic yd; mix steam pasteurized at 70°C for 60 min.

[c] SunGrow, Bellevue, WA.

[d] USDA Forest Service Nursery in Coeur D'Alene, Idaho.

and *Russula* species were not considered for testing since it is known that these genera do not grow *in vitro* and are primarily associated with mature trees and not seedlings. *Laccaria* and *Hebeloma* species, typically used as fungal inoculum, are rare in whitebark pine forests. Fungi as sporocarps (mushrooms/truffles) were identified using classical taxonomic methods; ectomycorrhizae on roots were identified using molecular techniques. The latter includes: DNA extraction, PCR, sequencing of the Internal Transcribed Spacer region followed by comparison to sequences in Genbank or our own DNA library (Mohatt 2006).

Twenty-five strains of native fungi from whitebark pine forests were screened as inoculum for whitebark pine seedlings. Tissue was removed from sporocarps using sterile technique and plated out on Petri dishes of Modified Melin Norkrans media (Brundrett and others 1996). Ectomycorrhizae on roots were surface sterilized with hydrogen peroxide or 10 percent Clorox solution, rinsed with sterile water and plated out on MMN.

The presence or absence of growth *in vitro* was used as an initial screening measure to identify potentially useful fungi. Strains that showed vigorous growth in culture were used to develop various types of soil and liquid fungal inoculum that was applied to whitebark pine seedlings. In addition, spore slurries produced by grinding fresh sporocarps with distilled water and stored at 5° C until application were also tested on seedlings. Out of 25 strains, ten were tested as spore slurries. Also, two new strains of *Suillus sibiricus* (CLC 2421 and CLC 2440) were used in trials. The fungi were then evaluated for their ability to form mycorrhizae on whitebark pine seedling roots in the greenhouse.

Whitebark Pine Seedlings for Experiments 1-3

Approximately 300 two to four-week-old whitebark pine seedlings were obtained from the USDA Forest Service Nursery in Coeur D'Alene, Idaho (Burr and others 2001). Seedling lots were from various locations and included lots 7425 and 7029, and 'extras'. At the Idaho nursery seedlings were originally grown under standard conditions in a substrate mix of Canadian Sphagnum peat moss and sawdust (8:2 by volume) in Styrofoam® blocks (91cells, 130 cm^3). Additional pre-germinated whitebark pine seedlings were planted into Ray Leach cone-tainers™ (3.8 cm x 14 cm, 115 cm^3) containing soil mix 1 or soil mix 2 after radicals reached a length of approximately 0.5 cm. At the Plant Growth Center (Montana State University), seedlings were subsequently grown under standard greenhouse conditions (22°C. day and 18°C night temperatures, 16 hr photoperiod). Seedling root systems were randomly examined before inoculation and 14/15 were free of nursery mycorrhizae such as E-strain or *Thelephora*. One seedling was minimally colonized by a nursery type of ectomycorrhizal fungus.

Several soil substrates were used in the various experiments reported in this paper. The components of these soil types are described in Table 1. Soil mix 1, soil mix 2 and the peat:sawdust mixture were used in Experiment 1. Soil mix 2 and the peat:sawdust mix were used in Experiment 2. Soil mix 2, the peat:vermiculite mix and the peat:bark mix were used in Experiment 3.

Experiment 1: Comparison of 4 inoculation methods

Selected native mycorrhizal fungi (16 strains) were used to develop various types of inoculum. Four general methods were used in the initial trial as a starting point towards development of a standard method for inoculation of whitebark pine seedlings with native mycorrhizal fungi in the greenhouse. Confounding factors are inherent in this approach (comparisons of whole methods) but gave information which directed follow-up experiments. Trials were also determined by the availability of materials (seeds, seedlings, fungi). Comparisons were made by assessing the frequency and abundance of colonization on seedlings roots by mycorrhizal fungi. Replication was N = 14 for each treatment.

METHOD 1: Soil inoculum 1 (agar plugs) & seedlings grown in Styrofoam® blocks

Modified Melin Norkrans liquid medium was added at a ratio of 85-100 ml to 250-300 ml of a substrate mixture containing Canadian Sphagnum peat moss and Vermiculite (volume ratio 1:9). The substrate mix was added to Mason jars and sterilized (45 min. at 121°C). The soil inoculum was prepared by adding 10 colonized agar plugs (0.5 x 0.5 cm) of actively growing mycorrhizal cultures to the sterile substrate mix. The soil inoculum was incubated for 4 to 6 weeks at 20°C. Seedlings in Styrofoam® blocks in peat:sawdust (8:2) mixture were used for this method. Approximately 5 g of soil were removed from the top layer of the cells with a scoop. Five grams of mycorrhizal inoculum were placed in the created space adjacent to the root system and re-covered with removed soil. Mycorrhizal fungi were allowed to establish and grow for 6 to 10 months before evaluation of fungal colonization.

METHOD 2: Soil inoculum 2 (liquid) and seedlings grown in Styrofoam® blocks

Liquid cultures were prepared by transferring 8 agar plugs (0.5 x 0.5 cm) of actively growing mycorrhizal cultures to glass flasks containing 150 ml of sterile MMN media. The cultures were placed onto a rotary shaker and grown for 4 to 6 weeks at 20°C. Liquid cultures were added at a ratio of 85-100 ml to 250-300 ml of a sterile substrate mixture containing Canadian Sphagnum peat moss and Vermiculite (volume ratio 1:9). The soil inoculum was incubated for 4 to 6 weeks at 20 °C. Seedlings in Styrofoam® blocks in peat:sawdust (8:2) mixture were also used for this method. As described above, 5 g of mycorrhizal inoculum were added into the created space adjacent to the root system and re-covered with removed soil. Mycorrhizal fungi were allowed to establish as described earlier.

METHOD 3: Spore inoculum & seedlings grown in Soil Mix 2 in Ray Leach single cells

Mature fruiting bodies of *Suillus sibiricus*, *Rhizopogon subpurpureus*, *Rhizopogon* cf *evadens*, *Rhizopogon* cf *molligleba*, and *Rhizopogon* cf *olivaceofusca* collected in whitebark pine forests in Montana were carefully cleaned. The hymenium of each was removed, cut in small pieces, and ground separately for 1 min in a coffee grinder with 10 ml of sterile distilled water. The ground materials were diluted into 100 ml sterile distilled water and stored in glass bottles at 4˚C. Seedlings in Ray Leach single cells in soil mix 2 were used to test this method. Approximately 5 ml of one type of spore slurry was added to each seedling with a pipette. Mycorrhizal fungi were allowed to establish as above.

METHOD 4: Soil inoculum 1 (agar plugs) & seedlings grown in Soil Mix 1 in Ray Leach single cells.

This method is the same as Method 1 except that seedlings were in soil mix 1 and in Ray Leach single cells.

Experiment 2: Comparison of types of spore inoculum (with and without fertilizer).

Spore slurries were most effective in Experiment 1, subsequently this method was used to examine the efficacy of various types of spore treatments on mycorrhizal colonization. Treatments included: full strength slurry, slurry diluted 1:10, dried spores, and frozen spores. Spore slurry of one *Suillus sibiricus* strain (CLC 2440) was selected for the trial. In addition, three levels of fertilization were added as three additional treatments plus a control.

For the spore slurries, fresh fruiting bodies were processed as described above for spore slurries. A hematocytometer was used to determine the number of spores per volume, which was generally around 10^6spores/ml. Spore slurries were used full strength or diluted 1:10 with distilled water. Spores for the 'frozen treatment' came from pieces of sporocarp frozen at 0°C for several weeks and then subjected to the same treatment. Spores for the 'dried treatment' came from sporocarps dried on a dehydrator and subsequently subjected to the grinder. Spore solutions were stored at 4°C and shaken well before use. Approximately 2 ml of the respective spore solutions were applied just below the soil surface close to the root system of seedlings grown in peat:sawdust in Styrofoam® blocks. Control seedlings were not inoculated. Mycorrhizal fungi were allowed to grow for at least 5 months before the root colonization was evaluated. The fertilizer treatments consisted of the application of 200 ppm of NPK (Scotts® Peters General Purpose 20-20-20) applied to saturation once (treatment 1), twice (treatment 2) or three times (treatment 3) a week. N=7 seedlings were used for each treatment.

Experiment 3: Effects of soil substrate type on mycorrhizal colonization

Seedlings were planted in three different soil substrates types in Ray Leach containers: peat:non-composted bark, peat:vermiculite and Soil Mix 2 (described in Table 1). Seedlings were inoculated with *Rhizopogon* CLC 2544 and *Suillus sibiricus* strains CLC 2375, 2421 and 2440, using full-strength spore slurry as described above. Controls were not inoculated. Seedlings were inoculated and mycorrhizal fungi were allowed to establish under greenhouse conditions for 5 months before evaluation. N=7 for each treatment.

Evaluation of mycorrhizal colonization

Seedlings were carefully extracted from the Styrofoam® blocks or Ray Leach containers. The roots of each seedling were immersed in distilled water and soil particles were removed by gentle agitation. For the non-destructive sampling technique the intact root system of each seedling was placed in petri plates containing distilled water and examined with a dissecting microscope (Nikon SMZ 1500, Meridian Instrument Company, Inc., Kent, WA). Ectomycorrhizal root tips were recognized by the presence of a mantle, extramatricular hyphae or rhizomorphs for some, and the dichotomous branching typical of pines. The frequency of mycorrhizal colonization was determined by presence/absence of mycorrhizae of the fungal strain. Quantification of mycorrhizal colonization was also assessed as either the number of mycorrhizal root tips per seedling or the estimated percentage of the root system that was colonized (0-100 percent) on each seedling (Brundrett and others 1996). Application of statistical analysis was difficult due to the patchy nature of results. Assessment in all trials was non-destructive in that seedlings were able to be transplanted after assessment. Effects on plant parameters were also measured but are not reported here.

Results

All sixteen of the strains that were tissue cultured onto Petri "plates" grew *in vitro* on MMN media (Table 2, column 6, M+). Six showed vigorous mycelial growth (M++) and were selected for further testing. These included: *Suillus subalpinus* CLC 2341, *S. cf subvariegatus* CLC 2344, *S. sibiricus* CLC 2345, *Suillus sp* CLC 2199, *Rhizopogon subbadius* CLC 2294 and *Cenococcum geophilum* VT 1009. These six were then tested for their ability to grow in "liquid" MMN media and peat:vermiculite (Table 2, columns 7 and 8). All six were able to grow in both substrates and were applied as a liquid or soil based inoculum to seedlings (Table 2, column 9) and all but *Cenococcum* formed mycorrhizae. An additional eight fungal strains were added as spore slurries (Table 2, column 6, S) directly to seedlings; these were primarily over-ripe suilloid fungi not suitable for tissue culturing. All formed mycorrhizae except *Thaxterogaster*.

While it was not possible to test all methods using all fungal strains, Experiment 1 showed that mycorrhizal colonization of whitebark pine seedlings is possible using Methods 1, 2 and 3 (Table 3). However, colonization did not occur with Method 4 using Soil Mix 1; this soil mix was found to be fungal suppressive due to the Sunshine Mix which concurs with results for other trials using this soil mix (not reported here). Mycorrhizal colonization occurred using either a liquid or agar plug initiated soil inoculum, although colonization was 'patchy' (not consistent within a treatment). The spore method produced the highest colonization rate in the shortest time period for all fungi tested with high frequency ratings. There were fungal effects as well with certain strains of *Suillus* out-performing other groups as soil inoculum. With

Table 2. Initial screening of native ectomycorrhizal fungi for potential use as inoculum for whitebark pine seedlings as assessed by growth characteristics on various substrates.

No.	Mycorrhizal species	Location	Source	Host	Plate[a]	Liquid[b]	Soil[c]	Seedling[d]
CLC 2035	*Rhizopogon subpurp.*	New World	sporocarp	*P. albicaulis*	M+	na	na	na
CLC 2036	*Rhizopogon* sp.	New World	sporocarp	*P. albicaulis*	M+	na	na	na
WO 81.1	*Tricholoma moseri*	New World	sporocarp	*P. albicaulis*	M -	na	na	na
Rhiz 1w	*R.* cf *ochraceorubens*	Waterton Park	sporocarp	*P. contorta*	M+	na	na	na
Hyp 1	*R.* cf *salebrosus*	Waterton Park	sporocarp	*P. flexilis*	M+	na	na	na
GDP 1	*Rhizopogon.* sp. 1	Glacier Park	roots	*P. flexilis*	M+	na	na	na
UB 7	*Rhizopogon* sp. 2	Fridley Burn	native soil	*P. albicaulis*	M+	na	na	na
CLC 2199	*Suillus* sp. (veil)	Yellowstone	sporocarp	*P. albicaulis*	M++	+	+	+
CLC 2294	*R. subbadius*	Yellowstone	sporocarp	*P. flexilis*	M++	+	+	+
CLC 2341	*S. subalpinus*	New World	sporocarp	*P. albicaulis*	M++	+	+	+
CLC 2344	*S. cf subvariegatus*	New World	sporocarp	*P. albicaulis*	M++	+	+	+
CLC 2345^{a}	*S. sibiricus (thick)*	Yellowstone	sporocarp	*P. albicaulis*	M++	+	+	+
CLC 2345^{b}	*S. sibiricus (thin)*	New World	sporocarp	*P. albicaulis*	M+	na	na	na
CLC 2346	*S.* cf *brevipes*	Yellowstone	sporocarp	Conifers	M -	na	na	na
CLC 2347^{c}	*S. subalpinus*	Yellowstone	sporocarp	*P. albicaulis*	M+	na	na	na
VT 1009	*Cenococcum geophil.*	Eastern US	roots	Conifers	M ++	+	+	-
CLC 2375	*S. sibiricus*	Beartooths	sporocarp	*P. albicaulis*	S	na	na	+
CLC 2377	*R. subpurpurascens*	Beartooths	sporocarp	*P. albicaulis*	S	na	na	+
CLC 2379	*R.* cf *evadens* R 1	Yellowstone	sporocarp	*P. albicaulis*	S	na	na	+
CLC 2380^{a}	*R.* cf *molligleba* R2	Yellowstone	sporocarp	*P. albicaulis*	S	na	na	+
CLC 2380^{b}	*R.* sp. (yellow) R3	Yellowstone	sporocarp	*P. albicaulis*	S	na	na	+
CLC 2381^{a}	*R. olivaceofuscus* 4,5	New World	sporocarp	*P. albicaulis*	S	na	na	+
CLC 2382	*Thaxterogaster* sp.	New World	sporocarp	*P. albicaulis*	S	na	na	-
NW Hyp 1	*Hypogeous* 1	New World	sporocarp	*P. albicaulis*	S	na	na	na
NW Hyp 2	*Hypogeous* 2	New World	sporocarp	*P. albicaulis*	S	na	na	na

[a] growth on Petri 'plates' of MMN (M+ = growth, M++ = vigorous growth, M- = poor growth).
[b] growth in 'liquid' MMN media (+ = growth, na = not tested).
[c] growth in peat:vermiculite (1:9 v/v) 'soil' mix (+ = growth, na = not tested).
[d] fungi used to inoculate whitebark pine seedlings.
S = spores from fruiting bodies used for direct inoculation of seedlings.

spores *Rhizopogon* species were also able to colonize seedlings at acceptable rates. Seedlings that were well colonized with mycorrhizal fungi exhibited a darker green color and root systems were often more well-developed (data not shown).

In Experiment 2, the application of fertilizer reduced mycorrhizal colonization to almost negligent levels (Figure 1, A and B) regardless of the type of spore inoculum applied. The lightest application (F1) had the highest frequency of colonization compared to heavier doses, but at all three levels, colonization of the overall root system was less than 7 percent and not acceptable. All types of spore inoculum (including slurries, dried or frozen spores) were effective in mycorrhizal colonization when applied without fertilizer with colonization levels up to 23 percent and frequencies of 70-100 percent. Differences in colonization levels were negligible between the full and 1:10 diluted spore slurry. The dried inoculum lagged behind in percent colonization but not in frequency of seedlings infected.

In Experiment 3, there was little mycorrhizal colonization in the peat:bark substrate for all four of the fungal strains tested (Fig. 2). All four fungi colonized seedling roots in both peat:vermiculite and soil mix 2 covering 7-28 percent of the roots systems in a majority of seedlings with high frequencies of 45-100 percent. There was also variation within strains of *Suillus sibiricus*, and results suggest that particular strains had a preference for soil type in this small trial.

Discussion

The main goal of this project was to initiate the development of an effective method for inoculation of whitebark pine seedlings with native ectomycorrhizal fungi under nursery conditions. We have made significant progress in capturing and storing native fungi from whitebark pine forests in the GYE for this project (a rather difficult task since fungi rarely fruit) and in screening them for potential as inoculum for whitebark pine seedlings. Mycorrhizal colonization was successful with numerous strains of native ectomycorrhizal fungi using several methods in the greenhouse. However, results were inconsistent within treatments (sometimes ranging from 0 to 100 percent colonization). Methods need to be refined for more consistent and reliable mycorrhizal colonization before moving to a larger scale that can be integrated into nursery protocol. However, a small successful trial using older seedlings is reported later in the discussion along with management recommendations.

Fungal strains

A total of 25 strains of native ectomycorrhizal fungi (Table 2) were tested in this initial trial and additional strains have been tested since; this includes native mycorrhizal fungi now being tested on limber pine (*Pinus flexilis* James). We

Table 3. Experiment 1: A comparison of four methods used to inoculate strains of ectomycorrhizal fungi onto whitebark pine seedlings in the nursery. Methods are summarized; for details see Table 1 and method section.

Method	Isolate Number	Fungus	Colonization frequency(%)	Average colonization(%)	Average No. mycorrhizae	Time (months)
Method 1: Soil inoculum 1 (agar plugs) & seedlings grown in Styrofoam® blocks (in peat:sawdust)						
1	CLC 2199	*Suillus* sp. (veil)	16.7	<1	0.7	9
1	CLC 2341	*Suillus subalpinus*	25.0	<1	0.3	9
1	CLC 2344	*Suillus cf subvariegatus*	16.7	0–25	19.7	6
1	CLC 2345[a]	*Suillus sibiricus*	0.0	0	0.0	9
1	CLC 2345[a]	*Suillus sibiricus*	16.7	<1	0.2	10
1	CLC 2345	*Suillus sibiricus* 3	0.0	0	0.0	6
1	CLC 2345	*Suillus sibiricus* 3	40.0	<1	1.2	9
1	CLC 2345[b]	*Suillus sibiricus*	100.0	0–25	38.9	9
1	CLC 2345[b]	*Suillus sibiricus*	100.0	25–50	47.0	10
1	CLC 2294	*Rhizopogon subbadius*	33.3	0–25	22.3	6
1	CLC 2294	*Rhizopogon subbadius*	16.7	<1	6.5	9
1	CLC 2294	*Rhizopogon subbadius*	16.7	<1	0.3	10
1	CLC 2294	*Rhizopogon subbadius*	33.3	0–25	7.2	10
1	VT 1009	*Cenococcum geophilum*	16.7	<1	0.8	9
1	Control	Control	0.0	0	0.0	9
Method 2: Soil inoculum 2 (liquid) & seedlings grown in Styrofoam® blocks (in peat:sawdust)						
2	CLC 2035	*Rhizopogon subpurpurascens*	16.7	<1	4.0	9
2	CLC 2199	*Suillus* sp. (veil)	100.0	25-50	47.5	9
2	CLC 2341	*Suillus subalpinus*	60.0	0-25	37.8	9
2	CLC 2344	*Suillus cf subvariegatus*	25.0	0-25	48.0	9
2	CLC 2345	*Suillus sibiricus* 3	0.0	0	0.0	9
2	CLC 2294	*Rhizopogon subbadius*	0.0	0	0.0	9
2	CLC 2035	*Rhizopogon subpurpurascens*	16.7	<1	4.0	9
Method 3: Spore inoculum & seedlings grown in Soil Mix 2 in Ray Leach single cell containers						
3	CLC 2375	*Suillus sibiricus*	100.0	25-50	49.0	5
3	CLC 2377	*Rhizopogon subpurpascans*	100.0	25-50	30.0	5
3	CLC 2379	*Rhizopogon* cf *evadens*	100.0	0-25	6.0	5
3	CLC 2380[a]	*Rhizopogon* cf *molligleba*	100.0	25-50	33.7	5
3	CLC 2381	*Rhizopogon* cf *olivaceofusca*	100.0	25-50	59.3	5
Method 4: Soil inoculum 1 (agar plugs) & seedlings in Soil Mix 1, Ray Leach single cell containers						
4	CLC 2035	*Rhizopogon subpurpurascens*	0.0	0	0.0	9
4	CLC 2199	*Suillus* sp. (veil)	0.0	0	0.0	9
4	CLC 2341	*Suillus subalpinus*	0.0	0	0.0	9
4	CLC 2344	*Suillus cf subvariegatus*	0.0	0	0.0	9
4	CLC 2345	*Suillus sibiricus* 3	16.7	<1	0.5	9
4	CLC 2294	*Rhizopogon subbadius*	0.0	0	0.0	9
4	VT 1009	*Cenococcum geophilum*	0.0	0	0.0	9

have found suilloids in all whitebark pine studied (Mohatt and others 2008) and as a dominant group on seedlings roots (Mohatt 2006). Also, whitebark pine seedlings planted for various management strategies such as after fire (Trusty and Cripps 2010) and along Dunraven Pass in Yellowstone National Park (Cripps and Trusty 2007) also hosted suilloid fungi. This suggests that suilloid fungi specific to 5-needle pines are important in whitebark pine systems and are multi-stage fungi appropriate for young seedlings as well as mature trees.

Results from additional fungal strains suggest a large variety of suilloids can be used as inoculum as long as they occur with 5-needle pines. While some strains of *Suillus* and *Rhizopogon* out-performed other strains in the trials reported here (particularly *Suillus sibiricus*), we have subsequently found that strain performance is also dependent on inoculum type, soil substrate, pH of the system, fertilizer regime, and other conditions. The inconsistent results where some seedlings were 100 percent colonized with no colonization for others within a treatment suggest seedling genetics may also play a role. Caution is therefore advised in limiting selection to just a few strains. Also, we do not yet know if the strains that perform well in the nursery enhance survival on out-planting, however field trials are underway. As stated before, often the most effective inoculum comes from beneath the tree species being inoculated (Davey and others 1990). We are recommending regional sources of fungal inoculum be identified and restricted to particular growing regions for whitebark pine management.

A primary fungus in commercial inoculum, *Rhizopogon roseolus,* associates more with lodgepole pine, while the main species in whitebark pine systems in the Greater Yellowstone Area are ecotypes of *R. evadens* and *R. milleri* (Mohatt and others 2008). Inoculum with *Paxillus involutus* or *Scleroderma*

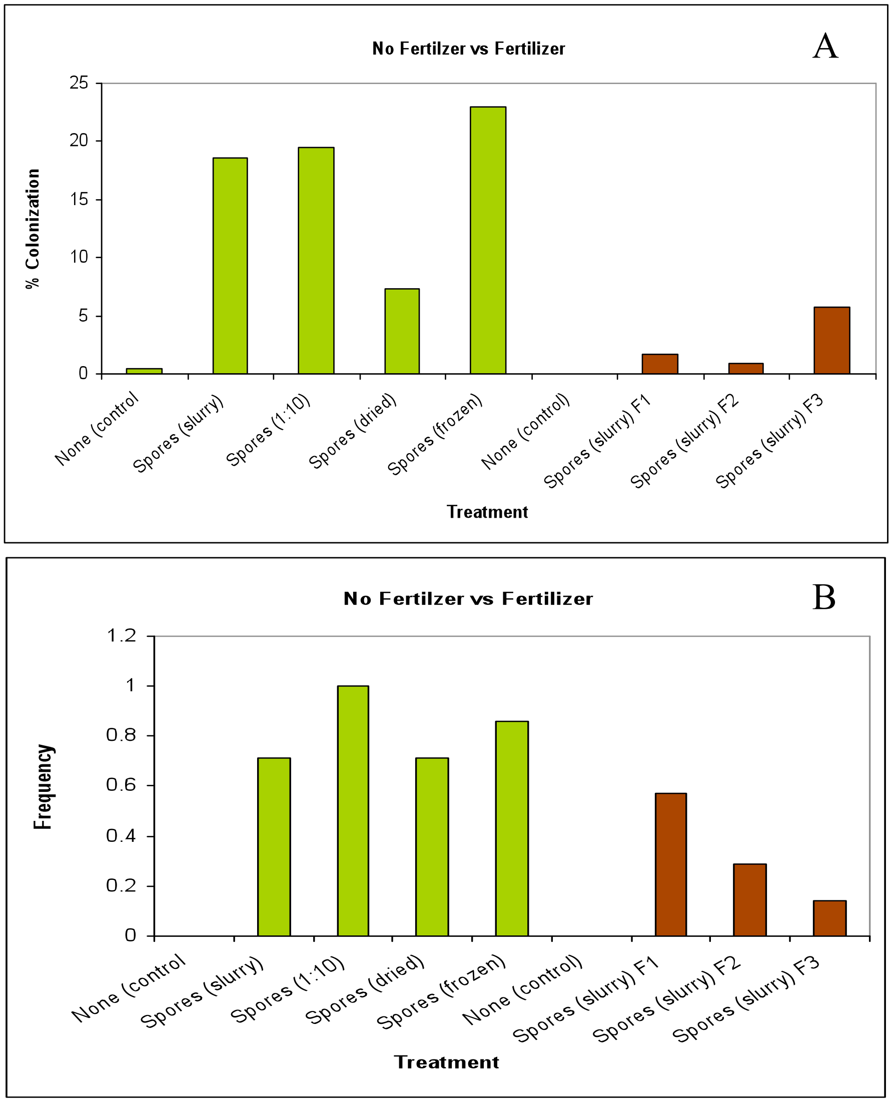

Fig. 1. Experiment 2, mycorrhizal colonization of whitebark pine seedlings after inoculation with various types of spore slurry with and without fertilizer (F1=once a week, F2=twice a week, F3=three times a week). A. % colonization of root system. B. frequency of colonization (no. seedlings colonized).

species is not recommended as these fungi are for acidic soils and are not known in whitebark pine systems. Similarly, *Hebeloma* species, often used in commercial inoculum, have only been recorded once on our whitebark pine sites. Alien fungi risk alteration of the food chain since small and large mammals depend on particular suilloids for food in these sensitive systems (Ashkannejhad and Horton 2005; Izzo and others 2005). In addition, the specific physiology of the native fungi may not be functionally redundant with that of those in commercial inoculum. Commercial inoculum could also serve to promote other tree species.

Inoculation Methods

Mycorrhizal colonization of whitebark pine was successful using either spore slurries or soil (mycelial) inoculum; two of the three soil inoculation methods tested showed the potential to be used with whitebark pine seedlings. Fresh spore slurries (method 3) were the most effective method tested resulting in 100 percent colonization of all seedlings inoculated with suilloids. This method is simple and spores can easily be directly added to seedlings in Styrofoam® blocks or Ray Leach containers. A drawback is that fresh spore slurries are not always available at inoculation time. These fungi fruit and produce spores in the fall and seedlings were inoculated directly afterwards resulting in high colonization rates. However, fruiting does not occur every year and it is often difficult to get to these locations at the correct time (Mohatt 2006). These high elevations sites are prone to drought which prevents fungal fruiting. Inoculation in spring would allow colonization just before fall planting. Therefore, we tested reduced amounts of spores (dilution of slurries) and storage methods for spores (freezing and drying). All of these treatments resulted in mycorrhizal colonization and methods need to be refined with larger trials. In subsequent trials, we learned that some spore slurries maintain viability for several months, however colonization was not always as consistent as in the preliminary trial if older or dried inoculum is used. We are currently testing the shelf life of spore slurries.

The soil inoculum also produced mycorrhizae in the greenhouse whether initiated with agar plugs or liquid medium. Mixing soil inoculum into the substrate when possible would likely improve colonization, but this may not be

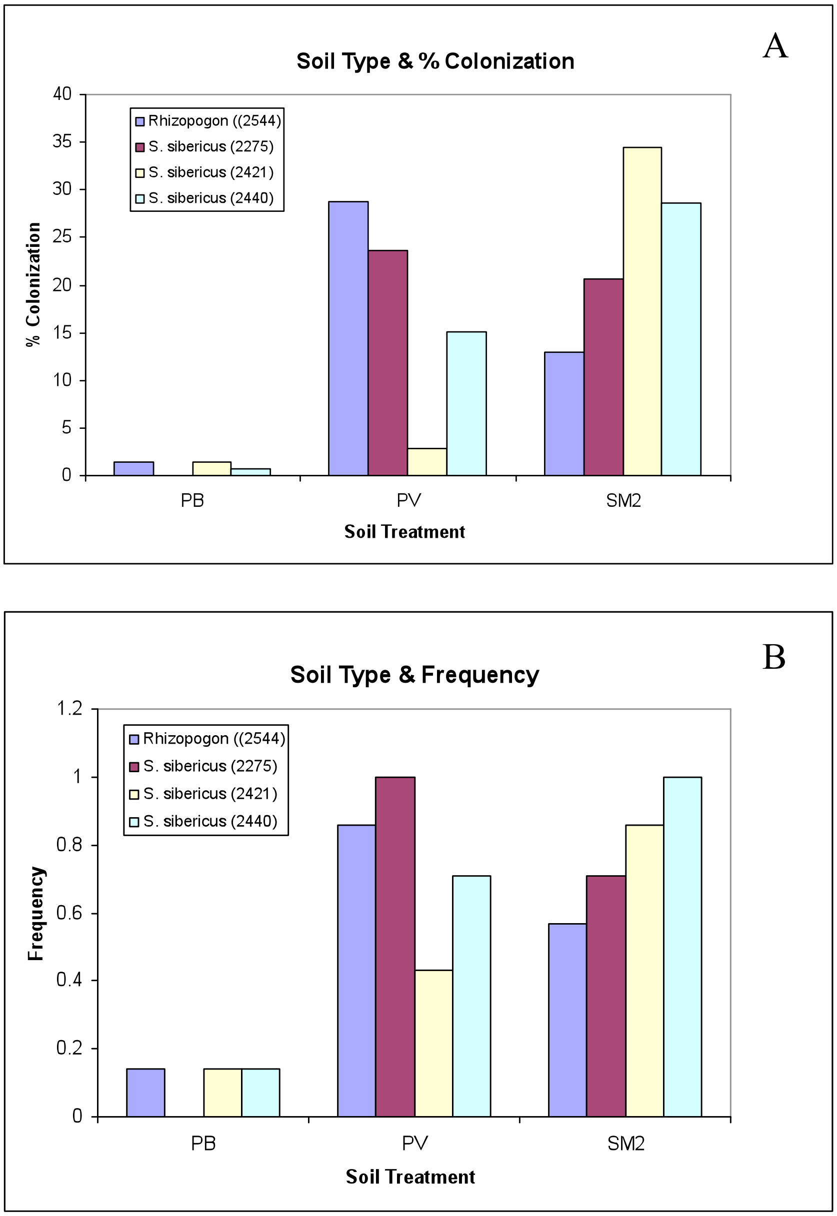

Fig. 2. Experiment 3, mycorrhizal colonization of whitebark pine seedlings after inoculation with 4 strains of fungi in three soil substrate types: peat:non-composted bark (1:1), peat:vermiculite (1:1) and Soil Mix 2 (p:MSU mix:v, 1:1:1). A. % colonization of root system. B. frequency of colonization (no. seedlings colonized).

feasible under most nursery situations. Liquid inoculum has drawbacks including the tendency for contamination. The benefit of using a soil inoculum is that it contains only the fungus of interest, it is pathogen free, and may be generated in the nursery. Unlike spore inoculum, genetic diversity of the fungus is kept to a minimum. Also, fungal sporocarps do not need to be collected each year. In a survey of many large scale trials, Brundrett and others (2005) found that regardless of conditions and fungi, mycelial slurries produced 35 percent colonization of root systems of Eucalyptus seedlings and spore suspensions 49 percent, with the latter being more cost effective when applied on a large scale in the nursery. Our data suggest this proportion may apply to whitebark pine systems as well.

Substrate Effects

There is a concern that certain types of substrate may not be amenable to mycorrhizal colonization. In Experiment 1, method 4, Soil Mix 1 (containing Sunshine Mix) prevented mycorrhizal colonization possibly due to the high pH level. Therefore, we tested soil substrates to determine which are suppressive and which conducive to mycorrhizal colonization. In Experiment 3, we tested three soil substrates with four strains of native mycorrhizal fungi to examine their effect on mycorrhizal colonization. These trials were done without fertilizer. The peat:bark precluded mycorrhizal colonization of native fungi and promoted pathogenic and nursery ECM fungi such as *Thelephora* and will not be used in future trials. Both the peat:vermiculite substrate and

Fig. 3. Successful mycorrhizal colonization of whitebark pine seedlings with a native suilloid fungus. The seedling was inoculuated at the MSU Plant Growth Center under nursery conditions. White areas on branched short roots are ectomycorrhizae of the fungus. Inset shows the fungus covering short roots and mycelium extending into the soil.

Soil Mix 2 were conducive to mycorrhizal colonization by suilloid fungi for the four strains tested. Experiments since have suggested that a different soil mix 3 (1:1:1 by volume, MSU mix: vermiculite: peat) and a peat:composted bark mix recently used at the Idaho nursery may be preferable for mycorrhizal colonization. The latter has been found to be acceptable for growth of whitebark pine seedlings (Eggleston, personal communication). One factor may be that substrate pH is around 5.5 which is recommended for conifers and also for many ectomycorrhizal fungi.

Possible soil substrates are currently being tested at the Idaho nursery for whitebark pine both to save money (primarily on peat) and to promote growth. Davis and others (2009) report that the peat:bark mixture was preferable to the peat:sawdust mixture for larch. Both peat:sawdust and peat:composted bark have also been tested for whitebark pine (Kent Eggleston, personal communication) and while colonization can occur in either substrate, new evidence from our lab suggests the latter may be preferable for inoculation purposes.

Parladé and others (2004) found that pines inoculated with *Rhizopogon* could be colonized in peat:bark (1:1 by volume) and peat:vermiculite (1:1 by volume), but that pines in the bark mixture benefited more from inoculation which increased survival by 23 percent in the field. However, Rincon and others (2005) found that *Pinus taeda* seedlings in a 1:1 peat:composted bark mix had reduced colonization of *Rhizopogon,* while those in peat:vermiculite were 80 percent colonized. This again suggests that methods need to be developed for each tree species and system.

Fertilizer Effects

In Experiment 2, the fertilizer added at 200 ppm of 20:20:20 once/twice/three times a week was detrimental to the seedlings (browning needle tips) and promoted infection of *Thelephora* which is a greenhouse strain of mycorrhizal fungus that can cause 'choke disease'. We initially wanted to examine high levels of fertilization to check the 'cap' on fertilization, but found that even at fertilization level 1 (once a week), mycorrhization was highly suppressed. In subsequent experiments, we found that some suilloid fungi can tolerate a light fertilizer treatment.

While fertilization is known to reduce mycorrhization, it is possible under some fertilization regimes (Khasa and others 2001). Reducing fertilization to once every 15 days can allow both mycorrhization and good seedling growth (Khasa and others 2001). Also, application of higher levels of inoculum can overcome suppression by liquid fertilizer but not that caused by the time-release fertilizer Osmocote (Castellano and others 1985). It may be that constant release of nutrients prevents spore germination or changes pH. Also, different fungal strains vary in their tolerance to fertilizer (level and type) and need to be tested individually. Davey and others (1990) suggest that ectomycorrhizae can form with some fertilization but might overload seedlings with phosphate and depress growth. The use of exponential fertilization has been shown to not only save on fertilizer use (45 percent less!) for *Pinus monticola* (Dumroese and others 2005) but to also be conducive to mycorrhizal colonization (Quoreshi and Timmer 1998); this offers a possible method for whitebark pine inoculation.

In a recent experiment we inoculated (spore slurries) 16 month old whitebark pine seedlings that had been grown in typical conditions at the Coeur D'Alene Nursery. Fertilization was stopped one month before inoculation to help promote colonization. Stunningly, a majority of seedlings were found to be well colonized after only two months and ectomycorrhizae covered a majority of their root systems (Fig. 3)! If this method can be shown to give consistent results (effective colonization) it would be a 'simple' way to inoculate whitebark pine seedlings. Large adjustments to typical nursery regime would not be necessary. The new peat:composted sawdust media used by the Coeur D'Alene was shown to be conducive to mycorrhizal colonization in this small trial.

Survival in the Field

The older seedlings described above are now out-planted in Waterton-Glacier International Peace Park and survival will be assessed in the next two years. The ultimate goal is to increase survival in the field. This has been shown to be possible under certain circumstances, primarily where natural inoculum is lacking (Wiensczyk and others 2002). However, inoculation can 'jump-start seedlings where appropriate fungi are found in the soil and when there is replacement by other fungi (Davey and others 1990).

For ponderosa pine seedlings inoculated with *Rhizopogon* survival increased on a dry, harsh site from 71 percent to 93 percent, a 22 percent increase, but inoculation did not make a difference on a second site (Steinfeld and others 2003). Parladè and others (2004) report a 23 percent increase in survival for *Pinus taeda* inoculated with *Rhizopogon* after 43 mo. and found inoculation to be cost effective. Seedling size is sometimes a concern at out-planting. Stenströme and Ek (1990) found that while colonized pine seedlings were smaller than controls at planting, they were 50 percent larger after 2.5 years. Inoculation often produces 'bushier' root systems that may be pre-conditioned to soil exploration on out-planting (Khasla and others 2009). This would be in contrast to the root systems we have examined in out-plantings of whitebark pine that have retained their container shape for at least 5 years (Trusty and Cripps 2010).

For whitebark pine, the use of suilloid fungi specific to 5-needle pine could possibly give these pines a competitive edge over other pine species and fir. Therefore, it is recommended that regionally-appropriate native mycorrhizal fungi be used for inoculation of nursery grown whitebark pine seedlings. Preservation of native strains is also important as a management tool as ecotypes are likely to disappear in areas where forests decline. Determining when inoculation is deemed necessary is outside the scope of the present report but see Wiensczyk and others (2002).

Current Recommendations

Currently we are recommending that managers minimize practices detrimental to soil microbes, seedlings be planted within a year of disturbances before ECM viability declines, seedlings be planted near inoculum sources (living whitebark pines or in soil previously in whitebark pine) and planted seedlings be monitored for mycorrhizal colonization. In areas where native ECM fungi specific for whitebark pine are likely to be absent, inoculation of seedlings in the greenhouse should be considered. These areas include severe burns, areas not previously in whitebark pine, ghost forests, and areas where planted whitebark pine seedlings have a low survival rate. We recommend that only regionally-appropriate native mycorrhizal fungi be used for inoculation of nursery grown whitebark pine seedlings. Commercial mycorrhizal inoculum *should not* be used in sensitive whitebark pine systems to minimize the risk of importing alien fungi. At present our data suggest that older seedlings can be inoculated 3-4 months before out-planting if fertilization is reduced one month before inoculation if the soil media is appropriate.

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References

Ashkannejhad, S.; Horton, T. R. 2005. Ectomycorrhizal ecology under primary succession on coastal sand dunes: interactions involving *Pinus contorta*, suilloid fungi and deer. New Phytologist. 169: 345-354.

Brundrett, M.; Boucher, N.; Dell, B.; Grove, T.; Malajczuk, N. 1996. Working with Mycorrhizas in Forestry and Agriculture. ACIAR Monograph 32. 374 p.

Brundrett, M.; Malajczuk, N.; Mingquin, G.; Daping, X.; Snelling, S.; Dell, B. 2005. Nursery inoculation of Eucalyptus seedlings in Western Australia and southern China using spores and mycelial inoculum of diverse ectomycorrhizal fungi from different climatic regions. Forest Ecology and Management. 209: 193-205.

Bruns, T. D.; Bidartondo, M. I.; Taylor, L. 2002. Host specificity in ectomycorrhizal communities: what do the exceptions tell us? Integrative and Comparative Biology. 42: 352-359.

Burr, K.; Eramian, A.; Eggleston, K. 2001. Growing whitebark pine seedlings for restoration. Pp. 325-345. In: Tomback, D. F., S. F. Arno and R. E. Keane. eds. Whitebark Pine Communities: ecology and restoration. Island Press, Washington, DC.

Castellano, M. A.; Trappe, J. M.; Molina, R. 1985. Inoculation of container-grown Douglas-fir seedlings with basidiospores of *Rhizopogon vinicolor* and *R. colossus*: effects of fertility and spore application rate. Canadian Journal of Forest Research. 15: 10-13.

Cripps, C. L. 2002. Mycorrhiza. Pp. 21-23. In: Pscheidt, J. W. and C. M. Ocamb (eds.), Pacific Northwest Plant Disease Management Handbook. Oregon State University Press, Corvallis, OR.

Cripps, C. L. (editor) 2004. Fungi in Forest Ecosystems: Systematics, Diversity and Ecology. New York Botanical Garden Press, NY. 363 p.

Cripps, C. L.; K. Mohatt. 2005. Preliminary results on the Ectomycorrhizal Fungi of Whitebark Pine Forests. Nutcracker Notes. 7: 9-11.

Cripps, C. L.; P. Trusty. 2007. Whitebark pine restoration program, Dunraven Pass (Monitoring mycorrhizal status of seedlings). Greater Yellowstone Coordinating Committee Project Report. 2007.

Cripps, C. L.; Smith, C.; Carolin, T.; Lapp, J. 2008. Ectomycorrhizal fungi with whitebark pine. Nutcracker Notes. 14: 12-14.

Davey, C. B.; Schenck, C. A. 1990. Mycorrhizae and realistic nursery management. Pp. 67-77. In: Rose, R., S. J. Campbell and T. D. Landis, eds. Proceedings of the Western Forest Nursery Association, Aug. 13-17, Roseburg, OR. GTR RM-200. USDA FS, Rocky Mountain Forest and Range Experiment Station.

Davis, A. S.; Eggleston, K.; Pinto, J. R.; Dumroese, R. 2009. Evaluation of three growing substrates for Western larch seedling production at the USDA Forest Service Coeur d'Alene Nursery. U.S. Department of Agriculture Forest Service Proceedings, RMRS-P-58.

Dumroese, K. 2008. Observations on root disease of container whitebark pine seedlings treated with biological controls. Native Plants Journal 9(2): 92-97.

Dumroese, K.; Page-Dumroese, D.S.; Salifu, K.F.; Jacobs, D.F. 2005. Exponential fertilization of *Pinus monticola* seedlings: nutrient uptake efficiency, leaching fractions, and early out-planting performance. Canadian Journal of Forest Reseach 35: 2961-2967.

Eggleston, K. 2010. [Personal Communication]. April 19, 2010. U.S. Department of Agriculture Forest Service Nursery, Coeur D'Alene, ID.

Izlar, D. 2007. Assessment of whitebark pine seedling survival for Rocky Mountain plantings. M.Sc. Thesis, University of Montana, Missoula, MT.

Izzo, A. D.; Meyer, M.; Trappe, J. M.; North, M.; Bruns, T. D. 2005. Hypogeous ectomycorrhizal fungal species on roots and in small mammal diet in a mixed-conifer forest. Forest Science. 51: 243-254.

Keane, R. E.; Arno, S. F. 2001. Restoration concepts and techniques. Pp. 367-400. In: Tomback, D. F., S. F. Arno and R. E. Keane, eds. Whitebark Pine Communities: ecology and restoration. Island Press, Washington, DC.

Keane, R. E.; Parsons, R. A. 2010. Management guide to ecosystem restoration treatments: whitebark pine forests of the Northern Rocky Mountains, U.S.A. U.S. Department of Agriculture, Forest Service, General Technical Report RMRS-GTR-232.

Khasa, P. D.; Sigler, L.; Chakravarty, P.; Dancik, B. P.; Erickson, L.; McCurdy, D. 2001. Effect of fertilization on growth and ectomycorrhizal development of container-grown and bare-root nursery conifer seedlings. New Forests. 22: 179-197.

Khasa, P. D.; Piché, Y.; Coughlan, A. P. (eds.). 2009. Advances in Mycorrhizal Science and Techology. NRC Research Press, Ottawa, 2009. 197 p.

Landis, T.; Tinus, R.; McDonald, S.; Barnett, J. 1990. The Container Tree Nursery Manual. Vol 5: Nursery Pests and Mycorrhizae. U.S. Department of Agriculture, Forest Service, Agriculture Handbook. 674.

Logan, J.; Macfarlane, W.; Willcox, L. 2010. Whitebark pine vulnerability to climate-driven mountain pine beetle disturbance in the Greater Yellowstone Ecosystem. Ecological Applications. 20(40): 895-902.

McCaughey, W.; Scott, G.; Izlar, K. 2009. Whitebark pine planting guidelines. Western Journal of Applied Forestry. 24(3): 163-166.

Mahalovich, M. F.; Dickerson, G. A. 2004. Whitebark pine genetic restoration program for the Intermountain West (United States). In: Sniezko, R. A., S. Samman, S. E. Schlarbaum, H. B. Kriebel (eds.). Breeding and genetic resources of five-needle pines: growth, adaptability and pest resistance. Proc RMRS-P-32, Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station: 181-187.

Mohatt, K. R. 2006. Ectomycorrhizal fungi of whitebark pine (*Pinus albicaulis*) in the Greater Yellowstone Ecosystem. M.Sc. Thesis, Montana State University, Bozeman, MT.

Mohatt, K. R.; Cripps, C. L.; Lavin, M. 2008. Ectomycorrhizal fungi of whitebark pine (a tree in peril) revealed by sporocarps and molecular analysis of mycorrhizae from treeline forests in the Greater Yellowstone Ecosystem. Botany. 86: 14-25.

Molina, R.; Trappe, J. 1984. Mycorrhiza management in Bareroot nurseries. In: Duryea, M. L. and T. D. Landis, eds. Forest Nursery Manual: Production of Bareroot seedlings. JijhoffJunk Publishers for Forest Research Laboratory, Oregon State University, Corvallis: 211-223.

Moser, M. M. 1956. Die Bedeutung der Mykorrhiza für Aufforestungen in Hochlagen. Forstwiss. Cbl. 75: 8-18.

Moser, M.M. 2004. Subalpine conifer forests in the Alps, the Altai, and the Rocky Mountains: A comparison of their fungal populations. Pp. 151-158. In: Cripps, C.L., ed. Fungi in Forest Ecoysystems: systematics, diversity and ecology. New York Botanical Garden Press, N.Y.

Parladé, J.; Luque, J.; Pera, J.; Rincón, A. M. 2004. Field performance of *Pinus pinea* and *P. Halepensis* seedlings inoculated with *Rhizopogon* spp. and out-planted in formerly arable land. Annals of Forest Science. 61: 507-514.

Quoreshi, A. M.; Timmer, V. R. 1998. Exponential fertilization increases nutrient uptake and ectomycorrhizal development of black spruce seedlings. Canadian Journal of Forestry Research. 28: 674-682.

Riley, L. E.; Coumas, C. M.; Danielson, J. F.; Berdeen, J. C. 2007. Seedling nursery culture of whitebark pine at Dorena Resource Center: headaches, successes and growing pains. U.S. Department of Agriculture, Forest Service, R6-NR-FHP-2007-01: 122-131.

Rincon, A.; Parladé, J.; Pera, J. 2005. Effects of ectomycorrhizal inoculation and the type of substrate on mycorrhization, growth and nutrition of containerized *Pinus pinea* L. seedlings produced in a commercial nursery. Annals of Forest Science. 62: 817-822.

Schwandt, J. 2006. Whitebark pine in peril. U.S. Department of Agriculture, Forest Service, R1-06-28. Missoula, MT.

Smith, S. E.; Read, D. J. 1997. Mycorrhizal Symbiosis. Academic Press, Inc., San Diego, CA.

Smith, C., Wilson, B.; Rasheed, S.; Walker, R.; Carolin, T.; Shepard, B. 2008. Whitebark pine blister rust in the Rocky Mountains of Canada and northern Montana. Canadian Journal of Forest Research. 38(5): 982-995.

Steinfeld, D.; Amaranthus, M.; Cazares, E. 2003. Survival of Ponderosa pine (*Pinus ponderosa*) Dougl. Ex Laws.) seedlings outplanted with *Rhizopogon* mycorrhizae inoculated with spores at the nursery. Journal of Arboriculture. 29(4): 197-208.

Stenström, E.; Ek, M. 1990. Field growth of *Pinus sylvestris* following nursery inoculation with mycorrhizal fungi. Canadian Journal of Forest Research. 20: 914-918.

Tomback, D. F.; Arno, S. F.; Keane, R. E. 2001. The compelling case for management intervention. Pp. 3-25. In: Tomback, D. F., S. F. Arno, and R. E. Keane, eds. Whitebark Pine Communities: ecology and restoration. Island Press, Washington, DC.

Trusty, P.; Cripps, C. L. 2010. Impact of fire on the mycorrhizal community with planted and natural seedlings (Fridley Burn, Montana). Hi-Five Symposium, Missoula, MT, June 28-30, 2010.

Whipps, J. M. 2004. Prospects and limitations for mycorrhizas in biocontrol of root pathogens. Canadian Journal of Botany 82: 1198-1227. (Special issue on Mycorrhizae)

Weisleitner, H. 2008. [Personal communication]. Federal Nursery of Austria, Innsbruck, Austria.

Wiensczyk, G.; Durall, D.; Jones, M; Simard, S. 2002. Ectomycorrhizae and forestry in British Columbia: A summary of current research and conservation strategies. Extension Note. B.C. Journal of Ecosystems and Management. 2(1): 1-20.

The Proactive Strategy for Sustaining Five-Needle Pine Populations: An Example of its Implementation in the Southern Rocky Mountains

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Abstract—The imminent invasion of the non-native fungus, *Cronartium ribicola* J.C. Fisch., that causes white pine blister rust (WPBR) and the current mountain pine beetle (*Dendroctonus ponderosae* Hopkins, MPB) epidemic in northern Colorado limber pine forests will severely affect the forest regeneration cycle necessary for functioning ecosystems. The slow growth and maturity of limber pine enables trees to persist on the landscape for centuries, but without sufficient regeneration opportunities these traits will inevitably hinder the ability of limber pine to adapt to novel stresses such as WPBR or climate change. The current MPB outbreak will result in the death of many mature limber pines, including many with genetic resistance to WPBR. It will be decades until advanced regeneration develops into seed-producing mature trees in much of this region. This development will be limited further by WPBR which rapidly kills susceptible young trees. Efforts to sustain limber pine and Rocky Mountain bristlecone pine in the southern Rockies were initiated in 2001. The Northern Colorado Limber Pine Conservation Program, described here, is an example of the Proactive Strategy being implemented at a local scale. The program is a cooperative partnership between the USFS Rocky Mountain Research Station, Rocky Mountain National Park (RMNP), USFS Forest Health Management, and several Ranger Districts on the Arapaho-Roosevelt National Forest. It is designed to 1) conserve limber pine genetic diversity and 2) collect needed data to assist land managers in making informed decisions for preparation of a management plan intended to sustain resilient limber pine ecosystems in northern Colorado. The cooperative effort aims to provide immediate protection of limber pine from MPB, facilitate seed collections for WPBR resistance tests, and store and use seed for conservation, research and restoration. Seedlings are being screened for WPBR resistance to determine frequencies of resistance across the landscape among populations and to identify resistant seed trees for future seed collections. The seedling tests will also estimate population differentiation along the elevation gradient to refine seed transfer guidelines. Surveys of forest health, biotic damage, rust incidence, and trends in advanced regeneration will help project persistence of these populations after passage of the MPB epidemic. These data will provide a basis for evaluations of proactive management options on a site specific basis before northern Colorado ecosystems are impaired by WPBR; this should shorten the time frame to return to functioning ecosystems. Focusing management on proactively maintaining genetic diversity and a functional regeneration cycle will promote sustained adaptive capacity and ecosystems resilience to novel stresses such as WPBR and climate change.

Introduction

There are still five-needle pine populations in North America that have not yet been invaded by *Cronartium ribicola* J.C. Fisch., the non-native, invasive pathogen that causes white pine blister rust (WPBR) (fig. 1). White pine blister rust will invade new areas where five-needle pines occur and will cause high mortality, potentially causing local extirpations. Options are available to land managers to help mitigate the impacts of rust and also to speed the recovery of the ecosystems. However, data is necessary to provide science-based information for developing those options. The Proactive Strategy framework is a template for the collection of this information in order to develop proactive management options. The proactive measures considered for WPBR will also assist with alleviating impacts of mountain pine beetle (*Dendroctonus ponderosae* Hopkins, MPB) and climate change. Any high elevation five-needle pine ecosystem not yet impacted by WPBR can be a candidate for proactive management.

Early awareness of the threat of WPBR to the remaining healthy high-elevation ecosystems offers unique opportunities for gathering information, capturing genetic resources, preparing the landscape for invasion, mitigating impacts of infection, and initiating preparations for restoration. Since high elevation ecosystems are especially vulnerable to climate change and mountain pine beetle activity has escalated recently in some of the five-needle pine ecosystems (Gibson and others 2008, Diaz and Eischeid 2007, Pepin and Lundquist 2008, Salzer et al. 2009)), both stressors add urgency and complexity to managing these mountain ecosystems. The Proactive Strategy was developed as a management tool to promote population and ecosystem resiliency in high-elevation five-needle pine ecosystems not yet infected by WPBR or in the early stages of infestation (Schoettle and Sniezko 2007; Keane and Schoettle this proceedings).

Recent discoveries of new WPBR infection centers in Colorado, Nevada and Arizona verify that the spread of the fungus continues (e.g. Blodgett and Sullivan 2004; Vogler and Charlet 2004; Kearns and Jacobi 2007, Fairweather and Geils 2011), although most five-needle pine populations

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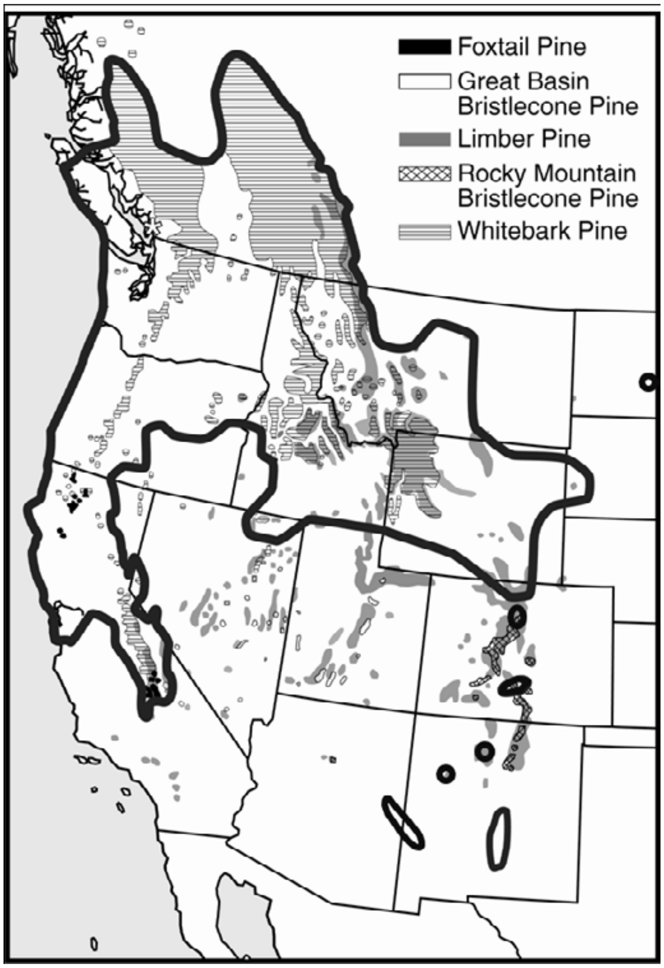
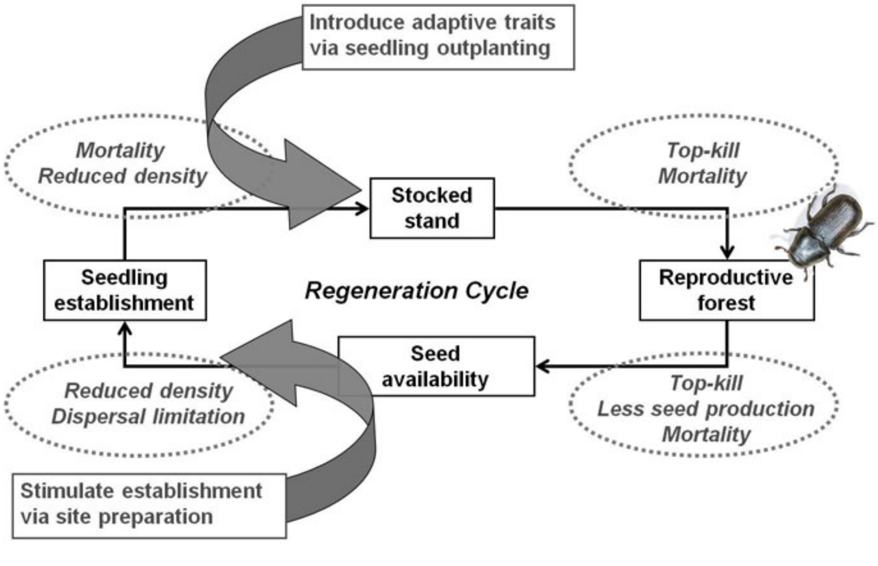


Figure 1. Map of western North America showing the current infection front of white pine blister rust (bold line; adapted from Samman and others 2003 and Schoettle and Sniezko 2007) and the distribution of each of the high elevation five-needle pine species. Note that many but not all populations within the infection areas are infected.

in these states are still healthy. Risk analyses of the currently rust-free areas of Colorado reveal that up to 50% of the five-needle pine habitats have climatic conditions that can regularly support disease success, suggesting that once the inoculum is in the area, disease incidence will increase (Kearns 2005; Howell and others 2006). The basic options for these areas include 1) 'no action': do nothing and let pine populations degrade and impacts cascade through the ecosystems, 2) 'reactive': wait to see if populations become degraded and then implement restoration treatments or 3) 'proactive': implement treatments before ecosystem degradation to maximize resiliency of the pine populations and mitigate ecosystems impacts. The detrimental impacts of WPBR in whitebark pine ecosystems (see Tomback and others 2001) demonstrate consequences of the 'no action' option in the early stages of infestation, an outcome which, in combination with the stress of MPB and climate change, has led to a petition for listing of whitebark pine as an endangered species under the Endangered Species Act (NRDC 2008).

Natural selection for traits that support survival under new conditions, such as an introduced pathogen or climate change, requires a foundation of genetic diversity and regeneration opportunities to pass the traits on to the next generation (Aitken and others 2008; St Clair and Howe 2009). Therefore, a sustainable population in the presence of WPBR requires traits for genetic rust resistance and a functioning regeneration cycle (Schoettle and Sniezko 2007). All of the high-elevation five-needle pines have at least one mechanism of resistance to WPBR (Hoff and others 1980). However, the frequency of trees with rust resistance appears to be low. These pines also have a slow regeneration cycle: they are not prolific seeders, they have delayed maturation and the adults are very long-lived. Proactive measures that enhance a functioning regeneration cycle in healthy populations can facilitate an increase in frequency of rust-resistant traits (Fig. 2). For example, artificial regeneration with rust-resistant seedling stock can increase the frequency of resistance in a healthy population that has very low resistance. If moderate frequencies of resistance exist in the healthy population, stimulating natural regeneration through site

Figure 2. Flow diagram of the forest regeneration cycle and the points of interaction with WPBR and management interventions. White pine blister rust can cause impacts at all stage (ovals) and the mountain pine beetle preferentially kills larger trees. Broad arrows depict intervention options for increasing rust resistance and population resiliency. (Redrawn from Schoettle and others 2009)



preparation results in greater numbers of individuals (and genotypes) on which natural selection for resistance can act (Schoettle and Sniezko 2007). These measures will be more effective at sustaining high mountain ecosystem services if implemented proactively in functioning ecosystems rather than reactively in degraded ecosystems where the regeneration cycle is impaired by WPBR. Many factors need to be weighed when making the decision to commit toward one or both of these proactive paths.

The Proactive Strategy provides a science-based foundation to better guide management decisions before ecosystem impacts curtail any options. This strategy, initiated in 2001 to sustain limber pine and Rocky Mountain bristlecone pine in the southern Rockies includes seed collections, forest health monitoring and studies of rust resistance, fire ecology, epidemiology, and regeneration dynamics (Schoettle 2004a; Schoettle and Sniezko 2007; Schoettle and others 2007; Burns and others 2010; Keane and Schoettle this proceedings, Kearns 2005; Kearns and Jacobi 2007). In this paper, we will present a summary of the intensive Northern Colorado Limber Pine Conservation Program as an example of the Proactive Strategy. The paper will provide guidance to land managers with concerns about the future viability of their five-needle pine populations. New science-based information is now available to help managers weigh some of the proactive management alternatives.

Urgency and Timing of the Proactive Strategy

Continued discoveries of WPBR infections in northern Colorado, including in Rocky Mountain National Park (RMNP) in 2009 and 2010, in conjunction with mountain pine beetle (MPB) populations increasing to epidemic levels heightens the concern over the health and future of limber pine in northern Colorado (Schoettle and others 2008; Schoettle and others 2009). The impact of these stressors together will severely affect pine regeneration cycles required for sustaining populations and ecosystem functions (Fig. 2). Although the slow growth and maturity of limber pine enable trees to persist on the landscape for centuries, the ability of limber pine to adapt to novel stresses, such as WPBR and climate change, will be hindered without sufficient regeneration opportunities. Moreover, the MPB outbreak will result in the death of many mature trees and, as a consequence, decades will pass until advanced regeneration can mature enough to produce seed. The ability to produce seed could take 30-50 years in limber pine. This recovery will be limited further by WPBR killing susceptible young trees as the pathogen expands its distribution.

WPBR can reduce the genetic diversity of pine populations (Kim and others 2003) and even cause population extirpation (Tomback and others 2001), so genetic conservation efforts should precede WPBR impacts. In light of the ongoing spread of WPBR and current MPB epidemic, capturing genetic diversity in the form of seed is an important step towards keeping proactive management options open into the future. The death of seed-producing mature trees by MPB will restrict our ability to capture the species' full genetic diversity and test for WPBR resistance. Current rust resistance testing technology requires the sowing of seed for artificial rust inoculation of seedlings. Non-reproductive young pine trees, which will escape MPB attack, cannot be screened for resistance until they mature; therefore without seed collections from the current overstory trees, gene conservation and tests of heritable WPBR resistance will be limited for the foreseeable future. Seed from base populations are also important for studies of genetic structure and seed transfer in order to develop restoration protocols, although technologies using genomics may ease that requirement in the future.

The Northern Colorado Limber Pine Conservation Program

In 2008, USFS Rocky Mountain Research Station (RMRS), Rocky Mountain National Park (RMNP), USFS Rocky Mountain Region Forest Health Management, and several National Forest districts initiated an intensive program to conserve limber pine and provide information for the development of limber pine management plans for Rocky Mountain National Park and northern Colorado; a process we are calling the Proactive Strategy. Approximately 1,100 ha and 41,000 ha of limber pine occurs in RMNP and Arapaho and Roosevelt National Forests, respectively. Most are in isolated populations east of the Continental Divide. Aside from the ecological functions that limber pine provides to high-elevation ecosystems including snow retention, wildlife food sources and facilitating the establishment of other tree species (see Schoettle 2004b), this long-lived species is aesthetically and historically important to visitors of the national park (2.9 million visitors in 2009; http://www.nps.gov/romo/parkmgmt/statistics.htm) and national forests. Limber pine occurs along scenic highways, along popular trails and at vista points that contribute to the visitor experience. Even people that do not visit these sites appreciate the high elevation pine species and value their continued existence (Meldrum and others this proceedings).

The objectives of the cooperative program to conserve and sustain limber pine on the northern Colorado landscape are 5-fold: (1) provide protection to limber pine from MPB so immediate seed collections can be made for WPBR resistance tests, genetic conservation, and research; (2) screen seedlings for WPBR resistance to determine the frequency of resistance across the landscape among populations and to identify resistant parent trees for future seed collections; (3) estimate population differentiation along the elevation gradient to refine seeds transfer guidelines; (4) survey forest health, biotic damage incidence and advanced regeneration to project persistence of these populations after MPB invasion; and (5) prepare management plans for northern Colorado.

1) Protection of Limber Pine from MPB for Seed Collections

Twenty-seven limber pine populations, stratified by elevation, were identified in RMNP and Arapaho and Roosevelt National Forest lands in spring 2008 (Figs. 3 and 4). Each population contains mature limber pine trees from which 10 to 15 individual seed trees were tagged and georeferenced for seed collections and MPB protection. Selected trees are spaced >60m from one another to increase sampling of non-related parent trees and the chances progeny will capture the pollen cloud of the population (and thus much of the genetic diversity); the sampling area per site ranged from approximately 9 to 12 ha.

Protection of limber pine seed trees from MPB on the 27 sites involves annual spraying with insecticides (at sites accessible by vehicle) or applying verbenone, a bark beetle anti-aggregate pheromone, on trees in more remote areas and within the National Park. Two pouches of verbenone are applied to each seed tree per year. Rocky Mountain National Park coordinates a network of citizen volunteers to help install the verbenone pouches at the park sites. This emergency short-term protection of the seed trees from MPB provides time to collect seeds during the epidemic.

Annual seed collections are attempted from each of the georeferenced seed trees at the 27 limber pine sites; bulk seed collections from other trees in each population are also being made (see Appendix for sampling details). Collections are made in late August through September and sometimes as late as early October, depending on seed maturation timelines. Generally, in northern Colorado, limber pine seeds mature at lower elevation sites in early September and at higher elevation sites by mid to late September. A bulk population collection from each site includes two to four cones from each of approximately 20 additional trees (not the georeferenced seed trees) evenly spaced throughout the population. Citizen volunteers also assist with cone collections each fall at the RMNP sites. Though 2008, 2009 and 2010 were not peak cone production years for limber pine in northern Colorado, collections were made from 201 individual seed-trees and an additional 23 bulk seed lots. Some of these were

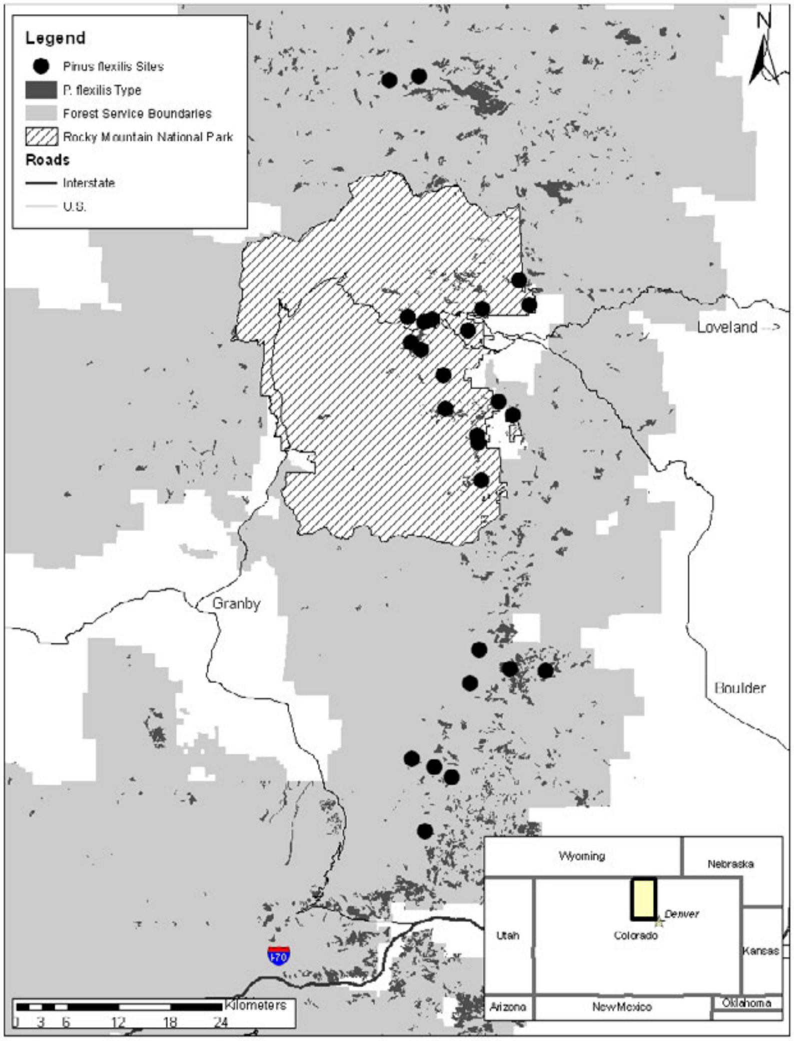


Figure 3. Map of the 27 sites used in the Northern Colorado Limber Pine Conservation Program.

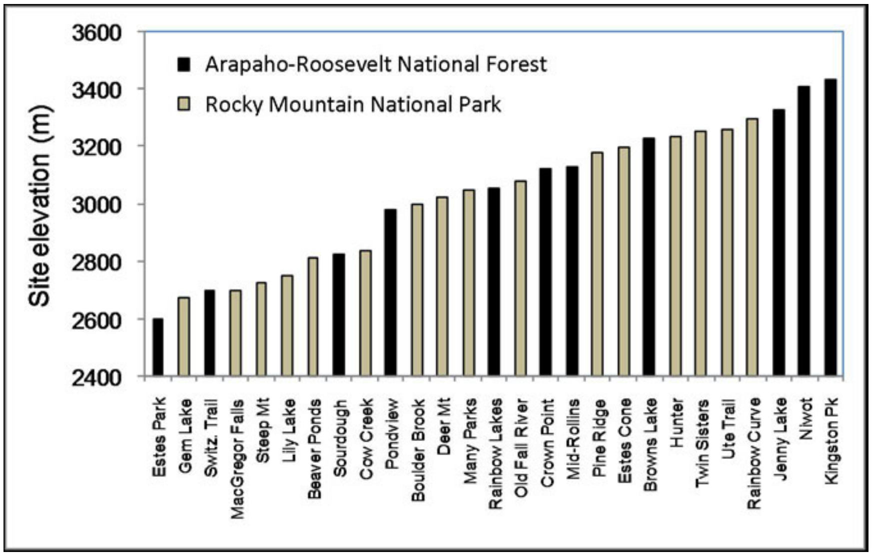


Figure 4. Distribution of the 27 sites used in the Northern Colorado Limber Pine Conservation Program with respect to elevation.

sampled in multiple years, bringing the total number of seed lots collected from the 27 sites in the past three years to 287. Seedlots with sufficient seed were used for rust resistance testing (see below) and a common garden study to assess variation among sources in growth parameters (see below). Remaining seed is archived at -80°C for gene conservation, research and small scale outplanting projects.

2) White Pine Blister Rust Resistance Screening

Seed collections from bulk and individual tree collections are being tested for genetic resistance to WPBR at the Forest Service Dorena Genetic Resource Center (DGRC, Cottage Grove, OR). The initial tests are examining the incidence of canker-free seedlings ('complete' resistance) following artificial inoculation with rust (see Vogler and others 2006 for more information on complete resistance). Testing of the bulk seed lots will estimate the natural frequency of complete resistance in each of the national park and forest sites (populations) and seed lots from the individual seed-tree (family) collections will identify resistant trees that can be used as seed sources for future outplanting. Inoculation of seedlings from bulk seed lots was done in 2009 and from the individual seed-tree lots in 2010 using protocols developed for limber pine by RMRS and DGRC personnel in previous testing at DGRC. Disease development on seedlings will be tracked for two years post-inoculation and seed-tree (parent tree) resistance will be inferred from the proportion of canker-free progeny in each family. Earlier WPBR screenings have confirmed complete resistance in limber pine and refined the data collection methods to quantify disease development for this species (Kinloch and Dupper 2002; Schoettle and others in preparation). The stratification of sampling sites will help define the relationships between genetic resistance and elevation in this region, i.e., to explore whether negative correlations exist between rust resistance and other adaptive traits. The rust screening results will guide the design of additional bulk collections that will be needed to support future large-scale proactive or restorative measures.

3) Population Differentiation

Five seed zones have been defined for limber pine in the Interior West to guide seed transfer for artificial regeneration (Mahalovich 2006; Burns and others 2008). All of the limber pine populations in southeastern Wyoming, Colorado and northern New Mexico are in one zone with a recommended maximum elevational movement of seed of approximately 200 m. To refine this recommendation in northern Colorado, a common garden study of seedlings from the bulk seed lots is underway to assess population differentiation in growth traits. The results will help quantify adaptive traits of limber pine (i.e., differences in growth as well as in the timing of the growth period) from locations along the elevation gradient and refine seed transfer recommendations to reduce the possibility of maladaptation of future outplanting efforts.

4) Trends in Advanced Regeneration

Forest health and stand structure surveys were conducted in each of the 27 limber pine sites in the national park and surrounding national forest in order to estimate population resiliency to MPB-caused mortality. Surveys were conducted in 2009 during the initial escalation of the MPB epidemic in the limber pine type. Ten plots (0.02 ha each), spaced 50 m apart within each site were surveyed for site characteristics, disturbances, advanced regeneration, overstory density, tree health, crown class and biotic damages of all tree species (Klutsch and others this proceedings). Data collected specifically on limber pine included: seedling microsite, seed cone production, estimated tree ages, and annual shoot growth. Ground cover and canopy cover were also estimated in subplots. These data will provide projections of the persistence of these populations (as advanced regeneration) if all of the large reproductive limber pine are killed in the current MPB epidemic.

5) *Pulling It All Together and Building a Management Plan*

Protection of seed-trees will continue until the MPB epidemic subsides or further prioritization is possible given the results of the other components of the program. For example, the current resistance tests of seedlings from the individual-tree seed lots (i.e., families) will identify those seed-trees having heritable complete resistance; the seed-trees would then be a priority for continued MPB protection and seed collections for accumulating resistant seed stock to be used in future outplantings. The resistance being identified in these tests may be similar to complete resistance in western white pine and sugar pine (Kinloch and Dupper 2002). Selective pressure on the rust over time can lead to the rust overcoming at least one form of complete resistance in some pine species (Kinloch and others 1999, 2003, 2008). We do not know if this selection for virulence in the rust will occur in the limber pine-WPBR pathosystem in northern Colorado, but monitoring for symptoms of WPBR on the field trees having complete resistance (from the seedling rust resistance testing) will be useful for detecting changes in rust virulence over time. Known rust-susceptible seed-trees, as identified in rust resistance testing, may also be biological indicators of early WPBR presence at a site. Ultimately, we would like to know the frequency and distribution of all types of genetic resistance to the WPBR fungus. These tests are among the first for the species. The first prototype for the longer-term tests for limber pine was initiated in 2007 and could be extended to more parent trees pending additional funding. With further support and time, a more comprehensive look at the available array of resistances in these populations is possible and would be beneficial to building seed collections with more durable WPBR resistance and, ultimately then supporting future restoration projects. Knowledge of the type of resistance, their frequency and their geographic distribution will provide land managers with baseline data to augment their decisions on the need for or type of appropriate treatment for sustaining a population into the future.

Rust resistance data from the bulk seed collections will provide frequency estimates of complete resistance in each population. In addition, this resistance frequency may be present in all age classes of a population (i.e., not just in the mature trees of the population) because seed dispersal, in the absence of disturbance, is often local and rust is not yet putting selective pressure on the pine populations. The combined information on stand structure and bulk seedlot resistance data will give information about the likelihood that resistance traits will persist in the population, even if MPB kills the mature trees. For example, if a site has healthy advanced regeneration in limber pine and the resistance test of the bulk seedlot reveals resistance, we can suspect that the advanced regeneration also contain resistant genotypes. Therefore, the advanced regeneration at these sites may be prioritized for protection from post-MPB activities, e.g., dead tree removal or prescribed burning. In contrast, if advanced regeneration density is low at a site, yet the resistance test of the bulk seedlot reveals resistance at the site, then protection of the mature trees from further MPB impacts and site preparations to stimulate regeneration may be warranted. Furthermore, if a site has neither advanced regeneration nor any resistance, the common garden study can identify which of the other populations that did show resistance have similar survival and growth traits and can serve as seed sources for artificial regeneration of rust resistant seed or seedlings on the site. Likewise, enrichment plantings with seedlings from resistant parents can also be used in any site to increase the limber pine population and potentially increase local genetic variation. The results will be useful for designing additional bulk collections that will support future large-scale proactive or restoration measures.

Integration of the results from these data with results from other studies will provide the foundation for development of long-term management plans for limber pine in RMNP and northern Colorado. Data collection for these initial studies will be complete in 2013 when a management plan for limber pine will be prepared. Information about the genetic structure of these limber pine populations, persistence of populations after the MPB epidemic, rust resistance traits and current advanced regeneration trends will allow informed evaluations of proactive management options on a site-specific basis in northern Colorado. In addition, the sampling design described here will contribute information on the elevational distribution and coincidence of growth traits, stand structures and frequencies of resistance—information that may be relevant to other areas and possibly other pine-WPBR pathosystems.

Guidelines for successful outplanting techniques of limber pine seedlings in the Rocky Mountain region are under development (Casper and others, this proceedings) and will be applicable to northern Colorado should artificial regeneration be recommended. Furthermore, past research reveals that limber pine regenerates well after fire in this area (Coop and Schoettle 2009) indicating that the use of fire as a management tool may be an option to stimulate regeneration near populations that have resistance. Research on the colonization dynamics of limber in MPB-disturbed landscapes would also complement this program. Further investigation into the consequences of long-distance seed movement on tree performance, especially in light of possible climate change-WPBR interactions, is also recommended. Information from all of these studies would also contribute data to parameterize population or landscape models for limber pine, opening more opportunities to use modeling management tools. As more data and analyses are gathered (e.g., on rust resistance, regeneration following management treatments, etc.) management recommendations and activities can be modified accordingly.

Conclusions

The Northern Colorado Limber Pine Conservation Program is an example of implementing the Proactive Strategy to facilitate the development of a management plan. This program contributes site-specific scientific data and tools for decision-making about the need for and/or trade-offs of intervention to promote sustainability of northern Colorado limber pine populations in the presence of multiple stressors (WPBR and MPB). Some of the information, tools and activities, such as estimating rust resistance frequency, understanding natural regeneration dynamics, and capturing the pine's full genetic diversity via seed collections, can only be taken advantage of from a healthy forest that has not yet had its processes disrupted by these stressors. Likewise, some management options, such as stimulating regeneration in populations with high levels of rust resistance, are best implemented in a healthy forest. The early availability of information will facilitate the regulatory process if interventions are prescribed and permit the inclusion of science-based information in prioritizing sites for strategic planning. Gathering and using this information before the loss of ecosystem functions allows land managers the widest range of management options for maximum resiliency of limber pine, mitigating future impacts on these ecologically important ecosystems in northern Colorado.

This Proactive Strategy framework can be adapted for other five-needle pine species threatened by WPBR and/or MPB and possibly for other pathosystems. An intensive location-based program, such as that implemented in northern Colorado, is especially appropriate for administrative units that want to use local genotypes as much as possible, such as national parks. Understanding the interaction of the species' life history traits and ecology with resistance mechanisms will highlight factors that limit the species' sustainability in the presence of the pathogen. Focusing management on proactively maintaining genetic diversity and a functional regeneration cycle will promote sustained adaptive capacity and ecosystem resiliency.

Acknowledgements

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Appendix—Cone Collection Guidelines and Field Forms

Cone collection guidelines and field forms used for seed collection on *P. flexilis* and *P. aristata* in the southern Rocky Mountains and also for *P. flexilis* in Montana and for *P. longaeva* in Nevada. Collections are for gene conservation, rust resistance screening and research. These protocols have been adapted from those for *P. albicaulis* (Mahalovich personal communication).

This document outlines three tasks that should be conducted at each site: 1) 10 individual tree cone collections, 2) bulk cone collection, and 3) site characterization. Figure 5 is the cone collection field sheet and key; Figure 6 is a field data sheet. Additional information and photos are available upon request to Anna Schoettle (aschoettle@fs.fed.us).

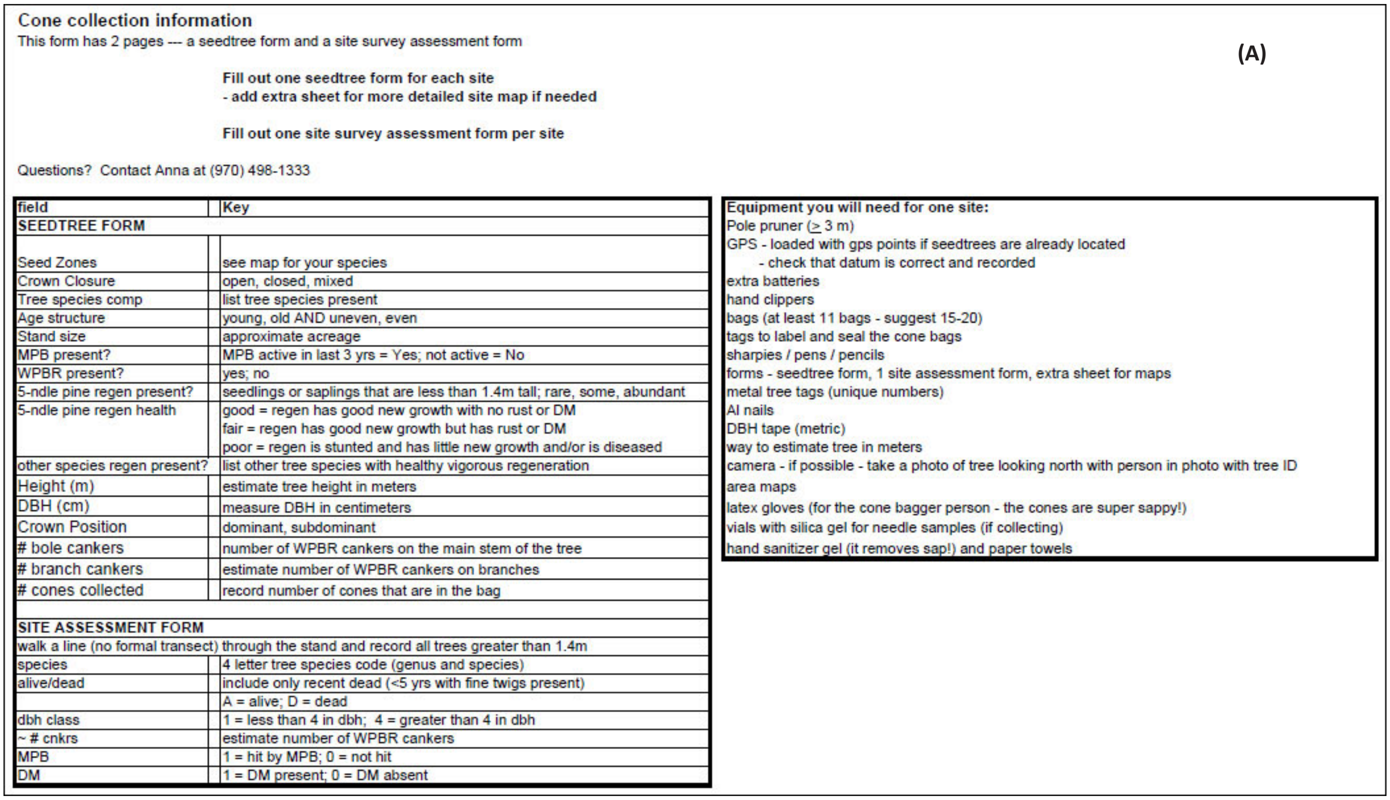
Check cone and seed ripening:

Before collecting cones at a site, cut several cones on site and inspect the embryo for development. The embryo will be filling at least 90 percent of the cavity in the endosperm when the seeds are ripe enough to collect (Figure 7). The embryo should be matte in finish with no jelly-like texture.

Individual tree cone collection:

a. Find, tag (north side of tree) and GPS cone bearing trees, each 200 ft away from each other. If there is rust on site select 9 phenotypically resistant (no visible cankers) seed trees and 1 susceptible (cankered) seed tree. If there is no rust on site, select 10 healthy mature trees (minimize dwarf mistletoe [DM] presence).

Spacing the trees: The easiest way to space the trees is to GPS the first tree ("Main Menu → Mark → Waypoint"), then set your GPS unit to find that point (Find → Waypoint) and walk away from it until you are ~200 ft away and then start looking for the second tree and so on. Be careful if you are not moving in a straight line that you aren't doubling back and getting close to a former seed tree—you may need to do a "go to nearest waypoints" (Find → Waypoint) to make sure you are ~200 ft away from all your trees. Waypoints should be named the same as the TREE ID and marked as Site Initials (2 to 3 letters) and tag number in the GPS. Each seed tree should have a unique tag and ID number, even among sites. Example: UTE3426. Set GPS to Datum WGS84 under Settings/Setup → Units → Datum.



Cone collection information

This form has 2 pages --- a seedtree form and a site survey assessment form

(A)

Fill out one seedtree form for each site
- add extra sheet for more detailed site map if needed

Fill out one site survey assessment form per site

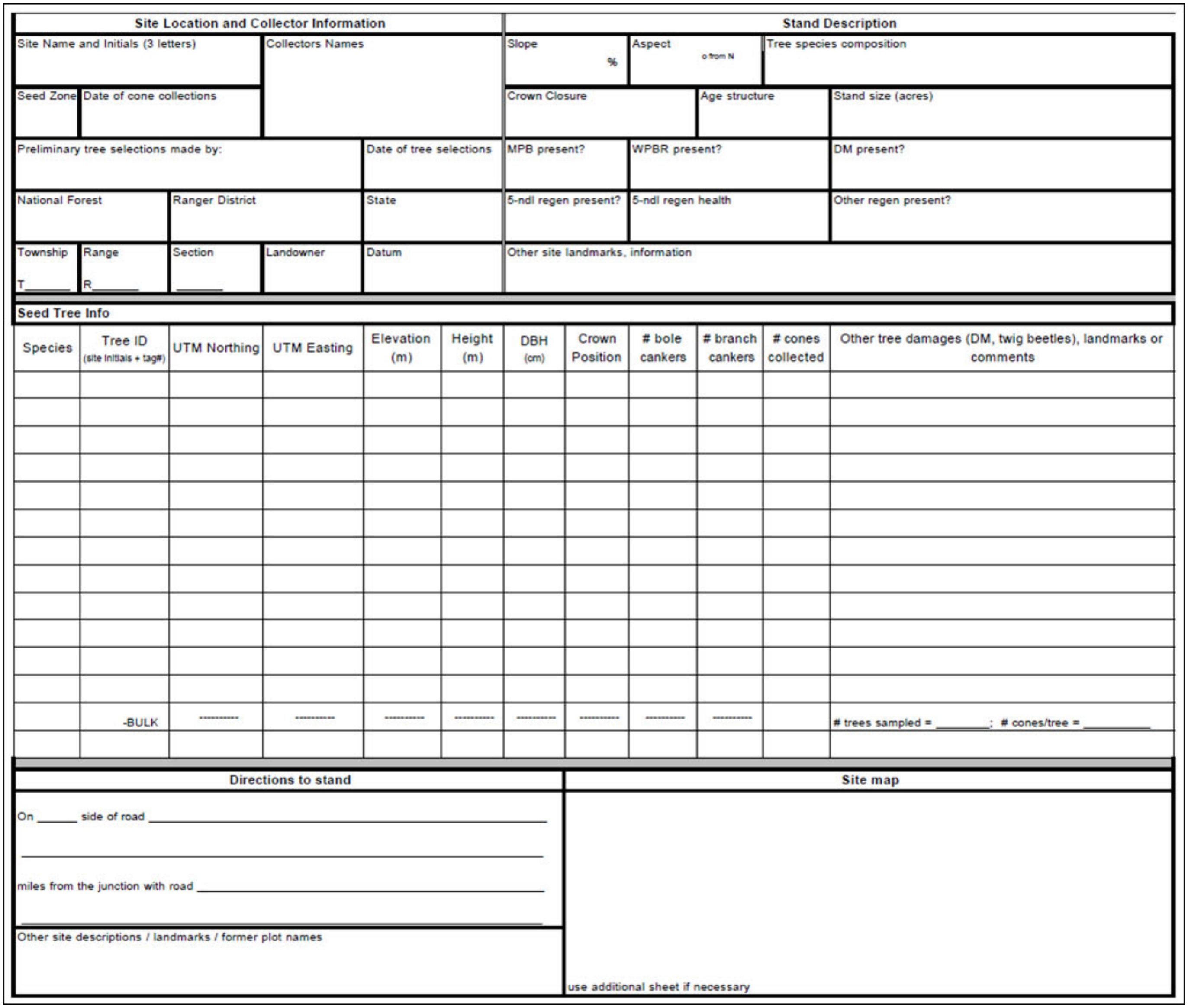
Questions? Contact Anna at (970) 498-1333

field	Key
SEEDTREE FORM	
Seed Zones	see map for your species
Crown Closure	open, closed, mixed
Tree species comp	list tree species present
Age structure	young, old AND uneven, even
Stand size	approximate acreage
MPB present?	MPB active in last 3 yrs = Yes; not active = No
WPBR present?	yes; no
5-ndle pine regen present?	seedlings or saplings that are less than 1.4m tall; rare, some, abundant
5-ndle pine regen health	good = regen has good new growth with no rust or DM fair = regen has good new growth but has rust or DM poor = regen is stunted and has little new growth and/or is diseased
other species regen present?	list other tree species with healthy vigorous regeneration
Height (m)	estimate tree height in meters
DBH (cm)	measure DBH in centimeters
Crown Position	dominant, subdominant
# bole cankers	number of WPBR cankers on the main stem of the tree
# branch cankers	estimate number of WPBR cankers on branches
# cones collected	record number of cones that are in the bag
SITE ASSESSMENT FORM	
walk a line (no formal transect) through the stand and record all trees greater than 1.4m	
species	4 letter tree species code (genus and species)
alive/dead	include only recent dead (<5 yrs with fine twigs present)
	A = alive; D = dead
dbh class	1 = less than 4 in dbh; 4 = greater than 4 in dbh
~ # cnkrs	estimate number of WPBR cankers
MPB	1 = hit by MPB; 0 = not hit
DM	1 = DM present; 0 = DM absent

Equipment you will need for one site:
Pole pruner (≥ 3 m)
GPS - loaded with gps points if seedtrees are already located
    - check that datum is correct and recorded
extra batteries
hand clippers
bags (at least 11 bags - suggest 15-20)
tags to label and seal the cone bags
sharpies / pens / pencils
forms - seedtree form, 1 site assessment form, extra sheet for maps
metal tree tags (unique numbers)
Al nails
DBH tape (metric)
way to estimate tree in meters
camera - if possible - take a photo of tree looking north with person in photo with tree ID
area maps
latex gloves (for the cone bagger person - the cones are super sappy!)
vials with silica gel for needle samples (if collecting)
hand sanitizer gel (it removes sap!) and paper towels

Figure 5. Field cone collection key (A) and form (B).

(B)



Site Location and Collector Information

Site Name and Initials (3 letters)

Collectors Names

Seed Zone

Date of cone collections

Preliminary tree selections made by:

Date of tree selections

National Forest

Ranger District

State

Township T______

Range R______

Section ______

Landowner

Datum

Stand Description

Slope %

Aspect o from N

Tree species composition

Crown Closure

Age structure

Stand size (acres)

MPB present?

WPBR present?

DM present?

5-ndl regen present?

5-ndl regen health

Other regen present?

Other site landmarks, information

Seed Tree Info

Species	Tree ID (site initials + tag#)	UTM Northing	UTM Easting	Elevation (m)	Height (m)	DBH (cm)	Crown Position	# bole cankers	# branch cankers	# cones collected	Other tree damages (DM, twig beetles), landmarks or comments
	-BULK	----------	----------	----------	----------	----------	----------	----------	----------		# trees sampled = ________; # cones/tree = __________

Directions to stand

On ______ side of road ________________________________

____

miles from the junction with road ________________________________

____

Other site descriptions / landmarks / former plot names

Site map

use additional sheet if necessary

Tree selection criteria: Healthy trees with cones! Single stemmed trees are preferred over multi-stemmed clumps. Multi-stem clumps can have multiple individuals and our "individual tree collections" must be from just one individual. If it is unavoidable to select a multi-stemmed clump then tag just one stem and be absolutely certain that all the cones are from just that stem. Note on form that tree is in a multi-stem clump. Make every effort to find single stem trees!

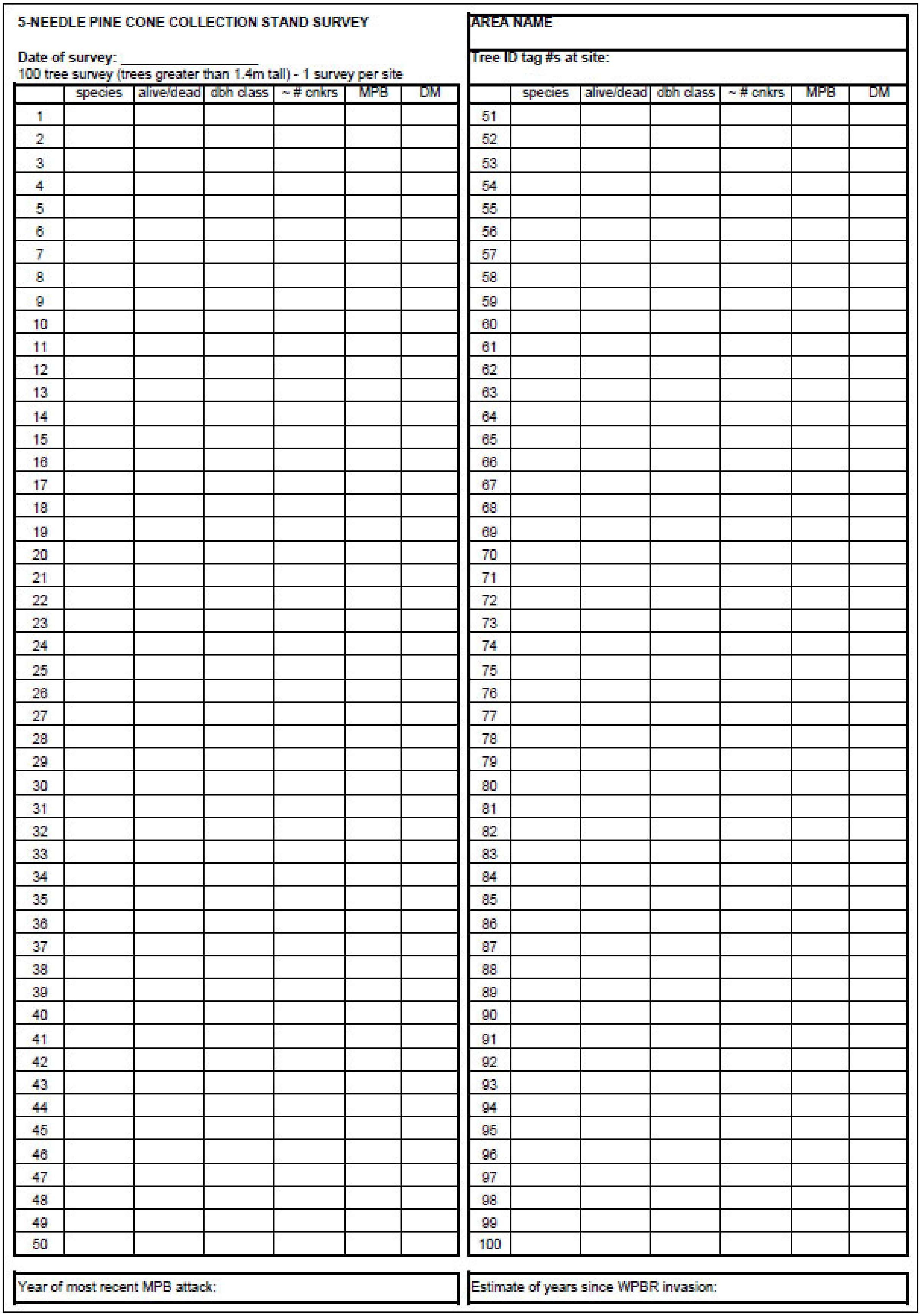
b. Record tree tag number, waypoint and associated information (ht, dbh, etc) as requested on the SEED TREE form (Fig. 5).

c. For each seed tree: Verify that the embryo fills at least 80 to 90 percent of the cavity in several seeds to determine if the seeds are ripe (Fig. 7). If ripe, collect at least 20-40 cones from as high in the crown as your pole pruner can reach. Try to collect only fully formed green cones (no small dry brown ones—they have aborted) from the upper third of the crown. Clip off the terminal branch with the cones, have the collector immediately retrieve the cones, detach cones from the twig and put only the cones in the burlap bag (fill each bag only half full—use 2 bags per seed tree if needed (see below). If you are not 100% sure that the cone you are picking up was cut from the sample tree do not include it (for the genetic analyses we have to be absolutely certain of the mother tree of the seeds).

Don't forget the bulk collection (see below)

d. Label both sections of the paper tag with the species, seed zone, elevation, Forest, District, collection date, collector name and TREE ID—detach lower portion and put it in the bag—use upper portion with a zip-tie to cinch the top of the burlap bag closed (within 6-8 inches of the top of the bag). Fill the bag only half full; we expect only 1 burlap bag per seed tree but if the cones are large and you need a second bag fill out a complete second tag and note on the tag that it is "1 of 2 bags" or "2 of 2 bags".

e. Fill out the field SEED TREE (Fig. 5) and SITE condition form (Fig. 6) for each site.



5-NEEDLE PINE CONE COLLECTION STAND SURVEY

AREA NAME

Date of survey: ____________________

100 tree survey (trees greater than 1.4m tall) - 1 survey per site

Tree ID tag #s at site:

	species	alive/dead	dbh class	~ # cnkrs	MPB	DM
1						
2						
3						
4						
5						
6						
7						
8						
9						
10						
11						
12						
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48						
49						
50						

	species	alive/dead	dbh class	~ # cnkrs	MPB	DM
51						
52						
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Year of most recent MPB attack:

Estimate of years since WPBR invasion:

Figure 6. One-hundred tree forest health condition form

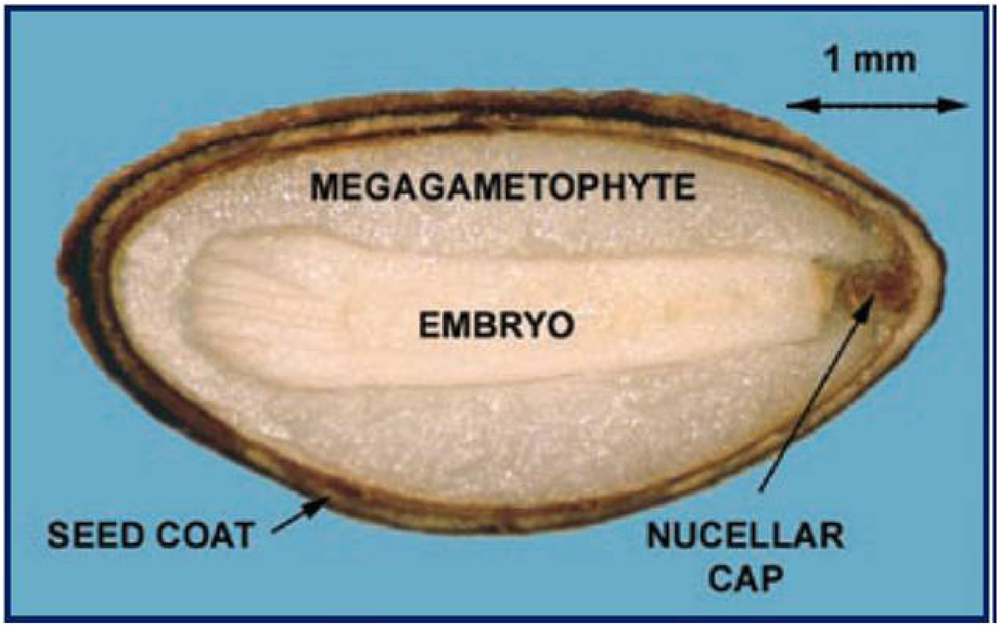

Figure 7. Photo of a healthy western white pine seed cut longitudinally revealing a fully mature embryo (from Kolotelo 1997 as presented in Owens 2004). The embryo fills the entire cavity in this photo. Seeds are mature enough for collection when the embryo is no less than 90 percent of the cavity. A healthy seed will have a bright white endosperm.

f. Keep the cones out of direct sun (especially in the back of a vehicle). Get them to a dry cool place with good ventilation between bags as soon as possible.

Bulk cone collection:

a. At each site, we want a bulk collection of cones that is a composite of equal number of cones from each of 20 trees (do not include trees with individual seed collections; select cones from high in the crown).

To do this, assess the amount of cone production in the site—if it is light then decide to collect 2 cones from each of the 20 trees; if it is a good cone producing site, select 4 cones from each of the 20 trees. The trees for the bulk need not be tagged or GPSed—they should however be somewhat evenly spaced throughout the population. The easiest way to do this is to collect from 2 trees for the bulk in between each individual seed tree you are collecting from. Keep track of the number of trees that contribute to the bulk sample (tally bulk tree numbers as you collect). Combine the 2 (or 4) cones from each tree into one burlap bag. Enter number of trees sampled and number of cones per tree on the SEED TREE FORM (Fig. 5).

b. Label the paper tag (upper and lower portions) with site name-BULK, "BULK from XXXX trees", GPS coordinates of the population, your name, date. As before, place the bottom half of the tag in the bag and use a zip tie to seal the burlap bag with the upper portion.

Site assessment:

It is important to have associated stand condition and forest health information at the time of the cone collections. For example, if a seed tree is recorded as being WPBR-free and the population has an estimated WPBR incidence of 60 percent, then that seed tree would be considered a putatively resistant tree. However, if that same tree was in a population with an estimated WPBR incidence of 5 percent it is much more likely to have escaped infection than be disease-free due to resistance. Any type of reputable stand assessment plot(s) can be used. If the site is co-located with a recent (past 2 yrs) stand health assessment then no further assessment is needed (unless the condition has significantly changed). Please provide a reference to the former data set, when it was collected and by whom, site name in the former study and a summary of the rust/MPB status of the site. At a minimum a 100 tree survey should be conducted.

100 tree survey: Walk a line through the population and record each tree (of all species) that is greater than 1.4 m tall onto the form (Fig. 6) along with the requested information. This does not need to be formal transect—try to cover the entire area within the population where the seed trees are located.

References

Aitken, Sally N.; Yeaman, Sam; Holliday, Jason A.; Wang, Tongli; Curtis-McLane, Sierra. 2008. Adaptation, migration or extirpation: climate change outcomes for tree populations. Evolutionary Applications. 1: 95-111.

Blodgett, James T.; Sullivan, Kelly F. 2004. First report of white pine blister rust on Rocky Mountain bristlecone pine. Plant Disease. 88: 311.

Burns, Kelly S.; Blodgett, James T.; Conklin, David; Fairweather, MaryLou; Geils, Brian; Guyon, John; Hoffman, James; Jackson, Marcus; Jacobi, William R.; Kearns, Holly S. J.; Schoettle, Anna W. 2010. White Pine Blister Rust in the Interior Mountain West. In: Adams, J. comp. 2010. Proceedings of the 57th Western International Forest Disease Work Conference; 2009 July 20-24; Durango, CO. Forest Health Technology Enterprise Team, Fort Collins, CO. Pp 57-65.

Burns, Kelly S.; Schoettle, Anna W.; Jacobi, William R.; Mahalovich, Mary F. 2008. Options for the management of white pine blister rust in the Rocky Mountain Region. Gen. Tech. Rep. RMRS-GTR-206. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station. 26 p. http://www.fs.fed.us/rm/pubs/rmrs_gtr206.html

Coop, Jonathon C.; Schoettle, Anna W. 2009. Regeneration of Rocky Mountain bristlecone pine (*Pinus aristata*) and limber pine (*Pinus flexilis*) three decades after stand-replacing fires. Forest Ecology and Management. 257: 893-903.

Diaz, H .F.; Eischeid, J. K. 2007. Disappearing "alpine tundra" Köppen climatic type in the western United States. Geophys. Res. Lett. 34: L18707.

Fairweather, M. L.; Giels, B. W. 2011. First report of the white pine blister rust pathogen, *Cronartium ribicola*, in Arizona. Plant Disease 'First Look' paper doi: 10.1094/PDIS-10-10-0699.

Gibson, Ken; Skov, Kjerstin; Kegley, Sandy; Jorgensen, Carl; Smith, Sheri; Witcosky, Jeff. 2008. Mountain pine beetle impacts in high elevation five needle pines: current trends and challenges. Forest Health Protection Report R1-08-020. U.S. Department of Agriculture, Forest Service. 32 p.

Hoff, Raymond; Bingham, Richard; MacDonald, Geral, I. 1980. Relative blister rust resistance of white pines. European Journal of Forest Pathology. 10: 307-316.

Howell, Brian; Burns, Kelly S.; Kearns, Holly S. J.; Witcosky, Jeff J.; Cross, Frank J. 2006. Biological Evaluation of a Model for Predicting Presence of White Pine Blister Rust in Colorado Based on Climatic Variable and Susceptible White Pine Species Distribution. Biological Evaluation R2-06-04, Rocky Mountain Region Renewable Resources, Lakewood, CO: U.S. Department of Agriculture, Forest Service. 15 p.

Kearns, Holly S. J. 2005. White pine blister rust in the central Rocky Mountains: Modeling current status and potential impacts. Fort Collins, CO: Colorado State University. 243 p. Dissertation.

Kearns, Holly S.J.; Jacobi, William R. 2007. The distribution and incidence of white pine blister rust in central and southeastern Wyoming and northern Colorado. Canadian Journal of Forest Research. 37: 462-472.

Kim, Mee-Sook; Brunsfeld, Steven J.; McDonald, Geral I.; Klopfenstein, Ned B. 2003. Effect of white pine blister rust (*Cronartium ribicola*) and rust-resistance breeding on genetic variation in western white pine (*Pinus monticola*). Theoretical and Applied Genetics. 106: 1004-1010.

Kinloch Bohun B., Jr.; Davis, Dean A.; Burton, Deems. 2008. Resistance and virulence interactions between two white pine species and blister rust in a 30-year field trial. Tree Genetics and Genomes. 4: 65-74.

Kinloch, Bohun B., Jr.; Dupper, Gayle E. 2002. Genetic specificity in the white pine-blister rust pathosystem. Phytopathology. 92: 278-280.

Kinloch Bohun B., Jr.; Sniezko Richard A.; Barnes, Gerald D.; Greathouse, Tom E. 1999. A major gene for resistance to white pine blister rust in western white pine from the Western Cascade Range. Phytopathology. 89: 861-867.

Kinloch, Bohun B., Jr.; Sniezko, Richard A.; Dupper, Gayle E. 2003. Origin and distribution of Cr2, a gene for resistance to white pine blister rust in natural population of western white pine. Phytopathology. 93: 691-694.

Kolotelo, D. 1997. Anatomy and Morphology of Conifer Seed. B.C. Min. For., Nursery and Seed Operations Branch, For. Nurs. Tech. Series 1.1.

Mahalovich, Mary F. 2003. [Email correspondence to Anna Schoettle] June 4. Files included Cone collection guidelines. doc, WBP Survey Form rev 04-03.xls, WBP Location and GPS Record rev 05-2003.xls. On file at: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Fort Colins, CO.

Mahalovich, Mary F. 2006. Limber pine seed transfer guidelines. U.S. Department of Agriculture Forest Service Regions 1-4. Internal Report, 4 pp. Prepared February 27, 2006.

Natural Resources Defense Council. 2008. A petition to list the whitebark pine, *Pinus albicaulis*, as an endangered species under the Endangered Species Act. December 8, 2008. 58 p.

Owens, J.N. 2004. The reproductive biology of western white pine. Forest Genetics Council of B.C. Extension Note 04, April 2004, p. 40.

Pepin N.C.; Lundquist J.D. 2008. Temperature trends at high elevations: patterns across the globe. Geophys. Res. Lett. 35**:** L14701.

Samman, Safiya; Schwandt, John W.; Wilson, Jill L. 2003. Managing for Healthy White Pine Ecosystems in the United States to Reduce the Impacts of White Pine Blister Rust. Forest Service Report R1-03-118. Missoula, MT: Department of Agriculture, Forest Service. 10 p.

Salzer, M. W.; Hughes, M. K.; Bunn, A. G.; Kipfmueller, K. F. 2009. Recent unprecedented tree-ring growth in bristlecone pine at the highest elevations and possible causes. P Natl Acad Sci USA. 106: 20348-20353.

Schoettle, Anna W. 2004a. Developing proactive management options to sustain bristlecone and limber pine ecosystems in the presence of a non-native pathogen. In: Shepperd, W. D., L. G. Eskew, compilers. Silviculture in special places: Proceedings of the National Silviculture Workshop; 2003 September 8-11; Granby, CO. Proceedings RMRS-P-34. Fort Collins, CO: U.S. Department of Agriculture Forest Service, Rocky Mountain Research Station: 46-155. Available at: http://www.fs.fed.us/rm/pubs/rmrs_p034/rmrs_p034_146_155.pdf

Schoettle, A. W. 2004b. Ecological roles of five-needle pines in Colorado: Potential consequences of their loss. In: Sniezko, Richard; S. Samman; S. Schlarbaum; H. Kriebel; eds. Breeding and genetic resources of five-needle pines: growth adaptability and pest resistance. 2001 July 24-25; Medford, OR. IUFRO Working Party 2.02.15. Proceedings RMRS-P-32. Ogden, UT: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station: 124-135. Available at: http://www.fs.fed.us/rm/pubs/rmrs_p032/rmrs_p032_124_135.pdf

Schoettle, Anna W.; Rochelle, S. G. 2000. Morphological variation of *Pinus flexilis* (Pinaceae), a bird-dispersed pine, across a range of elevation. American Journal of Botany. 87: 1797-1806.

Schoettle, Anna W.; Sniezko, Richard A. 2007. Proactive intervention to sustain high elevation pine ecosystems threatened by white pine blister rust. Journal of Forest Research. 12(5): 327-336.

Schoettle, Anna W.; Sniezko, Richard A.; Burns, Kelly S.; Freeman, Floyd. 2007. Preparing the landscape for invasion—Early intervention approaches for threatened high elevation white pine ecosystems. In: Goheen, E. M.; R. A. Sniezko, tech. coords. Proceedings of the conference Whitebark Pine: a Pacific Coast Perspective. 2006 Aug 27-31, Ashland, OR. R6-NR-FHP-2007-01. Portland, OR: Pacific Northwest Region, Forest Service, U.S. Department of Agriculture: 72-75. http://www.fs.fed.us/r6/nr/fid/wbpine/proc.shtml

Schoettle, Anna W.; Burns, Kelly S.; Costello, Sheryl; Witcosky, Jeff; Howell, Brian; Connor, Jeff. 2008. A race against beetles: Conservation of limber pine. Nutcracker Notes. 14: 11-12.

Schoettle, Anna W.; Sniezko, Richard A.; Burns, Kelly S. 2009. Sustaining *Pinus flexilis* ecosystems of the Southern Rocky Mountains (USA) in the presence of *Cronartium ribicola* and *Dendroctonus ponderosae* in a changing climate. In: Breeding and Genetic Resources of Five-Needle Pines Conference, IUFRO Working Party 2.02.15, Yangyang, Republic of Korea, 2008 September 22-26. Ed. By Noshad, D.; Noh, E.; King, J.; Sniezko, R. Yangyang: Korea Forest Research Institute: 63-65. http://www.iufro.org/download/file/4989/1191/20215-yangyang08-proceedings.pdf/

St. Clair, Bradley; Howe, Glen. 2009. Genetic options for adapting forests to climate change. Western Forester. 54(1): 9-11.

Tomback, Diana F.; Arno, Stephen F.; Keane, Robert E., editors. 2001. Whitebark Pine Communities: Ecology and Restoration. Island Press, Washington, DC.

Vogler, Det. R.; Charlet David A. 2004. First report of the white pine blister rust fungus (*Cronartium ribicola*) infecting whitebark pine (*Pinus albicaulis*) and *Ribes* spp. in the Jarbidge Mountains of northeastern Nevada. Plant Disease. 88: 772.

Vogler, D. R.; Delfino-Mix, A.; Schoettle, A. W. 2006. White pine blister rust in high-elevation white pines: screening for simply-inherited, hypersensitive resistance. In: Guyon, J. C., compiler. Proceedings of the 53th Western International Forest Disease Work Conference; 2005 September 26-30; Jackson, WY. Ogden, UT: USDA Forest Service, Intermountain Region. Pp 73-82.

Whitebark and Limber Pine Restoration and Monitoring in Glacier National Park

Extended Abstract

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Abstract—Whitebark pine (*Pinus albicaulis*) and limber pine (*Pinus flexilis*) are keystone species important to watersheds, grizzly and black bears, squirrels, birds, and other wildlife. Both high elevation five-needled pines have dramatically declined in Glacier National Park primarily due to white pine blister rust (*Cronartium ribicola*) and fire exclusion, with mountain pine beetle (*Dendroctonus ponderosae*) as a potential threat. In 1997, we began collecting seed from trees that show phenotypic rust resistance in order to establish a restoration and monitoring program to maintain healthy whitebark and limber pine ecosystems in the park. Most of the seed has been propagated into seedlings through a cooperative agreement with the US Forest Service (FS) Coeur d'Alene Nursery. From 2000 to 2007, we planted nearly 6,400 whitebark and 4,700 limber pine seedlings. Following monitoring in 2010, 41 percent of all planted whitebark seedlings had survived, while only 6 percent of limber pine survived. In addition to restoration monitoring, we established blister rust monitoring plots as well as a program to monitor individual "plus" trees; trees that potentially have genetic resistance to blister rust. Currently, we are working with a FS regional geneticist to determine if our designated "plus" trees are actually producing blister-rust resistant seedlings.

Introduction

Whitebark pine and limber pine populations have declined dramatically in Glacier National Park, largely due to the introduction of the non-native fungus white pine blister rust. Severe climatic events, mistletoe infections, fire exclusion, and/or mountain pine beetles may have also contributed to the poor health of these trees. Whitebark pine mortality has been estimated at 44 percent within the park, with at least 78 percent of the remaining live trees infected (Kendall and Keane 2001). Kendall and Keane (2001) have also estimated limber pine mortality in Glacier National Park at 39 percent, with 78 percent of the remaining live trees infected. Extensive blister rust surveys on both five-needled pines were conducted in the mid 1990s, and many areas were re-surveyed between 2003 and 2009. The monitoring has shown a continual decline in the percentage of healthy whitebark and limber pine trees in the park (Asebrook and others in press). On the other hand, recent fires have burned into the habitat of both pine species, affording an opportunity to re-establish the pines in many areas.

In an effort to restore both species to Glacier National Park, restoration activities began in 1997 when seeds were collected from "plus" trees that showed potential for genetic resistance. Park staff began to grow seedlings in 1998, followed by the first planting of whitebark pine in 2000, and the first planting of limber pine in 2002. Sites were selected based on accessibility for planting, appropriate habitat characteristics, and recent burn activity. Planting years were chosen based on the availability of seedlings. In addition, seeds from whitebark pine plus trees were directly planted at three sites in 2006 and 2007.

Overall, the whitebark and limber pine restoration program at Glacier National Park is complex, involving monitoring of "plus" trees, cone collection, production of seedlings, plantings, monitoring seedling survival, and ongoing research concerning the rust resistance of park trees and the use of ectomycorrhizae for increased survival and growth.

Monitoring Methods

The survival of planted whitebark and limber pine seedlings was monitored using circular plots installed at planting sites. The number of plots established at each site aimed to capture a minimum of 20 percent of the total planted seedlings. Circular plots ranged from a 5m to 20m radius, and were permanently marked with a nail in the center. Individual trees were located by measuring a distance and azimuth from this center nail. For each monitoring, height and width were measured for each tree and given a health rank from 1 to 5 (dead to healthy).

Overall, 56 plots were installed at four sites between 2000 and 2007 to monitor whitebark pine seedlings (table 1). A total of 1,577 whitebark pine seedlings are currently being monitored, capturing 21 percent of total planted seedlings. Forty-seven plots were installed at 13 sites between 2002 and 2006 to monitor limber pine seedlings (table 1). A total of 1,089 limber pine seedlings are currently being monitored, capturing 23 percent of total planted seedlings. All whitebark pine was planted in areas burned by wildfire while all limber pine was planted in non-burned areas, due to the fact that no limber pine habitat has burned by wild or prescribed fire in Glacier National Park.

In addition, a total of 723 whitebark pine seeds were planted in caches, shallow seed storage areas beneath the soil, along seven transects at three locations in the park in 2006 and 2007. Seeds were cached in groups, mimicking the natural planting schemes of Clark's nutcrackers (*Nucifraga columbiana*).

In: Keane, Robert E.; Tomback, Diana F.; Murray, Michael P.; and Smith, Cyndi M., eds. 2011. **The future of high-elevation, five-needle white pines in Western North America: Proceedings of the High Five Symposium.** 28-30 June 2010; Missoula, MT. Proceedings RMRS-P-63. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station. 376 p. Online at http://www.fs.fed.us/rm/pubs/rmrs_p063.html

Table 1. Monitoring plot establishment for whitebark and limber pine seedlings.

Site	Year(s) Planted	# Plots Established	# Trees Planted	Mean # Trees Monitored	% Trees Monitored
Whitebark pine					
Flattop Mtn.	2001, 2002	38	5,160	921	18
Grinnell Point	2000	7	96	96	100
Caper Peak	2006	2	139	139	100
Red Eagle	2007	9	2,000	421	21
TOTAL		**56**	**7,395**	**1,577**	**21**
Limber pine					
Apikuni Flats	2002	2	160	25	16
Baring Creek	2004, 2006	8	700	162	23
Altyn Peak	2002, 2004	3	360	67	19
Dead Horse Pt.	2002, 2004, 2006	8	1,312	261	20
Firebrand Pass	2002	2	140	38	27
Poia Lake trailhead	2002	2	160	41	26
Rocky Point	2002	2	150	37	25
Scenic Point	2002, 2005	10	900	223	25
Sun Point	2002, 2004	4	470	107	23
Two Med CG	2002	2	160	35	22
Two Med store	2003	1	26	26	100
Two Med RS	2002	2	140	38	27
Wild Goose turnout	2002	1	100	29	29
TOTAL		**47**	**4,778**	**1,089**	**23**

Monitoring Results

Whitebark Pine

Except for one site, three- to eight-year whitebark pine seedling survival was between 31 percent and 54 percent (table 2). These results are in keeping with 11 other sites monitored in Montana, Idaho, and Wyoming where three- to eight-year survival rates typically ranged from 29 percent to 50 percent (Izlar 2007).

The relatively high survival rates for whitebark pine seedlings likely were due to the fact that all seedlings were planted in areas burned by wildfire that had deep, high-nutrient soil with excellent planting microsites. There also was no competing vegetation for the seedlings, and possibly the higher elevation whitebark sites did not experience higher air temperatures that can cause seedling desiccation. This was the case at the Red Eagle Campground site that was lower in elevation and had high sun exposure. All of the seedlings in that location were brittle by year two after planting.

Whitebark pine seed that was cached had less success. Only three out of 723 seeds germinated in year one with one seedling dying in that same season. By comparison, data from Waterton Lakes National Park documented that 144 out of 338 (43 percent) cached seeds germinated by year 2 (Smith and others 2007).

Limber Pine

Although limber pine seedling survival has been very low, survival rates have increased as planting projects have continued. At sites planted in 2002 and 2003, five- to seven-year survival ranged between 0.2 percent and 8 percent (table 3). At sites planted in 2004 and 2005, five year survival increased to 14 percent and 15 percent (table 3). Despite the positive trend, these survival rates were well below the 85 percent year one survival, 74 percent year two survival, and 69 percent year three survival at Waterton Lakes National Park (Smith and others 2007).

Poor survival for the earliest plantings was likely due to three factors. First, both plantings were followed by

Table 2. Whitebark pine seedling survival (percent).

Site	Year Planted	Survival						
		Year 1	Year 2	Year 3	Year 4	Year 5	Year 7	Year 8
Grinnell Pt.	2000					41		
Flattop Mt.	2001	52			35	34		31
Flattop Mt.	2002			48	46		41	
Caper Peak	2006		46					
Red Egle Mt.	2007	75	55	54				
Red Egle CG	2007	91	0	0				

Table 3. Limber pine seedling survival (percent).

		Survival					
Site	**Year Planted**	**Year 1**	**Year 2**	**Year 3**	**Year 4**	**Year 5**	**Year 7**
various	2002	49	0.5		0.5	0.5	0.2
Two Med store	2003	96		35		8	
various	2004	46	34	25	23	15	
Scenic Pt.	2005	26	14	14		14	
Baring Ck.	2006	13	3	3			

hot, dry summers. Air temperatures were above average and precipitation was low in 2003 and 2004, resulting in heat stress to the seedlings. Second, our experience planting five-needled pines was limited. Seedlings were not always planted in favorable microsites, and overall site selection may have been poor, including rocky soil, areas of soil creep, areas not burned, and areas with high vegetative competition. As better sites were chosen in 2004 and 2005, seedlings were more consistently planted in microsites and survival increased. Temperature and precipitation levels were also average for those years.

Planting at Baring Creek in 2006 was the exception, with only 3 percent survival in year three. Although this site had relatively low vegetative competition, planting areas were highly exposed with few suitable microsites. In addition, experimental shade netting that was used on a majority of the seedlings did not hold up, negatively impacting the trees. Finally, 2007 temperatures were above average with low precipitation, resulting in heat stress to the seedlings.

Future Management

The future management of whitebark and limber pine at Glacier National Park will continue with active restoration of both five-needled pine species. At present, we have identified 62 whitebark and two limber pine trees as "plus" trees that appear to show genetic resistance to blister rust. We will continue to monitor these trees and search for new trees to add to the plus tree pool. Whitebark seed from Glacier's plus trees is currently part of a USFS Coeur d'Alene Nursery project to assess the genetic resistance of plus trees to blister rust (Mahalovich and others 2006). We will continue to investigate the resistance of the park's trees and continue collecting cones and growing seedlings from trees with phenotypic rust resistance. In addition, we are cooperating with Montana State University to investigate the potentially positive effects of inoculating whitebark and limber pine seedlings with certain *Suillus* mycorrhizae, an associated mushroom (Cripps and others 2008; Mohatt and others 2008).

Future management will also include finding additional planting sites for whitebark and limber pine, and incorporate appropriate planting techniques as they are identified (McCaughey and others 2009; Izlar 2007). These include the use of favorable microsites, growing vigorous trees, clumping trees when planting, and using burned areas whenever possible to plant in areas with reduced overstory and competition.

Literature Cited

Asebrook, J.M.; Hintz, J.L. [In press]. Glacier National Park blister rust surveys: 2003-2009. Unpublished technical report. West Glacier, MT, National Park Service, Glacier National Park.

Cripps, C.; Smith C.; Carolin, T.; Lapp, J. 2008. Ectomycorrhizal fungi with whitebark pine. Nutcracker Notes. 14: 12-14.

Izlar, D.K. 2007. Assessment for whitebark pine seedling survival for Rocky Mountain plantings. Missoula, MT, University of Montana. 84 p. Thesis.

Kendall, K.C.; Keane, R.E. 2001. Whitebark pine decline: infection, mortality, and population trends. In Tomback, D.F.; Arno, S.F.; Keane, R.E. Whitebark pine communities: Ecology and restoration. Washington, DC, Island Press: pages 221-242.

Mahalovich, M.F.; Burr, K.E.; Foushee, D.L. 2006. Whitebark pine germination, rust resistance and cold hardiness among seed sources in the Inland Northwest: planting strategies for restoration. In: National Proceedings: Forest and Conservation Nursery Association; 2005 July 18-20; Park City, UT. RMRS-P-43. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station: 91-101.

McCaughey, Ward; Scott, Glenda L.; Izlar, Kay. 2009. Whitebark pine planting guidelines. Western Journal of Applied Forestry. 24(3): 163-166.

Mohatt, K.R.; Cripps, C.L.; Lavin, M. 2008. Ectomycorrhizal fungi of whitebark pine (a tree in peril) revealed by sporocarps and molecular analysis of mycorrhizae from treeline forests in the Greater Yellowstone Ecosystem. Botany. 86: 14-25.

Smith, C.M.; Poll, G.; Gilles, C.; Praymak, C.; Miranda, E.; Hill, J. 2007. Limber pine seedling and seed survival project, Waterton Lakes National Park, 2003-2006. Unpublished technical report. Waterton Park, AB: Parks Canada, Waterton Lakes National Park. 33 p.

Restoration of Whitebark Pine Forests in the Northern Rocky Mountains, USA

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Abstract—Whitebark pine (*Pinus albicaulis*) has been declining across much of its range in North America because of the combined effects of mountain pine beetle epidemics, fire exclusion policies, and widespread exotic blister rust infections. Whitebark pine seed is dispersed by a bird, the Clark's nutcracker, which caches seed in open, pattern-rich landscapes created by fire. This study was initiated in 1993 to investigate the effects of various restoration treatments on tree populations, fuel dynamics, and vascular plant cover on five sites in the U.S. northern Rocky Mountains. The objective of this study was to restore whitebark pine ecosystems using treatments that emulate the native fire regime—primarily combinations of prescribed fire, silvicultural cuttings, and fuel enhancement cuttings. The main effects assessed included tree mortality, fuel consumption, and vegetation response measured just prior to the treatment, 1 year after the treatment(s), and 5 years post-treatment. We found that, while all treatments that included prescribed fire created suitable nutcracker caching habitat with many birds observed caching seed in the burned areas, there has yet to be significant regeneration in whitebark pine. All burn treatments resulted in high mortality in both whitebark pine and subalpine fir (>40 percent). Fine woody fuel loadings marginally decreased after fire but coarse woody debris more than doubled because of falling snags. Vascular species decreased in cover by 20 to 80percent and remained low for five years. While the treatments were successful in creating conditions that favor whitebark pine regeneration, the high level of blister rust mortality in surrounding seed sources has reduced available seed which then forced the nutcracker to reclaim most of the cached seed. Manual planting of whitebark pine seedlings is required to adequately restore these sites. A set of management guidelines is presented to guide restoration efforts.

Introduction

Whitebark pine (*Pinus albicaulis*) forests are declining across most of the species range in North America (Arno 1986; Kendall and Keane 2001) due to three factors: (1) recent and historical major mountain pine beetle (*Dendroctonus ponderosae*) outbreaks that have killed many cone-bearing whitebark pine trees (Arno 1986; Tomback and others 2001; Waring and Six 2005), (2) fire exclusion management policies that have reduced the area burned in whitebark pine forests resulting in a decrease of suitable conditions for whitebark pine regeneration (Keane and Arno 1993; Kendall and Keane 2001), and (3) the introduction of the exotic fungus white pine blister rust (*Cronarium ribicola*) to the western U.S. (circa 1910) that has killed many whitebark pine trees (Hoff and others 1980; Murray and others 1995; Kendall and Keane 2001). The cumulative effects of these three agents have resulted in a rapid decrease in mature whitebark pine, especially in the more mesic parts of its range (Keane and Arno 1993). What's worse is that predicted changes in northern Rocky Mountain climate brought about by global warming could further exacerbate whitebark pine decline by increasing the frequency and duration of beetles epidemics, blister rust infections, and severe wildfires (Logan and Powell 2001; Blaustein and Dobson 2006; Running 2006). How can society restore these invaluable ecosystems to their historical dominance?

In this paper, the results of an extensive, long-term study, called Restoring Whitebark Pine Ecosystems, are presented where the effects of several types of ecosystem restoration treatments implemented on five high elevation sites in the northern Rocky Mountains, USA are investigated. This paper is a summary of the Keane and Parsons (2010b) results presented as a comparison of treatment effects for seven major treatment types across the five sites. There is a companion report (Keane and Parsons 2010a) that presents detailed pictorial, anecdotal, and statistical summaries of all measurements and observations for each treatment unit at each time interval to serve as a guide to land management.

Whitebark Pine Ecology

Whitebark pine is a long-lived, seral tree of moderate shade tolerance (Minore 1979). It can live well over 400 years (one tree is more than 1300 years old), but on many sites it is eventually replaced, in the absence of fire, by the shade-tolerant subalpine fir (*Abies lasiocarpa*), and also by spruce (*Picea engelmannii*), and mountain hemlock (*Tsuga mertensiana*) in the mesic parts of its range (Arno and Hoff 1990; Keane 2001). Lodgepole pine (*Pinus contorta*) can outcompete whitebark pine during early successional stages in some subalpine forests, but both species often share dominance in upper subalpine forests (Day 1967; Mattson and Reinhart 1990).

The Clark's nutcracker (*Nucifraga columbiana*) plays a critical role in the dispersal of whitebark pine's heavy, wingless seed (Tomback 1982; Lorenz and others 2008). The bird harvests seed from purple cones during late summer and early fall, then carries these seeds, up to 100 of them in a sublingual pouch, to sites up to 10 km away, where it buries up to 15 seeds in a cache 2-3 cm below the ground surface (Tomback 1998; Lorenz and others 2008). Many of these

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caches are reclaimed during the following months but those seeds that remain unclaimed eventually germinate and grow into whitebark pine seedlings (Tomback 2005). Nutcrackers appear to prefer to cache in open areas where the ground is visible from above and they appear to cache near objects on the ground, such as rocks, logs, and snags, because it reclaims seed from caches by pattern recognition (Hutchins and Lanner 1982; Lanner 1996; Tomback and others 1993). Open areas with complex patterns that occur in high mountain settings are often created by wildland fire (Morgan and Bunting 1990).

Three types of fires describe the diverse array of fire regimes in whitebark pine forests (Morgan and Bunting 1990; Morgan and others 1994). Some high elevation whitebark pine stands experience non-lethal surface fires (called underburns in this study) because sparse fuel loadings foster low intensity fires (Keane and others 1994). The more common, mixed-severity fire regime is characterized by fires of mixed severities in space and time that create complex mosaics of tree survival and mortality on the landscape. Mixed severity fires can occur at 60- to 300-year intervals in patches that are often 1 to 100 ha, depending on topography and fuels, and these openings provide important caching habitat for the Clark's nutcracker (Morgan and Bunting 1990; Arno and others 2000; Norment 1991; Tomback and others 1993). Many whitebark pine forests in northwestern Montana, northern Idaho and western Washington originated from large, stand-replacement fires that occurred at long time intervals (greater than 250 years) (Keane and others 1994; Murray 1996).

Whitebark pine benefits from wildland fire because it is better adapted to surviving and regenerating after fire than its associated shade-tolerant trees (Arno and Hoff 1990). Whitebark pine can survive low severity fires better than its competitors can because it has thicker bark, thinner crowns, and deeper roots (Arno and Hoff 1990). It also readily colonizes large, stand-replacement burns because nutcrackers transport the seed great distances (Lorenz and others 2008; Tomback 2005). Nutcrackers can disperse whitebark pine seeds up to 100 times farther (over 10 km) than wind can disperse seeds of its competitors (McCaughey and others 1985; Tomback and others 1993). It is on open, burned sites where whitebark pine can successfully grow and mature to healthy cone producing trees in the absence of competition (Arno and Hoff 1990).

The critical assumption of this study is that whitebark pine ecosystems can be restored from the damaging effects of blister rust, mountain pine beetles, and fire exclusion by implementing treatments that emulate wildland fire regimes to remove competitors and create habitat suitable for nutcracker caching. The primary objective of these treatments was to increase whitebark pine regeneration to provide for future whitebark pine cone crops. We hypothesized that those living, cone-producing whitebark pine seed sources at or near the restoration sites will possess some degree of blister rust-resistance because they have already survived decades of rust infection (Arno and others 2001).

Methods

This study was implemented on five sites in the northern Rocky Mountains of the United States (figure 1, table 1). Whitebark pine is experiencing heavy rust mortality on all sites except for the Blackbird Mountain site. All sites are in the *Abies lasiocarpa/Luzula hitchcockii* (ABLA/LUHI) habitat type with most sites in the *Vaccinium scoparium* phase, but some in the *Menziesia ferruginea* phase (Pfister and others 1977). Prior to treatment, the overstory of most sites consisted of 200 to 400 year old overstory whitebark pine and lodgepole pine with encroaching subalpine fir and scattered large Engelmann spruce (table 1).

Each site was divided into treatment areas and each treatment area was further divided into treatment units (figure 2; example from the Beaver Ridge site). The treatment area is described by the major treatment implemented within the area, and the treatment unit is defined as a sub-area within the treatment area within which a secondary or minor treatment was implemented. We tried to replicate treatment units within a site to satisfy statistical requirements for analysis of variance but found that replication was nearly impossible due to the limited extent of most study sites (most were confined by ridgetop settings), the diversity of biophysical characteristics within each site (complex aspect, slope, drainage, and species composition conditions), pseudo-replication issue (Hurlbert 1984), and a consistent lack of accessible homogeneous areas. Each study site always included a control unit adjacent to the treatment units.

Two broad types of treatments were investigated in this study (table 2), both designed to reduce subalpine

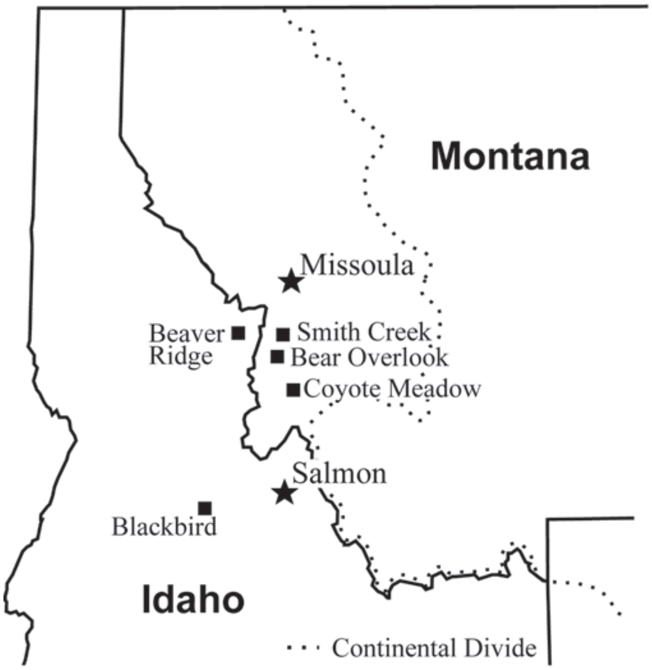

Figure 1. Study sites in the Restoring Whitebark Pine Ecosystems study.

Table 1. Description of the five sites included in the study Restoring Whitebark Pine Ecosystems (RWPE) study. All sites experienced a 1930-1934 mountain pine beetle epidemic and all but Blackbird Mountain had evidence of the 1910 fire.

Study Site Attribute	**Smith Creek (SC)**	**Bear Overlook (BO)**	**Coyote Meadows (CM)**	**Blackbird Mountain (BM)**	**Beaver Ridge (BR)**
National Forest	Bitterroot	Bitterroot	Bitterroot	Salmon	Clearwater
Elevation (m MSL)	2,100-2,250	2,070-2,250	2,340-2,425	2,400-2,460	2,010-2,250
Aspect	Southeast	Southeast	Northwest	South	South
Habitat type[a]	ABLA/LUHI	ABLA/LUHI	ABLA/LUHI, ABLA/MEFE	ABLA/LUHI	ABLA/LUHI
Cover type[b]	WP-LP	WP-LP	WP-SF	WP-SF	WP-LP
Overstory whitebark pine density (ha^{-1})	158	96	47	115	30
Overstory subalpine fir density (ha^{-1})	195	80	93	337	156
Historical fire regime	Mixed severity	Mixed Severity	Mixed Severity	Stand-replacement	Stand-replacement
Rust infection (%)[c]	85	70	90	<1	51
Rust mortality (%)[c]	95	93	91	<1	88
Number and type of treatment units[d]	3 MO, MN, LO	2 LO, LF	5 LO, MO, MF, HO, HF	2 HO, HF	6 LO, MO, MF, MN, HO, HF
Pre-treatment measurement year	1995	1996	1993, again in1996	1997	1997
Prescribed burn year(s)	1996	1999	2000	1999	1999, 2000, 2002
Plots compromised by wildfire[e]	20 (5)	0 (0)	44 (30)	6 (6)	28 (0)

[a] Habitat type is taken from Pfister and others (1977) where ABLA is *Abies lasiocarpa*, LUHI is *Luzula hitchcockii*, MEFE-*Menziesia ferruginea*

[b] Cover type acronyms are WP-whitebark pine, SF-subalpine fir, LP-lodgepole pine

[c] Infection and mortality levels were estimated from the tree data collected on the plots.

[d] Treatment unit codes are defined in table 2.

[e] A number of sites were burned by unplanned wildfires that burned some but not all of the plots. Number of control plots lost is in parentheses.

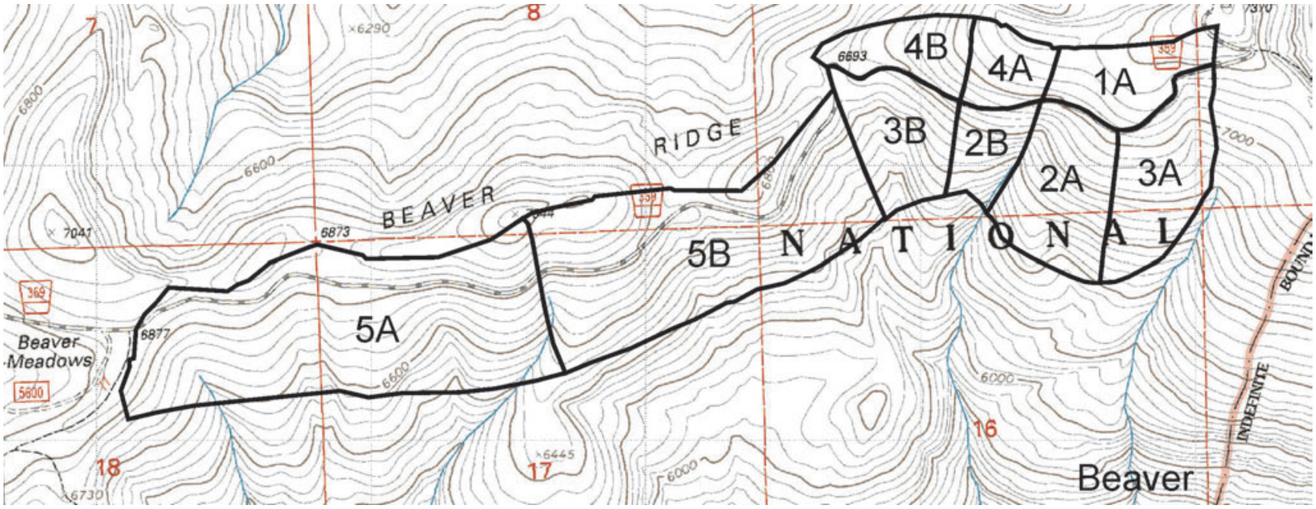

Figure 2. Treatment unit design for the Beaver Ridge study site where 1A is the control, 2A and 2B are nutcracker openings and no burning with and without tree planting, 3A and 3B are nutcracker openings with prescribed burning with and without tree planting, 4A and 4B are low severity prescribed burns with and without fuel enhancement, and 5A and 5B are high severity prescribed burns with and without fuel enhancement.

Table 2. The seven treatment type combinations (prescribed burn and tree cutting treatment) summarized in this study. Not all combinations could be reported because a majority of the study sites were burned in unplanned wildfires and uncontrolled prescribed burns (see table 1).

Prescribed burn treatment	Tree cutting treatment	Study Sites	Code
Low intensity, low severity underburn (Low)	Burn only, no cutting	BR, BO, CM, SC	LO
	Fuel enhancement	BR, BO	LF
Moderate intensity, mixed severity (Moderate)	Burn only, no cutting	BR, CM	MO
Nutcracker Openings	BR, SC	MN	
	Fuel enhancement	BR, CM	MF
High intensity, stand replacement (High)	Burn only, no cutting	CM, BM	HO
	Fuel enhancement	CM, BM	HF
No Fire (None)[a]	Nutcracker Openings	BR	N/A

[a] This treatment unit was burned by a wildfire and an uncontrolled prescribed burn so it's results are not reported here.

fir competition and to create desirable nutcracker caching habitat. The primary treatment was prescribed fire and it was implemented at three intensity levels to mimic the three types of fire regimes common in whitebark pine. A high intensity prescribed fire was used to mimic stand-replacement fire where more than 90 percent of the overstory was targeted to be killed by fire, while the moderate severity prescribed fire simulated effects from a mixed severity fire where patches of stand-replacement fire are mixed with varying severities of non-lethal surface fires (10-90 percent overstory mortality). The underburn fire was emulated with a low intensity prescribed fire. Silvicultural tree cuttings, the second type of treatment, were implemented at various levels of species selection and intensity to achieve stated objectives (table 2). First, we created cutting treatments called "Nutcracker Openings" where all trees except whitebark pine trees were cut within near-circular areas of 1 to 3 ha to entice the nutcrackers to cache seeds there. Between the nutcracker openings, but within the major treatment unit, we used group selection cuttings to remove all subalpine fir and spruce and leave all lodgepole and whitebark pine trees. A cutting treatment called *fuel enhancement* was also used to enhance the effectiveness of prescribed burning by cutting small and large fir and spruce trees and positioning them in areas with low fuel loadings. Fuel enhancement increased fuel loadings by 0.3 to 2.8 kg m^{-2} depending on the level and distribution of natural fuels.

Sampling Methods

We installed 10 plots within each treatment unit to record changes in ecological conditions. We systematically located these plots across the treatment units using a random start because attempts to randomly establish plots failed due to odd treatment unit shapes, variable fuel conditions, and concerns about finding plots in later years.

Sampling methods are described in detail in Keane and Parsons (2010a). In general, circular 0.04 ha plots were permanently located in all treatment units with all trees above 12 cm DBH (diameter at breast height) being tagged and measured for species, DBH (diameter breast height), height, crown height, and rust damage (Lutes and others 2006). The same measurements were taken on all live trees less than 12 cm DBH and greater than 1.37 meters tall (saplings), except that DBH was estimated to 2.5 cm diameter classes. Tree seedlings (trees less than 1.37 m in height) were counted by 0.3 m height classes on a 125 m^2 circular plot nested within the 0.04 ha plot. Surface fuels were measured using Lutes and other (2006) techniques on two 15.2 m transects that originated at plot center and extended in opposite directions (figure 3). Vertically projected foliar cover and heights of each vascular plant species was visually estimated within each of four, 1 m^2 microplots at each plot (figure 3) using the Lutes and others (2006) cover classes. Ground covers for rock, bare soil, wood, duff/litter, and moss were also estimated in each microplot using the same cover class categories.

Tree, fuel, and undergrowth plant species measurements were taken prior to the treatment, one year after each treatment, and five years after each treatment. Some units received two or more treatments (table 2) and we measured after each treatment type, but this report only summarizes the measurements after the last treatment was implemented. Photographs of each plot were taken in two directions at each of the measurement times.

Analysis Methods

Tree mortality was computed as percent of trees killed by species for three size classes: seedlings, saplings, and overstory trees. All ten plots within each treatment unit were used in the tree mortality calculations. We also included an assessment of snags (dead trees above 11 cm DBH) by comparing pre- and post-disturbance densities. Downed woody fuel loadings were computed from planar intercept counts using the protocols in FIREMON (Lutes and others 2006). Fuel consumption was computed as the difference in loading from pre-treatment and post-treatment measurements calculated as an average across all 20 transects in the treatment unit. We used the 60 observations of duff plus litter depth (three measurements on each of two transects for 10 plots) to

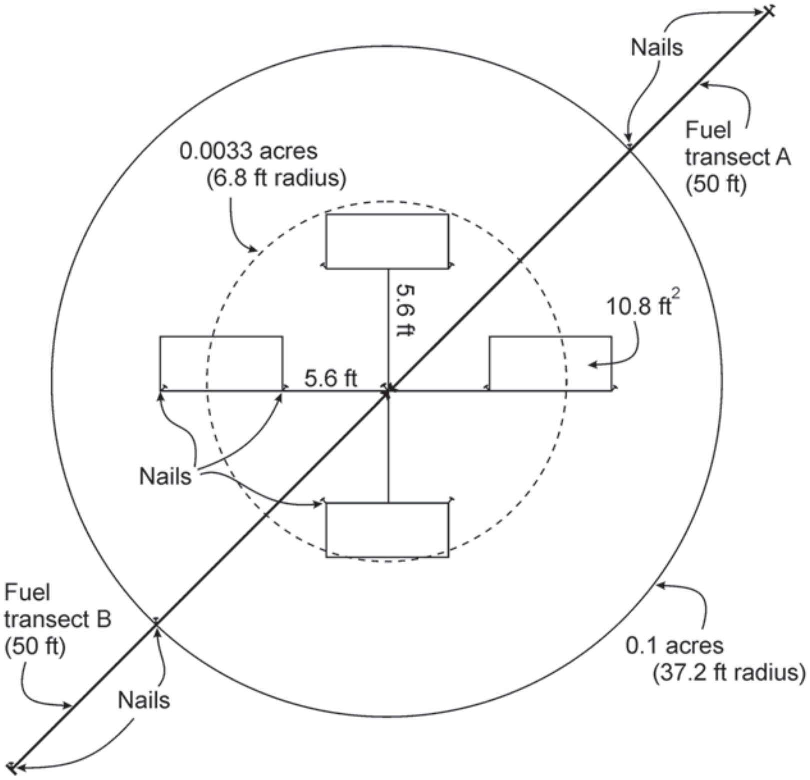

Figure 3. Diagram of the sample plot design used in the study.

calculate duff and litter consumption. Duff and litter depth was converted to loading using a bulk density of 31 kg m^{-3} (Brown 1981). We used all 40 microplots (four at each of ten plots) within each treatment unit as observations in the calculation of plant species cover response and ground cover changes (wood, rock, bare soil, duff/litter). For brevity and simplicity, seven major treatment combinations are used to present results of this restoration study. Combinations were developed by combining treatment units into similar groups across sites based on the prescribed burn intensity and the secondary cutting treatment (table 2).

Results

Summarized study results for the seven treatment type combinations across all sites are presented in table 3. Tree mortality was highest (55 to 88 percent) in treatment units with moderate to high intensity prescribed burns (HO, HF in table 3), and on any treatment with a fuel enhancement cutting (LF, MF, HF). Mortality for whitebark pine was comparable to that for subalpine fir for nearly all treatment combinations. Fire-caused mortality was highest for mature trees of both species on sites with high burn coverage (>60 percent of area burned). Moderate intensity prescribed fire (MO, MN, MF) had the greatest range of mortality across all species and size classes (19 to 88 percent) because of the patchy nature of the fires and the great diversity of site conditions across the five sites (Keane and Parsons 2010a). Most importantly, there were no detectable increases in seedling whitebark pine or subalpine fir after five years (except for the LO treatment; table 3). Whitebark pine snag densities did not change significantly after five years (except for 78 percent reduction in MF treatment) because fallen snags were replaced by fire-killed trees, but the overall trend was a 10 to 40 percent decrease in number of snags. In contrast, subalpine fir snags increased significantly for most treatments mainly because there were few fir snags prior to treatment.

New whitebark pine regeneration was rarely detected on any of the treatment units and only one site (Blackbird Mountain) had significant whitebark seedlings, probably because this site was in an area of few blister rust infections (Keane and Parsons 2010a). Some whitebark pine seedlings were survivors of the cutting and burning treatments and had marginal vigor. It is unknown whether the residual regeneration will have the capacity to release and grow into mature trees (Keane and others 2007). Subalpine fir trees were twice as plentiful as whitebark pine trees before and after all treatments for both trees and seedlings. Post-treatment fir densities are highest on sites that were burned without fuel enhancement and they tended to decrease over the five years.

Major changes in fuel loadings were detected in nearly all treatments but the direction of this change differed by woody size class (table 3, 4). Fine woody fuels (1, 10, 100 hr) marginally decreased in all treatment combinations except for LO because of extensive fuel consumption by the prescribed fires. Fine fuels were mostly unconsumed in the LO treatment because of the low coverage of the prescribed burn (<31 percent of area burned). However, logs increased significantly in all seven treatment combinations and, in some cases, this increase was striking (two to eight times greater) (tables 5, 6). Even though there was significant log consumption (10 to 50 percent) for most fires, especially in rotten logs, the

Table 3. Treatment effects for tree, fuel, and ground cover measurements averaged across all units within each of the seven treatment types (see table 2) expressed as percent change after five years from pre-treatment condition. Numbers in bold indicate statistically significant difference (p<0.05) between pre- and five year post-treatment measurements.

	Low Rx Fire		**Moderate Rx Fire**			**High Rx Fire**	
Category[a]	No cutting (LO)	Fuel enhance (LF)	No cutting (MO)	Nut-cracker Opening (MN)	Fuel enhance (MF)	No cut (HO)	Fuel enhance (HF)
				Whitebark pine (Pinus albicaulis) tree density percent change			
Seedling	-41.21	-54.35	**-82.87**	**-79.00**	-70.34	29.17	-40.69
Sapling	-31.03	-29.26	-19.44	**-88.52**	-47.85	**-63.39**	**-61.13**
Trees	**-47.20**	-37.84	**-88.37**	**-68.00**	-56.00	**-80.00**	**-86.15**
Snags	16.28	-17.28	-36.00	-8.94	**-78.26**	-25.29	10.00
				Subalpine fir (Abies lasiocarpa) tree density percent change			
Seedling	10.98	16.15	-34.08	**-87.37**	-18.79	-46.55	**-84.31**
Sapling	-17.62	-40.71	-40.52	-43.57	**-84.70**	-32.30	**-69.92**
Tree	**-58.05**	**-47.06**	-40.83	-40.63	**-75.00**	**-84.85**	**-84.73**
Snags	**188.10**	-33.33	19.18	20.69	**126.32**	**276.92**	29.73
				Fuel loading percent change			
Duff+Litter	**868.97**	**241.29**	**119.44**	-27.13	**138.64**	-40.25	-23.81
1 hr	**102.92**	-12.94	49.79	**-65.13**	**218.44**	-50.40	-18.42
10 hr	-16.97	-36.74	-49.76	**-72.07**	42.06	-10.77	-36.83
100 hr	-39.43	-12.00	-39.79	**-68.30**	45.80	-27.55	**-49.63**
1000 hr snd	-17.02	-12.34	**62.30**	**-45.29**	**97.08**	11.12	-22.30
1000 hr rot	**173.82**	143.35	**414.27**	**-30.95**	**778.00**	**342.74**	**398.90**
				Ground cover percent change			
Wood	**5.70**	4.44	**13.73**	-1.81	**12.61**	-1.17	-1.09
Rock	2.64	0.84	3.25	2.00	2.78	**11.06**	**17.66**
Soil	**5.72**	**7.60**	**6.74**	**8.37**	**5.98**	**19.24**	**22.65**
Duff+Litter	**39.32**	**17.63**	**19.69**	-5.85	**16.93**	8.96	-3.96
				Burn cover (%)			
After burn	31	54	56	91	81	61	90

[a] Categories for trees are seedling (tree height < 1.37 m), sapling (DBH<11.5 cm), trees (DBH>11.6 cm), snags (dead trees DBH>11.6); for fuels are 1 hr (dia<0.5 cm), 10hr (dia<2.5cm), 100hr (dia<7.6 cm), 1000hr (dia>7.6 cm); duff+litter refers to both litter and duff layers.

extensive log load increases were a result of prescribed fires weakening the numerous standing dead whitebark pine snags causing them to fall (table 3). Nearly all fallen whitebark pine snags were trees that had been previously killed by mountain pine beetle or blister rust. Duff and litter increased after low intensity prescribed burns (241 to 868 percent) because of the contribution of scorched needles from standing trees. Prescribed fires tended to increase bare soil and rock cover because of the corresponding decrease in duff/litter and woody cover (table 4), but the magnitude and variability of these changes were entirely dictated by the intensity and coverage of the fire. Woody cover increased in some units because of the fallen snags, whereas duff+ litter cover increased because of fallen scorched foliage. Rock and soil cover, however, increased in nearly all treatment combinations with the most significant increases in fuel-enhanced units with high burn cover and intensity. We feel that an increase in rock and bare soil cover creates more fine scale pattern within the unit thereby improving nutcracker caching potential (McCaughey and Weaver 1990; Tomback and others 1993; Tomback 2005).

Most treatment units in this study had low vascular plant diversity with microplots averaging only five species and the sites having only 20 to 25 species (Keane and Parsons 2010b). We selected four common undergrowth plant species that were dominant across all sites and treatment unit combinations, and found that these species declined in cover after treatment (20 to 100 percent) (figure 4). Elk sedge (*Carex geyeri,* CAGE) increased in cover after five years for all but the most severe burn treatments. Grouse whortleberry (*Vaccinum scoparium,* VASC) cover declined the most after nearly all treatments, but most sites recovered at least half pre-burn cover by the fifth year.

Discussion

All high and moderate intensity prescribed fire-cutting treatment combinations were effective at creating desirable nutcracker caching habitat as evidenced by the abundant nutcracker caching observed on nearly all sites (Keane and Parsons 2010a). These treatments were also successful at removing subalpine fir competition thereby creating desirable growing conditions for surviving and newly regenerating whitebark pine. However, the expected whitebark pine regeneration from the observed caching has not yet materialized with nearly all sites having few or no new whitebark pine seedlings (table 3). This is probably a result of several factors:

Table 4. Fuelbed characteristics at pre-treatment, 1 year after treatment, and 5 years after treatment. Rx stands for prescribed fire, and bold numbers indicate statistical significance ($p<0.05$) from pre-treatment condition

	Low Rx Fire		**Moderate Rx Fire**			**High Rx Fire**	
Sample Time	No cutting (LO)	Fuel enhance (LF)	No cutting (MO)	Nut-cracker Opening (MN)	Fuel enhance (MF)	No Cut (HO)	Fuel enhance (HF)
Fine fuel loadings (kg m^{-2})							
Pre	0.65	0.76	1.05	0.97	0.37	0.71	0.94
1 year	0.39	0.76	0.70	**0.37**	0.47	0.52	0.73
5 year	0.46	0.63	0.64	**0.30**	0.57	0.53	0.50
Sound log loading (kg m^{-2})							
Pre	2.64	3.94	3.75	11.71	1.72	4.35	4.64
1 year	**7.34**	**8.81**	**21.80**	7.37	**16.77**	**13.40**	**19.65**
5 year	**7.22**	**9.58**	**19.30**	8.09	**15.08**	**19.24**	**23.14**
Duff and litter loading (kg m^{-2})							
Pre	0.12	0.34	0.55	0.61	0.31	1.04	1.07
1 year	0.37	0.68	0.33	**0.07**	0.35	0.75	**0.68**
5 year	**1.13**	**1.15**	**1.21**	0.45	**0.74**	**0.62**	0.82
Bare soil cover (%)							
Pre	2.38	4.98	1.68	5.01	6.03	4.50	3.19
1 year	**14.40**	**16.08**	**19.62**	**38.51**	**17.69**	**29.59**	**36.05**
5 year	**8.09**	**12.58**	**8.41**	**13.38**	**12.00**	**23.74**	**25.84**

1. Many of the cached seeds were probably reclaimed by the nutcrackers during the years following caching. The populations of cone-producing whitebark pine at or near our study areas were so low that the nutcrackers are consuming many seeds during caching and reclaiming many cached seeds so it is doubtful that the bird left sufficient seed in the ground to provide for adequate regeneration (McKinney and Tomback 2007).
2. Severe environmental conditions could have killed many emerging seedlings. These steep, high mountain sites experience deep snowpack, especially the Beaver Ridge site, which had over 50 feet in 1997, and the heavy snow tended to creep down slope and pull young seedlings out of the ground.
3. Soils were highly erosive. Spring snowmelts generate abundant water that usually scours the topsoil away from those seedlings that are rooted in it, especially in recently burned sites.
4. The five-year evaluation period was too short for effectively evaluating regeneration dynamics. In these severe sites, a 10 or 20-year measurement might more accurately describe the success of our treatments. Some have identified a lag period of up to 40 years for whitebark pine to become established in upper subalpine zones due to severity of the disturbance and the site (Agee and Smith 1984; Arno and Hoff 1990).

We found that it was difficult to implement prescribed fires to mimic non-lethal surface and mixed severity fires for a number of reasons. First, the shrub and herbaceous fuels on most sites were rarely dry enough to sufficiently carry a fire under our prescriptions (desired conditions of burning) resulting in a light fire with low tree mortality and low burn coverage. In contrast, fire intensities on fuel enhanced sites were sometimes too high resulting in unwanted high whitebark pine mortality and extensive reductions in the stabilizing undergrowth plant community (table 4; figure 4). It takes a delicate balance of sufficient fuels and dry fuel moistures to implement an effective prescribed burn that reduces subalpine fir overstory and understory while allowing survival of mature whitebark pine trees. The lack of experience in burning high elevation ecosystems may have influenced fire crews to implement prescribed burns under wetter than desired moisture conditions thereby achieving lower than desired fire intensity and lower burn coverage across the stand (table 4).

Contrary to the restoration goals, the level of subalpine fir mortality was nearly the same as whitebark pine mortality and many fir trees remained after treatment (table 3). Our objective was to kill the majority of subalpine fir (>80 percent) and leave whitebark pine (>80 percent), yet we seemed to kill both tree species at the same rate regardless of diameter. This could be due to the mentioned inexperienced burn crews, but it is more likely that whitebark pine is not as fire tolerant as the literature would suggest (Ryan and Reinhardt 1988). We also found that many whitebark pine trees were killed by *Ips* spp. (originating from populations in unburned slash) and mountain pine beetle after burning (Baker and Six 2001). Because of this, it may be difficult to keep whitebark pines alive in units treated with prescribed burns so alternative non-burn treatments may be warranted, especially in areas with high beetle populations.

Management Implications

Based on the findings of this study, we recommend the following in designing and implementing whitebark pine restoration activities:

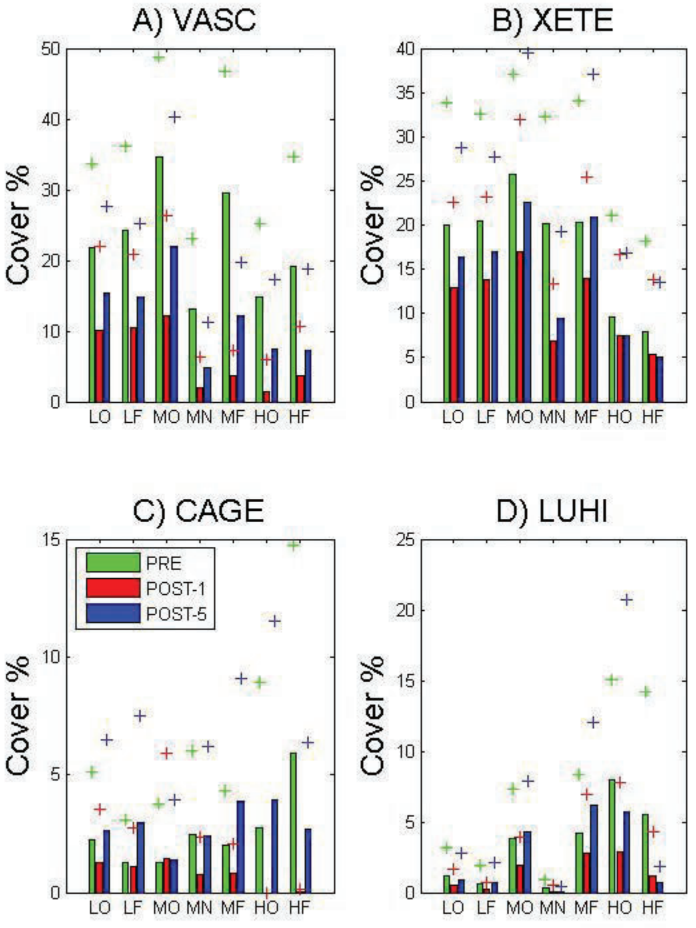

Figure 4. Changes canopy cover of the four dominant undergrowth plant species across each of the treatment combinations – a) *Vaccinium scoparium* (VASC), b) *Xerophyllum tenax* (XETE), c) *Carex geyeri* (CAGE), and d) *Luzula hitchcockii* (LUHI). Treatment combination codes are described in table 2. The symbol + represent standard error of the data.

- **Emulate historical fire regime**. Use the observed fire regime for a potential treatment site to guide design of the whitebark pine restoration treatment. Craft treatment specifics around the native fire regime effects.
- **Use prescribed burning**. Try to use prescribed burning as one of the restoration tools if economically possible. Prescribed burning can be enhanced by the following.
  - *Augmenting fuelbeds*. Fuel enhancement cuttings should be implemented one year prior to a prescribed burn to ensure burn objectives are fully realized. The addition of cured slash to discontinuous fuelbeds facilitates burn effectivness by providing additional fine fuel to 1) aid fire spread into all areas of the stand and 2) augment quickly drying fine fuel levels so the burn can be implemented in moister conditions.
  - *Burning under appropriate conditions*. Wait until the first hard frost in late summer or early fall before implementing a prescribed burn because we found shrub and herbaceous fuels were much drier after the first hard frost.
- **Use wildland fire use**. Pro-active, controlled management-ignited prescribed burns, such as those used in this study, many not always be possible due to access, cost, and risk considerations. Wildland fire use (letting lightning fires burn under acceptable conditions) may have a wider use in land management.
- **Plant, plant, plant**. Sites experiencing high whitebark pine blister rust-caused mortality (above 20 percent) and high rust infection (above 50 percent) or sites experiencing high beetle mortality should be planted with potentially rust-resistant seedlings after treatment, including wildland fire use. Potentially rust resistant seeds can be collected from surviving whitebark pine trees (Hoff and others 2001).
- **Monitor results**. There is a lack of comprehensive studies investigating effects of restoration treatment in whitebark pine. It is critical to monitor treatment effects to ensure future restoration success for others.

Acknowledgements

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References

Agee, J. K.; Smith, L. 1984. Subalpine tree reestablishment after fire in the Olympic Mountains, Washington. Ecology. 65: 810-819.

Arno, S. F. 1986. Whitebark pine cone crops a diminishing source of wildlife food. Western Journal of Applied Forestry. 9: 92-94.

Arno, S F.; Hoff, R. 1990. *Pinus albicaulis* Engelm. Whitebark Pine. Pages 268-279. In: Silvics of North America. Vol. I. Conifers. Agr. Handbook. USDA For. Service.

Arno, S. F.; Parsons, D. J.; Keane, R. E. 2000. Mixed-severity fire regimes in the northern Rocky Mountains: consequences of fire exclusion and options for the future. Pages 225-232. In: Wilderness science in a time of change conference, Volume 5: wilderness ecosystems, threat, and management, Missoula, MT. May 23-27, 1999. U.S. Dept. of Agriculture Forest Service Rocky Mountain Research Station. General Technical Report RMRS-P-15-VOL-3. Fort Collins, CO.

Arno, S. F.; Tomback, D. F.; Keane, R. E. 2001. Whitebark pine restoration: a model for wildland communities. Pages 416-419. In: D. F. Tomback, S. F. Arno, and R. E. Keane (editors): Whitebark pine communities: ecology and restoration. Island Press, Washington, DC.

Baker, K. M.; Six, D. L. 2001. Restoring whitebark pine (*Pinus albicaulis*) ecosystems: a look at endemic bark beetle distribution. Pages 501-502. In: Society of American Foresters 2000 National Convention. Society of American Foresters, Bethesda, MD. Washington, DC, USA.

Blaustein, A. R.; Dobson, A. 2006. Extinctions: A message from the frogs. Nature. 439: 143-144.

Brown, J. K. 1981. Bulk densities of nonuniform surface fuels and their application to fire modeling. Forest Science. 27: 667-683.

Day, R. J. 1967. Whitebark pine in the Rocky Mountains of Alberta. Forestry Chronicle. 43:278-282.

Hoff, R.; Bingham, R. T.; McDonald, G. I. 1980. Relative blister rust resistance of white pines. Eur. J. For. Path. 10: 307-316.

Hoff, R. J.; Ferguson, D. E., McDonald, G. I.; Keane, R. E. 2001. Strategies for managing whitebark pine in the presence of white pine blister rust. Pages 346-366. In: D. F. Tomback, S. F. Arno, and R. E. Keane (editors): Whitebark pine communities: ecology and restoration. Washington, DC: Island Press c2001.

Hurlbert, S. H. 1984. Pseudoreplication and the design of ecological field experiements. Ecological Monographs. 54: 187-211.

Hutchins, H. E.; Lanner, R. M. 1982. The central role of Clark's nutcrackers in the dispersal and establishment of whitebark pine. Oecologia. 55: 192-201.

Keane, R. E. 2001. Successional dynamics: modeling an anthropogenic threat. Pages 159-192. In: Tomback, D.; S. Arno, and R. Keane, editors. Whitebark pine communities: ecology and restoration. Island Press, Washington, DC, USA.

Keane, R. E.; Arno, S. F. 1993. Rapid decline of whitebark pine in Western Montana: Evidence from 20-year remeasurements. Western Journal of Applied Forestry. 8: 44-47.

Keane, R. E.; Arno, S. F. 2000. Restoration of whitebark pine ecosystems in western Montana and central Idaho. Pages 324-330. In: Proceedings of the Society of American Foresters 1999 national convention, Portland, OR, September 11-15, 1999. Bethesda, MD: Society of American Foresters c2000.

Keane, R. E.; Gray, K. L.; Dickinson, L. J. 2007. Whitebark pine diameter growth response to removal of competition. U.S. Department of Agriculture, Forest Service Rocky Mountain Research Station Research Note RMRS-RN-32. Ogden, UT.

Keane, R. E.; Morgan, P.; Menakis, J. P. 1994. Landscape assessment of the decline of whitebark pine (*Pinus albicaulis*) in the Bob Marshall Wilderness Complex, Montana, USA. Northwest Science. 68: 213-229.

Keane, R.E.; Parsons, R.A. 2010a. A management guide to ecosystem restoration treatments: the whitebark pine forests of the Northern Rocky Mountains. USDA Forest Service Rocky Mountain Research Station General Technical Report RMRS-GTR. Fort Collins, CO.

Keane, R. E.; Parsons, R. A. 2010b. Restoring whitebark pine forests of the northern Rocky Mountains, USA. Ecological Restoration. 28: 56-70.

Kendall, K.; Keane, R.E. 2001. The decline of whitebark pine. Pages 123-145 *in* D. Tomback, S.F. Arno, and R.E. Keane, editors. Whitebark pine communities: Ecology and Restoration. Island Press, Washington, DC, USA.

Lanner, R.M. 1996. Made for each other: A symbiosis of birds and pines. Oxford University Press, New York, New York, USA.

Logan, J. A.; Powell, J. A. 2001. Ghost forests, global warming, and the mountain pine beetle (*Coleoptera: Scolytidae*). American Entomologist. 47: 160-173.

Lorenz, T. J.; Aubry, C.; Shoal, R. 2008. A review of the literature on seed fate in whitebark pine and the life history traits of Clark's Nutcracker and pine squirrels. USDA Forest Service Pacific Northwest Research Station General Technical Report PNW-GTR-742. Portland, OR.

Lutes, D. C.; Keane, R. E.; Caratti, J. F.; Key, C. H.; Benson, N. C.; Sutherland, S. C.; Gangi, L. J. 2006. FIREMON: Fire effects monitoring and inventory system. USDA Forest Service Rocky Mountain Research Station General Technical Report RMRS-GTR-164-CD. Fort Collins, CO, USA.

Mattson, D. J.; Reinhart, D. P. 1990. Whitebark pine on the Mount Washburn Massif, Yellowstone National Park. Pages 106-117. In: Proceedings—Symposium on whitebark pine ecosystems: Ecology and management of a high-mountain resource. USDA Forest Service, Intermountain Research Station General Technical Report INT-270. Ogden, UT.

McCaughey, W. W.; Schmidt, W. C.; Shearer, R. C. 1985. Seed-dispersal characteristics of conifers in the Inland Mountain West. Pages 11-22. In: Proceedings from the Conifer Tree Seed in the Inland Mountain West Symposium, Missoula, MT.

McCaughey, W. W.; Weaver, T. 1990. Biotic and microsite factors affecting whitebark pine establishment. Pages 319-324. In: Schmidt, W. C. and K. MacDonald (Compilers). Proceedings—Symposium on Whitebark Pine Ecosystems: Ecology and management of a high mountain resource. USDA Forest Service Intermountain Research Station General Technical Report INT-270. Ogden, UT.

McKinney, S. T.; Tomback, D. F. 2007. The influence of white pine blister rust on seed dispersal in whitebark pine. Canadian Journal of Forest Research. 37: 1044-1057.

Minore, D. 1979. Comparative autecological characteristics of northwestern tree species: a literature review. General Technical Report PNW-87, U.S. Department of Agriculture, Forest Service, Pacific Northwest Forest and Range Experiment Station, Portland, OR, USA.

Morgan, P.; Bunting, S. C. 1990. Fire effects in whitebark pine forests. Pages 319-324. In: Schmidt, W. C. and K. MacDonald (Compilers). Proceedings—Symposium on Whitebark Pine Ecosystems: Ecology and management of a high mountain resource. USDA Forest Service Intermountain Research Station General Technical Report INT-270. Ogden, UT.

Morgan, P.; Bunting, S. C.; Keane, R. E.; Arno, S. F. 1994. Fire ecology of whitebark pine (*Pinus albicaulis*) forests in the Rocky Mountains, USA. Pages 136-142. In: Proceedings of the international symposium Subalpine stone pines and their environment: The status of our knowledge, St. Moritz, Switzerland.

Murray, M. P. 1996. Landscape dynamics of an island range: Interrelationships of fire and whitebark pine (*Pinus albicaulis*). University of Idaho, Moscow, ID, Ph.D. Dissertation.

Murray, M. P.; Bunting, S. C.; Morgan, P. 1995. Whitebark pine and fire suppression in small wilderness areas. General Technical Report INT-GTR-320, U.S. Department of Agriculture, Forest Service, Intermountain Research Station, Ogden, UT, USA, Missoula, MT, USA.

Norment, C. J. 1991. Bird use of forest patches in the subalpine forest-alpine tundra ecotone of the Beartooth Mountains, Wyoming. Northwest Science. 65: 2-9.

Pfister, R. D.; Kovalchik, B. L.; Arno, S. F.; Presby, R. C. 1977. Forest habitat types of Montana. U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station General Technical Report INT-34. Ogden, UT, USA.

Running, S. W. 2006. Is global warming causing more, larger wildfires. Science. 313: 927-928.

Ryan, K. C.; Reinhardt, E. D. 1988. Predicting postfire mortality of seven western conifers. Canadian Journal of Forest Research. 18: 1291-1297.

Tomback, D. F.; Arno, S. F.; Keane, R. E. 2001. Whitebark pine communities: Ecology and Restoration. Island Press, Washington, DC, USA.

Tomback, D. F. 1982. Dispersal of whitebark pine seeds by Clark's nutcracker: a mutualism hypothesis. J. of Animal Ecol. 51: 451-467.

Tomback, D. F. 1998. Clark's Nutcracker. In A. Poole and F. Gill, editors. The Birds of North America No. 331. The Birds of North America Inc.

Tomback, D. F. 2005. The impact of seed dispersal by the Clark's Nutcracker on whitebark pine: Multi-scale perspective on a high mountain mutualism. Pages 181-201. In: G. Broll and B. Kepline, editors. Mountain Ecosystems: Studies in treeline ecology. Springer.

Tomback, D. F.; Sund, S. K.; Hoffman, L. A. 1993. Post-fire regeneration of *Pinus albicaulis*: height-age relationships, age structure, and microsite characteristics. Canadian Journal of Forest Research. 23: 113-119.

Waring, K. M.; Six, D. L. 2005. Distribution of bark beetle attacks after whitebark pine restoration treatments: a case study. Western Journal of Applied Forestry. 20: 110-116.

No Free Lunch: Observations on Seed Predation, Cone Collection, and Controlled Germination of Whitebark Pine from the Canadian Rockies

Extended Abstract

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Abstract—Whitebark pine is a keystone species of high elevation forests in western North America that is experiencing rapid decline due to fire exclusion policies, mountain pine beetle, and the introduced pathogen, white pine blister rust. Restoration activities include collecting cones and growing seedlings from individuals that show mechanisms for resistance to blister rust infections. Collecting viable whitebark pine seeds is challenging due to high rates of cone harvest by wildlife prior to seed maturation. This has led to the practice of placing protective coverings over the cones early in the summer, and then collecting them when they fully mature in September. We investigate if the added time, expense, and complications of using protective coverings over cone bearing branches are required for the collection of viable whitebark pine seeds. Aside from anecdotal sources, there appears to be no quantitative information demonstrating this is necessary. We determined the optimal time for cone collection by comparing the timing of seed development and germination rates compared to the timing of seed harvest by wildlife in a stand in Banff National Park, in the northern region of its range. Results clearly indicate that in to collect viable seeds from whitebark pine, protective coverings must be put over unripe cones so that collections can be made at any time from late August to late September.

Introduction

Whitebark pine (*Pinus albicaulis*) is the sole North American stone pine (*Pinus* subsection *Cembrae*), a group of five pine species found at high elevations in the northern hemisphere, characterized by large, wingless seeds and indehiscent cones (McCaughey and Tomback 2001). In the Rocky Mountains, whitebark pine extends from 42 to 54 degrees north (Ogilvie 1990). It is an extremely long-lived species, with specimens in Canada found to be over 1100 years old (Luckman and Youngblut 1999). Whitebark pine is a keystone species of high elevation sites due to the many ecological roles it plays in these often steep, harsh environments (Tomback and others 2001). Whitebark pine seeds have a high nutritional value (Lanner and Gilbert 1994) and form a major component of the diets of many birds and mammals, including Clark's nutcracker (*Nucifraa columbiana*), red squirrels (*Tamiasciurus hudsonicus*), and grizzly bears (*Ursus arctos*) (Vander Wall and Hutchins 1983, Mattson and others 2001, Lorenz and others 2008). Clarks nutcracker is the only seed dispersal vector for whitebark pine regeneration because they harvest the seeds and cache them throughout the landscape to be retrieved throughout the following year; it is the un-retrieved seeds that can germinate and grow into new seedlings (Tomback 2001). However, Clark's nutcrackers and squirrels will often compete for seeds during the cone maturation process and often harvest all cones during poor cone crops or in areas with few whitebark pine trees (McKinney and Tomback 2007).

Whitebark pine is a pioneer species at upper subalpine elevations, where it often facilitates the establishment of other tree species following stand-replacing fire, and is a climax species at tree line, where the conditions are too harsh for other species (Callaway 1998). The pine also plays an important role in slowing snowmelt, regulating spring runoff and stabilizing soils at high elevations (Farnes 1990).

The rapid decline of whitebark pine is well documented in the United States (Kendall and Keane 2001) and gaining better awareness in Canada (Wilson 2007; Smith and others 2008). This decline is due to several anthropogenic factors. Whitebark pine can form continuously regenerating climax communities at the upper tree line, but is often reliant on burned areas to regenerate at lower elevations (Arno 2001). The successful fire exclusion policies of the last century have reduced the availability of burned areas for regeneration and promoted successional development of more shade-tolerant species, such as Engelmann spruce (*Picea engelmannii*) and subalpine fir (*Abies lasiocarpa*) (Kendall and Keane 2001). In the past, mountain pine beetle attacks on whitebark pine stands sporadically caused severe damage in some areas (Kendall and Keane 2001). Now, the interaction of warming climatic conditions and fire exclusion appears to be allowing pine beetle to expand its range up in elevation and further endanger whitebark pine stands (Raffa and others 2008).

The greatest concern for the survival of whitebark pine as a species is white pine blister rust, which is caused by the fungus, *Cronartium ribicola*. (Kendall and Keane 2001). This non-native disease has killed up to 60 percent and infected up to 97 percent of the trees in some areas in the Canadian Rocky Mountains (Smith and others 2008). Over several years, the infection spreads from needles into the branches and proceeds towards the main stem. The tree's ability to reproduce is eliminated once the infection kills the upper, cone-bearing branches by choking off nutrients, although it may be many years before the tree completely dies (Keane and Morgan 1994).

The impacts of losing whitebark pine on the landscape are manifold. The heavy reliance by grizzly bears and Clark's nutcracker on whitebark seeds will result in reduced habitat value of high elevation forests (Tomback and Kendall 2001).

In: Keane, Robert E.; Tomback, Diana F.; Murray, Michael P.; and Smith, Cyndi M., eds. 2011. **The future of high-elevation, five-needle white pines in Western North America: Proceedings of the High Five Symposium.** 28-30 June 2010; Missoula, MT. Proceedings RMRS-P-63. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station. 376 p. Online at http://www.fs.fed.us/rm/pubs/rmrs_p063.html

The loss of this food source may increase negative human – bear interactions by forcing bears to search for other sources of food at lower elevations where human densities are much higher (Mattson and others 1992). The loss of whitebark could change forest structure by altering successional development at lower elevations (Keane and Morgan 1994). At treeline, whitebark pine often initiates krummholz tree islands, so their loss could result in fundamental changes to vegetation structure (Resler and Tomback 2008).

An important conservation effort for whitebark pine populations is the harvest of seeds from cones in trees that show phenotypic resistance to blister rust. Planting blister rust-resistant seedlings grown from those seeds is considered a major component of the future whitebark forest management in the United States, and in Canada (McDonald and others 2004; Smith and others 2008). However it is difficult to collect viable whitebark pine seeds due to the high rates of cone harvest by Clark's nutcracker and red squirrels prior to seed maturation. This has led to the practice of placing protective coverings over the cones early in the summer, and then collecting them when they fully mature in September (Murray 2007). There are two main difficulties with this practice. The first is the cost of having to visit each tree twice in the season to cage and then retrieve the cones. The second is the damage to the tree caused by climbing onto the softer bark found near the cones, although, soft shoes and care may alleviate the latter problem. This leads to an important question of whether there is a time during the seed population's maturation process where cones can be harvested early enough to avoid significant predation, and yet still produce seed that can germinate. If this were true, it would cut the cost of harvesting drastically. Further, is it possible to visually recognise this point in the development of the seeds through observing key features in either the female cones or field dissection of individual seeds to look at the embryos?

Here we investigate the optimal time for cone collection by comparing the timing of seed development and germination rates versus the timing of seed harvest by wildlife. Our primary purpose is to determine if the added time, expense and complications of using protective coverings over cone bearing branches are required for the collection of viable whitebark pine seeds. Secondarily, we wanted to document the morphological changes that occur to the visible cone, and to the seed embryo, through the summer maturation process. We wanted to determine if there was a clear correlation between germination success of seeds and observable characteristics in the exterior cone appearance and with the embryo. This information will allow cone collectors to assess the likely germination rates of seeds based on cone appearance in the field.

Materials and Methods

Study Area

The study was located in the northern part of the whitebark pine range, on the west slope of Mt. Hector, in Banff National Park, Alberta, Canada (51º 35' 08" N 116º 17' 36" E) at 2000m elevation (Figure 1). The average slope of the study site was 62 percent. Walker and others (1982) characterizes the ecosystem type present at this site as having open mixed coniferous vegetation in the upper subalpine eco-region, with calcareous colluvial parent material, and medium textured brunisols or regosols. The site was located in an avalanche path with an understory dominated by *Shepherdia canadensis, Arctostaphylos uva-ursi, Fragaria virginiana, Castilleja miniata*, and several grass species. Repeated breaking and re-sprouting of branches and stems by snow avalanches has created stunted whitebark pine

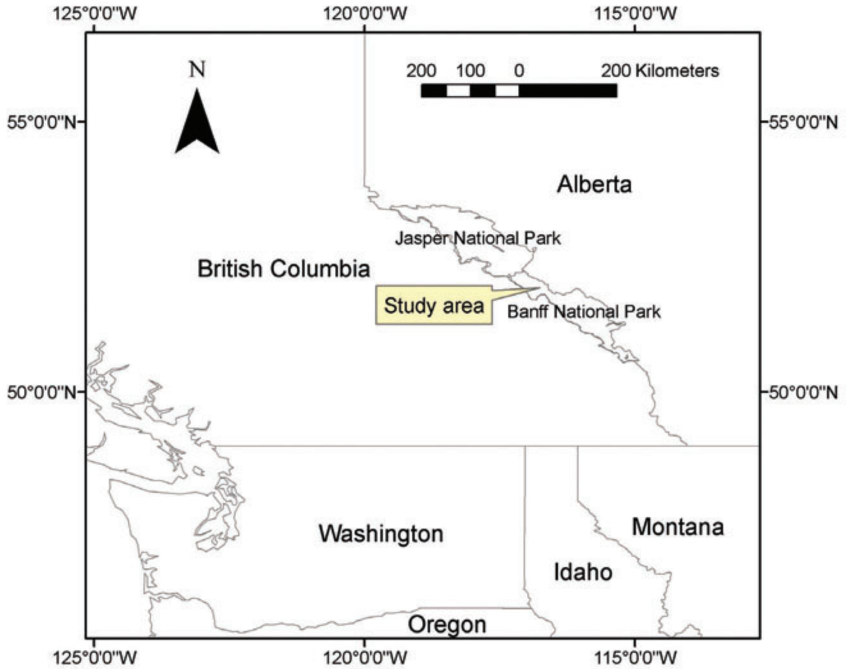

Figure 1. Study location in Banff National Park, Alberta.

growth forms that allowed easy access to cones from mature trees at ground level.

This area experiences a continental climate. The nearby records from Lake Louise document the recent mean January and July temperatures at -13.8° C and 12.0° C, respectively (Environment Canada 2010).

Cone Observations and Collections

Ten healthy whitebark pine trees with accessible cone bearing branches were located in June 2006. Five of these trees were randomly selected for cone collections and 30 protective cages were placed over cone bearing branches, protecting 72 cones from harvest by wildlife. The remaining five trees had no protective coverings placed over their cones, and were used to monitor timing and rates of wildlife harvest. At the end of June 2006, the numbers of seed bearing cones were counted on each tree, as observed through 8x40 binoculars from marked and recorded locations on the ground. Thereafter, every 11 to 13 days until September 16th, the number of complete, or only partial harvested (<50 percent) cones remaining were recorded from those same locations. Every 11 to 13 days from July 16th until September 16th, a seed lot was collected from 12 protected cones that were randomly selected from the trees with caged branches, for a total of six seed lots from six time periods. The timing of seed and cone development in whitebark pine can vary from site to site and year to year (Halstrom 1993). For this reason, a dissection of three of these cones was completed in the field, where qualitative descriptions of cone and seed development were made. The remaining cones from each collection were dried in a well-ventilated area at room temperature. In late September, seeds could be more easily extracted from the cones, with each cone yielding between 40 and 75 seeds, which were dried at room temperature for 21 days (Young and Young 1992). The six collections resulted in seed lot sizes between 344 and 522 seeds per collection date.

Seed Stratification and Germination

Methods outlined by Burr and others (2001) were followed to break physiological dormancy. All 2,322 seeds were placed in mesh bags and washed for 48 hours under running water, allowing seeds to begin water uptake. All seeds were kept moist and in the dark during a 30-day warm stratification at 21 to 23 degrees Celsius followed with 60-day cold stratification at 2 to 4 degrees Celsius. Every week throughout this period, moldy seeds were removed, and the remaining seeds were cleaned by placing them under a one-hour running water soak.

Each of the six seed lots were evenly and randomly divided into four replicates for germination trials. Twenty five seeds were placed in each 100 x 15mm Petri dish, which were each lined with two United Scientific Supplies Inc. 9 cm circle filter paper. The filter paper was kept moist to allow seeds to uptake water by wicking throughout the germination trial. In a greenhouse, the Petri dishes were randomly placed under a 12 hr photoperiod at 22° C during the day and 15° C at night. Each week for the next seven weeks, all seeds with emerged radicles exceeding 5mm in length and showed geotropic curvature were deemed to have germinated (Pitel and Wang 1990).

Seed coat dormancy is sometimes dealt with by making a 2 mm nick at the radicle end with a scalpel along the visible line separating the two halves of the seed, which will allow the radicle to emerge from the hardened seed coat (Pitel and Wang 1990). Those seeds that had not yet germinated after the fourth week of the germination trial were nicked in an attempt to increase germination rates.

Data Analysis

The total percent germination was calculated for each replicate from each of the six seedlots. Seeds developing mould during the stratification process and germination trial were included in this calculation as ungerminated seeds. These data were examined for departures from normality as suggested by Sokal and Rohlf (1995), however, no transformations were necessary. The null hypothesis, that there was no difference in germination of seeds between harvest dates, was tested using a one-way ANOVA. A Tukey's HSD post hoc test was used to determine which harvest date means were different. These analyses where only carried out on the collection periods where there was at least some germination recorded (the last four collection periods).

The percent predation of cones was calculated by dividing the number of cones observed on each date by the total number of cones initially observed on each of the five trees in late June. Similar to the germination data, these predation data were assessed for departure from normality. The null hypothesis, that there was no difference in the amount of predation of whitebark pine cones between assessment periods, was tested using a one-way ANOVA. A Tukey's HSD post hoc test was also used to determine which harvest date means were different. With these data, only the middle three recording periods were used in the statistical analysis, as there was no variation in the first two and last three measurement periods (Figure 2). All of these statistical procedures were carried out using R 2.91 (RCDT 2009).

Results

Predation and Germination Trends

Clark's nutcrackers began harvesting the unprotected whitebark pine cones at the start of July, with the birds picking at a few cones but never taking more than 50 percent of the seeds from any one cone. Red squirrels began removing cones and nutcrackers began picking out all the seeds after July 16th. Virtually all cones and seeds had been removed by August 9th (Figure 2). All protective coverings were effective in preventing harvest of cones by wildlife.

At this time, seeds harvested from the trees were just starting to show a low level of germination success. This

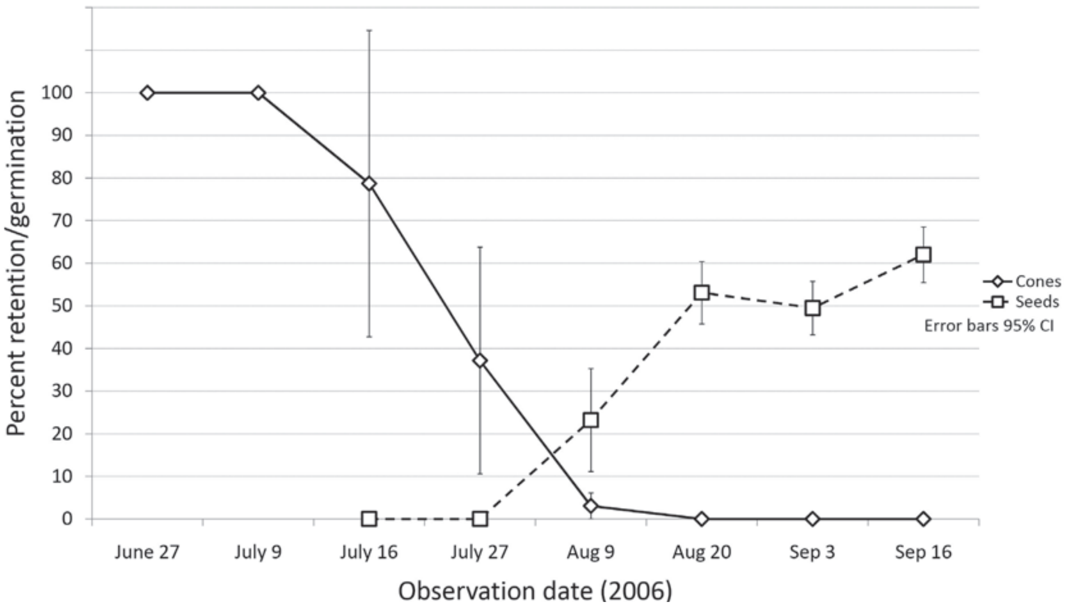

Figure 2. Comparison between the observed percent of cones remaining on study trees to success of seeds germinating from seedlots harvested at the same time of the observations.

success significantly increased over the next two weeks, levelling off to range between 50 percent and just over 60 percent (Figure 2).

Cone Descriptions

Seedlots that had low or no germination were characterized by cones that were very sticky, purple-red in colour, and the cone scales were very difficult to remove by hand. Once the cone scales were removed, some cone scale tissue was still attached to the seed coat (Figure 3). Seeds were soft and easy to cut in half. Seeds that were cut in half revealed embryos that were less than 50 percent of the length of the embryo cavity. The megagametophyte tissue was clear or white and shrunk away from the seed coat.

Figure 3. Appearance of immature cones and seeds harvested on August 9th, 2006. Note the dark red-purple colour of the cone surface and the cone scale tissue still adhering to the seeds.

Conversely, seedlots that had 50 percent germination rates or greater were characterized by cones that were purple—brown, and dry to somewhat sticky to touch. The cone scales were opened slightly or, if closed, came off with little difficulty, exposing two red—brown seeds that were easily removed (Figure 4). No cone scale tissue remained attached to seed coat, and seed coats were very hard. When seeds were sliced in half, embryos extended about 90 percent along the length of the embryo cavity. The mega gametophyte tissue was solid white and did not shrink away from the seed coat, even when left overnight. For a complete qualitative description of each seedlot dissection, see Leslie (2007).

Discussion

The primary goal of this research was to determine if placing protective coverings over whitebark pine cones early in the season is necessary when collecting seeds for restoration purposes. This study showed that during the 2006 field season in this area of Canadian Rockies it was necessary to do so because by the time seeds became mature, almost all cones had been harvested by wildlife. Aside from anecdotal sources, there appears to be no other quantitative information demonstrating this is necessary.

To maximize cone availability, the ideal time to make collection would be just prior to the beginning of wildlife harvest. However, at this time, cones are not yet mature, and no germination is expected. There have been some previous attempts in Alberta to collect seed early and finish its maturation in a controlled nursery environment, but this has not led to successful germination (Barnhardt, personal communication). Waiting until the middle of August when reasonable germination of seeds may be expected means that there may be no cones left to harvest for restoration purposes. There may be a very small window of opportunity for collecting viable seeds without protective coverings in the

Figure 4. Appearance of mature cones and seeds harvested on Sept 16th, 2006. The seeds now are light brown colour and are easily removed from the cone scales.

first week of August, given the data (Figure 2). However even during this time, the numbers of undamaged cones available, and the germination rates of their seeds, would likely be quite small.

The 2006 cone crop in the Canadian Rockies was generally very poor when compared to observations during the previous three summers. During years of good cone crop, slower rates of cone harvest by wildlife is expected (McKinney and Tomback 2007). However, collections for restoration purposes will be taking place in stands where there is a very high rate of blister rust incidence (Mahalovich and Dickerson 2004) where the cone crop will be very small due to the large number of dead, or reproductively dead trees. Where areas of higher blister rust infection have lowered densities of cones produced, these cones are subjected to greater rates of harvest by wildlife, and there are reduced levels of seed dispersal by Clark's nutcracker (McKinney and others 2009). While our study area had low infection rates, the poor cone crop during the study year may have mimicked a cone crop that could be expected when making collections for restoration purposes in areas with high infection rates, such as the stands in the southern border regions (Smith and others 2008).

Recommendations

Our results suggest that when collecting viable whitebark pine seeds, the placing of protective coverings over the cones is necessary. The timing of seed and cone development in whitebark pine can vary between sites and years (Burr and others 2001), so we recommend a visual inspection of the cone and seed development prior to collection. To ensure collection of viable seeds, the optimal time to collect the cones is when the cone is mature to the point that the cone scales are easily removed and dark orange or red seeds are exposed. The seeds should easily come out of the cone and the seed coat should be hard with no cone scale tissue still attached. We believe that this condition is a strong enough indicator of seed maturity that destructive sampling of a subset of cones is not necessary. In this study, mature seed development was reached by August 20th, but could be slightly earlier or later depending on local conditions.

The germination in the first four weeks before mechanical scarification took place shows that it is not critical to spend the extra time and effort required in this process for mid August seed lots. However, improved germination in the week following the nicking of the seed coat, especially in the two most mature seed lots from September (Leslie 2007), suggests that seed coat dormancy is an issue, especially for the more developed seeds with a harder seed coat.

Germination trials indicate that seeds become fully mature in late August, and remain viable through mid-September (Figure 2). However, because the maturation rate of seeds is variable, and this study was conducted near the northern extent of its range, the timing of cone collection should be based on the stage of cone and seed development rather than the time of year. Seeds are more easily extracted later, as cones dry out and become less sticky. Cone scales open slightly and seeds fall out, making the extraction process easier the longer you wait, but the germination potential will not increase significantly. By mid September, no further development of the seeds is expected and access to the stands may be limited due to the early onset of winter in these high elevation sites.

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References

Arno, Stephen F. 2001. Community types and natural disturbance processes. In: Tomback, Diana F.; Arno, Stephen F.; Keane, Robert E., eds. Whitebark pine communities: ecology and restoration. Washington, DC. Island Press: 74-88.

Barnhardt, Leonard. 2011. [Letter to Brendan Wilson]. January 24. On file at Selkirk College, Castlegar, BC.

Burr, Karen E.; Eramian, Aram; Eggleston, Kent. 2001. Growing whitebark pine seedlings for restoration. In: Tomback, Diana F.; Arno, Stephen F.; Keane, Robert E., eds. Whitebark pine communities: ecology and restoration. Washington, DC. Island Press: 325-345.

Callaway, Ragan M. 1998. Competition and facilitation on elevation gradients in subalpine forest of the northern Rocky Mountains, USA. Oikos. 82(3): 561-573.

Environment Canada. 2010. Canadian Climate Normals 1971-2000 [Homepage of National climate data and information archive] [online]. Available: www.climate.weatheroffice.gc.ca/climate_normals/index_e.html, [2010, March 8].

Farnes, Phillip E. 1990. SNOTEL and snow course data describing the hydrology of whitebark pine ecosystems. In: Schmidt, W. C.; MacDonald, K. J., eds. Proceedings of the symposium of whitebark pine ecosystems: Ecology and management of a high mountain resource; 29-31 March 1989 Bozemon, MT. General Technical Report INT-270. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station: 302-304.

Halstrom, Lars. 1993. Northern region genetic resource program—Whitebark pine program summary. [Homepage of Nutcracker Notes. No.2.] [online]. Available:http://www.whitebarkfound.org/Nutcracker-Notes/number2.htm [2010, March 8].

Keane, Robert E.; Morgan, P. 1994. Decline of whitebark pine in the Bob Marshall Wilderness Complex of Montana, USA. In: Schmidt, W. C.; Holtmeier, F. K., eds. Proceedings of the workshop on subalpine stone pines and their environment: The status of our knowledge, St. Moritz, Switzerland, 5-11 September 1992. General Technical Report INT-309. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station: 245-253.

Kendall, Katherine C.; Keane, Robert E. 2001. Whitebark pine decline: infection, mortality, and population trends. In: Tomback, Diana F.; Arno, Stephen F.; Keane, Robert E., eds. Whitebark pine communities: ecology and restoration. Washington, DC. Island Press: 221-242.

Lanner, R. M.; B. K. Gilbert. 1994. Nutritive value of whitebark pine seeds and the question of their variable dormancy. In: Schmidt, W. C.; Holtmeier, F. K. eds. Proceedings of the workshop on subalpine stone pines and their environment: The status of our knowledge, St. Moritz, Switzerland, 5-11 September 1992. General Technical Report INT-309. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station: 206-211.

Leslie, Adrian. 2007. Collecting and germinating whitebark pine seeds for restoration purposes in the Canadian Rocky Mountains. Kamloops, BC: Thompson Rivers University. 22 p. Thesis.

Lorenz, Teresa J.; Aubry, Carol; Shoal, Robin. 2008. A review of the literature on seed fate in whitebark pine and the life history traits of Clark's nutcracker and pine squirrels. Gen. Tech. Rep. PNW-GTR-742. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station. 62 p.

Luckman, B.; Youngblut, D. 1999. Millennial-aged trees from Banff National Park. Research Links (Parks Canada). 7(3): 15-17.

Mahalovich, M. F.; Dickerson, G. A. 2004. Whitebark pine genetic restoration program for the intermounain west (United States). In: Sniezko, Richard A.; Samman, Safiya; Schlarbaum, Scott E.; Kriebel, Howard B., eds. Breeding and genetic resources of five-needle pines: growth, adaptability and pest resistance. 2001 July 23-27; Medford, OR, USA. IUFRO Working Party 2.02.15. Proceedings RMRS-P-32 Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station: 181-187.

Mattson, D. J.; Blanchard, B. M.; Knight, R. R. 1992. Yellowstone grizzly bear mortality, human habituation and whitebark pine seed crops. Journal of Wildlife Management. 56: 432-442.

Mattson, D. J.; Kendall, K. C.; Reinhart, D. P. 2001. Whitebark pine, grizzly bears, and red squirrels. In: Tomback, Diana F.; Arno, Stephen F.; Keane, Robert E., eds. Whitebark pine communities: ecology and restoration. Washington, DC. Island Press: 121-136.

McCaughey, W. W.; Tomback, D. F. 2001. The natural regeneration process. In: Tomback, Diana F.; Arno, Stephen F.; Keane, Robert E., eds. Whitebark pine communities: ecology and restoration. Washington, DC. Island Press: 105-120.

McDonald, G.; Zambino, P.; Sniezko, R. 2004. Breeding Rust-resistant five-needle pines in the Western United States: Lessons from the past and a look to the future. In: Sniezko, Richard A.; Samman, Safiya; Schlarbaum, Scott E.; Kriebel, Howard B. eds. Breeding and genetic resources of five-needle pines: growth, adaptability and pest resistance. 2001 July 23-27; Medford, OR, USA. IUFRO Working Party 2.02.15. Proceedings RMRS-P-32 Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station: 28-50.

McKinney, Shawn T.; Fiedler, Carl E.; Tomback, Diana F. 2009. Invasive pathogen threatens bird-pine mutualism: implications for sustaining a high-elevation ecosystem. Ecological Applications. 19(3): 597-607.

McKinney, Shawn T.; Tomback, Diana F. 2007. The influence of white pine blister rust on seed dispersal in whitebark pine. Canadian Journal of Forest Research. 37(6): 1044-1057.

Murray, Michael P. 2007. Cone collecting techniques for whitebark pine. Western Journal of Applied Forestry. 22(3): 153-155.

Ogilvie, R. T. 1990. Distribution and ecology of whitebark pine in western Canada. In: Schmidt, W. C.; MacDonald, K. J., eds. Proceedings of the symposium of whitebark pine ecosystems: Ecology and management of a high mountain resource; 29-31 March 1989 Bozemon, MT. General Technical Report INT-270. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station: 54-60.

Pitel, J. A.; Wang, B. S. P. 1990. Physical and chemical treatments to improve germination of whitebark pine seed. In: Schmidt, W. C.; MacDonald, K. J., eds. Proceedings of the symposium of whitebark pine ecosystems: Ecology and management of a high mountain resource; 29-31 March 1989 Bozemon, MT. General Technical Report INT-270. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station: 130-133.

Raffa, Kenneth F.; Aukema, Brian H.; Bentz Barbara J.; Carroll, Allan L.; Hicke, Jeffrey A.; Turner, Monica G.; Romme, William H. 2008. Cross-scale drivers of natural disturbances prone to anthropogenic amplification: the dynamics of bark beetle eruptions. BioScience. 58(6): 501-517.

Resler, Lynn M.; Tomback, Diana F. 2008. Blister rust prevalence in krummholz whitebark pine: Implications for treeline dynamics, Northern Rocky Mountains, Montana, U.S.A. Arctic, Antarctic and Alpine Research. 40(1): 161-170.

R Development Core Team. 2009. R: A language and environment for statistical computing. [Homepage of R Foundation for Statistical Computing, Vienna, Austria]. [online]. Available: http://www.R-project.org [2010, March 8].

Smith, Cyndi M.; Wilson, Brendan C.; Rasheed, Salman; Walker, R.; Carolin, T.; Shepherd, B. 2008. Whitebark pine and white pine blister rust in the Rocky Mountains of Canada and northern Montana. Canadian Journal of Forest Research. 38(5): 982-995.

Sokal, Robert R.; Rohlf, F. James. 1995. Biometry: the principles and practice of statistics in biological research. 3d ed. New York: W. H. Freeman and Company. 887 p.

Tomback, Diana F.; Arno, Stephen F.; Keane, Robert E. 2001. The compelling case for management intervention. In: Tomback, Diana F.; Arno, Stephen F.; Keane, Robert E., eds. Whitebark pine communities: ecology and restoration. Washington, DC. Island Press: 3-28.

Tomback, Diana F.; Kendall, Katherine C. 2001. Biodiversity losses: The downward spiral. In: Tomback, Diana F.; Arno, Stephen F.; Keane, Robert E., eds. Whitebark pine communities: ecology and restoration. Washington, DC. Island Press: 243-262.

Vander Wall, S. B.; Hutchins, H. E. 1983. Dependence of Clark's nutcracker, *Nucifraga columbiana,* on conifer seeds during the post fledgling period. Canadian Field-Naturalist. 97(2): 208-214.

Walker, B. D.; Taylor, W. S.; Allan, D. T.; Wells, R. E. 1982. Ecosection/Ecosite descriptions. In Holland, W. D.; Coen, G. M. eds. Ecological (biophysical) land classification of Banff and Jasper National Parks. Alberta Institute of Pedology, Edmonton, AB. University of Alberta: 168-512.

Wilson, Brendan C. 2007. Status of the whitebark pine (*Pinus albicaulis*) in Alberta. Alberta Sustainable Resource Development, Edmonton, AB, Canada, Wildlife Status Report 63: 22 p.

Young, James A.; Young, Cheryl G. 1992. Seeds of woody plants in North America. Portland, OR: Dioscorides Press. 407 p.

Extended Abstract

Highlights of the Forest Health Protection Whitebark Pine Restoration Program

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Background

In 2005, Forest Health Protection (FHP) initiated a rangewide health assessment for whitebark pine (*Pinus albicaulis*). This assessment summarized the forest health condition of whitebark pine throughout its range and also documented information needs, potential restoration strategies, and challenges to restoration that need to be addressed (Schwandt 2006). This led to the creation of a national whitebark pine restoration program coordinated by FHP.

Forest Health Issues

The introduction of white pine blister rust (*Cronartium ribicola*) to fragile whitebark pine ecosystems has disrupted natural regeneration processes by rapidly killing young whitebark pine and causing mortality and reduced cone crops in mature trees. Mountain pine beetle (*Dendroctonus ponderosae*) which kills mature whitebark pine, and competition from other tree species in mixed stands also threaten long-term survival of whitebark pine ecosystems. As a result, whitebark pine populations have declined dramatically and have actually disappeared from many parts of its historic range (Schwandt 2006). For example, the Idaho Panhandle National Forest ecologist recently created a map depicting approximately 200,000 acres of suitable habitat in northern Idaho and surrounding areas where whitebark pine would have been a major stand component at some point during the past 300-500 years. Although scattered individual whitebark pines still exist in much of this area, it has completely disappeared from some areas, and current inventories show whitebark pine to be a major component on only about 4,000 acres of this historic range.

The urgency for whitebark pine restoration has recently increased due to large outbreaks of mountain pine beetle, where over 90 percent of mature trees can be killed, including those that may be resistant to white pine blister rust (Kegley and Schwandt, this proceedings). Without direct intervention the prognosis for many whitebark pine populations is bleak (Schwandt 2006; Tomback and others 2001).

Restoration Program

In 2007, the Whitebark Pine Restoration Program was initiated by FHP to provide seed money for projects that promote all phases of whitebark pine restoration. The primary goals are to protect and enhance existing whitebark pine populations, provide appropriate regeneration opportunities, and increase the proportion of whitebark pine with natural resistance to white pine blister rust.

An interdisciplinary technical committee was selected to develop a process to solicit and evaluate restoration proposals. Team members include representatives from the United States Department of Agriculture Forest Service (USFS) silviculture, FHP, genetics, and research programs, as well as the United States Department of the Interior Bureau of Land Management (BLM), the National Park Service (NPS), and universities. Proposals were solicited for six focus areas:

- Assessing whitebark pine ecosystem health (survey and monitoring)
- Harnessing natural blister rust resistance (operational cone collections)
- Conserving genetic diversity (rust screening, plus tree selection and cone collections)
- Silvicultural treatments to enhance restoration (thinning, planting, burning, etc.)
- Special whitebark pine ecosystem-related projects (nutcracker monitoring, nursery projects, mycorrhizal work, direct seeding trials) to help fill information gaps
- Education and outreach projects to increase public awareness (educational materials, publications, interpretive signs)

Proposals needed to include a brief description of the project, its geographic location, purpose, and scope as well as expected results. They also included a funding request, an explanation of how funds would be used, and what matching funds might be available. The technical committee evaluated all proposals and ranked them based on several criteria including:

- Scope of project
- Technical merit
- Measures (likelihood) of success
- Budget and cost efficiency

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Proposals for gene conservation or with broad geographic and ecological application and including matching funds received highest priority.

Program funding in 2007 and 2008 from the FHP Washington Office was $200,000 but additional FHP contributions from USFS Regions 1, 4, and 6 added an extra $67,320 in 2007 and $198,900 in 2008. In subsequent years, the base funding was reduced to $150,000 but USFS Regional contributions have more than doubled these amounts. The program is very popular and although requests far outweigh funding levels, the program has helped to fund more than 100 projects that have spent more than $3,000,000 on whitebark pine restoration projects throughout the western US (table 1).

The success of this program is largely due to the tremendous support of a wide array of cooperators that have more than doubled the total FHP investment each year. Cooperators include state and private agencies, foundations, and universities as well as over 30 national forests across five USFS regions, 10 national parks (including three in Canada), and several native American tribes. Cooperators also include a broad spectrum of environmental and hunting groups as well as several ski areas. In 2009, the Whitebark Pine Ecosystem Foundation provided $30,000 that helped fund several whitebark pine planting projects, and in 2010 the program assisted American Forest Magazine with producing a special educational article and they set aside $10,000 to assist with planting projects.

Future Plans

Although the need for whitebark pine restoration activities far exceeds the current funding levels, the current program has been instrumental in assisting with surveys, cone collections, silvicultural treatments as well as educational and special projects to promote whitebark pine restoration.

Whitebark pine is currently under consideration for listing as a threatened and endangered (T&E) species in both Canada and the United States (COSEWIC 2010, NRDC 2008). Whether listing as a T&E species helps or hinders the restoration process remains to be seen, but these activities will likely increase the level of interest in whitebark pine restoration. Regardless of the outcome of the T&E requests, successful restoration of whitebark pine will require long-term support and commitment to developing and implementing restoration strategies.

Literature Cited

COSEWIC. 2010. COSEWIC assessment and status report on the whitebark pine *Pinus albicaulis* in Canada. Committee on the Status of Endangered Wildlife in Canada. Ottawa. 55 p.

NRDC. 2008. [Online]. A petition to list the whitebark pine, *Pinus albicaulis*, as an endangered species under the Endangered Species Act. 66 p. Available at: http://docs.nrdc.org/legislation/files/leg_08120801a.pdf [2010, September].

Schwandt, J. W. 2006. Whitebark pine in peril: a case for restoration. Missoula, MT: U.S. Department of Agriculture Forest Service, Report R1-06-28.

Tomback, D. F.; Arno, S. F.; Keane, R. E. 2001. The compelling case for management intervention. In: Tomback, D. F.; Arno, S. F.; Keane, R. E., eds. Whitebark pine communities: ecology and restoration. Washington, DC. Island Press: 3-25.

Table 1. Whitebark pine restoration program funding history.

	Totals	2007	2008	2009	2010
# Proposals Received	211	56	64	52	39
$$ Requested from FHP	4,661,135	1,005,700	1,981,134	960,851	713,450
Total Matching Funds	3,824,302	850,500	1,202,290	878,532	892,980
# Projects Funded	106	24	26	35	21
Forest Health Funds	1,448,032	267,320	398,900	481,612	300,200
Match for Funded Projects	1,782,358	291,700	433,850	444,683	612,125
TOTAL FUNDS INVESTED	3,230,390	559,020	832,750	926,295	912,325

Note: This table only lists projects that were submitted to this FHP sponsored program. The FHP western bark beetle program funds approximately $200,000 annually for projects dealing with protecting whitebark pine from mountain pine beetle, and there are additional FHP Monitoring and Special Technology Development projects that focus on whitebark pine. In addition, FHP initiated a Gene Conservation Program in 2010 to collect cones from five-needle pines. FHP is currently developing a Monitoring on the Margins program to identify and monitor critical populations of high elevation pines. Many national forests and other agencies also fund projects outside the purview of this program so the totals in this table represent only a portion of all funds spent on whitebark pine each year.

Whitebark Pine Direct Seeding Trials in the Pacific Northwest

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Background

Whitebark pine (*Pinus albicaulis*) is a critical species in many high elevation ecosystems and is currently in serious decline due to white pine blister rust (*Cronartium ribicola*), mountain pine beetle (*Dendroctonus ponderosae*), and competition from other species (Schwandt 2006; Tomback and Achuff 2010; Tomback and others 2001). Many areas needing restoration are very remote or in areas where the planting of seedlings may not be logistically or politically feasible. Consequently, it is important to determine if direct planting of seeds is practicable and which treatments enhance germination and chances of survival.

Collecting seed and growing whitebark pine seedlings is an expensive, complex and labor-intensive process that takes several years (Burr and others 2001; Farmer 1997). There is limited information related to direct seeding, but McCaughey (1990) studied regeneration of whitebark pine seed under three shade levels, three seedbed types, two sowing types and four predator exclusion levels. He found germination increased with shade cover and planting depth and was significantly higher on exposed mineral soil than litter or burned seedbeds. Seeds sown on the surface and not protected by rodent exclosures were all eaten by rodents.

Recent advancements in seed treatments have greatly improved germination success in nurseries, but have not been tested in the field. Direct seeding field trials to test these seed treatments, as well as rodent repellants, were established on two sites in late fall of 2005 and 2006, and four additional trials were installed in the fall of 2009. Results from these and additional tests may greatly improve the cost efficiency and feasibility of whitebark pine restoration across its range.

Objectives

The objectives of our direct seeding trials were:

- to develop techniques for direct sowing of whitebark pine seeds,
- to determine the germination success of seeds and survival of seedlings,
- to compare the survival of seedlings from directly planted seeds with that of outplanted nursery-grown seedlings in the same study areas; and
- to compare germination success of 3-seed caches with individual seeding.

Methods

Test sites were selected across the West and were in typical whitebark pine habitats with easy access that had recently experienced either natural or prescribed fire. The 2005 test site was a harsh, exposed site on Vinegar Hill near Baker City, OR (figure 1). The 2006 test site was a more mesic site on Mt. Bachelor near Bend, OR (figure 2). The 2009 sites were: Fairy Lake on the Gallatin National Forest near Bozeman, MT (figure 3), Thompson Peak on the Lolo National Forest near Plains, MT (figure 4), Ulm Peak on the Idaho-Montana state line west of Thompson Falls, MT (figure 5), and Gold Pass on the Idaho-Montana state line west of St. Regis, MT (figure 6).

Approximately 1000 seeds, collected from local seed sources, were planted at each site in a randomized complete block design with five replicates of eight treatments of 20 seeds per treatment. Treatments included: a 30-day warm stratification, scarification by sanding, a combination of warm stratification plus scarification, and control. The two early trials included three seed treatments to control rodent predation (using Thiram®, Ropel®, and hot pepper). At the Mt. Bachelor site, some of the seeds were planted in small peat pots to test the effect of improved moisture availability on germination and survival. The 2009 trials also included a

Figure 1. Vinegar Hill installation (November, 2006) with logs for shade.

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Figure 2. Mt. Bachelor site, installed September, 2007.

Figure 3. Fairy Lake installation (September, 2009) using snags and standing trees for shade.

Figure 4. Thompson Peak installation (September, 2009) using logs for shade.

Figure 5. Ulm Peak installation (September, 2009) using snow fence for shade.

Figure 6. Gold Pass installation (September, 2009) using snow fence for shade.

Figure 7. Germinating seedlings from 3-seed cache next to dead planted seedling at Thompson Peak site (July, 2010).

Figure 8. Row of germinating warm-stratified seed at Gold Pass (July, 2010).

planting of three-seed caches next to two-year old seedlings (figure 7).

Survival of germinants may be an even bigger challenge than enhancing germination; so half of the treatments were protected from rodent predation by hardware cloth cages. In addition, all treatments were placed behind logs (figures 1, 4), snow fences (figures 5, 6), or standing trees and snags (figure 3) to provide shade.

Installation of these trials was accomplished by U.S. Forest Service District and Forest Health Protection personnel. Germination and survival will be documented each spring and fall for all sites for at least three years.

Results

2005 and 2006 Trials

The majority of seed germination occurred the first spring following planting for all treatments. Some germination did occur the second year, especially for the control and scarification treatments, but no seeds germinated after two years. Warm stratification significantly improved germination, especially the first year at both sites. Seed scarification improved germination somewhat but did not improve on the warm stratification, even when combined with it. The rodent repellants appeared to have no positive effect and actually reduced germination in some replicates. The peat pots tended to be more of a source of curiosity for the rodents than a deterrent as many were dug up and scattered across the hillside.

Under the harsh conditions at Vinegar Hill, 43 percent of the warm-stratified seeds germinated, and 25 percent of the seeds that were both scarified and warm-stratified, germinated. The scarify only and control treatments had 20 percent and 17 percent germination respectively (table 1). There was very little evidence of rodent predation, and seeds treated with rodent repellants had less germination than the uncaged controls. Only 20 percent of all seeds germinated, and most of the seedlings were killed by heat shortly after they emerged. After three years, only 16 percent of seedlings were still alive, which is only two percent of the total seeds planted.

Germination and survival at Mt. Bachelor was much higher but followed the same pattern as Vinegar Hill. Germination of the caged warm-stratified seeds was over 70 percent; the caged warm-stratified plus scarified seeds was 56 percent; the scarified seeds was 43 percent; and the caged control was 51 percent (table 2). Although micro-site was very important to seedling survival, shade logs had little or no effect on germination and survival. However, survival at the Mt. Bachelor site was much greater on cooler, northern aspects (25 percent) than hotter aspects (<3 percent). Survival was considerably greater for caged seeds at both sites.

Preliminary Results From 2009 Trials

Germination by the end of July, 2010, at all four sites followed the same pattern found at the Mt. Bachelor and Vinegar Hill, except that the cages did not have a noticeable

Table 1. Annual percent germination by treatment at Vinegar Hill (planted November, 2005).

Treatment (100 seeds each)	2006	2007	2008	Total % germinated
Warm stratification (caged)	38.0	5.0	0.0	**43.0**
Warm stratification & scarified (caged)	25.0	0.0	0.0	**25.0**
Scarified only (caged)	11.0	9.0	0.0	**20.0**
Control (caged)	9.0	8.0	0.0	**17.0**
Control (no cage)	5.0	4.0	0.0	**9.0**
Thiram® rodent repellant (no cage)	6.0	5.0	0.0	**11.0**
Hot pepper (no cage)	0.0	7.0	0.0	**7.0**

Table 2. Annual percent germination by treatment at Mt. Bachelor (planted October, 2006).

Treatment	No. germinated	2007	2008	2009	Total % germinated
Warm stratification (no cage)	78	39.0	0.0	0.0	**39.0**
Warm stratification (caged)	144	71.0	1.0	0.0	**72.0**
Warm stratification with peat pot (no cage)	104	48.0	4.0	0.0	**52.0**
Warm stratification & scarified (caged)	112	50.0	6.0	0.0	**56.0**
Scarified only (caged)	86	30.0	13.0	0.0	**43.0**
Control (caged)	102	25.0	26.0	0.0	**51.0**
Control (no cage)	50	22.0	3.0	0.0	**25.0**
Ropel® rodent repellant	36	18.0	0.0	0.0	**18.0**
Ropel® rodent repellant in peat pot	16	8.0	0.0	0.0	**8.0**
Hot pepper (no cage)	20	9.0	1.0	0.0	**10.0**

effect on germinant survival at this early stage in the study. Germination of the warm stratified and warm plus scarified seeds at Gold Pass and Thompson Peak varied from 46 to 64 percent while germination of the scarified only and control seeds were less than half these levels (table 3). Germination of warm and warm-scarified seeds at Ulm Peak was 50.5 and 41.5 percent, respectively, while germination of the scarified only and control seeds was only 5.5 and 3.5 percent, respectively. The Fairy Lake site had very poor germination for all treatments, but germination of the warm-stratified and warm-scarified seeds (18-22 percent) was still much better than the scarified only (6 percent) or control seed treatments (7 percent).

Although the warm-stratified treatment outperformed all the other treatments, it is still premature to recommend this treatment since additional germination can be expected for at least one more year, and this treatment may have an effect on survival that has not been evaluated as yet. With the exception of the Thompson Peak site where 85 percent of the 3-seed caches had some germination by the end of July 2010, very few of these caches had any germination the first year. However, these seed were not treated, so they may not germinate until the second year.

Future Plans

Additional monitoring will be needed to better determine if the preliminary differences continue to hold up over time. The 2009 trials will be remeasured in the fall of 2010, and in the spring and fall of 2011, to document additional germination as well as mortality. Three additional trials were installed in the fall of 2010:

- Toboggan Ridge above the Lochsa River on the Clearwater National Forest in ID
- Yellowstone Club ski area near Big Sky, MT
- Southeast side of Mt. Hood in OR.

The Idaho and Montana installations included a ectomycorrhizal treatment developed by Montana State University (Mohatt and others 2008) on some of the seed as well as some of the seedlings. Additional sites in other areas may be added in the future to determine which treatments provide the best germination and survival across the range of whitebark pine.

Table 3. Average percent germination by treatment and site.

Site\Treatment	Warm Stratification	Warm Stratification + Scarify	Scarify Only	Control	Total germination
Gold Pass	64.0	46.0	23.5	20.5	38.5
Thompson Peak	53.0	54.0	20.5	22.0	37.4
Ulm Peak	50.5	41.5	5.5	3.5	25.3
Fairy Lake	22.0	18.0	6.0	7.0	13.3
Average germination	**47.4**	**39.9**	**13.9**	**13.3**	**28.6**

Literature Cited

Burr, K. E.; Eramian, E.; Eggleston, K. 2001. Growing whitebark pine seedlings for restoration. In: Tomback, D. F.; Arno, S. F.; Keane, R. E., eds. Whitebark pine communities: ecology and restoration. Washington, DC: Island Press: 325-345.

Farmer, R. E. 1997. Seed ecophysiology of temperate and boreal zone forest trees. Delray Beach, FL. St. Lucie Press.

McCaughey, W. W. 1990**.** Biotic and microsite factors affecting *Pinus albicaulis* establishment and survival. Bozeman, MT: Montana State University. Dissertation.

Mohatt, K.; Cripps, C. L.; Lavin, M. 2008. Ectomycorrhizal fungi of whitebark pine (a tree in peril) as revealed by sporocarps and molecular analysis of mycorrhizae from treeline forests in the Greater Yellowstone Ecosystem. Canadian Journal of Botany. 86: 14-25.

Schwandt, J. W. 2006. Whitebark pine in peril: a case for restoration. Missoula, MT: U.S. Department of Agriculture Forest Service, Report R1-06-28.

Tomback, D. F.; Achuff, P. 2010. Blister rust and western forest biodiversity: ecology, values and outlook for white pines. Journal of Forest Pathology. 40: 186-225.

Tomback, D. F.; Arno, S. F.; Keane, R. E. 2001. The compelling case for management intervention. In: Tomback, D. F.; Arno, S. F.; Keane, R. E., eds. Whitebark pine communities: ecology and restoration. Washington, DC: Island Press. 3-25.

Guidelines for Whitebark Pine Planting Prescriptions

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Abstract—Whitebark pine (*Pinus albicaulis*) is a keystone species in high-elevation ecosystems of the western United States. Unfortunately many fragile subalpine ecosystems are losing whitebark pine as a functional community component due to the combined effects of an introduced disease, insects and succession. Planting whitebark pine is one part of a multifaceted restoration strategy (Keane and Arno 2001). Once seedlings are established, they have the potential to be a long term seed source where existing trees have been lost. The practice of growing and planting whitebark pine is relatively new compared to traditional conifers, and with the high cost of cone collection and seedling production, survival is particularly important. This paper describes the planting guides created by Scott and McCaughey (2006) and further refined by McCaughey and others (2009). The planting guidelines should help increase survival making wise use of limited funds, and further the restoration of whitebark pine.

Ecological Environment

Whitebark pine is adapted to a wide range of ecological conditions however it has a specialized niche with a distinct competitive advantage on windswept ridge tops, shallow soils, and high elevation sites. It is typically a pioneer species in the more mesic portions of its range, and it is successional to shade tolerant species such as subalpine fir (*Abies lasiocarpa*) and Engelmann spruce (*Picea engelmannii*). In the drier portions it maintains itself in a self-perpetuating climax species. In the Northern Rockies, it is present on a variety of habitat types defined by Pfister and others (1977) although it is most common as a long lived seral on the *Abies lasiocarpa-Pinus albicaulis/vaccinium scoparium* and *Abies lasiocaropa/Luzula hitchcockii* types (Arno and Hoff 1989).

Whitebark pine is most successful in establishing where there is a gap in the forest canopy (Arno and Weaver 1990, Larson and Kipfmueller 2010). It appears to be relatively shade intolerant, with less tolerance than subalpine fir and spruce and more tolerance than lodgepole pine (*Pinus contorta*) (Arno and Hoff 1989). Larson and Kipfmueller (2010) found seedlings, but few saplings, under a subalpine overstory but there were established saplings in canopy breaks. Izlar (2007) found fewer whitebark pine where it was outcompeted by faster growing lodgepole pine, spruce and Douglas-fir. When whitebark pine and lodgepole pine coexisted, Moody (2006) found whitebark pine to be below the dominant lodgepole pine canopy layer.

The presence of ground vegetation has a strong effect on the ability for whitebark pine to establish. Seedlings planted in the presence of grouse whortleberry (*Vaccinium scoparium*) had higher survival and growth than if planted in bare ground or other vegetation (Perkins 2004). Grouse whortleberry likely produces positive effects from reduced evapotranspiration, but the greater benefits may be from mycorrhizal relationships or other beneficial below ground interactions. Seedlings did not survive well when planted with sedges or similar ground vegetation and were especially outcompeted by species such as beargrass (*Xerophyllum tenax*) which has a tough fibrous root system.

Whitebark pine grows in cold, windy, snowy climatic zones (Arno and Hoff 1989). On these relatively harsh sites, planted seedlings survive best when they are protected by microsites which reduce the light intensity and stem heating (Izlar 2007) and also moderate cold conditions. Young seedlings, while drought resistant, are not frost resistant (McCaughey 1994) further emphasizing the benefits of microsites. Planted seedlings that were protected from moving snow and soil also survived better (Izlar 2007). In areas where soil movement was occurring, planted seedlings were protected by large stable material uphill from the planted seedling; the material caused moving snow and soil to be redirected away from the seedling. Material below the seedling however caused soil to "pool" around the seedlings, partially covering it.

Guidelines for Planting Prescriptions

The following planting guides presented by McCaughey and others (2009) incorporate the ecological and adaptive properties of whitebark pine into tree planting prescriptions to optimize survival and establishment and develop stands for long term restoration.

1. Plant large, hardy seedlings with good root development. Good tree vigor and fibrous roots systems give the seedlings the best advantage on harsh sites.
2. Reduce overstory competition to increase light and day length to improve the effective growing season.
    a. Whitebark pine is relatively shade intolerant requiring open conditions to establish and grow well.
    b. In early seral stages, whitebark pine does not tend to dominate and create wide crowned individuals because

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of competition and crowding from faster growing species.

3. Emphasize planting in areas where whitebark pine is growing or is known to have grown in the past.
    a. Avoid planting in areas where other species are establishing because they tend to outcompete whitebark pine seedlings. For example, burned lodgepole pine stands typically regenerate quickly with high seedling density that will rapidly outcompete whitebark pine seedlings.
    b. Do no plant in 'mixed plantings' with other conifers. Whitebark pine can be easily outcompeted by faster growing tree species such as lodgepole pine, Douglas-fir and Engelmann spruce. Whitebark pine is slow growing and terminal growth will slow when shaded.
4. Reduce most understory vegetation especially grasses and sedges to reduce competition for available soil moisture.
    a. Do not aggressively remove grouse whortleberry during site preparation. If grouse whortleberry is not present, a planting spot with bare mineral soil is the best alternative.
    b. Avoid areas of highly competitive vegetation. For example avoid beargrass areas as it is an extremely hardy, competitive plant, and has a very tough and fibrous root system making it difficult for planting any type of tree.
5. Consider ridge tops or exposed slopes which are generally the most suitable for planting. Avoid planting in swales or frost pockets considering the topographic position as well as the actual planting spot. Gopher activity increases where soils are deeper thus increasing mortality of planted trees. Young whitebark seedlings do not appear to be frost hardy during certain times of the growing season.
6. Provide microsites for newly planted trees to improve water utilization, reduce light intensity and stem heating, and protect the seedlings from wildlife trampling. A favorable microsite is one of the most critical conditions for survival. Stumps, rocks, and large logs are favorable microsites. Large material uphill from the planted seedling protects it from moving snow and soil, but microsites that are downslope of seedlings can cause soil to pool and partially bury seedlings. Microsites should be stable and not able to roll over or onto seedlings.
7. Avoid planting seedlings next to tall snags. Dead trees will, in time, fall. There are several reports of seedlings being uprooted in the root ball of falling trees. Downed trees or broken off snags are better microsite choices.
8. Do not overcrowd planted trees to avoid long-term inter-tree competition. Open grown trees produce the largest crowns and the most cones; tree form is not important. Adjust spacing guides based on expected survival. For example if the prescription is for 100 live seedlings per acre (247 per hectare) and typical survival is 50 percent, then the planting density should be 200 trees per acre (494 trees per hectare) with spacing averaging 15 ft x 15 ft (4.5 m x 4.5 m).
9. Plant when there is adequate soil moisture. Summer and fall planting may avoid the need for long expensive snow plows and delayed entry due to heavy spring snow loads, however recent dry summers may be limiting the summer plant window.

Additional observations

The best chance for success in restoring and maintaining whitebark pine is from planting seedlings with blister rust resistance. Cones should be collected from trees expressing resistance using criteria established by Mahalovich and Dickerson (2004) as a first but critical step towards improving rust resistance. The Forest Service has an aggressive blister rust resistance breeding program, and are establishing seed orchards. We hope the orchards will be producing rust resistant seed for many seed zones in Montana and Idaho in the next five to six years (Mahalovich 2010).

Nursery managers in the western U.S. have been producing increasingly better quality whitebark pine seedlings. Seedlings are generally grown in a large container for two growing seasons; a 10 in^3 container is most common. These larger containers allow for extensive root development which whitebark pine needs, while two growing seasons allow seedlings to develop height and larger caliper. Managers should continue testing various containers and cultural practices to grow target seedlings prescribed for varying site conditions. There is promising research on the benefits of inoculating seedlings with beneficial mycorrhizae, and practices are being developed for seed scarification which will enhance germination success and reduce handling and contamination. As an alternative to planting, seeding trials are in progress to more easily artificially reforest whitebark pine in hard to access areas.

Conclusion

Silviculturists are planting whitebark pine as one tool for whitebark pine restoration. Planting prescriptions for whitebark pine are similar to those for other species on harsh sites; however, whitebark pine grows in ecosystems typically avoided for planting with other conifers. Incorporating these planting guides should help enhance survival and establishment success. With proper attention to planting prescriptions, improved genetic rust resistance, and healthy tree stock, we can augment blister rust resistance and survival of planted trees where natural seed sources are limited. These planting guides should continually be updated based on research and monitoring of planted whitebark pine.

References

Arno, Stephen F.; Weaver, Tad. 1990. Whitebark pine community types and their patterns on the landscape. In: Schmidt, Wyman C. (proj. ldr.). Proceedings—Symposium on Whitebark pine ecosystems: Ecology and management of a high-mountain resource. 1989; Bozeman, MT. Gen Tech. Rep. INT-270.

Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station: 97-105.

Arno, Stephen F.; Hoff, Raymond J. 1989. Silvics of whitebark pine (*Pinus abicaulis*). Gen. Tech. Rep. INT-253. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station. 11 p.

Izlar, Deborah Kay. 2007. Assessment of whitebark pine seedling survival for Rocky Mountain plantings. Missoula, MT: University of Montana, MT. 76 p. Thesis.

Keane, R. E.; Arno, S. F. 2001. Restoration concepts and techniques. In: Tomback, D. F.; Arno, S. F.; Keane, R. E., tech. eds. Whitebark pine communities: Ecology and restoration. Island Press, Washington, DC: 367-400.

Larson, Evan R.; Kipfmueller, Kurt F. 2010. Patterns in whitebark pine regeneration and their relationship to biophysical site characteristics in southwest Montana, central Idaho, and Oregon, USA. Canadian Journal of Forestry Research. 40: 476-487.

Mahalovich, M. F.; Dickerson, G. A. 2004. Whitebark pine genetic restoration program for the Intermountain West (USA). In: Sniezko, R. A.; Samman, S.; Schlarbaum, S. E.; Kriebel, H. B. (eds). Proceedings—Breeding and genetic resources of five-needle pine: growth, adaptability and pest resistance; 2001. Medford, OR. Proc. RMRS-P-32. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station: 181-187.

Mahalovich, Mary Frances. 2010. [Personal communication]. April 26. Moscow, ID: U.S. Department of Agriculture, Forest Service, Northern Region.

McCaughey, Ward. 1994. Silvicultural treatments and whitebark pine plantation and regeneration trial results. In: Kendall, K. C.; Coen, B.; Keane, B.; Donner, B.; Brewer, K., tech coords. Proceedings—Research and management in whitebark pine ecosystems 1994. West Glacier, MT: 35-40.

McCaughey, Ward; Scott, Glenda L.; Izlar, Kay L. 2009. Whitebark pine planting guidelines. Western Journal of Applied Forestry. 24(3): 163-166.

Moody, Randall John. 2006. Post-fire regeneration and survival of whitebark pine (*Pinus albicualis* Engelm.). Vancouver, British Columbia. 108 p. Thesis.

Perkins, Judy L. 2004. *Pinus albicaulis* seedling regeneration after fire. Missoula, MT: University of Montana. 144 p. Thesis.

Pfister, R. D.; Kovalchik, B. L.; Arno S. F.; Presby, R. C. 1977. Forest habitat types of Montana. Gen. Tech. Rep. INT-GTR-34. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station. 174 p.

Scott, Glenda L., McCaughey, Ward W. 2006. Whitebark pine guidelines for planting prescriptions. In: Riley, L. E.; Dumroese, R. K.; Landis, T. D., tech cords. National Proceedings: Forest and Conservation Nursery Associations—2005; Park City, UT. Proc. RMRS-P-43. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station: 84-90.

Limber Pine Seed and Seedling Planting Experiment in Waterton Lakes National Park, Canada

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Abstract—Limber pine plays an important role in the harsh environments in which it lives, providing numerous ecological services, especially because its large, wingless seeds serve as a high energy food source for many animals. Limber pine populations are declining due to a combination of white pine blister rust, mountain pine beetle, drought, and fire suppression. Outplanting of seedlings is a common strategy to aid in restoration efforts, but the success of revegetation methods in limber pine habitats is little known. To aid in restoration efforts in Waterton Lakes National Park, in southwestern Alberta, and other impacted areas, we studied the survival of limber pine planted as seeds and those planted as seedlings. At our experimental site, 11 percent of the seeds had germinated and seedlings were still alive after three years, while 72 percent of the seedlings that were planted directly survived. Restoration efforts are likely to have greater success when limber pine is planted in groups of five as seedlings rather than as seeds and there may be benefit to planting seedlings in burned areas near cover such as rocks or stumps.

Introduction

Limber pine (*Pinus flexilis*) is a distinctive five-needled white pine that grows as individual trees (up to 12 m), in clusters of trees, or in krummholz form. These trees sometimes reach ages of 1000 years or more (Schoettle 2004a). Its range extends from southwestern Alberta and southeastern British Columbia to New Mexico, Arizona and eastern California, with notable outliers in the Dakotas, Nebraska, eastern Oregon and southwestern California (Steele 1990). It generally occurs on exposed ridges across a wider range of elevations, from 870 m to 3810 m, than any other tree in its range.

While limber pine is not economically important for timber, the species is ecologically vital. In the harsh environments where it grows, limber pine provides wind amelioration, shade and snowdrift accumulation to facilitate other species (Baumeister and Callaway 2006). Limber pine is an effective pioneer species, colonising disturbed areas after fires or avalanches (Donnegan and Rebertus 1999). Once established, it serves as a nurse tree for a variety of shade-tolerant tree species, which eventually out-compete the shade-intolerant limber pine as the habitat nears successional maturity (Baumeister and Callaway 2006, Donnegan and Rebertus 1999).

The large, wingless seeds of limber pine serve as a high energy food source for a variety of animals, including red squirrels (*Tamiasciurus hudsonicus*) (Hutchins and Lanner 1982), grizzly bears (*Ursus arctos*) (Kendall 1983), black bears (*U. americanus*) (McCutchen 1996), and a host of bird species, such as Clark's nutcrackers (*Nucifraga columbiana*) (Benkman and others 1984, Schoettle 2004a, Schoettle and Negron 2001). Limber pine cones open when mature (Benkman and others 1984), providing birds and mammals with easy access to large seeds. Clark's nutcrackers, in particular, store seeds for later use in caches of from 1-5 seeds each (Lanner and Vander Wall 1980), buried 2-3 cm in the ground. Many buried seeds that remain uncollected germinate and grow into trees. Propagation of the species in this manner is one of the few ways in which limber pine is disseminated, and accounts for its having evolved with cones that expose seeds upon maturity (Tomback and others 1990).

Limber pine forests, particularly in the central and northern parts of the species range, are declining due to a combination of white pine blister rust (*Cronartium ribicola*), a non-native fungus that severely affects all five-needled pines (Gautreau 1963, Kearns and Jacobi 2007, Schoettle and others 2008), mountain pine beetle (*Dendroctonus ponderosae*) (Kearns and Jacobi 2007, ASRD and ACA 2007), drought (Kendall and others 1996, Achuff 1997), and fire suppression (Schoettle 2004a, 2004b). In Montana, considerable mortality has also been associated with the needle pathogen *Dothistroma septospora* (Jackson and Lockman 2003).

In Waterton Lakes National Park (WLNP), in southwestern Alberta, 78 percent of limber pine trees surveyed in 1995-96 were infected, and rust had already killed at least 45 percent of surveyed trees (Kendall and others 1996, Kendall 2003). Regeneration in most stands was poor, and many seedlings were already infected with the rust fungus and they probably will never reach maturity. Based on these and other surveys, limber pine was listed as an Endangered species under *The Wildlife Act* in Alberta in 2008 (Government of Alberta 2010).

As limber pine populations decline in health and size, a range of restoration options have been proposed, which include proactive (before rust arrives) and reactive (after rust arrival). Proactive actions include creating regeneration opportunities by maintaining a mosaic of mixed age classes across the landscape (Schoettle and Sniezko 2007); increasing the frequency of rust-resistant traits in the population (Schoettle and others 2009); and reducing pest populations

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(Schoettle and Sniezko 2007). Active management such as protecting putatively resistant trees from mountain pine beetle attack (Schoettle and others 2008); testing these trees for genetic resistance; collecting seed, and; outplanting seedlings (Burns and others 2008) have also been proposed.

Outplanting of two- or three-year old seedlings has been generally recommended as being more desirable than planting seeds but the potential survivorship and long-term success rate of either revegetation method has largely been untested for the high elevation 5-needle pines (see Schwandt and others, this proceedings, for recent experiments with whitebark pine, *Pinus albicaulis*). Collecting limber pine seed is a labour-intensive process (Ward and others 2006), and thus expensive, making seeds precious. Growing seedlings is also an expensive and complex process (Burr and others 2001). The primary argument in favor of planting seeds is that it is more cost effective: less technical expertise and fewer facilities are required, and there is no two-to-three year delay waiting for seedlings to germinate and grow in the nursery. Planted seeds may be susceptible to predation by small rodents or birds.

Our objective was to compare the survivorship and health of limber pine planted as seeds and as seedlings under an array of microsite conditions. We hypothesized that the planted seedlings would have better survival and health than sown seeds.

Methods

Study Site Description

The study site was located in WLNP (49°3'N, 113°47'W) on a morainal ridge at an elevation of 1650 m. The area is moderately well drained with an Orthic Black Chernozemic soil. The slope was negligible. Prior to a wildfire in 1998, limber pine was the dominant tree species on the ridge. The stand was determined to be approximately 90 years of age and was rated as mature prior to the fire (Achuff and others 2002). The fire killed the majority of the limber pine trees, and now the site is dominated by early successional, post-disturbance vegetation.

The site had both burned and unburned areas. Several young limber pine trees were very small and growing only in the unburned area. The ground cover consisted of common juniper (*Juniperus communis*) and bearberry (*Arctostaphylos uva-ursi*), with several other grass and forb species. The burned area had less ground cover, with bearberry and small junipers growing sparsely. There was more grass growing on the burned area than on the unburned area, but total cover was less than the unburned area. The site was exposed to full sun with no shade being cast by anything other than a few limber pine snags and rocks.

Material

The limber pine seeds were collected in September 1999, in Glacier National Park, Montana, approximately 50 km southeast of the planting site, and sent to the U.S. Forest Service Tree Nursery in Coeur d'Alene, ID. The seeds were sown in 2000 and propagated following techniques outlined in Landis and others (1999). Prior to sowing, the seeds were x-rayed and the fill rate was 60 percent, which is analogous to the expected germination rate (McLaughlin, personal communication). The seedlings were three years old when planted. Seedlings were stored at 0°C until one month prior to planting.

Planting and Monitoring Protocol

In 2003, we planted 3-yr seedlings and sowed seeds at the site. A total of 345 seedlings were planted in 101 clusters in October, 2003. A total of 340 seeds were also planted in 100 caches in October of 2003. Seeds and seedlings were planted under the following paired treatments: (1) burned vs. unburned, (2) protected vs. unprotected, (3) near vegetation vs. in the open, and (4) 1, 3 or 5 seeds per cache or seedlings per cluster (table 1). Five replicates of each treatment combination were planned, however, due to a lack of enough seedlings and sufficient unburned area, several treatments were not completed (table 1).

Table 1. Matrix of treatment type and number of seeds/seedlings planted. The total sample size was 340 seeds and 345 seedlings. Number of replicates of each treatment is in parentheses. Zeros indicate that there were no plantings of that particular combination.

		Burned		Unburned	
Cluster/cache size	**Open/near vegetation**	**Protected**	**Unprotected**	**Protected**	**Unprotected**
1 seed	Near veg.	5 (5)	5 (5)	0	0
1 seed	Open	5 (5)	5 (5)	0	0
3 seeds	Near veg.	15 (5)	15 (5)	15 (5)	15 (5)
3 seeds	Open	15 (5)	15 (5)	15 (5)	15 (5)
5 seeds	Near veg.	20 (4)	25 (5)	25 (5)	20 (4)
5 seeds	Open	30 (6)	25 (5)	25 (5)	30 (6)
1 seedling	Near veg.	5 (5)	5 (5)	0	0
1 seedling	Open	5 (5)	5 (5)	0	0
3 seedlings	Near veg.	3 (1)	21 (7)	0	18 (6)
3 seedlings	Open	21 (7)	21 (7)	15 (5)	21 (7)
5 seedlings	Near veg.	5 (1)	50 (10)	5 (1)	25 (5)
5 seedlings	Open	35 (7)	35 (7)	25 (5)	25 (5)

Figure 1. Photo-degradable netting used to protect seedlings from herbivory.

Figure 2. Hardware cloth used to protect seeds from herbivory and pilfering.

Plantings were within 1-m^2 plots within the sites to aid in re-locating them during monitoring. Each cache or cluster was marked with a numbered tag. Maps of the planting area were made, with codes for each treatment type. Seedlings were planted by digging a hole that was deep enough (approximately 20-25 cm) to allow the top of the soil plug to be flush with the surrounding soil level, while ensuring that roots were not bent or "j-rooted." The root balls were loosened by hand before planting, and were tamped in carefully with excavated soil to ensure that no air pockets were next to the roots. Seeds were planted at a depth of approximately 3 cm to mimic the depth of a typical Clark's nutcracker cache (Lanner and Vander Wall 1980). Seeds were then covered with soil so that no mounding was visible.

Fifty-three seed caches and 37 seedling clusters were physically protected from herbivory and pilfering with photo-biodegradable plastic netting for seedlings (figure 1) and with steel wire mesh with 0.64-mm grid, called "hardware cloth," for seeds (figure 2). The netting was cut into 15-cm lengths and stretched over the top of the seedlings to completely cover them. The hardware cloth was cut into 20-cm x 20-cm squares with the edges bent approximately 2 cm into the ground to prevent small mammals from digging under the cloth and pilfering seeds. The square was affixed to the ground using 6-cm long aluminum fence staples. In two instances large sheets of hardware cloth, measuring approximately 1 m x 60 cm, were also used to protect six caches together.

Seeds were cached and seedlings planted in either an open, exposed location or near natural objects (either existing rocks or vegetation, or rocks and downed woody debris were placed in their vicinity). Natural objects were positioned within 5-10 cm of the seedlings or seeds and were approximately the same height as the seedlings. Rocks and vegetation were situated to protect the seeds and seedlings from the prevailing southwest wind.

Seeds and seedlings were planted in groups of 1, 3 or 5, mimicking the natural caching behaviour of Clark's nutcracker (Lanner and Vander Wall 1980). The numbers of seeds (caches) and seedlings (clusters) planted were randomly assigned.

The site was monitored weekly from May 7 to August 31 in 2004, and May 18 to August 31 in 2005. In 2006, monitoring occurred bimonthly, starting on May 17 and ending on August 31. Data were not collected for each individual seed or seedling, but rather for each cache or cluster. The emergence of seedlings and the number of seedlings emerged was noted for each seed cache. Then seedlings, whether planted as seeds or seedlings, were monitored for growth and survivorship. The number of seedlings in each cluster was counted and the height of the tallest seedling in the cluster was measured in centimetres. The measurement was made from the ground surface to the tip of the upper bud, needles extending past the bud were not included in the measurement. The overall health and vigor of the majority of the seedlings in each cluster was rated by assigning each cluster to one of the following two categories: healthy (only green needles present) or unhealthy (dead with no needles or only brown needles present, or alive with high number of brown needles or flagging). From these categories, dead vs. live and healthy vs. unhealthy were used in subsequent analyses, described below.

Statistical Analyses

We analyzed seedling survival or seed germination data using logistic regression. Our binomial response variables were (a) seedling survival to the end of monitoring and (b) seed germination. Because the pattern of germination was non-linear in relation to cache size, we treated cache size as a categorical variable.

We analyzed the survival of individuals, but we expected the survival of individuals in the same cache or cluster would be correlated. To account for this correlation in the analyses, we included a random intercept (Breslow and Clayton 1993) using *xtlogit* with a random intercept in Stata 8.2 (StataCorp 2003). In 11 cases seeds germinated, but there was no follow-up information to indicate when the seedling subsequently died. These cases were excluded from the survival analysis, but included in the germination analysis.

Seedling health was assessed for each cluster of seedlings based on whether the seedlings were healthy (0) or unhealthy (1). The health rating at the end of 2006 was used to assess the effects of the covariates (planted as seed or seedling, number planted, burned or unburned, protected or unprotected, exposed or near objects) on seedling health. We used the 2006 data because it was at the end of monitoring. All of the clusters with seedlings had a rating of 0 or 1 so logistic regression was used in the analysis. Because clusters were planted in smaller plots within the site (plots were sometimes separated by many meters) the clusters were not necessarily independent, so we used plot as a grouping variable (random intercept) in *xtlogit* (StataCorp 2003).

The height of the tallest seedling in each cluster was measured regularly through each year. We used the growth during 2006 (final measurement minus the first measurement). The data were not normally distributed because many values were close to zero. Data were analysed with Poisson, using *poisson* and *xtpoisson* (StataCorp 2003).

Results

Seed emergence was first observed on June 10, 2004, eight months after planting. Of the 338 seeds that were planted, 144 (43 percent) germinated by the end of 2006. Of these, 136 seeds had germinated in 2004, eight germinated in 2005, and no seeds germinated in 2006. There were no significant differences in germination among the different cache sizes (table 2), but the trend was that a greater proportion of the seeds in three-seeded caches germinated than in one- or five-seeded caches (figure 3). The measure of correlation within clusters (*Rho*) was significant, indicating there is significant correlation of the response within clusters.

Of the 354 seedlings planted, over 28 percent (100 seedlings) had died by the end of monitoring in 2006 (table 3). In contrast, of the 133 seeds that germinated for which we had information about their longevity, 96 (72 percent) had died by the end of monitoring in 2006. Data on seedlings from both origins (seed or seedling) were combined in the first analysis, then seedlings from the two origins were analysed separately (table 4). The strongest effect on seedling survival was their origin (sown as a seed or planted as a seedling). Seedlings showed first-year survival of 85 percent when planted as seedlings as compared to 65 percent when planted as seeds. The only other significant variable was the number of seeds/seedlings planted. Survival increased with the number of seeds/seedlings in the cluster (figure 3). When the data were split by origin, the number planted was only significant for the seedling data. There was a trend towards an effect of exposure on survival of the combined data; seedlings in the open had a greater probability of dying than those near cover.

Analysis of the seedling health initially combined seedlings sown as seeds and those planted as seedlings before analysing these separately (table 5). Seedlings generated from field-sown seed had a better health rating than those planted as seedlings (origin variable in table 5). The results from both the combined data and the seedling data suggest that seedlings are healthier in larger clusters and in burned sites (figure 4). There were no significant effects in the analysis of seedlings from seeds, suggesting that the significant effects seen in the combined data (number planted and burned) are the result of effects on the individuals planted as seedlings. In contrast to the seedling data, there was no effect of the number of seeds planted on health of the seed

Table 2. Seed germination analysis using logistic regression. The table includes coefficient for each covariate, their standard errors, and the probability that the coefficients differ from 0. The reference categories (dummy variable=0) were seeds, burned, protected, and near vegetation. *Rho* is the proportion of the total variance contributed by within-group (cluster) correlation. The *p* value for *Rho* is a test of whether *Rho* differs from zero, suggesting that including the grouping (shared frailty) is appropriate.

Covariate	Percent mean germination [b]	Coefficient	SE	*p*
No. planted 3 vs. 1[a]	0.50/0.25	1.12	0.67	0.073
No. planted 5 vs. 1[a]	0.39/0.25	0.62	0.66	0.350
Burned	0.38/0.48	0.30	0.32	0.347
Protection	0.39/0.46	0.45	0.32	0.154
Exposure	0.40/0.45	0.28	0.31	0.367
Constant		-1.68	0.66	0.011
Rho		0.20	0.08	χ^2_{01} =9.23, p=0.001

[a] Post-hoc comparison of 3 vs. 5, χ^2=3.13, p=0.077.

[b] First number is for first covariate in pair; second number is for second covariate or opposite.

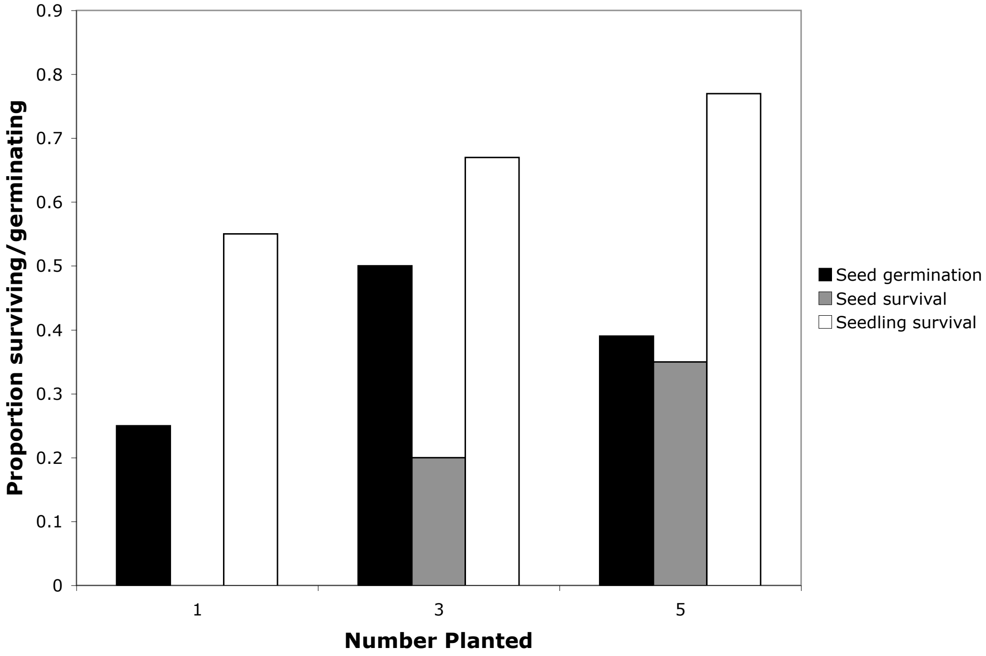

Figure 3. Seed germination and seedling survival as a function of the number that were planted in each cluster. Seed survival is the proportion of seedlings surviving of those seeds that germinated. Seedling survival is the survival of individuals planted as seedlings.

Table 3. Annual and cumulative mortality of seedlings that germinated from seeds and those planted as seedlings. Number of seedlings that died each year are shown with annual percent mortality in parentheses, and cumulative mortality as of the end of monitoring in 2006.

	Annual mortality[a] of seedlings planted	
Year	**(*n*=133)**	**(*n*=354)**
2004	47 (35%)	54 (15%)
2005	29 (22%)	32 (9%)
2006	20 (15%)	14 (4%)
Total dead (cumulative mortality)	96 (72%)	100 (28%)

[a] Annual percent mortality = number of trees that died in that year/number of seedlings at the end of year 1.

origin data. This is likely because there were no seedlings surviving at the end of 2006 that originated from caches of a single seed (figure 3) so the comparison is over a narrower range between caches with three or five seeds, which limits the potential to see an effect with this small sample size. There was significant correlation of clusters which warranted a random intercept for both the combined and seedling-only data.

Growth of the seedlings appeared independent of most of the covariates measured. The exception was the origin variable; individuals planted as seedlings grew faster than those from seeds. This is expected because they are also much taller (mean=16.33 cm vs. mean=3.25, respectively). When we corrected the growth for the final height of the seedling, analysing cm of growth/cm of final height rather than just cm of growth, this effect was no longer significant in the model (Coef.=-0.99, SE=0.65, p=0.129) and the other conclusions were unchanged (unreported results). Protected seedlings were 1.58 cm taller than unprotected seedlings in the seedling-only data.

Discussion

In our experiment, only 11 percent of the seeds that germinated were still alive after three years, while 72 percent of the seedlings that were planted directly survived. All seedlings were healthier in larger clusters and in burned plots.

Of 338 seeds planted, 144 (43 percent) germinated during our study, most of them in the first season after planting. This is lower than in a field experiment (buried in pots) in Kananaskis Country, Alberta, which reported 64.2 percent germination for one-year-old protected (wire mesh) seeds, but higher than the 2.4 percent reported for unprotected seeds (Webster 1998). Glacier National Park nursery reported germination rates of 68-80 percent (Evans and others 2001), while seeds sown at the Couer d'Alene nursery had germination rates of 88-95 percent (Carolin, personal communication).

While the percent of viable seeds can be expected to decline over time, and we do not know the rate of that decline, the seeds had only been stored for three years before planting, a length of time which likely would not have significant effects on germination (Evans and others 2001). Seed survival and germination success are dependent upon factors such as temperature and moisture (Carolin 2006). de Chantal and others (2003) observed that seeds sown earlier in the spring had higher rates of emergence and survival than from summer sowings due to more moisture and cooler temperatures. During the three years of our study (2004-06), the monthly average temperatures during growing season (May through September) was very similar to that of the 12-year average (table 6), at an Environment Canada weather station

Table 4. Seedling survival analysis results using logistic regression. The table includes the mean percentages for the groups, the coefficient for each covariate, their standard errors, and the probability that the coefficients differ from 0. The reference categories (dummy variable=0) were seeds, burned, protected, and near vegetation. *Rho* is the proportion of the total variance contributed by within-group (cluster) correlation. The *p* value for *Rho* is a test of whether *Rho* differs from zero, suggesting that including the grouping (random effect) is appropriate.

Origin[a]	**Covariate**	**Percent mean survival**[b]	**Coefficient**	**SE**	***p***
Seeds & seedlings combined	Origin (seed/seedling)	0.72/0.28	-2.95	0.48	<0.001
	No. planted (1, 3 or 5)	0.54/0.47/0.35	-0.43	0.15	0.005
	Burned/unburned	0.37/0.44	0.23	0.39	0.566
	Protected/unprotected	0.39/0.41	0.59	0.41	0.148
	Near/exposed	0.37/0.42	0.70	0.40	0.080
	Constant		2.39	0.78	0.002
	Rho		0.45	0.09	χ^2_{01}=36.56, p<0.001
From seedlings	No. planted (1, 3 or 5)	0.45/0.33/0.23	-0.39	0.17	0.020
	Burned/unburned	0.26/0.32	0.43	0.45	0.336
	Protected/unprotected	0.26/0.29	0.56	0.49	0.253
	Near/exposed	0.25/0.31	0.63	0.47	0.183
	Constant		-0.69	0.78	0.373
	Rho		0.41	0.10	χ^2_{01}=25.3, p<0.001
From seeds	No. planted (1, 3 or 5)	1/0.80/0.65	-0.66	0.44	0.139
	Burned/unburned	0.78/0.67	-0.21	0.84	0.807
	Protected/unprotected	0.65/0.77	0.55	0.80	0.492
	Near/exposed	0.68/0.75	0.95	0.83	0.255
	Constant		3.68	2.00	0.066
	Rho		0.60	0.21	χ^2_{01}=9.70, p=0.001

[a] Seedlings from germinated seeds or from planted seedlings.

[b] First number is for first covariate in pair; second number is for second covariate or opposite.

Table 5. Seedling health results from logistic regression. The table includes mean percentages for each group, the coefficient for each covariate, their standard errors, and the probability that the coefficients differ from 0. The reference categories (dummy variable=0) were seeds, burned, protected, and near vegetation. *Rho* is the proportion of the total variance contributed by within-group (cluster) correlation. The *p* value for *Rho* is a test of whether *Rho* differs from zero, suggesting that including the grouping (shared frailty) is appropriate. Because the response is 0= healthy and 1=unhealthy, the negative coefficient for number planted indicates that health improves with an increase in the number of seeds/seedlings planted.

Origin[a]	**Covariate**	**Percent mean health**[c]	**Coefficient**	**SE**	***p***
Seeds & seedlings combined (*n*=112)	Origin (seed/seedling)	0.18/0.31	1.78	0.88	0.043
	No. planted (1, 3 or 5)	0.85/0.38/0.18	-0.60	0.24	0.012
	Burned/unburned	0.30/0.27	1.77	0.81	0.028
	Protected/unprotected	0.23/0.32	-0.64	0.57	0.258
	Near/exposed	0.20/0.35	-0.75	0.68	0.271
	Constant		0.96	1.24	0.438
	Rho		0.36	0.16	χ^2_{01}=8.79, p=0.002
From seedlings (*n*=89)	No. planted (1, 3 or 5)	0.85/0.40/0.20	-0.72	0.29	0.013
	Burned/unburned	0.29/0.33	3.48	1.49	0.020
	Protected/unprotected	0.25/0.33	-0.79	0.73	0.279
	Near/exposed	0.21/0.37	-1.28	1.00	0.201
	Constant		3.09	1.30	0.018
	Rho		0.45	0.18	χ^2_{01}=10.65, p=0.001
From seeds (*n*=23)	No. planted (1, 3 or 5)	n/a /0.30/0.11	0.044	0.657	0.947
	Burned/unburned	0.38/0.06	-1.18	1.22	0.334
	Protected/unprotected	0.15/0.21	-0.50	1.12	0.654
	Near/exposed	0.16/0.20	0.027	1.03	0.979
	Constant		-0.42	2.79	0.881
	Rho[b]				

[a] Seedlings from germinated seeds or from planted seedlings.

[b] A random effect did not improve model fit so was not included.

[c] First number is for first covariate in pair; second number is for second covariate or opposite.

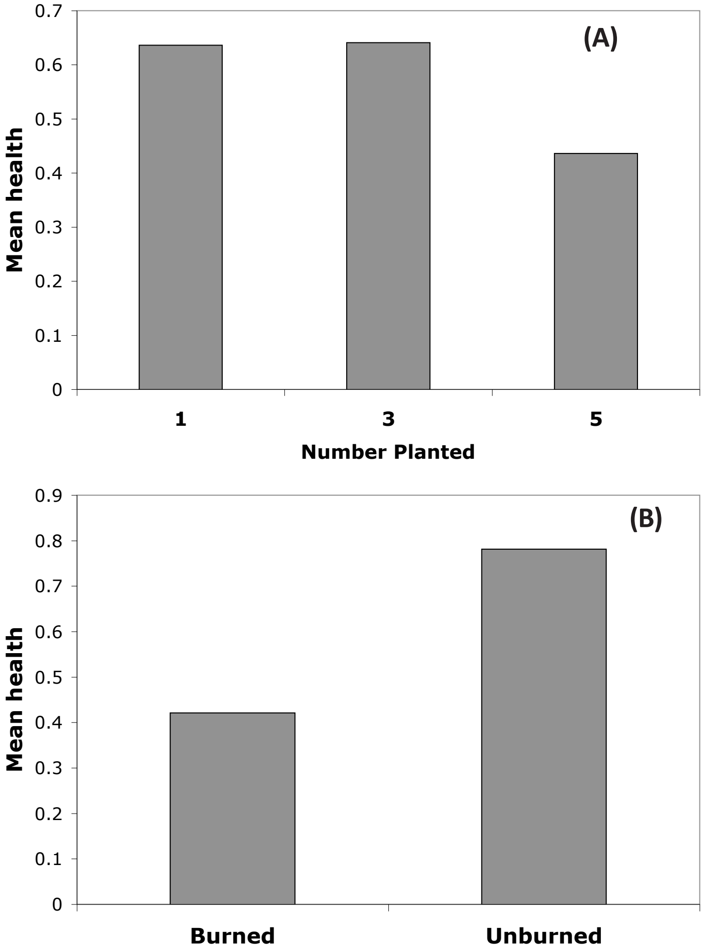

Figure 4. Mean health measures for the two significant covariates from the logistic regression of the seedling only data. Health improved (lower values) with an increase in the number of seedlings planted (A) and seedling health was better in burned than unburned areas (B).

approximately 10 km away. Precipitation was higher during the study than during the 12-year average (table 7). Thus, temperature and moisture did not appear to be limiting factors for germination. In other environments, unpredictable summer precipitation leads to fall planting, which is followed by more predictable winter moisture (Carolin 2006).

Schwandt and others (2007) and McLane (2010) observed significantly greater first-year germination in whitebark pine (*Pinus albicaulis*) seeds after stratification. McLane (2010) also noted that seeds with heavier initial weights were more likely to germinate and survive. Of those seeds that germinated most did so after the first winter but some continued to germinate after the second winter. This result demonstrates that limber pine, similar to whitebark pine (Tomback and others 2001), can have delayed germination and a small, short-duration soil seed bank.

Survival was much higher for individuals that were planted as seedlings (85 percent) than when planted as seeds (65 percent). This was higher than first-year survival (average 51 percent) at 13 different sites in Glacier National Park, MT (Carolin 2006).

Seedling survival after three years was substantially higher when planted as seedlings (72 percent) rather than as seeds (28 percent). This may be explained by the difference in ages at the end of monitoring; by 2006 those planted as seedlings were six years old, and may have passed a critical threshold for survival. Environmental conditions may affect seedlings differently at different stages of growth (Chambers and MacMahon 1994).

Survival and seedling health were improved when more seedlings were planted together in a cluster. Singly-planted seedlings had the lowest survival rate at the end of three monitoring seasons while three- and five-clustered seedlings had higher survival rates. Once emerged, seedling growth and survivorship are enhanced by the presence of other vegetation or seedlings (de Chantal and others 2003, Feldman and others 1999, Powell 1996, Coop and Schoettle 2009) that may alleviate the abiotic effects of the surrounding environment, thus making the microclimate more suitable. The presence of other vegetation may promote growth since soil nutrients, density and moisture are retained, due to an established root system from the other plants, rather than being leached during periods of higher precipitation (Coop and Schoettle 2009).

During the initial stages of seedling growth, high rates of emergence from seed clusters serve as protection against harsh environments for other seedlings in the cluster. In turn, survival increases (Donnegan and Rebertus 1999, Schoettle 2004a). The benefit of being in a larger cluster may not be a long-term effect. It is conceivable that the increased competition from being surrounded by more seedlings may result in lower survival once the seedlings are large enough to compete with one another. As the seedlings progress to later life stages, the requirements for survival and growth change. When root systems become established, competition for resources becomes evident (Powell 1996). Direct sunlight may become limited due to shade from other seedlings. The factors that once maintained the fitness level of the young tree could now contribute to the reduced survival, growth, health and reproductive output of clustered individuals (Powell 1996).

Seedling health was marginally better in burned areas than unburned areas. Burned soils have a higher mineral concentration than unburned soils, offering more nutrients for individuals with growing root systems, thus having a positive effect on the growth of seedlings (Coop and Schoettle 2009). Protection of seedlings appeared to increase seedling height slightly. Baumeister and Callaway (2006) found that the effects of protective covering had a negligible effect on seedling survivorship in their study. Microsites created by downed logs, stumps and and rocks significantly increased whitebark pine seedling survival, height and growth during their first year after planting (Izlar 2007).

Conclusions

Restoration of limber pine is time-consuming and expensive, so determining the appropriate methods of revegetation

Table 6. Monthly and annual average temperature (°C) at Waterton Park Gate, Alberta, 1996-2007 (Environment Canada 2011). Empty cells denote no data available for that month.

	Jan	Feb	Mar	Apr	May	June	July	Aug	Sept	Oct	Nov	Dec	AVE
1996	-12.9	-4.2	-5.9	5.7	6.3	13.4	15.8	16.9	9.6	4.7	-7.3	-10.6	2.6
1997	-8.3	-1.1	-2.0	1.4	9.0	12.9	15.4	15.7	13.6	5.8	0.2	-0.9	5.2
1998	-6.7	0.0	-2.2	6.0	10.2	11.5	18.1	17.3	13.5	7.6	0.2	-6.0	5.8
1999	-4.1	-0.1	1.0	4.2	8.0	11.7	13.8	16.4	10.0	7.0	4.9	0.8	6.1
2000	-5.9	-3.6	0.9	4.7	8.8	12.1	16.1	15.6	10.0	5.7	-3.7	-7.3	4.5
2001	-0.6	-9.1	0.1	2.2	10.9	12.1	15.8	16.4	12.7	5.9	3.0	-4.1	5.5
2002	-4.6	-2.6	-11.4	-0.1	6.6	12.8	17.8	13.6	10.0	1.6	3.6	-0.8	3.9
2003	-1.8	-4.3	-1.8	5.0	8.6	13.5	17.5	17.6	11.0	8.1	-3.1	-1.3	5.8
2004	-6.7	-1.1	2.6	6.3	7.2	11.8	16.5	15.7	11.0	5.4	2.1	-2.7	5.7
2005	-5.3	-1.0	0.4	4.6	8.8	11.8	16.6	14.1	10.3	7.4	1.5	-3.7	5.5
2006	1.4	-4.6	-2.6	6.6	11.1	13.9	18.3	15.7	12.2	4.4	-2.7	-0.1	6.1
2007	-3.7	-52.0	3.5	3.8	9.8	12.7	19.3	14.9	10.3	7.0	0.1		2.3
Average 2004-06													
	-3.5	-2.2	0.1	5.8	9.0	12.5	17.1	15.2	11.2	5.7	0.3	-2.2	5.8
Average 1996-2007													
	-4.9	-7.0	-1.5	4.2	8.8	12.5	16.8	15.8	11.2	5.9	-0.1	-3.3	4.9

Table 7. Total monthly and annual precipitation (mm) at Waterton Park Gate, Alberta, 1996-2007 (Environment Canada 2011). Empty cells denote no data available for that month.

	Jan	Feb	Mar	Apr	May	June	July	Aug	Sept	Oct	Nov	Dec	TOTAL
1996	60.8	38.9	42.2	26.3	121.7	68.2	10.4	27.4	77.8	23.5	79.1	62.0	638.3
1997	44.6	25.9	36.2	43.1	128.0	135.6	13.4	61.2	17.8	42.2	36.8	10.7	595.5
1998	39.5			61.1	92.8	171.6	13.6	14.4	39.0	3.4	52.7	44.4	532.5
1999	23.2	5.8	10.0	53.8	43.6	60.2	48.0	26.2	50.4	53.0	74.0	19.3	467.5
2000	31.8	22.0	32.8	42.0	25.8	55.2	12.2	24.0	67.0	6.4	15.0	22.5	356.7
2001	17.8	32.3	28.0	116.4	6.8	153.4	25.2	4.8	18.0	19.3	28.7	10.2	460.9
2002	37.4	39.6	53.3	52.3	125.3	157.2	16.0	68.6	77.1	31.1			657.9
2003	11.0	13.3	50.3	46.9	54.0	32.8	10.8	3.6	41.4	125.0	73.9	43.5	516.5
2004	94.3	12.2	33.9	36.6	85.7	132.6	29.6	100.6	35.6	50.2	24.4	41.5	687.2
2005	202.4	44.2	41.6	42.6	29.2	260.4	26.0	138.0	129.0	41.0	41.2	26.3	1021.9
2006	28.6	90.1	52.8	54.3	48.2	114.0	17.8	16.4	62.1	56.3	67.5	22.8	630.9
2007	14.3	28.1	21.6	53.6	81.8	32.8	1.8	12.0	78.8	38.6	18.5		381.9
Average 2004-06													
	108.4	48.8	42.8	44.5	54.4	169.0	24.5	85.0	75.6	49.2	44.4	30.2	780.0
Average 1996-2007													
	50.5	32.0	36.6	52.4	70.2	114.5	18.7	41.4	57.8	40.8	46.5	30.3	579.0

is important to success. While the results of our study should be considered preliminary, pending confirmation by other field experiments, we draw the following conclusions from our three seasons of monitoring:

- seedling survival was significantly higher when planted as seedlings rather than grown from field-sown seeds;
- survival was significantly improved, and seedling health somewhat improved, when more seedlings were planted together in a cluster;
- survival was marginally better in seedlings planted near cover;
- seedling health was marginally better in burned areas than unburned areas; and
- protection of seedlings appeared to increase seedling height slightly.

In areas where mortality of limber pine is high, and white pine blister rust is reducing natural regeneration, resource managers are considering revegetating suitable sites. Restoration efforts are likely to have greater success when limber pine is planted in groups of five as seedlings rather than as seeds and there may be benefit to planting them with cover. The benefit of larger clusters may wane, however, if a greater number of seedlings produces greater competition and higher mortality over the long-term. Seedlings are likely to survive well in both burned and unburned areas and the overall effect of seedling protection showed little widespread benefit.

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Literature Cited

Achuff, Peter L. 1997. Special plant and landscape features of Waterton Lakes National Park, Alberta. Unpublished Technical Report. Waterton Park, AB: Parks Canada, Waterton Lakes National Park.

Achuff, Peter L.; McNeil, Ron L.; Coleman, Mary L.; Wallis, Cliff; Wershler, Cleve. 2002. Ecological land classification of Waterton Lakes National Park, Alberta, Vol. I: integrated resource description. Unpublished Technical Report. Waterton Park, AB: Parks Canada, Waterton Lakes National Park.

ASRD and ACA (Alberta Sustainable Resource Development and Alberta Conservation Association). 2007. Status of the limber pine (*Pinus flexilis*) in Alberta. Wildlife Status Report No. 62. Edmonton, AB: Alberta Sustainable Resource Development. 17 p.

Baumeister, D.; Callaway, R. M. 2006. Facilitation by *Pinus flexilis* during succession: a hierarchy of mechanisms benefits other plant species. Ecology. 87: 1816-1830.

Benkman, C. W.; Balda, R. P.; Smith, C. C. 1984. Adaptations for seed dispersal and the compromises due to seed predation in limber pine. Ecology. 65: 632-642.

Breslow, N. E.; Clayton, D. G. 1993. Approximate inference in generalized linear mixed models. Journal of the American Statistical Association. 88: 9-25.

Burns, K. S.; Schoettle, A. W.; Jacobi, W. R.; Mahalovich, M. F. 2008. Options for management of the white pine blister rust in the Rocky Mountain Region. Gen. Tech. Rep. RMRS-GTR-206. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station. 26 p.

Burr, K. E.; Eramian, E.; Eggleston, K. 2001. Growing whitebark pine seedlings for restoration. Pp 325-345 In: Whitebark pine communities: ecology and restoration. Washington, DC: Island Press.

Carolin, Tara. 2003. [Personal communication]. West Glacier, MT: U.S. National Park Service, Glacier National Park.

Carolin, Tara. 2006. Whitebark and limber pine restoration in Glacier National Park: monitoring results. Nutcracker Notes. 10: 14.

Chambers, J. C.; MacMahon, J. A. 1994. A day in the life of a seed: fates and movements of seeds and their implications for natural and managed systems. Annual Review of Ecology and Systematics. 25: 263-292.

Coop, J. D.; Schoettle, A. W. 2009. Regeneration of Rocky Mountain bristlecone pine (*Pinus aristata*) and limber pine (*Pinus flexilis*) three decades after stand-replacing fires. Forest Ecology and Management. 257: 893-903.

de Chantal, M.; Leinonen, K.; Ilvesniemi, H.; Westman, C. J. 2003. Combined effects of site preparation, soil properties and sowing date on the establishment of *Pinus sylvestris* and *Picea abies* from seeds. Canadian Journal of Forest Research. 33: 931-945.

Donnegan, J. A.; Rebertus, A. J. 1999. Rates and mechanisms of subalpine forest succession along an environmental gradient. Ecology. 80: 1370-1384.

Environment Canada. 2011. National climate data and information archive. Ottawa, ON. [Online]. Available: http://climate.weatheroffice.gc.ca/advanceSearch/searchHistoricData_e.html [February 22, 2011].

Evans, J.; Luna, T.; Wick, D. 2001. Propagation protocol for production of container *Pinus flexilis* James plants (172 ml conetainers), Glacier National Park, West Glacier, MT. [Online]. Available: http://www.nativeplantnetwork.org [August 8, 2010].

Feldman, R.; Tomback, D. F.; Koehler, J. 1999. Cost of mutualism: competition, tree morphology, and pollen production on limber pine clusters. Ecology. 80: 324-329.

Gautreau, E. 1963. Effects of white pine blister rust in limber pine stands of Alberta. 1963. Canada Department of Forestry: Forest Entomology and Pathology Branch. Ottawa, ON. Bi-monthly Progress Report. 19(4): 3.

Government of Alberta. 2010. Species assessed by Alberta's Endangered Species Conservation Committee: short list. [Online]. Available: http://www.srd.alberta.ca/BioDiversityStewardship/SpeciesAtRisk/SpeciesSummaries/SpeciesAtRiskFactSheets [July 30, 2010].

Hutchins, H. E.; Lanner, R. M. 1982. The central role of Clark's nutcracker in the dispersal and establishment of whitebark pine. Oecologia. 55: 192-201.

Izlar, K. D. 2007. Assessment of whitebark pine seedling survival for Rocky Mountain plantings. M.Sc. thesis. Missoula, MT: University of Montana. 76 p.

Jackson, Marcus; Lockman, Blakey. 2003. Update on limber pine decline and mortality on the Lewis and Clark National Forest, Montana. Forest Health Protection Report 03-4. Missoula, MT: USDA Forest Service, Rocky Mountain Research Station. 8 p.

Kearns, Holly S. J.; Jacobi, William R. 2007. The distribution and incidence of white pine blister rust in central and southeastern Wyoming and northern Colorado. Canadian Journal of Forest Research. 37: 462-472.

Kendall, Katherine C. 1983. Use of pine nuts by black and grizzly bears in the Yellowstone area. International Conference on Bear Research and Management. 5: 166-173.

Kendall, Katherine C. 2003. Whitebark pine study master database. West Glacier, MT: U.S. Geological Survey, Northern Rocky Mountain Science Center.

Kendall, Katherine C.; Ayers, Dayna; Schirokauer, David. 1996. Limber pine status from Alberta to Wyoming. Nutcracker Notes. 7: 16-18.

Landis, R. D.; Tinus, R. W.; McDonald, S. E.; Barneti, J. P. 1999. Seedling propagation. In: The container tree nursery manual. Agriculture Handbook, No. 674, Vol. 6. Washington, DC: U.S. Department of Agriculture.

Lanner, Ronald M.; Vander Wall, S. B. 1980. Dispersal of limber pine seed by Clark's nutcracker. Journal of Forestry. 78: 637-639.

McCutchen, H. E. 1996. Limber pine and bears. Great Basin Naturalist. 56(1): 90-92.

McLane, Sierra C. 2010. Assisting whitebark pine's migration. Nutcracker Notes. 18: 10-11.

McLaughlin, Marie. 2010. [Personal communication]. Coeur d'Alene, ID: U.S. Department of Agriculture, Forest Service, Coeur d'Alene Nursery.

Powell, M. L. 1996. A greenhouse study of the effects of cache size and relatedness on seed germination, seedling survival, robustness, and root grafting in whitebark pine. Masters Thesis. Denver, CO: University of Colorado.

Schoettle, A. W. 2004a. Developing proactive management options to sustain bristlecone and limber pine ecosystems in the presence of a non-native pathogen. Pp 146-155 In: Silviculture in special places: proceedings of the 2003 national silviculture workshop. Proceedings RMRS-P-34. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station.

Schoettle, A. W. 2004b. Ecological roles of five-needle pines in Colorado: potential consequences of their loss. Pp 124-135 In: Breeding and genetic resources of five-needle pines: growth, adaptability, and pest resistance. Proceedings RMRS-P-32. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station.

Schoettle, A. W.; Negron, J. F. 2001. First report of two cone and seed insects on *Pinus flexilis*. Western North American Naturalist. 61: 252-254.

Schoettle, A. W.; Sniezko, R. A. 2007. Proactive intervention to sustain high-elevation pine ecosystems threatened by white pine blister rust. Journal of Forest Research. 12: 327-336.

Schoettle, A. W.; Sniezko, R. A.; Burns, K. S. 2009. Sustaining *Pinus flexilis* ecosystems of the Southern Rocky Mountains (USA) in the presence of *Cronartium ribicola* and *Dendroctonus ponderosae* in a changing climate. Pp 63-65 In: Breeding and Genetic Resources of Five-Needle Pines, Proceedings of the Conference 2008. Yangyang, Korea: Korea Forest Research Institute.

Schoettle, A. W.; Burns, K. S.; Costello, S.; Witcosky, J.; Howell, B.; Connor, J. 2008. A race against beetles: conservation of limber pine. Nutcracker Notes. 14: 11-12.

Schwandt, J. W.; Tomback, D. F.; Keane, R. E.; McCaughey, W. W.; Kearns, H. S. J. 2007. First year results of a whitebark pine seed planting trial near Baker City, OR. Pp 132-138 In: Whitebark pine: a Pacific Coast perspective, August 27-31, 2006, Ashland, OR. Report R6-NR-FHP-2007-01. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Region.

StataCorp. 2003. Stata statistical software: release 8.0. College Station, TX: Stat Corporation.

Steele, R. 1990. *Pinus flexilis* James. Pp 348-354 *in* Silvics of North America, Volume 1, Conifers. Agriculture Handbook, No. 654. Washington, DC: U.S. Department of Agriculture.

Tomback, Diana F.; Hoffmann, L. A.; Sund, S. K. 1990. Coevolution of whitebark pine and nutcrackers: implications for forest regeneration. Pp 118-129 In: Symposium on whitebark pine ecosystems: ecology and management of a high-mountain resource. General Technical Report INT-270. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experimental Station.

Tomback, Diana F.; Anderies, Angela J.; Carsey, Katherine S.; Powell, Mary L.; Mellmann-Brown, Sabine. 2001. Delayed seed germination in whitebark pine and regeneration patterns following the Yellowstone fires. Ecology. 82: 2587-2600.

Ward, Kimiora; Shoal, Robin; Aubry, Carol. 2006. Whitebark pine cone collection manual. Portland, OR: USDA Forest Service, Pacific Northwest Region. 20 p.

Webster, K. L. 1998. The importance of regional dynamics in local limber pine (*Pinus flexilis*) populations. M. Sc. Thesis. Calgary, AB: University of Calgary.

Restoration Planting Options for Limber Pines in the Southern Rocky Mountains

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1. Limber Pine (*Pinus flexilis*) populations in the southern Rocky Mountains are severely threatened by the combined impacts of mountain pine beetles and white pine blister rust. Limber pine's critical role in these high elevation ecosystems heightens the importance of mitigating these impacts.
2. To develop forest-scale planting methods, six limber pine seedling planting trial sites were installed extending from the Medicine Bow National Forest in southern Wyoming to the Great Sand Dunes National Park and Preserve in southern Colorado.
3. Seedlings were purchased from the Colorado State Forest Service nursery and were three years old, container-grown, and originated from a Colorado seed source.
4. Six plots were installed at each site and were split between high and low density canopy conditions, with three plots in each. In each of the six plots treatments were: presence/absence of a nurse object; and presence/absence of Terra-Sorb Hydrogel. The Hydrogel treatment was omitted at two sites due to planting logistics and national park regulations.
5. Terra-Sorb Hydgrogel (Pittsburgh, PA) is a potassium-based copolymer gel that absorbs up to 200 times its weight in water. Hydrogels are commonly used in horticulture, although scientific literature shows mixed results for tree survival. The hydrogel treatment consisted of dipping seedling roots in the hydrogel slurry before planting, per manufacturer directions. The roots of hydrogel control seedlings were dipped in water before planting.
6. We created nurse objects by burying 50-cm tall tree stem segments (20-40 cm in diameter) 10 cm into the ground. Seedlings were planted as close as possible to the object at the four cardinal directions to further test exposure stress. In the object control treatment we planted seedlings in an east/west orientation 40 cm apart.
7. There were six replicates of each treatment combination, with 432 seedlings planted in each of the four sites with the Terra-Sorb Hydrogel treatment and 216 seedlings planted in each of the two sites without hydrogel treatments, for a total of 2,160 seedlings.
8. After the first growing season overall seedling survival was greater than 90 percent. More seedlings were healthy in the dense canopy treatment, compared to the open canopy treatment (p=0.0012). There was no statistical difference in tree health between hydrogel treatments.
9. We will continue monitoring health and survival of the outplanted seedlings and the incidence of natural regeneration in 2010. Results from this project will be used to develop limber pine planting protocols for the southern Rocky Mountains.

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High Elevation White Pines Educational Website

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Abstract—The high elevation five-needle white pines are facing numerous challenges ranging from climate change to invasion by a non-native pathogen to escalation of pest outbreaks. This website (http://www.fs.fed.us/rm/highelevationwhitepines/) serves as a primer for managers and the public on the high elevation North American five-needle pines. It presents information on each of the five high elevation five-needle pines, their ecosystems and the factors that threaten them. The species covered include Rocky Mountain bristlecone pine (*Pinus aristata*), Great Basin bristlecone pine (*P. longaeva*), whitebark pine (*P. albicaulis*), foxtail pine (*P. balfouriana*) and limber pine (*P. flexilis*). Threats discussed include white pine blister rust, mountain pine beetle, climate change and other pests. The site outlines management options, includes links to reports and documents and provides an exercise for teachers to include in their curriculum. Photographs are free to download and use in presentations. The site was initiated in 2006 and is continually being revised; an expanded version will include updated links to documents and reports, further information on genetic conservation efforts for each species as well as monitoring protocols.

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