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SPECIAL FEATURE: REVIEW

Alien pests threatening biodiversity of forest ecosystems

Proactive intervention to sustain high-elevation pine ecosystems threatened by white pine blister rust

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Abstract Only recently have efforts begun to address how management might prepare currently healthy forests to affect the outcome of invasion by established non-native pests. *Cronartium ribicola*, the fungus that causes the disease white pine blister rust (WPBR), is among the introductions into North America where containment and eradication have failed; the disease continues to spread. Ecosystem function is impaired by high rust-caused mortality in mature five-needle white pine forests. This paper evaluates five proactive management options to mitigate the development of impacts caused by white pine blister rust in threatened remote high-elevation five-needle pine ecosystems of western North America. They are: reducing pest populations; managing forest composition; improving host vigor; introducing resistant stock with artificial regeneration; and diversifying age class structure to affect the natural selection process for resistance. Proactive intervention to manage and facilitate evolutionary change in the host species may sustain host populations and ecosystem function during pathogen naturalization.

Keywords Evolution of resistance · Exotic pathogen · *Pinus aristata* · *Pinus albicaulis* · *Pinus flexilis*

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Introduction

Globalization has increased the rate and likelihood of movement of organisms beyond their native distributions (Mack et al. 2000; Mack and Lonsdale 2001). While a species may not be a significant pest in its place of origin, it can become invasive in the new ecosystems. Non-native pests present a novel stress on native ecosystems because of the lack of co-evolution and natural enemies. Forests are among the ecosystems being impacted by non-native pests and pathogens (Liebold et al. 1995). Non-native organisms have severely reduced some forest species populations (e.g. chestnut blight), altered forest composition (e.g. gypsy moth), and threaten habitat for an endangered species (e.g. white pine blister rust, *Cronartium ribicola* J.C. Fisch., and the grizzly bear). Currently, invasive species strategies focus on preventing introduction, early detection and eradication, containment and control of the pest and, when those efforts are unsuccessful, mitigation of impacts, and restoration of the degraded forest.

Once the non-native organism is established, eradication, containment, and control have been challenging and often ineffective. In those cases, the non-native pest is commonly left to “run its course” through the remaining vulnerable ecosystems. There is a growing interest in managing ecosystems toward accommodating the non-native organism to mitigate ecosystem impacts during the naturalization process. Management of forest structure and composition can play a role in the suppression and spread of non-native pests (Waring and O’Hara 2005), yet its role in preparing vulnerable ecosystems for invasion and altering the outcome of invasion has been under explored.

The fungus that causes the disease white pine blister rust (WPBR) is among the introductions into North America where containment and eradication efforts have failed

(Maloy 1997). Since its introduction from Europe in the early 1900s, WPBR has caused economic and ecological impacts and still threatens five-needle pine ecosystems. The fungus is now a permanent resident of North America and continues to spread (Fig. 1). All of the nine five-needle white pine species in North America are susceptible to the lethal disease (Bingham 1972; Hoff et al. 1980). Although the noncommercial five-needle pine species primarily grow in remote high-elevation mountain areas, they too are threatened. It was thought that the remote dry habitats occupied by the high-elevation species would not support rust establishment, however, many of these sites are now infected. Impacts are occurring in limber, whitebark, Rocky Mountain bristlecone, and foxtail pine ecosystems; Great Basin bristlecone pine is the only North American five-needle pine species not yet infected in the field (Table 1). There is no biological or environmental reason to expect the remaining populations to escape infection in the future (Kinloch 2003). A risk analysis for WPBR in Colorado shows that approximately half of Colorado's susceptible pines lie in areas with average climatic conditions conducive to infection (Kearns 2005). Favorable conditions for WPBR may also occur in the other areas intermittently.

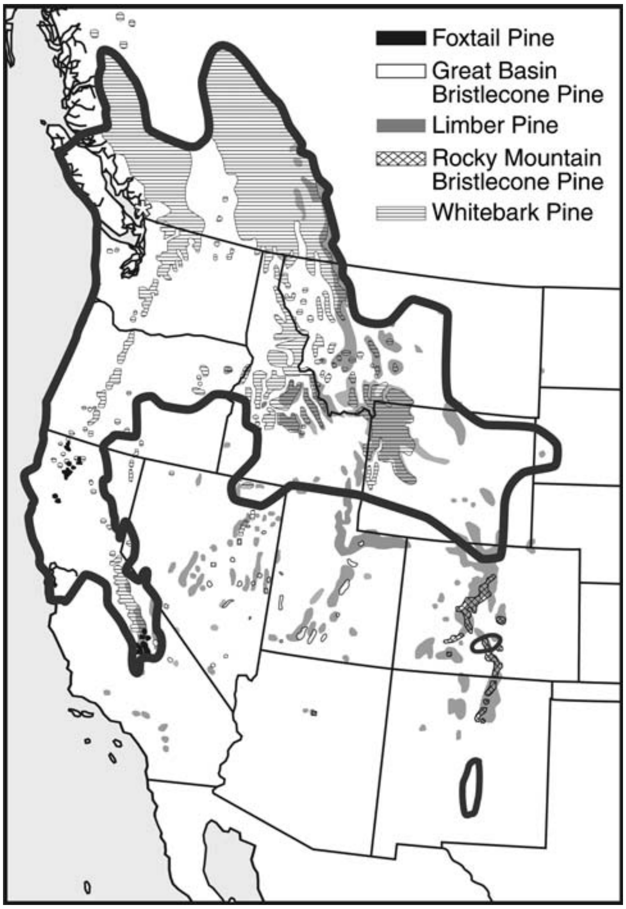

Fig. 1 Map of western North America showing the current infection front of white pine blister rust (*bold line*; adapted from Samman et al. 2003) and the distribution of each of the noncommercial high-elevation five-needle pine species. Note that many but not all stands within the infection areas are infected. The *white asterisk* marks the location of the one and only introduction of WPBR into western North America, which occurred in 1910

All of the North American five-needle pine species have some heritable resistance to WPBR (Bingham 1972). The frequency of resistance is low in all species; some infected areas have experienced greater than 90% mortality. Increasing the frequencies of durable resistance or tolerance traits within the populations is accepted as a promising avenue for the co-existence of five-needle pines and WPBR (Samman et al. 2003). Breeding programs to exploit these natural traits within some of the commercial white pine species are underway and resistant stock is available for reforestation or restoration (McDonald et al. 2004). Restoration strategies, also based on increasing genetic resistance of the pine host, are being developed for some of the noncommercial species as the ecological consequences of the disease become more evident and awareness of the pine species' unique ecological roles has increased (Hoff et al. 2001; Mahalovich and Dickerson 2004; Schoettle 2004a, 2004b). The current management approaches are strongly focused on restoration of severely affected areas.

Only recently have efforts begun to address how management might prepare the currently uninfected noncommercial white pine areas to affect the outcome of invasion (Schoettle 2004b). The premise of proactive intervention is to prepare the landscape such that upon WPBR invasion:

1. the distribution of five-needle pine species is minimally constricted;
2. ecosystem function and services are continued and self-sustaining; and
3. restoration efforts later would be unnecessary or reduced.

Eliminating the threat of WPBR invasion has proven futile (Maloy 1997), thus the objective of proactive intervention is to position the ecosystem to increase the frequency of rust-resistance and tolerance in five-needle pine populations and avoid ecosystem collapse. In short, the objective is to facilitate the evolution of rust-resistance in the five-needle pine populations. While contrary to current conservation approaches that would advocate preservation of native genotypes, facilitating evolutionary change in the host species (i.e. increasing the frequency of resistance genes in five-needle pines) may enable naturalization of the non-native organism while sustaining host populations and ecosystem function (Kilpatrick 2006).

Table 1 The nine five-needle white pine species in North America and the year that white pine blister rust was discovered in native forests (McDonald and Hoff 2001)

Species	Common name	Year of first infection/detection
Timber species		
Pinus strobus L.	Eastern white pine	1915
P. monticola Dougl.	Western white pine	1922
P. lambertiana Dougl.	Sugar pine	1961
P. strobiformis Engelm.	Southwestern white pine	1970
Non-timber species		
P. albicaulis Engelm.	Whitebark pine	1926
P. balfourniana Grev. and Balf.	Foxtail pine	1942
P. flexilis James	Limber pine	1945
P. aristata Engelm.	Rocky Mountain bristlecone pine	2003
P. longaeva Bailey	Great Basin bristlecone pine	NA

NA: no infections in native forests have been detected as of 2006

The success of a proactive strategy to increase rust resistance on the landscape will be dependent on the size of the original population (absolute number of individuals available for selection), the frequency of genetically resistant individuals in each stand, the type of resistance mechanisms, the disease hazard, consequences of rust-resistance selection (mortality of susceptible individuals) on the ecosystem functions, and the availability of sites suitable for natural regeneration and future reproduction. This paper will examine the management options for the uninfected areas in preparation for invasion from this tenet. It will review proactive options proposed for this and other non-native invasions and evaluate the efficacy of each to the WPBR pathosystems in remote high-elevation five-needle pine ecosystems of western North America.

Consequences of no intervention

The impacts of WPBR on high-elevation forests in the northern United States demonstrate the consequences of no intervention. These whitebark and limber pine forests have been challenged by WPBR for over 50 years and the impacts have been extensive and far reaching with cascading effects on ecosystem function and biodiversity (Tomback and Kendell 2001). With no intervention to alter the trajectory of interaction between WPBR and the traditionally unmanaged high-elevation North American five-needle pines forests, WPBR can be expected to continue impacting the ecosystems as it spreads. WPBR is a lethal disease that causes tree mortality at all life stages thereby affecting all aspects of the regeneration cycle (Fig. 2). The infections on the pines are perennial and result in branch or stem cankers that kill the distal tissue via girdling.

Extinction of the five-needle pine species is not imminent; however, WPBR may cause local extinctions and impact genetic diversity, gene flow, and possibly the distribution of adaptive traits, and ecosystem functions. During the early stages of infection of mature trees, reduced seed availability due to top-kill or branch death directly impacts wildlife species (Mattson 1992), regeneration (Tomback et al. 1995), and potentially the mutualism with seed-dispersing birds (McKinney 2004). With increasing tree mortality, changes in forest structure expand the impacts to include altered snow capture, watershed hydrology, community diversity, wildlife habitat, and the sustainability of the forest type on the site (Kendell and Arno 1990; McDonald and Hoff 2001). Seedlings and saplings are especially susceptible and are often killed within 1–3 years of infection. Reduced five-needle pine regeneration capacity affects forest recovery after disturbances (especially fire), slows succession (Rebertus et al. 1991; Donnegen and Rebertus 1999), and impacts other species' distributions due to the lack of facilitation (Rebertus et al. 1991; Bekker 2005; Baumeister and Callaway 2006).

The life history traits of the high-elevation five-needle pines are unlikely to promote the evolution of rust-resistance within populations without intervention. These species have adaptive traits that enable them to persist for many years on harsh sites (Schoettle 1994; Schoettle and Rochelle 2000; Schauer et al. 2001). Trees of Great Basin bristlecone pine are thought to be the oldest living organisms on earth, reaching life spans of over 4,500 years old (Schulman 1958; Curry 1965). Rocky Mountain bristlecone pine and limber pine commonly live over 1,000 years and the bristlecone pine can exceed 2,500 years old (Brustein and Yamaguchi 1992). Their longevity is also a result of the lack of frequent stand-replacing disturbances. Given that these species tend to be pioneer species, opportunities for regeneration are rare. As a result, even where trees with heritable rust-resistance persist on a site in the presence of WPBR, without regeneration opportunities the number of individuals with rust-resistance and tolerance in the five-needle pine population will not increase. The life history strategies of high-elevation five-needle pines toward

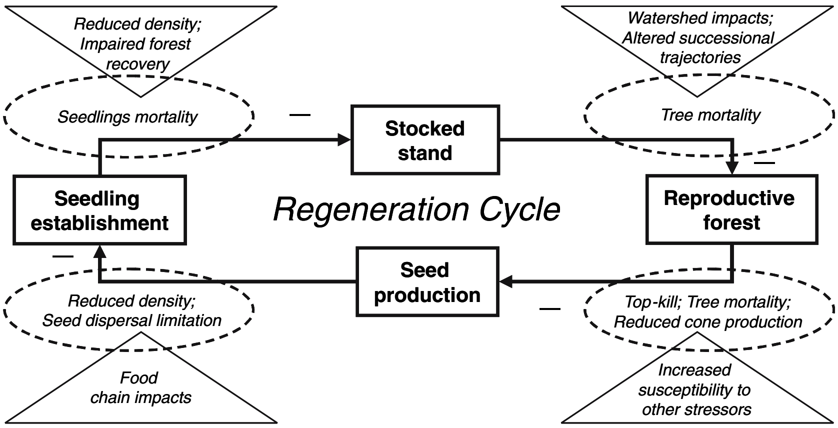

Fig. 2 The impacts of WPBR (*ovals*) at each stage of the forest regeneration cycle (*rectangles and arrows*). The *triangles* reflect the ecosystem impact of the disruption of the regeneration cycle by WPBR at each stage. White pine blister rust causes mortality of both young and old trees. High rust-caused mortality in a mature population can affect the sustainability of the population

persistence and away from adaptive change in response to stress support the observations that relying on natural events alone may not sustain five-needle pine ecosystems once WPBR has become established in an area.

Proactive intervention options

In this section we will discuss five different management approaches that could be implemented prior to, or during the early stages of, invasion by WPBR and assess their efficacy to minimize ecological impact of the disease and promote long-term ecosystem sustainability. We will examine each option for its suitability for application in the threatened high-elevation pine forests of western North America by applying the current knowledge of the ecology of the pines, blister rust biology, the pathosystem and ecological genetics. The strategies discussed include mitigating impacts in forests by:

1 reducing pest populations;
2 managing forest composition;
3 increasing host vigor;
4 introducing resistant stock with artificial regeneration; and
5 diversifying age class structure to affect the selection process.

1 Mitigating impacts via reducing pest populations

Reducing the intensity of stress imposed on an ecosystem can affect how it responds (Liebold et al. 1998). Historical efforts to eliminate rust via eradication of its alternate host, *Ribes*, failed (Maloy 1997). However, reducing the cover of *Ribes* in the northeastern United States is acknowledged to have reduced local intensification of the disease (from 9 to 4% rust incidence over the 70 year program) and impacts on eastern white pine (Ostrofsky et al. 1988). In contrast to the closed canopy plantations and forests of eastern North America, spores can spread over long distance in the well-ventilated open western forests. *Ribes* management to control spread has not been deemed successful under western conditions (McDonald and Hoff 2001; Toko et al. 1967). Long-distance atmospheric spore dispersal is suspected to be responsible for the isolated infection centers of WPBR in New Mexico (~960 km from the nearest known source of inoculum; Hawksworth 1990) and central Colorado (~300 km from the nearest known source of inoculum; Blodgett and Sullivan 2004).

Ribes in close association with high-elevation five-needle pines may be involved in local disease intensification in the west yet the relationship is not simple (Newcomb 2003). In addition, recently species other than *Ribes* have been shown to serve as alternate hosts for WPBR (McDonald et al. 2006). It is not known at this time how significant these hosts are in the epidemiology of the disease. Local *Ribes* control in accessible, high-value areas may reduce the frequency of wave infection years and, therefore, extend the time before impacts are obvious. Reducing the density of the alternate host may slow impacts to provide more time to develop and implement genetic approaches but by itself this approach will not facilitate increases in rust resistance in the five-needle pine species or stop the spread of the disease in the west.

Similarly, suppression approaches that retain susceptible trees on site will not contribute to increasing rust-resistance and the future sustainability of the population. Removal of WPBR cankers by pruning may extend the life of the tree but it does not affect the number of rust-resistant trees in the population or the ability of the stand to contribute to forest recovery after a disturbance in the presence of the rust. Although this approach may be suitable for plantations of commercial five-needle pines so that trees reach merchantable size, or for high value areas such as campgrounds, it is not an attractive approach for the wilderness-type forests of the high-elevation five-needle pines.

2 Mitigating impacts in forests via managing forest composition

Removal or management away from preferred host species can affect the outcome of an invasion on an ecosystem (Gottschalk 1993). This approach was applied to western white pine when the threat of WPBR was realized; planting of western white pine ceased and the land area was managed for other species (Mielke 1943). The combination of WPBR-caused mortality and changes in management practices has converted forests where western white pine accounted for over 30% of the trees to forests that now have a western white pine component of less than one-tenth of that (Samman et al. 2003). Unfortunately, the replacement forest type on these historically western white pine sites is highly susceptible to native pests and pathogens. Management away from western white pine may have reduced the impacts of WPBR but resulted in the loss of the white pine timber industry and did not improve overall forest health.

Management to reduce the high-elevation five-needle pines in forests may not sustain ecosystem function in many cases because some functions are uniquely provided by the pine species and other species cannot grow on many of the harsh sites currently occupied by the pines. Whitebark and limber pine are considered keystone species for their roles as an essential food source for black and grizzly bears (*Ursus* ssp.; Kendell 1983; McCutchen 1996; Felicetti et al. 2003), corvids (e.g. Clarks nutcrackers, *Nucifraga columbiana*; Tomback 1978; Tomback and Kramer 1980), red squirrels (*Tamaisciurus hudsonicus*; Hutchins and Lanner 1982) and other small rodents. These species and Rocky Mountain bristlecone are essential in the reforesting of post-fire subalpine landscapes (Baker 1992; Tomback et al. 1995; Donnegen and Rebertus 1999). For harsh sites dominated by high-elevation five-needle pines there are no replacement tree species to reduce forest vulnerability to WPBR. The high-elevation five-needle pines are very tolerant of abiotic stresses but are poor competitors. As a result, these pines dominate harsh sites not because they prefer the environmental conditions but because other species cannot grow there (Lepper 1974). On the less harsh sites, removal of the five-needle pine component will prevent succession to other subalpine conifers and accelerate ecosystem impacts (Tomback and Kendell 2001; Schoettle 2004a, 2004b).

In the case of the high-elevation five-needle pine–WPBR pathosystem, management in favor of the pine species may assist naturalization. Maximizing the size of the population on which selection will act is especially important since some resistance mechanisms may be present in only 1 of 10,000 trees (Kinloch et al. 2003). On the less harsh sites, the noncommercial five-needle pine species of western North America are early seral and are successionally replaced by more shade tolerant species in the absence of disturbance (Rebertus et al. 1991; Donnegen and Rebertus 1999). The fire suppression policies of the 1900s have unwittingly reduced the cover by five-needle pines on the landscape. Restoring a natural fire regime in these forests before WPBR invasion will increase regeneration and the five-needle pine component of the forests and provide a larger population size for natural selection of rust resistance (option 5, below).

3 Mitigating impacts in forests via increasing host vigor

Stand structure can affect the likelihood and outcome of an invasion for some pests via host vigor and tolerance to episodic attacks (Gottschalk 1993; Gottschalk et al. 1998; Schmid and Mata 2005). Due to the lack of co-evolution between North American five-needle pines and WPBR, increased host vigor may not convey greater defense and may in fact provide better food quality for a more aggressive WPBR parasitism. Lachmund (1934) found that canker growth rate, a measure of *C. ribicola* reproduction, was three times greater on western white pine trees growing under optimal conditions compared to those having poor vigor.

Improving tree vigor may, however, prevent damage or loss of trees by other agents. The five-needle pines are hosts to mountain pine beetle (*Dendroctonus ponderosae* Hopkins) (Amman 1982) and, in the case of limber pine, can be a preferred host (Langor et al. 1990). Removal of competing vegetation to improve tree vigor and reduce susceptibility to bark beetle attack (Schmid and Mata 2005) is currently being employed to protect large sugar pines in Oregon and limber and bristlecone pines in Colorado. In addition, removal of understory ladder fuels may reduce the risk of tree mortality in the event of a wildfire thereby retaining a greater number of individuals on the landscape for the WPBR selective pressure to act on. These treatments may also cause a transitory increase in *Ribes* cover (Schoettle et al. 2003) and potential increase in rust hazard. Therefore, stand manipulation may present a trade-off between lowering the risk of tree loss by other agents and increasing rust intensification. The trade-off may be acceptable since manipulation also offers regeneration opportunities for five-needle pines resulting in an increased population size for natural selection, as discussed below.

4 Mitigating impacts in forests via introducing resistant stock with artificial regeneration

Outplanting pest-resistant tree stock is the principal restoration approach for forests impacted by non-native pests and pathogens, including WPBR, in North America

(Sniezko 2006). Within a proactive approach this option requires identifying resistant host genotypes and outplanting them on sites in advance or at an early stage of infection. 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 reach reproductive maturity (McCaughey and Schmidt 1990). 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. Seed trees with resistance traits can be identified in already impacted sites or by progeny screening for resistance using artificial inoculation techniques of native genotypes local to each population (Danchok et al. 2003, Dorena Genetic Resource Center Manual. USDA Forest Service, unpublished document).

Transfer resistant genotypes via artificial regeneration

This option would require identifying seed trees with heritable resistance or tolerance to WPBR in already infected areas and culturing and outplanting their progeny into the threatened areas. Seed-transfer guidelines are essential for application of this proactive option given the high probability of long-distance seed transfers, because close proximity of an uninfected site to one with sufficient selection pressure to identify rust-resistant seed trees (80–90% mortality, Hoff et al. 1994) is unlikely. With improper seed transfer the possibility of failure may be high not due to WPBR mortality, but mal-adaptation and transplant failure on the harsh high-elevation sites. Experimentally verified seed transfer and transplant or direct seeding guidelines are not available for most of the noncommercial five-needle pine species. Seed-transfer guidelines are based on how much adaptive variation is attributed to the geographic location of the seed source and limits the consequences of any negative genotype by environment interactions. Patterns of variation for the adaptive traits provide insight into how a species is suited to its environment. Geographic variation in cold hardiness in whitebark pine recommends restricting transfer among mountain ranges (Mahalovich and Hoff 2000; Mahalovich et al. 2006) and indicates risk of fall cold injury of seedlings if seed is transferred from areas with warmer winter temperature to those with colder winters (Bower and Aitken 2006). Latitudinal variation in growth phenology among Rocky Mountain Bristlecone pine seed sources also suggests potential limitations to seed transfer even for this narrowly distributed species (Schoettle, unpublished data). More information is needed on patterns of genetic variation in adaptive traits for limber, foxtail, and the bristlecone pine species.

Identify resistant local genotypes and increase their representation via artificial regeneration

Ex situ progeny screening to identify seed trees with resistant traits from uninfected sites would be a large effort. Although cumbersome, in the absence of verified seed-transfer guidelines this approach has the advantage over the previous option of avoiding potential poor performance of the transplanted seedlings. Unfortunately, there are currently few known predictors of WPBR resistance that can be used to guide selection of potential seed trees for testing (Woo et al. 2001). Development of indirect measures of resistance would greatly expedite locating putatively resistant seed trees in uninfected stands. Tools being developed in molecular genetics could provide this capacity in the future. Geographic variation in resistance has been observed for sugar pine and western white pine (Kinloch 1992; Kinloch et al. 2003), whitebark pine (Mahalovich et al. 2006) and may exist in the other white pines. Initial range-wide screenings are underway for some, but not all, of the high-elevation five-needle species and will identify parent trees with resistance traits.

Rust-resistance screenings of progeny from native populations will provide baseline data on the frequency of resistance over the landscape from which prioritization of stands for further application of this or other approaches could be focused. In addition, screening uninfected populations for rust resistance will identify susceptible individuals that can be used to focus monitoring efforts to detect invasion in the early stages. Extra seed from these or other seed collections can also be archived for ex situ conservation of genetic diversity for the species. Overall, this is a promising approach for the high-elevation white pines and one that could supplement others such as option 5, below.

5 Mitigating impacts in forests via diversifying age class structure to affect the selection process

All life stages of the pine host are susceptible to WPBR although the time trajectory for mortality after infection is greater for older trees than younger trees (Smith and Hoffman 2000; Conklin 2004). One could consider managing a landscape for older tree age classes to slow the impacts in the short run; however, it would not increase the number of resistant individuals on the landscape. Attempts to promote regeneration after rust-resistance selection in a mature stand (Hoff et al. 1976, 1994) may be ineffective due to seed-limitations (Tomback et al. 1995; McKinney 2004). In addition, the mortality of mature susceptible trees during the selection process will likely result in impacts to ecosystem functions and the surviving resistant individuals will be at risk for loss over time to succession, wildfire, or other pests and pathogens. Alternatively, diversifying the age class structure by stimulating regeneration in a healthy mature ecosystem before rust invasion will provide a larger population size and enable resistance selection upon invasion in both the younger and older cohorts simultaneously. This proactive approach positions the ecosystem for rapid and efficient natural selection for resistance in the younger cohort while the older cohort sustains ecosystem function (Schoettle 2004b).

Significant gains in resistance to blister rust can be achieved in one generation of selection (Krebill and Hoff 1995). Rapid selection in younger cohorts may enable sustained ecosystem function through the high mortality phase of the first generation of rust-resistance selection. Rust-resistance of progeny reflects the level of selection pressure in the parent population (Table 2). For example, less than 1% of the progeny from original whitebark pine populations were canker-free when experimentally inoculated with rust, while over 40% of the progeny from survivors of a population after sustained selective pressure (>90% rust-caused mortality) were canker-free (McDonald and Hoff 2001). Considering that whitebark pine is among the most susceptible of the high-elevation white pines (Bingham 1972), the gains could be even greater after one generation of selection in the other high-elevation pines. Initial estimates of resistance in native populations of Rocky Mountain Bristlecone and Great Basin Bristlecone pine may be as high as 12 and 26%, respectively (Vogler et al. 2006). Progeny from putatively resistant southwestern white pine seed trees (identified in stands in the first generation of selection) were over 60% canker-free following experimental rust inoculation (Sniezko, unpublished data).

This approach generates a mosaic of different age classes on the landscape before invasion such that upon infection, natural selection for resistance would be rapid in the young cohorts and would concurrently proceed more slowly in the older cohort (Fig. 3). In an extensive survey in the western United States of infected stands with an average rust infection intensity of 35%, approximately 80% of the infected small trees (5–10 cm diameter) already had severe damage that would likely cull these susceptible individuals from the population in the near future; in contrast only approximately 30% of the infected larger trees (45–50 cm diameter) were at that stage of selection (Smith and Hoffman 2000). In addition, the younger tree age classes experienced a disproportionate amount of the mortality by WPBR; 35% of those trees killed by WPBR were in the 5 cm diameter class and all trees killed by WPBR in this survey were less than 30 cm diameter (Smith and Hoffman 2000). It is evident in this survey that the selection for resistance was preceding more rapidly in the small than the large trees. There are two reasons for these differences. First, lethal stem cankers develop more rapidly upon infection of a smaller tree due to the closer proximity of the infection point (needle on a twig or stem) to the main stem. Second, ontogenetic factors of resistance to blister rust are present in at least some old five-needle pines (Patton 1961; Bingham 1966; Kinloch and Byler 1981) and this resistance is not expressed by the tree's young progeny (Kinloch and Davis 1996).

Table 2 Whitebark pine seedlings grown from seed collected from three high-mortality stands (>90% by blister rust), three moderate mortality stands (40–60%), and three low-mortality stands (<10%) were tested for WPBR symptoms (cankers) following experimental inoculation with WPBR spores. Just one generation of rust-resistance selection provides useable levels of heritable resistance in whitebark pine (Hoff, unpublished data, presented in McDonald and Hoff 2001)

Parent stand mortality (%)	Number of progeny tested	Percent of progeny canker-free (%)
<10	226	0.9
40–60	134	11.9
>90	304	44.4

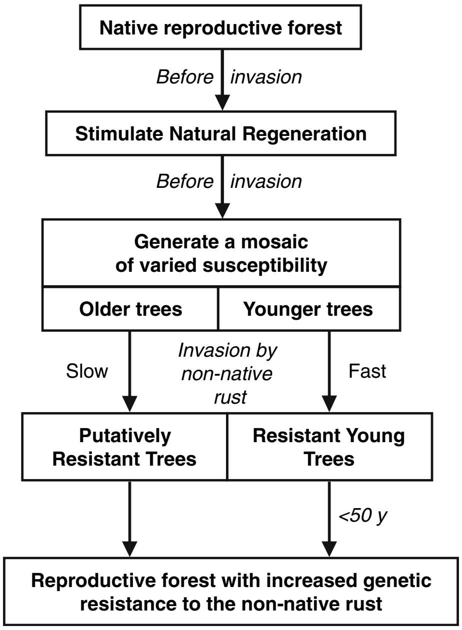

Fig. 3 Schematic diagram of the proactive intervention option Mitigating impacts in forests via diversifying age class structure to affect the selection process as it applies to white pine blister rust in western North America

The selection process in established young cohorts within a mature landscape during the early stages of invasion will have little effect on the ecological functioning of the ecosystem. The rapid selection for rust resistance in a population of young trees will enable survivors to mature and contribute to the reproductive capacity of the landscape before, or soon after, high levels of mortality occur in the older cohorts. As a result, the time when the regeneration cycle is compromised by WPBR and the ecosystem is at risk of impacts would be minimized (Fig. 2). The rate of mortality in a native young population upon invasion would be partially offset by the high number of seedlings in a regenerating population compared to a mature stand (Hoff et al. 1976). At the same frequency of resistance, a stand with thousands of individuals (progeny generation) should fare better than a stand with a much more modest number of individuals (mature trees). Nesting young cohorts of trees within a landscape of mature individuals prior to invasion will facilitate natural selection in the young cohorts upon invasion before high tree mortality of the older trees thereby uncoupling selection for rust resistance from ecosystem impacts across the landscape.

Genetic resistance would continue to increase given repeated future natural regeneration opportunities after the population of selected seedlings reach reproductive maturity. With sufficient regeneration opportunity three to four generations may be sufficient to sustain the white pines in the presence of the rust (Hoff et al. 1976; Neuenschwander et al. 1999; McDonald and Hoff 2001). Accelerating the generation time and natural selection process through silvicultural treatments will reduce the ecological consequences of mortality in any one cohort.

Similar to option 4 above, this option would reduce the vulnerable time when forest recovery from disturbance is compromised by WPBR since the young trees would already be established at the time of selection and would be that much closer to maturity. The older trees would retain site occupancy and ecosystem function during the early invasion and selection process. This option would also eliminate mal-adaptation concerns and does not require transplant guidelines.

This approach positions the ecosystem to utilize natural processes to provide resilience upon invasion. It may be especially suitable for ecosystems in which minimal management has occurred historically and extensive restoration intervention is unlikely yet the risk of ecological impacts is high. A patchwork of treatment areas across the landscape can generate reservoirs of resistant genotypes and traits for eventual spread to other areas by gene flow. Creation of canopy openings and removal of understory species is needed to support establishment of these shade intolerant five-needle pines. Pilot studies have been initiated to refine guidelines for generating gaps and site preparation to preferentially encourage five-needle pine regeneration (Schoettle et al. 2003). Assessment of the efficacy of this option for different species and geographic locations can be improved with knowledge of the frequency of heritable rust resistance in the native populations since the success of this approach relies on indigenous resistance within the population. If sufficient resistance is present and sufficient regeneration is encouraged, this approach will accelerate the development of a forest with greater resistance that will be more capable of sustaining itself.

Conclusions

Proactive intervention is an option for ecosystems vulnerable to established non-native invaders that are still spreading. Management before ecosystem function is impaired may be more successful than restoring function after ecosystem collapse. An interdisciplinary knowledge base of the pest, host, and ecosystem is essential when evaluating and developing both restoration and proactive options. Restoration of areas devastated by non-native invaders often dominates the attention of forest mangers and their actions. Taking a broader view of the invasion beyond the crisis areas reveals opportunities where management can alter the outcome of the invasion in the threatened areas. The spread of an established non-native organism may be inevitable but the devastation caused by the organism may be mitigated with early, informed intervention. Concurrent efforts to manage impacted and threatened areas may provide the best prognosis for the vulnerable ecosystems. Proactive management moves past the idea of protecting the hosts from exposure to the established non-native invader and shifts toward facilitating naturalization by preparing the landscape to sustain ecosystem function into the future in the presence of the invader. For WPBR, this means facilitating evolution of genetic resistance in the pine host to the non-native pathogen. Positioning the ecosystem for greater resilience upon invasion is especially important for traditionally minimally managed ecosystems where the risk of ecological impacts is high. These ecosystems may be remote but they are not out of reach for invasion by non-native organisms.

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