

Proactive Limber Pine Conservation Strategy for the Greater Rocky Mountain National Park Area

Anna W. Schoettle, Kelly S. Burns, Christy M. Cleaver, J. Jeff Connor



Schoettle, Anna W.; Burns, Kelly S.; Cleaver, Christy M.; Connor, J. Jeff. 2019.

Proactive limber pine conservation strategy for the Greater Rocky Mountain National Park Area. Gen. Tech. Rep. RMRS-GTR-379. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station. 81 p.

Abstract

This proactive conservation strategy addresses the unique situation of limber pine in the Greater Rocky Mountain National Park Area (GRMNPA). The target area includes Rocky Mountain National Park and surrounding areas of northern Colorado and southern Wyoming. The GRMNPA is at the infection front for white pine blister rust (WPBR) where populations were also impacted by the recent mountain pine beetle epidemic and are threatened by climate change. This is the first proactive conservation strategy for a five-needle pine species in North America. It focuses on timing specific monitoring efforts and interventions to sustain healthy limber pine populations and ecosystems during invasion and naturalization of WPBR, thereby putting limber pine on a trajectory that reduces the probability of ecosystem impairment in the future. The high frequency of complete resistance to WPBR in limber pine populations in the GRMNPA is a distinctive feature of this area's ecology. Having this information and other site-based genetic and disturbance ecology information before WPBR affects the populations is also unique and warranted the development of this proactive conservation strategy. The strategy outlines recommendations to promote (1) ex situ and in situ limber pine conservation and protection, (2) increased limber pine population size and sustained genetic diversity, (3) treatments to maintain durability of genetic resistance to WPBR, (4) monitoring forest health conditions for early detection of WPBR and changes in pathogen virulence, and (5) coordinated management actions within and among agencies. The recommendations apply to the GRMNPA and possibly to all of the southern Rockies; the approach used can be applied further. The recommendations herein are expected to be relevant for at least 20 years.

Keywords: *Pinus flexilis*, five-needle white pine, white pine blister rust, genetic disease resistance, gene conservation, regeneration, proactive management, resilience, *Cronartium ribicola*, *Dendroctonus ponderosae*

All Rocky Mountain Research Station publications are published by U.S. Forest Service employees and are in the public domain and available at no cost. Even though U.S. Forest Service publications are not copyrighted, they are formatted according to U.S. Department of Agriculture standards and research findings and formatting cannot be altered in reprints. Altering content or formatting, including the cover and title page, is strictly prohibited.

Cover photo: Limber pine along Lake Haiyaha (J. J. Connor, NPS).

Authors

Anna W. Schoettle is a Research Plant Ecophysiologicalist with the USDA Forest Service, Rocky Mountain Research Station in Fort Collins, Colorado.

Kelly S. Burns is a Plant Pathologist with the USDA Forest Service, Forest Health Protection in Lakewood, Colorado.

Christy M. Cleaver was a Research Associate at Colorado State University in Fort Collins, Colorado, at the time of writing; she is now a Plant Pathologist with the USDA Forest Service, Forest Health Protection in Coeur d'Alene, Idaho.

J. Jeff Connor is a Natural Resource Specialist (retired) from the DOI National Park Service, Rocky Mountain National Park in Estes Park, Colorado.

Pesticide Precautionary Statement

This publication reports research involving pesticides. It does not contain recommendations for their use, nor does it imply that the uses discussed here have been registered. All uses of pesticides must be registered by appropriate State and/or Federal agencies before they can be recommended.

CAUTION: Pesticides can be injurious to humans, domestic animals, desirable plants, and fish or other wildlife if they are not handled or applied properly. Use all pesticides selectively and carefully. Follow recommended practices for the disposal of surplus pesticides and pesticide containers.

The use of trade or firm names in this publication is for reader information and does not imply endorsement by the U.S. Department of Agriculture of any product or service.

Preface

This strategy for the conservation of limber pine is applicable to the Greater Rocky Mountain National Park Area (GRMNPA), which includes Rocky Mountain National Park (RMNP) and surrounding areas of northern Colorado and southern Wyoming. An earlier version was prepared specifically for RMNP; however, the genetic and ecological characteristics of RMNP and the greater area are sufficiently similar that the authors have expanded the reference area. The recommendations in this strategy apply to this greater area and possibly to all of the southern Rockies; the approach we used can be applied further. The information used in this strategy is the most current available and includes site-based research on genetics, adaptive variation, regeneration dynamics, disturbance regimes, forest health condition, and ecological interactions of limber pine as well as extrapolation of research from limber pine in other parts of its distribution and other five-needle pines, where we thought it necessary and appropriate. We expect the recommendations herein will continue to be relevant for at least 20 years.

This geographic area is at the infection front for white pine blister rust (WPBR). As the disease continues to spread and intensify, the forest health condition of limber pine will change. Consequently, continued monitoring (as recommended in this strategy) and consultation between the National Park Service, U.S. Forest Service Forest Health Protection (FHP), and Rocky Mountain Research Station (RMRS), and local university collaborators are encouraged in order to assess and interpret the changes to these ecosystems over time. Given the dynamic nature of the landscape, the scheduled timing and intensity of specific actions recommended in this strategy will be adapted, reevaluated, and refined as new information becomes available.

This strategy is the outcome of a collaboration between RMNP, RMRS, and FHP. Begun in 2008 by Jeff Connor, Natural Resource Specialist for RMNP, this partnership was requested by RMNP and put into action products of the Proactive Strategy Research Program initiated by Schoettle in 2001, introduced in 2004 (Schoettle 2004a) and further developed in 2007 (Schoettle and Sniezko 2007). We established a network of limber pine sites in and around RMNP for (1) protection from mountain pine beetle, (2) forest characterization, (3) collection of seed for gene conservation, (4) genetic studies including common-garden experiments, and (5) WPBR resistance testing. These studies were accomplished with additional collaborations with Colorado State University (Fort Collins, Colorado), U.S. Forest Service Dorena Genetic Resource Center (Cottage Grove, Oregon), and Mountain Studies Institute (Silverton, Colorado), and they complement other collaborative studies with Great Sand Dunes National Park and Preserve.

Other plans to manage effects of WPBR for high-elevation five-needle pines exist. However, most of the other strategies outline approaches and actions to restore function to populations and ecosystems that have already undergone high WPBR-caused mortality in whitebark pine—a species that has been shown to now warrant designation as endangered in the United States and Canada. These plans include:

- Managing for Healthy White Pine Ecosystems in the United States to Reduce the Impacts of White Pine Blister Rust (Samman et al. 2003)
- Whitebark Pine Restoration Strategy for the Pacific Northwest Region 2009–2013 (Aubry et al. 2008)
- Management Guide to Ecosystem Restoration Treatments: Whitebark Pine Forests of the Northern Rocky Mountains, U.S.A. (Keane and Parsons 2010)

- Whitebark Pine Strategy for the Greater Yellowstone Area (Greater Yellowstone Coordinating Committee Whitebark Pine Subcommittee 2011)
- A Range-wide Restoration Strategy for Whitebark Pine (*Pinus albicaulis*) (Keane et al. 2012)
- Strategies, Tools, and Challenges for Sustaining and Restoring High Elevation Five-Needle White Pine Forests in Western North America (Keane and Schoettle 2011)
- Alberta Whitebark Pine Recovery Plan 2013–2018 (Alberta Whitebark and Limber Pine Recovery Team 2014b)

Only three restoration or conservation plans address limber pine. Many of the interventions recommended herein are shared with these restoration strategies, though they differ in their timing, site prioritization, and specifics. These plans are:

- White Pine Blister Rust in the Rocky Mountain Region and Options for Management (Burns et al. 2008)
- White Pines, Blister Rust, and Management in the Southwest (Conklin et al. 2009)
- Alberta Limber Pine Recovery Plan 2014–2019 (Alberta Whitebark and Limber Pine Recovery Team 2014a)

This conservation strategy addresses the unique situation of limber pine in RMNP and the southern Rockies. It recommends proactive conservation actions specific to the southern Rockies based on knowledge from the RMNP/RMRS/FHP program and other research that provides site-based information gathered before ecosystem impairment by WPBR. It focuses on timing the specific monitoring efforts and interventions to sustain healthy limber pine populations and ecosystems during invasion and naturalization of WPBR, thereby putting limber pine on a trajectory that reduces the probability of ecosystem impairment in the future. The high frequency of complete resistance to WPBR in limber pine populations in RMNP and surrounding areas is a unique feature of this area's ecology. That we have this information and the other site-based genetic and disturbance ecology information before WPBR affects the populations is unique. This situation justifies developing a conservation strategy specific to RMNP and the greater area.

Respectfully,

Anna W. Schoettle, Kelly S. Burns, Christy M. Cleaver, and J. Jeff Connor

Executive Summary

Limber pine (*Pinus flexilis*) is common in northern Colorado and southern Wyoming and grows along the full elevation gradient from the Pawnee National Grasslands to the alpine treeline. It occurs on Federal Forest Service, National Park Service, and Bureau of Land Management (BLM) lands as well as State, county, and private lands and grows in designated wilderness areas. Limber pine is a keystone species that maintains ecosystem structure and function. It defines the alpine treeline, grows on exposed sites too harsh for other tree species, often becomes established on a site soon after disturbance, facilitates forest succession and the growth of understory species, aids in soil stabilization and snowpack retention and melt, and produces seeds that are a food source for birds, small mammals, and bears. Here, we outline a strategy for conserving limber pine that is applicable to the Greater Rocky Mountain National Park Area (GRMNPA), which includes Rocky Mountain National Park (RMNP) and surrounding areas of northern Colorado and southern Wyoming.

Limber pine has been designated a Species of Management Concern in RMNP, and maintains biodiversity in the park and greater landscape. Additionally, as long-lived and wind-defiant trees, limber pines are admired for their aesthetic value and cultural significance throughout their distribution, including the sentinel on Knife Edge along Trail Ridge Road and another by Lake Haiyaha. Most of the limber pine within RMNP occurs in designated wilderness managed under Class I Revegetation Guidelines.

Throughout the GRMNPA, limber pine is declining due to the combined effects of recent severe droughts and the climate-exacerbated mountain pine beetle (MPB, *Dendroctonus ponderosae*) outbreak. It is also imminently threatened by the invasion of the nonnative pathogen *Cronartium ribicola*, which causes the lethal disease white pine blister rust (WPBR) in five-needle white pines. In North America, WPBR has spread through much or part of the range of eight out of nine white pine species, affecting community composition and function. WPBR was confirmed in southern Wyoming in the 1990s, in northern Colorado in 1998, and in RMNP in 2010. It is expected to spread, kill trees, and negatively affect biodiversity, ecosystem processes, and other resources, compounding the impacts of changing climate. These stressors are causing widespread mortality throughout much of limber pine's range and basal area losses are projected to exceed 40 percent by 2030. Consequently, limber pine is listed as a Special Status Species on BLM land in Wyoming and is recommended for endangered status in Canada. Loss of this keystone species would ultimately lead to cascading ecological consequences and loss of biodiversity in the GRMNPA. Sustaining limber pine populations cannot be achieved with a "no action" option.

The U.S. Forest Service Rocky Mountain Research Station (RMRS) began the Five-Needle Pine Proactive Strategy Research Program in 2001, with a focus on conservation and management of limber pine and Rocky Mountain bristlecone pine (*P. aristata*) in the southern Rockies. In 2008, a collaboration between RMNP, RMRS, and U.S. Forest Service Forest Health Protection (FHP) initiated an intensive effort to conserve limber pine genetic diversity in and around RMNP. The intensive RMNP program and the broader Proactive Strategy research provide the site-based information necessary to develop this Proactive Limber Pine Conservation Strategy for the GRMNPA. The objectives are to: (1) conserve genetic diversity and populations of limber pine throughout the GRMNPA, (2) provide science-based recommendations appropriate for the GRMNPA (in and outside of wilderness) to sustain healthy high-elevation ecosystems, and (3) encourage and

facilitate coordination among a variety of land managers to preserve the genetic integrity of native flora and fauna in the southern Rocky Mountains and support collaborative efforts to ensure the future health of limber pine.

Managers in the GRMNPA are in a unique and enviable position in western North America, as they are proactively focusing on this threatened species while the ecosystems are still largely in “healthy” condition (that is, before WPBR-caused mortality of reproductive trees). This proactive approach enables informed management to avoid and mitigate ecological impacts before they are expressed. Many western national parks and national forests are in a reactive mode, managing the species only after WPBR-caused mortality of limber pine and other five-needle pines. Learning from the ecological effects from losses of whitebark pine (*Pinus albicaulis*) and limber pine in the northern Rockies, RMNP and other entities have opted to implement proactive conservation activities in an effort to shift limber pine’s trajectory toward resilience and away from endangered species status. Natural regeneration processes with supplemental planting or seeding before and early in the spread of WPBR will increase the number of trees on the landscape and will offset future mortality. Early intervention will reduce the potential need for restoration later during naturalization of WPBR. Recent research and products from RMRS, FHP, and RMNP provide unique and timely area-specific knowledge that includes the following:

- The ecosystems are still in the early stages of WPBR invasion, allowing time before severe ecological impacts are expressed.
- Post-fire habitats in the GRMNPA are conducive to successful natural regeneration of limber pine.
- Genetic resistance to WPBR, conferred by a single dominant resistance allele (*Cr4*), is present in native populations of limber pine in the GRMNPA at high frequency (~20 percent), although this resistance may be overcome by the rust with time (i.e., it may not be durable).
- Genetic resistance to WPBR that is conferred by multiple genes (more likely to be durable) may be present in the GRMNPA at low frequencies.
- MPB outbreaks in the GRMNPA are cyclical; dwarf mistletoe (*Arceuthobium cyanocarpum*) is common and other native pests are present.
- Climate change is projected to shift limber pine populations to higher elevations in RMNP as well as intensify the effects of native pests and pathogens throughout the region.

The Proactive Conservation Strategy recommends continued and expanded application of the current proactive management approach because it offers the best opportunity to prepare the landscape for greater resilience before WPBR-caused impacts develop and to sustain populations as the disease spreads.

The major focal areas for management activities are:

- **Promote ex situ conservation:** Continue and expand efforts to collect and archive limber pine genetic diversity through seed collections.
- **Promote in situ conservation:** Protect limber pine trees from MPB, WPBR, and fire to minimize mortality when and where land designations and management objectives permit.
- **Increase population size and sustain genetic diversity:** Increase the number of limber pine trees on the landscape through planting or seeding, or both, immediately to offset future mortality and to sustain viable genetically diverse, self-sustaining populations.

- **Locate treatments to maintain durability of qualitative WPBR resistance:** Minimize selective pressure on the rust by planting trees with a range of susceptibilities in low-WPBR-risk areas to reduce the probability of the proliferation of genotypes virulent to *Cr4*.
- **Discover, develop, and deploy local quantitative WPBR-resistant sources:** Research quantitative (polygenic) WPBR resistance types in limber pine in the GRMNPA and establish a seed orchard/clone bank of these genotypes (which can be protected from fire and other stresses) to provide seed for future planting projects.
- **Monitor pines and rust:** Monitor limber pine health and monitor for early detection of WPBR and WPBR virulence.
- **Coordinate management actions within and among agencies:** Preserve and diversify the age- and size-class distribution of limber pines as well as all successional stages across the landscape through fuels treatments, vegetation management, and planned fire.

The major focal area for leadership activities is:

- **Interagency coordination and cooperation for efficient use of resources for effective management outcomes:** The U.S. Forest Service has an “all lands” strategic approach that emphasizes consideration of the greater landscape and that crosses administrative boundaries in management planning. RMNP also takes into consideration the greater landscape surrounding the park, referred to as the Protected Area Centered Ecosystem, when managing resources. Further, RMNP focuses on continued leadership in limber pine conservation in the southern Rockies through research, genetic resource management, and coordination with other agencies and parks. RMNP managers strive to continue research on limber pine ecosystems and the WPBR pathosystem and encourage infrastructure that supports management objectives (e.g., a seed orchard/clone bank). Maintaining viable seed sources and seed collections helps to fulfill the park’s obligation as an International Biosphere Reserve.

Acknowledgments

We thank the contributors to this document including Sparkle Malone, Brian Howell, Jennifer Ross, Bob Cain, Sky Stephens, and William Jacobi. We also thank reviewers Ben Bobowski, Diana Tomback, Mike Battaglia, William Jacobi, Erin Borgman, and Amy Chambers, whose comments greatly improved the document. We also thank Jeff Witcosky, Richard Snieszko, Angelia Kegley, Betsy Goodrich, Jen Klutsch, Jonathan Coop, William Jacobi, John Popp, Mike Antolin, and Phyllis Pineda-Bovin



for their assistance with the research that provided much of the science foundation for the strategy. We extend our thanks to the RMNP coordinators whose commitment made this project possible including Paul McLaughlin, Scott Esser, Erin Borgman, Brian Verhulst, John Mack, Dale Loper, and Judy Visty, and the crew of exceptional volunteers over the years.

We also recognize the contributions of Sheryl Costello, U.S. Forest Service Rocky Mountain Region Entomologist, who tragically lost her life doing what she loved—mountain climbing. Her high degree of professionalism and expertise played an important role in the early development of this strategy.

Table of Contents

SECTION 1. PURPOSE AND NEED	1
1.1. Purpose and Need.....	1
1.2. Federal Forest Service and Park Service Policy	10
1.3. Objectives for Limber Pine Conservation	12
SECTION 2. STRATEGY FOR CONSERVATION ACTIONS	14
2.1. Consequences of Doing Nothing.....	14
2.2. The Time to Act Is Now.....	15
2.3. Cornerstones of Management.....	16
2.3.1. <i>Support Regeneration and Increased Population Size to Maintain Adaptive Capacity</i>	16
2.3.2. <i>Manage Genetic Resistance to White Pine Blister Rust for Sustainability</i>	16
2.3.3. <i>Foster Early Awareness and Engagement to Enhance Opportunity for Success</i>	17
SECTION 3. RECOMMENDED CONSERVATION ACTIONS	18
3.1. Promote Ex Situ Conservation	19
3.2. Promote In Situ Conservation	19
3.3. Increase Population Size and Sustain Genetic Diversity.....	20
3.4. Locate Treatments to Maintain Durability of Qualitative Resistance to White Pine Blister Rust.....	22
3.5. Discover, Develop, and Deploy Local Quantitative White Pine Blister Rust-Resistant Seed Sources.....	23
3.6. Monitor Pines and Rust	24
3.7. Coordinate Management Actions Within and Among Agencies.....	27
SECTION 4. RESOURCES TO EXECUTE THIS STRATEGY	28
SECTION 5. GUIDELINES FOR MANAGEMENT OF LIMBER PINE.....	29
5.1. Limber Pine Seed Collections—Bulk Cone Collections.....	29
5.2. Limber Pine Seed Collections—Individual Tree Collections.....	31
5.3. Limber Pine Seed Storage and Database	33
5.4. Protecting Limber Pine from Mountain Pine Beetle (MPB)	34
5.5. Sanitation Pruning to Remove White Pine Blister Rust (WPBR) Infections	36
5.6. Planting Limber Pine Seedlings	38
5.7. Direct Seed Limber Pine.....	40
5.8. Seed Transfer / Source Guidelines.....	41
5.9. Natural Regeneration	41
5.10. Locating Treatments and Selecting Seed Sources to Maintain Durability of WPBR Resistance.....	43
5.11. Testing for Quantitative Resistance to WPBR.....	44
5.12. Monitoring—Forest Health.....	45
5.13. Monitoring—Early Detection of WPBR in Riparian Areas.....	46
5.14. Monitoring – Rust Virulence	47
5.15. Consider Limber Pine During Fuel Treatments and Planned and Unplanned Fire.....	47
5.16. Limber Pine Seed Orchard / In Situ Clone Bank	49

SECTION 6. BACKGROUND	51
6.1. Overview.....	51
6.2. Evolutionary History of Limber Pine	55
6.3. Genetic Diversity	55
6.4. Natural History Traits	56
6.5. Community Dynamics.....	56
6.6. Clark's Nutcracker Ecology.....	57
6.7. Natural Regeneration Facilitated by Clark's Nutcracker	58
6.8. Mountain Pine Beetle Biology and Control	60
6.9. White Pine Blister Rust Biology and Control	61
6.10. Dwarf Mistletoe Biology and Control	64
6.11. Susceptibility to Other Biotic Damage Agents.....	64
6.12. Role of Fire in Limber Pine Ecology	65
6.13. Sensitivity to Abiotic Damage Agents: Nitrogen Deposition and Climate Change.....	66
SECTION 7. REFERENCES	68

Abbreviations Used Herein

BLM	United States Department of the Interior, Bureau of Land Management
d.b.h.	diameter at breast height (4.5 ft, 1.37 m)
FHP	USDA Forest Service, Forest Health Protection
FSM	Forest Service Manual
GRMNPA	Greater Rocky Mountain National Park Area
MPB	mountain pine beetle (<i>Dendroctonus ponderosae</i>)
NPS	United States Department of the Interior, National Park Service
RMNP	Rocky Mountain National Park
RMRS	USDA Forest Service, Rocky Mountain Research Station
ROMN	Rocky Mountain Inventory and Monitoring Network
USDA	United States Department of Agriculture
USFS	USDA Forest Service
WPBR	white pine blister rust (<i>Cronartium ribicola</i>)

SECTION 1. PURPOSE AND NEED

1.1. Purpose and Need

Limber pine (*Pinus flexilis*) is the only tree designated as a Species of Management Concern in Rocky Mountain National Park (RMNP) and is of management interest on other Federal, State, and county lands (Burns et al. 2008). It is declining in the Greater RMNP Area (GRMNPA) from the combined effects of native insects, drought, and climate change and is further threatened by a lethal, nonnative pathogen. Specifically, limber pine has succumbed to the recent mountain pine beetle (MPB, *Dendroctonus ponderosae*) outbreak and is imminently threatened by the nonnative fungal pathogen *Cronartium ribicola*, which causes white pine blister rust (WPBR). The combined threats of MPB, WPBR, limber pine dwarf mistletoe (*Arceuthobium cyanocarpum*), and climate change have caused widespread decline and mortality in limber pine. These threats have also reduced the capacity for forest recovery throughout a significant portion of the species' range (Cleaver et al. 2015; Smith et al. 2013); a 40 percent loss in basal area of limber pine is projected by 2030 in the absence of intervention (Krist et al. 2014).

White pine blister rust was detected on limber pine in southern Wyoming in the 1990s, in northern Colorado on limber pine in 1998 (Johnson and Jacobi 2000), and in south-central Colorado in 2003 on limber and Rocky Mountain bristlecone pine (*P. aristata*) (Blodgett and Sullivan 2004). In 2010, WPBR was confirmed on limber pine in RMNP (Schoettle et al. 2011a, 2018a). The incidence and severity of the disease are expected to increase over time, leading to negative impacts on biodiversity, ecosystem processes, and other natural resources. White pine blister rust kills trees of all ages. It kills seedlings and saplings most rapidly, thereby impairing post-disturbance recovery, and therefore resilience of the overall forest landscape. The purpose of this strategy is to coordinate management objectives and implement proactive strategies and tools to sustain limber pine populations and ecosystems in the GRMNPA.

As a foundation and keystone species, especially at high elevations and in harsh habitats, limber pine affects ecosystem stability and processes, and it also has a disproportionately large influence on biodiversity relative to its abundance. Limber pine is the only five-needle white pine species in most of the GRMNPA and is an important ecosystem component across its patchy, broad distribution in western North America (Schoettle 2004b; Steele 1990). Limber pine occurs range-wide across a greater span of elevations (2,250 ft to 12,500 ft [870 m to 3,810 m]) than any of the other white pine species (Schoettle and Rochelle 2000; Steele 1990). In the GRMNPA it has a broader elevational range than any other conifer species (5,250 ft to 11,155 ft [1,600 m to 3,400 m]) and is the only tree species found at all elevations up to treeline (Goetz et al. 2010). Limber pine defines the lower treeline in the Pawnee National Grassland and the upper alpine treeline in RMNP. Limber pine is often replaced at the alpine treeline by two other five-needle pines outside the GRMNPA—Rocky Mountain bristlecone pine (*P. aristata*) to the south and whitebark pine (*P. albicaulis*) to the north—highlighting the unique physical and ecological conditions of the GRMNPA.

Limber pine is shade-intolerant and typically occurs in open, low-density stands on dry, rocky, windswept sites that are free of competition from other tree species (Schoettle 2004b; Schoettle and Rochelle 2000). It is often the first tree species to regenerate after fire and facilitates forest succession (Baumeister and Callaway 2006; Donnegan and Rebertus 1999). Additionally, limber pine aids in soil stabilization and snowpack retention and also provides a food source for squirrels, other rodents, bears, and birds, particularly Clark’s nutcrackers (*Nucifraga columbiana*), which benefit limber pine by providing long-distance seed dispersal (Tomback and Taylor 1987). The nutcracker-limber pine interaction is similar to that of whitebark pine—an iconic natural history story in the West.

Limber pine is also admired for its cultural importance and significance, aesthetic value, and symbolism as a survivor, and it is a favorite with mountain visitors. The pine’s large, nutritious seeds were an important food source for Native Americans, and other parts of the tree were used for medicinal and ceremonial purposes (Moerman 1998, 2009; Tomback et al. 2011). Limber pine inhabits historically significant popular mountain passes of the Rocky Mountains and provides a unique connection with American history (Peattie 1991). One particular limber pine beside the route of the first transcontinental railroad, named “The Old Pine Tree,” is deemed the “most photographed object in Wyoming,” (Peattie 1991, p. 35). Limber pine is a long-lived species; some individuals in the GRMNPA are more than 1,000 years old (Schoettle 2004b). Their unique, gnarled appearance signals strength and endurance despite fierce winds at exposed, high-elevation sites. Several iconic and frequently photographed stands of limber pine exist in RMNP, including the stand on Knife Edge along Trail Ridge Road and another along Lake Haiyaha (fig. 1).



Figure 1—Limber pine along Lake Haiyaha (J. J. Connor, NPS).

In the GRMNPA, limber pine occurs on nearly 130,000 ac (52,609 ha), yet most of the area is suitable for the species (fig. 2). The majority of limber pine within the GRMNPA occurs on lands administered by the U.S. Forest Service (USFS) (53 percent), followed by the National Park Service (NPS) (14 percent), Bureau of Land Management (BLM) (3 percent), Colorado State Forest Service (3 percent), and Wyoming Department of Forestry (0.5 percent). Limber pine occurs on about 5,500 ac (2,225 ha) in the park and much of the forested eastern front of RMNP is also potential limber pine habitat. A large portion of limber pine's distribution within the GRMNPA occurs on privately owned lands (26 percent).

The native and nonnative biological disturbance agents, combined with a warming climate, are threatening limber pine in the GRMNPA and throughout much of its distribution. **Of the 13 pine species attacked by MPB, limber pine is a preferred host (Cerezke 1995).** Mountain pine beetles, native to western North America, have caused widespread mortality of pines throughout much of its range (Chapman et al. 2012; Raffa et al. 2008; Smith et al. 2015). In Colorado, 3.4 million ac (1.4 million ha) have been affected since the start of the most recent outbreak in 1996 (USFS Rocky Mountain Region 2014). Increased average monthly temperatures have favored MPB in this latest epidemic (Chapman et al. 2012), and **climate change increases the likelihood of expansion of MPB into higher elevations in the Rocky Mountains, where outbreaks historically have been rare (Raffa et al. 2008).**

In the GRMNPA, the effects of MPB from 1996 to 2015 are evident throughout the distribution of pine hosts (figs. 3 and 4). On evaluated plots in RMNP, only 55 percent of limber pine trees were categorized as healthy (Kelly Burns, personal communication 2013). The effects of the MPB-caused mortality of limber pine in the GRMNPA are not uniform; the proportion of a plot with MPB activity ranged from 33 to 96 percent in subareas of the GRMNPA (average of 63 percent) (Cleaver et al. 2015). The percentage of stems killed by MPB also varied from 6 to 32 percent within infested plots (Cleaver et al. 2015). In northern Colorado (excluding RMNP), MPB was active in 71 percent of the plots with an average incidence of 14 percent (as of 2011) (Cleaver et al. 2015), similar to the incidence in RMNP (average incidence of 19 percent; range of 0–49 percent). Impacts to limber pine include mortality of mature, cone-bearing trees—some of which may have genetic resistance to WPBR—and possible loss of genetic diversity. Stressors such as drought, disease, and insects (limber pine engraver [*Ips woodi*], and twig beetles [*Pityophthorus* spp. and *Pityogenes* spp.]) (Millar et al. 2007; USFS 2011a,b) may lead to increased susceptibility to bark beetles.

Assessments in 2011 and 2012 of more than 22,500 limber pine trees in central Colorado, Wyoming, and southern Montana indicated that only half were categorized as healthy, another quarter were declining or dying, and the remaining quarter were dead primarily due to MPB, WPBR, and dwarf mistletoe (Cleaver et al. 2015; Cleaver et al. 2017). Incidence of WPBR on limber pine was 26 percent, incidence of dwarf mistletoe was 9 percent, and 18 percent were killed by bark beetles (Cleaver et al. 2015). Additionally, in subalpine forests of the Colorado Front Range, drought and warmer temperatures are increasing the rate of limber pine mortality, even in the absence of bark beetles (Smith et al. 2015).

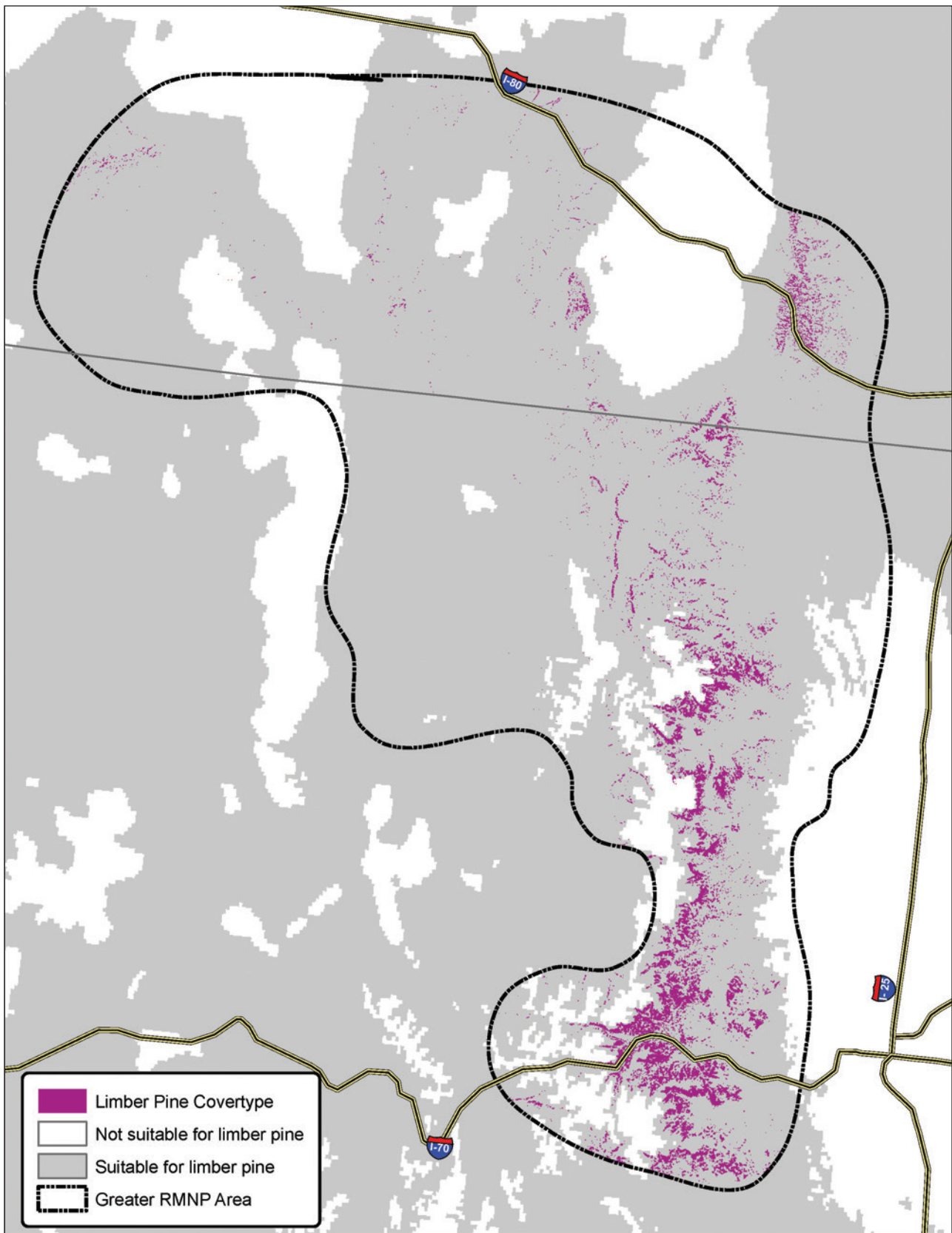


Figure 2—Current limber pine distribution (purple) and suitable limber pine habitat (gray) in the GRMNP. Limber pine suitability was determined based on climate (temperature and precipitation) thresholds. Limber pine research plot locations throughout the Front Range were used to create a subsample of the PRISM 30-year normals (1981-2010; <http://prism.nacse.org/normals/>) products. Thresholds for minimum and maximum mean annual temperature, and mean annual precipitation were identified for sample locations. Values greater than or less than the thresholds were classified as non-suitable (white).

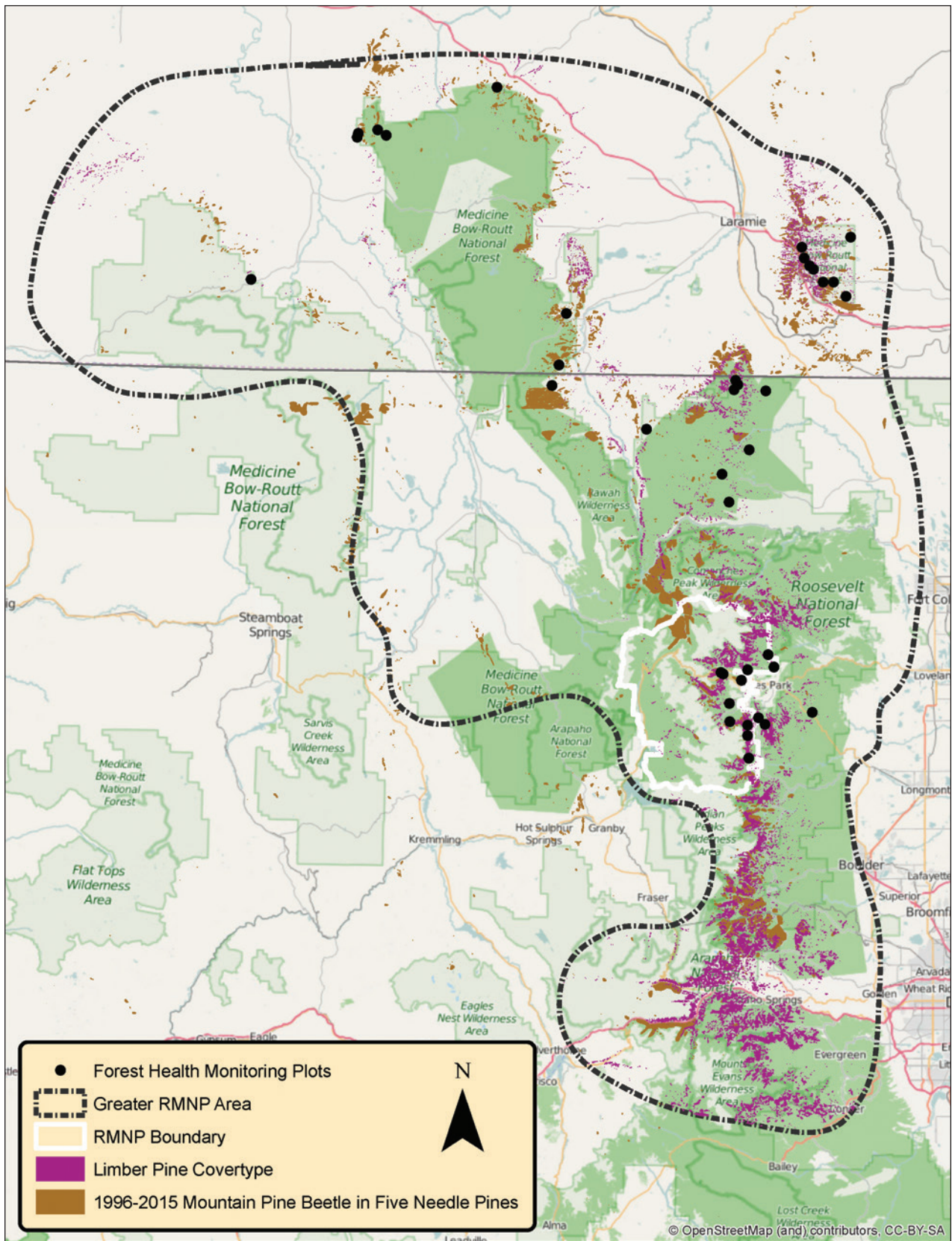


Figure 3—Map showing concentrated areas of limber pine mortality (tan) caused by mountain pine beetle based on U.S. Forest Service Aerial Detection Surveys from 1996-2015. Limber pine distribution is indicated by purple. Forest health monitoring plots are indicated by black circles.

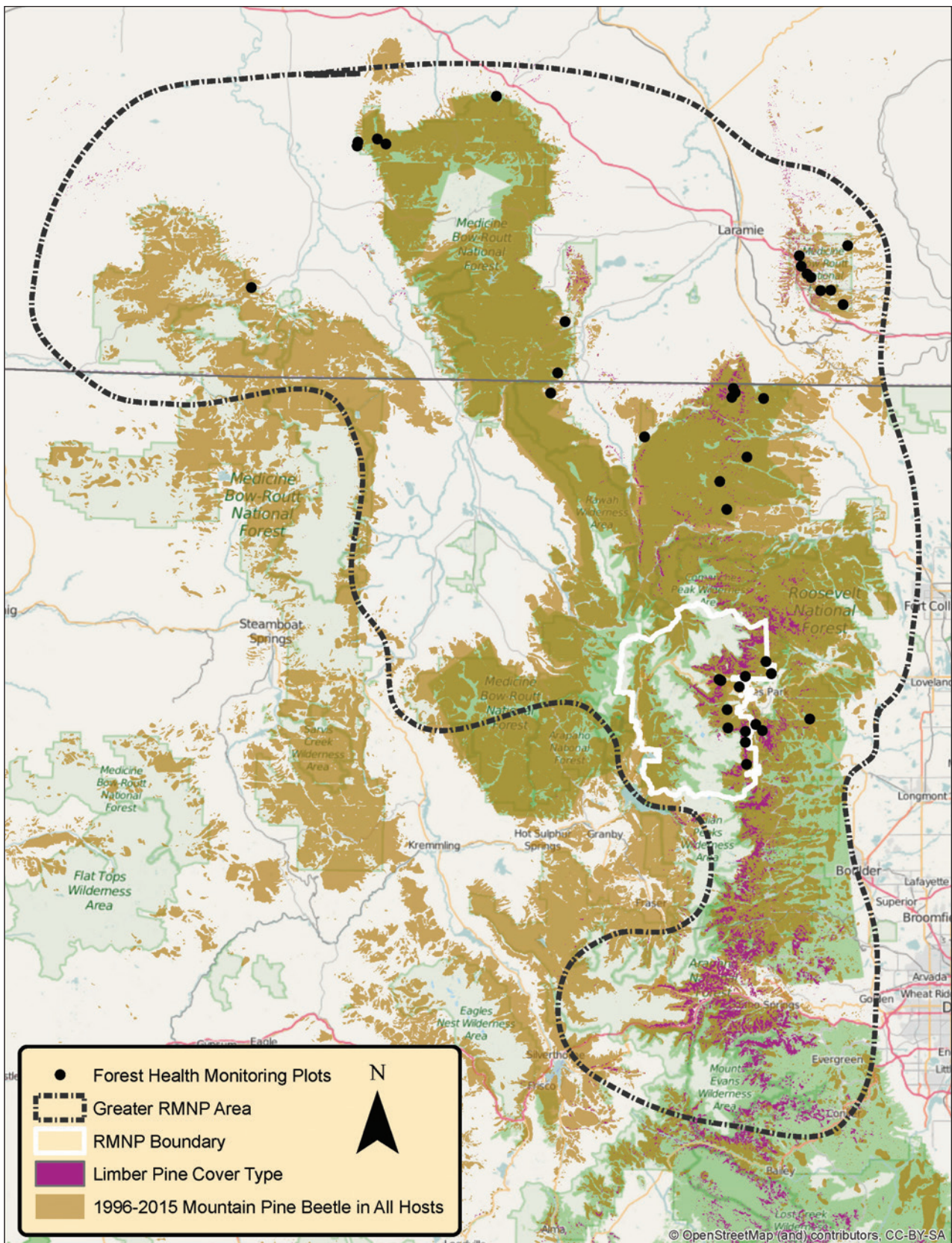


Figure 4—Map showing concentrated areas of mortality of all pines (tan) caused by mountain pine beetle based on U.S. Forest Service Aerial Detection Surveys from 1996-2015. Limber pine distribution is indicated by purple.

Over the entire GRMNPA, dwarf mistletoe is present in about 30 percent of the evaluated plots at an average incidence of almost 9 percent (calculated from data from Cleaver et al. 2015). In northern Colorado, dwarf mistletoe was found on limber pine in 33 percent of evaluated plots in 2011 (outside of RMNP) with an incidence of 7 percent (Cleaver et al. 2015). Dwarf mistletoe is a greater problem within RMNP, as it was present in 60 percent of evaluated study areas in 2009 and has an overall incidence of 12 percent (arithmetic mean) (Klutsch et al. 2011). Before the most recent MPB epidemic, the native limber pine dwarf mistletoe was the most damaging agent of limber pine after WPBR range-wide (Taylor and Mathiasen 1999). This species of dwarf mistletoe is especially virulent and has caused extensive mortality in limber, whitebark, Great Basin bristlecone (*Pinus longaeva*), and Rocky Mountain bristlecone pine (*Pinus aristata*) (Mathiasen and Hawksworth 1988). Dwarf mistletoe infections cause decreased growth, vigor, and seed production and increased mortality and may render the host susceptible to other diseases or insects, including MPB and *Ips* beetles (Geils et al. 2002; Taylor and Mathiasen 1999). Seedlings are susceptible to infection and rapid mortality, and severe infections in mature trees can reduce cone and seed production and quality (Geils et al. 2002).

As WPBR continues to spread, limber pine will undergo extensive mortality in the GRMNPA and throughout the southern Rocky Mountains (figs. 3 and 5). White pine blister rust has caused widespread mortality of trees in other populations, such as eastern white pine (*Pinus strobus*), western white pine (*Pinus monticola*), sugar pine (*Pinus lambertiana*), and high-elevation white pine species, including northern populations of whitebark pine and limber pine (Geils et al. 2010; Tomback and Achuff 2010; Tomback et al. 2011). Major economic and ecological losses have ensued and continue in affected areas. **Western white pine, a once-prized timber species, is now sparsely dispersed and currently occupies only 5 percent of its historical area (Man 2013).** In addition, whitebark pine, a foundation species, is declining across much of its range (Tomback and Achuff 2010). Populations of all WPBR-susceptible species risk extirpation as the pathogen continues to expand. Attempts to eradicate the disease or control it directly have failed (Maloy 1997). The U.S. Fish and Wildlife Service (2011) determined in 2011 that whitebark pine warranted Endangered Species status protection under the Endangered Species Act, and Canada designated whitebark pine as endangered in 2012 under the Species at Risk Act (Government of Canada 2012). Assessment of limber pine by the Committee on the Status of Endangered Wildlife in Canada determined it to be endangered in Canada, and the species was recommended for legal listing in November 2014 (Government of Canada 2014); formal proposal for the national listing as endangered is pending. The pine has been listed as endangered in Alberta for several years (Government of Alberta 2014). **Limber pine in Wyoming, where it is more common than in any other State, is on the Bureau of Land Management Wyoming's Special Status Species list (Bureau of Land Management Wyoming 2013).** The same factors that led to endangered status for whitebark pine and limber pine elsewhere threaten the GRMNPA and southern Rocky Mountains five-needle pine ecosystems.

It is only a matter of time until WPBR becomes common within currently uninfested portions of the GRMNPA. Since its introductions to western North America in the early 1900s, WPBR continues to spread and intensify within the ranges of

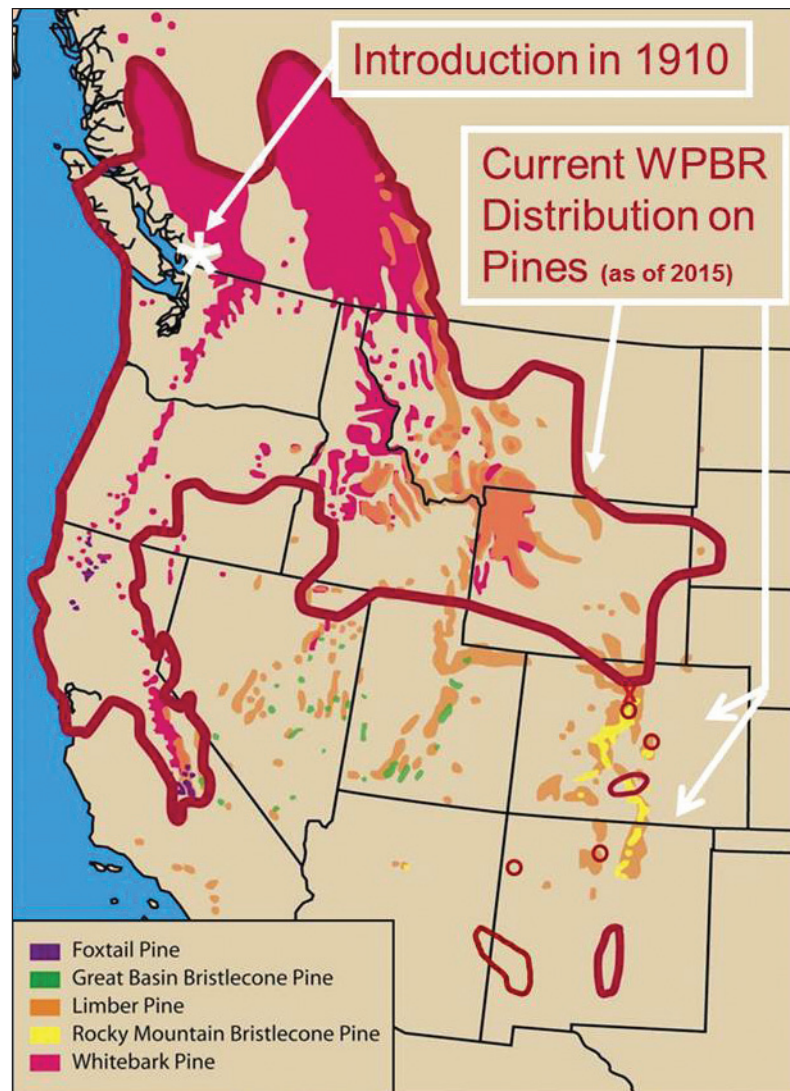


Figure 5—Map of the distribution of high elevation five-needle pines and the current (as of 2015) WPBR infection fronts in western North America. Note that not all stands of five-needle pines behind the infection front are infested.

susceptible and highly vulnerable hosts, including limber pine (fig. 6) (Blodgett et al. 2005; Burns 2006; Burns et al. 2011; Cleaver 2014; Kearns and Jacobi 2007; Maloney 2011; Smith and Hoffman 2001; Smith et al. 2013). White pine blister rust causes cankers that lead to a loss of vigor and ultimately death and also affects reproduction and regeneration by killing cone-bearing branches and seedlings.

Within the GRMNPA, WPBR is most common in the Laramie Range, being present in ~84 percent of evaluated plots with an average incidence of ~24 percent. It occurs in 58 percent of the plots in northern Colorado (excluding RMNP) with an incidence of 8 percent, and 18 percent of the plots in the Medicine Bow Mountains with an incidence of 2 percent (Cleaver et al. 2015). WPBR has been found in only one area of RMNP. Several infected trees were identified in 2010 and a larger infestation of about 65 trees was discovered in 2017; cankers were removed through sanitation pruning. Infections are sparse in areas south of the park, yet new infections continue to be found.

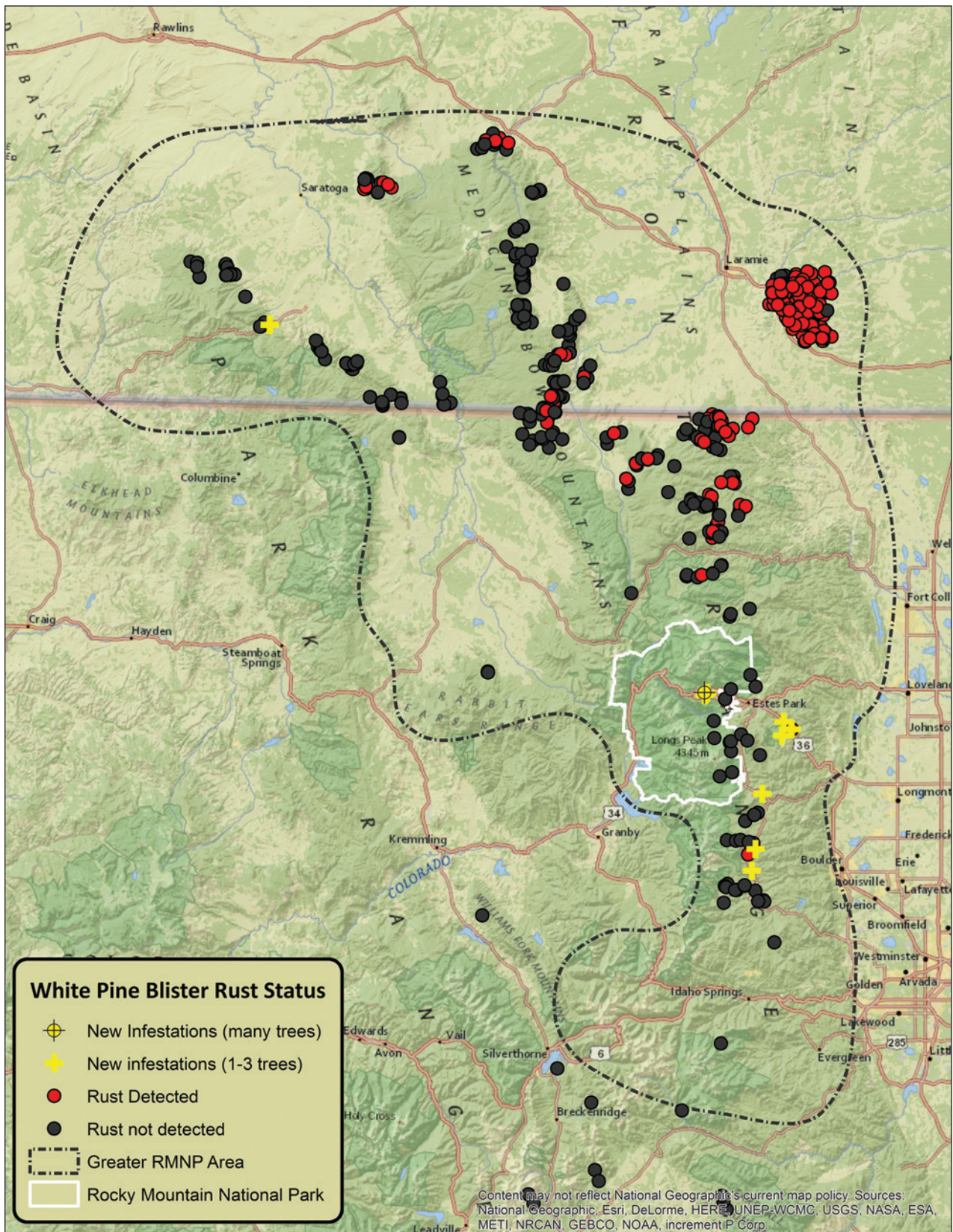


Figure 6—Map of WPBR presence and absence in the GRMNP. New infestations are also noted as of 2018.

Fifty-three percent of the limber pine habitat in Colorado is at risk for annual WPBR infection (Kearns et al. 2014); remaining habitat may also become invaded but may not support annual infections. Important factors found to positively influence WPBR risk (potential distribution) include density of limber pine, density of *Ribes inereme*, presence of ponderosa pine (*Pinus ponderosa*), stream density, relative humidity in May and September, maximum temperature in May, and mean May precipitation (Cleaver 2014; Kearns et al. 2014). Riparian areas have both the micrometeorological conditions and the abundance of alternate hosts that permit WPBR infection and sporulation, including cool, humid conditions, and *Ribes inerme*; we developed risk maps (figs. 2 and 7) to identify these potential areas for early detection of WPBR in the GRMNPA.

Further background information related to limber pine health and condition in general and specifically in the GRMNPA can be found in Section 6 of this document.

1.2. Federal Forest Service and Park Service Policy

The U.S. Forest Service is obligated by law and regulations, such as Executive Order 13112, to respond to invasive species that threaten terrestrial and aquatic resources of the National Forest System and to collaborate with Federal, State, and local partners to address invasive species that can spread from adjacent lands. The USFS policy for invasive species management and research has recently been updated by direction provided in Forest Service Manual (FSM) 2900 and FSMs 3400 and 4000. The most recent USFS Strategic Plan (2015, p. 11) highlights the goal to “sustain our nation’s forests and grasslands” under which it articulated the subgoals to “develop and apply detection, prediction, prevention, mitigation, treatment, restoration, and climate adaptation methods, technologies, and strategies for addressing disturbances such as wildfire, human uses, invasive species, insects, extreme weather events (e.g., storms), and changing climatic conditions;” “collaborate with other Federal agencies, State agencies, private landowners, communities, and American Indian tribes to improve the health and resilience of the land;” and “coordinate inventory, monitoring, and assessment activities across all lands to improve our adaptive management of natural resources.”

The USFS National Strategic Framework for Invasive Species Management (2013) presents the agency’s approach to addressing invasive species. The framework acknowledges that “proactive management to increase the resilience of threatened ecosystems to impacts by pending invasions might also be more cost effective than later restoration of degraded ecosystems,” (p. 11) and states that “the Forest Service will optimize efficacy and cost effectiveness of treatment by timing interventions to maximize forest health benefits,” (p. 10).

The NPS is guided in its decisions about resources by the requirements of the 1916 Organic Act, which states the agency’s purpose: “to promote and regulate the use of national parks in conformance with their fundamental purpose, which is to conserve the scenery and the natural and historic objects and the wildlife therein and to provide for the enjoyment of the same in such manner and by such means as would leave them unimpaired for the enjoyment of future generations,” (p. 535).

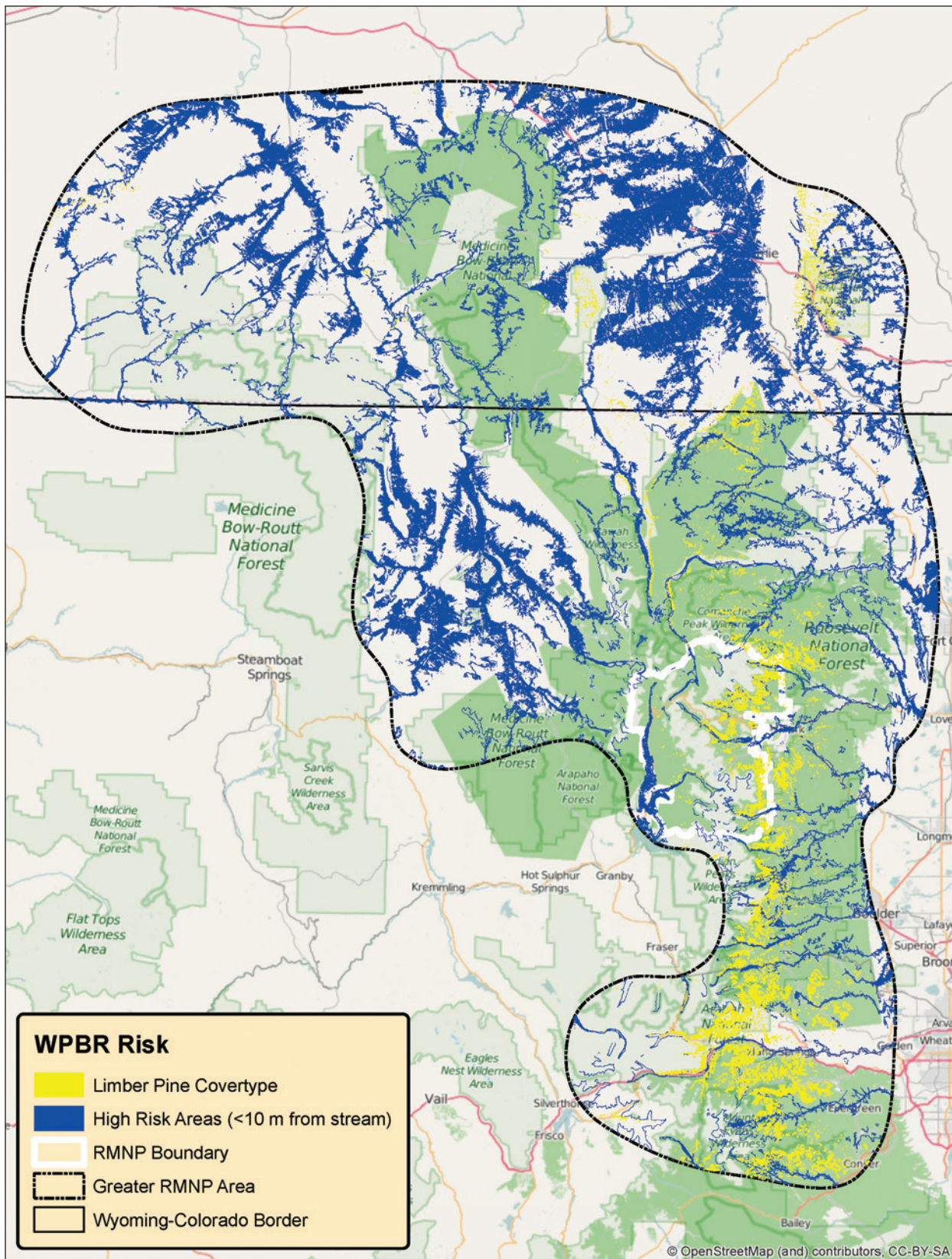


Figure 7—Map showing current distribution of limber pine (yellow) and areas with high risk of WPBR establishment in the GRMNP (blue). High-risk areas were delineated by buffering streams or water bodies to a change of 33 ft [10 m] in elevation (rather than Euclidean distance).

This authority was further clarified in the National Parks and Recreation Act of 1978: “Congress declares that...these areas, though distinct in character, are united... into one national park system.... The authorization of activities shall be construed and the protection, management, and administration of these areas shall be conducted in light of the high public value and integrity of the National Park System and shall not be exercised in derogation of the values and purposes for which these various areas have been established, except as may have been or shall be directly and specifically provided by Congress,” (p. 166).

The requirements placed on the NPS by the Organic Act and other environmental laws mandate that resources be passed on to future generations “unimpaired” (NPS 2006a). Great strides can be made to increase the probability of conserving limber pine and sustaining the healthy network of interacting elements that make up the high-elevation ecosystems in the park with the timely implementation of this Proactive Limber Pine Conservation Strategy. Continuing to take action early in the disease invasion and as WPBR continues to spread will enhance the resilience of the limber pine populations in the park for future generations.

As a designated International Biosphere Reserve since 1977, RMNP is also tasked with conservation of biological resources, including preservation of native flora and fauna. Preserving ecological integrity “in the context of ecological restoration refers to the reestablishment, on a disturbed site, of an ecological community that has a high degree (1:1 in the absolute case) of ecological integrity with the community that would have been present on the site had the disturbance not occurred,” (NPS 2006b, pp. 8-9). Ecological integrity should be maintained and restored to the best of current knowledge and ability. The Proactive Limber Pine Conservation Strategy will guide the park toward preservation and conservation of limber pine and its communities by maintaining genetic diversity, population size, and ecological processes while increasing genetic resistance to WPBR during the unavoidable invasion of WPBR. Sustaining viable limber pine populations will position the park to become a seed resource for surrounding areas and fulfill the intent of the International Biosphere Reserve.

The Wilderness Act of 1964 applies to RMNP and USFS lands. Most of RMNP was designated as wilderness under the Omnibus Public Lands Management Act of 2009 (National Park Service 2014). Under the 1964 Act, Federal managers of RMNP, USFS, and other Class I wilderness areas are obligated to preserve the natural and wilderness character of the land by restricting trammeling by humans.

1.3. Objectives for Limber Pine Conservation

Controlling the effects of infestation of invasive exotic species within the GRMNPA is an ongoing challenge for land managers. Invasive exotic species threaten natural and cultural resources (Burns et al. 2008; NPS 2003, 2006b). White pine blister rust threatens natural resource integrity and the ecological function and biodiversity of limber pine ecosystems. Because RMNP management goals include control of the establishment and perpetuation of nonnative species, management of WPBR is warranted in the Park; similar goals to sustain ecosystem health apply

to USFS lands (USFS 2013). Unfortunately, direct control of WPBR (i.e., eradication) is not possible (Geils et al. 2010; Schwandt et al. 2010). However, the effect of WPBR can be mitigated with strategies that promote host and forest resilience before and during WPBR establishment.

The long-term impact from WPBR, MPB, dwarf mistletoe, changing climatic conditions, and other damaging agents does not favor this species of management concern or the ecosystem processes and biodiversity that limber pine supports. We have learned from whitebark pine ecosystems in the northern Rockies that slow-growing, high-elevation, five-needle white pines, including limber pine, are not sustainable in the presence of WPBR without intervention (Barringer et al. 2012; Fiedler and McKinney 2014; McKinney et al. 2009; Smith et al. 2008). Though other restoration plans exist, mostly for affected whitebark pine ecosystems, this conservation strategy addresses the unique situation of limber pine in the southern Rockies. It recommends proactive conservation actions specific to the southern Rockies founded on site-based scientific information of the ecosystems before they are impaired by WPBR. It focuses on timing specific monitoring efforts and interventions to sustain healthy limber pine populations and ecosystems during invasion and naturalization of WPBR, thereby increasing the probability of putting limber pine on a trajectory that does not lead to ecosystem impairment in the future. The unique genetic composition of limber pine populations in the GRMNPA (relative to resistance to WPBR) and the other site-based disturbance ecology information are features unique to this area, and the fact that we have this information before the populations are greatly impacted by WPBR provides an opportunity to develop a targeted conservation strategy specific to the GRMNPA.

The overall objectives of this conservation strategy for the GRMNPA are to (1) conserve the genetic diversity of limber pine and to maintain the capacity for adaptation in the face of abiotic and biotic change, and (2) guide the implementation of strategies appropriate for the GRMNPA to promote self-sustaining montane and subalpine limber pine ecosystems in the presence of WPBR.

This strategy recommends that the land management agencies continue to play an important role within the southern Rocky Mountains to ensure the future presence of limber pine by initiating concerted, coordinated, and comprehensive research, management, and monitoring efforts. In addition, as a designated International Biosphere Reserve, RMNP should continue to serve as a limber pine seed source for areas within the surrounding GRMNPA. RMNP is expected to “manage the natural and cultural resources of the National Park Service to increase resilience in the face of climate change and other stressors,” (NPS 2012a) and when “confronted with continuous and dynamic change and the goal of preserving ecological integrity, NPS management strategies, must be expanded to encompass a geographic scope beyond park boundaries to larger landscapes and to consider longer time horizons. Specific tactics include improving the representation of unique ecosystem types within the National Park System, prioritizing the protection of habitat that may serve as climate refugia, ensuring the maintenance of critical migration and dispersal corridors and strengthening the resilience of park ecosystems,” (NPS 2012b).

SECTION 2. STRATEGY FOR CONSERVATION ACTIONS

2.1. Consequences of Doing Nothing

The ecological consequences of no management have been documented in white-bark pine stands severely impacted by WPBR in the northern Rocky Mountains (Burns et al. 2008). Most of these stands have been exposed to WPBR for over 50 years, resulting in severe changes in ecosystem function and biodiversity (Ellison et al. 2005; Tomback and Kendall 2001). Without management intervention, WPBR will spread and intensify throughout the range of limber pine, as it has in other parts of Wyoming, Montana, and southern Alberta, resulting in extensive mortality (Smith et al. 2013; Cleaver et al. 2015; Cleaver et al. 2017), unsustainable limber pine populations, and cascading ecological impacts.

Ecological impacts include a decline in seed production, which disrupts the interaction with Clark's nutcracker, in turn leading to reduced regeneration (e.g., McKinney et al. 2009) and loss of a food source for many small birds and mammals and even bears (Burns et al. 2008). Reduced regeneration will slow successional processes, including post-disturbance recovery and species distribution due to the lack of facilitation by limber pine (Baumeister and Callaway 2006; Rebertus et al. 1991). Other ecological effects due to tree mortality include changes in forest structure, composition, and hydrology and the loss of soil and snow retention, biodiversity, and wildlife habitat (Tomback and Achuff 2010). If limber pine dies on harsh sites where it is the only tree species, these areas may become treeless, vulnerable to erosion, and less able to capture and retain snow (Schoettle 2004b). Pressure by WPBR may result in a shift in the stress-tolerance traits that allow limber pine to survive in harsh environments, effectively contracting its fundamental and realized niches (Schoettle 2004b; Vogan and Schoettle 2015).

Should land managers within the GRMNPA choose the no action option and allow WPBR to become established, extensive restoration activities will be required in the future with highly uncertain outcomes. Most land managers to the north of GRMNPA have unwittingly found themselves with only "reactive" restoration approaches available to them (Keane et al. 2012). Consequently, most WPBR management actions have met with inconsistent and sometimes poor success (Keane and Parsons 2010). The GRMNPA is at the WPBR infection front and therefore managers have the option to implement proactive management to mitigate future impacts.

Mortality of seed-producing trees, combined with the added impacts of upslope migration due to climate change and inertia of postglacial dynamics, may render limber pine unable to support upper-elevational range expansion. **Even limber pine with complete WPBR resistance may be at risk if the WPBR pathogen evolves and overcomes the resistance.** Experience in the five-needle pine ecosystems of the northern Rocky Mountains and the listing of whitebark pine as endangered (precluded) under the Endangered Species Act suggest that choosing a no action option early in the invasion will not conserve limber pine in the GRMNPA, which faces the same challenges.

2.2. The Time to Act Is Now

The GRMNPA is in the enviable position of having some time to implement this biologically sound and efficient conservation strategy to respond to the challenges facing limber pine before the resource is impaired and in crisis. Our recommendation is to extend and expand the current proactive management approaches because they offer the greatest opportunity to sustain limber pine and landscape biodiversity. Early intervention will reduce the need for restoration in the future. Proactive intervention recommends conservation of genetic diversity of limber pine ecosystems and initiating actions to increase their resilience before WPBR invasion or impacts to maintain ecosystem processes (Schoettle and Sniezko 2007) (fig. 8). The southern Rocky Mountains currently afford this opportunity, even though it has long been lost for the heavily impacted areas of the northern Rockies.

The Proactive Limber Pine Conservation Strategy builds on what was learned from past experience and what we are continuing to learn about site-specific pre-impact ecology within the GRMNPA. The strategy recommends timely management for limber pine to avoid the magnitude of impacts that we see for whitebark pine ecosystems in the northern Rocky Mountains. In that area, the damage to and losses of whitebark pine from WPBR are so great that many whitebark pine communities are nonfunctional and the populations endangered (e.g., Fiedler and McKinney 2014; Smith et al. 2008). The U.S. Fish and Wildlife Service has downgraded the urgency of the listing of whitebark pine under the Endangered Species Act due to recent activity, suggesting that proactive efforts such as those recommended in this strategy may also help to avoid listing limber pine in the future.

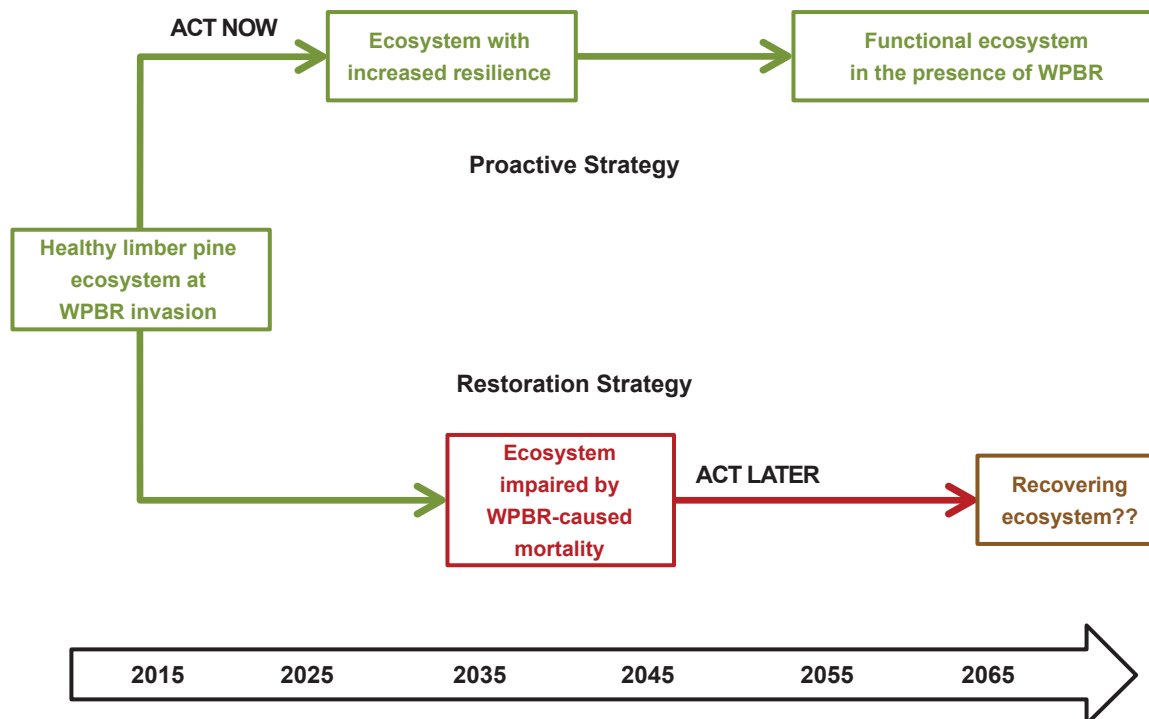


Figure 8—Proactive versus restoration strategy flow diagram (adapted from Keane and Schoettle 2011).

Because most of the GRMNPA ecosystems are still healthy, natural processes are key to this conservation strategy. Natural regeneration combined with planting or direct seeding or both can increase the population size to offset future mortality due to natural selection as WPBR continues to spread (Schoettle and Sniezko 2007). Diversifying age and size classes on the landscape promotes WPBR resistance selection in young trees while larger, mature trees facilitate ecosystem function and services (Schoettle and Sniezko 2007). When the landscape contains a sufficient frequency of WPBR-resistant trees combined with sufficient regeneration, the probability of long-term population sustainability is increased (Field et al. 2012; Schoettle et al. 2012).

2.3. Cornerstones of Management

The three cornerstones of proactive management—with the aim of conserving limber pine genetic diversity and creating sustainable, resilient populations—are the following.

2.3.1. Support Regeneration and Increased Population Size to Maintain Adaptive Capacity

Increasing the population size of limber pine via planting and direct seeding will buffer the effects of future high mortality and support a diverse mosaic of age classes on the landscape. The extent of the land area of suitable habitat supporting limber pine, as well as the density of regeneration, should be increased. Limber pine's life history strategy does not promote rapid adaptation to nonnative stresses, such as WPBR, with which it did not coevolve; thus, **natural processes alone may not support viable populations in the presence of these multiple interacting stressors without management support to increase population sizes (Field et al. 2012).**

2.3.2. Manage Genetic Resistance to White Pine Blister Rust for Sustainability

Genetic resistance to WPBR has been detected in all of the North American five-needle pines (Sniezko et al. 2011) and is an essential component of intervention and restoration strategies (Keane and Schoettle 2011; Schoettle and Sniezko 2007). With infection by WPBR, susceptible individuals are killed, and those trees with genetic resistance survive. Ultimately, the long-term prognosis of a population impacted by this disease depends on the frequency of resistance in the population, the size of the population, and the balance between regeneration and mortality (Field et al. 2012). The greater population size and frequency of resistance, the greater the probability there will be enough surviving trees to sustain the population (Schoettle et al. 2012).

Limber pine exhibits both complete (qualitative) (confirmed in the GRMNPA) and partial (quantitative) resistance to WPBR (Schoettle et al. 2011b; Schoettle et al. 2014). **Although complete resistance may provide immunity, it could eventually be overcome by a more virulent race of the pathogen (Kinloch et al. 2004; Schoettle et al. 2014).** Complete resistance to WPBR is conferred by a dominant allele for resistance, the *Cr4* allele in limber pine, which is recognized by the rust fungus (*avcr4* allele) and prevents the fungus from sporulating on the pine host. As a result, *Cr4* places strong selective pressure on the rust, and rust genotypes that

infect susceptible pines are the only ones that complete their life cycle and maintain the population. However, when trees carrying the *Cr4* allele become more common (through mortality of susceptible trees or selective planting of *Cr4* trees), a mutation in the rust that enables the fungus to overcome *Cr4* (*vcr4* allele)—and, therefore, sporulate on a *Cr4* tree—can rapidly increase in frequency in the rust population. Greater *vcr4* frequency may occur, especially if the rust population is isolated with low gene flow from other populations. This evolution of virulence reduces the durability—and therefore the sustained effectiveness—of *Cr4* resistance. Currently, there is no evidence for virulence (*vcr4*) in the rust populations in the GRMNPA or elsewhere. The only method at this time to detect virulence is through detection of successful sporulation on a known *Cr4* tree; we recommend monitoring for this occurrence, as discussed next. **But virulence has evolved to overcome complete resistance in western white pine and sugar pine (Kinloch and Dupper 2002) and is expected to arise eventually for *Cr4* (Schoettle et al. 2014).**

Conditions conducive to rapid proliferation of a mutation that leads to virulence include high frequencies of complete resistance, local presence of the susceptible alternate hosts for the rust, a habitat that restricts gene flow into the area from other rust sources, and conditions that support frequent (annual) infection events (Burdon and Thrall 2008). For *C. ribicola* and limber pine in the GRMNPA, high-risk areas include wind-protected riparian areas with *Ribes* and nearby limber pine trees, which describes the habitat in which WPBR was first found in RMNP (just east of the Beaver Ponds area; Schoettle et al. 2018a) and in northern Colorado (Sand Creek area; Johnson and Jacobi 2000). **To manage for sustained durability of *Cr4* for as long as possible, plantings of limber pine enriched in *Cr4* genotypes should be avoided in and near riparian areas.**

Traits that confer partial, or quantitative, resistance to WPBR, such as bark reaction, needle shed, or slow canker growth, reduce the number or severity of infections, enabling the tree to survive with the disease (Sniezko et al. 2004). This type of resistance is likely controlled by multiple genes and has been found at low frequency in limber pine from the southern Rockies (Schoettle et al. 2011b). **Quantitative resistance is more durable than qualitative resistance and every effort should be made to detect and then increase the frequency of this type of resistance in the GRMNPA.** The early engagement in limber pine management and the high frequency of complete resistance in the native limber pine populations provide time to research quantitative resistance, if initiated immediately (the progeny test takes 5–7 years). The presence of complete resistance to WPBR in the GRMNPA and the likelihood of partial resistance in local limber pine populations provide reason for optimism that the naturally occurring local genetic diversity can supply the material needed to manage the effects of WPBR in the GRMNPA if deployed early.

2.3.3. Foster Early Awareness and Engagement to Enhance Opportunity for Success

Colorado and the southern Rocky Mountains are part of only a few remaining areas that contain limber pine populations not yet impacted by WPBR. There is evidence that the public is in favor of early intervention (Bond et al. 2011), and this support should be capitalized on with community and volunteer involvement in the implementation of this conservation strategy.

SECTION 3. RECOMMENDED CONSERVATION ACTIONS

The GRMNPA ecosystems are at risk due to the introduction of the nonnative pathogen that causes the lethal disease WPBR and its interactions with other native stresses and climate change. Managers of the GRMNPA cannot rely on past forest conditions to provide the information and targets needed to maintain forest sustainably into the future with these stressors. The complexities of changing climate, insects and diseases, changing land use patterns, and other influences will create new unique environmental conditions and landscape patterns that need to be considered. Management strategies that build in flexibility, reversibility, and alternative pathways are more likely to succeed in an uncertain future (Means 2011; Millar et al. 2007).

The GRMNPA is in a unique position to manage limber pine because of the following suite of conditions:

- The ecosystems are still in the early stages of WPBR invasion, and therefore ecological processes are still functioning and have not yet been impaired.
- Postfire habitats in the GRMNPA are conducive to successful natural regeneration of limber pine.
- Genetic resistance to WPBR, conferred by a single dominant allele for resistance (*Cr4*), is present in native populations of limber pine in the GRMNPA at high frequency; however, this type of resistance could be overcome by the rust if a virulent strain evolves.
- Genetic resistance to WPBR that is conferred by multiple genes, which is less likely to be overcome by the rust, may be present in the GRMNPA at low frequencies.
- Climate change is projected to shift limber pine populations to higher elevations as well as intensify the impacts of other native pests and pathogens.

Consequently, the recommended management activities for this conservation strategy are as follows:

- **Promote ex situ conservation:** Continue and expand efforts to collect and archive limber pine genetic diversity through bulked and individual-tree seed collections.
- **Promote in situ conservation:** Protect limber pine trees from MPB, WPBR, and fire to minimize mortality when and where land designations and management objectives permit.
- **Increase population size and sustain genetic diversity:** Increase the number of limber pine trees across the landscape through planting or seeding, or both, and planned and unplanned fire management as soon as possible to offset future mortality and to sustain viable genetically diverse, self-sustaining populations.
- **Locate treatments to maintain durability of qualitative resistance to WPBR:** Minimize selective pressure on the rust by planting trees with a range of susceptibilities in low-WPBR-risk areas to reduce the probability of the proliferation of rust genotypes virulent to *Cr4*.
- **Discover, develop, and deploy local quantitative WPBR-resistant sources:** Research quantitative (polygenic) WPBR resistance types in limber pine in the GRMNPA and establish a seed orchard/clone bank of these genotypes to provide material for future planting projects in the GRMNPA.
- **Monitor pines and rust:** Monitor limber pine health, WPBR incidence, and WPBR virulence at the landscape, stand, and tree scales.

- **Coordinate management actions within and among agencies:** Preserve and diversify the age- and size-class distribution of limber pines as well as early-to-late successional stages across the landscape through fuels treatments, vegetation management, and fire.

The major focal area for leadership activities is to:

- **Continue coordinated limber pine conservation in the southern Rockies through research, genetic resource management, and interagency cooperation:** Continue to support research on limber pine ecosystems and the WPBR pathosystem and encourage infrastructure that supports management objectives. RMNP should pay special attention to maintaining viable seed sources and seed collections to further achieve its obligation as an International Biosphere Reserve.

The recommendations described in the following subsections provide justification for the guidelines for limber pine management described in Section 5.

3.1. Promote Ex Situ Conservation

Continue and expand efforts to collect bulked and individual-tree seed collections from throughout the GRMNPA to archive genetic diversity, and to use for propagation and outplanting, further scientific study, and WPBR partial resistance testing.

Because WPBR has not yet caused mortality of mature limber pine trees in much of the GRMNPA, the limber pine populations still represent historical genetic diversity and therefore their full adaptive capacity. **This genetic diversity should be preserved before WPBR mortality has the chance to cause a genetic bottleneck, the loss of rare alleles (Kim et al. 2003), and the loss of stress-tolerance traits (Vogan and Schoettle 2015).** Some collections have been made, but additional collections are needed at other sites (see Section 5, guidelines 1 and 2). It is estimated that limber pine seed can retain viability for at least 10 years, and possibility much longer, when stored at -0.4 to -4 °F (-18 to -20 °C). Tree and bulked seed collections should continue to be made during good cone production years at least every 8–10 years to ensure a viable collection. The sites for collections should be stratified by elevation and habitat type (when possible) and include areas targeted for planting or seed sowing to best supply the needed sources to conform to the seed transfer guidelines. Each seed accession should be retained for at least 20 years or longer (pending the results of seed viability assessments) for possible genetic studies to test for genetic changes in the populations over time (see Section 5, guideline 3). We expect collection of seeds to pose no conflict with wilderness character or values.

3.2. Promote In Situ Conservation

Protect limber pine trees from MPB, WPBR, and fire to minimize limber pine mortality when and where land designations and management objectives permit.

Maintaining a viable natural seed source is essential for population sustainability and recovery. Verbenone should be used each year to protect any limber pine tree that has undergone rust resistance testing (i.e., known genotype individuals), or is intended for use in resistance testing, and also to protect additional high-value and at-risk trees (recommend >15 trees per site; see Section 5, guideline 4). **Carbaryl is preferred and more effective;** however, in remote areas, verbenone is easier to

deploy. Within RMNP, all limber pine in Class III areas should be classified as high-value trees, and chemical insecticides used in accordance with the established protocols developed under the 2005 Bark Beetle Management Plan (NPS 2005a).

There are no chemical treatments effective against WPBR; however, we recommend sanitation pruning (excision of cankered branches) to extend the lifespan of an infected tree (Burns et al. 2008; Crump et al. 2011; Jacobi et al. 2017; see Section 5, guideline 5). It is imperative to tag the treated tree so it is not mistaken as canker-free (and therefore putatively genetically resistant to WPBR) in future monitoring efforts. Sanitation pruning efforts should be targeted in riparian areas in late spring when the *C. ribicola* aecia are most clearly visible.

Limber pine trees of all ages should be preserved during any fuels treatments implemented in the GRMNPA. In addition, fuels treatments in other forest types that surround these limber pine areas or in areas that would facilitate fire spreading into the area (i.e., where fire starts in a low-elevation area and moves up, as have several recent wildfires) should be implemented. A landscape-level assessment to optimize placement of fuels treatment is needed.

When there are planned wildland fires, scratch lines, fire lines, and removing duff and vegetation around trees can be used to protect individual trees or a stand of limber pines (see Section 5, guideline 15). Trees whose progeny have been tested for WPBR resistance are especially important to protect. During unplanned events, locations of limber pine trees as resources at risk should be provided to fire management teams to consider for protection to the highest degree possible. These areas and the genetically tested trees within RMNP are identified in the park's FIRE database as resource values at risk; that way, when fire incident managers come onsite from other areas, they know to protect them. Similar identification should be made for tested trees on other public lands.

3.3. Increase Population Size and Sustain Genetic Diversity

Increase the number of limber pine trees across the landscape through planting or direct seeding, or both, and planned and unplanned fire management as soon as possible to offset future mortality to sustain viable genetically diverse, self-sustaining populations.

Increasing the number of limber pines in a population by planting, direct seeding, and facilitating natural regeneration will help offset mortality and reduced regeneration caused by MPB, WPBR, and dwarf mistletoe and reduce the probability of population extirpation (Field et al. 2012). Seed sources for seedling planting and seed sowing should contain a mix of bulked seed collections from a range of elevations similar to that of the target site to provide locally adapted genotypes and enough genetic diversity to support adaptation to climate warming (see Section 5, guidelines 6–8). Until trees with quantitative (partial) resistance are identified, we recommend using bulked seedlots. We do not recommend using seeds only from the trees with complete resistance to WPBR (*Cr4*) because of concerns about rapid proliferation of rust genotypes virulent to *Cr4* that could arise via mutation (see next subsection).

Suitable target planting and seeding sites include recent burns and stands opened or expected to be opened by overstory mortality (e.g., due to MPB or spruce beetle) or disturbed by road work or other mechanical treatment. We recommend avoiding planting or seeding in areas with high presence of dwarf mistletoe unless the overstory is removed to prevent infection of the young trees. If dwarf mistletoe presence is moderate to low, the infected overstory needs to be removed before limber pine saplings reach 3 ft (0.9 m) tall or 10 years old, whichever is first (Worrall 2014). Consultation with FHP for management recommendations in areas with dwarf mistletoe is recommended. Microsites selected for planting and direct seeding should mimic those found in naturally regenerating stands (Coop and Schoettle 2009) to maintain a natural spatial arrangement and make the management treatment less conspicuous to forest visitors. Planting success is greatest when seedlings or seeds are planted near objects in open or semi-open stands (Casper et al. 2016; Smith et al. 2011).

In addition to the aforementioned site characteristics for limber pine planting, seeding, and management, we recommend targeting areas with low rust risk (figs. 2 and 7) and areas with low fire hazard for greatest success. Planting in high-WPBR-risk locations may be futile and may increase selective pressure for the proliferation of virulence in the rust (see subsection 3.4). Riparian areas are conducive to WPBR infection because they have the high humidity and cool temperatures optimal for spore development, release, transport, and germination, and *Ribes* species, which serve as the best alternate hosts for *C. ribicola*. Riparian areas are associated with high WPBR risk so we recommend avoiding these areas for planting or seeding (see subsection 3.4). To define these areas more accurately, further study is needed on the distribution of suitable alternate WPBR hosts and environmental conditions.

Conditions are favorable for limber pine germination in the GRMNPA, though establishment may be curtailed by competition from other tree and plant species (Stohlgren et al. 1998) and reduced seed sources due to overstory mortality (MPB, WPBR). Manipulations of forest cover through planned or unplanned fire or other disturbance may result in limber pine establishment if a nearby healthy seed source and good site conditions are present (see Section 5, guideline 9).

Planting seedlings generates a much higher long-term establishment rate than sowing seed (72-percent and 11-percent, respectively; Smith et al. 2011); however, direct seeding is still a viable option (see Section 5, guideline 7). Because many seeds are lost to predation, direct seeding with valuable WPBR-resistant seed is not recommended. When seed stock with quantitative WPBR resistance is developed, planting seedlings will be desirable for a more successful outcome. However, the immediate goal is to increase the number of limber pines on the landscape, so direct seeding with bulked seedlots is a good option that is affordable and nonintrusive to wilderness values. Furthermore, gene frequencies in a bulked seedlot are similar as those for natural regeneration, making this approach compatible with Class I wilderness values. Direct seeding below the soil surface ensures a higher success rate than surface-sown seeds, which are largely taken by rodents (McCaughey 1990). Loss to rodents of sown seeds can also be high; more than 50 percent loss of whitebark pine seed has been reported (Pansing 2014). In a limber pine planting study, 43 percent

of limber pine seeds planted at a depth of 1.2 in (3 cm) germinated by the second year and seedlings from 11 percent of sown seed survived after 3 years (Smith et al. 2011). Similarly, other whitebark pine seed sowing trials have reported 13 percent germination (Schwandt et al. 2011) and preliminary results indicate survival of up to 35 percent (Arno 2015).

Target density for artificial regeneration should supplement natural regeneration, and therefore increase seedling densities to offset future mortality from WPBR, dwarf mistletoe, bark beetles, or other damage agents. Average density of postfire natural regeneration (trees <4 in [10 cm] d.b.h.) of limber pine after the Ouzel Fire was 194 stems ac^{-1} (480 stems ha^{-1}) (Coop and Schoettle 2009). Postfire limber pine regeneration density measurements by Shankman and Daly (1988) were 117 stems ac^{-1} (288 stems ha^{-1}) at Sundance, 118 stems ac^{-1} (292 stems ha^{-1}) at Rollins Pass, and 206 stems ac^{-1} (508 stems ha^{-1}) at Niwot Ridge. Natural regeneration for trees <54 in [137 cm] in height in existing stands of limber pine in northern Colorado to southern Montana, including stands impacted by WPBR, MPB, and dwarf mistletoe, ranged from 0 to 783 stems/ ac^{-1} (1,935 stems ha^{-1}) and averaged 57 stems ac^{-1} (141 stems ha^{-1}) (Cleaver 2014). In Boulder County, where WPBR is in the early stages of infection, mean limber pine regeneration density in existing stands was 79 stems ac^{-1} (194 stems ha^{-1}) and ranged from 0 to 412 stems ac^{-1} (1,019 stems ha^{-1}) (Cleaver 2014). Natural limber pine regeneration for trees less than 54 in (137 cm) in height in existing stands along the northern Colorado Front Range, including 17 sites in RMNP, averaged 199 stems ac^{-1} (492 stems ha^{-1}) (Klutsch et al. 2011). Overall, we propose to use artificial regeneration to supplement and double the average natural regeneration density of 200 stems ac^{-1} . Assuming 50 percent pilfering and 11 percent seedling establishment rate from direct seeding, it would require a direct seeding rate of 3,636 seeds ac^{-1} (8,985 seeds ha^{-1}) and assuming 72 percent of planted seedlings successfully establish it would require a planting rate of 278 seedlings ac^{-1} (685 seedlings ha^{-1}) to yield the artificial regeneration supplemental target establishment density of 200 stems ac^{-1} (494 stems ha^{-1}) and an average total seedling density (natural plus artificial regeneration) of approximately 400 stems ac^{-1} (988 stems ha^{-1}).

3.4. Locate Treatments to Maintain Durability of Qualitative Resistance to White Pine Blister Rust

Select seed sources and locate treatment units to minimize selective pressure on the rust. This will lower the probability of the proliferation of rust genotypes virulent to Cr4, should they evolve via mutation, and may reduce the buildup of WPBR spore loads.

Every effort should be made to slow the proliferation of rust virulence (i.e., an evolved mechanism whereby a mutation enables the rust to overcome Cr4 resistance) to provide additional time to detect and deploy quantitative resistance in the GRMNPA (see Section 5, guideline 10). Wind-protected riparian areas with *Ribes* and nearby Cr4 limber pine are particularly conducive to the rapid proliferation of virulence should it arise. To manage for sustained durability of Cr4, plantings of limber pine enriched in Cr4 genotypes should be avoided in and near riparian areas early in the invasion timeline (figs. 2 and 7). We recommend planting or

direct seeding of limber pine using only bulked seedlots and planting or seeding no closer than 33 ft (10 m) in elevation from an active stream bed. Repeated seeding or planting of bulked seedlots (with both resistant and susceptible genotypes) is recommended as mortality increases. In addition, sanitation pruning should be done in these areas to prolong the life of the trees and to potentially reduce inoculum densities. The efficacy of pruning should be reevaluated with FHP and RMRS annually.

3.5. Discover, Develop, and Deploy Local Quantitative White Pine Blister Rust-Resistant Seed Sources

Research quantitative (polygenic) WPBR resistance types in limber pine in the GRMNPA and establish a seed orchard/clone bank of these genotypes to provide seed for future planting projects in and around the park.

Whereas *Cr4* resistance can sustain nearly a fifth of the original limber pine population for a limited number of rust generations, research to identify, build, and deploy seed stocks with the more durable quantitative WPBR resistance in the GRMNPA should begin immediately (see Section 5, guidelines 2 and 11). To sustain limber pine populations into the future, the frequency of trees with quantitative resistance must be increased to well above the suspected current frequency of ~1 percent in southern Rockies limber pine populations (Schoettle and Sniezko unpublished data on file at RMRS, Fort Collins, Colorado; Schoettle et al. 2011b). Individual tree seed collections can be tested for WPBR resistance using established artificial inoculation protocols at USFS facilities. Testing can only take place 5–7 years after the seed is collected, so we recommend commencing studies as soon as possible for timely results. The USFS operates several artificial inoculation facilities to test for resistance to WPBR; however, none of them are in the southern Rockies. If funds for testing are not available, families could be prescreened at field planting sites in areas with WPBR (e.g. the Southern Rockies Rust Resistance Trial site in south Wyoming) to identify those families that appear to have partial resistance for additional testing at the artificial inoculation testing facilities. This would reduce the number of families, and therefore the cost, that need to be tested under controlled conditions. Our past research on rust resistance of limber pine in the GRMNPA was done at the USDA Forest Service Dorena Genetic Resource Center (Cottage Grove, Oregon). Use of molecular methods to detect resistance to WPBR is encouraged when they become available.

After the inoculation test, the seedlings that express traits associated with quantitative resistance should be grafted to root stock and established in a seed orchard/clone bank (see Section 5, guideline 16) to mature and provide a source of seed (frequency of the traits can be determined by testing the first-generation progeny). Until then, field collected seed can be used to support planting or seeding projects. Scion from the seed trees that bore the resistant progeny could also be grafted for the clone bank. Quantitative resistance has been identified in limber pine from the southern Rockies, including some families from the GRMNPA; no seed sources from RMNP have been tested (Schoettle and Sniezko unpublished data). We recommend that clones (grafts) from these resistant genotypes (provided by RMRS and Great Sand Dunes National Park and Preserve) be immediately established in a RMNP clone bank to fulfill the park's mandate to be a source of genetic diversity to

promote sustained forest health in the park and surrounding areas. Additional sites for clone banks should also be considered. Other clones from the future tests can be added later.

3.6. Monitor Pines and Rust

Monitor limber pine health, WPBR occurrence, and WPBR virulence at the landscape, stand, and tree scales.

The existing monitoring network should be enhanced and expanded throughout the GRMNPA. Ten of the 17 research areas and 39 long-term monitoring plots are a good start for forest health monitoring at the landscape and stand scales. Establishing long-term monitoring plots in the remaining seven research areas within RMNP and in areas outside of the park that have not been surveyed extensively (e.g., the Arapaho and Routt National Forests) should be a priority in the near future (figs. 3 and 9). A remeasurement schedule of 5 years would be adequate to detect changes (forest health monitoring; see Section 5, guideline 12). For early WPBR detection and study of invasion dynamics, additional plots should be established in riparian areas to identify infection centers and areas where management for durability of resistance measures should be exercised (figs. 2 and 10) (early detection monitoring; see Section 5, guideline 13) as have been established in RMNP (Cleaver et al. 2017). In addition, those forest trees inferred to have *Cr4* resistance by WPBR resistance progeny testing, should be inspected each spring for signs and symptoms of WPBR as monitors for the evolution of virulence to *Cr4* (*vcr4*) in the rust (virulence monitoring; see Section 5, guideline 14). As soon as virulence is detected or suspected (i.e., a known *Cr4* tree is found with signs or symptoms of WPBR), FHP and researchers should be notified and consulted.

The Rocky Mountain Inventory and Monitoring Network (ROMN) is focused on long-term ecological monitoring in six parks including RMNP. Integrating five-needle pine monitoring with the network's monitoring programs would benefit the monitoring systems already in place; a regionwide database is currently being established as a collaborative effort between ROMN and FHP. Streamlining with the goals of ROMN and implementing early-detection WPBR monitoring allow for early warning of altered conditions so proper and cost-effective management decisions may be employed (Fancy et al. 2009).

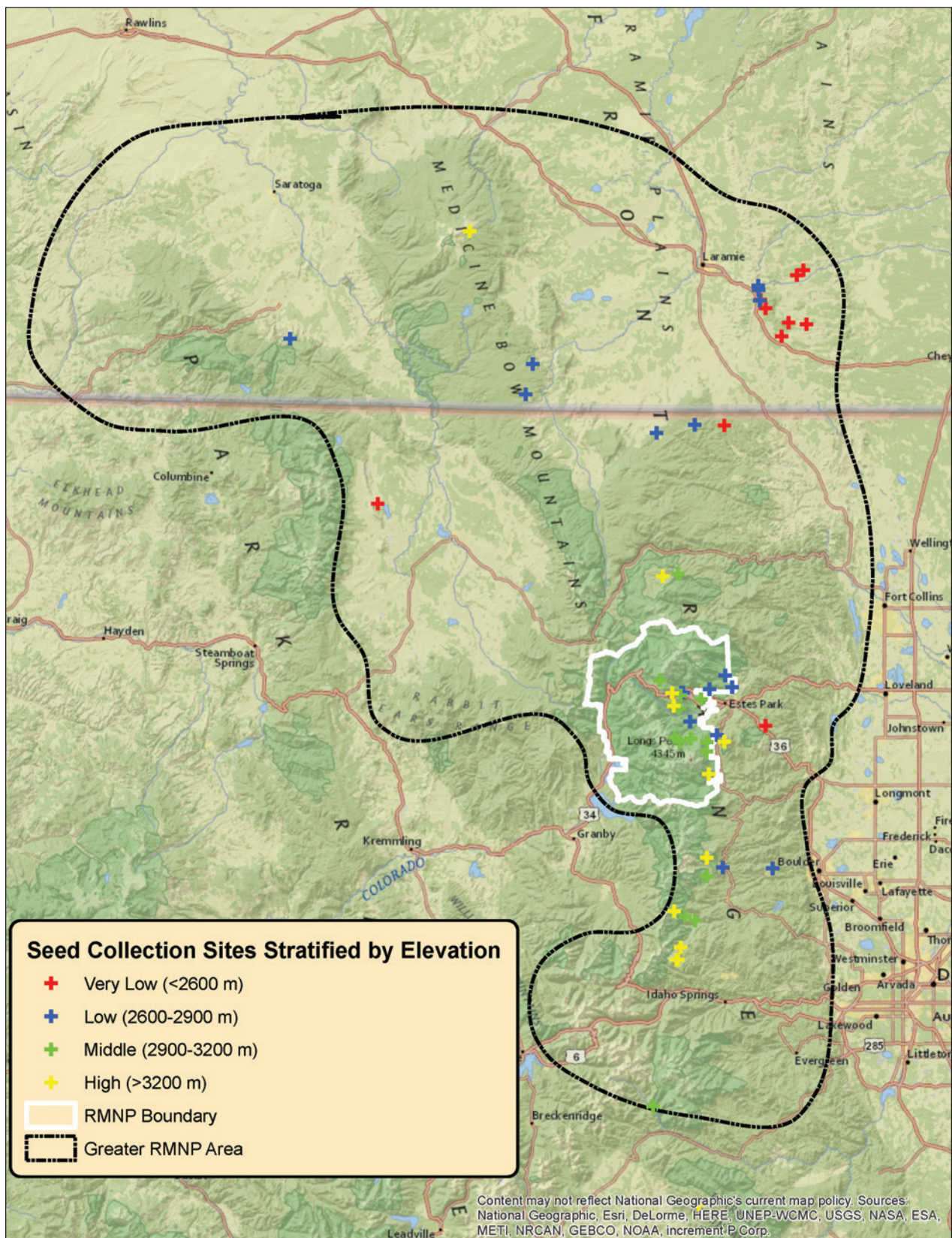


Figure 9—Map showing limber pine seed collection and research sites in the GRMNPA (Schoettle et al. 2011a, Schoettle et al. 2013). Sites were stratified by elevation to sample the ecological and genetic variation of limber pine in the area.

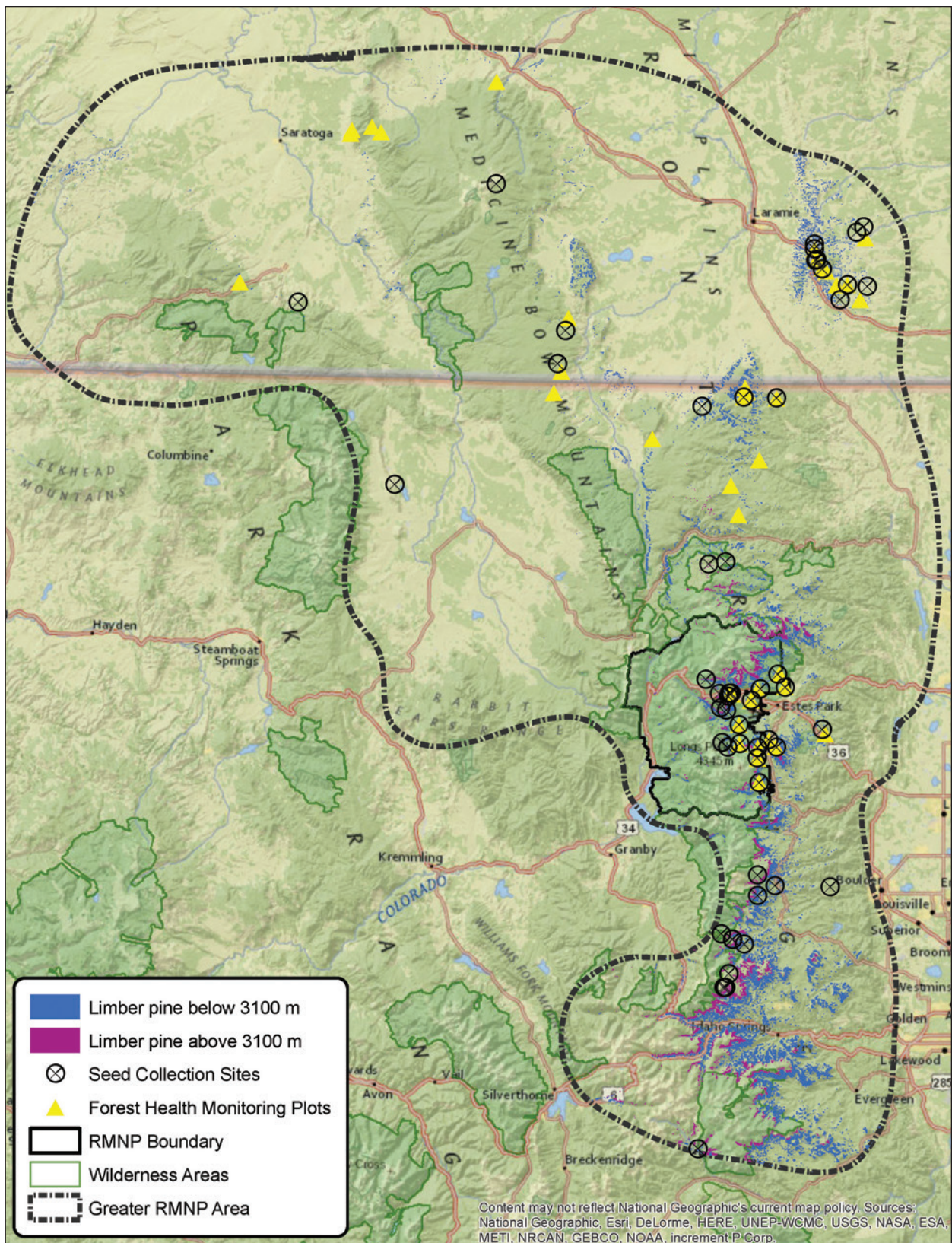


Figure 10—Map showing wilderness, current distribution of limber pine stratified by elevation, research sites, and forest health monitoring plots in the GRMNP.

3.7. Coordinate Management Actions Within and Among Agencies

Preserve and diversify the age- and size-class distribution of limber pines as well as early-to-late successional stages across the landscape through fuels treatments, vegetation management, and planned fire.

Using fire to benefit the resource and incorporating limber pine objectives and management when applicable will help sustain limber pine on the landscape. Fire regimes vary across the distribution of limber pine, with harsh, rocky sites receiving fire less often. In more productive areas, fire can be beneficial to limber pine by reducing competition and by providing a seedbed for Clark's nutcracker seed caching and habitat for planting or direct seeding through the creation of openings in the forest canopy (Coop and Schoettle 2009; see Section 5, guidelines 9 and 15). While occasional wildfires can be beneficial for limber pine regeneration, large, unplanned wildfires may threaten valuable stands of limber pine. RMNP fire managers have been notified of locations of high-value limber pine and other resources at risk (long-term monitoring plots, known WPBR-resistant trees) so that they may be considered for fire protection; similar notification should be made to other public land managers. Management activities that increase resilience of other tree species on the landscape can help lower MPB hazard for lodgepole, ponderosa, and limber pine. Management activities that reduce fire hazard in ponderosa pine and Douglas-fir (*Pseudotsuga menziesii*) forest types can also limit fire spread into higher elevations where limber pine grows.

SECTION 4. RESOURCES TO EXECUTE THIS STRATEGY

Implementing the recommendations of this strategy will require administration and management to coordinate efforts, consult with local experts, secure resources to achieve the goals, work across agencies and with different divisions within an agency (i.e., vegetation, fire, wilderness, and the Learning Center staffs), provide oversight for clone bank planting and maintenance, and compile information to assess and communicate current conditions and outcomes. RMNP has established a Limber Pine Coordinator position for at least 5 years. Because the GRMNPA is at the infection front for WPBR, limber pine forest conditions will be very dynamic during the next 10–30 years, and close consultation among agencies and experts will aid in interpreting those changes and adapting projections and management. FHP is a particularly good resource as it has responsibility for assisting with forest health management across all land ownerships. Close coordination with local FHP professionals can help with funding, focusing, and facilitating this work. RMRS also shares a cross-border mandate and can provide advice on the latest research findings and research opportunities to assist managers in their limber pine conservation efforts. The USFS Regional Geneticist for the Rocky Mountain Region is another resource to consult.

SECTION 5. GUIDELINES FOR MANAGEMENT OF LIMBER PINE

5.1. Limber Pine Seed Collections—Bulk Cone Collections

Purpose of activities:

- Archive genetic diversity.
- Create a seed reserve for:
 - WPBR resistance screening and research.
 - Propagation and seedling outplanting.
 - Direct seeding.

Timing of activity:

- At least every 8–10 years during good cone production years.
- Limber pine produces cones every 3–5 years; 2008 and 2011 were the best cone years over the period 2008–2015. Collecting early in the masting cycle will result in the best seed collections.

Activity (i.e., collection) priorities:

- Accessible stands stratified across the GRMNPA (can be co-located with the individual tree collections) (Section 5, guideline 2).
- Stands that fulfill the recommended geographic distribution of seed sources (see USFS Handbook FSH 2409.26f R-1 (Seed Handbook) and consult with Regional USFS Geneticist).
- Stands threatened with extirpation, i.e., with a high incidence of WPBR, low limber pine stem density, high levels of mortality (any cause), or any combination of those factors (Cleaver et al. 2015).

Description of activity:

- Site selection criteria:
 - Stratify sites by elevation, habitat type (when possible), and areas targeted for planting or seed sowing to best supply the needed sources and to conform to seed transfer guidelines (Section 5, guideline 8).
 - Collect from 2–3 sites for each 328 ft [100 m] elevation band (i.e., 9,190–9,518 ft, 9,518–9,846 ft [2,801–2,900 m, 2,901–3,000 m]) spaced across the GRMNPA.
- Tree selection criteria:
 - Select healthy single-stemmed trees or multi-stemmed clumps with cones. When sampling from clumps, make sure to collect from only one stem. Be careful to maintain a 100 ft. [30 m] spacing between all sampled trees.
 - Avoid collecting from trees that are heavily infested with dwarf mistletoe.
- Follow guidelines for bulk cone collections (see Appendix in Schoettle et al. 2011a)
 - Collect an equal number of cones from each of 20+ trees per site (40+ trees is better). To do this, assess the amount of cone production on site—if it is light, collect 2 cones per tree; if it is good, collect 4 cones per tree; and if it is excellent, collect 6 cones per tree.
 - Select cones from high in the crown.

- Do not include trees with individual seed collections.
- Verify seed ripeness prior to collection (see Appendix in Schoettle et al. 2011a).
- Collect only fully formed green cones (no small dry brown ones—they have aborted) (fig. 11).
- Only collect cones cut from the tree; do not collect cones from the ground.
- Keep the cones out of direct sun (especially in the back of a vehicle). Move them to a dry, cool place with good ventilation between bags as soon as possible.
- Seed can be extracted when cones have opened. See Section 5, guideline 3, *Limber Pine Seed Storage and Database*.
- Data Collection:
 - Enter the number of trees sampled and the number of cones per tree on the SEED TREE form (Schoettle et al. 2011a, Appendix).
 - Complete the SITE SURVEY form to provide associated stand condition and forest health information at the time of the collection (Schoettle et al. 2011a, Appendix).



Figure 11—Healthy limber pine cone cluster that is close to mature for collection (A.W. Schoettle, USFS).

5.2. Limber Pine Seed Collections—Individual Tree Collections

Purpose of activity:

- Archive genetic diversity.
- Create a seed reserve for:
 - Further scientific study.
 - WPBR partial resistance testing.
 - Outplanting.

Timing of activity:

- At least every 8–10 years during good cone production years.
- Limber pine produces cones every 3–5 years; 2008 and 2011 were the best cone years from 2008–2015. Collecting early in the masting cycle will result in the best seed collections.

Activity (i.e., collection) priorities:

- Accessible stands stratified across the GRMNPA. Include healthy and declining stands stratified spatially and by elevation.
- Stands at risk for extirpation, i.e., those with a high incidence of WPBR, low limber pine stem density, high levels of mortality, or any combination of those factors (Cleaver et al. 2015).
- Phenotypically resistant trees and trees with confirmed resistance.

Description of activity:

- Site selection criteria:
 - Stratify sites by elevation, habitat type (when possible), and areas targeted for planting or seed sowing to best supply the needed sources and to conform to seed transfer guidelines (see Section 5, guideline 8).
- Tree selection criteria:
 - Select healthy trees with cones. Single-stemmed trees are preferred over multi-stemmed clumps because clumps may consist of multiple individuals; for the genetic analyses, we have to be absolutely certain of the mother tree of the seeds. 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. If you are not 100 percent certain that the cone you cut was from the sample tree, do not include it.
 - If WPBR is on site, select 8–9 phenotypically resistant (no or few visible cankers) seed trees and 1–2 susceptible (cankered) seed trees. If there is no WPBR on site, select 10 healthy, mature trees.
 - Avoid collecting from trees that are heavily infested with dwarf mistletoe.
- Follow the guidelines for individual tree collections (see Appendix in Schoettle et al. 2011a)
 - Maintain a 200 ft. (61 m) spacing between sample trees.
 - Place a numbered tag on the north side of each tree and collect global positioning system (GPS) coordinates. Use site name and tag number on all bags of cones from that tree.
 - Verify seed maturity before collecting cones (see Appendix in Schoettle et al. 2011a).
 - Collect 20–40 cones from each tree from as high in the crown as possible (fig. 12).

- Collect only fully formed green cones (no small dry brown ones—they have aborted).
- Keep the cones out of direct sun (especially in the back of a vehicle). Move them to a dry cool place with good ventilation between bags as soon as possible.
- Seed can be extracted when cones have opened. See Section 5, guideline 3, *Limber Pine Seed Storage and Database*.
- Data Collection:
 - Enter each sampled tree and the number of cones per tree on the SEED TREE form (see Appendix in Schoettle et al. 2011a). Note if WPBR is on site and sample tree is infected.
 - Complete the SITE SURVEY form to provide associated stand condition and forest health information at the time of the collection (see Appendix in Schoettle et al. 2011a).
 - Update the FIRE database (RMNP) or similar National Forest database with the location of sampled trees.



Figure 12—Using a pole pruner to collect cones from a limber pine tree in RMNP (A.W. Schoettle, USFS).

5.3. Limber Pine Seed Storage and Database

Purpose:

- Preservation of genetic diversity of the species before WPBR-imposed bottleneck.
- For RMNP, which is an International Biosphere Reserve, maintain seed collection as a seed reserve for other management units.
- Outplanting.

Priorities:

- Individual tree seed collections
- Bulk seed collections

Description and guidelines:

- Seed Storage
 - Use USFS plant-nursery facilities to store seed, or alternatively, use private facilities.
 - Cleaned seed (i.e., seed cleaned of all twig, needle, wing, and cone debris) should be stored in impermeable bags sealed to exclude as much free airspace as possible. Bags should be labelled with collection date, sample name, species, latitude, longitude, and elevation and stored in a walk-in or chest freezer at -4 °F (-20 °C). Seeds retain viability when stored at -0.4 °F to -4 °F (-18 °C to -20 °C) for at least 10 years. High-quality, large chest freezers or a walk-in freezer will be needed. A generator backup or alarm system is warranted.
 - Conduct an initial seed germination test of each seed lot, if possible.
 - Each seed collection accession should be retained for at least 20 years for possible genetic studies to test for genetic changes in the populations over time. Assess viability through germination tests (with 60-day, 35.6 °F [2 °C] stratification) before deciding to discard.
 - Do not discard individual tree seed collections without prior consultation with RMRS and FHP.
 - Do not combine seed lots.
 - Add to seed collection during good cone production years.
- Seed Database
 - If seed is not being archived by a USFS plant nursery or managed by the Regional Geneticist, maintain a database (or Excel spreadsheet) for all seed collections. Record the date of collection, full site name, site abbreviation, waypoint name (tree tag number), latitude, longitude, elevation, datum, number of trees in the sample, type of collection (individual vs. bulk), WPBR resistance testing (yes or no) and date, phenotype of seed tree in the field (individual only; WPBR infected or not infected), WPBR on site (yes or no), mass (g) of sample, uses (see below), and notes. Site data requested on the datasheet should also be added. For “uses” add a column each time seed is sampled from the lot, and identify the project for which it was used. If percent germination is determined, note it with the date of the test.

5.4. Protecting Limber Pine from Mountain Pine Beetle (MPB)

Purpose of treatment:

- To preserve seed sources and minimize limber pine mortality due to MPB.

Timing of treatment:

- Consult with FHP annually to assess treatment needs and to optimize treatment time based on treatment type and the expected timing of beetle flights.
- Spray or verbenone additional seed trees, including all trees sampled for individual-tree seed collections, if there are 3 years of increasing MBP populations.¹

Treatment priorities:

- Trees confirmed to have complete WPBR resistance (*Cr4*) (virulence monitors—see Section 3.6).
- All trees that have undergone or are planned to undergo WPBR resistance testing (protecting the trees with known genetic susceptibility is also important as a control seed source for research studies and resistance trials).
- Cone-producing trees.
- High-value trees and at risk trees.
- Sites with reasonable access.

Description of treatments:

Carbaryl is a registered, preventive insecticide spray that is very effective for protecting uninfested trees from bark beetle attack for 1–2 years. A licensed and insured applicator is required and treatments can only be done on accessible sites and more than 50 feet from surface water.

Verbenone is an anti-aggregation pheromone that sends a ‘no vacancy’ signal to bark beetles. Its effectiveness in protecting limber pine has not been adequately studied, but it has shown success for protecting individual whitebark pines from beetle attacks (Kegley and Gibson 2004). Verbenone comes in 7.5-gram pouches that are easy to apply (figs. 13a,b) and fairly inexpensive. It is recommended for inaccessible sites, sites near surface water, or in areas where spraying insecticides is not an option. The guideline for individual tree protection is to apply one 7.5-gram pouch before the beetle flight (late May or early June) and add another 7.5-gram pouch later in the summer (late July or early August). Using verbenone for stand protection has had more variable results (Bentz et al. 2005). In a recent study, 40 high-dose verbenone pouches (with a verbenone emission rate up to 50 mg/d per pouch) per acre significantly reduced the number of MPB attacks compared to untreated stands. However, some mortality in large diameter trees still occurred. Consult with FHP for the most current treatment standards.

When treatment is complete, update the FIRE database (RMNP) or similar National Forest database with the location of treated trees.

¹ *MPB populations have returned to endemic levels in the greater RMNP Area as of 2016. In the future, a good indicator that another epidemic is beginning would be if beetle populations increase for 3 consecutive years in and around the tree or stand needing protection.*



Figure 13a—Verbenone pouches in RMNP (A.W. Schoettle, USFS).



Figure 13b—Stapling verbenone pouches to a limber pine seed tree in RMNP (A.W. Schoettle, USFS).

5.5. Sanitation Pruning to Remove White Pine Blister Rust (WPBR) Infections

Purpose of treatment:

- Prolong the life of existing, high-value trees.
- Attempt to reduce local *C. ribicola* spore load early in the invasion.

Timing of treatment:

- Late spring (mid-May to early June) when *C. ribicola* aecia are most visible.
- Yearly when paired with early detection monitoring, every 5 years for sites with incidence >20% (total host trees/infected trees), and every 10 years on sites where incidence is <20%.
- Consult with FHP annually on when to stop pruning at early detection sites, but a general guideline is to continue pruning until WPBR incidence reaches 30 percent on the site.

Treatment priorities:

- Riparian areas (33 ft [10 m] in elevation relative to active stream bed) for early detection.
- High-value trees in campgrounds, administrative sites, or points of interest.
- Do not treat tagged seed trees or tree samples for cones or rust resistance testing.
- Areas that are unique or have ecological or aesthetic value.

Description of treatment:

- In early detection areas, collect GPS coordinates (latitude and longitude), tag trees at the base using oval tag numbers (WPBR-#) specifically designated for infected and pruned trees (so the tree is not mistaken as canker-free and therefore putatively genetically resistant to WPBR), and maintain a database of treated trees. Do not prune tagged seed trees at research sites. Notify FHP as soon as possible when new infestations are found.
- Only prune branch cankers that are more than 6 in (15 cm) from the main stem using extension pole side-cutting pruners (Crump et al. 2011) (fig. 14).
- Stem cankers that have spread less than halfway around the stem's circumference and branch cankers within 6 in (15 cm) of the main stem can be scribed (Schnepf and Schwandt 2006) (figs. 15a,b).
- Do not prune a tree if more than 60 percent of the crown needs to be removed or if it has a stem canker that extends more than halfway around the stem's circumference.
- Pruning is not recommended on sites with moderate to high disease incidence (>30 percent) on highly susceptible trees or short trees (<20 ft [6.1 m]) with more than 3 branch cankers, medium height trees (20.1–30 ft [6.13–9.1 m]) with more than 6 branch cankers, and tall trees (>30.5 ft [10 m]) with more than 10 branch cankers (Jacobi et al. 2017). Ten cankers on tall trees is three times the mean canker count in this area (Kearns 2005, Cleaver et al. 2015), so such trees are likely very susceptible or the environment is highly conducive for future infections.
- Care should be taken to minimize damage to trees during treatment. Leaving the branch collar intact will promote a smaller wound. When cutting branches larger than 1.5 in (4 cm) in diameter, make an undercut to prevent bark from stripping as the branch is severed.
- Pruned branches can be left on the ground and tools do not need to be sanitized between trees. After pruning, cut side branches off so the infected branch lies flat on the ground and cover the canker with a layer of duff, soil, moss, or other material to prevent spore movement.
- See Schnepf and Schwandt (2006), Burns et al. (2008), Crump et al. (2011), and Jacobi et al. (2017).



Figure 14—WPBR-infected branch that should be pruned (K.S. Burns, USFS).



Figure 15a—After pruning a branch with a WPBR canker, potentially invaded tissue on the main stem is removed (scribed) with the goal of removing the entire infection (sanitation) (K.S. Burns, USFS).



Figure 15b—Scribing treatment to contain the growth of *C. ribicola* and prevent its spread around the main stem of the tree (K.S. Burns, USFS).

5.6. Planting Limber Pine Seedlings

Purpose of treatment:

- Increase the number of limber pine trees on the landscape to offset mortality by WPBR.
- Increase the number of seedlings with partial resistance to WPBR.
- Restore or regenerate, or both, limber pine where they have been reduced by natural and anthropogenic agents.
- Assure the future of limber pine on the landscape.
- Provide for future seed sources for areas where local sources have been diminished.

Treatment priorities:

- Recent burned stands in limber pine habitat.
- Stands with low age class diversity.
- Sites with easy access.
- Stands with overstory mortality or expected mortality.
- Campground, recreational, and administrative sites.
- Sites with low fire and WBPR risk.

Description of treatment:

Planting guidelines:

- Plan early to plant before limber pine populations have declined. Planted seedlings can successfully establish in the understory (Casper et al. 2016).
- Avoid planting in areas with high dwarf mistletoe without first pruning dwarf mistletoe infected branches from the nearby limber pines in the overstory.
- Avoid planting within 33 ft (10 m) in elevation from active stream bed. See WPBR risk map (fig. 7).
- Use a mix of bulked seed collections from a range of elevations similar to that of the target site to provide the locally adapted genotypes and enough genetic diversity to support adaptation to climate warming (see Section 5, guideline 8, *Seed Transfer / Source Guidelines*).
- Use bulked seeds for establishing seedlings (until seeds sources with quantitative resistance are identified).
- Plant 2-0 seedlings (fig. 16).
- Plant in the fall (Smith et al. 2011).
- Use seed from the clone bank for seedlings with WPBR partial resistance when available.
- Assess the frequency of genetically resistant seedling within your seed lot and adjust your planting density accordingly. Frequency of resistance can be estimated from previous tests of component lots or a new rust resistance test of a subsample of the planting stock should be conducted.
- Anticipate mortality when determining density and long-term goal. Plant 278 seedlings acre⁻¹ (685 seedlings ha⁻¹) for a projected artificial regeneration establishment density of 200 trees acre⁻¹ (494 trees ha⁻¹) to supplement natural regeneration.
- Repeated planting may be needed with bulk lots that contain susceptible genotypes.
- Microsite selection for planting should mimic those found in naturally regenerating stands (see Coop and Schoettle 2009) to maintain a natural spatial arrangement and promote establishment.
- Planting success is greatest when seedlings are planted near objects (on the north or west side), in the presence of vegetation, and in open or semi-open stands (Casper et al. 2016, Smith et al. 2011).



Figure 16—Planted limber pine seedling. Tagging is only required when coordinated with research assessments (C. Jensen, USFS).

5.7. Direct Seed Limber Pine

Purpose of treatment:

- Increase number of limber pine trees on the landscape to offset current and future high mortality.
- Increase the frequency of WPBR-resistant trees on the landscape.
- Assure the future of limber pine on the landscape.
- Restore or regenerate, or both, limber pine where they have been reduced by natural and anthropogenic agents.
- Provide seed sources for areas where local seeds have been diminished.

Treatment priorities:

- Remote areas where planting seedlings may not be feasible.
- Wilderness or other areas with poor access or management restrictions.
- Recently burned stands in limber pine habitat, especially within 10 years if natural limber pine regeneration has not established. However, earlier seeding is best to augment natural regeneration, promote resilience, and offset high mortality by WPBR.
- Sites with low fire and WBPR risk.

Guidelines for direct seeding:

- Seed sources for sowing should contain a mix of bulked seed collections from a range of elevations similar to that of the target site to provide locally adapted genotypes and enough genetic diversity to support adaptive capacity to climate warming (see Section 5, guideline 8—*Seed Transfer / Source Guidelines*).
- Use bulked seed lots.
- Sow in the fall (Smith et al. 2011).
- Assess the frequency of genetically resistant seedling within your seed lot and adjust your planting density accordingly. Frequency of resistance can be estimated from previous tests of component lots or a new rust resistance test of a subsample of the planting stock should be conducted.
- Seeds should be sown 0.8–1.6 in (2–4 cm) deep (McCaughy 1990) in clusters of 3 seeds—do not surface-sow (because they will be lost to predation on the surface).
- Target sowing 3,636 seeds acre⁻¹ (8,985 seeds ha⁻¹) from bulked seed lots for a target establishment density of 200 trees acre⁻¹ (494 trees ha⁻¹).
- Repeated seeding may be needed to keep susceptible genotypes on the landscape to delay evolution of virulence to complete resistance.

Where to plant seeds:

- Target seeding sites include recent burns, stands opened or expected to be opened by overstory mortality, or stands disturbed by road work or other mechanical treatment in the areas of potential limber pine habitat.
- Avoid seeding in areas with dwarf mistletoe without first pruning dwarf mistletoe infected branches from the nearby overstory.
- Avoid sowing within 33 ft (10 m) in elevation from active stream bed. See WPBR risk map (fig. 7).
- Microsite selection should mimic those found in naturally regenerating stands (Coop and Schoettle 2009) to maintain a natural spatial arrangement. Success is greatest when seeds are planted near objects and in the presence of vegetation in open or semi-open stands (Casper et al. 2016, Smith et al. 2011).

5.8. Seed Transfer / Source Guidelines

Purpose:

- Seed movement guidelines ensure seed is adapted to the growing conditions of the target planting area.

Priorities:

- Consider climate change.

Seed transfer guidelines:

- The GRMNPA is one seed zone that is stratified by elevation (Mahalovich 2006; Borgman et al. 2015).
- For a given target site elevation, seed sources should be a mix of bulked seed lots from sources down to 656 ft (200 m) below the target site to sources up to 656 ft (200 m) above the target site elevation; this will provide enough diversity to provide adaptive capacity for climate change.
- Restrict upward or downward movement of seed to 656 ft (200 m).

Building seed stock from multiple elevations while considering climate change:

- Conservation of the genetic diversity of limber pine in the GRMNPA requires conservation of genotypes at all elevations.
- To include enough diversity, we recommend that at least 2–3 bulked samples be collected from each 328 ft (100 m) elevation band.

Other considerations:

- RMNP can serve as a seed source for northern Colorado and southern Wyoming, but it is not recommended that the seed be moved to more southerly sites outside the GRMNPA (Borgman et al. 2015).
- Movement beyond these recommendations may be warranted if the material has quantitative resistance to WPBR.

5.9. Natural Regeneration

Purpose:

- To offset the current or future increase in limber pine mortality, good natural regeneration and supplemental planting or direct seeding will be required (fig. 17).
- Maintain genetic diversity.
- Diversify size and age class structure and successional stages across the landscape.
- Decrease costs of regeneration.

Priorities:

- Any area with canopy disturbance within approximately 7.5 miles (12 km) of a limber pine seed source; this is the average distance that the Clark's nutcracker transports and caches seeds.
- Ideally, this should be done before WPBR has impacted local limber pine seed sources through tree mortality.
- Local extinctions can occur if stands of limber pine decline and seed sources are not close enough to provide adequate regeneration; in these cases, planting or seeding will be needed.



Figure 17—New limber pine germinant (A.W. Schoettle, USFS).

Description and guidelines:

- Retain seed-producing trees in a variety of areas to ensure nutcrackers have a source of seeds to cache.
- At least 20–50 cone-bearing trees per acre are needed to be considered a seed source (Keane et al. 2012).
- Nutcrackers will cache seed in openings or closed canopies, steep slopes, needle litter, rocks, and tree trunks (Lorenz et al. 2008).
- Creation of forest openings is a suggested management option to increase nutcracker caching habitat; however, adequate seed source, nutcracker population, and good site conditions must exist (Keane and Parsons 2010).
- Manipulations of forest cover through planned or unplanned fire or other disturbance may result in limber pine establishment if there is a nearby healthy seed source and good site conditions.
- Monitoring for natural regeneration should take place 5 years post-disturbance and the amount of augmentation with planting or direct seeding required can be determined 10 years post-disturbance. Early augmentation with planting or seeding with stock that has partial resistance to WPBR is recommended.
- Natural regeneration capacity is reduced by WPBR, MPB, dwarf mistletoe, seed predation, drought, fire suppression, and other insects and diseases; prioritize planting or direct seeding in these areas.
- Any habitat that is suitable for natural regeneration should also be supplemented with direct seeding or seedling planting.
- Conditions are favorable for limber pine germination in the GRMNPA, though establishment may be curtailed by competition by other tree species (Stohlgren et al. 1998) and reduced seed sources due to overstory mortality (MPB, WPBR) or damage (dwarf mistletoe, WPBR).
- Clearing competing vegetation from established seedlings and sapling can help survival.

5.10. Locating Treatments and Selecting Seed Sources to Maintain Durability of WPBR Resistance

Purpose:

- Position treatments and select seed sources to minimize selective pressure on the rust, to lower the probability of the proliferation of rust genotypes that can overcome (i.e., become virulent to) *Cr4*, and to minimize the build-up of WPBR spore loads (fig. 18).

Description and guidelines:

- Bulked seed lots should be used throughout the GRMNPA until seed sources with quantitative resistance are available.
- Plantings of limber pine should be avoided in and near riparian areas (no closer than 33 ft [10 m] elevation of the stream-bed channel).
- Sanitation pruning (Section 5, guideline 5) should be done in riparian areas until WPBR incidence is ≥ 30 percent in the area or until advised to stop by FHP, to reduce the build-up of the local rust population.



Figure 18—White pine blister rust on limber pine (A.W. Schoettle, USFS).

5.11. Testing for Quantitative Resistance to WPBR

Purpose:

- Research quantitative (polygenic, partial) WPBR resistance types in limber pine in the GRMNPA and establish a seed orchard/clone bank of these genotypes to provide seed for future planting projects. Use field collected seed from trees tested to reveal partial resistance traits until seed orchard or clone banks mature.
- Quantitative resistance is less likely to be overcome by the WPBR pathogen over time and is more durable than qualitative complete (*Cr4*) resistance.
- Partial resistance is likely low in the GRMNPA limber pine populations and needs to be increased to sustain limber pine population health.

Timing:

- Quantitative resistance studies should be initiated as soon as possible, as tests take 5–7 years after the seed is available.
- The goal is to plant seedlings or seed with partial resistance established in the field before *Cr4* is overcome.

Description and guidelines:

- Existing individual tree seed lots may be used (consult with RMRS to select appropriate lots and make arrangements for testing). Additional selections and collections of healthy seed trees in stands that have WPBR-infected and declining trees may be useful to identify putatively resistant seed trees.
- Consider seedling field plantings in areas of high rust (e.g. Southern Rockies Rust Resistance Trial site on the Medicine Bow NF) to prescreen lots for possible resistance and prioritize families for further testing used controlled inoculation technology.
- The USFS has several facilities for testing for quantitative resistance to WPBR using controlled inoculation technologies. The Dorena Genetic Resource Center has experience with limber pine (fig. 19).
- Pricing will vary and is currently below \$2,000 per individual-tree seed lot.



Figure 19—Artificial inoculation process at the Dorena Genetic Resource Center (A.W. Schoettle, USFS).

5.12. Monitoring—Forest Health

Purpose of treatment:

- Monitor limber pine health at the landscape, stand, and tree scales.
- Enhance and expand the existing monitoring network throughout the GRMNPA.

Timing of treatment:

- Remeasure monitoring network every 5 years to detect changes.

Treatment priorities:

- Established monitoring network.

Description of treatment:

- Follow protocols and recommendations in Cleaver et al. 2017.
- Within RMNP, the 17 research areas stratified across elevations plus the 13 forest health monitoring plots are a good start; additional areas should be added.
- Ten of the FHP plots within the Park were installed within research areas; monumented plots should also be installed in the remaining 7 research areas (fig. 20).
- Thirty-three FHP plots were installed within the GRNMPA outside of RMNP in 2006, and were remeasured in 2011 and 2016 (K.S. Burns, personal communication).
- Use the Whitebark Pine Monitoring protocol (Greater Yellowstone Coordinating Committee Whitebark Pine Subcommittee 2011).
- Increase the number of plots.
- Stratify by distance from stream and elevation.
- Include riparian areas for early detection of WPBR (see Section 5, guideline 13).



Figure 20—Data collection during the installation of a forest health plot (K.S. Burns, USFS).

5.13. Monitoring—Early Detection of WPBR in Riparian Areas

Purpose of treatment:

- Early detection of WPBR.
- Enhance and expand existing monitoring network into areas at high risk for WPBR.

Timing of treatment:

- Annual late-spring monitoring in high hazard areas with follow-up sanitation pruning if infections are found.
- Fall monitoring of *Ribes* to assess rust production and risk.

Treatment priorities:

- Riparian area plots to identify infection centers.
- Established monitoring network.

Description of treatment:

- Follow protocols and recommendations in Cleaver et al. 2017.
- Within RMNP, an assessment transect has been established in each of six riparian areas for early WPBR detection monitoring (Cleaver et al. 2017).
- Within the GRMNPA outside of RMNP, establish similar transects in riparian areas.
- Assess health of limber pines in late spring (last week of May and first 2 weeks of June) when *C. ribicola* aecia are most visible (fig. 18).
- Assess alternate hosts for signs of infection in the fall (fig. 21).
- Mitigate WPBR infections on limber pine as necessary by sanitation pruning (see Section 5, guideline 5).

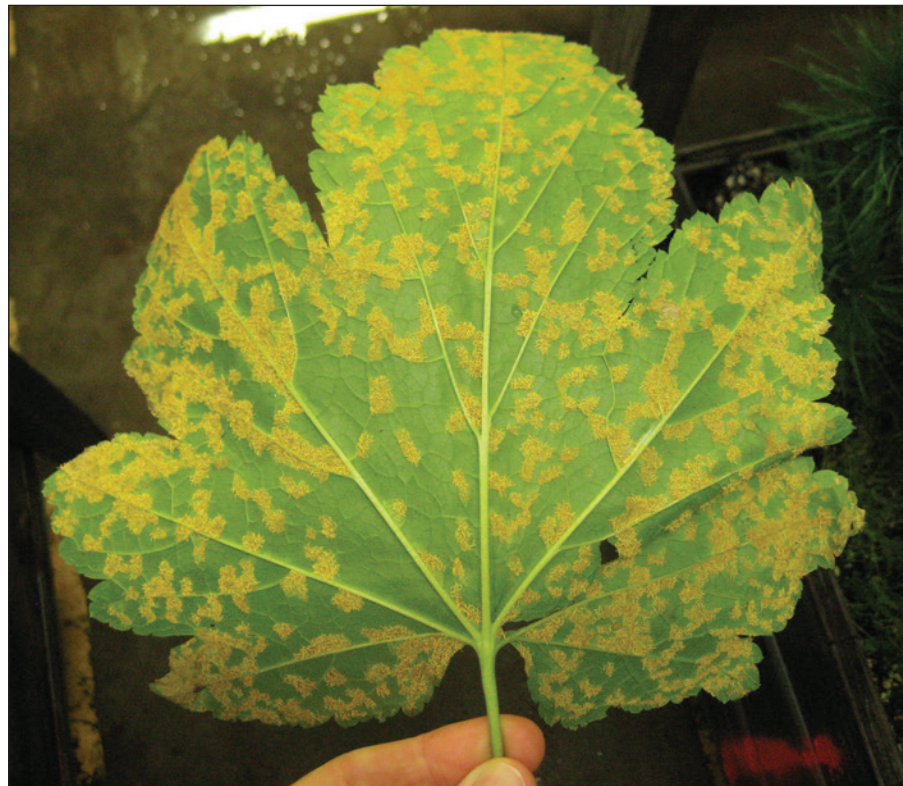


Figure 21—*C. ribicola* fruiting on the underside of a *Ribes* leaf (A.W. Schoettle, USFS).

5.14. Monitoring – Rust Virulence

Purpose of treatment:

- Monitor for WPBR virulence at the tree scale.
- Look for evidence of WPBR disease on known *Cr4* trees.

Timing of treatment:

- Annual monitoring of *Cr4* trees for cankers in the spring (late May to early June).

Treatment priorities:

- Trees inferred to have *Cr4* resistance by WPBR resistance testing.

Description of treatment:

- Follow protocols and recommendations in Cleaver et al. 2017.
- Each tree that has been determined to carry the *Cr4* allele through rust resistance testing will serve as a “virulence monitor”. Consult with FHP and RMRS for the most current listing and location of *Cr4* trees.
- If the disease is detected on one of these trees, it may indicate that the rust has evolved virulence and the *Cr4* allele will no longer provide immunity.
- As soon as virulence is detected or suspected, FHP and RMRS should be notified.

5.15. Consider Limber Pine During Fuel Treatments and Planned and Unplanned Fire

Purpose of treatment:

- Minimize limber pine mortality due to fuels treatments, and planned and unplanned fire (fig. 22).
- Provide habitat for planting or direct seeding to increasing the number of limber pine trees on the landscape.
- Stimulate natural regeneration via manipulations of forest cover through planned or unplanned fire or other disturbance.

Treatment priorities:

- Work with fire management to identify areas where fire would be detrimental (i.e., result in loss of seed bearing limber pine) or beneficial to limber management goals (i.e., create areas where fire is near a seed source).
- Protect limber pine with known resistance genotypes from fire (i.e., those trees whose progeny have been through rust resistance testing).

Description of treatment:

Planned and unplanned fire:

- List trees with known resistance genotypes on the valued resource list for fire protection.
- Retain limber pine during fuels treatments.
- Post-fire planting or seeding limber pine.
- Creation of forest openings is a suggested management option to increase nutcracker caching habitat; however, adequate seed source, nutcracker population, and good site conditions must exist (Keane and Parsons 2010) (fig. 23).
- Fire suppression considerations: protect seed sources by letting fire burn near but not in limber pine stands.
- Diversify size and age classes and successional stages across the landscape.



Figure 22—Forest fire in a subalpine forest within the GRMNPA (U.S. Forest Service).



Figure 23—Evidence of Clark's nutcracker foraging on limber pine (A.W. Schoettle, USFS).

Fuels treatments or harvesting for other objectives:

- Do not cut limber pine during fuels treatments or other harvesting operations, unless necessary.
- Consider planting or seeding with limber pine.
- Avoid damaging residual live limber pine during slash burning.

5.16. Limber Pine Seed Orchard/In Situ Clone Bank

Purpose:

- Establish a seed orchard/clone bank of quantitative (polygenic) WPBR resistance genotypes to provide seed for future planting projects within the GRNMPA.
- Produce improved seed for outplanting.
- Increasing the frequency of partial resistance on the landscape will significantly increase the sustainability of limber pine populations in the presence of WPBR.

Priorities:

- Clones (grafts) from quantitative (polygenic) WPBR resistance types should be established as soon as possible in a GRMNP clone bank (fig. 24).
- A clone bank will help fulfill RMNP's mandate to be a source of genetic diversity to promote sustained forest health in the park and greater surrounding areas.



Figure 24—Successful limber pine graft (A.W. Schoettle, USFS).

Description and guidelines:

- Great Sand Dunes National Park and Preserve and RMRS conducted a test of the partial resistance of 74 limber pine families from the southern Rockies at the Dorena Genetic Resource Center. Surviving seedlings that showed evidence of partial resistance are being grafted and will be available for a planting in a clone bank in 2017–2018. If additional studies are conducted in the GRMNPA, additional grafts could be added to the planting.
- Orchard-derived seeds will be valuable and are thus not recommended for direct seeding. Field collected seed from trees that revealed resistance traits in testing should be used to support plantings until orchards mature.
- Planting seedlings derived from the clone bank or forest trees, or both, with quantitative resistant to WPBR should begin as soon as possible. Collaborate with researchers and tree improvement professionals to explore hormone treatments to accelerate flowering and cone production.

Specification for clone bank/seed orchard:

- Accessible for protection from fire and MPB and within the range for potential supplemental watering.
- At least 1–2 acres (0.4–0.8 ha) and able to support 200–500 clones.
- A gentle slope (<15%) will allow for operation of machinery.
- Source of water for irrigation (e.g., nearby creek, holding tank, accessible by water truck).
- Good drainage.
- No residual overstory.
- Site preparation will be required during start up to remove shrubs, herbs, weeds, and grass.
- Low rust risk/hazard site preferred.
- Tall fencing required.
- Single ownership, not crossing administrative boundaries.

Potential locations of a clone bank/seed orchard in RMNP:

Hidden Valley Picnic Area—Located where the former parking lot was, adjacent to the road heading into the picnic area. There is limber pine in the area. Hidden Valley Creek is nearby and this site is not far from the Beaver Pond limber pine site. This site is near where WPBR was confirmed, so it may not be a desirable site; however, it is a higher elevation site. A new WPBR infestation was identified in this area in 2017 (K.S. Burns and B. Verhulst, personal communication).

Glacier Basin Campground—Located in the southeast corner of the campground, the Group Loop area, or near the Borrow Pit area. This site is near Glacier Creek, so the plan should specify the estimated distance required away from a stream. There should be enough distance away from the creek. This is a higher elevation site. There is limber pine in the area.

Tortilla Flats—Located in the vicinity of the Fire Office and Hotshot Dorm. Beaver Brook is in the area but a location could be found far enough away. Lower elevation site near headquarters. Currently no limber pine in the area.

Greenhouse/Nursery/Maintenance Area—This area may be suitable with respect to low WPBR risk; it is, however, a lower elevation site.

SECTION 6. BACKGROUND

6.1. Overview

Rocky Mountain National Park, established in 1915, is located in north-central Colorado and encompasses about 265,828 ac (107,577 ha). The park lies within Larimer, Boulder, and Grand Counties and is bordered by the towns of Estes Park, Allenspark, and Glen Haven on the east and Grand Lake on the west. The park is surrounded by Federal, State, local, and privately owned lands. With RMNP at its core, the GRMNPA includes ecosystems within and around the Brush Creek/Hayden, Laramie, and Parks Ranger Districts of the Medicine Bow-Routt National Forest and the entire Arapaho-Roosevelt National Forest.

Ninety-six percent of the limber pine in RMNP occurs within designated wilderness areas. The majority of land within RMNP, which is mostly backcountry wilderness, has been given permanent protection since 2009, when 249,339 ac (100,904 ha; 94 percent of the total park acreage) were designated as wilderness under the Omnibus Public Lands Management Act of 2009 (NPS 2014) (fig. 10). The designation offered a unique opportunity to provide protection of ecosystems and biodiversity extending beyond park boundaries, as four wilderness areas (Indian Peaks, Comanche Peaks, Neota, and Never Summer) (fig. 25) and three national forests (Routt, Roosevelt, and Arapaho) surround RMNP. In contrast, only about 10 percent of the limber pine population occurs within designated wilderness in the GRMNPA.

Management activities within the wilderness must honor the integrity of the Wilderness Act of 1964 by preserving wilderness character. Certain management activities in wilderness areas are permitted when exotic invasive species threaten native species. According to the NPS Wilderness Policy, “management actions, including the restoration of extirpated native species, the alteration of natural fire regimes, the control of invasive alien species, the management of endangered species, and the protection of air and water quality, should be attempted only when the knowledge and tools exist to accomplish clearly articulated goals,” (NPS 2006a, p. 83). Management of the wilderness areas surrounding RMNP is guided by the USFS Manual for Wilderness Management, Management of Insect and Diseases (FSM 2324.1), which states that control of insect or plant disease outbreaks is permitted when “it is necessary to prevent unacceptable damage to resources on adjacent lands or an unnatural loss to the wilderness resource due to exotic pests,” (USFS 2007).

Type and magnitude of visitor use vary throughout the park and create differences in disturbance type and quantity, which in turn requires different management strategies. Therefore, RMNP has divided areas of land within the park using a disturbance classification system with three categories: Natural Areas (Class I), High Use Areas (Class II), and Heavily Impacted Areas (Class III). Each of these is defined in the RMNP Vegetation Restoration Management Plan Version 2 (NPS 2006b). Here we will also use this system and will consider Class I to include all designated wilderness within RMNP, Class II to include non-wilderness wildlands such as areas within 200 ft (60 m) of park roads, and Class III to include administrative areas.

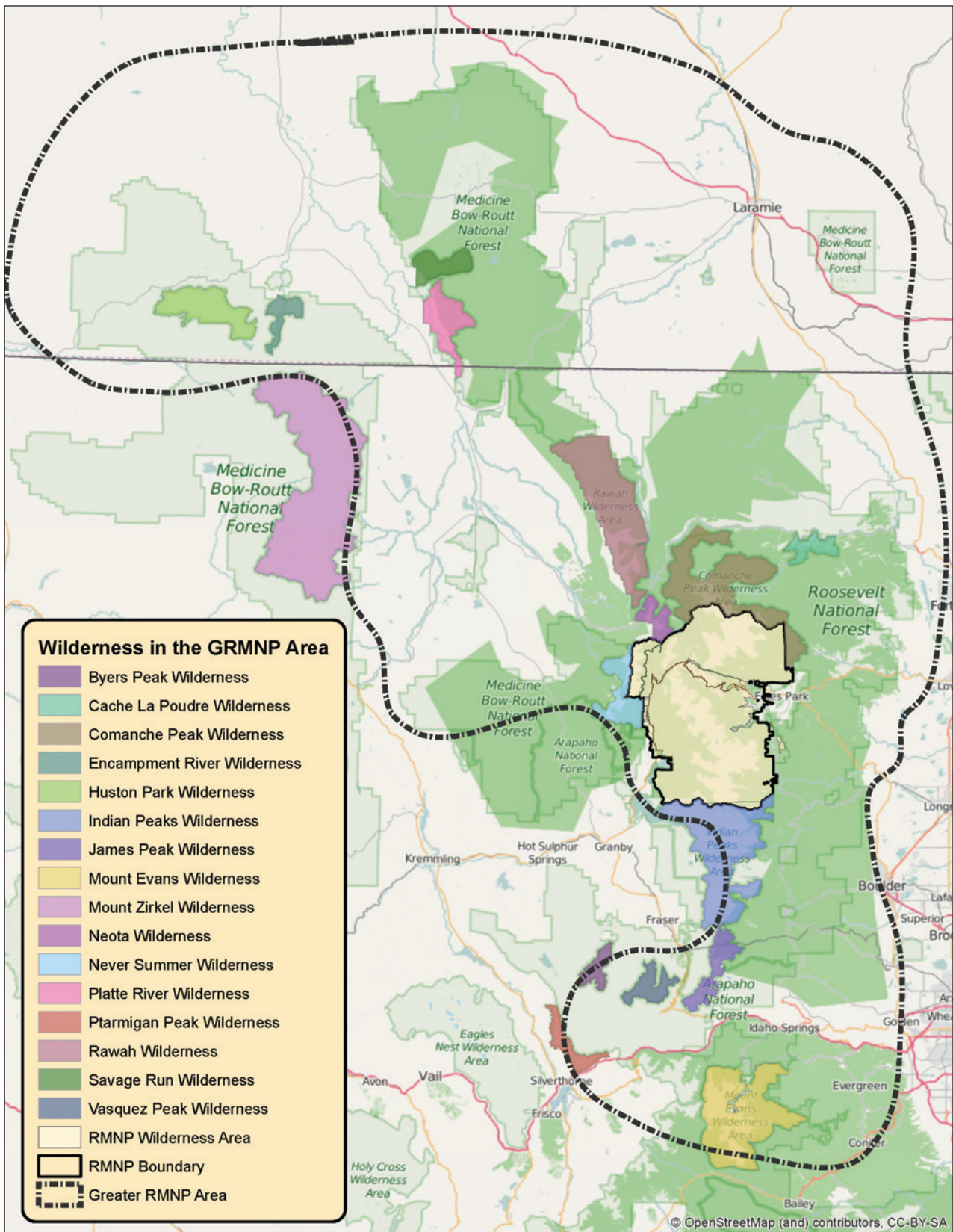


Figure 25—Map showing designated wilderness within the GRMNPA.

Rocky Mountain National Park, in collaboration with the USFS, established a program in 2008 to begin limber pine conservation in the park and to build the science foundation to address specific knowledge deficiencies that restricted efficient and effective management for limber pine conservation. This effort is built on the RMRS Five-Needle Pine Proactive Strategy Research Program begun in 2001. The science provides guidance for (1) assessing ecosystem health, (2) developing management recommendations, and (3) reducing the uncertainty of possible outcomes of interventions and consequences of inaction. The goal is to conserve limber pine and promote self-sustaining five-needle pine ecosystems in the presence of WPBR and other disturbances using available tools and methods that are compatible with land-use designations.

The information network to develop a sound conservation program must include (1) forest health evaluations, (2) data describing genetic structure and disease resistance, and (3) evaluation of population structure and dynamics (fig. 26) (Schoettle 2004a; Schoettle et al. 2011a). Sustaining population resilience requires maintaining recovery capacity after disturbance and sufficient genetic diversity to support adaptation over time. Therefore, conservation approaches must be considered within an evolutionary perspective (Schoettle et al. 2012). Tree longevity is not enough for multigenerational sustainability; sustainability depends on an intact regeneration cycle, sufficient tree population size, and, in the presence of WPBR, increased disease resistance to support survival and recovery capacity (fig. 27) (Schoettle and Sniezko 2007, Schoettle et al. 2018b). The speed at which this cycle completes a round (i.e., generation time or maturation duration) and the intensity of a selective pressure (mortality) dictates the rate of potential adaptive change given sufficient genetic diversity. If the selection is too great and the maturation time is too long, the number of individuals will decline and the population will be unsustainable (Field et al. 2012). Each stage in the regeneration cycle must be present and in balance, along with functional community landscape structure (i.e., seed dispersal via Clark's nutcracker), for maximum resilience.

RMNP and RMRS identified 17 limber pine research sites in the park (plus one that was abandoned due to hazardous cliffs) and 35 sites outside the park to serve as the sampling framework for the site-based research on which to lay the foundation for this conservation strategy (fig. 9) (Schoettle et al. 2011a, 2013). This cross-boundary network of sites was stratified by elevation to capture the full breadth of limber pine habitats in the greater geographic area. These sites were the focus of seed collections for conservation, WPBR resistance testing, and common garden studies as well as deployment of verbenone (which repels MPB attack) and regeneration and forest health assessments. To date, seed has been collected from 53 sites within the GRMNPA (18 in the park, 35 outside the park) (fig. 9). In addition, long-term forest health monitoring plots, independent of this network, were installed in 29 limber pine stands throughout the GRMNPA in 2006 and in 10 of the 17 research sites within the park in 2013 (fig. 10). The Proactive Limber Pine Conservation Strategy is an extension of this program.

Integrated Interdisciplinary Program to Build a Science Foundation for Proactive Management

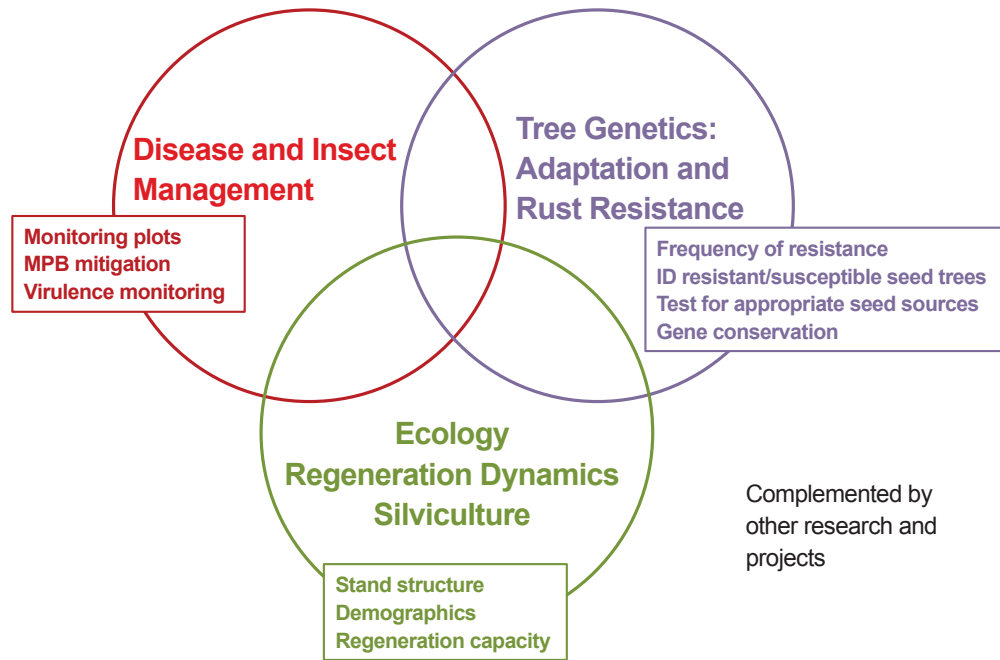


Figure 26—Diagram showing disciplines critical for providing the science foundation for the Proactive Strategy aimed at managing high elevation five-needle pine ecosystems threatened by WPBR (adapted from Schoettle et al. 2011a).

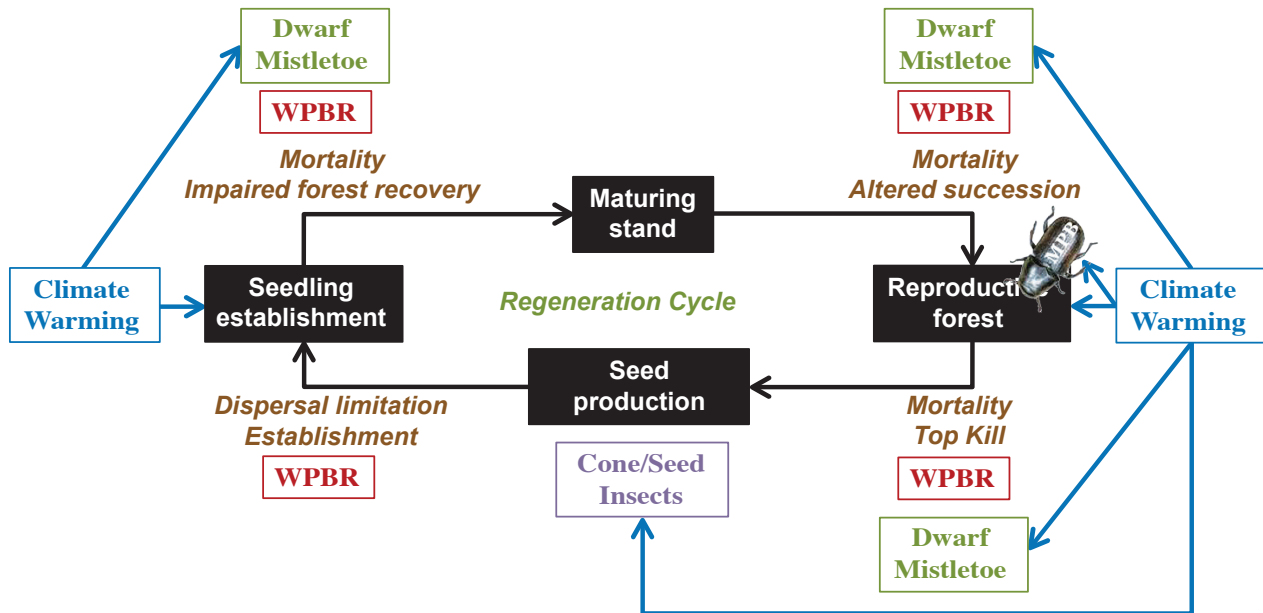


Figure 27—Forest regeneration cycle and damage agents (adapted from Schoettle and Sniezko 2007). White pine blister rust (WPBR) affects the regeneration cycle at all points (brown text), while mountain pine beetle (MPB) only impacts larger mature trees, and cone and seed insects only impact seed production. Dwarf mistletoe can infect trees of all ages. Climate change may directly impact insect populations and seedling establishment and tree growth and may indirectly affect other interactions within the cycle.

6.2. Evolutionary History of Limber Pine

The biogeographic history of a species contributes context to management and restoration options (Noss 1999). During the last glacial maximum (18,000 ± 4,000 years ago), evidence indicates there were at least four limber pine glacial refugia including western Kansas and Nebraska (Wells and Stewart 1987), the Great Basin, Fremont County in Colorado, and Bighorn County in Wyoming (Mitton et al. 2000). In addition, macrofossil evidence suggests that limber pine persisted during glaciation at low elevations near the eastern base of the Rocky Mountains south of Pikes Peak (Wells 1976). Today in the Front Range, limber pine is most commonly found above 7,875 ft (2,400 m) (Wells 1965); however, a few anomalous populations occur on escarpments of the High Plains with the pine persisting as low as 5,250 ft (1,600 m) around 37 mi (60 km) east of Cheyenne, Wyoming, and Fort Collins, Colorado. The remarkable populations of limber pine on the Pawnee National Grassland are widely disjunct and extremely local, and may be relicts of Plainswide Pleistocene populations (Wells and Stewart 1987). They are also possibly the populations most immediately vulnerable to climate change (Means 2011). As the glaciers receded, the mountains were progressively colonized from the low-elevation refugia with the aid of seed dispersal by Clark's nutcrackers (Mitton et al. 2000). During the early Holocene (approximately 11,500 years ago), limber pine had expanded to elevations of 8,200 ft (2,500 m) (Anderson et al. 2000). Its upslope migration has continued since the late Holocene and the end of the little ice age (1890) and is projected to continue (Monahan et al. 2013).

6.3. Genetic Diversity

The genetic diversity of a species and its distribution across the landscape, along with regeneration, dispersal, and disturbance dynamics, are important components of the species' adaptive capacity to novel stresses (see Aitken et al. 2008). Across its range, limber pine is considered a moderate generalist with broad tolerances to abiotic stresses. Genetic variation can be accessed from (1) neutral markers that reflect migration and genetic drift dynamics; (2) common garden studies that grow trees from different geographic sources in a common environment or set of environments such that differences among sources in growth, phenology, cold hardiness, or other adaptive traits are inferred as attributable to adaptive genetic differentiation among sources; and (3) genomic markers such as single nucleotide polymorphisms that reflect variation in adaptive traits (Menon et al. 2018). In addition, some inferences can be made from in situ studies of variation in traits among trees naturally growing in different environments; however, it is not possible to ascribe any differences to genetics versus the environment.

In the southern Rocky Mountains, a common garden study showed slight differentiation among populations from New Mexico and southern Colorado compared to those from northern Colorado and southern Wyoming (Borgman et al. 2015), suggesting that seed sources with a makeup similar to those from the GRMNPA extend from latitudes of about 40° N to 42° N in this region. In this area, neutral genetic marker studies (Latta and Mitton 1997; Schuster and Mitton 2000), in situ studies (Schoettle and Rochelle 2000; Schuster et al. 1989), and common garden studies (Reinhardt et al. 2011) have all detected genetic differences in limber pine from

different elevations. Local adaptation to conditions along the elevation gradient is common in tree species and may result from strong local selection, differences in phenology, or limited gene flow among limber pine populations. As a result of this pattern of genetic structure, seed sources for planting or sowing projects should be from elevations slightly above and below that of the target treatment site to provide sufficient genetic diversity for adaptation to climate change yet avoid potential maladaptation (see Section 5, guideline 8).

6.4. Natural History Traits

The same life history traits that enable limber pine to tolerate natural stresses also hinder rapid adaptive change to novel stresses. Limber pine is tolerant of cold and drought, but also has a slow growth rate (Schoettle and Rochelle 2000), long lifespan (>1,000 years), delayed maturity (>50 years), and a protracted regeneration dynamic (Coop and Schoettle 2009); it is not a prolific seed producer. This species' evolutionary strategy does not position it favorably for rapid adaptation to novel stresses, such as WPBR, with which it did not coevolve, and the interactions with intensifying native stresses. **The combination of rapid mortality, impaired recovery, slow maturation, and long generation time may not support viable populations in the presence of these multiple interacting stressors in the future without management intervention to increase the number of individuals and the frequency of genetic resistance to WPBR (Field et al. 2012).**

6.5. Community Dynamics

Limber pine is often the first species to colonize an area after fire (Donnegan and Rebertus 1999) and is capable of doing so in suitable habitat within its elevational range (see fig. 2). Clark's nutcrackers can cache seed across the undisturbed landscape as well as in the central areas of large burns where wind-dispersed seeds of other conifer species are scarce (Tomback et al. 1990). The germination of multiple seeds from one cache results in a cluster of seedlings that are often related, as the cache is frequently a product of a seed harvest by a nutcracker from a single or several parent trees (Carsey and Tomback 1994). The clustered distribution of seedlings facilitates successful establishment of limber pine (Donnegan and Rebertus 1999). Often, more than one seedling in a cluster survives, and together they form a multi-genet tree with stems contiguous or fused at the base. However, as trees mature, the clustered distribution may reduce the reproductive output (Feldman et al. 1999) and lifespan of individuals (Donnegan and Rebertus 1999) compared to trees growing singly.

The dynamic of stands containing limber pine depends on the site. Limber pine forms self-regenerating stands on dry rocky sites and at treeline, but tends to be limited to early successional stages on more mesic sites, where they are often replaced by more shade-tolerant species (Schoettle 2004b). Dry sites can be occupied by limber pine at any elevation within the species' range and are often windswept and accumulate little snow. Limber pine dominates xeric sites, not because they provide the optimal physical environment for limber pine growth (Lepper 1974; Schoettle and Rochelle 2000), but because the conditions are not suitable for the growth of other species and therefore competition is minimal. Competition is likely to be

the largest limitation defining the realized niche of limber pine and the location of sustainable limber pine stands (Schoettle 2004b). On dry sites, limber pines have been reported to live more than 1,500 years in Colorado (Schuster et al. 1995) and more than 2,000 years in Nevada and California (Lanner 1984). The stands tend to be open and support continual recruitment of limber pine (Knowles and Grant 1983; Stohlgren and Bachand 1997). Sexual maturity may take more than 50 years (Schoettle 2004b), and open-grown limber pine produces good cone crops.

The frequency of mast years is usually every 3 to 6 years. On harsh sites, limber pine stands persist not only because of the extreme longevity of some individuals, the lack of competing tree species, and sustained regeneration (Coop and Schoettle 2009), but also because catastrophic disturbance (i.e., wildfire) is rare on dry, rocky sites. While rocky ridges and dry slopes are the most visible habitat occupied by limber pine, scattered occurrence of limber pine throughout the forested region of the GRMNPA is typical (Marr 1977; Schoettle and Rochelle 2000). On the more mesic sites, limber pine's early post-disturbance dominance succeeds over time to other conifer species (Rebertus et al. 1991). Limber pine acts as a nurse tree, mitigating the harsh open environment after disturbances and facilitating the establishment of Engelmann spruce (*Picea engelmannii*) and subalpine fir (*Abies lasiocarpa*) (Donnegan and Rebertus 1999; Rebertus et al. 1991). Such facilitation accelerates limber pine's mortality due to the close proximity of, and competition by, the succeeding species. Limber pine also facilitate establishment of other conifers above tree line during the formation of tree islands in the krummholz zone (Schoettle and Richards, unpublished data on file at RMRS, Fort Collins, Colorado). Limber pine regeneration occurs frequently throughout all stand types along the elevation gradient (Brown and Schoettle 2008), yet successful establishment in late successional stands on mesic sites is rare (Stohlgren et al. 1998).

Seral limber pine is more likely to maintain apical dominance and retain an erect forest tree form and is suspected to produce fewer cones per tree than those trees on more open and drier sites (Lepper 1974). Seed yields for limber pine can also be reduced by some of the same cone and seed insects that affect co-occurring conifer species (Hedlin et al. 1980; Schoettle and Negrón 2001) as well as by WPBR infection, bark beetle attack, and dwarf mistletoe infection. Due to the lower seed yields in successional stands, it is unclear what proportion of seed from these sites is consumed by animals versus dispersed and cached. Therefore, the relative contribution of progeny from seral compared to persistent limber pine stands to the recolonization of nearby disturbances is unknown (Schoettle 2004b).

6.6. Clark's Nutcracker Ecology

Clark's nutcracker occupies coniferous forests of western North America, particularly forests dominated by pine species producing large, wingless seeds (Tomback 1998). Whitebark pine is a primary food source and obligate mutualist (Tomback and Linhart 1990) of Clark's nutcracker, but across its range the Clark's nutcracker also consumes seeds from other pines. In the southern Rocky Mountains, nutcrackers harvest seeds from limber and southwestern white pine (*Pinus strobiformis*) (Samano and Tomback 2003) and also Colorado pinyon (*Pinus edulis*), ponderosa,

and Rocky Mountain bristlecone (Tomback 1998) pine. Limber pine is considered a mutualist of Clark's nutcracker (Lanner 1980), and seed dispersal patterns influence distribution, postdisturbance establishment, and population genetics (Tomback 2001). The dependence of all these pines to varying degrees on seed dispersal by nutcrackers makes the bird an important connecting "mobile link" (Tomback and Kendall 2001) essential to the conservation of limber pine.

The morphological and behavioral adaptations of Clark's nutcracker allow for year-round access to their primary food source (Tomback 1978). Nutcrackers extract seeds from cones with a long, pointed bill. They can carry 50 or more seeds, depending on seed size, in a sublingual pouch. They use an extraordinary spatial memory to retrieve cached seeds from thousands of locations for up to a year (Tomback 1978; Vander Wall and Hutchins 1983), using objects such as rocks, trees, or logs for visual reference (Kamil and Balda 1985; Tomback 1980, 2001). About three to five seeds are stored per cache (Tomback 2001) at depths of about 0.8–1.2 in (2–3 cm) (Lanner and Vander Wall 1980; Tomback 1982). Clark's nutcrackers cache limber pine seeds ranging in distance from within 0.3 mi (0.5 km) to several miles away from the seed tree (Lanner and Vander Wall 1980). Typical seed caching distances by Clark's nutcrackers for other pines, mainly whitebark pine, range from a few feet to a few miles (Hutchins and Lanner 1982; Lorenz et al. 2011; Tomback 1978, 2001; Vander Wall and Balda 1977), with a maximum dispersal distance of 20 mi (32 km) (Lorenz et al. 2011). Tomback and Taylor (1987) found that color-banded nutcrackers in RMNP often traveled back and forth over the Continental Divide looking for tourist handouts within the course of a day—a distance of about 9 mi (14 km). Site types for seed caching include exposed, south-facing, steep slopes; areas with an open canopy or terrain; and disturbed sites, especially burned areas (Tomback 1978).

Limber pine across most of its range conforms to a meta-population structure whereby a regional population comprises many local small populations and a subset of these local populations become extinct over time primarily from fire and advancing succession (Hanski 1999; Webster and Johnson 2000). Long-distance seed dispersal by Clark's nutcrackers, moving seeds from the larger and more productive stands, is essential for maintaining this population structure, through recolonization of disturbed sites (Brown and Schoettle 2008) and the founding of new populations in suitable areas.

6.7. Natural Regeneration Facilitated by Clark's Nutcracker

Research with whitebark pine suggests that the number of seeds cached by a single Clark's nutcracker per season is prodigious (35,000 to 98,000); given adequate cone production, nutcrackers cache enough seeds to feed themselves and their young and to account for losses to rodents (Hutchins and Lanner 1982; Tomback 1982). Roughly 45 percent of whitebark pine caches are retrieved (Tomback 1982). Working in the Cascade Range with whitebark pine, Lorenz et al. (2011) suggested that only about 15 percent of seeds are cached in habitat suitable for successful germination, but this merits further study. If the seeds are viable and not lost to predation, they may germinate given adequate conditions of temperature and moisture (Tomback 1982). This suggests that more than 2,000 seeds per bird may potentially

germinate, and the seedling survival rate for cached seeds is relatively successful at more than 55 percent through the first year, diminishing to 25 percent by the fourth year (Tomback 1982). All these studies are based on whitebark pine, a species with indehiscent (closed at maturity) cones that depends on Clark's nutcracker for primary seed dispersal. These estimates may underestimate limber pine seed available for regeneration because the cones of limber pine open readily at maturity, allowing for dispersal of the wingless (or near-wingless) seeds via gravity, fierce winds (for short distances; Anna Schoettle, personal observation 2004), or rodents (Tomback et al. 2005); however, these dispersal mechanisms are less reliable than that provided by Clark's nutcracker.

Capacity for natural regeneration of limber pine is reduced by WPBR, MPB, dwarf mistletoe, seed predation, drought, and fire suppression (McCaughey and Tomback 2001), all of which affect seed availability and therefore dispersal by nutcrackers (McKinney et al. 2009). Opportunity for natural dispersal of WPBR-resistant limber pine may diminish if mortality is high enough to no longer support stand visitation by nutcrackers (McKinney and Tomback 2007; McKinney et al. 2009). Ultimately, a reduction in the carrying capacity of nutcracker populations by mortality of five-needle white pines will exacerbate the decline in limber and other five-needle pine species (McKinney et al. 2009). For whitebark pine ecosystems, a target of 405 cones ac^{-1} (1,000 cones ha^{-1}) is recommended to maintain a high probability of Clark's nutcracker visitation and seed dispersal, and an estimated basal area of 8.7 $\text{ft}^2 \text{ac}^{-1}$ (2 $\text{m}^2 \text{ha}^{-1}$) (Barringer et al. 2012) to 21.8 $\text{ft}^2 \text{ac}^{-1}$ (5 $\text{m}^2 \text{ha}^{-1}$) (McKinney et al. 2009) is suggested to produce that amount. Clark's nutcrackers are not likely to visit a stand with fewer than 53 cones ac^{-1} (130 cones ha^{-1}) (McKinney et al. 2009). However, Barringer et al. (2012) found that there was some probability of nutcracker stand visitation at even very low cone densities. Lorenz and Sullivan (2010) did not find a correlation between cone density and probability of seed dispersal in whitebark pine. Critical limber pine production levels for nutcracker visitation are unknown.

Postfire natural regeneration was especially successful after the 1978 Ouzel Fire in RMNP, with limber pine regeneration occurring within the burn interior and far from seed sources (Coop and Schoettle 2009). Other studies have indicated postfire dominance of limber pine on the Colorado Front Range and within the GRMNPA, including Sundance, Boulder Brook, and Longs Peak burns (Huckaby 1991; Rebertus et al. 1991; Shankman and Daly 1988). Successful natural regeneration of limber pine is highly dependent on caching by Clark's nutcracker, and not all Colorado Front Range postfire sites have been successfully colonized by limber pine, even when limber pine previously dominated the site, adequate seed sources were available nearby, and appropriate environmental conditions existed (Huckaby 1991; Shankman and Daly 1988).

Limber pine begins to establish postfire within the first decade (Huckaby 1991; Shankman and Daly 1988). Rebertus et al. (1991) examined limber pine on three northern Colorado sites and indicated that time until initial colonization was inconclusive but that peak colonization took several decades. Coop and Schoettle (2009) also reported sustained periods of limber pine establishment after stand-replacing fire such that areas are still accumulating new recruits more than 30 years after the

disturbance. Likewise, limber pine seedling establishment was successful in small disturbances (i.e., tree fall) within an otherwise intact forest (Brown and Schoettle 2008). Others evaluating whitebark pine regeneration recorded germination as early as 2 to 5 years (Tomback 1986; Tomback et al. 1993), whereas others found 5 years was not long enough and recommend at least 10 years (Keane and Parsons 2010). Regeneration can be delayed during periods of drought or in areas with seasonal drought.

It may take several decades until postfire tree density reaches that of surrounding unburned stands (Coop and Schoettle 2009; Klutsch et al. 2015), and colonization of limber pine occurs more slowly with increasing elevation and on xeric sites (Donnegan and Rebertus 1999; Shankman and Daly 1988). In the upper subalpine, reports indicate that it may take up to 40 years for whitebark pine to establish after a disturbance (Arno and Hoff 1990). Thus, enhancing natural regeneration of limber pine through planting and direct seeding as soon as possible will yield the greatest long-term benefit (Coop and Schoettle 2009).

Creation of forest openings is a suggested management option to increase nutcracker caching habitat; however, the efficacy of this technique will be limited if seed availability is reduced because of high stand mortality from WPBR and MPB, nutcracker retrieval of seed, and poor site conditions (Keane and Parsons 2010).

6.8. Mountain Pine Beetle Biology and Control

Mountain pine beetle is native to western North America, and limber pine is a preferred host (Cerezke 1995). Mountain pine beetle larvae develop under the bark of susceptible pines, and typically complete one life cycle per year (Safranyik and Carroll 2006). Initially, swarms of beetles attack a tree, and once the tree's defense system is overcome, the tree dies within a year. The cause of death is the combination of the excavation of galleries by adults and larvae and a mutualistic fungus carried by the beetle; both synergistically kill the tree (Hubbard et al. 2013; Solheim and Krokene 1998). Under endemic conditions, MPB prefers stressed pines, typically smaller in diameter, whereas larger diameter pines are preferred during epidemics (Safranyik and Carroll 2006). Studies in lodgepole pine (*Pinus contorta*) indicate that MPB attacks trees greater than 8 in (20.3 cm) diameter at breast height (d.b.h.) (Gibson et al. 2009); saplings and seedlings are not attacked. The endemic-epidemic cycle is largely driven by population size of MPB, host availability, and climatic conditions (Safranyik and Carroll 2006). Observations suggest that endemic populations of MPB may remain more active and continue to contribute to mortality in limber pine stands (Robert Cain, Regional Entomologist, R2 Forest Service, Forest Health Protection, personal communication 2015). Temperature thresholds of beetle life stages limit the distribution of MPB on a landscape of suitable hosts. The previous MPB outbreak in lodgepole pine in the GRMNPA occurred during the early 1980s; it ended abruptly following lethally cold October temperatures in 1983 and 1984 (Chapman et al. 2012; Lessard et al. 1987; Malm 2009). The intensity and broad elevational range of the most recent epidemic is attributed to recent climate warming (Raffa et al. 2008). Dense, even-aged stand conditions and drought in the early 2000s are thought to have increased the susceptibility of trees to attack, along with warmer winter temperatures; in fact, in contrast to previous

outbreaks, trees were attacked up to alpine treeline (Logan and Powell 2001). With continued climate warming, we can expect an increase in MPB epidemic periodicity, intensity, and elevational range.

It is common for secondary bark beetles, such as engraver beetles (*Ips* sp.) and twig beetles (*Pityophthorus* and *Pityogenes* spp.), to increase to very high population levels during a mountain pine beetle epidemic, and then cause significant tree mortality as the mountain pine beetle epidemic subsides (Evenden and Gibson 1940; Witcosky 2017). In such an instance, an outbreak of secondary bark beetles may occur over 2 to 3 years, causing significant additional tree mortality, and then decline abruptly.

Direct control of MPB can be achieved with timely spraying of the tree bole with a registered insecticide such as Carbaryl (1-naphthyl methylcarbamate). Anti-aggregation pheromones (semiochemicals, e.g., verbenone) can offer moderate control for individual trees (Kegley and Gibson 2004). The Arapaho, Roosevelt, and Medicine Bow National Forests have utilized both techniques to protect select high-value limber pine trees and populations with confirmed WPBR resistance. Since 2008, RMNP has deployed verbenone to protect 10–15 limber pine seed trees dispersed throughout the 17 research sites within the park. Two 7.5-g (0.3-oz) packets are deployed, one in early summer (May/June) and the other later (July/August) to ensure a continuous elution rate. Of the 275 trees treated with verbenone from 2008 to 2012 in RMNP, 41 trees were unsuccessfully attacked (20 percent) and 5 died from MPB attack (2 percent). Because beetle pressure was not controlled among sites, these data cannot definitively address the efficacy of verbenone treatment. However, the very low mortality for treated trees as compared to mortality of 19 percent of limber pine >5 in (12.7 cm) d.b.h. in RMNP during the recent MPB epidemic suggests that verbenone may have helped deter lethal MPB attacks on treated trees.

6.9. White Pine Blister Rust Biology and Control

Cronartium ribicola, the pathogen that causes WPBR, is native to Asia (Hunt 2003). It was accidentally introduced into eastern North America numerous times in the early 1900s on infected seedlings from Europe, and it is suspected that there was only a single introduction into western North America (Brar et al. 2015; Hunt 2009). Despite extensive spread, the pathogen populations in eastern and western North America are still distinct and show no evidence of gene flow across the Great Plains (Hamelin et al. 2000).

The complex life cycle of *C. ribicola* requires five spore stages, three of which are infective, and both a primary host (five-needle white pines, subgenus *Strobus*) and an alternate host (*Ribes*, *Castilleja*, and *Pedicularis* spp.) (McDonald et al. 2006; Zambino et al. 2006) (fig. 28). *Cronartium ribicola* requires living host tissue for survival. The needles of the primary white pine host may become infected during conditions of cool temperatures and high relative humidity in fall and exhibit yellow spots the following spring. In late spring of the next year, orange aeciospores, the durable, thick-walled fungal spores produced on the five-needle pine host, are wind-blown several hundred miles to infect the alternate hosts

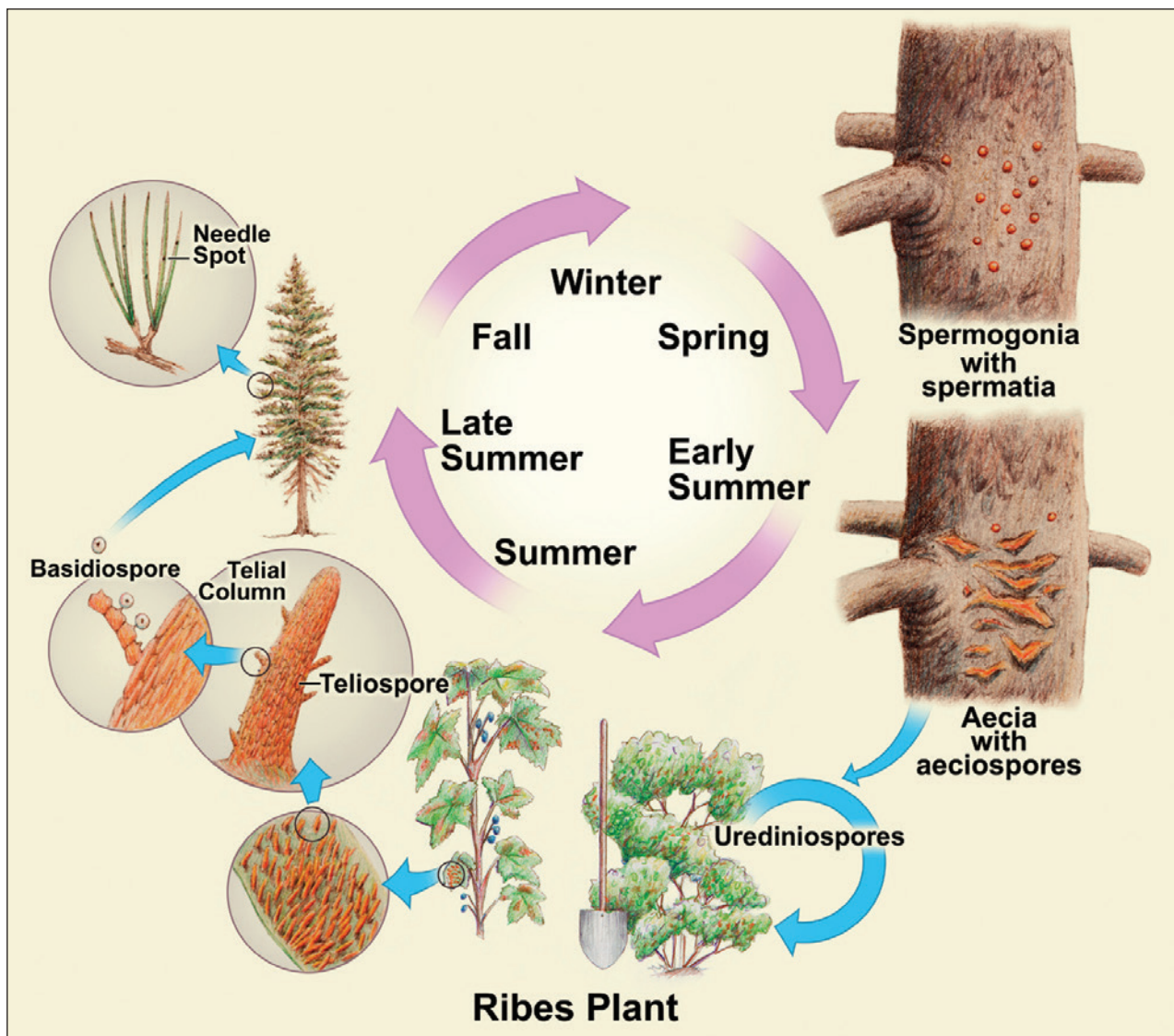


Figure 28—Life cycle of *Cronartium ribicola*. Species other than *Ribes* can also serve as the alternate host (W.R. Jacobi, Colorado State University).

(Frank et al. 2008). Urediniospores are produced on the leaves of the alternate host midsummer and can magnify WPBR infection in nearby alternate host species. Impacts to alternate host species (all deciduous) are minimal because the infection generally remains in the leaves and these are typically shed in fall (Stewart and Rankin 1914). Produced in late summer on the alternate hosts after 48 hours of 100 percent relative humidity and temperatures ≤ 68 °F (20 °C), fragile, thin-walled basidiospores are dispersed typically less than a thousand feet to five-needle pine hosts (Van Arsdell et al. 1956; Zambino 2010).

Once the host is infected, the fungus colonizes the inner bark of the pine, expanding through the branch and toward the main bole; it causes tissue death (cankers) that may result in decreased vigor, branch death, topkill, or entire-tree mortality. White pine blister rust can ultimately cause a reduction in canopy and cone-bearing branches and can infect and kill seedlings. Time from infection to mortality in

mature trees may be years to decades depending on infection location and tree size (Geils et al. 2010). There is no evidence for tree-to-tree transmission of this disease.

Important factors found to positively influence tree damage or mortality expected as a result of WPBR include: years infested, percentage of large trees, density of *Ribes inerme*, relative humidity in June, higher September daily minimum temperature, and mean May precipitation (Cleaver 2014; Kearns et al. 2014). Spread and intensification of WPBR are increased during years of favorable weather, resulting in a wave year phenomenon (Kinloch 2003). Despite complex meteorological requirements for sporulation and infection, there are no limitations for WPBR where white pines and susceptible *Ribes* species interact (Kinloch 2003). Species of all WPBR alternate hosts—*Ribes*, *Castilleja*, and *Pedicularis*—are common in the GRMNPA, including *R. cereum*, *R. inerme*, *R. montigenum*, *P. groenlandica*, *C. rhexifolia*, and *C. occidentalis*. Both *R. inerme* and *R. montigenum* are Class B alternate hosts of WPBR, expressing intermediate levels of incidence, whereas *R. cereum* is a Class D alternate host—thought to be less significant in WPBR spread (Van Arsdel and Geils 2004). However, because of the extensive coverage of *R. cereum* in the GRMNPA, it may have a greater role in the epidemiology of the disease than its ranking suggests.

Van Arsdel (1972) described slope bases, narrow valleys, and small openings in the overstory as the topographic positions and stand structure types with the micrometeorological conditions most suitable for WPBR infection. Riparian areas are conducive to the micrometeorological conditions and abundance of alternate hosts that permit WPBR infection and sporulation, including cool, humid conditions and presence of *Ribes inerme*; therefore, we developed risk maps (figs. 2 and 7) to identify potential areas for early detection of WPBR.

Efforts to control WPBR have limited success. Determining white pine resistance to WPBR and establishing rust-resistance breeding programs have been the most promising, but time-consuming, options (Burns et al. 2008). *Ribes* eradication was not successful in the western United States; chemical controls are not practical on a forest scale, and thinning was found to increase WPBR infection by exposing more foliage to inoculum (Burns et al. 2008; Maloy 1997; Schwandt et al. 1994). Preventive and sanitation pruning (i.e., removal of infected branches) can prolong the life of infected trees but is labor-intensive and therefore feasible only early in the infection process or for high-value trees; it is too expensive for application at a forest scale (Burns et al. 2008; Crump et al. 2011, Jacobi et al. 2017). While sanitation pruning does not contribute to an increase in the overall frequency of disease resistance in the forest and therefore resilience, it may retain high-value trees and enable tree survival to provide other ecosystem services (e.g. slope stabilization or diet for wildlife).

Natural genetic resistance (lower susceptibility) to WPBR colonization is present in each of the North American white pine species, including limber pine (King et al. 2010). Assessments of resistance are made with progeny tests and artificial inoculations with *C. ribicola* (see Sniezko et al. 2011). Limber pine in the GRMNPA has a high frequency of complete resistance conferred by a dominant resistance allele—*Cr4* (Schoettle et al. 2014). Complete resistance, or major gene resistance (MGR),

provides immunity; however, the rust can evolve and overcome it. Partial or quantitative resistance is polygenic and thus is suspected to be more durable over time, but it occurs at low frequencies. Partial resistance slows the progression of the fungus, enabling trees to mature and even reproduce when infected. Quantitative resistance appears to occur in limber pine in the southern Rockies (Schoettle and Sniezko, unpublished data on file at RMRS, Fort Collins, Colorado); 84 families total with 43 families across 8 sites within the GRMNPA have been tested (no RMNP seed sources were included). A balance of genetic resistance and the number of individuals to offset mortality within the pine populations is needed to sustain populations in the presence of the rust (Schoettle et al. 2012).

6.10. Dwarf Mistletoe Biology and Control

Dwarf mistletoe is a native, leafless, parasitic plant that extracts both water and nutrients from its host. It disseminates short distances (33 ft [10 m] on average), by forceful ejection of sticky seeds to nearby branches and occasionally by long-distance transport by birds and mammals (Hawksworth and Wiens 1996). The many species of dwarf mistletoe are generally host specific, but can cross hosts on occasion. Due to the long life cycle of dwarf mistletoe (4–5 years), lateral tree-to-tree spread occurs at a rate of about 1.5 to 2 ft (0.5 to 0.6 m) per year in even-aged stands and more rapidly in uneven-aged stands as seeds readily fall down onto the understory trees and branches (Taylor and Mathiasen 1999). Once a tree becomes infected, survival time depends on tree size and severity of infection. Heavily infected trees of less than 9 in (23 cm) d.b.h. may die within 7–17 years, while larger trees may die within 10–25 years (Hawksworth and Geils 1990). The mortality rate of infected trees may be increased by additional stress factors including drought (Page 1981; Smith 1983) and bark beetles (Kenaley et al. 2006; McCambridge et al. 1982; Millar et al. 2007). Heavily infected stands (e.g., the Boulder Brook stand in RMNP) may no longer be contributing to regeneration because seed production is suppressed, and any established seedlings are likely to become infected and die.

Limber pine dwarf mistletoe is common in the GRMNPA, and the most effective control is pruning infected branches or removal of all infected trees by cutting or fire. Pruning delays mortality in high-value trees with moderate infections that are concentrated within the lower half of the crown (Hawksworth and Johnson 1993). Ethephon, the generic name for trade product Florel® (Lawn and Garden Products, Fresno, California), is an ethylene-releasing plant growth regulator that causes mistletoe shoots to abscise but does not kill the parasite's roots, and therefore needs to be reapplied every few years. This could be an option for advanced regeneration and high-value trees but is not feasible or recommended at a landscape scale.

6.11. Susceptibility to Other Biotic Damage Agents

Limber pine is susceptible to other insects, diseases, and damaging agents. Common insects include the limber pine engraver (*Ips woodi*) and twig beetles (*Pityophthorus* spp. and *Pityogenes* spp.); both attack and can cause mortality in stressed and weakened trees (Witcosky 2017). Several other insects have been reported on limber pine including ponderosa pine budworm (*Choristoneura lambertiana*), woolly aphid (*Pineus coloradensis*), and multiple cone and seed insects

(Schoettle and Negron 2001; Steele 1990) that can reduce seed yields. Diseases affecting limber pine, but less commonly in Colorado, include root diseases (causal agents: *Armillaria* spp. and *Phaeolus schweinitzii*); wood-decay fungi (*Fomitopsis pinicola* and *Porodaedalea pini*); and foliar diseases such as brown felt blight (*Neopeckia coulteri*), a common snow mold of conifers (Steele 1990), and *Bifusella* species (reported in Colorado and Wyoming; Kelly Burns, USFS, personal communication 2015). *Dothistroma* needle blight (*Dothistroma septospora*) has not yet been found in Colorado (Taylor and Walla 1999). Additionally, limber pine trees are susceptible to wild animal damage, particularly elk (*Cervus elaphus*) antler rubbing and porcupine (*Erethizon dorsatum*) damage (Steele 1990).

6.12. Role of Fire in Limber Pine Ecology

The presettlement role of fire in limber pine forests remains the subject of considerable uncertainty. Limber pine probably was exposed to 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 and, in the high-elevation subalpine forests of the northern Colorado Front Range, it is an early colonist of extensive, high-severity burns. The degree to which high-severity fire was typical in limber pine forests is unclear.

Following fire, regeneration dynamics take from decades to centuries (Brown and Schoettle 2008). Where open stands border grassy openings, limber pine trees often exhibit fire scars indicative of fairly frequent but low-intensity fire. Because of the great ages attained by limber pine, they potentially offer very long fire history reconstructions in such settings. Whether or not fire suppression has led to declines in limber pine—through successional shifts to shade-tolerant competitors or shifts to a stand-replacing fire regime—remains an open question that deserves further inquiry. **In any case, reestablishing presettlement fire regimes, whatever they were, may not be as important as determining appropriate disturbance regimes given current conditions and management objectives.** In the face of the WPBR and MPB threats and uncertain consequences of climate change, fire management (both prevention and application) can be a tool to promote resilient landscapes (Coop and Schoettle 2011). Appropriate fire management may be used to conserve valuable stands, promote regeneration and diversify age-class structures and alter the balance between this species and its competitors (Schoettle and Sniezko 2007).

Limber pine appears to benefit from infrequent stand-replacing fires that permit multiple successional stages across the landscape (Brown and Schoettle 2008; Coop and Schoettle 2011). In the Colorado Front Range, limber pine is often an early seral species following high-severity fire, forms self-replacing stands on xeric sites, and succeeds to spruce and fir (*Abies* spp.) on mesic sites (Donnegan and Rebertus 1999; Peet 1981; Rebertus et al. 1991; Veblen 1986). *Ribes* species, alternate hosts of WPBR, are also early successional species that can establish a site after disturbance, including fire, thus contributing to WPBR hazard (Coop and Schoettle 2009; Zambino 2010). Limber pines have thin bark, which makes them highly susceptible to fire; however, typical open, low-density stands do not provide excessive fuels,

allowing for the survival of large trees (Steele 1990). Stand-replacing fires can lead to extinction of local populations of limber pine (Webster and Johnson 2000). Summer drought, which is projected to intensify in the western United States, contributes to increased frequency of large wildfires (Westerling et al. 2006). Fire season length, as well as frequency and severity of unplanned wildfires, is expected to increase with climate change, resulting in an overall increase of area burned by wildfire (McWethy et al. 2010). Protecting limber pine from fire when possible maintains genetic diversity and allows retention of cone-bearing and WPBR-resistant trees.

6.13. Sensitivity to Abiotic Damage Agents: Nitrogen Deposition and Climate Change

The GRMNPA, located near the growing population of the northern Colorado Front Range communities, is vulnerable to the damaging effects of anthropogenic nitrogen pollution (vehicle or industrial emissions and agricultural sources) deposited in rain or snow or as dry particles (NPS 2005b). Critical thresholds of nitrogen deposition have been recorded in RMNP and are altering ecosystem structure and function (Baron et al. 2000). High-elevation ecosystems are the most vulnerable because high-elevation plants are adapted to a nitrogen-limited environment, and short growing seasons limit time for plant nitrogen uptake. Additionally, the rocky, shallow soils lack adequate chemical buffering against the acidifying effects of excess nitrogen (Colorado Department of Public Health and Environment 2014). High foliar nitrogen levels increase susceptibility of pines and *Ribes* to WPBR (McDonald and Dekker-Robertson 1998; Van Arsdel 1972; Zambino 2010). Other potential consequences to limber pine and conifer ecosystems include loss of biodiversity; increased potential for insect and disease outbreaks; shift in growth phenology, increasing susceptibility to spring cold damage; and a decrease in general health and resilience to climate change (Fenn et al. 2003; Schoettle 1999).

Regional warming has already contributed to increasing mortality in western U.S. trees, including limber pine (Smith et al. 2015; van Mantgem and Stephenson 2007). Most general circulation models suggest a substantial reduction in suitable range for limber pine by 2090 (Crookston and Rehfeldt 2015). Changing climate, including increasing temperatures and altered snowpack and precipitation patterns, impact limber pine growth and can affect interaction with associated insects and pathogens. In the southern Rocky Mountains, temperatures have risen 0.9–1.8 °F (0.5–1 °C) over the last 30 years, with higher elevations warming more quickly in some areas (McWethy et al. 2010). A projected annual mean temperature increase of 3.6 °F (2 °C) is expected by 2050, with more precipitation occurring as rain instead of snow (McWethy et al. 2010). In RMNP, the bioclimatic envelope for limber pine is projected to expand upward in elevation and become fragmented (Monahan et al. 2013). Consequently, under a warmer climate it is also likely that populations may move upslope in the GRMNPA.

Climate change-caused warming may increase the likelihood of new, larger, or more frequent native and nonnative insect and disease outbreaks (McWethy et al. 2010). The drought of the early 2000s has been associated with the MPB epidemic

in the southern Rocky Mountains (Chapman et al. 2012). Increased sustained warming is also expected to expand, in both latitude and elevation, suitable habitat for MPB (Bentz et al. 2010). Warming conditions may also increase the occurrence of cone and seed insects that currently are less common at higher elevations (Schoettle and Negrón 2001). Predicting how climate change will affect WPBR and dwarf mistletoe is less certain (Kliejunas 2011). Warmer and drier conditions in the future may reduce the frequency of WPBR infection (which requires cool, wet conditions; Sturrock et al. 2011); warmer temperatures could expand the range of dwarf mistletoe because its distribution is limited by cold temperatures (Hawksworth and Wiens 1996). Drought stress in limber pine, an effect of climate change, may reduce host defenses, resulting in greater tree mortality (Millar et al. 2007).

SECTION 7. 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(1): 95-111.
- Alberta Whitebark and Limber Pine Recovery Team. 2014a. Alberta limber pine recovery plan 2014-2019. Alberta Environment and Sustainable Resource Development, Alberta Species at Risk Recovery Plan No. 35. Edmonton, AB. 61 p.
- Alberta Whitebark and Limber Pine Recovery Team. 2014b. Alberta Whitebark Pine Recovery Plan 2013-2018. Alberta Environment and Sustainable Resource Development, Alberta Species at Risk Recovery Plan No. 34. Edmonton, AB. 63 p.
- Anderson, R.S.; Betancourt, J.L.; Mead, J.I.; Hevly, R.H.; Adam, D.P. 2000. Middle-and late-Wisconsin paleobotanic and paleoclimatic records from the southern Colorado Plateau, USA. *Palaeogeography, Palaeoclimatology, Palaeoecology* 155(1): 31-57.
- Arno, S. 2015. Coeur d'Alene hosts whitebark conference. *Nutcracker Notes* 27: 9-10.
- Arno, S.F.; Hoff, R.J. 1990. *Pinus albicaulis* Engelm. whitebark pine. *Silvics of North America* 1: 268-279.
- 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. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Region. 212 p.
- Baron, J.S.; Rueth, H.M.; Wolfe, A.M.; Nydick, K.R.; Allstott, E.J.; Minear, J.T.; Moraska, B. 2000. Ecosystem responses to nitrogen deposition in the Colorado Front Range. *Ecosystems* 3(4): 352-368.
- Barringer, L.E.; Tomback, D.F.; Wunder, M.B.; McKinney, S.T. 2012. Whitebark pine stand condition, tree abundance, and cone production as predictors of visitation by Clark's nutcracker. *PLoS One* 7(5): e37663.
- Baumeister, D.; Callaway, R.M. 2006. Facilitation by *Pinus flexilis* during succession: A hierarchy of mechanisms benefits other plant species. *Ecology* 87(7): 1816-1830.
- Bentz, B.J.; Kegley, S.; Gibson, K.; Their, R. 2005. A test of high-dose verbenone for stand-level protection of lodgepole and whitebark pine from mountain pine beetle attacks. *Journal of Economic Entomology* 98(5): 1614-1621.
- Bentz, B.J.; Regniere, J.; Fettig, C.J.; Hansen, E.M.; Hayes, J.L.; Hicke, J.A.; Kelsey, R.G.; Negron, J.F.; Seybold, S.J. 2010. Climate change and bark beetles of the western United States and Canada: Direct and indirect effects. *BioScience* 60(8): 602-613.
- Blodgett, J.T.; Schaupp Jr., W.C.; Long, D.F. 2005. Evaluation of white pine blister rust and mountain pine beetle on limber pine in the Bighorn National Forest. Golden, CO: U.S. Department of Agriculture, Forest Service, Renewable Resources, Biological Evaluation R2-05-08. 19 p.
- Blodgett, J.T. Sullivan, K.F. 2004. First report of white pine blister rust on Rocky Mountain bristlecone pine. *Plant Disease* 88(3): 311-311.
- Bond, C.A.; Champ, P.; Meldrum, J.; Schoettle, A.W. 2011. Investigating the optimality of proactive management of an invasive forest pest. In: R.E. Keane, D.F. Tomback, M. Murray, and C.M. Smith, 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, Montana. Proceedings RMRS-P-63. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station. p. 295-302. <https://www.fs.usda.gov/treearch/pubs/4571>.

- Borgman, E.M.; Schoettle, A.W.; Angert, A.L. 2015. Assessing the potential for maladaptation during active management of limber pine populations: A common garden study detects genetic differentiation in response to soil moisture in the Southern Rocky Mountains. *Canadian Journal of Forest Research* 45: 496-505.
- Brar, S.; Tsui, C. . M.; Dhillon, B.; Bergeron, M.J.; Joly, D L.; Zambino, P.J.; El-Kassaby, Y.A.; Hamelin, R.C. 2015. Colonization history, host distribution, anthropogenic influence and landscape features shape populations of white pine blister rust, an invasive alien tree pathogen. *PLoS ONE* 10(5): e0127916.
- 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(3): 339-347.
- Burdon, J. J.; Thrall, P. H. 2008. Pathogen evolution across the agro-ecological interface: Implications for disease management. *Evolutionary Applications* 1(1): 57-65.
- Bureau of Land Management Wyoming. 2013. Limber Pine (*Pinus flexilis*), Special Status. Retrieved November 10, 2014, from <http://www.blm.gov/wy/st/en/programs/forestry/sp-status.html>.
- Burns, K.; Blodgett, J.; Jackson, M.; Howell, B.; Jacobi, W.; Schoettle, A.; Casper, A.M.; Klutsch, J. 2011. Monitoring limber pine health in the Rocky Mountains and North Dakota. In: R.E. Keane, D.F. Tomback, M. Murray, and C.M. Smith, 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, Montana. Proceedings RMRS-P-63.* Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station. p. 47-50. <https://www.fs.usda.gov/treesearch/pubs/4571>.
- Burns, K.S. 2006. White pine blister rust surveys 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.
- 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. General Technical Report RMRS-GTR-206. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station. 26 p.
- 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(3-4): 402-411.
- Casper, A.M.; Jacobi, W.R.; Schoettle, A.W.; Burns, K.S. 2016. Restoration planting options for limber pine (*Pinus flexilis* James) in the southern Rocky Mountains. *Journal of the Torrey Botanical Society* 143(1):21-37.
- Cerezke, H.F. 1995. Egg gallery, brood production, and adult characteristics of mountain pine beetle, *Dendroctonus ponderosae* Hopkins (Coleoptera: Scolytidae), in three pine hosts. *The Canadian Entomologist* 127(06): 955-965.
- Chapman, T.B.; Veblen, T.T.; Schoennagel, T. 2012. Spatiotemporal patterns of mountain pine beetle activity in the southern Rocky Mountains. *Ecology* 93(10): 2175-2185.
- Cleaver, C.M. 2014. Limber pine health in the southern and central Rocky Mountains. M.S. Thesis, Colorado State University, Fort Collins, CO. 136 p.
- Cleaver, C.M; Burns K.S.; Schoettle, A.W. 2017. Limber Pine and White Pine Blister Rust Monitoring and Assessment Guide for Rocky Mountain National Park. Final Report prepared by Rocky Mountain Research Station for Rocky Mountain National Park for Inter-Agency Agreement 15-IA-11221633-157. <https://www.fs.usda.gov/treesearch/pubs/56244>.

- Cleaver, C.M.; Jacobi, W.R.; Burns, K.S.; Means, R.E. 2015. Limber pine in the central and southern Rocky Mountains: Stand conditions and interactions with blister rust, mistletoe, and bark beetles. *Forest Ecology and Management* 358: 139-153.
- Cleaver, C.M.; Jacobi, W.R.; Burns, K.S.; Means, R.E. 2017. Limber pine regeneration and white pine blister rust in the central and southern Rocky Mountains. *Forest Ecology and Management* 63(2):151-164.
- Colorado Department of Public Health and Environment. 2014. Rocky Mountain National Park initiative: 2012 Nitrogen deposition milestone report. Colorado Department of Public Health and Environment, Department of the Interior National Park Service, and the Environmental Protection Agency, Retrieved from https://www.colorado.gov/pacific/sites/default/files/AP_PO_RMNP-Initiative-2013-Milestone-Report.pdf.
- 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.
- 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(3): 893-903.
- Coop, J.D.; Schoettle, A.W. 2011. Fire and high-elevation, five-needle pine (*Pinus aristata* and *P. flexilis*) Ecosystems in the southern Rocky Mountains: What do we know? In: R.E. Keane, D.F. Tomback, M. Murray, and C.M. Smith, 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, Montana. Proceedings RMRS-P-63. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, p. 164-175. <https://www.fs.usda.gov/treearch/pubs/4571>.
- Crookston, N.L.; Rehfeldt, G.E. 2015. Research on forest climate change: Potential effects of global warming on forests and plant climate relationships in western North America and Mexico. USDA Forest Service, Rocky Mountain Research Station, Moscow, ID. Retrieved March 18, 2015, from <http://forest.moscowfs.wsu.edu/climate/>
- Crump, A.; Jacobi, W.R.; Burns, K.S.; Howell, B.E.; William, R. 2011. Pruning to manage white pine blister rust in the southern Rocky Mountains. Research Note RMRS-RN-44. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station. 10 p.
- Donnegan, J.A.; Rebertus, A. J. 1999. Rates and mechanisms of subalpine forest succession along an environmental gradient. *Ecology* 80(4): 1370-1384.
- Ellison, A.M.; Bank, M.S.; Clinton, B.D.; Colburn, E.A.; Elliott, K.; Ford, C.R.; Foster, D.R.; Kloeppe, B.D.; Knoepp, J.D.; Lovett, G.M. 2005. Loss of foundation species: Consequences for the structure and dynamics of forested ecosystems. *Frontiers in Ecology and the Environment* 3(9): 479-486.
- Evenden, J.C.; Gibson, A.L. 1940. A destructive infestation in lodgepole pine stands by the mountain pine beetle. *Journal of Forestry* 38: 271-275.
- Fancy, S.G.; Gross, J.E.; Carter, S.L. 2009. Monitoring the condition of natural resources in U.S. National Parks. *Environmental Monitoring and Assessment* 151(1-4): 161-174.
- Feldman, R.; Tomback, D.F.; Koehler, J. 1999. Cost of Mutualism: Competition, Tree Morphology, and Pollen Production in Limber Pine Clusters. *Ecology* 80: 324-329.
- Fenn, M.E.; Baron, J.S.; Allen, E.B.; Rueth, H.M.; Nydick, K.R.; Geiser, L.; Bowman, W.D.; Sickman, J.O.; Meixner, T.; Johnson, D.W. 2003. Ecological effects of nitrogen deposition in the western United States. *BioScience* 53(4): 404-420.
- Fiedler, C.E.; McKinney, S.T. 2014. Forest structure, health, and mortality in two Rocky Mountain whitebark pine ecosystems: Implications for restoration. *Natural Areas Journal* 34(3): 290-299.

- Field, S.G.; Schoettle, A.W.; Klutsch, J.G.; Tavener, S.J.; Antolin, M.F. 2012. Demographic projection of high-elevation white pines infected with white pine blister rust: A nonlinear disease model. *Ecological applications* 22(1): 166-183.
- 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. *International Journal of Biometeorology* 52(7): 653-666.
- Geils, B.W.; Cibrián Tovar, J.; Moody, B. 2002. Mistletoes of North American conifers. General Technical Report RMRS-GTR-98. Ogden, UT: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, 123 p.
- Geils, B.W.; Hummer, K.E.; Hunt, R.S. 2010. White pines, *Ribes*, and blister rust: A review and synthesis. *Forest Pathology* 40(3-4): 147-185.
- Gibson, K.; Kegley, S.; Bentz, B. 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.
- Goetz, S.; Hansen, A.; Piekielek, N.; Gross, J.; Melton, F.; Hiatt, S.; Theobald, D. 2010. Landscape conditions and trends in and around Rocky Mountain National Park: Initial Summary Results. Ecological condition of U.S. National Parks: Enhancing decision support through monitoring, analysis, and forecasting. Park analysis of landscapes and monitoring support (PALMS). Report on file at Rocky Mountain National Park, Estes Park, Colorado.
- Government of Alberta. 2014. Species assessed by Alberta's endangered species conservation committee. Retrieved November 10, 2014, from <http://esrd.alberta.ca/fish-wildlife/species-at-risk/documents/SpeciesAssessed-EndangeredSpecies-Jul18-2014.pdf>
- Government of Canada. 2012. Order amending Schedule 1 to the Species at Risk Act. Canada Gazette Part II, Vol 146, No. 14, SOR/2012-113, June 20, 2012 [online]. Retrieved March 19, 2015, from http://www.sararegistry.gc.ca/virtual_sara/files/orders/g2-14614i_e.pdf
- Government of Canada. 2014. COSEWIC Wildlife Species Assessments (detailed version), November 2014; Limber pine. Wildlife Species Assessment. Retrieved September 29, 2017 from http://www.registrelep-sararegistry.gc.ca/virtual_sara/files/cosewic/sr_Limber%20Pine_2014_e.pdf
- Greater Yellowstone Coordinating Committee Whitebark Pine Subcommittee. 2011. Whitebark pine strategy for the Greater Yellowstone Area. 41 p.
- Hamelin, R.C.; Hunt, R.S.; Geils, B.W.; Jensen, G. ; Jacobi, V.; Lecours, N. 2000. Barrier to gene flow between eastern and western populations of *Cronartium ribicola* in North America. *Phytopathology* 90(10): 1073-1078.
- Hanski, I. 1999. Metapopulation ecology. Oxford University Press, Oxford. 328 p.
- Hawksworth, F.G.; Geils, B.W. 1990. How long do mistletoe-infected ponderosa pines live? *Western Journal of Applied Forestry* 5(2): 47-48.
- Hawksworth, F. G.; Johnson, D. W. 1993. Protect your trees from dwarf mistletoe. General Technical Report RMN-225. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station, 8 p.
- Hawksworth, F.G.; Wiens, D. 1996. Dwarf mistletoes: Biology, pathology, and systematics. *Agricultural Handbook* 709. U.S. Department of Agriculture, Forest Service, Washington, D.C., 410 p.
- Hedlin, A.F.; Yates III, H.O.; Tovar, D.C.; Ebel, B.H.; Koerber, T.W.; Merkel, E.P. 1980. Cone and seed insects of North American conifers. U.S. Department of Agriculture, Forest Service, Washington. 122 p.

- Hubbard, R.M.; Rhoades, C.C.; Elder, K.; Negron, J. 2013. Changes in transpiration and foliage growth in lodgepole pine trees following mountain pine beetle attack and mechanical girdling. *Forest Ecology and Management* 289: 312-317.
- Huckaby, L.S. 1991. Forest regeneration following fire in the forest-alpine ecotone in the Colorado Front Range M.S. Thesis, Colorado State University, Fort Collins, CO. 103 p.
- Hunt, R.S. 2003. White pine blister rust. *Recent Research Developments in Mycology* 1: 73-85.
- Hunt, R.S. 2009. History of western white pine and blister rust in British Columbia. *The Forestry Chronicle* 85(4): 516-520.
- Hutchins, H.E.; Lanner, R.M. 1982. The central role of Clark's nutcracker in the dispersal and establishment of whitebark pine. *Oecologia* 55(2): 192-201.
- Jacobi, W.R.; Bovin, P.P.; Burns, K.S.; Crump, A.; Goodrich, B.A. 2017. Pruning limber pine to reduce impacts from white pine blister rust in the southern Rocky Mountains. *Forest Science* 63(2): 218-224.
- Johnson, D.; Jacobi, W.R. 2000. First report of white pine blister rust in Colorado. *Plant Disease* 84(5): 595-595.
- Kamil, A.C.; Balda, R.P. 1985. Cache recovery and spatial memory in Clark's nutcrackers (*Nucifraga columbiana*). *Journal of Experimental Psychology: Animal Behavior Processes* 11(1): 95.
- Keane, R.E.; Parsons, R.A. 2010. Management guide to ecosystem restoration treatments: Whitebark pine forests of the northern Rocky Mountains, USA. 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.; Schoettle, A.W. 2011. Strategies, tools, and challenges for sustaining and restoring high elevation five-needle white pine forests in western North America. In: R.E. Keane, D.F. Tomback, M. Murray, and C.M. Smith, 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, Montana. Proceedings RMRS-P-63. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station. p. 276-294. <https://www.fs.usda.gov/treearch/pubs/4571>.
- Keane, R.E.; Tomback, D.F.; Aubry, C.A.; Bower, A.D.; Campbell, E.M.; Cripps, C.L.; Jenkins, M.B.; Mahalovich, M.F.; Manning, M.; McKinney, S.T.; Murray, M.P.; Perkins, D.L.; Reinhardt, D.P.; Ryan, C.; Schoettle, A.W.; Smith, C.M. 2012. A range-wide restoration strategy for whitebark pine (*Pinus albicaulis*). General Technical Report RMRS-GTR-279. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station. 108 p.
- 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. *Canadian Journal of Forest Research* 37(2): 462-472.
- Kearns, H.S.J.; Jacobi, W.R.; Reich, R.M.; Flynn, R.L.; Burns, K.S.; Geils, B.W. 2014. Risk of white pine blister rust to limber pine in Colorado and Wyoming, USA. *Forest Pathology* 44(1): 21-38.
- Kegley, S.; Gibson, K.E. 2004. Protecting whitebark pine trees from mountain pine beetle attack using verbenone. Rep. 04-08. Missoula, MT: U.S. Department of Agriculture, Forest Service, Northern Region, Forest Health Protection. 4 p.
- Kenaley, S.C.; Mathiasen, R.L.; Daugherty, C.M. 2006. Selection of dwarf mistletoe-infected ponderosa pines by *Ips* species (Coleoptera: Scolytidae) in northern Arizona. *Western North American Naturalist* 66(3): 279-284.
- Kim, M.S.; Brunfeldt, S.J.; McDonald, G.I.; Klopfenstein, N.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(6): 1004-1010.

- King, J.; David, A.; Noshad, D.; Smith, J. 2010. A review of genetic approaches to the management of blister rust in white pines. *Forest Pathology* 40(3-4): 292-313.
- Kinloch, B.B. 2003. White pine blister rust in North America: Past and prognosis. *Phytopathology* 93(8): 1044-1047.
- Kinloch, B.B.; Dupper, G.E. 2002. Genetic specificity in the white pine-blister rust pathosystem. *Phytopathology* 92(3): 278-280.
- 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.
- Kliejunas, J.T. 2011. A risk assessment of climate change and the impact of forest diseases on forest ecosystems in the western United States and Canada. General Technical Report PSW-GTR-236. Vallejo, CA: U.S. Department of Agriculture, Forest Service, Pacific Southwest Research Station. 70 p.
- Klutsch, J.G.; Goodrich, B.A.; Jacobi, W.R. 2015. Post-fire regeneration dynamics in whitebark pine (*Pinus albicaulis*) forests in Wind River and Absaroka Mountains, Wyoming, USA. *Journal of Forestry Research* DOI 10.1007/s11676-015-0064-6.
- Klutsch, J.G.; Goodrich, B.A.; Schoettle, A.W. 2011. Limber pine forests on the leading edge of white pine blister rust distribution in northern Colorado. In: R.E. Keane, D.F. Tomback, M. Murray, and C.M. Smith, 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, Montana. Proceedings RMRS-P-63. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station. p. 222-225. <https://www.fs.usda.gov/treearch/pubs/4571>.
- Knowles, P.; Grant, M.C. 1983. Age and size structure analyses of Engelmann spruce, ponderosa pine, lodgepole pine, and limber pine in Colorado. *Ecology* 64(1): 1-9.
- Krist, F.J.; Ellenwood, J.R.; Woods, M.E.; McMahan, A.J.; Cowardin, J.P.; Ryerson, D.E.; Sapio, F.J.; Zweifler, M. O.; Romero, S. A. 2014. 2013-2027 National Insect and Disease Forest Risk Assessment. U.S. Department of Agriculture, Forest Service, Forest Health Technology Enterprise Team. 199 p.
- Lanner, R.M. 1980. Avian seed dispersal as a factor in the ecology and evolution of limber and whitebark pines. In: B. P. Dancik and K. O. Higginbotham, eds. *Proceedings, Sixth North American Forest Biology Workshop*. Edmonton, Alberta 11-13 August, 1980. University of Alberta, Edmonton, Alberta, Canada. p. 15-48.
- Lanner, R.M. 1984. *Trees of the Great Basin*. Reno, NV: University of Nevada Press. 215 p.
- Lanner, R.M.; Vander Wall, S.B. 1980. Dispersal of limber pine seed by Clark's nutcracker. *Journal of Forestry* 78(10): 637-639.
- Latta, R.G.; Mitton, J.B. 1997. A comparison of population differentiation across four classes of gene marker in limber pine (*Pinus flexilis* James). *Genetics* 146(3): 1153-1163.
- Lepper, M.G. 1974. *Pinus flexilis* James, and its environmental relationships. Ph.D. Dissertation. University of California Davis, Davis California, USA. 197 p.
- Lessard, G.D.; Hildebrand, D.M.; Haneman, D.M. 1987. *Forest Pest Conditions in the Rocky Mountain Region 1986*. USDA Forest Service, Rocky Mountain Region. Timber, Forest Pest, and Cooperative Forest Management, Lakewood, Colorado, USA. 52 p.
- Logan, J.A.; Powell, J.A. 2001. Ghost forests, global warming, and the mountain pine beetle (Coleoptera: Scolytidae). *American Entomologist* 47(3): 160.
- 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. General Technical Report PNW-GTR-742. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station. 68 p.

- Lorenz, T.J.; Sullivan, K.A. 2010. Comparison of survey methods for monitoring Clark's Nutcrackers and predicting dispersal of whitebark pine seeds. *Journal of Field Ornithology* 81(4): 430-441.
- Lorenz, T.J.; Sullivan, K.A.; Bakian, A.V.; Aubry, C.A. 2011. Cache-site selection in Clark's Nutcracker (*Nucifraga columbiana*). *The Auk* 128(2): 237-247.
- Mahalovich, M.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.
- Malm, K.E. 2009. Temperature influences on phenology and population growth of mountain pine beetle populations in Northern Colorado M.A. Thesis, University of Colorado, Boulder, Colorado. 89 p.
- Maloney, P.E. 2011. Incidence and distribution of white pine blister rust in the high-elevation forests of California. *Forest Pathology* 41(4): 308-316.
- Maloy, O.C. 1997. White pine blister rust control in North America: A case history. *Annual Review of Phytopathology* 35: 87-109.
- Man, G. 2013. Major forest insect and disease conditions in the United States: 2012. USDA Forest Service Forest Health Protection, FS-1023. 44 p.
- Marr, J.W. 1977. The development and movement of tree islands near the upper limit of tree growth in the southern Rocky Mountains. *Ecology* 58(5): 1159-1164.
- Mathiasen, R.L.; Hawksworth, F.G. 1988. Dwarf mistletoes on western white pine and whitebark pine in northern California and southern Oregon. *Forest Science* 34: 429-440.
- McCambridge, W.F.; Hawksworth, F.G.; Edminster, C.B.; Laut, J.G. 1982. Ponderosa pine mortality resulting from a mountain pine beetle outbreak. Research Paper RM-235. Fort Collins, CO: U.S. Department of Agriculture Forest Service, Rocky Mountain Forest and Range Experiment Station. 7 p.
- McCaughey, W.W. 1990. Biotic and microsite factors affecting *Pinus albicaulis* establishment and survival. Ph.D. Dissertation, Montana State University, Bozeman, MT. 78 p.
- McCaughey, W.W.; Tomback, D.F. 2001. The natural regeneration process. Whitebark pine communities: Ecology and restoration. Edited by D.F. Tomback, S.F. Arno, and R.E. Keane. Island Press, Washington, DC: 105-120.
- McDonald, G.I.; Dekker-Robertson, D.L. 1998. Long-term differential expression of blister rust resistance in western white pine. In: Jalkanen, R. editor. *First IUFRO Rusts of Forest Trees Proceedings*. Rovaniemi, Finland: The Finnish Forest Research Institute. p. 285-295.
- McDonald, G.I.; Richardson, B.A.; Zambino, P.J.; Klopfenstein, N.B.; Kim, M.S. 2006. *Pedicularis* and *Castilleja* are natural hosts of *Cronartium ribicola* in North America: A first report. *Forest Pathology* 36(2): 73-82.
- 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.
- 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(6): 1044-1057.
- McWethy, D.B.; Gray, S.T.; Higuera, P.E.; Littell, J.S.; Pederson, G.T.; Ray, A.J.; Whitlock, C. 2010. Climate and terrestrial ecosystem change in the U.S. Rocky Mountains and Upper Columbia Basin: Historical and future perspectives for natural resource management. National Park Service, Natural Resource Report NPS/GRYN/NRR—2010/260. Fort Collins, CO.

- Means, R.E. 2011. Synthesis of lower treeline limber pine (*Pinus flexilis*) woodland knowledge, research needs, and management considerations. In: R.E. Keane, D.F. Tomback, M. Murray, and C.M. Smith, 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, Montana. Proceedings RMRS-P-63. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station. p. 29-36. <https://www.fs.usda.gov/treearch/pubs/4571>.
- Menon, M.; Bagley, J.C.; Friedline, C.; Whipple, A.V.; Schoettle, A.W.; Leal-Saenz, A.; Wehenkel, C.; Molina-Freaner, F.; Flores-Renteria, L.; Gonzalez-Elizondo, M.S.; Snieszko, R.A.; Cushman, S.A.; Waring, K.M.; Eckert, A.J. 2018. The role of hybridization during ecological divergence of southwestern white pine (*Pinus strobiformis*) and limber pine (*P. flexilis*). *Molecular Ecology*. 27(5): 1245-1260.
- Millar, C.I.; Westfall, R.D.; Delany, D.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.
- 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.
- Moerman, D.E. 1998. Native American ethnobotany. Timber Press, Portland, OR. 927 p.
- Moerman, D.E. 2009. Native American medicinal plants: An ethnobotany dictionary. Timber Press, Portland, OR. 800 p.
- Monahan, W.B.; Cook, T.; Melton, F.; Connor, J.; Bobowski, B. 2013. Forecasting distributional responses of limber pine to climate change at management-relevant scales in Rocky Mountain National Park. *PLoS One* 8(12): e83163.
- National Park Service [NPS]. 2003. Invasive exotic plant management plan and environmental assessment, Rocky Mountain National Park. Estes Park, Colorado: Retrieved from http://www.nps.gov/romo/parkmgmt/upload/exotic_plant_ea_final.pdf.
- National Park Service [NPS]. 2005a. Bark beetle management plan environmental assessment. Rocky Mountain National Park, Colorado. 82 Retrieved from http://www.nps.gov/romo/parkmgmt/upload/pine_beetle_ea_07-05.pdf.
- National Park Service [NPS]. 2005b. Nitrogen deposition: Issues and effects in Rocky Mountain National Park. Retrieved December 12, 2014, from <http://www.nature.nps.gov/air/Permits/ARIS/docs/romoNFactSheetV11200505Final.pdf>
- National Park Service [NPS]. 2006a. Management Policies 2006. 168 p. Retrieved from <http://www.nps.gov/policy/MP2006.pdf>.
- National Park Service [NPS]. 2006b. Vegetation Restoration Management Plan Version 2. Estes Park, CO: Rocky Mountain National Park, 114 p. Retrieved from http://www.nps.gov/romo/parkmgmt/upload/vegetation_restoration_management_plan_ver2.pdf.
- National Park Service [NPS]. 2012a. A call to action. Preparing for a second century of stewardship and engagement. Retrieved from http://www.nps.gov/calltoaction/PDF/Directors_Call_to_Action_Report_2012.pdf.
- National Park Service [NPS]. 2012b. Revisiting Leopold: Resource stewardship in the National Parks. Washington, D.C.: Retrieved from http://www.nps.gov/calltoaction/PDF/LeopoldReport_2012.pdf.
- National Park Service [NPS]. 2014. Wilderness. Rocky Mountain National Park, Colorado. Retrieved December, 8, 2014, from <http://www.nps.gov/romo/naturescience/wilderness.htm>
- Noss, R.F. 1999. Assessing and monitoring forest biodiversity: A suggested framework and indicators. *Forest Ecology and Management* 115(2): 135-146.

- Page, J.M. 1981. Drought-accelerated parasitism of conifers in the mountain ranges of northern California. *Environmental Conservation* 8(03): 217-226.
- Pansing, E.R. 2014. The influence of cache site and rodent pilferage on whitebark pine seed germination in the northern and central Rocky Mountains. M.S. Thesis, University of Colorado Denver, Denver, Colorado, USA. 97 p.
- Peattie, D.C. 1991. A natural history of western trees. Houghton Mifflin Harcourt, Boston, MA. 751 p.
- Peet, R. K. 1981. Forest vegetation of the Colorado Front Range. *Vegetation* 45(1): 3-75.
- 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: The dynamics of bark beetle eruptions. *BioScience* 58(6): 501-517.
- 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.
- Reinhardt, K.; Castanha, C.; Germino, M.J.; Kueppers, L.M. 2011. Ecophysiological variation in two provenances of *Pinus flexilis* seedlings across an elevation gradient from forest to alpine. *Tree physiology* 31(6): 615-625.
- Safranyik, L.; Carroll, A.L. 2006. The biology and epidemiology of the mountain pine beetle in lodgepole pine forests. In: Safranyik, L., Wilson, W. eds. *The mountain pine beetle: A synthesis of biology, management and impacts on lodgepole pine*. Natural Resources Canada, Canadian Forest Service, Pacific Forestry Centre, Victoria, B.C., p. 3-66.
- Samano, S.; Tomback, D.F. 2003. Cone opening phenology, seed dispersal, and seed predation in southwestern white pine (*Pinus strobiformis*) in southern Colorado. *Ecoscience* 10(3): 319-326.
- 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. Forest Service Report R1-03-118. Missoula, MT: U.S. Department of Agriculture, Forest Service. 10 p.
- Schnepf, C.; Schwandt, J.W. 2006. Pruning western white pine: A vital tool for species restoration. PNW 584. University of Idaho Cooperative Extension System. 62 p.
- Schoettle, A.W. 1999. Effect of two years of nitrogen deposition on shoot growth and phenology of Engelmann Spruce (*Picea engelmannii* Parry ex Engelm.) seedlings. *Journal of Sustainable Forestry* 10(1-2): 181-189.
- Schoettle, A.W. 2004a. Developing proactive management options to sustain bristlecone and limber pine ecosystems in the presence of a non-native pathogen. In: *Silviculture in Special Places: Proceedings of the National Silviculture Workshop*. 2004. Shepperd, W.D.; Eskew, L.G., compilers. September 8-11, 2003; Granby, CO. Proceedings RMRS-P-34. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station. p. 46-155.
- Schoettle, A.W. 2004b. Ecological roles of five-needle pines in Colorado: Potential consequences of their loss, p. 124-135. In: Sniezko, R.A., Samman, S., Schlarbaum, S.E., Kriebel, H.B., eds. 2004. *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. 259 p.
- Schoettle, A.W.; Connor, J.; Mack, J.; Pineda Bovin, P.; Beck, J.; Baker, G.; Sniezko, R.A.; Burns, K.S. 2013. Establishing the science foundation to sustain high-elevation, five-needle pine forests threatened by novel interacting stresses in four western National Parks. *George Wright Forum* 30. 302-312.

- Schoettle, A.W.; Goodrich, B.A.; Klutsch, J.G.; Burns, K.S. 2018a. White pine blister rust confirmed on limber pine (*Pinus flexilis*) in Rocky Mountain National Park. In: Proceedings of the IUFRO Joint Conference: Genetics of Five-Needle Pines, Rusts of Forest Trees, and Strobosphere. June 15-20 2014, Fort Collins, CO. A.W. Schoettle, R.A. Sniezko, and J.T. Kliejunas, tech. coord. U.S. Department of Agriculture, Forest Service Proceedings RMRS-P-76. p. 201-204
- Schoettle, A.W.; Goodrich, B.A.; Klutsch, J.G.; Burns, K.S.; Costello, S.; Sniezko, R.A.; Connor, J. 2011a. The proactive strategy for sustaining five-needle pine populations: An example of its implementation in the southern Rocky Mountains. In: R.E. Keane, D.F. Tomback, M. Murray, and C.M. Smith, 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, Montana. Proceedings RMRS-P-63. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station. 323-334. <https://www.fs.usda.gov/treesearch/pubs/4571>.
- Schoettle, A. W.; Jacobi, W. R.; Waring, K. M.; Burns, K. S. 2018b. Regeneration for resilience framework to support regeneration decisions for species with populations at risk of extirpation by white pine blister rust. *New Forests*—in press. doi: 10.1007/s11056-018-9679-8.
- Schoettle, A.W.; Klutsch, J.G.; Sniezko, R.A. 2012. Integrating regeneration, genetic resistance, and timing of intervention for the long-term sustainability of ecosystems challenged by non-native pests: A novel proactive approach. In: Proceedings of the 4th International Workshop on the Genetics of Host–Parasite Interactions in Forestry: Disease and Insect Resistance in Forest Trees. R.A. Sniezko, A.D. Yanchuk, J.T. Kliejunas, K.M. Palmieri, J.M. Alexander, and S.J. Frankel, tech. coord. General Technical Report PSW-GTR-240. Albany, CA: U.S. Department of Agriculture, Forest Service, Pacific Southwest Research Station. p. 112-123.
- Schoettle, A.W.; Negron, J.F. 2001. First report of two cone and seed insects 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.
- 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.
- Schoettle, A.W.; Sniezko, R.A.; Kegley, A.; Burns, K.S. 2011b. Preliminary overview of the first extensive rust resistance screening tests of *Pinus flexilis* and *Pinus aristata*. In: 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. Edited by R.E. Keane, D.F. Tomback, M.P. Murray, C.M. Smith. USDA For. Serv. Proc. RMRS-P-63. p. 265-269.
- Schoettle, A.W.; Sniezko, R.A.; Kegley, A.; Burns, K.S. 2014. White pine blister rust resistance in limber pine: Evidence for a major gene. *Phytopathology* 104(2): 163-173.
- Schuster, W.S.; Alles, D.L.; Mitton, J.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, W.S.; Mitton, J.B. 2000. Paternity and gene dispersal in limber pine (*Pinus flexilis* James). *Heredity* 84(3): 348-361.
- Schuster, W.S.; Mitton, J.B.; Yamaguchi, D.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(1): 101-111.

- Schwandt, J.; Chadwick, K.; Kearns, H.; Jensen, C. 2011. Whitebark pine direct seeding trials in the Pacific Northwest. In: R.E. Keane, D.F. Tomback, M. Murray, and C.M. Smith, 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, Montana. Proceedings RMRS-P-63. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station. 357-361. <https://www.fs.usda.gov/treesearch/pubs/4571>.
- 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.
- Schwandt, J.W.; Marsden, M.A.; McDonald, G.I. 1994. Pruning and thinning effects on white pine survival and volume in northern Idaho. In: Baumgartner, D.M., J.E. Lotan, and J.R. Tonn (eds.). Proceedings of the Symposium on interior cedar-hemlock-white pine forests: Ecology and Management. March 2-4, 1993. Spokane, Washington. Department of Natural Resource Sciences, Washington State University, Pullman, WA. p. 167-172.
- Shankman, D.; Daly, C. 1988. Forest regeneration above tree limit depressed by fire in the Colorado Front Range. *Bulletin of the Torrey Botanical Club* 114(4): 272-279.
- Smith, C.M.; Langor, D.W.; Myrholm, C.; Weber, J.; Gillies, C.; Stuart-Smith, J. 2013. Changes in white pine blister rust infection and mortality in limber pine over time. *Canadian Journal of Forest Research* 43(10): 919-928.
- Smith, C. M.; Poll, G.; Gillies, C.; Praymak, C.; Miranda, E.; Hill, J. 2011. Limber pine seed and seedling planting experiment in Waterton Lakes National Park, Canada. In: R.E. Keane, D.F. Tomback, M. Murray, and C.M. Smith, 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, Montana. Proceedings RMRS-P-63. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station. p. 365-374.
- 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(5): 982-995.
- Smith, J. M.; Paritsis, J.; Veblen, T.T.; Chapman, T. B. 2015. Permanent forest plots show accelerating tree mortality in subalpine forests of the Colorado Front Range from 1982 to 2013. *Forest Ecology and Management* 341: 8-17.
- Smith, J.P.; Hoffman, J.T. 2001. Site and stand characteristics related to white pine blister rust in high-elevation forests of southern Idaho and western Wyoming. *Western North American Naturalist* 61(4): 409-416.
- Smith Jr., R.S. 1983. Diseases of eastside pine types. In: Robson, T.F. and Standiford, R.B., eds. Management of the eastside pine type in northeastern California. Proceedings of a symposium, 1982 June 15–17, Susanville, CA. Publication SAF 83-06, Northern California Society of American Foresters, p. 79-81.
- Sniezko, R.; Bower, A.; Kegley, A. 2004. Variation in *Cronartium ribicola* field resistance among 13 *Pinus monticola* and 12 *P. lambertiana* families: Early results from Happy Camp. 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., p. 203-208.
- Sniezko, R.A.; Mahalovich, M.F.; Schoettle, A.W.; Vogler, D.R. 2011. Plenary paper: Past and current investigations of the genetic resistance to *Cronartium ribicola* in high-elevation five-needle pines. In: R.E. Keane, D.F. Tomback, M. Murray, and C.M. Smith, 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, Montana. Proceedings RMRS-P-63. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station. p. 246-264. <https://www.fs.usda.gov/treesearch/pubs/4571>.
- Solheim, H.; Krokene, P. 1998. Growth and virulence of mountain pine beetle associated blue-stain fungi, *Ophiostoma clavigerum* and *Ophiostoma montium*. Canadian Journal of Botany 76(4): 561-566.
- Steele, R. 1990. *Pinus flexilis* James. In: R.M. Burns and B.H. Honkala (Technical coordinators), Silvics of North America, Conifers. Agricultural Handbook 654. U.S. Department of Agriculture, Forest Service, Washington, DC, 348-354. Retrieved from http://www.na.fs.fed.us/pubs/silvics_manual/Volume_1/pinus/flexilis.htm.
- Stewart, F.C.; Rankin, W.H. 1914. Does *Cronartium ribicola* over-winter on the currant? Bulletin Number 374. Geneva, NY: New York Agricultural Experiment Station. 53 p.
- Stohlgren, T.J.; Bachand, R.R. 1997. Lodgepole pine (*Pinus contorta*) ecotones in Rocky Mountain National Park, Colorado, USA. Ecology 78(2): 632-641.
- Stohlgren, T.J.; Bachand, R.R.; Onami, Y.; Binkley, D. 1998. Species-environment relationships and vegetation patterns: Effects of spatial scale and tree life-stage. Plant Ecology 135(2): 215-228.
- Sturrock, R.N.; Frankel, S.J.; Brown, A.V.; Hennon, P.E.; Kliejunas, J.T.; Lewis, K.J.; Worrall, J.J.; Woods, A. J. 2011. Climate change and forest diseases. Plant Pathology 60(1): 133-149.
- Taylor, J.E.; Mathiasen, R.L. 1999. Limber pine dwarf mistletoe. Forest Insect and Disease Leaflet No. 171. Missoula, MT: U.S. Department of Agriculture, Forest Service, Northern Region. 8 p.
- Taylor, J.E.; Walla, J.A. 1999. First report of *Dothistroma septospora* on native limber and whitebark pine in Montana. Plant Disease 83(6): 590-590.
- Tomback, D.F. 1978. Foraging strategies of Clark's nutcracker. Living Bird 16(1977): 123-160.
- Tomback, D.F. 1980. How nutcrackers find their seed stores. Condor 82: 10-19.
- Tomback, D.F. 1982. Dispersal of whitebark pine seeds by Clark's nutcracker: A mutualism hypothesis. The Journal of Animal Ecology 51(2): 451-467.
- Tomback, D.F. 1986. Postfire regeneration of Krummholz whitebark pine: A consequence of Nutcracker seed caching. Madrono 33(2): 100-110.
- Tomback, D.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, D.F. 2001. Clark's nutcracker: Agent of regeneration. Whitebark Pine Communities: Ecology and Restoration. Edited by D.F. Tomback, S.F. Arno, and R.E. Keane. Island Press, Washington, DC: p. 89-104.
- 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.
- Tomback, D.F.; Achuff, P.; Schoettle, A.W.; Schwandt, J.W.; Mastrogiuseppe, R.J.; Keane, R.; Tomback, D.; Murray, M.; Smith, C. 2011. The magnificent high-elevation five-needle white pines: Ecological roles and future outlook. In: R.E. Keane, D.F. Tomback, M. Murray, and C.M. Smith, 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, Montana. Proceedings RMRS-P-63. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station. p. 2-28.

- Tomback, D.F.; Hoffman, L.A.; Sund, S.K. 1990. Coevolution of whitebark pine and nutcrackers: Implications for forest regeneration. In: W.C. Schmidt; K.J. McDonald, comps. 1990. Proceedings—symposium on whitebark pine ecosystems: Ecology and management of a high-mountain resource, March 29-31, 1989, Bozeman, MT. General Technical Report INT-270. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station. p. 118-130.
- Tomback, D.F.; Kendall, K.C. 2001. Biodiversity losses: The downward spiral. Whitebark pine communities: Ecology and restoration. Edited by D.F. Tomback, S.F. Arno, and R.E. Keane. Island Press, Washington, DC: p. 243-262.
- Tomback, D.F.; Linhart, Y. B. 1990. The evolution of bird-dispersed pines. *Evolutionary Ecology* 4(3): 185-219.
- Tomback, D.F.; Schoettle, A.W.; Chevalier, K.E.; Jones, C.A. 2005. Life on the edge for limber pine: Seed dispersal within a peripheral population. *Ecoscience* 12(4): 519-529.
- Tomback, D.F.; Sund, S.K.; Hoffmann, L.A. 1993. Post-fire regeneration of *Pinus albicaulis*: Height-age relationships, age structure, and microsite characteristics. *Canadian Journal of Forest Research* 23(2): 113-119.
- Tomback, D.F.; Taylor, C.L. 1987. Tourist impact on Clark's nutcracker foraging activities in Rocky Mountain National Park. *Wildlife Management and Habitats*: p. 158-172.
- U.S. Fish and Wildlife Service. 2011. Endangered and threatened wildlife and plants; 12-month finding on a petition to list *Pinus albicaulis* as Endangered or Threatened with critical habitat. *Federal Register* 76: 42631-42654.
- U.S. Forest Service [USFS]. Forest Service Handbook, FSH 2409.26f R-1 Seed Handbook, Missoula Montana: U.S. Department of Agriculture, Forest Service. Retrieved September 29, 2017, from http://fswweb.kootenai.r1.fs.fed.us/peers/silviculture/Reforestation/Seed/FSH2409.26F_Seed_Handbook.rtf
- U.S. Forest Service [USFS]. 2011. Forest Service Manual, Invasive Species Management, FSM 2900. Washington DC: U.S. Department of Agriculture, Forest Service.
- U.S. Forest Service [USFS]. 2009. Forest Service Manual, Forest Health Protection, FSM 3400. Washington DC: U.S. Department of Agriculture, Forest Service.
- U.S. Forest Service [USFS]. 2005. Forest Service Manual, Research and Development, FSM 4000. Washington DC: U.S. Department of Agriculture, Forest Service.
- U.S. Forest Service [USFS]. 2007. Forest Service Manual, Wilderness management, FSM 2324.1 Management of insects and diseases. Washington, DC: U.S. Department of Agriculture, Forest Service.
- U.S. Forest Service [USFS]. 2011a. Limber pine engraver. Retrieved April 9, 2015, from http://www.fs.usda.gov/Internet/FSE_DOCUMENTS/stelprdb5347205.pdf
- U.S. Forest Service [USFS]. 2011b. Twig beetles. Retrieved April 9, 2015, from http://www.fs.usda.gov/Internet/FSE_DOCUMENTS/stelprdb5320259.pdf
- U.S. Forest Service [USFS]. 2013. Forest Service National Strategic Framework for Invasive Species Management. FS-1017, August 2013. Retrieved August 26, 2016 from: http://www.fs.fed.us/foresthealth/publications/Framework_for_Invasive_Species_FS-1017.pdf
- U.S. Forest Service [USFS] Rocky Mountain Region. 2014. Aerial survey shows mountain pine beetle epidemic declining, spruce beetle numbers escalating. Retrieved November 10, 2014, from <https://www.fs.usda.gov/detail/r2/news-events/?cid=STELPRDB5447293>
- U.S. Forest Service. 2015. Forest Service Strategic Plan: FY 2015–2020. FS-1045, June 2015. Retrieved August 26, 2016 from: http://www.fs.fed.us/sites/default/files/strategic-planpercent5B2percent5D-6_17_15_revised.pdf

- Van Arsdel, E.P. 1972. Biology of rust resistance in forest trees: Proceedings of a NATO-IUFRO advanced study institute. In: Bingham, R.T., Hoff, R., McDonald, G.I., eds. 1969 August 17-24; Moscow, ID. Misc. Publ. no. 1221. Washington, DC: U.S. Department of Agriculture, Forest Service. p. 479-491.
- Van Arsdel, E.P.; Geils, B.W. 2004. The *Ribes* of Colorado and New Mexico and their rust fungi. FHTET 04-13. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Forest Health Protection, Forest Health Technology Enterprise Team. 32 p.
- Van Arsdel, E.P.; Riker, A.J.; Patton, R.F. 1956. The effects of temperature and moisture on the spread of white pine blister rust. *Phytopathology* 46(6): 307-318.
- Van Mantgem, P.J.; Stephenson, N.L. 2007. Apparent climatically induced increase of tree mortality rates in a temperate forest. *Ecology Letters* 10(10): 909-916.
- Vander Wall, S.B.; Balda, R.P. 1977. Coadaptations of the Clark's nutcracker and the pinon pine for efficient seed harvest and dispersal. *Ecological Monographs* 47: 89-111.
- Vander Wall, S.B.; Hutchins, H.E. 1983. Dependence of Clark's Nutcracker, *Nucifraga columbiana*, on conifer seeds during the postfledging period. *Canadian Field Naturalist* 97(2): 208-214.
- 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.
- Vogan, P.J.; Schoettle, A.W. 2015. Selection for resistance to white pine blister rust affects the abiotic stress tolerances of limber pine. *Forest Ecology and Management* 344: 110-119.
- Webster, K.L.; Johnson, E.A. 2000. The importance of regional dynamics in local populations of limber pine (*Pinus flexilis*). *Ecoscience* 7(2): 175-182.
- Wells, P.V. 1965. Scarp woodlands, transported grassland soils, and concept of grassland climate in the Great Plains region. *Science* 148(3667): 246-249.
- Wells, P.V. 1976. Macrofossil analysis of wood rat (*Neotoma*) middens as a key to the Quaternary vegetational history of arid America. *Quaternary Research* 6(2): 223-248.
- 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(1): 94-106.
- 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(5789): 940-943.
- Witcosky, J.J. 2017. Notes on the biology of *Ips woodi* in limber and Rocky Mountain bristlecone pines in Colorado and Wyoming and its response to the *Ips* pheromone components ipsdienol and ipsenol in the field. Golden, CO: U.S. Department of Agriculture, Forest Service, State and Private Forestry and Tribal Relations, Biological Evaluation R2-17-01. 31 p.
- Worrall, J. 2014. Dwarf mistletoes: Ecology and management in the Rocky Mountain Region. U.S. Department of Agriculture, Forest Service, Forest Health Management, Rocky Mountain Region. 48 p. Retrieved from http://www.fs.usda.gov/Internet/FSE_DOCUMENTS/fsbdev3_039584.pdf.
- Zambino, P.J. 2010. Biology and pathology of *Ribes* and section their implications for management of white pine blister rust. *Forest Pathology* 40(3-4): 264-291.
- Zambino, P.J.; Richardson, B.A.; McDonald, G.I.; Klopfenstein, N.B.; Kim, M.-S. 2006. A paradigm shift for white pine blister rust: Non-*Ribes* alternate hosts of *Cronartium ribicola* in North America. In: 53rd Annual Western International Forest Disease Work Conference, Jackson, WY, 2005 September 26-30. Guyon, J.C., comp. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Region. p. 161-163.

In accordance with Federal civil rights law and U.S. Department of Agriculture (USDA) civil rights regulations and policies, the USDA, its Agencies, offices, and employees, and institutions participating in or administering USDA programs are prohibited from discriminating based on race, color, national origin, religion, sex, gender identity (including gender expression), sexual orientation, disability, age, marital status, family/parental status, income derived from a public assistance program, political beliefs, or reprisal or retaliation for prior civil rights activity, in any program or activity conducted or funded by USDA (not all bases apply to all programs). Remedies and complaint filing deadlines vary by program or incident.

Persons with disabilities who require alternative means of communication for program information (e.g., Braille, large print, audiotope, American Sign Language, etc.) should contact the responsible Agency or USDA's TARGET Center at (202) 720-2600 (voice and TTY) or contact USDA through the Federal Relay Service at (800) 877-8339. Additionally, program information may be made available in languages other than English.

To file a program discrimination complaint, complete the USDA Program Discrimination Complaint Form, AD-3027, found online at [How to File a Program Discrimination Complaint](#) and at any USDA office or write a letter addressed to USDA and provide in the letter all of the information requested in the form. To request a copy of the complaint form, call (866) 632-9992. Submit your completed form or letter to USDA by: (1) mail: U.S. Department of Agriculture, Office of the Assistant Secretary for Civil Rights, 1400 Independence Avenue, SW, Washington, D.C. 20250-9410; (2) fax: (202) 690-7442; or (3) email: program.intake@usda.gov.



To learn more about RMRS publications or search our online titles:

www.fs.fed.us/rmrs/rmrs-publishing-services

www.fs.usda.gov/treesearch