



United States
Department
of Agriculture

Forest Service

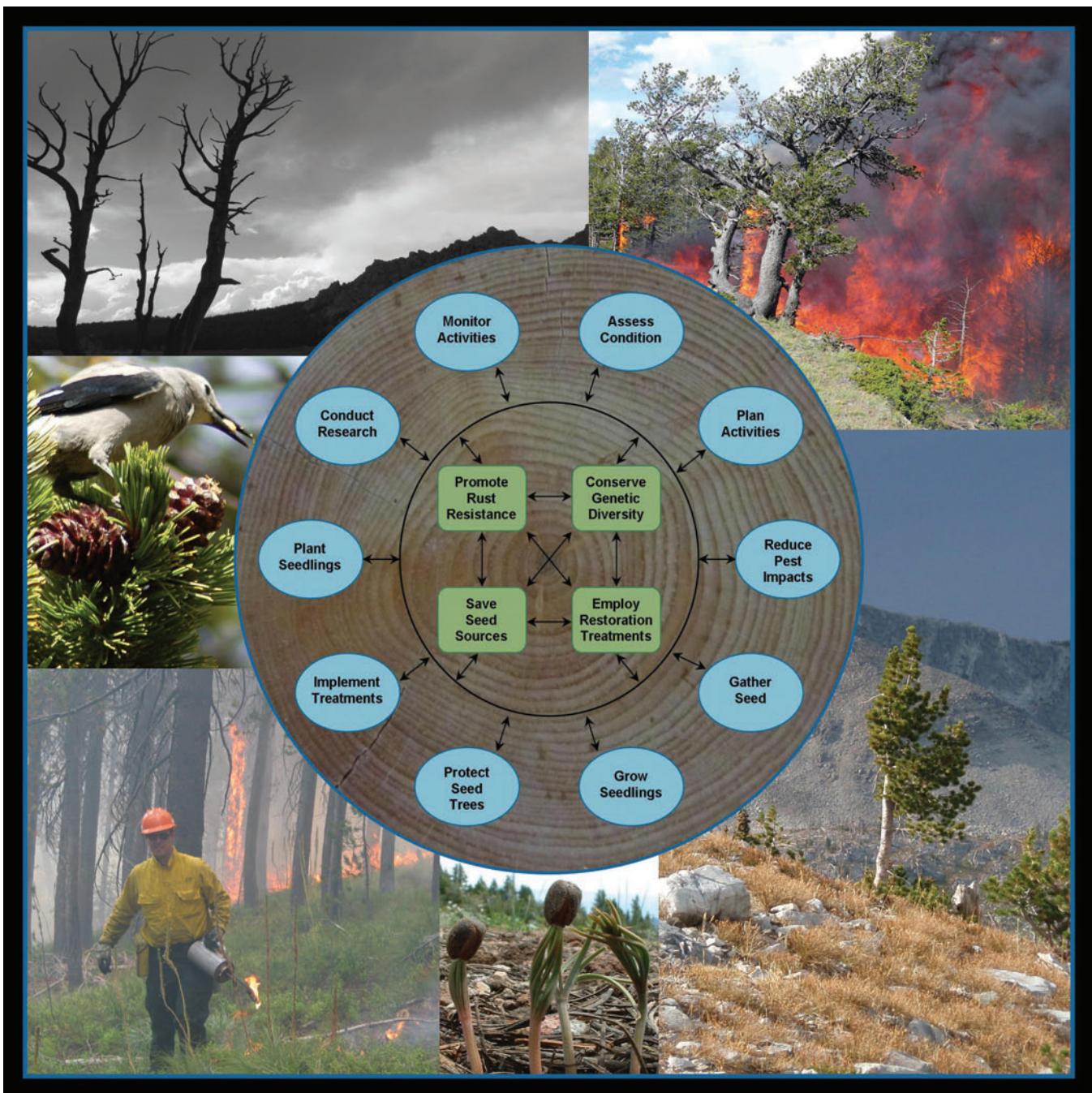
Rocky Mountain
Research Station

General Technical
Report RMRS-GTR-279

June 2012

A Range-Wide Restoration Strategy for

Whitebark Pine (*Pinus albicaulis*)



Keane, Robert 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.; Reinhart, D.P.; Ryan, C.; Schoettle, A.W.; Smith, C.M. 2012. **A range-wide restoration strategy for whitebark pine (*Pinus albicaulis*)**. Gen. Tech. Rep. RMRS-GTR-279. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station. 108 p.

ABSTRACT

Whitebark pine (*Pinus albicaulis*), an important component of western high-elevation forests, has been declining in both the United States and Canada since the early Twentieth Century from the combined effects of mountain pine beetle (*Dendroctonus ponderosae*) outbreaks, fire exclusion policies, and the spread of the exotic disease white pine blister rust (caused by the pathogen *Cronartium ribicola*). The pine is now a candidate species for listing under the Endangered Species Act. Within the last decade, with major surges of pine beetle and increasing damage and mortality from blister rust, the cumulative whitebark pine losses have altered high-elevation community composition and ecosystem processes in many regions. Whitebark pine is a keystone species because of its various roles in supporting community diversity and a foundation species for its roles in promoting community development and stability. Since more than 90 percent of whitebark pine forests occur on public lands in the United States and Canada, maintaining whitebark pine communities requires a coordinated and trans-boundary effort across Federal and provincial land management agencies to develop a comprehensive strategy for restoration of this declining ecosystem. We outline a range-wide strategy for maintaining whitebark pine populations in high mountain areas based on the most current knowledge of the efficacy of techniques and differences in their application across communities. The strategy is written as a general guide for planning, designing, implementing, and evaluating fine-scale restoration activities for whitebark pine by public land management agencies, and to encourage agency and inter-agency coordination for greater efficiency. The strategy is organized into six scales of implementation, and each scale is described by assessment factors, restoration techniques, management concerns, and examples.

Keywords: whitebark pine, ecosystem restoration, fire regime, blister rust, mountain pine beetle, grizzly bear, Clark's nutcracker, seed dispersal, regeneration, red squirrels, upper subalpine communities, climate change

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

You may order additional copies of this publication by sending your mailing information in label form through one of the following media. Please specify the publication title and series number.

Publishing Services

Telephone	(970) 498-1392
FAX	(970) 498-1122
E-mail	rschneider@fs.fed.us
Website	http://www.fs.fed.us/rm/publications
Mailing address	Publications Distribution Rocky Mountain Research Station 240 West Prospect Road Fort Collins, CO 80526

EXECUTIVE SUMMARY

Whitebark pine (*Pinus albicaulis*) forests are declining across most of their range in North America because of the combined effects of mountain pine beetle (*Dendroctonus ponderosae*) outbreaks, fire exclusion policies, and the exotic pathogen *Cronartium ribicola*, which infects five-needle white pines and causes the disease white pine blister rust. The loss of this high-elevation tree species poses serious consequences for upper subalpine ecosystems, both in terms of impacts on biodiversity and losses in ecosystem processes; whitebark pine is now a candidate species for listing under the Endangered Species Act. Large, nutritious seeds produced by whitebark pine are an important food for many bird and small mammal species, as well as grizzly (*Ursus arctos horribilis*) and black bears (*Ursus americanus*), and whitebark pine communities provide habitat for many additional wildlife species. Whitebark pine seed dispersal by Clark's nutcrackers (*Nucifraga columbiana*) combined with hardy seedlings results in early whitebark pine community development after fire and other disturbances; whitebark pine seedlings survive on harsh, arid sites and may act as nurse trees to less hardy conifers and vegetation. Whitebark pine at higher elevations, where it is common in many regions, helps regulate snow melt and reduce soil erosion. For these collective functions, whitebark pine is considered both a keystone species for promoting community diversity and a foundation species for promoting community stability. Since more than 90 percent of whitebark pine forests exist on public land in the United States and Canada, it is important that government natural resource management agencies play an important role in ensuring future presence of this tree species by initiating concerted, coordinated, and comprehensive restoration efforts. This is best accomplished through a coordinated, trans-boundary restoration strategy that includes shared infrastructure and expertise for conserving seeds, growing blister rust-resistant seedlings, protecting trees, restoring ecosystem processes, and promoting natural regeneration. We detail a multi-scale strategy for restoring whitebark pine across its range in the western United States and Canada. The strategy was compiled by researchers, land managers, and resource specialists for use as a reference for prioritizing, designing, and implementing successful whitebark pine restoration activities across many scales from stands to landscapes to its entire range. The whitebark pine restoration strategy consists of the following principles: (1) promote rust resistance, (2) conserve genetic diversity, (3) save seed sources, and (4) employ restoration treatments. These guiding principles are then used to implement the whitebark pine restoration strategy using a set of possible actions:

1. assess condition,
2. plan activities,
3. reduce pest impacts,
4. gather seed,
5. grow seedlings,
6. protect seed sources,
7. implement restoration treatments,
8. plant burned areas,
9. support research, and
10. monitor activities.

The strategy is also organized by six spatial scales of analysis and organization:

1. range-wide,
2. region (National Forest Region or Provincial Regions),
3. forest (National Forest, National Park, and Canadian Forest District),
4. landscape (watershed or landform),
5. stand, and
6. tree.

At each scale, we present four important factors in the restoration strategy: (1) assessment, (2) restoration actions, (3) management concerns, and (4) an example. Strategic restoration plans are presented for the coarse-scale strategies, while illustrated examples are presented for the finer scales (tree, stand, and landscape).

AUTHORS

Robert E. Keane is a Research Ecologist with the U.S. Forest Service, Rocky Mountain Research Station at the Missoula Fire Sciences Laboratory in Missoula, Montana. His most recent research includes (1) developing ecological computer simulation models for exploring landscape, fire, and climate dynamics; (2) sampling, describing, modeling, and mapping fuel characteristics, and (3) investigating the ecology and restoration of whitebark pine. He received his B.S. degree in Forest Engineering from the University of Maine, Orono; his M.S. degree in Forest Ecology from the University of Montana, Missoula; and his Ph.D. in Forest Ecology from the University of Idaho, Moscow.

Diana F. Tomback is a Professor in the Department of Integrative Biology University of Colorado Denver, an Evolutionary Ecologist and Conservation Biologist, and volunteer Director of the Whitebark Pine Ecosystem Foundation, a non-profit organization based in Missoula, Montana. Her current research examines several aspects of the interaction between Clark's nutcrackers and whitebark pine, including: (1) timeframe of post-fire regeneration of whitebark pine, (2) detecting changes in nutcracker seed dispersal services as whitebark pine declines, and (3) the role of whitebark pine in vegetation dynamics at treeline. She received her B.A. and M.A. degrees in Zoology from the University of California at Los Angeles, and her Ph.D. in Biological Sciences from the University of California at Santa Barbara.

Carol A. Aubry is a Forest Geneticist with the U.S. Forest Service, Olympic National Forest in Olympia, Washington. She works on National Forests in the Pacific Northwest, and her work focuses on the protection and management of forest genetic resources, including (1) whitebark pine conservation and restoration, and (2) climate change adaptation strategies for forest tree species. She received her B.S. degree in Biology from the University of Hartford, Connecticut; her M.S. degree in Forestry from Yale School of Forestry and Environmental Studies; and her Ph.D. in Forest Genetics from Oregon State University, Corvallis.

Andrew D. Bower is a Forest Geneticist with the U.S. Forest Service, Olympic National Forest in Olympia, Washington. Andrew is the U.S. Forest Service Pacific Northwest Region Whitebark Pine Restoration Program Lead and has been involved in research on genetic issues with whitebark pine since 2001. He received his B.S. degree in Forestry from the University of California, Berkeley; his M.S. degree in Forest Science from Oregon State University; and his Ph.D. in Forest Sciences from the University of British Columbia.

Elizabeth M. Campbell is a Research Ecologist with the Pacific Forestry Centre, Canadian Forest Service in Victoria, British Columbia, Canada. She received her B.Sc.H. degree in Biology at Queen's University Ontario; her M.Sc. degree in Biology from the University of Victoria, British Columbia; and her Ph.D. degree in Forest Ecology from the Université du Québec à Montréal Centre d'études de la forêt, Quebec. Her most recent work includes (1) a study of mountain pine beetle outbreaks in whitebark pine ecosystems, (2) describing, modeling, and projecting the potential impacts of biotic disturbances and climate change on boreal and temperate forest dynamics, and (3) incorporating the concepts of socio-ecological resilience into forest ecosystem management.

Cathy L. Cripps is an Associate Professor at Montana State University, Plant Sciences and Plant Pathology Department in Bozeman, Montana, and editor of the journal "Fungi in Forest Ecosystems." She received her B.Sc. degree in Natural Resources from the University of Michigan and her M.S. degree and Ph.D. in Biology (Mycology) from Virginia Polytechnic Institute. Her research examines the mycorrhizal fungi associations with whitebark and limber pine. This includes discovery of the native fungi associated with the pines and inoculation of seedlings with native strains in the greenhouse.

Melissa B. Jenkins is a Silviculturist with the U.S. Forest Service, Flathead National Forest in Kalispell, Montana. She was the first Chair of the Greater Yellowstone Coordinating Committee, Whitebark Pine Subcommittee (2001-2002), and wrote the first whitebark pine restoration guidelines for the Greater Yellowstone Ecosystem in 2005. She received a B.S. degree in Ecosystem Management and Forestry from the State University of New York College of Environmental Science and Forestry in 1981 and has been a certified Silviculturist with the Forest Service since 1993.

Mary F. Mahalovich is a Regional Geneticist with the U.S. Forest Service, Northern, Rocky Mountain, Southwestern, and Intermountain Regions and based at the Forestry Sciences Laboratory in Moscow, Idaho. Her program management and research includes genecology; identifying, harnessing and deploying blister rust-resistant five-needle pines; and gene

conservation. She received her B.S. degree in Forest Management from Northern Arizona University, Flagstaff; her M.S. degree in Forest Genetics from the University of California, Berkeley; and her Ph.D. in Forestry and Genetics from North Carolina State University, Raleigh.

Mary Manning is the Regional Vegetation Ecologist for the Northern Region of the U.S. Forest Service in Missoula, Montana. Her work is primarily in ecosystem classification and inventory and monitoring, with a special emphasis on non-forested vegetation and riparian/wetland ecosystems. She holds a B.S. degree in Natural Resources Management, with a minor in Range Management, from California Polytechnic State University, San Luis Obispo, and an M.S. degree in Rangeland Ecology from University of Nevada, Reno.

Shawn T. McKinney is the Assistant Unit Leader of the USGS Maine Cooperative Fish and Wildlife Research Unit, University of Maine, Orono. His research includes modeling community interactions across a range of whitebark pine habitat contexts, investigating Clark's nutcracker spatial foraging patterns, and exploring the consequences of blister rust invasion on natural selection and the future adaptive ability of whitebark pine. He received a B.A. degree in Biology, History, and Environmental Studies from the University of Colorado, Boulder; an M.S. degree in Biology from the University of Colorado Denver; and a Ph.D. in Forest Ecology from the University of Montana, Missoula.

Michael P. Murray is a Forest Pathologist for the Ministry of Natural Resource Operations located at the Kootenay Lake Forestry Centre, in Nelson, British Columbia, Canada. His current research includes (1) whitebark pine dynamics and long-term monitoring, (2) climate-driven tree declines, (3) ameliorating forest root diseases, and (4) fire-pathology interactions. He received his B.A. degree in environmental science from the State University of New York, Plattsburgh; his M.S. degree in Natural Resources from Humboldt State University, Arcata, California; and his Ph.D. in Forest Ecology from the University of Idaho, Moscow.

Dana L. Perkins is a Forest Ecologist and Five-Needle Pine Coordinator for Idaho Bureau of Land Management. Her research involves development of whitebark pine tree-ring chronologies, study of historic and current mountain pine beetle epidemics and how they influence stand structure, and conservation and restoration of whitebark pine on lower treeline and mountain islands of BLM administered lands. She received her B.S. degree in Animal Science and Wildlife Biology from the University of New Hampshire, Durham; her M.S. degree in Renewable Natural Resources at the Laboratory of Tree Ring Research, University of Arizona, Tucson; and her Ph.D. in Ecology from Utah State University, Logan.

Dan P. Reinhart is a Supervisory Resource Management Specialist with Yellowstone National Park. He is the Park's Representative with the Greater Yellowstone Coordinating Committee, Whitebark Pine Subcommittee and Terrestrial and Aquatic Invasive Species subcommittees. His research involves relationships of red squirrels and grizzly bears in whitebark pine habitats, Yellowstone grizzly bear food habits and habitat use, and participation in the monitoring and management of whitebark pine and wilderness in the Yellowstone Ecosystem.

Chris Ryan is the Wilderness, Wild and Scenic Rivers and Outfitter Guide Program Leader for the U.S. Forest Service Northern Region, Montana. She was the Forest Service Representative for the Arthur Carhart National Wilderness Training Center. Her 30-year Forest Service career has focused on wilderness management in areas such as Alpine Lakes in Washington State and the Boundary Waters Canoe Area Wilderness in Minnesota. Chris has a Bachelor's degree in Resource Geography from Central Washington University in Ellensburg, Washington.

Anna W. Schoettle is a Research Plant Ecophysicist with the U.S. Forest Service, Rocky Mountain Research Station in Fort Collins, Colorado. Her recent research on high-elevation five-needle pines includes regeneration requirements and population dynamics, resistance to white pine blister rust, gene conservation, and genetic structure studies toward the development of restoration strategies for impacted and threatened populations. She received both her B.S. degree in Biology and Botany and her M.S. degree in Plant Physiology from Cornell University, Ithaca, New York, and her Ph.D. in Physiological Ecology from the University of Wyoming, Laramie.

Cyndi M. Smith is an Ecosystem Scientist with Parks Canada at Waterton Lakes National Park in Waterton Park, Canada. She has undertaken research, monitoring, and restoration projects for both whitebark and limber pine. She obtained her B.E.Sc. degree from the University of Waterloo at Waterloo, Ontario, and her M.Sc. in Wildlife Ecology from Simon Fraser University at Burnaby, British Columbia. Cyndi has also been volunteer Associate Director of the Whitebark Pine Ecosystem Foundation since 2006.

ACKNOWLEDGMENTS

We are grateful to the members of the Whitebark Pine Ecosystem Foundation for providing material and reviews of this document. We also thank the following people who helped with the preparation of this report: Eva Karau, Signe Leirfallom, Aaron Sparks, and Don Helbrecht, of the U.S. Forest Service, Rocky Mountain Research Station, Missoula Fire Sciences Laboratory. We also thank Barry Bollenbacher and Bryan Donner, U.S. Forest Service, Northern Region, for extensive review of the several iterations of this publication.

CONTENTS

1. Introduction.....	1
Structure of This Report.....	2
Whitebark Pine Ecology.....	2
Taxonomy	2
Distribution	3
Autecology	4
Vegetation Community Characteristics	5
Successional Dynamics	7
Pine-Bird Interactions	8
Squirrels.....	11
Genetics.....	13
Ectomycorrhizal Fungi.....	15
Fire Regimes.....	17
Importance of Whitebark Pine.....	20
Ecological Processes and Ecosystem Services	20
Recreation.....	20
Cultural Heritage.....	21
Timber.....	21
Grizzly and Black Bears	22
Current Status.....	23
Blister Rust	24
Mountain Pine Beetle	25
Fire Exclusion.....	28
Climate Change.....	28
Extent of Decline.....	30
Other Whitebark Pine Issues	30
Whitebark Pine Restoration in Wilderness	30
Conservation Efforts for Whitebark Pine.....	33
2. Whitebark Pine Restoration Strategy	35
The Strategy.....	35
Important Restoration Concepts.....	38
Historical Range and Variability.....	38
Physiological Constraints.....	38
Assembly Rules	39
Proactive Approach	39
Central Tenets of the Restoration Strategy.....	39

3. National and Regional Direction	41
U.S. Forest Service.....	41
U.S. National Park Service.....	42
Canadian Land Management Agencies.....	42
British Columbia	42
Alberta	43
4. Restoration By Spatial Scale.....	45
Range-Wide Scale.....	45
Assessments	45
Restoration Actions.....	46
Management Concerns.....	47
A Range-Wide Prioritization for Whitebark Pine.....	47
Regional Scale	50
Assessments	50
Restoration Actions.....	50
The Northern, Rocky Mountain, and Intermountain Regions Genetic Restoration Program for Whitebark Pine	50
Management Concerns.....	52
The U.S. Forest Service Northern Region Restoration Strategy for Whitebark Pine	52
The Pacific Northwest Region Restoration Strategy for Whitebark Pine	55
The Greater Yellowstone Area Whitebark Pine Restoration Strategy.....	59
Forest Scale.....	59
Assessments	60
Restoration Actions.....	60
Management Concerns.....	61
Example: Implementation of the Greater Yellowstone Restoration Decision Guidelines for the Caribou-Targhee National Forest.....	61
Landscape Scale.....	63
Assessments	64
Restoration Actions.....	67
Management Concerns.....	68
Example: Restoration Decision Guidelines for Watersheds on the Caribou-Targhee National Forest	70
Stand Scale	70
Assessments	70
Restoration Actions.....	73
Management Concerns.....	77
Example	78
Tree Scale	80
Assessments	80
Restoration Actions.....	81
Management Concerns.....	82
Example	83
5. Implementation of Restoration Strategy.....	85
Decision Support Systems	86
6. Discussion.....	87
Future Research.....	88
Restoration Barriers and Challenges	89
Limitations	89
7. The Range-Wide Perspective	91
References	92
Appendix A—Whitebark Pine Tree Improvement Program	107

1. Introduction

Whitebark pine (*Pinus albicaulis* Engelm.) forests are declining throughout their range in North America because of the combined effects of historical and current mountain pine beetle (*Dendroctonus ponderosae* Hopkins Coleopteran: Curculionidae, Scotytinae) outbreaks, fire exclusion management policies, and the introduced pathogen *Cronartium ribicola*, which causes the disease white pine blister rust in five-needle white pines (Keane and Arno 1993; Kendall and Keane 2001; Murray and Rasumussen 2003; Schwandt 2006; Tomback and Achuff 2010) (Figure 1.1). The loss of this high-elevation tree species poses serious consequences for upper subalpine ecosystems, both in terms of the impacts on biodiversity and in losses of valuable ecosystem processes and services (Tomback and others 2001a; Tomback and Achuff 2010). The large, nutritious seeds produced by whitebark pine are an important food for birds and small mammals, as well as bears; whitebark pine communities provide habitat for many additional wildlife species; and rapid seed dispersal by Clark's nutcrackers (*Nucifraga columbiana* Wilson) combined with hardy seedling growth results in early whitebark pine community development after fire and other disturbances (Hutchins 1994; Mattson and others 2001; Tomback and Kendall 2001; Tomback and others 2001c). Furthermore, whitebark pine seedlings survive on harsh, high-elevation droughty sites and may eventually act as nurse trees to less hardy conifers and vegetation (Callaway 1998; Callaway and others 1998; Tomback and others 2001c). At upper subalpine elevations, where it is common in many regions (Resler and

Tomback 2008), whitebark pine helps regulate snow melt and reduce soil erosion (Farnes 1990). For these collective functions, whitebark pine is considered both a keystone species for promoting community diversity and a foundation species for promoting community stability (Ellison and others 2005; Tomback and others 2001a; Tomback and Achuff 2010). The loss of whitebark pine would potentially affect fire regimes, recreational experiences, and aesthetic perceptions (Keane and others 2002a; McCool and Freimund 2001; Tomback and others 2001a; Tomback and Achuff 2010).

Given limited budgets, personnel, and funding, the success of whitebark pine restoration efforts can be greatly enhanced by a coordinated strategy that integrates the latest scientific findings into a comprehensive plan for conserving the species. Since more than 90 percent of whitebark pine forests exist on public lands, including those managed by the U.S. Forest Service and National Park Service in the United States and by Provincial and Federal agencies in Canada, government land management agencies play key roles in ensuring the survival of this ecologically valuable tree species (Keane 2000; Tomback and Achuff 2010). If an inter-agency and even trans-boundary restoration strategy was developed that shared a common plan, infrastructure, and expertise, as well as other individual agency strengths for implementation, it could lead to more efficient use of scarce resources by integrating successful, cost-effective efforts for restoring this declining species.



Figure 1.1. A declining whitebark pine stand in the northern Rocky Mountains of the United States (photo courtesy of Steve Arno).

The first step toward a comprehensive, range-wide restoration effort is to craft feasible strategies at multiple levels so landscapes can be prioritized for treatment and so restoration techniques can be designed to return the species to its historical prominence and function (Keane and others 1996). Even in regions where whitebark pine losses are not yet great, such as the southern Sierra Nevada and interior Great Basin ranges, proactive strategies may help prevent or mitigate the severe declines experienced in, for example, the Northern Continental Divide Ecosystem (see Schoettle and Snieszko 2007; Smith and others 2008).

In this report, we describe a multi-scale strategy for restoring whitebark pine across its range in the western United States and Canada. It was compiled by researchers, land managers, and resource specialists to use as a reference for prioritizing, designing, and implementing successful whitebark pine restoration activities from stands to landscapes to National Forests to Regions, and ultimately, to the entire species' range. This effort was based on a number of existing conservation plans and strategies (Aubry and Shoal 2008; Jenkins 2005; Keane and Arno 2001; Schwandt 2006; Shoal and others 2008; Wilson and Stuart-Smith 2001). The strategy has a set of principles with an associated array of possible actions to guide the design, planning, and implementation of restoration activities.

Structure of This Report

This report provides managers with the information needed to develop plans to restore whitebark pine. The first section presents basic ecological principles and knowledge that are important in understanding and implementing whitebark pine restoration strategies and treatments. Next, we present our general restoration strategy by defining our guiding principles, detailing restoration actions, and discussing the underlying concepts and ecological foundation of the rangewide strategy. We then discuss the major national and regional direction for the government agencies that manage whitebark pine in the context of this restoration strategy. Subsequently, we present information needed to implement the restoration strategy at six spatial scales. The entire range of whitebark pine in the United States and Canada is presented as the coarsest scale. Regional or province-wide assessments are the next finer scale, and finer yet is the forest scale that can be represented by a National Forest in the United States or national or provincial park in Canada. The landscape scale is nested within the forest or park scale, and it is usually defined by watersheds, ranger districts, or landforms. Landscapes are comprised of stands, the next smaller spatial scale, and it is at this scale where the majority of proactive restoration treatments and efforts are accomplished. The last scale is the tree. In landscape ecology, the next finer scale is used to provide the detail to the scale in question, while the next coarser scale provides the context in which to interpret that detail.

We also present a list of assessments that could be used for prioritizing and planning restoration treatments at a particular scale. Next, we list the tools and actions that promote

and implement restoration treatments at that scale. Last, we present examples of restoration strategies designed specifically for a given scale using available data from various land management agencies. While the examples can be used to guide restoration activities, they may also be modified to develop alternative strategies that emphasize other important management concerns. We provide examples because it is impossible to construct standardized restoration strategies at finer scales due to the diversity of whitebark pine communities and their complex ecological processes, management issues, and public concerns. In other words, there is no “one size fits all” approach to developing landscape level restoration strategies. The examples may contain spatial data of mixed resolution and accuracy out of necessity because of the paucity of spatial data available to land management. In many cases, land managers are not able to wait for a consistent, area-wide data set before moving forward to develop their restoration strategy and implement treatments. In that case, the best available information should be used and then updated as more accurate information becomes available.

Whitebark Pine Ecology

The design and interpretation of any restoration effort demands a working knowledge of the autecology and synecology of species to be restored. This section contains a brief synopsis of whitebark pine ecology, emphasizing important concepts needed to understand the basic tenets of ecosystem restoration presented in this report. More detailed overviews are found in the contributed volume edited by Tombak and others (2001b), which may provide the most definitive source for background material on whitebark pine to date, and from Arno and Hoff (1990), which contains important silvicultural characteristics of whitebark pine.

Taxonomy

Pines are gymnosperms and classified in the class Pinopsida, order Pinales, and Division Coniferophyta (USDA NRCS 2009). Whitebark pine is further classified in the subgenus *Strobus*, a group known both as haploxyylon pines for having one rather than two fibrovascular bundles per needle, and the soft pines for their light wood. Traditionally, whitebark pine was placed in section *Strobus* and in subsection *Cembrae* (Little and Critchfield 1969; Price and others 1998) as the only North American species of the “stone pine” group. The stone pines all have cones and seeds adapted to seed dispersal by birds—the “nutcrackers” (genus *Nucifraga*).

Recent genetic studies have suggested that *Cembrae* pines do not form a distinct group (Gernandt and others 2005). Gernandt and others (2005) recommended merging two five-needle white pine subsections—*Strobi* and *Cembrae*—into a new subsection *Strobus* placed within the new pine section *Quinquefoliae*. This arrangement suggests that the closest relatives of whitebark pine are not only the *Cembrae* pines but several other five-needle white pines (Syring and others 2007).

Distribution

Whitebark pine has the largest and northern-most distribution of all five-needle white pines (Tomback and Achuff 2010). It is found in the upper subalpine and treeline forests of the United States and Canada, including the northern Rocky Mountains, Great Basin, Sierra Nevada and Cascades, and northern coastal ranges (Arno and Hoff 1990; McCaughey and Schmidt 2001) (Figure 1.2). Its distribution is split into two broad sections: the western section includes the Sierra Nevada and Klamath Mountains of California and Cascade Mountains of Oregon, Washington, and British Columbia; and the Olympic Mountains of Washington and coastal ranges through the Bulkley Mountains of British Columbia to about 55° N latitude. The eastern section comprises the Rocky Mountains from the Salt River and Wind River ranges of western Wyoming north through the Greater Yellowstone Area (GYA), Idaho, Montana, Alberta and British Columbia. The northern-most whitebark pine stands in the Rocky Mountains occur north of Willmore Wilderness Provincial Park at about 54° N latitude. Whitebark pine also grows in the Great Basin ranges of northern and eastern Nevada and in the Blue and Wallowa Mountains of northeastern Oregon, as well as in other isolated, outlying stands. These two distributional regions are connected by scattered populations

in northeastern Washington and southern British Columbia (Little and Critchfield 1969; Ogilvie 1990).

Whitebark pine forms extensive forests in the northern Rocky Mountains of the United States and it is also abundant on the eastern slope of the Cascades and Coast Ranges; however, it assumes a more patchy distribution at the northern end of its distribution in the Canadian Rockies and Coast Ranges of British Columbia (Arno and Hoff 1990). Whitebark pine grows on soils classified as Inceptisols (Typic Cryochrepts), in deeper volcanic ash deposits as Andic Cryochrepts or as Lithic Cryochrepts (USDA 1975). Among the Typic Cryochrepts these include the less, well-developed Entisols (Cryorthents in granitic substrates) and better developed Alfisols (Mollic and Typic Cryoboralfs), Inceptisols, and Mollisols (Argillic and Typic Cryoborolls) (Hansen-Bristow and others 1990). Some dry-sites in semiarid regions have a thick, dark surface horizon and are classified as Mollisols (Typic Cryoborolls), whereas soils that have a dark surface but low base saturation are classified as Typic Cryumbrepts (USDA 1975). Whitebark pine typically does not occur on limestone soils, except in wetter areas near and north of the Canadian border (reviewed in Weaver 2001). In the northern-most Canadian Rocky Mountains, whitebark pine grows exclusively on siliceous soils as opposed to limestone.

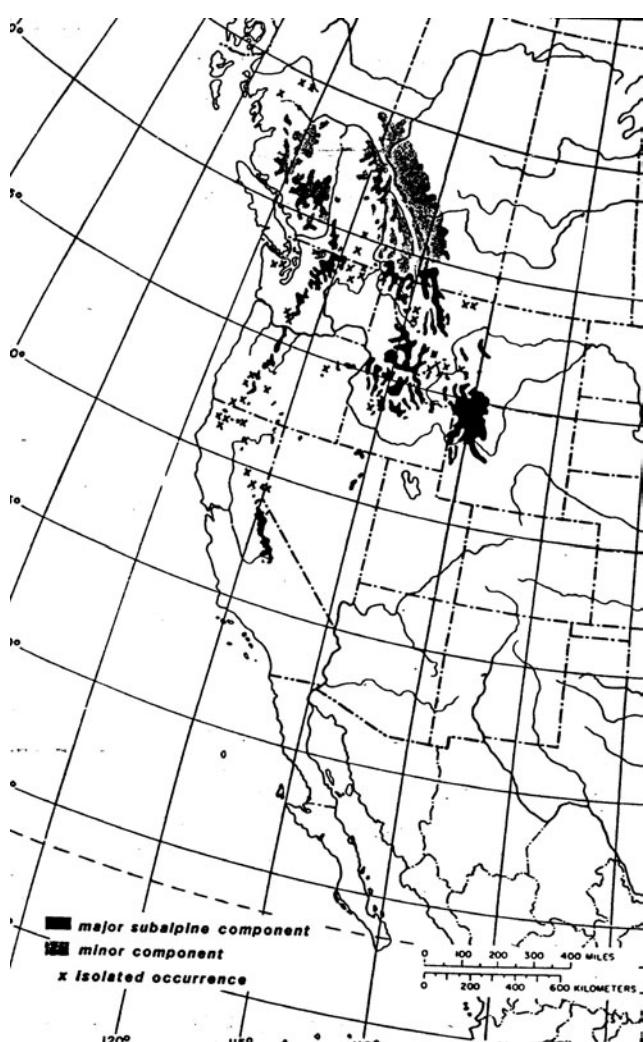


Figure 1.2. The range of whitebark pine, from Arno and Hoff (1990).

Autecology

Whitebark pine is a long-lived tree of moderate shade tolerance (Minore 1979) (Figure 1.3). It is common to find mature whitebark pine trees well over 400 years of age, especially on harsh growing sites (the oldest is more than 1,275 years) (Luckman and others 1984; Perkins and Swetnam 1996). Well-formed, thrifty individuals often have smooth, grey bark, especially in the tree crowns, which may appear white-ish in bright sunlight (Arno and Hoff 1990). Whitebark pine is slow growing in both height and diameter, and it rarely grows faster than most of its competitors except on the most severe sites (Arno and Hoff 1990).

Whitebark pine cones are purple in color, somewhat egg-shaped, and grow at the tips of branches, primarily in the upper tree crown (Figure 1.4). These cones contain about 60 large, wingless seeds depending on the magnitude of the cone crop (Forcella and Weaver 1980; Owens and others 2008; Weaver and Forcella 1986). Tomback (1982) reported a mean

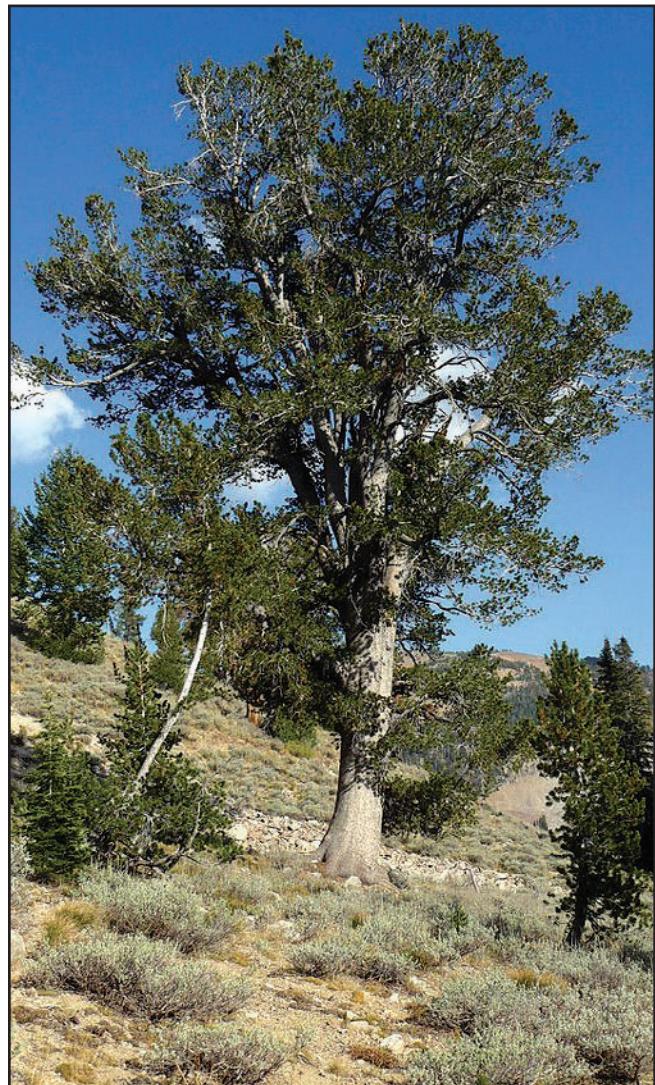


Figure 1.3. Typical mature whitebark pine tree. Note the unique lyrate crown growth form.



Figure 1.4. Whitebark pine cones arrayed upward on the upper portions of whitebark pine tree crowns. Note the purple color and abundant sap.

of 45 filled seeds per cone, whereas Weaver and Forcella (1986) reported 75 seeds per cone. These seeds are highly nutritious and are eaten by many insect, bird, and mammal species (Hutchins and Lanner 1982; Tomback and Kendall 2001). High nutritive value in whitebark pine seeds is characterized by 21 percent protein (Lanner and Gilbert 1994) and fat content ranging from 28 percent (Robbins and others 2006) to 52 percent (Lanner and Gilbert 1994). The cones remain closed after ripening because the scales lack principal fibrous tissues that pull them open (Harlow and others 1964). The seeds are relatively large, weighing on average 0.175 g each, with thick seed coats (McCaughay and Tomback 2001; Tomback and Linhart 1990) (Figure 1.5). Whitebark pine starts producing cones around 30 to 60 years of age, although trees must attain good canopy volume to have high cone production, usually at about 125 to 250 years of age (Arno and Hoff 1990; Krugman and Jenkinson 1974) (Figure 1.3). The frequency of large, cone crops within a given stand varies regionally by climate and population level, from yearly to every two or three to five years in many areas, although a few cones are produced within a stand nearly every year (Arno and Hoff 1990; Crone and others 2011; Krugman and Jenkinson 1974; Tomback and others 2001c).

Whitebark pine seeds are primarily dispersed and sown by Clark's nutcracker, a bird related to crows, ravens, and jays (avian Family Corvidae) (see the "Pine-Bird Interactions" section). Whitebark pine has many morphological characteristics that are adaptations for its mutualistic relationship with

Figure 1.5.
Whitebark pine
seeds.



the Clark's nutcracker (Lanner 1982, 1996; Tomback 1983; Tomback and Linhart 1990). The closed cones ensure availability of seeds to nutcrackers. The seeds lack seed wings, which for most conifers serve to disperse seeds away from parent trees, slowing seed fall and lengthening seed dispersal distance (Figure 1.5). Winged seeds, however, are not useful with closed cones and would slow seed harvest for nutcrackers. When nutcrackers harvest winged seeds from other tree species, they clip or rub off each wing before placing the seed in their throat pouch. Thus, the wingless and large seeds make for efficient foraging. Although whitebark pine cone and seed traits are well adapted to this mutualism, widespread seed predation by pine squirrels (*Tamiasciurus* spp.) appears to select for heavier cone scales, thicker seed coats, and fewer seeds per cone, which reduces the efficiency of nutcrackers (Siepielski and Benkman 2007). Whitebark has a distinctive “candelabra” or lyrate growth form, with essentially a flat-topped, shrub-like canopy, which may increase canopy area for cone production while serving to display cones to the bird (Lanner 1982, 1996) (Figure 1.3). The cones usually grow perpendicular in their long axis from the tips of vertically oriented branches, providing easy access to the birds (Figure 1.4) (Lanner 1982; Tomback 1978). As a result, the cones are in plain sight from flying nutcracker’s view because they are purple, at the branch’s end, and at the top of the lyrate crown (Figure 1.3).

Vegetation Community Characteristics

Whitebark pine forests occur in two high mountain biophysical settings (Figure 1.6). On productive upper subalpine sites, whitebark pine is the major seral species that

is replaced by the more shade-tolerant subalpine fir (*Abies lasiocarpa* [Hook.] Nutt.), Engelmann spruce (*Picea engelmannii* Parry ex. Engelm), or mountain hemlock (*Tsuga mertensiana* [Bong.] Carrière), depending on geographic region (Arno and Weaver 1990). These sites, referred to as “seral whitebark pine sites” in this report, support upright, closed-canopy forests in the upper subalpine lower transition to timberline, just above or overlapping with the elevational limit of the shade-intolerant lodgepole pine (*Pinus contorta* Douglas ex. Louden) (Figure 1.7) (Arno and Weaver 1990; Pfister and others 1977), and the two species can often share dominance. Other minor species found with whitebark pine on these sites are Douglas-fir (*Pseudotsuga menziesii* [Mirb.] Franco), limber pine (*Pinus flexilis* James), and alpine larch (*Larix lyallii* Parl) (Pfister and others 1977).

Whitebark pine can also successfully dominate high-elevation settings (called “climax whitebark pine sites” in this report) on harsh sites in the upper subalpine forests and at treeline on relatively dry, cold slopes (Arno 1986; Arno and Weaver 1990; Steele and others 1983) (Figure 1.8). Other species, such as subalpine fir, spruce, and lodgepole pine, can occur on these sites but as scattered individuals with truncated growth form (Arno and Hoff 1990; Arno and Weaver 1990; Cooper and others 1991; Pfister and others 1977). Alpine larch is often found on north-facing climax whitebark pine sites, often in association with sub-surface water (Arno and Habeck 1972). Whitebark pine can also occur as krummholz, elfin forests, clusters, groves, tree islands, and timber atolls in the alpine treeline ecotone (Arno and Hoff 1990; Tomback 1989) and as a minor seral in lower subalpine sites (Cooper and others 1991; Pfister and others 1977).

Figure 1.6. Elevational range of whitebark pine showing the two site types often associated with this species (from Keane 2001b).

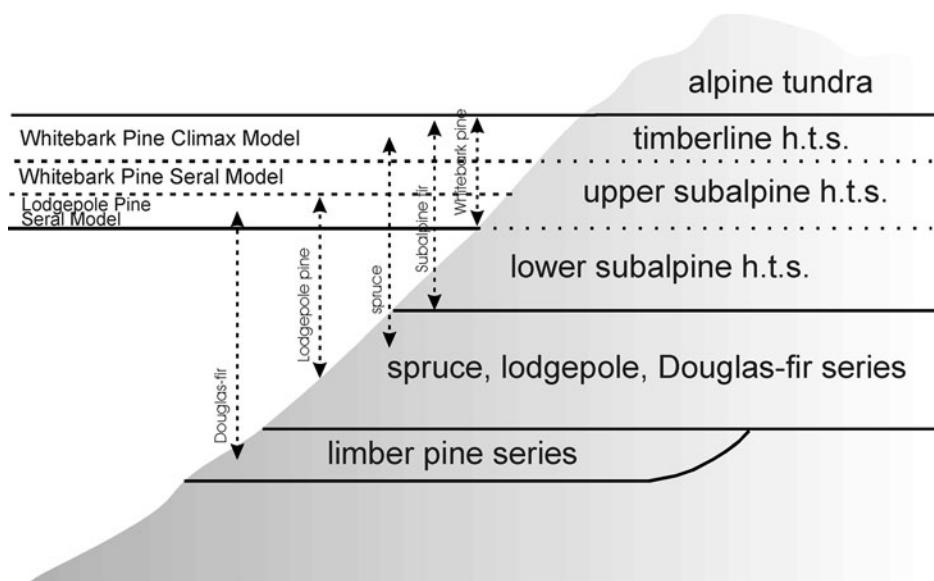
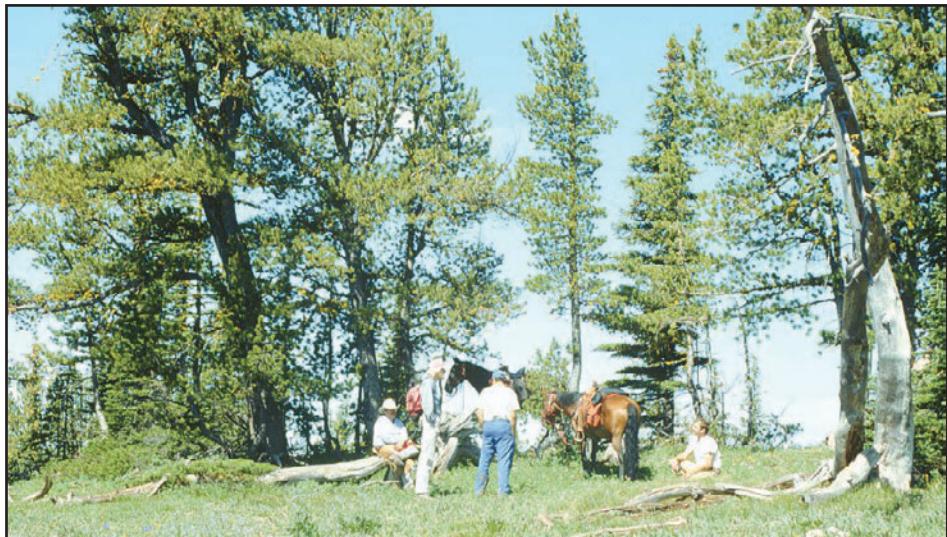


Figure 1.7. Mature whitebark pine in the later stages of development with the shade-tolerant subalpine fir becoming established in the overstory and dominant in the understory without disturbance. This successional replacement is typical on seral whitebark pine sites.

Figure 1.8. Old whitebark pine in the later stages of development on sites where whitebark pine is the indicated climax species. Subalpine fir can occur on these sites, but they are typically scattered individuals and do not successional replace whitebark pine.



Whitebark pine forests often contain unique assemblages of plant species (Tombback and Kendall 2001). Most whitebark pine forests, especially the seral types, have low diversity in vascular plants (Forcella 1978), with the majority of understory plant cover composed of grouse whortleberry (*Vaccinium scoparium* Leiberg ex. Coville), huckleberry (*Vaccinium membranaceum* Douglas ex. Torr.), menziesia (*Menziesia ferruginea* Sm.), Hitchcock's smooth woodrush (*Luzula glabrata* [Hoppe ex. Rostk.] Desv. var. *hitchcockii* [Hämet-Ahti] Dorn), and common beargrass (*Xerophyllum tenax* [Pursh.] Nutt), with minor components of sedge (*Carex* spp. mostly Ross' sedge (*C. rossii* Boott) and Geyer's sedge (*C. geyeri* Boott), Pink Mountain-heath (*Phyllodoce empetriflora* [Sm.] D. Don), and broadleaf arnica (*Arnica latifolia* Bong), depending on geographical area, aspect, and elevation (Arno and Weaver 1990; Campbell 1998; Keane and Parsons 2010b; Pfister and others 1977). Other plants that may be occasional dominants include Idaho fescue (*Festuca idahoensis* Elmer), Parry's rush (*Juncus parryi* Engelm.), and Wheeler bluegrass (*Poa nervosa* [Hook.] Vasey) (Arno and Weaver 1990; Aubry and others 2008a). In the Cascade range, whitebark pine can also be found with russet buffaloberry (*Shepherdia canadensis* [L.] Nutt.), kinnikinnick (*Arctostaphylos uva-ursi* [L.] Spreng.), and pipsissewa (*Chimaphila umbellata* [L.] W. Bartram). High-elevation climax stands of whitebark pine support many unique alpine, subalpine, and montane undergrowth species assemblages, some of which are only found in association with whitebark pine (Forcella 1978; Tombback and Kendall 2001). Forcella and Weaver (1977) found that whitebark pine forests had unexpectedly high biomass, but low productivity.

In Montana, the major habitat type where whitebark pine occurs as a major seral species is subalpine fir/woodrush habitat type in both the grouse whortleberry and *Menziesia* phase (Pfister and others 1977). It also occurs as a major seral species on the rarer subalpine fir/*Ribes montigium* and subalpine fir/*Clematis pseudoalpina* habitat types found on the east side of the Continental Divide. Climax habitat types include whitebark, whitebark-subalpine fir, and subalpine fir-whitebark, but Pfister and others (1977) did not classify these treeline and upper subalpine sites in detail. Whitebark pine is also a major seral species in the Engelmann spruce/grouse whortleberry and subalpine fir/arnica habitat types of western Wyoming (Steele and others 1983). In the Cascades, whitebark pine is found primarily in the parkland plant association type (PAG3201) (Aubry and others 2008a). Johnson (2004) identified several whitebark pine plant associations in the mountains between the Cascades and Rockies.

Successional Dynamics

As previously described, whitebark pine is eventually replaced, in the absence of fire, by the shade-tolerant subalpine fir, spruce, and mountain hemlock on the productive, seral whitebark pine sites (Arno and Hoff 1990; Campbell

and Antos 2003; Keane 2001b) (Figure 1.7). It can take 50 to 250 years for subalpine fir to replace whitebark pine in the overstory depending on the local environment and previous fire history (Arno and Hoff 1990; Keane 2001b). Successional processes vary considerably among and within regions (Campbell and Antos 2003; Keane 2001b); whitebark pine may occur as a minor to major seral component depending on biophysical settings, available seed sources, and disturbance type and severity.

Whitebark pine competes with lodgepole pine during early successional stages in the lower portions of its elevational range (Arno and others 1993; Mattson and Reinhart 1990). Lodgepole pine usually has the competitive advantage over whitebark pine when it establishes from seed after a stand-replacing disturbance event because of its fast growth, serotiny, and copious seed production. Because lodgepole pine is less shade-tolerant than whitebark pine, it is more of an associate than a competitor in some whitebark pine forests, especially near treeline (Murray 1996). Kipfmüller and Kupfer (2005) described the complexity of successional development pathways after gradients of disturbance in central Idaho and western Montana. There are several successional pathway diagrams detailed in Keane (2001b) for use in modeling seral whitebark pine types, and we provide a simplified pathway for seral whitebark pine sites (Figure 1.9) to better understand the successional pathways in whitebark pine communities.

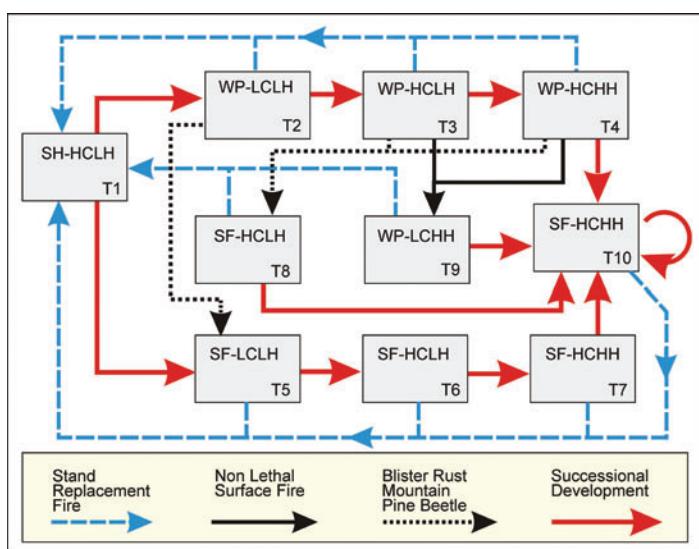


Figure 1.9. A generalized example of a successional pathway for a seral whitebark pine site. SH = mountain shrub, WP = whitebark pine, and SF = subalpine fir. Structural stage names: LCLH = low cover low height early succession stage, HCLH = high cover low height mid-serial stage, HCHH = high cover high height late succession stage, and LCHH = low cover high height disturbance maintained late succession stage (from Keane 2001b).

Pine-Bird Interactions

The Clark's nutcracker (Figure 1.10) and whitebark pines have intertwined fates: they participate in a coevolved, mutualistic interaction (Lanner 1982; Tomback 1982, 1983; Tomback and Linhart 1990). Essentially, whitebark pine has evolved a nearly exclusive dependence on nutcrackers to disperse its large wingless seeds, and in turn, nutcrackers utilize fresh and stored whitebark pine seeds as an important food source. The key behavior that benefits the whitebark pine is the tendency of nutcrackers to bury thousands of whitebark pine seeds each year as food stores in small clusters or "seed caches" across diverse forest terrain (Hutchins and Lanner 1982; Tomback 1982). These seed caches are retrieved by nutcrackers primarily in spring and summer months as an important food source for themselves and their young. However, not all seed caches may be recovered, particularly following a large cone crop. Snowmelt, spring rains, and summer showers stimulate seed germination, leading to whitebark pine regeneration (Tomback 1982; Tomback and others 2001c). Whereas whitebark pine depends nearly exclusively on nutcrackers, nutcrackers harvest and cache seeds of other large-seeded pines (see Tomback 1978, 1998). This section describes the important interactions between the bird and pine based on information presented in Hutchins and Lanner (1982), Tomback (1978, 1982, 1983, 1998, 2001, 2005), and Tomback and Linhart (1990).

There are two nutcracker species worldwide—the Clark's nutcracker (Figure 1.10), which ranges throughout the higher mountains of the western United States and Canada, and the spotted or Eurasian nutcracker (*Nucifraga caryocatactes*), which is widely distributed across the higher mountains of Europe and north-central and eastern Asia (Tomback 1983). Both nutcrackers have co-evolved relationships with pines historically classified together as *Cembrae* or "stone pines" (see Taxonomy section) within the pine family Pinaceae, and the white pine (soft pine) subgenus *Strobus*. The Eurasian *Cembrae* pines include four species—Swiss stone pine (*Pinus cembra*), Siberian stone pine (*P. sibirica*), Korean pine (*P. koraiensis*), and Japanese stone pine (*P. pumila*). In North America, the sole *Cembrae* pine is whitebark pine. Fossil evidence indicates that the *Cembrae* pines may be the most recent pines to evolve (Tomback 2005). New genetic evidence suggests that these pines may not form a related (monophyletic) group, but rather evolved similar traits through convergence, perhaps selected in part by nutcracker seed dispersal (Gernandt and others 2005).

Nutcrackers belong to the avian family Corvidae (along with ravens, crows, and jays), whose members tend to hide food for future use and are distinguished by superior cognitive abilities (Tomback 2005; Tomback and Linhart 1990). Nutcrackers have specialized traits for foraging on conifer seeds: a bill that is long, sturdy, and pointed and used to remove the scales of closed cones, peck or crack open seeds, and store and recover seed caches; a well-developed spatial memory that enables each bird to retrieve thousands of seed caches each year; a functional incubation patch in males as well as in females (unlike most corvids), enabling males to



Figure 1.10. The Clark's nutcracker. (Photo courtesy of Diana Tomback.)

incubate eggs or brood nestlings while females recover seed caches; an early nesting strategy, so that young are independent by late summer in time to cache their own seeds; and the sublingual pouch, a sac-like structure developed from the floor of the mouth with an opening under the tongue, which is used to transport conifer seeds and other nuts. For Clark's nutcrackers, the filled pouch may hold as many as 100 or more whitebark pine seeds.

Ancestors of the whitebark pine and the Clark's nutcracker most likely evolved in Eurasia, and progenitor species reached North America via the Bering Strait land bridge during the Pleistocene (Lanner 1980, 1990; Tomback 1983, 2001, 2005). Clark's nutcracker rapidly expanded its range beyond that of whitebark pine, through the ranges of other large-seeded pines, such as limber, southwestern white (*Pinus strobiformis*), Colorado piñon (*P. edulis*), and single-leaf piñon (*P. monophylla*) (Tomback 1983; Tomback and others 2011). Seeds of these pines are dispersed by Clark's nutcrackers as well, but importance of the interaction varies with the pine and geographic area. Nutcrackers also use seeds of other conifers, including ponderosa (*P. ponderosa*), Jeffrey (*P. jeffreyi*), the bristlecone (*P. aristata* and *P. longaeva*) pines, and Douglas-fir. In fact, the more widespread and frequent cone producers, such as ponderosa and Douglas-fir, may represent stable, if less preferred, food sources for nutcrackers. Similarly, Eurasian nutcrackers use a variety of relatively large-seed pines and hazelnuts (*Corylus avellana*) beyond the *Cembrae* pines; and seed use also varies geographically (as an example, see Mattes 1984; Swanberg 1956).

Clark's nutcracker life history is closely tied to *Pinus* spp. seed production (Tomback 1978, 1998). Nutcrackers forage on fresh pine seeds throughout the summer and fall and use their seed caches for winter and spring food, as well as for feeding nestlings (Mewaldt 1956; Vander Wall and Hutchins 1983). The seed caches of a single nutcracker yield an estimated 1.8 to 5.0 times the energy required to survive the winter (Tomback 1982; Vander Wall and Hutchins 1983; Vander Wall and Balda 1977). Based on metabolic requirements, Tomback (1982) estimated that a local population of nutcrackers consumes about 55 percent of their stored seeds. Furthermore, nutcrackers are sensitive to rates of energy gain: they increase their foraging efficiency by selecting trees with ripe cones and higher cone densities, and cones with higher proportions of edible seeds (Tomback 1978; Tomback and Kramer 1980; Vander Wall and Hutchins 1983; Vander Wall and Balda 1977).

Nutcrackers begin to harvest seeds as early as mid-July once cones are produced, removing pieces of unripe seeds from resinous cones, to feed themselves or their dependent juveniles (Tomback 1978). In the early summer, nutcrackers forage in subalpine forests and assess developing cone crops (Vander Wall and Hutchins 1983). This behavior presumably alerts birds to imminent seed shortages (Vander Wall and others 1981). Depending on the severity of cone crop failure, nutcrackers either emigrate regionally or irrupt synchronously from large geographic areas, such as the Sierra Nevada range, in search of food (Bock and Lepthien 1976; Davis and Williams 1957). The surviving nutcrackers apparently return to subalpine forests in the spring following mass migration and again assess the current year's cone crop (Vander Wall and others 1981). Thus, the size, mortality, and reproductive rates of nutcracker populations are likely closely associated with cone production of their preferred *Pinus* species. In early summer the nutcrackers act as seed predators, and the lost seeds are a price the trees pay for seed dispersal services later in the summer. Throughout the summer, nutcrackers also retrieve whitebark pine seed caches made the previous year. By mid to late August, nutcrackers are able to harvest intact seeds with brown seed coats; this appears to be the stimulus for caching seeds. In a good cone crop year, nutcrackers continue to store whitebark pine seeds until October or November. When cone crops are low to moderate, nutcrackers are in a race for the seeds against pine squirrels—the Douglas squirrel or chickaree (*Tamiasciurus douglasii*) of the Pacific ranges and widely distributed American red squirrel (*T. hudsonicus*)—that rapidly cut down cones as a winter food supply (see “Squirrels” section).

During fall, many nutcrackers move down to lower elevations or travel to other areas where they search for cones in other large-seeded conifers. Some birds spend the winter at lower elevations or moving up and down in elevation, retrieving caches and foraging in cones for remaining seeds, insects, and other foods. Nutcrackers begin courting as early as December and begin nest-building in March or earlier; young generally fledge in April or May (Tomback 1998). Most nutcrackers breed at mid-elevations, although some

breed within the subalpine zone. Adults feed young seeds retrieved from caches and some insect material. From May to early July, depending on snowpack depth, nutcrackers return to subalpine elevations, many in family groups, and retrieve caches made in previous years.

Continued decreased cone production capacity within declining whitebark pine forests, coupled with the tendency of nutcrackers to emigrate when cone crops are small, could result in fewer seed dispersal events in many whitebark pine forests. This outcome is especially of concern because high-mortality stands have lower cone abundance (McKinney and Tomback 2007), yet could harbor a higher frequency of rust-resistant alleles than similar stands with low mortality (Hoff and others 1994). Whether there exists a threshold of whitebark pine cone production necessary to elicit seed dispersal by nutcrackers, and whether the nutcracker-whitebark pine mutualism risks local and even regional disruption, are important questions for whitebark pine restoration planning. The following paragraphs are useful to address these questions and are excerpted from McKinney and others (2009).

The frequency of nutcracker occurrence in a whitebark pine forest is strongly associated with the number of available cones, and thus potential food-energy for the bird. The proportion of total observation hours with at least one Clark's nutcracker sighting increased linearly with increasing whitebark pine cone production across 24 research sites in the U.S. Rocky Mountains (McKinney and Tomback 2007; McKinney and others 2009). Nutcrackers are unlikely to occur when cone production averages fewer than 130 cones ha^{-1} . Furthermore, because nutcracker occurrence is strongly associated with cone production, it is also positively correlated with live whitebark pine basal area and negatively correlated with whitebark pine tree mortality. This suggests that measurable site variables that correlate to whitebark pine abundance, such as basal area and tree mortality, can be important indicators of cone production, and thus, bird occurrence. An often ignored component of cone production, also related to density, is an effective pollen cloud. When the number of reproductively mature conifers falls below 4 trees ha^{-1} , a sufficient pollen cloud is not present during female strobili receptivity for adequate fertilization, resulting in poor seed set or an increase in selfed seed (Robledo-Arnuncio and others 2004; Smith and others 1998) thereby limiting cone production available for seed caching.

Cone production is also a strong predictor of the probability of nutcracker seed dispersal. This relationship is consistent with what is known about nutcracker cognitive abilities as they relate to assessments of potential energy. It appears that by the time seed dispersal behavior begins (mid-August to early September), nutcrackers have decided whether or not to settle in an area, and this decision is largely determined by the magnitude of the existing cone crop. Moreover, there is a threshold of whitebark pine cone production below which there is a rapid decline in both the frequency of nutcracker occurrence and probability of seed dispersal. If cone production declines from 700 to 300 cones ha^{-1} , for example, the estimated likelihood of

nutcracker occurrence declines from 0.4 to 0.1, and probability of seed dispersal declines from 0.7 to 0.3 (McKinney and others 2009).

Nutcrackers typically place from 1 to 15 seeds within a cache, although rare caches with more than 30 seeds have been observed; average cache sizes are 3 to 5 seeds (Hutchins and Lanner 1982; Tomback 1978, 1982). Nutcrackers select diverse microsites for caching, burying caches 1 to 3 cm under various substrates, such as forest litter, mineral soil, gravel, or pumice. Nutcrackers place many caches at the base of trees near the trunk or exposed roots and these microsites tend to experience early snowmelt. Nutcrackers also cache next to fallen trees and rocks, in fallen trees, in open terrain, among plants, on rocky ledges, and in rock fissures. They place some of their caches in trees, tucking seeds in cracks, holes, and under the bark (Lorenz and others 2008; Tomback 1978). They will also cache whitebark pine seeds at and above treeline, among patches of conifers and in small depressions in open areas. Whitebark pine seeds may be cached near source trees or transported 32 km or farther, often to higher or to lower elevations, where whitebark pine cannot grow as well (Lorenz and others 2011; Tomback 1978). Studies have indicated that nutcrackers may transport seeds long distances, (piñon pine, for example, is dispersed 22 km; Vander Wall and Balda 1977). Nutcrackers appear to cache across a variety of terrain within their home range but also within communal storage areas, which are steep and south-facing slopes used by a local population of nutcrackers for caching. These slopes tend to be within 3 to 4 km of source trees.

Estimates of the numbers of whitebark pine seeds stored per bird within one season have been based on different assumptions and for different geographic regions, but vary from 35,000 seeds in about 9500 caches in the eastern Sierra Nevada, California (Tomback 1982), to 98,000 seeds in 30,600 caches in the Absaroka Mountains, Wyoming (Hutchins and Lanner 1982). With these estimates, a population of 25 nutcrackers would store from 95,000 to 750,000 caches (Tomback 1982). Seeds in unclaimed nutcracker caches germinate following snow melt and spring and summer rains, resulting in single seedlings or clusters of seedlings appearing throughout a caching area (Tomback 1982) (Figure 1.11). However, the nutcracker caching mode of seed dispersal has exerted selection pressure on both the seed structure and timing of germination in whitebark pine, as well as in other *Cembrae* pines (McCaughay 1993; McCaughey and McDonald 1993; Tillman-Sutela and others 2008). Both planting and natural experiments indicate that whitebark pine seeds typically require two or more winter dormancy cycles before they germinate (McCaughay 1993; Tomback and others 2001c). Therefore, seeds often do not germinate within the next growing season following seed caching, but rather two or more growing seasons later, and germination appears to correspond to higher moisture availability. Delayed germination

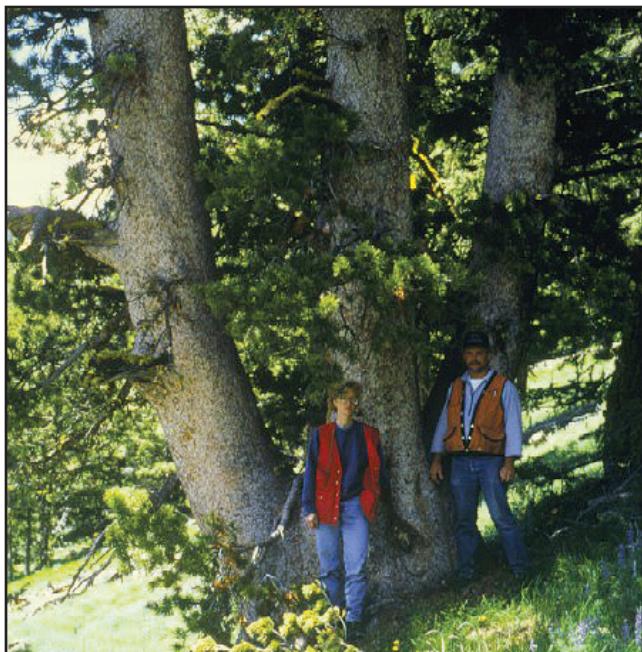


Figure 1.11. A cluster of whitebark pine seedlings that germinated from unretrieved seed cached by the Clark's nutcracker.

may result from the short growing season in the subalpine zone coupled with the fact that nutcrackers are caching a proportion of seeds before seed development is complete, resulting in underdeveloped embryos (Tomback and others 2001c). Seeds may also have physiological resistance to germination until available moisture is sufficient, which may be an adaptation to increase survival.

Seed dispersal by nutcrackers has diverse influences on the ecology of whitebark pine. For example, the sites selected by nutcrackers for seed caching, along with the environmental suitability of these sites for seed germination and seedling survival, determine where whitebark pine occurs on the landscape (Tomback 1983, 2001, 2005). The tendency of nutcrackers to cache seeds below and above the current elevational distribution of whitebark pine enables whitebark pine to respond rapidly to climate cooling or warming with changes in elevational and even latitudinal distribution. This influence is particularly important now, with climate warming predicted to cause an upward and northward shift in whitebark pine distribution (Tomback 2005; Tomback and Achuff 2010). Secondly, seed dispersal by nutcrackers is responsible for the genetic population structure of whitebark pine at several spatial scales (Tomback 2005). At the local level, the seed caching mode of seed dispersal results in a unique fine-scale genetic population structure. Because two or more whitebark pine seeds are often cached together, several seedlings from a cache may survive and produce a “tree cluster” growth form. This growth form appears to be a single tree with multiple stems that are tightly clustered or fused at the base or part way up the stem. Genetic studies confirm that most of these tree cluster growth forms contain distinct individuals, each arising from a different seed within a cache. Also, because nutcrackers harvest from several seeds to an entire pouch-load of seeds from a single tree, there is a high probability that the seeds within a cache are genetically related (Rogers and others 1999; Tomback and Linhart 1990; Tomback 2001, 2005). Finally, within a given area, nutcrackers cache at random with respect to caches already present, and with seeds from different source trees. Consequently, the seedlings among neighboring caches are usually unrelated, resulting in a random genetic pattern among clusters.

At the landscape and regional scale, we see the influence of nutcracker caching behavior as well on genetic population structure (Dimmick 1993; Hutchins and Lanner 1982; Tomback 1978). As mentioned, nutcrackers can disperse seeds over distances that are far greater than the mean distances traveled by wind-dispersed conifer seeds, and can easily move seeds over mountain passes and into adjacent drainages. Wind blows pollen over long distances as well. Consequently, researchers have found very little genetic differentiation among whitebark pine populations at both landscape and regional scales (Bower and others 2011; Brueckner and others 1998; Jørgensen and Hamrick 1997; Mahalovich and Hipkins 2011; Rogers and others 1999); this genetic differentiation is lower than found for most wind-dispersed conifer seeds (Brueckner and others 2001; Rogers and others 1999) or animal-ingested seeds (Hamrick and others 1992).

Squirrels

The North American red squirrel (*Tamiasciurus hudsonicus*) is a highly efficient, voracious consumer of conifer



Figure 1.12. The red squirrel competes with the Clark’s nutcracker for whitebark pine seeds.

seeds (Figure 1.12). Squirrels cut down conifer cones using their sharp teeth and strong temporal muscles and either eat seeds in situ or carry cones off to be stored for later use. Cone storage sites, called middens, are often large, conspicuous piles (for example, 1 m height by 10 m diameter) of cone debris that deeply cover the ground to the exclusion of living plants (Finley 1969) (Figure 1.13). Red squirrels are highly territorial, with the midden serving as the territorial hub, and home ranges are often small (less than 5 ha). They are thus central place foragers (Elliot 1974; Smith 1968)—a behavior describing the need to return to a particular place to hoard (consume or feed offspring) food. Due to their high foraging efficiency and central-place foraging lifestyle, red squirrels can greatly diminish cone crops at a local level (sometimes near 100 percent, Flyger and Gates 1982) and exert tremendous selection pressure on conifer cone morphology at a population level (Benkman and others 1984; Smith 1970). Moreover, red squirrels preferentially select tree species based on cone energy content (Smith 1970), foraging first on the highest energy species before moving on to the next highest energy species (Hutchins and Lanner 1982; Smith 1970). This adaptation is significant to the fate of whitebark pine because it has the greatest cone energy content of all sympatric species in U.S. northern

Figure 1.13. A squirrel midden site consisting of cached whitebark pine cones.



Rocky Mountain upper subalpine forests (whitebark pine = 27.7 Kcal cone⁻¹, next highest subalpine fir = 15.7 Kcal cone⁻¹) (Smith 1970; Tomback 1982). Indeed, red squirrels are the primary pre-dispersal seed predator of whitebark pine in the Rocky Mountains, taking more than 80 percent of the cone crop in some areas (Hutchins and Lanner 1982; McKinney and Tomback 2007).

Squirrels climb whitebark pine trees and rip or bite cones off the branches and let them drop to the ground (Finley 1969). The fallen cones are then collected and placed in middens for winter storage (Reinhart and Mattson 1990) (Figure 1.13). These middens can be in depressions on the ground, in hollowed logs, and around tree bases. Whitebark pine regeneration is rarely successful from middens because of (1) the deep depths that the squirrels store cones, (2) the high amounts of *Fusarium* spp. fungus in the discarded cone scales, and (3) the high use of cones by bears and other rodents. Optimum squirrel habitat within the whitebark pine zone consists of habitats with high overstory-basal area and high species diversity on moderate slopes (Podruzny and others 1999). Optimum stand characteristics that favor red squirrels are when total stand basal area is greater than 40 m² ha⁻¹ and whitebark basal area represents 15 to 50 percent of the total basal area (Mattson 2000).

Although red squirrels appear to favor whitebark pine seeds, their residence in whitebark pine forests (or any other type) is dependent on forest structure and tree species composition (Fisher and Bradbury 2006; Mattson and Reinhart 1997). Squirrels need to store enough cones to survive long boreal winters (Steele 1998); over time, this requirement is best met in mature mixed conifer species forests (often those with high basal area and tree species diversity) and not frequently met in forests where whitebark pine makes up greater than 50 percent of stand basal area (McKinney and Fiedler 2010). Squirrel energy requirements may be met in

whitebark pine dominant stands during high cone production years, but cone production of necessary quantities usually does not occur with enough frequency to maintain resident populations of squirrels. Therefore, red squirrel occurrence in dominant whitebark pine stands is often transient, with a higher number of cones eaten in situ and a lower number of active middens relative to mixed species forests (Mattson and Reinhart 1997; McKinney and Fiedler 2010). Thus, for the squirrel, a trade-off may exist between selection at the tree level (whitebark pine for its high energy seeds) and at the stand level (an annual cone crop large enough for population maintenance) (McKinney and Fiedler 2010).

Cone predation within a given forest is directly associated with red squirrel residential status. For example, in U.S. central and northern Rocky Mountain forests, the proportion of total squirrel detections comprised of active middens was positively and significantly correlated with whitebark pine pre-dispersal cone predation ($r = 0.65, p < 0.05$) (McKinney and Fiedler 2010). As cone production increases, squirrel predation also increases at both tree and stand levels; however, the strength of the relationship between production and consumption is dependent on the degree to which whitebark pine is a dominant component of the stand (McKinney and Fiedler 2010; McKinney and Tomback 2007). Pre-dispersal cone predation decreases with increasing proportion of total stand basal area comprised of whitebark pine. Therefore, as whitebark pine becomes more of a dominant component of canopy structure, conditions for squirrel residence become less favorable and cone predation declines.

In summary, whitebark pine-dominated forests, such as climax forests, are sub-optimal squirrel habitat. Conversely, red squirrels thrive in mixed species forests containing whitebark pine. The reason for the disparity between the two forest types in red squirrel residential status appears due to a higher degree of uncertainty in annual cone crops (Reinhart

and Mattson 1990). For example, during a three year study, average year-to-year differences in whitebark pine cone production within sites was 87 percent relative to mean cone production (the absolute difference between two years divided by the mean of the years, multiplied by 100) (McKinney and Fiedler 2010). Higher uncertainty appears to be directly related to lower diversity of conifer species because of the greater chance of cone crop failure. Squirrels still, however, prefer whitebark pine cones to the cones of sympatric conifers and will disperse into pure to nearly pure whitebark pine stands to harvest cones, especially after disturbances such as wildfire (McKinney and Fiedler 2010; McKinney and Tomback 2007). Whitebark pine-dominant stands (for example, stands with greater than 50 percent of total basal area comprised of whitebark pine) will have a larger proportion of their annual initial cone crop available for seed dispersal relative to mixed conifer species stands.

Genetics

A key component of any whitebark pine restoration program is the planting of rust-resistant seeds or seedlings for reforestation (Keane and Parsons 2010b; Mahalovich and Dickerson 2004; Mahalovich and others 2006). However, the wide movement of seeds away from the source of collection increases the risk of maladaptation, which could lead to reduced growth and survival (Campbell 1979; Mahalovich 2012). Seed transfer should be guided by natural levels of genetic variation and local adaptation in quantitative traits specific to the species in question (Morgenstern 1996; Hufford and Mazer 2003; McKay and others 2005). Understanding genetic structure is also necessary for predicting the possible effects of climate change (St. Clair and others 2005). Current predictions of future climates may complicate seed transfer. A diverse mixture of seed sources can balance suitability of individuals to current and future environments (Bower and Aitken 2008). An individual's genetic makeup, in interaction with its environment, determines the amount of variation in measurable characters (quantitative traits) such as growth, survival, tolerance to biotic and abiotic stress, and disease resistance. Genetic variation is quite important because it provides the raw material for adaptation to new environments. The amount and structure of genetic variation within a population are influenced by many factors including gene flow, mutation, genetic drift, and selection (Frankham and others 2002). Knowledge of a species' genetic structure is essential to ensure that management activities do not adversely affect the amount and patterns of genetic diversity.

Genetic variation and population structure may be assessed with two types of traits: (1) molecular markers controlled by a single gene and (2) quantitative traits controlled by many gene loci. Molecular markers include allozymes, which differ in amino acid sequence and can be visualized with gel electrophoresis, and differences in DNA (Deoxyribonucleic acid) sequence fragments. DNA fragments that are used as markers are often in sections of DNA that do not control a specific gene (non-coding) and therefore

are not acted upon by natural selection (they are selectively neutral). Thus, while they are useful to distinguish distinct breeding groups, the genetic differences do not imply differences in adaptation (Reed and Frankham 2001). To examine potential adaptive variation other methods must be used.

Genecology is the study of genetic variation and its relationship to environmental variation. Differences in seed sources grown in a common environment are thereby attributed to genetics, and when this genetic variation is correlated with the physiographic (for example, latitude, longitude, elevation, and distance from the coast) and climatic variables (temperature, rainfall, and growing season) of the seed source location, it may indicate a trait has responded to selection and has adaptive value. The amount of differentiation among seed sources facilitates ascribing a species' adaptive strategy from low (generalist), moderate (intermediate) to high (specialist). A direct management application of these types of studies is the development of seed transfer guidelines. Quantitative traits, such as growth, survival, biomass production, and biotic and abiotic stress tolerance, are generally considered better indicators of adaptation and are measured on trees growing in the field (usually in seedling common gardens or field test sites). In these types of tests, individuals from multiple geographic origins are grown together in the same environment. The organization of genetic differences among populations (genetic structure) of a species can be estimated by using both molecular markers and quantitative traits. Since quantitative traits are usually subject to the effects of natural selection, while molecular markers are usually not, the difference between these measures of genetic structure is often taken as evidence of natural selection resulting in local adaptation (Merila and Crnokrak 2001; Spitze 1993).

Genetic variation within whitebark pine has been assessed in several studies using neutral molecular markers at scales ranging from a single watershed to most of its range, and whitebark pine appears to have lower levels of genetic differences among populations than other wind-dispersed pines. Several allozyme studies assessing genetic variation and differentiation found that levels of whitebark pine genetic diversity (expected heterozygosity) were within the range of other stone pines (*Pinus* subsection *Cembrae*: Politov and others 1992; Jørgensen and Hamrick 1997), but somewhat below that of wind-dispersed pines in the subgenus *Strobus* (Bruederle and others 2001; Ledig 1998). Only about 4.9 percent of the measured genetic variation in allozymes is due to genetic differences among populations, while the vast majority of variation resides within populations (Bower and others 2011; Bruederle and others 1998; Jørgensen and Hamrick 1997; Krawkowsky and others 2003; Mahalovich and Hipkins 2011; Stuart-Smith 1998; Yandell 1992). This estimate of population differentiation is slightly higher than the mean for the four other *Cembrae* pines (4.6 percent) (Belokon and others 2005; Goncharenko and others 1993a, 1993b; Krutovskii and others 1995; Potenko and Velikov 1998, 2001; Tani and others 1996) and is consistent with wind-dispersed pines that typically have less than 10 percent

of their genetic diversity among populations (Ledig 1998). Thus, populations of bird-dispersed pines do not appear to be strongly differentiated using putatively neutral molecular markers. Additionally, Jorgensen and Hamrick (1997) reported that populations that have colonized areas covered by Pleistocene glaciers were more differentiated than populations from non-glaciated areas. Populations in the northern (western British Columbia), eastern (Rocky Mountains), and southern (Oregon and California) regions of the species' range are differentiated for monoterpenes (Zavarin and others 1991), allozymes (Yandell 1992), and organelle DNA (Richardson and others, 2002b).

The population genetic structure of whitebark pine is strongly affected by seed dispersal by Clark's nutcracker. In general, based on molecular markers, whitebark pine appears to have lower levels of genetic differences among stands than most wind-dispersed pines. Caching of seeds by the Clark's nutcracker was first implicated as the cause of the "tree cluster" or multi-stemmed growth form of whitebark pine in the early 1980s (Lanner 1982; Tomback 1982). Linhart and Tomback (1985) and Furnier and others (1987) found more than two genetically distinct individuals in the majority of multi-stemmed clumps, indicating that these stems had arisen from different seeds. Furnier and others (1987) also found that individual stems within clumps were often related, presumably because multiple seeds from the same tree or even the same cone were cached together. While stems within clumps were often related, there was little genetic structure among clumps, with the distance among them not correlated to how closely they were related. These results were supported by Rogers and others (1999), who found little genetic differentiation among watersheds, but also found that differentiation between elevations was moderate and differentiation within thickets of clumps was strong. Individuals within krummholz thickets often shared one or both parents, most likely because of the seed-caching behavior of the Clark's nutcracker.

In whitebark pine populations, inbreeding depression may result from the tendency of whitebark pine stems to grow in clusters of clumps of genetically related individuals (Figure 1.11). Inbreeding depression and reduced fitness typically accompany an increase in homozygosity in progeny that comes from matings among relatives. From two populations in southern British Columbia, Krakowski and others (2003) reported an inbreeding rate for whitebark pine of 27 percent, presumably as a result of the growth structure of clumps of related individuals. This rate is considerably higher than for most wind-pollinated conifers, which typically have inbreeding rates of less than 10 percent (Ledig 1998). Bower and Aitken (2007) confirmed the inbreeding rate for these populations; however, they reported that inbreeding rates ranged from 2 to 12 percent from five populations in Oregon and Montana. The areas where the Oregon and Montana populations were sampled were not glaciated at the last glacial maximum, so the higher level of inbreeding in the southern British Columbia populations may reflect postglacial colonization patterns and processes. Bower and Aitken (2007) also reported little evidence of inbreeding on quantitative traits,

with only one trait (biomass) in only one geographic region (southern British Columbia) showing a reduction that was correlated with the level of inbreeding. Therefore, relative to other threats faced by whitebark pine, inbreeding depression does not appear to be of great concern.

DNA markers from mitochondria and chloroplasts have also been used to study population genetic structure and biogeographic patterns of whitebark pine (Richardson and others 2002a). The DNA of these organelles is inherited maternally and paternally, respectively. Microsatellites (tandemly repeated DNA sequences) were used to assess genetic structure from 41 populations that covered most of the species' range. Richardson and others (2002a) found that whitebark pine populations clustered by genetic similarity into three main groups: Sierra Nevada, Yellowstone, and all others (northern Cascades, northern Idaho, central Idaho, and southern Oregon); the level of genetic differentiation (0.046) among these three groups was similar to the values reported from allozyme studies. Based on the geographic patterns observed with the DNA markers, the authors inferred three glacial refugia—southern Oregon, central Idaho, and the Yellowstone area—with a subsequent post-glacial colonization route northward into Canada and a secondary contact zone between the Oregon and Idaho populations in the Washington Cascades. This probable secondary contact zone was confirmed with a finer-scale sampling study at the location of the proposed contact zone (Richardson and others 2002b). This contact zone is supported by results of a recent molecular marker study of Oregon and Washington populations, which separated "northern" and "southern" populations here, but also showed that Olympic peninsula populations are genetically distinct from all other populations (Bower and others, unpublished data).

A few studies have assessed genetic variation in quantitative traits such as cold hardiness, growth, phenology, stem form, and disease resistance. Mahalovich and others (2006) found significant differences among sources for late winter cold injury (cold hardiness), survival, height growth and blister rust resistance, with most of the differentiation attributed to sources from the GYA. Cold hardiness and rust resistance show opposite geographic patterns, with sources in the northwest having higher rust resistance and lower cold hardiness, and southeastern sources having lower rust resistance and higher cold hardiness. Most trait correlations are favorable, and unfavorable correlations with cold hardiness can be managed through zoning, a restricted selection index (Mahalovich 2012; Mahalovich and others 2006), or site-specific planting prescriptions to avoid frost pockets and swales (McCaughay and others 2009). Family heritabilities for survival, height, cold hardiness, and blister rust resistance are moderate to high ($h^2_F = 0.68\text{--}0.99$). Gentle clines in elevation for height and rust resistance and moderate clines in cold hardiness characterize whitebark pine as having a generalist to intermediate adaptive strategy in the Northern Rockies (Mahalovich 2012). Moreover, adaptation to heterogeneous environments does not appear to be as strongly related to phenotypic plasticity as in western white pine.

Until whitebark pine seed orchards reach reproductive maturity, reforestation planting should be met with cone collections from rust-resistant areas, as identified by their progeny in rust screening trials. Similar to other conifers in the northern Rockies, whitebark pine is likely to have different adaptive strategies and response to geo-climatic traits in various parts of the species range; therefore, seed transfer is not approached from a “one size fits all” perspective. Both population structure in molecular traits (Mahalovich and Hipkins 2011) and patterns of genetic variation in key adaptive traits (Mahalovich 2012; Mahalovich and others 2006) characterize seed transfer in the Inland West (Idaho, Montana, Nevada and Wyoming) as follows:

- Geographically broad ($\pm 1.85^\circ$ latitude, $\pm 2.15^\circ$ longitude) characterized by five seed zones.
- Within seed zones, proven rust-resistant seed sources are top priority, followed by phenotypically rust-resistant sources waiting genetic testing in rust screening trials.
- Where cold hardiness is problematic (McCaughey and others 2009), transfer is further restricted to ± 245 m in elevation.
- Rather than transferring rust-resistant sources large distances across zones and traversing as much as 1600 m in elevation, risking maladaptation or outright mortality, correlation breakers (sources exhibiting both rust resistance and cold hardiness) should be utilized within a seed zone (Mahalovich and others 2006).
- In anticipation of climate change, transfer of rust-resistant seed sources should be unidirectional from colder (northerly latitude, higher elevations, or both) to milder climates within the local temperature envelope and seed zone.

Bower and Aitken (2006) found that the level of cold hardiness varies throughout the year from below -70°C in the winter to -9°C in the summer. Acclimation and de-acclimation to cold often occurs rapidly over a period of two to three weeks in the fall and spring, respectively; however, even during the period of active shoot elongation, whitebark pine shows greater hardiness to cold than most conifers (see also Mahalovich and others 2006). Geographic regions differed in cold hardiness in all seasons except in winter. Interior and northern sources were higher and California was lower in hardiness in the fall, with opposite patterns in the spring. Bower and Aitken (2008) proposed seed transfer guidelines based on population variation in quantitative traits:

- Seeds can be moved without substantial risk of maladaptation from seed collection site to planting sites differing up to 1.9°C in mean temperature of the coldest month in the northern region, and 1.0°C in the Rocky Mountain region; however, maladaptation could still occur if the seeds are not from a rust-resistant source.
- Differences in mean temperature of the coldest month correspond to approximately 4.6° latitude or 505 km for the northern region, and 320 m in elevation in the

Rocky Mountain region based on a 20 percent risk of maladaptation; however, late winter cold hardiness in a larger representative sample from the Rocky Mountain region (Mahalovich 2012) restricts elevation transfers to only 245 m.

- Where blister rust resistance has been demonstrated in rust screenings, it may be necessary to move seeds farther to take advantage of this resistance. However, this increases the risk of maladaptation, which must be weighed against the need for restoration (see previous discussion on correlation breakers).
- In the southern region, the lack of correspondence between the seedling and climatic traits means that seeds can be freely moved within this region; however, movement between mountain ranges is to be avoided.
- Except for the Inland West populations, seed movement should be unidirectional from milder to colder climates within the local temperature envelope to account for predicted warming due to climate change.

Ectomycorrhizal Fungi

Whitebark pine, like other pines, requires ectomycorrhizal (ECM) fungi for survival in nature (Read 1998; Mohatt and others 2008); this beneficial biotic factor should be taken into account in management strategies to help ensure establishment, maintenance, and conservation of this pine species.

There are 7000 to 10,000 species of ECM fungi associated with trees and woody shrubs (Taylor and Alexander 2005). Whitebark pine hosts only a small subset currently assessed at fewer than 50 species (Mohatt and others 2008; Molina and Trappe 1994). These ECM fungal species can be grouped ecologically into (1) generalists that associate with many trees such as pines, spruce, and fir (*Amphinema*, *Cenococcum*, *Piloderma*, and thelephoroid fungi); (2) associates of high-elevation western conifers (*Cortinarius*, *Russula*, *Lactarius*, *Tricholoma*, *Hygrophorus*, and fungi associated with snowbanks); and (3) specialists specific for pines such as five-needle pines or stone pines (*Suillus*, *Rhizopogon*, and *Chroogomphus*) (Cripps and Antibus 2010). The last group (the suilloids) has a long history of association with stone pines on a hemispheric scale (Wu and others 2000). Suillloid fungi are host-specific on some level; some are restricted to pines, five-needle pines, or stone pines (Grubisha and others 2002; Moser 2004). Several host-specific suillloid fungi occur with whitebark pine, and there is a risk that this important group of fungi will decline in western North America as whitebark pine declines (Mohatt and others 2008). ECM fungi are successional; some occur with young trees and others with mature trees. However, suillloid fungi appear to span all tree ages.

The conservation of species and genetic diversity in ECM fungi are important because these fungi (as species or strains) vary in host specificity; soil preference; host age requirements; dispersal strategies; ability to enhance nitrogen

(N) or phosphorus (P) uptake; types of N and P accessed; and protective abilities against pathogens, drought, heavy metals, and soil grazers (Tedersoo and others 2009). The ECM community as a whole provides a vast array of benefits to trees and forests.

Negative Impacts on ECM Fungi

Practices and impacts potentially threatening to the maintenance of ECM diversity in the soil include tree cutting, soil removal, mechanical disturbance, soil compaction, erosion, mining activities, liming, N-deposition, fertilization, high-severity fire, reduction of tree age diversity, and promotion of certain grasses. Additional detrimental effects may result from removal of certain understory or reservoir plants, woody debris, nurse trees, and other microsite components (reviewed in Wiensczk and others 2002). In general, these practices should be minimized to maintain high ECM fungal diversity in the soil.

If hosts are lost or removed, studies suggest that ECM viability in the soil declines rapidly after two to three years (Haggeman and others 1999). Recovery of ECM communities from cutting, thinning, and burning may take decades (Visser 1995). It is not known how long whitebark pine ghost forests maintain viable ECM propagules (spores). Adverse management activities should be particularly minimized around “plus” trees and in relatively intact mature forests with healthy seedling regeneration. The impact on soil microbes under the canopy from Carbaryl and other chemicals used to prevent host attack by mountain pine beetles needs investigation.

Fire can affect ECM communities in soil with varying results, depending on the severity of the fire, forest type, and other factors (Cairney and Bastias 2007). High-intensity fires may eliminate ECM communities because of the deep depth of heating in the soil, the loss of original tree hosts, and changes in abiotic conditions, including an increase in soil surface temperature (Neary and others 1999). A comparison of the ECM fungi on whitebark pine seedlings in a severe burn and adjacent unburned forest revealed a shift in ECM fungal species, but the functional significance of this shift is unknown (Trusty and Cripps 2010). Five years after the fire, seedlings in the burn were partially colonized by suilloids, likely due to the availability of a nearby inoculum source (adjacent unburned forest), the presence of vectors (deer and small mammals) that import inoculum, and a management plan that included planting one year after the burn (Trusty and Cripps 2010). The adverse effects of long delays before planting should be considered for severe burns (Wiensczk and others 2002). In contrast, there is no evidence that light burns affect ECM fungi in whitebark pine forests, but a loss of seedlings could reduce ECM diversity due to the successional nature of these fungi. While some fungal species survive and rapidly re-colonize after fire, others do not, and removal of the duff layer can be problematic for some ECM fungi (Smith and others 2005).

Strategies for Maintaining ECM Fungi

Whitebark pine management strategies should consider factors known to help maintain diversity of ECM fungi in the soil. These include maintaining an intact forest floor, promoting the continuous presence of living host trees, and maintaining multiple age forests (Wiensczk and others 2002). In particular, maintenance of soil organic matter, nurse trees, logs (not stumps), and other microsite components may enhance fungal diversity (Tedersoo and others 2008). For whitebark pine, we know that ectomycorrhizae occur in soil as well as in nurse logs (Cripps and others 2008). Microsites play a significant role in whitebark pine seedling establishment in general (McCaughey and others 2009). Management strategies that promote continuous host presence also function to preserve spore banks in soil (Kjöller and Bruns 2003). Since ECM fungi are successional, a mixed host age structure helps maintain fungal diversity for the next generation of trees. When continuity of the host is lost and plantings do not occur before spore banks become non-viable, it is possible that host-specific fungi will be lost.

Special consideration should be given to identification and preservation of ECM diversity “hot spots” and reservoirs of five-needle pine ECM fungi (the suilloids) in whitebark pine forests. Whitebark pine may derive some competitive advantage from these specialist fungi that do not form mycorrhizae with lodgepole pine, spruce, or fir. *Suillus* spp. associated with whitebark pine are restricted to five-needle or stone pines (Cripps and Antibus 2010). Host restriction is less clear for the *Rhizopogon* spp., which are also found with whitebark pine. Suilloids are important as ECM fungi that occur on all tree age classes from young seedlings to mature trees (Visser 1995) and because they have been used successfully for restoration purposes with other pines (Steinfeld and others 2003). They are also important in the food chain (Izzo and others 2005; Johnson 1996). *Rhizopogon* produces reproductive structures underground and is dependent on mammals (for example, squirrels, deer, and bears) for spore dispersal, while *Suillus* spores are dispersed primarily by wind but also by animals (Ashkannejhad and Horton 2005). Practices that help maintain mammal vectors also promote these plant-fungal associations.

A few studies have examined planting whitebark pine seedlings with understory plants as a revegetation strategy (Mellman-Brown 2002; Perkins 2004). Some, such as *Arctostaphylos* spp., are potential reservoir plants that could share certain ECM fungi with pine seedlings. *Arctostaphylos* spp. are known to host five-needle pine ECM fungi for European stone pine (Krpata and others 2007) and limber pine (Cripps, personal observation). However, *Arctostaphylos* spp. are uncommon beneath whitebark pine in many areas. In one study, plant competition reduced survival of *Pinus cembra* seedlings planted in *Arctostaphylos* spp. (Haselwandter 1997); however, *Arctostaphylos* spp. as an understory benefited Douglas-fir seedling regeneration (Horton and others 1999). A *Vaccinium* spp. understory may

enhance seedling survival (Perkins 2004), but there is no definitive evidence to date that *Vaccinium* spp. share ECM fungi with whitebark pine seedlings; *Vaccinium* spp. typically host ericoid fungi.

The following is a list of management actions that can improve ECM diversity and accessibility:

- Minimize practices detrimental to soil microbes, as previously mentioned.
- Enhance practices that preserve the diversity of native ectomycorrhizal (ECM) fungi in soil.
- Plant seedlings near inoculum sources (living whitebark pines).
- Plant seedlings within a year after disturbances before ECM viability declines.
- Assess soils to determine if native ECM fungi are present.
- Inoculate nursery seedlings with *native* five-needle pine ECM fungi when lacking.
- Use native ECM fungal inoculum from the same or adjacent seed transfer regions.
- Monitor ECM colonization of planted seedlings.
- Minimize importation of alien ECM fungi (commercial inoculum or nursery fungi).
- Conserve and preserve suilloid fungi specific to five-needle pines.

Inoculation of Nursery-Grown Seedlings

Inoculation of nursery seedlings with native fungi should be considered when soils lack appropriate ECM fungi and when it is unlikely that soils will be imported in a timely manner (Brundrett and others 1996; Khasa and others 2009). Areas at high risk for lack of ECM fungi for whitebark pine are ghost forests, severe burns, and planting areas not previously inhabited by whitebark pine. This is particularly true for areas a distance from an inoculum source with few/no animal vectors present. Soils can be assessed for the presence of appropriate native ECM fungi through observation or with bioassay techniques (planting seedlings in native soils under greenhouse conditions). The use of site-adapted, host-specific native fungi that occur with whitebark pine is highly recommended as inoculum. This excludes the use of generally available commercial inoculum containing generalist fungi or those that promote lodgepole pine, spruce, fir, and other conifers.

Suillus spp. have been used successfully to regenerate stone pines in Europe for 50 years (Weisheitner, personal communication). Inoculation and colonization of whitebark pine seedlings with native fungi has been successful under greenhouse conditions, and *Suillus* spp. were the most vigorous colonizers for whitebark pine in greenhouse studies (Cripps and Grimme 2010). Fungal strains used in inoculation should be restricted to the appropriate seed transfer region or larger adjacent region (Sierra Nevada and northern

Rocky Mountains). The transfer of exotic and alien ECM fungal species (including those in commercial inoculum) to whitebark pine areas should be minimized. The goal of inoculation is not to enhance growth of the pine, but to increase its survival and overall health. If possible, inoculated seedlings should be monitored to gain information. Some fungi specific for whitebark pine can be preserved in culture for at least several years by various methods (Cripps and Grimme 2009).

There is no evidence that ECM fungi can directly mitigate the impacts of whitebark pine blister rust or mountain pine beetles. These detrimental organisms primarily affect the above-ground portion of trees, whereas ECM fungi occur on roots. However, appropriate ECM fungi are known to improve the general health of plants, enhance drought tolerance (a factor in beetle kill), and promote resistance to other pathogens. ECM fungi are critical to sustaining whitebark pine forests, and strategies that promote their continued existence should be considered.

Fire Regimes

Whitebark pine fire regimes are quite complex and variable in space and time, but in general, all three types of fire severities describe whitebark pine fire dynamics: non-lethal, stand-replacing, and mixed-severity (Arno and Hoff 1990; Barrett 2008; Campbell and others 2011; Larson and others 2010; Morgan and others 1994b; Murray 2008; Siderius and Murray 2005). Some whitebark pine stands may experience low-intensity, non-lethal surface fires (sometimes called underburns or low-severity fires) because of sparse surface and canopy fuel loadings and unique topographical settings (Figure 1.14). These sites are mostly found in the southern parts of the species range in the Rocky Mountains or on high, dry ridges and may represent only a small portion of existing whitebark pine forests (less than 10 percent) (Keane and others 1994; Morgan and others 1994b). Whitebark pine can survive low-intensity surface fires better than most of its competitors, especially subalpine fir, because it has somewhat thicker bark, higher and thinner crowns, and deeper roots (Arno and Hoff 1990; Morgan and Bunting 1990; Ryan and Reinhardt 1988). As a result, non-lethal surface fires have historically maintained whitebark pine dominance in the overstory and prolonged whitebark pine cone production by stalling succession (Keane 2001b).

The more common, mixed-severity fire regime is characterized by severities that are highly variable in space and time, creating complex patterns of tree survival and mortality on the landscape (Murray and others 1998; Romme and Knight 1981; Siderius and Murray 2005) (Figure 1.15). Mixed-severity fires can occur at 60- to more than 300-year intervals and sometimes over 500 years, depending on drought cycles, fuel conditions, landscape burn history, and high wind events (Arno and Hoff 1990; Morgan and others 1994b; Walsh 2005). Individual mixed-severity fires can be non-lethal surface fires with differential



Figure 1.14. A low-intensity, non-lethal surface fire burning in a whitebark pine forest. The species is able to survive some of these fires because of high crowns and deep roots. However, the thin bark makes it susceptible to mortality when intensities are higher.



Figure 1.15. A common pattern created by mixed-severity fire in Yellowstone National Park.

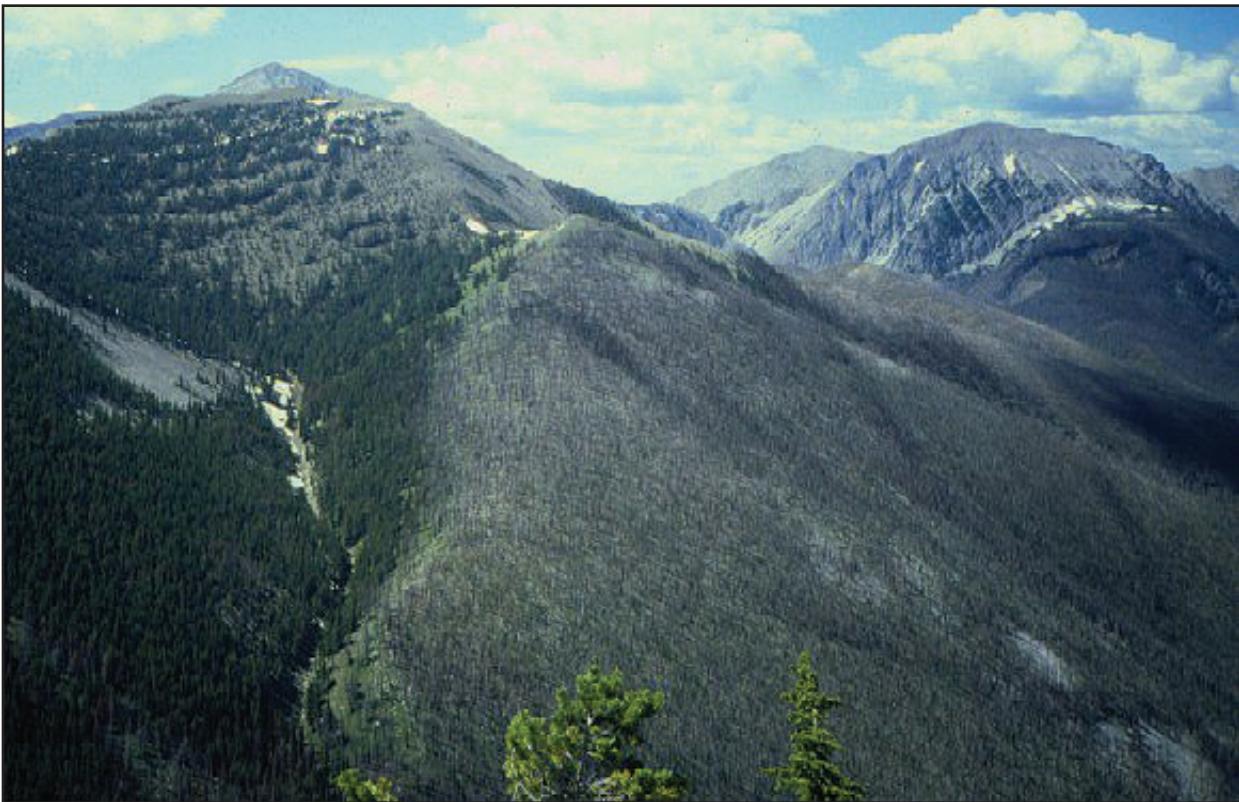


Figure 1.16. Large burned areas created by stand-replacement fires in whitebark pine.

mortality, variable mortality stand-replacement fires, and, most often, fires that contain elements of both (Morgan and others 1994b). Sometimes fires burn in sparse ground fuels at low-severities, killing the smallest trees and the most fire-susceptible overstory species, often subalpine fir (Walsh 2005). Severities increase if the fire enters areas with high fuel loads or if there are high winds or drought conditions because these situations facilitate fire's entrance into tree crowns, thereby creating patches of fire-killed mortality (Lasko 1990). Burned patches are often 1 to 30 ha in size, depending on topography and fuels, and these openings provide important caching habitat for the Clark's nutcracker (Norment 1991; Tomback and others 1990) (Figure 1.15).

Many whitebark pine forests in the northern Rocky Mountains, Cascades, and Greater Yellowstone Area experience periodic large, stand-replacement fires that occur at long time intervals (greater than 250 years) (Figure 1.16). Stand-replacement fires also occurred within mixed-severity fire regimes but as infrequent events (Morgan and Bunting 1989; Romme 1980). These fires are usually wind-driven; often originate in lower, forested stands (Murray and others 1998); and create large burned patches on the landscape that may be distant from tree seed sources (Beighley and Bishop 1990) (Figure 1.16). Whitebark pine has an advantage over its competitors in that it readily colonizes large, stand-replacement burns because its seeds are transported great distances by Clark's nutcracker (Lorenz and others 2008; Tomback 1982, 2005). Nutcrackers can disperse whitebark

pine seeds up to 100 times farther (over 10 km) than wind can disperse seeds of subalpine fir and spruce (McCaughay and others 1985; Tomback and others 1990, 1993). Since nutcrackers often prefer open sites with many visual cues for seed caching, stands burned by mixed-severity or stand-replacement fire provide favorable sites for nutcracker caching and competition free seedling growth (McCaughay and Weaver 1990; Sund and others 1991; Tomback 1998). Murray and others (1995) found that larger burns were associated with greater volume per hectare of whitebark pine as compared to smaller burns in the Bitterroot Mountains.

Whitebark pine benefits from wildland fire because it is better adapted to surviving fire and also to regenerate in burned areas than associated shade-tolerant trees (Arno and Hoff 1990). Without fire, most seral whitebark pine forests would be successional replaced by subalpine fir or some other shade-tolerant high-elevation species. Fire, whitebark pine, and the Clark's nutcracker form an important high-mountain ecological triangle. Virtually all whitebark pine regeneration comes from nutcracker caches, where unclaimed seeds eventually germinate and grow into seedlings. These seeds are often cached in open, pattern-rich landscapes that facilitate efficient retrieval of seeds, and these landscapes are commonly created by wildland fire. Once whitebark pine seeds cached in burned areas have germinated, those seedlings have a good chance to grow into mature trees because they can grow free from competition for a long time. Remove any one of the sides of the triangle and this keystone ecosystem is lost.

Importance of Whitebark Pine

Whitebark pine occurs in seven western states and two Canadian provinces; it has the broadest latitudinal distribution of any five-needle white pine in the United States and Canada (Tombback and Achuff 2010). In the northern Rocky Mountains alone, whitebark pine communities represent about 10 to 15 percent of the forested landscape (Arno 1986). More than 95 percent of whitebark pine in the United States occurs on public lands, including National Forests, Wilderness Areas, and National Parks. The three largest Wilderness Areas in the western United States each comprise about 25 to 50 percent potential whitebark pine forest habitat (Keane 2000).

The importance of whitebark pine, however, transcends its widespread occurrence in that, throughout its distribution, whitebark functions as both a keystone and foundation species (Tombback and Achuff 2010; Tombback and others 2001a). Keystone species promote community diversity disproportionately in relation to their abundance through interactions with other species (Mills and others 1993; Soulé and others 2003). Foundation species are regarded as a single species that influences community structure by "...creating locally stable conditions for other species, and by modulating and stabilizing fundamental ecosystem processes" (Dayton 1972; Ellison and others 2005). Whitebark pine assumes these ecological roles as a result of the following traits: large, nutritious seeds; seed dispersal by Clark's nutcrackers; hardy, robust seedlings; and tolerance for cold, windy sites (McKinney and Tombback 2011). This section details the value of whitebark pine to society.

Ecological Processes and Ecosystem Services

Whitebark pine promotes regional biodiversity as a keystone species in several ways (for reviews, see Tombback and Achuff 2010; Tombback and others 2011). Its large seeds are an important wildlife food, supporting a community of granivorous mice, squirrels, and birds, as well as grizzly and black bears (Ferner 1974; Hutchins 1994; Hutchins and Lanner 1982; Mattson and others 1991; Tombback 1978, 1982; Tombback and Kendall 2001). Whitebark pine grows at the highest forest elevations, providing habitat and nesting sites for many diverse species including grouse, deer, elk, birds of prey, foxes, coyotes, and other predators (Tombback and Kendall 2001; Tombback and others 2001a). Across its broad latitudinal distribution and eastern and western ranges, whitebark pine encompasses a variety of forest communities with different associates, successional stages, and understory diversity (Arno 2001; Arno and Hoff 1990; Tombback and Kendall 2001).

Whitebark pine promotes biological community development and stability after disturbance and within climax and treeline communities. Because nutcrackers readily cache seeds in burned or otherwise disturbed terrain and in large forest openings, whitebark pine regeneration occurs rapidly. The seedlings tolerate harsh conditions and poor

soils, although regeneration may be delayed by droughty conditions (Tombback 1986; Tombback and others 1990, 1993). As whitebark pine seedlings grow, they provide shade and favorable micro-environments for the establishment of other conifers and understory vegetation (Callaway 1998). Furthermore, whitebark may act as a "nurse" tree on harsh sites in the subalpine zone, protecting smaller spruce and fir from strong winds and ice abrasion (Callaway 1998). In the Rocky Mountain Front of Montana, east of the Continental Divide, treeline conditions are particularly extreme. There, the microsites selected by nutcrackers for caching seeds combined with the hardiness of whitebark pine seedlings result in the establishment of solitary whitebark pine trees that moderate wind effects on their leeward side and enable the establishment of other conifers, resulting in the development of tree islands. Consequently, whitebark pine is the most common species to initiate tree islands in these harsh environments (Resler and Tombback 2008).

The higher mountains of the world are increasingly recognized as important "water towers" that play crucial roles in supplying water for downstream agriculture and human consumption (Messerli and others 2004). Throughout much of its broad range, whitebark pine inhabits the highest elevations where other conifers are often sparse. Whitebark pine forests and treeline communities stabilize and shade snowpack, thus regulating melt-off and downstream flow; stabilizing loose, rocky soils; and reducing erosion (Arno and Hammerly 1984; Arno and Hoff 1990; Farnes 1990; Hann 1990).

Recreation

Each year, tens of millions of people visit whitebark pine forests in National Parks, National Forests, Wilderness Areas, and ski areas (Cole 1990). Murray (2005) estimated that nearly 2.5 million mountain tourists encounter whitebark pine stands every year in Oregon alone. These picturesque forests often surround high-elevation lakes or viewpoints, where most day-hikes end, and treeline whitebark pine communities accompany trails leading up to and down from mountain passes. The most common recreational activities in and around whitebark pine forests are horsepacking, skiing, hiking, camping, and fishing (Figure 1.17). Snowmobiling, four-wheel driving, and mountain biking are additional forms of recreation providing access to these scenic, high-elevation communities. Whatever the activity, visitors to whitebark pine generally (1) enjoy and appreciate the high-mountain scenery, (2) assume the forests have not been altered by humans, and (3) have sought out these forests for their remoteness and isolation. Studies have shown that intensive recreational use of high-elevation areas, particularly through hiking, use of pack stock, and creation of campsites, has resulted in forest degradation (Cole 1990). Guidelines for responsible recreation in these areas and enforcement of these guidelines would reduce further impacts.

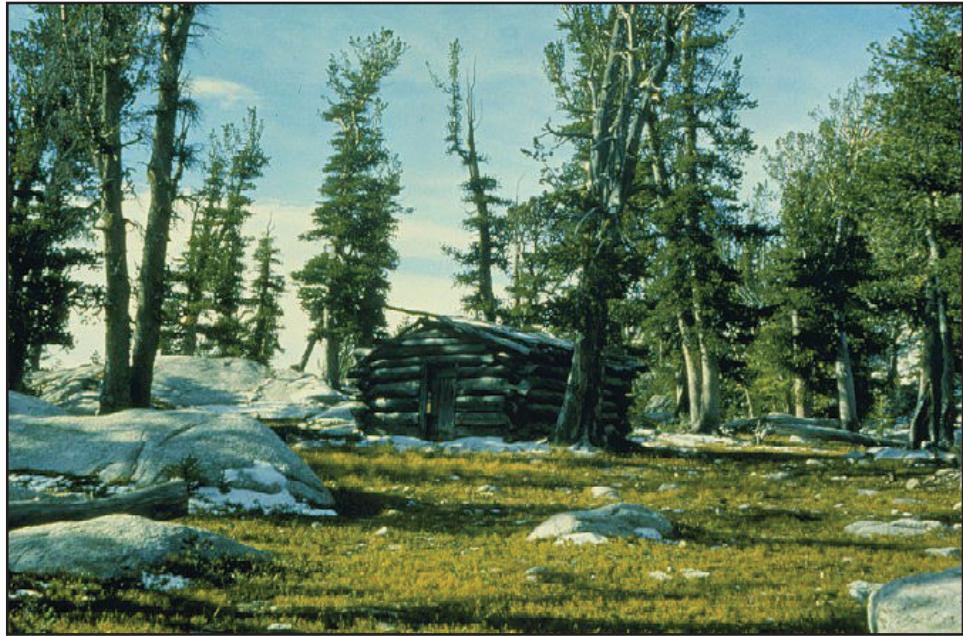


Figure 1.17. Park-like stand of whitebark pine trees on a climax site that is a popular hiking destination. (Photo courtesy of Steve Arno.)

Cultural Heritage

In years of good cone production, whitebark pine seeds were harvested by many Native Americans (First Peoples) of the United States and Canada. The seeds were traditionally served as an important winter food source, eaten raw or roasted. Seeds were also cooked, mashed, and mixed with service berries (Moermond 1998). For example, the interior Salish from British Columbia to Montana extensively harvested whitebark pine seeds, which were apparently more popular than seeds from the lower-elevation ponderosa pine (*Pinus ponderosa*) (Lee 2003). Archeological sites, such as the high-elevation campsites found along the Bitterroot Divide near Lolo Pass in Montana indicate that Native Americans used whitebark pine seeds for both short- and long-term food supplies (Losensky 1990). Cheff (1993) described his trips with the Flathead tribe into the Mission Mountains of Montana to harvest whitebark pine seeds. There, the trees would be literally bent over with the weight of whitebark pine cones, and it took only a short time to harvest a packhorse load. Women of the southern Okanagan and Thompson tribes in British Columbia often gathered cones in late summer while the men were hunting. The cones were dry-baked in an earthen oven for a day, and the seeds were extracted and stored for winter cooking or for trading for other goods (Turner and others 1980, 1991). Native Americans still value whitebark pine seeds, and are maintaining traditional seed collecting activities.

The Secwepemc and Flathead Salish also harvested the inner bark (cambium and secondary phloem tissues) of a variety of pines, including whitebark pine, for food and medicine (Kuhmlein and Turner 1991; Turner and others 1980). In the spring, pine bark was generally stripped from the north side of trees, with harvesters being careful not to over strip or girdle trees, and the sweet and juicy cambium was eaten or used as a medicine for stomach problems like

ulcers (Kuhmlein and Turner 1991; Turner and others 1980). The “catface” scars indicative of bark stripping have recently been found on whitebark pine in northwestern Montana, providing evidence that the inner bark of this species might have been used as a food source in this region (Arno and others 2008). The fibrous roots of whitebark pine were used to sew bark together and to weave water tight containers (Antos and others 1996), and the wood was used for firewood (Losensky 1990).

Timber

The scale of commercial logging of whitebark pine has been limited by the remote high elevations settings and the relatively poor quality of its timber—notably its twisted grain, brittleness, and growth form (Rockwell 1911). In fact, John Muir (1894) referred to whitebark pine as the “dwarf pine,” noting its growth habit as a small tree or prostrate form and occurrence at the highest elevations in the Sierra Nevada. However, beginning in the mid-1800s, whitebark pine was harvested in association with the growing mining industry throughout the American West. From 1860 to 1940, for example, billions of board feet of whitebark pine were cut to support the Montana mining industry; the wood was used for fuelwood in smelters and to heat miners’ homes (Losensky 1990). In Montana and Idaho, whitebark pine saplings were widely used by ranchers as fence posts (Rockwell 1911). In the northern Rocky Mountains of the United States and Canada, whitebark pine attains a growth form similar to lodgepole pine (*Pinus contorta*) on well-developed soils and protected sites; it has been commercially harvested along with lodgepole pine (Day 1967; Rockwell 1911). Commercially usable stem lengths exceeding 18 m (60 ft) have been recorded for whitebark pine, with records from southern British Columbia and Alberta (Day 1967).

Presently, however, whitebark pine is not a commercially important timber species and harvest throughout its range is negligible for two reasons. First, its remote locations preclude accessibility for the extensive timber harvesting equipment and road building. Second, the trees are short, gnarled, and have extensive taper, thereby decreasing their timber desirability; whitebark pine trees rarely grow to a size and structure that would be considered high-quality for lumber or other wood products. While the wood is generally as strong as other soft pines, it is considerably weaker than the hard pines and its wood grain is often spiraled (Kasper and Szabo 1970; Keenan and others 1970). Whitebark pine trees cut for timber in the lower reaches of its elevational limit are often within a timber sale for lodgepole pine. Less than 1000 ha of the whitebark pine forests in the United States are harvested during any given year (Losensky 1990). Chew (1990) presented some possible target stand conditions for whitebark pine forests in the northern Rockies, while Eggers (1990) presented alternative silvicultural recommendations for managing whitebark pine for grizzly bear and wildlife. The British Columbia Ministry of Forests encourages forest professionals to make minor amendments to harvest and planting planning to help conserve the species (B.C. Ministry of Forests 2008).

Grizzly and Black Bears

Grizzly and black bears consume substantial amounts of pine seeds in only small parts of their historical North American range (Figure 1.18). Heaviest bear use of seeds occurs in the GYA and the eastern front of the Montana Rocky Mountains, which are regions that experience a continental climate (Mattson and others 2001). Many researchers have found that pine seeds are an important food source for grizzly bears in these regions (Craighead and others 1982; Felicetti and others 2003; Kendall 1983; Kendall and Keane 2001; Mattson 1997; Mattson and Reinhart 1994). Year-to-year variation in whitebark pine cone production impacts grizzly bear ecology and demographics in the GYA (Interagency Grizzly Bear Study Team 2009), particularly influencing rates of movement (Blanchard and Knight 1991), diet (Felicetti and others 2003; Mattson 1997; Mattson and others 1991), mortality rate (Blanchard 1990, Mattson and others 1992), distribution of bears (Haroldson and others 2004), probability of survival (Haroldson and others 2006), and reproductive rates (Schwartz and others 2006).

Whitebark pine seeds have several features that make them a valuable food source for bears. They are large, which makes the seed easier to eat and more energetically rewarding for grizzly bears to consume. They are highly nutritional—whitebark pine seeds are characterized by 21 percent protein (Lanner and Gilbert 1994) and lipid contents ranging from 28 percent (Robbins and others 2006) to 52 percent (Lanner and Gilbert 1994). And they are easy to obtain from squirrel middens. The seeds are especially important for female grizzly bears; reproductive success

of females is contingent on the accumulation of body fat. Female grizzly bears in the GYA derive 40 to 50 percent of their fall nutrition from whitebark pine nuts (Felicetti and others 2003). Female grizzly bears that frequently use whitebark pine seeds exhibit substantially higher reproductive rates (larger litters, more likely to reproduce, and reproduce at a significantly earlier age) than females who consumed few pine seeds (Mattson and others 2001; Robbins and others 2006). Feeding on whitebark pine seeds also promotes high survivorship of sub-adult males and adult females.

The abundance of red squirrels and their middens of stored whitebark cones are important influences on the extent and character of black and grizzly bear use of whitebark pine seeds in any region. In the GYA, bears acquire almost all (greater than 90 percent) whitebark pine seeds by excavating red squirrel middens (Mattson and Reinhart 1994). Red squirrels typically harvest whitebark pine and other conifer cones in August and September to cache in territorial middens (Hutchins 1994; Kendall 1983). Bears seek out these hoards to excavate and consume whitebark pine seeds in their attempt to accumulate body fat prior to hibernation (Mattson and others 1994). Whitebark pine cone crops vary in size annually, and, when whitebark pine seeds are abundant and available, bears almost exclusively consume pine seeds (Mattson and others 2001).

Most middens excavated by bears coincide with years of large cone crops (Mattson and others 2001; Podruzny and others 1999). Grizzly bear use of squirrel middens can start as early as late July; heavy use typically does not occur until the last week of August or the first week of September and persists until bears den in late October and early November. If a substantial number of cones remain in squirrel middens, bear use resumes typically by early June of the following year and lasts until cones are depleted. When bears feed on pine seeds, they feed on virtually nothing else (Mattson and others 2001).

Because of the relationships among whitebark pine seeds, red squirrels, and bears, management of whitebark pine and grizzly bear habitats should take into account red squirrel densities and cone harvesting opportunities (Mattson and others 2001; Reinhart and Mattson 1990). Red squirrels require a diverse conifer species overstory in order to maximize foraging during variable pine cone crop years (Smith 1968). Density of red squirrel middens excavated by Yellowstone grizzly bears was highest in forest types dominated by a mix of whitebark pine and lodgepole pine (Mattson and Reinhart 1997). The best red squirrel habitat within the whitebark pine zone consists of forest habitats with high overstory basal area and high conifer species diversity on moderate slopes (Reinhart and Mattson 1990; Podruzny and others 1999). Optimum stand characteristics that favor red squirrels and grizzly bear use of whitebark pine seeds occur when conifer basal area is greater than $40\text{m}^2 \text{ha}^{-1}$ and whitebark pine basal area represents 15 to 50 percent of the total basal area (Mattson 2000). Management practices for whitebark pine forests



Figure 1.18. Grizzly bears eating whitebark pine seeds. (Photo courtesy of Kate Kendall.)

where bears frequently consume pine seeds should strive to optimize red squirrel habitat. Restoration efforts should also strive to maintain wildlife relationships by maximizing conifer species overstory diversity and preserving mature, seed-producing whitebark pine trees. In grizzly bear habitat, permanent access must be limited (Mattson and others 2001). Restoration efforts throughout whitebark pine range would benefit all wildlife species that take advantage of the foraging value of whitebark pine seeds. Grizzly bears may suffer from the short-term effects of large-scale disturbances, such as fire, mountain pine beetle outbreaks, and timber harvest, which remove cone-producing whitebark pine and reduce squirrel densities and midden sizes. The 1988 fires in Yellowstone burned 30 percent of cone-producing whitebark pine stands in the north and 12 percent in the east portion of the Park, potentially affecting the availability, amount, and distribution of food sources for bears in the Park (Renkin and Despain 1992).

Annual variation in whitebark pine cone production indirectly relates to human-caused bear mortality and adverse encounters. During years of abundant whitebark pine cone crops in the Greater Yellowstone Area, bears forage almost exclusively on pine seeds in the high-elevation whitebark pine zone (Mattson and others 2001; Podruzny and others 1999). When bears stay in the more remote whitebark pine zone, they are farther away from human facilities, campgrounds, big game hunting areas, and potential human-bear conflicts. Human-bear conflicts are the leading cause of bear mortality. During years when bears eat few pine seeds, conflicts with humans and associated bear mortality increase dramatically (Mattson and others 1992). National Forest System, Bureau of Land Management, and National Park System in Idaho, Montana, Washington, and Wyoming have adopted Interagency Grizzly Bear Guidelines for managing lands to favor grizzly bear use

over human use while emphasizing actions that contribute to grizzly bear recovery and conservation (IGBC 1986).

Current Status

The rapid decline of whitebark pine across most of its range in North America is mostly a result of multiple recent human-caused and natural events (Arno 1986; Kendall 1995; Kendall and Keane 2001; Tomback and others 2001a; for recent reviews, see Tomback and Achuff 2010 and Tomback and others 2011). First, several major natural mountain pine beetle outbreaks over the last 70 years have killed many cone-bearing whitebark pine trees across the species' range (Arno 1986; Baker and others 1971; Waring and Six 2005). The most recent mountain pine beetle outbreak, which began in the late 1990s, has achieved unprecedented intensity and geographic extent, driven by rising temperatures that many associate with anthropogenic climate warming (Logan and Powell 2001). Next, an extensive and successful fire exclusion management program in western North America has reduced the area that can be potentially inhabited by the shade-intolerant whitebark pine. Because of fewer fires now, late successional whitebark pine communities are increasingly common and early successional communities are increasingly rare, resulting in a cumulative decline of whitebark pine at a landscape scale over time (Keane and Arno 1993; Morgan and Bunting 1990; Murray and others 2000). And finally, potentially the most threatening events were multiple introductions of the exotic fungal pathogen *Cronartium ribicola* to the western United States and Canada in the early 1900s, which causes the disease white pine blister rust (Geils and others 2010; McDonald and Hoff 2001). Whitebark pine is among the most susceptible to blister rust of the five-needle white pines (Hoff and others 1980; Kendall and Keane 2001; Schwandt 2006).

The cumulative effects and interactions of these three agents have resulted in a rapid decrease in mature whitebark pine, particularly in the more mesic parts of its range (Campbell and Antos 2000; Elderd and others 2008; Keane and Arno 1993; Six and Adams 2007). Moreover, predicted changes in northern Rocky Mountain climate brought about by global climate change could further accelerate the decline of this important tree species by increasing the frequency, intensity, and duration of beetles and fire (Logan and Powell 2001; Romme and Turner 1991; Running 2006). In the following sections, we detail the current threats to whitebark pine and the extent of decline across the species' range.

Blister Rust

White pine blister rust is an exotic fungal disease of five-needle pines, including white, stone, and foxtail pines (Burns and others 2007). It was introduced to western North America around 1910 on infected eastern white pine nursery stock grown in France and shipped to Vancouver British Columbia. Since then, it has spread throughout the range of most five-needle pines in the United States and Canada. It was once thought that cold, dry, and hot

environments of western North America were inhospitable to the rust, but the rust now infects pines in even the most severe climates (Burns and others 2008; Resler and Tomback 2008).

Cronartium ribicola has a complex life cycle involving five different spore types on two groups of alternate hosts (Figure 1.19). Blister rust cankers on the white pine hosts produce aeciospores, which transmit the disease to the alternate hosts, which most commonly comprise shrubs of genus *Ribes*, but also may include plants of the genera *Pedicularis* and *Castilleja* (Geils and others 2010). Basidiospores produced by the alternate hosts are fragile, short-lived spores that infect pines by entering needle stomata. This stage of the life cycle is most climatically limited, requiring moderate temperatures and high humidity for spore production and transmission to pines. Basidiospores typically may travel only a short distance by wind—most often a few hundred meters but up to about 8 km. Spores that germinate within the needle tissue produce hyphae, which then grow into the vascular system and the needle stem (see McDonald and Hoff 2001; Geils and others 2010 and references therein). The hyphae grow down the branch and eventually into the tree bole. There, they eventually form a canker in which spore structures called

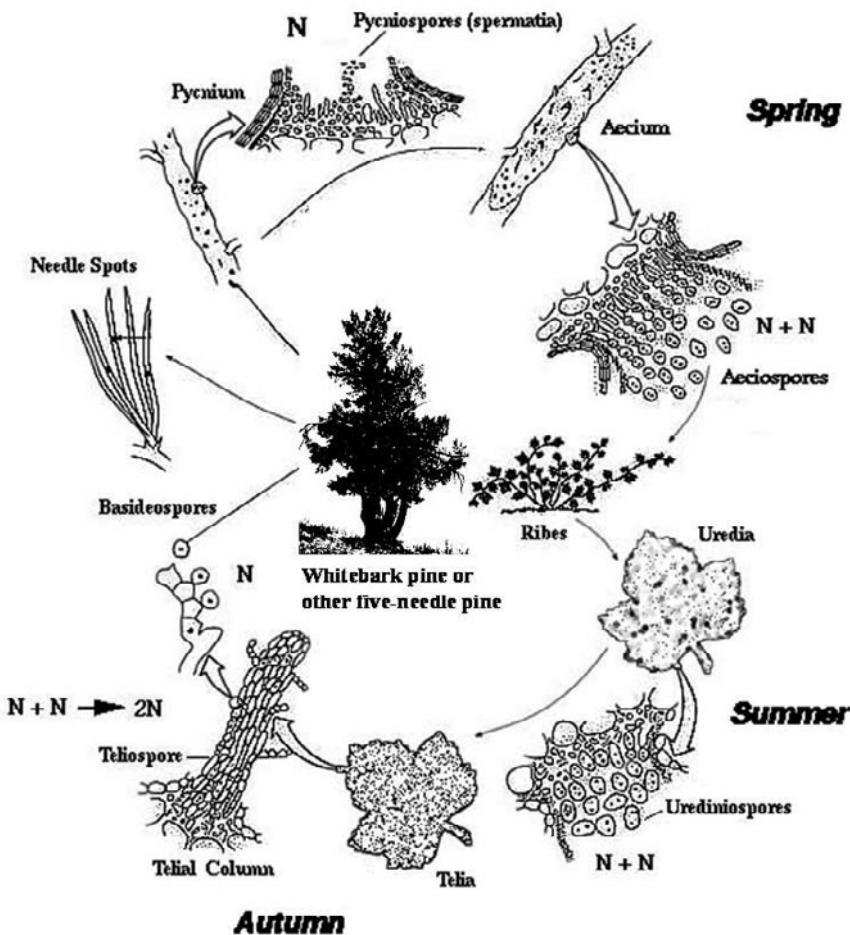


Figure 1.19. Life cycle of the blister rust (from McDonald and Hoff 2001).



Figure 1.20. A whitebark pine stand killed by white pine blister rust.

pycnia produce pycniospores, which are not infectious but are needed for fertilization by insects. Aeciospores are produced from fertilized pycnia the following year in the early summer within bright orange blisters or aecia. These aeciospores are hardy with thick walls and can travel great distances (more than 100 miles) to infect *Ribes* spp. Fragile orange urediniospores are produced in uredinia pustules on the underside of *Ribes* spp. leaves to infect other *Ribes* spp. shrubs throughout the summer. In the fall, teliospores form on infected *Ribes* spp. leaves and these germinate to form the basidiospores that infect the pine.

White pine blister rust damages and kills whitebark pine trees by girdling branches and stems (Hoff 1992) (Figure 1.20), thereby reducing seed cone production within trees and across forest stands. In the Bitterroot Mountains of western Montana and eastern Idaho for example, whitebark pine cone production was significantly lower in stands with higher rust damage (canopy kill and tree mortality) compared to stands with lower rust damage that were otherwise not different in forest structure, composition, slope, and elevation (McKinney and Tomback

2007). Across a broader geographic area—from northwest Wyoming to northwest Montana—whitebark pine cone production was positively correlated with live whitebark pine basal area and negatively correlated with whitebark pine tree mortality at the site level (McKinney and others 2009). Thus, blister rust directly constrains the ability of individual trees and forest stands to contribute propagules, and hence genetic material, to subsequent generations. This reduction in regeneration potential is further exacerbated by a suite of vertebrate species interactions that are altered both directly and diffusely by disproportionate whitebark pine mortality and reduced seed cone availability.

Resistance of whitebark pine to white pine blister rust ranges from 33 percent in a small sample ($n = 3$) (Hoff and others 1980) to 47.4 percent ($n = 108$) (Mahalovich and others 2006; Mahalovich 2012) in the Inland Northwest and 26.3 percent ($n = 43$) on the Pacific Coast (Sniezko and others 2007). Seeds from the healthy trees in stands heavily infected and damaged by blister rust would have the highest probability of being somewhat resistant to blister rust. If opportunities for regeneration are not provided until most of the whitebark is dead or no longer producing cones, the surviving (rust-resistant) trees will be at such low numbers that virtually all of their seeds will be eaten (McKinney and Tomback 2007). Some landscapes contain so few apparent rust-resistant whitebark pine seed sources that there is major concern that nutcrackers will consume a majority of the seed collected and their cached seed will be mostly reclaimed.

There have been many failed attempts at the control of white pine blister rust in the past. Attempts at eradicating *Ribes* spp. during 1940 to 1960 were largely unsuccessful because the shrubs can vegetatively regenerate from rhizomes and their seeds are stored in the soil where they can be activated for germination by future fires. Aerial applications of antibiotic solutions in diesel oil sprayed on whitebark pine to combat blister rust were mostly ineffective and costly (Brown 1969; Maloy 1997). Several management actions, such as pruning infected branches and thinning infected trees, may forestall rust mortality (Fins and others 2001).

Mountain Pine Beetle

The principal agent of insect-caused mortality of whitebark pine is the mountain pine beetle (Figure 1.21). It is a native, cambial-feeding bark beetle of all the western pines, including western white, whitebark, limber, and lodgepole pines. Its entire life cycle is spent beneath the bark of host trees, except when adults emerge from brood trees and fly in search of new host trees. Trees defend themselves with various chemicals, but these matchhead-size beetles can overwhelm these defenses with a mass attack strategy through sheer numbers of beetles (Logan and Powell 2001). Mountain pine beetles range from the Pacific Coast east to the Black Hills of South Dakota and from northern British Columbia and western Alberta south into northwestern Mexico.



Figure 1.21. The mountain pine beetle.

Mountain pine beetle is recognized as an aggressive and economically important forest insect responsible for tree mortality across large areas, and as an integral component of forest ecosystem dynamics for its role in stand thinning and redistribution of resources and nutrients for tree regeneration (Raffa and others 2008). Beetle outbreaks can cause dramatic tree mortality over extensive areas in only a few years, often killing the largest host trees in high-density stands. Beetles are present at low and endemic levels when population dynamics are considered “stable” or self-regulating and tree losses are negligible (Berryman 1986). However, mountain pine beetles can reach epidemic levels, killing up to 80 to 95 percent of suitable hosts when populations are unstable, environmental conditions are favorable, and host species plentiful (Berryman 1986). Forest managers should consider the 95 percent figure a realistic upper bound of overstory mortality in epidemic conditions, including the circa 2000 (1998 to present) west-wide epidemic (Schwandt 2006). Gibson and others (2008) reported that of all the high-elevation five-needled pine species, whitebark pine has sustained the highest mortality in nine western states.

Mountain pine beetles are native to high-elevation pine forests. Periodic outbreaks have occurred since the evolution of bark beetles and gymnosperms millions of years ago. For the 100+ years for which we have records, mountain pine beetles have impacted host stands, including whitebark and limber pine in many parts of the United States and Canada (Figure 1.22). In the early Twentieth Century, Craighead

(1925) and Bureau of Entomology mentions that Renner (1929) documented the start of the widespread mountain pine beetle epidemic that occurred during the historically warm and dry period of the 1930s (Arno and Hoff 1990; Ciesla and Furniss 1976; Perkins and Swetnam 1996). Pre-Twentieth Century mountain pine beetle-caused mortality dates, such as 1730, 1819, and 1887, have been inferred from whitebark pine tree-ring records (Perkins and Swetnam 1996) and lake core sediments with *Dendroctonus* spp. remains, and whitebark pine pollen has been found dating back to the Holocene approximately 8200 years before present (Brunelle and others 2008).

Most of the mountain pine beetle life cycle is completed under the bark where the insect disrupts the connectivity of the water transport system of the tree, damaging the tree by mechanically girdling the stem with adult and larvae galleries in the phloem, and introducing a blue stain fungus that inhibits water transport and may kill the tree (Gibson and others 2009). Signs of mountain pine beetle attack are pitch tubes and fine boring dust in bark crevices and around tree bases, which are made when beetles bore into the bole of the tree. On successfully attacked trees, pitch tubes are abundant on the surface of the bole and may extend more than 5 m up the stem. Pitch tubes are cream- to dark red-colored masses of resin mixed with boring dust and are approximately 1 cm in length. Unsuccessful attacks are called “pitch outs”; the tree’s resin response is to pitch out the beetles as they attempt to bore into the inner bark. These pitch tubes are generally larger in size, lighter in color, and widely scattered over the trunk. Whitebark pine, like other pines, may sustain “strip attacks” where a vertical portion of inner bark is killed while the rest of the stem is unaffected and continues to transport

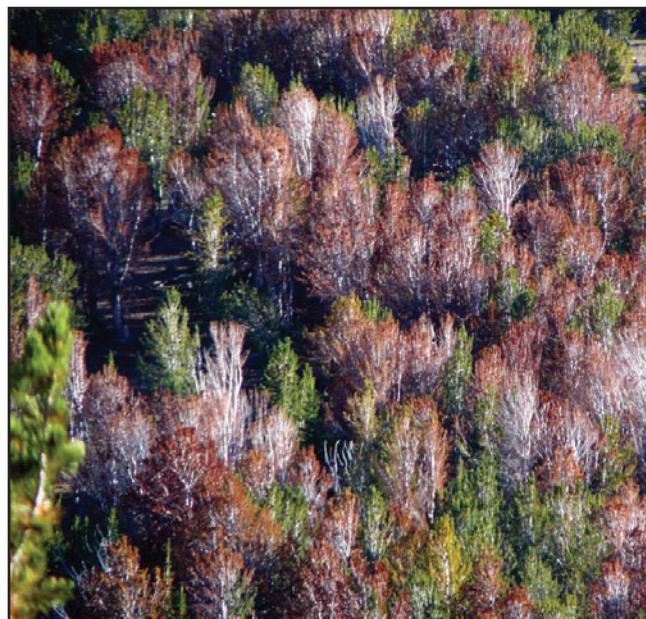


Figure 1.22. Whitebark pine stand killed by mountain pine beetles.

water and nutrients. Foliage of successfully attacked trees generally fades uniformly through the crown from yellowish green to shades of orange, rust, and red. Whitebark pine crowns generally fade to a rust color the year after attack, but may take two to three years in some individuals. Size, stress, and health of the tree are factors that affect the foliage fade rate.

Adult mountain pine beetles begin attacking trees in the early summer in pheromone-mediated mass attacks that overcome most of a tree's chemical defenses. Beetles develop through four stages: egg, larva, pupa, and adult (Gibson and others 2009). Adults mate and then lay eggs that hatch into larvae that develop in the phloem of the tree completing the life cycle—a one year or univoltine life cycle. Larval growth is aided by a symbiotic fungi *Grosmannia clavigera* and *Ophiostoma montium* (Adams and Six 2007; Six 2003; Six and Paine 1998). Adult beetles deposit the fungi in the tree as they excavate galleries where the females lay eggs. The fungi colonize the phloem and sapwood of the infected tree, with the fungal hyphae providing nutrition to beetle larvae (Six 2003). Adult beetles also feed on fungal spores in the pupal chambers before emergence and dispersal from the host tree. One to several months after the tree is infested, the sapwood discolors to a bluish tint caused by the fungi. Adult bark beetle galleries found under the bark are J-shaped and vertically aligned with the stem; larvae galleries are perpendicular to the adult galleries and terminate in pupae chambers. Adult galleries range in length from 5 to 7 cm to more than 60 cm and are diagnostic of mountain pine beetle attack.

Beetle life cycles take one to two years, and many empirical, laboratory, and modeling research studies have been undertaken to understand the causes of life cycle variability (Bentz and others 1991; Logan and Powell 2001; Powell and others 1996). Over most of its range, the beetle has one generation per year, but two generations have been observed in cooler, high-elevation areas, including whitebark forests. These forests have generally been associated with decreasing beetle-caused mortality levels because the cold environment creates unfavorable heat balance for beetle development (Amman 1973; Logan and Bentz 1999). Cool temperatures may retard development, resulting in longer life cycles and/or a disruption of critical timing of summer emergence necessary for a coordinated and successful mass attack. Mountain pine beetles have mechanisms to survive in sub-zero temperatures; however, sustained sub-freezing temperature may result in mortality in all life stages (Amman and Cole 1983; Regniere and Bentz 2007).

Beetle development is under direct temperature control (Logan and Bentz 1999), and warm temperatures favor successful brood development, beetle survivorship, and successful attacks (Amman 1972, 1973; Bentz and others 1991; Logan and Bentz 1999; Reid and Gates 1970). The climate conditions during the early Twentieth Century epidemic and the current epidemic have been characterized by above average departures in summer temperatures. This has contributed to outbreak extent and magnitude by improving conditions for the mountain pine beetle's adaptive

seasonality and population build up (Logan and Bentz 1999; Logan and Powell 2001). Generally, epidemics collapse due to one of two factors: (1) an extreme cold snap (less than 0° F) in early fall or late spring and winter temperatures below -34° F (Cole and others 1989); (2) a lack of susceptible host trees. Resource managers may be prudent to assume that the epidemic of the proportions that North America is currently experiencing will collapse when mountain pine beetle has run out of suitable hosts. The upper bound of 95 percent mortality of the overstory, or the "worst case scenario" (Berryman 1986), provides a quantitative metric of stand structure that silviculturists can use for restoration actions. Forecasting a cold event is nearly impossible due the high temperature variability in time and space.

Mountain pine beetle mortality influences canopy condition, stand structure, species composition, forage production, wildlife habitat, fuel loading, water yields, and aesthetics. Following the death of the overstory, advanced regeneration from shade-tolerant tree species (subalpine fir, for example) is expected to release. Species composition plays a critical role at this time; if the stand has succeeded to shade-tolerant species, it would be expected that the stand composition would shift to that shade-tolerant species mixture. If the stand composition is homogenous or climax whitebark, whitebark would be expected to persist on the site. White pine blister rust-infected regeneration, suppressed seedlings, changing climates, and other disturbances confound the expected successional trajectory, and management intervention may be needed to maintain whitebark pine. A combination of silvicultural treatments, prescribed fire, fuel reduction, and planting of blister rust-resistant seedlings may be recommended. Resource managers should integrate actions that help whitebark pine ecosystems forestall beetle impacts and protect seed resources (Millar and others 2007).

It has been well established that tree size, age, and stand density are factors positively correlated with tree mortality (Hamilton 1986; Hamilton and Edwards 1976; Lee 1971; Yoda and others 1963). For the whitebark pine-mountain pine beetle system, diameter and basal area were significant predictors of beetle caused mortality in the reconstructed MPB outbreak of the 1930s (Perkins and Roberts 2003). This is consistent with MPB-host susceptibility characteristic of other pines (Amman and others 1977; Berryman 1982; Cole and Amman 1980; Olsen and others 1996; Stevens and others 1980; Schmid and Mata 1992; Shore and Safranyik 1992). Mountain pine beetles prefer to attack large trees in dense stands. Whitebark pine stands with basal areas greater than $10 \text{ m}^2 \text{ ha}^{-1}$ or with a stand density index (SDI) greater than 80 were attacked during the 1930s epidemic (Perkins and Roberts 2003). Other studies are being conducted to quantify vulnerable stand structures.

Approaches to forestall or reduce mountain pine beetle-caused mortality have covered a broad spectrum. Efforts by the U.S. Forest Service in the early part of the Twentieth Century were aimed largely at killing beetles. The Forest Service, organized in 1905, was faced with its first beetle outbreak in the northern Rocky Mountains within a few

years of its inception. Infested trees were peeled, piled and burned, and treated with toxic chemicals—or an array of those treatments in varying combinations—for more than 50 years. Finally realizing the futility of trying to kill enough beetles to halt an outbreak, Forest Service entomologists and silviculturists began to recognize that stands of certain conditions experienced higher numbers of beetle-killed trees. By the 1970s, it was noted that lodgepole and ponderosa pine stands, especially susceptible to beetle outbreaks, shared similar characteristics—generally larger-diameter, older trees, in more densely stocked stands (Amman and others 1977). That recognition led to thinning studies and ultimately management recommendations directed at altering susceptible stand conditions to reduce beetle-caused mortality to acceptable levels (McGregor and others 1987). Current recommendations include reducing stand stocking to levels promoting vigorous tree growth and creating more open conditions that are less likely to attract and support beetle outbreaks (Safranyik and Wilson 2006).

Fire Exclusion

In general, the effects of fire exclusion in whitebark pine forests are not yet manifest because of the long fire return intervals associated with the ecosystem. Therefore, fire exclusion effects can only be evaluated at the landscape level by assessing the decrease in the extent of whitebark pine forests (early to mid-seral stands) and increase in subalpine fir (late seral) forests (Keane and others 1994). A major reduction in high-elevation fires since circa 1929 has led to the successional replacement of whitebark pine with subalpine fir on the more productive sites in some parts of its range (Barrett 2008; Keane 2001b). Keane and others (1994) found that subalpine fir communities comprised about 12 to 22 percent of the landscapes in the Bob Marshall Wilderness Complex, but a modeling effort estimated subalpine fir abundance between 3 to 12 percent historically (Keane 2001b; Keane and others 1990, 1996). A similar trend is evident in the Cascade Mountains, where late seral species have replaced dominance by seral whitebark pine in roughly 12.5 percent of stands (Siderius and Murray 2005).

Whitebark pine will continue to decline as long as fire exclusion limits wildland fire from creating caching sites for the nutcracker in competition-free growing environments suitable for whitebark pine regeneration, and blister rust kills trees faster than whitebark pine can regenerate. Burning creates good caching habitat for Clark's nutcrackers by exposing the ground to create a pattern-rich environment, and it creates optimal growing conditions for whitebark regeneration by removing its competitors (Tomback and others 1993). Burning near areas with moderate to high levels of blister rust infection and mortality would favor natural selection of rust-resistant individuals because the surviving cone-bearing trees would likely contain rust-resistant genes unless nutcrackers reclaim most of their cached seed (Hoff and others 2001; Kendall and Keane 2001; McKinney and Tomback 2007; McKinney and others 2009).

Climate Change

Predicted global warming has the potential to significantly impact whitebark pine ecosystems (Bartlein and others 1997; Romme and Turner 1991). Because of its long life span, whitebark pine may be a species that is able to last through major climatic cycles, but its complex regeneration processes may make it difficult to adjust to rapid climate change. It is speculated that increasing temperatures could “push” the species off the mountain by moving its lower elevational limits above the tallest peaks (Bartlein and others 1997; Schrag and others 2008; Warwell and others 2007). Conventional wisdom is that less hardy, shade-tolerant conifer species would be able to establish in those higher-elevation stands where whitebark pine currently dominates (Romme and Turner 1991; Koteen 1999). Bioclimatic envelope statistical modeling that relates climate to a species' current geographical distribution has shown dramatic decreases in whitebark pine over the next 50 years (Figure 1.23) (McDermid and Smith 2008; Warwell and others 2007). However, recent modeling efforts have shown that whitebark pine might be maintained on the landscape if increases in large, stand-replacement fires create large, competition-free burned areas (Loehman and others 2011). And, if tree dispersal enables range shifts to occur, this will lead to new northern distributional range (Hamann and Wang 2006; McKenney and others 2007). Moreover, whitebark pine also shows promise for being maintained in the northern Rockies because of high levels of genetic diversity (Mahalovich and Hipkins 2011; Richardson and others 2002a); moderate to high heritabilities in key adaptive traits (Mahalovich 2012); demonstrated blister rust resistance (Hoff and others 1980; Mahalovich and others 2006; Sneizko and others 2007); minimal inbreeding (Bower and Aitken 2007; Mahalovich and Hipkins 2011); and generalist adaptive strategies (Mahalovich 2012).

Many scientists believe that most major ecosystem changes caused by global climate change will be facilitated by major shifts in the disturbance regimes, which have already been observed in some whitebark pine ecosystems (Gardner and others 1996; Swetnam and Betancourt 1998). The current mountain pine beetle outbreaks that are killing more whitebark pine than historical records indicate are probably a result of warmer winter temperatures that facilitate expansion and establishment of beetle populations in the higher-elevation whitebark pine zone (Logan and others 2003; Logan and Powell 2001). Jewett (2009) found that the highest mortality in whitebark pine occurred on warmer, drier sites in the GYA, and this relationship was probably mediated by mountain pine beetles. A warmer climate may also accelerate the spread of blister rust (Koteen 1999). Although effects of global climate change could be severe for whitebark pine, they are also complex and difficult to predict; therefore, potential climate change effects should never be used as an excuse for not implementing restoration projects (Hobbs and Cramer 2008). Instead, climate change predictions could be used to guide the design, approach, and

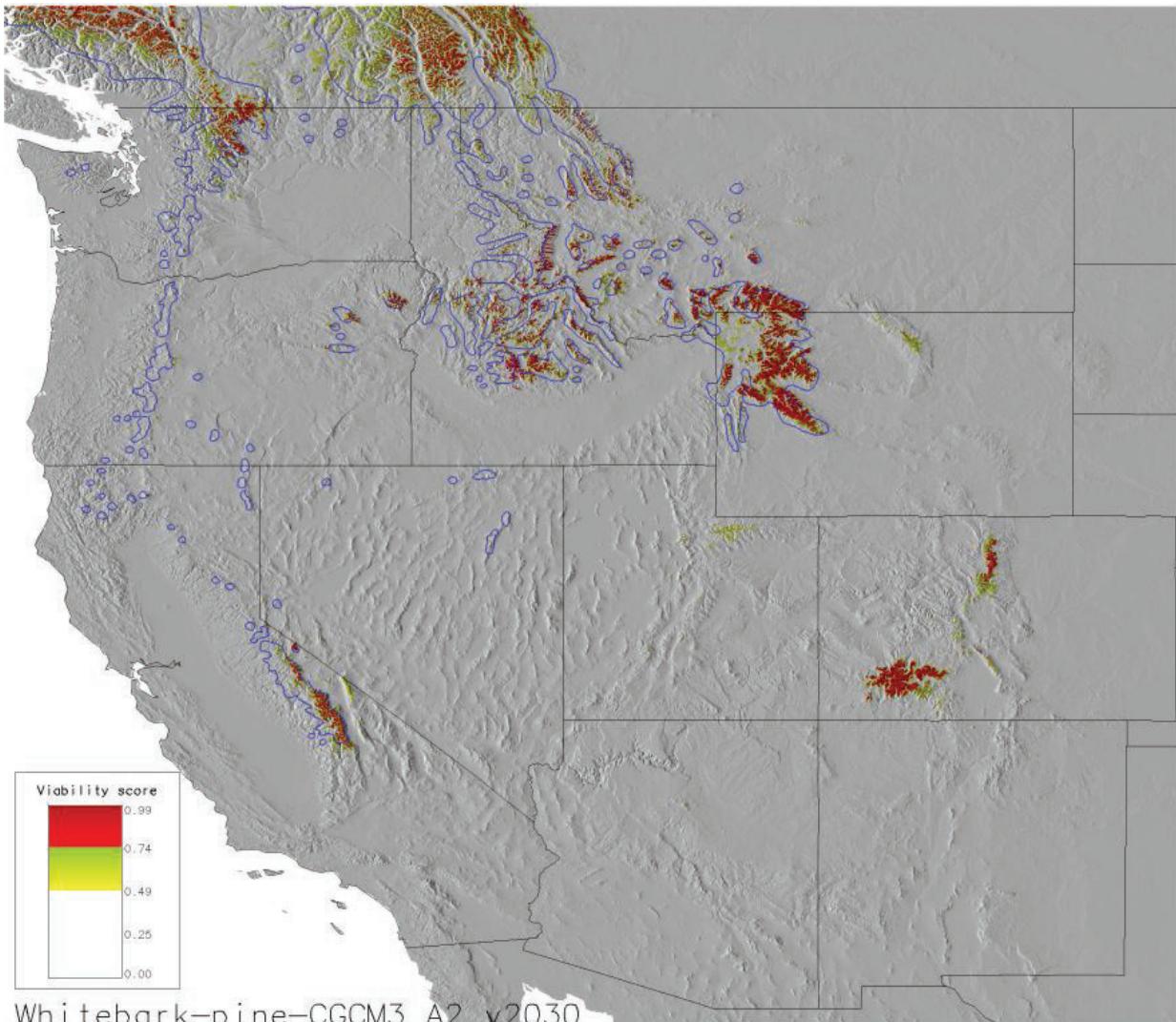


Figure 1.23. The decline in the range of whitebark pine over the next 50 years, as predicted from a niche modeling or bioclimatic species envelope modeling approach. Blue lines indicate current range and red and yellow indicate predicted viable range in 50 years (Warwell and others 2007).

kinds of restoration activities across the range of whitebark pine, with different activities emphasized in some bioclimatic regions or for specific site conditions.

It is important to evaluate the effects of climate change on all ecological interactions and processes that influence whitebark pine abundance. All life stages and ecosystem processes should be considered; not just growth response (Koteen 1999), but also effects on phenological and regeneration processes, such as seed dispersal, germination, and ecesis (Chuine 2010; Loehle and LeBlanc 1996; Price and others 2001). Moreover, climate change effects should be evaluated at landscape scales to include shifts in disturbance and abiotic interactions (Gardner and others 1996). If wildland fires are expected to increase in frequency and size (Brown and others 2004; Keeton and others 2007; Running 2006; Ryan 1991), then whitebark pine populations could actually increase in extent because nutcrackers disperse seeds into large burns more effectively than wind can disperse the seeds of whitebark pine's competitors, providing there are

sufficient seed sources left on the landscape (Tomback and others 1990). Bunn and others (2003) emphasized the importance of accounting for microsite variability in assessing whitebark pine climate change response; high-elevation microsite changes, coupled with increased fire activity, could increase whitebark pine regeneration and growth as climates change. If disturbances are predicted to increase (Flannigan and others 2008; Logan and Powell 2001), then disturbance adaptations might determine future landscape compositions and structures; and whitebark pine has many adaptations to disturbance that might allow it to remain on the high-elevation landscape. Maintaining whitebark pine on the high mountain landscape using fire could create resilient and resistant landscapes that are critical for future conservation efforts and effective at sequestering carbon (Craig 2009). In summary, while it appears that climate change can adversely affect whitebark pine populations, the actual magnitude and direction of climate response should be evaluated at several scales, especially at the local level (Keane and others

2008b), and these responses should not preclude restoration efforts (Hobbs and Cramer 2008).

Extent of Decline

There is now no doubt that whitebark pine is declining across most of its range. In general, trees in the mesic, warmer portions of whitebark pine's range are experiencing the greatest mortality from beetles and rust (Kendall and Keane 2001). But even the driest, coldest parts of the range are now experiencing blister rust infections (Bockino 2008; Resler and Tombback 2008). Keane and Morgan (1994b) performed a comprehensive analysis to predict those areas where decline from rust is the most rapid and found little correlation to climate averages or geography. Keane and Arno (1993) found a major line of demarcation that could be approximated by the 46th N latitude, where Montana and Idaho whitebark pine forests north of this latitude are in the worst state of decline.

A number of assessments document the rapid decline of whitebark pine (Table 1.1). The Whitebark and Limber pine Information System (WLIS) database is a compilation of all plot data documenting the decline in whitebark and limber pine in the Pacific Northwest and Rocky Mountains (Lockman and others 2007); it has recently been improved and updated (<http://www.fs.fed.us/r1-r4/spf/fhp/prog/programs2.html>). In Montana's Rocky Mountains, Peterson (1999) assessed the extensive decline of whitebark pine in Glacier National Park. In the Bitterroot Mountains of Montana, Arno and others (1993) documented that whitebark pine has migrated 200 m higher in elevation because of past fire suppression efforts, and Hartwell (1997) found a 75 percent decrease in whitebark pine. In Idaho, Kegley and others (2001) found 23 to 44 percent mountain pine beetle mortality and approximately 20 percent blister rust infection for whitebark pine in the Selkirk Mountains.

Many have addressed the decline in the Pacific Northwest. Goheen and others (2002) found 44 percent of whitebark pine stands were healthy and 46 percent were infected with blister rust on the Umpqua National Forest. Ward and others (2006a) synthesized results of assessments conducted in Washington and Oregon (see their Appendix A) and found percent mortality ranged from 0 to 100 percent with an average of approximately 44 percent. By 2004, Oregon had experienced up to 54 percent mortality in some places with a wide range of infected live trees (0 to 90 percent depending on location) (Murray 2005). Smith and others (2008) found that 27 percent of whitebark pine was healthy and 73 percent was infected with blister rust in the southern Rocky Mountains of Canada. The infection levels decreased to 16 percent in the central Canadian Rockies and increased again to about 60 percent near the northern limit of the range of whitebark pine in Jasper National Park. Between 1996 and 2003/04 infection levels increased from 43 percent to 71 percent and mortality increased from 26 percent to 61 percent in eight stands in Waterton Lakes National Park.

Province-wide model projections of the climatic suitability of beetle habitat in British Columbia (Carroll and others 2006) overlaid with the range of whitebark pine indicated that the percentage of whitebark pine's range at high risk to beetle outbreaks would double between 1981 and 2010, and then double again between 2001 and 2070. A GIS intersection of aerial survey data of beetle outbreaks, the range of whitebark pine in British Columbia (obtained from inventory data), and climate suitability projections for the normal period showed that, as of 2007, the number of infestations in previously unsuitable whitebark pine ecosystems was three times greater than during the previous outbreak in the 1980s. Field studies at eight sites and observations over other parts of British Columbia indicated that once mountain pine beetles infested stands, they killed between 50 to 100 percent of large, mature cone-bearing whitebark pine within one to four years of infestation initiation.

The GYA has historically had the lowest blister rust and mountain pine beetle infections and mortality compared with most of whitebark pine's range (Jewett and others 2011). However, recent increases in blister rust infection (now over 20 percent) and extensive mountain pine beetle mortality are now causing major declines of whitebark pine in the GYA (Hatala and others 2010; Hicke and Logan 2009; Jewett 2009).

Other Whitebark Pine Issues

Several other administrative, societal, or ecological issues in whitebark pine may be important to its restoration and management across its range. We discuss two major issues that play an important role in the restoration of whitebark pine ecosystems.

Whitebark Pine Restoration in Wilderness

In the United States, whitebark pine is most commonly found in remote upper subalpine sites, which, on Federal lands, is frequently Congressionally designated Wilderness. In fact, approximately 84 percent of whitebark pine occurs on Federal land and 48 percent occurs in designated and recommended Wilderness (Keane 2000). This latter designation poses challenges, both legal and philosophical, for whitebark pine restoration efforts. From a practical standpoint, restoration is logically challenging in areas that have no roads and where motorized equipment and mechanical transport is prohibited. In this section, we discuss the legal and philosophical dilemmas to whitebark pine restoration in Wilderness and then suggest the role Wilderness can play in restoration and the most compatible methods of restoration.

The Wilderness Act, signed by President Lyndon Johnson in 1964, defines wilderness as, "...an area where the earth and its community of life are untrammeled by man retaining its primeval character and influence managed so as to preserve its natural conditions and generally appears to have been affected primarily by the forces of nature, with the

Table 1.1. Summary of results from studies that documented decline of whitebark pine in the U.S. and Canada. Numbers in parentheses represent the mean of the given range (“NF” is National Forest and “—” indicates data unavailable).

Study Year	Geographic Area	Rust Infection (%)	Overall Decline (%)	Sources
United States				
1992	Southern Bitterroot NF	—	14	Arno and others (1993)
1992	Western Montana	20-90 (61)	30-90 (51)	Keane and Arno (1993)
1993	Bob Marshall Wilderness	10-99 (48)	10-80 (44)	Keane and others (1994)
1995	Sundance Burn Idaho	29	—	Tomback and others (1995)
1995	Eastern Cascades	27	2	Hadfield and others (1996)
1996	Bitterroot NF	—	29	Hartwell and Alaback (1997)
1997	Intermountain region	2-100 (36)	1	Smith and Hoffman (1998, 2000)
2000	Selkirk Mountains	33-82 (53)	22-45 (34)	Kegley and others (2001)
2000	Crater Lake NP	0-20 (12)	—	Murray and Rasumussen (2000, 2003)
2001	Umpqua NF	70	10	Goheen and others (2002)
2003	Western Cascades, Washington	65-84 (76)	26-53 (41)	Shoal and Aubry (2004)
2003	Eastern Cascades	21-84 (48)	6-42 (16)	Shoal and Aubry (2004)
2004	Medicine Bow NF	0-100 (16)	—	Kearns and Burns (2005)
2005	Washington, Oregon	0-100 (69)	0-89 (35)	Summary of multiple studies in Ward and others (2006)
2007	Oregon, Washington	5-73 (27)	1-61 (21)	Shoal (2007)
2008	Mt Rainier, North Cascades	22	31	Rochefort (2008)
2008	Greater Yellowstone, Teton NP	85	70	Bockino (2008)
2008	Glacier NP	73	60	Smith and others (2008)
2008	Central Idaho	—	31	Hicke and Logan (2009)
2008	Greater Yellowstone	20	—	Greater Yellowstone Whitebark Pine Monitoring Group (2008)
Canada				
1997	British Columbia	0-100 (45)	0-64 (21)	Campbell (1998), Campbell and Antos (2003)
2001	British Columbia	11-53 (31)	2-35 (19)	Zeglen (2002, 2007)
2007	Canadian Rocky Mtns	98	57	Smith and others (2008)

imprint of man's work substantially unnoticed" (Section 2 (c) P.L. 88-577). The word "untrammeled" was chosen carefully by the authors of the Wilderness Act to describe the untamed, free will aspects of wilderness. The idea was to allow natural processes to prevail, to allow nature to take its course, without human manipulation. Howard Zahniser, the key author of the Wilderness Act said, "Once management undertakes to improve the wilderness...by manipulating natural process in the wilderness itself, the fragile wilderness quality of the area being managed is in jeopardy." Based on this definition, any type of restoration would be considered "trammeling" the wilderness. However, the definition also states that wilderness is protected and managed to preserve *natural conditions*. If whitebark pine occurred naturally but is in jeopardy due to some type of human influence, should intensive manipulation (trammeling) be allowed in order to restore natural conditions? Therein lays the philosophical dilemma when interpreting the Wilderness Act.

To ensure some level of consistency in interpretation of the Wilderness Act and to provide guidance on philosophical dilemmas, Wilderness Management Policy has been developed for the Federal agencies that manage wilderness. In general, Forest Service policy does not allow for vegetative manipulation or broad-scale restoration actions in wilderness, except where the objectives cannot be met outside of wilderness, the loss is due to human influence, and there is no reasonable expectation that natural reforestation will occur. The following are passages from the Forest Service Manual that relate to the topic of whitebark pine restoration:

- FSM 2320—Introduction. "Manage wilderness to ensure that human influence does not impede the free play of natural forces or interfere with natural successions in the ecosystem."
- FSM 2320.2—Objectives. 2. "Maintain wilderness in such a manner that ecosystems are unaffected by human manipulation and influences so that plants and animals develop and respond to natural forces."
- 2323.5—Management of Forest Cover. "Manage forest cover to retain the primeval character of the environment and to allow natural ecological processes to operate freely."
- 2323.54—Reforestation. "Allow reforestation only if a loss of the wilderness resource has occurred, due to human influence, and there is no reasonable expectation of natural reforestation."
- 2323.04b states that the Chief has the authority to approve vegetative cover manipulation or any reforestation activities.

Two other sections of the Forest Service Wilderness Management Policy that provide direction on restoration of whitebark pine are fire and threatened and endangered species:

- 2324.2—Management of Fire. Objectives. 1. "Permit lightning caused fires to play, as nearly as possible, their natural ecological role within wilderness."

- 2324.22—Policy. 7. "Do not use prescribed fire in wilderness to benefit wildlife, maintain vegetative types, improve forage production, or enhance other resource values."
- 2323.3—Management of Wildlife and Fish. Objectives. 3. "Provide protection for known populations and aid in recovery in areas of previous habitation, of Federally listed threatened or endangered species and their habitats."
- 2323.32—Policy. 4. "Manage wilderness to protect known populations of Federally listed threatened or endangered species where necessary for their perpetuation and aid in their recovery in areas of previous habitation. When alternative areas outside of wilderness offer equal or better protection, take actions to recover threatened or endangered species outside of wilderness areas first."

The National Park Service policy under National Park Service Management Policy 2006 is as follows:

- 6.3.1—General Policy. "The National Park Service will take no action that would diminish the wilderness eligibility of an area possessing wilderness character until that wilderness designation has been completed. All management decisions affecting wilderness will further apply the concept of "minimum requirement" for the administration of the area regardless of wilderness category."
- 6.3.6—Scientific Activities in Wilderness. "The statutory purpose of wilderness includes scientific activities, and these activities are encouraged and permitted when consistent with the Services responsibilities to preserve and manage wilderness."
- 6.3.6.2—Monitoring Wilderness Resources. "As appropriate, wilderness monitoring programs may assess physical, biological, and cultural resources and social impacts. Monitoring programs may also need to assess potential problems that may originate outside of wilderness to determine the nature, magnitude, and probable source of those impacts."
- 6.3.7—Natural Resource Management. "The National Park Service recognizes that wilderness is a composite of resources with interrelated parts. Without natural resources, especially indigenous and endemic species, a wilderness experience would not be possible. Natural resources management in wilderness will include and be guided by a coordinated program of scientific inventory, monitoring, and research. The principle of non-degradation will be applied to wilderness management, and each wilderness area's condition will be measured and assessed against its own unimpaired standard. Natural process will be allowed, insofar as possible, to shape and control wilderness ecosystems. 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 knowledge and tools exist to accomplish clearly articulated goals.”

Currently, the only activities related to whitebark pine restoration that are occurring in wilderness are monitoring and inventory activities, caging and collecting cones from blister rust-resistant trees, and allowing controlled wildfire to restore successional advanced whitebark pine stands. Cone collection has low impacts and does not require any manipulation or prohibited activity, and wildfires are encouraged because they are supported by law and policy and have many resource benefits. Other activities that have been suggested but not implemented are planting of putatively blister rust-resistant seedlings, sowing blister rust-resistant seeds, mechanical thinning, and prescribed fire. All of these activities involve manipulation that would typically not be allowed in wilderness. Prior to any of these activities being implemented, the following steps must be taken:

- Determine that the loss of whitebark pine is due, in fact, to human intervention.
- Determine that restoration objectives cannot be accomplished entirely outside of wilderness.
- Determine if there is a reasonable expectation that human intervention will result in a significant improvement in whitebark pine survival.
- Determine if the analysis has proven that whitebark pine restoration actions are the minimum requirement or minimum tool necessary to meet the objectives.
- Determine the adverse effects of restoration actions on the other qualities of wilderness character (untrammeled, undeveloped, and outstanding opportunities).
- Determine if the timing, frequency, location, or intensity of the restoration actions can be altered to mitigate these adverse effects.
- Determine if the activity can be accomplished without the support of motorized equipment or mechanical transport.

If the project passes these tests, a National Environmental Policy Act environmental assessment and analysis will need to be completed, including public scoping.

One major restoration activity that is specifically excluded by policy from Forest Service Wilderness Areas is tree planting, and especially planting rust-resistant whitebark pine seedlings. Keane and Parsons (2010a) have found that planting whitebark pine seedlings in areas of high mortality of mature, seed-producing tree mortality may be essential for preventing local extirpation. On the other hand, Landres (2010) presented a rationale for taking a “hands off” approach to restoration and allowing whitebark pine to further decline. Since nearly half of whitebark pine’s range occurs in wilderness or protected settings, the ability to plant seedlings or seed may have vast implications to the success of range-wide restoration strategies.

Conservation Efforts for Whitebark Pine

At this time, the effects of cumulative losses of whitebark pine are gaining recognition, particularly after the massive mountain pine beetle outbreaks of the past decade coupled with increasing damage and mortality from white pine blister rust. The decline of whitebark pine and other impacted five-needle white pines was brought to the attention of the Chief of the U.S. Forest Service through the reports, “Managing for Healthy White Pine Ecosystems in the United States to Reduce the Impacts of White Pine Blister Rust” (Samman and others 2003), and “Whitebark Pine in Peril: A Case for Restoration” (Schwandt 2006). More recent efforts to highlight the decline in five-needle white pines include: the publication of a special issue of “Forest Pathology” in 2010 on white pine blister rust, edited by C. G. Shaw and B. W. Geils, and the 2010 conference and proceedings “The High Five Symposium: The Future of High-Elevation Five-Needle White Pines in Western North America,” organized by the Whitebark Pine Ecosystem Foundation, a 501 (c) 3 non-profit group dedicated to the restoration of whitebark pine (Keane and others 2011). Finally, whitebark pine achieved national media attention upon announcement in July, 2011, that it was listed as a candidate species under the Endangered Species Act (U.S. Fish and Wildlife Service 2011a, 2011b). This is the first widely distributed forest tree in the United States to warrant listing.

The status of whitebark pine is continually being evaluated at national, state, and provincial levels. First of all, whitebark pine is categorized as *vulnerable* (high risk of extinction in the wild in the medium-term future) both on the global IUCN Red and NatureServe List (IUCN 2007; NatureServe 2009). In the United States, whitebark pine was listed as a Species of Concern in western Washington in 2004 and in eastern Washington in 2009 by the U.S. Fish and Wildlife Service (2007, 2009). In December 2008, the Natural Resources Defense Council (2008), a U.S. non-profit, tax-exempt organization, submitted a petition to the U.S. Fish and Wildlife Service to list whitebark pine as an Endangered Species under the Federal Endangered Species Act. The 12-month finding (previously mentioned) concluded that listing was in fact warranted, but current listing was precluded by “higher priority actions to amend the Lists of Endangered and Threatened Wildlife and Plants” (U.S. Fish and Wildlife Service 2011b). The finding further stated that “We will develop a proposed rule to list *P. albicaulis* as our priorities and funding will allow.” Whitebark pine has been added to the candidate species list and waits updating through the annual Candidate Notice of Review.

The Committee on the Status of Endangered Wildlife in Canada (COSEWIC) has recommended that whitebark pine be Federally listed as Endangered under the Species at Risk Act (SARA) in Canada. In Alberta, whitebark pine was recently listed as an Endangered Species under The Wildlife Act because of ongoing and projected population declines in the province and because the status of neighboring populations in Montana and British Columbia, which

are also declining due to blister rust infections and mountain pine beetle outbreaks, reduce the likelihood of population “rescue” through seed dispersal to Alberta by the Clark’s nutcracker. This listing provides legal protection for whitebark pine in Alberta and necessitates the development of a recovery strategy for the species.

In 2007, the Conservation Data Centre at the British Columbia Ministry of the Environment added whitebark pine to its Blue List. Species on the Blue List are of special concern because of characteristics that make them particularly sensitive to human activities or natural disturbance events. Whitebark pine was added to this list because most populations are infected by the exotic blister rust fungus; a significant proportion of mature forests are now being killed by a mountain pine beetle outbreak; and a severe decline (70 to 90 percent) is expected over the next 70 years due to

expanding mountain pine beetle outbreaks, continued blister rust infections, fire protection activities that facilitate successional replacement, climate change, and increased pressure to log subalpine forests. While adding whitebark pine to the Blue List does not confer legal protection, it does highlight the species for more formal designation as a Threatened (or Endangered) species, either provincially under the British Columbia Wildlife Act, or nationally by the COSEWIC. It also calls attention to the species for special consideration under Operational Planning Regulations in the Forest Practices Code of British Columbia Act, and forest professionals in British Columbia are beginning to help conserve whitebark pine by making minor adjustments to landscape-level forest stewardship plans as well as harvesting and site plans (for example, adjustment of cutblock boundaries).

2. Whitebark Pine Restoration Strategy

The Strategy

The range-wide whitebark pine restoration strategy consists of a set of principles coupled with associated actions to guide the design, planning, and implementation of restoration activities throughout the range of whitebark pine (Schoettle and Sniezko 2007; Schwandt 2006) (Figure 2.1). The guiding principles represent broad areas of emphasis that need to be addressed when restoring whitebark pine. They were taken from a number of sources and represent the most current research in whitebark pine conservation (Aubry and others 2008a; Elderd and others 2008; Fins and others 2001; McKinney 2004; McKinney and others 2009; Schoettle and Sniezko 2007; Schultz 1989; Schwandt and others 2006; Sniezko and others 2004; Waring and O'Hara 2005):

1. **Promote rust resistance.** The most important action in restoring whitebark pine is to ensure that future populations of the species have some resistance to blister rust by increasing the frequency of trees with genetic resistance to the blister rust pathogen. All restoration

plans and activities must first address how natural or planted whitebark pine regeneration will survive with blister rust, now a naturalized species in North America (Geils and others 2010). To accomplish this, managers must (a) support selective breeding programs to develop and deploy blister rust-resistant whitebark pine, (b) facilitate and accelerate natural selection for blister rust-resistant genotypes in stands by reducing competition to increase survival of healthy putative rust-resistant trees in high blister rust areas, providing openings for natural seed dispersal and seedling survival, and (c) plant seedlings from trees known to have some level of blister rust resistance.

2. **Conserve genetic diversity.** The full genetic diversity across the range of whitebark pine must be preserved for the future by collecting and archiving seeds and growing and planting genetically diverse seedlings. During the process of selecting rust-resistant lineages for growing seedlings and planting, we must be careful not to lose the broad genetic diversity inherent in the species. Other

Whitebark Pine Strategy

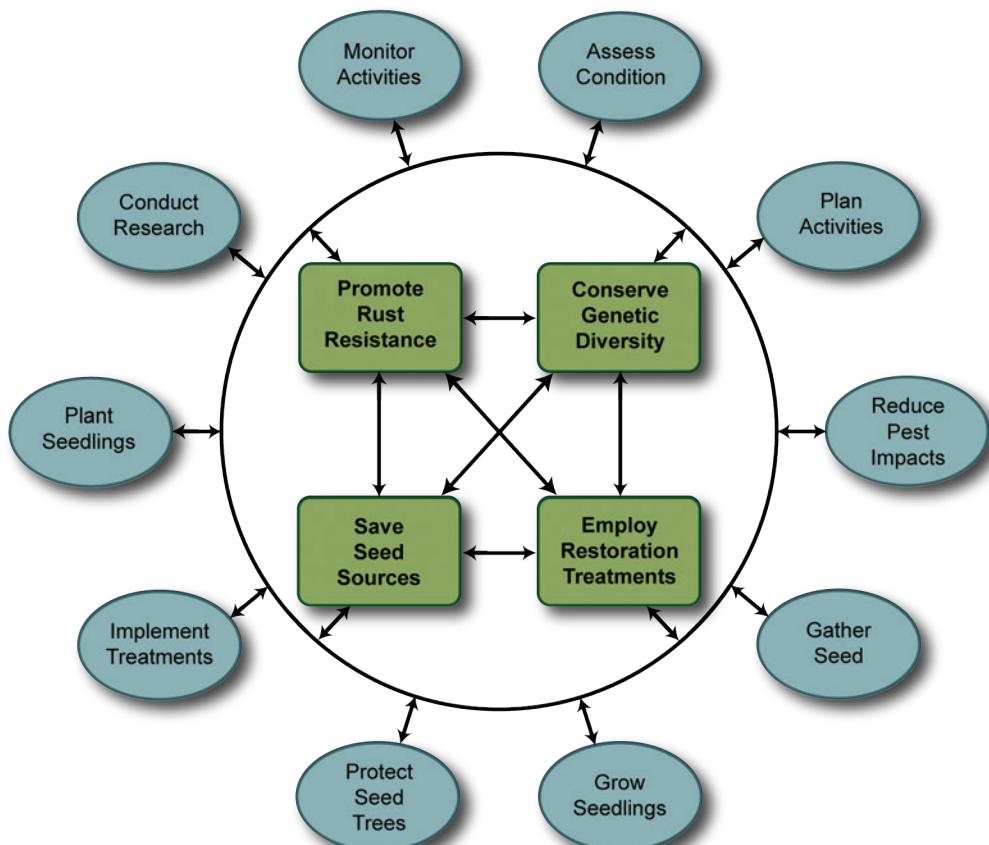


Figure 2.1. The range-wide restoration strategy.

critical activities include archiving pollen; developing seed orchards to produce blister rust-resistant seeds; and establishing clone banks to archive the selections possessing desirable characteristics of blister rust resistance, cold hardiness, and mountain pine beetle tolerance.

3. **Save seed sources.** Mature, seed-producing, putatively rust-resistant whitebark pine trees in regions that are experiencing rapid decline must be protected from other native or exotic disturbances so that the apparent rust-resistant seeds can be harvested in the future. These disturbances include bark beetles, unwanted wildland fire, and timber cutting. Identification and prioritization of areas that contain rust-resistant and genetically diverse trees can be accomplished with comprehensive genetics profiles using data generated from regional genetics programs and collaborative partnerships with research.
4. **Employ restoration treatments.** Areas where whitebark pine forests are declining due to insects, disease, or advanced succession should be considered for restoration treatments to create sustainable whitebark pine populations. Proactive restoration includes managing to limit the spread of blister rust; using fire in successional advanced communities to encourage whitebark pine regeneration; implementing silvicultural cuttings to reduce competing vegetation to increase the vigor of surviving trees and reduce the likelihood of mountain pine beetle attacks; planting rust-resistant seedlings to accelerate the effects of selection; and promoting natural regeneration and diverse age class structures to maintain ecosystem function and reduce landscape level beetle hazard, and to provide large populations for selection for rust resistance.

These principles are used to guide whitebark pine restoration plans at various spatial scales in conjunction with the following set of possible actions. One or more of these actions constitute meaningful steps toward restoring whitebark pine ecosystems.

1. **Assess condition.** Conduct assessments that document the status and trend of whitebark pine within regions. This includes inventory and monitoring projects, GIS mapping and modeling, and remote sensing applications.
2. **Plan activities.** Design plans and possible treatments for restoring whitebark pine ecosystems. This includes prioritizing, locating, and scheduling areas to treat.
3. **Reduce disturbance impacts.** Implement proactive measures to reduce the risk of blister rust, mountain pine beetle, and other disturbance impacts on whitebark pine forests. This may include *Ribes* spp. removal, pruning branches with cankers, spraying fungicide or insecticide, thinning, and treating fuels around rust-resistant trees to reduce wildfire-caused mortality.
4. **Gather seeds.** Collect seeds from trees that are proven rust-resistant or phenotypically rust-resistant in areas exposed to blister rust, and from trees not tested in areas yet to be exposed to blister rust for archiving genetic diversity and variation. These seeds can be used for operational planting, and possibly for direct seeding. Seed collections should be made throughout the distributional range of whitebark pine to capture the range of genetic diversity before it is reduced by the threats to whitebark pine. Seed inventories should be managed and periodically assessed for seed viability and to ensure that effective population sizes are being maintained in space and time. This will enable agencies to be proactive in conservation and to provide a buffer for climate change.
5. **Grow seedlings.** Grow whitebark pine seedlings from seeds of proven (genetically tested in a rust screening) rust-resistant trees; document levels of rust resistance performance in the parent trees and their seedlings; and establish seed orchards, and plant their seedlings in areas that have been treated with the appropriate site prescriptions.
6. **Protect seed sources.** Protect valuable rust-resistant, seed-producing whitebark pine from future mortality caused by disturbance, climate change, and competition.
7. **Implement treatments.** Create conditions that encourage whitebark pine regeneration, conserve seed sources, and promote rust resistance. This includes creating nutcracker caching habitat, reducing competing vegetation, and decreasing surface and canopy fuels using direct or indirect treatments, manipulating forest composition, and diversifying age-class structure.
8. **Plant seedlings.** Plant rust-resistant seedlings or sow seeds directly in treated or burned areas, especially in areas experiencing heavy whitebark pine mortality. Areas with few whitebark pine seed sources will doubtfully produce enough seed to provide for nutcracker energy requirements and adequate whitebark pine regeneration. Because blister rust is at the northern periphery and elevational limits of whitebark pine's range, which are important climate change fronts, seedlings should be planted from rust-resistant parent trees at both the elevational and northern limits.
9. **Monitor activities.** Pre- and post-activity field sampling is critical to document the success or failure of restoration treatments. Limited research funding will preclude extensive assessments of novel restoration treatments and activities, so monitoring will play an important role in providing critical information on the efficacy of restoration approaches. Install, maintain, and collect periodic data in replicated long-term genetic tests to assess the durability of rust resistance under operational conditions and natural inoculum; measure adaptive traits on older seedlings; and periodically reassess seed transfer guidelines and seed source performance under changing climatic conditions.

10. Conduct research. Researchers must continuously develop new and more efficient methods and techniques for identifying blister rust-resistant parent trees, thinning successional stands, growing seedlings, planting seeds and seedlings, and collecting cones. Development of genomic techniques for rapid testing of trees for genetic resistance would save years of greenhouse work and would make proactive restoration planning far easier and less costly. Research should seek to improve the restoration process by providing vital information on state-of-the-art techniques and protocols that will hopefully make restoration efforts more effective and cheaper.

This restoration strategy and its associated actions are discussed at six spatial scales of analysis (Figure 2.2) (Keane and others 1996): (1) whitebark pine's entire range (coarsest scale); (2) regional scale using the U.S. Forest Service Pacific Northwest and Northern Regions as examples; (3) forest scale that is equivalent in size to National Forests and National Parks; (4) landscape scale, which could be watersheds, management units, or landforms; (5) stand scale where most proactive restoration activities take place; and (6) tree level where intensive treatments are needed to protect individual whitebark pines. At each scale, we detail four important factors in the restoration strategy:

- *Assessments*—We present various assessments that can be used to prioritize restoration treatments. These factors describe ownership concerns (wilderness and land management agency, for example), ecosystem characteristics (successional stage and threatened species), and whitebark pine decline (percent rust infection and percent mortality).
- *Restoration Actions*—We present a set of possible tools, treatments, and management actions that can be conducted at the landscape and tree scale to restore whitebark pine ecosystems.
- *Management Concerns*—We detail important issues, barriers, and limitations facing land management for the restoration actions.
- *Examples*—An example or actual implementation of an aspect of the restoration strategy for that scale is included. Actual restoration plans are presented for the coarse-scale strategies, while illustrated examples are presented for the finer-scales (tree, stand, and landscape). We provided summaries of regional, broad-area, and National Forest strategies. The finer-scale examples can be repeated for other areas within the range of whitebark pine.

This strategy and the details of its implementation were integrated from a number of sources and are based on the

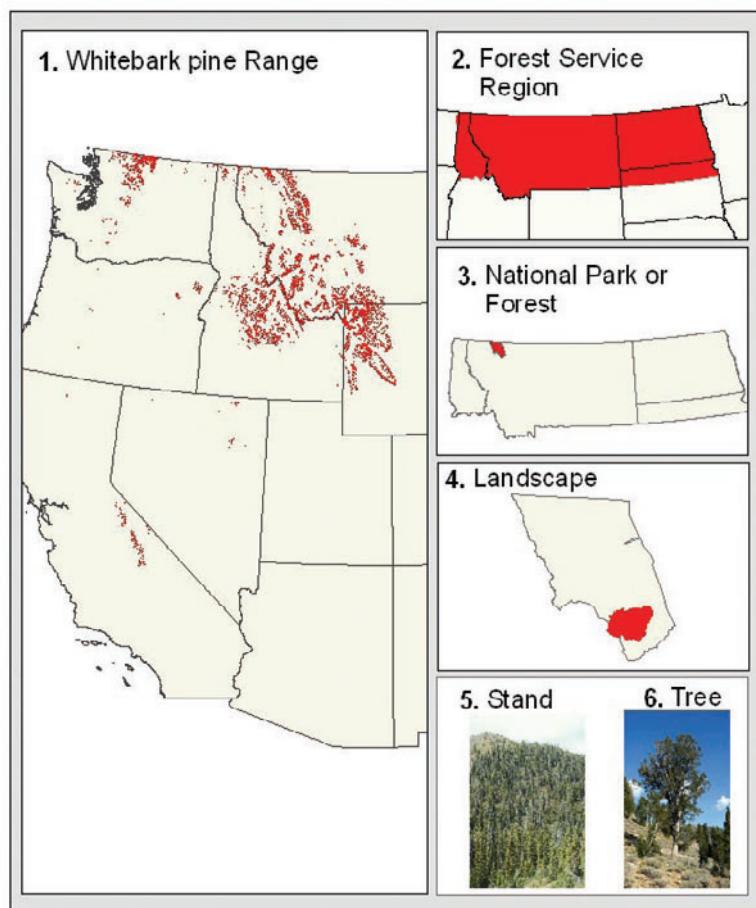


Figure 2.2. The six scales implemented in this whitebark pine restoration strategy.

latest research and perspectives. This strategy also emphasizes the importance of enhancing rust resistance on the landscape based on a number of foundation documents (Burns and others 2007, 2008; Fins and others 2001; Hoff and others 2001; Keane and Arno 2001; Schwandt and others 2006; Schoettle and Snieszko 2007). Several restoration plans for regional and local implementation also provided information used here (Aubry and others 2008; Jenkins 2005; Peterson 1999; Wilson and Stuart-Smith 2001). In the next section, we detail important restoration concepts that provide background for this strategy.

Important Restoration Concepts

The range-wide whitebark pine restoration strategy is built on some important concepts that were used to provide the foundation and context. First, we assume that because whitebark pine's decline is due to an exotic disease, proactive management is needed to ensure that whitebark pine is sustained on future landscapes and restoration should be based on credible science (Hobbs and Cramer 2008). Some people question the need for active restoration management, especially in ecosystems with exotic introductions (Higgs 1997) or wilderness settings (Landres 2010), but we feel that both "reactive" restoration to current conditions and proactive restoration in anticipation of losses are critical for long-term whitebark pine conservation (Schoettle and Snieszko 2007; Snieszko and others 2004). Others suggest a trial-and-error or "tinkering" approach over scientific evidence (Cabin 2007), but we feel that restoration treatments based on the most current scientific information will have the greatest success and will be the most efficient. Schoettle and Snieszko (2007) presented five proactive options for sustaining high-elevation five-needle pine ecosystems threatened by blister rust that overlap with the restoration steps presented above: (1) reduce pest populations, (2) manage forest composition, (3) increase host vigor, (4) plant rust-resistant seedlings, and (5) diversify age classes (also see Keane and Schoettle 2011). The role of whitebark pine as a keystone species becomes increasingly important as whitebark pine becomes more dominant within stands; and thus whitebark pine communities have a higher value than stands that have whitebark pine as a minor component. Therefore, restoration efforts should concentrate on restoring forest communities and not just the species.

Historical Range and Variability

This range-wide strategy is primarily based on the notion that historical conditions provide the most appropriate reference for comparing and assessing whitebark pine status, and historical conditions provide important sideboards and targets for designing and implementing restoration treatments. Historical ecology is used to guide many restoration efforts (Egan and Howell 2001; Perera and others 2004), and the concept of Historical Range and Variability (HRV) is often used to implement historical ecology into restoration

planning (Apfelbaum and Chapman 1997; Landres and others 1999; Morgan and others 1994a). HRV is the broad historical envelope of possible ecosystem conditions or characteristics, such as fire regime, vegetation cover type area, or patch size distribution that provides a representative span of reference conditions to guide land management (Landres and others 1999).

This range-wide strategy assumes that the goal of any restoration treatment or policy is to maintain whitebark pine forests within their historical range. Some feel that HRV will no longer be a viable concept in the future because of expected climate warming and expanding human activities across the landscape (Millar and others 2007). However, we feel at this time that past climates and ecosystem conditions represent considerably less uncertainty than do future predictions of climate and ecosystem response; therefore, HRV represents the best possible reference for guiding restoration in the near term until ecosystem simulation technologies improve and more reliable climate forecasts become available (Keane and others 2009). In fact, large variations in climate over the past several centuries are already represented in many HRV time series. In the meantime, it is doubtful that the use of HRV to guide management efforts will result in inappropriate activities considering the great genetic variation within most species, especially whitebark pine (Davis and others 2005; Rehfeldt and others 1999), the longevity of whitebark pine (Arno and Hoff 1989), and the robustness inherent in regional landscapes that display the broad range of conditions in HRV projections (Keane and others 2009). Restoration plans can be changed as simulation technology improves and as more knowledge becomes available. When ecosystem models have sufficient reliability to generate future trajectories of whitebark pine populations, we suggest a melding of HRV with the future range of variability (FRV) to assess if management actions are outside the envelope of both the past and future conditions (Keane and others 2009).

Physiological Constraints

Another restoration foundation concept is that conservation efforts incorporate adaptation and physiological limitations into their design. The idea of conservation physiology specifically addresses a species' physiological response to the changing environment and disturbance regimes (Wikelski and Cooke 2006). In short, we must know the tolerance limits for all phases of whitebark pine's life cycle for any restoration plan to be effective (for a simple example, don't plant whitebark pine seedlings where they cannot grow) (Cooke and Suski 2008). This seems in conflict with the HRV concept and global climate change, but we emphasize that this physiological approach can be better guided by the HRV of the species range and distribution than any prediction of global climate change environments with biophysical envelop modeling (for example, Warwell and others 2007). Ecophysiological constraints identified from new research can be addressed as climate changes in the future to provide a basis for conserving these high-elevation ecosystems.

Assembly Rules

Last, we base this strategy on the idea of “assembly rules” in restoration ecology (Temperton and others 2004). The species composition of ecosystems is shaped by interactions among species, including pests and diseases, mutualists and competitors, physical disturbance factors, climate, and multiple abiotic factors (soils, for example) (Wilson and others 1996). It is important to include these interactions in restoration designs to ensure that restored ecosystems are sustainable in the future (Luh and Pimm 1993). For example, proactive restoration treatments for whitebark pine should include prescribed burning to emulate the effects of historical disturbance where geographically appropriate (Keane 2001a; Murray and others 1997). Given that the blister rust pathogen is now well-integrated into our western mountain ecosystems and that future warming trends are predicted, the assembly rules approach to whitebark pine restoration entails planting rust-resistant seedlings and even planting seedlings from lower latitudes (Funk and others 2008). This strategy, if supported by geo-climatic analyses of genetic data where blister rust resistance is one of the key adaptive traits, would ensure that whitebark pine survives into the future (Bradley and Pregitzer 2008).

Proactive Approach

Not all whitebark pine ecosystems have been invaded by white pine blister rust, though all are vulnerable to impacts. There is an opportunity with proactive management to enhance currently healthy ecosystems to retain ecosystem function during the naturalization process of the rust (Schoettle and Sniezko 2007). The goal of proactive intervention in these ecosystems is to increase resiliency and sustainability of ecosystem functions in the presence of the spreading rust and other threats such that ecosystem impairment in the future is mitigated (Schoettle and Sniezko 2007). Healthy, functional ecosystems are better able to respond to management than heavily impacted ecosystems. Therefore, more management options are available and the potential for a successful outcome is improved. We know that blister rust can kill trees of all ages and disease impacts the regeneration capacity of pine populations (Schoettle and Sniezko 2007). As a result, efforts to stimulate regeneration after the population is heavily impacted may be compromised due to seed and disperser limitations (Keane and Parsons 2010b; McKinney and others 2009). Interventions in healthy ecosystems can avoid possible regeneration failure that constrain management options and affect outcomes. Sometimes waiting for populations to be impacted before acting is not advisable.

Promoting early selection and establishment of resistant genotypes provides time for the resistant seedlings to mature to seed-bearing age before high mortality occurs in the mature susceptible trees, thereby reducing the time where the ecosystem’s recovery capacity is compromised. Three approaches, two at the stand scale and one at the landscape scale, have been developed to proactively facilitate an

increase in rust resistance and mitigate the impact of the mortality of rust-susceptible trees (Schoettle and Sniezko 2007). Stimulating natural regeneration can increase population size, multiply genetic combinations, and promote efficient selection for resistance in the younger cohorts when rust arrives. Additionally, planting rust-resistant seedlings before rust has impacted an area can directly introduce rust-resistant genotypes to the population. Diversifying the age class structure across the landscape will also result in rust resistance selection (mortality of susceptible pines) proceeding at different rates in different patches that ultimately reduces the impact of mortality in any one cohort on ecosystem services. A mosaic of stand structures and ages positions the ecosystem for rapid and efficient natural selection for resistance in the younger cohort while the older cohort sustains ecosystem function (Schoettle 2004). A structurally diverse landscape is also more resilient to mountain pine beetle impacts and has greater adaptive capacity to climate change. To conduct these interventions requires resources and process-level information on how these little-studied ecosystems respond to perturbation.

Unique opportunities and challenges face researchers and land managers interested in proactively increasing the resiliency of whitebark pine ecosystems, including the need to: (1) educate and engage the public and managers to manage for resiliency, (2) conserve genetic diversity from native populations before they are impacted by rust and other stresses, (3) research patterns, processes, and responses of native ecosystems to provide process-level understanding of ecosystem behavior, and (4) develop and implement management actions that increase the resiliency of whitebark pine ecosystems to prepare them for change.

Central Tenets of the Restoration Strategy

Here, we describe three central tenets upon which the implementation of restoration treatments presented in this plan are based, listed in order of importance:

1. *Lands having high blister rust infection and mortality have the highest priority for restoration.* This is a result of a number of factors, including the following (Schwandt 2006):
 - a. Whitebark pine populations are the lowest in these areas because of decades of decline (Kendall and Keane 2001; McKinney and others 2009).
 - b. There may be a higher frequency of rust-resistant seeds in these areas because rust has likely killed most of the trees that were highly susceptible to the rust (Hoff and others 2001).
 - c. There may be a lower potential for these areas to naturally regenerate to whitebark pine (McKinney and Tomback 2007; McKinney and others 2009; Tomback 2008).
2. *Lands having high mountain pine beetle mortality have a higher priority for restoration* (Perkins and Roberts 2003; Six and Adams 2007). This is because:

- a. Potentially rust-resistant, cone-bearing whitebark pine trees will be killed by the beetles.
 - b. Mountain pine beetle mortality, coupled with rust mortality and fire exclusion effects, will exacerbate the decline of the whitebark pine ecosystem (Six and Adams 2007).
 - c. Seed dispersal will be limited because there will be fewer whitebark pine cone-bearing trees (McKinney and Tomback 2007; McKinney and others 2009; Tomback 2008).
3. *Lands that are in the later stages of successional development have a higher priority for restoration* (Keane 2001b; Keane and Arno 2001). Whitebark pine mortality and cone loss from these stands are the highest because:
- a. These are the stands where whitebark pine occurs in low densities with low vigor because of increased competition from shade-tolerant associates.
 - b. Most mature whitebark pine trees are dying or dead from competition, fire, insect, and disease.
 - c. Many surviving, mature whitebark pine suffer high rates of red squirrel cone predation (McKinney and Fiedler 2010).

In areas where blister rust and mountain pine beetle are at low levels (causing sporadic damage and mortality), it may also be considered prudent to begin proactive restoration work. This work (Schoettle and Sniezko 2007) entails:

1. Managing the spread of blister rust by controlling alternate hosts, usually *Ribes* spp. (care should be taken to limit *Ribes* spp. increases from disturbance) (see Tomback and Achuff 2010).
2. Screening accessible, healthy trees in search of blister rust-resistant parent trees.
3. Thinning or using fire in successional advanced communities to encourage whitebark pine regeneration, which provides selection opportunities.
4. Thinning and reducing competing vegetation to increase the vigor of trees and reduce the likelihood of mountain pine beetle attacks.
5. Planting rust-resistant seedlings from local trees to accelerate the effects of selection.
6. Promoting natural regeneration and diverse age class structures to maintain ecosystem function and provide large populations for selection for rust resistance.

3. National and Regional Direction

Government natural resource agencies are responding to the widespread degradation of natural ecosystems and watersheds, losses of biodiversity, and declining ecosystem function by engaging in strategic planning to mitigate the effects as efficiently and strategically as possible. Ecosystem degradation is often a result of a number of widely different anthropogenic factors, such as altered natural disturbance regimes, habitat destruction, fragmentation, invasive species, loss of natural buffer zones, and climate change. The varied causes and consequences of anthropogenic activities complicate management plans, especially a range-wide restoration strategy such as that detailed in this report. Below are the directions of two Government sources—U.S. Forest Service and Canadian land management agencies—for conducting nationwide restoration activities to preserve critical upper subalpine ecosystems. These directives set the context for many of the details of this restoration strategy for whitebark pine.

U.S. Forest Service

The U.S. Forest Service created an Executive Integration Team that chartered a Restoration Framework Team to develop “a strategic, integrated, science-based framework for restoring and maintaining forest and grassland ecological condition” across the United States (Day and others 2006). Under this charter, a restoration framework team recognized that the nation’s forests and grasslands face serious threats to their long-term health, productivity, and diversity. Foremost are non-native invasive species, altered disturbance regimes, and climate change. These diverse threats affect aquatic and terrestrial ecosystems in virtually every region of the country. Agency and public concern about some of these threats has led to the National Fire Plan (<http://www.fs.fed.us/r1/pgr/afterfire/nfp.html>), Healthy Forests Initiative and Healthy Forests Restoration Act (<http://www.fs.fed.us/projects/hfi/>), Invasive Species Strategy (<http://www.invasivespeciesinfo.gov/toolkit/controlus.shtml>), and various administrative actions to help facilitate restoration actions. Nevertheless, the magnitude of ecosystem restoration needs appears to greatly exceed the organizational and financial capacity of the agency. Many forest and grassland ecosystems, such as whitebark pine, continue to degrade at a rate that can be mitigated by restoration actions. The Forest Service must improve its productivity and effectiveness to achieve restoration objectives. New approaches are needed to clarify and focus the agency’s policy for ecosystem restoration.

This framework offers recommendations to improve the agency’s ability to restore ecosystems (Day and others 2006):

- Adopt a national policy regarding ecosystem restoration, including defining ecosystem restoration as “the process

of assisting the recovery of an ecosystem that has been degraded, damaged, or destroyed.”

- Increase productivity of the agency’s restoration efforts through improved integration of various programs spanning all deputy areas.
- Effectively apply national, forest, and project planning to engage Forest Service resources, partners, and stakeholders in identifying and implementing restoration needs and priorities.
- Use budget and performance incentives to increase accomplishment of ecosystem restoration objectives.

Protection of valuable resources and restoration of severely degraded areas were the primary reasons for creating the Forest Service and establishing the National Forests and Grasslands. Day and others (2006) stated that implementing the recommendations in this Framework will greatly strengthen the agency’s ability to fulfill its mission of sustaining “the health, productivity, and diversity of the nation’s forests and grasslands to meet the needs of present and future generations.” The following are the goals of the national strategy:

1. Reduce the risk from catastrophic wildland fire. Restore the health of the nation’s forests and grasslands to increase resilience to the effects of wildland fire.
2. Reduce the impacts from invasive species. Restore the health of the nation’s forests and grasslands to be resilient to the effects of invasive insects, pathogens, plants, and pests.
3. Provide outdoor recreational opportunities. Provide high-quality outdoor recreational opportunities on forests and grasslands, while sustaining natural resources, to meet the nation’s recreational demands.
4. Help meet energy resource needs. Contribute to meeting the nation’s energy need.
5. Improve watershed condition. Increase the number of forest and grassland watersheds that are in fully functional hydrologic condition.
6. Conduct mission-related work in addition to that which supports the agency goals. Conduct research and other mission-related work to fulfill statutory stewardship and assistance requirements.

The establishment of the Sustainable Land Management Board of Directors (SLMBOD) and their “Restoration and Maintenance” performance measures was intended as an incentive for integrated ecosystem restoration project planning and implementation by allowing line officers to justify higher unit cost for program-specific outputs when the project

results in multiple, reportable outcomes meeting a wide range of established desired condition objectives. Under the direction of the SLMBOD, the Forest Service developed a national strategy for restoration and maintenance of ecosystems with the objective to re-establish and retain ecological resilience of National Forest System lands and associated resources to achieve sustainable management and to provide a broad range of ecosystem services. Intact, resilient landscapes will have greater capacity to respond to and survive natural disturbances and large-scale threats to sustainability, especially under changing and uncertain future environmental condition, such as those driven by climate change and increasing human use.

Chapter 10 of the Fiscal Year 2009 Initial Program Direction includes guidance regarding the establishment of a single performance measure and target. The Program Direction recognizes that ecological restoration and maintenance to achieve sustainable landscapes requires an integrated approach, including restoration of water quality and watershed processes, vegetative condition, air quality, and fish and wildlife populations. During this initial effort to establish and define this new performance measure, the focus is on integrated terrestrial vegetation management designed to meet ecosystem restoration objectives.

U.S. National Park Service

The National Park Service (NPS) administers a broad range of programs that serve the conservation and recreation needs of the National Park System. Management Policies (USDI NPS 2006) is the basic service-wide document to guide management to preserve, unimpaired, the natural and cultural resources and values of the National Park System for the enjoyment, education, and inspiration of this and future generations.

Restoration of natural ecosystems is a tenet of NPS management policies. The NPS strives to understand, maintain, restore, and protect the inherent integrity of park resources, processes, systems, and values. This includes re-establishing natural functions and processes that have been damaged or compromised in the past. Landscapes that have been disturbed by natural phenomena such as landslides, hurricanes, and fires will be allowed to recover naturally. Impacts on natural systems resulting from human disturbances include introduction of nonnative species; contamination of air, water, and soil; changes to hydrologic patterns and sediment transport; and disruption of natural processes. The NPS will seek to return disturbed areas to natural conditions and processes. Examples of restoration efforts are:

- removal of exotic species,
- restoration of abandoned mineral lands, roads, or disrupted waterways,
- restoration of natural soundscapes or visibility, and
- restoration of native plants and animals.

Canadian Land Management Agencies

There is no national direction in Canada regarding the conservation or restoration of whitebark pine or whitebark pine ecosystems, which occur almost entirely on public Crown Lands, including provincial protected areas such as provincial parks, ecological reserves, wildlife management areas, and wilderness areas. The provinces of Alberta and British Columbia have slightly different management mandates and legislation. Therefore, any restoration direction is specified at the provincial level for Alberta and British Columbia.

British Columbia

In British Columbia, the Ministry of Environment's Conservation Framework provides a set of decision support tools to enable collaboration between government and non-government resource managers and practitioners using defined criteria: (1) to prioritize species and ecosystems for conservation; and (2) to determine the most appropriate and effective management actions, including ecosystem and habitat protection and restoration, stewardship, and species and population management. The Ministry of Forests Ecosystem Classification system is used to delineate ecosystems that may cross administrative boundaries such as British Columbia Forest Service Region and district boundaries. The conservation framework provides a decision key for reassigning status ranks (assignment to the British Columbia Red List means that the species is extirpated, endangered, or threatened, and assignment to the Blue List means that the species and ecosystems are of special concern) based on new information; initiating a provincial and/or Federal legal listing process; starting a full recovery/restoration planning process; and initiating on-the-ground protection measures. In most instances, species and ecosystems are formally listed under the provincial Wildlife Act and the Federal Species At Risk Act (SARA) before on-the-ground restoration actions are formally implemented with provincial-level guidance.

A recovery and restoration process and plan would become mandatory if whitebark pine was moved to British Columbia's Red List, and prioritization of activities would be undertaken at the provincial level. The Ministry of Environment published a document on guidelines for ecological restoration on public and private lands. This document lays out the philosophy of ecological restoration and provides general guidelines for setting restoration goals and objectives, setting restoration priorities, and planning restoration projects. There is not yet a formal province-wide restoration plan for whitebark pine, but several conservation actions have been initiated:

- A provincial inventory of whitebark pine and its communities has been completed.
- Province-wide surveys of blister rust infections and mountain pine beetle infestation have been undertaken.

- The British Columbia Ministry of Forests in collaboration with the Canadian Forest Service and the University of British Columbia produced first approximation projections of climate change impacts on whitebark pine, including climate change impacts on disturbance (Carroll and others 2006; Hamann and Wang 2006).
- The British Columbia Conservation Data Centre added whitebark pine to its Blue List in 2007 with the justification that although the species currently occurs in relatively high numbers over a fairly large range in the province, major declines of 75 to 90 percent are expected “due to a severe negative long-term trend expected from mountain pine beetle infections, the white pine blister rust epidemics, climatic warming trends, and successional replacement.”
- Following the British Columbia assessment, the Deputy Chief Forester for the British Columbia Ministry of Forests and Range issued a letter asking resource managers and forest professionals to take voluntary measures to conserve whitebark pine during forestry activities by considering the species in planning and operational activities.
- The British Columbia Ministry of Forests has surveyed in situ protection of all tree species in British Columbia protected areas, including whitebark pine (Hamann and Wang 2006).
- The British Columbia Ministry of Forests and Forest Genetics Council of British Columbia has drafted a gene conservation strategy for whitebark pine (Krakowski 2001).

- The British Columbia Ministry of Forests has collected cones and seed for storage to conserve genetic diversity and to test for rust resistance to blister rust.
- Because of the mandate to minimize anthropogenic damage and restore damaged ecosystems, local restoration activities have occurred within some protected areas in British Columbia.

The British Columbia Forest Service divides the province into three administrative regions: Coast Forest Region, Northern Interior Forest Region and Southern Interior Forest Region (<http://www.for.gov.bc.ca/mof/regdis.htm#rco>).

Alberta

In Alberta, whitebark pine was recently approved for legal listing as Endangered because of an ongoing and projected decline in populations across the province. Although there are neighboring whitebark pine populations in Montana and British Columbia, blister rust and mountain pine beetle are present in both geographic regions, reducing the likelihood of seed dispersal (Alberta Sustainable Resource Development and Alberta Conservation Association 2007). Furthermore, there may be insufficient quality habitat for successful establishment of emigrant pines given the presence of blister rust and mountain pine beetles in Alberta, even if nutcrackers could disperse seeds from Montana or British Columbia. Therefore, rescue of Alberta whitebark pine populations from other jurisdictions is unlikely. The Alberta provincial government is working on a gene conservation strategy.

4. Restoration By Spatial Scale

In this chapter, we describe how the range-wide whitebark pine restoration strategy (Figure 2.1) can be implemented across the six scales of analysis (Figure 2.2). Several elements are discussed at each scale. First, we present *a description of the scale* to provide spatial context for the following four topics. Next, the *assessment factors* that can be accomplished at that scale are discussed. Then, we suggest possible *restoration actions* to help guide managers to develop range-wide-to-local restoration plans. This is followed by a discussion of *management concerns* that may need to be addressed. Last, *examples* of restoration actions at the scale under discussion are presented. For the coarsest scales, a detailed restoration plan is provided instead of examples to guide local restoration action implementation. For example, at the scale of whitebark pine's range, we have combined a number of spatial data layers to create a prioritization of possible regions for restoration.

Range-Wide Scale

This is the coarsest scale of analysis and is defined in this report as all lands that encompass the entire range of whitebark pine in the contiguous United States (lower 48 states) and western Canada (Figure 1.2). In this report, the range of whitebark pine can be spatially stratified into five broad regions (see next section) to correspond to other conservation and restoration efforts (Figure 4.1). These geographic regions include nearly all whitebark pine in the United States and Canada.

Assessments

Several core GIS layers are required for a comprehensive assessment of restoration potential and priority at this coarse scale. A key layer is a digital range map of the spatial distribution of whitebark pine. Keane (2000) developed a digital range map using an empirical approach where the elevational limits of whitebark pine were predicted using data from Pfister and others (1977). Other spatial distribution maps include digitized versions of the Little and Critchfield (1969) range map, the Arno and Hoff (1990) range map, and the Warwell and others (2007) empirical bio-envelope distributional map. Another important digital layer is a coarse-scale land ownership map provided by the U.S. Forest Service that shows Regions, National Forests, Wilderness Areas, and National Parks. Finer delineations of management emphasis areas would also be useful.

Perhaps the most important data layers for this assessment are digital maps representing the decline of whitebark pine across its range. Helmbrecht and Keane (in prep) have developed a GIS layer that maps the levels of rust infection

in whitebark pine across the western United States. This map was created using gradient modeling where environmental factors such as temperature, precipitation, and topography were used to predict rust infection levels using statistical models based on data provided in the WLIS database (Lockman and others 2007). Kearns (2005) used a similar approach in predicting blister rust levels in Colorado that was later evaluated by Howell and others (2006). Kendall and Keane (2001) developed a map of whitebark pine mortality and rust infection, but the map detail may be too coarse for a comprehensive restoration plan. A map of current mountain pine beetle outbreaks and mortality is also important, but it may have to be created for the entire range of whitebark pine.



Figure 4.1. Broad regions used in this report to stratify geographical areas within the range of whitebark pine in the United States and Canada.

Other important maps included in this assessment represent the current major issues associated with whitebark pine forests. A critical map used here is the current distribution of grizzly bear range across the range of whitebark pine. Other important maps might be species distributions of lynx and other endangered endemic plants and animals of whitebark pine communities. Human settlement maps, such as the wildland-urban interface (WUI) and county population level, would help identify those few whitebark pine lands that are adjacent to development. Last, transportation maps of road and trail densities could help identify those areas that have access for proactive restoration activities. Additional maps that could be used to plan restoration are based on bioclimatic models that attempt to show the changes in whitebark pine elevation and latitudinal distribution with climate change (Hamann and Wang 2006; McKenney and others 2007; Schrag and others 2007; Warwell and others 2007). These predictions are informative but must be regarded as coarse-scale predictions because they do not incorporate many local environmental and physical variables (Keane and others 2008b).

Restoration Actions

One of the most important actions at this coarse scale is the creation of a range-wide genetic resistance program to promote the conservation of rust resistance in whitebark pine. This program would identify and mark possible rust-resistant, cone-producing trees in high blister rust areas (Mahalovich and Dickerson 2004), while seeking the greatest amount of genetic variation possible. Cone collections from these trees could provide an immediate seed source for operational reforestation, ex situ genetic conservation, and seedlings for blister rust resistance screening (for example, the Pacific Northwest Region ex situ gene conservation strategy described by Bower and Aubry [2009]). Pollen can be collected for genetic conservation and to advance blister rust resistance in seed and breeding orchards. Data from rust screenings can uniquely identify whitebark pine seed sources that provide high levels of blister rust resistance.

In 2001, Mahalovich and Dickerson (2004) created a multi-state restoration program (Idaho, Montana, Nevada, and Wyoming) designating permanent leave trees and selecting the healthiest, least infected trees in high blister rust- and mountain pine beetle-affected areas. Leave trees are elevated to elite-tree status based on their rust-resistant progeny in the rust screenings, and used as (1) a source of scion for root stock grafts in seed orchard creation, (2) a seed source for operational collections, and (3) seed trees for natural regeneration. Survivors of the blister rust screening are planted in clone banks for genetic conservation purposes to serve as donors for future seed orchard establishment and to facilitate selective breeding. Along with this program came recommendations about mixed seedling plantings following published seed transfer guidelines and suggestions for planting seedlings from other seed zones with warmer climates. However, genetics data for the U.S. northern Rockies region analyzed with geo-climatic variables do not support planting of whitebark

pine seedlings from warmer climates because there is both the blister rust resistance and late winter cold hardiness issues due to the span of over 1600 m in elevation from northwest to southeast. This allows a bet-hedging strategy facilitating whitebark pine survival and genetic migration under current and near future climate.

Another important action is the prioritization of regions or subregions for coarse-scale planning, such as allocating national resources for finer-scale restoration efforts. In one example, prioritization could involve the distribution of funding to regional scale stratifications (National Forest and Regions). Another example could involve the implementation of the rust-resistance program for determining when and where to allocate valuable restoration funds. Prioritization might be based on the status and health of whitebark pine forests, the likelihood for favorable outcomes, or the decision to establish whitebark pine “core areas” from which seeds eventually could be dispersed to neighboring areas (Tomback and Achuff 2010). It could also be based on numerous other concerns such as available management expertise, grizzly bear population distribution, available research results, extent of potential whitebark pine areas, and favorable land management policies (wilderness versus non-wilderness).

Other important restoration actions at this level include developing the knowledge, experience, and resources needed to implement effective restoration strategies. This involves an integrated basic and applied research program aimed at obtaining the knowledge and data that will be useful in the conservation of whitebark pine. Developing, collecting, and maintaining the comprehensive spatial data that provide context for restoration actions are also important tasks to proactively gain necessary information to evaluate risk and design restoration plans at multiple scales. Mapping the distribution of the species, threats to this species, spatial context (land ownership, wilderness, and roads, for example), forest structure and developmental stages (successional stage), and condition (level of mortality) at various scales is an important first step. Standard GIS spatial analysis techniques can be used on available digital maps describing ecology and management issues to provide the critical spatial information needed for many restoration efforts. Developing supporting technologies for whitebark pine management is also critical—for example, finding new ways to harvest cones; improving nursery techniques to reduce seedling costs; exploring new ways to regenerate whitebark pine using seed planting techniques; and developing standardized methods for monitoring, inventorying, and describing whitebark pine health, populations, and seed production.

Education is also effective at this level. Education and training programs for agency personnel is critical for planning and implementing successful whitebark pine restoration programs. Educating the public on the plight of whitebark pine is also critical in that it might improve support for restoration projects. The Whitebark Pine Ecosystem Foundation (www.whitebarkfound.org) is dedicated to restoring whitebark pine ecosystems throughout its range, and one of its missions is to educate people about the values and potential for restoration.

Management Concerns

A major concern is that some regions might be funded for restoration over others because of their higher prioritization. It will be difficult in the restoration prioritization process to decide funding allocation based on regional and range-wide parameters. Just because there are fewer whitebark pine trees in one region does not mean that region should get less funds for restoration—all whitebark pine forests are important for conservation. The design and development of prioritization analysis methods are critical for implementing range-wide restoration policies and actions. Another major concern is that maps will be included in range-wide assessments that may not match the scale of analysis. For example, a layer that depicts whitebark pine cover types may not be appropriate at the range-wide scale of analysis because cover types are quite variable within coarse resolutions and grain sizes.

A Range-Wide Prioritization for Whitebark Pine

The following is a proposed coarse-scale prioritization strategy to restore whitebark pine across its range in the United States. This strategy is not a final product but rather a baseline for conducting future prioritization efforts, and it should be improved as additional spatial data layers, new inventory and monitoring data, and new research become available. We realize that any prioritization is ultimately governed by the objective(s) of that prioritization, which can be as simple as determining where to allocate resources or as difficult as deciding which wilderness areas should be targeted for whitebark pine restoration.

Comprehensive, consistent, and accurate spatial data layers are desperately needed for successful prioritization plans. Unfortunately, few data layers were available to use for this prioritization effort. First, we found no data layers for all lands in Canada that represented whitebark pine. Second, most other data layers were inconsistent or too general across the entire range of whitebark pine, so Canada was not included in this analysis. Despite our best efforts, we were unable to locate or modify any coarse-scale data layers that were useful in the context of whitebark pine management. As a result, this prioritization has two parts. The first part is the description of limited prioritization effort using existing data layers, and the second part is a list of prioritization criteria that can be used for a coarse-scale effort once suitable data layers are available.

The three spatial data layers that we used to identify lands that are in the greatest need for restoration are:

- **Whitebark pine range** (Figure 4.2a). We used the Helmbrecht and Keane (in prep.) layer because it is consistent with the following blister rust infection layer.
- **Rust infection map** (Figure 4.2b). We used the Helmbrecht and Keane (in prep.) infection map to identify those regions that have the highest rust infections and used a 50 percent infection rate to identify low (less than 50 percent) and high (greater than 50 percent) infection areas.
- **Grizzly bear habitat** (Figure 4.2c).
- **Ownership** (Figure 4.3). Only Federally administered lands were included in this layer along with various agency geographic boundaries.

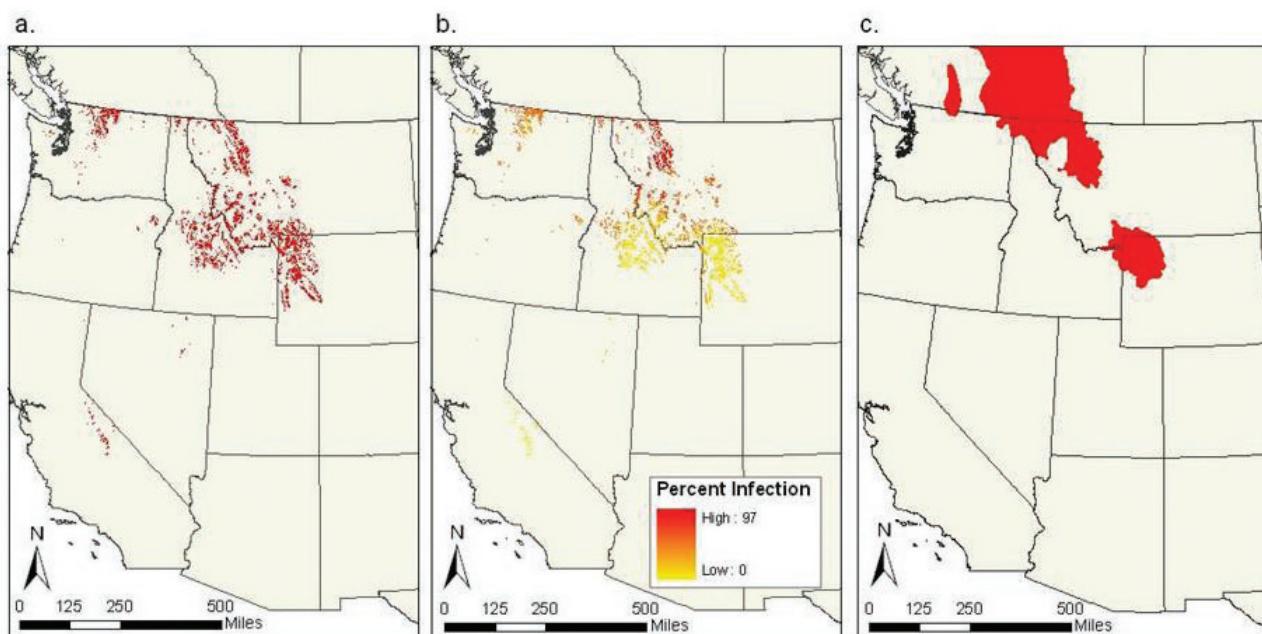


Figure 4.2. Maps used in the prioritization of whitebark pine areas for restoration: (a) empirically derived range map from distributional data (whitebark pine shown in red) (Helmbrecht and Keane [in prep.]), (b) rust infection level for whitebark pine across its range outside of Canada by Helmbrecht and Keane [in prep.]), and (c) range of the grizzly bear (shown in red) in the western United States.

Figure 4.3. Federal ownership digital layer across the range of whitebark pine in the western United States and lands within the Regions of the USDA Forest Service.

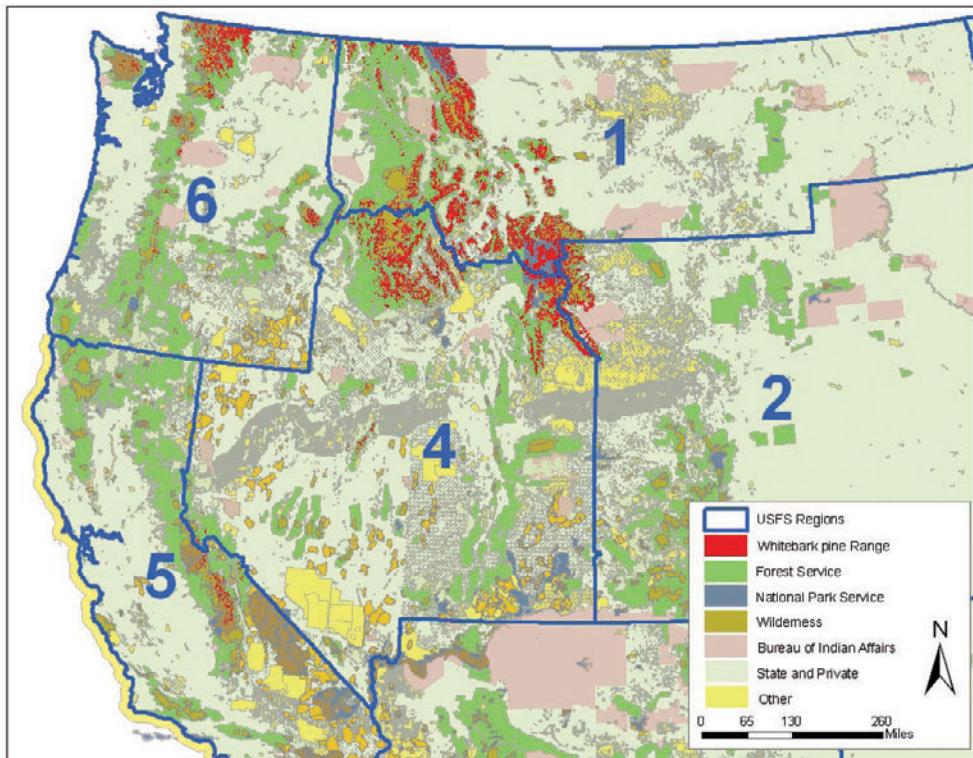


Figure 4.4. Range-wide prioritization of whitebark pine restoration.

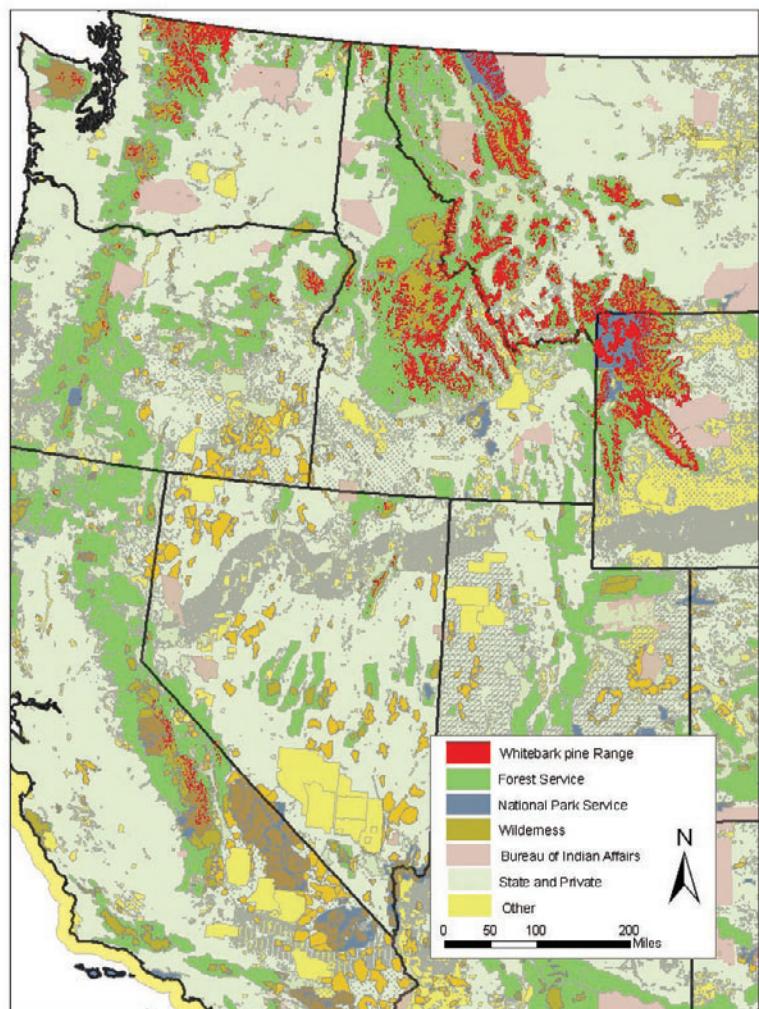


Table 4.1. Hectares of whitebark pine range by Forest Service Region and land ownership type in the western United States.

Land ownership	Whitebark pine range	Blister rust infection (>50%)	Grizzly bear range	Restoration plan*
<i>U.S. Forest Service Regions</i>				
Northern (Region 1)	2,757,580	1,274,020	62,831,600	844,372
Rocky Mountain (Region 2)	418,650	284	12,045,300	87
Intermountain (Region 4)	1,805,190	21,083	12,023,900	3,747
Pacific Northwest (Region 6)	668,967	153,958	4,283,170	8,085
Pacific Southwest (Region 5)	119,155	0	0	0
<i>Land ownership</i>				
Forest Service	2,708,687	688,818	387,544	328,932
National Park Service	584,111	139,538	317,308	139,538
Private or State lands	166,241	35,816	17,400	20,616
Wilderness	2,178,084	537,229	461,192	329,938
Centennial Mountains Sheep Experimental Station	3,047	1,691	1,672	1,691
Bureau of Indian Affairs	71,391	38,608	29,884	33,476
Bureau of Land Management	55,922	6,707	5,284	2,121
Department of Defense	2,362	1,268	384	437
Fish and Wildlife Service	168	7	52	7
Total hectares	5,770,013	1,449,682	1,220,720	856,757

*This range-wide restoration plan includes only areas with >50% blister rust infection that are also within the range of grizzly bears.

Based on these layers, we prioritized National Forest Regions (Figure 4.3) (not the regions in Figure 4.1) by overlapping these spatial layers and summing the area of overlap by the landscape stratifications (Figure 4.4). The total area in need of whitebark pine restoration is summarized in Table 4.1 by land ownership and National Forest Regions. This final layer forms the core prioritization areas for possible reference in planning coarse-scale restoration programs.

Many other data layers should be added to this analysis once they become available. Layers that describe whitebark pine range loss rates from climate change predictions (<http://forest.moscowfsl.wsu.edu/climate/>) could be used to target areas where whitebark pine is most at risk. We could also add layers that describe road and trail density to identify areas for proactive treatment using prescribed fire or mechanical cuttings (Keane and Parsons 2010b). Layers portraying whitebark pine mortality from disturbance would

also be valuable, such as a fire severity atlas (fire severity of recent fires) and mountain pine beetle damage maps.

This core prioritization can be augmented with any number of other layers to focus the prioritization for multiple objectives. Regions could be prioritized based on the extent of designated wilderness and areas that allow controlled wildfires. Also, care should be exercised when deciding priorities based on the extent of whitebark pine forest area within a region unless area is specifically part of the objective. Instead, it might be more appropriate to use percent of total area if the prioritization objective does not need to incorporate area itself in the decision process. We also urge caution when mixing scales in the GIS overlay process. In summary, it is impossible at this time to anticipate the ultimate objectives of Federal land management agencies for whitebark pine restoration planning. Therefore, we suggest that our core prioritization layer summarize conditions that are important for all planning efforts.

Regional Scale

This scale defines large regions that are important to stratify for restoration planning for whitebark pine across its range. In this report, we use U.S. Forest Service Regions and Canadian Provinces as our spatial delineation for simplicity and consistency, but we could easily have used Bailey's (1995) sections, the regions in Figure 4.1, or major mountain ranges. Regions can be described by land divisions within the range of whitebark pine. These divisions might be along ecological boundaries, such as the seed transfer zones presented by Hoff and others (2001), hydrological subdivisions such as Level 4 code HUC (Hydrologic Unit Code) (USGS 1987) watersheds, or mapping zones such as the ecological zones used by the EROS Data Center (Rollins and others 2006).

Assessments

Essentially the same layers used for range-wide assessments can be used at this regional scale because the main action for restoration at this scale is again prioritization. At the regional scale, the emphasis for prioritization can be on other, more specific factors such as:

- **Amount of funding available.** How much money is available to perform restoration actions? Low funding might indicate that planning and analysis tasks could be performed in preparation for future implementation, while high funding levels might indicate that restoration treatments can be implemented and assessments can be designed to emphasize lands that can have proactive treatments.
- **Available human resources.** How many people are experienced in whitebark pine restoration planning and activities? Can some restoration efforts be contracted out? The depth of available expertise is an important factor when deciding if a region has the ability to conduct restoration activities. This is especially true if prescribed burning and silvicultural cuttings are being considered.
- **Current management.** Can current management plans hinder whitebark pine restoration plans? For example, wildland fire use can only be considered if areas within the region are covered by fire management plans. U.S. Forest Service policy of not planting trees in wilderness could also affect any proactive restoration plans. Management plans for Endangered or Threatened Species might also influence restoration actions in some areas.

Restoration Actions

The design of a gene conservation strategy through seed collections and a blister rust screening program for restoration efforts is perhaps the most important restoration activity that is efficiently accomplished at this scale. Development of

a regional cone collection program using the seed zones described by Mahalovich and Hipkins (2011) would represent a significant step to ensure sufficient seeds are available for planting post-burn or post-treatment areas with viable whitebark pine seeds or seedlings that are putatively resistant to blister rust.

Another important activity is the regional development of a selective breeding program for whitebark pine, as was discussed at the range-wide scale. There is a general consensus among land managers that we should continue a genetic restoration program with an emphasis on selective breeding for white pine blister rust resistance. Identifying and collecting seeds from phenotypic rust-resistant individuals for this program is a high priority, and participation by all National Forests, Bureau of Land Management, and National Park Service and Canadian partners in the whitebark pine's range is strongly encouraged. Stands with high infection levels are a high priority for cone collections from phenotypically resistant trees (Hoff and others 2001).

The Northern, Rocky Mountain, and Intermountain Regions Genetic Restoration Program for Whitebark Pine

An Inland West Genetics Shared Services Agreement established in 1995 provides the framework for a multi-region, multi-agency, trans-boundary partnership covering Idaho, Montana, Nevada, Wyoming, and Alberta, Canada (Mahalovich 2000; Mahalovich and Dickerson 2004). The Northern, Rocky Mountain, and Intermountain Regions; USDI National Park Service; USDI Bureau of Land Management; Parks Canada; and Alberta Tree Seed Centre are active participants. Program goals include:

1. complete operational cone collections for planting to improve critical wildlife habitat and restore properly functioning watersheds,
2. designate plus trees and collect cones for rust screening and genetic conservation,
3. evaluate patterns of genetic diversity in molecular markers and genetic variation in adaptive traits,
4. refine seed transfer guidelines,
5. establish production seed and breeding orchards of blister rust-resistant whitebark pine,
6. compile a comprehensive genetics profile for conserving highly diverse and rust-resistant populations across the landscape,
7. develop clone banks and a live-tree network across the landscape for gene conservation, and
8. install long-term genetic tests to monitor the durability of rust resistance.

Rust resistance testing of seedling progenies of candidate plus trees is performed at the U.S. Forest Service Coeur d'Alene Nursery, Coeur d'Alene, Idaho. Mahalovich and

Dickerson (2004) provided the sampling design for seed collections to capture rust-resistant candidate trees and to capture desirable gene complexes by broadly sampling the physiographic and elevational breadth of the species. Each agency voluntarily participates in gene conservation cone collections for the National Center for Genetic Resources Preservation in Fort Collins, Colorado. Field activities are facilitated among partners within each seed zone (for example, GYA Subcommittee and the Northern Continental Divide working group) to optimize available resources.

The program began with cone collections in 1991 when provisional seed transfer and operational cone collection guidelines were delineated using known blister rust infection levels and physiography (Mahalovich and Hoff 2000). Genecology and molecular genetics studies ran concurrently with a rust screening and cold hardiness trial (1999 to 2005) (see “Genetics” section). Phase II was initiated in 2001, following the numerous wildfires in 2000. Approximately 1024

plus tree selections among five seed zones comprised the testing population. Designating new plus trees is ongoing to replace those plus trees lost to mountain pine beetle and fire and to meet gene conservation objectives. Three rust screenings of over 95,000 seedlings in 2011 are under evaluation. At the completion of each screening, two performance tests are established in whitebark pine cover type.

Recently, each National Forest and two National Parks developed a 10-year comprehensive seed procurement plan summarizing: (1) number of pounds of blister rust-resistant seeds needed for operational planting, (2) number of seedlings needed for coordinating production needs at nurseries and for determining acreages for seed orchard establishment, and (3) number of planting acres for large-scale disturbance to have enough seeds on hand for climate change as the severity of mountain pine beetle epidemics and increases in uncontrolled wildfires are attributed to warming trends and drought conditions. Four production seed orchards are under development to meet planting needs in the northern Rockies.

A comprehensive genetics profile (Mahalovich and Hipkins 2011) is periodically updated as new plus trees are selected in the genetics program and evaluated in rust screening, genecology, and molecular studies. Areas with high genetic diversity, blister rust resistance, or rare alleles facilitate restoration efforts and facilitate identification of new candidate locations for the U.S. Forest Service Research Natural Areas program (Evenden and others 2001). A recent compilation of these genetic resources is incorporated in a GIS layer (Figure 4.5). There is sufficient genetic diversity, genetic variation, and absence of inbreeding to support the continuation of a rust resistance screening and genetic restoration program (Mahalovich and Hipkins 2011).

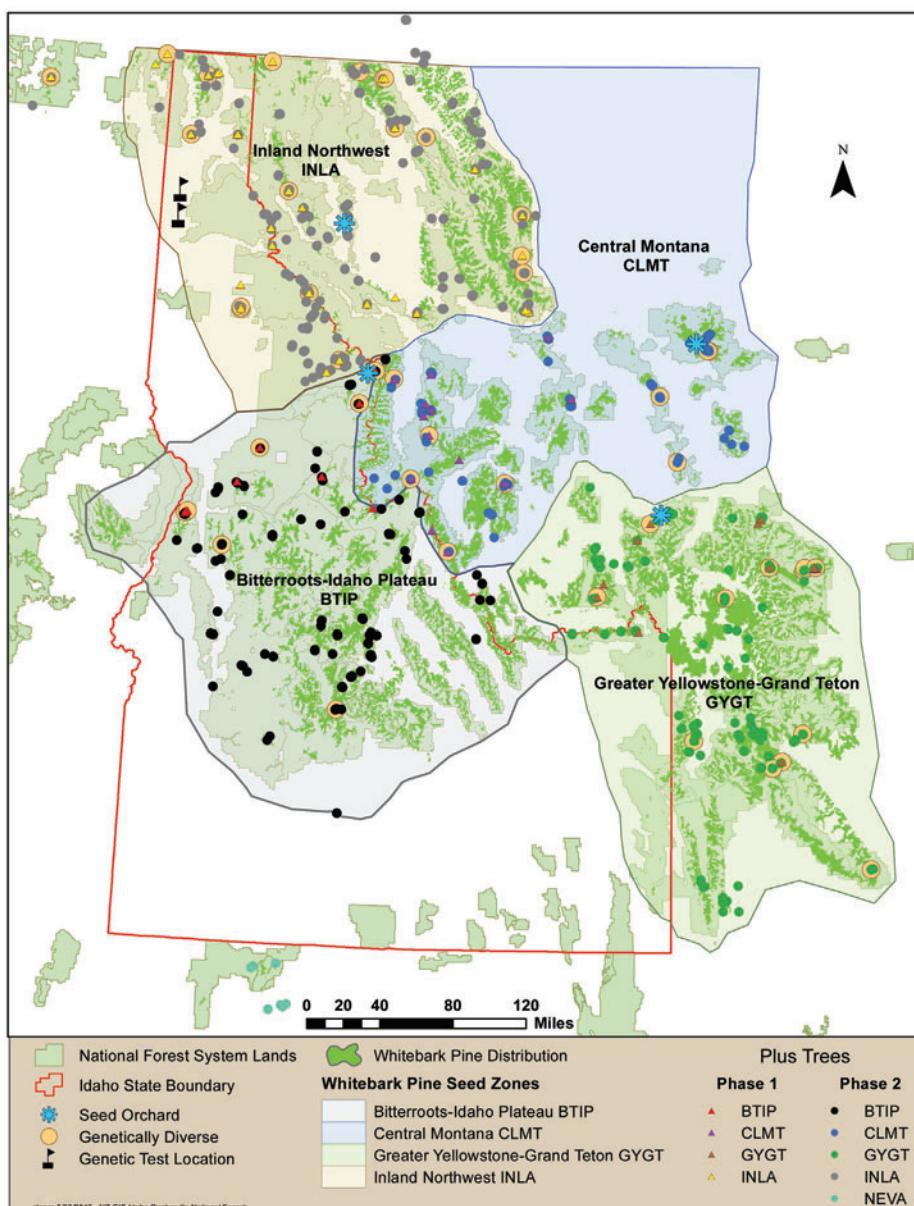


Figure 4.5. A compilation of genetic resources in the northern Rocky Mountains.

Management Concerns

The consistent representation of whitebark pine status and trends across all lands within a region is one of the major concerns at this scale. Spatial data layers portraying vegetation, rust infection, and beetle-caused mortality are often inconsistent in detail and accuracy across an entire region. Another major concern is that management issues that are important to National Forests, National Parks, and Provincial Forests will not be represented by the suite of available data layers. For example, the current status of mountain pine beetle mortality might not be represented in National Forests where the outbreak is just starting. As with the range-wide scale, the design and development of prioritization analysis methods are critical for implementing region-wide restoration policies and actions, and prioritization variables have different weights across areas within the region. For example, National Forests with low abundance of whitebark pine might receive low priority, but active management of whitebark pine in these areas might be critical to avoid their extirpation.

The U.S. Forest Service Northern Region Restoration Strategy for Whitebark Pine

The Northern Region's Integrated Restoration and Protection Strategy (IRPS) draws upon the basic premises of the national strategic goals and uses integrated objectives to prioritize and accomplish regional ecosystem restoration and protection of values at risk. The scale of consideration for the Strategy is the Northern Region of the U.S. Forest Service, which includes 12 National Forests located within the perimeter of northeastern Washington, northern Idaho, and Montana, and the National Grasslands in North Dakota and northwestern South Dakota. The Strategy is intended to be dynamic and will be continually amended as needed to address new information, changes in conditions, and changes in national priorities. The intent is to develop a common vision for addressing resource conditions across geographic areas independent of National Forest administrative boundaries. This Strategy is needed to promote integration among programs and budgets and to set priorities for investments in restoration and protection projects. It also sets the stage for addressing the relationships between wildfire and wildland fire use for the future.

The focus of the Northern Region's IRPS is to:

- Restore and maintain high-value watersheds in a properly functioning condition;
- Restore and maintain wildlife habitats, including restoring resilient vegetation conditions where appropriate, to meet ecological and social goals; and
- Protect people, structures, and community infrastructure (roads, bridges, and power corridors) in and associated with the WUI.

The strategy uses the foci described above, including resiliency of vegetation, which contributes to the distribution

and quantity of specific vegetation categories across the Northern Region, and characterizes the values that may be at risk in the event of uncharacteristic and geographically large fire events.

Some management tools that help achieve desired conditions for vegetation, specifically to promote ecosystem resiliency, diversity, and watershed health, include: (1) wildland fire use, (2) prescribed burning, (3) mechanical fuel treatments, (4) road restoration, and (5) elimination or reduction of invasive species. The mix of tools that are used for restoration and protection projects address specific conditions within the general land categories. For example, mechanical treatments may not be appropriate where backcountry and wilderness values are priorities. Likewise, wildland fire use may not be the most appropriate tool in the WUI. Some of the specific resources and values that are addressed by this strategy and that are influenced by natural processes and cultural treatments are:

- community infra-structure,
- old growth forest,
- threatened, endangered, and sensitive wildlife and plant species,
- wildlife habitat, including resilient vegetation conditions,
- watersheds and fish habitat,
- municipal watersheds, and
- recreation facilities.

Three focus areas for strategy implementation are: (1) identifying values that are directly threatened by potential large geographic scale fires; (2) restoring and maintaining watersheds and fish habitat; and (3) maintaining resilient vegetation conditions that restore wildlife habitat. The following are specific action items used to build a spatial map of priority areas that are regionally significant:

1. Protect people, structures, and community infra-structure (roads, bridges, and power corridors) that may be influenced by large geographic scale fire and large mountain pine beetle outbreaks.
2. Identify areas or watersheds that are fish and watershed restoration areas.
3. Promote opportunities to restore resilient vegetation that also function as key wildlife habitats.
4. Identify municipal watersheds.
5. Identify recreation areas that may be threatened by disturbance based on past investments and the level of people that use these areas.

The Strategy recognizes that resource conditions and values may vary at the Forest/Grassland or Ranger District scale. Areas outside the potential path of a "geographic fire" risk area or that are not spatially located on the map of priority areas that are regionally significant may still be a high

priority for treatment at local scales; individual units can use this same approach to address those unique situations.

Whitebark pine restoration is addressed in Scenario 2a under Theme 2 “Terrestrial Species: Unique Wildlife Habitats.” Whitebark pine was identified during the 1998 Northern Region Overview as a rare landscape element because it is an important species and dominates a unique plant community. A number of spatial data layers are used as input in the prioritization process. Because the Northern Region IRPS Whitebark Pine Restoration Strategy is still under development, we present our interpretation of these layers in the context of this report. While our analysis is detailed and comprehensive, it is meant for illustration purposes. It does not replace IRPS, even though it will be quite similar to the finished product since we are using the same data layers.

The analysis has a core restoration plan that includes core data layers that describe ecological processes important in whitebark pine conservation. We used the Helmbrecht and Keane (in prep.) white pine blister rust data layer to determine areas that have greater than 50 percent infection

(Figure 4.6a). In this layer, we also included points that correspond to trees found to be susceptible to blister rust based on field sampling. To describe damage from mountain pine beetle, we used data from the Aerial Detection Survey conducted by the Northern Region (Figure 4.6b). For prioritization purposes, we only included those areas that had more than three dead trees per acre due to mountain pine beetle. Spatial information for crown fire potential was based on data created with the large fire simulator FSIM for the Northern Region (Figure 4.6c). This data layer shows areas that are considered to have the potential for crown fire according to the following criteria: (1) flame length greater than 6 ft, (2) areas where the canopy cover is greater than 10 percent using the LANDFIRE cover layer (Rollins 2009), and (3) areas where the Scott and Burgan (2005) Fire Behavior Fuel Model values are greater than or equal to 161.

The spatial overlay of these layers is shown in Figure 4.7 by land ownership to form the core whitebark pine restoration plan, and the summary statistics are described in Table 4.2. In short, the majority of land that is high priority

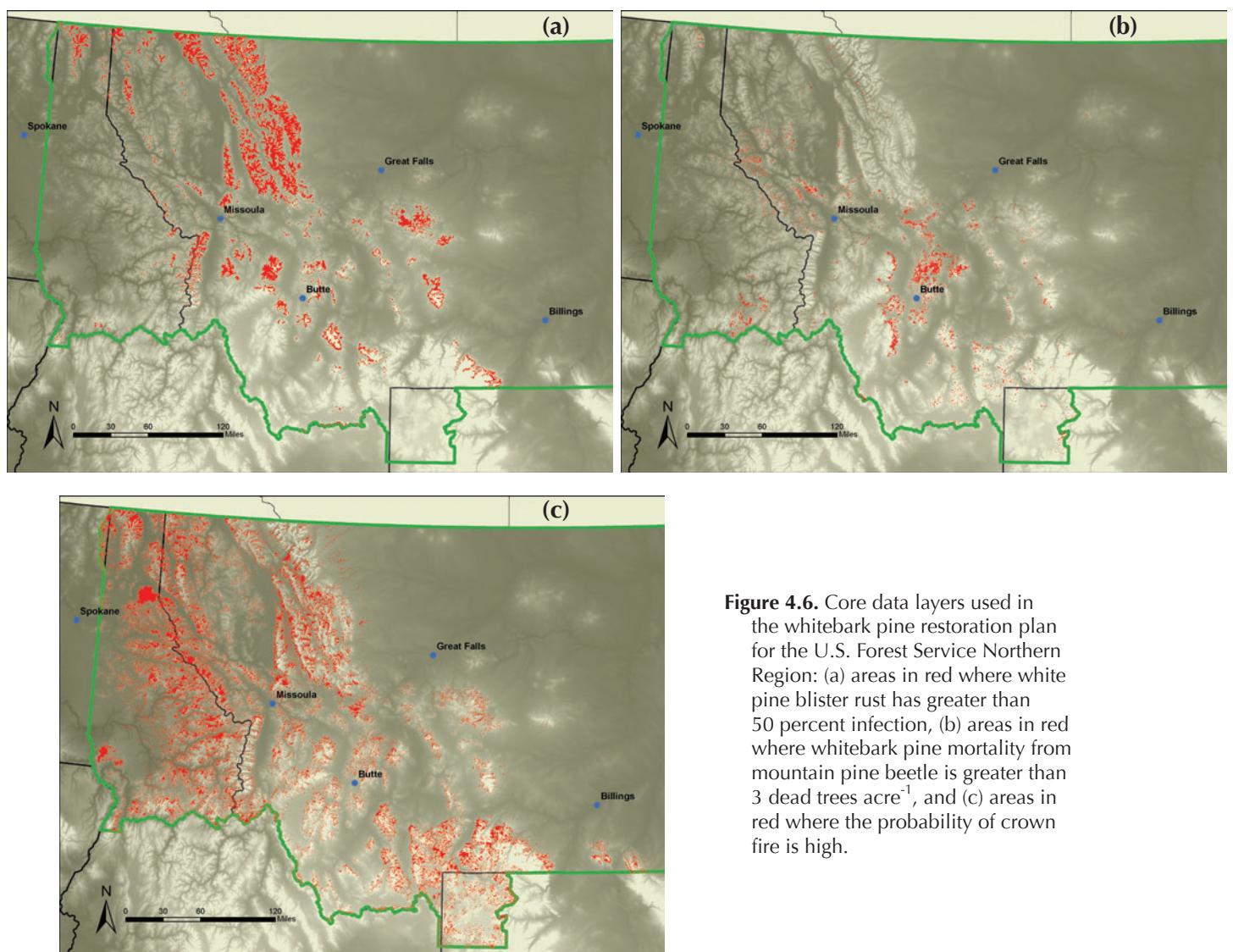


Figure 4.6. Core data layers used in the whitebark pine restoration plan for the U.S. Forest Service Northern Region: (a) areas in red where white pine blister rust has greater than 50 percent infection, (b) areas in red where whitebark pine mortality from mountain pine beetle is greater than 3 dead trees acre⁻¹, and (c) areas in red where the probability of crown fire is high.

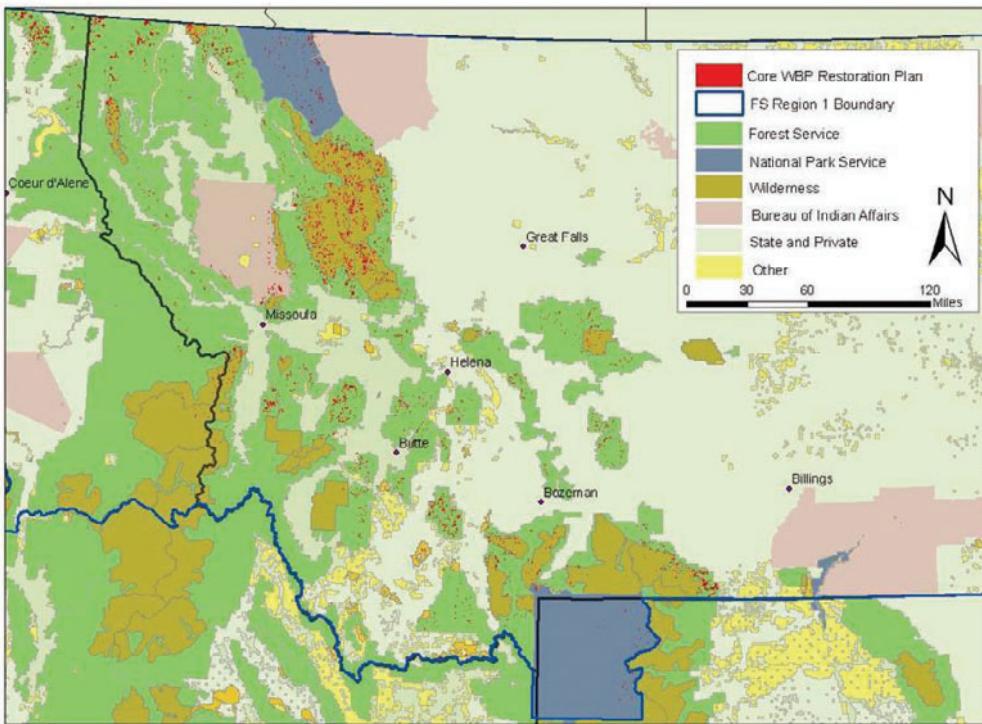


Figure 4.7. The core whitebark pine (WBP) restoration plan by land ownership. Conservation areas are shown in red.

for restoration occurs in protected areas (wilderness) of the Crown of the Continent ecosystem (Glacier National Park and the Bob Marshall Wilderness Complex). We then adjusted this core restoration plan by excluding all lands that have burned since 1988, based on the Northern Region fire atlas compiled from the project Monitoring Trends in Burn Severity (Figure 4.8). This adjustment, as shown in Figure 4.9 and Table 4.2, still has most of the critical lands that need restoration included within Montana wilderness. It is important to note that most of the lands in this restoration plan can be treated using wildland fire (wildland fire use or controlled wildfires) (Table 4.3) under the Northern Region's Appropriate Management Response area designations (Figure 4.10).

The Northern Region's IRPS used these findings along with the Ecosystem Management Decision Support (EMDS) Tool to determine priority areas for treatment based on resource value, indicators of risk, levels of departure, and potential response to various treatments on 6th HUC (USGS 1987) watersheds. In EMDS, as in most prioritization efforts, there are two tasks involved in determining final prioritization scores: spatial data analysis (EMDS logic engine) and data layer weighting. The spatial data analysis was previously described, while the weighting of the layers used in the analysis followed a more subjective approach. All scenarios, including the whitebark pine scenario, are scored (weighted) using three components—Value, Risk, and Feasibility—that total to a score of 100 based on the weights given each of the three values. These components and the associated treatment options will vary based on several criteria, including: (1) location (roaded, non-roaded, and wilderness), and (2) type of vulnerability (shade-tolerant tree dominance due

to fire exclusion, blister rust, mountain pine beetle, and probability of crown fire). The weighting of each of these data layers was assigned based on the importance to managers of each issue. The Value component was assigned a value of 40, all of which is assigned to the percent of whitebark pine occurrence in a 6th code HUC watershed. The Risk component was given a score of 30, with 20 assigned to crown fire burn probability, 5 assigned to blister rust damage, and 5 assigned to insect occurrence (and mortality) from 2002 to 2009. The Feasibility component had a value of 30, with 25 assigned to non-wilderness and non-roadless areas, and 5 assigned to Monitoring Trends in Burn Severity (MTBS) data layers with moderate- to high-severity fire (www.mtbs.gov) to identify where recent site preparation was provided by the fire, thus enabling planting of whitebark pine seedlings, if necessary. The EMDS model was run for each scenario to determine which 6th code HUC (USGS 1987) watersheds received the highest score for the greatest number of scenarios. These watersheds will likely be given priority for various treatments. For example, certain 6th code HUC watersheds may have a number of resource values at risk that can be treated to meet the restoration objectives. These watersheds will therefore rank higher in priority for treatment compared to a watershed with a single value identified, or if less risk is identified. The opportunity scores for whitebark pine are shown in Figure 4.11. The red watersheds are the highest opportunity areas for whitebark restoration since they have the highest values at risk and the greatest potential for restoration. The Northern Region plans to revisit the Value, Risk, and Feasibility weights through an adaptive management process to test the assumptions, validate the prioritization process, and respond to changes on the

Table 4.2. Hectares of whitebark pine range in zones of threat by land ownership type in USDA Forest Service Northern Region.

Land ownership	Blister rust infection (>50%)	Mountain pine beetle (≥ 3 dead trees ac^{-1})	High crown fire potential	Grizzly bear range	Core plan	Adjusted plan	Grizzly bear adjusted plan
Forest Service	643,547	103,657	241,751	229,148	127,189	123,033	60,711
National Park Service	139,450	8,274	75,867	308,764	9,441	9,346	9,346
Private or State lands	34,124	2,515	7,808	12,576	4,505	4,483	3,040
Wilderness	411,921	10,272	173,837	260,832	70,487	65,034	55,659
Centennial Mountains—Sheep Experimental Station	1,545	262	350	1,600	233	233	233
Bureau of Indian Affairs	35,692	1,349	5,008	18,372	4,520	4,505	4,126
Bureau of Land Management	5,220	1,400	2,333	1,304	729	729	211
Department of Defense	248	0	284	148	102	102	102
Fish and Wildlife Service	7	0	22	52	7	7	7
Bureau of Reclamation							
Total hectares	1,271,755		127,728	507,260	832,796	217,213	207,473
							133,436

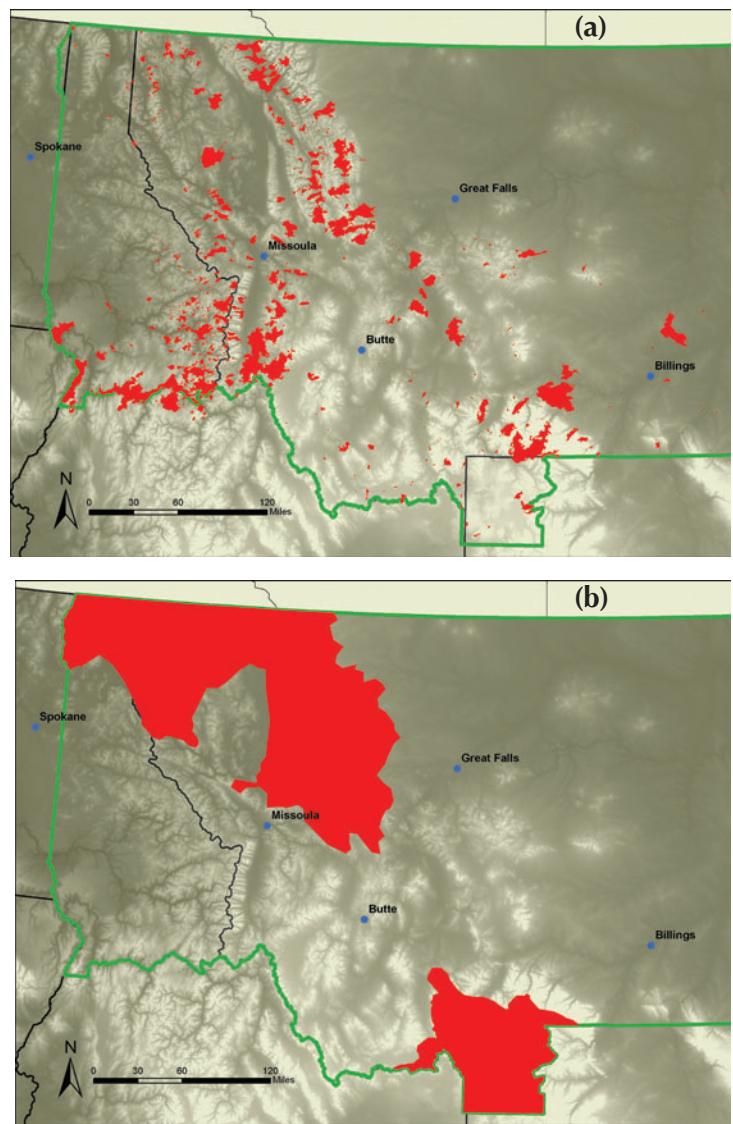


Figure 4.8. Data layers (shown in red) used to adjust the core restoration plan (a) to address wildland fire issues using a spatial data layer showing areas that have burned in wildfires since 1988 and (b) to identify grizzly bear range.

landscape (for example, large fires and beetle killed trees). A 2050 version of the IRPS is being developed as part of the Regional Climate Change vulnerability assessment to project increases in vulnerability of the key elements identified in 2011. In this way, IRPS is a process based framework that can be periodically refined and modified.

The Pacific Northwest Region Restoration Strategy for Whitebark Pine

A comprehensive, regional plan for restoring whitebark pine was written for the U.S. Forest Service Pacific Northwest Region (PNW) (Aubry and others 2008a; Aubry and Shoal 2008). Like the range-wide strategy, the PNW Strategy also included several scales of analysis from the

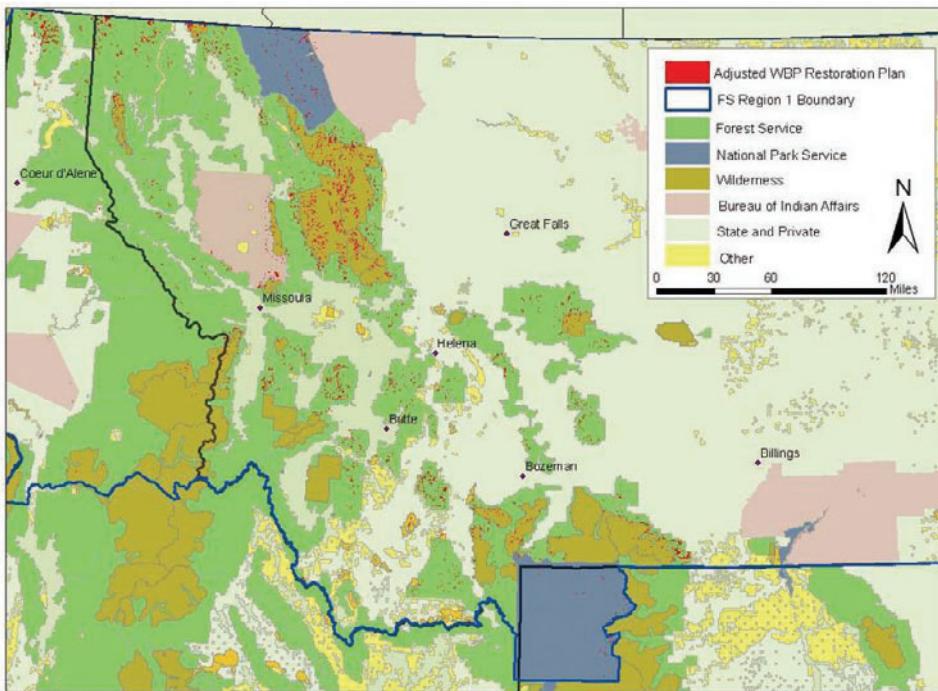


Figure 4.9. The adjusted restoration plan that excludes all lands burned since 1988. Restoration areas are shown in red.

Table 4.3. Hectares of whitebark pine restoration plans by Appropriate Management Response (AMR) categories in USDA Forest Service Northern Region.

AMR	Restoration plan		
	Core	Adjusted	Grizzly bear
Resource Benefit with Plan	122,129	115,707	70,640
Resource Benefit	51,657	49,477	32,601
Protection	9,973	9,739	4,724
Appropriate Suppression	6,641	6,116	2,129
Not Coded	26,215	25,836	22,767
Total hectares	216,615	206,876	132,860

regional level down to the landscape and stand levels. It is also supported by a number of ancillary documents that improve the efficacy of the strategy (Aubry and others 2008b; Lorenz and others 2008). The overriding goal of this Strategy is to *restore and conserve a network of viable populations of whitebark pine and associated species across the Pacific Northwest*. There are five objectives listed to complete this goal:

1. Restore degraded habitat.
2. Protect genetic resources through gene conservation.
3. Increase blister rust resistance in whitebark pine populations.
4. Evaluate the health and status of whitebark pine stands.
5. Increase our understanding of the threats to whitebark pine and develop practical and effective restoration techniques.

Aubry and others (2008a) used an ecoregion approach based on a framework for ecoregional planning (Dinerstein and others 2000; Groves 2003). The steps included: (1) conduct ecoregional assessment, (2) identify threats, (3) select sites for restoration and conservation, (4) create a biodiversity vision, (5) set long- and short-term goals, and (6) prioritize actions. The end result was a site-based conservation and restoration blueprint.

Forest personnel used their professional judgment to assign proposed actions to management units by considering fire history, mountain pine beetle activity, blister rust severity, size of the area, stand age, competition from other conifer species, and reproductive capability of whitebark pine. The framework also considered the logistics of traveling to an area and the existence of any special management designations, such as designated wilderness or research natural areas, and potential benefit versus cost of restoration. The entire region was divided into 30 conservation areas, and each conservation area was then stratified by management

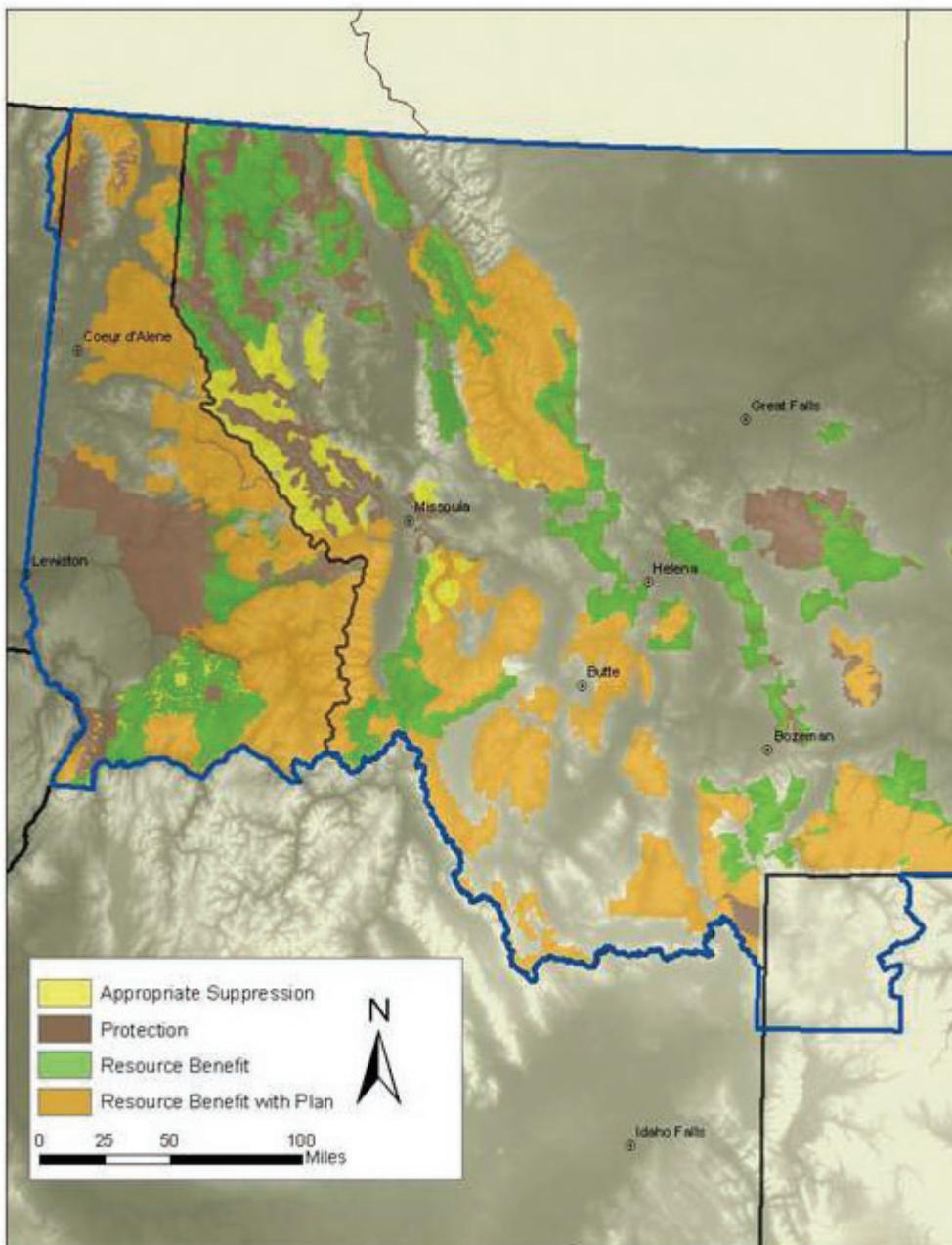


Figure 4.10. Areas describing Appropriate Management Response (AMR) for the Northern Region.

units with one or more of the following proposed actions assigned to each management unit:

1. **Safeguard habitat.** Conserve and safeguard from fire (both wild and prescribed).
2. **Collect cones.** Collect cones from mature whitebark pine stands with high potential for cone production.
3. **Restore.** Plant seed or seedlings, thin for conifer release, and/or prune. Included in this category are units that have burned or have high mortality due to mountain pine beetle infestation.
4. **Survey condition.** Survey to determine if whitebark pine is present, to record the general stand condition, and to determine what actions, if any, are needed.

5. **Survey seed trees.** Survey to determine if cone-bearing trees are present.

6. **No action.** Decide if management units have poor access, marginal habitat, or no need for planting or thinning.

A map showing conservation areas, management units, seed zones, and whitebark pine habitat is shown in Figure 4.11. Whitebark pine distribution and status varied greatly within the conservation areas and the nested management units. However, planting was needed in some part of every conservation area except for the Olympic Peninsula. Top priority for planting was given to management units located in grizzly bear habitat.

The PNW Restoration Strategy (Figure 4.12) also includes a genetics program with the following goals: gain an

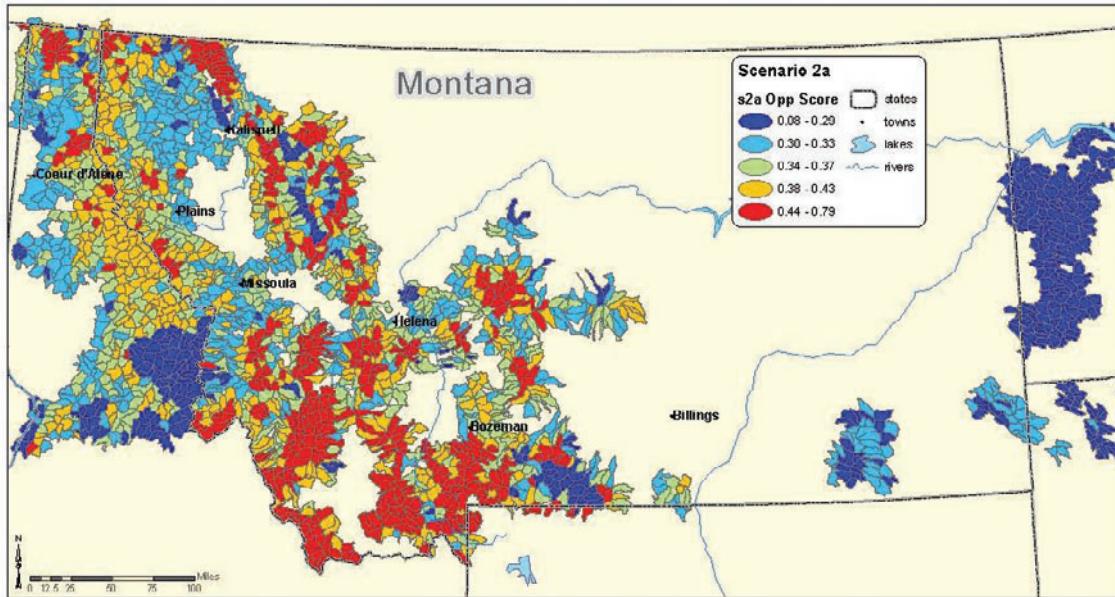


Figure 4.11. Opportunity scores for all 6th code HUC watersheds (USGS 1987) in the Northern Region IRPS prioritization for whitebark pine restoration with high scores indicating high opportunity for whitebark pine restoration activities. The code "s2a Opp Score" indicates the IRPS scenario 2a opportunity score.

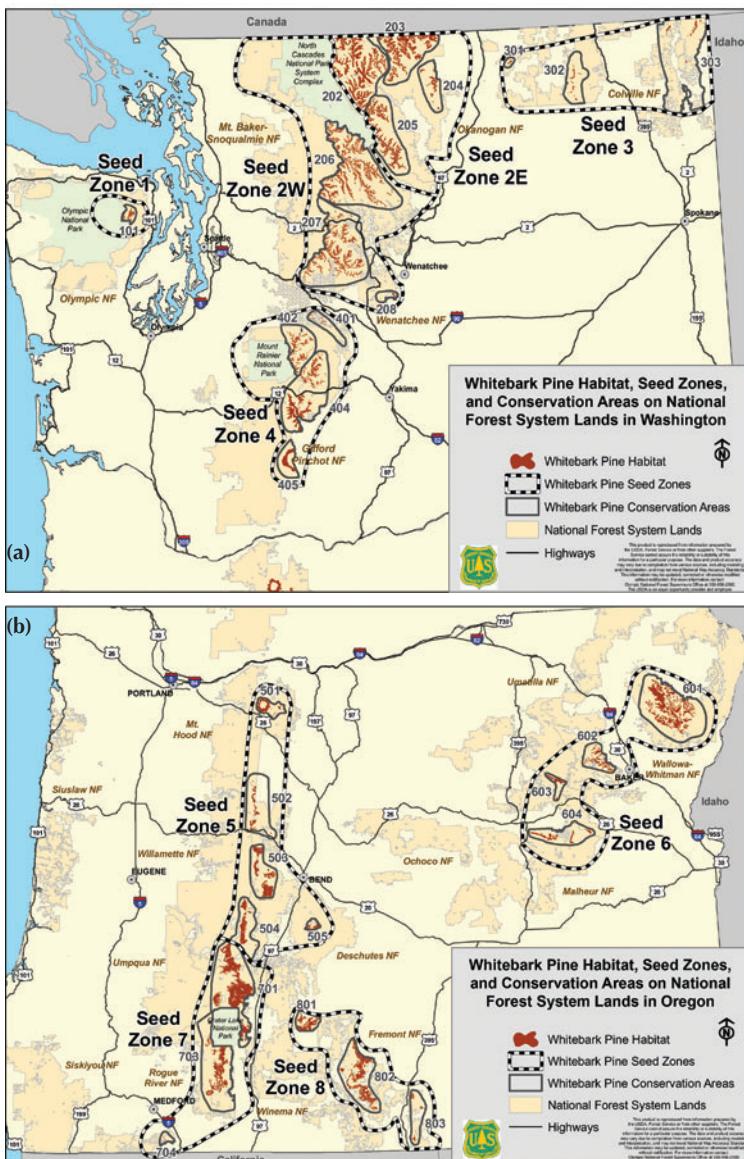


Figure 4.12. Map depicting the whitebark pine restoration strategy for the Pacific Northwest Region for the states of (a) Washington, and (b) Oregon (Aubrey and others 2008a).

understanding of the patterns of genetic diversity and adaptation in whitebark pine, use this knowledge to protect the whitebark pine genetic resource (gene conservation), and provide rust-resistant seeds for restoration. Rust resistance testing of seedling progenies to confirm resistance of candidate parent trees is conducted at the Forest Service Dorena Genetic Resource Center (DGRC). The regional ex situ gene conservation plan (Bower and Aubry 2009) outlines a sampling design for seed collection among populations across the region and long-term storage at both the DGRC and at the National Center for Genetic Resources Preservation under a memorandum of understanding with the USDA Agricultural Research Service in Fort Collins, Colorado.

A proactive approach is critical to prevent the permanent loss of whitebark pine habitat throughout much of whitebark pine distributional range in the Pacific Northwest. Aubry and others' (2008b) Strategy includes a five-year plan for 2009 to 2013 that targets the following activities:

- Collect seeds to meet gene conservation, rust resistance screening, and planting objectives.
- Assess the condition and determine restoration needs for all priority management units.
- Develop and implement a plan to plant seedlings in priority management units.
- Continue the ongoing rust screening program with emphasis on seed zones in grizzly bear recovery areas.
- Develop and implement a plan to treat mountain pine beetle in high risk units.
- Develop an approach for planting in designated wilderness areas that will allow the use of resistant plant material while maintaining wilderness character.
- Develop an approach to mitigate the predicted impacts of climate change.
- Develop monitoring plan(s) to track accomplishments, measure success of actions, provide information and feedback to improve procedures and outcomes of projects, and disseminate information.
- Work collaboratively to meet information needs.

A companion "Land Managers Guide" is available to plan and design local treatments (Shoal and others 2008). This PNW Strategy is easily the most comprehensive and detailed plan for a large region and provides the critical information to step concepts and knowledge presented in this report down to a finer scale. It serves as an excellent template for the development of strategies for other regions.

The Greater Yellowstone Area Whitebark Pine Restoration Strategy

As a foundation and keystone species of high-elevation ecosystems in the GYA, whitebark pine defines ecosystem structure, function, and process by providing snow capture, snow retention, carbon storage, biodiversity, and a food source for wildlife. Overstory mortality from combined

blister rust, beetle, and climate change is unprecedented in many areas of the GYA, resulting in the need for an approach to whitebark management that links Federal administrative units throughout the GYA. To protect healthy whitebark pine and restore whitebark pine in areas with extensive overstory mortality, appropriate management actions must be coordinated, consistent, efficient, and science-based. In response to the current situation in whitebark ecosystems, the Greater Yellowstone Coordinating Committee's Whitebark Pine Subcommittee, which has worked successfully across boundaries since its inception in 2000, developed this Whitebark Pine Strategy to promote the persistence of whitebark pine over time and space in the GYA by: (1) documenting the current condition of whitebark pine in the GYA; (2) establishing criteria to prioritize areas for management action; (3) identifying techniques and guidelines to protect and restore whitebark pine; and (4) facilitating communication and distribution of this information. This Strategy is intended to enable land management units to maximize the use of their limited resources to maintain whitebark pine as an important ecosystem component in the GYA.

The GYA Whitebark Pine Strategy is a living document that will be regularly updated to reflect changes in ecosystem conditions, advances in the understanding of whitebark pine ecosystems and management techniques, and improvements in the technology available to characterize and map whitebark pine. In addition, reviews by other resource staff such as fire managers, wildlife biologists, interpreters, and recreation specialists will provide the basis for integration of this strategy within individual management units as well as across the GYA. The Strategy contains four sections:

- **Section 1. Introduction, Purpose and Need, and Strategic Objectives.** Details the strategic objectives developed for assessing and conserving whitebark pine ecosystem condition in the GYA and describes the Whitebark Pine Subcommittee and its work to date.
- **Section 2. Methods.** Describes the assessment and prioritization of whitebark stands in the GYA by the Whitebark Pine Subcommittee.
- **Section 3. Site Selection, Management Strategies, and Action Plan.** Describes how whitebark stands within the GYA will be selected for management actions and addresses considerations for resistance, resiliency, and adaptive management relative to climate change. A three-year action plan based on current restoration and protection efforts and priorities is also presented.
- **Section 4. Tools for Protection and Restoration of Whitebark Pine Stands.** Describes potential tools and techniques for protecting and/or restoring whitebark pine stands (Table 4.4).

Forest Scale

The forest scale refers to any large consolidated area with multiple land management units that could include National

Table 4.4. The Greater Yellowstone Area whitebark pine restoration strategy simplified tools and techniques for restoration.

Protection	Restoration
<ul style="list-style-type: none"> • Apply verbenone and carbaryl to prevent mortality due to mountain pine beetle. • Prune to remove blister rust infection and/or improve fire resistance. • Prevent loss of high-value whitebark pine trees from fire. • Natural regeneration 	<ul style="list-style-type: none"> • Whitebark pine seed orchard • Participation in whitebark pine genetic conservation program • Collect whitebark pine seeds and cones. • Plant whitebark pine seedlings and seeds. • Development of guidelines and limitations for fire in whitebark pine stands • Creation of nutcracker openings • Thinning • Natural regeneration

Forests and National Parks. Once an assessment is completed at the forest scale, a landscape scale assessment (see the Landscape Scale section) and stand level assessment (see the Stand Scale section) are likely required to further refine the assessment of whitebark pine restoration needs.

Assessments

Assessments performed at this level can incorporate more detailed information than the range-wide and regional scales because wall-to-wall consistent data layers are more readily available. The following are some of the layers that are often available at this scale and the questions they can help address:

- **Vegetation cover types and age classes.** Where are the whitebark pine forests? How much of them are in late successional status? How much age class diversity is there within the area? Where should monitoring plots be located?
- **Habitat types (potential vegetation).** Where can whitebark pine grow, and where is it most likely to succeed to other conifers or be the dominant species?
- **Insect and disease aerial detection surveys.** Where has whitebark pine been killed by mountain pine beetle or other agents?
- **Blister rust infection levels.** Where has cone production been lost, and where are the best places to look for phenotypically rust-resistant trees to (1) collect seeds for planting, or (2) include in the genetic rust resistance breeding program?
- **Threatened and endangered species habitat.** Where could grizzly bears potentially use whitebark pine seeds collected from cones in squirrel middens? Can the process of prioritizing areas for restoration also help design projects in grizzly habitat that mitigate potential human-bear conflicts?
- **Roads and trails:** Where are potential treatment areas that are easily accessible?

Restoration Actions

An important restoration action implemented at this level is the collection of seeds from apparent rust-resistant whitebark pine trees, particularly from areas with high rust infection levels. Since whitebark pine is a species that can be planted across large regions, seed collection for whitebark pine is best employed at the forest scale. Mahalovich and Dickerson (2004) implemented an extensive whitebark pine tree improvement program for the Intermountain Region and summarized criteria for selecting plus trees for collecting cones (Appendix A). Trees that are considered desirable for harvesting seeds because of their observed rust resistance and robust qualities are called “plus” trees. Aeciospore collections for rust screening and pollen collections for seed orchard applications and breeding are also facilitated at the forest level.

Other genetics activities include establishing seed orchards and long-term genetic tests within their respective seed zones. Presently, there are four seed orchards at various stages of development servicing the Bitterroots-Idaho Plateau (Clearwater National Forest), Central Montana (Lewis and Clark National Forest), Greater Yellowstone-Grand Teton (Gallatin National Forest), and Inland Northwest (Lolo National Forest) seed zones. Seed orchards are genetically designed for broad adaptability with a minimum effective population size of 30. A further design goal is to separate ramets (multiple copies) of the same genotype by 24 m to minimize inbreeding through cross-pollination. Where seed zones cover a wide range in elevations, orchards are stratified by elevation band for cold hardiness considerations (for example, the Little Bear Seed Orchard on the Gallatin National Forest). Seedlings from the 110-seed source study (Mahalovich 2012; Mahalovich and others 2006), at the completion of the rust screening and cold hardiness trial, were planted on the Idaho Panhandle National Forests. Additionally, replicated, long-term performance tests are scheduled to be planted at the completion of each rust screening.

Another restoration action best conducted at this level is the inventory and monitoring of whitebark pine health and status. While some inventory and monitoring efforts are usually conducted at finer scales, the most effective are those that are coordinated at the broad or coarser scales. Many inventory and monitoring techniques are available for implementing programs that assess whitebark pine status. The most appropriate may be the inventory and monitoring methods on the Whitebark Pine Ecosystem Foundation web site (www.whitebarkfound.org) (Tomback and others 2005). These methods were developed specifically for whitebark pine and limber pine to be implemented at a broad-scale. Other methods that could be used are those in FIREMON (Fire Monitoring and inventory system) (Lutes and others 2006) and FFI (Lutes and others 2009), which are available at the FRAMES (Fire Research and Management Exchange System) web site (www.frames.gov). FIREMON and FFI contain detailed methods for measuring trees and rust conditions and a discussion on how to design a sampling strategy. Other inventory techniques include those in FSVEG and the Fire Monitoring Handbook (USDI 2001). Shoal and Aubrey (2006) also presented a set of core data attributes essential for whitebark pine surveys.

Management Concerns

The major concern at this level is that restoration resources may not be strategically or efficiently used across broad forest scale units, such as National Forests. Another potential concern is that there may not be enough personnel with sufficient time and experience to implement well-conceived whitebark pine restoration projects. Experienced personnel must be available to complete National Environmental Policy Act documents, pursue funding, and plan and implement treatments.

Example: Implementation of the Greater Yellowstone Restoration Decision Guidelines for the Caribou-Targhee National Forest

The process described in “Greater Yellowstone Area Decision Guidelines for Whitebark Pine Restoration” (Jenkins 2005) was used to prioritize whitebark pine restoration treatments on the Caribou-Targhee National Forest. General steps for implementing the guidelines were:

4. Prioritize the need for restoration at the stand scale by using the stand scale guidelines to determine a relative rating for each of the stands that have whitebark pine.

Prioritization can then be done at each of the three scales. In addition, priority ratings from all three scales for a stand (broad, mid, and stand) can be added to determine a total restoration priority rating for the stand. These scores can be compared to all other stands within the National Forest to determine which stands are the highest priorities for treatment considering multi-level priorities. For demonstration purposes, this process is illustrated using one principal watershed within the forest (broad-scale, Figure 4.13), all of the subwatersheds within that principal watershed (mid scale), and all of the stands within one subwatershed. The mid-scale analysis is discussed in detail in the Landscape Scale section and the stand analysis is discussed in detail in the Stand Scale section.

Step 1: Establish Whitebark Pine Vegetation Layer for the National Forest

A vegetation layer was created using the best information available for whitebark pine current and historic presence. Several different layers were joined to make the whitebark pine vegetation layer (WBP layer):

- Whitebark pine designations from the Grizzly Bear Cumulative Effects Model Map (CEM) (Weaver and others 1986).
- Stand examination data documenting the presence of whitebark pine.
- Whitebark plus tree location data.
- The 1966 Timber Inventory, whitebark pine component.
- Whitebark pine presence/absence map assembled by the USGS using satellite imagery.
- Local knowledge of employees and researchers familiar with the area.
- The 2130-m elevational band. Whitebark pine presence in this area is incidental at elevations below 2130 m, so everything below 2130 m was excluded. A validation assessment revealed that the layer tended to overestimate the amount of area with whitebark, but overall, it accurately predicted areas that are currently known to have whitebark pine. This was the best available information for the Caribou-Targhee National Forest at the time.

Step 2: Develop Forest-Scale Principal Watershed Process

Since whitebark pine is declining throughout its range, it was assumed that the greater the reduction from historical extent, the greater the loss of ecological function and the more urgent the need for restoration. The following losses were evaluated:

1. Establish a whitebark pine spatial data layer that displays where whitebark pine is located across the area of interest (Caribou-Targhee National Forest).
2. Prioritize the need for restoration at the broad-scale (Caribou-Targhee National Forest) by using the guidelines to determine a relative rating for each principal watershed that has whitebark pine.
3. Prioritize the need for restoration for each principal watershed by using the guidelines to determine a relative rating for each of its subwatersheds that have whitebark pine.

- **Loss to mountain pine beetle.** Aerial detection survey flights since 2000 were used to determine the number of acres lost (≥ 10 trees per acre killed by mountain pine

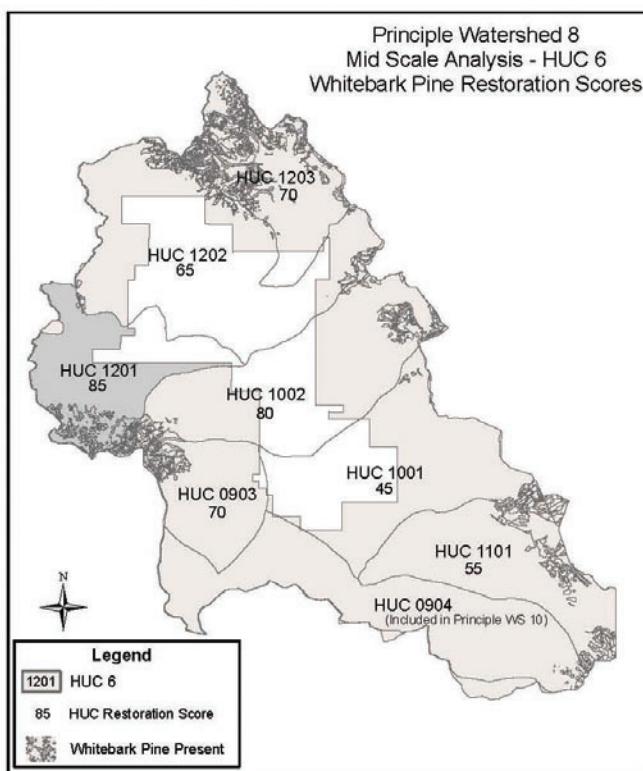
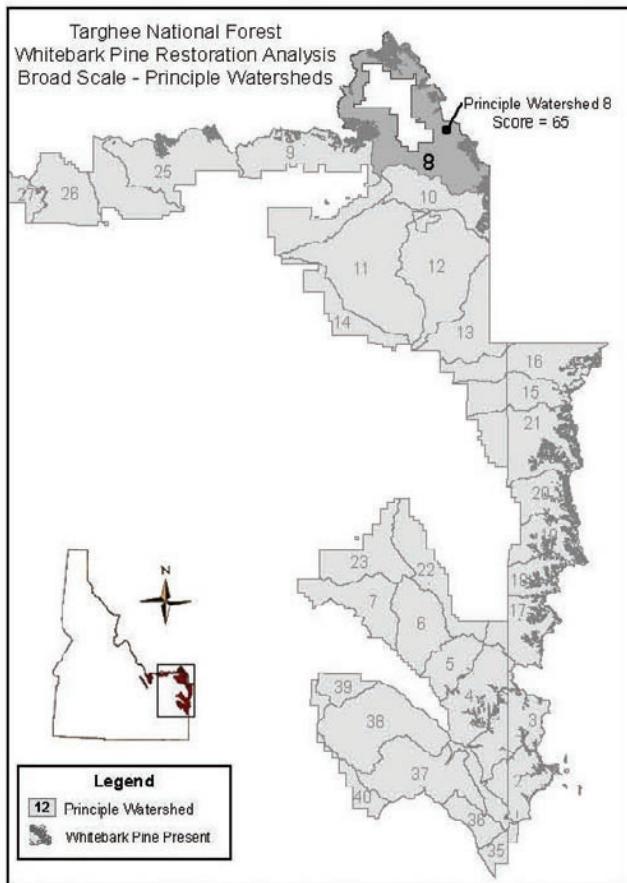


Figure 4.13. Broad-scale forest areas used by the Caribou-Targhee National Forests to implement the Greater Yellowstone Area whitebark pine restoration strategy. (a) all lands in the assessment area (forest) and (b) stands within one 6th code HUC watershed.

beetle is considered area lost). Mountain pine beetle typically kills the larger trees, which also tend to be the cone-bearing trees. Areas with high or increasing mountain pine beetle mortality were assigned a high priority for restoration.

- **Loss from stand replacing fire.** A fire history layer was intersected with the whitebark pine layer to identify whitebark lost from fire. The majority of the stand-replacing fire in the whitebark pine habitat occurred in 1988. Monitoring of the 1988 fire areas shows that whitebark pine is not adequately regenerating. Burned acres that have been planted with whitebark pine seedlings were excluded.

Since mature whitebark pine are more likely to be attacked by mountain pine beetles than young trees, it was assumed that maintaining a diversity of size classes would ensure that some stands are less likely to be killed by beetles. It also ensures that stands senescing out of cone production are being replaced. Small size classes are often limited in extent because fire exclusion has reduced the opportunities for whitebark pine to regenerate. The diversity of age classes needed was determined from the estimated fire return interval in the area for whitebark pine (200 to 325

years) and whitebark pine's prime cone production period (100 to 300 years). Areas with less than 25 percent in small size classes (seedling through pole less than 100 years old) were determined to have a high priority for restoration and areas with between 25 to 35 percent of the stands in small size classes were determined to have a moderate priority. The Targhee National Forest vegetation layer and the grizzly bear classifications were combined and then overlaid with the whitebark pine cover layer to identify young stand age classes.

In general, within areas where blister rust levels are high, trees with low rust resistance have either died or their cone-bearing branches have been killed. Rust-infected trees with more than 20 to 30 percent of the crown killed can no longer produce good cone crops (Keane and Arno 2001). Open conditions suitable for regeneration are important in areas that have moderate levels (25 to 75 percent) of infection so that trees with rust resistance will have the opportunity to regenerate. If restoration treatments are postponed until few cone-producing whitebark pine remain, then virtually all of the seeds produced by the resistant trees will be consumed. Areas with high infection levels (greater than 75 percent) were assigned the highest restoration priority.

Table 4.5. Broad-scale analysis for the Caribou-Targhee National Forests for restoring whitebark pine (WBP).

Consideration item	Weight	Principle watershed #8 rating	Principle watershed #8 score
1. Change from historical acres	10	0	0
2. Age class distribution	10	1	10
3. Successional potential and status	5	2	10
4. Areas far from WBP seed source	5	1	5
5. Grizzly bear use	20	1	10
6. Level of blister rust	10	1	10
7. Level/trend of mountain pine beetle	20	1	20
Score^a (weight x rating)^b			65

^aThe score is calculated by multiplying the weight for that consideration item by the rating given to that item. The purpose of weighting is to incorporate the relative importance of the consideration item. Land managers completing the analysis assign the weights and can adjust them to reflect local management direction. The consideration item ratings are defined as follows:

^bRatings are as follows:

Item 1. Small decrease or increase in acres = 0, moderate decrease = 1, large decrease in acres = 2

Item 2. Well distributed age classes = 0, Mod = 1, high percentage in older age classes = 2

Item 3. High percent landscape in whitebark pine climax = 0, Seral: High percent of whitebark = 0, high percent of landscape in lodgepole pine = 1, high percent of subalpine fir = 2

Item 4. Acres well distributed = 0, high mortality areas far from other seed sources = 1

Item 5. Grizzly bear use low = 0; use high and cannot support >13 percent whitebark pine = 1; grizzly bear use high and is supporting >13 percent of area with cone-bearing whitebark = 2, or same but is not supporting >13 percent = 3

Item 6. Rust infections low = 0, rust infections moderate = 1, rust infections high = 2

Item 7. Mountain pine beetle levels low and stable = 0, beetle levels high or increasing = 1

In stands where whitebark is seral, successional progression causes whitebark pine to be replaced by more shade-tolerant tree species (primarily subalpine fir and Engelmann spruce). It was assumed that the greater the representation of the shade-tolerant species, the greater the decline of less shade-tolerant species such as whitebark pine. Because lodgepole pine is a shade-intolerant seral species, it will not replace whitebark pine at the rate of subalpine fir or Engelmann spruce. Stands succeeding to spruce and fir have a higher priority than stands succeeding to lodgepole pine. Climax whitebark pine stands have a low priority because they are not successional replaced by other tree species.

Local extinctions may occur if stands of whitebark pine decline and seed sources are not close enough to provide adequate regeneration. Usually, 10 km was used as the maximum distance to expect nutcrackers to re-establish a whitebark stand, but that is a conservative estimate of nutcracker caching distance. All stands or polygons that were greater than 10 km from a whitebark pine seed source were assigned a high priority.

Whitebark pine seeds are an important source of energy for the grizzly bear (Felicetti and others 2003; Mattson and Reinhart 1994; Robbins and others 2006). In Bear Management Units (BMUs) with >13 percent of the area supporting mature whitebark pine, the relationship between

availability of squirrel middens and use of middens is strong (Mattson 2000). Areas in BMUs that have the capability to support greater than 13 percent cone-bearing whitebark, but do not currently do so, have the highest priority for restoration. Results of the forest- (broad) scale prioritization process along with the mid-scale and stand-scale prioritization are shown in Table 4.5 and Figure 4.13b.

Landscape Scale

The landscape scale refers to local areas that are geographically defined by the spatial dynamics of the biophysical processes, such as disturbance and vegetation development, that shape them. These landscapes can be variable in size, but Karau and Keane (2007) found that typical western U.S. landscapes could be anywhere from 50 to 200 km² (10,000 to 50,000 acres) to encompass the full range of spatial dynamics in disturbances, hydrology, and biophysical setting, or a little bigger than the size of a 6th code HUC watersheds (USGS 1987) or a landform (Holdorf and Donahue 1990). Generally, landscape assessments would be implemented on sub-areas within the broad-scale assessment and should be no smaller than about 5000 acres, or 7th code HUC watersheds (USGS 1987). A landscape is usually composed of and described by stands that are small areas of homogeneous vegetation

and site conditions (Turner and others 2001). Landscape composition is described by the plant species that dominate the stands that comprise the landscape, while landscape structure is the spatial pattern of stand types, such as patch density, contagion, and patch shape.

Assessments

Assessments performed at this scale would entirely depend on the availability, quality, and extent of appropriate GIS layers to describe the variables being assessed. Assessments will always differ across landscape for several reasons:

- Unique biophysical setting dictates the abundance and distribution of whitebark pine stands.
- Fire and other disturbance regimes will be dramatically different across landscapes comprising a broad area due to landform, topography, and orientation.
- Blister rust and mountain pine beetle impacts are highly heterogeneous across landscapes.
- Management issues will differ across landscapes and agencies depending on existing management plans and ownership.

Therefore, a one-size-fits-all approach to landscape assessments for whitebark pine restoration is often ineffective and inappropriate for most assessments, analyses, and applications.

Historical Range and Variation (HRV) Assessments

The concept of HRV is especially useful at the landscape scale (Morgan and others 1994a). In an operational context, the historical range and variation of landscape characteristics, mainly composition (species cover types) and structure (spatial pattern), can be used as a reference to compare with current conditions to calculate a measure of departure. This departure can then be used to prioritize landscapes for restoration (Keane and others 2007b). The assumption behind HRV is that the spatial arrangement, composition, and structure of vegetation communities on a landscape reflects the cumulative and interactive effects of past disturbance regimes, biophysical environments, and successional processes over long time periods. Historical fluctuations in landscape characteristics, such as species composition and structure, can provide an important reference for evaluating the current condition of the same landscape; a quantification of these fluctuations can be used to guide the design and implementation of restoration treatments (Keane and others 2009). Current landscape conditions can be compared with a set of historical landscape conditions to detect ecologically significant change, such as that incurred by fire exclusion and blister rust. This information can be used to plan and prioritize treatment areas where stands that have significantly departed from historical conditions may warrant treatment first.

In this report, we define HRV as the quantification of temporal fluctuations in ecological processes and characteristics prior to European settlement (prior to 1900) and before the introduction of blister rust. HRV is often highly scale-dependent and somewhat flawed conceptually due to climate change, human land use, and geologic processes. The variability of historical whitebark pine cover across a landscape, for example, depends on the range of years used to compute the HRV landscape cover statistics; fluctuations over a 1000-year period taken 10,000 years ago at the end of the last ice age would be dramatically different from a recent 1000-year time slice.

HRV has limitations in a spatial context. The HRV of a stand is meaningless unless it is described in the context of a landscape; for example, a subalpine fir stand might not be outside of HRV if the rest of the landscape is composed of whitebark pine. To use HRV in an operational context, it must be assumed that the record of historical conditions more or less reflects the range of possible conditions for future landscapes—an assumption that we now know to be overly simplistic because of documented climate change, exotic introductions, and human land use. The landscape must also be large enough to encompass the dynamics of most disturbance regimes that affect it—a task that is difficult due to the high variation of disturbance. Yet, despite its drawbacks, the HRV concept may well be indispensable to ecosystem management because it can be used to define limits of acceptable change and compare historical and current stand or landscape condition to prioritize for restoration treatments (Hessburg and others 1999; Swetnam and others 1999).

The HRV of landscapes can be quantified from three main approaches. The best approach is to obtain spatial chronosequences defined as sequences of maps from one landscape over many time periods. The second approach is to quantify HRV landscape characteristics by using vegetation maps from many similar, unmanaged landscapes taken from one or more time periods gathered across a geographic region (Hessburg and others 1999). This spatial series essentially substitutes space for time and assumes all landscapes in the series contain highly similar environmental, disturbance, topographical, and biological conditions (Pickett and others 1987). The third method involves simulating historical dynamics to produce a chronosequence of simulated maps to compute landscape statistics and metrics. Many spatially explicit ecosystem simulation models are available for quantifying HRV patch dynamics (Gardner and others 1999; Keane and others 2004; Mladenoff and Baker 1999). The LANDFIRE national mapping effort (www.landfire.gov) has simulated historical time series that can be used as reference in calculating departure of current from historical conditions, as described in this report.

Possible Assessment Criteria

The list of important landscape attributes that may be considered when prioritizing, planning, or designing treatments to restore whitebark pine is quite different at the landscape

level than for other restoration scales. Many of the factors that govern whitebark pine status and decline act primarily at the landscape scale (Keane and others 1996), such as disturbance, climate, and seed dispersal. Management responses to these factors require careful evaluation. While most proactive management actions are implemented at the stand level, the location of stands to be restored will entirely depend on the landscape in which they occur. The following are some important factors that could be used to prioritize, design, and select landscapes to restore:

1. Disturbance

- *Level of rust infection and mortality.* The extent of blister rust infection and mortality is an important factor in determining the kinds of restoration actions for a given landscape. In short, the higher the rust infection and mortality levels, the greater the need for restoration action, such as creating openings through thinning, and planting rust-resistant seedlings. In these stands, cone productivity is greatly diminished, and whitebark pine is declining as a functional ecosystem component. However, under these conditions, surviving trees may have the highest blister rust resistance, yet seeds for these stands are less likely to be dispersed because of intense competition among nutcrackers, squirrels, and other seed-users (McKinney and Tomback 2007). As previously mentioned, stands with the highest levels of rust infection (greater than 90 percent) and mortality (greater than 50 percent) are the best candidates for finding blister rust resistant trees, which can be designated plus trees and can be protected from seed predators and disturbance (Hoff and others 2001). Conversely, landscapes with low rust infection (less than 90 percent of stands) may not be good places to look for plus trees, but they may be suitable for proactive restoration treatments, such as reducing competition from shade-tolerant competitors through thinning and by creating openings to encourage natural regeneration through nutcracker caching (Hoff and others 2001; Keane and Arno 2001). Landscapes with greater than 50 percent of the area having high whitebark pine mortality (greater than 50 percent) should have high priority for restoration. At the same time, proactive treatment of healthier landscape should be considered, and even planting of rust-resistant seedlings, to create more resilient stands.
- *Level of mountain pine beetle outbreak.* The success or failure of restoration programs can be wholly dependent on the current level of mountain pine beetle on the landscape. Landscapes with evidence of impending or on-going mountain pine beetle outbreaks (patchy mountain pine beetle mortality or infestation) should be evaluated carefully before restoration is implemented. These stands may have the lowest priority for restoration actions such as silvicultural thinning or nutcracker openings to encourage seed caching (Keane and Arno 2001) because beetles in outbreak mode will kill many of the living whitebark pine trees that the restoration actions were designed to preserve. Conversely, landscapes that experienced major pine beetle epidemics in the past are good candidates for restoration through seedling planting, because of the lack of seed sources for regeneration and the open canopy conditions. Furthermore, we should be managing stand structure to mitigate future beetle outbreaks, as previously described. This entails maintaining multiple age classes within a stand or as a mosaic on the landscape.
- *Recent occurrence of fire.* A recent fire event might indicate that this landscape may not need treatment, or the landscape may need post-fire restoration treatments such as tree planting or site amelioration. A fire atlas (map of fire perimeters with burn dates) is essential for this assessment. If information on historical fire return intervals is lacking, managers need to consider that regenerating 2.5 percent of the total whitebark pine habitat type every 10 years is required to emulate a 400-year fire return interval to maintain the landscape within its historical range of variation over time. At 400 years, the long end of the fire return interval, most trees will be peaking in cone production. That would mean at a minimum, 25 percent of the seral whitebark pine type should have burned since 1900 to be within the maximum historical fire return interval range (Morgan and Bunting 1989).
- *Climate change.* Many believe whitebark pine is one of the most at-risk ecosystems in the western United States and that climate change will affect the whitebark pine distribution most severely, especially forests at the lowest elevational range (Koteen 1999; Romme and Turner 1991; Schrag and others 2008). While whitebark pine can grow in warmer, drier climates (Arno and others 1993), its vigor, reproductive potential, and regeneration success will surely decline, and it may be outcompeted by other forest species moving up in elevation. Therefore, as a hedge against potential shifts in climate, and the need for whitebark pine to disperse to new elevations or latitudes, restoration actions should be implemented above the current local lower elevational limits of whitebark pine and at the northern limits of whitebark pine in order to maintain healthy forests (Schoettle and Sniezko 2007; Tomback and Achuff 2010). Landscapes with topography that encompasses the full elevation range of whitebark pine might have higher potential for successful long-term restoration, while landscapes that have maximum elevations that are at

the historical lower elevational limits of whitebark pine might be difficult to restore in the future.

2. Successional Status

- *Landscape composition.* The composition of the landscape is an important indicator of the need for restoration. A landscape that is comprised mostly of stands dominated by shade-tolerant species (specifically subalpine fir) might indicate the absence of wildland fire and the need to initiate restoration actions. Conversely, the number of stands dominated by shade-intolerants (early seral species, such as whitebark pine) might indicate that restoration treatments might not be required. Modeling exercises have indicated that landscapes with greater than 10 to 20 percent of their area dominated by subalpine fir might be outside HRV and could be good candidates for initiating restoration activities (Keane 2001b). This threshold was estimated from simulation results for a landscape in north-central Montana. Vertical stand structure (seedling, sapling, pole, mature, and old growth, for example) is another indicator of successional stage; advanced stages have less structure than earlier seral stages. Landscapes composed primarily of stands in late seral stages (mature and old growth), especially if dominated by subalpine fir, should have a high priority for restoration. However, whitebark pine stands in the later stand structural stages might be used as a surrogate for the presence or abundance of cone-producing trees, which should be retained on the landscape. HRV concepts can be used as a reference to determine potential restoration thresholds based on stand structure.
- *Landscape structure.* The spatial patterns of stands comprising a landscape (patch distribution) can also indicate the status of important ecological processes. For example, landscapes composed of one or two patches (stands with same age class or vegetation characteristics) may need treatment to diversify and fragment the landscape (Keane and others 2002c). Conversely, landscapes with many fragmented small patches might need treatment to improve historical patch distributions. Landscape structure is usually described from a wide variety of landscape metrics that quantify size, shape, connectivity, contagion, and dimension of the landscape (McGarigal and Marks 1995). Reference conditions would be best taken from a simulated series of landscape histories where a small set of landscape metrics are used for comparison (Keane and others 2002a). We recommend that the indices of mean patch size (patch density), largest patch index, shape index, and contagion be used to match the native disturbance regime (Keane and others 2002b).
- *Departure from HRV of landscape composition and structure.* The current landscape composition,

computed as area by patch type (cover type, structural stage, or the combination, for example), can be compared to an historical time series of spatial layers to determine departure. The current condition can be quantified from any number of sources, including digitized stand maps and maps developed from remotely sensed imagery. Temporally deep historical spatial chronosequences are rare for most of the western United States, so most historical time series are developed using simulation modeling. The national LANDFIRE project is creating maps of current conditions from satellite imagery and historical time series from the landscape simulation model LANDSUM (www.landfire.gov) (Pratt and others 2006). These historical time series can also be created from other landscape models such as SIMMPPLE (Chew and others 2003), FVS-FFE (Reinhardt and Crookston 2003), and VDDT (Vegetation Dynamics Development Tool) (Beukema and Kurtz 1998). The comparison between current and historical is calculated using a departure index scaled from zero (totally departed) to 100 (exactly the same). The Fire Regime Condition Class (FRCC) mapped by the LANDFIRE project is derived from a departure index and can be used for this purpose. FRCC is an ordinal index from 1 (within HRV) to 3 (outside HRV), and it is available in a 1 km² national map (www.fs.fed.us/fuelman) and as a LANDFIRE map product at 30-m pixel resolution (www.landfire.gov).

3. Seed Sources

- *Distance.* Local extinctions can occur if whitebark pine declines to an extent where seeds are not abundant and sources are not close enough to provide adequate regeneration. Maximum dispersal distances documented in the literature range from 10 to greater than 30 km depending on geographical area and nutcracker population, but we feel 12 to 15 km is a good conservative maximum distance to expect nutcrackers to re-establish a whitebark stand (Lorenz and others 2008; Tomback 2005). Landscape assessments should identify areas where local extinctions are possible (greater than 12 to 15 km from a seed source) and prioritize these areas for regeneration treatments that involve planting. This can be done in a GIS using buffer analysis. Identified seed source areas should be assessed to evaluate if there are sufficient numbers of cone-bearing whitebark pine to provide the seed for regeneration. At least 20 to 50 cone-bearing trees per acre would be needed to be considered a good seed source (McKinney 2004).

4. Logistical Issues

- *Transportation network.* Critical for most restoration actions is a means to efficiently travel to the landscape to perform the treatments. Conducting

prescribed burns and tree cuttings is best done if the treatment units are near roads or trails. However, wildland fire use (WFU; allowing lightning fires to burn under acceptable conditions) may not need extensive transportation networks because no active suppression is involved. Landscapes with roads in whitebark pine forests would receive a high priority and those with trails may rate lower in priority.

- *Topography.* The complexity, orientation, and aspect of the topography will dictate the type, intensity, and extent of restoration activities. Landscapes with gentle slopes, for example, will be much easier to restore than steep, dissected topography. Landscapes with deep snows may be inaccessible for restoration equipment during critical times of the year.

5. Management Issues

- *Grizzly bear.* Any landscape where grizzly bears frequent could be considered high priority for restoration, especially if whitebark pine mortality is high and subalpine fir stands are extensive (greater than 20 percent in area). Management activities, such as prescribed burning, in critical grizzly bear whitebark pine habitat may not be desirable because these actions might actually reduce whitebark pine cone production in the short term. Restoration plans often prioritize treating areas with available access, which could cause potential future conflicts when cone-producing trees are close to human activities. Restoration activities themselves also cause disturbance, which discourages bear use of the area (Mattson and others 2001). Restoration treatments often focus on reducing the effects of competing shade-tolerant tree species, but mixed species stands have higher squirrel populations and therefore more squirrel middens. While bears require large areas free from human activities, restoration treatments bring humans into the whitebark zone, may remove cone-producing whitebark pine in the short term, or may reduce the population of squirrels or the size of middens. On the other hand, whitebark pine may need extensive management to avoid extirpation in the long term (Mattson and others 2001).
- *Land ownership and management direction.* The list of possible restoration actions for a landscape would entirely depend on the ownership of the landscape and how that landscape is managed. Roadless areas on National Forests may have a different set of restoration techniques when compared with National Parks or state lands. Landscapes with restrictions that may reduce the efficacy of restoration measures might be less desirable. Landscape management concerns are often locally important and must be addressed in any prioritization effort.
- *Wilderness.* Wilderness and recommended wilderness lands are treated quite differently from other public lands and, as such, are a special case in management.

Current wilderness policy with respect to whitebark pine restoration is detailed in the “Introduction” section.

- *Planning stage.* Landscapes that have completed burn plans could be some of the first to be restored, especially with wildland fire use or controlled wildfires. Those landscapes with completed NEPA analyses may also be considered high priority.

- *Human disturbance—structures and activities.*

Whitebark pine forests that are near areas or developments frequented by people, such as ski areas or popular hiking trails, may be undesirable for restoration if there is negative public opinion. However, proactive public education may be a win-win solution to this problem, actively engaging the public in understanding the reasons for whitebark pine resource management and even enlisting public support through “citizen science.” Interpretive information or other forms of public outreach at ski areas or at trailheads are good ways to inform the public about ecological challenges and potential solutions. Any restoration treatment may be made more desirable if it can also reduce fuels, improve ecosystem health, improve aesthetics, and have easy access.

Restoration Actions

Perhaps the most important restoration tool for landscape-level restoration applications is the use of controlled wildfires (CW). CW, which used to be called wildland fire use, prescribed natural fires, and “let burn” fires, are lightning-started fires that are allowed to burn under acceptable weather and site conditions that are specified in a fire plan (Black 2004). We feel the aggressive use of CW has the potential to be an efficient, economical, and ecologically viable method of restoring whitebark pine in many areas, especially wilderness. Landscapes where CW might be contra-indicated are those with few whitebark pine seed sources both near and distant, and in these places, planting is strongly advised. Otherwise, most CW will probably improve whitebark pine’s status and health if the fires are carefully monitored to avoid mortality of potentially rust-resistant trees. However, we highly recommend that burned areas in landscapes with high blister rust infection (greater than 50 percent) and mortality (greater than 20 percent) be planted with apparent rust-resistant whitebark pine seedlings (discussed at the stand and tree scale).

Uncontrolled wildfires, or wildland fires that are actively suppressed, may also be a possible restoration tool at the landscape level. Large wildfires may be important for whitebark pine restoration in those areas of its range that historically experienced extensive fires in a given year, such as the northern Rocky Mountains of the United States. Conventional wisdom is that wildfires today may burn larger areas more severely than the past because of the buildup of fuel from fire suppression efforts (Ferry and others 1995;

Van Wagendonk 1985), but recent research has found that these large fires actually leave a mosaic of intensities and severities that are similar to historical conditions (Keane and others 2008a). Land managers and fire suppression management teams should view wildfires as a possible mechanism for restoring high-elevation systems and use ecologically based decision support tools to decide whether or not to let wildfires create potential restoration sites for whitebark pine. Moreover, wildfire rehabilitation teams should evaluate the level of cone production and rust/beetle mortality in whitebark pine stands surrounding these large wildfires to assess if planting putative rust-resistant whitebark pine is necessary to ensure adequate regeneration.

Management Concerns

Seed Dispersal and Large Burns

Large burns (greater than 1000 ha) favor whitebark pine regeneration because wind-dispersed seeds of its competitor species take longer to disseminate into the center of large burned areas than whitebark seeds that are cached by nutcrackers flying up to about 30 km to cache their seeds (Lorenz and others 2008; Tomback and others 1990). However, seed dispersal for wind-dispersed conifers, such as subalpine fir and Engelmann spruce, can be rapid with favorable prevailing winds, thus reducing the effectiveness of large burns (Tomback and others 1990). If the prevailing winds do not favor seed dispersal into burns, whitebark pine seed dispersal by nutcrackers can result in more rapid regeneration. Burn areas can be attractive to nutcracker caching (Tomback and others 1990), but whitebark pine on-site seed sources are often killed during wildfires. Trees are killed not only directly from fire effects, but also because fire-damaged trees often attract mountain pine beetles.

A major management concern may be that cone-production

on or near the burned landscape might be insufficient for adequate regeneration of whitebark pine, because of high tree mortality and advanced successional processes. Between red squirrels cutting cones for storage in middens and Clark's nutcracker predispersal seed predation, few seeds may remain for seed dispersal (McKinney and Tomback 2007; McKinney and others 2009; Keane and Parsons 2010b). If whitebark pine seed sources are sparse or in poor condition then large burns must be planted with rust-resistant whitebark pine seedlings to ensure restoration success. Furthermore, between climate change and past fire exclusion policies, the area burned by wildfires and CW fires will be extensive during the next few decades. It is critical that periodic assessments be conducted to determine if too many or too few whitebark pine forest communities are being burned. Again, a landscape rotation or mean fire return interval of 400 years can be used to identify important burning thresholds and targets. One further concern is that with the combination of deteriorating seed sources and climate change, temperature and moisture regimes may be less favorable for germination of whitebark pine seeds cached in stand-replacing burns, and survival of seedlings. These processes may already be at work and explain observations of delayed regeneration of large burns in northwestern Montana (Tomback 2008).

Decline in Cone Production and Effects on Seed Dispersal

An analytically based model depicts the series of processes that occur following the arrival of blister rust within a whitebark pine stand and culminates with the creation of a positive feedback loop resulting in continued whitebark pine community decline (McKinney and Fiedler 2010) (Figure 4.14). The data to support this model were collected from 2001 to 2006 in 24 forest sites that ranged in size from 2 to 7 ha in the U.S. central and northern Rocky Mountains

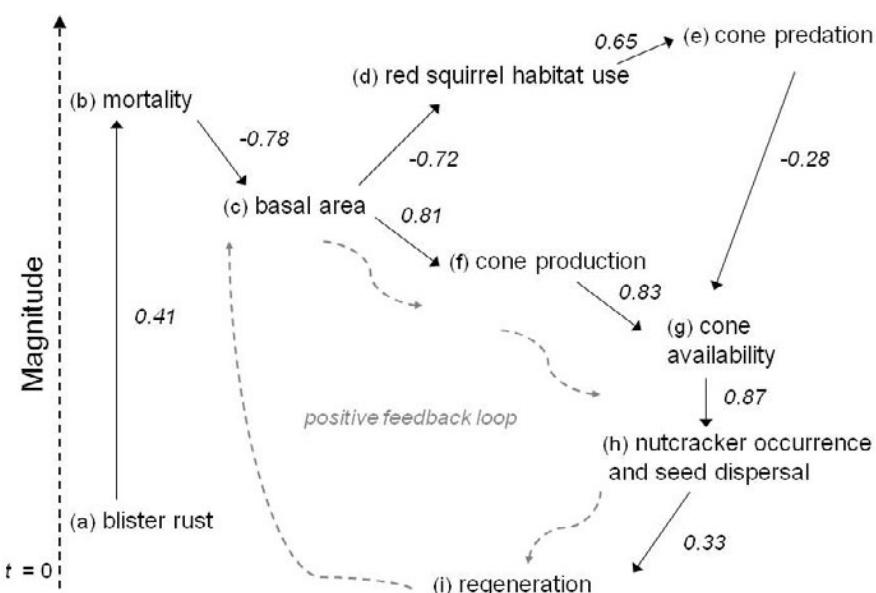


Figure 4.14. Analytically based model depicting the series of processes that occur following the arrival of blister rust within a whitebark pine stand (from McKinney and Fiedler 2010).

(McKinney and Fiedler 2010). Blister rust initially invades the stand, and rust-induced tree mortality increases with time. The correlation between rust infection and tree mortality is positive but weak, because as rust kills the most susceptible trees, the proportion of infected trees levels off while mortality continues to increase. As mortality increases, live whitebark pine basal area declines sharply. The decline in live whitebark pine basal area has an effect on red squirrel habitat use that depends on tree species composition. As the proportion of total stand basal area that is comprised of whitebark pine declines, red squirrel habitat use increases. There is a strong negative correlation between the proportion of stand whitebark pine basal area and the proportion of total squirrel detections comprised of active middens. As the proportion of middens increases, pre-dispersal cone predation increases. Greater cone predation results in fewer available cones at the time of nutcracker seed dispersal. Basal area and cone production are strongly and positively correlated ($r = 0.81$); thus, as whitebark pine basal area declines, cone production declines in a near linear fashion. Cone production declines that are due to a loss of live basal area are exacerbated by squirrel predation in mixed species forests and even whitebark pine-dominant forests that are adjacent to recently burned sites (fewer cones produced that suffer greater predation pressure) resulting in substantially fewer cones available at the time of seed dispersal (late summer to early fall) (McKinney and Tomback 2007; McKinney and Fiedler 2010).

Nutcrackers are highly sensitive to the available number (or density) of cones in a forest, and as nutcracker occurrence and seed dispersal behavior decline, regeneration opportunities decline (McKinney and others 2009). A lack of regeneration over time will eventually lead to a decline in mature, cone-producing trees. This begins the *positive feedback loop* whereby declining basal area leads to declining cone production, declining nutcracker seed dispersal activity, and ultimately, declining regeneration. Active management, such as planting rust-resistant seedlings, becomes a necessity at this point to prevent spiraling of the positive feedback loop to an end point of extirpation.

It is difficult to say exactly when in the previously described cycle of decline active management intervention is needed. Part of the uncertainty is due to differing management goals and priorities, and part is due to the complexities of habitat and landscape context of the forest in question. In the best of all worlds, proactive restoration would begin before decline is evident, helping to mitigate losses (Schoettle and Sniezko 2007). Decisions regarding an acceptable level of cone production decline and uncertainty of seed dispersal need to be made first, however, and the analytical model may be applied here for that purpose (McKinney and others 2009). For example, when we set a cutoff probability of seed dispersal to 0.70 (we want to be sure that 70 percent of the seeds will be dispersed by nutcrackers), 94.7 percent of all study sites with seed dispersal observed were correctly classified by the model. The logistic equation in McKinney and others (2009) predicts that a whitebark pine forest has

a seed dispersal probability greater than 0.70 with average cone production greater than 700 cones ha^{-1} .

Based on previous estimates of nutcracker energy requirements and the results from the seed dispersal model, a threshold of 1000 cones ha^{-1} averaged over a given site is needed for a high likelihood of nutcracker presence at the time of seed dispersal. For example, the model predicts a nutcracker seed dispersal probability of 0.83 for a site with mean production of 1000 cones ha^{-1} . The local spatial extent over which this magnitude of cone production must occur requires more detailed investigation. The estimate does, however, form a reasonably sound basis to begin to formulate whitebark pine management and restoration decisions.

If estimates of cone production are not readily obtainable for a given landscape, live whitebark pine basal area can be used instead as a predictor of cone production. Mean cone production was significantly correlated with mean basal area over the 24 sites sampled ($r = 0.81$). Graphical analysis of mean cone production plotted against basal area suggests that $5.0 \text{ m}^2 \text{ ha}^{-1}$ defines the lower limit of mean live whitebark pine basal area needed to produce an average of 1000 cones ha^{-1} . Furthermore, research sites where nutcracker seed dispersal was never observed over a three-year period had mean live whitebark pine basal area of $1.58 (\pm \text{SE } 0.78) \text{ m}^2 \text{ ha}^{-1} (n = 7)$; sites with nutcracker seed dispersal observed in some years (and not in others) had mean live basal area of $5.03 (\pm 1.01) \text{ m}^2 \text{ ha}^{-1} (n = 7)$; and sites with observations of nutcracker seed dispersal in all years had mean basal area of $15.27 (\pm 2.51) \text{ m}^2 \text{ ha}^{-1} (n = 10)$. Therefore, we estimate that whitebark pine forests with a mean basal area around $5.0 \text{ m}^2 \text{ ha}^{-1}$ will be able to produce approximately 1000 cones ha^{-1} , at least in some years, and consequently attract and maintain nutcrackers through the critical period of seed dispersal. However, because there is substantial variability in cone production among sites, the proposed cutoff value should be interpreted cautiously and accompanied by a site-specific evaluation of conditions (McKinney and Fiedler 2009).

Landslides with less than $5.0 \text{ m}^2 \text{ ha}^{-1}$ of live whitebark pine basal area and producing fewer than 1000 cones ha^{-1} will require planting of rust-resistant seedlings, especially with further whitebark pine losses highly likely. For example, given the high levels of rust infection and tree mortality, and the low levels of live basal area documented in northwestern Montana, it is likely that many whitebark pine forests in that region are no longer sustainable without restoration planting. However, data show that sites that exceed the $5.0 \text{ m}^2 \text{ ha}^{-1}$ threshold can still rely on nutcracker seed dispersal in some years, although these forests will lose whitebark pine over time as blister rust infection kills trees and damages canopies and as mountain pine beetle outbreaks continue. Managers are encouraged to identify such sites and use appropriate silvicultural treatments to increase nutcracker caching habitat, at least for the immediate future.

As an example, if a whitebark pine landscape has greater than $5.0 \text{ m}^2 \text{ ha}^{-1}$ of live basal area, is at least 10 ha in area, and is not isolated from other whitebark forests, it could serve as a natural seed source for a restoration project.

Removal (cutting) of competing shade-tolerant trees followed by prescribed burning at a location within 10 km of the whitebark seed source would likely attract nutcracker caching and increase the likelihood of natural regeneration (Keane and Arno 2001). Site-specific knowledge of whitebark pine forest attributes would also allow fire managers to make informed decisions regarding CW, which entails deciding when and where to allow lightning-ignited fires to burn. CW could be allowed to burn in subalpine forests where the probability of nutcracker seed dispersal is high and the potential for damage to humans and property is low. Finally, knowing which forests have whitebark pine basal area below 5.0 m² ha⁻¹ would allow managers to prioritize areas for planting with the limited number of rust-resistant seedlings available (Mahalovich and others 2006).

Here we have shown that specific forest stand conditions (proportion of stand basal area comprised of whitebark pine, total live whitebark pine basal area, and cone production) within a landscape are crucial elements in predicting the number of cones available for nutcrackers, nutcracker seed dispersal probability, and thus, the potential to contribute genetic material to future generations through natural regeneration. Natural regeneration, facilitated by restoration treatments, should include a higher proportion of rust-resistant individuals over time relative to the frequency of rust-resistance in parent trees because of a high mortality rate in susceptible trees. In some remote locations, the use of CW may be the best approach to whitebark pine restoration, given reasonably healthy seed sources. However, seedlings that are susceptible to blister rust have a poor chance of survival in areas of high blister rust infection levels (for example, Tomback and others 1995), and the need to plant rust-resistant seedlings may be inevitable. Planting rust-resistant seedlings may well be the best strategy for spreading genetic resistance to blister rust as rapidly as possible and ensuring that whitebark pine will remain on the landscape.

Example: Restoration Decision Guidelines for Watersheds on the Caribou-Targhee National Forest

Jenkins (2005) recognized that several factors should be included in landscape-scale assessments (Table 4.6). Of greatest importance is the extent of whitebark pine forests that currently exist in the assessment area compared to the historical levels of whitebark pine. Those areas with small changes in whitebark pine distributions and abundance require less active restoration. A large decrease in abundance (estimated at greater than 20 percent of historical levels) indicates a greater need for restoration. Jenkins (2005) also recognized that in addition to whitebark pine abundance, changes in size class distribution should be considered. Areas that have decreases (greater than 20 percent) in historical size class distribution levels have a greater need for restoration. This comparison to historical ranges of whitebark pine abundance and size class distributions to current

levels is consistent with the concepts of HRV (Keane and others 2002b; Landres and others 1999). Application of HRV to prioritize and design whitebark pine restoration efforts can be useful if interpreted in the appropriate ecological context (Keane and Karau 2010).

Stand Scale

The stand scale is the resolution at which most proactive management restoration efforts are targeted. A stand is defined here as an area of homogeneous vegetation composition and structural conditions, usually about 1 to 100 ha (2 to 250 acres). The delineation of a stand in a spatial analysis environment (GIS) is usually called a polygon. Planning and prioritization should rarely be conducted at the stand level because the complex processes that control whitebark pine abundance and decline are best described at the landscape and broader scales. However, most proactive restoration treatments are usually designed and implemented at this stand level. In this report, landscapes are composed of stands that are described by the trees and undergrowth that grow within their borders, and trees are usually described by basal area, density, and timber volume by species and size classes. The undergrowth is often described as cover, height, and density by species and size class.

Assessments

Assessments performed at this scale would be for several purposes: (1) to determine the health and condition of the stand to rank it compared to other stands for restoration priority, and (2) to determine the condition of the stand to inform design of restoration treatment. Assessments at the stand level usually involve inventory or monitoring. Many inventory and monitoring systems can be used to sample stand attributes, including FIREMON (Lutes and others 2006), FSVEG, and FFI (FEAT FIREMON Integration) (Lutes and others 2009). It is critical that any inventory or monitoring effort include an assessment of those factors that are contributing to whitebark pine decline, such as rust infection incidence, canopy kill, mountain pine beetle mortality, whitebark pine regeneration potential, and subalpine fir or other shade-tolerant species density and size classes. The WPEF methods for surveying whitebark pine are focused on health assessment of stands; using these methods and the variables described allows for meaningful comparisons among stands within and among geographic areas (Tomback and others 2005; www.whitebarkfound.org).

A multitude of variables can be used to describe stand conditions for assessing restoration concerns and designing appropriate management treatments. Previous fire history can be assessed by visual evidence within the stand such as fire scars on trees, age class structure of the stand, and charcoal in the soil. Successional status can be determined from the tree density by size class and species. The following are important stand attributes that may be considered in deciding how to treat a whitebark pine stand:

Table 4.4.1. Restoration Rating for Stands for the Targhee within HUC 1201. "SF" is subalpine fir, "WB" is whitebark pine, and "N/A" is not available. Numbers after "/" indicate weighting.

Stand #	Recent stand replacing event ¹	Distance to seed source >10 km ²	Successional status ³	GB management emphasized		No GB management	Blister rust ⁷	Mountain pine Beetle ⁸	Stand score	Total restoration need score
				Human disturbance >.5 mile ⁴	>174 BA and 15-50% WBP ⁵					
1	No	No	SF/20	.65/10	Maybe/10	N/A	Mod/10	Y/40	90	240*
2			SF/20	1/10	Maybe/10	N/A	Mod/10	Y/40	90	240*
3			WB/0	.5/0	N	N/A	Mod/10	Adj/40	50	200
4			SF/20	.1/0	Maybe/10	N/A	Mod/10	Adj/40	80	230
5			SF/20	.5/0	Maybe/10	N/A	Mod/10	Y/40	80	230
6			SF/20	.6/10	Maybe/10	N/A	Mod/10	Y/40	90	240*
7			SF/20	1-2/10	Maybe/10	N/A	Mod/10	Adj/40	90	240*
8			SF/20	1-2/10	Maybe/10	N/A	Mod/10	Adj/40	90	240*
9			SF/20	1-2/10	Maybe/10	N/A	Mod/10	.8mi/20	70	220
10			LP/10	1-2/10	N	N/A	Mod/10	.9mi/20	50	200
11			SF/20	1-2/10	N	N/A	Mod/10	Adj/40	80	230
12			SF/20	1-2/10	Maybe/10	N/A	Mod/10	.3mi/20	70	220
13			WB/0	1-2/10	N	N/A	Mod/10	.9mi/20	40	190
14			WB/0	2-3/10	N	N/A	Mod/10	1-2mi/20	40	190
15			WB/0	2-3/10	N	N/A	Mod/10	1-2mi/20	40	190
16			SF/10	2-3/10	Maybe/10	N/A	Mod/10	1-2mi/20	60	210
17			WB/0	2-3/10	N	N/A	Mod/10	1-2mi/20	40	190
18			WB/0	2-3/10	N	N/A	Mod/10	1-2mi/20	40	190
19			LP/10	2-3/10	N	N/A	Mod/10	1-2mi/20	50	200
20			WB/0	3-4/10	N	N/A	Mod/10	2mi/20	40	190
21			LP/10	2-3/10	Maybe/10	N/A	Mod/10	1-2mi/20	60	210
22			SF/20	2-3/10	Maybe/10	N/A	Mod/10	1-2mi/20	70	220
23			SF/20	2-3/10	Maybe/10	N/A	Mod/10	1-2mi/20	70	220
24			WB/0	2-3/10	N	N/A	Mod/10	1-2mi/20	40	190
25			SF/20	2-3/10	Maybe/10	N/A	Mod/10	1-2mi/20	70	220
26		✓	LP/10	3-4/10	Maybe/10	N/A	Mod/10	2.5mi/20	60	210
27		Yes/10	SF/20	.5/0	N; CSE	N/A	High/20	Y/40	90	240*
28		Yes/10	WB/0	.65/10	N; CSE	N/A	High/20	Y/40	80	230
29		Yes/10	WB/0	.5/0	N; CSE	N/A	High/20	Y/40	70	220
30	✓	No	WB/0	1-2/10	N	N/A	Mod/10	.6mi/20	40	190

"CSE" indicates stands with a stand exam.

* indicates highest rated stands.

Ratings are as follows:

¹Natural regeneration within 10 yrs = 0, regeneration within 20 yrs = 10, regeneration >20 yrs = 20

²Distance <10 km = 0, Distance >10 km = 10

³Whitebark pine climax = 0, climax with high mortality = 1, whitebark pine >40 percent = 0, lodgepole dominant = 10, subalpine fir dominant = 20

⁴Potential for human disturbance >.5 mi = 0, ≤.5 mi = 10

⁵Not capable of meeting or meets and is stable = 0, potentially but not currently meets = 10, meets but treatment needed to maintain = 20

⁶Accessibility poor = 0, accessibility fair = 10, accessibility good = 20

⁷Blister rust infection low = 0, rust infection moderate = 10, rust infection high = 20

⁸Mountain pine beetle low and stable = 0, beetle high or increasing within 1-3 mi = 10, high or increasing in or adjacent = 20

- **Disturbance History**

- *Blister rust infection and mortality.* Treatment objectives for these sites should emphasize rust-resistant whitebark pine regeneration rather than cone production. This is accomplished by treatments that favor remaining healthy trees (which could be rust resistant), and where blister rust infection levels are high, planting of seedlings from rust-resistant parent trees. Rust infection and mortality levels can be assessed using the WPEF rust sampling methods (Tombak and others 2005), but other inventory systems, such as FIREMON (Lutes and others 2006), FFI (Lutes and others 2009), and FSVEG, are available to assess rust damage.
- *Mountain pine beetle damage and mortality.* Although mountain pine beetles are native to whitebark pine ecosystems, outbreak levels should be quantified to maximize the success of restoration treatments; many treatments can be rendered ineffective if they are followed by mountain pine beetle infestations. Some treatments, such as thinning and burning, actually attract mountain pine beetles, which can then kill the same whitebark pine that have been favored by treatments. The standard inventory techniques mentioned above are available for estimating beetle levels and damage.
- *Time since last fire.* It is important to know if the time since last fire has been excessively long (greater than one fire rotation) or past the mean historical fire-free interval (greater than mean fire return interval), especially on seral whitebark pine sites, because wildfires can be used as restoration tools. If the stand has been burned within the last century, then it is doubtful that it would need immediate restoration actions unless post-burn whitebark pine recovery was hampered by blister rust or a lack of nutcracker caching and a need for planting is indicated. We recommend planting phenotypically rust-resistant seedlings in recently burned areas where the blister rust incidence in the surrounding seed source is greater than 50 percent or if losses to mountain pine beetle are severe. In contrast, climax whitebark pine communities are self-replacing over time in the absence of fire and other disturbances.
- *Fire regime and history.* Determining fire regime and historical fire intervals for any given stand will provide guidance as to fire regime characteristics and successional dynamics. Some stands may be prone to non-lethal surface fires that maintain whitebark pine dominance and kill subalpine fir, and the frequency of these fires could be used to craft an appropriate restoration action.

- **Successional Status**

- *Site type.* Climax whitebark stands will be dominated by whitebark pine or codominated by whitebark

and other conifers depending on site harshness. Generally, the drier and colder the site, the more dominant whitebark pine (Arno 2001). These climax stands usually occur at the highest whitebark pine elevations, but also may occur on particularly wind-swept or otherwise droughty sites where other tree species struggle to survive. In geographic or topo-edaphic regions where whitebark pine is one of the indicated climax species, succession to more shade tolerant tree species is not a concern. If mortality in climax stands due to blister rust and bark beetles is high (greater than 50 percent), managers may consider planting whitebark pine to meet appropriate forest cover objectives established during land management planning, especially if seedlings have some degree of rust resistance. In stands where whitebark pine is seral (seral whitebark pine types, see “Ecology” section), the successional progression causes the whitebark pine to be replaced by more shade-tolerant tree species (primarily subalpine fir and Engelmann spruce). The greater the representation of the shade-tolerant species, the greater the decline of more seral species such as whitebark pine. Succession is one of the three major factors causing the decline of whitebark pine throughout its range (Tombak and Achuff 2010; Tombak and others 2001a).

- *Seral stage.* Managers may consider treating stands with low to moderate representation of subalpine fir and spruce (less than 50 percent basal area) if this meets with other management objectives. Treating stands earlier in the successional process could reduce loss of the whitebark pine component, possibly increase cone production, and decrease the likelihood that the stand will support a crown fire that will kill cone-bearing whitebark pine. Any stand with greater than 50 percent basal area in subalpine fir and Engelmann spruce should have a high priority for treatment, especially if the landscape is composed of greater than 20 percent subalpine fir dominated stands by area. Stands with high densities of subalpine fir in the understory (greater than 2500 trees ha⁻¹) should also be prioritized for treatment.

- **Other Ecological Factors**

- *Distance to seed source.* Stands that are experiencing high levels of whitebark pine mortality due to blister rust, beetles, wildfire, or succession and that are greater than 12 to 15 km (general maximum distance to expect nutcrackers to re-establish a whitebark stand) from a productive whitebark pine seed source should be a high priority for treatment (for example, Lorenz and others 2008). Further decline of the stand might result in a local extirpation. Restoring whitebark pine in this situation may require planting since so many of the cone-bearing trees are lost.

- **Management Issues**

- *Red squirrel middens.* Grizzly bears obtain whitebark seeds from squirrel middens. In general, squirrels and their middens are more abundant in stands with high basal areas of mixed conifer species that produce more constant supplies of squirrel food compared to pure whitebark stands that produce highly variable seed crops (see “Squirrels” section). Midden size and probability of occupancy decrease with increasing elevation (Mattson and Reinhart 1997). Based on optimum conditions for bear use of squirrel middens, Mattson (2000) recommended an overall forest basal area greater than $40 \text{ m}^2 \text{ ha}^{-1}$ with whitebark basal area representing 15 percent to 50 percent of the total basal area. In the GYA, grizzly bear use of whitebark pine seeds increases with increasing squirrel densities and decreases with increasing whitebark pine basal area. Maximum bear use occurs at relatively low whitebark pine densities (basal area of 3 to $15 \text{ m}^2 \text{ ha}^{-1}$). Optimizing stand conditions for red squirrel midden production for grizzly bear use is somewhat at odds with optimum stand conditions for whitebark pine. Cone production is relatively low in stands younger than 100 years of age and reaches peak levels soon after. Moderate levels of cone production persist in stands 300 to 400 years old (Weaver and Forcella 1986). Conditions that optimize squirrel use should occur when the whitebark pine trees in the stand are at prime cone-producing age (100 to 300 years).
- *Grizzly Bears.* Grizzly bear foraging in whitebark pine will suffer from the removal of cone-producing whitebark pine, reduction of squirrel densities, or reduction in the size of squirrel middens (Mattson and others 2001). Restoration efforts should minimize impacts on these factors, but Podruzny and others (1999) preferred a no action approach, stating “we encourage caution in the management of whitebark pine habitats.” To prevent further loss of whitebark habitat and seed-producing trees in the grizzly bear’s range, cone harvesting or use of management-prescribed fires in the whitebark pine zone is discouraged. Bears avoid areas with on-going human activity, such as stand preparation for restoration activities. Management of whitebark pine forests for grizzly bears should emphasize maintaining large secure areas of diverse habitat types supporting stable numbers of whitebark pine trees and squirrels.

Restoration Actions

Wildland fire is the keystone disturbance that shapes most seral whitebark pine communities, so restoration treatments should be designed at the stand level to emulate fire’s historic effects on the landscape (Keane and Arno 2001; Perera and others 2004). While prescribed fire is the obvious tool,

mechanical cutting treatments can also be effective in accessible areas. Properly designed silvicultural thinning can simulate the effect of mixed severity and non-lethal surface fire in whitebark stands (Keane and Arno 2001). Treatment unit sizes and shapes should be similar to the patterns left by past fires, but must consider the amount and condition of available whitebark pine seed source in surrounding stands (Keane and Parsons 2010b). Treatments that create large areas for whitebark pine regeneration should be avoided if there is little seed available for caching unless planting rust-resistant seedlings is possible (McKinney 2004).

Whitebark pine is regenerated almost exclusively from Clark’s nutcracker seed caches. Therefore, restoration treatments that emphasize regeneration should optimize conditions that attract Clark’s nutcracker caching, or if not possible, plant seedlings instead. The optimum habitat for whitebark pine regeneration appears to be recently burned areas, because nutcrackers readily cache seeds in these open areas, and whitebark pine usually regenerates rapidly as a pioneering species under these conditions (Tomback and others 1990; Tomback and others 2001c). Burn patches greater than 5 to 10 acres were found to be attractive to Clark’s nutcrackers (Norment 1991; Tomback and others 2001c). Whitebark pine seedling survival depends on many factors, but the lack of competition, and the protected microsite conditions that nutcrackers select appear to be the most important (Izlar 2007; McCaughey and others 2009).

Basically, two major types of restoration treatments are best implemented in combination at the stand level: prescribed burning and mechanical cuttings. Other minor treatments can be used to augment or complement the two major treatment types. Most restoration treatments are designed to reduce or eliminate competing species and increase the regeneration opportunities for blister rust-resistant whitebark pine seedlings. Again, the primary objectives of these proactive restoration treatments are to: (1) mimic some historical disturbance process, mainly wildland fire, (2) facilitate whitebark regeneration and cone production, and (3) create optimum nutcracker caching habitat. Two sources are available as detailed references for evaluating, designing, and implementing whitebark pine treatments. Keane and Parsons (2010a, 2010b) summarized results of a 15-year whitebark pine restoration study by treatment across five diverse sites. Keane and Arno (2001a) presented additional summarized material that can be used for the same purpose.

Mechanical Cuttings

Mechanical cuttings are treatments that manipulate the stand by removing trees (Figure 4.15). It is important to note that traditional silviculture has limited effectiveness in these high mountain stands because of the severity of the site, unique autecology of whitebark pine, and bird-mediated seed dispersal (Keane and Arno 2000). Novel silvicultural strategies that are tailored to individual stands are needed to address restoration concerns in whitebark pine (Waring and O’Hara 2005). In general, most cuttings should attempt to

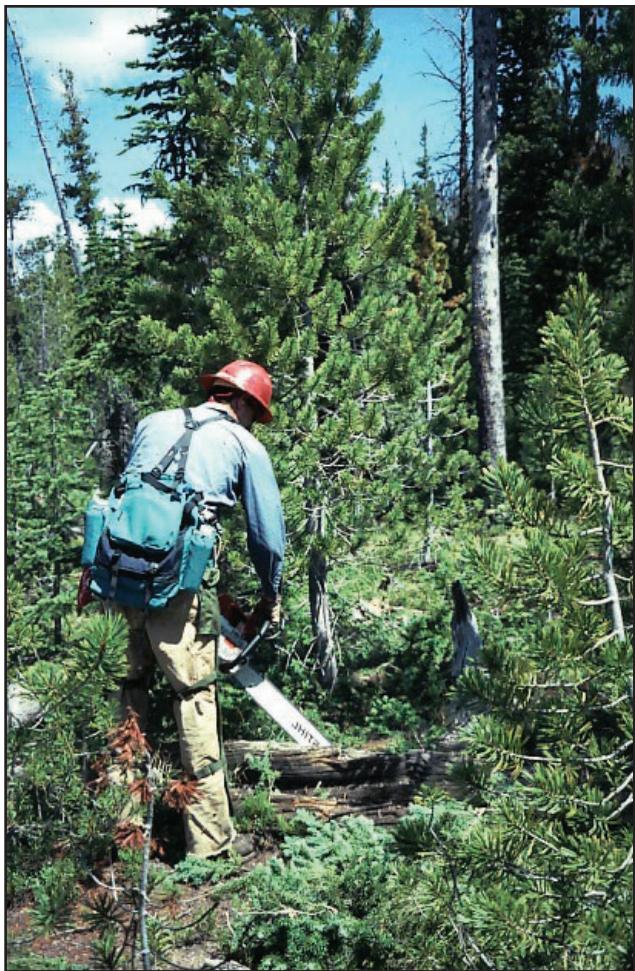


Figure 4.15. Mechanical cutting used for restoring whitebark pine stands.

eliminate subalpine fir and other shade-tolerant competitors while enhancing whitebark pine. Thinnings can be used to improve the health of potential cone-producing whitebark pine, while other cuttings can be used to create fuelbeds to support prescribed burning activities. Usually, mechanical cuttings are only effective when treated stands are in close proximity to roads and are easy to work (gentle slopes, few rocks, and few wet areas, for example).

Six types of mechanical cuttings are being used in restoration treatments for whitebark pine. Keane and Parsons (2010b) created *nutcracker openings* in successional advanced subalpine fir stands with healthy and dying, rust-infected whitebark pine (Figure 4.16). Nutcracker openings are a cutting treatment that attempts to mimic patchy, mixed severity fires. All trees except whitebark pine are cut in these openings. The size and shape of these cut areas may vary, but they can be anywhere from 1-30 acres based on a study by Norment (1991) who found that nutcrackers appeared to favor burn patches less than 15 ha in size. Other cutting treatments include *group selection cuts*, where all trees except whitebark pine are cut (group selections can be nutcracker openings), and *thinnings* where all non-whitebark pine trees

below a threshold diameter are cut (Burns and others 2008; Chew 1990; Eggers 1990). *Girdling* subalpine fir trees has also been attempted on some restoration efforts because it is a cheap, rapid means of killing competing subalpine fir (Jenkins 2005). However, to be effective, the girdling has to be done below the lowest live branches or those branches can form new boles. Girdling also leaves a large portion of the tree biomass on the site, which could provide fuel that fosters high severity wildfires that could kill the whitebark pine trees being restored. *Daylighting* (cutting of shade-tolerant competing species in a circle around whitebark pine trees) has been gaining favor among managers because it is cheap and easy, but there is little research on its effectiveness. One last cutting treatment is a fuel augmentation or *fuel enhancement* treatment where subalpine fir trees are directionally felled to increase fuel loadings and fuelbed contagion (Keane and Arno 1996, 2001). Keane and Parsons (2010a) found this treatment highly effective for facilitating prescribed burning.

It is important to reduce or remove the slash from the treatment area to (1) allow nutcrackers access to the ground for caching (Keane and Parsons 2010b), (2) reduce potential mortality from *Ips* spp. beetles (Baker and Six 2001), and (3) reduce the severity of unplanned wildfires (Keane and Arno 2000). This may be accomplished by (1) piling the slash and then burning the piles, (2) whole tree skidding to a landing that removes the boles and branches from the site, or (3) augmenting the cutting with a prescribed fire. Waring and Six (2005) found that *Ips* spp. beetles from slash piles move out and kill whitebark pine trees after one year. Cutting treatments can be offered as commercial timber harvests if (1) the trees are large enough, (2) the area is accessible by road, and (3) there is a market for the timber. Often, land management agencies have implemented cutting treatments using outside funding from various foundations or institutions because of the low timber value in treated stands.

Keane and Parsons (2010b) found that lodgepole pine trees could be left on site if they occur in low densities (less than 20 trees ha^{-1}). Whitebark pine can compete with lodgepole pine on most upper subalpine sites with acceptable whitebark pine regeneration and growth providing that over-story lodgepole pine cover is low (less than 50 percent) (Arno and Hoff 1990; Keane and Parsons 2010b). Elimination of shade-tolerant competitors is the most important requirement of any cutting, and it is critical that the cone-bearing trees are eliminated first. Subalpine fir can have frequent cone crops with numerous seeds that will create dense fir stands. The most effective cutting treatments will be those that eliminate the most subalpine fir trees, starting with the cutting of cone-bearing trees first and then eliminating the carpet of fir regeneration. The presence of residual subalpine fir seedlings and saplings after a cutting treatment can shorten its life span and render it ineffective after a short time. The implementation of a prescribed burn after a cutting treatment can kill the understory subalpine fir and make the treatment effective longer.



Figure 4.16. An example of nutcracker openings, a mechanical treatment used by Keane and Parsons (2010b) to mimic patchiness of mixed-severity fires.

Prescribed Burning

Prescribed burning may be the most desirable treatment because it best emulates wildland fire regimes (Figure 4.17), but it is also the most difficult and risky treatment to implement. Prescribed burns can be implemented at three intensities to mimic the three types of fire regimes common in whitebark pine forests (see “Fire Regimes” section). The primary objective of low-intensity prescribed fires is to kill the subalpine fir understory and perhaps the fir overstory and to preserve the whitebark pine component. Moderate-intensity prescribed burns can be used to mimic mixed-severity fires where passive crown fire behavior is common as dense subalpine fir crowns are torched, and these passive crown fires can burn patches of variable size depending on wind, canopy contagion, and fuel moisture conditions. A high-intensity prescribed burn is difficult to apply because it is usually implemented as a running or active crown fire that is difficult to control. However, this type of severe burn creates patches that are so large that seeds of whitebark pine competitors are unable to disperse into the center, allowing whitebark pine regeneration decades of competition-free growth after they have germinated from seeds cached by nutcrackers.

The ignition method for lighting the prescribed fires is important in the upper subalpine whitebark pine ecosystem. In previous restoration efforts, the prescribed fires were ignited using strip head-fires where the strip width was increased if higher fire intensities were desired. However, some study sites were too moist so they were burned with very wide strips. Keane and Arno (2000) used both the terra-torch and heli-torch in their study and burned large areas with the target high intensities, but these tools may not always be available (Figure 4.18). That leaves hand-held drip torches as the



Figure 4.17. Prescribed burning in whitebark pine (Keane and Parsons 2010b).

primary ignition technique, and, to be effective, these ignitions should be attempted under dry conditions, especially if high-intensity fires are the objective of the burn. Another way to achieve high-severity prescribed fires is to implement multiple prescribed burns where two or three burns are implemented in the same stand over 5 to 10 years, provided there are sufficient fine fuel accumulations.



Figure 4.18. Prescribed fire ignition is being implemented in a whitebark pine restoration site using the terra-torch.

We recommend a fuel enhancement cutting that is implemented one year prior to a prescribed burn to ensure that burn objectives are fully realized (Figure 4.19) (Keane and Parsons 2010b). The addition of cured slash to discontinuous fuelbeds improves burn effectiveness by providing additional fine fuel to: (1) aid fire spread into all areas of the stand, and (2) augment quickly drying fine fuel loadings so the burn can be implemented under moist conditions. Prescribed burns have a greater coverage and higher severity in stands where the fuels were enhanced (Keane and Arno 2001). Fuel enhancement is easy, cheap, and relatively quick, and enhancements can be done by timber crews, fire crews or contractors. Keane and Parsons (2010b) also found that shrub and herbaceous fuels were much drier after the first hard frost in late summer or early autumn. This frost kills the aboveground foliage that allows the plants to take water from the soil so the entire plant structure can dry sufficiently for burning.

Planting

As whitebark pine continues to decline across its range, there will be fewer seeds produced and available for nutcracker caching, resulting in fewer caches across the landscape, which in turn will reduce potential whitebark pine regeneration. Furthermore, those seeds produced in damaged stands are highly sought after by pre-dispersal seed predators, especially pine squirrels but also nutcrackers, leaving few seeds for nutcracker caching (McKinney and others 2009; McKinney and Tomback 2007). In high rust mortality areas, there may not be sufficient seeds to

naturally regenerate whitebark pine and planting may be the only option.

Trees should only be planted from seed collected from “plus” trees known to be rust-resistant—identified by seedling progeny in rust screenings—or at least from phenotypically rust-resistant cone-bearing trees that are healthy with 30 percent or more live-green crown in otherwise highly rust-infested stands. Once seeds are available from seed orchards, cone collections should shift from the field to the orchards, which have been designed for improved blister rust resistance, broad adaptability, and minimal inbreeding. It may be beneficial to plant whitebark pine on a variety of sites and to refine planting guidelines for a specific geographic area or stand condition that will optimize survival and growth of future plantings.

Scott and McCaughey (2006) and McCaughey and others (2009) have developed more detailed, extensive planting guidelines. On the broad scale, planting should be done on a variety of sites, including the more productive seral sites. When practical, planting crews should attempt to remove non-whitebark conifers to make planting more effective in the long term. Based on ecological and physiological information, planting trials, and experience in the northern Rocky Mountains, they recommended the following guidelines be included in planting prescriptions:

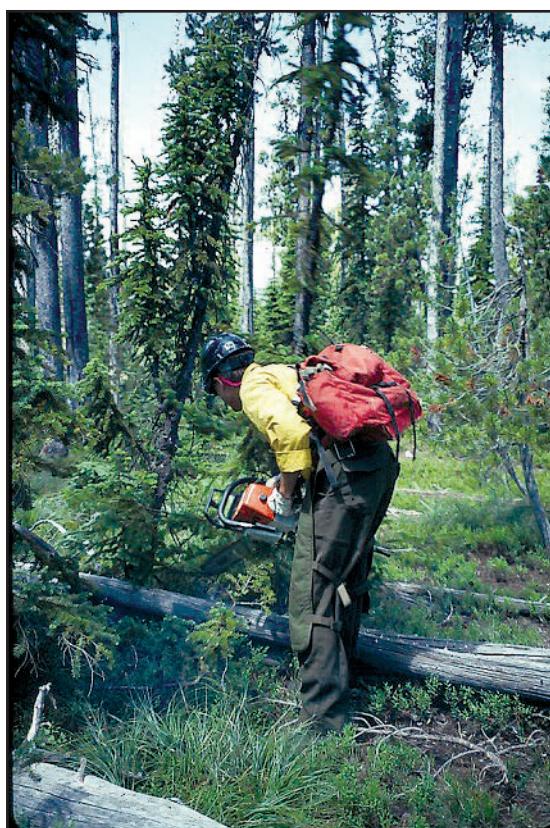


Figure 4.19. Fuel enhancement cutting used to augment the fuelbed to widen the prescribed burning window and allow fire to burn to more of the restoration stand.

- Reduce overstory competition to increase light and day length to improve the effective growing season.
- Reduce most understory vegetation, especially grasses and sedges, to reduce competition for available soil moisture. However, sparse vegetation and particularly grouse whortleberry may provide some shade, retain moisture, and provide other benefits.
- Avoid planting in swales or frost pockets; consider the topographic position as well as the actual planting spot. Young whitebark pine seedlings do not appear to be frost hardy during the growing season. Ridge tops or exposed slopes are suitable.
- Provide shade and protection for newly out-planted trees to improve water utilization and to reduce light intensity and stem heating. Planting by stumps or other stationary shade is important.
- Plant where there is some protection from heavy snow loads and drifting snow. Stumps, rocks, and large logs are favorable microsites
- Do not overcrowd out-planted trees to avoid long-term inter-tree competition. Open grown trees have the largest crowns and produce the most cones. Tree form is not as important because the purpose is to establish trees for long-term regeneration, cone production purposes, aesthetics, and a variety of other reasons that do not include timber production. Adjust spacing guides based on expected survival. At 50 percent survival, planting density should be 6.1 m by 6.1 m (20 ft by 20 ft), producing 247 live seedlings ha^{-1} (100 acre^{-1}).
- Plant when there is adequate soil moisture. Summer and fall outplanting have been successful, thereby avoiding the need for long expensive snow plows and delayed entry due to heavy spring snow loads.
- Plant large, hardy seedlings with good root development.

Whitebark pine seedlings take five to seven years to become fully established and start significant height growth (McCaughey and Tomback 2001). Perkins (2004) found that grouse whortleberry has a positive effect and upland sedges (*Carex* spp.) have a negative effect on the growth and survival of planted whitebark pine seedlings (Tomback and others 1993). Planting spot selection should be adjusted to take advantage of this information.

It may be useful to inoculate whitebark pine seedlings with ECM fungi for survival in nature since whitebark pine shares a complex, mutualistic ecological relationship with various species of ectomycorrhizae (Mohatt and others 2008; Read 1998) (see “Introduction” section). Pre-assessment of soils for the presence of appropriate native ECM fungi can be accomplished through use of bioassay techniques (planting seedlings in soils to be tested under greenhouse conditions). Inoculation of nursery seedlings with native fungi should be considered when soils lack appropriate ECM fungi and it is unlikely they will be imported in a timely manner (Brundrett and others 1996; Khasa and others 2009). Areas at high risk for absence of ECM fungi

for whitebark pine are: ghost forests, severe burns, and species shift areas (not previously in whitebark pine). This is particularly true for areas a long distance from an inoculum source with few/no animal vectors present. The use of site-adapted host specific native fungi that occur with whitebark pine as inoculum is highly recommended. This excludes the use of commercial inoculum containing generalist fungi or those for/from lodgepole pine, spruce, fir, and other conifers. Inoculation and colonization of whitebark pine seedlings with native fungi has been successful under greenhouse conditions (Cripps and Grimme 2010). *Suillus* species have been used to successfully regenerate stone pines in Europe for 50 years (Weisheit personal communication) and *Suillus* spp. were the most vigorous colonizers for whitebark pine in greenhouse studies (Cripps and Grimme 2010). The goal of inoculation is not to enhance growth of the pine, but to increase its survival rate and overall health. Inoculated seedlings should be subsequently monitored for colonization and survival. Planting trials using whitebark pine seedlings inoculated with native fungi were initiated in 2010.

Management Concerns

Scorching and wounding of trees can weaken trees and expose them to further damage by attracting mountain pine beetles, even at endemic beetle population levels. Managers should avoid scorching and wounding of 6 inch diameter breast height (DBH) and larger whitebark pine trees during restoration treatments. Changes in microclimate that occur when adjacent trees are removed can also stress whitebark pine in the short term and make them more susceptible to mountain pine beetle attack (Baker and Six 2001). Managers should protect high-value trees, which are those both bearing cones and exhibiting phenotypic blister rust resistance, as discussed in the “Tree Scale” section. If active outbreaks of mountain pine beetle are occurring locally, or if beetle populations are increasing, managers may consider delaying the restoration treatments until the outbreak is over.

There is little information available documenting the release of whitebark pine after the removal of any competition. Keane and others (2007a) conducted a limited release study based on only 48 trees in Montana, United States, and found that the magnitude of release after surrounding competing trees were cut was dependent on pre-cut tree density, tree age, and tree size. Basically, the youngest, largest trees in dense stands had the greatest potential for release and saplings older than 70 to 100 years may not release following treatment. Keane and Morgan (1994a) found that most of the apparent advanced regeneration in mature whitebark pine stands was quite old (greater than 100 years). Moreover, the understory regeneration had a wide range—from 30 to 270 years of age for trees less than 1 inch DBH. It is doubtful that all seedlings and saplings will release following a treatment to remove competition. Designing restoration prescriptions to release whitebark pine is risky since only a few of the youngest, most vigorous trees will release, but the majority of older understory regeneration may not have the capacity

to release. If release cuttings are desired, we suggest that the age structure of the understory be assessed to evaluate the potential for release (Keane and others 2007a).

The likelihood and rate of natural regeneration establishment depends primarily on the abundance of seed sources, the proximity of those seed sources to treated area, and the harshness of the site. Productive sites with abundant adjacent seed sources will likely establish natural regeneration within 10 years. However, recent studies and observations (Tombback 2008) suggest that areas with limited seed production will have limited natural regeneration, especially during warming temperature trends. Planting is the indicated treatment on these disturbed sites because it can increase rust resistance by using seedlings from suitable seed sources with the highest known levels of resistance.

Previously, planting success for whitebark pine was quite low due to the lack of guidelines and experience in these high-elevation systems. However, current efforts are showing great promise, and the Scott and McCaughey (2006) guidelines should help increase the survival of planted whitebark pine seedlings. There are some factors that might influence planting success:

- *Snow.* Heavy snow loads may harm or break seedlings, and the creep and glide of these heavy snow packs downslope could pull seedlings from the ground (Holler and others 2009). Seedlings should be planted near stable microsites (logs and stumps, for example). Heavy snow can also decrease the growing season because of late melt dates (Keane and Parsons 2010a).
- *Sun.* Insolation can kill many planted seedlings, but this can be mitigated with the selection of microsites that provide at least partial shade in planting sites.
- *Disease.* Damping off fungus occurs in deep duff and decomposing organic material.
- *Competition.* Grass competes with whitebark pine seedlings; seedlings should not be planted next to grass clumps or in graminoid tussocks. Whitebark pine should not be planted under closed or semi-closed canopies, or on sites near other conifers.

Here are some other precautions that managers should take when designing stand-level restoration treatments:

- Where cone-producing whitebark pine need to be released from competition to maintain adequate whitebark presence in the stand, emphasize removing competing trees within one to one-half of dominant tree height around individual or small groups of whitebark pine.
- Emphasize restoration treatments that minimize the mortality of whitebark pine, especially cone-bearing trees. If prescribed burning is needed, emphasize burning in stands that currently have low whitebark basal area (0 to 1 m^{-2} hectare $^{-1}$ or 0 to 5 ft^{-2} acre $^{-1}$). Consider using preventive bark beetle treatments (see “Tree Level” section).

- If openings need to be created to attract nutcracker caching, emphasize keeping them relatively small (50 to 100 m diameter) to optimize bird caching and provide sunlight to promote whitebark regeneration.
- Emphasize removal of many non-whitebark conifers as other management considerations will allow. This would reduce the competition experienced by individual whitebark pine of all ages and could reduce the likelihood of a stand-replacing fire.
- If possible, coordinate regeneration treatments with a good cone crop.
- Consider that many small understory whitebark pines are old and appear suppressed (poor growth, gray bark, irregular shaped bole) and these trees are unlikely to become cone-bearing, even with removal of competition (Keane and others 1994).
- Design regeneration treatments that minimize the potential for seeding from other tree species (i.e., large, stand-replacing fires upwind from seed sources).

If grizzly bears frequent the treatment area, then the following are some suggestions:

- Emphasize management that maintains or restores area in cone-bearing whitebark pine where possible. Consider controlling natural fires that may burn cone-bearing trees or protect these mature whitebark pine trees using fuel treatments, and avoid harvesting any whitebark pine.
- Prioritize management of habitat for red squirrels in areas that are capable of supporting cone-bearing whitebark pine.
- Protect areas that may be providing key habitat for bears, especially those areas where whitebark pine is limited due to losses from fire, bark beetle or succession.
- Emphasize maintaining cone-bearing whitebark pine in areas that are farthest from human disturbances. Avoid restoration treatments that create access that may increase human use of whitebark areas.
- Avoid restoration activities in whitebark pine forests when bears are most likely to be using them (last week in August through mid-November). Consider allowing treatments to occur if surveys for bears show that the area is not currently being used by bears or if area cone crops are known to be light.

Example

This example was taken from a treatment unit located at Beaver Ridge, Clearwater National Forest (Figure 4.20a) that was included in a whitebark pine study (Keane and Arno 1996, 2001; Keane and Parsons 2010b). The study is extensively detailed in Keane and Parsons (2010b) and the following is a summary of that discussion. The treatment is a moderate intensity prescribed burn with fuel enhancement (Unit 5A) (Figure 4.20b).

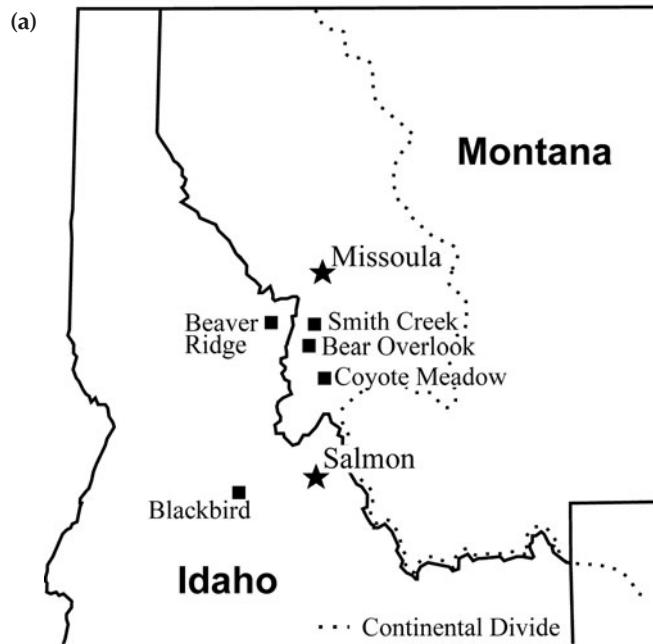
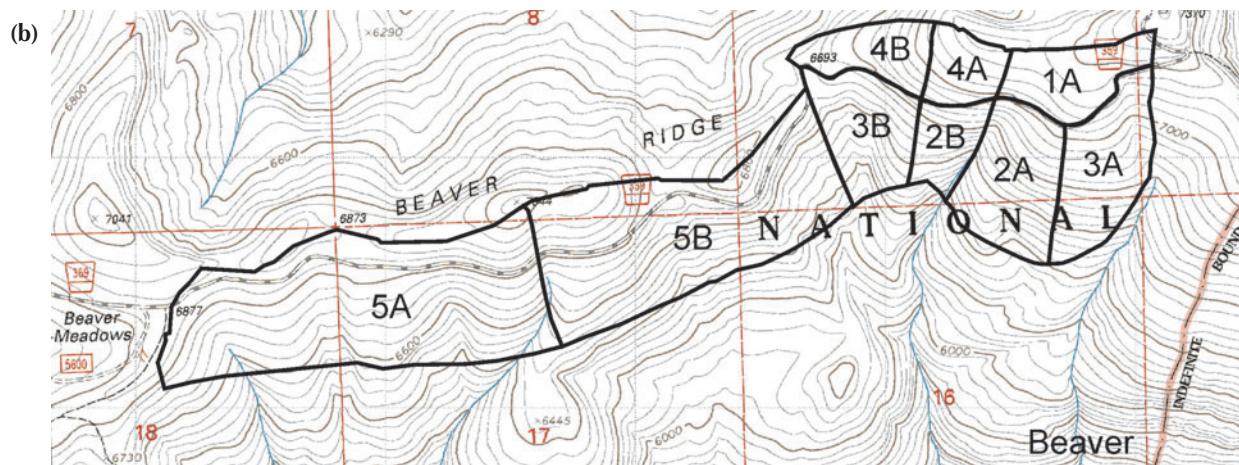


Figure 4.20. An example of a stand-level restoration activity implemented in a whitebark pine stand on Beaver Ridge of the Clearwater National Forest, Idaho. (a) location of the five stands in the Keane and Parsons (2010b) study with Beaver Ridge location shown, and (b) the Beaver Ridge study stands with the stand discussed as Unit 5A.



The Powell Ranger District wrote a comprehensive “District-Wide whitebark pine restoration integrated analysis” in May of 1997 and included research in their planning effort. They selected two areas for treatment: the Blacklead Mountain site and Beaver Ridge site in the fall of 1997. A request for comment was mailed to interested people in May of 1997, the NEPA analysis for the Categorical Exclusion was finished that summer and a decision memo was written and mailed in mid September of that year. The cutting treatments were implemented in the summer of 1998 and 1999. District personnel successfully obtained funding (over \$30,000) for this project from a number of sources including the Nez Perce Tribe, Rocky Mountain Elk Foundation, National Fish and Wildlife Foundation, U.S. Forest Service Research, and Hazardous fuels.

The District implemented a fuel enhancement treatment by cutting any subalpine fir or Engelmann spruce tree that could be used to increase fuel loadings and improve

continuity of the fuelbed. They directionally felled these trees to fill in bare soil gaps within the fuelbed, but, in many parts of the stand, there were insufficient subalpine fir trees to optimally augment the fuelbed. The District fire crew did some of the saw work but most was accomplished through an experienced contract crew. The cutting was done in September 1998. The District estimated that they spent around \$20 to \$40 per acre for slashing this unit.

This unit was burned in September 12, 2002, by Powell Ranger District fire crews using strip headfires with strips varying from 10 to 60 ft wide. Fuels were mostly dry with fine material around 10 to 15 percent (1 hr = 10 percent, 10 hr = 14 percent, 100 hr = 14 percent), coarse woody debris (1000 hr) around 20 percent for sound logs and 19 percent for rotten logs, and live fuels at around 100 to 160 percent (154 percent for herbs and 100 percent for shrubs). Weather conditions at the time of the fire were sunny, warm (60 to 70 °F), with 5 to 10 mph winds and relative humidity

around 30 percent. Weather preceding the burn was typical fall conditions with cool days and cold nights.

This prescribed burn was originally designed to mimic a stand-replacement fire using a high-intensity prescription, but logistical concerns and insufficient fuels, even with the fuel enhancement cuttings, demanded a less intense fire. Thus, the district implemented a mixed severity burn at the high end of the mixed-severity category. Flame lengths on this unit were variable from 1 to 10 ft high with passive crown fire behavior observed throughout the burn. Many trees were killed by the fire but in very patchy distributions, especially above the road near the ridgeline. Many subalpine fir trees crowned during the fire but there were large patches of 100-year old lodgepole pine that did not crown and many survived the prescribed burn. The fire was primarily carried through the shrub (*Vaccinium* spp.) and herb (*Xerophyllum tenax*, for example) fuelbeds so flame lengths were often low and creeping in lodgepole pine patches. This burn met nearly all burn plan prescriptions but the tree mortality was highly variable. The burn was extensive and covered most of the unit (greater than 60 percent) and consumed many fine fuels. The prescribed burning was estimated at \$600 per ha for 40+ ha. Unfortunately, the burn severity patterns inside the research plots were somewhat different than the severity distribution outside the plots.

The combination of cutting and burning were successful in removing many subalpine fir and spruce trees, but the low level of fuel augmentation coupled with the moist burning conditions did not allow the fire to achieve burn severities to mimic stand-replacement or high intensity mixed severity fire. Keane and Parsons (2010a) suggested burning when fuels are drier and relative humidity is lower. The chances of accomplishing a prescribed crown fire might be low in this forest type and mixed severity burns might be the conservative choice. Again, whitebark pine tree regeneration was marginal on this site, which could be a result of high whitebark pine mortality on this isolated ridge resulting in little nutcracker caching. Keane and Parsons (2010a) recommended that burned areas with high levels of blister rust mortality be planted with whitebark pine seeds or seedlings to ensure future dominance of this species. The collection of the seed from phenotypic rust-resistant whitebark pine trees will increase the chance that the planted stock or seed will survive the exotic disease infection. Keane and Parsons (2010a) suggested that an evaluation of the success of natural regeneration must be made at least a decade or two after burning.

Tree Scale

The finest scale included in this strategy is the tree level where treatments are designed for individual trees. These trees can be any size and age but they are usually cone-producing mature whitebark pine or vigorous advanced whitebark pine regeneration (tree planting was covered at the stand scale). Again, planning and prioritization analyses are rarely conducted at this scale because the factors that

control tree dynamics are manifest at broader scales. In this report, we describe the tree from a set of measurable characteristics, such as species, diameter at breast height, height, crown base height, and, of course, rust infection level.

Assessments

There are few assessments that need to be made at the tree scale to promote whitebark pine restoration efforts. Perhaps the most common assessment is the identification of individual trees that are the most valuable to sustaining viable, rust-resistant whitebark pine populations. These trees are most often mature, cone-producing whitebark pine trees that outwardly show signs of blister rust resistance (Mahalovich and Dickerson 2004). The primary sign would be a healthy tree with no blister rust flagging or blisters in a stand where most other whitebark pine trees have been killed by the rust (Hoff 1992) (Figure 4.21), with 30 percent or more live green crown. Since blister rust resistance is positively correlated with growth (Mahalovich 2012; Mahalovich and others 2006), dominant and co-dominant specimens should be favored (Mahalovich, personal communication). Area surveys for blister rust and mountain pine beetle incidence and for plus tree designations indicate that whitebark pine exhibits a negative relationship between blister rust resistance and mountain pine beetle tolerance. During moderate rust infestations (50 to 90 percent mortality levels), specimens with few to no beetle attacks may possess desirable genes for insect tolerance. These trees are extremely valuable and it is suggested that efforts be made to protect these surviving relics from beetles, rust, and competing conifers. In particular, cone-bearing plus trees in the rust resistance breeding program must be kept alive until their offspring are evaluated for rust resistance. Those plus trees whose progeny exhibit resistance will be extremely important for future cone collections and scion material for grafting and use in rust-resistant seed orchards. Identification and mapping of the location of individual high value whitebark pine trees is important for planning. Tree location information should be used when making resource management decisions such as fire use planning.

Other assessments might be to identify individual subalpine fir, spruce, or mountain hemlock trees that pose the greatest threat to whitebark pine survival. These trees might be out-competing whitebark pine trees for light, water, or nutrients, or they could be providing heavy, adjacent canopy and surface fuels that could foster lethal wildland fire and contribute to killing healthy, cone-bearing whitebark pine. This is especially important in the whitebark pine community types where many mature whitebark pine trees are surrounded by a “skirt” of subalpine fir regeneration (Arno and Weaver 1990). Prioritizing mature stands with high rust mortality containing healthy, apparently rust-resistant cone-bearing trees is very important in assessing the potential of an area to regenerate to viable whitebark pine communities.

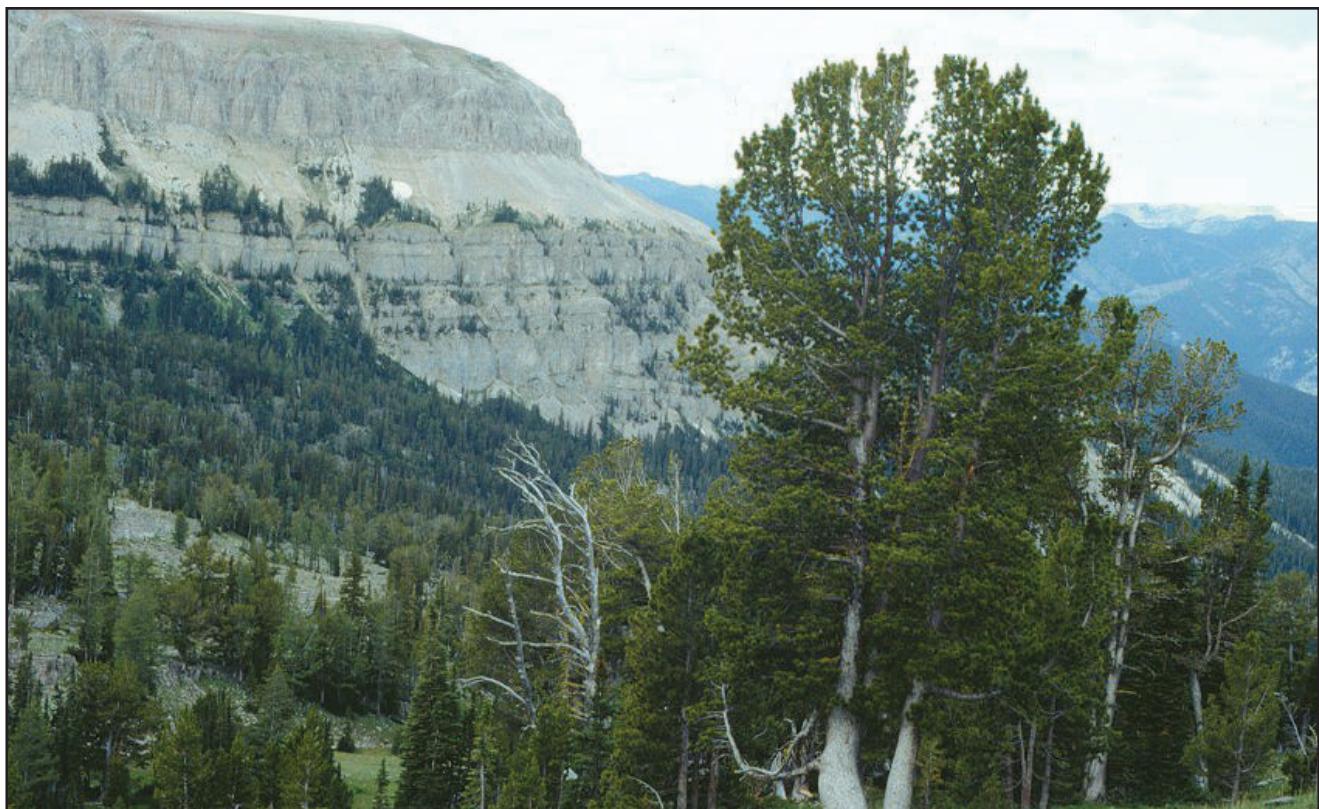


Figure 4.21. Mature, cone-producing whitebark pine tree with apparent blister rust resistance because it is surrounded by dead or dying whitebark pine.

Restoration Actions

Probably the most common tree-level restoration activity is the protection of trees from disturbance agents, primarily fire, beetles, and rust. The best trees to protect from these agents are those that have been identified as important sources for phenotypic rust-resistant seeds (“plus” trees) (Mahalovich and Dickerson 2004). Protection of trees from damage from wildland fire (prescribed, CW, or wildfire) is difficult and costly, and yet often successful (Keane and Parsons 2010a; Murray 2007c). Mechanical manipulation of fuel surrounding the trees by (1) raking or blowing (via leaf blower) litter and duff away from tree bases, (2) cutting competing fir and spruce, or (3) manual removal of downed woody, shrub, and herbaceous fuels has been attempted with mixed success (Keane and Parsons 2010b) (Figure 4.15). Fire crews have wrapped large whitebark pine with fire shelters to protect against fire mortality with limited success (Keane and Parsons 2010b). Modification of ignition patterns by controlling burn severity using head fires ignited in thin strips may be the most successful way to minimize whitebark pine fire-caused mortality in prescribed burning or back-burning in wildfires.

Cone collection also occurs at the individual-tree level (Halstrom 1995; Mahalovich and Dickerson 2004). Acquiring cones can serve several purposes. First, collected seeds can be sown in a nursery to produce seedlings for planting in

recently burned areas or restoration projects (Keane and Parsons 2010a). In a wind-pollinated outcrossed breeding system, bulked collections should contain a minimum of 20 cone-bearing trees separated by 60 m (200 ft) in distance (Mahalovich and Dickerson 2004). Additional seeds can be stored for future operational use in planting whitebark pine seedlings. Acquisition of cones is also required for blister rust screening procedures (Mahalovich and Dickerson 2004). Genetic studies often depend on collected seeds for analysis. Furthermore, seeds are needed for rootstock production for seed orchard establishment. As whitebark pine declines in distribution, seeds should increasingly be collected and stored for ex situ conservation and long-term gene-banking.

Cone collecting can be challenging due to the remote and rugged character of whitebark pine habitat and the technical difficulties involved in saving cones from marauding animals, especially Clark’s nutcrackers and red squirrels. Based on field experiences, guidelines are available that can ensure successful collections (Murray 2007b; Ward and others 2006b). A basic procedure consists of several steps. The first step is stand and tree selection. Criteria used in this step may vary depending on purpose (rust screening versus long-term seed banking). Once trees are selected, the best method to access the cones must be determined usually by climbing, but orchard ladders, sectional ladders, and custom-made tree-tongs have proven advantageous at some locations (Davies and Murray 2006). These cones must be protected



Figure 4.22. Installing cone cages on whitebark pine near an on-looking nutcracker.



Figure 4.23. Collecting cones in whitebark pine trees
(Photo courtesy of Michael Murray).

from animal harvest by installing protective devices (stout hardware cloth or fine wire mesh cages) in the early summer to prevent animal access to the cones (Figure 4.22). Once cones ripen in late summer, the cages are removed and cones collected. Other techniques for cone harvest might include pruning, shooting, and mechanized lifts (Burr and others 2001) (Figure 4.23). Helicopters have been employed for cone harvesting in British Columbia. Cones should be stored in a dry, cool, and well-ventilated environment while awaiting seed extraction.

Another tree-level restoration action is pruning rust-infected branches to delay or prevent rust infection and mortality (Burns and others 2007, 2008). This involves cutting off the branches that have signs of rust infections at the bole to prevent rust infection of the main trunk. While this method can delay rust mortality, it is not a long-term solution and will probably be ineffective as additional branches are infected in subsequent years.

Management Concerns

All whitebark pine trees greater than 20 cm (8 inches) DBH (Diameter Breast Height) are susceptible to mountain pine beetle, but recent research has found that the beetle can successfully reproduce in whitebark pine as small as 10 cm (4 inches) DBH (Logan and Powell 2001; Logan and others 2003). Changing the microsite conditions around a tree by removing competing trees can also cause stress and make the trees more susceptible to mountain pine beetle attack in the short-term (Baker and Six 2001). Managers should strongly consider protecting valuable rust-resistant trees from mountain pine beetle. Carbaryl is the most effective pesticide treatment, especially when beetles are at epidemic levels. Carbaryl has shown to provide greater than 90 percent protection for two years (Gibson and Bennett 1985). The anti-aggregation pheromone Verbenone is also currently

being used to protect whitebark pine trees during beetle epidemics (Bentz and others 2005; Kegley and Gibson 2004).

Even when mountain pine beetle populations are at endemic levels, managers should consider using Verbenone or spraying Carbaryl on high value trees within the stands where restoration treatments are implemented (Baker and Six 2001). Since mountain pine beetle populations can build in stressed trees in treatment areas and spread to other areas, managers should consider treating high value trees in adjacent stands as well. When mountain pine beetle is at epidemic levels, widespread mortality is likely. In mechanical or prescribed burn treatment areas, using Carbaryl on high value trees within or nearby the stand during epidemic situations is strongly recommended. Carbaryl provides two years of effective protection and is the best way to protect trees from mountain pine beetle. Application can be difficult because the solution must be sprayed on the tree bole to a point of runoff (approximately 4 to 5 gallons of solution per tree) up until the bole is 5 inches in diameter or less.

Verbenone is purchased in plastic pouches that are easily tacked on the tree. It is much easier to apply, but the level of protection is significantly lower than Carbaryl. Current studies are working to improve Verbenone's effectiveness. Bubble pouches containing the pheromone are placed on the tree prior to mountain pine beetle flight (usually late June through September). Verbenone is not as effective when beetles are at epidemic levels. Current studies are assessing the effectiveness of Verbenone when combined with other measures such as pheromone baited funnel traps. For more information on the use of Carbaryl and Verbenone, managers should contact a local State and Private Forestry, Forest Health Protection/Monitoring representative.

Collecting cones by climbing the tree may be damaging to the tree. Wounding from climbing spikes or chain steps may facilitate mountain pine beetle attack. These wounds could be entry avenues for pathogens and may attract wildlife gnawing (porcupines and squirrels, for example). Care should also be taken when cutting subalpine fir or removing

surface fuels around valuable cone collection trees to avoid wounding.

Example

The activities employed in the Keane and Parsons (2010b) study provides comprehensive examples of the protection of high quality rust-resistant trees. Historic blazed trees at the Blackbird Mountain study site were protected using fire shelters because they were deemed archeological relics. This protection yielded mixed results with about half the blazed trees damaged by the prescribed burn. Surface fuels were removed from the base of some trees at the Smith Creek and Bear Overlook site using hand piling and raking. Verbenone patches were placed on mature whitebark pine trees on the Smith Creek site from 1998-2000 to protect against possible endemic mountain pine beetle attacks. At the Beaver ridge site, subalpine regeneration "skirts" around large whitebark pine trees were manually cut and piled, and several healthy, cone-producing whitebark pine trees in the control unit were selected as plus-trees; cones were harvested from these trees for three years.

To help abate the loss of trees due to blister rust disease, Crater Lake National Park collected cones for resistance testing from portions of the Park with the highest degree of blister rust incidence. Mature trees with no cankers were selected as disease-resistant candidates. The particular technique used to cage and collect depended on each tree's physical traits and proximity to a road. Climbing, orchard ladders, and tree tongs were employed. Wire-mesh cages (0.2 to 0.5 mm) were installed in early summer. Retrieval and cone collection in late September and early October yielded about 265 cones from 88 cages. By late October, all cones were delivered to the Dorena Genetic Resource Center for formal rust resistance testing. Each collecting technique had distinct strengths and weaknesses that are detailed in Murray (2007a, 2007b).

5. Implementation of Restoration Strategy

In this report, we present various methods, data, and models that could be used to implement a viable range-wide restoration strategy, and at the coarsest scale (the species range) we have presented a strategy for prioritizing whitebark pine regions. However, the implementation of the strategy at finer scales depends on many biological, abiotic, political, and societal factors that occur across all scales of organization and space. The available resources ultimately govern any restoration effort, and this includes not only funding, but also the number of trained resource professionals, experienced managers, and knowledgeable decision makers that can engage in restoration planning and implementation. Experience in prescribed burning and restoration treatments in whitebark pine systems, for example, is not as common as experience in burning other ecosystems.

One of the greatest challenges in designing restoration projects at any scale is the clear articulation of project objectives to comprehensively inform the prioritization, design, and implementation of that project. While seemingly obvious, this is easily the least understood concept in conducting restoration activities. Without an explicit statement of objectives, it is problematic, and perhaps impossible, to plan and implement a restoration project that can be evaluated for effectiveness and success. A clear objective makes key restoration analyses and decisions easy, such as (1) prioritization criteria, (2) variables to measure and monitor, (3) treatment design criteria, (4) appropriate spatial and temporal scales, and (5) future research. The restoration objective would provide the foundation for building a comprehensive restoration plan.

Planning and prioritizing regions, landscapes, and stands in this strategy demands a comprehensive technique to rank

the factors being prioritized in an objective, consistent, and efficient manner. Prioritization matrix approaches are the simplest to implement at any scale of analysis. The selected factors for assessment are assigned a relative importance for each item being prioritized (stands, landscapes for example) based on management objectives, available resources, and critical issues of the day (Jenkins 2005). Keane and Arno (2000) present a comprehensive multiple scale method of deciding where restoration activities should be implemented and what type of treatment is the best based on disturbance regimes, primarily wildland fire.

Decision Support Systems

There is a wide array of decision tools to aid in the prioritization of areas for restoration (Reynolds and Hessburg 2005). Hessburg and others (2007) used a logic model called EMDS to prioritize watersheds for fuel treatments in the central Rocky Mountains. They summarized fine-scale spatial data (30-m pixel resolution) up to a coarse-scale analysis unit (6th code HUC watersheds) and then assigned a rating system using fuzzy logic to rate watersheds according to hazard and risk. A similar analysis was completed by the Northern Region of the U.S. Forest Service for whitebark pine (see “Region Scale” section). Cipollini and others (2005) presented an expert opinion based decision analysis technique for prioritizing prairie openings for restoration. Any of these tools provide the platform that would evaluate selected factors with a minimum of subjectivity and inconsistency.

6. Discussion

While this strategy provides critical information for planning and implementing whitebark pine restoration efforts at multiple scales, its success lies in the ability of managers to tailor restoration designs to local conditions. In nature, it is impossible to design a strategy that will work everywhere with the same level of effectiveness. It is left up to the manager to craft a restoration plan that will be successful for a specific area by addressing critical local conditions such as rust infection levels, mountain pine beetle mortality, fuel loadings, successional status, HRV, public issues, and whitebark pine mortality. Hopefully this range-wide strategy provides helpful direction on how to design restoration projects and details those efforts that need to be accomplished at the appropriate scale.

The success of future whitebark pine restoration efforts will be greatly dependent on the lessons learned in previous attempts (Keane and Parsons 2010b). Everyone will benefit by the detailed documentation of the successes and failures of all restoration efforts (Logan and others 2008). Therefore, monitoring restoration treatments is required for providing the critical information needed to fine tune this restoration strategy to local areas. The first need for monitoring is a system of protocols, databases, and sampling methods for implementing a monitoring project. Several monitoring systems are available, including FIREMON (Lutes and others 2006), the FIREMON-FEAT Integration (Lutes and others 2009), the U.S. Forest Service's FSVEG, and the National Park Service's Fire Monitoring Handbook (USDI 2001). Another need is the collation of all monitoring data into one database for analysis (WLIS, for example, Lockman and others 2007). This can be accomplished by research and management at various time intervals. These data then need to be analyzed at the local, regional, and national scales to document ecosystem responses to restoration treatments for modifying restoration designs. Next, results from these monitoring efforts should be published so they are readily available. Possible publication outlets include research journals, management journals, government reports, and the Whitebark Pine Ecosystem Foundation's newsletter *Nutcracker Notes*. Last, these monitoring efforts need to be maintained well into the future because of the long response times in whitebark pine ecosystems. There is a role for both management and research in whitebark pine restoration monitoring—management could collect the data while research could analyze and report the data, for example. However, the primary role of research should be to learn more about whitebark pine ecology and devise effective restoration approaches so management can adapt their methods to respond to these new discoveries.

There is great concern among managers that treating declining whitebark pine ecosystems during a time of

widespread climate change, rust infections, and mountain pine beetle outbreaks might destroy the important remaining whitebark pine seed sources. Allowing lightning fires to burn as CWs and proactively lighting prescribed fire might kill valuable putatively rust-resistant, cone bearing whitebark pine trees. These concerns are valid, but we should consider the alternative. Wildfires will happen regardless of our best suppression efforts, especially in this high-elevation ecosystem where uncontrolled wildfires would have a greater chance of killing valuable rust-resistant individuals than managed fires (CW) because they burn under drier, hotter, and windier conditions. Even if uncontrolled wildfires don't occur, vegetation succession will, and the result will put an even greater competitive stress on the remaining shade-intolerant whitebark pine trees. Seeds from these surviving trees would have less chance of being planted in favorable sites free of competition because there are fewer burned areas on the landscape due to fewer fires. Mountain pine beetle impacts on whitebark pine are devastating, but these impacts are no reason to suspend restoration activities. In fact, this might be the most important time to initiate restoration actions on the landscape to ensure whitebark pine will continue to inhabit high-elevation forests into the future and prevent the conversion of sites to subalpine fir. We feel that the key to successful restoration in the future is the planting of rust-resistant whitebark pine seedlings after wildland fires, whether these fires are controlled, uncontrolled, or prescribed. It is also important that the genetic diversity of these seedlings is maximized to ensure whitebark pine remains on the landscape as the climate changes. Maintaining a diversity of age classes that contain putative rust-resistant whitebark pine is critical to sustaining the species over long time periods because it provides the resilience to survive unwanted wildfires and the resistance to beetle outbreaks, disease, and climate shifts. In the meantime we must concentrate our efforts on ensuring the continued presence of whitebark pine on the high elevations of Canada and the United States by following the strategy presented here.

While the strategy presented in this report may seem complex and complicated because we described it by scale, we feel that, in general, it can be summarized by these major tasks:

- *Collect whitebark pine seed.* Gather as much seed as possible for genetic testing, gene conservation, rust screening, and operational planting.
- *Grow rust-resistant whitebark pine seedlings.* Cultivate as many seedlings as possible to out-plant to disturbed areas.
- *Let wildfire do the work.* Proactive stand-level treatments are expensive and time-consuming. Let wildfire treat

potentially declining areas to reduce competing subalpine fir and create caching habitat.

- *Save the relics.* Save as many putative rust-resistant cone-bearing trees as possible for reasons stated above.
- *Plant burned areas.* Plant all burned areas with rust-resistant whitebark pine seedlings. Hopefully, seed planting technology can be developed to reduce the cost of seedling establishment. Do not depend on nutcracker dispersal, especially in areas where whitebark pine populations are too low.
- *Patch in the holes.* Use stand-level treatments to restore high value or critical declining stands, especially those stands that are distant from seed sources, that contain putative rust-resistant cone-bearing trees, or that are too valuable to lose from uncontrolled wildfire (critical grizzly bear habitat, for example).
- *Measure then measure again.* Inventory and monitoring are critical tasks that need to be implemented so that we can evaluate if treatments are successful and adjust treatments to improve efficacy.

Future Research

There are many unanswered questions concerning the management and ecology of whitebark pine, and critical research is needed in many areas to improve the success and efficiency of restoration treatments. These research efforts need to be well organized, encompass more than one scale, and include more than one geographic area. Schwandt (2006) posed several questions that illustrate our research needs:

- What are the frequency, genetic basis, and geographical distribution for blister rust resistance?
- How do we define and model factors that affect rust infection?
- What is the role of nutcrackers in declining stands?
- How can we reduce mountain pine beetle impacts?

We would like to add the following high priority topics for guiding future research in whitebark pine restoration (Aubry and others 2008a; Keane and Parsons 2010b):

- *Regeneration dynamics:* How do we shorten the regeneration lag time for high-elevation ecosystems? Are there more cost-efficient methods of regenerating declining whitebark pine stands than planting seedlings? Will planting seeds work? How long must you wait to evaluate the success of restoration treatments? Should we plant seedlings in a cluster or as individuals? What are the roles of microsites in seedling survival and success?
- *Species autecology:* What are life history attributes of whitebark pine throughout its range? What are the species ecophysiological characteristics (stomatal conductance, light compensation point, specific leaf

area for examples) so that models can be built that mechanistically simulate this species? How long does it take for regeneration to become established in burned whitebark pine stands?

- *Cone production:* Do restoration treatments actually increase whitebark pine cone production? What level of cone production is needed to sustain whitebark pine on a landscape? How do we determine which stands to plant and which stands to allow for natural regeneration? How can we efficiently count and collect cones?
- *Nutcracker interactions:* At what level of cone production do nutcrackers become seed predators rather than dispersal vectors? Where do most of the seeds come from to regenerate large burned areas to whitebark pine? What is the interaction between squirrels and nutcrackers?
- *Blister rust resistance:* How can we best evaluate the level of rust resistance in individual whitebark pine? What level of rust resistance in a whitebark pine population is needed to sustain that population into the future? How can we accelerate rust resistance in whitebark pine?
- *Restoration techniques:* What are novel restoration techniques that are effective and economically feasible? What role does prescribed fire, either as wildland fire use or management ignited burns, play in whitebark pine restoration? What monitoring techniques are best for evaluating the success of restoration activities? What techniques minimize rust-beetle-climate change impacts while still retaining seed-producing, rust-resistant individuals on the landscape?
- *Fire management:* How is fuel best managed in whitebark pine restoration plans? How often are prescribed burns needed and what areas are best restored using prescribed fire, wildfire, and wildland fire use?
- *Climate change:* What is the influence of changing climates on life cycles of blister rust, cone and seed insects, mountain pine beetle, and any other exotic insect, disease, or plant invader? How will it affect fire? How will it affect whitebark pine ecosystem dynamics? How do we structure gene conservation, and planting guidelines to correspond to changes in climate?
- *Ecosystem modeling:* Can we simulate whitebark pine ecosystem processes under future climates and disturbances? Do we know enough about possible influences to create comprehensive models? How can these models inform management decisions? How do we explore ecological interactions and relationships across large time and space scales with landscape modeling?

Researchers and managers should promote extensive public education concerning the ecology and decline of whitebark pine across North America. Non-governmental entities such as The Whitebark Pine Ecosystem Foundation (www.whitebarkfound.org) are good resources and often willing partners in any public education efforts. It is

incumbent on resource specialists to tell the story of whitebark pine to facilitate effective and timely restoration efforts.

Restoration Barriers and Challenges

Humans have caused much of whitebark pine's decline, so now it appears that humans will now have to put forth great effort to keep from losing this keystone species in high-elevation western North American ecosystems. The conditions contributing to this pine's decline took decades to develop so we expect that successful restoration will take decades and even centuries to accomplish. The first step is education. Public education is critically needed so that society will understand the scope and depth of the problem and be willing to support restoration. Access to nearby whitebark communities may provide important opportunities for public education, especially at heavily used recreational facilities, such as ski areas and National Parks. Land management agencies need to educate their staff on the ecology and management of this unique high-elevation ecosystem. The lack of comprehensive research in ecology and restoration is also a major barrier to conducting efficient and successful restoration treatments. Few research funds are being spent on this ecosystem and there are few scientists that have an extensive knowledge of this complex ecosystem. Little is known about this intricate ecosystem and it is vital that research provide the information needed for the sustainable management of whitebark pine ecosystems.

There will also be many challenges in implementing a comprehensive restoration program across the range of whitebark pine. Since whitebark pine has marginal value as timber, there will be fewer Federal funds available to pay for large restoration efforts. Many lower elevation ecosystems are also declining (for example, western larch, aspen, and ponderosa pine) and their economic value is much higher than whitebark pine (Ferry and others 1995; Hann 1990). The remote setting is also a challenge for restoration activities; the number of restoration options for treating whitebark pine stands decreases with decreasing accessibility to declining whitebark pine stands. In the United States, most whitebark pine forests are found in wilderness or National Parks (Keane 2000) and often in the most remote parts of these protected areas. In grizzly bear habitats, managers should also be concerned about development of facilities near or within the whitebark pine zone. Proximity to roads and town sites reduced the probability of bear use by 66 and 92 percent, respectively (Mattson and Reinhart 1997).

There are also barriers to restoration in society and land management policies. The public lack of trust in land management agencies coupled with the inability of diverse environmental groups to find "common ground" may limit any restoration plan proposed by Government agencies (Salwasser and Huff 2001). The fight for funding for the restoration efforts may be difficult and short lived as more

issues become important to the public. Conflicting regulations and laws also pose a significant barrier to whitebark pine restoration. Endangered species, such as Canadian lynx, may require habitat (subalpine fir sapling stands, for example) that could supersede any whitebark pine restoration. The wilderness policies for the Forest Service, as another example, prevent planting of rust-resistant whitebark pine seedlings. These barriers must be overcome to ensure a successful and long-term program of restoring whitebark pine on North American landscapes.

Limitations

The restoration strategy presented here may have limitations that must be considered for its implementation. First, this strategy and the examples presented herein are based on information, technology, and data that were available during the 5 to 10 years prior to the publication of this report, so there may be more current information (see Keane and others 2011). The strategy is designed to be improved as (1) new restoration technologies are developed, (2) additional research is completed, and (3) more data become available. This strategy, while comprehensive, is not exclusive, and it is incumbent on land management agencies to incorporate new technology and information in future analyses. This strategy is not intended to be implemented as a one-size-fits-all approach across the range of whitebark pine because of the tremendous variation in this ecosystem. The guidelines presented in this document are provided for reference and are not designed to be implemented in the same way across the range of whitebark pine. This report is meant to guide land managers as to which attributes to consider when evaluating the condition of their whitebark pine communities and to provide a rationale for active restoration. Managers should use this information along with specific management direction established for their National Park or National Forest to determine when, where, and if active restoration should occur.

Managers must also consider that what is best for whitebark pine in the long term may not be what is best for other species in that ecosystem, such as the grizzly bear and lynx, especially in the short term. According to Mattson and others (2001), "Insofar as we understand them, the means for conserving whitebark and grizzly bears may seem somewhat incompatible." While bears require large areas free from human activities, restoration treatments bring humans into the whitebark zone. Grizzly bears may suffer from the short-term effects of anything that removes cone-producing whitebark pine or reduces the population of squirrels or the size of middens. On the other hand, whitebark pine may need extensive management for it to remain abundant in the long term. These decision guidelines are an attempt to emphasize restoration treatments while minimizing negative short-term effects on grizzly bears.

7. The Range-Wide Perspective

We have the knowledge, skills, and experience to successfully restore whitebark pine forests across the species' entire range, even though blister rust and climate change will make this task more difficult and complex. There is concern among some scientists and managers that treating declining whitebark pine ecosystems during a time when mountain pine beetle outbreaks are rampant, extensive blister rust infection looms large, and climates are rapidly changing, might be a fruitless, counterproductive, and inefficient use of restoration funding. However, we feel these factors only further highlight the pressing need for immediate action to prevent the loss of this species and provide a solid rationale for strategic research and management planning for the conservation of this ecosystem. Sustaining ecosystem function on these valued upper subalpine landscapes so that they will be resistant and resilient to climate change requires that we conserve as many parts of this ecosystem as we can. The potentially devastating impacts of the combination of white pine blister rust, mountain pine beetles, and the unknown effects of climate change suggest that the time to restore these ecosystems cannot be delayed. Losing whitebark pine ecosystems before the full range of climate change impacts are manifest could lead to a less resilient forest and dramatic shifts in high-elevation ecosystems of western North America.

The successful restoration of whitebark pine ecosystems will take from decades to centuries. Two major factors will ultimately govern the time it takes: (1) the magnitude of resources available over time to conduct restoration efforts, and (2) the commitment of natural resource agencies to conduct restoration activities for the long term, most likely for many decades. Available resources can be in the form of funding, personnel, collaborative planning efforts, or public support. The success of this restoration strategy ultimately depends on the effective and strategic allocation of resources across multiple time and spatial scales. Not all whitebark pine forests need to be restored immediately, but a plan must be in place to prioritize those areas in the greatest need for restoration, and to also proactively prepare additional healthy ecosystems to be more resilient to the on-going threats. Conversely, the dedication of adequate resources targeted at restoration does not always ensure a successful restoration effort or program. The most successful strategy is one that is: (1) implemented across all levels of organization; (2) fully

integrated in planning, protection, and treatment activities across many land management agencies at various scales of management; and (3) focused on specific local areas rather than implemented at low intensity across the entire species range. Thus, restoration efforts for whitebark pine need not be implemented across an entire National Forest or National Park; the most successful programs will concentrate limited restoration resources on high-priority sites where potential restoration success is high. As funds become available and as results of previous restoration efforts are evaluated, this process can be repeated on additional sites with new, revised restoration treatments designed from information learned from previous treatments. This is why it is critical that all treatments and actions be monitored to adapt to unanticipated effects of disturbance, climate change, and ineffective treatment prescriptions (Logan and others 2008).

The key to successful whitebark pine restoration is facilitating the increase in rust resistance on the landscape, whether through natural selection or planting of rust-resistant pine seedlings after disturbance, and the creation of high-elevation landscapes that are resilient to climate change. Wildland fires, whether wildfires, CW, or prescribed fires, are important disturbances for whitebark pine restoration and important components of management plans because they create diverse shifting mosaics of upper subalpine communities. It is also vital that the genetic diversity of planted seedlings be maximized while also including rust resistance traits to ensure whitebark pine forests remain on the landscape as the changes in climate and disturbance alter landscape processes. The free flow of genetic material across the landscape using bird-assisted seeding along with human-assisted planting may be our best strategy for sustaining whitebark pines on the high-elevation landscape.

This document is based on the state-of-knowledge at the time of writing. However, ongoing research on whitebark pine ecology, seed dispersal, fire dynamics, white pine blister rust resistance, grizzly bear use of whitebark pine seeds, mountain pine beetle protection methods, whitebark pine planting guidelines, effects of global climate change, and successional processes will inform future restoration efforts in an adaptive management strategy. These restoration guidelines should be revised as needed when this new information becomes available and as additional issues and items for consideration arise.

References

- Adams, A. S.; Six, D. L. 2007. Temporal variation in mycophagy and prevalence of fungi associated with developmental stages of *Dendroctonus ponderosae* (Coleoptera: Curculionidae). *Environmental Entomology* 36:64-72.
- Alberta Sustainable Resource Development and Alberta Conservation Association. 2007. Status of the whitebark pine (*Pinus albicaulis*) in Alberta. Alberta Sustainable Resource Development, Wildlife Status Report No. 63, Edmonton, Alberta. 22 p.
- Amman, G. D. 1972. Some factors affecting oviposition behavior of the mountain pine beetle. *Environmental Entomology* 1:691-695.
- Amman, G. D. 1973. Population changes of the mountain pine beetle in relation to elevation. *Environmental Entomology* 2:541-548.
- Amman, G. D.; Cole, W. E. 1983. Mountain pine beetle dynamics in lodgepole pine forests. Part II: population dynamics. General Technical Report INT-145, USDA Forest Service, Intermountain Forest and Range Experiment Station, Ogden, UT, USA. 59 p.
- Amman, G. D.; McGregor, M. D.; Cahill, D. B.; Klein, W. H. 1977. Guidelines for reducing losses of lodgepole pine to mountain pine beetles in unmanaged stands in the Rocky Mountains. General Technical Report INT-36, USDA Forest Service, Intermountain Forest and Range Experiment Station, Ogden, UT, USA. 19 p.
- Antos, J.; Coupe, R.; Douglas, G.; Evans, R.; Goward, T.; Ignace, M.; Lloyd, D.; Parish, R.; Pojar, R.; Roberts, A. 1996. Pages 121-144 in: Plants of Southern Interior. Parish, R.; Coupe, R.; Lloyd, D., editors. B.C. Ministry of Forests and Lone Pine Publishing. Vancouver, British Columbia.
- Apfelbaum, S. I.; Chapman, K. A. 1997. Ecological restoration: a practical approach. Pages 301-322 in: *Ecosystem management: applications for sustainable forest and wildlife resources*. Yale University Press, New Haven, CT, USA.
- Arno, S. F.; Habeck, J. R. 1972. Ecology of alpine larch (*Larix lyallii* Parl.) in the Pacific Northwest. *Ecological Monographs* 42:417-450.
- Arno, S. F.; Hammerly, R. P. 1984. *Timberline: Mountain and Arctic Forest Frontiers*. The Mountaineers, Seattle, WA. 123 p.
- Arno, S. F.; Ostlund, L.; Keane, R. E. 2008. Living artifacts: the ancient ponderosa pines of the west. *Montana the Magazine of Western History* 58:55-62.
- Arno, Stephen F.; Tomback, D. F.; Keane, R. E. 2001. Whitebark pine restoration: a model for wildland communities. Pages 416-419 in: Tomback, D. F.; Arno, S. F.; Keane, R. E., editors. *Whitebark pine communities: ecology and restoration*. Island Press, Washington DC, USA.
- Arno, S. F.; Reinhardt, E. D.; Scott, J. H. 1993. Forest structure and landscape patterns in a subalpine lodgepole pine type: a procedure for quantifying past and present conditions. General Technical Report INT-294, USDA Forest Service, Intermountain Research Station, Ogden, UT, USA. 22 p.
- Arno, Stephen F. 1986. Whitebark pine cone crops: a diminishing source of wildlife food. *Western Journal of Applied Forestry* 9:92-94.
- Arno, Stephen F. 2001. Community types and natural disturbance processes. Pages 74-89 in: Tomback, D. F.; Arno, Stephen F.; Keane R. E., editors. *Whitebark pine communities: ecology and restoration*. Island Press, Washington, DC, USA.
- Arno, Stephen F.; Hoff, Raymond. 1990. *Pinus albicaulis* Engelm. Whitebark pine. Pages 268-279 in: *Silvics of North America*. Vol. I. Conifers. Agriculture Handbook. USDA Forest Service.
- Arno, Stephen F.; Weaver, Tad. 1990. Whitebark pine community types and their patterns on the landscape. Pages 97-105 in: Schmidt, W. C.; McDonald, K. J., compilers. *Proceedings—symposium on whitebark pine ecosystems: ecology and management of a high-mountain resource*. General Technical Report INT-270, USDA Forest Service, Intermountain Research Station, Ogden, UT, USA.
- Ashkannejhad, S.; Horton, T. R. 2005. Ectomycorrhizal ecology under primary succession on coastal sand dunes: interactions involving *Pinus contorta*, suilloid fungi and deer. *New Phytologist* 169:345-354.
- Aubry, C.; Goheen, D.; Shoal, R.; Ohlson, T.; Lorenz, T.; Bower, A.; Mehmel, C.; Snieszko, R. A. 2008a. Whitebark pine restoration strategy for the Pacific Northwest 2009-2013. Region 6 Report, USDA Forest Service, Pacific Northwest Region, Portland, OR, USA. 212 p.
- Aubry, C.; Shoal, R. 2008. Whitebark pine restoration strategy for the Pacific Northwest. USDA Forest Service Pacific Northwest Region, Portland, OR, USA. 55 p.
- Aubry, C.; Shoal, R.; Ohlson, T. 2008b. Land managers guide to whitebark pine restoration in the Pacific Northwest 2009-2013. Region 6 Report, USDA Forest Service, Pacific Northwest Region, Portland, OR, USA. 33 p.
- Augare, Kodi. 2010. Personal communication. July, 2010.
- British Columbia Ministry of Forests. 2008. Whitebark pine bulletin. Issue 1. B.C. Ministry of Forests and Range. Victoria, British Columbia.
- Bailey, R. G. 1995. Description of the ecoregions of the United States: second edition. Miscellaneous Publication Number 1391, USDA Forest Service, Washington, DC, USA. 108 p.
- Baker, B. H.; Amman, G. D.; Trostle, G. C. 1971. Does the mountain pine beetle change hosts in mixed lodgepole and whitebark pine stands? Research Note INT-151, USDA Forest Service, Intermountain Forest and Range Experiment Station, Ogden, UT, USA. 7 p.
- Baker, K. M.; Six, D. L. 2001. Restoring whitebark pine (*Pinus albicaulis*) ecosystems: a look at endemic bark beetle distribution. Pages 501-502 in: Society of American Foresters 2000 National Convention; 16-20 November 2000; Washington, DC. Society of American Foresters, Bethesda, MD, USA.
- Barrett, S. W. 2008. Role of fire in the Mission Mountains northwestern Montana-fire regimes and fire regime condition class. Report on file at the Missoula Fire Sciences Laboratory, Missoula, MT, USA.
- Bartlein, P. J.; Whitlock, C.; Shafer, S. L. 1997. Future climate in the Yellowstone National Park region and its potential impact on vegetation. *Conservation Biology* 11:782-792.
- Beighley, M.; Bishop, J. 1990. Fire behavior in high-elevation timber. *Fire Management Notes* 51:23-28.
- Belokon, M. M.; Belokon, Y. S.; Politov, D. V.; Altukhov, Y. P. 2005. Allozyme polymorphism of Swiss stone pine *Pinus cembra* L. in mountain populations of the Alps and eastern Carpathians. *Russian Journal of Genetics* 41:1268-1280.
- Benkman, C. W.; Balda, R. P.; Smith, C. 1984. Adaptations for seed dispersal and the compromises due to seed predation in limber pine. *Ecology* 65:632-642.
- 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 (Coleoptera:

- Curculionidae: Scolytinae) attacks. *Journal of Economic Entomology* 98:1614-1621.
- Bentz, B. J.; Logan, J. A.; Amman, G. D. 1991. Temperature dependent development of mountain pine beetle and simulation of its phenology. *Canadian Entomology* 123:1083-1094.
- Berryman, A. A. 1982. Mountain pine beetle outbreaks in Rocky Mountain lodgepole pine forests. *Journal of Forestry* 80:410-413.
- Berryman, A. A. 1986. *Forest Insects Principles and Practices of Population Management*. Plenum Press, New York. 279 p.
- Beukema, S. J.; Kurz W. A. 1998. Vegetation dynamics development tool: users guide version 3.0. ESSA Technologies Ltd., West 8th Avenue, Vancouver, British Columbia.
- Black, A. 2004. Wildland fire use: the “other” treatment option. Research Note RMRS-RN-23-6-WWW, USDA Forest Service, Rocky Mountain Research Station, Ft. Collins, CO, USA. 2 p.
- Blanchard, B. 1990. Relationships between whitebark pine cone production and fall grizzly bear movements. Page 362 in: Schmidt, W. C.; McDonald, K. J., compilers. *Proceedings—symposium on whitebark pine ecosystems: ecology and management of a high-mountain resource*. General Technical Report INT-270, USDA Forest Service, Intermountain Research Station, Ogden, UT, USA.
- Blanchard, B.; Knight, R. 1991. Movements of Yellowstone grizzly bears, 1975-1987. *Biological Conservation* 58:41-67.
- Blaustein, A. R.; Dobson, A. 2006. Extinctions: a message from the frogs. *Nature* 439:143-144.
- Bock, C. E.; Leptien, L. W. 1976. Synchronous eruptions of boreal seed-eating birds. *The American Naturalist* 110:559-571.
- Bockino, N. K. 2008. Interactions of white pine blister rust, host species, and mountain pine beetle in whitebark pine ecosystems in the Greater Yellowstone. Thesis, University of Wyoming, Laramie.
- Bower, A. D.; Aitken, S. N. 2006. Geographic and seasonal variation in cold hardiness of whitebark pine (*Pinus albicaulis* Engelm.). *Canadian Journal of Forestry Research* 36:1842-1850.
- Bower, A. D.; Aitken, S. N. 2007. Mating system and inbreeding depression in whitebark pine (*Pinus albicaulis* Engelm.). *Tree Genetics and Genomes* 3:379-388.
- Bower, A. D.; Aitken, S. N. 2008. Ecological genetics and seed transfer guidelines for *Pinus albicaulis* (Pinaceae). *American Journal of Botany* 95:66-76.
- Bower, A. D.; Aubry, C. 2009. Whitebark pine ex situ gene conservation for the Pacific Northwest Region. PNW Region Document. USDA Forest Service, Pacific Northwest Region, Olympia, WA, USA.
- Bower, A. D.; McLane, S. C.; Eckert, A.; Jorgensen, S.; Schoettle, A.; Aitken, S. 2011. Conservation genetics of high elevation five-needle pines. Pages 104-123 in: Keane, R. E., editor. “High-Five” Symposium: The future of high-elevation five-needle white pines in western North America, 2010 June 28-30. Missoula, MT, USA. Proceedings RMRS-P-63, USDA Forest Service, Rocky Mountain Research Station, Fort Collins, CO, USA.
- Bradley, K. L.; Pregitzer, K.S. 2008. Ecosystem assembly and terrestrial carbon balance under elevated carbon dioxide. *Trends in Ecology and Evolution* 22:538-547.
- Brown, D. H. 1969. Aerial application of antibiotic solutions to whitebark pine infected with *Cronartium ribicola*. *Plant Disease Reporter* 53:487-489.
- Brown, T. J.; Hall, B. L.; Westerling, A. L. 2004. The impact of Twenty-First Century climate change on wildland fire danger in the western United States: an applications perspective. *Climatic Change* 62:365-388.
- Bruederle, L. P.; Rogers, D. P.; Krutovskii, K. V.; Politov, D. V. 2001. Population genetics and evolutionary implications. Pages 137-158 in: Tomback, D. F.; Arno, S. F.; Keane, R. E., editors. *Whitebark pine communities: ecology and restoration*. Island Press, Washington, DC, USA.
- Bruederle, L. P.; Tomback, D. F.; Kelly, K. K.; Hardwick, R. C. 1998. Population genetic structure in a bird-dispersed pine, *Pinus albicaulis* (Pinaceae). *Canadian Journal of Botany* 76:83-90.
- Brundrett, M.; Boucher, N.; Dell, B.; Grove, T.; Malajczuk, N. 1996. Working with mycorrhizas in forestry and agriculture. Australian Centre for International Agriculture Research Monograph 32. 374 p.
- Brunelle, A.; Rehfeldt, J.; Bentz, B.; Munson, S. 2008. Holocene records of Mountain Pine beetle infestation in the U.S. northern Rocky Mountains. *Forest Ecology and Management* 255:836-846.
- Bunn, A. G.; Lawrence, R. L.; Bellante, G. J.; Waggoner, L. A.; Graumlich, L. J. 2003. Spatial variation in distribution and growth patterns of old growth strip-bark pines. *Arctic, Antarctic, and Alpine Research* 35:323-330.
- Burns, K. S.; Schoettle, A. W.; Jacobi, W. R.; Mahalovich, M. F. 2007. White pine blister rust in the Rocky Mountain Region and options for management. Report R2-07-04, USDA Forest Service, Rocky Mountain Region Renewable Resources, Golden, CO, USA. 37 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. Report RMRS-GTR-206, USDA Forest Service, Rocky Mountain Research Station, Fort Collins, CO, USA. 26 p.
- Burr, K. E.; Eramian, A.; Eggleton, K. 2001. Growing whitebark pine seedlings for restoration. Pages 325-346 in: Tomback, D. F.; Arno, S. F.; Keane, R. E., editors. *Whitebark pine communities: ecology and restoration*. Island Press, Washington, DC, USA.
- Cabin, R. J. 2007. Science-driven restoration: a square grid on a round earth. *Restoration Ecology* 15:1-7.
- Cairney, J. W.; Bastias, B. A. 2007. Influences of fire on forest soil fungal communities. *Canadian Journal of Forest Research* 37:207-215.
- Callaway, R. M. 1998. Competition and facilitation on elevation gradients in subalpine forests of the northern Rocky Mountains, USA. *Oikos* 82:561-573.
- Callaway, R. M.; Sala, A.; Keane, R. E. 1998. Replacement of whitebark pine by subalpine fir: consequences for stand carbon, water, and nitrogen cycles. Final Report RJVA-INT-95086, USDA Forest Service, Fire Sciences Laboratory, Missoula, MT, USA.
- Campbell, E. M. 1998. Whitebark pine forests in British Columbia: composition, dynamics and the effects of blister rust. Dissertation. University of Victoria, British Columbia.
- Campbell, E. M.; Antos J. A. 2000. Distribution and severity of white pine blister rust and mountain pine beetle on whitebark pine in British Columbia. *Canadian Journal of Botany* 30:1051-1059.
- Campbell, E. M.; Antos, J. A. 2003. Postfire succession in *Pinus albicaulis*-*Abies lasiocarpa* forests of southern British Columbia. *Canadian Journal of Botany* 81:383-397.
- Campbell, Elizabeth M.; Keane, Robert E.; Larson, Evan; Murray, Michael P.; Schoettle, Anna W.; Wong, Carmen. 2011.

- Disturbance ecology of high-elevation five-needle pine ecosystems in Western North America. Pages 154-163 *in:* Keane, Robert E.; Tomback, Diana F.; Murray, Michael P.; Smith, Cyndi M., editors. The future of high-elevation, five-needle white pines in western North America: Proceedings of the High Five Symposium; 28-30 June 2010; Missoula, MT. Proceedings RMRS-P-63, USDA Forest Service, Rocky Mountain Research Station, Fort Collins, CO, USA.
- Campbell, R. K. 1979. Genecology of Douglas-fir in a watershed in the Oregon Cascades. *Ecology* 60:1036-1050.
- Carroll, A. L.; Régnière J.; Logan, J. A.; Taylor, S. W.; Bentz, B. J.; Powell, J. A. 2006. Impacts of climate change on range expansion by the mountain pine beetle. Mountain Pine Beetle Working Paper 2006-14. Natural Resources Canada, Canadian Forest Service, Pacific Forestry Centre, Victoria, British Columbia.
- Cheff, B. 1993. Indian Trails and Grizzly Tales. Stoneydale Press Publishing Company, Stevensville, MT.
- Chew, J. D. 1990. Timber management and target stands in the whitebark pine zone. Pages 310-314 *in:* Schmidt, W. C.; McDonald, K. J., compilers. Proceedings—symposium on whitebark pine ecosystems: ecology and management of a high-mountain resource. General Technical Report INT-270, USDA Forest Service, Intermountain Research Station, Ogden, UT, USA.
- Chew, J. D.; Stalling, C.; Moeller, K. 2003. Integrating knowledge for simulating vegetation change at landscape scales. *Western Journal of Applied Forestry* 19:102-108.
- Chuine, I. 2010. Why does phenology drive species distribution? *Philosophical Transactions of the Royal Society B* 365:3149-3160.
- Ciesla, W. M.; Furniss, M. M. 1975. Idaho's haunted forests. *American Forests* 81:32-35.
- Cipollini, K. A.; Maruyama, A. L.; Zimmerman, C. L. 2005. Planning for restoration: a decision analysis approach to prioritization. *Restoration Ecology* 13:460-470.
- Cole, D. N. 1990. Recreation in whitebark pine ecosystems: demand, problems, and management strategies. Pages 305-309 *in:* Schmidt, W. C.; McDonald, K. J., compilers. Proceedings—symposium on whitebark pine ecosystems: ecology and management of a high-mountain resource. General Technical Report INT-270, USDA Forest Service, Intermountain Research Station, Ogden, UT, USA.
- Cole, W. E.; Amman, G. D. 1980. Mountain pine beetle dynamics in lodgepole pine forests. Part 1. Course of an infestation. General Technical Report INT-89, USDA Forest Service, Intermountain Forest and Range Experiment Station, Ogden, UT, USA: 56.
- Cole, W. E.; Amman, G. D.; Jensen, C. E. 1989. Mountain pine beetle dynamics in lodgepole pine forests. Part III: Sampling and modeling of mountain pine beetle populations. General Technical Report INT-188. USDA Forest Service, Intermountain Forest and Range Experiment Station, Ogden, UT, 46 p.
- Cooke, S. J.; Suski, C. D. 2008. Ecological restoration and physiology: an overdue integration. *BioScience* 58:957-961.
- Cooper, S. V.; Neiman, K. E.; Roberts, D. W. 1991. Forest habitat types of northern Idaho: a second approximation. General Technical Report INT-236, USDA Forest Service, Intermountain Research Station, Ogden, UT.
- Craig, R. K. 2009. "Stationarity is dead"—long live transformation: five principles for climate change adaptation law. Florida State University: 61.
- Craighead, F. C. 1925. Bark beetle outbreaks and rainfall deficiency. *Journal of Economic Entomology*. 18:577-586.
- Craighead, J. J.; Summer, J. S.; Scaggs, J. B. 1982. A definitive system for analysis of grizzly bear habitat and other wilderness resources utilizing LANDSAT multispectral imagery and computer technology. Monograph No. 1, Wildlife Wildlands Institute, University of Montana Foundation, Missoula, MT, USA.
- Cripps, C. L.; Antibus, R. K. 2010. Native ectomycorrhizal fungi of limber and whitebark pine: necessary for forest sustainability? Pages 37-44 *in:* Keane, Robert E.; Tomback, Diana F.; Murray, Michael P.; Smith, Cyndi M., editors. 2011. The future of high-elevation, five-needle white pines in Western North America: Proceedings of the High Five Symposium; 28-30 June 2010; Missoula, MT. Proceedings RMRS-P-63, USDA Forest Service, Rocky Mountain Research Station, Fort Collins, CO, USA.
- Cripps, C. L.; Grimme, E. 2009. Soil microbes that sustain YNP whitebark pine forests: inventory of native mycorrhizal fungi and their preservation. Report to Greater Yellowstone Coordinating Committee. USDI National Park Service, West Yellowstone, Montana, USA.
- Cripps, C. L.; Grimme, E. 2010. Inoculation and successful colonization of whitebark pine seedlings with *native* mycorrhizal fungi under greenhouse conditions. Pages 312-322 *in:* Keane, Robert E.; Tomback, Diana F.; Murray, Michael P.; Smith, Cyndi M., eds. The future of high-elevation, five-needle white pines in western North America: Proceedings of the High Five Symposium; 28-30 June 2010; Missoula, MT. Proceedings RMRS-P-63, USDA Forest Service, Rocky Mountain Research Station, Fort Collins, CO.
- Cripps, C. L.; Smith, C.; Lapp, J.; Carolin, T. 2008. Assessment of ectomycorrhizal fungi with whitebark pine: Waterton-Glacier International Peace Park. *Nutcracker Notes* 14:12-14.
- Crone, E. E.; McIntire, E. J. B.; Brodie, J. 2011. What defines mast seeding? Spatio-temporal patterns of cone production by whitebark pine. *Journal of Ecology* 99:438-444.
- Davies, M. A.; Murray, M. 2006. Tree tong puts whitebark pine cones within reach. Tech Tip 0624-2354-MTDC. USDA Forest Service, Missoula Technology and Development Center, Missoula, MT, USA. 8 p.
- Davis, J.; Williams, L. 1957. Irruptions of the Clark nutcracker in California. *The Condor* 59.
- Davis, M. B.; Shaw, R. G.; Etterson, J. R. 2005. Evolutionary responses to changing climates. *Ecology* 86:1704-1714.
- Day, K.; Berg, J.; Brown, H.; Crow, T.; Morrison, J.; Nowacki, G.; Puckett, D.; Sallee, R.; Schenck, T.; Wood, B. 2006. Ecosystem restoration: a framework for restoring and maintaining the National Forests and Grasslands. USDA Forest Service, Washington, DC, USA.
- Day, R. J. 1967. Whitebark pine in the Rocky Mountains of Alberta. *Forestry Chronicle* 43:278-282.
- Dayton, P. K. 1972. Toward an understanding of community resilience and the potential effects of enrichments to the benthos at McMurdo Sound, Antarctica. Pages 81-96 *in:* Parker, B. C., editor. Proceedings of the colloquium on conservation problems in Antarctica. Allen Press, Lawrence, Kansas, USA.
- Dimmick, C.R. 1993. Life history and the development of cache-recovery behaviors in Clark's nutcracker. PhD. Dissertation. Northern Arizona University, Flagstaff, AZ, USA. 209 p.
- Dinerstein, E.; Powell, G.; Olson, D.; [and others]. 2000. A workbook for conducting biological assessments and developing biodiversity visions for ecoregion-based conservation. Available: <http://conserveonline.org/docs/2003/10/13wkbk.pdf>. Accessed March 18, 2008.

- Egan, D.; Howell, E. A., editors. 2001. The Historical Ecology Handbook. Island Press, Washington, DC, USA.
- Eggers, D. E. 1986. Management of whitebark pine as potential grizzly bear habitat. General Technical Report INT-207, USDA Forest Service, Intermountain Research Station, Missoula, MT, USA.
- Eggers, D. E. 1990. Silvicultural management alternatives for whitebark pine. Pages 324-328 in: Schmidt, W. C.; McDonald, K. J., compilers. Proceedings—symposium on whitebark pine ecosystems: ecology and management of a high-mountain resource. General Technical Report INT-270, USDA Forest Service, Intermountain Research Station, Ogden, UT, USA.
- Elderd, B. D.; Dushoff, J.; Dwyer, G. 2008. Host-pathogen interactions, insect outbreaks, and natural selection for disease resistance. *The American Naturalist* 172:829-842.
- Elliott, P. F. 1974. Evolutionary responses of plants to seed-eaters: pine squirrel predation on lodgepole pine. *Evolution* 28:221-231.
- Ellison, A. M.; Bank, M. S.; Clinton, B. D., [and others]. 2005. Loss of foundation species: consequences for the structure and dynamics of forested ecosystems. *Frontiers in Ecology and the Environment* 3:479-486.
- Evenend, A. G.; Moeur, M.; Shelly, J. S.; Kimball, S. F.; Wellner, C. A. 2001. Research natural areas on National Forest Systems lands in Idaho, Montana, Nevada, Utah, and western Wyoming: a guidebook for scientists, managers, and educators. General Technical Report RMRS-GTR-69, USDA Forest Service, Rocky Mountain Research Station, Fort Collins, CO, USA. 84 p.
- Farnes, P. E. 1990. SNOWTEL and snow course data: describing the hydrology of whitebark pine ecosystems. Pages 302-305 in: Schmidt, W. C.; McDonald, K. J., compilers. Proceedings—symposium on whitebark pine ecosystems: ecology and management of a high-mountain resource. General Technical Report INT-270, USDA Forest Service, Intermountain Research Station, Ogden, UT, USA.
- Felicetti, L. A.; Schwartz, C. C.; Rye, R. O.; Haroldson, M. A.; Gunther, K. A.; Phillips, D. L.; Robbins, C. T. 2003. Use of sulfur and nitrogen stable isotopes to determine the importance of whitebark pine nuts to Yellowstone grizzly bears. *Canadian Journal of Zoology* 81(5):763-770.
- Ferner, J. W. 1974. Habitat relationships of *Tamiasciurus hudsonicus* and *Sciurus aberti* in the Rocky Mountains. *Southwest Nut* 18:470-473.
- Ferry, G. W.; Clark, R. G.; Montgomery, R. E.; Mutch, R. W.; Leenhouts, W. P.; Zimmerman, G. T. 1995. Altered fire regimes within fire-adapted ecosystems. Pages 222-224 in: Our Living Resources: a report to the nation on the distribution, abundance, and health of U.S. plants, animals and ecosystems. USDI, National Biological Service, Washington, DC.
- Finley, R. B. 1969. Cone caches and middens of *Tamiasciurus* in the Rocky Mountain Region. Miscellaneous Publication 51:233-273. University of Kansas Museum of Natural History.
- Fins, L.; Byler, J.; Ferguson, D.; Harvey, A. E.; Mahalovich, M. F.; McDonald, G. I.; Miller, D.; Schwandt, J.; Zack, A. 2001. Return of the giants: restoring white pine ecosystems by breeding and aggressive planting of blister rust-resistant white pines. University of Idaho Station Bulletin 72:1-22.
- Fisher, J. T.; Bradbury, S. M. 2006. Understory protection harvest expedites recolonisation of boreal forest stands by North American red squirrels. *Forest Ecology and Management* 234:40-47.
- Flannigan, M. D.; Stocks, B. J.; Turetsky, M. R.; Wotton, B. M. 2008. Impact of climate change on fire activity and fire management in the circumboreal forest. *Global Change Biology* 15:549-560.
- Flyger, V.; Gates, J. E. 1982. Pine squirrels (*Tamiasciurus hudsonicus* and *T. douglasii*). Pages 230-238 in: Chapman, J. A.; Feldhamer, G. A., editors. *Wild Mammals of North America: Biology, Management and Economics*. John Hopkins University Press, Baltimore, MD, USA.
- Forcella, F. 1978. Flora and chorology of the *Pinus albicaulis-Vaccinium scoparium* association. *Madrono* 25:139-150.
- Forcella, F.; Weaver, T. 1977. Biomass and productivity of the subalpine *Pinus albicaulis-Vaccinium scoparium* association in Montana, USA. *Vegetatio* 35:95-105.
- Forcella, F.; Weaver, T. 1980. Food production in the *Pinus albicaulis-Vaccinium scoparium* association. *Proceedings of the Montana Academy of Science* 39:73-80.
- Frankham, Richard; Ballou, Johnathon D.; Briscoe, David A. 2002. *Introduction to Conservation Genetics*. Cambridge University Press, Cambridge, United Kingdom. 617 p.
- Funk, J. L.; Cleland, E. E.; Suding, K. N.; Zavaleta, E. S. 2008. Restoration through reassembly: plant traits and invasion resistance. *Trends in Ecology and Evolution* 23:695-703.
- Furnier, G. R.; Knowles, P.; Clyde, M. A.; Dancik, B. P. 1987. Effects of avian seed dispersal on the genetic structure of whitebark pine populations. *Evolution* 41:607-612.
- Garcia, R.; Siepielski, A. M.; Benkman, C. W. 2009. Cone and seed trait variation in whitebark pine (*Pinus albicaulis*: PINACEAE) and the potential for phenotypic selection. *American Journal of Botany* 96:1050-1054.
- Gardner, R. H.; Hargrove, W. W.; Turner, M. G.; Romme, W. H. 1996. Climate change, disturbances and landscape dynamics. Pages 149-172 in: Walker, B. H.; Steffen, W. L.; editors. *Global change and terrestrial ecosystems*. Cambridge University Press, Cambridge, MA, USA.
- Gardner, R. H.; Romme, William H.; Turner, M. G. 1999. Predicting forest fire effects at landscape scales. Pages 163-185 in: Mladenoff, D. J.; Baker, W. L., editors. *Spatial modeling of forest landscape change: approaches and applications*. Cambridge University Press, Cambridge, United Kingdom.
- Geils, Brian W.; Hummer, Kim E.; Hunt, Richard S. 2010. White pines, *Ribes*, and blister rust: a review and synthesis. *Forest Pathology* 40:147-185.
- Gernhardt, D.S.; Geada López, G.G.; Ortiz Garcia, S.; Liston, A. 2005. Phylogeny and classification of *Pinus*. *Taxon* 54:29-42.
- Gibson, K.; Skov, K.; Kegley, S.; Jorgensen, C.; Smith, S.; Witcosky, J. 2008. Mountain pine beetle impacts in high-elevation five-needle pines: current trends and challenges. R1-08-020, USDA Forest Service, Forest Health Protection, Missoula, MT, USA.
- Gibson, K. E.; Bennett, D. D. 1985. Carbaryl prevents attacks on lodgepole pine by the mountain pine beetle. *Journal of Forestry* 83(2):109-112.
- Goheen, E. M.; Goheen, D. J.; Marshall, K.; Danckoh, R. S.; Petrick, J. A.; White, D. E. 2002. The status of whitebark pine along the Pacific Crest National Scenic Trail on the Umpqua National Forest. General Technical Report PNW-GTR-530, USDA Forest Service, Pacific Northwest Research Station, Portland, OR, USA.
- Goncharenko, G. G.; Padutov, V. E.; Silin, A. E. 1993a. Allozyme variation in natural populations of Eurasian pines. 2. Genetic variation, diversity, differentiation, and gene flow in *Pinus*

- sibirica* DuTour in some lowland and mountain populations. *Silvae Genetica*. 42:246-253.
- Goncharenko, G. G., Padutov, V. E.; Silin, A. E. 1993b. Allozyme variation in natural populations of Eurasian pines. 1. Population structure, genetic variation, and differentiation in *Pinus pumila* (Pall) Regel from Chukotsk and Sakhalin. *Silvae Genetica*. 42:237-246.
- Greater Yellowstone Coordinating Committee Whitebark Pine Subcommittee. 2011. Whitebark pine strategy for the Greater Yellowstone Area. USDA Forest Service and USDI National Park Service, West Yellowstone, MT, USA. 41 p.
- Greater Yellowstone Whitebark Pine Monitoring Working Group. 2008. Monitoring Whitebark Pine in the Greater Yellowstone Ecosystem: 2007 annual report. Pages 50-56 in: Schwartz, C. C.; Haroldson, M. A.; West, K., editors. Yellowstone grizzly bear investigations: annual report of the Interagency Grizzly Bear Study Team, 2007. U.S. Geological Survey, Bozeman, MT, USA.
- Groves, C. R. 2003. Drafting a Conservation Blueprint. Island Press, Washington, DC, USA. 457 p.
- Grubisha, L.; Trappe, J.; Molina, R.; Spatafora, J. 2002. Biology of the ectomycorrhizal genus *Rhizophogon*. VI. Re-examination of infrageneric relationships inferred from phylogenetic analyses of ITS sequences. *Mycologia* 94:607-619.
- Haggeman, S.; Jones, M.; Gillespie, M.; Bradfield, G.; Durall, D. 1999. Effects of clear-cut logging on the diversity and persistence of ectomycorrhizae at a subalpine forest. *Canadian Journal of Forest Research* 29:1856-1870.
- Halstrom, L. 1995. Reforestation of whitebark pine in the northern region. Pages 113-114 in: Western International Forest Disease Work Conference. Idaho Department of Lands, Whitefish, MT, USA.
- Hamann, A.; Wang, T. 2006. Potential effects of climate change on ecosystem and tree species distribution in British Columbia. *Ecology* 87:2733-2786.
- Hamilton, D. A., Jr. 1986. A logistic model of mortality in thinned and unthinned mixed conifer stands of northern Idaho. *Forest Science* 32:989-1000.
- Hamilton, D. A., Jr.; Edwards, B. M., 1976. Modeling the probability of individual tree mortality. Research Paper INT-185, USDA Forest Service, Intermountain Research Station, Ogden, UT, USA. 22 p.
- Hamrick, J. L.; Godt, M. J. W.; Sherman-Broyles, S. L. 1992. Factors influencing levels of genetic diversity in wood plant species. *New Forests* 6:95-124.
- Hann, W. J. 1990. Landscape and ecosystem-level management in whitebark pine ecosystems. Pages 335-339 in: Schmidt, W. C.; McDonald, K. J., compilers. Proceedings—symposium on whitebark pine ecosystems: ecology and management of a high-mountain resource. General Technical Report INT-270, USDA Forest Service, Intermountain Research Station, Ogden, UT, USA.
- Hanson-Bristow, K. C.; Montagne, C.; Schmid, G. 1990. Geology, geomorphology, and soils within whitebark pine ecosystems. Pages 62-71 in: Schmidt, W. C.; McDonald, K. J., compilers. Proceedings—symposium on whitebark pine ecosystems: ecology and management of a high-mountain resource. General Technical Report INT-270, USDA Forest Service, Intermountain Research Station, Ogden, UT, USA.
- Harlow, W. M.; Cote, W. A., Jr.; Day, A. C. 1964. The opening mechanism of pine cone scales. *Journal of Forestry* 62:538-540.
- Haroldson, M. A.; Podruzny, S. 2011. Whitebark pine cone production. 2011 project summary. U.S. Geological Survey, Northern Rocky Mountain Science Center, Interagency Grizzly Bear Study Team. 2 p. Available: <http://www.nrmsc.usgs.gov/research/igbst-home.htm>.
- Haroldson, M. A.; Schwartz, C. C.; Cherry, S.; Moody, D. S. 2004. Possible effects of elk harvest on fall distribution of grizzly bears in the Greater Yellowstone Ecosystem. *Journal of Wildlife Management* 68(1):129-137.
- Haroldson, M. A.; Schwartz, C. C.; White, G. C. 2006. Survival of independent grizzly bears in the Greater Yellowstone Ecosystem, 1983-2001. Temporal, spatial and environmental influences on the demographics of the Yellowstone grizzly bear. *Wildlife Monographs* 161:33-42.
- Hartwell, M. G. 1997. Comparing historic and present conifer species compositions and structures on forested landscape of the Bitterroot Front. Contract completion report RJVA-94928, USDA Forest Service, Rocky Mountain Research Station, on file at the Missoula Fire Sciences Laboratory, Missoula, MT, USA.
- Haselwandter, K. 1997. Soil micro-organisms, mycorrhiza, and restoration ecology. *Restoration Ecology and Sustainable Development* 1:65-80.
- Hatala, J. A.; Crabtree, R. L.; Halligan, K. Q.; Moorcroft, P. R. 2010. Landscape-scale patterns of forest pest and pathogen damage in the Greater Yellowstone Ecosystem. *Remote Sensing of the Environment* 114:375-384.
- Helmbrecht, D.; Keane, R. E. [In prep.]. Mapping blister rust infection across the range of whitebark pine. USDA Forest Service, Rocky Mountain Research Station, Fort Collins, CO, USA.
- Hessburg, P. F.; Smith, B. G.; Salter, R. B. 1999. A method for detecting ecologically significant change in forest spatial patterns. *Ecological Applications* 9:1252-1272.
- Hessburg, P. F.; Reynolds, K. M.; Keane, R. E.; James, K. M.; Salter, R. B. 2007. Evaluating wildland fire danger and prioritizing vegetation and fuels treatments. *Forest Ecology and Management* 247:1-17.
- Hicke, J. A.; Logan, J. 2009. Mapping whitebark pine mortality caused by a mountain pine beetle outbreak with high spatial resolution satellite imagery. *International Journal of Remote Sensing* 30:4427-4441.
- Higgs, E. S. 1997. What is good ecological restoration? *Conservation Biology* 11:338-348.
- Hobbs, R. J.; Cramer, V. A. 2008. Restoration ecology: interventionist approaches for restoring and maintaining ecosystem function in the face of rapid environmental change. *Annual Review Environmental Resources* 33:39-61.
- Hoff, R. J. 1992. How to recognize blister rust infection on whitebark pine. Research Note INT-406, USDA Forest Service, Intermountain Research Station, Ogden, UT, USA.
- Hoff, R.; Bingham, R. T.; McDonald, G. I. 1980. Relative blister rust resistance of white pines. *European Journal of Forest Pathology* 10:307-316.
- Hoff, R. J.; Ferguson, D. E.; McDonald, G. I.; Keane, R. E. 2001. Strategies for managing whitebark pine in the presence of white pine blister rust. Pages 346-366 in: *Whitebark Pine Communities: Ecology and Restoration*. Island Press, Washington, DC, USA.
- Hoff, R. J.; Hagle, S. K.; Krebill, R. G. 1994. Genetic consequences and research challenges of blister rust in whitebark pine forests. Pages 118-126 in: Schmidt, W. C.; Holtmeier, F. K., editors. Proceedings—International workshop on subalpine stone pines and their environment: the status of our knowledge. General Technical Report INT-GTR-309, USDA Forest Service, Intermountain Research Station.

- Holdorf, H.; Donahue, J. 1990. Landforms for soil surveys in the northern Rockies. Miscellaneous Publication No. 51, USDA Forest Service, Montana Forest and Conservation Experiment Station, Missoula, MT, USA.
- Holler, P.; Fromm, R.; Leitinger, G. 2009. Snow forces on forest plants due to creep and glide. *Forest Ecology and Management* 257:546-552.
- Horton, T.; Bruns, T.; Parker, V. 1999. Ectomycorrhizal fungi associated with *Artostaphylos* contribute to *Pseudotsuga menziesii* establishment. *Canadian Journal of Botany* 77:93-102.
- Howell, B.; Burns, K. S.; Kearns, H. S. J. 2006. Biological evaluation of a model for predicting presence of white pine blister rust in Colorado based on climatic variables and susceptible white pine species distribution. *Biological Evaluation R2-06-04*, USDA Forest Service, Lakewood, CO, USA.
- Hufford, K. M.; Mazer, S. J. 2003. Plant ecotypes: genetic differentiation in the age of ecological restoration. *Trends in Ecology and Evolution* 18:147-155.
- Hutchins, H. E. 1994. Role of various animals in dispersal and establishment of whitebark pine in the Rocky Mountains, U.S.A. General Technical Report INT-GTR-309, USDA Forest Service, Intermountain Research Station, Ogden, UT, USA.
- Hutchins, H. E.; Lanner, R. M. 1982. The central role of Clark's nuthatches in the dispersal and establishment of Whitebark pine. *Oecologia* 55:192-201.
- Interagency Grizzly Bear Committee. 1986. Interagency grizzly bear guidelines. 108 p. Available: <http://www.igbconline.org/html/igbeguidelines.html>.
- Interagency Grizzly Bear Study Team. 2009. Yellowstone grizzly bear mortality and conflict reduction report. Interagency Grizzly Bear Study Team, Northern Rocky Mountain Science Center, Montana State University, Bozeman, MT, USA. 53 p. Available: www.igbconline.org/YellowstoneMortalityReportFinalv2.pdf.
- Izlar, D. K. 2007. Assessment of whitebark pine seedling survival for Rocky Mountain plantings. Thesis. University of Montana, Missoula.
- Izzo, A. D.; Meyer, M.; Trappe, J.; North, M.; Bruns, T. 2005. Hypogeous ectomycorrhizal fungal species on roots and in small mammal diet in a mixed-conifer forest. *Forest Science* 51:243-254.
- Jenkins, M. M. 2005. Greater Yellowstone area decision guidelines for whitebark pine restoration. Silvicultural Report on file at the Caribou Targhee National Forest Island Park Ranger District, USDA Forest Service, Idaho.
- Jewett, J. T. 2009. Spatiotemporal relationships between climate and whitebark pine mortality in the Greater Yellowstone Ecosystem. Thesis, Montana State University, Bozeman. 77 p.
- Jewett, J. T.; Lawrence, R. L.; Marshall, L. A.; Gessler, P. E.; Powell, S. L.; Savage, S. L. 2011. Spatiotemporal relationships between climate and whitebark pine mortality in the Greater Yellowstone Ecosystem. *Forest Science* 57(4):320-335.
- Johnson, C. 1996. Interactions between mammals and ectomycorrhizal fungi. *Trends in Ecology and Evolution* 11:503-507.
- Johnson, C. G. 2004. Alpine and subalpine vegetation of the Wallowa, Seven Devils, and Blue Mountains. R6-NR-ECOL-TP-03-04, USDA Forest Service, Pacific Northwest Region, Portland, OR, USA.
- Jørgensen, S. M.; Hamrick, J. L. 1997. Biogeography and population genetics of whitebark pine, *Pinus albicaulis*. *Canadian Journal of Forest Research* 27:1574-1585.
- Karau, E. C.; Keane, R. E. 2007. Determining landscape extent for succession and disturbance simulation modeling. *Landscape Ecology* 22:993-1006.
- Kasper, J. B.; Szabo, T. 1970. The physical and mechanical properties of whitebark pine. *The Forest Chronicle* 46:315-316.
- Keane, R.; Arno, S. F.; Brown, J. K.; Tombak, D. F. 1990. Modelling stand dynamics in whitebark pine (*Pinus albicaulis*) forests. *Ecological Modelling* 51:73-95.
- Keane, R.; Morgan, P.; Menakis, J. 1994. Landscape assessment of the decline of whitebark pine (*Pinus albicaulis*) in the Bob Marshall Wilderness Complex, Montana, USA. *Northwest Science* 68:213-229.
- Keane, R. E. 2000. The importance of wilderness to whitebark pine research and management. Pages 84-93 in: *Proceedings of the symposium: Wilderness Science: in a time for change. Volume 3: wilderness as a place for scientific inquiry*. General Technical Report RMRS-P-15-VOL-3, USDA Forest Service, Rocky Mountain Research Station, Missoula, MT, USA.
- Keane, R. E. 2001a. Can the fire-dependent whitebark pine be saved? *Fire Management Notes* 61:17-20.
- Keane, R. E. 2001b. Successional dynamics: modeling an anthropogenic threat. Pages 159-192. in: Tombak, D.; Arno, S.; Keane, R., editors. *Whitebark Pine Communities: Ecology and Restoration*. Island Press, Washington, DC, USA.
- Keane, R. E.; Arno, S. 2000. Restoration of whitebark pine ecosystems in western Montana and central Idaho. Pages 324-330 in: *Society of American Foresters 1999 National Convention*. Society of American Foresters, Portland, OR, USA.
- Keane, R. E.; Arno, S. F. 1993. Rapid decline of whitebark pine in Western Montana: Evidence from 20-year remeasurements. *Western Journal of Applied Forestry* 8:44-47.
- Keane, R. E.; Arno, S. F. 1996. Whitebark pine (*Pinus albicaulis*) ecosystem restoration in western Montana. Pages 51-54 in: *The use of fire in forest restoration—a general session at the annual meeting of the Society of Ecosystem Restoration: Taking a broader view*. General Technical Report INT-GTR-341, USDA Forest Service, Intermountain Research Station, Seattle, WA, USA.
- Keane, R. E.; Arno, S. F. 2001. Restoration concepts and techniques. Pages 367-400 in: *Whitebark Pine Communities: Ecology and Restoration*. Island Press, Washington, DC, USA.
- Keane, R. E.; Karau, E. C. 2010. Evaluating the ecological benefits of wildfire by integrating fire and ecosystem models. *Ecological Modeling* 221:1162-1172.
- Keane, R. E.; Morgan, P. 1994a. Decline of whitebark pine in the Bob Marshall Wilderness Complex of Montana, U.S.A. Pages 245-253 in: *Proceedings—International workshop on subalpine stone pines and their environment: the status of our knowledge*; St. Moritz, Switzerland, 5-11 September, 1992. General Technical Report INT-GTR-309, USDA Forest Service, Intermountain Research Station, Ogden, UT, USA.
- Keane, R. E.; Morgan, P. 1994b. Landscape processes causing whitebark pine decline in the Bob Marshall Wilderness Complex. Pages 22-33 in: *Proceedings from a workshop on Research and management in whitebark pine ecosystems*. Glacier National Park, General Report Number 3, West Glacier, MT, USA.
- Keane, R. E.; Parsons, R. 2010a. Restoring whitebark pine forests of the northern Rocky Mountains, USA. *Ecological Restoration* 28:56-70.
- Keane, R. E.; Parsons, R. A. 2010b. A management guide to ecosystem restoration treatments: whitebark pine forests of the northern Rocky Mountains. General Technical Report RMRS-GTR-232, USDA Forest Service, Rocky Mountain Research Station, Fort Collins, CO, USA.

- Keane, R. E.; Schoettle, Anna. 2011. Strategies, tools, and techniques for restoring high elevation five needle pines. Pages 276-294 in: Keane, Robert E.; Tomback, Diana F.; Murray, Michael P.; Smith, Cyndi M., editors. 2011. The future of high-elevation, five-needle white pines in Western North America: Proceedings of the High Five Symposium; 28-30 June 2010; Missoula, MT. Proceedings RMRS-P-63. USDA Forest Service, Rocky Mountain Research Station, Fort Collins, CO, USA.
- Keane, R. E.; Agee, J.; Fule, P.; Keely, J.; Key, C.; Kitchen, S.; Miller, R.; Schulte, L. 2008a. Ecological effects of large fires in the United States: benefit or catastrophe. International Journal of Wildland Fire 17:696-712.
- Keane, R. E.; Cary, G.; Davies, I. D.; Flannigan, M. D.; Gardner, R. H.; Lavorel, S.; Lennihan, J. M.; Li, C.; Rupp, T. S. 2004. A classification of landscape fire succession models: spatially explicit models of fire and vegetation dynamic. Ecological Modelling 256:3-27.
- Keane, R. E.; Garner, J.; Teske, C.; Stewart, C.; Paul, H. 2002a. Range and variation in landscape patch dynamics: implications for ecosystem management. Pages 19-26 in: Barras, Stan J., editor. Proceedings: 1999 National Silviculture Workshop; 5-7 October 1999; Kalispell, MT. Proceedings RMRS-P-19, USDA Forest Service, Rocky Mountain Research Station, Ogden, UT, USA.
- Keane, R. E.; Gray, K. L.; Dickinson, L. J. 2007a. Whitebark pine diameter growth response to removal of competition. Research Note RMRS-RN-32, USDA Forest Service, Intermountain Region, Ogden, UT, USA.
- Keane, R. E.; Hessburg, P. F.; Landres, P. B.; Swanson, F. J. 2009. A review of the use of historical range and variation (HRV) in landscape management. Forest Ecology and Management 258:1025-1037.
- Keane, R. E.; Holsinger, L.; Parsons, R.; Kathy, G. 2008b. Climate change effects on historical range of variability of two large landscapes in western Montana, USA. Forest Ecology and Management 254:274-289.
- Keane, R. E.; Menakis, J. P.; Hann, W. J. 1996. Coarse scale restoration planning and design in Interior Columbia River Basin ecosystems—an example using whitebark pine (*Pinus albicaulis*) forests. Pages 14-20 in: The use of fire in forest restoration—a general session at the annual meeting of the Society of Ecosystem Restoration: Taking a broader view. General Technical Report INT-GTR-341, USDA Forest Service, Intermountain Research Station, Seattle, WA, USA.
- Keane, R. E.; Parsons, R.; Hessburg, P. 2002b. Estimating historical range and variation of landscape patch dynamics: limitations of the simulation approach. Ecological Modelling 151:29-49.
- Keane, R. E.; Rollins, M. G.; Zhu, Z. 2007b. Using simulated historical time series to prioritize fuel treatments on landscapes across the United States: the LANDFIRE prototype project. Ecological Modelling 204:485-502.
- Keane, R. E.; Veblen, Thomas; Ryan, Kevin C.; Logan, Jesse; Allen, Craig; Hawkes, B. 2002c. The cascading effects of fire exclusion in the Rocky Mountains. Pages 133-153 in: Baron, Jill S., editor. Rocky Mountain Futures: An Ecological Perspective. Island Press, Washington, DC, USA.
- Keane, Robert E.; Tomback, Diana F.; Murray, Michael P.; Smith, Cyndi M., editors. 2011. The future of high-elevation, five-needle white pines in Western North America: Proceedings of the High Five Symposium; 28-30 June 2010; Missoula, MT. Proceedings RMRS-P-63, USDA Forest Service, Rocky Mountain Research Station, Fort Collins, CO, USA. 376 p.
- Kearns, H. S. J. 2005. White pine blister rust in the central rocky mountains: modeling current status and potential impacts. Dissertation. Colorado State University, Fort Collins.
- Kearns, H. S. J.; Burns, K. S. 2005. Distribution, incidence, and severity of white pine blister rust on the Medicine Bow National Forest. Biological Evaluation R2-06-01, USDA Forest Service, Golden, CO, USA.
- Keenan, F. J.; Glavicic, M. R.; Swindle, P. W.; Cooper, P. A. 1970. Mechanical properties of whitebark pine. The Forestry Chronicle 46:322-325.
- Keeton, W. S.; Mote, P. W.; Franklin, J. F. 2007. Climate variability, climate change, and western wildfire with implications for the urban-wildland interface. Advances in the Economics of Environmental Resources 6:225-253.
- Kegley, S.; Gibson, K. 2004. Protecting whitebark pine trees from mountain pine beetle attack using verbenone. Forest Health Protection Report 04-8, USDA Forest Service Northern Region, Missoula, MT, USA.
- Kegley, S.; Schwandt, J.; Gibson, K. E. 2001. Forest health assessment of whitebark pine on Pyramid Pass, Russell Mountain, and Burton Ridge in the Selkirk Mountains on the Idaho Panhandle National Forests. Report 01-8, USDA Forest Service, Northern Region, Missoula, MT, USA.
- Kendall, K. C. 1983. Use of pine nuts by grizzly and black bears in the Yellowstone Area. Bears: Their Biology and Management 5:166-173.
- Kendall, K. C. 1995. Whitebark pine: ecosystem in peril. Pages 228-230 in: Our Living Resources. USDI National Biological Service, Washington, DC.
- Kendall, K. C.; Keane, R. E. 2001. Whitebark pine decline : infection, mortality, and population trends. Pages 221-242 in: Tomback, D.F.; Arno, S. F.; Keane, R. E., editors. Whitebark Pine Communities: Ecology and Restoration. Island Press, Washington, DC, USA.
- Khasa, P.; Piché, Y.; Coughlan, A., editors. 2009. Advances in Mycorrhizal Science and Technology. NRC Research Press, Ottawa. 197 p.
- Kipfmüller, K. F.; Kupfer, J. A. 2005. Complexity of successional pathways in subalpine forests of the Selway-Bitterroot Wilderness Area. Annals of the Association of American Geographers 95:495-510.
- Kjøller, R.; Bruns, T. D. 2003. *Rhizopogon* spore bank communities within and among California pine forests. Mycologia 95:603-613.
- Koteen, L. 1999. Climate change, whitebark pine, and grizzly bears in the greater Yellowstone ecosystem. Pages 343-364 in: Schneider, S. H.; Root, T. L., editors. Wildlife Responses to Climate Change. Island Press, Washington, DC, USA.
- Krakowski, J. 2001. Conservation genetics of whitebark pine (*Pinus albicaulis* Engelm.) in British Columbia. Thesis, University of British Columbia, Vancouver.
- Krakowski, J.; Aitken, S. N.; El-Kassaby, Y. A. 2003. Inbreeding and conservation genetics in whitebark pine. Conservation Genetics 4:581-593.
- Krpata, D.; Muhlmann, O.; Kuhnert, R.; Ladurner, H.; Göbl, F.; Peintner, U. 2007. High diversity of ectomycorrhizal fungi associated with *Arctostaphylos uva-ursi* in subalpine and alpine zones: potential inoculum for afforestation. Forest Ecology and Management 250(3):167-175.
- Krugman, S. L.; Jenkinson, J. L. 1974. *Pinus* L. pine. Pages 598-638 in: Schopmeyer, C. S., technical coordinator. Seeds of woody plants in the United States. USDA Forest Service Agriculture Handbook No. 450, Washington, DC, USA.

- Krutovskii, K. V.; Politov, D. V.; Altukhov, Y. P. 1995. Isozyme study of population genetic structure, mating system and phylogenetic relationships of the five stone pine species (subsection *cembrae*, section *strobi*, subgenus *strobis*). Pages 279-304 in: Baradat, P.; Adams, W. T.; Müller-Starck, G., editors. Population Genetics and Genetic Conservation of Forest Trees. SPB Academic Publishing, Amsterdam, the Netherlands.
- Kuhmlein, H.; Turner, N. 1991. Traditional Plant Foods of Canadian Indigenous Peoples: Nutrition, Botany and Use. Gordon and Breach, Philadelphia.
- Landres, P. 2010. Let it be: a hands-off approach to preserving wildness in protected areas. Pages 88-105 in: Cole, D. N.; Yung, L., editors. Beyond Naturalness: Rethinking Park and Wilderness Stewardship in an Era of Rapid Change. Island Press, Washington, DC, USA.
- Landres, P. B.; Morgan, Penelope; Swanson, F. J. 1999. Overview and use of natural variability concepts in managing ecological systems. Ecological Applications 9:1179-1188.
- Lanner, R. M. 1980. Avian seed dispersal as a factor in the ecology and evolution of limber and whitebark pines. Pages 14-48 in: Dancik, B. P.; Higginbotham, O., compilers. Proceedings of the 6th North American Forest Biology Workshop. University of Alberta, Edmonton.
- Lanner, R. M. 1982. Adaptations of whitebark pine for seed dispersal by Clark's nutcracker. Canadian Journal of Forest Research 12:391-402.
- Lanner, R. M. 1990. Biology, taxonomy, evolution, and geography of stone pines of the world. Pages 14-24 in: Schmidt, W. C.; McDonald, K. J., compilers. Proceedings—symposium on whitebark pine ecosystems: ecology and management of a high-mountain resource. General Technical Report INT-270, USDA Forest Service, Intermountain Research Station, Ogden, UT, USA.
- Lanner, R. M. 1996. Made for Each Other: A Symbiosis of Birds and Pines. Oxford University Press, New York, USA.
- Lanner, R. M.; Gilbert, B. K. 1994. Nutritive value of whitebark pine seeds, and the question of their variable dormancy. Pages 206-211 in: Schmidt, W. C.; Holtmeier, F. K. compilers. Proceedings—international workshop on subalpine stone pines and their environment: the state of our knowledge. General Technical Report INT-GTR-309, USDA Forest Service, Intermountain Research Station, Ogden, UT, USA.
- Lantz, G. 2010. Imperiled in high places. American Forests Spring: 34-47.
- Larson, E. R. 2009. Status and dynamics of whitebark pine (*Pinus albicaulis* Engelm.) forests in southwest Montana, central Idaho, and Oregon, USA. Dissertation. University of Minnesota, Minneapolis.
- Larson, E. R.; Kipfmüller, K. F. 2010. Patterns in whitebark pine regeneration and their relationships to biophysical site characteristics in southwest Montana, central Idaho, and Oregon, USA. Canadian Journal of Forest Research 40:476-487.
- Larson, E. R.; Van de Gevel, S.; Grissino-Mayer, H. 2010. Variability in fire regimes of high-elevation whitebark pine communities, western Montana USA. Ecoscience 16:382-398.
- Lasko, R. J. 1990. Fire behavior characteristics and management implications in whitebark pine ecosystems. Pages 319-323 in: Schmidt, W. C.; MacDonald, K. J., compilers. Proceedings—symposium on white bark pine ecosystems: Ecology and management of a high-mountain resource. General Technical Report INT-270, USDA Forest Service, Intermountain Research Station, Ogden, UT, USA.
- Ledig, F. T. 1998. Genetic variation in *Pinus*. Page 527 in: Richardson, D. M., editor. Ecology and Biogeography of *Pinus*. Cambridge University Press, Cambridge, United Kingdom.
- Lee, I. 2003. Whitebark pine: keystone species in peril. Ecoforestry 11:28-31.
- Lee, Y. 1971. Predicting mortality for even-aged stands of lodgepole pine. Forestry Chronicle 47:29-32.
- Linhart, Y. B.; Tomback, D. F. 1985. Seed dispersal by nutcrackers causes multi-trunk growth form in pines. Oecologia 67:107-110.
- Little, E. L., Jr.; Critchfield, W. B. 1969. Subdivisions of the genus *Pinus* (pines). Miscellaneous Publication 1144, USDA Forest Service, Washington, DC, USA.
- Lockman, I. B.; DeNitto, G.; Courter, A. W.; Koski, R. D. 2007. WLIS: the whitebark-limber pine information system and what it can do for you. Pages 146-147 in: Proceedings of the conference—Whitebark pine: a Pacific Coast perspective. R6-NR-FHP-2007-01, USDA Forest Service, Pacific Northwest Region, Ashland, OR, USA.
- Loehle, C.; LeBlanc, D. 1996. Model-based assessments of climate change effects on forests: a critical review. Ecological Modelling 90:1-31.
- Loehman, Rachel A.; Corrow, Allissa; Keane, Robert E. 2011. Modeling climate changes and wildfire interactions: effects on whitebark pine (*Pinus albicaulis*) and implications for restoration, Glacier National Park, Montana, USA. Pages 176-188 in: Keane, Robert E.; Tomback, Diana F.; Murray, Michael P.; Smith, Cyndi M., editors. 2011. The future of high-elevation, five-needle white pines in Western North America: Proceedings of the High Five Symposium; 28-30 June 2010; Missoula, MT. Proceedings RMRS-P-63, USDA Forest Service, Rocky Mountain Research Station, Fort Collins, CO, USA.
- Logan, J. A.; Bentz, B. J. 1999. Model analysis of mountain pine beetle (Coleoptera: Scolytidae) seasonality. Environmental Entomology 28:924-934.
- Logan, J. A.; Macfarlane, W. W.; Willcox, L. 2008. Effective monitoring as a basis for adaptive management: a case history of mountain pine beetle in Greater Yellowstone Ecosystem whitebark pine. iForest 2:19-22.
- Logan, J. A.; Powell, J. A. 2001. Ghost forests, global warming, and the mountain pine beetle (Coleoptera: Scolytidae). American Entomologist 47:160-173.
- Logan, J. A.; Regniere, J.; Powell, J. A. 2003. Assessing the impacts of global warming on forest pest dynamics. Frontiers in Ecology and the Environment 1:130-137.
- Lorenz, T. J. [in prep]. Rodent abundance in whitebark pine stands and rodent predation and dispersal of whitebark pine seed in central Idaho (Salmon-Challis National Forest), eastern Montana (Gallatin National Forest) and central Washington (Okanogan-Wenatchee National Forest).
- 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, USDA Forest Service, Pacific Northwest Research Station, Portland, OR, USA.
- Lorenz, T. J.; Sullivan, K. A.; Bakian, A. V.; Aubry, C. A. 2011. Cache-site selection in Clark's nutcracker. The Auk 128:237-247.
- Losensky, B. J. 1990. Historical uses of whitebark pine. Pages 191-201 in: Schmidt, W. C.; MacDonald, K. J., compilers. Proceedings—symposium on white bark pine ecosystems: Ecology and management of a high-mountain resource. General Technical Report INT-270, USDA Forest Service, Intermountain Research Station, Ogden, UT, USA.

- Luckman, B. H.; Jozsa, L. A.; Murphy, P. J. 1984. Living seven-hundred-year-old *Picea engelmannii* and *Pinus albicaulis* in the Canadian Rockies. Arctic and Alpine Research 16:419-422.
- Luh, H.-K.; Pimm, S. L. 1993. The assembly of ecological communities: a minimalist approach. Journal of Animal Ecology 62:749-765.
- Lutes, D. C.; Benson, N. C.; Keifer, M.; Caratti, J. F.; Streetman, S. A. 2009. FFI: a software tool for ecological monitoring. International Journal of Wildland Fire 18:310-314.
- Lutes, D. C.; Keane, R. E.; Caratti, J. F.; Key, C. H.; Benson, N. C.; Sutherland, S.; Gangi, L. J. 2006. FIREMON: fire effects monitoring and inventory system. General Technical Report RMRS-GTR-164-CD, USDA Forest Service, Rocky Mountain Research Station, Fort Collins, CO, USA.
- Mahalovich, M. F. 2000. Whitebark pine restoration strategy-some genetic considerations. Nutcracker Notes 11:6-9.
- Mahalovich, M. F. 2012. Genetic differentiation of *Pinus albicaulis* Engelm. populations from the Northern Rocky Mountains. The Americas Journal of Plant Science and Biotechnology, Special Issue on Rusts.
- Mahalovich, M. F.; Burr, K. E.; Foushee, D. L. 2006. Whitebark pine germination, rust resistance, and cold hardiness among seed sources in the Inland Northwest: planting strategies for restoration. In: Riley, L. E.; Dumroese, R. K.; Landis, T. D., technical coordinators. 2006. National proceedings: Forest and Conservation Nursery Associations—2005. Proceedings RMRS-P-43, USDA Forest Service, Rocky Mountain Research Station, Fort Collins, CO, USA. 160 p. Available: <http://www.rngr.net/nurseries/publications/proceedings>.
- Mahalovich, M. F.; Dickerson, G. A. 2004. Whitebark pine genetic restoration program for the Intermountain West (United States). In: Snieszko, R. A.; Samman, S.; Schlarbaum, S. E.; Kriebel, H. B., editors. 2004. Breeding and genetic resources of five-needle pines: growth, adaptability and pest resistance; 23-27 July 2001; Medford, OR, USA. IUFRO Working Party 2.02.15. Proceedings RMRS-P-32, USDA Forest Service, Rocky Mountain Research Station, Fort Collins, CO, USA.
- Mahalovich, M. F.; Hipkins, V. D. 2011. Molecular genetic variation in whitebark pine (*Pinus albicaulis* Engelm.) in the Inland West. Pages 124-139 in: Keane, Robert E.; Tomback, Diana F.; Murray, Michael P.; Smith, Cyndi M., editors. 2011. The future of high-elevation, five-needle white pines in Western North America: Proceedings of the High Five Symposium; 28-30 June 2010; Missoula, MT. Proceedings RMRS-P-63. USDA Forest Service, Rocky Mountain Research Station, Fort Collins, CO, USA.
- Mahalovich, M. F.; Hoff, R. J. 2000. Whitebark pine operational cone collection instructions and seed transfer guidelines. Nutcracker Notes 11:10-13.
- Maloy, O. C. 1997. White pine blister rust control in North America: a case history. Annual Review of Phytopathology 35:87-109.
- Mattes, H. 1984. The role of animals in Cembran pine forest regeneration. Proceedings of 3rd IUFRO Workshop. Ber Eidgenoss Anstalt Forst Versuch 270:195-205.
- Mattson, D. J. 1997. Use of ungulates by Yellowstone grizzly bears *Ursus arctos*. Biological Conservation 81:161-177.
- Mattson, D. J. 2000. Causes and consequences of dietary differences among Yellowstone grizzly bears (*Ursus arctos*). Dissertation, University of Idaho, Moscow. 173 p.
- Mattson, D. J.; Blanchard, B. M.; Knight, R. R. 1991. Food habits of Yellowstone grizzly bears, 1977-1987. Canadian Journal of Zoology 69:1619-1629.
- Mattson, D. J.; Blanchard, B. M.; Knight, R. R. 1992. Yellowstone grizzly bear mortality, human habituation, and whitebark pine seed crops. Journal of Wildlife Management 56:432-442.
- Mattson, D. J.; Reinhart, D. P. 1990. Whitebark pine on the Mount Washburn Massif, Yellowstone National Park. Pages 106-117 in: Schmidt, W. C.; McDonald, K. J., compilers. Proceedings—symposium on whitebark pine ecosystems: ecology and management of a high-mountain resource. General Technical Report INT-270, USDA Forest Service, Intermountain Research Station, Ogden, UT, USA.
- Mattson, D. J.; Kendall, K. C.; Reinhart, D. P. 2001. Whitebark pine, grizzly bears, and red squirrels. Pages 121-137 in: Tomback, D. F.; Arno, S. A.; Keane, R. E., editors. Whitebark Pine Communities: Ecology and Restoration. Island Press, Washington, DC, USA.
- Mattson, D. J.; Reinhart, D. P. 1994. Bear use of whitebark pine seeds in North America. Pages 212-220 in: Schmidt, W. C.; Holtmeier, F. K., compilers. Proceedings of the international workshop on subalpine stone pines and their environment: the status of our knowledge. General Technical Report INT-GTR-309, USDA Forest Service, Intermountain Research Station, Ogden, UT, USA.
- Mattson, D. J.; Reinhart, D. P. 1997. Excavation of red squirrel middens by grizzly bears in the whitebark pine zone. Journal of Applied Ecology 34:926-940.
- Mattson, D. J.; Reinhart, D. P.; Blanchard, B. M. 1994. Variation in production and bear use of whitebark pine seeds in the Yellowstone area. Pages 205-220 in: Diennial scientific conference on the Greater Yellowstone Ecosystem. USDI National Park Service, Natural Resources Publication Office, Yellowstone National Park, WY, USA.
- McCaughay, W. W. 1993. Delayed germination and seedling emergence of *Pinus albicaulis* in a high elevation clearcut in Montana, USA. Pages 67-72 in: Edwards, D. G. W., compiler. Dormancy and barriers to germination. Proceedings of an International Symposium of the International Union of Forestry Research Organizations (IUFRO) Project Group P2.04.00. Forestry Canada, Pacific Forestry Centre, Victoria, British Columbia.
- McCaughay, W. W.; McDonald, K. J. 1993. Workshop proceedings. Pages 1-56 in: Management of whitebark pine ecosystems—an international and regional perspective. Eastside Chapter of SAF, Intermountain Research Station, Gallatin National Forest, Bozeman, MT, USA.
- McCaughay, W.; Schmidt, W. C. 2001. Taxonomy, distribution, and history of whitebark pine. Pages 29-41 in: Tomback, D. F.; Arno, S. A.; Keane, R. E., editors. Whitebark Pine Communities: Ecology and Restoration. Island Press, Washington, DC, USA.
- McCaughay, W.; Scott, G. L.; Izlar, K. L. 2009. Whitebark pine planting guidelines. Western Journal of Applied Forestry 24:163-166.
- McCaughay, W.; Tomback, D. F. 2001. The natural regeneration process of whitebark pine. Pages 105-122 in: Tomback, D. F.; Arno, S. A.; Keane, R. E., editors. Whitebark Pine Communities: Ecology and Restoration. Island Press, Washington, DC, USA.
- McCaughay, W. W.; Schmidt, W. C.; Shearer, R. C. 1985. Seed-dispersal characteristics of conifers in the inland mountain west. In: Proceedings from the Conifer tree seed in the Inland Mountain West symposium, Missoula, MT, USA.
- McCaughay, W. W.; Weaver, T. 1990. Biotic and microsite factors affecting whitebark pine establishment. Pages 140-150 in: Schmidt, W. C.; McDonald, K. J., compilers. Proceedings—symposium on whitebark pine ecosystems: ecology and

- management of a high-mountain resource. General Technical Report INT-270, USDA Forest Service, Intermountain Research Station, Ogden, UT, USA.
- McCool, S. F.; Freimund, W. A. 2001. Threatened landscapes and fragile experiences: conflict in whitebark pine restoration. Pages 263-288 in: Tomback, D. F.; Arno, S. A.; Keane, R. E., editors. Whitebark Pine Communities: Ecology and Restoration. Island Press, Washington, DC, USA.
- McDonald, G. I.; Hoff, R. J. 2001. Blister rust: an introduced plaque. Pages 193-220 in: Tomback, D. F.; Arno, S. F.; Keane, R. E., editors. Whitebark Pine Communities: Ecology and Restoration. Island Press, Washington, DC, USA.
- McDermid, G. J.; Smith, I. U. 2008. Mapping the distribution of whitebark pine (*Pinus albicaulis*) in Waterton Lakes National Park using logistic regression and classification tree analysis. Canadian Journal of Remote Sensing 34:356-366.
- McGarigal, K.; Marks, B. J. 1995. FRAGSTATS: spatial pattern analysis program for quantifying landscape structure. General Technical Report PNW-GTR-351, USDA Forest Service, Pacific Northwest Research Station, Portland, OR, USA.
- McGregor, M. D.; Amman, G. D.; Schmitz, R. F.; Oakes, R. D. 1987. Partial cutting lodgepole pine stands to reduce losses the mountain pine beetle. Canadian Journal of Forest Resources 17:1234-1239.
- McKay, J. K.; Christian, C. E.; Harrison, S.; Rice, K. J. 2005. How local is local? A review of practical and conceptual issues in the genetics of restoration. Restoration Ecology 13:432-440.
- McKenney, D. W.; Pedlar, J. J.; Lawrence, L.; Campbell, K.; Hutchinson, M. F. 2007. Potential impacts of climate change on the distribution of North American trees. Bioscience 57: 939-948.
- McKinney S.; Fiedler, C. 2010. Tree squirrel habitat selection and predispersal seed predation in a declining subalpine conifer. Oecologia 162:697-707.
- McKinney, S. T. 2004. Evaluating natural selection as a management strategy for restoring whitebark pine. Thesis, University of Colorado, Denver.
- McKinney, S. T.; Fiedler, C. E.; Tomback, D. F. 2009. Invasive pathogen threatens bird-pine mutualism: implications for sustaining a high-elevation ecosystem. Ecological Applications 19:597-607.
- McKinney, S. T.; Fiedler, C. E.; Tomback, D. F. 2010. Altered species interactions and implications for natural regeneration in whitebark pine communities. Pages 56-63 in: Keane, Robert E.; Tomback, Diana F.; Murray, Michael P.; Smith, Cyndi M., editors. 2011. The future of high-elevation, five-needle white pines in Western North America: Proceedings of the High Five Symposium; 28-30 June 2010; Missoula, MT. Proceedings RMRS-P-63, USDA Forest Service, Rocky Mountain Research Station, Fort Collins, CO, USA.
- McKinney, S. T.; Tomback, D. F. 2007. The influence of white pine blister rust on seed dispersal in whitebark pine. Canadian Journal of Forest Research 37:1044-1057.
- McKinney, S. T.; Tomback, D. F. 2011. Altered community dynamics in Rocky Mountain whitebark pine forests and the potential for accelerating declines. Pages 45-78 in: Richards, K. E., editor. Mountain Ecosystems: Dynamics, Management and Conservation. Nova Science Publishers, Hauppauge, NY.
- Mellman-Brown, S. 2002. The regeneration of whitebark pine in the timberline ecotone of the Beartooth Plateau, Montana and Wyoming. Dissertation, Westfälischen Wilhelms-Universität Münster.
- Merila, J.; Crnokrak, P. 2001. Comparison of genetic differentiation at marker loci and quantitative traits. Journal of Evolutionary Biology 14:892-903.
- Messerli, B.; Viviroli, D.; Weingartner, R. 2004. Mountains of the world: vulnerable water towers for the 21st Century. Ambio: 29-34.
- Mewaldt, L. R. 1956. Nesting behavior of the Clark nutcracker. The Condor 58:3-23.
- Millar, C. I.; Stephenson, N. L.; Stephens, S. L. 2007. Climate change and forests of the future: managing in the face of uncertainty. Ecological Applications 17(8):2145-2151.
- Mills, L. S.; Soulé, M. E.; Doak, D. F. 1993. The keystone-species concept in ecology and conservation. BioScience 43(4):219-224.
- Minore, D. 1979. Comparative autecological characteristics of northwestern tree species: a literature review. General Technical Report PNW-87, USDA Forest Service, Pacific Northwest Forest and Range Experiment Station, Portland, OR, USA.
- Mladenoff, D. J.; Baker, W. L. 1999. Spatial Modeling of Forest Landscape Change. Cambridge University Press, Cambridge, United Kingdom.
- Moerman, D. E. 1998. Native American Ethnobotany. Timber Press, Portland, OR, USA. 927 p.
- Mohatt, K. R.; Cripps, C. L.; Lavin, M. 2008. Ectomycorrhizal fungi of whitebark pine (a tree in peril) revealed by sporocarps and molecular analysis of mycorrhizae from treeline forests in the Greater Yellowstone Ecosystem. Botany 86:14-25.
- Molina, R.; Trappe, J. 1994. Biology of the ectomycorrhizal genus, *Rhizopogon*. I. Host associations, host specificity and pure culture syntheses. New Phytologist 126:653-675.
- Morgan, P.; Aplet, G. H.; Haufner, J. B.; Humphries, H. C.; Moore, M. M.; Wilson, W. D. 1994a. Historical range of variability: a useful tool for evaluating ecosystem change. Journal of Sustainable Forestry 2:87-111.
- Morgan, P.; Bunting, S. C. 1989. Whitebark pine: fire ecology and management. Women in Natural Resources 11:52.
- Morgan, P.; Bunting, S. C. 1990. Fire effects in whitebark pine forests. Pages 166-170 in: Schmidt, W. C.; McDonald, K. J., compilers. Proceedings—symposium on whitebark pine ecosystems: ecology and management of a high-mountain resource. General Technical Report INT-270, USDA Forest Service, Intermountain Research Station, Ogden, UT, USA.
- Morgan, P.; Bunting, S. C.; Keane, Robert E.; Arno, S. F. 1994b. Fire ecology of whitebark pine (*Pinus albicaulis*) forests in the Rocky Mountains, USA. Pages 136-142 in: Proceedings—International workshop on subalpine stone pines and their environment: the status of our knowledge; St. Moritz, Switzerland, 5-11 September, 1992. General technical report INT-GTR-309, USDA Forest Service, Intermountain Research Station, Ogden, UT, USA.
- Morgenstern, Ken E. 1996. Geographic Variation in Forest Trees. UBC Press, Vancouver, British Columbia. 209 p.
- Moser, M. M. 2004. Subalpine conifer forests in the Alps, the Altai, and the Rocky Mountains: a comparison of their fungal populations. Pages 151-158 in: Cripps, C. L., editor. Fungi in forest ecosystems: systematics, diversity and ecology. New York Botanical Garden Press, New York.
- Muir, John. 1894 (1977 reprint). The Mountains of California. Ten Speed Press, Berkeley, CA. 381 p.
- Murray, M. P. 1996. Landscape dynamics of an island range: interrelationships of fire and whitebark pine (*Pinus albicaulis*). Dissertation. University of Idaho, Moscow.
- Murray, M. P. 2005. Our threatened timberlines: the plight of whitebark pine ecosystems. Kalmiopsis 12:25-29.

- Murray, M. P. 2007a. A comparison of cone collecting techniques for whitebark pine. Pages 109-112 in: Goheen, E. M.; Sniezko, R. A., technical coordinators. Proceedings of the conference—Whitebark pine: a Pacific Coast perspective; 27-31 August 2006, Ashland, OR. R6-NR-FHP-2007-01, USDA Forest Service, Pacific Northwest Region, Portland, OR, USA.
- Murray, M. P. 2007b. Cone collecting techniques for whitebark pine. *Western Journal of Applied Forestry* 22(3):153-155.
- Murray, M. P. 2007c. Fire and Pacific Coast whitebark pine. Pages 51-60 in: Goheen, E. M.; Sniezko, R. A., technical coordinators. Proceedings of the conference—Whitebark pine: a Pacific Coast perspective; 27-31 August 2006. Ashland, OR. R6-NR-FHP-2007-01, USDA Forest Service, Pacific Northwest Region, Portland, OR, USA.
- Murray, M. P. 2008. Fires in the high Cascades: new findings for managing whitebark pine. *Fire Management Today* 68:26-29.
- Murray, M. P.; Bunting, S. C.; Morgan, P. 1995. Whitebark pine and fire suppression in small wilderness areas. General Technical Report INT-GTR-320, USDA Forest Service, Intermountain Research Station, Ogden, UT, USA.
- Murray, M. P.; Bunting, S. C.; Morgan, P. 1997. Subalpine ecosystems: the roles of whitebark pine and fire. Pages 295-310 in: Fire effects on rare and endangered species and habitats. International Association of Wildland Fire, Couer d'Alene, ID, USA.
- Murray, M. P.; Bunting, S. C.; Morgan, P. 1998. Fire history of an isolated subalpine mountain range of the intermountain region, United States. *Journal of Biogeography* 25:1071-1080.
- Murray, M. P.; Rasumussen, M. 2003. Non-native blister rust disease on whitebark pine at Crater Lake National Park. *Northwest Science* 77:87-91.
- Natural Resources Defense Council. 2009. A petition to list the whitebark pine, *Pinus albicaulis*, as an endangered species under the Endangered Species Act. [online] Available: http://docs.nrdc.org/legislation/files/leg_08120801a.pdf.
- NatureServe. 2009. *Pinus albicaulis*. NatureServe Explorer (Version 7.1). [online]. Available: <http://www.natureserve.org/explorer>.
- Neary, D. G.; Klopatek, C. C.; DeBano, L. F.; Folliott, P. F. 1999. Fire effects on belowground sustainability: a review and synthesis. *Forest Ecology and Management* 122:51-71.
- Norment, C. J. 1991. Bird use of forest patches in the subalpine forest-alpine tundra ecotone of the Beartooth Mountains, Wyoming. *Northwest Science* 65:1-10.
- Ogilvie, R. T. 1990. Distribution and ecology of whitebark pine in western Canada. Pages 54-60 in: Schmidt, W. C.; McDonald, K. J., compilers. Proceedings—symposium on whitebark pine ecosystems: ecology and management of a high-mountain resource. General Technical Report INT-270, USDA Forest Service, Intermountain Research Station, Ogden, UT, USA.
- Olsen, W. K.; Schmid, J. M.; Mata, S. A. 1996. Stand characteristics associated with mountain pine beetle infestations in ponderosa pine. *Forest Science* 42:310-327.
- Owens, J. N.; Kittirat, T.; Mahalovich, M. F. 2008. Whitebark pine (*Pinus albicaulis* Engelm.) seed production in natural stands. *Forest Ecology and Management* 255:803-809.
- Perera, A. H.; Buse, L. J.; Weber, M. G., editors. 2004. Emulating natural forest landscape disturbances: concepts and applications. Columbia University Press, New York, USA.
- Perkins, D. L.; Roberts, D. W. 2003. Predictive models of whitebark pine mortality from mountain pine beetle. *Forest Ecology and Management* 174:495-510.
- Perkins, D. L.; Swetnam, T. W. 1996. A dendroecological assessment of whitebark pine in the Sawtooth-Salmon River region, Idaho. *Canadian Journal of Forest Research* 26:2123-2133.
- Perkins, J. L. 2004. *Pinus albicaulis* seedling regeneration after fire. Dissertation, University of Montana, Missoula.
- Peterson, K. T. 1999. Whitebark pine (*Pinus albicaulis*) decline and restoration in Glacier National Park. Thesis. University of North Dakota, Grand Forks.
- Pfister, R. D.; Kovalchik, B. L.; Arno, S. F.; Presby, R. C. 1977. Forest habitat types of Montana. General Technical Report INT-34, USDA Forest Service, Intermountain Forest and Range Experiment Station, Ogden, UT, USA.
- Pickett, S. T. A.; Collins, S. L.; Armesto, J. J. 1987. Models, mechanisms, and pathways of succession. *The Botanical Review* 53:335-371.
- Podruzny, S.; Reinhart, D. P.; Mattson, D. J. 1999. Fire, red squirrels, whitebark pine, and Yellowstone grizzly bears. *Ursus* 11:131-140.
- Politov, D. V.; Krutovskii, K. V.; Altukhov, K. V. 1992. Isozyme loci characteristics of gene banks of populations of cedar pines. *Genetika* 28:76-95.
- Potenko, V. V.; Velikov, A. V. 1998. Genetic diversity and differentiation of natural populations of *Pinus koraiensis* (Sieb. et Zucc.) in Russia. *Silvae Genetica* 47:202-208.
- Potenko, V. V.; Velikov, A. V. 2001. Allozyme variation and mating system of coastal populations of *Pinus koraiensis* Sieb. et Zucc. in Russia. *Silvae Genetica* 50:117-122.
- Powell, J. A.; Logan, J. A.; Bentz, B. J. 1996. Local projections for a global model of mountain pine beetle attacks. *Journal of Theoretical Biology* 179:243-260.
- Pratt, S. D.; Holsinger, L.; Keane, R. E. 2006. Modeling historical reference conditions for vegetation and fire regimes using simulation modeling. General Technical Report RMRS-GTR-175, USDA Forest Service, Rocky Mountain Research Station, Fort Collins, CO, USA.
- Price, D. T.; Zimmerman, N. E.; van der Meer, P. J.; [and others]. 2001. Regeneration in gap models: priority issues for studying forest responses to climate change. *Climatic Change* 51(3-4):475-508.
- Price, R. A.; Liston, A.; Strauss, S. H. 1998. Phylogeny and systematics of *Pinus*. Pages 49-68 in: Richardson, D. M., editor. *Ecology and Biogeography of Pinus*. Cambridge University Press, Cambridge, United Kingdom.
- Raffa, K. F.; Aukema, B. H.; Bentz, B.; 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* 58:501-517.
- Read, D. J. 1998. The mycorrhizal status of *Pinus*. Pages 324-340 in: Richardson, D. M., editor. *Ecology and Biogeography of Pinus*. Cambridge University Press, Cambridge, United Kingdom.
- Reed, David H.; Frankham, Richard. 2001. How closely correlated are molecular and quantitative measures of genetic variation? A meta-analysis. *Evolution* 55(6):1095-1103.
- Régnière, J.; Bentz, B. J. 2007. Modeling cold tolerance in the mountain pine beetle, *Dendroctonus ponderosae*. *Journal of Insect Physiology* 53:559-572.
- Rehfeldt, G. E.; Ying, C. C.; Spittlehouse, D. L.; Hamilton, D. A. 1999. Genetic responses to climate in *Pinus contorta*: niche breadth, climate change, and reforestation. *Ecological Monographs* 69:375-407.

- Reid, R.W.; Gates, H. 1970. Effect of temperature and resin on hatch of eggs of the mountain pine beetle (*Dendroctonus ponderosae*). The Canadian Entomologist 102:617-622.
- Reinhart, D. P.; Mattson, D. J. 1990. Red squirrels in the whitebark pine zone. Pages 256-263 in: Schmidt, W. C.; McDonald, K. J., compilers. Proceedings—symposium on whitebark pine ecosystems: ecology and management of a high-mountain resource. General Technical Report INT-270, USDA Forest Service, Intermountain Research Station, Ogden, UT, USA.
- Reinhardt, E.; Crookston, N. L. 2003. The fire and fuels extension to the Forest Vegetation Simulator. General Technical Report RMRS-GTR-116, USDA Forest Service, Rocky Mountain Research Station, Fort Collins, CO, USA.
- Renkin, R. A.; Despain, D. G. 1992. Fuel moisture, forest type and lightning caused fire in Yellowstone National Park. Canadian Journal Forest Research 2:37-45.
- Renner, E. A. 1929. Letter to District Forester, Ogden, UT. USDA Forest Service Archives, Forestry Science Laboratory, Logan, UT, USA.
- Resler, L. M.; Tombak, D. F. 2008. Blister rust prevalence in Krummholz whitebark pine: implications for treeline dynamics, northern Rocky Mountains, MT, USA. Arctic, Antarctic, and Alpine Research 40:161-170.
- Reynolds, K. M.; Hessburg, P. F. 2005. Decision support for integrated landscape evaluation and restoration planning. Forest Ecology and Management 207:263-278.
- Richardson, B. A.; Brunsfeld, S. J.; Klopfenstein, N. B. 2002a. Assessing Clark's nutcracker seed-caching flights using maternally inherited mitochondrial DNA of whitebark pine. Canadian Journal of Forestry Research 32:1103-1107.
- Richardson, B. A.; Brunsfeld, S. J., Klopfenstein, N. B. 2002b. DNA from bird-dispersed seed and wind-disseminated pollen provides insights into postglacial colonization and population genetic structure of whitebark pine (*Pinus albicaulis*). Molecular Ecology 11:215-227.
- Robbins, C. T.; Schwartz, C. C.; Gunther, K. A.; Servheen, C. 2006. Grizzly bear nutrition and ecology studies in Yellowstone National Park. Yellowstone Science 14(3):19-26.
- Robledo-Arnuncio, J. J.; Alía, R.; Gil, L. 2004. Increased selfing and correlated paternity in a small population of a predominantly outcrossing conifer, *Pinus sylvestris*. Molecular Ecology 13:2567-2577.
- Rockwell, F. I. 1911. The white pines of Montana and Idaho—their distribution, quality, and uses. Forestry Quarterly 9: 219-231.
- Rogers, D. L.; Millar, C. I.; Westfall, R. D. 1999. Fine-scale genetic structure of whitebark pine (*Pinus albicaulis*): associations with watershed and growth form. Evolution 53:74-90.
- Rollins M. G. 2009. LANDFIRE: a nationally consistent vegetation, wildland fire, and fuel assessment. International Journal of Wildland Fire 18:235-249.
- Rollins, M. G.; Keane, R. E.; Zhu, Z. 2006. An overview of the LANDFIRE prototype project. General Technical Report RMRS-GTR-175, USDA Forest Service, Rocky Mountain Research Station, Fort Collins, CO, USA.
- Romme, W. H. 1980. Fire frequency in subalpine forests of Yellowstone National Park. Pages 27-30 in: Proceedings of the fire history workshop. General Technical Report RM-81, USDA Forest Service, Rocky Mountain Forest and Range Experiment Station, Tucson, AZ, USA.
- Romme, W. H.; Knight, D. H. 1981. Fire frequency and subalpine forest succession along a topographic gradient in Wyoming. Ecology 62:319-326.
- Romme, W. H.; Knight, D. H.; Yavitt, J. B. 1986. Mountain pine beetle outbreaks in the Rocky Mountains: regulators of primary productivity? American Naturalist 127:484-494.
- Romme, W. H.; Turner, M. G. 1991. Implications of global climate change for biogeographic patterns in the Greater Yellowstone Ecosystem. Conservation Biology 5:373-386.
- Running, S. W. 2006. Is global warming causing more, larger wild fires. Science 313:927-928.
- Ryan, K. C. 1991. Vegetation and wildland fire: implications of global climate change. Environment International 17:169-178.
- Ryan, K. C.; Reinhardt, E. D. 1988. Predicting postfire mortality of seven western conifers. Canadian Journal of Forest Research 18:1291-1297.
- Safranyik, L.; Wilson B. 2006. The mountain pine beetle: a synthesis of biology, Management and Impacts in Lodgepole Pine. Natural Resources Canada, Canadian Forest Service, Victoria, British Columbia.
- Salwasser, H.; Huff, D. E. 2001. Social and environmental challenges to restoring whitebark pine. Pages 401-432 in: Tombak, D.; Arno, Stephen F.; Keane, R. E., editors. Whitebark Pine Communities: Ecology and Restoration. Island Press, Washington, DC, USA.
- Samman, S.; Schwandt, J. W.; Wilson, J. L. 2003. Managing for healthy white pine ecosystems in the United States to reduce the impacts of white pine blister rust. Report R1-03-118, USDA Forest Service, Forest Health and Protection, Missoula, MT, USA.
- Schmid, J. M.; Mata, S. A. 1992. Stand density and mountain pine beetle-caused tree mortality in ponderosa pine stands. Research Note RM-515, USDA Forest Service, Rocky Mountain Forest and Range Experiment Station, Fort Collins, CO, USA. 4 p.
- Schoettle, A. W. 2004. Developing proactive management options to sustain bristlecone and limber pine ecosystems in the presence of a non-native pathogen. Pages 146-155 in: Shepperd, W. D.; Eskew L. G., editors. Silviculture in special places: proceedings of the national silviculture workshop. Proceedings RMRS-P-34, USDA Forest Service, Rocky Mountain Research Station, Ft. Collins, CO, USA.
- Schoettle, A. W.; Snieszko, R. A. 2007. Proactive intervention to sustain high-elevation pine ecosystems threatened by white pine blister rust. Journal of Forest Research 12:327-336.
- Schrag, A. M.; Bunn, A. G.; Graumlich, L. J. 2007. Influence of bioclimatic variables on tree-line conifer distribution in the Greater Yellowstone Ecosystem: implications for species of conservation concern. Journal of Biogeography 35:698-710.
- Schultz, J. R. 1989. Using disease resistant white pine to meet multiple resource objective. Northern Journal of Applied Forestry 6:38-39.
- Schwandt, J. W. 2006. Whitebark pine in peril: a case for restoration. Report R1-06-28, USDA Forest Service, Forest Health and Protection, Missoula, MT, USA.
- Schwandt, J. W.; Kliejunas, J.; Lockman, B.; Muir, J. 2006. White pines and blister rust in western North America: spread, impacts and restoration. Pages 65-68 in: Proceedings of the 53rd Western International Forest Disease Work Conference; 26-29 August 2005; Jackson, WY. USDA Forest Service, Intermountain Region, Ogden, UT, USA.
- Schwandt, J. W.; Lockman, I. B.; Kliejunas, J. T.; Muir, J. A. 2010. Current health issues and management strategies for white pines. Forest Pathology 40:226-250.
- Schwartz, C. C.; Haroldson, M. A.; Cherry, S. 2006. Reproductive performance for grizzly bears in the Greater Yellowstone Ecosystem, 1983-2002. Wildlife Monographs 161:18-23.

- Scott, G. L.; McCaughey, W. W. 2006. Whitebark pine guidelines for planting prescriptions. Pages 84-90 in: National proceedings: Forest and Conservation Nursery Associations—2005. Proceedings RMRS-P-43, USDA Forest Service, Rocky Mountain Research Station, Fort Collins, CO, USA.
- Scott, J.; Burgan R. E. 2005. A new set of standard fire behavior fuel models for use with Rothermel's surface fire spread model. General Technical Report RMRS-GTR-153, USDA Forest Service, Rocky Mountain Research Station, Fort Collins, CO, USA. 72 p.
- Shoal, R. 2007. The status and distribution of whitebark pine in Oregon and Washington. Pages 28-29 in: Proceedings of the conference whitebark pine: a Pacific Coast perspective. USDA Forest Service, Pacific Northwest Region, Ashland, OR, USA.
- Shoal, R.; Aubry, C. 2004. The status of whitebark pine on four National Forests in Washington State. Regional Document. USDA Forest Service, Pacific Northwest Region, Olympia National Forest, Olympia, WA, USA.
- Shoal, R.; Aubry, C. 2006. Core data attributes for whitebark pine surveys. Regional Document. USDA Forest Service, Pacific Northwest Region, Portland, OR, USA.
- Shoal, R. Z.; Lorenz, T.; Aubry, C. 2008. Land managers guide to whitebark pine restoration techniques. Report. USDA Forest Service, Pacific Southwest Region, Olympia, WA, USA.
- Shore, T. L.; Safranyik, L. 1992. Susceptibility and risk rating systems for the mountain pine beetle in lodgepole pine stands. Information Report BC-X-336. Forestry Canada, Pacific and Yukon Region, Pacific Forestry Centre, Victoria, British Columbia. 12 p.
- Siderius, J.; Murray, M. P. 2005. Fire knowledge for managing Cascadian whitebark pine ecosystems. Report 01B-3-3-26, to the Interagency Joint Fire Sciences Program. 44 p.
- Siepielski, A. M.; Benkman, C. W. 2007. Selection by a predispersal seed predator constrains the evolution of avian seed dispersal in pines. Functional Ecology 21:611-618.
- Six, D. L. 2003. A comparison of mycangial and phoretic fungi of individual mountain pine beetles. Canadian Journal of Forest Research 33:1331-1334. doi:10.1139/x03-047.
- Six, D. L.; Adams, J. 2007. White pine blister rust severity and selection of individual whitebark pine by the mountain pine beetle (Coleoptera: Curculionidae, Scolytinae). Journal of Entomological Science 42:345-353.
- Six, D. L.; Paine, T. D. 1998. Effects of mycangial fungi and host tree species on progeny survival and emergence of *Dendroctonus ponderosae* (Coleoptera: Scolytidae). Environmental Entomology 27:1393-1401.
- Smith, C. 1968. The adaptive nature of social organization in the genus of three squirrels *Tamiasciurus*. Ecological Monographs 38:31-63.
- Smith, C. 1970. The coevolution of pine squirrels (*Tamiasciurus*) and conifers. Ecological Monographs 40:349-371.
- Smith, C.; Hoffman, J. 1998. Status of white pine blister rust in Intermountain Region white pines. Report R4-98-02, USDA Forest Service, Intermountain Region, State and Private Forestry, Boise, ID.
- Smith, C.; Hoffman, J. 2000. Status of white pine blister rust in the intermountain west. Western North American Naturalist 60:165-179.
- Smith, C.; Wilson, B. C.; Rasheed, S.; Walker, R. C.; Carolin, T.; Shepherd, B. 2008. Whitebark pine and white pine blister rust in the Rocky Mountains of Canada and northern Montana. Canadian Journal of Forest Research 38:982-995.
- Smith, C. C.; Hamrick, J. L.; Kramer, C. L. 1988. The effects of stand density on frequency of filled seeds and fecundity in lodgepole pine (*Pinus contorta* Dougl.). Canadian Journal of Forest Research 18:453-460.
- Smith, J. E.; McKay, D.; Brenner, G.; McIver, J.; Spatafora, J. 2005. Early impacts of forest restoration treatments on the ectomycorrhizal fungal community and fine root biomass in a mixed conifer forest. Journal of Applied Ecology 42:526-535.
- Sniezko, R. A. 2008. White pine blister rust resistance and genetic conservation of the nine five-needle pine species of the United States. Pages 68-70 in: Noshad, D.; Woon, N. E.; Sniezko, R. A., editors. Breeding and genetic resources of five needle pines. Korean Forest Research Institute, Yanqyang, Korea.
- Sniezko, R. A.; Kegley, A.; Danchok, R.; Long, S. 2007. Variation in resistance to white pine blister rust among whitebark pine families from Oregon and Washington—early results and implications for conservation. Pages 82-97 in: Goheen, E. M.; Sniezko, R. A., technical coordinators. Proceedings of the conference Whitebark pine: a Pacific Coast perspective; 2006 August 27-31; Ashland, OR. R6-NR-FHP-2007-01, USDA Forest Service, Pacific Northwest Region, Portland, OR.
- Sniezko, R. A.; Tomback, D. F.; Rochefort, R. M.; Goheen, E.; Hunt, R.; Beatty, J. S.; Murray, M. P.; Betlejewski, F. 2004. Exotic pathogens, resistant seed, and restoration of forest tree species in western North America. Pages 21-27 in: Second conference on Klamath-Siskiyou ecology; Siskiyou Field Institute, Cave Junction, OR, USA.
- Soulé, M. E.; Estes, J. A.; Berger, J.; Martinez del Rio, C. 2003. Ecological effectiveness: conservation goals for interactive species. Conservation Biology 17:1238-1250.
- Spitze, K. 1993. Population structure in *Daphnia obtusa*: quantitative genetic and allozymic variation. Genetics 135:367-374.
- St. Clair, J.; Bradley, Nancy; Mandel, L.; Vance-Borland, Ken W. 2005. Genecology of Douglas fir in western Oregon and Washington. Annals of Botany 96:1199-1214.
- Steele, M. A. 1998. *Tamiasciurus hudsonicus*. Mammalian Species 586:1-9.
- Steele, R.; Cooper, S. V.; Ondov, D. M.; Roberts, D. W.; Pfister, R. D. 1983. Forest habitat types of eastern Idaho-western Wyoming. General Technical Report INT-144, USDA Forest Service, Intermountain Forest and Range Experiment Station, Ogden, UT, USA.
- Steinfeld, D.; Amaranthus, M.; Cazares, E. 2003. Survival of ponderosa pine (*Pinus ponderosa* Dougl. Ex Laws.) seedlings outplanted with *Rhizopogon* mycorrhizae inoculated with spores at the nursery. Journal of Arboriculture 29(4):197-208.
- Stevens, R. E.; McCambridge, F. M.; Edminster, C. B. 1980. Risk rating guide for mountain pine beetle in Black Hills ponderosa. Research Note RN-385, USDA Forest Service, Rocky Mountain Forest and Range Experiment Station, Ogden, UT, USA.
- Stuart-Smith, G. J. 1998. Conservation of whitebark pine in the Canadian Rockies: blister rust and population genetics. Thesis. University of Alberta, Edmonton.
- Sund, S. K.; Tomback, D. F.; Hoffman, L. 1991. Post fire regeneration of *Pinus albicaulis* in western Montana: patterns of occurrence and site characteristics. Unpublished report, USDA Forest Service, Intermountain Research Station, on file at: Intermountain Fire Sciences Laboratory, Missoula, MT, USA.
- Swanberg, P. O. 1956. Territory in the thick-billed nutcracker *Nucifraga caryocatactes*. Ibis 98:412-419.
- Swetnam, T. W.; Allen, C. D.; Betancourt, J. L. 1999. Applied historical ecology: using the past to manage for the future. Ecological Applications 9:1189-1206.

- Swetnam, T. W.; Betancourt, J. L. 1998. Mesoscale disturbance and ecological response to decadal climatic variability in the American Southwest. *Journal of Climate* 11:3128-3147.
- Syring, J.; Farrell, K.; Businsky, R.; Cronn, R.; Liston, A. 2007. Widespread genealogical nonmonophyly in species of *Pinus* subgenus *Strobus*. *Systematic Biology* 56(2):163-181.
- Tani, N.; Tomaru, N.; Araki, M.; Ohba, K. 1996. Genetic diversity and differentiation in populations of Japanese stone pine (*Pinus pumila*) in Japan. *Canadian Journal of Forest Research* 26:1454-1462.
- Taylor, A. F. S.; Alexander, I. 2005. The ectomycorrhizal symbiosis: life in the real world. *Mycologist* 19:102-112.
- Tedersoo, L.; May, T. W.; Smith, M. E. 2009. Ectomycorrhizal lifestyle in fungi: global diversity, distribution, and evolution of phylogenetic lineages. *Mycorrhiza* 20:217-263.
- Tedersoo, L.; Suvi, T.; Jairus, T.; Köljalg, U. 2008. Forest microsite effects on community composition of ectomycorrhizal fungi on seedlings of *Picea abies* and *Betula pedula*. *Environmental Microbiology* 10(5):1189-1201.
- Temperton, V. M.; Hobbs, R. J.; Nuttle, T.; Halle, S., editors. 2004. Assembly rules and restoration ecology: bridging the gap between theory and practice. Island Press, Washington, DC, USA.
- Tillman-Sutela, E.; Kauppi, A.; Karppinen, K.; Tomback, D. F. 2008. Variant maturity in seed structures of *Pinus albicaulis* (Engelm.) and *Pinus sibirica* (du Tour): key to a soil seed bank, unusual among conifers? *Trees-Structure and Function* 22(2):225-236.
- Tomback, D. F. 2008. Preliminary pattern of investigation of the magnitude and time-frame of post-fire whitebark pine regeneration within selected areas in the Bob Marshall Wilderness Area and adjacent lands. Joint Venture Agreement Final Report JVA 03-JV-112222022-251, on file at Missoula Fire Sciences Laboratory, USDA Forest Service, Missoula, MT, USA.
- Tomback, D. F. 1978. Pre-roosting flight of the Clark's nutcracker. *The Auk* 95:554-562.
- Tomback, D. F. 1982. Dispersal of whitebark pine seeds by Clark's nutcracker: a mutualism hypothesis. *Journal of Animal Ecology* 51:451-467.
- Tomback, D. F. 1983. Nutcrackers and pines: coevolution or coadaptation? Pages 179-223 in: Nitecki, M. H., editor. Coevolution. University of Chicago Press, Chicago.
- Tomback, D. F. 1986. Post-fire regeneration of krummholz whitebark pine: a consequence of nutcracker seed caching. *Madroño* 33:100-110.
- Tomback, D. F. 1989. The broken circle: fire, birds and whitebark pine. Pages 14-17 in: Walsh, T., editor. Wilderness and wildfire. Miscellaneous Publication 50, University of Montana, School of Forestry, Montana Forest and Range Experiment Station.
- Tomback, D. F. 1998. Clark's nutcracker (*Nucifraga columbiana*). *The Birds of North America* 331:1-23.
- Tomback, D. F. 2001. Clark's nutcracker: agent of regeneration. Pages 89-104 in: Tomback, D. F.; Arno, S. F.; Keane, R. E., editors. Whitebark Pine Communities: Ecology and Restoration. Island Press, Washington, DC, USA.
- Tomback, D. F. 2005. The impact of seed dispersal by the Clark's nutcracker on whitebark pine: multi-scale perspective on a high mountain mutualism. Pages 181-201 in: Broll, G.; Kepline, B., editors. Mountain Ecosystems: Studies in Treeline Ecology. Springer.
- 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.; Mastrogiovanni, R. J. 2011. The magnificent high-elevation five-needle white pines: ecological roles and future outlook. Pages 2-28 in: Keane, Robert E.; Tomback, Diana F.; Murray, Michael P.; Smith, Cyndi M., editors. 2011. The future of high-elevation, five-needle white pines in Western North America: Proceedings of the High Five Symposium; 28-30 June 2010; Missoula, MT. Proceedings RMRS-P-63, USDA Forest Service, Rocky Mountain Research Station, Fort Collins, CO, USA.
- Tomback, D. F.; Anderies, A. J.; Carsey, K. S.; Powell, M. L.; Mellmann-Brown, S. 2001c. Delayed seed germination in whitebark pine and regeneration patterns following the Yellowstone fires. *Ecology* 82:2587-2600.
- Tomback, D. F.; Arno, S. F.; Keane, R. E. 2001a. The compelling case for management intervention. Pages 3-28 in: Tomback, D.; Arno, Stephen F.; Keane, R. E., editors. Whitebark Pine Communities: Ecology and Restoration. Island Press, Washington, DC USA.
- Tomback, D. F.; Arno, S. F.; Keane, R. E. 2001b. Whitebark Pine Communities: Ecology and Restoration. Island Press, Washington, DC, USA. 440 p.
- Tomback, D. F.; Clary, J. K.; Koehler, J.; Hoff, R. J.; Arno, S. F. 1995. The effects of blister rust on post fire regeneration of whitebark pine: the Sundance Burn of northern Idaho (USA). *Conservation Biology* 9:654-664.
- Tomback, D. F.; Hoffman, L. A.; Sund, S. K. 1990. Coevolution of whitebark pine and nutcrackers: implications for forest regeneration. Pages 118-129 in: Schmidt, W. C.; McDonald, K. J., compilers. Proceedings—symposium on whitebark pine ecosystems: ecology and management of a high-mountain resource. General Technical Report INT-270, USDA Forest Service, Intermountain Research Station, Ogden, UT, USA.
- Tomback, D. F.; Keane, R. E.; McCaughey, W. W.; Smith, C. M. 2005. Methods for surveying and monitoring whitebark pine for blister rust infection and damage. Whitebark Pine Ecosystem Foundation. Available: www.whitebarkfound.org.
- Tomback, D. F.; Kendall, K. 2001. Biodiversity losses: a downward spiral. in: Tomback, D.; Arno, S. F.; Keane, R. E., editors. Whitebark Pine Communities: Ecology and Restoration. Island Press, Washington, DC, USA.
- Tomback, D. F.; Kramer K. A. 1980. Limber pine seed harvest by Clark's nutcracker in the Sierra Nevada: timing and foraging behavior. *The Condor* 82:467-468.
- Tomback, D. F.; Linhart, Y. B. 1990. The evolution of bird-dispersed pines. *Evolutionary Ecology* 4:185-219.
- Tomback, D. F.; Sund, S. K.; Hoffman, L. A. 1993. Post-fire regeneration of *Pinus albicaulis*: height-age relationships, age structure, and microsite characteristics. *Canadian Journal of Forest Research* 23:113-119.
- Trusty, P.; Cripps, C. L. 2010. Impact of fire on the mycorrhizal community with planted and natural seedlings (Fridley Burn, Montana). Pages 312-322 in: Keane, Robert E.; Tomback, Diana F.; Murray, Michael P.; Smith, Cyndi M., editors. 2011. The future of high-elevation, five-needle white pines in Western North America: Proceedings of the High Five Symposium; 28-30 June 2010; Missoula, MT. Proceedings RMRS-P-63. USDA Forest Service, Rocky Mountain Research Station, Fort Collins, CO, USA.
- Turner, M. G.; Gardner, R. H.; O'Neill, R. V. 2001. Landscape Ecology in Theory and Practice. Springer-Verlag, New York, USA.
- Turner, N.; Bouchard, R.; Kennedy, D. 1980. Ethnobotany of the Okanagan-Colville Indians of British Columbia and

- Washington. Occasional papers of the Royal British Columbia Museum, No. 21, Victoria, British Columbia.
- Turner, N.; Thompson, L. C.; York, A. Z. 1991. Thompson ethnobotany. Royal British Columbia Museum, Memoir No. 3, Victoria, British Columbia.
- U.S. Department of Agriculture, Soil Conservation Service. 1975. Soil taxonomy. Agriculture Handbook 436. USDA Soil Conservation Service, Washington, DC, USA. 754 p.
- U.S. Department of the Interior, National Park Service [USDI NPS]. 2001. Fire Monitoring Handbook, National Interagency Fire Center, Boise, ID, USA.
- U.S. Department of the Interior, National Park Service [USDI NPS]. 2006. Management Policies 2006. 168 p.
- U.S. Fish and Wildlife Service. 2007. Endangered, threatened, proposed, and candidate species, critical habitat, and species of concern in western Washington. Western Washington Fish and Wildlife Office, WA, USA. Available: www.fws.gov/westwaf/wo/pdf/species_list_Aug2007.pdf.
- U.S. Fish and Wildlife Service. 2011a. Grizzly bear (*Ursus arctos horribilis*) Five-year review: summary and evaluation. U.S. Fish and Wildlife Service, Grizzly Bear Recovery Office, Missoula, MT, USA. 205 p. Available: <http://www.iqbconline.org/>.
- U.S. Fish and Wildlife Service. 2011b. 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(138):42631-42654.
- Van Wagendonk, J. W. 1985. Fire suppression effects on fuels and succession in short-fire-interval wilderness ecosystems. Pages 119-126 in: Proceedings—symposium and workshop on wilderness fire; Missoula, Montana; 15-18 November 1983. USDA Forest Service, Intermountain Forest and Range Experiment Station, Ogden, UT, USA.
- 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.; Hoffman, S.; Potts, W. K. 1981. Emigration behavior of Clark's nutcracker. The Condor 83:162-170.
- Vander Wall, S. B.; Hutchins, H. E. 1983. Dependence of Clark's nutcracker, *Nucifraga columbiana*, on conifer seeds during the postfledging period. The Canadian Field-Naturalist 97:208-214.
- Visser, S. 1995. Ectomycorrhizal fungal succession in Jack pine stands following wildfire. New Phytologist 129:389-401.
- Walsh, J. R. 2005. Fire regimes and stand dynamics of whitebark pine (*Pinus albicaulis*) communities in the Greater Yellowstone Ecosystem. Thesis, Colorado State University, Fort Collins.
- Ward, K.; Shoal, R.; Aubry, C. 2006a. Whitebark pine in Washington and Oregon: a synthesis of current studies and historical data. Regional Document. USDA Forest Service, Pacific Northwest Region, Portland, OR, USA.
- Ward, K.; Shoal, R.; Aubry, C. 2006b. Whitebark pine cone collection manual. Report, USDA Forest Service, Pacific Northwest Region, Portland, OR, USA.
- Waring, K. M.; O'Hara, K. L. 2005. Silvicultural strategies in forest ecosystems affected by introduced pests. Forest Ecology and Management 209:27-41.
- Waring, K. M.; Six, D. L. 2005. Distribution of bark beetle attacks after whitebark pine restoration treatments: a case study. Western Journal of Applied Forestry 20:110-116.
- Warwell, M. V.; Rehfeldt, G. E.; Crookston, N. L. 2007. Modeling contemporary climate profiles of whitebark pine (*Pinus albicaulis*) and predicting responses to global warming. Pages 139-142 in: Proceedings of the conference whitebark pine: a Pacific Coast perspective; 27-31 August 2006; Ashland, OR. R6-NR-FHP-2007-01, USDA Forest Service, Pacific Northwest Region.
- Weaver, T. 2001. Whitebark pine and its environment. Pages 41-73 in: Tomback, D. F.; Arno, S. F.; Keane, R. E., editors. Whitebark Pine Communities: Ecology and Restoration. Island Press, Washington, DC, USA.
- Weaver, T.; Forcella, F. 1986. Cone production in *Pinus albicaulis* forests. General Technical Report INT-203, USDA Forest Service, Intermountain Range and Experiment Station, Missoula, MT, USA.
- Weisleitner, H. 2008. [Personal communication]. Research Scientist, Federal Nursery of Austria, Innsbruck, Austria.
- Wiensczyk, G.; Durall, D.; Jones, M.; Simard, S. 2002. Ectomycorrhizae and forestry in British Columbia: a summary of current research and conservation strategies. B. C. Journal of Ecosystems and Management 2(1):1-20.
- Wikelski, M.; Cooke, S. J. 2006. Conservation physiology. Trends in Ecology and Evolution 21(2): 333-421.
- Wilson, B. C.; Stuart-Smith, G. J. 2001. Whitebark pine conservation for the Canadian Rocky Mountain National Parks. KNP01-01, Parks Canada, Radium Hot Springs, British Columbia, Canada.
- Wilson, J. B.; Wells, T. C. E.; Trueman, I. C.; Jones, G.; Atkinson, M. D.; Crawley, M. J.; Dodd, M. E.; Silvertown, J. 1996. Are there assembly rules for plant species abundance? An investigation in relation to soil resources and successional trends. Journal of Ecology 84:527-538.
- Wu, Q.-X.; Mueller, G.; Lutzoni, F.; Huang, Y.-Q.; Guo, S.-Y. 2000. Phylogenetic and biogeographic relationships of eastern Asian and eastern North American disjunct *Suillus* species (fungi) as inferred from nuclear ribosomal RNA ITS sequences. Molecular Phylogenetics and Evolution 17:37-47.
- Yandell, U. G. 1992. An allozyme analysis of whitebark pine (*Pinus albicaulis* Engl.). Thesis, University of Nevada, Reno.
- Yoda, K.; Kira, T.; Ogawa, H.; Hozumi, K. 1963. Intraspecific competition among higher plants. II. Self-thinning in over-crowded pure stands under cultivated and natural conditions. Journal 1024 Biology. Osaka City University 14:107-129.
- Zavarin, E.; Rafii, Z.; Cool, L. G.; Snajberk, K. 1991. Geographic monoterpenoid variability of *Pinus albicaulis*. Biochemical Systematics and Ecology 19:147-156.
- Zeglen, S. 2002. Whitebark pine and white pine blister rust in British Columbia, Canada. Canadian Journal of Forest Research 32:1265-1274.
- Zeglen, S. 2007. Current conditions and the state of our efforts regarding whitebark pine in British Columbia. Pages 36-39 in: Proceedings of the conference—Whitebark pine: a Pacific Coast perspective. R6-NR-FHP-2007-01, USDA Forest Service, Pacific Northwest Region, Ashland, OR, USA.

Appendix A—Whitebark Pine Tree Improvement Program

In areas where whitebark pine is a component of upper subalpine forests, it is on the edge of its species distribution, or there are only scattered whitebark pine trees, skip over the stand evaluation criteria and focus on the individual tree selection criteria. When damaging agents are minimal or whitebark pine occurs as scattered trees, units are asked to select the best available trees from a broad sample to meet the gene conservation goals for the project. If more than one growth habit occurs on a unit, efforts should be made to balance selections among the different forms (for example, erect/one main stem, erect/multiple stems, and Krummholz/prostrate).

Whitebark Pine Plus Tree Selection Stand and Individual Tree Criteria

Stand-Level Selection Criteria

- Vigorous and representative of the species.
- Habitat type where whitebark pine normally occurs.
- Within the recognized range of the species.
- Broadly sample the geography and range of elevations throughout the forest. When infection levels are low and whitebark pine grows in both mixed (e.g., lodgepole pine and subalpine fir) and pure stands, balance the number of selections between mixed and pure stands.
- Overall composition has a high proportion of living or dead whitebark pine well represented throughout the stand.
- Easily accessible by road or trail, if at all possible.
- Uniformly and heavily infected with blister rust (10 or more cankers per tree on the average). Average infection level for the stand is determined by carefully counting both live and dead cankers on a representative sample of 100 living or dead whitebark pines in the stand.
- Presence/absence of cankers (bole and branch) for the 100-tree survey determines overall stand infection level.
- A more detailed tally of the number of main-bole and branch cankers for the 100-tree survey will provide a stand average (cankers/tree) for the individual tree selection criteria below. Count the actual number of main-bole cankers and estimate the number of branch cankers in the following categories: 0 = no cankers present, 1-9 cankers, 10-20, 21-40, 41-75, 76-150, and 150+ cankers. (It is recommended that complete bole and branch canker tallies be determined for about three trees so that one's eye can more readily determine estimated branch canker amounts by category.)
- The combined total of main-bole cankers and estimated branch cankers is equal to the number of cankers per tree. The average number of cankers/tree for the overall 100-tree survey then yields the stand average. When rust infection is heavy and infection is high, allowances are made for the possible presence of difficult to see or undetectable cankers.
- Selection of resistant trees in uniform stands with confirmed blister rust mortalities of at least 90 percent is preferable.
- In stands with 50-90 percent infection due to blister rust, select individuals with no more than five cankers.

- If representative sampling of the genetic base within a seed zone is not being met in stands with greater than 50 percent infection due to rust, then selections will be relaxed to include selections from stands with less than 50 percent infection.
 - Not less than 25 years old and from 35 to 100 ft tall so that the stand will:
 - Have had 25 years of exposure to blister rust.
 - Be of cone bearing age.
 - Be producing pollen.
 - Be easily and safely climbable.
- Of moderately open stand density so the plus tree will:
 - Be easy to examine from the ground.
 - Have persistent branches to the ground for climbing ease.
 - Have full crowns for better cone bearing potential (30% or more live-green crown).

Individual Tree Selection Criteria

Relatively free of blister rust when compared to the infection level in the stand as a whole. Allowable infection in the candidate tree is summarized as follows:

Stand average (cankers/tree)	Candidate tree limit
10 to 20	No cankers
21 to 40	1 canker
41 to 75	2 cankers
76 to 150	3 cankers
151+	4 or 5 cankers

The presence or absence of cankers in a potential candidate tree is determined by examining the tree from the ground with binoculars and by climbing the tree and examining each individual whorl from bottom to top. (Even in the most heavily infected stands, it is possible to find canker-free trees).

- Dominant or co-dominant trees are preferable, but the erect/multiple stems or Krummholz growth form categories may lend themselves to intermediate or suppressed tree crown class categories.
- Far enough apart to be unrelated; there should be a minimum of 300 ft between selected trees.
- Free of other insects (mountain pine beetle) and diseases.
- Have a history or the potential to bear cones.
- Be within 5 to 10 chains from the nearest road or trail, unless intervening vegetation is sparse enough that longer lines of sight are possible.
- Select no more than three of the best candidates in any given stand.
- Take care to avoid collections from limber pine, when whitebark and limber pine are intermixed on the same forest. The operational cone collection guidelines for whitebark pine provide additional information on how to distinguish the two species by cone morphology, strobilus color, and pollen catkin color.
- No squirrel cache cone collections for plus tree assignments.

Runty, seriously deformed, diseased, or insect-attacked trees should be avoided, as these characteristics are likely inherited and passed on to progeny.



The Rocky Mountain Research Station develops scientific information and technology to improve management, protection, and use of the forests and rangelands. Research is designed to meet the needs of the National Forest managers, Federal and State agencies, public and private organizations, academic institutions, industry, and individuals. Studies accelerate solutions to problems involving ecosystems, range, forests, water, recreation, fire, resource inventory, land reclamation, community sustainability, forest engineering technology, multiple use economics, wildlife and fish habitat, and forest insects and diseases. Studies are conducted cooperatively, and applications may be found worldwide.

Station Headquarters

Rocky Mountain Research Station
240 W Prospect Road
Fort Collins, CO 80526
(970) 498-1100

Research Locations

Flagstaff, Arizona
Fort Collins, Colorado
Boise, Idaho
Moscow, Idaho
Bozeman, Montana
Missoula, Montana

Reno, Nevada
Albuquerque, New Mexico
Rapid City, South Dakota
Logan, Utah
Ogden, Utah
Provo, Utah

The U.S. Department of Agriculture (USDA) prohibits discrimination in all of its programs and activities on the basis of race, color, national origin, age, disability, and where applicable, sex (including gender identity and expression), marital status, familial status, parental status, religion, sexual orientation, political beliefs, genetic information, reprisal, or because all or part of an individual's income is derived from any public assistance program. (Not all prohibited bases apply to all programs.) Persons with disabilities who require alternative means for communication of program information (Braille, large print, audiotape, etc.) should contact USDA's TARGET Center at (202) 720-2600 (voice and TDD).

To file a complaint of discrimination, write to: USDA, Assistant Secretary for Civil Rights, Office of the Assistant Secretary for Civil Rights, 1400 Independence Avenue, S.W., Stop 9410, Washington, DC 20250-9410.

Or call toll-free at (866) 632-9992 (English) or (800) 877-8339 (TDD) or (866) 377-8642 (English Federal-relay) or (800) 845-6136 (Spanish Federal-relay). USDA is an equal opportunity provider and employer.

www.fs.fed.us/rmrs



To learn more about RMRS publications:

www.fs.fed.us/rm/publications

www.treesearch.fs.fed.us