Whitebark Pine: Ecological Importance and Future Outlook

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Abstract

Whitebark pine (*Pinus albicaulis*) ranges widely throughout the western United States and Canada. On wind-swept sites, it assumes picturesque shapes with sparse canopies and twisted trunks. Whitebark pine is one of eight "five-needled" white pines (Subgenus *Strobus*, Family Pinaceae) found in the West, but the only North American species in Subsection *Cembrae*, a taxon characterized by large, wingless seeds, cones that do not open, and seed dispersal by the nutcrackers. Clark's nutcracker (*Nucifraga columbiana*, Family Corvidae) is the primary disperser of whitebark pine seeds. The coevolved, mutualistic whitebark pine-nutcracker interaction shapes the population genetic structure of whitebark pine, engineers tree growth forms, and facilitates rapid regeneration of whitebark pine after fire. Whitebark, regarded as both a foundation and keystone species, provides multiple ecosystem services: Its seeds are an important wildlife food; it stabilizes soil and protracts snow melt at high elevations; it initiates community development after fire and serves as a nurse tree for other conifers on stressful sites. These ecosystem services, as well as the biodiversity supported by whitebark pine communities, are diminishing nearly rangewide from the spread of *Cronartium ribicola*, an exotic fungal pathogen that causes white pine blister rust in five-needled white pines. Blister rust cankers kill tree branches, reducing cone production and rendering trees non-reproductive years before trees succumb to the disease. Blister rust infection levels in whitebark pine stands are highest in the northern Rocky Mountains of the United States, with survey averages greater than 80%. Recently, the threat posed by blister rust in this region has been overshadowed by mortality in whitebark pine from outbreaks of mountain pine beetles (*Dendroctonus ponderosae*). Also, in the northern Rocky Mountain and Intermountain ranges, whitebark pine is experiencing successional replacement by shade-tolerant species. Restoration techniques developed for whitebark pine include thinning and burning to reduce competition and prepare seedbeds for natural regeneration or planting seedlings. Seedlings with genetic resistance to blister rust are currently viewed as the most promising approach to restoring whitebark pine communities. Whitebark pine trees with genetic resistance to blister rust are being identified and can be protected against mountain pine beetles. In short, restoration techniques are available, but restoration requires a high level of commitment over time and dependable funding. Without this commitment, we risk the loss of whitebark pine and greatly diminished western forest biodiversity.

Introduction

The dedication of an entire symposium to a single high elevation Pacific Coast conifer, whitebark pine (*Pinus albicaulis*, Family Pinaceae, Subgenus *Strobus*) and its high elevation relatives, the "five-needled" white pines, indicates how our perspectives as forest researchers and managers have evolved over the last quarter century. First of all, the concepts integral to ecosystem management have raised our awareness of the importance of intact forest ecosystems, not just for their commercial and value but also for the ecosystem services and the biodiversity they comprise. Secondly, research has provided us with better understanding of the role and function of whitebark pine ecosystems, and the current synergism of threats to these ecosystems—invasive disease, pine beetle outbreaks, and advancing ecological succession. We also acknowledge the ecological value of the other Pacific Coast five-needled white pine ecosystems and the similarly uncertain future they face.

The realization that these ecosystems are and will be disappearing from the Pacific mountain landscape over the coming decades raises questions of how well we understand the ecological role of these pines, particularly in this region, and how ecosystems will be affected in their absence. Most importantly, we need to ask whether we understand what management intervention is necessary and sufficient to restore these ecosystems.

When the 20th century history of western forest management is written, whitebark pine should have a special place as a symbol of new priorities. Although the threat posed by the exotic pathogen *Cronartium ribicola* to all five-needled white pines was previously recognized, the looming possibility of regional extirpations of whitebark pine raises concerns about ecological consequences, indicating the importance of these values to management objectives. In some regions, restoration strategies are already being planned. This paper summarizes why whitebark pine has become the focus of our attention: its ecological importance, major threats, current status, and future outlook.

Distribution and taxonomy

Whitebark pine (*Pinus albicaulis*), a tenacious survivor of the harsh upper subalpine zone and treeline ecotone, ranges widely throughout the western United States and Canada (Fig. 1). Its latitudinal range, from about 37^{o} to 55^{o} N, is among the broadest of the *Strobus* pines; whitebark pine ranges longitudinally from 107^{o} to 128^{o} (Olgivie 1990, McCaughey and Schmidt 2001). “In much of its geographic range whitebark pine is primarily a timberline tree, confined to sites that are so cold, snowbound, rocky, or wind-scoured that its competitors are suppressed by the harsh environment….” (Arno 2001). Thus, whitebark pine occupies sites not tolerated by other subalpine conifers, and consequently may range higher in elevation. On wind-swept sites, such as the rim of Crater Lake, it assumes picturesque shapes with sparse canopies and twisted trunks.

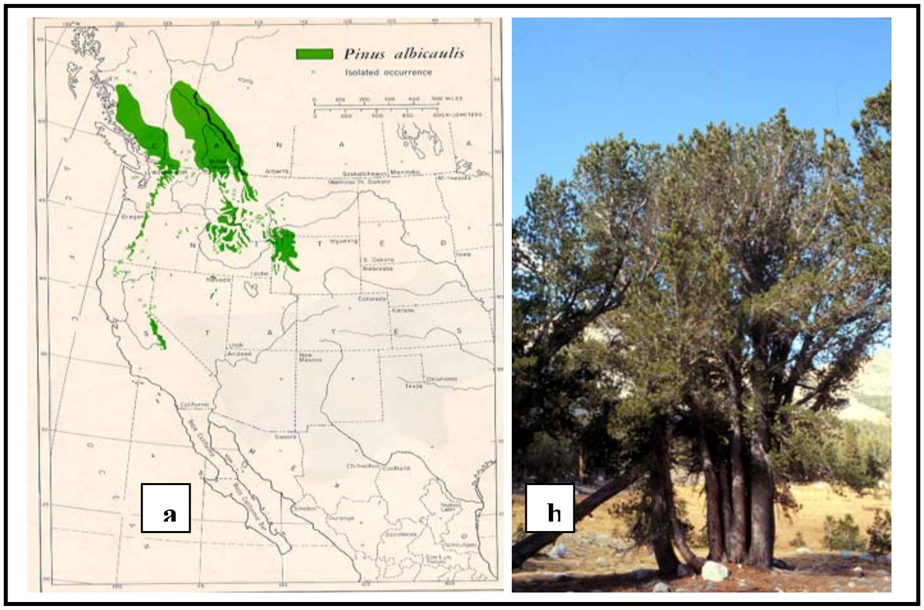

Fig. 1. a. Map of the general distribution of whitebark pine (from Critchfield and Little 1966). The Canadian distribution is patchier than indicated here (see Olgivie 1990). b. Whitebark pine with multiple stems, Tioga Pass, Yosemite National Park, California (Photo: D. F. Tomback).

Whitebark pine is divided into a Rocky Mountain and western or Pacific Coast distribution, connected by a series of ranges in the inter-mountain regions of northeastern Washington and southern British Columbia (Ogilvie 1990, McCaughey and Schmidt 2001). In the Rocky Mountains, whitebark pine ranges in elevation from 3,200 m in western Wyoming to 900 m at its northern limit; and in the west from about 3,660 m in the southern Sierra Nevada to 900 m to its northern limit in the Coast Mountains of British Columbia (Arno and Hoff 1990, Ogilvie 1990).

Whitebark pine has been traditionally classified in Subgenus *Strobus*, Section *Strobus*, Subsection *Cembrae* (Price et al. 1998). According to this scheme, whitebark pine is the only North America member of the *Cembrae*, a taxon considered to be coevolved with nutcrackers (*Nucifraga* spp.). The monophyly of *Cembrae* pines and *Strobus* pine taxonomy, however, are being challenged by recent molecular analyses (e.g., Gernandt et al. 2005)

Community types

Whitebark pine and its high elevation relatives are considered to be "stress-tolerant" pines, capable of extremely slow growth rates under adverse conditions (McCune 1988). Throughout its range, whitebark pine forms climax communities (i.e., self-replacing) on harsh, upper subalpine sites and at treeline, where it usually occurs as krummholz growth forms. Because of slow growth rates, whitebark pine is generally outcompeted on favorable sites, but it is capable of growing throughout the upper subalpine zone in absence of competition (Arno 2001).

Disturbance provides whitebark pine the opportunity to colonize favorable upper subalpine sites: In the northern Rocky Mountains of the United States and southern Canada, and Intermountain Region, where fire at subalpine elevations occurs in both stand-replacement and mixed-severity regimes, whitebark pine forms early seral communities after disturbance and often persists late in succession (Arno 2001, Tomback et al. 2001, Campbell and Antos 2003). Seral whitebark pine communities in the upper subalpine zone may also be more common in the Pacific Coast ranges than previously realized, as suggested by recent fire history studies in the Cascade Range (e.g., Murray 2006, also this proceedings). This possibility requires further study.

Seed dispersal and ecological impact

Whitebark pine seeds are primarily dispersed by Clark's nutcracker (*Nucifraga columbiana*, Family Corvidae), resulting in an interaction that shapes many aspects of the ecology and population biology of whitebark pine (Tomback and Linhart 1990, Tomback 2001).

Nutcrackers have both behavioral and morphological adaptations for an annual cycle that is based on the year-round use of fresh and stored pine seeds (Vander Wall and Balda 1977, Tomback 1978). Nutcrackers possess a sublingual or "throat" pouch, in which 100 or more whitebark pine seeds may be transported to seed caching sites (Fig. 2a) (Tomback 1978, Hutchins and Lanner 1982). They have a sturdy, long, pointed bill that enables them to dig into unripe whitebark pine cones and tear off cone scales for access to seeds. Their well-developed spatial memory permits each bird to remember the precise locations of thousands of seed caches that it stores in late summer and fall (Vander Wall 1982, Kamil and Balda 1985). Nutcrackers retrieve cached pine seeds aided by their spatial memory in order to feed themselves and their young during winter and spring (Mewaldt 1956). Unretrieved seeds that are exposed to snow melt or summer rains may germinate and lead to whitebark pine regeneration (Tomback 1982). Basic information pertaining to nutcracker harvest, transport, and caching of whitebark pine seeds is reported in Box 1.

Box 1. Summary of typical whitebark pine caching behavior by Clark's nutcrackers. Information based on Tomback(1978, 1982) and Hutchins and Lanner (1982).

- One nutcracker may carry maximum loads of 100 or more seeds, although average pouchloads may contain fewer seeds.
- Caches typically consist of 1-15 seeds, with means ranging from 3 to 5 seeds per cache.
- Nutcrackers typically bury seeds 1 to 3 cm under soil substrate.
- Caching substrate may consist of soil, gravel, pumice, or duff.
- Selected sites for seed caching are both under forest canopy and on open terrain, the latter especially including steep, southerly slopes and recently burned areas.
- Nutcrackers transport seeds from a few meters to 12 km from parent trees.

The adaptations of whitebark pine for interaction with Clark's nutcrackers include large, wingless seeds, which provide nutcrackers an energy-rich food that is obtained efficiently (Fig. 2b) (Lanner and Gilbert 1994, Tomback 1978). Nutcrackers not only gain more nutrition per foraging effort compared to smaller conifer seeds but they also place the harvested seeds directly in their sublingual pouch without the need to remove the seed wings (Tomback 1978). The ripe seeds are retained in cones, which do not open, and seed release depends on nutcrackers. Furthermore, whitebark pine canopy morphology appears to make cones more visible and accessible to nutcrackers: the cones are horizontally-oriented on the tips of upwardly-directed branches (Tomback 1978, Lanner 1982).

Fig. 2. a. Clark's nutcracker, with a partially filled sublingual pouch, standing on a whitebark pine branchtip. b. Whitebark pine cones, Crater Lake National Park. (Photos: D.F. Tomback)

Seed dispersal by nutcrackers has important consequences for the distribution, successional status, growth form, and population genetic structure of whitebark pine (Tomback and Linhart 1990, Tomback 2001). Where whitebark pine grows is determined by the cache-site preferences of nutcrackers in conjunction with the environmental tolerances of whitebark pine seeds and seedlings. Whitebark pine seedlings are morphologically robust and tolerant of harsh sites (Arno and Hoff 1990, McCaughey and Tomback 2001). Nutcrackers cache whitebark pine seeds widely throughout the upper subalpine zone landscape (Box 1), but also within the treeline ecotone and above treeline, as well as below the lower elevational limit of whitebark pine. Consequently, whitebark can respond to climate warming or cooling with changes in elevational patterns of recruitment. Seed dispersal by nutcrackers after fire leads to rapid establishment and formation of early seral whitebark pine communities (Tomback et al. 2001a).

The population genetic structure of whitebark is influenced on multiple scales by nutcracker seed dispersal (Tomback 2001, Tomback 2005 for detailed overview). First of all, the tendency of nutcrackers to bury more than one seed per cache often results in a "tree cluster" growth form, comprising genetically distinct stems (resembling the tree in Fig. 1b) that tend to be genetic relatives (e.g., Rogers et al. 1999). Stems within clusters tend to be closely related to each other, because nutcrackers typically harvest many seeds from the same parent tree. This growth form leads to a clumped population dispersion pattern for whitebark pine. Furthermore, neighboring trees or tree clusters tend not to genetically related—a pattern that emerges when different nutcrackers cache seeds from different trees haphazardly within an area. On a regional scale, whitebark pine populations are not geographically genetically differentiated, possible because of long-distance seed dispersal by nutcrackers (e.g., Bruederle et al. 1998). On a rangewide scale, mitochondrial DNA haplotype distribution suggests how nutcrackers impacted whitebark pine migration from Pleistocene glacial refugia (Richardson et al. 2002a, 2002b). There are three distinct mitochondrial DNA haplotypes, each likely representing a Pleistocene refugium, and the boundaries between haplotypes appear to reflect geographical limits to seed dispersal by nutcrackers.

Whitebark pine as a foundation and keystone species: Why we are concerned about losing whitebark pine.

There is a growing recognition that single species may exert important influences that shape or define the character of entire ecosystems. These important species are considered *foundation species*: "A single species that defines much of the structure of a community by creating locally stable conditions for other species, and by modulating and stabilizing fundamental ecosystem processes" (Dayton 1972, cited in Ellison et al. 2005). Whitebark pine is an important foundation species, providing ecosystem services with respect to community development, watershed stability and hydrology, and treeline community development, as outlined below (Box 2). It may also be regarded as a *keystone species*, which by definition has greater effects on biodiversity than its abundance or density would suggest (e.g., Krebs 2001). Whitebark pine supports biodiversity in part through its large, nutritious seeds, which comprise an important wildlife food, but by also providing wildlife habitat especially at the highest elevations (Box 2). Whitebark pine seeds are high in fat (52% by weight) (Lanner and Gilbert 1994). At least 12 species of birds from five families and mammals from three families are known to feed on whitebark pine seeds—among them the black bear (*Ursus americanus*) and the grizzly bear (*Ursus arctos*), which usually obtain seeds by raiding the middens of red squirrels (*Tamiasciurus hudsonicus*) (Tomback and Kendall 2001). Whitebark pine seeds are a major food for grizzly bears in the Greater Yellowstone Area, and considered important for the long-term viability of the population (Mattson et al. 1992).

Box 2. The foundation and keystone roles of whitebark pine, based on overviews in Tomback and Kendall (2001) and Tomback et al. (2001b) and references therein unless noted otherwise.

- Broad geographic distribution and ecological tolerances lead to a wide array of community types (Arno 2001).
- Seeds are an important wildlife food.
- Found at the highest treeline elevations
- Most often initiates tree island formation in the northern Rocky Mountains (L.M. Resler and D. F. Tomback, unpublished data).
- Grows to the highest elevations in the treeline ecotone, providing wildlife habitat.
- Slows snow melt and run-off in the treeline ecotone (Farnes 1990).
- Reduces soil erosion at high elevations.
- Establishes rapidly after fire and other disturbances (Tomback et al. 20011).
- Tolerates harsh conditions after fire.
- Facilitates community development after disturbance.
- On harsh sites, acts as a "nurse" tree (Callaway 1998).

Losses of whitebark pine from watershed to regional scales thus results in diminished ecosystem services, altered community structure, including greater homogeneity of forests, and reduced carrying capacity for wildlife.

Why whitebark pine is declining

Three factors have caused widespread losses of whitebark pine: the spread and intensification of *Cronartium ribicola*, the introduced pathogen that causes white pine blister rust; recent mountain pine beetle (*Dendroctonus ponderosae*) upsurges; and the successional replacement of whitebark pine by more shade-tolerant species. The threat posed by each factor varies in importance geographically.

Cronartium ribicola, accidentally introduced to western North America in 1910, has spread nearly rangewide in whitebark pine (Fig. 3). The disease has a complex life cycle with five spore stages, requiring two hosts for completion of a cycle (e.g., McDonald and Hoff 2001). One host group, the “five-needled” white pines of subgenus *Strobus*, is perennially infected by the disease, producing aeciospores most years, which then infect alternate hosts. The alternate hosts, which grow new leaves each spring, comprise various species of the genus *Ribes* (Family Grossulariaceae) and, as recently discovered, the herbaceous species *Pedicularis racemosa* and *Castilleja miniata* (Family Orobanchaceae) (McDonald et al. 2006). Blister rust, growing on the leaves of alternate hosts, releases basidiospores in late summer, which start new infections on infected and uninfected pines. The fungus enters the stomates of pine needles and grows into the branch or stem of a tree, producing a sporulating canker within about 3 years.

Trees with blister rust disease are weakened and experience reduced radial growth (L. Daniels, personal communication). Blister rust cankers in the tree canopy kill branches and thus reduce or eliminate seed production years before the trees themselves succumb to the disease. Blister rust cankers that develop on stems usually girdle and kill the tree. However, a small number of trees within each population (< 5%) show genetic resistance to blister rust and are the basis for restoration strategies speeding up natural selection.

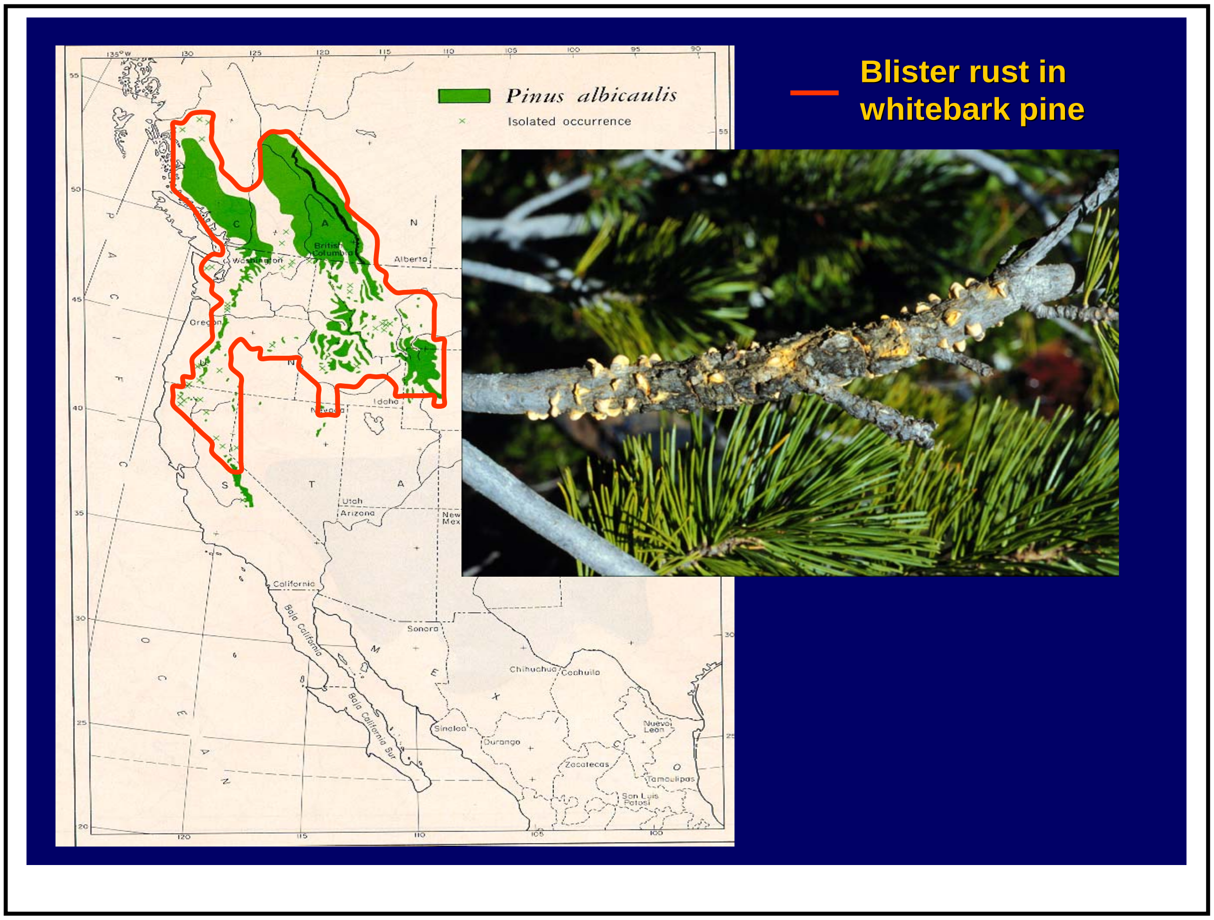

Fig. 3. Map showing the distribution of *Cronartium ribicola* within the range of whitebark pine (modified from Critchfield and Little 1966). Inset picture of a blister rust canker on a whitebark pine branch, with aeciospore sacs (Photo: D.F. Tomback)

Blister rust now infects whitebark pine nearly rangewide (Fig. 3), with the exception of the southern Sierra Nevada (P. Maloney and J. Dunlap, this proceedings) and several Great Basin ranges (J. Guyon, pers. commun.). The highest levels of blister rust infection, mortality, and canopy damage occur in the northern Rocky Mountains of the U.S., including western Montana, Glacier National Park, the Bob Marshall Wilderness Complex, and the Blackfeet Reservation, with average infection levels over 80% (e.g., Keane and Arno 1993; Keane et al. 1994; Kendall et al. 1996). Mean infection levels are now about 20 to 70% in most other regions, including the northernmost limits of whitebark pine's distribution (Schwandt 2006, D.F. Tomback and P. Achuff, unpublished data). Furthermore, as whitebark pine cone production diminishes, nutcracker numbers may decline, or the birds may avoid subalpine elevations, reducing the possibility of seed dispersal (Tomback and Kendall 2001). Blister rust alone has the potential to cause local, if not regional and even range-wide extirpation of whitebark pine in the absence of management support.

Currently, large-scale outbreaks of mountain pine beetles in whitebark pine are occurring in the northern Rocky Mountains and Intermountain Region of the United States—including areas where blister rust infection levels are high. In 2005 in the Greater Yellowstone Area, aerial flyovers indicated that nearly 720,000 whitebark pine trees had been killed by mountain pine beetles in 2004 (Gibson 2006). Upsurges in mountain pine beetle populations have occurred in the same regions in the past, leaving behind stands of old snags or "grey

ghosts" (e.g., Perkins and Swetnam 1996). These periodic outbreaks may be driven by higher temperatures, which are favorable to beetle development; this does not bode well for global warming trends (Logan and Powell 2001). With mountain pine beetles rapidly killing whitebark pine trees in many populations along with blister rust, the losses of whitebark pine are accelerating. Furthermore, mountain pine beetles are killing trees that are genetically resistant to blister rust.
The third threat to whitebark pine is successional replacement, possibly exacerbated by fire suppression. Studies in the northern Rocky Mountains and Intermountain region have documented shifts to late seral communities (e.g., Keane and Arno 1993, Murray et al. 2000). Historically, the landscape comprised a mosaic of different successional stages, maintaining relatively more whitebark pine than today.

Restoration—the last hope for whitebark pine

The challenge is to prevent local and even regional extirpation of whitebark pine where blister rust infection levels are high, and many trees have already been lost. A major restoration strategy is to speed up natural selection by planting genetically rust-resistant seedlings. The primary objective is to maintain whitebark pine on the landscape until genetic resistance to blister rust is well-distributed throughout populations.

This strategy requires that rust-resistant whitebark pine trees be identified and protected against mountain pine beetles, for example with verbenone pouches (e.g., Bentz et al. 2005), and cones collected to grow seedlings for outplanting. Genetic resistance in whitebark pine has been recently verified: Seedlings were grown from seed collections from 108 potentially rust-resistant whitebark pine trees in the Intermountain and Northern Rocky Mountain region and then screened for blister rust resistance. Overall, 48% of the parent trees demonstrated at least one genetic resistance mechanism (Mahalovich et al. 2006). Seedbed preparation through prescribed fire or thinning may be necessary prior to planting seedlings to reduce competition. Seedlings may also be planted in new and old burns, particularly in areas with little potential for natural whitebark pine regeneration. Direct seeding rather than planting seedlings may be a useful alternative technique that deserves further study, particularly for wilderness areas where disturbance must be minimized. Additional strategies include encouraging natural regeneration by creating "nutcracker openings" in mature forests, and using burning and thinning to reduce competitors of whitebark pine in late seral communities (Keane and Arno 2001).

Whitebark pine restoration is a multi-generational stewardship commitment that should be built into regional National Forest plans, with dependable funding. The goal is the spread of genetic resistance to blister rust throughout whitebark pine populations over time. Without management intervention, the losses of whitebark pine and also its high elevation relatives will have major consequences for western forest biodiversity. Collectively, the high elevation five-needled white pines represent a multiplicity of community types across broad environmental, elevational, topographic, and geographic spectrums. Losing this magnitude of biodiversity would be a national tragedy.

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