

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

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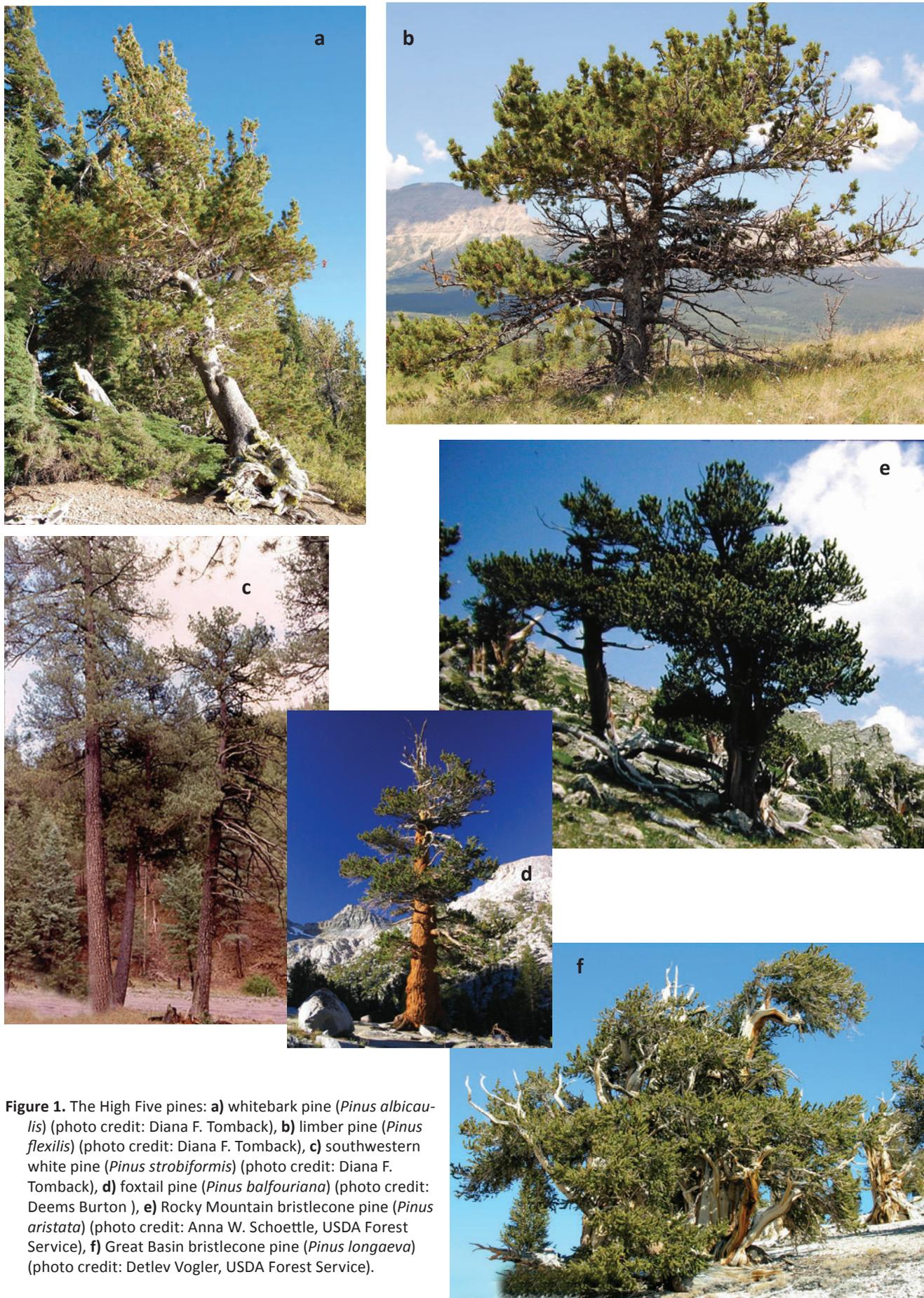
**Abstract**—The High Five symposium is devoted to exchanging information about a small group of pines with little commercial value but great importance to the ecology of high-mountain ecosystems of the West. These High Five pines include the subalpine and treeline species—whitebark (*Pinus albicaulis*),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

## Why the High Five Pines?

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

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

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



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

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

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

## Taxonomy and Distribution

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

### Taxonomy

The traditional classification of the High Five pines places whitebark pine in Section *Strobos*, Subsection *Cembrae*, as the only North American member of a taxon that otherwise comprises European and Asian species (Table 1). The *Cembrae* pines or stone pines were traditionally considered a monophyletic group with derived traits adapted to avian seed dispersal by the nutcrackers, Clark's (*Nucifraga columbiana*) and the Eurasian or Spotted nutcracker (*N. caryocatactes*).

Among these derived traits are indehiscent (non-opening) cones and relatively large, wingless seeds (Lanner 1990; Tomback and Linhart 1990; Price and others 1998). Limber and southwestern white pine, also traditionally classified in Section *Strobos* but in Subsection *Strobi*, are closely related species (Andresen and Steinhoff 1971). Both species have large, wingless seeds but cones that open when seeds have matured. The three "foxtail" pines, the Rocky Mountain and Great Basin bristlecones and foxtail, are considered distant relatives of the other pines and placed in Section *Parrya*, Subsection *Balfourianae*. The seeds of these species are small and winged and the cones open when seeds ripen—traits common for seed and cone morphology within the genus *Pinus* (Tomback and Linhart 1990).

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

### Distribution

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

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

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Genus <i>Pinus</i> L.
Subgenus <i>Strobos</i> Lemmon
Section <i>Parrya</i> Mayr (foxtail pines)
Subsection <i>Balfourianae</i> Engelm.
<b>Rocky Mountain bristlecone pine, <i>P. aristata</i> Engelm.</b>
<b>Foxtail pine, <i>P. balfouriana</i> Grev. &amp; Balf.</b>
<b>Great Basin bristlecone pine, <i>P. longaeva</i> D.K. Bailey</b>
Section <i>Strobos</i> (white pines)
Subsection <i>Strobi</i> Loudon
Mexican white pine, <i>P. ayacahuite</i> Ehrenb. ex Schltdl.
<b>Southwestern white pine, <i>P. strobiformis</i> Engelm.</b>
Chiapas white pine, <i>P. chiapensis</i> (Martínez) Andresen
<b>Limber pine, <i>P. flexilis</i> James</b>
Sugar pine, <i>P. lambertiana</i> Dougl.
Western white pine, <i>P. monticola</i> Dougl. ex D. Don
Eastern white pine, <i>P. strobus</i> L.
Subsection <i>Cembrae</i> Loudon (stone pines)
<b>Whitebark pine, <i>P. albicaulis</i> Engelm.</b>

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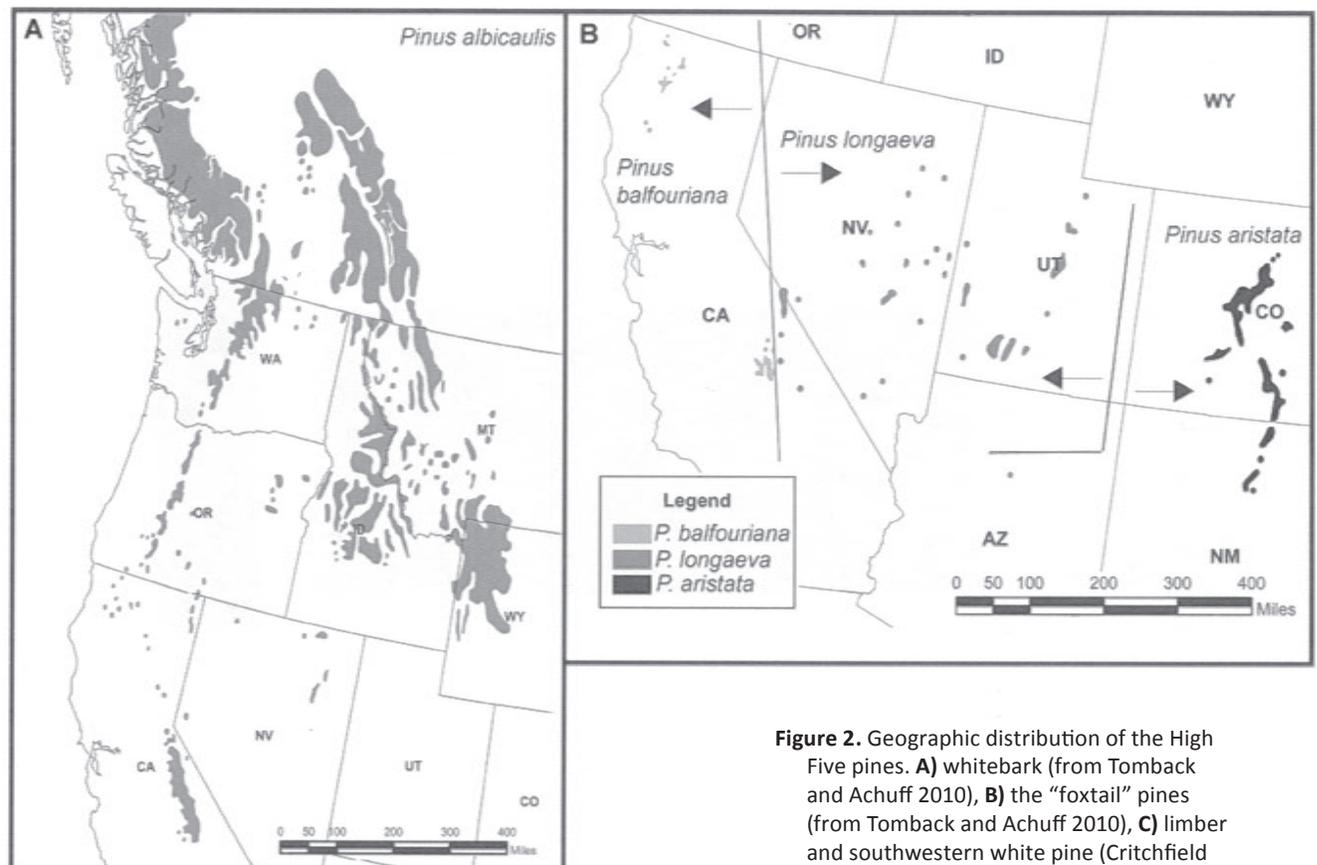
Whitebark pine has the largest geographic distribution of all U.S. and Canadian white pines, but the narrowest elevational limits, inhabiting only the upper subalpine forest zone up to the limits of treeline (Figure 2A, Table 2) (Arno and Hoff 1990; Tomback and Achuff 2010). Reflecting its tolerance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

Limber pine is nearly as broadly distributed as whitebark pine, but occurs at lower latitudes and over more arid regions, including the southern Sierra Nevada, southern California, the U.S. Southwest, the southern Rocky Mountains, and many Great Basin mountain ranges, occurring as far east as the Black Hills, South Dakota (Thilenius 1970; Steele 1990) (Figure 2C, Table 2). Farjon and Styles (1997) note that it has been collected in several locations in northern Mexico as well. Particularly noteworthy about limber pine is its broad elevational tolerance—broader perhaps than any other species within the Pinaceae. Within a given region, limber pine may occur at both lower and upper treeline and in patchy stands at all elevations in between (Steele 1990; Schoettle

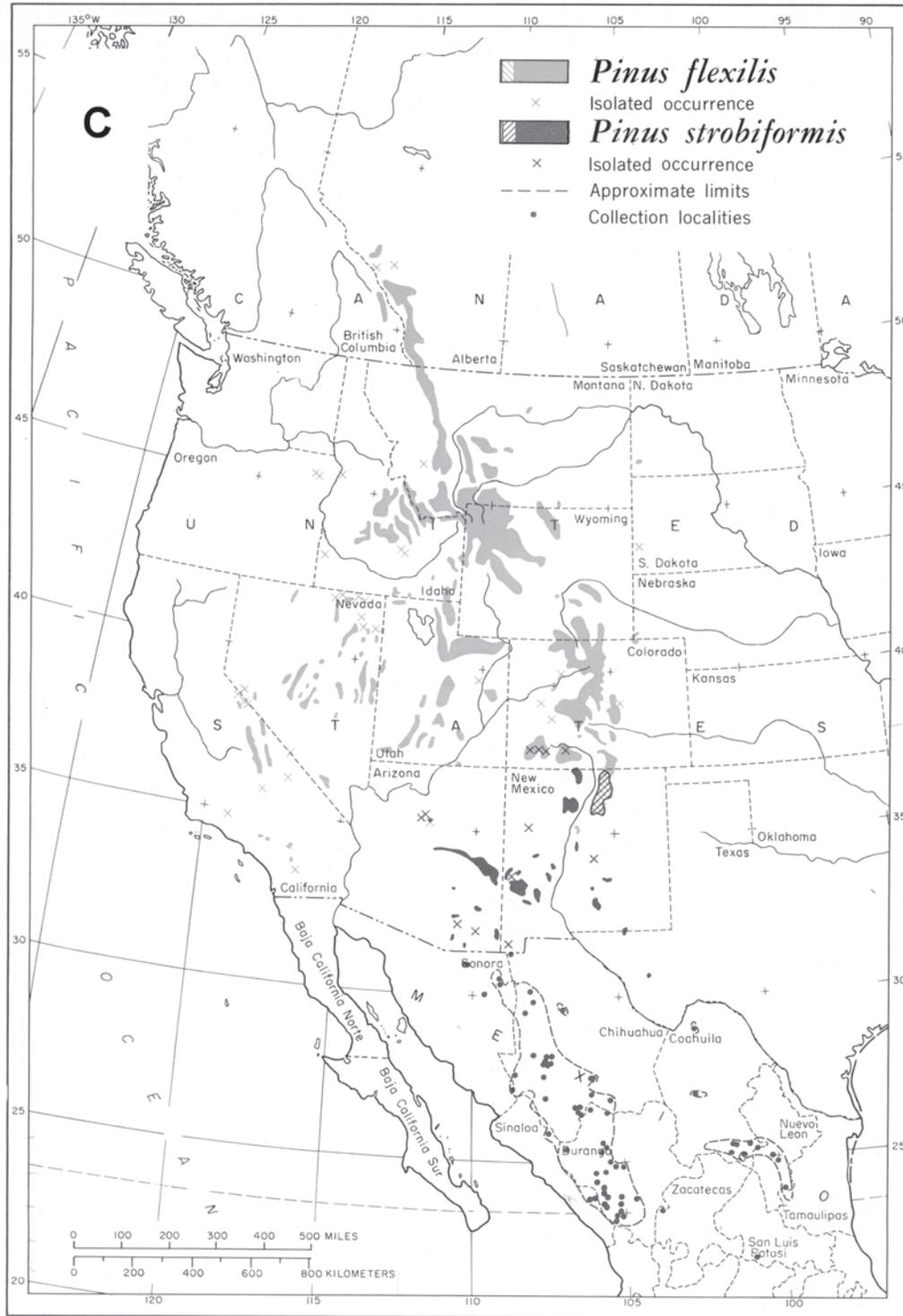
2004; Tomback and Achuff 2010). For example, on the eastern plains of southern Wyoming and northern Colorado, limber pine occurs as isolated populations on rocky escarpments at elevations of 1600 m or lower, and in the Front Range of Colorado from the lower montane forest zone up to treeline to 3300 m (Schuster and others 1995; Schoettle and Rochelle 2000). Throughout western Wyoming and along the eastern Rocky Mountain Front of Montana and southern Alberta, limber pine forms woodlands on arid foothills, ridges, and escarpments, but also occurs at subalpine and treeline elevations (Knight 1994; Achuff and others 2002; Resler and Tomback 2008).

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

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



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



Tertiary relics confined to high elevations,” and notes their extreme tolerance of low moisture and prolonged drought. Both foxtail pine and Rocky Mountain bristlecone pine have disjunct distributions. Foxtail pine occurs at subalpine and treeline elevations in the vicinity of Sequoia and Kings Canyon National Park and south to Olanche Peak in the southern Sierra Nevada but also in the Klamath Mountains of northern California (ca. 1700 to 2500 m elevation) (Mastrogiussepe 1972; Eckert and Sawyer 2002).

Both bristlecone pines have a wider elevational tolerance than foxtail pine. Rocky Mountain bristlecone pine occurs throughout much of Colorado and northern New Mexico, but a small population also occurs in northern Arizona; elevations range from about 2800 to 3600 m (Hawksworth and Bailey 1980). Great Basin bristlecone pine has the greatest elevational range, occurring from subalpine to treeline elevations (about 2300 to 3500 m) throughout the higher desert mountain ranges of the Great Basin.

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

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

## Community Ecology

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

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

### Whitebark Pine

Despite occurring within only a narrow elevational range, whitebark pine is found in a diversity of community types, and varies greatly within and across its range in prevalence, species composition, elevation, and successional status (Arno 2001 and references therein; Tomback and Kendall 2001). These different community types form in relation to climate

at a regional scale, but also in response to local factors, such as soil depth and bedrock type, or topography (Daubenmire 1968; Franklin and Dyrness 1973). Arno and Weaver (1990) note that “whitebark pine is abundant in regions having humid, snowy winters and long, dry periods in summer...” They further note that as summers become wetter at more northerly latitudes, whitebark pine abundance decreases.

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

Fire is the primary disturbance factor that renews seral whitebark pine communities. Fire regimes in whitebark pine communities are complex, and range from small, localized fires and low intensity burns caused by lightning strikes in treeline and extremely harsh upper subalpine sites to mixed-severity burns to stand-replacing fires (Tomback 1986; Arno 2001; Keane 2001; Walsh 2005). Fire return-intervals vary with a number of factors, including ignition frequency, drought frequency, local topography, forest structure, and

forest composition. Steep terrain with heterogeneous forest structure and available fuels tend to support mixed-severity burns, and large expanses of continuous subalpine forest tend to support stand-replacing burns (Arno 2001). Overall, the mean fire return intervals for whitebark pine communities range from about 30 to 400 years (Table 4-5 in Arno 2001). Regeneration of recently burned areas may occur fairly rapidly as a result of seed dispersal by Clark's nutcracker, depending on proximity and health of seed sources, local snow depth, and moisture availability (Tomback and others 1990; Tomback and others 1993; Tomback and others 2001b).

### **Limber Pine**

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

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

achieved maximum ages of less than 200 years, whereas the oldest trees from upper treeline had ages greater than 1500 years.

### **Southwestern White Pine**

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

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

### **Foxtail Pine**

Foxtail pine, which has a disjunct distribution in California, comprises a minor to major species in upper subalpine and treeline communities of both its northern and southern populations (for overviews, see Bailey 1970; Mastrogioseppe and Mastrogioseppe 1980; Eckert and Sawyer 2002; Tomback and Achuff 2010). Although all three pines in the *Balfourianae* tolerate poorly developed soils, wind, and prolonged drought, foxtail pine grows under the most mesic conditions. Foxtail pine appears to be shade-intolerant at all life stages, occurs on a variety of substrates, and grows at high elevations on slopes and ridges. In the Klamath Mountains, which experience a maritime climate, foxtail pine occurs on all slope aspects, principally in mixed conifer forests on south- and west-facing slopes. The pine dominates west-facing slopes and commonly associates with red fir (*Abies magnifica*), Jeffrey (*Pinus jeffreyi*), lodgepole (*Pinus contorta*), and whitebark pine. On

ridgetops, it associates with mountain hemlock (*Tsuga mertensiana*), western white pine (*Pinus monticola*), and red fir, which are all restricted to the northern and eastern aspects with deeper soils and snowpack (Mastrogiuseppe 1972). Foxtail pine communities in more northern stands include montane zone conifers such as Douglas-fir, white fir, and incense cedar (*Calocedrus decurrens*) (Mastrogiuseppe 1972; Mastrogiuseppe and Mastrogiuseppe 1980; Eckert and Sawyer 2002).

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

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

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

### **Rocky Mountain Bristlecone Pine**

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

Within the southern Rocky Mountains, bristlecone pine typically grows on igneous and volcanic soils on steep, south-facing slopes at elevations between 2,750 and 3,670 m (Hawksworth and Bailey 1980; Baker 1992). The maximum ages attained are about 2,400 years (Brunstein and

Yamaguchi 1992). Ancient trees are found on extremely arid sites, such as bedrock, talus slopes, south-facing slopes, and in small stands separated from larger forested areas. These individuals are protected from fire by isolation and sparse fuels.

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

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

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

### **Great Basin Bristlecone Pine**

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

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

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

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

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

## Seed Dispersal

Within the genus *Pinus* there is much variation in seed size, seed and wing morphology, cone size, and cone morphology. Seed size alone varies by two orders of magnitude—for example, the differences in seed mass averages

of 0.0035 g for jack pine (*Pinus banksiana*) and 0.9072 g for Torrey pine (*Pinus torreyana*) (Table 3 in Tomback and Linhart 1990). The various morphologies of cone and seed traits are assumed to be the product of selection for effective seed dispersal, given the constraints of taxonomy, life history, and environmental conditions (Tomback and Linhart 1990; Keeley and Zedler 1998; Lanner 1998). However, seed dispersal from cones by wind appears to be the ancestral condition within the genus *Pinus*, and among species of the Pinaceae in general (for example, Lanner 1980).

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

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

### ***Pines Dependent on Nutcrackers for Primary Seed Dispersal***

#### **Whitebark pine**

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

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

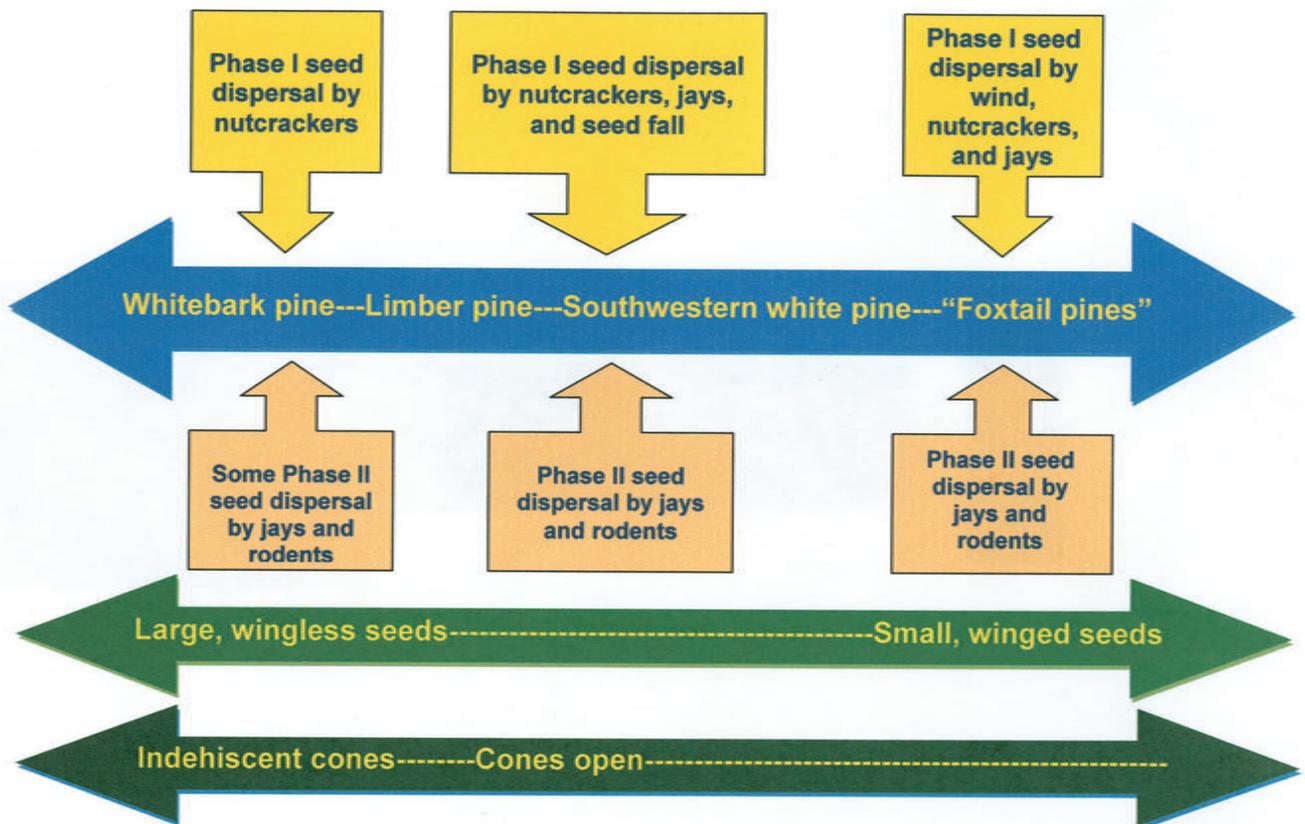
Species	Mean seed mass (g)	Seed wing	Cones open	Phase I seed dispersal <sup>1</sup>	Phase II seed dispersal <sup>2</sup>
Whitebark	0.157 <sup>b</sup> 0.099 <sup>b</sup>	No <sup>3</sup>	No	Nutcrackers	Rodents, jays?
Limber	0.093 <sup>a</sup> 0.085 <sup>d</sup>	No <sup>3</sup>	Yes	Nutcrackers, jays, seed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

<sup>1</sup> Phase I seed dispersal refers to mode of dispersal of seeds from cones.

<sup>2</sup> Phase II seed dispersal refers to mode of seed movement from substrate or cache to final "safe site."

<sup>3</sup> For a small proportion of trees, seeds bear short seed wing remnants.

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



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



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

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

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

Pine squirrels compete with nutcrackers for pine seeds. In mid-summer, they efficiently cut down the cones of nearly all

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

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

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

buried caches (Tillman-Sutela and others 2008). Buried seeds may be stimulated to germinate by snowmelt and summer precipitation, leading to regeneration (Sidebar) (Tomback 1982; McCaughey 1990).

Steller's jays (*Cyanocitta stelleri*) harvest and cache whitebark pine seeds to a limited extent: they cannot open closed cones, and have not been observed caching seeds in the ground in whitebark pine communities (Hutchins and Lanner 1982). At this time, it is not known to what extent cached nutcracker seeds might be pilfered by mice and

squirrels and either consumed or re-cached, which would constitute Phase II seed dispersal (Figure 4). Caches are likely to be less prone to discovery if well-dispersed and in harsh, wind-swept sites, open terrain, rocky ledges, and in volcanic substrates, where rodent populations may be sparse, and where many whitebark pine communities grow. Regardless, nutcrackers as dispersers determine where and how far seeds are moved from source trees; secondary dispersers move seeds locally.

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## Sidebar: What Is A Nutcracker Worth—In Dollars?

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

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

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

- 1) Although multiple seed sources are used to maintain genetic diversity, here we base the costs on obtaining seeds from one tree only. It is typical to place 30 cone cages per tree, each cage protecting a whorl of cones. One tree would thus produce an excess of the seeds needed to plant 440 seedlings.
- 2) Maturing cones require protection from foraging nutcrackers and pine squirrels. These calculations assume that cages for protecting cones are already available.
- 3) Parent trees known to be genetically resistant or potentially resistant to the blister rust pathogen are protected from mountain pine beetle with applications of verbenone or carbaryl, but this is not included in cost calculations.
- 4) Also, costs of identifying and screening parent trees, travel and transportation, and cone storage are not included.

### Estimated costs:

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

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

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

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## Limber pine

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

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

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

Seed fall leads to Phase II or secondary seed dispersal in limber pine. The population genetic structure of limber pine, discussed below, provides evidence that Phase I seed dispersal by nutcrackers is more important in core populations than gravity dispersal. Although not studied specifically for limber pine seeds within the core range, diurnal secondary

dispersers, including Steller's jays, chipmunks, and golden-mantled ground squirrels (*Spermophilus lateralis*), forage on the forest floor for conifer seeds and then distribute the seeds within caches, which may lead to seedling production (Breindel 2000; Samano and Tomback 2003; Vander Wall 1992). Nocturnal seed dispersers, especially deer mice (*Peromyscus maniculatus*) harvest and cache pine seeds as well, including large, wingless seeds (Vander Wall 1997; Vander Wall 2003). Because larger pine seeds are preferred by rodents, it is likely that limber pine seeds are harvested and cached by secondary dispersers (Vander Wall 2008). Secondary seed dispersal tends to be over much shorter distances than nutcracker seed dispersal—for example, within about 60 m of seed sources (Vander Wall 1992).

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

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

### How seed dispersal by nutcrackers impacts pine ecology and population biology

Seed dispersal by Clark's nutcrackers has profoundly influenced the ecology, population genetic structure, and distribution of both whitebark and limber pine (for overview for whitebark pine, see Tomback 2005): 1) Nutcracker selection of topography and location for seed caching, coupled with the environmental requirements of whitebark and limber pine seeds for germination and seedling survival, determine where trees grow (Lanner 1980; Tomback 1982; Tomback and Linhart 1990). 2) After fire or other disturbance, nutcrackers will cache seeds in open terrain, leading to the pioneering status of both whitebark and limber pine (Lanner and Vander Wall 1980; Tomback and others 2001b). 3) Seedlings originating within a whitebark or limber pine seed cache may produce a "tree cluster" growth form—a multi-genet cluster of trunks, often composed of siblings, contiguous or fused at the base (Linhart and Tomback 1985; Carsey and Tomback 1994; Rogers and others 1999). This is a common growth form in both whitebark and limber pine

on harsher sites, and represents a highly “clumped” population dispersion pattern. 4) Long distance seed dispersal by nutcrackers results in lower than expected genetic differentiation among neighboring and regional populations (Schuster and others 1989; Jorgensen and Hamrick 1997; Rogers and others 1999; Bruederle and others 2001). 5) Seed dispersal by nutcrackers enabled whitebark and limber pine to migrate out of refugia following the retreat of Pleistocene glaciers. Nutcracker seed dispersal along mountain corridors, and limits to dispersal, may explain current range-wide population structure of mitochondrial DNA haplotypes (Mitton and others 2000; Richardson and others 2002a,b).

### ***Pines With Mixed Seed Dispersal Strategies***

#### **Southwestern white pine**

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

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

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

proceedings) determined that cones in the Chiricahua Mountains were more frequently pendulous in orientation than in the San Juan Mountains, and had larger seeds.

#### **The “foxtail pines”**

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

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

## **Ecological Importance**

### ***Foundation and Keystone Functions***

A foundation species is viewed as “A single species that defines much of the structure of a community by creating locally stable conditions for other species, and by modulating and stabilizing fundamental ecosystem processes” (Dayton 1972 cited in Ellison and others 2005). Keystone species influence community diversity to a greater extent than predicted by their abundance or through their interactions with

other species (for example, Mills and others 1993; Soulé and others 2003). Whitebark pine has been regarded as both a foundation and keystone species in subalpine and treeline ecosystems with influences on biodiversity that transcend its elevational range (Tomback and others 2001a; Ellison and others 2005; Tomback and Achuff 2010). These ecological roles result primarily from four characteristics of whitebark pine: large, nutritious seeds; seed dispersal by nutcrackers; hardy, robust seedlings; and high tolerance for cold and extremely windy sites (McKinney and Tomback 2011). The other high-elevation five-needle white pines share some or all of these traits and thus serve to varying degrees as foundation and keystone species.

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

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

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

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

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

### **Ecosystem Services**

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

### **Native American Use of the High Five Pines**

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

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

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

*Limber pine*

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

**Medicinal uses***Limber pine*

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

*Rocky Mountain bristlecone pine*

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

**Ceremonial uses***Limber pine*

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

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

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

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

### ***Aesthetics: the High-Mountain Experience***

All the high-elevation white pines may be found on extremely harsh sites—on steep, rocky slopes, ridges, and canyon walls—with wind-sculpted irregular or flagged crowns. But, southwestern white pine may also grow as a magnificent, tall and full-crowned old-growth tree on favorable sites. Under the harshest conditions, whitebark, limber, and the foxtail pines assume massive, gnarled, bark-stripped forms with twisted wood—forms that are the product of a millennium or more of survival under adverse conditions (Tomback and Achuff 2010). The progressive loss of bark

on the stout trunks, known as cambial die-back, eventually leaves isolated strips of live bark surrounded by exposed, weathered wood, supporting remnant canopies (Tang and others 1999; Schauer and others 2001; Bunn and others 2003). Visitors to high elevations may perceive these trees as ‘survivors’ and symbolic of perpetual struggle. The snags of the dead “warriors” are frequently photographed by hikers.

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

### **Threats**

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

### White Pine Blister Rust

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

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

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

Whitebark pine is infested by blister rust to varying degrees throughout its distribution in both the U.S. and Canada, up to the pine's northern limits, again with the exception of interior Great Basin ranges (Tomback and Achuff 2010; Schwandt and others 2010). The highest incidence of blister rust infection is in the northern U.S. and southern Canadian Rocky Mountains, and particularly in the Northern Continental Divide Ecosystem (Northern Divide), which includes the Bob Marshall Wilderness Area, and Glacier and Waterton Lakes National Parks (for example, Kendall and Keane 2001; Smith and others 2008). Throughout the Northwestern U.S. and Northern Divide, infection levels in some stands may range as high as 90 to 100 percent. Even within the more xeric regions, such as the Greater Yellowstone, incidence of blister rust appears to be increasing during this past decade (GYWPMWG 2010).

As whitebark pine experiences more damage and mortality, cone production declines within stands. In the Northern Divide, the extensive and widespread loss of whitebark pine has greatly diminished the functional roles and ecosystem services provided by the pine. With reduced cone production, red squirrels harvest most available cones, and Clark's nutcrackers may not reliably visit stands to harvest and cache seeds (Smith and others 2008; McKinney and Tomback 2007; McKinney and others 2009). Thus, whitebark pine regeneration may be greatly reduced.

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

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

### Mountain Pine Beetle

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

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

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

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

### **Fire Exclusion**

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

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

Whitebark pine has experienced altered fire frequencies since the late 1800s, particularly in some areas of the central and northern Rocky Mountains (Morgan and Bunting 1990; Keane and Arno 1993; Murray and others 2000; Murray 1998; for overview, see Tomback and Achuff 2010). However, Walsh (2005) found no evidence for suppression after compiling fire histories from stands from multiple locations in the Greater Yellowstone Area. It is also likely that

subalpine forests with long fire return intervals may not yet be outside their historical range of variability (Agee 1993; Chappell and Agee 1996).

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

### **Climate Change**

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

A number of bioclimatic models, also referred to as “niche-based” models have recently been used to predict the distribution of white pine species under different temperature scenarios (Hamann and Wang 2006; McKenny and others 2007; Warwell and others 2007; Schrag and others 2008). In general, these models predict shifts to higher elevations and more northern latitudes, with losses of lower elevation and more southern populations (Tomback and Achuff 2010). According to interpretation of these models, forest tree species have the option of three responses, or possibly a combination within a species, to rapidly changing climate: migration to track their niches, adaptation in current distributions to changing conditions, or population extirpation (Aitken and others 2008). However, niche-based models produce coarse-scale predictions, not incorporating information on topographic variation within regions, potentially leading to persistence, or species-specific ecological or phenological processes that affect survival, such as timing

of bud-break or flowering or the requirements for seedling germination and survival or mediation of response to climate through other processes or interactions, such as damage and mortality from blister rust and fire (Tomback and Resler 2007; Keane and others 2008; Morin and Thuiller 2009; Chuine 2010; Loehman and Keane, these proceedings). The high elevation white pines are among the most vulnerable species to climate change, because of little area to support these pines above current treeline, patchy and isolated “sky island” populations without ‘migration corridors,’ stressed southern populations, and, especially, current forest health challenges from the blister rust pathogen, mountain pine beetle outbreaks, and advancing succession from fire suppression. The velocity of climate change within montane landscapes, however, is predicted to be comparatively slow because of steep and complex topography. Plants may be able to keep pace with change based on historic rates of migration (Loarie and others 2009).

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

## Conservation Status of the High Five Pines

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

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

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

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

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

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

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

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

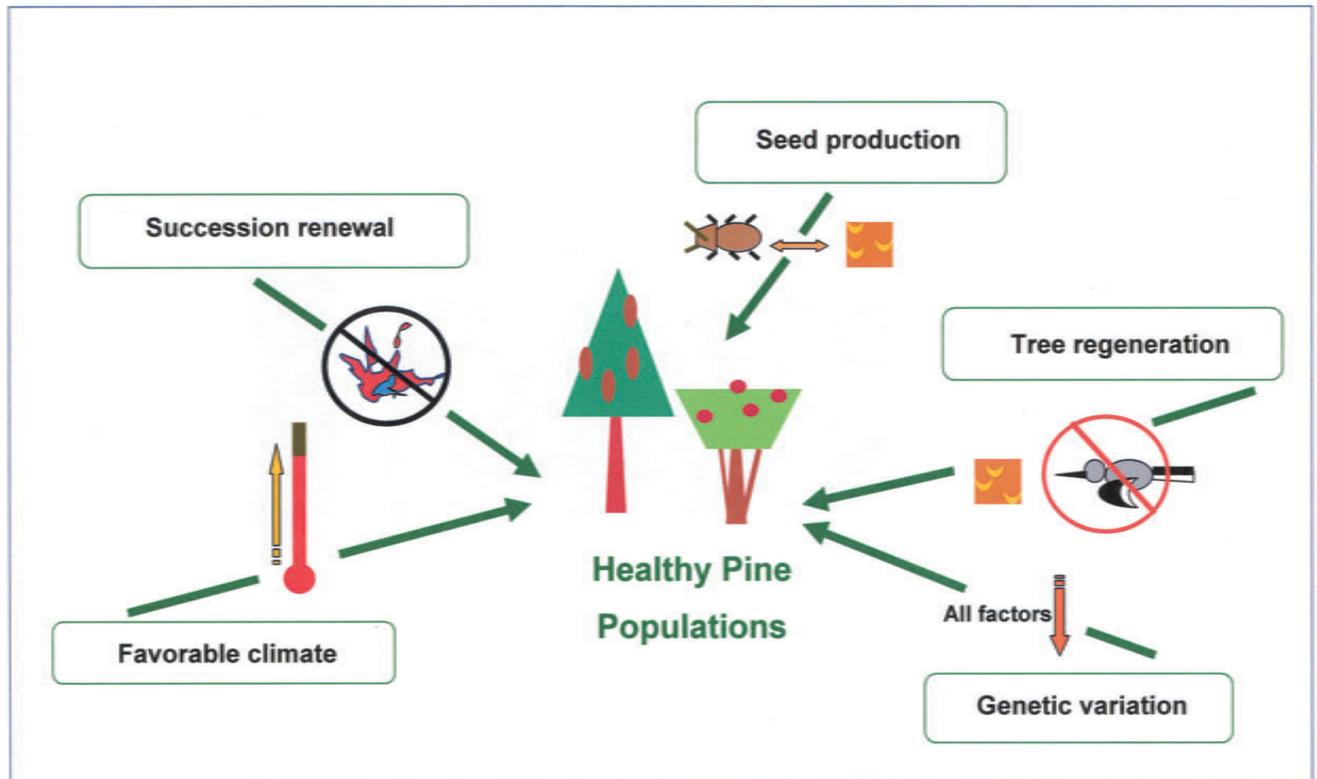
Southwestern white pine is considered to be of *Least Concern* by IUCN and to be *Secure* globally and nationally in the USA by NatureServe. It is *Not Ranked* in the four states in which it occurs. Foxtail pine is considered *Conservation Dependent* by the IUCN and *Secure* both globally and in the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

states. Great Basin bristlecone pine is ranked as *Vulnerable* by the IUCN but *Secure* both globally and nationally in the U.S. by NatureServe. Two states rank this pine as *Vulnerable* and it is *Not Ranked* in one state.

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

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

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



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

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

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

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

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