Mountain Pine Beetle Impacts in High-Elevation Five-Needle Pines: Current Trends and Challenges

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On the cover:

Mountain pine beetle-caused mortality in whitebark pine, Yellowstone National Park, 2004 (Ken Gibson, USFS)

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EXECUTIVE SUMMARY

Present Conditions

High-elevation five-needle pines, keystone species in fragile ecosystems throughout western North America, are being beset by changing climates, the introduction of non-native pests, and the reduction of naturally occurring fires. Bark beetles and diseases are threatening tree species growing in these ecosystems; the most serious short-term threat is a native insect, the mountain pine beetle. While not unprecedented, mountain pine beetle populations in high-elevation, five-needle pine stands are presently at higher levels than previously recorded. In most stands throughout the West, populations have increased dramatically within the past 8-10 years, infesting more than 1.2 million acres and killing as many as six million five-needle pines. We anticipate beetle populations will remain high as long as weather conditions are conducive to beetle survival and/or until most mature host trees have been killed.

Reducing Beetle-Caused Mortality

Management efforts to reduce beetle-caused mortality in these ecosystems are largely untried or infeasible. Individual trees can be protected from attack by using insecticides or bark beetle pheromones. More long-term efforts to reduce beetle-caused impacts on these sites are largely undeveloped and unknown.

Unanswered Questions

Mountain pine beetles pose significant short-term threats to mature host trees on high-elevation sites. Unfortunately, an even more insidious long-term threat is posed by the introduced pathogen that causes white pine blister rust. This disease, in combination with mountain pine beetles, threatens the sustainability of five-needle pine communities. Blister rust affects all aspects of the forest regeneration process and will impair ecosystem recovery long after the current beetle epidemic is over (Schoettle and Sniezko 2007). Restoration efforts underway to combat the effects of white pine blister rust and other threats may well benefit stands striving to overcome the effects of mountain pine beetle. At the very least, efforts should be integrated to foster improved forest health in these often-delicate ecosystems.

Critical to the success of lessening impacts from mountain pine beetle will be finding answers to the following questions.

- How do mountain pine beetle life cycles vary from low to high elevations throughout its range?
- How might we better assess overall impacts of the beetle on hosts on these sites and on associated resources?
- What constitutes "high-hazard" conditions for beetle outbreaks in these stands?

- What is the role of natural or prescribed fire in maintaining healthful forest conditions on these sites; and how does excessive beetle-caused mortality influence fire behavior?
- Might genetic studies underway for blister rust resistance also explore genetic resistance to bark beetles?
- How does white pine blister rust alter stand susceptibility to mountain pine beetle?
- Can silvicultural intervention improve forest recovery after a beetle epidemic and mitigate the effects of the next one?

Much remains to be done before we will significantly reduce beetle-caused mortality in the short term, facilitate recovery after the current outbreak is over, and help reduce impacts of future ones on these high-elevation sites. Most of those challenges are beyond the scope of this paper. Still, we are confident that united and multi-disciplined efforts can and will preserve these critical, keystone species.

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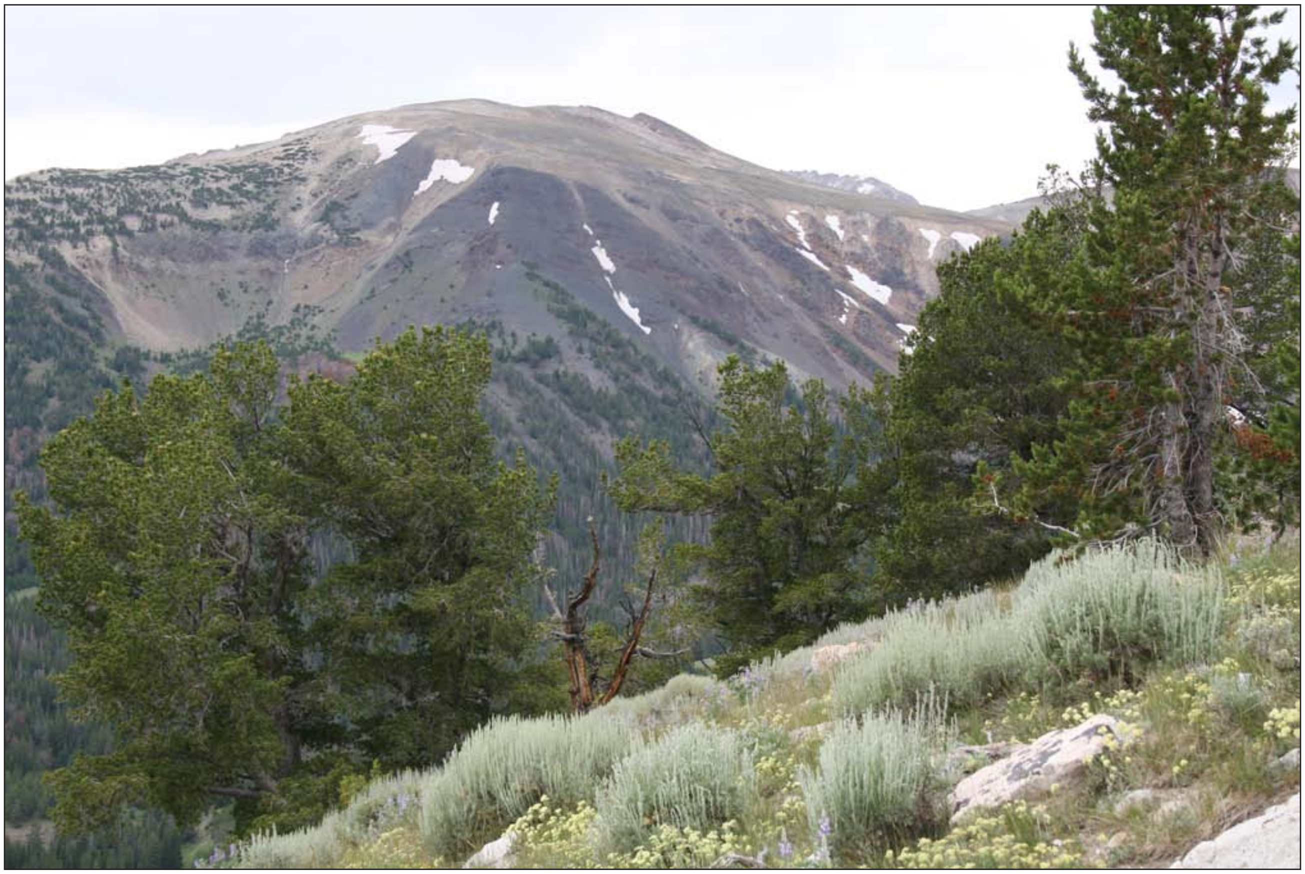

Sandy Kegley, USDA Forest Service

INTRODUCTION

A diverse group of five-needle pines native to western North America have captured the imagination of many for being long-lived and thriving in what can be considered harsh environmental conditions. These pines include whitebark pine (*Pinus albacaulis* Engelm.), limber pine (*P. flexilis* James), foxtail pine (*P. balfouriana* Grev. & Balf.), Rocky Mountain bristlecone pine (*P. aristata* Engelm.), and Great Basin bristlecone pine (*P. longaeva* Bailey). These pine species provide important ecosystem services in high-elevation settings (Schoettle 2004), including stabilizing soil, improving snow retention, pioneering revegetation of alpine and subalpine sites following fire, providing resources and cover for wildlife, and facilitating the establishment by other tree species associated with these white pines (Rebertus et al. 1991, Baumeister and Callaway 2006). In this report, we focus on five species of five-needle pines and present information on tree mortality trends caused by mountain pine beetles. We also discuss challenges and opportunities facing forest managers that, when adequately addressed, will help ensure these pine species remain an integral part of high-elevation landscapes.

MOUNTAIN PINE BEETLE

Mountain pine beetle (MPB), *Dendroctonus ponderosae* Hopkins (Figure 1), kills more pines throughout its range than all other insect pests combined. Mortality experienced during periodic outbreaks recorded over the past one hundred years has devastated host stands in many parts of the United States and Canada.

Ryan Bracewell, USDA FS

Figure 1. Mountain pine beetle adult (*Dendroctonus ponderosae*).

Currently, MPB populations are at outbreak levels across much of western North America. In 2007, more than four million forested acres were infested to some extent in the United States, and another 50 million acres have been impacted in western Canada. Approximately 85 percent of these beetle-killed trees have been lodgepole pine; however, many high-elevation five-needle pines have been killed as well.

Nearly six million high-elevation five-needle pines have been killed by MPB in the United States over the past five years. Whitebark pines on almost half a million acres and other five-needle pines on 124,000 acres were killed by MPB in 2007 alone (Figure 2). These are the highest levels of MPB-caused whitebark pine mortality ever recorded. In some stands, more than 160 whitebark pines per acre have been killed during the past three years; this extreme level of mortality represents over 90 percent of the trees greater than five inches diameter-at-breast-height (DBH) in those stands (Region 1 FHP, unpublished data).

The current MPB epidemic is likely to continue to intensify and expand over the next several years barring severely cold temperatures that could cause high levels of larval mortality. Depletion of suitable host trees will also result in local reductions of MPB populations. Warmer-than-normal temperatures increase susceptibility of high-elevation host trees via drought stress and increase survival of MPB. Mild winters, warmer and drier summers, and highly susceptible stands create ideal conditions for MPB population expansion. Present conditions appear to be similar to those that created high-elevation "ghost forests" in the mid- to late-1930s (Ciesla and Furniss 1975, Logan and Powell 2001).

Ken Gibson, USDA Forest Service

Figure 2. Whitebark pine killed by mountain pine beetle, Yellowstone National Park, 2004.

High levels of MPB-caused pine mortality are not unprecedented. During the first 30 years of the 1900s, MPB ravaged many pine stands in the western United States. In 1905, MPB survey and management efforts were implemented in the U.S. concentrating on merchantable stands of lodgepole and western white pine. High-elevation pines, usually considered unmerchantable, were not easily surveyed and not reported to the same extent. However, significant MPB infestations in whitebark and limber pines were reported during that period.

Figure 3. Battling a mountain pine beetle infestation, Yellowstone National Park ca. 1930. Image provided by Mal Furniss.

During the winter of 1932-1933, considerable beetle mortality was reported in Montana, eastern Idaho, and Yellowstone National Park (Figure 3). On the Beaverhead National Forest, MPB-killed trees were reduced from over 17 million in 1932 to little more than 900,000 in 1933. However, beetle-killing temperatures were not uniform throughout the region: the Targhee National Forest reported an unexpected increase in infestation the same year (Evenden 1933).

By the end of the 1930s and into the early 1940s, many national forests reported low-level MPB infestations. At the time, many believed the collapse of the historic MPB outbreak was "no doubt due largely to the near exhaustion of host material" (1935 Intermountain Region Forester Annual Letter to the Chief). An interesting observation, attributed to A.L. Gibson (1939), lends an historical perspective: "Losses in whitebark pine have been general over the entire forest and heavy in some areas. While the loss of this timber from an aesthetic and watershed protection standpoint would be regrettable, if our present surmise that mountain pine beetle outbreaks may 'boil over' into adjoining lodgepole pine stands when they reach a certain status is correct, the elimination of mature whitebark pine might remove a menace to lodgepole pine stands." His musings likely do not reflect current sentiment with regard to whitebark pine elimination.

LIFE CYCLE OF MOUNTAIN PINE BEETLE

MPB have four life stages: egg, larva, pupa, and adult. Development occurs in the phloem under the bark of host trees. Female beetles initiate attack, enter the inner bark, attract mates, and then construct vertical egg galleries parallel with the wood grain in the phloem. After mating, eggs are laid in niches along the sides of the galleries. Following egg hatch, larvae feed in the phloem, mining perpendicular to parent galleries (Figure 4). At maturity, larvae pupate and then emerge as adults to initiate new attacks. Development time varies by location and is primarily dependent upon temperature.

In low-elevation lodgepole pine forests, attack to adult emergence generally takes one year. In higher elevations and in more northern latitudes, two years may be required to complete development. Extremely cold winter temperatures can kill developing brood, though most MPB larvae are relatively cold-hardy. There have been occasional reports of MPB outbreaks subsiding, at least in part, due to extreme cold winter temperatures (Evenden 1934, Evenden

Figure 4. Mountain pine beetle brood and galleries in whitebark pine.

and Gibson 1940, Lessard et al. 1987). In high-elevation stands, beetle mortality in winter may be minimal due to relatively thicker bark and deep snow that insulate overwintering larvae (Gibson 1935a). Colder-than-normal temperatures during summer and fall can delay beetle development, forcing a large proportion of the population to enter the winter as eggs and early instar larvae—life stages that are especially vulnerable to subfreezing conditions (Amman 1973). In addition, unusually cold temperatures in the fall and spring months can be lethal when beetle life stages are not yet adapted to cold temperatures (Bentz and Mullins 1999).

Some beetles developing in whitebark pine can emerge in one year while others, including some from the same trees, emerge in two years (Bentz and Schen-Langenheim 2007). One- and two-year life cycles were also reported during the warm years between 1931-1934 (Gibson 1935a). MPB populations in lodgepole pine stands at elevations between 8,700 and 9,900 feet in 2004 in the central Rocky Mountains typcially completed their life cycle in one year (Tishmack et al. 2005). Bentz and Schen-Langenheim (2007) found that, at one site at 9,500 ft elevation in central Idaho, 40 percent of beetles completed their life cycle in one year while 60 percent took two years. Summer temperatures were important in determining one- or two-year development times. Warmer than average temperatures, particularly during the summer, appeared to shorten the time interval required for beetles to complete development.

Flight period of MPB varies by host species. Based on the few studies that have monitored beetle activity at high elevations, MPB flights occur earlier in whitebark pine stands than lower elevation lodgepole pine. In addition, beetle emergence at high-elevation whitebark pine sites occurred over a 60-day period, whereas emergence occurred within a 14-day period at low elevation lodgepole pine (Bentz and Schen-Langenheim 2007). An extended flight period is not atypical for MPB and is also known to occur in beetles emerging from western white pine (*Pinus monticola* Dougl.) (DeLeon et al. 1934).

EFFECTS OF CLIMATE ON MOUNTAIN PINE BEETLE AND ITS HIGH-ELEVATION HOSTS

MPB are native to high-elevation pine stands (Figure 5), and outbreaks have been recorded throughout history. Beetle remains found in lake sediments dating back to the Holocene (around 8,000 years ago) may indicate epidemic populations occurred during a period that was cooler and wetter than present (Brunelle et al. 2008). More recently, MPB outbreaks have occurred during periods of warmer-than-average temperatures and drought. For example, during the unusually warm, dry years of the late 1920s and early 1930s (NOAA 2006), there is evidence of large MPB outbreaks in whitebark pine in Idaho, Montana, and Yellowstone National Park (Gibson 1935b, Evenden 1944, Perkins and Swetnam 1996, Furniss and Renkin 2003). In recent years, MPB has expanded its range into more northern latitudes and higher elevations—areas previously thought to be climatically unsuitable for beetle outbreaks (Carroll et al. 2003). The extent of more recent outbreaks in high-elevation forests over the past 10 years has been attributed, at least in part, to warmer-than-normal temperatures (Bentz and Schen-Langenheim 2007).

Bob Oakes, USDA Forest Service

Figure 5. Whitebark pine killed by mountain pine beetle.

Currently, stand conditions in conjunction with warmer temperatures and drought have left high-elevation five-needle pine forests more susceptible to successful MPB attack. Implicating factors in the increase of mortality in these stands include longer periods when conifers are in summer drought, an associated decline in host vigor and defensive chemicals, and more favorable conditions for MPB survival and development.

HIGH-ELEVATION FIVE-NEEDLE PINES AND THEIR SUSCEPTIBILITY TO MOUNTAIN PINE BEETLE

All five-needle pines are suitable hosts for MPB (Furniss and Carolin 1977, Wood 1982). In laboratory studies, limber pine (Figure 6) was been shown to be more favorable for MPB development, survival, and brood production than lodgepole pine (Cerezke 1995, Langor 1989, Langor et al. 1990); and whitebark pine yielded more beetles than lodgepole pine in a study by Amman (1982). In one field study, MPB selected whitebark pine more often than lodgepole pine (Bockino 2007). Current Rocky Mountain bristlecone pine mortality is attributed to MPB. MPB has not been confirmed in the recently killed Great Basin bristlecone pines reported in Nevada; however, it is the most-likely culprit. MPB-caused mortality in foxtail pines has only recently been reported (Kliejunas and Dunlap 2007).

Ken Gibson, USDA Forest Service

Figure 6. Limber pine killed by mountain pine beetle, Yellowstone National Park.

During their analysis of tree mortality during the 1970–1985 MPB epidemic in the northern Rocky Mountains, Bartos and Gibson (1990) found that MPB prefers larger-diameter whitebark pine trees. Perkins and Swetnam (1996) reported a similar preference for large-diameter trees after examining whitebark pine mortality following the 1908 – 1940 mountain pine beetle outbreak in the Sawtooth-Salmon Region of Idaho. In addition to tree diameter, Perkins and Roberts (2003) also found that basal area per acre, trees per acre, and number of stems in a tree cluster were significant predictors of tree attack.

STATUS OF CURRENT MPB OUTBREAKS

Mortality of high-elevation, five-needle pines across western North America (Figure 7) has been increasing significantly for the past several years (Figure 8). These MPB epidemics began at different times in different regions, beginning 10-12 years ago.

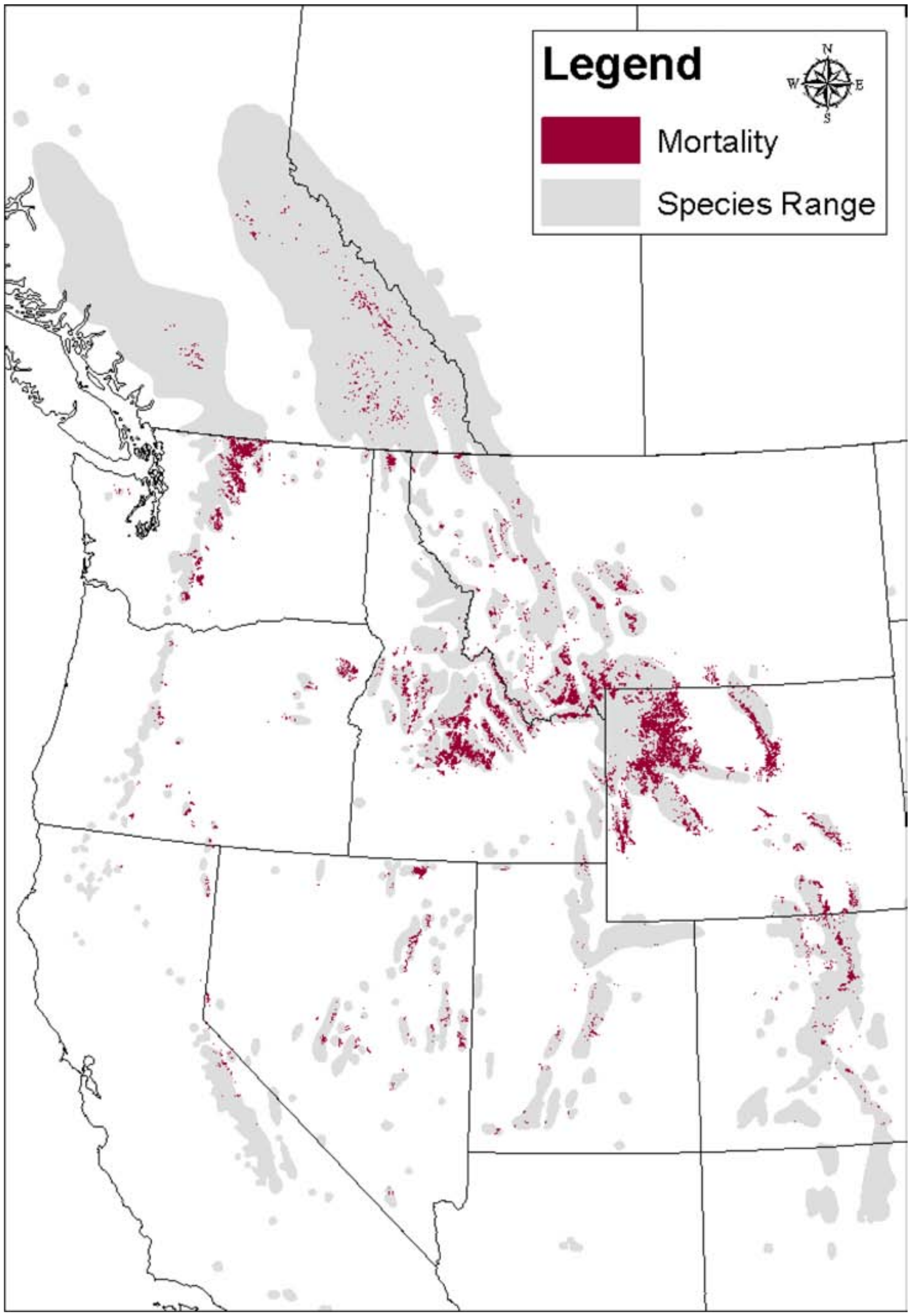

Figure 7. MPB-caused mortality of four pine species (whitebark, limber, Rocky Mountain bristlecone, and Great Basin bristlecone) in the western United States (1998-2007 ADS) and British Columbia (2006-2007) throughout the distributions of these tree species (United States Geological Survey).

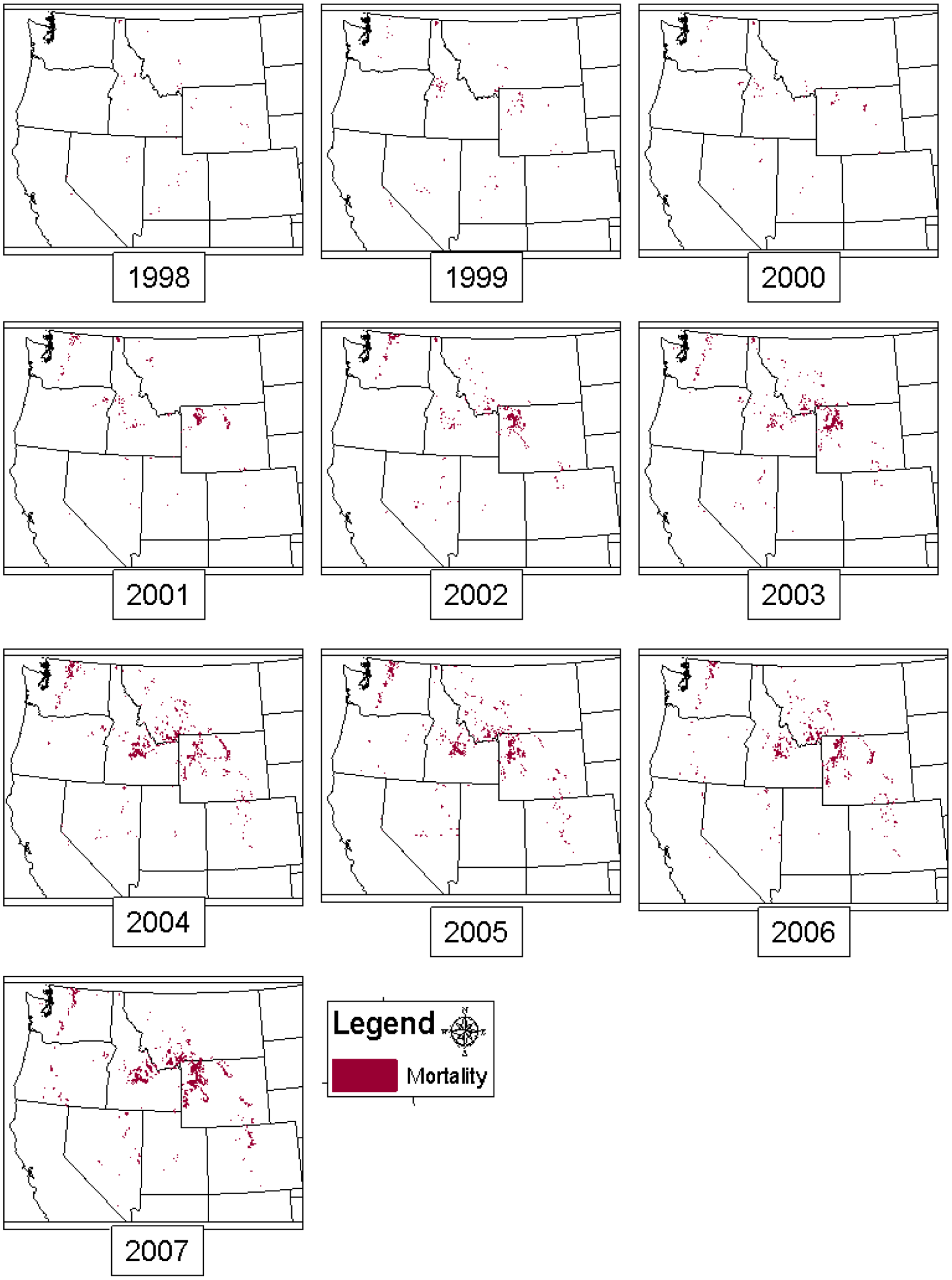

Figure 8. MPB-caused mortality of five pine species (whitebark, limber, Rocky Mountain bristlecone, Great Basis bristlecone, and foxtail pines), 1998-2007 (ADS).

AERIAL DETECTION SURVEYS

Forest health personnel perform aerial detection surveys (ADS) over western forests of all ownerships to assess biotic and abiotic impacts. These surveys are intended to detect new insect activity, monitor trends of current outbreaks, provide general location information, and subjectively estimate levels of defoliation and mortality. These data provide estimates of mortality by tree species; however, not all forested acres are flown annually. ADS techniques and disclaimers can be found in “Aerial Detection Survey Accuracy Assessment” (http://www.fs.fed.us/r1-r4/spf/fhp/aerial/gisdata.html).

ADS data from 1998–2007 was used to describe recent mortality trends of five pine species: whitebark, limber, Rocky Mountain bristlecone, Great Basin bristlecone, and foxtail pines. Numbers of acres of bark beetle-caused mortality in each of these tree species were estimated for California, Colorado, Idaho, Montana, Nevada, Oregon, Utah, Washington, and Wyoming. Numbers of trees killed per acre vary markedly and are not available for every surveyed area.

Most forest stands experience continued mortality for many consecutive years, with some host trees being killed each year. Cumulative acres of mortality (Figure 9) reflects the total number of acres affected over the entire period 1998-2007, not the sum of each years’ affected acres: this avoids recounting the same acres experiencing additional mortality each year. However, some forests contain more than one susceptible host species, such as those containing both whitebark and limber pine: acres of mortality may include acres counted twice to account for mortality in each species separately.

GROUND PLOT SURVEYS

Permanent or yearly plots to collect impact data have been installed in a few locations. These have been helpful in monitoring changes in tree health of high-elevation pines. Many of these areas are not routinely surveyed from the air, and ground plots provide a more accurate estimate of local conditions, including number of dead trees, cause of death, and presence of other damage agents.

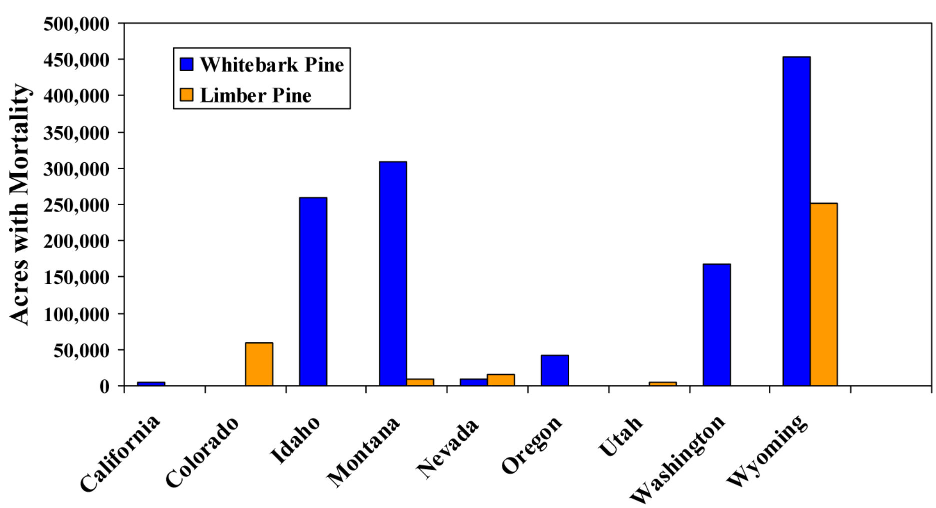

Figure 9. Cumulative acres that include whitebark and limber pine trees killed by MPB reported in each of nine western states by aerial detection survey from 1998-2007).

Conditions by Host Type

Whitebark pine. The number of acres with whitebark pine mortality far exceeds that of any other five-needle pine species and has been increasing for the past 10 years (Figure 10). Mortality of whitebark pine has been recorded in each of the nine western states reported here, with Idaho, Montana, and Wyoming having the greatest number of affected acres (see Figure 9). Whitebark pine mortality began to increase in Idaho and Wyoming in 1999 and in Montana in 2002 (Table 1). The number of acres with reported mortality approximately doubled in these states from 2003 to 2004 and has continued to increase in subsequent years. In Washington State, whitebark pine mortality increased dramatically between 1999 and 2002 and has remained at high levels. In Oregon, whitebark pine mortality increased later and fewer acres were affected.

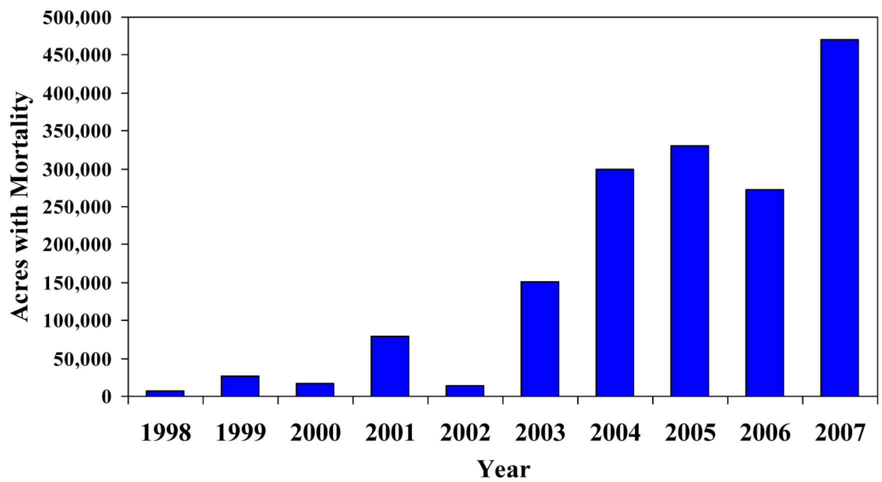

Figure 10. Total acres with MPB-killed whitebark pine each year (1998-2007 ADS) in California, Idaho, Montana, Nevada, Oregon, Washington, and Wyoming.

Table 1. Acres with MPB-killed whitebark pine in nine western states (1998-2007 ADS).

State	Years									
	1998	1999	2000	2001	2002	2003	2004	2005	2006	2007
California	100	0	0	0	200	200	100	80	1,600	3,100
Colorado	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A
Idaho	4,200	13,200	12,100	25,600	22,900	32,900	67,100	51,800	44,700	85,400*
Montana	2,400	8,600	200	1,000	32,400	62,500	102,000	108,000	118,000	117,000*
Nevada	30	0	0	0	0	10	700	400	2,800	6,400
Oregon	0	0	1,100	3,900	60	3,100	5,700	3,000	11,400	21,700
Utah	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A
Washington	200	3,000	2,500	15,000	32,800	22,500	35,400	38,400	23,800	31,800
Wyoming	400	1,400	1,500	33,400	49,200	30,100	89,600	129,000	70,700	205,000*
Total Acres	7,330	26,200	17,400	78,900	137,560	151,310	300,600	330,680	273,000	470,400

* includes acres that are classified as "high-elevation five-needle pine"
'N/A' indicates that whitebark pine is not found in these states

The outbreak is less severe but increasing in California. While more than 60 percent of 49 ground plots established in California since 2004 had some level of MPB activity, overall mortality levels on the plots were low (less than 1 percent) (Kliejunas and Dunlap 2007; Dunlap and Maloney, unpublished data). In plots with MPB evidence, the percentage of beetle-attacked trees ranged from 2 to 32 percent. A greater proportion of plots from the Eldorado National Forest to Yosemite National Park had MPB evidence than plots further south in the Sierra Nevada Range (Dunlap and Maloney, unpublished data).

On ground plots from five different locations in northern Idaho, whitebark pine mortality caused by MPB ranged from 15 to 90 percent. Mature whitebark pine with average diameter at breast height of 14 to 20 inches were killed by the beetles (Kegley et al. 2004). Ground-collected data from the past four field seasons in Montana and Yellowstone National Park (10 to 30 variable-radius plots from selected locations each year) show extreme amounts of MPB-caused mortality in some whitebark pine stands. Mortality ranged from 38 to 96 percent of the trees over 5 inches DBH. In one stand in Yellowstone National Park, more than 160 whitebark pines per acre—92 percent of the trees equal to or greater than 5 inches DBH—have been killed in this recent outbreak (Region 1 FHP, unpublished data).

Limber pine. Acres with limber pine mortality have been increasing steadily for the past 10 years (Figure 11 and Table 2). California and Idaho reported the least number of acres with limber pine mortality; Colorado and Wyoming reported the most (see Figure 9). Mortality of limber pine throughout northern and central Colorado (Figure 8) began to increase in 2002, with a noticeable increase in 2007 (Table 2). In Wyoming, limber pine mortality is primarily in the south central and western portions of the state. The level of limber pine mortality scattered throughout high elevations of Utah and Nevada has been relatively constant for the past 10 years. In Montana, limber pine mortality on the eastern slope of the Rocky Mountains increased somewhat in 2003 but has since decreased.

Fourteen ground plots in limber pine were installed in California from 2004 to 2005 (Kliejunas and Dunlap 2007). No tree mortality caused by MPB was detected in those plots. Millar et al. (2007) studied three disjunct limber pine stands on the Inyo National Forest in California: these stands experienced high levels (50 to 75 percent) of tree mortality in the late-1980 to 1990s. This period of time corresponded with a state-wide protracted low-precipitation period in areas where conifer mortality was extremely high in the Sierra Nevada Range; the mortality was attributed to drought, stocking levels,

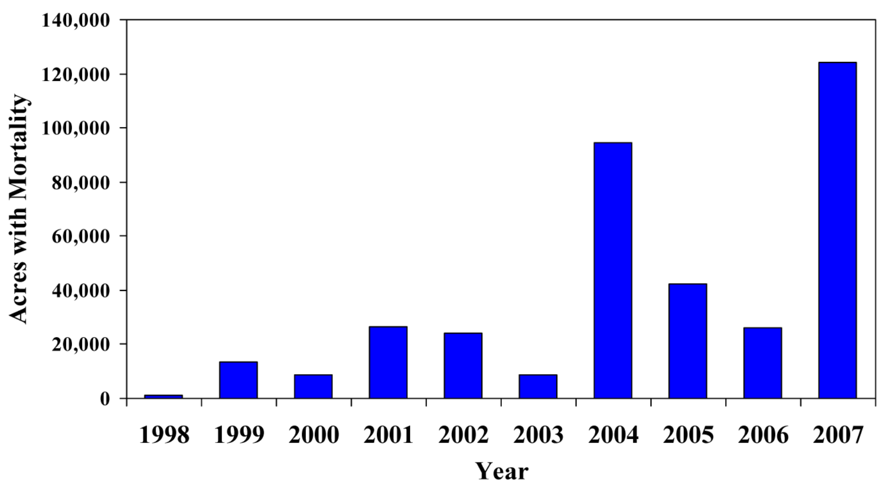

Figure 11. Total acres with MPB-killed limber pine each year (1998-2007 ADS) in California, Colorado, Idaho, Montana, Nevada, Oregon, Utah, and Wyoming.

Table 2. Acres with MPB-killed limber pine in nine western states (1998-2007 ADS).

STATE	YEARS									
	1998	1999	2000	2001	2002	2003	2004	2005	2006	2007
California	0	200	100	200	0	0	0	0	0	0
Colorado	100	200	100	300	1,300	0	4,800	4,200	3,900	48,100
Idaho	0	0	0	0	20	0	0	30	200	60
Montana	0	0	60	30	500	6,300	1,600	1,400	200	*
Nevada	200	1,500	800	1,500	2,800	2,200	3,100	1,800	600	1,600
Oregon	0	0	0	0	0	0	0	0	0	0
Utah	600	1,100	300	700	200	300	500	300	170	1,000
Washington	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A
Wyoming	200	10,400	7,200	23,600	19,300	0	84,400	34,600	21,000	73,000
Total Acres	1,100	13,400	8,560	26,330	24,120	8,800	94,400	42,330	26,070	123,760

* may be included in acres that are classified as "high-elevation five-needle pine" in Table 1
N/A indicates that limber pine is not found in these states

and mountain pine beetle. The authors concluded that, although mortality levels were high during the protracted drought event in the 1980s, thinning improved stand resilience and mortality events such as this were not necessarily detrimental to long-term forest health.

Rocky Mountain bristlecone pine. Mortality of Rocky Mountain bristlecone pine was detected in three non-sequential years, with an increase in acres for 2007 (ADS). All recorded mortality took place in Colorado in 2002 (900 acres), 2004 (4,400 acres), and 2007 (46,500 acres). None of this mortality occurred in pure bristlecone pine stands but was part of general mortality in stands with a mix of Rocky Mountain bristlecone pine, limber pine, and lodgepole pine. Bristlecone pine mortality was observed throughout central Colorado from the high-elevation sites west of Boulder south to the northern end of the San Luis Valley.

Great Basin bristlecone pine. Mortality of Great Basin bristlecone pine has been detected during the past three years, including 100 acres in 2005, 60 acres in 2006, and 300 acres in 2007 (ADS). This mortality has all occurred on the east side of central Nevada in the Snake Mountain Range and in Great Basin National Park. Five ground plots on the Inyo National Forest and in Death Valley National Park showed no evidence of MPB activity (Kliejunas and Dunlap 2007).

Foxtail pine. No foxtail pine mortality has been detected by ADS. Twelve ground plots, six each in the northern and southern occurrences of California's foxtail pine, were installed between 2004 and 2005 (Kliejunas and Dunlap 2007). Two of the six northern plots had some level of MPB activity, and recently increasing levels of MPB-caused tree mortality was detected near some of the northern plots. Evidence of MPB was not found in any of the southern plots.

Conditions by State

California. Whitebark pine mortality has been increasing in California over the past few years. Most of the mortality is in the Warner mountain range in the northeastern part of the state and on the north slope of Mt. Shasta. Current levels of mortality in foxtail, limber, and Great Basin bristlecone pines are low. Root disease is known to be killing Great Basin bristlecone pines on the Inyo National Forest.

Colorado. Limber pine mortality has been increasing in scattered patches along the spine of the Rocky Mountains in central Colorado (see Table 2 and Figure 9). The largest areas with mortality were reported in 2007 in north central Colorado along the Continental Divide west of Denver. Mortality of Rocky Mountain bristlecone pine was not reported until 2002, but the number of affected acres has increased dramatically since then.

Idaho. Whitebark pine mortality began increasing in northern Idaho in 1999 and across central Idaho in 2002 (see Table 1 and Figure 8). The most widespread mortality was reported in the Selkirk Mountains of northern Idaho and in southern Idaho from the Sawtooth, Boulder-White Clouds, Pioneer, Salmon River, Lost River, and Lemhi mountains east to the Montana border near Dubois. An estimated 843,000 acres of potential whitebark pine habitat are in designated wilderness areas in Idaho (Keane 2000). These wilderness areas are not surveyed by ADS; therefore, MPB-caused mortality information is lacking for those forests. However, expectations are that MPB-caused mortality rates in wilderness areas are similar to those of other whitebark pine stands. In far southeastern Idaho where limber pine is the dominant five-needle pine, MPB-caused limber pine mortality is increasing with building MPB populations.

Montana. In the late 1990s, Montana had only small, scattered groups of MPB-caused mortality in whitebark and limber pine (see Figure 8). By 2001, beetle populations began to spread throughout the ranges of these hosts. Heaviest mortality was seen in the southwest corner of the state, north and northwest of Yellowstone National Park. In 2007, mortality of individual five-needle pine species was not recorded but recorded as five-needle pine group. Most of this mortality was likely whitebark pine. Currently, whitebark pine stands and some limber pine stands throughout central Montana are also heavily infested with MPB.

Nevada. Nevada has experienced continuing, patchy mortality of limber pines on high ridge tops throughout the state (see Table 2 and Figure 8). Whitebark pine mortality has increased during the last two years (see Table 1), particularly in the northwestern corner of the state. In 2006 and 2007, mortality of Great Basin bristlecone pine in the Snake Range and Great Basin National Park on the eastern edge of Nevada was detected by aerial survey.

Oregon. Whitebark pine mortality was low throughout Oregon between 1998 and 2005 (see Table 1). Mortality increased in the last two years but is still confined to small, scattered groups of trees (see Figure 8). Whitebark pine mortality occur along the ridge of the Cascade Range and in the northeast corner of the state.

Utah. Limber pine mortality has been reported at consistent and notable levels during the past 10 years (see Table 2), and is distributed throughout high elevations of Utah's mountain ranges (see Figure 8). This mortality is distributed throughout high elevations of Utah's mountain ranges (see Figure 8). Whitebark pine is not known to exist in the state. No Great Basin bristlecone pine mortality attributable to MPB has been observed in Utah.

Washington. Mortality of whitebark pines increased in Washington between 1999 and 2001 and has been at consistently high levels since 2002 (see Table 1). Mortality is almost exclusively along the eastern side of the Cascade Mountains throughout the entire range where whitebark pines are found. MPB-caused mortality is particularly extensive in northern Washington (see Figures 7 and 8).

Wyoming. Some of the most extensive areas of whitebark and limber pine mortality are in Wyoming (see Figure 7 and Table 1). Mortality was reported throughout the host ranges in the late 1990s, but the number of acres of mortality increased dramatically in 2001 (see Tables 1 and 2). Acres with whitebark and limber pine mortality have been very high for the last five years. In the 2007 survey of Yellowstone National Park, mortality of individual five-needle pine species was not recorded separately but was lumped together into a five-needle pine group. Most of this mortality is likely whitebark pine mortality, based on the previous years' survey results, and was represented here as such.

British Columbia, Canada. MPB-caused tree mortality in lodgepole pine stands has been at unprecedented levels across British Columbia during the past decade. Most of this mortality has been in lodgepole pine; however, aerial surveys have recorded the species of affected trees only in the last two years. In 2006 and 2007, whitebark pine was killed on 21,800 and 35,200 acres, respectively (Westfall and Ebata 2007). Mortality was observed on the east side of British Columbia in the Rocky Mountains, with higher amounts in the Coast Range (see Figure 7).

OTHER AGENTS OF CHANGE AT HIGH-ELEVATION SITES

White Pine Blister Rust

White pine blister rust, caused by *Cronartium ribicola* J. C. Fisch., an invasive fungal pathogen that infects five-needle pines, has become established throughout most of the ranges of all five-needle pines in this report. The fungus (Figure 12) is contributing to increased losses in whitebark pine and limber pine in the northern and central Rocky Mountains in particular (Figure 13). Blister rust rapidly kills smaller trees and is responsible for losses of most natural regeneration in many places (Schwandt 2006).

Sandy Kegley, USDA Forest Serv.

Figure 12. Sporulating white pine blister rust.

Some populations of Rocky Mountain bristlecone pine have recently been infected (Blodgett and Sullivan 2004). However, white pine blister rust has not been confirmed on Great Basin bristlecone pine in California, Nevada, or Utah.

Sandy Kegley, USDA Forest Service

Figure 13. Whitebark pine with top-kill caused by white pine blister rust.

Schwandt (2006) presents a detailed account of threats posed by white pine blister rust to the survival of whitebark pine and described challenges and opportunities in restoration efforts presently facing resource managers. Many of the issues and concerns surrounding long-term species survival are similar in the wake of high levels of MPB-caused tree mortality in most high-elevation five-needle pines. Both MPB and blister rust reduce seed availability for reforestation and therefore may impair forest recovery (Schoettle and Sniezko 2007).

Secondary Bark Beetles

Secondary bark beetle species, such as *Pityogenes* spp. and *Ips* spp., are often found in the branches and boles of five-needle pines attacked by MPB and in smaller trees stressed by drought, injury, or disease (Figure 14). These secondary bark beetle populations may also build with increasing MPB populations. Rarely do these secondary beetles attack healthy five-needle pine regeneration; *Ips woodi* Thatcher attacks and infests smaller limber pines in southern Wyoming that are stressed by drought and/or severely infected with white pine blister rust. The biology of these secondary bark beetles is generally not well known (Wood 1982).


Sandy Kegley, USDA Forest Serv.

Figure 14. Galleries made by secondary bark beetles in whitebark pine.

Climate Change

Increasing temperatures are noticeably affecting MPB activity in some areas (Carroll et al. 2003). Changes in MPB population dynamics are associated with higher temperatures during summer and absence of lower-than-normal temperatures during winter. A complete discussion of these changes is outside the scope of this publication.

Westerling et al. (2006) noted that warming conditions contribute to increased wildfire activity in western United States. The same features associated with wildfire frequency—earlier snowmelt, higher summer temperatures, longer fire seasons, and an expanded vulnerable area of high-elevation forests—are factors that also may contribute to increasing MPB-caused mortality in high-elevation five-needle pines. Drought, in conjunction with increasing temperatures, also affects tree condition and may be associated with increased populations of MPB.

MANAGEMENT ALTERNATIVES TO REDUCE BEETLE-CAUSED TREE MORTALITY

Approaches to forestall or reduce MPB-caused tree mortality have covered a broad spectrum. Efforts by forest entomologists in the early part of the twentieth century were aimed largely at killing beetles: infested trees were peeled, piled and burned, and treated with insecticides—or an array of those treatments in combination—for more than 50 years. Eventually recognizing the futility in trying to kill beetles directly, entomologists and silviculturists began to consider other approaches to managing forest stands to reduce beetle-caused tree mortality. Before long, they recognized that higher numbers of beetle-killed trees were associated with certain stand conditions.

By the 1970s, it became apparent that highly susceptible lodgepole and ponderosa pine stands shared similar characteristics: generally, they were larger-diameter, older trees in more densely stocked stands (Amman et al. 1977). That recognition led to thinning studies and ultimately to management recommendations directed at altering stand conditions to reduce susceptibility to beetle attack and tree mortality to more acceptable levels (McGregor et al. 1987). Current recommendations include reducing stand stocking to levels that promote vigorous tree growth and result in more-open conditions that beetles find less desirable (Safranyik and Wilson 2006). Creating a mosaic of age and size classes and promoting species diversity where feasible have proven successful at lowering the levels of tree mortality for some forest types.

Historically, silvicultural manipulation in high-elevation pine stands has been very limited. It is largely unknown how reducing tree density would affect tree health or MPB outbreaks in these areas. In lodgepole and ponderosa pine stands, reducing stand susceptibility through sanitation and green tree thinning can do much to lessen subsequent beetle-caused tree mortality over the longer term. However, such treatments in high-elevation stands may be impractical, ineffective, or yield unanticipated results. Studies suggest the use of prescribed burns or "prescribed" natural fires may successfully reduce stand susceptibility (Figure 15). Re-introduction of fire on these sites may also provide a basis for restoration efforts in stands already adversely impacted by beetles and/or white pine blister rust (Keane 2000).

Bob Keane, USDA Forest Service

Figure 15. Use of fire in five-needle pine stands to enhance restoration efforts.

As genetic-based restoration programs are developed and implemented to foster or enhance blister rust resistance in high-elevation five-needle pines, it will be even more critical to prevent MPB attacks on older, cone-bearing trees (Schwandt 2006).

Short-term treatments, such as insecticide applications, are very successful in preventing attacks on individual trees (Gibson and Bennett 1985, Fettig et al. 2006) but may not be feasible in many high-elevation locations. Other methods, such as the use of the MPB anti-aggregative pheromone, verbenone (trimethyl-bicyclo-heptenone), have been shown to prevent MPB attacks on individual trees (Bentz et al. 2005, Kegley et al. 2003, Kegley and Gibson 2004) (Figure 16). Verbenone has been less efficacious in other situations but may be the only option available in many areas.

Sandy Kegley, USDA Forest Serv.

Figure 16. Verbenone pouches placed to protect a whitebark pine.

PRESENT CHALLENGES AND OPPORTUNITIES FOR REDUCING MPB-CAUSED MORTALITY

MPB-caused mortality can be devastating to high-elevation, five-needle pine stands. Numbers of acres harboring beetle-killed trees are at or near record-setting levels in many areas in western North America. Relatively conservative estimates suggest that nearly one million five-needle pines have been killed by MPB in the western United States in each of the past several years. Mortality of that magnitude has severely impacted many sites directly and has affected restoration efforts being implemented to offset the combined effects of MPB, white pine blister rust, fire exclusion, and climate change. Unquestionably, we need long-term solutions to maintain and restore pines in these delicate high-elevation sites. However, short-term treatments that protect mature, cone-bearing trees will increase future management options and restoration efforts.

Short-Term Preventive Measures

Individual-Tree Treatment. Insecticide applications on individual trees are the most efficacious preventive treatment available. Carbaryl insecticide, applied at its registered rate of 2 percent active ingredient in a water-based spray, provides nearly 100 percent protection of treated trees for up to two years (Gibson and Bennett 1985). Recently, success has been exhibited with synthetic pyrethroid insecticides, but they usually only afford one year of protection (Fettig et al. 2006). Limited treatments in whitebark pine have also been effective.

Where insecticidal treatments are feasible, they would be the short-term treatment of choice. Where they are not feasible—and that may often be the case on many fragile and inaccessible sites—the only other currently available treatment is the application of anti-aggregation pheromones. While treatment effects can be variable and less efficacious when beetle populations are high, verbenone was found to protect 80 percent or more of individually treated whitebark pines for one year (Kegley et al. 2003, Kegley and Gibson 2004). Site assessments should be conducted prior to application to determine the need and likelihood of success.

Area-Wide Treatment. Some reductions in tree mortality have been obtained by applying verbenone across small areas (Bentz et al. 2005, Progar 2003). Product labels (dependent upon manufacturer) suggest small-area (greater than a couple of acres) protection may be achieved by using a minimum of 20 pouches per acre (maximum 60 pouches per acre) in a grid pattern throughout the treatment area. Favorable results have been obtained with 20 pouches per acre (Bentz et al. 2005) and 40 per acre (Progar 2003); other tests have had less-than-satisfactory results despite similar application rates (Progar 2005). Most area-protection efforts have been carried out in lodgepole pine stands. Aerial application of verbenone for area protection is being evaluated. Success of any area-protection program will likely be dependent upon beetle populations, tree species, and site and stand characteristics. Treatment effectiveness may be enhanced when integrated with other bark beetle management techniques, such as sanitation thinning.

Long-Term Preventive Measures

The most effective, long-term means of reducing tree mortality caused by MPB are silvicultural treatments that emphasize diversity of age, size, and species composition, thereby altering overall stand susceptibility. Over the past several decades, reducing bark beetle-caused mortality through sanitation thinning has been successful. McGregor et al. (1987) showed MBP-caused losses could be markedly reduced in susceptible lodgepole pine stands through basal area reductions. Sartwell and Dolph (1976) had similar results in ponderosa pine stands. More recently, Schmid et al. (2007) also demonstrated the benefit of thinning ponderosa pine to reduce stand susceptibility (Figure 17). Such thinning has been carried out in operational settings with good results for nearly three decades. While we can only surmise that similar results might be obtained on high-elevation sites, we do not have experimental data or operational observations to make reliable recommendations. Where feasible, hazard-reducing silvicultural treatments in selected high-elevation stands may be warranted and effectively implemented. At the very least, we would encourage additional silvicultural research on these sites.

Ken Gibson, USDA Forest Service

Figure 17. Thinning host stands can reduce mountain pine beetle-caused mortality.

Typical silvicultural treatments (such as thinning) will be difficult to conduct effectively and economically on most whitebark pine sites. Keane (2001) has suggested that more liberal let-burn policies or the judicious use of prescribed fires will offer the best hope for reducing MPB-caused impacts and may be the most effective means of restoring healthy conditions to these sites.

RESTORING ECOSYSTEM HEALTH ON HIGH-ELEVATION SITES

Natural disturbances—those caused by fire, insects, disease, or weather phenomena—are part of ongoing processes on these sites, and five-needle pines have accommodated those vagaries with marked success. Today, fire exclusion, the introduction of white pine blister rust, and possibly climate change have exacerbated the effects of these natural disturbances and are now threatening the very survival of some stands (Schmidt and McDonald 1990).

Restoring ecosystem health may not directly reduce MPB-caused tree mortality, particularly while outbreaks are in progress, but re-establishing natural ecosystem processes—specifically, a more-natural role for fire—may result in five-needle pine ecosystems that are less susceptible to MPB and promote selection for resistance to blister rust infections (Schoettle and Sniezko 2007). Management efforts to reduce the effects of MPB, white pine blister rust, and fire exclusion should result in more resilient stands less sensitive to future climate trends (Figure 18).

Figure 18. Healthy whitebark pine stand.

Speaking from an ecosystem perspective, Hann (1990) noted that alpine/subalpine communities are diverse, complex mosaics of often sparse vegetation where human-caused disturbances are disruptive of natural processes. Management efforts to reduce all impacts will be difficult and challenging—and will need to be monitored to document effectiveness.

Keane (2000) reported on whitebark pine forest decline due to MPB, white pine blister rust, and advancing succession (a result of more than 70 years of fire exclusion) and concluded that their conservation and restoration will be nearly impossible without the reintroduction of fire. Later, Bockino (2007) suggested the role of fire suppression in whitebark pine decline may not be fully understood, especially in the Greater Yellowstone Ecosystem. Still, many believe human activity has—directly through fire exclusion and indirectly through white pine blister rust introduction—contributed to the precarious condition in which we find many whitebark and other five-needle pine stands today. Clark's nutcracker is thought to be the primary means of natural regeneration of whitebark and limber pines, and some now believe that fire may be especially important in restoration efforts because of the apparent preference of Clark's nutcracker to cache seeds in recently burned sites (Tomback 2001).

ADDITIONAL CHALLENGES AND UNANSWERED QUESTIONS

1. How do MPB life cycles vary from low to high elevations throughout its range?

   We know that MPB life cycles vary with temperature and that life cycles require between one and two years to complete in whitebark pine at certain locations. A better understanding of how temperature affects MPB success at varied elevations in all high-elevation five-needle pines is needed to correctly implement management strategies to reduce beetle-caused mortality.

2. How might we better assess overall impacts of MPB on these sites and on associated resources?

   A ground survey to determine the extent of mortality and what is left in areas that experienced recent MPB outbreaks in Idaho, Montana, and Wyoming is currently underway (Schwandt, personal communication). Clearly, more assessments are needed to fully understand MPB impacts on high-elevation resources throughout its range.

3. What constitutes "high-hazard" for MPB outbreaks in high-elevation stands?

   Stand characteristics of high-hazard lodgepole and ponderosa pine forests have been identified and silvicultural treatments to reduce hazard in these forests have been implemented. Corresponding conditions in high-elevation forests are not fully defined but are urgently needed in order to develop management strategies to reduce high-hazard conditions. Perkins and Roberts (2003) have described conditions—tree diameter, basal area, trees per acre, and number of stems in a cluster—in whitebark pine stands in central Idaho that can be associated with MPB-caused mortality. How applicable those criteria may be across the range of whitebark pine or in other host species is unknown.

4. What is the role of natural or prescribed fire in maintaining healthful forest conditions on high-altitude sites; and how does excessive beetle-caused mortality influence fire behavior—positively or negatively?

Keane (2000) seems convinced the natural role of fire must be re-established on whitebark pine sites if health and resiliency of those fragile ecosystems are to be restored and maintained. Bockino (2007) is less certain about the role of fire, at least in some of those ecosystems. Additional research is needed to address some of these critical issues.

5. How many mature trees are needed in a stand to maintain populations of nutcrackers sufficient to provide adequate natural regeneration?

6. Might genetic studies underway for blister rust resistance also explore genetic resistance to bark beetles? Are bark beetles killing five-needle pines most resistant to blister rust?

   While extreme beetle populations may overwhelm the healthiest trees, we often observe otherwise "susceptible" hosts that are not killed during MPB outbreaks. There is more to that phenomenon than we currently know.

7. Can silvicultural treatments hasten forest recovery following MPB outbreaks and lessen the effects of future ones?

CONCLUSION

Restoration of high-elevation five-needle pine ecosystems, such as the whitebark pine forests devastated by blister rust, fire exclusion, or MPB, may be difficult using more traditional silvicultural treatments or fire. Whatever means of restoration are ultimately selected, it now seems apparent that, without some type of proactive intervention, whitebark and other five-needle pine ecosystems will continue to decline (Arno 1986, Keane 2000, Schoettle and Sniezko 2007).

The combined effects of insects, diseases, management philosophies, and climate changes have high-elevation, five-needle pines on the brink of disaster. Cooperative efforts of entomologists, plant pathologists, silviculturists, geneticists, ecologists, other resource specialists, and private citizens will be required to successfully protect, preserve, and restore critical stands of these keystone species throughout their range. Reducing MPB-caused mortality will be a crucial first step in that process.

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APPENDIX:
RANGE, DISTRIBUTION, AND ECOLOGY OF HIGH-ELEVATION FIVE-NEEDLE PINES

WHITEBARK PINE

The species (Figure 19) is broadly distributed in the northern Rocky Mountains, including in Idaho, Montana, and northwestern Wyoming, and extends into the Canadian provinces of British Columbia and Alberta, at elevations of 5,400 to 7,200 ft (Critchfield and Little 1966, Little 1971, Arno and Hoff 1990, Ogilvie 1990). It is also found along the crest of the Sierra Nevada, in the Klamath Mountains, in higher elevations in the Warner mountain range, and in the southern Cascades in California. In Oregon and Washington, it occurs along the Cascade range from about 3,000 ft to 7,200 ft elevation. Isolated populations exist in the Blue and Wallowa mountains in northeastern Oregon, on mountain peaks in northeastern Washington, and in northern and northeastern Nevada. Figure 20 illustrates the geographic range of whitebark pine.

K.D. Swan, USDA Forest Service

Figure 19. Whitebark pine.

A. Schoettle, USDA Forest Service

Figure 20. Geographic range of whitebark pine.

Whitebark pine is generally found on cold, windswept, exposed, and moist sites at high elevations and at timberline (Arno and Weaver 1990, Arno and Hoff 1990) (Figure 19). Whitebark pine may be associated with lodgepole pine and limber pine on drier sites and with subalpine fir, Engelmann spruce, alpine larch, and mountain hemlock on moister sites in the northern Rocky Mountains. In California, whitebark pine is associated with mountain hemlock, California and Shasta red fir, western white pine, foxtail pine, limber pine, and Sierra lodgepole pine.

Whitebark pine may act as a pioneer following fire (Arno and Weaver 1990, Arno and Hoff 1990). Fire return intervals in whitebark pine systems appear to be on the order of 50 to 300 years (Arno 1980). At timberline, the species is often considered climax. In the subalpine vegetation zones across its range, whitebark pine is generally considered seral. Whitebark pine is considered intolerant of shade or competition. The species is slow-growing and long-lived, attaining ages of over 1,000 years (Perkins and Swetnam 1996).

Whitebark pine cones are produced at irregular intervals and are closed at maturity. Seeds of whitebark pine are large and wingless. Small rodents and birds, especially Clark's nutcracker, disseminate many of the seeds produced by this species. The seeds of whitebark pine are an important food source of grizzly bears, which often raid squirrels' seed caches.

LIMBER PINE

Limber pine (Figure 21) is widely distributed across western North America (Little 1971, Steele 1990) and exists on a wide range of elevations from 2,850 ft to 12,500 ft, where it may occur at upper tree line or on dry exposed ridgetops at lower elevation (Schoettle and Rochelle 2000) (Figure 20). Its range extends along the Rocky Mountains from New Mexico through Colorado, Wyoming, Idaho, and Montana and into Canadian Provinces of British Columbia and Alberta. In also occurs in Nevada, Arizona, and Utah, with outlying populations existing in North Dakota, South Dakota, Nebraska, and Oregon. In California, it occurs on the mountain tops in the southern and east-central part of the state and on the east side of the Sierra Nevada Range in Inyo County. Figure 22 illustrates the geographic range of limber pine.

Along the Rocky Mountains, limber pine may be found associated with whitebark pine in Wyoming, Idaho, and Montana and with Rocky Mountain bristlecone pine in Colorado. Associated tree species include white fir, lodgepole pine, Douglas-fir, quaking aspen, Engelmann spruce, and subalpine fir. Common associates in California include whitebark, foxtail, Great Basin bristlecone, Jeffrey, and lodgepole pines; white fir; and western juniper. Rebertus et al. (1991) and Schuster et al. (1995) observed limber pines reaching nearly 1,300 years of age along the northern Front Range of Colorado. Most stands in California are sparse, with scattered, slow growing, relic trees 500 to 1,500 years old (Schulman 1954); a few stands are closed-canopy, with straight-stemmed, fast-growing trees mostly less than 200 years old (Millar et al. 2007). Schoettle (2004) discussed the available information on the ecology of limber pine.

Limber pine is generally intolerant of shade and is considered an early seral species across most of its range (Steele 1990). It may occur as a pioneer following fire (Rebertus et al. 1991, Donnegan and Rebertus 1999) and can establish and maintain populations in very dry and windy environments. In mesic sites in Colorado, the species has been replaced by Engelmann spruce (Picea engelmanii Parry) and subalpine fir (Abies lasiocarpa [Hook.] Nutt.). Limber pine can persist on xeric sites, such as steep, south-facing slopes, ridgetops, and rock outcrops (Rebertus et al. 1991, Donnegan and Rebertus 1999).

Dave Powell, USDA FS UGA 0806050

Figure 21. Limber pine.

A. Schoettle, USDA Forest Service

Figure 22. Geographic range of limber pine.

Most seeds of limber pine are large and wingless. Large seed crops are produced every two to four years (Steele 1990). Clark's nutcracker is the primary seed disperser for limber pine. Small rodents have also been shown to contribute to seed dispersal (Lanner and Vander Wall 1980, Tomback et al. 2005).

Foxtail Pine

Foxtail pine (Figure 23) is endemic to California and exists in two disjunct areas: in the inner north coast ranges (Siskiyou, Scott and Yolly Bolly Mountains) in northwestern California and in the southern Sierra Nevada (Critchfield and Little 1966). Most of the foxtail pines in the south occur in Sequoia-Kings Canyon National Park. Figure 24 illustrates the geographic range of foxtail pine.

Northern and southern populations are separated by about 300 miles and are considered distinct subspecies (Oline et al. 2000, Mastrogiuseppe and Mastrogiuseppe 1980). In the north, foxtail pine grows primarily on scattered peaks and ridges between 6,600 ft and 10,000 ft and is found in the mixed conifer type with Shasta red fir, lodgepole pine, and Jeffrey pine. In the south, it is found between 7,200 to almost 12,100 ft, most often growing in pure stands or mixed with lodgepole, limber, and western white pines.

Foxtail pine is a long-lived species (2,500 years and more), shade intolerant, adapted to high-elevation sites with droughty conditions, and has similar ecological values as other high-elevation white pines (Bailey 1970). Seed of this species have wings, providing an opportunity for wind dissemination. Otherwise, seed dissemination in foxtail pine is undocumented.

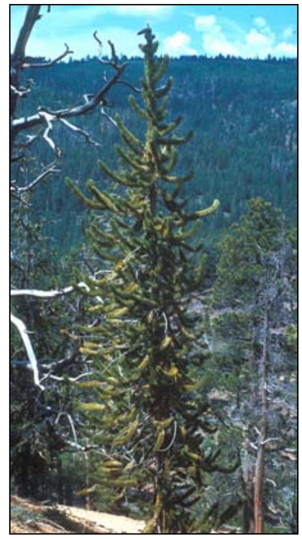
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Figure 23. Foxtail pine.


A. Schoettle, USDA Forest Service

Figure 24. Geographic range of foxtail pine.

ROCKY MOUNTAIN BRISTLECONE PINE

The range of Rocky Mountain bristlecone pine (Figure 25) includes the central Rocky Mountains in Colorado and extends south into the Sangre de Cristo Mountains of northern New Mexico. An isolated population also occurs in Arizona on San Francisco Peaks (Bailey 1970). Figure 26 illustrates the geographic range of Rocky Mountain bristlecone pine.

Rocky Mountain bristlecone pine has been recorded to reach at least 2,400 years of age (Brunstein and Yamaguchi 1992). It has a narrow elevation range: from 9,000 ft to 12,040 ft (Baker 1992). Schoettle (2004) presents information on the ecology of Rocky Mountain bristlecone pine.

Rocky Mountain bristlecone is a long-lived species that occupies dry, windswept sites at timberline and in the subapine zone. It is considered a pioneer species and regenerates well following fire (Baker 1992). Associated tree species include Douglas-fir, limber pine, Engelmann spruce, subalpine fir, and aspen. In the absence of disturbance, Rocky Mountain bristlecone pine may yield to these associated species (Baker 1992). This species appears to facilitate the establishment of other tree species, including Engelmann spruce (Schoettle 2004).

Patterns of seedling establishment of Rocky Mountain bristlecone pine are suggestive of dissemination by small mammals or birds (Schoettle 2004). Seeds of this species have wings, providing an opportunity for wind dissemination.

Figure 25. Rocky Mountain bristlecone pine.

A. Schoettle, USDA Forest Service

Figure 26. Geographic range of Rocky Mountain bristelcone pine.

GREAT BASIN BRISTLECONE PINE

Great Basin bristlecone pine (Figure 23) is distributed in small populations throughout Nevada, Utah, and portions of California. It occurs at high elevations throughout Nevada, including the Snake and Shell creek ranges; and in southwestern and central Utah, including the Markagunt, Paunsaugunt, Sevier, and Wasatch plateaus and Escalante Mountains. In California, Great Basin bristlecone is restricted to the White Mountains, the Inyo Mountains, and the Panamint Range in Mono and Inyo counties. Figure 28 illustrates the geographic range of Great Basin bristlecone pine.

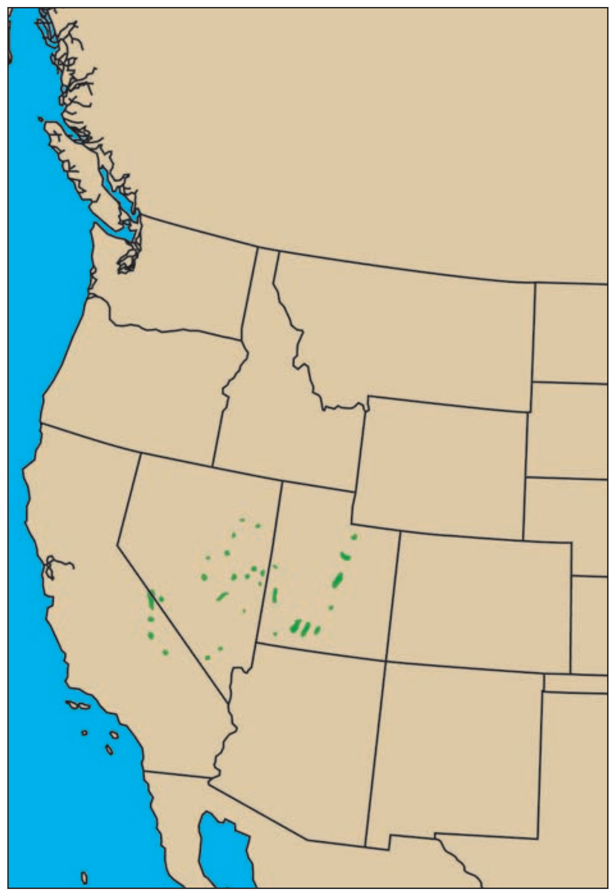
This species is of special note due to the great age of some individuals, which exceed 4,000 years (Schulman 1958, Curry 1965, Ferguson 1968). The "Methuselah" tree in the Ancient Bristlecone Pine Forest in the White Mountians is approximately 4,700 years old and is the oldest known tree in North America and the oldest individual in the world.

Conifer associates of Great Basin bristlecone pine include lodgepole, ponderosa, and singleleaf piñon pines; subalpine and white firs; Douglas-fir; Engelmann spruce; Rocky Mountain, Utah, and western junipers; and quaking aspen (Hiebert and Hamrick 1984, Lanner 1988). In California, limber pine is the only associate; however, extensive stands of singleleaf pinyon exist downslope.

Seeds of Great Basin bristlecone pine are small and winged and are thought to be disseminated by wind, small mammals, and birds. At high elevations, regeneration in this species is most frequently observed from seed caches of Clark's nutcracker (Lanner 1988).

Mary Ellen (Mel) Harte, UGA5001050

Figure 27. Great Basin bristlecone pine.



A. Schoettle, USDA Forest Service

Figure 28. Geographic range of Great Basin bristelcone pine.