

Disturbance Ecology of High-Elevation Five-Needle Pine Ecosystems in Western North America

Elizabeth M. Campbell, Canadian Forest Service, Natural Resources Canada, Victoria, BC; **Robert E. Keane**, USDA Forest Service, Rocky Mountain Research Station, Missoula Fire Sciences Laboratory, Missoula, MT; **Evan R. Larson**, Department of Geography, University of Wisconsin-Platteville, Platteville, WI; **Michael P. Murray**, British Columbia Forest Service, Nelson, BC; **Anna W. Schoettle**, USDA Forest Service, Rocky Mountain Research Station, Fort Collins, CO; **Carmen Wong**, Parks Canada, Whitehorse, YK

Abstract—This paper synthesizes existing information about the disturbance ecology of high-elevation five-needle pine ecosystems, describing disturbance regimes, how they are changing or are expected to change, and the implications for ecosystem persistence. As it provides the context for ecosystem conservation/restoration programs, we devote particular attention to wildfire and its interactions with mountain pine beetle (*Dendroctonus ponderosae* Hopkins) outbreaks and white pine blister rust (*Cronartium ribicola* J.C. Fisch.).

Patterns of fire disturbance and post-fire regeneration in high-elevation five-needle pine ecosystems are highly variable over space and time. While stand-replacing fires predominate in some regions, mixed severity fire regimes that include low intensity surface fires and crown fire components, appear most common. Fire disturbance provides critical regeneration opportunities for most high-elevation five-needle pines but fire exclusion over the last century is having some impacts—such as major declines of whitebark pine (*Pinus albicaulis* Engelm.). Historic mountain pine beetle outbreaks caused episodes of mature high-elevation five-needle pine death over large regions. While these pines have adapted to this historic pattern of disturbance, global climate change is causing the geographic expansion of beetle outbreaks that are killing high-elevation pines in places with no history of major impacts. Expanding beetle outbreaks and exotic blister rust infections, which continue to intensify and spread into the southernmost geographic range of high-elevation five-needle pines, reduce the density of seed bearing trees and hasten succession. Global climate change may also generate more frequent severe fires. This may pose a threat to some pines and generate regeneration opportunities for others, provided beetle outbreaks and blister rust have not reduced the density of seed-bearing trees below critical thresholds.

High-elevation five-needle pine ecosystem responses to disturbance are complex and while there is still much to learn, management efforts are moving forward to conserve and restore these critical components of mountain landscapes. Given the complexity and uncertainty of ecosystem response to disturbance, a cautious yet proactive approach to management will be necessary to build ecosystem resilience to future disturbances, whether natural or human-caused.

Introduction

Disturbances are key natural components of forest ecosystems. Variation in the type, timing and severity of disturbances generate forest heterogeneity, which is linked to biodiversity and ecosystem resilience to subsequent perturbations and environmental change (Gunderson and

others 2009). However, substantial alterations to historical disturbance regimes—the type, timing and severity of disturbances—can compromise the capacity of ecosystems to recover from disturbance and persist on landscapes. Human interactions with ecosystems are the primary cause of recent major changes in disturbance regimes.

In western North America, land use activities (including wildland fire management, livestock grazing, logging and planting patterns), global climate change caused by increased greenhouse gas emissions, and introduction of the Eurasian white pine blister rust fungus (*Cronartium ribicola* J.C. Fisch.) are altering historical disturbance regimes and threatening the persistence of high-elevation five-needle (high-five) pine ecosystems dominated by whitebark pine (*Pinus albicaulis* Engelm.), limber pine (*P. flexilis* James), Rocky Mountain bristlecone pine (*P. aristata* Engelm.), Great Basin bristlecone pine (*P. longaeva* D.K. Bailey), fox-tail pine (*P. balfouriana* Grev. & Balf.), and southwestern white pine (*P. strobiformis* Engelm.) (Campbell and Carroll 2007; Keane 2001; Tomback and Achuff 2010). In this paper, we synthesize existing information about the disturbance regimes of high-five pine ecosystems and describe how they are changing or are expected to change. We devote particular attention to the importance of wildfire and its interactions with other major disturbances—mountain pine beetle (*Dendroctonus ponderosae* Hopkins) outbreaks and the white pine blister rust epidemic—since this provides most of the context for interpreting threats to high-five pine decline and the design of ecosystem conservation and/or restoration programs.

Fire Disturbance

Fire is a component of the disturbance regimes of most high-five pine ecosystems. We currently know the most about fire disturbance in the whitebark pine ecosystem, which is more widely distributed than any of the other high-five pine ecosystems. The presence of charcoal in lake sediment cores from the northern U.S. Rocky Mountains indicates that fires burned in areas supporting whitebark pine for at least the past 14,000 years (Brunelle and Whitlock 2003; Minckley and others 2007). Tree-ring studies, which provide more temporally precise information about fires over the last several hundred years, indicate complex and highly variable fire regimes in space and time. Severe stand-replacing,



Figure 1. Evidence for past fires in whitebark pine forests including a) fire-scarred whitebark pine trees indicative of surface fires, b) charred remnant wood, and c) dense, post-fire cohorts of whitebark pine indicative of stand-replacing fires. Photos by E. Larson.

partial-stand replacing and low-severity surface fires all occur in whitebark pine ecosystems with mean fire-return intervals ranging from 13 to 400+ years (figure 1, table 1). Mixed-severity fire regimes, which are very common in whitebark pine ecosystems, include low intensity surface fire and crown fire components that typically create complex patterns of tree death and survival in stands and over landscapes (Murray and others 1998; Romme and Knight 1981). Burned patches typically range from 1 to 30 ha in size, depending on weather, topography and fuel connectivity (Norment 1991; Tomback and others 1993). Large stand-replacement fires occur within mixed-severity fire regimes but as infrequent events that often originate in lower elevation forests and move to whitebark ecosystems when weather conditions facilitate fire spread (Morgan and Bunting 1990; Murray and others 1998). In dense mixed-conifer subalpine forests, which are most extensive in the U.S. Rocky Mountains and in mountain ranges of British Columbia, whitebark pine fire regimes are often characterized by large stand-replacement fires occurring over long time intervals (250+ years) (Campbell and Antos 2003; Romme 1980).

With somewhat thicker bark, higher and thinner crowns, and deeper roots, whitebark pine is better adapted to survive low intensity surface fires than its shade-tolerant competitors (Morgan and others 1994). When surface fires are relatively frequent, mature cone-bearing whitebark pine survive fires that generally kill competing species, such as subalpine fir (*Abies lasiocarpa* [Hook.] Nutt.) and Engelmann spruce (*Picea engelmannii* Parry ex. Engelm.), which have denser canopies that typically extend to the ground. Such disturbances delay the successional process (Keane 2001) typically producing stands with fire-scarred whitebark pine and multiple post-fire cohorts of this species (figure 2). Whitebark pine is also well adapted to severe, large stand-replacing fires because the Clark's nutcracker (*Nucifraga columbiana* Wilson) can disperse whitebark pine seeds up to 100 times farther (over 10 km) than wind can disperse the seeds of its major competitors (Tomback 2005). As such, the species can more readily colonize large burned areas and seedlings can grow without competition for some time unless lodgepole pine—with predominantly serotinous cones—were a significant component of the pre-burned stand (Campbell and

Table 1. Tree-ring studies reporting fire-return intervals for whitebark pine forests (modified from Arno 2001).

Fire-free interval (yrs)	Methods	Geographic area	Source
13–46	Fire-scar and age-structure analyses	Russell Peak, Wyoming	Morgan and Bunting 1990
19–350+	Fire-scar and age-structure analyses	Lolo National Forest, Montana	Larson and others 2009
20–173	Fire-scar and age-structure analyses	Selway-Bitterroot Wilderness, Montana/Idaho	Kipfmüller 2003
57–94	Fire-scar and age-structure analyses	Bitterroot Valley, West Montana	Arno 1980; Arno and Petersen 1983
50–119	Fire-scar and age-structure analyses	Big Hole Range, Montana/Idaho	Murray and others 1998
47–250+	Fire-scar and age-structure analyses	Cascade Range, Oregon/Washington	Siderius and Murray 2005
55–304	Fire-scar and age-structure analyses	Bob Marshall Wilderness, NW Montana	Keane and others 1994
80–300	Age-structure analysis	Yellowstone National Park, Wyoming	Mattson and Reinhardt 1990
66–>350	Fire-scar and age-structure analyses	Yellowstone National Park, Wyoming	Barrett 1994
300–400	Fire-scar and age-structure analyses	Yellowstone National Park, Wyoming	Romme 1982

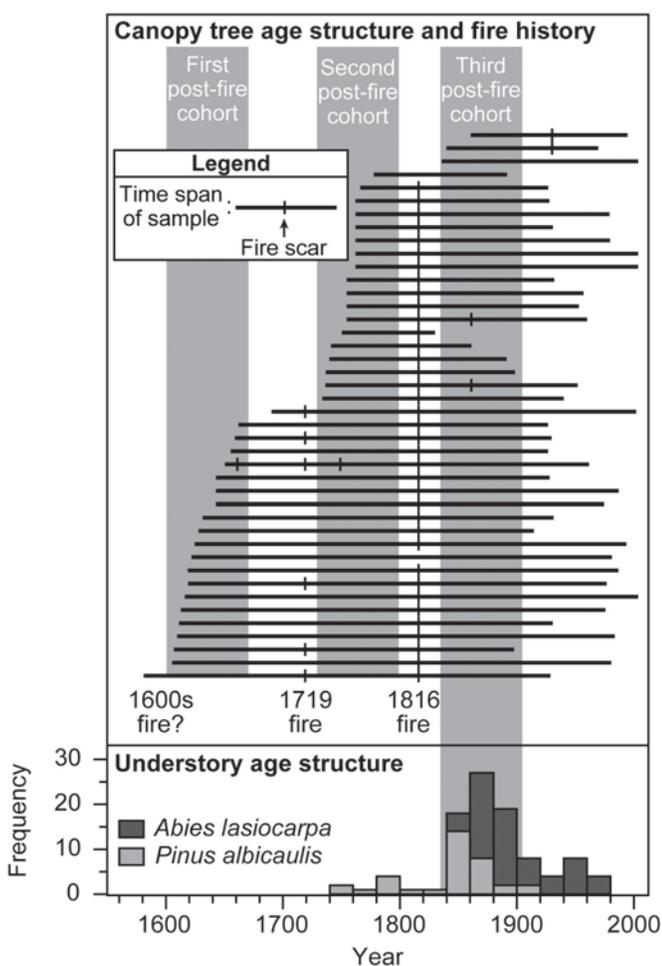


Figure 2. Age structure and fire history of a whitebark pine forest on Point Six, near Missoula, Montana. The lack of fire since the widespread 1816 fire event likely reflects the effects of fire suppression on this forest. Also note that subalpine fir was establishing in this forest within one decade of the most recent widespread fire. Restoration plans have been developed for the whitebark pine forests on Point Six. For more detail about fire on this site, see Larson and others 2009.

Antos 2003; Kipfmüller and Kupfer 2005). However, in the upper subalpine zone, generally beyond the altitudinal limits of lodgepole pine, crown fires commonly leave scattered unburned patches that serve as important biological legacies, resulting in subalpine fir and Engelmann spruce colonizing burns synchronously with whitebark pine (Campbell and Antos 2003). Fire disturbance is less important near the timberline or on dry sites where whitebark pine's tolerance to harsh environments permits it to thrive in places other subalpine tree species cannot. Much of what we know about the fire ecology of whitebark pine ecosystems comes from research in the U.S. and southern Canada. Information from the northern part of the range, in Canada, is sparse; however preliminary data (Haeussler and others 2009; Clason and others 2010) suggest that patterns of whitebark pine response to fire disturbance are broadly similar to the patterns described above.

Our knowledge about the fire ecology of other North American high-five pine ecosystems is limited and needs further study. A few studies report mixed-severity fire regimes for high-five pine ecosystems dominated by limber pine, Rocky Mountain bristlecone pine and Great Basin bristlecone pine in Colorado, Nevada and Utah, with mean fire return intervals ranging from 11 to 129 years (Brown and Schoettle 2008; Coop and Schoettle 2009; Kitchen 2010). On an isolated desert mountain range in Arizona, frequent low-intensity surface burns dominate a mixed-severity fire regime in southwestern white pine ecosystems—mean fire return intervals range from 4 to 22 years (Iniguez and others 2009). Fire disturbance is considered rare in the driest southern U.S. landscapes where Great Basin bristlecone pine, foxtail pine and limber pine dominate dry, rocky ridges; and, when fires do occur, they are usually small and of low severity due to sparse fuels. Caprio and Lineback (2002) report mean and maximum fire-return intervals in foxtail pine ecosystems as 187 and 580 years, respectively. Like whitebark pine, fire scars have been found on all other high-five pine species, indicating that they can also survive low-intensity surface fires (Iniguez and others 2009; Brown and Schoettle 2008; Kitchen 2010; Ryerson 1983).

Mounting evidence suggests temporal variations in fire activity are linked to natural global ocean-atmospheric processes. The El Niño/Southern Oscillation (ENSO), the Pacific Decadal Oscillation (PDO), and the Atlantic Multidecadal Oscillation (AMO) may influence patterns of drought occurrence from regional to continental spatial scales, and from seasonal to multidecadal temporal scales, synchronizing fire activity over large areas (McCabe and others 2004; Skinner and others 2006). Recent studies report more frequent severe fires in subalpine forests in western Colorado during cool phases of the PDO and ENSO and warm phases of the AMO (Schoennagel and others 2007). However, the relative influence of these natural phenomena may vary spatially and even reduce fire activity in subalpine forests of other regions. The influence of ocean-atmospheric oscillations on regional climate and linkages to fire activity remains an active area of research.

Human land use activities can also influence temporal patterns of fire activity. Since the early 1930s, fire suppression programs in the U.S. have successfully limited the extent of wildland fire in many western North American ecosystems (Keane and others 2002). Information about the effects of fire exclusion policies on high-five pine ecosystems come from two different kinds of studies in the U.S.: stand-level tree-ring analyses and landscape-level assessments. Using fire scar and tree age data, some stand-level tree-ring studies readily detect a reduction in fire activity that could be attributed to fire suppression management (Brown and Schoettle 2008; Buechling and Baker 2004; Kitchen 2010; Larson and others 2009; Murray and others 1998; Sherriff and others 2001). However, because tree-ring studies are labour intensive work, many are based on too few samples (that is, stands) to make definitive conclusions about the effects of fires suppression across landscapes. Moreover, while they can detect the effects of fire suppression in regions where frequent surface fires were historically common, in moist/cool regions where fire return intervals are longer, the effects of fire suppression are not yet manifest at the stand-level and generally not yet detectable. In these regions, the effects of fire suppression can be examined at the landscape-level by assessing areal extent of early to mid-seral pine stands and increases in late-seral stands in high-elevation landscapes (Keane and others 1994). Using this approach, Keane (2001) reported that a major reduction in high-elevation fires since about 1929 has led to the successional replacement of whitebark pine by subalpine fir on the most productive sites in parts of its range. Although subalpine fir communities currently comprise about 12-22 per cent of the landscapes in the Bob Marshall Wilderness Complex (Keane and others 1994), modelling efforts estimated that historical landscapes in this area had 3-13 per cent late-seral subalpine fir stands. Similarly, Murray and others (2000) show that nearly 50 per cent of the landscape has shifted to late successional stands over the last 250 years in the Big Hole Range of Idaho and Montana.

In Canada, fire suppression programs have been effective reducing the extent of forest area burned since the late 1950s (Cumming 2002). However, very little information is

available about the effects of fire exclusion policies on high-five pine ecosystems. While there has been a tendency to let fire burn in remote locations of Canada, this is most common in boreal forest zones north of the geographic range of high-five pines. A summary of fire data for British Columbia, indicated a clear decrease in the extent of fire in subalpine zones where whitebark pine occurs (Campbell, unpublished data). Given these data, we expect fire exclusion policies are having the same impacts on high-five pines in Canada as they are in the U.S.

There is much yet to learn about the fire ecology of high-elevation five-needle pine ecosystems and the effects of fire suppression. Some analogies can be drawn from high-elevation pine ecosystems of Eurasia. For example, Cembran pine (*Pinus cembrae* L.), which shares many life-history traits with the taxonomically similar North America high-elevation pines, currently occurs as fragmented populations in mountain landscapes where fire has been suppressed for centuries. During the Holocene, when the climate was warmer and fire disturbance was more frequent, Cembran pine was much more abundant, even in valleys and above the current timberline (Ali and others 2005). Moderately frequent surface fires, which promote Cembran pine regeneration (Genries and others 2009a), resulted in the expansion of Cembran pine forests, while very frequent fires occurred to the detriment of the species (Genries and others 2009b).

Other Disturbances and Interactions With Fire

High-elevation pines are subject to damaging agents other than fire—such as localized insect infestations of *Ips* spp. bark beetles (Campbell, unpublished data) or the pine leaf adelgid (*Pineus pinifolia*, Fitch) (Woods, unpublished data) and dwarf mistletoe infections (Mathiasen and Daugherty 2001; Mathiasen and Hawksworth 1988)—but mountain pine beetle (MPB) outbreaks and the introduced white pine blister rust (WPBR) fungus are the only other major disturbances. All high-five pines are currently being attacked by MPB (see Bentz and others, this proceedings) with the most beetle-caused deaths during this outbreak occurring among whitebark, limber and Rocky Mountain bristlecone pines (Gibson and others 2008). Over the last several decades, WPBR has caused widespread pine decline and death throughout most of the geographic range of whitebark pine and limber pine, and in all but the western extent of southwestern white pine's range (Campbell and Antos 2000; Schoettle and Sniezko 2007; Smith and others 2006). WPBR is currently limited to a small portion of Rocky Mountain bristlecone pine's range and it has yet to be found on Great Basin bristlecone pine (see Tomback and others, this proceedings), presumably because the arid climate of these regions slows infection. However, the disease continues to spread and it is expected to intensify wherever five-needle pines occur (Schoettle and Sniezko 2007). Most of the context for interpreting high-elevation five-needle pine ecosystem decline, and its conservation, come from

understanding the interactions among these three major disturbances: fire, MPB, and WPBR.

In many areas, whitebark pine deaths caused by MPB outbreaks and concurring WPBR hasten forest succession, converting pine stands to forests dominated by the shade-tolerant conifers, such as subalpine fir, Engelmann spruce (Jackson and Campbell 2008; Keane 2001; Kipfmüller and Kupfer 2005). This, in turn, increases the potential for high-severity crown fires because of greater canopy bulk densities and multi-layered canopy of spruce-fir forests (Reinhardt and others 2006). These high severity fires then kill most of the whitebark pine that survived past MPB outbreaks and were potentially blister rust-resistant trees. Continued rigorous management to suppress wildland fire may result in the same cycle of spruce-fir dominance fostering large, crown fires, particularly in mesic forests where severe fires were more common historically (Keane and others 2002). While not well studied, the same interactions among fire, MPB and WPBR might be expected in mesic forests where other high-five pines occur as seral species in mixed forests, particularly among the high-five pines that depend almost entirely on nutcracker to disperse seed. In northern British Columbia, however, where MPB have killed whitebark pine and balsam bark beetle (*Dryocoetes confusus*, Swaine) infestations that have killed subalpine fir, stands are succeeding to shade-tolerant mountain hemlock (*Tsuga mertensiana*, [Bong.] Carr.) (Clason and others 2010), which would generate stands with similar canopy fuels a tendency for crown fires.

Wildland fire disturbance is pivotal to the persistence of some high-five pine ecosystems. Newly burned patches provide regeneration opportunities for these shade-intolerant species. Burns can be colonized by seed from putatively blister rust-resistant pines in nearby maturing forests where pines are at increasing risk of loss due to other pests and pathogens, wildfire or successional replacement. When seed sources are plentiful in the landscape, due to high rust resistance or low rust incidence, wildfire disturbance stimulates regeneration and efficient natural selection for rust resistance (Hoff and others 1976; Schoettle and Sniezko 2007). However, if the density of seed-bearing trees is low (that is, tree basal area < 5 m²/ha), due to blister rust, successive MPB outbreaks and decades of fire suppression, colonization of open habitat may be limited by inadequate seed, limited nutcracker dispersal, and a relative increase in the rate of seed predation by nutcrackers and squirrels (Haeussler 2010; Larson 2009; McKinney and others 2009). By generating a forest landscape mosaic with diverse age class and patch structures, fires also facilitate ecosystem resistance to subsequent disturbances. For example, given that the beetle rarely attacks small pine trees, young, fire-originated pine stands generally persist in landscapes during beetle population outbreaks and a sufficient proportion of young stands in landscapes could prevent catastrophic losses of pine during MPB outbreaks (Li and others 2005). Some forest patches created by previous fires could also act as fire-breaks and reduce the likelihood of the severity of future fire impacts.

It is often presumed that MPB outbreaks increase the likelihood and intensity of crown fire disturbances because they increase forest fuels. However, studies about the interaction between MPB outbreaks and fire have yielded mixed results. Jenkins and others (2008) report an increase in surface fire intensity due to an increase in fine surface fuels (for example, pine needles). However, these studies could not determine if increased surface fire intensity would lead to more severe crown fires. Some argue that the increased risk of intense fires following MPB outbreaks is short-lived (as fine fuels quickly decompose) and fire risk decreases again until later successional stages when shade-tolerant species, such as spruce and subalpine fir, grow to fill the gaps left by dead pines and increase crown fire risk (Lynch and others 2006). Most recently, Simard and others (2011) found that the interaction between fire and MPB outbreaks is the opposite of what is widely presumed; rather than increase the probability high intensity crown fires, outbreaks decrease crown fire risk in the short term by thinning pine forests. Studies conducted following the last MPB outbreak report similar findings (Despain 1990; Schmid and Amman 1992). While these studies focus predominantly on lodgepole pine (*Pinus contorta*, Dougl.) forests, we expect they can be applied similarly to subalpine forests containing high-elevation five-needle pines. In fact, many sites dominated by high-elevation pines are probably at even lower risk of crown fires following MPB outbreaks because of their more open canopies.

In regions where fire disturbance is infrequent, bark beetle outbreaks may play a more important role in high-elevation pine regeneration dynamics. For example, in southern Alberta, MPB and *Ips* spp. outbreaks create forest gaps that facilitate self-perpetuation of whitebark pine in subalpine forests (Wong and others, submitted). This historic role for bark beetle outbreaks has also been suggested for whitebark pine forests in Montana (Larson and others 2009; Larson and Kipfmüller 2010) and for lodgepole pine forests in Oregon (Stuart and others 1989). Similar to wildfire disturbance, MPB outbreaks may provide regeneration opportunities that facilitate natural selection of blister rust-resistant whitebark pine (Larson, in press).

High-elevation pines are often considered more susceptible to attack by MPB when they are stressed by WPBR infections. However, while WPBR infections appear to make pines more susceptible to attack by MPB when beetles are at endemic population levels (Six and Adams 2007), during population outbreaks, there is no correlation between WPBR infection and susceptibility to beetle infestation. During outbreaks, beetles kill mature pines regardless of vigor or health (Bockino 2008; Jackson and Campbell 2008).

Global Climate Change

Global warming has the potential to significantly impact high-elevation pine ecosystems. Like all species, high-five pines respond to environmental changes by adapting *in situ* or by migrating to more suitable habitat. Despite moderate

levels of genetic diversity, many wonder if temperate trees species can rapidly adapt—given their long generation times—or migrate at a sufficient pace to keep up with rapid climate change (Aitken and others 2008).

Bioclimatic envelope models, which quantify relationships between climate and a species occurrences, project dramatic reductions in the geographic distribution of climatically suitable habitat for whitebark pine over the next century (Hamman and Wang 2006; Warwell and others 2007) and similar results could be expected for other high-five pines. Warwell and others (2007) speculate that increasing temperatures could “push” whitebark pine off mountains by moving its lower elevational limits above the tallest peak. Conventional wisdom suggests that this would occur because less cold-hardy, shade-tolerant conifer species would establish more abundantly and out-compete whitebark pine at high elevations where it currently dominates (Koteen 1999).

Interpretations about the persistence of high-five pines from bioclimate envelope models, however, are not simple because climate influences a complex array of multi-scaled, interacting ecological processes that determine species ranges, not all of which are captured with these modelling techniques (Araujo and Guisan 2006). More information about the constraining effects of local topoedaphic conditions on climate change impacts will be important to high-five pine conservation efforts in a changing climate (Lafleur et al. 2010; Mbogga and others 2010; Hof and others 2011). For example, we may expect high-elevation five-needle pines

to remain free of competition and persist on sites with shallow soils (including rock outcrops) despite climate change. In addition, a greater understanding of the potential effects of climate change on growth, regeneration processes, and dispersal rates, which may come from mechanistic models, can also provide insights into the management of high-five pines in a changing climate. For example, recent mechanistic modelling work in British Columbia, which considers frost and drought thresholds, suggests decreased whitebark pine seedling survivorship could contribute to range reductions (Nitschke and Campbell, in prep.).

Most major ecosystem changes caused by global climate change will likely be precipitated by shifts in disturbance regimes (Dale and others 2001). Such shifts have already been observed in high-five pine ecosystems. For example, current mountain pine beetle outbreaks are killing more whitebark pine, and probably other high-five pines, than at any time in the historical record, and this trend is expected to continue to the end of the century as warmer winter temperatures facilitate the survival and reproduction of beetles in high-elevation zones (Bentz and others, this proceedings; Campbell and Carroll 2007; Logan and Powell 2001) (figure 3). Although many suggest that a warmer climate would accelerate the spread of blister rust where temperature is limiting (Koteen 1999), increased aridity in other regions may retard the spread and intensification of WPBR infections (Boland and others 2004).

A warmer climate may also increase in frequency and size of wildfires (Keeton and others 2007; Ryan 1991; Running

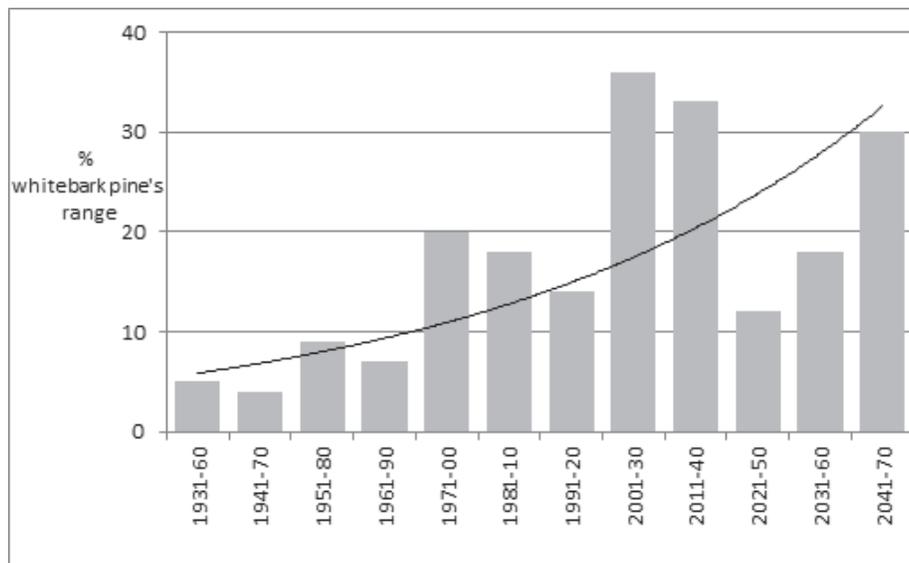


Figure 3. Historical and future projections indicating the percentage of whitebark pine’s range in British Columbia that is climatically suitable habitat for mountain pine beetle. Beetle outbreak risk is high in these areas. Indices of climatically suitable habitat were calculated for each map pixel based on climate threshold values for critical beetle life-stages (see Carroll and others 2006). Weather station data were used to calculate historical climate suitability indices and the Canadian Global Climate Model (CGCM), for a mid-range climate change scenario (A2), was used to project indices of climate suitability into the future. Indices were calculated for 30-year normal periods. Classes of climatically suitable habitat were derived from indices and mapped. The range of whitebark pine was then overlaid on these maps to calculate percentage of the range where outbreak risk is high.

2006). While an increase in fire size frequency and size may pose a threat to southern high-five pines with limited and isolated geographic ranges, it may benefit other pines, for example, whitebark pine (Loehman and Keane, in prep). Provided that sufficient seed sources remain on the landscape, and that microsites favouring establishment exist (Moody 2006), whitebark pine populations could increase as a result of increased fire activity. Coincidentally, increased fire activity that generates more young pine stands on landscapes could reduce the impact of future MPB outbreaks.

While disturbance rates are expected to increase with climate change, high-five pines may possess some capacity to adapt to changed disturbance regimes and persist in landscapes as the climate changes, particularly with some proactive management. Variability in high-five pine responses to current disturbance agents—including variability in responses to MPB outbreaks due to site, stand age, and genetics, or variability in the incidence and timing of blister rust deaths due to genetic resistance and tree size (Jackson and Campbell, 2008; Hof and others 2011; Jewett 2009; Schoettle and Snieszko 2007; Wong and others, submitted; Yanchuk and others 2008)—can provide insights and guide management actions to minimize disturbance impacts in a rapidly changing climate. High-five pine species with limited geographic ranges are likely most vulnerable to the increased frequency and extent of disturbances expected to accompany global climate change.

The effects of global climate change could be severe for high-five pine ecosystems. However, not only is the degree of future climate change uncertain, the response of high-five pine ecosystems to climate change are complex and difficult to predict. As such, the potential for major climate change effects should not be used as an excuse for not implementing restoration projects (Hobbs and Cramer 2008), but it could guide the choice of restoration activities used over the range of high-five pines, with differing activities occurring in some climatic regions or on some sites.

Management

The exotic white pine blister rust, wildfire suppression, MPB outbreaks, and global climate change are causing a rapid decline of whitebark pine and posing serious threats to other high-five pines. Management to stem the threats to high-five pine ecosystems is essential and described in greater detail throughout this proceedings (for example, see Schoettle and others, and references therein). Management can take two complementary approaches: targeted actions to minimize the impacts of on-going disturbances, and proactive management that enhances ecosystem resilience to future disturbances, natural or human-caused.

In the short term, targeted efforts could be used to protect highly-valued trees, or small groups of trees during a disturbance. If pines are not resistant to blister rust, pruning blister rust cankers from individual trees can prolong their life (Burns and others 2008). During MPB outbreaks, applying insecticides or treating putatively blister-rust resistant

trees with verbenone will protect seed sources and the genetic material needed to develop rust-resistance strains of high-five pines (see Bentz and others, this proceedings). During slow moving lightning-ignited fires, actions can also be taken to protect pine seed sources from the fire. In 2006, during the Bybee fire at Crater Lake National park (OR), crews removed flammable debris and installed fire lines at the base of putatively rust-resistant whitebark pine to improve their chance of survival (Murray 2007).

Over the longer-term, proactive management that builds high-five pine ecosystem resilience to future disturbances should be a key aspect of conservation strategies. Understanding, and harnessing, high-five pine response diversity to disturbance and environmental change can help achieve this goal. For example, selection, breeding, and future out-planting of high-five pines with a range of rust-resistance mechanisms will help to minimize the impact of the exotic blister rust fungus. Also, because forests of various ages, and on various sites, exhibit differential responses to blister rust infection, MPB outbreaks, fire, and probably even global climate change, diversifying forest age class structure across site types and over subalpine landscapes can help to build high-five pine ecosystem resilience to future disturbance (Schoettle and Snieszko 2007). Fire management can play a central role in achieving this goal by maintaining, or increasing, the proportion of pine-dominated forests in subalpine landscapes. This may include actions that decrease fuel loads to reduce the risk of severe crown fires and protect mature seed-bearing pines. It may also include controlled management of lightning-ignited burns or prescribed burns that reintroduce fire.

Fire has been reintroduced in subalpine landscapes of the Rocky Mountains of Alberta, Idaho, and Montana to promote whitebark pine regeneration. These prescribed fires had mixed results. In Montana, despite pre-fire thinning treatments to control the spread of fire and protect mature, cone-bearing and putatively blister rust-resistant trees, many overstory whitebark pines died on most burns. While competing spruce and fir regeneration were often markedly reduced and the numbers of nutcrackers caching seed in the post-burn environment increased, five years after the burn, whitebark pine regeneration was insignificant at most sites (Haeussler 2010; Keane and Parsons 2010). A better understanding of whitebark pine regeneration dynamics in areas without severe blister rust will provide valuable baselines for evaluating management in areas with severe infections and help assess the needs for out-planting seedlings. Also, detailed guidelines to identify high-priority target stands (*sensu* Shoal and others 2008), including stands where introducing fire poses too large a risk, should be developed for prescribed burning.

Acknowledgements

Yves Bergeron, Sybille Haeussler and Diana Tomback reviewed this paper, providing many helpful suggestions that help to improve the manuscript. We also thank Brad

Hawkes insight on fire suppression effects in Canada and mountain pine beetle–fire interactions. John Parminter provided spatial data on fire occurrence in British Columbia.

References

- Aitken, S. N.; Yeaman, S.; Holliday, J. A.; Wang, T.; Curtis-McLane, S. 2008. Adaptation, migration or extirpation: Climate change outcomes for tree populations. *Evolutionary Applications*. 1: 95–111.
- Ali, A.; Carcaillet, C.; Talon, B.; Roiron, R.; Terral, J.-F. 2009. *Pinus cembra* (arolla), a common tree in the inner French Alps since the early Holocene and above the present tree line: a synthesis based on charcoal data from soils and travertines. *Journal of Biogeography*. 32: 1659–1669.
- Araujo, M. B.; Guisan, A. 2006. Five (or so) challenges for species distribution modelling. *Journal of Biogeography*. 33: 1677–1688.
- Arno, S. F.; Hoff, R. 1990. *Pinus albicaulis* Engelm. Whitebark Pine. Pages 268–279 in *Silvics of North America*. Vol. I. Conifers. Agr. Handbook. U.S. Department of Agriculture, Forest Service.
- Arno, S. F.; Petersen, T. D. 1983. Variation in estimates of fire intervals: A closer look at fire history on the Bitterroot National Forest. General Technical Report GTR-INT-301, Ogden, UT: U.S. Department of Agriculture, Forest Service Intermountain Forest and Range Experiment Station.
- Barrett, S. W. 1994. Fire regimes on andesitic mountain terrain in northeastern Yellowstone National Park, Wyoming. *International Journal of Wildland Fire*. 4: 65–76.
- Bockino, N. K. 2008. Interactions of white pine blister rust, host species, and mountain pine beetle in whitebark pine ecosystems in the Greater Yellowstone. M.S. Thesis. University of Wyoming, Laramie, WY.
- Boland, G. J.; Melzer, M. S.; Hopkin, A.; Higgins, V.; Nassuth, A. 2004. Climate change and plant diseases in Ontario. *Canadian Journal of Plant Pathology*. 26: 335–350.
- Brown, P. M.; Schoettle, A. W. 2008. Fire and stand history in limber pine (*Pinus flexilis*) and Rocky Mountain bristlecone (*Pinus aristata*) stands in Colorado. *International Journal of Wildland Fire*. 17: 339–347.
- Brunelle, A.; Whitlock, C. 2003. Postglacial fire, vegetation, and climate history in the Clearwater Range, Northern Idaho, USA. *Quaternary Research*. 60: 307–318.
- Buechling, A.; Baker, W. L. 2004. A fire history from tree rings in a high-elevation forest of Rocky Mountain National Park. *Canadian Journal of Forest Research*. 34: 1259–1273.
- Burns, K. S.; Schoettle, A. W.; Jacobi, William R.; Mahalovich, M. F. 2008. Options for the management of white pine blister rust in the Rocky Mountain Region. Gen. Tech. Rep. RMRS-GTR-206. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station. 26 p.
- Campbell, E.; Carroll, A. 2007. Climate-related changes in the vulnerability of whitebark pine to mountain pine beetle outbreaks in British Columbia. *Nutcracker Notes*. 12: 13–15.
- Campbell, E.; Antos, J. 2000. Distribution and severity of white pine blister rust and mountain pine beetle on whitebark pine in British Columbia. *Canadian Journal of Forest Research*. 30: 1051–1059.
- Campbell, E.; Antos, J. 2003. Postfire succession in *Pinus albicaulis*-*Abies lasiocarpa* forests of southern British Columbia. *Canadian Journal of Botany*. 81: 383–397.
- Caprio, A. C.; Lineback, P. 2002. Pre-twentieth century fire history of Sequoia and Kings Canyons National Park: a review and evaluation of our knowledge. Pages 180–199 in *Proceedings—Symposium on Fire in California ecosystems: integrating ecology, prevention and management*: November. Association for Fire ecology. [Place of publication unknown].
- Carroll, A. L.; Régnière, J.; Logan, J.; Taylor, S.; Bentz, B.; Powell, J. P. 2006. Impacts of climate change on range expansion by mountain pine beetle. Mountain Pine Beetle Initiative Working Paper. 2006–14. Ottawa, ON: Canadian Forest Service.
- Clason, A.; MacDonald, E.; Haeussler, S. 2010. Ecosystem change at Whitebark Pine's northern limit. *Nutcracker Notes*. 18: 12–13.
- Coop, J. C.; Schoettle, A. W. 2009. Regeneration of Rocky Mountain bristlecone pine (*Pinus aristata*) and limber pine (*Pinus flexilis*) three decades after stand-replacing fires. *Forest Ecology and Management*. 257: 893–903.
- Cumming, S. G. 2002. Effective fire suppression in boreal forests. *Canadian Journal of Forest Research*. 35: 772–786.
- Dale, V. H.; Joyce, L. A.; McNulty, S.; Neilson, R. R.; Ayres, M. P.; Flannigan, M. D.; Hanson, P. J.; Irland, L. C.; Lugo, A. E.; Peterson, J.; Simberloff, D.; Swanson, F. J.; Stocks, B. J.; Wotton, B. M. 2001. Climate change and forest disturbances. *BioScience*. 51: 723–734.
- Despain, D. G. 1990. Yellowstone vegetation. Consequences of environment and history in a natural setting. Roberts Rinehart Publishers, Boulder, Colorado.
- Genries, A.; Mercier, L.; Lavoie, M.; Muller, D.; Radakovitch, O.; Carcaillet, C. 2009a. The effect of fire frequency on local cembra pine populations. *Ecology*. 476–476.
- Genries, A.; Morin, X.; Chauchard, S.; Carcaillet, C. 2009b. The function of surface fires in the dynamics of formerly grazed old subalpine forest. *Journal of Ecology*. 97: 728–741.
- Gibson, K.; Skov, K.; Kegley, S.; Jorgensen, C.; Smith, S.; Witcosky, J. 2008. Mountain pine beetle impacts in high-elevation white pines: current trends and challenges. Report # R1-08-020 Missoula, MT. U.S. Department of Agriculture, Forest Service. 32 p.
- Gunderson, L.; Allen, C. R.; Holling, C. S. 2009. *Foundations of Ecological Resilience*. Washington: Island Press. 466 p.
- Haeussler, S. 2010. Exploring whitebark pine at its northern limits. *Nutcracker Notes*: 18:11–22
- Haeussler, S.; Woods, A.; White, K.; Campbell, E.; LePage, P. 2009. Do whitebark pine—lichen ecosystems of west central British Columbia display tipping point behaviour in response to cumulative stress? Bulkley Valley Centre for Natural Resources Research & Management. Research Report. Smithers, BC. 23 p.
- Hamann, A.; Wang, T. 2006. Potential effects of climate change on ecosystem and tree species distribution in British Columbia. *Ecology*, 87: 2773–2786.
- Hobbs, R. J.; Cramer, V. A. 2008. Restoration ecology: Interventionist approaches for restoring and maintaining ecosystem function in the face of rapid environmental change. *Annual Review Environmental Resources*. 33: 39–61.
- Hof, C.; Levinsky, I.; Araújo, M. B.; Rahbek, C. 2011. Rethinking species' ability to cope with climate change. *Global Change Biology*. Accepted Article doi:10.1111/j.1365-2486.2011.02418.x.
- Hoff, R. J.; McDonald, G. I.; Bingham, R. T. 1976. Mass Selection for blister rust resistance: A method for natural regeneration of western white pine. Research Note INT-202, Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station. 11 p.
- Iniguez, J. M.; Swetnam, T. W.; Baisan, C. H. 2009. Spatially and temporally variable fire regime on Rincon Peak, Arizona, USA. *Fire Ecology*. 5: 3–21
- Jackson, S.; Campbell, E. 2008. Assessing the threat of mountain pine beetle to whitebark pine in British Columbia. Project Report, FIA-FSP Project #M07-5048. BC Ministry of Forests and Range, Victoria, BC.

- Jenkins, M. J.; Hebertson, E.; Page, W.; Jorgensen, C. A. 2008. Bark beetles, fires, and implications for forest management in the Intermountain West. *Forest Ecology and Management*. 16-34.
- Jewett, J. T. 2009. Spatiotemporal relationships between climate and whitebark pine mortality in the Greater Yellowstone Ecosystem. Thesis. Montana State University, Bozeman, MT, USA.
- Keane, R. E. 2001. Successional dynamics: modeling an anthropogenic threat. Pages 159-192. *in* Whitebark pine communities: ecology and restoration. Washington: Island Press.
- Keane, R. E.; Veblen, T.; Ryan, K. C.; Logan, J.; Allen, C.; Hawkes, B. 2002. The cascading effects of fire exclusion in the Rocky Mountains. Pages 133-153 *in* Rocky Mountain Futures: An Ecological Perspective. Washington: Island Press.
- Keane, R. E.; Parsons, R. A. 2010. A management guide to ecosystem restoration treatments: Whitebark pine forests of the Northern Rocky Mountains. General Technical Report RMRS-GTR-232, U.S. Department of Agriculture, Forest Service Rocky Mountain Research Station, Fort Collins, CO.
- Keane, R.; Morgan, P.; Menakis, J. 1994. Landscape assessment of the decline of whitebark pine (*Pinus albicaulis*) in the Bob Marshall Wilderness Complex, Montana, USA. *Northwest Science*. 68: 213-229.
- Keeton, W. S.; Mote, P. W.; Franklin, J. F. 2007. Climate variability, climate change, and western wildfire with implications for the urban-wildland interface. *Advances in the Economics of Environmental Resources*. 6: 225-253.
- Kitchen, S. 2010. Historic Fire Regimes of Eastern Great Basin Mountains Reconstructed from Tree Rings. Ph.D. Dissertation. Brigham Young University. Provo, UT. 166 p.
- Kipfmüller, K. F. 2003. Fire-climate-vegetation interactions in subalpine forests of the Selway-Bitterroot Wilderness Area, Idaho and Montana, USA. Ph.D. Dissertation. The University of Arizona, Tucson, AZ, USA. 322 p.
- Kipfmüller, K. F.; Kupfer, J. A. 2005. Complexity of successional pathways in subalpine forests of the Selway-Bitterroot Wilderness Area. *Annals of the Association of American Geographers*. 95: 495-510.
- Koteen, L. 1999. Climate change, whitebark pine, and grizzly bears in the greater Yellowstone ecosystem. Pages 343-364 *in* S. H. Wildlife responses to climate change. Washington: Island Press.
- Lafleur, B.; Paré, D.; Munson, A. D.; Bergeron, Y. 2010. Response of northeastern North American forests to climate change: Will soil conditions constrain tree species migration? *Environmental Reviews*. 18: 279-289.
- Larson, E. R. 2009. Status and dynamics of whitebark pine (*Pinus albicaulis* Engelm.) forests in southwest Montana, central Idaho, and Oregon, U.S.A. Ph.D. Dissertation. University of Minnesota, Minneapolis, MN, USA. 176 p.
- Larson, E. R. (In press) Influences of the biophysical environment on blister rust and mountain pine beetle, and their interactions, in whitebark pine forests. *Journal of Biogeography*.
- Larson, E. R.; Kipfmüller, K. F. 2010. Patterns in whitebark pine regeneration and their relationships to biophysical site characteristics in southwest Montana, central Idaho, and Oregon, USA. *Canadian Journal of Forest Research*. 40: 476-487.
- Larson, E. R.; van de Gevel, S. L.; Grissino-Mayer, H. D. 2009. Variability in fire regimes of high-elevation whitebark pine communities, western Montana, USA. *Ecoscience*. 16: 282-298.
- Li, C.; Barkley, H.; Hawkes, B.; Taylor, S. 2005. Lodgepole pine forest age class dynamics and susceptibility to mountain pine beetle outbreaks. *Ecological Complexity*. 3: 232-239.
- Logan, J. A.; Powell, J. A. 2001. Ghost forests, global warming, and the mountain pine beetle (Coleoptera: Scolytidae). *American Entomologist*. 47: 160-173.
- Lynch, H. J.; Renkin, R. A.; Crabtree, R. L.; Moorcroft, P. R. 2006. The influence of previous mountain pine beetle (*Dendroctonus ponderosae*) activity on the 1988 Yellowstone fires. *Ecosystems*. 9: 1318-1327.
- Mathiasen, R. L.; Daugherty, C. M. 2001. Susceptibility of foxtail pine and western white pine to limber pine dwarf mistletoe in northern California. *Western Journal of Applied Forestry*. 16: 58-60.
- Mathiasen, R. L.; Hawksworth, F. J. 1988. Dwarf mistletoes on western white pine and whitebark pine in northern California and southern Oregon. *Forest Science*. 34: 429-440.
- Mattson, D. J.; Reinhart, D. P. 1990. Whitebark pine on the Mount Washburn Massif, Yellowstone National Park. Pages 106-117 *in* Proceedings—Symposium on whitebark pine ecosystems: Ecology and management of a high-mountain resource. Bozeman, MT: U.S. Department of Agriculture, Forest Service.
- Mbogga, M. S.; Wang, X. L.; Hamann, A. 2010. Bioclimate envelope model predictions for natural resource management: dealing with uncertainty. *Journal of Applied Ecology*. 47: 731-740.
- McCabe, G. J.; Palecki, M. A.; Betancourt, J. L. 2004. Pacific and Atlantic Ocean influences on multidecadal drought frequency in the United States. *Proceedings of the National Academy of Sciences*. 101: 4136-4141.
- McKinney, S. T.; Fiedler, C. E.; Tomback, D. F. 2009. Invasive pathogen threatens bird-pine mutualism: implications for sustaining a high-elevation ecosystem. *Ecological Applications*. 19: 597-607.
- Minckley, T. A.; Whitlock, C.; Bartlein, P. J. 2007. Vegetation, fire, and climate history of the northwestern Great Basin during the last 14,000 years. *Quaternary Science Reviews*. 26: 2167-2184.
- Moody, R. 2006. Post-fire regeneration and survival of whitebark pine (*Pinus albicaulis* Engelm.). M.Sc. Thesis. University of British Columbia, Vancouver, BC. 108 p.
- Morgan, P.; Bunting, S. C. 1990. Fire effects in whitebark pine forests. Pages 166-170 *in* Symposium on Whitebark Pine Ecosystems: Ecology and Management of a High-Mountain Resource. General Technical Report GTR-INT-270. Ogden, UT: U.S. Department of Agriculture, Forest Service Intermountain Forest and Range Research Station.
- Morgan, P.; Bunting, S. C.; Keane, R. E.; Arno, S. F. 1994. Fire ecology of whitebark pine (*Pinus albicaulis*) forests in the Rocky Mountains, USA. Pages 136-142 *in* Proceedings—Symposium on subalpine stone pines and their environment: The status of our knowledge. General Technical Report GTR-INT-309. Ogden, UT: U.S. Department of Agriculture, Forest Service Intermountain Research Station.
- Murray, M. 2007. Fire and Pacific Coast whitebark pine. Pages 51-60 *in* Whitebark pine: a Pacific Coast perspective. R6-NR-FHP-2007-01. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Region.
- Murray, M. P.; Bunting, S. C.; Morgan, P. 1998. Fire history of an isolated subalpine mountain range of the intermountain region, United States. *Journal of Biogeography*. 25: 1071-1080.
- Murray, M. P.; Bunting, S. C.; Morgan, P. C. 2000. Landscape trends (1753-1993) of whitebark pine (*Pinus albicaulis*) forests in the West Big Hole Range, Idaho/Montana, U.S.A. *Arctic, Antarctic, and Alpine Research*. 32: 412-418.
- Norment, C. J. 1991. Bird use of forest patches in the subalpine forest-alpine tundra ecotone of the Beartooth Mountains, Wyoming. *Northwest Science*. 65: 1-10.
- Reinhardt, E. J.; Scott, H.; Gray, K. L.; Keane, R. E. 2006. Estimating canopy fuel characteristics in five conifer stands in the western United States using tree and stand measurements. *Canadian Journal Forest Research*. 36: 1-12.

- Romme, W. H. 1980. Fire frequency in subalpine forests of Yellowstone National Park. Pages 27-30 in Proceedings of the fire history workshop. Tucson, AZ: U.S. Department of Agriculture, Forest Service Rocky Mountain Forest and Range Experiment Station.
- Romme, W. H. 1982. Fire and landscape diversity in subalpine forests of Yellowstone National Park, Wyoming. *Ecological Monographs*. 52: 199-221.
- Romme, W. H.; Knight, D. H. 1981. Fire frequency and subalpine forest succession along a topographic gradient in Wyoming. *Ecology*. 62: 319-326.
- Running, S. W. 2006. Is global warming causing more, larger wildfires. *Science*. 313: 927-928.
- Ryan, K. C. 1991. Vegetation and wildland fire: implications of global climate change. *Environment International*. 17: 169-178.
- Ryerson, D. 1983. Population structure of *Pinus balfouriana* Grev. & Balf. along the margins of its distribution area in the Sierran and Klamath regions of California. Thesis. Sacramento, CA: California State University. 197 p.
- Schmid, J. M.; Amman, G. D. 1992. *Dendroctonus* beetles and old-growth forests in the Rockies. Pages 51-59 in Proceedings of the workshop on: Old growth forests in the Southwest and Rocky Mountain region. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station. Gen. Tech. Rep. RM-213.
- Schoettle, A. W.; Sniezko, R. A. 2007. Proactive intervention to sustain high-elevation pine ecosystems threatened by white pine blister rust. *Journal of Forest Restoration*. 12: 327-336.
- Sherriff, R.; Veblen, T. T.; Sibold, J. S. 2001. Fire history in high elevation subalpine forests in the Colorado Front Range. *Ecoscience*. 8: 369-380.
- Shoal, R. Z.; Lorenz, T.; Aubry, C. 2008. Land managers guide to whitebark pine restoration techniques. USDA Forest Service Pacific Southwest Region, Olympia, WA.
- Siderius, J.; Murray, M. 2005. Fire knowledge for managing Cascadian whitebark pine ecosystems. Final report to the Interagency Joint Fire Sciences Program, (#01B-3-3-26). 44 p.
- Skinner, W. R.; Shabbar, E.; Flannigan, M. D.; Logan, K. 2006. The association between circulation anomalies in the mid-troposphere and area burned by wildland fire in Canada. *Journal of Geophysical Research*. 111, D14106, doi:10.1029/2005JD006738.
- Simard, M.; Romme, W. H.; Griffin, J. M.; Turner, M. 2011. Do mountain pine beetle outbreaks change the probability of active crown fire in lodgepole pine forests? *Ecological Monographs*. 81:3-24.
- Smith, C.; Wilson, B.; Rasheed, S.; Walker, R.; Carolin, T.; Sheperd, B. 2008. Whitebark pine and blister rust in the Rocky Mountains of Canada and northern Montana. *Canadian Journal of Forest Research*. 38: 982-995.
- Six, D. L.; Adams, J. 2007. White pine blister rust severity and selection of individual whitebark pine by the mountain pine beetle (Coleoptera: Curculionidae, Scolytinae). *Journal of Entomological Science*. 42: 345-353.
- Stuart, J. D.; Agee, J. K.; Gara, R. I. 1989. Lodgepole pine regeneration in an old, self-perpetuating forest in south central Oregon. *Canadian Journal of Forest Research*. 19: 1096-1104.
- Tomback, D. F. 2005. The impact of seed dispersal by the Clark's Nutcracker on whitebark pine: Multi-scale perspective on a high mountain mutualism. Pages 181-201 in *Mountain Ecosystems: Studies in treeline ecology*. New York, NY: Springer.
- Tomback, D.; Achuff, P. 2010. Blister rust and western forest biodiversity: ecology, values, and outlook for white pines. *Forest Pathology*. 40: 186-225.
- Tomback, D. F.; Sund, S. K.; Hoffman, L. A. 1993. Post-fire regeneration of *Pinus albicaulis*: height-age relationships, age structure, and microsite characteristics. *Canadian Journal of Forest Research*. 23: 113-119.
- Warwell, M. V.; Rehfeldt, G.; Crookston, N. 2007. Modeling contemporary climate profiles of whitebark pine (*Pinus albicaulis*) and predicting responses to global warming. Pages 139-142 in *Proceedings of the conference whitebark pine: a Pacific Coast perspective*. Ashland, OR. Ashland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Region.
- Yanchuk, A.; Murphy, J.; Wallin, K. 2008. Evaluation of genetic variation of attack and resistance in lodgepole pine in the early stages of a mountain pine beetle outbreak. *Tree Genetics Genomes*. 4: 171-180.

The content of this paper reflects the views of the author(s), who are responsible for the facts and accuracy of the information presented herein.
