

**Status and Dynamics of Whitebark Pine
(*Pinus albicaulis* Engelm.) Forests in Southwest
Montana, Central Idaho, and Oregon, U.S.A.**

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Dedication

For your encouragement, patience, support, patience,
advice, patience, smile, patience, laughter, patience, and Love...

For carrying into the field a pack that was too heavy in 2006,
our baby in your belly in 2007, and our baby on your back in 2008...

For sharing with me the beauty of the field,
my joys and frustrations, my break throughs and break downs...

For raising our beautiful baby into a beautiful child...

For making my life more wonderful
every instant I am alive...

I dedicate this work to my wife, Danica.

I love you.



Abstract

Whitebark pine (*Pinus albicaulis*) is a vital component of high-elevation forest communities across western North America, but declines in its health and dominance have raised concerns about the potential loss of this foundation species from many of the places it is currently found. The factors implicated as driving mechanisms of these declines include the exotic fungal disease white pine blister rust (*Cronartium ribicola*), outbreaks of the native mountain pine beetle (*Dendroctonus ponderosae*), climate change, and fire suppression, but much of the research that links these mechanisms with whitebark pine declines is geographically restricted to the Northern Rockies, an important but relatively small part of the range of whitebark pine. My dissertation research developed baseline data on the status of whitebark pine communities and critically assessed the effects of blister rust, mountain pine beetle, and fire suppression on whitebark pine communities across the central distribution of the species. Specifically, I assessed (1) blister rust infection levels and the causes and rates of whitebark pine mortality, (2) patterns in the abundance and distribution of whitebark pine regeneration, and (3) patterns in disturbance, succession, and the effects of fire suppression on the structure and composition of the whitebark pine communities at my sites. Blister rust rates were generally lowest in western Oregon and highest in central Idaho. Mortality rates varied widely but mountain pine beetle activity was the primary cause of whitebark pine death at most sites. Whitebark pine regeneration was nearly ubiquitous and more abundant on cooler, drier sites with lower subalpine fir abundances and higher rates of mountain pine beetle-related mortality. Many of the stands I examined contained post-fire cohorts, but several stands also contained cohorts that established following episodes of

mountain pine beetle-related mortality, illustrating the need for multiple lines of evidence when reconstructing fire history in whitebark pine forests. Patterns in succession and forest composition were strongly influenced by site-specific climate conditions and I found limited evidence of advancing succession due to fire suppression at my sites. The diverse and complex dynamics of whitebark pine communities require a nuanced discussion of its current and future status.

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Chapter 1: Diversity and Uncertainty in Whitebark Pine Communities and the Inspiration for this Research

The Ecology and Decline of Whitebark Pine Communities

To those who have spent time in the mountains of western North America, few images are more symbolic of high-elevation environments than the graceful silhouettes of whitebark pine (*Pinus albicaulis* Engelm.) trees. This hardy species is often found as the sole tree inhabiting harsh and windswept slopes of mountain ridges and crests in ancient and twisted forms, bent low before the winds but gripping the mountain side with such tenacity as to weather the most brutal storms (Figures 1a–1c). In mountain valleys and at lower elevations, whitebark pines mingle with other subalpine tree species and can grow to be large trees with full, spreading canopies that provide shelter to myriad wildlife species as well as the occasional hiker (Figures 1d, 1e). Individual whitebark pine trees can achieve extremely old ages, with several individuals growing in remote settings found to be over 1,000 years old (Perkins and Swetnam 1996; Luckman and Youngblut 1999; Kipfmueller 2008). These trees have recorded volumes of ecological data in their growth rings over the centuries, and it is these data that may provide critical insights into our understanding of the past, present, and future dynamics of this singular tree species.

Whitebark pine is an important component of several subalpine forest community types (Arno 2001). Near treeline and on droughty, southerly slopes, whitebark pine is often found as scattered individual trees or as the dominant species of open woodlands. In these settings, whitebark pine plays a crucial role stabilizing loose soils and catching snow (Arno and Hammerly 1984), thereby maintaining the headwaters of many alpine

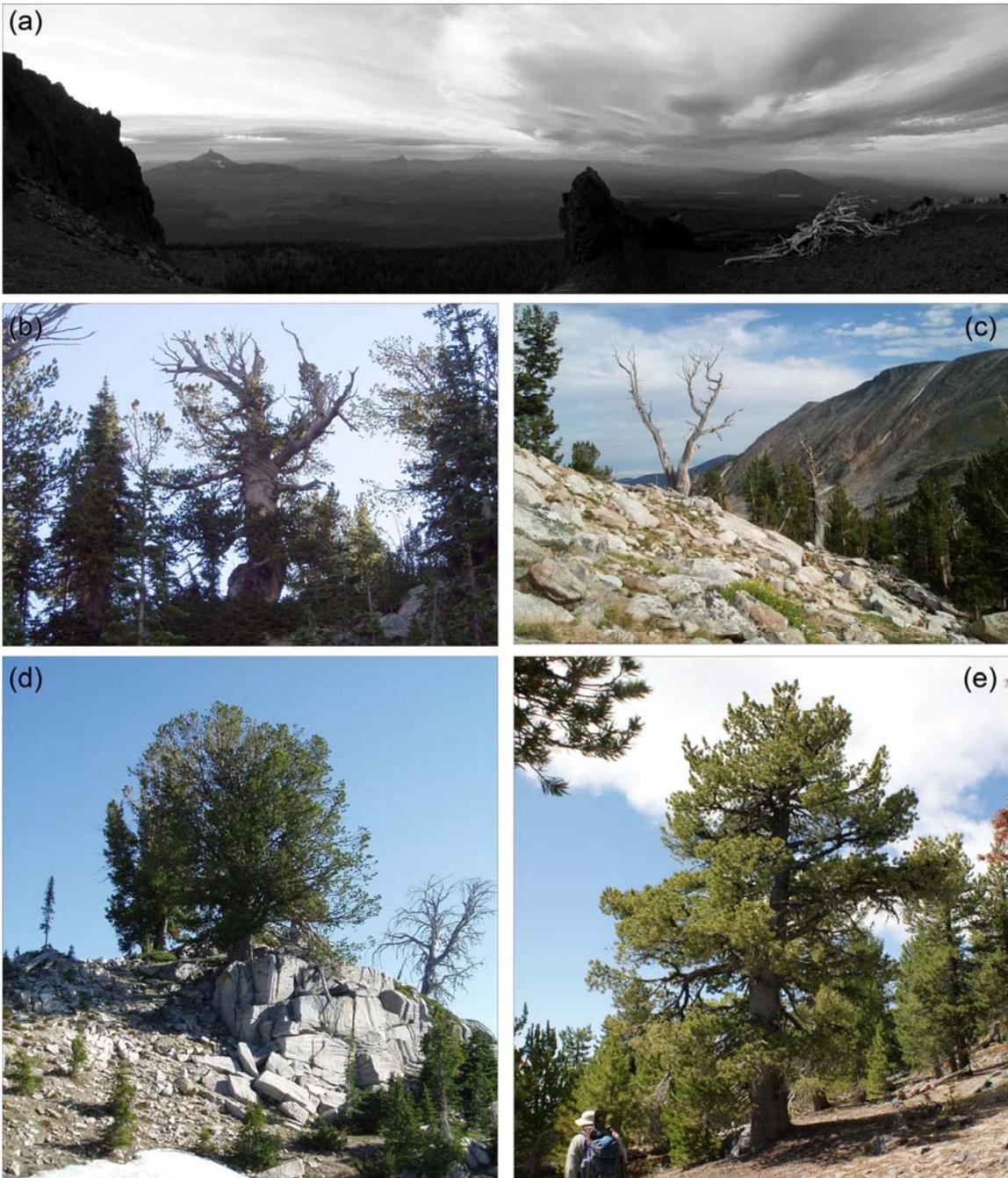


Figure 1. Whitebark pine (*Pinus albicaulis* Engelm.) trees exhibiting characteristics of wind and age (a) on Black Crater in central Oregon, (b) at the crest of Glacier Pass in the Wallowa Mountains, and (c) on the slopes above Goddess Lake in the Pioneer Mountains, and open grown whitebark pine with spreading canopies in (d) the Lakes Basin area of the Wallowa Mountains and (e) on the rim of Newberry Caldera, Paulina Peak.

watersheds that provide critical sources of moisture throughout the year for surrounding communities and ecosystems (Farnes 1990). The presence of whitebark pine at these harsh sites ameliorates microsite conditions sufficiently to facilitate increased biodiversity in both plant and animal communities (Tomback and Kendall 2001). At more moderate sites, whitebark pine is a co-dominant species with other subalpine conifers, in particular subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.), Engelmann spruce (*Picea engelmannii* Parry ex Engelm.), and mountain hemlock (*Tsuga mertensiana* (Bong.) Carr.) (Weaver and Dale 1974). In many of these sites, the physical presence of whitebark pine provides shelter from wind, sun, and ice that facilitates the establishment and growth of other less hardy tree species where they would otherwise be unable to survive or more limited in growth (Callaway 1998). In lower subalpine zones, whitebark pine often pioneers recently disturbed sites and is considered a seral species that is eventually succeeded in dominance by more shade-tolerant tree species (Pfister and Arno 1980); however, the long life span of whitebark pine and intermediate shade tolerance often result in whitebark pine maintaining its presence in a stand, albeit at lower levels, throughout the history of many lower subalpine forest stands until the next disturbance event creates openings sufficient for whitebark pine to regenerate abundantly (Campbell and Antos 2003).

In many of the community types that it exists, whitebark pine serves as the foundation species of an intricate ecosystem involving Clark's nutcrackers (*Nucifraga columbiana*), red squirrels (*Tamiasciurus hudsonicus*), black bears (*Ursus americanus*), and grizzly bears (*Ursus arctos*) (Ellison et al. 2005). The seeds of whitebark pine are relatively large and rich in fat and protein, making them a favorite food for a variety of

mountain wildlife (Arno 1986). Whitebark pine seeds are somewhat inaccessible, however, as the cones are indehiscent, meaning that they do not open of their own accord (Owens, Kittirat, and Mahalovich 2008). The evolution of indehiscence in whitebark pine is probably the result of a mutualistic relationship between the tree and the Clark's nutcracker, which serves as the primary dispersal mechanism for whitebark pine (Lanner 1982; Tomback 1982; Hutchins and Lanner 1982). The beak of the bird is perfectly adapted to remove the seeds from the cones, after which the nutcracker stores up to a few dozen pine seeds in a sublingual pouch. Once their pouch is full, the birds typically fly to nearby forest openings or windswept slopes where they bury the seeds in a cache that they can return to later in the year for food (Tomback 2005). Nutcrackers can disperse whitebark pine seeds over a range of distances, with individual birds having been observed caching seeds as near as the at the base of the tree from which they were picked up to as far as 13 km away (Tomback 1982; Hutchins and Lanner 1982). The birds tend to bury the seeds at the ideal depth for germination, and those seeds that are forgotten or otherwise unrecovered are the source of the next generation of whitebark pine (Lanner 1996). Red squirrels also prey on whitebark pine seeds by cutting entire cones down and gathering them together in middens that can contain hundreds of whitebark pine cones. The concentrated food sources provided by squirrel middens have lured the other major players in whitebark pine ecosystems into the picture – grizzly bears and black bears (Felicetti et al. 2003). Bears frequently travel through whitebark pine forests to search out and raid squirrel middens in preparation for winter hibernation (Mattson and Reinhart 1997). The importance of whitebark pine seeds as a food source for bears is clearly illustrated by the nearly perfect inverse relationship between whitebark pine seed

production and the number of human-bear interactions in Yellowstone National Park, with bears more frequently seeking out food at low elevations when whitebark pine seeds are unavailable at high elevations (Mattson, Kendall, and Reinhart 2001). The status of whitebark pine forests are therefore intimately linked with the well being of these animal species, and it is in large part these connections that inspired the rising concern over the rapidly diminishing health and dominance of whitebark pine in many parts of the species' range due to the synergistic effects of several factors (Kendall and Keane 2001).

The mountain pine beetle (*Dendroctonus ponderosae* Hopkins) is a bark beetle native to North America that has long been recognized as an important factor in the dynamics of lodgepole pine (*Pinus contorta* Dougl. ex Loud.) forests (Amman and Baker 1972; Romme, Knight, and Yavitt 1986), but its historical role in whitebark pine forests is less certain (Bartos and Gibson 1990). Documented twentieth-century mountain pine beetle outbreaks caused extensive mortality in whitebark pine forests from the central Rocky Mountains to the Pacific Northwest (Bartos and Gibson 1990; Perkins and Swetnam 1996; Kipfmüller, Swetnam, and Morgan 2002; Larson, van de Gevel, and Grissino-Mayer 2009), with sun-bleached skeletons of long-dead whitebark pine etched with the j-shaped galleries of mountain pine beetle larvae providing stark evidence of these past events (Ciesla and Furniss 1975; Arno and Hammerly 1984). Over the past decade mountain pine beetle populations have frequently reached epidemic levels, resulting in massive mortality of lodgepole pine and whitebark pine across much of western North America (Raffa et al. 2008). These outbreaks have raised concerns over the potential role of climate change in driving unprecedented mountain pine beetle activity, particularly in whitebark pine forests that were previously thought to be too cold

to regularly support large beetle populations (Logan et al. 1995; Logan and Powell 2001; Hicke et al. 2006).

The introduction of the exotic white pine blister rust (*Cronartium ribicola* (A. Dietr.) J.C. Fisch.) in Vancouver, British Columbia, in the early 1900s brought an additional disturbance agent into whitebark pine forests that has had and will continue to have profound influences on these systems (Kinloch 2003). Blister rust was first documented on whitebark pine in the coastal range of British Columbia in 1926 and by 1938 was found in northern Idaho (Childs, Bedwell, and Englerth 1938). Since that time blister rust has spread throughout most of the range of whitebark pine (McDonald and Hoff 2001). Surveys have found highly variable blister rust infection rates and severities within and across different landscapes, with infection rates in individual stands ranging from 0–100 percent at sites throughout the Canadian Rocky Mountains, U.S. Northern Rockies, and the Pacific Northwest (Keane and Arno 1993; Campbell and Antos 2000; Smith and Hoffman 2001; Goheen 2002; Zeglen 2002; Smith et al. 2008). Blister rust typically infects and kills the upper branches and crowns of whitebark pine first, which is where the majority of cones are produced in healthy trees. Declines in cone production below a certain threshold due to increased blister rust infection rates may accelerate the loss of whitebark pine from areas of high blister rust incidence by disrupting the relationship between whitebark pine and the Clark's nutcrackers (McKinney, Fiedler, and Tomback 2009). Blister rust may further unravel the fabric of forest communities within the treeline ecotone by reducing the presence of whitebark pine in treeline environments where it plays a critical pioneer role that facilitates vegetation development (Tomback and Resler 2007; Resler and Tomback 2008). Evidence also suggests that blister rust may

increase the susceptibility of individual whitebark pine trees to mountain pine beetle infestation (Six and Adams 2007). The evolutionary novelty and interactions with other causes of decline may result in white pine blister rust having the most striking and long-lasting effects on whitebark pine communities.

Climate change may affect whitebark pine communities directly through warmer temperatures and indirectly through interactions with other disturbance processes.

Warmer temperatures have been associated with a general shift upward in elevation of forest ecosystems at some locations in the past (Kullman 2001; Fagre, Peterson, and Hessler 2003), and future warming has been predicted to result in large reductions in the aerial extent of whitebark pine habitat (Bartlein, Whitlock, and Shafer 1997; Schrag, Bunn, and Graumlich 2008). In many cases, whitebark pine habitat is limited to the upper-most elevations of the mountain ranges in which it is currently found, and the upward migrations of montane tree species could essentially push whitebark pine off the tops of these mountains. Indirectly, warmer temperatures are also a concern for their potential to exacerbate future mountain pine beetle outbreaks (Negron et al. 2008) and drive increased fire frequency and severity in subalpine forests through reduced snowpack and longer fire seasons (Fagre, Peterson, and Hessler 2003; Westerling et al. 2006).

Finally, fire suppression has been widely implicated as one of the primary causes of declines in whitebark pine communities (Keane 2001a). Many stands of whitebark pine include fire-scarred trees that serve as evidence of past low-severity fires (Arno 1980; Larson, van de Gevel, and Grissino-Mayer 2009). The exclusion of low-severity fires from these stands through fire suppression and grazing over the past century is

thought to have enabled fire-intolerant species to increase in abundance and successional replace whitebark pine (Morgan et al. 1994). In addition to outcompeting whitebark pine, encroachment by fire-intolerant species into previously open whitebark pine forests adds ladder fuels that would likely result in higher severity fires than historically occurred at these sites, further driving disturbance regimes out of their historical range of variability (Morgan and Bunting 1990). Additionally, it has been suggested that suppression of subalpine forest fires has reduced the number of fire-created forest openings that provide ideal habitat for whitebark pine regeneration (Keane 2001a).

As dire as the case of whitebark pine may appear to be in light of these factors, uncertainty and hope also exist with respect to the future of this species. The mountain pine beetle outbreaks currently ravaging western forests are unprecedented in the historical records, yet mortality from these outbreaks is rarely 100 percent (Rocca and Romme 2009) and while historical records only extend over the past century, evidence suggests that whitebark pine and mountain pine beetles have coexisted for millennia (Brunelle et al. 2008). The introduction of blister rust to North America has profoundly changed the dynamics of whitebark pine communities, but the drier conditions that are projected for many areas because of climate change may result in less suitable conditions for the successful spread of blister rust spores and an overall reduction in the effects of this disease on whitebark pine communities (Boland et al. 2004). Research also suggests that the selective pressures of blister rust-related mortality may result in increased resistance to the disease over relatively few generations and programs breeding rust-resistant whitebark pine are showing some signs of success (McDonald and Hoff 2001).

Climate is changing rapidly, but the models forecasting declines in whitebark pine habitat are based on species climate envelopes derived from modern records which may not reflect the climate conditions under which many of these forests established. These models also incorporate static interpretations of current forest dynamics that may not accurately predict changes in species' competitive interactions that may following changes in climate (Williams et al. 2004). Novel climates will emerge and competitive interactions will change along with climate and therefore these models should be interpreted cautiously (Davis et al. 1998). Additionally, if climate change results in more frequent fires this essentially counters the possible effects of fire suppression and may therefore actually increase the availability of sites suitable for whitebark pine regeneration. Fire suppression has resulted in dramatic changes in the structure of some forest systems, particularly the dry forests of the American Southwest, but applying this paradigm to subalpine forests is likely inappropriate in many cases due to the fundamentally different dynamics that govern the fire regimes of these forest systems (Schoennagel, Veblen, and Romme 2004). Furthermore, much of the evidence used to suggest the encroachment of fire intolerant species into whitebark pine forests is based on tree size distributions and static age-structure data, both of which can provide false impressions of the actual dynamics governing a stand (Johnson, Miyanishi, and Kleb 1994).

In addition to these sources of uncertainty, a significant portion of the research from which these conclusions have been drawn was conducted in the U.S. Northern Rockies (e.g., Tomback, Arno, and Keane 2001b and references within), a region that includes a large proportion of the distribution of whitebark pine in the U.S. but is not

representative of the broad geographic and environmental distribution of whitebark pine as a whole. While the body of research investigating many aspects of whitebark pine communities has grown over recent years, several basic yet critical questions remain with respect to the dynamics of whitebark pine forests across much of the species range and the likelihood that answers to these questions will embody more complexity than is currently granted to whitebark pine communities is high. A more nuanced perspective on whitebark pine communities is needed as incomplete information is forming the foundation of management and restoration activities as well as efforts to list the species under the U.S. Endangered Species Act (NRDC 2008). Although my dissertation may read like a critique of current efforts, I did not undertake this research to undermine the important work being done by the many people and groups interested and concerned with the plight of whitebark pine, but rather I hoped to provide insight into some of the lingering questions concerning the status and dynamics of this embattled species and in doing so help develop a more complete understanding of whitebark pine communities.

Description of the Dissertation

My research examined several key aspects of whitebark pine communities in areas that at the time I developed my project had little published information available. Specifically, I documented the status of whitebark pine in terms of blister rust rates, mortality, and forest composition and examined patterns in regeneration, disturbance, and succession in whitebark pine communities along a roughly east-west transect across the central distribution of the species (Figure 2). Documenting the status of whitebark pine is an important step toward assembling the baseline data that will be critical to monitor

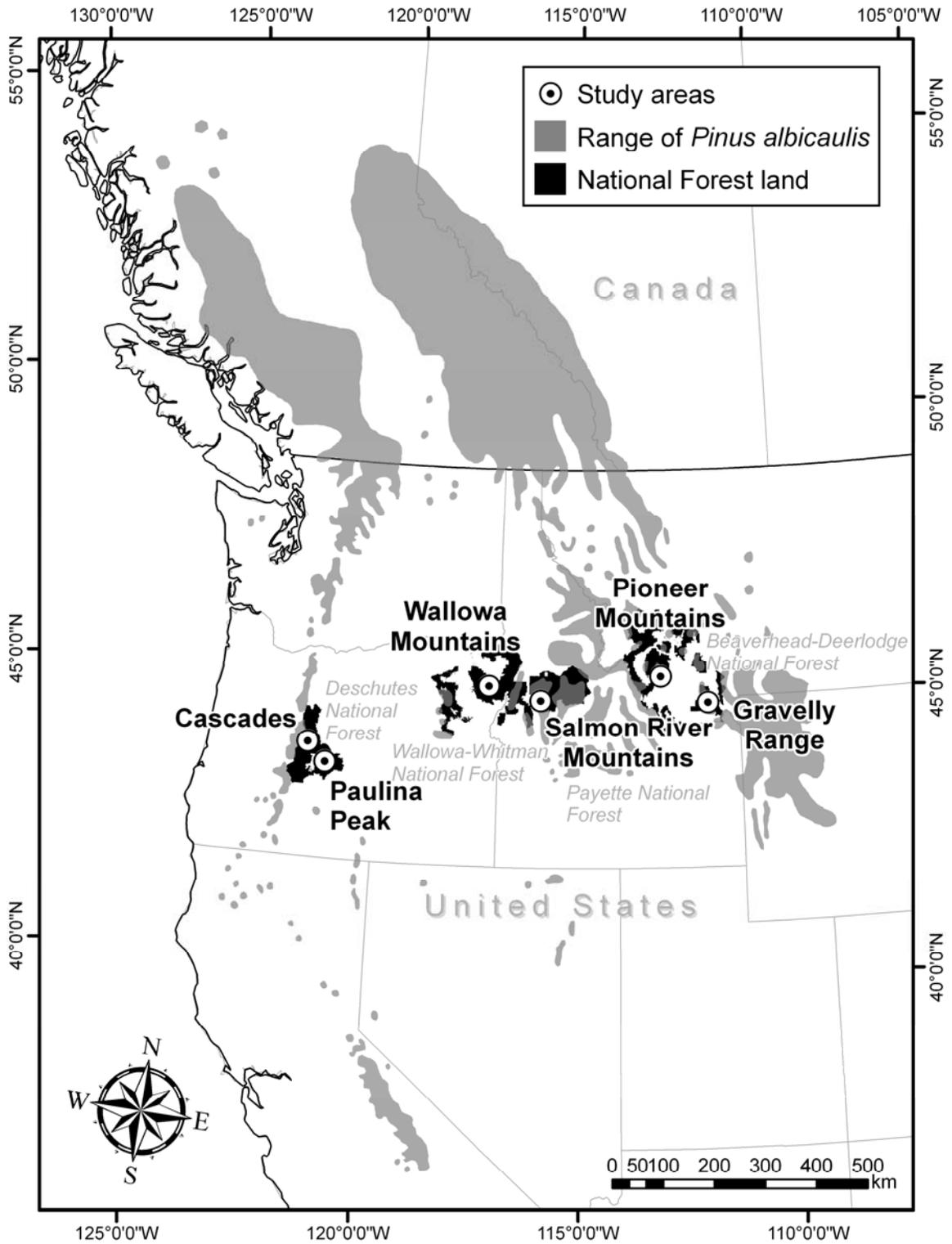


Figure 2. Study area map.

future changes in whitebark pine communities and to assess the effects of management activities. Examining patterns in regeneration, disturbance, and succession is in a sense assessing the “vital traits” (sensu Noble and Slatyer 1980) of not just whitebark pine as a species, but more so of the entire communities that are supported and would be utterly transformed in the absence of this foundation species (Ellison et al. 2005). Therefore the topics I covered in my dissertation provided insight into both a static snapshot of current conditions and the mechanisms that influence whitebark pine community dynamics in an attempt to create a more holistic understanding of this complex system.

I relied heavily on dendroecological methods to describe the history of the stands I studied (Kipfmüller and Swetnam 2001) and coupled these methods with traditional metrics of stand structure and composition (Cottam and Curtis 1956). One of the key principles of dendroecology I employed was that of crossdating, or comparing patterns in ring width and other structural features among trees that grew in similar environments to ensure that the exact year that each ring represents is assigned accordingly (Douglass 1922). Crossdating enabled me to describe tree and stand ages, the occurrence of past disturbances, and the timing and causes of tree mortality with accuracy and temporal precision that is not attainable through simple ring counts, particularly for dead trees and trees growing as slowly as many of those included in this study (Figure 3). The application of these methods together granted me a more complete understanding of the dynamics of these communities than would be possible using either approach alone.

The structure of my dissertation includes this introductory chapter followed by three research chapters that attended to the different aspects of whitebark pine communities listed above and a closing chapter that synthesized the results of my

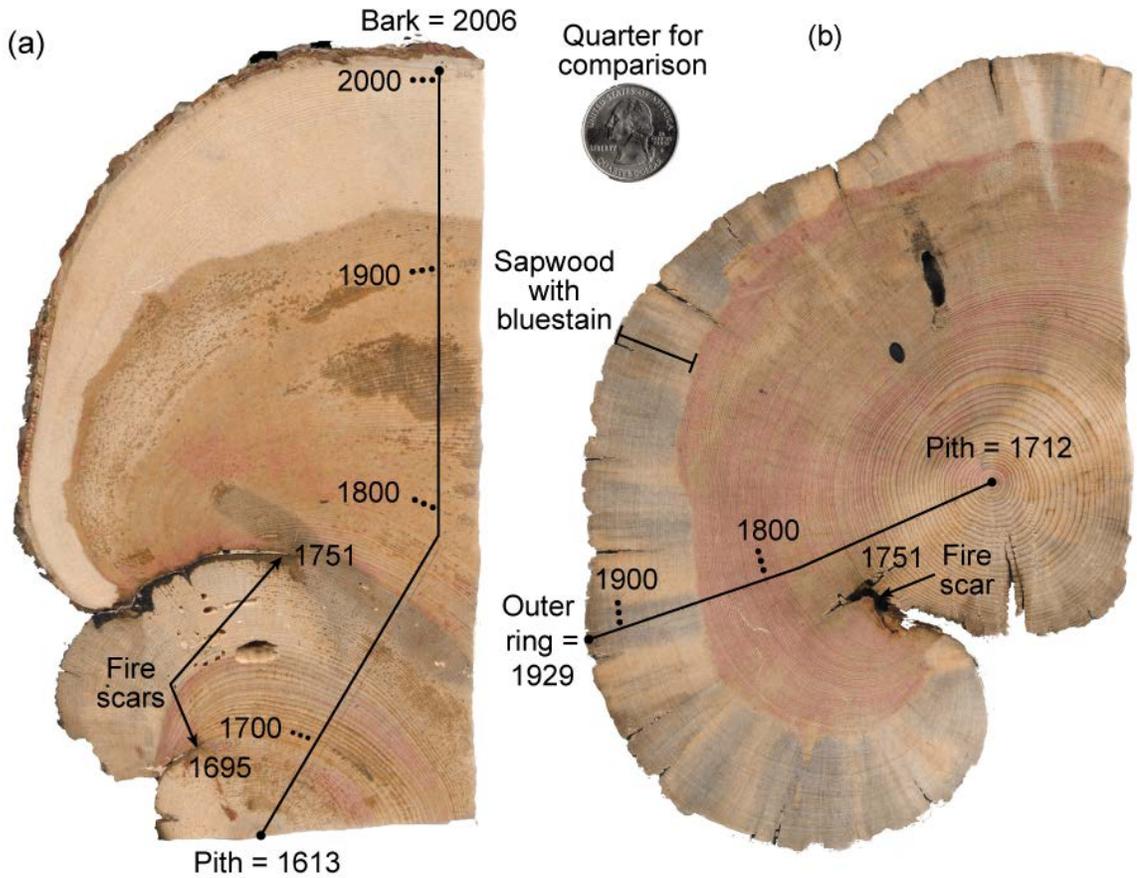


Figure 3. Tree-ring samples illustrating the slow growth rates of whitebark pine at my sites. Both samples were collected on the south slopes of Baldy Mountain in the Pioneer Mountains. The sample shown in (a) was taken from a live tree 22 cm in diameter at breast height that was 397 years old and contained two fire scars. The sample shown in (b) was 13.5 cm diameter at breast height, had recorded a fire in 1751, and was 227 years old when it was killed by mountain pine beetles (*Dendroctonus ponderosae* Hopkins) as indicated by j-shaped galleries on the bole of the tree and the bluestain fungus visible in the sapwood of the sample. The quarter is included as a size comparison.

dissertation. Each of the research chapters was written as a stand alone publication and therefore some redundancy exists with respect to their introductions and descriptions of study sites and methods; however, when taken together the results and conclusions from each chapter coalesce into what I believe is an important and useful body of information that will help inform the management and restoration of whitebark pine communities.

In Chapter 2 I present data on the general forest composition and structure, rates of blister rust infection, patterns and causes of whitebark pine mortality, and levels of whitebark pine regeneration I observed at my study sites. These data are offered as contributions to the efforts that are currently underway to develop baseline data on the overall status of whitebark pine communities across the full range of the species spearheaded by the Whitebark Pine Ecosystem Foundation (Tomback et al. 2005). In Chapter 3 I explore patterns in whitebark pine regeneration as they relate to disturbance and the biophysical environment at the site and landscape scales. This complements other research on whitebark pine regeneration focused on the mechanisms of regeneration as they are related to seed availability and the caching habits of Clark's nutcrackers and post-fire environments (e.g., Tomback 1994; Tomback et al. 2001). In Chapter 4 I describe patterns in disturbance and succession in whitebark pine forests and use these data along with site-specific climate data to critically assess the relative influences of climate and fire suppression and other disturbances on forest composition at my study sites. The results of this endeavor provide a lens through which to examine management activities in the context of site specific conditions to help increase the efficacy and ecological basis of restoration activities in whitebark pine forests. Chapter 5 serves as a summary and synthesis of the primary findings of my dissertation research.

Chapter 2. The Status of Whitebark Pine Communities in Southwest Montana, Central Idaho, and Oregon, U.S.A.

Introduction

Whitebark pine is a symbol of high-elevation environments across western North America. This long-lived tree species (1000+ yrs) (Perkins and Swetnam 1996; Luckman and Youngblut 1999; Kipfmueller 2008) is found along the crests of the Cascades and Sierra Nevada and throughout the northern Rocky Mountains (Arno and Hoff 1990) inhabiting harsh and windswept slopes at and above treeline in twisted forms. In these environments whitebark pine plays a crucial role stabilizing loose soils and catching snow (Arno and Hammerly 1984), thereby maintaining the headwaters of many alpine watersheds that provide critical sources of moisture throughout the year for surrounding human communities and low-elevation ecosystems (Farnes 1990). The shelter provided by whitebark pine trees at these harsh sites ameliorates microsite conditions and facilitates increased biodiversity among plant and animal communities (Callaway 1998; Tomback and Kendall 2001).

At lower elevations, whitebark pine is a component of several subalpine community types, including open woodlands near treeline where it is the dominant species, upper-subalpine forests as a co-dominant species along with subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.), Engelmann spruce (*Picea engelmannii* Parry ex Engelm.), lodgepole pine (*Pinus contorta* Dougl. ex Loud.), and mountain hemlock (*Tsuga mertensiana* (Bong.) Carr.), and lower subalpine habitat types as a seral species mixing with the above species as well as Douglas fir (*Pseudotsuga menziesii* (Mirbel) Franco) on

occasion (Pfister and Arno 1980; Arno 2001). In many of these settings, whitebark pine serves as the foundation species of an ecosystem involving Clark's nutcrackers (*Nucifraga columbiana* Wilson), red squirrels (*Tamiasciurus hudsonicus* Trouessart), black bears (*Ursus americanus* Pallas), and grizzly bears (*Ursus arctos* L.) (Ellison et al. 2005) and provides a critical food source for a variety of other mountain wildlife (Arno 1986). Yet in spite of its broad environmental tolerance and distribution, whitebark pine and the communities it supports are diminishing (Tomback, Arno, and Keane 2001b).

The presence and dominance of whitebark pine in high-elevation forests have undergone dramatic declines over the last 80 years, and a great amount of concern exists pertaining to its future status on the landscape (Tomback, Arno, and Keane 2001a). Twentieth century outbreaks of the native mountain pine beetle (*Dendroctonus ponderosae* Hopkins) caused extensive mortality in whitebark pine forests from the central Rocky Mountains to the Pacific Northwest (Bartos and Gibson 1990; Perkins and Swetnam 1996; Kipfmüller, Swetnam, and Morgan 2002), with abundant sun-bleached whitebark pine snags across these regions providing stark evidence of these past events (Ciesla and Furniss 1975; Arno and Hammerly 1984). The ongoing invasion of the exotic white pine blister rust (*Cronartium ribicola* (A. Dietr.) J.C. Fisch.) that began in the early 1900s has devastated northern whitebark pine populations (McDonald and Hoff 2001; Murray and Rasmussen 2003; Smith et al. 2008) and is likely to spread throughout the range of whitebark pine and other five-needle pine in the future (Kinloch 2003). Fire suppression has been implicated in the decline of whitebark pine as well (Keane 2001a), with less frequent fires decreasing the occurrence of forest openings critical for whitebark pine regeneration, increasing the susceptibility of aging stands to future beetle outbreaks,

and enabling fire-intolerant species to encroach upon mature stands of whitebark pine (Morgan et al. 1994). The synergistic effects of these disturbance agents may be amplified by changes in climate that could lead to reductions in the aerial extent of whitebark pine habitat across the species' range (Bartlein, Whitlock, and Shafer 1997; Schrag, Bunn, and Graumlich 2008). As a result, whitebark pine is at a risk of extirpation from many of the regions in which it is currently found (Kendall and Keane 2001).

Management and restoration strategies are actively being designed and implemented in response to these pressures on whitebark pine communities (e.g., Burr, Eramian, and Eggleston 2001; Hoff et al. 2001; Keane and Arno 2001; Waring and Six 2005; Novotny et al. 2006; Bower and Aitken 2008) and a concerted effort is underway to develop baseline data that will be critical to inform and assess the effectiveness of these efforts (e.g., Campbell and Antos 2000; Goheen 2002; Zeglen 2002; Six and Newcomb 2005; Smith et al. 2008). The geographic coverage of reports on the status of whitebark pine communities has increased over recent decades (Smith and Hoffman 2000; Goheen 2002; Murray and Rasmussen 2003; Ward, Shoal, and Aubry 2006; Rochefort 2008), yet numerous gaps remain in the spatial extent of these data. Additionally, patterns in structure, composition, and mortality in whitebark pine forests vary both within landscapes and across mountain ranges (Morgan and Murray 2001), necessitating consideration of multiple spatial scales of variability to inform management decisions. To address these needs, my goals for this project were to: 1) provide baseline data on the composition and health of whitebark pine communities at multiple sites within six mountain ranges across the central distribution of whitebark pine; 2) compare rates of blister rust infection and mountain pine beetle-related mortality among these

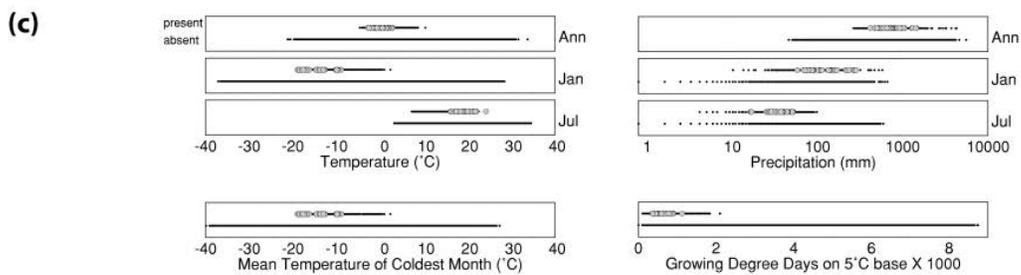
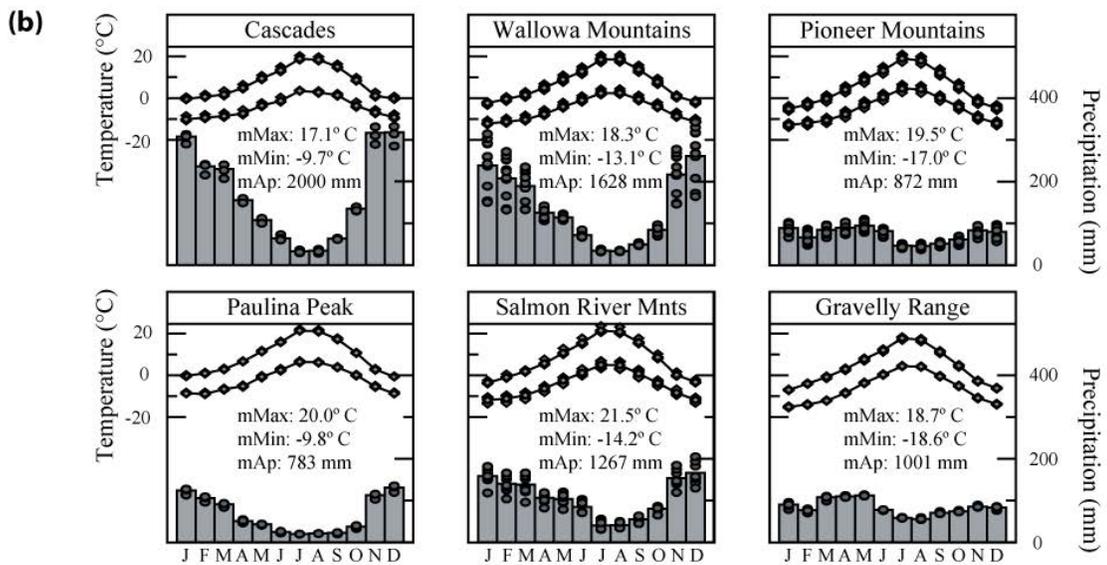
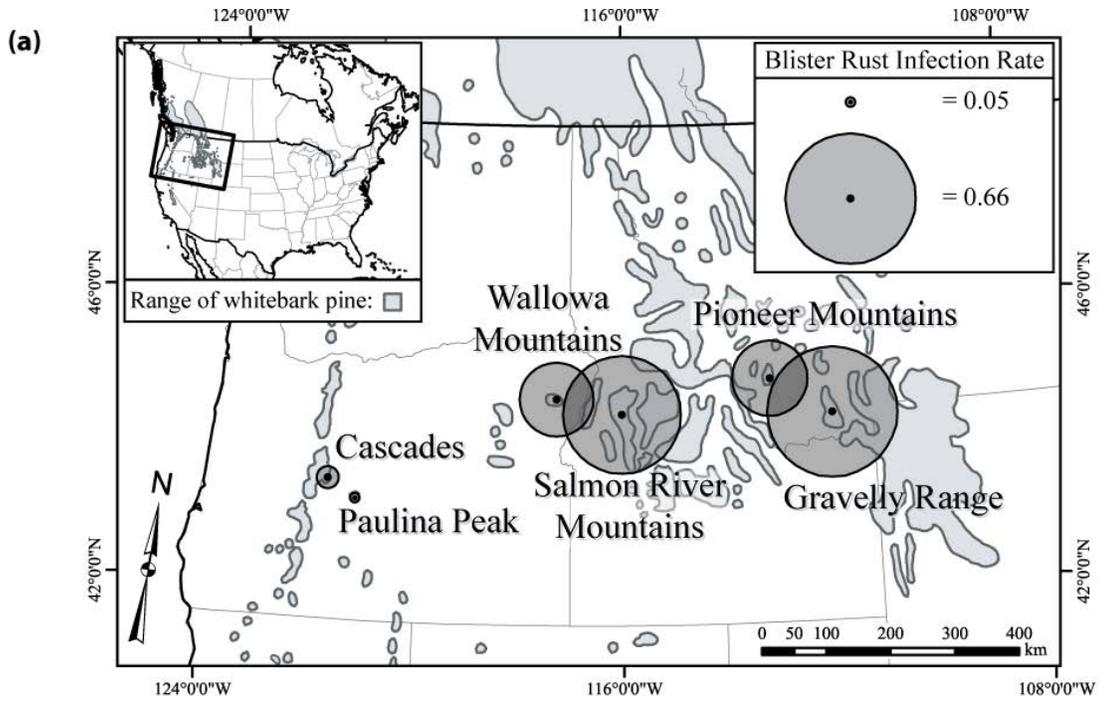
mountain ranges; 3) determine if patterns of blister rust infection and mountain pine beetle-related mortality exist within the whitebark pine populations of each range based on tree size and age; and 4) quantify the relationships between the biophysical environment and rates of blister rust infection and mountain pine beetle-related mortality at my sites.

Methods

Study Area Description

Whitebark pine is widely distributed across the western United States, with the native range of the species spanning 36° to 55° N longitude and 108° to 127° W latitude. My study area extends from southwest Montana to western Oregon between ca. 42° and 45° N with sites in the Gravelly Range and Pioneer Mountains of Montana, the Salmon River Mountains of Idaho, and the Wallowa Mountains, Paulina Peak, and Cascade Range of Oregon (Figure 1a). These mountain ranges are included within the boundaries of the Beaverhead–Deerlodge National Forest, the Payette National Forest, the Wallowa–Whitman National Forest, and the Deschutes National Forest, respectively. The topographic character of these ranges varies greatly. The Gravelly Range is generally rolling, while the Pioneer Mountains, Salmon River Mountains, and Wallowa Mountains are each an extensive mountain range and highly dissected by glacial valleys and ridges. Paulina Peak and the Cascades are younger, relatively isolated volcanic mountains with more regular terrain. Paulina Peak is the remnant of Newberry Volcano with a high-elevation rim bordering the south and east sides of what is now Newberry Caldera. My sites in the Cascades were located on Mount Bachelor, a relatively young volcanic

Figure 1. Study area information including (a) the location of mountain ranges included in this study with respect to the range of whitebark pine, mean blister rust (*Cronartium ribicola* (A. Dietr.) J.C. Fisch.) infection rate for each mountain range, (b) climographs for each mountain range based on plot-level climate data, and (c) the distribution of my plots in the climate space of whitebark pine. The climographs represent the mean monthly maximum, mean monthly minimum, and mean monthly precipitation for each plot as scatter points with the overall means of each of these variables for each mountain range indicated by the line graphs (temperature) and the bar graphs (precipitation). The data were derived from PRISM climate grids for the United States (PRISM Group, Oregon State University, <http://www.prismclimate.org>, created 13 Nov 2008) (Daly et al. 2002; Daly et al. 2008). The climate space of whitebark pine is adapted from Thompson *et al.* (1999) who used the 1951–1980 climate normals, while the data for my sites is based on 1971–2000 climate normals provided in the PRISM data.



mountain with a regular conical shape, and Black Crater, an irregularly shaped cinder cone.

Broad similarities existed in the annual patterns of temperature and precipitation at my sites as well as some distinct differences. In general, the sites shared a common pattern of drier summers and wetter winters, although the peak in winter precipitation was much more pronounced in the Cascades, Wallowa Mountains, and Salmon River Mountains than at the other sites (Figure 1b). Mean total annual precipitation among the different mountain ranges was affected by regional-scale rain shadows and ranged from 783 mm across the sites on Paulina Peak up to 2,000 mm at the Cascades sites, while mean monthly maximum and minimum temperatures exhibited a gradient in extremes from the western, more maritime sites to the eastern, more continental sites (Figure 1b). Climate conditions within each landscape was highly influenced by the general topography of the mountain ranges, with more variable topography and climate in the Pioneer Mountains, Salmon River Mountains, and Wallowa Mountains contrasting with less variability in the Gravelly Range, Paulina Peak, and the Cascades (Figure 1b). The climatic settings of my study sites represent a relatively wide range within the overall distribution of whitebark pine (Figure 1c) despite an increase in mean July temperatures that is evident when comparing the current climate normals (1970–2000) to those used in the Climate-Vegetation atlas (1951–1980) (Thompson, Anderson, and Bartlein 1999).

My study sites were located in the upper forest zones of each mountain range where whitebark pine was the dominant or co-dominant tree species. In addition to whitebark pine, several other tree species occurred in at least one site including subalpine fir, Engelmann spruce, lodgepole pine, Douglas-fir, and mountain hemlock. Groundcover

communities varied considerably between the mountain ranges and among the individual sites within each range by the different slope, aspect, substrate, and topographic positions of each site. Some of the more common species included *Arnica spp.*, *Vaccinium scoparium* Leib. ex Coville, *Lupinus spp.*, *Ribes spp.*, *Juniperus spp.*, and *Penstemon spp.*

Data Collection

I used a geographic information system (ESRI 2006) to identify the geographic centroid of 60 upper-elevation stands that contained whitebark pine in the National Forests based on geospatial stand inventory data provided by each Forest and aerial photographs viewed in Google Earth (Google 2006). The selected stands existed on a variety of slopes and aspects, and were near treeline yet still appeared to have relatively continuous canopies. The Universal Transverse Mercator (UTM) coordinates of each stand centroid were marked on field maps and programmed into a handheld Global Positioning System (GPS) device. In the field, I found that two of the stand centroids were located on cliff edges or other unsafe slopes, four were in forest openings, one was approximately 25 m off shore in a lake, and one was on the margins of a treeless wetland. In these cases I adjusted the plot location 100 m in a randomly chosen direction. In addition, two of the larger stands in the Wallowa Mountains appeared relatively heterogeneous in disturbance history, structure, and composition. I therefore used aerial photographs, stand inventory maps, and the GPS to randomly select up to two additional sites within these stand boundaries.

A 0.1 ha circular plot was placed at the centroid or adjusted centroid of each stand to collect site characteristic and forest demographic information. I recorded the elevation,

average slope, aspect, topographic position (valley bottom, lower slope, middle slope, upper slope, or ridge top), microsite characteristics (concave, concave/straight, straight, convex/straight, convex), dominant forest floor species (based on percent coverage), and the presence or absence of *Ribes spp.*, *Castilleja spp.*, and *Pedicularis spp.*, all of which serve as alternate hosts to the blister rust causing pathogen *Cronartium ribicola* (McDonald et al. 2006). The species, diameter at breast height (d.b.h.), canopy class, and health of all trees were recorded within the 0.1 ha plot. Canopy class was defined as canopy (≥ 50 percent of the tree canopy exposed to direct overhead light) and subcanopy (< 50 percent of the tree canopy exposed to overhead light). Tree health was subjectively categorized as alive (healthy canopy, fully capable of reproduction), declining (partial canopy dieback but still capable of producing cones or the presence of pitch tubes due to active mountain pine beetle infestation), and dead. All living whitebark pine trees were visually searched from multiple angles for evidence of blister rust infection including active cankers, inactive cankers, rodent chew, and flagging branches. Dead whitebark pine trees were not surveyed for blister rust due to the tendency of most dead trees in the plots to have lost their small branches and sloughed off their bark, greatly reducing the reliability of identifying past infections. All dead trees were inspected for physical damage, char, and j-shaped mountain pine beetle galleries to determine the proximate cause of death. Increment cores were collected along two radii of all living and dead trees ≥ 5 cm d.b.h. within the 0.05 ha plot to determine stand age, disturbance history (Kipfmüller and Swetnam 2001), and to detect the presence of blue-stain fungus, an indicator of mountain pine beetle-related mortality (Solheim 1995). Additional cores

were taken through the scar face and healing lobes of any trees in the coring plot that displayed basal or strip-kill scars to date the causal event (Means 1989).

All of the increment cores were air dried, glued into core mounts, and sanded using progressively finer grit sand paper until individual xylem cells were clearly visible under 7–45x magnification. I developed master chronologies for each mountain range and crossdated each core included in my analyses (Stokes and Smiley 1996). The inner dates of cores that did not reach the pith of a tree but exhibited sufficient curvature in the inner rings were corrected using pith-estimators based on concentric circles (Appelquist 1958). Cores that were rotten near the center and did not contain pith or sufficient curvature to estimate the rings to pith were assigned minimum ages and excluded from age-structure analyses. Minimum stand age was determined as the age of the oldest tree in the plot and was used as a measure of the time since the last stand-replacing disturbance (Kipfmüller and Baker 1998). I summarized the age-structure data into 10-yr age classes and identified cohorts where the sum of trees that established over any 30 year period (3 consecutive age-structure bins) was ≥ 5 trees and ≥ 25 percent of the total number of cored trees in the plot (Wells, Duncan, and Stewart 2001). I assigned cohort establishment dates, fire scar dates, and mountain pine-beetle related mortality events to decadal bins and used these to calculate a decadal disturbance frequency for each plot.

I collected site-specific climate data for each of my plots. The climate data were sampled from ASCII grids of the Spline climate data set developed by Rehfeldt (2006) and the PRISM climate data set developed by the PRISM Group at Oregon State University (Daly, Neilson, and Phillips 1994; Daly et al. 2000; Daly et al. 2002). The climate variables obtained included mean monthly maximum temperatures (T_{\max}), mean

monthly minimum temperatures (T_{\min}), and mean monthly precipitation (ppt) from the PRISM data set, and a suite of variables derived from combinations of temperature and precipitation data available in the Spline data set including degree days $>0^{\circ}$ C, degree days $>5^{\circ}$ C, the length of the frost-free period, the mean Julian date of the first autumn frost, and dryness indices for the year, summer, and growing season (Rehfeldt et al. 2006). I included both monthly values and seasonalized values for the PRISM data including spring (MAM), summer (JJA), fall (SON), and winter (DJF). In all I obtained 70 variables describing various aspects of the site-specific climate conditions for each plot.

I calculated a suite of standard forest metrics (frequency, relative frequency, basal area, relative basal area, and importance values) (Cottam and Curtis 1956) for each species present in the inventory plots as well as the same metrics stratified by canopy class and health category. In addition to the raw variables of slope, aspect, and elevation, I converted plot aspect to a linear metric (IASP), calculated relative elevation (rElev), determined a topographic relative moisture index (TRMI), and derived a relative TRMI (rTRMI) for each plot. Linear aspect was calculated as follows:

$$IASP_i = 1 + \cos \frac{\pi(aspect_i - 45)}{180} \quad (1)$$

where $IASP_i$ and $aspect_i$ are the IASP and aspect of site i , respectively. This results in a value from 0 (warmer, drier SW-facing slopes) to 2 (cooler, moister NE-facing slopes). Relative elevation was calculated by subtracting the elevation of the lowest plot within a mountain range from the elevation of each of the other plots and represented an estimation of the elevational position of each stand within the distribution of sampled

whitebark pine stands in each of the mountain ranges. The TRMI was developed to quantify the effects of stand-scale topography on effective moisture availability in mountainous landscapes (Parker 1982). TRMI values range from 0–60, and are calculated as the sum of values assigned to slope steepness (0–10), slope configuration (0–10), slope aspect (0–20), and slope position (0–20). Lower numbers indicate sites with less moisture availability and higher numbers indicate sites with greater moisture availability. To enhance my abilities to use the TRMI in comparisons between mountain ranges I also calculated a rTRMI for each site as follows:

$$rTRMI_s = \frac{TRMI_s \times MAP_s}{\frac{1}{n} \sum_{i=1}^n TRMI_i} \quad (2)$$

where $TRMI_s$ and MAP_s are the TRMI and mean annual precipitation (PRISM data) for site s , respectively, and $TRMI_i$ is the TRMI for the i th site. From these data I obtained a total of 235 variables describing the forest composition and physical setting of each plot, hereafter referred to as stand variables.

Data Analyses

I compared median rates of blister rust infection and mountain pine beetle-related mortality between the different mountain ranges using non-parametric Kruskal-Wallis one-way ANOVA by ranks tests (Legendre and Legendre 1998). I used a non-parametric Mann–Whitney U -test to determine if the presence or absence of alternate hosts to *Cronartium ribicola* influenced blister rust infection rates. To visually explore the relationships between tree size and age and blister rust and mountain pine beetle-related

mortality rates I graphed the frequency distributions of whitebark pines unaffected and affected by these agents and calculated probability density functions of each distribution using a Weibull function (Weibull 1951). I supplemented my visual analyses by conducting Kolmogorov–Smirnov two-sample tests to compare the d.b.h. and age distributions for each category (Burt and Barber 1996). Statistical analyses were conducted using R (R Development Core Team 2008).

I conducted stepwise multiple regressions to model blister rust infection rates and mountain pine beetle-related mortality rates as functions of the stand and climate variables for each plot. Researchers have identified a variety of biophysical variables that are related to blister rust infection levels in whitebark pine forests (Campbell and Antos 2000; Smith and Hoffman 2001; Smith et al. 2008), but the specific results are not always consistent between studies. I therefore included the full suite of stand and climate variables as potential independent variables in the stepwise regression to determine if other unexplored relationships existed between patterns in blister rust infection rates and the biophysical environment. In each analysis, blister rust and mountain pine beetle rates were used as the dependent variables and predictor variables were included in the regression through forward and backward selection based on the criteria of $\alpha \leq 0.1$. I interpreted the results of each regression using partial correlations of the included variables to identify the most parsimonious model that also included the most ecologically meaningful relationships. I used MINITAB v15 (MINITAB Inc. 2006) to conduct the stepwise regressions and the function `pcor.test` in R (R Development Core Team 2008) to calculate the partial correlations.

Results

I inventoried 4,176 trees in 60 plots over the summers of 2006–2008, of which 2,346 were cored. Of the trees inventoried, 2,666 were whitebark pine. Stand composition varied widely between the mountain ranges with whitebark pine dominating the canopy layer at 37 sites and the subcanopy at 33 sites (Table 1). The dominant forest floor species varied widely both within and among the mountain ranges, with *Vaccinium scoparium* being the most common dominant ($n = 17$, Table 1). At the scale of the mountain ranges, whitebark pine density was greatest in the Pioneer Mountains and least in the Wallowa Mountains and Salmon River Mountains (Figure 2a). The proportion of alive whitebark pine trees was greatest in the Wallowa Mountains and lowest in the Salmon River Mountains while the proportion of whitebark pine in decline was relatively similar among the different ranges (Figures 2a, 2b). Blister rust infections were observed on 37 percent ($n = 660$) of the living whitebark pine trees I inventoried for this study, with the lowest rates occurring in the Cascades and on Paulina Peak (Figure 2b). Blister rust infections were observed on at least one tree in 54 of the 60 plots, with rates of infection in individual plots ranging from 0–100 percent (Table 1). Blister rust infection rates were significantly higher ($t = -2.53$, d.f. = 26, $p = 0.019$) in stands where an alternate host for *Cronartium ribicola* was present (mean rate = 0.55, $n = 17$) than where those species were lacking (mean rate = 0.22, $n = 42$). Out of the total 2,666 whitebark pine trees inventoried, 33 percent ($n = 887$) were dead. Mountain pine beetle activity was the primary cause of mortality with 83 percent ($n = 619$) of all dead whitebark pine exhibiting extensive pitch tubes, beetle galleries, and/or blue stain fungus (Table 2, Figure 2b). An active outbreak was occurring in the Gravelly Range during the 2007 field

Table 1. Forest age, disturbance, and dominance by plot and range.

Plot ID	n trees	Stand age (yrs)	TSC* (yrs)	DDF [‡]	BR rate [†]	MPB rate [‡]	PIAL mort [§]	Dominant Species [◊]		
								Canopy	Sub-canopy	Understory
Cascades										
1	88	400	140	0.05	0.13	0.64	0.46	PIAL	ABLA	<i>Carex spp.</i>
2	59	354	80	0.08	0.00	0.64	0.58	TSME	PIAL	<i>Penstemon spp.</i>
3	125	146	90	0.34	0.12	0.87	0.40	PIAL	PIAL	<i>Penstemon spp.</i>
4	73	451	150	0.09	0.12	0.57	0.41	PIAL	PIAL	<i>Juncus parryi</i>
5	35	360	120	0.03	0.24	0.82	0.50	PIAL	PIAL	<i>Penstemon spp.</i>
6	101	235	240	0.13	0.07	0.50	0.70	PIAL	PIAL	Grass spp.
CAS:	481	324	137	0.12	0.11	0.65	0.50			
Gravelly Range										
1	121	508	110	0.04	0.43	0.85	0.30	PIAL	PIAL	<i>Arnica alpina</i>
2	149	230	110	0.04	0.42	0.91	0.47	ABLA	ABLA	<i>Lupinus spp.</i>
3	91	222	90	0.05	0.94	1.00	0.08	PIAL	PIAL	<i>Lupinus spp.</i>
4	60	359	90	0.06	0.86	0.50	0.17	PIAL	PIAL	<i>Lupinus spp.</i>
5	66	75	80	0.13	0.61	0.75	0.18	PIAL	PIAL	Grass spp.
6	51	191	90	0.16	0.70	0.57	0.27	ABLA	PIAL	<i>Vaccinium scoparium</i>
7	70	288	280	0.17	0.55	0.79	0.70	PIAL	PIAL	<i>Ribes spp.</i>
8	70	446	140	0.09	0.54	0.88	0.56	ABLA	PIAL	<i>Lupinus spp.</i>
GRA:	678	290	124	0.09	0.66	0.82	0.35			
Paulina Peak										
1	97	391	120	0.05	0.17	0.19	0.40	PIAL	PIAL	Grass spp
2	112	367	80	0.14	0.00	0.67	0.30	PICO	PIAL	Grass spp
3	153	261	110	0.11	0.00	0.75	0.13	PICO	PICO	<i>Arctostaphylos spp.</i>
4	98	323	320	0.03	0.06	0.63	0.31	PICO	PICO	Grass spp.
5	61	329	100	0.09	0.00	1.00	0.19	PIAL	PIAL	<i>Penstemon spp.</i>
6	25	337	340	0.09	0.14	1.00	0.39	PIAL	PIAL	<i>Lupinus spp.</i>
7	137	171	70	0.23	0.02	0.68	0.44	PICO	PIAL	<i>Juncus parryi</i>
PAU:	683	311	163	0.11	0.05	0.60	0.34			
Pioneer Mountains										
1	173	257	190	0.04	0.23	0.13	0.05	PIAL	PIAL	<i>V. scoparium</i>
2	95	509	60	0.04	0.10	0.92	0.48	PIAL	PIAL	<i>V. scoparium</i>
3	48	542	490	0.06	0.20	0.86	0.58	PIAL	PIAL	<i>Juniperus spp.</i>
4	59	538	550	0.15	0.33	0.98	0.82	PICO	PIAL	<i>V. scoparium</i>
5	70	191	100	0.05	0.26	1.00	0.05	PIAL	PIAL	<i>V. scoparium</i>
6	66	573	570	0.03	0.64	0.80	0.50	PIEN	PIAL	<i>V. scoparium</i>
7	122	293	100	0.14	0.45	1.00	0.09	PIAL	PIAL	<i>V. scoparium</i>
8	76	446	230	0.18	0.69	0.80	0.13	PIAL	PIAL	<i>Vicia spp.</i>
9	83	432	130	0.07	0.47	0.50	0.03	PIAL	PIAL	<i>Juniperus spp.</i>
10	65	286	70	0.14	0.88	0.60	0.09	PIAL	PIAL	Grass spp.
11	64	597	220	0.05	0.70	0.00	0.03	PIAL	PIAL	Grass spp.
12	108	346	270	0.09	0.19	0.00	0.02	PIAL	PIAL	<i>Juniperus spp.</i>
13	28	808	810	0.01	0.39	0.40	0.36	PIAL	PSME	<i>V. scoparium</i>
14	148	530	110	0.06	0.28	0.27	0.08	PIAL	PIAL	<i>V. scoparium</i>
PIO:	1205	453	279	0.08	0.38	0.78	0.20			

(Table 1 continued)

Salmon River Mountains										
1	21	169	170	0.12	0.83	0.80	0.45	PIAL	PIAL	<i>Carex spp.</i>
2	33	274	60	0.11	0.89	0.90	0.53	PICO	PICO	Grass spp.
3	28	205	210	0.10	1.00	0.50	0.86	PICO	ABLA	Grass spp.
4	42	231	90	0.17	0.70	0.72	0.64	PIAL	ABLA	<i>Lupinus spp.</i>
5	14	183	180	0.11	0.00	1.00	0.33	ABLA	ABLA	<i>Phlox hoodii</i>
6	34	239	40	0.13	na	1.00	1.00	ABLA	ABLA	<i>Carex spp.</i>
7	42	209	80	0.14	0.50	0.63	0.67	ABLA	ABLA	<i>Lupinus spp.</i>
8	54	345	110	0.06	0.70	0.80	0.33	PIAL	PIAL	<i>Salix spp.</i>
9	33	454	450	0.09	0.38	1.00	0.76	PIAL	ABLA	<i>Lupinus lyallii</i>
10	53	367	230	0.16	0.50	0.44	0.95	ABLA	ABLA	<i>Phlox hoodii</i>
11	46	181	40	0.17	1.00	0.30	0.91	ABLA	ABLA	Grass spp
12	54	43	50	0.23	0.22	0.00	0.18	PIAL	ABLA	<i>Salix spp.</i>
SRM:	454	242	143	0.13	0.60	0.67	0.69			
Wallowa Mountains										
1	29	654	80	0.02	0.17	na	0.00	PICO	ABLA	<i>V. scoparium</i>
2	60	254	120	0.04	0.11	na	0.00	PIAL	ABLA	<i>V. scoparium</i>
3	55	158	70	0.06	0.00	na	0.00	PICO	PICO	<i>V. scoparium</i>
4	62	900	200	0.03	0.17	na	0.00	PICO	ABLA	<i>V. scoparium</i>
5	78	285	270	0.11	0.09	0.44	0.29	ABLA	ABLA	<i>V. scoparium</i>
6	36	383	90	0.03	0.13	na	0.00	PIAL	ABLA	<i>Arenaria aculeata</i>
7	78	278	80	0.04	0.10	na	0.00	ABLA	ABLA	<i>V. scoparium</i>
8	31	491	490	0.04	1.00	0.60	0.83	ABLA	ABLA	<i>Phyllodoce empetriformis</i>
9	59	693	100	0.03	0.27	0.00	0.15	PIAL	ABLA	<i>P. empetriformis</i>
10	41	306	140	0.03	0.92	0.33	0.33	PIAL	ABLA	<i>V. scoparium</i>
11	60	496	500	0.02	0.75	0.27	0.26	PIAL	PIAL	<i>Juncus parryi</i>
12	42	556	560	0.04	0.50	0.50	0.09	PIAL	ABLA	<i>Juncus parryi</i>
13	44	293	220	0.03	0.55	0.25	0.17	PIAL	ABLA	<i>V. scoparium</i>
WLA:	675	442	225	0.04	0.38	0.36	0.17			

* Time-since-cohort establishment. The number of years since the establishment of the most recent cohort identified in the age-structure data.

^α Decadal Disturbance Frequency. The rate of disturbance per decade at a site based on fire scar, mountain pine beetle-related mortality, and post-disturbance cohort establishment data.

[†] Rate of blister rust infection among living whitebark pine (na indicates no living whitebark pine in plot)

[‡] Rate of dead whitebark pine showing evidence of mountain pine beetle-related mortality (na indicates no dead whitebark pine in plot)

[§] Proportion of all whitebark pine inventoried that were dead

[◇] Dominant species for canopy and subcanopy are based on importance values and for understory on percent coverage. Species codes are based on the first two letters of the Latin binomial name of each species (e.g., *Pi-nus al-bicaulis* = PIAL).

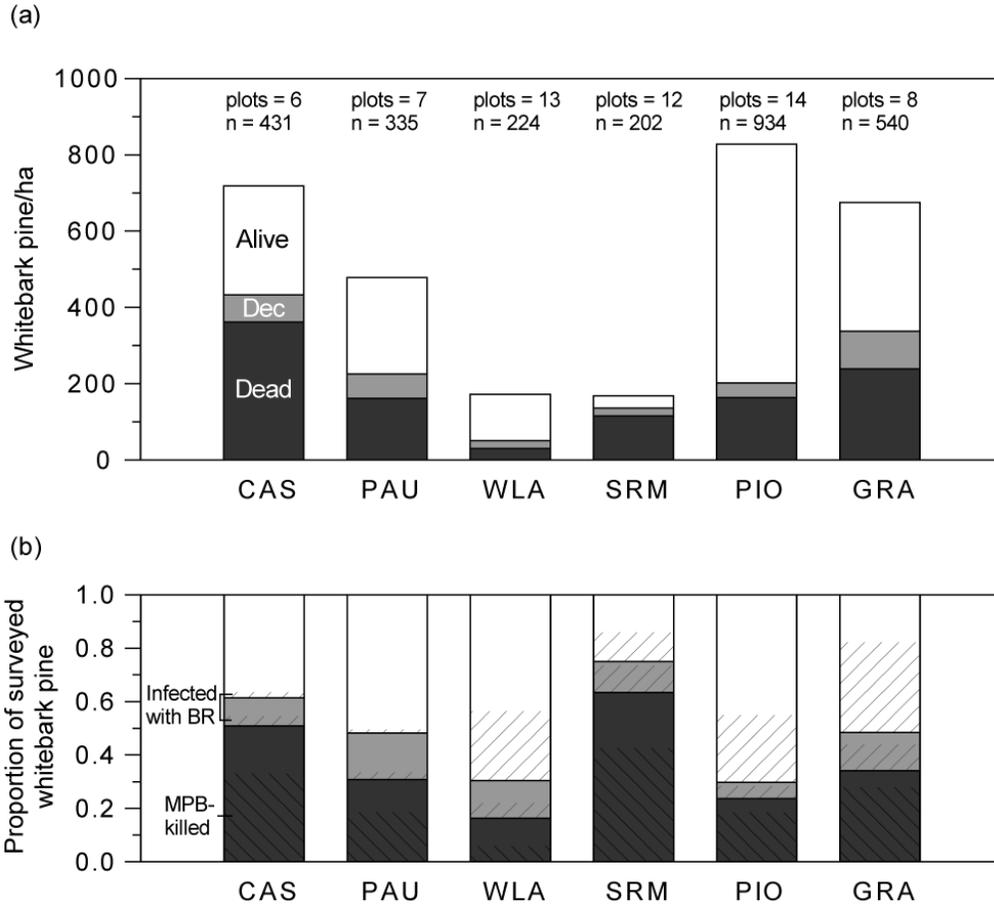


Figure 2. Whitebark pine (a) density and health and (b) rates of blister rust and mountain pine beetle (*Dendroctonus ponderosae* Hopkins)-related mortality by health category in 60 plots across six mountain ranges. Health categories for (a) and (b) are alive (healthy canopy, fully capable of reproduction), declining (DEC; partial canopy dieback but still capable of producing cones, or the presence of pitch tubes due to active mountain pine beetle infestation), and dead. In (b) the proportion of living and declining trees with blister rust are indicated by grey hatching, while the proportion of dead trees showing evidence of mountain pine beetle-related mortality are indicated by black hatching. Site codes are as follows: CAS = Cascades; PAU = Paulina Peak; WLA = Wallowa Mountains; SRM = Salmon River Mountains; PIO = Pioneer Mountains; GRA = Gravelly Range.

Table 2. Results of Kruskal-Wallis one-way ANOVA by ranks test for differences in blister rust rates and mountain pine beetle-related mortality between mountain ranges.

Range	Blister rust infection			MPB mortality rate		
	Median	\bar{X} rank	Z	Median	\bar{X} rank	Z
Cascades	0.11	14	-2.4	0.64	28	0.1
Gravelly Range	0.58	43	2.4	0.82	35	1.4
Paulina Peak	0.02	9	-3.4	0.68	31	0.7
Pioneer Mountains	0.36	33	0.7	0.70	27	-0.2
Salmon River Mountains	0.70	40	2.3	0.76	30	0.7
Wallowa Mountains	0.17	28	-0.5	0.33	12	-2.9
	$H = 25.3, \text{d.f.} = 5, p < 0.000$			$H = 9.6, \text{d.f.} = 5, p = 0.087$		

season, and a relatively high number of recent beetle-killed pines may indicate an impending outbreak on Paulina Peak. Crossdated tree ring-samples collected from dead trees provided evidence of multiple episodes of mountain pine beetle-related mortality during the late 1800s and early 1900s in all of the mountain ranges, as well as limited evidence of beetle-caused mortality in the form of blue stain fungus during the late 1600s and 1700s for two sites in the Pioneer Mountains. I found evidence of past fires in 35 percent ($n = 21$) of my plots either in the form of fire-scarred trees and/or post-fire cohorts.

I was able to assign accurate inner dates or pith estimations to 87 percent ($n = 2,046$) of the cored trees, with the majority of the undated cores taken from rotten trees. Pith was included in 16 percent ($n = 365$) of the cores and the average correction for cores that did not include pith was 7 ± 5 SD years (range: 1–30 years). Minimum stand ages ranged from 40–900+ years (Table 1), with individual stands exhibiting 0–2 cohorts. In general, disturbance frequency was highest in the Salmon River Mountains and lowest in the Wallowa Mountains. A detailed discussion of the disturbance histories and successional dynamics of these stands is provided elsewhere (see Chapter 4).

Significant differences in blister rust infection rates ($H = 25.3$, d.f. = 5, $p < 0.000$) existed between the different mountain ranges, with the lowest rates on Paulina Peak and the highest rates in the Salmon River Mountains (Table 2, Figure 1a). Rates of mountain pine beetle-related mortality were relatively homogenous across the different mountain ranges ($H = 9.6$, d.f. = 5, $p = 0.087$) with the exception of the Wallowa Mountains where the rate was lower (Table 2). The distributions of trees infected by blister rust were significantly different ($p < 0.05$) from the distribution of rust-free trees at three of the six mountain ranges with respect to d.b.h. (Figure 3a) and two of the six ranges with respect

to tree age (Figure 3b), although the Weibull distributions in most cases were visually similar. With respect to the overall similarity of d.b.h. and age distributions across the study area stratified by blister rust, 30 percent ($n = 20$) of the 66 total distribution comparisons based on d.b.h. and 42 percent ($n = 28$) of the possible relationships based on tree age showed no significant differences (Figures 3a, 3b). The distributions of mountain pine beetle killed or infested trees were significantly different ($p < 0.05$) within all of the mountain ranges with respect to d.b.h. (Figure 4a) and all but the Wallowa Mountains in terms of age (Figure 4b), with the distributions of mountain pine beetle-affected trees including more larger diameter and older trees. D.b.h. and age distributions stratified by mountain pine beetle activity showed relatively low similarity across the study area, with only 15 percent ($n = 10$) of the 66 distribution comparisons showing no difference with respect to d.b.h. and 18 percent ($n = 12$) showing no difference with respect to tree age (Figures 4a, 4b).

The selected stepwise regression models explained 64 percent and 58 percent of the variance in blister rust infection rates and mountain pine beetle-related mortality rates, respectively (Table 3). Blister rust infection rates were higher in more open forests on steeper slopes and cooler, moisture aspects that included a greater proportion of stand basal area represented by whitebark pine. With respect to climate conditions, blister rust infection rates were higher at sites with colder minimum December temperatures and warmer spring temperatures. Mountain pine beetle-related mortality was highest at sites with lower density stands composed of larger whitebark pines with generally younger stand ages, as well as at sites with cooler June temperatures, higher August temperatures, and relatively drier springs.

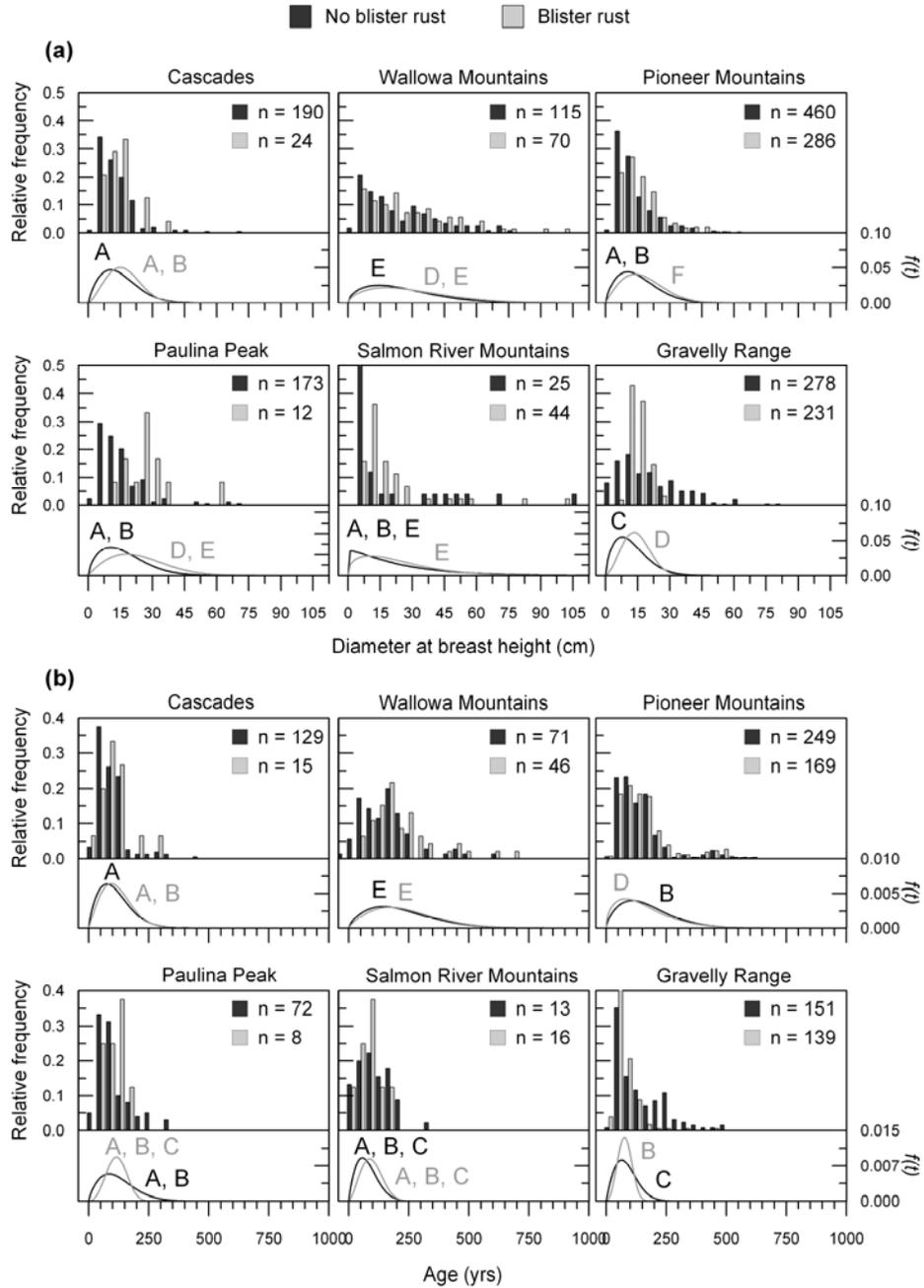


Figure 3. Distributions of whitebark pine (a) diameter and (b) age, stratified by the presence or absence of blister rust infection. The lower pane in each graph shows the Weibull distribution for each category. Different letters above the Weibull distributions indicate significantly different distributions ($p < 0.05$) based on Kolmogorov–Smirnov two-sample tests. The distributions include only living whitebark pine.

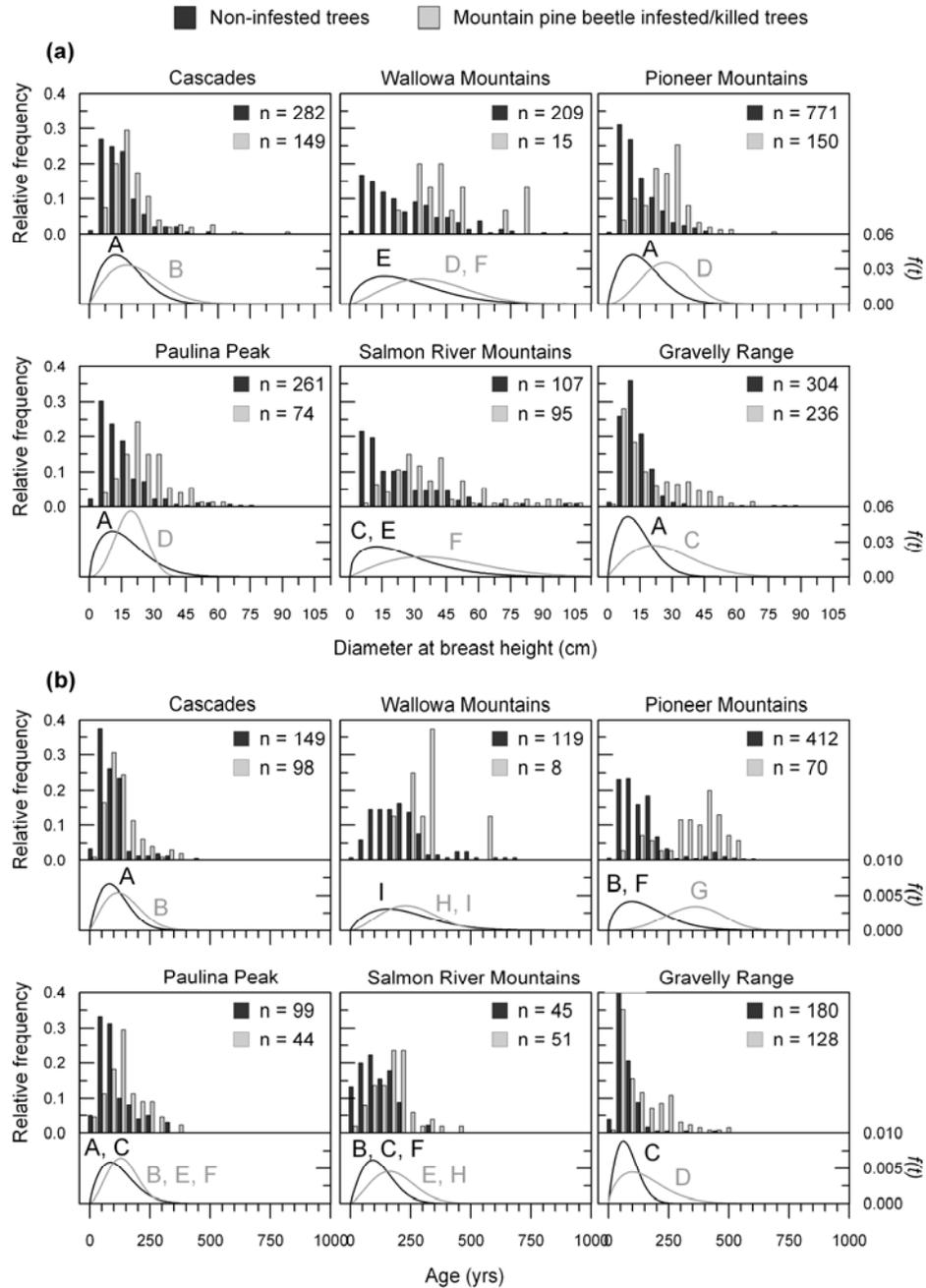


Figure 4. Distributions of whitebark pine (a) diameter and (b) age, stratified by evidence for mountain pine beetle-related mortality. The lower pane in each graph shows the Weibull distribution for each category. Different letters above the Weibull distributions indicate significantly different distributions ($p < 0.05$) based on Kolmogorov–Smirnov two-sample tests. The distributions for non-infested trees include both living trees and dead trees that showed no evidence of beetle-related mortality. The trees included in the infested/killed distributions displayed at least one of the following lines of evidence for mountain pine beetle attack: extensive pitch tubes, j-shaped galleries, or bluestain fungus in their sapwood.

Table 3. Results of stepwise multiple regressions relating blister rust infection rates and mountain pine beetle-related mortality rates to stand and climate variables.

Blister rust infection rate regression						
Step:	9 of 10	Variable	r_{partial}	coef.	t	p
Intercept:	-2.624	December T_{min}	-0.64	-0.1730	-6.1	0.000
r^2 :	0.64	Canopy trees/ha	-0.18	-0.0003	-2.2	0.034
PRESS:	2.66	Slope	0.43	0.0070	3.5	0.001
		IASP	0.35	0.1220	2.7	0.008
		PIAL relative basal area/ha	0.41	0.4900	3.2	0.002
		Spring T_{max}	0.50	0.1540	4.2	0.000
		Whitebark pine basal area/ha	-0.27	-0.0053	-2.0	0.053
Mountain pine beetle-related mortality rate regression						
Step:	6 of 7	Variable	r_{partial}	coef.	t	p
Intercept:	0.125	Canopy PIAL basal area/ha	0.44	0.0126	3.4	0.013
r^2 :	0.58	October T_{min}	0.53	0.2960	4.1	0.000
PRESS:	2.69	June T_{min}	-0.50	-0.3570	-3.8	0.000
		Stand age	-0.44	-0.0009	-3.3	0.002
		Spring ppt	-0.31	-0.0014	-2.3	0.029
		Canopy PIAL/ha	-0.28	-0.0004	-1.9	0.060

Discussion

Composition and Health of Whitebark Pine Communities in Southwest Montana, Central Idaho, and Oregon

Patterns in vegetation and disturbance are created through the influences of a diverse array of climatic, landscape, and biological factors and their legacies that operate across multiple scales (Delcourt, Delcourt, and Webb III 1982; Turner 2005). With respect to whitebark pine, these factors are further complicated by the broad distribution of this species across mountainous environments that tend to sharpen environmental gradients and increase landscape diversity (Beniston 2003). It is no surprise, then, that the forests at my sites exhibited wide variability in composition, age, disturbance frequency, and disturbance effects, yet this diversity stands out as an important finding as it underscores the complexity in forest systems broadly defined as whitebark pine communities.

The blister rust infection rates I observed at my sites generally agree with the regional patterns of blister rust described elsewhere (Smith and Hoffman 2000; Kendall and Keane 2001) and complement previous studies that have identified a North-South gradient in blister rust infection levels (Campbell and Antos 2000; Zeglen 2002; Smith et al. 2008) with evidence of increasing blister rust infection rates from west to east across my study area. In addition to this gradient, the sites with the lowest blister rust infection rates are more isolated from more contiguous portions of the range of whitebark pine (cf, Morgan and Murray 2001). For example, Paulina Peak, with the lowest blister rust rates of the mountain ranges included in this study, is a single peak separated by over 40 km

from the nearest neighboring population of whitebark pine in the Cascades. In contrast, the Gravelly Range and the Salmon River Mountains, which show the highest rates of blister rust infection, are a part of or in close proximity to extensive and widespread populations of whitebark pine. Similarly, the Pioneer Mountains and Wallowa Mountains are less isolated than Paulina Peak or the Cascades, but more so than the Gravelly Range and Salmon River Mountains. The whitebark pine forests in these ranges likewise show moderate levels of rust infection. While these differences may diminish in the future as infections become more widely established on the landscape (Kinloch 2003), these patterns illustrate the important interactions between landscape structure, in terms of the isolation of whitebark pine populations, and the mechanisms driving the spread of invasive species such as blister rust (With 2002).

In contrast to other assessments of whitebark pine forests that found white pine blister rust to be a dominant cause of mortality and limited evidence of mountain pine beetle activity (Keane, Morgan, and Menakis 1994; Campbell and Antos 2000; Zeglen 2002; Smith et al. 2008), I found mountain pine beetle activity to be the dominant mortality agent for whitebark pines across my study area for at least the past 100 years. Even the forests in the Wallowa Mountains, where the overall proportion of mountain pine beetle-related mortality was lower than elsewhere, most of the dead trees were too old and decayed to determine a cause of death. This makes it unlikely that the trees with an undetermined cause were infected with blister rust, as the disease only arrived in this range ca. 1960s (McDonald and Hoff 2001). Additionally, while recent research indicates that increasing severity of blister rust infections on individual trees may increase the likelihood of that tree to be attacked by mountain pine beetles (Six and Adams 2007), a

large proportion of the beetle-caused mortality occurred prior to the development of severe blister rust at these sites (McDonald and Hoff 2001) and even at the time of this study many of the whitebark pine infected with blister rust across my study area were in relatively good health as indicated in Figure 3b. These results suggest that where declines have occurred in the whitebark pine forests of my study area, mountain pine beetle activity is at least as important if not more so than blister rust in driving these changes.

Although whitebark pine mortality rates were relatively high in many of the mountain ranges included in this study, the conditions of whitebark pine in the Salmon River Mountains warrant special consideration. Whitebark pine at my sites in the Salmon River Mountains were undergoing severe declines with the highest rates of mortality (0.69) reported in this study, and the second highest rates of blister rust infection (0.60) and mountain pine beetle-related mortality (0.67). Several of the sites surveyed had also been burned over by recent severe fires, although many of the trees that initially appeared to have been killed by fire had actually been killed earlier by mountain pine beetles. The combined effects of these disturbances occurring at my sites in close temporal proximity may have initiated the downward spiral in ecosystem function forewarned about by many researchers (e.g., Tomback and Kendall 2001; Smith et al. 2008; McKinney, Fiedler, and Tomback 2009). However, some whitebark pine regeneration was observed at these sites (see Chapter 3) and peak levels of whitebark pine regeneration can lag disturbance events by a decade or more, given sufficient seed source (Tomback, Sund, and Hoffmann 1993). If whitebark pine is able to persist on the landscape despite these disturbances, long-term benefits may result for the species through accelerated adaptations to the modern environment. Natural selection is strongly influenced by extreme selective pressures

(Siepielski and Benkman 2007). This translates to higher proportions of blister rust resistant whitebark pine in areas regenerating in the presence of more severe blister rust infections (Hoff et al. 2001). The Salmon River Mountains may therefore provide a suitable environment for the evolution of increased blister rust resistance in whitebark pine and warrant special attention from management efforts aiming to facilitate this process.

Intra-Population Variability in Blister Rust and Mountain Pine Beetle Rates

At the scale of individual organisms, the likelihood of being affected by agents such as blister rust or mountain pine beetles is strongly influenced by a variety of site-specific environmental and physiological factors, yet shifting the scale of analysis to the landscape can often reveal patterns that elucidate broad-scale dynamics and ecological mechanisms (Levin 1992). My assessment of the patterns of blister rust infection and mountain pine beetle-related mortality among trees of different sizes and ages within and among the mountain ranges included in this study provide clear illustrations of the dynamics of these two agents.

Blister rust infections in whitebark pine forests occur due to the aerial dispersal of basidiospores from alternate hosts infected with *Cronartium ribicola* to the needles of susceptible whitebark pines (Hoff and Hagle 1990). The spatial dispersal of basidiospores is dictated by wind patterns and suitable moisture conditions which over time may create a relatively homogenous distribution of infection on the landscape (McDonald and Hoff 2001). This homogenization is evident in the generally similar size and age distributions of whitebark pine with and without blister rust at my sites. Even while blister rust

infection levels reported in this and other studies varied between individual stands within the same landscapes (e.g., Campbell and Antos 2000; Smith and Hoffman 2001; Smith et al. 2008), it is clear that at the landscape scale, blister rust is affecting trees of all sizes and ages at nearly equal proportions to their overall representation on the landscape.

In contrast to the dispersal of basidiospores, the distribution of mountain pine beetles, among other bark beetles, is dictated by the proximity and direction of suitable food sources and topographic barriers on the landscape (Amman 1978; Hadley 1994), while the likelihood of successful infestations of individual trees is related to bark and phloem thickness, among other factors such as stand structure- and climate-induced stress (Amman 1972). This results in a non-random distribution of trees affected by mountain pine beetle and a greater susceptibility of larger trees to successful beetle attacks (Perkins and Roberts 2003). My results showed exactly this pattern, with the size and age distributions of beetle-killed whitebark pine all shifted toward larger and older trees.

The Influences of Climate and Forest Structure on the Agents Driving Whitebark Pine Declines

Patterns in blister rust infection and mountain pine beetle-related mortality in whitebark pine forests have been linked to variations in stand and climatic settings (Campbell and Antos 2000; Smith and Hoffman 2001; Perkins and Roberts 2003; Smith et al. 2008), but variability in the type and strength of relationships identified suggests that geographic differences influence the interactions of these species. Similar to other studies, stands on steeper slopes with more open canopies, as indicated by the inverse partial correlations of canopy tree density and whitebark pine basal area/ha, were

associated with higher blister rust infection rates in my study area (Jacobi et al. 1993; Campbell and Antos 2000). This can be attributed to the greater exposure of individual trees to the wind-dispersed basidiospores that cause blister rust. The tendency for higher blister rust infection levels to occur in stands with more north and north-easterly aspects across my study area likely reflects the importance of local-scale topography in creating conditions suitable for infection. Basidiospore production peaks in late summer, the driest time of the year at my sites, yet the spores require a period of continuous high humidity to survive and successfully infect host pine trees (McDonald and Hoff 2001). The cooler and moister conditions on northerly aspects appear to provide sufficiently different conditions to result in more successful infections and higher blister rust rates. Similar to my findings, Smith and Hoffman (2001) identified a relationship linking higher blister rust infection rates with more northerly aspects but did not include this in their regression model due to the relationship being only marginally significant. The overall distribution of my study sites appear to be in drier areas than those assessed by Smith and Hoffman, which may accentuate the importance of this relationship. The positive correlation with spring temperatures likely reflects the importance of an early start for blister rust to complete its life cycle within the relatively short growing season of high-elevation environments (Mielke and Kimmey 1935). The inverse correlation between mean minimum December temperatures and blister rust infection rates is more likely an indicator of the sites where rust is more prevalent rather than a climatic mechanism. In other words, the sites with the coldest winter temperatures in my study area are those with more continental locations and climates, placing them nearer to regions in the

Northern Rockies with larger populations of whitebark pine and higher rates of blister rust infection.

Mountain pine beetle population dynamics are influenced by complex interactions between biotic and abiotic aspects of the environment over a broad spectrum of spatiotemporal scales (Raffa et al. 2008). As previously stated, larger trees offer more abundant food for mountain pine beetles, but their thicker bark also offers protection from extreme winter cold that can kill overwintering beetles (Amman 1978). Therefore stands of larger trees offer both food and shelter that enable beetle populations to remain at higher levels over several years, likely resulting in higher beetle-related mortality rates. My finding of higher mountain pine beetle-related mortality rates in stands with greater canopy whitebark pine basal area is consistent with this tendency. The weak correlation between lower canopy whitebark pine density and higher rates of blister rust likely reflects the lower stem densities associated with mature whitebark pine forests that are composed of larger trees (Weaver, Forcella, and Dale 1990). The pattern of higher beetle-related mortality rates and younger forest age may at first appear contradictory; however, whitebark pine regenerates well underneath beetle-killed canopies in my study area (see Chapter 3) and this relationship likely reflects the young forests developing in stands that experienced high rates of mortality during 19th and 20th century mountain pine beetle outbreaks. With respect to climate, sites with warmer minimum August temperatures and less spring precipitation experience more intense late-season drought, which may in turn result in increased stress and susceptibility of individual trees to mountain pine beetle attack (Mattson and Haack 1987), although the relationship between drought stress and insect attack is not without its critics (e.g., Larsson 1989). Warmer August temperatures

may also result in a relatively longer season for the development and maturation of mountain pine beetles and their larvae (Bentz, Logan, and Amman 1991) that could result in higher mortality rates.

Implications of a Changing Environment for Patterns in Blister Rust, Mountain Pine Beetles, and Whitebark Pine Ecosystems

The Earth's ecosystems are being dramatically altered at an unprecedented pace due to rapidly changing climate and the introduction of exotic species world-wide (Mack et al. 2000; IPCC 2007). Understanding the past, present, and future effects of these changes is a daunting task due to the complexity of interactions, feedbacks, and ecological surprises that may occur in already dynamic systems (Paine, Tegner, and Johnson 1998), yet is critical for managers and scientists working to minimize the ecological degradation of our planet (Swetnam, Allen, and Betancourt 1999). Whitebark pine ecosystems provide an example where all of these factors of environmental change are coalescing. Synergistic relationships between the exotic blister rust and the native mountain pine beetle have already been documented, as increasing blister rust infection severity leads to greater susceptibility to successful mountain pine beetle attacks (Six and Adams 2007). In addition to this interaction, my results illustrate a potential amplification of blister rust infection rates in surviving trees due to mountain pine beetle-related mortality. Beetle outbreaks rarely result in 100 percent mortality (Rocca and Romme 2009), but rather they thin and open forest canopies through selective mortality of dominant trees and shift the overall population structure toward smaller, younger trees (Sibold et al. 2007). This structural change will reduce the number of large whitebark

pine suitable for mountain pine beetle attack, but may also result in more exposure of surviving whitebark pine to basidiospores and higher blister rust infection levels. Furthermore, whitebark pine seed production is diminished following mountain pine beetle outbreaks due to the loss of mature, cone-producing trees, while blister rust infections often occur in the top and outer branches of infected trees further reducing the potential for surviving whitebark pine to produce cones. The pattern of forest renewal following mountain pine beetle outbreaks (see Chapter 3) may therefore be disrupted, leading to severe declines and potential extirpation of whitebark pine where both mountain pine beetle outbreaks and high levels of blister rust occur. The combined influences of these agents will undoubtedly have profound influences on the structure, composition, and vitality of whitebark pine forests on future landscapes, but what the specific outcomes of these changes are likely to be remains less certain.

Chapter 3. Patterns in Whitebark Pine Regeneration and Their Relationships to Biophysical Site Characteristics in Southwest Montana, Central Idaho, and Oregon, U.S.A.

Introduction

The continued persistence of whitebark pine (*Pinus albicaulis* Engelm.) as an important species in high elevation forests of western North America is a topic of major concern among land managers and researchers (Tomback, Arno, and Keane 2001a). Dramatic declines have been observed in the health and dominance of whitebark pine across the species' range over the last 40 years (Keane and Arno 1993; Kendall and Keane 2001). These declines have been attributed to the invasive white pine blister rust (*Cronartium ribicola* (A. Dietr.) J.C. Fisch.) (Kinloch 2003), advancing succession as a result of fire suppression (Keane and Arno 1993), and episodic mountain pine beetle (*Dendroctonus ponderosae* Hopkins) outbreaks over the 20th Century (Perkins and Swetnam 1996; Campbell and Antos 2000; Kipfmüller, Swetnam, and Morgan 2002). Concern over the deterioration of whitebark pine forests is based on the potential cascade of ecological effects that may result due to the critical role the species fills in subalpine forest communities through enhanced biodiversity (Arno and Hoff 1990; Tomback and Kendall 2001), regulation of hydrology and watershed dynamics (Farnes 1990), and as the foundation of an ecosystem involving Clark's nutcrackers (*Nucifraga columbiana* Wilson), red squirrels (*Tamiasciurus hudsonicus* Trouessart), grizzly bears (*Ursus arctos* L.), and black bears (*Ursus americanus* Pallas) (Ellison et al. 2005).

In response to these declines, active management and restoration projects in whitebark pine forest are becoming increasingly common (Keane and Arno 2001), yet to persist over the long term the trees themselves must adapt to changes in the biotic and abiotic environment, particularly with respect to blister rust (Hoff et al. 2001). Change and adaptation in species and natural systems occurs through selective processes that operate at the scale of generations, and therefore successful whitebark pine regeneration will be one critical component of the long-term success of this species (Hoff, Bingham, and McDonald 1980; Kendall and Keane 2001).

Early research on whitebark pine regeneration focused primarily on the mutualistic relationship between whitebark pine and its primary dispersal agent, the Clark's nutcracker, and the ecological and evolutionary implications of this relationship, particularly with respect to the behavioral tendencies of Clark's nutcrackers when they create seed caches (Lanner 1982; Tomback 1982; Hutchins and Lanner 1982; Tomback, Hoffman, and Sund 1990). Clark's nutcrackers preferentially cache whitebark pine seeds in open and recently disturbed settings (McCaughey and Tomback 2001; Tomback 2005), and most studies of the patterns and abundances of whitebark pine regeneration have focused on post-fire settings (e.g., Tomback 1986; McCaughey 1990; Tomback, Sund, and Hoffmann 1993; Tomback et al. 1995; Tomback et al. 2001). Clark's nutcrackers have also been documented caching whitebark pine seeds in a variety of other microsites (Hutchins and Lanner 1982) and recent research identified variable levels of advanced whitebark pine regeneration across a wide spectrum of biophysical settings including stands that had experienced high levels of mortality related to 20th century mountain pine beetle outbreaks (Mellmann-Brown 2005; Moody 2006; Larson 2007). Additionally, the

community dynamics and spatial patterns of animal-dispersed plants are highly influenced by the non-random behaviors of their dispersalists (Gomez 2003; Westcott et al. 2005; Jordano et al. 2007), yet few assessments of patterns in whitebark pine regeneration at the landscape-scale have been conducted (but see Zeglen 2002). A more complete understanding of where whitebark pine regeneration is likely to occur and succeed would enhance management and restoration activities in whitebark pine communities, particularly with respect to site selection for the outplanting of blister rust-resistant whitebark pine seedlings (Hoff et al. 2001) and the application of prescribed fire (Keane and Arno 2001). In response to this need, my study seeks a better understanding of the spatial patterns in natural whitebark pine regeneration and how these patterns relate to the biophysical environment. My guiding questions for this research were: 1) Is whitebark pine regenerating and do levels of regeneration vary within and among the landscapes included in my study area? 2) How do patterns of whitebark pine regeneration relate to the biophysical environment? 3) How do patterns of whitebark pine regeneration relate to past disturbances and in particular mountain pine beetle outbreaks?

Study Area

Whitebark pine is widely distributed across the western United States, with the native range of the species spanning 36° to 55° N longitude and 108° to 127° W latitude. Within this range, whitebark pine habitat is found from the lower subalpine zone to the upper forest limits and timberline (Arno and Hoff 1990). My study area extends from southwest Montana to western Oregon between ca. 42° and 45° N with study sites in the Gravelly Range and Pioneer Mountains of Montana, the Salmon River Mountains of

Idaho, and the Wallowa Mountains, Paulina Peak, and Cascade Range of Oregon (Figure 1). These mountain ranges are located within the Beaverhead-Deerlodge National Forest, the Payette National Forest, the Wallowa-Whitman National Forest, and the Deschutes National Forest, respectively. The topographic character of these ranges varies greatly. The Gravelly Range is generally rolling, while the Pioneer Mountains, Salmon River Mountains, and Wallowa Mountains are each an extensive mountain massif and highly dissected by glacial valleys and ridges. Paulina Peak is the remnant of Newberry Volcano with a high-elevation rim bordering the south and east sides of what is now Newberry Caldera. My sites in the Cascades were located on Mount Bachelor, a relatively young volcanic mountain with a regular conical shape, and Black Crater, an irregularly shaped cinder cone..

Broad similarities and a few distinct differences existed in the annual patterns of temperature and precipitation at my sites based on site-specific climate data obtained from the PRISM dataset (PRISM Group, Oregon State University, <http://www.prismclimate.org>, created 13 Nov 2008) (Daly et al. 2002; Daly et al. 2008). In general, the sites shared a common pattern of drier summers and wetter winters, although the peak in winter precipitation was much more pronounced in the Cascades, Wallowa Mountains, and Salmon River Mountains than at the other sites (Figure 1). Mean total annual precipitation among the different mountain ranges was affected by regional-scale rain shadows and ranged from 783 mm across the sites on Paulina Peak up to 2,000 mm at the Cascades sites, whereas mean monthly maximum and minimum temperatures exhibited a gradient in extremes from the western, more maritime sites to the eastern, more continental sites (Figure 1). The climate conditions within each

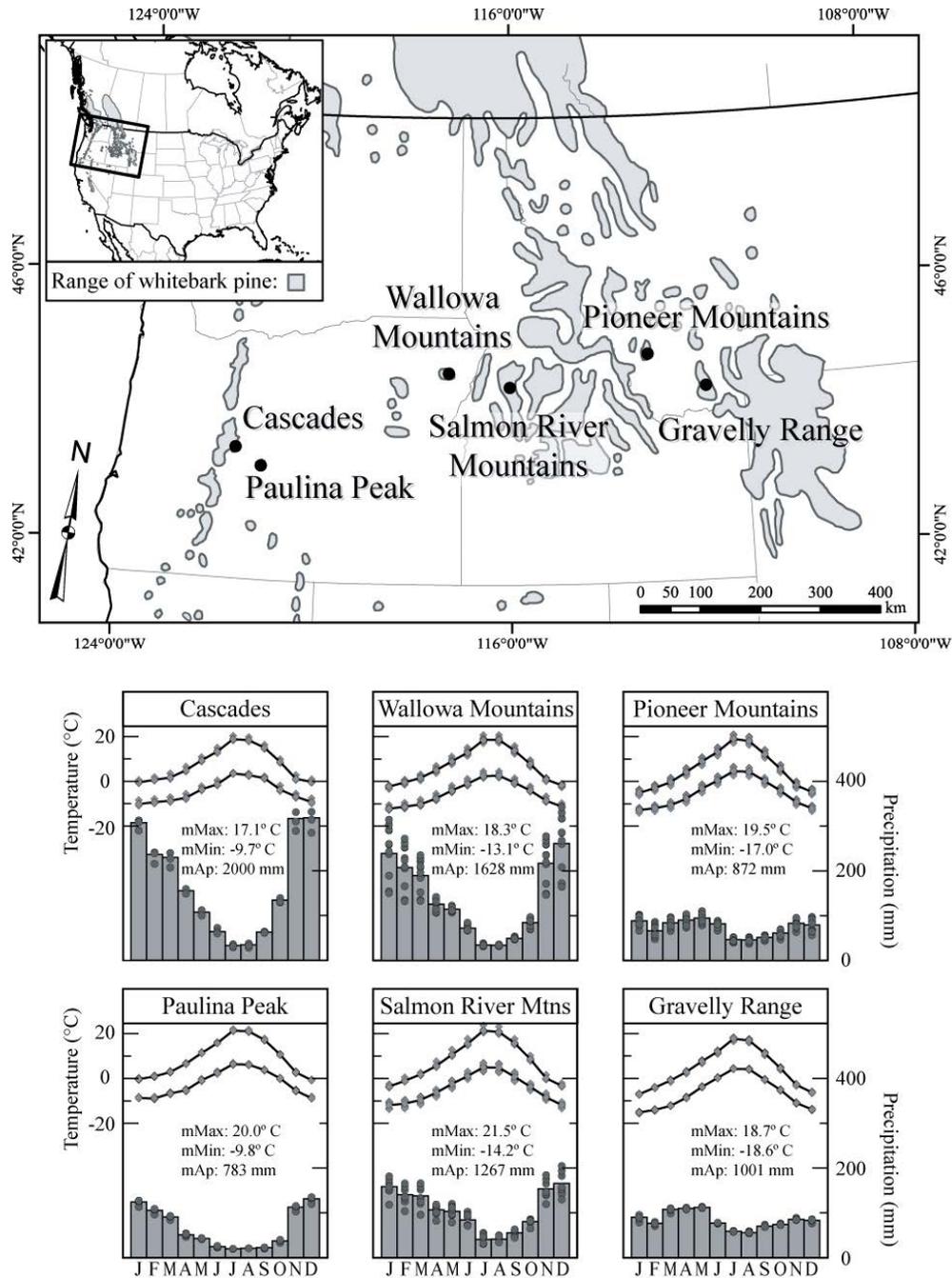


Figure 1. Study area showing the range of whitebark pine (gray shading), location of studied mountain ranges (black dots), and climographs for each mountain range. The climographs represent the mean monthly maximum, mean monthly minimum, and mean monthly precipitation for each plot as scatter points with the overall means of each of these variables for each mountain range indicated by the line graphs (temperature) and the bar graphs (precipitation). The data were derived from PRISM climate grids for the United States (PRISM Group, Oregon State University, <http://www.prismclimate.org>, created 13 Nov 2008) (Daly et al. 2002; Daly et al. 2008).

landscape were influenced by the general topography of the mountain ranges, with more variable topography and climate in the Pioneer Mountains, Salmon River Mountains, and Wallowa Mountains contrasting with less variability in the Gravelly Range, Paulina Peak, and the Cascades (Figure 1).

My study sites were located in the upper forest zones of each mountain range where whitebark pine was the dominant or co-dominant tree species (Table 1). In addition to whitebark pine, several other tree species occurred in at least one site including subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.), Engelmann spruce (*Picea engelmannii* Parry ex Engelm.), lodgepole pine (*Pinus contorta* Dougl. ex Loud.), Douglas-fir (*Pseudotsuga menziesii* (Mirbel) Franco), and mountain hemlock (*Tsuga mertensiana* (Bong.) Carr.). Herbaceous communities varied considerably between the mountain ranges and among the individual sites within each range due to differences in the slope, aspect, substrate, and topographic position of each site. Dominant species based on percent ground cover included *Arnica alpine* (L.) Olin, *Juniperus* spp., *Lupinus* spp., *Penstemon* spp, *Phlox hoodii*, *Ribes* spp., *Phyllodoce empetriformis* (Sm.) D. Don, *Vaccinium scoparium* Leib. Ex Coville, and *Salix* spp.

Methods

Data Collection and Processing

I used a geographic information system (ESRI 2006) to identify the geographic centroid of 60 upper-elevation stands among the different mountain ranges that contained whitebark pine based on geospatial USDA Forest Service stand inventory data provided

Table 1. Site setting, stand structure, and stand composition for each mountain range. Values are means \pm 1 SD. Species codes for importance values are based on the first two letters of the Latin binomial name of each species (e.g., *Pinus albicaulis* = PIAL).

Range	n	Elevation (m)	Density (trees/ha)	Basal Area (m ² /ha)	Importance Values				
					PIAL	ABLA	PIEN	PICO	TSME
Cascades	6	2330 \pm 41	802 \pm 130	31 \pm 4	179 \pm 6	6 \pm 4	0 \pm 0	0 \pm 0	14 \pm 7
Gravelly Range	8	2887 \pm 27	848 \pm 120	34 \pm 4	176 \pm 12	22 \pm 11	2 \pm 1	0 \pm 0	0 \pm 0
Paulina Peak	7	2306 \pm 29	976 \pm 165	36 \pm 5	112 \pm 20	0 \pm 0	0 \pm 0	74 \pm 21	13 \pm 6
Pioneer Mountains	14	2728 \pm 27	1051 \pm 177	38 \pm 5	152 \pm 12	2 \pm 1	9 \pm 5	31 \pm 12	0 \pm 0
Salmon River Mountains	12	2369 \pm 26	378 \pm 38	30 \pm 4	112 \pm 13	74 \pm 11	2 \pm 1	11 \pm 7	0 \pm 0
Wallowa Mountains	13	2348 \pm 35	519 \pm 45	25 \pm 3	92 \pm 14	73 \pm 10	4 \pm 2	31 \pm 15	0 \pm 0

by each National Forest. I viewed aerial photographs in Google Earth (Google 2006) to confirm the vegetation type at each plot. These stands existed on a variety of slopes and aspects, and were near treeline yet still appeared to have relatively continuous canopies. The Universal Transverse Mercator (UTM) coordinates of each stand centroid were marked on field maps and programmed into a handheld Global Positioning System (GPS) device. In the field I found that two of the stand centroids were located on cliff edges or other unsafe slopes, four were in forest openings, one was approximately 25 m off shore in a lake, and one was on the margins of a treeless wetland. In these cases I adjusted the plot location 100 m in a randomly chosen direction. In addition, two of the larger stands in the Wallowa Mountains appeared relatively heterogeneous in disturbance history, structure, and composition. I therefore used aerial photographs, stand inventory maps, and the GPS to randomly select up to two additional sites within these stand boundaries.

A 0.1 ha circular plot was placed at the centroid or adjusted centroid of each stand to collect site characteristic and forest demographic information. I recorded the elevation, average slope, aspect, topographic position, microsite characteristics, and substrate type for each plot. The species, diameter at breast height (d.b.h.), canopy class, and health of all trees were recorded within the 0.1 ha plot. Canopy class was defined as canopy (≥ 50 percent of the tree canopy exposed to direct overhead light) and subcanopy (< 50 percent of the tree canopy exposed to overhead light). Tree health was subjectively categorized as alive (healthy canopy, fully capable of reproduction), declining (partial canopy dieback but still capable of producing cones, or the presence of pitch tubes due to active mountain pine beetle infestation), and dead. All living whitebark pine trees were visually searched for evidence of blister rust infection including active cankers, inactive cankers, rodent

chew, and flagging branches. I did not survey dead whitebark pine trees for blister rust due to the tendency of most dead trees in my plots to have lost their small branches and sloughed off their bark, greatly reducing my ability to identify past infections. All dead trees were inspected for physical damage, char, and j-shaped mountain pine beetle galleries to determine the cause of death. I tallied all saplings (≥ 2 cm diameter at ground level [d.g.l.] and < 5 cm diameter at breast height [d.b.h.]) by species and all seedlings (< 2 cm d.g.l.) by species within a nested plots of 0.05 ha and 0.01 ha, respectively. Increment cores were collected along two radii as low on the bole as possible from all living and dead trees ≥ 5 cm d.b.h. within the 0.05 ha plot to determine stand age and disturbance history and to detect the presence of blue-stain fungus, an indicator of mountain pine beetle-related mortality (Solheim 1995). Additional cores were taken through the scar face and healing lobes of any trees in the coring plot that displayed basal or strip-kill scars to date the event that caused the scar (Means 1989).

All of the increment cores were air dried, glued into core mounts, and sanded using progressively finer grit sand paper until individual xylem cells were clearly visible under 7–45x magnification (Stokes and Smiley 1996). I used the list method to develop master chronologies of marker rings for each mountain range (Yamaguchi 1990) and visually crossdated each core. The inner dates of cores that did not reach the pith of a tree but exhibited sufficient curvature in the inner rings were corrected using pith-estimators based on concentric circles (Applequist 1958). Cores that were rotten near the center and did not contain pith or sufficient curvature to estimate the rings to pith were assigned minimum ages and excluded from my age-structure analyses. Cores taken from scarred trees were examined in the context of multiple lines of evidence, including field notes on

the presence or absence of charcoal, stand structure data, timing of other injuries in the same plot, and presence or absence of blue stain at the scar face, to assign a cause to the injury (physical abrasion, mountain pine beetle strip kill, fire, or unknown disturbance).

I summarized the age-structure data into 10-yr age classes and calculated a number of disturbance-related metrics. Minimum stand age was determined as the age of the oldest tree in the plot and was used as a measure of the time since the last stand-replacing disturbance (Kipfmüller and Baker 1998). I identified cohorts where the sum of trees that established over any 30 year period (3 consecutive age-structure bins) was ≥ 5 trees and ≥ 25 percent of the total number of cored trees in the plot (Wells, Duncan, and Stewart 2001), and used the time since the last cohort establishment as an estimate of the time since the last disturbance, stand replacing or not. I assigned cohort establishment dates, fire scar dates, and mountain pine-beetle related mortality events to decadal bins and used these to calculate a decadal disturbance frequency for each plot.

I collected site-specific climate data for each of my plots. The climate data I used were sampled from the Spline climate data set developed by Rehfeldt (2006) and the PRISM climate data developed by the PRISM Group at Oregon State University (Daly, Neilson, and Phillips 1994; Daly et al. 2000; Daly et al. 2002). The climate variables I obtained included mean monthly maximum (Tmax) and minimum temperatures (Tmin) and mean monthly precipitation (ppt) from the PRISM data, and mean annual precipitation (MAP) and mean annual temperature (MAT) from the Spline data set. I seasonalized the monthly variables into spring (MAM), summer (JJA), fall (SON), and winter (DJF) variables, and included a number of derived variables related to the length of the growing season and the number of degree days (Table 2a) (Rehfeldt et al. 2006).

Table 2. Biophysical variables calculated for each site including (a) derived climate variables and (b) stand and site metrics calculated for each site.

(a)		(b)	
Code	Climate variable	Code	Stand metrics
D100	Julian date the sum of degree days reaches 100	Freq	Frequency ¹
DD0	Degree-days <0° C	RF	Relative frequency ¹
DD5	Degree-days >0° C	BA	Basal area (m ²) ¹
FFP	Julian date of the first freezing date of autumn	rBA	Relative basal area ¹
FDAY	Length of the frost-free period	IV	Importance values ([RF + rBA] × 100) ¹
GSDD5	Degree-days >5° C accumulating in the frost-free period	lASP	Linear aspect (Cosine[Aspect+45])
GSP	Growing season precipitation (April to September)	Elev	Elevation
MMAX	Mean maximum temperature in the warmest month	rElev	Relative elevation (see text for definition)
MMIN	Mean minimum temperature in the coldest month	TRMI	Topographic relative moisture index
MTCM	Mean temperature in the coldest month	rTRMI	Relative topographic relative moisture index (see text and equation (1) for definition)
MTWM	Mean temperature in the warmest month	Min Age	Minimum age of stand
SDAY	Julian date of the last freezing date of spring	DDF	Decadal disturbance frequency
ADI	Annual dryness index (DD5/MAP)	TSC	Time-since-cohort-establishment
SMI	Summer dryness index (GSDD5/MAP)		
GDI	Growing season dryness index (GSP/DD5)		

¹ Calculated for each permutation of species present, canopy class (C = canopy, S = sub-canopy), and health category (A = alive, DEC = declining, D = dead)

Following Rehfeldt et al. (2008), I also calculated a growing season dryness index (GDI) as the ratio of total summer precipitation to the degree-days >5 C° that accumulate during the frost-free season based on the Spline data (Table 2b). Lower values of the GDI indicate sites more likely to experience drought conditions.

I calculated a suite of standard forest metrics (frequency, relative frequency, basal area, relative basal area, and importance values) (Cottam and Curtis 1956) for each species present and stratified by canopy class and health category (Table 2b). In addition to the raw variables of slope, aspect, and elevation, I converted plot aspect to a linear metric (IASP), calculated relative elevation (rElev), and determined a topographic relative moisture index (TRMI) and a relative TRMI (rTRMI) for each plot. Relative elevation was calculated by subtracting the elevation of the lowest plot within a mountain range from the elevation of each of the other plots and represented an estimation of the elevational position of each stand within the distribution of sampled whitebark pine stands in each of the mountain ranges. The TRMI was developed to quantify the effects of stand-scale topography on effective moisture availability in mountainous landscapes (Parker 1982). TRMI values range from 0–60, and were calculated as the sum of values assigned to slope steepness (0–10), slope configuration (0–10), slope aspect (0–20), and slope position (0–20). Lower numbers indicate sites with less moisture availability and higher numbers indicate sites with greater moisture availability. To allow for TRMI comparisons between mountain ranges I calculated a rTRMI for each site as follows:

$$rTRMI_s = \frac{TRMI_s \times MAP_s}{\frac{1}{n} \sum_{i=1}^n TRMI_i} \quad (1)$$

where $TRMI_s$ and MAP_s are the TRMI and mean annual precipitation (PRISM data) for site s , respectively, and $TRMI_i$ is the TRMI for the i th site. This measure incorporates site-specific precipitation and topography to produce a measure of effective moisture availability that is comparable across sites with similar topography but different climate regimes.

Data Analysis

I used two nonparametric tests and ordination analyses to explore the potential relationships between whitebark pine regeneration and site biophysical characteristics across my study area. I used Kruskal-Wallis' one-way ANOVA by ranks to assess the overall similarity in levels of whitebark pine regeneration between the different mountain ranges and Kendall's τ correlation analyses to describe the strength of the relationships between individual biophysical site characteristics and whitebark pine regeneration.

I used both unconstrained (Principal Coordinates Analysis; PCO) and constrained (Canonical Correlation Analysis; CCorA) ordinations to address the multicollinearity in my environmental variables and to further assess the relationships identified in my correlation analyses. Due to the similarity in the results of my Kendall's τ correlation analyses comparing seedling and sapling densities to biophysical site characteristics, I used only the variables identified as significant with respect to sapling density to create a matrix \mathbf{X} that I ordinated using Canonical Analysis of Principal Coordinates (CAP). CAP is conducted by first using PCO on any type of dissimilarity matrix or distance measure, and then conducting CCorA on the axes of the PCO (Anderson and Willis 2003; Anderson and Robinson 2003). This approach allows for flexibility in the choice of

dissimilarity or distance measures and by conducting the CCorA on the PCO axes produces less arbitrary results for the CCorA. Using this approach CAP has been shown to be effective in identifying ecological patterns in multivariate data that are otherwise masked in the results of unconstrained ordinations (Anderson and Willis 2003). Matrix **Y** for the CCorA was composed of whitebark pine seedling and sapling densities. My ordinations were based on a symmetrical Gower dissimilarity matrix due to the different states of the biophysical variables (Legendre and Legendre 1998). All ordinations were conducted using the program CAP v.12 (Anderson and Robinson 2004), with the program determining the number of PCO axes (m) to include in the canonical analysis by sequentially increasing the number of m and each time calculating the residual error. The number of axes resulting in the minimum residual error is chosen, with the test run on 9999 random permutations.

Results

I inventoried 1,240 living seedlings, 3,051 living saplings, and 4,176 trees in 60 plots during the summers of 2006–2008 (Table 3). Of these, 1,004, 1,546, and 2,666 were whitebark pine, respectively. I observed whitebark pine regeneration in 97 percent ($n = 58$) of my plots, with seedling densities ranging from 0–17,000/ha and sapling densities ranging from 0–2,680/ha (Table 3). Increment cores were collected along two radii from 2,346 trees and I was able to assign accurate inner dates or pith estimations to 87 percent ($n = 2,046$) of these. The majority of the undated cores collected from trees with rotten centers. Pith was included in 16 percent ($n = 365$) of the cores and the average correction for cores that did not include pith was 7 ± 5 SD years (range: 1–30 years). Stand setting,

Table 3. Whitebark pine regeneration rates, blister rust rates on alive trees (% BR), frequency of mountain pine beetle-killed whitebark pine (PIAL-MPB), minimum stand age (Min Age), time since cohort establishment (TSC) and decadal disturbance frequency (DDF) for each mountain range. Values are means \pm 1 SD.

Range	PIAL seedlings/ha	PIAL saplings/ha	% BR	PIAL- MPB	Min Age	TSC	DDF
Cascades	1233 \pm 326	703 \pm 93	0.11 \pm 0.03	0.67 \pm 0.06	324 \pm 46	137 \pm 24	0.12 \pm 0.05
Gravelly Range	375 \pm 158	467 \pm 113	0.63 \pm 0.07	0.78 \pm 0.06	290 \pm 50	124 \pm 23	0.09 \pm 0.02
Paulina Peak	6086 \pm 2113	840 \pm 160	0.06 \pm 0.03	0.70 \pm 0.10	311 \pm 28	163 \pm 44	0.11 \pm 0.03
Pioneer Mountains	3107 \pm 1072	866 \pm 189	0.41 \pm 0.06	0.59 \pm 0.10	453 \pm 44	279 \pm 62	0.08 \pm 0.01
Salmon River Mountains	92 \pm 29	252 \pm 43	0.61 \pm 0.10	0.67 \pm 0.09	242 \pm 31	143 \pm 34	0.13 \pm 0.01
Wallowa Mountains	215 \pm 108	149 \pm 33	0.37 \pm 0.10	0.34 \pm 0.07	442 \pm 59	225 \pm 49	0.04 \pm 0.01

structure, and composition varied widely between the mountain ranges (Tables 1, 3). Overall, blister rust infections were observed on 37 percent ($n = 660$) of the living whitebark pine trees I inventoried, with rates of infection in individual plots ranging from 0–100 percent. Out of the 2,666 whitebark pine trees inventoried, 33 percent ($n = 887$) were dead. Mountain pine beetle activity was the primary cause of mortality with 83 percent ($n = 619$) of all dead whitebark pine exhibiting extensive pitch tubes, beetle galleries, and/or blue stain fungus. I found evidence of past fires in 35 percent ($n = 21$) of my plots in the form of fire-scarred trees and/or post-fire cohorts. In general, disturbance frequency was highest in the Salmon River Mountains and lowest in the Wallowa Mountains (Table 3). A detailed discussion of the status, structure, and disturbance histories of these stands is provided elsewhere (see Chapter 4).

Whitebark pine seedling and sapling abundances varied significantly between the six mountain ranges (seedlings: $H = 33.29$, $p < 0.000$; saplings: $H = 33.66$, $p < 0.000$) (Table 4). My correlation analyses identified a number of significant relationships between biophysical site characteristics and both seedling and sapling abundance (Table 5). The strongest relationship for both categories of regeneration was an inverse relationship with the importance of subalpine fir. Both seedlings and saplings were positively correlated with the density of whitebark pine as well as the density of dead trees and mountain pine beetle-killed whitebark pine. Whitebark pine regeneration was positively correlated with overall stand density and the density of lodgepole pine and mountain hemlock. Elevation and whitebark pine regeneration was positively correlated, with relative elevation showing a stronger relationship than absolute elevation. Several climate variables were significantly related to both seedling and sapling abundance,

Table 4. Results of Kruskal-Wallis' one-way ANOVA by ranks test for differences in whitebark pine seedling and sapling densities between mountain ranges. The test results for both seedlings and saplings indicated significant differences exist between the mountain ranges.

Range	n	Seedlings			Saplings		
		Median	Mean rank	Z	Median	Mean rank	Z
Cascades	6	1000	42.6	1.79	720	43.9	1.98
Gravelly Range	8	200	25.1	-0.95	470	31.5	0.17
Paulina Peak	7	6700	49.0	2.98	920	45.2	2.37
Pioneer Mountains	14	900	42.7	2.99	600	42.3	2.88
Salmon River Mountains	12	100	16.1	-3.20	220	20	-2.34
Wallowa Mountains	13	100	18.5	-2.81	100	12.8	-4.13

illustrating the general pattern of greater whitebark pine regeneration at the cooler, drier sites of my study area. The direction of these relationships was similar between seedlings and saplings, but the strength of the relationships was greater with respect to sapling abundance in almost all cases. Whitebark pine sapling density was also weakly but significantly related to the disturbance frequency of my sites.

The CAP results refined the patterns I identified in my correlation analyses. The first two axes of the unconstrained PCO ordination explained 68 percent of the variance in the biophysical variables significantly related to whitebark pine sapling density. A biplot of the axis scores clearly illustrated systematic differences in the multivariate structure of the biophysical variables between the mountain ranges, indicating that each range has a unique physical and climatic envelope (Figure 2a). The constrained CCorA ordination was based on the first 5 axes of the PCO, which together explained 94 percent of the variance in the biophysical variables. The CCorA generally agreed with my correlation analyses (Table 5) and highlighted the underlying similarities in the relationships between site biophysical characteristics and whitebark pine regeneration across my study area (Figure 2b). Whitebark pine seedling abundance was correlated at -0.54 with CCorA axis 1 and -0.26 with CCorA axis 2 while sapling abundance was correlated at -0.59 and 0.19 with the axes, respectively (Figure 2b). In the context of the CCorA ordination, these results indicate that both seedlings and saplings are generally more abundant at higher, drier, and colder sites with denser forests, more whitebark pine, and higher levels of mountain pine beetle mortality, and less abundant at warmer, wetter sites with greater subalpine fir importance. These patterns hold both within and among the different mountain ranges. The different relationships between seedling and sapling

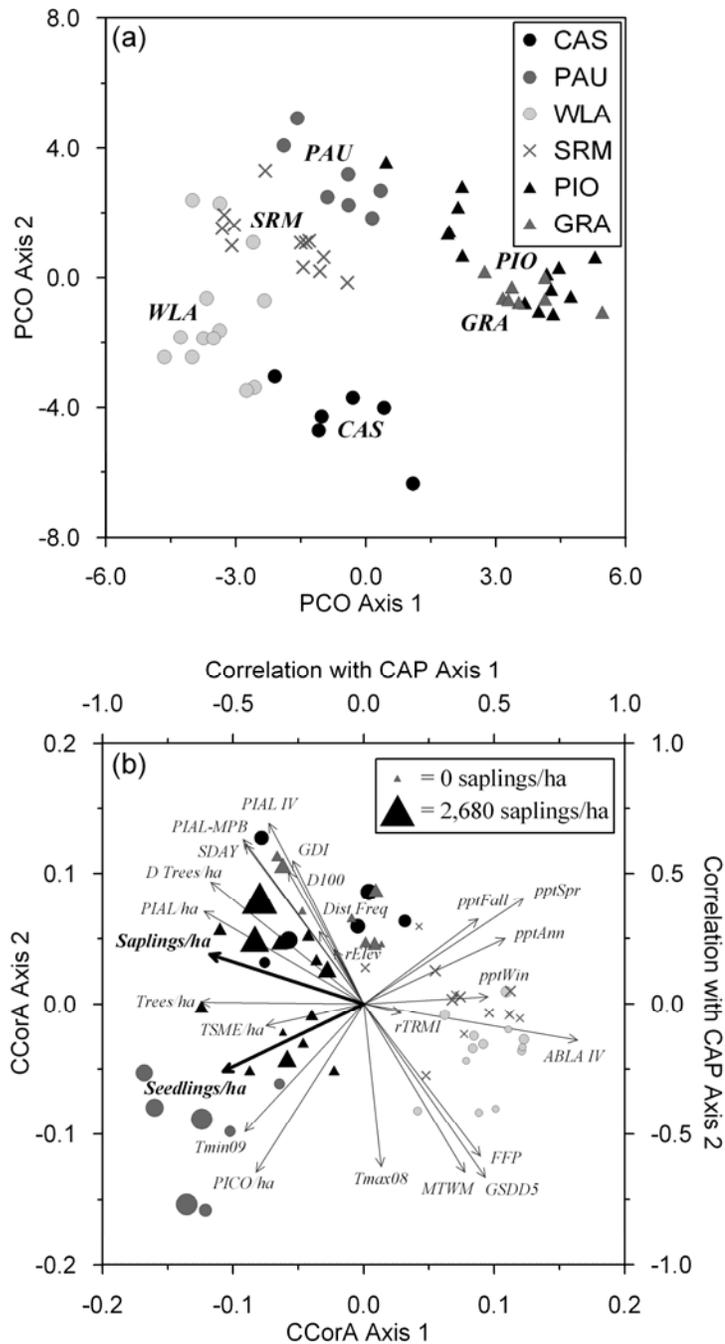


Figure 2. Ordinations of the biophysical variables significantly correlated to whitebark pine sapling abundance using (a) Principal Coordinates analysis and (b) Canonical Correlation Analysis. Site codes in (A) indicate the approximate centroid of each range in ordination space. Symbols in (b) are scaled by sapling density. The correlations of the original variables with the two canonical axes are represented by vectors in (b).

Table 5. Significant Kendall's τ rank correlations between biophysical site characteristics and whitebark pine seedling and sapling densities and correlations between biophysical site characteristics and axes 1 and 2 of the Canonical Correlation Analysis. In many cases significant correlations were identified between closely related variables such as monthly and seasonal precipitation variables or variations on forest metrics (e.g., relative frequency, relative basal area, and importance values). In these cases I listed the single variable with the strongest relationship. Species codes are as follows: ABLA = *Abies lasiocarpa*; PIAL = *Pinus albicaulis*; PICO = *Pinus contorta*.

Seedlings Variable	Kendall's τ		Saplings Variable	Kendall's τ		CCorA	
	τ	<i>p</i>		τ	<i>p</i>	Axis 1	Axis 2
ABLA IV	-0.429	0.000	ABLA IV	-0.455	0.000	0.819	-0.139
C trees/ha	0.422	0.000	PIAL/ha	0.415	0.000	-0.610	0.354
A C PIAL/ha	0.393	0.000	D Trees/ha	0.395	0.000	-0.585	0.466
pptFall	-0.283	0.001	GSDD5	-0.373	0.000	0.483	-0.665
MTWM	-0.281	0.001	MTWM	-0.350	0.000	0.387	-0.645
PICO/ha	0.276	0.001	PIAL-MPB	0.342	0.000	-0.460	0.630
D trees/ha	0.274	0.001	SDAY	0.329	0.000	-0.452	0.610
pptSpr	-0.266	0.001	Trees/ha	0.316	0.000	-0.622	0.007
GSDD5	-0.235	0.004	GDI	0.298	0.000	-0.271	0.548
SDAY	0.223	0.006	FFP	-0.296	0.000	0.447	-0.584
rElev	0.216	0.007	PIAL IV	0.283	0.001	-0.362	0.692
PIAL-MPB	0.192	0.015	pptSpr	-0.260	0.002	0.613	0.404
GDI	0.167	0.030	pptFall	-0.247	0.003	0.439	0.325
			D100	0.245	0.003	-0.288	0.507
			pptAnn	-0.241	0.003	0.541	0.251
			rElev	0.231	0.004	-0.112	0.207
			PICO/ha	0.215	0.008	-0.411	-0.645
			pptWin	-0.214	0.008	0.475	0.028
			Dist Freq	0.189	0.017	-0.169	0.276
			Tmax08	-0.160	0.035	0.067	-0.625
			TSME/ha	0.158	0.037	-0.374	-0.083
			Tmin09	0.157	0.038	-0.454	-0.490
			rTRMI	-0.149	0.047	0.142	-0.034

abundance and CCorA axis 2 indicate that although more whitebark pine regeneration occurred in the relatively colder sites across the landscape, within the context of this pattern seedling density was greater on warmer sites while saplings density was greater at the cooler sites.

Discussion

The Presence of Early and Advanced Whitebark Pine Regeneration

The nearly ubiquitous presence of whitebark pine seedlings and saplings across my study area was encouraging, as past landscape-scale assessments of whitebark pine have reported patchy occurrences of regeneration (Zeglen 2002) or abundant seedlings with few saplings present (Weaver, Forcella, and Dale 1990). The presence of seedlings at nearly all of my sites reflects two consecutive mast years in 2005 and 2006 that occurred across my study area (personal communication, Bob Keane, Research Ecologist, USDA Fire Sciences Lab). Whitebark pine seed germination often lags when the seeds are cached by Clark's nutcrackers by 1–2 years (Tomback et al. 2001), suggesting these mast events could have provided the seed source for the abundance of recently emerged whitebark pine seedlings I observed; however, the advanced regeneration I documented in the form of saplings indicates that there have been multiple episodes of successful whitebark pine establishment at my sites over the recent past. Additionally, abundant seed production would do little for regeneration without the availability of sites suitable for regeneration. While whitebark pine regeneration is often associated with recently burned or otherwise disturbed settings (Tomback, Sund, and Hoffmann 1993; McCaughey and Tomback 2001), my results are more similar to a recent study in British

Columbia that found comparable densities of whitebark pine seedlings between recently burned sites and nearby undisturbed settings (Moody 2006). This suggests that whitebark pine is not limited to the role of a post-fire pioneer species at my study sites even in the presence of more shade-tolerant species such as subalpine fir and mountain hemlock.

The mountain ranges with the lowest densities of regeneration illustrate contrasting mechanisms behind these patterns. The stands in the Wallowa Mountains that I examined were quite open in terms of stand density and total basal area and would seem to provide ample locations for whitebark pine regeneration (Tomback 1982), yet regeneration levels were relatively low compared to other sites. The Wallowa Mountains exhibited the lowest mean rates of blister rust infection, mountain pine beetle activity, and disturbance frequencies of the ranges included in my study, and had a corresponding greater importance of subalpine fir, possibly suggesting that these stands were successional advanced in the absence of disturbance. The inverse relationship between subalpine fir and whitebark pine regeneration identified in my correlation analyses and CAP suggests that subalpine fir may limit whitebark pine regeneration through resource competition and shading on suitable sites (Keane et al. 1990a). Therefore the lower rates of regeneration in the Wallowa Mountains may be the result of advancing succession due to a general lack of disturbance. The Salmon River Mountains are climatically similar to the Wallowa Mountains and also exhibited low levels of regeneration. In the case of the Salmon River Mountains, however, the low levels of regeneration and greater importance of subalpine fir are more likely the result of the compounded effects of multiple recent disturbances. Most stands in the Salmon River Mountains experienced high levels of mountain pine beetle related mortality from the late 1980s to the present in addition to

two large fires that burned across two sites in 1989 and three sites in 1994 (Gibson 2005). Large, infrequent disturbances that occur in close temporal succession such as these events often have different ecological effects than either disturbance alone (Paine, Tegner, and Johnson 1998). As a result, whereas whitebark pine regeneration was positively correlated with mountain pine beetle-caused mortality elsewhere in my study area, the fires that burned following mountain pine beetle activity at these sites may have killed whatever whitebark pine regeneration was alive at the time while also killing nearby seed sources that may have survived the mountain pine beetle outbreaks, resulting in the relatively low levels of regeneration in Idaho. These results suggest a disturbance frequency-dependent pattern in whitebark pine regeneration that may have important implications for the ecological response of whitebark pine communities across the species range. In particular, the low levels of whitebark pine regeneration at sites affected by multiple closely-timed disturbance events is a foreboding pattern in the context of expanding mountain pine beetle outbreaks (Raffa et al. 2008) and increasing mid- and high-elevation fire activity in the western United States (Westerling et al. 2006).

The Relationships Between Whitebark Pine Regeneration and Biophysical Site Characteristics

Similar to other tree species that exist across the gradient from lower subalpine forests to upper subalpine forests, patterns in whitebark pine regeneration reflect both local-scale factors as well as the overall dominant environmental gradients of regional climate and changing elevation (e.g., Pollmann and Veblen 2004). The relationships between whitebark pine regeneration and biophysical site characteristics that I identified

agreed well with the known distribution of whitebark pine and the niche it occupies (Arno and Hoff 1990; Weaver 2001; Rehfeldt, Ferguson, and Crookston 2008). The strong correspondence between axis 1 of my CCorA and several measures of temperature and moisture availability illustrates whitebark pine's ability to regenerate in harsh environments and provides a mechanism for whitebark pine dominance of timberline communities and xeric sites in the subalpine forests of the Northern Rockies and Pacific Northwest (Arno and Hammerly 1984; Arno 2001). The differing relationships between seedling and sapling densities and CCorA axis 2 potentially illustrate the differential effects of the biophysical environment on whitebark pine germination success versus successful establishment. McCaughey (1990) found that while warm temperatures were important for facilitating whitebark pine seed germination, some of the most common causes of death among emerging whitebark pine seedlings were heat scorch and drought. Similarly, Moody (2006) found that whitebark pine seedlings were more abundant following longer growing seasons contingent on there being sufficient moisture available throughout the season. These relationships seem to play out in my study area with the greater seedling densities found at the sites with longer, warmer growing seasons compared to the greater sapling densities at the colder sites within the context of the overall gradient of axis 1 toward colder sites in general. The implications of this are that while seedlings are more likely to emerge at warmer sites, they are also more likely to suffer heat damage and higher mortality rates, and therefore seedlings on cooler sites with lower initial seedling success have higher sapling recruitment rates (McCaughey 1990; Tomback, Sund, and Hoffmann 1993). This differential response likely affected the spatial patterning and structure of whitebark pine communities in the past, and may play

an important role in the future dynamics of whitebark pine forests in the context of global warming.

The strong inverse relationship between whitebark pine seedling and sapling density and the importance of subalpine fir at my sites provides an interesting illustration of the complexity of regeneration dynamics in whitebark pine communities. Subalpine fir is more tolerant of shade than whitebark pine (Alexander, Shearer, and Shepperd 1990), but less tolerant of drought and winter desiccation, and often depends on whitebark pine to become established at harsh sites (Callaway 1998). In moderate sites, however, subalpine fir often dominates the understory of whitebark pine forests as they age and transition into later successional stages (Keane, Morgan, and Menakis 1994; Kipfmüller and Kupfer 2005). Indeed, subalpine fir was the dominant understory species (based on importance values) in 22 of the 35 sites in my study at which it occurred, yet neither subalpine fir importance or whitebark pine regeneration densities showed a significant relationship to stand age and the presence of recently emerged and advanced regeneration at these sites suggests that whitebark pine regeneration was not yet precluded from these stands. Campbell and Antos (2003) observed similar patterns of whitebark pine regeneration throughout the history of several stands in a chronosequence study of succession in whitebark pine-subalpine fir forests in British Columbia. Whitebark pine regeneration densities were significantly different among the landscapes included in my study and these patterns may not hold true across the entire range of whitebark pine, but the presence of whitebark pine regeneration in later-successional subalpine forests may play an important role in the persistence of whitebark pine on the modern landscape, albeit at lower densities.

The Role of Mountain Pine Beetles in Whitebark Pine Regeneration

The declines in whitebark pine forests due to blister rust are likely unprecedented as this disease is a novel disturbance with respect to the recent evolutionary history of whitebark pine (McDonald and Hoff 2001) and fire suppression activities are potentially causing shifts of many whitebark pine forests outside of their natural range of variability in terms of structure and composition (Keane, Morgan, and Menakis 1994; Murray, Bunting, and Morgan 2000; Larson, van de Gevel, and Grissino-Mayer 2009). In contrast, mountain pine beetle has been a disturbance agent in whitebark pine forests for millennia (Brunelle et al. 2008), and while recent warming may have exacerbated current mountain pine beetle outbreaks (Logan and Powell 2001), this warmth may not be unprecedented in the evolutionary history of whitebark pine in North America when compared to the increased seasonality and temperature extremes associated with periods such as the Holocene Solar Optimum (MacDonald, Cwynar, and Whitlock 1989; Ruddiman 2000). It would therefore make sense if the tree species were adapted to occasional severe and widespread mountain pine beetle outbreaks similar to recent beetle epidemics. The strong relationship between rates of mountain pine beetle-killed whitebark pine and whitebark pine regeneration density indicate that stand-scale gap-phase dynamics may be one response of whitebark pine forests to mountain pine beetle outbreaks.

Gap dynamics have been extensively studied in forest ecosystems world wide (e.g., Platt and Strong 1989 and papers mentioned therein), yet while the patchy mortality of most mountain pine beetle outbreaks creates numerous forest openings and canopy gaps of varying sizes (Raffa et al. 2008; Rocca and Romme 2009), relatively little

research has examined how these disturbances may influence whitebark pine regeneration. In part, this is due to a broad focus on the historical role of fire as the dominant disturbance process in most forest types of western North America (Attwell 1994; Swetnam and Betancourt 1998; Keane et al. 2002; Allen et al. 2002; Hessburg, Agee, and Franklin 2005), including whitebark pine communities (Keane 2001a; Arno 2001). It also reflects the uncertainty and relatively limited data available on the long-term role of mountain pine beetles in whitebark pine ecosystems (Kipfmüller, Swetnam, and Morgan 2002). Yet while research suggests that warming temperatures are enabling mountain pine beetle outbreaks to reach whitebark pine forests in climatic settings that were previously too harsh to support large beetle populations (Logan and Powell 2001; Hicke et al. 2006), Brunelle et al. (2008) found evidence that mountain pine beetle outbreaks have occurred in whitebark pine ecosystems since at least the mid Holocene. In other forest types, mountain pine beetle outbreaks act as secondary disturbances with strong influences on patterns in stand development (Sibold et al. 2007; Nigh, Antos, and Parish 2008). My research adds to this growing literature by indicating that mountain pine beetle-caused mortality in whitebark pine forests can serve as an effective mechanism for creating canopy gaps and forest openings that appear to be attractive seed caching areas for Clark's nutcrackers (Hutchins and Lanner 1982; Tomback 1982) and are suitable sites for whitebark pine regeneration.

Management Implications

The existence of landscape-scale relationships between whitebark pine regeneration and the biophysical environment offer several opportunities to increase the

efficacy of management and restoration activities in whitebark pine communities. Outplanting of blister rust-resistant seedlings and saplings is an expensive and labor-intensive endeavor (Hoff et al. 2001), but is considered one of the more effective strategies for managing whitebark pine in the presence of white pine blister rust (Schoettle and Sniezko 2007). In the context of my research, targeting stands in colder, drier settings for outplanting may give the planted whitebark pine the greatest chance of establishment and eventual maturation. Planting beneath canopies of mature whitebark pine experiencing an active mountain pine beetle outbreak may also be an effective approach, as the resources made available by mountain pine beetle disturbances appear to provide an optimal environment for whitebark pine regeneration. Additionally, stands where the mature trees are killed by mountain pine beetle may be less susceptible to future outbreaks due to the dearth of larger living trees that are the preferred host of beetle infestations (Amman 1972; Stuart 1984; Waring and Pitman 1985) and, depending on the susceptibility of the landscape to fire (Turner and Romme 1994; Peterson 2002), offer the longest potential disturbance-free growing period for the planted trees.

The advanced natural regeneration I observed in mountain pine beetle-created gaps may also serve as an important asset to management aimed at increasing blister rust resistance in whitebark pine. Blister rust infection levels across my study area were moderate relative to other regions (Smith and Hoffman 2000; Smith et al. 2008), yet the susceptibility of early and advanced regeneration to white pine blister rust (Tomback et al. 1995) may result in differential mortality among the regeneration I observed with a greater proportion of surviving seedlings and saplings representing rust-resistant genotypes. Rust resistance has been documented to increase rapidly over only a few

generations (Hoff et al. 2001) and the greater levels of regeneration found at my study sites affected by 20th century mountain pine beetle outbreaks may act as a catalyst for the development of white pine blister rust resistance in whitebark pine. Natural regeneration in this context may provide a key mechanism for this foundation species to adapt to its changing environment and should be closely monitored as it could be a critical step in maintaining the presence of whitebark pine communities in western North America.

Chapter 4. Disturbance, Succession, and the Effects of Fire Suppression in Whitebark Pine Communities of Southwest Montana, Central Idaho, and Oregon, U.S.A.

Introduction

Disturbance and succession are fundamental processes that influence the structure and composition of ecological communities and any changes to these processes likewise produce changes in ecosystem dynamics. This holds potent implications for many of the Earth's ecosystems as they undergo rapid and potentially unprecedented changes due to shifting global climate conditions, anthropogenic modification of disturbance regimes, and the spread of invasive species (Mack et al. 2000; IPCC 2007). My ability to understand and predict the ecological effects of these changes is limited by the complexity of most ecosystems and made more difficult where ecosystem processes function on long time scales. Subalpine forest communities provide an example of such systems, where short growing seasons, relatively infrequent disturbances, and the great longevity of many subalpine tree species result in forest dynamics that play out over centuries to millennia. On these time scales even the foundation of ecosystem change and community succession varies with the continually shifting backdrop of local and regional climate conditions (Kutzbach 1976). It is therefore challenging to determine if modern changes to these systems are the result of natural processes or human-induced disturbances that warrant restoration activities. This uncertainty is particularly important for ecosystems that are undergoing apparently unprecedented declines and are subject of strong calls for active management intervention and restoration. Whitebark pine

communities provide a model for this problem due to their position at the convergence of a number of cultural and environmental factors driving ecological change.

The label of whitebark pine community is broadly applicable to subalpine forests across western North America that include the conifer tree species whitebark pine (*Pinus albicaulis* Engelm.) (Arno 2001). Whitebark pine is found along the crests of the Cascades and Sierra Nevada and throughout the northern Rocky Mountains (Arno and Hoff 1990). It fills a number of ecological roles including the physical maintenance of the headwaters of mountain watersheds (Farnes 1990), the amelioration of microsite conditions that facilitate increased plant and animal biodiversity (Callaway 1998; Tomback and Kendall 2001), and the production of a critical food source for a variety of mountain wildlife (Arno 1986). Whitebark pine is largely dependent on the Clark's nutcracker (*Nucifraga columbiana* Wilson) for seed dispersal (Tomback 1982; Lanner 1996), and the mutualistic relationship between these species serves as the foundation for a tightly woven ecosystem that includes whitebark pine, Clark's nutcrackers, red squirrels (*Tamiasciurus hudsonicus* Trouessart), black bears (*Ursus americanus* Pallas), and grizzly bears (*Ursus arctos* L.) (Ellison et al. 2005). Due to the myriad ecosystems services provided by whitebark pine, recent declines in whitebark pine communities have raised concerns among managers and scientists over the current and future status of this species (Tomback, Arno, and Keane 2001b).

The factors implicated in the declines of whitebark pine include outbreaks of the native mountain pine beetle (*Dendroctonus ponderosae* Hopkins), the spread of the invasive white pine blister rust (*Cronartium ribicola* (A. Dietr.) J.C. Fisch.), climate change, and fire suppression (Tomback, Arno, and Keane 2001a), yet it is the effects of

fire suppression that have received a bulk of the attention while being founded on relatively little quantitative data. Fire suppression is thought to have reduced fire frequency in whitebark pine communities, thereby decreasing the occurrence of forest openings critical for whitebark pine regeneration, increasing the susceptibility of aging stands to future beetle outbreaks, and enabling fire-intolerant species to encroach upon mature stands of whitebark pine (Morgan et al. 1994; Keane 2001a). It is commonly called on as a leading cause of declines in whitebark pine communities, with an example drawn from one of the primary and most comprehensive sources on whitebark pine communities: “Whitebark pine communities are declining because of two forces, fire suppression and the introduction of an exotic fungal disease” (p. 417, Arno, Tomback, and Keane 2001). The issue arises in that this statement and others like it are based on a relatively limited data set that specifically examines and quantifies whitebark pine forest fire regimes, much of which is restricted to the U.S. Northern Rockies (Arno 1980; Morgan and Bunting 1990; Keane, Morgan, and Menakis 1994; Murray, Bunting, and Morgan 1998). Even in this region an assessment of stand dynamics in whitebark pine forests found fire-intolerant species had established as early as the 1700s in many stands, well before fire suppression was a factor on the landscape (van de Gevel 2008) and a detailed study of the fire regimes of three whitebark pine forests found only one of three had shifted outside of its historical range of fire frequency due to fire suppression (Larson, van de Gevel, and Grissino-Mayer 2009). Additionally, one of the few studies to explicitly address whitebark pine fire history and succession outside of the U.S. Northern Rocky Mountains found that whitebark pine had not been successional excluded from stands that were over 500 years old (Campbell and Antos 2003). Furthermore, research

across western North America suggests that the fire regimes of most high-elevation forests are still operating within their historical range of variability and have not been affected by modern fire suppression (e.g., Romme 1982; Johnson, Fryer, and Heathcott 1990; Sherriff, Veblen, and Sibold 2001; Buechling and Baker 2004). All of these factors create considerable uncertainty with respect to the actual effects of fire suppression in whitebark pine forests, yet despite this uncertainty prescribed fire is suggested as a primary management tool in whitebark pine restoration activities with the justification that fire has been removed from this system (Keane and Arno 2001). While fire suppression has affected some forests (Larson, van de Gevel, and Grissino-Mayer 2009), management strategies uniformly based on a paradigm of the pervasive effects of fire suppression are likely inappropriate for whitebark pine ecosystems across the broad range of this species and require a more nuanced perspective informed by site-specific data. It is therefore critical that management and restoration activities move forward with the best possible knowledge of what factors have led to the declines in whitebark pine forests and what management activities are ecologically warranted to encourage their restoration.

To address this uncertainty my research examined patterns of disturbance and succession in whitebark pine communities to better understand the mechanisms underlying the declines of this foundation species. In particular I examined the relative roles of stand processes and climate in driving forest composition to illustrate the potential effects of fire suppression in whitebark pine forests. I approached this problem by seeking answers to the following questions: 1) How do patterns in disturbance and forest structure and composition in whitebark pine communities vary in different biophysical settings? 2) What are the relative influences of disturbance, time, and climate

in driving whitebark pine forest composition? 3) Do whitebark pine forests show any structural and/or compositional changes that may be related to fire suppression? I then used the answers to these questions to broadly assess disturbance, succession, and the effects of fire suppression in the whitebark pine communities.

Methods

Study Area

My study area extends from southwest Montana to western Oregon between ca. 42° and 45° N with sites in the Gravelly Range and Pioneer Mountains of Montana, the Salmon River Mountains of Idaho, and the Wallowa Mountains, Paulina Peak, and Cascade Range of Oregon (Fig. 1). These mountain ranges are included within the boundaries of the Beaverhead–Deerlodge National Forest, the Payette National Forest, the Wallowa–Whitman National Forest, and the Deschutes National Forest, respectively. The topographic character of these ranges varies considerably. The Gravelly Range is generally rolling, while the Pioneer Mountains, Salmon River Mountains, and Wallowa Mountains are each an extensive mountain range and highly dissected by glacial valleys and ridges. Paulina Peak and the Cascades are younger, relatively isolated volcanic mountains with more regular terrain. Paulina Peak is the remnant of Newberry Volcano with a high-elevation rim bordering the south and east sides of what is now Newberry Caldera. The sites in the Cascades were located on Mount Bachelor, a relatively young volcanic mountain with a regular conical shape, and Black Crater, an irregularly shaped cinder cone.

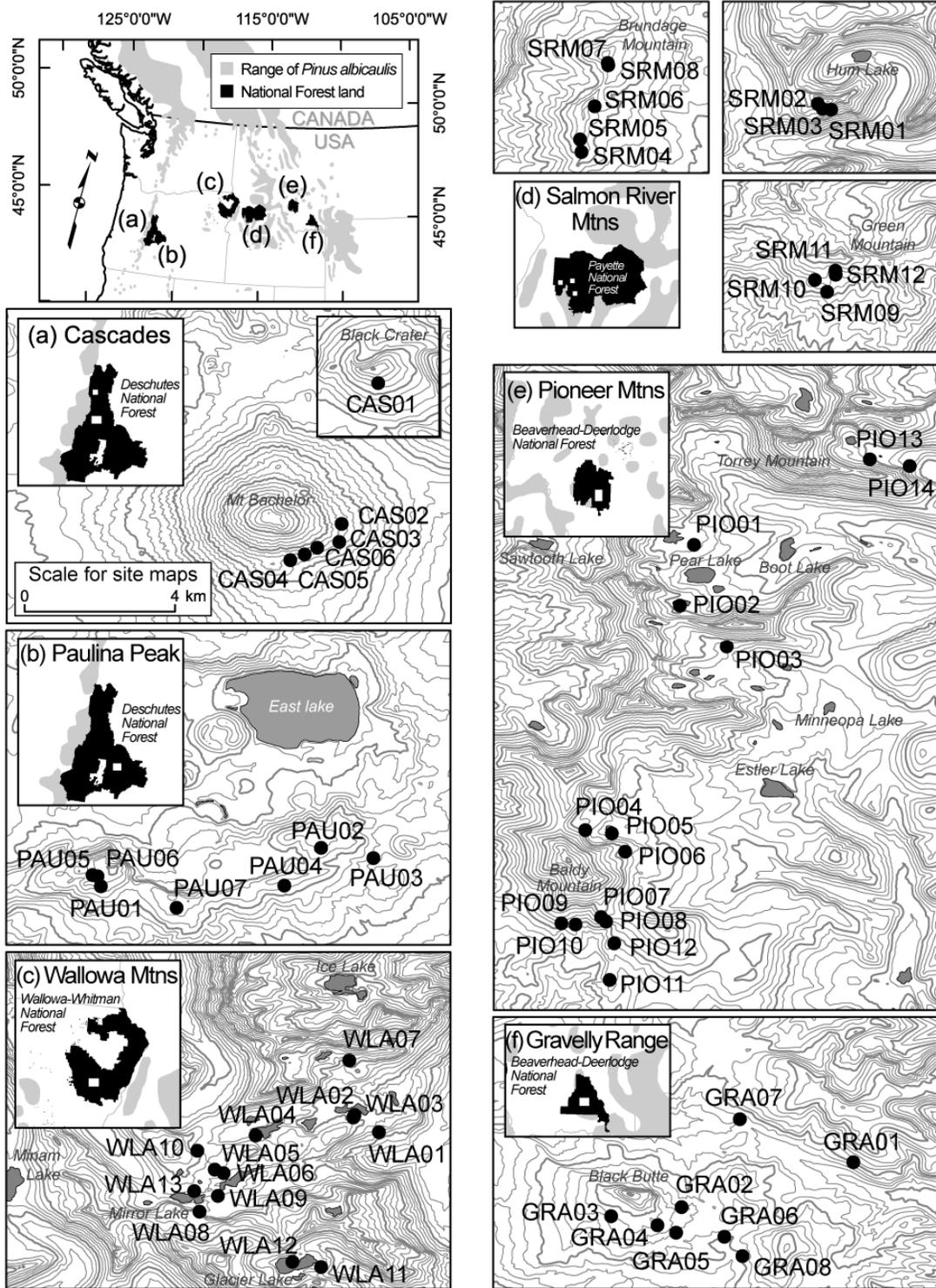


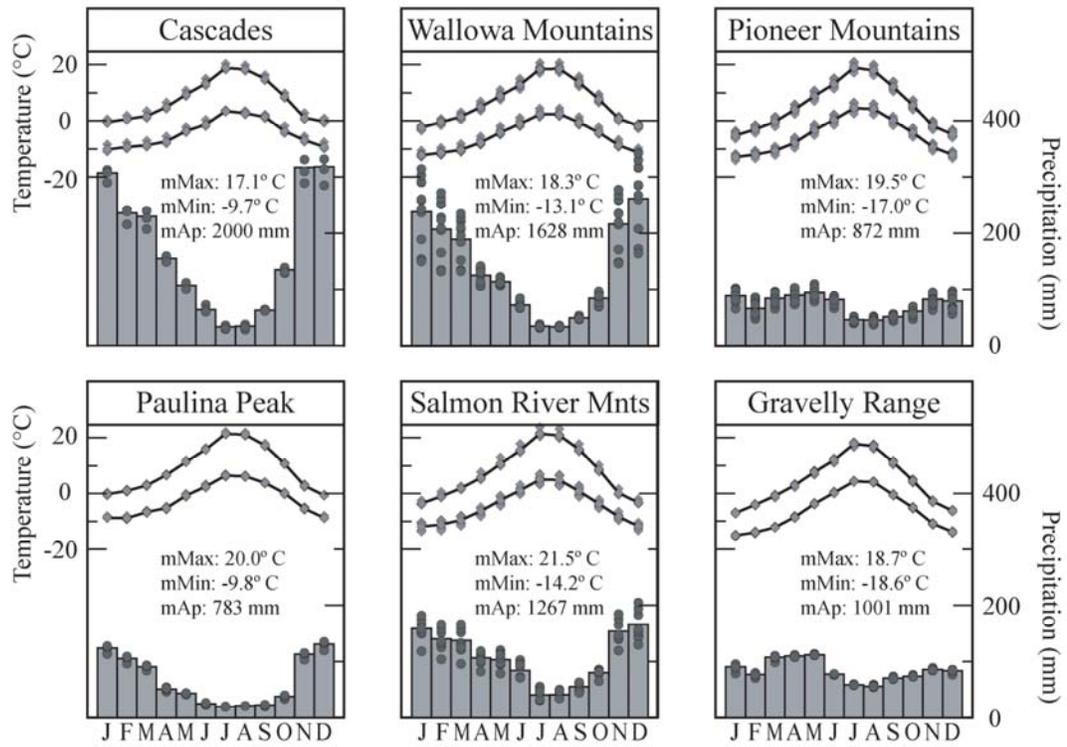
Figure 1. Study area and site maps. Letters on the study area map correspond to the site maps. The white rectangles within the national forest boundaries in each site map indicate the areas depicted in the study site maps. The site map scale is shown in (a) and is the same for all site maps. Contour intervals are 20 m with index contours every 100 m.

Broad similarities existed in the annual patterns of temperature and precipitation at my sites as well as some distinct differences. In general, the sites shared a common pattern of drier summers and wetter winters, although the peak in winter precipitation was more pronounced in the Cascades, Wallowa Mountains, and Salmon River Mountains than at the other sites (Fig. 2a). Mean total annual precipitation among the different mountain ranges was affected by regional-scale rain shadows and ranged from 783 mm across the sites on Paulina Peak up to 2,000 mm at the Cascades sites, while mean monthly maximum and minimum temperatures exhibited a gradient in extremes from the western, more maritime sites to the eastern, more continental sites. Variability in climate conditions within each landscape was highly influenced by the general topography of the mountain ranges, with more variable topography and climate in the Wallowa Mountains, Salmon River Mountains, and Pioneer Mountains contrasting with less variability in the Gravelly Range, Paulina Peak, and the Cascades. The climatic settings of my study sites represent a relatively wide range within the overall distribution of whitebark pine (Fig. 2b), although the distribution of July temperatures at my sites based on 1971–2000 climate normals was systematically higher than the July temperatures used in the Climate-Vegetation atlas that were based on the 1951–1980 climate normals (Thompson, Anderson, and Bartlein 1999).

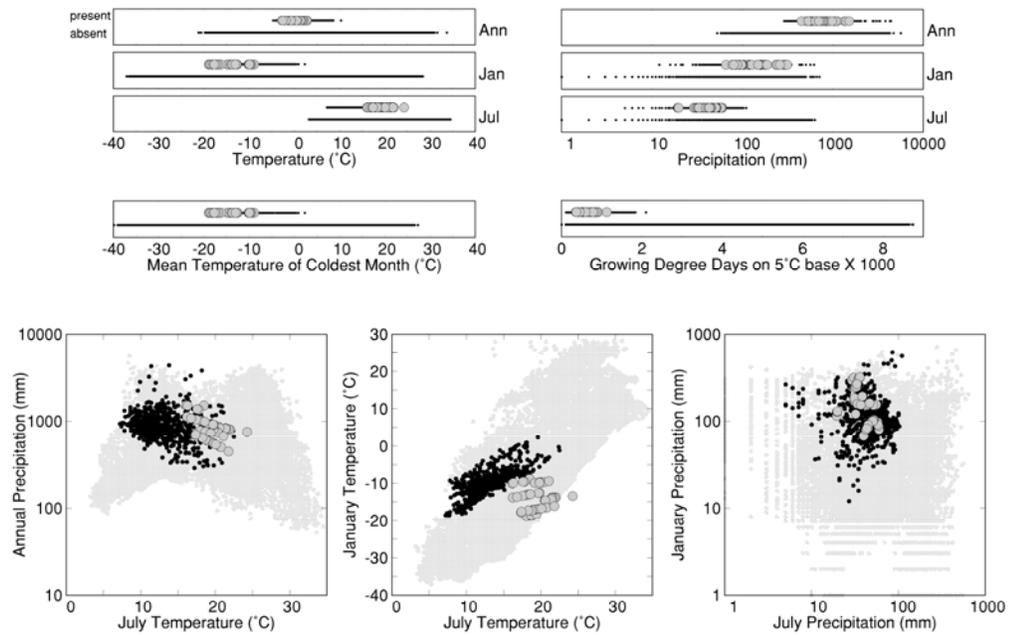
My study sites were located in the upper forest zones of each mountain range where whitebark pine was the dominant or co-dominant tree species. In addition to whitebark pine, several other tree species occurred in at least one site including subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.), Engelmann spruce (*Picea engelmannii* Parry ex Engelm.), lodgepole pine (*Pinus contorta* Dougl. ex Loud.), Douglas-fir (*Pseudotsuga*

Figure 2. Climate conditions for my sites represented by (a) climographs for each mountain range based on plot-level climate data, and (b) the distribution of the my plots (grey dots) in the climate space of whitebark pine (black dots). The climographs represent the mean monthly maximum, mean monthly minimum, and mean monthly precipitation for each plot as scatter points with the overall means of each of these variables for each mountain range indicated by the line graphs (temperature) and the bar graphs (precipitation). The data were obtained from PRISM climate grids for the United States (PRISM Group, Oregon State University, <http://www.prismclimate.org>, created 13 Nov 2008) (Daly et al. 2002; Daly et al. 2008). The climate space of whitebark pine is adapted from Thompson *et al.* (1999) who used the 1951–1980 climate normals, while the data for my sites is based on 1971–2000 climate normals provided in the PRISM data.

(a)



(b)



menziesii (Mirbel) Franco), and mountain hemlock (*Tsuga mertensiana* (Bong.) Carr.).

Associated plant communities varied considerably between the mountain ranges and among the individual sites within each range by the different slope, aspect, substrate, and topographic positions of each site. Some of the more common species included *Arnica spp.*, *Vaccinium scoparium* Leib. ex Coville, *Lupinus spp.*, *Ribes spp.*, *Juniperus spp.*, and *Penstemon spp.*

Data Collection: Field Methods

I used a geographic information system (GIS) (ArcMap v9.2, ESRI) to identify the geographic centroid of 60 upper-elevation stands that contained whitebark pine in the National Forests based on geospatial stand inventory data provided by each National Forest. I confirmed the vegetation at each site using aerial photographs viewed in Google Earth (v2.0–4.1). The selected stands existed on a variety of slopes and aspects, and were near treeline yet still appeared to have relatively continuous canopies. The Universal Transverse Mercator coordinates of each stand centroid were marked on field maps and programmed into a handheld geographic positioning system (GPS) device. Once in the field I found that eight of the stand centroids were located in or near water features or on cliff edges or other unsafe slopes. In these cases I adjusted the plot location 100 m in a randomly chosen direction. In addition, two of the larger stands in the Wallowa Mountains appeared relatively heterogeneous in disturbance history, structure, and composition. I therefore used aerial photographs, stand inventory maps, and the GPS to randomly select up to two additional sites within these stand boundaries.

A 0.1 ha circular plot was placed at the centroid or adjusted centroid of each stand to collect site characteristic and forest structure, composition, and demographic information. I recorded the elevation, average slope, aspect, topographic position (valley bottom, lower slope, middle slope, upper slope, or ridge top), and microsite characteristics (concave, concave/straight, straight, convex/straight, convex). I recorded the species, diameter at breast height (d.b.h.) and canopy class of all trees ≥ 5 cm d.b.h. within the plot. Canopy class was defined as canopy ($\geq 50\%$ of the tree canopy exposed to direct overhead light) and subcanopy ($< 50\%$ of the tree canopy exposed to overhead light). All dead trees were inspected for physical damage, char, and j-shaped mountain pine beetle galleries to determine the proximate cause of death. Increment cores were collected along two radii of all living and dead trees ≥ 5 cm d.b.h. within a nested 0.05 ha subplot centered on the stand centroid. Additional cores were taken through the scar face and healing lobes of any trees in the coring plot that displayed basal or strip-kill scars to date the event that caused it (Means 1989), and cross sections were taken from fire-scarred trees where sampling permission and wilderness restrictions permitted. I tallied all saplings (≥ 2 cm diameter at ground level [d.g.l.] and < 5 cm d.b.h.) by species within the 0.05 ha subplot and all seedlings (< 2 cm d.g.l.) by species within a nested 0.01 ha subplot.

Data Collection: Climate and Stand Variables

I collected site-specific climate data for each of my plots. The climate data were sampled using a GIS (ESRI 2006) from grids of the Spline climate data set developed by Rehfeldt (2006) and the PRISM climate data set developed by the PRISM Group at

Oregon State University (Daly et al. 2002). The climate variables obtained included mean monthly maximum temperatures, mean monthly minimum temperatures, and mean monthly precipitation from the PRISM data set, and mean annual precipitation, mean growing season precipitation (April–September), mean annual temperature, and mean temperature of the warmest month, and mean minimum temperature of the coldest month from the Spline data set. I seasonalized the monthly PRISM variables into spring (March–May), summer (June–August), fall (September–November), and winter (December–February) variables. I also obtained a number of derived variables from the Spline data set, including degree days $>5^{\circ}\text{C}$, the length of the frost-free period, the mean Julian dates of the last spring frost and first autumn frost, and dryness indices for the year, summer, and growing season (Rehfeldt et al. 2006). Following some of my initial analyses I also calculated a measure of potential productivity by multiplying mean summer precipitation and the length of the frost free period. From these data I obtained a total of 70 variables describing different aspects of the site-specific climate conditions for each plot. A high degree of multicollinearity existed among these variables, but I retained them in their original form rather than in a reduced form (e.g., principle components) so as to retain as much resolution as possible in the data set in the occasion that particular aspects of climate, such as temperature during a single month, would not be smoothed and lost from my analysis. To compensate for the multicollinearity in this data set I used partial correlations and stepwise regression to aid my interpretations of analyses that identified specific variables as important.

I calculated a suite of standard forest metrics (frequency, relative frequency, basal area, relative basal area, and importance values) for each species present in the inventory

plots as well as the same metrics stratified by canopy class (Cottam and Curtis 1956). In addition to the raw variables of slope, aspect, and elevation, I converted plot aspect to a linear metric (IASP), calculated relative elevation (rElev), and determined a topographic relative moisture index (TRMI) for each plot. Linear aspect was calculated as $1 + \cos(\pi(\text{aspect} - 45)/180)$ and results in a value from 0 (warmer, drier SW-facing slopes) to 2 (cooler, moister NE-facing slopes). Relative elevation was calculated by subtracting the elevation of the lowest plot within a mountain range from the elevation of each of the other plots and represented an estimation of the elevational position of each stand within the distribution of sampled whitebark pine stands in each of the mountain ranges. The TRMI was developed to quantify the effects of stand-scale topography on effective moisture availability in mountainous landscapes (Parker 1982). TRMI values range from 0–60, and were calculated as the sum of values assigned to slope steepness (0–10), slope configuration (0–10), slope aspect (0–20), and slope position (0–20). Lower numbers indicate sites with less moisture availability and higher numbers indicate sites with greater moisture availability.

Stand and Disturbance History Reconstruction

All of the increment cores and fire-scar samples were prepared and crossdated following standard dendrochronological methods (Stokes and Smiley 1996). The inner dates of cores that did not reach the pith of a tree but exhibited sufficient curvature in the inner rings were corrected using pith-estimators based on concentric circles (Applequist 1958). Cores that were rotten near the center and did not contain pith or sufficient curvature to estimate the rings to pith were assigned minimum ages and used to

determine minimum stand age but were excluded from my age-structure analyses.

Because of the at-risk status of whitebark pine I did not collect saplings to determine an age-to-coring-height correction. Therefore the tree age data used in this paper should be considered the minimum age of the trees rather than the absolute date of germination.

I used both the minimum stand age and the time since the last cohort established (TSC) as measures of stand development. Minimum stand age was determined as the minimum age of the oldest living tree in the plot and was used as a measure of the time since the last stand-replacing disturbance (Kipfmüller and Baker 1998). To calculate the TSC for each plot, I first summarized the age-structure data into 10-yr bins, and then defined individual cohorts as any period of 30 years (three consecutive 10-yr age-structure bins) that included the inner dates of ≥ 5 trees and $\geq 25\%$ of the total number of cored trees in the plot (Wells, Duncan, and Stewart 2001). Decadal cohort dates were assigned by the first 10-yr bin of each period that satisfied these requirements. The TSC was calculated as the number of years since the most recent cohort established at each site. I used non-parametric Kruskal-Wallis one-way ANOVA by ranks test (Legendre and Legendre 1998) to determine if differences in stand age and TSC existed between the different mountain ranges that could influence my interpretation of the results of other analyses.

I described the disturbance history of each site using fire scar dates, mountain pine beetle-related mortality dates, and cohort establishment dates. The dates of all fire scars were assigned to the decade in which they occurred to match the scale used for the age-structure data and to accommodate the uncertainty of core-derived fire dates (Barrett and Arno 1988). I used the outer rings of trees showing evidence of mountain pine beetle-

related mortality to determine the probable death date for each tree, then summed the number of beetle-killed trees by decade to account for potential inaccuracies of death dates due to erosion of the cambial surface following death. Tree establishment cohorts in the age-structure of high-elevation conifer forests of western North America typically follow moderate- to high-severity disturbance events (Parker and Peet 1984), and I therefore included all cohort establishment dates that did not follow an identified fire event as evidence of an unidentified disturbance. I then divided the minimum stand age by the total number of disturbance events to calculate a decadal disturbance frequency DDF for each plot. I used non-parametric Kruskal-Wallis one-way ANOVA by ranks test (Legendre and Legendre 1998) to identify differences in disturbance frequency that would help me broadly characterize the disturbance regimes of the different mountain ranges.

Analyses of Vegetation Composition and Succession

I used aspects of vegetation reconstructions (Hett and Loucks 1976), chronosequence methods (Brubaker 1981), and multivariate analyses (Minchin 1987) to assess patterns in forest composition and succession at my sites. Each of these methods has its strengths and weakness, and I therefore sought to strengthen my analyses by incorporating elements of all of them. I began my analyses by visually examining the stand history data of each individual plot for patterns in disturbance and species establishment over time using size-age graphs, d.b.h. distributions, frequency distributions of mountain pine beetle-related mortality, and fire and cohort establishment events. The shape of tree size and age distributions can be used to infer stand dynamics

(Hett and Loucks 1976; Whipple and Dix 1979). I therefore calculated Weibull distributions of tree d.b.h. and age by species for each plot (Weibull 1951; Bailey and Dell 1973) to enhance my ability to visually compare forest structure within and among the mountain ranges. I also combined the plot data by mountain range and calculated overall tree d.b.h. and age frequency distributions by species to assess landscape-scale patterns of forest development (Parker and Peet 1984). While these analyses are based on static age-structure data and may not capture the full scope of establishment and mortality rates (Johnson, Miyanishi, and Kleb 1994), they do offer insight as to how the current forest structure developed and can help predict future conditions at a site (Enright 1982).

I developed chronosequences by iteratively ranking and sorting the plots within each mountain range by stand age, TSC, and DDF and examined each sorting for emergent patterns in the relative frequency, relative basal area, and importance value of each species by plot. I did not control my site selection as stringently as would be required for a true chronosequence approach (Pickett 1989), but chronosequence studies are most appropriately used to describe broad, landscape-scale patterns in succession (Foster and Tilman 2000) and I therefore believed that the relatively coherent climate regimes of the different mountain ranges would allow me to identify similarly general patterns in succession at my sites if they occurred. Furthermore, most models of succession in whitebark pine forests currently in use are applied at a landscape scale similar to the scale of my analyses (e.g., Keane et al. 1990a; Keane 2001b).

I examined compositional differences in the canopy and subcanopy layers of my sites visually and with a non-parametric ordination analysis to determine potential future changes in species composition (Kipfmüller and Kupfer 2005). I first graphed overall

species composition of canopy and subcanopy layers for each mountain range and visually examined the graphs for differences. To further visualize the relationships between canopy and subcanopy species importance values and to quantify potential mechanisms driving these differences I applied a two-dimensional nonmetric multidimensional scaling (NMDS) to a similarity matrix calculated using the Bray-Curtis coefficient and species importance values for the canopy and subcanopy of each site as separate plots. This resulted in two locations for each plot within the ordination space – one based on canopy composition and the other based on subcanopy composition. I used Pearson correlations to compare the ordination axes with the original species variables and the stand and climate variables to interpret the environmental patterns represented by the ordination space. I calculated the angle and Euclidean distance between the two points for each plot to identify the direction and magnitude of change in the composition between canopy layers in ordination space and calculated Pearson correlations between the distance of change and the suite of stand and climate variables collected for each plot. I used NMDS due to its robustness for identifying multivariate, nonlinear relationships within ecological datasets (Legendre and Legendre 1998) and the Bray-Curtis coefficient for its effectiveness as a measure of ecological distance among variables of similar units and scales (Faith, Minchin, and Belbin 1987). I conducted the NMDS using PC-ORD (McCune and Mefford 2006).

Assessing the Role of Fire Suppression in Driving Succession in Whitebark Pine Communities

I used direct evidence in the form of fire scars and indirect evidence in the form of stand composition data to assess the potential influences of fire suppression on the whitebark pine forests at my sites. Fire-scar data were key components of early research documenting the effects of fire suppression on fire-dependent forest systems (e.g., Frissell 1973; Kilgore and Taylor 1979; Dieterich 1983; Swetnam 1993), but this approach is most effective where fires were relatively widespread and recurred at intervals much shorter than the typical lifespan of individual trees. Fire frequency varies widely in whitebark pine forests (Arno 1980; Larson, van de Gevel, and Grissino-Mayer 2009), limiting the use of fire-scar data to examine the effects of fire suppression in only those few stands that recorded multiple fires in the pre-fire suppression era. Changes in stand structure and composition have also been used to describe the effects of fire suppression (Cooper 1960; Heinselman 1973), and indeed the most commonly cited effects of fire suppression in whitebark pine forests are shifts in species composition due to the increased presence of fire intolerant/shade tolerant species, particularly subalpine fir (Keane et al. 1990b; Keane, Morgan, and Menakis 1994; Murray, Bunting, and Morgan 2000). I therefore examined my age-structure data by species for tree and cohort establishments in the early 1900s that might have resulted from the suppression and exclusion of fires. In addition to my static age-structure data which may not be representative of the composition of the forests at my sites in the past due to a loss of evidence through death and decay (Johnson, Miyanishi, and Kleb 1994), I modeled forest composition across my sites with respect to whitebark pine and subalpine fir to determine

what stand and climate variables influenced stand composition with respect to these two species. To conduct these analyses I calculated a ratio of living whitebark pine frequency to living subalpine fir frequency (PIAL:ABLA) that ranged from 1 (pure whitebark pine) to 0 (pure subalpine fir), and used linear stepwise regression to identify the significant predictors of this ratio from the full suite of stand and climate variables for my sites. I conducted two stepwise regressions: one based on all of my sites ($n = 60$) and one based only on sites where both species were present ($n = 33$). I postulated that if fire suppression had caused succession to advance that this would be most strongly reflected where fire had been excluded from a stand for a longer period of time and where fire had historically been more frequent. Therefore I would see an inverse relationship between PIAL:ABLA and stand age, TSC, and DDF, indicating that there was more subalpine fir at sites that were older, had existed longer since the last cohort established, and had experienced more frequent disturbances in the past. Conversely, if fire suppression was not a significant driver in stand composition then other factors should provide more explanatory power in the ratio of whitebark pine to subalpine fir. I also compared the residuals from my model to the full suite of stand and climate variables using Spearman rank correlations to determine if deviations from my model showed any consistent relationships with these variables. Again, if fire suppression were influencing the structure at my stands I expected to see an inverse correlation between the residuals and stand age, TSC, and DDF indicating that my model under predicted the relative frequency of subalpine fir where stands were older, had existed longer since the last cohort, and had experienced more frequent disturbances in the past. The stepwise process included predictor variables in the regression through forward and backward selection

based on the criteria of $\alpha \leq 0.1$. To facilitate my interpretation of the final regression results I calculated partial correlations between PIAL:ABLA and each of the individual variables included in the final model. I used MINITAB v15 to conduct the stepwise regressions (MINITAB Inc. 2006) and the function `pcor.test` in R to calculate partial correlations (R Development Core Team 2008).

Results

Stand and Disturbance History

I inventoried 4,176 trees, 3,051 saplings, and 1,202 seedlings in 60 plots over the summers of 2006–2008. Stand structure and composition varied widely within and among the mountain ranges (Table 1). Stand densities ranged from 40–2,680 living stems/ha, with generally denser stands on Paulina Peak and in the Pioneer Mountains and less dense stands in the Salmon River Mountains. Total stand basal area of living trees ranged from as low as 0.9 m²/ha in one stand in the Salmon River Mountains that had been affected by a recent mountain pine beetle outbreak and severe fire up to 38.1 m²/ha in one stand in the Pioneer Mountains. The most common dominant canopy species were whitebark pine ($n = 37$) and lodgepole pine ($n = 10$). Whitebark pine was also the most common subcanopy dominant ($n = 33$), while subalpine fir was the second most common dominant subcanopy species ($n = 21$) and was particularly prevalent in the Wallowa Mountains. Of the 13 sites where neither whitebark pine nor lodgepole pine dominated the canopy, 11 showed evidence of recent mountain pine beetle activity (Figure 3). I observed whitebark pine seedlings at 47 sites and saplings at 57 sites, with densities varying by an order of magnitude within and among the different mountain ranges (Table 1).

Table 1. Stand information. Density, basal area, and dominance are based on living trees.

Plot ID	Density (stems/ha)	Basal area (m ² /ha)	Dominant Species [†]		Stand age (yrs)	TSC* (yrs)	DDF [‡]	PIAL seedling / sapling density (#/ha)
			Canopy	Sub-canopy				
Cascades								
1	270	7.0	PIAL	ABLA	400	140	0.05	400 / 980
2	490	17.9	TSME	PIAL	354	80	0.08	1,800 / 360
3	280	3.7	PIAL	PIAL	146	90	0.34	1,300 / 740
4	670	9.8	PIAL	PIAL	451	150	0.09	2,500 / 700
5	330	12.5	PIAL	PIAL	360	120	0.03	700 / 900
6	100	7.0	PIAL	PIAL	235	240	0.13	700 / 540
CAS:	357	9.6	PIAL	PIAL	324	137	0.12	1,233 / 703
Paulina Peak								
1	500	23.6	PIAL	PIAL	391	120	0.05	6,700 / 1,040
2	690	15.7	PICO	PIAL	367	80	0.14	17,000 / 1,320
3	930	11.4	PICO	PICO	261	110	0.11	6,900 / 1,340
4	630	17.3	PICO	PICO	323	320	0.03	6,900 / 540
5	500	24.5	PIAL	PIAL	329	100	0.09	4,100 / 380
6	120	12.5	PIAL	PIAL	337	340	0.09	100 / 340
7	850	20.2	PICO	PIAL	171	70	0.23	900 / 920
PAU:	603	17.9	PIAL	PIAL	311	163	0.11	6,086 / 840
Wallowa Mountains								
1	230	5.6	PICO	ABLA	654	80	0.02	0 / 20
2	540	35.6	PIAL	ABLA	254	120	0.04	0 / 0
3	470	7.3	PICO	PICO	158	70	0.06	0 / 80
4	250	8.8	PICO	ABLA	900	200	0.03	0 / 100
5	550	19.0	ABLA	ABLA	285	270	0.11	1,400 / 220
6	310	6.7	PIAL	ABLA	383	90	0.03	100 / 100
7	720	25.0	ABLA	ABLA	278	80	0.04	100 / 280
8	260	14.2	ABLA	ABLA	491	490	0.04	100 / 20
9	510	36.8	PIAL	ABLA	693	100	0.03	300 / 40
10	290	11.2	PIAL	ABLA	306	140	0.03	300 / 240
11	460	13.5	PIAL	PIAL	496	500	0.02	0 / 280
12	320	26.0	PIAL	ABLA	556	560	0.04	0 / 340
13	350	26.1	PIAL	ABLA	293	220	0.03	500 / 220
WLA:	405	18.1	PIAL	ABLA	442	225	0.04	215 / 149
Salmon River Mountains								
1	40	2.2	PIAL	PIAL	169	170	0.12	100 / 0
2	300	6.9	PICO	PICO	274	60	0.11	300 / 480
3	420	4.7	PICO	ABLA	205	210	0.10	200 / 380
4	110	9.1	PIAL	ABLA	231	90	0.17	200 / 100
5	260	6.2	ABLA	ABLA	183	180	0.11	100 / 200
6	280	13.1	ABLA	ABLA	239	40	0.13	0 / 320
7	410	25.3	ABLA	ABLA	209	80	0.14	0 / 120
8	60	0.9	PIAL	PIAL	345	110	0.06	0 / 220
9	100	5.9	PIAL	ABLA	454	450	0.09	0 / 360
10	170	9.5	ABLA	ABLA	367	230	0.16	0 / 160
11	100	3.6	ABLA	ABLA	181	40	0.17	100 / 220
12	180	6.2	PIAL	ABLA	43	50	0.23	100 / 460
SRM:	203	7.8	PIAL	ABLA	242	143	0.13	92 / 252

(Table 1 continued)

Pioneer Mountains								
1	1630	37.1	PIAL	PIAL	257	190	0.04	900 / 520
2	560	14.6	PIAL	PIAL	509	60	0.04	600 / 2,080
3	360	32.6	PIAL	PIAL	542	490	0.06	600 / 640
4	160	23.5	PICO	PIAL	538	550	0.15	11,200 / 2,680
5	1320	38.1	PIAL	PIAL	191	100	0.05	200 / 160
6	390	33.3	PIEN	PIAL	573	570	0.03	5,300 / 900
7	1070	20.8	PIAL	PIAL	293	100	0.14	3,200 / 1,160
8	550	14.3	PIAL	PIAL	446	230	0.18	3,900 / 580
9	790	21.2	PIAL	PIAL	432	130	0.07	700 / 420
10	460	12.2	PIAL	PIAL	286	70	0.14	100 / 540
11	470	16.5	PIAL	PIAL	597	220	0.05	300 / 380
12	830	24.5	PIAL	PIAL	346	270	0.09	12,300 / 360
13	170	20.4	PIAL	PSME	808	810	0.01	3,300 / 1,080
14	2680	33.3	PIAL	PIAL	530	110	0.06	900 / 620
<i>PIO:</i>	817	24.5	<i>PIAL</i>	<i>PIAL</i>	453	279	0.08	3,107 / 866
Gravelly Range								
1	680	11.5	PIAL	PIAL	508	110	0.04	0 / 0
2	740	6.6	ABLA	ABLA	230	110	0.04	600 / 480
3	520	5.7	PIAL	PIAL	222	90	0.05	600 / 680
4	430	8.6	PIAL	PIAL	359	90	0.06	100 / 460
5	430	6.8	PIAL	PIAL	75	80	0.13	100 / 280
6	350	7.7	ABLA	PIAL	191	90	0.16	300 / 760
7	220	7.3	PIAL	PIAL	288	280	0.17	1,300 / 940
8	260	7.0	ABLA	PIAL	446	140	0.09	0 / 140
<i>GRA:</i>	454	7.6	<i>PIAL</i>	<i>PIAL</i>	290	124	0.09	375 / 467

[†] Dominant species for canopy and subcanopy are based on importance values of living trees. Species codes are based on the first two letters of the Latin binomial name of each species (e.g., *Pinus albicaulis* = PIAL).

* Time-since-cohort establishment. The number of years since the establishment of the most recent cohort identified in the age-structure data.

[‡] Decadal Disturbance Frequency. The rate of disturbance per decade at a site based on fire scar, mountain pine beetle-related mortality, and post-disturbance cohort establishment data.



Figure 3. Examples of sites currently dominated by subalpine fir due to high rates of mountain pine beetle-related mortality among canopy whitebark pine. Photos were taken (a) on Brundage Mountain in Idaho, (b) on Green Mountain in Idaho, and (c) in the Gravelly Range of Montana.

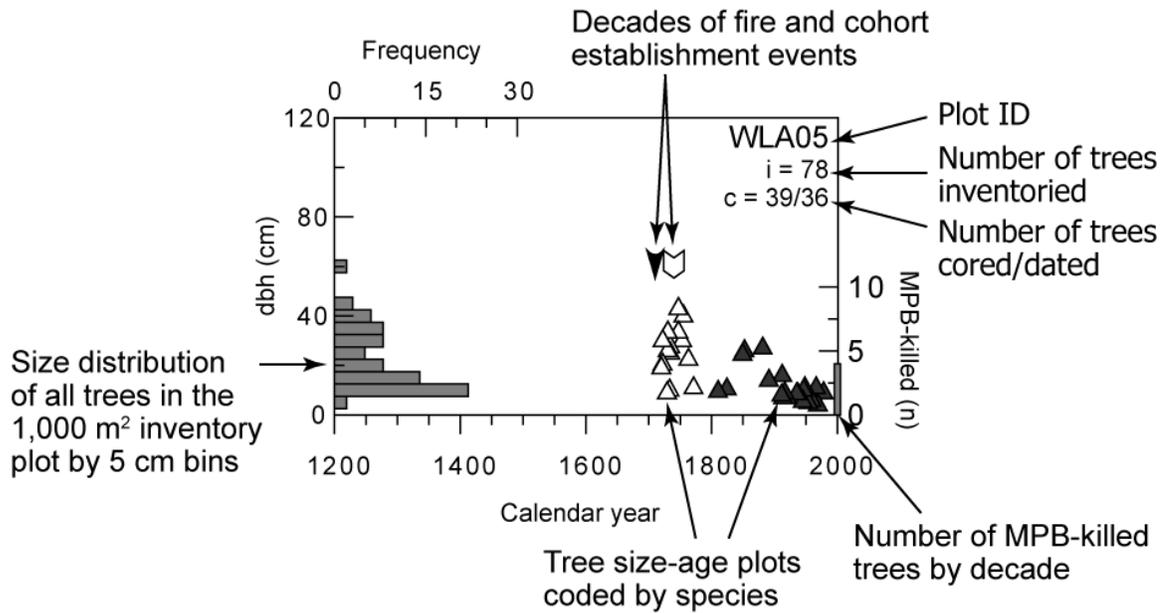
I collected increment cores from 2,346 of the inventoried trees and were able to assign accurate inner dates or pith estimations to 2,046 of these (87%). Pith was included in 16% ($n = 365$) of the cores and the average correction for cores that did not include pith was 7 ± 5 SD years (range: 1–30 years). Stand ages ranged from 40–900+ years and there were significant differences in median stand age among the different mountain ranges (Table 2). In general, the stands in the Salmon River Mountains were younger than in the other mountain ranges, while stands were older in the Pioneer Mountains and Wallowa Mountains. Individual stands exhibited 0–2 cohorts, and although the median TSC in the Pioneer Mountains was twice that of the Gravelly Range, Paulina Peak, and Salmon River Mountains, no significant differences existed between the ranges (Table 2). Disturbance rates were significantly higher in the Salmon River Mountains, significantly lower in the Wallowa Mountains, and no different among the remaining ranges (Table 2).

Analyses of Vegetation Composition and Succession

The oldest trees in 47 of the 60 stands I sampled were whitebark pine, and lodgepole pine was the oldest tree present at 10 of the remaining sites (Figures 4–10). Whitebark pine establishment occurred relatively continuously over the past 150–200 years in the stands I sampled in the Cascades and on Paulina Peak (Figures 5, 6), but more episodically in the other ranges where it appeared to be more closely related to disturbance events. The age-structure data for several sites suggests that whitebark pine established as nearly pure stands and as mixed stands with lodgepole pine following fires as illustrated with examples from the Wallowa Mountains and Pioneer Mountains (Figures 11a), yet there and elsewhere subalpine fir often established on site within a few

Table 2. Results of Kruskal-Wallis one-way ANOVA by ranks test for differences in stand age, time-since-cohort establishment (TSC), and decadal disturbance frequency (DDF) between mountain ranges.

Range	Stand age			TSC			DDF		
	Median (yrs)	Mean rank	Z	Median (yrs)	Mea n rank	Z	Median rate	Mea n rank	Z
Cascades	357	29	-0.2	130	30	-0.1	0.087	33	0.3
Gravelly Range	259	24	-1.2	100	25	-0.9	0.073	34	0.6
Paulina Peak	329	28	-0.5	110	29	-0.3	0.091	36	0.8
Pioneer Mountains	478	41	2.6	205	38	1.7	0.056	29	-0.4
Salmon River Mountains	220	18	-2.8	100	24	-1.5	0.122	45	3.2
Wallowa Mountains	383	37	1.6	140	34	0.7	0.034	13	-4.1
	$H = 14.8$, d.f. = 5, $p = 0.011$			$H = 5.2$, d.f. = 5, $p = 0.386$			$H = 22.1$, d.f. = 5, $p < 0.000$		



Species and event key	
△	<i>Pinus albicaulis</i>
△	<i>Pinus contorta</i>
▲	<i>Picea engelmannii</i>
▲	<i>Pseudotsuga menziesii</i>
▲	<i>Abies lasiocarpa</i>
▲	<i>Tsuga mertensiana</i>
▽	Cohort
▽	Fire

Figure 4. Legend for graphs of individual stand histories.

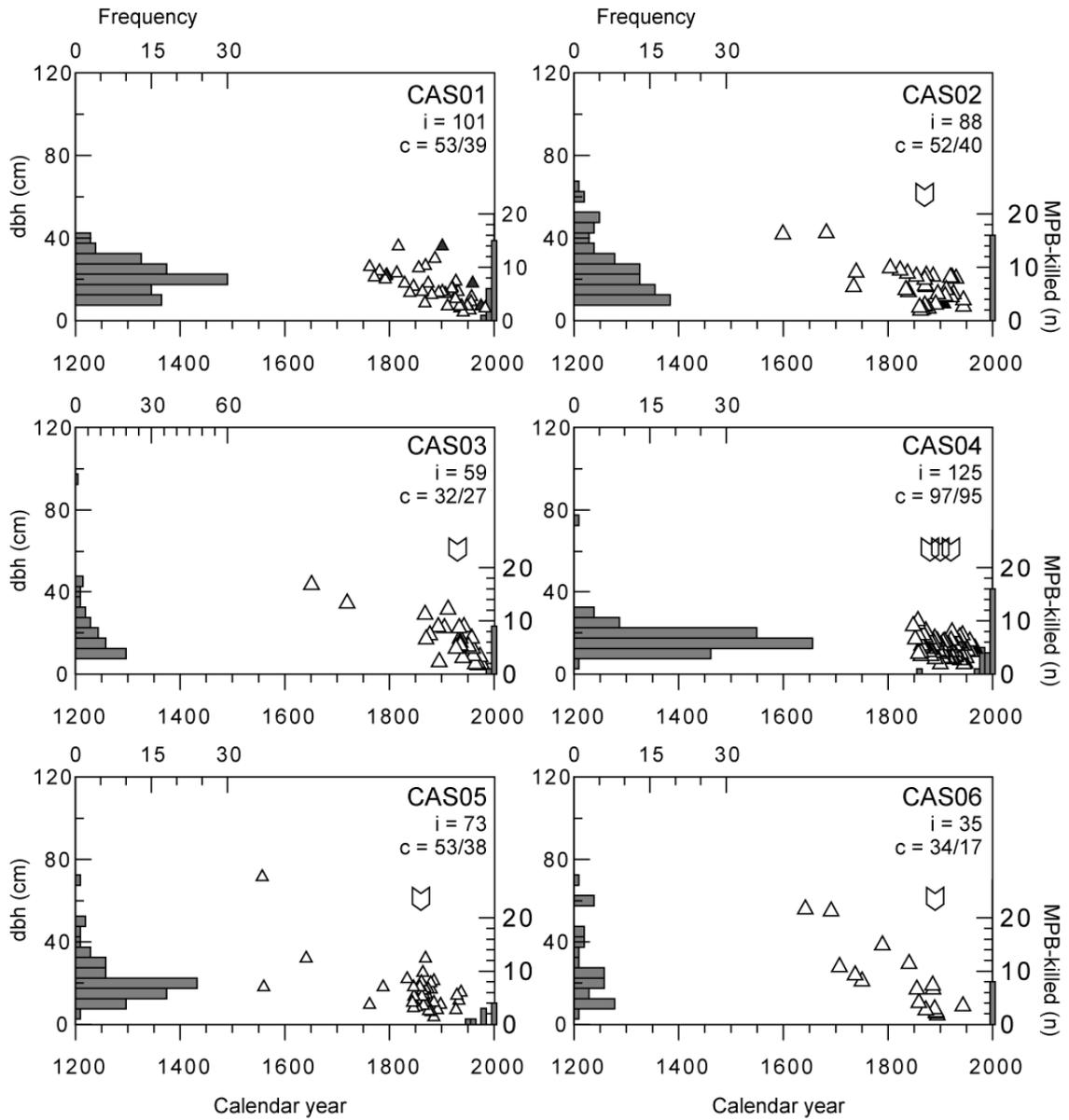


Figure 5. Individual stand histories for the Cascades.

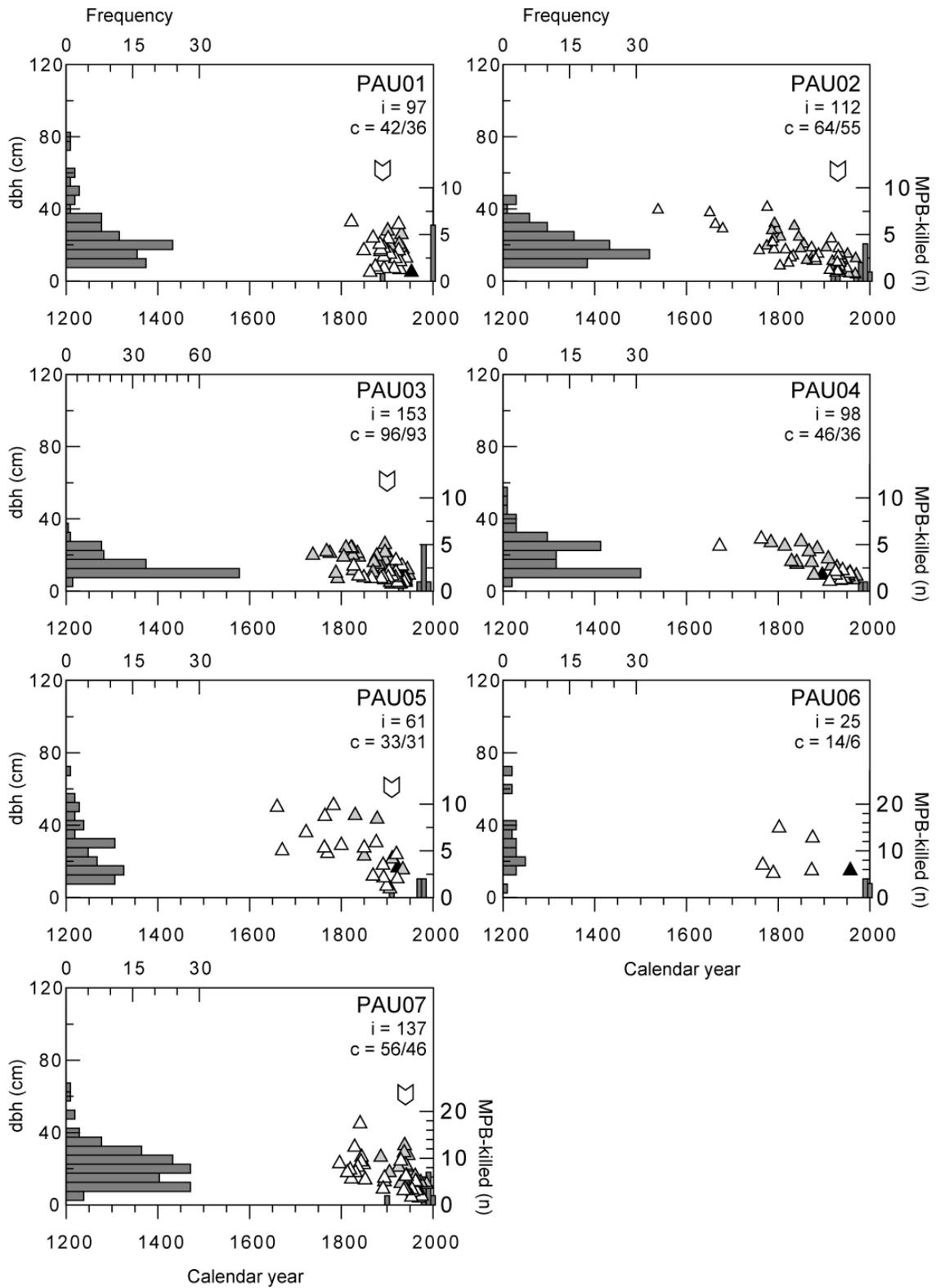


Figure 6. Individual stand histories for Paulina Peak.

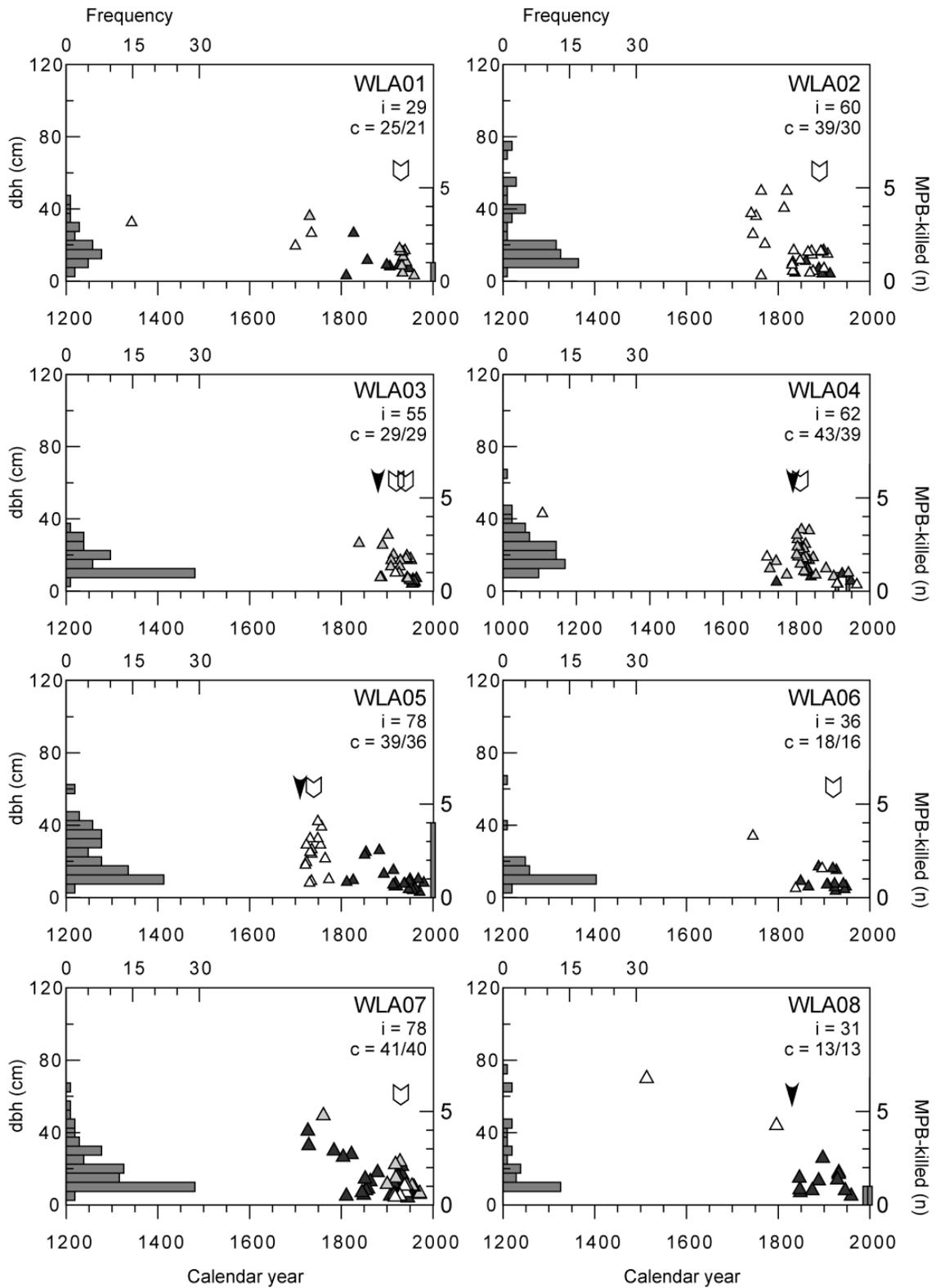


Figure 7. Individual stand histories for the Wallowa Mountains.

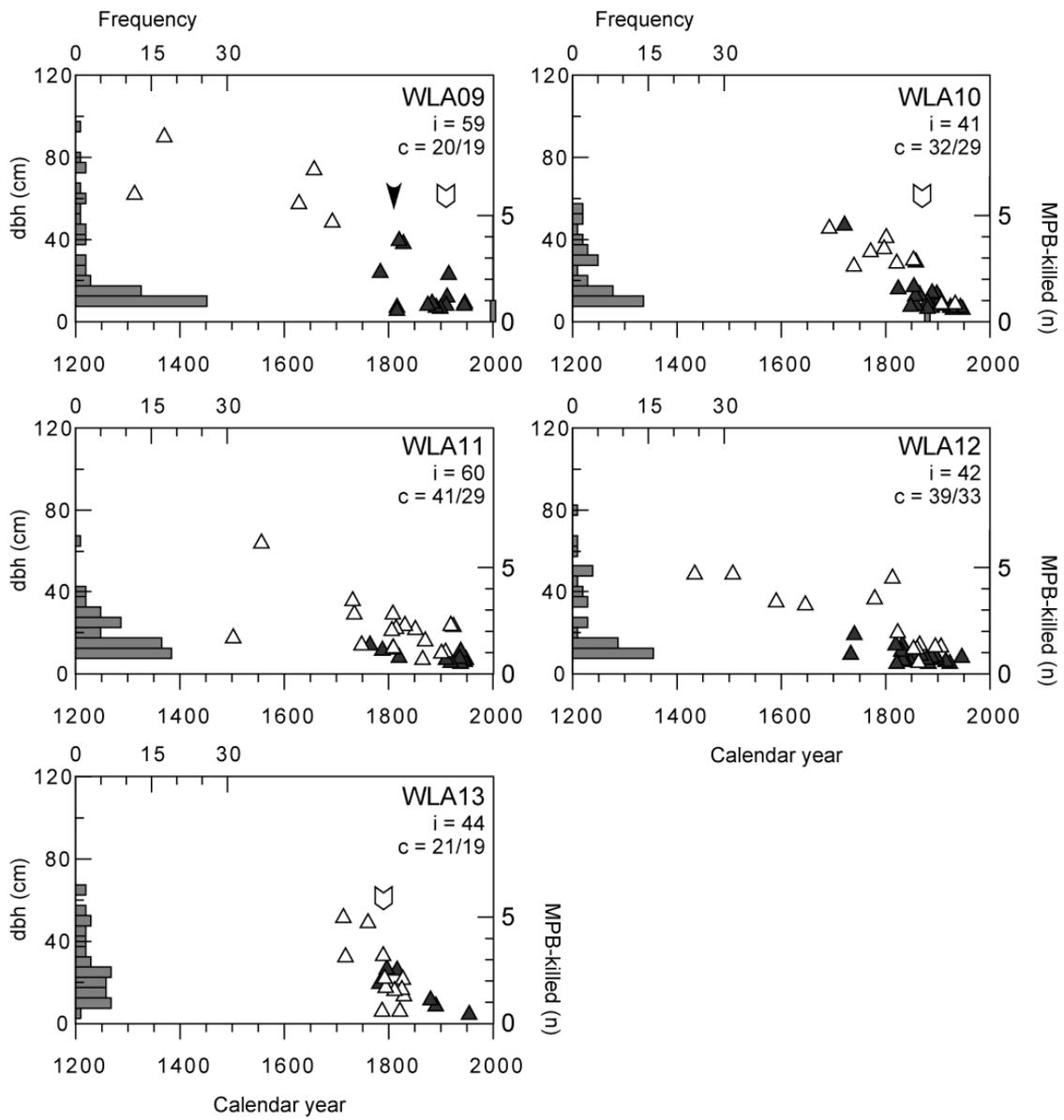


Figure 7. Continued

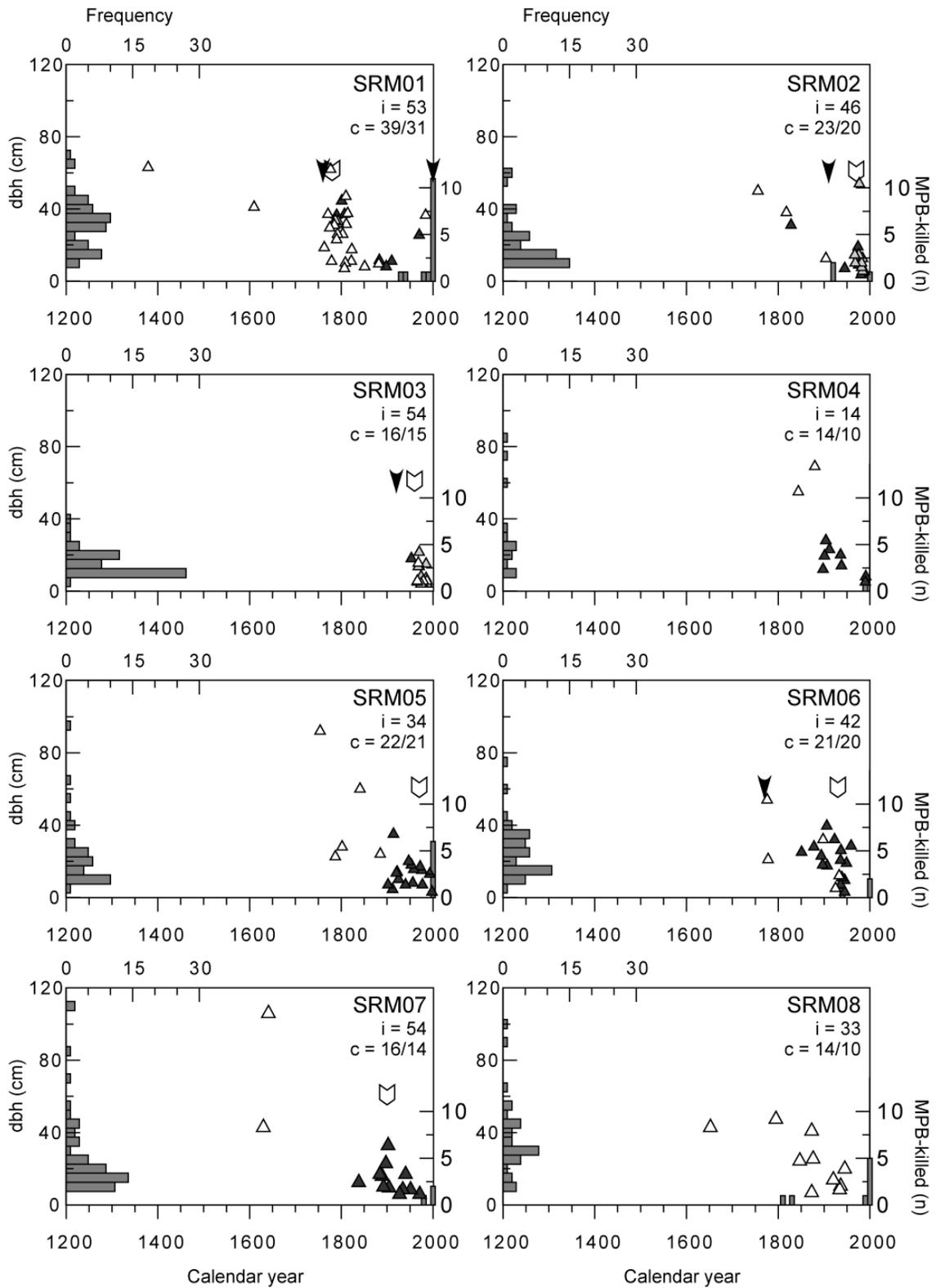


Figure 8. Individual stand histories for the Salmon River Mountains.

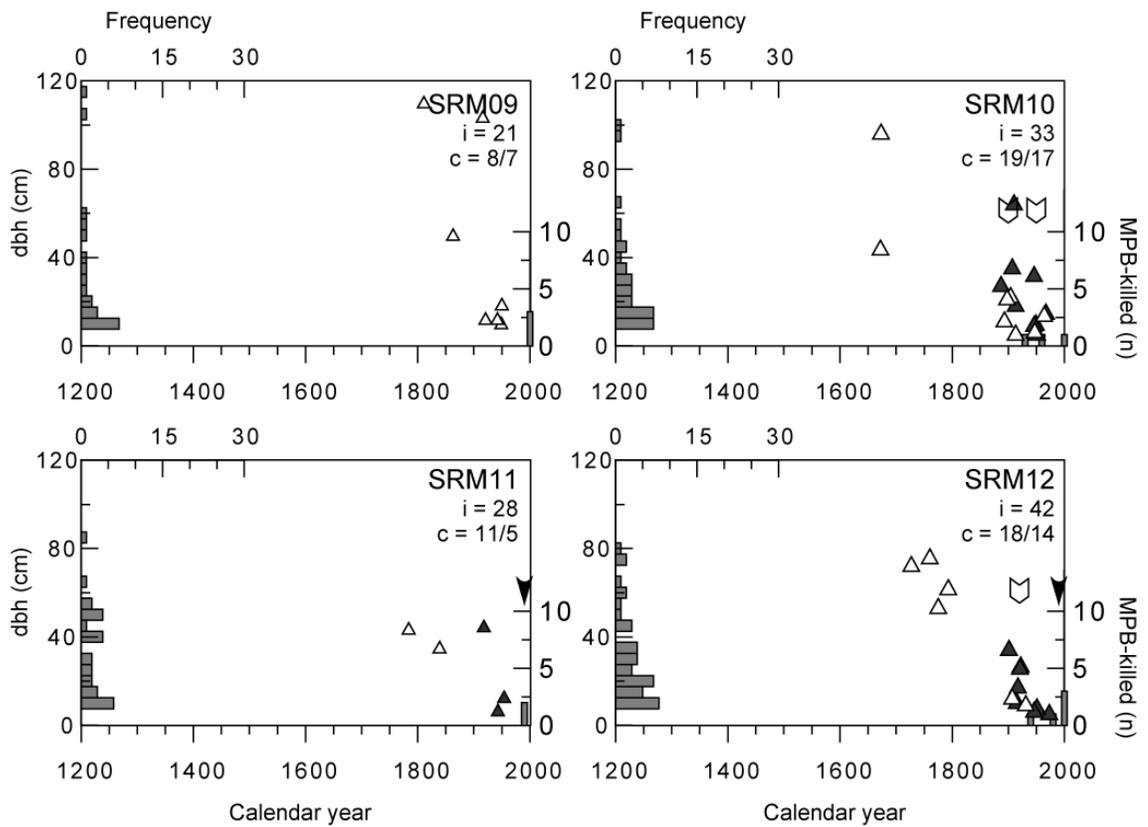


Figure 8. Continued

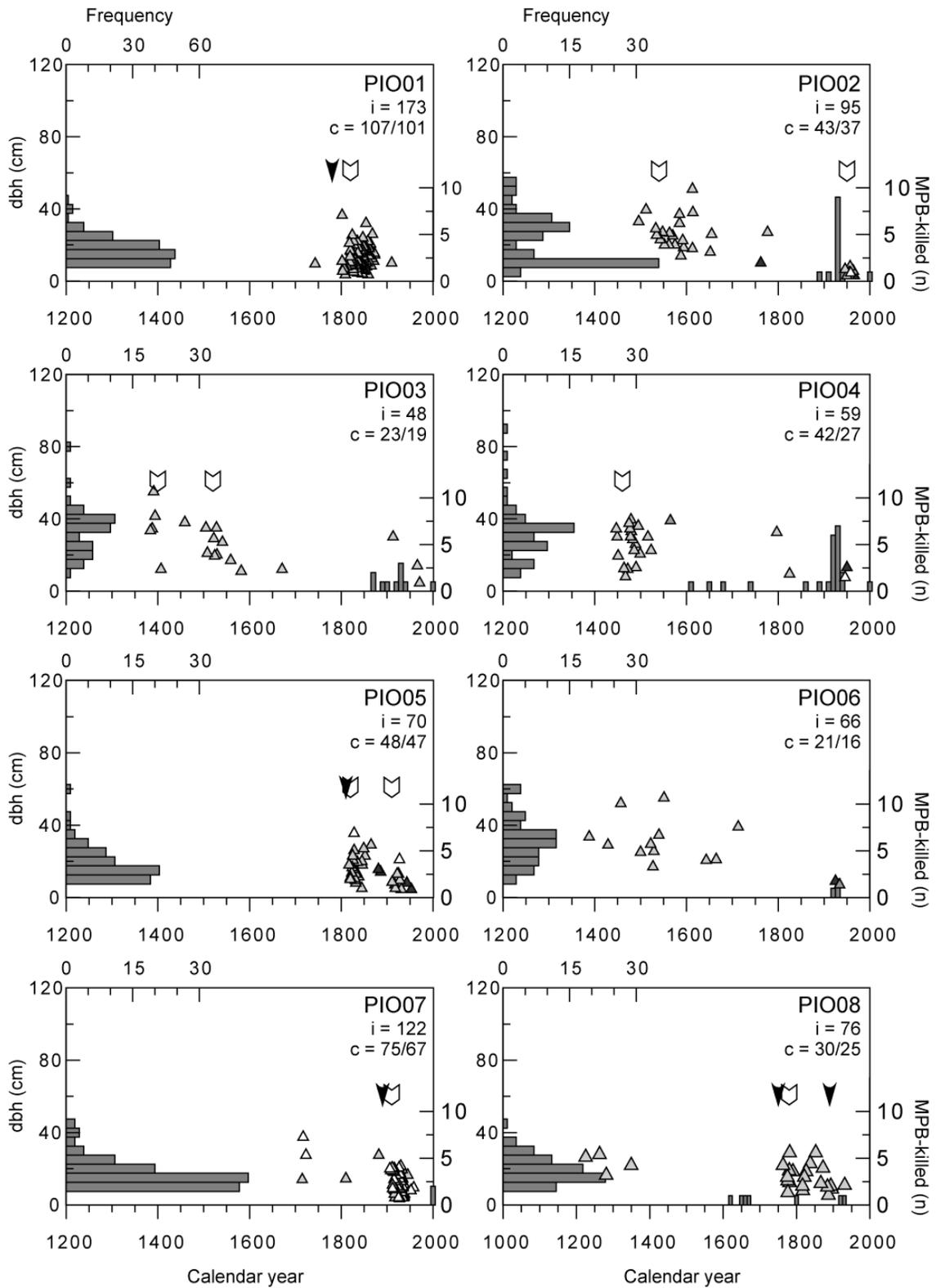


Figure 9. Individual stand histories for the Pioneer Mountains.

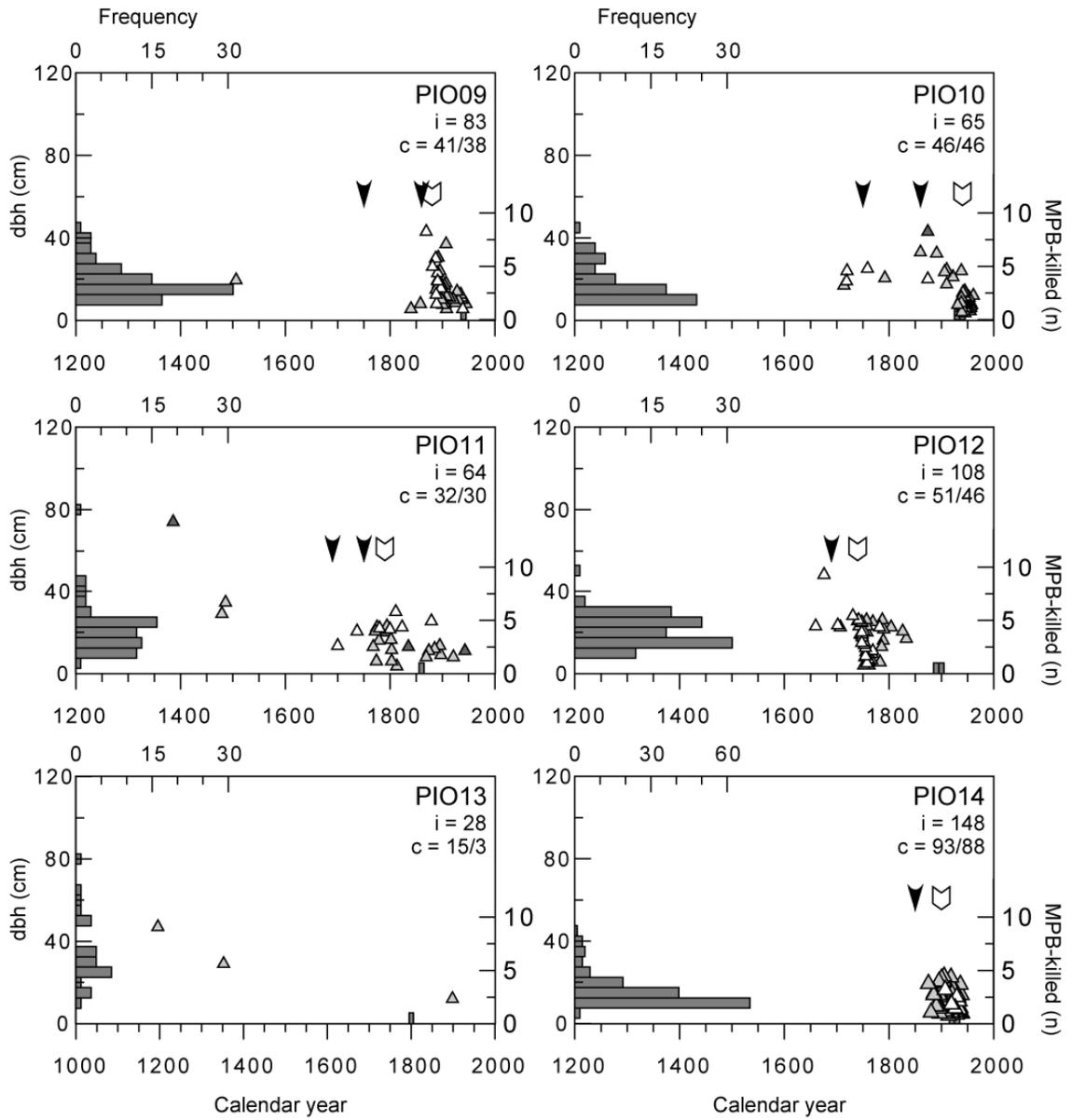


Figure 9. Continued

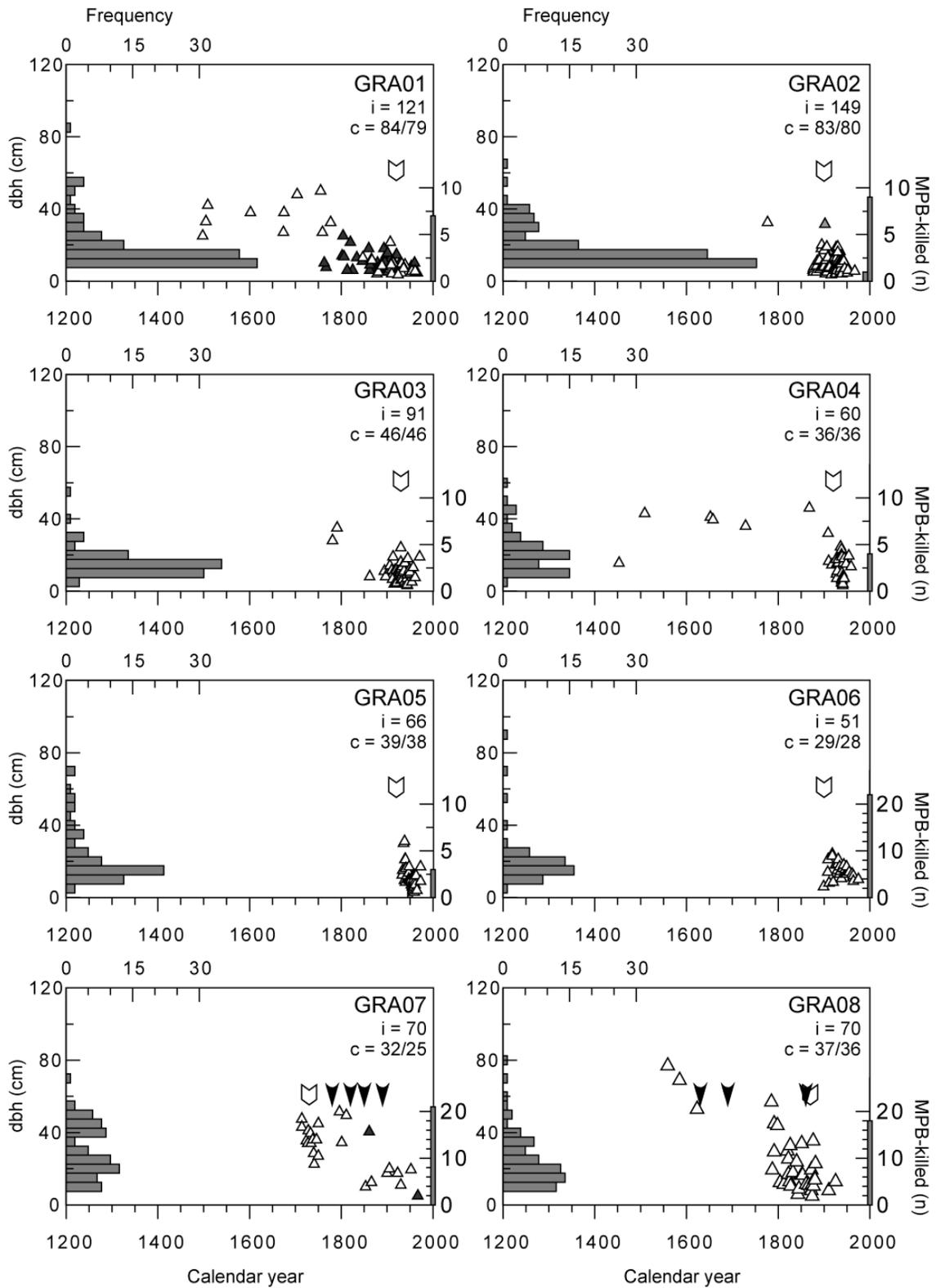


Figure 10. Individual stand histories for the Gravelly Range.

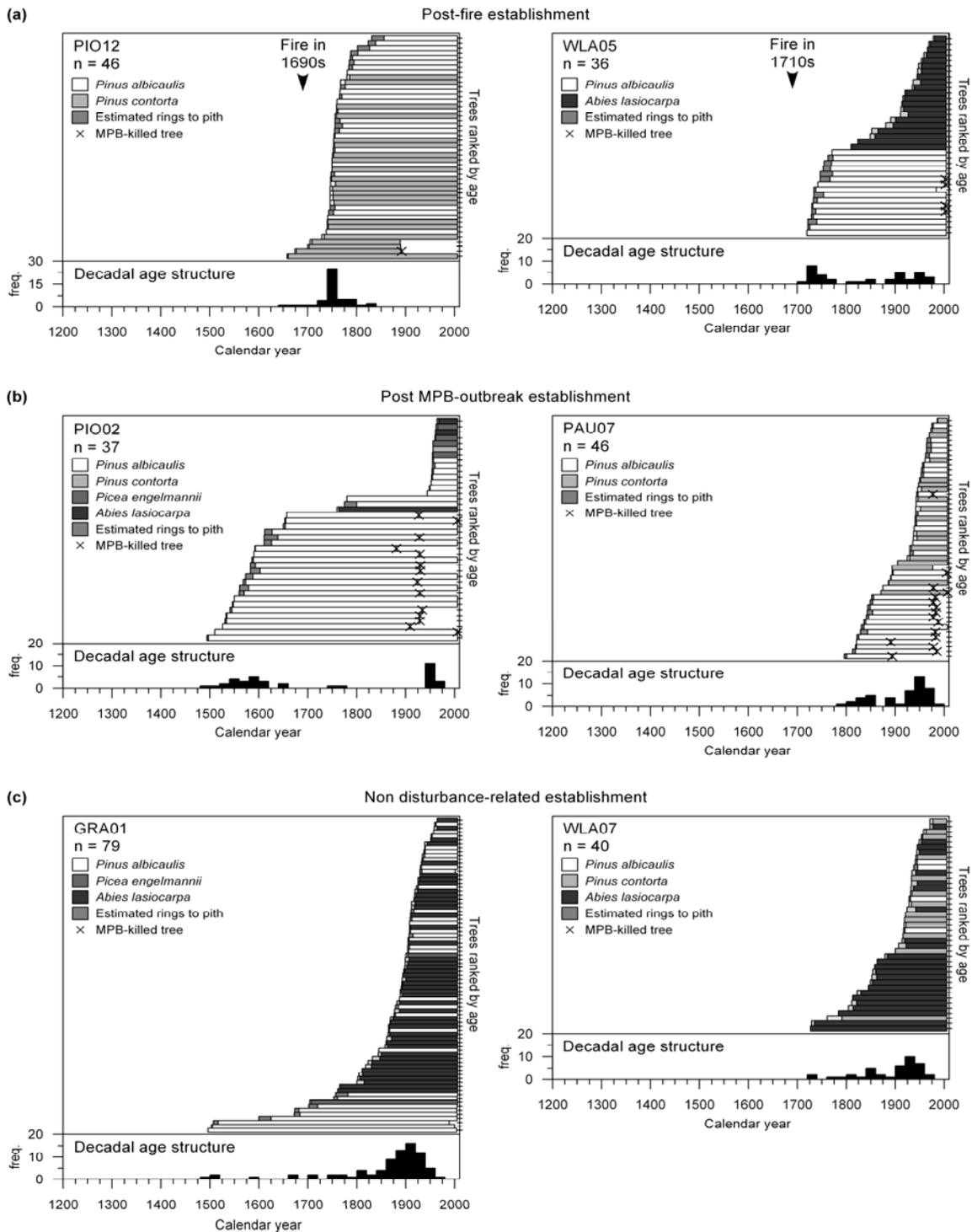


Figure 11. Stand reconstructions illustrating (a) post-fire cohorts and successional shifts to shade-tolerant species, (b) post-mountain pine beetle outbreak cohorts and releases, and (c) unusual patterns of tree establishment with no identified disturbance event and whitebark pine and lodgepole pine (*Pinus contorta* Dougl. Ex Loud.) establishing in stands with large components of subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.).

decades following fires. Subalpine fir established more abundantly than other species during the past century at several sites in the Salmon River Mountains and Wallowa Mountains and one site in the Gravelly Range, yet sporadic whitebark pine establishment co-occurred with subalpine fir during this time at many of these sites (Figures 7, 8, 10).

Seven of the stands that I sampled contained trees that had recorded multiple fires (one in the Salmon River Mountains, four in the Pioneer Mountains, and two in the Gravelly Range; Figures 8, 9, 10) and 15 additional stands contained direct evidence of at least one past fire. I encountered and crossdated mountain pine beetle-killed trees in 48 of the 60 stands. The earliest dates of mortality likely caused by mountain pine beetles were derived from the outer rings of trees that had fallen onto talus in plot PIO04 of the Pioneer Mountains and dated to the late 1600s (Figure 9). Other mountain pine beetle-related tree deaths dated to the late 1800s in the Cascades, Paulina Peak, and Pioneer Mountains. Mountain pine beetle-related mortality occurred in the late 1900s and early 2000s in nearly every range, including a recent outbreak in the Salmon River Mountains, an active outbreak in the Gravelly Range at the time of sampling in 2007, and evidence of an impending outbreak in the Cascades and Paulina Peak during 2008. Of the 12 stands that did not include beetle-killed trees, 7 were in the Wallowa Mountains. A number of stands exhibited what appeared to be post-mountain pine beetle outbreak cohorts (Figure 11b). In addition to these apparent post-disturbance cohorts, five stands in the Gravelly Range showed the establishment of nearly pure whitebark pine cohorts in the early 1900s at roughly the same time that fires ceased to be recorded elsewhere in the mountain range (Figure 10). Several stands displayed unexpected patterns of species establishment, including cohorts of whitebark pine and lodgepole pine establishing following periods

dominated by subalpine fir establishment at sites in the Gravelly Range and Wallowa Mountains (Figure 11c).

Weibull distributions for each species by plot illustrated high variability in the d.b.h. and age distributions of whitebark pine that contrasted with the nearly identical distributions of subalpine fir both within and among the mountain ranges where it was present (Figures 12a, 12b). The distributions of lodgepole pine showed an intermediate level of variability relative to whitebark pine and subalpine fir, and the relatively low sample depth of most other species limited my ability to compare their distributions. A number of separate peaks in the whitebark pine age distributions are not apparent in the d.b.h. distributions, and overall the d.b.h. distributions are more similar to each other than the age distributions. Examined at the landscape scale, the d.b.h. distributions of whitebark pine and subalpine fir approach inverse-J shapes in several ranges, while the distributions of lodgepole pine were more peaked (Figure 13a). In general, the whitebark pine age distributions exhibited multiple and more distinct peaks than the whitebark pine d.b.h. distributions in the Pioneer Mountains and Paulina Peak. The same was true for lodgepole pine in the Wallowa Mountains and the Pioneer Mountains (Figure 13b). In contrast to the whitebark pine and lodgepole pine distributions, the d.b.h. distributions of subalpine fir were generally more peaked than the age distributions for the same sites. The only age distributions that appear near to an inverse-J shape are the whitebark pine distributions in the Cascades and Gravelly Range. All other age distributions contained cohorts indicative of past disturbances.

The strongest patterns in compositional change that I identified in my chronosequence analyses emerged when the plot data were ranked by TSC and I have

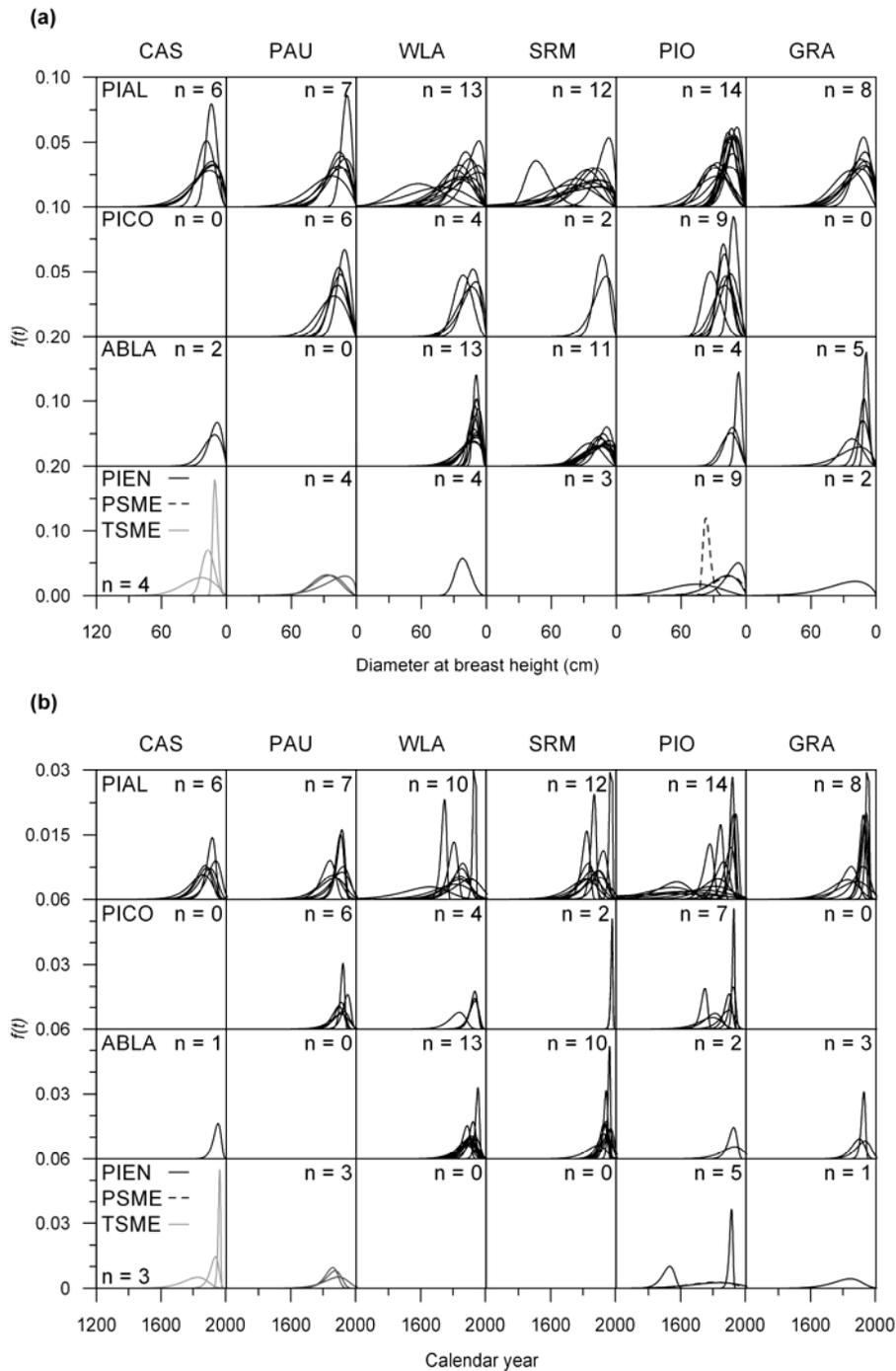


Figure 12. Weibull probability functions of (a) tree diameter at breast height distributions and (b) tree age distributions by species and mountain range. Site codes are CAS = Cascades, PAU = Paulina Peak, WLA = Wallowa Mountains, SRM = Salmon River Mountains, PIO = Pioneer Mountains, and GRA = Gravelly Range. Species codes are based on the first two letters of the Latin binomial name of each species (e.g., *Pinus albicaulis* = PIAL). The number of plots in which each species was present is given in the upper-right corner of each graph.

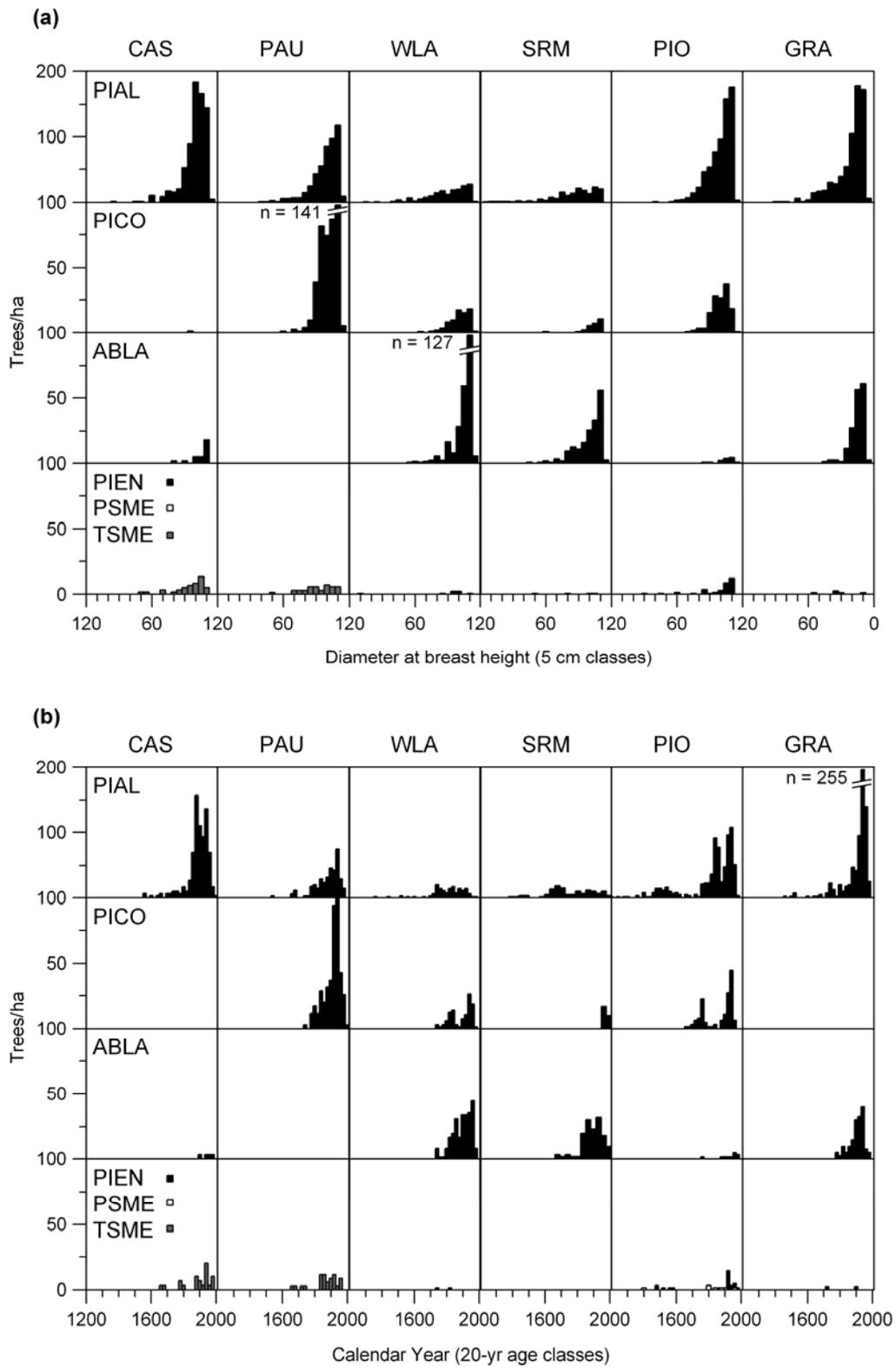


Figure 13. Trees per hectare by (a) diameter at breast height and (b) establishment date by decade for the species in each mountain range.

presented only those results here (Figure 14). In the Cascades and on Paulina Peak, mountain hemlock increased somewhat in relative frequency in the older stands and markedly in relative basal area and importance, but at both ranges it was less abundant to non-existent at the oldest sites. Patterns in the relative frequency of whitebark pine were not consistent within and across the different mountain ranges, but with the exception of the Cascades the relative basal area and importance of whitebark pine were generally higher in older stands. Subalpine fir was present only at the youngest and oldest stand in the Cascades. In the Wallowa Mountains and Salmon River Mountains, subalpine fir showed high relative frequency across stands of all ages but represented a relatively small proportion of the living basal area in most stands and therefore had overall moderate importance values. Two stands in the Salmon River Mountains were exceptions to this and were completely dominated by subalpine fir with respect to relative frequency, relative basal area, and importance (SRM02, SRM11). Both stands had experienced high levels of mountain pine beetle-related mortality and had been burned in recent severe fires. In the Gravelly Range subalpine fir made up a greater component of forest composition in the older stands. I observed no other clear patterns of difference in the forest composition when ranked by TSC.

Compositional differences in the canopy and subcanopy layers showed consistent trends across most of the mountain ranges included in my study (Figure 15). The relative frequency, relative basal area, and importance of lodgepole pine decreased from the canopy to the subcanopy in all of the ranges in which it was present. On Paulina Peak and in the Pioneer Mountains, ranges where subalpine fir was relatively scarce, the decreases in lodgepole pine were balanced by increases in the relative frequency, relative basal

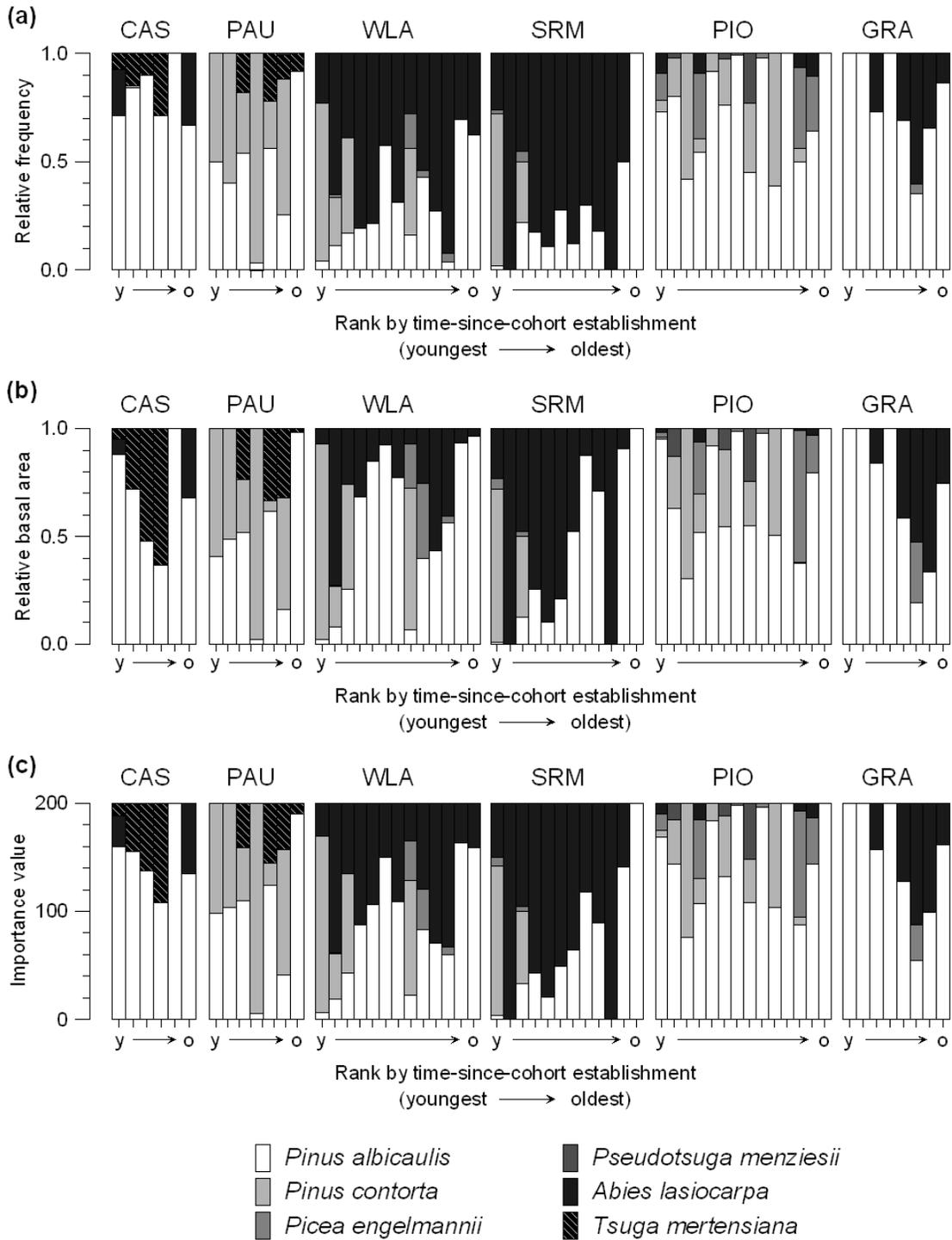


Figure 14. Patterns in species (a) relative frequency, (b) relative basal area, and (c) importance values with the plots for each mountain range ranked by time-since-cohort establishment.

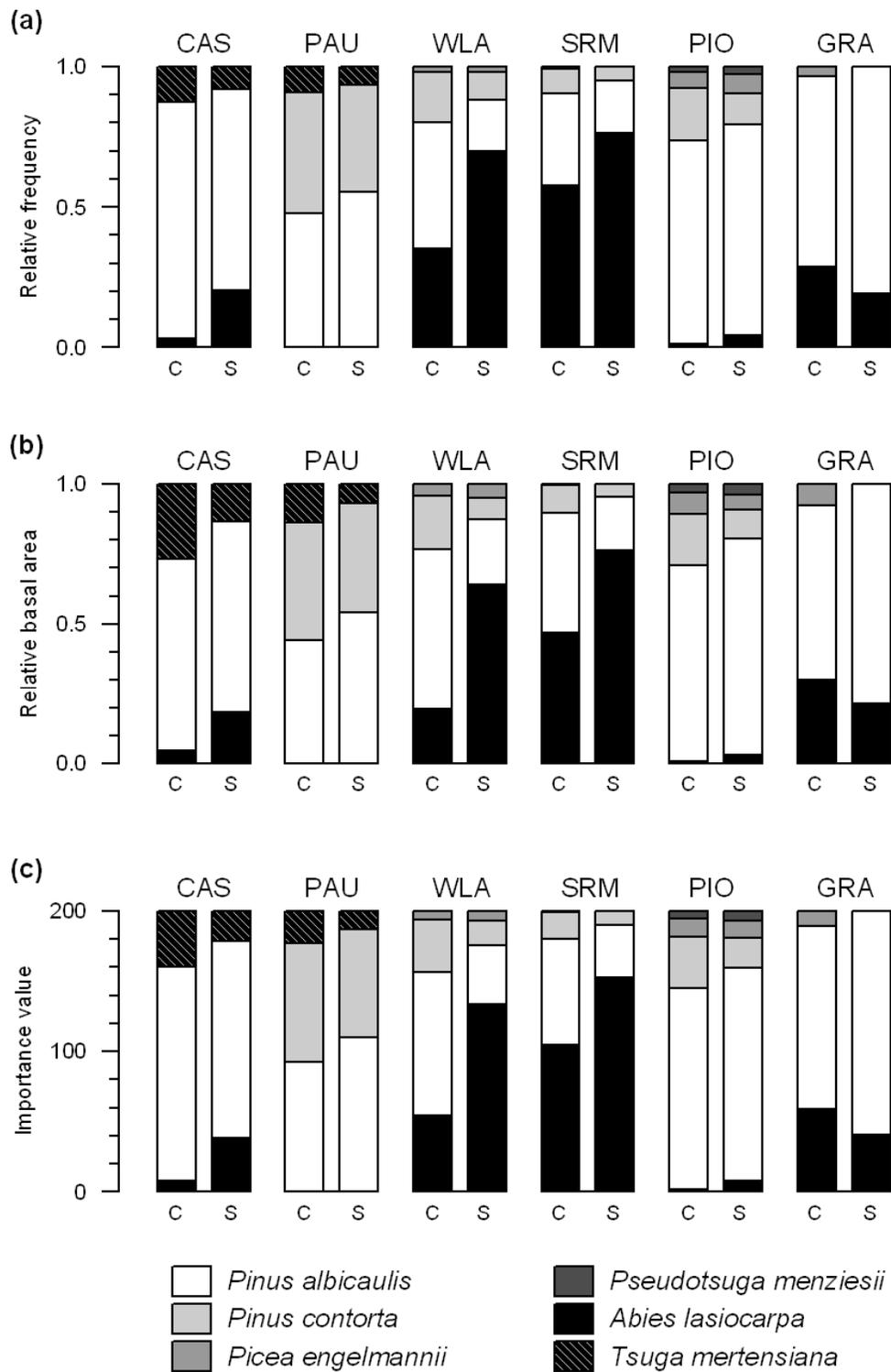


Figure 15. Patterns in species (a) relative frequency, (b) relative basal area, and (c) importance values by canopy class for all species combined by mountain range.

area, and importance of whitebark pine in the subcanopy. In the Cascades, Wallowa Mountains, and Salmon River Mountains the relative frequency, relative basal area, and importance of subalpine fir increased at the expense of all other species present. In contrast, subalpine fir relative frequency, relative basal area, and importance were lower in the subcanopy than in the canopy while whitebark pine increased in all of these measures in the Gravelly Range. The changes in the values of subalpine fir were remarkably similar between the Wallowa Mountains and the Salmon River Mountains despite the significant differences in stand age and DDF between these ranges. The relative frequency, relative basal area, and importance of mountain hemlock were greater in the canopy than subcanopy in the Cascades and on Paulina Peak.

My NMDS ordination retained 94% of the variance in the original species data, with axis 1 explaining 66% and axis 2 explaining 28% of the variance, respectively. The primary gradients represented by Axis 1 were a positive correlation with whitebark pine importance and an inverse correlation with subalpine fir importance, while Axis 2 was most strongly correlated with lodgepole pine importance and inversely correlated with subalpine fir importance, but to a lesser extent (Table 3). Two dominant patterns emerged from my ordination of importance values by canopy class: a shift from greater lodgepole pine importance in the canopy to greater whitebark pine importance in the subcanopy, and a shift from whitebark pine dominance of the canopy to subalpine fir dominance of the subcanopy (Figure 16a). The largest and most consistent differences between canopy and subcanopy composition existed at sites in the Wallowa Mountains and Salmon River Mountains, while differences were relatively less pronounced and less consistent at sites in the other mountain ranges (Figure 16a). The greatest magnitude of difference between

Table 3. Pearson correlation coefficients of species importance variables with ordination axes shown in Fig. 16a.

Species IV	Correlations (<i>r</i>)	
	Axis 1	Axis 2
<i>Pinus albicaulis</i>	0.94	-0.03
<i>Abies lasiocarpa</i>	-0.88	-0.57
<i>Pinus contorta</i>	-0.20	0.89
<i>Picea engelmannii</i>	-0.04	-0.21
<i>Pseudotsuga menziesii</i>	0.10	0.19
<i>Tsuga mertensiana</i>	0.25	0.08

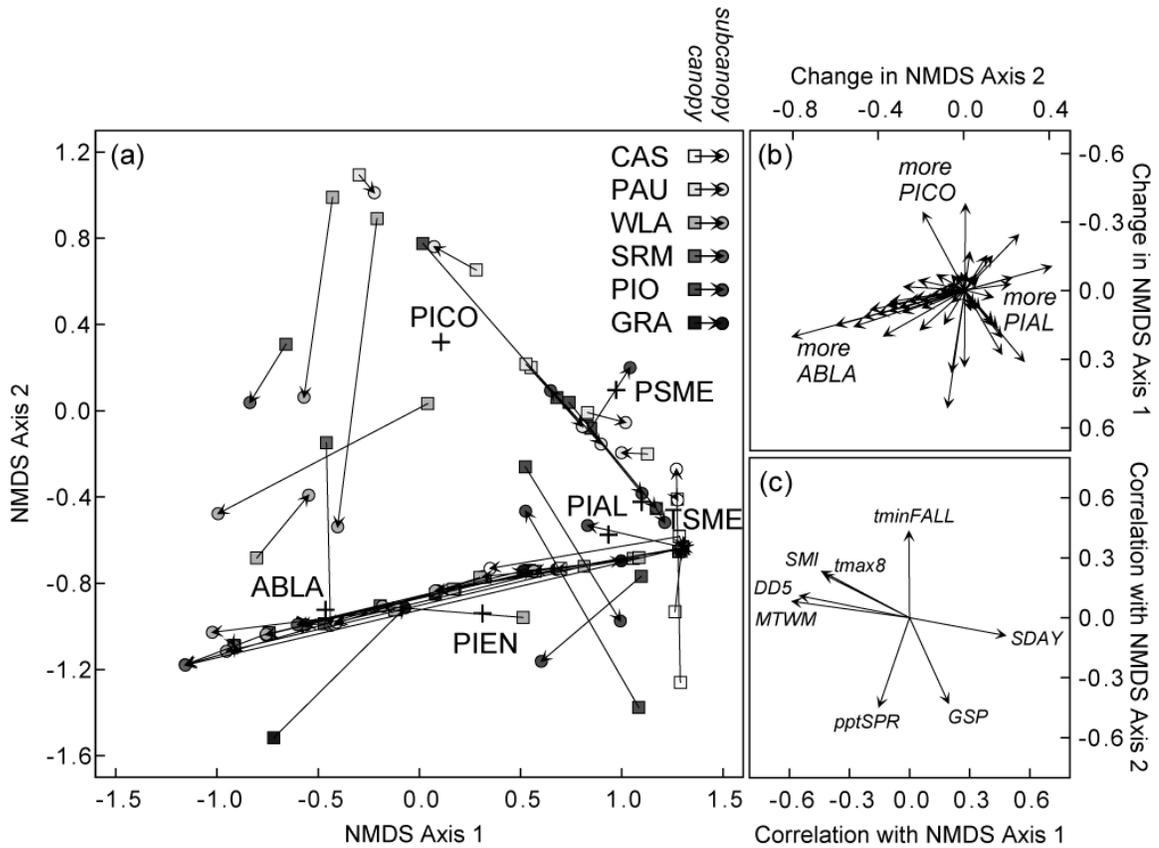


Figure 16. Differences in species importance values for canopy and subcanopy strata as illustrated using two-dimensional nonmetric multidimensional scaling ordination of canopy and subcanopy importance values. Fig. 16a shows the species scores and the position of the canopy of each plot connected by a vector to the position of the subcanopy of the same plot in ordination space. Fig. 16b represents the direction and magnitude of the vectors in Fig. 16a. The vectors in Fig. 16c represents the direction and strength of the significant Pearson correlations of the ordination axes with stand and climate variables.

canopy classes existed at sites in the Wallowa Mountains and Salmon River Mountains, and while these sites created the dominant pattern in direction and magnitude of differences in ordination space, variability did exist in the direction and magnitude of change at several other sites (Figure 16b). The NMDS axes showed significant correlations ($p < 0.001$) with several climate variables but no stand age variables (Figure 16c). In general, axis 1 was inversely correlated with the overall summer warmth and precipitation and growing season length of a site, while axis 2 was positively correlated with fall temperatures and inversely correlated with spring temperatures and growing season precipitation. Distance in ordination space from the canopy to the subcanopy was significantly correlated with the length of the frost free period, annual precipitation, and the interaction of temperature and moisture as represented by $\text{pptSUM} \times \text{FFP}$, but showed no relationship with stand age, TSC, or DDF (Table 4).

Assessing the Role of Fire Suppression in Driving Succession in Whitebark Pine Communities

Of the seven stands that recorded multiple fires only one stand in the Salmon River Mountains recorded a fire in the 2000s (Figs. 8) while the other six stands in the Pioneer Mountains and Gravelly Range recorded no fires after the 1800s (PIO10, GRA01–06; Figs. 9, 10). Twenty five stands across all six mountain ranges contained cohorts that established in the 1900s, but only the seven stands mentioned above showed evidence of altered fire regimes and even there the species composition of the cohorts was exclusively lodgepole pine and whitebark pine (Figs. 9, 10). Additionally, many of

Table 4. Pearson correlation coefficients of the distance in composition from the canopy to subcanopy position in ordination space with stand and climate variables.

Variable	<i>r</i>	<i>p</i> -value
pptSUM × FFP ^a	0.48	< 0.000
FFP ^b	0.35	0.006
MAP ^c	0.35	0.007
Stand age	0.13	0.319
TSC	-0.04	0.756
DDF	-0.18	0.160

^a summer precipitation (June–August) multiplied by the frost-free period

^b Frost-free period

^c Mean annual precipitation

the newly established whitebark pine in the Gravelly Range were growing in areas that had little evidence of trees previously occupying the area (Fig 17).

The stepwise process identified mean temperature of the warmest month, the annual dryness index, and mean minimum temperature of the coldest month as significant predictors that together explained 75% of the variance in PIAL:ABLA when all sites were included (Table 5, Figure 18a). The same variables plus mean maximum fall and spring temperatures explained 73% of the variance in PIAL:ABLA for sites where both whitebark pine and subalpine fir were present (Table 5, Figure 18b). These results indicate that whitebark pine is overall relatively more abundant than subalpine fir at sites with cooler temperatures during the warmest month, drier annual conditions, and with higher minimum temperatures during the coldest month, as well as at sites with cooler fall temperatures and warmer spring temperatures. The lack of a significant relationship with any measure of stand age or disturbance frequency suggests fire suppression has not influenced stand composition at these sites.

The residuals from the two regressions showed no relationship with stand age, TSC, or DDF but were significantly correlated with a number of climate variables, indicating that the PIAL:ABLA ratio was generally overestimated at sites with warmer growing seasons and warmest months and underestimated at sites with less growing season precipitation and less moisture available over the course of the year (Table 6). The residuals from the regression based on only those stands where both species were present also showed a significant inverse correlation with the number of mountain pine beetle-killed trees at each site, indicating that the PIAL:ABLA ratio was over predicted for stands with higher levels of mountain pine beetle-related mortality (Table 6). A



Figure 17. Examples of areas with recently established whitebark pine trees in the Gravelly Range (a) on the southwest slopes and (b) south slopes of Black Butte.

Table 5. Results of the stepwise regression using biophysical site characteristics to model the ratio of whitebark pine to subalpine fir at my sites.

<i>n</i> = 60	Variable	<i>r</i> _{partial}	coef.	<i>t</i>	<i>p</i>
Intercept: 5.636	MTWM ^a	-0.86**	-0.436	-12.74	< 0.001
<i>r</i> ² : 0.75	ADI ^b	0.78**	1.38	9.20	< 0.001
PRESS: 2.20	MMIN ^c	0.69**	0.073	7.06	< 0.001
<i>n</i> = 35	Variable	<i>r</i> _{partial}	coef.	<i>t</i>	<i>p</i>
Intercept: 6.349	MTWM	-0.44*	-0.198	-2.37	0.025
<i>r</i> ² : 0.73	ADI	0.37*	0.740	1.96	0.061
PRESS: 0.94	MMIN	0.64**	0.165	4.53	< 0.001
	T _{max} Fall	-0.51*	-0.478	-3.25	0.003
	T _{max} Spring	0.41*	0.330	2.51	0.018

^a Mean temperature of the warmest month

^b Annual dryness index (Degree days >5° C/Mean annual precipitation)

^c Mean minimum temperature in the coldest month

* significant partial correlation at *p* < 0.05

** significant partial correlation at *p* < 0.001

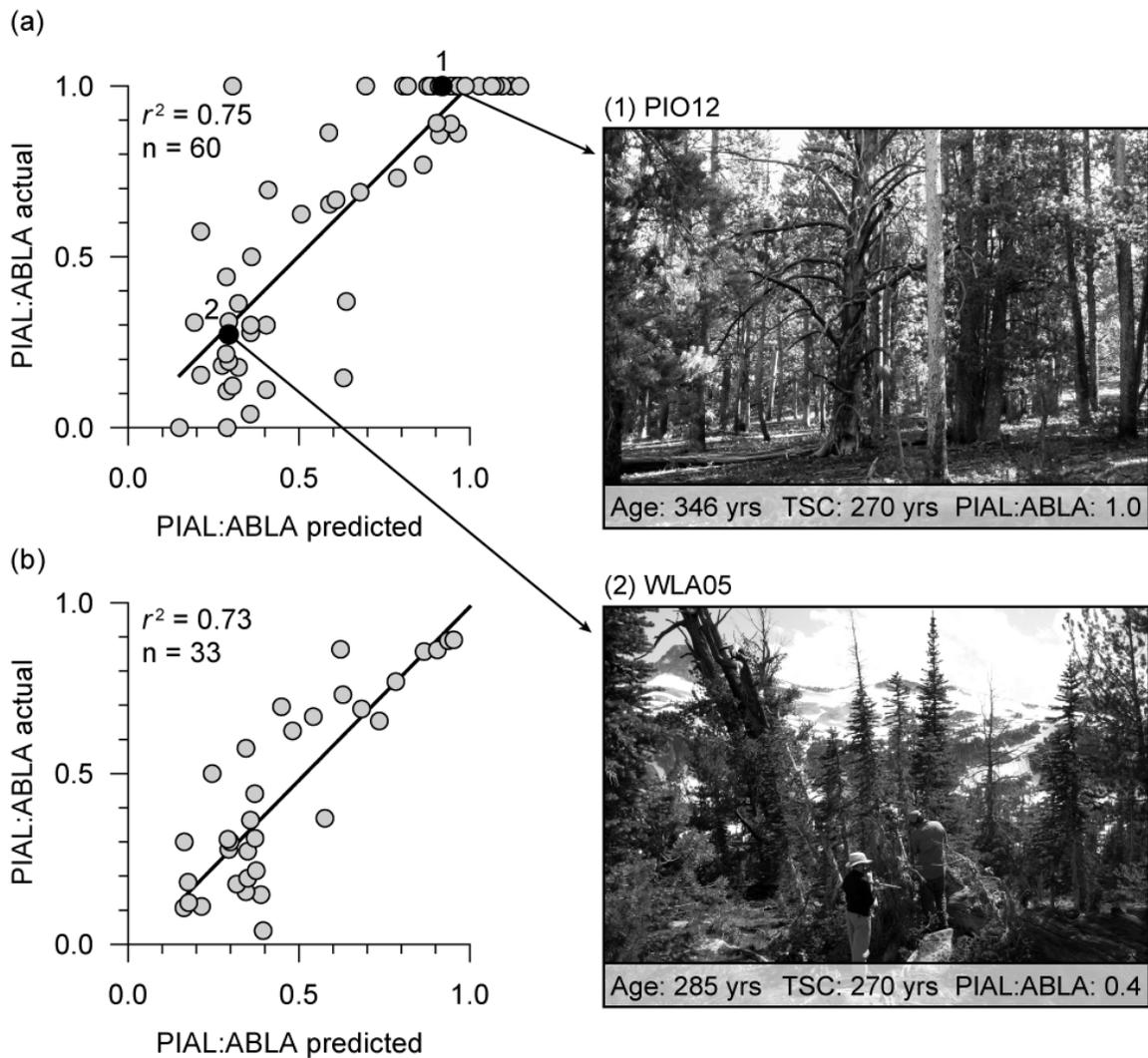


Figure 18. Predicted vs. actual ratios of whitebark pine to subalpine fir frequencies as determined through stepwise regression using (a) data from all plots ($n = 60$) and (b) data from only those plots that contained both species ($n = 33$). The photographs illustrate the differences in forest structure and composition of similarly aged forests at plot (1) PIO12 and (2) WLA05.

Table 6. Spearman rank correlations between the PIAL:ABLA regression residuals and select stand and climate variables.

variable	All sites		Both species present	
	r_s	p	r_s	p
Stand age	-0.03	0.795	-0.12	0.376
TSC	0.04	0.785	-0.07	0.574
DDF	-0.07	0.617	-0.02	0.866
DD5 ^a	0.30	0.022	0.55	< 0.000
GSP ^b	-0.30	0.021	-0.31	0.001
MTWM	0.35	0.006	0.60	< 0.000
ADI	0.36	0.004	0.35	0.007
MPB-killed ^c	-0.13	0.339	-0.29	0.024

^a Degree days >5° C

^b Growing season precipitation (April–September)

^c number of mountain pine beetle-killed whitebark pine in a plot

comparison of two sites that shared similar patterns in disturbance history, stand setting, and basal area yet show markedly different PIAL:ABLA ratios illustrates the results of the regression analysis (Table 7, Figure 18).

Discussion

Disturbance and the Structure and Composition of Whitebark Pine Communities

At a coarse scale the structure and composition of the forests at my sites reflected patterns of succession observed in whitebark pine forests elsewhere, yet at the scale of individual stands the variability in composition and structure within and across the different mountain ranges highlighted the diverse forms that whitebark pine communities can take. In general, the high proportion of stands with single cohorts indicates that most of these forests developed following severe, stand-replacing disturbances (Parker and Peet 1984), while the few stands that contained multiple cohorts more likely developed under mixed-severity disturbance regimes (Larson, van de Gevel, and Grissino-Mayer 2009) and the stands that contained no post-disturbance cohorts experienced low-severity disturbances associated with climax whitebark pine communities (Arno 2001). The peaks in the density and Weibull distributions of tree age that are not apparent in the distributions of tree size suggest a convergence of size structure in whitebark pine forests that has been observed in other subalpine forest types where as stands that at first appear quite different become more structurally similar over time (Kashian et al. 2005). The pattern of early whitebark pine and lodgepole pine establishment following fire and more abundant subalpine fir later in the stand history that is displayed by many stands follows both conceptual and observed patterns of succession for seral whitebark pine

Table 7. Descriptions of sites showing common histories but contrasting ratios of whitebark pine to subalpine fir.

Plot ID	Slope	Aspect	Stand age (yrs)	TSC (yrs)	DDF	Tree density (stems/ha)			Basal area (m ² /ha)			PIAL: ABLA
						PIAL	ABLA	All	PIAL	ABLA	All	
PIO12	18	220	346	270	0.09	490	0	830	13.0	0.0	34.6	1.00
WLA05	15	280	285	270	0.11	310	470	780	21.4	12.9	34.2	0.40

communities (e.g., Keane 2001b; Campbell and Antos 2003; Kipfmüller and Kupfer 2005). In addition to this pattern, however, are multiple examples of stands with structure and composition that cannot be explained using the current models of whitebark pine forest succession. This suggests that succession in whitebark pine forests is more complex than currently recognized.

The ecological versatility of whitebark pine is likely the source of some of the diversity in forest structure and composition at my sites. Whitebark pine is often considered a pioneer species, but does not entirely share the traits common to classic pioneer species. The representation of whitebark pine early in most stand histories and often as the oldest tree at a site agrees with the pioneering nature of whitebark pine due to the long-distance dispersal by Clark's nutcracker (Tomback 1982; Hutchins and Lanner 1982) and the relative hardiness of whitebark pine seedlings and saplings (McCaughey 1990), yet while most pioneer species are intolerant of shade, whitebark pine exhibits moderate shade tolerance. This was illustrated in my study by the continuous establishment of whitebark pine alongside mountain hemlock, subalpine fir, and Engelmann spruce at many sites, albeit at lower levels than directly following disturbance events (Fig. 19). This is similar to the findings of Campbell and Antos (2003) who found whitebark pine established abundantly following disturbances but also throughout the history of whitebark pine-subalpine fir stands in excess of 500 years of age. The class of early successional species was assigned to whitebark pine due to its shade tolerance relative to its primary competitors subalpine fir and mountain hemlock, but in contrast to classic early successional species whitebark pine can tolerate moderate levels of shade (Arno and Hoff 1990) and has been observed to release following mechanical treatments

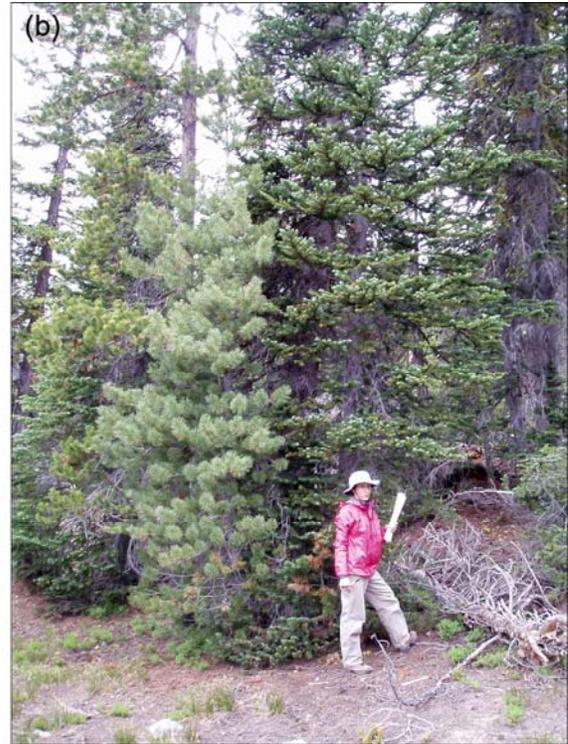


Figure 19. Examples of young whitebark pine growing out from underneath mature (a) subalpine fir and (b) Engelmann spruce (*Picea engelmannii* Parry ex Engelm.) in the Wallowa Mountains.

to open forest canopies (Keane, Gray, and Dickinson 2007). The ability of whitebark pine to persist on sites for long periods is also facilitated by the life span of individual whitebark trees that frequently approaches 500 years and occasionally surpasses 1,000 years (Perkins and Swetnam 1996; Luckman and Youngblut 1999; Kipfmueller 2008). The archetypal description of a species as a pioneer often does not capture the complexity of species life histories and competitive interactions (Glenn-Lewin 1980), and a more appropriate label for whitebark pine may be a super species following the concepts of Huston and Smith (1987). Releasing whitebark pine from the confines of the categorical label of an “early successional species” is an important step for increasing our ability to acknowledge and incorporate complexity into conceptions and models of whitebark pine communities.

The frequent occurrence of fire scars and charcoal at my sites agreed with research that emphasizes the important role of fire in whitebark pine forests (Arno 2001), but my results also illustrate the importance of mountain pine beetles in this system, particularly over the recent past. The synchrony and nearly ubiquitous presence of mountain pine beetle-related mortality over the late 1900s and early 2000s appears unprecedented across my study area, although regional-scale outbreaks have occurred in the past (Bartos and Gibson 1990; Perkins and Swetnam 1996) and helped to spur concern over declines in whitebark pine forest (Keane and Arno 1993). The legacies of disturbances on these scales can linger in the structure and composition of vegetation communities for centuries (Foster, Knight, and Franklin 1998), and the effects of the recent mountain pine beetle outbreaks will be important drivers in the dynamics of these forests at a time of rapid climate change and the intensification of blister rust infections.

The immediate effects of mountain pine beetle outbreaks are a shift in species composition from the host pine species to non-host spruce and fir, essentially accelerating succession (*sensu* Veblen et al. 1991). Mountain pine beetles preferentially attack and kill larger trees (Amman and Baker 1972), and therefore landscape-scale outbreaks greatly reduce mature trees that serve as seed sources for post-disturbance regeneration. Mortality rates from mountain pine beetle outbreaks are rarely 100% (Rocca and Romme 2009), however, and the release of resources following canopy mortality can initiate a period of release among subcanopy trees (Romme, Knight, and Yavitt 1986) that has been associated with the establishment of post-outbreak cohorts of both pine and fir species in lodgepole pine forests (Sibold et al. 2007). The presence of whitebark pine seedlings and saplings in the understory of nearly all of my sites may therefore offset the reduction in seed source and provide the means by which whitebark pine can persist on sites that experience high levels of mountain pine beetle-related mortality as seen at PAO07 and other sites (see Chapter 3). Evidence for this dynamic is visible in several of my stands that contain post-mountain pine beetle outbreak cohorts (Fig. 20).

The occurrence of post-mountain pine beetle outbreak cohorts holds important implications for the current understanding of whitebark pine community dynamics. Fire scar evidence clearly illustrates the historical role of fire in whitebark pine communities (Arno 1980; Morgan and Bunting 1990; Larson, van de Gevel, and Grissino-Mayer 2009), but a large portion of the fire history research used to describe whitebark pine forest fire regimes was based on age-structure data (e.g., Romme 1982; Keane, Morgan, and Menakis 1994; Murray, Bunting, and Morgan 1998). Multiple lines of evidence including age structure and fire scar data can be used to minimize the uncertainty



Figure 20. A cohort of whitebark pine established under a mountain pine beetle-killed canopy.

regarding the type of disturbance that initiated past cohorts, but where these complementary data are lacking the possibility of fire or mountain pine beetle activity must be considered. Additionally, episodic regeneration following mountain pine beetle outbreaks provides a mechanism for the persistence of whitebark pine on landscapes in the absence of fire, a topic of primary concern among management communities (Keane 2001a). The abundant whitebark pine regeneration I observed at many of my sites may provide a mechanism for these forests to recover following the current widespread mountain pine beetle-related disturbances. Given sufficient seed source or stocking of regeneration prior to recent outbreaks, the high levels of mortality in whitebark pine forests across western North America caused by mountain pine beetle may provide suitable habitats for extensive renewal of whitebark pine forests (see Chapter 3), which in turn may enhance the species' ability to adapt to the changing modern environment. In the largest sense this may be an illustration of how disturbance processes can act to keep otherwise long-lived biotic communities in balance with the varying biophysical environment (Sousa 1984).

One of the primary critiques of retrospective studies such as mine is the inability to describe what parts of the forest have been lost from a site through disturbance, death, and decay (Johnson, Miyanishi, and Kleb 1994) and my data serve to illustrate this uncertainty and its relevance to the concept of fire suppression leading to declines in whitebark pine forests. As with research in other subalpine forests, I found that most species established on site within the first few decades following a disturbance (Johnson and Fryer 1989; Parish and Antos 2002; Campbell and Antos 2003; Kipfmüller and Kupfer 2005), and while I observed mountain hemlock of equal or greater age than the

co-occurring whitebark pine in the Cascades and on Paulina Peak, I found relatively few subalpine fir more than 200 years old. The question then is if the modern establishment of subalpine fir soon after fires is indicative of past post-disturbance dynamics, then why are old subalpine fir trees so rare at my sites? The two possibilities are that 1) the subalpine fir represented in age-structure data are the first individual firs to establish in that stand and have done so because of changing disturbance regimes; or 2) that subalpine fir occurred at these sites throughout their history but the individual trees that established earlier have since died and decomposed. The most common argument in support of the first possibility is that fire suppression has enabled subalpine fir to increase in abundance and importance at sites where it had previously been excluded due to frequent, low-severity fires (Tomback, Arno, and Keane 2001a), yet I have no evidence of frequent fires at most of my sites and therefore lack a mechanism by which fire suppression could influence stand structure. My results, and in particular the Weibull distributions showing nearly identical size and age distributions of subalpine fir across stands of varying ages, make a strong case for the second possibility where the age-structure of subalpine fir is more reflective of the species' demographic characteristics, namely the shorter lifespan than whitebark pine (Shea 1985; Alexander, Shearer, and Shepperd 1990), rather than successional processes. The relative differences in the life span of whitebark pine and subalpine fir may result in forest dynamics similar to the gap dynamics of mature spruce-fir forests in the Front Range of the Rocky Mountains where Engelmann spruce persists in stands due to its long life span despite the more abundant regeneration of subalpine fir (Veblen 1986). No absolute conclusion can be drawn on this matter for exactly the reasons discussed by Johnson et al. (1994), but the lack of confidence should be

considered an important caveat to the suggestion of widespread influence of fire suppression on advancing succession and declines in whitebark pine communities and future research should examine the role of gap dynamics in whitebark pine forests.

The Relative Influences of Disturbance, Time, and Climate on Whitebark Pine Forest Composition

The finding of broad influences of climate on plant distributions is by no means novel (Clements 1916; Daubenmire 1966; Rehfeldt, Ferguson, and Crookston 2008), yet this relationship has generally been described at the scale of landscapes or regions and rarely at the scale of individual stands where autogenic and stochastic processes are more often called upon to explain site-specific differences in community composition and structure (Halpern 1989). It was therefore striking to find no relationship between compositional differences and stand age or TSC at my sites, as this lack of relationship contrasts sharply with most conceptual descriptions of succession in whitebark pine communities (Morgan and Bunting 1990; Keane 2001b). Instead it appears that climate, not time since disturbance or stand age, is the dominant factor driving differences in forest composition across my study area. The significant relationships between differences in canopy and subcanopy composition, the significant correlations between climate variables and the ordination axes, and the lack of clear patterns of differences in composition among stands of different ages all lend support to this conclusion, which is further corroborated by my regression analysis of the factors related to the variations in the ratio of whitebark pine to subalpine fir. The explanation for why climate is the dominant factor driving forest composition at my sites rests in the interactions of

landscape configuration and the vital attributes of the tree species that make up whitebark pine communities.

The presence of plant species within a community is primarily determined by three factors characterized as species' vital traits: 1) the ability of propagules to persist or arrive on a site, 2) conditions amenable to establishment and growth at a site, and 3) the time taken to reach reproductive maturity (Noble and Slatyer 1980). In the case of whitebark pine communities it is possible that the second factor, the conditions required for a species to establish and grow, plays the dominant role in community composition for the following reasons. Disturbances in subalpine environments are patchy and often of mixed severity, particularly in whitebark pine communities (Romme 1982; Howe and Baker 2003; Larson, van de Gevel, and Grissino-Mayer 2009). This creates patches of undisturbed forest that serve as biological legacies and seed sources for the surrounding matrix of disturbed sites (Turner et al. 1997). Patch sizes in upper subalpine forests are often relatively small (Daubenmire and Daubenmire 1968), and a nearest neighbor analysis conducted using the USFS-delineated stands including and surrounding my plots showed mean distances of 277–1,278 m between stand centroids across my study area (Table 8). The distance over which wind-dispersed subalpine tree seeds can travel range from ca. 60 m for the heavy-seeded lodgepole pine to 200+ m for subalpine fir, Engelmann spruce, and mountain hemlock (Alexander, Shearer, and Shepperd 1990; Alexander and Shepperd 1990; Lotan and Critchfield 1990; Means 1990), while Clark's nutcrackers have been observed dispersing whitebark pine seeds greater than 12 km in a single flight (Tomback 1978; Hutchins and Lanner 1982). The distances for wind dispersed species also do not account for extreme events that can vastly increase the

Table 8. Mean stand size and nearest neighbor based on stand centroids for the stands included and surrounding my study plots.

Mountain Range	Mean stand size (m ²)	Nearest neighbor (m)		
		Mean	Min.	Max.
Cascades	3,015,531	1,278	456	3,099
Paulina Peak	1,905,547	1,160	447	2,942
Wallowa Mountains	689,063	538	146	1,932
Salmon River Mountains	204,270	277	10	952
Pioneer Mountains	231,540	290	44	1,400
Gravelly Range	253,624	296	22	967

distance propagules may travel (Nathan 2006). The dispersal distance for most subalpine tree species is thus not trivial when compared to the typical patch size in my study area, which helps to explain the arrival of most species to a site within the first few decades following a disturbance as has been documented elsewhere (Johnson and Fryer 1989; Antos and Parish 2002; Campbell and Antos 2003; Kipfmueller and Kupfer 2005). Therefore I suggest that the effects of propagule arrival and maturation likely vary less across my sites than do the effects of climate on individual trees abilities to establish at a site.

The climate spaces occupied by the different species present at my sites are difficult to separate in many cases, and made more so due to the importance of what conditions are suitable specifically for establishment rather than survival once established. Additionally, climate extremes may have a relatively greater influence on species regeneration than overall mean conditions (Easterling et al. 2000), yet little information is available on the specific effects of extreme climate conditions on the species considered in my study. I therefore offer a rather crude assessment of the relative hardiness of whitebark pine compared to the two other dominant tree species I encountered at my sites: subalpine fir, and lodgepole pine. Whitebark pine seedlings are relatively more tolerant of drought and temperature extremes than subalpine fir (McCaughey 1990) and the presence of whitebark pine and its close relative limber pine (*Pinus flexilis* James) facilitate the establishment and growth of subalpine fir through shade and protection from ice abrasion and winter desiccation (Hadley and Smith 1986; Callaway 1998; Donnegan and Rebertus 1999). Whitebark pine is slightly more cold tolerant than lodgepole pine while lodgepole pine is better adapted to drought conditions

(Brunelle et al. 2008). As shown in my ordination, lodgepole pine was more dominant at the warmer sites with less growing season precipitation, whereas subalpine fir was more common at the warmer, wetter sites where it would be less dependent on facilitation by whitebark pine. These simple differences in climate tolerances, if representative of their ability to establish at a site, agree with my findings linking site-specific climate to variations in stand composition at my sites. Additionally, due to climate variability and changing microsite conditions through stand development and biotic feedbacks, the settings that influence the establishment of different species will change over time, resulting in non-stationary patterns of forest structure and composition.

At first glance it may appear that I am calling for the re-application of the concept of climate-dictated climax communities (e.g., Clements 1936), but that is not my goal. Rather, I argue that the role of climate in setting the stage on which succession plays out must be acknowledged and more explicitly included in models of succession for plant communities that extend across broad environmental gradients. In such cases successional change will occur at different rates and in different patterns on a site-by-site basis and the ability to generalize management applications from one area to the next is limited and ecologically unfounded, particularly in mountain environments where environmental gradients are sharpened and made more complex by highly variable topography and relief. I therefore present here a species-specific conceptual model of forest succession that explicitly incorporates the role of climate while emphasizing the gradients along which climate conditions vary across the range of whitebark pine. The model I present is focused specifically on the relative composition of a forest with respect to whitebark pine and subalpine fir and draws heavily from the results of my regression

analyses. This model is easily modified to incorporate other co-occurring species and combining models for multiple species would create a model of whitebark pine community succession, but I instead focused on subalpine fir due to its presence in nearly every part of the range of whitebark pine (Fig. 21) and it being the primary competitor of whitebark pine in most settings that is also most frequently cited as evidence of advancing succession in whitebark pine forests (Keane 2001b).

The model is based on gradients of time, climate, and species composition with consideration given to species performance under different settings and different disturbance events. I employed the concept of gradients rather than pathways to guide the development of my model because in a sense pathways are too constraining for a process as variable as succession and because of the deep roots of gradients in ecological theory and meaningful applicability for describing natural systems (ter Braak and Prentice 1988). Additionally, while most successional models include cycles or loops that suggest succession is cyclical I contend that the applicability of this view is generally limited for succession in subalpine forests due to the long time span on which succession occurs that includes periods of unique climate conditions, disturbance regimes, and landscape configurations. Cyclic models of succession may be particularly inappropriate for whitebark pine communities due to the novel disturbance regimes now operating in all whitebark pine communities and the pace at which modern climate is changing. Essentially I argue for a model that approaches succession from the perspective of a continuum and is equally applicable for describing past as well as future changes in the composition of whitebark pine communities.

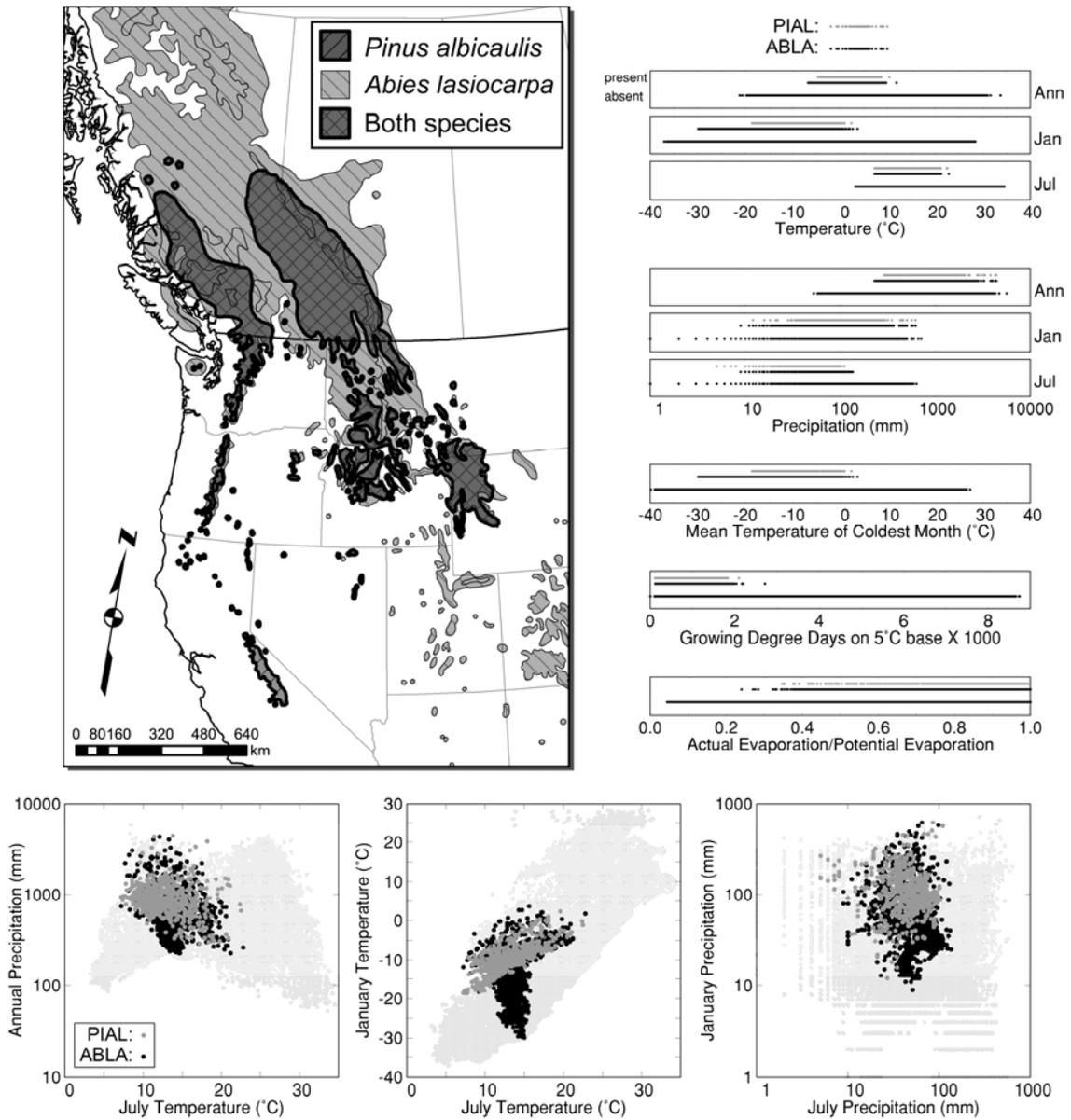


Figure 21. Geographic and climatic distribution of whitebark pine and subalpine fir. Adapted from Thompson et al. (1999).

I developed species performance curves on which to base my model from my understanding of the climate and shade tolerances of whitebark pine and subalpine fir as well as their competitive and facilitative interactions (Fig. 22) (Daubenmire and Daubenmire 1968; Pfister et al. 1977; Callaway 1998; Arno 2001; Sala et al. 2001). At the coldest, driest sites whitebark pine is able to establish and tolerate harsh conditions while subalpine fir is only able to persist at low populations in the shelter of mature whitebark pine trees. This results in a facilitative relationship between the two species where whitebark pine establishes early and continuously and subalpine fir abundance slowly increases with no deleterious effects on whitebark pine. In warmer and wetter environments, whitebark pine becomes more productive and establishes more abundantly and earlier in the stand history, while subalpine fir can establish on the site even in the absence of whitebark pine and increases in abundance at an increasing rate over time due to the positive feedbacks produced by earlier established fir. Whitebark pine still operates as a facilitator for subalpine fir establishment and growth, and therefore accelerates the population growth of subalpine fir over time. At still warmer and wetter sites the relationship between whitebark pine and subalpine fir becomes one of tolerance, where whitebark pine establishes more abundantly early in the stand history but as subalpine fir abundance builds up over time the performance of whitebark pine diminishes. In these communities whitebark pine will likely persist due to its long life span but whitebark pine regeneration will diminish over time. Finally in the warmest and wettest sites subalpine fir is a major competitor of whitebark pine and will eventually outcompete all but a few whitebark pine in the stand in the absence of disturbance. These descriptions align

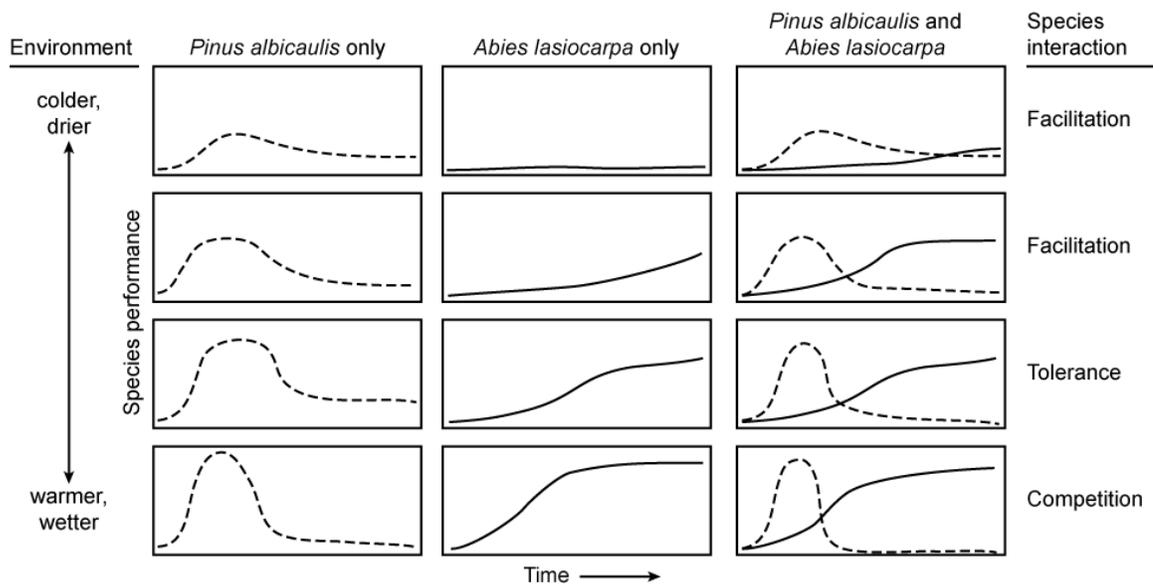


Figure 22. Theoretical species performance curves for whitebark pine and subalpine fir under varying environmental conditions and the resulting species interactions (sensu Connell and Slatyer 1977; Pickett, Collins, and Armesto 1987).

generally with the climax, co-climax, major seral, and minor seral whitebark pine communities described by Arno (2001).

The use of species performance curves such as those described above is limited in two ways that are also related to the shortfalls of most models of succession: 1) the implicit suggestion that succession can be divided into separate categories or pathways and 2) that climate and species interactions are static over time. As was illustrated by the stands I considered in this study, forest composition varies continuously along the primary environmental gradients influencing various aspects of vegetation communities. To incorporate this variability, I translated the species performance curves into my final successional model based on gradients that illustrate the continuous variability in stand composition that I identified in my research. In this model there are no clear-cut categories of climax, co-climax, or seral whitebark pine communities, but rather a continuous gradient of composition that varies in line with environmental conditions and time (Fig. 23a). Disturbances such as fire that set back succession (Fig. 23b) and mountain pine beetle outbreaks that accelerate succession (Fig. 23c) can also be incorporated into this model, with corresponding effects on forest composition. The effects of blister rust infection can also be illustrated with this model as a shortened gradient from pure whitebark pine to pure subalpine fir that still reflects the climatic limitations to subalpine fir establishment (Fig. 23d). An additional strength to this model is the ability to incorporate climate variability into a successional model. Climate varies continuously over all spatial and temporal scales (Kutzbach 1976), and a constant rate and direction of successional change (illustrated by the path A in Fig. 24) is highly unlikely to occur, particularly on the time scales of succession in whitebark pine

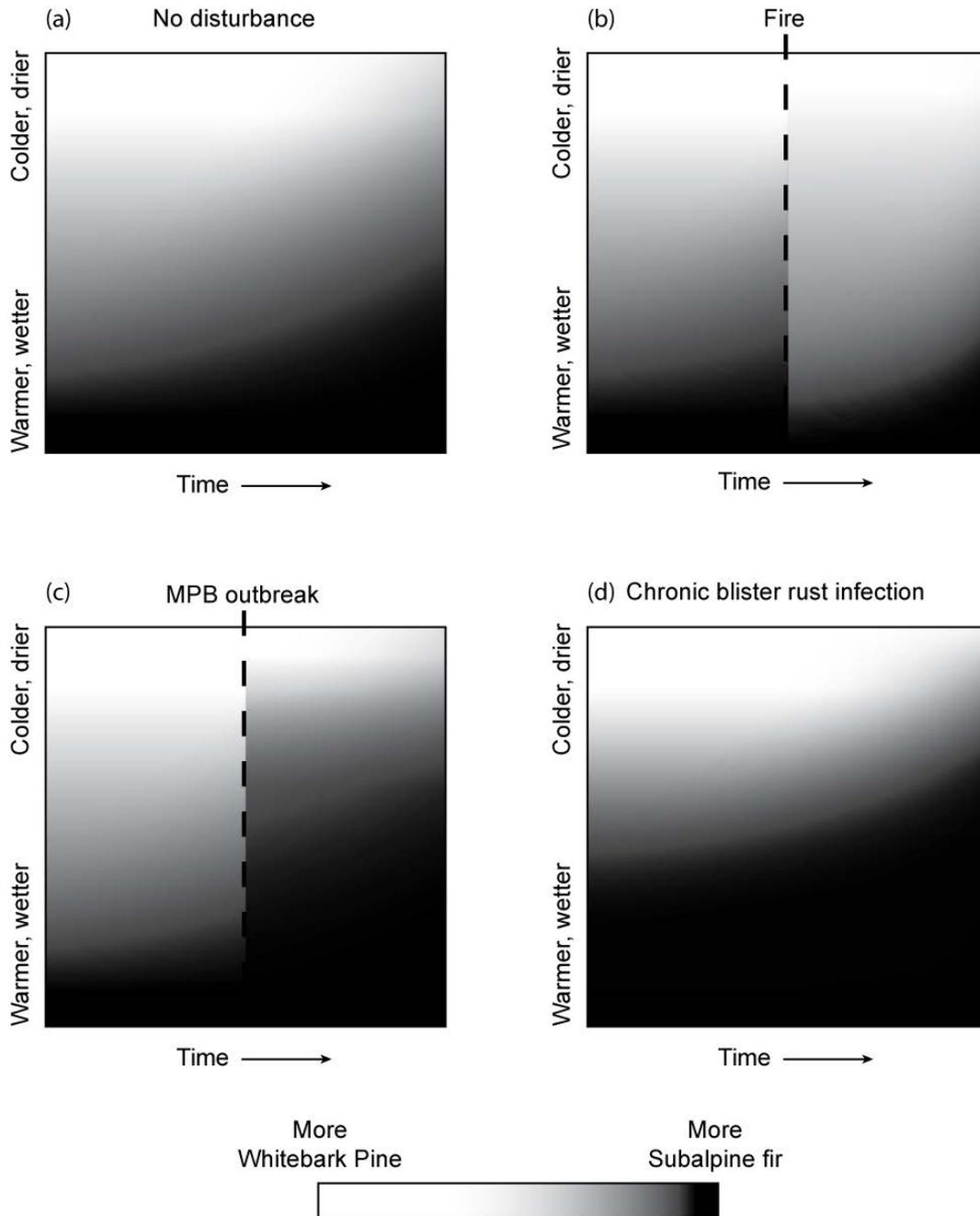


Figure 23. Gradient models of succession with respect to whitebark pine and subalpine fir across varying environmental conditions and time with (a) no disturbance, (b) the effects of fire, (c) the effects of a mountain pine beetle outbreak, and (d) with chronic blister rust infection.

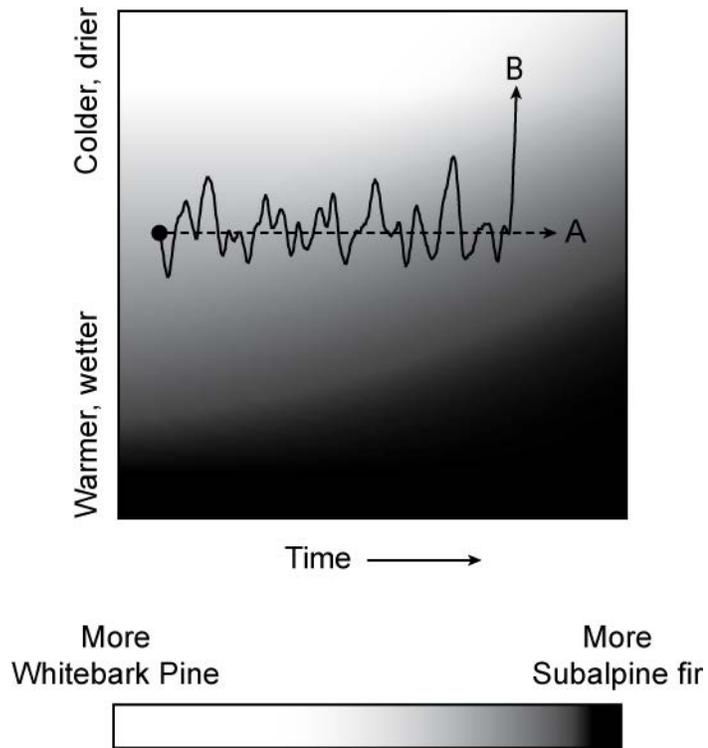


Figure 24. Illustration of successional change over time under static climate conditions (line A) and variable climate conditions (line B). Line B is drawn from 150 years of reconstructed Palmer's Drought Severity Index for the Wallowa Mountains smoothed using a 20-yr spline (Cook et al. 1999).

communities. What is more likely is that the rate and trajectory of succession in a particular stand will change over time as climate changes (illustrated by the path B in Fig. 24). This dynamic aspect of succession is often lacking from conceptual models but can be integrated with my proposed gradient model of succession. Recent developments in the quantification of species-climate relationships (Rehfeldt, Ferguson, and Crookston 2008) offer an opportunity to increase the articulation and utility of this model through a better understanding of the environmental gradients that drive community composition successional dynamics.

The Effects of Fire Suppression on Whitebark Pine Communities

My results suggest that fire suppression has likely had a minimal effect on the composition of most of the whitebark pine forests across my study area and that where fires have been excluded from the landscape the structural and compositional changes are not the same as those described for forests in the Northern Rockies (Keane 2001b). The few stands that historically experienced recurrent fires that have since been excluded are not advancing successional in terms of species composition, and in fact the exclusion of fire from these sites may have resulted in increased stand density through increased whitebark pine regeneration. In other forest types affected by fire suppression, increased stand densities have resulted in declines in forest health and resiliency to disease and pest outbreaks (Hemstrom 2001; Allen et al. 2002). In the context of this discussion it is interesting to note that of the mountain ranges I examined, the Gravelly Range showed the greatest structural effects from fire exclusion and also experienced the highest rates of mountain pine beetle-related mortality (see Chapter 2). The probability of mountain pine

beetle outbreaks in lodgepole pine forests increases with greater stand density (Waring and Pitman 1985), suggesting that the high rates of mountain pine beetle-related mortality in the Gravelly Range may be an indirect result of fire suppression through increased stand density. With respect to the forests at my other sites, several lines of evidence support the conclusion that fire suppression has had limited effects on forest structure and composition. The wide range in fire frequency and the relatively small proportion of the stands that recorded multiple fires agrees with the findings of previous research describing whitebark pine forest fire regimes (Arno 2001; Larson, van de Gevel, and Grissino-Mayer 2009). The majority of my sites are in rugged terrain where fire suppression efforts have only been effective for ca. 60 years (Pyne 2001). This length of time, when compared to fire-free intervals that can range up to several centuries make it unlikely that fire suppression has moved these stands outside of the historical range of variability in structure and composition (Schoennagel, Veblen, and Romme 2004). Of the stands that contained 20th century cohorts, most could be attributed to documented disturbance events including mountain pine beetle outbreaks and only seven showed a decrease in fire activity over the same time period. Finally, my ability to predict over 70% of the variability in stand composition among my sites based solely on climate variables leaves a relatively small proportion of the variance in stand composition to be explained by ecological legacy effects, the type and timing of past disturbances, and other stochastic processes that influence stand development (e.g., Halpern 1989; Foster, Knight, and Franklin 1998). It therefore seems that the effects of fire suppression, like so many other aspects of complex ecosystems, vary on a site-by-site basis.

Chapter 5. Conclusions and Synthesis

Variability in the Status and Dynamics of Whitebark Pine Communities

The common theme that I observed throughout my dissertation research was one of variability in whitebark pine communities. Blister rust infection rates, mountain pine beetle-related mortality, whitebark pine regeneration, and stand structure and composition all varied among and within the different mountain ranges included in my study. In general, the whitebark pine communities in the Wallowa Mountains and Pioneer Mountains appeared vigorous and relatively healthy, with moderate rates of blister rust infection but little decline in tree health, moderate to high levels of regeneration, and little to no evidence of advancing succession due to fire suppression. Whitebark pine populations in the Cascades and on Paulina Peak also appeared to be relatively healthy with the possibility that this may change if the mountain pine beetle activity I observed at these sites grows to epidemic proportions, but at the time of my study I observed moderate to high rates of mortality balanced by the lowest rates of blister rust infection among my sites, widespread and abundant whitebark pine regeneration, and little evidence of advancing succession. The vigor of whitebark pine in the Salmon River Mountains and Gravelly Range contrasted sharply with those of the other ranges and appeared to be in steep declines as a result of high mortality rates associated with recent and ongoing mountain pine beetle activity and severe fires, high rates of blister rust infection among the surviving trees, and moderate to low levels of regeneration, as well as several potential cases of structural changes due to fire suppression in the Gravelly Range. The important caveat to all of this, however, is that there were stands that stood as

exceptions to the general patterns within each range. Some stands appeared to be in decline in the Pioneer Mountains, Wallowa Mountains, Cascades, and on Paulina Peak while the whitebark pine at a few plots in the Gravelly Range and Salmon River Mountains seemed to be relatively healthy. The variability in the health of whitebark communities across my study area calls for a more nuanced discussion about the status of this singular species.

The Overarching Influence of Climate on Whitebark Pine Communities

Site-specific climate conditions were identified as important factors in all aspects of whitebark pine communities that I assessed. Differences in moisture and temperature regimes were significant influences on blister rust infection rates, mountain pine beetle-related mortality rates, patterns and abundances of whitebark pine regeneration, and differences in forest composition and succession. Climate therefore appears to be an important driver of the variability I observed in the structure and dynamics of whitebark pine communities across my study area, but the critical factor to recognize is that it was not just regional-scale gradients in climate that were important, but also site-specific variability in climate conditions. Spatially continuous and accurate climate data have only recently become available, but now that they are, an incredible opportunity exists to explicitly integrate site-specific climate conditions with landscape-scale successional models to increase the resolution of our ability to model current and future vegetation changes.

The other implication of my results linking so many aspects of whitebark communities to climate conditions is that because climate is changing it should be

expected that changes in the structure, composition, and dynamics of whitebark pine forests will occur as well. What the specific changes will be is uncertain as shifting and novel climate conditions modify disturbance regimes and competitive interactions among species, but that changes will occur is certain. As temperatures rise, so too may the rates of blister rust, mountain pine beetle activity, and the abundance of subalpine fir in whitebark pine communities, while successful whitebark pine regeneration may decline. Yet increasing temperatures may induce more frequent and severe drought conditions and fires which may set back succession and have a confounding influence on effects of temperature in many of these cases. Over time these changes may become clear, but for the time being it is critical to expand the understanding of the influences of climate on whitebark pine community dynamics so that scientists and managers can move into the future as well prepared as possible.

Implications for Management and Research of Whitebark Pine

The basic implication of my research is that management of whitebark pine communities must be informed by site-specific data that incorporates climate as well as stand conditions and consideration of disturbance history. Variability in the status and dynamics of whitebark pine forests requires a fine-scale approach to managing this species that may be present in the management community but is lacking from the peer-reviewed literature. Whitebark pine communities may appear simple when compared to other forest systems due to the relatively few tree species that are typically present and the slow successional dynamics that govern ecological change in these settings, but their existence over areas of diverse topography, extreme environmental gradients, and long-

term variability in climate and disturbance types, frequencies, and interactions result in diverse and complex composition, structure, and dynamics. As a result, whitebark pine communities may be at risk of extirpation from some regions, but they appear to be healthy in others and generalizations about the declines of this species do little to improve our overall understanding and management of whitebark pine communities. To draw on a phrase used in the recent U.S. presidential elections, sweeping statements about the declines of whitebark pine and their causes are similar to using an axe where a scalpel is required. More specific language should be used that explicitly acknowledges the spatial variability in the status of whitebark pine communities and acknowledges the uncertainty relating to some aspects of the dynamics of these forests. Furthermore, the ubiquitous call on fire suppression as a primary factor causing the declines of whitebark pine communities is inaccurate for much of my study area. The potential therefore exists that fire suppression has played a less important role in driving whitebark pine community dynamics in other areas as well. More detailed information is required about the historical fire regimes and modern changes in patterns of disturbance, succession, and forest structure and composition in whitebark pine forests to better inform where restoration activities are warranted to counter the potential effects of fire suppression. Fire is without a doubt an important disturbance agent in whitebark pine communities, but so too is mountain pine beetle activity, and both disturbances take place in the context of site-specific climate and environmental conditions that broadly influence patterns in regeneration, stand composition, and succession. The resulting variability in whitebark pine community structure and function limits the ability to generalize from research conducted in whitebark pine forests in one region to another and this complexity must be

incorporated into management and restoration activities in whitebark pine forests lest generalizations blur the effects of fire suppression and natural variability and cause more harm than good.

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