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Landscape Level Dynamics in an Endangered Mountain Ecosystem, Northern Rocky Mountains, U.S.A.

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To the Graduate Council:

I am submitting herewith a dissertation written by Saskia L. van de Gevel entitled "Landscape Level Dynamics in an Endangered Mountain Ecosystem, Northern Rocky Mountains, U.S.A.." I have examined the final electronic copy of this dissertation for form and content and recommend that it be accepted in partial fulfillment of the requirements for the degree of Doctor of Philosophy, with a major in Geography.

Henri D. Grissino-Mayer, Major Professor

We have read this dissertation and recommend its acceptance:

Sally Horn, Ken Orvis, Wayne Clattebuck

Accepted for the Council:

Carolyn R. Hodges

Vice Provost and Dean of the Graduate School

(Original signatures are on file with official student records.)

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LANDSCAPE LEVEL DYNAMICS IN AN ENDANGERED MOUNTAIN ECOSYSTEM, NORTHERN ROCKY MOUNTAINS, U.S.A.

A Dissertation
Presented for the
Doctor of Philosophy
Degree
The University of Tennessee, Knoxville

Saskia L. van de Gevel
August 2008

DEDICATION

This dissertation is dedicated to my family and friends
for their love, support, and humor.
I would especially like to recognize my parents,
Dr. A.A.J.S. van de Gevel and Ms.Veronica King.

"Life is a great adventure, and the worst of all fears is the fear of living."
— Theodore Roosevelt

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ABSTRACT

The purpose of this dissertation research was to investigate the extent of natural and anthropogenic impacts on declining whitebark pine communities. My research used dendroecology to study multicentury changes in these threatened communities to assess current and past forest dynamics and the overlapping effects of white pine blister rust, mountain pine beetle, and climate change in the northern Rocky Mountains.

I created whitebark pine (host) and subalpine fir (nonhost) chronologies and collected species composition, stand structure, and forest health data in sites along a latitudinal transect through the Rocky Mountains in western Montana. The stand-structure data indicate over 70% of whitebark pines at all sites are declining or dead. The high mortality of whitebark pines was caused by the overlapping effects of past (1880s, 1920s, and 1970s) and current mountain pine beetle outbreaks, and more recently by white pine blister rust infection. Whitebark pine populations, in the majority of our sites, are being successionally replaced by subalpine fir, grand fir, and Engelmann spruce in all levels of the forest strata (trees, saplings, and seedlings). Shade-tolerant trees began establishing between 150 and 300 years ago at all sites, a finding that suggests 20th century fire suppression is not responsible for the successional replacement of whitebark pine forests.

Whitebark pine and subalpine fir growth respond strongly to drought and precipitation. This indicates wet conditions from precipitation and snowpack melt in the previous summer enhance tree growth during the following growing season. My climate reconstruction results support other climate reconstructions, east of the Continental

Divide, that found precipitation and Palmer Drought Severity Index (PDSI) have more of an influence on subalpine forest growth than temperature. The reconstruction data contribute an important high-elevation component to existing drought reconstructions from lower elevations in the northern Rocky Mountains. Whitebark pine communities should continue to be monitored as continued periods of drought will likely make whitebark pines more susceptible to mountain pine beetle attack and weaken their resistance to white pine blister rust infection.

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INTRODUCTION

1.1 Purpose

The purpose of this dissertation research is to investigate the extent of natural and anthropogenic impacts on declining whitebark pine (*Pinus albicaulis* Engelm.) communities in Montana using ecological and dendrochronological methods. Whitebark pine is limited in distribution to high elevations in the mountains of western North America, where it has been present through most of the Holocene (Tomback *et al.* 2001). Whitebark pine is a subalpine keystone species of critical importance for maintaining biodiversity in mountain ecosystems and for supporting wildlife species such as Clark's nutcrackers (*Nucifraga columbiana* Wilson), black bears (*Ursus americana* Pallas), and grizzly bears (*Ursus arctos* L.), and exists in areas that are highly sensitive to climate change (Tomback *et al.* 2001). I studied multicentury changes in these threatened communities by evaluating whitebark pine tree-ring patterns to assess current and past forest dynamics and the overlapping effects of human disturbances, fire exclusion, white pine blister rust, mountain pine beetle, and global climate change. A lack of research on these topics has hindered the response of land managers to the dramatic decline in whitebark pine communities. Consequently, an urgency exists to implement management practices that will slow the succession to shade-tolerant species, and decrease the severity of decline in whitebark pine communities in western North America.

1.2 Biogeography of Whitebark Pine

Whitebark pine is a long-lived tree species found in many high elevation and subalpine forest communities of western North America (Arno and Hoff 1989). Whitebark pine forms extensive contiguous stands in high elevation forests in the Rocky Mountains of Wyoming, Idaho, and Alberta, and smaller disjunct populations in eastern and southwestern Oregon, California, and Nevada. The species is restricted at its upper elevations by severe climate conditions and at lower elevations by competition from other tree species (Arno and Hammerly 1984). Whitebark pine is a pioneer species that fills a crucial niche in watershed protection, catching and retaining snow, and stabilizing rock and soil in harsh and recently disturbed areas (Tomback *et al*. 2001) (Figure 1.1).

Whitebark pine fossil pollen records suggest the species survived the last glaciation south of its present range in North America (Nowak *et al.* 1994). These southern populations may have been the seed source for postglacial colonization of whitebark pine in the Sierra Nevada (Anderson 1990). Less is known about whitebark pine in the northern Rocky Mountains as only trace amounts of haploxylon pine pollen have been found before 12,000 BP (Anderson 1990, Beiswenger 1991, Whitlock *et al.* 1995). Warmer and drier postglacial climates, initiated approximately 10,000 BP, restricted whitebark pine and associated conifers to higher elevations across mountain ranges in North America (Whitlock 1993). Subfossil wood, over 8,000 years old, has been found above current treeline, indicating that whitebark pine grew above its current elevation in the early Holocene (Luckman 1988, Clague and Mathewes 1989). During the late

Figure 1.1. Whitebark pine tree on Ajax Peak, in the Beaverhead-Deerlodge National Forest (photograph taken by Saskia van de Gevel).

Holocene, whitebark pine populations have extended to lower elevations in montane forests (Mehringer *et al.* 1977, MacDonald *et al.* 1998).

Whitebark pine is also a food source of critical importance to Clark's nutcrackers, red squirrels (*Tamiasciurus hudsonicus* Erxleben), grizzly bears, and black bears (Mattson *et al*. 2001, Tomback 2001). Whitebark pine seeds are picked and cached by nutcrackers and squirrels, and bears rely upon these seed caches in the northern Rocky Mountains (Mattson *et al*. 2001). Cached seeds that escape predation are in turn a major source of regeneration for whitebark pine (Tomback *et al*. 2001). The availability of whitebark pine seeds directly influences the number of human conflicts with grizzly bears that result in management actions. In the Yellowstone Basin, more conflicts occur between grizzly bears and humans during low seed crop years, and grizzly bears experience higher mortality at these times (Mattson and Reinhart 1986).

1.3 Natural and Anthropogenic Disturbances in Whitebark Pine Ecosystems

The combination of advancing encroachment by fire-intolerant species such as subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.) and Engelmann spruce (*Picea engelmannii* Parry ex Engelm.), infestation by mountain pine beetle (*Dendroctonus ponderosae* Hopk.), and the epidemic of white pine blister rust (*Cronartium ribicola* JC Fischer) have devastated whitebark pine populations north of 45° N latitude in western North America (Kendall and Keane 2001, Tomback *et al.* 2001). Due to natural (mountain pine beetle) and anthropogenic (climate change, fire suppression, and the introduction of white pine blister rust) disturbances, the whitebark pine ecosystem of the northern Rockies is diminishing. If whitebark pine conservation efforts are not successful in the next 15 to 20 years, this species will likely become extinct (Tomback *et al.* 2001).

Ecologists recognize that natural disturbance cycles that involve fire, wind, or pathogens are important components in most landscapes, and that few ecosystems ever achieve a steady-state climax (Bormann and Likens 1979, White 1979, Christensen 1989). Tree reproduction in many forest ecosystems occurs in episodes associated with major disturbances. Thus, the distribution of ages in a population is often a sensitive indicator of the history of disturbance in a stand (Christensen 1989). Conventional models of succession show that whitebark pine dominates during early stages of succession and regenerates after stand-level fires that occur at long return intervals of 200 years or more (Fischer and Bradley 1987). The long lifespan (up to 1000 yrs) of whitebark pine makes it an important component of mid- and late-successional forests. Research shows that this ecosystem experiences both stand-replacing fires, which occur at long intervals and initiate forest succession, and low-severity surface fires, which occur throughout stand development and create and maintain an open canopy (Arno and Peterson 1983, Fischer and Bradley 1987, Larson 2005, Larson *et al.* 2008). Stand-replacing fires kill most trees and result in juvenile recruitment, which alters the age structure of the stand. Low-severity fires produce fire scars on trees but do not dramatically change stand composition.

1.4 White Pine Blister Rust Distribution

White pine blister rust is an exotic pathogen first discovered in North America on a currant plant (*Ribes* spp.) in Geneva, New York, in 1906. The pathogen soon spread to the Great Lakes region and British Columbia. Eastern white pine seedlings that had been exposed to white pine blister rust were sold from tree nurseries in Germany and France to North America from 1890 to 1914 (Tomback *et al.* 2001). Blister rust first appeared on whitebark pine in the coastal range of British Columbia in 1926 and spread to northern Idaho by 1938 (Childs *et al.* 1938). Soon after the discovery of blister rust, infected white pine trees were destroyed and a *Ribes* eradication program was begun (Tomback *et al.* 2001). Millions of *Ribes* shrubs were pulled out of stream bottoms, forested uplands, and mountain slopes on public lands across western North America (Hoff 1992). Herbicides such as actidione and phytoactin were also used during the *Ribes* eradication program, although with limited success. The eradication effort of removing *Ribes* shrubs was abandoned in 1966 due to the complex life cycle of white pine blister rust.

Blanchard and Tattar (1997) reported that white pine blister rust is now found throughout the entire range of five-needled pines in North America. Worsening the situation, whitebark pine is also the most vulnerable white pine species, with fewer than one in 10,000 trees showing resistance to blister rust (Kendall 1994). The range of whitebark pine affected by white pine blister rust is expanding and infection is intensifying. Currently, the degree of infestation of whitebark pine decreases southward throughout all parts of its range, including the Cascade-Sierra Nevada chain, the Bitterroot Mountains, and along the Continental Divide of the Rocky Mountains (Hoff 1992). In Washington State, northern Idaho, northwest Montana, southern Alberta, and British Columbia, 40–100% of whitebark pine are dead in most forest stands, and 50–100% of the living trees are infested with white pine blister rust (Tomback *et al.* 2001).

Keane (1995) found that 98% of the whitebark pine populations in the Columbia River Basin have disappeared since the turn of the century. During a project to reconstruct landscape patterns of whitebark pine in western Montana, Arno *et al.* (1993) found that 14% of the stands were dominated by whitebark pine around 1900, but none of these stands were dominated by whitebark pine in the 1990s. Of the remaining living trees in these whitebark pine stands, 80% were infected with white pine blister rust, and more than one-third of their cone-bearing crowns were dead (Arno *et al*. 1993). Furthermore, the extent of forest stands with cone-bearing trees had declined by half.

1.4.1 Blister Rust Disease Cycle

White pine blister rust alternates between five-needle pines and *Ribes* species. White pine blister rust is a heteroecious rust fungus that produces several spore types and requires two host types to complete its life cycle (Bega 1978, Blanchard and Tatter 1997) (Figure 1.2). The disease initially infests a tree through the needles and girdles branches, but can travel to the main stem, where it usually leads to trunk girdling and death of the tree. Disease infection takes place through white pine needle stomata in the fall, grows into the branches and stems, and erupts as spore-producing cankers that kill the branches, thus ending cone production, and ultimately killing the tree (Bega 1978, Blanchard and Tatter 1997).

The first symptoms of white pine blister rust on white pines are yellow brown cankers that appear on infected pine branches (Figure 1.3). The fungus grows in the phloem and bark with no visible symptoms for at least three years before spores are produced. In the spring of the 3rd or 4th years, spermatia are formed, followed by the

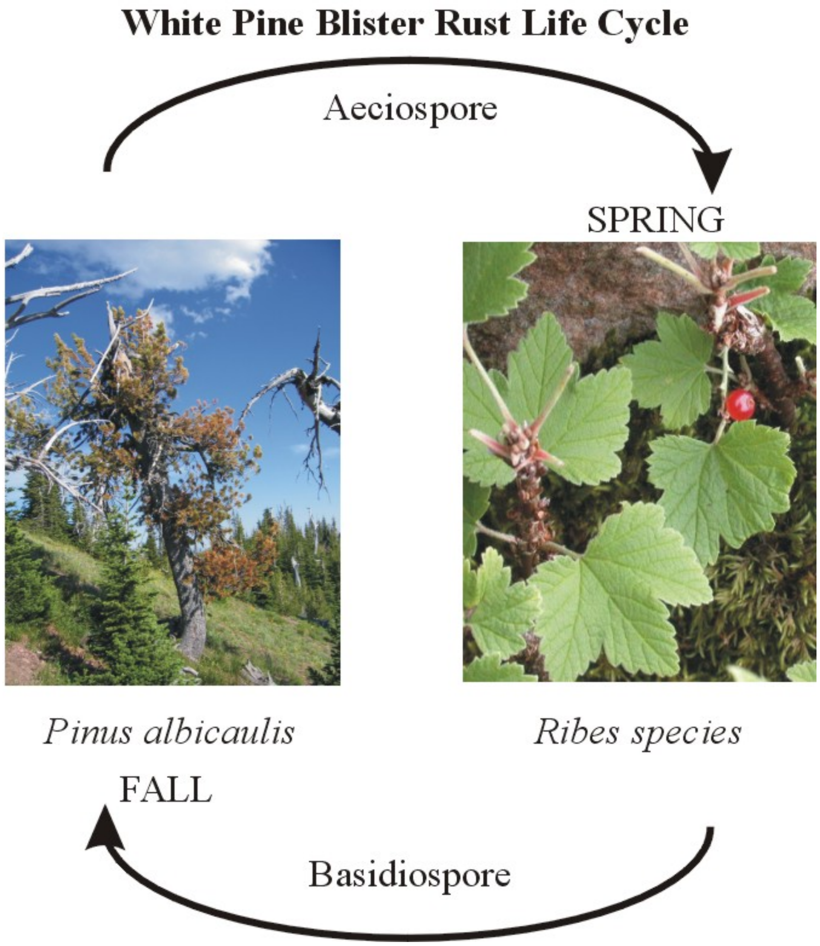

Figure 1.2. White pine blister rust life cycle (photographs taken by Saskia van de Gevel).

Figure 1.3. Yellow cankers caused by white pine blister rust evident on the bark of a whitebark pine tree (photograph taken by Saskia van de Gevel).

production of aeciospores in white blisters that break through the bark. Aeciospores, which can be wind-dispersed up to 1300 km, are capable of infecting only *Ribes* species. Approximately ten days after infection, urediniospores develop on the lower surface of *Ribes* leaves and continue to accumulate throughout the summer. Urediniospores are able to reinfect *Ribes* species, thus intensifying the disease on this host. In the fall, teliospores and basidiospores are produced on *Ribes* species and are dispersed to *Pinus* species, thereby completing the life cycle.

1.4.2 Blister Rust Resistance

The loss of whitebark pine trees from white pine blister rust has significantly reduced whitebark pine regeneration. Tomback *et al*. (2001) described the situation as being so grim that land managers are faced with several difficult decisions. If fire or cutting techniques are used to open the whitebark pine stands for regeneration, the few remaining whitebark pine trees may be an inadequate seed source. Clark's nutcrackers may also complicate the whitebark pine regeneration efforts because they could consume the limited supply of unripened seeds before the seeds ripen. Currently, a combination of using blister rust-resistant whitebark pine, prescribed fire, and silvicultural techniques is in use to conserve whitebark pine ecosystems (Tomback *et al*. 2001).

Exotic invasive species, such as white pine blister rust, have produced major changes in forest ecosystems (Salwasser and Huff 2001). Eradication of white pine blister rust has failed, but management actions can be used to change the severity of its effect on whitebark pine ecosystems. Increasing the level of genetic resistance is one option to reverse severe losses in whitebark pine caused by white pine blister rust. In areas where blister rust has infected and killed most of the whitebark pine, one or more trees often have no visible cankers, which suggests the possibility of genetically controlled resistance to blister rust (Hoff *et al.* 2001). Hoff *et al*. (2001) performed a test in 1989 to investigate the level of resistance to blister rust in whitebark pine seedlings in high mortality whitebark pine stands. The results suggested that surviving whitebark pine seedlings possessed usable levels of heritable resistance. The researchers proposed that the next step was to use seed collection, seed transfer, and gene conservation to incorporate the resistance genes into future generations of whitebark pine, with the limitation that whitebark pine material (seeds, seedlings, or pollen) be transferred no more than 80 km from the point of origin. However, land managers must consider that planting genetically-resistant whitebark pine seedlings could eliminate unknown desirable genetic qualities and variation (Salwasser and Huff 2001).

1.5 Mountain Pine Beetle Ecology

Mountain pine beetle outbreaks have killed millions of *Pinus* trees over thousands of square kilometers in the northern Rockies during the 20th century (Romme *et al.* 1986). The mountain pine beetle is the most destructive of the native biotic agents in mature *Pinus* forests in western North America (Safranyik and Carroll 2006). The major hosts for mountain pine beetle include, in addition to whitebark pine, ponderosa pine (*Pinus ponderosa* Douglas ex C. Lawson), lodgepole pine (*Pinus contorta* Douglas ex Loudon), and western white pine (*Pinus monticola* Douglas ex D. Don). Extensive mountain pine beetle outbreaks in the northern Rockies occurred between 1925 and 1935 and between 1970 and 1980 (Arno and Hoff 1989), and more recently in the early 2000s. The series of outbreaks that occurred from 1925 to 1935 in Idaho and Montana killed an estimated 1.4 billion lodgepole pines and vast numbers of whitebark pines (Safranyik and Carroll 2006). Extensive outbreaks in the western US and Canada during the late 1970s and early 1980s killed almost 2 million hectares of *Pinus* trees. A massive infestation, extending over 12 million hectares, also devastated lodgepole and whitebark pine stands in the northern Rocky Mountains and in central British Columbia in the early 2000s (Safranyik and Carroll 2006).

This native bark beetle constructs “J” shaped egg galleries in the infected tree’s inner phloem (Figure 1.4), and the larvae feed on the phloem tissue (Amman *et al.* 1989). The beetle galleries impede water and nutrient transport within the tree and can introduce a secondary pathogen, a blue staining fungus (*Ophiostoma* spp.) that clogs the sapwood of living trees (Kipfmueller and Swetnam 2002). The combination of beetle galleries and blue staining fungus girdles trees and cuts off nutrient flow, leading to the death of the tree. The beetles tend to selectively attack larger, older trees that have a thicker phloem. Because mountain pine beetle larvae develop within the phloem tissue of their hosts, large-diameter trees with their thicker phloem are the optimal resource for the beetle (Amman *et al.* 1989). Younger trees are usually not killed because they lack an adequate food supply for the beetles.

1.5.1 Mountain Pine Beetle Life Stages

The mountain pine beetle has four life stages: egg, larvae, pupa, and adult. All of the life stages occur behind the bark of the host tree with the exception of adult beetle

Figure 1.4. Mountain pine beetle J-shaped galleries on a whitebark pine log in the Beaverhead-Deerlodge National Forest (photograph taken by Saskia van de Gevel).

dispersal (Safranyik and Carroll 2006). Adult beetles construct egg galleries in the phloem of the tree in a direction parallel to the stem. Once female beetles have mated, they deposit their eggs (approximately 60 eggs per female) in niches cut in the sides of the galleries and cover them with boring dust. Larvae pass through four instar stages, each of which is separated by moulting. During the last instar stage, the feeding areas around the parental galleries are cleared of debris. The prepupal and pupal growth periods are passed in this chamber. Adults first appear pale and soft, until they become harder and turn a dark brown color before they emerge. Adult beetles range in length from 3.7 to 7.5 mm and have strong cylindrical bodies. Beetle populations normally have one generation per year. Temperatures affect the number of generations per year. During warm summers, parent adults may re-emerge to establish a second brood. In cooler summers, and at higher elevations, some or all of the brood may require two years to mature (Safranyik and Carroll 2006).

1.5.2 Mountain Pine Beetle Control

Several natural factors affect abundance of mountain pine beetles, including sub-zero winter temperatures, nematodes, woodpeckers, predaceous insects, and insect parasites. The current latitudinal and elevational range of mountain pine beetle is not limited by available host trees (Carroll *et al.* 2003). The potential of the mountain pine beetle to expand north and east has been restricted by climatic conditions unfavorable for brood development. Temperature and moisture are the two most important abiotic factors that affect mountain pine beetle development and survival (Thompson and Shrimpton 1984, Safranyik and Carroll 2006). For a mountain pine beetle outbreak to develop, two requirements must be met. First, a sustained period of favorable weather must occur over several years (Safranyik 1978), such as summer heat accumulation and winter minimum temperatures. In areas where summer heat accumulation is limited or where winter minimum temperatures are below a critical threshold, mountain pine beetle infestations cannot establish and persist (Safranyik and Carroll 2006). The second requirement for outbreak development is that an abundance of susceptible host trees must be present (Safranyik 1978). The physiological effects of temperature are important for establishing and regulating beetles' growth and development rates, cold-hardiness, and in determining survival. An increase in the number of infestations since 1970 in formerly climatically unsuitable habitats indicates that mountain pine beetle populations have expanded into high-elevation areas (Safranyik and Carroll 2006). Given the rapid colonization by mountain pine beetles of former climatically unsuitable areas during the last several decades, continued warming in the northern Rockies associated with climate change will allow the beetle to further expand its range northward, eastward, and toward higher elevations.

Direct mountain pine beetle control measures, such as cutting and burning infested trees, applying oil or chemical sprays, or thinning dense *Pinus* forests, were used for decades in many parts of western North America (Safranyik and Carroll 2006). In addition to thinning stands to reduce susceptibility, individual high-value trees were successfully protected by applications of pesticides to uninfested tree boles. However, the control techniques have been proven limited in *Pinus* forests because the outbreaks have occurred over large areas in short periods of time. Most control measures are now considered generally uneconomical, although beetle populations have been manipulated with pheromone technology to avoid outbreaks in some large *Pinus* stands (Bentz and Kegley 2005).

1.6 Dendroecology

Trees are dependable annual biorecorders of environmental processes during the Holocene in portions of North America (Brubaker and Cook 1983, Luckman and Kearney 1986, Luckman 1988, Benson *et al.* 2002, Barclay *et al.* 2006). In most geographic regions, climate patterns in any year cause a response by trees in the volume of wood the tree produces which varies the widths of tree rings. Changing year-to-year environmental conditions cause fluctuations in tree growth over time, which allow dendrochronologists to compare ring patterns in trees at the forest stand, landscape, and regional spatial scales. Crossdating uses the year-to-year fluctuations in tree growth by matching patterns of ring widths from one tree with corresponding patterns for the same years from another tree (Fritts 1976, Schweingruber 1988). Crossdating is possible because climate is largely a regional phenomenon, affecting trees within a geographic region in a similar way, so that related patterns of ring widths are produced among many trees. Dendrochronologists accurately assign calendar dates to tree rings by matching the sequence of tree-ring widths against a known reference chronology. Eventually, sequences from individual trees are combined into a reference chronology for a particular location, so that any new tree-ring samples collected can be crossdated against the reference chronology. Crossdating the chronologies of dead and living trees makes it possible to recreate forest landscapes on century and millennial scales (Grissino-Mayer 2001).

Furthermore, crossdating helps identify problematic rings, such as false rings (a dark band of cells within the ring that is not a true ring), and helps identify locally absent or discontinuous rings (produced when growth regulators do not reach certain points in the trunk of the tree), both of which could reduce the temporal accuracy of ecological reconstructions (Stokes and Smiley 1996, Grissino-Mayer 2001). To ensure a high level of confidence in the dates assigned to tree rings, dendrochronologists inspect both visual and statistical relationships to identify a probable match. Only after a tree-ring series has been accurately crossdated, both graphically and statistically, can calendar dates for the tree rings in a wood sample be assigned with annual resolution (Stokes and Smiley 1996, Grissino-Mayer 2001). Dendroecological techniques help evaluate the age structure and tree-growth patterns to document changing stand conditions related to disturbance, stand development, or climatic variation (Payette *et al.* 1990, Foster *et al.* 1996). Such analyses can also help assess relationships between climate, site conditions, and tree growth to evaluate factors that influence the growth of a plant community (Cook and Kairiukstis 1989).

The longevity of whitebark pine trees provides an opportunity for temporally extensive tree-ring reconstructions of past disturbance regimes and ecological events. In addition, the sensitivity of many subalpine species to changes in their environment suggests whitebark pine may also be an excellent indicator of global climate change (LaMarche and Stockton 1974, Fritts 1976, Perkins and Swetnam 1996, Luckman and Youngblut 1999, Kipfmueller 2003, Mann 2008). The annual nature of tree-ring formation and the ability to statistically link tree growth with climate are important tools for understanding climate variability on a temporal scale (Kipfmueller 2003).

1.6.1 Northern Rocky Mountains

Dunwiddie (1977) was the first dendrochronologist to study whitebark pine. He investigated tree invasion of a subalpine meadow in the Wind River Mountains of western Montana. He dated approximately 340 trees and saplings of whitebark pine, lodgepole pine, and Engelmann spruce in a 13 m by 8 m plot that extended along a clear edge of mature forest, to determine the age and growth trends within the samples. Tree growth rates increased with increased distance from the forest edge, which indicated that factors other than climate may have restricted tree regeneration within the meadow. Tree invasion was slow and relatively steady between 1889 and1940, after which a significant acceleration in tree establishment rates occurred until a sudden cessation of establishment after 1962. When compared to the grazing records, meadow invasion increased slightly when the area was heavily grazed, and the shift to rapid invasion occurred when grazing pressure was reduced, but still present on the landscape. Cattle were removed from the landscape in the early 1960s. Grazing facilitated the establishment of young trees by removing competition with meadow vegetation. With the complete removal of cattle from the area, seedlings could no longer out-compete the meadow grasses and shrubs, and trees could not become established.

Arno (1976) developed tree ring-based fire histories for study areas in the Bitterroot National Forest in western Montana. The study areas covered a wide range of elevations and forest types. He used non-crossdated fire-scarred samples collected from living trees and age-structure data to describe the frequency and severity of fires in the Bitterroot Mountains. Arno mentioned that numerous whitebark pine trees in the study area contained multiple fire scars. Age structure data were relatively uneven-aged, but still indicated post-fire tree establishment cohorts. He emphasized the spatial variability in the fire regimes of the study areas, and suggested mixed-severity fires played a more important role in the northern Rockies than was previously recognized. Fire activity and instrumental meteorological data were compared and showed a correlation between drought conditions and years of widespread fires. Arno concluded that fire has and will continue to be a major ecological component of forests in the Bitterroot National Forest and suggested several management techniques for reducing fuel loads and maintaining forest health. Arno and Pederson (1983) later used these results and reanalyzed them spatially to emphasize the importance of using the appropriate scale when reporting results of fire history research.

Romme (1982) examined the diversity and evenness of species after fires in a subalpine watershed in Yellowstone National Park, Wyoming. Romme found 15 fires since 1600, seven which were major fires that burned more than four ha, and initiated secondary forest succession. Although whitebark pine was only a small component of the subalpine forest, many of the whitebark pines showed multiple fire scars. Most of the upland forest area was burned by large fires in the middle and late 1700s. Fires in the 1800s and 1900s were smaller and occurred at longer intervals. Fire frequency in the Yellowstone study area is partly controlled by fuels in the understory and forest floor. Typically, fuels capable of supporting a crown fire usually do not develop until a stand is over 300 years old. Therefore, fire ignitions in younger stands usually extinguished naturally before spreading more than a few hectares. Crown fires became more likely whenever lightning ignites small fuels during warm, dry, windy weather. The subalpine plateaus of Yellowstone National Park had a natural fire cycle between 300 and 400 years when large areas burned during a short period, followed by a long, relatively fire-free period. Landscape diversity was highest in the early 1800s, which followed the large fires in the 1700s, then declined in the late 1800s during a 70-year period when no major fires occurred and the landscape was dominated by even-aged forests. Romme interpreted these landscape reconstructions to indicate that the Yellowstone subalpine ecosystem is a nonsteady-state system characterized by long-term disturbance regimes that changed landscape composition and diversity.

Mattson and Reinhardt (1990) also examined the fire history of subalpine forests in the Greater Yellowstone Ecosystem. They evaluated stands using aerial photographs, age-structure, stand composition, and site characteristics in 5–26 variable radius forest inventory plots evenly distributed throughout each stand. The fire history was derived from stand age-structure and indicated a MFI of 80–300 years. The distribution of whitebark pine was closely related to a site warmth index, as opposed to subalpine fir and Engelmann spruce that were more sensitive to wind exposure. Whitebark pine and lodgepole pine were highly competitive where they coexisted, gained early dominance of most stands, and eventually lost stand dominance to shade-tolerant fir and spruce. Extremely cold and exposed sites were dominated by whitebark pine.

Barrett (1994) investigated the fire history of three forest types on the Absaroka Mountains in the northeast corner of Yellowstone National Park. Fire-scar and age structure data were gathered in low-elevation Douglas-fir forests, mid-elevation lodgepole pine forests, and high-elevation whitebark pine forests, and composite fire chronologies were constructed for all sites. The MFI was over 350 years in most whitebark pine forests. Barrett noted, however, that several whitebark pines contained multiple fire scars, and that tree age was highly variable in whitebark pine stands, indicating a mixed-severity fire regime. Four stands of whitebark pine at treeline experienced MFIs of 66–204 years. Fire suppression had not influenced high-elevation whitebark pine ecosystems.

Keane *et al.* (1994) conducted a landscape assessment of the effects of blister rust and fire suppression on whitebark pine forests in the Bob Marshall Wilderness Complex, Montana. The study combined satellite imagery with field reconnaissance and stand data to evaluate the disturbance history and recent shifts in whitebark pine populations. The fire history was determined using non-crossdated, fire-scarred samples and age-structure data. Blister rust infections were identified on 83% of the 32 inventoried whitebark pine, and high mortality rates due to blister rust were reported for 22% of the landscape containing whitebark pine. The study documented little to no whitebark pine regeneration. Subalpine fir dominated 14% of the total subalpine landscape, approximately 7% more than its historical composition. Regeneration throughout the study area was almost exclusively subalpine fir. Fire suppression and the blister rust-induced mortality of whitebark pine allowed subalpine fir to establish throughout the Bob Marshall Wilderness Complex.

Morgan and Bunting (1990) crossdated 14 fire-scarred samples and found MFIs of 13–46 years for whitebark pine forests on Russell Peak, Wyoming. The fire history showed a period of frequent fire activity between 1700 and 1850 that corresponded with the establishment of a large cohort of whitebark pine. Fire activity began to decrease after 1850, and the last fire occurred in 1894. Morgan and Bunting hypothesized that whitebark pine forests burn often when young with abundant fine fuels under an open canopy, go through a period of relatively infrequent fires as the canopy closes, and then burn in old age as fuel loads develop. Subalpine fir encroachment and insect-caused mortality also contributed to fuel loading.

Perkins and Swetnam (1996) successfully built a whitebark pine tree-ring chronology over 1000 years in length, and while they found their samples difficult to date, they suggested that whitebark pine could be used to relate disturbance regimes and climate on a multi-millennial scale. They constructed tree-ring chronologies from four sites in central Idaho that all extended at least 700 years, and included the oldest known living whitebark pine at the time (> 1270 years old). Crossdating with other tree-ring chronologies from the region was problematic due to relatively low inter-annual ring-width variability (chronology mean sensitivity ranged from 0.12–0.17), but the authors succeeded by using several distinct marker rings. Correlation coefficients within and between sites ranged from 0.5–0.6, which indicated strong statistical crossdating for high-elevation trees. The peak mortality caused by a mountain pine beetle outbreak was determined by the outer ring of sampled snags to be 1930, and was synchronous at all four sites.

Murray *et al.* (1998) reconstructed the fire history of subalpine forests of the West Big Hole mountain range to determine if their isolated study area would be more affected by fire suppression than larger mountain ranges. The study area straddles the Continental Divide along the southwestern border of Montana and Idaho and includes six watersheds, three to the east and three to the west of the divide. Fire-scar and age-structure data were collected in plots centered along a transect from the base to the head of each watershed. Fire dates were estimated to be accurate within 10 years. Fire history data extended back to 1754 for all sites. West side historical fire regimes were classified as mixed-severity and smaller relative to the more widespread, non-stand-replacing fires that characterized the east side fire regimes. A dramatic shift toward smaller fires occurred on both sides of the divide in 1874, with west side fires shifting toward non-stand replacing and east side fires becoming more mixed-severity. The authors suggested that fire suppression was not likely the cause of these landscape level changes, but that the widespread introduction of cattle and sheep may have reduced fuels sufficiently to affect the fire regimes of the area. Compared to larger mountain ranges, fires in the West Big Hole area were generally smaller and more frequent, due to a concentration of lightning strikes and close proximity of the range to steppe communities.

Murray *et al.* (2000) used data from their 1998 study to compare over 200 years of whitebark pine growth to successional trends in six areas of the West Big Hole mountain range. The authors found a decrease in whitebark pine dominance that they attributed to successional replacement by fire-intolerant species, grazing, and fire suppression. Size class and species composition data were collected along an elevational transect in each watershed, and species dominance was calculated at 20-year intervals using ring-width-derived basal areas for distinct size classes. Mid-seral forests dominated all six watersheds until 1950, when late-seral stands became more dominant on the landscape. Overall, an 85% increase in basal area was found among all species since the 1870s, while whitebark pine dominance had decreased steadily over the same period. The authors suggested fire suppression and grazing may be the cause of advancing succession, and proposed active management may be required to maintain the historically whitebark pine dominated structure and composition of this landscape.

Kipfmueller (2003) conducted a fire history of subalpine forests that contained whitebark pine, and examined the fire-climate relationships in four watersheds in the Selway Bitterroot Wilderness Area, on the border between Montana and Idaho. Fire dates were obtained from 96 crossdated fire-scarred samples collected from lodgepole pine, whitebark pine, and Douglas fir, and fire extent was estimated using stand boundaries coupled with stand age-structure data. The fire history data illustrated mixed-severity fire regimes in all four watersheds, with numerous small fires and seventeen widespread fire years identified over the past 800 years. MFI values ranged from 20–170 years at the watershed scale to 139–341 years for individual stands. A reduction in fire activity occurred across all four sites *ca.* AD 1935, and was likely the result of fire suppression. Superposed epoch analyses (SEA) were used to assess the influence of climate prior to the fire events, and revealed a significant relationship between two consecutive dry years and widespread fire events.

Kipfmueller and Kupfer (2005) analyzed over 1,100 tree cores from 23 stands in four watersheds to better understand successional processes in subalpine forests for establishment patterns after fires. The data for this study came from Kipfmueller's (2003) dissertation work in the Selway Bitterroot Wilderness Area, on the border between Montana and Idaho. Successional changes were quantified by using the time-since-fire to determine the length of time the stand developed without fire as a disturbance. Stand composition and structural traits were compared using nonmetric multidimensional scaling and ordination with respect to environmental variables, including time-since-fire, topographic relative moisture index, slope, aspect, and elevation. The authors created a conceptual model of the multiple successional pathways that are evident in the study sites. Whitebark pine was the most important tree species in the overstory in only two of the 23 sites. Surprisingly, whitebark pine was an important species in the understory of two other sites with lodgepole pine as the most important associated overstory species. The authors found lodgepole pine dominated sites after fire events, but as the stand aged, other disturbance events altered succession through host-specific mortality. In the absence of stand-initiating disturbance over long periods of time, whitebark pine historically had a chance to dominate the forest canopy. Whitebark pines were present in old stands, but many were dead from mountain pine beetle outbreaks in the 1930s and 1980s.

Bunn *et al.* (2003) compared strip-bark and entire-bark high-elevation whitebark pine trees in the Greater Yellowstone Ecosystem. Their dataset contained 27 pairs of strip-bark and entire-bark trees, and allowed direct comparisons of the influence of tree growth form on tree-ring growth rates over time and space. The authors conducted a temporally and spatially explicit analyses of tree locations and growth rates related to the abiotic environment. After finding spatial structure to the strip-bark tree distribution, they assessed the relationship between environmental variables and presence or absence of strip-bark trees using a spatially explicit regression. Growth patterns of the strip-bark trees were compared to neighboring entire-bark trees. The whitebark pine samples showed the complexity of climate-growth relationships within a species and demonstrated the importance of considering tree physiognomy and microsite variation in developing climatically sensitive tree-ring chronologies. Time-series plots were constructed from the 15 datable strip-bark chronologies and their neighboring entire-bark trees showed nearly identical growth rates and coherent trends until 1875. The strip-bark time series also showed a consistent pattern of postindustrial increased growth rates similar to studies in the White and Sierra Nevada Mountains of California.

Larson (2005) and Larson *et al.* (2008) created an extensive fire history for three mountains in the Lolo National Forest. The three sites differed significantly in fire regimes, topography, and local climate. Fire suppression was evident after *ca.* 1920, although tree establishment at the sites was related to major fire events that occurred in the late 1800s. The fire regimes of each site were considered mixed-severity fire regimes, but distinct differences in fire frequency and severity existed between them. The forest on one of the sites, Point Six, was outside of its historical range of variability and may provide a suitable site for a prescribed burn. The forests on Morrell Mountain and Mineral Peak remained within their historical ranges and likely do not warrant management intervention at this time. All three sites contained at least one post-disturbance tree establishment cohort and had experienced at least one widespread fire over their histories.

Grissino-Mayer *et al.* (2006) and Daniels *et al.* (2006) used dendroecological methods to assess whitebark pine fire and disturbance histories during the 13th Annual North American Dendroecological Fieldweek on Morrell Mountain in western Montana. Grissino-Mayer collected 21 fire-scarred whitebark pine samples and found a fire return interval approximately every 50 years. Daniels found living whitebark pine over 500 years old but many of the whitebark pine had died from mountain pine beetle and white pine blister rust. The basal area increment of living whitebark pine trees significantly decreased between 1951 and 2000. Some subalpine fir trees were over 300 years old, suggesting that a stand-replacing fire had not burned that site in the past 300 years.

Mann (2008) reconstructed climate and assessed the effects of climate variability on specific environmental processes in the subalpine ecosystem of western Montana using whitebark pine and subalpine fir. This study also examined the climate response of whitebark pine and subalpine fir to treeline dynamics and fire history. Trees in excess of 400 years of age were found at the western Beaverhead, Gravely Range, and Mineral Peak sites. Numerous deadwood remnants of whitebark pine were also found at all sites. The most long-lived tree in all chronologies was obtained at the western Beaverhead site and contained 607 rings.

The growth response of whitebark pine and subalpine fir to PDSI was more significant than the growth response to precipitation and temperature. The author found the most significant relationship between whitebark pine growth and PDSI found in the previous year's June and July. The PDSI indices were strongly correlated to growth from June to August, with July having the highest correlation. Drought conditions late in the previous year (August-September) affected bud break and the initiation of growth more than climate during the current year's growing season. The reconstructed June–July PDSI revealed both interannual and decadal trends for the period 735–2005. Since AD 750, eight periods of protracted extreme drought and five periods of extreme wetness have occurred. The most severe extended drought occurred between 1434 and 1462, a period that had an average PDSI of –2.21 for the 28-year period. Two additional periods of extended drought, AD 1145–1167 and AD 764–782, lasted 23 and 19 years, respectively.

In terms of wetness, the most extreme period and longest in duration occurred between AD 894 and 918.

1.6.2 Sierra Nevadas/Cascades

Peterson *et al.* (1990) conducted a dendroecological assessment of long-term growth trends in the subalpine forests of the central Sierra Nevada. They focused on high-elevation lodgepole pine and whitebark pine because these trees were sensitive to small changes in the environmental factors that impacted their growth. The study examined changes in basal area of each species, calculated from ring widths, for the late 1700s up to the 1980s. Principle components analyses found climate explained between 22−40% of the variance in basal area for whitebark pine, depending on age class. Climate-response analyses found tree growth was significantly affected by spring temperature and annual precipitation. A trend of increasing basal area at an increasing rate, independent of climate, was found in the whitebark pine chronologies, similar to patterns of increased growth found in Great Basin bristlecone pine (*Pinus longaeva* D.K. Bailey) in the nearby White Mountains (Graybill and Idso 1993). The authors suggested a possible effect of atmospheric CO_2 fertilization on growth in upper-elevation trees.

Garfin (1998) used whitebark pine tree-ring data to examine the relationship of shifting pressure systems and tree growth in the Sierra Nevada of California. He found winters that preceded years of high growth in whitebark pine were warm and wet, caused by anomalously low pressure in the northern Pacific Ocean, anomalously high pressure over northwestern Canada, and anomalously low pressure across the southern United States, all of which leads to a southwesterly flow of warm maritime air into

California. Extreme low growth in whitebark pines was associated with a shift in the Westerlies north of their mean position and enhanced ridging in the northeast Pacific, which advects cool dry air into the Sierra Nevada. Garfin concluded that synoptic dendroclimatological studies such as his may provide insight about atmospheric circulation that will increase understanding of past climate variability derived from tree-ring studies.

Millar *et al.* (2004) is the only whitebark pine study to examine annual branch growth of krummholz whitebark pine in the Sierra Nevada. The authors studied whitebark pine establishment on formerly persistent snowfields and dated vertical branch emergence in krummholz whitebark pine. Mean annual branch growth at six treeline sites increased significantly over the 20th century (ranged 130–400%), with significant accelerations in rate from 1920 to 1945 and after 1980. Growth stabilized from 1945 to 1980. Similarly, invasion of six snowfield slopes began in the early 1900s and continued into snowfield centers throughout the 20th century, with significantly accelerated mean invasion from 1925 to 1940 and after 1980. The lack of new vertical branches growth after 1980 and the death of seven vertical branches around 1980 showed unfavorable growing conditions in the Sierra Nevada. All ecological responses were significantly correlated with minimum temperature fluctuations.

1.6.3 Canadian Rockies

Luckman *et al.* (1984) was the first to document several whitebark pines with ages in excess of 700 years in the Canadian Rockies. Luckman followed his preliminary assessment with several projects that used evidence obtained from subalpine tree species to describe periods of glacial advance in the Canadian Rockies (Luckman 1994, 1995, 2000). Luckman examined the fluctuation in glacial advance and retreat during the Neoglacial period, when glaciers were at their Holocene minimum. Studies of Holocene glacial activity have shown that the Neoglacial period was asynchronous, with advances ranging from 8,000 B.P. (Denton and Karlen 1973) to 3,000 years B.P. (Luckman *et al.* 1993). Luckman found glaciers throughout the region were advancing down valley between 3,300 and 2,800 years ago. Following this advance, most glaciers appear to have retreated up valley and may have only begun to readvance during the Little Ice Age (LIA) glacial events of the last 900 years (Luckman 1986, 1993, 1995, 2000).

In studies within the southern Canadian Rockies, exposed stumps have been used to distinguish Holocene glacial advances by crossdating floating tree-ring series to living tree-ring chronologies (*e.g.* Luckman 1995, Smith and Laroque 1996) or by assigning 14C dates to perimeter wood samples (Luckman 1996, 1998). Luckman used establishment dates of tree stands on moraines to estimate the date of glacial advance and retreat. Remnant and sub-fossil trees and stumps were also crossdated to construct death-date charts, thereby giving an estimate of both the timing and rate of glacial advance. These data were synthesized and compared to reconstructions of temperature and precipitation. They provided evidence of region-wide glacial advances during 1200−1300 and 1400−1600, and abundant evidence of regionally synchronous advances in the early 1700s and early 1800s (Luckman and Villalba 2001). Summer temperature was the primary driver of these fluctuations, but precipitation also played a strong role in some areas. Luckman also directed research on extending chronologies throughout the

Canadian Rockies, and eventually found two whitebark pine trees that were at least 1,013 and 1,049 years of age (Luckman and Youngblut 1999). The vegetation of the Columbia Icefield area, in the Canadian Rockies, was characterized by subalpine forests and expansive alpine tundra, with most valley bottoms characterized by Engelmann spruce and lodgepole pine forests. Restricted stands of subalpine fir, whitebark pine and krumholtz spruce characterized treeline (Luckman and Kavanagh 1998, 2000, Luckman and Youngblut 1999).

1.7 Fire Regimes in Whitebark Pine Ecosystems

Research shows that the whitebark pine ecosystem experiences both stand-replacing fires, which occur at long intervals and initiate forest succession, and low-severity surface fires, which occur throughout stand development and suppress the establishment of fire-intolerant species (Arno and Peterson 1983, Larson 2005). Studies focused on frequent, low-severity fires have found that active fire suppression and grazing in the late 1800s and early 1900s led to decreased fire activity (*e.g.*, Kilgore and Taylor 1979, Dieterich 1983, Barrett 1994, Touchan *et al.* 1995, Grissino-Mayer *et al.* 1996, Swetnam and Betancourt 1998, Grissino-Mayer *et al.* 2004) and resulted in dramatic increases in forest density and fuel loads (Brown and Wu 2005). Other researchers highlight the important role of climatic variations as a source for recent changes in fire activity (Mast *et al.* 1998, Schoennagel *et al.* 2005, Sibold *et al.* 2006). Regardless of the source of these changes, the recent increases in large wildfire activity (Stephens 2005, Westerling *et al.* 2006) have amplified pressure on land managers in the western United States to implement thinning practices, prescribed fire programs, and wildland fire use programs to restore the historical structure and disturbance processes to forests. The term “restoration” should be used carefully because comparing current wildfire activity with the historical range in variability of wildfires in these forest systems is complicated. Forests are affected by many ecological processes in addition to the influence of humans and climate on their fire regimes (Larson *et al.* 2008).

1.8 Climate Change in the Northern Rocky Mountains

Climate change assessments based on computer models, paleoecological studies of past climatic conditions, and small-scale experiments suggest extensive disruptions of most ecological communities occurring under generally accepted future climate scenarios (McCarty 2001). Atmospheric CO_2 levels will most likely double from preindustrial values within 100 years (Korner *et al.* 1996). The doubling of CO_2 and other greenhouse gases could increase average temperatures 1.4–5.6 °C, which will affect precipitation patterns, soil moisture, snow and ice cover, and other environmental variables (IPCC 2001). The Earth’s mean global temperature has increased 0.6 ºC since 1900, and the rate of warming has varied, occurring most rapidly between 1925 and 1944 and between 1978 and 2004 (Walther *et al.* 2002). Temperature changes vary geographically and tend to be greatest during the coldest months (McCarthy 2001). Temperature records developed from valley floor meteorological stations in the Canadian Rockies indicate that significant temperature differences occur between seasons (Luckman and Kavanagh 2000). Winter (January–March) conditions show the largest interannual range (12.7 °C) and the greatest warming trend (3.4 °C per 100 years) rather than the spring and summer

(Luckman and Kavanagh 2000). The differences in seasonality are important because most proxy climate records use biological indicators that respond primarily to growing season conditions.

Climate changes more rapidly with elevation (about 1 °C per 160 m) than with latitude (about 1 °C per 150 km)(IPCC 2001), so rapid changes in mountain communities are expected as climate continues to warm (McCarty 2001). Treeline advances upslope in response to climate warming have been observed in mountain vegetation studies (Prentice 1992, Mann 2008), but site (*e.g.* aspect) and species differences influence the rate of advance (Luckman and Kavanagh 2000). The effects of global and regional climate changes on vegetation will be moderated by microclimate effects, local topography, and site conditions (Luckman and Kavanagh 2000). Asymmetry in warming between regions will contribute to the heterogeneity in ecological responses across systems (Walther *et al.* 2002). Climate will change over a few decades while the response of many species might take centuries. The modern fragmented landscape provides little flexibility for ecosystems to adjust to rapid climate changes (Walther *et al.* 2002). Areas that may become climatically suitable to support species may be too disjunct or remote from their current distributions for successful dispersal. Integrating species' responses to land use and land cover changes, the effects of CO_2 fertilization, and the effects of climate change, are important when assessing the resiliency of complex ecosystems, such as whitebark pine.

The highly irregular topography of the northern Rocky Mountains results in a wide range of weather conditions, as well as unique microclimates. Terrain ranges from rugged ridges and glacial features to gentle slopes. Mountains in the northern Rockies are influenced by North Pacific weather patterns and are located in a transitional zone between continental and maritime climates (Arno and Hammerly 1984). Continental atmospheric patterns likely affect the relationship between the ecology of mountain pine beetles, white pine blister rust, and whitebark pine growth. The interacting feedbacks between these variables and climate are important for understanding changing fire regimes in whitebark pine ecosystems. One of the most widespread concerns of global warming on whitebark pine ecosystems is an overall reduction in area, with a loss of disjunct whitebark pine communities (Haslett 1997).

Instrumental climate records are limited in length, therefore proxy climate data, such as from tree rings, have been useful in extending precipitation and temperature records (Woodhouse 2001). Perkins and Swetnam (1996) used climate-response analyses with whitebark pine and found a similar signal among their four sites in Idaho, with a positive correlation between ring width and winter/spring precipitation, and a negative correlation between ring width and summer (May–July) temperatures, indicating tree growth at these sites is both moisture and temperature limited. The study concluded that whitebark pine has excellent potential for dendroclimatological and dendroecological research.

Biondi *et al.* (1999) used tree ring data from whitebark pines (Perkins and Swetnam 1996) and Douglas firs, to develop an 858-year proxy record of July temperatures for east-central Idaho. The correlation of their proxy series with instrumental July temperatures was 0.47 (1895–1992) with this value improving to 0.55 when the 1895–1903 period was removed.

Kipfmueller (2003) found his whitebark pine chronologies correlated to temperature, snowpack conditions, and PDO. Whitebark pine growth was significantly related to warm July temperatures, but a potential climate switch was identified in the mid 1900s, when the response of whitebark pine to warmer summer temperatures diminished and was replaced by a negative relationship to spring temperatures. Kipfmueller hypothesized that this shift may be related to changing snow pack conditions and resulting moisture stress, and is potentially an expression of shifting PDO signal. Despite the shifting climate-tree growth relationship, the climate reconstruction of the whitebark pine chronology explained 36% of the variance in summer temperature over the calibration period.

Luckman and Wilson (2005) used tree-ring data from Engelmann spruce to reexamine summer temperatures (May–August) in the Canadian Rockies for the last millennium. The maximum temperature reconstruction, which explained 53% of the variation, revealed warm intervals during the first half of the eleventh century, the late 1300s, and the early 1400s. A portion of the reconstruction, however, showed below-normal temperatures for the period between 1901 and 1980, with prolonged cool periods between 1200 and 1350 and between 1450 and the late 1800s. The most extreme cool period was observed in the late 1690s. The reconstructed cool periods agreed with regional records of glacial advances between 1150 and the 1300s, and in the early 1500s, early 1700s, and 1800s.

Wilson *et al.* (2007) studied temperature divergence between cooler reconstructed and warmer instrumental large-scale temperatures in the Extratropical Northern Hemisphere (ENH). They hypothesized that the temperature divergence in the 1980s is partly related to chronologies used from previous reconstructions that showed divergence against local temperatures in the recent period. The authors only used tree-ring data and published local/regional reconstructions that showed no divergence against local temperatures. One of the datasets used in the reconstruction was a whitebark pine summer temperature reconstruction from Idaho (Biondi *et al.*1999). The authors found that these correlations were generally consistent back into the 19th century (r = 0.41, 1868–1992). The tree-ring proxy time series were chosen because they showed relatively robust estimates of local/regional temperatures, showed no divergence in the recent period with the instrumental records, and allowed replication up to the year 2000 in the final reconstructed time series. The authors hypothesized that the use of tree-ring based proxies that show no divergence at the local-scale could result in better estimates of hemispheric temperatures in the recent (post-mid-1980s) period where all other tree-ring based ENH hemisphere reconstructions diverge below the increasing trends in the instrumental data. The authors developed a new, completely independent reconstruction of ENH annual temperatures from 1750 to 2000.

1.9 Objectives

Knowledge of the complex dendroecology and stand dynamics of whitebark pine ecosystems is essential to the long-term management and conservation of this declining foundation species. The primary objectives of my research are to:

1. Construct whitebark pine tree-ring chronologies from long-lived trees and subfossil wood from six mountains in the Beaverhead-Deerlodge, Lolo, and Flathead National Forests, in western Montana.

2. Analyze the relationship between climate and whitebark pine growth.
3. Reconstruct climate variables using the whitebark pine chronologies.
4. Compare climate with fluctuations in tree growth associated with disturbance events.
5. Reconstruct the age structure of whitebark pine forests in the Beaverhead-Deerlodge, Lolo, and Flathead National Forests.
6. Assess the successional status of subalpine fir and Engelmann spruce in subalpine areas historically dominated by whitebark pine.
7. Compare the long-term impacts of human-related (climate change, fire-suppression and the introduction of white pine blister rust) and natural (mountain pine beetle) disturbances in the Beaverhead-Deerlodge, Lolo, and Flathead National Forests.
8. Compare tree growth patterns in whitebark pine and subalpine fir chronologies from the Beaverhead-Deerlodge, Lolo, and Flathead National Forests.
9. Determine whether distinct spatial and/or temporal patterns exist in the disturbance regimes of these forests locally, at the individual site level, and regionally, by comparing and contrasting the sites with each other.
10. Compare methods in dendroecology to distinguish suppression and release patterns in whitebark pine growth related to landscape-level disturbance events.

1.10 Organization of the dissertation

The remainder of my dissertation consists of five chapters. In Chapter 2, I provide site descriptions, geologic history, and land-use history of the six study sites in the Lolo, Flathead, and Beaverhead-Deerlodge National Forests in western Montana. In Chapter 3, I compare six whitebark pine chronologies developed from the study sites to evaluate landscape level trends on a multicentury scale. I separate the tree-ring variance explained by disturbance regimes and climate changes in the whitebark pine chronologies. The tree-ring data from the Lolo, Flathead, and Beaverhead-Deerlodge National Forests are analyzed separately, but comparisons are made between them to examine the spatiotemporal scale of disturbance events in the whitebark pine ecosystem. Chapter 4 provides an in-depth comparison of whitebark pine and subalpine fir chronologies from three study sites: Morrell Mountain in the Lolo National Forest, Ajax Peak in the Beaverhead-Deerlodge National Forest, and Hornet Peak in the Flathead National Forest. I examine growth suppression and release events caused by climate, white pine blister rust, and mountain pine beetle. Resulting forest composition and structure changes are statistically analyzed and discussed. Chapter 5 focuses on the relationship between drought and mountain pine beetle outbreaks. I statistically analyze the relationship between mountain pine beetle outbreaks with climate factors (temperature, precipitation, and PDSI). I summarize the major finding of my dissertation in Chapter 6 and suggest recommendations for future research. The Appendices contain details of chronologies developed from the dendroecological samples.

CHAPTER 2

DESCRIPTION OF THE NORTHERN ROCKY MOUNTAINS

2.1 The Northern Rocky Mountains

The Northern Rocky Mountains are characterized by generally north to south-oriented mountain ranges separated by wide flat valley floors. Weather conditions are affected by slope and aspect along the Continental Divide, becoming progressively cooler and more humid from lower to higher elevations. Climatic zones range from the semiarid and relatively warm valley bottoms through a range of cool, moist conditions in the middle elevations, to the cold, moist subalpine and alpine region characterized by bedrock escarpments, talus slopes, and glacial features from the Pleistocene epoch (Arno and Hammerly 1984, Overbay 1986). The topographic variety in the northern Rockies facilitates the development of diverse plant and animal communities (Figure 2.1).

2.1.1 Geology and Soils

Tectonic forces elevated the Rocky Mountain area during the Laramide orogeny in the Late Cretaceous, approximately 40–70 million years ago (mya), and also caused the differential uplift of individual mountain ranges (Johns 1970, Peterson 1986). The mountain-building process formed collinear folds and subparallel faults that run throughout the northern Rockies. Although tectonic activity had its greatest impact on the Northern Rocky Mountains during the Late Cretaceous, folding and faulting still occur today on a much smaller scale.

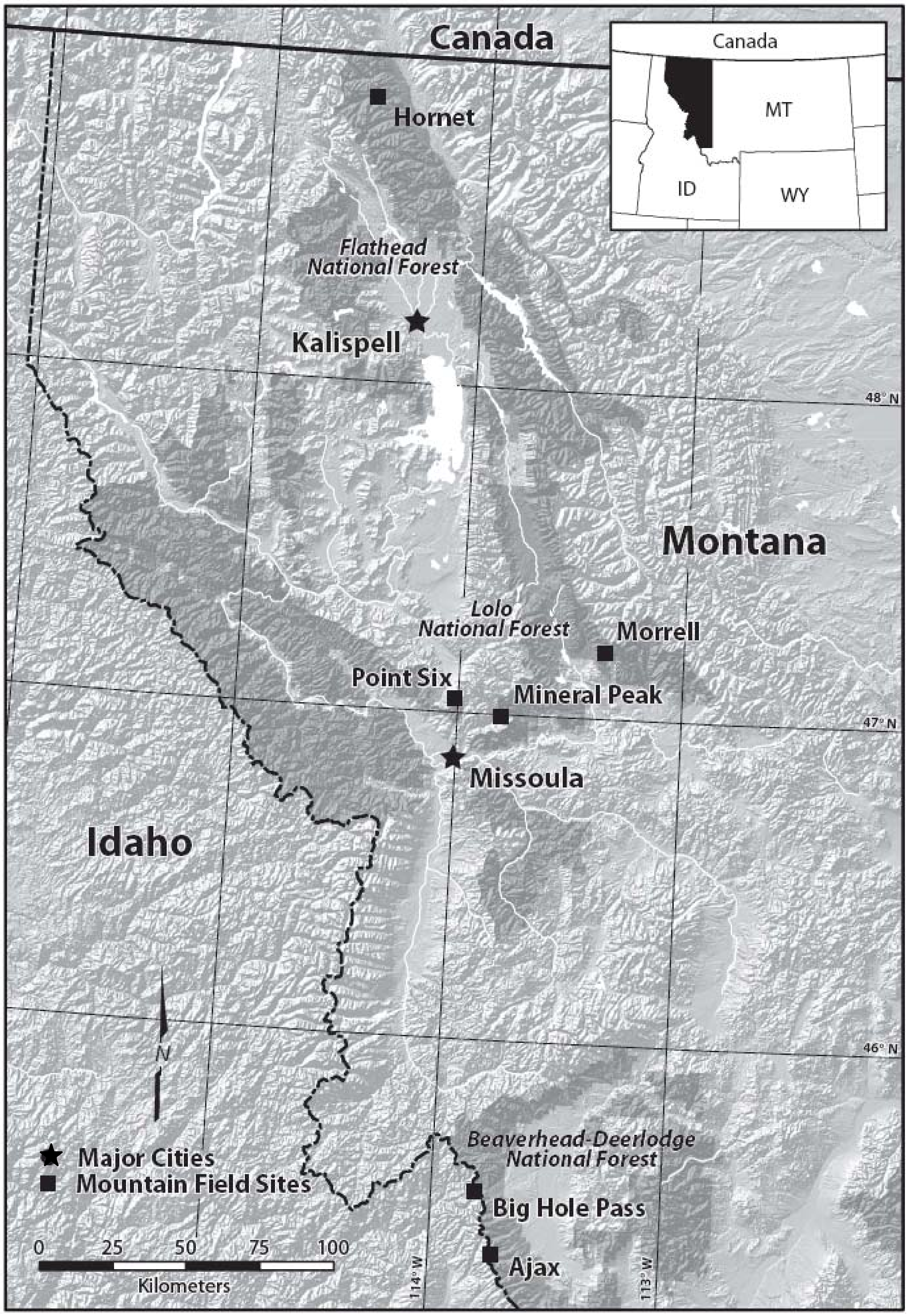

Figure 2.1 Terrain map of western Montana. The Continental Divide is marked by a black dashed line. Map produced by Tracy Pollock, from the University Of Tennessee Department of Geography Cartographic Laboratory.

The ice advance of the Wisconsin glaciation, which ended approximately 10,000 years ago, removed evidence of earlier glaciations (Johns 1970). The Cordilleran ice sheet entered Montana from Canada as individual lobes that filled the valleys, but at its glacial maximum, ice covered most of western Montana. Alpine glaciers merged with the Cordilleran ice sheet during the glacial advance. The advance and retreat of the glaciers were irregular and experienced relatively brief reversals. At the Montana/Canadian boundary, the ice reached a maximum altitude of over 2200 m (Daly 1912). Cirques, U-shaped valleys, moraines, and mountain lakes are the most common glacial features visible today in the Northern Rocky Mountains.

The Precambrian Belt, consisting of mainly quartzites and argillites, is evident in the surface geology of northwestern Montana (Pfister *et al.* 1977). The Bitterroot Range west of the Bitterroot Valley, the Sapphire and Anaconda-Pintlar Ranges, and the Continental Divide from Butte to Helena are comprised of the Idaho and Boulder Batholiths. The Continental Divide area is the most geologically complex area of the northern Rockies (Perry 1962). Composition of the batholiths is predominantly granitic with inclusions of schist and gneiss. The remainder of the mountains in the Montana Rockies consists of volcanic and sedimentary rocks (Pfister *et al.* 1977). The valleys contain a thick layer of alluvium deposits from streams and past glaciations.

Montana forest soils are rocky and prone to erosion from wind and water. In high-elevation sites in the Montana Rockies, Cryochrepts (well drained with moderately rapid permeability and slow runoff) are the major soil subgroup (Pfister *et al.* 1977). The Typic Cryochrepts are the most common, although thick deposits of volcanic ash in some areas form Andic Cryochrepts (Nimlos 1963). These soil types are generally found in glacial till areas and are deep to very deep. Large stones and boulders are present on the surface and in the soil profile. Surface soils at high elevations are acidic, gravelly loams and silts, with duff depths not exceeding 4 cm (Pfister *et al.* 1977). The surface soils are young, showing less leaching, weathering, and horizon development than Spodosols, although they are strongly acidic. Mean pH values of 4.8 to 5.0 were found for the upper soil horizons in high-elevation forest types, largely composed of Typic Cryochrepts (Pfister *et al.* 1977).

2.1.2 Climate

The Rocky Mountains provide a barrier to the flow of air across western North America and profoundly influence local climates. The northern Rockies are influenced by North Pacific weather patterns and are located in a transition zone between continental and maritime climates (Arno and Hammerly 1984). The area west of the Continental Divide has mild, wet, cloudy weather throughout the year, with the exception of a dry period in July and August. The climate east of the Continental Divide is continental, with warm summers and precipitation falling between May and September. Winter conditions are influenced by subzero Arctic air followed by warm, dry chinook winds (Pfister *et al.* 1977). Mountain weather is much cooler than in the valleys. High elevations receive 2 to 3 times the amount of annual precipitation, mainly in the form of snow. Mean annual precipitation ranges from 64–114 cm. Thus, the lower elevational limits for tree growth are controlled by moisture while the upper elevational limits are controlled primarily by temperature (Pfister *et al.* 1977).

2.1.3 Vegetation

Plant succession and disturbance regimes affect the processes of change as vegetation communities develop over time. In the northern Rockies, forests rarely progress toward a steady-state or climax condition. In a traditional succession model, forests are initiated after a major disturbance, such as a stand-replacement fire (Peet 2000). The disturbed site enters a relatively short period in which grasses, forbs, or shrubs dominate. The initial disturbed period is typically followed by the dominance of tree species that require open sunlight (shade-intolerant or early seral species). In the final forest succession stage, shade-tolerant or climax species germinate below the shade-intolerant species and eventually dominate the site. Forest types in the northern Rockies experience frequent disturbances from fire, insects, and disease, amplified by periodic drought conditions (Monnig 1992). Depending on the site, the interval between disturbances can range from less than a decade to more than a century.

Forested portions of northern Idaho and western Montana have distinct forest communities (Peet 2000) (Table 2.1). Stands of open, old-growth ponderosa pine (*Pinus ponderosa* Douglas ex C. Lawson) cover the lower montane slopes of the Rockies. At mid-elevation montane communities, vast areas are covered by stands of western white pine (*Pinus monticola* Douglas ex D. Don), usually mixed with western larch (*Larix occidentalis* Nutt.), grand fir (*Abies grandis* (Douglas. ex D. Don) Lindl.), and other conifers. Douglas-fir (*Pseudotsuga menziesii* (Mirbel) Franco) is also present but seldom abundant. In the subalpine ecotone, mixed stands of subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.), Engelmann spruce (*Picea engelmannii* Parry ex Engelm.), and

Table 2.1 Vegetation classification by climate and habitat in the northern Rocky Mountains. Adapted from Peet (2000).

Moisture Classification	**Forest Climate Type**	**Habitat Type Groups**	**Species in Habitat Types**
Dry	Warm Dry Forest	Warm and Dry	ponderosa pine, Douglas-fir, grass types
		Moderately Warm and Dry	mostly Douglas-fir and dry grand fir types
		Moderately Warm and Moderately Dry	Douglas-fir, twinflower, and mostly grand fir types
Moist	Warm Moist Forest	Moderately Warm and Moist	grand fir, queencup, beadlily types
		Moderately Cool and Moist	western redcedar, western hemlock, queencup, beadlily types
	Cool Moist	Cool and Moist	subalpine fir, queencup, beadlily, menziesia types
	Cold Moist	Cool and Moderately Dry	subalpine fir, beargrass, dwarf huckleberry types
	Riparian	Moderately Cool and Wet	western red cedar, devil's club types
		Cool and Wet	subalpine fir, bluejoint types
Cold	Cold	Cold and Moderately Dry	subalpine fir, grouse whortleberry, woodrush types
		Cold	whitebark pine and alpine larch types

whitebark pine (*Pinus albicaulis* Engelm.) are present at high elevations. The understory of the subalpine ecotones is dominated by grouse whortleberry (*Vaccinium scoparium* Leib. ex Coville), Geyer's sedge (*Carex geyeri* Boot.), beargrass (*Xerophyllum tenax* Nutt.), and slender hawkweed (*Hieracium gracile* Hook.) (Peet 2000).

Tree reproduction in many forest ecosystems occurs in episodes associated with major disturbances. Thus, the distribution of ages in a population is often a sensitive indicator of the history of disturbance in the stand (Christensen 1989). Tree size is highly dependent on the growth site and is not indicative of tree age. Although whitebark pine diameters may not exceed 30 cm due to harsh high-elevation environments, many of these trees are hundreds of years old. Healthy whitebark pine and other old-growth forests in the high elevations of the Northern Rocky Mountains are uncommon, but have several distinct characteristics:

- The age of the dominant trees are significantly older than the average time between disturbance events.
- The dominant trees are approaching their average life expectancy.
- Forest composition and structure are more complex than younger stands.
- The rate of change in these older stands is slower than younger stands.
- Defects and broken crowns are evident in both living and dead trees (Pfister *et al.* 1977, Peet 2000).
- Abundant snags and dead woody debris are also common in old-growth forests.

2.1.4 Land-Use History

Land-use studies provide a background for understanding the development of modern vegetation (Christensen 1989, Foster 1992). Land-use history has been used to analyze the change from pre-European to present forest conditions (Foster 1992, Orwig and Abrams 1994, Ruffner and Abrams 1998). Land management agencies are recommending the application of land-use history techniques to quantify the range and variability of ecological processes since pre-European settlement (Swetnam *et al.* 1999). Historical ecologists emphasize the context of land-use history to compare past locations and times with current conditions (Swetnam *et al.* 1999). Combining historical information from different sources has proven to be an effective tool for evaluating land-use practices (Christensen 1989, Foster *et al.* 1998, Motzkin *et al.* 1999). Information about 19th and 20th century forest and landscape conditions can be attained from regional surveys, journals and legal documents, regional histories, and long-term permanent plots (Foster 1988, Foster 1992).

Settlers of European origin from the eastern U.S. began to occupy the Rocky Mountains after the Lewis and Clark expedition in 1805–1806 (Parks *et al.* 2005). The arrival of railroads in the late 19th century created an economy for farming and industrial mining for the industrial revolution in the eastern U.S and Europe. The mining and agricultural economy drew a diverse population to the northern Rockies (Parks *et al.* 2005). Ranchers began to spread across the federal grasslands of the region, which led to the growth of the wheat farming industry. The valleys of the northern Rockies were moderately grazed and logged in the early 20th century (Pfister *et al.* 1977). The low-elevation forests by streams and open areas were used by cattle, horses, and sheep.

Although livestock grazing intensity has decreased in most of the northern Rockies, livestock grazing is still permitted on portions of most public lands. In addition to ranching, timber also became an important natural resource industry (Parks *et al.* 2005). Heavy logging was associated with mining, railroad building, and settlement in the 1870s. Logging continues today with the exception of several wilderness areas in Montana. Approximately 50% of low-elevation Montana forests have been logged (Pfister *et al.* 1977).

Wilderness areas are an important part of the Northern Rocky Mountains. The expansive roadless areas are linked by minimally-roaded mountain ranges (Parks *et al.* 2005). The wilderness areas provide an important habitat for many animal species, including large carnivores such as the grizzly bear, wolf (*Canis lupus* L.), and other animals that rely on large tracts of land (Ament and Craighead 1998). The wilderness areas in the northern Rockies are surrounded by an increasingly fragmented landscape from road building, development, and recreational activities (Johnson *et al.* 2003).

2.2 The Flathead National Forest

The Flathead National Forest (FNF) occupies over 930,700 ha in the Northern Rocky Mountains of northwestern Montana (Alt and Hyndman 1986, McCay 1994). The FNF is 89% forest land and 11% nonforest or water. Over 45% of the forest land in FNF is designated as wilderness (O'Brien 1999). The Canada/United States border is the northern boundary of FNF. Approximately 210 kilometers of the FNF boundary is shared with Glacier National Park along the Flathead River. The Flathead Indian Reservation is located west of the southern portion of the forest. The FNF also shares boundaries with the Lewis and Clark National Forest on the east, the Lolo National Forest on the south, and the Kootenai National Forest on the west.

2.2.1 Geology and Soils

The topography of the FNF is typical of glaciated lands, featuring high alpine basins and broad U-shaped valleys (McCay 1994). Continental, alpine, and valley glaciations occurred in the FNF. The Wisconsin glaciation influenced the shape of the land as well as the composition of the soils. During the last ice age, the glacier that filled the Rocky Mountain Trench pushed south through the Flathead Valley and into the Mission Valley. Ice that filled the Flathead Valley was about 2000 m thick at the Canadian border (Alt and Hyndman 1986). The ice thinned so rapidly southward that the glacier ended just south of Flathead Lake. Eventually, the ice age summers were warm enough to melt enormous volumes of ice.

The soils in the FNF are young and have a silty texture (Fenneman 1931). A volcanic ash surface mantle ranges from 10–20 cm in thickness. The bedrock is mostly meta-sedimentary argillites, quartzites, and limestones from the Precambrian era. Most of the mountain ranges have been formed by block faults. A vertical component of over 2000 m related to the Lewis Thrust also contributes to the elevation of the ranges east of the Rocky Mountain Trench, specifically where the FNF adjoins Glacier National Park (Fenneman 1931). Most of the mountain ranges run north-south and stand 1500–2100 m above sea level, with the highest peaks reaching altitudes of 2200 to 2700 m. The slopes of these mountain ranges are typically greater than 60%.

2.2.2 Climate

The weather in the FNF is cool and maritime influenced. The forest lies within the National Oceanic and Atmospheric Administration's Montana Climate Division 1 (Western). Annual precipitation varies from 40 cm in the valley bottoms to more than 250 cm on the mountain tops. In the valleys, 50% of the precipitation falls as snow, while in higher elevations, 80% of the precipitation is snow. Air temperatures range from –40 °C to over 38 °C. The growing season ranges from 60 to 90 days, depending primarily on the elevation and aspect (O'Brien 1999).

2.2.3 Vegetation

The most common forest types in the FNF are spruce-fir (47%), Douglas-fir (19%), lodgepole pine (17%), Engelmann spruce (6%), larch (5%), and whitebark pine (3%) (O'Brien 1999). Grand fir, ponderosa pine, and aspen forest types are uncommon but do occur. Over 81% of all trees in the FNF are less than 10 cm diameter breast height (DBH), and almost half of those are subalpine fir. The FNF has over 66 million snags (i.e., dead, standing trees) greater than 10 cm DBH. The largest snags (greater than 48 cm DBH) are estimated at 1.2 snags per hectare. The most abundant species of snags in this largest size class are Engelmann spruce and western larch (O'Brien 1999).

Habitat types describe the potential of a site to support various plant communities as determined by climatic, soil, topographic characteristics. Habitat types are subdivided by specific combinations of potential overstory and understory indicator plant species (Pfister *et al.* 1977) (Table 2.1). The most common habitat type group in the FNF is the cool moist group, occurring in 48% of the forest area, and consists of spruce, fir, Douglas-fir, lodgepole pine, Engelmann spruce, larch, and whitebark pine (O'Brien 1999). Whitebark pine is part of the cool vegetation groups and has both even-aged and uneven-aged stands at high elevations that extend treeline. Whitebark pines are only found at higher elevations in the FNF, specifically from 1800 m to 2400 m.

2.2.4 Land-Use History

Fur trappers started to settle in the FNF area in the early 1820s (McKay 1994). However, the hostility of the Blackfeet and other tribes in the plains east of the Rocky Mountains led to a slower exploration of northwestern Montana by the fur companies and independent fur traders. Fur companies entered the western slopes of the Rocky Mountains through British Territory in the north to avoid conflict with the Blackfeet Indians. The Hudson Bay Company established trading posts in the valleys from 1846–1870 (Barbouletos 1998). In 1846, Fort Connah was built to provide supplies (such as buffalo meat, pemmican, horse accessories, saddle blankets, and animal skins) to travelers in the region (McKay 1994). A population survey was conducted when Fort Connah was built and the majority of the area was populated by Native Americans: 450 Flatheads, 600 Kalispels, and 350 Kootenais. Only 15 European settlers were surveyed at that time. The Hellgate Treaty of 1855 established the Flathead Indian Reservation in the Flathead Valley for the Flathead, Kalispel, and Kootenai tribes. After the reservation was established, the fur traders could not prevent the exploration and eventual settlement of western Montana by miners, ranchers, and other Europeans. During the flow of miners into the area in the 1860s, the settlement of towns and communities depended on the location of trading posts, topography, and government land policies. Many of these settlers were French-Canadian, Scottish, or of Iroquois heritage. The most significant impact on the settlement of the Flathead area was the building of the Great Northern Railroad in 1891. By 1895, the Upper Flathead Valley had approximately 3,000 occupants (McKay 1994). The Forest Homestead Act in 1906 also encouraged settlement of agricultural lands within the boundary of the Flathead Forest Reserve.

The earliest forest surveys were conducted from 1898–1899, after the Forest Reserves in Montana were established on February 22, 1897 as part of The Organic Act (McKay 1994). John Muir and Gifford Pinchot traveled together to the Flathead Valley for the National Forest Commission in the late 1890s and commented on the natural beauty of the area and the abundant wildlife (Muir 1898). The Forest Reserves were managed by the General Land Office until 1905, when the USDA Forest Service was created (McKay 1994). The reserved land was mainly used for grazing, not for harvesting timber.

Fires have been recorded by the Forest Service in the FNF since the late 1800s. The 1889 fire in Montana burned approximately 35,600 hectares, but the area had not been settled, so the effects of the fire were not devastating (Ensign 1889). The 1889 fire year was exceptionally dry and is a year of widespread fire across the northwestern United States (Barrett *et al.* 1997, Kipfmueller and Swetnam 2000, Heyerdahl *et al.* 2001, Hessl *et al.* 2004). The 1910 fire, in comparison, burned over 1,214,050 hectares in Montana and Idaho, and destroyed entire towns. Over half of the fires in 1910 were started by railroad operations and people who wanted work (Pyne 1982). After the 1910 fire, the Forest Service built fire towers on high peaks and started coordinating transportation and communication systems (McKay 1994). The majority of the fires on the FNF have been caused by lightning rather than human ignitions (McKay 1994). In the northern Rockies, approximately one in every 25 lightning strikes has the necessary characteristics to start a fire (Pyne 1982). Large wildfires occurred in the FNF in 1910, 1919, 1926, 1929, 1931, 1934, 1940, 1946, and 1958 (Wolff 1980). More recent fires have also been recorded, such as the fires that occurred in 2003 when over 125,450 ha of forests in northwestern Montana burned (Peterson 2007). The Robert Fire and Wedge Canyon Fire burned approximately 5,260 hectares and 8,500 hectares, respectively, on the FNF from July to September of 2003. The FNF has since salvage harvested approximately 1,820 hectares of trees killed or injured from the fires (EPA 2004).

2.3 The Beaverhead-Deerlodge National Forest

The Beaverhead-Deerlodge National Forest (BDNF), located in southwestern Montana, encompasses 1,356,600 hectares divided into nine separate management sections (DeBlander 2001). The BDNF ranges in elevation from 1400 m at the Beaverhead River to 4000 m at the summit of Tweedy Mountain in the East Pioneer Range (Klepper 1950). The East Pioneer, Tobacco Root, Pintlar, Beaverhead, Gravelly, Snowcrest, Tendoy, and Centennial Ranges all experienced Pleistocene alpine glaciations (DeBlander 2001). Southwestern Montana is semiarid and the cold, frost-prone climate is unsuitable for the establishment of tree species that are not cold-adapted. The diverse topography of the BDNF, high relief, and climatic variability result in diverse alpine environments (DeBlander 2001).

2.3.1 Geology and Soils

The Big Hole Valley, which dissects the BDNF, is the highest and widest of the broad mountain valleys in western Montana (Alt and Hyndman 1986). The valley separates the two large mountain ranges on BDNF, the Pioneer and Bitterroot Ranges. Volcanic rocks filled the bottom of the valley, while much of the bedrock on the Bitterroot Range is granite (Alt and Hyndman 1986). The Big Hole Valley was created over 70 million years ago when a portion of the upper crust detached and moved east from the Idaho Batholith. The Big Hole Valley is deeper than surrounding valleys with fill sediments, with areas over 4,200 m deep.

More than half of the 27 mountain ranges in Montana are on the BDNF (Cooper *et al.* 1997). The crests of the southern Beaverhead, Gravelly, Snowcrest, and Tendoy Mountains are composed of Mesozoic and upper Paleozoic limestones, sandstones, and quartzites. The southern end of the Beaverhead Mountains is composed of calcareous Beaverhead Conglomerate. The highest point in the Gravelly Mountains, Black Butte, is composed of Quaternary basalt. The high country of the Tobacco Root Mountains is composed of the Tobacco Root Batholith. Most of the alpine terrain in the Pioneer Mountains is underlain by granite of the Pioneer Batholith. However, the high peaks at the northern end of the Pioneer Range have both intrusive igneous and Paleozoic limestones and dolomites. The majority of the Anaconda Mountains is granitic. The Madison Mountains are composed primarily of Precambrian gneiss and schist with part of the eastern side underlain by Mesozoic limestone (Cooper *et al.* 1997). Elevations in the Beaverhead and Gravelly Mountains range from 1750 to 3400 m (DeBlander 2001).

2.3.2 Climate

The climate of the BDNF is typical of higher elevations in southwestern Montana with very cold, dry winters and mild summers. The forest lies within the National Oceanic and Atmospheric Administration's Montana Climate Division 2 (Western). The BDNF is in the rainshadow of Oregon's Blue Mountains and central Idaho's high mountain mass, resulting in lower amounts of precipitation from Pacific storm systems when compared to areas in northern Montana (Ross and Hunter 1976). Mean annual precipitation varies from 36–120 cm with the majority of precipitation falling in the winter as snow (Ross and Hunter 1976). Summers are typically dry with orographically generated precipitation events (DeBlander 2001). The mean January temperature is approximately 5 °C, while the mean July temperature is 15 °C (DeBlander 2001). Local climate in the BDNF is modified by elevation, aspect, topographic position, and position relative to prevailing westerly winds and large-scale topographic features.

2.3.3 Vegetation

Southwestern Montana is the most floristically diverse region of the state (Cooper *et al.* 1997). Forest composition in the BDNF consists mostly (78%) of smaller-diameter tree (less than 10 cm DBH), while the remaining 22% are larger diameter trees (greater than 10 cm DBH). Snags and downed woody debris are an important component of forest ecosystems by providing habitat for wildlife species and acting as carbon sinks. The BDNF has over 71 million snags greater than 10 cm DBH. The largest snags (greater than 48 cm DBH) have a density estimated at 0.2 snags per hectare. The most abundant species of snags in this largest size class are whitebark pine, followed by Douglas-fir and Engelmann spruce (DeBlander 2001).

The BDNF has different forest types, with lodgepole pine (*Pinus contorta* Dougl. ex Loud.) being the most common species at 47% of the total forest land area. Lodgepole pine is followed in abundance by Douglas-fir (22%), spruce and fir (12%), whitebark pine (11%), Engelmann spruce (5%), and limber pine (*Pinus flexilis* James) (2%). Whitebark pines are only found at higher elevations in the BDNF, specifically from 2130–3020 m. Past glaciation and modern periglacial climates have resulted in environmental gradients that produce communities with high diversity (Peet 2000). The BDNF has more than 70 forest habitat types grouped by temperature gradients and moisture availability. The most common habitat group is the cool and dry group, composed of lodgepole pine, Douglas-fir, spruce, fir, whitebark pine, and Engelmann spruce (DeBlander 2001). Whitebark pine stands are most abundant (over 80,900 ha) in the cold habitat type, with lodgepole pine, spruce, fir, and Engelmann spruce as the associated species. Understory vegetation includes mountain grasslands dominated by Idaho fescue (*Festuca idahoensis* Elmer) and shrublands dominated by mountain big sagebrush (*Artemisia tridentata* Nutt.) (Peet 2000).

2.3.4 Land-Use History

USDA Forest Inventory Analysis crews noted considerable impacts from both anthropogenic and natural disturbances in the BDNF forest stands (DeBlander 2001). The field crews found that 27% of the forested area in the BDNF had no visible signs of disturbance, 26% of the forest showed signs of disease damage, 15% of the stands had been logged, 12% had signs of wind and weather damage, 9% had evidence of fire, and 8% showed signs of insect and animal damage. The remaining 3% of the BDNF had been disturbed through road building, land clearing, and mining.

The Lemhi, Flathead, Shoshoni, Bannock, Crow, Blackfeet, and Nez Perce Indian tribes used the BDNF as hunting grounds prior to the arrival of European settlers (Burlingame 1942). The year-round Lemhi presence in the BDNF was caused by raiding by the Blackfeet which pushed them into the southwestern corner of Montana (Burlingame 1942). The Nez Perce maintained buffalo hunting grounds in the valleys of the BDNF. On August 9, 1877, Colonel Joseph Gibbon and the U.S. Army ambushed and attacked the Nez Perce encampment in the Big Hole Valley, driving the tribe across the Continental Divide and into north-central Montana (Munday 2001).

The first record of European movement into the BDNF occurred in August 1805 when the Lewis and Clark expedition traveled through the Big Hole Valley and made contact with the Lemhi Indian tribe (Appleman 1975). By 1830, the American Fur Company began operations in the area; buffalo hides were also an important source of trade (Burlingame 1957). Fur trappers also brought the smallpox epidemic which decimated the Blackfeet Indians and other tribes in the area (Munday 2001). Homesteaders were slow to settle in the area because many were afraid of grizzly bear attacks on their milking cows or in their houses. Therefore, many settlers did not have doors on their houses (Silve 2005). Gold was discovered in the BDNF in 1863 and within a year 10,000 miners had begun working these deposits (Barsness 1962). Hydraulic mining operations began in the 1870s and their effect on the landscape can still be seen today in the form of exposed talus slopes (Burlingame 1957).

2.4 The Lolo National Forest

The Lolo National Forest (LNF) administers 841,400 hectares, of which 95% is forest land and 5% is nonforest or water resources (DeBlander 2000). Wilderness areas are designated as 8% of the total managed area. The LNF is approximately 190 km long and 60–180 km wide, segmented by valleys (Overbay 1986). The forest is located west of the Continental Divide and is influenced by both continental and maritime climates (DeBlander 2000). These climates provide a wide range of environmental gradients that produce highly-diverse forests. Elevation ranges from less than 732 m at the Clark Fork River to 2743 m at Lolo Peak (Overbay 1986).

2.4.1 Geology and Soils

The topography of the LNF has been sculpted by the weathering, erosion, and past glaciation (Peterson 1986). The bedrock of the region is composed of Proterozoic igneous rock, overlain in places with Devonian and Cambrian sedimentary rock (Alt and Hyndman 1972) and Quaternary sediments from glacial activity (Alt 2001). The LNF is located on the western end of the Garnet Range and at the northern edge in the Sapphire tectonic block at the junction of the Clark Fork fault and the Blackfoot thrust plate (Alt 2001). The Clark Fork fault and Blackfoot thrust plate are overlaid by the Belt formation which consists mostly of Precambrian sedimentary rock formations made up of the Snowslip Formation and the Mount Shields Formation (Alt 2001). The Snowslip Formation consists of argillite and siltite with thin beds of fine-grained quartzite (Alt 2001). Thin beds of limestone and flat pebble conglomerate also occur. Soils are poorly developed in high elevations of the LNF, and the underlying geology is composed of a mix of Quaternary and Cenezoic glacial deposits, Precambrian shales and siltstones, and Precambrian argillites and quartzites (Ross *et al.* 1955)

2.4.2 Climate

The climate of the LNF is representative of higher elevations in western Montana, with very cold, dry winters and mild summers. The forest lies within the National Oceanic and Atmospheric Administration's Montana Climate Division 1 (Western). Average annual temperature is 6° C, with summer and winter temperatures averaging 13° C and –2° C, respectively (NCDC 2007). Average annual precipitation is 42 cm, with the majority falling in the winter and early spring. Precipitation increases with elevation and over two-thirds of the precipitation falls as snow. The snowmelt, which is approximately half of the annual precipitation, is the primary source of ground water recharge and streamflow (Overbay 1986). The western section of the LNF lies in the rainshadow of the Bitterroot Mountains and results in lower amounts of precipitation from Pacific storm systems when compared to areas in the eastern section of the LNF (Overbay 1986). Summers are typically dry with orographically-generated precipitation events.

2.4.3 Vegetation

Tree sizes in the LNF resemble an inverse-J distribution of many smaller-diameter trees (less than 10 cm DBH), and fewer larger-diameter trees (greater than 10 cm DBH). The LNF has over 66 million snags greater than 10 cm DBH. The largest snags (greater than 48 cm DBH) are estimated at 0.44 snags per hectare. The most abundant species of snags in this largest size class are whitebark pine, Douglas-fir, and western larch (DeBlander 2000).

The most common forest type is Douglas-fir, which is 41% of the total forest land area. Douglas-fir is followed in abundance by lodgepole pine (21%), spruce and fir (18%), larch (6%), ponderosa pine (4%), western red cedar (3%), and grand fir, Engelmann spruce, and whitebark pine (each 2%). Whitebark pines are only found at higher elevations in the LNF, specifically from 1830–2710 m. The LNF includes more than 80 forest habitat types (DeBlander 2000). The forest habitat types are grouped by temperature gradients and moisture availability in the biophysical environment. The most common habitat group is the moderate warm/dry, composed of Douglas-fir, ponderosa pine, grand fir, and lodgepole pine. Second most common are the cool/moist and cool/moderate dry habitat type groups which include Douglas-fir, Engelmann spruce, spruce, fir, mountain hemlock (*Tsuga mertensiana* (Bong.) Carr.), larch, and lodgepole pine. Whitebark pine is not a major component of any habitat type group but is found in the cold and cold/moderate dry groups with spruce, fir, and lodgepole pine.

Common understory plants include grouse whortleberry, red mountain-heath (*Phyllodoce empetriformis* (Sm.) D. Don), woodrush (*Carex luzulina* Olney), and beargrass (Peet 2000). Areas above treeline are dominated by shrub and herbaceous plant communities of elk sedge (*Carex garberi* Fern.), pinegrass (*Calamagrostis rubescens* Buckl.), twin flower (*Linnaea borealis* L.), shooting star (*Dodecatheon* L.), yellow avalanche-lily (*Erthronium grandiflorum* Pursh), mountain arnica (*Arnica montana* L.), arrowleaf ragwort (*Senecio triangularis* Hook.), and dwarf blueberry (*Vaccinium caespitosum* Michx.) (Peet 2000).

2.4.4 Land-Use History

The LNF was used by the Blackfeet, Kootenai, and the Salish Indian tribes before European settlers arrived in the 1800s (Sutton 2000). In September 1805, the Lewis and Clark Expedition passed through the LNF on the Lolo Trail with great difficulty as the game was scarce and the snowfall was early (Devlin 2001). On the expedition's return trip through the area, the Blackfeet attacked and killed a number of party members (Appleman 1975). However, by 1830, the Blackfeet population had been reduced to 10,000 people as a result of smallpox (Hafen 1982). The Lolo Trail was historically used by the Salish Indians to travel from the west to dig for camas roots and to access salmon and steelhead fishing on the Clearwater and Snake Rivers (Devlin 2001). The Nez Perce, from the plateaus of central Idaho, came east on the Lolo Trail to hunt buffalo (Devlin 2001). In the summer of 1877, over 750 Nez Perce tried to escape General Oliver Otis Howard's army by crossing the trail into northwestern Montana (McWhorter 1984). This trail was regularly maintained with intentionally-set fires (Lewis and Ferguson 1999, Barrett 2000). Although the importance of fires set by American Indians in the West is still debated (Vale 2002, Pyne 2003, Barrett *et al.* 2005), significant impacts to local vegetation structure and communities around occupied sites have been documented in the LNF region (Arno *et al.* 1997, Barrett and Arno 1999).

The LNF is relatively rich in mineral resources, and mining operations have existed in the region nearly continuously following a gold and silver rush in the mid-1860s (Harrison *et al.* 1969, Safford 2004). Prospecting occurred throughout the region, and several abandoned mines are now scattered across the landscape. Following the initial rush for precious metals, mining interests broadened to include numerous mineral resources including antimony, barite, copper, sapphire, gold, and silver. By the late 1980s, mining activity occurred on 107 ha of the LNF. Sand and gravel extraction also occurred at several sites, and while oil and gas have not yet been exploited within the forest, large-scale exploration began in the mid-1980s with over 372,310 ha under lease for mining (Overbay 1986).

Large-scale logging was restricted by terrain and did not begin until the region was opened to railroads in the late 19th century (DeBlander 2000). Since the 1920s, logging operations have focused on clear-cutting operations at low and mid-elevation forests of ponderosa pine, Douglas-fir, western larch, and lodgepole pine (Overbay 1986). Due to inaccessibility, many high-elevation forests in the LNF have never been logged (DeBlander 2000). However, over 410,000 ha have been deemed appropriate for future harvesting (Overbay 1986).

CHAPTER 3

TRENDS IN WHITEBARK PINE GROWTH RELATED TO CLIMATE AND MOUNTAIN PINE BEETLE OUTBREAKS IN THE MONTANA ROCKY MOUNTAINS

Portions of this chapter that refer to whitebark pine ecology and study site descriptions were taken from Chapters 1 and 2 of this dissertation. The use of "we" in this chapter refers to Dr. Henri Grissino-Mayer and Evan Larson, who will be co-authors on the manuscript submitted from this chapter. Dr. Grissino-Mayer and Evan Larson assisted in the identification of relevant literature, location of sample sites, field collection, and verifying the accuracy of dated samples.

In this chapter, we compare six whitebark pine chronologies to evaluate multicentury radial growth and climate trends along a north-south transect in the Montana Rocky Mountains. Our objective was to use the whitebark pine chronologies to partition the proportion of tree-ring variance explained by mountain pine beetle outbreaks and the proportion of variance explained by climate in the 20thcentury. *Manuscript to be submitted to Ecological Applications*.

3.1 Introduction

Whitebark pine (*Pinus albicaulis* Engelm.) ecosystems have been shown to be highly sensitive to climate variability (Perkins and Swetnam 1996, Biondi *et al.* 1999, Luckman and Villalba 2001, Tomback *et al.* 2001, Kipfmueller 2003), with relatively small changes in temperature and precipitation having significant effects on species productivity and community disturbance regimes (Tomback and Resler 2007). Our understanding of how whitebark pine communities have been influenced by changing climate conditions is therefore critical in understanding the current decline of whitebark pine throughout its range. Studying climate and vegetation dynamics at multicentury scales may provide insight into the resiliency of complex ecosystems in the northern Rocky Mountains of the western U.S.

Dendroclimatological studies on whitebark pine have shown the complexity of climate-growth relationships within this species and demonstrated the importance of considering microsite variation in developing climatically-sensitive whitebark pine chronologies (Perkins and Swetnam 1996, Kipfmueller 2003, Bunn *et al.* 2003). Previous studies have been conducted on whitebark pine climate response in the northern Rocky Mountains west of the Continental Divide in Idaho (Perkins and Swetnam 1996, Kipfmueller 2003), but little is know about the response to climate in whitebark pine east of the Continental Divide in Montana (Mann 2008). West of the Continental Divide, summer temperatures have been the primary driver of whitebark pine growth fluctuations (Perkins and Swetnam 1996, Luckman *et al.* 1997, Biondi *et al.* 1999, Kipfmueller 2003), but drought has shown a stronger relationship to whitebark pine growth patterns east of the Continental Divide (Mann 2008). More dendroclimatological research is needed to compare climate-growth response in whitebark pine populations on a landscape-level scale in the northern Rocky Mountains.

Climate patterns affect the relationship between the ecology of mountain pine beetles (*Dendroctonus ponderosae* Hopk.) and whitebark pine mortality. Mountain pine beetle attacks occur more frequently during periods with warmer temperatures (Campbell *et al.* 2007). Warming climate conditions expand the geographic range of mountain pine beetles by increasing the area available for the beetles to complete their life cycle. An increase in the number of infestations since 1970 in formerly climatically unsuitable habitats indicates that mountain pine beetle populations have expanded into high-elevation areas (Carroll *et al.* 2003). Therefore, whitebark pine may be more vulnerable to mountain pine beetle outbreaks under current warming conditions than during previous outbreaks between 1920 and 1940 and between 1970 and 1980. Whitebark pine is already in peril due to white pine blister rust (*Cronartium ribicola* JC Fischer), and the overlapping effects of the current mountain pine beetle outbreak will likely intensify its decline. The effects of climate change are important when assessing the flexibility of whitebark pine ecosystems to recover from mountain pine beetle outbreaks and other landscape-level disturbances. Consequently, an urgency exists to understand the influence of climate change on the severity of mountain pine beetle outbreaks and white pine blister rust infections, both of which are contributing to the decline in whitebark pine ecosystems.

Mountain pine beetle epidemics killed a large proportion of mature whitebark pine trees in the Rocky Mountains of the United States during the 20th century (Ciesla and Furniss 1975, Furniss and Carolin 1977, Romme *et al.* 1986), and the insect is considered the most destructive of the native biotic agents in mature *Pinus* forests in western North America (Safranyik and Carroll 2006). The major hosts for mountain pine beetle include whitebark pine, ponderosa pine (*Pinus ponderosa* Douglas ex C. Lawson), lodgepole pine (*Pinus contorta* Douglas ex Loudon), and western white pine (*Pinus monticola* Douglas ex D. Don). Extensive mountain pine beetle outbreaks in western North America occurred in the 1880s, 1930s, and 1970s, and more recently in the early 2000s (Arno and Hoff 1989, Taylor *et al.* 2006). The series of outbreaks that occurred from 1920 to 1940 in Idaho and Montana killed an estimated 1.4 billion lodgepole pines and vast numbers of whitebark pine (Safranyik and Carroll 2006). Extensive outbreaks in western North America during the late 1970s and early 1980s killed almost 2 million hectares of *Pinus* trees. A massive infestation, extending over 12 million hectares, also devastated lodgepole and whitebark pine stands in the northern Rocky Mountains and in central British Columbia in the early 2000s (Safranyik and Carroll 2006).

Dendroecological methods for detecting mountain pine beetle outbreaks in whitebark pine and lodgepole pine forests have relied mostly on growth release periods beginning almost a decade after the outbreak event (Heath and Alfaro 1990, Alfaro *et al.* 2004, Taylor *et al*. 2006, Campbell *et al.* 2007). In lodgepole pine forests, climate-tree growth relationships have been explored that compared mountain pine beetle outbreak periods using correlation analysis and ordination techniques (Campbell *et al.* 2007). The inter-relationships between whitebark pine growth, climate response, and mountain pine beetle outbreak periods, however, have not yet been studied. We propose to contribute to these dendroecological methods by developing a new approach for decoupling radial-growth signatures related to climate and mountain pine beetle outbreaks in the northern Rocky Mountains.

In this study, we interpret radial growth patterns of six whitebark pine chronologies to distinguish the relative influence of climate response and mountain pine beetle outbreaks in whitebark pine populations in western Montana. The specific objectives of this study were to: (1) develop tree-ring chronologies for whitebark pine along a latitudinal transect through western Montana, (2) determine which climate variables exert the most influence on whitebark pine growth and reconstruct climate over the length of the chronologies, and (3) partition the response of whitebark pines to that caused by known mountain pine beetle outbreaks during the 20th century, and to that caused by climate in the 20th century.

3.2 Study Site

We sampled whitebark pine-dominated forests located on a north-south transect that extended from the Montana/Canada border to the western side of Yellowstone National Park. We chose to sample along a north-south transect to evaluate landscape-level climate and mountain pine beetle outbreak trends. Our study sites were located in whitebark pine forests that cover six peaks in western Montana (Figure 3.1). The sites varied in elevation from 2,040 m to 2,535 m (Table 3.1). Mean annual temperature ranges are similar, but a gradient of decreasing precipitation exists from west to east that creates different precipitation regimes among the six sites. Soils are poorly developed at all sites. The underlying geology is composed of a mix of Quaternary and Cenozoic glacial deposits, Precambrian shales and siltstones, and Precambrian argillites and quartzites (Ross *et al.*1955, Raines and Johnson 1996). Subalpine fir, Engelmann spruce, and lodgepole pine were present in the stands we examined. Forest cover on Point Six and Ajax Peak were relatively continuous, although the forests on Morrell Mountain, Big Hole Pass, and Hornet Peak were broken by a few alpine meadows, and the forest on Mineral Peak was dissected by open talus. Herbaceous cover on the sites was dominated by grouse whortleberry (*Vaccinium scoparium* Leib. ex Coville), red mountain-heath (*Phyllodoce empetriformis* (Sm.) D. Don), smooth woodrush (*Luzula hitchcockii* Hamet-Ahti), bear grass (*Xerophyllum tenax* (Pursh) Nutt.), and elk sedge (*Carex geyeri* Boott).

Evidence of disturbances was common at each site. Whitebark pine had experienced differing rates of mortality in each stand, predominantly from mountain pine beetle activity that we identified by the presence of J-shaped galleries on the boles of

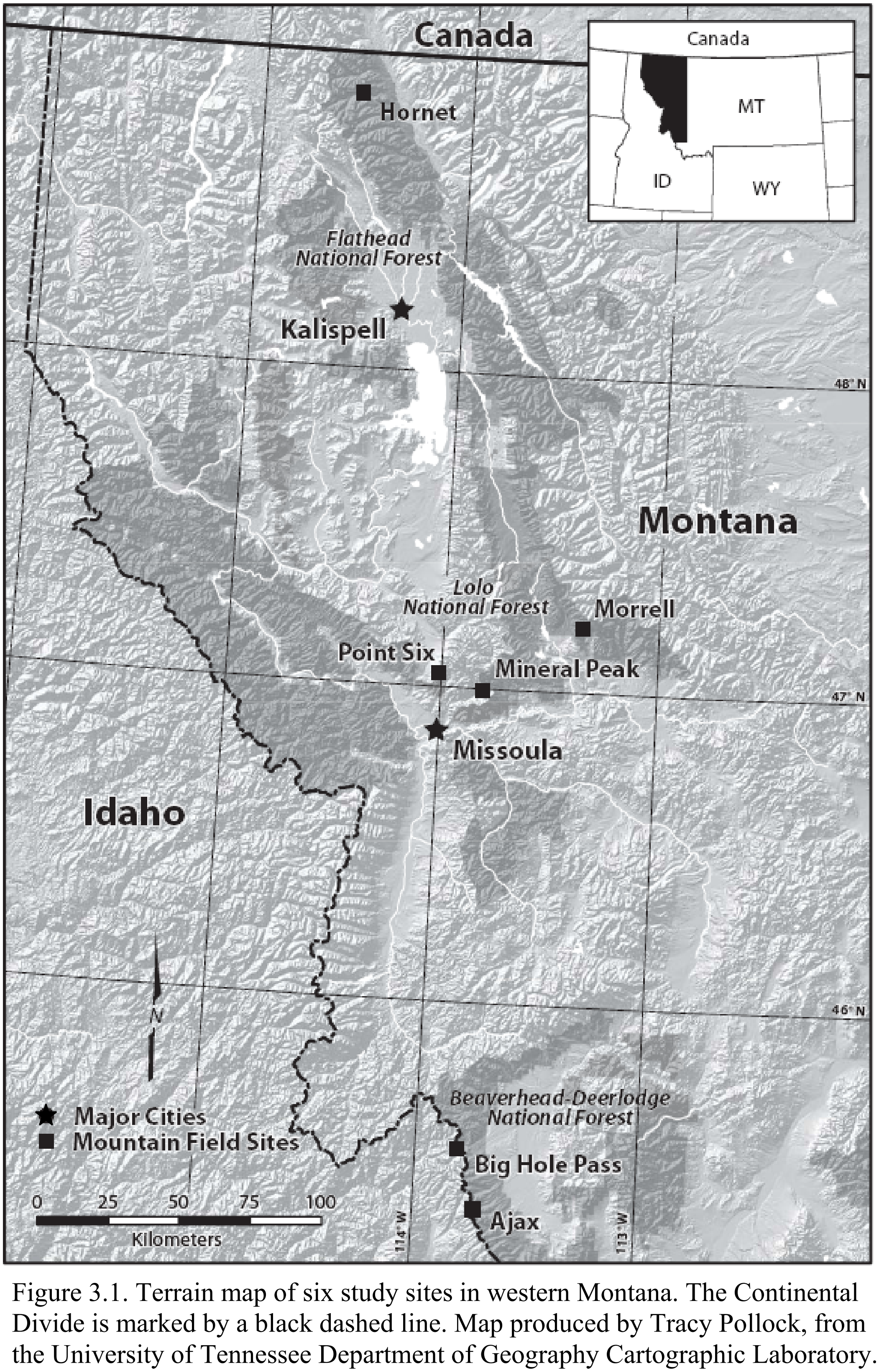

Figure 3.1. Terrain map of six study sites in western Montana. The Continental Divide is marked by a black dashed line. Map produced by Tracy Pollock, from the University of Tennessee Department of Geography Cartographic Laboratory.

Table 3.1. Study site locations in Montana.

Study Site	**National Forest**	**Elevation (m)**	**Latitude (Degrees N)**	**Longitude (Degrees W)**
Hornet Peak	Flathead	2040	48.52.44	114.31.33
Mineral Peak	Lolo	2250	47.00.13	113.48.51
Morrell Mountain	Lolo	2370	47.11.53	113.21.25
Point Six	Lolo	2350	47.02.34	113.59.14
Ajax Peak	Beaverhead-Deerlodge	2535	45.20.25	113.42.57
Big Hole Pass	Beaverhead-Deerlodge	2255	45.31.14	113.48.16

dead trees. We also observed several dead trees with what appeared to be old blister rust cankers at the sites in our northern (Flathead National Forest) and central (Lolo National Forest) sites. Blister rust was abundant in all sites, with living whitebark pine trees exhibiting open cankers or flagging (red needles due to the recent mortality of a branch or stem) in their upper canopies. Evidence of past fires was common, especially in our central sites, with whitebark pine trees displaying multiple fire scars. We did not observe any fire-scarred fir or spruce.

3.2.1 Land-Use History

Fires have been recorded by the USDA Forest Service in the Flathead, Lolo, and Beaverhead-Deerlodge National Forests since the late 1800s. The 1889 fire in Montana burned approximately 35,600 hectares (Ensign 1889). The 1889 fire year was exceptionally dry and is a year of widespread fire across the northwestern United States (Barrett *et al.* 1997, Kipfmueller and Swetnam 2000, Heyerdahl *et al.* 2001, Hessl *et al.* 2004). The 1910 fire, in comparison, burned over 1,214,050 hectares in Montana and Idaho (McKay 1994). After the 1910 fire, the USDA Forest Service built fire towers on high peaks and started coordinating transportation and communication systems (McKay 1994). Fire towers were built on Hornet Peak (northern site), Mineral Peak, and Morrell Mountain (central sites) in the 1920s. A radio tower was constructed on Point Six (central site) in the early 1960s. Point Six site is also fragmented by several ski runs and a utility road to the radio facility on the peak of the mountain. More recent fires have been recorded in the northern and central sites, such as the fires that occurred in 2003 when over 125,450 ha of forests in northwestern Montana burned (Peterson 2007). Fire towers were not present on Ajax Peak and Big Hole Pass (southern sites). However, gold was discovered at Ajax Peak in 1863, which led to hydraulic mining operations in the 1870s (Barsness 1962). The effects of mining on the landscape can still be seen today in the form of exposed talus slopes (Burlingame 1957, Barsness 1962).

3.3 Methods

3.3.1 Field Methods

The whitebark pine samples used in this study were part of a larger project designed to study the current status of the whitebark pine ecosystem in Montana. Many of the whitebark pine samples selected for dendroclimatological analysis were affected by the mountain pine beetle and some samples exhibited fire scars that could diminish the strength of the overall climate signal. Whitebark pine tree-ring data were collected in four 0.05 ha fixed-radius (r = 12.66 m) plots on each of the six mountains selected (24 overstory plots total). We collected increment cores from two radii of each tree in the plot by either coring the tree twice on opposite sides of the tree, or by coring straight through the tree. All cores were taken at or below 30 cm above the root collar and along the contour of the slope to minimize the effects of reaction wood on the growth patterns in each sample (Fritts 1976). Core samples were labeled and placed in paper straws for storage and protection. We used a chainsaw to collect 5 to 10 cross-sections from whitebark pine snags, stumps, and logs to extend the tree-ring information from the cores back in time, and examined cross-sections for fire and mountain pine beetle scars at each of the six mountain sites (Arno and Sneck 1977). We visually examined each cross-section and noted the presence or absence of fire (*i.e.*, internal fire scars), mountain pine beetle galleries, and blue-stain fungus on each sample. All samples were labeled and then wrapped with plastic wrap for transport back to the laboratory.

3.3.2 Laboratory Methods

All samples were frozen at –40 °C for 48 hours to kill any pathogens and/or insects that may have been transported along with the samples. After allowing all samples to dry, fragile cross-sections were glued to plywood for stabilization. Cores were allowed to air-dry completely in the straws and were then glued to wooden core mounts with cells vertically aligned to ensure a transverse view of the wood surface. Cores and cross-sections were examined for blue-stain fungus in the outer tree rings, indicating mountain pine beetle presence. Cross-sections were given an initial flat surface using a band saw to remove deep chain saw cuts prior to sanding, then each cross-section and core sample was sanded using a belt sander, beginning with ANSI 80-grit (177−210 µm) and using progressively finer-grit belts until ANSI 400-grit (20.6−23.6 µm) (Orvis and Grissino-Mayer 2002). This process produced a wood surface with cellular features clearly defined under 10x magnification for clear ring identification.

3.3.3 Crossdating and Chronology Construction

We used visual, graphical, and statistical crossdating to assign precise calendar years to the growth rings of the core and cross-section samples. Visual crossdating relied on recognition of characteristic patterns of wide and narrow rings common to each study site that were likely related to regional climate (Fritts1976), graphical crossdating was accomplished using the skeleton-plot method (Stokes and Smiley 1996), and statistical crossdating was accomplished using ring-width measurements and the computer program COFECHA (Holmes 1983, Grissino-Mayer 2001).

We drew two radii on each cross-section extending from the pith to the outermost complete ring, and measured along each radius, bypassing particularly eroded and degraded portions of the surface. We measured the ring widths on all samples to 0.001 mm accuracy with a Velmex measuring stage coupled with MEASURE J2X software. We confirmed the graphical crossdating and relative placements of all tree-ring series using COFECHA, which uses segmented time-series correlation techniques to confirm the previously-assigned temporal placements of all tree rings (Grissino-Mayer 2001). Because crossdating is a high-frequency process (pattern matching of sequences of individual rings), COFECHA removes all low-frequency trends using both spline-fitting algorithms and autoregressive modeling (Grissino-Mayer 2001). Such trends could also be caused by natural (*e.g.*, mountain pine beetle outbreaks and fire events) and human (*e.g.*, blister rust infestation, logging, and mining) disturbances that otherwise could mask the climate signal desirable for accurate crossdating. We tested consecutive 50-year segments (with 25-year overlaps) on each series with a master chronology created from all other series at each of the six study sites. We also tested our six whitebark pine chronologies with other chronologies from Montana and Idaho. Crossdating was verified when the correlation coefficient for each tested segment exceeded 0.32 ($p < 0.01$), although coefficients were usually much higher. The final suggested placement made by COFECHA had to be convincing both graphically (similar patterns in wide and narrow rings) and statistically (correlation significant at $p < 0.001$) (Grissino-Mayer 2001).

Crossdating quality was assessed by two statistical descriptors. The average mean sensitivity was used to measure the strength of the year-to-year variability in all series. Values of 0.25 or higher are common for tree-ring data from the western U.S. (DeWitt and Ames 1978). We also used the interseries correlation as the average of all Pearson correlation coefficients calculated for each series to compare to all other series in the chronology (Grissino-Mayer 2001).

We standardized all measurement series in the six chronologies to remove effects from age-related growth trends that could add noise to the series unrelated to the climate signal desired in chronology development (Cook 1987, Fritts 2001). We removed the age-related growth trend of each sample using the program ARSTAN (Cook 1985), which fits a negative exponential trend curve or straight line to the growth of the sample using the least squares technique. ARSTAN then creates an index for that year by dividing the actual ring-width by the value predicted by the regression (Fritts 1976, Cook 1985). The indices were then averaged for each year across all series to create a single index series for each site (Cook 1985).

3.3.4 Instrumental Climate Data

The climate-tree growth relationships for each of the six chronologies were analyzed using divisional climate data obtained from the National Climatic Data Center (NCDC 2007). For the Beaverhead-Deerlodge National Forest chronologies, we used climate data from NOAA Climate Division Montana 2 (Southwestern). For the Flathead and Lolo National Forest chronologies, we used climate data from NOAA Climate Division Montana 1 (Western). The climate variables used in the climate response analysis included monthly average temperature, monthly total precipitation, and monthly Palmer Drought Severity Index (PDSI). PDSI is used by the National Weather Service to monitor drought and wetness conditions in the United States and is a measure of the moisture conditions during the growing season. PDSI describes the severity of both wet and dry periods and incorporates temperature, precipitation, and evapotranspiration as an estimate of soil moisture availability as a monthly index (Palmer 1965). The index is a weighted average of estimated soil moisture conditions for the current and preceding months resulting in a strong month-to-month autocorrelation that represents soil moisture condition changes over time (Stahle *et al.* 1988). PDSI generally ranges from –6 to +6, with negative values indicating dry periods and positive values indicating wet periods. PDSI values from –2.0 to –3.0 are considered a moderate drought, values from –3.0 to –4.0 are considered a severe drought, and values less than –4.0 are considered an extreme drought. PDSI has been used in dendroclimatic studies and is often significantly correlated with tree-ring indices in North America (Grissino-Mayer and Butler 1993, Watson and Luckman 2001, Woodhouse 2001).

We also compared whitebark pine growth with precipitation, maximum temperature, minimum temperature, and dewpoint temperature using the PRISM data set. PRISM (parameter-elevation regressions on independent slopes model) is a regression-based model that uses point data, a digital elevation model, and climate parameterization to generate repeatable estimates of annual, monthly, and event-based climate parameters for locations at any given point (Daly *et al.* 1994, 2002, Johnson *et al.* 2000). These estimates are represented on a regular grid, making them GIS-compatible. PRISM data provide 103 years of high-resolution monthly temperature and precipitation maps for the contiguous 48 states (Daly *et al.* 2002), as well as detailed precipitation and temperature maps for Canada, China and Mongolia (Daly *et al.* 2000a,b) and the European Alps.

3.3.5 Statistical Analysis of Climate Response and Reconstructions

Climatic variables that influence whitebark pine growth were assessed using both biological and statistical modeling. The program PRECON (Fritts and Shashkin 1994) was used to conduct correlation analysis and response function analysis (RFA) for each of the ARSTAN tree-ring chronologies from 1895 to 2004. We wanted to use the longest possible climate record for the biological models of tree growth. We used the ARSTAN chronologies instead of the STANDARD and RESIDUAL chronologies because we found stronger relationships between climate variables and the ARSTAN chronologies. RFA was used in conjunction with correlation analysis to examine the climatic effects on ring widths by applying a multivariate, biological model of tree growth (Grissino-Mayer and Fritts 1995). The RFA examines the climatic effects on tree growth using principal components of the normalized climate dataset to reduce the effects resulting from covariance among the independent variables (Grissino-Mayer *et al*. 1989). Included with the climate data as possible predictors were growth indices from prior years to assess biological inertia in the tree-ring record (Grissino-Mayer and Fritts 1995). A bootstrap method provides confidence intervals for the response coefficients. The resulting response function coefficients indicate the separate influences that precipitation and temperature have on monthly tree growth (Grissino-Mayer *et al*. 1989). RFA and stepwise regression were conducted using the six whitebark pine chronologies and 30 monthly variables: 15 variables for mean monthly temperature and 15 variables for monthly total precipitation. The 15 months began with the June of the previous growing season and ended with August of the current growing season. We chose to begin the interval in the previous June because summer (June–August) climate conditions are likely to impact whitebark pine growth during the subsequent growing season.

Correlation analysis was used as a complement to response function analysis by statistically determining the strength of association between climate variables and whitebark pine growth. Pearson correlation coefficients were calculated between growth indices and climate variables (temperature, precipitation, and PDSI) for a 20-month period (previous May–current December). Seasons were determined for each climate variable based on sequences of months during which the climatic variable exhibited statistically significant relationships with whitebark pine growth. Seasonalizing climate data are important because they illustrate the longer period during which a climatic variable has the greatest effect on tree growth (Grissino-Mayer and Butler 1993, Grissino-Mayer 1995).

We selected the seasonal variable with the strongest relationship with tree growth to develop a regression equation that predicted the selected climatic variable for the full length of the whitebark pine chronologies. We tested different subsets of climate data and found the earlier periods (1895–1939) were sparse and less consistent when compared to recorded climate data beginning in 1940. Therefore, we used the strongest period of instrumental records (1940–present) to compute a transfer function and reconstruct the seasonal climate variable over the length of the chronologies. Standard regression diagnostics (Studentized residuals and Cook's d) ensured that our reconstructions minimized violations of the least squares regression. Outliers that exceeded tolerances after inspection of the Studentized residuals (< –2 or > +2) and Cook's d (approximately 0.1) statistics were evaluated for possible removal from the model (Grissino-Mayer 1995).

3.3.6 Separating Disturbance from Climate

We used PRECON to develop 100-year time series plots that incorporated the results from the stepwise regression. The stepwise regression uses the months with significant climate effects to show those periods during the 20th century when tree growth was above or below that modeled from the observed climate variables. Declines in growth not associated with climate could be caused by large-scale disturbances, such as mountain pine beetle outbreaks, that contribute to the mortality of mature whitebark pines within a stand. Smaller-diameter whitebark pines that survived the periodic mountain pine beetle outbreaks were expected to show an increase in growth within a decade following the outbreak (Taylor *et al.* 2006, Campbell *et al.* 2007). The mountain pine beetle outbreaks between 1925 and 1935 and between 1970 and 1980 are expected to have influenced whitebark pine growth, thus reducing the strength of the overall climate signal. We used PRECON to create residual chronologies (actual tree growth minus predicted tree growth) in the 20th century to distinguish the separate influences of mountain pine beetle outbreak periods and climate in whitebark pine growth. Creating such residual chronologies also allowed us to infer mountain pine beetle outbreak trends along a latitudinal transect through western Montana.

3.4 Results

3.4.1 Chronology Development

The six whitebark pine chronologies developed from the Flathead, Lolo, and Beaverhead-Deerlodge National Forests in Montana were developed using 322 series (Table 3.2). The site chronologies varied in length, with the shortest record from Ajax Peak (1832–2005) and the longest from Mineral Peak (1171–2003). Individual tree series ranged from 50–726 years in length. Interseries correlation and mean sensitivity were used to compare statistical quality in each site chronology. Mean sensitivity values between 0.20 and 0.24 are common for whitebark pine tree-ring data from Montana and Idaho (Perkins and Swetnam 1996, Biondi *et al.* 1999, Kipfmueller 2003, Larson 2005, Mann 2008). Our chronology mean sensitivities ranged from 0.21 to 0.24. Interseries correlations for whitebark pine chronologies in the northern Rocky Mountains range between 0.41 and 0.70 (Perkins and Swetnam 1996, Biondi *et al.* 1999, Kipfmueller 2003, Larson 2005, Mann 2008). The Ajax Peak chronology had the highest interseries correlation (0.52), followed by Morrell Mountain (0.51), Big Hole Pass (0.50), Hornet Peak (0.48), Mineral Peak (0.47), and Point Six (0.47). The interseries correlation and mean sensitivity of our six whitebark pine chronologies were representative of other whitebark pine chronologies from Montana (Larson 2005, Mann 2008). We compared our six site chronologies with other whitebark pine and Douglas-fir chronologies from the northern Rocky Mountains and found the correlation coefficients were significant ($p < 0.001$) (Table 3.3). The strong relationship between our sites in Montana and neighboring sites in Idaho indicates a similar climate signal across the Continental Divide.

Table 3.2. Summary data of the six whitebark pine chronologies from Montana.

Study Site	National Forest	Period of Record	Number of Samples	Interseries Correlation	Mean Sensitivity
Hornet Peak	Flathead	1682–2005	64	0.48	0.23
Mineral Peak	Lolo	1171–2003	76	0.47	0.21
Morrell Mountain	Lolo	1489–2003	60	0.51	0.24
Point Six	Lolo	1581–2003	62	0.47	0.22
Ajax Peak	Beaverhead-Deerlodge	1832–2004	33	0.52	0.21
Big Hole Pass	Beaverhead-Deerlodge	1778–2004	27	0.50	0.22

Table 3.3. Correlation coefficients between our six whitebark pine chronologies and other tree-ring chronologies from Montana and Idaho.

Study Site	Species	Correlation Coefficient	Number of Years	P-value
Hornet Peak				
Upper Sand Pass, Idaho (Perkins 1996)	whitebark pine	0.38	314	$p < 0.001$
Mineral Peak				
Selway-Bitterroot, Idaho (Kipfmueller 2003)	whitebark pine	0.46	831	$p < 0.001$
Morrell Mountain				
Selway-Bitterroot, Idaho (Kipfmueller 2003)	whitebark pine	0.39	511	$p < 0.001$
Point Six				
Selway-Bitterroot, Idaho (Kipfmueller 2003)	whitebark pine	0.37	421	$p < 0.001$
Ajax Peak				
Selway-Bitterroot, Idaho (Kipfmueller 2003)	whitebark pine	0.36	171	$p < 0.001$
Helena, Montana (Ferguson 1965)	Douglas-fir	0.41	134	$p < 0.001$
Big Hole Pass				
Selway-Bitterroot, Idaho (Kipfmueller 2003)	whitebark pine	0.40	225	$p < 0.001$

A few similar marker rings occurred in the chronologies, but we found noticeable differences among the six whitebark pine chronologies, likely due to differences in microclimates and disturbance histories. Visual and graphical crossdating were aided by especially narrow growth rings formed in AD 1601, 1641, 1698, 1782, 1838, 1899, and 1906. A pattern of consecutive narrow rings in 1753, 1754, and 1755, followed by a wide ring in 1756, also provided a strong ring signature in the three central sites in the Lolo National Forest. Figures 3.2–3.7 illustrate the entire length of the six whitebark pine chronologies.

3.4.2 Climate Response

Whitebark pine showed different climate responses at each site, but results from the response function analysis (RFA) showed that monthly climate variables were less important to whitebark pine growth than prior years' growth in these biological models. In the most northern site, Hornet Peak, the RFA showed 54% of the whitebark pine variance was explained by climate ($r^2 = 0.23$) and prior growth ($r^2 = 0.31$). The central sites had similar results with over 40% of the variance explained by climate and prior growth. At Mineral Peak, 58% of the variability was explained by climate ($r^2 = 0.26$) and prior growth ($r^2 = 0.32$). For Morrell Mountain, 44% of the variance was explained by climate ($r^2 = 0.16$) and prior growth ($r^2 = 0.28$). Of the central sites, Point Six had the most variance explained, 72%, by climate ($r^2 = 0.16$) and prior growth ($r^2 = 0.56$). The southern sites, Ajax Peak and Big Hole Pass, had over 50% of the whitebark pine variance explained by climate and prior growth. For Ajax Peak, 52% of the variance was

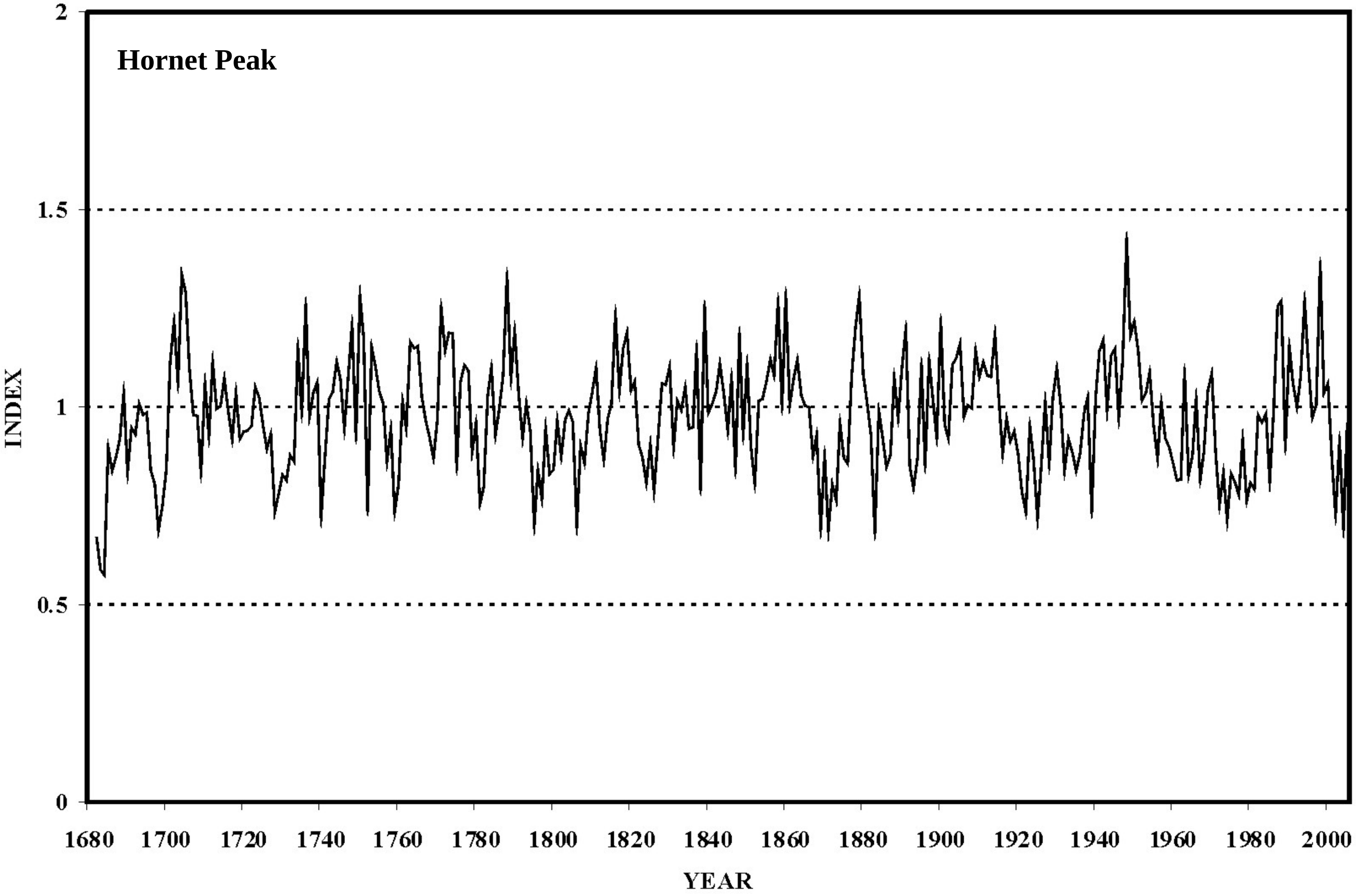

Figure 3.2. Hornet Peak whitebark pine chronology.

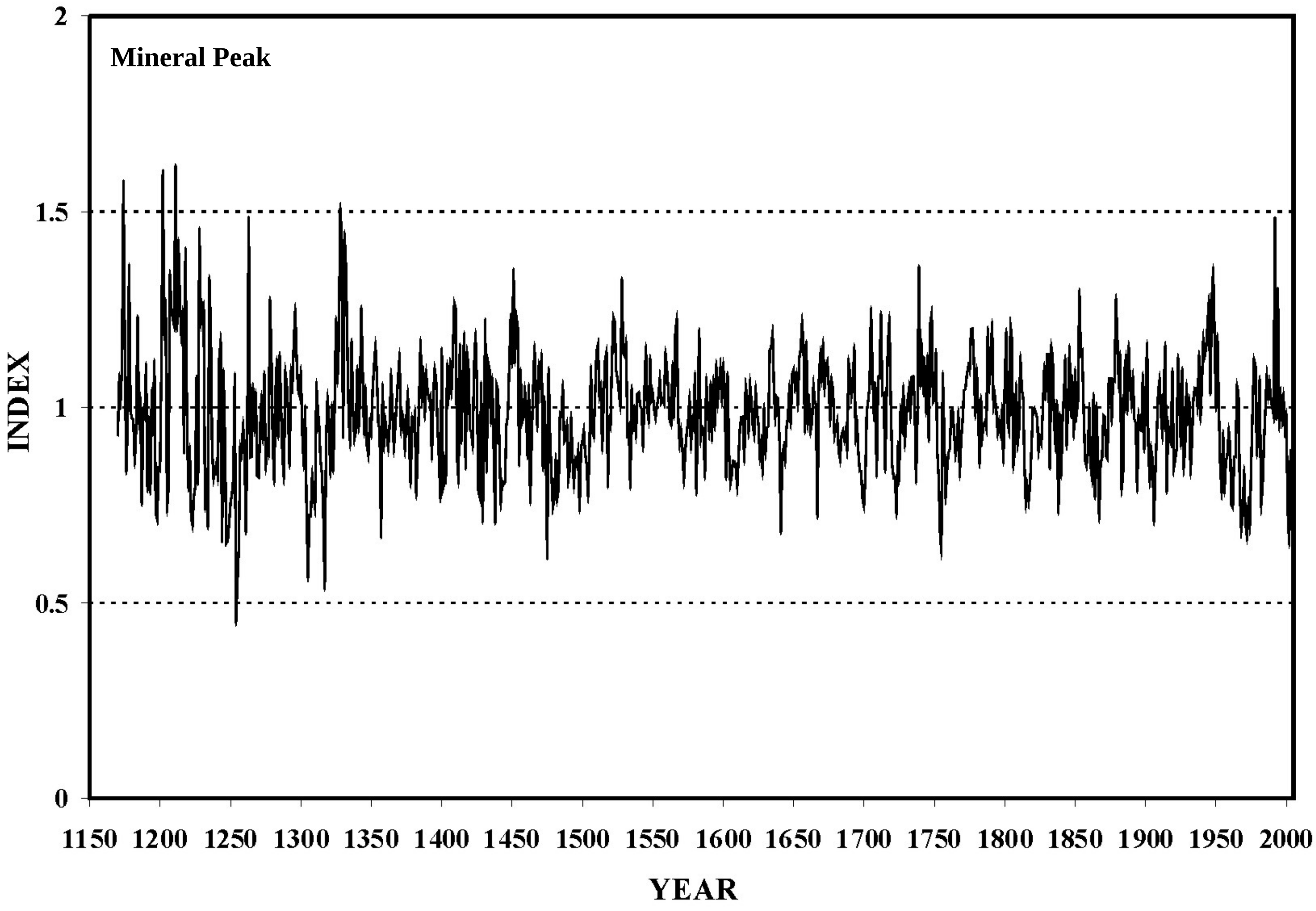

Figure 3.3. Mineral Peak whitebark pine chronology.

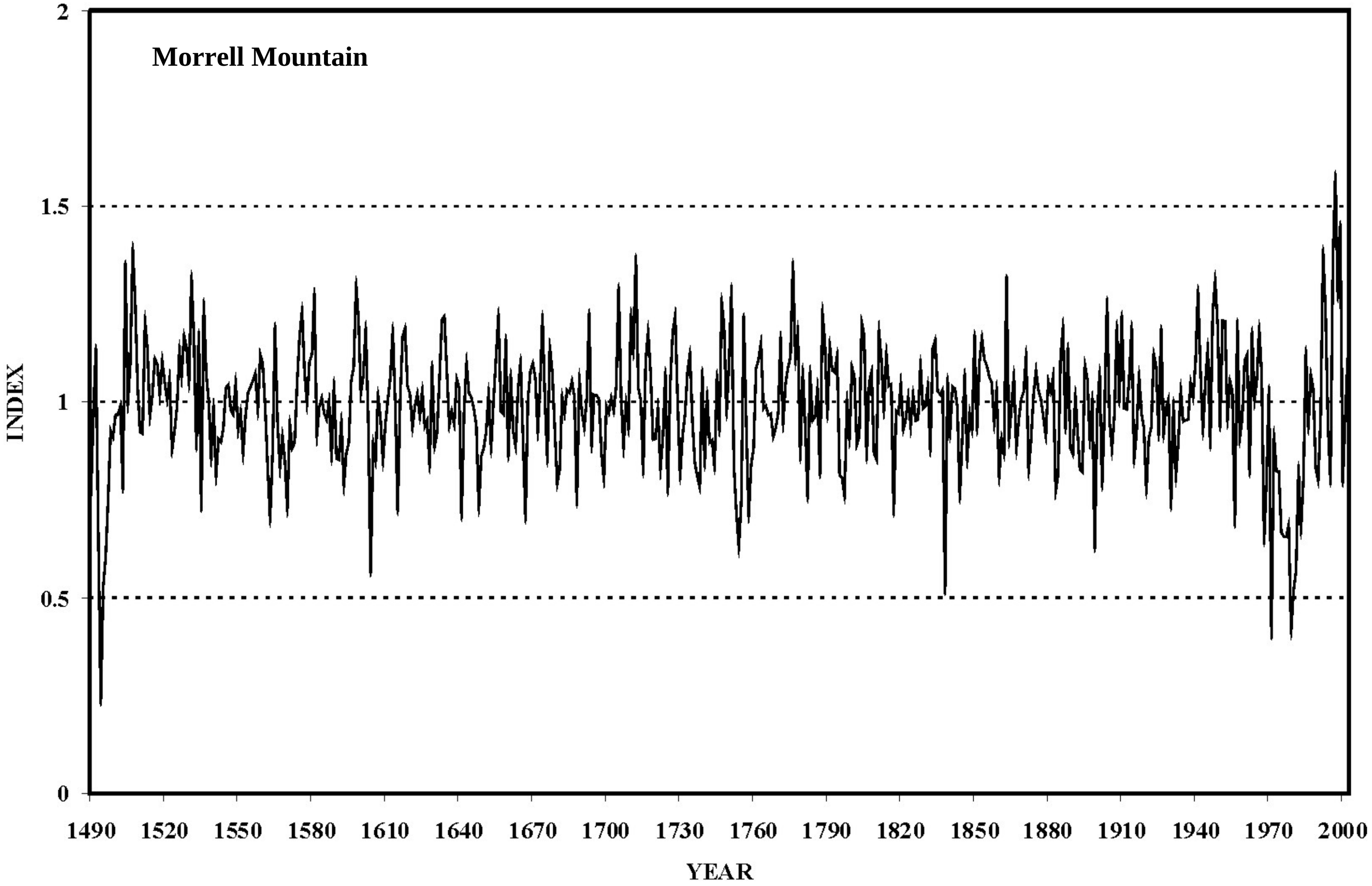

Figure 3.4. Morrell Mountain whitebark pine chronology.

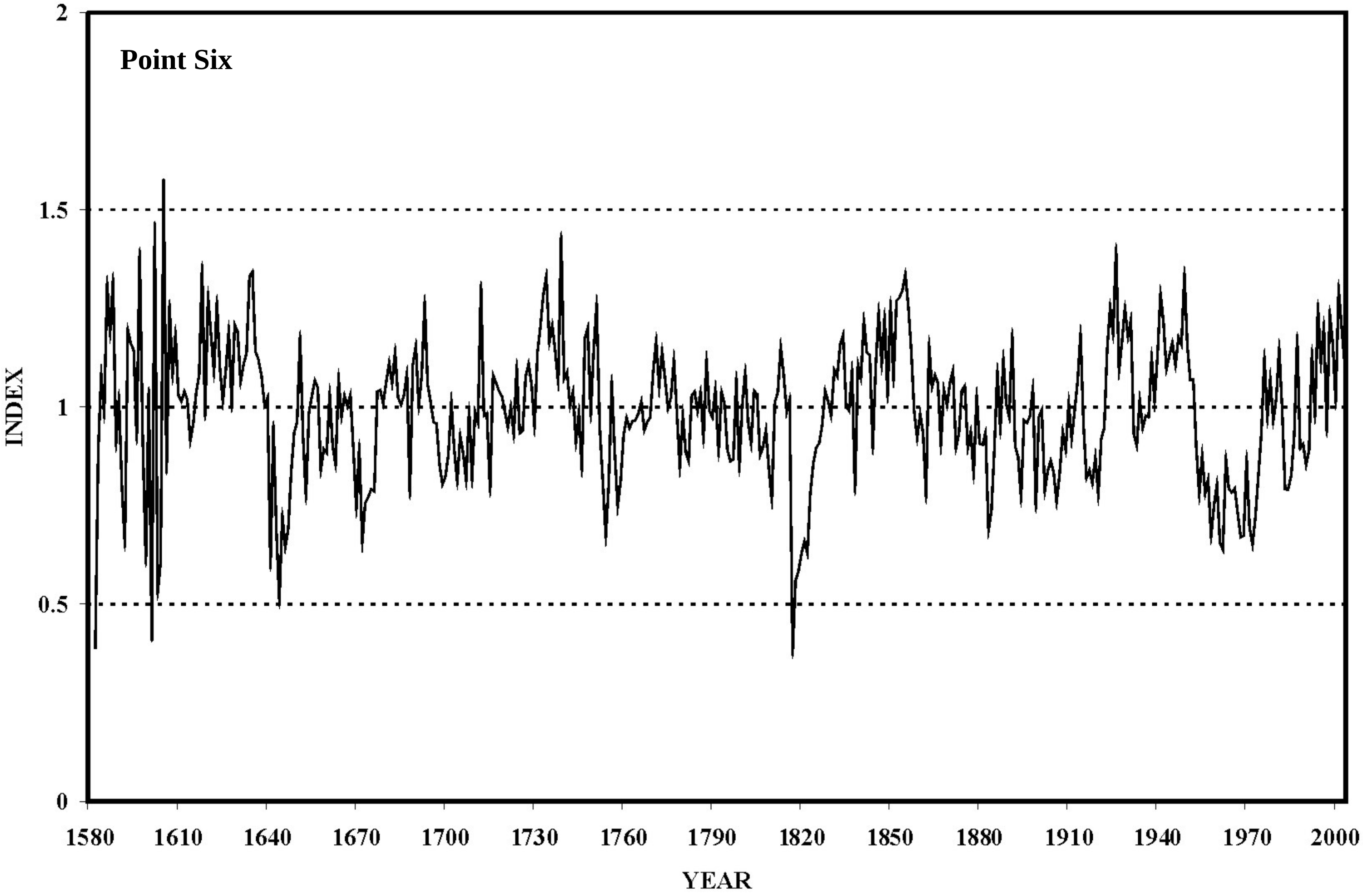

Figure 3.5. Point Six whitebark pine chronology.

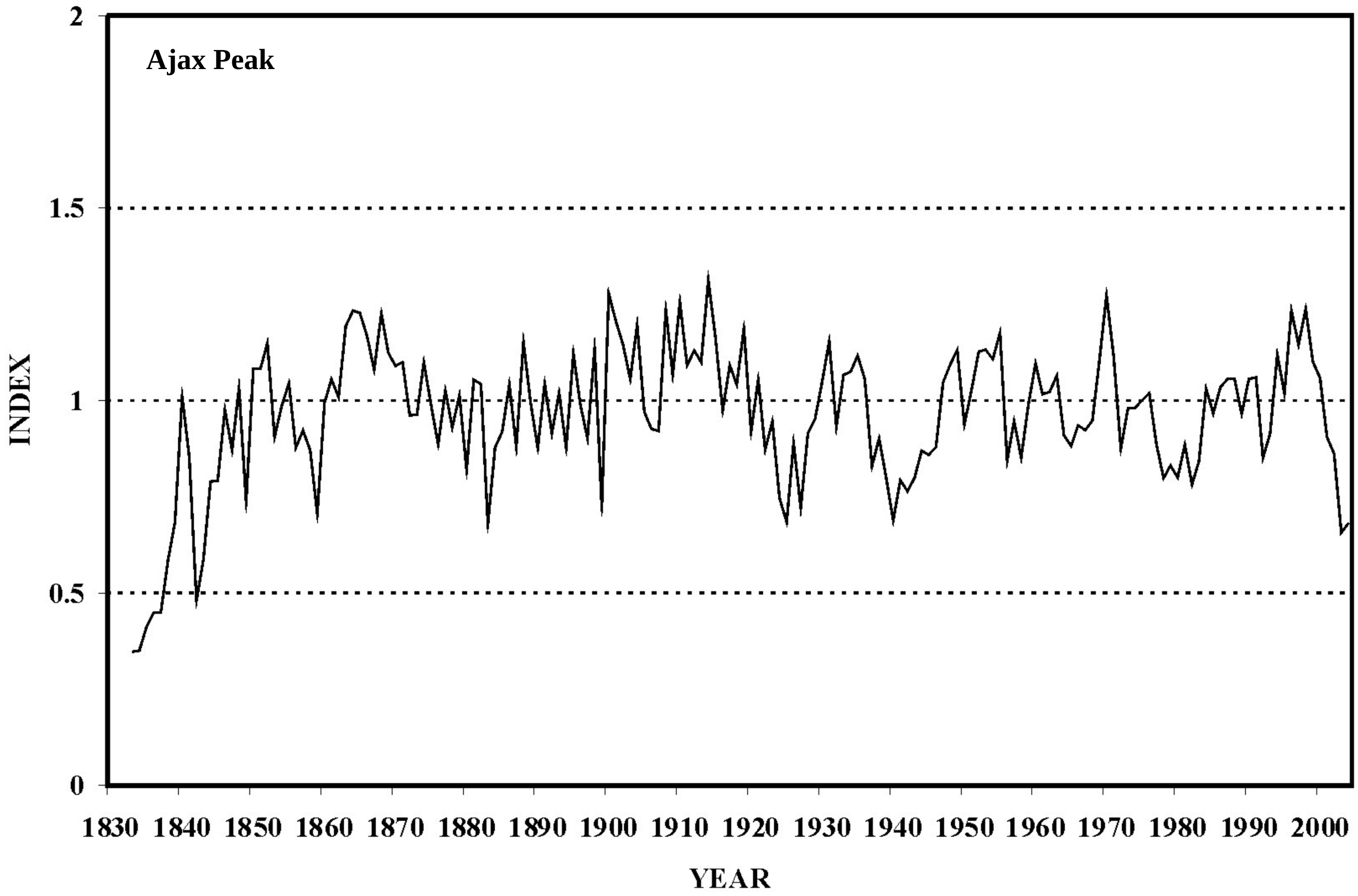

Figure 3.6. Ajax Peak whitebark pine chronology.

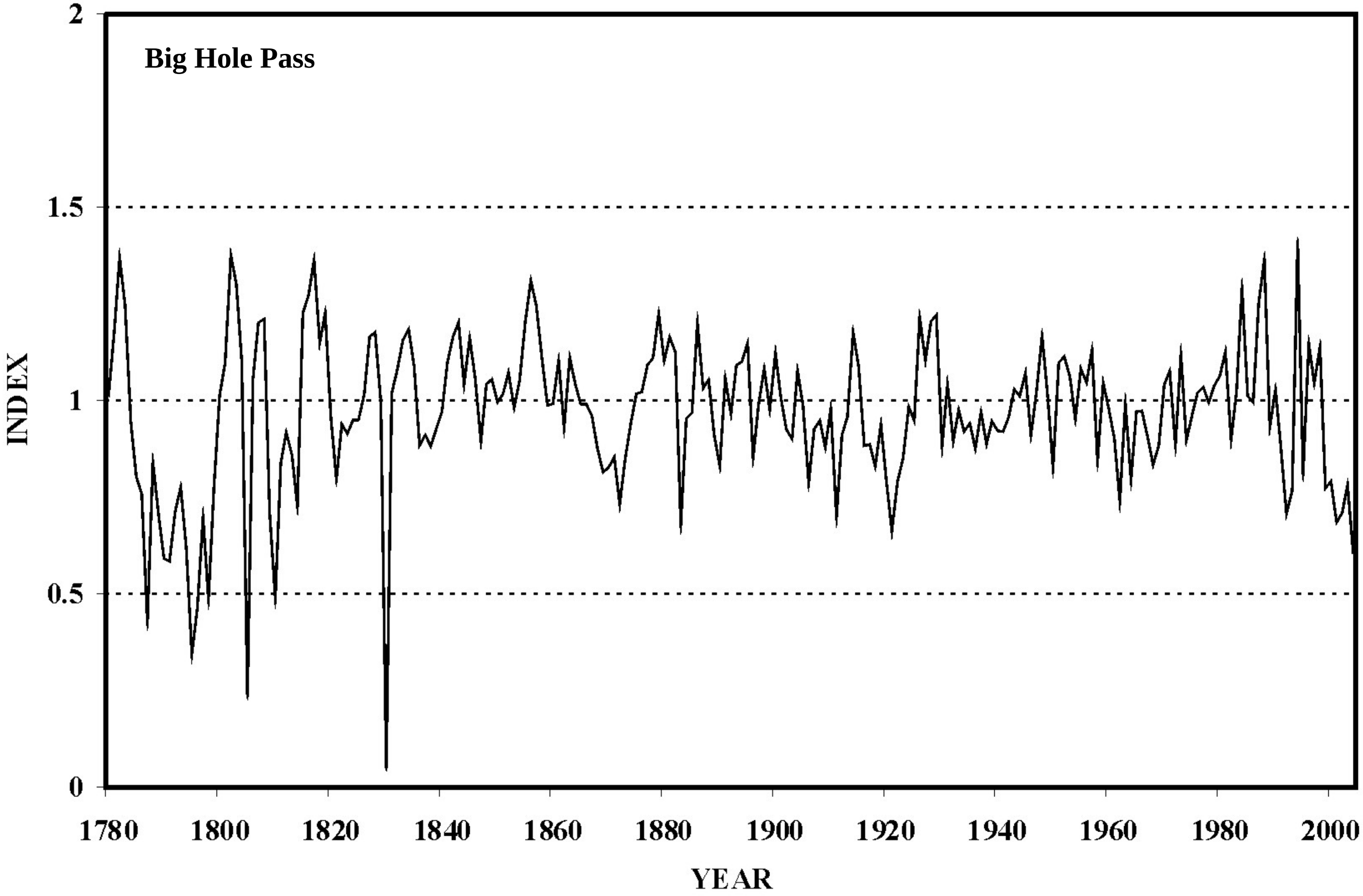

Figure 3.7. Big Hole Pass whitebark pine chronology.

explained by climate ($r^2 = 0.17$) and prior growth ($r^2 = 0.35$). At Big Hole Pass, 56% of the variability was explained by climate ($r^2 = 0.41$) and prior growth ($r^2 = 0.15$). Of the whitebark pine chronologies, the Big Hole Pass chronology had the strongest response to climate in comparison to prior growth.

The RFA revealed which climate variables were impacting whitebark pine growth and showed the importance of further investigation of the influence of drought, seasonalizing climate variables, and creating lagged climate variables. Specifically, the RFA showed a significant positive relationship between whitebark pine growth and the previous year's summer precipitation and the current year's spring temperature in most of the sites (Figures 3.8–3.10). Hornet Peak, the most northern site, responded differently from the central and southern sites with significant temperature and precipitation relationships in the previous fall season (Figure 3.8). Morrell Mountain, one of the central sites, showed a strong positive relationship with November precipitation, but the response was weaker than with the previous year's summer precipitation (Figure 3.9b).

The correlation analysis indicated a strong response between whitebark pine growth and precipitation and PDSI in our site chronologies from 1940–2005 (Figures 3.11–3.13). Ajax Peak and Big Hole Pass had the highest positive correlations between tree growth and spring and previous summer PDSI. The positive correlation indicates that these sites are responding well to a combination of precipitation, temperature, and available soil moisture. The growing season (June to September) begins when temperatures warm and snowpack begins to thaw. Whitebark pine seem to respond well

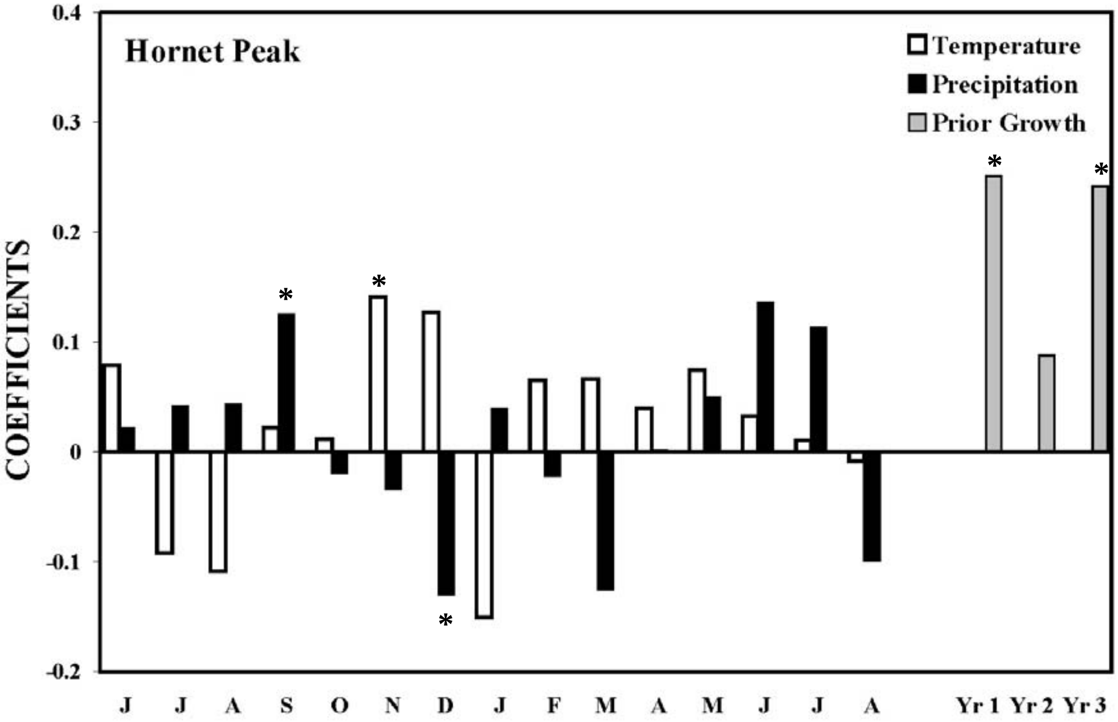

Figure 3.8. Results from the response function analysis for Hornet Peak, showing the effects of temperature and precipitation (1906–2005) on whitebark pine growth. Statistically significant relationships are indicated by * ($p < 0.05$).

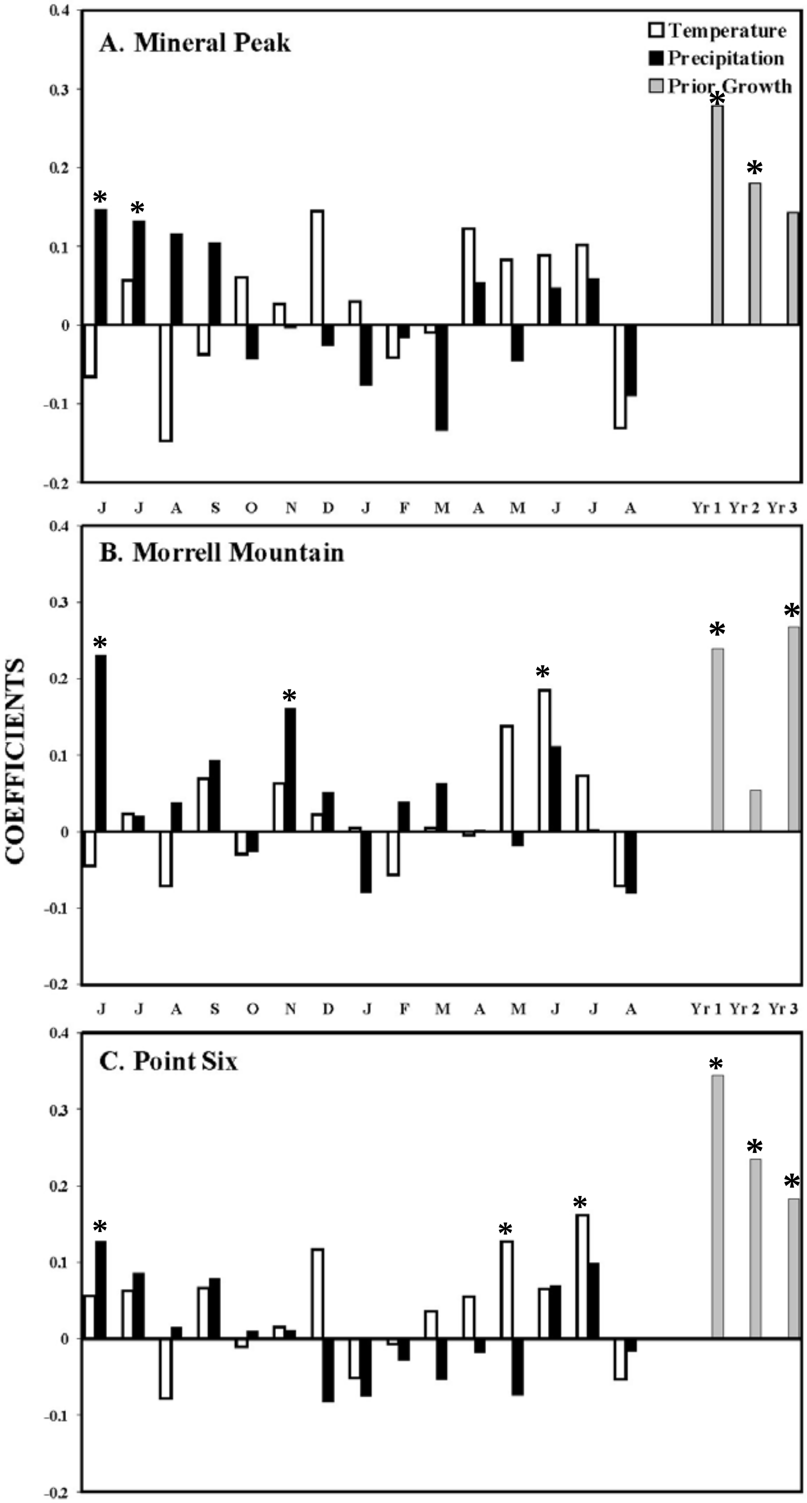

Figure 3.9. Results from the response function analysis for (A) Mineral Peak, (B) Morrell Mountain, and (C) Point Six, showing the effects of temperature and precipitation (1904–2003) on whitebark pine growth. Statistically significant relationships are indicated by * ($p < 0.05$).

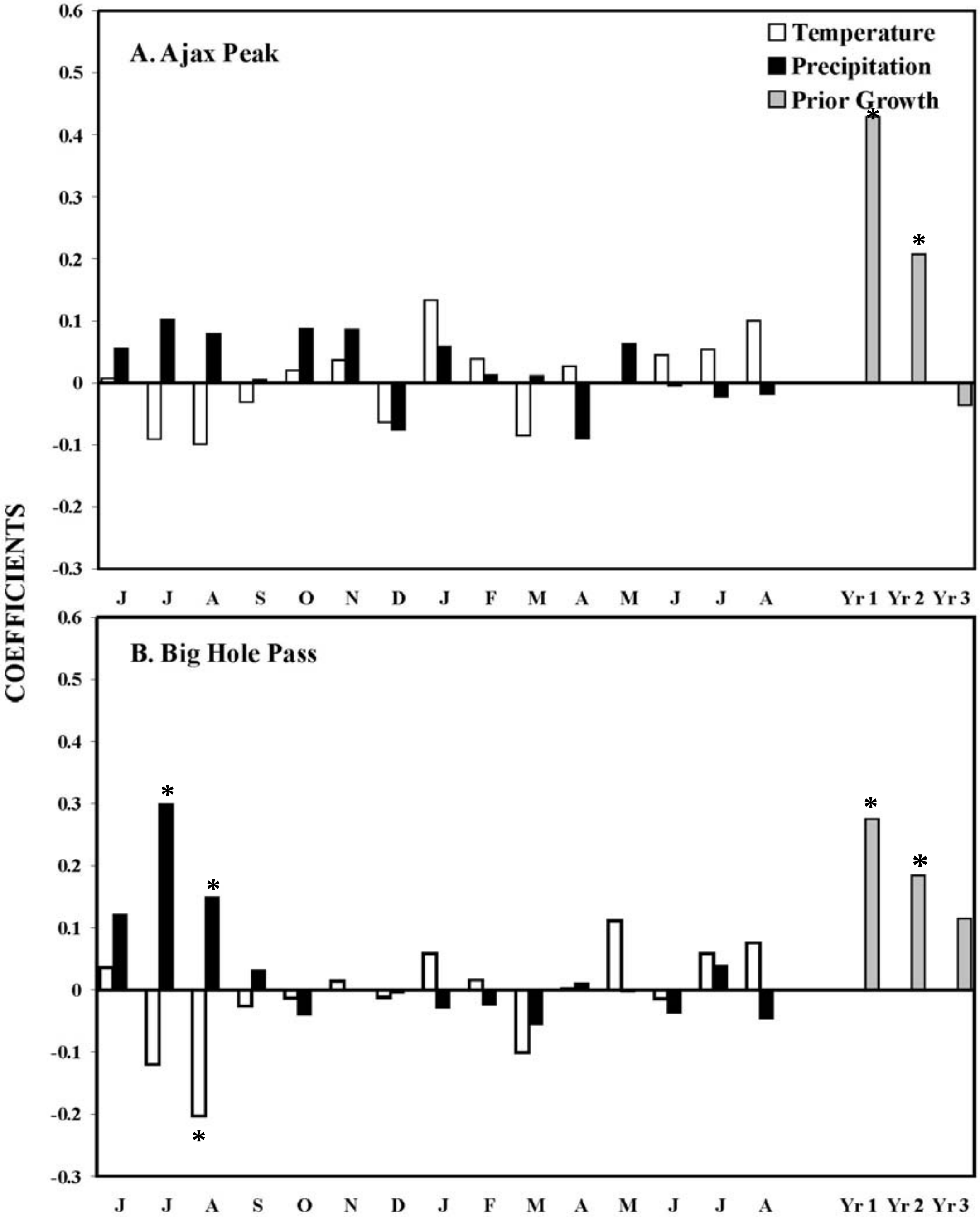

Figure 3.10. Results from the response function analysis for (A) Ajax Peak, and (B) Big Hole Pass showing the effects of temperature and precipitation (1905–2004) on whitebark pine growth. Statistically significant relationships are indicated by * ($p < 0.05$).

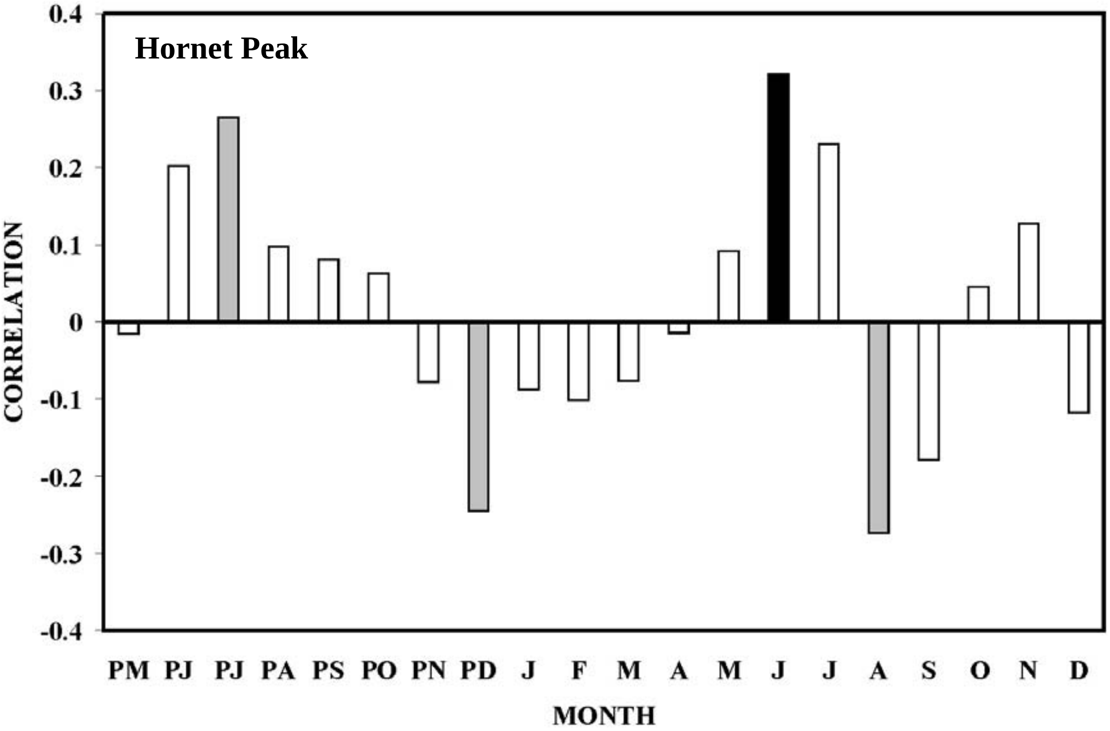

Figure 3.11. Correlation analysis between the Hornet Peak chronology and regional precipitation. Month abbreviations preceded with a "P" indicate the previous year. Gray solid bars indicate significant values of $p < 0.05$, and black solid bars indicate higher significant values of $p < 0.01$.

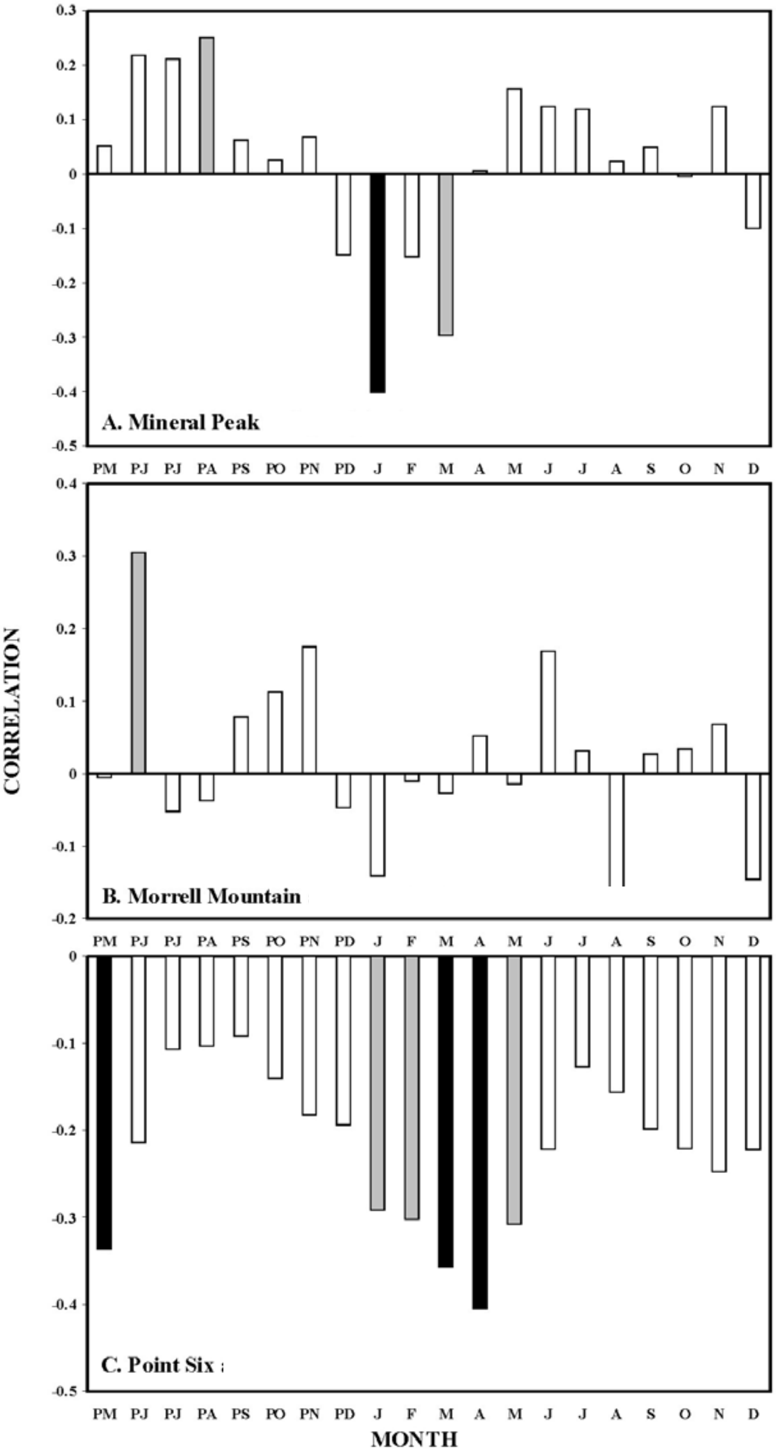

Figure 3.12. Correlation analysis for the Lolo National Forest between (A) Mineral Peak and precipitation, (B) Morrell Mountain and precipitation, and (C) Point Six PDSI. Month abbreviations preceded with a "P" indicate the previous year. Gray solid bars indicate significant values of $p < 0.05$, and black solid bars indicate higher significant values of $p < 0.01$.

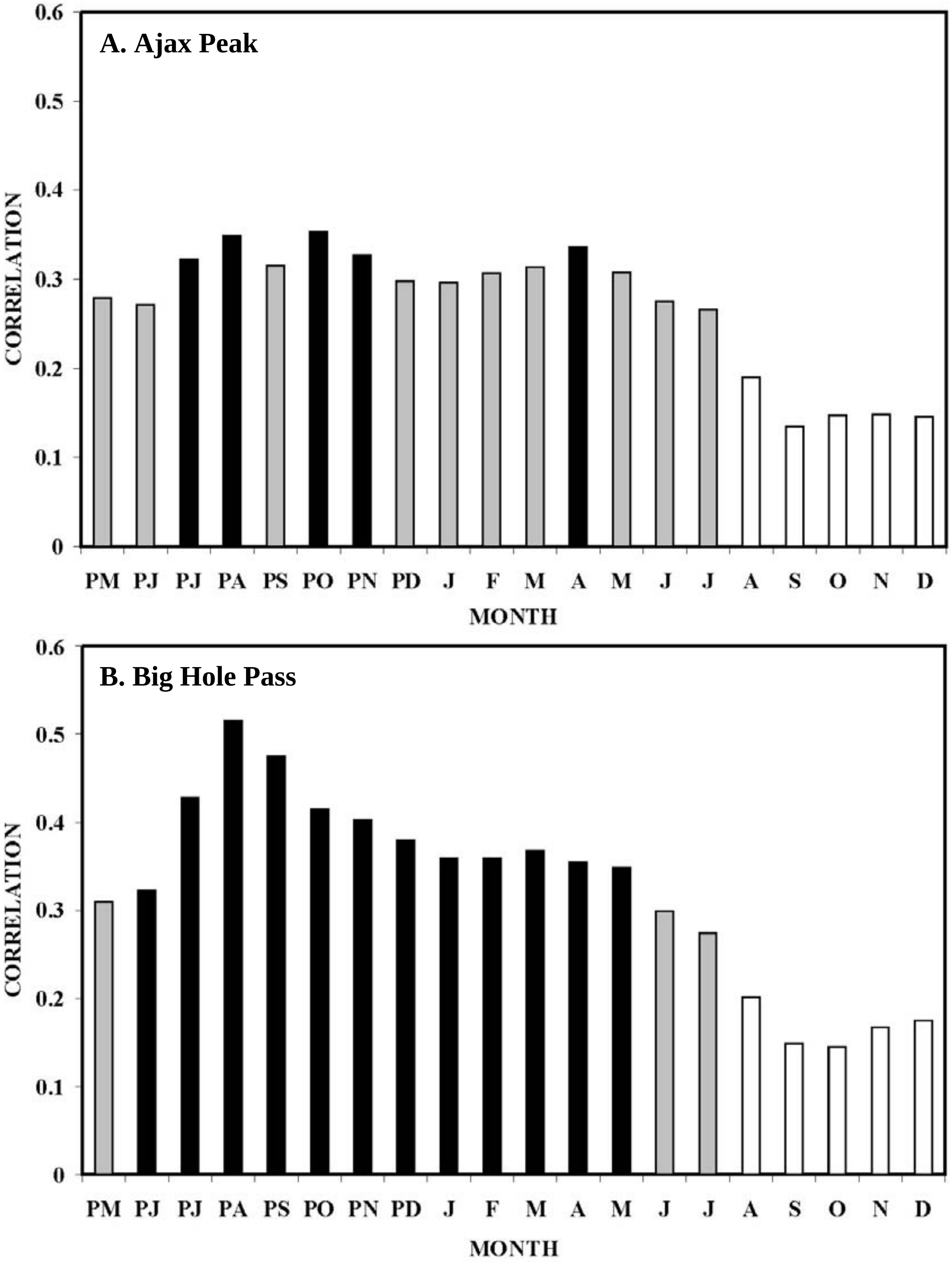

Figure 3.13. Correlation analysis for the Beaverhead-Deerlodge National Forest between the (A) Ajax Peak chronology and regional PDSI and the (B) Big Hole Pass chronology and PDSI. Month abbreviations preceded with a "P" indicate the previous year. Gray solid bars indicate significant values of $p < 0.05$, and black solid bars indicate higher significant values of $p < 0.01$.

to the available soil moisture in the current spring and also the previous spring in the Beaverhead-Deerlodge National Forest. Conversely, Point Six had a strong negative relationship with tree growth and PDSI for previous and current months. The whitebark pine at Point Six had an inverse relationship with PDSI that shows trees respond well during dry periods in the spring.

Hornet Peak, Morrell Mountain, and Mineral Peak had the highest correlations between tree growth and precipitation. The positive correlations in the previous summer indicate that an increase in precipitation in the previous year's summer results in increased tree growth during the current growing season. We found a strong negative relationship with tree growth at Hornet Peak, Mineral Peak, and Point Six during the winter months when precipitation is in the form of snow and snowpack levels are high. Hornet Peak also had a strong positive correlation to June precipitation. We also analyzed site-specific PRISM climate parameter data and found the strongest relationships between our whitebark pine chronologies and PRISM precipitation data (Figures 3.14–3.16). However, correlations between our chronologies and PRISM data were weaker than with the divisional climate data from NOAA.

Seasonalized variables were developed and analyzed using the results from the correlation analysis for PDSI at Ajax Peak, Big Hole Pass, and Point Six, and precipitation at Hornet Peak, Mineral Peak, and Morrell Mountain. The seasons during which precipitation and PDSI exhibited the strongest statistical relationship with tree growth occurred in the previous summer and current spring. The Big Hole Pass whitebark pines responded the strongest to climate (PDSI, $r = 0.51$, $p < 0.001$) of all the sites, followed by Mineral Peak (precipitation, $r = 0.44$, $p < 0.001$), Hornet Peak (precipitation,

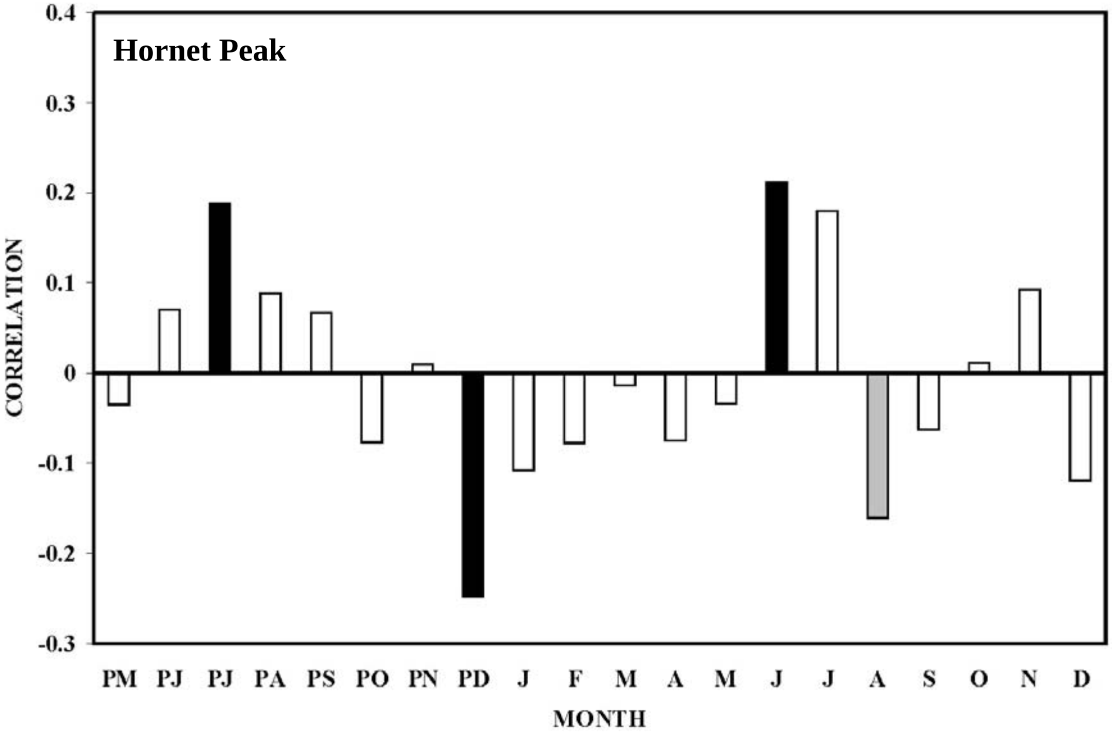

Figure 3.14. Correlation analysis for the Flathead National Forest, between the Hornet Peak chronology and PRISM precipitation. Month abbreviations preceded with a "P" indicate the previous year. Gray solid bars indicate significant values of $p < 0.05$, while black solid bars indicate higher significant values of $p < 0.01$.

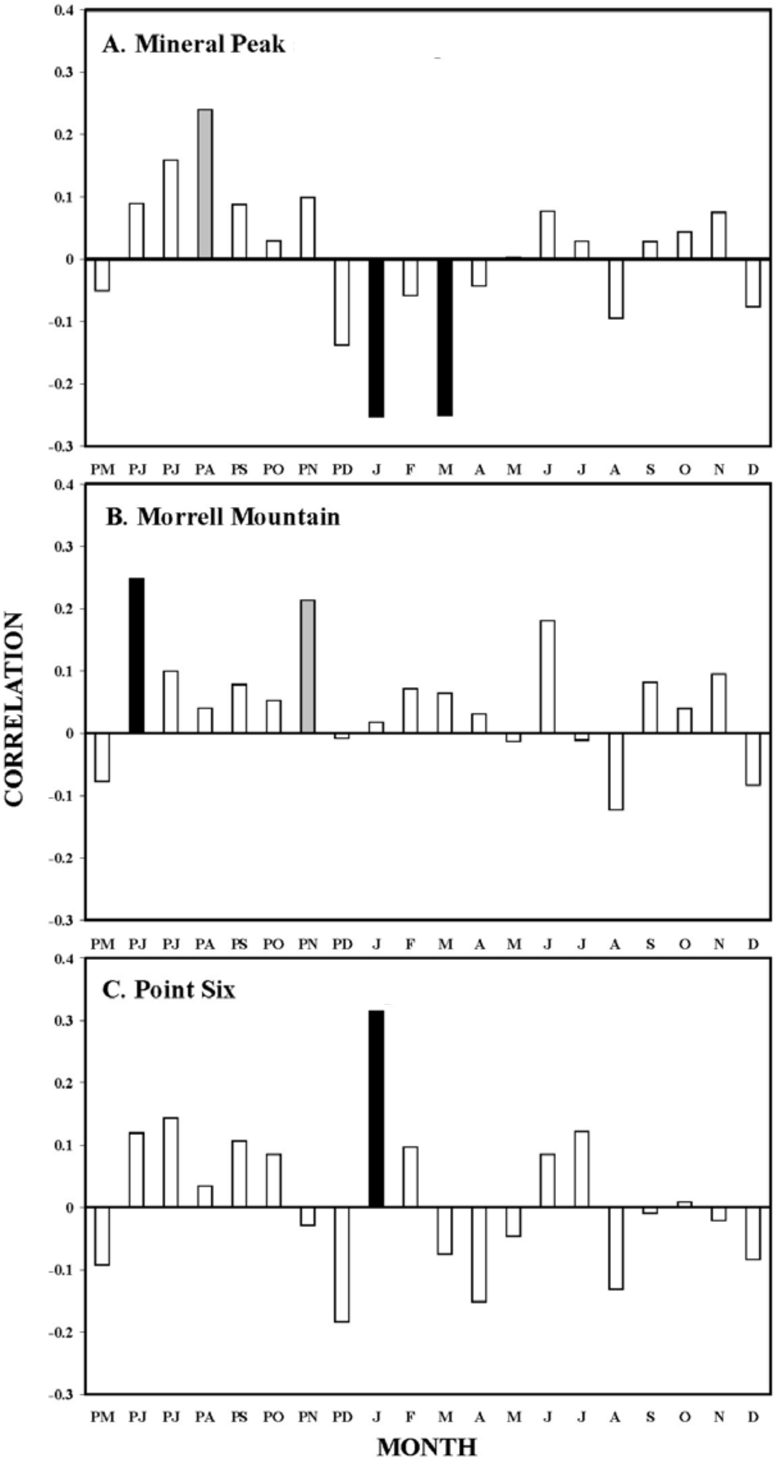

Figure 3.15. Correlation analysis for the Lolo National Forest between (A) Mineral Peak, (B) Morrell Mountain, and (C) Point Six and chronologies and PRISM precipitation data. Month abbreviations preceded with a "P" indicate the previous year. Gray solid bars indicate significant values of $p < 0.05$, while black solid bars indicate higher significant values of $p < 0.01$.

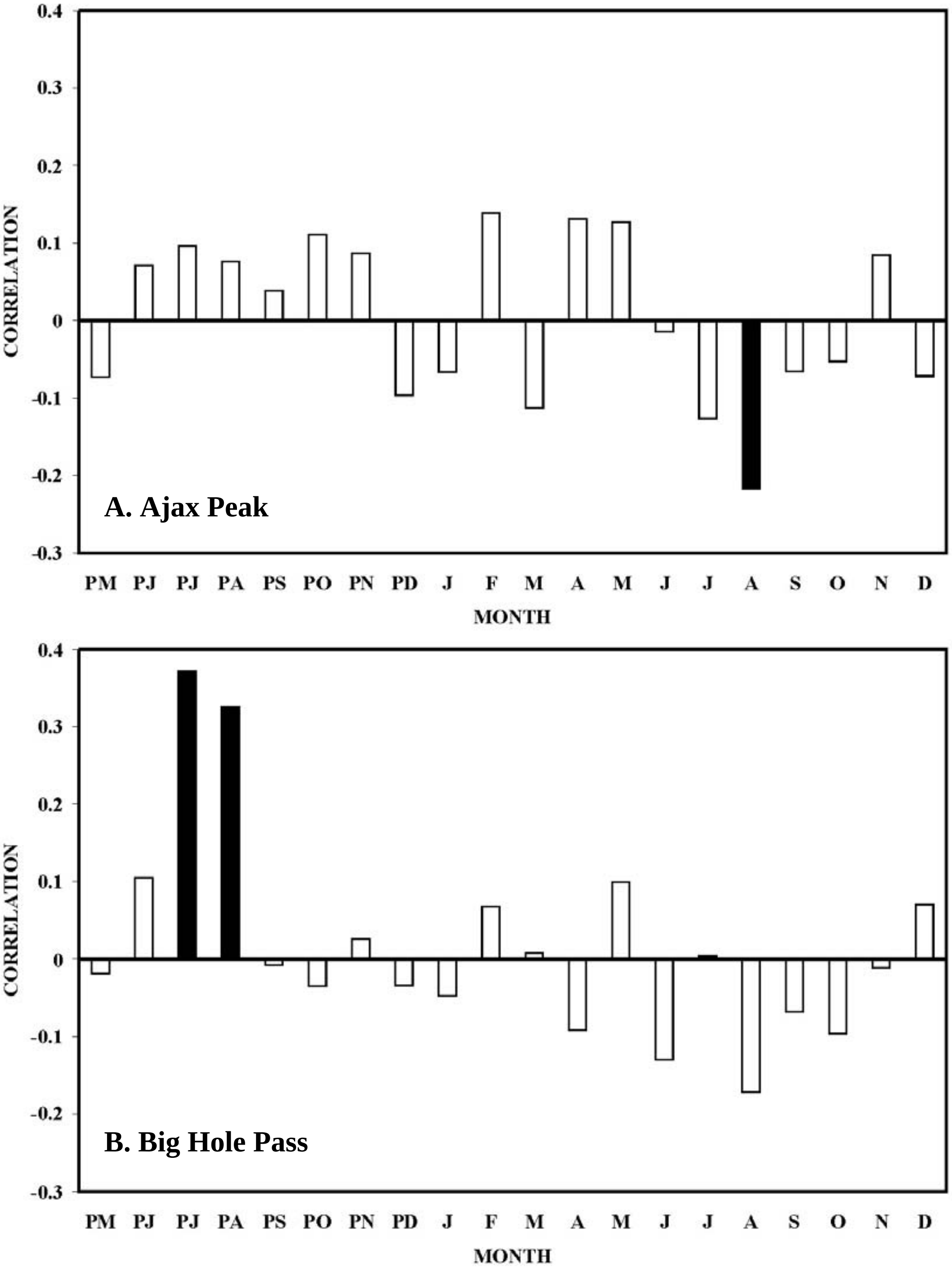

Figure 3.16. Correlation analysis for the Beaverhead-Deerlodge National Forest between (A) Ajax Peak and (B) Big Hole Pass chronologies and PRISM precipitation data. Month abbreviations preceded with a "P" indicate the previous year. Gray solid bars indicate significant values of $p < 0.05$, while black solid bars indicate higher significant values of $p < 0.01$.

$r = 0.36$, $p < 0.01$), Ajax Peak (PDSI, $r = 0.35$, $p < 0.01$), Point Six (PDSI, $r = -0.35$, $p < 0.01$), and Morrell Mountain (precipitation, $r = 0.30$, $p < 0.05$) (Table 3.4).

Regression models were based on our calibration period from 1940–2005. Our climate reconstruction models explained between 12% and 36% of the variability in our chronologies (Table 3.5). Outlier observations identified by high Studentized residuals were removed from the calibration models. Outlier years in the Ajax Peak and Big Hole Pass chronologies were 1985and 1989. Hornet Peak only had one outlier year in 1993. Point Six did not have any outlier years, Morrell Mountain had outlier years in 1940 and 1961, and Mineral Peak had outliers in 1950, 1972, and 1973. These outlier years may have been caused by disturbance events, such as fire or mountain pine beetle outbreaks, that corrupted the relationship between climate and tree growth during that year. Models showed a relatively close fit between the actual and estimated precipitation and PDSI values (Figures 3.17–3.19), with the exception of years influenced by exogenous disturbances. We used the regression equation developed from the calibration period (1940–2005) to reconstruct precipitation or PDSI for the entire period for each of the six whitebark pine chronologies (Figure 3.20–3.25).

Early portions of the six site reconstructions showed high variability characteristic of low sample depth in the tree-ring chronologies. The higher level of variance in the early portion of the reconstruction does not necessarily reflect a climate period with high variability and exceptional events shifting to a more moderate climate regime (Mann 2008). We retained these early portions of the reconstructions, however, to help differentiate between climate anomalies and possible disturbance events.

Table 3.4. Seasonal climate data for each site.

Study Site	**Period**	**Climate Variable**	**Season**	**Correlation Coefficient**
Hornet Peak	1940–2005	Precipitation	June–July	0.36**
Mineral Peak	1940–2003	Precipitation	January–March	0.44***
Morrell Mountain	1940–2003	Precipitation	pJune	0.30 *
Point Six	1940–2003	PDSI	January–May	-0.35**
Ajax Peak	1940–2004	PDSI	pJuly–pOctober	0.35**
Big Hole Pass	1940–2004	PDSI	pAugust–pSeptember	0.51***

* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$

Table 3.5. Seasonal climate reconstruction equations for each site.

Study Site	**Reconstruction Equation**
Hornet Peak	Reconstructed (June–July precipitation)$_t = 2.62(\mathrm{TR})_t + 0.90$
Mineral Peak	Reconstructed (January–March precipitation)$_t = -3.48(\mathrm{TR})_t + 8.03$
Morrell Mountain	Reconstructed (pJune precipitation)$_t = 8.90(\mathrm{TR})_t - 8.68$
Point Six	Reconstructed (January–May PDSI)$_t = -4.91(\mathrm{TR})_t + 4.87$
Ajax Peak	Reconstructed (pJuly–pOctober PDSI)$_t = 8.90(\mathrm{TR})_t - 8.65$
Big Hole Pass	Reconstructed (pAugust–pSeptember PDSI)$_t = 12.20(\mathrm{TR})_t - 11.77$

TR is the tree-ring index for year t

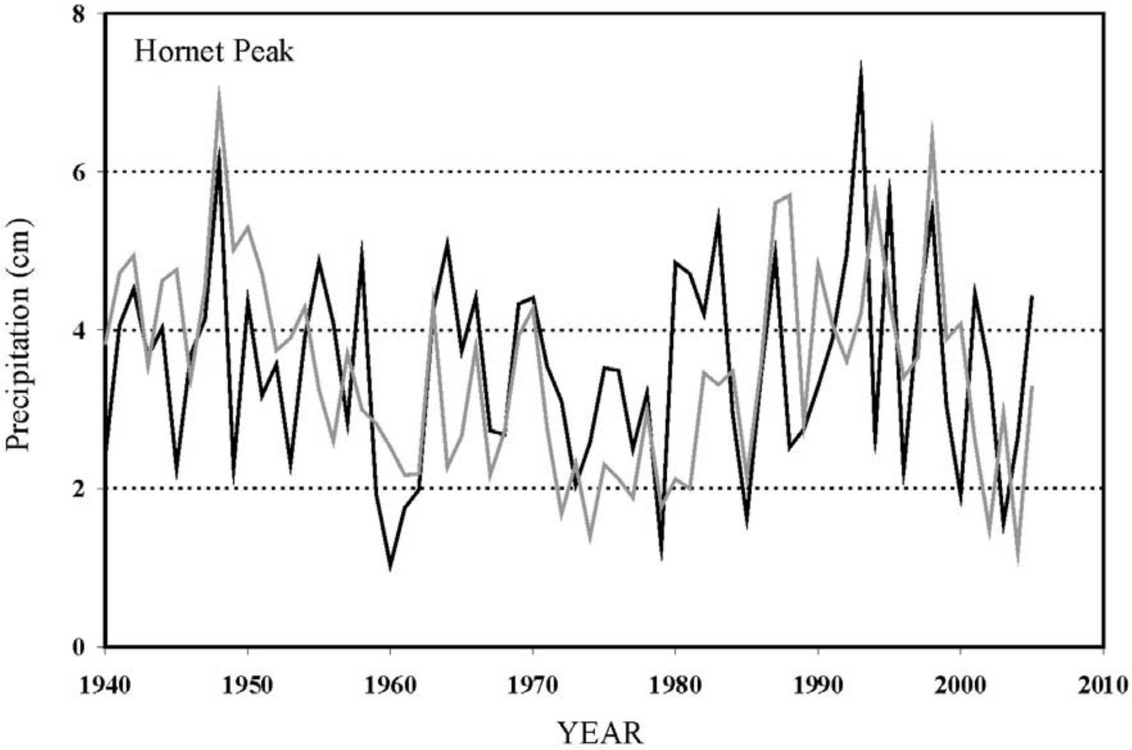

Figure 3.17. Observed (black line) and reconstructed (gray line) Hornet Peak precipitation (June–July).

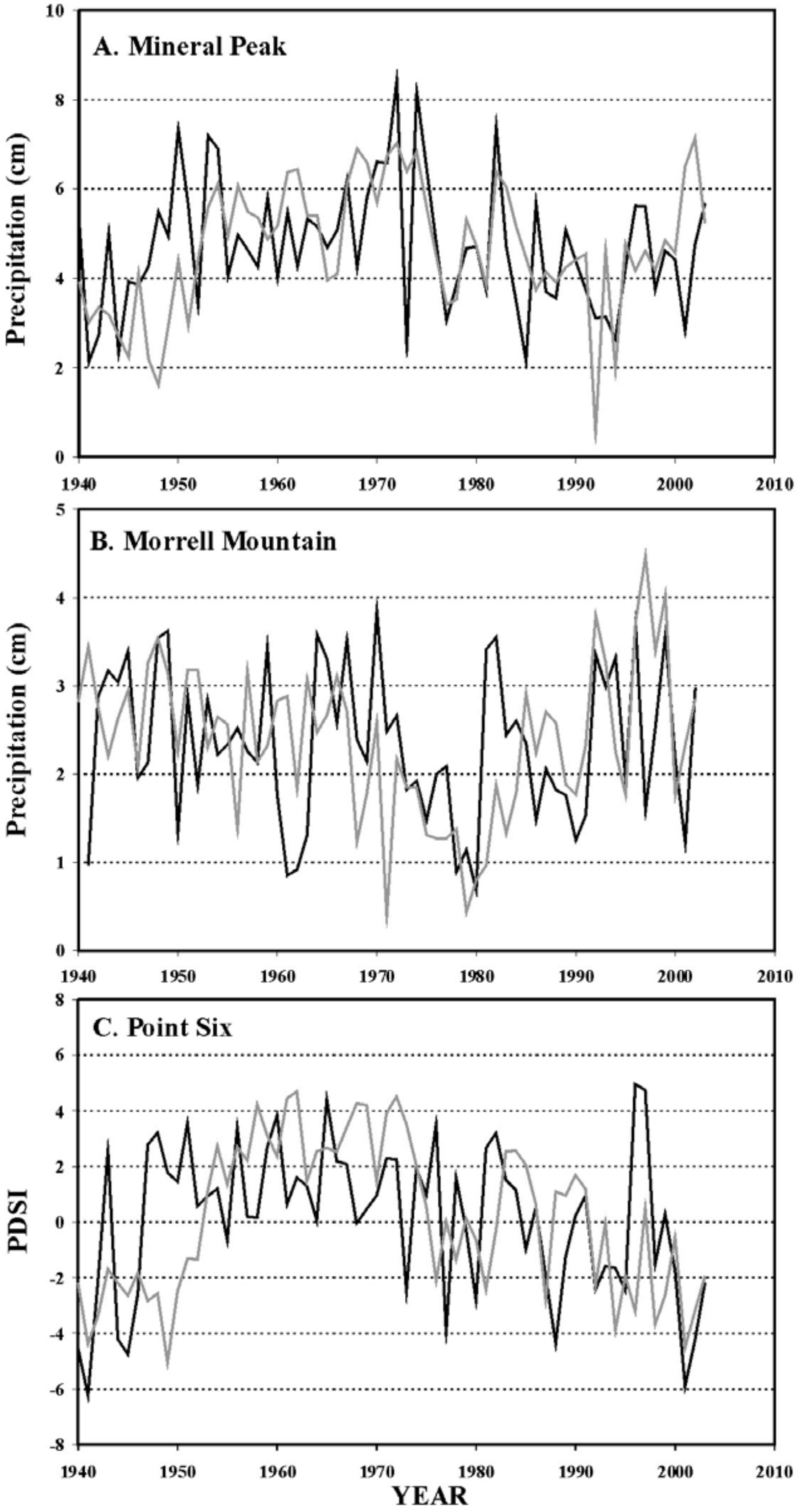

Figure 3.18. Observed (black line) and reconstructed (gray line): (A) Mineral Peak precipitation (January–March), (B) Morrell Mountain precipitation (previous June), and (C) Point Six PDSI (January–May).

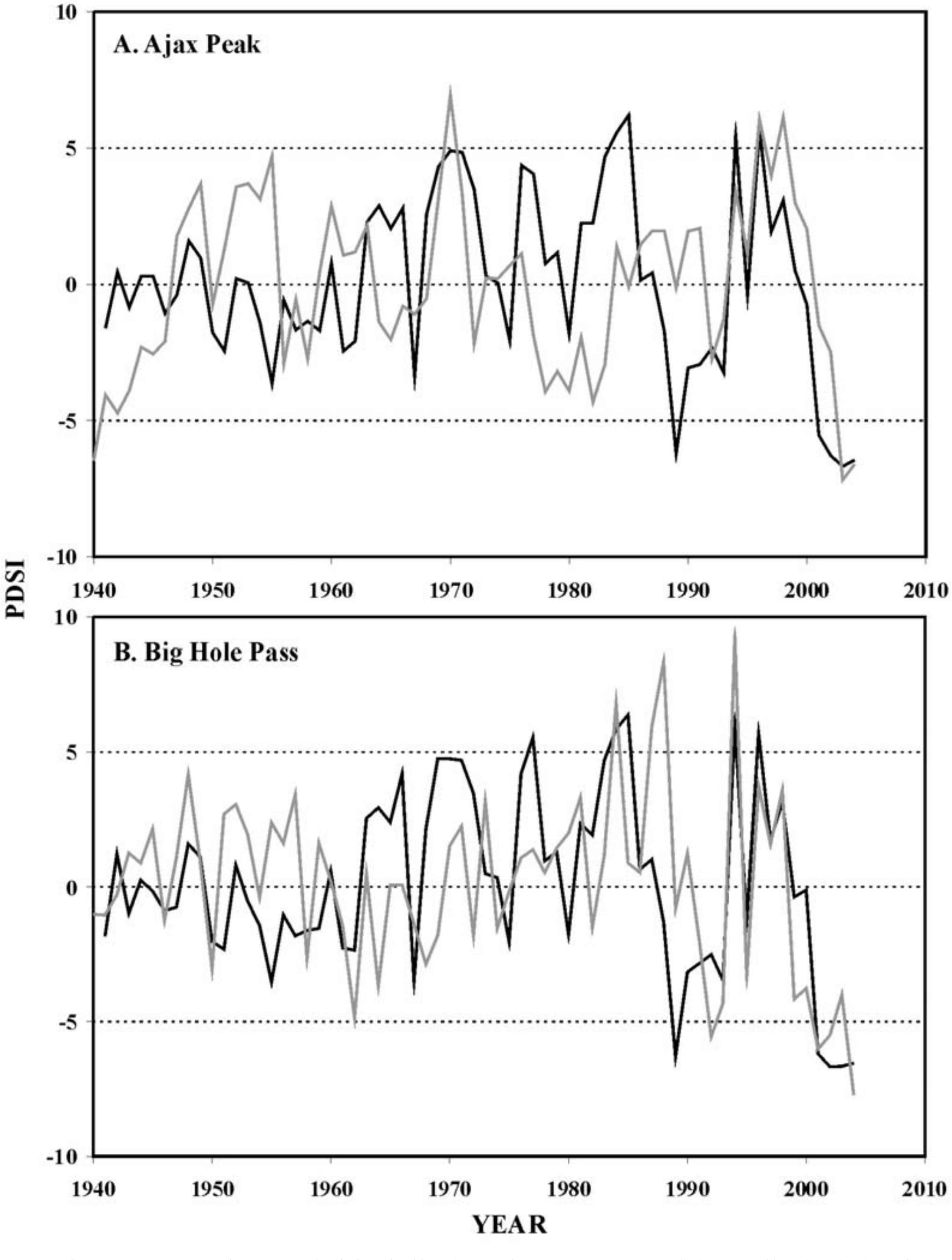

Figure 3.19. Observed (black line) and reconstructed (gray line): (A) Ajax Peak PDSI (previous July–previous October), and (B) Big Hole Pass PDSI (previous August–previous September).

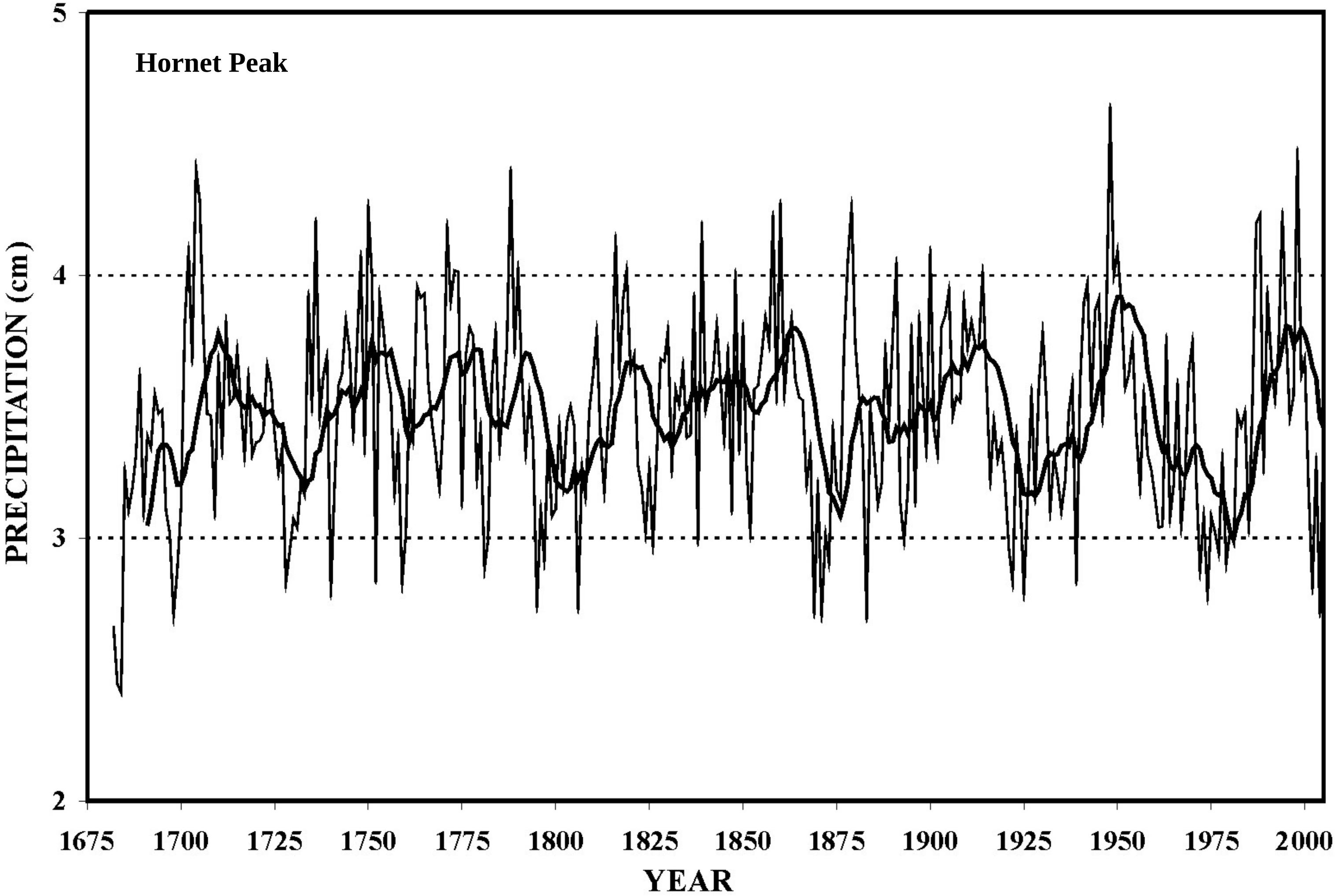

Figure 3.20. Reconstructed Hornet Peak June–July precipitation for the period AD 1682–2005. The thick black line is a 10-year moving average that shows interannual trends in the reconstruction.

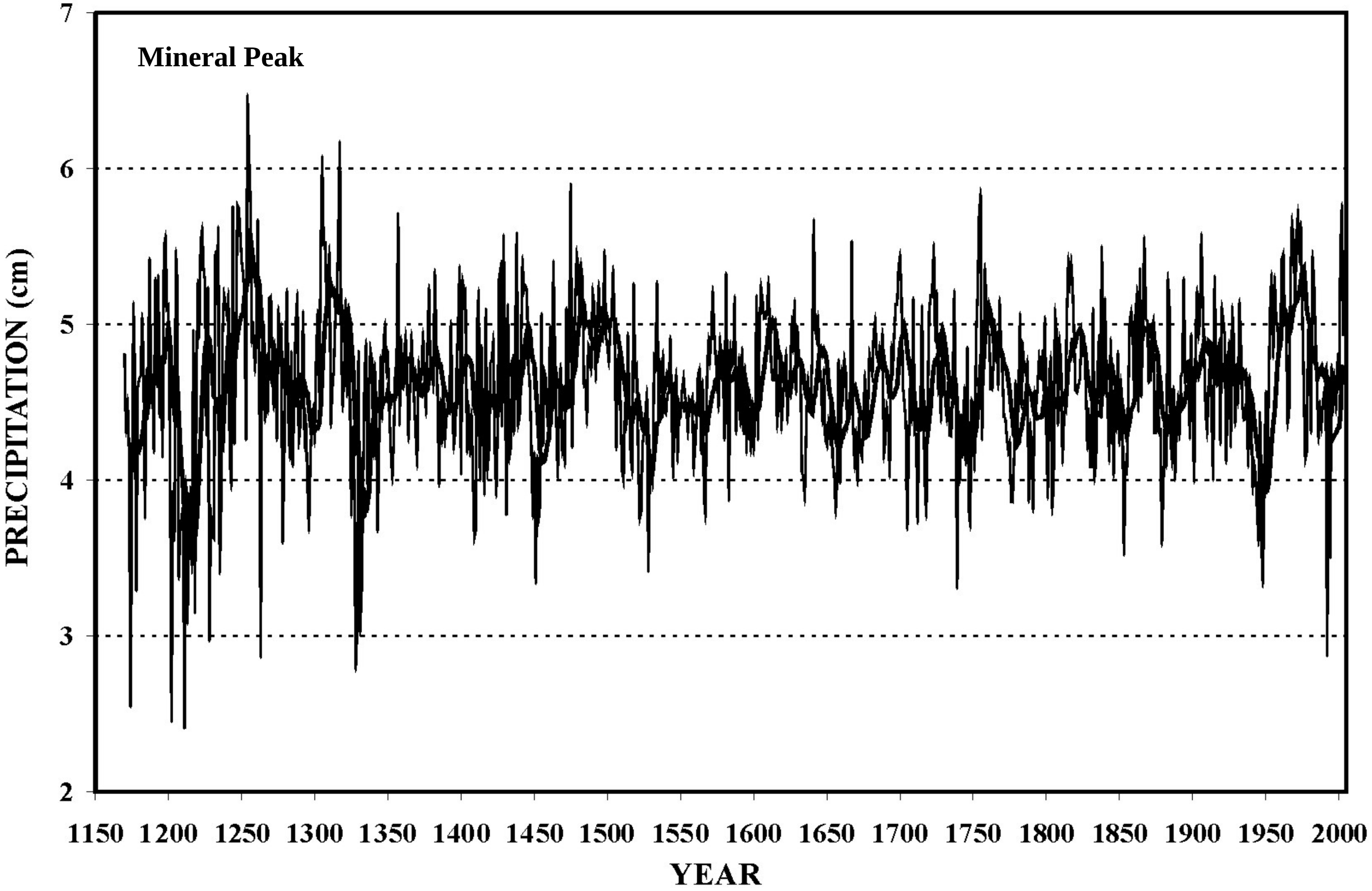

Figure 3.21. Reconstructed Mineral Peak January–March precipitation for the period AD 1171–2003. The thick black line is a 10-year moving average that shows interannual trends in the reconstruction.

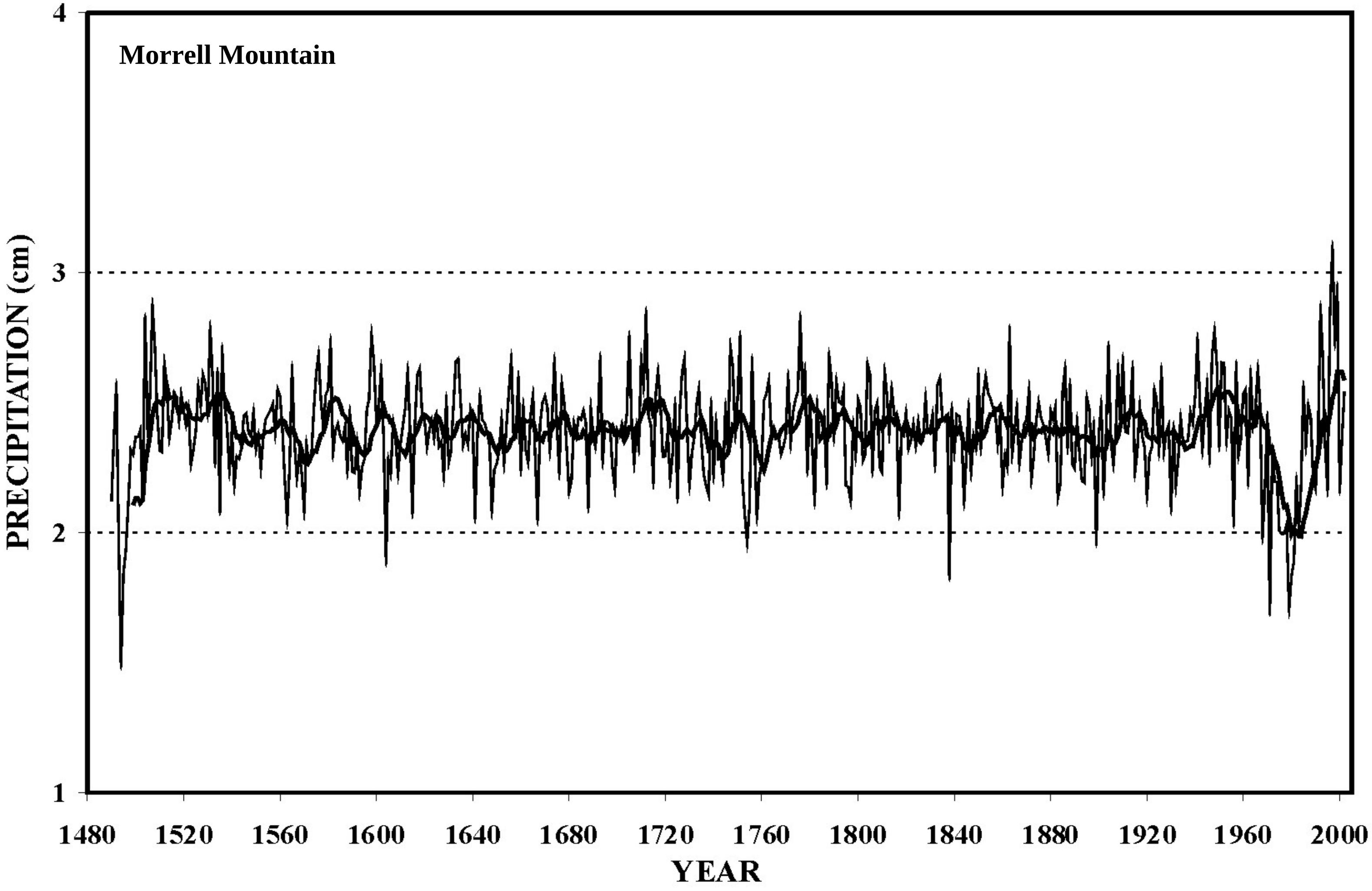

Figure 3.22. Reconstructed Morrell Mountain previous June precipitation for the period AD 1489–2003. The thick black line is a 10-year moving average that shows interannual trends in the reconstruction.

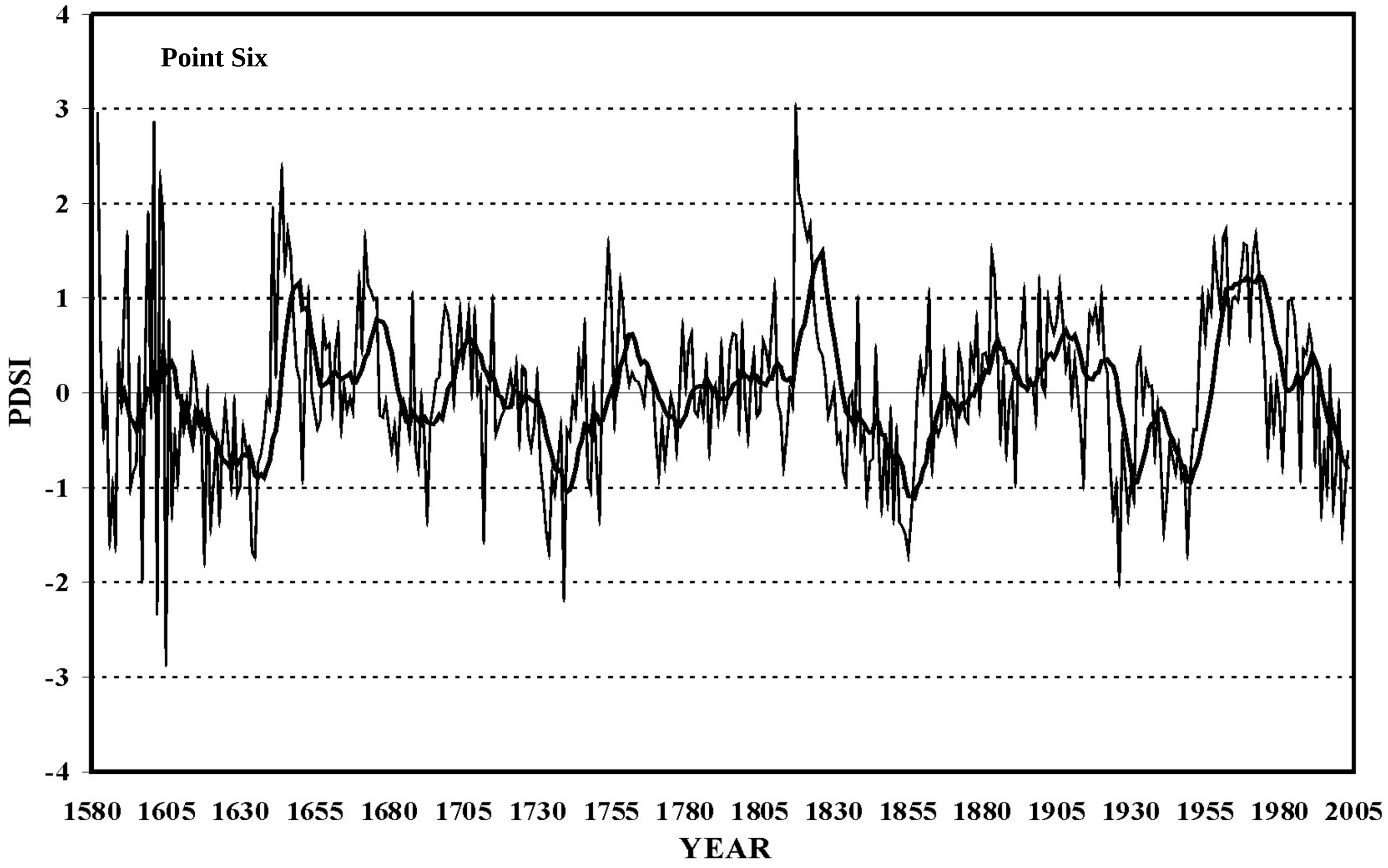

Figure 3.23. Reconstructed Point Six January–May PDSI for the period AD 1581–2003. The thick black line is a 10-year moving average that shows interannual trends in the reconstruction.

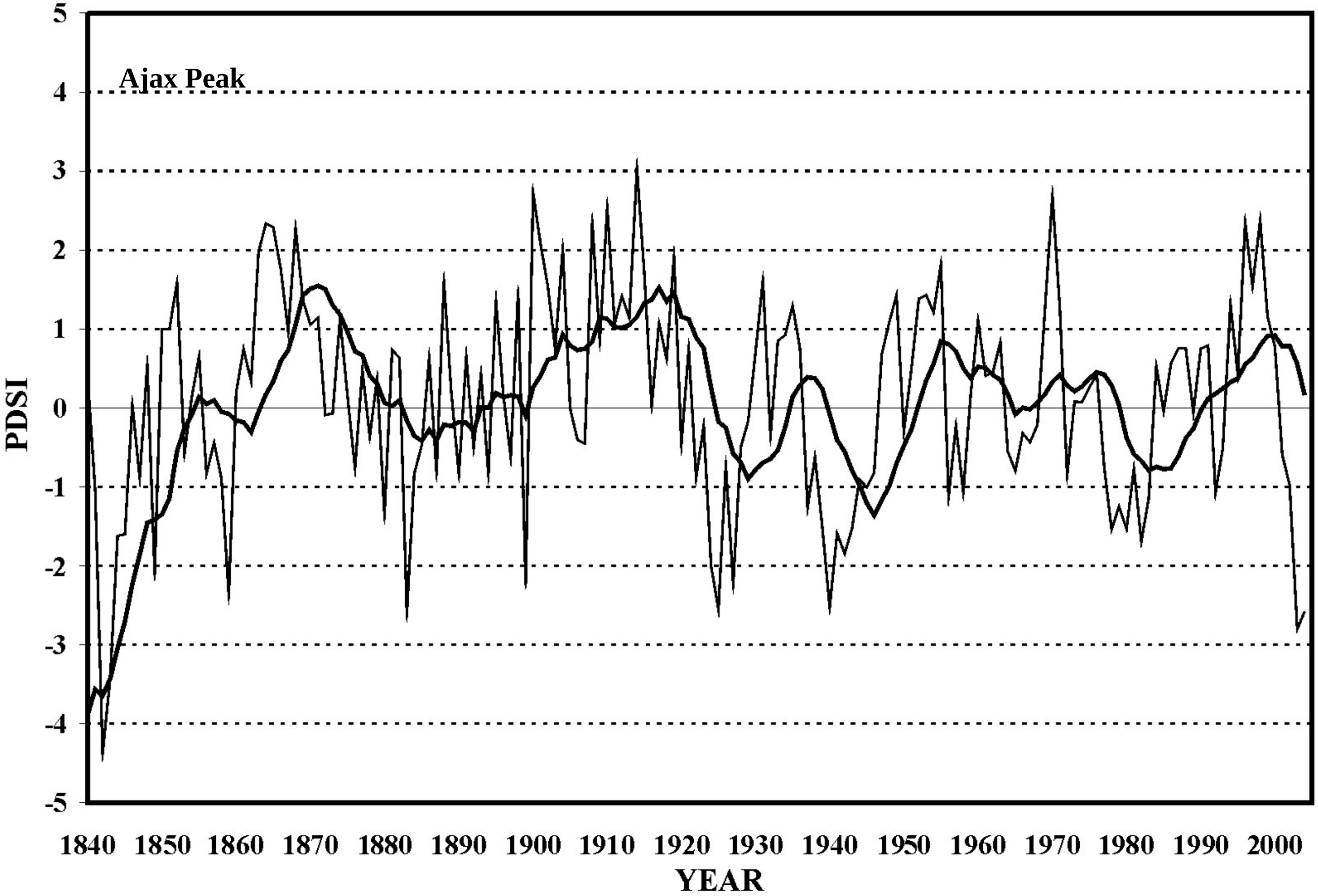

Figure 3.24. Reconstructed Ajax Peak previous July–previous October PDSI for the period AD 1832–2004. The thick black line is a 10-year moving average that shows interannual trends in the reconstruction.

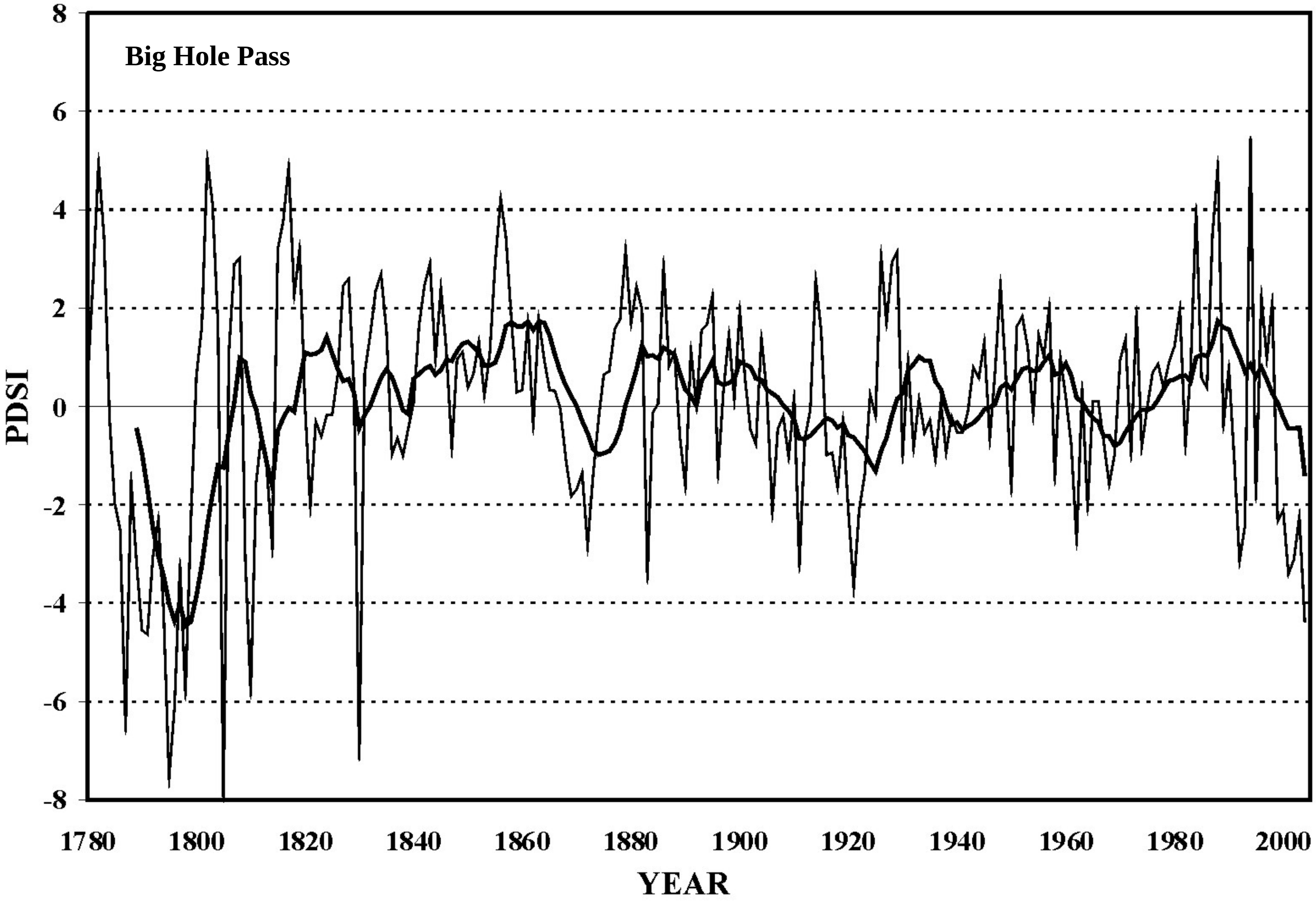

Figure 3.25. Reconstructed Big Hole Pass previous August–previous September PDSI for the period AD 1778–2005. The thick black line is a 10-year moving average that shows interannual trends in the reconstruction.

Therefore, climate trends in the data where the sample depth is low should be considered more carefully.

The PDSI reconstructions showed periods of moderate drought (PDSI values from –2 to –3) on a multicentury scale. An 1883 drought was present in both the Ajax Peak and Big Hole Pass reconstructions. Other common drought patterns include the early 1920s and the early 2000s. Point Six provided the longest PDSI reconstruction and showed moderate droughts that pre-dated the other reconstructions in 1602, 1605, and 1739. We also found a common extremely wet year (PDSI values above 3.0) in 1817 in the Big Hole Pass and Point Six reconstructions.

Hornet Peak and Morrell Mountain precipitation reconstructions showed a relatively dry period at both sites in the 1970s. Earlier dry periods at Hornet Peak included the mid-1700s, 1869–1873, 1883, and the 1920s. Morrell Mountain experienced less frequent dry years (1494, 1604, 1754, 1838, and 1899) when compared to Hornet Peak and Mineral Peak. Mineral Peak was the longest precipitation reconstruction but only had one dry year (1739) in common with another reconstructions (Point Six PDSI). Other dry years in the Mineral Peak reconstruction included 1174, 1202, 1211, 1263, 1328, 1451, 1528, 1853, 1879, 1948, and 1992.

3.4.3 Separating Disturbance Events and Climate Response

Mountain pine beetle outbreaks may have caused anomalous growth patterns in our climate reconstructions. In the site climate models used for the reconstructions, some of the identified outliers appeared to have been related to mountain pine beetle outbreaks in the western United States during the period from 1940 to 2005. Between 1970 and

1985, an extensive pine beetle outbreak occurred in the western United States and Canada (Safranyik and Carroll 2006). The whitebark pine chronologies at Morrell Mountain and Point Six showed below-average growth from 1970 to 1975 while precipitation and PDSI were relatively high in the early 1970s. Mineral Peak shows an inverse relationship in the early 2000s, with whitebark pine growth declining during a period of increasing precipitation. The next step was to explore whitebark pine growth without the influence of climate to examine the mountain pine beetle outbreak periods in the chronologies more closely.

The residual chronologies developed to examine the periodicity of departures from the mean, independent of climate, showed disturbance patterns at each site throughout the 20th century (Figures 3.26–3.28). The time series plot for our most northern site, Hornet Peak, indicated that actual whitebark pine growth agreed relatively well with predicted growth, although positive departures (indicating non-climate growth releases) were found in the 1940s and 1980s, a decade after known mountain pine beetle outbreaks (Figure 3.26). The three central sites showed different patterns of growth unrelated to climate over the past 100 years (Figure 3.27). The Mineral Peak time series plot revealed a close relationship between actual and predicted whitebark pine growth, but the residual chronology showed peaks in growth in the 1940s and 1990s. The Morrell Mountain time series plot showed that the predicted whitebark pine growth deviated from actual growth between 1965 and 1980. This 15-year growth suppression indicated a possible mountain pine beetle outbreak. Following the growth suppression, whitebark pines at Morrell Mountain showed a release from 1982 to 1986. Point Six exhibited a growth suppression beginning in 1952 and ending in 1975.

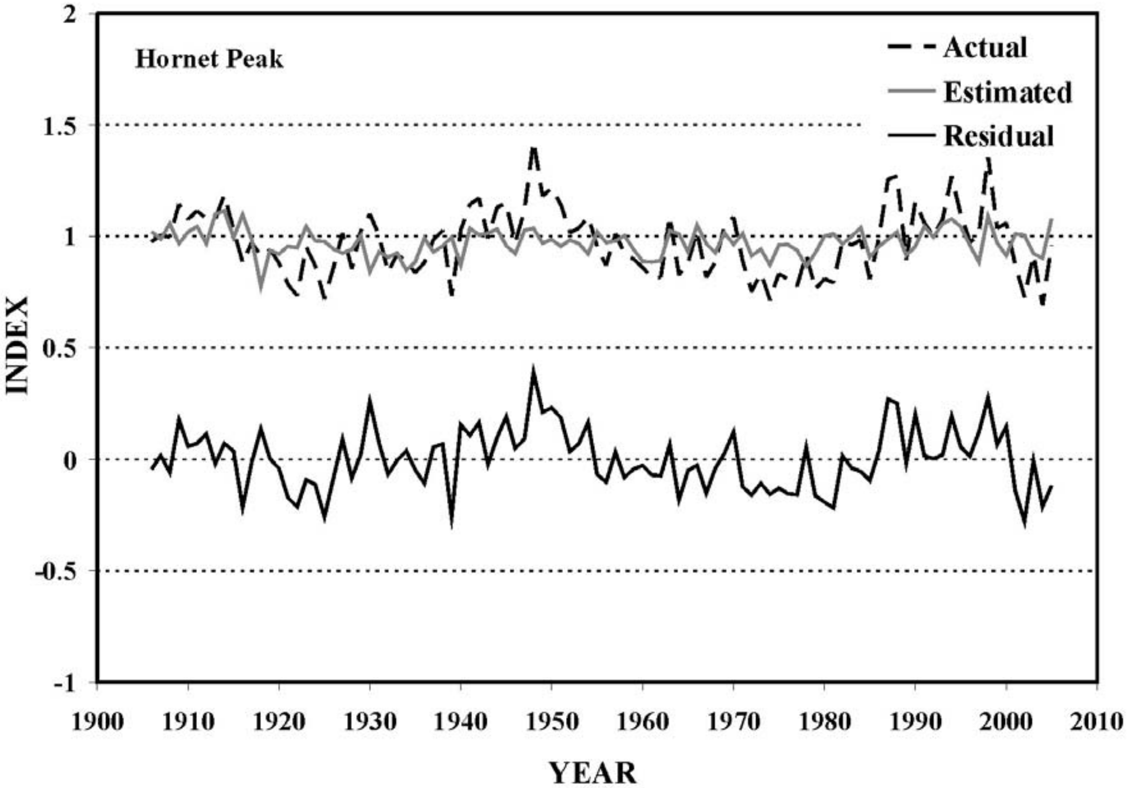

Figure 3.26. Actual and estimated indices of tree growth and their residuals developed for whitebark pines growing on Hornet Peak. "Actual" indicates the actual whitebark pine growth, "estimated" indicates the estimated annual whitebark pine growth based on the significant climate variables, and "residual" is the difference between the actual and estimated chronologies.

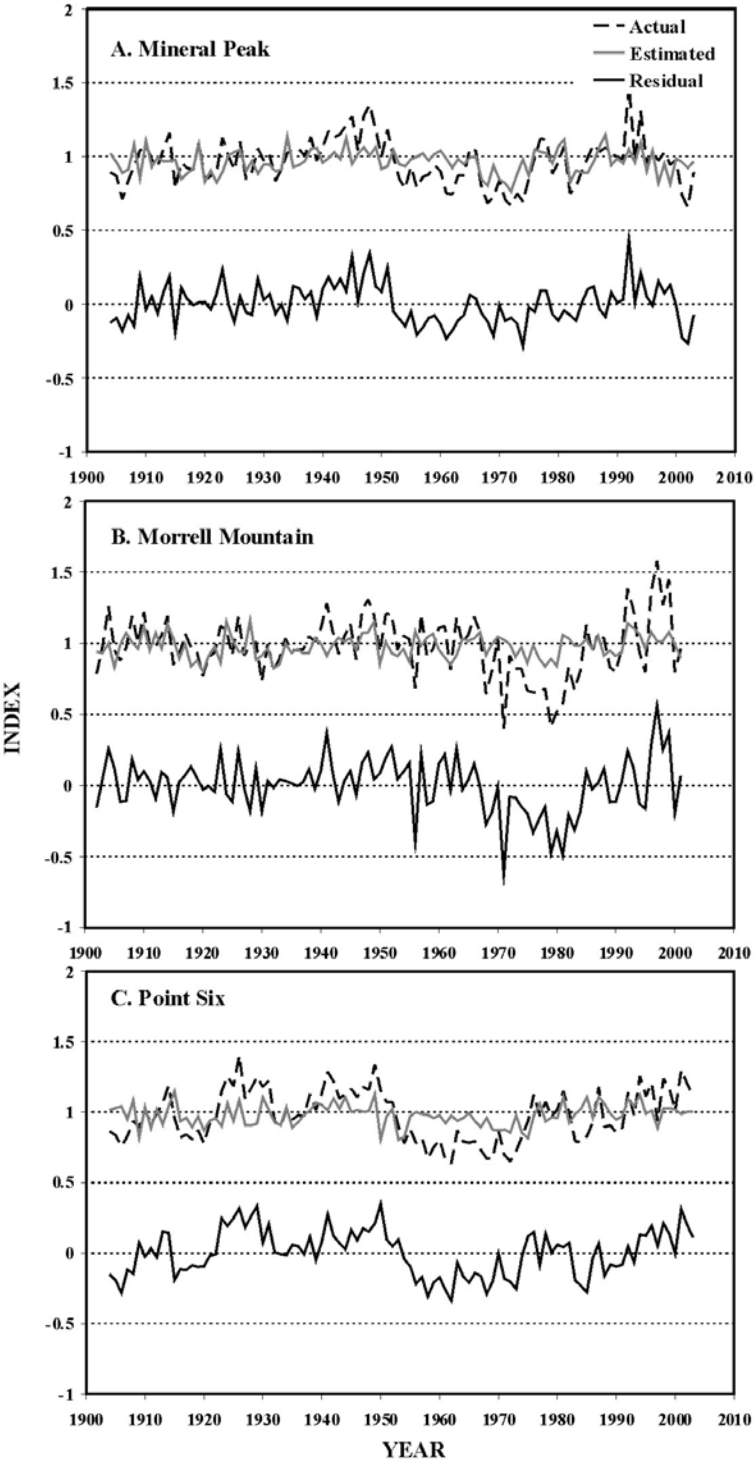

Figure 3.27. Actual and estimated indices of tree growth and their residuals developed for whitebark pines growing on (A) Mineral Peak, (B) Morrell Mountain, and (C) Point Six. “Actual” indicates the actual whitebark pine growth, “estimated” indicates the estimated annual whitebark pine growth based on the significant climate variables, and “residual” is the difference between the actual and estimated chronologies.

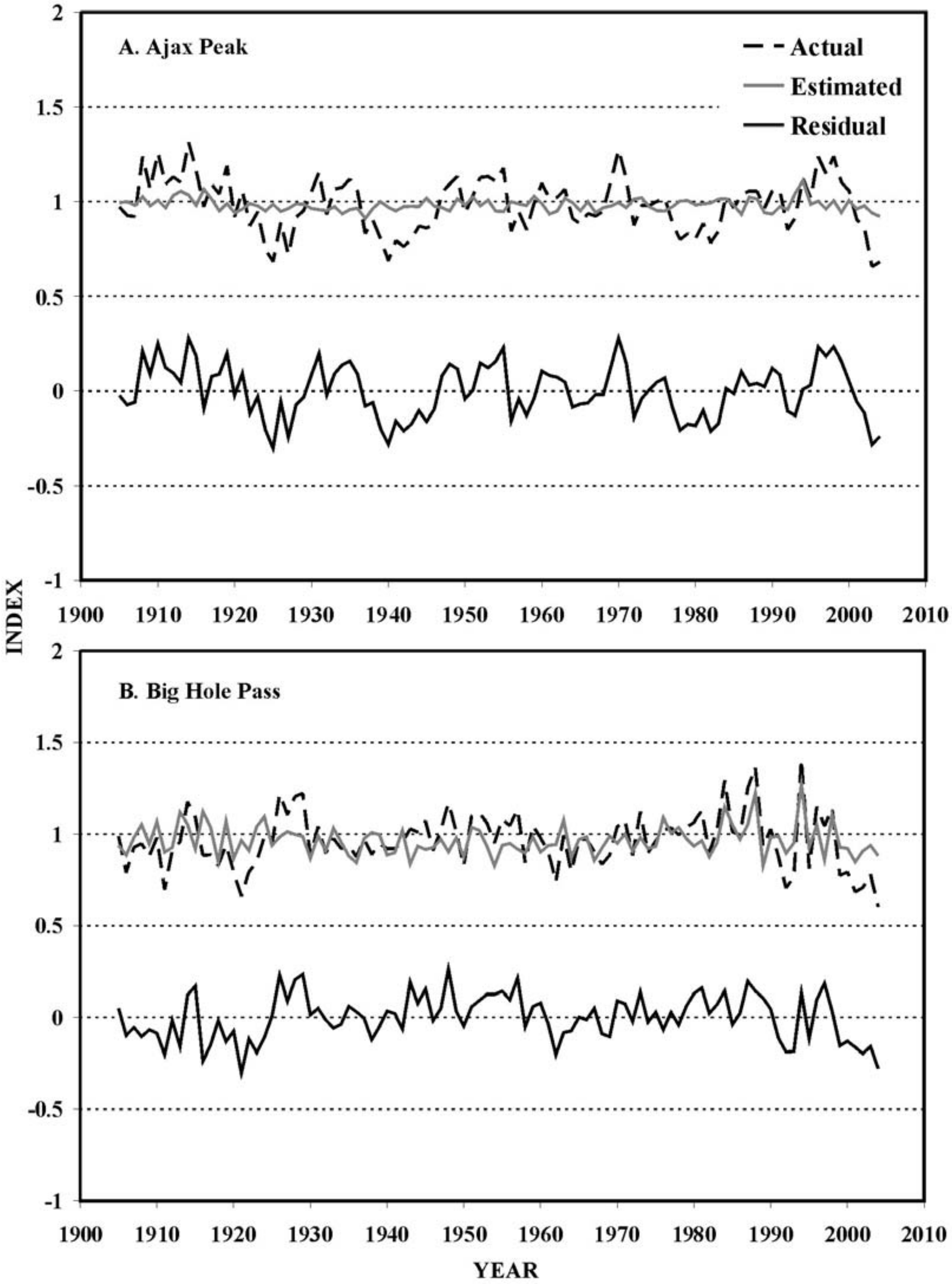

Figure 3.28. Actual and estimated indices of tree growth and their residuals developed for whitebark pines growing on (A) Ajax Peak, and (B) Big Hole Pass. “Actual” indicates the actual whitebark pine growth, “estimated” indicates the estimated annual whitebark pine growth based on the significant climate variables, and “residual” is the difference between the actual and estimated chronologies.

Our southern sites also showed asynchronous growth patterns, similar to the central sites (Figure 3.28). In comparison to the other sites, whitebark pines at Ajax Peak were the least responsive to temperature and precipitation over the 20thcentury (Figure 3.28). Therefore, more periodic positive and negative growth departures are evident at this site. Ajax Peak experienced growth suppressions in the 1920s, 1940s, and the 1980s. Growth releases at Ajax Peak occurred in 1970 and in the late 1990s. Conversely, the time series plot for Big Hole Pass indicated that the actual whitebark pine growth closely matched the predicted growth, with only one growth suppression period in the 1920s.

3.5 Discussion

3.5.1 Chronology Development

Interseries correlations were highly significant at all six sites, with an average of 0.49. Whitebark pine chronologies in Idaho had higher interseries correlations, but these sites were located at higher elevations in open-canopied forests (Perkins and Swetnam 1996, Kipfmueller 2003). Our chronologies were developed as part of a larger study to examine successional dynamics in the subalpine forest. Therefore, our interseries correlations were lower because the majority of whitebark pines chosen for chronology development were not from park-like treeline stands, but were from closed groupings in which trees influenced by competition from other individuals, in addition to natural and anthropogenic disturbances. All sites chronologies had average mean sensitivities, signifying that necessary variability exists in the tree-ring patterns from climatic factors to ensure successful crossdating and extraction of the dominant climate signal. The commonality of marker rings along our latitudinal transect and the significant correlations between neighboring chronologies in Montana and Idaho further indicate a regional climatic influence.

3.5.2 Climate Analyses

Response function analysis for the six sites resulted in different climate signals likely related to differences in elevation, microclimate conditions, and disturbances at the sites. In the northern Rocky Mountains, climate-response models typically explain 30–55% of the variance in ring-width indices (Kipfmueller 2003, Gray *et al.* 2004, Mann 2008), because tree growth is related to moisture availability in high-elevation sites. The whitebark pine growth data from all sites had between 16% and 41% of the variance explained by climate, which makes these data sets less climatically-sensitive than other northern Rocky Mountain sites. With the exception of Big Hole Pass, one of the most southern sites, the whitebark pines in our study were more responsive to prior growth than climate. Big Hole Pass had 41% of the whitebark pine variance explained by climate, making it a more climatically sensitive site compared to the other sites. Whitebark pines at Big Hole Pass are the most climatically sensitive in our study because the site is located on the Continental Divide in a semiarid region with an open, grassy understory, and little competition from competing shade-tolerant species.

Although the growing season for whitebark pine only lasts from June to September, we found growth correlated with drought and precipitation patterns throughout the year. Tree growth is clearly responsive to drought and precipitation and its seasonal distribution, but to varying degrees along the latitudinal transect. Whitebark pine growth at most of the study sites (with the exception of Point Six), showed a statistically significant positive relationship between tree growth and previous summer precipitation or PDSI. This indicates wet conditions from precipitation and snowpack melt in the previous summer months enhance whitebark pine growth during the following growing season. Previous year's precipitation affects water and nutrient storage, and the initiation of growth in the current growing season (Fritts 1976). During the winter season, when available moisture is low due to accumulated snowpack conditions, whitebark pines may favor respiration over photosynthesis. When low precipitation and soil moisture levels occur, trees experience water stress which results in decreased photosynthesis. Water stress causes lower amounts of carbohydrate storage and lower amounts of growth hormones to be produced which causes a reduction in cambial growth and results in the formation of a narrow ring (Fritts 1976). If favorable precipitation and snowmelt conditions occur in the previous summer, the carbohydrate reserves are available for the current year's growth (Fritts 1976). The seasonal fluctuations in precipitation and drought also reflect the fluctuations in snowpack. Snowpack variability is a central force that limits tree growth at high-elevation sites (Peterson 1998), therefore the timing of snowpack melt is important in understanding wet conditions in whitebark pine forests.

Whitebark pine growth response to PDSI at Point Six, Ajax Peak, and Big Hole Pass (central and southern sites) was more significant than with precipitation at Hornet Peak, Mineral Peak, and Morrell Mountain (northern and central sites). PDSI represents the overall environmental conditions by incorporating temperature, precipitation, and the available water content of soil, which better represents the conditions necessary for tree growth more than the precipitation and temperature indices alone (Fritts 1976, Cook *et al.* 2004). Point Six showed a completely different response to PDSI than the other sites.

Although Point Six PDSI response was significant in the previous May, and from January–May, it was a negative response. Given whitebark pine's short growing season, any extended period of snowpack (October–June) would result in lower than average growth at the microsite level which could create noise in the climate signal. The inverse climate-growth relationship at Point Six may also reflect complex microsite conditions. Point Six is dissected by ski runs and artificial snow is blown early during the ski season which contributes to snowpack accumulation throughout the winter. Snow was still on the ground in late June when we sampled this site during our field seasons, indicating that heavy snow accumulation persists into the growing season and likely causes an extended photosynthetically inactive period and delays the beginning of tree growth (Fritts 1976). Tree growth in any year in moisture-stressed trees is often related to a climatic window that includes part of the previous and current summers (Watson and Luckman 2002). Therefore, if the June–September growing season is further shortened due to high accumulations of snowpack, the window for whitebark pine photosynthesis is narrower. Although precipitation in the form of snow occurs throughout the year at Point Six, the water is not available to whitebark pines until the late summer when temperatures are warmer and snowpack begins to melt. The longer snowpack period at Point Six contributes to the inverse relationship between tree growth and PDSI. Point Six is an example of the important influence of land-use history on climate-growth response in whitebark pine forests.

In contrast to Point Six, the most significant positive relationship between whitebark pine growth and PDSI found in this study occurred in the previous year's summer in Ajax Peak and Big Hole Pass in the southern portion of the study area. This indicates that drought (precipitation and temperature) conditions are critical during the previous growing season and, to a lesser extent, during the winter season in our southern sites. Moisture conditions late in the previous year's growing season may affect the current year's bud break and the initiation of growth more than climate during the current year's growing season. Drought may cause a reduction in current growth, but cause an increase in carbohydrate storage for the following year's growth (Fritts 1976). Our seasonal PDSI correlation results from these southern sites are similar to the results obtained by Mann (2008) from the same region, except he found stronger relationships between tree growth and current summer PDSI.

The northern and central sites (Hornet Peak, Mineral Peak, and Morrell Mountain) responded to precipitation during different periods throughout the year, indicating microsite conditions may influence the amount of available precipitation for tree growth. Hornet Peak is the lowest in elevation of the study sites and therefore may experience an earlier snowpack melt, which could explain the strong positive correlation to previous July precipitation and current June precipitation. Morrell Mountain whitebark pines also responded favorably to snowmelt in the previous June. Hornet Peak and Mineral Peak had a significant negative response to precipitation during December and January, indicating that winter snowpack conditions are important for understanding tree growth at these sites.

Future snowpack conditions will directly influence the significant relationship between whitebark pine growth and available moisture (precipitation and PDSI). Climate change will reduce the depth, duration, and distribution of snowpack in the northern Rocky Mountains (Marshall *et al.* 2008). Snow cover has already significantly decreased every month (except November and December) from 1966 to 2005 in western North America (IPCC 2007). Continued warming will cause snowpack to melt earlier during the year which will lengthen the whitebark pine growing season. Photosynthesis and transpiration by whitebark pine and other high-elevation plant species will remove the available soil moisture earlier in the summer and will therefore experience drought stress later in the summer causing reduced tree growth in any given year. Large snowpack reductions will also eliminate the insulation that prevents soil from freezing during winter cold waves in high elevations (Marshall *et al.* 2008), which will further negatively affect whitebark pine growth.

3.5.3 Climate Reconstruction

The reconstructed PDSI and precipitation values revealed specific dry years and longer drought periods during the entire length of the reconstructions. The climate reconstruction results support other climate reconstructions, east of the Continental Divide, that found precipitation and PDSI have a greater influence on subalpine forest growth than temperature (Cook *et al.* 2004, Gray *et al.* 2004, Mann 2008). We compared our results to a regional summer PDSI reconstruction (data points 68 and 84 from Cook *et al.* 2004) from lower-elevation sites in the northern Rocky Mountains, and found a few similar dry years between the lower-elevation PDSI reconstruction and our high-elevation PDSI and precipitation reconstructions across western Montana. Similar dry years between our studies included 1174, 1263, 1328, 1583, 1739, 1782, 1883, and 1992. These years are important because the mixed-conifer chronologies used in the Cook *et al.* (2004) reconstructions were not affected by the same disturbance events that could have affected our reconstructions. Therefore, dry years and droughts in common between our PDSI reconstructions and the Cook *et al.* (2004) PDSI reconstructions are independent of mountain pine beetle disturbance.

A few of our driest single years (1263, 1274, 1278, and 1583) from our longest precipitation reconstruction (Mineral Peak) also matched other regional drought reconstructions. Drought records from the western United States that span the 13th-century indicate a severe, multidecadal drought at this same time (Woodhouse and Overpeck 1998). Tree-ring chronologies from Nebraska, New Mexico, the Great Basin, and northeastern Utah also showed sharp decreases in tree growth around this time (Grissino-Mayer 1996, Hughes and Graumlich 1996, Woodhouse and Overpeck 1998, Gray *et al.* 2004). We also noted the influence of the late-1500s megadrought (Grissino-Mayer 1996, Cook *et al.* 1999, Stahle *et al.* 2000) in the Mineral Peak reconstruction. Our reconstructed winter precipitation dropped over 1.5 cm from 1572 to 1600. Many tree-ring records have described the spatial and temporal extent of this megadrought. Stahle *et al.* (2000) conducted an analysis of tree-ring chronologies during the late 1500s and found strong evidence for this same drought extending from the southwestern United States through the Rocky Mountains. Grissino-Mayer (1996) also suggested that this drought was the most severe drought in the Southwest over the past 2000 years.

Our reconstruction data contribute an important high-elevation component to existing drought reconstructions in the northern Rocky Mountains. Further analysis should be conducted on the links between Pacific modes and high-elevation precipitation to understand the influence of multidecadal oscillations on drought regimes in our sites. For example, the Mineral Peak winter precipitation reconstruction could be further explored to reconstruct snowpack conditions and examine the influence of the Pacific Decadal Oscillation (PDO) on long-term snowpack fluctuations. Detailed analysis and testing of specific hypotheses regarding the effects of PDO on long-term precipitation and PDSI trends are necessary for understanding the influence of teleconnections on whitebark pine tree growth in western Montana.

3.5.4 Distinguishing Climate Response from Mountain Pine Beetle Response

The PDSI and precipitation reconstructions showed a strong relationship between the preconditioning effects of drought on disturbance events at our study sites. For example, Hornet Peak and Morrell Mountain experienced a drought in the 1970s, during a mountain pine beetle outbreak. Hornet Peak, Point Six, Ajax Peak, and Big Hole Pass also had a drought period in the mid-1920s which may have caused the whitebark pines to be more susceptible to the mountain pine beetle outbreak that occurred from 1920 to 1940. The effects of disturbance events are difficult to distinguish from the climate signal in our reconstructions prior to the early 1900s. However, multiple sites experienced a dry year in 1883 which would have made whitebark pine trees more susceptible to a mountain pine beetle attack during a reported 1880s outbreak period (Alfaro *et al.* 2004, Taylor *et al.* 2006). Therefore, earlier values derived from the reconstructions should be interpreted conservatively in the context of possible disturbance events. Further dendroclimatological research should be conducted on sites where the mountain pine beetle influence appears to be minimal. Whitebark pines at Big Hole Pass had the strongest response to climate and the least amount of influence from disturbance events of our sites. This would be an ideal site for further studies using whitebark pine for climate reconstructions in the Rocky Mountains of Montana.

Asynchronous patterns between the actual and expected climate response in the time series plots, particularly in Hornet Peak, Morrell Mountain, Point Six, and Ajax Peak, are most likely due to mountain pine beetle outbreaks. The departure from expected growth during the 1970s and 1980s is clearly seen at these sites and is interpreted here as an indication of the landscape-level mountain pine beetle outbreak. An earlier mountain pine beetle outbreak from 1920 to1940 affected whitebark pine growth at Hornet Peak, Mineral Peak, Ajax Peak, and Big Hole Pass. Hornet Peak and Ajax Peak were the only two sites that exhibited growth departures from both mountain pine outbreaks during the 20th century.

In addition to mountain pine beetles outbreaks, other landscape-level patterns in the whitebark pine chronologies were evident. The whitebark pine chronologies showed a sharp growth decline in the study sites from 1998–2005. This decrease in radial growth is likely related to a contribution of drought, mountain pine beetle outbreaks, and white pine blister rust infections. Although both white pine blister rust and mountain pine beetle were present at each site, the megadrought from 1999–2007 has also impacted these sites. According to Cook *et al.* (2004), over 50% of the United States experienced moderate to severe drought conditions in 2002, with record or near-record precipitation deficits throughout the western United States. Severe drought conditions have continued to affect the western United States through 2007 (Marshall *et al.* 2008). Droughts restrict biological activity in whitebark pine and change processes within the whitebark pine ecosystem. Continued periods of drought will likely stress whitebark pines and make them more susceptible for mountain pine beetle attack and weaken their resistance to white pine blister rust infection. The results of this study substantiate the importance of drought in whitebark pine communities. We suggest that climate change, especially increased periods of drought, may increase the threat to whitebark pine survival by changing biological processes, reducing whitebark pine productivity, and increasing stress which makes whitebark pines more susceptible to insects and pathogens. Further research should be conducted on the climate-growth relationships of subalpine tree species that are non-hosts for the mountain pine beetle and white pine blister rust, to examine community-level drought and disturbance responses in Montana.

CHAPTER 4

RESPONSE BY WHITEBARK PINE AND SUBALPINE FIR TO NATURAL AND ANTHROPOGENIC DISTURBANCES IN THE NORTHERN ROCKY MOUNTAINS, U.S.A.

Portions of this chapter that refer to whitebark pine ecology and study site descriptions were taken from Chapters 1 and 2 of this dissertation. The use of “we” in this chapter refers to Dr. Henri Grissino-Mayer and myself who will be co-authors on the manuscript submitted from this chapter. Dr. Grissino-Mayer assisted in the identification of relevant literature, field collection, and verifying the accuracy of dated samples.

In this chapter, we compare current stand conditions in whitebark pine communities in the Flathead, Lolo, and Beaverhead-Deerlodge National Forests in the northern Rocky Mountain of western Montana. We compare whitebark pine and subalpine fir chronologies from three study sites (one site from each national forest: Hornet Peak from the Flathead National Forest, Morrell Mountain from the Lolo National Forest, and Ajax Peak from the Beaverhead-Deerlodge National Forest) to examine changes in tree growth patterns that could possibly be attributed to fire suppression, white pine blister rust, and mountain pine beetle disturbance events. Changes in forest composition and structure are statistically analyzed and discussed. *Manuscript to be submitted to Canadian Journal of Forest Research.*

4.1 Introduction

Ecologists recognize that natural disturbance cycles that involve fire, insects, or pathogens are important components in most landscapes, and that few ecosystems ever achieve a steady-state climax (Bormann and Likens 1979, White 1979, Christensen 1989). By understanding disturbance regimes, we can identify the spatiotemporal trends, variations, and periodicities of events and processes that affect forest ecosystems (Swetnam *et al.* 1999). The types, frequencies, and spatial scales of disturbances are important variables that influence the structure and composition of high-elevation ecosystems in the northern Rocky Mountains (Veblen *et al.* 1991). Few ecosystems warrant more attention from managers and have greater research needs than do whitebark pine (*Pinus albicaulis* Engelm.) forests.

Whitebark pine is a long-lived tree species found in many high elevation and subalpine forest communities of western North America (Arno and Hoff 1989). Whitebark pine forms extensive contiguous stands in high-elevation forests in the Rocky Mountains of Montana, Wyoming, Idaho, and Alberta, as well as smaller disjunct stands in eastern and southwestern Oregon, California, and Nevada. The species is restricted at its upper elevations by severe climate conditions and at lower elevations by competition from other tree species (Arno and Hammerly 1984). It is a pioneer species that fills a crucial niche in watershed protection, catching and retaining snow, and stabilizing rock and soil in harsh and recently disturbed areas (Tomback *et al*. 2001). Whitebark pine is also a food source of critical importance to Clark's nutcrackers (*Nucifraga columbiana* Wilson), red squirrels (*Tamiasciurus hudsonicus* Erxleben), grizzly bears (*Ursus arctos* L.), and black bears (*Ursus americana* Pallas) (Mattson *et al*. 2001, Tomback 2001).

Conventional models of succession show that whitebark pine dominates during early stages of succession and regenerates after stand-level disturbances (*i.e.*, fire) that occur at long return intervals of 200 years or more (Fischer and Bradley 1987, Larson 2005, Larson *et al.* 2008). However, the long lifespan (up to 1000 years) of whitebark pine makes it an important component of mid- and late-successional forests. Currently, a successional shift is occurring in whitebark pine-dominated forests (Keane and Arno 1993, Kendall and Keane 2001, Tomback et al. 2001). Subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.) and Engelmann spruce (*Picea engelmannii* Parry ex Engelm.) are two species successionally replacing whitebark pine-dominated forests in the northern Rocky Mountains. Advancing succession has been observed in whitebark pine forests throughout their range and these forests are currently outside the historical range of variability for the species (Keane and Arno 1993, Murray *et al*. 2000). This divergence from historical conditions is likely the result of a combination of natural and anthropogenic changes in the disturbance regimes of whitebark pine communities.

The overlapping effects of mountain pine beetle, fire suppression, advancing encroachment by fire-intolerant plant species, and the introduction of white pine blister rust have contributed to the ongoing demise of the whitebark pine ecosystem of the northern Rocky Mountains of western North America. A relatively large body of research has been conducted on whitebark pine ecosystems to examine the relationship between fire suppression and white pine blister rust (Arno *et al.* 1993, Keane and Arno 1993, Tomback *et al.* 1995, Murray *et al.* 2000, Zeglen 2002, Kipfmueller and Kupfer 2005, Kearns and Jacobi 2007, Smith *et al.* 2008) and mountain pine beetle and white pine blister rust interactions (Campbell and Antos 2000, Campbell *et al.* 2007) in portions of British Columbia, Idaho, northwestern Montana, Wyoming, and Colorado. Although mountain pine beetle outbreaks and whitebark pine mortality have been examined in portions of Idaho and Montana (Perkins and Swetnam 1996, Murray *et al*. 2000, Kipfmueller 2003), the extent of the white pine blister rust epidemic has not been quantified throughout the Rocky Mountains of western Montana. More temporally-precise, site-specific data on the extent of white pine blister rust infection, past and current mountain pine beetle outbreaks, and resulting successional trends in whitebark pine communities throughout western Montana are needed to understand landscape-level declines in these whitebark pine communities.

Extensive mountain pine beetle outbreaks affected whitebark pine communities in the northern Rockies between 1925 and 1935 and between 1970 and 1980 (Arno and

Hoff 1989), and more recently in the early 2000s. The series of outbreaks that occurred from 1925 to 1935 in Idaho and Montana killed an estimated 1.4 billion lodgepole pines (*Pinus contorta* Douglas ex Loudon) and vast numbers of whitebark pine (Safranyik and Carroll 2006). Extensive outbreaks in the western U.S. and Canada during the late 1970s and early 1980s killed almost 2 million hectares of *Pinus* trees. A massive infestation, extending over 12 million hectares, has also devastated lodgepole and whitebark pine stands in the northern Rocky Mountains and in central British Columbia in the early 2000s (Safranyik and Carroll 2006).

An additional stressor currently affecting whitebark pine is white pine blister rust (*Cronartium ribicola* J.C. Fischer), an exotic pathogen first discovered in North America on a currant plant (*Ribes* spp.) in Geneva, New York, in 1906. The fungus soon spread to the Great Lakes region and British Columbia. White pine blister rust is now found throughout the entire range of five-needled pines in North America (Blanchard and Tattar 1997). Worsening the situation, whitebark pine is also the most vulnerable of the several white pine species, with fewer than one in 10,000 trees showing resistance to blister rust (Kendall 1994). The range of whitebark pine affected by white pine blister rust is expanding and infection is intensifying (Campbell and Antos 2000, Zeglen 2002, McKinney and Tomback 2007, Smith *et al.* 2008). Currently, the degree of infection in whitebark pine populations decreases southward throughout all parts of its range, including the Cascade-Sierra Nevada chain, the Bitterroot Mountains, and along the Continental Divide of the Rocky Mountains (Hoff 1992). In Washington State, northern Idaho, northwest Montana, southern Alberta, and British Columbia, 40–100% of whitebark pine are dead in most forest stands, and 50–100% of the living trees are infected with white pine blister rust (Arno *et al.* 1993, Campbell and Antos 2000, Kendall and Keane 2001, Tomback *et al.* 2001, Zeglen 2002, Smith *et al.* 2008). The extent of whitebark pine stands with cone-bearing trees has also declined by half (Tomback *et al.* 2001, McKinney and Tomback 2007).

Dendroecological techniques have only been used in a limited scope to study the current effects of mountain pine beetle, white pine blister rust, and fire suppression on whitebark pine growth (Perkins and Swetnam 1996, Kendall and Keane 2001, Kipfmueller and Kupfer 2005). Previous dendroentomological studies have analyzed radial growth patterns to examine the effects of insect disturbances on tree growth, such as defoliation episodes during spruce budworm and pandora moth outbreaks (Swetnam and Lynch 1993, Speer *et al.* 2001) and species-specific mortality events from spruce and mountain pine beetles (Veblen *et al.* 1991, Campbell and Antos 2000, Girardin *et al.* 2002, Sherriff 2006, Safranyik and Carroll 2006, Berg *et al.* 2006, Campbell et al. 2007). No research has been conducted that compared growth between the insect-host whitebark pine with nonhost species such as subalpine fir. Many studies exist that describe potential reasons behind the decline of whitebark pine forests (Keane and Arno 1993, Kendall and Keane 2001, Tomback *et al.* 2001, Kipfmeuller and Kupfer 2005), but one key approach that is lacking is an analysis that combines radial growth patterns from whitebark pine and from competing species. Growth comparisons between whitebark pine (host species to mountain pine beetle and white pine blister rust) and nonhost species could further clarify stand dynamics that affect whitebark pine communities throughout western North America. Such research could also clarify how these dynamics may have changed in the modern environment with the introduction of white pine blister rust.

In this study, we analyzed differential species' responses to natural and anthropogenic disturbances in subalpine forests of the northern Rocky Mountains in Montana. The specific objectives of this study were to: (1) examine growth suppression and release events caused by white pine blister rust and mountain pine beetle disturbance events in whitebark pines (host species) and subalpine firs (nonhost species), (2) quantitatively describe the current species composition and stand structure, (3) reconstruct the disturbance history of whitebark pine communities using forest inventory measures and dendroecological techniques, and (4) assess whitebark pine health along a latitudinal transect through the Rocky Mountains of western Montana.

4.2 Study Site

Our study sites were located in whitebark pine forests on eight peaks across three national forests in Montana, located on a north-south transect that extended from the Montana/Canada border to the western side of Yellowstone National Park. We chose to sample along a north-south latitudinal transect to evaluate landscape-level white pine blister rust and mountain pine beetle outbreak trends. The sites varied in elevation from 1,770 m to 2,535 m (Table 4.1). Mean annual temperature ranges are similar, but a gradient of decreasing precipitation exists from west to east that creates different precipitation regimes among the study sites. Soils are poorly developed at all sites. The underlying geology is composed of a mix of Quaternary and Cenozoic glacial deposits, Precambrian shales and siltstones, and Precambrian argillites and quartzites

Table 4.1. Study site locations in Montana.

Study Site	National Forest	Elevation (meters)	Latitude (Degrees N)	Longitude (Degrees W)
Big Mountain	Flathead	1770	48.31.25	114.22.50
Challenge	Flathead	1770	48.12.37	113.20.53
Hornet Peak	Flathead	2040	48.52.44	114.31.33
Mineral Peak	Lolo	2250	47.00.13	113.48.51
Morrell Mountain	Lolo	2370	47.11.53	113.21.25
Point Six	Lolo	2350	47.02.34	113.59.14
Ajax Peak	Beaverhead-Deerlodge	2535	45.20.25	113.42.57
Big Hole Pass	Beaverhead-Deerlodge	2255	45.31.14	113.48.16

(Ross *et al.*1955, Raines and Johnson 1996). Subalpine fir, Douglas-fir, lodgepole pine, Engelmann spruce, and grand fir (*Abies grandis* (Douglas. ex D. Don) Lindl.) were present in the stands we examined. Forest cover on Big Mountain, Challenge, Point Six, and Ajax Peak was relatively continuous, although the forests on Morrell Mountain, Big Hole Pass, and Hornet Peak were broken by a few alpine meadows. The forest on Mineral Peak was dissected by open talus. Common herbaceous plants on all sites included grouse whortleberry (*Vaccinium scoparium* Leib. ex Coville), red mountain-heath (*Phyllodoce empetriformis* (Sm.) D. Don), smooth woodrush (*Luzula hitchcockii* Hamet-Ahti), bear grass (*Xerophyllum tenax* (Pursh) Nutt.), and elk sedge (*Carex geyeri* Boott).

Evidence of disturbance was common at each site. The whitebark pines had experienced differing rates of mortality in each stand, predominantly from mountain pine beetle activity that we identified by pitch tubes and red boring dust on tree stems, by the presence of J-shaped galleries on the boles of dead trees, and by blue-staining fungus (*Ceratocystis montia* (Rumb.) Hunt.) in the outer tree rings once cross-sections were collected. We also observed several recently dead trees with what appeared to be old blister rust cankers at the sites in the Flathead and Lolo National Forests. Blister rust was abundant, with whitebark pine trees exhibiting open cankers or flagging (red needles due to the recent mortality of a branch or stem) in their upper canopies and on lower branches. Evidence of past fires was limited to northern sites, where many whitebark pine trees displayed multiple fire scars. We did not observe any fire-scarred fir or spruce.

4.3 Methods

4.3.1 Field Methods

Forest composition and age-structure data were collected in four 0.05 ha fixed-radius (r = 12.66 m) plots at the eight sites (32 overstory plots total). We sampled vertical forest structure (trees, saplings, and seedlings) within each fixed-radius overstory plot. The center of the plots were located from a random point within a whitebark pine-dominated stand by walking 50 m in a direction selected by the second hand of a watch. We tallied all trees by species and recorded diameter at breast height (DBH; height = 1.47 m) of all trees ≥ 5.0 cm DBH within each plot. Living tree crowns were classified into four categories (dominant, codominant, intermediate, and suppressed) based on the amount and direction of intercepted light (Oliver and Larson 1996).

Each whitebark pine was evaluated for tree health (healthy, declining, or dead), severity of white pine blister rust, and the presence or absence of mountain pine beetle. Overall tree health was based on the amount of dead needles in the crown. A tree was considered healthy if less than 5% of the tree crown was faded or had flagged branches. Whitebark pines that showed only one flagged branch from white pine blister rust were categorized as healthy because the crowns of the trees were still healthy overall. A tree was considered declining if more than 5% of the crown was showing stress. The presence of white pine blister rust was evaluated on the health of tree crowns as well (brown needles and flagged branches), and on the presence of cankers on the branches and stems of whitebark pine, following the methods of the Whitebark Pine Ecosystem Foundation (Tomback *et al.* 2005). Specific attention was given to finding active cankers (orange-yellow aecial blisters) on flagged branches during our early summer field months. We also examined trees for signs of rodent chewing as another indicator of white pine blister rust presence (Hoff 1992). Rodents chew on the branches and trunks of whitebark pine that have produced streams of resin during advanced white pine blister rust infections. Agents of whitebark pine mortality were distinguished between mountain pine beetle, white pine blister rust, or other causes.

Saplings less than 5.0 cm DBH but greater than 1.3 cm diameter at ground level (DGL) were tallied by species in the 32 overstory plots. We cut 4–8 subalpine fir saplings in each plot to obtain general ages of subalpine fir saplings at each site. Seedlings (less than 1.3 cm DGL) were tallied by species in nested fixed-radius 0.01 ha plots (r = 5.66 m). All understory data were later grouped by national forest and converted to saplings or seedlings per hectare. We also recorded UTM coordinates, percent slope, and aspect at each overstory plot center.

Dendroecological techniques and analyses were used to provide temporally precise information that would be helpful for assessing the ecological status of whitebark pine ecosystems. We sampled all living and standing dead trees in each plot for age using increment borers. We obtained two cores from each standing tree (healthy, declining, and dead) in each plot. All cores were taken at or below 30 cm above the root collar and along the contour of the slope to minimize the effects of reaction wood on the growth patterns in each sample (Fritts 1976). Core samples were labeled and placed in paper straws for storage and protection.

We used a chainsaw to collect 5 to 10 cross-sections from whitebark pine snags, stumps, and logs to extend the tree-ring information obtained from the cores back in time. A variety of disturbances can injure trees in the subalpine environment (Burrows and

Burrows 1976, Stuart *et al.* 1983, Butler *et al.* 1986, Morgan and Bunting 1990) causing erratic but characteristic patterns in the tree-ring record. We visually examined each cross-section and noted presence or absence of fire (*i.e.,* internal fire scars), mountain pine beetle galleries, and blue-staining fungus (Arno and Sneck 1977). All samples were labeled and then wrapped with plastic for transport back to the laboratory.

The mountain pine beetle is the most destructive of the native biotic agents in mature *Pinus* forests in western North America (Safranyik and Carroll 2006). During endemic mountain pine beetle infestations, beetles tend to select weaker, less vigorous trees for attack. However, tree size selection is not evident during epidemic conditions (Safranyik and Carroll 2006). Infested whitebark pines were recognized first by pitch tubes on their trunk and red boring dust in bark crevices and on the ground at the root collar. We also examined whitebark pine foliage for discoloration, as it changes from green to light greenish yellow, and then to reddish brown. The sapwood of attacked trees soon becomes discolored by blue-staining fungus. This blue-staining fungus is readily apparent in tree-ring samples, and is one type of evidence for past beetle activity (Amman *et al.* 1989, Perkins and Swetnam 1996). We also expected to find episodes of tree establishment temporally clustered around outbreak dates. Because mountain pine beetle do not infest subalpine fir, we expected to see release events in the subalpine fir ring widths following whitebark pine growth decline.

4.3.2 Laboratory Methods

All samples were frozen at –40 °C for 48 hours to kill any pathogens and/or insects that may have been transported along with the samples. After allowing all samples to dry, fragile cross-sections were glued to plyboard for stabilization. Cores were allowed to air-dry completely in the straws and were then glued to wooden core mounts with cells vertically aligned to ensure a transverse view of the wood surface. Cross-sections and cores were given an initial flat surface using a band saw to remove deep chain saw cuts prior to sanding, then the cross-sections and core samples were sanded using a belt sander, beginning with ANSI 80-grit (177−210 µm) and using progressively finer-grit belts until ANSI 400-grit (20.6−23.6 µm) (Orvis and Grissino-Mayer 2002). This process produced a wood surface with cellular features clearly defined under 10x magnification for clear ring identification.

4.3.3 Crossdating and Chronology Construction

We used visual, graphical, and statistical crossdating to assign exact calendar years to the tree rings of the whitebark pine and subalpine fir cores and whitebark pine cross-section samples. Visual crossdating relied on recognition of characteristic patterns of wide and narrow rings common to each site that were likely related to regional climate (Fritts 1976). Graphical crossdating was accomplished using the skeleton plot method (Stokes and Smiley 1996). Statistical crossdating was accomplished using ring-width measurements and the computer program COFECHA (Holmes 1983, Grissino-Mayer 2001).

We measured the ring widths on all samples to 0.001 mm accuracy with a Velmex measuring stage coupled with MEASURE J2X software. We confirmed the graphical crossdating and relative placements of all tree-ring series using COFECHA, which uses segmented time-series correlation techniques to confirm the previously-assigned temporal placements of all tree rings to the exact year each was formed (Grissino-Mayer 2001). Because crossdating is a high-frequency process (pattern matching of sequences of individual rings), COFECHA removes all low-frequency trends using both spline-fitting algorithms and autoregressive modeling (Grissino-Mayer 2001). Such trends could also be caused by natural (*e.g.* mountain pine beetle outbreaks and fire events) and human (*e.g.* blister rust infestation, logging, and mining) disturbances that otherwise could mask the climate signal desirable for accurate crossdating. We tested consecutive 50-yr segments (with 25-yr overlaps) on each series with a master chronology created from all other series by site.

Crossdating was verified when the correlation coefficient for each tested segment exceeded 0.32 ($p < 0.01$), although coefficients were usually much higher. The final suggested placement made by COFECHA had to be convincing both graphically (similar patterns in wide and narrow rings) and statistically (correlation significant at $p < 0.001$) (Grissino-Mayer 2001). Crossdating quality was assessed by two statistical descriptors. The average mean sensitivity was used to measure the strength of the year-to-year variability in all series and is an indicator of climate responsiveness (Fritts 1976). Values of 0.25 or higher are common for tree-ring data from the western U.S. (DeWitt and Ames 1978). We also used the interseries correlation as the average of all correlation coefficients calculated for each series to compare to all other series in the chronology (Grissino-Mayer 2001). The average interseries correlation is calculated by averaging the Pearson correlation coefficients calculated for each measurement series when correlated against a master chronology created from the remaining series (Grissino-Mayer 2001).

We standardized all measurement series in the six chronologies to remove effects from age-related growth trends that could add noise to the series unrelated to the climate signal desired in chronology development (Cook 1987, Fritts 2001). We removed the age-related growth trend of each sample using the program ARSTAN (Cook 1985), which fits a negative exponential trend line to the growth of the sample using the least squares technique. ARSTAN then creates an index for that year by dividing the actual ring-width by the value predicted by the regression (Fritts 1976, Cook 1985). The indices were then averaged for each year across all series to create a single index series for each site (Cook 1985).

4.3.4 Disturbance Regimes

We chose one representative site from each national forest to develop whitebark pine and subalpine fir chronologies, and to examine disturbance regimes in whitebark pine communities more closely. Subalpine fir was chosen as the nonhost species to compare to whitebark pine because of its abundance in whitebark pine communities. Tree reproduction in many forest ecosystems occurs in episodes associated with major disturbances. Thus, the distribution of ages in a population is often a sensitive indicator of the history of disturbance in a stand (Christensen 1989). Forest stand dynamics and disturbance patterns can also be inferred from suppression-release patterns in tree rings (Brubaker 1987, Lorimer and Frelich 1989, Nowacki and Abrams 1997, Ruffner and Abrams 1998, Rubino and McCarthy 2004). To quantify the extent of the disturbance (fire events, mountain pine beetle, or white pine blister rust) on stand and landscape scales, we calculated releases of tree growth over time in each of our samples from the whitebark pine and subalpine fir chronologies. The growth release events, defined as changes in radial growth relative to a pre-determined criterion, were identified for each tree-ring series in each chronology using the program JOLTS (Holmes 1999). We analyzed changes in ring width with respect to the running mean of the previous and subsequent 10 years. Release events were identified as periods in which ring width for a given year was at least 50% greater than the mean ring width of the 10 preceding and superseding years. The JOLTS program parameters were a release factor of 1.5 (*i.e.,* 50%), a 10-year moving average, and a five year minimum between release events (Veblen *et al.* 1991, Girardin *et al.* 2002, Berg *et al.* 2006). These criteria were chosen to reduce the number of release events caused by climatic anomalies and to isolate releases more likely caused by natural and anthropogenic disturbances.

The occurrence of releases in trees within and between study sites can identify disturbances as either a regionally extensive or localized event (Veblen *et al.* 1991). To determine if release events were stand-wide or local, we analyzed the temporal pattern of release episodes. Stand-wide disturbances were defined as release episodes where a minimum of 20% of individuals experienced simultaneous release. A stand-wide release event indicates an exogenous disturbance that removed or damaged overstory trees at a large spatial scale (*e.g.*, stand-replacing fires, mountain pine beetle outbreaks, and white pine blister rust).

Individual disturbance events in our whitebark pine-dominated stands were later disentangled by inspecting tree cores for blue-staining fungus from mountain pine beetle outbreaks and by quantifying declines in tree growth over a decade, indicating a possible white pine blister rust signature. We compared sites that are heavily infested with white pine blister rust (the Flathead and Lolo National Forests) to stands where white pine blister rust was thought to be absent (Beaverhead-Deerlodge National Forest) to find a unique tree-ring pattern indicative of when white pine blister rust first became present within the whitebark pine stands. For example, blister rust is known to have affected a small percentage of whitebark pines in the Flathead and Lolo National Forests in the 1960s (Hoff and Hagle 1990), therefore releases in surviving whitebark pines and all subalpine firs that occured in the 1970s could be a function of a white pine blister rust presence. However, known periods of mountain pine beetle outbreaks also occurred in the 1970s and 1980s. Unless these disturbances caused tree mortality, it is impossible for us to distinguish if releases in tree growth were associated with white pine blister rust infection, mountain pine beetle attack, or both during the 1970s and 1980s. If the mountain pine beetle outbreak did kill an individual tree, we would expect to see blue-staining fungus in the sapwood. The southern sites, in the Beaverhead-Deerlodge National Forest, are higher-elevation and have a cool, dry climate that is thought to be poorly suited for blister rust infection. We will compare the southern sites that have not been affected by blister rust since the 1960s with the central and northern sites where blister rust has been present during the past 40 years. We will also compare the mountain pine beetle outbreaks between 1925 and 1935 and between 1970 and 1980 in the whitebark pine (host) and subalpine fir (nonhost) chronologies at all sites. We would expect to see releases in surviving whitebark pines and all subalpine firs within a decade of know mountain pine beetle outbreaks in each of the sites.

Relative importance values were calculated for each species in each national forest as the average of the relative density (number of individuals) and relative dominance (basal area) (Cottam and Curtis 1956, Abrams *et al.* 2001). Importance values helped describe past and current forest composition as a function of tree density and size (dominance). Dominance values are particularly useful for projecting future overstory composition after stand-wide disturbances. Canopy class structure was also analyzed for species composition in the dominant, codominant, intermediate, and suppressed canopy classes in each national forest.

4.4 Results

4.4.1 Forest Composition

The dominant species in Montana subalpine forests were whitebark pine, subalpine fir, and grand fir (Table 4.2). Living whitebark pine composed 59% of the dominant trees in the Beaverhead-Deerlodge National Forest (BDNF). Basal area (m^2/ha) for living whitebark pine ranged from 26 m^2/ha in the BDNF to 5 m^2/ha in the FNF. Subalpine fir had the second highest basal area as a species and ranged from 8 m^2/ha in the Lolo National Forest (LNF) to 6 m^2/ha in the BDNF. Grand fir was only important in the Flathead National Forest (FNF) and had a relatively high basal area (6 m^2/ha). The BDNF had the highest basal area of the national forests (45 m^2/ha), which reflected the large size of the living whitebark pine and other species present in our study sites. High whitebark pine mortality was evident in the FNF and LNF where dead whitebark pines had the second highest importance values in both forests, even above living whitebark pines (Table 4.2). In healthier whitebark pine stands in the BDNF, living whitebark pines had the highest importance value (60%) compared to associated species.

Table 4.2. Density, dominance, and importance of trees (≥ 5 cm DBH) from the Flathead, Lolo, and Beaverhead-Deerlodge National Forests in Montana. Values shown are per hectare.

FLATHEAD NATIONAL FOREST

Species	Trees/ Ha	Rel Density	Ba/Ha	Rel Dominance	Rel Importance
grand fir	193	23.87	6.26	21.79	22.83
subalpine fir	221	27.37	8.00	27.84	27.60
lodgepole pine	25	3.09	1.53	5.32	4.20
Engelmann spruce	55	6.79	1.47	5.13	5.96
Douglas-fir	2	0.21	0.07	0.26	0.23
whitebark pine (living)	118	14.61	5.09	17.73	16.17
whitebark pine (dead)	194	24.07	6.30	21.93	23.00
TOTAL	807	100	28.72	100	100

LOLO NATIONAL FOREST

Species	Trees/ Ha	Rel Density	Ba/Ha	Rel Dominance	Rel Importance
subalpine fir	609	51.11	8.84	29.71	40.41
Engelmann spruce	8	0.70	0.65	2.19	1.44
lodgepole pine	5	0.42	0.18	0.60	0.51
whitebark pine (living)	168	14.07	7.17	24.09	19.08
whitebark pine (dead)	402	33.70	12.92	43.41	38.56
TOTAL	1192	100	29.77	100	100

BEAVERHEAD-DEERLODGE NATIONAL FOREST

Species	Trees/ Ha	Rel Density	Ba/Ha	Rel Dominance	Rel Importance
subalpine fir	113	12.13	6.15	13.72	12.92
lodgepole pine	85	9.16	3.60	8.04	8.60
Douglas-fir	73	7.82	5.09	11.35	9.58
whitebark pine (living)	563	60.65	26.36	58.83	59.74
whitebark pine (dead)	95	10.24	3.61	8.06	9.15
TOTAL	928	100	44.80	100	100

Ha is hectare
Rel Density is Relative Density (relative stems per hectare)
Ba is basal area (m^2)
Rel Dominance is Relative Dominance (relative m^2/ha)
Rel Importance is Relative Importance ((Rel Density + Rel Dominance) / 2)

The most abundant species in the tree layer (individuals ≥ 5 cm DBH) based on relative density were also whitebark pine, subalpine fir, and grand fir. Whitebark pine relative density was highest in the BDNF (61%) where whitebark pine mortality was relatively low (10%). The FNF and LNF had low relative densities of living whitebark pine (15% and 14%). Subalpine fir had the highest density in the LNF (51%), even over living and dead whitebark pine trees combined. Compared to the FNF and LNF, the BDNF had the lowest densities of subalpine fir (12%) and the highest densities of living whitebark pine (61%).

The understory densities and species varied across the national forests (Figure 4.1). Six species were found in the sapling layer: whitebark pine, subalpine fir, Engelmann spruce, grand fir, lodgepole pine, and Douglas-fir (Figure 4.1). Of these species, subalpine fir had the highest number per hectare in the LNF (1,522 saplings/ha). Whitebark pine saplings were most abundant in the LNL (300 saplings/ha) but many of these showed signs of white pine blister rust. The BDNF had a rather low but even distribution of saplings and seedlings between five species. The FNF and LNF had the highest number of subalpine fir seedlings (2,699 and 2,432 seedlings/ha). The relatively high number of grand fir seedlings (1,866 seedlings/ha) in the FNF contributed to the national forest having the highest number of seedlings per hectare (5,006). Whitebark pine seedlings were most abundant in the LNF with 750 seedlings per hectare.

Subalpine forest species were grouped and values were standardized at the hectare level to reveal canopy class distribution patterns between the national forests (Figure 4.2). Whitebark pine was the leading dominant canopy species in subalpine sites in each

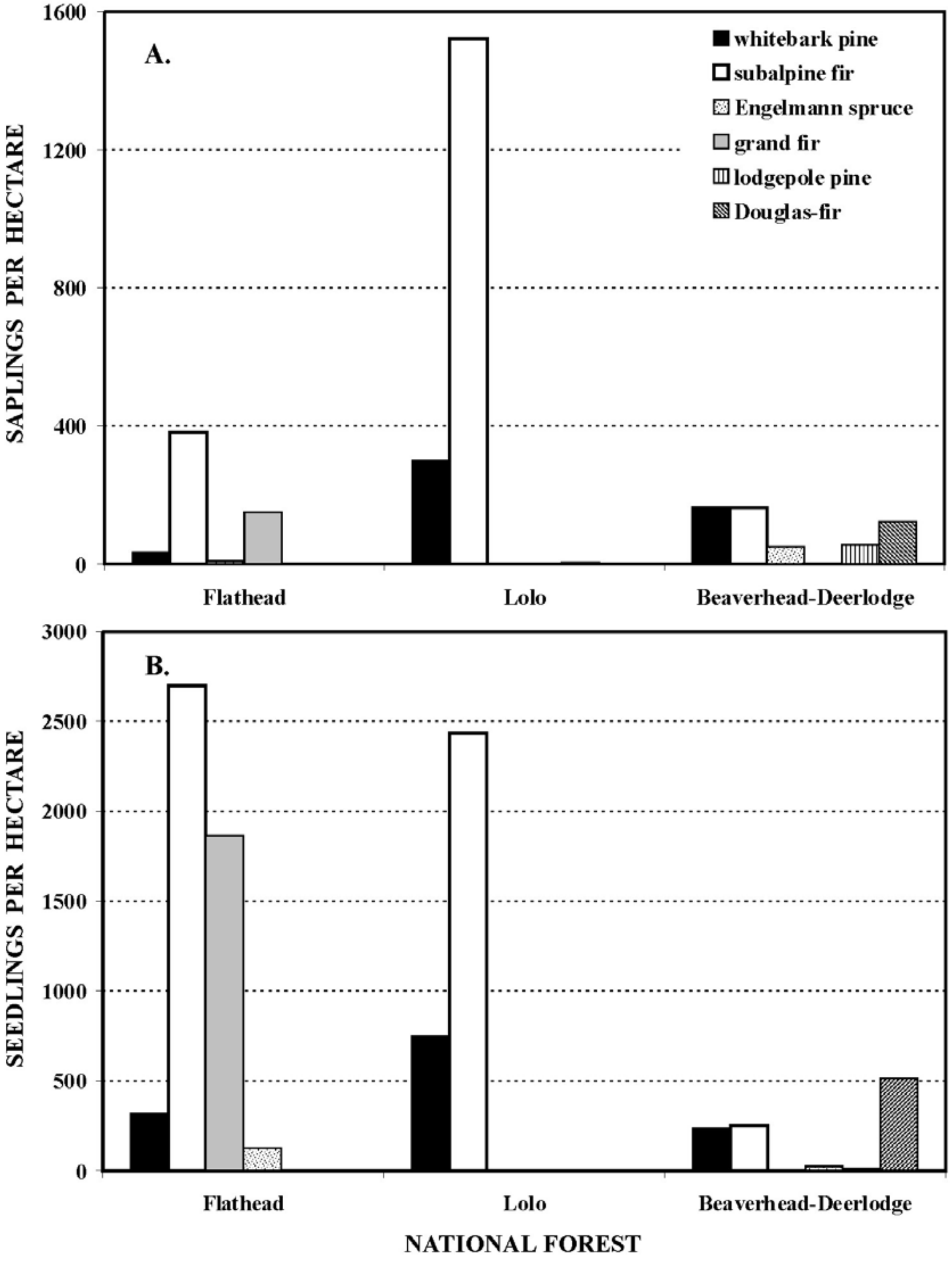

Figure 4.1. Density for: (A) saplings and (B) seedlings per hectare by national forest in Montana. Saplings: less than 5.0 cm DBH but greater than 1.3 cm DGL; Seedlings: less than 1.3 cm DGL. Note: y-scale varies.

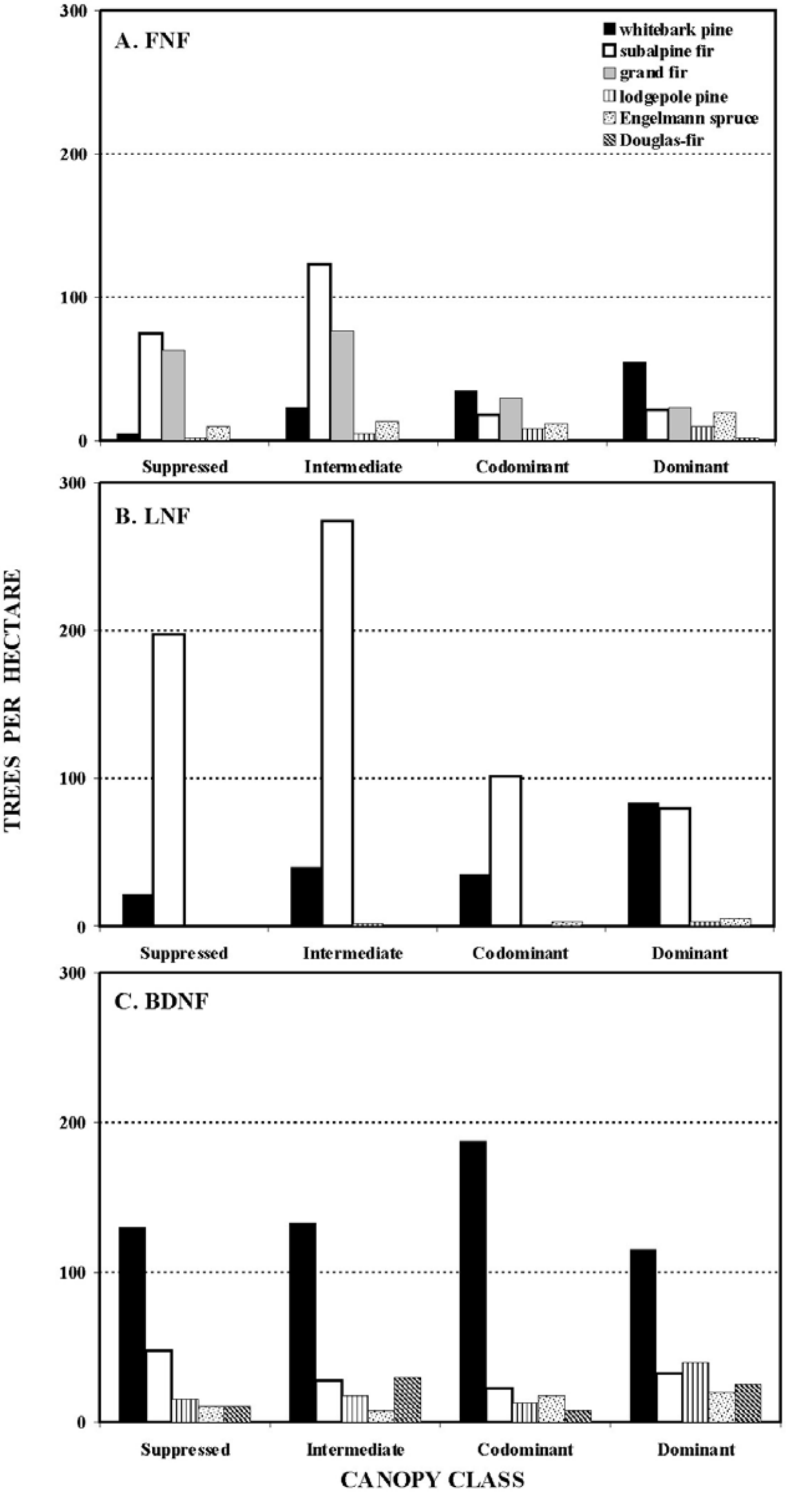

Figure 4.2. Canopy class distributions per hectare by group. Canopy class categories are based on the amount and direction of intercepted light (Oliver and Larson 1996).

national forest. Historically, whitebark pine would have been represented by more trees per hectare in the dominant and codominant canopy classes, similar to the pattern found in the BDNF (Figure 4.2c), where whitebark pine was the most abundant species in all canopy classes. Although whitebark pine was also the most abundant in dominant and codominant canopy positions in the FNF (Figure 4.2a), the number of trees per hectare is low compared to the LNF and BDNF. The number of trees per hectare is highest in the intermediate and suppressed canopy classes in the FNF and LNF (Figure 4.2a,b). In the LNF, subalpine fir was the most abundant species in the suppressed, intermediate, and codominant canopy classes. Subalpine fir was the second most abundant species, after whitebark pine, in the dominant canopy class (Figure 4.2b).

4.4.2 Forest Health

We completed health surveys on 805 whitebark pine trees (≥ 5 cm DBH) in our 32 overstory plots in the FNF, LNF, and BDNF. Of the 805 whitebark pines examined, 30% (n = 238) were alive, 20% were declining (n = 159), and 50% were dead (n = 407). In general, many of the larger diameter (≥ 30 cm DBH) dead whitebark pines showed evidence of mountain pine beetle in the form of "J"-shaped egg galleries in the phloem of the affected tree. The smaller diameter whitebark pines (5–30 cm DBH) that were recently dead or declining had evidence of white pine blister rust in the form of new and old cankers, rodent chewing, and flagged branches.

The BDNF had the highest number of living whitebark pines (563/ha), compared to the LNF (168/ha) and FNF (118/ha) (Table 4.3). Although the BDNF had the healthiest population of whitebark pines, approximately 40% had white pine blister rust (n = 228). Over half of the living whitebark pines in the LNF (78%) and the FNF (56%) showed symptoms of white pine blister rust (Table 4.3). Most of the whitebark pines in the FNF and the LNF are declining or dead (Figure 4.3). Almost 75% of the whitebark pines in the BDNF remain healthy, but only 14% of the whitebark pines in the FNF and 7% in the LNF are healthy. The LNF had the highest percentage of dead whitebark pines (71%), followed by the FNF (62%), and the BDNF (14%).

4.4.3 Disturbance History

The six whitebark pine and subalpine fir chronologies were developed using 229 samples from the FNF, LNF, and BDNF (Table 4.4). The site chronologies varied in length, with the shortest whitebark pine record from Ajax Peak (1832–2005) and the longest from Morrell Mountain (1489–2003). Subalpine fir chronologies ranged from 1797–2004 at Ajax Peak to 1860–2005 at Hornet Peak. Subalpine fir chronologies had low sample depth and proved difficult to crossdate because many of the samples were from interior forest trees that were in intermediate or suppressed canopy classes.

The interseries correlation and mean sensitivity of our three whitebark pine chronologies were representative of other whitebark pine chronologies from Montana (Larson 2005, Mann 2008). Interseries correlations for whitebark pine chronologies in the northern Rocky Mountains range between 0.41 and 0.70 (Perkins and Swetnam 1996, Biondi *et al.* 1999, Kipfmueller 2003, Larson 2005, Mann 2008). Mean sensitivity values between 0.20 and 0.24 are common for whitebark pine tree-ring data from Montana and Idaho (Perkins and Swetnam 1996, Biondi *et al.* 1999, Kipfmueller 2003, Larson 2005, Mann

Table 4.3. Living whitebark pine and white pine blister rust status by national forest in Montana. Values are per hectare.

National Forest	Living whitebark pine	Whitebark pine with blister rust	Percent of whitebark pine with blister rust
Flathead (FNF)	118	66	56
Lolo (LNF)	168	131	78
Beaverhead-Deerlodge (BDNF)	563	228	40

Table 4.4. Summary data of whitebark pine and subalpine fir chronologies from Montana.

Study Site	Species	Period of Record	Number of Samples	Interseries Correlation	Mean Sensitivity
Hornet Peak (FNF)	whitebark pine	1682–2005	64	0.48	0.23
	subalpine fir	1860–2005	20	0.43	0.24
Morrell Mountain (LNF)	whitebark pine	1489–2003	60	0.51	0.24
	subalpine fir	1830–2003	23	0.50	0.28
Ajax Peak (BDNF)	whitebark pine	1832–2004	33	0.52	0.21
	subalpine fir	1797–2004	29	0.49	0.22

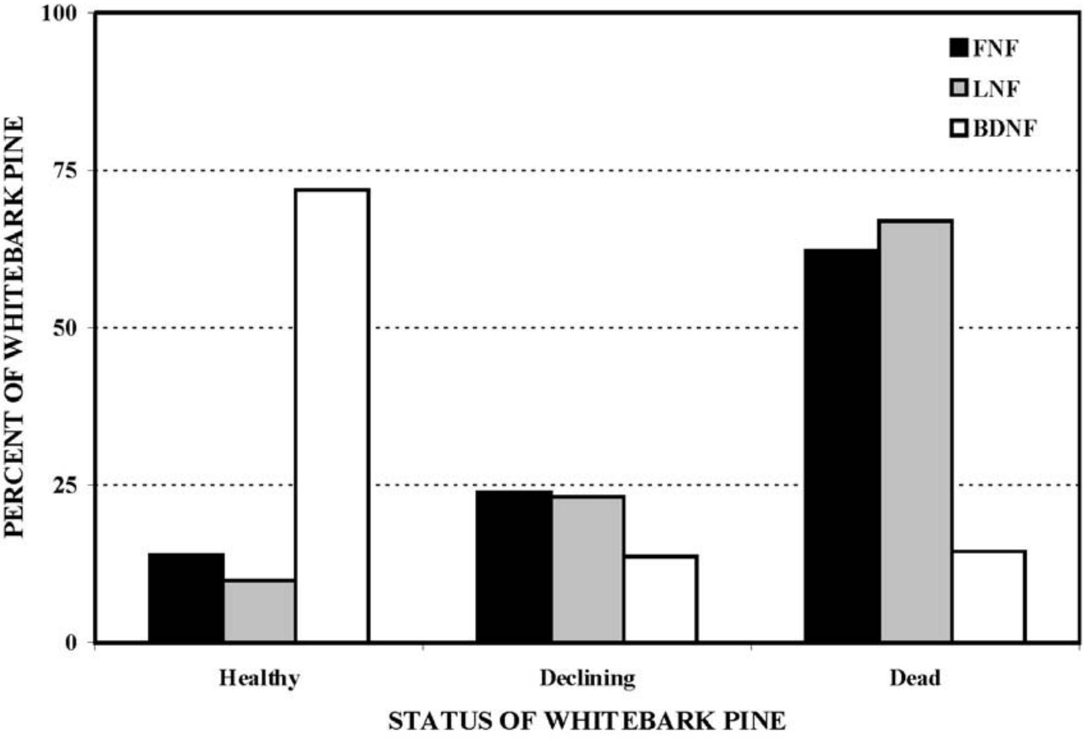

Figure 4.3. Comparing the health status of whitebark pine populations between national forests in Montana. FNF = Flathead National Forests, LNF = Lolo National Forest, and BDNF = Beaverhead-Deerlodge National Forest.

2008). The mean sensitivity for the whitebark pine chronologies from western Montana ranged from 0.21 to 0.24.The Ajax Peak chronology had the highest interseries correlation (0.52), followed by Morrell Mountain (0.51), and Hornet Peak (0.48). Our subalpine fir chronologies had lower interseries correlations (0.43 at Hornet Peak, 0.50 at Morrell Mountain, and 0.49 at Ajax Peak) than a recent study that used subalpine fir to reconstruct treeline advancement in Glacier National Park (interseries correlation was 0.55), but we found the Morrell Mountain subalpine fir mean sensitivity was higher (0.28) than that found in the other study (0.26) (Bekker 2005).

Hornet Peak, our northern-most site in the FNF, showed continual establishment of all species from 1675–1850 (Figure 4.4a). The last whitebark pine to establish at Hornet Peak occurred in 1854 after a pulse of tree establishment from 1790 to 1850. Subalpine fir and grand fir have continued to establish since 1850. The whitebark pine and subalpine fir chronologies showed above-average growth in 1880 but then did not show similar growth patterns again until both showed a decrease in growth between 1998 and 2005 (Figure 4.4 b,c). Whitebark pine had below-average growth in 1698, 1795, 1806, 1870, 1883, the 1920s, 1939, and the 1970s. A steady decrease in growth also occurred from 1948 to 1960. Subalpine fir had years of below average growth in 1867, 1914, 1924, 1938, and 1989.

Morrell Mountain, in the eastern LNF, showed two discrete patterns of whitebark pine establishment over the last 500 years (Figure 4.5a). The first cohort established over a 50-year period starting in 1500. Continual tree establishment has occurred since 1700, with a group of whitebark pines becoming established around 1800. A large number of subalpine firs have established since 1700, including a pulse of small diameter trees in

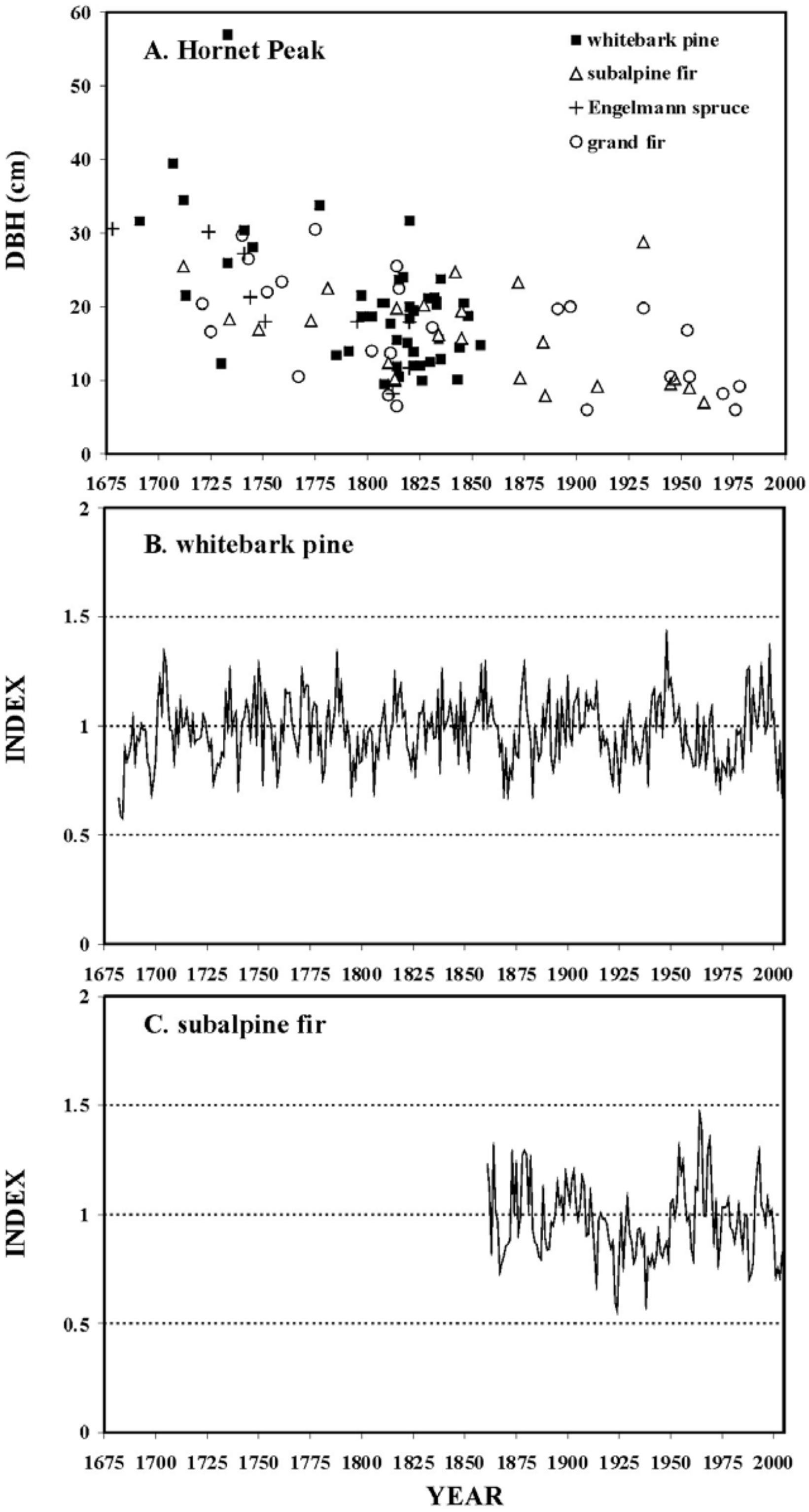

Figure 4.4. (A) Age-diameter relationships for cored trees, (B) the ARSTAN chronology for whitebark pine, and (C) subalpine fir from Hornet Peak in the Flathead National Forest.

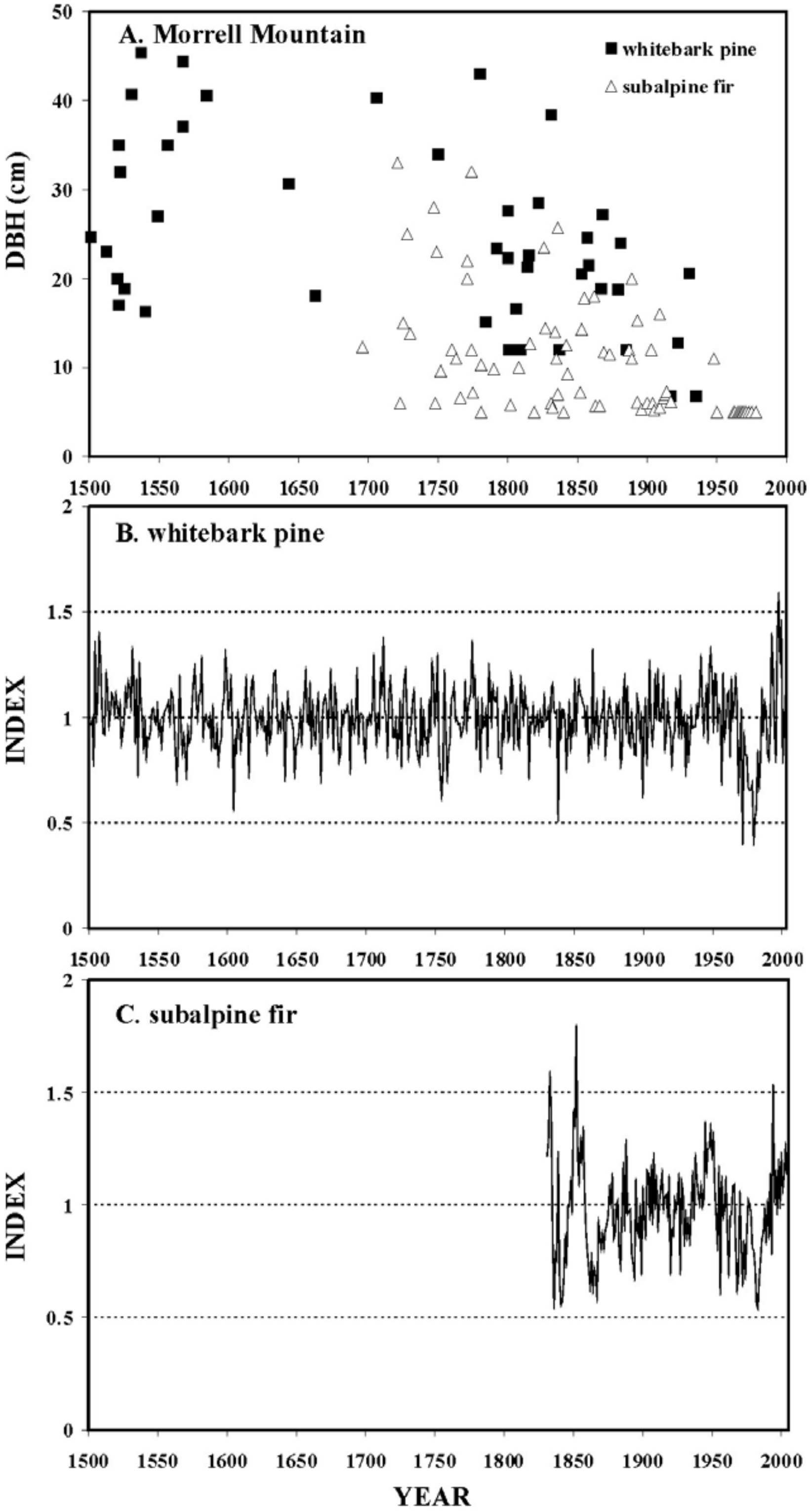

Figure 4.5. (A) Age-diameter relationships for cored trees, (B) the ARSTAN chronology for whitebark pine, and (C) subalpine fir from Morrell Mountain in the Lolo National Forest.

the 1970s. Many of the subalpine firs, independent of tree age, had diameters less than 15 cm DBH. The smaller-diameter subalpine firs were not included in the subalpine fir chronology because crossdating quality was poor in the interior forest trees. The whitebark pine and subalpine fir chronologies showed a similar growth decline from 1977 to 1984 (Figure 4.5 a,b). Both chronologies showed peaks in growth during the 1990s, but whitebark pine began a steady decrease in growth in 1997. While subalpine fir experienced a period of decreased growth from 1852 to 1868, whitebark pine growth experienced a peak in growth in 1863. Years of low growth in whitebark pine occurred in 1604, 1754, 1838, 1899, 1930, 1956, 1971, and 1979. Subalpine fir also had below-average growth in 1956.

Ajax Peak, on the Continental Divide in the Beaverhead-Deerlodge National Forest, has had continual tree establishment since the 1830s (Figure 4.6a). A few older whitebark pine, subalpine fir, and Engelmann spruce individuals were found that established in the 1700s. Whitebark pine trees continued to establish into the 1970s, which is later than both Hornet Peak (1860s) and Morrell Mountain (1950s). Although establishment of whitebark pine has been steady, whitebark pine growth has significantly decreased since 1998 (Figure 4.6b). Similar patterns emerged between whitebark pine and subalpine fir in the 1800s (Figure 4.6 b,c). The years 1838 and 1899 showed particularly low growth, while both chronologies experienced a growth peak in 1863. The same 1800s trend also occurred in the Morrell Mountain whitebark pine chronology, which indicates a similar climate signal between the Ajax Peak and Morrell Mountain sites. Whitebark pine had periods of below-average growth from 1930–1940 and 1970–1983. Subalpine fir experienced low growth from 1972 to 1974, but had average growth

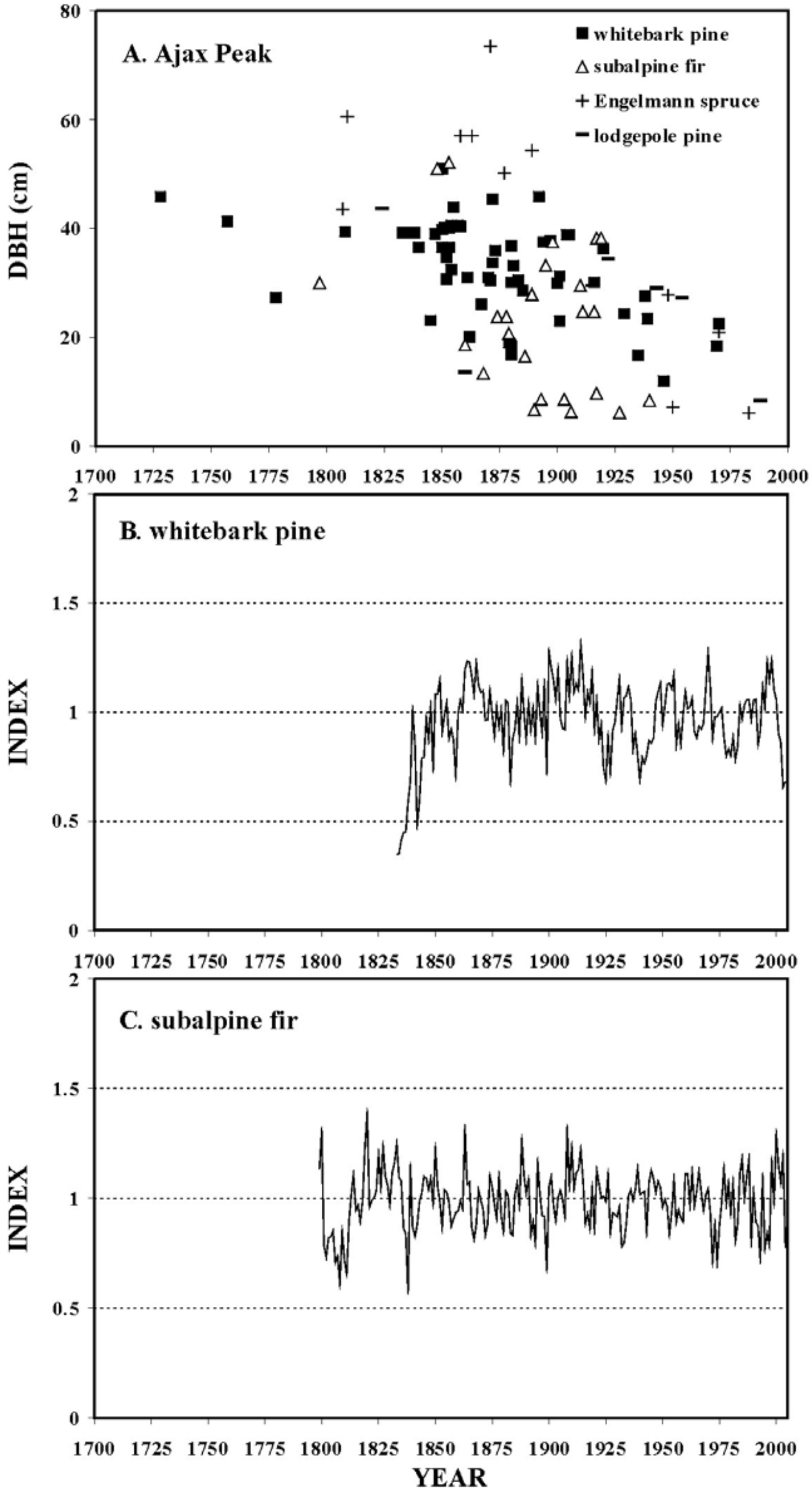

Figure 4.6. (A) Age-diameter relationships for cored trees, (B) the ARSTAN chronology for whitebark pine, and (C) subalpine fir from Ajax Peak in the Beaverhead-Deerlodge National Forest.

in the 1980s. A growth pulse occurred from 1997 to 2003, during a sharp decrease in whitebark pine growth.

Of the 229 whitebark pine and subalpine fir trees analyzed using the 10-year running mean method, 183 (80%) exhibited release events. A total of 566 release events were detected from the 229 individuals with some trees experiencing multiple releases during their lifespan. All release events detected using the 10-year running mean method were visually checked for accuracy using the raw ring-width measurements for the 229 whitebark pine and subalpine fir individuals. Ajax Peak had the lowest number of releases per tree in whitebark pine (1.39) and subalpine fir (2.28), while Morrell Mountain had the highest frequency of release events per tree in both species (3.12) (Table 4.5).

Our sites experienced very few stand-wide release events, although we observed distinct cohorts of release events throughout the length of the chronologies (Figures 4.7–4.9). Whitebark pines from Hornet Peak experienced frequent releases between 1690–1710, 1730–1745, 1790–1810, 1930–1945, and 1960–1990 (Figure 4.7a). The largest release cohort occurred from 1960–1990 when individual whitebark pines were experiencing an average growth increase of over 50% almost every year. In 1980, 20% of the whitebark pines experienced a growth release. Subalpine firs at Hornet Peak had a stand-wide disturbance in 1880, followed by a high frequency of releases from 1930 to 1990. Over 20% of the subalpine firs experienced releases in 1944, 1946, 1954, and 1962 (Figure 4.7b).

Whitebark pines at Morrell Mountain experienced stand-wide releases between 1500 and 1506, 1525, 1973, 1979, and 1984 (Figure 4.8a). Other periods of release

Table 4.5. Growth release data from 229 whitebark pine and subalpine fir series in study sites from Montana.

Study Site	**Species**	**Number of Samples**	**Series with Releases**	**Releases in all Trees**	**Mean Number of Releases per Tree**
Hornet Peak	whitebark pine	64	46	142	2.22
	subalpine fir	20	18	52	2.60
Morrell Mountain	whitebark pine	60	55	187	3.12
	subalpine fir	23	20	73	3.12
Ajax Peak	whitebark pine	33	21	46	1.39
	subalpine fir	29	23	66	2.28

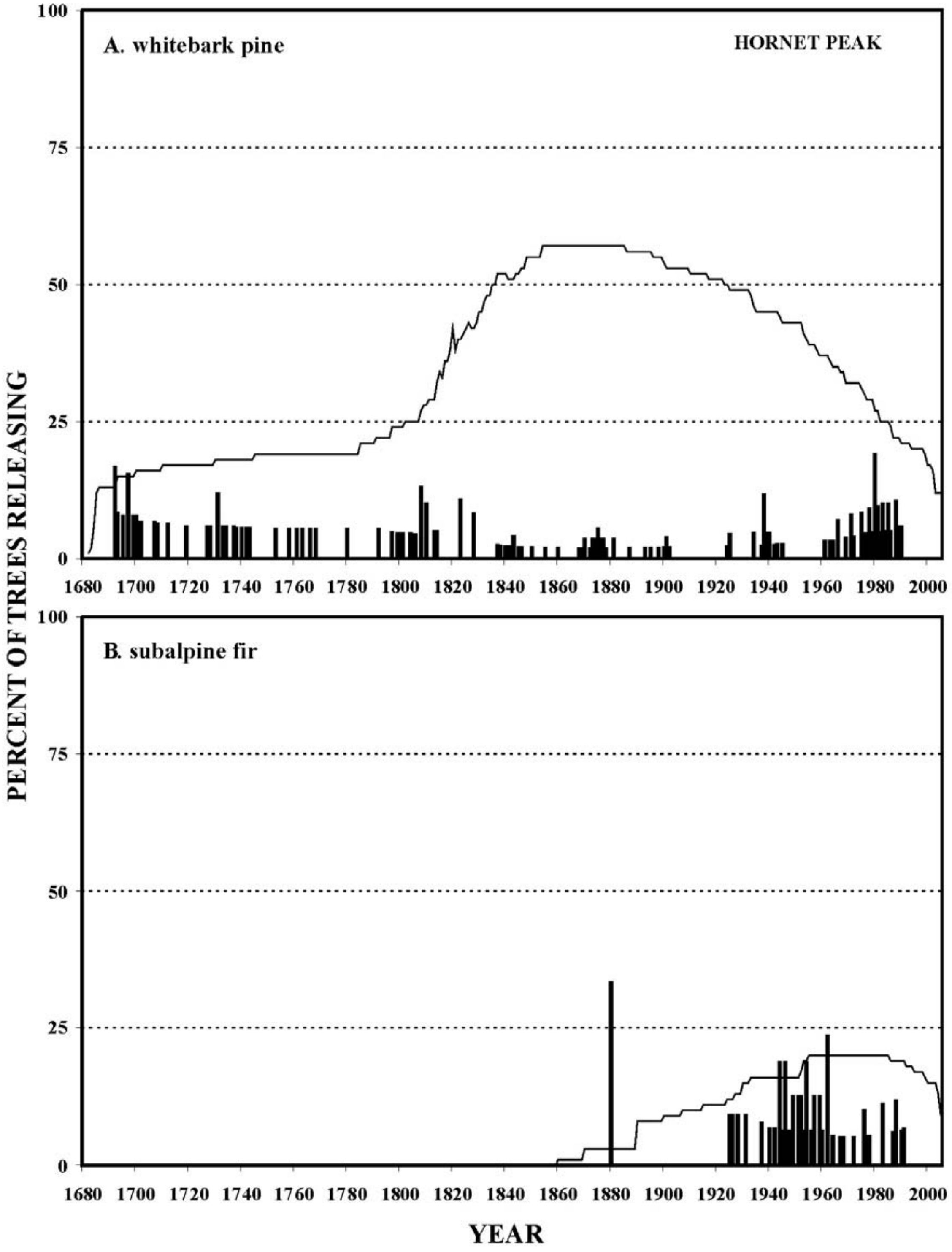

Figure 4.7. Detected release events using the 10-yr running mean method for whitebark pine and subalpine fir individuals sampled from Hornet Peak. Each black bar represents the percentage of trees that experienced a release event by year. The black line represents the sample depth.

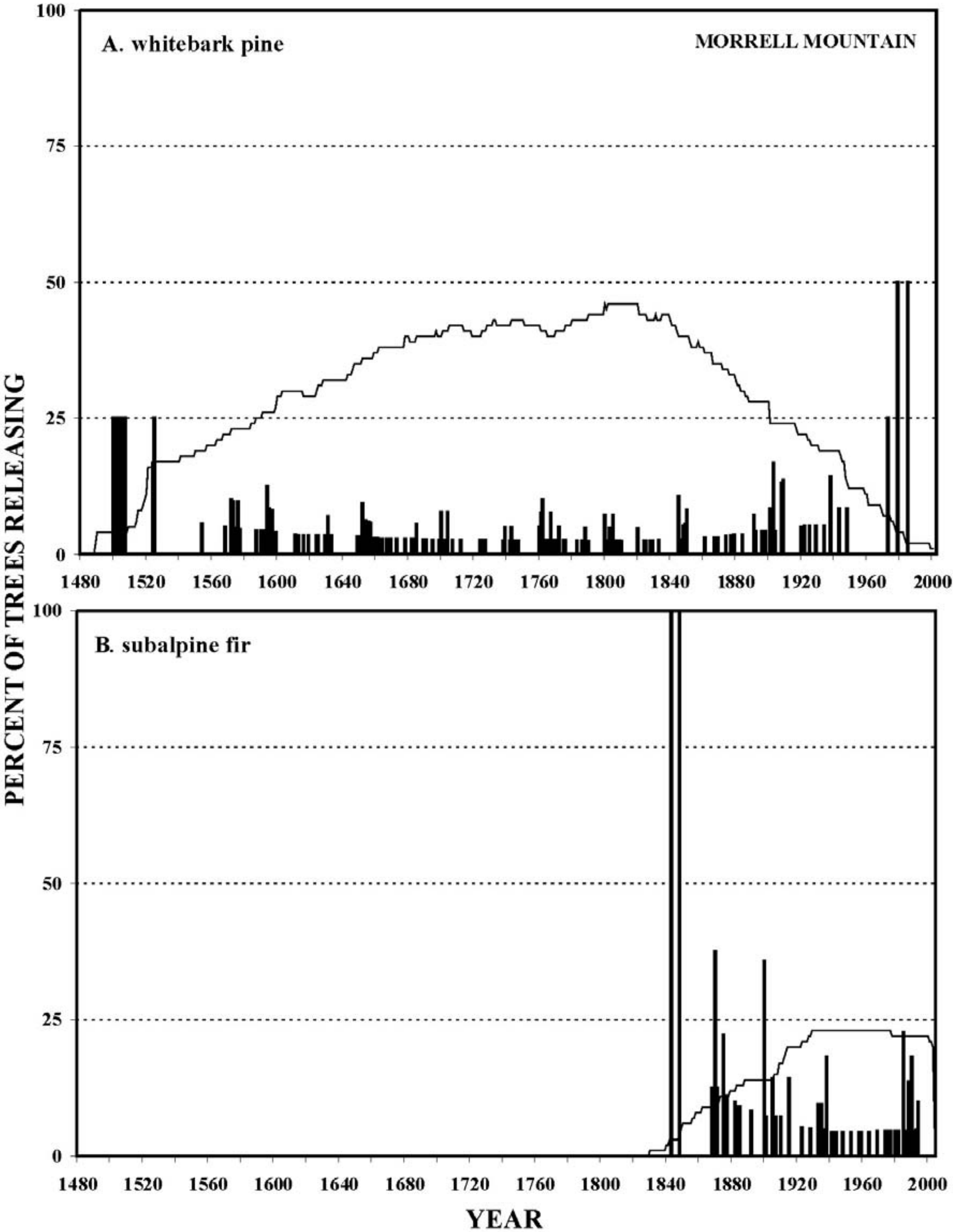

Figure 4.8. Detected release events using the 10-yr running mean method for whitebark pine and subalpine fir individuals sampled from Morrell Mountain. Each black bar represents the percentage of trees that experienced a release event by year. The black line represents the sample depth.

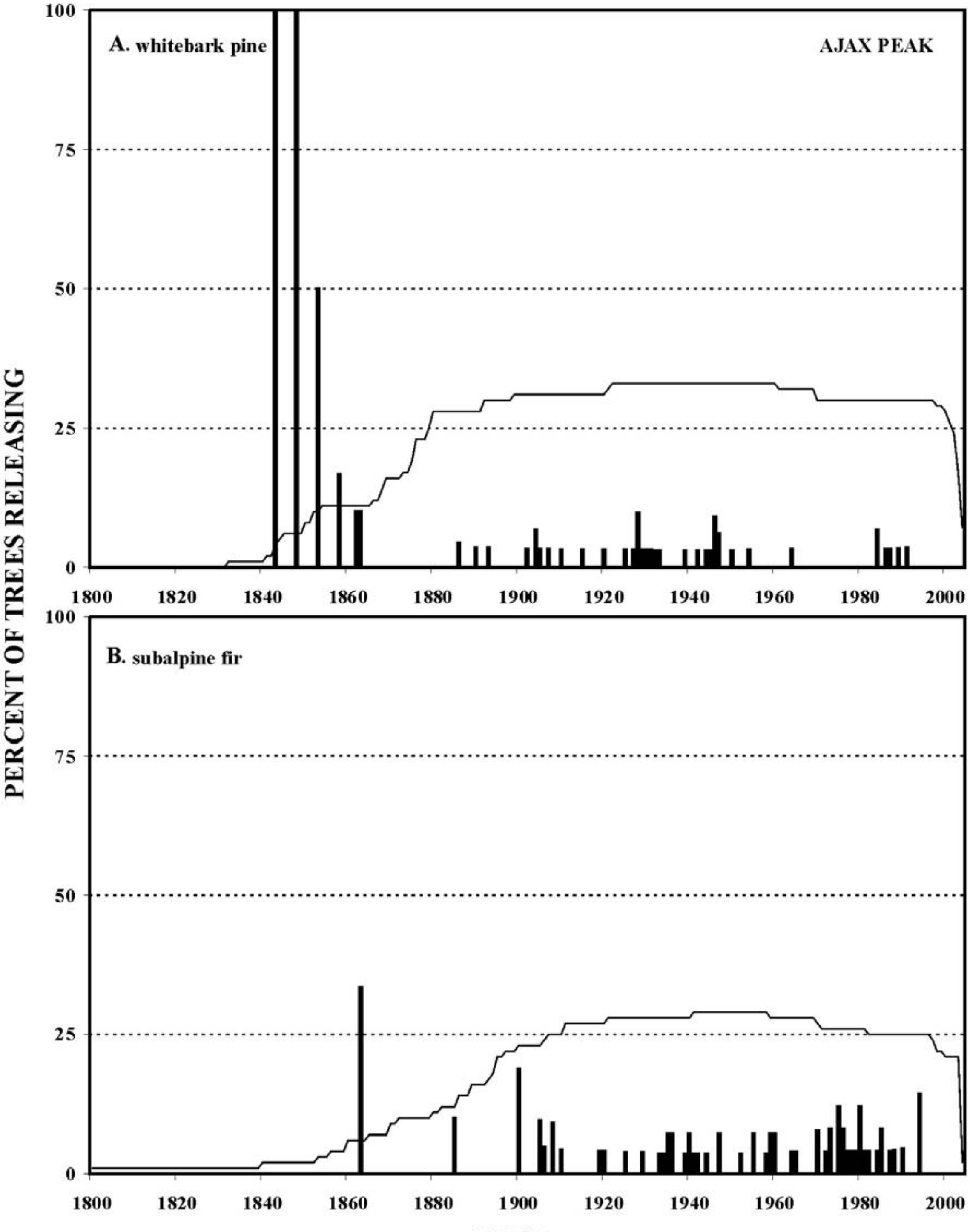

Figure 4.9. Detected release events using the 10-yr running mean method for whitebark pine and subalpine fir individuals sampled from Ajax Peak. Each black bar represents the percentage of trees that experienced a release event by year. The black line represents the sample depth.

occurred from 1890–1910 and 1920–1950. Subalpine fir and whitebark pine did not experience releases during the same years, but they both had a release pulse in the mid-1980s. Subalpine fir had stand-wide releases in 1843, 1848, 1870, and 1900 (Figure 4.8b). Over 20% of the subalpine firs experienced releases in 1875, 1938, 1985, and 1990. Whitebark pines from Ajax Peak experienced stand-wide releases in 1843, 1848, and 1853 (Figure 4.9a). Ajax Peak and Morrell Mountain both had stand-wide releases in 1843 and 1848, which indicates regionally important disturbance or climatic events that affected western Montana in the mid-1840s (Figures 4.8 and 4.9). Periods of release pulses in whitebark pines included 1927–1933 and 1944–1947. Subalpine fir only responded similarly to whitebark pine at Ajax Peak in 1863 (Figure 4.9b). Other years that showed a release pulse in subalpine fir included 1900, 1975, 1982, and 1994.

4.5 Discussion

4.5.1 Forest Composition

High-elevation subalpine forests in the Rocky Mountains of western Montana were historically dominated by whitebark pine. Currently, the combination of advancing encroachment by fire-intolerant species such as subalpine fir and Engelmann spruce, mountain pine beetle outbreaks, and the epidemic of white pine blister rust have devastated whitebark pine populations north of 45 °N in western North America (Kendall and Keane 2001, Tomback *et al.* 2001). Whitebark pine populations, in the majority of our sites, were being successionally replaced by subalpine fir, grand fir, and Engelmann spruce in all levels of the forest strata (trees, saplings, and seedlings). Our southern-most sites in the BDNF had the highest number of living whitebark pine in all canopy classes.

These sites also had the lowest densities of competing species which may contribute to their relatively healthy whitebark pine populations. Shade-tolerant species, such as subalpine fir, grand fir, and Engelmann spruce, established throughout the stand history of our whitebark pine-dominated sites, with individual subalpine firs having established in the early 1700s.

The establishment of shade-tolerant species over the past 300 years shows that forest succession in whitebark pine communities in not a result of 20th century fire suppression, contrary to what has been suggested by previous studies (Tomback *et al.* 1995). The age structure of our sites indicates that tree establishment is linked with stand-replacing fires during the 1700s and 1800s and that 20th century fire suppression and stand-thinning disturbances, such as mountain pine beetle outbreaks, have not significantly affected tree establishment. This suggests fire suppression may not be responsible for the advanced succession found in these whitebark pine forests in western Montana. Although canopy disturbances by mountain pine beetles are predicted to favor tree establishment, our understory results do not generally show pulses of tree establishment after known mountain pine beetle outbreaks. However, subalpine fir establishment did occur during a mountain pine beetle outbreak in the 1970s at Morrell Mountain. Overall, we expected to see distinct cohorts of tree establishment during the 20th century as a result of fire suppression and stand-thinning disturbances at our sites in western Montana, but found there was little new establishment of either whitebark pine or shade-tolerant species since 1940.

Our canopy class and understory results show the future trajectory of these historically whitebark pine-dominated forests. In the absence of stand-wide disturbance, shade-tolerant species will likely increase in dominance as understory individuals are recruited to larger size and canopy classes and shade-tolerant species will continue to successionally replace whitebark pine. In the understory, subalpine fir, whitebark pine, grand fir, and Douglas-fir were the most abundant species in the sapling and seedling plots. However, many of the understory whitebark pines showed signs of white pine blister rust in the form of flagged branches and cankers on the stem, indicating that most understory whitebark pines will not survive the next decade.

Our results on understory composition in whitebark pine communities of western Montana support the reported lack of healthy whitebark pine regeneration that has been documented throughout western North America (Keane *et al.* 1994, Kendall and Keane 2001, Tomback 2001, Tomback *et al.* 2001, Zeglen 2002, Smith *et al.* 2008). Subalpine fir and Engelmann spruce are shade-tolerant species that can competitively exclude whitebark pine in the understory and lower canopy classes because they can remain suppressed in the understory until the occurrence of disturbance events allows them to recruit. Many subalpine fir saplings in our study sites were over 100 years old and still remained healthy in the understory. As more shade-tolerant individuals crowd the understory, and as trees in the suppressed and intermediate canopy positions reach codominant and dominant positions in the canopy, the forest will change from a whitebark pine-dominated forest to a spruce-fir forest. Whitebark pines will continue to be competitively excluded from successful recruitment into larger canopy classes by shade-tolerant species. In addition to the loss of whitebark pine as an important subalpine species, dense spruce-fir forests can lead to more severe fire regimes (Keane *et al.* 2001).

4.5.2 Forest Health

The process of tree death is complex and is commonly a result of numerous contributing factors that overlap in time (Manion 1981, van Mantgem *et al.* 2004). For example, blister rust infection may not directly lead to whitebark pine mortality, but may weaken tree defense mechanisms, leading to lethal mountain pine beetle infestations (Smith *et al.* 2008, Tomback and Resler 2008, Tomback and Achuff 2008). Many of the larger whitebark pines (> 30 cm DBH) in the FNF and LNF exhibited signs of both white pine blister rust infection and attack from the mountain pine beetle. Therefore, we can hypothesize that the presence of both of these mortality agents will lead to the death of declining whitebark pines in our sites within the next decade. Furthermore, weakened whitebark pines are actually more susceptible to attack by mountain pine beetles (Six and Adams 2007). Unlike mountain pine beetles which prefer to attack larger trees, blister rust threatens multiple aspects of the regeneration process by not only reducing available cone crops before a tree dies, but also by causing sapling and seedling mortality (McDonald and Hoff 2001). Whitebark pines in the overstory and understory at all of our sites showed branch or stem cankers from white pine blister rust. We agree with the current opinion that white pine blister rust is threatening the sustainability of high-elevation whitebark pine stands throughout its range (Tomback and Achuff 2008). Our results support the effort to understand the current status of white pine blister rust in whitebark pine forests throughout its range. We are the first to report white pine blister rust presence in whitebark pine forests in the BDNF, which should alert land managers to monitor and assess blister rust spread throughout southwestern Montana.

The high frequency of white pine blister rust and mountain pine beetle outbreaks, together with the contributing effects of fire suppression, all suggest the significant role of disturbance in determining whitebark pine population trajectories over the next few decades. Infection and mortality levels varied considerably across western Montana, but over 70% of the whitebark pine in all sites were either declining or dead. The high mortality of whitebark pine in the FNF and LNF was caused by the overlapping effects of past and current mountain pine beetle outbreaks, and more recently by white pine blister rust infection. We observed recently dead trees with what appeared to be old blister rust cankers at the sites in the FNF and LNF. Blister rust was abundant in all our sites, with whitebark pine trees exhibiting open cankers or flagging in their upper canopies and on lower branches. Most of the whitebark pines in the BDNF had cankers form directly on the main stem that will likely cause mortality within 10 years (Hunt 1991, Zeglen 2002).

Our study was the first to find a white pine blister rust signature in whitebark pine chronologies. Although whitebark pine may not show immediate external symptoms of blister rust infection, the tree-ring record can show radial growth declines from blister rust before external tree symptoms appear. Since 1998, we observed a steady decline in whitebark pine growth at all our sites, but the decline in the BDNF was different because there were no overlapping effects from mountain pine and blister rust, only blister rust was present at these sites. Blister rust had expanded significantly in BDNF sites from the 2003 to 2004 field seasons, but growth in these trees had been declining since 1998. We found that using dendroecological methods on whitebark pine and possibly other blister rust host tree species could be used to detect blister rust presence before visible external symptoms appear at least three years after a tree has been infected (Hoff 1992). More dendroecological research should be conducted in whitebark pine populations in southwestern Montana and other areas where blister rust is thought to be limited or absent, to determine if blister rust is present in these forests. Early blister rust detection could help land managers find blister rust-resistant whitebark pines earlier for conservation purposes.

4.5.3. Disturbance History

Hornet Peak has been heavily influenced by natural and anthropogenic disturbances throughout the stand history. Hornet Peak and the surrounding Flathead National Forest experienced wildfires in 1910, 1919, 1926, 1929, 1931, 1934, 1940, 1946, and 1958 (Wolff 1980), but these fires were not large enough to influence whitebark pine establishment because most of the trees established from 1675 to 1850. The largest cohort of tree establishment at Hornet Peak occurred around 1810, indicating a large fire could have created conditions favorable for tree establishment. In fact, many of the whitebark pines in the chronology established in 1817. We would have expected to see cohorts of tree establishment following fires in the early 20th century but only a few subalpine firs and grand firs established during this period. The last whitebark pine to establish at Hornet Peak occurred in 1854 at the end of a large 1810–1850 establishment period. However, subalpine fir and grand fir have continued to establish since 1850, indicating a lack of fire or other stand-wide disturbance to facilitate whitebark pine establishment. A large disturbance occurred around 1880 that favorably affected growth in the whitebark pine and subalpine fir chronologies. This disturbance could be a mountain pine beetle outbreak that affected larger (>30 cm DBH) whitebark pines but created favorable conditions for release in smaller whitebark pines and competing shade-tolerant species. Alfaro *et al*. (2004) also found an 1880s mountain pine beetle outbreak signal from lodgepole pines in British Columbia. Whitebark pines at Hornet Peak had below-average growth periodically throughout the length of the chronology but most notably during mountain pine beetle outbreaks in the 1920s, 1930s, and the 1970s. Surviving whitebark pines and nonhost trees, such as subalpine firs, showed a cohort of release events from 1960 to 1990, during a period of a mountain pine outbreak. Our nonhost species, subalpine fir, also had asynchronous years of below average growth in the chronology indicating that the growth reductions in whitebark pine are likely due to mountain pine beetle outbreaks and white pine blister rust infection.

Morrell Mountain had a similar pulse of release events from 1960 to 1990 which were also caused by the mountain pine beetle. Morrell Mountain experienced fires in 1711, 1751, 1754, 1796, 1830, 1836, 1843, 1898, and 1919 (Larson 2005, Larson *et al.* 2008). Fires in the early 1700s likely influenced forest age-structure by creating conditions that favored tree establishment. Mountain pine beetle-caused mortality peaked in the 1970s and 1980s, but a cluster of mortality dates in the late 1920s suggests the stand may have been affected by previous outbreaks. The whitebark pine and subalpine fir chronologies showed a similar growth decline from 1977 to 1984, during a mountain pine beetle outbreak. Further research should focus on climate data during this mountain pine beetle outbreak to isolate drought conditions or other climatic anomalies that affected both host and nonhost species. Morrell Mountain had the highest frequency of release events from natural and anthropogenic disturbances throughout the length of the chronologies.

Fire history information was not available for Ajax Peak. However, a large cohort of tree establishment in the mid-1800s indicates a possible stand-replacing fire occurred. Gold mining was also conducted near Ajax Peak in the late 1800s (Burlingame 1957) and exposed talus slopes from mining are still evident today. Ajax Peak had the shortest chronology, with many of the living trees in the chronologies establishing in the 1870s. Murray *et al.* (2000) also found similar establishment dates in the 1870s in the West Big Hole mountain range. They found a decrease in whitebark pine dominance that they attributed to successional replacement by fire-intolerant species, grazing, and fire suppression. Whitebark pines at Ajax Peak and Morrell Mountain showed similar growth suppression patterns in 1838 and 1899, while both chronologies experienced a growth peak in 1863. The growth trends in the 1800s indicate a similar climate signal between the Ajax Peak and Morrell Mountain sites. The similar growth trends between Morrell Mountain and Ajax Peak is interesting because Ajax Peak had the lowest frequency of release events of the study sites. Although mountain pine beetle mortality occurred in the late 1920s–1930s, the outbreak did not cause a large growth release in the surviving whitebark pines or in the subalpine firs, which indicates the 1930s outbreak might not have had a severe impact on the high-elevation whitebark pines at Ajax Peak. Although Ajax Peak had the healthiest population of whitebark pine, the Ajax Peak chronology showed a decrease in growth since the late 1990s caused by white pine blister rust presence at the site.

Stand-wide release episodes occurred in the study sites, usually early or late in the site release records when sample size was small. However, similarities in the LNF and BDNF release record in 1843 and 1848 indicate regionally important disturbance or climatic events that affected western Montana in the mid-1840s. In the northern Rocky Mountains, such disturbance events may have included fires, mountain pine beetle outbreaks, and extreme climatic events, among other factors. We also found release cohorts following mountain pine beetle outbreaks during the 20th century at our sites. In contrast to stand-replacing fires, mountain pine beetle outbreaks are selective mortality agents that do not create extensive areas of exposed mineral soil. Plant responses to insect disturbances include growth suppressions in attacked trees and growth releases in understory or competing trees (Veblen *et al*. 1991). Release responses in our whitebark pine and subalpine fir series were largely asynchronous, which is what we would expect from host and nonhost trees during host-specific mortality periods. Our study found that using release episodes between species and sites was necessary to interpret mountain pine beetle outbreaks on a landscape scale. The chronologies only showed a small spike in growth during mountain pine beetle outbreaks compared to episodic periods of release in the whitebark pine and subalpine fir series. Therefore, we would recommend further research into using both suppression and release measures of host and nonhost series and mortality dates of host trees to clarify the extent and intensity of mountain pine beetle outbreaks in whitebark pine communities in western North America.

The overlapping effects of mountain pine beetle and white pine blister rust are hastening the decline of whitebark pine in our northern and central sites in western Montana. The mountain pine beetle will continue to move south until it attacks our southern sites as well. Whitebark pine currently has very little resistance to mountain pine beetle and white pine blister rust, and is unlikely to evolve more resistance before populations are dramatically reduced across western North America (Campbell and Antos

2000, Tomback *et al.* 2001). However, conservation efforts in the form of planting blister rust-resistant whitebark pine seedlings and prescribed fire are currently being used by land managers in select whitebark pine communities (Hoff *et al.* 2001). The data from this study can be used by land managers to prioritize areas for conservation on a landscape scale. For example, our northern and central sites with high levels of infection, canopy kill, and overstory and understory mortality could be replanted with blister rust-resistant trees. These replanted trees would later need protection from mountain pine beetle by applying semiochemicals (Kegley and Gibson 2004).

CHAPTER 5

DIFFERENTIATING THE EFFECTS OF CLIMATE AND MOUNTAIN PINE BEETLE ON GROWTH OF WHITEBARK PINE AND SUBALPINE FIR IN THE NORTHERN ROCKY MOUNTAINS, U.S.A.

Portions of this chapter that refer to whitebark pine ecology, study site descriptions, and methods were taken from Chapters 1, 2, and 3 of this dissertation. The use of "we" in this chapter refers to Dr. Henri Grissino-Mayer and myself who will be co-authors on the manuscript submitted from this chapter. Dr. Grissino-Mayer assisted in the identification of relevant literature, field collection, and verifying the accuracy of dated samples.

In this chapter, we examine whitebark pine and subalpine fir response to climate and mountain pine beetle outbreaks in the Flathead, Lolo, and Beaverhead-Deerlodge National Forests in the northern Rocky Mountain of western Montana. We compare whitebark pine and subalpine fir chronologies from three study sites (one site from each national forest: Hornet Peak from the Flathead National Forest, Morrell Mountain from the Lolo National Forest, and Ajax Peak from the Beaverhead-Deerlodge National Forest) to understand the contributing effects of climate to host and non-host species response to mountain pine beetle outbreaks in the 20th century. *Manuscript to be submitted to Dendrochronologia.*

5.1 Introduction

The interacting and entangled relationships between climate, mountain pine beetle (*Dendroctonus ponderosae* Hopk.) outbreak periods, and growth of whitebark pine (*Pinus albicaulis* Engelm.) and subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.) has not yet been studied. This research was initiated to first evaluate the climate-tree growth relationship of these two subalpine tree species, and then attempt to separate the effects caused by mountain pine beetle. Although climate is known to affect high-elevation whitebark pine ecosystems (Perkin and Swetnam 1996, Biondi *et al.* 1999, Luckman and Villalba 2001, Kipfmueller 2003, Mann 2008), little is known about which climate variables affect the growth of these two species in Montana. Understanding climate response in subalpine forests is important because climatic fluctuations may increase or decrease the vulnerability of whitebark pine to mountain pine beetle outbreaks, and affect the advancing succession of subalpine fir in declining whitebark pine forests. This approach to disentangling the effects of both climate and mountain pine beetle is possible because whitebark pine is the host species (and should therefore harbor the signal caused by mountain pine beetle) while subalpine fir is the nonhost species (and should therefore contain a stronger climate signal).

Climate patterns (both short-term (annual to interannual) and long-term (decadal and interdecadal)) affect the relationship between the ecology of mountain pine beetles and whitebark pine mortality. Attacks by mountain pine beetles occur more frequently during periods with warmer temperatures and drought conditions (Campbell *et al*. 2007). Warming climate conditions expand the geographic range of mountain pine beetles by increasing the area available for the beetles to complete their life cycle. An increase in the number of infestations since 1970 in formerly climatically unsuitable habitats indicates that mountain pine beetle populations have expanded into high-elevation subalpine forests (Carroll *et al*. 2003). Therefore, whitebark pine may be more vulnerable to mountain pine beetle outbreaks under current warming conditions than during previous outbreaks between 1920 and 1940 and between 1970 and 1980. Whitebark pine is already in peril due to white pine blister rust (*Cronartium ribicola* JC Fischer), and the overlapping effects of the current mountain pine beetle outbreak will likely intensify its decline. The effects of these changes in climate are important when assessing the flexibility of whitebark pine ecosystems to recover from mountain pine beetle outbreaks that may be intensified, infestations of blister rust that are geographically extensive, and other landscape-level disturbances, including thos caused by humans (*e.g.*, logging and fire exclusion practices). Consequently, an urgency exists to understand the influence of climate change on the severity of mountain pine beetle outbreaks and white pine blister rust infections that contribute to the decline in whitebark pine ecosystems.

Mountain pine beetle epidemics killed a large proportion of mature whitebark pine trees in the Rocky Mountains of the United States during the 20th century (Ciesla and Furniss 1975, Furniss and Carolin 1977, Romme *et al*. 1986). The insect is considered the most destructive of the native biotic agents in mature *Pinus* forests in western North America (Safranyik and Carroll 2006). The major hosts for mountain pine beetle include whitebark pine, ponderosa pine (*Pinus ponderosa* Douglas ex C. Lawson), lodgepole pine (*Pinus contorta* Douglas ex Loudon), and western white pine (*Pinus monticola* Douglas ex D. Don). Extensive mountain pine beetle outbreaks in western North America occurred in the 1880s, 1930s, and 1970s, and more recently in the early 2000s (Arno and Hoff 1989, Alfaro *et al.* 2004, Taylor *et al.* 2006). The series of outbreaks that occurred from 1920 to 1940 in Idaho and Montana killed an estimated 1.4 billion lodgepole pines and vast numbers of whitebark pine (Safranyik and Carroll 2006). Extensive outbreaks in western North America during the late 1970s and early 1980s killed almost 2 million hectares of *Pinus* trees. A massive infestation, extending over 12 million hectares, has also devastated lodgepole and whitebark pine stands in the northern Rocky Mountains and in central British Columbia in the early 2000s (Safranyik and Carroll 2006).

Tree-ring reconstructions of defoliating insects have used both host and nonhost species to differentiate the response in tree growth caused by insect outbreaks from the response in growth caused by climate (Fritts 1976, Brubaker and Greene 1979, Ferrel 1980, Swetnam *et al.* 1985, Fritts and Swetnam 1991, Swetnam and Lynch 1993, Speer 2000, Campbell *et al*. 2005). These studies sampled separate tree species that were susceptible and unsusceptible to the insect, and examined tree-ring characteristics associated with known insect outbreaks. Multicentury tree-ring chronologies are ideal for differentiating long-term growth patterns associated with both climate and insects because they provide replicated observations of multiple past outbreaks and multiple short-term and long-term climatic fluctuations that may be synchronous or asynchronous (Swetnam and Lynch 1993). Dendroecological methods for detecting mountain pine outbreaks in whitebark pine and lodgepole pine forests have relied mostly on detecting periods of growth releases beginning almost a decade after the outbreak event (Heath and Alfaro 1990, Alfaro *et al.* 2004, Taylor *et al*. 2006, Campbell *et al.* 2007), but no study hascompared whitebark pine growth with growth of a nonhost species to determine outbreak periods and climatic influences. Therefore, we propose to use a new technique to identify discrete mountain pine beetle outbreak periods by first minimizing the over-riding effects of climate by comparing host and nonhost tree species.

The objectives of this study were to: (1) develop tree-ring chronologies for both whitebark pine (host) and subalpine fir (nonhost) along a latitudinal transect through western Montana, (2) determine which climate variables exerted the most influence on whitebark pine and subalpine growth during the 20th century, and (3) using the host and nonhost chronologies, determine mountain pine beetle outbreak characteristics, such as timing, frequency, as well as evaluate possible relationships between climatic patterns and outbreaks.

5.2 Study Site

Our study sites were located in whitebark pine forests on three peaks across three national forests in Montana, located on a north-south transect that extended from the Montana/Canada border to the western side of Yellowstone National Park. We chose to sample along a north-south latitudinal transect to evaluate trends in landscape-level mountain pine beetle outbreaks. The sites varied in elevation from 2,040 m to 2,535 m (Table 5.1). Ranges of mean annual temperature are similar, but a gradient of decreasing precipitation exists from west to east that creates different precipitation regimes among the study sites. Soils are poorly developed at all sites. The underlying geology is composed of a mix of Quaternary and Cenozoic glacial deposits, Precambrian shales and siltstones, and Precambrian argillites and quartzites (Ross *et al.*1955, Raines and Johnson 1996). Subalpine fir, Douglas-fir, lodgepole pine, Engelmann spruce, and grand fir (*Abies grandis* (Douglas. ex D. Don) Lindl.) were present in the stands we examined. Forest cover on Ajax Peak was relatively continuous, although the forests on Morrell Mountain and Hornet Peak were broken by a few alpine meadows. Common herbaceous plants on all sites included grouse whortleberry (*Vaccinium scoparium* Leib. ex Coville), red mountain-heath (*Phyllodoce empetriformis* (Sm.) D. Don), smooth woodrush (*Luzula hitchcockii* Hamet-Ahti), bear grass (*Xerophyllum tenax* (Pursh) Nutt.), and elk sedge (*Carex geyeri* Boott).

Evidence of disturbances was found at each site. The whitebark pines had experienced differing rates of mortality in each stand, predominantly from mountain pine beetle activity that we identified by pitch tubes and red boring dust on tree stems,

Table 5.1. Study site locations in Montana.

Study Site	**National Forest**	**Elevation (meters)**	**Latitude (Degrees N)**	**Longitude (Degrees W)**
Hornet Peak	Flathead	2040	48.52.44	114.31.33
Morrell Mountain	Lolo	2370	47.11.53	113.21.25
Ajax Peak	Beaverhead-Deerlodge	2535	45.20.25	113.42.57

the presence of J-shaped galleries on the boles of dead trees, and by blue-staining fungus (*Ceratocystis montia* (Rumb.) Hunt.) in the outer tree rings once cross-sections were collected. We also observed several recently dead trees with what appeared to be old blister rust cankers our sites, particularly at Ajax Peak. Blister rust was abundant, with whitebark pine trees exhibiting open cankers or flagging (red needles due to the recent mortality of a branch or stem) in their upper canopies and on lower branches. Evidence of past fires was limited to Hornet Peak and Morrell Mountain, where many whitebark pine trees displayed multiple fire scars. We did not observe any fire-scarred subalpine fir trees.

5.3 Methods

5.3.1 Field Methods

The whitebark pine and subalpine fir samples used in this study were part of a larger project designed to study the stand histories of the whitebark pine ecosystem in Montana. Many of the whitebark pine samples selected for analysis were affected by the mountain pine beetle that could diminish the strength of the overall climate signal. Whitebark pine and subalpine fir tree-ring data were collected in four 0.05 ha fixed-radius (r = 12.66 m) plots on each of the three mountains selected (12 overstory plots total). We collected increment cores from two radii of each tree in the plot by either coring the tree twice on opposite sides of the tree, or by coring straight through the tree. All cores were taken at or below 30 cm above the root collar and along the contour of the slope to minimize the effects of reaction wood on the growth patterns in each sample (Fritts 1976). Core samples were labeled and placed in paper straws for storage and protection. We used a chainsaw to collect 5 to 10 cross-sections from whitebark pine snags, stumps, and logs to extend the tree-ring information from the cores back in time, and examined cross-sections for fire and mountain pine beetle scars at each of the three mountain sites (Arno and Sneck 1977). We visually examined each cross-section and noted the presence or absence of fire (*i.e.*, internal fire scars), mountain pine beetle galleries, and blue-stain fungus on each sample. All samples were labeled and then wrapped with plastic wrap for transport back to the laboratory.

5.3.2 Laboratory Methods

All samples were frozen at –40 °C for 48 hours to kill any pathogens and/or insects that may have been transported along with the samples. After allowing all samples to dry, fragile cross-sections were glued to plywood for stabilization. Cores were allowed to air-dry completely in the straws and were then glued to wooden core mounts with cells vertically aligned to ensure a transverse view of the wood surface. Cores and cross-sections were examined for blue-stain fungus in the outer tree rings, indicating the presence of mountain pine beetles. Cross-sections were given an initial flat surface using a band saw to remove deep chain saw cuts prior to sanding, then each cross-section and core sample was sanded using a belt sander, beginning with ANSI 80-grit (177−210 μm) and using progressively finer-grit belts until ANSI 400-grit (20.6−23.6 μm) (Orvis and Grissino-Mayer 2002). This process produced a wood surface with cellular features clearly defined under 10x magnification for clear ring identification.

5.3.3 Crossdating and Chronology Construction

We used visual, graphical, and statistical crossdating to assign precise calendar years to the growth rings of the core and cross-section samples. Visual crossdating relied on recognition of characteristic patterns of wide and narrow rings common to each study site that were likely related to regional climate (Fritts1976); graphical crossdating was accomplished using the skeleton-plot method (Stokes and Smiley 1996); and statistical crossdating was accomplished using ring-width measurements and the computer program COFECHA (Holmes 1983, Grissino-Mayer 2001).

We measured the ring widths on all samples to 0.001 mm accuracy with a Velmex measuring stage coupled with MEASURE J2X software. We confirmed the graphical crossdating and relative placements of all tree-ring series using COFECHA, which uses segmented time-series correlation techniques to confirm the previously-assigned temporal placements of all tree rings to the exact year each was formed (Grissino-Mayer 2001). Because crossdating is a high-frequency process (pattern matching of sequences of individual rings), COFECHA removes all low-frequency trends using both spline-fitting algorithms and autoregressive modeling (Grissino-Mayer 2001). Such trends could also be caused by natural (*e.g.* mountain pine beetle outbreaks and fire events) and human (*e.g.* blister rust infection, logging, and mining) disturbances that otherwise could mask the climate signal desirable for accurate crossdating. We tested consecutive 50-yr segments (with 25-yr overlaps) on each series with a master chronology created from all other series by site.

Crossdating was verified when the correlation coefficient for each tested segment exceeded 0.32 ($p < 0.01$), although coefficients were usually much higher. The final suggested placement made by COFECHA had to be convincing both graphically (similar patterns in wide and narrow rings) and statistically (correlation significant at $p < 0.001$) (Grissino-Mayer 2001). Crossdating quality was assessed by two statistical descriptors. The average mean sensitivity was used to measure the strength of the year-to-year variability in all series and is an indicator of climate responsiveness (Fritts 1976). Values of 0.25 or higher are common for tree-ring data from the western U.S. (DeWitt and Ames 1978), although the International Tree-Ring Data Bank (ITRDB, 2008) reports average values of 0.21 for both subalpine fir and whitebark pine. We also used the average interseries correlation calculated in COFECHA by averaging the correlation coefficients for each measurement series when correlated against a master chronology created from the remaining series (Grissino-Mayer 2001). The average interseries correlation for 33 subalpine fir chronologies in the ITRDB is 0.59, while the average value for 12 whitebark pine chronologies is 0.53 (ITRDB 2008).

We developed a whitebark pine and subalpine fir chronology for each of our three sites (six chronologies total). We standardized all measurement series in the six chronologies to remove effects from age-related growth trends that could add noise to the series unrelated to the climate signal desired in chronology development (Cook 1987, Fritts 2001). We removed the age-related growth trend of each sample using the program ARSTAN (Cook 1985), by first fitting either a negative exponential trend curve or straight line to the growth series of the sample using the least squares technique. ARSTAN then creates an index for that year by dividing the actual ring-width by the value predicted by the regression (Fritts 1976, Cook 1985). The indices were then averaged for each year across all series to create a single index series for each site for each species (Cook 1985).

5.3.4 Instrumental Climate Data

The climate-tree growth relationships for each of the six chronologies were analyzed using divisional climate data obtained from the National Climatic Data Center (NCDC 2007). For the Beaverhead-Deerlodge National Forest chronologies, we used climate data from NOAA Climate Division Montana 2 (Southwestern). For the Flathead and Lolo National Forest chronologies, we used climate data from NOAA Climate Division Montana 1 (Western). The climate variables used in the climate response analysis included monthly average temperature, monthly total precipitation, and monthly Palmer Drought Severity Index (PDSI). PDSI is used by the National Weather Service to monitor drought and wetness conditions in the United States and is a measure of the moisture conditions during the growing season. PDSI describes the severity of both wet and dry periods and incorporates temperature, precipitation, and evapotranspiration as an estimate of soil moisture availability as a monthly index (Palmer 1965). PDSI has been used in dendroclimatic studies and is often significantly correlated with tree-ring indices in North America (Grissino-Mayer and Butler 1993, Watson and Luckman 2001, Woodhouse 2001). The index is a weighted average of estimated soil moisture conditions for the current and preceding months resulting in a strong month-to-month autocorrelation that represents soil moisture condition changes over time (Stahle *et al.* 1988). PDSI generally ranges from –6 to +6, with negative values indicating dry periods and positive values indicating wet periods. PDSI values from –2.0 to –3.0 are considered a moderate drought, values from –3.0 to –4.0 are considered a severe drought, and values less than –4.0 are considered an extreme drought.

5.3.5 Statistical Analysis of Climate Response

Correlation analysis was used to statistically determine the strength of association between climate variables and tree growth of both whitebark pine and subalpine fir. Correlation coefficients were calculated between growth indices and climate variables (temperature, precipitation, and PDSI) for a 20-month period from previous May to current December. Seasons were determined for each climate variable based on sequences of months during which the climatic variable exhibited statistically significant ($p < 0.05$) relationships with whitebark pine and subalpine fir tree growth. Seasonalizing climate data is important because these seasons illustrate the longer period over which a climatic variable has the greatest effect on tree growth (Grissino-Mayer and Butler 1993, Grissino-Mayer 1995).

5.3.6 Separating Disturbance from Climate

We used the program OUTBREAK (Holmes and Swetnam 1994) for comparing our whitebark pine (host) and subalpine fir (nonhost) chronologies to detect mountain pine beetle outbreaks between1860 and 2005. First, we developed tree-level ARSTAN chronologies from 20 whitebark pine trees and 20 subalpine fir trees for each site. Although we had more series in each of the six chronologies used for climate analyses, the program OUTBREAK requires each tree analyzed be represented by two radii. The tree-level chronologies were important because they give a better representation for growth within a tree and assure that individual trees are not overrepresented in the final chronology (Swetnam *et al.* 1995, Speer *et al.* 2001, Speer 2007). The climatic variation contained in the whitebark pine chronologies was removed by subtracting the variation found in the subalpine fir chronologies by assigning growth suppression parameter values in OUTBREAK. We assigned a 100% growth suppression period of at least five years to identify a mountain pine beetle outbreak. OUTBREAK automates the correction of host chronologies and applies growth suppression criteria to identify dates of insect outbreaks (Swetnam *et al.* 1995, Speer *et al.* 2001, Campbell *et al.* 2005).

The corrected indices (OUTBREAK chronology) record radial growth in the host species after reduction or elimination of the climate signal found in the nonhost species chronology. Although OUTBREAK has not previously been used to detect mountain pine beetle outbreaks, we felt confident that the program would detect outbreaks after examining the whitebark pine cores for periodic growth suppressions during the 20th century. The timing of mountain pine beetle outbreaks in western North America is known to have been in the 1880s, 1920–1940, and 1970–1980 (Alfaro *et al.* 2004, Safranyik and Carroll 2006, Taylor *et al.* 2006). We were also expecting to see the tree-ring signature of the mountain pine beetle outbreak that is currently spreading through western North America.

5.4 Results

5.4.1 Chronology Development

The six whitebark pine and subalpine fir chronologies developed from Hornet Peak, Morrell Mountain, and Ajax Peak represented 229 samples (Table 5.2). The site chronologies varied in length, with the shortest whitebark pine record from Ajax Peak (1832–2005) and the longest from Morrell Mountain (1489–2003). Subalpine fir chronologies ranged from 1800–2004 at Ajax Peak to 1860–2005 at Hornet Peak. Subalpine fir chronologies had low sample depth and proved difficult to crossdate because many of the samples were smaller diameter trees (< 15 cm diameter breast height).

The interseries correlation and mean sensitivity of our three whitebark pine chronologies were representative of other whitebark pine chronologies from Montana (Larson 2005, Mann 2008) and typical for whitebark pine chronologies in the western U.S. (ITRDB 2008). Average interseries correlations for whitebark pine chronologies in the northern Rocky Mountains range between 0.41 and 0.70 (Perkins and Swetnam 1996, Biondi *et al.* 1999, Kipfmueller 2003, Larson 2005, Mann 2008), while we observed values between 0.48 and 0.52. Mean sensitivity values between 0.20 and 0.24 are common for whitebark pine tree-ring data from Montana and Idaho (Perkins and Swetnam 1996, Biondi *et al.* 1999, Kipfmueller 2003, Larson 2005, Mann 2008). The mean sensitivity for the whitebark pine chronologies from western Montana ranged from 0.21 to 0.24, typical of values found for other regional whitebark pine chronologies.

The Ajax Peak chronology had the highest interseries correlation (0.52), followed by Morrell Mountain (0.51), and Hornet Peak (0.48). Our subalpine fir chronologies had lower interseries correlations (0.43 at Hornet Peak, 0.50 at Morrell Mountain, and 0.49 at Ajax Peak) than a recent study that used subalpine fir to reconstruct treeline advancement in Glacier National Park (interseries correlation was 0.55), but we found the Morrell Mountain subalpine fir chronology mean sensitivity was higher (0.28 in comparison to

Table 5.2. Summary data of whitebark pine and subalpine fir chronologies from Montana. FNF is the Flathead National Forest, LNF is the Lolo National Forest, and BDNF is the Beaverhead-Deerlodge National Forest.

Study Site	Species	Period of Record	Number of Samples	Interseries Correlation	Mean Sensitivity
Hornet Peak (FNF)	whitebark pine	1682–2005	64	0.48	0.23
	subalpine fir	1860–2005	20	0.43	0.24
Morrell Mountain (LNF)	whitebark pine	1489–2003	60	0.51	0.24
	subalpine fir	1830–2003	23	0.50	0.28
Ajax Peak (BDNF)	whitebark pine	1832–2004	33	0.52	0.21
	subalpine fir	1800–2004	29	0.49	0.22

0.26) than the other study (Bekker 2005).

A few similar marker rings occurred in the whitebark pine and subalpine fir chronologies, but we found noticeable differences among the chronologies, likely due to differences in microclimates and disturbance histories. Visual and graphical crossdating were aided by especially narrow growth rings that formed in whitebark pines in AD 1601, 1641, 1698, 1782, 1838, 1899, and 1906. A pattern of consecutive narrow rings in 1753, 1754, and 1755, followed by a wide ring in 1756, also provided a strong tree-ring signature in the Morrell Mountain chronology. Marker rings among the subalpine fir chronologies included 1867, 1899, 1972, 1974, and 1993. The narrowest rings in both the whitebark pine and subalpine fir chronologies occurred in 1838 and 1899. Figures 5.1–5.3 illustrate the entire length of the whitebark pine and subalpine fir chronologies.

5.4.2 Climate Response

The correlation analysis indicated a strong response between whitebark pine and subalpine fir growth and precipitation and PDSI in our site chronologies from 1940–2005 (Figure 5.4). Whitebark pines at Hornet Peak and Morrell Mountain had the highest correlations between tree growth and precipitation. The positive correlations in the previous summer indicate that an increase in precipitation in the previous year's summer result in increased tree growth. We found a strong negative relationship with whitebark pine growth at Hornet Peak during the winter months when precipitation is in the form of snow and snowpack levels are high. The growing season (June to September) begins when temperatures warm and snowpack begins to thaw.

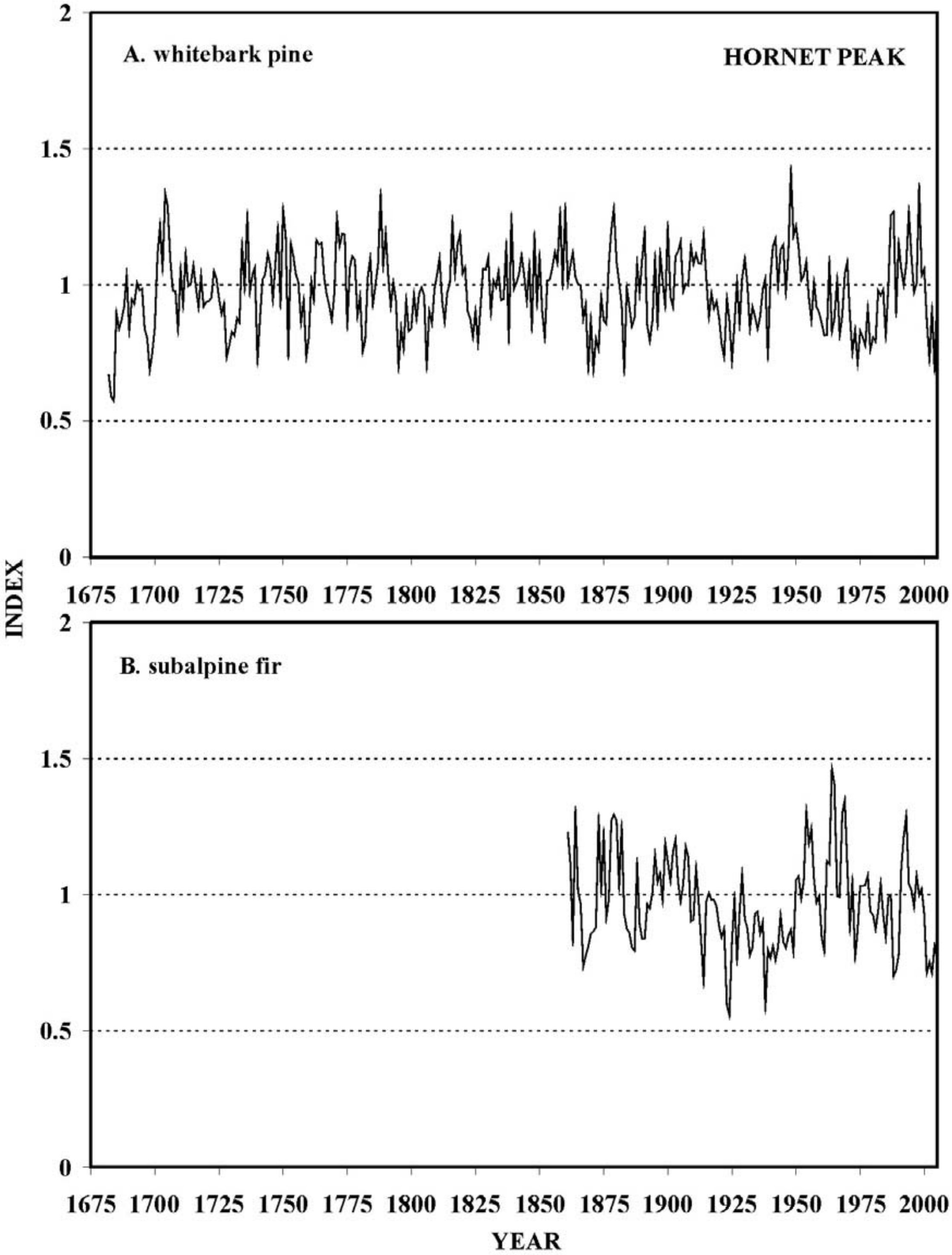

Figure 5.1. The ARSTAN chronology for: (A) whitebark pine and (B) subalpine fir from Hornet Peak in the Flathead National Forest.

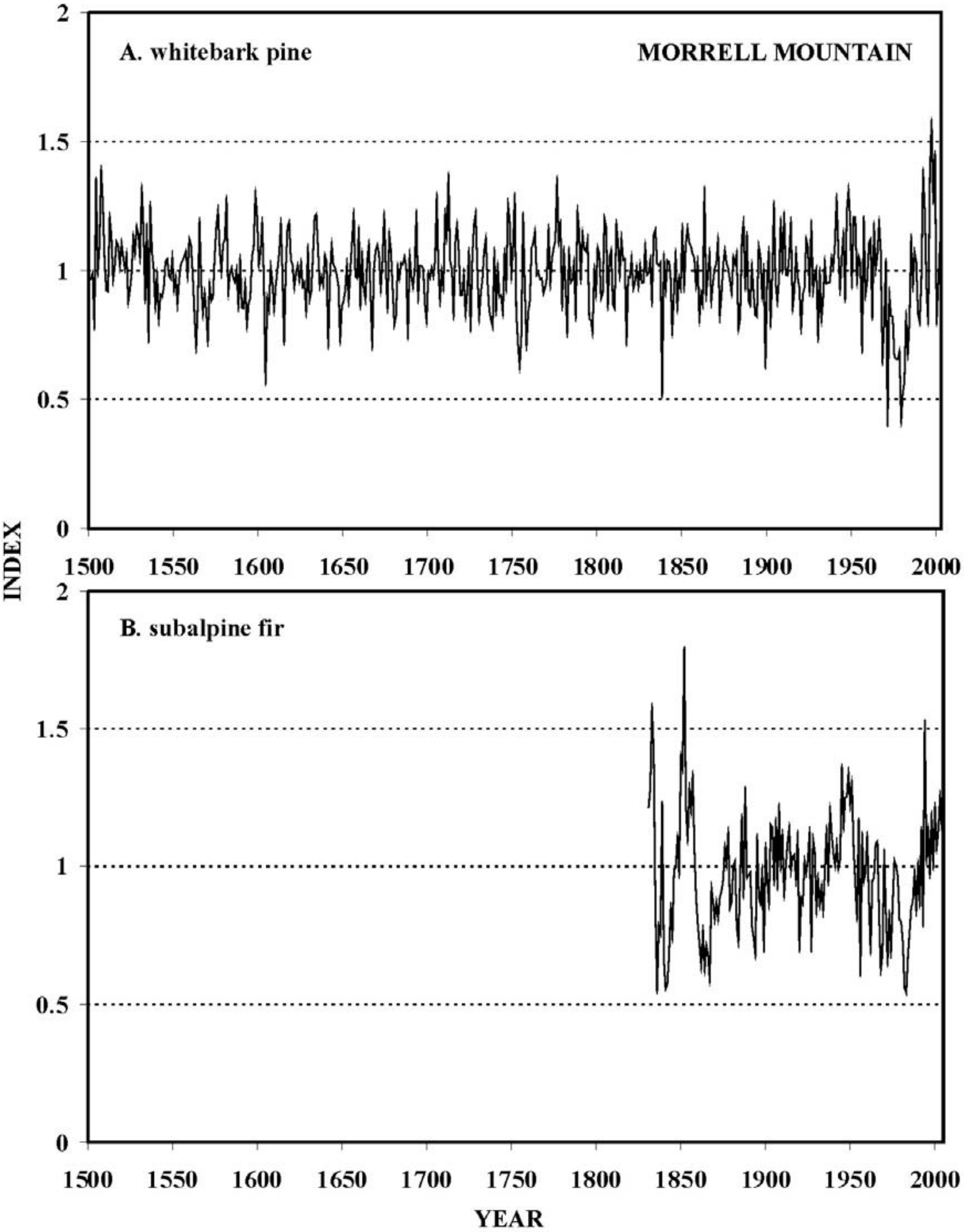

Figure 5.2. The ARSTAN chronology for: (A) whitebark pine and (B) subalpine fir from Morrell Mountain in the Lolo National Forest.

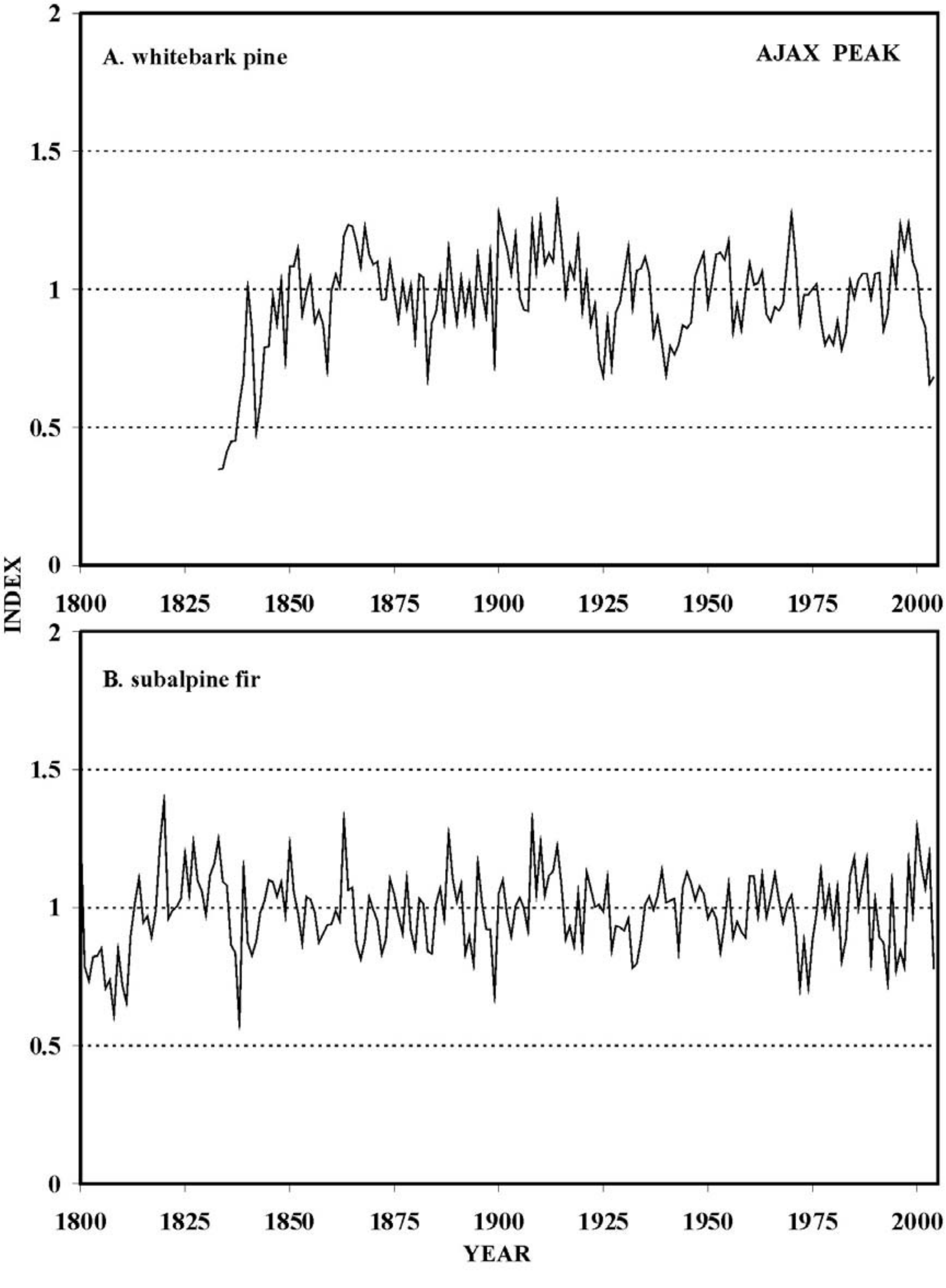

Figure 5.3. The ARSTAN chronology for: (A) whitebark pine and (B) subalpine fir from Ajax Peak in the Beaverhead-Deerlodge National Forest.

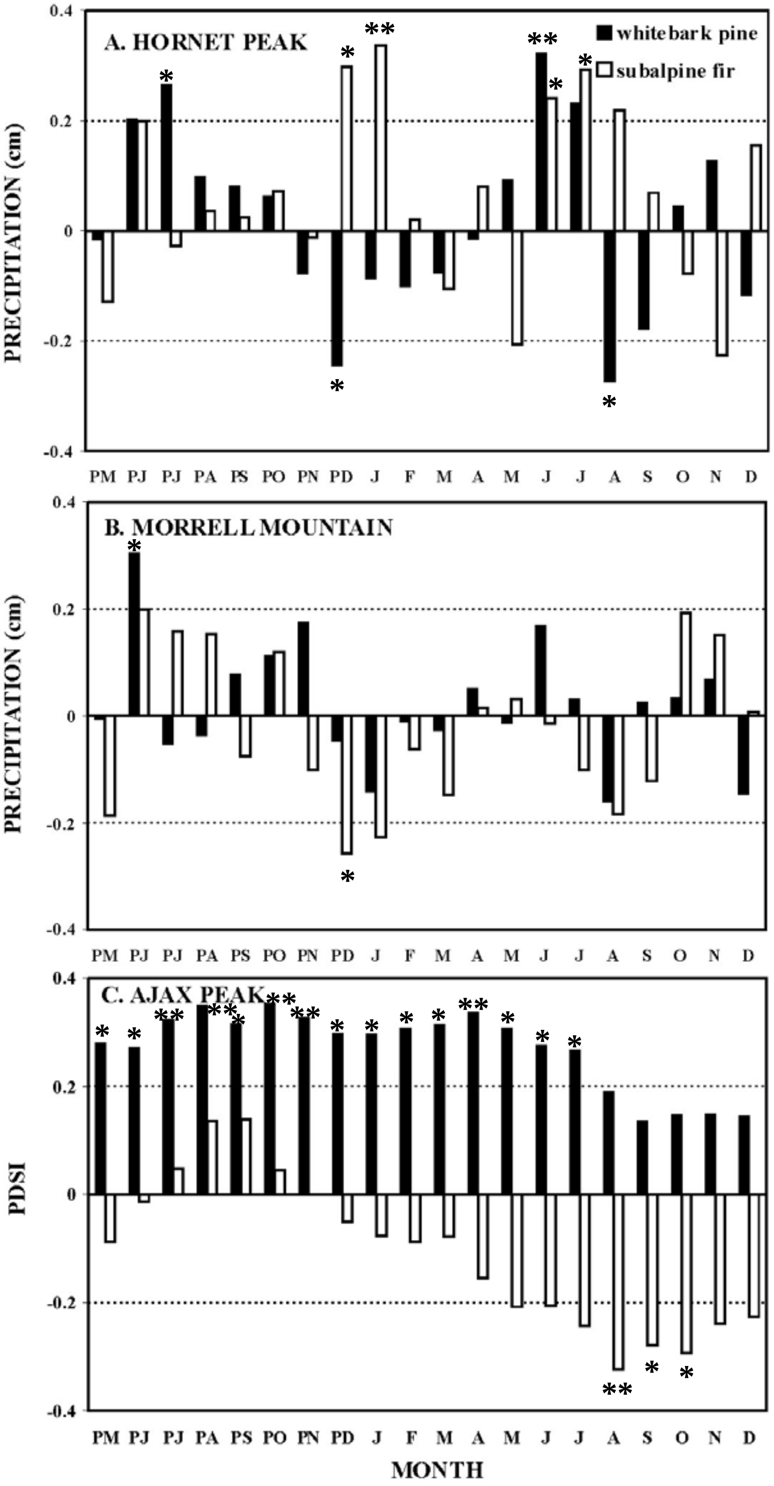

Figure 5.4. Correlation analysis for our three sites: (A) Hornet Peak and precipitation, (B) Morrell Mountain and precipitation, and (C) Ajax Peak and PDSI. Month abbreviations preceded with a "P" indicate the previous year. Black solid bars are whitebark pine and white solid bars are subalpine fir. * is $p < 0.05$, ** is $p < 0.01$

Whitebark pines at Hornet Peak also had a strong positive correlation to June precipitation. The climate response of subalpine firs at Hornet Peak was opposite of the whitebark pines during the winter. The positive correlations between subalpine fir growth during December and January precipitation show that subalpine firs respond favorably to high snowpack accumulations. We also found a strong positive correlation between subalpine firs and available moisture in the summer (June and July).

Tree growth at Morrell Mountain was less responsive to fluctuations in precipitation than at Hornet Peak. We found a strong positive relationship between whitebark pines and precipitation in the previous June, and significantly negative response in subalpine firs to snowpack accumulation during December. Whitebark pines at Ajax Peak had the highest positive correlations between tree growth and spring and previous summer PDSI. The positive correlation indicates that these sites are responding well to a combination of precipitation, temperature, and available soil moisture. The subalpine firs at Ajax Peak responded negatively to available moisture from August to October when there is likely a late summer drought from snowpack melting and new snow beginning to accumulate.

Seasonalized variables were developed for PDSI at Ajax Peak and precipitation at Hornet Peak and Morrell Mountain. The seasons during which precipitation and PDSI exhibited the strongest statistical relationship with whitebark pine growth occurred in the previous summer and current spring (Table 5.3). Whitebark pines at Hornet Peak responded the strongest to climate of the three sites (precipitation, $r = 0.36$, $p < 0.01$), followed by Ajax Peak (PDSI, $r = 0.35$, $p < 0.01$), and Morrell Mountain (precipitation, $r = 0.30$, $p < 0.05$). Subalpine firs at two of the study sites had inverse relationships with

Table 5.3. Seasonal climate data for whitebark pine and subalpine fir chronologies at each study site (1940–2005).

Study Site	**Species**	**Climate Variable**	**Season**	**Correlation Coefficient**
Hornet Peak	whitebark pine	Precipitation	June–July	0.36**
	subalpine fir	Precipitation	June–July	0.34**
Morrell Mountain	whitebark pine	Precipitation	pJune	0.30*
	subalpine fir	Precipitation	December–March	–0.31*
Ajax Peak	whitebark pine	PDSI	pJuly–pOctober	0.35**
	subalpine fir	PDSI	August–October	–0.31*

* $p < 0.05$; ** $p < 0.01$

PDSI (Ajax Peak) and precipitation (Morrell Mountain). Although the subalpine firs responded significantly to seasonalized variables at each site, each site was different. Hornet Peak was the site that showed the strongest positive relationship between summer precipitation and tree growth of both tree species, but Morrell Mountain and Ajax Peak had different inverse seasonal growth responses between species. Subalpine firs at Hornet Peak responded the strongest to climate of the three sites (precipitation, $r = 0.34$, $p < 0.01$), followed by Ajax Peak (PDSI, $r = –0.31$, $p < 0.05$), and Morrell Mountain (precipitation, $r = –0.31$, $p < 0.05$).

The relationships between tree growth and the significant seasonal climate variables were different in each site from 1940–2005 (Figures 5.5–5.7). Hornet Peak had the strongest association between tree growth and summer temperatures. Patterns of years with low summer precipitation in 1960, 1978, and in the 1990s also corresponded to years of low growth in whitebark pines and subalpine firs at Hornet Peak (Figure 5.5). Whitebark pines at Morrell Mountain responded to favorable summer precipitation from 1940 to 2003 but a few years of low growth in 1956 and 1971 do not correspond to the precipitation record (Figure 5.6). Whitebark pine growth during 1971 could be a response to a mountain pine beetle outbreak. Subalpine firs at Morrell Mountain had an inverse relationship to winter precipitation that is obvious in years 1956, 1972, and 1982. However, we found some years where subalpine firs responded positively to increases in precipitation in 1962 and 1968. Ajax Peak whitebark pines and subalpine firs had the most complex relationship with seasonalized climate variables. We found a highly significant positive relationship between whitebark pines and the previous summer/fall PDSI, that can be seen clearly in 1970, 1994, and 1996. Subalpine firs at Ajax Peak

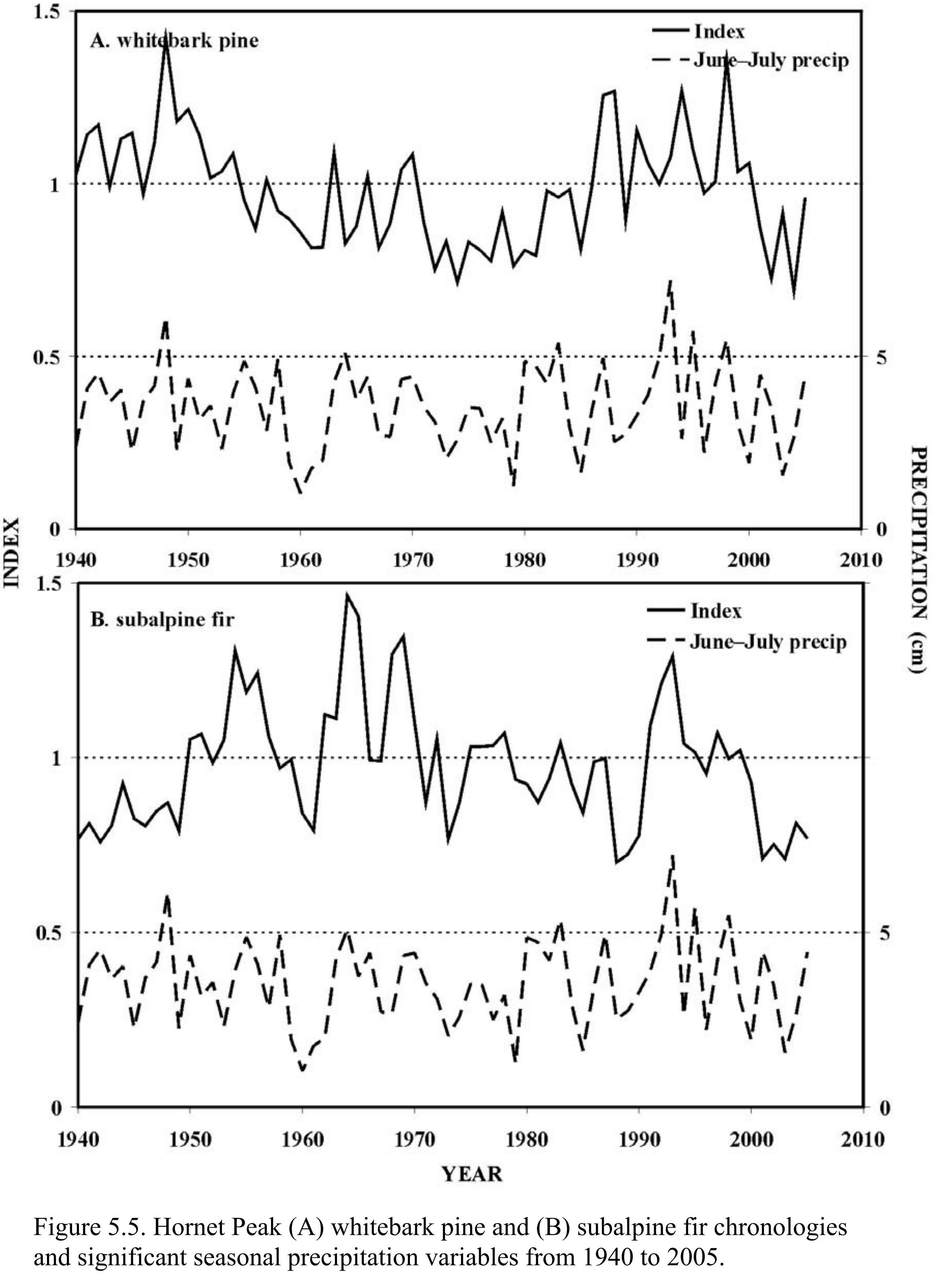

Figure 5.5. Hornet Peak (A) whitebark pine and (B) subalpine fir chronologies and significant seasonal precipitation variables from 1940 to 2005.

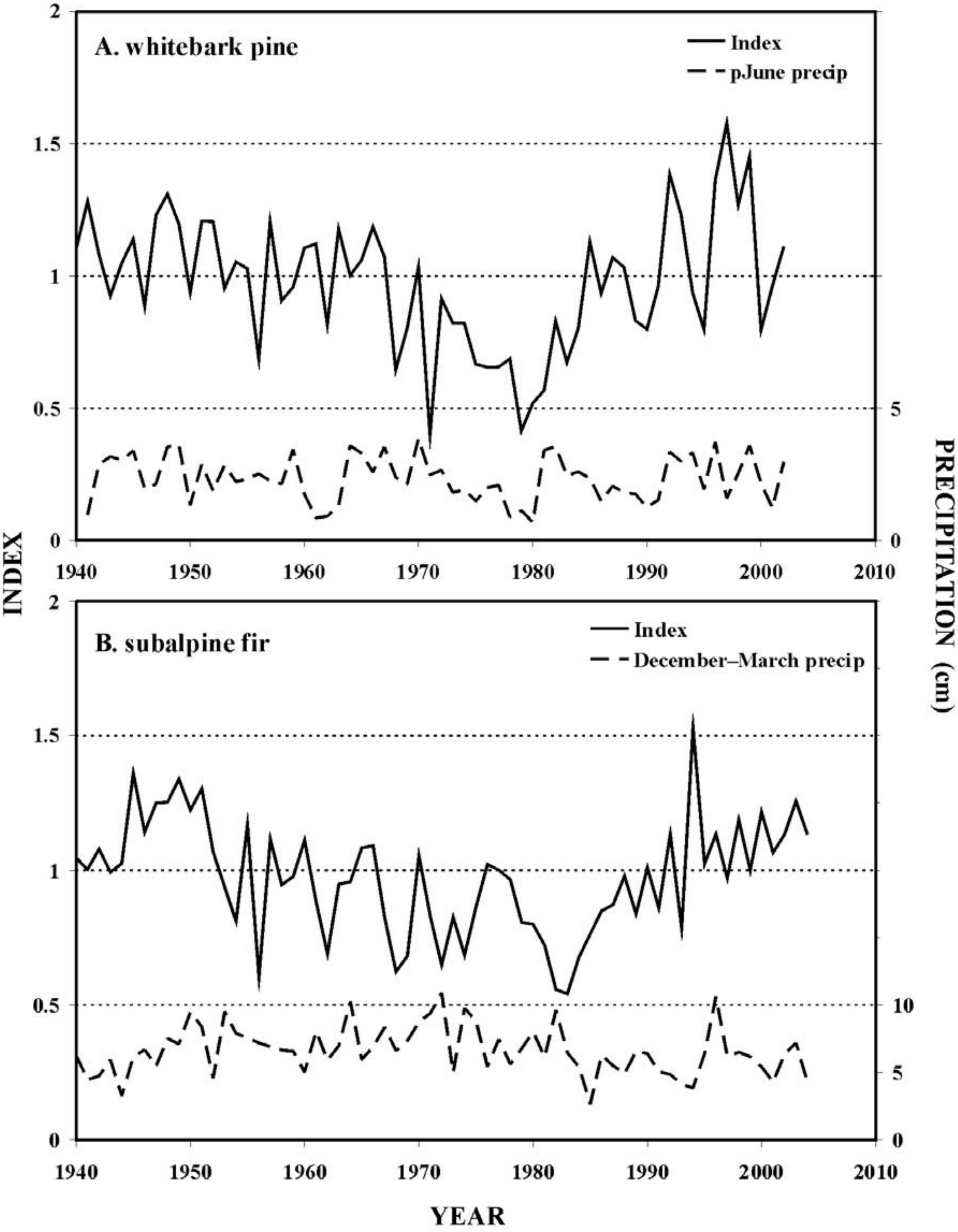

Figure 5.6. Morrell Mountain (A) whitebark pine and (B) subalpine fir chronologies and significant seasonal precipitation variables from 1940 to 2003.

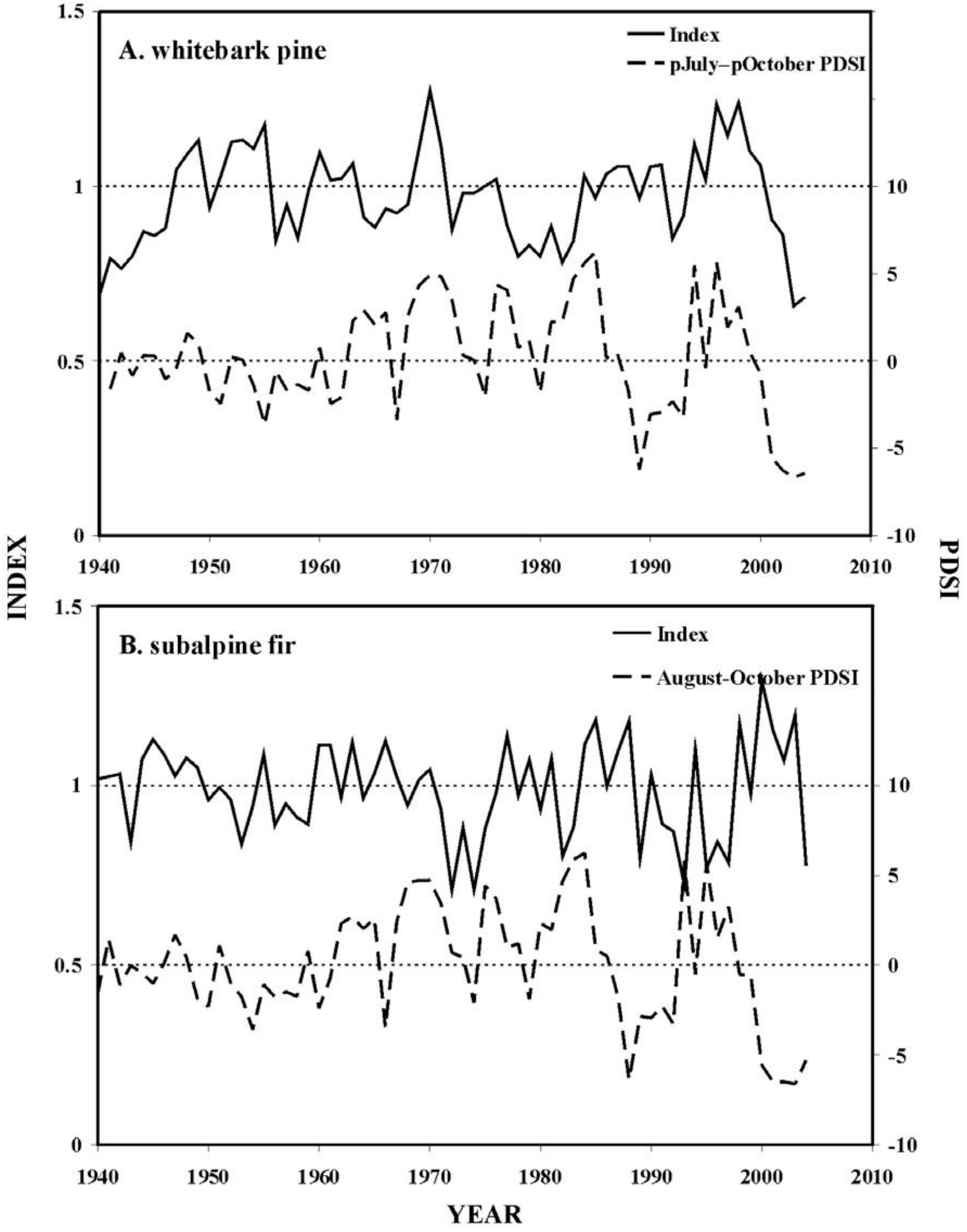

Figure 5.7. Ajax Peak (A) whitebark pine and (B) subalpine fir chronologies and significant seasonal PDSI variables from 1940 to 2004.

showed an inverse relationship to current summer/fall PDSI, most clearly in 1966, 1982, 1993, and 1996 (Figure 5.7).

5.4.3 OUTBREAK chronologies and whitebark pine mortality

The OUTBREAK chronologies helped identify years of extreme low growth in the whitebark pines attributed to non-climatic influences in the Rocky Mountains of western Montana. A comparison of these chronologies with known mountain pine beetle outbreaks in the 1880s, 1920–1940 and 1970–1980 indicates that a few of these low growth years do correspond with known outbreaks (Figure 5.8). Periods of reduced growth were common between the OUTBREAK chronologies in the 1880s, 1920s (except Morrell Mountain), and the 1970s. The year 1883 was one of the lowest growth years in the chronologies and corresponds with a mountain pine beetle outbreak that occurred in Canada in the 1880s (Alfaro *et al.* 2004, Taylor *et al.* 2006). The 1880s mountain pine beetle outbreak has yet to be documented in the western U.S. However, the 20th century mountain pine beetle outbreaks were less synchronous. Hornet Peak and Ajax Peak showed low growth in the 1920s, particularly in 1926 and 1925, respectively. Low growth years at these sites in 1977 and 1980 also coincided with a known outbreak period. Whitebark pines at Morrell Mountain responded similarly to whitebark pines at Hornet Peak and Ajax Peak in the 1970s, but low growth in 1906, 1909, 1916, 1918, the 1940s, and 1958 were asynchronous with the other sites, which could be from a different type of exogenous disturbance at Morrell Mountain. The Morrell Mountain and Ajax Peak OUTBREAK chronologies also showed a recent sharp decrease in growth since 1998. The patterns of outbreaks were clear in our site OUTBREAK chronologies, but we

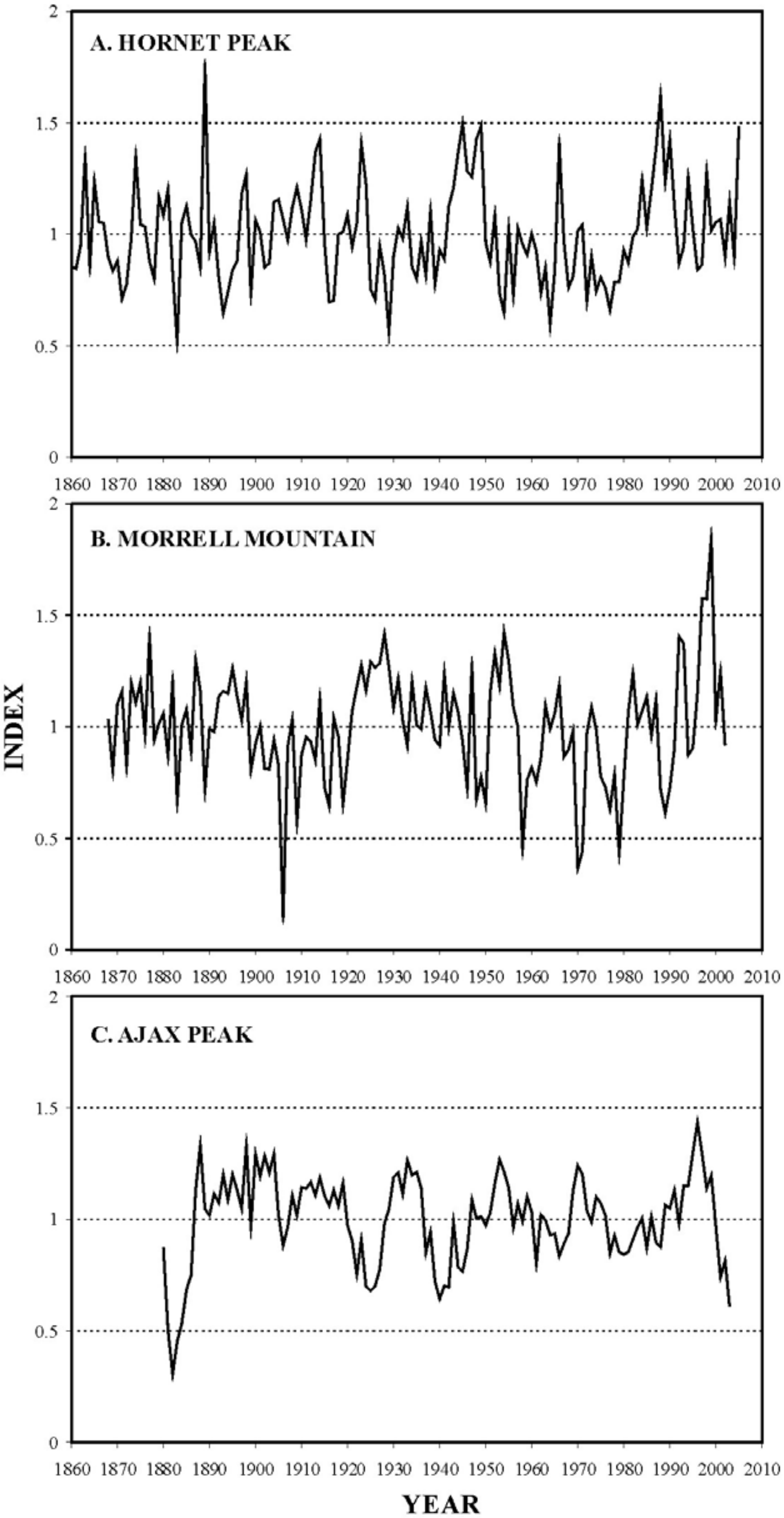

Figure 5.8. OUTBREAK chronologies from: (A) Hornet Peak, (B) Morrell Mountain, and (C) Ajax Peak. These chronologies have had climatic effects removed or minimized.

found no major differences in duration and intensity of mountain pine beetle outbreaks between the three sites (Table 5.4). The duration of the outbreaks is consistent with other findings in whitebark pine ecosystems in Idaho (Perkins and Swetnam 1996) and lodgepole pine studies in western North America (Cole and Amman 1980, Safranyik and Carroll 2006).

Mortality by decade for 65 whitebark pine trees that died during the 20th century revealed that the timing of tree death was asynchronous throughout western Montana (Figure 5.9). Whitebark pine mortality occurred every decade during the 20th century at Hornet Peak and Morrell Mountain, although the current decade shows the highest mortality rates of whitebark pines in the past century. Hornet Peak showed the largest cohort of tree death in the 1980s, after the mountain pine beetle outbreak that occurred from 1970 to 1980. Morrell Mountain had the highest frequency of whitebark pine death during the 1940s, after the mountain pine beetle outbreak from 1920 to 1940. Ajax Peak had the healthiest whitebark pine population and only showed one tree death in the 1960s and 1990s. However, eight whitebark pines died recently at Ajax Peak from 2000 to 2004.

5.5 Discussion

5.5.1 Chronology Development

The average interseries correlations for whitebark pines were highly significant at our three sites, with an average of 0.49. Our whitebark pine chronologies were developed as part of a larger study to examine successional dynamics in subalpine forests. Therefore, our interseries correlations were lower than neighboring whitebark pine

Table 5.4. Duration and severity of mountain pine beetle outbreaks at each site, as estimated from ring-width suppression in corrected (OUTBREAK) chronologies.

Study Site	**Period**	**Average Duration (years)**	**Average Departure**	**Average Maximum Growth Reduction (%)**
Hornet Peak	1860–2005	9.06	–1.7	48
Morrell Mountain	1868–2002	10.05	–2.3	77
Ajax Peak	1880–2003	9.80	–2.3	69

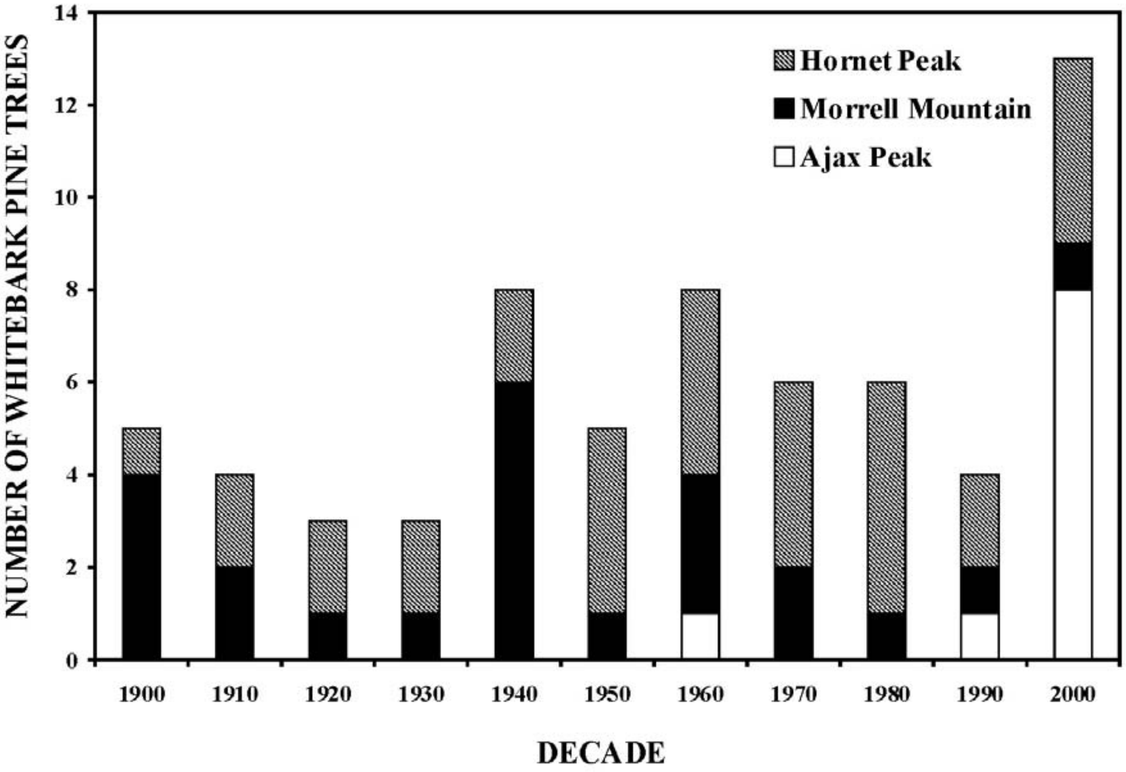

Figure 5.9. Crossdated mortality dates of 65 whitebark pine trees during the 20th century by site.

chronologies in Idaho (Perkins and Swetnam 1996, Kipfmueller 2003) because the majority of whitebark pines chosen for chronology development were not from park-like treeline stands, but were influenced by competition from other species and other stand effects, in addition to natural and anthropogenic disturbances. The whitebark pine chronologies had average mean sensitivities, signifying that necessary variability exists in the tree-ring patterns from climatic factors to ensure successful crossdating and extraction of the dominant climate signal. The commonality of marker rings between sites along our latitudinal transect indicates a regional climatic influence.

The subalpine fir chronologies proved to be more difficult to crossdate than the whitebark pine chronologies. Although we were able to build subalpine chronologies for each site, sample size was relatively low. One of the reasons we had between 20 and 30 subalpine firs in each chronology is that many of the smaller-sized subalpine firs common in each site would not crossdate due to erratic tree-ring patterns likely caused by particular stand dynamics processes. In most cases, these smaller-diameter subalpine firs were over 100 years old and showed little ring-width variability because subalpine fir is a shade-tolerant species that grows well in the intermediate and suppressed canopy classes. Subalpine firs can live in the lower canopy classes and understory up to 300 years at these sites, but these trees cannot be used successfully to study subalpine fir growth trends in dendroecological studies. Only subalpine firs greater than 15 cm diameter breast height were successfully crossdated.

5.5.2 Climate Analyses

We were expecting to see different relationships between tree growth and climate variables between the three sites due to microsite conditions such as elevation, aspect, and slope, but we were surprised to find different species' responses to climate within two of our sites. Unlike the whitebark pines and subalpine firs at Hornet Peak, which both responded well to summer precipitation, the subalpine firs at Morrell Mountain and Ajax Peak responded to different seasons than the whitebark pines and had inverse relationships with precipitation and PDSI. The negative relationships between subalpine fir growth and drought stress in the late summer and snowpack accumulations in the winter were different than the whitebark pine growth response to the same climate variables. Whitebark pine and subalpine fir are the two most common species at Morrell Mountain and Ajax Peak but they react differently to climatic conditions. The differences between the climate-growth relationships of whitebark pines and subalpine firs could also be related to added noise from stand dynamics and disturbance events.

Although the growing season for high-elevation subalpine forest only lasts from June to September, we found growth correlated with different climate variables throughout the previous summer and current year (Fritts 1976). Whitebark pine and subalpine fir growth rates in Montana are influenced by drought and precipitation patterns during the previous summer, previous winter, and current summer. Tree growth is clearly responsive to drought and precipitation and its seasonal distribution. Whitebark pine growth at most of the study sites showed a statistically significant positive relationship between whitebark pine growth and previous summer precipitation or PDSI. Subalpine fir growth showed a negative relationship between tree growth and previous fall/winter precipitation and PDSI. This indicates wet conditions from precipitation and snowpack melt in the previous summer months enhance tree growth during the following growing season, but that late in the growing season and into the fall/winter, trees become stressed. The seasonal fluctuations in precipitation and drought also reflect the fluctuations in snowpack. Snowpack variability is a central force that limits tree growth at high-elevation sites (Peterson 1998), therefore the timing of snowpack melt is important in understanding wet conditions in subalpine forests.

Whitebark pines and subalpine firs responded to seasonalized precipitation and PDSI data differently during the instrumental climate record (1940–2005). Growth anomalies occurred at each site that could not be explained by precipitation and PDSI. These asynchronous years were clear in the whitebark pine chronologies with some of them matching periods of mountain pine beetle outbreaks in the 1970s. Morrell Mountain was the site where this trend was most apparent and was also the most difficult site to interpret because climate-growth relationships were relatively weak for both species. Only one month was significant with whitebark pine and subalpine fir growth, which indicates that disturbance regimes could be affecting this site more than climate.

Whitebark pine growth and subalpine fir response to precipitation at Hornet Peak was more significant than with precipitation at Morrell Mountain and PDSI at Ajax Peak. Subalpine fir response to precipitation and PDSI was inverse at two sites (Morrell Mountain and Ajax Peak) during the fall and winter seasons. Fall and winter precipitation and PDSI variation has a large impact on tree growth in our sites. Given the short growing season at these high-elevation sites, any extended period of snowpack (October–June) would result in lower than average growth at the microsite level which could create noise in the climate signal. The inverse climate-growth relationship of subalpine firs at Morrell Mountain and Ajax Peak may also reflect a heavy snow accumulation that persists into the growing season and likely causes an extended photosynthetically inactive period and delays the beginning of tree growth (Fritts 1976). In contrast to subalpine firs at Morrell Mountain and Ajax Peak, the most significant positive relationship between whitebark pine and subalpine fir growth and precipitation and PDSI occurred in the current summer and previous year's summer. This indicates that drought (precipitation and temperature) conditions are critical during the current and previous growing season in our sites. Moisture conditions late in the previous year's growing season may affect this year's bud break and the initiation of growth more than climate during the current year's growing season. Drought may cause a reduction in current growth, but an increase in the tree's reserves for the following year's growth (Fritts 1976). Our seasonal PDSI correlation results from whitebark pines at Ajax Peak are similar to those found by Mann (2008) from the same region, except he found stronger relationships between whitebark pine growth and current summer PDSI.

Tree growth in these subalpine forests will undoubtedly become more stressed with continued changes in temperature, precipitation, and snowpack. Climate models for the Rocky Mountains of Montana show an average reduction in snowpack of approximately 33% over the next 80 years (Zimmerman *et al.* 2006). Continued warming will cause snowpack to melt earlier in year which will lengthen the subalpine forest growing season. Photosynthesis and transpiration by whitebark pine, subalpine fir, and other high-elevation plant species will remove the available soil moisture earlier in the summer and trees will experience drought stress later in the summer. We already see the negative relationship between late summer drought stress and subalpine fir growth at Ajax Peak. Longer growing seasons with less available moisture at the end of the summer will negatively impact growth of both whitebark pine and subalpine fir. Continued periods of drought will likely stress subalpine forests and make whitebark pines more susceptible to mountain pine beetle attack and weaken their resistance to white pine blister rust infection. The results of this study substantiate the importance of drought in whitebark pine communities. We suggest that climate change, especially increased periods of drought, may increase the threat to whitebark pine survival by changing biological processes, reducing whitebark pine productivity, and increasing stress which makes whitebark pines more susceptible to insects and pathogens.

5.5.3 OUTBREAK chronologies and whitebark pine mortality

This was the first study conducted that used the program OUTBREAK to examine mountain pine beetle outbreaks in western North America. Our results did show mountain pine beetle outbreaks that matched the historical record, but our results were clouded by other disturbance events that appeared as outbreaks at one of our sites (Morrell Mountain). We would recommend using OUTBREAK for disturbance detection in whitebark pine forests, but the mountain pine beetle parameters should be changed from a minimum 5-year growth suppression to a minimum 9-year growth suppression to exclude other exogenous disturbances from being recorded as mountain pine beetle outbreaks. Although whitebark pine trees provide long tree-ring records of climate fluctuations and disturbance events, more calibration of the effects of mountain pine beetle outbreaks on whitebark pine growth should be conducted in OUTBREAK before multicentury mountain pine beetle outbreak reconstructions should be attempted.

One of the assumptions of OUTBREAK is that the nonhost species has a similar climatic response as the host species (Swetnam and Lynch 1993, Speer 2007). We showed that only one of our sites had a similar climatic response between species (Hornet Peak), and that the whitebark pines and subalpine firs at the other two sites had completely different climatic responses. Therefore, we would recommend examining climate response by site and perhaps choosing a different nonhost species that might be more climatically sensitive, which could have possibly helped omit disturbances that were unrelated to mountain pine beetle outbreak periods. Other species that might be more climatically sensitive that were abundant in the whitebark pine communities in Montana included Engelmann spruce and grand fir.

The recorded growth suppressions in the 1880s, 1920s (except Morrell Mountain), and the late 1970s–early 1980s at our sites are interpreted here as an indication of landscape-level mountain pine beetle outbreaks. Morrell Mountain has been impacted by disturbances such as logging, road-cutting, and fire during the 20th century (Larson *et al.* 2008), therefore this site is not ideal for determining a mountain pine beetle outbreak signature. However, Hornet Peak and Ajax Peak had less anthropogenic disturbance and were more reliable sites for mountain pine beetle outbreak detection. These two sites also exhibited growth suppressions from all three mountain pine outbreaks between 1860 and 2005. We also found the first record in the western U.S. of the 1880s mountain pine beetle outbreak that was only recently discovered in British Columbia (Alfaro *et al.* 2004, Taylor *et al.* 2006), in our sites in western Montana. More research should be conducted on the extent of the 1880s outbreak throughout the range of whitebark pine communities throughout the western U.S. Our results support other studies on the landscape-level periodicity of mountain pine beetle outbreaks that have been conducted in western North America (Perkins and Swetnam 1996, Heath and Alfaro 1990, Alfaro *et al.* 2004, Taylor *et al*. 2006, Campbell *et al.* 2007).

Previous mountain pine beetle studies have used dendroecological methods such as growth releases in surviving whitebark pine and lodgepole pine trees and tree mortality dates to help identify mountain pine beetle outbreaks (Heath and Alfaro 1990, Alfaro *et al.* 2004, Taylor *et al*. 2006, Campbell *et al.* 2007). Because mountain pine beetles tend to kill larger trees and avoid smaller trees, we would recommend examining both suppression (from attacked trees) and release periods (from surviving trees) to pinpoint outbreak occurrence more precisely. Mortality dates were also useful in determining the severity of mountain pine beetle outbreaks by site. We found that the mountain pine outbreak from 1970–1980 was more severe in terms of whitebark pine mortality at our sites than the mountain pine beetle outbreak from 1920–1940. More whitebark pines that died during the 19th and 20th centuries should be analyzed for mortality dates and growth departures during and after mountain pine beetle outbreak periods, to compare the severity of outbreaks across western North America.

In addition to mountain pine beetles outbreaks, other landscape-level patterns in the whitebark pine chronologies were evident. The Morrell Mountain and Ajax Peak whitebark pine chronologies showed a sharp growth decline in the study sites from 1998–2004. This decrease in radial growth at Morrell Mountain is likely related to the overlapping effects of drought, mountain pine beetle outbreaks, and white pine blister rust infections. We did not see any evidence of mountain pine beetle attack at Ajax Peak but white pine blister rust was apparent. Therefore, we hypothesize the recent decline in whitebark pine growth at Ajax Peak is not related to the current mountain pine beetle outbreak but is a signature of white pine blister rust.

CHAPTER 6

CONCLUSIONS AND FUTURE RESEARCH

The overall purpose of this study was to integrate ecological and dendrochronological methods to investigate the extent of natural and anthropogenic impacts on declining whitebark pine communities in the northern Rocky Mountains of Montana. Previous research on whitebark pine ecosystems has been limited because investigators have not examined the overlapping effects of stand dynamics, disturbance regimes, and climate patterns in the northern Rocky Mountains. Thus, this research fills a void in our knowledge of the long-term record of climate and disturbance history of whitebark pine ecosystems in Montana. This chapter summarizes the major findings and makes recommendations for future research.

6.1 Whitebark pine growth, climate, and mountain pine beetle outbreaks

1. Our six whitebark pine chronologies crossdated well with neighboring tree-ring chronologies from Montana and Idaho.

Interseries correlations were highly significant at all six research sites, with an average of 0.49. Our interseries correlations were slightly lower than neighboring whitebark pine chronologies because the majority whitebark pines chosen for chronology development were not from park-like treeline stands, but were in mixed-conifer stands, in addition to natural and anthropogenic disturbances. Our multicentury chronologies had significant mean sensitivities, signifying that necessary variability exists in the tree-ring patterns from climatic factors to ensure successful crossdating and extraction of the dominant climate signal. The commonality of marker rings along our latitudinal transect and the significant correlations between neighboring chronologies in Montana and Idaho further indicate a regional climatic influence.

2. Climate response function analysis revealed differences in our sites related to elevation, microclimate conditions, and disturbance histories.

The whitebark pine growth data from all sites had between 16% and 41% of the variance explained by climate, which makes these datasets less climatically-sensitive than other northern Rocky Mountain sites. With the exception of Big Hole Pass, one of the most southern sites, the whitebark pines in our study were more responsive to prior growth than climate. Big Hole Pass had 41% of the whitebark pine variance explained by climate, making it the most climatically sensitive site in our study.

3. Previous summer and current spring precipitation and PDSI were the most important seasonal climate variables affecting whitebark pine growth.

Whitebark pine growth in Montana is influenced by drought and precipitation patterns during the previous summer and current spring. Tree growth is clearly responsive to drought and precipitation and its seasonal distribution. This indicates wet conditions from precipitation and snowpack melt in the previous summer and spring months enhance whitebark pine growth during the following growing season. The seasonal fluctuations in precipitation and drought also reflect the fluctuations in snowpack.

4. Reconstructed PDSI and precipitation values revealed dry years and drought periods during the length of the reconstructions.

Our climate reconstruction results support other climate reconstructions, east of the Continental Divide, that found precipitation and PDSI have more of an influence on subalpine forest growth than temperature. We compared our results to regional summer PDSI reconstructions from lower-elevation sites in the northern Rocky Mountains, and found a few similar dry years between the lower-elevation PDSI reconstruction and our high-elevation PDSI and precipitation reconstructions across western Montana. Similar dry years between our studies included 1174, 1263, 1328, 1583, 1739, 1782, 1883, and 1992. Our reconstruction data contribute an important high-elevation component to existing drought reconstructions from lower elevations in the northern Rocky Mountains.

5. Asynchronous patterns between the actual and expected climate response in whitebark pine during the 20th century are most likely due to mountain pine beetle outbreaks.

The departure from expected whitebark pine growth during the 1970s and 1980s is clearly seen at these sites and is interpreted here as an indication of the landscape-level mountain pine beetle outbreak. An earlier mountain pine beetle outbreak from 1920 to 1940 affected whitebark pine growth at Hornet Peak, Mineral Peak, Ajax Peak, and Big Hole Pass. Hornet Peak and Ajax Peak were the only two sites that exhibited growth departures from both mountain pine outbreaks during the 20th century.

6. The 1998–2005 decrease in whitebark pine radial growth is likely related to drought, mountain pine beetle outbreaks, and white pine blister rust infections.

Although both white pine blister rust and mountain pine beetle were present at each site, the megadrought from 1999–2007 also impacted these sites. Droughts restrict whitebark pine's biological activity and change processes within the whitebark pine ecosystem. Continued periods of drought will likely stress whitebark pines and make them more susceptible for mountain pine beetle attack and weaken their resistance to white pine blister rust infection. The results of this study substantiate the importance of drought in whitebark pine communities. We suggest that climate change, especially increased periods of drought, may increase the threat to whitebark pine survival by changing biological processes, reducing whitebark pine productivity, and increasing stress, that make whitebark pines more susceptible to insects and exotic pathogens.

6.2 Whitebark pine and subalpine response to disturbance

1. Successional shift from whitebark pine-dominated forests to shade-tolerant forests.

This study supports other research that has found whitebark pine communities are being successionally replaced by subalpine fir, grand fir, and Engelmann spruce in all levels of the forest strata (trees, saplings, and seedlings). Our southern-most sites in the BDNF had the highest number of living whitebark pine in all canopy classes. These sites also had the lowest densities of competing species which may contribute to their relatively healthy whitebark pine populations. Shade-tolerant species, such as subalpine fir, grand fir, and Engelmann spruce, established throughout the stand history of our whitebark pine-dominated sites, with individual subalpine firs having established in the early 1700s. An important finding of our study is that the establishment of shade-tolerant species over the past 300 years indicates that forest succession in whitebark pine communities in not a result of 20th century fire suppression, contrary to what has been suggested by previous studies.

2. Whitebark pine are declining throughout our sites from mountain pine beetle and white pine blister rust.

The high frequency of white pine blister rust and mountain pine beetle outbreaks, suggest the significant role of insects and pathogens in determining whitebark pine population trajectories over the next few decades. Infection and mortality levels varied considerably across western Montana, but over 70% of the whitebark pine in our sites were either declining or dead. The high mortality of whitebark pine in our sites was caused by the overlapping effects of past and current mountain pine beetle outbreaks, and more recently by white pine blister rust infection.

3. White pine blister rust can be detected using dendroecological techniques before external symptoms appear on whitebark pines.

Our study was the first to find a white pine blister rust signature in whitebark pine chronologies. Although whitebark pine may not show immediate external symptoms of blister rust infection, the tree-ring record can show radial growth declines from blister rust before external tree symptoms appear. Since 1998, there has been a steady decline in whitebark pine growth at all our sites, but the decline in the southern sites was different because there were no overlapping effects from mountain pine and blister rust as only blister rust was present at these sites. Blister rust had expanded significantly in the southern sites from the 2003 to 2004 field seasons, but growth in these trees had been declining since 1998.

4. Release events from mountain pine beetle outbreaks and climate events were evident in the tree-ring record, but the releases were asynchronous and not standwide.

Only a few stand-wide release episodes occurred in the study sites, usually early or late in the site release records. Similarities in the central and southern release records in 1843 and 1848 indicate regionally important disturbance or climatic events affecting western Montana in the mid-1840s. Release responses in our whitebark pine and subalpine fir series were largely asynchronous, which is what we would expect from host and non-host trees during host-specific mortality periods, such as mountain pine beetle outbreaks.

6.3 Comparing whitebark pine and subalpine growth to climate and response to mountain pine beetle outbreaks

1. Subalpine fir chronologies were more difficult to crossdate than whitebark pine

The subalpine fir chronologies proved to be more difficult to crossdate than the whitebark pine chronologies. One of the reasons we had between 20 and 30 subalpine firs in each chronology is that many of the smaller-sized subalpine firs common in each site would not crossdate due to stand dynamics. A few similar marker rings occurred in the whitebark pine and subalpine fir chronologies, but we found noticeable differences among the chronologies, likely due to differences in microclimates and disturbance histories. Visual and graphical crossdating were aided by especially narrow growth rings that formed in whitebark pines in AD 1601, 1641, 1698, 1782, 1838, 1899, and 1906. Marker rings among the subalpine fir chronologies included 1867, 1899, 1972, 1974, and 1993. The narrowest rings in the whitebark pine and subalpine fir chronologies did respond similarly in 1838 and 1899.

2. Whitebark pine and subalpine fir responded differently to drought

Whitebark pine and subalpine fir growth in Montana are influenced by drought and precipitation patterns during the previous summer, previous winter, and current summer. Subalpine fir response to precipitation and PDSI was inverse at two sites during the fall and winter seasons. Given the short growing season at these high-elevation sites, any extended period of snowpack (October–June) results in lower than average growth at the microsite level which adds noise to the climate signal. The most significant positive relationship between whitebark pine and subalpine fir growth and precipitation and PDSI occurred in the current summer and previous year’s summer. This indicates that drought (precipitation and temperature) conditions are critical during the current and previous growing season in western Montana. The results of this study substantiate the importance of drought in whitebark pine communities.

3. A new technique was used to examine mountain pine beetle outbreaks

This was the first study conducted that used the program OUTBREAK to examine mountain pine beetle outbreaks in western North America. Our results did show mountain pine beetle outbreaks that matched the historical record (in the 1880s, 1920s, and 1970s). We would recommend using OUTBREAK for disturbance detection in whitebark pine forests, but the mountain pine beetle parameters should be changed from a minimum 5-year growth suppression to a minimum 9-year growth suppression to exclude other exogenous disturbances from being recorded as mountain pine beetle outbreaks. Although whitebark pine trees provide long tree-ring records of climate fluctuations and disturbance events, more calibration of the affects of mountain pine beetle outbreaks on whitebark pine growth should be conducted in OUTBREAK before multicentury mountain pine beetle outbreak reconstructions should be attempted.

6.4 Recommendations for Future Research

This study demonstrated the importance of climate on natural and anthropogenic disturbances that impact the development of whitebark pine communities. This work contributes to ecological data on forest succession and forest health in whitebark pine communities, and adds new knowledge on the application of dendroecological techniques to separate climate and disturbance on a landscape scale. Major areas for future studies include: (1) the influence of multidecadal oscillations on drought regimes in high-elevation whitebark pine forests in Montana, (2) the preconditioning effects of drought on mountain pine beetle outbreaks, and (3) the comparison of the severity of mountain pine beetle outbreaks and white pine blister rust infection in whitebark pine communities across western North America.

Instrumental climate records suggest that summer precipitation and winter snowpack in western Montana vary significantly over decadal to multidecadal temporal scales. Because instrumental climate records are limited to the 20th century, and are from low-elevation climate stations, knowledge of the range of variability associated with these moisture anomalies and their impacts on high-elevation ecosystems and physical processes are limited. Understanding long-term climate trends can show decadal and multidecadal- scale shifts between persistent drought and wet events prior to the instrumental period (before 1900). Decadal-scale dry and wet events, in conjunction with periods of high and low snowpack, are drivers of whitebark pine ecosystem processes in the northern Rocky Mountains in Montana.

Our reconstructed climate data contribute an important high-elevation component to existing drought reconstructions in the northern Rocky Mountains. Further analyses should be conducted on the trends in Pacific modes and high-elevation precipitation to understand the influence of multidecadal oscillations on drought regimes in whitebark pine ecosystems. For example, our longest precipitation reconstruction from Mineral Peak should be used to reconstruct snowpack conditions and examine the influence of the Pacific Decadal Oscillation (PDO) on long-term snowpack fluctuations. Detailed analysis and testing of specific hypotheses regarding the affects of PDO on long-term precipitation and PDSI trends is necessary for understanding the influence of teleconnections on whitebark pine tree growth in the northern Rocky Mountains. Research questions that should be explored include: (1) Do large-scale climatic anomalies from El Niño Southern Oscillation (NIÑO3) and PDO indices have differential affects on snowpack and drought stress across the northern Rocky Mountains?, (2) Do combined warm phases (positive PDO during El Niño) or combined cool phases (negative PDO during La Niña) promote drought stress, fire occurrence, or mountain pine beetle outbreaks in the northern Rocky Mountains, and (3) How do these oscillations affect winter season length, timing of the first snowfall, and snowpack depth, which would significantly impact whitebark pine biological function?

We also suggest additional research should be conducted on the preconditioning effects of drought on mountain pine beetle outbreaks. Climate change may affect the dynamics mountain pine beetle populations directly, through the physiological processes of individual insects, and indirectly, through their host trees. Water stress on host trees induced by drought has been proposed as a cause of mountain pine beetle outbreaks in several studies in western North America. Changes in climate, particularly towards drier conditions, may increase the frequency of outbreaks. Dendroecologists can use tree-ring techniques to help determine if droughts do precondition trees for mountain pine beetle outbreaks. Whitebark pine growth comparisons before and after drought years could be used to examine mountain pine beetle outbreak periodicity in western North America. Superposed epoch analysis (SEA) could be used to identify how many years whitebark pines have experienced growth suppressions associated with drought before a mountain pine beetle outbreak occurred. SEA would superimpose disturbance events present in the whitebark pine chronologies into a composite history and then average the climate characteristics prior to, during, and after the disturbance events into a common window. The timing of mountain pine beetle outbreaks in the 1880s, 1920, and 1970s and associated droughts could be compared using SEA in the Dendrochronology Program Library software, EVENT (Holmes and Swetnam 1994).

In addition to the study of historical mountain pine beetle outbreaks and their impact on whitebark pine communities, continued monitoring of the ecological status of whitebark pine ecosystems is also important. If we do lose whitebark pine as a major component in subalpine forests in western North America, what are the ecological effects of this loss in terms of biodiversity, landscape vegetation patterns, and habitat loss? We can study examples of forest ecosystems that have already severely declined as a result of exotic pathogen and insect introduction to hypothesize about the future of whitebark pine ecosystems. In the eastern U.S., we have two examples of forest ecosystems that now differ in structure, composition, and function, as a result of exotic species introduction during the 20th century. First, American chestnut (*Castanea dentata*) forests were replaced by oaks (*Quercus spp.*) and eastern hemlock (*Tsuga canadensis*) in the Appalachian Mountains after the introduction of chestnut blight (*Cryphonectria parasitica*). Second, eastern hemlock is now disappearing due to an introduced insect, the hemlock woolly adelgid (*Adelges tsugae*). This rapidly spreading insect kills hemlocks of all sizes and age-classes within 4–15 years of infestation (Orwig *et al*. 2002). Hemlock has no apparent resistance to the adelgid and rarely recovers from attack (Orwig *et al*. 2002). What has happened to these tree species exemplifies the worst possible scenario for whitebark pine ecosystems.

Conservation efforts on the part of the Whitebark Pine Ecosystem Foundation, land managers, and ecologists throughout western North America are using different forest management techniques to mitigate the loss of whitebark pine through its range. Their efforts will hopefully prevent whitebark pine from becoming another functionally-extinct species. Planting blister rust-resistant whitebark pine seedlings and prescribed fire are conservation techniques currently being used by land managers in select whitebark pine communities. However, in order to preserve a viable seed source of whitebark pines, these conservation efforts should be focused rangewide. The data from this study can be used by land managers to prioritize areas for conservation on a landscape scale. For example, sites with high levels of infection, canopy kill, and overstory and understory mortality could be replanted with blister rust-resistant trees. These replanted trees would later need protection from mountain pine beetle by applying semiochemicals (Kegley and Gibson 2004).

In conclusion, this study showed the importance of using dendroecological techniques to separate the influence of climate and disturbance events on whitebark pine growth in the northern Rocky Mountains. To understand climate and disturbance patterns on a larger spatial scale, studies could use similar techniques to determine the preconditioning effects of climate on the spatial distribution, periodicity, and severity of mountain pine beetle outbreaks across western North America. More research should also focus on reconstructing drought and mountains pine beetle outbreaks in the northern Rocky Mountains. Therefore, we should develop longer and more robust (*i.e.*, high sample depth back in time) whitebark pine tree-ring chronologies from sites that are climatically sensitive (Big Hole Pass) and from sites that are not as climatically sensitive but have recorded all known mountain pine beetle outbreaks (Ajax Peak and Hornet Peak). This is especially important in southwestern Montana where little research has been conducted in whitebark pine communities. Subalpine fir proved to be a promising nonhost tree species in most sites and should continue to be explored as a control for mountain pine beetle outbreak detection in whitebark pine communities in the northern Rocky Mountains. Additional studies are needed to further monitor disturbance processes and successional changes throughout the range of whitebark pine in western North America.

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APPENDICES

APPENDIX A1. Statistical descriptions for whitebark pine series from Hornet Peak, Flathead National Forest, Montana.

Seq	Series	Interval		No. Years	Corr. w/ Master	Mean Sens.	Std. Dev.	Auto Corr.	AR ()
1	horn009A	1797	2005	209	0.500	0.221	0.372	-0.012	2
2	horn009B	1797	1999	203	0.472	0.239	0.346	-0.015	1
3	horn013A	1820	2005	186	0.557	0.200	0.382	-0.024	1
4	horn013B	1820	2005	186	0.576	0.251	0.484	-0.016	1
5	horn014A	1811	2005	195	0.451	0.213	0.494	-0.019	1
6	horn015A	1745	2005	261	0.449	0.177	0.420	0.008	1
7	horn021A	1822	2005	184	0.452	0.253	0.456	-0.019	1
8	horn030A	1820	2005	186	0.586	0.224	0.579	0.014	2
9	horn030B	1820	2005	186	0.573	0.212	0.467	-0.020	2
10	horn035A	1832	2002	171	0.425	0.253	0.354	-0.048	1
11	horn035B	1832	1999	168	0.524	0.231	0.502	-0.015	2
12	horn055A	1825	1986	162	0.473	0.389	0.463	-0.077	1
13	horn057A	1848	2005	158	0.489	0.238	0.437	0.022	1
14	horn057B	1848	2005	158	0.607	0.241	0.413	-0.015	1
15	horn060A	1808	2005	198	0.485	0.248	0.496	-0.070	2
16	horn060B	1817	2005	189	0.408	0.258	0.516	-0.006	2
17	horn003A	1814	2002	189	0.393	0.236	0.466	0.004	1
18	horn003B	1814	2002	189	0.463	0.252	0.338	-0.043	1
19	horn006A	1815	2001	187	0.472	0.245	0.466	-0.038	1
20	horn008a	1785	1944	160	0.477	0.267	0.392	-0.007	1
21	horn008b	1785	1933	149	0.380	0.249	0.352	-0.008	2
22	horn012A	1822	1943	122	0.509	0.220	0.414	0.020	1
23	horn015A	1835	1976	142	0.499	0.202	0.323	-0.080	2
24	horn016B	1791	1979	189	0.493	0.202	0.409	-0.032	1
25	horn022A	1844	1975	132	0.521	0.235	0.468	-0.009	1
26	horn024a	1730	1900	171	0.389	0.133	0.426	0.008	1
27	horn033A	1809	1934	126	0.534	0.227	0.402	-0.026	1
28	horn033B	1808	1932	125	0.398	0.239	0.344	-0.021	1
29	horn034A	1819	1957	139	0.506	0.195	0.428	-0.039	2
30	horn034B	1819	1966	148	0.645	0.224	0.372	0.016	1
31	horn036A	1824	1952	129	0.568	0.259	0.386	-0.009	1
32	horn037A	1854	1998	145	0.622	0.242	0.439	-0.039	2
33	horn037B	1854	1989	136	0.469	0.255	0.422	-0.005	1
34	horn038A	1837	1968	132	0.602	0.227	0.397	-0.047	1
35	horn038B	1837	1958	122	0.519	0.277	0.431	-0.008	2
36	horn039A	1829	1985	157	0.512	0.235	0.421	0.042	1

APPENDIX A1. *continued*

Seq	Series	Interval		No. Years	Corr. w/ Master	Mean Sens.	Std. Dev.	Auto Corr.	AR ()
37	horn040A	1830	1981	152	0.604	0.236	0.412	-0.002	1
38	horn040B	1830	1979	150	0.520	0.283	0.434	0.002	1
39	horn041A	1835	1974	140	0.573	0.262	0.439	-0.076	1
40	horn044A	1846	1993	148	0.590	0.225	0.456	0.009	1
41	horn049A	1817	1986	170	0.556	0.231	0.364	-0.064	1
42	horn049B	1817	1962	146	0.550	0.198	0.340	-0.031	2
43	horn061A	1815	1963	149	0.493	0.283	0.522	0.024	1
44	horn064A	1826	1952	127	0.454	0.259	0.448	-0.044	2
45	horn067A	1833	2002	170	0.559	0.257	0.427	0.022	1
46	horn074A	1802	1981	180	0.394	0.219	0.440	0.007	1
47	horn080A	1814	1909	96	0.523	0.254	0.402	-0.053	1
48	Horn409A	1686	1933	248	0.436	0.206	0.418	-0.004	1
49	Horn409B	1685	1895	211	0.551	0.189	0.412	-0.029	1
50	Horn410A	1684	1922	239	0.421	0.205	0.376	-0.023	1
51	Horn410B	1684	1899	216	0.485	0.214	0.375	-0.043	1
52	Horn411A	1700	1954	255	0.483	0.200	0.524	0.003	2
53	horn402A	1685	1924	240	0.379	0.225	0.243	-0.040	1
54	horn402B	1685	1815	131	0.442	0.254	0.500	-0.012	2
55	horn403A	1684	1968	285	0.391	0.229	0.415	0.023	1
56	horn403B	1685	1820	136	0.423	0.231	0.432	0.004	1
57	Horn404A	1682	1820	139	0.442	0.222	0.496	0.020	1
58	Horn404B	1683	1820	138	0.403	0.216	0.495	-0.038	1
59	horn406A	1684	1826	143	0.451	0.226	0.421	-0.014	4
60	horn406B	1685	1840	156	0.474	0.331	0.464	-0.007	1
61	Horn407A	1685	1820	136	0.453	0.254	0.349	-0.005	1
62	Horn412A	1693	1916	224	0.376	0.192	0.467	0.010	1
63	Horn412B	1693	1885	193	0.400	0.208	0.355	-0.032	1
64	Horn419B	1710	1953	244	0.370	0.180	0.400	0.001	2
Total or Mean				10951	0.482	0.231	0.423	-0.015	

APPENDIX A2. Statistical descriptions for whitebark pine series from Mineral Peak, Lolo National Forest, Montana.

Seq	Series	Interval		No. Years	Corr. w/ master	Mean Sens.	Std. Dev.	Auto Corr.	AR ()
1	mp1001a	1560	1696	137	0.505	0.154	0.246	-0.069	1
2	mp1001b	1521	1733	213	0.488	0.146	0.406	-0.037	1
3	mp1002a	1603	1776	174	0.382	0.203	0.140	-0.055	1
4	mp1003a	1672	1962	291	0.437	0.186	0.255	-0.035	1
5	mp1003b	1670	1962	293	0.415	0.203	0.225	0.012	1
6	mp1004a	1351	1867	517	0.473	0.188	0.223	0.008	1
7	mp1004b	1344	1957	614	0.490	0.184	0.210	-0.007	2
8	mp1008a	1541	1673	133	0.444	0.206	0.353	-0.021	1
9	mp1008b	1531	1686	156	0.434	0.164	0.338	0.014	2
10	mp1009c	1791	1983	193	0.402	0.222	0.375	-0.015	1
11	mp1010a	1623	1971	349	0.557	0.230	0.354	-0.018	1
12	mp1010b	1622	1785	164	0.564	0.216	0.307	0.017	1
13	mp1010c	1812	1974	163	0.499	0.209	0.355	-0.010	1
14	mp1011a	1600	1712	113	0.498	0.151	0.354	-0.031	1
15	mp1011b	1587	1771	185	0.434	0.189	0.494	-0.010	2
16	mp1012a	1171	1396	226	0.628	0.243	0.658	-0.009	3
17	mp1012b	1179	1383	205	0.604	0.232	0.505	-0.021	1
18	mp1013a	1687	1922	236	0.431	0.288	0.470	-0.025	1
19	mp1013b	1678	1922	245	0.438	0.258	0.424	-0.011	1
20	mp1014a	1613	1742	130	0.646	0.197	0.435	-0.039	2
21	mp1014b	1619	1738	120	0.663	0.157	0.467	-0.039	1
22	mp1017a	1467	1736	270	0.427	0.234	0.178	0.002	1
23	mp1017b	1441	1690	250	0.423	0.235	0.259	-0.005	1
24	mp2002a	1562	1786	225	0.508	0.213	0.577	-0.057	1
25	mp2002b	1562	1970	409	0.404	0.200	0.444	0.006	1
26	mp2004a	1664	1892	229	0.423	0.227	0.189	-0.016	1
27	mp2009c	1785	1962	178	0.414	0.228	0.325	-0.064	1
28	mp2010a	1554	1823	270	0.392	0.208	0.441	-0.056	1
29	mp2010b	1555	1790	236	0.436	0.226	0.428	-0.033	2
30	mp2012a	1404	1497	94	0.571	0.237	0.241	-0.010	1
31	mp2012b	1419	1976	558	0.541	0.208	0.225	-0.011	2
32	mp2012c	1508	1976	469	0.608	0.194	0.303	-0.008	1
33	mp2013a	1537	1952	416	0.565	0.176	0.273	-0.009	1
34	mp2013b	1588	1952	365	0.562	0.170	0.242	-0.015	1
35	mp3001c	1891	1997	107	0.460	0.221	0.542	-0.072	1
36	mp3003a	1522	1984	463	0.408	0.169	0.280	-0.017	2
37	mp3003b	1526	1816	291	0.421	0.169	0.305	-0.008	1
38	mp3004a	1506	1816	311	0.521	0.193	0.154	-0.015	1
39	mp3004b	1464	1679	216	0.557	0.233	0.198	0.007	1
40	mp3006a	1434	1951	518	0.490	0.206	0.145	-0.001	1
41	mp3006b	1434	1853	420	0.526	0.200	0.190	-0.013	1

APPENDIX A2. *continued*

Seq	Series	Interval		No. Years	Corr. w/ master	Mean Sens.	Std. Dev.	Auto Corr.	AR ()
42	mp3007a	1265	1409	145	0.476	0.180	0.215	-0.050	1
43	mp3007b	1263	1805	543	0.416	0.179	0.213	0.005	1
44	mp3009a	1591	1832	242	0.476	0.186	0.267	-0.041	1
45	mp3011a	1579	1828	250	0.382	0.246	0.304	-0.010	1
46	mp3011b	1579	1832	254	0.466	0.242	0.552	0.004	1
47	mp3011c	1845	1998	154	0.433	0.255	0.412	-0.048	1
48	mp3012a	1754	1956	203	0.428	0.225	0.301	0.017	1
49	mp3012b	1754	1828	75	0.380	0.233	0.150	-0.126	1
50	mp3013a	1400	1762	363	0.484	0.223	0.292	-0.028	2
51	mp3013b	1267	1801	535	0.430	0.229	0.285	-0.015	2
52	mp3015a	1630	1964	335	0.494	0.186	0.436	-0.010	1
53	mp3015b	1628	1830	203	0.510	0.183	0.463	-0.009	1
54	mp3016a	1620	1982	363	0.441	0.276	0.141	-0.005	2
55	mp3016a	1620	1981	362	0.476	0.271	0.153	-0.023	1
56	mp4042A	1865	1992	128	0.472	0.266	0.739	-0.074	1
57	mp1017a	1912	2003	92	0.401	0.291	0.382	-0.021	1
58	mp1040a	1889	2003	115	0.396	0.213	0.437	-0.083	1
59	mp1042a	1910	2002	93	0.406	0.254	0.351	-0.076	1
60	mp1052a	1930	2002	73	0.479	0.277	0.270	-0.024	1
61	mp1053a	1926	2002	77	0.455	0.222	0.226	0.072	1
62	mp1063a	1913	2003	91	0.411	0.291	0.442	-0.037	1
63	mp2017a	1908	2002	95	0.414	0.203	0.484	-0.045	1
64	mpr002A	1550	1953	404	0.405	0.201	0.208	-0.009	1
65	mp4027A	1367	1506	140	0.375	0.250	0.333	0.021	1
66	mp4042A	1865	1992	128	0.472	0.266	0.739	-0.074	1
67	mpr002B	1536	1958	423	0.439	0.225	0.214	0.033	1
68	mpr105A	1536	1791	256	0.408	0.302	0.367	-0.023	1
69	mpr005A	1252	1451	200	0.363	0.190	0.168	-0.043	1
70	mp2007A	1527	1883	357	0.490	0.203	0.128	-0.004	1
71	mp2007B	1504	1870	367	0.451	0.204	0.194	-0.007	2
72	mp1004A	1555	1712	158	0.428	0.204	0.600	-0.004	1
73	mp1004B	1555	1707	153	0.394	0.213	0.565	0.016	1
74	mpr001A	1557	1816	260	0.549	0.230	0.179	-0.006	1
75	mp1002A	1580	1883	304	0.473	0.272	0.133	0.009	1
76	mp1002B	1568	1793	226	0.503	0.213	0.118	-0.012	1
Total or Mean				19319	0.471	0.231	0.298	-0.014	

APPENDIX A3. Statistical descriptions for whitebark pine series from Morrell Mountain, Lolo National Forest, Montana.

Seq	Series	Interval		No. Years	Corr. w/ Master	Mean Sens.	Std. Dev.	Auto Corr.	AR ()
1	mmt3008a	1732	1969	238	0.543	0.261	2.620	-0.035	1
2	mmt3008b	1697	1968	272	0.539	0.307	2.590	-0.018	1
3	mmt022a	1490	1960	471	0.441	0.212	2.520	-0.010	1
4	mmt022b	1490	1925	436	0.444	0.223	2.680	0.011	1
5	mmt2014b	1743	1900	158	0.399	0.255	2.810	-0.022	1
6	mmt2013b	1780	1948	169	0.476	0.250	2.780	-0.033	1
7	mmt3006a	1624	1840	217	0.515	0.200	2.570	-0.024	2
8	mmt2002a	1489	1974	486	0.432	0.199	2.750	-0.058	1
9	mmt2002b	1489	1977	489	0.477	0.273	2.670	-0.007	1
10	mmt2003a	1599	1764	166	0.479	0.259	2.680	0.011	1
11	mmt2006a	1643	1943	301	0.448	0.281	2.740	-0.043	2
12	mmt2006b	1652	1857	206	0.494	0.257	2.810	-0.009	1
13	mmt2007a	1625	1750	126	0.437	0.207	2.590	-0.002	1
14	mmt2007b	1584	1800	217	0.499	0.197	2.860	-0.053	1
15	mmt2007c	1659	1800	142	0.471	0.238	2.580	-0.034	1
16	mmt2008a	1678	1820	143	0.503	0.183	2.660	0.005	1
17	mmt2008b	1678	1844	167	0.469	0.209	2.460	0.028	1
18	mmt2009a	1685	1865	181	0.571	0.202	2.650	-0.073	1
19	mmt2009b	1705	1875	171	0.574	0.203	2.490	-0.067	1
20	mmt2016a	1728	1871	144	0.396	0.304	2.760	-0.045	1
21	mmt2016b	1770	1852	83	0.388	0.291	2.740	-0.001	1
22	mmt3004a	1725	1860	136	0.538	0.206	2.790	0.038	1
23	mmt3004b	1701	1882	182	0.542	0.220	2.630	-0.022	1
24	mmt001a	1541	1947	407	0.422	0.244	2.870	-0.051	1
25	mmt003a	1567	1885	319	0.565	0.210	2.740	-0.021	1
26	mmt003b	1591	1887	297	0.535	0.248	2.500	-0.028	1
27	mmt004a	1521	1880	360	0.503	0.215	2.790	-0.013	1
28	mmt004b	1600	1900	301	0.485	0.204	2.390	-0.038	1
29	mmt008a	1646	1820	175	0.661	0.325	2.600	-0.062	1
30	mmt008b	1628	1851	224	0.572	0.339	2.630	-0.044	1
31	mmt011a	1801	1946	146	0.543	0.220	2.600	-0.059	2
32	mmt011b	1802	1946	145	0.534	0.211	2.420	-0.041	3
33	mmt012a	1519	1916	398	0.609	0.218	2.550	-0.001	1
34	mmt012b	1521	1697	177	0.511	0.191	2.620	-0.009	1

APPENDIX A3. *continued*

Seq	Series	Interval		No. Years	Corr. w/ Master	Mean Sens.	Std. Dev.	Auto Corr.	AR ()
35	mmt012c	1790	1900	111	0.571	0.289	2.690	-0.025	1
36	mmt013b	1520	1839	320	0.551	0.236	2.560	-0.027	2
37	mmt014a	1587	1917	331	0.560	0.290	2.740	-0.017	2
38	mmt014b	1550	1831	282	0.477	0.263	2.740	-0.038	1
39	mmt015a	1515	1865	351	0.587	0.255	2.620	-0.001	1
40	mmt015b	1521	1930	410	0.582	0.222	2.540	-0.042	1
41	mmt016a	1521	1982	462	0.610	0.233	2.660	-0.010	1
42	mmt016b	1600	1983	384	0.586	0.220	2.710	-0.039	1
43	mmt017a	1572	1958	387	0.490	0.224	2.980	-0.019	1
44	mmt017b	1563	1946	384	0.512	0.285	2.590	-0.019	1
45	mmt018a	1514	1713	200	0.453	0.239	2.860	-0.036	1
46	mmt018b	1515	1680	166	0.568	0.196	2.650	-0.020	1
47	mmt019a	1603	1879	277	0.475	0.175	2.450	-0.027	1
48	mmt019b	1557	1843	287	0.470	0.164	2.700	-0.032	1
49	mmt020a	1518	1976	459	0.623	0.193	2.620	-0.047	1
50	mmt020b	1509	1825	317	0.546	0.214	2.830	-0.039	1
51	mmt021a	1521	1760	240	0.545	0.234	2.750	-0.024	1
52	mmt1004a	1662	1733	72	0.434	0.304	2.910	-0.066	1
53	mmt1101a	1831	1944	114	0.413	0.213	2.840	-0.046	1
54	mmt2003a	1857	1998	142	0.396	0.347	2.630	-0.074	1
55	mmt2024a	1525	1615	91	0.356	0.228	2.710	-0.049	2
56	mmt1004b	1835	1960	126	0.443	0.338	2.820	-0.037	1
57	mmt1057a	1776	1923	148	0.420	0.326	2.510	-0.031	1
58	mmt1061a	1800	1900	101	0.349	0.294	2.830	0.021	1
59	mmt2023a	1647	1718	72	0.361	0.241	2.550	0.013	2
60	mmt2027a	1800	2002	203	0.423	0.257	2.590	-0.038	1
Total or Mean				14687	0.509	0.237	2.980	-0.026	

APPENDIX A4. Statistical descriptions for whitebark pine series from Point Six, Lolo National Forest, Montana.

Seq	Series	Interval		No. Years	Corr. w/ Master	Mean Sens.	Std. Dev.	Auto Corr.	AR ()
1	ps1001a	1753	1950	198	0.523	0.206	0.473	-0.044	1
2	ps1001c	1753	1957	205	0.457	0.201	0.398	-0.037	1
3	ps1002a	1735	1898	164	0.471	0.194	0.493	-0.035	1
4	ps1002b	1735	1949	215	0.410	0.231	0.391	-0.056	1
5	ps1003a	1764	1878	115	0.478	0.173	0.409	-0.043	1
6	ps1003b	1764	1926	163	0.631	0.204	0.354	0.001	1
7	ps1003c	1764	1923	160	0.565	0.189	0.290	-0.035	2
8	ps1004a	1759	2003	245	0.451	0.202	0.322	-0.032	1
9	ps1004b	1818	1996	179	0.544	0.180	0.366	-0.027	1
10	ps1005a	1760	2002	243	0.433	0.207	0.388	-0.025	1
11	ps1006a	1757	1952	196	0.493	0.216	0.444	-0.017	1
12	ps1006b	1757	1816	60	0.527	0.135	0.546	0.045	4
13	ps1007b	1761	1976	216	0.434	0.233	0.333	0.038	1
14	ps1008a	1617	2003	387	0.524	0.280	0.417	-0.022	2
15	ps1008b	1617	1808	192	0.468	0.311	0.395	0.004	1
16	ps1008c	1824	2003	180	0.499	0.246	0.437	-0.044	1
17	ps1009b	1650	1812	163	0.460	0.240	0.396	-0.010	1
18	ps1009c	1828	1985	158	0.394	0.210	0.383	-0.038	1
19	ps1009d	1828	1985	158	0.417	0.222	0.398	-0.022	1
20	ps1013a	1633	1811	179	0.477	0.237	0.354	-0.042	1
21	ps1013b	1633	1929	297	0.424	0.238	0.334	-0.048	2
22	ps1014a	1608	1897	290	0.429	0.213	0.302	-0.008	3
23	ps1014b	1608	1846	239	0.462	0.217	0.408	-0.040	1
24	ps1015a	1581	1928	348	0.433	0.229	0.319	0.010	1
25	ps1016a	1618	1976	359	0.514	0.222	0.443	-0.044	1
26	ps1016b	1618	1816	199	0.495	0.236	0.361	-0.006	1
27	ps2001a	1629	1913	285	0.500	0.250	0.383	0.025	1
28	ps2001b	1643	1906	264	0.470	0.221	0.394	-0.030	1
29	ps2002a	1662	1926	265	0.471	0.184	0.291	-0.021	2
30	ps2002b	1671	1814	144	0.455	0.185	0.361	0.024	1
31	ps2003c	1882	1973	92	0.403	0.248	0.504	-0.038	4
32	ps2004a	1655	1926	272	0.433	0.294	0.278	-0.018	1
33	ps2004b	1654	1816	163	0.453	0.231	0.478	-0.068	1
34	ps2011a	1621	1731	111	0.486	0.256	0.523	0.008	1
35	ps2011c	1867	1985	119	0.426	0.272	0.541	-0.034	2

APPENDIX A4. *continued*

Seq	Series	Interval		No. Years	Corr. w/ Master	Mean Sens.	Std. Dev.	Auto Corr.	AR ()
36	ps2012a	1762	1972	211	0.537	0.182	0.324	-0.033	1
37	ps2012b	1643	1813	171	0.404	0.231	0.421	-0.033	1
38	ps2013a	1606	1816	211	0.416	0.228	0.335	0.005	1
39	ps2013b	1606	1980	375	0.435	0.226	0.397	-0.040	1
40	ps2014a	1621	1979	359	0.473	0.205	0.365	-0.055	1
41	ps2014b	1621	1979	359	0.473	0.190	0.354	-0.023	1
42	ps2016a	1659	1776	118	0.431	0.177	0.369	0.014	2
43	ps2016b	1672	1929	258	0.519	0.186	0.304	-0.010	1
44	ps2016c	1671	1897	227	0.570	0.195	0.306	-0.020	1
45	ps3001a	1821	1949	129	0.407	0.297	0.465	-0.025	1
46	ps3001b	1756	1938	183	0.442	0.255	0.388	-0.058	1
47	ps3002b	1734	1852	119	0.501	0.195	0.301	-0.036	1
48	ps3003c	1763	1885	123	0.441	0.208	0.560	-0.005	3
49	ps3004a	1742	1877	136	0.448	0.218	0.425	-0.068	2
50	ps3004b	1742	1889	148	0.432	0.225	0.409	0.028	1
51	ps3005a	1743	1845	103	0.480	0.232	0.301	0.001	1
52	ps3006b	1737	1837	101	0.455	0.181	0.383	-0.055	1
53	ps3007a	1768	1925	158	0.464	0.216	0.365	0.001	1
54	ps3007b	1768	1924	157	0.441	0.184	0.493	-0.009	1
55	ps3008a	1757	1929	173	0.488	0.239	0.386	0.014	2
56	ps3008b	1757	1929	173	0.451	0.291	0.361	0.011	1
57	ps3009a	1762	1929	168	0.495	0.192	0.455	-0.003	1
58	ps3009b	1762	1901	140	0.468	0.158	0.419	-0.025	2
59	ps3010a	1750	1930	181	0.607	0.239	0.374	-0.014	1
60	ps3010b	1750	1929	180	0.546	0.241	0.405	-0.050	1
61	psx013a	1760	1952	193	0.468	0.231	0.349	-0.025	1
62	psx019a	1644	1928	285	0.466	0.273	0.321	-0.044	1
Total or Mean				12362	0.473	0.223	0.381	-0.022	

APPENDIX A5. Statistical descriptions for whitebark pine series from Ajax Peak, Beaverhead-Deerlodge National Forest, Montana.

Seq	Series	Interval		No. Years	Corr. w/ Master	Mean Sens.	Std. Dev.	Auto Corr.	AR ()
1	AJX3002A	1875	2002	128	0.533	0.188	0.535	-0.039	5
2	AJX3002b	1875	2000	126	0.547	0.229	0.280	-0.022	1
3	ajx3003a	1844	2004	161	0.464	0.242	0.276	-0.031	1
4	AJX3012a	1852	1999	148	0.387	0.208	0.369	-0.035	1
5	AJX3012B	1852	2002	151	0.507	0.178	0.430	-0.059	2
6	ajx3014a	1832	2002	171	0.560	0.226	0.380	-0.027	1
7	ajx3017a	1868	2002	135	0.556	0.232	0.257	-0.092	1
8	ajx3017b	1868	1969	102	0.610	0.223	0.433	-0.062	1
9	AJX3030a	1850	1997	148	0.481	0.225	0.445	-0.036	1
10	AJX3030b	1850	1960	111	0.477	0.206	0.519	-0.042	1
11	ajx3031a	1869	2004	136	0.526	0.236	0.317	-0.052	1
12	ajx3031b	1869	2003	135	0.683	0.211	0.396	-0.036	1
13	ajx3036a	1854	2003	150	0.399	0.186	0.393	0.029	1
14	ajx3036b	1873	2001	129	0.578	0.244	0.280	-0.063	3
15	ajx3059a	1845	2004	160	0.484	0.181	0.424	-0.020	1
16	ajx3060a	1843	2004	162	0.563	0.187	0.362	-0.060	1
17	ajx3060b	1843	2004	162	0.574	0.213	0.440	-0.095	1
18	ajx4006a	1922	2002	81	0.566	0.216	0.429	0.046	1
19	ajx4006b	1921	2002	82	0.492	0.219	0.294	-0.083	1
20	ajx4015a	1880	2000	121	0.668	0.200	0.341	-0.099	1
21	ajx4027a	1892	2003	112	0.583	0.176	0.421	-0.043	1
22	ajx4027b	1892	2003	112	0.606	0.193	0.464	-0.017	1
23	ajx4026a	1876	2003	128	0.533	0.163	0.480	-0.011	1
24	ajx4046b	1876	2003	128	0.558	0.144	0.519	-0.065	1
25	ajx3004a	1876	1969	94	0.500	0.200	0.519	0.024	1
26	ajx3023a	1841	2001	161	0.413	0.209	0.394	-0.016	1
27	aj3046a	1876	2003	128	0.473	0.180	0.303	-0.050	1
28	ajx3038a	1866	2003	138	0.530	0.247	0.505	0.029	1
29	ajx4012a	1879	2003	125	0.454	0.225	0.390	-0.050	1
30	ajx4021a	1880	2003	124	0.432	0.257	0.472	-0.024	1
31	ajx4036a	1879	2004	126	0.462	0.236	0.403	-0.033	1
32	ajx3016a	1880	2002	123	0.570	0.207	0.389	-0.116	1
33	ajx3058a	1899	2004	106	0.407	0.221	0.421	0.062	1
Total or Mean:				4304	0.518	0.209	0.400	-0.037	

APPENDIX A6. Statistical descriptions for whitebark pine series from Big Hole Pass, Beaverhead-Deerlodge National Forest, Montana.

Seq	Series	Interval		No. Years	Corr. w/ Master	Mean Sens.	Std. Dev.	Auto Corr.	AR ()
1	BIG3004b	1956	1992	37	0.465	0.242	0.558	-0.081	1
2	BIG3005A	1870	2003	134	0.553	0.198	0.445	0.010	1
3	BIG3013b	1801	2002	202	0.649	0.240	0.284	-0.029	1
4	big3033a	1852	2004	153	0.482	0.217	0.450	-0.055	1
5	BIG3037a	1820	1933	114	0.608	0.192	0.289	-0.004	1
6	BIGF53	1869	1982	114	0.432	0.284	0.360	-0.040	1
7	BIGF53B	1885	1985	101	0.371	0.151	0.609	0.000	1
8	big2001a	1865	1949	85	0.512	0.219	0.406	-0.044	2
9	big2009a	1931	2004	74	0.494	0.190	0.498	0.031	1
10	big2010a	1952	2004	53	0.453	0.155	0.498	0.006	1
11	big2016a	1876	1948	73	0.384	0.255	0.544	0.039	1
12	big2044a	1943	1969	27	0.435	0.172	0.548	-0.116	1
13	big2048a	1926	1967	42	0.410	0.266	0.510	-0.009	1
14	big3039a	1930	2004	75	0.500	0.187	0.483	-0.056	1
15	big4021a	1778	2003	226	0.572	0.254	0.254	-0.039	1
16	big2001a	1865	1949	85	0.512	0.219	0.406	-0.044	2
17	big2004a	1922	1999	78	0.491	0.216	0.489	0.000	1
18	BIG3005b	1870	2004	135	0.540	0.194	0.449	-0.009	1
19	big3011a	1886	2004	119	0.635	0.261	0.520	-0.059	1
20	big3012a	1866	1904	39	0.451	0.204	0.485	-0.010	1
21	BIG3012b	1863	1885	23	0.621	0.332	0.878	-0.059	1
22	big3017a	1842	1907	66	0.391	0.181	0.553	-0.046	1
23	BIG3022b	1844	1940	97	0.399	0.200	0.463	-0.011	2
24	BIG3050a	1837	1927	91	0.424	0.199	0.422	-0.037	1
25	big3086a	1888	2004	117	0.539	0.216	0.381	-0.045	1
26	big4016a	1832	1961	130	0.373	0.345	0.346	-0.047	1
27	big4017a	1882	1991	110	0.461	0.164	0.394	-0.033	2
Total or Mean				2600	0.502	0.223	0.422	-0.028	

VITA

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