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ECOLOGY OF TREELINE WHITEBARK PINE (*PINUS ALBICAULIS*)
POPULATIONS IN CENTRAL IDAHO: SUCCESSIONAL STATUS,
RECRUITMENT AND MORTALITY, AND A SPRING TEMPERATURE
RECONSTRUCTION FROM WHITEBARK PINE TREE RINGS

by

Dana Lee Perkins

A dissertation submitted in partial fulfillment
of the requirements for the degree

of

DOCTOR OF PHILOSOPHY

in

Ecology

Approved:

UTAH STATE UNIVERSITY
Logan, Utah

2001

ABSTRACT

Ecology of Treeline Whitebark Pine (*Pinus albicaulis*) Populations in Central Idaho:
Successional Status, Recruitment, and Mortality, and A Spring Temperature
Reconstruction from Whitebark Pine Tree Rings

by

Dana Lee Perkins, Doctor of Philosophy

Utah State University, 2001

Major Professor: Dr. David W. Roberts
Department: Forest Resources

This research investigated the successional status of treeline whitebark pine (*Pinus albicaulis*) populations on 14 stands in central Idaho and used empirical statistical models to determine the principal factors affecting recruitment and mortality. The longest lived whitebark pines from four additional high-elevation sites were used to develop a tree-ring chronology to reconstruct over 1,000 years of average April-May temperature.

The assessment of stand structures using size-frequency distributions generally provides evidence that treeline whitebark pine populations are currently self-sustaining in areas of low to nonexistent incidence of white pine blister rust (*Cronartium ribicola*). However the presence of subalpine fir (*Abies lasiocarpa*) in all size classes on sample plots suggests potential replacement of, or codominant climax with whitebark pine.

Inference from Poisson regression models suggests that stand structure variables are important to whitebark pine establishment, which may be constrained by interference competition and available growing space. Subalpine fir establishment appears to be constrained by distance to seed source at lower elevations and by favorable site water-balance effects on northly aspects.

Inferences from logistic regression models calibrated from pre-epidemic stand conditions and post-epidemic mortality levels surrounding a historic mountain pine beetle (*Dendroctonus ponderosae*) outbreak suggest that density and tree size variables are significant predictors of stand and individual tree attack. The significance of the predictor variables in these models corroborates the susceptible host characteristics identified in other pine-mountain pine beetle system risk assessments.

A composite whitebark pine tree-ring chronology from 24 trees from four sites was used to develop a 1028-year long reconstruction of spring temperature for the Sawtooth-Salmon River region of central Idaho. The chronology was calibrated against Ketchum and New Meadows, Idaho US Historical Stations, April-May average monthly temperature using half-sample calibration-verification tests for the period that contained historic climate data, 1909-1992. The chronology accounted for 41% of the variability in the climatic data and successfully simulated medium to high frequency trends. A 19th century cold period coincides with the "Little Ice Age." Neither the instrumental nor the proxy temperature records show evidence of warming in the 20th century.

(175 pages)

ACKNOWLEDGMENTS

I gratefully acknowledge the expert assistance and vision of Dr. Dave Roberts and his encouragement to execute this research. I also thank my committee members for their assistance and brainstorming on various components of the project. Much appreciation is extended to the Rocky Mountain Research Station, USDA Forest Service, and the Sawtooth National Recreation Area and Sawtooth National Forest USDA Forest Service for financial support, use of facilities, and equipment. Thanks to Dennis Ferguson and Dave Turner for encouragement and good advice. Special thanks to Jim Rineholt, Greg Clark, Dave Bassler, Sharon Bradley, and Deb Bumpus for applied ecology opportunities in the subalpine forests of central Idaho.

I also thank my family and friends for their patience and encouragement throughout this graduate program. Special thanks to Kelly McCloskey and my sister Holly Coiner for their well reasoned and practical approach to graduate school endeavors, and their gracious hospitality. Thanks to Marti Aitken for rendering site maps for this manuscript and to Karen Shideler and Roger Anderson for invaluable field assistance. Finally a very special thank you is extended to Denis Norton for his unfailing support, encouragement, and inspiration.

Dana Lee Perkins

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CHAPTER 1

INTRODUCTION

High-elevation, treeline forests are an important component of the vegetation in the northern Rocky Mountains (Daubenmire 1943, Steele et al. 1981, 1983, Peet 1988). These forests are composed of a few species of subalpine conifers that range across successional types and vary from closed-storied stands to open-storied stands to krummholz forms. Upper treeline forests constitute small areas on landscape scales, but occur on the highest elevations that support trees growing in an upright form. They are critical for watershed protection (Farnes 1990), are considered sensitive indicators of global climate change (LaMarche and Stockton 1974, Ross 1990, Stevens and Fox 1991), and provide habitat for wildlife at the upper limit of forested vegetation. Heat and site water constraints are the most common limitation to upper treeline, but biotic factors affect the abundance and distribution of species as well (Tranquillini 1979, Lloyd 1997).

In the cold, dry mountain ranges of central Idaho the upper timberline is dominated by whitebark pine (*Pinus albicaulis* Engelm.). This long-lived pine occurs on harsh, rocky, exposed sites and at elevations above 2,700 meters, and is generally the only species that provides shade to delay snow melt through the early summer. Temperature reconstructions from whitebark pine tree rings exceed 1,000 years (Biondi et al. 1999, Chapter 4) and provide baseline information for studying climatic variability. Whitebark pine is a keystone species (Paine 1969, Krebs 1994, Lanner 1996) of critical importance to wildlife species dependent on its nutritious seeds. Recreationists value whitebark pine as an aesthetic component of treeline landscapes.

Regional attention to whitebark pine population levels has been stimulated by reports that current environmental conditions have led to higher rates of mortality than establishment (Arno 1986, Keane et al. 1990, Keane and Arno 1993, Keane et al. 1994).

Recognized factors causing whitebark pine decline in the northern Rocky Mountains include an exotic fungus, white pine blister rust (*Cronartium ribicola*), infestation of whitebark pine by mountain pine beetle (*Dendroctonus ponderosae*) (Coleoptera: Scolytidae), and successional replacement by shade tolerant species as a result of fire suppression (Arno and Hoff 1989, Keane et al. 1990, Morgan and Bunting 1990, Kendall and Arno 1990, Keane and Arno 1993). Current research efforts have focused primarily on the exotic blister rust fungus, which has been responsible for severe pine mortality and reduced cone crops in whitebark pine over much of its northern distribution (Keane et al. 1994).

Conservation of species such as whitebark pine that are threatened by environmental change requires understanding the processes determining population and community structure. Ecological status and trends must be assessed; is the population stable or self sustaining, increasing or decreasing? Abiotic and biotic factors influencing life history characteristics, including disturbances, must be identified and the degree that they affect populations investigated (Schemske et al. 1994). In the following section I present the background biology of whitebark pine that was eloquently summarized by Arno and Hoff (1989). In the last section I present a conceptual model that serves as a framework to address questions of self-sustainability and motivates the discussion of biotic factors affecting whitebark pine.

BACKGROUND

Whitebark pine is a slow growing, long-lived, stone pine (subgenus *Strobus*, section *Strobus*, subsection *Cembrae*) of high-elevation forests and timberlines of the northwestern United States and southwestern Canada. It is one of five stone pines worldwide and the only stone pine in North America. The northern distribution limit is in the Canadian Coastal Mountains of British Columbia and its southern limit is in the California Sierra

Nevada Mountains. The distribution of whitebark is split between the inland Rocky Mountain Ranges and the Coastal Ranges of the Cascade, and Sierra Nevada. It occupies harsh, cold sites characterized by rocky, poorly developed soils and snowy, wind-swept exposures (Arno and Hoff 1989). Throughout its range, whitebark pine may occur as a climax alpine species, including a krummholz form in communities above tree line, or as a seral species or climax co-dominant with subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.). Other common tree associates in the Northern Rockies are lodgepole pine (*Pinus contorta* Dougl.), Engelmann spruce (*Picea engelmannii* Parry), and less commonly mountain hemlock (*Tsuga mertensiana* (Bong.) Carr.) and alpine larch (*Larix lyallii* Parl.) (Arno and Hoff 1989).

Whitebark pine seeds are not wind dispersed; they develop in indehiscent cones that are harvested by Clark's nutcrackers (*Nucifraga columbiana*). Nutcrackers cache or consume seeds and those not retrieved from caches may germinate and become established as seedlings (Lanner 1980, Tomback 1978, 1982, Hutchins and Lanner 1982). Corvids, such as Clark's nutcracker and other *Nucifraga* spp., have evolved with Cembrae pines over centuries and are critical components in pine regeneration dynamics, ultimately responsible for the geographic range, spacing, successional status, and genetics of the stone pines (Hutchins and Lanner 1982, Lanner 1982, Tomback 1982, Lanner 1996). Red squirrels (*Tamiasciurus hudsonicus*) also harvest cones and store them in middens. Black bears (*Ursus americana*) and the endangered grizzly bear (*Ursus arctos horribilis*) raid these middens for the energy-rich food that the seeds provide (Kendall 1983, Mattson and Jonkel 1990).

The most serious threat to the persistence of whitebark pine is white pine blister rust, an exotic fungus native to Eurasia that was introduced to the west coast of the United States and Canada in the early 20th century (Hoff et al. 1980, Hoff and Hagle

1990, Hoff et al. 1992, Tomback et al. 1995, Smith 1997, Smith and Hoffman 2000). In northwestern Montana, environmental conditions favorable to the propagation of white pine blister rust have resulted in severe pine mortality and reduced whitebark pine cone crops (Arno 1986, Kendall and Arno 1990, Mattson and Jonkel 1990, Keane and Arno 1993, Keane et al. 1994). Decline of whitebark pine populations on 20-year remeasurement plots in northwestern Montana showed 42% mortality rate over the measurement period (Keane and Arno 1993). The threat of local extinction of whitebark pine from blister rust is possible in the mesic northwestern range of whitebark pine partly because humid weather enhances fungus spore dissemination (Arno and Hoff 1989). The geographic spread of blister rust to the south and eastern range of whitebark pine, including Yellowstone National Park is expected to have devastating effects on the species and the wildlife dependent on its nutritious seed, particularly the grizzly bear (Keane and Arno 1993). It appears that it is only a matter of time and favorable weather conditions before it spreads throughout the pine's distribution. Research efforts are concentrated on rust resistance and documenting rates of decline and spread of blister rust (Hoff and Hagle 1990, Hoff et al. 1992, Keane and Arno 1993, Kendall and Keane 2000). Areas with low to nonexistent blister rust are currently the only areas where the natural variability of factors affecting whitebark pine populations may be assessed.

Mountain pine beetles are the most common natural damaging agents of whitebark pine and are responsible for mortality of mature trees (Arno 1970, Ciesla and Furniss 1975, Arno 1986, Arno and Hoff 1989, Bartos and Gibson 1990, Perkins and Swetnam 1996). As a phytophagous, cambial-feeding insect of western conifers, mountain pine beetle is recognized as an aggressive forest insect responsible for large timber losses, and as an integral component of forest ecosystem dynamics for its role in stand thinning, redistribution of resources for regeneration, and for fuel load enhancement (Peterman

1978, Romme et al. 1986). Mountain pine beetles may kill trees previously weakened by blister rust (Keane and Arno 1993).

Stand-replacing fires adjacent to treeline whitebark pine stands have historically spread to high-elevation stands either as small spot fires resulting in the death of small clumps of trees, or as larger stand-replacing fires when fuel conditions and intensity permit (Arno and Hammerly 1984, Murray 1996). Lightning strikes are common in treeline stands, resulting in the death of one to several trees. Mean fire return intervals in seral whitebark pine stands range from 50 to 300 years (Arno 1986, Arno and Hammerly 1984) and on rocky treeline sites events may exceed 350 years (Barrett 1994, Romme 1982). Gap producing disturbances resulting in the death of a few trees, such as those caused by lightning strikes or spot fires, occur on shorter time intervals (Watt 1947, Arno 1986, Pickett and White 1985). On lower elevation, less harsh sites, fire suppression of the last 80 years has favored the successional replacement of shade intolerant whitebark pine by shade tolerant species such as subalpine fir (Arno and Hoff 1989, Murray 1996). Only on treeline stands, where understory fuels are generally insufficient to carry wildfire, and where environmental conditions are generally limiting for establishment of competitors do whitebark pine populations appear to be self-sustaining.

A south-central Idaho study area was chosen for this research because field surveys from 1995-1997 showed that white pine blister rust was only present in low amounts (Smith 1997, Smith and Hoffman 2000, Perkins pers. observ.). Accordingly, its effects as a confounding factor in studying treeline whitebark pine dynamics are currently negligible. However, many stands in this region experienced high mortality of large diameter trees in a widespread mountain pine beetle epidemic between 1920 and 1940 (Arno 1970, Ciesla and Furniss 1975, Arno 1986). Therefore a mixture of mountain pine beetle-disturbed and

nondisturbed stands was sampled to provide a comparison of the effects of disturbance on successional dynamics, recruitment and mortality.

CONCEPTUAL FRAMEWORK

The dynamics of the treeline whitebark pine populations are a consequence of the interactions among abiotic and biotic factors that enhance or mitigate population levels. Abiotic factors include the site heat and water balance, radiation loads, and nutrient availability. Principal biotic factors are Clark's nutcracker, mountain pine beetle, and more shade tolerant tree species. Whitebark pine populations are promoted by Clark's nutcracker; seeds not consumed or retrieved from caches may become established as seedlings. This is a positive effect for trees and nutcrackers (Fig. 1-1). Mountain pine beetles feed on and kill trees and reduce whitebark pine population levels. Thus, whitebark pine has a positive effect on mountain pine beetles and mountain pine beetles have a negative effect on whitebark pine (Fig. 1-1). Description of high elevation whitebark pine forests as a system is appealing because it provides a conceptual model to integrate information from the parts to make inferences about the whole. The integrity of the system depends upon whitebark pine's relative stability and self sustainability as represented by the tree in Figure 1-1. The functional components that influence the whole are represented by the nutcracker and beetle in Figure 1-1. This simple schematic represents a complex system and serves to highlight the interactions affecting a unique, long-lived species that is endangered primarily because of human activities.

In the second chapter I quantitatively describe the successional status of treeline whitebark pine stands by fitting the frequently used reverse-J or negative exponential distribution (Leak 1964, 1965, Whipple and Dix 1979, Parker 1988) to whitebark pine size class data. This distribution is the theoretical ideal for a self-perpetuating population and may imply a stable size distribution, a necessary but not sufficient assumption of some

demographic models. I measure the departure from the theoretical distribution using the coefficient of determination R^2 . The objective of this chapter is represented by the tree in Fig. 1-1.

In the third chapter, I use generalized linear models (McCullagh and Nelder 1989) and generalized additive models (Hastie and Tibshirani 1990) (log-linear regression) to predict whitebark pine and subalpine fir seedling density as a function of stand structure and environmental site variables. Prediction of seedling density is useful in its own right, but more importantly these models elucidate ecological mechanisms related to recruitment success. The objective of this chapter is represented by the nutcracker in Fig. 1-1.

In the fourth chapter, I use a generalized linear model (logistic regression) to explain the probability of mountain pine beetle attack and death of whitebark pine as a function of tree and stand-level variables. Again the model is useful for prediction and identifies susceptibility characteristics of whitebark pine that are common to other pine species. The objective of this chapter is represented by the beetle in Fig. 1-1.

In the fifth chapter I present a spring temperature reconstruction from whitebark pine tree rings. The long-lived individuals (mean age equals 430 years) that constitute the chronology have survived disturbances or lived on extreme sites where the return interval of disturbances has left them intact. Their usefulness for a climate reconstruction is caused by their sensitivity to site heat and water constraints on high-elevation treeline sites. The objective of this chapter is again represented by the tree in Fig. 1-1.

Finally in the last chapter I summarize the implications of these interacting inputs and outputs to conjecture what processes are structuring treeline whitebark pine populations.

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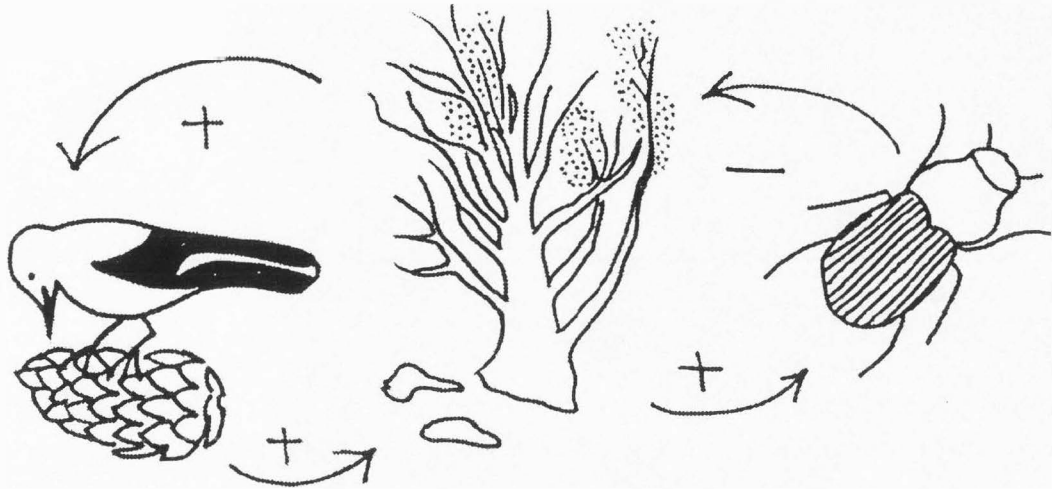


Fig. 1-1. Schematic representation of the whitebark pine system with principal biotic components, Clark's nutcracker and mountain pine beetle. The arrows connecting the variables represent the direction of effect and rates of change between the biotic state variables of the system.

CHAPTER 2
STAND STRUCTURE AND SUCCESSIONAL STATUS OF TREELINE WHITEBARK
PINE STANDS

Abstract. Diameter distributions from 14 treeline whitebark pine (*Pinus albicaulis* Englem.) stands in central Idaho were analyzed for successional status. Nine stands had experienced widespread mortality during a mountain pine beetle (*Dendroctonus ponderosae*) (Coleoptera: Scolytidae), epidemic ca. 1930 and five were unaffected by mountain pine beetles. Reconstructed stand structures prior to the ca. 1930 mountain pine beetle epidemic for the attacked (disturbed) and nonattacked (undisturbed) stands were compared to current (1998) stand structures. Size class distributions were compared to negative exponential and multimodal forms indicating self-sustaining climax status. Inspection of the direction of change of stand structure reveals that three of the undisturbed stands have destabilized and two show little change, as assessed by goodness of fit to the negative exponential curve. Four of the disturbed stands increased in stability and three showed little change. Only two disturbed stands decreased in stability. Thus mountain pine beetle infestations may be beneficial for maintaining the self-replacing status of treeline stands. Lags in recruitment following disturbance may be expected after mortality of large diameter cone-producing trees. The presence of subalpine fir in all size classes suggests a successional replacement of whitebark pine by subalpine fir or potential codominant status.

INTRODUCTION

On time scales of decades to thousands of years, treeline forests are generally considered self-perpetuating, stable, and representative of the edaphic and climatically limited climax (Clements 1928, 1936, Daubenmire 1943, Whittaker 1953, 1975, Veblen

1986, Peet 1988). By definition, a climax plant community or population is self-replacing in the absence of disturbance and returns to the same end community following disturbance (Clements 1936, Daubenmire 1943, Whittaker 1953, Hall et al. 1995). Stability is intrinsically linked to the climax theme because a balance between inputs (births) and outputs (deaths) is maintained resulting in a stable or steady state population. Fluctuations about the average or changes in absolute abundance of population levels are accepted in this framework as long as the relative proportions of classes are maintained. Cycles may also be considered steady state as long as they are regular and without trend (Pielou 1977).

On treeline sites in the northern Rocky Mountains, whitebark pine (*Pinus albicaulis* Engelm.) occurs in nearly pure, single species stands and is considered the climax species (Weaver and Dale 1974, Steele et al. 1981, 1983, Arno 1986, Peet 1988, Arno and Hoff 1989). It is classified as intermediate to intolerant of shade (Arno and Hoff 1989) and is considered drought tolerant (Arno and Hoff 1989, Tomback et al. 1993). Whitebark pine is considered to be better adapted to the harsh conditions found on treeline sites than its principal codominant and competitor, subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.) (Arno and Hoff 1989, Callaway 1998). It conforms to the life history patterns of other long-lived pines, investing heavily in roots and stems as juveniles, maturing later, and typically forming open-canopied stands (Platt et al. 1988, Arno and Hoff 1989). Its importance has been recognized for watershed protection (Farnes 1990, Arno and Hoff 1989), as a mutualist with Clark's nutcracker (*Nucifraga columbiana*)—its seed dispersal agent (Lanner 1980, Tomback 1982, Hutchins and Lanner 1982, Lanner 1982)—and has been called a keystone species of subalpine ecosystems (Lanner 1996). Mountain pine beetle (*Dendroctonus ponderosae*) (Coleoptera: Scolytidae) is the most common natural damaging agent, killing mature trees in endemic and epidemic

infestations (Ciesla and Furniss 1975, Arno 1986, Arno and Hoff 1989, Bartos and Gibson 1990, Perkins and Swetnam 1996). Wind-throw, wildfire, lightning, and other pathogens (Hoff and Hagle 1990) also kill trees.

Considerable research in the Rocky Mountains has focused on the successional status of moderately tolerant and shade tolerant subalpine species such as Engelmann spruce (*Picea engelmannii* Parry) and subalpine fir and shade intolerants such as lodgepole pine (*Pinus contorta* Dougl.) and limber pine (*Pinus flexilis* James) (Hanley et al. 1975, Whipple and Dix 1979, Peet 1981, Johnson and Fryer 1989, Knowles and Grant 1983, Parker and Peet 1984, Parker 1988, Veblen 1986). The successional status of treeline forests of whitebark pine has received less attention (but see Parker 1988 and Sneath 1980) for several reasons. First, research efforts on whitebark pine have focused primarily on the exotic white pine blister rust fungus (*Cronartium ribicola*) responsible for considerable mortality, and reduced cone crops over much of its northern distribution (Hoff et al. 1992, Keane and Arno 1993, Keane et al. 1994). Whitebark pine decline has severe consequences to the wildlife dependent on its nutritious pine nuts, including the Clark's nutcracker, red squirrel (*Tamiasciurus hudsonicus*) (Reinhart and Mattson 1990), black bear (*Ursus americanus*), and endangered grizzly bear (*Ursus arctos horribilis*) (Kendall 1983, Arno 1986, Mattson and Jonkel 1990, Kendall and Arno 1990, Mattson et al. 1993, Keane and Arno 1993). Second, research in the last decade has demonstrated the positive effects of fire on whitebark pine recruitment (Tomback et al. 1993) and on stand dynamics with simulation models (Keane et al. 1990). On stands where whitebark pine is seral, it is increasingly being replaced by shade tolerant subalpine fir because of fire suppression (Arno 1986, Morgan and Bunting 1990, Keane et al. 1994). Information on the effects of fire are critical to management activities focusing on conservation and restoration of the species and again research has been prioritized here. Finally, whitebark

pine is not generally a species of commercial interest; historically there has been little concern about stand structure and successional dynamics of this high-elevation pine.

The biological integrity of high-elevation ecosystems, particularly biodiversity and watershed protection, and the importance of whitebark pine to endangered species have raised both scientific and public awareness of the need to understand the processes affecting whitebark pine populations. Therefore, the purpose of this research was to determine the successional status of whitebark pine forests near treeline through analyses of stand structure. It appears that only on treeline stands and in areas with low to nonexistent incidence of blister rust is whitebark pine self-perpetuating as the climax species.

Forest researchers characterize stand structure and interpret successional status using both age and size class frequency distributions (Knowles and Grant 1983, Hanely et al. 1975, Whipple and Dix 1979, Veblen 1986, Lorimer 1980). Age-frequency distributions capture the time-varying mortality and recruitment rates to the extent that estimates of pith dates and decomposition schedules allow (Lloyd 1997). Ideally they yield the most information on time-defined successional status, evenness of age classes, and provide the resolution to compare with historical environmental conditions (Veblen 1986). For instance, age-based dendrochronological methods have enabled researchers to reconstruct both establishment and mortality rates on 100 year to millennium scales and compare them to climatic variations and disturbance (Lloyd 1997, Villaba and Veblen 1997).

Size, as a proxy for age, is an easier variable to obtain, may be more closely related to endogenous stand dynamics such as growth release following disturbance (Peet 1981), may be a better indicator than age of reproductive capacity (Harper 1967, 1977), and historically has been the variable of interest for commercial timber values (de Liocourt 1898, Reineke 1933, Leak 1964, Knowles and Grant 1983). For these first three reasons,

particularly ease of measurement and the effects of mountain pine beetle disturbance (Chapter 4, Perkins and Swetnam 1996) I chose to use size frequency distributions.

Independent of whether age or size variables are used for structural analyses, the frequency distribution that characterizes a stable, self-replacing all-aged population is known as the reverse-J, inverse-J, or J-shaped probability distribution (Leak 1965). It is a negative exponential function, $y = ae^{-rx}$, where e is the base for natural logarithms, x represents the size or age class variable on a continuous scale and y is the number of trees per age or size class. The constants a and r are positive and reflect the structure of the population distribution.

To evaluate stand structure and successional status of treeline whitebark pine populations, I focused on the following questions: (1) Is there evidence that whitebark pine are self-perpetuating populations as evinced by negative exponential diameter distributions? (2) Is there evidence of a negative exponential diameter distribution prior to a large-scale disturbance, a mountain pine beetle epidemic of ca. 1930? (3) How does the mountain pine beetle epidemic change the shape of the size-frequency distribution? (4) In the 70 years since the mountain pine beetle epidemic, has stand structure attained a semblance of pre-disturbance form? (5) Is there evidence of successional advance (encroachment) of subalpine fir on high-elevation sites?

This work is intended to serve as a framework for understanding the processes structuring treeline whitebark pine populations. A quantitative description of the current stand structure is expected to be useful for silvicultural management decisions for restoration and conservation of the species.

METHODS

Study Area

A central Idaho study area was chosen because field surveys from 1995-1997 showed that white pine blister rust was only present in low amounts (Smith 1997, Smith and Hoffman 2000, Perkins pers. observ.). Accordingly, its effects as a confounding factor in characterizing stand structure are currently negligible. However, many of these stands experienced high mortality of large diameter trees in a widespread mountain pine beetle epidemic between 1920 and 1940 (Arno 1970, Ciesla and Furniss 1975, Arno 1986). Evidence of the epidemic is still apparent 70 years later with ghost forests of persistent snags. Not all high-elevation stands were attacked in this epidemic (Chapter 4); therefore a mixture of attacked and nonattacked stands was sampled to provide a comparison of the effects of disturbance on successional dynamics.

Fourteen treeline whitebark pine stands located within the Sawtooth National Recreation Area, the Sawtooth National Forest, and the Challis National Forest were sampled during the field season of 1998 (Fig. 2-1). Stands were located in six mountain ranges within the study area. Four sites were located near summits in the White Clouds Mountains (WC), three in the Headwater Mountains (HW), two in the Smoky Mountains (SM), three in the Salmon River Mountains (SR), one in the Boulder Mountains (BM), and one in the Sawtooth Mountains (SW) (Fig. 2-1). The Headwater Mountains are not identified in Fig. 2-1; they were considered either part of the Sawtooth or Smoky Mountains and form the divide between the Salmon and Big Wood rivers. Elevations ranged from 2,700 to 3,000 m (8,800 to 9,800 ft). Stand names and physical site attributes are summarized in Table 2-1.

Sample stand selection criteria were: (1) whitebark pine was the dominant species with composition greater than or equal to 60% of total basal area; (2) stand elevations

were between 2,700 m (8,800 ft) and an upper edaphic treeline bordering an unvegetated rock ridgetop; (3) stand extent was as large an area as possible with homogeneous structure, constant aspect and slope; (4) tree form was upright (krummholz form trees were not sampled); (5) mountain pine beetle attacked and nonattacked stands within the same watershed were chosen whenever possible. The last criterion was relevant to objectives characterizing host susceptibility in Chapter 4. Here the importance of disturbed stands was for assessing structural patterns following disturbance. Beyond these criteria, selection of sites was restricted by access within a day. Aerial photographs and ground reconnaissance or both were used to identify potential stands. Attacked and nonattacked stands were differentiated by abundance of whitebark pine snags with visible J-shaped adult beetle galleries and lack of fine limbs. The first criterion, adult galleries, had been used previously to determine beetle attack (Perkins and Swetnam 1996) and the second, no fine limbs, was a consistently observed characteristic of trees killed in the 1920-1940 period. Stands composed of $\geq 15\%$ beetle-killed snags were considered attacked stands; stands composed primarily of living whitebark pines with few beetle killed trees were considered nonattacked stands. These were readily identifiable on aerial photographs. Selected stands often extended below 2,700 m (8,800 ft) but were not sampled below this elevation because in this geographic region their character was distinctly seral succeeding to subalpine fir. Implicit in the near-treeline criterion is the idea that these stands represent the climax whitebark pine community (Whittaker 1975, Steele et al. 1981).

The study area in the central Idaho region is semiarid with an average annual precipitation of 82 cm (32 in.) and ranges from less than 38 cm (15 in.) in the southern section and valleys to greater than 152 cm (60 in.) on some mountain peaks. Most precipitation falls as snow and rain during winter and spring; at elevations above 2,700 m, most precipitation falls as snow. Annual temperatures range from average minimum of

-6° C (22° F) to average maximum of 8° C (46° F) with a mean of 2° C (36 °F) (Steele et al. 1981). Extreme cold temperatures of -34° to -47° C (-30° to -50° F) are recorded from December through February (Steele et al. 1981). Winds redistribute snow around whitebark pine trees to form snowdrifts that may linger until July and occasionally August. Granitic bedrock of the Sawtooth and Idaho Batholiths forms the core of the study area, with Tertiary volcanic and sedimentary forms on southerly and easterly ranges (Williams 1961).

Across the study area, tree associates are lodgepole pine, subalpine fir, Douglas-fir (*Pseudotsuga menziesii* Mirbel Franco), and Engelmann spruce. Habitat types are in the PIAL/ABLA or PIAL series (Steele et al. 1981). Landscape vegetation mapping on the Sawtooth National Forest identified 4.1% of the land area as climax whitebark pine vegetation (Redmond et al. 1997).

Field Collections

Seven to ten 0.04-ha (1/10 acre) plots with a nested 0.008-ha (1/50 acre) subplot were established randomly on each site, except for one site, RRB, which only had three plots. For each plot, elevation, aspect, slope, location coordinates, the presence of old wood, and charcoal were recorded. On each 0.04-ha plot, the diameter at breast height (DBH, 1.5 m (4.5 ft.) above ground surface) and species of all trees ≥ 10.2 cm (4.0 in) DBH were recorded; on each 0.008-ha plot the DBH and species of all trees less than 10.2 cm DBH (4 in.) were recorded. Additionally, the first trees north and south on a clockwise arc from plot center were cored with an increment borer for age determination. To maximize the precision of age estimates, trees were cored close to ground level, generally 30-35 cm (12-14 in.) from the ground surface. Individual trees were recorded as attacked and killed by mountain pine beetles *versus* not attacked.

Analyses

To reconstruct the stand structure prior to the mountain pine beetle epidemic, the diameter of trees ca. 1930 (DBH30) was estimated from the subset of cored trees as:

$$DBH30 = DBH98 - 2 * RI$$

where DBH98 was the diameter at breast height recorded in 1998 and RI was the radial increment measured to the nearest 0.25 cm (0.10 in.) along the increment core from the 1930 through the 1998 annual ring. A least squares regression was used to calculate the DBH30 of all live trees sampled as:

$$DBH30 = (a + b\sqrt{DBH98})^2$$

The regression was significant ($p < 0.001$) with 53% of the variability in DBH30 explained by DBH98 (Table 2-2). The regression model was thus considered adequate to reconstruct diameters of trees that survived the ca. 1930 epidemic. The model fit and evidence of the random distribution of model errors are shown in Fig. 2-2.

For both the pre-epidemic and 1998 stand structure analyses, average abundances were normalized to a per ha basis, and will be referred to as densities in this paper. Reconstructed diameters ca. 1930 and 1998 sample diameters were used to generate standard stand-level forest metrics (Husch et al. 1982) including basal area (m^2/ha), trees per ha (*tph*), mean basal area (*mba*), quadratic mean diameter (*dq*), and stand density index (*sdi*) (Reineke 1933, Long and Daniel 1990). Sampled 1998 diameters were also used to generate local density metrics including basal area per 0.04 ha of live and dead trees (*lbplt* and *dbplt*) and live and dead trees per 0.04 ha (*ltplt* and *dtplt*). The 0.04 ha basis reflects the local area environment of trees on subplots.

Size-Age Relationships and Size Frequency Distributions

Linear regressions of age against size have proven useful for inference of trends related to age structure. The problems associated with size as a surrogate for age are well known. Trees have differential growth rates related to environmental and autogenic effects (Smith et al. 1997). Nonetheless I assessed the variability in age that could be explained by diameter using a least squares regression. Local density metrics as well as DBH were included as independent variables. To maximize the precision of age estimates, only increment cores from sample trees that included the pith or were within ten years of the pith were used in regression analyses. Curvature of rings on cores was compared with concentric circles on a plastic template to estimate the number of annual rings to the pith.

Size-frequency histograms and distributions were calculated for the two principal species, whitebark pine and subalpine fir. Douglas-fir and lodgepole pine were present in small amounts, so their distributions are not reported. All size frequency distributions were plotted over 5-cm diameter classes. Seedlings density was generally two orders of magnitude greater than pole size or dominant tree density so densities were transformed to the natural logarithm scale and plotted against the midpoints of the diameter classes. Because the tree densities were transformed to the logarithm scale, the negative exponential curve was fitted in the natural log scale using least squares regression (Hett 1971). I used the coefficient of determination (R^2) to measure the departure from the idealized stable size distribution (reverse-J) (Parker 1988).

RESULTS

The effect of the mountain pine beetle disturbance of the 1920-1940 period is reflected in the changes in tree density on the sampled stands (Table 2-3). Basal area (ba_{30}), trees per ha (tph_{30}), mean basal area (mba_{30}), quadratic mean diameter (dq_{30}),

and stand density index (*sdi*30) were all lower in nonattacked than attacked stands. The implications of these differences to host susceptibility characteristics of whitebark pine are discussed in Chapter 4. The nonattacked stands have continued to increase in basal area and density, while most of the attacked stands have not reached their pre-1930s stocking levels. Across all sites charcoal remnants, down log remnants and old, pre-epidemic snags were observed.

Size-Age Relationships

Regression analysis with age as a function of diameter and local density metrics revealed that only diameter was significantly correlated ($p \leq 0.001$) with age. Local basal area and trees per 0.04 ha did not reduce the variability in the regression sufficiently to retain them as predictors in a multiple regression. This is not surprising because individuals occur in open-canopied stands near treeline with mean basal areas of 18 m²/ha (80 ft²/acre) (Table 2-2). The regression equation was:

$$\text{Age} = -47.6329 + 42.5113 \sqrt{\text{DBH}}$$

with 55% of the variability in age explained by DBH (Table 2-4). The model fit is shown in Fig. 2-3.

Size-Frequency Distributions

Size frequency distributions of both pre-mountain pine beetle epidemic (ca. 1930) and current (1998) stand structures revealed two patterns: (1) a negative exponential (reverse-J) distribution and (2) a multimodal distribution. Whitebark pine seedling densities are high on all sites (Appendix A). The natural log transform of the frequencies for each size class appears in Fig. 2-4 for the undisturbed stands and in Fig. 2-5 for the mountain pine beetle disturbed stands. The straight line fit of the logarithmic

transformation of the negative exponential distribution suggests a self-perpetuating population ($R^2 \geq 0.90$) on six of the 14 stands prior to the beetle epidemic (Table 2-5, Figs. 2-4, 2-5). Of these six stands, two (AVL and BGH) were subsequently attacked and four (AND, ASO, CRS, NRR) were not. Two of the four undisturbed stands, CRS and NRR, have since departed from a previous stable size distribution. The two attacked stands that exhibited stable size distributions before the epidemic (AVL and BGH) have not significantly departed from the negative exponential distribution in the 70 years since the disturbance (Fig. 2-5).

Prior to the epidemic eight stands were characterized by the multimodal distributions (Parker 1988). Coefficients of determination ranged from 0.50 to 0.88 for the idealized fit to the negative exponential distribution (Figs. 2-4, 2-5). The multimodal distribution may be described as modification of Whipple and Dix's (1979) bimodal distribution (Parker 1988). This distribution is associated with (1) a high number of seedlings and saplings, and (2) with two or more size classes with higher density than adjacent smaller and larger classes. Such distributions indicate episodic or pulse recruitment, usually following a disturbance, and may achieve an all-aged, self-replacing population over time (Whipple and Dix 1979). Of the eight stands characterized by multimodal distributions, seven were attacked and one was not (Table 2-5 and Fig. 2-4, 2-5). The nonattacked stand (BLP) showed little change in size structure (Fig. 2-4) since the outbreak while four of the seven stands (ABK, BLK, RRB, and TLK) increased in approaching a stable size distribution with the BLK distribution showing the best fit to the stable size distribution with an $R^2 = 0.97$. Two of the attacked stands departed (GOA and SIL) further from the stable size distribution and one showed little change (TWP) (Fig. 2-5). On attacked stands, BGH, BLK, GOA, SIL, TLK, and TWP, the pre-epidemic reconstructed distributions are skewed right to include the large diameter

trees that were attacked by beetles (Chapter 4). This is manifest by the less negative slope of the straightline fit to the transformed negative exponential curve (Appendix B).

Recruitment densities for whitebark pine are currently higher than those of subalpine fir (Fig. 2-4) on 12 out of 14 stands. Average whitebark pine densities across all sites for the 2.5- and 7-cm size class are 1346 and 116 per ha (545 and 47 per acre) as compared to 728 and 27 per ha (295 and 11 per acre) for subalpine fir (Appendix A). For the 1998 assessment, a depression in the density of the the 7-cm diameter class is evident on four of the nonattacked stands and to lesser extent on most of the attacked stands.

Subalpine fir is generally present in all size classes, with abundance decreasing with size (Fig. 2-4, third column). On three stands, CRS, NRR, and GOA, subalpine fir seedling densities exceed whitebark pine seedling densities. On sites ABK, GOA and to a lesser extent NRR, subalpine fir occurs in all size classes and appears to be codominant with whitebark pine (Fig. 2-4). Subalpine fir canopy dominants on these three stands share equivalent size classes with the dominant whitebark pines.

All stands are uneven or all-aged stands as inferred from size-age relations and diameter distributions. The variability in size class abundances appears to be greater in the current assessment than in the pre-epidemic assessment primarily due to the depression in the sapling (7 cm) size class (Fig. 2-4, center column).

DISCUSSION

The quantitative assessment of stand structures generally provides evidence that treeline whitebark pine populations are currently self-sustaining. Negative exponential and multimodal diameter distributions, with high abundances in the seedling class are reported for both pre-epidemic and current conditions.

Current whitebark pine seedling densities are high. With the assumptions of a typical survivorship curve, and analogous death-rate curves, seedlings in the smallest size

class would be expected to sustain the greatest mortality in the transition to the next size class, as there is a decreasing risk of death with age or size (Harcombe 1987, Deevey 1947, Pearl 1928). An alternative "U-shaped mortality curve" (Goff and West 1975, Harcombe 1987) also exhibits high mortality in the early size class, levels out for vigorous overstory trees, and shows increasing mortality in larger size classes. The first part of either of these curves likely describes the survivorship function of small size class whitebark pine. No inference of recovering or increasing densities is possible because of the usual difficulties of static life-table data (Harper 1977, Caswell 1989, Gotelli 1995, Ross et al. 1982).

On the nonattacked stands a depression in the densities of whitebark pines is evident in the 6-cm diameter class (Fig.3). From the age-size regression I estimated that these individuals established as cohorts approximately 40 to 70 years ago (Fig. 2-2) and overlap the period of the 1930's drought. This period is also concurrent with mountain pine beetle epidemic (Arno 1970, Ciesla and Furniss 1975, Perkins and Swetnam 1996). Seedling establishment may have been limited by drought conditions and above average summer temperatures (Biondi et al. 1999) and/or by low seed availability because of the widespread beetle-caused mortality of mature cone bearing trees. However, the depression is also apparent in the six cm subalpine fir seedling class. This may be evidence that "safe site" conditions (Harper 1977, Tomback et al. 1993) for both species were more limited by climatic variables than life history characteristics. In previously burned sites in northwestern Montana, Tomback et al. (1993) found high levels of whitebark pine and subalpine fir recruitment from 1977 to 1985. They attributed the synchronous pulse of recruitment to environmental site conditions. Rather than high levels of recruitment, my finding of low levels of levels of recruitment may also be related primarily to environmental site variables. Differentiating among possible mechanisms responsible for this period of low recruitment is difficult and requires further research.

Stability has had a long and arguable association with the concept of climax (McIntosh 1980, West et al. 1981, Davis 1981, Pielou 1991, Hall et al. 1995 and references therein). If stability is the ability to recover from disturbance, and refers to stable size, reverse-J, negative exponential, and self-replacing size distributions as defined here, it appears that treeline stands of whitebark pine are stable. In fact, it appears that the mountain pine beetle disturbance may enhance stability. Inspection of the direction of change of stand structure (Table 2-5) reveals that of the undisturbed stands, four of which were stable before the epidemic, three have destabilized and two show little change as assessed by goodness of fit to the negative exponential curve. Of the disturbed stands, four increased in stability, three decreased in stability, and two showed little change. Thus mountain pine beetle infestations may be beneficial for maintaining the self-replacing status of treeline stands. This is not surprising: while beetles reduce the absolute abundance of large diameter cone-bearing trees, the newly available growing space, and increased radiation may provide suitable caching sites for Clark's nutcracker and subsequent whitebark pine regeneration (see Chapter 3). Additionally, advance regeneration is released and survivors of the disturbance may be expected to increase in size. Implicit in this explanation of regeneration is that sufficient cone-bearing trees with viable seed are available to be cached. This is generally not problematic because nutcrackers will fly distances of up to 22 km (Vander Wall and Balda 1977, Tomback 1978, 1982, Hutchins and Lanner 1982) carrying seeds to cache in openings. Reproductive survivors of the epidemic were the likely seed sources for post-epidemic recruitment. Additionally, in younger, nonattacked stands, time lags until individuals become reproductive likely resulted in pulse recruitment. This explanation also assumes low variability in environmental conditions with respect to the generation time of trees.

Mechanistically this explanation is the same as the Romme et al. (1986) suggestion that mountain pine beetles regulate primary productivity in lodgepole pine forests.

The most recent beetle disturbance of ca. 1930 has been preceded by other beetle infestations. The oldest cross-dated death date of a whitebark pine killed by mountain pine beetles in this area before the ca. 1930 epidemic is 1819; two other trees that were probable beetle-kills died in 1887 and 1730 (Perkins and Swetnam 1996). Although there was only one tree per date for all three past events, it is reasonable to suggest that mountain pine beetle infestations are recurrent and cyclical in this species as they are in other hosts (Chapter 4). In this work, old remnant down logs and snags that were older than the ca. 1930 beetle-killed snags, and that did not have fire scars or charcoal may be indirect evidence of previous beetle-caused mortality. Further dendroecological and palynological research is needed to identify the magnitude, extent, and frequency of past mountain pine beetle infestations.

Stand-replacing fires adjacent to whitebark pine stands have historically spread to high-elevation stands either as small spot fires resulting in the death of small clumps of trees, or when fuel conditions and intensity permit, as larger stand-replacing fires (Arno and Hammerly 1984). Lightning strikes are also common and generally kill one to several trees. Wildfire charcoal remnants found on all sites are evidence that wildfire disturbances are affecting climax treeline whitebark pine forests either by stand-replacing events at mean fire return intervals ≥ 350 years (Barrett 1994, Romme 1982); 50 to 300 years (Arno 1986, Arno and Hammerly 1984); or on shorter intervals as gap-producing disturbances (Watt 1947, Arno 1986, Pickett and White 1985). Wildfires are infrequent in high-elevation subalpine ecosystems (Agee 1993); however, they are important and understudied processes affecting stand structure of treeline whitebark pine forests.

Although this work supports previous observations of whitebark pine as self-sustaining and as the climax dominant on cold, dry sites of the northern Rockies (Weaver and Dale 1974, Arno and Hoff 1989, Peet 1988, Steele et al. 1981), the presence of subalpine fir in all size classes suggests potential replacement of whitebark pine by subalpine fir or codominant status with whitebark pine. Successional replacement of whitebark pine by fir is possible, particularly in the absence of fire. Facilitation of subalpine fir by whitebark pine likely explains the co-occurrence of these species on abiotically stressed sites (Callaway 1998).

While temperature is most strongly associated with limiting physical treeline (Wardle 1974, LaMarche 1974, LaMarche and Stockton 1974, Tanquillini 1979, Stevens and Fox 1991) and species composition, it appears that disturbances are equally important in maintaining self-sustaining treeline whitebark pine populations.

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Table 2-1. Physical site attributes of sampled whitebark pine stands. Sites are: NRR = North Railroad Ridge, BLP = Blackman Peak, ASO = Assout Basin, CRS = The Cross, AND = Anderson Peak, BLK = Blackman Peak Beetle Kill, ABK = Anderson Peak Beetle Kill, SIL = Silver Peak, AVL = Avalanche Peak, TLK = Titus Lake Peak, GOA = Goat, TWP = Twin Peaks, BGH = Big Hill, RRB = Railroad Ridge Beetle Kill.

Mountain range	Site	Elevation (meters)	Aspect (deg)	Slope (deg)	Stand status	Longitude (UTM)	Latitude (UTM)	Number of plots
WC	NRR	2800	23	10	non-attacked	0695400	4891300	10
WC	BLP	2900	180	30	non-attacked	0687900	4880700	10
SR	ASO	2900	75	30	non-attacked	0707900	4927500	7
HW	CRS	2700	290	20	non-attacked	0683800	4861100	10
SM	AND	2900	300	15	non-attacked	0691700	4849500	7
WC	BLK	3000	200	30	attacked	0688800	4880500	8
SM	ABK	2900	320	20	attacked	0691600	4849300	7
BL	SIL	2800	260	30	attacked	0698000	4855400	7
HW	AVL	2700	180	17	attacked	0683800	4861800	10
HW	TLK	2900	290	20	attacked	0683300	4858100	8
SW	GOA	2700	125	30	attacked	0657900	4893700	8
SR	TWP	2900	180	20	attacked	0700300	4940400	8
SR	BGH	2900	240	20	attacked	0707200	4927800	8
WC	RRB	2900	135	25	attacked	0695600	4890300	3

Table 2-2. Regression statistics for reconstructed diameter at breast height ca. 1930,
 $n = 153$, $R^2 = 0.53$.

	Estimator	SE	T-Stat	p > T
Slope	1.08337	0.08337	12.3005	0.0001
Intercept	-2.2921	0.29047	-4.95125	0.0001

Table 2-3. Stand summary metrics for whitebark pine. The first five rows of the table are stands that were not attacked by mountain pine beetles ca. 1930. Abbreviations are *ba30*= basal area (m²/ha) ca. 1930, *tph30* = trees/ha, *mba30* = mean basal area, *dq30* = quadratic mean diameter (cm), *sdi30* = stand density index, *babk* = basal area of beetle killed whitebark pine, and *tphbk* = trees killed by beetle/ha. Abbreviations are the same for the 1998 equivalent metrics.

Site	<i>ba30</i>	<i>tph30</i>	<i>mba30</i>	<i>dq30</i>	<i>sdi30</i>	<i>babk</i>	<i>tphbk</i>	<i>ba98</i>	<i>tph98</i>	<i>mba98</i>	<i>dq98</i>	<i>sdi98</i>
NRR	3.4	178	0.05	15	33	0	0	26.6	640	0.10	23	221
BLP	3.9	195	0.05	16	38	0	0	29.2	687	0.11	23	241
ASO	4.6	27	0.41	46	30	0	0	12.9	642	0.05	16	123
CRS	5.1	210	0.06	18	47	0	0	26.6	477	0.14	27	208
AND	6.7	289	0.06	17	63	0	0	39.5	714	0.14	26	309
ABK	13.1	403	0.08	20	114	12.2	338	11.0	289	0.09	22	93
SIL	14.0	272	0.13	26	111	11.5	188	11.0	158	0.17	30	83
AVL	16.3	356	0.11	24	132	10.6	143	28.9	506	0.14	27	226
TLK	16.5	195	0.21	33	119	14.7	101	16.8	454	0.09	22	143
GOA	18.4	124	0.37	44	119	16.8	59	8.5	136	0.15	28	64
TWP	21.6	257	0.21	33	156	20.4	183	9.2	249	0.09	22	78
BLK	26.4	316	0.21	33	190	25.3	249	9.6	343	0.07	19	87
BGH	32.1	479	0.17	29	242	30.3	380	12.4	331	0.09	22	106
RRB	50.3	889	0.14	27	393	46.8	734	15.4	222	0.17	30	115

Table 2-4. Regression statistics for the age-diameter relationship of whitebark pine. $n = 87$, $R^2 = 0.55$.

	Estimator	SE	T-Stat	p > T
Slope	-47.6329	18.3289	-2.59878	0.0110273
Intercept	42.5113	4.18629	10.1549	0.0001

Table 2-5. Coefficients of determination for
the natural log fit of the negative
exponential to the midpoints of
whitebark pine diameter classes.

Site	Stand status	1930 R^2	1998 R^2
AND	nonattacked	0.93	0.72
ASO	nonattacked	0.99	0.94
BLP	nonattacked	0.88	0.85
CRS	nonattacked	0.96	0.27
NRR	nonattacked	0.92	0.46
ABK	attacked	0.61	0.76
AVL	attacked	0.93	0.87
BGH	attacked	0.93	0.91
BLK	attacked	0.76	0.97
GOA	attacked	0.73	0.59
RRB	attacked	0.50	0.68
SIL	attacked	0.82	0.63
TLK	attacked	0.69	0.84
TWP	attacked	0.80	0.79

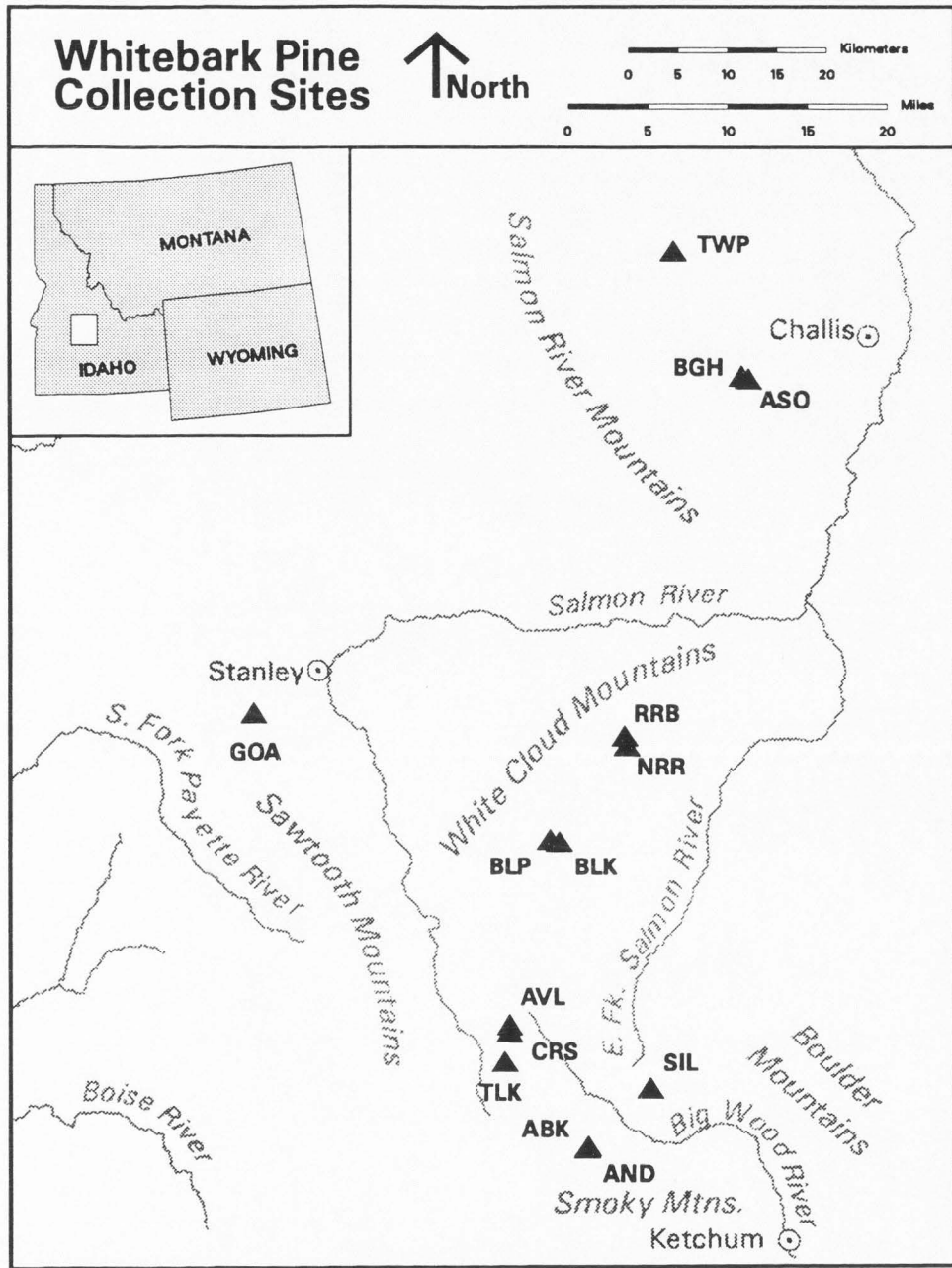


Fig. 2-1. Central Idaho study area and sampled whitebark pine sites.

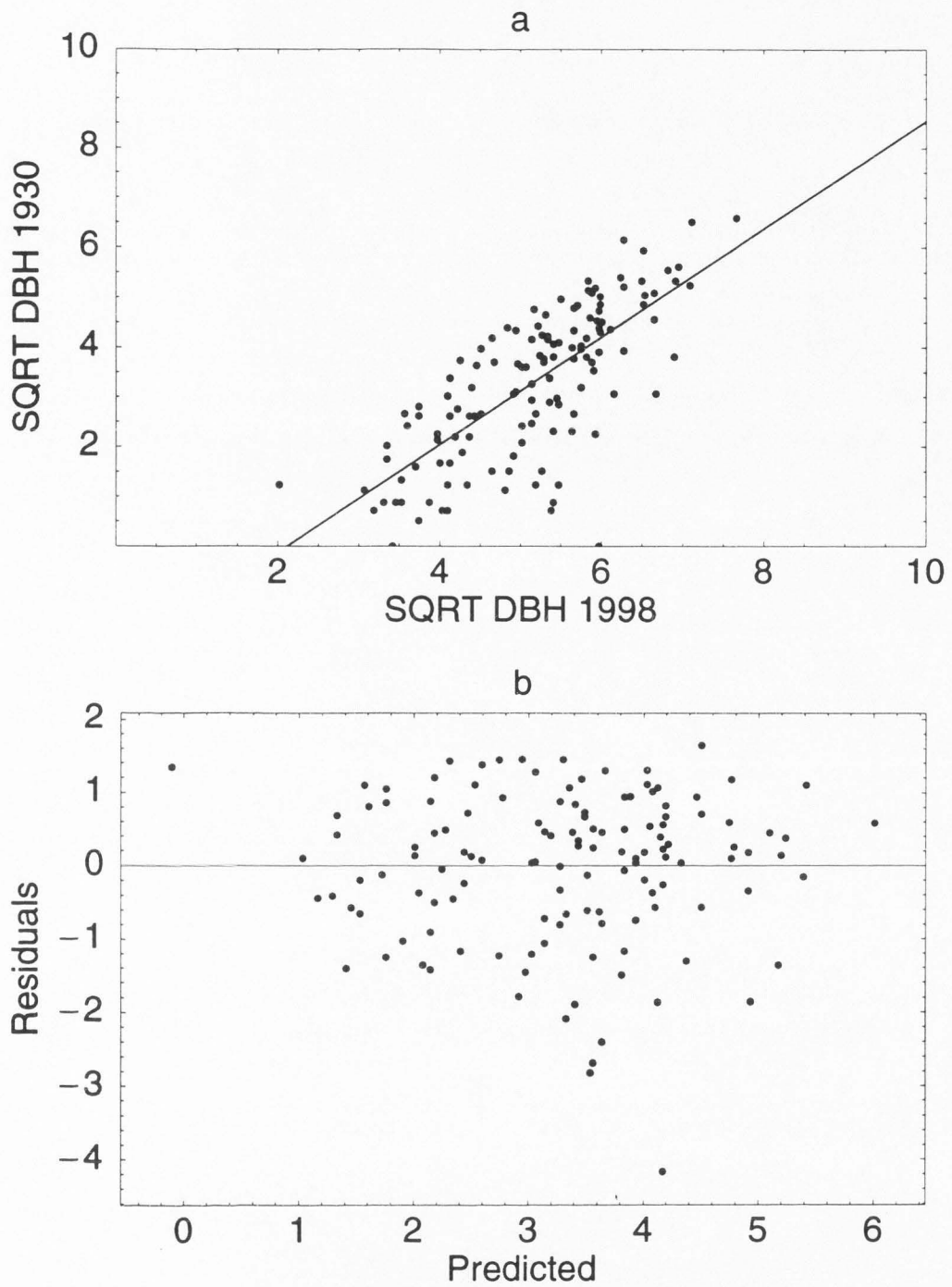


Fig. 2-2. a) Whitebark pine least square regression of diameter classes ca. 1930 against diameters in 1998. b) Residual *versus* predicted values of the regression.

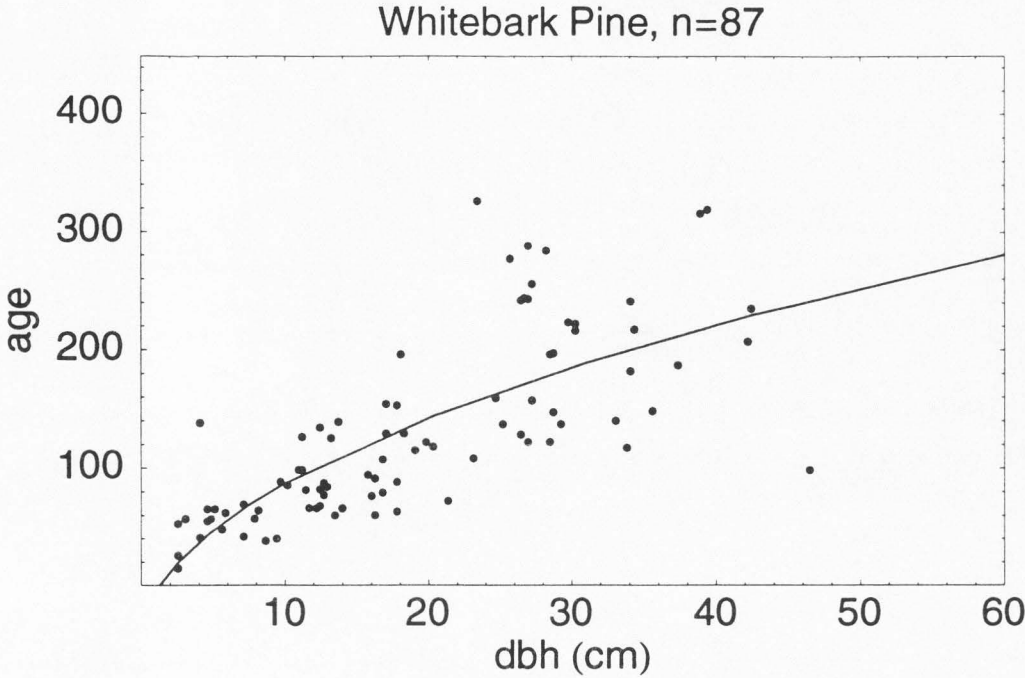


Fig. 2-3. Age-diameter regression for whitebark pine from fourteen near treeline stands in the Sawtooth Salmon River Region. $Age = -47.6329 + 42.5113\sqrt{DBH}$. $R^2 = 0.55, n = 87$.

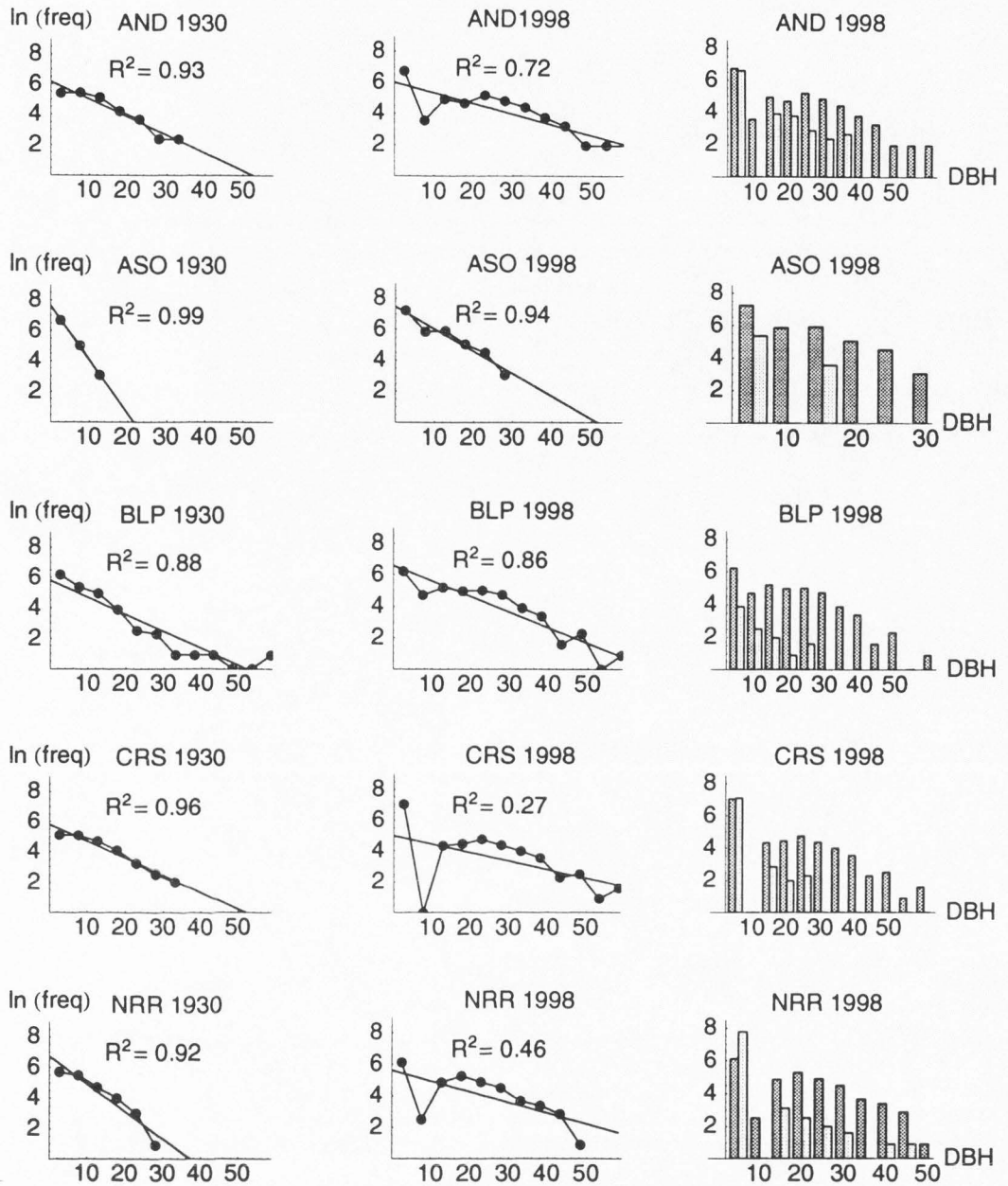


Fig. 2-4. Size-frequency distributions of whitebark pine ca. 1930 and 1998 (left and center column) from the five undisturbed stands. Points are midpoints of 5 cm diameter size classes. The straight line is the regression fit to the natural log frequency of midpoints of the size classes. The right column is the same 1998 whitebark pine size class data plotted as a histogram (dark grey bars) with subalpine fir (light grey bars).

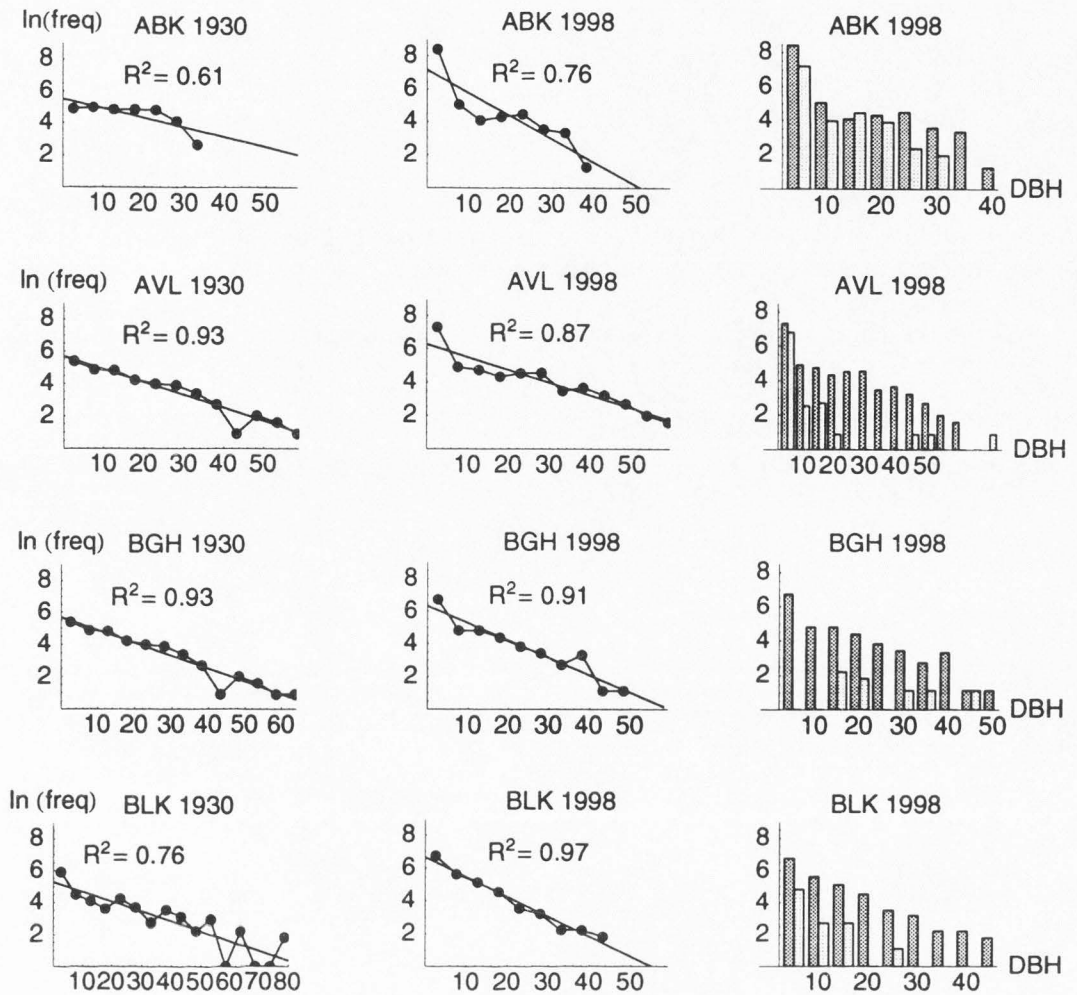


Fig. 2-5. Size-frequency distributions of whitebark pine ca. 1930 and 1998 (left and center column) from the nine mountain pine beetle disturbed stands. Points are midpoints of 5 cm diameter size classes. The straight line is the regression fit to the natural log frequency of midpoints of the size classes. The right column is the same 1998 whitebark pine size class data plotted as a histogram (dark grey bars) with subalpine fir (light grey bars).

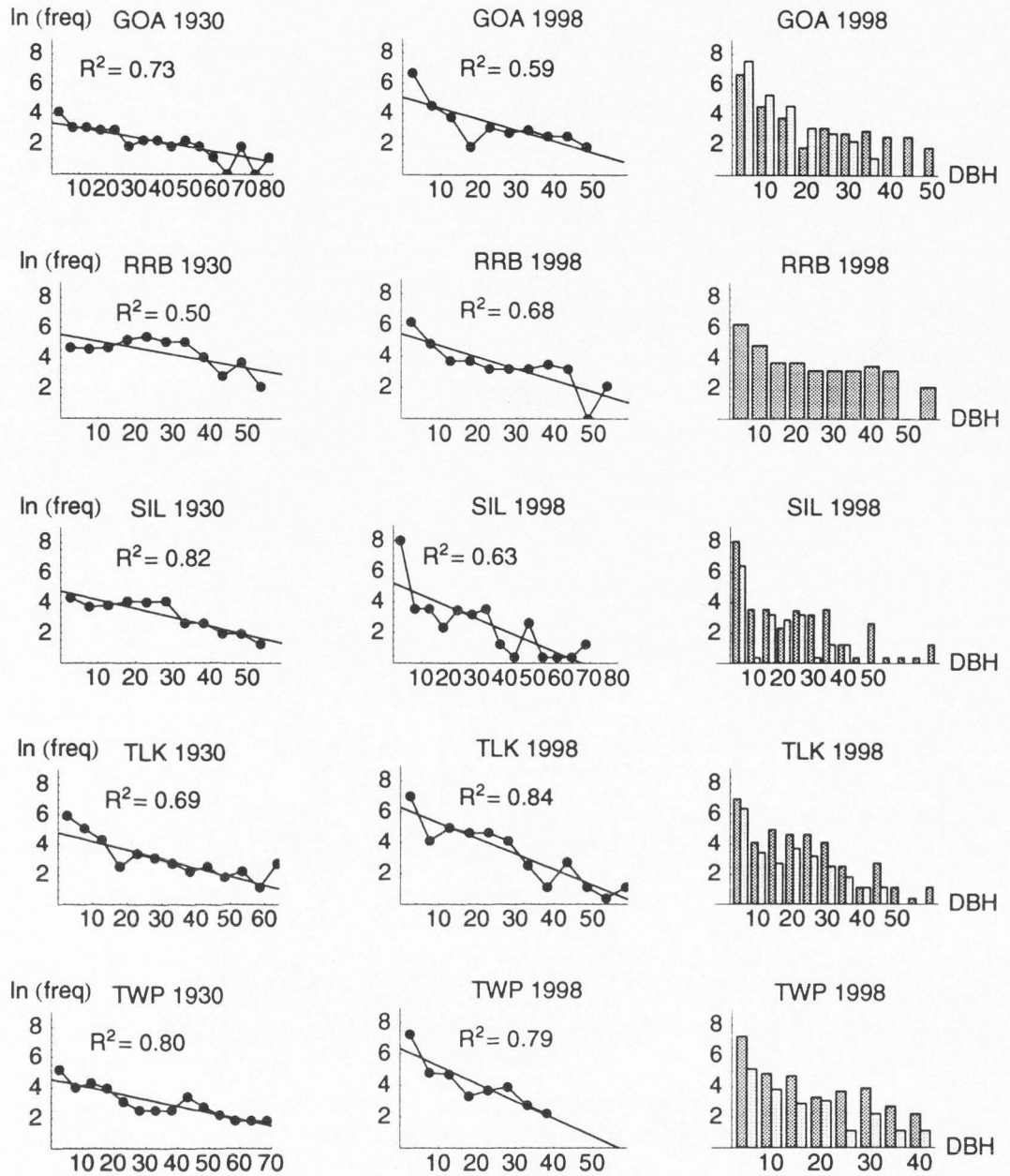


Fig. 2-5. Continued.

CHAPTER 3

PREDICTIVE MODELS OF SEEDLING RECRUITMENT OF WHITEBARK PINE
AND SUBALPINE FIR IN TREELINE STANDS IN CENTRAL IDAHO

Abstract. The influence of environmental factors and stand structure on whitebark pine (*Pinus albicaulis* Engelm.) and subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.) seedling density was analyzed with generalized linear and generalized additive models. Whitebark pine seedling densities on treeline stands in central Idaho were negatively correlated with the density of live trees (per 0.04 ha) and dead tree basal area (m^2/ha), and positively correlated with density of dead trees (per 0.04 ha) ($p \leq 0.001$). Subalpine fir seedling densities were negatively correlated with elevation and positively correlated with northerly aspects ($p \leq 0.001$). Stand structure variables appear to be more important for whitebark pine establishment which may be constrained by interference competition and available growing space. Subalpine fir establishment appears to be influenced by distance to seed source at lower elevations and by favorable site water-balance effects on northerly aspects.

INTRODUCTION

Seedling recruitment, the establishment of new individuals in a plant community, affects community composition, succession and population dynamics. Following disturbance, the species that become established define the initial conditions of the successional trajectory. On high-elevation treeline sites in the northern Rocky Mountains, whitebark pine (*Pinus albicaulis* Engelm.) is considered the climax dominant and is generally self-replacing (Chapter 2). Natural disturbances including wildfire, mountain pine beetle (*Dendroctonus ponderosae*) (Coleoptera: Scolytidae) infestations, avalanches, and windthrow reduce site biomass, which increase radiation loads, and provide growing

space for shade intolerant whitebark pine seedlings. For whitebark pine, seedling recruitment also depends on: (1) the productivity and periodicity of seed crops (Weaver and Dale 1974, Weaver and Forcella 1986); (2) the population levels of Clark's nutcracker (*Nucifraga columbiana*) and their caching behavior and retrieval of whitebark pine seeds (Tomback 1978, 1982, Lanner 1980, Hutchins and Lanner 1982, Tomback et al. 1990); (3) the probability of viable seed germinating (McCaughey and Weaver 1990, McCaughey 1993); (4) and the 'safe site' (Harper 1977) conditions of the environment (McCaughey and Weaver 1990).

The influence of site conditions on whitebark pine and subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.) seedling recruitment is investigated in this paper.

Environmental site variables and stand structure characteristics were used as independent variables in generalized linear models (GLM—McCullagh and Nelder 1989) and generalized additive models (GAM—Hastie and Tibshirani 1990) to predict both whitebark pine and subalpine fir seedling density. Identification of variables associated with high seedling density is expected to be useful for restoration and conservation activities and for understanding ecological mechanisms structuring whitebark pine communities at upper treeline.

Background

Whitebark pine is a stone pine (subgenus *Strobus*, section *Strobus*, subsection *Cembrae*) of subalpine forests and timberlines of the northwestern United States and southwestern Canada. It is one of five stone pines worldwide and the only stone pine in North America. Whitebark seeds are not wind dispersed; they develop in indehiscent cones that are harvested by nutcrackers and squirrels (Arno and Hoff 1989, Reinhart and Mattson 1990). Nutcrackers cache or consume seeds and those not retrieved from caches may germinate to become seedlings (Lanner 1980, Tomback 1978, 1982, Lanner 1996).

Corvids, such as Clark's nutcracker and other *Nucifraga spp.*, have evolved with Cembrae pines over centuries and are critical components in pine regeneration dynamics, ultimately responsible for the geographic range, spacing, successional status, and genetics of the stone pines (Hutchins and Lanner 1982, Lanner 1982, Tomback 1982, Lanner 1996). Red squirrels (*Tamiasciurus hudsonicus*) also cut cones from trees and bury them in middens, but little regeneration results from their caching activities (Lanner 1996). Nutcrackers cache and recover whitebark pine seeds year-round from forest floor sites, burns, along meadow edges, in clearcuts, above treeline and on rocky outcrops (Hutchins and Lanner 1982). A preference for caching on south slopes and in openings has been documented (Vander Wall and Balda 1977, Tomback et al. 1993). Nutcrackers may fly up to 22 km from source seed trees to cache seeds (Vander Wall and Balda 1977, Tomback 1978, 1982). While nutcrackers are the primary regulator of seed distribution, environmental site conditions are the primary factors limiting successful establishment.

Regional attention to whitebark pine population levels has been stimulated by reports that current environmental conditions have led to higher rates of mortality than establishment (Arno 1986, Keane et al. 1990, Keane and Arno 1993, Keane et al. 1994). Recognized factors causing whitebark pine decline in the northern Rocky Mountains include an exotic fungus, white pine blister rust (*Cronartium ribicola*), infestation of whitebark pine by mountain pine beetle, and successional replacement by shade tolerant species as a result of fire suppression policies (Arno and Hoff 1989, Keane et al. 1990, Morgan and Bunting 1990, Keane and Arno 1993, Kendall and Arno 1990). Blister rust acts as a confounding factor in seedling establishment dynamics (Tomback et al. 1995) so that natural variability of factors affecting recruitment in treeline communities is best assessed in areas of low blister rust incidence.

While white pine blister rust is the most common exotic threat to whitebark pine, mountain pine beetle is the most common natural damaging agent that kills trees (Arno and Hoff 1989). Mountain pine beetles devastated whitebark pine forests in a widespread epidemic of the 1920-1940s from southern Canada to northern Wyoming (Arno 1970, Ciesla and Furniss 1975, Arno and Hoff 1989). Throughout its northern Rocky Mountain distribution, a high percentage of whitebark pine dominants was killed (Arno 1986). In central Idaho a dendrochronologically determined maxima of beetle-caused mortality occurred in 1930 (Perkins 1995, Perkins and Swetnam 1996) where stands with large diameter trees and high basal area were generally more likely to be attacked (Chapter 4). However, not all whitebark pine stands were attacked in this epidemic; a mosaic of disturbed and nondisturbed stands exists across the high-elevation landscape in this region (Chapter 4). In disturbed stands, the structural characteristics, such as the abundance, size, and spacing of beetle-killed snags, are different from stands that were not disturbed. Such differences are expected to affect microsite characteristics and the success of seedling establishment.

The principal codominant with whitebark pine on treeline sites in the northern Rocky Mountains is subalpine fir. Facilitation of subalpine fir by whitebark pine may explain the co-occurrence of these species on high-elevation, abiotically stressed sites (Callaway 1998). Large subalpine fir are 2-4 times more aggregated with live and dead whitebark pine than are seedlings (Callaway 1998). Winter snowpack likely protects seedlings from wind and blowing ice and snow, but once trees grow above the average snow depth they become increasingly vulnerable to winter damage without the protection of larger whitebark pine. Subalpine fir was present in all size classes on climax whitebark pine stands in central Idaho (Chapter 2). Potential increases in abundance may occur in the absence of fire and with climate change.

The assessment of stand structure characteristics and environmental site variables in relation to subalpine fir and whitebark pine seedling densities is expected to be useful for evaluating establishment potential of these species on high elevation sites. The use of the GLM and GAM methods is intended to enhance understanding of biotic and abiotic mechanism affecting seedling recruitment and, secondly, to serve the purpose of prediction (Hilborn and Mangel 1997).

METHODS

Study Area

A central Idaho study area was chosen because field surveys from 1995-1997 showed that white pine blister rust was only present in low amounts (Smith 1997, Smith and Hoffman 2000, Perkins pers. observ.). Accordingly, its effects as a confounding factor of whitebark pine regeneration is currently negligible. However, many of these stands experienced high mortality of large diameter trees in the widespread mountain pine beetle epidemic between 1920 and 1940 (Ciesla and Furniss 1975, Arno 1986). Evidence of the epidemic is still apparent 70 years later with ghost forests of persistent snags. Because not all high-elevation stands were attacked in this epidemic (Chapter 4), a mixture of attacked and nonattacked stands was sampled to provide a comparison of the effects of disturbance on recruitment success.

Fourteen treeline whitebark pine stands located within the Sawtooth National Recreation Area, the Sawtooth National Forest, and the Challis National Forest were sampled during the field season of 1998 (Fig. 2-1). Stands were located in six mountain ranges within the study area. Four sites were located near summits in the White Clouds Mountains (WC), three in the Headwater Mountains (HW), two in the Smoky Mountains (SM), three in the Salmon River Mountains (SR), one in the Boulder Mountains (BM),

and one in the Sawtooth Mountains (SW) (see Fig. 2-1). The Headwater Mountains are not identified in Fig. 2-1; they were considered either part of the Sawtooth or Smoky Mountains and form the divide between the Salmon and Big Wood rivers. Elevations ranged from 2,700 to 3,000 m (8,800 to 9,800 ft). Stand names and physical site attributes are summarized in Table 2-1.

Sample stand selection criteria were the following: (1) whitebark pine was the dominant species with composition greater than or equal to 60% of total basal area; (2) stand elevations were between 2,700 m (8,800 ft) and an upper edaphic treeline bordering an unvegetated rock ridgetop; (3) stand extent was as large an area as possible with homogenous structure, constant aspect and slope; (4) tree form was upright (krummholz form trees were not sampled); (5) mountain pine beetle attacked and nonattacked stands within the same watershed were chosen whenever possible. The last criterion was relevant to objectives characterizing host susceptibility in Chapter 4. Here the importance of disturbed stands was for assessing structural differences as related to recruitment densities following disturbance. Beyond these criteria, selection of sites was restricted by access within a day. Aerial photographs and ground reconnaissance or both were used to identify potential stands. Attacked and nonattacked stands were differentiated by abundance of whitebark pine snags with visible J-shaped adult beetle galleries and lack of fine limbs. The first criterion, adult galleries, had been used previously to determine beetle attack (Perkins 1995, Perkins and Swetnam 1996) and the second, no fine limbs, was a consistently observed characteristic of trees killed in the 1920-1940 period. Stands composed of $\geq 15\%$ beetle-killed snags were considered attacked stands; stands composed primarily of living whitebark pines with few beetle killed trees were considered nonattacked stands. These were readily identifiable on aerial photographs. Selected stands often extended below 2,700 m (8,800 ft) but were not sampled below this elevation

because in this geographic region their character was distinctly seral. Implicit in the near-treeline criterion is the idea that these stands represent the climax whitebark pine community (Whittaker 1975, Steele et al. 1981).

The study area in central Idaho region is semiarid with an average annual precipitation of 82 cm (32 in.) and ranges from less than 38 cm (15 in.) in the southern section and valleys to greater than 152 cm (60 in.) on some mountain peaks. Most precipitation falls as snow and rain during winter and spring; at elevations above 2,700 meters, most precipitation falls as snow. Annual temperatures range from average minimum of -6°C (22°F) to average maximum of 8°C (46°F) with an mean of 2°C (36°F) (Steele et al. 1981). Extreme cold temperatures of -34° to -47°C (-30° to -50°F) are recorded from December through February (Steele et al. 1981). Winds redistribute snow around whitebark pine trees to form snowdrifts that may linger until July and occasionally August. Granitic bedrock of the Sawtooth and Idaho Batholiths forms the core of the study area, with Tertiary volcanic and sedimentary forms on southerly and easterly ranges (Williams 1961).

Across the study area, tree associates are lodgepole pine (*Pinus contorta* Dougl.) subalpine fir, Douglas-fir (*Pseudotsuga menziesii* (Mirbel) Franco), and Engelmann spruce (*Picea engelmannii* Parry). Habitat types are in the PIAL/ABLA or PIAL series (Steele et al. 1981, 1983). Landscape assessment on the Sawtooth National Forest and Sawtooth National Recreation Area identified 3.8% of the area as climax whitebark pine vegetation (Redmond et al. 1997).

Field Collections

Seven to ten 0.04-ha (1/10 acre) plots with a nested 0.008-ha (1/50 acre) subplot were established randomly on each site, except for one site (RRB) which only had three plots. For each plot, elevation, aspect, slope, and location coordinates were recorded. On

each 0.04-ha plot, the diameter at breast height (DBH, 1.5 m (4.5 ft) above ground surface) and species of all trees ≥ 10.2 cm (4.0 in) were recorded; on each 0.008-ha plot the DBH, height, and species of all trees less than 10.2 cm DBH (4 in) were recorded. In total 109 plots were sampled. Individual trees were recorded as attacked and killed by mountain pine beetles *versus* not attacked.

Analyses

Basal area for the local per 0.04 ha (1/10 acre) of live and dead trees (*lbplt* and *dbplt*), and density of live and dead trees per 0.04 ha (*ltplt* and *dtplt*) were calculated from basic sample data and employed to characterize the local canopy structural components surrounding the smaller seedling plot. Aspect (deg) was transformed to aspect value (*av*) as: $av = \cos(\text{aspect} - 30)$. Aspect values range from -1 to 1 ; an aspect value of zero represents WNW (300 deg) and ESE (120 deg) aspects while an aspect value of 1 represents NNE (30 deg) aspects and -1 represents SSW (210) aspects. Aspect values of zero are similar in terms of site radiation loads and site water balance during the growing season.

Environmental site variables aspect value (*av*), slope (*sl*), and elevation (*el*); structural characteristics (*ltplt*, *dtplt*, *lbplt*, *dbplt*); stand disturbance status (attacked or not attacked by mountain pine beetles); and site were assessed as independent variables in both generalized linear and generalized additive models to predict seedling densities. Because the response variable is a count ≥ 0 of seedlings, the models were fit as a Poisson regression. The generalized linear Poisson model (GLM) is written:

$$\ln(\mu) = b_0 + b_1x_1 + b_2x_2 + \dots b_nx_n,$$

so that

$$\mu = e^{(b_0 + b_1x_1 + b_2x_2 + \dots b_nx_n)}$$

The general form for a GLM is:

$$g(\mu) = \alpha + \beta^T \mathbf{x} = \alpha + \sum_{i=1}^n \beta_i x_i$$

where $g(\mu)$ is the link function that relates the mean of the response variable to the predictors, α is the intercept or constant term, β^T is the vector of regression (or slope) coefficients, and \mathbf{x} is the vector of independent variables. General additive models (GAMs) were compared to the GLMs because nonlinearities in the response could be extracted in a non-parametric, data-driven manner. Thus these models allow the data to determine the shape of the response curve, but reduce the degrees of freedom to fit the model and are less parsimonious.

The general form for a GAM is:

$$g(\mu) = \alpha + \sum_{i=1}^n f_i(x_i)$$

The GAM is a sum of non-parametric smoothing functions $f_i(x_i)$ developed for smoothing scatterplots (Yee and Mitchell 1991), where α and $g(\mu)$ are as above for the Poisson regression. Analyses of deviance methods (Hastie and Pregibon 1992) were used to determine the most parsimonious model and to test for significance of all parameters. To approximate the general linear model goodness of fit statistic, the coefficient of determination, R^2 , for the Poisson regression models, a quasi R^2 was calculated as: $1 - (\text{residual deviance}/\text{null deviance})$ (Yee and Mitchell 1991).

RESULTS

Whitebark pine seedling density was negatively correlated with $ltplt$, $dbplt$, and positively correlated with $dtplt$. The GLM model for whitebark pine seedling density (μ_w) is:

$$\mu_w = e^{(2.99942 - 0.03418ltplt - 1.41723dbplt + 0.08638dtplt)}$$

with a quasi R^2 of 0.30.

Subalpine fir seedling density is negatively correlated with elevation and positively correlated with northerly aspects. The GLM model for subalpine fir seedling density (μ_s) is:

$$\mu_s = e^{(25.25753 - 0.00251el + 0.98764av)}$$

with a quasi R^2 of 0.45. The contribution of the independent variables to the predicted whitebark pine densities is shown in Fig. 3-1 and similarly for subalpine fir in Fig. 3-2. Analyses of deviance of the model predictors with the chi-square test statistic (Venables and Ripley 1999) demonstrated statistical significance ($p \leq 0.001$) for all terms included in the models.

As expected, the GAMs achieved a lower residual deviance than the GLMs although at a cost of higher residual degrees of freedom. The GAM model for whitebark pine seedling density (with the same predictors as the GLM) reduced the residual deviance from 670.90 to 525.49, with a reduction of 9 degrees of freedom and raised the quasi R^2 from 0.30 to 0.45 (Table 3-1). The GAM model for subalpine fir seedling density reduced the residual deviance from 706.12 to 660.62, with a reduction of 6 degrees of freedom and raised the quasi R^2 from 0.45 to 0.49 (Table 3-1).

Seedling density decreases strongly from 0 to 20 live trees per plot and decrease more slowly beyond 20 (Fig. 3-3). For the whitebark pine GAM, when $dbplt$ and $dtplt$ are held at their mean (solid line Fig. 3-3 upper left), the effect of density of live trees is higher than when they are held at their minimum (stippled line Fig. 3-3 upper left). At their maximum values (dotted line Fig. 3-3 upper left), the effect of the density of live trees is reduced. Seedling density decreased strongly from 0 to 0.6 m² dead basal area per plot and decreased more slowly beyond 0.6 basal area. When $ltplt$ and $dtplt$ are held constant at the three levels, seedling density is highest when dead tree basal area is low

(Fig. 3-3 upper right). Seedling density increases strongly from 0 to ≈ 15 dead trees per plot and decreases less strongly beyond 15 trees. Fig. 3-3 (lower left) shows the greatest difference in the effects of the density of dead trees with respect to constant mean and maximum *ltptl* and *dbplt* on seedling density. At the maximum number of live trees and the maximum dead tree basal area (dotted line) there are almost no seedlings, i.e. there is almost no contribution of density of dead trees to the predicted seedling density. However at mean levels of the *ltptl* and *dbplt* seedling density increases significantly with dead tree density. The minimum level is not plotted because when dead tree basal area is at its minimum, i.e. zero, the number of dead trees must also be zero.

Plots of the contribution of elevation to subalpine fir seedling abundance while holding aspect value at its mean (westerly aspect), minimum (southerly aspect), and maximum (northeasterly aspect) revealed that seedling densities were highest on lower elevation sites (Fig. 3-4) on northeasterly aspects (Fig. 3-4). This is the same result as shown in the parametric log-linear model.

Evidence of the random distribution of residuals and the 95% confidence limit for the GAM models is shown in Figs. 3-5 and 3-6. As the number of samples decreases, the confidence interval widens. Comparisons of the fitted GLM and GAM for both species models revealed little difference in the shape of the response curves (Fig. 3-1 vs 3-3 and Fig. 3-2 vs 3-4). The slight irregularities of the GAMs are not distinct departures from the general shape of the GLMs and are likely sampling effects.

The models presented above are parsimonious and general, but they do not explain a high degree of deviance. The inclusion of site as a categorical variable showed that differences among sites were significant and improved the goodness of fit for both species models. For the whitebark pine log-linear model, the residual deviance was reduced from 671 to 394 and the quasi R^2 increased from 0.30 to 0.59. For the subalpine

fir log-linear model, the residual deviance was reduced from 706 to 535 and the quasi R^2 increased from 0.45 to 0.59. Similar reductions in deviance are shown when seedling density is modeled by the GAMs (Table 3-1). The addition of site to the subalpine fir models confounded the response to aspect value. With elevation and aspect value as the only independent variables, subalpine fir density was positively associated with northwesterly to northeasterly aspects. When site was added, seedling densities were positively associated with southwesterly as well as northerly aspects. Sites ABK (NW aspect) and SIL (SW aspect) had higher abundances of whitebark pine seedlings and sites GOA (SE aspect) and NRR (NE aspect) had higher abundances of subalpine fir seedlings than all other plots and likely contribute to the confounding effects of site as a predictor variable (Figs. 3-7 and 3-8).

DISCUSSION

Stand structure variables, live trees per plot (*ltplt*), dead trees per plot (*dtplt*) and dead basal area per plot (*dbplt*), were the best predictors of seedling density for whitebark pine. Environmental site variables, aspect value (*av*) and elevation (*el*) were the best predictors of seedling density for subalpine fir. Disturbance history (whether the stand was attacked by mountain pine beetles or not), was not a significant predictor variable for either species.

The assessment of whitebark pine seedling densities in climax treeline whitebark pine stands supports previous work that whitebark pine recruitment is higher on open sites (Tomback 1978, Arno 1986, McCaughey and Weaver 1990, Tomback et al. 1990, 1993, Arno 1986). Inverse correlations with stand structure variables (*ltplt*, *dbplt*) may be explained by biotic and abiotic mechanisms: low whitebark pine seedling densities may be attributed in part to interference competition for light and below ground resources with live trees, and to shading from the large diameter snags. Shading from both live and dead

trees reduces incident radiation and lowers ambient air temperatures on already cool high-elevation sites, thus limiting growth. However, shade cast by some dead trees (the positive association with *dtplt*) may be beneficial to seedling establishment by reducing evapotranspiration. McCaughey (1993) found that seedling establishment was enhanced by partial shade in experimental plots. Another explanation is that dead trees serve as landmarks and visual cues for nutcrackers to retrieve seeds from caches (Vander Wall 1982, Balda and Kamil 1989, Kamil and Jones 1997) Snags are also used by nutcrackers to wipe the pine cone resin off their bills (pers. obser., Tomback 1982) and a behavioral preference for caching in stands with some dead snags is reasonable.

The result that subalpine fir seedling density was negatively correlated with elevation suggests that habitat is unsuitable or that proximity to seed source at lower elevations is important to recruitment success. This is not surprising nor is the fact that recruitment densities are higher on northerly aspects where cool and moist conditions are favorable to seedling germination. More interesting is the lack of facilitation of subalpine fir seedlings by whitebark pine as measured by stand structural variables. This result supports Callaway's (1998) findings that seedlings may be protected from blowing snow and ice while trees are small and below the snow surface, and do not require facilitation.

Site confounds the response of subalpine fir seedling density to aspect value and is not easily interpreted. Multivariate interactions between site variables are common in ecological systems. Unmeasured variables are likely correlated with sites. Expanding the set of potential predictor variables to include amount of bare mineral soil, type of substrate, and amount and type of understory vegetation (McCaughey and Weaver 1990, McCaughey 1993, Tomback et al. 1993) may reveal associations of environmental variables significant to recruitment success that were not considered here.

For the subalpine tree species and the set of predictor variables used in this analysis, the parametric GLM models are more parsimonious and are preferred over the GAM models. While the GAM models produced a better fit as determined by the goodness of fit statistic, the overall shape of the non-parametric curves did not reveal any significant improvements over the log-linear GLM. Both species models were calibrated from treeline sites in the geographic area of central Idaho, and require validation with independent data outside the region.

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Table 3-1. Summary statistics of Poisson regressions GLMs and GAMs. Abbreviations:
 wb = whitebark pine, sf = subalpine fir, df = degrees of freedom displayed in parenthesis.

Model	Null deviance	Residual deviance	Quasi R^2
GLMs			
$wb = f(ltplt, dbplt, dtplt)$	958 (108)	671 (105)	0.30
$sf = f(el, av)$	1294 (108)	706 (106)	0.45
$wb = f(ltplt, dbplt, dtplt, site)$	958 (108)	394 (92)	0.59
$sf = f(el, av, site)$	1294 (108)	535 (93)	0.59
GAMs			
$wb = f(s(ltplt), s(dbplt), s(dtplt))$	958 (108)	524 (96)	0.45
$sf = f(s(el) + s(av))$	1294 (108)	661 (100)	0.49
$wb = f(s(ltplt), s(dbplt), s(dtplt), site)$	958 (108)	329 (83)	0.66
$sf = f(s(el), s(av), site)$	1294 (108)	494 (87)	0.62

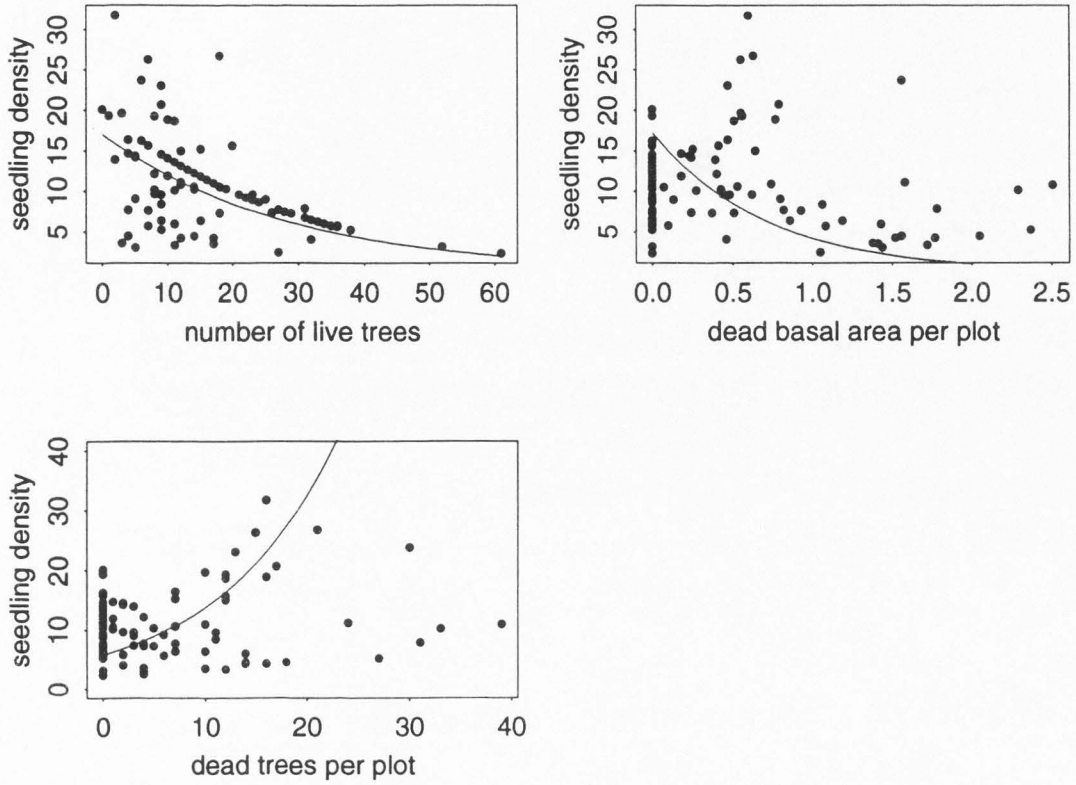


Fig. 3-1. Log-linear model of seedling densities of whitebark pine. Each frame shows the contribution of each of the independent variables to the predicted seedling density while holding the other variables constant at their mean. The log-linear equation is $\mu_w = e^{(2.99942 - 0.03418ltplt - 1.41723dbplt + 0.08638dtplt)}$

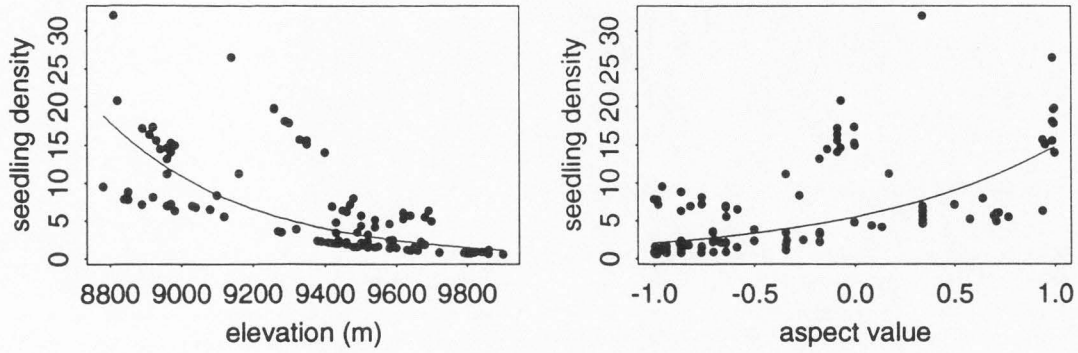


Fig. 3-2. Log-linear model of seedling densities of subalpine fir showing the contribution of each of the independent variables to the predicted seedling density while holding the other variables constant at their mean. The log-linear equation is

$$\mu_s = e^{(25.25753 - 0.00251el + 0.98764av)}$$

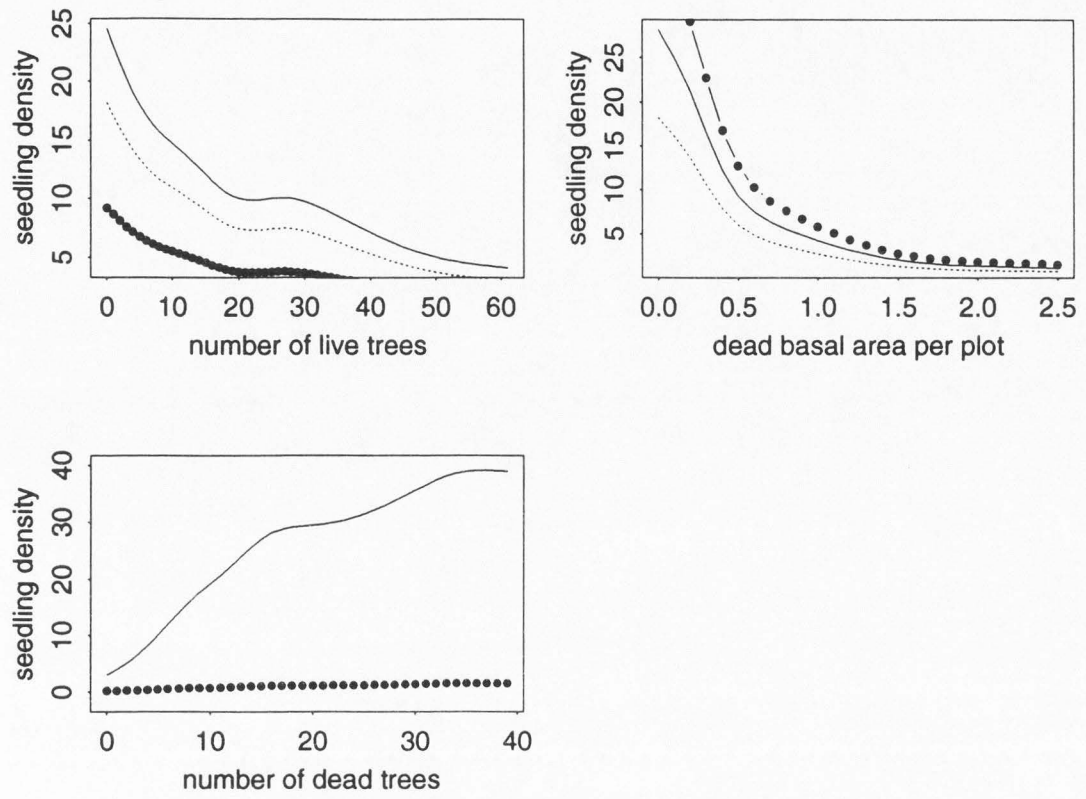


Fig. 3-3. Generalized additive model of whitebark pine seedling densities. Each line represents the contribution of the independent variable while holding the other variables at their mean (solid line), minimum (stippled line) and maximum (dotted line).

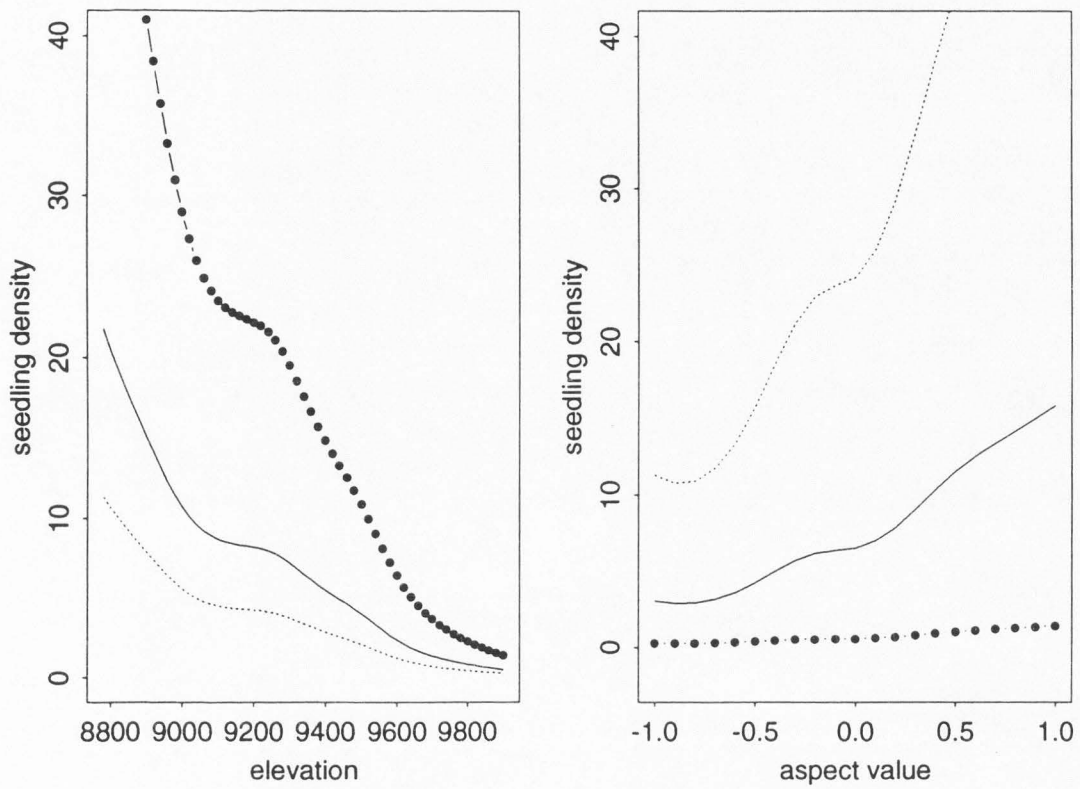


Fig. 3-4. Generalized additive model of subalpine fir seedling densities. The solid line represents the contribution of one independent variable while holding the other variable at its mean (solid line), minimum (stippled line) and maximum (dotted line).

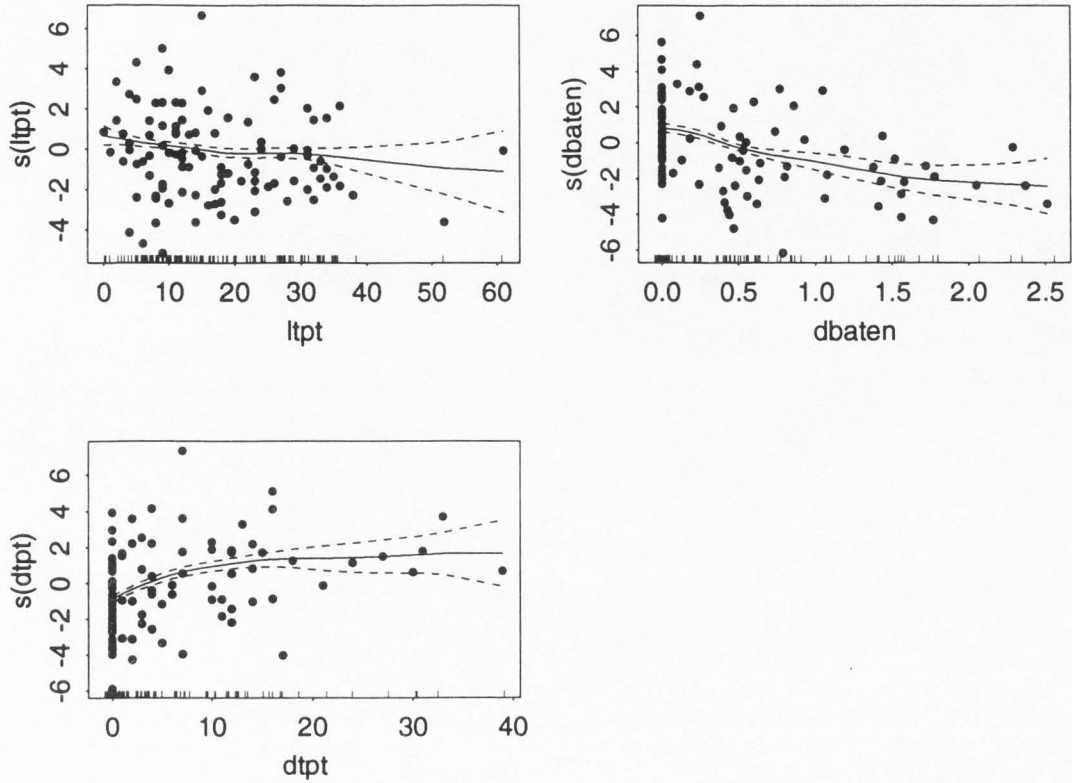


Fig. 3-5. Fitted function of the log of whitebark pine seedling densities and with confidence limits (stippled line) and residuals displayed (points).

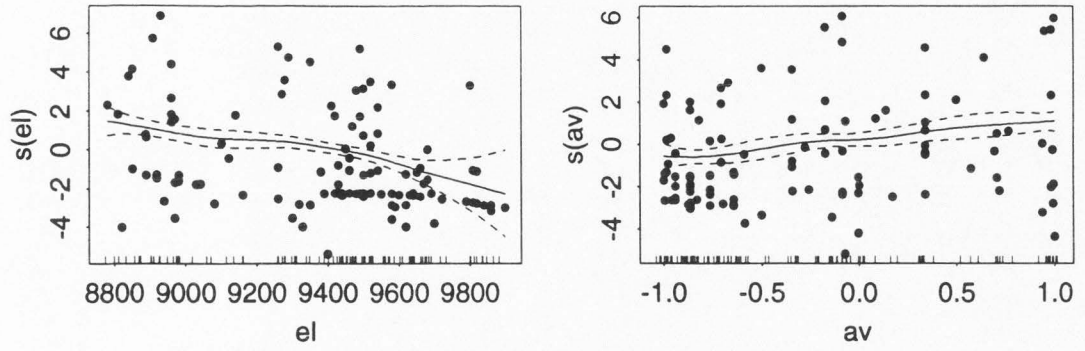


Fig. 3-6. Fitted function of the log of subalpine fir seedling densities and with confidence limits (stippled line) and residuals displayed (points).

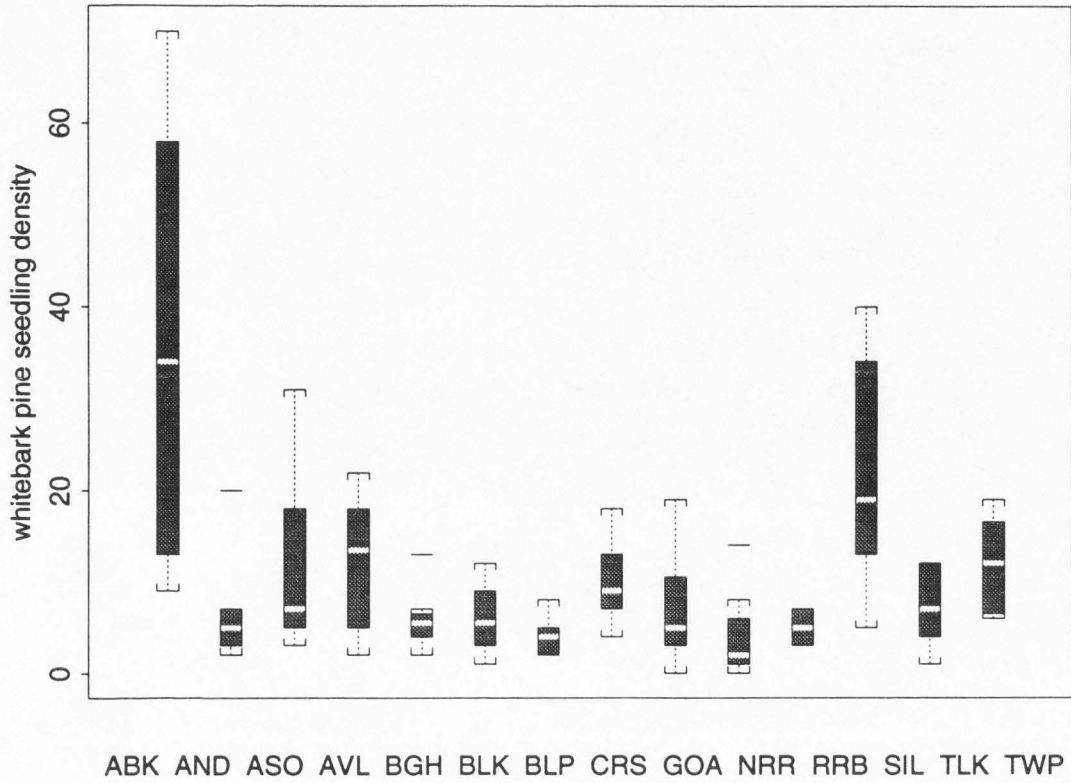


Fig. 3-7. Box plots of observed densities of whitebark pine seedlings.

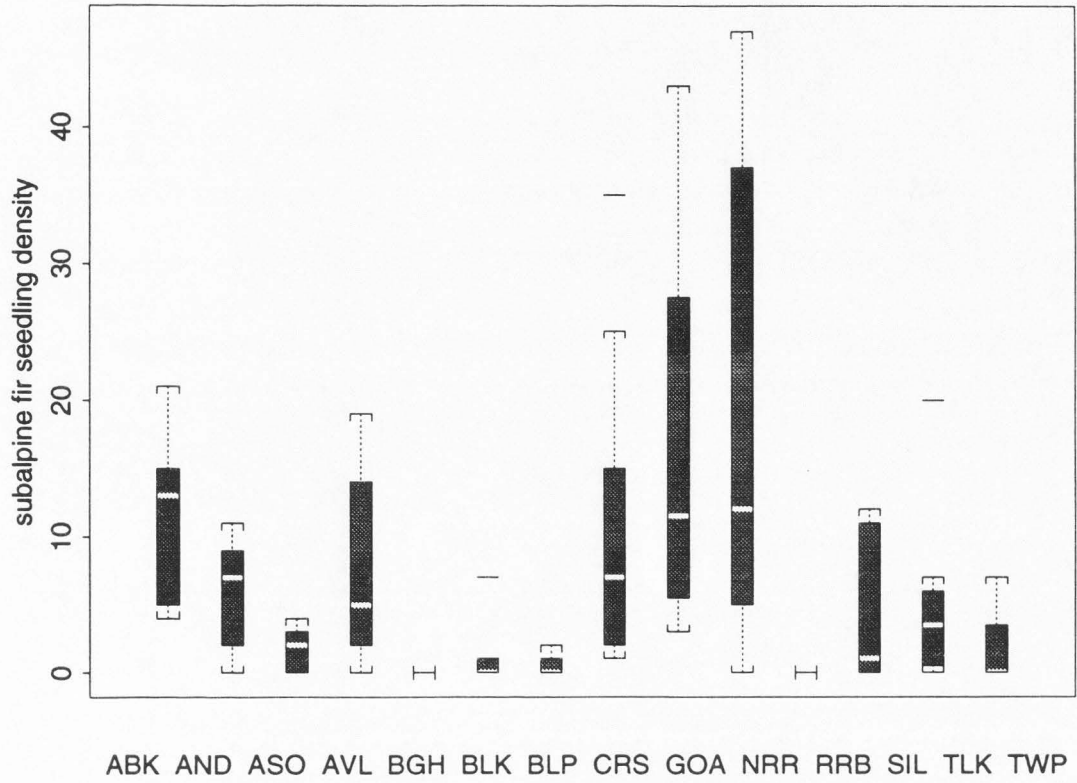


Fig. 3-8. Box plots of observed densities of subalpine fir seedlings.

CHAPTER 4
PREDICTIVE MODELS OF MOUNTAIN PINE BEETLE ATTACK ON
WHITEBARK PINE

Abstract. Stand-level and tree-level data collected from whitebark pine (*Pinus albicaulis* Engelm.) stands in central Idaho were used to develop statistical models to estimate the probability of attack and mortality of whitebark pine caused by mountain pine beetle (*Dendroctonus ponderosae*) (Coleoptera: Scolytidae). Logistic regression models were calibrated from pre-epidemic stand conditions and post-epidemic mortality levels resulting from a historic widespread mountain pine beetle outbreak that occurred from 1920-1940. Basal area (m^2/ha) and *SDI* (stand density index) were significant predictors of stand attack ($p \leq 0.001$). Tree diameter, basal area per plot, trees per plot, and number of stems in a tree clump were significant predictors of individual tree attack ($p \leq 0.001$). The models may be used to estimate anticipated cumulative mortality in currently or potentially infested whitebark pine stands. Predictor variables selected by the models corroborate the susceptible host characteristics identified in other mountain pine beetle-caused pine mortality systems. This work presents evidence of the generality of host susceptibility characteristics across pine species and over elevation gradients.

INTRODUCTION

Regional attention to whitebark pine (*Pinus albicaulis* Engelm.) population levels has been stimulated by reports that current environmental conditions have led to higher rates of mortality than establishment (Arno 1986, Keane et al. 1990, Keane and Arno 1993, Keane et al. 1994). Recognized factors causing whitebark pine decline in the northern Rocky Mountains include an exotic fungus, white pine blister rust (*Cronartium ribicola*), infestation of whitebark pine by mountain pine beetle (*Dendroctonus*

ponderosae) (Coleoptera: Scolytidae), and successional replacement by shade tolerant species as a result of fire suppression policies (Arno 1986, Arno and Hoff 1989, Keane et al. 1990, Morgan and Bunting 1990, Keane and Arno 1993, Kendall and Arno 1990, Hoff and Hagle 1990). Historically the principal natural mortality agent of whitebark pine was the mountain pine beetle (Ciesla and Furniss 1975, Arno 1986, Arno and Hoff 1989, Bartos and Gibson 1990, Perkins and Swetnam 1996). As a phytophagous, cambial-feeding insect of western conifers, it is recognized as an aggressive forest insect responsible for large timber losses, and as an integral component of forest ecosystem dynamics for its role in stand thinning and redistribution of resources for regeneration (Amman 1977, Peterman 1978, Romme et al. 1986). While host susceptibility characteristics of economically valuable western pines have been described and used in risk and hazard rating systems (Cole and Amman 1980, Stevens et al. 1980, McGregor et al. 1981, Schmid and Mata 1992, Shore and Safranyik 1992) and in models of mortality and attacks (Cole et al. 1976, Schenk et al. 1980, Cole and McGregor 1983, Anhold and Jenkins 1987, Powell et al. 1996, Negron et al. 1999) little quantitative information about the host susceptibility characteristics of whitebark pine has been documented.

There are several reasons for the lack of research on mountain pine beetle–whitebark pine interactions. First, research efforts have focused primarily on the exotic blister rust fungus responsible for severe pine mortality and reduced cone crops in whitebark pine over much of its northern distribution (Arno 1986, Keane et al. 1994). Whitebark pine is a keystone species in this region (Lanner 1996) and a mutualist with Clark's nutcracker (*Nucifraga columbiana*), its seed dispersal agent (Lanner 1980, Tomback 1982, Hutchins and Lanner 1982, Lanner 1982). Its decline has severe consequences for the wildlife dependent on its nutritious pine nuts, including the red squirrel (*Tamiasciurus hudsonicus*) (Reinhart and Mattson 1990), black bear (*Ursus*

americanus), and endangered grizzly bear (*Ursus arctos horribilis*) (Kendall 1983, Arno 1986, Mattson and Jonkel 1990, Kendall and Arno 1990, Mattson et al. 1993). The second reason for the lack of research on pine beetle–whitebark pine relations is that the cause of death is confounded in regions of high blister rust incidence. Trees may be killed by either blister rust or mountain pine beetle, or they may be weakened by blister rust, fire, and other pathogens and subsequently killed by mountain pine beetle (Keane and Arno 1993, Smith 1997, Smith and Hoffman 2000). Finally, whitebark pine is not generally a species of commercial interest; hence there has been little concern about the loss of timber volume from beetle-caused mortality.

The natural variability of host selection by mountain pine beetle and mortality levels sustained by whitebark pine populations are important for understanding natural disturbance related population dynamics. Therefore, this research was initiated to analyze the tree-level and stand-level host susceptibility characteristics of whitebark pine and to use this information to develop predictive models of probability of attack by mountain pine beetle.

Mountain pine beetle devastated whitebark pine forests in a widespread epidemic of the 1920-1940s from southern Canada to northern Wyoming (Arno 1970, Ciesla and Furnis 1975, Arno and Hoff 1989). Throughout its northern Rocky Mountain distribution, a high percentage of whitebark pine dominants was killed (Arno 1986). In central Idaho a dendrochronologically determined maxima of beetle-caused mortality occurred in 1930 (Perkins and Swetnam 1996) where large diameter trees were attacked more frequently than small trees and the duration of the outbreak in whitebark pine was 8-12 years. These characteristics are also typical of infestation in the most common host, lodgepole pine (Roe and Amman 1970, Cole and Amman 1980).

The work presented here used a logistic regression model calibrated from pre-epidemic stand conditions and post-epidemic mortality levels of ca. 70 years ago. The dry cold climate of central Idaho favors the persistence of beetle-killed snags, such that it was possible to reconstruct pre-epidemic stand structure using forest metrics as independent variables. Beetle-killed trees that were alive before the epidemic and trees that are still alive were used in the reconstruction. The model's usefulness is to estimate anticipated cumulative mortality in currently or potentially infested whitebark pine stands. Predictor variables in the model also corroborate susceptible host characteristics identified in other beetle-caused pine mortality systems.

Results from this research are expected to provide resource specialists with quantitative information useful for reducing mountain pine beetle-caused mortality in high-elevation whitebark pine communities.

METHODS

Study Area

A central Idaho study area was chosen because field surveys from 1995-1997 showed that white pine blister rust was only present in low amounts (Smith 1997, Smith and Hoffman 2000, Perkins pers. observ.). Accordingly, blister rust effects as a confounding factor in determining cause of tree mortality in this region are currently negligible. Fourteen treeline whitebark pine stands located within the Sawtooth National Recreation Area, the Sawtooth National Forest, and the Challis National Forest were sampled during the field season of 1998. Stands were located in six mountain ranges within the study area. Four sites were located near summits in the White Clouds Mountains (WC), three in the Headwater Mountains (HW), two in the Smoky Mountains (SM), three in the Salmon River Mountains (SR), one in the Boulder Mountains (BM),

and the one in the Sawtooth Mountains (SW) (Fig. 2-1). The Headwater Mountains are not identified in Fig. 2-1; they were considered either part of the Sawtooth or Smoky Mountains and form the divide between the Salmon and Big Wood rivers. Elevations ranged from 2700 to 3000 m (8800 to 9800 feet). Stand names and physical site attributes are summarized in Table 2-1.

Sample stand selection criteria were: (1) whitebark pine was the dominant species with composition greater than or equal to 60% of total basal area; (2) stand elevations were between 2680 m (8800 ft) and an upper edaphic treeline bordering an unvegetated rock ridgetop; (3) stand extent was as large an area as possible with homogeneous structure, constant aspect and slope; (4) paired mountain pine beetle attacked and unattacked stands within the same watershed were chosen whenever possible; and (5) tree form was upright (krummholz form trees were not sampled). Beyond these criteria, selection of sites was restricted by access within a day. Aerial photographs and ground reconnaissance or both were used to identify potential stands. Attacked and nonattacked stands were differentiated by abundance of whitebark pine snags with visible J-shaped adult beetle galleries and lack of fine limbs. The first criterion, adult galleries, had been used previously to determine beetle attack (Perkins and Swetnam 1996) and the second, no fine limbs, was a consistently observed characteristic of trees killed in the 1920-1940 period. Stands composed of $\geq 15\%$ beetle-killed snags were considered attacked stands; stands composed primarily of living whitebark pines with few beetle killed trees were considered nonattacked stands. These were readily identifiable on aerial photos. Selected stands often extended below 2,680 m (8,800 ft) but were not sampled below this elevation because in this geographic region their character was distinctly seral, complicated by the successional advance of subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.). Implicit in the

near-treeline criterion is the idea that these stands represent the climax whitebark pine community (Whitaker 1975, Steele et al. 1981, 1983).

Field Sampling

Seven to ten 0.04-ha (1/10 acre) plots were established randomly on each of the attacked and nonattacked stands, except for one site, RRB, which only had three plots. For each plot, elevation, aspect, slope, and location coordinates were recorded. On each plot, diameter at breast height (DBH, 1.5 m [4.5 ft above ground surface]) and species of trees ≥ 10.2 cm (4.0 in) were recorded. Additionally, the first trees north and south on a clockwise arc from plot center were cored with an increment borer for age determination and measured with a clinometer for height. To maximize the precision of age estimates, trees were cored close to ground level, generally 30-35 cm (12-14 in.) from the ground surface. Individual trees were recorded as attacked and killed versus not attacked; stands were recorded as attacked ($\geq 15\%$ mortality) *versus* not attacked.

Analyses

To reconstruct the stand structure prior to the mountain pine beetle epidemic, the diameter of trees ca. 1930 (DBH30) was estimated from the subset of live cored trees as:

$$DBH30 = DBH98 - 2 * RI$$

where DBH98 was the diameter at breast height recorded in 1998 and RI was the radial increment measured to the nearest 0.25 cm (0.10 in.) along the increment core from the 1930 through the 1998 annual ring. Trees with reconstructed DBH30 less than 10.2 cm (4.0 in.) were not used in further analyses and reduced the sample size to 134 trees. From this subset a regression model was used to calculate the DBH30 of all live trees sampled:

$$DBH30 = (a + b\sqrt{DBH98})^2$$

The regression equation, standard diagnostics and plots of residuals versus predicted values were calculated using the software *Mathematica* ver. 3.0 (Wolfram 1996) (see Table 2-2 and Fig. 2-2). Diameters of beetle killed trees that died in the epidemic and were recorded in 1998 were used in ca. 1930. The reconstructed diameters were then used to generate standard forest metrics (Husch et al. 1982) including basal area of the tree ca. 1930 (*batr30*), basal area per 0.04 ha ca. 1930 (*baplt30*), and trees per 0.04 ha ca. 1930 (*tplt30*). The number of stems in a tree clump was also recorded because tree regeneration initiates from Clark's nutcracker seed caches (Lanner 1980, 1982, Hutchins and Lanner 1982, Tomback 1982). The 0.04 ha basis reflects the local area environment of a tree and the number of stems reflects the more immediate biomass arrangement of the caching site. The latter was anticipated as a potential predictor variable reflective of the spatial component of beetle movement from stem to stem. Stand-level attributes including stand density index, SDI (*sdi*) (Reineke 1933, Long and Daniel 1990), quadratic mean diameter (*dq*), basal area (*ba*), and mean basal area (*mba*) were calculated ca. 1930 and 1998 for all 14 stands (Husch et al. 1982, Avery and Burkhart 1994).

Stand-level and tree-level metrics were tabulated with physical site attributes for two fundamental analyses: (1) Stand-level metrics were used for a stand-level logistic regression model to explain the probability of attack as a function of stand-level variables. (2) Tree-level metrics constituted the set of independent variables used in a 10-fold cross-validated logistic regression model for probability of individual tree attack given that the stand was attacked.

The utility of logistic regression to describe a discrete event as a function of independent site and stand variables is well established for forest tree mortality (Hamilton 1974, Hamilton and Edwards 1976, Hamilton 1986, Berryman 1986). In logistic regression the dependent or response variable, tree survivorship status (*tsts*), is dichotomous taking

the values of zero or one. The response distribution for logistic regression is the binomial distribution established through a logit link function that relates the log of the odds of attack with the linear predictor of independent variables (Hastie and Pregibon 1992). The model can be expressed as:

$$\ln(p/(1-p)) = b_0 + b_1x_1 + b_2x_2 + \dots b_nx_n$$

where p is the probability of attack, $x_1, x_2 \dots x_n$ are the predictor variables and $b_0, b_1 \dots b_n$ are coefficients determined in the logistic regression. The model is then back transformed to generate probabilities of attack as:

$$p = 1/(1 + e^{-(b_0 + b_1x_1 + b_2x_2 \dots b_nx_n)})$$

Logistic regression employing 10-fold cross validation was accomplished with S-PLUS (MathSoft 1999). Analyses of deviance methods (Hastie and Pregibon 1992) were used to search for a parsimonious model and to identify the significance of parameters. To approximate the general linear model goodness of fit statistic (the coefficient of determination, R^2) for the logistic regression model, a quasi R^2 was calculated as: $1 - (\text{residual deviance}/\text{null deviance})$ (Cutler pers. comm.). To avoid the bias inherent in using the same data to develop and test the model, and to account for within-site dependencies, the analyses were 10-fold cross-validated as follows. Trees in each of the attacked stands were partitioned into ten segments. One segment was withheld and the remaining nine were used to calibrate the model. The 10th segment was then used to test the prediction against the known status to validate the model. This was repeated 10 times for each site leaving out each segment in turn. The predictions of the 10 independently verified models were compared to the actual survivorship status for each tree in a contingency (cross-tabulation) table. Percent correctly predicted, percent error of omission, and percent error of commission were calculated as well as bias of the models.

Bias describes the model's errors in a directional sense with respect to actual and predicted attacks. A negative value indicates a tendency to underpredict and a positive value indicates a tendency to overpredict attacks. From a managerial perspective, over prediction of beetle attacks is less problematic than underprediction. For a cross-tabulation of the form:

	<i>Predicted</i>	
<i>Actual</i>	False	True
False	a	c
True	b	d

Bias is calculated as:

$$\frac{(c + d) - (b + d)}{(b + d)}$$

Differences in the significance of the independent variables across stands were explained by a qualitative interpretation of size-frequency distributions ca. 1930. Finally, trees in all stands were pooled and the 10-fold cross-validation assessment of the logistic model was repeated to see if the pooled model was significantly worse than the stand-specific models.

RESULTS

The least squares regression for reconstructed diameter ca. 1930 was significant ($p < 0.001$) with 53% of the variability in DBH30 explained by DBH98 (see Table 2-2). The regression model was thus considered adequate to reconstruct diameters of trees that survived the ca. 1930 epidemic. The model fit and evidence of the random distribution of model errors are shown in Fig. 2-2.

Stand-Level Model

Nine stands met the criteria for attacked and five stands met the criteria for nonattacked stands (Table 2-1). Attacked and nonattacked paired stands were located adjacent to each other for stands ABK and AND, BLK and BLP, and AVL and CRS. Stands ASO and BGH and RRB and NRR were also paired but were separated by a ridge and not adjacent (Fig. 2-1).

Differences in nonattacked versus attacked stands are apparent in Table 4-1. Basal area (*ba30*), trees per ha (*tph30*), mean basal area (*mba30*), quadratic mean diameter (*dq30*) and stand density index (*sdi30*) before the outbreak were lower on unattacked as compared to attacked stands (Table 4-1). On attacked stands, approximately 60-400 trees/ha were killed by mountain pine beetles. Site RRB was a small stand with only three plots; trees killed by beetles per ha is likely overestimated at 734.

The implication of having paired stands is that they generally experienced the same beetle pressure and that structural rather than environmental site variables would differentiate susceptibility. This was shown with basal area (*ba30*) and stand density index (*sdi30*) as the only significant predictors in logistic regression models. Both stand density index and basal area are positively correlated with beetle attack ($p \leq 0.001$). These two models explained stand attack perfectly for the 14 stands:

$$\ln(p/(1-p)) = -76.9344 + 0.8840 \text{ sdi30}$$

$$\ln(p/(1-p)) = -64.9297 + 6.5671 \text{ ba30}$$

The probability of correctly predicting 14 out of 14 stands was 0.002 calculated using the probability mass function of a binomial random variable (Ross 1976).

Tree-Level Model

Analyses of the pooled tree-level data set identified four significant ($p < 0.001$) independent variables: diameter ca. 1930, (*dbh30*), basal area 0.04 ha ca. 1930 (*baplt30*), trees per 0.04 ha ca. 1930 (*tplt30*), and number of stems in a tree clump (*nstms*).

Analyses of deviance of the model predictors with the chi-square test statistic (Venables and Ripley 1999) demonstrated statistical significance ($p < 0.001$) for all four variables in the 10-fold cross-validation models. Results from cross-validation models were cross-tabulated with observed tree attacks on each stand in contingency tables (Appendix C). The mean of the percent of trees correctly predicted was 90%. Number correctly predicted, errors of omission and commission, and bias are tabulated in Table 4-2. Models from two stands tended to slightly underpredict tree mortality but generally all bias metrics were close to zero (Appendix C).

Analyses of the coefficients of the independent variables revealed that *dbh30* was the most consistently significant ($p < 0.001$) on all nine sites, followed by *nstms* on seven sites, *baplt30* on five sites, and *tplt30* on two sites (Table 4-3). The difference in the significance of the predictors may be explained in part by size frequency distributions (Fig. 4-1) and stand summary metrics (Table 4-1). For instance, on the Goat site (GOA) the quadratic mean diameter was large at 43.7 cm (17.2 in.) with a low stocking of 124 trees per ha (50 trees per acre). With few large diameter trees, nearly all of which were selected by beetles, the contribution of *baplt30* and *tplt30* as predictors was negligible (Fig. 4-1). On Anderson Peak (ABK), beetles selected small diameter trees (there were no large ones) and *nstms* was significant with intermediate significance for *tplt30*. On two stands, Titus Lake Peak (TLK) and Big Hill (BGH), all four predictors are significant; both stands are dominated by the abundance of large diameter trees at high to moderate

stocking levels (Fig. 4-1). Local basal area was significant on AVL, BGH, BLK, TLK, and TWP stands that lost small as well as large diameter trees (Fig 4-1).

The cross tabulation for the pooled data set of all trees across all sites dropped to 85% correct in predicting tree fate (Table 4-4). The logistic equation for the pooled data set was:

$$\ln(p/1 - p) = -6.0167 + 0.1954 \text{ dbh30} + 0.0944 \text{ baplt30} + 0.0668 \text{ tplt30} + 0.5792 \text{ nstms}$$

The quasi R^2 was 0.44. The contribution of diameter ca. 1930 (*dbh30*) and number of stems (*nstms*) to the model fit is shown in Fig. 4-2. The bias was 0.011, indicating a potential to slightly overpredict tree mortality.

DISCUSSION

It has been well established that tree size, age, and stand density are factors correlated with tree mortality (Yoda et al. 1963, Lee 1971, Hamilton and Edwards 1976, Hamilton 1986). For the whitebark pine-mountain pine beetle system, that tree diameter and basal area were positive significant predictors in the logistic models is not surprising and is consistent with mountain pine beetle-host susceptibility characteristics identified by others (Amman et al. 1977, Cole and Amman 1980, Stevens et al. 1980, Berryman 1982, Shore and Safranyik 1992, Schmid and Mata 1992, Olsen et al. 1996). Stand-level characteristics associated with attack are also qualitatively similar to other mountain pine beetle-pine host systems. For instance, whitebark pine stands with basal areas below 7 m²/ha (30 ft²/acre) and average diameters below 18 cm (7 in.) were not attacked in the early 20th century epidemic. These characteristics are similar to susceptibility characteristics found in lodgepole pine stands where host basal areas below 18 m²/ha (80 ft²/acre) and diameters less than 20 cm (8 in.) are seldom attacked (Cole and Amman 1969, Amman et al. 1977) and in ponderosa pine stands where thresholds for attack are

28 m²/ha (120 ft²/acre) for basal area and 25 cm (10 in.) at DBH (Sartwell and Stevens 1975). This work presents evidence of the generality of host susceptibility characteristics across pine species and over elevation gradients.

The significance of number of stems (*nstms*) as positively correlated with individual tree attack implicates distance between stems as a spatial constraint related to the probability that mountain pine beetles will attack a tree. Whitebark pine trees with multiple stems in clumps are more likely to be attacked than single stems. Donnegan and Rebertus (1999) also found that mortality of mid-successional stage limber pine (*Pinus flexilis* James) was correlated with its clumped pattern. The *nstms* variable indirectly incorporates a spatial component identified by Bentz et al. (1993) as needed to improve risk/hazard rating systems and by Powell et al. (1996) to incorporate dispersal effects. Mitchell and Preisler (1991) used a logistic regression spatial analysis of lodgepole pine attack by mountain pine beetles and found that among small diameter classes spatial relationships among trees and tree size were the most important covariates. Their explanation may capture the variability I could not explain with the significance of the four independent variables.

High elevations are generally associated with decreasing beetle-caused mortality levels because of unfavorable heat balance for beetle development (Amman 1973). However, elevation is not correlated with beetle attack of trees or stands during the epidemic conditions of the ca. 1930 outbreak. This may be explained in part by the narrow elevation band \approx 300 m (1,000 ft) of the study area and by the concurrent above average departures in summer temperatures during the widespread "dust bowl drought" years (ca. 1930) (Finklin 1988, Perkins and Swetnam 1996, Biondi et al. 1999) Warm temperatures would likely have favored successful brood development, beetle survivorship, and successful attacks (Reid and Gates 1970, Amman 1972, 1973, Bentz et al. 1991,

Logan and Bentz 1999). The infestation also occurred at the start of the longest sustained low growth period for the last 200 years as represented in whitebark tree-ring width chronologies (Perkins 1995, Perkins and Swetnam 1996). This growth suppression likely reflects poor growing conditions for trees, low tree vigor and may support the plant-drought stress hypothesis (Mattson and Haack 1987), which suggests that water-stressed individuals are more susceptible to damaging agents than non-water-stressed individuals.

The logistic regression models presented here explain the probability of whitebark pine tree attack by mountain pine beetle based on tree and stand-level characteristics calibrated in the pre-epidemic phase of a historic outbreak. Bentz et al. (1993) in their review of four risk and hazard rating systems note that the population phase (beginning, increasing, or declining) is important for a risk model's ability to accurately predict mortality. Because the reconstructed DBH at 1930 was the foundation for calculating pre-epidemic stand conditions and the assessment of mortality was post-epidemic, the model may be suited for estimates of cumulative mortality anticipated in mountain pine beetle epidemics. Both the tree- and stand-level models are limited to whitebark pine in the geographic area of central Idaho, and require verification with independent data outside the region.

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Table 4-1. Stand summary metrics ca. 1930. The first five rows are stands that were not attacked by mountain pine beetle. *ba30* = basal area (m^2/ha) *tph30* = trees per ha, *mba30* = mean basal area, *dq30* = quadratic mean diameter (cm), *sdi30* = stand density index, *babk* = basal area of trees killed by mountain pine beetles, *tphbk* = trees killed by mountain pine beetles/ha.

Site	<i>ba30</i>	<i>tph30</i>	<i>mba30</i>	<i>dq30</i>	<i>sdi30</i>	<i>babk</i>	<i>tphbk</i>
NRR	3.4	178	0.05	15	33	0	0
BLP	3.9	195	0.05	16	38	0	0
ASO	4.6	27	0.41	46	30	0	0
CRS	5.1	210	0.06	18	47	0	0
AND	6.7	289	0.06	17	63	0	0
ABK	13.1	403	0.08	20	114	12.2	338
SIL	14.0	272	0.13	26	111	11.5	188
AVL	16.3	356	0.11	24	132	10.6	143
TLK	16.5	195	0.21	33	119	14.7	101
GOA	18.4	124	0.37	44	119	16.8	59
TWP	21.6	257	0.21	33	156	20.4	183
BLK	26.4	316	0.21	33	190	25.3	249
BGH	32.1	479	0.17	29	242	30.3	380
RRB	50.3	889	0.14	27	393	46.8	734

Table 4-2. Number of trees correctly predicted (attacked or not attacked), errors of omission and commission, and bias.

Percentages are in parentheses.

Site	Correct	Errors of omission	Errors of commission	Bias
ABK	114 (91)	4 (3)	7 (6)	0.028
AVL	130 (90)	7 (5)	7 (5)	0
BGH	148 (93)	5 (3)	7 (4)	0.008
BLK	86 (83)	6 (6)	11 (11)	0.061
GOA	39 (95)	1 (2.5)	1 (2.5)	0
RRB	99 (87)	4 (3)	11 (10)	0.071
SIL	61 (80)	7 (9)	8 (11)	0.018
TLK	64 (98)	1 (2)	0 (0)	-0.030
TWP	77 (95)	3 (4)	1 (1)	-0.036

Table 4-3. Significance table of the four independent variables used in the tree-level logistic regression model. 0 = significant ($p < 0.001$), 1 = not significant ($p > 0.1$), .5 = $0.001 < p < 0.1$.

Site	<i>dbh30</i>	<i>nstms</i>	<i>baplt30</i>	<i>tplt30</i>
ABK	0	0	1	.5
AVL	0	0	0	1
BGH	0	0	0	0
BLK	0	1	0	1
GOA	0	1	1	1
RRB	0	0	1	.5
SIL	0	0	1	.5
TLK	0	0	0	0
TWP	0	0	0	1

Table 4-4. Cross-tabulations of logistic model

prediction versus actual tree survivorship

status. $\chi^2 = 349.70$, $df = 1$, ($p \leq 0.0001$)

Correctly predicted = 84%, errors of omission = 8%,

errors of commission = 8%, bias = 0.011.

Actual	Predicted		Row total
	False	True	
False	194	75	269
True	68	573	641
Col. total	262	648	910

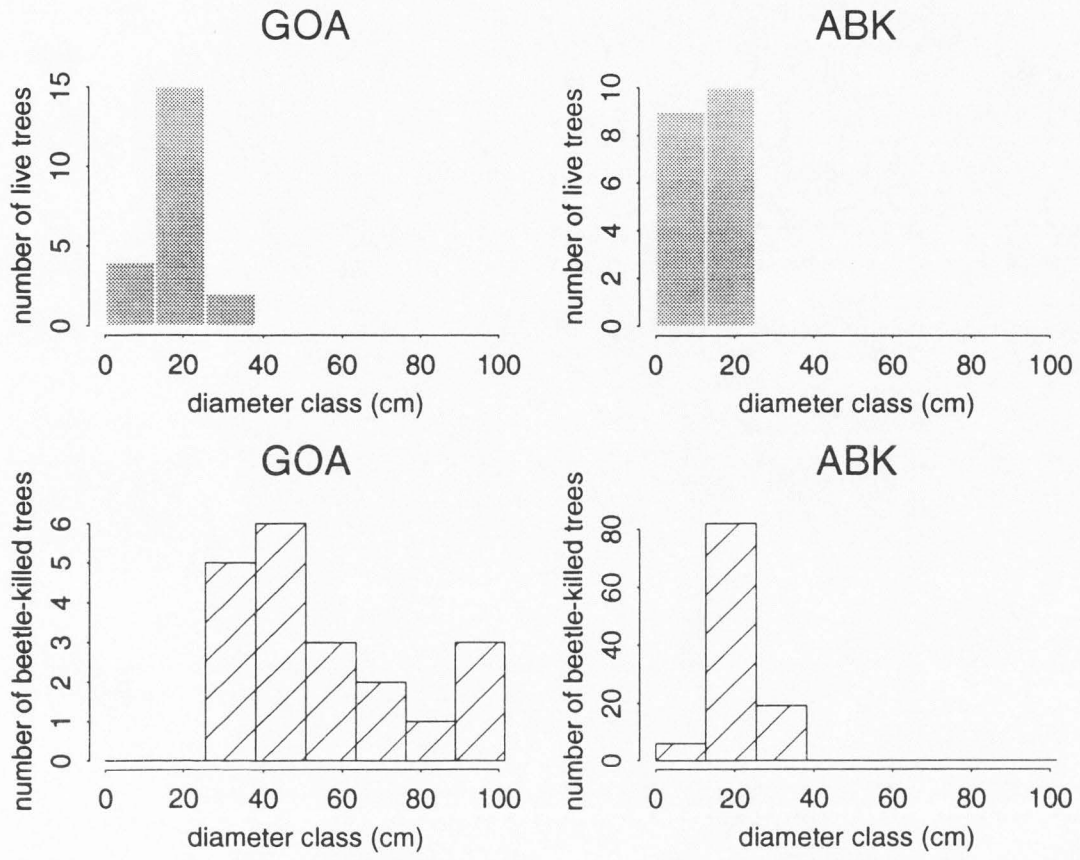


Fig. 4-1. Size-frequency distributions of attacked and nonattacked whitebark pines ca. 1930. Solid bars are live, nonattacked trees and hatched bars are trees attacked and killed by mountain pine beetles.

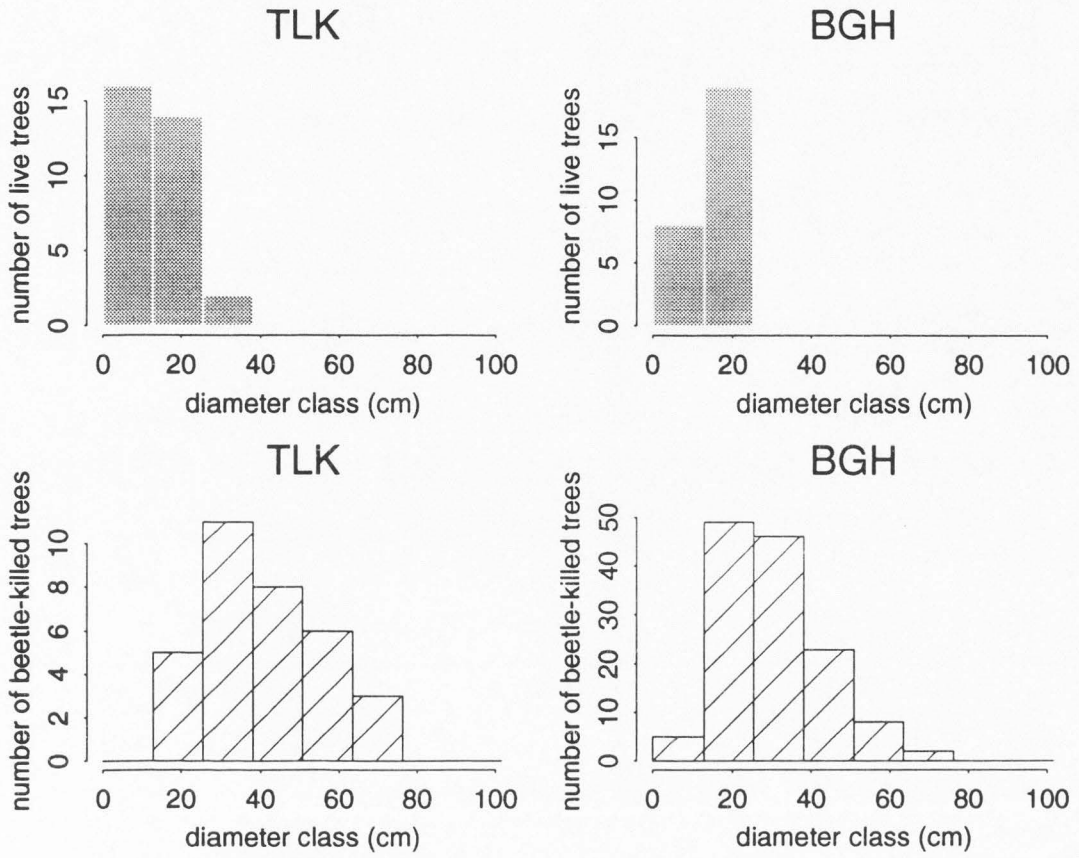


Fig. 4-1. Continued.

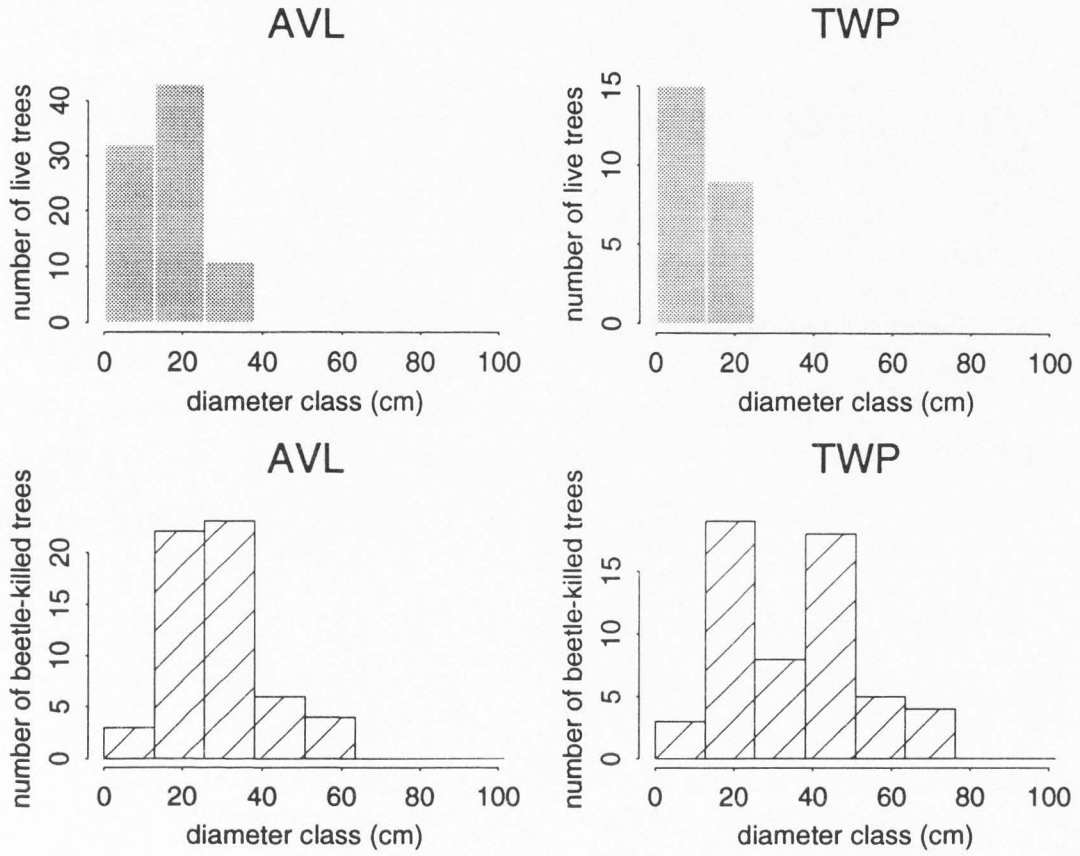


Fig. 4-1. Continued.

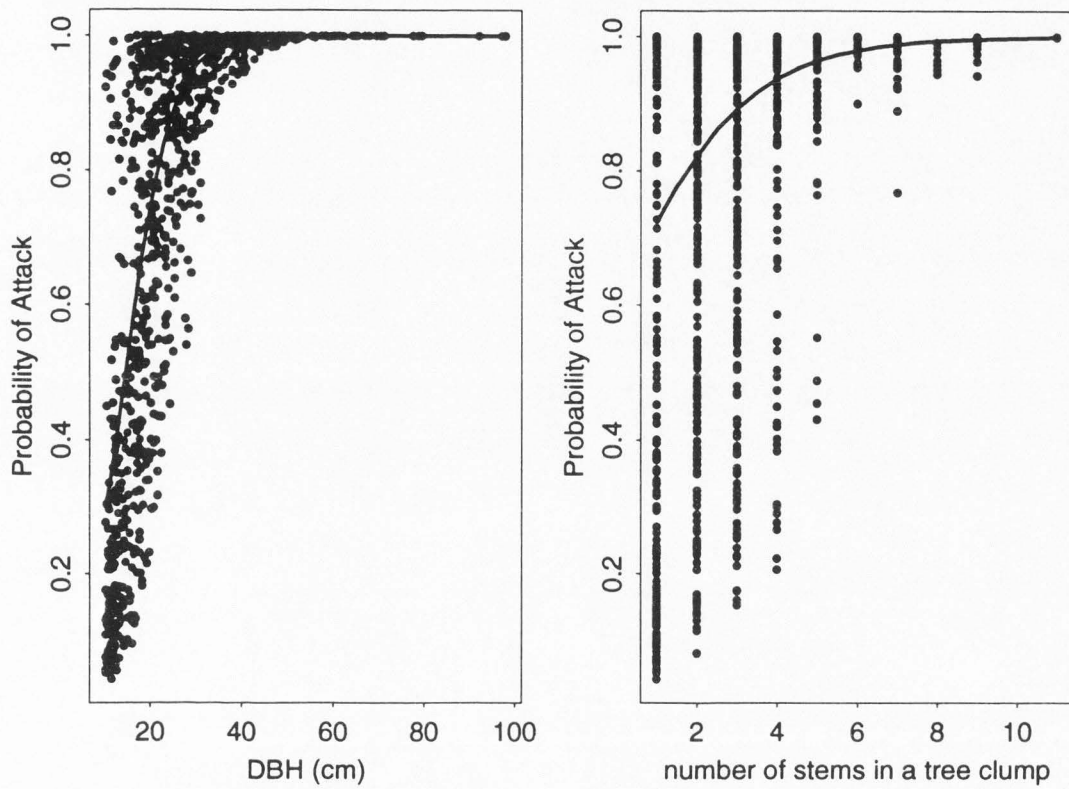


Fig. 4-2. Fitted logistic regression model plotted against *dbh30* and *nstms*. The equation for the probability of tree attack (p) is:

$$p = 1/1 + e^{-6.0167+0.1954 \text{ dbh30}+0.0944 \text{ baplt30}+0.0668 \text{ tplt30}+0.5792 \text{ nstms}}$$

CHAPTER 5
A SPRING TEMPERATURE RECONSTRUCTION FROM
WHITEBARK PINE TREE RINGS

Abstract. A high-elevation whitebark pine (*Pinus albicaulis* Engelm.) tree-ring chronology was used to develop a 1028-year long reconstruction of spring temperature for the Sawtooth-Salmon River region of central Idaho. The chronology was developed using 53 measurement series from 24 trees collected on four sites, and spans the interval A.D. 965 to 1992. Series were selected from live and dead trees for continuous long segment lengths and high inter-series correlation within and between the sites. The chronology was calibrated against Ketchum and New Meadows, Idaho US Historical Stations, April-May average monthly temperature using half-sample calibration-verification tests for the period that contained historic climate data, 1909-1992. The chronology accounted for 41% of the variability in the climatic data and successfully simulated medium to high frequency trends. Below average departures from mean spring temperatures occurred ca. 1080-1150, 1260-1460, and 1720-1925. The 19th century cold period coincides with the "Little Ice Age." The warmest interval ca. 965-1080 is greater in magnitude than any other period in the reconstruction and is concurrent with the "Medieval Warm Period." Neither the instrumental nor the proxy temperature records show evidence of warming in the 20th century.

INTRODUCTION

Inferences about paleoclimatic variability from tree-ring chronologies have been constrained by the length of the chronologies and the spatial network of chronology sites. Millennium length chronologies have been increasingly sought to quantify the spatial and time varying properties of climate variables of the distant past (Bradley and Jones 1995,

Biondi et al. 1999). In response to the need for paleoclimatic information this research was initiated to (1) construct a millennium-length tree-ring chronology for the northwestern U.S. and (2) reconstruct temperature using a calibration equation that relates tree-ring indices of annual growth to temperature.

Four previously published whitebark pine (*Pinus albicaulis* Engelm.) chronologies from the Sawtooth-Salmon River region of central Idaho were long and well replicated, and had demonstrated dendroclimatic potential (Perkins and Swetnam 1996). The dominant climate signal from response function and correlation analyses (Guiot 1990) was spring temperature (Perkins and Swetnam 1996). Annual ring-width growth was inversely correlated with average monthly May temperature from the Idaho central mountains (NOAA climate division 4) instrumental record (NCDC, Asheville, North Carolina) (Perkins and Swetnam 1996). Because all four sites showed a similar climate signal, it was reasonable to construct a composite chronology using the longest ring-width series from both living and dead trees at each site. The standardized composite chronology was then calibrated against instrumental climate data from sites that were geographically proximal to chronology site elevations.

The addition of this 1000-year spring temperature reconstruction is expected to be integrated with other regional paleoclimatic information to enhance understanding of climate variability on spatial as well as temporal scales in the northern Rocky Mountains.

METHODS

The composite chronology was developed from ring-width series from four previously published central Idaho whitebark pine chronologies (Fig. 5-1). Details about site descriptions, field collections, chronology development and crossdating characteristics can be found in Perkins (1995) and Perkins and Swetnam (1996). Individual trees selected for the composite chronology had long and continuous ring-width series from both live and

dead trees. Each series was chosen for long segment length (Cook et al. 1995), high interseries correlations ($r \geq 0.43$) with their respective master site chronologies, and high interseries correlations across sites ($r \geq 0.43$) for the composite chronology. Additionally, trees living between A.D. 800-1300 were selected to increase sample size in the early part of the chronology. Crossdating was verified for the composite chronology with the quality control crossdating program COFECHA to ensure measured series were accurately dated (Holmes 1983). Crossdating is accomplished when cores from the same tree and from different trees within a stand share a common pattern of wide and narrow annual rings or other diagnostic features. The synchronicity of these patterns allows assignment of an exact calendar year to each tree ring (Douglass 1941, Fritts 1976). The COFECHA algorithm calculates running correlation coefficients between a single series and a master composite that excludes the series being tested. Crossdating was confirmed if the highest significant correlation occurred at the dated position.

Three important steps characterize a dendroclimatic reconstruction (Fritts 1976, 1991, Bradley and Jones 1995): (1) standardization or detrending of the tree ring parameter; (2) calibration of the site chronology with with instrumentally recorded climate data and the production of the reconstruction with the calibration equations; (3) verification of the reconstruction from an independent period not used in the initial calibration.

After crossdating was verified, each series was standardized to remove nonstationary time domain trends (Fritts 1976, Cook 1985, 1987). The standardization of the tree ring width series removes the biological age trend of the tree, non-climatic and individualistic disturbance effects, and normalizes the tree ring series to a common mean where the relative variance is emphasized (Fritts 1976, Holmes et al. 1986). Generally, widely spaced, open-canopied trees can be detrended with simple exponential or linear

functions to remove the biological age trend and still preserve the long frequency variations desirable for climate reconstructions (Fritts 1976). Smoothing splines have been commonly used to detrend forest interior ring-width series because of competition and endogenous disturbance patterns manifest in the tree-ring series (Cook 1985, 1987). In this study a 32-year smoothing spline (Reinsch 1967, Cook and Peters 1981) was chosen for detrending because individual trees showed asynchronous periods of above and below average growth due in part to intraspecific competition between multiple stems and by mechanical damage to stems within clumps. Whitebark pine trees commonly grow in a multiple stem form because tree regeneration initiates from Clark's nutcracker (*Nucifraga columbiana*) seed caches (Tomback 1978, Lanner 1980, Hutchins and Lanner 1982, Tomback 1982). In the multiple stem form, growth rings often lack circuit uniformity and grow away from the tree centerline.

Division of the observed ring-width values by the expected value from the smoothing spline function produced the index values for each series. The indices were then averaged for all measured series to produce a master ring-width index for each year. Standardization with the 32-year smoothing spline preserved 50% of the amplitude frequency response at the 32-year wavelength but lost all variance at the 60-year frequency. As a result of this standardization method, high to medium frequency variations are preserved and long frequency trends are lost. Detrending and development of the final master chronology were performed with procedures in the computer program ARSTAN (Cook 1985). The STANDARD chronology from the ARSTAN output was used for all analyses.

Response function and correlation analyses (Guiot 1990, Fritts et al. 1990) from the four previously published chronologies had shown a significant inverse relationship with average monthly May temperature from the Idaho-central mountains (division 4)

instrumental record (NCDC, Asheville, North Carolina) (Perkins and Swetnam 1996). To investigate climate-tree growth relations on smaller, local scales, the five nearest US Idaho historical weather stations with approximately 100 years of continuous climate data were selected: Challis, Cambridge, Ketchum, Mackay, and New Meadows. Climate variables investigated were monthly mean temperature and monthly total precipitation by individual station, regionalized monthly mean temperature and monthly total precipitation from Idaho climate division 4 (Central Mountains), and Idaho division 4 Palmer Drought Severity Index (PDSI). A 20-month period of meteorologic data from previous May through following December was analyzed to detect autocorrelation effects.

Investigation of climate-growth response was accomplished using PRECONK (Fritts et al. 1991, Fritts and Shashkin 1995) while SAS correlation routines (Schlotzhauer and Littell 1987) were used to identify months in which temperature and precipitation had significant effects on annual ring width growth. The analysis of tree ring growth and climate variables followed standard dendrochronological methods (Fritts 1976, 1991, Cook and Kairiukstis 1990) of correlation coefficients and response functions. Response function analysis regresses principal components (eigenvectors) of climate variables upon the master index chronology to calculate a set of coefficients (weights) that correspond to the original set of climate variables. A bootstrap method provides confidence intervals for the response coefficients (Guiot 1990).

The climate variable with the most significant response function and correlation coefficients was used for reconstruction. For the calibration and verification steps of the reconstruction, the period of climatic observations (1909-1992) was divided into half-sample subsets. Each half-period was calibrated with a regression model and then verified on the half withheld from the calibration. Studentized residuals and Cook's d were the diagnostics used to identify outliers that adversely affected the model.

Verification tests included correlation analyses, reduction of error (RE) tests, the product mean test, and the sign products test (Fritts 1976, Fritts et al. 1990)

After verification, the entire instrumental period was used to develop a new regression equation to maximize the number of observations and therefore the degrees of freedom used to calculate model significance (Briffa et al. 1990). The final step was to apply the transfer equation to the chronology to predict the past average April-May temperature for the period A.D. 965 - 1992.

RESULTS

Crossdating/Standardization

The composite chronology was composed of 53 series from 24 trees and was 1267 years in length (Table 5-1, Fig. 5-2). Four trees from Railroad Ridge (RRR), eight trees from Sandpass (SDP), six trees from Twin Peaks (TWP), and six trees from Upper Sand Pass (UPS) comprised the final chronology. The strength of the crossdating was reflected by a high interseries correlation of 0.55 (Table 5-1). The mean sensitivity of 0.22, a measure of the relative change between adjacent ring widths (Douglass 1936), reflects the low year-to-year variance typical of Rocky Mountain conifers near treeline (LaMarche and Stockton 1974, Fritts and Shatz 1975). Mean segment length was 457 years, of substantial length to mitigate the effects of the "segment length curse" (Cook et al. 1995). The "curse" is related to the fact that the maximum resolvable wavelength in the climate reconstruction is only as long as the ring-width series itself, and chronologies composed of short overlapping segments may be expected to represent variable climatic, site, age, and stand structure conditions.

Climate-Growth Relations

The most significant relationship between climate and tree-growth was an inverse relationship with April and May temperature for the single climate stations New Meadows, Ketchum, and Cambridge. The highest Pearson correlation coefficients ($p < 0.0001$) occurred with the STANDARD chronology. Although the correlation coefficients with Cambridge and New Meadows were approximately equal, New Meadows and Ketchum were selected as potential predictor variables because they were the closest in elevation and distance to the chronology sites (Fig 5-1). Ketchum and New Meadows station data were averaged to create a spring temperature variable for average April-May temperature. This variable improved the correlation coefficients from the individual months to produce the strongest regional temperature signal (Table 5-2).

Calibration/Verification

A simple linear regression was calculated on half-sample subsets for the periods 1909-1950 and 1951-1992. Verification of the calibration equation for each subset withheld from the calibration period was performed using program VFY of the International Tree-Ring Data Bank Program Library (Holmes 1992). Initial regression models indicated that only 21% to 34% of the variance in climate could be explained by tree growth. Outlier observations identified using Cook's d and Studentized residuals were removed from the calibration model and significantly improved the correlations. After removal of outlier years 1910, 1914, 1920, 1925, 1940, and 1948, the F-values, the ratio of model to error variance, were statistically significant ($p < 0.0001$) with improved R^2 values of 0.37 and 0.41.

All verification diagnostics on both half periods were statistically significant ($p < 0.05$) with the exception of the product means test for the late period calibration. A

possible explanation is that the period calibrated in 1951-1992 was a recovery growth period (above average growth) but was verified during the suppressed growth period of the 1930's drought and concurrent mountain pine beetle epidemic (below average growth) (Ciesla and Furniss 1975, Arno and Hoff 1989, Perkins and Swetnam 1996) The non-parametric sign test indicates that the number of similarities in the sign of departures between climate and ring-width indices was larger than the number of dissimilarities (Fritts 1976). The reduction of error statistic was positive, indicating that the calibration model provides a better estimate of climate on the verification period than the mean of the calibration period (Fritts 1976).

After the double calibration and verification on the half-period subsets, the full set 1909-1992, less five missing station values and outliers, was used for the simple least square regression. The first order linear equation (transfer function) relating ring-width index to average April-May temperature was:

$$y_t = -7.78x_t + 14.95$$

where y_t was the predicted spring temperature ($^{\circ}$ C) and x_t was the standard ring-width index at year t ($n = 73$) (Table 5-2). The R^2 for the full set regression was 0.41, retaining the same level of variance explained as the half-set model (Table 5-3). The instrumental mean temperature of 7.28° C was substituted for the five missing station values in years 1957, 1978, 1983, 1984, and 1992 for the plot of observed and expected values (Fig. 5-3).

The observed versus predicted spring temperature values reveal generally synchronous agreement in periods 1911-1920, 1927-1938, 1945-1970, and 1973-1981. The effects of outliers and missing values in periods of poor agreement, 1982-1992 and 1920-1925, were also evident (Fig. 5-3). Although the composite chronology spanned the interval A.D. 726-1992, only the period A.D. 965-1992 was used for the reconstruction

because there were fewer than three trees from A.D. 726-965. Reconstructed temperature was converted to standard deviation units (z-scores) to provide an objective method to detect the magnitude of temperature deviation (Grissino-Mayer 1995), and smoothed with a 50-year smoothing spline to detect longer frequency trends (Grissino-Mayer 1995) and facilitate visual comparisons with other temperature reconstructions (Fig. 5-5).

DISCUSSION

The reconstruction of average April-May temperature shows high variability on annual to decadal scales with oscillations close to the mean (Fig. 5-4). The length and magnitude of the climate anomalies discussed here are influenced by the chronology standardization procedure and care must be used in their interpretation (Cook and Kariukstis 1990). The smoothed reconstruction reveals low-frequency departures for up to 200 years for cool periods interspersed with higher frequency, decade-scale oscillations for warm periods (Fig. 5-5).

The most striking departure from the mean in the smoothed reconstruction is the above-average warm period beginning in 965 and persisting for over 100 years until about 1080. The expectation is that the amplitude of departure from the mean would decrease with an increase of samples. However, the trees in this period come from three different sites (RRR, SDP, TWP), so endogenous stand influences on the ring widths may be averaged out and inference about warmth is not unreasonable. From 1080 to 1250, three additional periods of persistent (> 10 year) warming occurred. These as well as the initial 10th century warming are concurrent with the "Medieval Warm Period" (Lamb 1977, Williams and Wigley 1983, Briffa et al. 1992), beginning around A.D. 900 and lasting until ca. 1450. This period is reported to be highly variable in length and magnitude with asynchronous periods of warming and cooling differentiated by region, species used in reconstructions, and methodology. Such variability is apparent in the early "Medieval

Warm Period” of 965-1080 being followed by cool years between 1090-1150. More samples are needed to clarify the climate response in the early period of the reconstruction. Other notable warm periods shown in the smoothed reconstruction are centered around 1470, 1510, and 1710 and are 10-20 years in duration.

Toward the present, a period of average or just below average temperature lasted for 200 years starting ca. 1260 and ending ca. 1460. Another 200-year cool period occurred from ca. 1725-1925 (Fig. 5-5). This period falls within the “Little Ice Age,” ca. 1400-1900 (Lamb 1977, Grove 1988, Briffa et al. 1992, Bradley and Jones 1995). The “Little Ice Age” is of disputed duration, characterized by geographic variability and anomalous warm-cool oscillations in an otherwise widely recognized period of glacial advance (Pielou 1991, Bradley and Jones 1995). In North America, the 19th century is generally acknowledged as the coldest (Jones and Bradley 1995), and the spring temperature reconstruction supports this for central Idaho. Neither the instrumental nor the proxy temperature records show evidence of warming in the 20th century. While the 1930’s drought was a period of above average summer temperatures, April-May temperatures were cool.

Comparisons of the average April-May temperature reconstruction with other temperature reconstructions from western North America generally reveal similarities with the 19th and 20th centuries broadly consistent with the Little Ice Age. Graumlich and Brubaker (1986) reconstructed annual temperature from conifers at timberline from the Cascade Mountains of Washington and reported a cool period from 1860-1900, which agrees with the spring temperatures reported here. Other periods, including a significant 20th century warming trend were notably dissimilar. In a nearby reconstruction of July temperature from arid-site Douglas-firs (*Pseudotsuga menziesii*) and whitebark pines (Biondi et al. 1999), continuity between spring and summer temperature was seen around

1150, 1420, 1600, 1660-1725, and the 1940s (Fig. 5-6). Similarities in cool periods were not apparent. Luckman and others (1997) reconstructed summer temperature from densiometric and ring width analyses of subalpine conifers near the Columbia Icefield, Alberta, Canada. The cold periods 1650-1690, and the first half of the 19th century, were notably similar between their reconstruction and this one. Additionally there were segments of overlap in the cold periods around 1220, 1260, 1280, and 1330. Their reported warm period from 1350-1440 agrees with the summer temperature from the Douglas-fir/whitebark chronology (Biondi et al. 1999) but is markedly different from the average to slightly below average departure of spring temperature in this reconstruction. Spring temperature appears to have little seasonal persistence with summer temperatures.

CONCLUSIONS

High elevation and northern latitude tree ring chronologies from the northern hemisphere have proven utility for summer temperature reconstruction (LaMarche 1974, LaMarche and Stockton 1974, Briffa et al. 1990, 1992, 1998, Graumlich 1993, Luckman et al. 1997, Biondi et al. 1999). Heat and water constraints on conifer physiology at upper treeline have been well studied (Wardle 1974, Tranquillini 1979). Carbon assimilation is limited by the length and magnitude of warm temperatures during the growing season and by water availability to plants. Thus temperature and precipitation are two of several environmental variables that interact in a complex, nonlinear manner to constrain tree distribution, affect tree growth, and provide the biological justification for dendroclimatology (Fritts 1976). On high-elevation sites in the northern hemisphere, annual tree ring growth of conifers is generally positively correlated with with spring and/or summer temperature (LaMarche and Stockton 1974, Graumlich and Brubaker 1986, Peterson et al. 1990, Luckman et al. 1997) and winter and spring precipitation (Kienast and Schweingruber 1986, Peterson et al. 1990, Graumlich 1993).

Inverse correlations of growth with spring temperature are less common but have also been reported. LaMarche and Stockton (1974) noted both inverse correlations with spring temperature and positive correlations with summer temperature in near-treeline bristlecone pine (*Pinus longaeva* D.K. Bailey and *P. aristata* Engelm.) tree ring series from the Colorado Front Range and Great Basin, Nevada. They suggested that the inverse relationship is explained by the loss of photosynthates from respiration on warm spring days.

Biondi (1993) investigated the climatic response of European beech (*Fagus sylvatica* L.) in the mountains of central Italy and reported that annual ring-width growth was inversely correlated with April temperature, and positively correlated with December precipitation. His interpretation is that adequate winter snowfall coupled with cool springs slowed rates of snow melt and provided sufficient water for trees during the dry growing season. Perkins and Swetnam (1996) also suggested that whitebark pine annual ring growth may be favored by cool springs and delayed snow melt, a site water-balance effect.

Another possible explanation for below average ring-width growth with warm spring temperatures, is that radiation loads are enhanced by light reflected off the snow surface at high elevations, thereby raising ambient air temperatures and resulting in early onset of photosynthesis and transpiration. Water may be unavailable to roots at still low soil temperatures, resulting in desiccation, xylem cavitation, reduced photosynthate, and subsequent reduced annual ring growth (Fritts 1976, LaMarche and Stockton 1974, Tranquillini 1979) Graumlich (1991) also found an inverse correlation between lodgepole pine (*Pinus contorta* Dougl.) growth and April temperature but suggested it was not easily interpretable. The physiological explanations for above average ring-width growth with cool spring temperatures and below average growth with warm temperatures require further research to clarify the relationship of tree growth, spring heat budgets and site

water availability. Precipitation varies widely within the central Idaho region and with elevation (Emmett 1975, Steele 1981). Including snowpack measurements from elevations near the site chronologies as a potential predictor variables may improve the climate reconstruction from these high-elevation trees as well as provide insights to the ecophysiological processes affecting whitebark pine.

Lowered sensitivity of high-latitude tree growth to summer temperatures has been reported in recent decades (Briffa et al. 1998). Thus spring temperature reconstructions may become increasingly important for detecting past climate variability. The spring temperature reconstruction presented here is among the longest climate reconstructions in North America and is expected to be useful for testing climate simulation models and enhancing the spatial and temporal network of proxy climate data.

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Table 5-1. Crossdating statistics.

Time interval	AD 726-1992
Chronology length	1267 years
Number of trees	24
Number of cores (series)	53
Mean segment length	467 years
Series inter-correlation	0.55
Average mean sensitivity	0.22
Mean standard deviation	0.18 mm

Table 5-2. Pearson's correlation coefficients for Idaho US
historical weather stations and spring temperature.

	April	May	April-May
Ketchum	-0.42	-0.34	-0.47
New Meadows	-0.42	-0.36	-0.48
Ketchum-New Meadows			-0.49

Table 5-3. Calibration statistics for average April-May temperature and tree growth for the periods 1909-1950, 1951-1992 and 1909-1992.

Period	Slope	Intercept	F-value	p > F	R ²
1909-1950	-6.96	14.68	21.2	0.0001	0.37
1951-1992	-5.77	12.77	22.5	0.0001	0.41
1909-1992	-7.78	14.95	49.14	0.0001	0.41

Table 5-4. Results of verification tests between observed and predicted temperature between 1909-1950 and 1951-1992.

Calib. period	Verif. period	Correl. coeff.	Reduction of error	Product means test	Signs test
1909-1950	1951-1992	0.53	0.87	2.55	13
1951-1992	1909-1950	0.45	0.18	* 1.15	13

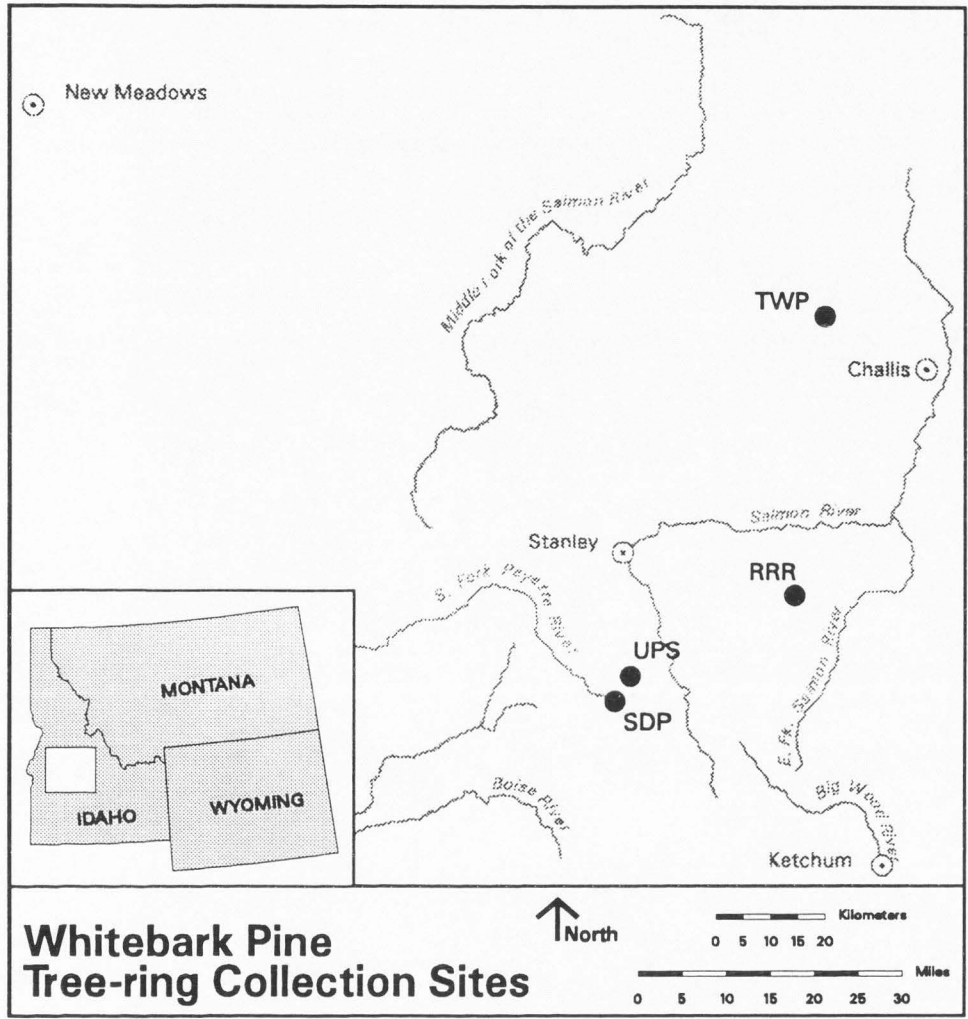


Fig. 5-1. Central Idaho whitebark pine chronology sites. RRR, Railroad Ridge; SDP, Sandpass; UPS, Upper Sandpass; TWP, Twin Peaks.

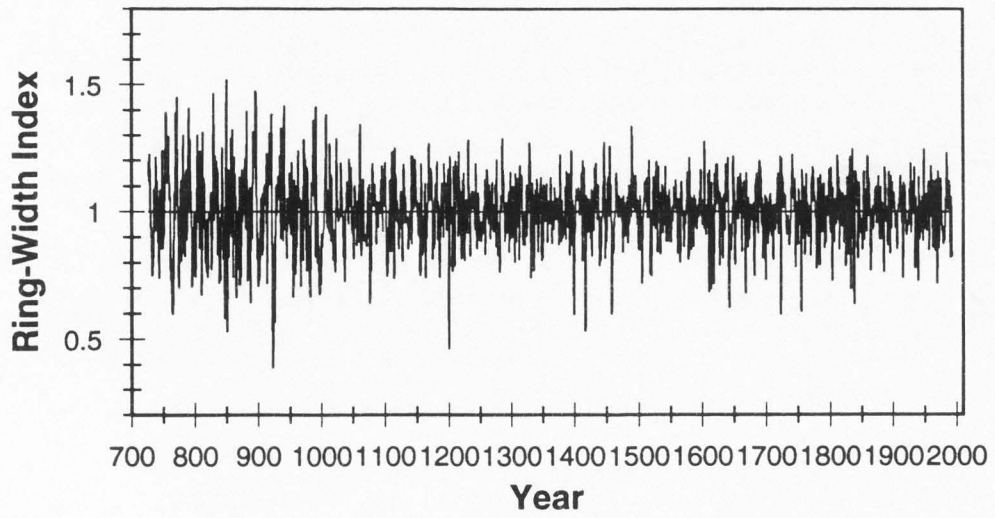


Fig. 5-2. Whitebark pine master ring-width chronology

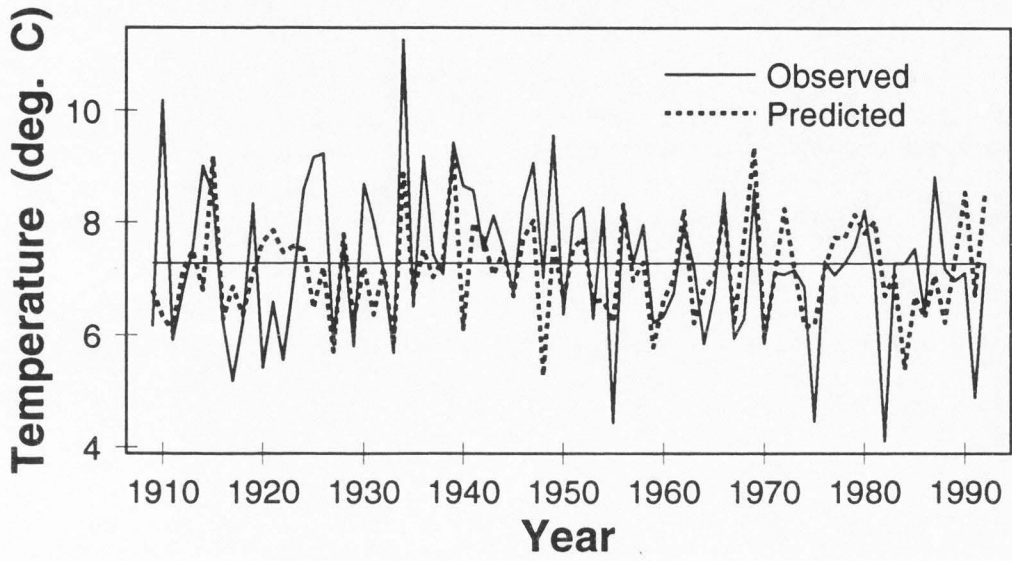


Fig. 5-3. Instrumental and predicted spring temperatures.

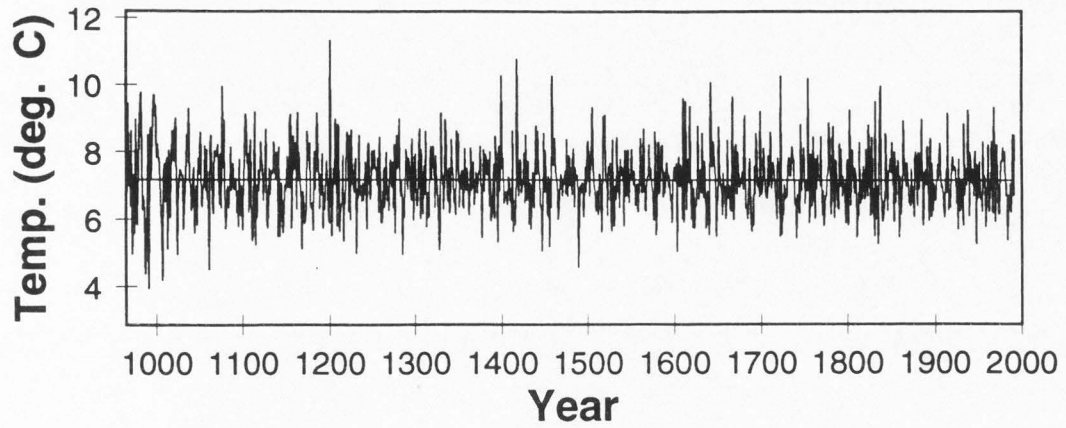


Fig. 5-4. Reconstructed average April-May temperatures.

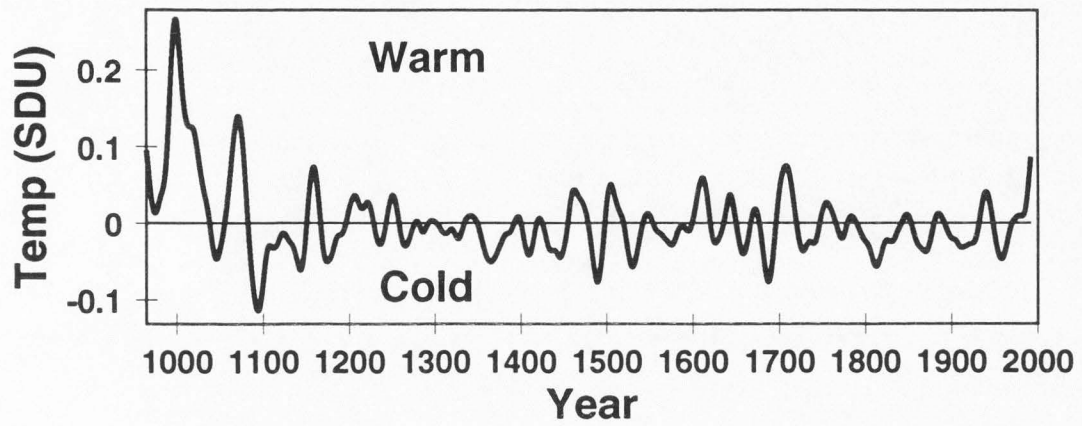


Fig. 5-5. Fifty-year smooth on average April-May temperatures in SDU units.

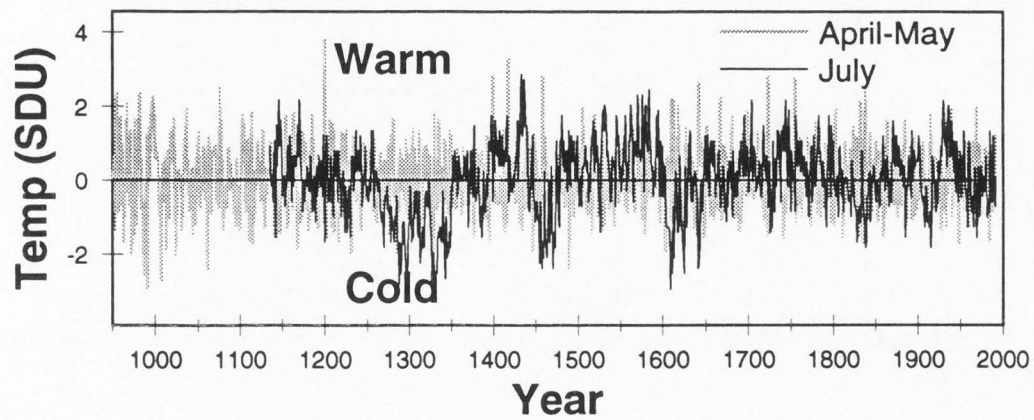


Fig. 5-6. Comparison of reconstructed average April-May and July temperatures from tree rings from central Idaho.

CHAPTER 6

CONCLUSION

The traditional definition of plant population or community stability, self-perpetuation in the absence of disturbance, often applied to shade tolerant climax dominants, is not appropriate for the cold, dry environments of treeline where shade intolerant whitebark pines occur. Although these are often called climax, and are sustainable high-elevation forests, they are so because of the stabilizing influences of disturbances. I have used another common definition of stability, the ability of populations or communities to recover from disturbance to the same pre-disturbance association, and have used as a metric the stable size, reverse-J, or negative exponential distribution as evidence of self-sustainability. It appears that treeline stands of whitebark pine are currently self-perpetuating or stable.

This self-replacing state may be explained in part by past mountain pine beetle infestations (Chapter 4). Mountain pine beetles attack large-diameter trees in high-density stands creating gaps (openings) and providing growing space for recruitment (Chapter 3). Thus beetles, as disturbance agents, act as a negative feedback regulatory mechanism to maintain self-perpetuating whitebark pine forests. Reproductive survivors of the ca. 1930 mountain pine beetle epidemic are the seed sources for the next generation of trees.

Clark's nutcrackers disperse the heavy non-winged whitebark pine seeds across landscapes and are the principal agent of whitebark pine establishment. However, local-scale stand structural variables affect seedling establishment much as they do wind-dispersed intolerant pines. Live overstory trees have a negative effect on seedling establishment probably as a consequence of belowground interference competition for patchy and limited nutrients and water, and aboveground interference for light. Large dead trees also have a negative effect on establishment, but few smaller dead trees may

cast enough shade to reduce evapotranspiration, increase long wave radiation re-emittance, and create favorable microsite conditions for seedlings, thereby positively affecting establishment.

As a result of this research, the conceptual model (Fig. 1-1) has been expanded (Fig. 6-1). The addition of the seedling whitebark pine represented schematically by the small scraggly tree is positively affected by Clark's nutcracker, but negatively affected by large live trees (Fig. 6-1). Establishment depends on open canopy conditions, such as those created by mountain pine beetles or fire. Thus the net effect of mountain pine beetle on seedling establishment is positive (signs of arrows: $- * - = +$, Fig. 6-1).

The addition of subalpine fir to the schematic (fir tree silhouette Fig. 6-1) represents the potential successional trend toward subalpine fir as a codominant. Large shade tolerant subalpine fir will replace intolerant whitebark (negative interaction) (Fig. 6-1). Whitebark pine facilitate intermediate to mature subalpine fir (positive interaction) and the effect of mature whitebark pine on subalpine fir establishment appears to be negligible (no interaction) (Chapter 3 and Fig. 6-1).

The conceptual model summarizes the direction of influence of the dispersal agent Clark's nutcracker; a primary disturbance agent, mountain pine beetle; and the principal competitor, subalpine fir, on treeline populations of whitebark pine. This system approach incorporates interactions of biotic factors and indirectly abiotic factors structuring whitebark pine populations. The identification and direction of influence of these factors result from the empirical statistical models used in this research (Chapter 3 and 4). Their predictive power is robust in statistical terms and may be useful for management activities involving conservation and restoration of whitebark pine.

MOUNTAIN PINE BEETLE DISTURBANCE

Large diameter whitebark pine in dense stands are more susceptible to mountain pine beetle attacks and mortality than are small trees and stands with low basal areas (Chapter 4). Thus, as whitebark pine stands mature they become susceptible to infestation by mountain pine beetles (Chapter 4). The gaps created by death of overstory trees may be beneficial to whitebark pine recruitment (Chapter 3) in areas of low white pine blister rust, but this effect would be reversed with the spread of blister rust. Beetle-caused mortality of mature cone-bearing trees, especially those with natural blister rust resistance, is expected to be devastating to whitebark pine populations (Chapters 1-5). Thinning practices should be evaluated critically with respect to blister rust presence and mountain pine beetle population levels. Rust-resistant and vigorous trees may be treated with an insecticide to give them temporary protection from beetle attack.

Tree-level and stand-level susceptibility characteristics of whitebark pine are similar to other pines that are attacked by mountain pine beetles (Chapter 4). While the qualitative generalization is similar, the quantitative thresholds are different (Chapter 4). As a management strategy for other pines, reduction of basal area, group selection, and thinning of stands have reduced basal areas and improved individual tree vigor, thereby lowering the risk of individual tree and stand attack. This may be recommended for whitebark pine as well, but needs experimental field verification.

SUCCESSIONAL STATUS

While this work corroborates that upper treeline whitebark pine stands in central Idaho are self-sustaining, a cautious interpretation is advised. Whitebark pine's principal competitor, subalpine fir, is present in all size classes, suggesting potential replacement of whitebark pine or codominant status with whitebark pine. Patchy, low to moderate

severity fires would enhance whitebark pine populations by killing subalpine fir and opening the sites for regeneration. Alternatively, with downslope fuel build-up, increased fuel loading from the fall of large ca. 1930 beetle-killed snags, and projected global warming, the likelihood of lethal stand replacing high-elevation wildfires increases. Thus the potential for whitebark pine conversion to non-forested, alpine parklands over centennial time frames is as reasonable as successional replacement of whitebark pine by subalpine fir in the absence of stabilizing disturbances.

The restoration of fire to these high-elevation forests is recommended, but this is not a simple management issue. Loss of blister rust-resistant individuals and trees of high dendrochronological value is possible. Alternatively, without periodic fire to create openings for seedling establishment, and thin stands, other shade tolerant species such as subalpine fir will replace whitebark pine. One advantage of prescribed fire in these habitats is that they are remote and rocky. Patchy, low severity fires would be expected and are less threatening to humans. Although there would be a temporary loss of aesthetic values, primarily to recreationists, on decadal to centennial scales the species would have the best chance to perpetuate itself.

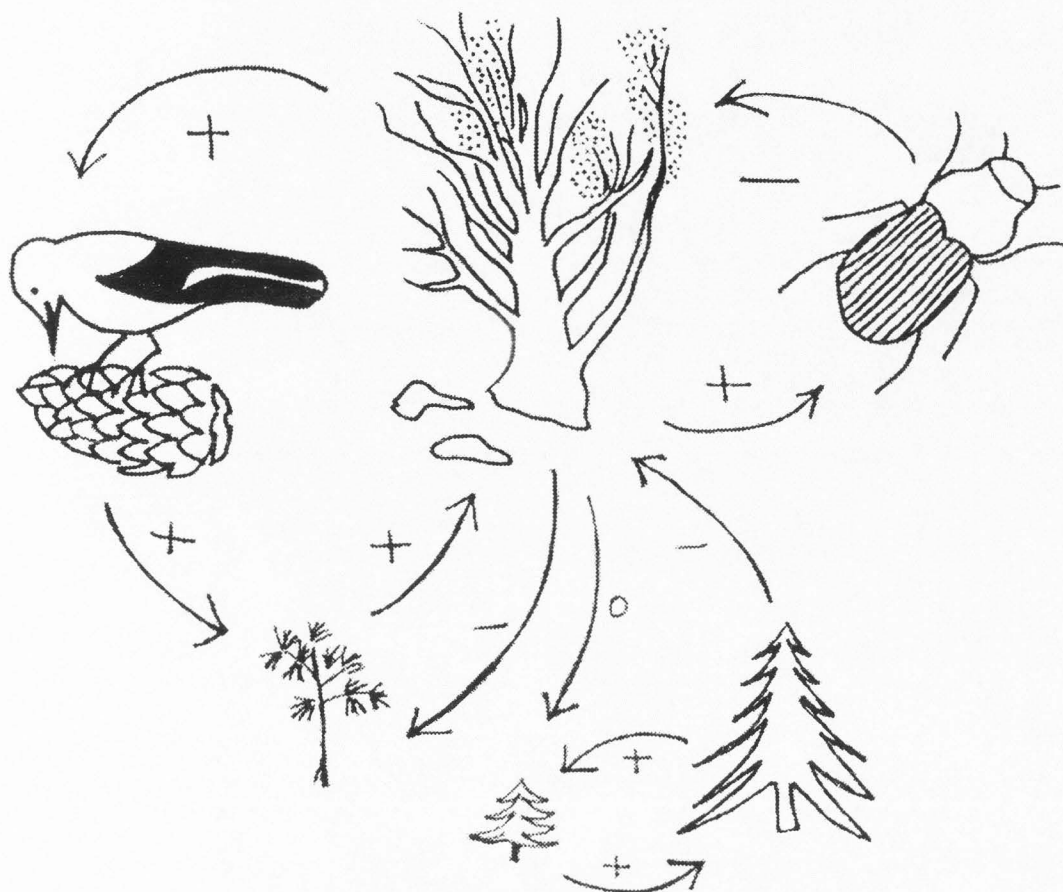


Fig. 6-1. Revised schematic representation of the whitebark pine system with principal biotic components, Clark's nutcracker mountain pine beetle, and subalpine fir. The arrows connecting the variables represent the direction of effect and rates of change between the biotic state variables of the system.

APPENDICES

APPENDIX A.
DENSITIES OF WHITEBARK PINE AND SUBALPINE FIR LISTED
BY DIAMETER CLASSES

ABK 1930

mdpt	w30freq	w30logfreq	w30relfreq	w30cumfreq
2.54	134.086	4.89848	0.184466	134.086
7.62	144.671	4.97447	0.199029	278.757
12.7	127.029	4.84441	0.174757	405.786
17.78	127.029	4.84441	0.174757	532.814
22.86	119.971	4.78725	0.165049	652.786
27.94	59.9857	4.09411	0.0825243	712.771
33.02	14.1143	2.64719	0.0194175	726.886

ABK 1998

mdpt	wfreq	wlogfreq	wrelfreq	wcumfreq	afreq	alogfreq	arelfreq	acumfreq
2.54	4481.29	8.40767	0.909091	4481.29	1358.5	7.21414	0.869074	1358.5
7.62	158.786	5.06756	0.0322119	4640.07	52.9286	3.96894	0.03386	1411.43
12.7	59.9857	4.09411	0.0121689	4700.06	84.6857	4.43895	0.0541761	1496.11
17.78	74.1	4.30542	0.0150322	4774.16	49.4	3.89995	0.0316027	1545.51
22.86	88.2143	4.47977	0.0178955	4862.37	10.5857	2.35951	0.00677201	1556.1
27.94	35.2857	3.56348	0.0071582	4897.66	7.05714	1.95404	0.00451467	1563.16
33.02	28.2286	3.34033	0.00572656	4925.89	0	0	0	0
38.1	3.52857	1.26089	0.00071582	4929.41	0	0	0	0

AND 1930

mdpt	w30freq	w30logfreq	w30relfreq	w30cumfreq
2.54	222.3	5.40403	0.298578	222.3
7.62	229.357	5.43528	0.308057	451.657
12.7	165.843	5.11104	0.222749	617.5
17.78	67.0429	4.20533	0.0900474	684.543
22.86	38.8143	3.65879	0.0521327	723.357
27.94	10.5857	2.35951	0.014218	733.943
33.02	10.5857	2.35951	0.014218	744.529

AND 1998

mdpt	wfreq	wlogfreq	wrelfreq	wcumfreq	afreq	alogfreq	arelfreq	acumfreq
2.54	846.857	6.74153	0.530973	846.857	723.357	6.5839	0.843621	723.357
7.62	35.2857	3.56348	0.0221239	882.143	1	0	0.00116626	724.357
12.7	137.614	4.92445	0.0862832	1019.76	49.4	3.89995	0.0576132	773.757
17.78	105.857	4.66209	0.0663717	1125.61	42.3429	3.7458	0.0493827	816.1
22.86	176.429	5.17292	0.110619	1302.04	17.6429	2.87033	0.0205761	833.743
27.94	123.5	4.81624	0.0774336	1425.54	10.5857	2.35951	0.0123457	844.329
33.02	81.1571	4.39639	0.050885	1506.7	14.1143	2.64719	0.0164609	858.443
38.1	42.3429	3.7458	0.0265487	1549.04	0	0	0	0
43.18	24.7	3.2068	0.0154867	1573.74	0	0	0	0
48.26	7.05714	1.95404	0.00442478	1580.8	0	0	0	0
53.34	7.05714	1.95404	0.00442478	1587.86	0	0	0	0
58.42	7.05714	1.95404	0.00442478	1594.91	0	0	0	0

ASO 1930

mdpt	w30freq	w30logfreq	w30relfreq	w30cumfreq
2.54	790.4	6.67254	0.814545	790.4
7.62	151.729	5.02209	0.156364	942.129
12.7	21.1714	3.05265	0.0218182	963.3

ASO 1998

mdpt	wfreq	wlogfreq	wrelfreq	wcumfreq	afreq	alogfreq	arelfreq	acumfreq
2.54	1376.14	7.22704	0.580357	1376.14	211.714	5.35524	0.857143	211.714
7.62	352.857	5.86606	0.14881	1729.	1	0	0.00404858	212.714
12.7	370.5	5.91485	0.15625	2099.5	35.2857	3.56348	0.142857	248.
17.78	158.786	5.06756	0.0669643	2258.29	0	0	0	0
22.86	91.7429	4.51899	0.0386905	2350.03	0	0	0	0
27.94	21.1714	3.05265	0.00892857	2371.2	0	0	0	0

AVL 1930

mdpt	w30freq	w30logfreq	w30relfreq	w30cumfreq
2.54	222.3	5.40403	0.310345	222.3
7.62	130.91	4.87451	0.182759	353.21
12.7	125.97	4.83604	0.175862	479.18
17.78	69.16	4.23642	0.0965517	548.34
22.86	54.34	3.99526	0.0758621	602.68
27.94	49.4	3.89995	0.0689655	652.08
33.02	29.64	3.38912	0.0413793	681.72
38.1	14.82	2.69598	0.0206897	696.54
43.18	2.47	0.904218	0.00344828	699.01
48.26	7.41	2.00283	0.0103448	706.42
53.34	4.94	1.59737	0.00689655	711.36
58.42	2.47	0.904218	0.00344828	713.83
63.5	2.47	0.904218	0.00344828	716.3

AVL 1998

mdpt	wfreq	wlogfreq	wrelfreq	wcumfreq	afreq	alogfreq	arelfreq	acumfreq
2.54	1494.35	7.30945	0.699422	1494.35	901.55	6.80412	0.960526	901.55
7.62	135.85	4.91155	0.0635838	1630.2	12.35	2.51366	0.0131579	913.9
12.7	116.09	4.75437	0.0543353	1746.29	14.82	2.69598	0.0157895	928.72
17.78	76.57	4.33821	0.0358382	1822.86	2.47	0.904218	0.00263158	931.19
22.86	93.86	4.5418	0.0439306	1916.72	1	0	0.00106542	932.19
27.94	96.33	4.56778	0.0450867	2013.05	1	0	0.00106542	933.19
33.02	32.11	3.46917	0.0150289	2045.16	1	0	0.00106542	934.19
38.1	39.52	3.67681	0.0184971	2084.68	1	0	0.00106542	935.19
43.18	24.7	3.2068	0.0115607	2109.38	2.47	0.904218	0.00263158	937.66
48.26	14.82	2.69598	0.00693642	2124.2	2.47	0.904218	0.00263158	940.13
53.34	7.41	2.00283	0.00346821	2131.61	1	0	0.00106542	941.13
58.42	4.94	1.59737	0.00231214	2136.55	1	0	0.00106542	942.13
63.5	0	0	0	0	1	0	0.00106542	943.13
68.58	0	0	0	0	2.47	0.904218	0.00263158	945.6

BGH 1930

mdpt	w30freq	w30logfreq	w30relfreq	w30cumfreq
2.54	324.188	5.78132	0.35	324.188
7.62	104.975	4.65372	0.113333	429.163
12.7	67.925	4.2184	0.0733333	497.088
17.78	111.15	4.71088	0.12	608.238
22.86	61.75	4.12309	0.0666667	669.988
27.94	64.8375	4.17188	0.07	734.825
33.02	64.8375	4.17188	0.07	799.663
38.1	46.3125	3.83541	0.05	845.975
43.18	33.9625	3.52526	0.0366667	879.938
48.26	15.4375	2.7368	0.0166667	895.375
53.34	12.35	2.51366	0.0133333	907.725
58.42	9.2625	2.22597	0.01	916.988
63.5	3.0875	1.12736	0.00333333	920.075
68.58	3.0875	1.12736	0.00333333	923.162
73.66	3.0875	1.12736	0.00333333	926.25

BGH 1998

mdpt	wfreq	wlogfreq	wrelfreq	wcumfreq	afreq	alogfreq	arelfreq	acumfreq
2.54	833.625	6.72578	0.647482	833.625	1	0	0.0404858	1
7.62	123.5	4.81624	0.0959233	957.125	1	0	0.0404858	2
12.7	123.5	4.81624	0.0959233	1080.63	9.2625	2.22597	0.375	11.2625
17.78	80.275	4.38546	0.0623501	1160.9	6.175	1.82051	0.25	17.4375
22.86	46.3125	3.83541	0.0359712	1207.21	1	0	0.0404858	18.4375
27.94	30.875	3.42995	0.0239808	1238.09	3.0875	1.12736	0.125	21.525
33.02	15.4375	2.7368	0.0119904	1253.53	3.0875	1.12736	0.125	24.6125
38.1	27.7875	3.32459	0.0215827	1281.31	1	0	0.0404858	25.6125
43.18	3.0875	1.12736	0.00239808	1284.4	3.0875	1.12736	0.125	28.7
48.26	3.0875	1.12736	0.00239808	1287.49	0	0	0	0

BLK 1930

mdpt	w30freq	w30logfreq	w30relfreq	w30cumfreq
2.54	370.5	5.91485	0.47619	370.5
7.62	89.5375	4.49466	0.115079	460.038
12.7	58.6625	4.0718	0.0753968	518.7
17.78	37.05	3.61227	0.047619	555.75
22.86	67.925	4.2184	0.0873016	623.675
27.94	40.1375	3.69231	0.0515873	663.813
33.02	15.4375	2.7368	0.0198413	679.25
38.1	33.9625	3.52526	0.0436508	713.212
43.18	21.6125	3.07327	0.0277778	734.825
48.26	9.2625	2.22597	0.0119048	744.088
53.34	18.525	2.91912	0.0238095	762.612
58.42	1	0	0.00128526	763.613
63.5	9.2625	2.22597	0.0119048	772.875
68.58	1	0	0.00128526	773.875
73.66	1	0	0.00128526	774.875
78.74	6.175	1.82051	0.00793651	781.05

BLK 1998

mdpt	wfreq	wlogfreq	wrelfreq	wcumfreq	afreq	alogfreq	arelfreq	acumfreq
2.54	849.063	6.74413	0.577731	849.063	123.5	4.81624	0.784314	123.5
7.62	277.875	5.62717	0.189076	1126.94	15.4375	2.7368	0.0980392	138.938
12.7	166.725	5.11635	0.113445	1293.66	15.4375	2.7368	0.0980392	154.375
17.78	92.625	4.52856	0.0630252	1386.29	1	0	0.00635072	155.375
22.86	33.9625	3.52526	0.0231092	1420.25	3.0875	1.12736	0.0196078	158.463
27.94	24.7	3.2068	0.0168067	1444.95	0	0	0	0
33.02	9.2625	2.22597	0.00630252	1454.21	0	0	0	0
38.1	9.2625	2.22597	0.00630252	1463.48	0	0	0	0
43.18	6.175	1.82051	0.00420168	1469.65	0	0	0	0

BLP 1930

mdpt	w30freq	w30logfreq	w30relfreq	w30cumfreq
2.54	484.12	6.18233	0.525469	484.12
7.62	214.89	5.37013	0.233244	699.01
12.7	140.79	4.94727	0.152815	839.8
17.78	49.4	3.89995	0.0536193	889.2
22.86	12.35	2.51366	0.0134048	901.55
27.94	9.88	2.29051	0.0107239	911.43
33.02	2.47	0.904218	0.00268097	913.9
38.1	2.47	0.904218	0.00268097	916.37
43.18	2.47	0.904218	0.00268097	918.84
48.26	1	0	0.00108541	919.84
53.34	1	0	0.00108541	920.84
58.42	2.47	0.904218	0.00268097	923.31

BLP 1998

mdpt	wfreq	wlogfreq	wrelfreq	wcumfreq	afreq	alogfreq	arelfreq	acumfreq
2.54	506.35	6.22723	0.388994	506.35	49.4	3.89995	0.645161	49.4
7.62	111.15	4.71088	0.085389	617.5	12.35	2.51366	0.16129	61.75
12.7	180.31	5.19468	0.13852	797.81	7.41	2.00283	0.0967742	69.16
17.78	143.26	4.96466	0.110057	941.07	2.47	0.904218	0.0322581	71.63
22.86	150.67	5.01509	0.11575	1091.74	4.94	1.59737	0.0645161	76.57
27.94	113.62	4.73286	0.0872865	1205.36	0	0	0	0
33.02	49.4	3.89995	0.0379507	1254.76	0	0	0	0
38.1	29.64	3.38912	0.0227704	1284.4	0	0	0	0
43.18	4.94	1.59737	0.00379507	1289.34	0	0	0	0
48.26	9.88	2.29051	0.00759013	1299.22	0	0	0	0
53.34	1	0	0.000768232	1300.22	0	0	0	0
58.42	2.47	0.904218	0.00189753	1302.69	0	0	0	0

CRS 1930

mdpt	w30freq	w30logfreq	w30relfreq	w30cumfreq
2.54	165.49	5.10891	0.308756	165.49
7.62	158.08	5.0631	0.294931	323.57
12.7	108.68	4.68841	0.202765	432.25
17.78	59.28	4.08227	0.110599	491.53
22.86	24.7	3.2068	0.0460829	516.23
27.94	12.35	2.51366	0.0230415	528.58
33.02	7.41	2.00283	0.0138249	535.99

CRS 1998

mdpt	wfreq	wlogfreq	wrelfreq	wcumfreq	afreq	alogfreq	arelfreq	acumfreq
2.54	1160.9	7.05695	0.708899	1160.9	1197.95	7.08837	0.971944	1197.95
7.62	1	0	0.000610646	1161.9	1	0	0.000811339	1198.95
12.7	76.57	4.33821	0.0467572	1238.47	17.29	2.85013	0.0140281	1216.24
17.78	86.45	4.45957	0.0527903	1324.92	7.41	2.00283	0.00601202	1223.65
22.86	116.09	4.75437	0.0708899	1441.01	9.88	2.29051	0.00801603	1233.53
27.94	79.04	4.36995	0.0482655	1520.05	0	0	0	0
33.02	54.34	3.99526	0.0331825	1574.39	0	0	0	0
38.1	34.58	3.54328	0.0211161	1608.97	0	0	0	0
43.18	9.88	2.29051	0.00603318	1618.85	0	0	0	0
48.26	12.35	2.51366	0.00754148	1631.2	0	0	0	0
53.34	2.47	0.904218	0.0015083	1633.67	0	0	0	0
58.42	4.94	1.59737	0.00301659	1638.61	0	0	0	0

GOA 1930

mdpt	w30freq	w30logfreq	w30relfreq	w30cumfreq
2.54	61.75	4.12309	0.294118	61.75
7.62	21.6125	3.07327	0.102941	83.3625
12.7	21.6125	3.07327	0.102941	104.975
17.78	18.525	2.91912	0.0882353	123.5
22.86	18.525	2.91912	0.0882353	142.025

27.94	6.175	1.82051	0.0294118	148.2
33.02	9.2625	2.22597	0.0441176	157.463
38.1	9.2625	2.22597	0.0441176	166.725
43.18	6.175	1.82051	0.0294118	172.9
48.26	9.2625	2.22597	0.0441176	182.163
53.34	6.175	1.82051	0.0294118	188.338
58.42	3.0875	1.12736	0.0147059	191.425
63.5	1	0	0.00476304	192.425
68.58	6.175	1.82051	0.0294118	198.6
73.66	1	0	0.00476304	199.6
78.74	3.0875	1.12736	0.0147059	202.688
83.82	1	0	0.00476304	203.688
88.9	1	0	0.00476304	204.688
93.98	3.0875	1.12736	0.0147059	207.775
99.06	6.175	1.82051	0.0294118	213.95

GOA 1998

mdpt	wfreq	wlogfreq	wrelfreq	wcumfreq	afreq	alogfreq	arelfreq	acumfreq
2.54	787.313	6.66863	0.775076	787.313	1883.38	7.54082	0.844875	1883.38
7.62	92.625	4.52856	0.0911854	879.938	200.688	5.30175	0.0900277	2084.06
12.7	43.225	3.76642	0.0425532	923.163	95.7125	4.56135	0.0429363	2179.78
17.78	6.175	1.82051	0.00607903	929.338	21.6125	3.07327	0.00969529	2201.39
22.86	21.6125	3.07327	0.0212766	950.95	15.4375	2.7368	0.00692521	2216.83
27.94	15.4375	2.7368	0.0151976	966.388	9.2625	2.22597	0.00415512	2226.09
33.02	18.525	2.91912	0.0182371	984.913	3.0875	1.12736	0.00138504	2229.18
38.1	12.35	2.51366	0.0121581	997.263	0	0	0	0
43.18	12.35	2.51366	0.0121581	1009.61	0	0	0	0
48.26	6.175	1.82051	0.00607903	1015.79	0	0	0	0

NRR 1930

mdpt	w30freq	w30logfreq	w30relfreq	w30cumfreq
2.54	296.4	5.69171	0.409556	296.4
7.62	239.59	5.47893	0.331058	535.99
12.7	111.15	4.71088	0.153584	647.14
17.78	54.34	3.99526	0.0750853	701.48
22.86	19.76	2.98366	0.0273038	721.24
27.94	2.47	0.904218	0.00341297	723.71

NRR 1998

mdpt	wfreq	wlogfreq	wrelfreq	wcumfreq	afreq	alogfreq	arelfreq	acumfreq
2.54	456.95	6.12457	0.412027	456.95	2383.55	7.77635	0.978702	2383.55
7.62	12.35	2.51366	0.0111359	469.3	1	0	0.000410607	2384.55
12.7	130.91	4.87451	0.11804	600.21	22.23	3.10144	0.00912779	2406.78
17.78	195.13	5.27367	0.175947	795.34	12.35	2.51366	0.00507099	2419.13
22.86	133.38	4.8932	0.120267	928.72	7.41	2.00283	0.0030426	2426.54
27.94	91.39	4.51514	0.0824053	1020.11	4.94	1.59737	0.0020284	2431.48
33.02	39.52	3.67681	0.0356347	1059.63	1	0	0.000410607	2432.48
38.1	29.64	3.38912	0.0267261	1089.27	2.47	0.904218	0.0010142	2434.95
43.18	17.29	2.85013	0.0155902	1106.56	2.47	0.904218	0.0010142	2437.42
48.26	2.47	0.904218	0.00222717	1109.03	0	0	0	0

RRB 1930

mdpt	w30freq	w30logfreq	w30relfreq	w30cumfreq
2.54	107.033	4.67314	0.0928571	107.033
7.62	98.8	4.5931	0.0857143	205.833
12.7	107.033	4.67314	0.0928571	312.867
17.78	181.133	5.19923	0.157143	494.
22.86	222.3	5.40403	0.192857	716.3
27.94	156.433	5.05263	0.135714	872.733
33.02	156.433	5.05263	0.135714	1029.17
38.1	57.6333	4.0541	0.05	1086.8
43.18	16.4667	2.80134	0.0142857	1103.27
48.26	41.1667	3.71763	0.0357143	1144.43
53.34	8.23333	2.10819	0.00714286	1152.67

RRB 1998

mdpt	wfreq	wlogfreq	wrelfreq	wcumfreq	afreq	alogfreq	arelfreq	acumfreq
2.54	494.	6.20254	0.588235	494.	0	0	0	0
7.62	123.5	4.81624	0.147059	617.5	0	0	0	0
12.7	41.1667	3.71763	0.0490196	658.667	0	0	0	0
17.78	41.1667	3.71763	0.0490196	699.833	0	0	0	0
22.86	24.7	3.2068	0.0294118	724.533	0	0	0	0
27.94	24.7	3.2068	0.0294118	749.233	0	0	0	0
33.02	24.7	3.2068	0.0294118	773.933	0	0	0	0
38.1	32.9333	3.49449	0.0392157	806.867	0	0	0	0
43.18	24.7	3.2068	0.0294118	831.567	0	0	0	0
48.26	1	0	0.00119076	832.567	0	0	0	0
53.34	8.23333	2.10819	0.00980392	840.8	0	0	0	0

SIL 1930

mdpt	w30freq	w30logfreq	w30relfreq	w30cumfreq
2.54	77.6286	4.35194	0.2	77.6286
7.62	42.3429	3.7458	0.109091	119.971
12.7	45.8714	3.82584	0.118182	165.843
17.78	59.9857	4.09411	0.154545	225.829
22.86	56.4571	4.03348	0.145455	282.286
27.94	59.9857	4.09411	0.154545	342.271
33.02	14.1143	2.64719	0.0363636	356.386
38.1	14.1143	2.64719	0.0363636	370.5
43.18	7.05714	1.95404	0.0181818	377.557
48.26	7.05714	1.95404	0.0181818	384.614
53.34	3.52857	1.26089	0.00909091	388.143

SIL 1998

mdpt	wfreq	wlogfreq	wrelfreq	wcumfreq	afreq	alogfreq	arelfreq	acumfreq
2.54	3052.21	8.02362	0.940217	3052.21	617.5	6.42568	0.892857	617.5
7.62	35.2857	3.56348	0.0108696	3087.5	1.5	0.405	0.00144592	618.5
12.7	35.2857	3.56348	0.0108696	3122.79	24.7	3.2068	0.0357143	643.2
17.78	10.5857	2.35951	0.00326087	3133.37	17.6429	2.87033	0.0255102	660.843
22.86	31.7571	3.45812	0.00978261	3165.13	24.7	3.2068	0.0357143	685.543
27.94	24.7	3.2068	0.0076087	3189.83	1.5	0.405	0.00144592	686.543
33.02	35.2857	3.56348	0.0108696	3225.11	3.52857	1.26089	0.00510204	690.071
38.1	3.52857	1.26089	0.00108696	3228.64	3.52857	1.26089	0.00510204	693.6
43.18	1	0	0.000308044	3229.64	0	0	0	0
48.26	14.1143	2.64719	0.00434783	3243.76	0	0	0	0
53.34	1	0	0.000308044	3244.76	0	0	0	0
58.42	1	0	0.000308044	3245.76	0	0	0	0
63.5	1	0	0.000308044	3246.76	0	0	0	0
68.58	3.52857	1.26089	0.00108696	3250.29	0	0	0	0

TLK 1930

mdpt	w30freq	w30logfreq	w30relfreq	w30cumfreq
2.54	376.675	5.93138	0.508333	376.675
7.62	157.463	5.05919	0.2125	534.138
12.7	74.1	4.30542	0.1	608.238
17.78	12.35	2.51366	0.0166667	620.588
22.86	27.7875	3.32459	0.0375	648.375
27.94	21.6125	3.07327	0.0291667	669.988
33.02	15.4375	2.7368	0.0208333	685.425
38.1	9.2625	2.22597	0.0125	694.688
43.18	12.35	2.51366	0.0166667	707.038
48.26	6.175	1.82051	0.00833333	713.213
53.34	9.2625	2.22597	0.0125	722.475
58.42	3.0875	1.12736	0.00416667	725.563
63.5	15.4375	2.7368	0.0208333	741.

TLK 1998

mdpt	wfreq	wlogfreq	wrelfreq	wcumfreq	afreq	alogfreq	arelfreq	acumfreq
2.54	1096.06	6.99948	0.680077	1096.06	586.625	6.37439	0.811966	586.625
7.62	61.75	4.12309	0.0383142	1157.81	30.875	3.42995	0.042735	617.5
12.7	145.113	4.97751	0.0900383	1302.93	15.4375	2.7368	0.0213675	632.938
17.78	104.975	4.65372	0.0651341	1407.9	40.1375	3.69231	0.0555556	673.075
22.86	104.975	4.65372	0.0651341	1512.88	24.7	3.2068	0.034188	697.775
27.94	61.75	4.12309	0.0383142	1574.63	12.35	2.51366	0.017094	710.125
33.02	12.35	2.51366	0.00766284	1586.98	6.175	1.82051	0.00854701	716.3
38.1	3.0875	1.12736	0.00191571	1590.06	3.0875	1.12736	0.0042735	719.388
43.18	15.4375	2.7368	0.00957854	1605.5	3.0875	1.12736	0.0042735	722.475
48.26	3.0875	1.12736	0.00191571	1608.59	0	0	0	0
53.34	1	0	0.000620472	1609.59	0	0	0	0
58.42	3.0875	1.12736	0.00191571	1612.68	0	0	0	0

TWP 1930

mdpt	w30freq	w30logfreq	w30relfreq	w30cumfreq
2.54	175.988	5.17041	0.358491	175.988
7.62	55.575	4.01773	0.113208	231.563
12.7	74.1	4.30542	0.150943	305.663
17.78	52.4875	3.96058	0.106918	358.15
22.86	21.6125	3.07327	0.0440252	379.763
27.94	12.35	2.51366	0.0251572	392.113
33.02	12.35	2.51366	0.0251572	404.463
38.1	12.35	2.51366	0.0251572	416.813
43.18	30.875	3.42995	0.0628931	447.688
48.26	15.4375	2.7368	0.0314465	463.125
53.34	9.2625	2.22597	0.0188679	472.388
58.42	6.175	1.82051	0.0125786	478.563
63.5	6.175	1.82051	0.0125786	484.738
68.58	6.175	1.82051	0.0125786	490.913

TWP 1998

mdpt	wfreq	wlogfreq	wrelfreq	wcumfreq	afreq	alogfreq	arelfreq	acumfreq
2.54	1420.25	7.25859	0.791738	1420.25	169.813	5.13469	0.617978	169.813
7.62	123.5	4.81624	0.0688468	1543.75	46.3125	3.83541	0.168539	216.125
12.7	108.063	4.68271	0.060241	1651.81	18.525	2.91912	0.0674157	234.65
17.78	27.7875	3.32459	0.0154905	1679.6	21.6125	3.07327	0.0786517	256.263
22.86	40.1375	3.69231	0.0223752	1719.74	3.0875	1.12736	0.011236	259.35
27.94	49.4	3.89995	0.0275387	1769.14	9.2625	2.22597	0.0337079	268.613
33.02	15.4375	2.7368	0.00860585	1784.58	3.0875	1.12736	0.011236	271.7
38.1	9.2625	2.22597	0.00516351	1793.84	3.0875	1.12736	0.011236	274.787

APPENDIX B.
DIAGNOSTICS FOR THE NATURAL LOG FIT OF A NEGATIVE
EXPONENTIAL FUNCTION TO THE MIDPOINTS OF 5-CM
DIAMETER CLASSES

ABK 1930

ParameterTable ->	Estimate	SE	TStat	PValue
1	5.51294	0.438055	12.585	0.0000562461
x	-0.0602626	0.0213914	-2.81714	0.0372336

RSquared -> 0.613491, AdjustedRSquared -> 0.536189,

EstimatedVariance -> 0.330646,

ANOVATable ->	DF	SumOfSq	MeanSq	FRatio	PValue
Model	1	2.6241	2.6241	7.9363	0.0372336
Error	5	1.65323	0.330646		
Total	6	4.27733			

ABK 1998

ParameterTable ->	Estimate	SE	TStat	PValue
1	7.17591	0.754345	9.51277	0.0000769513
x	-0.140798	0.0322127	-4.37087	0.00471456

RSquared -> 0.760999, AdjustedRSquared -> 0.721166,

EstimatedVariance -> 1.12468,

ANOVATable ->	DF	SumOfSq	MeanSq	FRatio	PValue
Model	1	21.4866	21.4866	19.1045	0.00471456
Error	6	6.7481	1.12468		
Total	7	28.2347			

AND 1930

ParameterTable ->	Estimate	SE	TStat	PValue
1	6.16838	0.297228	20.7531	4.81005 10
x	-0.11767	0.0145144	-8.10711	0.000463083

RSquared -> 0.929304, AdjustedRSquared -> 0.915165,

EstimatedVariance -> 0.152224,

```

ANOVA Table ->
      DF  SumOfSq  MeanSq  FRatio  PValue
Model  1    10.005   10.005   65.7253  0.000463083
Error  5     0.761119  0.152224
Total  6     10.7661

```

AND 1998

```

ParameterTable ->
      Estimate  SE      TStat  PValue
      1  6.0205   0.481804  12.4957  1.99466 10-7
      x -0.0687723  0.0137013  -5.01938  0.000522214

```

RSquared -> 0.715862, AdjustedRSquared -> 0.687448,

EstimatedVariance -> 0.692771,

```

ANOVA Table ->
      DF  SumOfSq  MeanSq  FRatio  PValue
Model  1    17.4538   17.4538  25.1942  0.000522214
Error  10    6.92771   0.692771
Total  11    24.3815

```

ASO 1930

```

ParameterTable ->
      Estimate  SE      TStat  PValue
      1  7.63068   0.157264  48.5214  0.0131185
      x -0.356288  0.0181269  -19.6553  0.0323614

```

RSquared -> 0.997418, AdjustedRSquared -> 0.994836,

EstimatedVariance -> 0.0169591,

```

ANOVA Table ->
      DF  SumOfSq  MeanSq  FRatio  PValue
Model  1     6.5518   6.5518  386.329  0.0323614
Error  1     0.0169591  0.0169591
Total  2     6.56876

```

ASO 1998

```

ParameterTable ->
      Estimate  SE      TStat  PValue
      1  7.48256   0.330757  22.6226  0.0000226125
      x -0.144884  0.0188611  -7.68164  0.00154452

```

RSquared -> 0.936516, AdjustedRSquared -> 0.920645,

EstimatedVariance -> 0.160657,

ANOVA Table ->	DF	SumOfSq	MeanSq	F Ratio	P Value
Model	1	9.48001	9.48001	59.0076	0.00154452
Error	4	0.64263	0.160657		
Total	5	10.1226			

AVL 1930

Parameter Table ->	Estimate	SE	T Stat	P Value
1	5.68855	0.256625	22.1667	1.7681 10 ⁻¹⁰
x	-0.0799211	0.00673557	-11.8655	1.30604 10 ⁻⁷

RSquared -> 0.927532, AdjustedRSquared -> 0.920944,

EstimatedVariance -> 0.213083,

ANOVA Table ->	DF	SumOfSq	MeanSq	F Ratio	P Value
Model	1	30.	30.	140.791	1.30604 10 ⁻⁷
Error	11	2.34391	0.213083		
Total	12	32.3439			

AVL 1998

Parameter Table ->	Estimate	SE	T Stat	P Value
1	6.2885	0.33027	19.0405	3.46859 10 ⁻⁹
x	-0.0776187	0.00939209	-8.26427	8.84796 10 ⁻⁶

RSquared -> 0.872283, AdjustedRSquared -> 0.859511,

EstimatedVariance -> 0.325527,

ANOVA Table ->	DF	SumOfSq	MeanSq	F Ratio	P Value	
						-6
Model	1	22.2329	22.2329	68.2982	8.84796	10
Error	10	3.25527	0.325527			
Total	11	25.4882				

BGH 1930

Parameter Table ->	Estimate	SE	T Stat	P Value	
					-10
1	5.68855	0.256625	22.1667	1.7681	10
					-7
x	-0.0799211	0.00673557	-11.8655	1.30604	10

RSquared -> 0.927532, AdjustedRSquared -> 0.920944,

EstimatedVariance -> 0.213083,

ANOVA Table ->	DF	SumOfSq	MeanSq	F Ratio	P Value	
						-7
Model	1	30.	30.	140.791	1.30604	10
Error	11	2.34391	0.213083			
Total	12	32.3439				

BGH 1998

Parameter Table ->	Estimate	SE	T Stat	P Value	
					-8
1	6.33002	0.351754	17.9956	9.32664	10
x	-0.106201	0.0120082	-8.84401	0.0000210692	

RSquared -> 0.90721, AdjustedRSquared -> 0.895612,

EstimatedVariance -> 0.307001,

ANOVA Table ->	DF	SumOfSq	MeanSq	F Ratio	P Value
Model	1	24.0125	24.0125	78.2165	0.0000210692
Error	8	2.45601	0.307001		
Total	9	26.4685			

BLK 1930

ParameterTable ->	Estimate	SE	TStat	PValue
1	5.2831	0.427657	12.3536	6.43712 10
x	-0.0615133	0.00911768	-6.74659	9.37072 10

RSquared -> 0.764771, AdjustedRSquared -> 0.747969,

EstimatedVariance -> 0.729416,

ANOVATable ->	DF	SumOfSq	MeanSq	FRatio	PValue
Model	1	33.2004	33.2004	45.5165	9.37072 10
Error	14	10.2118	0.729416		
Total	15	43.4123			

BLK 1998

ParameterTable ->	Estimate	SE	TStat	PValue
1	6.66624	0.208552	31.9643	7.58386 10
x	-0.121393	0.00791299	-15.341	1.20557 10

RSquared -> 0.971116, AdjustedRSquared -> 0.966989,

EstimatedVariance -> 0.0969528,

ANOVATable ->	DF	SumOfSq	MeanSq	FRatio	PValue
Model	1	22.8174	22.8174	235.346	1.20557 10
Error	7	0.678669	0.0969528		
Total	8	23.4961			

BLP 1930

ParameterTable ->	Estimate	SE	TStat	PValue
1	5.80483	0.461557	12.5766	1.87668 10
x	-0.11165	0.0131256	-8.50631	6.8519 10

RSquared -> 0.878578, AdjustedRSquared -> 0.866436.

EstimatedVariance -> 0.635771,

ANOVA Table ->	DF	SumOfSq	MeanSq	F Ratio	P Value	
						-6
Model	1	46.0027	46.0027	72.3574	6.8519	10
Error	10	6.35771	0.635771			
Total	11	52.3605				

BLP 1998

Parameter Table ->	Estimate	SE	T Stat	P Value	
					-8
1	6.59457	0.43869	15.0324	3.42445	10
x	-0.0989948	0.0124753	-7.93527	0.0000126424	

RSquared -> 0.862955, AdjustedRSquared -> 0.84925,

EstimatedVariance -> 0.574333,

ANOVA Table ->	DF	SumOfSq	MeanSq	F Ratio	P Value
Model	1	36.165	36.165	62.9686	0.0000126424
Error	10	5.74333	0.574333		
Total	11	41.9083			

CRS 1930

Parameter Table ->	Estimate	SE	T Stat	P Value	
					-6
1	5.79677	0.211637	27.3902	1.2138	10
x	-0.111774	0.0103348	-10.8153	0.000117253	

RSquared -> 0.959007, AdjustedRSquared -> 0.950808,

EstimatedVariance -> 0.0771769,

ANOVA Table ->	DF	SumOfSq	MeanSq	F Ratio	P Value
Model	1	9.02749	9.02749	116.971	0.000117253
Error	5	0.385884	0.0771769		
Total	6	9.41337			

CRS 1998

ParameterTable ->	Estimate	SE	TStat	PValue
1	4.98734	1.00995	4.93819	0.000588748
x	-0.0547482	0.0287206	-1.90623	0.0857365

RSquared -> 0.266524, AdjustedRSquared -> 0.193177,

EstimatedVariance -> 3.04405,

ANOVA Table ->	DF	SumOfSq	MeanSq	FRatio	PValue
Model	1	11.0612	11.0612	3.63372	0.0857365
Error	10	30.4405	3.04405		
Total	11	41.5017			

GOA 1930

ParameterTable ->	Estimate	SE	TStat	PValue
1	3.36821	0.314004	10.7267	3.00255 10
x	-0.0315884	0.00535473	-5.89916	0.0000138644

RSquared -> 0.659091, AdjustedRSquared -> 0.640152,

EstimatedVariance -> 0.492068,

ANOVA Table ->	DF	SumOfSq	MeanSq	FRatio	PValue
Model	1	17.124	17.124	34.8001	0.0000138644
Error	18	8.85722	0.492068		
Total	19	25.9812			

GOA 1998

ParameterTable ->	Estimate	SE	TStat	PValue
1	5.08587	0.629693	8.07673	0.0000407657
x	-0.0728249	0.0214966	-3.38774	0.00953178

RSquared -> 0.589255, AdjustedRSquared -> 0.537911,

EstimatedVariance -> 0.983831,

ANOVA Table ->	DF	SumOfSq	MeanSq	F Ratio	P Value
Model	1	11.2912	11.2912	11.4768	0.00953178
Error	8	7.87065	0.983831		
Total	9	19.1619			

NRR 1930

Parameter Table ->	Estimate	SE	T Stat	P Value
1	6.71554	0.489281	13.7253	0.000163247
x	-0.180759	0.0279008	-6.47862	0.00292555

RSquared -> 0.912991, AdjustedRSquared -> 0.891239,

EstimatedVariance -> 0.35156,

ANOVA Table ->	DF	SumOfSq	MeanSq	F Ratio	P Value
Model	1	14.7558	14.7558	41.9725	0.00292555
Error	4	1.40624	0.35156		
Total	5	16.1621			

NRR 1998

Parameter Table ->	Estimate	SE	T Stat	P Value
1	5.63555	0.76238	7.39205	0.0000767775
x	-0.0682695	0.0260263	-2.6231	0.0305033

RSquared -> 0.462389, AdjustedRSquared -> 0.395188,

EstimatedVariance -> 1.44213,

ANOVA Table ->	DF	SumOfSq	MeanSq	F Ratio	P Value
Model	1	9.9228	9.9228	6.88065	0.0305033
Error	8	11.5371	1.44213		
Total	9	21.4599			

RRB 1930

Parameter Table ->	Estimate	SE	T Stat	P Value
1	5.53184	0.472022	11.7194	9.41657 10
x	-0.0439937	0.0146459	-3.00383	0.0148638

RSquared -> 0.500637, AdjustedRSquared -> 0.445153,

EstimatedVariance -> 0.608908,

ANOVA Table ->	DF	SumOfSq	MeanSq	F Ratio	P Value
Model	1	5.49416	5.49416	9.02298	0.0148638
Error	9	5.48017	0.608908		
Total	10	10.9743			

RRB 1998

Parameter Table ->	Estimate	SE	T Stat	P Value
1	5.43886	0.556041	9.7814	4.29965 10 ⁻⁶
x	-0.0746519	0.0172528	-4.32694	0.00191365

RSquared -> 0.675353, AdjustedRSquared -> 0.639281,

EstimatedVariance -> 0.844968,

ANOVA Table ->	DF	SumOfSq	MeanSq	F Ratio	P Value
Model	1	15.8198	15.8198	18.7224	0.00191365
Error	9	7.60471	0.844968		
Total	10	23.4245			

SIL 1930

Parameter Table ->	Estimate	SE	T Stat	P Value
1	4.77213	0.295081	16.1722	5.85888 10 ⁻⁸
x	-0.0581922	0.00915578	-6.35579	0.00013197

RSquared -> 0.817799, AdjustedRSquared -> 0.797555,

EstimatedVariance -> 0.237964,

ANOVA Table ->	DF	SumOfSq	MeanSq	F Ratio	P Value
Model	1	9.61281	9.61281	40.3961	0.00013197
Error	9	2.14167	0.237964		
Total	10	11.7545			

SIL 1998

ParameterTable ->	Estimate	SE	TStat	PValue
1	5.22824	0.700916	7.45915	7.6409 10
x	-0.0776712	0.0170809	-4.54725	0.000669368

RSquared -> 0.632774, AdjustedRSquared -> 0.602172,

EstimatedVariance -> 1.7129, ANOVATable ->

	DF	SumOfSq	MeanSq	FRatio	PValue
Model	1	35.4184	35.4184	20.6774	0.000669368
Error	12	20.5548	1.7129		
Total	13	55.9732			

TLK 1930

ParameterTable ->	Estimate	SE	TStat	PValue
1	4.89192	0.43214	11.3202	2.11347 10
x	-0.055911	0.0113423	-4.92943	0.00045007

RSquared -> 0.688379, AdjustedRSquared -> 0.66005,

EstimatedVariance -> 0.604225,

ANOVA Table ->	DF	SumOfSq	MeanSq	FRatio	PValue
Model	1	14.6823	14.6823	24.2993	0.00045007
Error	11	6.64648	0.604225		
Total	12	21.3287			

TLK 1998

ParameterTable ->	Estimate	SE	TStat	PValue
1	6.29332	0.492681	12.7736	1.62002 10
x	-0.101027	0.0140107	-7.21073	0.0000288927

RSquared -> 0.838696, AdjustedRSquared -> 0.822565,

EstimatedVariance -> 0.724405,

ANOVA Table ->	DF	SumOfSq	MeanSq	F Ratio	P Value
Model	1	37.6651	37.6651	51.9946	0.0000288927
Error	10	7.24405	0.724405		
Total	11	44.9092			

TWP 1930

Parameter Table ->	Estimate	SE	T Stat	P Value
1	4.55075	0.261893	17.3764	7.15424 10
x	-0.0437648	0.00638219	-6.85734	0.0000175384

RSquared -> 0.79669, AdjustedRSquared -> 0.779747,

EstimatedVariance -> 0.239138,

ANOVA Table ->	DF	SumOfSq	MeanSq	F Ratio	P Value
Model	1	11.245	11.245	47.0232	0.0000175384
Error	12	2.86965	0.239138		
Total	13	14.1147			

TWP 1998

Parameter Table ->	Estimate	SE	T Stat	P Value
1	6.3466	0.544321	11.6597	0.0000239842
x	-0.111563	0.0232441	-4.79963	0.00300189

RSquared -> 0.793363, AdjustedRSquared -> 0.758924,

EstimatedVariance -> 0.5856, ANOVA Table ->

	DF	SumOfSq	MeanSq	F Ratio	P Value
Model	1	13.4901	13.4901	23.0364	0.00300189
Error	6	3.5136	0.5856		
Total	7	17.0037			

APPENDIX C.
DIAGNOSTICS FOR WHITEBARK PINE AND SUBALPINE FIR
SEEDLING GLM AND GAM MODELS

Call: glm(formula = pial ~ ltpt + dbaten + dtpt, family = poisson, data = seedmet)

Deviance Residuals:

Min	1Q	Median	3Q	Max
-5.701555	-1.935282	-0.4477544	1.262667	10.20418

Coefficients:

	Value	Std. Error	t value
(Intercept)	2.99942709	0.065182169	46.01607
ltpt	-0.03518273	0.003228502	-10.89754
dbaten	-1.41723270	0.113880846	-12.44487
dtpt	0.08638178	0.007067160	12.22298

(Dispersion Parameter for Poisson family taken to be 1)

Null Deviance: 958.1448 on 108 degrees of freedom

Residual Deviance: 670.9011 on 105 degrees of freedom

Number of Fisher Scoring Iterations: 4

Correlation of Coefficients:

	(Intercept)	ltpt	dbaten
ltpt	-0.8208116		
dbaten	-0.1894943	0.1198787	
dtpt	-0.1082170	0.0345843	-0.8665570

Call: gam(formula = pial ~ s(ltpt) + s(dbaten) + s(dtpt), family = poisson, data = seedmet)

Deviance Residuals:

Min	1Q	Median	3Q	Max
-5.390737	-1.742824	-0.5106744	1.001389	6.694528

(Dispersion Parameter for Poisson family taken to be 1)

Null Deviance: 958.1448 on 108 degrees of freedom

Residual Deviance: 524.4952 on 96.00785 degrees of freedom

Number of Local Scoring Iterations: 3

DF for Terms and Chi-squares for Nonparametric Effects

	Df	Npar	Df	Npar	Chisq	P(Chi)
(Intercept)	1
s(ltpt)	1	3	3	21.6054	7.90034e-05	
s(dbaten)	1	3	3	58.2233	0.00000e+00	
s(dtpt)	1	3	3	173.2858	0.00000e+00	

Call: glm(formula = abla ~ el + av, family = poisson, data = seedmet)

Deviance Residuals:

	Min	1Q	Median	3Q	Max
	-5.319722	-2.132915	-1.201543	0.5955277	6.06268

Coefficients:

	Value	Std. Error	t value
(Intercept)	25.257530226	1.2890586418	19.59378
el	-0.002511292	0.0001405334	-17.86971
av	0.987644262	0.0585393888	16.87145

(Dispersion Parameter for Poisson family taken to be 1)

Null Deviance: 1294.101 on 108 degrees of freedom

Residual Deviance: 706.1208 on 106 degrees of freedom

Number of Fisher Scoring Iterations: 5

Correlation of Coefficients:

	(Intercept)	el
el	-0.9995789	
av	0.2921415	-0.2969827

Call: gam(formula = abla ~ s(el) + s(av), family = poisson, data = seedmet)

Deviance Residuals:

	Min	1Q	Median	3Q	Max
	-5.455446	-2.212471	-0.9677311	0.8702807	5.903295

(Dispersion Parameter for Poisson family taken to be 1)

Null Deviance: 1294.101 on 108 degrees of freedom

Residual Deviance: 660.6156 on 100.2373 degrees of freedom

Number of Local Scoring Iterations: 4

DF for Terms and Chi-squares for Nonparametric Effects

	Df	Npar	Df	Npar	Chisq	P(Chi)
(Intercept)	1					
s(el)	1	2.9			30.67450	0.0000008171
s(av)	1	2.9			16.92066	0.0006592348

APPENDIX D.
CROSS-TABULATIONS OF ACTUAL NUMBER OF MOUNTAIN
PINE BEETLE ATTACKS AND PREDICTED NUMBER OF
ATTACKS BY STAND

<i>Actual</i>	<i>Predicted</i>		
ABK	False	True	Row Total
False	12	7	19
True	4	102	106
Col. Total	16	109	125
bias = 0.028			

<i>Actual</i>	<i>Predicted</i>		
AVL	False	True	Row Total
False	79	7	86
True	7	51	58
Col. Total	86	58	144
bias = 0			

<i>Actual</i>	<i>Predicted</i>		
BGH	False	True	Row Total
False	20	7	27
True	5	128	133
Col. Total	25	135	160
bias = 0.008			

<i>Actual</i>	<i>Predicted</i>		
BLK	False	True	Row Total
False	10	11	21
True	6	76	82
Col. Total	16	87	103
bias = 0.061			

<i>Actual</i>	<i>Predicted</i>		
GOA	False	True	Row Total
False	20	1	21
True	1	19	20
Col. Total	21	20	41
bias = 0			

<i>Actual</i>	<i>Predicted</i>		
RRB	False	True	Row Total
False	5	11	16
True	4	94	98
Col. Total	9	105	114
bias = 0.071			

<i>Actual</i>	<i>Predicted</i>		
SIL	False	True	Row Total
False	15	8	23
True	7	46	53
Col. Total	22	54	76
bias = 0.018			

<i>Actual</i>	<i>Predicted</i>		
TLK	False	True	Row Total
False	32	0	32
True	1	32	33
Col. Total	33	32	65
bias = -0.030			

<i>Actual</i>	<i>Predicted</i>		
TWP	False	True	Row Total
False	23	1	24
True	3	54	57
Col. Total	26	55	81
bias = -0.036			

VITA

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Summary:

Over twenty years of natural resource experience with an emphasis in forest and sub-alpine ecosystems. Research and applied experience in forest ecology, quantitative ecology, disturbance ecology, dendrochronology and dendroclimatology.

Education:

Ph.D. Utah State University, Ecology	2000
M.S. University of Arizona, Renewable Natural Resources	1995
B.S. University of New Hampshire, Animal Science	1976

Experience:

Research Ecologist, Rocky Mountain Research Station US	1994-2000
<ul style="list-style-type: none"> • Generated Ph.D. research proposal. • Funded by cooperatively by the Rocky Mountain Research Station and National Forest System USDA-FS. 	
Forest Ecologist, Sawtooth National Recreation Area USDA-FS	1998-2000
<ul style="list-style-type: none"> • Developed vegetation management plans. • Implemented whitebark pine seedling restoration project. • Author Biological Assessments/Biological Evaluations for aquatic and terrestrial vertebrates and terrestrial plants. • Conducted administrative study for the Boise National Forest USDA-FS. 	
Research Assistant, Laboratory of Tree Ring Research University of Arizona Tucson, Arizona	1992-1994
<ul style="list-style-type: none"> • Generated M.S. research proposal and established Cooperative Agreement with USDA-FS. • Granted \$38,000.00 in funding. 	
Math Tutor, Pima Community College Tucson, Arizona	1992
Senior Wildlife Technician, Idaho Department of Fish and Game	1990
<ul style="list-style-type: none"> • Documented wolverine activity. 	

- Owner-operator Sawtooth Mountain Guides, Stanley, Idaho 1985-1990
 Guide service for backcountry skiing and mountaineering.
 • Responsible for annual sales of \$80,000.00.
 • Client base of over 300 individuals—perfect safety record.
 • Supervised up to six mountain guides.
- Wildlife Biologist 1982-1984
 Wallowa–Whitman National Forest USDA-FS
 • Wrote recommendations for Environmental Assessments.
 • Developed wildlife habitat inventory field guide.

Skills:

Computer operating systems: UNIX, LINUX, Windows.
 Programming and software: *Mathematica*, S-PLUS, Perl, Excel.
 Geographic Information System analysis with ArcView.
 Nordic Ski Instructor, certified by Professional Ski
 Instructors of America since 1985.

Awards:

Competitive Graduate Student Research Award 1997
 The Women and Gender Research Institute,
 Utah State University, Logan, UT

Professional Societies:

Ecological Society of America
 Society of American Foresters
 Xi Sigma Pi

Publications:

- Dissertation Title: Ecology of Treeline Whitebark Pine (*Pinus albicaulis*) Populations in Central Idaho: Successional Status, Recruitment and Mortality, and A Spring Temperature Reconstruction from Whitebark Pine Tree-Rings.
- Perkins, D. L., and T. W. Swetnam. 1996. A dendroecological assessment of whitebark pine in the Sawtooth Salmon River region Idaho. *Canadian Journal of Forest Research* 26: 2123-2133.
- Perkins, D. L., and T. W. Swetnam. 1994. Long-Term Dynamics of Whitebark Pine: Tree-Ring Studies in Central Idaho. In *Workshop Proceedings: Research and Management in Whitebark Pine Ecosystems*. May 1994–Glacier National Park.
- Logan, J. A., P. V. Bolstad, B. J. Bentz, and D. L. Perkins. 1994. Assessing the Effects of Changing Climate on Mountain Pine Beetle Dynamics. In *Proceedings of the IUFRO Conference, Maui, Hawaii*. February 1994.
- Biondi, F., D. L. Perkins, D. R. Cayan, and M. K. Hughes. 1999. July temperature during the second millennium reconstructed from Idaho tree rings. *Geophysical Research Letters* 26:1445-1448.