Post-logging stand characteristics and crown development of whitebark pine (Pinus albicaulis)

by Todd Roger Kipfer

A thesis submitted in partial fulfillment of the requirements for the degree of Master of Science in Earth Sciences
Montana State University

Abstract:
Whitebark pine (Pinus albicaulis) is an important and potentially threatened high-elevation tree. In order to increase the knowledge of factors influencing whitebark pine growth characteristics for potential management strategies and actions, the competitive influence of neighboring trees on individual whitebark pine crown characteristics was assessed using a distance-dependent competition index. Approximately 300 subject whitebark pine trees and selected competing trees were measured in three study stands that were logged between 1968 and 1972. The study stands were in the Gallatin National Forest, Montana. The competition index quantified competitive pressure from the number, size, and spatial arrangement of competing trees using tree height ratios and inter-tree distances. The subject whitebark pine trees were identified according to whether or not they established before or after the logging. Those trees that established before the logging were not further evaluated. Regression analysis evaluated the relationships between the competition index, and four subject whitebark pine measures: (I) total tree height, (2) crown diameter, (3) crown diameter/total tree height, and (4) crown volume.

Significant inverse correlations between the competition index and each measure were found, but the percent variation in the measures' explained by the competition index was low. Subject whitebark pine tree ages and differences between stands were also significant factors affecting the four whitebark pine measures. Possible competition index thresholds were qualitatively identified. The results were similar to previous competition index/tree growth studies, and continued research on factors affecting whitebark pine growth characteristics was discussed.

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APPROVAL

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Todd Roger Kipfer

This thesis has been read by each member of the thesis committee and has been found to be satisfactory regarding content, English usage, format, citations, bibliographic style, and consistency, and is ready for submission to the College of Graduate Studies.

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ABSTRACT

Whitebark pine (*Pinus albicaulis*) is an important and potentially threatened high-elevation tree. In order to increase the knowledge of factors influencing whitebark pine growth characteristics for potential management strategies and actions, the competitive influence of neighboring trees on individual whitebark pine crown characteristics was assessed using a distance-dependent competition index. Approximately 300 subject whitebark pine trees and selected competing trees were measured in three study stands that were logged between 1968 and 1972. The study stands were in the Gallatin National Forest, Montana. The competition index quantified competitive pressure from the number, size, and spatial arrangement of competing trees using tree height ratios and inter-tree distances. The subject whitebark pine trees were identified according to whether or not they established before or after the logging. Those trees that established before the logging were not further evaluated. Regression analysis evaluated the relationships between the competition index and four subject whitebark pine measures: (1) total tree height, (2) crown diameter, (3) crown diameter/total tree height, and (4) crown volume. Significant inverse correlations between the competition index and each measure were found, but the percent variation in the measures explained by the competition index was low. Subject whitebark pine tree ages and differences between stands were also significant factors affecting the four whitebark pine measures. Possible competition index thresholds were qualitatively identified. The results were similar to previous competition index/tree growth studies, and continued research on factors affecting whitebark pine growth characteristics was discussed.

CHAPTER 1

INTRODUCTION

Mid-latitude, high-elevation environments exhibit a fragile complexity and have often, in the past, been relatively inaccessible to development. Although these landscapes in much of western North America have largely remained intact (Wardle 1968), increasing anthropogenic activity is creating impacts at large, ecosystem or landscape scales (Veblen 1987). Also, societal values of these high-mountain forest resources have undergone significant changes to include recreation, watershed management, wilderness, and wildlife preservation (Ives 1990). The effects of fire suppression, exotic species introductions, landscape fragmentation, global climate change, and other society-environment interactions could have potential deleterious impacts on high-elevation ecosystems. Specific solutions will likely rely on reactive measures, focused on specific ecosystem components because many of these impacts have only recently been observed and are now only partially understood. For example, management actions may become specifically focused on the maintenance of a specific species or a specific population that is identified as threatened.

Study Objectives

This study focuses on increasing the understanding of an important and potentially threatened high-elevation tree, whitebark pine (*Pinus albicaulis*), so that this information can be used to develop improved policies and more appropriate management actions. Specifically, this study quantifies the influence of competition from neighboring trees on the crown characteristics of individual, regenerating whitebark pine trees in logged stands. The growth characteristics of individual trees depend upon numerous factors that vary spatially and temporally. However, competition is an important factor influencing tree growth that has been successfully related to tree growth characteristics for many commercially important tree species (Lorimer 1983; Tomé and Burkhart 1989).

Four objectives were identified to evaluate the relationships between competition and whitebark pine crown characteristics. The objectives are: (1) to describe the crown characteristics of regenerating whitebark pine in the study stands, (2) to statistically compare crown characteristics for two types of whitebark pine in the study stands (i.e., those trees that established before the logging and survived, referred to as advance growth trees, and those trees that established after the logging, referred to as subsequent regeneration trees), (3) to quantify and describe the amount of competition from neighboring trees on individual whitebark pine for the study stands, and (4) to evaluate the variability in whitebark pine crown characteristics explained by the competition indices.

Management Implications

Whitebark pine (*Pinus albicaulis*) is an important, but potentially endangered, high-elevation resource (Kendall and Arno 1990). It occupies subalpine forest zones and forms upper timberline in the northwestern United States and western Canada. Whitebark pine populations, however, may be declining. Arno (1986) cites increased whitebark pine mortality and links it to insect and disease epidemics and successional replacement related to fire suppression. In western Montana and northern Idaho, blister rust (*Cronartium ribicola* J.C. Fisch. ex Rabenh.) has caused 80 to 90% mortality of whitebark pine stands. Blister rust is present in the Greater Yellowstone Ecosystem (GYE) but has not caused widespread mortality, probably due to the GYE's relatively cold and dry climate (Hoff and Hagle 1990).

The predicted impacts of potential climate change on whitebark pine forests within the GYE are severe, and climate change may constitute the most serious long-term threat to whitebark pine in the region. Romme and Turner (1991) anticipate a more fragmented and reduced whitebark pine zone as a consequence of climate change in the GYE for three different scenarios of climate change. The three likely climate scenarios were: (1) warmer and drier than the present; (2) warmer and drier, but with a compensating increase in plant water use efficiency; and, (3) warmer and wetter than the present. Under climate scenario (1), available habitat for whitebark pine forests, currently occupying approximately 250,000 hectares within Yellowstone National Park and the adjacent high peaks, is predicted to decrease by 90%. A similar habitat loss is predicted for climate scenario (2). Habitat loss for whitebark pine forests is also predicted for climate scenario (3), and because whitebark pine may currently be restricted to the drier summer climates that characterize the northern Rocky Mountains, the wetter conditions under this scenario may contribute to an increased reduction in whitebark pine or even local extinction. It is believed that relatively cool and dry conditions have prevented widespread blister rust infestation in the GYE (Hoff and Hagle 1990). Warmer and wetter conditions may bring about increased blister rust infestation in the GYE, magnifying the negative impacts of climate scenario (3) for whitebark pine populations.

Whitebark pine ecosystems provide significant wildlife habitat. The large seeds produced by whitebark pine are an important and preferred high-energy food source for several wildlife species including the endangered grizzly bear (*Ursus arctos horribilis*) (Craighead et al. 1982; Kendall 1983; Kendall and Arno 1990), the red squirrel (*Tamiasciurus hudsonicus*), and the Clark's nutcracker (*Nucifraga columbiana*) (McCaughey and Schmidt 1990).

Because of whitebark pine's predicted decline and its importance for high-elevation wildlife habitats, continued seed production and survival of naturally regenerating whitebark pine are pressing concerns for ecological researchers and land managers (Eggers 1986; Hillis 1986; Weaver and Forcella 1986; Tyers 1990). McCaughey and Weaver (1990) suggested that the probability of natural regeneration of whitebark pine in wildlife-sensitive areas is likely decreasing, and future management of whitebark pine forests will require assessment and management of factors such as competition and disease. Research aimed at finding ways to manage competition and disease for enhanced whitebark pine seed production, regeneration survival, and specific growth characteristics is only just now getting started.

The effects of silvicultural management options for maintaining or enhancing whitebark pine ecosystems are not well documented (Eggers 1990; Schmidt and McCaughey 1990). Management actions that may increase seed production by increasing the proportions of the crown that are fully exposed to light include: thinning, fertilization, and protection from insects and other seed destroying agents (Eggers 1990). The effect of these actions on residual whitebark pine seedlings and saplings is not well understood. Observations by Eggers (1990) indicate that advance growth whitebark pine seedlings and saplings have responded little to release (i.e., removal of forest competition) and additional data are needed.

Quantifying the influence of competing vegetation on conifer growth can help to determine silvicultural prescriptions, optimize management decisions, and provide a basis for growth models of young forest stands (Wagner and Radosevich 1991b). Neighboring species compete for necessary resources such as light, water, and nutrients, and this competition influences the structure and composition of a forest community (Spurr and Barnes 1980). The management of interspecific competition may also influence the rate and course of development for young conifer stands (Stewart et al 1984; Walstad and Kuch 1987). Resource managers interested in maximizing crown growth characteristics and seed production can also benefit from a better understanding of the relationships between whitebark crown growth characteristics and the competitive influence of neighboring trees.

Previous Studies

Biogeography

Geographers increasingly have assessed human influences on the spatial pattern and dynamics of vegetation (Veblen 1987). Many geographers have studied the effect of disturbance, anthropogenic and natural, on vegetation patterns and processes, focusing, for example, on fire (Vale 1979; Parker and Parker 1983; Veblen 1986; Veblen and Lorenz 1986), climate (Hansen-Bristow and Ives 1984), settlement and land use (Dando and Hansen 1990; Wyckoff and Hansen 1991), avalanches (Butler 1985; Malanson and Butler 1986), and tree falls (Beatty 1984; Veblen 1985). High-elevation forests have received increasing attention by American geographers with much of the work regionally focused in the American West (Ives and Hansen-Bristow 1983; Hansen-Bristow and Ives 1984; Hansen-Bristow and Ives 1985; Veblen 1986; Baker 1988; Parker 1988; Taylor 1990). The remainder of this review focuses on those aspects pertinent to this study.

Inter-Tree Competition and Tree Growth

The effect of competition on the growth of individual trees has been studied for many species (Tomé and Burkhart 1989) but not for whitebark pine. These studies have used individual tree growth models based on competition indices to quantify the amount of competition from neighboring trees. The growth of individual trees on specific sites depends upon many factors, including past growing conditions, genetic ability to grow, micro-environment, competitive status, and influence of local neighbors (Tomé and Burkhart 1989). For studies looking at incremental growth characteristics (i.e., growth over time), past-growing conditions and genetic ability to grow are introduced in growth models by incorporating initial tree dimensions. The influence of local neighbors is accounted for by interpreting stand densities and size structures at local or stand-level scales. The majority of these studies have focused on the growth of individual, economically important trees in plantations or homogeneous stands (Daniels et. al 1986; Tomé and Burkhart 1989; Wagner and Radosevich 1991b). Other studies have used competition-tree growth models to compare the shade tolerance of tree species (Lorimer 1983), to assess reproductive strategies in mixed species forests (Woods and Whittaker 1981), and to evaluate the susceptibility of individual trees to insect attack (Ellis 1979).

Competition indices can be categorized as either distance-independent or distance-dependent (Munro 1974; Tomé and Burkhart 1989). Distance-independent indices (using a whole stand approach) have been used to predict the mean ability of the average tree or whole stand to grow based on average measures of vegetation abundance throughout the stand. Distance-dependent indices (using an individual-tree or neighborhood approach) measure the influence of local neighbors on an individual subject tree's ability to grow. Although both approaches predict with a similar precision, distance-dependent indices are expected to provide a greater precision and are considered more satisfactory than distance-independent indices (Alemdag 1978; Firbank and Watkinson 1987; Goldberg 1987; Tomé and Burkhart 1989; Wagner and Radosevich 1991a). The influence of competition on stand dynamics cannot be fully examined with whole-stand approaches because individual trees in young stands are typically surrounded by a variation of species, growth forms, ages, origins, densities, proportions, and spatial arrangements that change through time (Firbank and Watkinson 1987; Wagner and Radosevich 1991a).

Neighborhood or distance-dependent models of competition can be divided into four types (Firbank and Watkinson 1987; Wagner and Radosevich 1991a). The first type quantifies the degree of crown overlap with neighboring trees (Newnham and Smith 1964; Bella 1971; Ek and Monserud 1974; Daniels et al. 1986); the second type counts the number of neighbors (Alemdag 1978; Firbank and Watkinson 1987); the third type measures the area available to individual trees (Brown 1965; Moore et al. 1973; Jensen 1974; Pelz 1978; Watkinson et al. 1983; Mithen et al. 1984; Daniels et al.

1986); and, the fourth type combines the number, size, and distance of neighbors in a composite statistic (Hamilton 1969; Hegyi 1974; Daniels 1976; Alemdag 1978; Daniels et al. 1986; Wagner and Radosevich 1991a and 1991b). Simple competition indices that include competitor size and inter-tree distances generally perform as well as the more complex competition-growth models that assess local spatial pattern (Lorimer 1983).

Previous studies using neighborhood models to assess individual tree growth in response to competition suggest an inverse relationship between the amount of competition from neighbors and individual tree growth performance. Daniels (1976) found correlations between simple distance-diameter competition indices and total height increments (r = -0.207 to -0.424) and diameter at breast height (dbh) increments (r = -0.141 to -0.456) of Loblolly pine (*Pinus taeda* L.) in Virginia tree plantations. Daniels et al. (1986) compared competition indices for correlation with annual dbh and basal area growth of loblolly pine. The analysis used simple correlation, contribution to multiple correlation, and multiple regression analysis to evaluate the contribution of the competition index. Negative simple correlation coefficients were interpreted to represent competitive stress and ranged from -0.6316 to -0.7143 for annual dbh and from -0.3807 to -0.5574 for tree basal area. In the multiple regressions, squared multiple correlation coefficients (R^2)

between pine basal area growth and distance-dependent competition indices ranged from 0.387 to 0.686. For pine diameter growth, the multiple correlation coefficients ranged from 0.249 to 0.652.

In a similar comparative study, Tomé and Burkhart (1989) compared distance-dependent competition indices for growth prediction in *Eucalyptus globulus* plantations. They found consistently significant correlations between calculated distance-dependent competition indices and dbh and basal area growth. Simple and multiple correlations were similar to those of Daniels et al. (1986). Simple distance-diameter indices explained subject tree growth variation with a precision similar to other indices. They also modified the existing indices based on the premise that neighboring trees larger than a subject tree contributed a competitive influence, whereas neighboring trees smaller than a subject tree were competitively influenced by the subject tree. Regression analysis evaluated the competition indices as predictor variables, and they found higher correlations using the modified indices.

Lorimer (1983) modified a distance-diameter competition index for interpreting changes in the index over time. His study examined natural hardwood stands where spatial variability was much higher than would be typically found in a tree plantation. Various modified indices were utilized as predictor variables against diameter growth in bivariate regressions. The search radius used to identify competitors, the distance function used in the index computation, and the criteria used to select and evaluate competitors were varied. Significant ($p < 0.05$) coefficients of determination (R^2) ranged from 0.07 to 0.74, depending upon the geography of the stand location (i.e., Nettleton, WI, Black Rock, NY, or Prospect Hill, MA) and the tree species selected as the subject species.

Other researchers have assessed the influence of interspecific competition in young plantations. In a study of *Pseudotsuga* menziesii saplings in the Oregon Coastal range, Wagner and Radosevich (1991a, 1991b) found significant relationships between calculated interspecific competition indices and *Pseudotsuga menziesii* growth measures. Multiple regression analysis used nine independent variables against four dependent variables. The independent variables included subject tree age, a competition index, the height of the tree after the first growing season after planting, slope, and slope azimuth. Dependent variables included total height, stem diameter, a stem volume index, and a crown volume index. Tree age accounted for between 34 and 42% of the variation in tree size. A competition index summing the percent cover for all woody species that were equal to or taller than the subject tree in a 2.1 meter radius neighborhood was the best predictor of *Pseudotsuga menziesii* height growth.

The effects of inter-tree competition on the morphological growth performance of individual whitebark pine trees has not been well documented. Previous studies have assessed whitebark pine incremental growth and stand dynamics. Peterson et al. (1990) used dendrochronological methods to assess long-term growth trends of whitebark pine in response to climatic and other environmental variables in the Sierra Nevada range. Weaver et al. (1990) studied successional patterns in 47 stands containing whitebark pine (*Pinus albicaulis-Vaccinium* scoparium habitat type (following Pfister et al. 1977) in Montana, Wyoming, and Idaho. Competition was assessed in terms of stand development rather than individual tree growth characteristics. One important result of their research applied to the gap size needed for seedlings to grow into saplings. Although the density of seedlings remained approximately constant across stands of different ages it was hypothesized that growth from seedling to sapling size could not be supported in stands older than 100 years. They suggested that clearings needed to be larger than 10 m^2 for seedlings to grow into saplings.

Geography and Ecology of Whitebark Pine

Analysis of the influence of competition on the crown characteristics of whitebark pine requires an assessment of the general geography and ecology of whitebark pine. From seed dispersal to geographic distribution, this high-elevation tree exhibits specialized characteristics that warrant attention for understanding crown characteristics and local stand factors.

The geography of whitebark pine extends from northern British Columbia to central California and west from the Pacific coastal ranges to the northern and coastal Rocky Mountains (Figure 1) (Arno and Hoff 1989; McCaughey and Schmidt 1990). Whitebark pine occupies an altitudinal range of 1520 to 3050 m (5000 - 10,000 ft) in Idaho and Montana (McCaughey and Schmidt 1990). Other available data on site characteristics of whitebark pine stands in the GYE show a wide range of elevations, slopes, and aspects (Hansen-Bristow et al. 1990). For example, whitebark pine stands occur at an altitudinal range of 2075 meters to 2895 m (6180 - 9500 ft) and slopes of 0% to 45% in a wide range of aspects in the Gallatin National Forest, Montana. In contrast, elevations ranged from 2400 m to 3050 m (7,710 - 10,000 ft) on slopes ranging from 5% to 90% in the Bridger-Teton National Forest, Wyoming. The trees here have a preference for south and west aspects.

The high-mountain landscapes which whitebark pine occupy are harsh areas characterized by instability (Hansen-Bristow et al. 1990). At its upper elevational limits, the harsh climatic conditions include extreme winter temperatures of -51°C (-60°F) and summer temperatures exceeding 38°C

(100°F) (McCaughey and Schmidt 1990). Strong winds and snowfall add to the harsh conditions. The soils of whitebark pine are typically thin and poorly developed and vary according to the parent bedrock (Hansen-Bristow et al 1990).

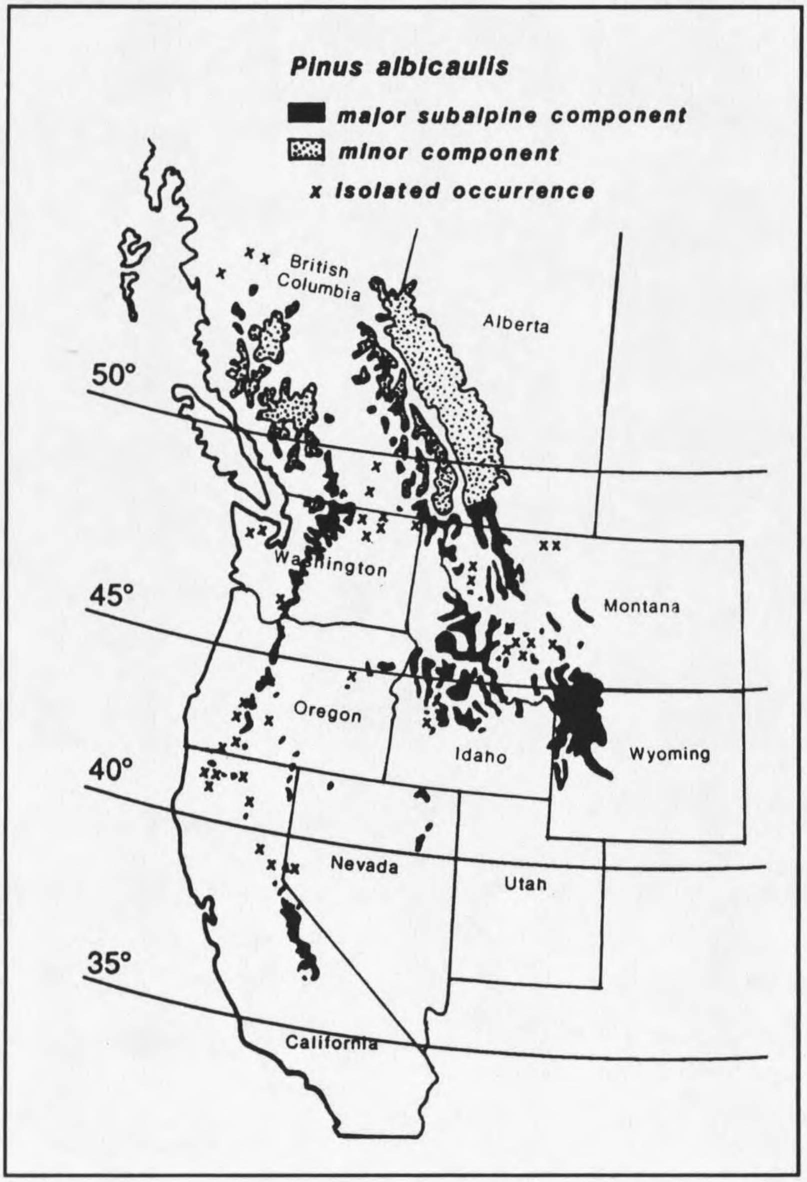

Figure 1. Geography of Pinus albicaulis in western North America (from Arno and Hoff 1989).

Needles of the pine are typically 3.8 to 6.4 cm (1.5 to 2.5 in) long and are in fascicles of five. The bark is thin, smooth, and white-gray on young stems and branches. It is about 1.3 cm (0.5 in) thick and broken into brown-white, plate-like scales with a red-brown inner bark on old trunks. The cones of whitebark pine are short-stalked and 3.8 to 7.6 cm (1.5 to 3.0 in) long (Preston 1968). The cones rapidly disintegrate from decay and depredation by animals when they reach the ground surface (Arno and Hoff 1989). The seeds are large (0.75 cm long) and wingless with a dark brown hard and thick shell (McCaughey and Schmidt 1990). Whitebark pine is extremely difficult to distinguish from limber pine (*Pinus flexilis*) when cones are not available. Identification of the number and position of resin canals of the needles (Ericson 1964) is the most effective method for differentiation of whitebark pine and limber pine in the field when cones are not available. Hendrickson and Lotan (1971), however, found Ericson's method to be unsatisfactory.

Whitebark pine typically shows a well-spread crown when grown in the open and an "upswept" upper crown similar to that of lodgepole pine in dense stands (McCaughey and Schmidt 1990). Near timberline, whitebark pine shows a prostrate form often called "krummholz." Whitebark pine is noted for multiple stems (also multi-trunked or multiple trunks) resulting from either basal branching or seed caching (Weaver and Jacobs 1990). Electrophoretic analysis revealed that two or more of the trunks of multiple stemmed *Pinus flexilis* and *Pinus albicaulis* trees were genetically distinct individuals in 20 of the 25 multi-trunk trees sampled (Linhart and Tomback 1985). The occurrence of multiple stems in whitebark pine has been shown in 8 to 79% of the trees in a study in Montana and Wyoming, and the occurrence of multiple stems decreased from open woodlands to almost zero in closed forests (Weaver and Jacobs 1990).

Reproduction in whitebark pine is heavily dependent upon the Clark's nutcracker (*Nucifraga columbiana*) and red squirrel (*Tamiasciurus hudsonicus*) for seed dissemination (McCaughey and Schmidt 1990). Predators harvest most or all seeds in some areas. Clark's nutcrackers and red squirrels harvest seeds and store them in caches, disseminating the seeds. The Clark's nutcracker may harvest and store as many as three to five times more seeds than it needs. Hutchins (1990) found that Clark's nutcracker caching is responsible for nearly all whitebark pine regeneration. Clark's nutcrackers have been observed caching whitebark pine seeds as far as 22 km from the seed source, thus effectively dispersing whitebark pine seeds to both disturbed and understory sites (Tomback et al. 1990).

Seed production is variable with poor seed crops and bumper crop years (Arno and Hoff 1989). Seed germination is highly variable (0 to 75%), and it is unknown how long the seeds remain viable in cached situations, although seeds have been observed to germinate after 2 years (McCaughey and Schmidt 1990). Weaver and Forcella (1986) evaluated cone production in whitebark pine forests, and found that stand size and canopy cover explained 52% of the variation in cone production. They hypothesized that average cone production of a stand is primarily determined by the number of fertile shoots per hectare and their interaction with weather conditions.

Whitebark pine is considered relatively competition- and shade-intolerant (Table 1) (Arno and Weaver 1990), although the trees may become more shade-tolerant with increasing age (McCaughey and Schmidt 1990). Because of its relatively low ability to compete, whitebark pine is restricted to harsh sites where more competitive trees are restricted or to less harsh sites where competition has been reduced by disturbance (Arno and Weaver 1990). Thus, disturbance is an important factor in the regeneration of whitebark pine.

Whitebark pine is frequently found growing with other high-elevation conifers, although it does form pure stands in relatively dry mountain ranges (Arno 1989). In mixed species stands, whitebark pine can form a long-lived seral co-dominant, eventually becoming replaced by the more shade tolerant species. In southwestern Montana, whitebark pine forms stands with lodgepole pine, subalpine fir, Douglas fir, and Engelmann spruce.

Table 1. Comparative tolerance of shade or competition for species associated with whitebark pine in the inland northwest. (From Arno and Weaver 1990)

Tolerance	Common name (species)
Very tolerant	Subalpine fir (*Abies lasiocarpa*) Mountain hemlock (*Tsuga mertensiana)*
Tolerant	Engelmann spruce (*Picea engelmannii*)
Intermediate or intolerant	**Whitebark pine** (*Pinus albicaulis*)
Very intolerant	Lodgepole pine (*Pinus contorta* var.latifolia) Alpine larch (*Larix lyallii*)

Pfister et al. (1977) classified forest habitat types of Montana using a modified version of Daubenmire's (1952) classification approach. This classification identifies habitat types by the potential climax tree species. Variations of each habitat type are subcategorized by the dominant understory species and called phases. Whitebark pine occurs in numerous habitat types and phases, existing as either an accidental, a minor seral species, a minor climax species, a major seral species, or a major climax species. In Montana, whitebark pine occurs as a major seral or climax species in the following habitat types: *Abies lasiocarpa* (ABLA), *Pinus albicaulis-Abies lasiocarpa* (PIAL-ABLA), *Larix lyallii-Abies lasiocarpa* (LALY-ABLA), and *Pinus albicaulis* (PIAL). Arno and Weaver (1990) summarize the landscape patterns of whitebark pine community types.

CHAPTER 2

METHODS

Study Area

Site Selection

Three logged stands in the Gallatin National Forest in Montana were sampled (Figure 2). The three stands were clear-cut logged between 1968 and 1972. The first two stands (hereafter individually identified as TEEPEE 01 and TEEPEE 02) were located in the Little Teepee Creek drainage on the southeastern edge of the Madison Range, approximately 2 km (3.2 mi) east of northwestern Yellowstone National Park and 7 km (4.4 mi) north-northeast of the Grayling Arm of Hebgen Lake. The final Moose Creek stand (MOOSE CR.) was located on the drainage divide between the Moose Creek drainage and the Swan Creek drainage that form the western slopes of the Gallatin Range, approximately 55 km (34 mi) north of the Teepee Creek stands and 17 km to the northeast of Big Sky, Montana. Sampling on the Moose Creek stand was not as

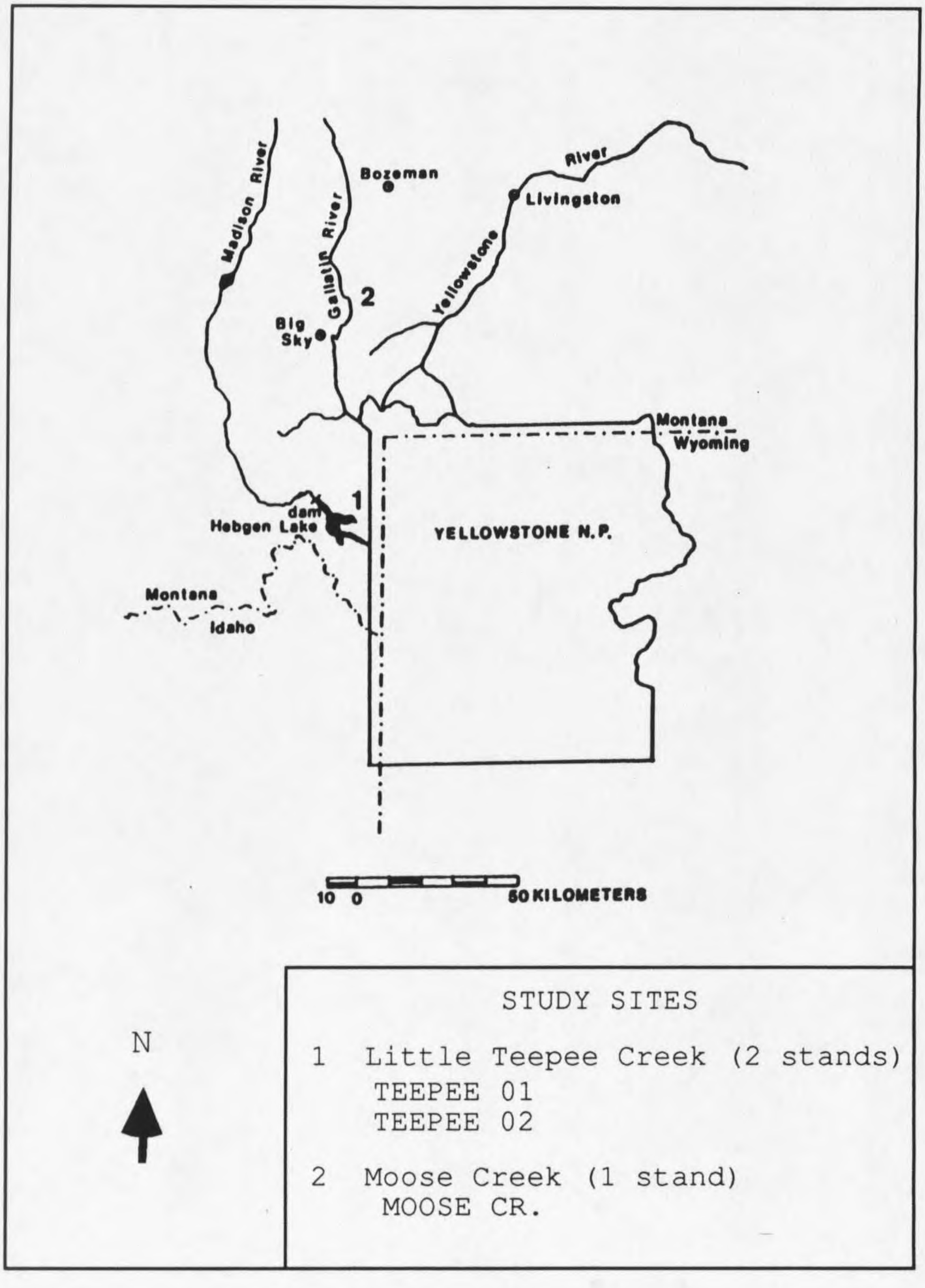

Figure 2. Map of the Yellowstone region showing the location of the two study areas that contain the three study stands.

extensive as on the two Teepee Creek stands due to the small number of whitebark pine trees in the stand. Table 2 lists general stand characteristics for the three study stands.

Table 2. General characteristics of the three study stands.

Stand	Elevation (m)	Aspect	Area (ha)	Year logged
TEEPEE 01	2450-2500	NW-NE	75	1968
TEEPEE 02	2500-2570	NE-SE	49	1970
MOOSE CR.	2130-2400	S-W	96	1972

These logged stands were selected through consultation with USDA Forest Service personnel, a USDA Forest Service database search, and individual site reconnaissance of numerous logged stands in the Gallatin National Forest. From a USDA Forest Service database search, logged stands above 1829 m (6000 ft) in the Gallatin National Forest were identified. These higher elevation, logged stands were considered to have the highest probability of containing whitebark pine. Many stands were eliminated due to difficulty with access and recent silvicultural thinning.

Criteria for selecting sites included stands logged over 15 years ago that contained whitebark pine trees. Stands with fewer than approximately 200 whitebark pine trees were considered to have too few whitebark pine for data collection needs and rejected. Once the potential sites were located, simple transects were delineated through the stands, and all observable whitebark pine trees were counted. This count produced a crude estimate of the number of whitebark pine in a stand. In the absence of cones, identification of whitebark pine in young stands was extremely difficult due to its similarity with limber pine (*Pinus flexilis*), and cross sections of fascicles were evaluated for the number and position of resin canals of the needles following Ericson (1964). Although this field method has been shown to yield errors between 44 and 47% of the time (Hendrickson and Lotan 1971), stands above approximately 2135 m (7000 ft) with a majority of field identifiable whitebark pine, determined by Ericson's method, were assumed to contain all whitebark pine.

Site Descriptions

Lodgepole pine (*Pinus contorta* var. latifolia) is the dominant tree species in all three stands. Subalpine fir (*Abies lasiocarpa*) is the second most numerous species in both of the two Teepee Creek stands, but in the lower elevation Moose Creek stand, Douglas-fir (*Pseudotsuga menziesii*) is the second most numerous species, reflecting a different habitat type. The number of whitebark pine varies in the three stands, with the largest number in the highest elevation Teepee Creek stand (TEEPEE 02) and the smallest number in the relatively lower elevation Moose Creek stand. Engelmann spruce (*Picea engelmannii*) is a minor component of the two Teepee Creek stands, occupying more north facing aspects, and was not found in the Moose Creek stand. Juniper (*Juniperus* spp.) is prevalent in the Moose Creek stand but rare in the relatively higher elevation Teepee Creek stands.

The understory of the logged stands varies, but Grouse Whortleberry (*Vaccinium scoparium*) was common with a conspicuous component of fire weed (*Epilobium* spp.). Grasses dominate the more open portions of the stands and are more common in the Moose Creek stand. Burned slash remnants from logging are very common in all three stands.

The Moose Creek stand is probably a different habitat type (Pfister et al. 1977) than the two Teepee Creek stands. Although not directly sampled, observations suggest that the two Teepee Creek stands are in an early phase of the *Abies lasiocarpa* /*Vaccinium scoparium* (ABLA/VASC) habitat type. The Moose Creek stand was not classified, but it is noticeably different from the two Teepee creek stands due to the presence of *Pseudotsuga menziesii* and the absence of *Abies lasiocarpa*.

Observed wildlife in the three stands included moose (*Alces alces*), coyote (*Canis latrans*), Clark's nutcracker, mule deer (*Odocoileus hemionus*), and small rodents (predominantly *Citellus* spp.). Throughout the Teepee Creek stands was numerous scat from bears (*Ursus* spp). Many bear scat contained a component of whitebark pine seeds.

Climatological information was obtained for the nearest climate stations. The Big Sky 3S climate station is located approximately 22 km (13.7 mi) to the southwest of the Moose Creek stand at an elevation of 2012 m (6600 ft). The Hebgen Dam climate station is located approximately 14 km (8.7 mi) to the west of the two Teepee Creek stands at an elevation of 2004 m (6489 ft). In general, both study areas are high-elevation sites characterized by extreme diurnal and seasonal climatic variability (Table 3).

Table 3. Mean annual precipitation and temperature for two climate stations nearby to the study stands.

Station	Mean annual precipitation cm (in)	Mean annual temperature °C (°F)
Big Sky 3S	44.63 (17.57)	3.39 (38.1)
Hebgen Dam	56.34 (22.18)	2.67 (36.8)

The only available soils information for the study areas was gleaned from a general soils map of Montana (US Department of Agriculture 1982). The soils of the Teepee Creek study stands can be generally characterized as mollisols-inceptisols-alfisols on gently sloping to very steep mountain slopes. The soils of the Moose Creek stand can be generally characterized as inceptisols-alfisols on gently sloping to very steep mountain slopes.

Data Collection

Data collection focused upon specific measures for selected whitebark pine trees, neighboring trees, and related factors such as understory grasses, forbs, and shrubs. The subject whitebark pine trees were identified by a systematic-random-systematic sampling procedure, using systematic transects with the distance to the initial points chosen randomly on each transect and 50 m spacing used for subsequent points. The transects were oriented north-south. For each point, the nearest whitebark pine tree greater than 0.5 m tall was selected. This method allowed for the selection of approximately 100 subject whitebark pine trees per stand.

For each subject whitebark pine tree, nested, fixed radius circular plots identified competitors. Previous studies have preferred a fixed angle gauge sweep centered at the subject tree to identify competitors (Tomé and Burkhart 1989). Simply, this method requires that with increasing distance from the subject tree, neighboring trees need to be larger in order to be selected. The application of this method was not possible for this study because of the relatively small tree sizes in the young study stands. However, three nested circular plots, each with specific tree size criteria for competitors, were utilized in order to approximate a fixed angle gauge sweep. This approach required that trees farther away from the subject tree be larger in order to be considered a competitor, such that:

(1) All tree seedlings and saplings were identified as competitors within 3.0 m radius plots centered at each

subject whitebark pine (seedlings were considered to be those trees less than or equal to 1.4 m in total tree height, and saplings were considered to be those trees greater than 1.4 m in total tree height but having a diameter-at-breast-height (dbh) less than 4.0 cm); (2) All trees with dbh greater than or equal to 4.0 cm and less than 10.0 cm were identified as competitors within the 6.0 m radius plots centered at each subject whitebark pine, and (3) All trees with dbh greater than or equal to 10.0 cm were identified as competitors within 9.0 m radius plots centered at each subject whitebark pine.

Specific measurements of the subject whitebark pine and the competing trees were selected as those considered best to calculate crown characteristics and distance-dependent competition. The whitebark pine growth characteristics evaluated by this study focused on measures of crown shape and size. Crown structure is an important factor in the productivity of forest stands. Crown structure, tree density, and the spatial distribution of trees contribute to the canopy structure, which affects stand productivity through control of within-stand light conditions (Kellomäki et al. 1985; Hashimoto 1990). Crown structure also influences seed production. Trees with narrow and suppressed crowns yield fewer seeds than open-grown trees or large dominant trees in closed forest stands with crowns well exposed to sunlight (Spurr and Barnes 1980). Crown form and horizontal canopy closure in the development of even-aged stands is often assumed to be invariant, but crown form does change because of mechanical and ecological factors as a tree grows (Zeide 1991). Trees grown in open conditions typically have full vigorous crowns that extend to or near the ground, while trees in dense stands tend to show small, narrow crowns with long cylindrical boles often without branches (Honer 1972).

Overall, five attributes were measured for each subject whitebark pine tree (Figure 3): (1) Tree age (AGE), (2) total tree height (H), (3) diameter-at-breast-height (DBH), (4) average live crown diameter (CD), and (5) height of the maximum crown diameter above the ground surface (CH). Tree age for each subject tree was determined by counting annual rings from tree cores taken by an increment borer or bole cross-sections from trees too small to core. Cores and cross-sections were taken as close to the ground surface as possible. The average live crown diameter (CD) was calculated from two perpendicular measurements taken at the widest portion of the crown.

Two crown measures were created from the measured crown characteristics. A ratio of the crown diameter to total tree height (CD/H) was used to evaluate the shape of the crown. This ratio represents how full or wide the crown is in relation to a tree's total height. Higher values of this ratio reflect trees with more horizontal crown growth

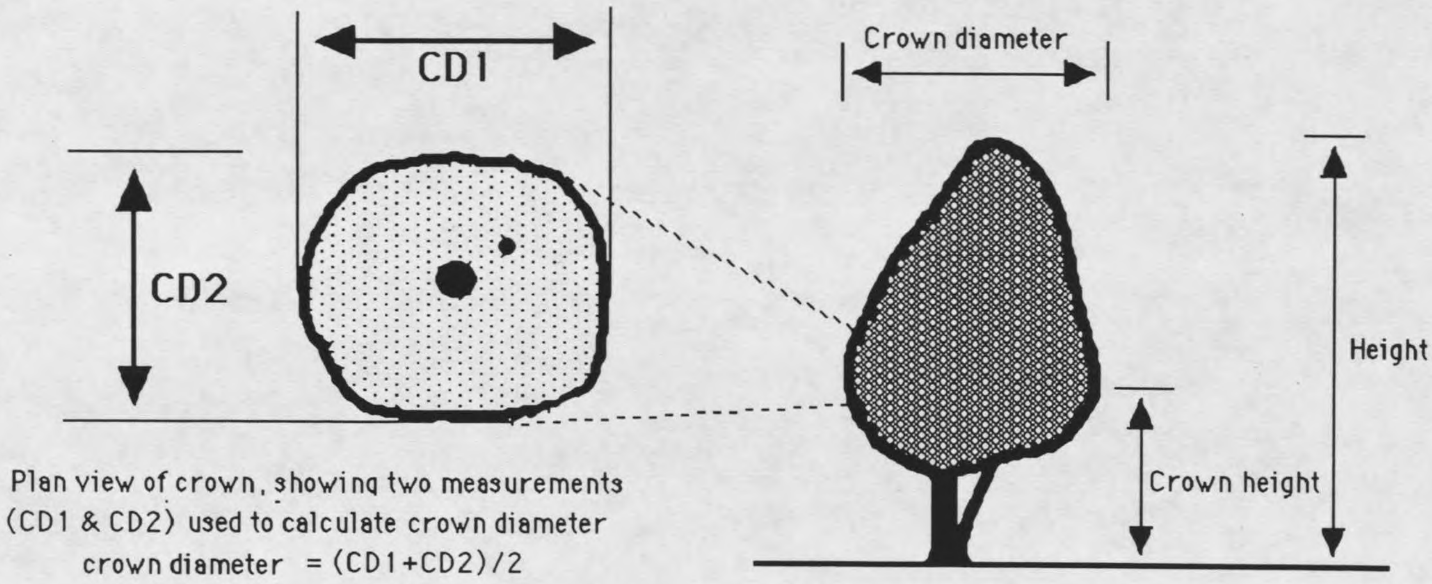

Figure 3. Crown measurements taken for each subject whitebark pine tree.

relative to the tree height (i.e., more diffuse crowns). A crown volume was also calculated by assuming the crown form was conical in shape. The crown volume was estimated from the equation for the volume of a cone (Volume = 1/3 * PI * R^2 * H) and measured crown characteristics. The crown volume allowed for a comparison of total crown size for the individual trees.

The subject whitebark pine trees were classified as advance growth and subsequent regeneration from an initial evaluation of the tree cores and bole cross-sections. Quick counts of the annual rings and evidence of previous suppression in the field (e.g., a cluster of suppressed annual rings preceding more widely spaced annual rings) often identified the advance growth trees. Subsequent laboratory analysis was used to compare the tree age to the age of the logging, and those trees older than the logging event were identified as advance growth. Trees younger than or the same age as the logging event were identified as subsequent regeneration.

Tree species (SPP), total tree height (H), distance from the subject whitebark pine to the competing tree (DIST), and diameter at breast height (DBH) were measured for the selected competing trees. These measures allowed for the computation of a distance-dependent competition index that could be compared to the subject whitebark pine crown measures.

Additional measures of the understory vegetation, slope, and aspect were taken for each subject whitebark pine. Slope angle was measured for the ground surface immediately surrounding each subject tree. No information was recorded for slope concavity or convexity. Slope aspect was measured to the nearest direction on an eight point scale (i.e., N, NE, E, SE, S, SW, W, and NW). Modified Braun-Blanquet percent ground cover class categories (Barbour et al 1987) were used to estimate ground cover for graminoids, forbs, shrubs, bare ground (included rocks and litter), and dead wood on the surface within the 3.0 meter radius plots. A visual estimate was used to measure the average height of the grasses, forbs, and shrubs. The presence of dominant understory species (not including trees, which were recorded separately) was also recorded. Although it was not expected that the grasses, forbs, and shrubs were contributing a significant amount of competition to the subject whitebark pine trees (expect for very small trees), the composition of the understory was considered to provide additional, important ecological information for interpreting the competitive influence of neighboring trees.

Analysis Methods

A series of tests was used to assess the influence of competition on the crown characteristics of individual *Pinus* *albicaulis*, where each successive stage depended upon the results from the previous stage. These stages allowed for the evaluation of competitive influence on the crown characteristics of whitebark pine by systematically evaluating the significance of factors such as competition index modifications, stand, advance growth, and subsequent regeneration.

First, characteristics of the subject whitebark pine trees and competing trees were described for each stand. Summary statistics (e.g., mean, standard deviation, minimum, and maximum) evaluated four subject whitebark pine measures for each stand. The selected whitebark pine measures were total tree height and three crown measures: crown diameter, ratio of the crown diameter to total tree height, and crown volume. Also, size structures were evaluated for the subject whitebark pine trees in all three stands, while age structures of the subject whitebark pine trees were evaluated only for the two Teepee Creek stands. Age data was not available for the Moose Creek stand.

Competing tree characteristics were also summarized. Descriptive statistics were evaluated to describe two competing tree measures by species for each stand. These measures were total tree height and distance between the competing tree and the subject whitebark pine. Additionally, tree species abundance of the competing trees was compared for each stand.

Second, crown characteristics were statistically compared between the advance growth and subsequent regeneration whitebark pine trees. Two sample, two-tailed *t*-tests tested for statistical differences of the four subject whitebark pine measures between the advance growth and subsequent regeneration trees. Statistical analyses were aided by the Minitab statistical software for the Macintosh computer (Schafer and Farber 1992). If the advance growth trees had significantly different crown characteristics from the subsequent regeneration trees, the advance growth trees would then be eliminated from further analysis. Because most of the advance growth trees existed in the suppressed understory conditions prior to the logging and because these historical conditions are not known, statistically significant differences between crown characteristics would eliminate the advance growth trees from further analysis. A competition index based upon existing, post-logging stand characteristics would not be expected to adequately represent the pre-logging conditions that influenced advance growth crown characteristics.

A distance-dependent competition index was selected and modified for whitebark pine to statistically evaluate the variability in whitebark pine crown characteristics explained by the variability in the competition index. A distance-diameter competition index was selected and modified for whitebark pine, and then competition index values were calculated for each subject whitebark pine. Descriptive statistics assessed the values of the competition indices for each stand.

A distance-weighted-size-ratio index or distance-diameter index (Hamilton 1969; Hegyi 1974; Daniels 1976; Alemdag 1978; Tomé and Burkhart 1989) was chosen as the index from which to develop a competition index. The distance-diameter index is a distance-dependent index that sums a size ratio of a diameter (dbh or basal diameter) of competing trees to the diameter of a subject tree. Typically, a distance-decay functions multiplied by a size ratio. The general theory is that larger competing trees, relative to the subject tree, contribute more competition to a subject tree than relatively smaller trees. A competing tree larger than a subject tree will have a size ratio greater than one, while a competing tree smaller than a subject tree will have a size ratio less than one. Also, it is assumed that with increasing distance between the subject tree and the competitor, the competitive influence will decrease, and thus, that the distance decay function can be multiplied by the size ratio. A common distance decay function is one over distance. Thus doubling the diameter of a competitor will double that tree's contribution to the index, and doubling the distance from the subject tree will cut its contribution in half. The most common form of a distance weighted size ratio index sums the ratios of diameters of a subject tree and its competitors, weighted by the distance from the subject tree (Lorimer 1983; Tomé and Burkhart 1989). This index can be written:

$$C.I. = \sum_{i=1}^{n} (Dj / Di) / DISTij \qquad (1)$$

where C.I. = competition index; D_j = diameter of competitor tree j; D_i = diameter of subject tree i; $DIST_{ij}$ = distance between trees i and j; and n = total number of competitors for each subject tree. The distance-diameter index summarized in Equation (1) was selected for two primary reasons. First, distance-diameter indices have been found to explain the variation of growth in trees with a precision similar to other indices while having the advantage of being easy to compute (Tomé and Burkhart 1989). Second, only one measure of a subject tree, the corresponding measure of each competitor, and the distance between the subject tree and competitor are needed. This relative simplicity has numerous advantages. Simple measures of competitive effects are more desirable because confounding present conditions that do not accurately reflect past growing conditions do not receive extensive detailed inclusion to the competition index. In the simple distance-diameter index, competitive influence is based on simple theory, and this simplicity could have future benefits if it was used later to assess specific management options.

Adaptation of the distance-diameter index to whitebark pine required several modifications. A diameter at breast height measure was not feasible because of the multiple stem form and the relative small size of the trees. The multiple stem form also prevented the use of a basal diameter measure. Hence, total tree heights were selected for the size ratio. Because the young trees are probably competing for canopy dominance, height was chosen to represent relative competitive ability. Height growth may provide a useful measure of relative competitive influence in young stands where canopy closure and maximum height growth have not yet occurred. Various distance weighting functions were also applied. The modified competition index can be written:

$$C.I. = \sum_{i=1}^{n} (Hj / Hi) * \text{function}(DISTij) \qquad (2)$$

where C.I. is the competition index, H_j is the total tree height of the subject tree, H_i is the total tree height of the competing tree and function($DIST_{ij}$) is a distance decay function (i.e., $1/DIST_{ij}$, $1/DIST^2{}_{ij}$, $e^{-DIST}{}_{ij}$). The competitive influence of a tree would, thus, be considered to decrease linearly with distance, to decrease with the square of the distance, or to decrease exponentially.

Regression analysis compared the influence of competition on the crown characteristics of the subject whitebark pine trees. This analysis stage allowed a quantitative assessment of the competitive influence of neighboring trees on whitebark pine crown measures. The regressions compared the predictive ability of competition indices using each of the three distance decay functions against total tree height and three crown measures (i.e., crown diameter, ratio of crown diameter to total tree height, and crown volume). Regressions that maximized the coefficient of determination (R^2) were desired. The coefficient of determination represents the percent explanation of the independent variable on the dependent variable.

First, competition index values (independent variables or predictor variables), were regressed against the four subject whitebark pine measures (dependent variables or response variables) for all the subject whitebark pine trees in the three stands. Also, bivariate scatterplots were visually inspected to evaluate the nature of the relationships between competition and tree characteristics. Advance growth trees were eliminated from this analysis stage if they had statistically different measures than the subsequent regeneration trees.

Factors other than competition can affect tree growth, and to evaluate unmeasured differences between stands, an indicator variable for stand was used in multiple regression analysis (Draper and Smith 1981). Also, the age of a tree is expected to be a significant factor for tree growth with the simple theory that older trees are larger, and age was included in the multiple regression analysis to test for significance. Stand and age were considered significant if the p-value from the *t*-test for the respective regression equation coefficient was less than 0.05. Finally, the data were assessed by tree type and/or stand if appropriate.

CHAPTER 3

RESULTS

Stand Characteristics

Subject Whitebark Pine Characteristics

Tree height and crown measures of the subject whitebark pine trees differed by stand (Table 4). Mean values for total tree height, crown diameter, the ratio of the crown diameter to total tree height, and a calculated crown volume were compared using two-tailed paired *t*-tests. P-values less than or equal to 0.05 were considered significant.

Subject tree total tree heights were significantly different between the Moose Creek stand and the two Teepee Creek stands (i.e., TEEPEE 01 and TEEPEE 02 combined) ($p = 0.0026$), between TEEPEE 02 and the Moose Creek stand ($p = 0.016$), and between and TEEPEE 01 and the Moose Creek stands ($p = 0.0037$). Differences between subject whitebark pine total tree heights were not significant between the two Teepee Creek stands ($p = 0.790$).

Table 4. Summary statistics of tree height, crown diameter, crown diameter/height, and crown volume for the subject whitebark pine trees by stand.

Measure/Stand	# Plots	Mean	*Standard error	Min	Max
Height (m)					
TEEPEE 01	104	2.00	0.065	0.50	4.40
TEEPEE 02	135	2.00	0.078	0.60	4.40
MOOSE CR.	72	2.26	0.065	1.10	3.10
Crown Diameter (m)					
TEEPEE 01	104	0.64	0.025	0.20	1.30
TEEPEE 02	135	0.71	0.033	0.15	1.75
MOOSE CR.	72	0.81	0.037	0.20	1.60
Crown Diameter/Height (m/m)					
TEEPEE 01	104	0.341	0.012	0.095	0.667
TEEPEE 02	135	0.373	0.014	0.083	0.792
MOOSE CR.	72	0.351	0.011	0.167	0.684
Crown Volume (m^3)					
TEEPEE 01	104	0.336	0.022	0.007	1.177
TEEPEE 02	135	0.233	0.040	0.004	2.125
MOOSE CR.	72	0.428	0.045	0.017	1.319

* standard error of the mean = standard deviation/$\sqrt{n}$

Crown diameter measures of the subject whitebark pine trees were significantly different between the Moose Creek stand and the two Teepee Creek stands (p = 0.005), between TEEPEE 01 and the Moose Creek stand (p = 0.000), and between TEEPEE 01 and TEEPEE 02 (p = 0.007). Crown diameter measures were not significantly different between TEEPEE 02 and the Moose Creek stand (p = 0.079).

Crown diameter to total tree height ratios of the subject whitebark pine trees were only significantly different between TEEPEE 01 and TEEPEE 02 (p = 0.0096). These ratios were not significantly different between the

Moose Creek stand and the two Teepee creek stands (p = 0.730), between TEEPEE 01 and the Moose Creek stand (p = 0.091), and between TEEPEE 02 and the Moose Creek stand (p = 0.160).

Crown volume measures of the subject whitebark pine trees were significantly different between the Moose Creek stand and the two Teepee Creek stands (p = 0.0026), between TEEPEE 01 and the Moose Creek stand (p = 0.000), and between TEEPEE 01 and TEEPEE 02 (p = 0.0055). Crown volume measures were not significantly different between TEEPEE 02 and the Moose Creek stand (p = 0.110).

Slope and aspect measures for the whitebark pine trees varied by stand (Figure 4). Aspects for stand TEEPEE 01 were predominantly north facing (i.e., NW, N, NE). In contrast, stand TEEPEE 02 faced predominantly east (i.e., NE, E, SE). The Moose Creek stand generally faces southeast. Mean slope measures for the three stands vary between 14.4° (16.0%) and 19.5° (21.7%), but very steep slopes approaching 45° (50%) exist in stand TEEPEE 02 (Table 5). Because slope and aspect affect many site factors including the quantity and quality of incoming solar radiation, microclimate characteristics, and soil characteristics (Spur and Barnes 1980), this variability may contribute to differences in stand structure and composition.

Table 5. Summary statistics of slope measure for ground surface immediately surrounding the subject whitebark pine trees by stand.

Stand	n	Mean	Standard Deviation	Min	Max
TEEPEE 01	135	14.4	5.3	4.0	24.0
TEEPEE 02	104	19.5	7.9	2.0	42.0
MOOSE CR.	72	19.1	6.6	4.0	32.0

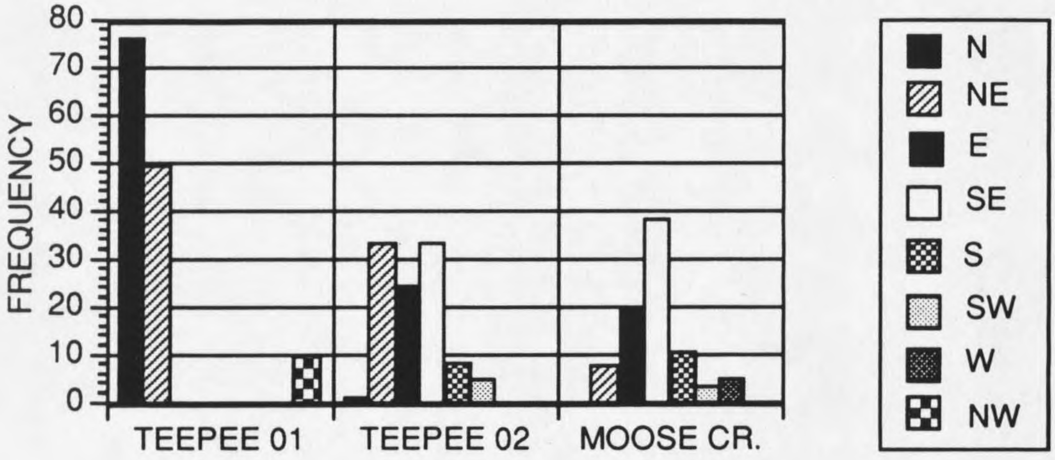

Figure 4 Aspects of the ground surface immediately surrounding the subject whitebark pine trees by stand.

Percent cover measurements for grasses, forbs, shrubs, bare ground, and dead wood were similar for the two Teepee creek stands, but the Moose Creek stand was more dense (Table 6). Mean values for the percent cover of bare ground are over 40% for the two Teepee Creek stands and below five percent for the Moose Creek stand. These data support observations that the understory of the Moose Creek stand was more densely vegetated than the understory of the two Teepee Creek stands.

Table 6. Understory characteristics (percent ground surface cover in 3.0 m circular plots surrounding the subject trees) for the three study stands.

Stand	Surface Cover Type	n	Mean (%)	Standard Deviation	Min	Max
TEEPEE 01	Grasses	135	17.8	14.4	5.0	75.0
	Forbs	135	9.6	4.0	1.0	25.0
	Shrubs	135	24.7	19.5	0.0	75.0
	Bare ground	135	40.4	18.2	1.0	85.0
	Dead wood	135	7.2	7.3	0.0	30.0
TEEPEE 02	Grasses	104	17.4	15.7	0.0	75.0
	Forbs	104	12.8	8.7	0.0	50.0
	Shrubs	104	11.8	12.3	0.0	50.0
	Bare ground	104	48.8	20.0	5.0	90.0
	Dead wood	104	9.7	12.0	0.0	80.0
MOOSE CR.	Grasses	72	32.8	18.1	5.0	75.0
	Forbs	72	22.1	9.1	0.0	40.0
	Shrubs	72	29.7	14.8	0.0	50.0
	Bare ground	72	4.1	3.9	0.0	20.0
	Dead wood	72	16.4	17.1	0.0	75.0

A four category size classification in which whitebark pine trees were categorized as seedlings, small saplings, large saplings, or trees illustrates whitebark pine tree size differences between the stands (Figure 5). The two Teepee Creek stands were very similar with a majority of the population consisting of seedlings and a small proportion as trees. The Moose Creek stand had relatively larger numbers of both small and large saplings with few seedlings and trees.

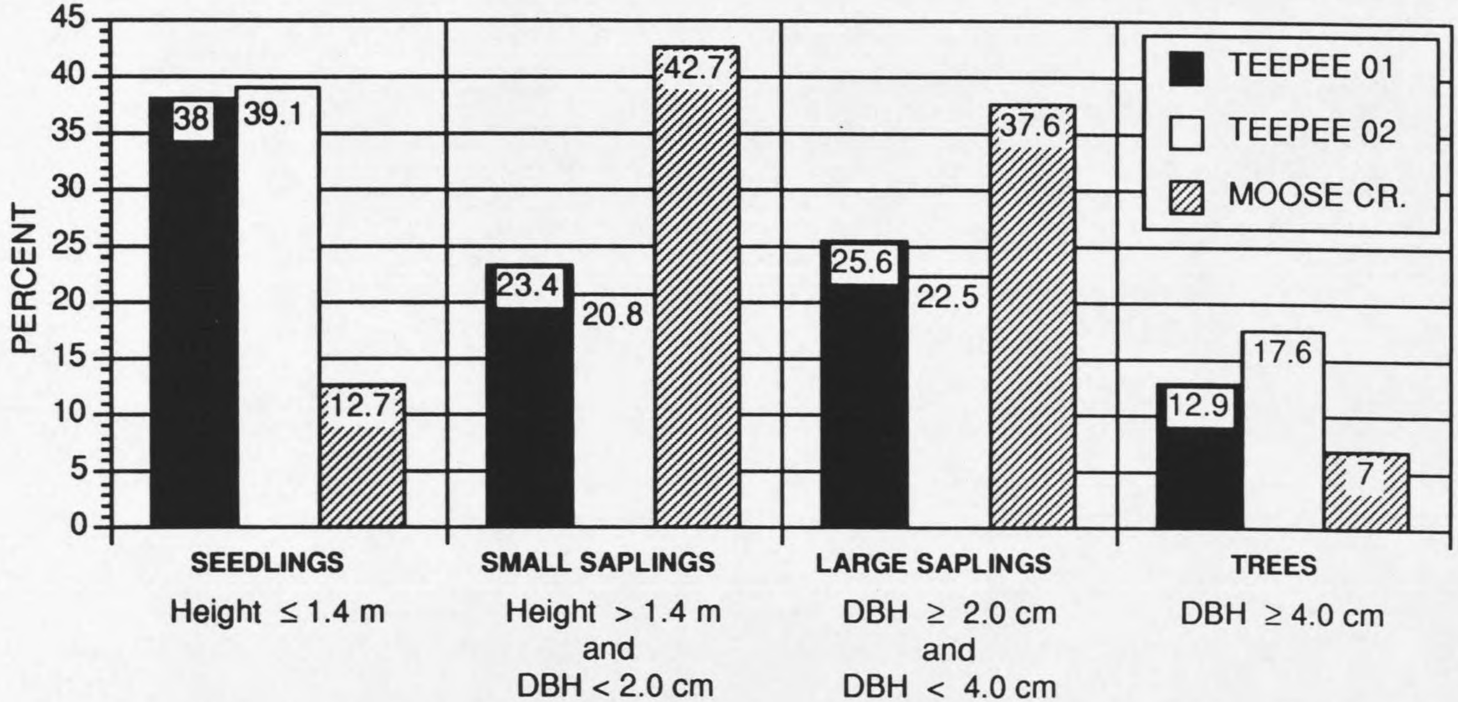

Figure 5. Four category size classification of whitebark pine trees

Stand densities appear to decrease with increasing elevation in the study stands. With an elevational range between 2130 and 2400 m, an average of 29.3 trees per study plot were measured in the Moose Creek stand. In contrast, the average number of trees per study plot decreased to 22.5 in stand TEEPEE 01 (2450 - 2500 m) and to only 15.9 in stand TEEPEE 02 (2500 - 2570 m).

Standardized by the number of plots (i.e., mean number of trees per plot by species), species composition and abundance vary in the study stands (Figure 6). Lodgepole pine is the most abundant tree in all three stands. In stand TEEPEE 02, whitebark pine is the second most numerous tree species, followed by subalpine fir. For the relatively lower elevation TEEPEE 01 stand, subalpine fir is the second most numerous tree, followed by whitebark pine. Engelmann spruce was a minor component in the two Teepee creek stands and not recorded in the Moose Creek stand. Douglas fir was the second most numerous tree in the Moose Creek stand, and whitebark pine was a relatively minor component in the Moose Creek stand.

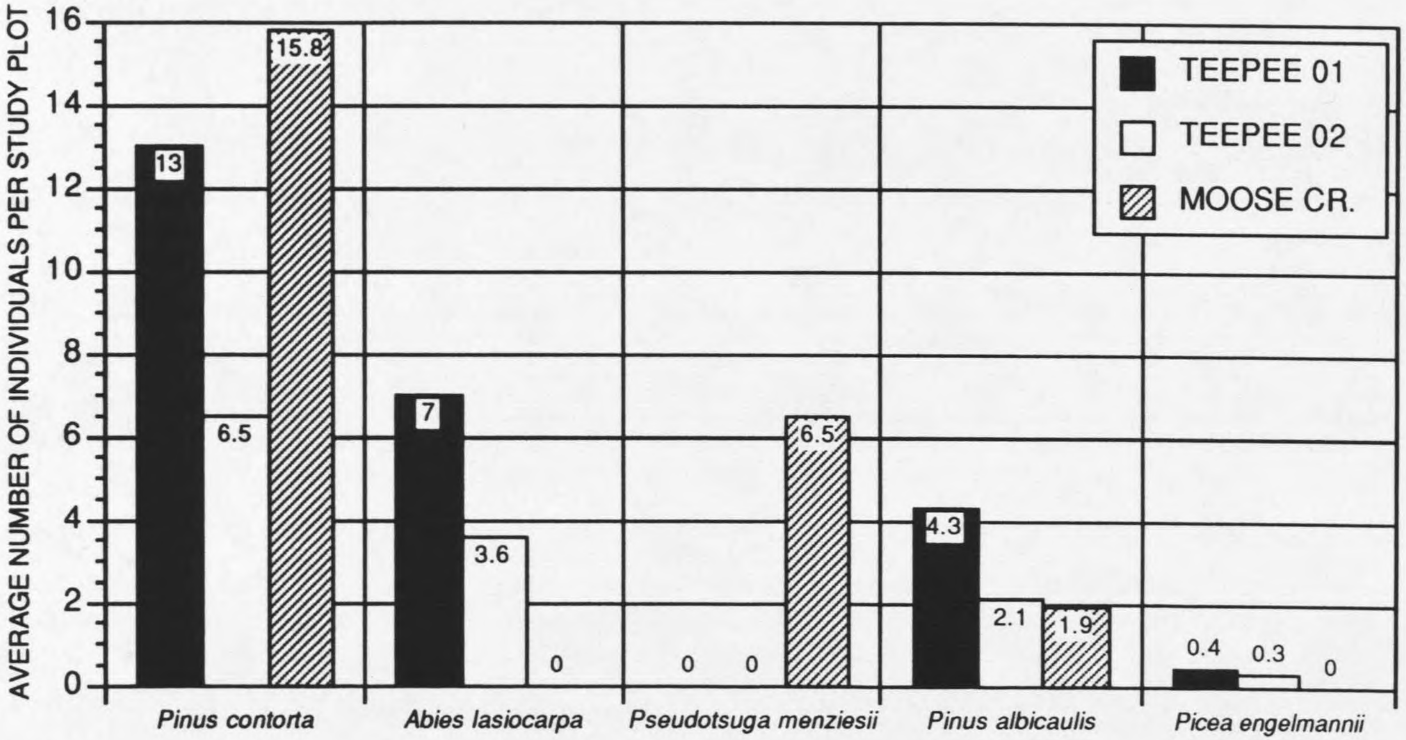

Figure 6. Average number of individuals per plot by species for each study stand.

Whitebark Pine Age Structures for TEEPEE 01 and TEEPEE 02

Whitebark pine ages in the higher elevation TEEPEE 02 stand ranged from 11 to over 50 years old. 68 (65.4%) of the trees were subsequent regeneration, and 36 (34.6%) of the trees were advance growth (Figure 7). A peak at 16 years suggests an above average whitebark pine seed production year. Alternatively, that peak may be due to systematically avoiding younger trees by sampling only those trees greater than 0.5 m tall.

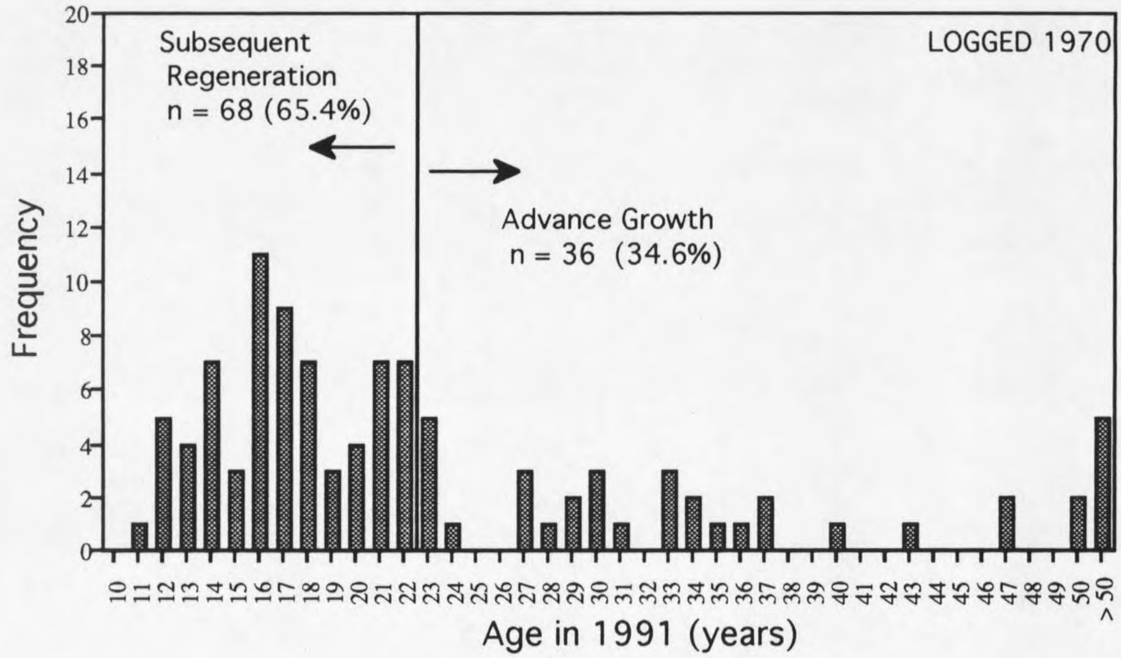

Figure 7. Age distribution for the subject whitebark pine trees in stand TEEPEE 02.

Whitebark pine ages in the TEEPEE 01 stand ranged from 10 to over 50 years old. 82 (60.7%) of the trees were classified as subsequent regeneration, and 53 (39.3%) of the trees were classified as advance growth (Figure 8). Similar to TEEPEE 02, a peak occurs at 17 years (8 years after the logging year). Because the peak in the age distribution occurs at 16 years for TEEPEE 01 and at 17 years for TEEPEE 02, the suggestion of an above average seed production year is supported.

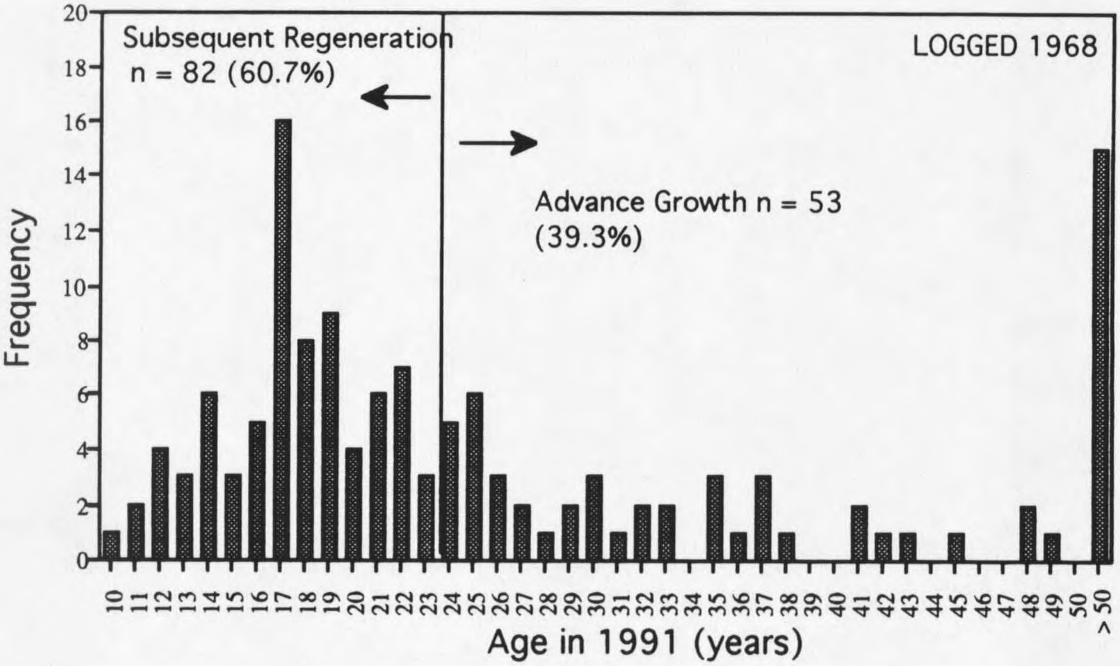

Figure 8. Age distribution for the subject whitebark pine trees in stand TEEPEE 01.

Competing Tree Characteristics

Average competing total tree heights and average distance of competing trees to the subject whitebark pine by species showed important differences between tree species in the three study stands (Table 7). The tallest trees tended to be lodgepole pine. This may be because of its colonizing nature and fast growth characteristics when grown in the open conditions that follow a disturbance. The whitebark pine trees had the shortest mean total tree height in the two Teepee Creek stands. Douglas fir had the shortest mean total tree height in the Moose Creek stand.

Competing whitebark pine trees tended to grow closer to the subject whitebark pine trees than other competing species. On average, the distance between the lodgepole pine trees and the subject whitebark pine trees was significantly greater than for any other tree species. The establishment by the shade-intolerant lodgepole pine trees occurred in gaps away from the whitebark pine trees, possibly due to an initial establishment of whitebark pine in the stands from Clark's nutcracker seed caching.

Table 7. Summary statistics of total tree height and distance between competing tree and subject whitebark pine for competing trees by species and stand.

			Height (m)		Distance (m)	
Stand	Species	n	Mean	Standard Deviation	Mean	Standard Deviation
TEEPEE 02	*Pinus albicaulis*	443	0.97	2.28	1.12	1.74
	Pinus contorta	678	1.16	3.53	1.57	3.33
	Abies lasiocarpa	492	1.40	2.55	1.50	2.22
	Pseudotsuga menziesii	-	-	-	-	-
	Picea engelmanni	42	5.49	2.55	1.81	2.72
	All trees	1655	1.61	2.87	1.55	2.53
TEEPEE 01	*Pinus albicaulis*	283	0.89	2.22	1.93	1.68
	Pinus contorta	1761	1.39	3.20	1.74	2.92
	Abies lasiocarpa	948	1.30	2.23	1.28	1.71
	Pseudotsuga menziesii	-	-	-	-	-
	Picea engelmanni	45	1.81	1.69	0.98	1.81
	All trees	3037	2.40	2.78	1.69	2.40
MOOSE CR.	*Pinus albicaulis*	141	0.38	1.33	0.65	1.92
	Pinus contorta	1138	1.19	3.48	1.76	3.81
	Abies lasiocarpa	-	-	-	-	-
	Pseudotsuga menziesii	466	1.66	1.72	0.69	1.70
	Picea engelmanni	-	-	-	-	-
	All trees	1745	1.76	2.77	1.65	2.69

Advance Growth and Subsequent Regeneration Whitebark Pine

Advance growth whitebark pine had significantly different characteristics than subsequent regeneration whitebark pine. Comparisons between advance growth and subsequent regeneration whitebark pine were done for all advance growth trees (n = 90) against all subsequent regeneration trees (n = 221). Also, trees from the Moose Creek stand were eliminated and comparisons were made for advance growth trees (n = 90) against subsequent regeneration trees (n = 149) in the two Teepee creek stands. The Moose Creek trees were eliminated because of its lack of advance growth whitebark pine.

Significant differences were found for total tree height (p = 0.000), crown diameter (0.049), crown diameter to tree height ratio (0.0002), and crown volume (0.014) by comparing all advance growth trees to all subsequent regeneration trees in the three study stands. Similar significant differences were found for total tree height (p = 0.0000), crown diameter (0.0006), crown diameter to tree height ratio (0.0004), and crown volume (0.0001) when the Moose Creek whitebark pine trees were eliminated.

Because there were significant differences between the advance growth trees and the subsequent regeneration trees, the advance growth trees were eliminated from further analysis.

Competition Indices

Competition index values were computed for each subject whitebark pine tree for each of the three study stands using three distance functions (1/distance, 1/distance^2, and $e^{-distance}$) (Table 8). Competition index values varied by stand, showing a wide range of values. Maximum competition index values calculated were over 60 using 1/distance, over

100 using 1/distance^2, and almost 20 using e$^{-distance}$. Competition index values for each of the three distance functions were highest in the Moose Creek stand. Index values were similar for the two Teepee Creek stands. Stand TEEPEE 02 had competition index values of zero; subject whitebark pine trees with competition index values of zero had no identified competitors.

Competition index values varied according to the distance function used. Index values calculated using 1/distance and 1/distance^2 were similar with mean values ranging from approximately 13 to 17 for the three study stands. Index values were substantially smaller using the e$^{-distance}$ function, ranging from 3.11 to 4.22 for the three study stands.

Table 8. Summary statistics of competition index values for subject whitebark pine trees (subsequent regeneration) by stand and competition index distance function.

Stand	Distance Function	n	Mean	Standard Deviation	Range
TEEPEE 01	1/distance	81	14.00	9.17	1.82 - 42.3
	1/distance^2	81	14.92	19.90	0.54 - 149.9
	e$^{-distance}$	81	3.11	2.404	0.18 - 10.3
TEEPEE 02	1/distance	68	12.98	12.98	0.00 - 63.7
	1/distance^2	68	13.12	13.12	0.00 - 67.0
	e$^{-distance}$	68	3.95	3.95	0.00 - 19.5
MOOSE CR.	1/distance	72	17.12	10.81	0.96 - 52.8
	1/distance^2	72	16.57	18.06	0.26 - 114.0
	e$^{-distance}$	72	4.22	3.69	0.03 - 18.1

Competition and Whitebark Pine Crown Characteristics

Bivariate Regression Analysis for Subsequent Regeneration Trees

The four subject whitebark pine tree measures (i.e., height, crown diameter, crown diameter to height ratio, and crown volume) were statistically correlated with the competition index values (Figures 9, 10, 11, and 12). R^2 values from bivariate regression analysis ranged from 0.027 to 0.131. The competition index was inversely related to each whitebark pine measure. There was considerable variability in the whitebark crown measures at lower levels of competition, and less variability at higher levels of competition. This changing variability may be an artifact of the lower number of subject trees with larger competition index values.

Total tree heights of the subject whitebark pine trees were statistically correlated with the competition index, but the R^2 values (0.033 for 1/distance, 0.027 for 1/distance^2, and 0.032 for $e^{-distance}$) indicate that the linearity of that relationship is poor (Figure 9). It is interesting to note that the intercept in the regression equation $y = a + bx$ can be interpreted to represent a maximum possible value for each tree measure in the absence of competition, although numerous trees are taller than the 2.047 intercept value would predict.

Crown diameters of the subject whitebark pine trees were statistically correlated with the competition index (Figure 10), although the R2 values were again quite low (0.131 for 1/distance, 0.096 for 1/distance^2, and 0.128 for $e^{-distance}$). The intercept value (0.820) of the regression equation poorly represents the maximum possible crown diameter; crown diameter values above 1.0 m are common.

The two calculated crown measures, crown diameter to tree height ratio and crown volume of the subject whitebark pine trees were also statistically correlated with the competition index (Figures 11 and 12). R^2 values for regressions using the crown diameter to tree height ratio were similar to those found using the crown diameter (0.122 for 1/distance, 0.079 for 1/distance^2, and 0.120 for $e^{-distance}$). Again, similar R^2 values were obtained in correlating competition index with crown diameter measures (0.092 for 1/distance, 0.058 for 1/distance^2, and 0.091 for $e^{-distance}$).

The 1/distance function used in the competition indices yielded slightly higher R^2 values for each of the four subject whitebark pine measures. Because of the relatively better explanation ability of the 1/distance function, the 1/distance^2 and $e^{-distance}$ distance functions were not evaluated in subsequent regressions.

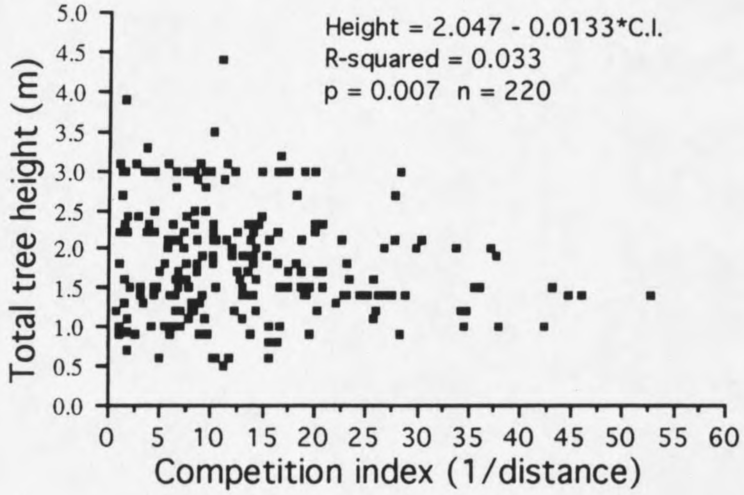

Figure 9. Bivariate scatterplot comparing competition index values with subject whitebark pine tree heights.

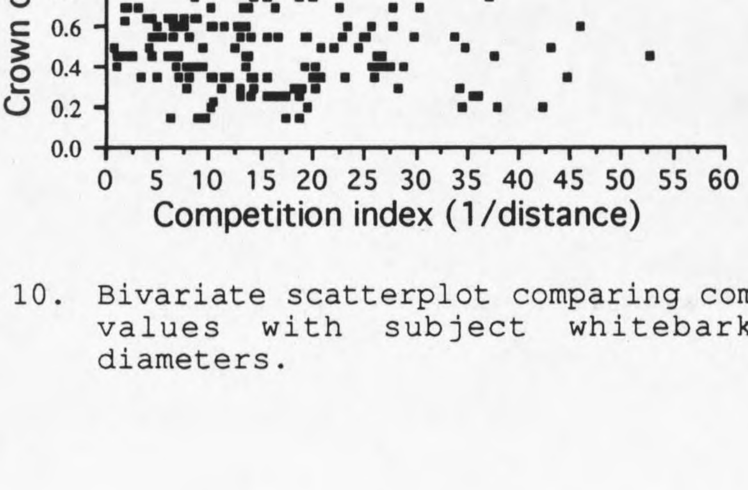

Figure 10. Bivariate scatterplot comparing competition index values with subject whitebark pine crown diameters.

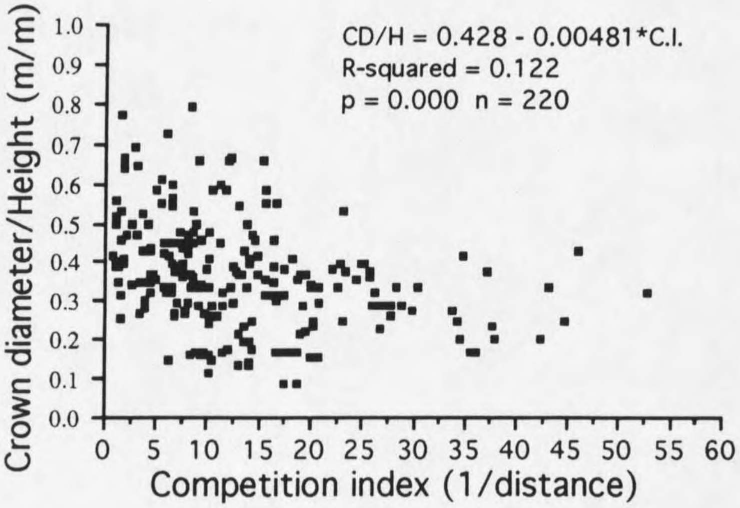

Figure 11. Bivariate scatterplot comparing competition index values with subject whitebark pine crown diameter to tree height ratios.

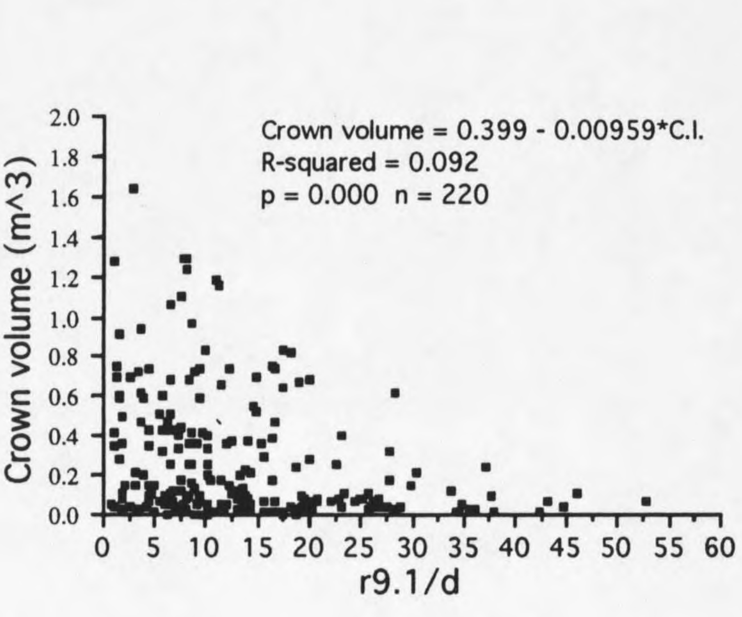

Figure 12. Bivariate scatterplot comparing competition index values with subject whitebark pine crown volume measures.

Multiple Regressions Using Stand and Tree Age

Indicator variables were included in multiple regressions to evaluate the influence of tree age and stand. Stand was a significant factor ($p \leq 0.005$ for *t*-tests of the age coefficient in the regression equations) for all subject whitebark pine measures except the crown diameter to tree height ratio ($p = 0.747$). Stand differences may represent factors that were not sampled for. Inclusion of stand as an indicator (TEEPEE 02 = 0, TEEPEE 01 = 1, and MOOSE CR. = 2) with the competition index in multiple regressions substantially increased the explanation of variability in whitebark pine tree heights, crown diameters, and crown volumes. The adjusted R2 values represent this increased explanation ($R^2 = 0.205$ for height, $R^2 = 0.250$ for crown diameter, and $R^2 = 0.248$ for crown volume). Stand, however, was not a significant factor between the two Teepee Creek stands ($p > 0.10$ for all four whitebark pine measures).

Subject whitebark pine tree ages were also included in the multiple regression analysis. Age data were not available for the Moose Creek stand, so age could not be assessed for the whitebark pine trees in the Moose Creek stand. Using only the subsequent regeneration whitebark pine trees in the two Teepee Creek stands, age was found to be a significant factor influencing whitebark pine measures ($p \leq$

0.005 for *t*-tests of the age coefficient in the regression equations).

From these multiple regression results, it was interpreted that age was a significant factor for height and crown measures (except crown diameter to tree height ratios) of the subsequent regeneration whitebark pine trees in the two Teepee Creek stands. Additionally, there were significant differences between the two Teepee Creek stands and the Moose Creek stand that influenced whitebark height crown measures, but there were not significant differences between stands TEEPEE 01 and TEEPEE 02.

Competition Thresholds

The form of the scatterplots comparing competition index values and whitebark pine height and crown measures suggests that a competition threshold exists below which some tree growth factor or factors are not limiting. In order to qualitatively assess a possible competition threshold, scatterplots were visually interpreted for competition values above which there is noticeably less variability in the general inverse relationship.

Competition thresholds were estimated for total tree height, crown diameter, crown diameter to tree height ratio, and crown volume for the subsequent regeneration trees in the two Teepee creek stands (Figures 13, 14, 15, and 16). No identifiable threshold was observed for the subject trees in the Moose Creek stand.

Competition thresholds were estimated at competition index values (using 1/distance) of approximately 17 for total tree heights (Figure 13), 22 for crown diameters (Figure 14), 22 for crown diameter to tree height ratios (Figure 15), and 18 for crown volumes (Figure 16). The majority of the whitebark pine trees had competition index values less than the estimated threshold values.

Bivariate regression analysis of the competition index against the four whitebark pine measures using only those trees greater than the threshold values yielded poor results for tree height ($R^2 = 0.128$, $p = 0.062$, $n = 27$), crown diameter ($R^2 = 0.146$, $p = 0.106$, $n = 18$), and crown volume ($R^2 = 0.091$, $p = 0.120$, $n = 27$). A statistically significant correlation, however, was found between the competition index and the crown diameter to tree height ratio ($CD/H = 0.846 - 0.0142*C.I.$: $R2 = 0.230$, $p = 0.000$, $n = 18$).

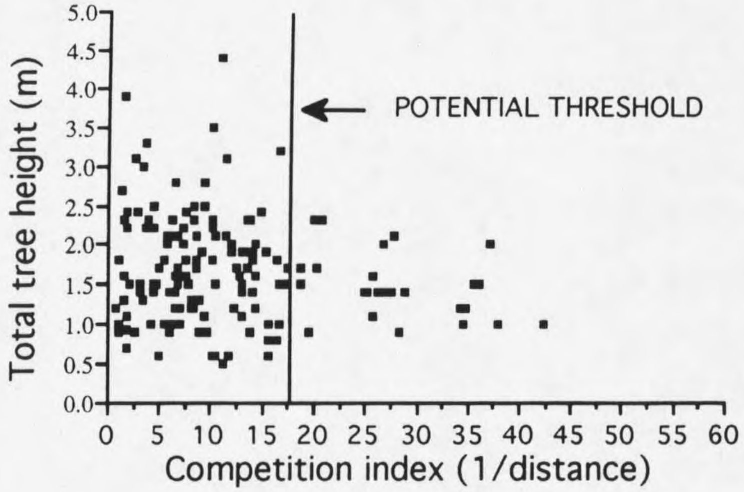

Figure 13. Scatterplot of competition index values and total tree heights showing a potential competition threshold.

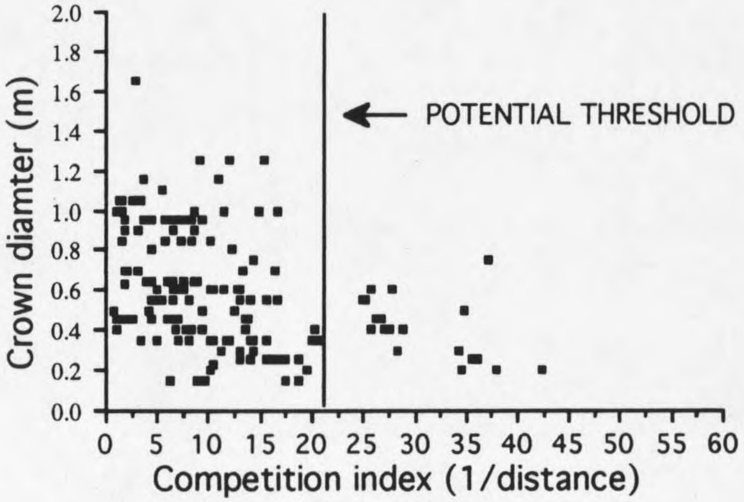

Figure 14. Scatterplot of competition index values and crown diameters showing a potential competition threshold.

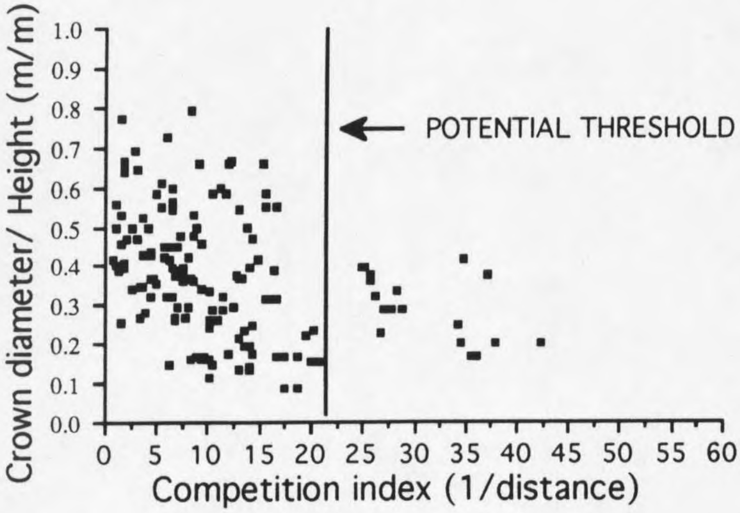

Figure 15. Scatterplot of competition index values and crown diameter/height ratios showing a potential competition threshold.

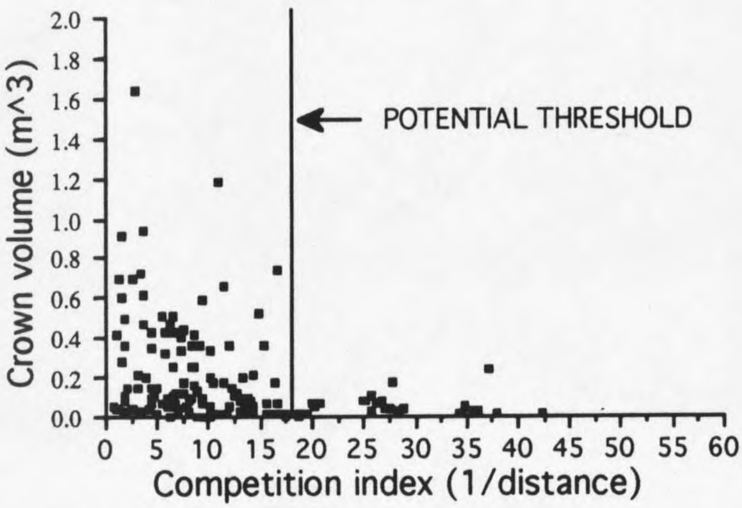

Figure 16. Scatterplot of competition index values and crown volumes showing a potential competition threshold.

CHAPTER 4

DISCUSSION

The competition index does not account for a very high proportion of the variation in crown characteristics of whitebark pine trees. Previous studies have published similar results, finding that competitive pressure explains approximately 20% of the variation in individual plant yield (Firbank and Watkinson 1987). Assessment of the influence of competition on the crown characteristics for whitebark pine is made additionally difficult by relying on present spatial relationships to evaluate a dynamic system; past growing conditions are unknown. Still, these results do provide important information for a potentially threatened tree.

Stand Characteristics

Subject Whitebark Pine Characteristics

Significant differences in whitebark pine measures were found between the three study stands. Whitebark pine measures in the Moose Creek stand were often significantly different from measures in the two Teepee Creek stands. Tree heights were different between the two Teepee Creek stands and the Moose Creek stand. Tree height is typically considered to be insensitive to tree spacing (Lanner 1985) and may reflect differences in site factors between the Teepee Creek stands and the Moose Creek stand. Crown diameters and crown volumes were different between TEEPEE 01 and the Moose Creek stand and between TEEPEE 01 and TEEPEE 02. Crown diameters are expected to be partially influenced by competition, responding to mechanical constraints as crowns begin to touch. Crown volumes reflect the overall size of a tree's crown, and total crown size could be an important characteristic to manage for increased seed production.

The crown diameter to tree height ratios were an exception to this general trend of differences between the Moose Creek stand and the two Teepee Creek stands. These ratios were significantly different between TEEPEE 01 and TEEPEE 02 only. The crown diameter to tree height ratio quantifies the shape of a tree, and larger values of the ratio may also be important for management goals such as increased seed production. Alternatively, tree shape may represent a characteristic crown form for young whitebark pine, and the relative similarity in this measure between stands may reflect this possibility.

The relatively small number of seedlings in the Moose Creek stand helps to explain some of the differences between whitebark pine measures between the Moose Creek stand and the Teepee Creek stands. Most of the whitebark pine trees in the Moose Creek stand were identified as small and large saplings. With relatively fewer seedlings, whitebark pine trees in the Moose Creek stand are, on average, larger than trees in the two Teepee Creek stands.

The low number of whitebark pine trees in the seedling size at the Moose Creek stand suggests that the majority of the whitebark pine establishment there may have occurred during and soon after the logging. This observation is supported by the field observation that none of the subject whitebark pine trees in the Moose Creek stand were identified as advance growth. The relatively greater stand density and more dense understory with few bare ground openings may have reduced pre-logging and recent whitebark pine establishment and survival at the Moose Creek stand. The lack of advance growth trees in the Moose Creek stand may be due to a higher mortality of understory whitebark pine during and after the logging, or there may have been few understory whitebark pine before the logging. Observations of adjacent mature forests suggests the latter.

The two Teepee Creek stands were very similar, and the age structures for the subject whitebark pine trees reinforce this similarity. Between 35 and 39 % of the whitebark pine trees were advance growth. Thus the advance growth trees are an important component of the whitebark pine trees in those two stands. Whitebark pine in the two Teepee Creek stands established both before and after the logging. Both stands showed similar age distributions with a large peak of trees that established approximately between 1974 and 1975, suggesting an above average seed crop year.

Competing Tree Characteristics

In the three study sites, whitebark pine trees are relatively minor components of the stands. Lodgepole pine is the dominant tree species in all three stands. Subalpine fir and Douglas fir are also important tree species. The ability of the whitebark pine trees to become mature overstory trees will depend upon their ability to grow relative to the lodgepole pine trees. In the mature forests adjacent to the Teepee Creek stands there are numerous suppressed understory whitebark pine and only a few mature whitebark pine in the overstory. These mature whitebark pine trees have straight boles and small crowns and are difficult to distinguish from lodgepole pine trees. Thus, the ability of the regenerating whitebark pine trees to grow into mature trees with full, vigorous crowns is doubted. Over the time period from establishment to maturity, competition is probably the most significant factor influencing whitebark pine crown characteristics in the study areas.

Competition Indices

A specific competition index value represents the competitive pressure exerted on a subject tree from the number, size, and spatial pattern of neighboring trees. An almost infinite combination of tree sizes, numbers, and spatial patterns is possible for each competition index value. For example, a competition index of x may represent a competitive pressure from several small trees near a subject tree or one or two larger trees farther away from a subject tree.

Additionally, the nature of the competition is unknown. Theoretically, trees compete for necessary resources such as light, nutrients, and space. Numerous mechanisms are possible for one plant to affect the growth of neighboring plants, and assessing these mechanisms requires long-term, intricate experiments (Barclay and Layton 1990). Hence, relationships in this study are estimations of the competitive pressure exerted by neighboring trees on subject trees; competition was not measured.

Advance Growth and Subsequent Regeneration Whitebark Pine

The advance growth trees had statistically different tree heights, crown diameters, crown diameter to tree height ratios, and crown volumes compared to the subsequent regeneration trees. The historical conditions that influenced characteristics of the advance growth tress could not be determined. Theoretically, an evaluation of tree stumps could give information on the size, number and spatial pattern of neighboring trees for the time period immediately preceding the logging, but many of the stumps were removed during the logging or site preparation procedures. Because of the differences between advance growth and subsequent regeneration whitebark pine trees in the study stands, the advance growth trees were eliminated from additional analysis.

Because advance growth and subsequent regeneration whitebark pine have statistically different tree heights and crown characteristics, the field identification of tree type may be important for forest management. Age data from tree cores or bole cross sections is the only certain way to identify the two types of trees, but these data are time consuming to collect and analyze, often requiring destructive sampling for small trees.

Advance growth was difficult to distinguish from subsequent regeneration in the field, although some advance growth showed a more dissected bark, had a noticeable needle litter on the ground surface below the tree, or had a twisting trunk appearance. Also, observations revealed that only 5% of the advance growth trees had multiple stem forms. In contrast, 68% of the subsequent regeneration trees had a multiple stem form. The multiple stem form may be either genetic or controlled by Clark's nutcracker seed caching (Weaver and Jacobs 1990). It is possible there is a high mortality of whitebark pine germinants in the understory of mature forests. Due to fewer surviving stems in a seed cache, the occurrence of multiple stems for understory whitebark pine may be decreased relative to trees grown in open conditions with higher germinant survival. Thus, the advance growth trees that established in the understory conditions prior to the logging may have a lower incidence of multiple stems than the subsequent regeneration trees. These observations suggest that the identification of advance growth may be made with simple field observations, although this identification procedure was not rigorously tested.

Competition and Whitebark Pine Crown Characteristics

Competition is a significant factor influencing whitebark pine crown characteristics. All relationships were inverse. Tree heights and crown volumes had poor correlations with the competition index. Tree heights were not expected to correlate strongly with competition. Poor correlations with crown volumes may be due to the sampling procedures. The relative vigor of the crowns was not recorded, and crowns with relatively sparse stem spacing within the crown were not separated from crowns with dense stem spacing. This distinction could easily be made in future studies by using crown vigor categories to weight crown volume measures.

Crown diameters and crown diameter to tree height ratios had good correlations with the competition index. Still, only 12 to 13% of the variation in these measures was explained by the competition index. The addition of age and an indicator variable for stand improved this relationship for the crown diameter measure, increasing the R^2 value to 0.250, but did not yield a significant correlation for the crown diameter to tree height ratio. Potentially, the crown diameter to tree height ratio may represent a characteristic crown shape for young whitebark pine trees in the stands.

The poor correlations between whitebark crown characteristics and the competition index may be due to unknown historical conditions. Many factors influence individual tree size. These factors include, local density, plant genotype, seed size, emergence time, and microhabitat variations. Historical conditions were not measured in this study and may have been important factors influencing crown characteristics. Emergence time was found to be an important factor influencing plant size for two annuals (*Agrostemma* *githago* L and *Triticum aestivum* L.) (Firbank and Watkinson 1987). Those plants that emerged first in a population and grew the fastest gained the largest share of resources. Additionally, competition from woody shrubs was found to be an important growth influencing factor for young Douglas fir trees (Wagner and Radosevich 1991b). Potentially, a competition index could incorporate conditions over time, but the use of incremental growth characteristics (i.e., annual) could provide some improvement without substantial efforts.

Finally, possible competition index thresholds were identified. These thresholds may be artifacts due to relatively few trees at higher competition values, or they may be values of competitive pressure where needed growth factors become limiting. Future studies are needed to further assess these threshold relationships. For such studies, multiple aged stands with varying tree densities should be sampled. To compare stands of different ages, the age independent competition index methods of Lorimer (1983) may provide a strong starting point.

A note on the use of regression methods for assessing competition and tree characteristics is needed. Regression analysis requires the assumption that the predictor variables are independent from the response variable: Firbank and Watkinson (1987) pointed out that "while a focal plant is affected by its neighbors, it is concomitantly affecting them." Regression analysis can comparatively evaluate the influences of competitive pressure on tree characteristics, but the actual relationships are much more complex than the linear regression models might suggest.

This study provides initial information on the relationships between whitebark pine crown characteristics and competitive pressures from neighboring trees. Before such information is applied to direct management strategies and actions, additional studies of competition and other factors influencing whitebark pine growth characteristics are recommended. For the GYE, these studies should include regenerating whitebark pine in a variety of stand ages and habitat types. Understanding these forest processes at physiological levels or scales of populations and communities can be important for the explanation of ecosystem level phenomena (Waring and Schlesinger 1985).

Timber harvests have provided an important but declining part of the GYE's regional economy (Powers 1991), and economic considerations are an important component of forest management policies. However, timber harvests can also have negative impacts. They have been a source of human-influenced degradation within the GYE, principally through accelerated slope failures, erosion, and sedimentation from roads (Marston and Anderson 1991). Additional disturbances such as fire, windthrow, and avalanches should also be considered. Although logged stands provide good access and possible whitebark pine regeneration sites, it is not believed that logging will be a major means for regenerating whitebark pine (Arno 1986). The importance of quantifying how neighboring trees influence whitebark pine crown characteristics in logged stands comes from increasing the knowledge of how a potentially manageable factor, competition, affects this important tree.

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APPENDIX

ORIGINAL DATA

Original data from this study are on file in digital form (tab delimited ASCI text files for DOS compatable computers) at the following locations:

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Bozeman, Montana 59715
(406) 994-3331

(2) Forestry Sciences Lab
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