

**Structure and dynamics of whitebark pine forests
in the South Warner Wilderness, northeastern California**

by

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ABSTRACT

I examined the structural characteristics and population dynamics of whitebark pine (*Pinus albicaulis*) across a 640 m elevational range in the Warner Mountains, northeastern California. I established permanent plots (8 x 50 m) at 90 m elevational intervals along six systematically located transects. Transects followed an east-west orientation, parallel to the slope. At each plot I inventoried physiographic conditions, stem density, basal area, height, and diameter, and I aged all single-stemmed individuals (>1.4 m) and the largest sound stem of multi-stemmed clusters. I also noted whether each stem occurred individually or as part of a multi-stemmed cluster.

Whitebark pine forest structure and dynamics vary with elevation. At low elevations whitebark pine began expanding downslope into sagebrush steppe habitat in the latter half of the 19th century. These stands are characterized by low stem density and basal area, and by relatively young, small trees. Forests at middle and high elevations exhibit age and size distributions typical of old, self-perpetuating stands. Other structural characteristics (density, basal area, and height) vary between middle and high elevation stands. Whitebark pine regeneration is occurring at all elevations, but sapling and seedling density are uniformly lower than that of tree density.

No differences were detected at different elevations in either the percentage of clustered vs. unclustered stems, or in the number of stems within each cluster. Trees

generally occur in clusters more often than saplings, and saplings generally occur in clusters more often than seedlings, suggesting that growth form (single stem vs. multi-stem) and cluster size may vary within an “individual” over time.

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INTRODUCTION

Whitebark pine (*Pinus albicaulis*)¹ occurs in the highest forests and at timberline in the primary mountain ranges of western North America. Although this high-mountain tree species has historically received relatively little attention, its resource values and importance have been increasingly recognized among both ecologists and land managers (Arno and Hoff 1989, Schmidt 1990, Keane and Arno 1993). Whitebark pine's large wingless seeds provide a major food source for many species of birds and mammals, including the black bear (*Ursus americanus*), the threatened grizzly bear (*Ursus arctos horribilis*), Clark's nutcracker (*Nucifraga columbiana*), and the red squirrel (*Tamiasciurus hudsonicus*) (Kendall and Arno 1990). Whitebark pine stands provide watershed protection by stabilizing soil and rock in harsh environments and by retaining snowpack (Arno and Hoff 1989). Occurring in subalpine and timberline areas heavily used by mountain recreationists, whitebark pine is also highly valued for its aesthetic qualities (Cole 1990).

Whitebark pine is the only North American representative of the five pine species known as the "stone pines" - members of subsection *Cembrae* of section *Strobus*, subgenus *Strobus*, genus *Pinus* (Critchfield and Little 1966). These species have traditionally been grouped into subsection *Cembrae* because of several diagnostic

¹ Scientific names follow *The Jepson Manual* (Hickman 1993) unless otherwise noted. See the manual for botanical authorities.

morphological features, including large wingless seeds and indehiscent cones. These features are thought to have resulted from coevolution between the trees and nutcrackers (*Nucifraga* spp.), the latter of which also show distinct morphological adaptations to pine seed dispersal, such as a sublingual pouch for seed storage, a very sturdy beak for ripping apart cones, and an excellent spatial memory for relocating pine seed cache sites (Lanner 1982, 1993, Tomback 1983, Tomback and Linhart 1990). Although some authors have thought that whitebark pine should be placed in subsection *Strobi* because of its morphological and ecological similarities to some *Strobi* species (Critchfield 1986, Millar and Kinloch 1991 cited by Krutovskii et al. 1994), recent studies based on isozyme and chloroplast DNA restriction fragment analyses indicate that the species does belong within subsection *Cembrae* (Krutovskii et al. 1994). Whitebark pine is thus more closely related to European and Asian pine species than it is to the other white pines of western North America, such as limber pine (*P. flexilis*), western white pine (*P. monticola*), and sugar pine (*P. lambertiana*), all of which are placed in subsection *Strobi*.

The distribution of whitebark pine can be split primarily into eastern and western populations. The eastern (or Rocky Mountain) population extends from the high ranges of eastern British Columbia and western Alberta along the principal ranges of the northern Rockies into northwestern Wyoming. The western population extends from the Coast Ranges of British Columbia south through the Cascades to the high Sierra Nevada. In addition to the two primary distributions whitebark pine also occurs

in isolated ranges in northeastern and south-central Oregon, northern Nevada, and the Klamath ranges and Warner Mountains of northern California (McCaughey and Schmidt 1990, Arno and Hoff 1989). Whitebark pine population dynamics vary in different parts of its range and at different altitudes; in the northern Rockies it is often a pioneer species after disturbances and is considered a transitional component of subalpine fir (*Abies lasiocarpa*) habitat types, while in drier ranges (such as the Sierra Nevada) and at timberline it often is considered the dominant self-maintaining species (Arno and Weaver 1990).

Much concern about the future of whitebark pine exists among biologists and land managers because the species is rapidly decreasing in abundance in many parts of its range. Remeasurement of permanent plots documented average mortality rates of 42% in some whitebark pine stands in western Montana over a 20 year period beginning in 1971 (Keane and Arno 1993). Whitebark pine mortality exceeds 90% in many areas of Glacier National Park (Lanner 1993). This decline has been caused principally by attacks of the introduced white pine blister rust (*Cronartium ribicola*), the mountain pine beetle (*Dendroctonus ponderosae*), and limber pine dwarf mistletoe (*Arceuthobium cyanocarpum*), and also by replacement by other subalpine tree species (notably subalpine fir). The combination of these factors is threatening the existence of whitebark pine in major parts of its range, and much

additional research into its biology and that of its parasites is necessary to develop the ⁴
management strategies necessary to guarantee the species' survival in the long term
(Lanner 1993).

QUESTIONS AND OBJECTIVES

Although the development of management strategies for ensuring the survival of whitebark pine and its valuable seed crops depends on a thorough knowledge of the species' habitat, competitive relationships, and patterns of stand development and regeneration, relatively little is known about its stand dynamics, especially within lower elevation stands where it competes with other tree species (Mattson and Reinhart 1990). This lack of knowledge appears to be particularly acute for stands in the southwestern portion of the species' range (Peterson et al. 1990), where whitebark pine often occurs as the sole or dominant self-maintaining species.

Extensive stands of whitebark pine in the Warner Mountains of extreme northeastern California have been described, but their dynamics have been little studied (Vale 1977, Riegel et al. 1990). As part of a study that focused primarily upon recent changes in lower-elevation white fir (*Abies concolor*) forests, Vale (1977) sampled size and age structure in several higher-elevation stands ("too few" in the author's words) dominated by whitebark pine and lodgepole pine (*P. contorta* ssp. *murrayana*). His limited data (from unknown elevations) suggested that whitebark pine was increasing while lodgepole pine was decreasing in abundance. He concluded that fire suppression was probably responsible for the changing forest composition, as he had also concluded for the lower-elevation forests.

In a more recent floristic classification of forest habitat types in the south Warner Mountains, Riegel et al. (1990) found that the composition and structure of whitebark pine-dominated habitat types vary in response to changes in elevation and aspect. In addition (and contrary to Vale's earlier [1977] conclusions) the study also reported that at lower elevations within whitebark pine habitat types both lodgepole pine and whitebark pine were successfully reproducing and appeared "persistent." At higher elevations (above 2713 m) whitebark pine was reported as both the canopy and reproductive dominant tree "whereas *P. contorta* is only occasional." The authors suggested that the dominance of whitebark at higher elevations may not be the result of lack of fire but rather that whitebark pine has a wider ecological amplitude than lodgepole pine. Several studies in other western ranges suggest that whitebark and lodgepole pine are often major competitors within overlapping parts of their elevational ranges (Jackson and Faller 1973, Parker 1988, Mattson and Reinhart 1990).

Charlet (1994) subjectively sampled the ages of several whitebark and lodgepole pines within the wilderness area, and his data indicated that some of the stands may be of great age and only infrequently subject to major disturbance. Eleven of 17 sampled whitebark pine trees were greater than 300 years old, and three of five sampled lodgepole pine trees were greater than 250 years old. A fire-scarred whitebark pine was estimated to be 820 years of age, and a 550 year-old specimen showed no signs of fire.

The Warner Mountains also offer an opportunity to study large stands of whitebark pine which are relatively unimpacted by white pine blister rust and limber pine dwarf mistletoe. Neither pathogen is currently a major threat within the South Warner Wilderness. I observed no dwarf mistletoe within the study area and estimated that a maximum of 6% of the trees within the study area were infected with blister rust, using a liberal interpretation of Hoff's (1992) identification methodology. Additionally, previous workers in the same vicinity estimated annual mortality at less than 1% in 1991 and 1993 (Riegel et al., unpublished data).

I undertook this study with the idea that a thorough investigation of the structure and population dynamics of whitebark pine across its elevational range within the South Warner Wilderness would provide greater insight into the composition of these subalpine forest stands, their history, and their current health, and would also determine their current regenerative status and likely future development patterns. It was hoped that the information yielded from the study would help to fill the literature gap in the dynamics of whitebark pine and would be valuable to biologists and land managers concerned with the status of this declining species.

The objectives of this project were:

- to describe the structure and composition of habitats in which whitebark pine is a dominant or important component within the south Warner Mountains
- to determine the size, age, and height distributions of whitebark pine and associated trees within these habitats

- to determine the current regenerative status and infer the population dynamics of the trees occurring in these habitats
- to establish permanent plots which will be of use to future researchers monitoring the long-term health and dynamics of these forests

DESCRIPTION OF THE STUDY AREA

Location

The Warner Mountains are located in Modoc County in extreme northeastern California, near the meeting of the California, Oregon, and Nevada borders (Figure 1). The range has a north-south orientation and is part of the Modoc National Forest. Most of the range south of Cedar Pass (State Highway 299) comprises the South Warner Wilderness. The wilderness encompasses approximately 28,647 ha and averages about 11 km in width and 26 km in length, with elevations ranging from 1457 to 3015 m (Riegel et al. 1990). The streams on the western slope of the mountains form the headwaters of the Pit River, while the eastern slopes drain into Surprise Valley, which is part of the Great Basin.

Climate

The climate of the Warner Mountains is considered continental, with cold, snowy winters and hot, dry summers (Pease 1965). Most precipitation falls between October and April, although thundershowers are occasional in the summer. Normal

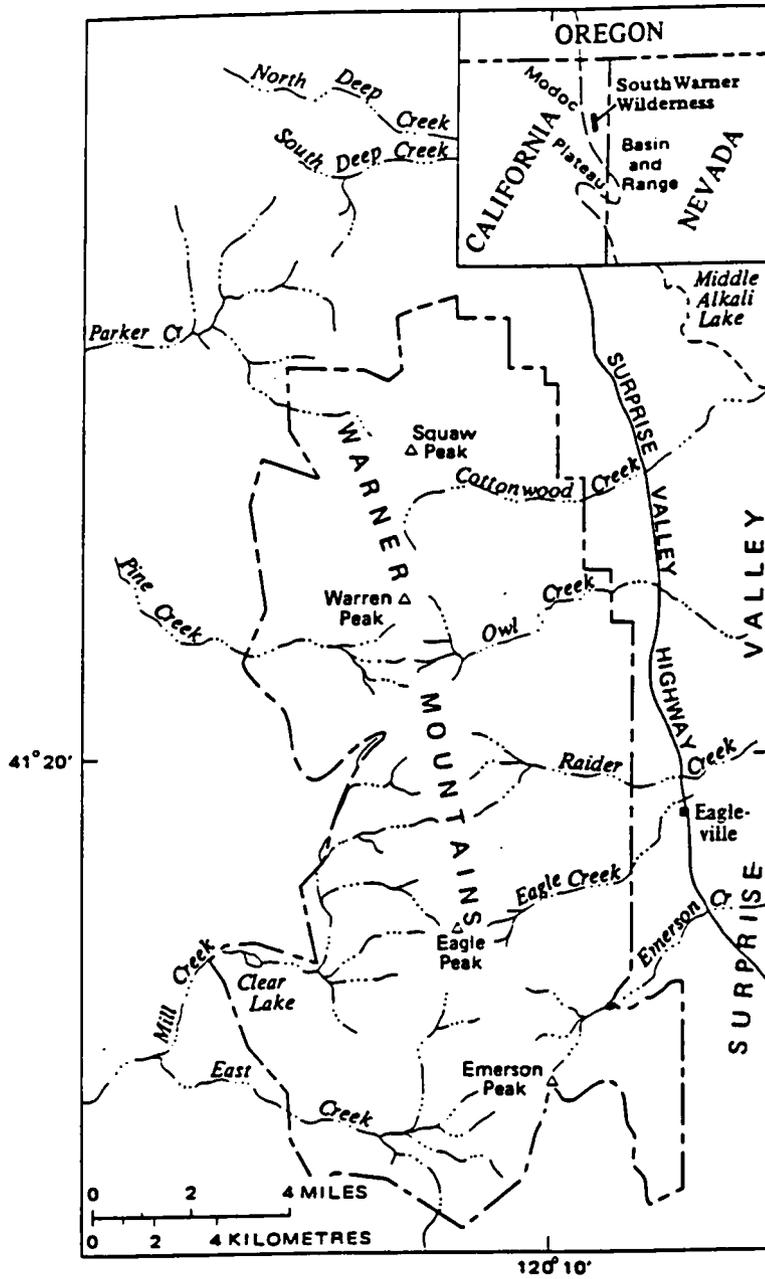


Figure 1. Location of the South Warner Wilderness.

(30 year average) annual precipitation from three nearby locations is as follows

(National Weather Service, 1997):

Alturas (on the Modoc Plateau on the west side of the mountains) -	30.51 cm
Jess Valley (on the southwestern edge of the mountains) -	46.15 cm
Cedarville (in Surprise Valley on the east side of the mountains) -	32.66 cm

Based on isohyetal contours, it is estimated that mean annual precipitation in the south Warners varies from 40.6 cm at their base to 63.5 cm near their crest (Rantz 1969). The snow pack averages 1077 mm in depth and contains an equivalent of 404 mm of water (State of California 1981). Snow typically remains near the crest of the ridge on the western slope of the mountains through June or early July and often lingers though the summer in sheltered patches on the eastern slope (Riegel 1982).

Geology and soils

The Warner Mountains have been uplifted by a west-dipping fault block created by a fault immediately to the east of the range (Duffield and Weldin 1976, Pease 1965). The Warner Mountains are considered to be the western edge of the Basin and Range mountain system; the block-faulted structure is characteristic of the Great Basin (although compositionally the rocks are related to the Modoc Plateau) and the east side of the range drains into Surprise Valley, which has no outlet. The general rock sequence of the Warner Mountains is Miocene volcanic rocks overlying Oligocene sedimentary rocks. The volcanic rocks consist of rhyolitic ash-flow tuff, andesite

flows, rhyolitic to andesitic air-fall pyroclastic deposits, basalt flows or small local rhyolite flows, while the sedimentary rocks consist of bedded siltstone and sandstone (Duffield and Weldin 1976). Soils within the wilderness are classified primarily as mollisols with some alfisols and entisols (Luckow 1986).

Habitats and vegetation

The flora of the Warner Mountains has been considered by some to be primarily Sierran in nature (Cronquist et al. 1972, Munz 1973), while others have considered it to be more aligned with the Great Basin and intermountain floras (Raven 1977, Harper et al. 1978, Raven and Axelrod 1978, Reveal 1979). The gently-tilted western slope of the wilderness supports large forest stands and a mosaic of sagebrush-steppe and spring-fed meadows. The steep, rocky eastern slope is dominated by big sagebrush (*Artemisia tridentata*) with scattered forests and meadows associated with drainages and springs (Riegel et al. 1990).

The coniferous forests of the Warner Mountains have been considered to be depauperate examples of Sierra Nevada and southern Cascade Range forests (Critchfield and Allenbaugh 1969), and are noted for the absence of four trees common to those ranges: red fir (*Abies magnifica*), sugar pine, Douglas-fir (*Pseudotsuga menziesii*), and mountain hemlock (*Tsuga mertensiana*) (Griffin and Critchfield 1972). Riegel (1982) and Riegel et al. (1990) described four series (*Cercocarpus ledifolius*, *Populus tremuloides*, *Abies concolor*, and *Pinus albicaulis*) containing nine forest

habitat types and two phases for the South Warner Wilderness' montane and subalpine habitats.

The major vegetation types within the study area are forests dominated by white fir, forests dominated by whitebark pine, and sagebrush-steppe areas. The white fir forests are dominated by white fir in both the canopy and the reproductive layers, with an understory of shrub species such as snowberry (*Symphoricarpos rotundifolius*) and sticky currant (*Ribes viscosissimum*), and herb species such as osmorhiza (*Osmorhiza chilensis*), false Solomons' seal (*Smilacina racemosa*), and white-veined wintergreen (*Pyrola picta*). Most of the fir-dominated habitats within the study area fall within the ABCO/OSCH (*Abies concolor/Osmorhiza chilensis*) habitat type. Jeffrey pine (*P. jeffreyi*) and whitebark pine are frequent associates of white fir. Whitebark pine forests are generally nearly pure stands of whitebark pine, except along their lower margins where white fir is an occasional associate. Riegel et al. (1990) identified three whitebark pine-dominated habitat types within the study area, which are defined by the occurrence of associated species and are located on an elevational/soil moisture gradient: 1) PIAL/STCA - whitebark pine/California needlegrass (*Stipa californica*)², 2) PIAL/PEGR - whitebark pine/slender penstemon (*Penstemon gracilentus*), and 3) PIAL/ARAC - whitebark pine/woody sandwort (*Arenaria aculeata*). The sagebrush-steppe habitats are generally located on gentle west-facing slopes and are dominated by big sagebrush. The most common, and sometimes codominant, associate of sagebrush

² *Stipa californica* Merr. & Burt Davy = *Achnatherum occidentale* (Thurber) Barkworth ssp. *californicum* (Merr. & Burt Davy) Barkworth in *The Jepson Manual*.

is mule's ears (*Wyethia mollis*). This vegetation type was identified as "sagebrush-*Wyethia* scrub" by Milligan (1968). Hereafter I generally refer to it as sagebrush habitat. Small quaking aspen stands (*Populus tremuloides*) are occasionally located on these slopes within the greater matrix of sagebrush.

Land use history

Since the settlement of Surprise Valley and the Alturas plains by European Americans in the 1860s, the primary use of the higher-elevation lands in the south Warner Mountains has been livestock grazing. Grazing intensity in the region increased rapidly after settlement, and by 1900 the number of cattle and sheep in the valleys adjacent to the Warners (and thus presumably using the Warners for seasonal forage) were 40,000 and 60,000, respectively (U.S. census data cited by Vale 1977). In addition, transient sheep flocks passed through the Warners seasonally on their way to shipping points south of the range, and/or from the Central Valley (Olmsted 1957). As a result, the Warner Mountains are said to have been severely overgrazed by the early 1900s (Vale 1977).³ Partly in response to overgrazing, a federal forest reserve was created in the Warners in 1904 at the behest of local ranchers. In 1934 the U.S. Forest Service established a "primitive area" in the southern Warners. However, widespread overgrazing continued until at least 1940, and local overgrazing continued

³ Vale makes this assertion based on allegations in several other papers, but he does not "specifically evaluate" these claims. See Brown (1951), Olmsted (1957), and Pease (1965).

beyond 1950. These conditions were documented by Vale (1977) based on research into annual grazing reports, periodic evaluations of range conditions, and official correspondence in files at the Modoc National Forest in Alturas. Grazing continues within the wilderness area which was created in 1964. The estimated carrying capacity of the wilderness is 4000 animal unit months (one animal unit month = the amount of forage required to sustain a cow and calf, or equivalent, for one month), and current forest management policies indicate that grazing will probably be maintained at or near these levels (Bordwell, personal communication).

With the advent of federal control over the Warner Mountains came a formal policy of fire suppression, and the Modoc National Forest has maintained a policy of suppressing fires within the wilderness (Riegel 1982, USDA Forest Service 1991). Between 1913 and 1993 there were 136 recorded fires within the present wilderness boundary (78% were caused by lightning). Most (87%) of these fires burned less than 0.4 ha. Although fire scars and charred wood are common throughout much of the study area, only three recorded fires have occurred in any of the six different square-mile sections occupied in part by the study area, and all were recorded as burning only 0.10 acre (0.04 ha). The largest recorded fires within the wilderness were 540 acres in 1981 and 1156 acres in 1987 (unpublished data, USDA Forest Service, Modoc National Forest, Warner Mountain Ranger District, Cedarville, CA).

METHODS

Stand selection

Previous workers observed that large forest stands dominated by whitebark pine occur within the South Warner Wilderness (Riegel et al. 1990). Using topographic maps, LANDSAT-generated images of vegetation types (Charlet 1989), and aerial photography, I located and compared large whitebark pine stands based on their size, density, elevational range, and topography. I chose one of the most extensive whitebark pine-dominated areas in the wilderness as the study area. It has a large elevational range (from approximately 2290 m to the crest of the mountains) with relatively little variation in aspect and a fairly uniform physiography. The site occurs on the western slope of the range in the vicinity of Eagle Peak (3015 m), the highest point in the range.

Sampling design

Transects and plots

The study area was sampled with a systematic plot arrangement. I established six equally-spaced transects which run from 2290 m to the crest of the mountains (which varies between 2835 and 3015 m within the study area). The transects are

located parallel to the slope in an east-west orientation and are approximately 412 m apart. I established 400 m² permanent plots⁴ at approximately 90 m elevational intervals along each of the transects (Figure 2). Because whitebark pine is often clumped, rectangular plots (8 x 50 m) were used rather than circular plots to minimize potential for bias (despite the greater boundary error of rectangular plots). Seven or eight plots were established along each transect (depending on the altitude of the ridgetop at the end of the transect) for a total of 44 plots. The center of each plot was marked in the field by a flagged and staked piece of 3/8" rebar extending approximately 8" above ground level. I marked plot locations on an enlarged U.S.G.S "Eagle Peak" 7.5-minute topographic map and on an aerial photograph.

Forest structure and composition

The frequent occurrence of whitebark pine in multi-stemmed clusters presents sampling difficulties, as it is difficult to determine whether a clump consists of one or more than one genet. Because of this difficulty, the sampling unit that I employed was the "stem" rather than the individual. A "stem" was defined as either a single-stemmed

⁴ Reasons for this choice of plot size include 1) 400m² plots have been used successfully in studies of whitebark pine ecology in a variety of areas and habitats in the northern Rocky Mountains (Keane and Morgan 1992), 2) the ECODATA protocol and analysis program used by the U.S. Forest Service (Region 1) as part of its ecosystem management strategy specifies this plot size, and thus data generated by this study can be easily analyzed in relation to data from other locations and made accessible to a variety of forest managers, and 3) preliminary, unpublished field studies in the Warner Mountains indicate that this plot size represents an adequate compromise between the amount of variation captured and the level of investigator effort necessary per plot (Riegel, personal communication).

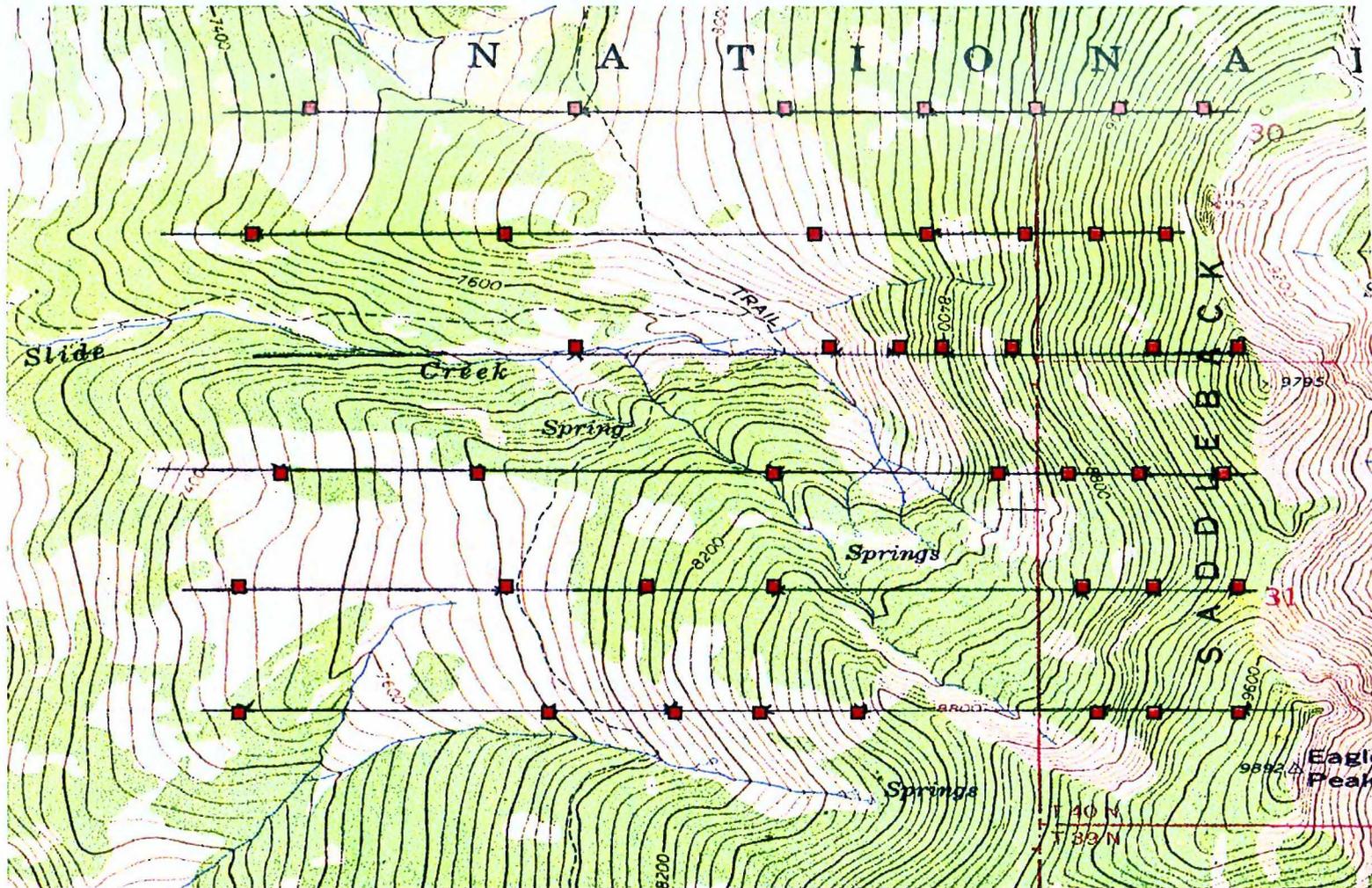


Figure 2. Map of study area (from USGS Eagle Peak 7.5 minute quadrangle) showing approximate locations of transects and plots. Transects are shown as horizontal dark lines, and plots are shown as red squares. North= \uparrow .

individual or a branch within a multi-stemmed cluster which had a high likelihood of being part of that cluster since the cluster's inception, regardless of whether the stem was genetically identical to the other stems in the cluster⁵. Stems within multi-stemmed clusters that were not obviously branched above the base of the cluster, or substantially smaller than the other primary stems in the cluster, were treated as individual trees, saplings, or seedlings, depending on their height. This sampling scheme required occasional "judgment calls" regarding whether a particular branch should be inventoried as a "stem" or simply ignored as an "after the fact" branch. Although I strove for consistency on these occasions, the wide variety of sizes, forms, and branching angles that I encountered in multi-stemmed clusters made completely objective decisions not always possible. It seems unlikely, however, that these rare instances would much impact the ultimate cluster size comparisons and results.

Variables recorded at each plot for each coniferous stem >1.4 m tall ("trees") included tree species, height class, and diameter at breast height (DBH). Height classes were in 1.5 m increments below 9 m, and in 3.0 m increments above 9 m. Stems were

⁵ Multi-stemmed whitebark pine clusters are known to arise in several ways, resulting in clusters in which the stems may or may not be genetically identical. Some authors have claimed that the clusters arise almost exclusively from different seeds cached at the same spot by Clark's nutcrackers and sometimes squirrels and/or chipmunks (Hutchinson and Lanner 1982, Linhart and Tomback 1985, Furnier et al. 1987). It is also claimed that the clusters may originate from independent seedlings germinating from a cone which may occasionally fall intact (Linhart and Tomback 1985). Weaver and Jacobs (1990) have shown that spontaneous basal branching occurs in both naturally-occurring and in greenhouse-grown specimens. I observed some seedling clusters in the field that were obviously comprised of independent seedlings, and others that had simply branched at ground level.

tagged with numbered aluminum tags (1999 total stems)⁶. Number, basal diameter, height, and health were also recorded for stems between 0.5 and 1.4 m tall (“saplings”), but they were not tagged. Basal area was calculated for each plot from the diameter data for trees and saplings. Numbers of seedlings (<0.5 m) were tallied within an 8 x 12.5 m subplot (one-quarter of each 400 m² macroplot). Whether each tree, sapling, and seedling occurred individually or as part of a multi-stemmed cluster was recorded to provide information about the distribution of multi-stemmed clusters along elevational and other environmental gradients.

Environmental variables inventoried at each plot included elevation, aspect, slope angle, slope configuration, topographic position, litter depth, ocular estimates of the amount of surface rock and downed wood abundance, habitat type (using a modification of the classification system of Riegel et al. 1990), and grazing sign. Parker’s (1982) topographic relative moisture index values (TRMI) were calculated from the topographic position, slope angle, aspect, and slope configuration data. Plants were inventoried by assigning ocularly-estimated cover class values to the dominant vascular plants of each growth form (trees, shrubs, and herbs), and by estimating overall cover values for each growth form.

⁶ A total of only 1999 tree stems were tagged in the field because of a shortage of tags on the last plot, although 2028 tree stems were actually inventoried. Due to the lack of tags each of several tree clusters on this plot received only one tag, which was placed on the largest sound stem of the cluster (the stem that was cored). The rest of the trees in each cluster were assigned a letter starting with the stem furthest south in the cluster, and progressing toward the north (e.g., stem 1984 was cored, and the other stems in the cluster were identified as stem 1984B and 1984C, with 1984B lying to the south of 1984C).

Age structure

Numerous studies have found poor correlations between the age and size of forest trees (Knowles and Grant 1983, Stewart 1986, Rebertus et al. 1991, Taylor and Halpern 1991). To obtain the most accurate and useful information possible about stand age structures, I cored all single-stemmed trees and the largest sound stem of multi-stemmed trees (896 stems total) as close as was practical to ground level with an increment borer.⁷ Saplings and seedlings were not involved in the age analysis. Several stems which qualified as trees based on the height criteria were not cored because their diameter was deemed too small to bear being cored (n=4). Because growth rates of individual trees can vary greatly and small, suppressed trees are often quite old (Parker and Peet 1984, Palik and Pregitzer 1995), I made no attempt to estimate the number of years required for each tree to reach coring height. Data are presented in terms of age at coring height.

⁷ Aging multi-stemmed tree clusters presents complications that have been approached in different ways by different investigators. Rebertus et al. (1991) aged multi-stemmed tree clusters of *P. flexilis* by coring the largest sound stem of the cluster and assuming that all individuals in the cluster probably germinated in the same year (thus also assuming that all stems were distinct genotypes). Alternatively, Peterson et al. (1990) aged the larger stem in two-stemmed clusters of *P. albicaulis* and a stem of "median dbh" in clusters with more than two stems. If stems in a cluster truly represent different genotypes germinated from the same Clark's nutcracker cache (Linhart and Tomback 1985, Furnier et al. 1987), it seems reasonable to assume that all stems (individuals) should be of the same or very similar age. Tomback et al. (1993) found that ages among *P. albicaulis* seedlings within 94 clusters differed by a mean of 1.5 years, with a range of 0 to 8 years. Determining the age of any stem within the cluster would thus provide a reasonably accurate estimate of the ages of all individuals within the cluster. I sampled the largest sound stem of each cluster, following the methodology of Rebertus et al. (1991).

In the laboratory, cores were mounted, planed, and then sanded with successively finer grades of sandpaper (to 600 grit). I counted growth rings with a binocular dissecting microscope and an illuminator (angled toward the core at approximately 30-45 degrees). For cores with very narrow growth rings, I sometimes used small amount of water to cause a slight expansion of the wood, which allowed easier distinction of ring boundaries. Age at coring height was recorded for those cores that passed through the pith of the stem. For those cores that were either off-center (failed to pass through the pith) or incomplete (those that failed to reach the pith or its vicinity due to rot, etc.), I recorded the number of countable rings as the minimum age. I then estimated the actual age of each core using the methodology of Applequist (1958) for off-center cores, and the methodology described in following section for incomplete cores. I used the estimated ages in the creation of the age distributions.

Additionally, I cored each stem of ten multi-stemmed clusters (elevation approximately 2500 m) to determine whether each stem in multi-stemmed clusters was the same age or nearly the same age as other stems in the cluster (sampled clusters averaged 3 stems; 29 cores total).

Data analysis

Forest structure and composition

Because I only inventoried two plots at 2930 m, the data gathered from that elevation could not be statistically compared to data from other elevations. After reviewing the data for many variables across all the inventoried elevations, I judged that the 2930 m plots were not substantially different from the 2830 m plots and merged the two into the “2830/2930 m” elevation band. This procedure created eight plots at that elevation, and allowed statistical comparisons to be made among all elevations.

Most forest structural characteristics (including stem density [trees, saplings, and seedlings], basal area, and tree diameter) were compared with respect to elevation by one-way analysis of variance (ANOVA) and the Kruskal-Wallis one-way ANOVA on ranks (a nonparametric test) when one-way ANOVA normality assumptions were not met. When significant differences ($p < 0.05$) among elevations were detected by an ANOVA test, the Tukey-Kramer multiple comparison procedure was used to pinpoint which elevations were actually different from one another (the alpha level considered significant was reduced to 0.10 for these multiple comparisons, as suggested by Hintze [1995]). The Tukey-Kramer multiple comparison procedure is a conservative test (i.e., two means must be very different for the difference to be considered significant) which employs an experimentwise error rate for the type I error. Significant differences ($p < 0.05$) detected by the Kruskal-Wallis one-way ANOVA test were further investigated with the aid of the Kruskal-Wallis Z-value multiple comparison procedure

(Hintze 1995, Sokal and Rohlf 1995). Data were transformed in several cases when equal-variance assumptions were not met. The transformations used were logarithmic ($\log[x]$), square root (\sqrt{x}), and reciprocal ($1/x$), which are appropriate for right-skewed data (Norman and Streiner 1994).

Tree height with respect to elevation was not compared statistically because the height data did not pass normality or equal variance tests, in raw form or after transformation. However, height means and standard deviations are presented in tables, boxplots, and histograms.

Mean number of stems per multi-stemmed cluster and the percentage of clustered stems vs. single stems for 1) trees and saplings, and 2) seedlings were compared with the Kruskal-Wallis one-way ANOVA test.

Cover estimates (canopy, shrub, and herb) and environmental parameters (slope, aspect, surface rock, litter depth, and down wood) were also compared with respect to elevation through ANOVA and multiple comparison procedures.

Age structure

Age structure data were analyzed primarily with respect to elevation. Boxplots and histograms were prepared comparing the ages of stems (by species) at each elevation. The age data did not lend itself to simple statistical comparison, because the primary differences among elevations were the presence of outliers rather than differing means. Nonetheless, means of tree age for each elevation are presented. The relationship between tree age and diameter was investigated by calculating Spearman

rank correlation coefficients and linear regression models for all trees and for trees at each elevation (by species).

Age structure data are presented with only the largest stem in a multi-stemmed cluster contributing to the structure of a plot, while density was calculated by considering each stem in a multi-stemmed cluster as an individual). The age structures presented here are therefore not based on all stems, which would require assigning the same age to every stem in a cluster as was calculated for the one that was cored. Instead they are the structure of the ages of each single-stemmed tree and each multi-stemmed cluster.

Various calculations related to the age analysis are presented in tabular form, including percentage of cores through the pith or off-center or incomplete, mean ages added to off-center cores, and mean ages added to incomplete cores.

Partial cores were extracted from 47 stems. Although I determined a minimum age for each stem by counting all the growth rings present on the partial cores, I also estimated the actual age of each tree. Estimated ages were calculated by first estimating the missing length for each core, and then estimating the number of growth rings occurring in the missing core section, using methods similar to those of Taylor and Halpern (1991) and Bingham (1993).

To predict total core length for each of the partial cores, I developed a regression equation relating core length (distance from cambium to pith) to tree diameter for all trees with complete cores (core length = $1.44 + 0.42(\text{DBH})$, $r^2=0.85$,

$p=0.0000$, $n=850$). The difference between predicted core length for each incompletely-cored tree and the length of its partial core was determined to be the missing length of each incomplete core. If the predicted core length was less than the actual length of the core fragment, the minimum age of the tree was used as its estimated age ($n=12$; 26% of the incomplete cores).

To calculate the average number of growth rings per centimeter of missing core for each tree, I calculated the mean number of rings per centimeter for all trees occurring at the same elevation as each partial-core tree with complete cores less than or equal in length to that of the missing core length for the particular tree in question. For example, to calculate the mean rings/cm of a tree growing at 2650 m with a missing length of 5.4 cm, I calculated the mean number of rings/cm for all trees occurring at 2650 m that had complete cores less than or equal to 5.4 cm in length. Lastly, the mean number of rings/cm was multiplied by the estimated length of the missing core section to determine the number of years to be added to the minimum age of each incomplete tree.

The benefit of this method of calculating rings/cm is that the rings upon which the calculation is based are those that were accumulated relatively early in the lives of the “model” trees (e.g., the age of the first 5.4 cm of a tree’s life is based on the first 5.4 and fewer cm of other trees growing at the same elevation). The weakness of this method is that this calculation assumes that the growth rate of the trees in question

occurred at approximately the same rate as it does today; the impacts of any possible climatic changes upon growth rate are not taken into account.

Five of the incomplete cores were calculated to have very small missing core lengths, which created a problem because there were few or no other trees with such small diameters that could be used to derive “rings/cm” values for the partial-core trees. In order to develop a sample large enough, the core length criteria for trees on which to base the rings/cm calculation was relaxed, allowing trees with slightly larger core lengths to be used as a basis for the calculation. Table 1 lists these trees, the missing core lengths, and the modified criteria which allowed a larger sample to be drawn as a basis for the rings/cm calculation. The amount the criteria is relaxed is not uniform relative to the missing core length because the sample upon which the calculation is based must be drawn from the same elevation as the tree in question, and different elevations had different numbers of trees of particular size ranges.

Table 1. Modified core length criteria for trees with incomplete cores and very small missing core lengths.

Tree #	Missing core length (cm)	Modified core length criteria (cm)
794	1.89	2.2
1035	0.65	2.0
1913	1.15	2.0
1126	1.12	2.0
992	1.18	1.5

RESULTS

Structure and composition

Environmental data

Most environmental parameters varied along an elevational gradient (Table 2, Figure 3). No significant differences were detected between the mean aspect of plots at each elevation (Kruskal-Wallis one-way ANOVA on ranks, $p=0.3456$ [Appendix A provides detailed statistical summary tables for all tested variables]), indicating that aspect throughout the study area is fairly uniform and unlikely to have a large effect on the structural and age differences present within the studied forest stands. I found slope angle to be a highly significant variable with respect to elevation (one-way ANOVA, $p=0.0000$), with the general trend of increasing slope with increasing elevation. Topographic relative moisture index (TRMI) values varied significantly with elevation (one-way ANOVA, $p=0.0000$), with the trend of decreasing values with increasing elevation. The percentage of surface rock is significantly higher above 2650 m (one-way ANOVA, $p=0.0003$). No significant differences at the various plot elevations were detected for litter depth (one-way ANOVA, $p=0.42$). The percentage of ground surface occupied by downed wood is significantly lower at 2290 m than at almost all other elevations (Kruskal-Wallis one-way ANOVA, $p=0.0080$), while the

Table 2. Summary of major environmental parameters with respect to elevation. Data are means and 1 SD.

Environmental Variable	Elevation (m)	2290	2380	2470	2560	2650	2740	2830/2930
	n	6¹	6¹	6¹	6¹	6	6	8
Aspect²	mean	287.8	268.8	272.3	279.8	267.5	273.2	283.0
	SD	27.6	15.3	40.5	18.9	15.4	20.7	20.4
Slope³	mean	8.7	10.0	15.5	15.5	21.2	26.2	24.95
	SD	3.4	2.8	6.1	6.1	4.3	3.3	2.4
TRMI value⁴	mean	33.8	31.7	26.3	27.7	23.8	19.7	19.9
	SD	3.3	2.3	5.1	5.6	5.3	2.1	2.9
Surface rock⁵	mean	7.3	11.0	8.8	5.8	11.8	31.2	38.1
	SD	7.5	15.5	13.0	5.6	7.5	15.2	22.3
Litter depth⁶	mean	1.2	0.7	0.9	1.2	1.0	0.6	0.9
	SD	0.4	0.6	0.8	0.6	0.4	0.5	0.5
Downed wood⁵	mean	5.3	1.0	1.8	5.8	5.2	6.5	5.4
	SD	5.0	0.0	1.2	5.8	2.0	4.8	2.7
Canopy cover⁵	mean	25.2	6.2	17.7	21.2	24.8	18.8	23.5
	SD	24.2	4.3	16.3	22.1	9.2	8.1	11.4
Shrub cover⁵	mean	11.2	25.5	16.2	11.8	4.3	1.3	0.1
	SD	8.9	24.0	23.1	16.5	5.8	1.5	0.4
Herb cover⁵	mean	29.8	27.6	32.2	28.4	28.2	14.5	7.0
	SD	20.7	14.9	13.5	10.7	11.8	12.6	5.4

Notes:

¹ n=5 for shrub cover at 2290, 2470, and 2560 m; n=5 for herb cover at 2290, 2380, 2470, and 2560 m

² North=0, east=90, south=180, west=270.

³ degrees

⁴ Topographic Relative Moisture Index (higher value = greater soil moisture availability)

⁵ percent

⁶ cm

downed wood values at other elevations are, for the most part, not significantly different from one another.

Significant differences in tree canopy cover percentage were detected among elevations (one-way ANOVA on log-transformed data, $p=0.0204$; Kruskal-Wallis one-way ANOVA with raw data, $p=0.0470$). The mean cover at 2380 m is significantly lower than that at 2650 m and 2830/2930 m. Variation in canopy cover was probably due to the overall structural and habitat diversity of the project area (i.e., some plots fell into or adjacent to relatively open scree-covered areas in the high elevation areas, while some plots fell into fairly open areas or along the forest edge within the sagebrush invasion habitats). Shrub cover varies significantly among elevations (Kruskal-Wallis one-way ANOVA, $p=0.002$), with the highest shrub cover values at 2380 m and then declining with increasing elevation to nearly zero cover at 2830/2930 m. Herb cover also varies significantly in response to elevation (one-way ANOVA, $p=0.011$), with low mean cover values at the highest elevations. The steep, dry slopes of the upper elevations have less plant cover and soil development upon the exposed bedrock and weathered scree than do the lower elevations.

I observed cows and/or sheep or their respective scat in all plots up to and including those at 2560 m. At 2650 m, four of six plots had cow and/or sheep scat but two plots had no sign of grazing. At 2740 m only one plot had indications of recent grazing, and at 2830 and 2930 m there was no evidence of recent grazing.

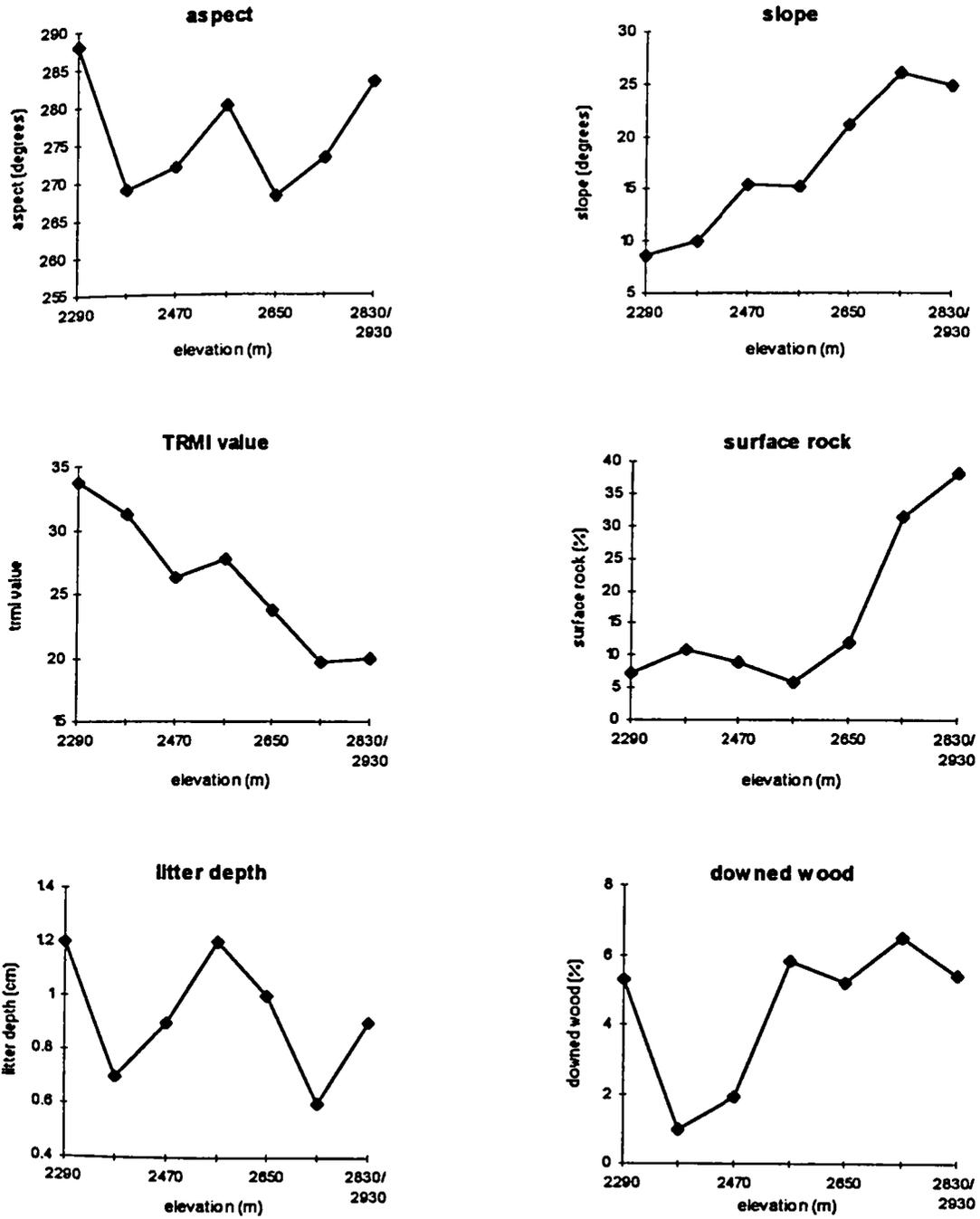


Figure 3. Means of major environmental parameters with respect to elevation.

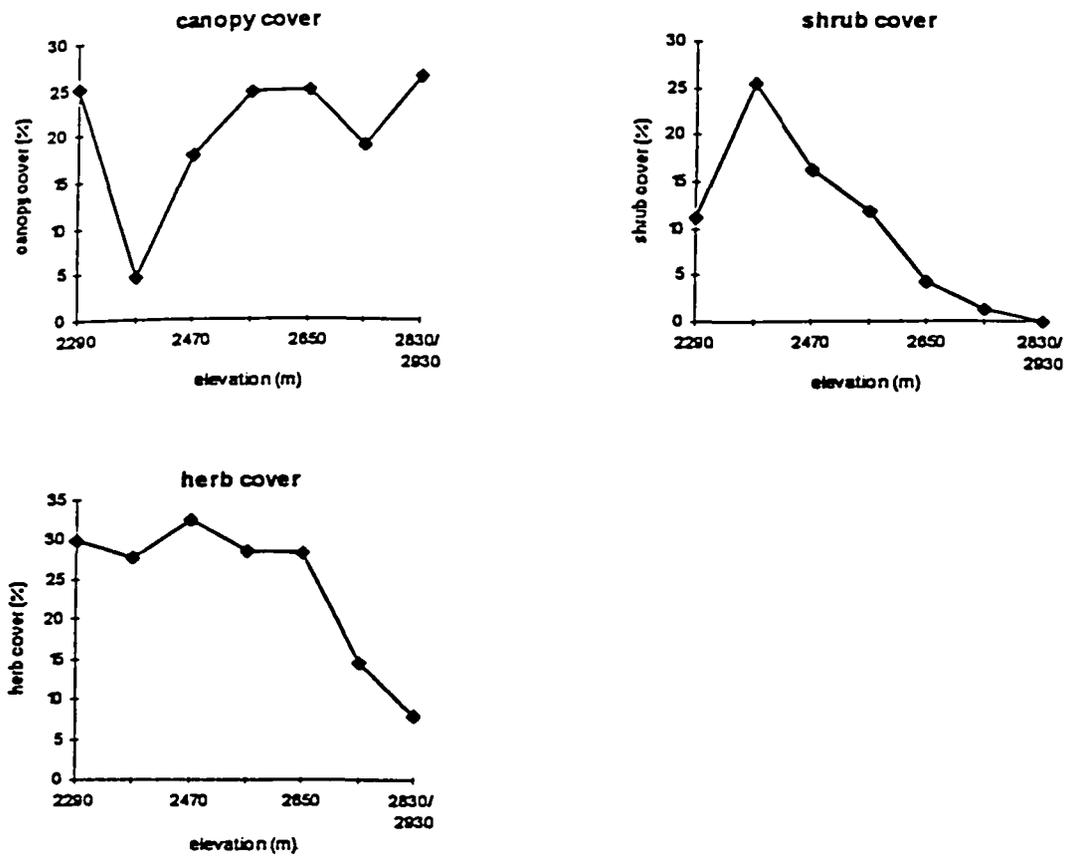


Figure 3. Means of major environmental parameters with respect to elevation, continued.

Classification of the plots into forest habitat types followed the designations of Riegel et al. (1990), although I also designated the “sagebrush” habitat type for those plots which supported white fir and whitebark pine yet were dominated by big sagebrush. Habitat types within the study area are essentially distributed along an elevational gradient (Table 3).

In summary, most environmental parameters vary along an elevational gradient. Low-elevation forests are dominated by white fir, middle elevations support sagebrush-dominated habitat, and the high elevations support whitebark pine-dominated woodlands and forests in the steeper, drier terrain. Canopy cover is high in the fir forest, low in the sagebrush habitats, and high in the three whitebark pine-dominated habitats. Shrub and herb cover are highest in the lower elevations, and consequently grazing is concentrated in these areas. Surface rock is much more prevalent in the higher areas, while downed wood is significantly less abundant in the sagebrush-dominated plots.

Density

White fir is the dominant tree species at 2290 m, near the upper end of the white fir band within the study area. At this elevation white fir tree, sapling, and seedling density are far higher than those of whitebark pine (Table 4). At 2380 m, where the vegetation is dominated by sagebrush, white fir tree and sapling densities are much lower than those of whitebark pine (although fir seedling densities are very high). Above 2380 m white fir is only incidental, and none were observed above

Table 3. Summary of plot habitat types for each elevation.

Elevation (m)	Number of plots consisting of habitat type (each asterisk represents one plot)s					
	Series Association	White fir ¹ ABCO/OSCH ³	Big sagebrush ² sagebrush	PIAL/STCA ⁴	Whitebark pine ¹ PIAL/PEGR ⁵	PIAL/ARAC ⁶
2290		*****	*			
2380			*****			
2470			***	**	*	
2560				***	***	
2650				***	*	**
2740					*	*****
2830/2930						*****

Notes:

¹ Riegel et al. (1990)

² Sawyer and Keeler-Wolf (1995)

³ ABCO/OSCH = *Abies concolor*/*Osmorhiza chilensis*

⁴ PIAL/STCA = *Pinus albicaulis*/*Stipa californica*

⁵ PIAL/PEGR = *P. albicaulis*/*Penstemon gracilentus*

⁶ PIAL/ARAC = *P. albicaulis*/*Arenaria aculeata*

Table 4. Mean density (stems/ha \pm 1 SD) values for trees, saplings, and seedlings with respect to elevation. PIAL = whitebark pine, ABCO = white fir.

	2290 m	2380 m	2470 m	2560 m	2650 m	2740 m	2830/2930 m
PIAL trees	108.3 \pm 91.7	229.2 \pm 169.9	675.0 \pm 407.4	662.5 \pm 258.7	1208.3 \pm 654.2	1158.3 \pm 393.6	2918.8 \pm 550.1
ABCO trees	462.5 \pm 351.7	37.5 \pm 68.5	4.2 \pm 10.2	4.2 \pm 10.2	-	-	-
Total trees	570.8 \pm 402.6	266.7 \pm 216.0	679.2 \pm 403.6	666.7 \pm 259.6	1208.3 \pm 654.2	1158.3 \pm 393.6	2918.8 \pm 550.1
PIAL saplings	87.5 \pm 125.2	54.2 \pm 92.8	25.0 \pm 31.6	41.7 \pm 56.3	237.5 \pm 218.4	166.7 \pm 80.1	668.8 \pm 338.8
ABCO saplings	412.5 \pm 652.6	4.2 \pm 10.2	4.2 \pm 10.2	-	4.2 \pm 10.2	-	-
Total saplings	504.2 \pm 773.9	58.3 \pm 102.1	29.2 \pm 29.2	41.7 \pm 56.3	241.7 \pm 217.8	166.7 \pm 80.1	668.8 \pm 338.8
PIAL seedlings	83.3 \pm 204.1	133.3 \pm 326.6	433.3 \pm 964.7	50.0 \pm 83.7	183.3 \pm 194.1	383.3 \pm 386.9	787.5 \pm 591.5
ABCO seedlings	3116.7 \pm 4764.2	666.7 \pm 1123.7	-	-	-	-	-
Total seedlings	3200.0 \pm 4931.1	800.0 \pm 1075.2	433.3 \pm 964.7	50.0 \pm 83.7	183.3 \pm 194.1	383.3 \pm 386.9	787.5 \pm 591.5

2650 m. Whitebark pine tree densities follow a trend of increasing density with increasing elevation and the mean densities among several elevations are significantly different from one another (one-way ANOVA, $p=0.0000$). Whitebark pine sapling densities are relatively low from 2290 to 2560 m and increase substantially above 2560 m, with the 2830/2930 m elevation supporting significantly higher densities than most other elevations (one-way ANOVA on log-transformed data, $p=0.0025$). Whitebark pine seedling density does not follow a clear pattern, though density at 2830/2930 m is significantly greater than at 2290 m (Kruskal-Wallis one-way ANOVA, $p=0.0385$).

I inventoried 53 dead, standing trees (2.6% of 2028 trees), and only one dead, standing sapling. Most of the plots (59.1%) had no snags, and only 3 plots had more than three snags. Although two of these plots were at 2650 m and one was at 2740 m, no clear patterns with regard to snag distribution were apparent (though a Kruskal-Wallis one-way ANOVA and Z-value test indicated that the mean number of snags at 2650 m was greater than that at 2380 m, $p=0.0359$). No snags were observed in any of the 2380 m plots (the sagebrush-dominated habitat).

Basal area

Overall basal area is lowest at the 2380 and 2470 m elevations, which are characterized primarily by sagebrush-dominated habitats (Table 5). White fir comprises most of the basal area at the 2290 m elevation, and contributes very little to

Table 5. Mean basal area (m²/ha ± 1 SD) values for whitebark pine (PIAL) and white fir (ABCO) with respect to elevation.

Species	2290 m	2380 m	2470 m	2560 m	2650 m	2740 m	2830/2930 m
PIAL	3.65 ± 4.94	5.69 ± 6.03	23.88 ± 19.79	55.25 ± 27.67	66.39 ± 20.48	40.92 ± 25.68	34.64 ± 8.17
ABCO	36.87 ± 30.64	1.87 ± 3.57	0.06 ± 0.08	0.01 ± 0	0.04 ± 0	-	-
Total	39.92 ± 34.96	6.94 ± 8.13	23.90 ± 19.77	55.26 ± 27.67	66.40 ± 20.47	40.925 ± 25.68	34.64 ± 8.17

the basal area totals at higher elevations. Whitebark pine basal area increases from a low mean of 3.65 m²/ha at 2290 m to its peak mean of 66.39 m²/ha at 2650 m, and then decreases at higher elevations. A one-way ANOVA test ($p=0.0000$) and multiple comparisons indicated that whitebark pine basal area at the lower elevations is generally significantly different from that at middle and upper elevations, and the basal area at 2830/2930 m is also significantly lower than that at 2650 m.

Height

Because data did not pass equal-variance and normality tests (in raw form or after transformations), I did not conduct statistical comparisons of mean tree height among elevations. The tallest trees occur at 2290m and are white fir. Because it is rare at higher elevations, white fir has little effect on the height distributions above 2380 m. The whitebark pine that occurs at 2290 m are generally of medium height. Mean height at 2380 is low, then increases to its highest value at 2560 m. Above 2560 m tree height declines with increasing elevation (Table 6, Figure 4).

Nearly all height classes are represented by white fir at 2290 m (Figure 5). No whitebark pine occurs in the tallest height classes at that elevation. At 2560 m there is a relatively even distribution occurs, with many trees in most height classes. The distributions at higher elevations indicate a trend of fewer tall trees with increasing elevation.

Table 6. Mean height class (± 1 SD) of whitebark pine (PIAL) and white fir (ABCO) trees with respect to elevation.

		2290 m	2380 m	2470 m	2560 m	2650 m	2740 m	2830/2930 m
PIAL	mean \pm SD	4.5 \pm 2.0	3.7 \pm 1.8	4.7 \pm 2.2	5.0 \pm 2.0	4.2 \pm 1.9	3.8 \pm 1.6	2.9 \pm 1.0
	n	26	55	162	153	290	278	934
ABCO	mean \pm SD	5.6 \pm 3.1	4.0 \pm 2.7	2	2	-	-	-
	n	111	9	1	1	-	-	-
All trees	mean \pm SD	5.4 \pm 2.9	3.7 \pm 1.9	4.6 \pm 2.2	5.0 \pm 2.0	4.2 \pm 1.9	3.8 \pm 1.6	2.9 \pm 1.0
	n	137	64	163	154	290	278	934

Note: Height classes are in 1.5 m increments below 9 m, and in 3 m increments above 9 m.

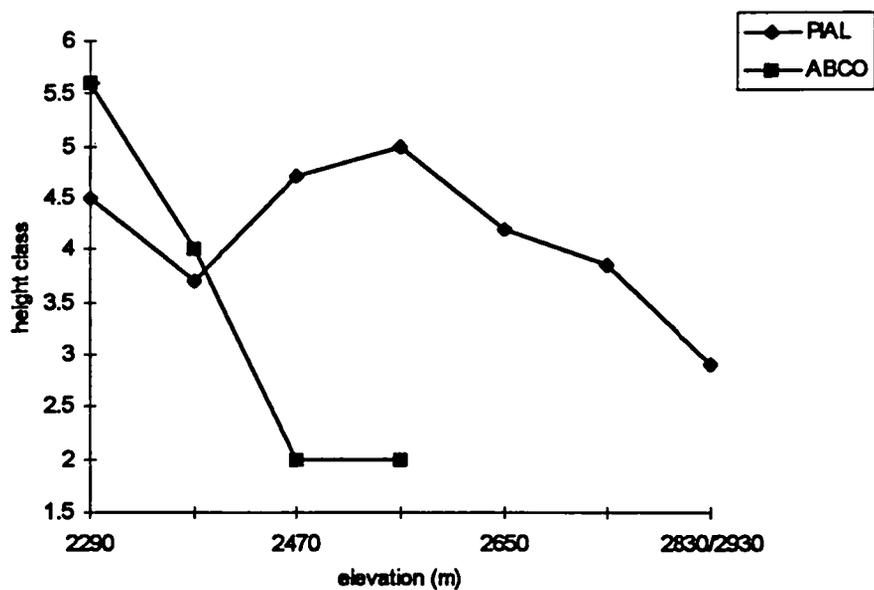


Figure 4. Mean height classes of whitebark pine (PIAL) and white fir (ABCO) trees with respect to elevation. Height classes are in 1.5 m increments below 9 m, and in 3 m increments above 9 m.

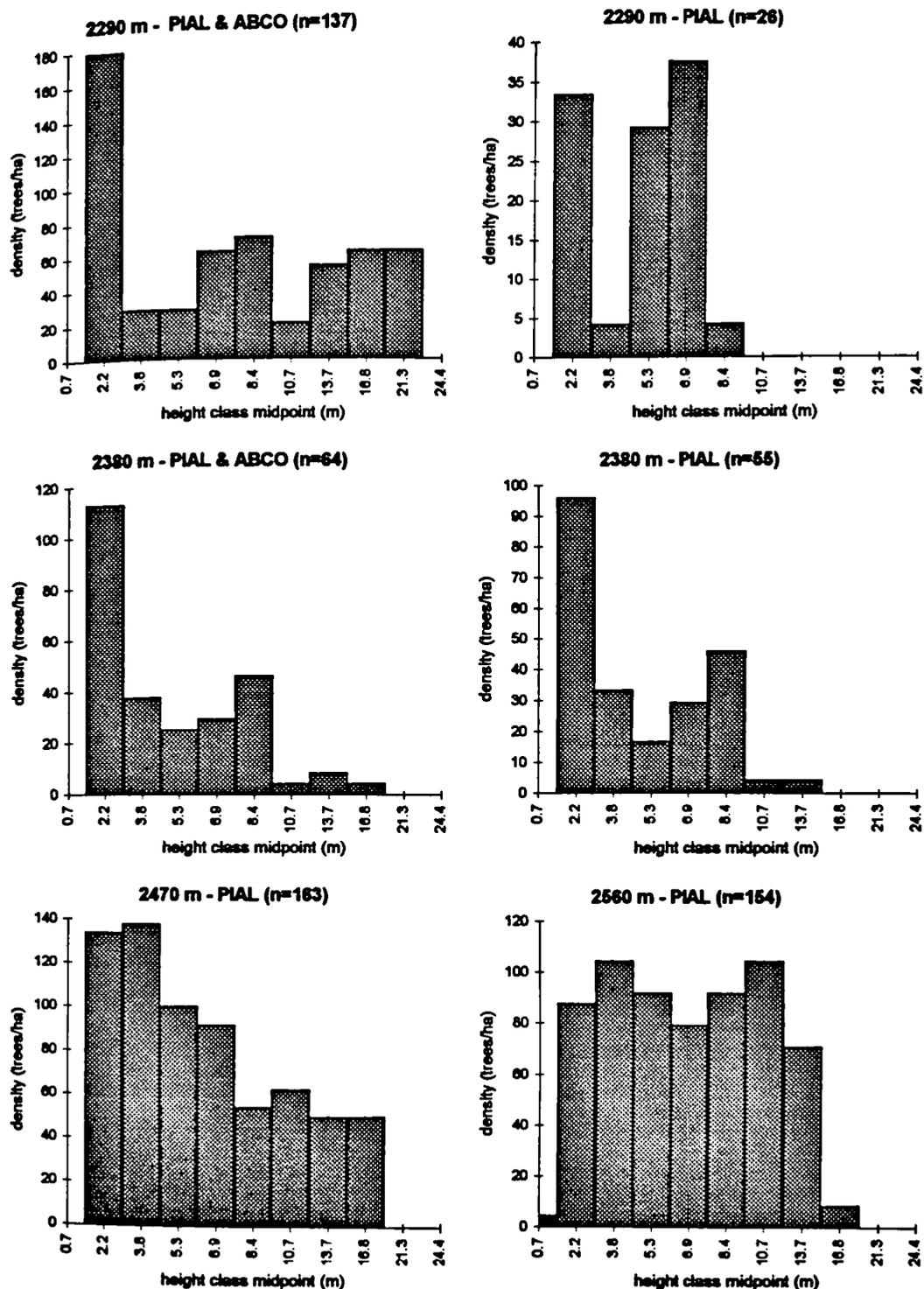


Figure 5. Tree height class (height classes in 1.5 m increments below 9 m and 3 m increments above 9 m) and density (trees/ha) distributions for each elevation (PIAL = whitebark pine, ABCO = white fir).

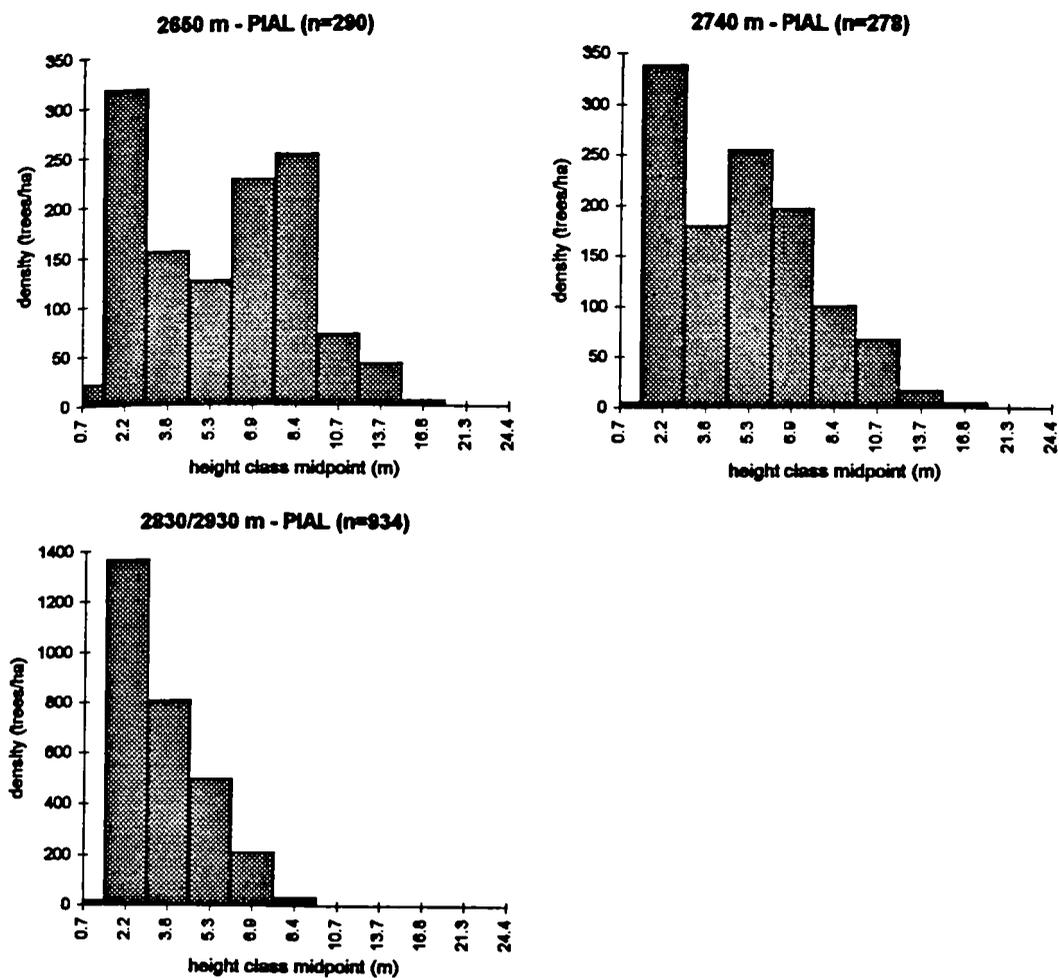


Figure 5. Tree height class (height classes in 1.5 m increments below 9 m and 3 m increments above 9 m) and density (trees/ha) distributions for each elevation (PIAL = whitebark pine, ABCO = white fir), continued.

Diameter

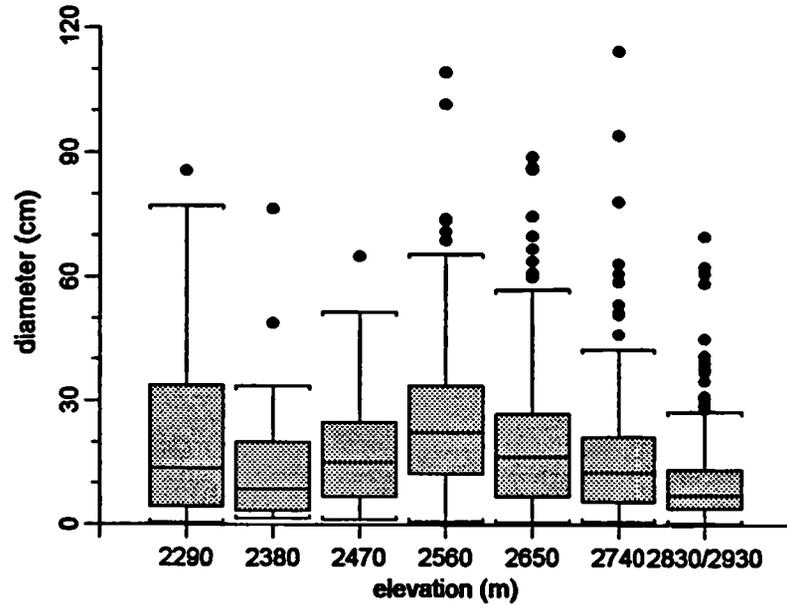
Much of the difference in diameter distributions among elevations occurs in outliers; large diameter trees are much more frequent at the middle and higher elevations than at the low elevations (Figure 6). Nonetheless, significant differences do occur in the mean diameter of whitebark pine at the various elevations (Kruskal-Wallis one way ANOVA on log-transformed data, $p=0.0000$), with the trend of small mean diameters at the lowest elevations, the largest diameters at 2560 m, and decreasing diameter with greater elevation (Table 7).

At 2290 and 2380 m, where white fir plays a significant role in the overall tree stem density, histograms show the distribution of all species and that of whitebark pine only (Figure 7). Above 2380 m, stems are whitebark pine except for one white fir at three elevations, so only a histogram of whitebark pine diameters is provided for each elevation.

Clustering/multi-stem analysis

When the mean number of stems per multi-stemmed cluster was compared with respect to elevation, no significant differences or trends were detected for whitebark pine trees (Kruskal-Wallis one-way ANOVA, $p=0.0919$), saplings (Kruskal-Wallis one-way ANOVA, $p=0.0938$), or seedlings (Kruskal-Wallis one-way ANOVA, $p=0.7585$). For trees, the group means for the various elevations range from 3.0 to 3.89, with an overall mean of 3.40 ($n=497$). On average, the 2560 m plots had the highest number

a)



b)

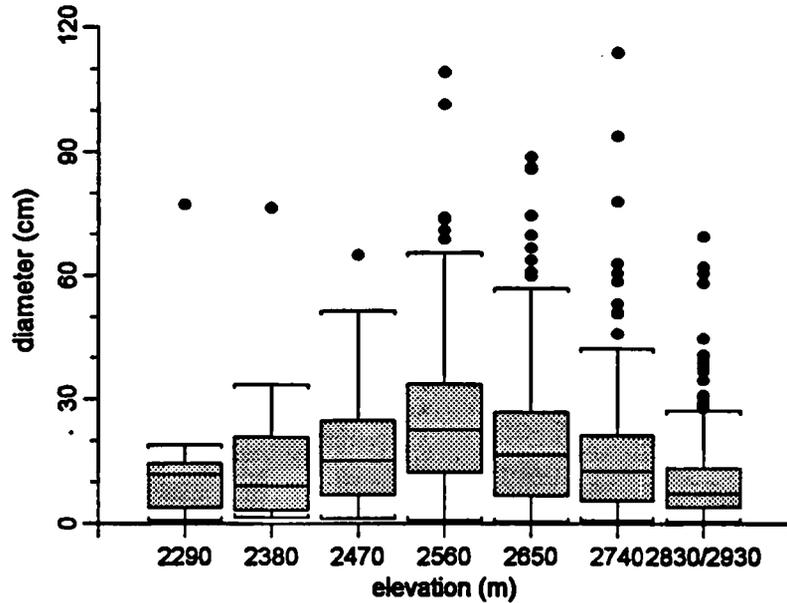


Figure 6. Boxplots of tree diameter (cm at DBH) with respect to elevation for a) whitebark pine and white fir, and b) whitebark pine only. Boxes represent the interquartile range (IQR = 25^{th} - 75^{th} percentiles) with the median shown as a crossbar. Upper (largest observation $\leq 75^{\text{th}}$ percentile plus 1.5 times IQR) and lower (smallest observation $\geq 25^{\text{th}}$ percentile minus 1.5 times IQR) adjacent values are displayed as T-shaped lines, and outliers are displayed as solid circles.

Table 7. Tree diameter mean (± 1 SD) and range for whitebark pine (PIAL) and white fir (ABCO) with respect to elevation.

		2290 m	2380 m	2470 m	2560 m	2650 m	2740 m	2830/2930 m
PIAL	mean \pm SD	12.6 \pm 14.3	12.9 \pm 12.3	17.2 \pm 12.4	26.4 \pm 19.1	19.7 \pm 15.8	15.7 \pm 14.3	9.5 \pm 7.7
	range	0.7 - 77.2	1.5 - 76.5	1.3 - 65.0	0.8 - 109.2	0.5 - 88.9	0.8 - 114.0	0.5 - 69.6
	n	26	55	162	159	290	278	933
ABCO	mean \pm SD	23.8 \pm 21.1	13.7 \pm 16.2	1.8	2.5	-	-	-
	range	0.5 - 85.6	2.3 - 48.8	-	-	-	-	-
	n	111	9	1	1	0	0	0
All trees	mean \pm SD	21.7 \pm 0.4	13.0 \pm 12.8	17.1 \pm 12.4	26.3 \pm 9.1	19.7 \pm 15.8	15.7 \pm 14.3	9.5 \pm 7.7
	range	0.5 - 85.6	1.5 - 76.5	1.3 - 65.0	0.8 - 109.2	0.5 - 88.9	0.8 - 114.0	0.5 - 69.6
	n	137	64	163	160	290	278	933

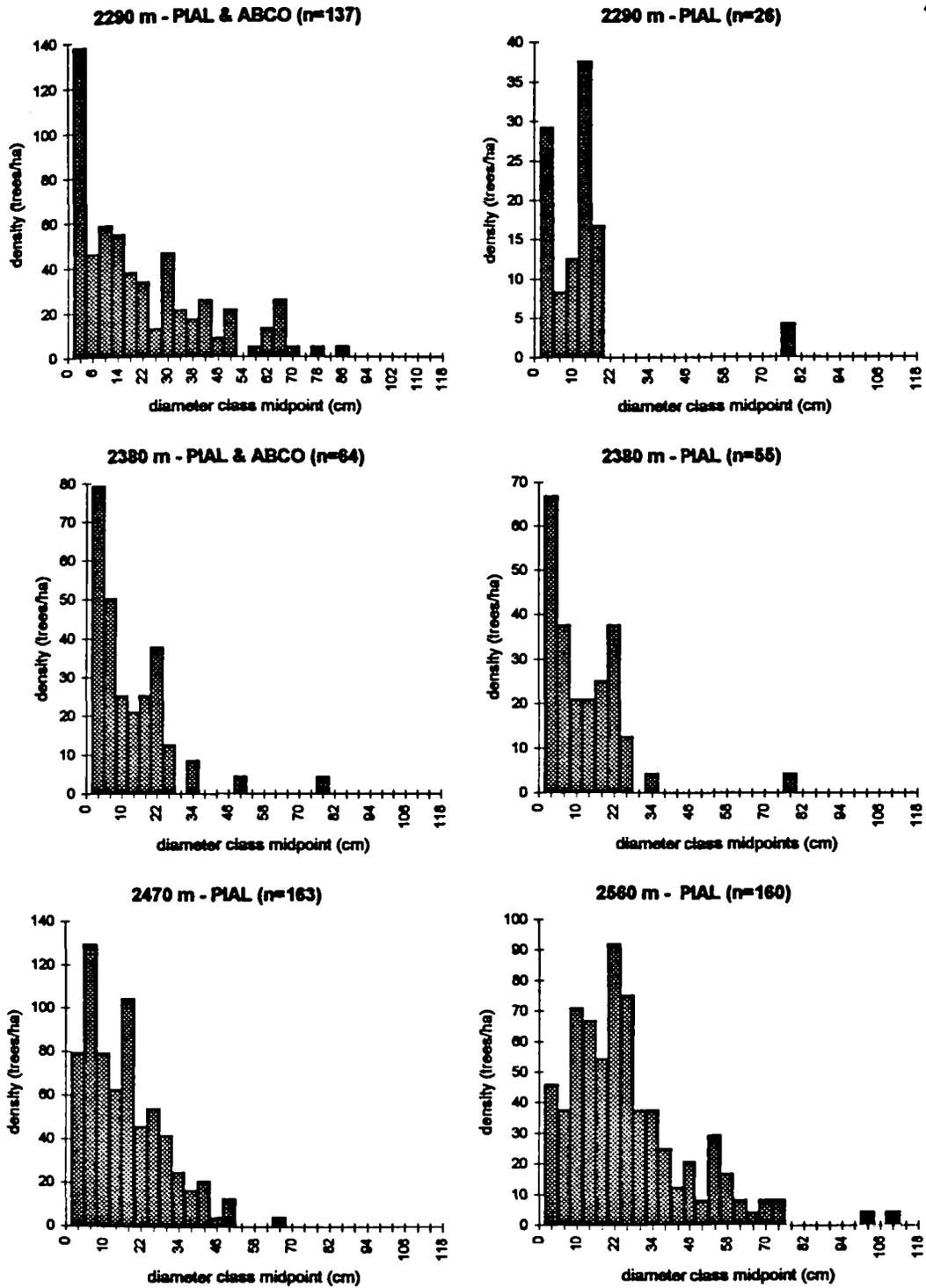


Figure 7. Diameter class (classes in 4 cm increments) and density distributions (trees/ha) for trees at each elevation (PIAL = whitebark pine, ABCO = white fir).

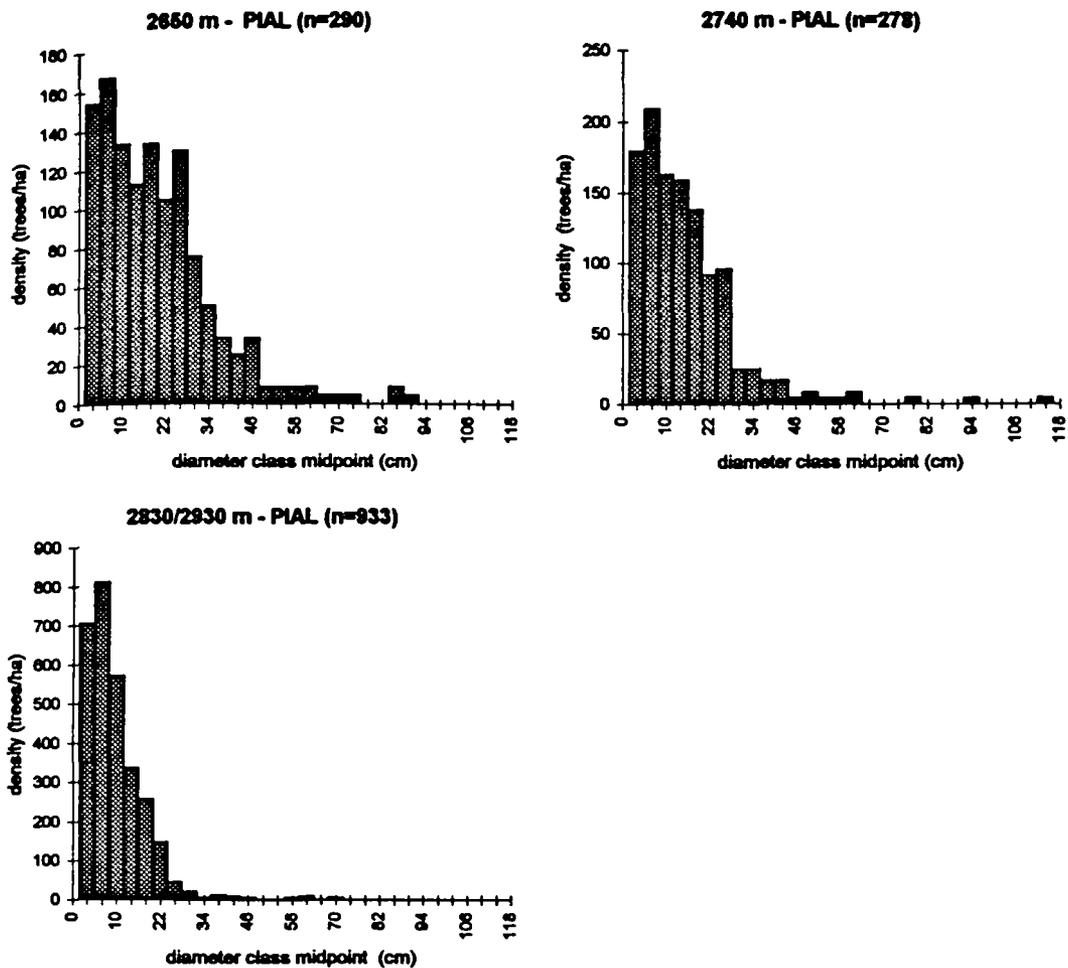


Figure 7. Diameter class (classes in 4 cm increments) and density distributions (trees/ha) for trees at each elevation (PIAL = whitebark pine, ABCO = white fir), continued.

of stems per multi-stemmed cluster (3.89, SD=1.82, n=36). The largest clusters that I inventoried occurred at 2830 m - one cluster had 17 stems and another had 16 stems. For saplings, the group means range from 2.0 to 3.86, with an overall mean of 2.91(n=64). The highest mean occurs at 2650 m. For seedlings, the group means range from 2.0 to 3.0, with an overall mean of 2.67 (n=52). The highest mean occurs at 2290 m, where only two clusters were sampled.

The percentage of clustered stems vs. non-clustered stems within plots was compared with respect to elevation, and no significant differences or trends were noted for whitebark pine trees (Kruskal-Wallis one-way ANOVA on log-transformed data, $p=0.9350$), saplings (one-way ANOVA, $p=0.6339$), or seedlings (one-way ANOVA, $p=0.2166$). At all but the two lowest elevations, the mean percentages of clustered tree stems within a plot were between 83% and 89%. The 2290 and 2380 m plots had a mean of 63% and 57% clustered stems, respectively. Sapling cluster percentages ranged from 33% to 69% and seedling percentages ranged from 17% to 67% of stems within clusters. Saplings and seedlings were infrequent at some elevations.

When each whitebark pine growth "site" (a single-stemmed individual or a single multi-stemmed cluster) was evaluated, clusters generally occurred more often in trees than in saplings, and more often in saplings than in seedlings (Figure 8). These differences could not be compared statistically because the data did not meet equal variance assumptions. No significant differences in cluster percentage occurred among

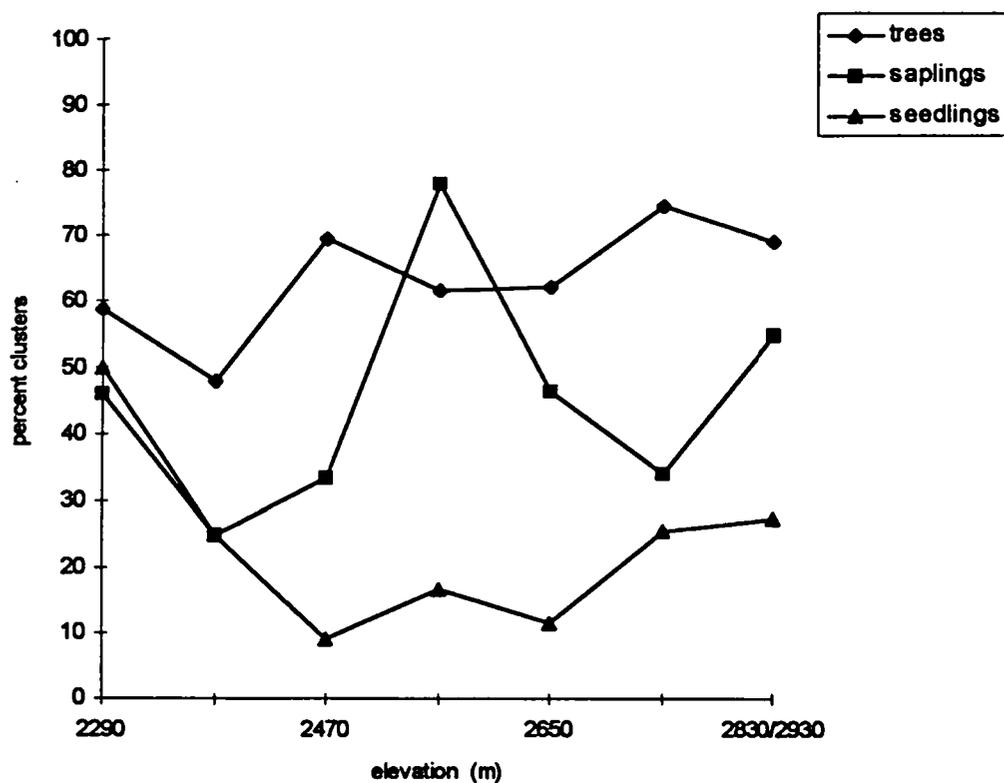


Figure 8. Percentage of whitebark pine "sites" occupied by multi-stemmed clusters at each elevation. Data are presented for tree (>1.4 m), sapling (>0.5 m and <1.4 m), and seedling (<0.5 m) clusters.

elevations for either trees (Kruskal-Wallis one-way ANOVA on log-transformed data, $p=0.7996$), saplings (one-way ANOVA, $p=0.5921$), or seedlings (one-way ANOVA, $p=0.3779$).

In summary, no differences were detected at different elevations in either the percentage of clustered vs. unclustered stems, or in the number of stems within each cluster for either trees, saplings, or seedlings. While the data for saplings and seedlings are perhaps problematic due to stem numbers at certain elevations, the number of trees is substantial. Because the results are the same for trees, saplings, and seedlings, it seems likely that even with greater numbers of stems in the latter groups significant differences in either of the examined measures would not be detected. Stem size may play a role in the occurrence of clusters; greater percentages of trees than saplings tend to occur in clusters, and greater numbers of saplings than seedlings tend to occur in clusters.

Age structure

Age distribution

Although the means at each elevation could not be compared statistically (normality and equal-variance assumptions were not met by either the raw or transformed data), the mean tree age is substantially lower at 2290, 2380, and 2470 m than it is at any higher elevation (Table 8, Figure 9).

Table 8. Mean tree age (± 1 SD) and range for whitebark pine (PIAL) and white fir (ABCO) with respect to elevation.

		2290 m	2380 m	2470 m	2560 m	2650 m	2740 m	2830/2930 m
PIAL	mean \pm SD	62.3 \pm 36.2	48.8 \pm 41.4	83.4 \pm 50.3	133.7 \pm 81.5	152.6 \pm 112.2	144.4 \pm 140.4	126.7 \pm 80.1
	range	24 - 156	18 - 187	13 - 269	22 - 423	43 - 759	42 - 868	28 - 703
	n	13	24	68	59	130	118	370
ABCO	mean \pm SD	66.3 \pm 32.8	41.4 \pm 21.5	-	20	-	-	-
	range	18 - 190	14 - 82	-	-	-	-	-
	n	102	9	-	1	-	-	-
All trees	mean \pm SD	65.9 \pm 33.1	46.8 \pm 36.9	83.4 \pm 50.3	131.8 \pm 82.1	152.6 \pm 112.2	144.4 \pm 140.4	126.7 \pm 80.1
	range	18-190	14 - 187	13 - 269	20 - 423	43 - 759	42 - 868	28 - 703
	n	115	33	68	60	130	118	370

Note: one white fir tree occurred in the 2470 m plots, but I lost the core for that specimen and thus failed to determine its age. The diameter and height data for that tree is included in the diameter and height tables and distributions.

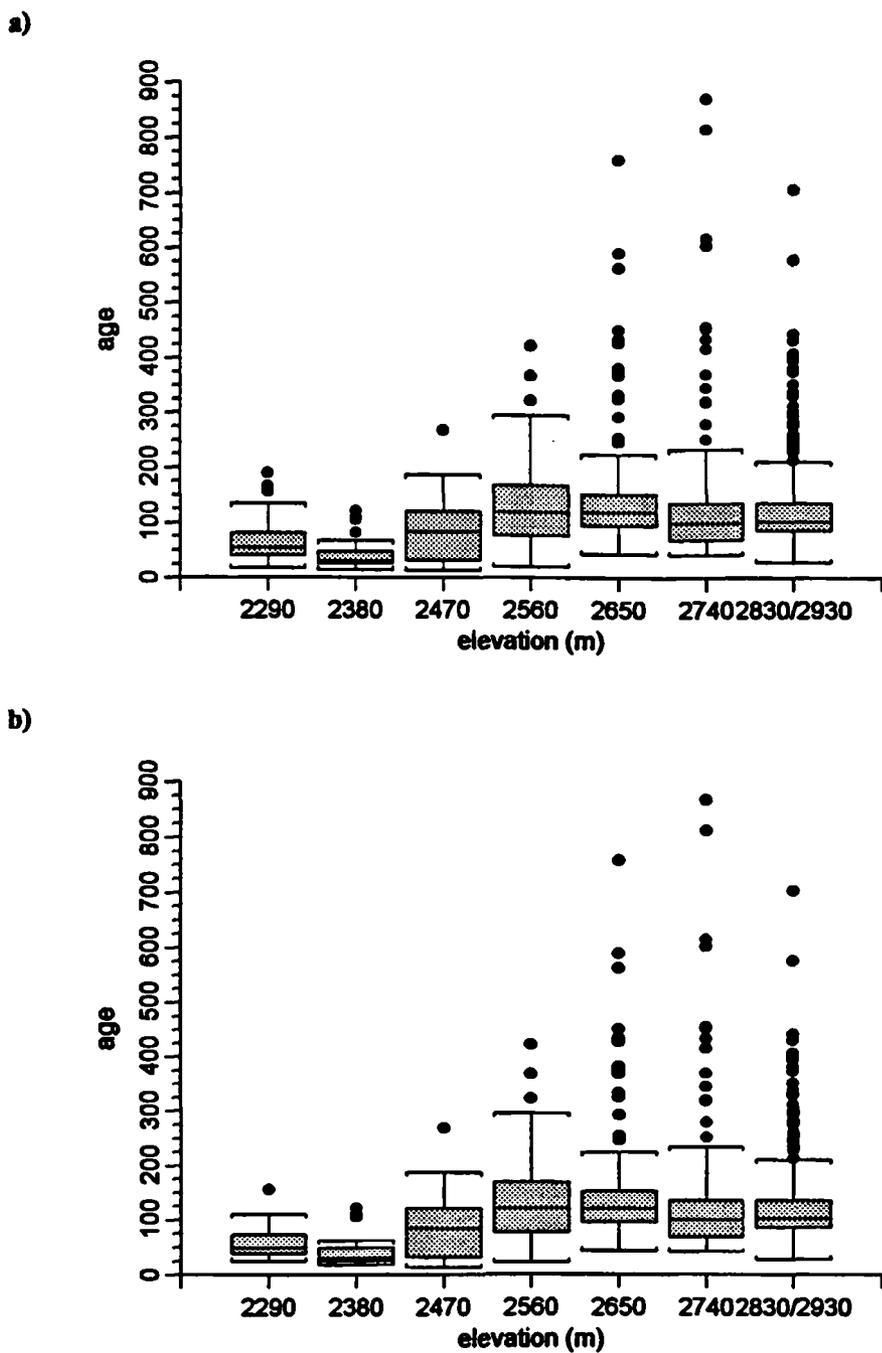


Figure 9. Boxplots of tree ages with respect to elevation, for a) whitebark pine and white fir, and b) whitebark pine only. Boxes represent the interquartile range (IQR = 25th-75th percentiles) with the median shown as a crossbar. Upper (largest observation $\leq 75^{\text{th}}$ percentile plus 1.5 times IQR) and lower (smallest observation $\geq 25^{\text{th}}$ percentile minus 1.5 times IQR) adjacent values are displayed as T-shaped lines, and outliers are displayed as solid circles.

Additionally, as is the case with the diameter data, the age ranges from the table and the age distributions shown in the boxplots are probably more telling than the mean ages. Outliers (much older trees) occur at a much greater frequency at higher elevations than at lower elevations. These “old” trees are oldest at higher elevations (outliers at low elevations are about 200-300 years old; those at higher elevations age generally 400-800 years old).

Differences in age distribution between elevations include a wide range in tree density (stems/ha) in the various age classes and the presence of occasional old, “emergent” trees at the higher elevations (and their notable absence from the lower elevations) (Figure 10). Across all elevations the majority of successful recruitment has occurred within the past 50-150 years. Recruitment has apparently occurred in a somewhat continuous fashion rather than through “pulses” of recruitment (the periodic or episodic recruitment of discrete cohorts resulting from disturbance or predictable stages in stand development). That the youngest age classes appear to be underrepresented at some of the higher elevations is probably more an artifact of the sampling procedure than a true approximation of age distribution. For example, at higher elevations it generally takes longer for stems to reach the minimum height that I considered a tree (1.4m), and a greater percentage of the individuals that fall within the younger age classes at those elevations are likely to be saplings and thus not be sampled.

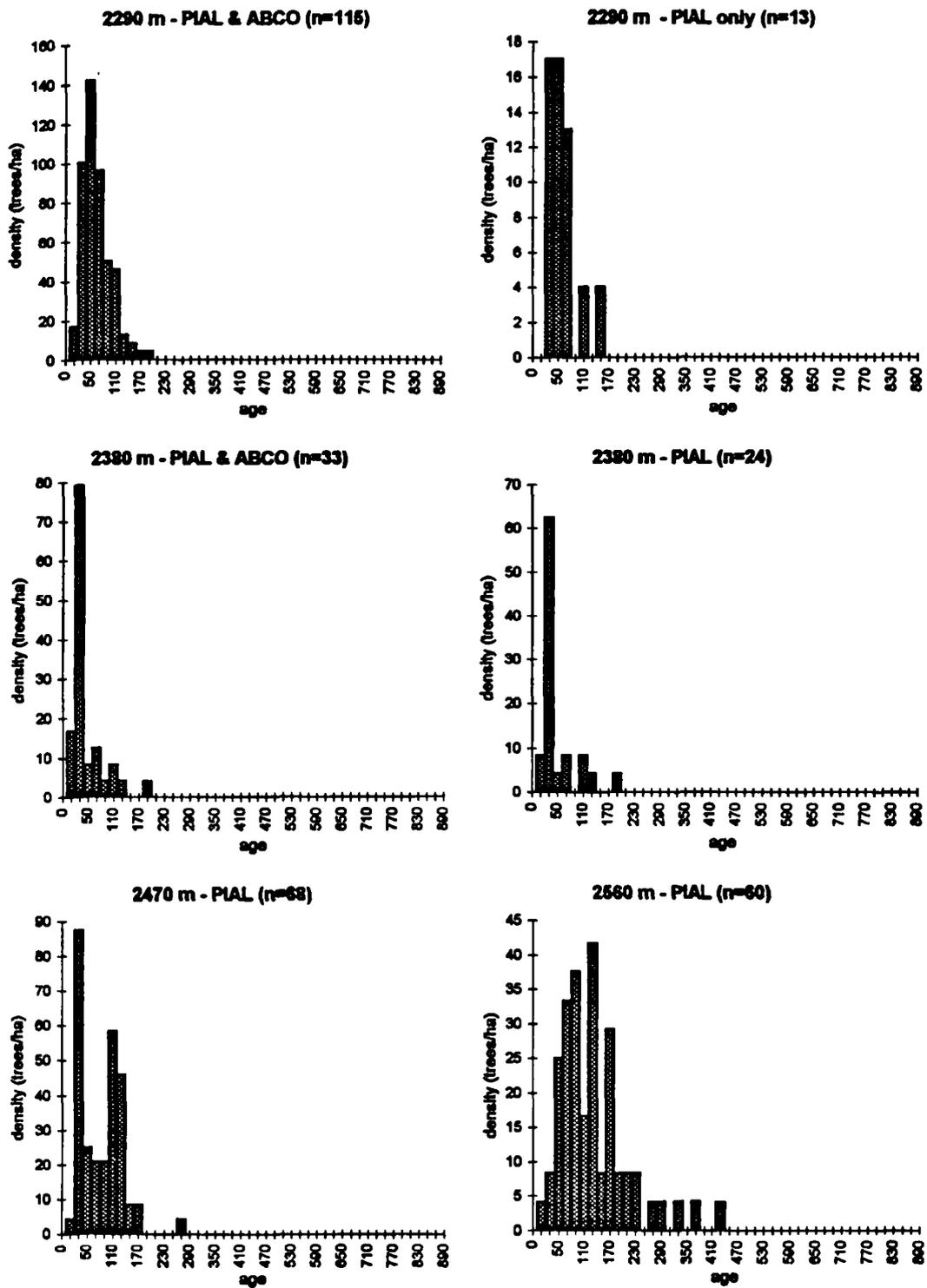


Figure 10. Tree age (age classes in twenty year increments) and density (trees/ha) distributions for trees at each elevation (PIAL = whitebark pine, ABCO = white fir).

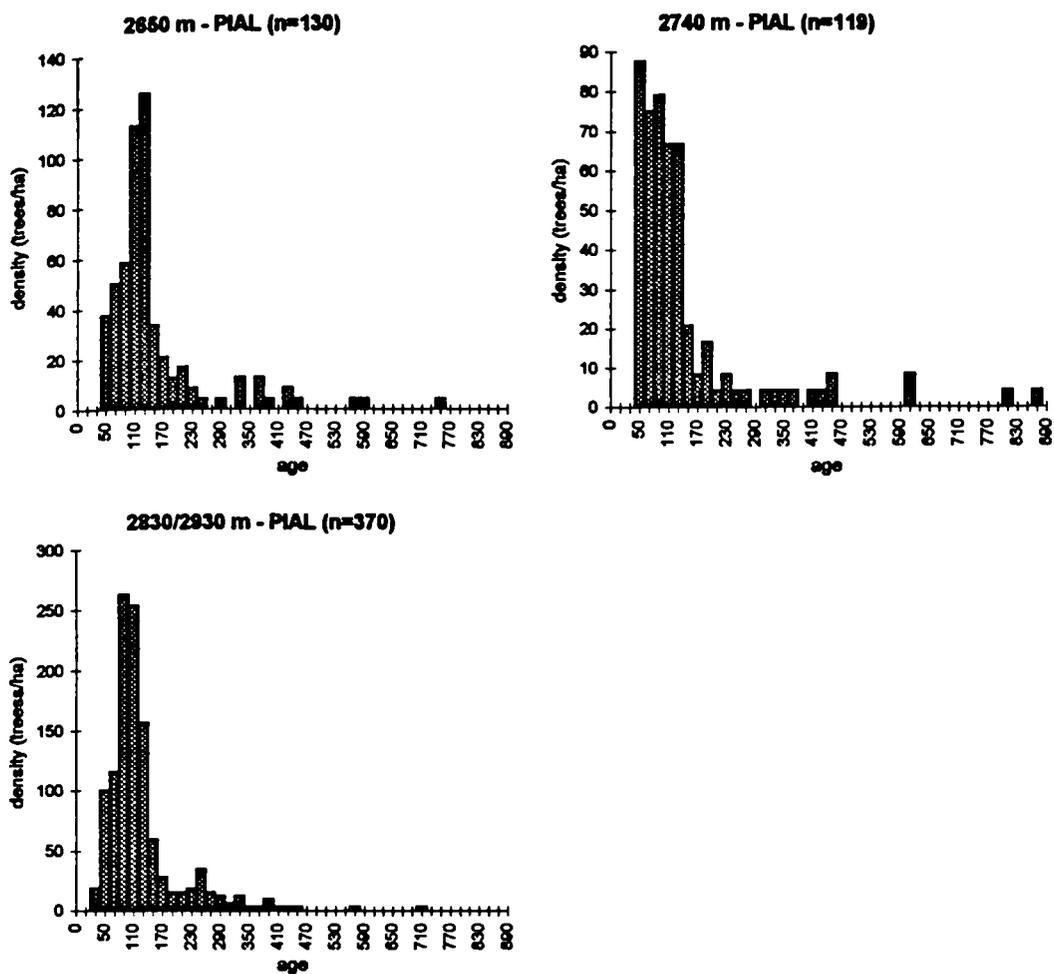


Figure 10. Tree age (age classes in twenty year increments) and density (trees/ha) distributions for trees at each elevation (PIAL = whitebark pine, ABCO = white fir), continued.

Age distribution was also analyzed with respect to habitat type (Figure 11). Mean whitebark pine ages within each of the three whitebark pine-dominated habitat types is significantly different from the mean age in both the white fir and sagebrush-dominated habitat types (Kruskal-Wallis one-way ANOVA on log-transformed data, $p=0.0000$). Mean ages within each whitebark pine habitat type are not significantly different from one another. These results mimic those in which age was compared to elevation.

In summary, stands are generally young at low elevations and older at higher elevations. At low elevations, particularly in white fir and sagebrush-dominated habitats, there are no trees greater than approximately 200 years old. Higher elevations support scattered older trees ranging from 400 to over 800 years old. The majority of trees at all elevations have been recruited within the past 50-150 years, and recruitment appears to have been more continuous than episodic.

Size/age relationships

Spearman rank correlation coefficients indicate a significant relationship between tree age and DBH both for all trees combined and for each species at most of the sampled elevations (Table 9). The regression models developed are highly significant in each case, yet the relatively low r^2 values indicate that diameter alone generally fails to describe most of the variation in the age data, and thus is not a very accurate predictor of age within the study site (Table 10).

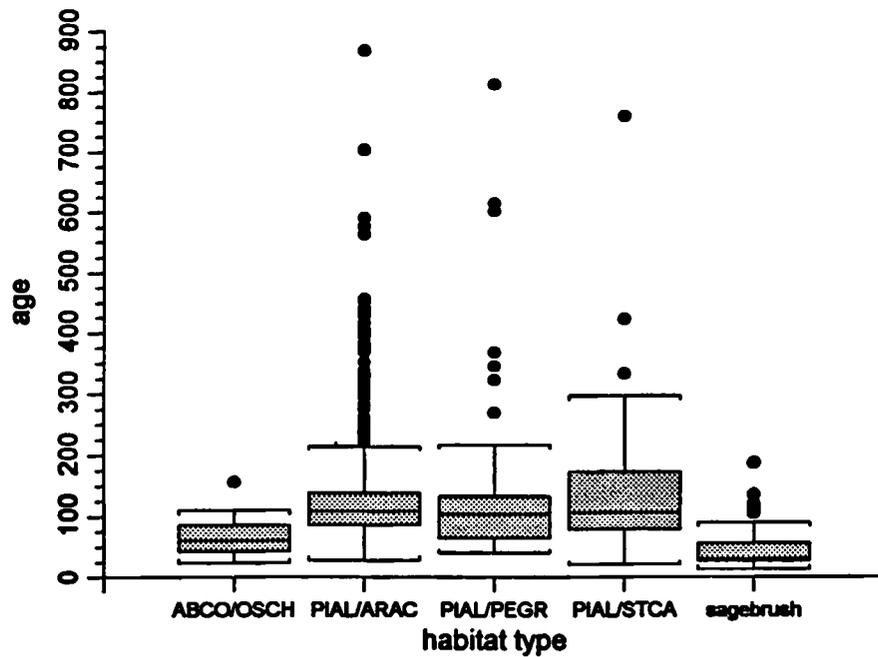


Figure 11. Boxplot comparing whitebark pine tree age distributions for each habitat type. ABCO/OSCH = white fir/osmorhiza, PIAL/ARAC = whitebark pine/woody sandwort, PIAL/PEGR = whitebark pine/slender penstemon, PIAL/STCA = whitebark pine/California needlegrass. Boxes represent the interquartile range (IQR = 25th-75th percentiles) with the median shown as a crossbar. Upper (largest observation \leq 75th percentile plus 1.5 times IQR) and lower (smallest observation \geq 25th percentile minus 1.5 times IQR) adjacent values are displayed as T-shaped lines, and outliers are displayed as solid circles.

Table 9. Spearman rank correlation coefficients for the relationship between tree age and DBH, presented in terms of species and elevation (PIAL = whitebark pine, ABCO = white fir).

	correlation coefficient	p value	n
All species, all elevations	0.59	0.0000	897
ABCO only, all elevations	0.74	0.0000	112
PIAL only, all elevations	0.66	0.0000	785
ABCO - 2290 m	0.73	0.0000	102
ABCO - 2380 m	0.46	0.2125	9
PIAL - 2290 m	0.77	0.0021	13
PIAL - 2380 m	0.60	0.0020	24
PIAL - 2470 m	0.84	0.0000	69
PIAL - 2560 m	0.78	0.0000	60
PIAL - 2650 m	0.68	0.0000	130
PIAL - 2740 m	0.76	0.0000	119
PIAL - 2830/2930 m	0.70	0.0000	370

Table 10. Best fit linear regression equations, r^2 values, and significance values of the regression models for the relationship between tree age and DBH, presented in terms of species and elevation (PIAL = whitebark pine, ABCO = white fir).

	regression equation	r^2	adjusted r^2	F	p	n
All species, all elevations	age = 55.03 + 3.57(DBH)	0.40	0.40	603.49	0.0000	897
ABCO only, all elevations	age = 39.69 + 1.04(DBH)	0.45	0.45	90.70	0.0000	112
PIAL only, all elevations	age = 49.95 + 4.49(DBH)	0.53	0.53	891.65	0.0000	785
ABCO - 2290 m	age = 41.89 + 1.00(DBH)	0.43	0.42	75.58	0.0000	102
ABCO - 2380 m	age = 27.20 + 1.04(DBH)	0.61	0.56	11.10	0.0126	9
PIAL - 2290 m	age = 39.85 + 1.58(DBH)	0.76	0.74	34.81	0.0001	13
PIAL - 2380 m	age = 18.15 + 2.27(DBH)	0.80	0.79	88.74	0.0000	24
PIAL - 2470 m	age = 29.98 + 2.97(DBH)	0.69	0.68	147.3	0.0000	69
PIAL - 2560 m	age = 41.30 + 3.03(DBH)	0.64	0.64	104.99	0.0000	60
PIAL - 2650 m	age = 36.49 + 4.82(DBH)	0.66	0.66	247.00	0.0000	130
PIAL - 2740 m	age = 10.47 + 6.98(DBH)	0.81	0.81	504.31	0.0000	119
PIAL - 2830/2930 m	age = 47.45 + 6.75(DBH)	0.59	0.59	522.15	0.0000	370

Additional age and core-related results

Forty-five percent of all cores passed through the pith of the cored tree, 50% of cores were off-center, and 5% were incomplete (Table B-1, Appendix B). The mean number of years added to each off-center core tends to be small (overall mean of 6.2 years) and indicates that most off-center cores were fairly close to the pith, and that the ages used in the analysis are generally reasonable estimates (Table B-2, Appendix B). The number of years added to the minimum age to estimate ages for incomplete cores (mean = 154.7 years, range = 0-749 years) was generally much greater than that for off-center cores (Table B-3, Appendix B)

I tried to core trees as close to ground level as practical, but coring height varied from tree to tree (mean=26.9 cm, SD=17.3, range 5.1-101.6 cm, n=448) as some trees were less accessible than others due to slope angle or physical interference from other stems in a particular cluster. Borer size also played a role in variable coring heights, as smaller borers can core closer to ground level due to their shorter handles (thus, small trees were usually aged closer to ground level than larger trees).

Ages of stems in completely sampled multi-stemmed clusters

Ninety percent of the 29 cores taken from ten completely sampled multi-stemmed clusters intersected the pith of the sampled stems (Table 11). I added very few years to the off-center cores (mean = 3.7 years, n=3) when estimating actual age at

coring height. Although cores were taken at the same height within each cluster (overall mean coring height = 25 cm, range =15-46 cm), stem ages at coring height within a cluster varied in most cases. In two of the 10 clusters the age range was very small (one year, three years), in two clusters the range was 7 years, and in the remaining clusters the range was at least 12 years (with two clusters having a 24 year range). In several cases the oldest stem is not the largest in diameter within the cluster, and in others a stem of much smaller diameter is nearly as old as larger stems.

Table 11. Summary of stem ages from completely aged multi-stemmed clusters.

cluster number	tree number	coring height (cm)	minimum age	pith/ off-center ¹	diameter (cm)	age	age range within cluster
C1	3001	15	83	p	9.4	83	3
	3002	15	86	p	14.5	86	
C2	3003	25	127	p	20.3	127	1
	3004	25	126	p	20.8	126	
C3	3005	15	123	p	13.2	123	24
	3006	15	133	p	15.5	133	
	3007	13	116	oc	12.4	122	
	3008	15	109	p	3.6	109	
C4	3009	30	88	p	17.8	88	7
	3010	30	93	p	22.6	93	
	3011	30	95	p	22.1	95	
C5	3012	15	65	p	4.6	65	24
	3013	15	89	p	8.6	89	
	3014	15	66	oc	4.3	69	
C6	3015	36	78	p	18.0	78	12
	3016	36	77	p	15.5	77	
	3017	36	67	p	15.2	67	
	3018	36	79	p	15.2	79	
	3019	36	76	p	10.2	76	
C7	3020	20	154	p	20.1	154	7
	3021	20	147	p	20.6	147	
C8	3022	20	126	p	13.2	126	19
	3023	20	145	p	15.2	145	
	3024	20	144	p	23.9	144	
C9	3025	46	124	p	11.9	124	15
	3026	46	137	oc	22.4	139	
C10	3027	36	142	p	14.7	142	13
	3028	36	142	p	22.9	142	
	3029	36	129	p	7.1	129	

¹ p = core intersected pith of tree, oc = core off-center

DISCUSSION

Species composition of the whitebark pine-dominated forests within the south Warner Mountains varies along an elevational/soil moisture availability gradient (Riegel et al. 1990). My results indicate that these forests also exhibit changing structural characteristics and population dynamics along this gradient. Although the gradient appears to be essentially continuous with respect to environmental parameters, when analyzed in terms of structure and age the habitats in which whitebark pine is an important component fall into three major categories.

The first or “low” stand type occurs at lower elevations (below approximately 2470 m) and is represented by developing whitebark pine “stands” within sagebrush-dominated habitats in what appears to be an expansion of the species’ range. These developing stands have structural characteristics coincident with young forest stands, including relatively young, short, and small trees, no snags, and limited downed wood. The environment of this stand type is characterized by gentle slopes, relatively well-developed soils, and a relatively high soil moisture index (TRMI).

The second and third stand types occur at higher elevations. Both types exhibit structural characteristics of self-perpetuating, old-growth stands, including all-sized diameter and all-aged age distributions, individual trees of great size and age, and occasional snags and high amounts of downed wood. Age structures are similar across the higher elevations, but structural components of the forest vary with elevation and

form the basis for the stand type distinctions. At medium elevations the forests are relatively open and support the tallest and largest diameter trees, and the highest basal areas. The environment of this “medium” stand type is characterized by moderately developed soils, and a medium soil moisture index and slope steepness. At higher elevations denser forests are composed of short, relatively small-diameter trees and have medium basal areas. Exposed rock, little soil development, and a lower soil moisture index characterize this “high” stand type.

Forest composition and structure

The pure stands of whitebark pine across such a wide elevational range in the Warner Mountains seem to be an anomaly; at other montane and subalpine locations in California whitebark pine often occurs with lodgepole pine, mountain hemlock, foxtail pine (*P. balfouriana*), red fir, western white pine, and/or limber pine (Clausen 1965, Parker 1988, Arno and Hoff 1989, Peterson et al. 1990, Sawyer and Keeler-Wolf 1995). Local dominance at middle elevations may in part be a result of the depauperate nature of the forests of the Warner Mountains, as most of these associates are not present within the range. However, previous studies within the Warners have described at least the lower elevation whitebark pine forests as having lodgepole pine as a frequently co-occurring species. Vale (1977) and Riegel et al. (1990) both addressed the likely competitive relationships and dynamics between the two pines, and

one of my initial goals was to clarify the dynamics of this relationship. However, I did not encounter a single lodgepole pine in any of my plots, and within the entire study area I only observed lodgepole pine in one small stand (less than one ha, at about 2380 m elevation). North of the study area I observed small lodgepole pine and mixed lodgepole/whitebark pine stands in the headwaters of Mill Creek, and Riegel (personal communication) notes other lodgepole stands along the South Fork of Palmer Creek and in the headwaters of Cottonwood Creek. Extensive stands of pure whitebark pine occur within the wilderness even in the lower portion of its range.

The relationship between density and basal area is similar to that found for high-elevation whitebark pine/lodgepole pine forests in a study in the central Sierra Nevada (Peterson et al. 1990). Lower basal area values (and lower mean diameters and heights) within “high” stand types probably result from environmental conditions (deep snow pack, low temperatures, harsh wind, short growing season, etc.) which are more limiting to tree growth than those at lower elevations. Lower stem density within “medium” stand types could be explained by either higher mortality or lower natality than at high elevations. As basal area and mean diameters are largest within the “medium” stands, competition for light may result in localized self-thinning as large trees shade out smaller stems. However, these “medium” stands are still relatively open compared to many forests (e.g., the white fir forests within the Warner Mountains) and generally do not appear to be light-limited. Interspecific competition for soil resources may also be more keen within these “medium” stands and result in lower establishment

rates, as shrub and herb cover are significantly higher in medium stands than they are in “high” stands. Differences in density values could also be related to differences in seed production and /or dispersal patterns within each stand type.

The overall density figures from my study site are comparable to those observed by Peterson et al. (1990), but the basal area figures from my study site are much higher (generally about 2-3 times as high). However, Peterson’s study sites were higher than mine (3170-3780 m versus 2280-2930 m), and both studies show declining basal area with increasing elevation. The basal area figures from this study are comparable to those reported from various *Pinus albicaulis/Vaccinium scoparium* woodlands in the northern Rockies (Weaver et al. 1990).

Clusters

The primary dispersal agent of whitebark pine is the Clark’s nutcracker, which generally caches 1-15 seeds in each caching location (Tomback et al. 1993). Several of these seeds often germinate and grow as a cluster, which has been shown to sometimes develop into the multi-stemmed growth form characteristic of many whitebark pine trees (Linhart and Tomback 1985, Furnier et al. 1987). However, 17-42% of the sampled clusters in these studies contained only one genotype, which indicates that “clusters” also occur as a result of basal branching. A greenhouse experiment found that single whitebark pine seedlings branched basally 85% of the time (Weaver and Jacobs 1990). Thus, multi-stemmed clusters arise from both basal branching and from

the germination of cached multiples of seeds, and in naturally-occurring specimens genetic analysis is necessary to determine which is the actual case.

Whichever way that multi-stemmed clusters appear, it is thought that stem number is ultimately controlled by competition among members of a clump - that multi-stemmed clusters function as independent stands and are subject to self thinning (Weaver and Jacobs 1990). Thus older clusters should have fewer stems than younger ones and that number per cluster should decline with canopy closure and other environmental conditions that heighten competition. I expected that there would be greater numbers of stems per cluster at higher elevations within the Warners, where stem density is high and basal area is low and little competition within the stands appears to be occurring. My results do not support these hypotheses, as no significant differences between elevations were noted in the mean number of stems/multi-stemmed cluster for either seedlings, saplings, or trees.

The proportion of individual whitebark pine "sites" occupied by multi-stemmed clusters rather than single-stemmed trees tended to be greater in tree sites than in sapling sites, and greater in sapling sites than in seedling sites. This result suggests an increase in the number of stems with cluster age, as size is significantly correlated with age. If the clusters are viewed as independent stands these data suggest that the reverse of thinning may be occurring with age -- stem number may be increasing. It also suggests that in my study site whitebark pine generally branches basally and that a greater proportion of clusters may arise through branching than through the successful

establishment of multiple seedlings from individual nutcracker caches. If each stem in a cluster was a distinct genotype developing from a separate seed and no post-germination basal branching occurred, I would not expect differences in stem number per cluster between different growth stages. Alternative explanations include delayed germination of one or more seeds within a cache for several years, and re-caching of seeds beneath established clusters. Both of these mechanisms have been observed (Tomback et al. 1993; King, personal communication) and may help to explain the patterns of older “sites” supporting greater numbers of stems.

The age data from multi-stemmed clusters also support the conclusion that many clusters have developed from either basal branching, delayed germination, or re-caching beneath established clusters (or some combination of all three mechanisms). While ages of stems within clusters were very similar in 4 of 10 clusters (seven year age range or less), in the other 6 clusters the age range varied from 12-24 years. Although the cores were taken as close to the ground as possible (from 15-46 cm, at the same level within a cluster), variation in the time required for each stem to reach coring height may account for some of the age discrepancies.

Stand development and dynamics

It is difficult to discern patterns of stand development within the study area from stand age and diameter structures alone. Within the higher-elevation forests it is

possible that the oldest, emergent trees represent either the few survivors of past stands that were destroyed by a disturbance such as fire or simply are the oldest remaining trees in a very old stand that has not undergone a “stand-replacing” disturbance in recent time (perhaps upward of 800-900 years). If the former scenario is correct, it is likely that the initial recolonization of the stands has been continuing since the disturbance occurred (possibly several hundred years). Slow growth on the high-elevation sites would preclude much competition for growing space, and it is possible that the “stem exclusion” phase of post-disturbance stand development (Oliver and Larson 1996) has only recently begun on the most favorable sites (i.e., 2560 m) and may never occur on poorer sites.

Fire has probably been the major historic disturbance factor within these stands. The large emergent trees all show signs of historic fire, and many smaller stems are also fire-scarred. All fire-scarred trees which I cored had rotten centers, precluding the dating of historic fires. Bits of charred wood were common on the ground within these stands as well. Fires in whitebark pine habitats are typically lightning-caused and are confined to very small areas due to generally sparse fuels and moist and cool environmental conditions, although large fires occasionally burn sizable stands, particularly after periods of drought (Arno and Hoff 1989). Recent data for the South Warner Wilderness indicate frequent small lightning-caused fires, but few large fires (although many natural fires which may have otherwise grown have been suppressed). Stand-replacing fires appear to be rare, and small fires, though common, may generally

have little effect on overall stand development because space is generally not limiting at most elevations.

The sagebrush-dominated habitats into which whitebark pine has been expanding within the past 100-150 years appear to have not supported conifer stands in recent time. I saw no standing snags, large fallen logs, or burnt coniferous wood in these areas, and downed wood in general was very scarce. Whitebark pine can be considered a harsh site specialist, as it is primarily adapted to timberline habitats characterized by short growing seasons, large temperature fluctuations, heavy snowfall, strong winds, and poorly developed mountain soils (McCaughey and Schmidt 1990, Arno and Hoff 1989). However, it clearly has the ecological amplitude to succeed in these lower, more favorable sites, and I suggest that a competitive relationship that historically kept most pine out of these sagebrush habitats within recent time was initially altered approximately 100-150 years ago. This time period coincides well with the beginning of grazing (and subsequent overgrazing) in the Warner Mountains, and possibly also with climatic change, as a period sometimes referred to as the Little Ice Age may have come to an end circa 1850-1880 (Jones and Bradley 1992, Taylor 1995).

Livestock grazing

The invasion of sagebrush by tree species has been well-documented in western North America, and the causes attributed to the invasions are generally livestock grazing, climatic fluctuation, and fire suppression (Cottam and Stewart 1940,

Burkhardt and Tisdale 1969, 1976, Patten 1969, Blackburn and Tueller 1970, Miller and Wigand 1994). As a result of livestock grazing, perennial grass density has been reduced while sagebrush density has increased in California sagebrush steppe (Young et al. 1977). Grazing can result in the invasion of shallow-rooted vegetation types by deeper-rooted types (i.e., as grasses and forbs are eaten, water losses from transpiration are slowed, which reduces full utilization of soil moisture and creates an “opening” which benefits the establishment of shrubs and trees) (Walter 1979, Robertson and Pearse 1943, Moir and Huckaby 1994). Once established, these deep-rooted plants may prosper, but may not reproduce well if grazing is removed and the shallow-rooted vegetation “closes” once again. Other grazing-related mechanisms for the invasion of sagebrush may include less frequent fires resulting from reduction of fine fuels, and additional safe sites for tree establishment beneath increased shrub cover (Miller and Wigand 1994).

Based upon the ages of trees occurring within a matrix of sagebrush, Vale (1975, 1977) concluded that livestock grazing was responsible for white fir invasion of sagebrush on the east side of the Warner Mountains, and for fir and yellow pine (*P. jeffreyi* and *P. ponderosa*) invasion of sagebrush on the western slope of the range. My tree age data for the 2290⁸ and 2380 m plots show that most trees established

⁸ Most plots at 2290 m were classified as ABCO/OSCH because they were dominated by white fir. However, these plots were at the high end of the white fir forest band at the sagebrush/fir ecotone. Sagebrush, mule’s ears, and other forbs typical of the sagebrush steppe were the dominant understory species. The idea that these plots represent relatively recent forest invasion is borne out by the tree age structures.

between 1915 and 1965. The presence of a few older trees indicates that successful establishment sometimes occurred in these habitats prior to livestock grazing. These data correspond well with Vale's studies which indicate a major invasion period for white fir and yellow pine that began in the 1920s and continued to the mid-1940s at one location and continued at least until 1960 at others. At 2470 m many trees are approximately 100-150 years old, and there are also many trees that are 20-40 years old (only three plots at 2470 m were classified as sagebrush habitat). My results support Vale's conclusions, and indicate that a similar invasion occurred at higher elevations as whitebark pine moved *downslope* into sagebrush steppe habitats after livestock grazing began and reached its highest rates of establishment after the Warners were said to have been severely overgrazed.

Climatic change

Numerous forest expansion events in western North America have been identified in the past 150 years (Franklin et al. 1971, Dunwiddie 1977, Scuderi 1987, Taylor 1995), suggesting a large scale causal mechanism such as climatic change. A warm, mesic period occurred in the late 1800s and early 1900s, providing conditions beneficial to tree establishment and growth and thus probably playing a role in the recent forest expansions (Miller and Wigand 1994; Taylor 1995). Recent research near treeline in the Sierra Nevada indicates that the horizontal growth rate of whitebark pine increased substantially between 1880 and 1965, but has recently declined. Additionally, growth initiation dates for vertical leaders extending above well-defined krummholz

mats begin in the 1920s and peak from 1940-1975 (King, personal communication). These data suggest that environmental conditions in California may have favored whitebark pine growth within much of the past century.

However, in a study comparing several tree invasion chronologies in the Rocky Mountains from Canada to Mexico, Moir and Huckaby (1994) concluded that climate warming itself (increases in regional annual mean temperatures) was insufficient to explain the tree invasions, and that while climatic change may “set the stage” for forest expansion, actual tree establishment also depends on many other factors.

In summary, the whitebark pine expansion into sagebrush steppe habitat in the Warner Mountains represents an additional forest expansion event which began in the late 19th century and has continued throughout much of the 20th century. Although, the expansion of trees into sagebrush steppe during this period has been widespread and well-documented, the reported expansions generally involve trees such as pinyon pine (*Pinus* spp.), juniper (*Juniperus* spp.), and ponderosa pine rather than subalpine species such as whitebark pine. I hypothesize that the combination of favorable climatic conditions for tree establishment and growth *and* changes in soil water availability, species composition, and the structural characteristics of sagebrush habitats resulting from the introduction of livestock have contributed to the whitebark pine expansion.

Regeneration

Whitebark pine regeneration is occurring across its the elevational range. However, although seedlings and saplings occur at all elevations and appear to follow generally the same patterns of density change with respect to elevation as do trees, their densities were uniformly lower than tree densities. Similar whitebark pine seedling and tree densities within the same stands have previously been interpreted as possible signs of decline (Jackson and Faller 1973); if these sapling and seedling density figures were added to size distribution curves (and age distribution curves as well, assuming that seedlings and saplings tend to be younger than trees), the curves could shift in many cases from an inverse-J shape (often cited as an indicator of an all-sized or all aged, self-maintaining stand) to a “declining” shape (Whipple and Dix 1979, Parker and Peet 1984). Parker (1988) found mean whitebark pine seedling densities to be intermediate compared to other species within higher elevation forests of the central Sierra Nevada, and also noted that the whitebark pine stands were primarily characterized by decreasing or random diameter distribution curves. He concluded that both of these results were related to the tree’s relative shade intolerance and the influence of climatic variability and dispersal patterns on its establishment and growth.

In developing stands of fir and yellow pine invading sagebrush in the Warner Mountains, Vale (1977) found low seedling densities in most plots and attributed the lack of establishment to a reduction in grazing intensity, which allowed sagebrush and other forbs to reutilize openings created by historic grazing (which also could reduce

nutcracker cache sites in sagebrush vegetation). The low number of seedlings and saplings relative to trees within the south Warner Mountains may be related to various phenomena, including poor cone crops and/or establishment in recent years due to climatic fluctuation, lack of disturbance such as fire, and reduction in grazing since establishment of the primitive area and wilderness. Low seedling and sapling density may or may not represent a long-term decline in establishment and density.

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APPENDIX A. SUMMARY TABLES FOR STATISTICAL ANALYSES

Table A-1. Statistical summary of comparisons of plot aspect (degrees) among elevations.

Kruskal-Wallis one-way ANOVA on ranks					
Method	DF	Chi-Square (H)	Prob Level		
Not Corrected for Ties	6	6.718624	0.347654		
Corrected for Ties	6	6.739522	0.345609		
Group	Count	Sum of Ranks	Mean Rank	Z-Value	Median
2290	6	169	28.17	1.1628	277.5
2380	6	95.5	15.92	-1.3509	266
2470	6	109.5	18.25	-0.8721	266
2560	6	144	24	0.3078	272.5
2650	6	102.5	17.08	-1.1115	267.5
2740	6	136	22.67	0.0342	275
2830/2930	8	233.5	29.19	1.628	282

Table A-2. Statistical summary of comparisons of plot slope (degrees) among elevations.

Analysis of Variance Table					
Source	DF	Sum of Squares	Mean Square	F-Ratio	Prob Level
A (elevation)	6	1826.951	304.4918	18.65	0.000000*
S(A)	37	604.2083	16.32995		
Total (Adjusted)	43	2431.159			
Total	44				

* Term significant at alpha = 0.05

Tukey-Kramer Multiple-Comparison Test
 Response: slope (degrees)
 Term A: elevation
 Alpha=0.100 Error Term=S(A) DF=37 MSE=16.32995 Critical Value=3.976182

Group	Count	Mean	Different From Groups
2290	6	8.666667	2470, 2650, 2830/2930, 2740
2380	6	10	2650, 2830/2930, 2740
2560	6	15.166667	2830/2930, 2740
2470	6	15.5	2290, 2830/2930, 2740
2650	6	21.166667	2290, 2380
2830/2930	8	24.875	2290, 2380, 2560, 2470
2740	6	26.166667	2290, 2380, 2560, 2470

Table A-3. Statistical summary of comparisons of plot TRMI value among elevations.

Analysis of Variance Table					
Source		Sum of	Mean		Prob
Term	DF	Squares	Square	F-Ratio	Level
A (elevation)	6	1146.011	191.0019	12.27	0.000000*
S(A)	37	575.875	15.56419		
Total (Adjusted)	43	1721.886			
Total	44				

* Term significant at alpha = 0.05

Tukey-Kramer Multiple-Comparison Test
 Response: trmi value
 Term A: elevation
 Alpha=0.100 Error Term=S(A) DF=37 MSE=15.56419 Critical Value=3.976182

Group	Count	Mean	Different From Groups
2740	6	19.66667	2470, 2560, 2380, 2290
2830/2930	8	19.875	2470, 2560, 2380, 2290
2650	6	23.83333	2380, 2290
2470	6	26.33333	2740, 2830/2930, 2290
2560	6	27.66667	2740, 2830/2930
2380	6	31.66667	2740, 2830/2930, 2650
2290	6	33.83333	2740, 2830/2930, 2650, 2470

Table A-4. Statistical summary of comparisons of surface rock (percent) among elevations.

Analysis of Variance Table					
Source		Sum of	Mean		Prob
Term	DF	Squares	Square	F-Ratio	Level
A (elevation)	6	6855.617	1142.603	5.69	0.000286*
S(A)	37	7425.542	200.6903		
Total (Adjusted)	43	14281.16			
Total	44				

* Term significant at alpha = 0.05

Tukey-Kramer Multiple-Comparison Test
 Response: surface rock
 Term A: elevation
 Alpha=0.100 Error Term=S(A) DF=37 MSE=200.6903 Critical Value=3.976182

Group	Count	Mean	Different From Groups
2560	6	5.833333	2740, 2830/2930
2290	6	7.333333	2740, 2830/2930
2470	6	8.833333	2830/2930
2380	6	11	2830/2930
2650	6	11.83333	2830/2930
2740	6	31.16667	2560, 2290
2830/2930	8	38.125	2560, 2290, 2470, 2380, 2650

Table A-5. Statistical summary of comparisons of litter depth (cm) among elevations.

Analysis of Variance Table					
Source		Sum of	Mean		Prob
Term	DF	Squares	Square	F-Ratio	Level
A (elevation)	6	1.871922	0.3119871	1.02	0.425879
S(A)	37	11.28552	0.3050141		
Total (Adjusted)	43	13.15744			
Total	44				

* Term significant at alpha = 0.05

Table A-6. Statistical summary of comparisons of downed wood abundance (percent) among elevations.

Kruskal-Wallis One-Way ANOVA on Ranks					
Method	DF	Chi-Square (H)	Prob Level		
Not Corrected for Ties	6	16.8257	0.009946		
Corrected for Ties	6	17.38814	0.007958		

Group	Count	Sum of Ranks	Mean Rank	Z-Value	Median
2290	6	143.5	23.92	0.2907	3.5
2380	6	42	7	-3.1805	1
2470	6	80.5	13.42	-1.8639	1.5
2560	6	150.5	25.08	0.5301	3
2650	6	170	28.33	1.197	5.5
2740	6	182	30.33	1.6074	4.5
2830/2930	8	221.5	27.69	1.2628	5.5

Kruskal-Wallis Multiple-Comparison Z-Value Test	
Different from groups (alpha = 0.10, Bonferroni test)	
2290	
2380	2650, 2740, 2830/2930
2470	
2560	
2650	2380
2740	2380
2830/2930	2380

Table A-7. Statistical summary of comparisons of canopy cover (percent) among elevations.

Kruskal-Wallis One-Way ANOVA on Ranks					
Method	DF	Chi-Square (H)	Prob Level		
Not Corrected for Ties	6	11.80758	0.066402		
Corrected for Ties	6	11.86695	0.065004		
Group	Count	Sum of Ranks	Mean Rank	Z-Value	Median
2290	6	142	23.67	0.2394	13.5
2380	6	51	8.5	-2.8727	5.5
2470	6	115.5	19.25	-0.6669	17.5
2560	6	125.5	20.92	-0.3249	12.5
2650	6	176	29.33	1.4022	23
2740	6	144	24	0.3078	15
2830/2930	8	236	29.5	1.704	27.5
Kruskal-Wallis Multiple-Comparison Z-Value Test					
Different from groups (alpha = 0.10, Bonferroni test)					
2290					
2380		2650, 2830/2930			
2470					
2560					
2650		2380			
2740					
2830/2930		2380			

Table A-8. Statistical summary of comparisons of chrub cover (percent) among elevations.

Kruskal-Wallis One-Way ANOVA on Ranks					
Method	DF	Chi-Square (H)	Prob Level		
Not Corrected for Ties	6	19.93878	0.00284		
Corrected for Ties	6	20.67912	0.002095		
Group	Count	Sum of Ranks	Mean Rank	Z-Value	Median
2290	5	142	28.4	1.4741	10
2380	6	202	33.67	2.8033	15
2470	5	127	25.4	0.8765	4
2560	5	112.5	22.5	0.2988	8
2650	6	120.5	20.08	-0.2029	1.5
2740	6	91.5	15.25	-1.2726	1
2830/2930	8	65.5	8.19	-3.372	0
Kruskal-Wallis Multiple-Comparison Z-Value Test					
Different from groups (alpha = 0.10, Bonferroni test)					
2290		2830/2930			
2380		2830/2930			
2470					
2560					
2650					
2740					
2830/2930		2290, 2380			

Table A-9. Summary of statistical comparisons of herb cover (percent) among elevations.

Analysis of Variance Table					
Source		Sum of	Mean		Prob
Term	DF	Squares	Square	F-Ratio	Level
A (elevation)	6	3326.767	554.4611	3.37	0.010548*
S(A)	33	5427.208	164.4609		
Total (Adjusted)	39	8753.975			
Total	40				

* Term significant at alpha = 0.05

Tukey-Kramer Multiple-Comparison Test
 Response: herb cover
 Term A: elevation
 Alpha=0.100 Error Term=S(A) DF=33 MSE=164.4609 Critical Value=3.996997

Group	Count	Mean	Different From Groups
2830/2930	8	7.875	2650, 2290, 2470
2740	6	14.5	
2380	5	27.6	
2650	6	28.16667	2830/2930
2560	5	28.4	
2290	5	29.8	2830/2930
2470	5	32.2	2830/2930

Table A-10. Summary of statistical comparisons of whitebark pine tree density (stems/400 m²) among elevations.

Analysis of Variance Table					
Source		Sum of	Mean		Prob
Term	DF	Squares	Square	F-Ratio	Level
A (elevation)	6	62754.89	10459.15	37.89	0.000000*
S(A)	37	10213.83	276.0496		
Total (Adjusted)	43	72968.73			
Total	44				

* Term significant at alpha = 0.05

Tukey-Kramer Multiple-Comparison Test
 Response: pial tree count
 Term A: elevation
 Alpha=0.100 Error Term=S(A) DF=37 MSE=276.0496 Critical Value=3.976182

Group	Count	Mean	Different From Groups
2290	6	4.333333	2740, 2650, 2830/2930
2380	6	9.166667	2740, 2650, 2830/2930
2560	6	26.5	2830/2930
2470	6	27	2830/2930
2740	6	46.33333	2290, 2380, 2830/2930
2650	6	48.33333	2290, 2380, 2830/2930
2830/2930	8	116.75	2290, 2380, 2560, 2470, 2740, 2650

Note: while statistical tests were conducted on raw data from 400 m² plots, the means and standard deviations presented within the body of the document are the values per hectare

Table A-11. Summary of statistical comparisons of whitebark pine sapling density (stems/400 m²) among elevations.

Analysis of Variance Table					
Source		Sum of	Mean		Prob
Term	DF	Squares	Square	F-Ratio	Level
A (elevation)	6	4.030403	0.6717338	4.69	0.002527*
S(A)	25	3.581853	0.1432741		
Total (Adjusted)	31	7.612256			
Total	32				

* Term significant at alpha = 0.05

Tukey-Kramer Multiple-Comparison Test
 Response: log (pial saplings)
 Term A: elevation
 Alpha=0.100 Error Term=S(A) DF=25 MSE=0.1432741 Critical Value=4.059185

Group	Count	Mean	Different From Groups
2470	3	0.2593837	2830/2930
2560	3	0.4336767	2830/2930
2290	4	0.5284858	2830/2930
2650	6	0.762408	2830/2930
2740	6	0.7649544	2830/2930
2380	2	0.7781513	
2830/2930	8	1.352255	2470, 2560, 2290, 2650, 2740

Note: while statistical tests were conducted on raw data from 400 m² plots, the means and standard deviations presented within the body of the document are the values per hectare

Table A-12. Summary of statistical comparisons of whitebark pine seedling density (stems/100 m²) among elevations.

Kruskal-Wallis One-Way ANOVA on Ranks					
Method	DF	Chi-Square (H)	Prob Level		
Not Corrected for Ties	6	11.60227	0.071453		
Corrected for Ties	6	13.30286	0.038471		

Group	Count	Sum of Ranks	Mean Rank	Z-Value	Median
2290	6	91	15.17	-1.5048	0
2380	6	96	16	-1.3338	0
2470	6	129.5	21.58	-0.1881	0.5
2560	6	101	16.83	-1.1628	0
2650	6	142.5	23.75	0.2565	1.5
2740	6	159	26.5	0.8208	4
2830/2930	8	271	33.88	2.769	8

Kruskal-Wallis Multiple-Comparison Z-Value Test
 Different from groups (alpha = 0.10, Bonferroni test)

2290	2830/2930
2380	
2470	
2560	
2650	
2740	
2830/2930	2290

Note: while statistical tests were conducted on raw data from 100 m² plots, the means and standard deviations presented within the body of the document are the values per hectare

Table A-13. Summary of statistical comparisons of the percentage of dead stems per plot among elevations.

Kruskal-Wallis One-Way ANOVA on Ranks					
Method	DF	Chi-Square (H)	Prob Level		
Not Corrected for Ties	6	10.71061	0.097743		
Corrected for Ties	6	13.49166	0.03586		
Group	Count	Sum of Ranks	Mean Rank	Z-Value	Median
2290	6	129	21.5	-0.2052	0
2380	6	81	13.5	-1.8468	0
2470	6	149.5	24.92	0.4959	1.219512
2560	6	107.5	17.92	-0.9405	0
2650	6	216	36	2.7701	3.102453
2740	6	139	23.17	0.1368	0
2830/2930	8	168	21	-0.3651	0.3333333
Kruskal-Wallis Multiple-Comparison Z-Value Test					
Different from groups (alpha = 0.10, Bonferroni test)					
2290					
2380	2650				
2470					
2560					
2650	2380				
2740					
2830/2930					

Table A-14. Summary of statistical comparisons of whitebark pine basal area (m²/400 m²) among elevations.

Analysis of Variance Table					
Source	DF	Sum of Squares	Mean Square	F-Ratio	Prob Level
A (elevation)	6	30.91198	5.151997	9.72	0.000002*
S(A)	36	19.08752	0.5302088		
Total (Adjusted)	42	49.9995			
Total	43				
* Term significant at alpha = 0.05					
Tukey-Kramer Multiple-Comparison Test					
Response: basal area (m ² /400m ²)					
Term A: elevation					
Alpha=0.100 Error Term=S(A) DF=36 MSE=0.5302088 Critical Value=3.980944					
Group	Count	Mean	Different From Groups		
2290	5	0.1460523	2830/2930, 2740, 2560, 2650		
2380	6	0.2276882	2830/2930, 2740, 2560, 2650		
2470	6	0.9552441	2560, 2650		
2830/2930	8	1.385655	2290, 2380, 2650		
2740	6	1.63686	2290, 2380		
2560	6	2.210169	2290, 2380, 2470		
2650	6	2.655701	2290, 2380, 2470, 2830/2930		

Note: while statistical tests were conducted on raw data from 400 m² plots, the means and standard deviations presented within the body of the document are the values per hectare

Table A-15. Summary of statistical comparisons of whitebark pine tree diameter among elevations.

Kruskal-Wallis One-Way ANOVA on Ranks					
Method	DF	Chi-Square (H)	Prob Level		
Not Corrected for Ties	6	285.1651	0.000000		
Corrected for Ties	6	285.1983	0.000000		
Group	Count	Sum of Ranks	Mean Rank	Z-Value	Median
2290	26	22893	880.5	-0.6681	1.086075
2380	55	49445.5	899.01	-0.7258	0.9730355
2470	162	183097	1130.23	4.3161	1.190163
2560	159	219983	1383.54	10.3444	1.359076
2650	290	341136.5	1176.33	7.5515	1.227643
2740	278	286814.5	1031.71	2.6173	1.11662
2830/2930	933	708286.5	759.15	-15.0153	0.881955
Kruskal-Wallis Multiple-Comparison Z-Value Test Different from groups (alpha = 0.10, Bonferroni test)					
2290	2560				
2380	2560, 2650				
2470	2560, 2830/2930				
2560	2290, 2380, 2470, 2650, 2740, 2830/2930				
2650	2380, 2560, 2740, 2830/2930				
2740	2560, 2650, 2830/2930				
2830/2930	2470, 2560, 2650, 2740				

Table A-16. Summary of statistical comparisons of number of tree stems per multi-stemmed cluster.

Kruskal-Wallis One-Way ANOVA on Ranks					
Method	DF	Chi-Square (H)	Prob Level		
Not Corrected for Ties	6	9.976605	0.125641		
Corrected for Ties	6	10.8869	0.091936		
Group	Count	Sum of Ranks	Mean Rank	Z-Value	Median
2290	7	1505	215	-0.6308	2
2380	12	3183	265.25	0.3968	3.5
2470	35	9906.5	283.04	1.4545	3
2560	36	10655	295.97	2.0376	3
2650	76	17711.5	233.05	-1.0522	3
2740	82	18309	223.28	-1.7747	2.5
2830/2930	249	62483	250.94	0.3011	3

Table A-17. Summary of statistical comparisons of number of sapling stems per multi-stemmed cluster among elevations.

Kruskal-Wallis One-Way ANOVA on Ranks					
Method	DF	Chi-Square (H)	Prob Level		
Not Corrected for Ties	6	8.497574	0.203867		
Corrected for Ties	6	10.83056	0.093757		
Group	Count	Sum of Ranks	Mean Rank	Z-Value	Median
2290	5	120.5	24.1	-1.0507	2
2380	1	42.5	42.5	0.5413	3
2470	1	19.5	19.5	-0.7037	2
2560	3	58.5	19.5	-1.2387	2
2650	7	329	47	2.1833	4
2740	9	239.5	26.61	-1.0235	2
2830/2930	38	1270.5	33.43	0.4853	2

Table A-18. Summary of statistical comparisons of number of seedling stems per multi-stemmed cluster among elevations.

Kruskal-Wallis One-Way ANOVA on Ranks					
Method	DF	Chi-Square (H)	Prob Level		
Not Corrected for Ties	6	2.627408	0.853945		
Corrected for Ties	6	3.390045	0.758537		
Group	Count	Sum of Ranks	Mean Rank	Z-Value	Median
2290	2	75	37.5	1.0468	3
2380	3	69.5	23.17	-0.3925	2
2470	10	267	26.7	0.0464	2
2560	1	16	16	-0.6996	2
2650	5	101.5	20.3	-0.9622	2
2740	13	353.5	27.19	0.1902	2
2830/2930	18	495.5	27.53	0.3558	2

Table A-19. Summary of statistical comparisons of percentage of clustered tree stems among elevations.

Kruskal-Wallis One-Way ANOVA on Ranks					
Method	DF	Chi-Square (H)	Prob Level		
Not Corrected for Ties	6	1.814634	0.935933		
Corrected for Ties	6	1.824906	0.935077		
Group	Count	Sum of Ranks	Mean Rank	Z-Value	Median
2290	4	87	21.75	0.2254	1.956425
2380	4	98	24.5	0.7213	1.974424
2470	6	132.5	22.08	0.3598	1.949511
2560	6	113	18.83	-0.3788	1.937531
2650	6	94.5	15.75	-1.0795	1.920304
2740	6	131	21.83	0.303	1.941918
2830/2930	8	164	20.5	0	1.939061

Table A-20. Summary of statistical comparisons of percentage of clustered sapling stems among elevations.

Analysis of Variance Table					
Source		Sum of	Mean		Prob
Term	DF	Squares	Square	F-Ratio	Level
A (elevation)	6	6408.53	1068.088	0.72	0.633853
S(A)	25	36848.79	1473.952		
Total (Adjusted)	31	43257.32			
Total	32				

* Term significant at alpha = 0.05

Table A-21. Summary of statistical comparisons of percentage of clustered seedling stems among elevations.

Analysis of Variance Table					
Source		Sum of	Mean		Prob
Term	DF	Squares	Square	F-Ratio	Level
A (elevation)	6	0.5453153	9.09E-02	1.56	0.216594
S(A)	18	1.050545	5.84E-02		
Total (Adjusted)	24	1.59586			
Total	25				

* Term significant at alpha = 0.05

Table A-22. Summary of statistical comparisons of percentage of clustered (vs. single stemmed) whitebark pine tree "sites" among elevations.

Kruskal-Wallis One-Way ANOVA on Ranks					
Method	DF	Chi-Square (H)	Prob Level		
Not Corrected for Ties	6	3.073018	0.799628		
Corrected for Ties	6	3.092747	0.797119		
Group	Count	Sum of Ranks	Mean Rank	Z-Value	Median
2290	4	90.5	22.63	0.3832	1.889076
2380	4	96	24	0.6312	1.911954
2470	6	123.5	20.58	0.0189	1.809894
2560	6	97	16.17	-0.9848	1.80103
2650	6	92.5	15.42	-1.1553	1.782564
2740	6	141.5	23.58	0.7007	1.834503
2830/2930	8	179	22.38	0.5072	1.826885

Table A-23. Summary of statistical comparisons of percentage of clustered (vs. single stemmed) whitebark pine sapling “sites” among elevations.

Analysis of Variance Table					
Source		Sum of	Mean		Prob
Term	DF	Squares	Square	F-Ratio	Level
A (elevation)	6	5905.988	984.3313	0.78	0.592051
S(A)	25	31472.14	1258.886		
Total (Adjusted)	31	37378.13			
Total	32				

* Term significant at alpha = 0.05

Table A-24. Summary of statistical comparisons of percentage of clustered (vs. single stemmed) whitebark pine seedling “sites” among elevations.

Analysis of Variance Table					
Source		Sum of	Mean		Prob
Term	DF	Squares	Square	F-Ratio	Level
A (elevation)	6	2174.744	362.4574	1.14	0.37791
S(A)	18	5706.008	317.0005		
Total (Adjusted)	24	7880.752			
Total	25				

* Term significant at alpha = 0.05

APPENDIX B. DIFFERENCES BETWEEN MINIMUM AGES AND ESTIMATED AGES FOR OFF-CENTER AND INCOMPLETE TREE CORES

Table B-1. Percentages of incomplete, off-center, and through-the-pith tree cores, broken down by elevation.

	2290 m	2380 m	2470 m	2560 m	2650 m	2740 m	2830/2930 m	Total
n	115	33	69	60	130	119	370	896
incomplete	7%	0	4%	8%	6%	8%	3%	5%
off-center	50%	58%	44%	60%	53%	45%	50%	50%
pith	43%	42%	52%	32%	41%	47%	47%	45%

Table B-2. Estimated ages and minimum ages for off-center tree cores, broken down by elevation.

Elevation (m)	n	mean estimated age	mean minimum age	mean years added
2290	58	70.5 (29.6)	65.2 (28.7)	5.3 (3.2)
2380	19	50.6 (43.3)	46.8 (42.0)	3.7 (2.3)
2470	30	71.8 (44.1)	67.8 (43.6)	4.0 (2.6)
2560	36	118.4 (67.0)	112.0 (66.4)	6.4 (4.5)
2650	69	148.5 (73.3)	140.8 (72.0)	7.6 (5.4)
2740	53	132.6 (97.9)	126.3 (96.6)	6.3 (6.6)
2830/2930	184	121.9 (65.3)	115.5 (64.0)	6.5 (4.6)
Total	452	114.4 (71.7)	108.2 (70.2)	6.2 (4.8)

Table B-3. Information related to estimating ages of incomplete tree cores, including missing core lengths, mean number of rings/cm of similar cores, minimum ages, and estimated ages.

Elevation (m)	Plot number	Tree number	Species	diameter (cm)	length of core (cm)	predicted complete core length	missing core length	mean rings/cm with 95%CI	years to add	minimum age	estimated age
2290	1-4-1	1035	ABCO	43.7	19.3	19.95	0.65	18.42 +/- 3.83	12	123	135
2290	1-4-1	1037	ABCO	48.0	10	21.78	11.78	12.88 +/- 1.86	152	38	190
2290	1-4-1	1047	ABCO	67.6	31.4	30.07	-1.33		0	102	102
2290	1-4-1	1049	ABCO	28.7	8	13.60	5.60	15.39 +/- 2.22	86	80	166
2290	1-4-1	1053	PIAL	77.2	34.9	34.16	-0.74		0	156	156
2290	1-5-1	1481	ABCO	65.5	34.1	29.21	-4.89		0	74	74
2290	1-5-1	1483	ABCO	66.3	35.1	29.54	-5.56		0	69	69
2290	1-6-1	1754	ABCO	63.5	36.2	28.35	-7.85		0	71	71
2470	1-3-3	769	PIAL	65.0	18.9	29.00	10.10	11.67 +/- 2.09	118	151	269
2470	1-3-3	791	PIAL	38.6	18.3	17.80	-0.50		0	125	125
2470	1-3-3	794	PIAL	28.2	11.5	13.39	1.89	20.40 +/- 13.75	39	106	145
2560	1-3-4	813	PIAL	26.7	8.8	12.74	3.94	32.08 +/- 16.68	126	34	160
2560	1-4-4	1101	PIAL	53.6	25.9	24.15	-1.75		0	368	368
2560	1-6-4	1827	PIAL	101.6	33.7	44.50	10.80	18.63 +/- 5.59	201	222	423
2560	1-6-4	1832	PIAL	73.7	36.4	32.66	-3.74		0	274	274
2560	1-6-4	1845	PIAL	45.2	13.3	20.60	7.30	24.14 +/- 8.88	176	120	296
2650	1-2-5	511	PIAL	85.9	35.9	37.82	1.92	58.38 +/- 5.52	112	339	451
2650	1-2-5	516	PIAL	66.8	25	29.75	4.75	33.73 +/- 5.32	160	403	563
2650	1-2-5	517	PIAL	47.5	6.7	21.57	14.87	20.52 +/- 14.31	305	130	435
2650	1-2-5	524	PIAL	56.9	21.8	25.55	3.75	39.54 +/- 6.50	148	229	377
2650	1-2-5	525	PIAL	46.5	12.2	21.14	8.94	26.64 +/- 3.93	238	190	428
2650	1-4-5	1126	PIAL	45.7	19.7	20.82	1.12	58.38 +/- 5.52	65	307	372
2650	1-4-5	1165	PIAL	74.7	8.7	33.09	24.39	18.67 +/- 2.59	455	135	590
2650	1-6-5	1884	PIAL	88.9	16.6	39.12	22.52	18.67 +/- 2.59	420	339	759

Table B-3. Summary table of incomplete core information, continued.

Elevation (m)	Plot number	Tree number	Species	diameter (cm)	length of core (cm)	predicted complete core length	missing core length	mean rings/cm with 95%CI	years to add	Minimum age	Age
2740	1-2-6	529	PIAL	60.7	21.5	27.17	5.67	25.10 +/- 4.04	142	310	452
2740	1-2-6	530	PIAL	35.8	12.1	16.62	4.52	27.79 +/- 4.98	126	193	319
2740	1-3-6	850	PIAL	3.8	1.5	3.05	1.55	73.83 +/- 15.35	115	17	132
2740	1-3-6	865	PIAL	50.8	9.5	22.97	13.47	19.39 +/- 2.34	261	194	455
2740	1-3-6	868	PIAL	63.0	21.7	28.14	6.44	23.51 +/- 3.41	151	265	416
2740	1-3-6	877	PIAL	30.2	8.8	14.25	5.45	25.19 +/- 4.24	137	296	433
2740	1-4-6	1250	PIAL	94.0	8.7	41.27	32.57	18.42 +/- 2.15	600	268	868
2740	1-5-6	1571	PIAL	78.0	21.1	34.49	13.39	19.39 +/- 2.34	260	355	615
2740	1-5-6	1596	PIAL	114.0	9.1	49.77	40.67	18.42 +/- 2.15	749	64	813
2740	1-6-6	1909	PIAL	47.2	34.3	21.46	-12.84	-	0	270	270
2740	1-6-6	1913	PIAL	26.9	11.7	12.85	1.15	45.87 +/- 22.99	53	138	191
2830	1-1-7	147	PIAL	26.7	9.9	12.74	2.84	41.40 +/- 4.86	118	213	331
2830	1-1-7	201	PIAL	29.5	12	13.93	1.93	54.23 +/- 9.41	104	208	312
2830	1-2-7	723	PIAL	18.0	11.4	9.08	-2.32	-	0	252	252
2830	1-3-7	891	PIAL	16.8	9.6	8.54	-1.06	-	0	99	99
2830	1-3-7	992	PIAL	37.8	16.3	17.48	1.18	64.6 +/- 26.61	76	305	381
2830	1-3-7	999	PIAL	62.2	13	27.81	14.81	24.01 +/- 1.80	356	347	703
2830	1-4-7	1318	PIAL	58.4	9.1	26.20	17.10	24.21 +/- 1.78	414	162	576
2830	1-4-7	1351	PIAL	40.9	11.4	18.77	7.37	28.18 +/- 2.33	208	233	441
2830	1-5-7	1715	PIAL	69.6	33.1	30.93	-2.17	-	0	430	430
2830	1-6-7	1955	PIAL	34.8	7.5	16.19	8.69	26.35 +/- 2.12	229	165	394
2930	1-1-8	324	PIAL	23.9	2.3	11.56	9.26	25.07 +/- 2.36	232	64	296
2930	1-4-8	1468	PIAL	23.4	7.4	11.34	3.94	32.14 +/- 3.73	127	280	407