The influence of forest structure on cone production in whitebark pine throughout the Greater Yellowstone Ecosystem
by David A Spector

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

Abstract:
This research focuses on relationships among whitebark pine (Pinus albicaulis) cone production and forest structure characteristics. I used counts of mature cones obtained from 103 trees at 11 plots over a 9-year period within the Greater Yellowstone Ecosystem. Whitebark pine cone count data, collected by the Interagency Grizzly Bear Study Team, were used in regression analyses with forest structure data. I quantified forest structure with measurements of crown size, basal area of competing trees, stem size and number, tree height, tree age, and understory composition. Results of regressions with cone production indicate that there are significant positive relationships with crown area (p = 0.00; R2 = 0.30), crown volume (p = 0.00; R2 = 0.25), and stem size (p =0.05; R2 = 0.04), while basal area of competing trees has a negative effect on cone production (p = 0.00; R2 = 0.10). Multiple regression analyses with forest structure measurements yielded a model that explains 36% of the variation in cone production (p = 0.00). These results may be useful for future stand assessments and management efforts directed at improving cone production for grizzly bear (Ursus arctos horribilis) forage and/or whitebark pine regeneration.

I found that cone production within sample plots was unrelated to topographic site characteristics, including aspect, elevation, and slope angle. I also conducted inventories of blister rust (Cronartium ribicola) infection and mountain pine beetle (Dendroctonus ponderosae) occurrence within all plots. Summaries suggest that the occurrence of these damaging agents are low (8% and <2%, respectively) throughout the Greater Yellowstone Ecosystem.

THE INFLUENCE OF FOREST STRUCTURE ON CONE PRODUCTION IN WHITEBARK PINE THROUGHOUT THE GREATER YELLOWSTONE ECOSYSTEM

by

David A. Spector

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APPROVAL

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David A. Spector

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

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ABSTRACT

This research focuses on relationships among whitebark pine (*Pinus albicaulis*) cone production and forest structure characteristics. I used counts of mature cones obtained from 103 trees at 11 plots over a 9-year period within the Greater Yellowstone Ecosystem. Whitebark pine cone count data, collected by the Interagency Grizzly Bear Study Team, were used in regression analyses with forest structure data. I quantified forest structure with measurements of crown size, basal area of competing trees, stem size and number, tree height, tree age, and understory composition. Results of regressions with cone production indicate that there are significant positive relationships with crown area ($p = 0.00$; $R^2 = 0.30$), crown volume ($p = 0.00$; $R^2 = 0.25$), and stem size ($p = 0.05$; $R^2 = 0.04$), while basal area of competing trees has a negative effect on cone production ($p = 0.00$; $R^2 = 0.10$). Multiple regression analyses with forest structure measurements yielded a model that explains 36% of the variation in cone production ($p = 0.00$). These results may be useful for future stand assessments and management efforts directed at improving cone production for grizzly bear (*Ursus arctos horribilis*) forage and/or whitebark pine regeneration.

I found that cone production within sample plots was unrelated to topographic site characteristics, including aspect, elevation, and slope angle. I also conducted inventories of blister rust (*Cronartium ribicola*) infection and mountain pine beetle (*Dendroctonus ponderosae*) occurrence within all plots. Summaries suggest that the occurrence of these damaging agents are low (8% and <2%, respectively) throughout the Greater Yellowstone Ecosystem.

CHAPTER 1

INTRODUCTION

High-mountain forests are important and fragile communities. They are sensitive to small changes in stress, resulting from either human or environmental pressures (Ross 1990). Anthropogenic influences, including fire suppression, exotic species invasion, domestic grazing, mineral exploration, timber harvesting, road building, and increases in mountain recreation, have damaged many high-mountain ecosystems throughout the west (Brown and Chambers 1990). These forests provide food and refuge for many plant and animal species, are prime recreation areas, and are important for snow catchment, which provides much of the water to the western United States. Protecting these ecosystems provides an important challenge to land managers.

Objectives and Hypotheses

Whitebark pine (*Pinus albicualis*) grows throughout the mountainous west in high-elevation forests up to treeline. A large concentration of whitebark pine exists in Yellowstone National Park, where it occupies 14% of the landscape (Despain 1990).

Until recently, whitebark pine has received very little research attention due primarily to its low timber value. However, it is a potentially threatened tree, due partially to anthropogenic causes. White pine blister rust (*Cronartium ribicola*), an exotic disease, has been epidemic throughout much of the range of whitebark pine (Hoff and Hagle 1990). Historical fire suppression practices have facilitated the encroachment of subalpine fir *(Abies lasiocarpa)* and Engelmann spruce *(Picea engelmannii)* into whitebark stands (Morgan and Bunting 1990) and have also encouraged mountain pine beetle (*Dendroctonus ponderosae*) infestations, both of which have caused considerable mortality of whitebark pine in the Yellowstone area (Kendall and Arno 1990). Whitebark pine seeds are an important food resource for threatened grizzly bears (*Ursus arctos horribilis*) in the Greater Yellowstone Ecosystem, as well as for various bird and rodent species. Fire suppression and insect and disease epidemics have reduced cone crops (Arno 1986), thus affecting forage for threatened grizzly bear populations in the Greater Yellowstone Ecosystem (Blanchard 1990; Mattson and Jonkel 1990; Mattson and Reinhart 1994). There is a need to better understand forest structure characteristics and where and why cone production is successful so that management efforts can be aimed at improving cone production for the wellbeing of grizzly bears and for more successful regeneration of whitebark pine. This project focuses on relationships among whitebark pine cone production and forest structure characteristics, as well as on the health of whitebark pine in the Greater Yellowstone Ecosystem. Three objectives were defined for this project:

1. To determine which forest structure characteristics are associated with cone production for individual trees.
2. To determine whether topographic site characteristics are associated with cone production at the stand level.
3. To describe the health of individual whitebark pine trees in terms of the amount of white pine blister rust and mountain pine beetle infestation.

Based on previous literature, hypotheses associated with the above-stated objectives are as follows:

1A. Trees with larger crowns (area and volume) produce more cones.

1B. Trees with bigger stems (total diameter at breast height) produce more cones.

1C. Multiple-stemmed trees have lower cone production than single-stem trees.

1D. Cone production increases as tree height increases.

1E. Cone production is not associated with age of trees.

1F. Cone production decreases as competition (total basal area) increases.

1G. Understory composition influences cone production.

2A. Cone production is not associated with site aspect.

2B. Cone production is not associated with site elevation.

2C. Cone production decreases as slope angle increases.

3A. Blister rust has yet to cause extensive damage to whitebark pine throughout the Greater Yellowstone Ecosystem.

3B. Current mountain pine beetle infestations are low in whitebark pine throughout the Greater Yellowstone Ecosystem.

Previous Literature

Competition and Crown Size

Whitebark pine is intolerant of competition from other species (Arno and Hoff 1989; Day 1967; Pfister et al. 1977; Steel et al. 1983). However, the influence of between-tree competition on cone production in whitebark pine stands is understudied. In other species, competition for sunlight has a direct influence on crown size and shape (Horn 1971; Rudolf 1959). Shading of leaves reduces photosynthesis, affecting leaf production and growth, eventually leading to the death of branches and altering crown size and shape (Wilson 1990). Shading has been shown to reduce cone production in Japanese stone pine (Khomentovsky 1994). Kipfer (1992) found that competition influences crown size and shape in whitebark pine, but did not relate this to cone production. Trees with larger crowns usually produce more cones (Fowels 1965; Wenger and Trousdell 1958). A greater spacing of trees allows for full crown development, and has been shown to increase the amount of cone production in red pine (*Pinus resinosa*)

(Overton and Johnson 1984; Stiell 1988) and in western larch (*Larix occidentalis*) (Schmidt 1997; Shearer and Schmidt 1987). Larger crowned Douglas firs (*Pseudotsuga menziesii*) also have greater cone production (Shearer 1986). Weaver and Forcella (1986) show that whitebark pine cone production is related to the number of fertile shoots, which is influenced by crown size and shape.

Stem Size and Number

Diameter of tree stems and cone production both depend on crown size (Pomeroy 1949; Shearer 1986; Stiell 1988; Wenger and Trousdell 1958). Therefore, an indirect relationship has been found between stem diameter at breast height (dbh) and cone production (Shearer 1986; Stiell 1988) for red pine (Godman 1962; Stiell 1988), loblolly pine (*Pinus taeda*) (Pomeroy 1949; Wenger and Trousdell 1958), Douglas fir and western larch (Shearer 1986). These are all single-stemmed trees, and Feldman, et al. (in press) suggest that multi-stemmed (multi-genet) limber pines (*Pinus flexilis*) often have lower cone production due to inter-tree competition between genets.

Tree Height and Age

Increased cone production has been noted in tall lodgepole pine (*Pinus contorta*) (Ying and Illingworth 1986), probably resulting from increased light interception.

Weaver and Forcella (1986) found overall stand age to be unrelated to stand cone production (cones/m^2).

Understory Composition

Perry (1994) suggests that understory plants in forest ecosystems compete for resources with trees, but may also be beneficial in ways that are not readily apparent. There is no research addressing the effects of understory vegetation on whitebark pine. Arno and Weaver (1990) and Weaver and Dale (1974) describe understory vegetation in whitebark pine stands within the Greater Yellowstone Ecosystem.

Topographic Site Characteristics

Previous studies have shown that stand elevation and stand aspect were not correlated to cone production in whitebark pine (Weaver and Forcella 1986) and Japanese stone pine (*Pinus pumila*) (Khomentovsky 1994). Lodgepole pine cone production is also unrelated to elevation (Ying and Illingworth 1986). However, in pinyon pine, (*Pinus edulis*) south-facing aspects have lower cone production (Floyd 1987). Slope angle influences the amount of water available for plant use. On steep slopes, more than half of rainwater reaching the ground can flow over the surface rather than being absorbed into the soil (Larcher 1975).

Blister Rust and Mountain Pine Beetle

White pine blister rust is an exotic disease brought to North America from Europe in 1910 that attacks all white pines, with whitebark pine being the most susceptible (Hoff and Hagle 1990). Since 1910, this disease has become epidemic throughout most of the whitebark pine range, but has yet to cause extensive mortality in the Greater Yellowstone Ecosystem (Berg et al. 1975; Carlson 1978; Hoff and Hagle 1990). This is likely due to the cool and dry continental climate in Yellowstone, which is poorly suited to blister rust teliospore germination (Krebill 1971 in Hoff and Hagle 1990).

Mountain pine beetle infestations have caused extensive mortality within the Greater Yellowstone Ecosystem during periodic epidemic outbreaks (Bartos and Gibson 1990). The last major infestation of mountain pine beetle in this area was during the early 1980's, in which 22% to 44% of the whitebark pine had been killed. These rates have declined significantly since then, with only isolated endemic populations reported (Bartos and Gibson 1990).

Quantity and Regularity of Cone Production

Weaver and Forcella (1986) suggest that temperature and precipitation throughout the cone maturation cycle has a "significant, but not dominant" influence on annual variations of cone production. McCaughey (1994) also suggests that fluctuations in amounts of annual cone yields can be influenced by climatic variations, as well as insects and diseases during reproductive bud formation, pollination, growth, and development.

Whitebark pine is generally considered to be a masting species, producing bumper crops every 3-5 years, often with several years of zero cone production in the interim (Krugman and Jenkinson 1974). Causes of these masting phenomena have not been explained specifically for whitebark pine. The primary hypothesis regarding the cause of masting behavior, the predator satiation hypothesis, proposes that large, synchronized, episodic seed crops benefit the plant by swamping seed predators, thus allowing more seeds to escape predation (Christensen and Whitham 1991; Ims 1990; Janzen 1971; Norton and Kelly 1988; Silverton 1980). However, this hypothesis only considers the evolutionary advantages of masting, and not the mechanisms by which masting is initiated and/or synchronized (Isagi et al. 1997).

Meteorological phenomena can influence the annual variations in the quantity of seed production (Allen and Plat 1990; Rehfeldt et al. 1971; Sharp and Sprague 1967; Sork et al. 1993; Weaver and Forcella 1986). However, annual fluctuations in weather are small when compared to the large fluctuation in seed production for many species, and may therefore not be a major influence on annual variations in quantity of seed production (Kelly 1994; Koenig et al. 1994). Weaver and Forcella (1986) and McCaughey (1994) suggest that annual variation in cone production for whitebark pine is only partially influenced by temporal variations in weather patterns. Lalonde and Roitberg (1992) propose a combination of the above theories, suggesting that small annual variations in seed production can be initiated by interactions between plant physiology and weather, and that these fluctuations can then be exacerbated in response to seed predators, thus promoting masting behavior. Cone and seed predators in whitebark pine include birds, squirrels, small rodents, and cone and seed insects.

Study Area

This study was carried out in the Greater Yellowstone Ecosystem which encompasses approximately 72,840 square kilometers (18 million acres) of predominately public land in the Rocky Mountains (Glick, et al., 1991). At its center, on a 2500-meter (8000-foot) plateau, is Yellowstone National Park, which is surrounded by several lowland areas and mountain chains ranging in elevation from roughly 900 meters (3000 feet) to 4000 meters (13,000 feet). Precipitation falls predominantly in the form of snow during the months of October to April (Baker 1944; Despain 1990; Dirks 1982). Summer precipitation is generally in the form of thunderstorms associated with frontal movement (Dirks 1982). Maximum daily temperatures during winter are usually below freezing, with January being the coldest month (Dirks 1982). Average summer temperatures range from 21°C (70°F) to 26°C (79°F) (Dirks 1982), with occasional freezing temperatures (Despain 1990). Forest ecosystems cover approximately 60% of the Greater Yellowstone Ecosystem (Glick, et al., 1991). These forests are dominated by conifers, including lodgepole pine, Douglas fir, Engelmann spruce, subalpine fir, limber pine, and whitebark pine.

The Interagency Grizzly Bear Study Team established 21 whitebark pine cone count plots, widely dispersed throughout the subalpine zone of the Greater Yellowstone Ecosystem. Each site contains 10 subject trees, and depending on the year of plot establishment, has a cone count record of 9 to 18 years. All subject trees are mature, non-krummholz, cone-producing trees. From these 21 plots, 12 were selected for this study. However, site J was removed from analyses due to heavy incidence of blister rust. Site characteristics of the remaining 11 stands were described by the Interagency Grizzly Bear Study Team (Table 1). These sites were chosen to represent a thorough distribution of habitat types, cover types, and geographic location within Greater Yellowstone Ecosystem (Figure 1).

Table 1: Descriptions of 11 whitebark pine cone count plots used in this study (data courtesy of the Interagency Grizzly Bear Study Team). Habitat types are described by Pfister et al. (1977) and cover types by Despain (1986).

SITE	ELEVATION METERS	SLOPE ANGLE %	ASPECT (DEGREES)	HABITAT TYPE	COVER TYPE
A	2560	12	100	ABLA/THOC-PIAL	WB3
B	2650	30	266	ABLA/VASC-PIAL	WB2
C	2715	26	115	ABLA/VASC-PIAL	WB3
F	2895	28	232	PIAL/FEID	WB
H	2835	8	119	ABLA/VASC-PIAL	NA
M	2745	50	230	PIAL/JUCO	WB
P	2680	30	220	ABLA/VAGL-VASC	WB3
Q	2925	35	224	ABLA/VASC-PIAL	WB2
R	2560	5	90	ABLA/ARCO-VASC-PIAL	SF1-WB3
S	2680	5	260	ABLA/VASC-PIAL	WB3
U	2680	5	70	ABLA/JUCO	WB

Habitat Types:

ABLA/THOC-PIAL -- *Abies lasiocarpa/Thalictrum occidentale-Pinus albicaulis* phase
subalpine fir/western meadowrue-whitebark pine phase

ABLA/VASC-PIAL -- *A. lasiocarpa/Vaccinium scoparium-P. albicaulis* phase
subalpine fir/ grouse whortleberry- whitebark pine phase

PIAL/FEID -- *P. albicaulis/ Festuca idahoensis*
whitebark pine/Idaho fescue

PIAL/JUCO -- *P. albicaulis/Juniperus communis*
whitebark pine/common juniper

ABLA/VAGL-VASC -- *A. lasiocarpa/V. globulare-V. scoparium* phase
subalpine fir/globe huckleberry- grouse whortleberry phase

ABLA/ARCO-VASC-PIAL – *A. lasiocarpa/Arnica cardifolia- V. scoparium- P. albicaulis* phase
subalpine fir/heartleaf arnica- grouse whortleberry- whitebark pine phase

ABLA/JUCO -- *A. lasiocarpa/ Juniperus communis*
subalpine fir/ common juniper

Cover Types:

WB -- Climax stand of whitebark pine
WB2 -- Mature stand of whitebark pine
WB3 -- Overmature stand of whitebark pine
SF1 -- Even-aged, dense stand of fir and spruce. Usually in cool, wet environment
NA -- Not available

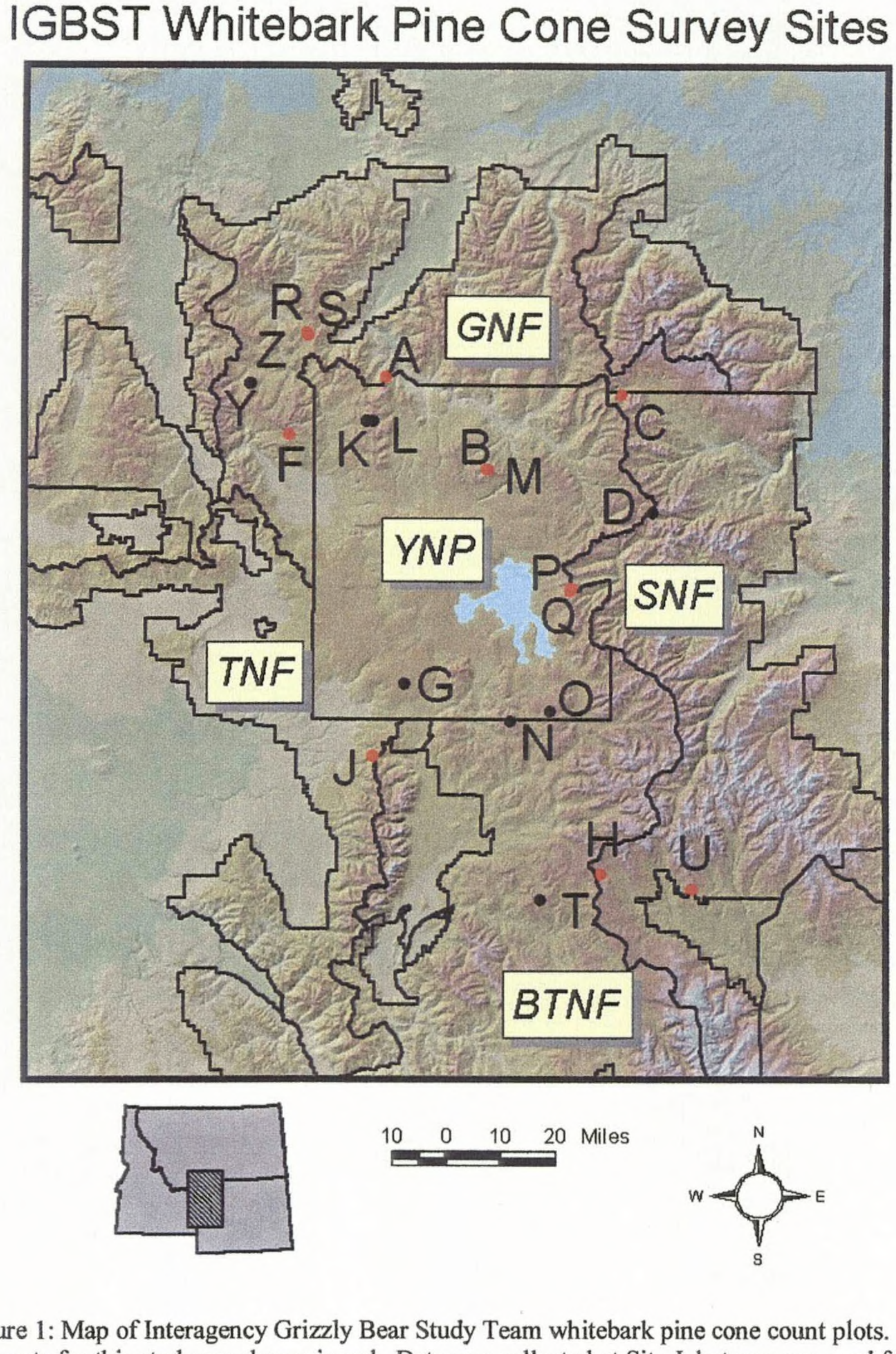

Figure 1: Map of Interagency Grizzly Bear Study Team whitebark pine cone count plots. Selected transects for this study are shown in red. Data was collected at Site J, but was removed from analyses due to heavy incidence of blister rust in subject trees.

YNP = Yellowstone National Park
GNF = Gallatin National Forest
TNF = Targhee National Forest
SNF = Shoshone National Forest
BTNF = Bridger-Teton National Forest

CHAPTER 2

GEOGRAPHY AND ECOLOGY OF WHITEBARK PINE

Whitebark pine is classified as a stone pine, and belongs to the genus *Pinus,* subgenus *Strobus*, subsection *Cembrae*. Other stone pines include Korean stone pine (*P. koraiensis*), Siberian stone pine (*P. sibirica*), Japanese stone pine *(P. pumila*), and Swiss stone pine (*P. cembra*). All stone pines have five-needled fascicles, cones that remain closed upon maturity, and large wingless seeds (Richardson 1998). Stone pines have co-evolved with nutcrackers (*Nucifraga spp.*), and rely on them for seed dispersal (Mattes, 1994).

Whitebark pine grows throughout the mountainous west from central British Columbia to central California and from central Alberta to northwest Wyoming (Figure 2). It grows in the subalpine zone to treeline and ranges in elevation from 1400-2100 meters (4500-7000 feet) in the north to 2400-3700 meters (8000-12,000 feet) in the south (Little et al. 1996). Whitebark pine stands are characterized by cold, snowy winters and relatively warm, dry summers, with an average minimum temperature in January of -11°C (12°F) and an average maximum temperature in July of 21°C (70°F) (Weaver 1990). Maximum snowpack ranges from 1-3 meters (3-10 feet) in the winter, and individual summer months can be rain free (Weaver 1990). Whitebark pine is most abundant on warm, dry exposures in moist mountain ranges and cool, moist exposures in semi-arid ranges (Arno and Hoff 1989). Whitebark pine typically grows in thin, nutrient-poor Cryochrepts and Cryoboralfs soils on landforms with relatively good drainage (Hansen-Bristow, et al. 1990).

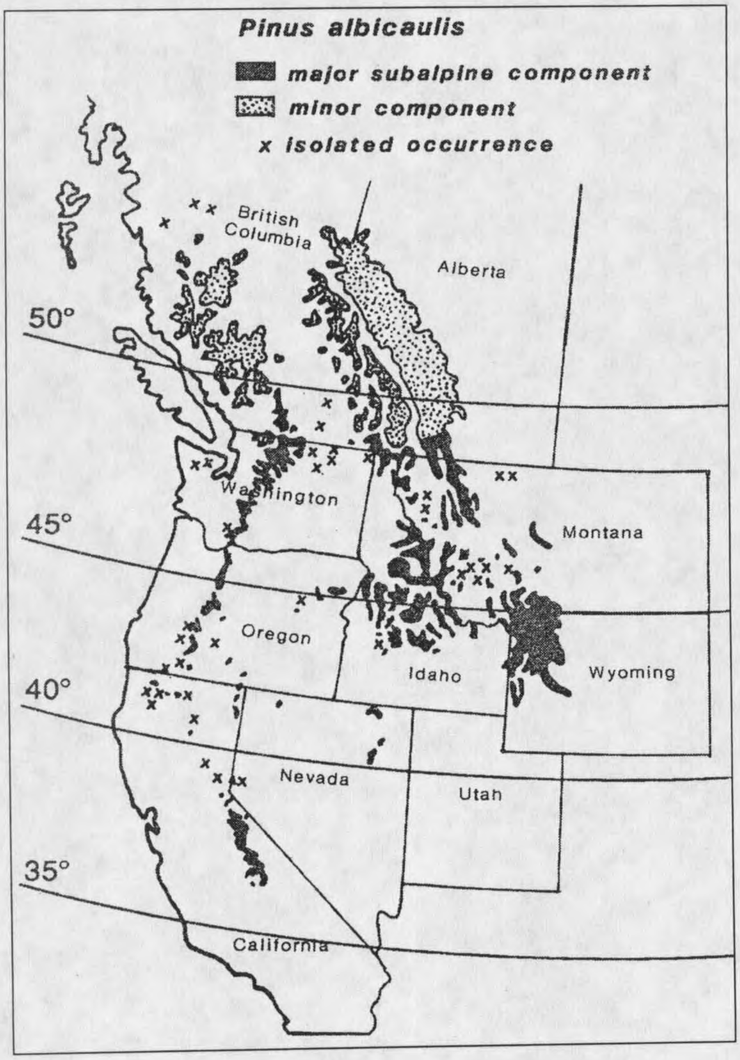

Figure 2: Distribution of whitebark pine (*Pinus albicaulis*) (from Arno and Hoff 1989).

In the Greater Yellowstone Ecosystem, whitebark pine grows in pure or mixed stands, often with lodgepole pine, Engelmann spruce, subalpine fir, and limber pine, and is considered intermediate or intolerant of competition and shade (Arno and Hoff 1989). Whitebark pine is found as a climax or major seral species in a variety of habitat types and phases with varying cover types (Arno and Hoff 1989; Arno and Weaver 1990; Pfister et al. 1977). Whitebark pine is primarily limited to harsh environments where other trees cannot compete, and sites where disturbance has reduced competition (Arno and Weaver 1990). Whitebark pine is a climax species primarily on high-elevation sites that are open and wind exposed (Mattson and Reinhart 1990; Morgan et al. 1994). In mixed stands, whitebark pine can exist as a long-lived seral co-dominant species with frequent low-intensity fires (Arno and Weaver 1990; Morgan et al. 1994). Stand-replacement fires also benefit whitebark pine due to its success at re-invading recently burned sites (Tomback et al. 1990). In the absence of fire, whitebark pine is eventually replaced by more shade tolerant subalpine fir throughout most of the northern Rocky Mountains (Morgan et al. 1994).

Near timberline, whitebark pine trees often grow in krummholtz form. These trees are shrub-like, often forming mats close to the ground (McCaughey and Schmidt 1990). In the subalpine zone, whitebark pine trees typically have rounded spreading crowns with upswept branches, rather than the more typical cone-shaped crowns of other subalpine conifers. They often have multiple stems, resulting from either basal branching or clustering from multiple seed caching by birds (Tomback et al. 1990; Weaver and Jacobs 1990). Whitebark pine needles are 4-7cm (1.3 –2.75 in) long, yellow-green with 1-4 faint white stomatal lines, and have 5 needles per fascicle (McCaughey and Schmidt

1990). The bark is smooth, whitish-gray on younger trees, and scaly, whitish-brown on mature trees. Mature cones are approximately 4-8 cm (1.5-3.25 in) long, egg-shaped, and dark purple-brown. They are highly resinous and contain large, wingless seeds. Each cone contains approximately 75± 28 seeds, comprising 30-50% of the cone's mass (McCaughey and Schmidt 1990; Weaver and Forcella 1986).

Limber pine has a very similar morphology to whitebark pine, and the two can be difficult to distinguish in field observations. The primary methods involve comparison of cones and the number and position of resin ducts in the needles. Cones of limber pine are longer and more slender than whitebark pine, green to yellow-brown, and open upon maturity (Little et al. 1996). However, cones are often absent or hard to see, and comparing resin ducts is often necessary. Limber pine needles have two resin ducts, whereas whitebark pine needles usually have three (Ericson 1964). This method, however, may produce misidentification 44% to 47% of the time (Hendrickson and Lotan 1971).

Cone and seed cycles, from initiation to maturity, take approximately 24 months. Whitebark pine are monoecious, with individual trees containing both male pollen cones (staminate strobili) and female seed cones (ovulate strobili) (McCaughey and Schmidt 1990). Bud onset begins in late August of the first year and then the buds become dormant throughout the fall and winter. Pistillate conelets emerge from these buds early the following spring, around the time of snowmelt (Weaver and Forcella 1986). During the summer, staminate cones grow to a length of 0.64 cm (0.25 in) and ovulate cones grow to 2.5 cm (1 in) (McCaughey and Schmidt 1990). Wind pollination of ovulate cones begins in mid-summer (McCaughey and Schmidt 1990; Weaver and Forcella

1986). After pollination, staminate cones fall from the tree and ovulate cones continue to grow. By mid-September of the second year, cones average 1.5 x 0.9 cm (0.6 x 0.4 in) (Weaver and Forcella 1986). In the following July, growth begins and cones develop until maturity (6.3 x 4.7 cm; 2.5 x 1.9 in) in early August (Weaver and Forcella 1986). Cones remain on the tree until predation or abscission occurs in mid-September to early October (Weaver and Forcella 1986). Whitebark pine reaches reproductive maturity at around 20-30 years (McCaughey and Schmidt 1990). Cone production varies significantly from tree to tree (Weaver and Forcella 1986) and from year to year (Krugman and Jenkinson 1974).

Species such as the Clark's nutcracker (*Nucifraga columbiana*), the red squirrel (*Tamiasciurus hudsonicus*), and the grizzly bear (*Ursus arctos horribis*) depend on whitebark pine seeds as a major food source (Hutchins and Lanner 1982; Kendall 1983; Knight et al. 1987 in McCaughey 1994; Reinhart and Mattson 1990). Conversely, whitebark pine rely on Clark's nutcrackers for seed dispersal. Clark's nutcrackers cache seeds on forest floors, above treeline, on rocky outcrops, meadow edges, clearcuts, burns, and often on sun and wind exposed aspects, as far as 22 km (12 miles) from a seed source, and as many as 3 to 5 times more seeds than it needs (Tomback et al. 1990). Nutcrackers store an average of 3.7 seeds per cache, with the number of seeds ranging from 1-15 (Tomback 1982). Red squirrels harvest and cache cones and seeds primarily within forest habitats, in large centralized middens (Reinhart and Mattson 1990).

Whitebark pine seeds have a high energy content and are particularly important as a fat source for grizzly bears, constituting approximately 40% of their fat intake (Mattson and Jonkel 1990). In fact, whitebark pine seeds are the most important fall food source for grizzly bears in Yellowstone, influencing feeding strategies and movements (Blanchard 1990). Grizzly bears access seeds primarily by digging up red squirrel caches (Mattson and Jonkel 1990). During low seed crop years, grizzly bears begin to move to lower elevations where they look for alternative food sources, such as campground trash containers and livestock (Mattson and Jonkel 1990). This results in increased human contact and human-induced grizzly bear mortality (Blanchard 1990).

CHAPTER 3

RESEARCH METHODS

Field Methods

I collected several measurements to assess forest structure, topographic site characteristics, and health of 120 trees within 12 sites. Photos were also taken of each tree from a recorded distance and angle to be used for future reference and to aid in field identification. These photos are held by the Interagency Grizzly Bear Study Team, USGS, Biological Resource Division, Forestry Sciences Lab, Bozeman, Montana.

Cone Counts

Cone count plots were established by the Interagency Grizzly Bear Study Team 9 to 18 years ago. Each plot is composed of 10 mature, cone-producing whitebark pine trees with crowns visible from at least two angles (Morgan and Bunting, 1992). Mature cones were counted annually by the Interagency Grizzly Bear Study Team from late July to early August, before significant predation occurred. Cones were counted from the ground using binoculars, viewing each crown from at least 2 vantage points.

Crown Size

Crown size measurements included two diameter measurements taken at right angles and a crown height measurement (see Tree and Crown Height). Both diameter measurements were made to include the farthest branch reaches. The direction of the diameter measurements for each tree was chosen to best measure the cross-sectional extent of the crown, rather than, for example, adhering to constant compass directions for all trees. A measure of crown area was then calculated by multiplying the two diameter measurements, and a measure of crown volume was calculated by multiplying the two diameter measurements and the crown height measurement. Due to the asymmetric crown shape and the large variation in crown structure in whitebark pine, calculations of crown area were based on a rectangle and calculations of crown volume were based on a hexahedron. Although this method over-estimates crown area and crown volume for each tree (by creating a box into which the entire crown fits), it was chosen because it can be done easily and in a timely manner in the field, thus allowing for continued use in future field assessments of whitebark pine stands.

Stem Size

The diameter at breast height (dbh) was measured for all stems on each subject tree using a standard dbh measuring tape to determine total stem size for each tree. Breast height was approximately 1.4 meters (4.5 feet) from the ground, measured from the uphill side of each stem. Diameter was measured in inches, rounded to the nearest half-inch, and converted to centimeters. Stems were defined as individual trunks within a tree cluster and branches that diverged from any of these trunks below breast height. A measure of total dbh was calculated for each tree by summing dbh measurements for all stems.

Tree Height and Crown Height

Tree height and crown height (used for crown volume calculations) were measured with a Spiegel-Relaskop instrument. Angle measurements were taken from an observation point 15.25 meters (50 feet) from the subject tree to the top of the tree, the bottom of the tree, and the bottom of the crown. Observation points were chosen so that a view of the whole tree was available. By measuring height in terms of feet (+ or -) from horizontal, the Relaskop is able to correct for potential height measurement errors associated with the effect of slope angle on elevation differences between the subject tree and the observation point. Tree height was calculated by subtracting the measured height to the bottom of the tree from the measured height to the top of the tree, and then converting from feet to meters. Similarly, crown height was calculated by subtracting the measured height to the bottom of the crown from the height to the top of the tree.

Age

Using a stem increment borer, a core was taken from each tree that had not been previously cored by the Interagency Grizzly Bear Study Team. Tree cores were taken at breast height, on the uphill side of the tree, from the largest diameter stem. Cores were mounted and growth rings were counted by eye to estimate age. Cores are stored in the Department of Earth Sciences, Montana State University, Bozeman.

Competition

Basal area from competing trees (square meters) surrounding each subject whitebark pine tree was measured with a Spiegel-Relaskop. Basal area is a function of tree diameter and stand density. Using the Bitterlich angle method (Bitterlich 1984), a fixed viewing angle within the Relaskop tool was chosen for each transect based on average stem diameter and the density of trees within the stand. The basal area factor was 20 for stands A, B, F, M, and S, and 40 for stands C, H, P, Q, R, and U. The variation of fixed viewing angles between sites does not affect the validity of comparison between sites (Bitterlich 1984). Each subject whitebark pine was used as a sampling point, and surrounding trees were measured in respect to the chosen fixed viewing angle. All surrounding trees whose stem diameters at breast height were larger than the chosen fixed viewing angle were counted as competing trees. This method includes small, nearby trees as well as large, farther away trees that may be in competition with the subject tree. Multiple stems of whitebark pine that branched below dbh were measured as individual trees. The number of trees counted was multiplied by the basal area factor (BAF), the value associated with the chosen fixed viewing angle, to determine the basal area in square meters of the competing trees.

Understory Composition

Understory was described by ocular estimation as percent of grass, forbs, woody shrubs, small trees, rock, dead wood, and bare ground within a 5-meter radius (16.4 feet) of each tree. The understory species composition was not recorded.

Topographic Site Characteristics

Elevation, slope aspect, and slope angle were measured and recorded by the Interagency Grizzly Bear Study Team at the time of transect establishment. Aspect was transformed into degrees from east to west (08 to 1808) and degrees from north to south

(08 to 1808) for separate regression analyses. No additional topographic site characteristics were recorded in the field.

Health

The relative health of the trees was described in terms of the amount of blister rust infection, amount of beetle infestation, and the presence, size, and type of visible scar such as animal damage, mechanical damage, or fire damage. Blister rust was identified using a field guide by Hoff (1992). The presence/absence of advanced stem cankers was noted, as well as the number of branches (flags), large and small, with infected (red) needles. Within the subset of infected branches per tree, the estimated percentage of infected needles was recorded. The relative evidence of beetle infestation was rated on a 0 to 3 scale where 0 was no evidence, 1 was evidence of bore holes, 2 was bore holes and pitch tubes obvious and numerous, and 3 was a browning crown with bore holes and pitch tubes. Scars were measured in length and width to determine area, and were described as animal damage, mechanical damage (ex. caused by falling trees or branches), or fire damage. Observations were supported by visual evidence from the surrounding environment, such as claw marks from bears, other fire scars on surrounding trees, or fallen trees adjacent to subject trees.

Analysis Methods

Development of Cone Production Indices

Average cone production from the Interagency Grizzly Bear Study Team data set was used as one measure of cone productivity. Due to large variations between trees in quantity and periodicity of cone production, averages for each tree and each plot were calculated based on the 9 years (1989-1997) of cone count data that all trees and plots had in common. This was necessary because cone production in whitebark pine can vary significantly from year to year. Using a different time series for some trees may give them a better chance of producing a large cone crop, thus elevating mean cone production for those trees beyond trees with a shorter cone count record. The opposite could also be true if the extended cone record included many years of poor cone record.

Whitebark pine is generally considered a masting species. However, some trees may produce cones more consistently, thus exhibiting less typical masting behavior than others. From a short-term perspective of grizzly bear management, higher value might be placed on non-masting, consistent cone producing trees, which provide a reliable fall food source for bears. In the long term, however, masting trees that swamp seed predator populations are more effective for whitebark pine regeneration. In order to account for both varying quantity and periodicity of cone production within the 9 years of cone production, a cone productivity index that attempts to treat masting and non-masting trees equally was developed in consultation with the Statistical Consulting Services, Department of Mathematical Sciences, Montana State University (Eva Marquez, Courtney Kellum, Dr. John Borkowski, and Dr. Jim Robison-Cox). This index was based on a modified process capability ratio. These ratios are commonly used in industry for monitoring the variability in production processes (Kotz and Lovelace 1998). The productivity index is:

$$PI = P_{0.5} / (P_{0.5} - P_{0.00135})$$

where PI is the productivity index for each tree, $P_{0.5}$ is the median of annual cone production for each tree, and ($P_{0.5}$ - $P_{0.00135}$) is a measure of the variability in cone production. Both measures are based on the fitted Weibull distribution curve of the annual cone production data for each tree. The Weibull distribution was used because the non-normality of the cone data required a flexible family of distributions to fit the data for each tree (Montgomery 1997). The shapes and probabilities associated with these distributions reflect smoothed versions of the trees' cone production processes, thus allowing for the calculations of more accurate values for median and measure of variability. The measure of variability was specifically chosen to represent the lower half of the cone production data ($\leq$0. 5) so that trees with a high variability of cone production above the median were not penalized. This equation was developed such that trees with a high variability below the median and a high proportion of zero cone years are penalized (i.e. are designated as poorer producers) and trees with lower variability and fewer zero cone years are benefited (i.e. are designated as better producers). Therefore, trees with lower means that produce cones fairly consistently may have similar PI values to trees that have a much higher mean but do not produce regularly.

Regression Analyses

I performed a regression analysis between forest structure data and the two measures of cone production (average cone production and the cone productivity index) on 103 trees from 11 plots (from the original 120 trees from 12 plots, site J was removed from analyses due to heavy incidence of blister rust, and within the remaining 110 trees, A6 and C4 are dead, and F3, F5, H9, and H10 are missing data). Using SAS statistical software (SAS Institute 1994), two separate analyses were carried out using the average cone production and the productivity index as dependent variables. For each analysis, simple regressions were performed between cone production and forest structure measurements and were evaluated at the 0.05 significance level. Forest structure data included crown size (area and volume), total dbh, number of stems per tree, tree height, tree age, total basal area of competing trees, basal area of whitebark pine, subalpine fir, and Engelmann spruce, and understory composition. All data, including dependent and independent variables, were centered and scaled (standardized) in order to reduce variations of scale between variables. For example, when comparing crown volume, whose scale ranges from 262 to 126,900, with total dbh, whose scale ranges from 8 to 95, difficulties in interpretation will arise as a result of large differences in scale. Centering and scaling helps to more accurately determine collinearity between independent variables and significance of independent variables in multiple linear regression models (Borkowski, pers. comm. 1999), and is recognized as the appropriate procedure when multiple linear regression models include interactions between variables and/or squared variables (Myers 1986). Centering and scaling were accomplished by finding the mean and standard deviation for all trees for each variable and calculating a new value for each tree as shown below:

$$A_1 = (A - \text{mean}) / \text{standard deviation}$$

where A_1 is the centered and scaled transformation for a given variable for an individual tree (ex: crown volume for tree Q4), A is the raw value for the same variable and tree, and the mean and standard deviation are calculated from raw data of the given variable from all trees. Centering and scaling do not change rank or value of each tree with respect to other trees.

Multiple linear regression models were developed for both measures of cone production (average and productivity index) using centered and scaled field data as explanatory variables. I used a stepwise selection procedure (Myers 1986) in choosing explanatory variables for models. This method is a combination of forward selection and backward selection procedures. It adds explanatory variables in the order of most influence to least influence, and considers whether there is any variable that should be deleted at every step. Final models were chosen based on supporting literature, multiple R-squared values, significance of explanatory variables at the 0.05 level, and lack of multicollinearity. Centered and scaled data were used for model development but were back-transformed to raw data scales for ease of application.

CHAPTER 4

RESULTS AND DISCUSSION

Whitebark Pine Cone-Count Data

The cone count data collected by the Interagency Grizzly Bear Study Team show that cone production for individual whitebark pine trees is spatially and temporally variable (Figure 3, Table 2). No patterns of cone production are evident across the study sites. The 9-year mean production of cones per tree per site varied from 3.7 to 24.6 among sites. Annual average cone production for trees within sites varied from 0 to 95 cones. Each site had years with zero cone production, confirming that whitebark pine is predominately a masting species. However, some trees produced more consistently over time, suggesting variation in this masting strategy. Trees in site U, for example, produce cones more consistently than other stands. These results encouraged the development of the productivity index to account for both quantity and periodicity in cone production. As previously mentioned, the intention of this index was to give near-equal values to masting trees and consistent cone-producing trees with similar average cone productions. However, tree F6 (range of 0 to 200) and U3 (range of 0 to 56) had similar means (30.67

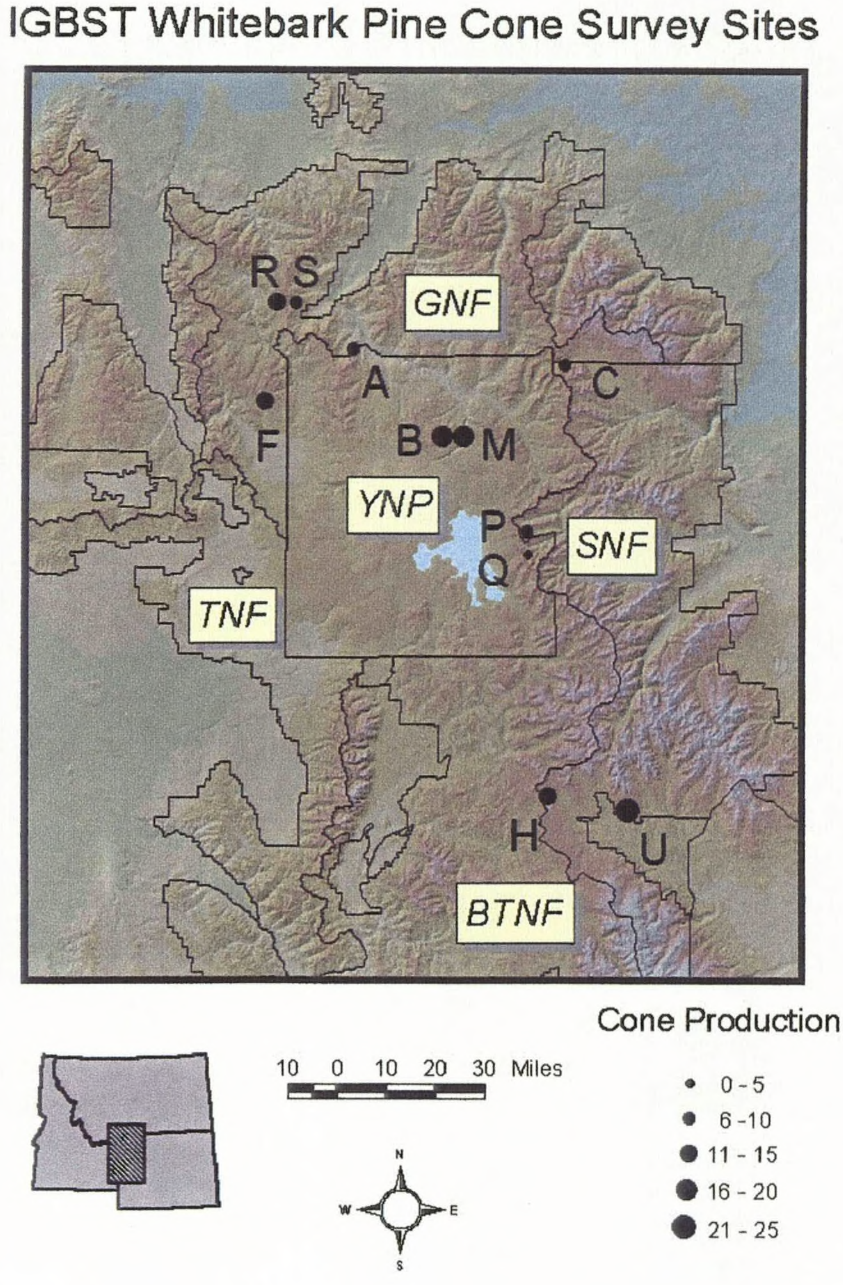

Figure 3: Map of 9-year mean production of cones per tree per site. Locations for sites R, S, B, M, P, and Q have been altered to avoid overlapping symbols.

YNP = Yellowstone National Park
GNF = Gallatin National Forest
TNF = Targhee National Forest
SNF = Shoshone National Forest
BTNF = Bridger-Teton National Forest

and 32.78, respectively), but quite different rankings (42 and 1 respectively) (Appendix A). Also, tree M9 (range of 0 to 325; mean of 80.33) ranked number 12. Thus, results of the cone productivity index did not characterize quantity and periodicity of cone production.as well as expected.

Tree M9 stands apart from other trees on all plots due to its considerably higher average cone production (80.3 cones/year). Although this tree is an outlier, it was kept in the analysis because its anomalies are due to biological differences, rather than error associated with measurement. However, this tree had a strong influence on slopes of regression lines (Appendix B). Additionally, the cone production data did not have a normal distribution (Figure 4). Therefore, the log transform of average cone production was used as the response variable in order to normalize the cone production data and effectively reduce the difference between cone production for M9 and the rest of the sample trees (Figure 5).

Table 2: Summary of average annual cone production for trees in each of the 11 sampled sites, and average cone production for trees per site per year from 1989 to 1997.

	Avg. Cones	1989	1990	1991	1992	1993	1994	1995	1996	1997
A	7.5	0.8	0.0	9.3	16.7	6.8	0.4	0.0	32.7	0.6
B	17.8	55.3	2.4	36.2	15.8	6.0	0.0	0.5	43.9	0.0
C	7.6	17.4	0.0	29.5	4.5	0.9	0.2	0.0	15.7	0.4
F	14.1	95.0	1.2	9.5	13.1	0.0	0.0	2.4	5.7	0.1
H	11.9	15.1	0.0	21.1	6.6	16.3	3.9	3.4	22.4	18.0
M	19.8	73.7	2.8	22.6	26.4	4.9	0.0	0.2	47.7	0.0
P	8.3	16.1	0.0	10.2	7.7	10.8	0.3	0.7	27.6	1.3
Q	3.7	8.3	0.0	11.0	1.9	5.6	0.0	1.5	4.2	0.8
R	13.7	22.9	0.3	11.4	17.0	19.1	0.0	0.0	52.7	0.0
S	8.2	35.3	0.0	1.3	18.4	3.3	0.0	0.6	15.3	0.0
U	24.6	28.3	0.0	36.6	14.7	30.4	24.4	27.7	29.8	29.2

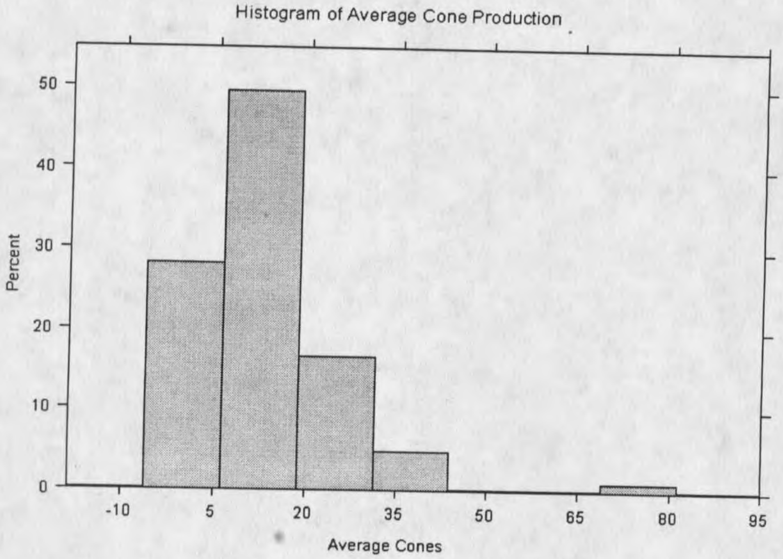

Figure 4: Histogram of average cone production for the 103 whitebark pine trees used in regression analyses.

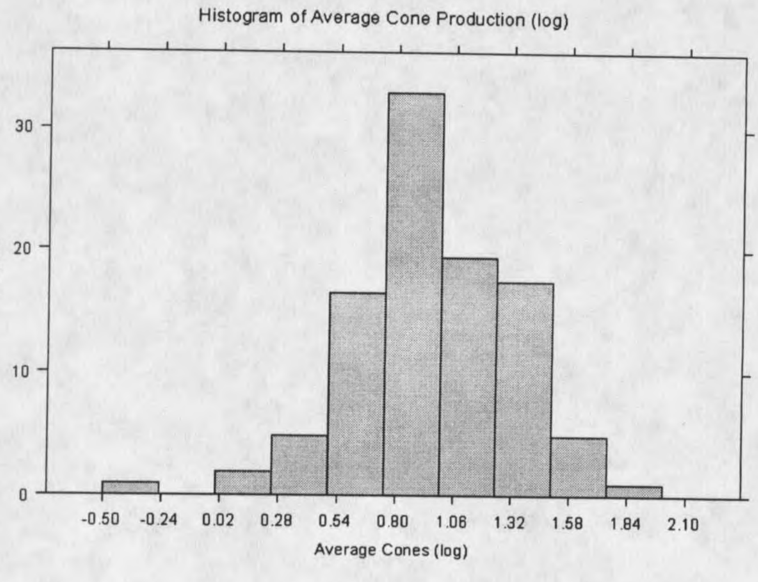

Figure 5: Histogram of the log transform of average cone production for the 103 whitebark pine trees used in regression analyses.

Simple Regression Analyses

The first objective for this research was to determine which forest structure characteristics are associated with cone production for individual whitebark pine trees. Forest structure measurements used in the analyses included crown area and volume, stem size, number of stems, tree height, tree age, competition from adjacent trees (basal area), and understory composition. Log transform of average number of cones was used as a simple measure of productivity, whereas a production index was used in an attempt to capture variability. However, results of regressions were better with the log of average cone production than with the productivity index. Thus, this discussion focuses on results of simple and multiple regression analyses of forest structure characteristics against the log of average cone production. All results of simple and multiple regression analyses are reported using raw data (i.e. not centered and scaled).

Crown Size

Crown size, measured in terms of crown area and crown volume, are correlated to log of average cone production substantially more than any other variable. Crown area explained 30 % of the variation in cone production ($p = 0.00$) and crown volume explained 25 % ($p = 0.00$) (Table 3). The z-test of the difference from the slope of the regression line for area (slope = 0.0055; S.E. = 0.0008) and for volume (slope = 0.0003;

S.E. = 0.0001) from a slope of zero are 6.9 and 3.0, respectively. These values are greater than 1.96, which is the critical value for determining significant difference (at 95% confidence level) of slopes of regression lines from zero. The slopes of the regression lines indicate that as crown area increased, cone production increased (Figure 6), and similarly, as the crown volume increased, cone production increased (Figure 7), supporting hypothesis 1A. These results supported similar findings suggesting that cone production was usually dependent upon crown size (Fowells 1965; Shearer 1986; Wenger and Trousdell 1958). This is a result of more fertile shoots per tree (Weaver and Forcella 1986). Crown size was expected to influence cone production because it represents photosynthetic potential.

Table 3: R^2 values for the log transform of average cones (Log Cones) and forest structure measurements with associated p-values.

Measure	Log Cones R^2	p-values
Crown Area	0.30	0.00
Crown Volume	0.25	0.00
Total DBH	0.04	0.05
Number of Stems	0.00	0.82
Total Tree Height	0.00	0.89
Age	0.01	0.40
Total Basal Area	0.10	0.00
Whitebark Pine Basal Area	0.05	0.03
Subalpine Fir Basal Area	0.01	0.30
Engelmann Spruce Basal Area	0.01	0.44
% Forbs	0.02	0.15
% Small Trees	0.01	0.30
% Shrubs	0.01	0.40
% Rocks	0.01	0.39
% Dead Wood	0.01	0.38
% Grass	0.00	0.82
% Bare Ground	0.00	0.58

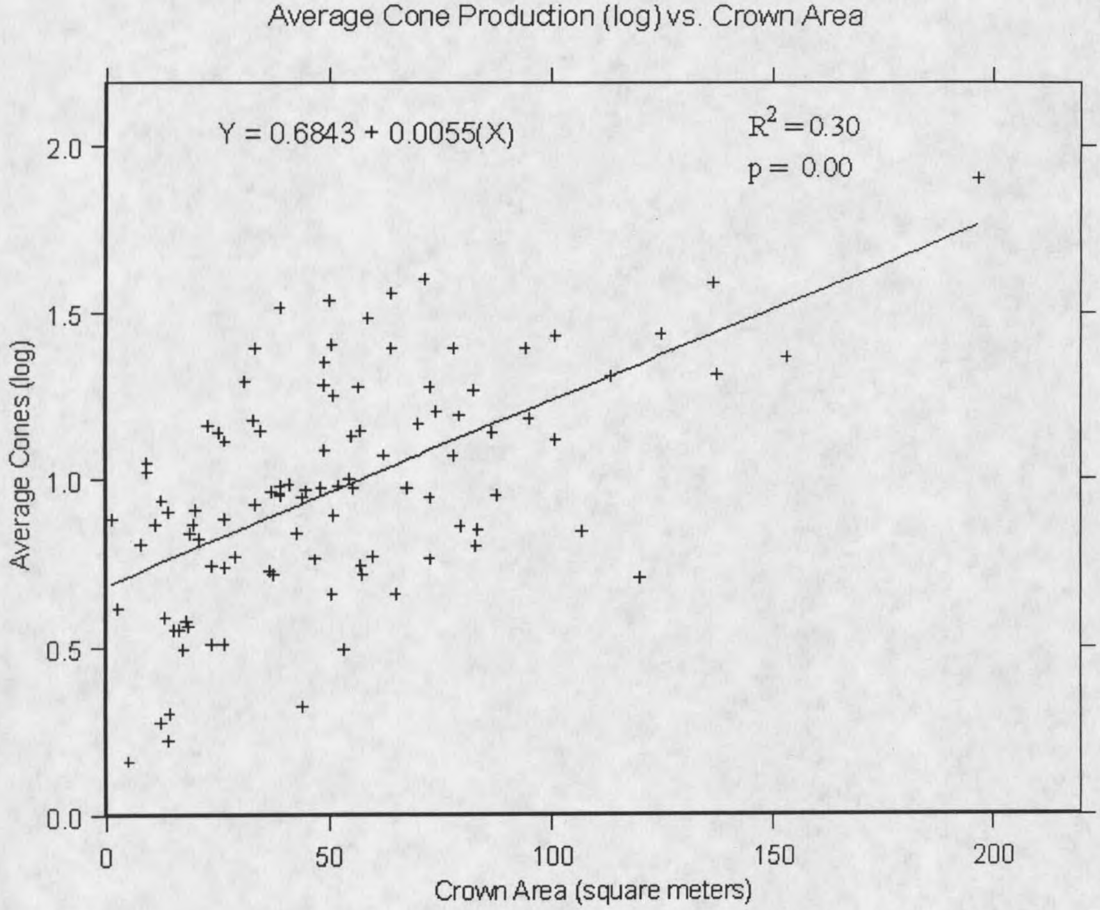

Figure 6: Scatterplot of crown area and log transform of average cone production of whitebark pine.

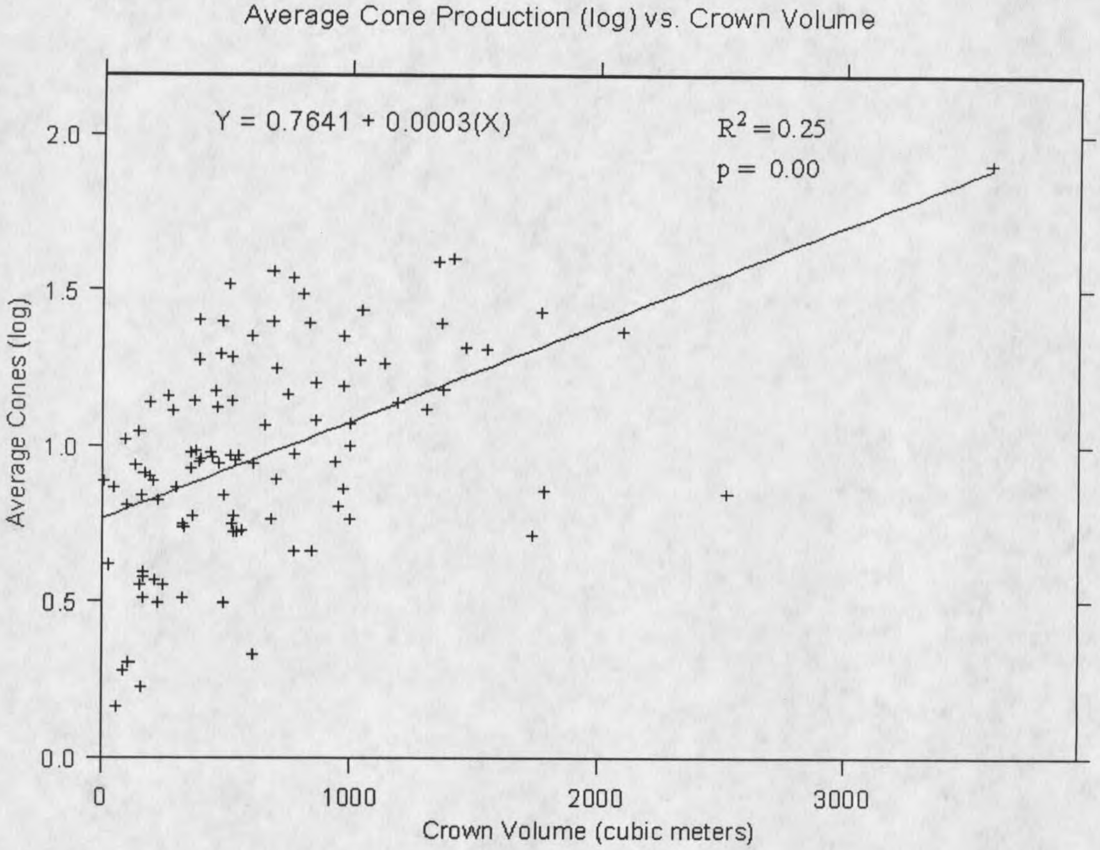

Figure 7: Scatterplot of crown volume and log transform of average cone production of whitebark pine.

Stem Size and Number

Stem size, as measured by total dbh, explained only 4 % (Table 3; Figure 8) of the variation in the log of average cone production, but is significant at the 95% confidence level ($p = 0.05$). The slope of the regression line (slope = 0.0021; S.E. = 0.0010) is significantly different than zero ($p \leq 0.05$), with a z-test value of 2.1, which is greater than the critical value of 1.96. This relationship suggests that cone production increases as stem size increases, supporting hypothesis 1B. Previous studies of single-stemmed trees suggested a relationship between stem size and cone production in red pine (Godman 1962; Stiell 1988), loblolly pine (Pomeroy 1949; Wenger and Trousdell 1958), Douglas fir and western larch (Shearer 1986). The relationship between stem size and cone production was not as evident in whitebark pine. It was likely due to frequent occurrences of multiple-stems, perhaps resulting in competition among multi-genet stems (Feldman et al. in press).

Stem number within the sample trees ranged from 1 to 6. There was no relationship between the number of stems and the log of cone production ($p = 0.82$; $R^2 = 0.0$) (Table 3; Figure 9).

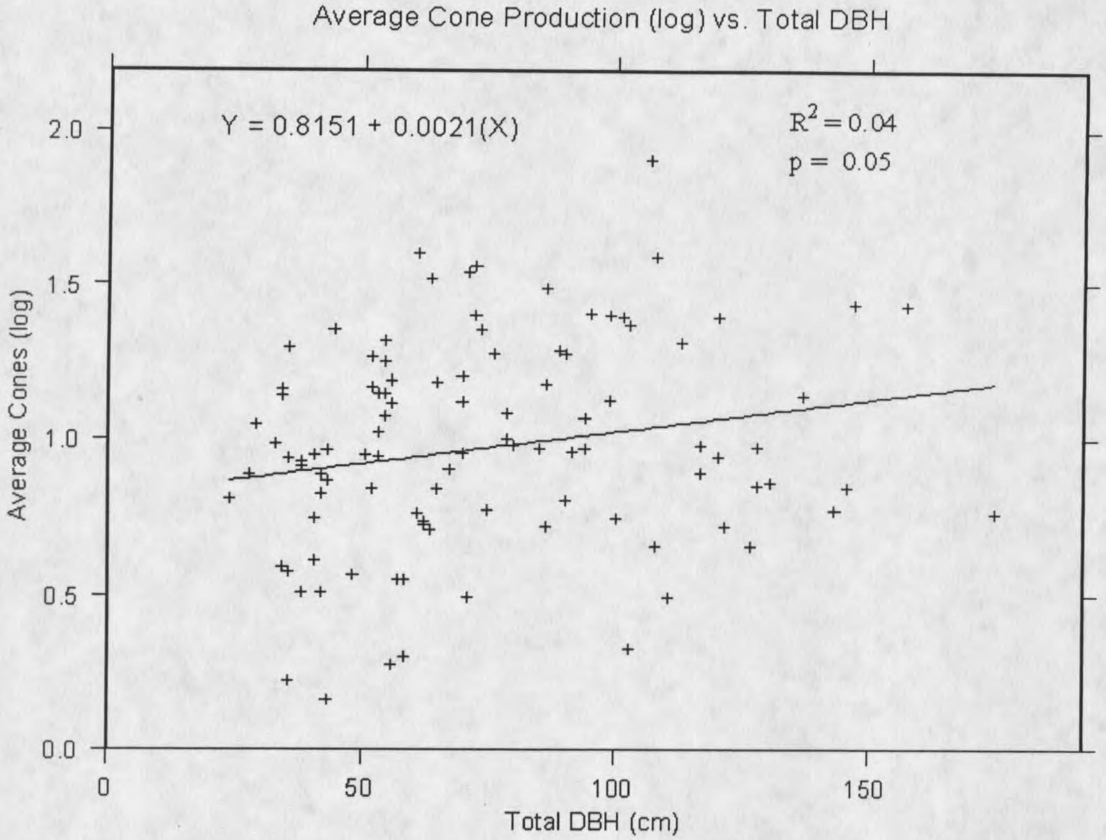

Figure 8: Scatterplot of total dbh and log transform of average cone production of whitebark pine.

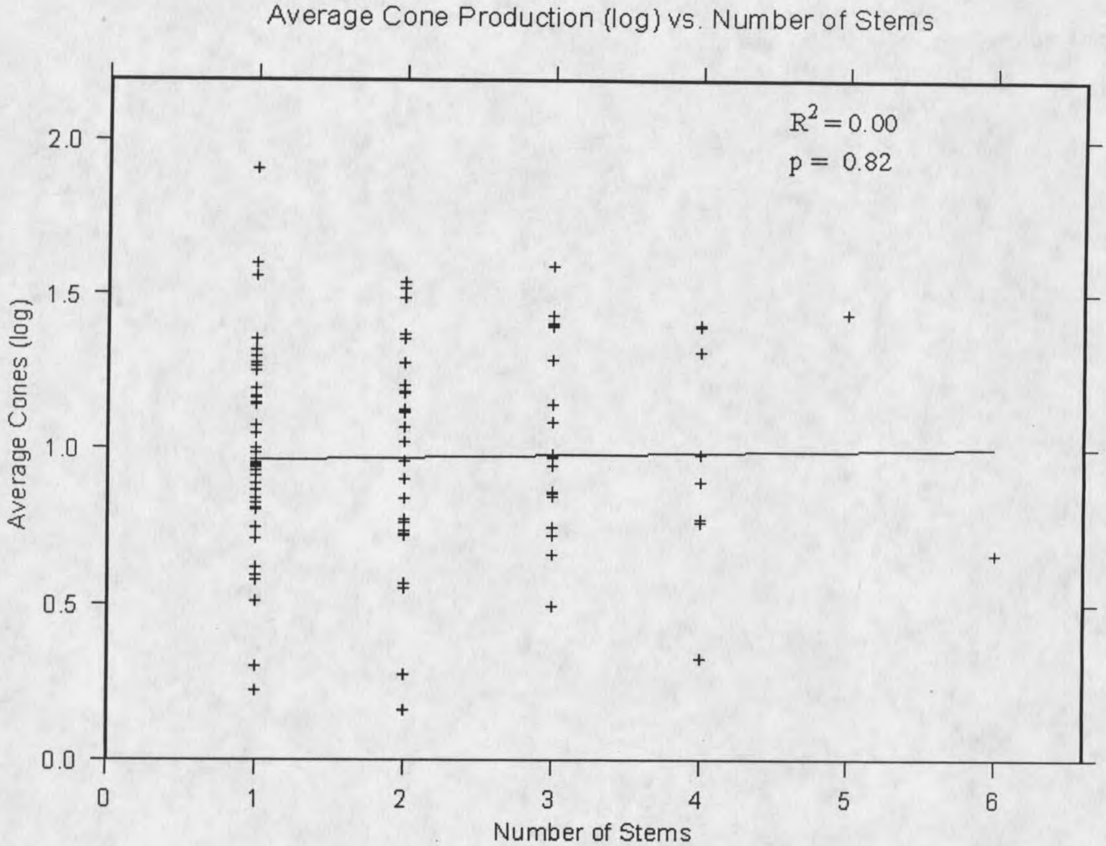

Figure 9: Scatterplot of number of stems and log transform of average cone production of whitebark pine.

Tree Height

Regression analysis between the log of average cone production and total tree height was nonsignificant ($p = 0.89$; $R^2 = 0.0$) (Table 3; Figure 10). These results do not support hypothesis 1D (taller trees have increased cone production). Ying and Illingsworth (1986) found that tall lodgepole pine have higher cone production. Lodgepole pine typically grows in dense stands where tall trees may have a photosynthetic advantage over shorter trees. In the whitebark pine stands in this study, however, density (as measured by basal area) was low, and height may not result in a photosynthetic advantage.

Age

Age had no influence on the log of average cone production ($p = 0.40$; $R^2 = 0.01$) (Table 3; Figure 11), as proposed in hypothesis 1E. This supports results from Weaver and Forcella (1986) which showed overall stand age to be unrelated to cone production. Additionally, it must be noted that all trees selected for this study were mature and capable of cone production.

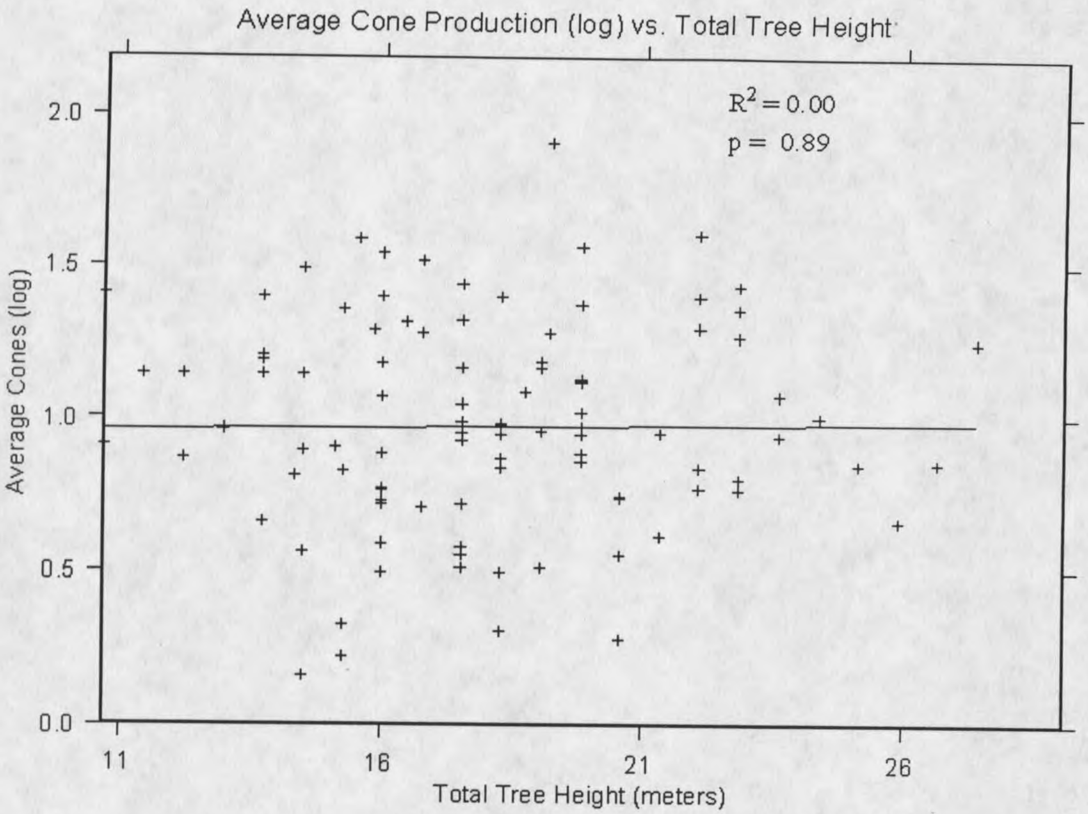

Figure 10: Scatterplot total tree height and log transform of average cone production of whitebark pine.

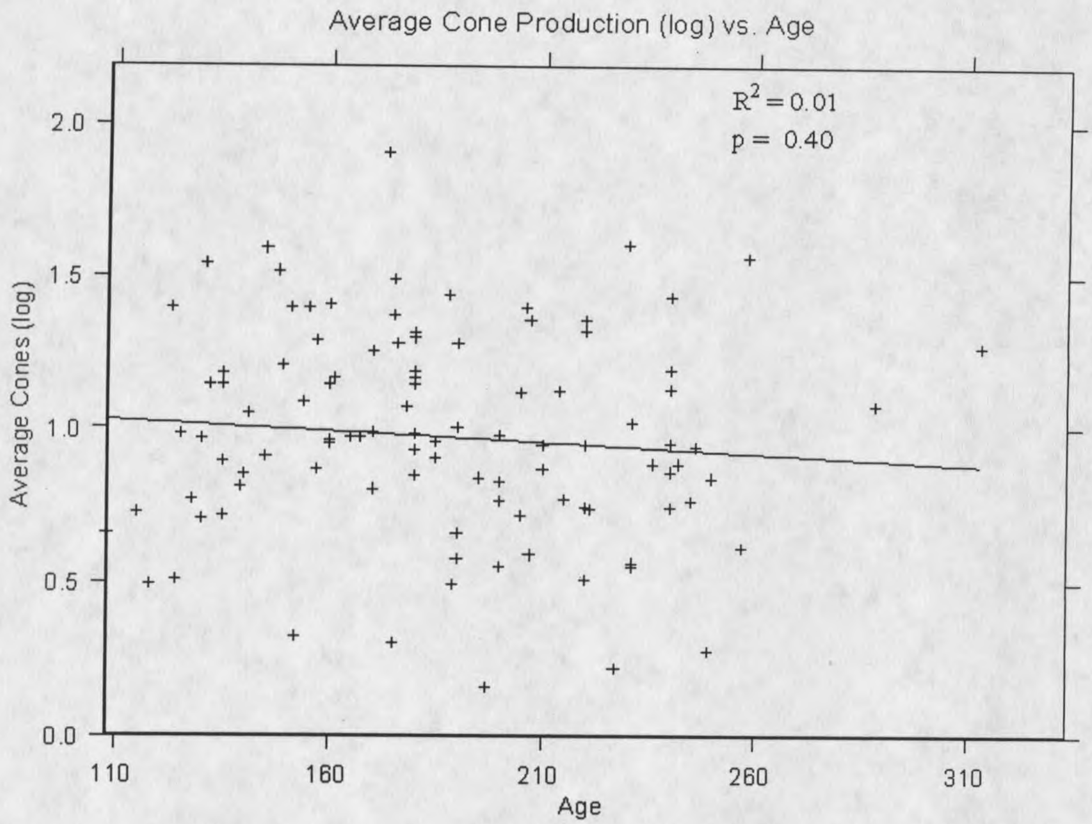

Figure 11: Scatterplot of age and log transform of average cone production of whitebark pine.

Competition

Regression with competition (R^2= 0.10), as measured by total basal area of competing trees, had a p-value of 0.00 (Table 3; Figure 12). The z-test value is 3.4, which is greater than 1.96, indicating the slope of the regression line (slope = -0.0188; S.E. = 0.0035) is significantly different (p [0.05) from zero. This relationship suggests that as competition increases, cone production decreases, thus supporting hypothesis 1F. However, this relationship was not as strong as expected, which could either be due to low stand density or to inappropriate use of basal area for measuring competition. Basal area is a function of both stem diameter and stand density. Trees in subject sites were widely spaced, and in most sites, the canopy was open. Cone production was more affected in denser, closed canopy stands, where shading influences crown size and shape (Khomentovsky 1994; Overton and Johnson 1984; Schmidt 1997; Shearer 1986; Shearer and Schmidt 1987; Stiell 1988). Regressions were also done with competing whitebark pine, subalpine fir, and Engelmann spruce (represented as subsets of total basal area). Whitebark pine had the only significant relationship with the log of average cone production (p = 0.03; R^2 = 0.05), with the slope of the regression line significantly different than zero (z-test value is 2.3) (Table 3; Figure 13). Subalpine fir and Engelmann spruce were non-significant (p = 0.30, 0.44; R^2= 0.01, 0.01, respectively) (Table 3; Figures 14 and 15). However, basal area may not accurately represent competition because it does not consider the influence of shading from surrounding trees. Further, this measurement may not accurately represent trees that are competing for water or nutrients.

For descriptive purposes, basal area measurements of competing trees were averaged for each stand and described as percent whitebark pine, subalpine fir, and Engelmann spruce, giving estimates of stand composition. Most of the competing trees were whitebark pine (from 41% to 98% of competition) and subalpine fir (2% to 47%). Engelmann spruce was determined to be in competition only in 5 study sites and as a considerably smaller component (0% to 23%) (Table 4).

Understory Composition

Understory composition was described as a percent of forbs, small trees, shrubs, rocks, dead wood, grass, and bare ground. All understory classes were regressed against average cone production (Table 3; Figures 16-22, respectively), and were insignificant. These results do not support hypothesis 1G (understory influences cone production). The lack of significance associated with these results may be a consequence of error associated with data collected by ocular estimation. Previous research suggests that understory plants often compete for resources with overstory trees (Perry 1994). For descriptive purposes, understory composition was averaged for each site (Table 5). Understory species composition was not recorded.

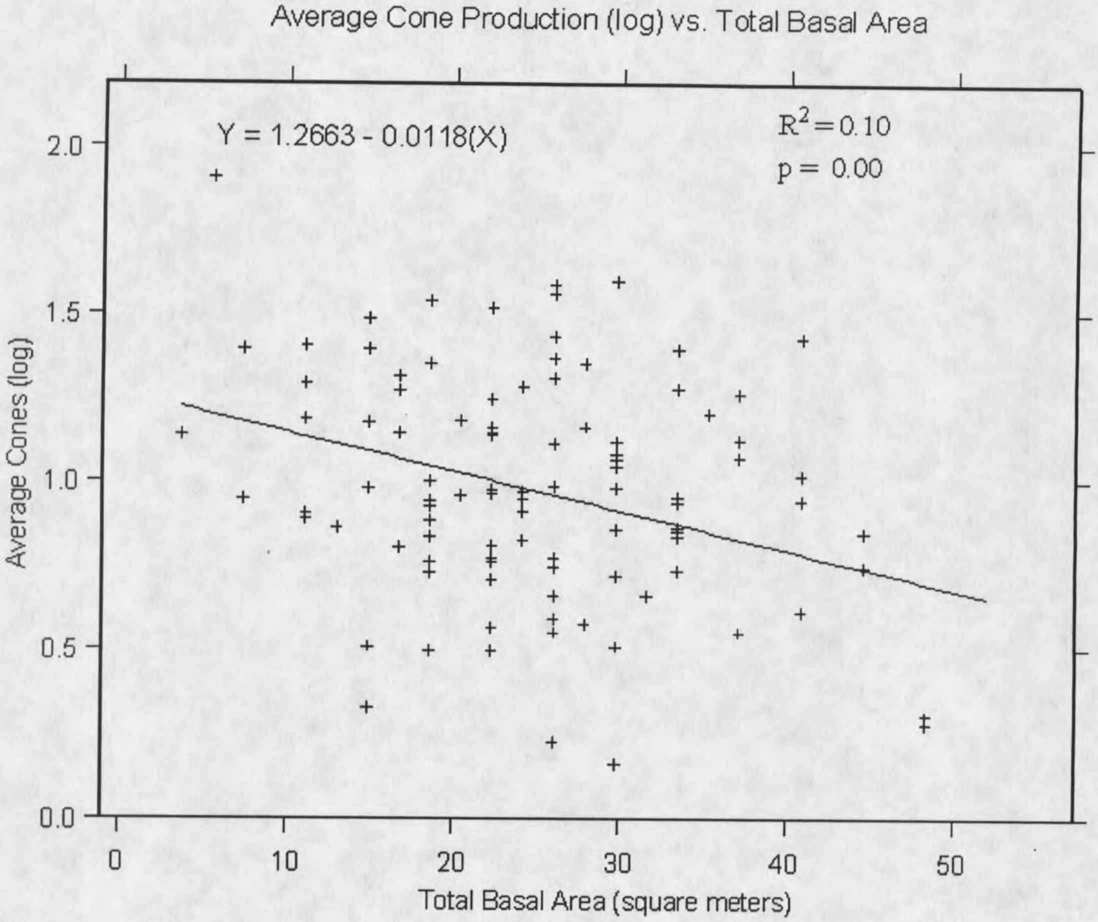

Figure 12: Scatterplot of total basal area of competing trees and log transform of average cone production of whitebark pine.

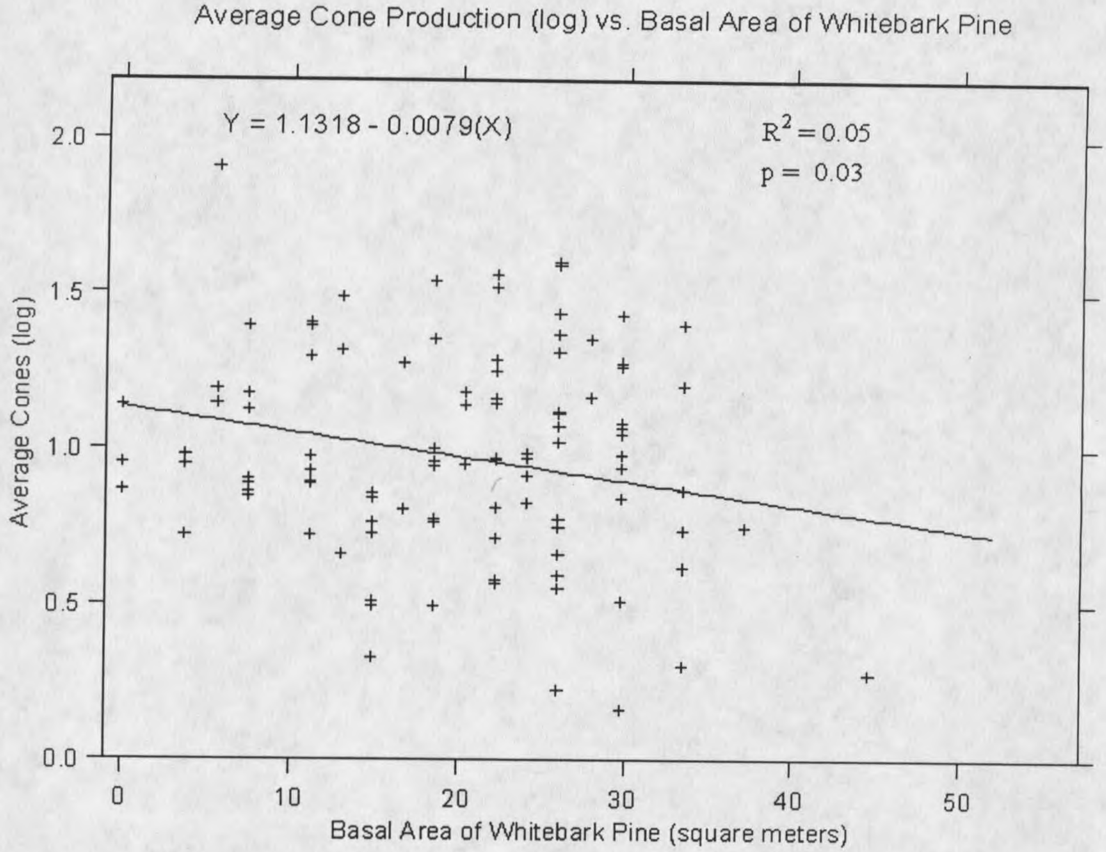

Figure 13: Scatterplot of basal area of competing whitebark pine and log transform of average cone production of whitebark pine.

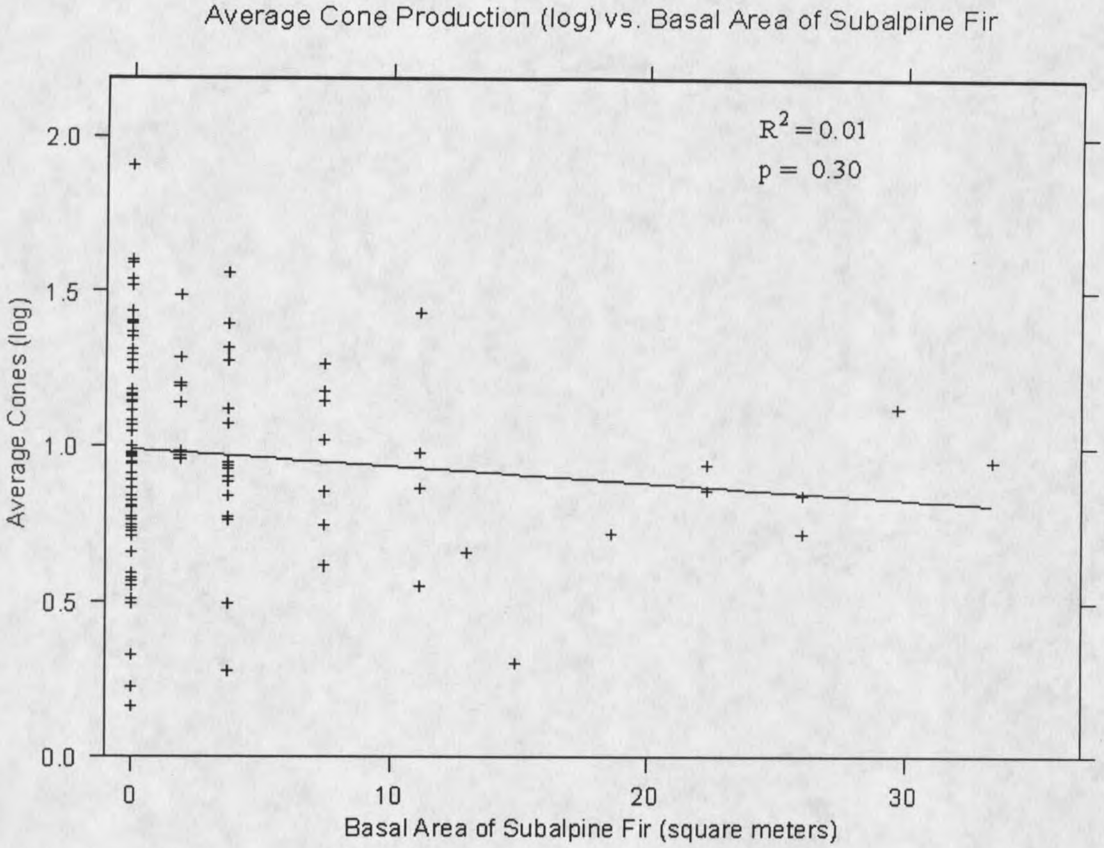

Figure 14: Scatterplot of basal area of competing subalpine fir and log transform of average cone production of whitebark pine.

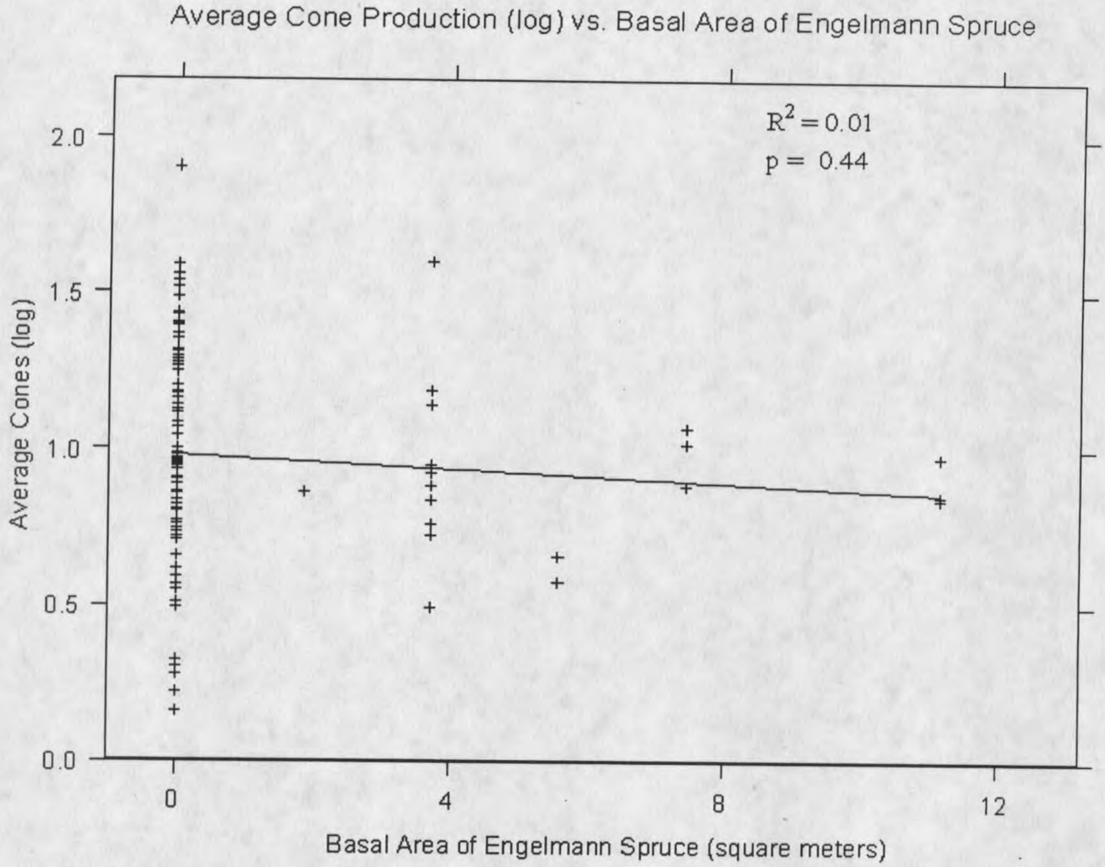

Figure 15: Scatterplot of basal area of competing Engelmann spruce and log transform of average cone production of whitebark pine.

Table 4: Average basal area for 10 subject whitebark pine trees (with range) per site and percent of that basal area of whitebark pine (WBP), subalpine fir (SAF), and Engelmann spruce (ENSP).

SITE	BASAL AREA SQ. METERS	% BASAL AREA WBP	% BASAL AREA SAF	% BASAL AREA ENSP
A	23 (17-30)	98%	2%	0%
B	27 (20-33)	98%	2%	0%
C	27 (7-48)	67%	33%	0%
F	21 (11-28)	97%	3%	0%
H	20 (15-26)	81%	13%	6%
M	23 (6-35)	97%	3%	0%
P	35 (19-48)	79%	14%	7%
Q	30 (22-52)	94%	3%	3%
R	29 (4-45)	41%	47%	10%
S	20 (11-32)	57%	20%	23%
U	20 (7-33)	96%	4%	0%

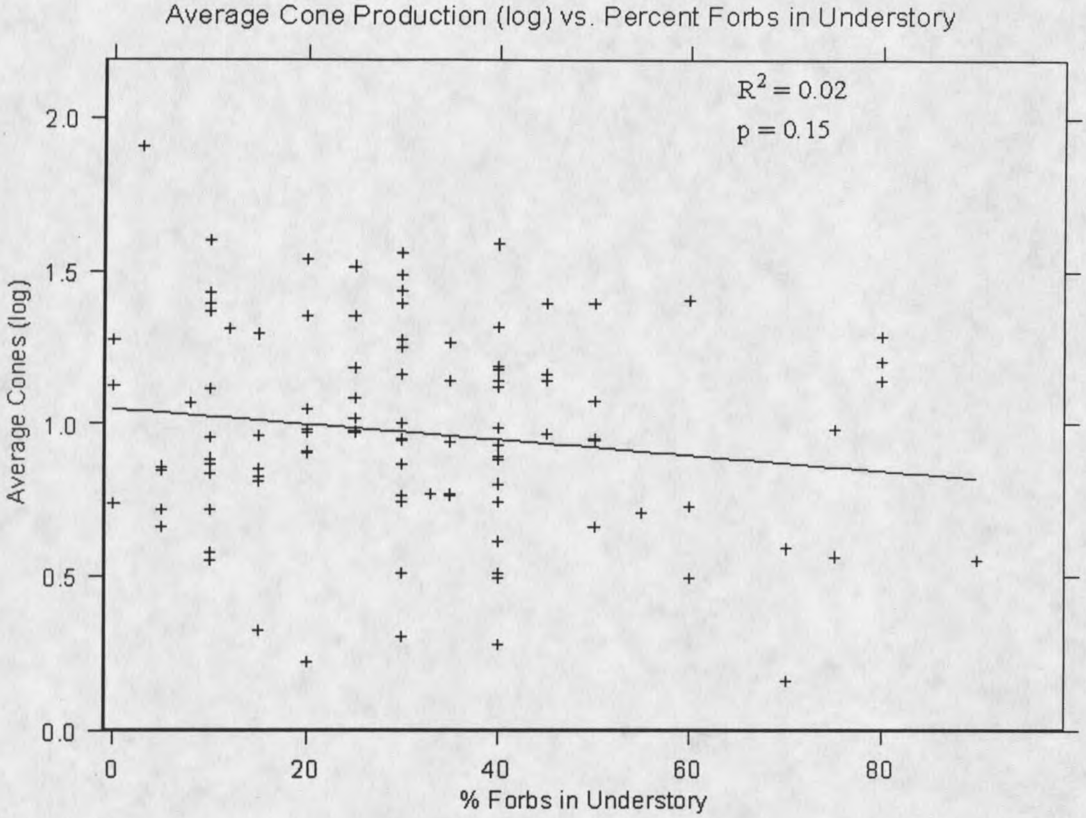

Figure 16: Scatterplot of percent forbs in understory and log transform of average cone production of whitebark pine.

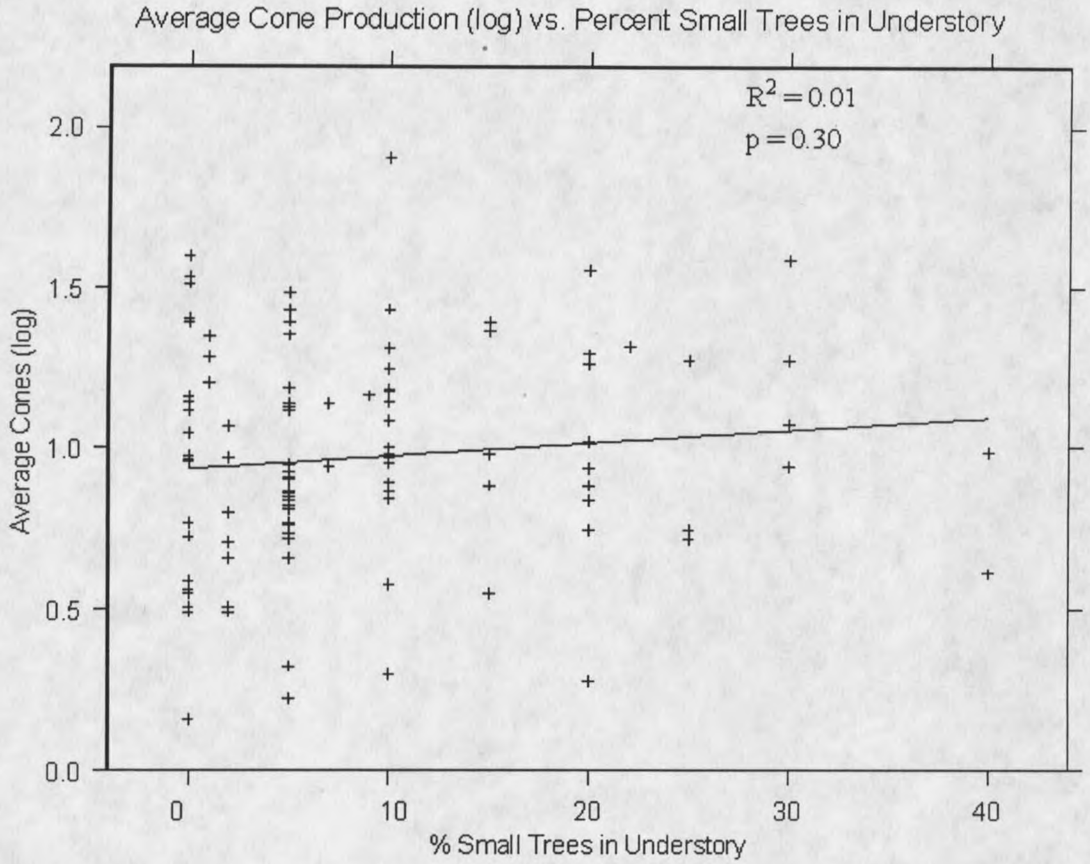

Figure 17: Scatterplot of percent small trees in understory and log transform of average cone production of whitebark pine.

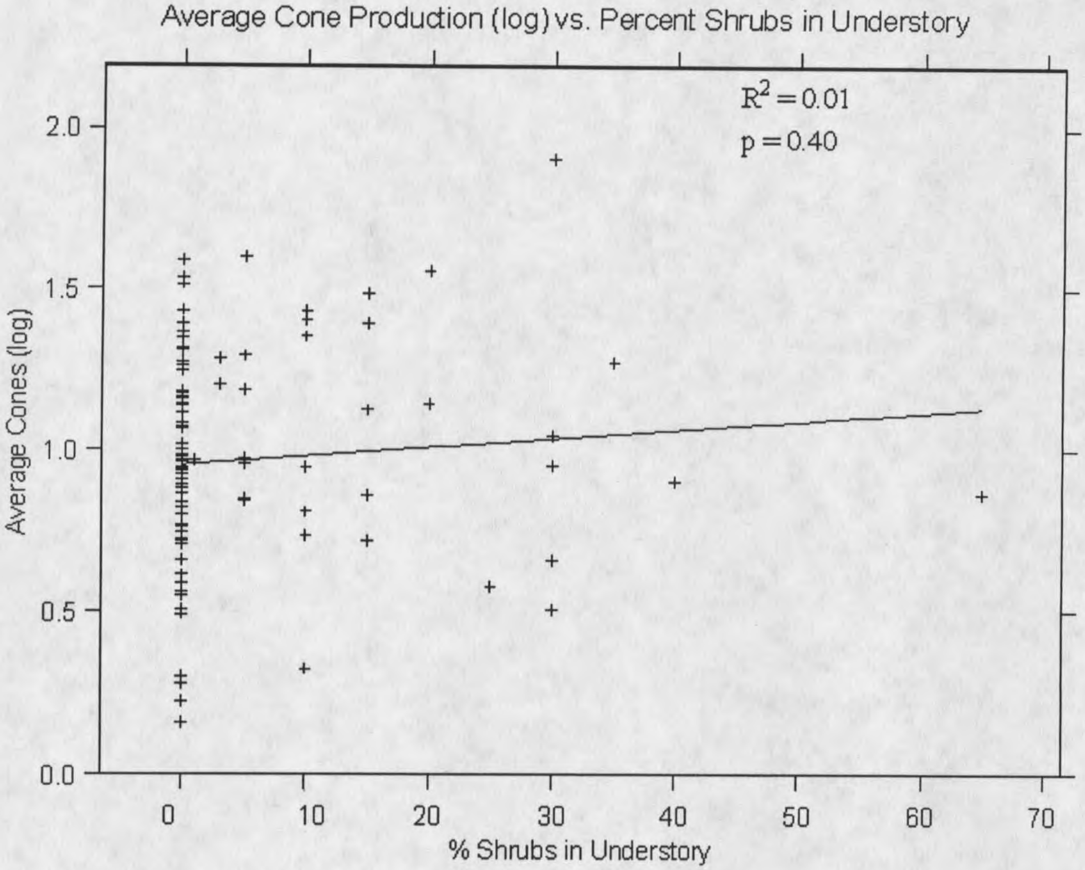

Figure 18: Scatterplot of percent shrubs in understory and log transform of average cone production of whitebark pine.

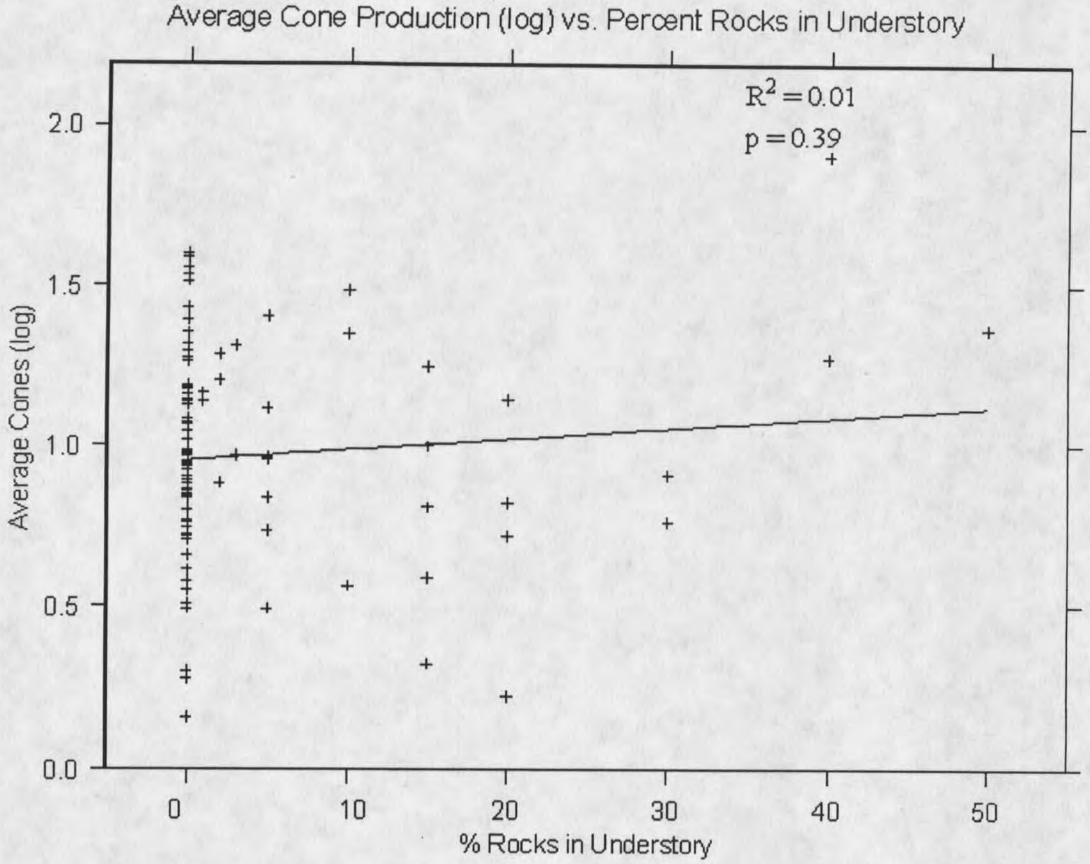

Figure 19: Scatterplot of percent rocks in understory and log transform of average cone production of whitebark pine.

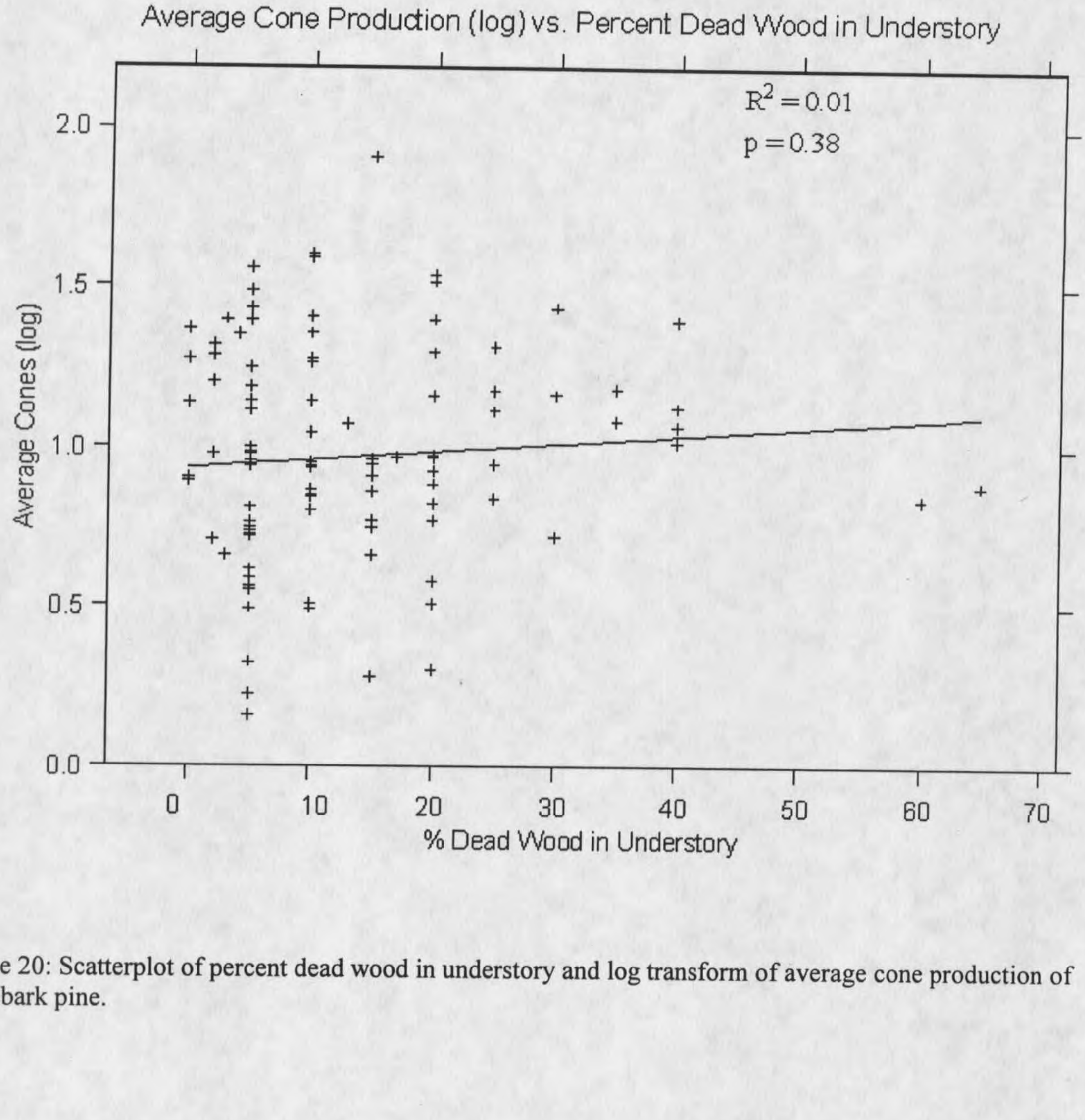

Figure 20: Scatterplot of percent dead wood in understory and log transform of average cone production of whitebark pine.

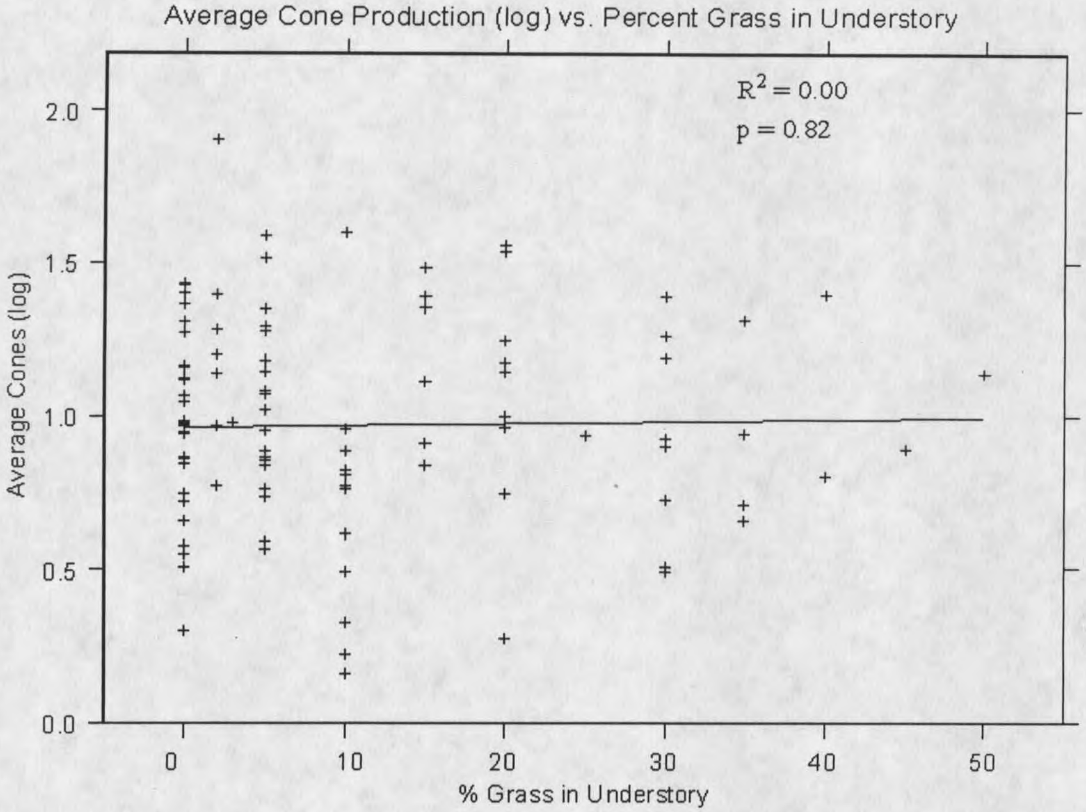

Figure 21: Scatterplot of percent grass in understory and log transform of average cone production of whitebark pine.

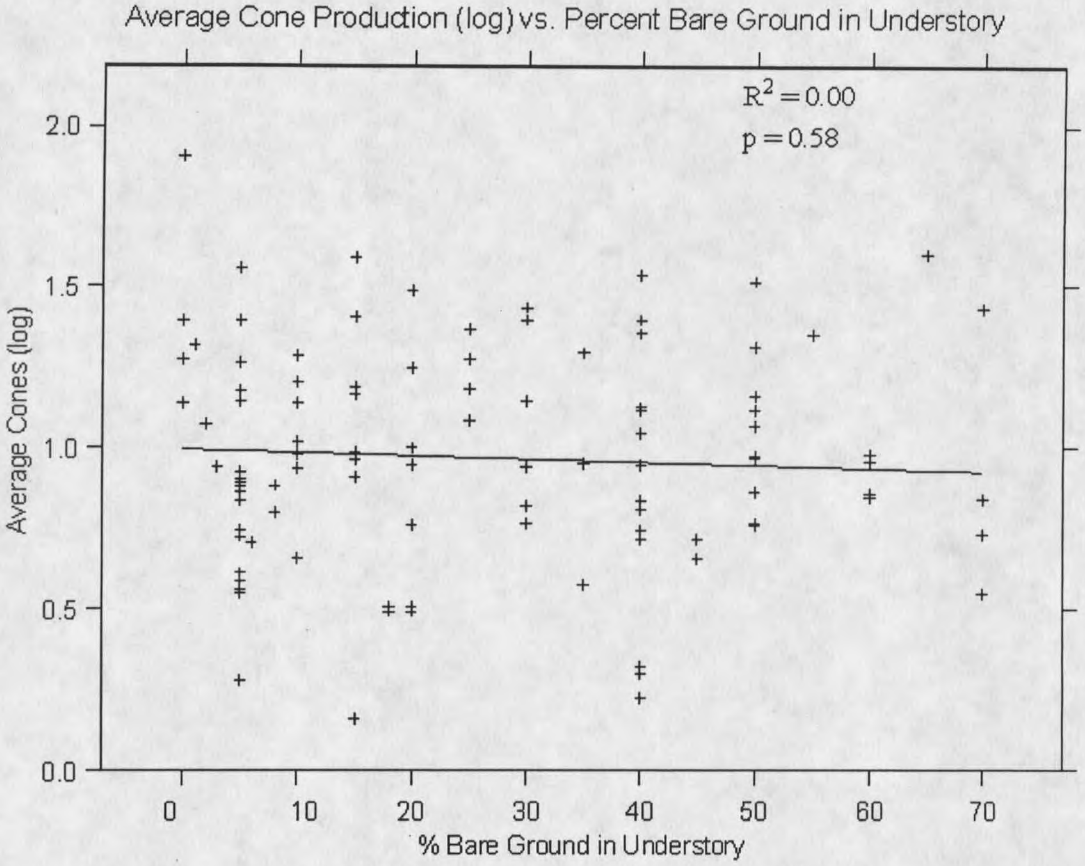

Figure 22: Scatterplot of percent bare ground in understory and log transform of average cone production of whitebark pine.

Table 5: Understory composition classes averaged (with range) for 10 subject trees at each site.

SITE	% FORBS	% GRASS	%WOODY SHRUBS	% SMALL TREES	% DEAD WOOD	% ROCKS	% BARE GROUND
A	47 (33-75)	27 (2-40)	0 (0)	5 (0-22)	7 (2-15)	0 (0)	14 (1-50)
B	26 (8-45)	2 (0-5)	0 (0)	15 (2-40)	25 (5-40)	1 (0-3)	32 (15-50)
C	22 (10-30)	0 (0)	3 (0-30)	16 (0-30)	11 (0-25)	8 (0-50)	41 (20-70)
F	33 (15-60)	12 (0-20)	4 (0-15)	2 (0-5)	10 (4-20)	13 (5-30)	26 (15-55)
H	33 (10-40)	18 (10-30)	0 (0)	7 (5-10)	18 (5-35)	7 (0-31)	16 (0-40)
M	33 (0-80)	4 (0-10)	10 (0-35)	7 (1-25)	7 (0-20)	13 (0-40)	27 (0-50)
P	32 (10-50)	14 (5-30)	0 (0)	23 (15-40)	26 (5-65)	0 (0-2)	6 (2-10)
Q	62 (0-90)	4 (0-10)	0 (0-10)	1 (0-5)	5 (5)	7 (0-20)	22 (5-70)
R	15 (0-45)	12 (0-50)	8 (0-30)	6 (0-10)	13 (0-40)	0 (0)	46 (0-70)
S	30 (5-60)	9 (0-30)	18 (0-65)	6 (0-10)	12 (0-20)	0 (0)	26 (5-50)
U	25 (10-45)	14 (0-40)	9 (0-30)	7 (0-20)	17 (5-40)	0 (0)	28 (0-50)

Multiple Regression Analysis

Correlation Among Forest Structure Characteristics

To effectively complete multiple regression analyses, it was necessary to examine the correlation between independent variables (Table 6). Crown volume was highly correlated with crown area and crown height because both were used in volume calculations. The relationship between total dbh and number of stems ($r = 0.81$; $p = 0.0001$) was explained due to greater overall wood production on multiple-stemmed trees when compared to single-stemmed trees. Crown area and crown volume were also correlated with total dbh ($r = 0.55$; 0.50, respectively; $p = 0.0001$). This suggested a dependence of stem diameter on crown size, which has been shown in other species, including loblolly pine (Wenger and Trousdell 1958), Douglas fir and western larch (Shearer 1986), and red pine (Stiell 1988). Age was poorly related to dbh and crown size. However, the relationship between stem size and age may be complicated, as an artifact of measurement, by the increase of total stem diameter by possibly younger stems on multiple-stemmed trees. Crown area was correlated with number of stems ($r = 0.26$; $p = 0.0088$), which suggested that multiple-stemmed trees may support lateral extension of crowns. Total tree height was correlated with age ($r = 0.42$; $p = 0.001$) as expected because height increases with age. Total basal area of competing trees was related to age of subject tree ($r = 0.28$; $p = 0.0033$), which may be due to the often even-aged nature of whitebark pine stands. Whitebark pine often pioneer disturbed sites (Arno and Weaver

1990; Tomback et al. 1990; Weaver and Dale 1974), forming widely-spaced, even-aged stands which increase in basal area with age. Total tree height also increased with basal area (r = 0.33; p = 0.0007), perhaps resulting from increase in age (Weaver and Dale 1974).

Table 6: Correlation matrix (r-values) for forest structure data used in multiple regression analyses. Associated p-values for each correlation are in parentheses, and correlations with p≤0.05 are in bold.

	TOTAL DBH	# OF STEMS	TOT. TREE HEIGHT	AGE	CROWN AREA	CROWN VOLUME	TOTAL BASAL AREA
TOTAL DBH	1						
# OF STEMS	**0.81 (0.0001)**	1					
TOTAL TREE HEIGHT	0.14 (0.1499)	-0.07 (0.5003)	1				
AGE	-0.19 (0.0611)	**-0.30 (0.0023)**	**0.42 (0.0001)**	1			
CROWN AREA	**0.55 (0.0001)**	**0.26 (0.0088)**	0.16 (0.1180)	-0.08 (0.4121)	1		
CROWN VOLUME	**0.50 (0.0001)**	0.18 (0.0703)	**0.30 (0.0020)**	-0.05 (0.6513)	**0.91 (0.0001)**	1	
TOTAL BASAL AREA	-0.03 (0.7536)	0.00 (1.0000)	**0.33 (0.0007)**	**0.28 (0.0033)**	-0.16 (0.1169)	-0.13 (0.1916)	1

Multiple Regression Model

A multiple regression analysis was conducted using the log transform of average cone production as the response variable with total dbh, crown area, crown volume, and total basal area of competing trees as predictor variables. These variables were chosen based on results of simple regressions and support of previous literature. Stepwise selection techniques were used in model development for determining significance of predictor variables. The regression model is:

$$Y = b_0 + b_1x_1 + b_2x_2$$

where Y is the log transform of average cone production (response variable), b_0 is the intercept coefficient, b_1 and b_2 are regression coefficients corresponding to each one of the selected predictor variables (x_1 and x_2), which include crown area ($p = 0.00$) and total basal area ($p = 0.00$). The resulting model is:

$$\text{Average cones (log)} = 0.9261 + 0.0051(\text{crown area}) - 0.0088(\text{total basal area})$$

where crown area and total basal area are measured in square meters. The model is appropriate for the data ($p < 0.00$), and explains 36% of the variation in average cone production, with all variables significant. Scatterplot of observed values versus predicted values (Figure 23) shows how well the model predicts the actual data. The ideal model, with an R^2 value close to one, would plot the actual data (dots) close to the predicted values (line). The residuals for the model are normally distributed, and satisfy Gauss-Markov conditions (Sen and Srivastava 1990). Average residual values for each site were calculated and mapped to determine whether a spatial pattern existed in the predictive ability of the model. There was no spatial pattern in the distribution of underpredicted and overpredicted sites (Figure 24).

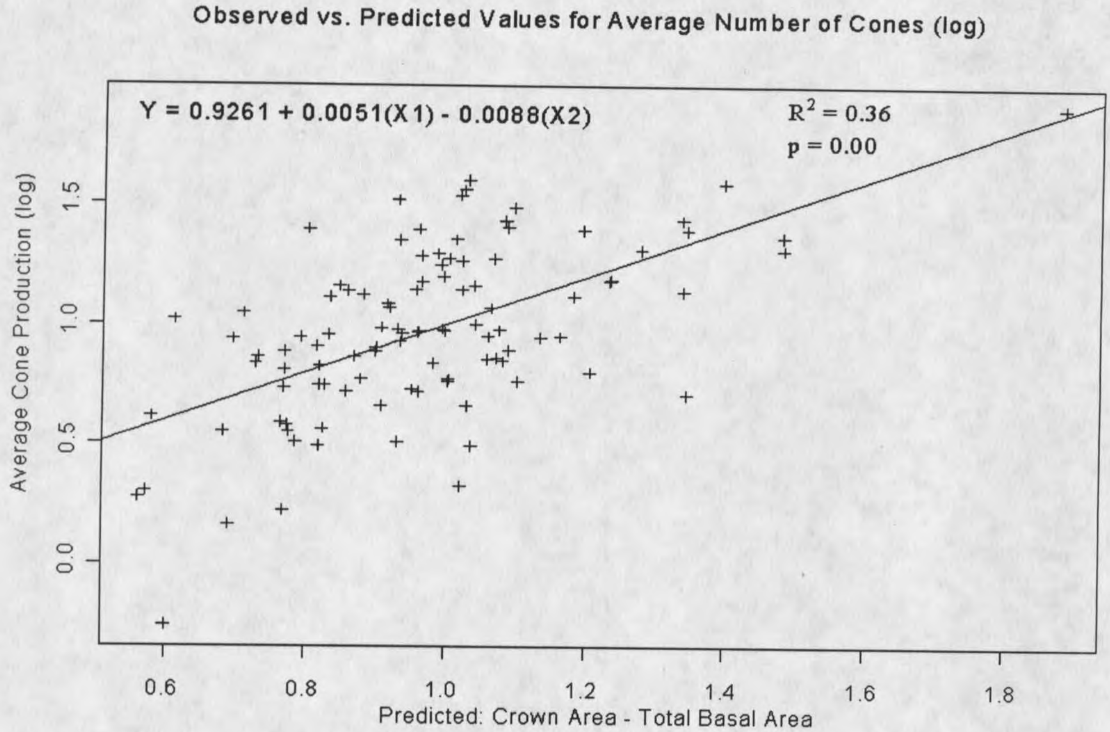

Figure 23: Observed verses predicted values for multiple regression model with the log transform of average cone production of whitebark pine and forest structure variables. (x_1 = crown area; x_2 = total basal area).

IGBST Whitebark Pine Cone Survey Sites

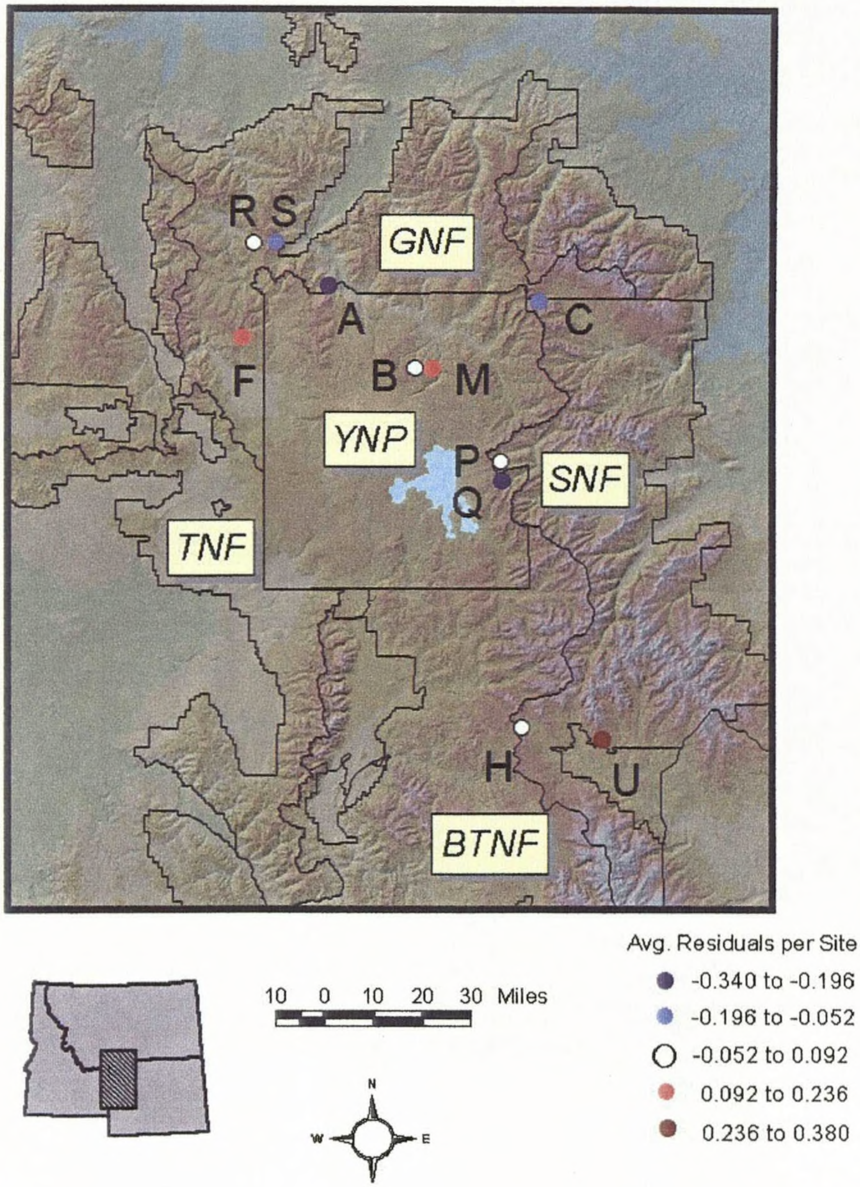

Figure 24: Map of residuals for multiple regression model with the log transform of average cone production of whitebark pine and forest structure variables. Blue represents sites where the model underpredicts, white where the model accurately predicts, and red where the model overpredicts. Locations for sites R, S, B, M, P, and Q have been altered to avoid overlapping symbols.

YNP = Yellowstone National Park
GNF = Gallatin National Forest
TNF = Targhee National Forest
SNF = Shoshone National Forest
BTNF = Bridger-Teton National Forest

Regression Analysis for Individual Plots

The second objective for this research was to determine whether topographic site characteristics were related to cone production in whitebark pine plots. Average cones per plot were regressed with aspect, elevation, and slope angle using data collected by the Interagency Grizzly Bear Study Team for 18 plots. Transformations of average cone production were not used for regressions with site characteristics because they did not help to normalize the data and did not improve the relationships. Simple regressions were insignificant (≤0.05), and a valid model could not be developed using these variables. Aspect and average cone production was regressed using (1) north/south and (2) east/west, and yielded R^2 values of 0.08 and 0.05, with p-values of 0.2453 and 0.3542, respectively. However, sites were not randomly distributed among aspects; thus, conclusions cannot made about this relationship (Figure 25). Results of regression between cone production and elevation were low and insignificant ($R^2 = 0.01$; $p = 0.80$) (Figure 26). Regression analysis with slope angle was also insignificant ($R^2 = 0.03$; $p = 0.50$) (Figure 27). Weaver and Forcella (1986) found that both aspect and elevation were unrelated to cone production in whitebark pine, and Khomentovsky (1994) found similar results for Japanese stone pine, a species that has similar morphology and ecology to whitebark pine.

Average Cone Production per Site vs. Aspect

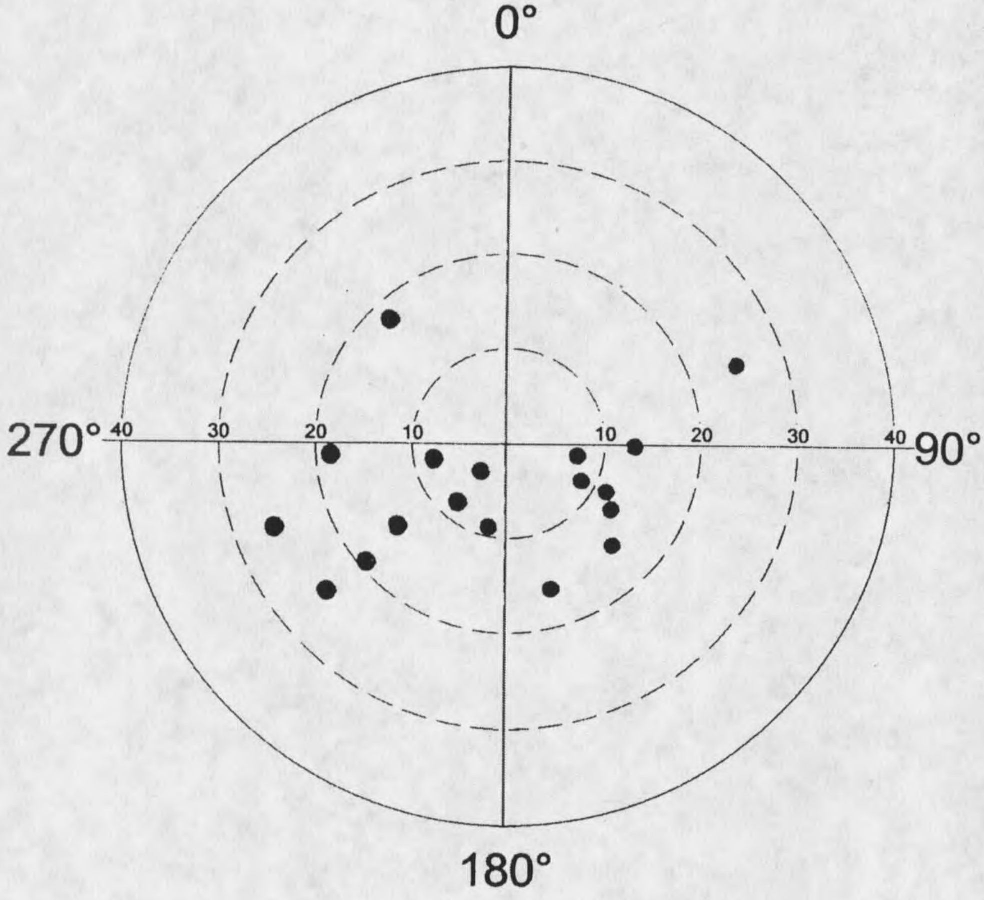

Figure 25: Average cone production per whitebark pine cone count site shown in relation to aspect. Cone production increases from center of circle.

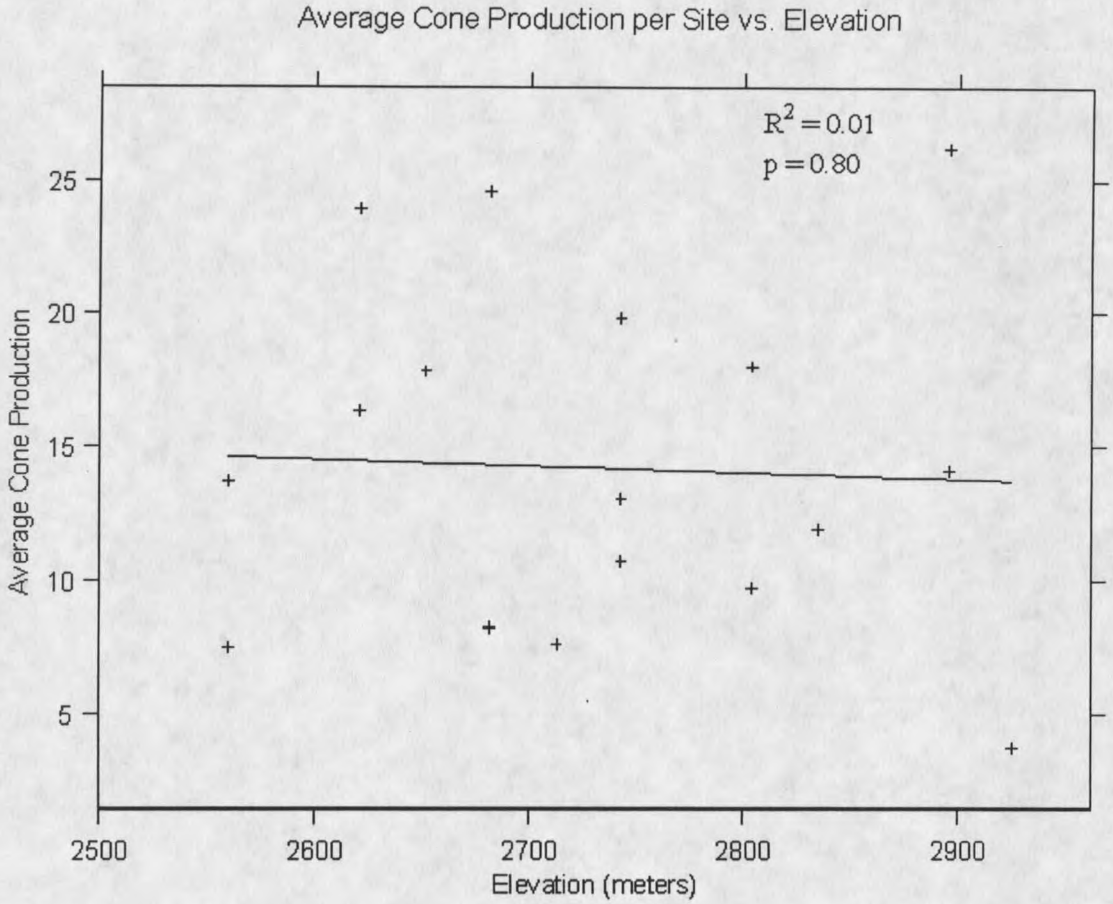

Figure 26: Scatterplot of elevation and average cone production for whitebark pine sites.

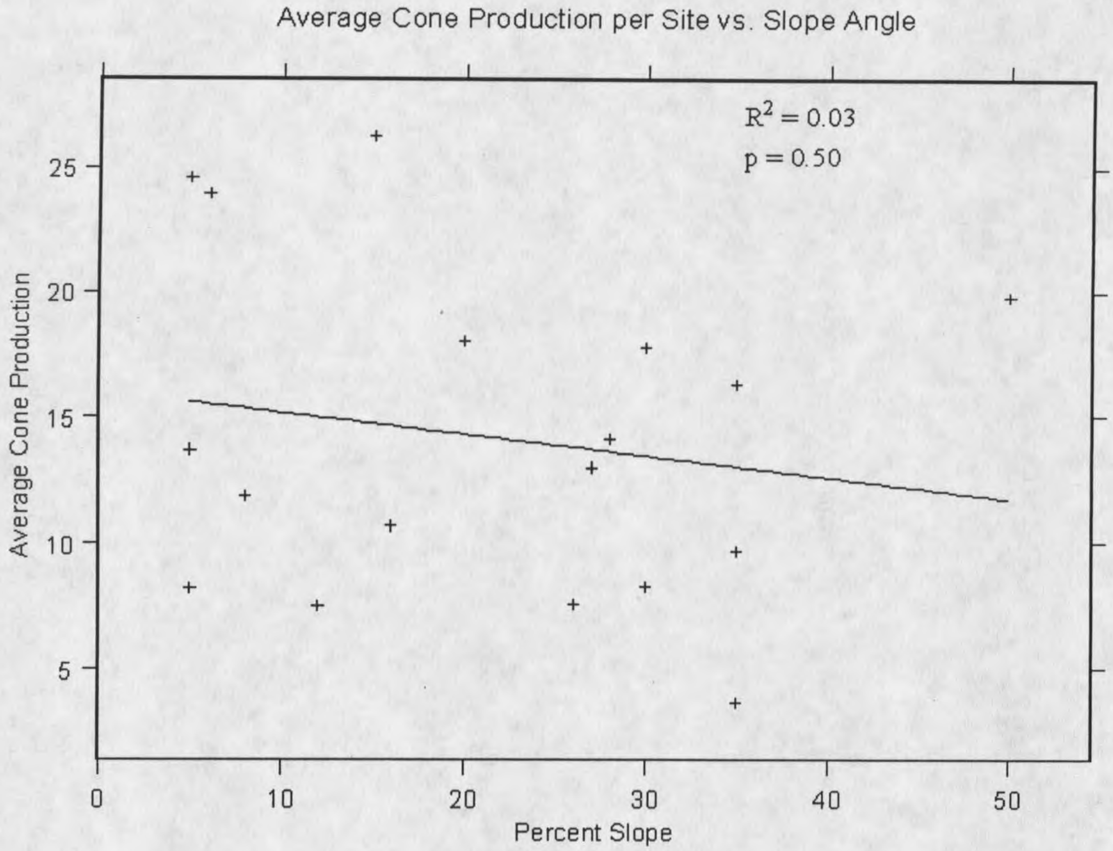

Figure 27: Scatterplot of slope angle and average cone production for whitebark pine sites.

Health of Whitebark Pine in the Greater Yellowstone Ecosystem

The final objective for this research was to characterize the amount of blister rust and beetle infestation in whitebark pine trees throughout the Greater Yellowstone Ecosystem. The size and type of scarring on the subject trees was also noted. Percentages of blister rust and beetle infestation are calculated using field data from all 120 trees from 12 sites. Thirty-one trees had either blister rust, beetle damage, or scarring (Table 7). Blister rust infected ~8 % of whitebark pine within the sample set of 120 trees. Two sites (H and J) out of 12 (~17 %) were infected with blister rust. Site H had 2 infected trees and site J had 8 infected trees. These results support findings by Hoff and Hagle (1990) suggesting that blister rust has yet to cause extensive mortality throughout the Greater Yellowstone Ecosystem. However, it is worth noting that both sites containing blister rust are in parts of the ecosystem which may have higher precipitation than other areas (Despain 1990) (Figure 28). Beetle infestation occurred in < 2% of the subject trees, in two sites (~17 %). Sites M and P each had 1 infected tree. Both sites are in areas which had no reported incidence of beetle infestation during the last epidemic outbreak in the late 1970's and early 1980's (Despain 1990). These results, however, may not accurately represent the health of whitebark pine communities throughout the ecosystem due to preferential selection of healthy trees and stands at the time of transect establishment 9-18 years ago.

Table 7: The relative health of trees described in terms of the amount of blister rust infection, amount of beetle infestation and the presence, size, and type of scars. Trees studied but not shown in this table do not have signs of blister rust, beetle infestation, or scarring.

SITE	TREE	BLISTER RUST # OF FLAGS	BLISTER RUST INFECTED NEEDLES (%)	BEETLE INFEST (0-3)	SCARS (SQ. CM)
A	9	0	0	0	1161-F
A	10	0	0	0	581-F
C	5	0	0	0	26-M
C	6	0	0	0	26-M
C	9	0	0	0	181
F	9	0	0	0	1613-M
H	1	12	25	0	0
H	2	0	0	0	129-M
H	3	10	10	0	0
H	8	0	0	0	1935-F
H	10	0	0	0	323-F
J	1	1	100	0	0
J	2	7	100	0	0
J	3	30	100	0	0
J	4	9	100	0	0
J	5	8	70	0	0
J	6	2	60	0	0
J	7	2	80	0	0
J	9	25	100	0	0
M	6	0	0	3	0
P	3	0	0	1	0
P	8	0	0	0	26-M
P	10	0	0	0	774-M
R	3	0	0	0	452-M
R	5	0	0	0	697-F
S	1	0	0	0	935-F
S	2	0	0	0	3710-F
S	3	0	0	0	1355-F
S	4	0	0	0	516-F
S	6	0	0	0	1290-F
S	9	0	0	0	97-M

Scars: caused by animal (A), mechanical (M), or fire (F)
Beetle infestation: 1 = evidence of some bore holes
2 = bore holes and pitch tubes obvious and fairly numerous
3 = browning crown with numerous bore holes and pitch tubes

IGBST Whitebark Pine Cone Survey Sites

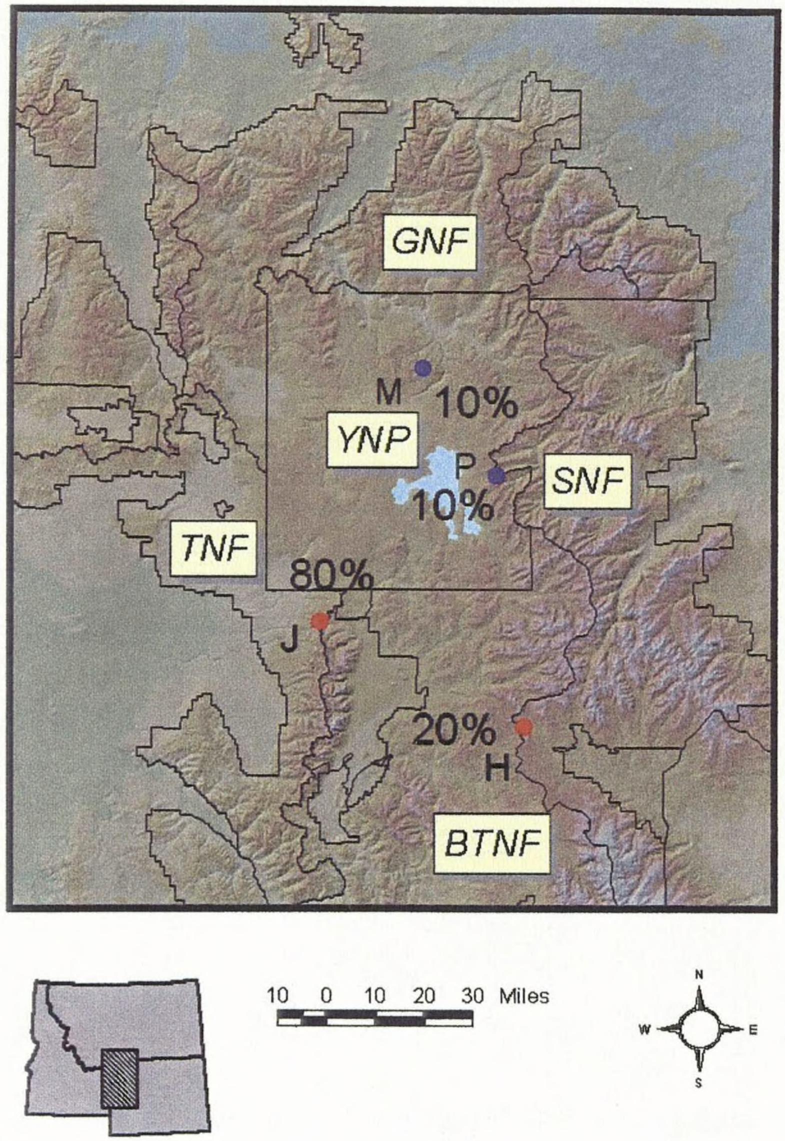

Figure 28: Map of whitebark pine sites which are infected with blister rust (red) and have evidence of beetle infestation (blue), with associated percentages of trees inflicted.

YNP = Yellowstone National Park
GNF = Gallatin National Forest
TNF = Targhee National Forest
SNF = Shoshone National Forest
BTNF = Bridger-Teton National Forest

CHAPTER 5

CONCLUSIONS

Crown size, as measured by crown area and crown volume, accounts for 30% ($p = 0.00$) and 25% ($p = 0.00$) of the variation in average cone production for individual whitebark pine trees. Regression with the amount of competition (measured in basal area) suggests that a relationship may exist ($R^2 = 0.10$; $p = 0.00$) such that cone production is reduced with increased basal area of surrounding trees. Regression with stem size (dbh) had an R^2 value of 0.04 ($p = 0.05$), but number of stems, tree height, and age all had nonsignificant relationships with cone production. A multiple regression analysis yielded a model that explains 36% of the variation ($p = 0.00$), using crown area and basal area of competing trees. Relationships among cone production and understory composition were inconclusive. Regressions among average cone production per site and topographic characteristics, including aspect, elevation, and slope angle were all nonsignificant. Results of regression analyses with forest structure characteristics were low, suggesting that other factors are influential, including soil characteristics and nutrient status, weather/climate, and genetic traits.

Blister rust and beetle infestation were low throughout the study plots within the Greater Yellowstone Ecosystem. Less than 8 % of subject trees (120) were infected with blister rust, and less than 2% had evidence of beetle damage. Blister rust was limited to two sites in the southern part of the ecosystem (H and J), and beetle infestation to two sites in the central part (M and P). These results suggest that both are low throughout the Greater Yellowstone Ecosystem. However, they may not accurately represent the health of whitebark pine communities due to preferential selection of healthy trees and stands at the time of transect establishment 9-18 years ago.

Management implications

These results give forest managers some ability to predict which trees within a stand are the larger cone producers. Future inclusion of soil, weather, and genetics data would likely improve the predictive ability of multiple regression models. While the ability to predict cone production is valuable, more information is needed in order to manage trees for higher cone production. Mattson et al. (1994) found that bears eat pine seeds from stands that produce more than 21 cones per tree. The average cone production from all 21 of the Interagency Grizzly Bear Study Team transects, for all recorded years, is 13.1 cones per tree. Therefore, it is important to continue identifying characteristics of strong cone-producing trees and subsequently manage stands for better cone production. These results alone indicate that stands managed to increase crown and stem sizes and decrease overall stand basal area would improve cone production. However, if management objectives are primarily addressing consumption of seeds by grizzly bears, care should be taken to maintain or encourage diversity of tree species within stands. Squirrel densities are higher in mixed-species stands, which provide larger food sources for grizzly bears (Reinhart and Mattson 1990). However, this type of management may favor successional replacement of whitebark pine. More information is needed in order to effectively manage whitebark pine forests for increased cone production and optimal grizzly bear habitat.

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APPENDICES

APPENDIX A

CONE PRODUCTION

Appendix A: Values of average cone production and values of productivity index (PI) with associated tree rankings.

	AVG CONES	AVG CONES RANK	PI	PI RANK
A1	4.56	94	0.73718	74
A2	9.56	48	0.88014	25
A3	5.11	92	0.83509	53
A4	3.11	107	0.6083	108
A5	3.22	105	0.73152	76
A7	5.89	81	0.82764	55
A8	6.33	80	0.85006	47
A9	8.78	59	0.86859	34
A10	20.67	19	0.9363	13
B1	38.78	3	0.9277	15
B2	18.89	23	0.87554	30
B3	9.67	47	0.82815	54
B4	27.22	9	0.91141	19
B5	9.33	52	0.87587	29
B6	20.44	20	0.91774	17
B7	15.22	30	0.86945	33
B8	12.11	41	0.85163	44
B9	11.67	43	0.87094	32
B10	14.56	32	0.83644	51
C1	5.56	85	0.8372	50
C2	5.22	90	0.82028	57
C3	23.33	16	0.90645	22
C5	3.56	102	0.82274	56
C6	9.56	48	0.8761	28
C7	3.22	105	0.68336	92
C8	8.89	57	0.87772	26
C9	2.00	110	0.66856	96
C10	8.78	59	0.85025	46
F1	9.11	55	0.72743	78
F2	9.22	54	0.6167	104
F3	7.22	71	0.76323	67
F4	8.11	64	0.7379	73
F5	8.44	62	0.60846	107
F6	30.67	7	0.85337	43
F7	6.67	77	0.65457	97
F8	13.89	34	0.69962	88
F9	25.33	11	0.85866	40
F10	22.44	18	0.80877	60
H1	13.00	40	0.90646	21
H2	6.89	75	0.86064	38
H3	5.89	81	0.85834	41
H4	5.78	83	0.86854	35

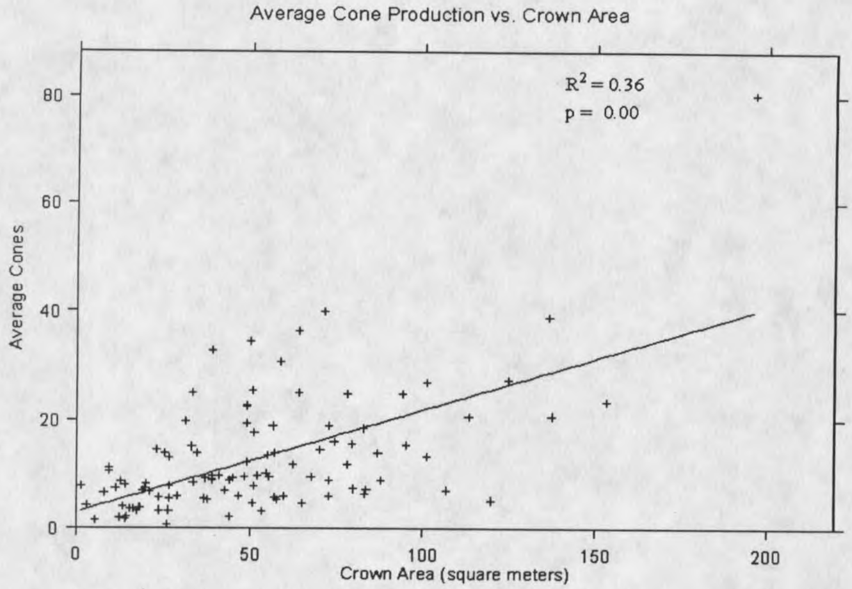
H5	17.67	27	0.94084	11
H6	10.00	46	0.91044	20
H7	8.44	62	0.91504	18
H8	15.00	31	0.94118	10
H9	30.44	8	0.96767	6
H10	5.56	85	0.84219	49
J1	9.43	51	0.72604	79
J2	0.29	117	0.44368	115
J3	1.29	114	0.6527	98
J4	3.29	104	0.68229	93
J5	18.57	25	0.86141	37
J6	4.29	96	0.7002	87
J7	4.86	93	0.7242	81
J8	3.86	99	0.70067	86
J10	6.57	78	0.78307	64
M1	13.78	36	0.81573	59
M2	19.22	22	0.85994	39
M3	15.89	28	0.81746	58
M4	9.33	52	0.77314	65
M5	7.33	69	0.741	72
M6	24.89	12	0.83542	52
M7	6.44	79	0.67605	95
M8	2.11	109	0.45126	114
M9	80.33	1	0.93838	12
M10	18.78	24	0.86781	36
P1	7.67	67	0.78466	63
P2	11.78	42	0.85078	45
P3	18.33	26	0.87748	27
P4	8.67	61	0.74609	70
P5	4.11	97	0.77238	66
P6	5.56	85	0.73694	75
P7	1.89	111	0.51618	112
P8	10.44	45	0.87539	31
P9	6.89	75	0.71342	83
P10	7.67	67	0.69512	89
Q1	5.44	88	0.67677	94
Q2	0.56	115	0.31516	116
Q3	13.11	39	0.85346	42
Q4	1.44	113	0.48581	113
Q5	0.56	115	0.22576	117
Q6	3.56	102	0.68694	91
Q7	1.67	112	0.54369	111
Q8	3.11	107	0.59045	109
Q9	3.67	101	0.70072	85
Q10	3.89	98	0.7103	84
R1	9.00	56	0.78797	61
R2	5.22	90	0.56485	110
R3	7.11	73	0.6519	99
R4	7.00	74	0.6873	90
R5	39.78	2	0.92066	16

R6	26.89	10	0.9038	24
R7	7.78	66	0.64807	100
R8	13.78	36	0.78787	62
R9	13.33	38	0.75348	68
R10	7.22	71	0.61005	106
S1	8.00	65	0.74814	69
S2	13.89	34	0.84615	48
S3	5.33	89	0.63355	101
S4	15.44	29	0.74498	71
S5	7.33	69	0.7259	80
S6	5.78	83	0.61977	103
S7	8.89	57	0.7187	82
S8	3.78	100	0.61458	105
S9	4.56	94	0.62026	102
S10	9.44	50	0.72752	77
U1	34.44	5	0.97346	5
U2	24.89	12	0.96744	7
U3	32.78	6	0.99055	1
U4	14.44	33	0.98844	2
U5	11.11	44	0.90564	23
U6	24.78	14	0.95978	9
U7	36.22	4	0.9743	4
U8	22.56	17	0.96363	8
U9	19.67	21	0.93139	14
U10	24.78	14	0.98041	3

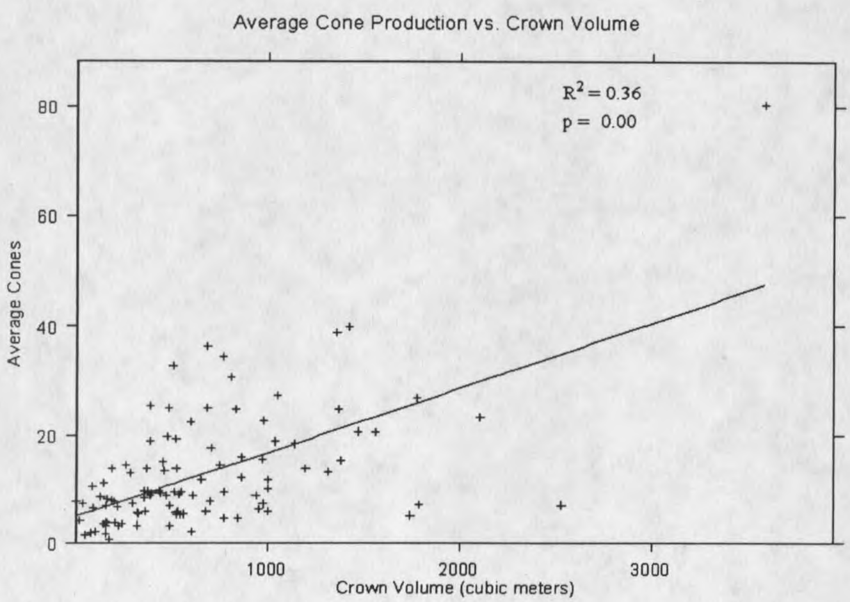
APPENDIX B

SCATTERPLOTS

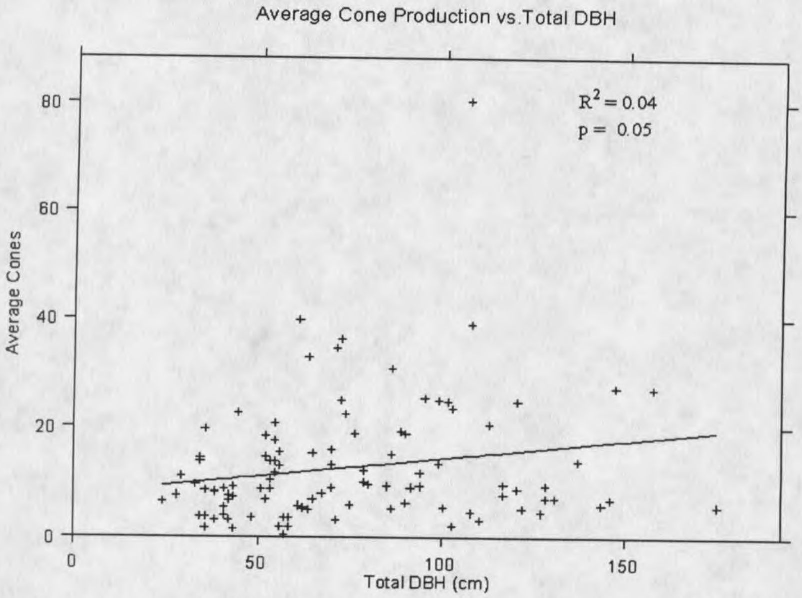
Appendix B: Scatterplots of forest structure variables using average cone production as the response variable.



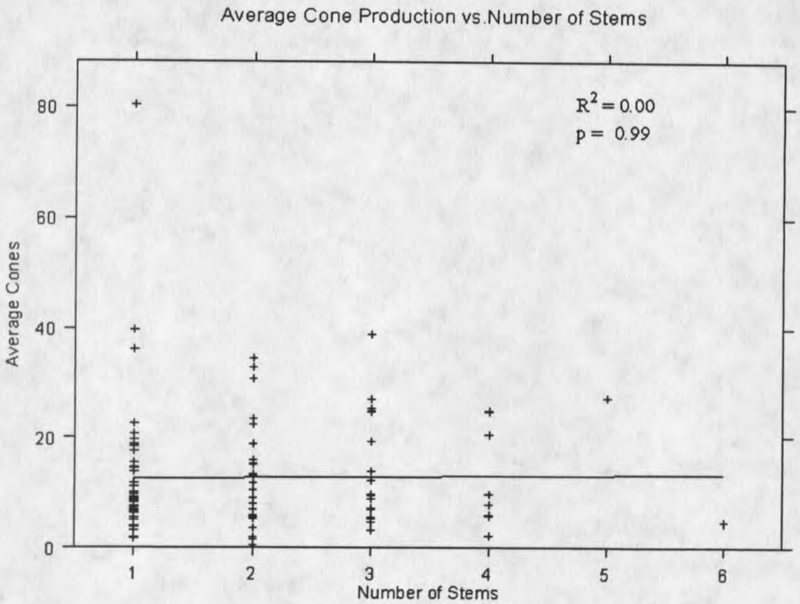
1: Scatterplot of crown area and average cone production of whitebark pine.



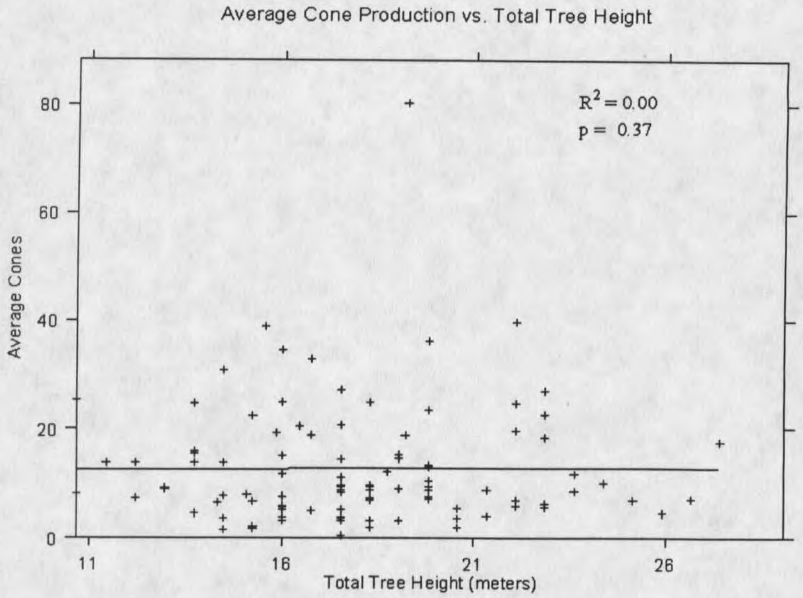
2: Scatterplot of crown volume and average cone production of whitebark pine.



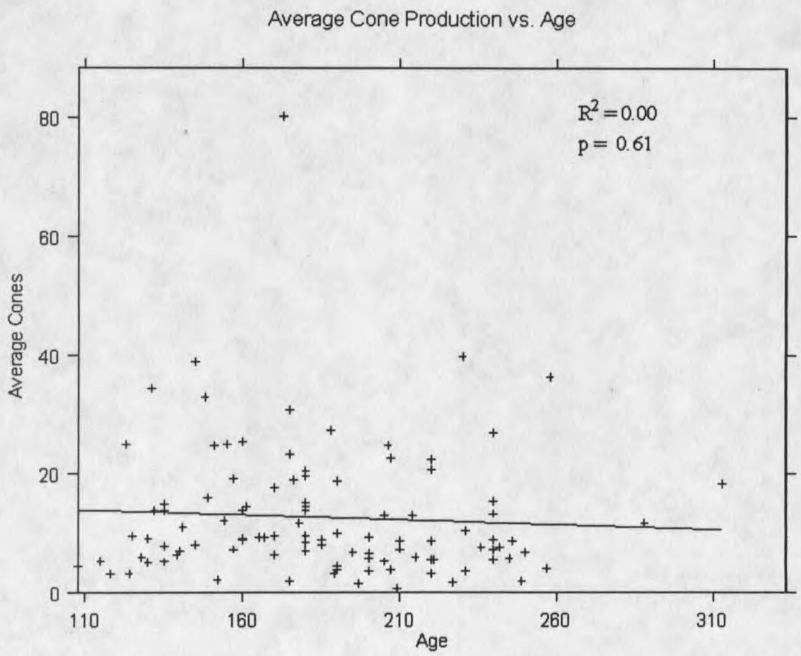
3: Scatterplot of total dbh and average cone production of whitebark pine.



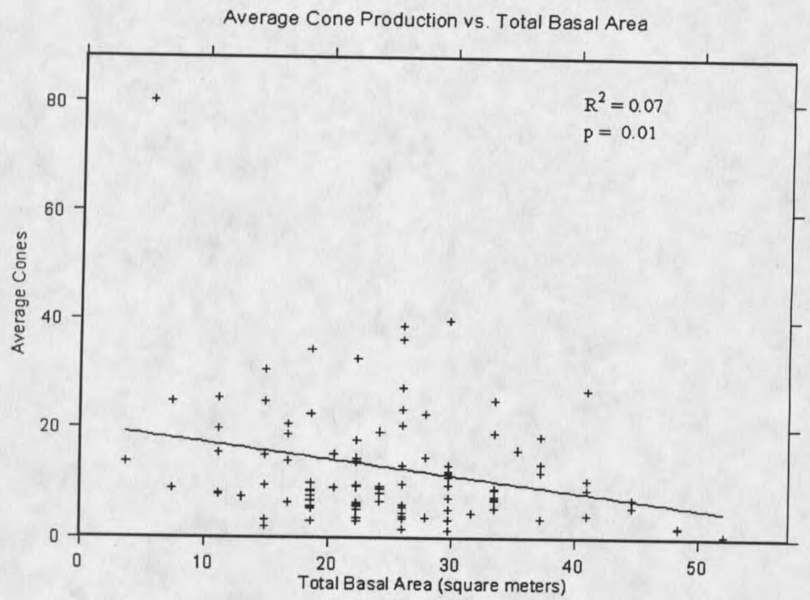
4: Scatterplot of number of stems per tree and average cone production of whitebark pine.



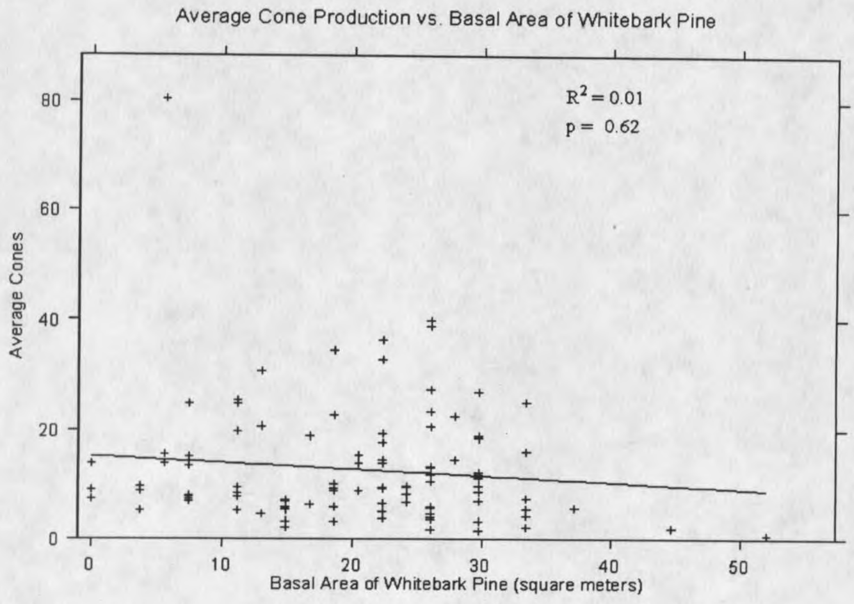
5: Scatterplot of total tree height and average cone production of whitebark pine.



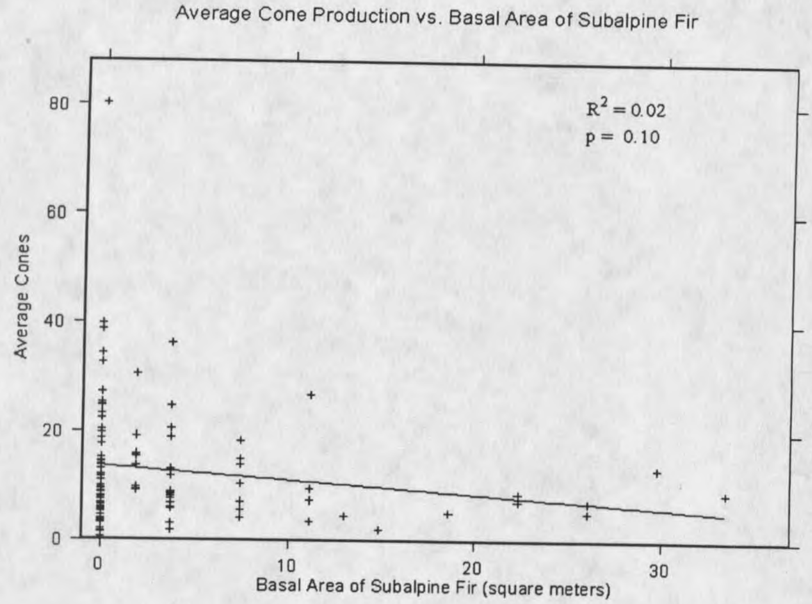
6: Scatterplot of age and average cone production of whitebark pine.



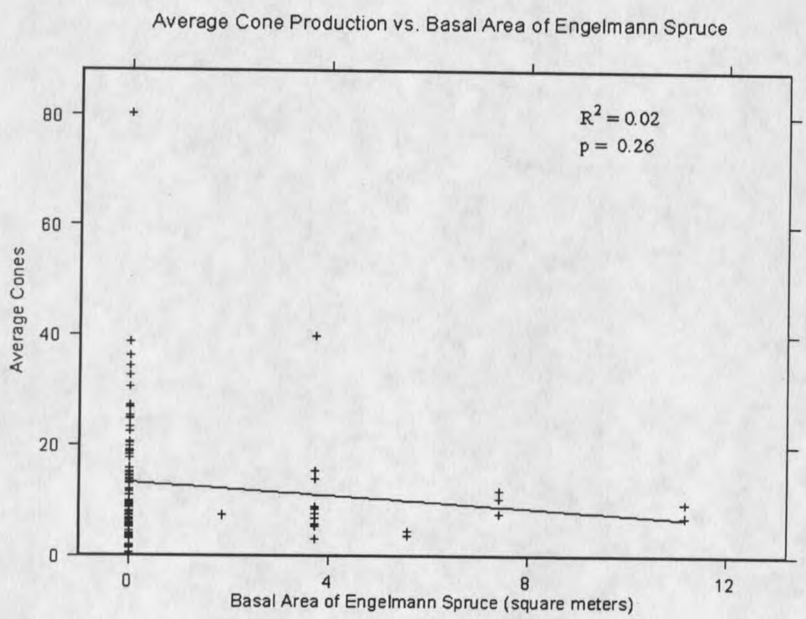
7: Scatterplot of total basal area and average cone production of whitebark pine.



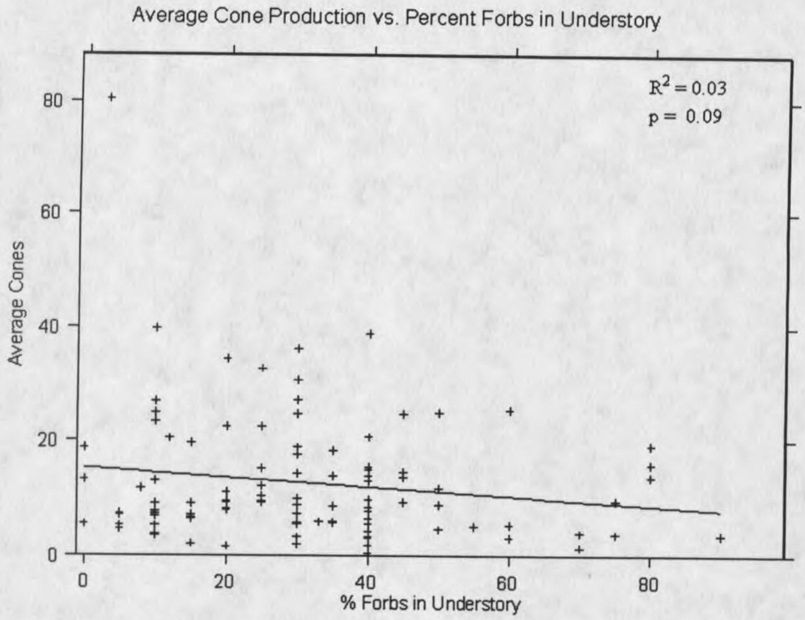
8: Scatterplot of whitebark pine basal area and average cone production of whitebark pine.



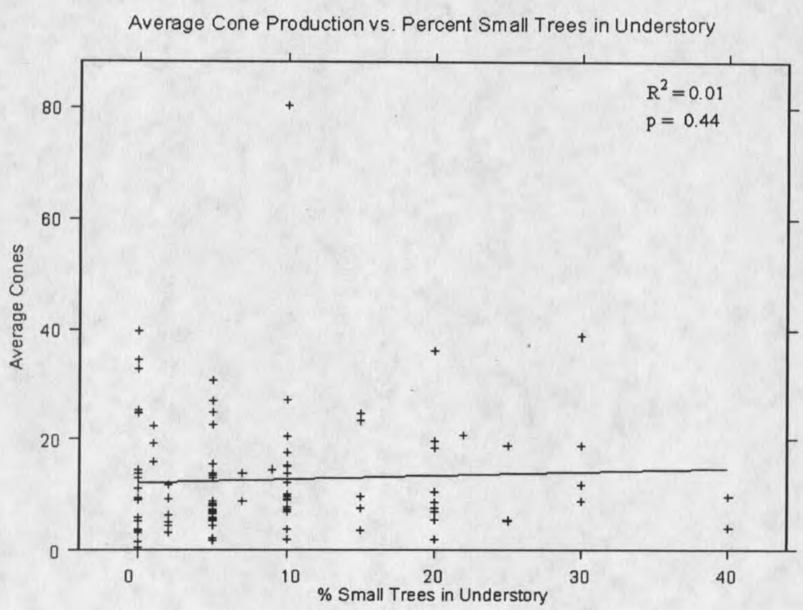
9: Scatterplot of subalpine fir basal area and average cone production of whitebark pine.



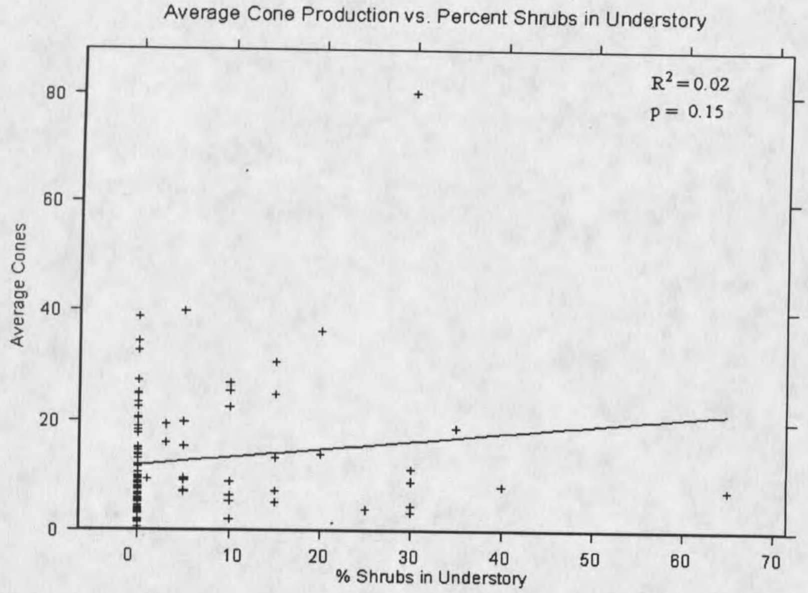
10: Scatterplot of Engelmann spruce basal area and average cone production of whitebark pine.



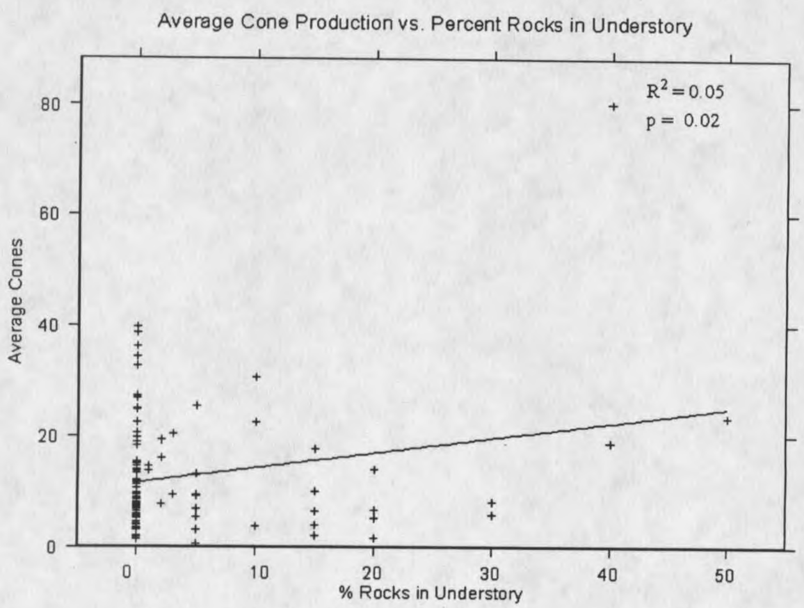
11: Scatterplot of percent forbs in understory and average cone production of whitebark pine.



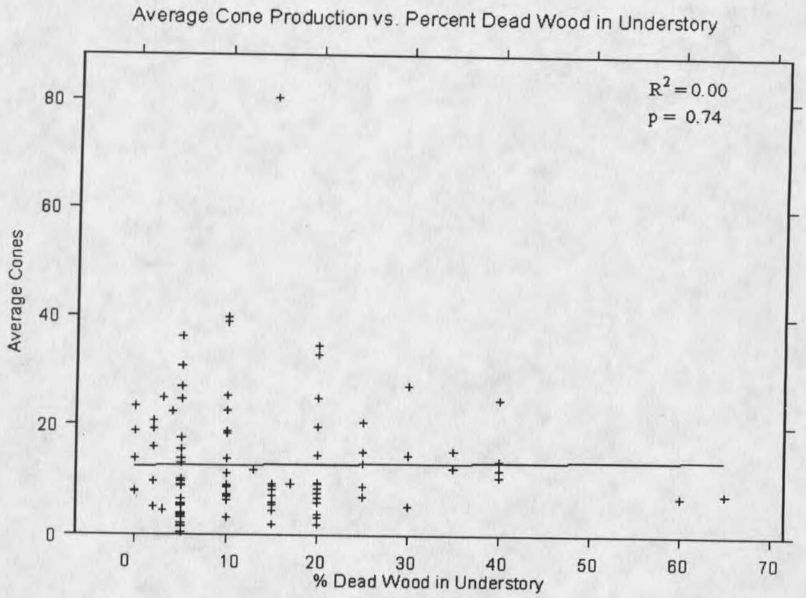
12: Scatterplot of percent small trees in understory and average cone production of whitebark pine.



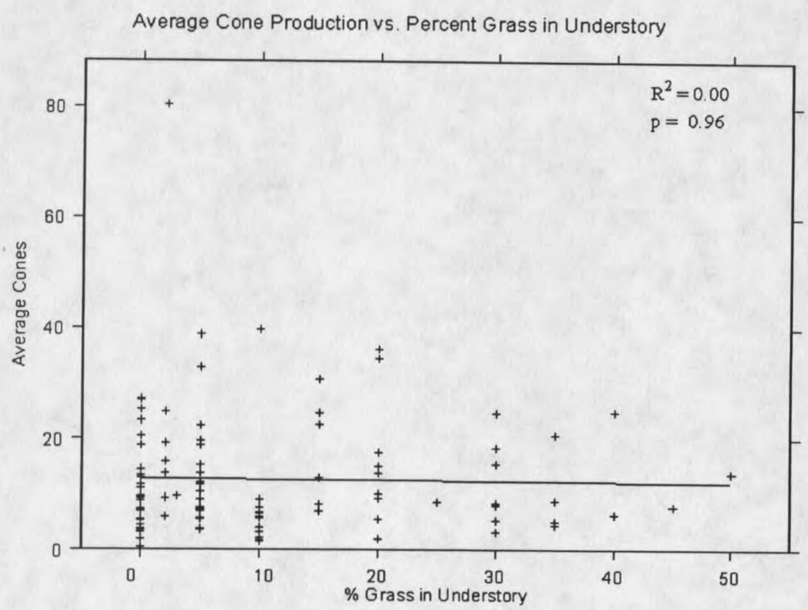
13: Scatterplot of percent shrubs in understory and average cone production of whitebark pine.



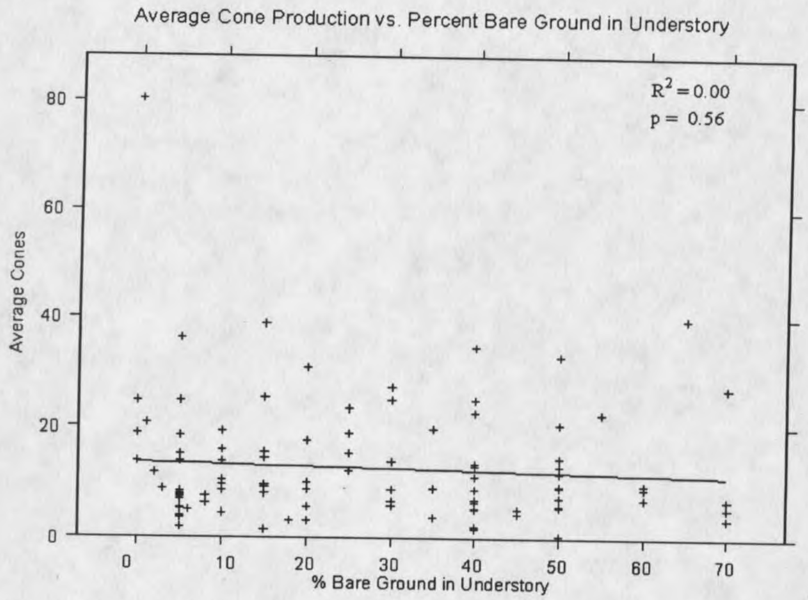
14: Scatterplot of percent rocks in understory and average cone production of whitebark pine.



15: Scatterplot of percent dead wood in understory and average cone production of whitebark pine.



16: Scatterplot of percent grass in understory and average cone production of whitebark pine.



17: Scatterplot of percent bare ground in understory and average cone production of whitebark pine.

APPENDIX C

FIELD DATA

Appendix C1: Field data including crown size, total basal area of competing trees, and subsets of competing trees that are whitebark pine (WBP), subalpine fir (SAF), and Engelmann spruce (ENSP).

STAND	TREE	CROWN AREA (SQ. M)	CROWN VOLUME (CUBIC M)	BASAL AREA TOTAL (SQ. M)	BASAL AREA WBP (SQ. M)	BASAL AREA SAF (SQ. M)	BASAL AREA ENSP (SQ. M)
A	1	65.0	842.5	26.0	26.0	0.0	0.0
A	2	52.0	436.1	29.7	29.7	0.0	0.0
A	3	120.0	1738.0	22.3	22.3	0.0	0.0
A	4	53.5	489.4	18.6	18.6	0.0	0.0
A	5	23.7	162.5	29.7	29.7	0.0	0.0
A	7	59.8	364.8	26.0	26.0	0.0	0.0
A	8	83.2	951.6	16.7	16.7	0.0	0.0
A	9	72.7	609.8	18.6	18.6	0.0	0.0
A	10	137.5	1467.0	16.7	13.0	3.7	0.0
B	1	136.7	1354.8	26.0	26.0	0.0	0.0
B	2	72.7	388.1	33.4	29.7	3.7	0.0
B	3	41.1	375.5	26.0	24.2	1.9	0.0
B	4	124.9	1046.7	26.0	26.0	0.0	0.0
B	5	55.6	550.4	24.2	24.2	0.0	0.0
B	6	113.4	1556.0	26.0	26.0	0.0	0.0
B	7	95.1	1377.5	20.4	20.4	0.0	0.0
B	8	49.1	859.8	29.7	29.7	0.0	0.0
B	9	78.0	654.2	29.7	29.7	0.0	0.0
B	10	70.2	749.3	27.9	27.9	0.0	0.0
C	1	23.7	325.0	26.0	26.0	0.0	0.0
C	2	37.6	544.8	29.7	11.1	18.6	0.0
C	3	153.3	2102.8	26.0	26.0	0.0	0.0
C	5	16.4	149.5	37.2	26.0	11.1	0.0
C	6	39.0	356.8	14.9	3.7	11.1	0.0
C	7	26.5	322.8	14.9	14.9	0.0	0.0
C	8	39.0	386.6	7.4	3.7	3.7	0.0
C	9	14.2	108.3	48.3	33.4	14.9	0.0
C	10	44.1	470.8	40.9	18.6	22.3	0.0
F	1	37.2	396.5	20.4	18.6	1.9	0.0
F	2	44.9	444.6	22.3	22.3	0.0	0.0
F	3	42.7	456.0	24.2	24.2	0.0	0.0
F	4	20.1	168.2	24.2	24.2	0.0	0.0
F	5	31.8	290.6	29.7	26.0	3.7	0.0
F	6	58.9	807.5	14.9	13.0	1.9	0.0
F	7	20.8	222.0	24.2	24.2	0.0	0.0
F	8	57.2	523.4	22.3	22.3	0.0	0.0
F	9	50.7	386.6	11.1	11.1	0.0	0.0
F	10	49.1	599.3	27.9	27.9	0.0	0.0
H	1	26.8	285.5	26.0	26.0	0.0	0.0
H	2	42.7	488.5	18.6	14.9	0.0	3.7
H	3	29.0	530.2	22.3	18.6	3.7	0.0

H	4	46.8	678.0	18.6	18.6	0.0	0.0
H	5	51.2	702.2	22.3	22.3	0.0	0.0
H	6	54.6	999.1	18.6	18.6	0.0	0.0
H	7	33.5	357.8	18.6	11.1	3.7	3.7
H	8	33.2	455.0	14.9	7.4	7.4	0.0
H	9	58.5	1025.9	22.3	11.1	7.4	3.7
H	10	35.7	652.5	22.3	22.3	0.0	0.0
J	1	11.2	85.7	20.4	13.0	7.4	0.0
J	2	9.2	70.1	7.4	7.4	0.0	0.0
J	3	26.8	265.1	16.7	13.0	3.7	0.0
J	4	24.7	113.0	22.3	16.7	5.6	0.0
J	5	17.8	149.5	13.0	9.3	3.7	0.0
J	6	16.9	141.7	9.3	5.6	3.7	0.0
J	7	7.5	17.2	14.9	9.3	5.6	0.0
J	8	12.3	121.5	11.1	5.6	5.6	0.0
J	10	49.1	561.8	9.3	5.6	3.7	0.0
M	1	25.2	192.0	22.3	20.4	1.9	0.0
M	2	49.0	522.4	24.2	22.3	1.9	0.0
M	3	74.3	860.9	35.3	33.4	1.9	0.0
M	4	48.3	515.4	24.2	22.3	1.9	0.0
M	5	19.5	297.4	33.4	33.4	0.0	0.0
M	6	64.1	683.9	33.4	33.4	0.0	0.0
M	7	7.8	95.2	22.3	22.3	0.0	0.0
M	8	44.1	605.3	14.9	14.9	0.0	0.0
M	9	196.5	3593.8	5.6	5.6	0.0	0.0
M	10	56.6	1034.8	16.7	16.7	0.0	0.0
P	1	26.6	202.5	18.6	11.1	3.7	3.7
P	2	62.4	999.1	37.2	26.0	3.7	7.4
P	3	82.8	1135.5	37.2	29.7	7.4	0.0
P	4	12.5	133.8	33.4	29.7	3.7	0.0
P	5	2.8	25.5	40.9	33.4	7.4	0.0
P	6	57.2	523.4	44.6	37.2	7.4	0.0
P	7	12.3	84.1	48.3	44.6	3.7	0.0
P	8	9.2	91.1	40.9	26.0	7.4	7.4
P	9	19.0	158.9	33.4	29.7	3.7	0.0
P	10	1.4	7.4	18.6	7.4	3.7	7.4
Q	1	26.8	326.2	33.4	33.4	0.0	0.0
Q	2	26.0	178.4	52.0	52.0	0.0	0.0
Q	3	101.2	1310.7	29.7	26.0	3.7	0.0
Q	4	5.2	55.5	29.7	29.7	0.0	0.0
Q	5	3.3	22.9	29.7	26.0	0.0	3.7
Q	6	15.3	245.3	26.0	26.0	0.0	0.0
Q	7	13.9	159.3	26.0	26.0	0.0	0.0
Q	8	17.4	225.1	22.3	14.9	3.7	3.7
Q	9	18.4	210.3	22.3	22.3	0.0	0.0
Q	10	13.3	162.0	26.0	26.0	0.0	0.0
R	1	39.0	535.2	33.4	0.0	33.4	0.0
R	2	57.7	527.6	29.7	3.7	26.0	0.0
R	3	83.6	1784.2	33.4	14.9	7.4	11.1
R	4	107.0	2528.4	44.6	7.4	26.0	11.1

R	5	71.5	1417.4	29.7	26.0	0.0	3.7
R	6	101.2	1773.3	40.9	29.7	11.1	0.0
R	7	51.1	700.9	11.1	11.1	0.0	0.0
R	8	87.0	1192.8	3.7	0.0	0.0	0.0
R	9	55.2	462.6	37.2	7.4	29.7	0.0
R	10	79.7	971.9	29.7	7.4	22.3	0.0
S	1	13.9	191.2	11.1	7.4	3.7	0.0
S	2	34.7	370.7	16.7	5.6	7.4	3.7
S	3	36.8	560.7	18.6	14.9	0.0	3.7
S	4	79.4	968.5	11.1	5.6	1.9	3.7
S	5	11.1	42.5	13.0	0.0	11.1	1.9
S	6	72.7	997.9	22.3	14.9	3.7	3.7
S	7	87.8	936.7	24.2	20.4	0.0	3.7
S	8	18.1	165.7	27.9	22.3	0.0	5.6
S	9	50.7	773.1	31.6	13.0	13.0	5.6
S	10	67.6	773.1	22.3	11.1	0.0	11.1
U	1	50.2	764.6	18.6	18.6	0.0	0.0
U	2	33.4	484.3	33.4	33.4	0.0	0.0
U	3	39.0	505.5	22.3	22.3	0.0	0.0
U	4	22.9	262.3	22.3	22.3	0.0	0.0
U	5	9.2	147.2	29.7	29.7	0.0	0.0
U	6	78.0	832.6	14.9	11.1	3.7	0.0
U	7	64.1	683.9	26.0	22.3	3.7	0.0
U	8	49.1	973.8	18.6	18.6	0.0	0.0
U	9	31.2	475.8	11.1	11.1	0.0	0.0
U	10	94.3	1365.4	7.4	7.4	0.0	0.0

Appendix C2: Field data including total dbh per tree, number of stems per tree, tree height, and age.

STAND	TREE	TOTAL DBH (CM)	# OF STEMS	TOTAL TREE HEIGHT (M)	AGE
A	1	127.0	6	13.7	108
A	2	116.8	4	18.3	125
A	3	63.5	1	16.8	130
A	4	110.5	3	18.3	118
A	5	38.1	1	19.1	124
A	7	143.5	4	16.0	128
A	8	90.2	1	22.9	170
A	9	120.7	3	19.8	220
A	10	54.6	1	17.5	220
B	1	108.0	3	15.5	145
B	2	76.2	1	16.8	176
B	3	33.0	1	17.5	170
B	4	147.3	5	17.5	188
B	5	85.1	3	17.5	167

B	6	113.0	4	16.5	180
B	7	64.8	2	19.1	180
B	8	78.7	3	18.7	154
B	9	94.0	2	16.0	178
B	10	52.1	1	19.1	161
C	1	40.6	1	20.6	220
C	2	86.4	2	16.0	205
C	3	102.9	2	19.8	175
C	5	58.4	2	20.6	200
C	6	80.0	3	18.3	180
C	7	41.9	1	17.5	220
C	8	40.6	1	17.5	160
C	9	58.4	1	18.3	175
C	10	53.3	1	18.3	210
F	1	91.4	2	13.0	160
F	2	43.2	1	13.0	130
F	3	161.3	6	12.2	
F	4	38.1	1	10.7	145
F	5	77.5	2	13.0	
F	6	86.4	2	14.5	175
F	7	41.9	1	15.2	200
F	8	53.3	1	11.4	180
F	9	95.3	3	10.7	160
F	10	73.7	2	15.2	220
H	1	55.9	2	19.8	205
H	2	52.1	1	18.3	195
H	3	74.9	2	22.1	215
H	4	175.3	4	22.9	245
H	5	54.6	1	27.4	170
H	6	78.7	1	24.4	190
H	7	38.1	1	17.5	180
H	8	86.4	2	16.0	135
H	9	95.3	2	22.1	
H	10	40.6	1	21.3	
J	1	31.8	2	9.9	90
J	2	44.5	2	11.4	100
J	3	83.8	4	12.2	100
J	4	45.7	2	9.1	70
J	5	30.5	1	10.7	90
J	6	47.0	2	11.4	90
J	7	20.3	1	7.6	65
J	8	33.0	1	11.4	75
J	10	83.8	3	14.5	90
M	1	34.3	1	12.2	132
M	2	88.9	3	15.8	157
M	3	69.9	2	13.7	149
M	4	94.0	3	19.8	165
M	5	43.2	1	18.3	157
M	6	72.4	3	18.3	155
M	7	24.1	1	14.3	139

M	8	102.9	4	15.2	152
M	9	106.7	1	19.2	173
M	10	90.2	2	19.2	190
P	1	41.9	1	19.8	242
P	2	54.6	1	23.6	288
P	3	52.1	1	22.9	313
P	4	35.6	1	23.6	246
P	5	40.6	1	21.3	257
P	6	100.3	3	20.6	240
P	7	55.9	2	20.6	249
P	8	53.3	2	19.8	231
P	9	64.8	2	22.1	250
P	10	27.9	1	16.0	236
Q	1	62.2	2	20.6	221
Q	2	57.2	2	17.5	209
Q	3	69.9	2	19.8	214
Q	4	43.2	2	14.5	197
Q	5	241.3	1	16.8	221
Q	6	57.2	2	17.5	231
Q	7	35.6	1	15.2	227
Q	8	71.1	3	16.0	189
Q	9	48.3	2	14.5	231
Q	10	34.3	1	16.0	207
R	1	69.9	1	19.1	185
R	2	121.9	3	17.5	135
R	3	128.3	3	26.7	140
R	4	146.1	3	25.1	180
R	5	61.0	1	22.1	230
R	6	157.5	3	22.9	240
R	7	116.8	4	14.5	135
R	8	137.2	3	14.5	135
R	9	99.1	2	19.8	240
R	10	130.8	3	19.8	240
S	1	67.3	2	15.1	185
S	2	54.6	1	13.7	160
S	3	62.2	2	16.0	115
S	4	55.9	1	13.7	240
S	5	43.2	1	12.2	210
S	6	61.0	2	16.0	200
S	7	50.8	1	21.3	240
S	8	35.6	1	17.5	190
S	9	108.0	3	25.9	190
S	10	128.3	3	18.3	200
U	1	71.1	2	16.0	131
U	2	99.1	4	16.0	123
U	3	63.5	2	16.8	148
U	4	34.3	1	17.5	180
U	5	29.2	1	17.5	141
U	6	120.7	4	13.7	151
U	7	72.4	1	19.8	258

U	8	44.5	1	22.9	207
U	9	35.6	1	22.1	180
U	10	101.6	3	22.1	206

Appendix C3: Field data of understory composition within a 5 -meter radius from each tree.

STAND	TREE	% BARE GROUND	% ROCKS	% FORBS	% GRASS	%WOODY SHRUBS	% SMALL TREES
A	1	10	0	50	35	0	2
A	2	10	0	75	3	0	10
A	3	6	0	55	35	0	2
A	4	18	0	40	30	0	2
A	5	18	0	40	30	0	2
A	7	50	0	33	2	0	0
A	8	8	0	40	40	0	2
A	9	3	0	50	35	0	7
A	10	1	0	40	35	0	22
B	1	15	0	40	5	0	30
B	2	25	0	30	5	0	30
B	3	15	0	40	0	0	40
B	4	30	0	30	0	0	10
B	5	50	3	20	0	0	10
B	6	50	3	12	0	0	10
B	7	25	0	25	5	0	10
B	8	25	0	25	5	0	10
B	9	50	0	8	0	0	2
B	10	15	1	45	0	0	9
C	1	40	0	30	0	0	25
C	2	40	20	10	0	0	25
C	3	25	50	10	0	0	15
C	5	70	0	10	0	0	15
C	6	60	0	20	0	0	15
C	7	20	0	30	0	30	0
C	8	40	0	30	0	0	5
C	9	40	0	30	0	0	10
C	10	30	0	30	0	0	30
F	1	60	5	15	10	5	0
F	2	15	5	45	20	0	0
F	3	30	10	30	20	0	0
F	4	15	30	20	15	0	5
F	5	20	5	30	20	15	0
F	6	20	10	30	15	15	5
F	7	30	20	15	10	0	5
F	8	30	20	40	5	0	0
F	9	15	5	60	0	10	0

F	10	55	10	25	5	0	1
H	1	40	5	10	15	0	5
H	2	40	5	10	15	0	5
H	3	30	0	35	10	0	5
H	4	20	30	30	10	0	5
H	5	20	15	30	20	0	10
H	6	20	15	30	20	0	10
H	7	5	0	40	30	0	5
H	8	5	0	40	20	0	10
H	9	5	0	40	20	0	10
H	10	0	0	40	20	0	5
J	1	5	1	55	20	0	14
J	2	20	1	60	5	0	10
J	3	25	0	50	15	0	8
J	4	8	7	55	10	0	5
J	5	45	5	20	20	0	5
J	6	5	0	60	5	0	15
J	7	5	45	10	20	0	15
J	8	10	0	45	10	0	20
J	10	30	5	50	5	0	5
M	1	10	1	80	2	0	7
M	2	10	2	80	2	3	1
M	3	10	2	80	2	3	1
M	4	50	0	25	2	1	2
M	5	50	0	30	5	0	5
M	6	40	0	50	2	0	5
M	7	40	15	15	10	10	5
M	8	40	15	15	10	10	5
M	9	0	40	3	2	30	10
M	10	0	40	0	0	35	25
P	1	8	2	40	10	0	20
P	2	2	0	50	5	0	30
P	3	5	0	35	30	0	20
P	4	10	0	35	25	0	20
P	5	5	0	40	10	0	40
P	6	5	0	40	20	0	20
P	7	5	0	40	20	0	20
P	8	10	0	25	5	0	20
P	9	5	0	10	5	0	20
P	10	5	0	10	5	0	15
Q	1	70	5	0	5	10	5
Q	2	50	5	40	0	0	0
Q	3	50	5	40	0	0	0
Q	4	15	0	70	10	0	0
Q	5	5	0	90	0	0	0
Q	6	5	0	90	0	0	0
Q	7	40	20	20	10	0	5
Q	8	20	5	60	10	0	0
Q	9	5	10	75	5	0	0
Q	10	5	15	70	5	0	0

R	1	35	0	10	5	30	10
R	2	45	0	5	0	15	5
R	3	60	0	15	5	5	5
R	4	70	0	5	0	5	10
R	5	65	0	10	10	5	0
R	6	70	0	10	0	10	5
R	7	5	0	40	45	0	10
R	8	0	0	45	50	0	5
R	9	40	0	0	0	15	5
R	10	60	0	5	0	15	5
S	1	5	0	20	30	40	5
S	2	5	0	35	20	20	10
S	3	5	0	60	30	0	0
S	4	15	0	40	30	5	5
S	5	5	0	10	0	65	10
S	6	50	0	35	5	0	5
S	7	20	0	50	0	10	5
S	8	35	0	10	0	25	10
S	9	45	0	5	0	30	5
S	10	50	0	25	0	5	0
U	1	40	0	20	20	0	0
U	2	30	0	10	40	0	0
U	3	50	0	25	5	0	0
U	4	50	0	30	0	0	0
U	5	40	0	20	0	30	0
U	6	5	0	45	30	15	0
U	7	5	0	30	20	20	20
U	8	40	0	20	15	10	5
U	9	35	0	15	5	5	20
U	10	0	0	30	15	0	15