The influence of soil on whitebark pine (Pinus albicaulis) cone production in the Greater Yellowstone Ecosystem
by Adam Walker Morrill

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 examined the relationships between whitebark pine (Pinus albicaulis) cone production and soil properties and foliar nutrient levels. Cone count data were collected by the Interagency Grizzly Bear Study Team from plots across the Greater Yellowstone Ecosystem (1980-1999). The data used in this study came from 8 of those plots (78 trees) and covered the years of 1989-1997. Soil properties measured included: electrical conductivity (EC), pH, percent coarse material, texture (% sand, % silt and % clay), percent organic matter and depth. Foliar nutrient levels were determined for the following nutrients: boron, calcium, copper, iron, potassium, magnesium, manganese, molybdenum, nitrogen, phosphorus, sulfur and zinc. These variables were regressed against cone production to determine their influence and significance. EC and pH both had significant positive correlations with cone production, and percent coarse material had a significant negative correlation with cone production. EC is a measure of the concentration of ions in solution, and in whitebark pine environments it can be used as an approximation of the amount of available nutrients. When soil pH levels approach neutral more nutrients necessary to plants become available. Percent coarse material limits the amount of surface area on which nutrients or water may be held, and thus limits productivity. All other variables had no significant relationships with cone production.

A multiple regression model using EC and pH significantly explained 38% of the variation in cone production. Percent coarse material was insignificant in the model because of its covariance with EC and pH, suggesting that it affected soil chemistry rather than water availability. A second multiple regression model, which used crown volume (Spector, 1999) and EC, significantly explained 59% of the variation in cone production. Soil pH was not used because of its correlation with EC, and because EC had more predictive power. The information gained from this study could be used to assist in site selection for planting of whitebark pine, and in developing other management strategies that increase whitebark pine cone production and provide better wildlife habitat.

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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 examined the relationships between whitebark pine (*Pinus albicaulis*) cone production and soil properties and foliar nutrient levels. Cone count data were collected by the Interagency Grizzly Bear Study Team from plots across the Greater Yellowstone Ecosystem (1980-1999). The data used in this study came from 8 of those plots (78 trees) and covered the years of 1989-1997. Soil properties measured included: electrical conductivity (EC), pH, percent coarse material, texture (% sand, % silt and % clay), percent organic matter and depth. Foliar nutrient levels were determined for the following nutrients: boron, calcium, copper, iron, potassium, magnesium, manganese, molybdenum, nitrogen, phosphorus, sulfur and zinc. These variables were regressed against cone production to determine their influence and significance. EC and pH both had significant positive correlations with cone production, and percent coarse material had a significant negative correlation with cone production. EC is a measure of the concentration of ions in solution, and in whitebark pine environments it can be used as an approximation of the amount of available nutrients. When soil pH levels approach neutral more nutrients necessary to plants become available. Percent coarse material limits the amount of surface area on which nutrients or water may be held, and thus limits productivity. All other variables had no significant relationships with cone production. A multiple regression model using EC and pH significantly explained 38% of the variation in cone production. Percent coarse material was insignificant in the model because of its covariance with EC and pH, suggesting that it affected soil chemistry rather than water availability. A second multiple regression model, which used crown volume (Spector, 1999) and EC, significantly explained 59% of the variation in cone production. Soil pH was not used because of its correlation with EC, and because EC had more predictive power. The information gained from this study could be used to assist in site selection for planting of whitebark pine, and in developing other management strategies that increase whitebark pine cone production and provide better wildlife habitat.

INTRODUCTION

Whitebark pine grows in the western mountains of North America (Figure 1). It is generally found between the high elevation forests and upper treeline. Until recently little research attention has been given to the species due to its low timber value. However whitebark pine is important for wildlife, microclimates, snowmelt accumulation and ablation, and for reduced erosion in the upper parts of watersheds.

Whitebark pine is currently in danger from an introduced disease, white pine blister rust (*Cronartium ribicola*). This disease is moving into the Greater Yellowstone Ecosystem (Figure 2) from the Pacific Northwest (where it was accidentally introduced in 1910) (Hoff and Hagle, 1990). Whitebark pine is of great value to grizzly bears (*Ursus arctos horribilus*) because the cones contribute to part of the bears' diet (due to the high fat content of the seeds) (Kendall and Arno, 1990; Mattson and Jonkel, 1990; Baskin 1998). This large supply of high fat and easily accessible food serves to keep the bears foraging in higher elevations. Without an adequate seed supply the bears will increase the geography of their search for other food sources. Unlike the area around Glacier National Park, Montana where the bears have an alternative food in the higher elevations (e.g. huckleberries, *Vaccinium globulare*), the bears of the Greater Yellowstone Ecosystem lack alternate sources of plant-derived food in the higher elevations (Baskin, 1998). As a result, when the whitebark pine cone crop declines, bears leave the higher elevations in search of other types of food (such as elk or bison) (Kendall and Arno,

Figure 1: Distribution of whitebark pine across North America (from Arno and Hoff, 1989).

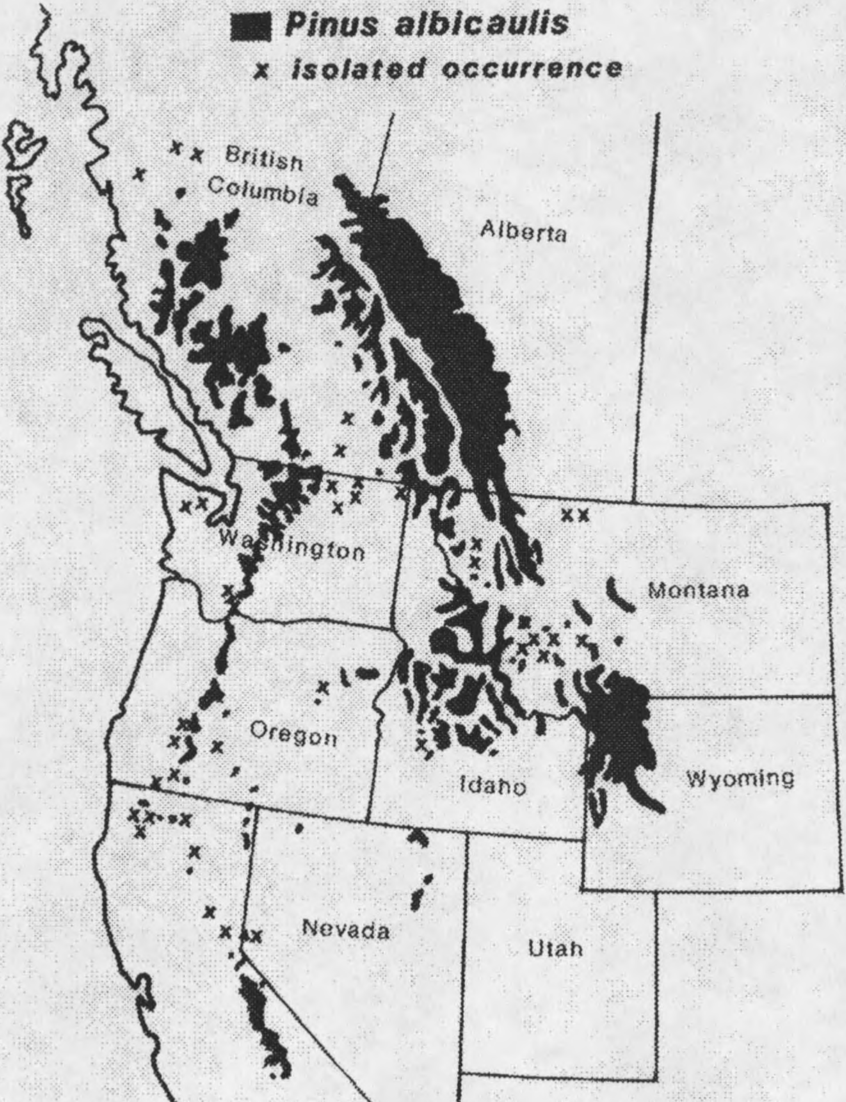
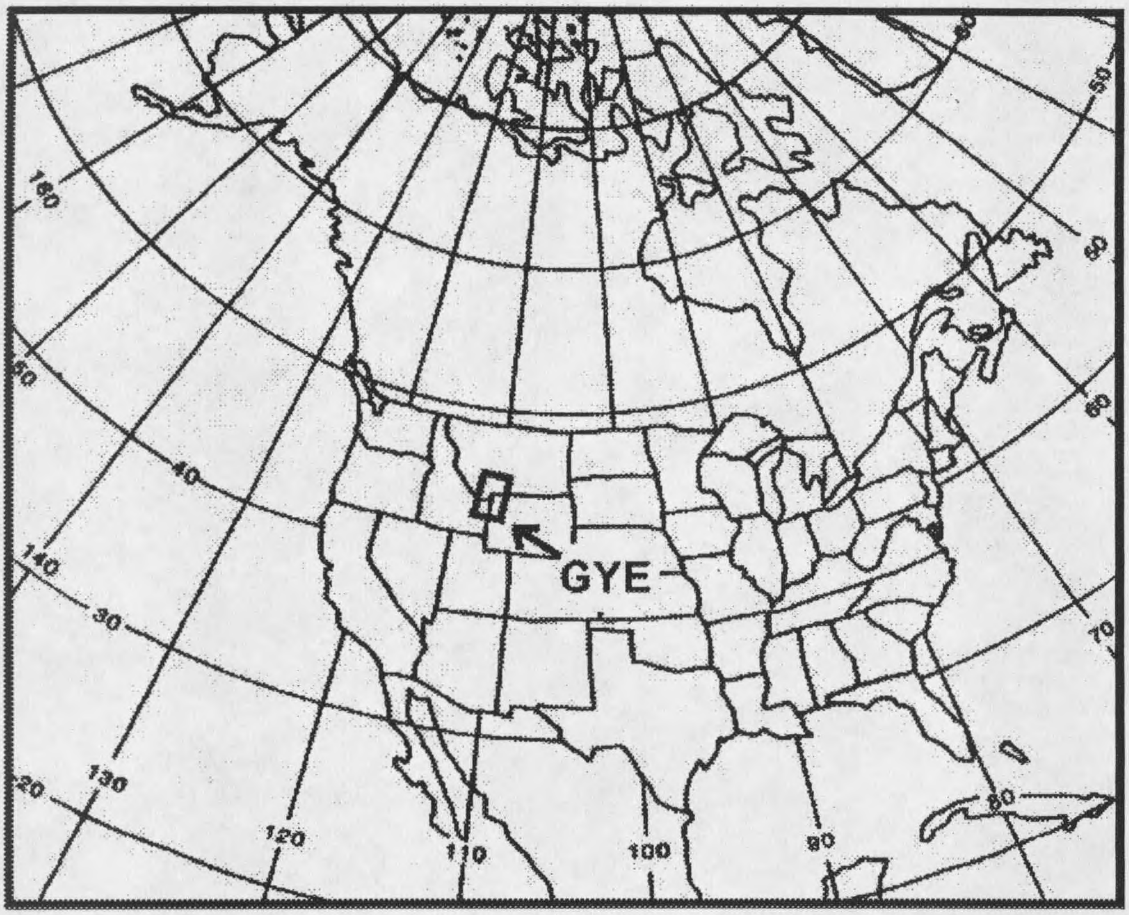


Figure 2: Location of the Greater Yellowstone Ecosystem (GYE).



1990) which may result in increased numbers of bear/human interactions (Blanchard, 1990; Kendall and Arno, 1990; Mattson and Jonkel, 1990). It has been documented that bear mortality (especially human-caused mortality) increases in years of low whitebark pine cone production (Mattson, 1998).

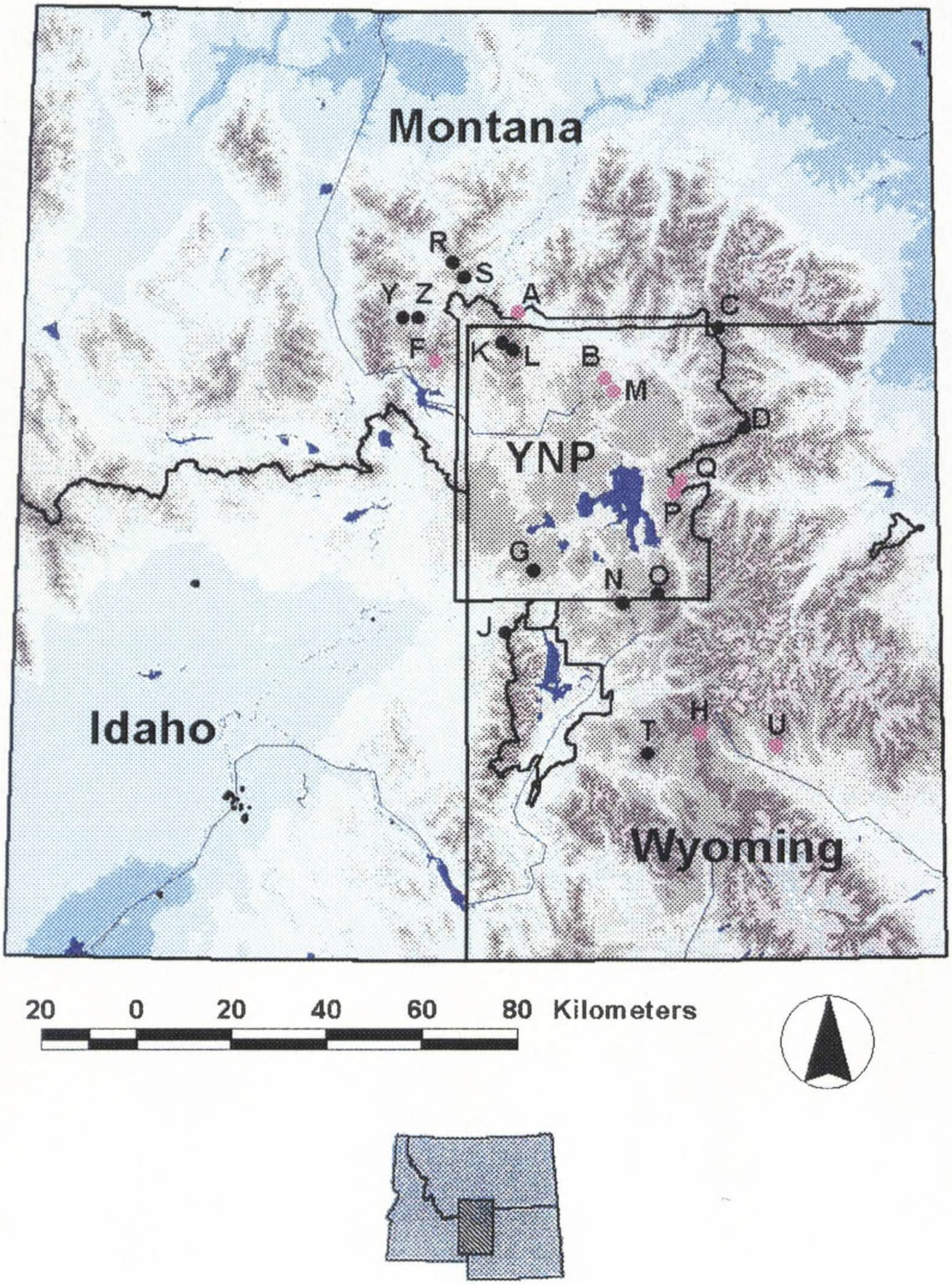
In 1980, the Interagency Grizzly Bear Study Team began collecting whitebark pine cone counts from sites around the Greater Yellowstone Ecosystem (Figure 3) in order to better understand whitebark pine cone production. Many factors, such as soils, climate, disease, ecology and genetics, may influence whitebark pine cone production, but to date there have been no studies that have examined the effects of soil on whitebark pine cone production (Arno, pers. comm.; Callaway, pers. comm.; Keane, pers. comm.; Montagne, pers. comm.).

Objectives and Hypotheses

The objective of my research was to determine if various soil properties affect whitebark pine (*Pinus albicaulis*) cone production in the Greater Yellowstone Ecosystem. There is a need to better understand what factors in the environment affect the cone production of whitebark pine. Soil properties studied included electrical conductivity, pH, texture, depth, and percent organic matter. Foliar nutrient concentrations were also studied, as a method of determining the use of soil nutrients by the tree. Soil properties should affect cone production because they strongly influence the potential productivity of a site (Powers et al., 1998).

The hypotheses of this study, based on previous literature, were:

Figure 3: Interagency Grizzly Bear Study Team cone count sites (sites used in this study are in red) (YNP = Yellowstone National Park).



1) Soils with higher electrical conductivity values contribute to higher cone production.
2) Soils with more neutral pH values will contribute to higher cone production.
3) Soils with lower proportions of coarse material (material greater than 2mm) contribute to higher cone production.
4) Soils with finer textures (lower in percent sand and higher percentages of silt and clay) contribute to higher cone production.
5) Soils with higher percentages of organic matter contribute to higher cone production.
6) Deeper soils contribute to higher cone production.
7) Trees with higher levels of nutrients have higher cone production

Increased knowledge about soils and cone production in whitebark pine stands will help in predicting the geography of high and low cone productivity sites. The long-term benefit of my research will be to assist in site selection for the artificial planting of whitebark trees, assuming that soils that produce cones well may also support transplanted trees. This study may also contribute towards decisions on possible fertilization applications for transplants and it provides new information on the nutritional requirements of whitebark pine for cone production.

Previous Literature

Soil Characteristics

Soil serves as the foundation on which plants grow, and as a reservoir for nutrients and moisture (Steila, 1976). Soil is a reflection of the environment (climate, biology, topography, parent material, and time) in which it exists (Jenny, 1941). Variability in environments results in different soils, with different productivity potentials, reflected in the productivity of plants. Since soil is essentially a summary of the surrounding environment, differences in soil can provide some insight into explaining differences in plant productivity.

Electrical Conductivity. Electrical conductivity (EC) is an indicator of the ion concentration in solution. Typically it is used for determining the degree to which soils may be salt-affected (Singer and Munns, 1996). In soils that are not salt-affected, such as forest soils, EC is correlated with cation exchange capacity (or the total amount of cations that the soil can hold), which is an important indicator of soil fertility (Singer and Munns, 1996), and exchangeable calcium and magnesium (McBride et al., 1990). Higher EC values can therefore be a good indicator of higher soil fertility in certain environments (McBride et al., 1990), especially in high mountain forests that typically have acidic, well drained soils (Price, 1981). Montagne and Munn (1980) found that EC ranged between 0.00 and 3.40 mmhos/cm (mean = 0.48), for the entire soil profile, in Gallatin National Forest under general forest cover.

Soil pH. Nutrients in the soil become insoluble (or not available for uptake by plants) at very high or very low pH levels (Waring and Schlesinger, 1985; Meurisse et al., 1991; Singer and Munns, 1996; Kimmins, 1997). Most macronutrients are soluble at a pH of 7.0 (or neutral) (Waring and Schlesinger, 1985; Meurisse et al., 1991; Singer and Munns, 1996; Kimmins, 1997). Increased acidity can also have a negative effect on microorganisms that are beneficial to plants (Armson, 1977). In whitebark pine stands, Weaver and Dale (1974) found that pH in Montana and Wyoming ranged between 4.9-5.7, Reed (1976) found that pH in Wyoming averaged 5.1, Baig (1972) found that pH in Alberta averaged 6.0, and in Banff and Jasper National Parks, Alberta pH averaged 5.4 (Holland and Coen, 1982).

Percent Coarse Material and Texture. The overall texture of a soil (which includes percent coarse material) is very important for plant productivity. Texture is a major control on water-holding capacity (Waring and Schlesinger, 1985; Singer and Munns, 1996; Kimmins, 1997) and nutrient retention (Meurisse et al., 1991; Singer and Munns, 1996). Soils that have higher proportions of coarse material and sand will have lower water-holding capacities. Water-holding capacity is especially important in mountain environments where water is usually a limiting resource (Price, 1981). Silt will increase the water-holding capacity of the soil and will weather more rapidly than sand, releasing more nutrients (Steila, 1976). Clay plays an important role in soil fertility because clay surfaces serve as the major reservoir for nutrients in the soil (Meurisse et al., 1991; Singer and Munns, 1996). In whitebark pine stands, Weaver and Dale (1974) found that percent coarse material in Montana and Wyoming ranged between 20-50, and

Baig (1972) found that percent coarse material in Alberta averaged 40. In whitebark pine stands, Weaver and Dale (1974) found that percent sand and clay in Montana and Wyoming averaged 42 ± 1.9 and 8.5 ± 1.7, respectively, Baig (1972) found that percent sand, silt and clay in Alberta averaged 51, 35, and 15, respectively, and in Banff and Jasper National Parks, Alberta percent sand, silt and clay averaged 40, 51, and 9, respectively (Holland and Coen, 1982).

Percent Organic Matter. Organic matter plays a similar role to clay in soil productivity in that it serves as a surface for nutrient and water retention (Waring and Schlesinger, 1985; Page-Dumroese et al., 1991; Singer and Munns, 1996; Kimmins, 1997). As organic matter decomposes it also serves as a source of nutrients (Waring and Schlesinger, 1985; Page-Dumroese et al., 1991; Singer and Munns, 1996; Kimmins, 1997). In whitebark pine stands, Weaver and Dale (1974) found in Montana and Wyoming that percent organic matter averaged 6.1 ± 1.8, Baig (1972) found in Alberta that percent organic matter averaged 8.7, and in Banff and Jasper National Parks, Alberta percent organic matter averaged 3.5 (Holland and Coen, 1982).

Soil Depth. Depth is important for soil productivity in that deeper soil will be able to retain more water for use by plants (Meurisse et al., 1991; Singer and Munns, 1996). Soil depth also influences the rooting zone of plants, and thus their access to resources. Both of these facts are more important in mountain environments where water and other resources are limited (Price, 1981). In whitebark pine stands, Baig (1972) found that soil depth in Alberta averaged 53 cm, and in Banff and Jasper National Parks, Alberta soil depth averaged 102 cm (Holland and Coen, 1982).

Plant Nutrition

The minerals that are necessary for adequate growth are mostly derived from a plant's substrate (Truog, 1951). If a plant does not have its nutritional requirements satisfied it will suffer negative physiological side effects including greater susceptibility to disease and drought, discoloration of leaves, malformation of fruits, retarded growth, lack of reproduction, and death (Kramer and Kozlowski, 1960; Jenny, 1980; Mead, 1984; Mauseth, 1995). However, moderate nutrient deficiencies can promote mycorrhizal associations (mutualistic relationships between tree roots and fungi) which serve to increase the tree's root surface area, thus increasing nutrient and water uptake (Kimmins, 1997). Seed production requires even more nutrients than what is necessary just for survival (Kramer and Kozlowski, 1960), so seed production should be dependent on the characteristics of the soil (including the nature of the soil's microflora). Although excessively high levels of nutrients can have negative effects (Kramer and Kozlowski, 1960), mountain soils and forest soils are typically low in nutrients (Kramer and Kozlowski, 1960; Price, 1981; Kimmins, 1997).

There are certain nutrients that are considered essential to plant growth and productivity. The essential nutrients are well identified and documented, but less is known about the proportions of these nutrients for optimal growth. This varies significantly between plant families, species and even between genotypes (Ericsson, 1994; Kimmins, 1997). As yet it is unknown what the optimal proportions are for whitebark pine. However, for some conifers the optimal proportions have been determined (Table 1).

The following nutrients have been shown to strongly influence the health and productivity of plants.

- Boron: necessary for sugar translocation and water absorption, deficiency will result in injury to apical meristems (Kramer and Kozlowski, 1979).
- Calcium: essential for enzyme functions in the plant (Mauseth, 1995), deficiency will result in injury to meristematic regions, especially root tips (Kramer and Kozlowski, 1979).
- Copper: assists with photosynthesis as part of a plastocyanin (Mauseth, 1995) and an enzyme activator (Singer and Munns, 1996).
- Iron: essential as part of a protein (nitrogenase) used in nitrogen fixation by other organisms (Mauseth, 1995).
- Magnesium: important because it is complexed as chlorophyll (Singer and Munns, 1996) and activates many enzymes (Mauseth, 1995).
- Manganese: important for chlorophyll synthesis (Mauseth, 1995), an enzyme activator (Singer and Munns, 1996) and can affect iron availability (Kramer and Kozlowski, 1979).
- Molybdenum: essential for nitrogen reduction and N_2 fixation (Mauseth, 1995; Singer and Munns, 1996).
- Nitrogen: important for amino acids, nucleic acids, and chlorophyll (Mauseth, 1995; Singer and Munns, 1996).

Table 1. Optimal proportions of some major nutrients (values are based on percent by weight and are relative to a nitrogen value equal to 100) for listed species (Ingestad, 1979).

NUTRIENT	*Pinus sylvestris* (Scots pine)	*Picea abies* (Norway spruce)	*Picea sitchensis* (Sitka spruce)	*Pinus nigra* (Corsican pine)	*Pseudotsuga menziesii* (Douglas fir)
N	100	100	100	100	100
K	45	50	55	50	50
P	14	16	16	20	30
Ca	6	5	4	5	4
Mg	6	5	4	4	5

- Phosphorus: essential for many functions in the plant (ATP, nucleic acids, etc.) (Mauseth, 1995; Singer and Munns, 1996) and is found in high levels in the fruits/seeds (Meyer et al., 1973), a substantial deficiency will inhibit nitrogen utilization (Kimmins, 1997) and may affect fruit/seed formation (Meyer et al., 1973).
- Potassium: important for amino acids and the osmotic balance (or the water transport) of the tree (Mauseth, 1995; Singer and Munns, 1996).
- Sulfur: important for amino acids (Mauseth, 1995; Singer and Munns, 1996).
- Zinc: activates many enzymes (Mauseth, 1995; Singer and Munns, 1996).

Factors Affecting Cone Production

Several factors, such as adverse weather, insect damage and other factors attributable to tree physiology, may contribute to poor cone crops (Allen, 1941). Weaver and Forcella (1986) also found that weather might contribute to poor cone production in whitebark pine. Temperature and precipitation have an important influence on all stages of cone development in whitebark pine throughout the year (McCaughey and Schmidt, 1990). Cone crops for western larch (*Larix occidentalis*) are significantly reduced when temperatures go below -4°C (25°F) at any phenological stage (Farnes et al., 1995).

Crown area and crown volume have significant positive correlations with cone production in whitebark pine (Spector, 1999). Crown area explains 30% of the variation in cone production, while crown volume explains 25%. In western white pine (*Pinus monticola*) it has been found that tree size, as well as genetics, explain 34-49% of the variation in cone production (Hoff, 1981). Hoff (1981) stated that the management of such factors as soil moisture, pH, and wind protection should also improve cone production. Fifty-four percent of the variation in cone production for Scots pine (*Pinus sylvestris*) can be explained by genetics (Savolainen et al., 1993).

Fertilizer and hormone treatments have also been found to increase cone production in some species. The application of nitrogen-based fertilizers is one of the oldest and most widely used methods for increasing cone production (Owens and Blake, 1985) and is a practical means for increasing cone production and reducing the length time between high production years (Edwards, 1986). Heidmann (1984) found that nitrogen/phosphorus fertilizers increased the number of cones for ponderosa pine (*Pinus ponderosa*) by two to four times depending on the amount of fertilizer used. Cone production in black spruce (*Picea mariana*) could be increased by four times when trees were injected with the gibberellin A4/7 (a hormone essential for seed development; Moore and Ecklund, 1975) (Brockerhoff and Ho, 1997). Wheeler and Bramlett (1991) also found that gibberellin treatments increased cone production in loblolly pine (*Pinus taeda*). The type of method used and timing of gibberellin treatments is also import for maximum cone yields (Bonnet-Masimbert, 1987).

REGIONAL SETTING AND SITE DESCRIPTION

Regional Setting

The area known as the Greater Yellowstone Ecosystem served as the regional setting for this research (Figures 2 and 3). The geology, climate, and physiography of the region affect the formation and character of the soils found here. The soils, in turn, may influence the distribution of the area's flora.

Geology

The oldest rocks in the Greater Yellowstone Ecosystem are the Precambrian basement rocks (plutonic and metamorphic) that are approximately 2.7 billion years old. These are found primarily in the northern half of the ecosystem. Over time these rocks were eroded, and the sediments were deposited to form the Belt Supergroup, outside the ecosystem. After this period of erosion (during the Paleozoic and the Mesozoic, approximately 500-150 million years ago), the Greater Yellowstone Ecosystem was covered by vast inland seas, swamps, and lakes. In the water bodies sediments accumulated to depths of several thousand meters. These sediments would later become the limestone, sandstone, and other sedimentary rocks that are found in the Greater Yellowstone Ecosystem. Then during the late Cretaceous (about 100-50 million years ago), as a result of a plate collision on the west coast of what would be North America, the region underwent a period of uplift known as the Laramide orogeny. This episode was the beginning of the Rocky Mountains. Approximately 50 million years ago volcanoes began to erupt in the region. These volcanoes erupted with andesite ash and lava flows, these flows would eventually form the Absaroka Volcanic Supergroup, which extends from southwest Montana through Yellowstone to northwest Wyoming. This volcanic activity stopped around 40 million years ago. After the volcanism stopped the area still underwent uplift and erosion (Fritz, 1985; Alt and Hyndman, 1986; Maughan, 1987; Kiver and Harris, 1999).

Then about 2.5 million years ago volcanism began again. This activity was associated with the Yellowstone Hot Spot and Caldera (Good and Pierce, 1996). Between 2.5 and 0.6 million years ago there occurred three major volcanic cycles that produced some of the largest known eruptions on earth (Huckleberry Ridge (2.0 Ma), Mesa Falls (1.3 Ma), and Lava Creek (0.6 Ma)) (Christiansen and Hutchinson, 1987). These large eruptions (and the smaller ones that were also part of the volcanic cycles) filled the Yellowstone basin with huge amounts of rhyolitic lava and ash flows . These lava flows produced a large plateau made of rhyolite, which is also known as the Yellowstone Plateau. Volcanic activity continued in the area until around 70,000 years ago (Christiansen and Hutchinson, 1987). The last lava flow formed the youngest rocks of the Pitchstone Plateau about 80-70 thousand years ago (Christiansen and Hutchinson, 1987).

During the last 2 million years there have been several episodes of glaciation in the Greater Yellowstone Ecosystem. There is clear evidence of two major glaciations in the region. The first one, and larger one (known as the Bull Lake glaciation), reached its maximum extent between 200 and 130 thousand years ago (Richmond, 1986). The second (known as the Pinedale glaciation) reached its maximum extent between 30 and 13 thousand years ago (Richmond, 1986). There were also smaller glacial periods between these two major events (Richmond, 1986).

Geology exerts a certain amount of influence on soil development and character as noted by Jenny (1941, 1980). Different rock compositions could influence the chemical characteristics of the soils. Soils formed on andesite tend to be more nutritious than soils formed on rhyolite (Despain, 1990). This is because andesite is more mafic, which means it is higher in elements like iron and magnesium (both of which are important to plants (Mauseth, 1995)) and lower in silica (which is not very beneficial to plants (Mauseth, 1995)) (Press and Siever, 1986; Despain, 1990). Soils derived from andesite may also be more productive than sedimentary rocks (e.g. sandstone) because andesite, when weathered, will produce more variety in the type of elements that are available to plants. Age of the parent material affects the amount of time the material has been exposed to weathering, and thus also affects the development of the soil. Geomorphology is also important to soil formation. Geomorphic processes, such as glacial scour, can remove soil which results in that surface having a soil with minimal development and productivity (Price, 1981). In contrast, areas of glacial deposition may be more productive due to the weathered material that is added, rather than removed from the site.

Climate

The ecosystem's continental position in North America (Figure 2) contributes to its dry and low temperature winters, but its mountainous position also induces more precipitation and milder summers than the surrounding lowlands (Dirks and Martner, 1982). Due to the latitude of the ecosystem (approximately 43-46°N), the area (during the winter) is influenced by the subpolar low and receives precipitation in the form of snow, and in the summer it receives precipitation from periodic thunderstorms rather than from frontal systems (Dirks and Martner, 1982). The area receives added moisture from the moist air masses that move in from the southwest by way of the Columbia-Snake River valley (Dirks and Martner, 1982). The highest precipitation months are usually May and June, averaging about 13 cm (5 inches) of precipitation falling in these months across Yellowstone and Grand Teton National Parks (Dirks and Martner, 1982).

Temperatures during the summer reach maximums between 21-27°C (70-80°F) and minimums are usually below 4°C (40°F) in Yellowstone and the Tetons (Dirks and Martner, 1982). Maximum temperatures during the winter average -7°C (20°F), while minimum temperatures average -18°C (0°F) (Dirks and Martner, 1982). The area during the winter will often experience temperature inversions (Dirks and Martner, 1982). According to Baker's (1944) climate divisions, the area within south-central Montana, at an elevation of about 2440 meters (8000 feet), has a growing season (daily average temperature above 6°C; 43°F) of about 110 days long (late May-mid September) and does not have a frost-free period. The portion of the ecosystem in western Wyoming at the same elevation has growing season that is about 165 days long (late April-mid

October) and a frost-free period that is 80 days (mid June-late August)(Baker, 1944). This information may be oversimplified, but it does illustrate obvious climatic differences between the two areas. This difference between these regions could be due to moisture input to western Wyoming from the Snake River valley, which would moderate temperatures. Additionally western Wyoming could be protected from polar air masses, moving into the area from the north, by the Absaroka and the Beartooth Ranges to the north (Locke, pers. comm.).

Climate affects soil development through the rate and degree to which weathering (or the breakdown of the parent material) occurs, with more occurring in environments that are warm and moist and less in environments that are cool and dry (Singer and Munns, 1996). Mountain environments in general have lower amounts of chemical weathering (which is necessary for the formation of clay) than lowland environments because of their low temperatures (Price, 1981). Precipitation affects the movement of material (clay and organic matter) through the soil, so when temperatures are below freezing, soil forming processes are restricted.

Flora

Organisms secrete organic acids that assist in the weathering process, they recycle nutrients, and they protect the soil from erosion (Singer and Munns, 1996). At the lowest elevations, in the Greater Yellowstone Ecosystem, exists grasslands and shrublands composed of many grass species (*Poa spp.*, *Calamagrostis spp.*, etc.) and sagebrush (*Artemisia tridentata*), willow (*Salix spp.*), bitterbrush (*Purshia tridentata*), Rocky Mountain maple (*Acer glabrum*), and serviceberry (*Amelanchier alnifolia*). Forests habitats make up 80% of the vegetation cover across Yellowstone National Park (Despain, 1990). Forest species found in the low-elevation forests include limber pine (*Pinus flexilis*), Rocky Mountain juniper (*Juniperus scopulorum*), Douglas fir (*Pseudotsuga menziesii*), and aspen (*Populus tremuloides*). With an increase in elevation, lodgepole pine (*Pinus contorta*) forests occur. These forests are usually dense and composed mainly of lodgepole pine. These lodgepole forests make up 60% of the total forest cover in the ecosystem. With increasing elevation, the forests are composed of Engelmann spruce (*Picea engelmannii*), subalpine fir (*Abies lasiocarpa*), and whitebark pine (*Pinus albicaulis*). The alpine habitat is at the highest elevations. The plants that grow here are usually small and remain close to the ground. This habitat is mainly composed of grasses, mosses, and lichens, and some krummholz tree-species such as Engelmann spruce, subalpine fir and whitebark pine. A localized, but very important, habitat that is found in the ecosystem is the riparian habitat. A wide variety of plants grow in this habitat ranging from willows (*Salix spp.)* and cottonwoods (*Populus spp.*) at the lower elevations, willows and aspen (*Populus tremuloides*) at the mid-elevations, and spruce and fir at the highest elevations (along stream sides and seeps) (Despain, 1990).

Geography of Whitebark Pine

Whitebark pine is distributed along two major north-south mountainous areas in western North America (Figure 1). The first extends from the coastal mountains of British Columbia south through the Cascades and into the Sierra Nevada. The second area covers the Rocky Mountains and extends from British Columbia and Alberta in the north, through Idaho and Montana, to Wyoming in the south (Arno and Hoff, 1989). In Canada whitebark pine is only a minor subalpine component, while south of the Canadian border it is a major subalpine component (Hansen-Bristow et al., 1990). Whitebark pine reaches its highest elevational range in the southern Sierra Nevada. Whitebark pine's elevational limits are lower in Canada due to its more northern location and the harsher climate (Hansen-Bristow et al., 1990).

The climate of whitebark pine stands (across its entire range) is characterized by low temperature, snowy winters, and moderate temperature, dry summers. Winter minimums average -11°C (12°F), and, on average, maximums do not exceed -2°C (28°F), while summer temperatures range from a minimum of 4°C (39°F) to a maximum of 21°C (70°F) (Weaver, 1990). Snow usually begins to fall by September or October, but snow does not often accumulate until November. The snow pack in the winter averages one to three meters. Spring runoff usually begins in May and continues through June. Rain totals for July through September range from 25mm to 180mm, but it is not uncommon for some months to be rain-free (Weaver, 1990).

Whitebark pine are typically found on a variety of soils (Cryochrepts, Cryoboralfs, Cryoborolls, and Cryorthents), which have minimal development (often due to steep topography) and are characterized as being fairly coarse in texture and nutrient poor (Hansen-Bristow et al., 1990). The low temperature, harsh environment, that is characteristic of subalpine ecosystems, limits the amount of chemical and biological weathering that occurs with these soils (Price, 1981).

Site Description

The Interagency Grizzly Bear Study Team maintains a total of 19 cone count sites throughout the Greater Yellowstone Ecosystem (Schwartz, pers. comm.) (Figure 3). For this study a sub-sample consisting of eight of those sites was used. The selected sites are displayed in Figure 3.

Geology

The geologic composition and age of the sites was summarized (Table 2). Sites B, M, P, and Q would be expected to have better nutrient pools in the soils than sites A and F, because of the location on andesitic substrates rather than on sedimentary substrates. Sites B, M and U have darker rocks than P and Q, which indicate that they have higher amounts of mafic minerals and lower amounts of silica (Press and Siever, 1986), thus producing soils that are higher in nutrients. All the sites, except F, were glacially eroded during the Pinedale glaciation (Pierce, 1979; Good and Pierce, 1996). This means that site F may have had more time for its soil to develop (possibly contributing to greater productivity), but because of its ridge-line location, would most likely not benefit from this head start due to soil loss as a result of mass wasting.

Vegetation

The ecology (habitat and cover types) of the sites (Table 3) should have some influence on the soil development. Soil development could be enhanced by denser vegetation (increased organic material, more biological weathering, reduced erosion, etc.), but increased competition for nutrients and moisture from other plants could have a

Table 2. Geologic composition and age for the Interagency Grizzly Bear Study Team cone count sites used in this study (from geology maps (U.S. Geological Survey, 1955; Keefer, 1957; U.S. Geological Survey, 1972) and soil surveys (Davis and Shovic, 1996)).

PLOT	COMPOSITION	AGE
A	o Sandstone and shale	o Upper Cretaceous
	o Intrusive dikes composed of rhyodacite, quartz monzonite, and granodiorite	o Early Eocene
B	o Dark-colored andesitic volcaniclastic rocks	o Early Eocene
	o Light-colored andesitic volcaniclastic rocks and andesite lava flows	o Late Eocene
F	o Limestone	o Mississippian
	o Calcareous Sandstone	o Jurassic/Cretaceous
H	o Tuffaceous claystone and sandstone	o Mid-Late Eocene
M	o Dark-colored andesitic volcaniclastic rocks	o Early Eocene
	o Light-colored andesitic volcaniclastic rocks and andesite lava flows	o Late Eocene
P	o Light-colored andesitic volcaniclastic rocks, andesite lava flows and intrusives of andesite, diorite, and quartz monzonite	o Late Eocene
	o Detrital Deposits	o Quaternary
Q	o Light-colored andesitic volcaniclastic rocks, andesite lava flows and intrusives of andesite, diorite, and quartz monzonite	o Late Eocene
	o Detrital Deposits	o Quaternary
U	o Dark-colored volcanic conglomerate and breccia	o Oligocene

Table 3. Habitat and cover types for the Interagency Grizzly Bear Study Team cone count sites used in this study (data from the Interagency Grizzly Bear Study Team, cover type descriptions from Despain (1990)).

PLOT	HABITAT	COVER TYPE
A	ABLA/THOC-PIAL	WB3
B	ABLA/VASC-PIAL	WB2
F	PIAL/FEID	WB
H	ABLA/VASC-PIAL	No Data
M	PIAL/JUCO	WB
P	ABLA/VAGL-VASC	WB3
Q	ABLA/VASC-PIAL	WB2
U	ABLA/JUCO	WB

Habitat Types:	Species:
ABLA/THOC-PIAL	-*Abies lasiocarpa/Thalictrum occidental-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/Vaccinium globulare-V. scoparium* phase subalpine fir/globe huckleberry-grouse whortleberry phase
ABLA/JUCO	-*A. lasiocarpa/J. communis* subalpine fir/common juniper

Cover Types:
WB – Climax stand of whitebark pine
WB2 – Mature stand of whitebark pine
WB3 – Over-mature stand of whitebark pine

negative effect on whitebark pine. Kipfer (1992) found that competition from other trees significantly decreased the crown size of whitebark, which is known to affect cone production (Spector, 1999). However, it is unclear whether these trees are competing for light or for soil resources.

Topography

The topography (slope and aspect) of the sites (Table 4) influences soils in that less steep slopes may have deeper and more productive soils than sites with steeper slopes, where soil is lost through the down-slope movement of material (Price, 1981). Thus sites H and U would be expected to have better deeper soils than other sites, because of their relatively flat slopes; site M would be expected to have shallower soils because of its very steep slope. Aspect influences the available energy and soil moisture at a given site. Sites with north-facing aspects (such as B and H) may retain more moisture (due to less evaporation and possible re-deposition of snow from southwest winds) which would contribute to higher plant productivity, but they may also experience lower temperatures, which would decrease plant productivity. So sites that have aspects that maximize average temperatures, while at the same time maximizing moisture levels, should have higher levels of plant productivity. Sites on southwest-facing slopes (plots F, M, P, and Q) will tend to be the warmest and the driest because of their exposure to the late afternoon sun, while northeast-facing slopes (plot U) will tend to be the coolest and the wettest because of their minimal solar exposure (Birkeland, 1999). So sites on northwest-facing and southeast-facing slopes (plots A and H) should have higher

Table 4. Topographic data for the Interagency Grizzly Bear Study Team cone count sites used in this study (data from the Interagency Grizzly Bear Study Team).

PLOT	ELEVATION (METERS)	SLOPE (%)	ASPECT (°)
A	2560	5-20	100
B	2652	30	266
F	2896	28	232
H	2835	8	119
M	2743	50	230
P	2682	30	220
Q	2926	35	224
U	2682	5	70

production because these aspects should have at least moderate amounts of both solar radiation and moisture.

Soils

The soils for the sites visited (Table 5) are all classified as low temperature soils (mean annual temperatures higher than 0°C and lower than 8°C; Soil Conservation Service, 1975). The Cryoborolls at sites B, F, M, P, and Q may be more productive because of their dark organic-rich surface horizon, which provides a source for nutrients and increased moisture retention (Singer and Munns, 1996). Site A's soil (Cryoboralf) may also be productive because of its clay accumulation, which increases moisture retention, and is a possible source of nutrients (Singer and Munns, 1996). Sites with lithic contacts (B, M, and Q) could possibly benefit from the bedrock contact in that the trees may be able to access water in rock fractures, or extract nutrients from the rock. A lithic contact could also have no effect or a negative effect. If the rock is heavily fractured, water may be completely drained away from the site and have a negative effect on the plants, and if the rock is not high in minerals that are important to plants it will not be beneficial to have that lithic contact (in the case of plots B, M, and Q, the lithic contact, which is primarily andesitic, would most likely be beneficial because of higher amounts of nutrients that are available).

Table 5. Soil types for the Interagency Grizzly Bear Study Team cone count sites used in this study (data for sites A, B, M, P, Q, and U were obtained from the Yellowstone National Park soil survey (1996), data for site F were obtained from the Gallatin National Forest soil survey (1996)). Soil descriptions were taken from Veseth and Montagne, 1980; Soil Conservation Service, 1975; Davis and Shovic, 1996; Rodman et al., 1996; and Singer and Munns, 1996.

STAND	SOIL TYPE
A	Typic Cryoboralf, Typic Cryochrept
B	Typic Cryoboroll, Lithic Cryoboroll
F	Typic Cryochrept, Typic Cryoboroll
H	No published data
M	Typic Cryoboroll, Lithic Cryoboroll, Pachic Cryoboroll, Argic Pachic Cryoboroll
P	Typic Cryoboroll, Typic Cryochrept, Argic Cryoboroll
Q	Typic Cryoboroll, Lithic Cryoboroll, Pachic Cryoboroll
U	No published data

Soil Types:	Descriptions:
Typic Cryoboralf –	Typical cold, cool (mean soil temperature is > 0°C and < 8°C) soil that is light-colored and has accumulations of illuviated clays in the subsoil horizons.
Typic Cryochrept –	Typical cold (mean soil temperature is > 0°C and < 8°C) soil that is light-colored, young and minimally developed.
(Typic) Cryoboroll –	Typical cold, cool (mean soil temperature is > 0°C and < 8°C) soil with a dark, organic-rich surface horizon.
Lithic –	Has a shallow lithic contact.
Pachic –	Has a thick surface horizon
Argic –	Has a horizon with significant clay accumulation.

METHODS

The Interagency Grizzly Bear Study Team maintains a total of 19 cone count sites throughout the Greater Yellowstone Ecosystem (Schwartz, pers. comm.) (Figure 3). For this study I selected a sub-sample of those sites. Plot cone productivity variations (high, medium and low producing plots were included to get a broad profile of cone production), and widespread geographical distribution of these sites were criteria for site selection. The sites visited as part of this study are displayed in Figure 3.

Field Methods

The measurements and samples collected in the field include surface soil samples, depth measurements, and foliage samples. All field data were collected during the summer of 1999.

Soil Samples

At each transect, soil samples were collected from each of the ten trees, except at sites A (where tree A6 was dead) and Q (where data was not collected from Q1 due to adverse weather conditions). Samples were collected at four points, at azimuths of N, E, S, and W, halfway between the trunk and the crown perimeter, to control for the variation in soil properties that occur with distance from the tree's trunk (Birkeland, 1984). If an obstacle to sampling was encountered (e.g. a rock, a surface root, etc.), the position of the sampling point was moved counter-clockwise around the tree until the obstruction was clear (the maximum move was 30 cm). A total of at least 200 grams of fine material (<2 mm) was collected from around each tree (approximately 50 grams from each sample point). Samples were collected from the surface mineral horizon (or A horizon) where the majority of a tree's fine roots exist (Beaton, 1973; Armson, 1977; Bowen, 1984; Wilson, 1984; Kimmins, 1997). Any overlying organic material (e.g. litter or humus) was removed so that only the surface mineral horizon was sampled. The samples were placed in zip-lock bags and labeled with the site's letter, tree number, and the aspect of the sample (N, S, E, W).

Soil Depth

Soil depth was measured at ten points around each tree. Measurements were taken at equal compass intervals of 36°. Measurements were taken at points halfway between the trunk and edge of crown. The depth at each point was determined by measuring the depth (to the nearest centimeter) to which a metal rod could be hammered into the soil until a solid object was encountered.

Foliar Samples

Foliage, in the form of needles, was collected for laboratory analysis to determine elemental composition. This method has been previously used in agriculture and forestry to determine the nutritional state of a plant, which is a reflection of the nutrient status of the soil (Kramer and Kozlowski, 1960; Beaton et al., 1965; Van Den Driessche, 1974; Zasoski et al., 1990; Fluckiger and Braun, 1995; Kimmins, 1997).

Approximately 40 grams of foliage was clipped from the lower part of the crown (closet to the ground) on the north-facing side. The consistent sampling position was chosen to reduce nutrient variation in the samples that could be attributed to differences in the amount of light received. It has been found that needles that receive more light will have nutrient levels that are diluted due to higher carbohydrate concentrations (Van Den Driessche, 1974). Because nutrient translocation occurs from older foliage to younger foliage (Van Den Driessche, 1974), all samples were collected from the same year of growth (1998) and were the youngest mature needles available. This previous year's growth (1998) was selected because not all sites had mature present year's (1999) foliage at the time of sampling, and because it has been shown that nutrient level will vary at different development stages (Van Den Driessche, 1974).

After the samples were clipped from the trees they were placed in paper bags to stop photosynthesis and to prevent condensation and molding (McCaughey, pers. comm.). Samples were labeled by site letter and tree number. Of the total number (78) of trees visited, 63 foliar samples were obtained (Table 6). The trees from which foliar samples were not taken either had no live needles within reach or had obvious signs of infection (e.g. discoloration of the needles). Infection has been found to taint analysis results (Van Den Driessche, 1974). Once out of the field, the samples were sealed in plastic bags and placed in a freezer (for no more than one week), to slow or stop continued biological functions and reduce nutrient loss, until they could be dried (Van Den Driessche, 1974; Armstrong, pers. comm.; McCaughey, pers. comm.).

Table 6. Interagency Grizzly Bear Study Team whitebark pine trees that were visited, sampled, and selected for foliar analysis.

PLOT	TREES VISITED	TREES SAMPLED	TREES SELECTED
A*	1,2,3,4,5,7,8,9,10	1,2,3,4,8,9	3,4,8
B	1,2,3,4,5,6,7,8,9,10	1,4,5,6,7,8,9,10	4,5,6,10
F	1,2,3,4,5,6,7,8,9,10	1,2,3,4,5,6,7,8,9,10	1,4,7,8,9
H	1,2,3,4,5,6,7,8,9,10	1,2,3,4,6,7,8,9,10	2,3,6,9,10
M	1,2,3,4,5,6,7,8,9,10	2,3,4,5,6,7,8,9,10	3,4,5,8,9
P	1,2,3,4,5,6,7,8,9,10	2,6,9	2,9
Q**	2,3,4,5,6,7,8,9,10	3,4,5,6,7,8,9,10	4,5,6,8
U	1,2,3,4,5,6,7,8,9,10	1,2,3,4,5,6,7,8,9,10	2,4,5,7,8

* Tree A6 was not visited because it is dead.
** Tree Q1 was not visited due to lightning.

Table 7. Mean whitebark pine cone production by year, and for the entire period (1989-1997) for the Interagency Grizzly Bear Study Team cone count sites used in this study.

PLOT	1989	1990	1991	1992	1993	1994	1995	1996	1997	AVG
A	0.8	0.0	9.3	16.7	6.8	0.4	0.0	32.7	0.6	7.5
B	55.3	2.4	36.2	15.8	6.0	0.0	0.5	43.9	0.0	17.8
F	95.0	1.2	9.5	13.1	0.0	0.0	2.4	5.7	0.1	14.1
H	15.1	0.0	21.1	6.6	16.3	3.9	3.4	22.4	18.0	11.9
M	73.7	2.8	22.6	26.4	4.9	0.0	0.2	47.7	0.0	19.8
P	16.1	0.0	10.2	7.7	10.8	0.3	0.7	27.6	1.3	8.3
Q	8.3	0.0	11.0	1.9	5.6	0.0	1.5	4.2	0.8	3.7
U	28.3	0.0	36.6	14.7	30.4	24.4	27.7	29.8	29.2	24.6

Lab Methods

Soil Samples

The soil samples were air dried, sieved and analyzed for percent coarse material (>2mm), percent sand, silt, and clay, percent organic matter, pH, and electrical conductivity (measured in mmhos/cm). The fine and coarse material for each sample (N, S, E, and W for each tree) were weighed and a percent coarse material value (based on the sample's total weight) was calculated for each sample. For the analysis of the remaining soil properties, the fines of the four samples from each tree were combined. In the combining process, equal portions were taken (using a riffle splitter) from each of the four samples and combined. The riffle splitter was used again to obtain the sub-samples for the lab tests. A standard set of procedures was followed in the analysis of the remaining soil properties (Appendix A).

Foliar Samples

In the lab, foliar samples were lightly rinsed with distilled water to remove any dust that might have affected the results (Van Den Driessche, 1974). Samples were dried in their paper bags in a drying oven at 50°C for approximately 2 days (until the samples were dry and could be ground for passage through a 2 mm screen)(Armstrong, pers. comm.). Only thirty-three samples were analyzed (out of 63 collected) due to budget restraints. Half of the samples from each plot (so that every plot was represented in the analysis) were randomly selected (Table 6) using computer generated random numbers. This was to ensure that the data would not be skewed by a non-random selection process

(Cherry, pers. comm). One tree with unusually high cone production was also included (even though it had not been randomly selected) because of its uniquely high productivity. The samples were analyzed by the Soil Analytical Lab at Montana State University, Bozeman (using digestion methods outlined by Chapman and Pratt (1961) and an Inductively Coupled Plasma emission spectrometer (Fisons Instruments, model: Accuris) for the analysis) for Total Kjeldahl Nitrogen (TKN) (organic nitrogen and ammonium), boron, calcium, copper, iron, potassium, magnesium, manganese, molybdenum, phosphorus, sulfur, and zinc.

Statistical Analysis Methods

Cone data from 1989-1997 were used in the analysis, because the sampled plots had these years of cone counts in common. The average number of cones per tree for the nine years was the basis for determining productivity. Using Microsoft Excel spreadsheet software, simple linear regressions were performed between all independent variables (EC, pH, % coarse material, % sand, % silt, % clay, % organic matter, mean soil depth, the foliar concentrations of each individual nutrient sampled, and the estimated total amount of each individual nutrient sampled) and the response variable (cone production) for all 78 trees sampled. The response variable used was the square root of the average number of cones per tree. This was used rather than the average number of cones per tree because these data (Figure 4) were not normally distribution, and therefore were transformed for linear regression analysis. The data for the average number of cones per tree (Figure 4) had a distribution similar to a Poisson distribution,

Figure 4. Histogram of the average number of whitebark cones per tree (1989-1997) for the trees from the Interagency Grizzly Bear Study Team cone count sites used in this study.

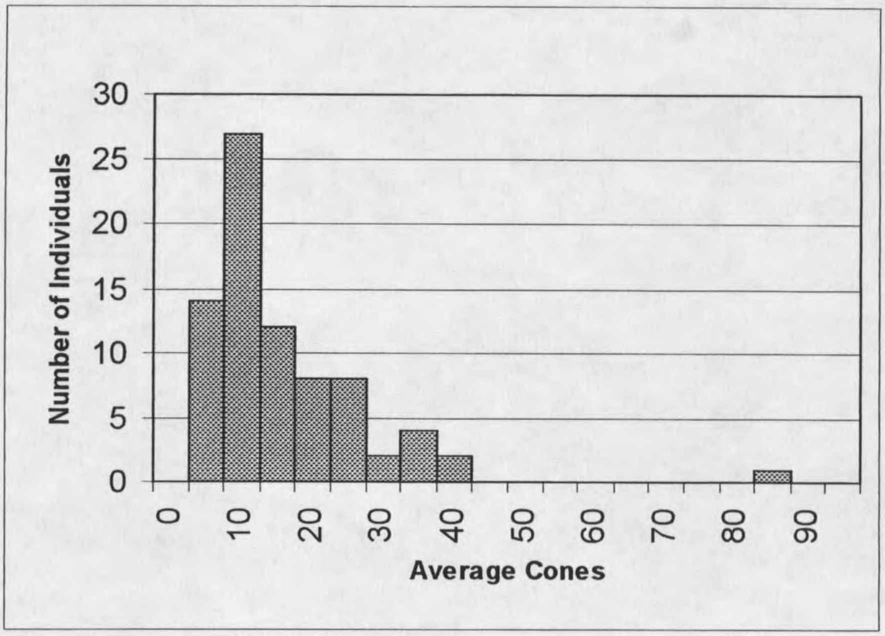
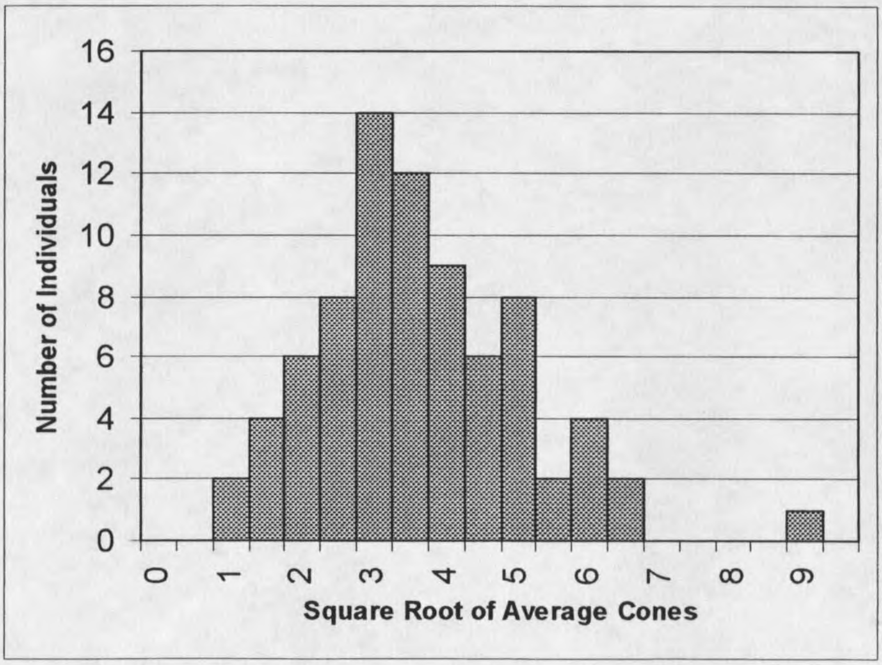


Figure 5. Histogram of the square root of the average number of whitebark cones per tree (1989-1997) for the trees from the Interagency Grizzly Bear Study Team cone count sites used in this study.



and therefore a square root transformation was used for normalization (Figure 5). This transformation is a fairly standard approach for analyzing this type of data (Snedecor and Cochran, 1980; Dixon and Massey, 1983; Cherry, pers. comm.). This transformation also reduced the effect of M9 as an outlier by bringing it in closer to the center of the distribution (Figure 4 (M9 = 85-90), Figure 5 (M9 = 9-9.5). The level of significance used for all regressions was $\propto = 0.05$.

To get the estimated total amount of any given nutrient in a tree, the nutrient concentration value was multiplied by crown volume using values collected by Spector (1999) for the same trees. Spector's study used the same sites and cone data as were used in this study. Spector (1999) examined to what extent tree morphology (tree and crown size, age, and number of stems) and competition influences whitebark pine cone production. It was found that crown size (both area and volume) and total basal area (a measurement of competition) were significantly correlated with cone production. Since crown volume was already correlated with cone production (Spector, 1999), these total nutrient estimates were regressed against the residuals of the regression of crown volume and the square root of average cones per tree for the same trees used in the foliar analysis (Appendix B). This would eliminate the variance that is explained by crown volume, and the total nutrient estimates would explain the remaining variance. Tree U1 was not included in the simple regression of depth verses square root of average cones per tree because I was unable to collect the data due to adverse weather conditions in the field.

A multiple linear regression model was developed using the square root of average cones per tree and the independent variables. A second model was developed using the square root of average cones per tree and the independent variables, and the independent variables measured by Spector (1999) for the same trees. A stepwise selection method determined which variables were included in the model based on their influence and significance. Scatter plots of residual distributions were used to determine the appropriateness of the models (Moore, 1995).

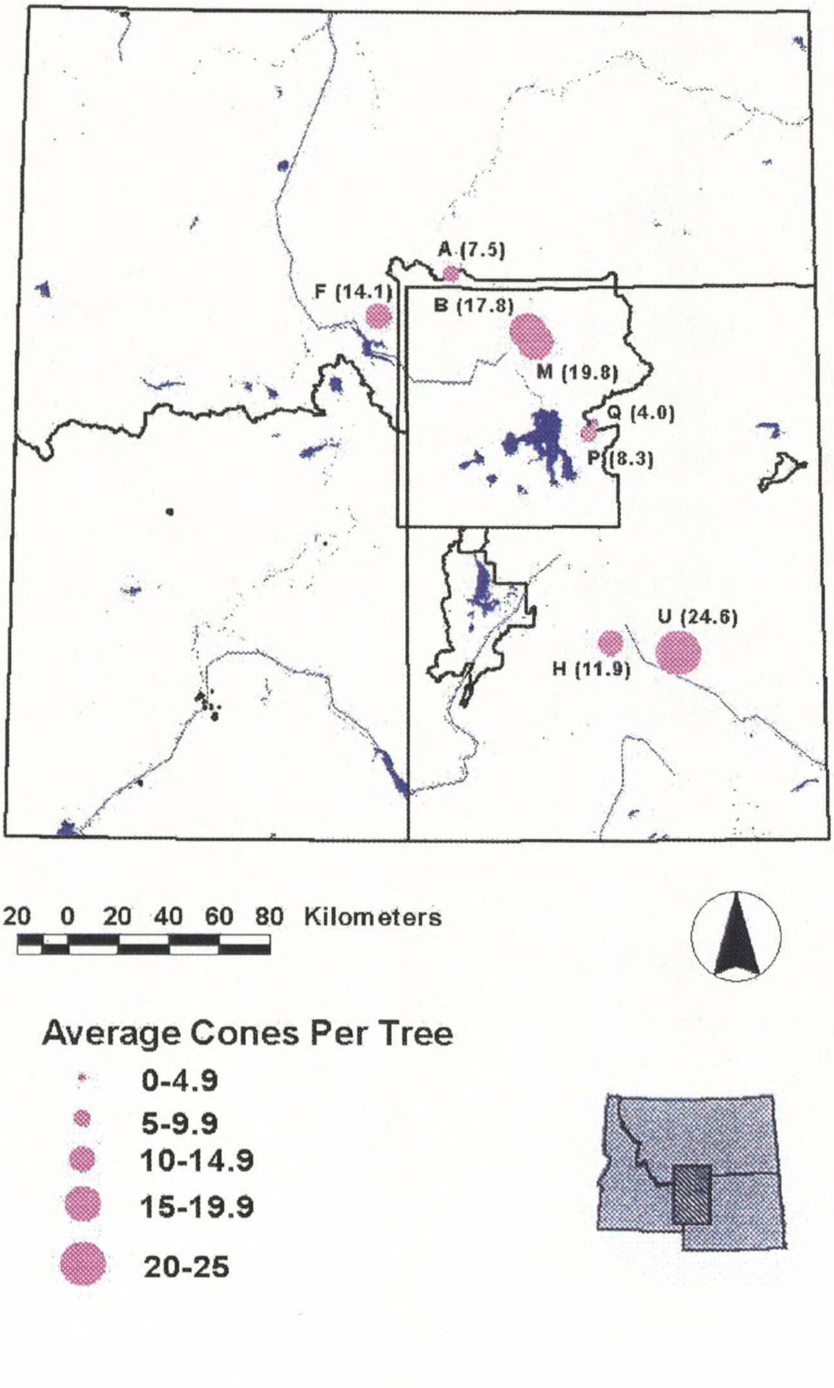
RESULTS AND DISCUSSION

Whitebark Pine Cone Data

Cone data from1989-1997 are summarized for the plots sampled (Table 7). There is a clearly identifiably low cone production year (1990) in which all the plots either produced below the average from 1989-1997 (for each individual plot) or no cones. There are no years in which all the plots had above average (plot average for the years used) cone crops, but in 1996 all sites except one (site F) had an above average year. There appears to be no obvious temporal pattern in cone production among plots.

It appears that there is also no apparent geographic pattern in cone production (Figure 6). Plot U is the most productive plot, averaging 24.6 cones per tree per year during the nine year measurement period, and plot Q was the least productive, averaging 3.7 cones per tree per year. Plot M's relatively high level of average productivity is not an accurate representation of the entire plot, because one tree (M9) is an unusually high producer (producing as many as 325 cones in one year), raising the plot's average from 13.1 to 19.8. This particular tree, even though it skews the plot's average, is included in the analysis because its high cone counts are not the result of errors in measurement (extremely low producers were also included for the same reason).

Figure 6. The average number of whitebark pine cones per tree (1989-1997), by plot, for the Interagency Grizzly Bear Study Team cone count sites used in this study.



Results of the Simple Regressions

Soil Properties

Electrical Conductivity. Mean EC values, measured in mmhos/cm, (Table 8 and Appendix C) ranged between 0.042 at site Q and 0.236 at site U; total range was 0.029 to 0.301. Results fall within the range found by Montagne and Munn (1980) (0.00-3.40, mean = 0.48) in the Gallatin National Forest (under general forest cover), but they are definitely on the low end of the range. This could be due to the fact that the sites used in the survey of the Gallatin National Forest may be dominated by calcareous soils, resulting in higher EC values, additionally the values measured by Montagne and Munn (1980) were average values for the entire soil profile.

EC was significantly correlated with the square root of average cones per tree and explained 33% of the variation (Table 9). The result of the t-test indicated that slope of the regression line (Figure 7) was also significant. This supports the hypothesis that an increase in EC should result in an increase in cone production. This was expected because extremely low EC values (near 0, which is equal to pure water) indicate a low concentration of ions present in the soil solution, thus low nutrient availability. EC however, did not appear to have any apparent geographic pattern (Figure 8), but the relationship between EC and square root of average cones per tree was seen at the plot level (Figure 8, Figure 9); plot U had a highest EC values and highest cone production, while plot Q had the lowest EC value and the lowest cone production.

Table 8. Mean (Range) of the eight soil variables measured for the Interagency Grizzly Bear Study Team cone count sites used in this study.

PLOT	Electrical Conductivity (mmhos/cm)	pH	% Coarse Material	% Clay	% Silt	% Sand	% Organic Matter	Depth(cm)
A	0.091 (0.076-0.11)	4.99 (4.57-5.27)	44 (40-48)	32 (29-42)	33 (24-40)	36 (30-42)	4.6 (3.8-5.7)	69 (36-90)
B	0.098 (0.065-0.144)	5.10 (4.68-5.51)	47 (37-73)	33 (31-36)	37 (34-39)	30 (26-34)	8.2 (5.7-10.8)	43 (34-53)
F	0.083 (0.045-0.122)	5.07 (4.47-6.10)	50 (32-66)	21 (18-25)	29 (25-33)	50 (43-57)	4.4 (3.1-5.8)	26 (19-33)
H	0.095 (0.067-0.129)	4.78 (4.56-5.03)	39 (31-52)	27 (25-29)	35 (32-38)	38 (33-42)	5.7 (4.7-7.6)	28 (16-39)
M	0.145 (0.096-0.250)	5.60 (5.19-6.39)	41 (28-47)	24 (21-26)	38 (30-43)	38 (34-49)	5.3 (4.2-6.4)	25 (11-34)
P	0.111 (0.096-0.133)	4.56 (4.38-4.72)	54 (42-63)	23 (18-26)	34 (33-37)	43 (40-47)	4.9 (4.1-7.3)	37 (26-49)
Q	0.042 (0.029-0.062)	4.93 (4.59-5.28)	71 (50-90)	22 (19-25)	32 (28-36)	46 (40-51)	6.6 (4.9-9.4)	27 (10-44)
U	0.236 (0.148-0.301)	5.90 (5.60-6.46)	17 (10-30)	27 (24-32)	27 (21-31)	47 (40-56)	5.8 (4.3-9.7)	57 (46-81)

Table 9. Results (R^2 and p-values) of the simple regressions between the eight soil variables measured and the square root of average cones per tree for whitebark pine.

VARIABLE	R^2	P-VALUE
Electrical Conductivity	0.33	0.00
pH	0.29	0.00
% Coarse Material	0.22	0.00
% Clay	0.02	0.29
% Silt	0.01	0.45
% Sand	0.00	0.82
% Organic Matter	0.00	0.88
Depth	0.00	0.70

Table 10. Dominant soil texture classes for the Interagency Grizzly Bear Study Team cone count sites used in this study.

PLOT	TEXTURE CLASS
A	Clay loam
B	Clay loam
F	Loam
H	Clay loam
M	Loam
P	Loam
Q	Loam
U	Sandy clay loam

Figure 7

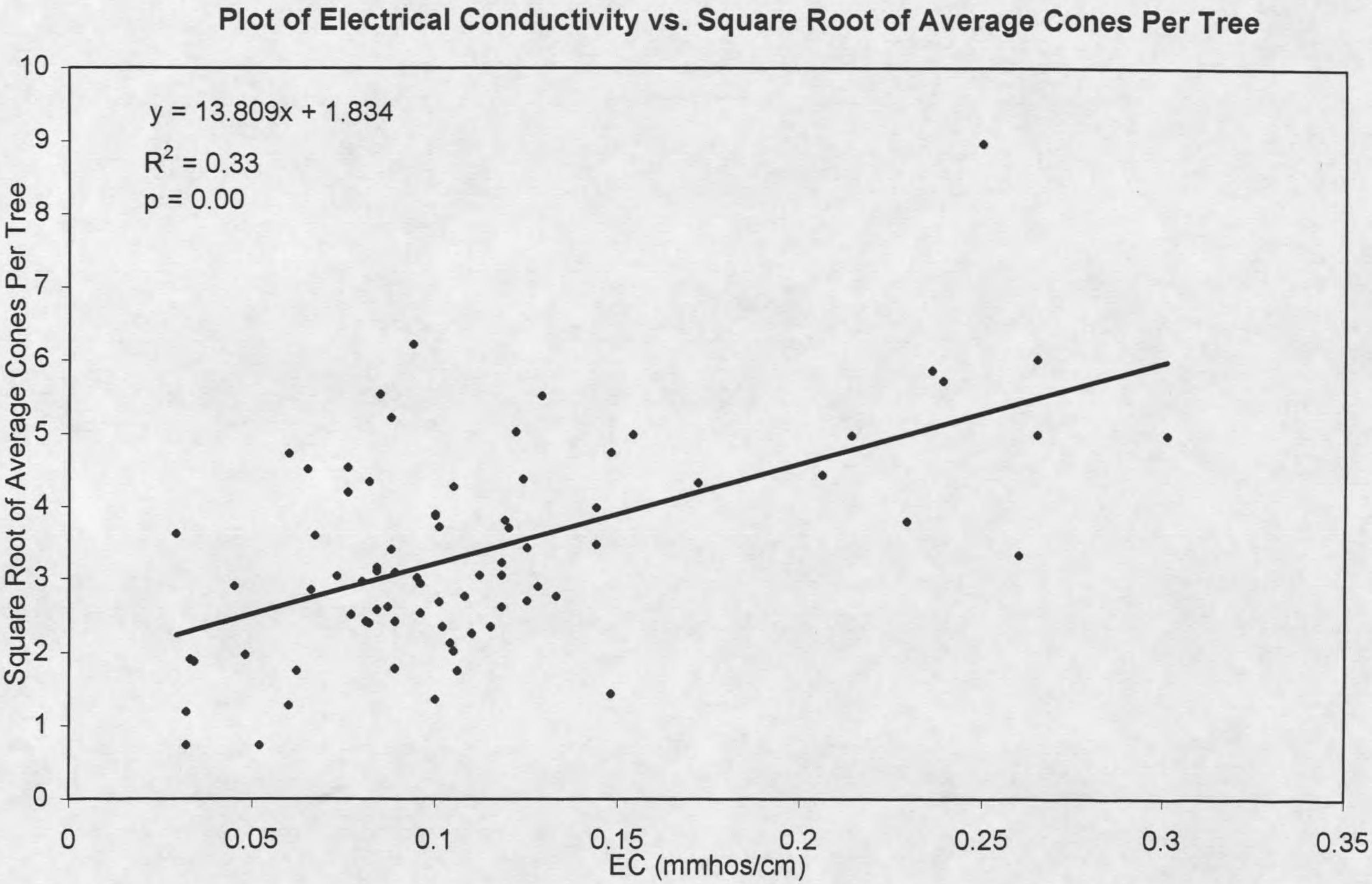

Plot of Electrical Conductivity vs. Square Root of Average Cones Per Tree
y = 13.809x + 1.834
R2 = 0.33
p = 0.00
Square Root of Average Cones Per Tree
0
1
2
3
4
5
6
7
8
9
10
EC (mmhos/cm)
0
0.05
0.1
0.15
0.2
0.25
0.3
0.35

Figure 8. Mean Electrical Conductivity (mmhos/cm) for the Interagency Grizzly Bear Study Team cone count sites used in this study.

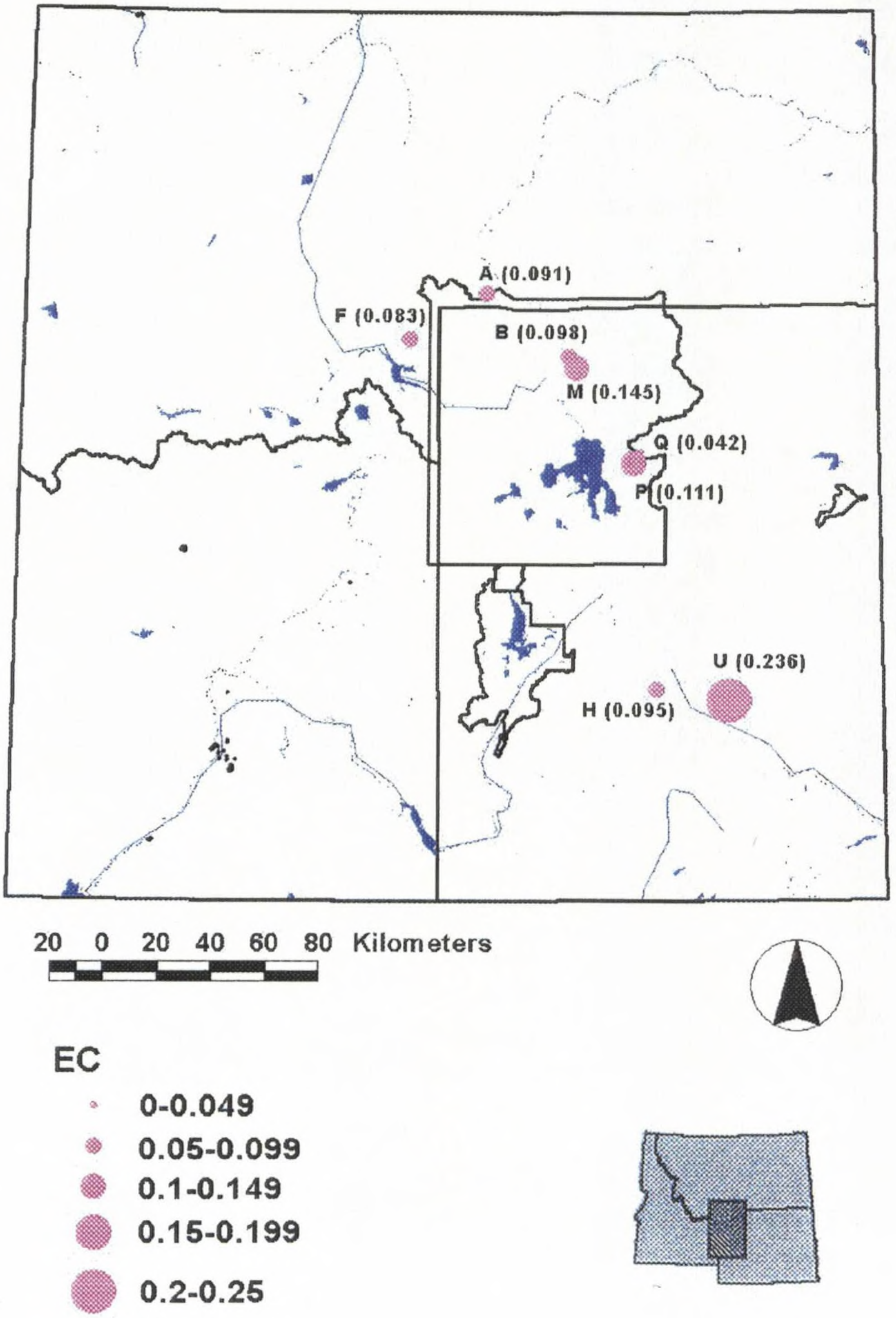
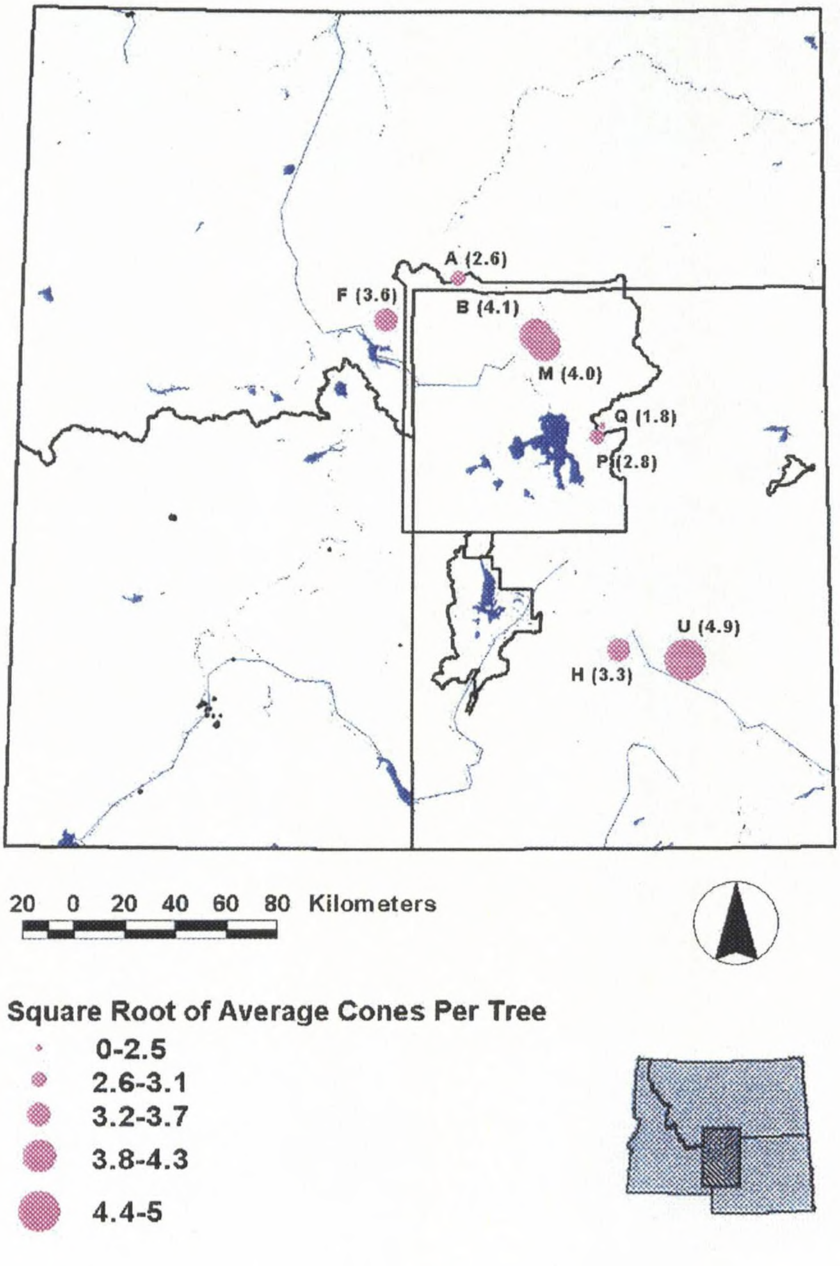


Figure 9. The square root of the average number of whitebark pine cones per tree (1989-1997), by plot, for the Interagency Grizzly Bear Study Team cone count sites used in this study.



Soil pH. Mean soil pH values (Table 8 and Appendix C) ranged between 4.56 at site P and 5.90 at site U; total range was 4.38 to 6.46. Results fall within the ranges found in whitebark pine stands (for the surface mineral horizon) by Weaver and Dale (1974) (4.9-5.7) in Montana and Wyoming, Reed (1976) (mean = 5.1) in Wyoming, Baig (1972) (mean = 6.0) in Alberta, and Holland and Coen (1982) (mean = 5.4) in Banff and Jasper National Parks, Alberta.

Soil pH was significantly correlated with the square root of average cones per tree, and explained 29% of the variation (Table 9). The result of the t-test indicated that slope of the regression line (Figure 10) was also significant. This supports the hypothesis that soils with a pH closer to 7 (neutral) were more productive. As a soil's acidity increases (decreasing pH) many nutrients become insoluble or precipitate out of solution, and are no longer available to plants (Waring and Schlesinger, 1985; Meurisse et al., 1991; Singer and Munns, 1996; Kimmins, 1997). Lower pH values may also negatively affect micro-fauna that are beneficial to the plant (Armson, 1977). There was no apparent geographic pattern of pH across the ecosystem (Figure 11), but the relationship between pH and square root of average cones per tree was apparent at the plot level (Figure 9, Figure 11); plots M and U had both higher pH values and higher cone production, while plots P and Q had lower pH values and lower cone production.

Percent Coarse Material. Mean percent coarse material (Table 8 and Appendix D) ranged between 17 at site U and 71 at site Q; total range was 10 to 90 percent. The range of values found in this study were much larger than those found in whitebark pine

Figure 10

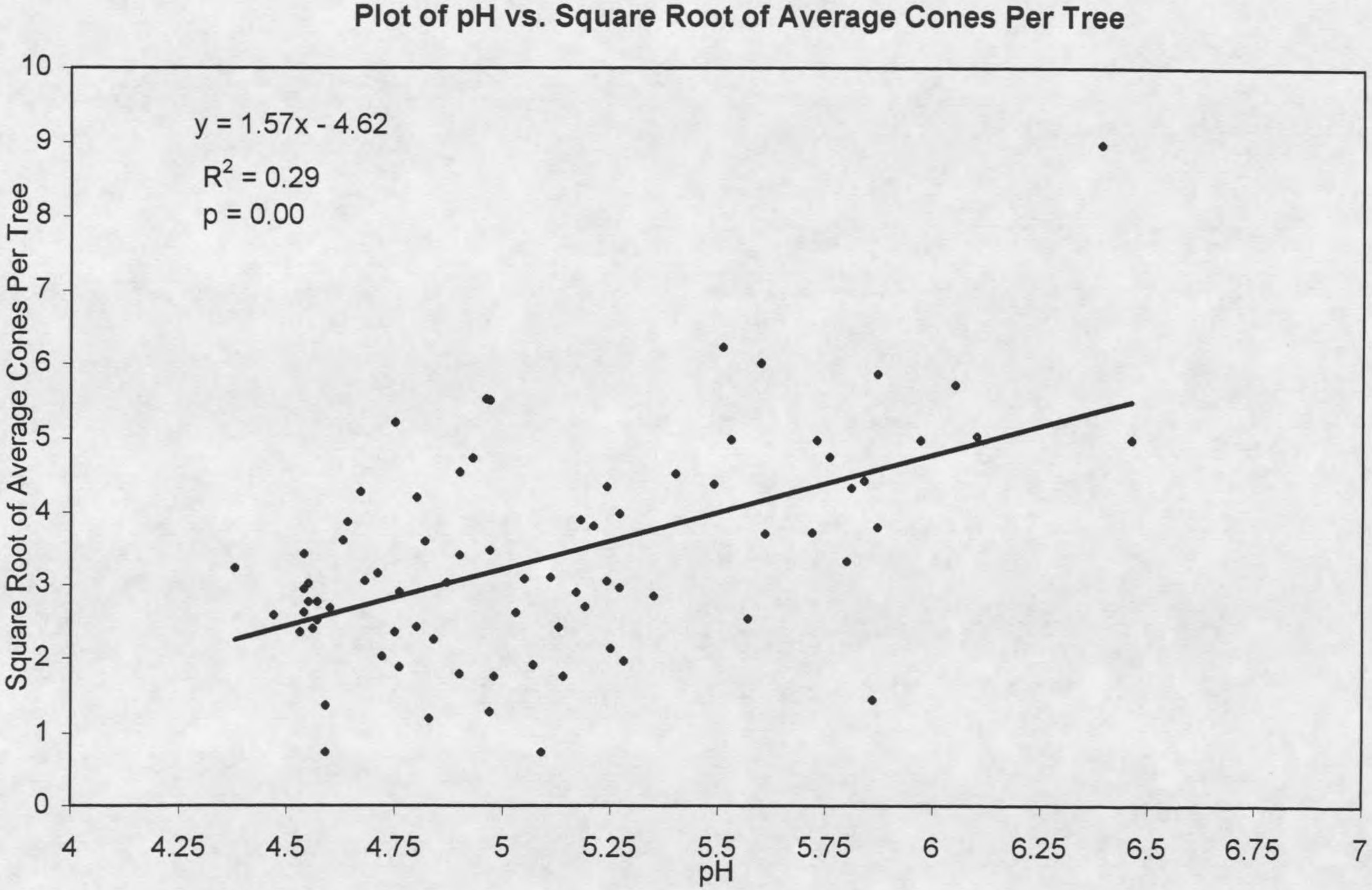
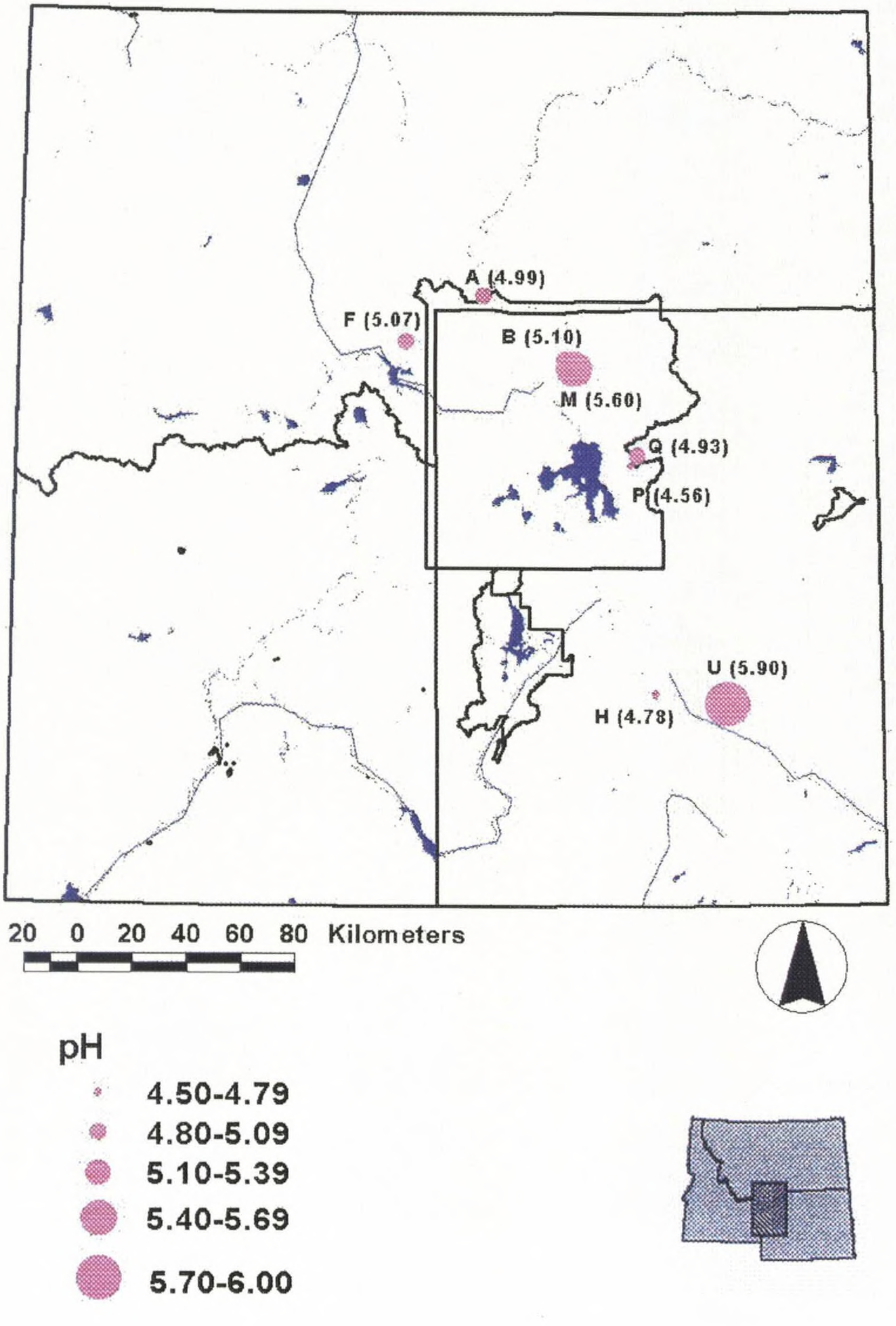

Plot of pH vs. Square Root of Average Cones Per Tree
y = 1.57x - 4.62
R^2 = 0.29
p = 0.00
Square Root of Average Cones Per Tree
0
1
2
3
4
5
6
7
8
9
10
pH
4
4.25
4.5
4.75
5
5.25
5.5
5.75
6
6.25
6.5
6.75
7

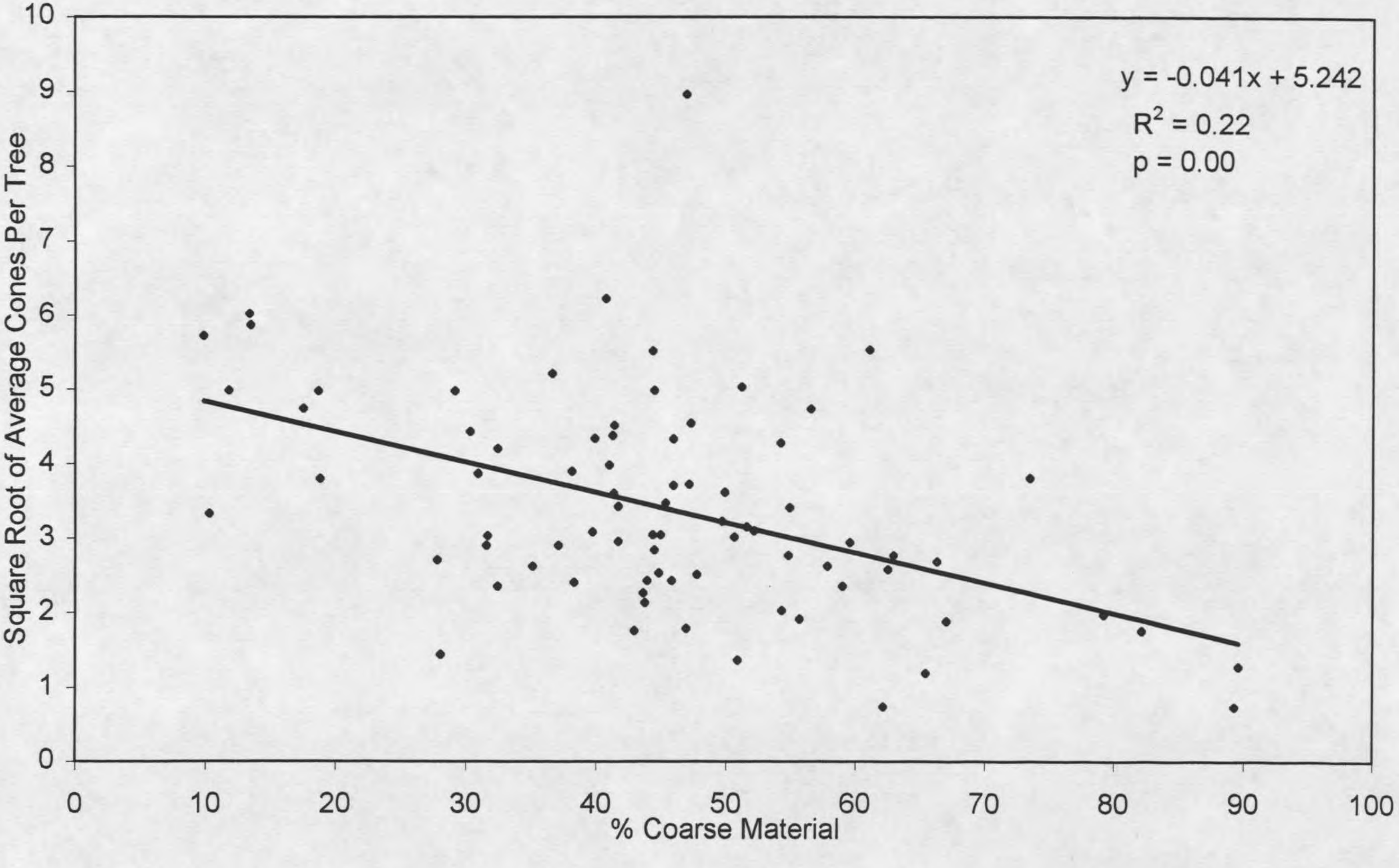
Figure 11. Mean pH values for the Interagency Grizzly Bear Study Team cone count sites used in this study.



stands (for the surface mineral horizon) by Weaver and Dale (1974) (20-50%) in Montana and Wyoming and by Baig (1972) (mean = 40%) in Alberta. This could indicate that the variability in coarse material in whitebark pine stands (in Montana, Wyoming and Alberta) is much larger than previously thought. However, a majority of the sites (95%) used by Weaver and Dale (1974) and half of the sites used by Baig (1972) were on slopes less than or equal to 20%, as compared to this study where a majority of the sites (75%) were on slopes greater than 20%. This might explain the difference in percent coarse material. On steeper sites fine material (< 2 mm) will be more easily transported away from the sites leaving behind the larger rock fragments and contributing to soils with higher percentages of coarse material.

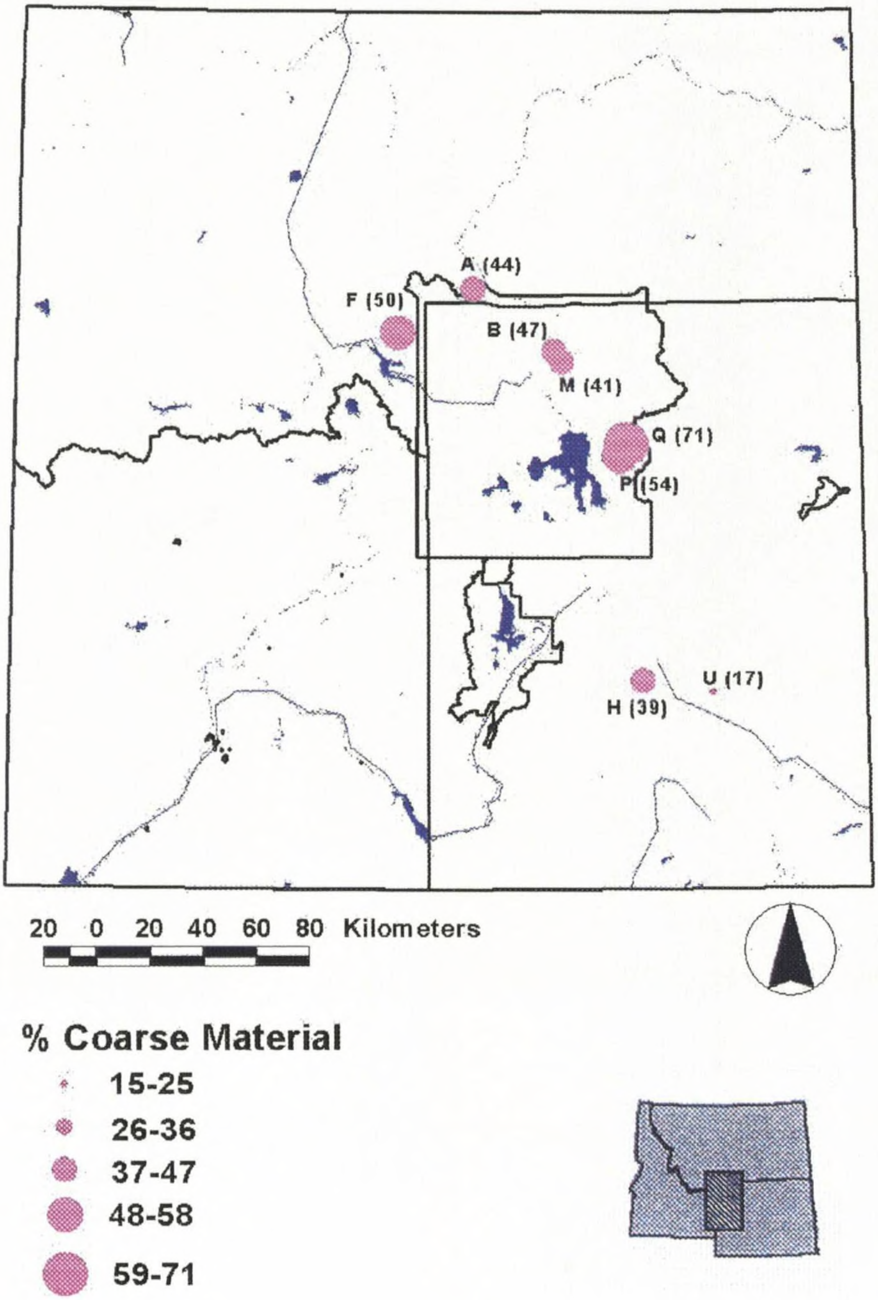
Percent coarse material was significantly correlated with the square root of average cones per tree and explained 22% of the variation (Table 9). The result of the t-test indicated that the slope of the regression line (Figure 12) was also significant. The relationship between percent coarse material and square root of average cones per tree was an inverse relationship, as was expected (as percent coarse material decreased the square root of average cones per tree increased). This supports the hypothesis that soils with a lower coarse fraction are more productive. Soils with a lower amount of coarse material retain more moisture and nutrients than soils higher in coarse material (Waring and Schlesinger, 1985; Page-Dumroese, et al., 1991; Singer and Munns, 1996; Kimmins, 1997). Percent coarse material had no apparent geographic pattern (Figure 13), but the relationship between percent coarse material and the square root of average cones per tree was apparent at the plot level (Figure 9, Figure 13); plot U had a low percentage of coarse

Firgure 12



Plot of Coarse Material vs. Square Root of Average Cones Per Tree

Figure 13. Mean percent coarse material for the Interagency Grizzly Bear Study Team cone count sites used in this study.

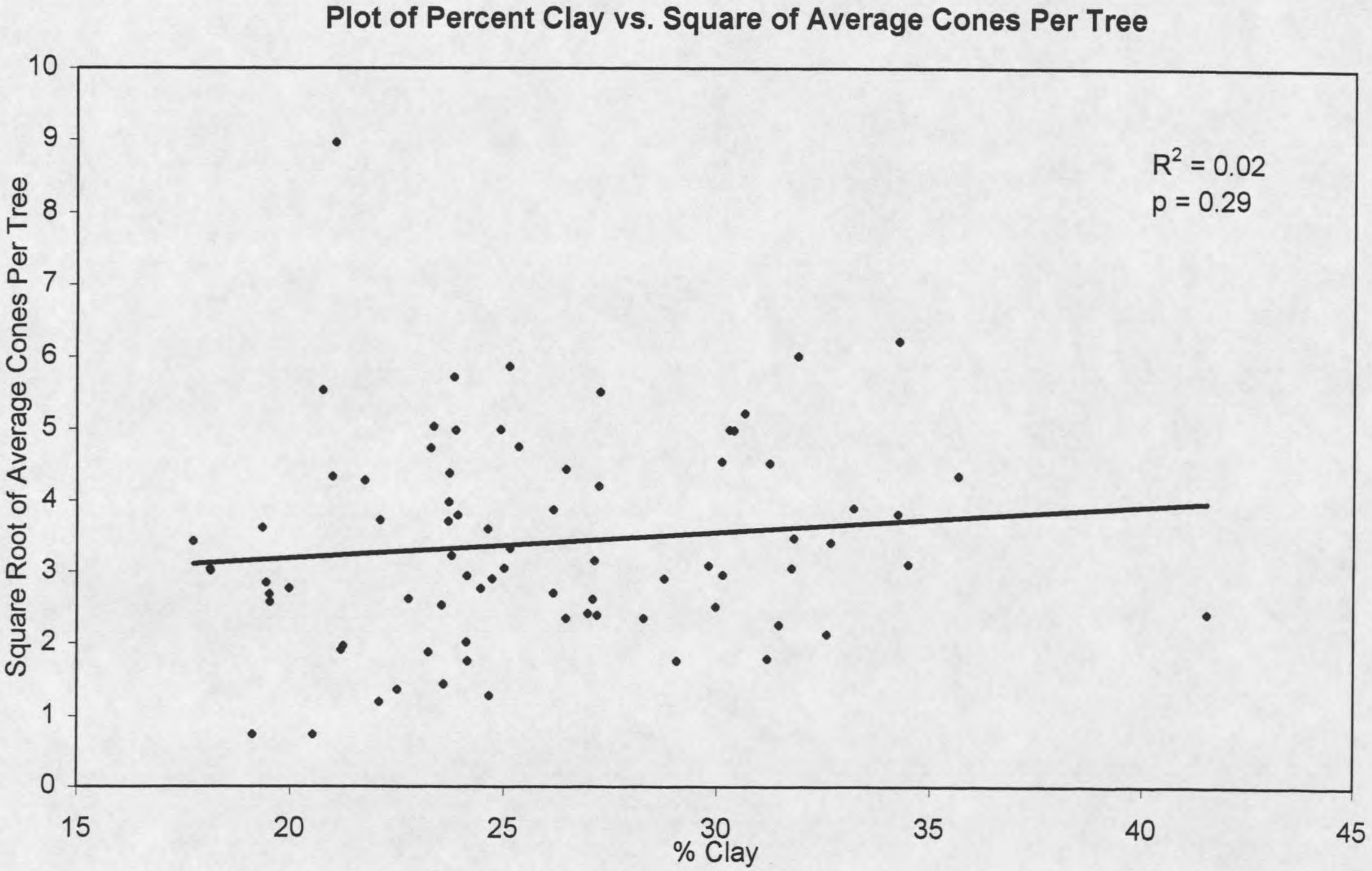


material and had a high level of cone production, while plots P and Q had high percentages of coarse material and low levels of cone production.

Soil Texture. Mean percent clay, silt and sand (Table 8 and Appendix C) ranged between 21 (site F) and 33 (site B), 27 (site U) and 38 (site M), and 30 (site B) and 50 (site F), respectively. Total ranges for percent clay, silt and sand were 18 to 42, 21 to 43, and 26 to 57, respectively (Table 8 and Appendix C). In whitebark pine stands Weaver and Dale (1974) (Montana and Wyoming), Baig (1972) (Alberta) and Holland and Coen (1982) (Banff and Jasper National Parks, Alberta) had average values for percent sand, for the surface mineral horizon, (42 ± 1.9, 51, and 40 respectively) that were similar to the results found in this study. Additionally, in whitebark pine stands, Baig (1972) (Alberta) had an average value for percent silt, for the surface mineral horizon, (35) that was similar to the results found in this study. However, Holland and Coen (1982) (Banff and Jasper National Parks, Alberta) had a higher average percent silt value, for the surface mineral horizon (51). In whitebark pine stands Weaver and Dale (1974) (Montana and Wyoming), Baig (1972) (Alberta) and Holland and Coen (1982) (Banff and Jasper National Parks, Alberta) had average values for percent clay, for the surface mineral horizon, (8.5 ± 1.7, 15, and 9 respectively) that lower than what was found in this study.

Percent clay, silt and sand were not significantly correlated with the square root of average cones per tree, and there were no apparent patterns in the data to suggest a non-linear relationship (Table 9, Figures 14-16). This does not support the hypothesis that

Figure 14



Plot of Percent Clay vs. Square of Average Cones Per Tree

Figure 15

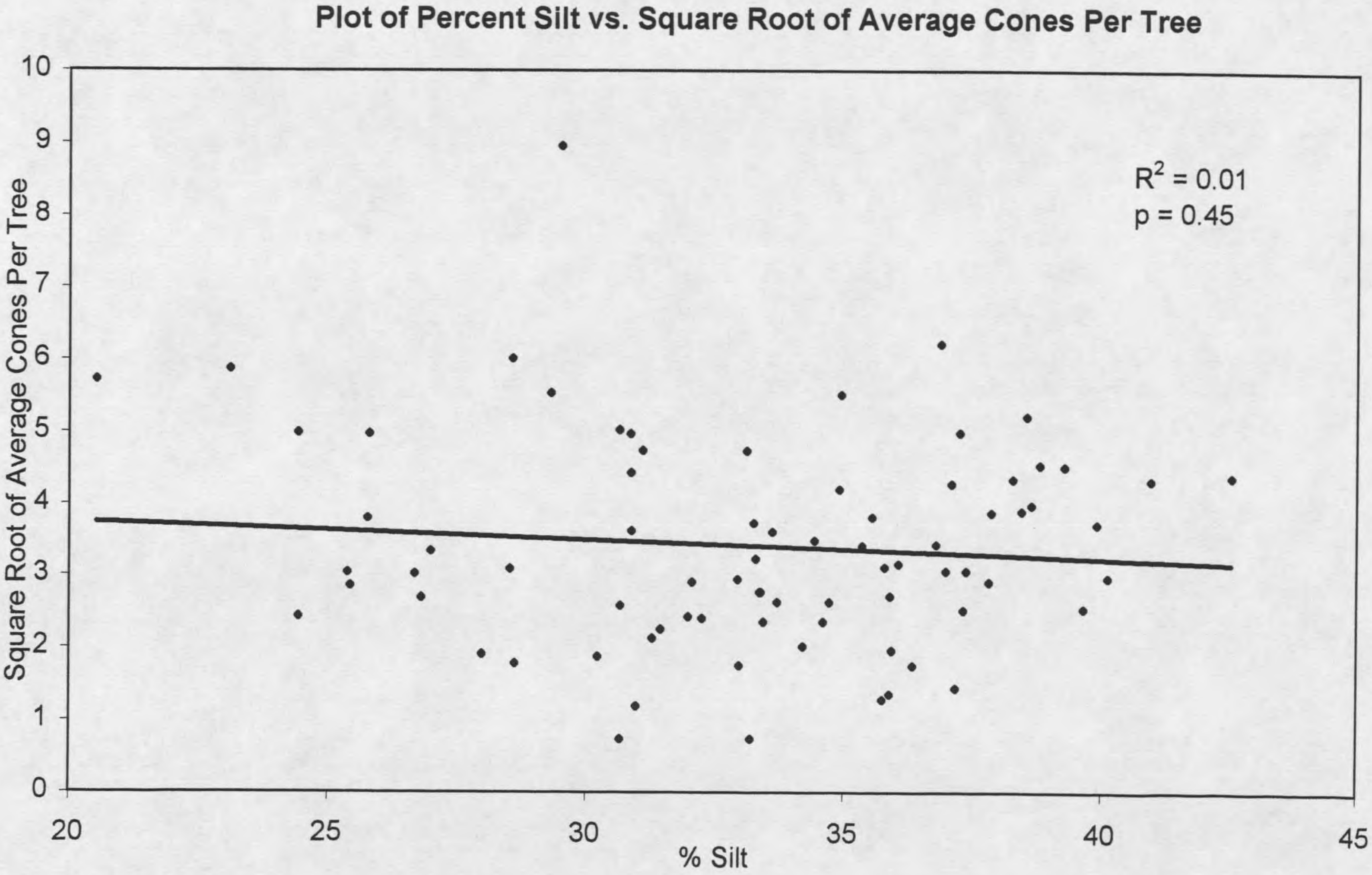
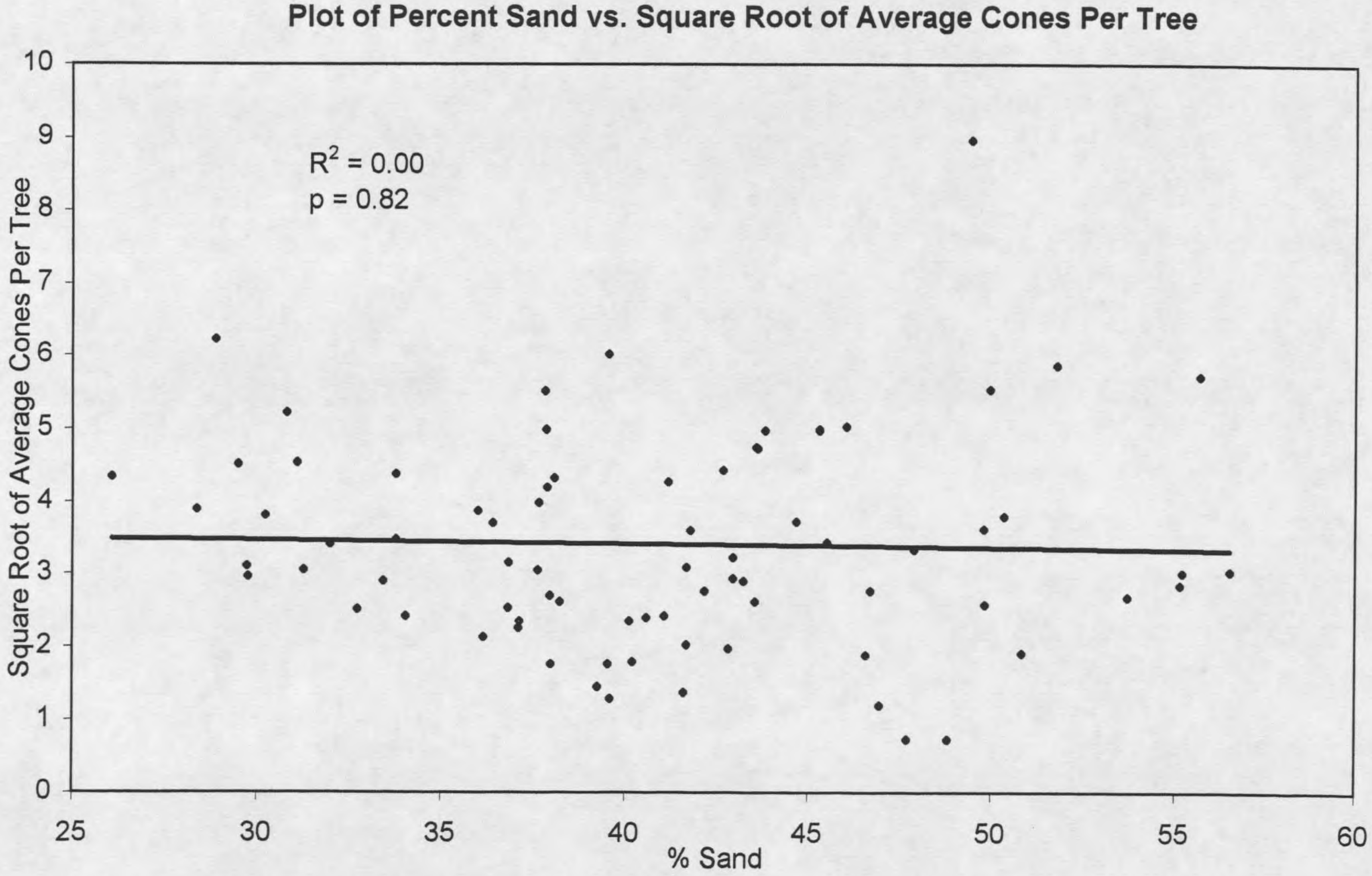

Plot of Percent Silt vs. Square Root of Average Cones Per Tree

Figure 16


Plot of Percent Sand vs. Square Root of Average Cones Per Tree
$R^2 = 0.00$
$p = 0.82$
Square Root of Average Cones Per Tree
0
1
2
3
4
5
6
7
8
9
10
% Sand
25
30
35
40
45
50
55
60

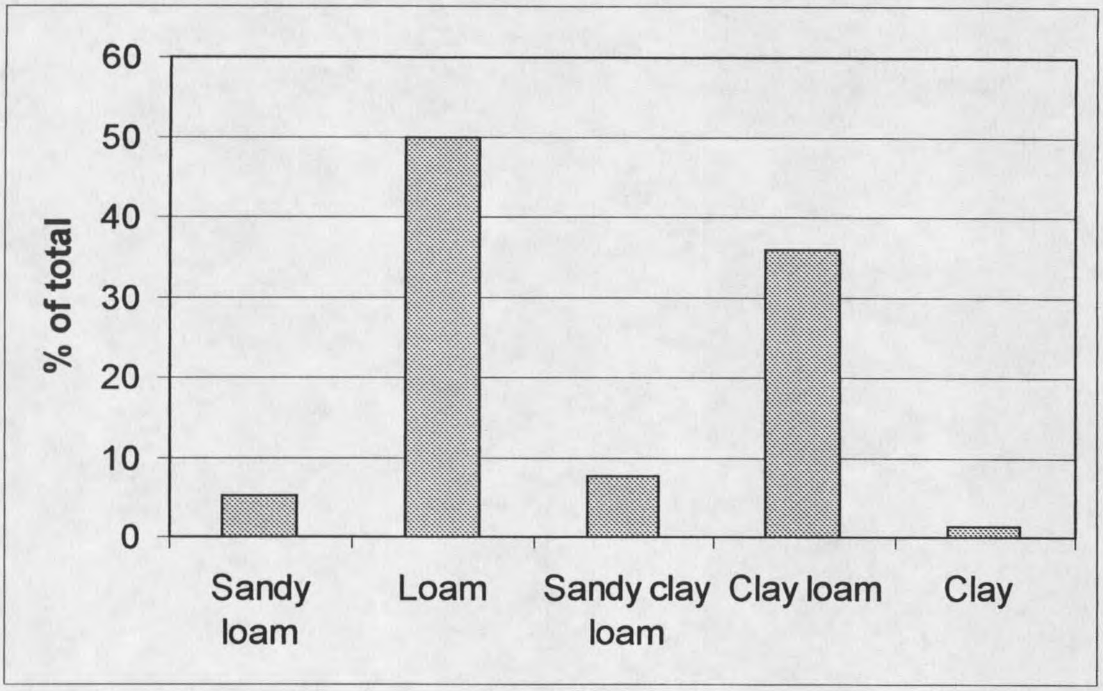
soils finer in texture (lower in percent sand and higher in percentages of silt and clay) are more productive because of increased nutrient and water retention (Price, 1981; Waring and Schlesinger, 1985; Meurisse, et al., 1991; Page-Dumroese, et al., 1991; Singer and Munns, 1996; Kimmins, 1997).

One explanation for why soil texture was not statistically significant was that when the values for sand, silt and clay are combined together to classify each sample as a specific texture class (e.g. loam, clay loam) (Figure 17, Table 10, Appendix E), there is little variation in soil texture between plots and individual trees. Eighty-six percent of the soils sampled were classified as either loam or clay loam, and every plot, except for U, was classified (based on the texture class that the majority of the trees had) as either loam or clay loam. This low variation in overall soil texture (relative to the variation in cone production) could explain why soil texture was not statistically significant in predicting the square root of average cones per tree.

Percent Organic Matter. Mean percent organic matter (Table 8 and Appendix C) ranged between 4.4 at site F and 8.2 at site B; total range was 3.1 to 10.8 percent. Results are similar to those found in whitebark pine stands for the surface mineral horizon by Weaver and Dale (1974) (Montana and Wyoming), Baig (1972) (Alberta) and Holland and Coen (1982) (Banff and Jasper National Parks, Alberta), with average values of 6.1 ± 1.8, 8.7 and 9 respectively.

The relationship between percent organic matter and the square root of average cones per tree was not statistically significant, and there was no apparent pattern in the

Figure 17. Histogram (by % of total) of the soil textural classifications for whitebark pine trees from the Interagency Grizzly Bear Study Team cone count sites used in this study.



data to suggest a non-linear relationship (Table 9, Figure 18). This does not support the hypothesis that soils with higher levels of organic matter are more productive (because organic matter serves at a surface for nutrient retention and as a nutrient pool for when the organic matter decomposes) (Waring and Schlesinger, 1985; Page-Dumroese, et al., 1991; Singer and Munns, 1996; Kimmins, 1997). One reason that the results are not as expected could be that the loss on ignition method for percent organic matter is not as accurate as other methods (e.g. Walkley-Black and Schollenberger methods) (Allison, 1965), but the other methods were not used due to cost considerations. Another reason for the results not being as expected could be due to the fact that in mountain environments decomposition is slow (Price, 1981), and higher levels of organic matter would only increase productivity if decomposition rates were also high (which is not the case in most mountain environments).

Soil Depth. Mean soil depth (Table 8 and Appendix F) ranged between 25 cm at site M and 69 cm at site A; total range was 10 to 90 cm. Results are similar to those found in whitebark pine stands by Baig (1972) in Alberta (mean = 53 cm), and are only slightly lower than those found by Holland and Coen (1982) in Banff and Jasper National Parks, Alberta (mean = 102 cm)

The relationship between soil depth and the square root of average cones per tree was not statistically significant, and there was no apparent pattern in the data to suggest a non-linear relationship (Table 9, Figure 19). This does not support the hypothesis that deeper soils because of increased water holding capacity (Meurisse, et al., 1991; Singer

Figure 18

Plot of Percent Organic Matter vs. Square Root of Average Cones Per Tree

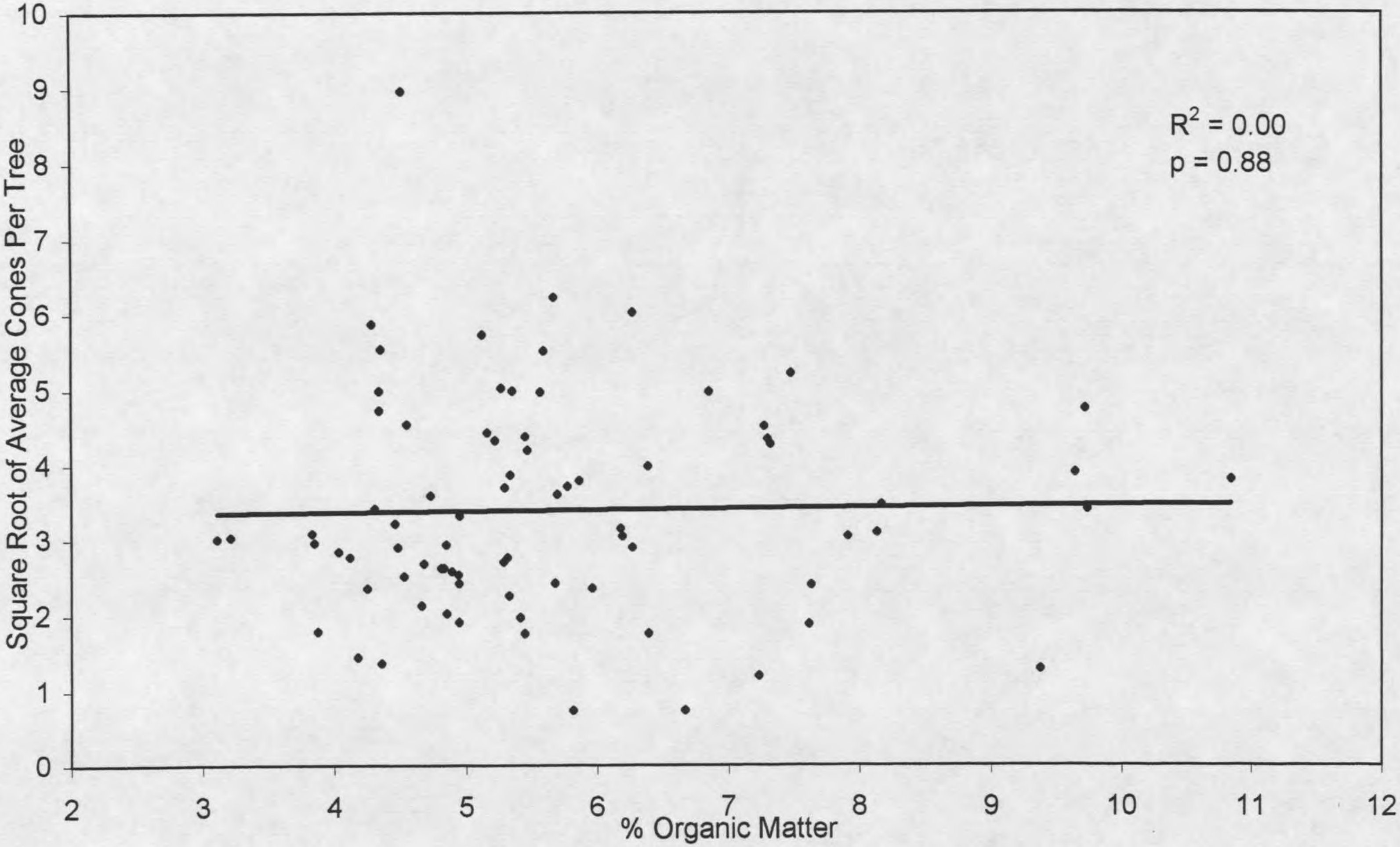
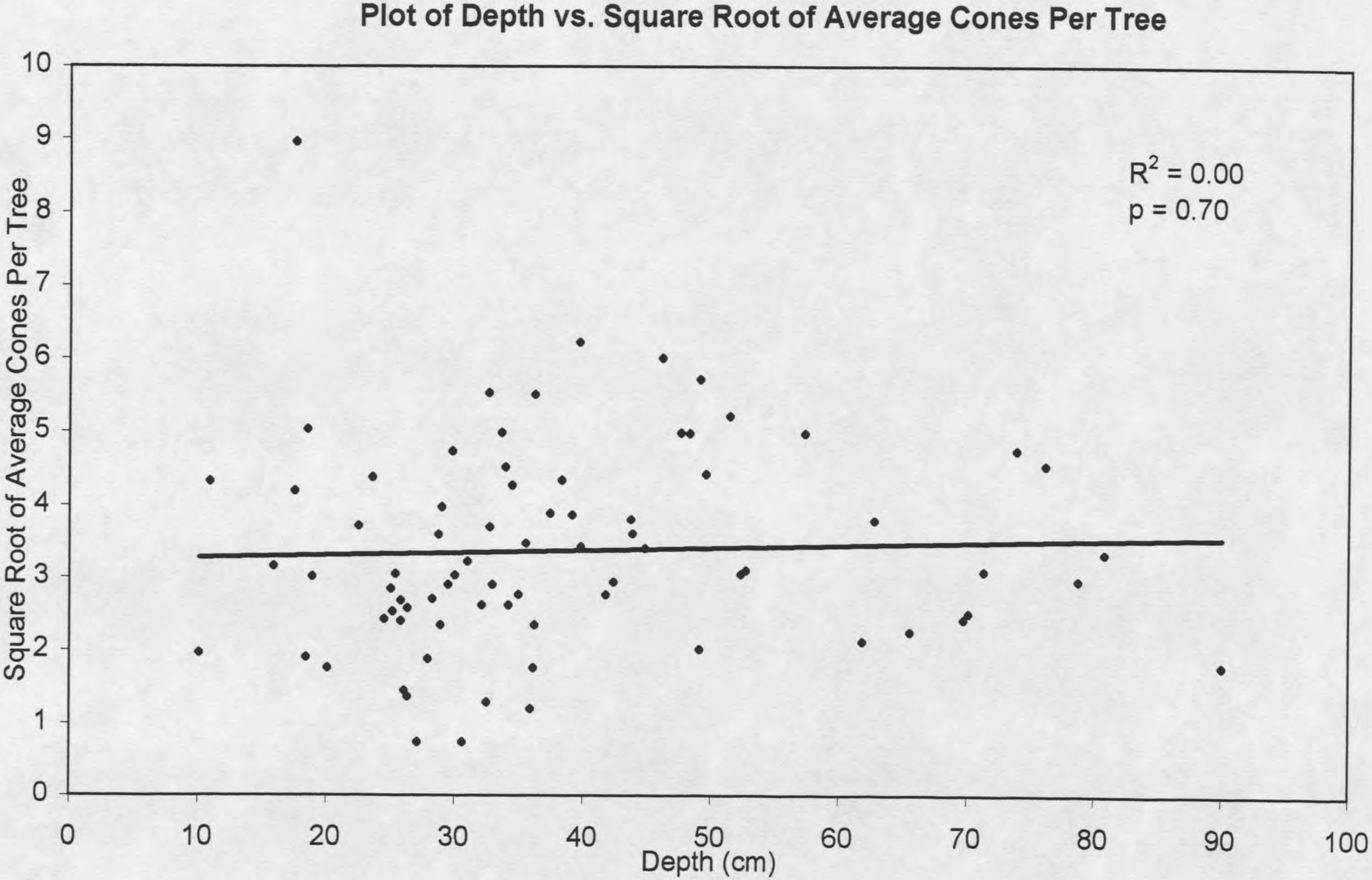


Figure 19


Plot of Depth vs. Square Root of Average Cones Per Tree
R² = 0.00
p = 0.70
Square Root of Average Cones Per Tree
10
9
8
7
6
5
4
3
2
1
0
0
10
20
30
40
50
60
70
80
90
100
Depth (cm)

and Munns, 1996) are more productive. This could be that it is very difficult to get an accurate estimate of depth without digging soil pits, which was not done in this study due to permit restrictions. The assumption that deeper soils would be found on sites with lower slopes was not entirely valid. The assumption was valid for plot U (slope = 5°, depth = 57 cm), but it was not valid for plot H (slope = 8°, depth = 28 cm) which had approximately the same depth as plot M (depth = 25 cm), which had the highest slope (50°).

Foliar Data

The results of the foliar analysis were summarized in Table 11 (all values are in Appendix G). All the nutrients that were analyzed in this study were not significantly correlated with the square root of average cones per tree (Table 12, Figures 20-30) (except molybdenum, which was not used in the analysis because all the samples were determined to have less than 0.5 mg/kg, and could not be accurately measured). This does not support the hypothesis that increased nutrient concentrations increase cone production. However, tree health is known to affect nutrient concentrations. Trees that are growing rapidly may tend to have lower nutrient concentrations due to dilution from increases in carbohydrates (Van Den Driessche, 1974; Armson, 1977), so an estimate of the total nutrient levels of the tree was also used. Tree M9, which is the most productive tree, did show signs of this dilution effect for all nutrients except copper (Figures 20-30, M9 is the point that has a square root of average cones per tree value between 9 and 10). However, all nutrients measured did not significantly explain any of the remaining

Table 11. Average amounts of the listed nutrients found in the foliage of selected whitebark pine trees from the Interagency Grizzly Bear Study Team cone count sites used in this study.

PLOT	B (mg/kg)	Ca (%)	Cu (mg/kg)	Fe (mg/kg)	K (%)	Mg (%)	Mn (mg/kg)	TKN (%N)	P (%)	S (%)	Zn (mg/kg)
A	22.1	0.437	2.4	70.3	0.445	0.122	685	1.10	0.132	0.077	37.7
B	22.0	0.478	2.0	69.9	0.371	0.125	754	0.99	0.112	0.065	29.4
F	21.6	0.593	2.2	74.5	0.302	0.143	581	1.02	0.110	0.066	35.9
H	16.7	0.517	2.0	59.6	0.378	0.127	1014	1.01	0.108	0.068	32.7
M	19.3	0.439	2.2	50.4	0.322	0.110	393	0.91	0.100	0.072	24.5
P	13.9	0.282	1.8	43.8	0.343	0.097	427	0.87	0.096	0.061	13.3
Q	17.9	0.407	2.0	58.8	0.414	0.131	875	1.07	0.123	0.072	29.6
U	23.6	0.428	2.0	51.2	0.372	0.157	287	0.99	0.105	0.064	18.7

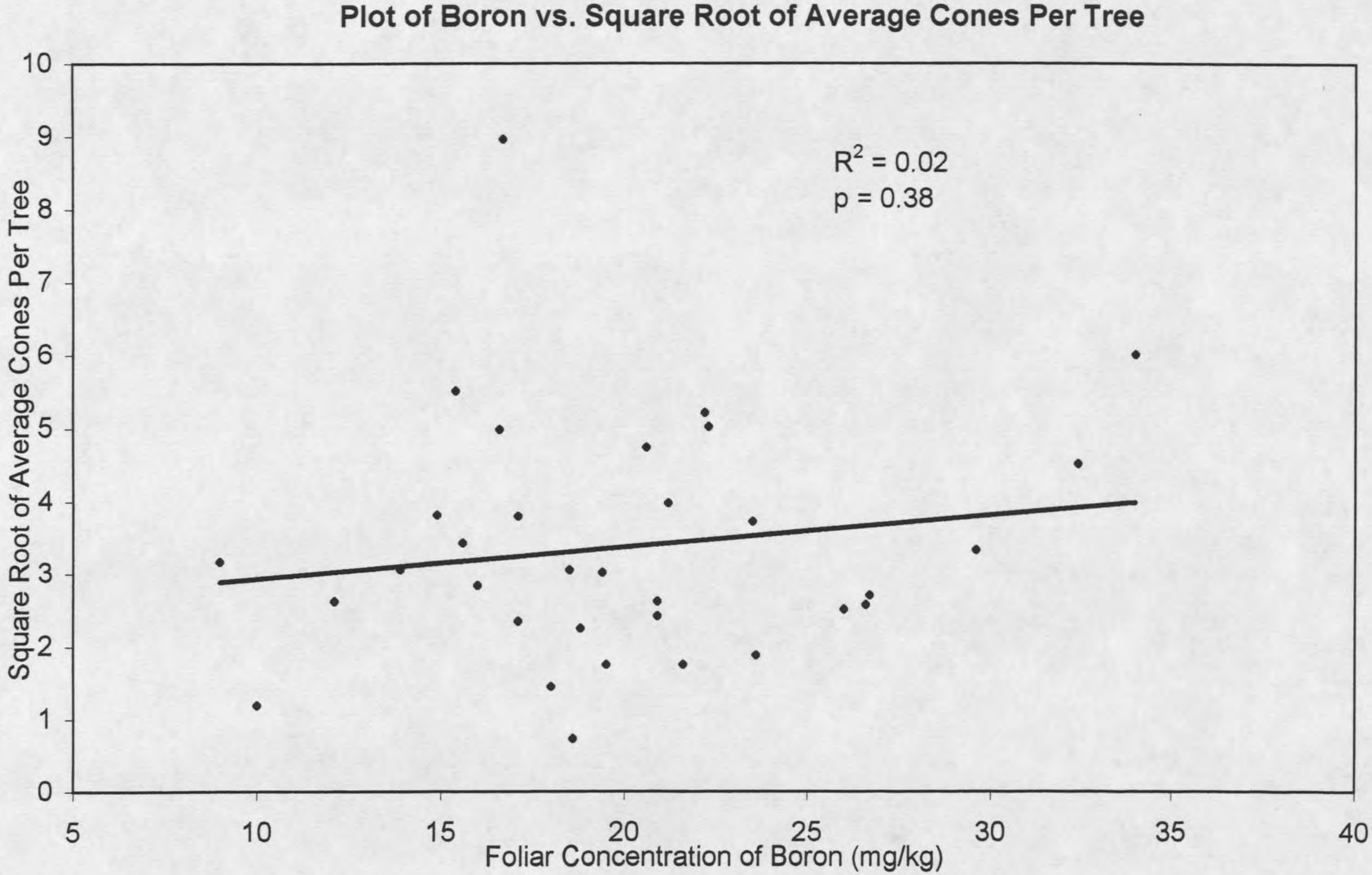
Table 12. Results (R^2 and p-values) of the simple regressions between the listed foliar nutrient concentrations and the square root of average cones per tree for whitebark pine.

VARIABLE	R^2	P-VALUE
Boron (mg/kg)	0.02	0.38
Calcium (%)	0.00	0.90
Copper (mg/kg)	0.09	0.09
Iron (mg/kg)	0.00	0.79
Potassium (%)	0.04	0.28
Magnesium (%)	0.00	0.81
Manganese (mg/kg)	0.11	0.06
Total Kjeldahl Nitrogen (TKN) (%)	0.04	0.24
Phosphorus (%)	0.01	0.55
Sulfur (%)	0.03	0.37
Zinc (mg/kg)	0.01	0.53

Table 13. Results (R^2 and p-values) of the regressions between the listed foliar nutrient concentrations multiplied by crown volume and the residuals of the regression of crown volume and the square root of average cones per tree for whitebark pine (Appendix B).

VARIABLE	R^2	P-VALUE
Boron	0.00	0.85
Calcium	0.00	0.72
Copper	0.00	0.88
Iron	0.00	0.76
Potassium	0.01	0.68
Magnesium	0.00	0.74
Manganese	0.03	0.34
Total Kjeldahl Nitrogen (TKN)	0.00	0.91
Phosphorus	0.00	0.96
Sulfur	0.00	0.93
Zinc	0.00	0.87

Figure 20



Plot of Boron vs. Square Root of Average Cones Per Tree

Figure 21

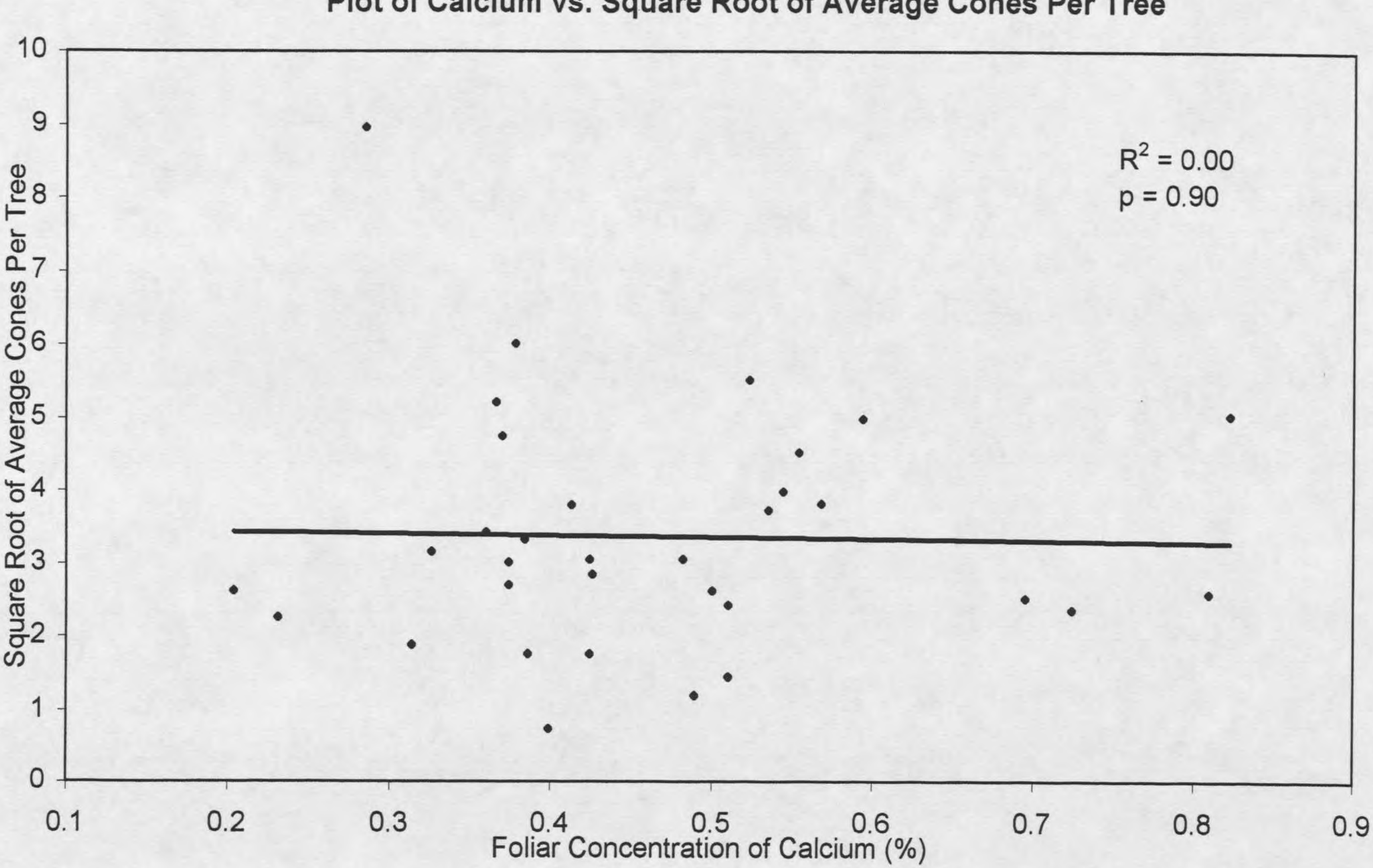

Plot of Calcium vs. Square Root of Average Cones Per Tree
$R^2 = 0.00$
p = 0.90
Square Root of Average Cones Per Tree
0
1
2
3
4
5
6
7
8
9
10
Foliar Concentration of Calcium (%)
0.1
0.2
0.3
0.4
0.5
0.6
0.7
0.8
0.9

Figure 22

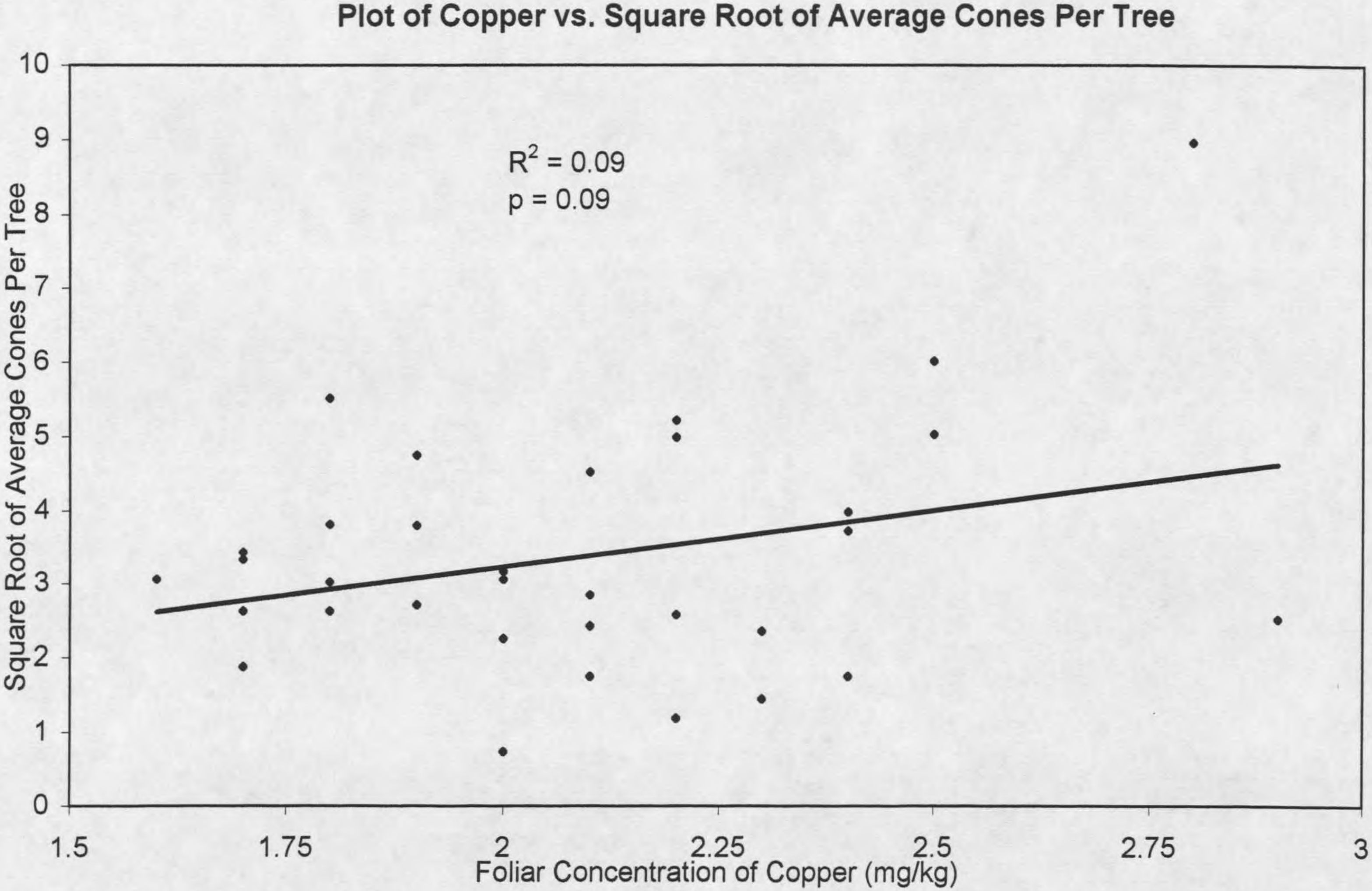

Plot of Copper vs. Square Root of Average Cones Per Tree
$R^2 = 0.09$
p = 0.09
Square Root of Average Cones Per Tree
0
1
2
3
4
5
6
7
8
9
10
1.5
1.75
2
2.25
2.5
2.75
3
Foliar Concentration of Copper (mg/kg)

Figure 23

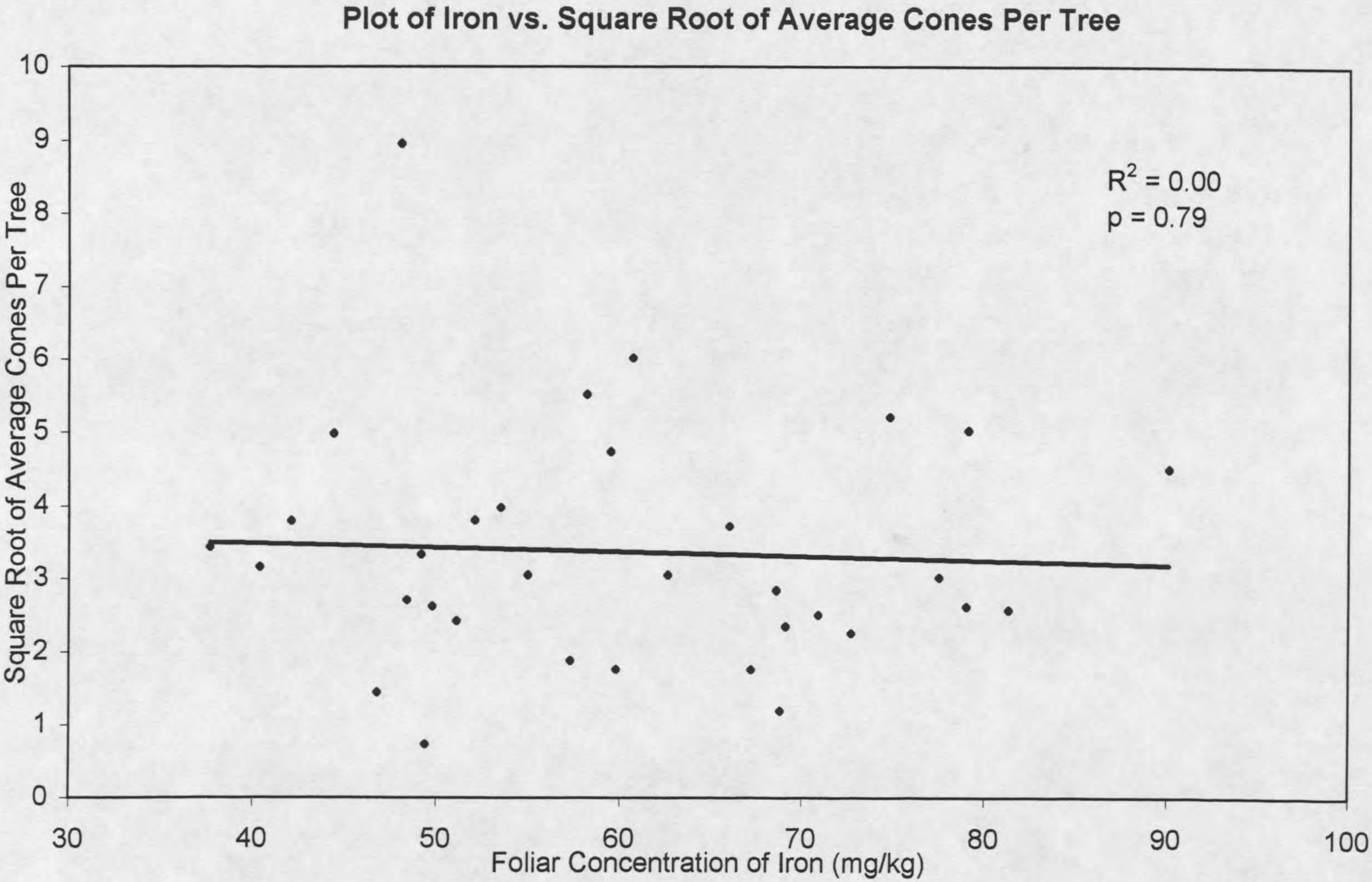

Plot of Iron vs. Square Root of Average Cones Per Tree
Square Root of Average Cones Per Tree
Foliar Concentration of Iron (mg/kg)
$R^2 = 0.00$
$p = 0.79$
0
1
2
3
4
5
6
7
8
9
10
30
40
50
60
70
80
90
100

Figure 24

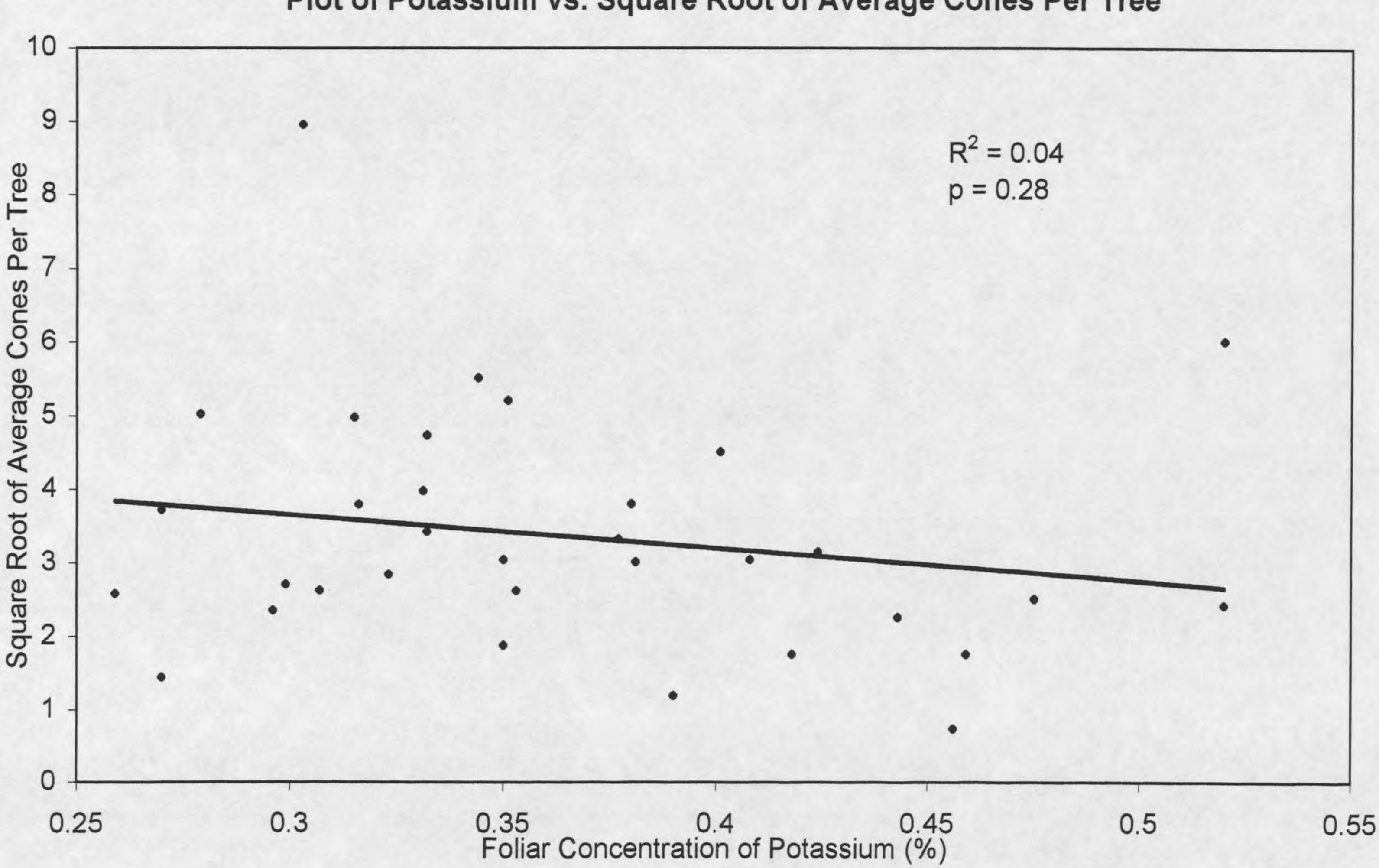

Plot of Potassium vs. Square Root of Average Cones Per Tree
R^2 = 0.04
p = 0.28
Square Root of Average Cones Per Tree
10
9
8
7
6
5
4
3
2
1
0
0.25
0.3
0.35
0.4
0.45
0.5
0.55
Foliar Concentration of Potassium (%)

Figure 25

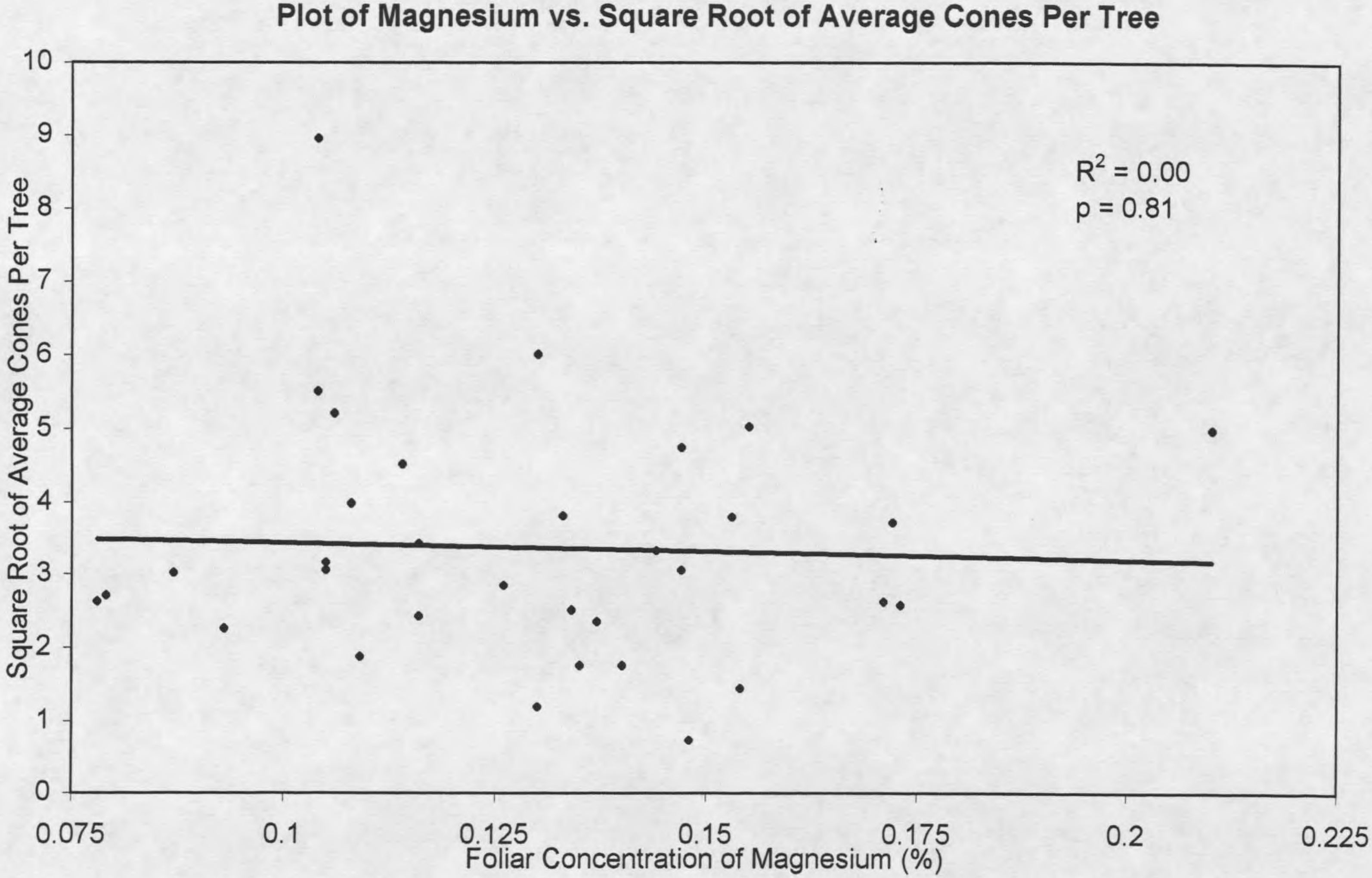

Plot of Magnesium vs. Square Root of Average Cones Per Tree
Square Root of Average Cones Per Tree
Foliar Concentration of Magnesium (%)
0
1
2
3
4
5
6
7
8
9
10
0.075
0.1
0.125
0.15
0.175
0.2
0.225
$R^2 = 0.00$
p = 0.81

Figure 26

Plot of Manganese vs. Square Root of Average Cones Per Tree

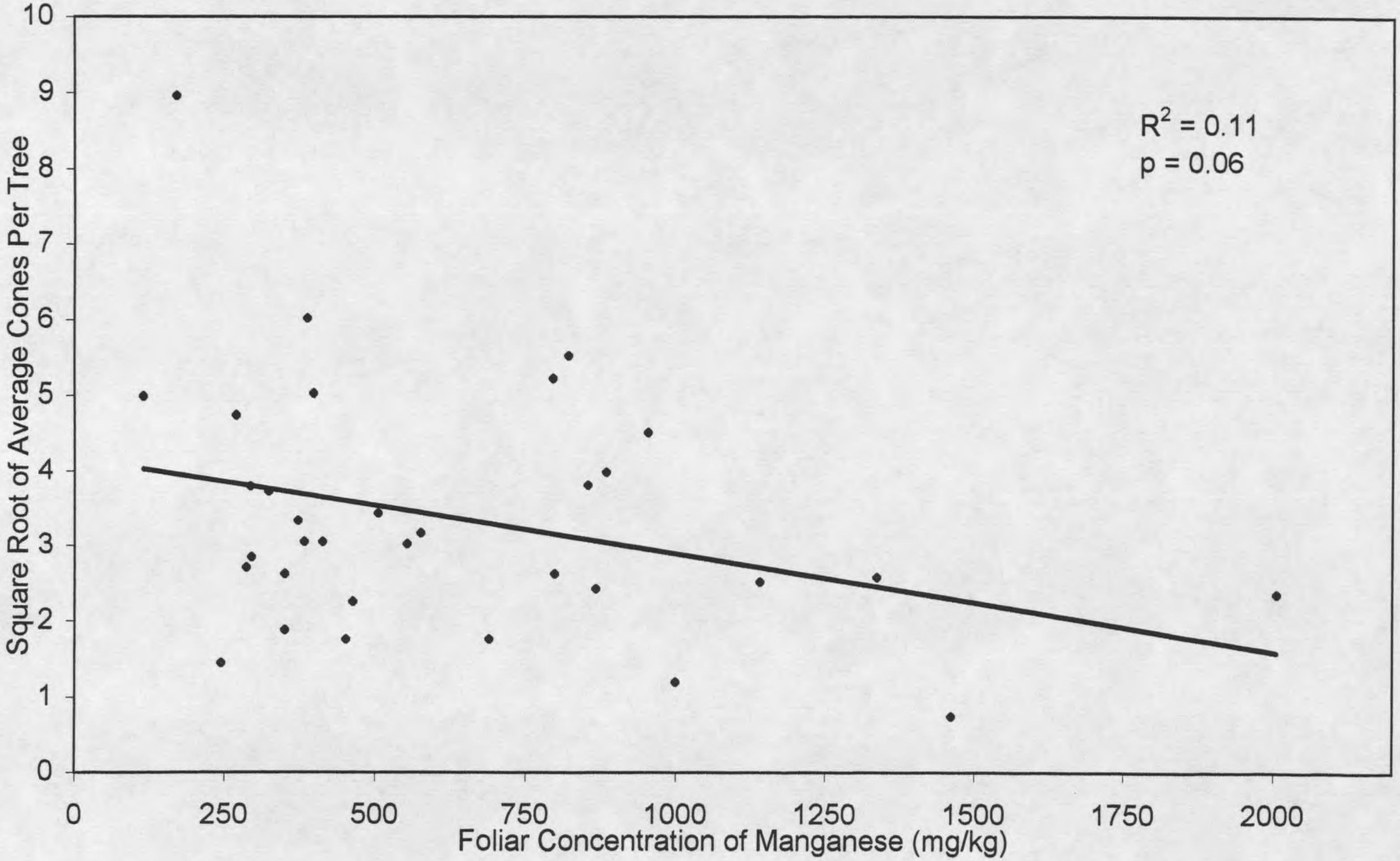


Figure 27

Plot of Total Kjeldahl Nitrogen vs. Square Root of Average Cones Per Tree

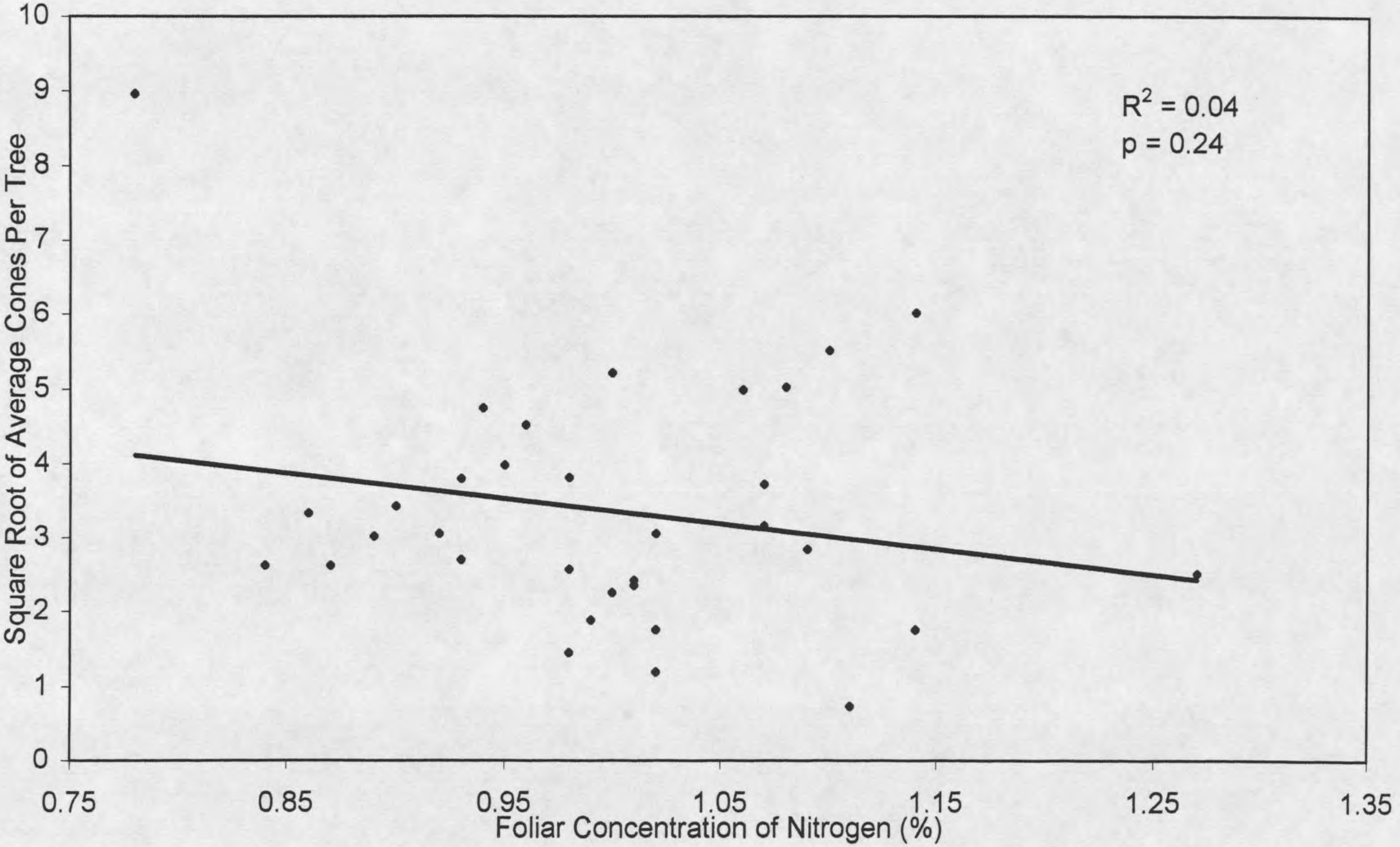


Figure 28

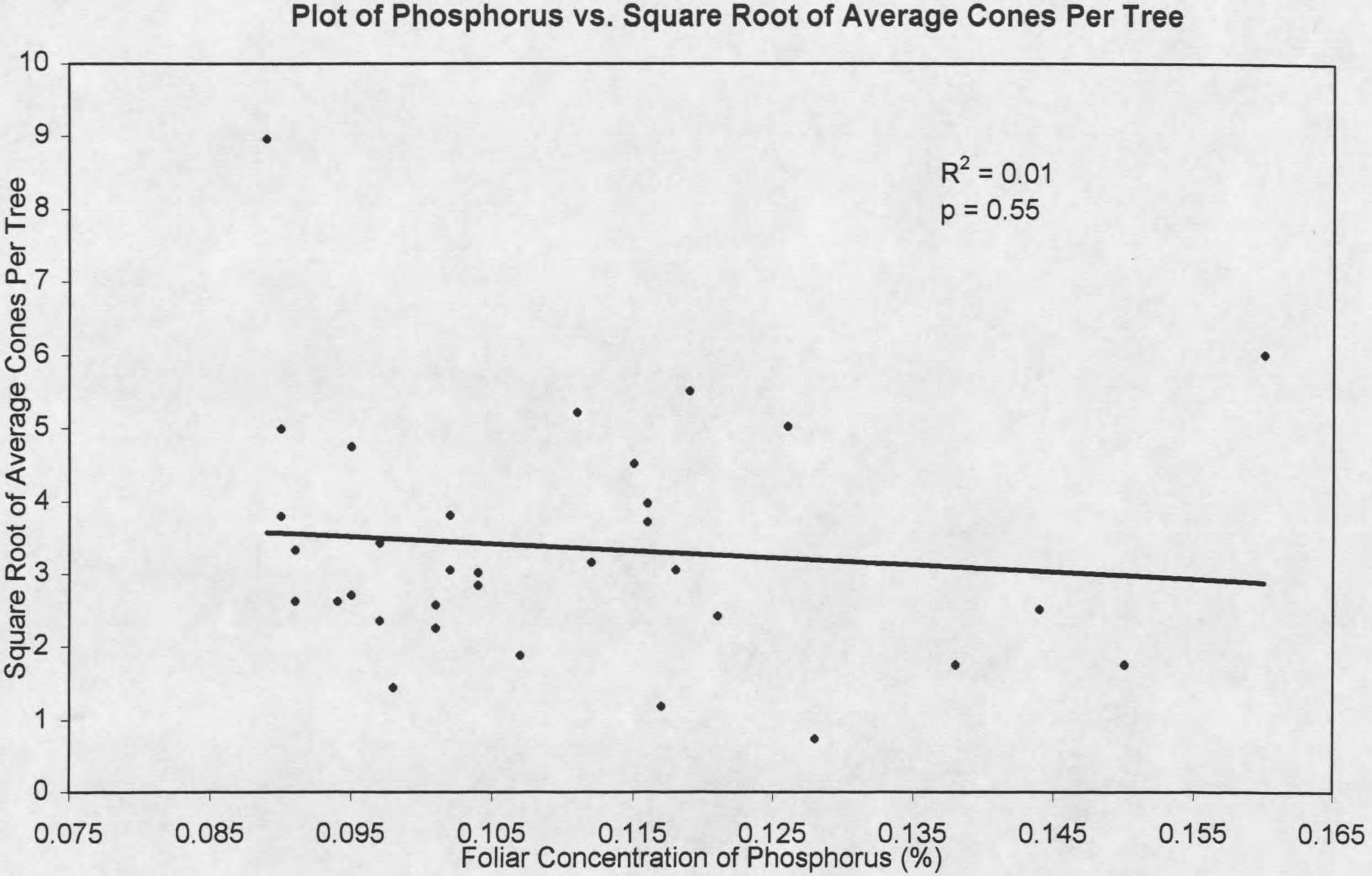
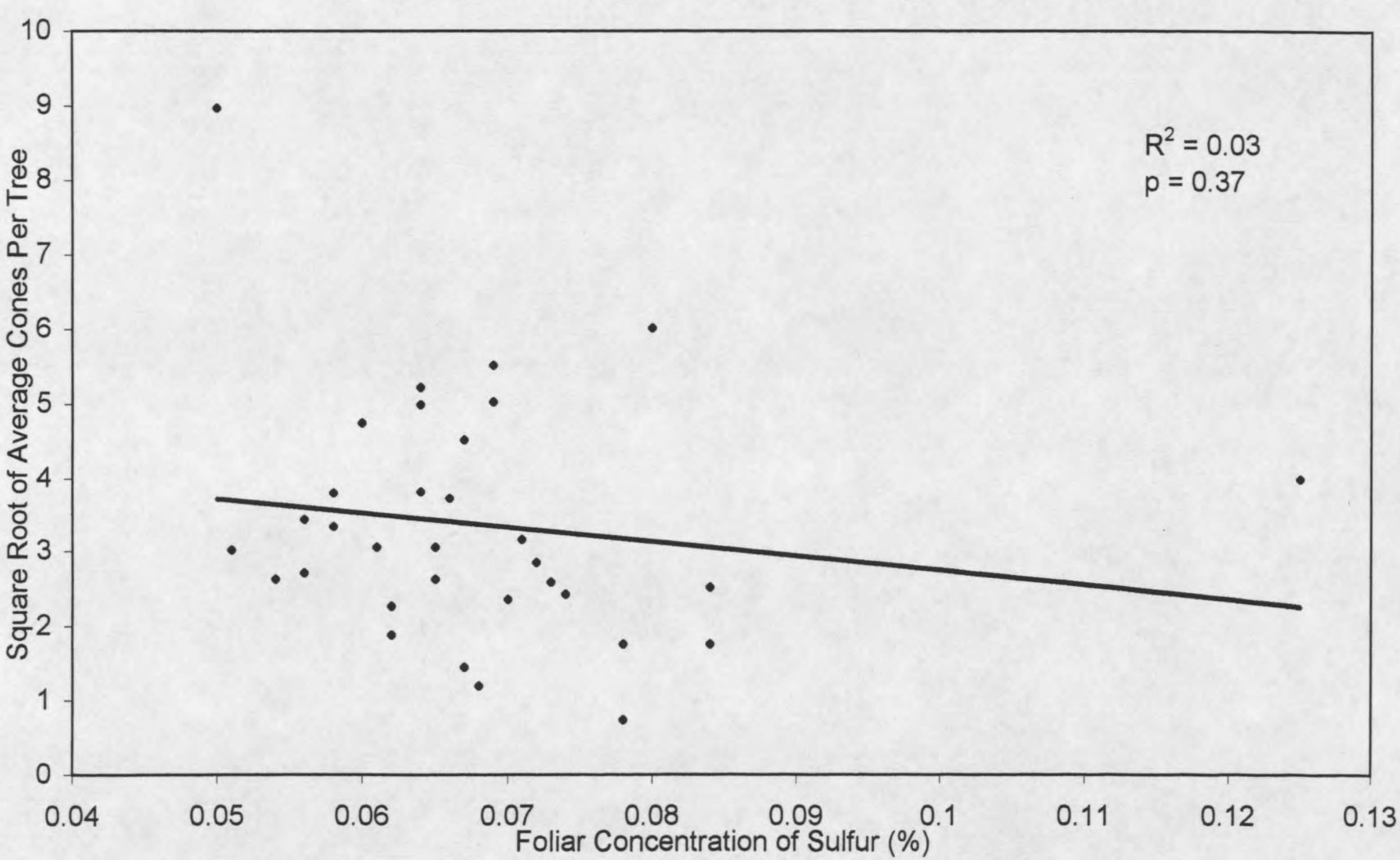
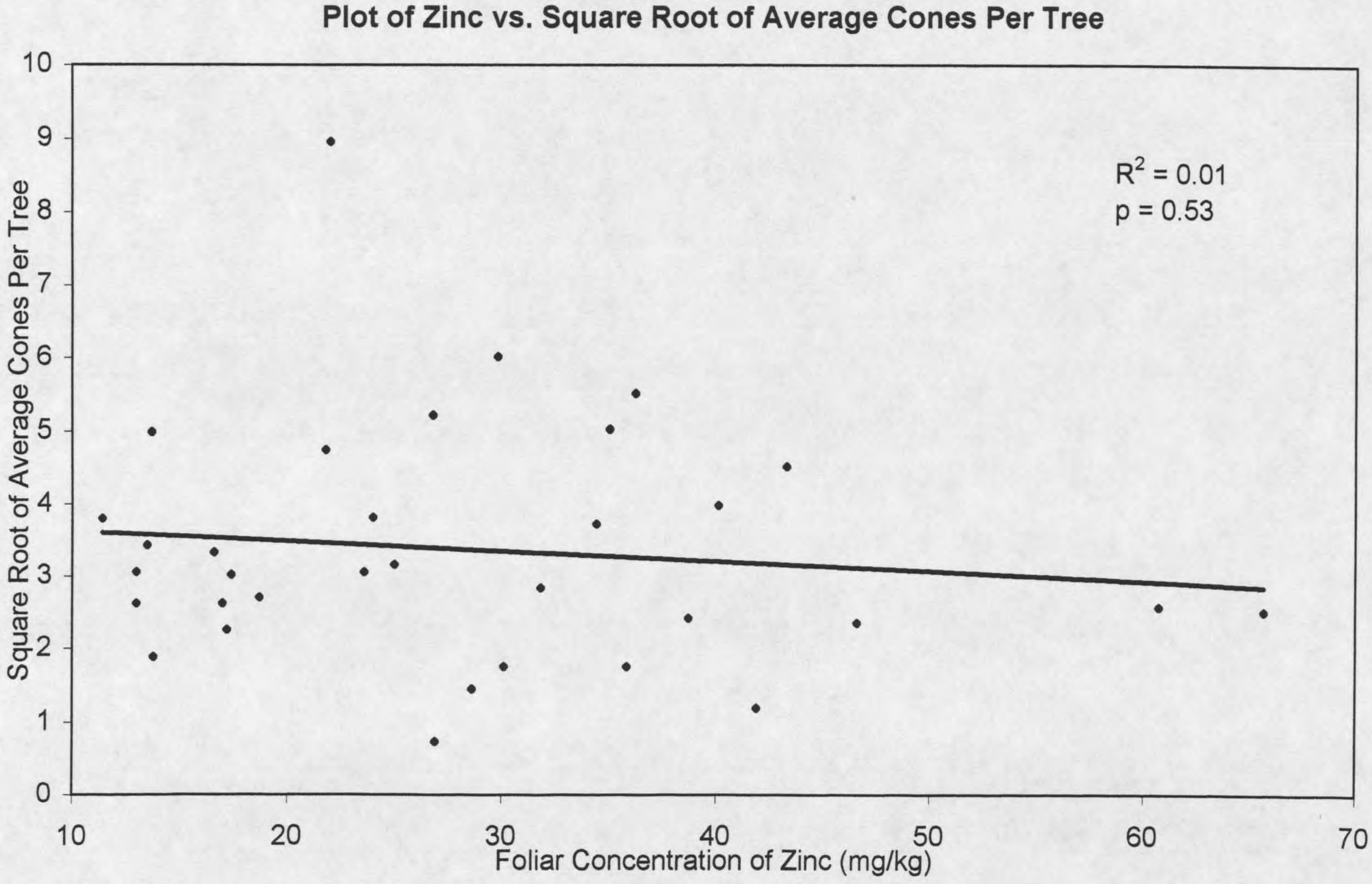

Plot of Phosphorus vs. Square Root of Average Cones Per Tree
$R^2 = 0.01$
p = 0.55
Square Root of Average Cones Per Tree
0
1
2
3
4
5
6
7
8
9
10
0.075
0.085
0.095
0.105
0.115
0.125
0.135
0.145
0.155
0.165
Foliar Concentration of Phosphorus (%)

Figure 29



Plot of Sulfur vs. Square Root of Average Cones Per Tree
Square Root of Average Cones Per Tree
0
1
2
3
4
5
6
7
8
9
10
0.04
0.05
0.06
0.07
0.08
0.09
0.1
0.11
0.12
0.13
Foliar Concentration of Sulfur (%)
$R^2 = 0.03$
$p = 0.37$

Figure 30


Plot of Zinc vs. Square Root of Average Cones Per Tree
Square Root of Average Cones Per Tree
0
1
2
3
4
5
6
7
8
9
10
Foliar Concentration of Zinc (mg/kg)
10
20
30
40
50
60
70
$R^2 = 0.01$
$p = 0.53$

variance from the regression of crown volume verses the square root of average cones per tree (Table 13), thus total nutrient estimates were not significantly correlated with the square root of average cones per tree. This does not support the hypothesis that increases in total nutrient levels increase cone production. This may be because for optimal production plants need nutrients in the proper ratios. If one nutrient is limited (e.g. a phosphorus deficiency will inhibit nitrogen use (Loveless, 1961; Beadle, 1966)), it may inhibit the use of another nutrient (Ingestad, 1979; Waring and Schlesinger, 1985; Ericsson, 1994; Kimmins, 1997). Table 14 shows the nutrient proportions (by weight) of each plot relative to the amount of nitrogen. All the sites have approximately the same proportions, again indicating that plant nutrition (in the plots used here) is not a predictor of cone productivity. However, when these values are compared with the values for other conifers that have optimal nutrient levels (Table 1), some differences are clearly evident. It appears that the plots in this study have higher proportions of calcium and magnesium. This could indicate the possibility of luxury consumption (or the point at which a plant continues to absorb a particular nutrient but does not continue to benefit from the increase of the nutrient) or toxic levels of these nutrients. Another possibility is that since these values are based on their amounts relative to nitrogen content, the plants have adequate amounts of calcium and magnesium and are in fact deficient in nitrogen. This may be more likely because nitrogen is typically a more of a limiting resource in mountain and forest environments (Price, 1981; Waring and Schlesinger, 1985; Kimmins, 1997), and because these soils are acidic, it is unlikely that the trees are experiencing toxic levels of calcium and magnesium. When the comparison is made between the two tables (Table 1

Table 14. Nutrient proportions for some major nutrients (values are based on percent by weight and are relative to a nitrogen value equal to 100) for selected whitebark pine trees from the Interagency Grizzly Bear Study Team cone count sites used in this study.

PLOT	N	K	P	Ca	Mg
A	100	41	12	40	11
B	100	37	11	48	13
F	100	30	11	58	14
H	100	37	11	51	13
M	100	35	11	48	12
P	100	39	11	32	11
Q	100	39	12	38	12
U	100	38	11	43	16

and 14) it is clear that the plots in this study have lower amounts of potassium and phosphorus than what has been found to be optimal for other tree species. A t-test was also performed to verify that there were significant differences between the values in tables 1 and 14 for potassium and phosphorus. The test confirmed the idea that the plots used in this study had significantly lower potassium and phosphorus levels, and that those plots are possibly deficient in those nutrients, suggesting that addition of potassium and phosphorus to these sites would increase cone production.

Results of Multiple Regression Analyses

Correlation between Independent Variables

Before proceeding with the development of a multiple regression model, the relationships between independent variables were first examined (Table 15). Percent coarse material is significantly negatively correlated with both pH and EC. The correlation between EC and coarse material is explained by the fact that as the proportion of fine material increases, the exchange complex is able to hold more ions, which results in an increase in EC. The negative relationship between coarse material and pH can similarly be explained. If the number of ions held on the exchange complex increases (especially calcium and magnesium), these ions could raise the pH. The relationship is not as strong because if the exchange complex was larger and held more hydrogen ions, the pH would decrease. The reason for the significant positive correlation between EC and pH is that as pH increases more ions are released into solution, which results in an

Table 15. Correlation matrix for the listed soil properties measured under whitebark pine at eight of the Interagency Grizzly Bear Study Team's cone count sites (sites A, B, F, H, M, P, Q and U) (significant correlations ($p \leq 0.05$) in **bold**, and corresponding R^2 values *italicized*, corresponding R values are not italicized).

	% Coarse Material	Electrical Conductivity (mmhos/cm)	pH	% Sand	% Clay	% Silt	Depth (cm)	% Organic Matter
% Coarse Material	1							
Electrical Conductivity (mmhos/cm)	**-0.66** ***0.44*** **p = 0.00**	1						
pH	**-0.49** ***0.24*** **p = 0.00**	**0.66** ***0.44*** **p = 0.00**	1					
% Sand	-0.01 *0.00* p = 0.95	0.15 *0.02* p = 0.18	0.08 *0.01* p = 0.49	1				
% Clay	**-0.25** ***0.06*** **p = 0.03**	0.10 *0.01* p = 0.38	0.09 *0.01* p = 0.41	**-0.77** ***0.59*** **p = 0.00**	1			
% Silt	**0.27** ***0.07*** **p = 0.02**	**-0.34** ***0.12*** **p = 0.00**	**-0.22** ***0.05*** **p = 0.05**	**-0.75** ***0.56*** **p = 0.00**	0.15 *0.02* p = 0.20	1		
Depth (cm)	**-0.36** ***0.13*** **p = 0.00**	**0.24** ***0.06*** **p = 0.03**	0.08 *0.01* p = 0.50	-0.22 *0.05* p = 0.06	**0.51** ***0.26*** **p = 0.00**	-0.21 *0.04* p = 0.07	1	
% Organic Matter	0.16 *0.03* p = 0.16	-0.06 *0.00* p = 0.61	0.01 *0.00* p = 0.95	**-0.45** ***0.20*** **p = 0.00**	**0.41** ***0.17*** **p = 0.00**	**0.27** ***0.07*** **p = 0.02**	0.03 *0.00* p = 0.81	1

increase in EC. However, if the solution is strongly acidic (low pH) then EC could also be higher because of the high amounts of hydrogen ions that would be present in solution.

The significant negative correlation between sand and clay may be the result of the measurement of soil texture. Since texture is based on percentages, if the proportion of sand were to increase, then silt, clay or both must decrease in the relative proportions. The strong correlation between sand and silt is the result of the method of calculation (silt is calculated by subtracting the proportion of sand and clay from 100%). Silt was not correlated with clay, perhaps because sand has a wider distribution of values than clay (Figures 14 and 16), thus silt is dependent on the proportion of sand. Clay and depth were also well correlated. More developed soils, which typically have higher proportions of clay, may also be typically deeper. Organic matter is also correlated (negatively) with sand. Soils that are more chemically weathered, and, as a result, lower in the proportion of sand, are to be expected to have higher amounts organic matter in the soil (which results from the decomposition of litter).

Multiple Regression Models

I used multiple regression analysis, with the percent coarse material, EC, and pH as the independent variables, and the square root of average cones per tree as the dependent variable. Stepwise selection techniques were used for determining which variables (based on their significance) would be included in the model. The resulting model was:

$$\text{Square Root of Average Cones Per Tree} = 9.276(\text{EC}) + 0.83(\text{pH}) - 1.878$$

where EC is measured in mmhos/cm. The model was significant ($p = 0.00$) and explained 38% of the variation in the square root of average cones per tree; all variables were significant. The residual plot (Figure 31) indicated the relationship was linear because the plot showed the residuals to be randomly distributed with no apparent pattern. Percent coarse material was not included because when all three variables were used it became statistically insignificant, indicating that much of the variance that it explained was also explained by EC and pH. This implies that the amount coarse material is more important for soil chemistry, rather than for the soil's moisture holding capacity. EC was more significant than pH in the model. One reason for this could be that higher levels of some nutrients, such as phosphorus, would increase EC but have no effect on pH. Thus EC would be a better indicator of site fertility (and cone productivity), as evident by the higher predictive power of EC (Table 9).

A second model combined the data from this study with the data collected by Spector (1999) (which indicated that crown size and basal area are good predictors of cone production). The resulting model was:

$$\text{Square Root of Average Cones Per Tree} = 0.0014(\text{crown volume}) + 10.504(\text{EC}) + 1.343$$

where crown volume is measured in meters cubed. Spector (1999) used crown area in his model, but crown volume had marginally more predictive power with the square root of average cones per tree for the trees selected in this study (Crown Volume: $R^2 = 0.41$, $p = 0.00$; Crown Area: $R^2 = 0.39$, $p = 0.00$ ($\alpha = 0.05$)). The model was significant ($p = 0.00$) and explained 59% of the variation in the square root of average cones per tree; all variables were significant. The residual plot (Figure 32) indicated the relationship was

Figure 31

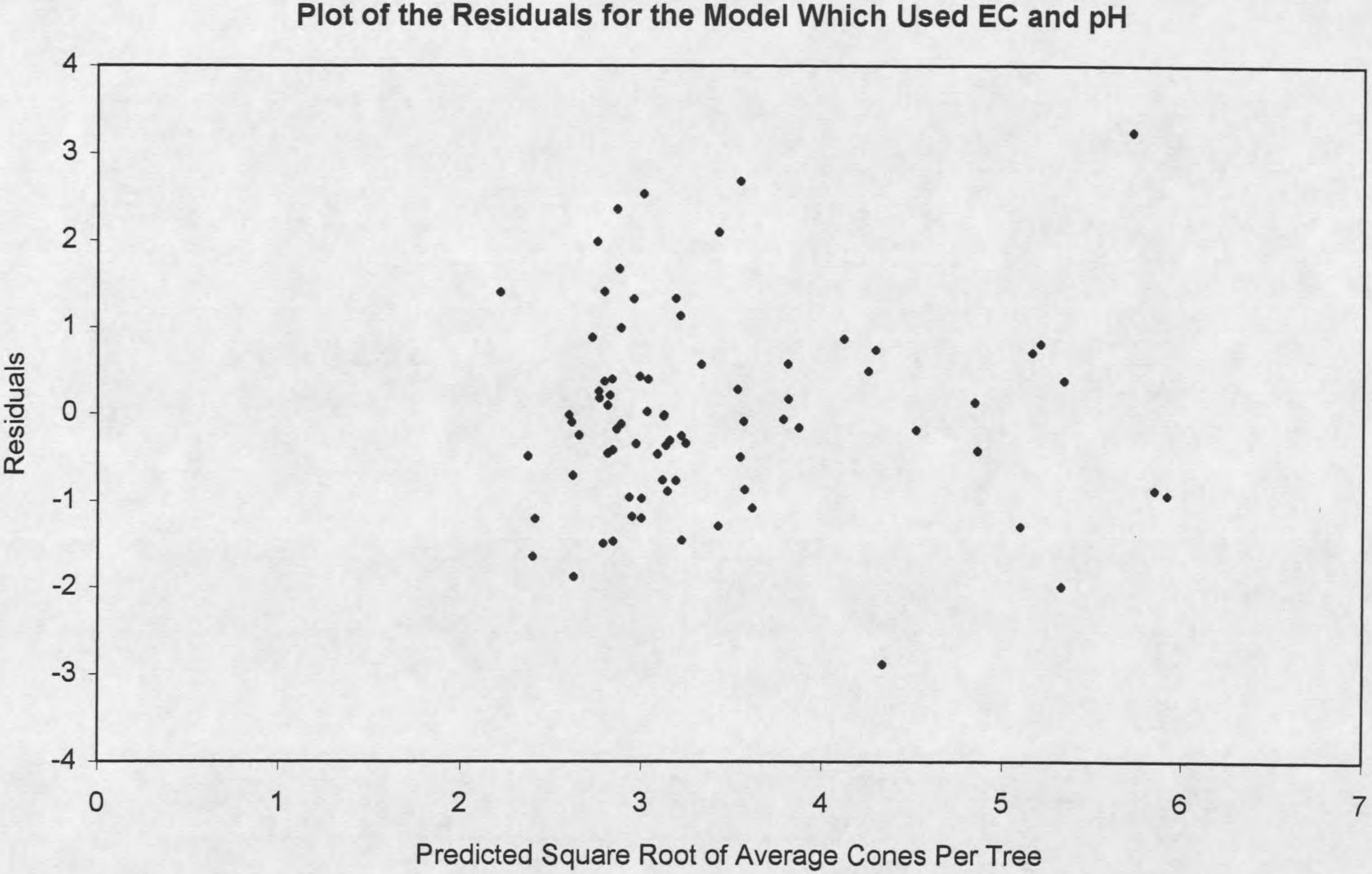
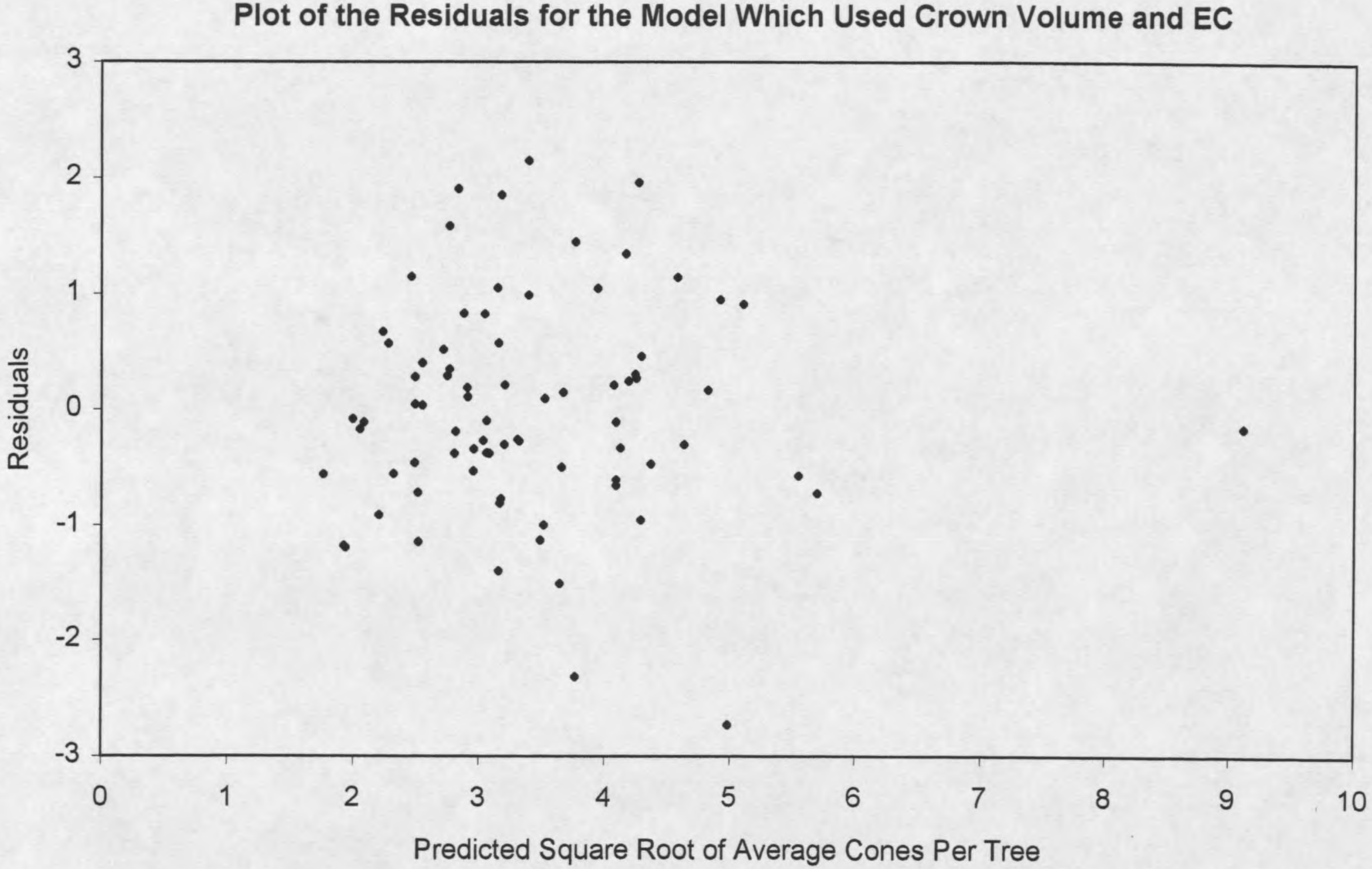

Plot of the Residuals for the Model Which Used EC and pH
Residuals
4
3
2
1
0
-1
-2
-3
-4
0
1
2
3
4
5
6
7
Predicted Square Root of Average Cones Per Tree

Figure 32


Plot of the Residuals for the Model Which Used Crown Volume and EC
Residuals
3
2
1
0
-1
-2
-3
0
1
2
3
4
5
6
7
8
9
10
Predicted Square Root of Average Cones Per Tree

linear because the plot showed the residuals to be randomly distributed with no apparent pattern. Basal area (Spector, 1999) and pH were not included in the model because they both became statistically insignificant.

CONCLUSIONS

Electrical conductivity had a significant and positive influence on cone production in whitebark pine. It explained 33% of the variation in the square root of average cones per tree. Soil pH also had a significant and positive influence on cone production; it explained 29% of the variation in the square root of average cones per tree. The percent coarse material of soil had a significant and negative influence on the square root of average cones per tree. It explained 22% of the variation in the square root of average cones per tree. Soil texture (% sand, % silt, % clay), percent organic matter and soil depth did not have significant relationships with cone production. Foliar nutrient levels (both concentrations and estimated total amounts) also did not have significant relationships with cone production. The foliar data did suggest that these trees might be deficient in nitrogen, phosphorus and potassium. A multiple regression using EC and pH significantly explained 38% of the variation in the square root of average cones per tree. An additional model using crown volume data from a previous study (Spector, 1999) and EC significantly explained 59% of the variation in the square root of average cones per tree. Since the results of the regression analyses (using soil properties) and the multiple regression analyses (using forest structure characteristics and soil properties) did not explain all of the variation in cone production, other factors such as genetics, climate, and moisture availability should be able to explain more of the remaining variation in cone production.

Management Implications

The results of this study contribute to researchers' abilities to better predict the geography of whitebark pine cone production. The information is useful as a guide in the selection of productive sites, for the artificial planting of whitebark pine. This research suggests that increasing EC and pH levels at sites would increase cone production. This could be accomplished through the addition of lime to sites with low EC and pH values. This would serve to raise pH levels, which would release more nutrients into solution and raise EC. However, more research is needed to determine how this would affect the use of the stands by wildlife, and if it might result in the successional replacement of whitebark pine by other species. Additionally the addition of nitrogen-phosphorus-potassium fertilizers would be expected to increase cone production since foliar concentrations indicated that the trees were deficient in these nutrients.

Future Research

More research needs to be done to give us a more complete understanding of whitebark pine cone production. From the knowledge gained from this study it is clear that more information is needed about the nutrient requirements of whitebark pine, especially in how they relate to cone production. This could lead to the development of management strategies involving fertilizer applications to increase cone production. However, it must be determined what extent this may impact whitebark pine ecology (e.g. successional replacement and wildlife use). Additionally, since soil moisture availability was not addressed in this study, its effects on cone production should also be examined. Future research should also focus on the effects of climate, especially at a micro-scale level, on cone production. The influence of genetics, which is known to affect cone production in other species (Hoff, 1981; Savolainen et al., 1993), should also be examined to see to what extent it affects whitebark pine cone production.

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REFERENCES CITED

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APPENDICES

APPENDIX A

Appendix A. Procedures for soil analysis.

1: Soil pH and Electrical Conductivity (1:1 procedure) (Clesceri et al., 1989; Page and Klute, 1982; U.S.S.L., 1954)

1) Weigh 20 grams air-dry soil into extraction racks and add 20ml of deionized water.
2) Shake for 3 minutes to suspend and allow 30 minutes to settle.
3) Calibrate pH and EC meters.
4) Gently mix wetted soil/sample into slurry.
5) Place electrode in the slurry.
6) Read the EC value.
7) Resuspend the slurry.
8) Place electrode in the slurry.
9) Wait for the pH meter to equalize.
10) Read the pH value.

2: Soil Organic Matter (Loss on Ignition Method) (Schulte, 1988; Schulte and Hopkins, 1996; Storer, 1984)

1) Weigh 10.0 ± 1.0 grams (or more may be used, 20.0 ± 1.0 grams was used) into a pre-weighed crucible (record to the nearest ± 0.001 grams). Prepare a crucible containing calcium (this is used as a blank in order to measure losses of alkali metals, if >0.05% change in weight occurs, furnace must be calibrated (all blanks were under 0.05% change)).
2) Place in drying oven for two hours at 105°C. Place in dessicator for one hour (a lid was placed over the crucible while in ovens and dessicators to prevent soil loss).
3) Record crucible + soil as initial weight to the nearest ± 0.001 grams.
4) Heat in muffle furnace to 360°C for two hours.
5) Place in drying oven at 105°C for one hour and place in dessicator for one hour.
6) Record crucible + soil as final weight to nearest ± 0.001 grams.

Calculation:

$$\text{LOI } \% = \frac{(\text{Initial wt at } 105^\circ\text{C} - \text{Final wt after } 360^\circ\text{C})}{(\text{Initial wt at } 105^\circ\text{C} - \text{crucible wt})} \times 100$$

3: Soil Texture (modified Bouyoucos Method) (A.S.T.M., 1985; Bouyoucos, 1936; Day, 1965; Gee and Bauder, 1979; Gee and Bauder, 1986; U.S.S.L., 1954)

1) Weigh 40.0 ± 0.05 grams of air-dry soil into 200ml container.
2) Add 10ml of 10% sodium hexametaphosphate $(NaPO_3)_6$ and 90ml of deionized water.
3) Close container and place on reciprocating horizontal shaker for sixteen hours.

4) Rinse soil slurry into graduate cylinder and add additional water (deionized) until volume equals 1 liter.
5) Fully suspend soil mixture with plunger (about 1 minute) using strong upward stokes of the plunger near the bottom to lift into suspension any particles that may have lodged there. Dislodge any sediment that remains in the lower corners by inclining the rod slightly and rotating it to impart a spinning motion to the disk. Finish with two or three slow smooth strokes.
6) Carefully remove plunger. (Tip plunger and touch off to side to remove adhering drops.)
7) Follow timetable below.

No. of seconds	
0	Note time that plunger was removed
20	Carefully insert the hydrometer
35	Familiarize yourself with hydrometer scale/markings
40	Read hydrometer "at the upper edge of the meniscus" at an angle of 10-20 degrees above plane of the liquid and record Bouyoucos scale value to the closest 0.5 g/L

8) Slowly remove hydrometer from suspension and rinse. Record the time and temperature on the data sheet.
9) Without remixing, reinsert hydrometer and take another reading at 2 hours. Record a second temperature.
10) Perform steps 2-9 for a blank (without soil sample).
11) Calculate all readings to reflect blank value and temperature adjustments.

Temperature Adjustment: For each degree above 67°F, add 0.2 to the reading to get the corrected hydrometer reading. For each degree less than 67°F, subtract 0.2 from the reading.

Blank Adjustment: Subtract or add appropriate value to make blank equal to zero.

12) Calculations:

$$\%\ \text{Sand} = \frac{\text{grams of sample(adjusted to be oven dry)} - \text{(40 sec corrected reading)}}{\text{grams of sample(adjusted to be oven dry)}} \times 100$$

$$\%\ \text{Clay} = \frac{\text{(2 hour corrected reading)}}{\text{grams of sample(adjusted to be oven dry)}} \times 100$$

$$\%\ \text{Silt} = 100\% - (\%\ \text{Sand} + \%\ \text{Clay})$$

APPENDIX B

Appendix B. Residuals for the regression between crown volume (Spector, 1999) and square root of average cones per tree for trees selected for foliar analysis.

PLOT	TREE	RESIDUALS
A	3	-2.8778
A	4	-1.2756
A	8	-1.2998
B	4	1.2411
B	5	-0.0870
B	6	-0.3111
B	10	0.3387
F	1	0.1352
F	4	0.3484
F	7	-0.0081
F	8	0.6302
F	9	2.1666
H	2	-0.4134
H	3	-0.6813
H	6	-0.7341
H	9	1.5762
H	10	-0.9567
M	3	0.3220
M	4	-0.0282
M	5	-0.0087
M	8	-1.7815
M	9	0.7045
P	2	-0.4645
P	9	0.1408
Q	4	-1.1083
Q	5	-1.5100
Q	6	-0.7436
Q	8	-0.8313
U	2	1.9580
U	4	1.1428
U	5	0.8691
U	7	2.6520
U	8	0.8955

APPENDIX C

Appendix C. Lab data for selected soil properties for sample trees within selected study plots.

PLOT	TREE	EC	pH	% Sand	% Clay	% Silt	% Organic Matter
A	1	0.104	5.25	36	33	31	4.7
A	2	0.089	5.05	42	30	29	3.8
A	3	0.11	4.84	37	31	31	5.3
A	4	0.106	4.98	38	29	33	5.5
A	5	0.089	4.9	40	31	29	3.9
A	7	0.089	5.13	34	42	24	5.7
A	8	0.077	4.57	33	30	37	4.5
A	9	0.08	5.27	30	30	40	3.9
A	10	0.076	4.9	31	30	39	4.6
B	1	0.094	5.51	29	34	37	5.7
B	2	0.082	5.24	26	36	38	7.3
B	3	0.084	5.11	30	34	36	8.1
B	4	0.088	4.75	31	31	39	7.5
B	5	0.112	4.68	31	32	37	7.9
B	6	0.065	5.4	29	31	39	7.3
B	7	0.1	5.18	28	33	38	9.6
B	8	0.144	4.97	34	32	34	8.2
B	9	0.088	4.9	32	33	35	9.7
B	10	0.119	5.21	30	34	36	10.8
F	1	0.095	4.55	55	18	27	3.1
F	2	0.073	4.87	57	18	25	3.2
F	3	0.101	4.6	54	20	27	4.7
F	4	0.066	5.35	55	19	25	4.0
F	5	0.045	5.17	43	25	32	4.5
F	6	0.085	4.96	50	21	29	4.4
F	7	0.084	4.47	50	20	31	4.9
F	8	0.101	5.72	45	22	33	5.8
F	9	0.122	6.1	46	23	31	5.3
F	10	0.06	4.93	44	23	33	4.3
H	1	0.067	4.82	42	25	34	4.7
H	2	0.087	5.03	38	27	35	4.8
H	3	0.081	4.8	41	27	32	4.9
H	4	0.082	4.56	41	27	32	7.6
H	5	0.076	4.8	38	27	35	5.5
H	6	0.084	4.71	37	27	36	6.2
H	7	0.128	4.76	33	29	38	6.3
H	8	0.1	4.64	36	26	38	5.3
H	9	0.129	4.97	38	27	35	5.6
H	10	0.115	4.75	37	28	35	6.0

M	1	0.12	5.61	36	24	40	5.3
M	2	0.124	5.49	34	24	43	5.5
M	3	0.144	5.27	38	24	39	6.4
M	4	0.118	5.24	38	25	37	6.2
M	5	0.125	5.19	38	26	36	5.3
M	6	0.154	5.53	38	25	37	5.4
M	7	0.096	5.57	37	24	40	4.9
M	8	0.148	5.86	39	24	37	4.2
M	9	0.25	6.39	49	21	30	4.5
M	10	0.172	5.81	38	21	41	5.2
P	1	0.133	4.57	42	24	33	5.3
P	2	0.125	4.54	46	18	37	4.3
P	3	0.105	4.67	41	22	37	7.3
P	4	0.096	4.54	43	24	33	4.8
P	5	0.105	4.72	42	24	34	4.9
P	6	0.102	4.53	40	26	33	4.3
P	7	0.1	4.59	42	23	36	4.4
P	8	0.118	4.38	43	24	33	4.5
P	9	0.118	4.54	44	23	34	4.8
P	10	0.108	4.55	47	20	33	4.1
Q	2	0.032	5.09	48	19	33	5.8
Q	3	0.029	4.63	50	19	31	5.7
Q	4	0.032	4.83	47	22	31	7.2
Q	5	0.052	4.59	49	21	31	6.7
Q	6	0.034	4.76	47	23	30	7.6
Q	7	0.06	4.97	40	25	36	9.4
Q	8	0.062	5.14	40	24	36	6.4
Q	9	0.033	5.07	51	21	28	4.9
Q	10	0.048	5.28	43	21	36	5.4
U	1	0.236	5.87	52	25	23	4.3
U	2	0.265	6.46	45	30	24	4.3
U	3	0.239	6.05	56	24	21	5.1
U	4	0.229	5.87	50	24	26	5.9
U	5	0.26	5.8	48	25	27	5.0
U	6	0.301	5.97	44	30	26	6.9
U	7	0.265	5.6	40	32	29	6.3
U	8	0.148	5.76	44	25	31	9.7
U	9	0.206	5.84	43	26	31	5.2
U	10	0.214	5.73	45	24	31	5.6

APPENDIX D

Appendix D. Lab data for percent coarse material for sample trees within selected study plots.

PLOT	TREE	N	S	E	W	MEAN
A	1	48	37	37	53	44
A	2	33	48	44	33	40
A	3	45	45	40	44	44
A	4	33	38	47	54	43
A	5	51	50	47	40	47
A	7	43	39	36	58	44
A	8	51	44	45	52	48
A	9	41	45	47	34	42
A	10	48	51	53	36	47
B	1	35	45	43	39	41
B	2	45	48	39	28	40
B	3	50	46	58	55	52
B	4	35	30	38	43	37
B	5	47	40	58	34	45
B	6	47	29	54	35	41
B	7	39	41	44	29	38
B	8	52	47	42	41	45
B	9	45	100	37	38	55
B	10	37	100	100	57	73
F	1	55	61	55	32	51
F	2	25	35	28	39	32
F	3	52	100	50	63	66
F	4	56	43	41	38	44
F	5	33	29	25	39	32
F	6	60	30	100	54	61
F	7	56	100	47	47	62
F	8	35	60	47	47	47
F	9	37	100	33	35	51
F	10	38	37	51	100	57
H	1	37	51	26	52	41
H	2	29	48	33	30	35
H	3	30	26	100	27	46
H	4	47	39	22	45	38
H	5	30	60	21	19	32
H	6	66	53	41	47	52
H	7	36	40	38	34	37
H	8	55	11	32	25	31
H	9	31	19	28	100	44
H	10	37	46	28	20	32
M	1	35	36	74	38	46

M	2	63	35	28	38	41
M	3	25	43	37	60	41
M	4	65	37	43	32	44
M	5	28	20	20	43	28
M	6	55	35	36	52	44
M	7	68	29	49	33	45
M	8	31	31	18	33	28
M	9	31	27	63	66	47
M	10	37	100	20	27	46
P	1	69	60	48	74	63
P	2	44	38	37	47	42
P	3	51	45	71	50	54
P	4	70	59	63	46	60
P	5	59	50	61	47	54
P	6	66	62	48	60	59
P	7	61	46	48	49	51
P	8	54	35	53	56	50
P	9	58	52	68	53	58
P	10	48	53	55	63	55
Q	2	57	100	100	100	89
Q	3	51	39	47	63	50
Q	4	63	54	74	70	65
Q	5	65	71	75	38	62
Q	6	36	74	58	100	67
Q	7	100	82	100	76	90
Q	8	61	100	78	89	82
Q	9	1	57	100	65	56
Q	10	100	48	100	69	79
U	1	15	12	18	9	13
U	2	14	12	17	3	12
U	3	10	11	13	5	10
U	4	29	17	15	14	19
U	5	14	13	10	5	10
U	6	25	14	13	23	19
U	7	18	11	24	0	13
U	8	22	15	15	18	17
U	9	23	29	46	22	30
U	10	24	33	30	29	29

APPENDIX E

Appendix E. Soil texture classes for sample trees within selected study plots.

PLOT	TREE	TEXTURE
A	1	Clay loam
A	2	Clay loam
A	3	Clay loam
A	4	Clay loam
A	5	Clay loam
A	7	Clay
A	8	Clay loam
A	9	Clay loam
A	10	Clay loam
B	1	Clay loam
B	2	Clay loam
B	3	Clay loam
B	4	Clay loam
B	5	Clay loam
B	6	Clay loam
B	7	Clay loam
B	8	Clay loam
B	9	Clay loam
B	10	Clay loam
F	1	Sandy loam
F	2	Sandy loam
F	3	Sandy loam
F	4	Sandy loam
F	5	Loam
F	6	Loam
F	7	Loam
F	8	Loam
F	9	Loam
F	10	Loam
H	1	Loam
H	2	Clay loam
H	3	Clay loam
H	4	Clay loam
H	5	Clay loam
H	6	Clay loam
H	7	Clay loam
H	8	Loam
H	9	Clay loam
H	10	Clay loam
M	1	Loam
M	2	Loam

M	3	Loam
M	4	Loam
M	5	Loam
M	6	Loam
M	7	Loam
M	8	Loam
M	9	Loam
M	10	Loam
P	1	Loam
P	2	Loam
P	3	Loam
P	4	Loam
P	5	Loam
P	6	Loam
P	7	Loam
P	8	Loam
P	9	Loam
P	10	Loam
Q	2	Loam
Q	3	Loam
Q	4	Loam
Q	5	Loam
Q	6	Loam
Q	7	Loam
Q	8	Loam
Q	9	Loam
Q	10	Loam
U	1	Sandy clay loam
U	2	Sandy clay loam
U	3	Sandy clay loam
U	4	Sandy clay loam
U	5	Sandy clay loam
U	6	Sandy clay loam
U	7	Clay loam
U	8	Loam
U	9	Loam
U	10	Loam

APPENDIX F

Appendix F. Field data for depth measurements taken at selected compass directions for sample trees within the selected study plots (there is no data for trees Q1 and U1).

PLOT	TREE	0	36	72	108	144	180	216	252	288	324	Mean
A	1	65	90	79	74	62	61	47	50	32	58	61.8
A	2	53	62	44	61	90	90	90	90	72	61	71.3
A	3	56	86	42	90	68	90	44	21	90	68	65.5
A	4	44	20	25	33	28	30	33	46	49	53	36.1
A	5	90	90	90	90	90	90	90	90	90	90	90
A	7	76	44	62	56	61	90	90	77	51	90	69.7
A	8	55	77	75	90	90	90	57	53	76	38	70.1
A	9	90	90	72	56	90	90	90	64	71	74	78.7
A	10	90	90	71	90	84	90	64	48	64	70	76.1
B	1	59.5	50	52	45	57	14	10	41	28	40	39.65
B	2	40	45	35	8	42	24	24	49	51	65	38.3
B	3	51	77	37	8	32	57	90	56	59	60	52.7
B	4	35	53	48	40	50	90	40	39	37	82	51.4
B	5	36	90	55	24	48	42	51	44	64	69	52.3
B	6	40	10	42	62	44	12	51	57	11	10	33.9
B	7	20	15	48	31	26	53	51	41	39	50	37.4
B	8	13	17	55	46	33	13	59	43	34	42	35.5
B	9	20	56	35	82	34	32	61	45	40	43	44.8
B	10	42	40	32	43	39	54	43	46	60	38	43.7
F	1	24	14	16	10	30	9	16	22	23	25	18.9
F	2	45	15	14	10	14	9	17	43	75	58	30
F	3	16	16	10	16	18	27	20	45	48	42	25.8
F	4	8	22	28	12	30	30	18	44	30	28	25
F	5	60	19	29	25	52	38	39	30	25	12	32.9
F	6	13	41	70	52	24	8	33	23	38	24	32.6
F	7	40	42	18	25	20	9	40	24	23	22	26.3
F	8	34	31	25	19	20	6	45	20	10	15	22.5
F	9	10	25	23	26	27	31	15	10	10	8	18.5
F	10	50	37	10	10	25	18	19	23	76	30	29.8
H	1	22	43	25	19	9	52	36	30	25	26	28.7
H	2	46	4	66	60	33	15	28	20	15	34	32.1
H	3	15	30	18	43	11	19	23	28	35	23	24.5

H	4	10	52	23	15	58	16	6	48	14	16	25.8
H	5	10	43	32	6	17	12	13	13	12	17	17.5
H	6	12	10	21	5	15	13	20	26	32	5	15.9
H	7	21	66	22	31	6	14	55	42	5	33	29.5
H	8	5	61	60	61	42	14	14	40	49	45	39.1
H	9	28	40	42	15	35	29	24	35	35	79	36.2
H	10	25	45	43	13	18	47	27	9	23	39	28.9
M	1	13.6	52	26.4	51.1	36	42.3	29.1	21.6	23	32.1	32.72
M	2	18.2	23.6	21.2	23.4	13.2	33.6	22.1	18.3	29.2	32.8	23.56
M	3	23.1	18.6	28.6	60.6	15.3	39.6	32.1	24.2	23.6	24	28.97
M	4	29.4	32.6	15.3	22.6	25	30.2	25.6	23.2	31.2	18.6	25.37
M	5	41	32	35.3	11	23.2	37.1	29.2	22.5	24	27.3	28.26
M	6	45.2	35.2	20.2	30.5	26.2	24	48.1	32.3	38	36.5	33.62
M	7	21	14.2	12.7	26.6	59.5	28.2	24	16.6	23.5	25	25.13
M	8	27	21	32	20	28.5	25.5	34	15	37.5	19.9	26.04
M	9	13.5	16	19.5	17.6	23.8	19.3	24.2	12.2	12.6	16.7	17.54
M	10	13	13	13	14	8	9.2	6.9	12.8	12	7.2	10.91
P	1	20	46	34.3	25.7	29.6	30.1	49.4	43.2	30.5	40.4	34.92
P	2	27	56.5	43.1	45.6	73	26.1	34.7	28	31	33	39.8
P	3	17	49.1	30	26.4	35.3	22.1	28.2	67	39.1	30	34.42
P	4	39.5	49.9	45.3	31	36.7	63.8	45.7	44.8	26	40.7	42.34
P	5	47.4	48	42.3	54.5	61.5	49	53.6	48.4	46.3	40	49.1
P	6	54.5	35	44	37.8	40.6	29	44	34.7	24.7	17.5	36.18
P	7	14.5	23.6	33	45.2	39.5	21.1	14.2	20	24.6	27.6	26.33
P	8	26.7	27	25.5	28.6	25.2	33.5	26.7	46.5	41.3	29	31
P	9	33.5	35.9	28	36	33	38.5	33.3	42.2	21.8	39.5	34.17
P	10	18	24.5	38.5	66.5	90	62.7	27.5	53.5	30	6.5	41.77
Q	2	25	35	28	28	24	26	21	23	13	48	27.1
Q	3	27	30	53	73	40	43	30	63	28	51	43.8
Q	4	27	43	27	25	45	38	39	52	33	30	35.9
Q	5	47	30	48	26	22	13	27	28	36	29	30.6
Q	6	24	33	34	48	44	15	21	14	18	28	27.9
Q	7	38	21	34	21	17	33	40	40	41	40	32.5
Q	8	5	20	15	25	30	13	10	45	23	15	20.1
Q	9	6	20	35	30	22	20	14	12	12	13	18.4
Q	10	18	8	6	18	8	10	8	5	8	12	10.1
U	2	59	49.9	35.6	46	51.3	47	63	44.3	52	27.9	47.6

U	3	42	39.5	36.5	43	47.3	53.5	48.6	60.3	67.3	53	49.1
U	4	54.5	45.3	63.5	67.3	73.5	59.3	63.3	64.5	67.5	68.3	62.7
U	5	90	89.6	90	63.5	81	69.9	71	83.5	79.3	90	80.78
U	6	61.3	65.6	54	51.6	59.3	67.5	53.5	63.5	65.1	31.5	57.29
U	7	37	41.3	45	39.5	68	53	56.3	49.3	26.5	45.3	46.12
U	8	68.3	70.3	65.6	73.5	55.6	81	76.3	74	90	83.5	73.81
U	9	51	41	65.5	46.3	41	46	39	58.7	43.6	63.5	49.56
U	10	10	22	74	57	60	54	39.5	55	81.5	30	48.3

APPENDIX G

Appendix G. Lab data for nutrient concentrations for selected sample trees within selected study plots.

PLOT	TREE	B(mg/kg)	Ca(%)	Cu(mg/kg)	Fe(mg/kg)	K(%)	Mg(%)	Mn(mg/kg)	TKN(%N)	P(%)	S(%)	Zn(mg/kg)
A	3	18.8	0.231	2	72.7	0.443	0.093	463	1	0.101	0.062	17.2
A	4	21.6	0.386	2.4	67.2	0.418	0.14	451	1.02	0.15	0.084	30.1
A	8	26	0.695	2.9	70.9	0.475	0.134	1141	1.27	0.144	0.084	65.7
B	4	22.2	0.366	2.2	74.8	0.351	0.106	796	1	0.111	0.064	26.8
B	5	18.5	0.424	2	62.6	0.35	0.147	412	1.02	0.118	0.065	23.6
B	6	32.4	0.554	2.1	90.1	0.401	0.114	954	0.96	0.115	0.067	43.3
B	10	14.9	0.568	1.8	52.1	0.38	0.133	854	0.98	0.102	0.064	24
F	1	19.4	0.374	1.8	77.5	0.381	0.087	553	0.89	0.104	0.051	17.4
F	4	16	0.426	2.1	68.6	0.323	0.126	294	1.09	0.104	0.072	31.8
F	7	26.6	0.809	2.2	81.3	0.259	0.173	1337	0.98	0.101	0.073	60.7
F	8	23.5	0.535	2.4	66	0.27	0.172	323	1.07	0.116	0.066	34.4
F	9	22.3	0.822	2.5	79.1	0.279	0.155	397	1.08	0.126	0.069	35
H	2	20.9	0.5	1.7	79	0.307	0.171	799	0.87	0.091	0.054	17
H	3	20.9	0.51	2.1	51.1	0.52	0.116	867	1.01	0.121	0.074	38.7
H	6	9	0.326	2	40.4	0.424	0.105	576	1.07	0.112	0.071	25
H	9	15.4	0.523	1.8	58.2	0.344	0.104	822	1.1	0.119	0.069	36.2
H	10	17.1	0.724	2.3	69.1	0.296	0.137	2004	1.01	0.097	0.07	46.6
M	3	21.2	0.544	2.4	53.5	0.331	0.108	884	0.95	0.116	0.125	40.1
M	4	13.9	0.482	1.6	55	0.408	0.105	382	0.92	0.102	0.061	13
M	5	26.7	0.374	1.9	48.4	0.299	0.079	286	0.93	0.095	0.056	18.7
M	8	18	0.51	2.3	46.8	0.27	0.154	244	0.98	0.098	0.067	28.6
M	9	16.7	0.285	2.8	48.1	0.303	0.104	170	0.78	0.089	0.05	22
P	2	15.6	0.36	1.7	37.7	0.332	0.116	504	0.9	0.097	0.056	13.5
P	9	12.1	0.204	1.8	49.8	0.353	0.078	350	0.84	0.094	0.065	13
Q	4	10	0.489	2.2	68.8	0.39	0.13	999	1.02	0.117	0.068	41.9
Q	5	18.6	0.399	2	49.4	0.456	0.148	1461	1.11	0.128	0.078	26.9
Q	6	23.6	0.314	1.7	57.3	0.35	0.109	350	0.99	0.107	0.062	13.8
Q	8	19.5	0.424	2.1	59.8	0.459	0.135	690	1.14	0.138	0.078	35.8
U	2	16.6	0.594	2.2	44.4	0.315	0.21	115	1.06	0.09	0.064	13.7
U	4	17.1	0.413	1.9	42.1	0.316	0.153	293	0.93	0.09	0.058	11.4
U	5	29.6	0.384	1.7	49.2	0.377	0.144	371	0.86	0.091	0.058	16.6
U	7	34	0.378	2.5	60.7	0.52	0.13	387	1.14	0.16	0.08	29.8
U	8	20.6	0.37	1.9	59.5	0.332	0.147	269	0.94	0.095	0.06	21.8