**Growth Response of Whitebark Pine to Climate in the
Pacific Northwest**

A thesis presented to the faculty of the department of
biology St. Joseph's University

In partial fulfillment of the requirements for the degree
of Master of Science

by
Pedram Patrick Daneshgar
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Abstract

In this study, dendrochronological methods were used to understand how whitebark pine responds to climate in the Pacific Northwest. Whitebark pine cores were extracted, dated and their growth patterns were correlated with monthly temperature and precipitation to determine the short-term effects of climate at 27 sites at Crater Lake, Mount Rainier, and North Cascades National Parks. Six of the 27 sites showed no significant correlation between climate and whitebark growth. The short-term analysis revealed that whitebark pine growth is limited by growing season length. Negative correlations between previous December and March precipitation and positive correlations were observed between January and March temperature at sites in both North Cascades and Mount Rainier suggesting that winter precipitation in the form of snowpack limits growth while warm winter temperatures promoted growth by decreasing the snowpack in the two northern parks. Whitebark pine growth cannot begin until soil temperatures rise above freezing allowing new roots to grow. June temperatures positively correlated with growth at Crater Lake suggesting most growth occurs in the late spring. Growth is presumed to cease in the summer when high summer temperatures cause respiration costs to exceed carbon gains from photosynthesis, however July precipitation may allow whitebark pine at Crater Lake to once again resume, allowing for storage of carbon, as evidenced by a positive correlation of previous July precipitation with growth at Crater Lake. Warm fall temperatures lead to productive growing seasons the following year at Crater Lake and Mount Rainier, presumably by increasing carbon stores. Using factor analysis on 20 mean basal area increment chronologies from 20 sites, four factors were extracted which account for 88% of the variability in the whitebark pine growth patterns. The first factor, which accounted for 35% of the variance, showed a growth increase in whitebark pine since the late 1950's. We believe a combination of increasing temperatures and carbon dioxide fertilization best explain this growth increase, however the effects of increasing nitrogen deposition cannot be completely ruled out. Factor 1 is significantly positively correlated with CO_2 ($r=0.668$, $p<0.001$) and annual temperature from the three climate divisions representing Mt. Rainer, North Cascades, and Crater Lake National Parks($r=0.569$, $p<0.001$ for WA division 5, $r=0.275$, $p=0.005$ for WA division 6, $r=0.495$, $p<0.001$ for OR division 5; Figure 3.2a-c). The second major factor showed a strong negative correlation with winter Pacific Decadal Oscillation (PDO) index($r=-0.2916$, $p=0.006$), with the time period of 1941 to 1970 the most strongly correlated ($r= -0.391$, $p=0.005$) suggesting that PDO is partially responsible for the trends observed in the growth. The third and fourth extracted factors correlated with the same climate variables that limited growth of whitebark pine in the short-term implying that their effects are seen in the long-term.

<u>Chapter 1: Introduction</u>

Whitebark Pine Ecology

An upper subalpine species, whitebark pine (*Pinus albicaulis*) is a long-lived, slow-growing conifer (Arno and Hoff 1989; McCaughey and Schmidt 2001). A short-needled pine, whitebark pine, can be recognized by their large, exposed, spreading crown (Lanner 1996; Arno and Hoff 1989), and a deep and spreading root system anchor whitebark pines into rock substrate (Arno and Hoff 1989). In general, whitebark pine are small trees with heights ranging from 10 to 15 m (Harlow and Harrar 1958). Whitebark pine are considered, by most, to be one of five stone pines worldwide along with Swiss stone pine (*Pinus cembra*), Korean stone pine (*Pinus koaiensis*), Siberian stone pine (*Pinus sibirica*), and Japanese stone pine (*Pinus pumila*)(McCaughey and Schmidt 2001). Stone pines are characterized by needles in groups of five, wingless seeds, and indehiscent cones (McCaughey and Schmidt 2001).

Whitebark pine are monecious (Arno and Hoff 1989). Pollen from the red, male strobili grow throughout the crown and are shed in early July (Arno and Hoff 1989). Whitebark pine female cones are oblong in shape, roughly 5-8 cm in length, dark brown to purple in color, usually appearing near the tips of the upper crown branches where they take a year to mature (McCaughey and Schmidt 2001; Arno and Hoff 1989). Cones ripen in September when the scales become somewhat loose (Arno and Hoff 1989). The scales do not completely expose the seeds, but when the cone is ripe the scales can be easily broken, particularly by Clark's nutcracker (Tomback 1978).

Whitebark pines seeds are large, wingless and are characterized by their delayed germination (Lanner and Gilbert 1992). The seeds are high in calories, which comes from the fact that they are fifty-two percent fat and only twenty-one percent protein (Lanner and Gilbert 1992). Studies suggest this is why whitebark pine seeds are a valuable resource for several kinds of wildlife (Kendall and Arno 1990; Lanner and Gilbert 1992).

Fossil records show that for the past 8,000 years, whitebark pine has been limited to western North America (McCaughey and Schmidt 2001). Pines did not exist in North America until the Cretaceous period and whitebark pine did not appear until the Tertiary period when the earth was still relatively cool (McCaughey and Schmidt 2001). Whitebark pine are believed to have evolved from Eurasian stone pines that crossed from northeast Asia to Alaska over the Bering Straight land bridge (Lanner 1996). Fossil pollen sites indicate that whitebark pine was present in the Yellowstone National Park region for more than 100,000 years, however glacial retreat 15,000 years ago has caused them to be restricted to high elevation sites (MacDonald et al. 1989). Global warming and the melting of glaciers caused whitebark pine to migrate to high elevations 8-10 thousand years ago (McCaughey and Schmidt 2001).

Whitebark pine is found between the longitudes of 107 and 128 degrees west and between 37 and 55 degrees north latitude (McCaughey and Schmidt 1990). Whitebark pine occurs predominantly in two ranges, an eastern and western range (McCaughey and Schmidt 2001). From the Kern River in southeastern California up through the Blue and Wallowa Mountains of Oregon

to the coastal ranges of the Bulkley Mountains in northern British Columbia make up the western range encompassing the Cascade Range (McCaughey and Schmidt 1990). The northern Rocky Mountains of British Columbia, Alberta, Idaho, Montana, Wyoming and Nevada compose the eastern range (McCaughey and Schmidt 1990).

Climate and competition limit whitebark pine's range to high elevation forests near the timberline (Arno and Hoff 1989) and many of the stands are geographically isolated (Arno and Hoff 1990; McCaughey and Schmidt 2001). Whitebark pine are excluded from growing at higher elevations by a cool growing season and/or wind induced drought (Weaver 2001). In the Cascades, the length of growing season influences whitebark pine growing patterns. Whitebark pine is outcompeted by subalpine fir (*Abies lasiocarpa*) and lodgepole pine (*Pinus contorta*) at lower elevations (Weaver 2001). White spruce (*Picea glauca*), Engelmann spruce *(Picea engelmannii)*, mountain hemlock (*Tsuga mertensiana*), and limber pines (*Pinus flexilis*) are also often found with whitebark pine (Weaver 2001).

Whitebark pine is distributed in cold, windy and snowy regions (Arno and Hoff 1989). Their small size suggests their roots uptake reduced amounts of water, which explains why they are commonly found on dry, exposed sites (Harlow and Harrar 1958). Short cool summers with temperatures of 13-15 $^{\circ}$C and long cold winters with temperatures between -9 $^{\circ}$C and -3 $^{\circ}$C define the whitebark pine climate (Arno and Hoff 1989). Communities of whitebark pine receive from 60 to 180 cm of mean precipitation a year, two thirds of which is

snow or sleet (Arno and Hoff 1989). Snowpack begins in late October and reaches its maximum depth of 60 to 125 cm in April (Weaver 2001). Whitebark pine occurs in cold snowy areas, not because it can't survive else where, but because the weather suppresses its competitors from establishing on these sites (Arno 2001). This suggests that whitebark pine may be the most drought and cold tolerant species at the timberline of the Cascades.

The soils of the whitebark pine zone are cold climate soils, typically classified as Inceptisols that tend to be weakly developed (Weaver 2001; Arno and Hoff 1989). Many of these Inceptisols are identified as Typic Cryochrepts. Usually glaciers previously covered the grounds where these soils are found (Arno and Hoff 1989). The soils have low temperatures and high acidity which limit nitrogen fixation and other microbial activity (Arno and Hoff 1989). Often, the soils also lack fine material, because most clay is washed away (Weaver 2001). Whitebark pine can also grow on exposed bedrock and hardened lava flows (Arno and Hoff 1989). Water is held in the soil by the high amounts of organic carbon, which come from decaying matter, helping whitebark pine cope with drought (Weaver 2001), however, whitebark pine are often found on steep slopes steep slopes with much of the nutrients and water moving downhill.

The Role of Whitebark Pine in the Environment

The large lipid-rich pine seed of whitebark pine is a source of food for several animals including red squirrels, black and grizzly bears, and birds such as the Clark's nutcracker (Lanner and Gilbert 1992). Almost all of the viable

seed produced by whitebark pine are harvested by mammals and birds (Kendal and Arno 1990). In stands where red squirrels predominate, up to 63% of the cached seeds will be by this squirrel species (Kendall and Arno 1990). When whitebark pine cone production is low, squirrel populations survive on other food sources, however the squirrels' nutrition comes predominantly from whitebark pine seeds.

Bears rely on squirrels to cache cones in order to provide access to whitebark pine seeds. The most valuable stands of whitebark pine to bears are the ones inhabited by squirrels. Studies in the Yellowstone area have revealed that whitebark pine cone crop has a positive correlation with the number of grizzly cubs that are born and raised the following year (Kendall and Arno 1990; Knight 1989). Poor whitebark pine crops are often followed by increased grizzly bear mortality (Kendall and Arno 1990; Knight 1989). A good seed crop would keep bears at higher elevations where whitebark pine grow (Mattson et al. 1992). High grizzly bear mortality occurs when seed crops are poor, forcing the bears to move to lower elevations where there are human facilities that put the bears in danger (Mattson et al. 1992). Thus bear populations are heavily influenced by whitebark pine productivity.

Clark's nutcracker and whitebark pine have evolved an important mutualistic relationship (Kendall and Arno 1990). While the Clark's nutcracker depends on the whitebark pine for food and nutrients, the trees depend on it for seed dispersal. The scales of whitebark pine do not open during ripening (Tomback 2001). The condition, called indehiscence, causes the wingless

seeds to be fixed in place (Tomback 2001). Wind alone can not dislodge the seeds, instead, the seeds must be freed by squirrels or Clark's nutcrackers, from the parent tree (Tomback 2001). Nutcrackers have long sturdy bills, which allows them to open ripe and unripe whitebark pine cones by ripping off the scales (Tomback 2001). The repetitive hacking at the cone causes some seeds to fall out and land on the ground while most of the seeds are carried away and harvested underground where they are more likely to germinate (Tomback 2001). Lanner (1996) states that Clark's nutcrackers are the only reliable source of germination. Throughout the year, nutcrackers will dig up these seeds (Lanner 1982). Often the amount of seeds that are cached exceeds the metabolic needs of the birds; it is the surplus seeds that germinate and eventually become adult trees (Lanner 1982). Nutcrackers can recognize caches by locating visual landmarks such as logs, rocks or other whitebark pine trees with most caches located strictly from the bird's memory (Lanner and Gilbert 1992, Lanner 1996).

When a nutcracker arrives at a cone, often they will remove the seeds and carry them elsewhere (Tomback 2001). This helps the tree because the seeds are moved away from it. Clark's nutcrackers can store up 150 seeds in their sublingual pouch (Krebill 1990). The pouch of an adult nutcracker can hold up to 20 ml, an anatomical characteristic that is unique to nutcrackers (Lanner 1982). This is important because the diet of juvenile nutcrackers is solely whitebark pine seeds so parent birds must be able to carry several seeds from caches back to their young (Lanner and Gilbert 1992).

Whitebark pine has also evolved to support the symbiosis with Clark's nutcracker. The seeds of the whitebark pine are of appropriate size that the nutcracker can easily shell, pouch, and cache them (Lanner 1982). Whitebark pine seeds are larger than other conifers (Lanner 1982). The large seeds benefit the pine by making them more attractive to nutcrackers and they benefit the nutcracker by allowing them to fill their pouches more rapidly and with fewer manipulations (Lanner 1982). Whitebark pine has evolved efficient means to display cones so that birds, which rely on visual acuity, can find them (Lanner 1982). The cones are high up in the crown where they are more obvious as opposed to other white pines whose cones are hidden by the long-needled limbs above them.

Whitebark pines contribute to their environment in other ways as well. In high-elevation exposed areas, they provide environments for less hardy vegetation to establish (Kendall and Arno 1990). The canopy of the whitebark pine forest spreads blocking out the light beneath it killing many sun-loving plants (Lanner 1996). Plants such as Grouse whortleberry, gooseberry, helianthella, and parrot's beak pedicularis benefit from the presence of whitebark pine (Lanner 1996).

Whitebark Pine Decline and Restoration

Forest succession and insect and disease epidemics have destroyed extensive stands of whitebark pine. In the seventies and eighties, thousands of acres, in the intermountain west, were lost to the mountain pine beetle with 225,000 acres of whitebark pine lost in the Flathead National Forest in western Montana (Kendall and Arno 1990). The larger older trees are ideal targets for mountain pine beetle because the larvae can survive better in thick inner bark (Arno 1986). Trees become more susceptible to beetle attacks when they are victims of other diseases (Campbell and Antos 2000).

Significant mortality of whitebark pine has occurred as a result of infections of dwarf mistletoe. This flowering parasitic plant has been found in the mountains of Montana, Idaho, Wyoming, Colorado, Utah, Nevada, and Oregon (Hoff and Hagle1989). Over 50 percent of the whitebark pine at Mount Shasta are dead as a result of mistletoe (Mathiasen and Hawksworth 1988). Whitebark pine has been classified as a primary host for dwarf mistletoe (Mathiasen and Hawksworth 1988). Dwarf mistletoes can reduce growth on heavily infected hosts, reduce seed and cone production, predispose their hosts to other diseases and insects, and increase mortality (Mathiasen and Hawksworth 1988). Dwarf mistletoe plays a major role on whitebark pine forest canopies as well. Invasion by the plant generally induces the trees to take a witches' broom formation (Mathiasen 1996).

The largest threat to whitebark pine populations is the fungus *Cronartium ribicola*, commonly called white pine blister rust (Hoff 1992). Blister rust was

accidentally introduced into western North America in 1910 from Eurasia (Kendall and Arno 1990). The effects of the fungus were not noticed by foresters until eleven years later (Hoff 1992). Within 25 years of the first infection, blister rust had spread over most of the range of western white pine, whitebark pine, limber pine, and sugar pine (Hoff 1992). It threatens all white pines, however whitebark pine seems to be most susceptible (Hoff 1992).

White pine blister rust has two hosts, the inner bark of white pines and leaves of currant and gooseberry bushes (Campbell and Antos 2000). The fungus moves from host to host via small spores that are not visible to the naked eye (Hoff 1992). The spores move, most often, in the fall when there are moist cool conditions (Arno 1986). The rust infects trees through stomata in the leaves (Campbell and Antos 2000). The fungus will grow through the leaf and branches eventually reaching the main stem (Campbell and Antos 2000). On the branches and trunk of the tree, the fungus will form cankers where there is colonization of the phloem by the fungus and a discoloration of the bark (Campbell and Antos 2000). At the cankers, the stems thicken, the bark cracks and resin is exuded (Bauman 1982). All the growth above the canker will die. Small trees die quickly while larger trees die slower by the process of branch dieback (Campbell and Bauman 2000). Mature whitebark pine undergo approximately twenty years of growth reductions before energy stores are reduced to the point where no growth occurs and the tree dies (DelPrato 1999).

Restoration of whitebark pine populations has been difficult. In the past, forest fires were efficient means to eradicate the whitebark pine populations of

beetles and dwarf mistletoe (Kendall and Arno 1990). This method works as long as whitebark pine is able to regenerate. Blister rust however, inhibits the species' ability to produce viable offspring by inhibiting cone production (Kendall and Arno 1990). For four decades, starting in the 1930s, efforts to control blister rust were made with little success (Kendall and Arno 1990). No biological or chemical control has proven to be effective (Bauman 1982).

In order to control blister run from destroying entire populations of whitebark pine, some measures can be taken that provide a temporary solution to the epidemic. First, branches and stems can be cut proximally to the discoloration of the cankers (Bauman1982). This prevents the fungus from spreading to the trunk of the tree. By exterminating all the secondary host plants, the currants and gooseberries, the blister rust can not survive and will eventually die out (Bauman 1982). Whitebark pine resistant to blister rust has been observed. There appears to be resistant forms in every stand (Hoff and Hagle 1989). Resistant whitebark pine, prematurely drop their needles after being infected to prevent the fungus from spreading (Hoff et al. 1980). Some whitebark pine have reactions that eliminate established bark infections such as necrosis around the infection to prevent the fungus from spreading (Hoff et al. 1980). These resistant forms can be used for restoration with seeds from resistant trees be gathered, germinated in a greenhouse, and saplings replanted planted at the timberline, where populations are decreasing.

Climate Change: Implications for Forests and Whitebark Pine

CO_2 levels are increasing in the atmosphere due to the burning of fossil fuels and conversion of forestland into agricultural land. Temperature increases have resulted from these increasing levels and have been well documented from many proxy records including tree-rings (Briffa et al. 1998). Jacoby and D'Arrigo (1995) showed evidence of recent warming of 0.5 to 1° C over the past century using maximum latewood densities of trees in Alaska. A 1,000-year tree-ring temperature record created by Briffa et al. (1995) to study summer warmth in Siberia demonstrated that the past century had been warmer relative to the past millenium. Using long instrumental climatic records dating back to 1750 from all over the Northern Hemisphere, Jones et al. (2002) observed a slight long-term warming especially during the cold season (from October to April).

The geographic distribution of forests is expected to shift as the climate changes. Simulations of climate change on conifer forests of the Pacific Northwest suggest that forest zones could migrate 500 to 1000 m up in elevation (Urban et al. 1993). The movement could lead to the extirpation of high-altitude species such as whitebark pine because the elevations to which these trees should migrate exceed the elevation range of many peaks. Lower elevation species such as Douglas fir (*Psuedotsuga menziesii*) and ponderosa pine (*Pinus ponderosa*) will move to higher altitudes and are likely to outcompete high elevation species, such as whitebark pine, for growing space (Urban et al. 1993). In mountainous terrain, the displacement caused by the climatic change would

imply a reduction in total areas dominated by forests and a decrease in subalpine species (Urban et al. 1993).

Regional climate models for the Pacific Northwest suggest that climatic change will result in an increase in temperature and precipitation but a decrease in snowfall in the Pacific Northwest (Leung and Wigmota 1999). Warming is expected to occur mostly in the winter with an average warming of 2 °C (Leung and Ghan 1999). There will be an increase in precipitation and a decrease in snowfall as a result of the increasing temperatures, especially in the higher latitudes implying less snowpack, with a reduction of about 60%, and a higher likelihood of winter flooding (Leung and Wigmota 1999). Climatic change could cause ecosystems in the Pacific Northwest to become drier in the summer, and thus more vulnerable to fire. When fire sweeps through a stand, lodgepole pine one of whitebark pine's competitors (particularly in the Rocky Mountains), are more likely to establish afterwards (Mattson et al. 2001).

Warming may cause the spread of blister rust to accelerate by creating conditions more conducive for infection such as increased ambient temperature and more variability in weather conditions (Koteen 1999). Greater rust infection will lead to decreased whitebark pine seed crops, tree deaths and population reductions (Mattson et al. 2001). This will affect populations of bears, squirrels and birds who depend on whitebark pine for its seeds. The implications of warming on whitebark pine may not all be bad. The warming may allow for less harsh conditions, which limit the harvesters such as Clark's nutcracker. If more

seeds are harvested then it is possible that more seeds will be cached in the region where whitebark pine can survive.

CO_2 that is released into the atmosphere is not only affecting vegetation through its potential to cause climatic change, but also through the possibility of CO_2 fertilization. Mid- and high-latitude forests in the Northern Hemisphere represent potential significant carbon sinks (Fang et al. 2001). Increasing amounts of CO_2 in the atmosphere may greatly affect forest productivity since forests posses 90% of the carbon found in terrestrial vegetation. Forest growth and composition is expected to change because CO_2 is often limiting to growth (Graham et al. 1990). The uptake of carbon due to the atmospheric increase will lead to an overall increased amount of forest biomass.

Several physiological changes have been observed to occur in trees due to elevated CO_2. Leaves grow larger in surface area in order to increase uptake of sunlight and CO_2, which in turn increases evapotranspiration, increasing water uptake. The concentration of CO_2 in plant leaves has been shown to increase monotonically while the ratio of CO_2 in the atmosphere and intercellularly has remained the same (Feng 1998). Photosynthetic rates increase when exposed to elevated CO_2, which is brought about by the increased availability of CO_2 at the chloroplast level (Ward and Strain 1999). This is not surprising considering that photosynthesis by terrestrial vegetation accounts for about half of the carbon that annually cycles between Earth and the atmosphere (Chapin and Ruess 2001). These changes are all above ground, however a high proportion of carbon

allocation occurs below ground in the roots and so elevated CO_2 levels also increase carbon storage in roots (Hogberg et al. 2001).

Reproduction of plant species will also be affected by climate change. Loblolly pines exposed to elevated CO_2, for three years, were twice as likely to reach reproductive maturity, and as a result produce three times as many cones and seeds, as trees grown at ambient CO_2 (LaDeau and Clark 2001). This study also demonstrated that there was disproportionate amount of carbon allocation to reproduction, resulting in trees reaching maturity sooner and at a smaller size when exposed to elevated carbon levels (LaDeau and Clark 2001). Elevated CO_2 affect seed germination, seed quality and seedling viability (Ward and Strain 1999). Tree seedlings have increased growth under elevated atmospheric CO_2 conditions (Naidu and Delucia 1999).

El Niño and Pacific Decadal Oscillation

Wind, precipitation and air temperatures vary over decadal time scales in the Pacific Northwest. The most well studied natural pattern of climate is the El Niño/Southern Oscillation (ENSO) pattern. ENSO generally refers to the occasional warming of the eastern tropical Pacific Ocean basin (Trenberth and Hoar 1996). This phenomenon, which is linked to global atmospheric circulation, is linked to basin-scale warming from the coast of South America to the International Dateline (Trenberth and Hoar 1996). The duration of El Niño has been observed to be roughly 6-to-8 months (Mantua et al. 1997). The climate pattern has caused an increase in precipitation over the state of California during the winter months. ENSO events have been implicated in warming and drying over the Pacific Northwest (Leung et al. 1999). Warming and drying in the Pacific Northwest would affect whitebark pine. There would be less snowpack in the winter limiting the start of each growing season in the northern part of the western range. These whitebark pine may have increased growth. The southern part of the western range, which is not limited as much by snow, but more by drought, may become even more limited by drought. Growth may decrease as a result of the drying effects of ENSO.

In the Pacific Northwest, an El Niño-like pattern exists called Pacific Decadal Oscillation (PDO). Pacific Decadal Oscillation variability is reported as an indexed value which is figured from sea surface temperature. Extremes in PDO are partially responsible for variations in North American climate and North

Pacific Basin (Mantua et al. 1997). PDO differs from ENSO in that it is much longer lived, with duration of 20-30 years (Mantua et al. 1997). Only two full PDO cycles have occurred in the past century. From 1890 to 1924 and 1947 to 1976, two low index PDO regimes occurred, while two high index PDO regimes dominated from 1925 to 1946 and from 1977 to the mid 1990's (Mantua et al. 1997). During a high index period, the Pacific Northwest is warm and dry, while during the low it is cold and wet (Mantua et al. 1999). Climate data from the Pacific region suggests that a cool regime began in 1998 (Mantua et al. 1997). Tree-rings have been used to reconstruct PDO, and demonstrate that fluctuations in PDO predate instrumental records (D'Arrigo et al. 2001).

Gershunov and Barnett (1999) demonstrated that ENSO has it greatest affect on the Pacific Northwest when its extremes are in phase with PDO extremes with summer rainfall and drought, and winter and spring flood events correlated with PDO events in the Pacific Northwest (Nigam et al. 1999). There are fluctuations in the dominance of sardines and anchovies that occur in 25-year periods in the Pacific Ocean as well (Chavez et al. 2003). For 25 years, the Pacific is warmer than average and there is a sardine regime, then there is a switch to a cold regime with an anchovy regime (Chavez et al. 2003). These shifts in regimes are very similar to shifts in PDO index and there may be a connection. Currently, the cause of PDO is not known but its effects are clearly observed in plant life. Peterson and Peterson (2001) found 49% of the variation in the growth of mountain hemlock at high elevations was attributed to winter PDO.

Tree rings and climate research

Andrew Ellicott Douglass, an astronomer working at the Lowell Observatory in Flagstaff, Arizona, began the systematic use of tree rings in 1901, while trying to study the cyclic nature of solar activity, particularly sunspots, on terrestrial climate (Robinson 1992). He decided on tree rings when he needed a historical record of climate. He proposed the idea that tree rings were a measure of food supply, which was a measure of precipitation (Douglass 1914). While trying to create growth curves for the trees he sampled, Douglass noticed that different trees were having the same patterns of thin and thick rings, which he tried to match from tree-to-tree and from this crossdating was established in 1904 (Robinson 1992).

Douglass wanted to use tree rings because there was no historical record of climate at his study sites. The methodology and applications of tree rings since then has been refined in order to study climate and species responses to climate. In 1976, Harold C. Fritts published a landmark book *Tree Rings and Climate*, which gave an explanation of the techniques used in extracting climatic information from tree rings (Cook and Kairiukstis 1992). Since then, the science of dendroclimatology has rapidly developed, but the book remains an important reference. In the nineties, Edward Cook and Julie Cole began using tree rings with simulation models in order to predict responses of forests in eastern North America to future climatic change (Cook and Cole 1991).

Today, tree rings are still being used to recreate past climate events and to understand various species growth responses to climate. North American tree

ring series were used to reconstruct Pacific Decadal Oscillation index for the Northeast Pacific region for years prior to 1700 when no instrumental records were kept (D'Arrigo et al. 2001). Kusniercyzk and Ettl (2002) showed that short-term growth response of ponderosa pine is most sensitive to non-growing season precipitation. Conifer chronologies from 387 sites from throughout the Northern Hemisphere demonstrated that summer temperatures strongly influence growth of most conifers with an optimal growing season occurring from April to September (Briffa et al. 2002). Tree ring studies have been used to understand the growth response of several subalpine species to climate. Mountain hemlock growth was negatively correlated with spring snowpack depth, positively correlated with growth-year summer temperature and showed sensitivity to Pacific Decadal Oscillation (Peterson and Peterson 2001). Huxman et al. (2003) showed that subalpine forests composed of lodgepole pine, Engelmann spruce, and subalpine fir are most optimally suited for productivity at cool growing season temperatures. Lodgepole pine and whitebark pine, in the Sierra Nevada, California have shown growth increases over time in all age classes of both species, which the authors suggest are caused by either stand dynamics, unevaluated climate variables or increases in atmospheric CO_2 concentrations (Peterson et al. 1990).

Organization of thesis

This thesis is the first attempt to understand the regional growth response of whitebark pine to climate. It examines the effects of climate in the short-term from a growing season to growing season standpoint. It also focuses on the effects of temperature and precipitation on growth. Additionally, I look at long-term trends in the growth of whitebark pine that have resulted from climate patterns and climate change. After this introduction the second chapter will discuss the methodology that was used for this project. The third chapter will show the results and the fourth chapter will encapsulate the entire project with a discussion. Lastly, in the fifth chapter, there will be an overall summary of the project.

Chapter 2: Methods

Area of study

Whitebark pine study sites were selected along the Cascade Mountains in North Cascades, Mount Rainier, and Crater Lake National Parks (Figure 2.1). Two climate types define the regions encompassed by these parks. West of the range is maritime climate and to the east is a combination of maritime and continental climates (Franklin and Dyrness 1973). All three parks occur at the crest of the Cascade Range and therefore contain both maritime and continental influences. Maritime climate presents generally mild temperatures with cloudy, wet winters and dry summers (Henderson et al. 1989). Most of the precipitation occurs at the start of October and continues until the end of March. The dominant westerlies bring in low-pressure systems from the Pacific Ocean (Franklin and Dyrness 1973). Summers are often characterized by extended periods of dry weather due to high-pressure systems forcing storm tracks northward.

East of the Cascade Range, the mixture of continental and maritime climate results in a greater fluctuation of temperatures. On this side of the range, winters are colder and summers are hotter. The climate is drier overall due to the rain shadow effect (Henderson et al. 1989). Whitebark pine is more commonly associated with the eastern Cascades being replaced by subalpine fir and mountain hemlock on the western sites.

Mean temperatures at Mount Rainier range from -7.0 to 17.4 $^{\circ}$C (NCDC 2002). Crater Lake has mean temperatures of -8.4 to 21.9 $^{\circ}$C (NCDC 2002).
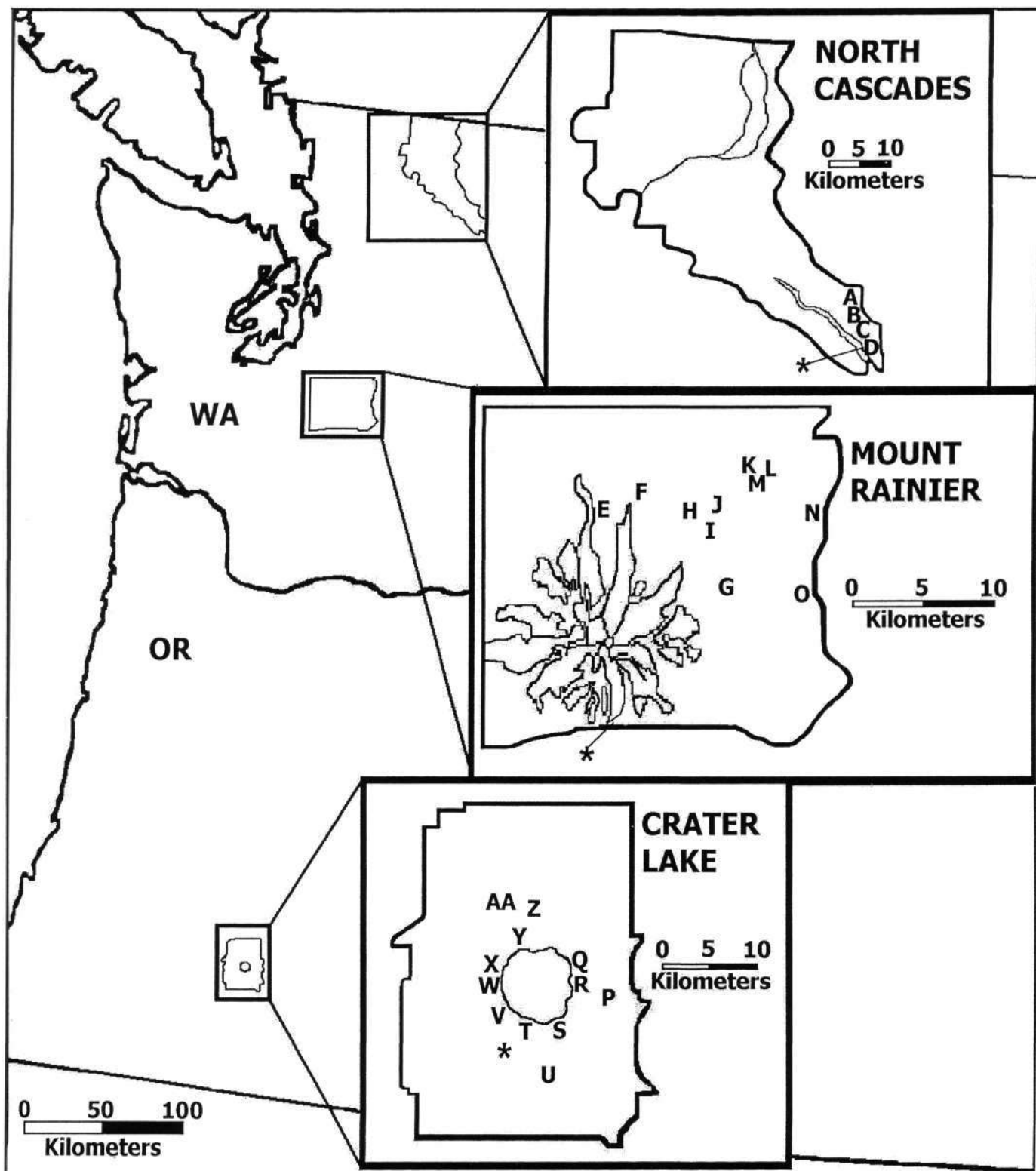
Figure 2.1 Location of the 27 sites and climate stations (asterisk) in North Cascades, Mount Rainier, and Crater Lake National Parks. See Table 2.1 for site names and characteristics.

North Cascades National Park reports mean temperatures of -11 to 22.5 $^{\circ}$C (NCDC 2002).

Mount Rainier receives an average annual precipitation of 265 centimeters and average annual snowfall of 1,362 centimeters, while Crater Lake receives 164 centimeters of rain and 1,324 centimeters of snowfall (Weaver 2001). Adiabatic temperature cooling causes the rain to freeze and become snow at elevations greater than 1000 meters at all three national parks throughout much of the rainy season. Generally, the snow throughout the winter accumulates until spring when higher temperatures allow for snowmelt (Peterson and Peterson 2001). There is an average snow accumulation in April of 259 centimeters in the North Cascades, 498 centimeters at Mount Rainier and 257 centimeters at Crater Lake (NRCS). The length of the growing season for whitebark pine depends on snowmelt and subsequent warming of the soils.

In the North Cascades, whitebark pine grows at elevations of 1,700 to 2,200 m (McCaughey and Schmidt 2001). At Mount Rainier, the trees grow at elevations of 1,800 to 2,100 meters (McCaughey and Schmidt 2001). Crater Lake whitebark pine grow from 2,100 to 2,600 meters (McCaughey and Schmidt 2001). Because most of the peaks in the Cascade Range are 1500 to 2200 meters, many stands are geographically isolated (Arno and Hoff 1989). Some of the study sites are dominated by whitebark pine, however many are mixed with other subalpine species such as subalpine fir, shasta fir, Engelmann spruce, mountain hemlock, and lodgepole pine. All but one of the twelve study sites at Crater Lake was dominated by whitebark pine (Table 2.1).

Table 2.1 Site and chronology characteristics. Mean sensitivity is an indication of the year-to-year variability in growth. Signal-to-noise ratio is an indication of the strength of a common signal in cores extracted from each site.

Park	ID	Site	Sample size	Chronology Length	Mean Sensitivity	Signal-to-noise ratios[ᵞ]	Dominant Species (> 50% of individuals)
North Cascades							
	A	Hidden Meadows	22	1795-1999	0.197	10.97	subalpine fir
	B	South Pass	24	1900-1999	0.228	7.62	whitebark pine
	C	Boulder Butte	30	1800-1999	0.247	6.64	whitebark pine
	D	Splawn Mtn.	31	1739-1999	0.211	12.79	subalpine fir
Mount Rainier							
	E	Mystic Lake	25	1752-1997	0.232	3.41	subalpine fir
	F	Skyscraper Mtn.	14	1782-1997	0.244	5.15	whitebark pine
	G	Summersland	17	1743-1997	0.222	11.38	subalpine fir
	H	Sunrise Camp	15	1720-1997	0.253	3.33	subalpine fir
	I	Shadow Lakes	23	1900-1997	0.196	5.04	subalpine fir
	J	Frozen Lake Trail	16	1814-1997	0.242	6.21	subalpine fir
	K	Palisades	16	1865-1997	0.226	4.86	subalpine fir
	L	Clover Lake	13	1785-1997	0.208	3.86	subalpine fir
	M	Sourdough	16	1884-1997	0.258	5.17	subalpine fir
	N	Crystal Mtn.	17	1663-1997	0.262	5.97	subalpine fir
	O	Deadwood Lakes	20	1906-1997	0.239	3.73	whitebark pine
Crater Lake							
	P	Mt. Scott	21	1729-2000	0.208	7.73	whitebark pine
	Q	Redcloud Cliff	24	1811-2000	0.240	3.41	whitebark pine
	R	Castle Rock	19	1840-2000	0.232	4.75	whitebark pine
	S	Dutton Ridge	20	1681-2000	0.199	5.87	whitebark pine
	T	Dyar Rock	19	1741-2000	0.211	4.78	whitebark pine
	U	Crater Peak	19	1791-2000	0.204	5.82	whitebark pine
	V	Discovery Point	19	1801-2000	0.229	5.85	mountain hemlock
	W	Watchman's Lookout	20	1796-2000	0.231	8.82	whitebark pine
	X	Hillman's Peak	22	1782-2000	0.228	4.75	whitebark pine
	Y	Llao Rock	21	1800-2000	0.224	4.90	whitebark pine
	Z	Grouse Hill	19	1711-2000	0.209	4.38	whitebark pine
	AA	Red Cone	20	1841-2000	0.228	3.35	whitebark pine

Mountain hemlock was found on all the sites and was more dominant on the western sites, while lodgepole pine and shasta fir were found at several of the Crater Lake sites. Nine of the eleven sites at Mount Rainier were dominated by subalpine fir. The remaining two were whitebark pine dominant. Mountain hemlock was found scattered throughout Mount Rainier as well. At North Cascades National Park there was a mixture of whitebark pine and subalpine fir. Two sites were whitebark pine dominant and two were subalpine fir dominant. Engelmann spruce, mountain hemlock and alpine larch (*Larix lyallii*) were also found at the North Cascades sites.

Climate Data

Divisional and local station data was acquired to compare with tree-ring data from each park (NCDC 2002). Divisional data are averages from all of the climate stations in that division. Divisional data have the advantage of including data for a larger region and are less likely to be impacted by equipment failure or localized events. The study sites in Mount Rainier are most closely associated with Washington Climate Division 5, which encompasses the western Cascade Mountains. The North Cascade sites occur in the Washington Climate Division 6. This division includes the eastern slope of the Cascades. Crater Lake is located in the high plateau region of Oregon, Climate Division 4. Local station data came from Paradise (at Mount Rainier), Stehekin (at North Cascades) and Crater Lake Headquarters (Figure 2.2). The Mount Rainier Paradise station is at 1,654 m and generally lies between 6.5 and 16 kilometers southwest of the study
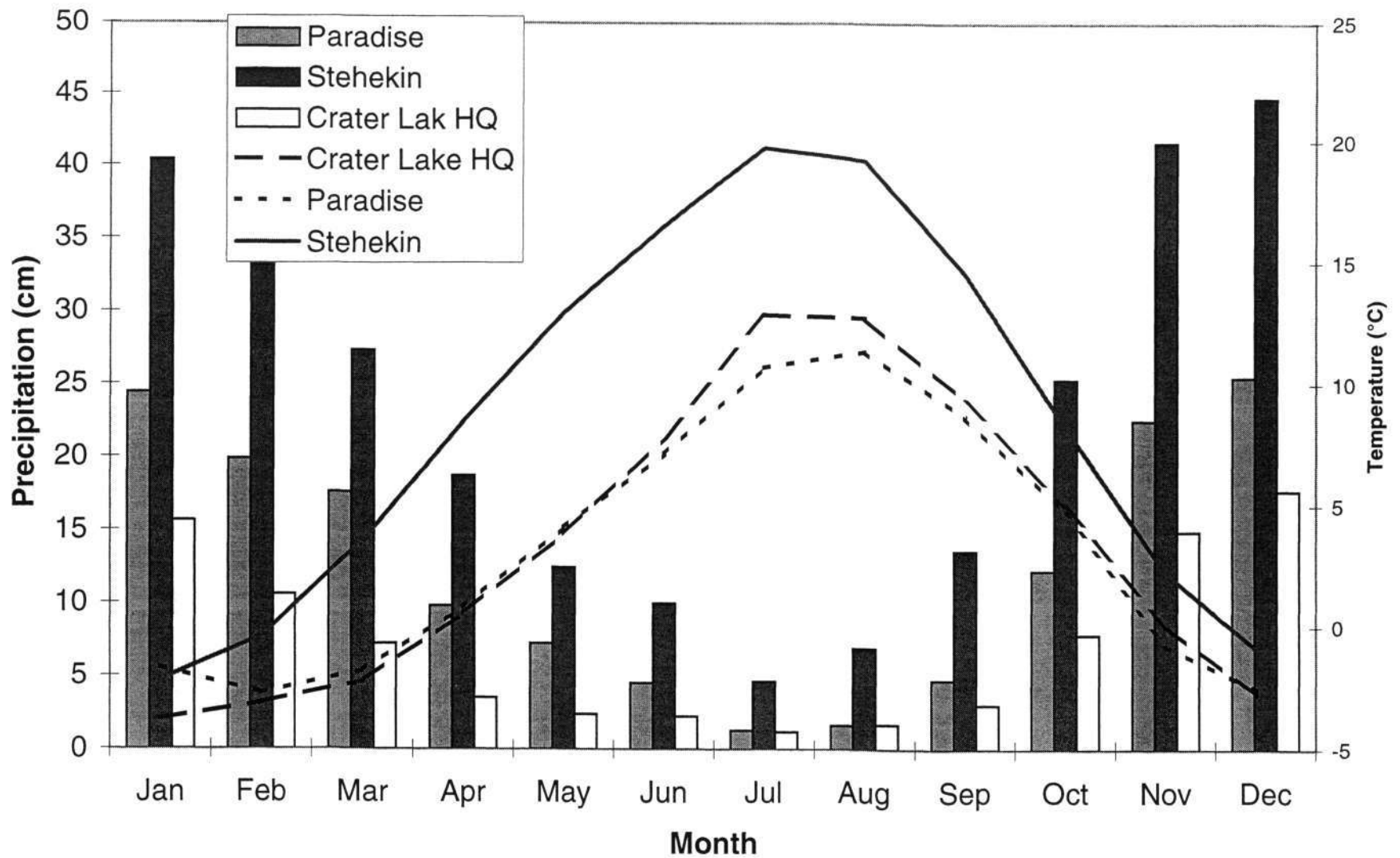
Figure 2.2 Monthly temperature (lines) and precipitation (bars) averages from Paradise, Mt. Rainier, Stehekin, North Cascades, and Crater Lake Headquarters climate stations for the time period of 1931 to 2000. Note that temperature at Stehekin is from 387 m.

sites. Crater Lake Headquarters is at 1,974 meters above sea level and lies about 2 kilometers south of the lake rim 1.5 to 11 kilometers away from study sites. Five kilometers west of the North Cascade sites, the Stehekin station is located at 387 meters above sea level. All three stations unfortunately are located at lower elevations than the study sites, but are the closest in proximity. No long-term climate data exists at any of the study sites and these 3 stations have the longest records of the nearby suitable stations. Correlation analysis between climate data and standardized ring-width chronologies was performed initially with divisional and local climate data to determine which was better suited for this study (i.e., strength of correlation). Local data showed stronger correlations with tree-ring chronologies (range divisional, vs. range local) and all results represent correlations with local climate data.

Crater Lake headquarters has temperature and precipitation data from 1930, and Paradise and Stehekin climate stations have temperature data from 1931 and precipitation data from 1919 to the present. Missing values for some monthly temperature and precipitation variables exist for each of the 3 stations. Crater Lake was missing 42 out of 840 temperature values and 37 of 840 precipitation values. Mount Rainer was missing 88 values out of 828 of temperature data and 88 out of 972 precipitation data. Stehekin was missing 26 of 828 temperature values and 20 out of 972 precipitation values. Missing values were estimated from a linear regression between the station data and the climate division data for monthly temperature and precipitation. There was a strong relationship between divisional and local temperature data: $R^2 = 0.90$ at Crater

Lake, $R^2 = 0.88$ at Mount Rainier, $R^2 = 0.77$ at North Cascades. This was true

for precipitation data as well: $R^2 = 0.89$ at Crater Lake, $R^2 = 0.88$ at Mount

Rainier, $R^2 = 0.78$ at North Cascades.

Core Sampling

Whitebark pine cores were sampled from 27 sites in three National

Parks in the Pacific Northwest (Figure 2.1 and Table 2.1). The three parks

encompass a large portion of whitebark pine's western range. The sites chosen

were originally part of another study examining the effects of white pine blister

rust (*Cronartium ribicola*) on whitebark pine (DelPrato 1999; Cottone 2001;

Cottone and Ettl 2001; Ettl and Cottone in press). For this study, however, only

adult trees free of blister rust infection were used. Trees were classified as

adults by being at least ten centimeters in diameter at breast height.

At each site, 13- 30 cores were extracted depending on the availability of

healthy trees. A manual increment borer was used to extract the cores

approximately 1.4 meters above the ground. The cores were stored in paper

straws to prevent mildew and they were transported to the laboratory. In many

cases 2 or more cores were extracted to obtain suitable samples, but only 1 core

from each tree was included in the analysis. In the laboratory, the whitebark pine

cores were air-dried then mounted into grooved wood blocks with wood glue.

The mounted cores were then sanded with four different grades of sandpaper

100, 150, 400 and 600 grit. Using progressively finer grades of sandpaper

allowed for the core to go from being round and rough to a flat, polished surface in which the boundaries of the tree-rings could be clearly visualized.

Crossdating and Standardization

The cores were visually crossdated matching marker years (years that are thinner or thicker than the years surrounding it) at each site (Stokes and Smiley 1968). The presence of marker years indicates that all the trees are reacting to climate in a similar manner resulting in the same ring-width patterns. The recognition of patterns of wide and narrow rings allows for crossdating with each ring being assigned a date with some certainty (Pilcher 1992). A Velmex incremental measuring machine attached to a personal computer was used to measure the ring-widths to the nearest 0.01mm. The measuring machine consists of a moving stage along a threaded metal rod. Attached to the stage was an ACU-RITE linear encoder. The encoder provides for digital outputs for the movement of the stage along the threaded rod. The program Measure J2X was used to record the ring-width data that was determined by the encoder. To insure that the data was measured accurately for each ring-width, a randomly selected 20-year segment of each core was remeasured (Ettl and Peterson 1995; Fritts 1976). These values were subtracted from the previously measured values. The differences were squared and added. If the sum of the squared differences between the 2 sets of measurements was greater than 0.073 mm^2 then the entire core was remeasured.

Crossdating was verified using the computer program COFECHA (Holmes 1983). This program calculates correlation coefficients between each core and a

master chronology created from the rest of the cores for 50-year periods within the same site. Tree cores that show similar growth patterns to other cores from the site yield high correlation coefficients. Low coefficients could imply that the dating or measuring of the core was done incorrectly. COFECHA also provides correlation coefficients for years both in the past (lag correlations −1, -2, -3 etc.) and the future (i.e. +1, +2, +3 etc.) allowing for the possibility that the correlation would be higher if the series were shifted. Generally, the data from cores showing lower correlation can be fixed by shifting the series so that they yield high correlation coefficients. Because the program works in 50-year increments and these increments overlap, problem areas on the core can be isolated to segments of 25 years. These 25-year portions are reexamined to locate possible errors. Cores were taken out of the site master data set if they could not be correlated with the others at that site.

Short-term Climate Analysis

In order to study the interannual growth patterns of whitebark, the climate-related growth signal was extracted from the cores by minimizing the noise (Cook and Briffa 1990). In this case, we aim to maximize the climate-related components while minimizing noise by standardizing trees to get the highest signal-to-noise ratio. A high ratio would suggest that there is a strong signal with little noise. Short-term analysis of the tree ring data focuses on the signal that remains after aging, endogenous and exogenous disturbances and other non-climatic factor effects are minimized. The standardization process removes long-term trends in growth and we address these trends with a separate analysis.

Standardization is done by dividing each ring-width value by its expected value:

$$I_t = R_t/G_t$$

where I_t is the relative tree index, R_t is the observed ring-width and G_t is the estimated growth trend (Cook et al. 1992). This process converts raw ring-width values into stationary, relative tree-ring indices that have a defined mean of 1.0 and relatively constant variance (Cook et al. 1992). The estimated growth trend, G_t, is calculated using the following function:

$$G_t = f(A_t, \delta D1_t, \delta D2_t)$$

where A_t is the age-size-related trend in the ring-width. $\delta D1_t$ and $\delta D2_t$ are the disturbance pulses caused by a local endogenous disturbance and a regional exogenous disturbance respectively (Cook et al. 1992). Considering the equation:

$$R_t = A_t + C_t + \delta D1_t + \delta D2_t + E_t$$

where C_t is the climatically related environmental signal and E_t is the largely unexplained year-to-year variability not related to other signals (Cook et al. 1992). The removal of G_t leaves the climatically related environmental signal C_t.

The computer program ARSTAN was used to standardize tree cores and create site chronologies (Cook and Holmes 1996). This program allows low frequency growth trends to be extracted from ring-width time series. Four different standardization treatments were performed for each site. For the first three methods of standardization a double-detrending was used to standardize the chronologies. Each series was first detrended by fitting a negative

exponential curve to the raw ring-widths. The raw ring-width measurements were divided by the fitted values to create standardized ring-width indices. Then in the second detrending, each series was fit with a cubic smoothing spline of varying stiffness, 25-, 50- or 128--year cubic spline. The cubic spline removes 50% of the growth variation over the time frame indicated, therefore eliminating some of the long-term growth trends. The fourth method of standardization involved no detrending. Instead the raw data was fit with a horizontal line along the ring-width mean. Again, indices were calculated by dividing the ring-width values by the fitted values. Site chronologies were created from the indices. The standardization method that yielded the highest signal-to-noise ratio was used for each site.

Mean sensitivities were calculated for each site using the computer program COFECHA (Holmes 1983) (Table 2.1). Mean sensitivity describes the year-to-year variation in ring-widths as a proportion to the mean ring-width (Fritts 1976). The mean sensitivities calculated were low, but other studies suggest that low mean sensitivities may be a characteristic of subalpine species. Studies involving subalpine fir in the Pacific Northwest have shown mean sensitivities of less than 0.3, with a mean of 0.21 (Peterson et al. 2002, Ettl and Peterson 1995). The mean sensitivity was 0.23 for our 27 whitebark pine chronologies.

Pearson bivariate correlation analysis was used to examine the relationship between whitebark pine growth and climate (Norusis 2000). Standardized site chronologies were correlated with monthly temperature and precipitation for a 17-month span. The 17-month period begins with May of the

year prior to the year the growth ring forms and ends with September of the current growing season. Bivariate correlations are performed when one variable is expected to have a linear relationship with an other variable (Kim 1978). Bivariate correlation analysis was performed on all site chronologies with the respective local climate variables. Partial correlation analysis was performed between the site chronologies and climate variables that were significantly correlated ($\alpha \leq 0.05$) from the bivariate analysis. Partial correlation analysis allows climate variables to be correlated with growth while controlling for intercorrelation among the climate variables. Results from the partial correlation analysis were used to describe the response of whitebark pine to climate. Our *initial analysis revealed a significant correlation between Mount Rainer sites and* winter precipitation. Therefore, we also correlated April snowpack data from Cayuse Pass, (2 kilometers east of Deadwood Lakes, Table 2.1, Figure 2.1) with site chronologies from Mount Rainier to examine the role of snowpack on tree growth.

Long-term Climate Analysis

Long-term trends of whitebark pine growth were examined without standardization in order to preserve possible trends in growth. The raw ring-width data was converted to basal area increments (BAI). Ring-widths normally have a decreasing trend over time as the diameter of the tree increases, because the same volume of wood needs to be added to an increasing circumference (Fritts 1976). Basal area increment represents annual wood volume and

therefore may be a better indicator of growth over long time periods. Basal area increments (BAI) were calculated by subtracting the total area (πr^2) of all previous growth years from the total area of the current growth year using the following equation:

$$BAI = \pi r_n^2 - \pi r_{(n-1)}^2$$

Where n is the current year and r is the radius of the tree. Basal area increment values, for each tree, were averaged together on a year-by-year basis within each site. The result was a single chronology of basal area increments for each site.

In order to ascertain common patterns in the long-term trends of whitebark pine growth among sites, factor analysis was performed on 21 of the 27 site chronologies. We excluded 6 sites (B, E, I, L, M, O) that did not date back to 1900 because the goal was to assess long-term trends in growth. Factor analysis assumes that the measured variables are linear combinations of some underlying source variables (Kim 1978). In this case, we use factor analysis to try and visualize underlying factors for the long-term growth patterns of whitebark pine. Extracted factors are indices, and because an index value is calculated for every year, we were able extract factor chronologies. These factor chronologies contain common growth patterns that are observed for all sites in this study, thereby providing a regional analysis of whitebark pine.

Factor chronologies were derived by performing a principal components analysis using Varimax rotation. Rotation was used to find the most meaningful and interpretable factorial structure. Rotation does not improve the fit between

the data and the factors, it just allows for a simpler factor structure to occur (Kim 1978). Rotated factor chronologies explain just as much covariation between the data and factor chronologies as the unrotated analysis, but we used the rotated factors because it is easier to interpret (Kim 1978).

Four factors explain 87.9% of the growth response (Table 2.2). Partial correlation analysis was used to determine relationships between the extracted factors and a variety of variables which were thought to influence growth over the long-term including the monthly temperature and precipitation variables used in the short-term analysis, annual temperature for each climate division, Pacific Decadal Oscillation index (PDO), and global atmospheric CO_2. The factors were correlated to monthly and seasonal PDO indices. A time series of global atmospheric CO_2 was calculated using the following exponential equation:

$C_a = 277.78 + 1.350 \ exp[0.01572(t-1740)]$

where t is the year (after Feng 1998) for the years 1890 to 2000. All four factor chronologies were plotted with the variables they significantly correlated with and these were smoothed using a trend line for visual purposes. The correlation coefficients between the factors and the variables stated in the results represent the calculated values prior to smoothing.

Table 2.2 Factors extracted from 21 mean basal area increment site chronologies using Varimax rotation in principal components analysis. All 21 chronologies used in analysis date back to at least 1900.

Factor	Rotated Eigen Values	Percent of variance	Cumulative percent of variance
1	7.381	35.149	35.149
2	5.859	27.900	63.049
3	3.492	16.627	79.675
4	1.734	8.257	87.932

Chapter 3: Results

Short-term analysis

Partial correlation analysis demonstrates several significant correlations between the standardized site chronologies and monthly climate variables (Table 3.1). All four sites in the North Cascades National Park showed significant correlation with some climate variables. Nine of eleven of the sites at Mount Rainier and eight sites out of twelve at Crater Lake had significant correlations with climate variables. Six of the 27 sites (sites K, N, P, R, U, V) did not correlate significantly with any climate variables. We presumed that these sites were responding differently to climate so we compared these sites to climate data from other stations (in most cases more eastern local climate stations) and found no significant correlation.

Significant partial correlations with winter climate variables were seen only for the two Washington parks (Table 3.1). Two site chronologies at Mount Rainier showed positive correlations with January temperature. Significant positive correlations with March temperature occurred for 3 out of the four sites at North Cascades and 4 sites at Mount Rainier. One site at North Cascades and two at Mount Rainier showed negative correlation with March precipitation (sites B, H, and L). December precipitation is negatively correlated with growth at six of eleven sites (sites E, F, G, J, M, O) at Mount Rainier (Table 3.1). Partial correlation with the same six sites and April snowpack are also negatively correlated. The six sites represent regions throughout the park, suggesting that the response is widespread for whitebark pine in Mount Rainier.

Table 3.1 Significant correlation coefficients (p≤ .05) from partial correlation analysis between standardized site chronologies and monthly climate variables.

A. North Cascades: Stehekin climate data from 1932 to 1999.

Climate variable	A	B	C	D
Previous August temperature	-0.355	-0.336		-0.356
March temperature		0.284	0.242	0.289
March precipitation		-0.246		

B. Mount Rainier: Paradise climate data from 1931 to 1997.

Climate variable	E	F	G	H	I	J	L	M
Previous October temperature			0.347	0.229	0.344	0.256		
January temperature		0.263				0.276		
March temperature	0.275		0.264			0.329		0.479
Previous December precipitation	-0.362	-0.398	-0.345			-0.444		-0.458
March precipitation				-0.398			-0.307	

C. Crater Lake: Headquarters climate data from 1930 to 2000.

Climate variable	Q	S	T	W	X	Y	Z	AA
Previous October temperature		0.287		0.318	0.316			
June temperature	0.381	0.403	0.391	0.447	0.476		0.296	0.402
Previous July precipitation	0.390		0.369			0.293		0.281

Summer temperature and precipitation also influenced the growth of whitebark pine (Table 3.1). Previous August temperature was negatively correlated with growth for three out of four of the sites in the North Cascades. Seven out of twelve sites at Crater Lake resulted in positive partial correlations of growth with June temperature. The seven sites represent the entire perimeter of the lake. A third of the sites at Crater Lake also showed positive partial correlation coefficients with previous July precipitation. Only correlations of October temperature with growth were observed for the fall season. Previous October temperature showed positive correlations with four sites at Mount Rainier and 3 sites at Crater Lake.

Long-term analysis

Principal components analysis resulted in four factors. The four factors explain 87.9 percent of the variance (Table 3.2). The components matrix created from factor analysis indicated that Factor one, had a loading greater than 0.452 for 15 of 21 sites indicating they are strongly associated (Table 3.3). Site V was the only site that showed a negative loading with Factor 1. The components matrix reveals a common trend for 14 of the 21 sites in relation to Factor two, including all of the Crater Lake sites.

Table 3.2 Factors extracted from 21 mean basal area increment site
chronologies using Varimax rotation in principal components analysis. All 21
chronologies used in analysis date back to at least 1900.

Factor	Rotated Eigen Values	Percent of variance	Cumulative percent of variance
1	7.381	35.149	35.149
2	5.859	27.900	63.049
3	3.492	16.627	79.675
4	1.734	8.257	87.932

Table 3.3 Components matrix of the four extracted factors. The values represent correlation coefficients between individual basal area increment chronologies and the factor chronologies.

	Factor			
Site	1	2	3	4
A	0.222	0.358	0.791	0.02804
C	0.624	0.685	0.300	-0.0569
D	0.788	0.203	0.394	-0.0333
F	0.700	0.585	0.292	-0.0202
G	0.318	-0.156	0.315	0.783
H	0.412	0.644	0.468	0.198
J	0.857	0.306	0.266	0.187
K	0.02338	0.0866	0.877	0.318
N	0.413	0.354	0.756	0.114
P	0.624	0.685	0.300	-0.0569
Q	0.687	0.498	0.09512	0.316
R	0.683	0.483	0.434	0.09607
S	0.362	0.874	0.0469	0.131
T	0.833	.181	-0.208	0.330
U	0.692	0.630	0.250	0.03411
V	-0.0826	0.413	0.114	0.788
W	0.452	0.773	0.259	0.179
X	0.612	0.686	0.309	-0.0817
Y	0.651	0.558	0.402	0.06013
Z	0.176	0.842	0.302	0.126
AA	0.757	0.484	0.07336	-0.0901

Factor 1 is significantly positively correlated with CO_2 (r=0.668, p<0.001) and annual temperature from the three climate divisions representing Mt. Rainer, North Cascades, and Crater Lake National Parks(r=0.569, p<0.001 for WA division 5, r=0.275, p=0.005 for WA division 6, r=0.495, p<0.001 for OR division 5; Figure 3.2a-c). The second factor was negatively correlated with winter Pacific Decadal Oscillation (PDO) (r=-0.2916, p=0.006; *Figure* 3.3), with the time period of 1941 to 1970 the most strongly correlated (r= -0.391, p=0.005).

Partial correlation analysis between the third and fourth factors with station monthly climate data showed similar results to those found in the short-term analysis (Table 3.4) and when the factors were plotted and smoothed, two long-term growth trends were evident by the shifts in the chronology over time (Figure 3.4). Factor three positively correlates with July precipitation and negatively correlates with July temperature, and the fourth factor positively correlated with June temperature at Crater Lake. Strong negative correlations between previous December precipitation and the fourth factor occurred at both Mount Rainier and North Cascades National Parks. Factor four is also negatively correlated with August temperature at North Cascades.
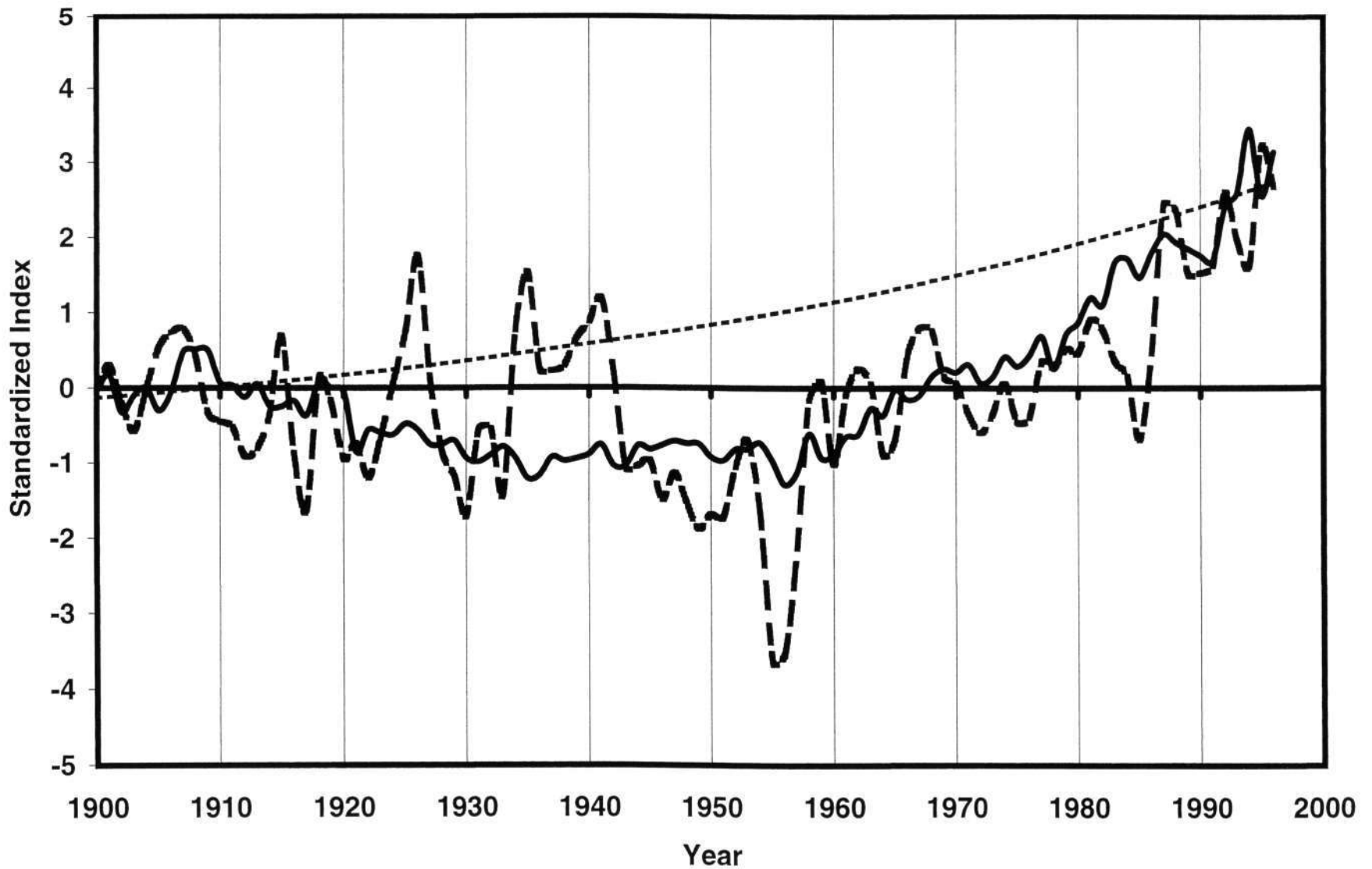
Figure 3.2a Indexed atmospheric CO_2 (small dashes), Washington climate division 5 annual temperature means (large dashes) and Factor 1 index chronology (solid line) from factor analysis. (atmospheric CO_2 with Factor 1 $r=0.668$, $p<0.001$; temperature means with Factor 1 $r=0.569$, $p<0.001$)
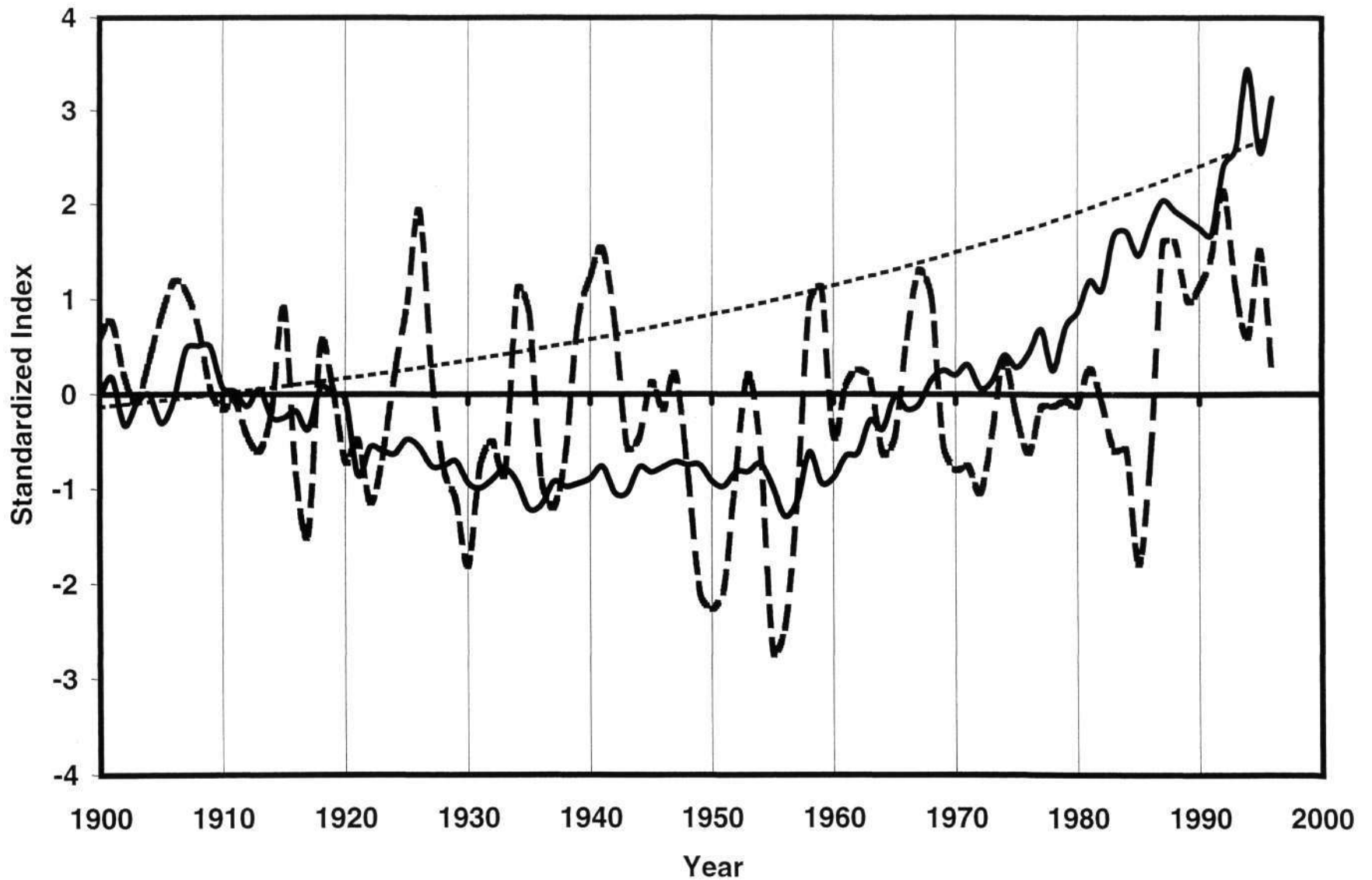
Figure 3.2b Indexed atmospheric CO_2 (small dashes), Washington climate division 6 annual temperature means (large dashes) and Factor 1 index chronology (solid line) from factor analysis. (atmospheric CO_2 with Factor 1 $r=0.668$, $p<0.001$; temperature means with Factor 1 $r=0.275$, $p=0.005$)
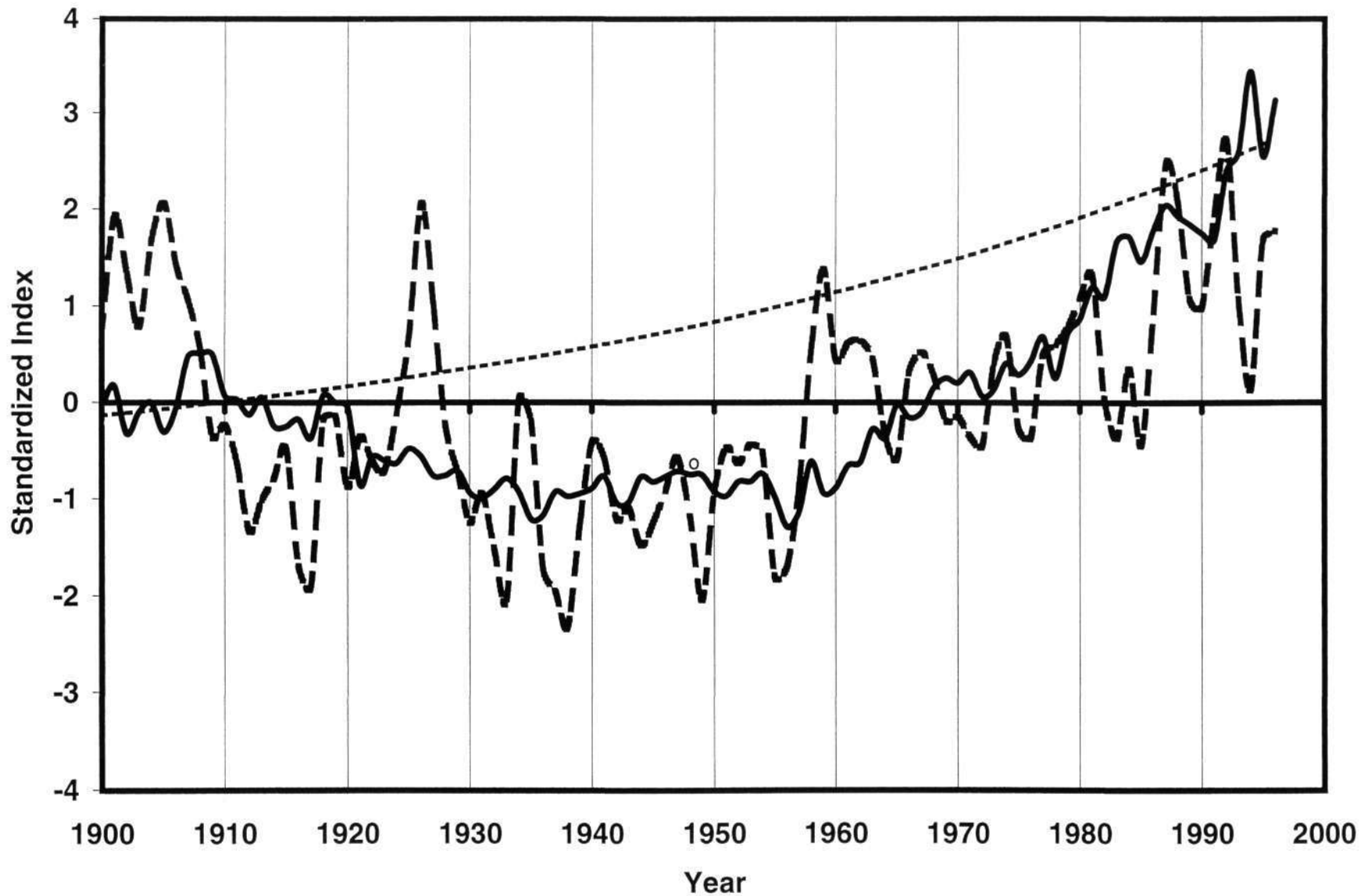
Figure 3.2c Indexed atmospheric CO_2 (small dashes), Oregon climate division 5 annual temperature means (large dashes) and Factor 1 index chronology (solid line) from factor analysis. (atmospheric CO_2 with Factor 1 $r=0.668$, $p<0.001$; temperature means with Factor 1 $r=0.495$, $p<0.001$)
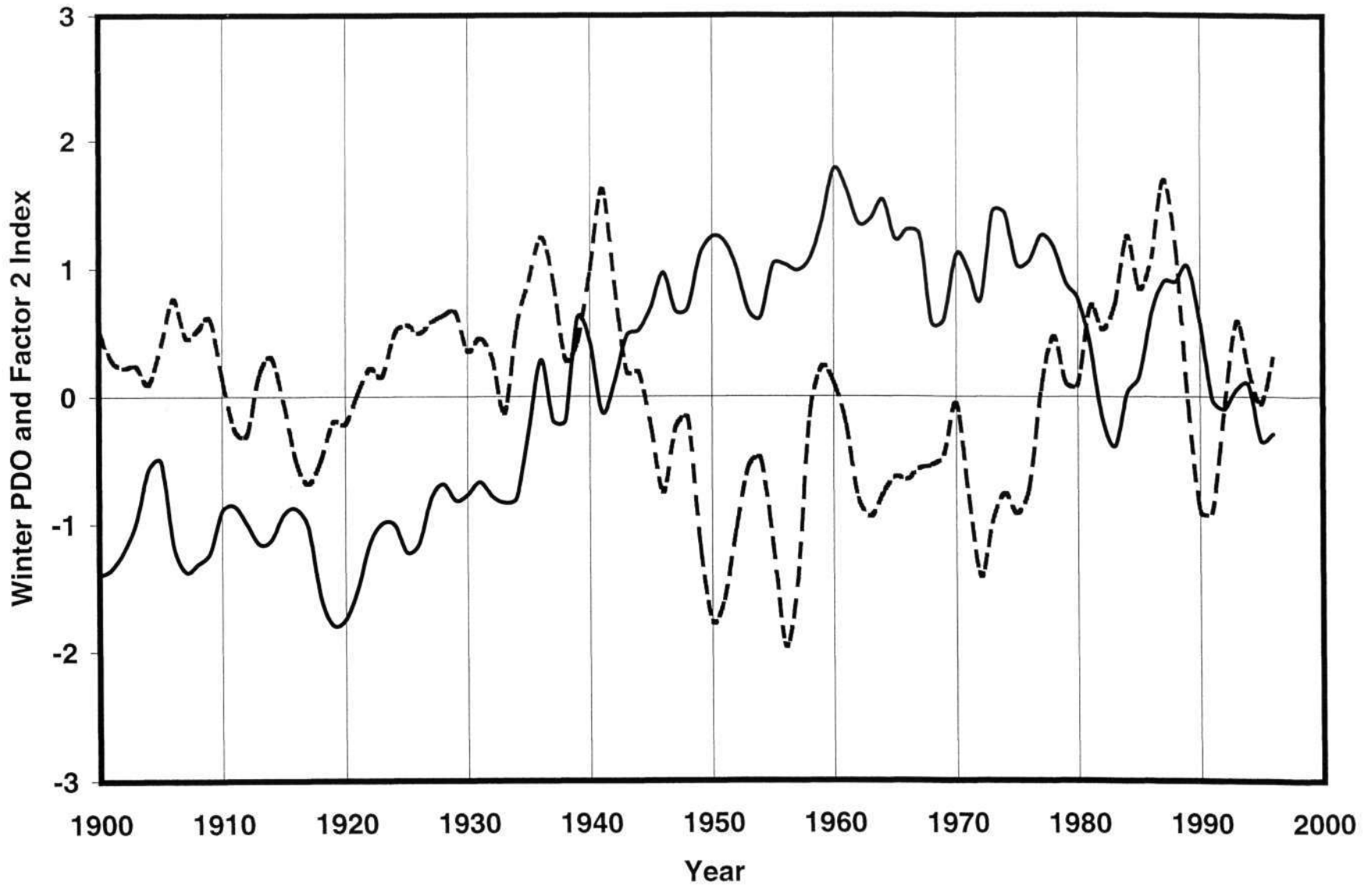
Figure 3.3 Plot of winter PDO index (dashed line) and Factor 2 index chronology (solid line) from factor analysis. These two were correlated giving r=-0.2916 and p=0.006.

Table 3.4 Partial correlation analysis between Factors 3 and 4 and monthly
climate variables that were also used in short-term analysis.

Factor 3 Station	Climate variable	Correlation coefficient (r)	P value
Crater Lake Headquarters	July precipitation	0.3207	0.041
Paradise	July temperature	-0.3716	0.003

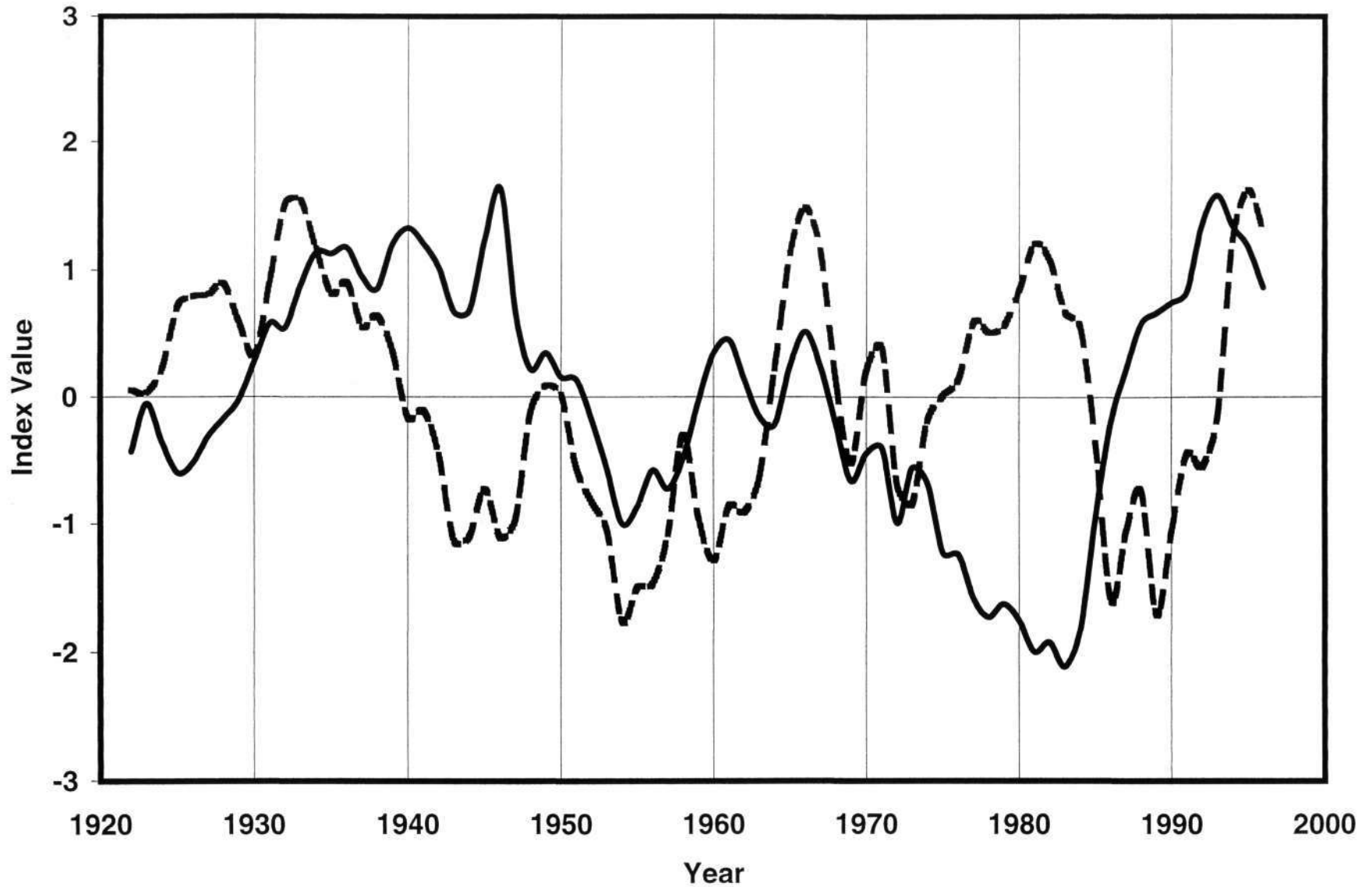| Factor 4 Station	Climate variable	Correlation coefficient (r)	P value
Crater lake headquarters	June temperature	0.3207	0.042
Paradise	Previous December precipitation	-0.4279	<0.001
Stehekin	Previous December precipitation	-0.2880	0.021
Stehekin	August temperature	-0.3811	0.002

Figure 3.4 Smoothed plot of Factor 3 (dashed line) and Factor 4 (solid line) index chronologies from factor analysis.

Chapter 4: Discussion

Short-term trends

At Mount Rainier and North Cascades National Parks, whitebark pine growth is limited by spring snowpack. Partial correlation analysis revealed a positive correlation between growth and January and March temperature at both Mount Rainier and North Cascades. The positive correlation suggests that warm temperatures lead to lower snowpack and therefore an earlier start to the growing season. Previous December precipitation and March precipitation at both Mount Rainier and North Cascades are also negatively correlated with growth implying that as snow increases, growth decreases. The fourth component extracted from factor analysis is also negatively correlated with previous December precipitation at Mount Rainier and the North Cascades. This suggests that snowpack affects the growth of whitebark pine on annual and longer time frames.

Almost twenty percent of the precipitation that falls annually at Mount Rainier is in December (Figure 4.1). No other month produces as much precipitation as December in any of the parks. This may be the reason why December precipitation correlated with growth while other winter months' precipitation did not. March precipitation probably occurs as snow and therefore affects the years' snowpack, thereby shortening the growing season.

Winter climate has been shown to affect the short-term growth response of several other subalpine species. Subalpine species delay bud break until the snow melts and soil temperatures rise above freezing (Worall 1983). During the early springs of 1999 and 2000, at Niwot Ridge, Colorado, springtime net carbon

uptake of lodgepole pine, Engelmann spruce, and subalpine fir, began within the first three days when night-time soil temperature rose above 0° C within the first 10 cm (Monson et al. 2002). Snow insulates the ground and prevents spring soil temperatures from rising above freezing. After snowmelt, respiration of subalpine species increased and net ecosystem CO_2 outputs decreased indicating net photosynthetic CO_2 uptake was taking place (Monson et al. 2002). Although no direct measurements of photosynthesis and respiration are available for the Pacific Northwest, we believe the same mechanism is involved.

There is some variability from park-to-park of whitebark pine's response to winter climate. In Washington, winter precipitation limits whitebark pine growth, and warm winter temperature presumably promote growth by decreasing snowpack. Crater Lake shows no significant correlation with winter precipitation or temperature. The northern parks were much wetter than Crater Lake to the south (Figure 2.2). Snowpack may have a lower impact on the growth of whitebark pine at Crater Lake because the snowpack melts sooner. In December, Mount Rainier averaged 10 cm more precipitation than Crater Lake, and in April, near the end of snow accumulation, Crater Lake receives half as much precipitation as Mount Rainier (NCDC). Because the total precipitation is less at Crater Lake, it can be assumed that a shorter time period is required for snow to melt. We conclude that as latitude decreases, so does the influence of snowpack on the growing season and so the growing seasons of whitebark pine start earlier heading south along the Cascade Range.

Growth at Crater Lake had a positive correlation with June temperature. The fourth extracted factor also had a positive correlation with June temperature suggesting that June temperature affects growth in the long-term as well. In the Sierra Nevada, in northern California, Peterson et al. (1990) found strong correlations between growth of whitebark pine, 60 years or older, with spring temperature. They suggest that the warm spring temperatures may allow for an earlier initiation of budbreak (Peterson et al. 1990). With mid-summer drought often halting growth, an earlier budbreak can provide a longer period of photosynthetic activity. More bole growth will result from the extended period of photosynthesis.

Dry regions in general show that increases in temperature are detrimental to carbon balance. In the Colorado Front Range, at a site with a low topographic relative moisture index, the growth of Engelmann spruce and subalpine fir were negatively correlated with June temperature (Villalba et al. 1994). Subalpine species in drought limiting regions are sensitive to high temperatures even in the spring. At Niwot Ridge, the largest fraction of annual carbon sequestration occurred in the early-growing season, during the first 30 days after budbreak (Monson et al. 2002). Maximum carbon uptake was observed during late May to early June during another study at the same site (Huxman et al. 2003). At Niwot Ridge, most bole growth of subalpine species occurred during the spring. We conclude that the influence of climate on the growth of whitebark pine at Crater Lake is intermediate to what we observed in Washington and what others observed in the arid regions of California (Peterson et al. 1990) and Colorado

(Villalba et al. 1994, Monson et al. 2002). Correlations of growth with temperature shifts from June at Crater Lake to August (albeit previous August) at North Cascades. When combined with the positive correlation between whitebark pine growth and spring temperatures in California (Peterson et al. 1990) the trend is even more apparent.

The negative correlation between previous August temperature and growth at North Cascades suggests that summer temperatures can be too warm for whitebark pine growth. Climate-growth correlations occur earlier in the Sierra Nevada (Peterson et al. 1990) and Crater Lake, than at Mount Rainier and North Cascades implying that warm summer temperatures are detrimental to the growth of whitebark pine. A decrease of 60 to 75% in net ecosystem production occurs in subalpine forests at Niwot Ridge in mid- to late-summer due to high temperatures (Huxman et al. 2003). Respiration costs at Niwot Ridge increase as temperatures rise, and the net ecosystem CO_2 uptake decreases, leading to less growth. In old-growth ponderosa pine, nighttime respiration doubles from May to July in central Oregon (Anthoni et al. 2002). As temperatures increase in the summer, there is an increase in respiration especially in the soil, which is exacerbated by drought. In 1999 and 2000, the highest respiration costs were observed at Niwot Ridge in August and in July respectively (Huxman et al. 2003). The year 2000 was drier, which explains an earlier increase in respiration costs (Huxman et al. 2003). Higher temperatures are accompanied by high respiration costs, thereby limiting growth. The enzymes of subalpine plants are believed to be the most efficient below 12° C (Huxman et al. 2003), and therefore summer

temperatures at all of our sites would likely be too high to maintain positive carbon balance in the summer. Temperature increases earlier in the growing season at Crater Lake than at Mount Rainier or North Cascades. An average temperature of $12°$ C occurs in June at Crater Lake and in late July at Mount Rainier (NCDC) demonstrating that the productivity of whitebark pine will be affected earlier at Crater Lake.

Photosynthesis and carbon uptake may occur in the late summer if there is adequate precipitation, or if cool temperatures remain, thereby either prolonging the growing season or providing stored carbon for the following growing season. Our study shows that high July precipitation at Crater Lake led to greater whitebark pine growth the following season (i.e. there was a positive correlation between previous July precipitation and growth). In both wet and dry sites in the Colorado Front Range, previous July precipitation was positively correlated with subalpine fir growth the following year (Villalba et al. 1994). We also observed that high summer temperatures decreased growth of whitebark pine. Previous August temperature negatively correlated with growth in three out of the four sites in the North Cascades. This suggests that if August temperatures were low, then growth the following year would increase. Ettl and Peterson (1995) found a negative correlation between growth of subalpine fir in the Olympic Mountains and previous August temperature as well. We believe that the same mechanism (temperatures becoming too warm to support positive carbon gain) is responsible for negative correlations with previous August temperature at North Cascades and previous July precipitation at Crater Lake.

The timing of the negative correlation of previous July precipitation at Crater Lake coming after positive correlations with growth in June suggests that increased respiration costs affect carbon gain (Monson et al. 2002), and therefore carbon stores for the following year.

Non-growing season photosynthesis is very important in the overall carbon balance for many conifers in the Pacific Northwest, especially at lower elevations (Emmingham and Waring 1977). Our results suggest that non-growing season photosynthesis is also important for whitebark pine. A positive correlation of growth with October temperatures from the previous year at both Mount Rainier and Crater Lake imply that as temperature increases in October so does the growth the following year. We interpret this to mean that more photosynthesis occurs in the fall as a result of warmer temperatures. Warmer temperatures may also indicate a delay of storm fronts, and therefore a decrease in precipitation falling as snow and presumably warmer soil temperatures. Less snow may also mean less snowpack that winter, and a subsequent earlier start to the subsequent growing season. Lodgepole pine is positively correlated with fall temperature in Colorado (Villalba et al. 1994), and subalpine fir is positively correlated with November temperatures (at lower elevation subalpine fir sites, Ettl and Peterson 1995) in the Olympic Mountains, Washington suggesting that positive carbon storage in the fall may be common among subalpine species. Huxman et al. (2003) showed an increase in net ecosystem CO_2 uptake in September and October in a subalpine forest suggesting enhanced carbon assimilation.

Long-term trends

The first extracted factor, representing 35% of the variance, shows a pronounced increase beginning in the late 1950's, and the positive correlation of this factor with all but one of the study sites implies a growth increase in whitebark pine at all three parks. We believe that this growth increase is not due to stand dynamics. In subalpine forests, disturbances such as fire, wind, bark beetles, and snow damage from drifts and avalanches commonly alter stand dynamics (Antos and Parrish 2002). Forest regeneration often follows these disturbances leading to growth increases in saplings that have replaced the dead trees. As the saplings become adult trees, there is more competition for water and other nutrients resulting an eventual decrease in radial growth of the new trees. In mature stands, (the factor analysis incorporates only chronologies that date back at least 100 years), radial growth typically decreases or levels off (Aber and Melillo 2001), but our results indicate radial growth is increasing. Neither stand maturation nor disturbance factors are sufficient to explain the observed growth increase. In fact, on many sites (particularly at Mt, Rainier and North Cascades) subalpine fir is becoming more common (as evidenced by recent meadow invasion by saplings(Rochefort 1999) and we would expect that the less shade tolerant whitebark pine would show reduced growth in response to subalpine fir. If stand dynamics played a major part in the growth increase, then we would need a cause that would explain the increase over a large area from northwestern Washington to southwestern Oregon.

The presence of blister rust throughout the Pacific Northwest could serve as a possible explanation for the observed growth increase. We surveyed blister rust on all of the stands as part of an ongoing study examining the effects of blister rust on whitebark pine in the Pacific Northwest (DelPrato 1999). It is possible that the observed growth increases are related to healthy trees being freed of competition from neighboring whitebark pine infected with blister rust. (It is important to note that the majority of the study sites occur in subalpine parkland habitat and dominant trees were sampled, thereby minimizing intraspecific competition.) DelPrato (1999) used tree-ring data to estimate the timing of blister rust infection on a site-by-site basis at Mt. Rainier. Many of the sites that show a growth increase beginning in the 1950's (i.e., G and O), do not show serious effects of blister rust until the later 1970's and therefore the growth increase is probably not related to blister rust dynamics on these sites. Some of the sites (i.e., E and F) however do show severe blister rust infections prior to 1950 (rust appeared at F in 1933), and therefore it is possible that blister rust-related mortality of infected whitebark pine has led to a growth increase of uninfected whitebark pine (DelPrato 1999). At Crater Lake some of the sites that show a growth increase (i.e., P, Q, and R) showed low levels of blister rust infection in 2001 (yet alone 1950) and therefore blister rust is an unlikely explanation for the growth increase (Ettl, unpublished data). In fact, 8 out of the 12 study sites have relatively low levels of blister rust infection, which suggests blister rust is an unlikely cause of the growth increases we observed at Crater Lake. In the North Cascades, 3 of 4 sites have less than 30% blister rust

infection implying that the fungus was not affecting the dynamics at these sites as well. In summary, though it is possible that blister rust related stand dynamics could explain the observed growth increase, it is an unlikely explanation for the majority of the sites.

Long instrumental climate records dating back to 1750 from cities throughout the Northern Hemisphere indicate that annual warming is occurring with much of the increase taking place in the cold season from October -April (Jones et al. 2002). Using the latewood densities of trees in Alaska, Jacoby and D'Arrigo (1995) recreated a climate history of the region, which shows evidence of recent warming of 0.5 to 1° C over the past century. Annual daily temperature means from three of the climate divisions in the Pacific Northwest, represented by the sites in this study, show an increasing trend as well (NCDC) (Figure 3.2). Positive correlations were observed when the first extracted factor was correlated with the annual temperature means from these climate divisions (r=0.569, p<0.001 for WA division 5; r=0.275, p=0.005 for WA division 6; and r=0.495, p<0.001 for OR division 5; Figure 3.2a-c). This would imply that whitebark pine growth is increasing with increasing temperature. Growth back to the start of the chronologies prior to the late 1950s is positively correlated with temperature as well suggesting that growth of whitebark pine is sensitive to temperature and that shifts in temperature would affect growth. An increase in temperatures, as predicted under most future climate scenarios (IPCC 2001) would presumably benefit the growth of whitebark pine throughout its range in the Pacific Northwest.

Climatic change is expected to affect whitebark pine and other subalpine species by impacting the factors that limit the growing season. This study shows that productivity of the growing season of whitebark pine is dependent on winter snowpack. Leung and Ghan (1999) using a regional-scale circulation model predict that warming will lead to a 50% reduction in snow cover in the Pacific Northwest. Increased warming has allowed for more productive growing seasons of subalpine species such as subalpine fir and mountain hemlock because of less snowpack and an earlier snowmelt in the Pacific Northwest (Peterson et al. 2002, Peterson and Peterson 2001). Growth of whitebark may be increasing with increasing temperature, because snowpack is decreasing and more growth is occurring earlier in the year as a result.

Increased CO_2 fertilization due to increasing levels of atmospheric CO_2 may account for some of the growth increase observed for whitebark pine. The sensitivity of tree growth, in the Northern Hemisphere, to climate has been shown to decrease, potentially due to growth increases, which are believed to be partially related to increases in atmospheric CO_2 concentrations (Briffa et al. 1998). Values calculated from an exponential equation for atmospheric CO_2 derived from data measured air samples and ice bubbles (Feng 1998) were standardized and correlated to the first extracted factor. The two were positively correlated and the factor demonstrated an exponential likeness to the curve for atmospheric CO_2 suggesting CO_2 fertilization. It should be noted that Factor 1 is below the CO_2 curve from 1940-1960 (Figure 3.2), a period when temperatures

were lower, but tracks the CO_2 data well since 1970, and I suspect that both temperature and CO_2 concentrations are responsible for the growth increase.

Increased levels of CO_2 enhance plant growth because levels of CO_2 are often limiting to plant growth, especially for high elevation vegetation, which are subject to low air-pressure and decreased CO_2 concentrations (LaMarche et al. 1984).. Photosynthesis should increase with increasing levels of atmospheric CO_2 because the stimulation of the carboxylation reaction of Rubisco should occur as a result of increasing levels of atmospheric CO_2 leading to increases in photosynthetic rates (Ward and Strain 1999). An increase in atmospheric CO_2 partial pressure would result in a reduction of the photorespiration-to-photosynthesis ratio, thereby increasing net photosynthesis (Tissue et al. 1999). An increase in photosynthesis should lead to an increase in available carbon and therefore an increase in radial growth.

Most forests in North America, including the stands in this study, are most likely limited by nitrogen availability (Fenn et al. 1998) and nitrogen deposition from any source including pollution would be expected to cause a growth increase. Because historic nitrogen deposition data is not available for the region, the possibility that increased nitrogen availability is causing the growth increase cannot be ruled out. Juvenile ponderosa pine subjected to high nitrogen treatments had an 88% increase in shoot weight when compared to juveniles grown at ambient conditions (Walker et al 1998). This would suggest that nitrogen deposition could be a factor in the growth increase. Earlier, we suggested that fertilization of CO_2 might contribute to the growth increase,

however CO_2 fertilization is limited by nitrogen in ponderosa pine and loblolly pine (*Pinus taeda*), which were shown to increase in biomass with increases in nitrogen uptake (Johnson et. 1998). CO_2 fertilization effects are short-lived in the absence of nitrogen additions (Schlesinger and Lichter 2001). Our study provides no mechanism for separating growth components into those attributable to CO_2 fertilization and nitrogen fertilization, and because both processes are closely associated, both may be involved in the growth increase of whitebark pine.

Winter Pacific Decadal Oscillation is negatively correlated with the second growth factor, which suggests that PDO is responsible for a portion of the growth variance of whitebark pine. This would imply that when PDO index is high and the Pacific Northwest is in a warm and dry phase (Mantua et al. 1997), that whitebark pine growth decreases. This result is at first glance surprising given the negative correlation of winter precipitation with growth at Mt. Rainier and North Cascades. However, the components matrix revealed that the second factor correlated with Crater Lake sites the most consistently suggesting that whitebark pine at Crater Lake are sensitive to winter PDO. The greatest correlation occurred during a cold and wet regime (1941-1970). This result suggests that at Crater Lake, a cold and wet regime enhances growth of whitebark pine, most likely because drought limits growth there. A cold regime most likely gives Crater Lake more snow making the sites wetter and less susceptible to drought. This suggests that whitebark pine at Crater Lake (and perhaps in California as well) are more sensitive to PDO than more northern sites.

Factors 3 and 4 account for nearly 25% of the variance in the basal area increment chronologies. These two factors correlated with six monthly climate variables (Figure 3.4) four of which were the same climate variables that showed significant correlations to growth of whitebark pine in the short-term suggesting that there is a short-term component to these factors. The limiting climate variables proved to be long-term trends as well because growth trends were evident in these two factors (Figure 3.4). In the short-term analysis, a negative correlation was observed between growth and previous December precipitation at both Mount Rainier and North Cascades. The fourth extracted factor had a negative correlation with previous December precipitation implying that the response to winter snowpack is a long-term trend. Peterson and Peterson (2001) also observed significant negative correlations between spring snowpack and - the growth of mountain hemlock in the Cascade and Olympic Mountains demonstrating that snowpack affects other subalpine species in the long-term as well.

Factor 4 positively correlated with June temperature at Crater Lake implying that over the long-term June has been an important month for the radial growth of whitebark pine at this park. Factor 4 negatively correlated to August temperature at North Cascades and Factor 3 negatively correlated to July temperature at Mount Rainier suggesting that increased respiration costs are consistently preventing growth from occurring in the late growing season over the long-term. There was a positive correlation between Factor 3 and July precipitation at Crater Lake, which demonstrates that whitebark pine may be able

to maintain production into July when increased precipitation lowers respiration costs.

The shift from June at Crater Lake, to July at Mt. Rainier, to August in the North Cascades is indicative of the timing of the growing season at each site. The northern most park has the latest period of climate-growth correlation. South of Crater Lake, in the Inyo National Forest in the Sierra Nevada, in northern California, whitebark pine growth showed positive correlations to climate in the spring (April to June) (Peterson et al. 1990) suggesting that as latitude decreases, the majority of the growth of whitebark pine occurs earlier in the year. Southern whitebark sites grow earlier in the year, most likely related to the temperature and water moisture availability at each site. The southern parks are warmer and as a result are not limited by snowpack, because warm temperatures prevent snowpack from forming which could potentially delay or limit the growth of whitebark pine (NCDC). The sites to the south are also drier (NCDC), which suggests that radial growth of southern whitebark pine is completed before summer drought. This response in the south has implications for northern whitebark pine, as well. Warming in the north, most likely will lead to decreases in snowpack and increase in summer drought, forcing whitebark pine to begin growth earlier. With warming, what is observed in the southern parks is likely to be observed in the north. Unfortunately for the southern whitebark pine, the shift in the timing of growth may not be as easy. Instead, they may lose out to more drought tolerant subalpine species.

The overall long-term response of whitebark pine is a growth increase suggesting that conditions are improving for whitebark pine throughout its range. High elevation species should benefit from the growth increases in regards to competition with species currently at lower elevations. Low elevation species have been projected to migrate up in elevation into the range of many subalpine species, due to warming, where they are expected to outcompete existing subalpine species (Franklin et al. 1992)). The growth increases we observed in this study bring into question the assumption that lower elevation species will be able to out compete current subalpine species as climate warms.

With temperatures rising as a result of global warming, snowpack, which was shown to limit whitebark pine growth in the northern parks, should decrease and decrease in importance as a limiting factor. The effects of global warming on snowpack however may be nullified in the coming years by a cold and wet Pacific Decadal Oscillation regime. Mantua et al. (1999) reported that there has been a shift in PDO index from high to low and that as of 1998 a cold and wet regime may have begun. If this holds true, then winter snowpack may stay the same or increase, remaining a limiting factor for whitebark pine. This study showed that drought limited Crater Lake whitebark pine, while snowpack did not. Whitebark at Crater Lake should be impacted by the PDO regime with an increase in moisture in the form of snow and summer precipitation. Potentially, then the whitebark pine at Crater Lake may no longer be limited by drought in summer, instead an accumulation of more snow in the winter could limit growth.

Chapter 5: Summary

In the short-term analysis, it was determined that whitebark pine is limited by the length of the growing season. At the two northern parks, the length of the growing season was influenced by winter snowpack, (i.e. winter precipitation is negatively and winter temperature positively correlated with growth).. Previous December precipitation and March precipitation at both Mount Rainier and North Cascades are negatively correlated with growth implying that as snow increases, growth decreases. Partial correlation analysis revealed a positive correlation between growth and January and March temperature at both Mount Rainier and North Cascades. This suggests that warm winter temperatures lead to lower snowpack and therefore an earlier start to the growing season. Snowpack was not limiting at Crater Lake. We believe this is because higher spring temperatures at Crater Lake, and overall lower winter precipitation (10 cm of precipitation less than at Mount Rainier in December) (NCDC).

Subalpine species, such as whitebark pine, can not begin growth until the snow melts and soil temperatures rise above freezing. At Niwot Ridge, Colorado, subalpine species, including lodgepole pine, Engelmann spruce and subalpine fir, show springtime net carbon intake begins when nighttime soil temperature within the first 10 cm rises above 0° C (Monson et al. 2000). After snowmelt, respiration of subalpine species increased and net ecosystem CO_2 exchange decreased (Monson et al. 2002). We believe the same mechanism is involved for whitebark pine in the Pacific Northwest even though no direct measurements of photosynthesis and respiration are available for the region.

Growth at Crater Lake had a positive correlation with June temperature. Peterson et al. (1990) found strong correlations with growth of whitebark pine in the Sierra Nevada, in northern California, and spring temperature, which they suggest may be due to earlier budbreak. An early budbreak gives the trees a head start on growth before mid-summer drought halts it, therefore a longer period of photosynthesis. Maximum carbon uptake was observed for subalpine species at Niwot Ridge during late May to early June (Huxman et al. 2003). The most bole growth of subalpine species occurs in the spring at Niwot Ridge..

Respiration costs increase as the summer progresses and temperatures rise causing net ecosystem CO_2 exchange to decrease leading to less growth. As temperature increases so does soil respiration , which is exacerbated by drought. Photosynthesis and carbon uptake can still occur in the late summer if there is adequate precipitation or cool temperatures, thereby prolonging the growing season or providing stored carbon for the following growing season. A positive correlation between previous July precipitation and growth at Crater Lake was observed. In the Colorado Front Range, previous July precipitation correlated with subalpine fir growth (Villalba et al. 1994). We also observed that high summer temperatures decreased the growth of whitebark pine, as demonstrated by previous August temperatures being negatively correlated with growth in the North Cascades. Summer precipitation and temperature are presumably linked to carbon balance, as it relates to transpiration and respiration, thereby influencing growth the following year.

In warm falls, photosynthesis can occur allowing for carbon stores to be replenished leading to increased growth the following growing season. A positive correlation with October temperatures from the previous year was found at both Mount Rainier and Crater Lake implying as temperature increases in October so does the amount of photosynthesis and growth the following growing season. Ettl and Peterson (1995) found a positive correlation between previous November temperature and subalpine fir growth in the Olympic Mountains. Warm fall temperatures could enhance growth the following year by increasing fall photosynthesis and therefore carbon stores, or by causing fall precipitation to not fall as snow. Fall snow would lead to increased snowpack, which has been shown to limit growth.

Four factors were extracted with principal components analysis from the basal area increment chronologies in order to examine long-term growth trends. The first factor, which accounted for 35% of the variance showed a pronounced growth increase beginning in the late 1950's. In mature stands, radial growth of old trees is expected to decrease or level off (Aber and Melillo 2001), but our study shows increases in radial growth even in the chronologies that dated before 1900. Stand dynamics was eliminated as a possible cause for the growth increase, although the possibility exists that the growth increase is related to blister rust dynamics on some sites. Neither disturbances nor maturity explain the growth increase.

Blister rust in the Pacific Northwest also affects stand dynamics by killing trees and leaving open spaces in the canopy, therefore the possibility of stand

dynamics as the cause of the observed growth increase was examined. Blister

rust was surveyed on all the sites as part of a separate study examining the

effects of the fungus on whitebark pine at Mount Rainier (DelPrato 1999).

DelPrato reported blister rust related mortality at several sites occurred prior to

the 1950's (F which was infected in 1933) and after the 1970's at others (such as

G and O). None of the infections seem to occur in the fifties suggesting blister

rust that caused mortality of whitebark pine did not cause the growth increase in

the healthy trees. At most of the Crater Lake and North Cascades sites, there

was less than 50% infection levels of whitebark pine, and many trees were in

early stages of infection in 2001, suggesting that blister rust-related growth

releases of sample trees is unlikely.

Annual temperature in the three climate divisions represented appeared to

have an increasing trend similar to the growth increase observed for Factor 1.

There were positive correlations between Factor 1 and the annual temperature

means from the three climate divisions (r=0.569, p<0.001 for WA division 5,

r=0.275, p=0.005 for WA division 6, r=0.495, p<0.001 for OR division 5) implying

that whitebark pine growth is increasing with increasing temperature. The

variations in Factor 1 prior to the 1950's also correlated with these temperature

data suggesting that whitebark pine are sensitive to fluctuations in temperature.

An increase in temperatures, as predicted under most future climate scenarios

(IPCC 2001) should benefit whitebark pine. Warming will cause snowpack,

which was limiting to growth at the two northern parks, to decrease. Using a

general circulation model, Leung and Ghan (1999) predict that snow cover will

decrease by 50% in the Pacific Northwest. The correlations of the first factor with temperature may be related to decreasing amounts of snowpack.

Increased CO_2 fertilization may also account for some of the growth increase observed in Factor 1. A positive correlation was observed between Factor 1 and atmospheric CO_2. Factor 1 is below the CO_2 curve from 1940-1960, a period when temperatures were lower, but tracks the CO_2 data well since 1970, suggesting that both temperature and CO_2 concentrations may be responsible for the observed growth increase. Photosynthesis should increase with increasing levels of atmospheric CO_2 because the stimulation of the carboxylation reaction of Rubisco should occur as a result of increasing levels of atmospheric CO_2 leading to increases in photosynthetic rates (Ward and Strain 1999). An increase in photosynthesis should lead to an increase in available carbon and therefore an increase in radial growth.

No historic nitrogen deposition data is available for the Pacific Northwest, therefore the possibility that the growth increase resulted from nitrogen availability cannot be ruled out. Nitrogen fixation has been shown to increase the growth of several species including ponderosa pine, which when exposed to elevated levels of nitrogen increased shoot weight by 88% (Walker et al. 1998). CO_2 fertilization is limited by nitrogen in ponderosa pine and loblolly pine (*Pinus taeda*), which were shown to increase in biomass with increases in nitrogen uptake (Johnson et. 1998). CO_2 fertilization and nitrogen fertilization prove to be interrelated and both may be involved in the growth increase of whitebark pine.

Winter PDO index significantly negatively correlated to our second growth factor, which implies that PDO is responsible for some of the variance in whitebark pine growth. When PDO index increases putting the Pacific Northwest in a warm and dry phase (Mantua et al. 1997), whitebark pine growth decreases. The correlation matrix revealed that Factor 2 correlated with many of the sites at Crater Lake, suggesting whitebark pine at this park are quite sensitive to PDO. The strongest correlation of PDO occurred during a cold wet regime (1941-1970), which makes sense because Crater Lake sites are limited by drought. When the index falls and the region becomes wetter, growth at Crater Lake improves. Mountain hemlock in the Olympic Mountains show negative correlations with PDO as well (Peterson and Peterson 2001) suggesting that many of the subalpine species in the Pacific Northwest are sensitive to this regional climate pattern.

Correlation analysis demonstrated that the last two factors, which account for 25% of growth variability, correlated with six monthly climate variables four of which were the same climate variables that showed significant correlations to growth of whitebark pine in the short-term suggesting that there is a short-term component to these factors. The correlations to the climate variables are also long-term trends as evidenced by the factor plots.

The fourth extracted factor had a negative correlation with previous December precipitation implying that the response to winter snowpack is a long-term trend. Factor 4 positively correlated with June temperature at Crater Lake implying that over the long-term June has always been a time for growth of

whitebark pine at this park. Factor 4 negatively correlated to August temperature at North Cascades and Factor 3 negatively correlated to July temperature at Mount Rainier. There was a positive correlation between Factor 3 and July precipitation at Crater Lake, which demonstrates that every year, whitebark pine can photosynthesize when increased summer precipitation allows them to compensate for high respiration costs.

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