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Growth-climate Relations of Lodgepole Pine in the North Cascades National Park, Washington

Abstract

Information about the sensitivity of lodgepole pine to climate will allow forest managers to maximize growth, better understand how carbon sequestration changes over time, and better model and predict future ecosystem responses to climate change. We examined the effects of climatic variability during the 20th century on the growth of lodgepole pine along an elevation gradient in the North Cascades National Park, Washington. Multivariate analysis and correlation analysis were used to simplify growth patterns and identify climate-growth relations. Mid-elevation chronologies correlated negatively with growing season maximum temperature and positively with growing season precipitation. By contrast, high-elevation chronologies correlated positively with annual temperatures and winter Pacific Decadal Oscillation index. Projected increases in summer temperatures will likely cause greater soil moisture stress in many forested ecosystems and the potential of extended summer drought periods over decades may significantly alter spatial patterns of productivity, thus impacting carbon storage. The productivity of lodgepole pine likely will decrease at sites with shallow, excessively drained soils, south and west facing aspects, and steep slopes, but increase at high-elevation sites.

Introduction

The concentration of carbon dioxide in the atmosphere has increased about 36% since 1800, due, in large part, to human activities (Intergovernmental Panel on Climate Change, 2001). This unprecedented rate of increase will continue to cause surface temperatures to rise, having both positive and negative impacts on forested ecosystems (Watson et al. 1996, Flannigan et al. 1998, Li et al. 2000, Cayan et al. 2001). Numerous studies have demonstrated that variation in climate has affected vegetation distribution and growth (e.g., Brubaker 1986, Innes 1991, Graumlich 1991, Peterson and Peterson 2001). Changes in vegetation distribution and growth may both positively and negatively affect ecosystem processes and functions, including productivity (Graumlich et al. 1989) and carbon sequestration.

Temperature and precipitation in the Pacific Northwest have increased more than global averages, a trend likely to continue into the future (Mote 2003). Although there is some uncertainty about

the exact changes in precipitation, future summers will likely be warmer and drier, and winters will be warmer and wetter than present (based on climate system model output) (Mote 2003, Mote et al. 2004). A warmer, wetter winter will cause more precipitation to fall as rain, a decrease in snowpack depth, and a longer growing season when compared to current conditions. While less certain, it is projected that climate change will also increase the frequency and perhaps intensity of disturbances such as forest fires (Westerling 2006, McKenzie et al. 2004) and outbreaks of insects such as mountain pine beetle (*Dendroctonus ponderosae*) (Logan and Powell 2001).

Our understanding of climatic effects on growth can be improved by sampling a range of sites with both extreme and moderate environmental conditions, because different growth-climate relations have been documented at separate elevations for several species (Kienast et al. 1987, Buckley et al. 1997, Holman 2006, Zhang and Hebda 2004).

Rising temperatures over the last century have increased the productivity of some high-elevation forests in Washington State (Graumlich et al. 1989). Altered forest productivity has been documented through increased growth in mountain hemlock (*Tsuga mertensiana*) (Graumlich et al. 1989),

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lodgepole pine (*Pinus contorta* var. *murrayana*) (Peterson et al. 1990), whitebark pine (*P. albicaulis*) (Peterson et al. 1990), bristlecone pine (*P. aristata*) (LaMarche et al. 1984), and other species across North America (McKenzie et al. 2001). Higher temperatures may not only facilitate growth of high elevation trees, but may also cause the tree line to rise throughout much of the North Cascades (Rochefort et al. 1994, Rochefort and Peterson 1996, Zolbrod and Peterson 1999). However, this advancing tree line may favor subalpine fir growth and regeneration (Alexander et al. 1990, Ettl and Peterson 1995).

High-elevation tree growth in the Pacific Northwest is typically limited by summer temperature and the depth of winter snowpack, though growth-climate relations vary spatially by topographic position, soil properties, and species (Peterson and Peterson 1994, Ettl and Peterson 1995, Peterson and Peterson 2001, Watson and Luckman 2002). For example, the root system of lodgepole pine varies considerably in form, depth, and soil type; however, roots tend to accumulate in upper soil horizons, and growth is limited in a large part by soil temperature (Körner 2003). In general, root growth does not typically occur when soil temperature is below 2° C (Teskey and Hinckley 1981). Therefore, the duration of the snowpack at high elevation can greatly affect the growth of lodgepole pine.

Longer, warmer summers may also result in significantly less tree growth and productivity at low elevations. Prolonged periods of water stress during the growing season can reduce a tree's ability to photosynthesize (Kozłowski and Pallardy 1997), leading to reduced rates of cambial activity and below average tree growth (Fritts 1966, Zaerr 1971, Brubaker 1980, Robertson et al. 1990). Dendroecological studies in the Pacific Northwest identify the negative effects of water stress on tree growth (Peterson and Peterson 1994, Ettl and Peterson 1995, Little et al. 1995, Peterson and Peterson 2001, Nakawatase 2006). Palmer Drought Severity Index (PDSI), which is essentially a surrogate for mean soil moisture (a combination of soil moisture supply and demand); can be used as another measure of water stress and can be used to identify a relationship between climate and growth.

In addition to annual climatic variation, there are two quasi-periodic atmospheric circulation

patterns connected with the Pacific Ocean influence the climate of the Pacific Northwest. The El Niño/Southern Oscillation (ENSO) has been identified as a key source of interannual climatic variations for the Pacific and has a periodicity of 2-7 yr (Rasmussen and Wallace 1983). The Pacific Decadal Oscillation (PDO), described as a long-lived El Niño-like pattern of climatic variability (Mantua et al. 1997), is a pattern of interdecadal variability of sea-surface temperatures in the North Pacific. The PDO phase (warm/dry or cool/wet) is associated with snowpack depth (lesser or greater) and air temperature and thus affects the soil temperature and length of the growing season and tree growth at low and high elevation sites (Peterson and Peterson 2001, Nakawatase 2006).

We used dendroecological methods to quantify the effects of climatic variability on lodgepole pine (*Pinus contorta* var. *latifolia*) growth at annual time scales along an elevation gradient in the North Cascades National Park, Washington. Lodgepole pine is widespread throughout the North Cascades and is an important ecological component of several forest assemblages (Larson 1972, Wellner 1975, McDougal 1975). Lodgepole pine is used for aesthetics, recreation, watershed management, wildlife, and wood production (Wellner 1975). It is adapted to a variety of climatic conditions (Satterlund 1975), and can dominate on sites with shallow or low-fertility soils on which other species grow poorly (Lotan and Critchfield 1990). Lodgepole pine has many uses and wide ecologic amplitude, however, little research has looked at growth-climate relations (Peterson et al. 1990, Graumlich 1991, Villalba et al. 1994, Biondi and Fessenden 1999, Antos and Parish 2002). A detailed picture of how lodgepole pine responds to climatic variability at different spatial and temporal scales (e.g., low versus high elevations and annual to decadal time scales) will provide the necessary information to improve management of growth and productivity of this species and to project and prepare for how ecosystem processes and functions may be altered in the future because of a warmer world.

Study Area

The study site is located on the southwest-facing slope of Ruby Mountain in Thunder Creek watershed, North Cascades National Park, Washington (Figure 1). The North Cascades span the transition

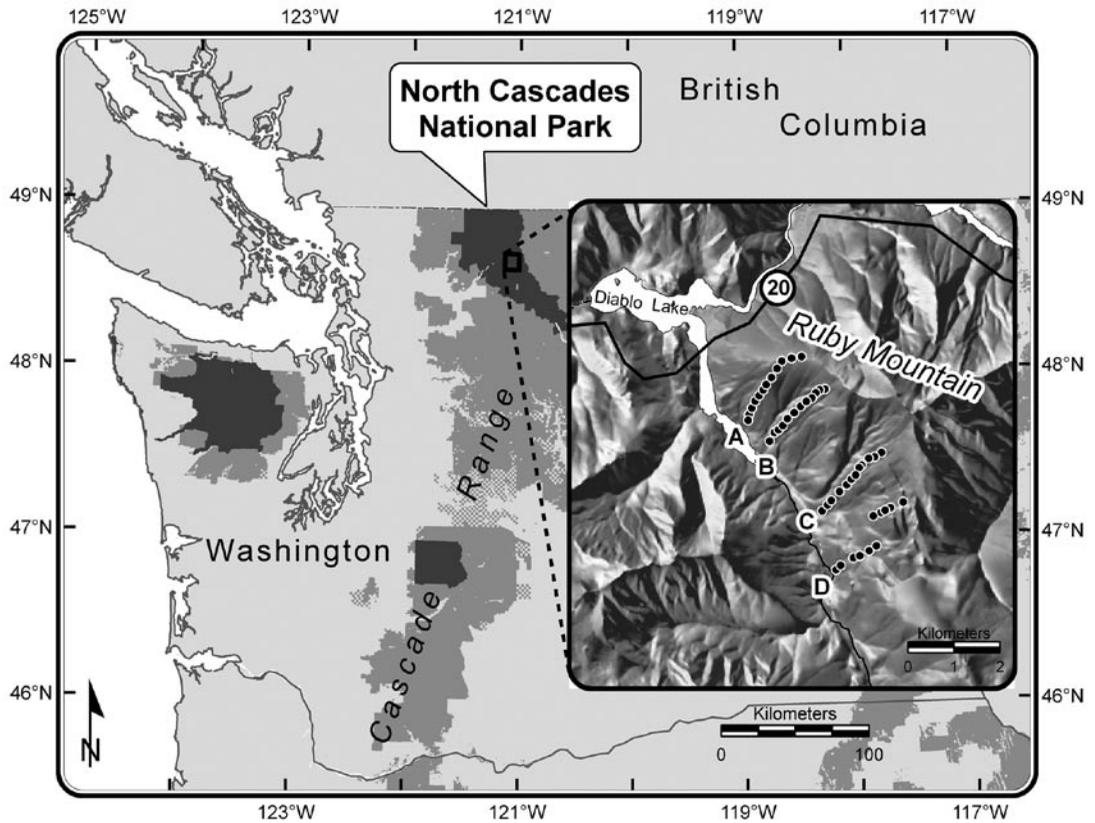


Figure 1. Location of the study site, Ruby Mountain, and individual plot locations (indicated by the small black dots). Transects are labeled A, B, C, and D.

between wet maritime weather associated with the Pacific Ocean and dry continental weather typical of the continental interior U.S. The geology of the study site was formed by oceanic, volcanic, tectonic, glacial, and erosion events. Bedrock is mostly composed of ancient oceanic rocks, including metamorphosed basalt, chert, and mantle, with exposed schist near the summit (Tabor and Haugerud 1999). Ruby Mountain has steep topographic relief with rocky benches and terraces, a result of glaciation during the last ice age (Tabor and Haugerud 1999). Soils are typically coarse and shallow and are generally classified as Andisols and Spodosols (Susan J. Prichard, University of Washington, personal communication).

The orographic effects of the geographic position of Ruby Mountain cause a wide range of local weather conditions, particularly at high elevations. Based on historic precipitation data (1934 - 2003) for the closest weather station (Diablo Dam, Wash-

ington, 300 m elevation and 5 km west of the study site), mean annual minimum temperature is 4.4°C, mean annual maximum temperature is 13.9°C, mean total snow fall is 133 cm, and mean annual precipitation is 168 cm. During the winter, low elevations typically experience a cool, wet maritime climate and high elevations experience deep snowpacks. Winter precipitation typically falls as snow above 1,000 m and is stored in the snowpack until it is released by the spring melt. Between July and September, low elevations experience relatively warm, dry weather, with little rainfall occurring, whereas higher elevations experience more moderate but dry weather.

The varied topography and distinct precipitation gradient found in this area (Larson 1972) strongly influence the vegetation pattern. Forest vegetation varies from maritime lowlands dominated by western hemlock (*Tsuga heterophylla*), western redcedar (*Thuja plicata*), and Douglas-fir

(*Pseudotsuga menziesii*) to subalpine sites dominated by subalpine fir (*Abies lasiocarpa*), Alaska yellow cedar (*Chamaecyparis nootkatensis*), and mountain hemlock, and dry inland sites dominated by Douglas-fir and lodgepole pine (Agee and Kertis 1987).

Forests of Ruby Mountain have never been harvested and, therefore, recent disturbance history consists of patchily distributed fires, snow avalanches, windstorms, and insect and disease outbreaks. Of these disturbances, fire is the most widespread and exerts the strongest controls on patterns of vegetative growth and reproduction. Mean fire return intervals for this area are generally 80 - 250 yr (Agee 1993, Prichard 2003). We have found evidence of fungal pathogens (root rot) and insect outbreaks (mountain pine beetle, *Dendroctonus ponderosae*) on individual trees or small groups of trees (author, personal observation).

Methods

Plot data and tree cores were collected during the summer of 2000 for a study of disturbance and succession (Prichard 2003). Four elevation transects were placed on Ruby Mountain, chosen because of its relatively consistent aspect and slope gradient. Plots were spaced at 100-m elevation intervals along the four transects (A – D) ranging from 465 m to 1546 m (Figure 1). These plots captured the growth variability of lodgepole pine along its entire elevation range within the watershed. Riparian areas, stream drainages, avalanche chutes, and cliffs were avoided. Plots were 0.05 ha in area and dominant and co-dominant lodgepole pine trees were cored once from the cross-slope sides at 140 cm height. Descriptive data collected on each plot included elevation, aspect, slope gradient, and geographic position (UTM coordinates).

Tree cores were mounted, sanded, and visually crossdated using standard procedures (Stokes and Smiley 1968). Of the 1125 cores originally collected, this study used 197 lodgepole pine cores that crossdated successfully. Individual ring widths were measured to the nearest 0.01 mm using a sliding stage measuring system (Robinson and Evans 1980). Measurements were verified by remeasuring a random 10-yr section of each core; cores were remeasured if the standard deviation of the absolute difference between the original measurement and the remeasurement was greater

than 0.05. The computer program COFECHA was used to detect measurement and crossdating errors by computing cross-correlations between individual series (Holmes 1999).

Lodgepole pine growth chronologies were developed from the crossdated ring-width series using the program CRONOL (Holmes 1999). Chronologies are composed of at least five trees per individual plot and were detrended. The crossdated measurement series were detrended by fitting a model to the series (negative exponential or linear regression) then standardized by dividing by the fitted values. These standardized growth indices removed the biological growth trend of each series that is associated with age and the increasing circumference of the tree. The plot chronology was then computed as a biweight robust mean of the detrended and standardized individual series (Cook et al. 1990). Chronologies were also pre-whitened by performing autoregressive modeling on the detrended ring-width measurement series to produce a residual chronology. The mean of these pre-whitened chronologies do not contain persistence (Holmes 1999).

Site characteristics (e.g., elevation, vegetation composition) and Pearson's product-moment correlation coefficients between individual growth chronologies and plot chronologies were used to compare intrasite and intersite relations and to guide exploratory analyses.

Descriptive statistics for each plot and species chronology were calculated, including mean sensitivity (Fritts 2001), intrasite correlation, intersite correlation, and percentages of the total number of chronologies of each autoregressive model order (1–4). Autoregressive models were chosen and developed using CRONOL (Holmes 1999) and verified with SPLUS (Insightful, Inc. 2003).

Multivariate Analysis

Factor analysis with oblique rotation was conducted to identify common modes of variability within the chronologies. After trying several different rotations, oblique (Promax) rotation was chosen over orthogonal rotation because it best represented growth patterns in the ring-width chronologies. We used principal components analysis (PCA) to determine how many factors to use in factor analysis (Insightful, Inc. 2003). Time series of factor scores (factor chronologies) were extracted, and factor loadings were used to

identify relations between the original ring-width chronologies and the factor chronologies.

Climate Data

Growth-climate relations were assessed by comparing species-specific plot chronologies with annual and seasonal climate variables. These climate variables were obtained from two local climate stations, Ross Dam (1961–1999) and Diablo Dam (1934–1999), both of which are within 5 km of the study site. Divisional climate data (Washington State Climate Division 5, 1932–1999) were not used for further analysis in this study because a preliminary analysis indicated that the local climate data are more strongly correlated with tree growth at the study site than divisional climate data. We examined annual, seasonal, and monthly temperature and precipitation variables for both Ross Dam and Diablo Dam climate stations for the current year of tree growth, the previous year of tree growth, and two previous years of tree growth.

Snowpack data were obtained from the Thunder Basin Snowpack Telemetry (SNOTEL) site located within the Thunder Creek drainage (Natural Resources Conservation Service 2003). This station has been collecting data from 1948 to the present. Annual, monthly, and spring snowpack depth and annual snow water equivalent were used to correlate with aggregated plot chronologies and factor chronologies. Snowpack data from the previous year and previous two years were also examined for significant correlations.

PDSI values were obtained from the National Oceanic and Atmospheric Administration Paleoclimatology Program for the period 1895–1995 at two locations in Washington State (grid point number 1, 122.5 W, 49 N; grid point number 8, 199.5 W, 49 N) (Cook et al. 1999). Two locations were used because the study site is on the transition between the wet, west side and the dry, east side of the Cascade Range. PDSI uses annual temperature and rainfall to quantify a measure of meteorological drought and is often considered to be a surrogate for soil moisture. Positive values thus represent higher soil moisture, and negative values represent lower soil moisture.

Monthly PDO and ENSO indices (ENSO indices in this study are represented by Nino3.4 sea surface temperature deviations from the mean) were obtained for the period 1900–1999 (Climate Impacts Group 2004) and transformed into

seasonal and annual values for comparison with tree growth. Positive values of the PDO are associated with higher winter temperatures, lower precipitation, and decreased snowpack accumulations; negative values typically represent lower temperatures, more precipitation, and potentially more snowpack (Mantua et al. 1997). Similarly, positive ENSO values (El Niño events) represent higher than average temperatures and less precipitation, whereas negative ENSO values (La Niña) represent cooler, wetter weather (Rasmussen and Wallace 1983).

Growth-Climate Relations

Pearson product-moment correlation coefficients (r) were calculated between factor chronologies and climate variables to assess which variables were significantly related to tree growth ($P < 0.05$). Climate variables used in this study include mean monthly temperature and total monthly precipitation from two years prior to the end of the growing season in which the ring was formed. Annual values were based on the hydrologic year from October through September. Annual and seasonal climate variables were used for correlations and were based on known seasonal weather patterns and previous studies. Other climate variables include total annual snowpack depth, total annual snow water equivalent, spring snowpack depth, and monthly snowpack depth. PDO and ENSO climate variables were also examined and include annual and previous year annual indices, winter (November–March) and previous year winter indices, summer (July–September) and previous year summer indices, and fall (September–October) and previous year fall indices.

We examined the relationship between lodgepole pine growth response and annual-to-decadal variability in the climate variables graphically, by calculating 5-yr running averages for factor chronologies and key climate variables. Moving averages were used for visual comparisons only, and no statistical analysis occurred on these averages, only on the detrended chronologies.

Results

Lodgepole pine was present in all four transects (A–D) and within 28 of the 47 plots, with most trees concentrated on transect A and C. Plots with fewer than five cores were combined with the nearest, most similar plots because we did

TABLE 1. Site elevation and descriptive statistics for lodgepole pine plots. Combined plots are indicated by *.

Elevation (m)	Plot	Number of cores	Mean intrasite correlation ¹	Mean sensitivity	% Auto-regressive model				
					order1	order 2	order 3	order 4	order 5
619	C3	10	0.32	0.17	90		10		
708-872	C4,5*	6	-0.01	0.14	67		33		
759	A4	5	0.22	0.17	40	60			
884-949	A5,6*	16	0.35	0.14	63	38			
954	C6	8	0.04	0.10	63	13	13	13	
1036-1316	C8,9,10*	10	0.19	0.15	60	20	20		
1168	A8	15	0.22	0.10	80	20			
1266	A9	11	0.35	0.11	73	9	9		1
1358	A10	7	0.26	0.15	71	14		14	
1469-1546	A11,12*	18	0.38	0.12	72	28			

¹Pearson product moment correlation coefficients

TABLE 2. Principal components and factor analysis for 10 lodgepole pine chronologies for the period 1932-1999.

PC	Principal components analysis			Factor analysis			
	Eigenvalue	Variance (%)	Cumulative variance	Factor	Eigenvalue	Variance (%)	Cumulative variance
1	0.2	40.0	40.0	1	2.2	24.0	24.0
2	0.1	21.0	61.0	2	2.0	23.0	46.0
3	0.1	12.0	73.0				
4	0.1	9.0	82.0				
5	0.1	6.0	88.0				
6	0.1	4.0	92.0				
7	0.1	3.0	95.0				
8	0.1	3.0	98.0				
9	0.0	2.0	100.0				

not want individual tree responses to override the overall influence of climate (e.g., some plots only contained a single lodgepole pine tree). Similarity of plots was based on intrasite and intersite correlations and similar elevation and vegetation composition. Nine individual plots were combined resulting in 10 site growth chronologies (Table 1) averaging 11 cores per plot.

Descriptive statistics were examined at the individual plot level (Table 1). Mean intrasite correlations range from -0.01 to 0.38, with the overall mean for all correlations 0.23 ± 0.13 (± 1 SE). Mean sensitivities for each core were averaged by plot and range from 0.10 to 0.17, with an overall mean of 0.135 ± 0.026 SE. Autoregressive models of the first order were sufficient to account for autocorrelation in 68% of plot chronologies, second order 20%, and third and fourth order models a combined 12%.

Multivariate Analysis

PCA determined that two principal components explained 61% of the variance in the 10 site chro-

nologies. Because each additional PC accounted for $\leq 12\%$ additional variance (Table 2), we used two factors in the factor analysis. Similar criteria have been used in other dendroecological studies (Peterson and Peterson 1994, Peterson and Peterson 2001, Peterson et al. 2002). Factor analysis was used to generate factor chronologies explaining 23–24% of the total variance within and among site chronologies (Table 2). These factor chronologies contain patterns of annual and decadal growth variability and therefore can be used to summarize the aggregated tree growth chronologies that are most closely related to them.

Factor loadings between factor chronologies and site chronologies over the period 1932–1999 show a correlation (1) between the first factor chronology (Factor 1) and low and mid-elevation plots in transect A and all plots in transect C, and (2) between Factor 2 and high-elevation plots in transect A (Table 3). Time series of the two factor chronologies have a combination of high-amplitude interannual growth variations and low-amplitude interdecadal growth variations as

TABLE 3. Factor loadings for lodgepole pine chronologies.

Chronology	Factor 1	Factor 2
C3	0.59	0.17
C4,5	0.45	----
A4	0.57	----
A5,6	0.74	0.34
C6	0.11	0.14
C8,9,10	0.66	0.37
A8	0.41	0.50
A9	0.17	0.63
A10	----	0.81
A11,12	0.28	0.70

shown by 5-yr moving averages (Figure 2). Factor 1 has brief periods of above average growth during the late 1930s, mid 1950s, late 1960s, and early 1980s, and periods of below average growth during the 1940s, early 1950s, mid 1970s, and early 1990s (Figure 2). In comparison, Factor 2 has a brief period of above-average growth during the mid 1950s, mid-to-late 1960s, and mid 1980s, and periods of below average growth during the 1940s, mid 1950s, mid 1970s, and early 1990s (Figure 2).

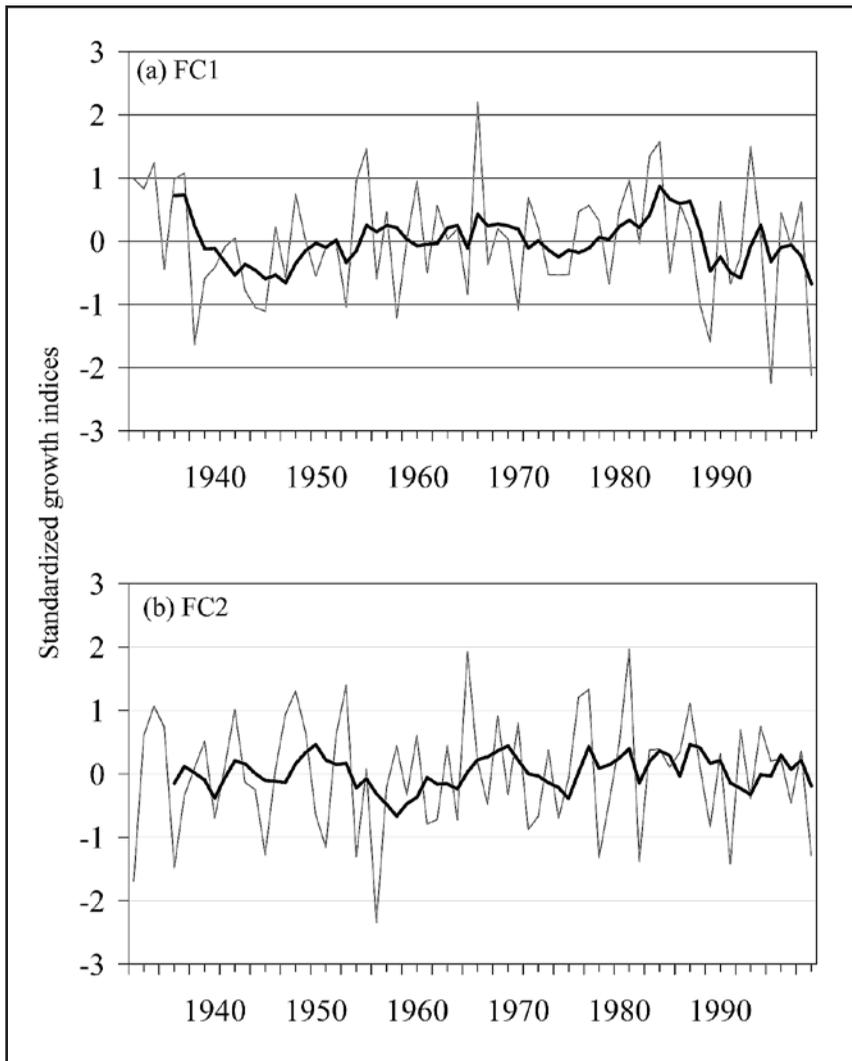


Figure 2. Factor score time series plots showing temporal variability in lodgepole pine growth: (a) FC1 (low/mid-elevation) and (b) FC2 (high-elevation). Thin lines represent annual values and thick lines represent smoothed 5-year running averages.

TABLE 4. Significant ($P < 0.05$) Pearson's product-moment correlation coefficients (r) between lodgepole pine factor chronology 1 (FC1 or low/mid elevation) and climate variables from Ross and Diablo climate stations, Thunder Basin SNOTEL station and PDSI indices.

Climate variable	FC 1 (low/mid elevation)		
	Diablo	Ross	Other
Growing season maximum temperature (May-Sep)	-0.40	----	----
Growing season average temperature (May-Sep)	-0.31	----	----
Summer temperature (Jun-Aug)	-0.26	----	----
Growing season precipitation (May-Sep)	0.32	0.38	----
Summer precipitation, previous year (Jul-Aug)	0.40	0.35	----
Winter precipitation (Nov-Mar)	0.25	----	----
Total annual snow water equivalent (Nov-Jun)	----	----	-0.35
PDSI at grid point number 8, 199.5 W, 49 N, 1895-1995	----	----	0.26
PDSI at grid point number 1, 122.5 W, 49 N, 1895-1995	----	----	0.44

Growth-Climate Correlations

Growing season temperatures and precipitation correlate with lodgepole pine growth at low/mid-elevations (represented by Factor 1, Table 4). Factor 1 is negatively correlated with growing season maximum temperature, growing season average temperature, summer temperature, and total annual snow water equivalent (Table 4). Factor 1 is positively correlated with growing season precipitation, previous year summer precipitation, winter precipitation, and PDSI (Table 4). Radial growth was highest during years of relatively low temperatures and high amounts of precipitation.

Previous year summer temperature and spring snow depth correlate with Factor 2. Radial growth was highest during years of low spring snowpack

and following years of relatively low summer temperatures. Factor 2 also correlates positively with annual and spring temperatures and negatively with previous year annual, previous year growing season, previous year spring, and previous two years fall temperatures (Table 5). Other significant growth-climate correlations include negative correlations with annual precipitation, total annual snow depth, total annual snow water equivalent, and April and May snow depth; and a positive correlation with annual ENSO values and winter and annual PDO indices (Table 5).

After plotting 5-year running averages of the Factors and key climate variables together (Figure 3), the correlation between Factor 1 and Diablo station growing season maximum temperature and

TABLE 5. Significant ($P < 0.05$) Pearson's product-moment correlation coefficients (r) between lodgepole pine factor chronology 2 (high elevation) and climate variables from Ross and Diablo climate stations, Thunder Basin SNOTEL station, and ENSO and PDO indices.

Climate variable	FC 2 (high elevation)		
	Diablo	Ross	Other
Annual temperature (Oct-Sep)	0.27	0.39	----
Spring temperature (Mar-Apr)	0.33	0.40	----
Growing season average temperature, previous year (May-Sep)	----	-0.33	----
Annual temperature, previous year (Oct-Sep)	----	-0.41	----
Spring temperature, previous year (Mar-Apr)	----	-0.35	----
Summer temperature, previous year (Jul-Aug)	-0.30	-0.56	----
Fall temperature, previous 2 years (Oct-Nov)	-0.42	-0.35	----
Annual precipitation (Oct-Sep)	-0.25	----	----
Total annual snow water equivalent (Nov-Jun)	----	----	-0.41
Total annual snow depth (Nov-Jun)	----	-0.45	-0.47
Spring snow depth (Apr-Jun)	----	----	-0.52
April snow depth	----	----	-0.48
May snow depth	----	----	-0.48
Annual ENSO (Nino3.4 SST anomalies) (Oct-Sep)	----	----	0.26
Winter PDO (Nov-Mar)	----	----	0.33
Annual PDO (Oct-Sep)	----	----	0.32

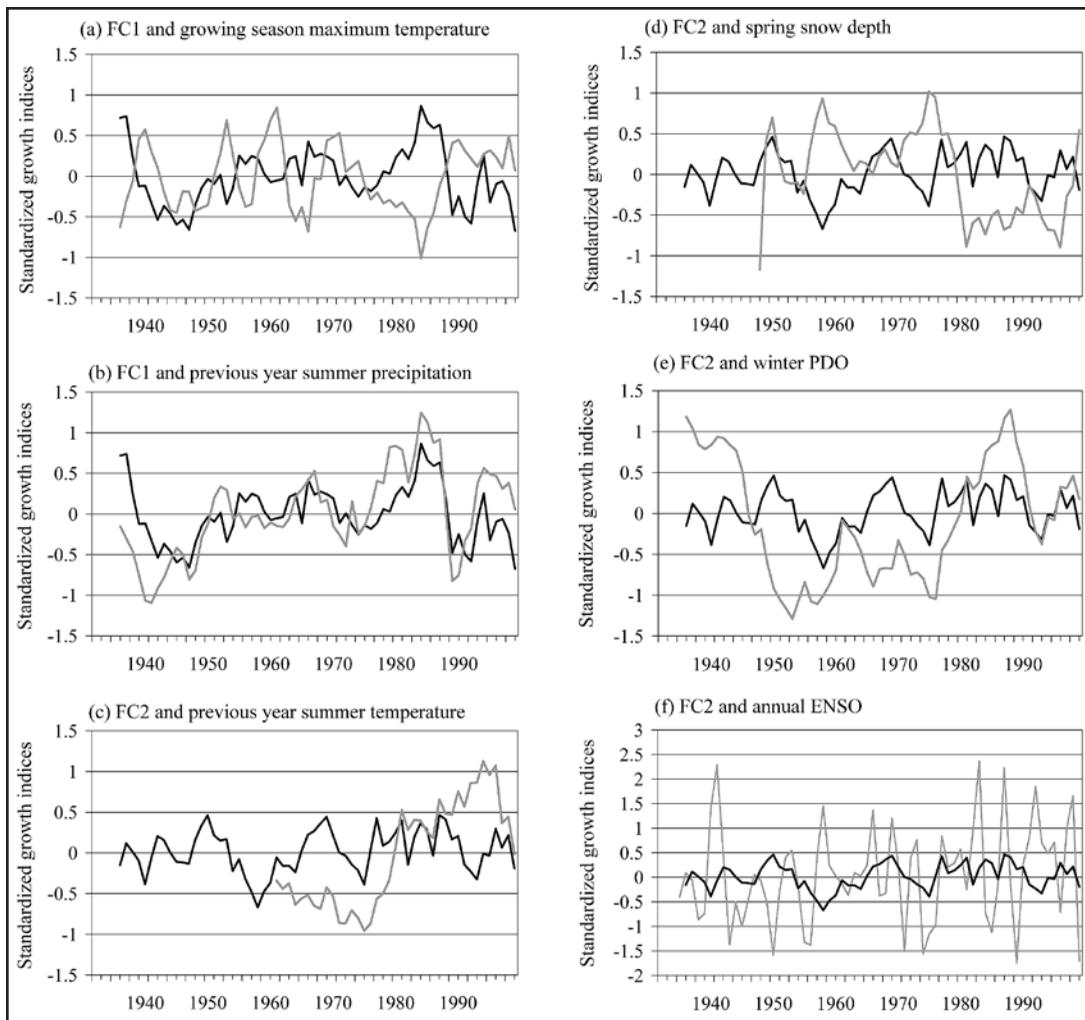


Figure 3. Temporal variability in lodgepole pine growth and key climate variables. Black lines represent 5-yr moving average of standardized growth indices and grey lines represent 5-yr moving averages of climate variables: (a) FC1 and Diablo station growing season maximum temperature; (b) FC1 and Diablo station previous year summer precipitation; (c) FC2 and Ross station previous year summer temperature; (d) FC2 and spring snow depth; (e) FC2 and winter Pacific Decadal Oscillation (PDO) index; and (f) FC2 and El Niño/Southern Oscillation (ENSO) index

Diablo station previous year summer precipitation is apparent (Figure 3a and 3b). Factor 2 is negatively correlated with previous year summer temperatures (Figure 3c) and spring snow depth (Figure 3d). A positive relationship can be seen between Factor 2 and winter PDO and annual ENSO indices (Figure 3e and 3f) (PDO and ENSO indices are correlated at 0.42, $P < 0.001$). High-elevation growth tends to be high when PDO index is positive and low when PDO index is negative.

Discussion

Based on our data and existing data in the literature, we conclude that much of the growth variation in lodgepole pine in the North Cascades National Park is driven by climatic variability at annual to decadal time scales. At low/mid-elevations, growth is affected by a combination of growing season temperature and precipitation (Table 4). These variables affect growth by influencing the site water balance and ultimately controlling the length of the summer drought period. At high eleva-

tions, growth is limited by length of the growing season, which is largely affected by previous year summer temperatures and total annual snow depth (Table 5). Higher temperatures will likely melt the snowpack earlier and warm soil temperatures more quickly, which can lengthen the growing season and lead to more growth.

The growth response to climate of lodgepole pine varies by elevation. Growth at low and mid-elevation responds positively to higher precipitation, but responds negatively to high precipitation at the highest elevations (Table 4 and Table 5). Moderate to strong correlations between radial growth and temperature and precipitation variables suggest that lodgepole pine growth is substantially affected by interannual variability in climate.

Low/mid-Elevation Growth

At low/mid-elevation sites (represented by Factor 1), a positive correlation with PDSI suggests that the radial growth of lodgepole pine is probably limited by low soil moisture since PDSI is essentially a surrogate for soil moisture. Factor 1 is above average when PDSI values are positive (wet years) and below average when PDSI values are negative (dry years). Similar results have been found between Douglas-fir and PDSI in the Pacific Northwest and the northern Rocky Mountains (Little et al. 1995, Watson and Luckman 2002, Nakawatase 2006).

Lodgepole pine growth is also reduced by high growing-season temperatures and low growing season precipitation. The amount of available soil moisture is probably limited by rocky, shallow soils at the study site, high growing-season temperatures, and low growing-season precipitation. Under these conditions, the rate of water loss from evapotranspiration exceeds the rate of water absorption by the roots, and trees undergo water stress (Larcher 2003).

Relations between other climate variables and growth at low/mid-elevations are consistent with the aforementioned drought stress phenomenon. For example, Factor 1 maintains a negative relationship with summer and growing season average temperatures (Table 4). Growth responds to changes in these temperatures in a similar way as it does to growing season maximum temperature. This relationship is not surprising because these climate variables are strongly collinear. Factor 1 also shows positive relations with previous year

summer precipitation and winter precipitation (Table 4). A positive relationship with winter precipitation and a negative relationship with total annual snow water equivalent seem inconsistent. However, snow water equivalent tends to be higher in years when winter and spring temperatures are higher, spring snowfall is high, and rain falls on snow. The result is earlier snowmelt and less available soil water during the summer.

High-Elevation Growth

Growth of lodgepole pine at high-elevation sites is limited by low temperature and deep spring snow. We believe that this relationship did not show up in high elevation transect C sites because high elevation transect A sites are higher in elevation (Table 1). Consequently, high elevation sites experience deeper snowpack, and represent the upper elevational limit of lodgepole pine on Ruby Mountain. Here, lodgepole pine experiences very short growing seasons, and like other species in subalpine environments, may be limited by frost, freezing winds, deep snowpack, and low soil temperatures (Hadley and Smith 1986, Körner 1998, 2003).

High spring snow depth also appears to limit the growth of lodgepole pine at high-elevation sites (Table 5). Deeper snow shortens the growing season by insulating the soil and maintaining soil temperatures under a threshold critical for growth (Coleman et al. 1992, Körner 1998).

Annual indices of ENSO and PDO are correlated with growth of high-elevation lodgepole pine. High-elevation growth displayed a positive relationship with annual ENSO (Nino3.4 SST deviations) and annual and winter PDO indices (Table 5). The most plausible explanation for these relations is that positive ENSO and PDO values typically translate into warm, dry climate in the Pacific Northwest. Higher than average temperatures that are associated with positive ENSO and PDO values reduce snowpack depth and raise soil temperatures, which extend growing season length and lead to above average growth.

Climate Change Effects

The results of this study suggest that lodgepole pine growth in a warmer climate will vary depending on elevation. Lodgepole pine at the highest elevations is limited by temperature and high snowpack depth (Table 5), so that warmer winters will not

only facilitate growth, but may cause the tree line of these sites to rise throughout much of the North Cascades. Both of these trends would increase forest productivity and carbon storage.

Warmer winters and less snow may exacerbate soil moisture deficits at lower elevations and likely reduce lodgepole pine growth (Table 4), especially if summer temperatures are higher and summer precipitation does not increase. The effects of longer summer droughts will be most pronounced on sites with rocky, well-drained soils, south and west facing aspects, and/or extreme slopes. Climate change is generally projected to increase the overall precipitation and it is likely that it will be in the form of rain and not snow during the winter; however, if the climate is wetter in the spring and summer, then there may be more soil moisture available for growth.

As climate changes, the species growth, regeneration, and dominance will shift. For example, lodgepole pine shares dominance with Douglas-fir at low/mid elevations and with subalpine fir at higher elevations. At low elevations, warmer, drier summers may translate into more favorable growing conditions for lodgepole pine than Douglas-fir (Hermann and Lavender 1990, Case and Peterson 2005), and at higher elevations increased temperatures and reduced snowpack may favor subalpine fir growth and regeneration as previously suggested.

The effects of a warmer climate on disturbances may have a greater affect on lodgepole pine distribution and productivity than direct climatic impacts on tree growth. Warmer, drier summers will increase the likelihood of fires (McKenzie et al. 2004), which could lead to changes in the distribution and abundance of plant species. While lodgepole pine is relatively intolerant to intense fires, regeneration immediately following fire is typically dominated by lodgepole pine because it can disperse large quantities of seeds from nearby trees and often has serotinous cones that open due to heating from fire (Lotan and Perry 1983). Warmer, drier summers may also lead to increased outbreaks of insects such as mountain pine beetle (*Dendroctonus ponderosae*) (Logan and Powell 2001).

Management Implications

Forest managers are presented with the increasingly difficult task of providing society with consumable and non-commodity goods while conserving

forest resources. If maximizing the productivity of particular sites is a management goal, then it is important to know how growth varies spatially and temporally across a management unit. Past tree growth-climate relations can be used to quantify the potential effects of future climate change on tree growth. Information about how lodgepole pine responds to climatic variability and change will allow managers to anticipate patterns of aboveground productivity and better understand how carbon dynamics may change over time. Because it is likely that the current trend of warming temperatures will continue into the future (IPCC 2001), many Pacific Northwest forested ecosystems, especially drier systems, may experience reduced soil moisture, increased water stress and altered disturbance regimes. Extended summer drought over decades could significantly affect which tree species are the most productive and abundant, thereby affecting carbon storage and future management success.

On lands managed for timber production, managers may want to consider potential shifts in species composition when planting trees. In a warmer climate, the abundance and productivity of Douglas-fir may decrease on sites with shallow, rocky soils, south and west facing aspects, and steep slopes. Therefore, managers may want to plant genotypes tolerant of a warmer climate or plant more drought-tolerant species such as lodgepole pine. For example, in the North Cascades, lodgepole pine is more dominant than Douglas-fir on high-elevation, drier sites and can surpass Douglas-fir in height growth and biomass accumulation (Larson 1972, Lotan and Critchfield 1990). In comparison, on more mesic sites, Douglas-fir is able to out-compete lodgepole pine for resources and therefore is the more dominant cover type (Larson 1972, Herman and Lavender 1990). There are also sites at intermediate elevations where Douglas-fir and lodgepole pine overlap in their dominance. At sites equally suitable for both species, a directional change in climate could significantly alter which species is more productive and more competitive.

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