

Fine-scale variability in growth–climate relationships of Douglas-fir, North Cascade Range, Washington

Michael J. Case and David L. Peterson

Abstract: Information about the sensitivity to climate of Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) is valuable because it will allow forest managers to maximize growth, better understand how carbon sequestration may change over time, and better model and predict future ecosystem responses to climatic change. We examined the effects of climatic variability on the growth of Douglas-fir along an elevational gradient in the North Cascade Range, Washington (USA), at annual timescales during the 20th century. Multivariate analysis and correlation analysis were used to identify climate–growth relationships. Mid-elevation chronologies were negatively correlated with growing season maximum temperature and positively correlated with growing season precipitation. In contrast, high-elevation chronologies were positively correlated with annual temperatures and negatively correlated with previous-year winter Pacific Decadal Oscillation index. Projected increases in summer temperatures will likely cause greater soil moisture stress in many forested ecosystems. The potential of extended summer drought periods over decades may significantly alter spatial patterns of productivity, thus impacting carbon storage. It is likely that the productivity of Douglas-fir in the Cascade Range will decrease at sites with shallow, excessively drained soils, south- and west-facing aspects, and steep slopes and will increase at high-elevation sites.

Résumé : L'information sur la sensibilité du douglas (*Pseudotsuga menziesii* (Mirb.) Franco) au climat est importante parce qu'elle permettra aux aménagistes forestiers de maximiser la croissance, de mieux comprendre comment la séquestration du carbone pourrait évoluer dans le temps et d'améliorer la modélisation et la prédiction des réactions futures des écosystèmes aux changements climatiques. Nous avons étudié les effets des variations climatiques sur la croissance du douglas le long d'un gradient altitudinal dans la partie nord de la chaîne des Cascades, dans l'état de Washington aux États-Unis, à des échelles de temps annuelles au cours du 20^e siècle. Des analyses multivariées et de corrélation ont été utilisées pour déterminer les relations entre le climat et la croissance. Les chronologies à moyenne altitude étaient négativement corrélées à la température maximale durant la saison de croissance et positivement corrélées aux précipitations durant la saison de croissance. À l'opposé, les chronologies à haute altitude étaient positivement corrélées aux températures annuelles et négativement corrélées à l'indice d'oscillation décennal du Pacifique de l'hiver précédent. L'augmentation projetée des températures estivales causera probablement des stress hydriques dans le sol de plusieurs écosystèmes forestiers. Le prolongement potentiel des périodes de sécheresse estivale pendant plusieurs décennies peut affecter significativement les patrons spatiaux de productivité et, par conséquent, avoir un impact sur le stockage du carbone. Il est probable que la productivité du douglas dans la chaîne des Cascades diminuera dans les stations à sols minces et drainage excessif, dans les stations exposées au sud et à l'ouest et sur les pentes fortes alors qu'elle augmentera dans les stations situées à haute altitude.

[Traduit par la Rédaction]

Introduction

Projected trends of carbon cycling and global warming suggest that by the year 2100, the concentration of atmospheric CO₂ will have more than doubled since 1850, and the Earth's average surface temperature will increase by 1.4 to 5.8 °C (IPCC 2001). Warming of the Earth's surface temperature, increased levels of CO₂, and changes in climatic

patterns may have substantial impacts on forested ecosystems (Watson et al. 1996; Flannigan et al. 1998; Li et al. 2000; Cayan et al. 2001). These climatic variations can affect the distribution, composition, and growth of forests, which, in turn, may influence ecosystem processes and functions, including forest productivity (Graumlich et al. 1989) and carbon sequestration. A wide range of studies has demonstrated that past climatic variability has affected tree spe-

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M.J. Case.^{1,2} Fire and Mountain Ecology Laboratory, College of Forest Resources, University of Washington, Box 352100, Seattle, WA 98195-2100, USA.

D.L. Peterson. USDA Forest Service, Pacific Northwest Research Station, 400 N 34th Street, Suite 201, Seattle, WA 98103, USA.

¹Corresponding author (e-mail: michael.case@wwfus.org).

²Present address: World Wildlife Fund, 1250 24th Street NW, Washington, DC 20037, USA.

cies distribution, forest growth, and forest productivity (e.g., Brubaker 1986; Graumlich 1991; Innes 1991; Peterson and Peterson 2001), and that species respond individually to changes in climatic regime (Brubaker 1986).

Warmer, wetter winters and warmer summers predicted for northwestern North America (Mote³) may result in significant alterations in forest productivity and ecosystem processes. For example, increasing temperatures over the last century have increased the productivity of some high-elevation forests in Washington State (USA) (Graumlich et al. 1989). Altered forest productivity at high elevations has also been documented by other studies examining the relationship between climate and tree growth for subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.) (Ettl and Peterson 1995a, 1995b; Peterson et al. 2002), mountain hemlock (*Tsuga mertensiana* (Bong.) Carrière) (Peterson and Peterson 2001), and other species across North America (McKenzie et al. 2001). High-elevation tree growth in the Pacific Northwest is typically limited by summer temperature and the amount of winter snowpack, though growth–climate relationships vary spatially by topographic position, soil properties, and species (Peterson and Peterson 1994, 2001; Ettl and Peterson 1995a; Watson and Luckman 2002). The understanding of climatic effects on tree growth can be improved by sampling a range of sites with both extreme and moderate environmental conditions. For example, species have different growth–climate relationships at separate elevations (Kienast et al. 1987; Buckley et al. 1997; Holman 2004; Zhang and Hebda 2004).

In the Pacific Northwest, there are two quasiperiodic atmospheric circulation patterns connected with the Pacific Ocean that influence the climate of this area, the El Niño – Southern Oscillation (ENSO) and Pacific Decadal Oscillation (PDO). ENSO has been identified as a key source of interannual climatic variations for the Pacific and has a periodicity of 2–7 years (Rasmussen and Wallace 1983). The 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 from the North Pacific. The PDO phase (warm–dry or cool–wet) is associated with variations in snowpack depth (lesser or greater) and thus tree growth at low- and high-elevation sites (Peterson and Peterson 2001; Peterson et al. 2002; Nakawatase 2003).

In this study, we used dendroecological methods to quantify the effects of climatic variability on Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) growth at annual timescales along an elevational gradient within the North Cascade Range, Washington. Douglas-fir is a common and productive species throughout the Cascade Range and a major component of Pacific Northwest forests, which store more carbon per unit area than any other forested area of North America (Turner et al. 1995). Although Douglas-fir growing on productive low-elevation sites has been assumed to be relatively insensitive to climate compared with subalpine species, Douglas-fir may be more sensitive to climatic variability on drier sites (Hessl and Peterson 2004). The combination of relatively high productivity and sensitivity to climate has implications for the management of carbon. Additionally, Douglas-fir forests managed on long rotations (100+ years) may serve as

substantial carbon sinks as global atmospheric concentrations of CO₂ continue to rise (Harmon et al. 1990; Harmon and Marks 2002). However, little information is available on the growth of Douglas-fir at moderate to high elevations (see Curtis et al. 1974; DeMars and Herman 1987), and growth information derived from lowland Douglas-fir forests is not applicable at higher elevations (Curtis et al. 1974). A detailed picture of how Douglas-fir responds to climatic variability at different spatial and temporal scales will improve management of growth and productivity of this species.

Study site

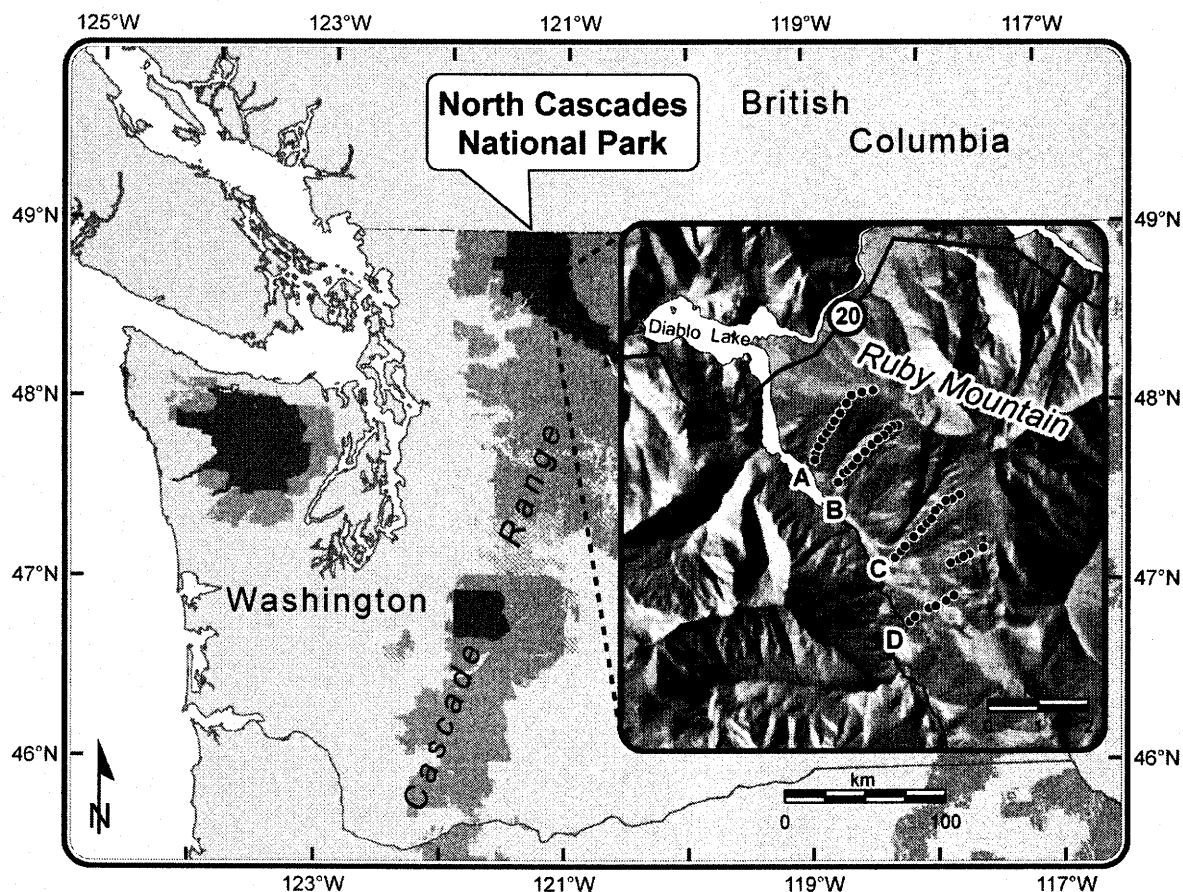
The study site is located on the southwest-facing slope of Ruby Mountain in Thunder Creek Watershed, North Cascades National Park, Washington (Fig. 1). The North Cascades span the transition between wet maritime weather associated with the Pacific Ocean and dry continental weather typical of eastern Washington. The geology of the study site was formed by oceanic, volcanic, tectonic, glacial, and erosional 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. The soil near the base of Ruby Mountain can be up to 150 cm deep and is classified as Typic Udutrands – Andic Haplorthods. Soil depth becomes shallower as elevation increases, and at the top of the study site the soil is about 50 cm deep and is classified as Typic Vitricryands – Andic Haplocryods (Briggs 2004).

Because of the geographic position of Ruby Mountain, orographic effects 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, Washington, 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 (Western Regional Climate Center, University of Nevada, Reno, Nevada). During the winter, low elevations typically experience a cool, wet maritime climate associated with the Pacific Ocean, and high elevations experience deep snowpacks. During the summer, low elevations experience relatively warm, dry weather, with little rainfall occurring between July and September, whereas higher elevations experience low temperatures and low rainfall. Winter precipitation typically falls as snow above 1000 m and is stored in snowpacks until it is released by the spring melt.

The varied topography and distinct precipitation gradient found throughout the North Cascades National Park (Larson 1972) strongly influence local variation in vegetation composition. Forest vegetation varies from maritime lowlands dominated by western hemlock (*Tsuga heterophylla* (Raf.) Sarg.), western redcedar (*Thuja plicata* Donn ex D. Don), and Douglas-fir; to subalpine sites dominated by subalpine fir, Alaska yellow cedar (*Chamaecyparis nootkatensis* (D. Don) Spach), and mountain hemlock; and dry inland sites domi-

³ P.W. Mote. Possible future climate. Chap. 5. In *Rhythms of change: an integrated assessment of climate impacts on the Pacific Northwest*. Edited by A.K. Snover, E.L. Miles, and the Climate Impacts Group. MIT Press, Cambridge, Mass. In review.

Fig. 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.



nated by Douglas-fir and lodgepole pine (*Pinus contorta* Dougl. var. *latifolia* Engelm.) (Agee and Kertis 1987).

Forests of Ruby Mountain have never been harvested, and therefore, recent disturbance history consists of discontinuously 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. However, evidence of fungal pathogens (root rot) and insect outbreaks (mountain pine beetle, *Dendroctonus ponderosae* Hopkins) has been found on individual trees or small groups of trees (M.J. Case, personal observation). Mean fire return intervals for this area are generally between 80 and 250 years (Agee 1993; Prichard 2003).

Methods

Data used for this analysis 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 to 1546 m (Fig. 1), thereby capturing the growth variability of Douglas-fir along its entire elevation range within the watershed. Riparian areas, perennial streams, avalanche chutes, and cliffs were avoided. Plots were 0.05 ha in area, corrected

for slope gradients. Dominant and codominant Douglas-fir 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).

After data collection was completed, tree cores were mounted, sanded, and visually cross-dated (Stokes and Smiley 1968). Of the 1125 cores originally collected, 86% (968) were cross-dated successfully, and of these 968, 501 were high-quality Douglas-fir cores suitable for dendroecological analysis (i.e., no rot or missing segments). 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-year 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 cross-dating errors by computing cross-correlations between individual series (Holmes 1999).

Douglas-fir growth chronologies were developed from the cross-dated ring-width series using the program CRONOL (Holmes 1999). Chronologies are composed of at least five trees per individual plot (the average number of cores per plot is 14) and were detrended. The cross-dated measurement series were detrended by fitting a model to the series (negative exponential or linear regression) and then stan-

standardized by dividing by the fitted values. This was done to remove 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 prewhitened by performing autoregressive modeling on the detrended ring-width measurement series to produce a residual chronology.

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 relationships and to guide exploratory analyses. After an in-depth analysis examining intersite correlations and individual plot growth patterns, we determined that coherent patterns of Douglas-fir growth could best be summarized by elevation groups. Because some plots had fewer than five cores, we combined them with the nearest plot that had the highest correlation between plot ring-width chronologies and most similar elevation and vegetation composition. While there is some crossover between the elevation groups, these categories best represent the growth pattern for Douglas-fir at that given elevation and have relatively similar means when compared. We were able to maintain the unique fine-scale variability found at particular elevations by aggregating individual plots into elevation groups, and this enabled us to increase our small sample size at some plots. Individual Douglas-fir plots were aggregated into one of four categories by transect: low elevation, mid elevation, high elevation, and very high elevation.

Descriptive statistics for each plot and species chronology were calculated, including mean sensitivity (Fritts 2001), intrasite 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 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 to determine how many factors to use in factor analysis (Insightful 2003). Time series of factor scores (factor chronologies) were extracted, and factor loadings were used to identify the relationships between the original ring-width chronologies and the factor chronologies.

Climatic data

Growth-climate relationships were assessed by comparing species-specific plot chronologies with annual and seasonal climatic variables. These climatic variables were obtained from two local climate stations, Ross Dam (1961–1999) and Diablo Dam (1934–1999). Both local climate stations are within 5 km of the study site. Divisional climatic 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 climatic data are more strongly correlated with tree growth at the study site than divisional

climatic data. We examined annual, seasonal, and monthly temperature and precipitation variables for both Ross and Diablo Dam climate stations for the current year of tree growth, the previous year of tree growth, and two prior years of tree growth (lag 2).

Snowpack data were obtained from the Thunder Basin Snowpack Telemetry site located within the Thunder Creek Watershed (Natural Resources Conservation Service 2003). This station has been collecting data from 1948 to the present. Annual, monthly, and spring snowpack depths and annual snow water equivalent were used for correlations with aggregated plot chronologies and factor chronologies. Snowpack data from the previous year and previous 2 years were also examined for significant correlations.

Palmer Drought Severity Index (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 both annual temperature and rainfall to quantify a measure of meteorological drought and is often considered to be a surrogate for soil moisture. Positive values 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 SST anomalies) 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 warmer winter temperatures, lower precipitation, and decreased snowpack depth; negative values typically represent cooler temperatures, more precipitation, and potentially greater snowpack depth (Mantua et al. 1997). Similarly, positive ENSO values (El Niño events) represent warmer than average temperatures and less precipitation, whereas negative ENSO values (La Niña events) represent cooler, wetter weather (Rasmussen and Wallace 1983). PDO and ENSO indices are both positively correlated with temperature and negatively correlated with precipitation near the study area (both Diablo and Ross climate stations), but neither is significantly correlated with the snowpack data used in this study.

Growth-climate relationships

Pearson product-moment correlation coefficients (r) were calculated between factor chronologies and climatic variables to assess which variables are significantly related to tree growth ($\alpha < 0.05$). Climatic variables used in this study include mean monthly temperature and total monthly precipitation from 2 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 climatic variables were used for correlations and were based on known seasonal weather patterns and previous studies. Other climatic variables include total annual snowpack depth, total annual snow water equivalent, spring snowpack depth, and monthly snowpack depth. PDO and ENSO climatic variables were also examined and include current-year and previous-year annual indices, current-year

(November–March) and previous-year winter indices, current-year (July–September) and previous-year summer indices, and current-year (September–October) and previous-year fall indices.

Multiple regression models of annual growth were created using multiple climatic variables that exhibited the strongest correlations with tree growth. Models were created with a forward stepwise procedure using factor scores and climatic data. Models were simplified to maximize the amount of variability that could be explained while minimizing the number of variables used. Autocorrelation was removed from both the growth chronologies and the climatic variables before regression models were created (Insightful 2003). These models were used as a diagnostic approach to explain the variability found within the factor chronologies and not to attempt to predict future variability.

To examine the relationship between Douglas-fir growth response and annual to decadal variability in the climatic variables graphically, 5-year running averages were calculated for factor chronologies and key climatic variables. Moving averages were used for visual comparisons only, and statistical analyses were not performed with these averages, but only with the detrended chronologies.

Results

The number of Douglas-fir trees varied by plot. However, Douglas-fir was present in all four transects (A–D) and within 41 of the 47 plots (absent only from the highest elevation plots). Plots with fewer than five cores were combined with the nearest, most similar plots. Similarity of plots was based on correlations between plot ring-width chronologies and similarity in elevation and vegetation composition. Nine plots were combined resulting in 33 site growth chronologies (Table 1). The number of cores per plot averaged 14.

Descriptive statistics were examined for individual plots (Table 1). While many of the chronologies are over 150 years old, some are younger (65 years old), and all chronologies were shortened to allow for unbiased correlations. Mean intrasite correlations of individual ring-width chronologies were computed using COFECHA, which analyzed 50-year-long segments, and they range from 0.16 to 0.65, with an overall mean for all correlations of 0.51 ± 0.11 (± 1 SD). Mean sensitivities were also calculated by COFECHA for each core and were averaged by individual plot and range from 0.18 to 0.26, with an overall mean of 0.22 ± 0.01 . Autoregressive modeling was conducted on individual cores and is summarized by plot chronologies. First-order autoregressive models were sufficient to account for autocorrelation in 71% of the plot chronologies, second-order models, in 21% of plot chronologies, and third- and fourth-order models combined, in 8% of plot chronologies.

Multivariate analysis

Principal component analysis determined that two principal components explain 81% of the variance in the 13 aggregated site chronologies. Each additional principal component accounts for less than 5% of additional variance (Table 2), therefore we decided to use two factors in the factor analysis. This criterion has been used in similar dendroecological studies (Peterson and Peterson 1994, 2001; Peterson et al.

2002). Factor analysis was used to generate factor chronologies explaining 25%–52% of the total variance within and among aggregated 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 1935–1999 show a strong relationship between low- and mid-elevation aggregated plots and the first factor chronology, and a moderate relationship between high- and very-high-elevation aggregated plots and the second factor chronology (Table 3). Because of these distinct spatial patterns, we refer to the first factor chronology (factor 1) as “low–mid elevation FC” and the second factor chronology (factor 2) as “high-elevation FC”. The low–mid elevation FC has a brief period of above-average growth during the mid to late 1940s, 1950s, 1960s, and 1980s, and periods of below-average growth during the 1970s and 1990s (Fig. 2). In comparison, the high-elevation FC has brief periods of above-average growth during the 1940s, 1960s, 1970s, and 1990s, and periods of below-average growth during the early 1960s, 1970s and 1980s (Fig. 2).

Growth–climate correlations

Douglas-fir growth at mid elevations (represented by factor 1, Table 4) is negatively correlated with growing season maximum temperature and positively correlated with growing season precipitation. Radial growth was highest during years of relatively low mean temperatures and high precipitation. This relationship is supported by the correlations between low–mid elevation FC and seasonal climatic variables, which show a consistent pattern of negative correlations with spring, summer, and growing season average temperatures and positive correlations with late-winter temperatures and spring and summer precipitation (Table 4). Other significant growth–climate correlations for the low–mid elevation FC include a positive correlation with previous-year summer precipitation, PDSI, and previous-year spring ENSO values (Table 4). These relationships are consistent with the sensitivity of low- to mid-elevation tree growth to growing season temperature and precipitation. A diagnostic multiple regression model including growing season temperature and precipitation explains 41% of the variance within the low–mid elevation FC (Table 5).

Annual temperatures correlate best with the high-elevation FC (represented by factor 2, Table 4). Radial growth was highest during years of relatively warm temperatures and lowest during cool years. High-elevation growth also correlates positively with winter, spring, and summer temperatures (Table 4, Fig. 3). More specifically, positive correlations are found with annual temperatures, growing season average and minimum temperature, spring temperature, previous-year fall temperature, and summer temperature from the previous 2 years (Table 4). High-elevation growth is negatively correlated with previous-year winter through summer temperatures (Fig. 3). The pattern of monthly growth and precipitation correlations also show that high-elevation growth is negatively affected by late-winter through spring precipitation (Fig. 3). Growth is positively correlated with annual, winter, and previous-year fall ENSO indices and previous year total annual snow

Table 1. Site descriptions and descriptive statistics for Douglas-fir individual plots.

Site name	Plot	Elevation (m)	<i>n</i> ^a	Intrasite correlation and length ^b	Mean sensitivity	% AR model order 1 ^c	% AR model order 2 ^c	% AR model order 3 ^c	% AR model order 4 ^c
A mid	A3	682	15	0.59 (81)	0.19	87	7	7	
	A4	759	15	0.64 (77)	0.21	100			
	A6	949	18	0.57 (82)	0.21	83	11	6	
A high	A7	1064	19	0.65 (106)	0.26	58	37	5	
	A8,9,10 ^d	1168–1358	8	0.42 (103)	0.23	75	25		
B low	B1	476	20	0.65 (33)	0.24	90	10		
	B2	483	16	0.52 (62)	0.22	88	13		
	B3	677	17	0.60 (74)	0.18	82	18		
B mid	B5	881	11	0.49 (65)	0.20	73	27		
	B6	962	11	0.55 (69)	0.20	73	27		
	B7	1043	18	0.50 (47)	0.22	89		11	
	B8	1133	16	0.51 (70)	0.20	88	6	6	
B high	B9	1228	22	0.57 (53)	0.23	64	36		
	B10	1325	13	0.38 (71)	0.20	69	15	15	
B very high	B11	1398	8	0.44 (103)	0.23	75	25		
C low	C1	465	14	0.47 (83)	0.25	79	21		
	C2	600	15	0.54 (95)	0.23	80	20		
	C3,4 ^d	619–708	22	0.45 (90)	0.24	64	32	5	
C mid	C5	872	16	0.58 (95)	0.24	75	19	6	
	C6	954	10	0.40 (64)	0.23	80	10	10	
	C7	1017	10	0.55 (74)	0.21	100			
	C8	1036	10	0.56 (92)	0.21	50	30	20	
C high	C9	1222	18	0.57 (58)	0.23	83	17		
	C10	1316	10	0.50 (111)	0.20	80	20		
	C11	1450	8	0.62 (106)	0.22	75	25		
D low	D1	504	7	0.36 (90)	0.22	57	43		
	D2,3 ^d	589–696	17	0.54 (107)	0.20	76	18	6	
	D4	732	13	0.52 (83)	0.26	69	31		
D mid	D5	863	9	0.16 (137)	0.22	78	22		
	D6,7 ^d	973–1061	16	0.53 (143)	0.22	50	25	19	6
D high	D8	1166	19	0.54 (123)	0.21	84	16		
	D9	1228	15	0.48 (117)	0.21	60	33		7
D very high	D11	1425	5	0.24 (119)	0.22	60	20	20	

^aSample size (*n*) is the number of cores.^bMean length of series (years) is given in parentheses. All correlation are significant at $p < 0.001$, except for plot D5.^cPercentages of the total number of chronologies with autoregressive model order (1–4) used in statistical analysis.^dCombined plots.

depth and negatively correlated with previous-year winter ENSO and previous-year PDO (Table 4). A multiple regression model including annual temperature and previous-year winter PDO explains 55% of the variance associated with high-elevation growth (Table 5).

After plotting 5-year running averages of the FCs and key climatic variables together (Fig. 4), the low-frequency relationships between the low–mid elevation FC and Diablo station growing season maximum temperature and between low–mid elevation FC and Ross station growing season precipitation become noticeable (Figs. 4a and 4b). A positive relationship is apparent between high-elevation growth and Ross station annual temperatures (Fig. 4d). These results are consistent with the aforementioned growth–climate correlations. A negative relationship can also be seen between high-elevation FC and previous-year winter PDO and previous-year winter ENSO indices (Figs. 4e and 4f) (PDO and ENSO indices are correlated at 0.42, $p < 0.001$). High-elevation

growth tends to be low when PDO indices are above average and high during below-average PDO phases.

Discussion

The growth response of Douglas-fir to climate varies by elevation. Differences in growth patterns found in this study likely reflect the differences in tree responses to climatic variability between low to mid elevations and high elevations. Relatively strong correlations between radial growth and temperature and precipitation variables suggest that tree growth is affected in large part by interannual climatic variability.

Low- to mid-elevation growth

At low to mid elevations (495–1133 m), the radial growth of Douglas-fir is limited by low growing season precipitation and high growing season temperatures. The amount of

Table 2. Principal components analysis (A) and factor analysis (B) for 33 Douglas-fir chronologies for the period 1935–1999.

(A) Principal components analysis.			
PC	Eigenvalue	Variance (%)	Cumulative variance (%)
1	3.1	72.0	72.0
2	1.1	9.0	81.0
3	0.8	5.0	86.0
4	0.7	3.0	89.0
5	0.6	3.0	92.0
6	0.5	2.0	94.0
7	0.5	2.0	96.0
8	0.4	1.0	97.0
9	0.3	1.0	98.0
10	0.3	1.0	99.0

(B) Factor analysis.			
Factor	Eigenvalue	Variance (%)	Cumulative variance (%)
1	6.7	52.0	52.0
2	3.3	25.0	77.0

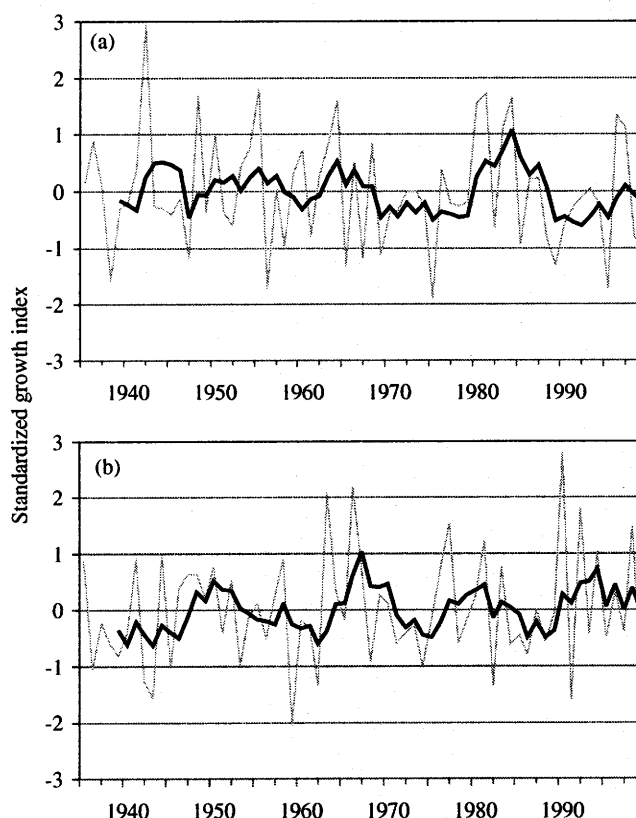
Table 3. Factor loadings for aggregated Douglas-fir chronologies.

Chronology	Factor 1	Factor 2
B low	0.88	0.21
C low	0.94	0.12
D low	0.88	0.17
A mid	0.86	0.28
B mid	0.78	0.49
C mid	0.89	0.36
D mid	0.77	0.37
A high	0.72	0.53
B high	0.44	0.63
B very high	0.52	0.59
C high	0.58	0.76
D high	0.78	0.41
D very high	0.28	0.68

Note: Factor 1 best represents "low" and "mid" plots, and factor 2 best represent "high" and "very high" plots.

available soil moisture is probably limited because of shallow soils at the study site, high temperatures during the growing season, and low growing season precipitation. Under these conditions, the day-to-day accumulative water loss likely exceeds the replenishment of water via absorption by the roots, and trees undergo progressive water stress (Larcher 2003).

Douglas-fir is likely affected by varying degrees of water stress at low- to mid-elevation sites at the study location. Water deficiency and stress are known to fluctuate throughout the year in response to precipitation and evaporation rates (Helms 1965; Phillips et al. 2003; Stout and Sala 2003), with prolonged periods of water stress drastically reducing a tree's ability to photosynthesize (Kozlowski and Pallardy 1997). A reduction in photosynthesis will lead to less food reserves (Lassoie 1982) and below-average tree growth (Fritts 1966; Zaerr 1971; Robertson et al. 1990). Other dendroecological

Fig. 2. Factor score time series plots showing temporal variability in Douglas-fir growth. Thin lines represent annual values and thick lines represent smoothed 5-year running averages.

studies in the Pacific Northwest also identified the negative effects of water stress on tree growth (Peterson and Peterson 1994, 2001; Little et al. 1995; Nakawatase 2003).

Reduced radial growth may also be exacerbated by the transfer of existing photosynthate to the root system in an effort to increase root absorption area (Waring and Pitman 1985; Waring 1991). Because stem growth is considered to be a rather low priority in the overall hierarchy of photosynthate allocation for trees, it is believed that reduced stem growth is likely to be a sensitive indicator of stress (Hanson and Weltzin 2000).

Relationships between other climatic variables and growth at low to mid elevations are consistent with the aforementioned drought stress phenomenon. For example, the low-mid elevation factor chronology maintains a negative relationship with spring, summer, and growing season average temperatures. Growth responds to changes in these temperatures in a similar way as it does to growing season maximum temperature. This is not surprising because these climatic variables are strongly correlated with growing season maximum temperatures, and all represent temperature during the growing season. Low- to mid-elevation growth also is positively correlated with PDSI. Similar results have been found between Douglas-fir and PDSI at other locations (Little et al. 1995; Watson and Luckman 2002; Nakawatase 2003). PDSI

Table 4. Correlation coefficients (*r*) between temporal variability in factor chronologies and seasonal and monthly climatic variables from Diablo Dam and Ross Dam climate stations and other climatic data sources.

Climate variable	Factor 1			Factor 2		
	Diablo (<i>n</i> = 65)	Ross (<i>n</i> = 39)	Other (<i>n</i> = 65)	Diablo (<i>n</i> = 65)	Ross (<i>n</i> = 39)	Other (<i>n</i> = 65)
Growing season max. temp. (May–Sept.)	−0.53**	−0.46*	—	—	—	—
Growing season max. temp., prior year (May–Sept.)	—	—	—	−0.29*	−0.48*	—
Growing season average temp. (May–Sept.)	−0.41**	−0.39*	—	0.26*	0.38*	—
Growing season average temp., prior year (May–Sept.)	—	—	—	−0.32*	−0.43*	—
Growing season min. temp. (May–Sept.)	—	—	—	0.32*	0.47*	—
Annual temp. (Oct.–Sept.)	—	—	—	0.28*	0.60**	—
Annual temp., prior year (Oct.–Sept.)	—	—	—	−0.31*	−0.43*	—
Spring temp. (Apr.–June)	−0.36*	—	—	—	—	—
Spring temp. (Apr.–May)	—	—	—	0.29*	0.42*	—
Summer temp. (June–Aug.)	−0.25*	−0.35*	—	—	—	—
Summer temp., prior year (July–Aug.)	—	—	—	−0.54**	−0.55**	—
Summer temp., prior 2 years (July–Aug.)	—	—	—	0.26*	—	—
Fall temp., prior year (Oct.–Nov.)	—	—	—	—	0.37*	—
Growing season precip. (May–Sept.)	0.38*	0.55**	—	—	—	—
Summer precip., prior year (July–Aug.)	0.28*	—	—	—	—	—
PDSI ^a grid point 8, 199.5°W, 49°N, 1895–1995	—	—	0.35*	—	—	—
PDSI ^a grid point 1, 122.5°W, 49°N, 1895–1995	—	—	0.32*	—	—	—
Spring ENSO ^b , prior year (Apr.–May)	—	—	0.29*	—	—	—
Annual ENSO ^b (Oct.–Sept.)	—	—	—	—	—	0.30*
Winter ENSO ^b (Nov.–May)	—	—	—	—	—	0.32*
Winter ENSO ^b , prior year (Nov.–Mar.)	—	—	—	—	—	−0.35*
Fall ENSO ^b , prior year (Sept.–Oct.)	—	—	—	—	—	0.29*
Winter PDO ^c , prior year (Nov.–Mar.)	—	—	—	—	—	−0.40*
Total annual snow depth, prior year (Nov.–June)	—	—	—	—	—	0.28** ^d

Note: **, significant at $p < 0.001$; *, significant at $p < 0.05$.

^aPalmer Drought Severity Index.

^bEl Niño – Southern Oscillation.

^cPacific Decadal Oscillation

^dSample size is 52.

Table 5. Diagnostic multiple regression models of growth–climate relationships for low–mid elevation and high-elevation Douglas-fir factor chronologies.

Factor	<i>R</i> ²	Predictor variable	Coefficient	<i>P</i>
Low–mid elevation	0.41	Growing season max. temp. (May–Sept.) Diablo Dam climate station	−0.37	0.015
		Growing season precip. (May–Sept.) Ross Dam climate station	0.39	0.011
High elevation	0.55	Annual temp. (Oct.–Sept.) Ross Dam climate station	0.56	0.000
		Winter PDO, prior year (Nov.–Mar.)	−0.43	0.001

Note: Growing season temperature and precipitation explains 41% of the variance within the low–mid elevation factor chronology, and annual temperature and previous-year winter Pacific Decadal Oscillation (PDO) explain 55% of the variance associated with the high-elevation factor chronology.

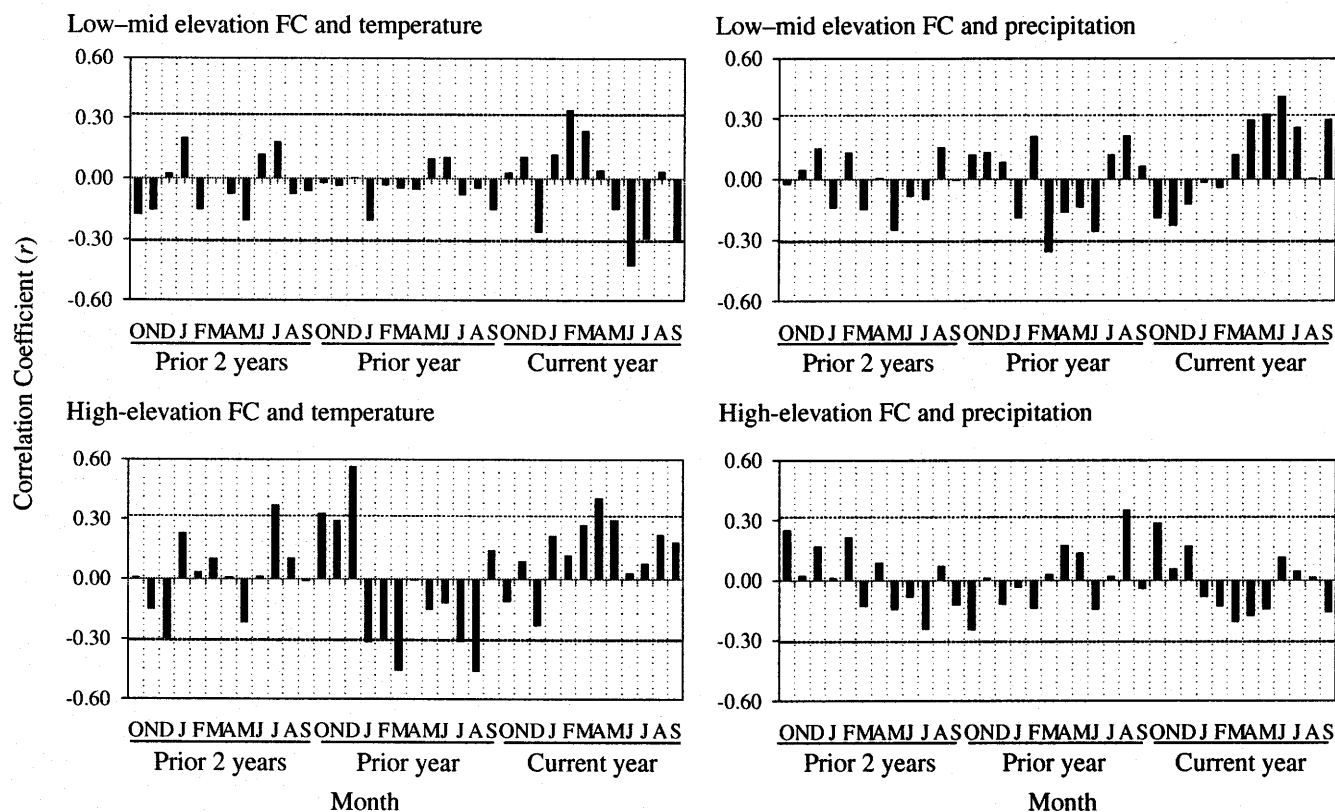
is a surrogate for mean soil moisture (a combination of soil moisture supply and demand, which integrates temperature, precipitation, soil moisture storage, and evapotranspiration). Low- to mid-elevation growth is above average when PDSI values are positive (wet years) and below average when PDSI values are negative (dry years).

The relationship between previous-year growth and climatic variables is most likely explained by (1) low soil moisture and (or) (2) a short growing season during the previous year of stem growth. For example, if in the previous year of growth Douglas-fir experiences high temperatures and low soil moisture supply, then respiration rates are high, photosynthate production and storage are low, and root growth is

likely reduced (Salo 1974; Lassoie and Salo 1981). However, the reduction in growth and low photosynthate production are not fully expressed until the current year of growth when the tree must compensate for the reduction in root growth, leading to a reduction in stem growth. Alternatively, a short growing season in the previous year can limit the amount of carbohydrates that are allocated to the production of new primordia, which will expand the next spring, and lead to reduced stem growth during the current year (Lassoie 1982).

Previous-year spring ENSO values (Nino3.4 SST anomalies) have a positive relationship with low- to mid-elevation growth. Although the addition of this climatic variable to the

Fig. 3. Correlations (r) between factor chronologies and mean monthly temperature and total monthly precipitation variables for 24 months (two hydrologic years, October–September) prior to the end of the current growth year. Climate variables are from Ross Dam climate station for the period 1961–1999. Statistical threshold values for significance of individual correlations are $r = 0.32$ ($p < 0.05$).



regression model did not measurably boost the amount of explained variability, it may explain important annual trends that are visible when examining the time series of the low-mid elevation chronology (Fig. 4c). Positive spring ENSO values indicate above-average spring temperatures that may create a longer growing season. This would enable trees to create and store additional carbohydrates for the following season, which would give trees a head start during the beginning of the growing season. Ultimately, this will lead to increased growth during the current year.

High-elevation growth

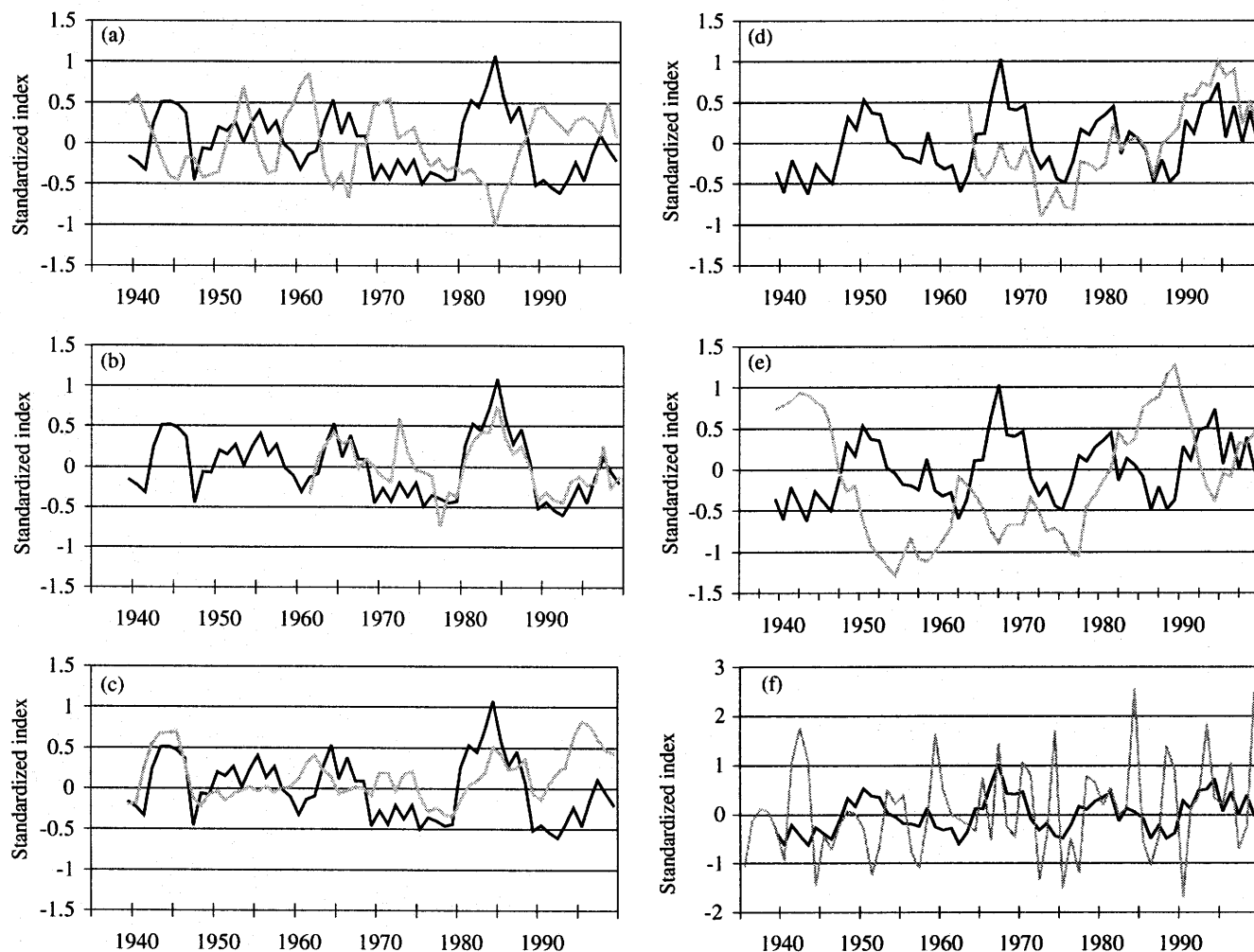
Growth of Douglas-fir at high-elevation sites (1036–1450 m) is limited by annual and growing season temperatures. High current-year temperatures lead to above-average growth, whereas low temperatures limit growth. However, it should be noted that short growing seasons, frost, freezing winds, low soil temperatures, and deep snowpacks limit the growth of trees at high elevations (Hadley and Smith 1986; Körner 1998, 2003). Although not much research has looked at the growth of Douglas-fir at high elevations, Douglas-fir is likely at the limit of its distribution at these sites, and length of the growing season and soil temperatures are important to tree growth (Hansen-Bristow 1986). Warm temperatures and early snowmelt can lengthen the growing season, warm soil temperatures,

and lead to increased photosynthesis and cambial growth (Coleman et al. 1992; Körner 1998).

However, high stem growth without increased carbohydrate storage during the growing season could lead to reduced growth in the following year (Colenutt and Luckman 1991; Graumlich 1991; Ettl and Peterson 1995a). This is supported by the positive relationship of high-elevation tree growth and fall temperatures and the negative relationship with previous-year summer temperatures, annual temperatures, growing season maximum temperatures, and growing season average temperatures (Table 4). A long growing season with high temperatures in the previous year could stimulate stem growth, resulting in less carbon being available for allocation to the roots and food reserves for the following year. Additionally, an exceptionally warm, dry summer may substantially increase water stress, producing high maintenance respiration rates and reducing photosynthesis, similar to the response that low- to mid-elevation Douglas-fir plots experience (Lassoie 1982; Larcher 2003).

Annual indices of ENSO and PDO are correlated with growth of high-elevation Douglas-fir. High-elevation growth displayed a positive relationship with winter and annual ENSO values during the current growth year and a positive relationship with current-year fall ENSO values and previous-year total annual snow depth. Accordingly, high-elevation growth

Fig. 4. Temporal variability in Douglas-fir growth and key climate variables. Black lines represent 5-year moving average of standardized growth indices and grey lines represent 5-year moving averages of climate variables: (a) low-mid elevation factor chronology (FC) and Diablo Dam climate station growing season mean maximum temperatures, (b) low-mid elevation FC and Ross Dam climate station growing season total precipitation, (c) low-mid elevation FC and previous-year spring El Niño – Southern Oscillation (ENSO), (d) high-elevation FC and Ross Dam climate station mean annual temperature, (e) high-elevation FC and previous-year winter Pacific Decadal Oscillation, and (f) high-elevation FC and previous-year winter ENSO.



had a negative relationship with previous-year winter ENSO values and previous-year winter PDO values. The most plausible explanation for these relationships is that positive ENSO and PDO values typically translate into warm, dry climate in the Pacific Northwest. The warmer temperatures associated with positive winter ENSO and PDO values lengthen the growing season by reducing snowpack depth and warming the soil. An extended growing season during the previous year of growth may reduce the amount of carbohydrates allocated for roots and carbohydrate reserves for the current year and therefore reduce the current-year growth (Lassoie 1982; Robertson et al. 1990; Larcher 2003).

Climatic-change effects

Temperature and precipitation in the Pacific Northwest have increased more than global averages have, a trend likely

to continue into the future (Mote 2003). Although there is some uncertainty about the exact changes in precipitation, summers will likely be warmer and drier, and winters warmer and wetter (based on climate system model output) (Mote 2003; Mote³). A warmer, wetter winter will cause more precipitation to fall as rain, a decrease in snowpack depth, and a longer growing season.

Because Douglas-fir at high elevations is limited by temperature, a warmer climate may allow the species to grow faster, as well as potentially expand its range in the North Cascades (Rocheffort et al. 1994; Zolbrod and Peterson 1999). However, because most photosynthesis and growth occurs during the summer months, and warmer, drier summers will lead to longer summer drought periods, it is likely that the growth of low- to mid-elevation Douglas-fir will decrease on dry sites. The effects of a longer summer dry period will be

most pronounced on sites with shallow, well-drained soils, south- and west-facing aspects, and extreme slopes. An increase in summer temperature without an increase in summer precipitation will likely decrease the productivity of Douglas-fir at low to mid elevations.

Although Douglas-fir is able to grow in a variety of environmental conditions, this study suggests that growth in a warmer climate will vary depending on elevation. At low to mid elevations, productivity may decrease on some sites, whereas at high elevations, Douglas-fir productivity may increase. Over time, a reduction in growth, and perhaps of regeneration in some areas, may reduce the dominance of Douglas-fir where other species are less limited by an altered climate (Isaac 1943; Hermann and Lavender 1968, 1990; Schneider et al. 1998). For example, at the study site, Douglas-fir shares dominance with lodgepole pine at mid to high elevations. At these elevations, warmer, drier summers may translate into more favorable growing conditions for lodgepole pine growth and regeneration (Larson 1972; Lotan and Critchfield 1990; M.J. Case and D.L. Peterson, submitted manuscript).

Conclusions

Douglas-fir growth in the North Cascade Range varies significantly by elevation and at annual and decadal time-scales. Much of this growth variation is driven by climatic variability. At low to mid elevations, growth is affected by a combination of growing season temperature and precipitation. These variables affect growth by influencing the site water balance and ultimately controlling the length of the summer drought period. As elevation increases, temperature becomes more important in regulating growth. At high elevations, growth is largely affected by annual temperatures. Warming temperatures due to human-induced increases of greenhouse gases will likely melt the snowpack earlier and warm soil temperatures more quickly, which can lengthen the growing season and lead to increased growth and changes in species composition.

Management implications

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. Current growth-climate relationships can be used to quantify the potential effects of a warmer climate on tree growth. Information about how Douglas-fir responds to climatic variability will allow managers to anticipate patterns of aboveground productivity and better understand how carbon sequestration may change over time.

If summer temperature continues to increase as expected, reduced soil moisture may increase stress in some Pacific Northwest forested ecosystems, especially in drier systems. Extended summer drought periods over decades may significantly affect which tree species are the most productive and abundant, thereby affecting carbon storage. For example, on some sites in the North Cascade Range, Douglas-fir is able to outcompete lodgepole pine for resources and therefore is the more dominant cover type (Larson 1972; Lotan and Critchfield 1990; M.J. Case and D.L. Peterson, submitted manuscript). In comparison, lodgepole pine is more dominant than Douglas-

fir on higher-elevation sites with shallow soils and surpasses Douglas-fir in height growth and biomass accumulation (Larson 1972; Hermann and Lavender 1990). On some sites at intermediate elevations, Douglas-fir and lodgepole pine overlap in their dominance. At these sites, equally suitable for both species, a directional change in climate could significantly alter which species is more productive.

On lands managed for timber production, managers may want to consider how site compatibility for tree species could change in a warmer climate. Growth of Douglas-fir would likely decrease on sites with shallow, rocky soils, south- and west-facing aspects, and steep slopes. Therefore, thinning Douglas-fir to increase individual tree vigor, planting Douglas-fir genotypes tolerant of a warmer climate, or planting more drought-tolerant species such as lodgepole pine may be potential management options.

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