Spatial variability in forest growth – climate relationships in the Olympic Mountains, Washington

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Abstract: For many Pacific Northwest forests, little is known about the spatial and temporal variability in tree growth – climate relationships, yet it is this information that is needed to predict how forests will respond to future climatic change. We studied the effects of climatic variability on forest growth at 74 plots in the western and northeastern Olympic Mountains. Basal area increment time series were developed for each plot, and Pearson's correlation analysis and factor analysis were used to quantify growth–climate relationships. Forest growth in the Olympic Mountains responds to climatic variability as a function of mean climate and elevation. Low summer moisture limits growth across all elevations in the dry northeastern Olympics. Growth at low elevations in the wet western Olympics is associated with phases of the Pacific Decadal Oscillation and with summer temperature. Heavy winter snowpack limits growth at high elevations in the western Olympics. In the warmer greenhouse climate predicted for the Olympic Mountains, productivity at high elevations of the western Olympics will likely increase, whereas productivity at high elevations in the northeastern region and potentially in low elevations of the western region will likely decrease. This information can be used to develop adaptive management strategies to prepare for the effects of future climate on these forests. Because growth–climate relationships on the Olympic Peninsula vary at relatively small spatial scales, those relationships may assist modeling and other efforts to provide more accurate predictions at local to regional scales.

Résumé : La variabilité spatiale et temporelle des relations entre la croissance des arbres et le climat sont largement inconnues pour plusieurs forêts de la région du nord-ouest du Pacifique, même si cette information est nécessaire pour prédire la réaction des forêts aux futurs changements climatiques. Les auteurs ont étudié les effets des variations climatiques sur la croissance de la forêt dans 74 placettes échantillons situées dans les parties ouest et nord-est des Montagnes Olympic. Des séries chronologiques d'accroissement en surface terrière ont été produites pour chaque placette et l'analyse de corrélation de Pearson ainsi que l'analyse factorielle ont été utilisées pour quantifier les relations entre la croissance et le climat. La croissance des forêts des Montagnes Olympic réagit différemment aux variations climatiques selon le climat moyen et l'altitude. Une faible humidité estivale limite la croissance à toutes les altitudes de la région sèche du nord-est des Montagnes Olympic. La croissance à faible altitude de la région humide de l'ouest des Montagnes Olympic est associée aux phases d'oscillation décennales du Pacifique et à la température estivale. Un épais couvert de neige limite la croissance à haute altitude dans la partie ouest des Montagnes Olympic. Avec le climat plus chaud prédit pour les Montagnes Olympic en raison de l'effet de serre, la productivité à haute altitude dans sa partie ouest augmentera probablement alors qu'elle devrait diminuer à haute altitude dans la région nord-est et possiblement à faible altitude dans la région ouest. Cette information peut être utilisée pour mettre au point des stratégies d'aménagement adaptatif dans le but de se préparer aux effets du climat futur sur ces forêts. Parce que les relations entre la croissance et le climat de la presqu'île Olympic varient à des échelles spatiales relativement grandes, ces relations peuvent être utiles pour la modélisation et les autres efforts visant à fournir des prédictions plus précises à des échelles variant de locale à régionale.

[Traduit par la Rédaction]

Introduction

The climate of the Pacific Northwest has become warmer and wetter (especially in winter) over the past century, and these trends are likely to continue in the future (JISAO 1999). A projected doubling of atmospheric CO_2 concentrations will likely cause annual temperatures in the Pacific Northwest to increase by 1.5–2.5 °C by the 2050s (Mote 2003). Precipita-

tion is likely to increase by 5%, primarily during the winter months (Johns et al. 1997; Boer et al. 1999).

How will forests respond to a changing climate? Biogeographic models and forest gap models predict widespread species migration under future climatic scenarios (Lenihan and Neilson 1995; Zolbrod and Peterson 1999). Such predictions provide insight into how species distribution and abundance may change given certain assumptions about species

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responses. For example, in forest gap models, species are assumed to respond to climate as a function of species-specific temperature limits. Factors not considered in these models include within-species genetic variability and the effects of climatic variables such as snow depth. To develop management strategies for mitigation and adaptation, it is important to know more specifically how forest growth responds to climatic variability and which factors limit growth.

Prior studies of tree growth responses to climatic variability in the Pacific Northwest concentrate on individual dominant species, often growing at the limits of their ranges (Brubaker 1980; Peterson and Peterson 1994, 2001; Ettl and Peterson 1995; Peterson et al. 2002). Although species respond individually to climatic variation rather than as species assemblages, considering forests in terms of individual species is not always practical from a management perspective. Thus, it is also important to understand how entire stands and landscapes, composed of multiple species and size classes, respond to environmental variability. Other studies have focused on growth–climate relationships at scales ranging from regional (Brubaker 1980; Peterson and Peterson 2001; Peterson et al. 2002; Case and Peterson 2005) to subcontinental (McKenzie et al. 2001) to continental (Briffa 1998). Growth may respond differently to climate in different biogeographic locations; however, relationships between climate and tree growth vary at smaller spatial scales as a function of aspect (Villalba et al. 1994), elevation (Ettl and Peterson 1995; Buckley et al. 1997), and species (Graumlich 1993; Peterson and Peterson 1994). Growth–climate relationships also vary at multiple temporal scales, and growth has been shown to respond to climate differently for different time periods within the 20th century (e.g., Solberg et al. 2002). Other factors, such as CO_2 fertilization and nitrogen deposition, also affect growth–climate relationships.

In this study, we quantified spatial variability in forest growth – climate relationships during the 20th century on the Olympic Peninsula, an ideal setting in which to study growth–climate interactions because of the variety of bioclimatic zones in close proximity. Spatial variation in growth was examined under different climatic regimes, in a variety of topographic settings, for multiple species groups, and for different time periods.

Study area

Climate

The Olympic Mountains are characterized by sharply contrasting climatic environments. On the western, coastal side of the Olympic Peninsula, the climate is mild and maritime, with heavy precipitation. Dry, almost continental climatic conditions characterize the "rainshadow" of the northeastern peninsula. Data were collected in the Hoh River and the Dungeness River watersheds as part of the Climate Landscape Interactions on a Mountain Ecosystem Transect project (Fagre et al. 2003) (Fig. 1). The Hoh River watershed represents conditions in the west side of the peninsula, and the Dungeness River watershed represents conditions in the northeast.

Lowland areas in the Hoh watershed receive roughly 250 cm of annual precipitation, and high elevations receive over 500 cm. In the Dungeness watershed, annual precipitation is less than 50 cm at low elevations and is as high as 200 cm at the

headwaters (Henderson et al. 1989). Winter precipitation falls mostly as snow at elevations above ~750 m. In both watersheds, 80% of precipitation falls between October and March, and only 5% falls in July and August. Consequently, low soil moisture is common in the summer, although low clouds and summer fog buffer the effects of low summer moisture on the west side of the mountains. Temperatures are slightly more extreme in the Dungeness watershed, averaging 0 °C in January and 24 °C in July, compared with 4 °C in January and 16 °C in July for the Hoh watershed (Smith and Henderson 1986).

Climate on the Olympic Peninsula is influenced by annual and decadal patterns in atmospheric circulation, sea-surface temperature, and sea-level pressure. The Southern Oscillation Index (SOI) (Zhang et al. 1997) and the Pacific Decadal Oscillation (PDO) (Mantua et al. 1997) are quasiperiodic patterns of climatic variability associated with precipitation and sea and air temperatures. Cool phases of the PDO and SOI (La Niña) (low index values) are associated with cool and wet winter conditions, and warm phases of the PDO and SOI (El Niño) (high index values) are associated with warm and dry winter conditions. Based on the length of measured record (approximately 100 years), the SOI shifts between warm and cool phases at 2- to 7-year intervals, and the PDO shifts between phases at 20- to 30-year intervals.

Forest landscapes

Glacial sediments are common on the Olympic Peninsula. Glacial sediments in the eastern peninsula are derived from the most recent continental glaciation, 13 000 to 20 000 years old, and composed mostly of granitic material. Soils are relatively shallow, poorly developed, and oxidized to a depth of only 60 cm. On the southwestern peninsula, depositions are older and soils are more developed where continental glaciers did not extend.

The Hoh River valley is wide and U-shaped. The river headwaters are steep and mountainous, whereas low elevations are moderately sloped. Lowland areas consist of temperate rainforests, typified by a heavy moss layer, abundant nurse logs, and deep, organic-rich soils. Forests are dominated by western hemlock (*Tsuga heterophylla* (Raf.) Sarg.), Sitka spruce (*Picea sitchensis* (Bong.) Carrière), and western redcedar (*Thuja plicata* Donn ex D. Don). At elevations above 350 m, Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) replaces Sitka spruce as the dominant tree species. At elevations exceeding roughly 500 m, silver fir (*Abies amabilis* (Dougl. ex Loud.) Dougl. ex J. Forbes) and western hemlock are dominant, and at elevations exceeding 1100 m, subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.) and mountain hemlock (*Tsuga mertensiana* (Bong.) Carrière) are dominant (Buckingham et al. 1995).

The Dungeness River valley is narrow and deep. The upper watershed is mountainous, the foothills are moderately sloped, and the valley bottom is flat. Lowland areas of the Dungeness watershed are dominated by Douglas-fir, western hemlock, and occasionally by western redcedar and grand fir (*Abies grandis* (Dougl. ex D. Don) Lindl.). At elevations exceeding 1000 m, silver fir, Douglas-fir, and western hemlock are dominant, and at elevations exceeding roughly 1500 m, subalpine fir and lodgepole pine (*Pinus contorta* Dougl. ex Loud. var. *latifolia* Engelm.) are dominant (Buckingham et al. 1995).

Fig. 1. Location of study and sample plots.
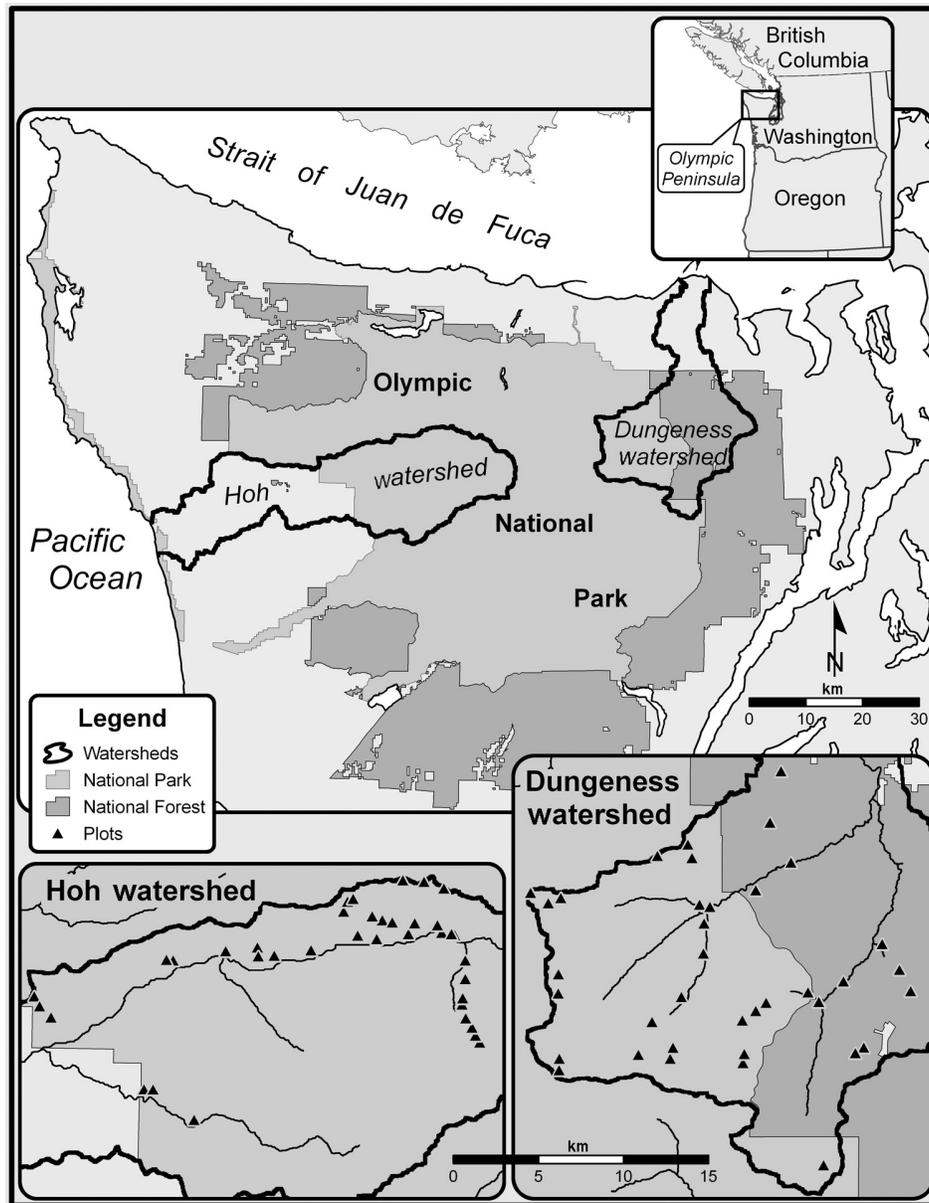
Methods

Data collection

A total of 74 plots were sampled, 37 in the Hoh watershed and 37 in the Dungeness watershed (Fig. 1). Plots were selected to represent a variety of forest types and topographic settings, following examination of vegetation maps, consultation with local ecologists, and extensive field reconnaissance. We classified plots into seven forest types (sensu Buckingham et al. 1995) based on elevation and dominant tree species. These classifications summarize plots into simplified units for analysis, as depicted in Fig. 2. High variability in structure and species composition exists within each forest type.

Actual plot location was subjective and based on modal concepts of forest types described above. Plots were 0.05 ha and circular (12.6 m radius). Plot descriptions include location, as gauged by a GPS unit, elevation, topographic position, aspect, and slope percent. In each plot, the height and diameter of all trees greater than 10 cm diameter at breast height (DBH) were measured. Trees from each 10 cm size class of a given species (two trees per 10 cm size class) were cored at DBH within each plot. Preference was given to trees with minimal damage to either boles or crowns. Two increment cores were sampled from the cross-slope sides of each tree. A total of 1079 trees were cored, 532 from the Hoh watershed and 547 from the Dungeness watershed.

Growth time-series development

Cores were mounted in grooved, wooden boards and sanded with increasingly fine grades of sandpaper. Cores were cross-dated and verified using the computer program COFECHA (Holmes 1983; Grissino-Mayer 2001). Beginning with the ring associated with the year 1895, ring widths were measured to the nearest 0.01 mm under magnification using an

Fig. 2. Classification of forest types, showing distribution of major tree species and biotic zones by elevation. Adapted from Buckingham et al. (1995).
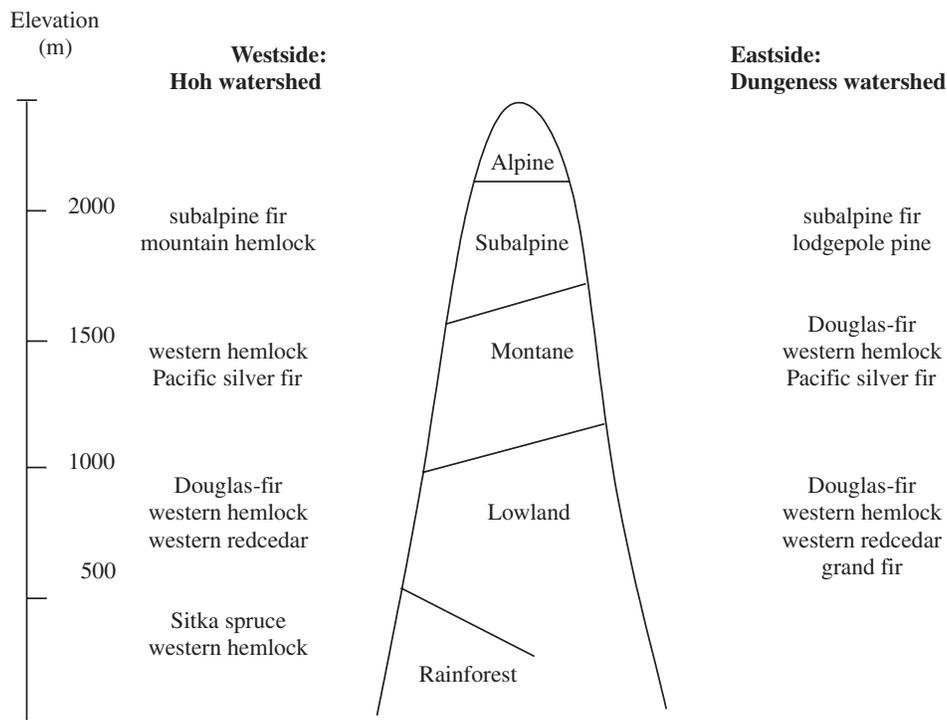
incremental measuring system equipped with a video camera and monitor. One core from each tree was selected for ring-width measurements based on its completeness and the length of its tree-ring record. The accuracy of core measurements was checked by remeasuring a randomly selected 20-year segment per core.

Ring-width measurements were converted into annual diameter increments using the following equation:

$$D_{t-1} = \frac{[D_t - (B_s D_t)] - R_t}{1 - B_s}$$

Here, B_s is a species-specific bark coefficient that accounts for the decrease in bark thickness for successively smaller diameter trees (Finch 1948; Smith and Kozak 1967; Bormann 1990). D_t is the DBH for year t. For the outermost ring, this value was estimated using the DBH value derived from field measurements. D_{t-1} is the DBH at year $t - 1$, and R_t is the ring width for year t, multiplied by 2. Annual diameter increments were then translated into annual basal area increments (BAI) using the following equation:

$$\text{BAI} = \pi \left(\frac{D_t}{2} \right)^2 - \pi \left(\frac{D_{t-1}}{2} \right)^2$$

Individual-tree BAI time series were then standardized by dividing each BAI by the tree mean BAI. Standardization gives equal weight to each time series by averaging trees of different size, age, species, and growth trend.

The final products were mean time series of growth for each plot. We used BAI because it is a practical and cost-efficient way to estimate growth. BAI is not subject to decreasing trends as a tree grows, and therefore detrending is unnecessary (although the effects of local stand competition on growth trends may still be evident). Using this method, we were able to sample widely across forest types and develop inferences for the whole watershed.

Descriptive statistics

Mean BAI, intraplot correlations, interplot correlations, common variances, and the slope of the growth time series were calculated over the time series of the cores to compare growth within and among plots. Mean BAI was calculated for each plot by taking the arithmetic mean for each year of every nonstandardized individual-tree BAI time series within the plot. This value represents the average growth per unit area per year for a given sample of trees alive at the time of data collection. Plots with fewer than five cores were combined with plots of similar elevation and species type to reduce within-plot variability, provided significant correlation among the individual-tree BAI time series existed. This was done for five plots in the Hoh watershed, producing three combined plots. No data for plots in the Dungeness watershed were combined.

Pearson's correlation coefficients expressed intraplot correlations between each individual-tree time series and the plot-growth time series. This value quantifies the coherence of year-to-year variability in BAI among trees within a plot and captures growth patterns at small spatial scales. Correlations among growth time series between plots within forest types were also calculated. Common variance was estimated by the percentage of variance explained by the first component in principal components analysis. This represents the percentage of variance within a plot that is captured by the mean plot time series. The slope of each growth time series was estimated using linear regression techniques and represents the general linear trend in the time series.

Table 1. Summary of important intercorrelations among climatic variables.

	Annual precip.	June–Sept. precip.	Oct.–May precip.	Annual temp.	June–Sept. temp.	Oct.–May temp.	Winter PDO	PDSI	Spring snow
Annual precipitation		+	+				−	+	+
June–Sept. precipitation	+				−			+	
Oct.–May precipitation	+						−	+	+
Annual temperature					+	+	+	−	−
June–Sept. temperature		−		+		+	+	−	
Oct.–May temperature				+	+		+	−	−
Winter PDO	−		−	+	+	+		−	−
PDSI	+	+	+	−	−	−	−		+
Spring snow	+		+	−		−	−	+	

Note: "+" indicates significant positive correlation and "−" indicates significant negative correlation between climatic variables ($\alpha < 0.05$).

Growth time series were prewhitened by fitting autoregressive models. Prewhitening removes the correlation of a time series with its own past or future values (autocorrelation), thereby retaining the portion of sample that is not related to the rest of the samples. The model order required to remove the serial correlation from the time series was identified based on the first-minimum Akaike information criterion. The Akaike information criterion is used to estimate expected uncertainty by taking simultaneously into account the goodness-of-fit of a model and the complexity of the model required to achieve that fit (Bozdogan 1987). The amount of variance explained by the autoregressive model was also calculated. Autoregressive modeling was conducted using the S-PLUS® version 6 statistical software package (Insightful, Inc., Seattle, Washington, 2002).

Factor analysis

Factor analysis identifies common modes of variability, or common growth patterns, among growth time series (Rencher 1995). Oblique or promax rotation of eigenvectors was chosen over orthogonal rotation to provide simple structure and better interpretations of BAI patterns. Coefficients of determination (r^2) describe the amount of variance within each mean growth time series explained by each of the factor variables.

Temporal stability of underlying growth patterns was explored by using factor analysis for different time ranges. The periods 1925–1946 (warm), 1947–1976 (cool), and 1977–1998 (warm) were selected because they coincide with PDO phases. A resampling approach was required because the number of observations (22–30 years) was less than the number of variables (plots). Factor analysis was performed 20 times for a random grouping of 21–29 plots. The periods 1920–1960 and 1960–2000 were also explored through factor analysis to further explore temporal stability for two equal time periods independent of known PDO phases.

Climatic data

Growth time series and factor-score time series were compared with annual and seasonal climatic variables for the length of the climatic record. Temperature and precipitation data from Divisional records were used in this study (Natural Resources Conservation Service 2003). Data for the Hoh watershed were obtained from Washington State Climate Division 1 for the West Olympic Coastal Region, with temperature data to 1914, and precipitation data to 1919. Data for the Dungeness watershed were obtained from Division 4 for the eastern Olympics and the Cascade foothills, with temperature data to 1931, and precipitation data to 1919.

Snowpack data were obtained from the monitoring station at Hurricane Ridge, Olympic National Park (National Climatic Data Center 2003). These data were recorded from 1950 to the present. Snowpack depth measurements on 1 April were used because most snow courses in this region reach their maximum snow water equivalent at this time (Cayan 1996). Regional instrumental Palmer Drought Severity Index (PDSI) values were obtained from the NOAA Paleoclimatology Program for the period 1895–1995 (Cook et al. 1999). PDSI provides a surrogate for mean soil moisture for a given year by combining temperature and rainfall information. Negative PDSI values indicate dry conditions, and positive values indicate wet conditions. The PDO index was obtained for 1900–2000 from instrumental sea surface temperature records (JISAO 2003).

Growth–climate correlations

Associations between climatic variables and growth were identified by calculating Pearson's correlation coefficients (r) between climatic variables and factor-score time series. Climatic variables include annual temperature and precipitation (based on a climate year from October to September), seasonal temperature and precipitation (based on a wet season (winter) from October to May and a dry season (summer) from June to September), annual PDSI, spring snowpack depth, and PDO index. The PDO index was aggregated into mean winter (November–March) and mean summer (June–September) components. Climatic variables were also considered at lags of 1 and 2 years.

Correlations were considered potentially significant if the correlation coefficient was significant at $\alpha = 0.05$. Only correlations showing consistency among similar plots are considered significant. The strength of correlations did not vary for plots or forest types with different sample sizes, which suggests that the sample sizes were sufficient to produce robust quantitative results. Degrees of freedom were adjusted when smoothed time series were compared.

Results

Climatic variability

A total of 48 climatic variables were included in this analysis. A correlation matrix assessed the intercorrelation of these variables (Table 1). Fifty-six of the total 1228 possible

pairwise correlations would be expected to be significantly correlated at random ($\alpha = 0.05$). There are 331 significant correlations, showing intercorrelations among climatic variables.

Precipitation is positively correlated with spring snowpack depth and PDSI and negatively correlated with winter PDO index. Temperature is positively correlated with previous-year temperature and PDO index and negatively correlated with spring snowpack depth and PDSI. Spring snowpack is positively correlated with PDSI and precipitation and negatively correlated with PDO index and temperature. Table 1 summarizes important intercorrelations among climatic variables. Many of the climatic variables exhibit low-frequency decadal variability, in addition to high-frequency interannual variability. The winter and summer PDO indexes show considerable decadal variability. Temperature and precipitation variables also display low-frequency variability. Spring snowpack depth does not show clear decadal variability, perhaps because of the short time span of the record.

Descriptive statistics

Plots included in the analysis cover topographic settings over an elevation range of 190 to 2000 m (see Nakawatase (2003) for more details). Each forest type is represented by 7 to 17 plots. A total of 733 tree cores were used, 354 cores in the Hoh watershed and 379 cores in the Dungeness watershed (data from all plots were used regardless of intraplot correlation). Average number of trees per plot is 20 in the Hoh watershed and 29 in the Dungeness watershed, and average number of cores per plot is 10.4 in the Hoh watershed and 10.2 in the Dungeness watershed.

Mean BAI varies from 0.076 to 0.890 $m^2 \cdot ha^{-1} \cdot year^{-1}$ in the Hoh watershed, and from 0.082 to 1.13 $m^2 \cdot ha^{-1} \cdot year^{-1}$ in the Dungeness watershed. No significant difference in mean BAI was detected between the watersheds. Average BAI tends to be lower at mid to high elevations and higher at low elevations, although this relationship with elevation is not statistically significant in the Hoh watershed (Hoh: $r = -0.238$, $p = 0.156$; Dungeness: $r = -0.553$ $p < 0.0001$). In the Dungeness watershed, average BAI is highest for the low- to mid-elevation Douglas-fir – western hemlock forest types. In the Hoh River watershed, average BAI is highest for Sitka spruce and western hemlock lowland forest types.

Mean intraplot correlations range from 0.25 to 0.78, averaging 0.48 ± 0.14 (SD, here and hereafter), with no significant difference between watersheds. The variance associated with the first principal component ranges from 23.4% to 73.7%, averaging 36.6% ± 7.4% in the Hoh watershed and 45.5% ± 10.4% in the Dungeness watershed. Common variance is significantly higher in the Dungeness watershed ($p = 0.0002$). There is a wide range in overall growth trends, estimated by the slope of the growth time series, from –0.018 to 0.005 in the Hoh watershed and from –0.010 to 0.020 in the Dungeness watershed. The slope of the growth time series is significantly higher in the Dungeness watershed ($p < 0.0001$), suggesting that 20th century growth increases are more pronounced here. These statistics do not vary as a function of elevation, forest type, or aspect.

Interplot correlation is highest between plots at similar elevations. In the Hoh watershed, correlations between high-

Table 2. Principal components analysis and factor analysis for the period 1920–2000.

(A) Principal components analysis.			
PC	Eigenvalue	Proportion of variance	Cumulative variance
1	3.8	0.204	0.204
2	2.6	0.093	0.297
3	2.1	0.064	0.362
4	1.8	0.049	0.412
5	1.8	0.044	0.456
6	1.6	0.039	0.495
7	1.6	0.035	0.530

(B) Factor analysis.			
Factor	Eigenvalue	Proportion of variance	Cumulative variance
1	10.4	0.149	0.149
2	8.9	0.127	0.276
3	4.3	0.061	0.337

elevation plots are greater than those between low- to mid-elevation plots ($p = 0.001$). There are no significant differences among interplot correlations within the three lower elevation forest types in the Hoh watershed. In the Dungeness watershed, interplot correlations among high-elevation plots are significantly lower than correlations among low- and mid-elevation plots ($p = 0.014$). No significant difference between interplot correlations within the low- and mid-elevation forest types in the Dungeness watershed was detected.

Growth time series show widely varying autocorrelation structure with model order ranging from 1 to 4. Significant autocorrelation at a lag of 1 year was found for 37% of the growth time series, a lag of 2 years for 35%, a lag of 3 years for 25%, and a lag of 4 years for 4%. First-order autocorrelation coefficients are positive for all plots and range from 0.042 to 0.972. Autocorrelation coefficients are highest at low elevations and decrease with increasing elevation ($r = 0.458$, $p < 0.0001$). This suggests that previous-year growth has a greater influence on current-year growth at lower elevations than at higher elevations. No difference in first-order autocorrelation coefficients was detected between watersheds.

Factor analysis

Three factors account for a significant proportion (34%) of the total variance within and among the growth time series (Table 2). Three factors were selected because principal component analysis identified three components each of which explains more than 5% of the variance among growth time series (Rencher 1995). This criterion has been used in similar studies of tree growth – climate relationships (Peterson and Peterson 1994, 2001; Peterson et al. 2002). Time series for different factor scores were uncorrelated following nonorthogonal rotation.

Growth time series with high amounts of variance explained by each of the factors can be separated by watershed and elevation or forest type (Table 3). Plots that correlate closely with factor 1 are located across elevations in the Dungeness watershed, primarily within low- to mid-elevation

Table 3. Coefficients of determination between growth time series and factor score time series.

Table 3 (*concluded*).

(A) Hoh River watershed.

Plot identification	r² Factor 1	Factor 2	Factor 3	R² Combined
Sitka spruce – western hemlock				
HO026.27	0.004	0.001	**0.309**	0.310
HO029	0.021	0.001	**0.130**	0.144
HO030	0.014	0.001	**0.291**	0.301
HO041	0.012	0.044	**0.312**	0.373
HO051.52	0.012	0.064	**0.281**	0.338
HO031	0.009	0.023	**0.336**	0.354
HO200	0.007	0.049	**0.270**	0.326
HO039.53	0.043	0.070	**0.253**	0.369
HO201	0.046	0.072	**0.082**	0.210
Douglas-fir – western hemlock				
HO036	**0.227**	0.142	0.195	0.570
HO004	**0.240**	0.012	0.154	0.392
HO204	0.026	0.030	**0.035**	0.096
HO055	**0.207**	0.065	0.172	0.441
HO205	**0.091**	0.018	0.063	0.185
HO037	0.015	0.054	**0.203**	0.277
HO001	0.075	**0.088**	0.060	0.228
Silver fir – western hemlock				
HO003	**0.092**	0.018	0.041	0.150
HO008	**0.281**	0.003	0.023	0.302
HO056	0.034	**0.098**	0.068	0.207
HO203	0.016	**0.333**	0.156	0.504
HO202	0.001	**0.133**	0.132	0.255
HO006	0.007	**0.448**	0.016	0.484
HO014	0.081	**0.085**	0.000	0.175
HO012	0.000	**0.514**	0.002	0.515
Subalpine fir – mountain hemlock				
HO005	0.019	**0.175**	0.126	0.333
HO013	0.013	**0.186**	0.001	0.207
HO019	0.013	**0.594**	0.012	0.625
HO018	0.022	**0.661**	0.005	0.705
HO059	0.026	**0.605**	0.002	0.646
HO020	0.027	**0.589**	0.004	0.634
HO023	0.001	**0.538**	0.010	0.543
HO011	0.001	**0.180**	0.002	0.186
HO206	0.022	**0.258**	0.009	0.282
HO022	0.061	**0.313**	0.055	0.443

(B) Dungeness River watershed.

Plot identification	r² Factor 1	Factor 2	Factor 3	R² Combined
Western hemlock – Douglas-fir – western redcedar				
DU204	**0.134**	0.132	0.022	0.306
DU203	**0.115**	0.076	0.031	0.238
DU207	**0.103**	0.006	0.068	0.190
DU020	**0.272**	0.071	0.020	0.373
DU017	**0.341**	0.021	0.002	0.372
DU018	**0.367**	0.016	0.015	0.405
DU019	**0.266**	0.005	0.045	0.307
DU016	**0.552**	0.016	0.003	0.560
DU002	**0.686**	0.006	0.000	0.693
DU026	**0.157**	0.008	0.013	0.177
DU035	**0.096**	0.011	0.046	0.149
DU010	**0.476**	0.055	0.010	0.570
DU013	**0.273**	0.017	0.007	0.312
DU205	0.030	**0.108**	0.070	0.214
DU012	**0.317**	0.012	0.007	0.351
DU003	**0.615**	0.012	0.015	0.623
DU206	**0.018**	0.031	0.031	0.084
Douglas-fir – western hemlock				
DU023	**0.351**	0.011	0.012	0.375
DU004	**0.395**	0.158	0.020	0.595
DU027	**0.478**	0.000	0.001	0.486
DU008	**0.366**	0.145	0.001	0.538
DU001	**0.425**	0.030	0.001	0.473
DU033	**0.440**	0.074	0.002	0.534
DU209	0.000	**0.038**	0.021	0.056
DU202	**0.198**	0.094	0.037	0.327
DU030	0.088	**0.242**	0.011	0.357
Subalpine fir – lodgepole pine				
DU032	0.031	**0.157**	0.039	0.234
DU015	**0.498**	0.063	0.030	0.627
DU028	0.081	**0.321**	0.013	0.434
DU062	0.011	**0.090**	0.008	0.113
DU208	0.000	**0.038**	0.021	0.056
DU005	**0.168**	0.153	0.042	0.387
DU200	0.001	0.073	**0.080**	0.150
DU104	0.025	**0.128**	0.004	0.156
DU039	**0.086**	0.047	0.002	0.142
DU066	0.000	**0.009**	0.002	0.011
DU106	**0.001**	0.000	0.000	0.002

Note: Coefficients of determination measure the variance in growth time series explained by each factor and the combination of all three factors. Plots are arranged by forest type and watershed. Bold values indicate the highest coefficient of determination for each plot.

western hemlock and Douglas-fir forests. High-elevation subalpine fir and silver fir plots in the Hoh watershed correlate closely with factor 2. Low-elevation Sitka spruce – western hemlock plots in the Hoh watershed correlate closely with factor 3. Together, the three factors explain up to 70% of the variance within the growth time series (Table 3).

When plotted over time, the factor scores show high-frequency variability but do not display clear long-term trends (Fig. 3). Factor analysis for the PDO-derived periods 1925–1946, 1947–1976, and 1977–1998, and the periods 1920–1960 and 1960–2000 produces groupings of plots associated

with each factor similar to those for the entire time range. This implies temporal stability of the factor groupings across the range of analysis.

Climatic variables related to summer moisture conditions are best correlated with growth in the Dungeness watershed, primarily in low- to mid-elevation Douglas-fir and western

Fig. 3. Time-series plots of factor scores. Thin lines are annual values, and thick lines are 5-year running averages.
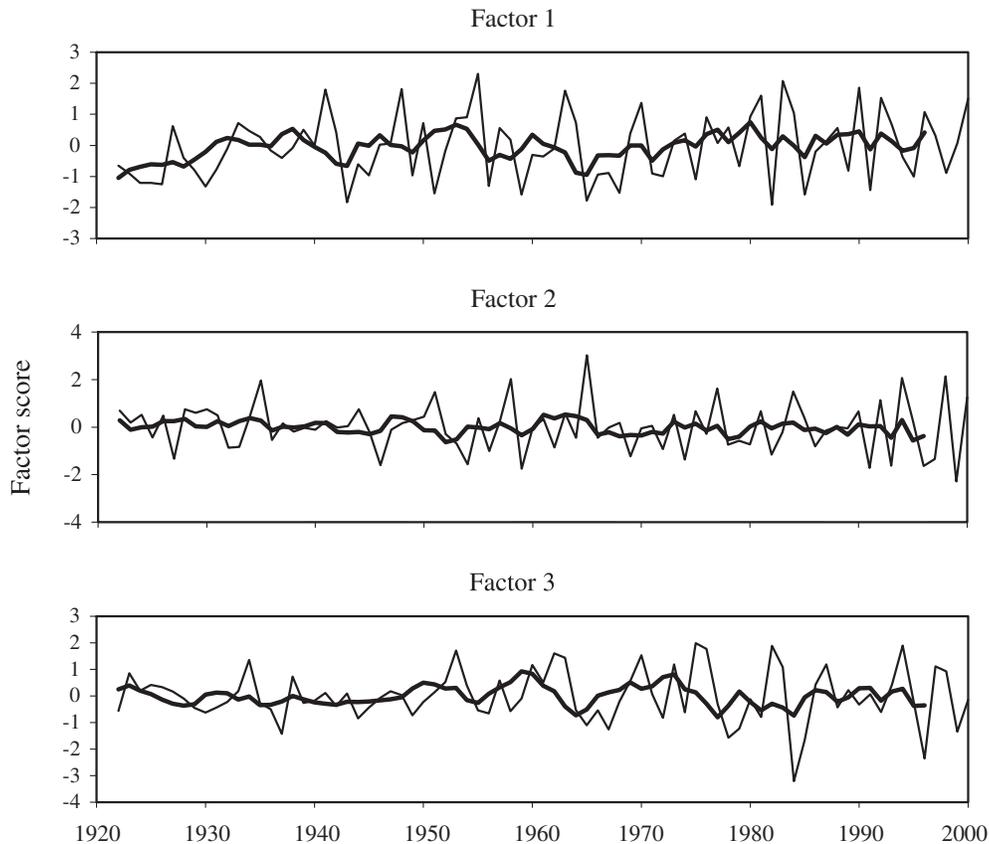
hemlock plots (factor 1). The time series of factor 1 scores is positively correlated with PDSI (Fig. 4), summer precipitation, and winter temperature (Table 4). Climatic variables related to snowpack depth are best correlated with growth for high-elevation subalpine fir, mountain hemlock, and silver fir plots in the Hoh watershed (factor 2). The time series of factor 2 scores correlates negatively with annual and winter precipitation (Fig. 4), spring snowpack depth, and PDSI. Factor 2 scores correlate positively with summer temperature, a variable associated with snowpack persistence (Table 4). Factor 2 scores also correlate positively with previous-year snowpack, and previous-year annual and winter precipitation.

No climatic variables are significantly correlated with factor 3 scores, associated with low-elevation Sitka spruce forests in the Hoh watershed (Table 4). To explore whether Sitka spruce growth is related to climatic variability at an alternate time step, correlations between 5-year moving averages of factor 3 scores and 5-year averages of climatic variables were calculated. Smoothed averages of factor 3 scores show significant negative correlation with smoothed averages of winter PDO ($p < 0.0001$) (Fig. 4) and summer temperature ($p = 0.039$).

Growth–climate relationships

At elevations above 1200 m, growth time series in the Hoh watershed are negatively correlated with spring snowpack depth, annual precipitation, winter precipitation, and PDSI (Fig. 5). A number of high-elevation growth time series correlate positively with annual and summer temperature. High-elevation growth time series also correlate positively

with previous-year annual precipitation, previous-year winter precipitation, previous-year snowpack, and previous-year PDSI. No significant correlations exist with climatic variables at lags of 2 years. Plots at lower elevations show no consistent trends in correlations.

Low- to mid-elevation growth time series in the Dungeness watershed are positively correlated with current- and previous-year summer precipitation and PDSI and current-year winter temperature (Fig. 6), although the relationship varies among plots. Growth at low to mid elevations is negatively correlated with spring snowpack depth. Mid-elevation growth time series also show a negative correlation with previous-year summer temperature. Growth at high elevation shows a significant negative correlation with current- and previous-year summer temperatures and a weak, positive correlation with previous-year summer precipitation. High-elevation growth time series are negatively correlated with spring snowpack depth, although this pattern is more variable than that for lower elevations. No significant correlations with climatic variables exist at lags of 2 years.
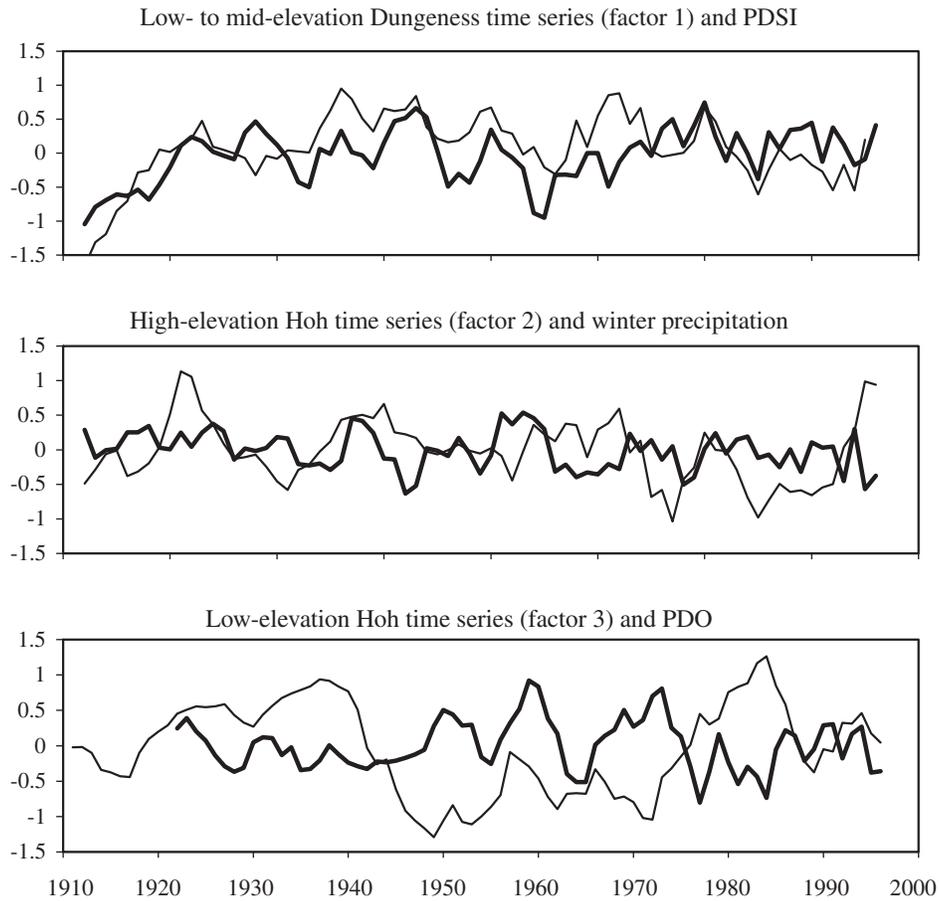
Discussion

Climatic influences on growth

Hoh River watershed
Snowpack depth limits growth for high-elevation subalpine fir – western hemlock and silver fir – western hemlock forests in the Hoh watershed. Growth is negatively related to annual precipitation, winter precipitation, PDSI, and spring

Fig. 4. Time-series plots of factor scores compared with selected climatic variables. Thick lines are 5-year moving averages of factor scores, and thin lines are 5-year moving averages of climatic variables. *Y*-axis units are used to denote both (1) factor scores and (2) standardized values of climatic variables with a mean of 0.

Low- to mid-elevation Dungeness time series (factor 1) and PDSI

High-elevation Hoh time series (factor 2) and winter precipitation

Low-elevation Hoh time series (factor 3) and PDO

Table 4. Coefficients of determination (r^2) between factor score time series and climatic variables.

| Climatic variable	Dungeness, low to mid elevation	Hoh, high elevation	Hoh, low elevation
Summer temperature	—	0.084	—
Winter temperature	0.080	—	—
Annual precipitation	—	–0.115	—
Annual precipitation, previous year	—	0.064	—
Summer precipitation	0.125	—	—
Winter precipitation	—	–0.150	—
Winter precipitation, previous year	—	0.078	—
Snow depth, Hurricane ridge, April 1	—	–0.096	—
Snow depth, previous year	—	0.094	—
Palmer Drought Severity Index	0.097	–0.118	—

Note: Sign retained to indicate direction of the relationship. All values shown are statistically significant ($p < 0.05$).

snowpack levels. Intercorrelation of these climatic variables suggests they can be attributed to a single overriding variable. The significant correlation between growth and annual precipitation is likely driven by the effects of winter precipitation on growth, because there is no relationship between growth and summer precipitation. The correlation between growth and winter precipitation is associated with snowpack depth, because winter precipitation at high elevation falls mainly as snow (National Climatic Data Center 2003). The

negative relationship between growth and PDSI indicates that growth is higher during dry years, which are typically years with low snowpack.

The relationship between high-elevation growth time series and snowpack depth suggests that growth in subalpine fir – mountain hemlock and silver fir – western hemlock forests in the Hoh watershed is limited by growing season length. Snowpack depth affects both the start and length of the growing season, primarily through its effects on soil tem-

Fig. 5. Correlations (*r*) between growth time series in the Hoh watershed and selected climatic variables. Each bar represents one plot, and plots are arranged in order of increasing elevation. Black bars indicate a significant correlation ($\alpha < 0.05$).

Increasing elevation →
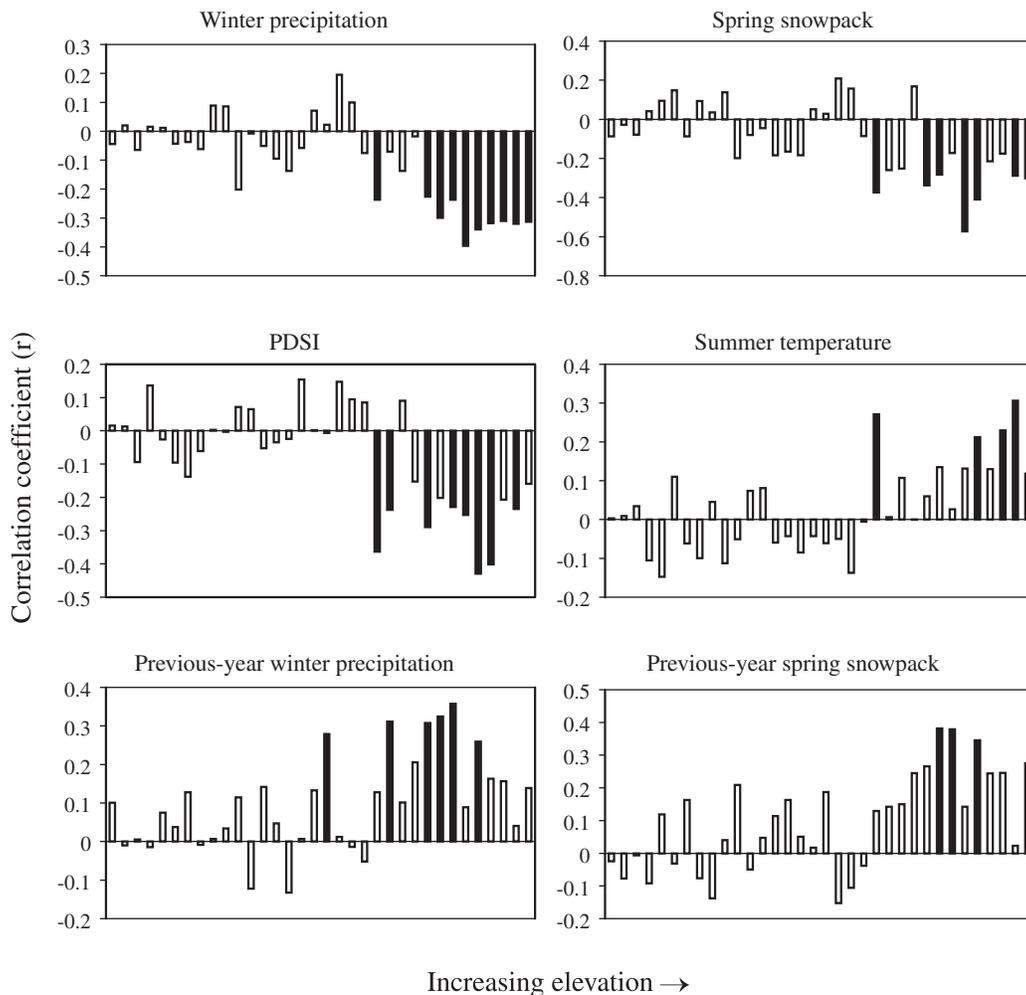
perature (Körner 1995). Leaf and shoot expansion for subalpine fir, silver fir, and mountain hemlock does not begin until after snowmelt, when soil temperature begins to warm (Worrall 1983; Hansen-Bristow 1986). Our data corroborate the importance of growing season length as a limiting factor for tree growth in high-elevation Pacific Northwest forests, including the Olympic Mountains (Ettl and Peterson 1995; Peterson et al. 2002; Holman and Peterson 2006) and the Cascade Range (Graumlich and Brubaker 1986; Peterson and Peterson 1994, 2001).

The positive relationship between high-elevation growth time series and summer temperature further supports the importance of growing season length in limiting growth. Warm summer temperatures lengthen the growing season by accelerating snowmelt, increasing soil temperatures, and supporting rapid leaf, shoot, and stem growth (Körner 1998).

The positive response of high-elevation growth to previous-year precipitation, previous-year snowpack, and previous-year PDSI can be explained by the tendency for low snowpack or precipitation years (below mean) to follow high snowpack or precipitation years (above mean). Medium and low snowpack or precipitation years follow high snowpack or precipitation years at a rate of about 70% for the length of the climatic record. In years with heavy snowpacks, the growing season is

short and stem growth is minimal, so a greater relative proportion of carbohydrate reserves is stored for use the following year (Waring 1991).

The lack of significant correlations between low- to mid-elevation growth in the Hoh watershed and climatic variables suggests that growth is not related to interannual variability of these climatic variables. However, growth in low-elevation Sitka spruce – western hemlock forests in the Hoh watershed is correlated with PDO index and possibly summer temperature at a lag of 1 year. One explanation for these relationships is that growth is responding to low-frequency variability in the PDO and possibly summer temperature. Climate at low elevations in the Hoh watershed is wet and mild, and growth responses to climatic variability may be somewhat buffered from one year to the next, supporting a low-frequency relationship. However, the only way to identify a relationship between low-frequency variability in two time series is by exploring the frequency domain through spectral analysis (Hessl et al. 2003).

Dungeness River watershed

The negative relationship between growth in the Dungeness watershed and summer temperature and the positive relationship between growth and summer precipitation and PDSI

Fig. 6. Correlations (*r*) between growth in the Dungeness watershed and selected climatic variables. Each bar represents one plot, and plots are arranged in order of increasing elevation. Black bars indicate a significant correlation (α < 0.05).
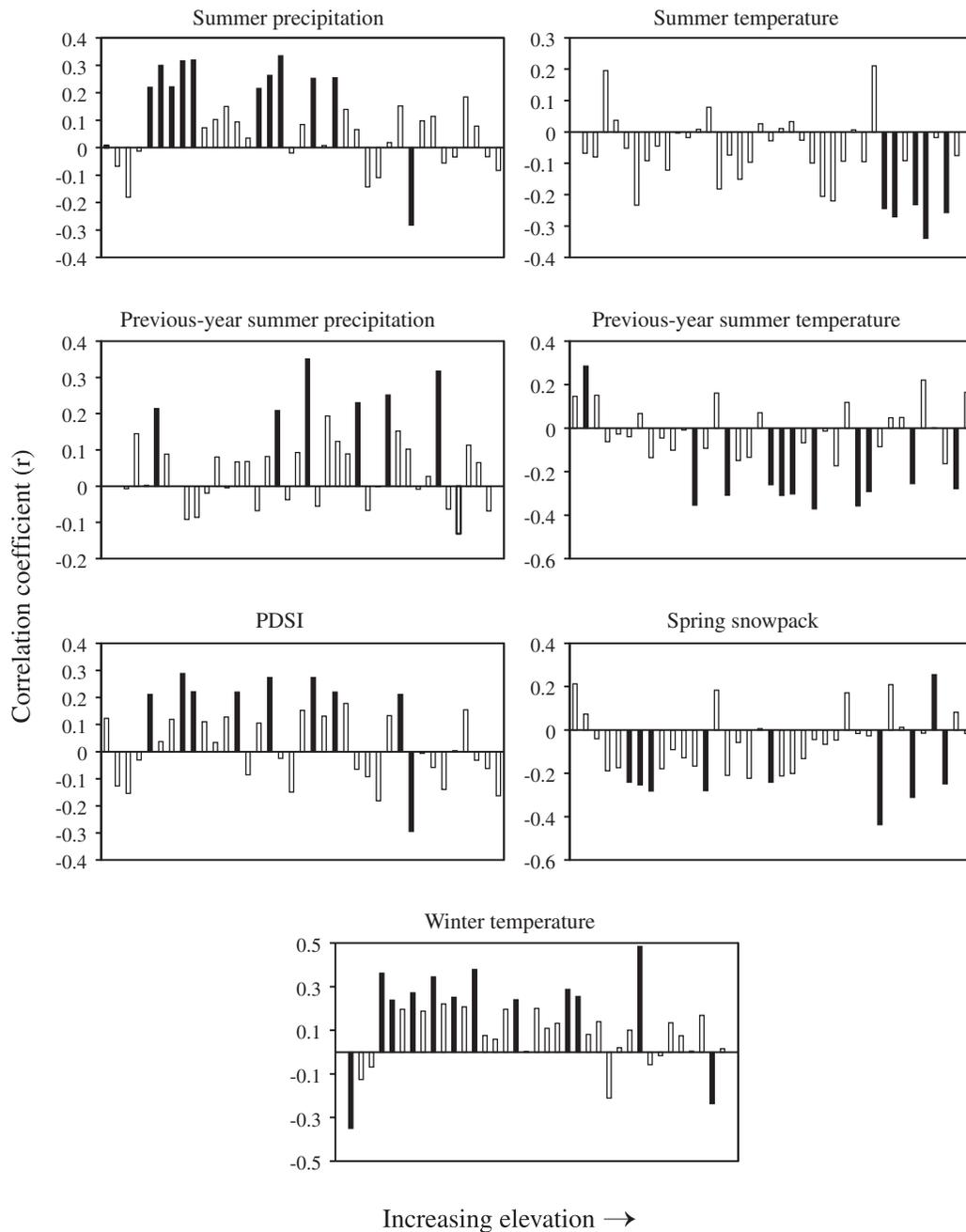

suggest that growth is limited by summer moisture deficit. Precipitation and temperature function together as growth limiting factors and in combination provide a rough indication of plot water balance (Stephenson 1998).

Growth in the Dungeness watershed also responds to previous-year summer precipitation and temperature. Previous-year climate can influence subsequent growth through its effects on energy reserves and leaf area, especially in drier locations (Colenutt and Luckman 1991; Villalba et al. 1994; Ettl and Peterson 1995). Warm and dry summer conditions increase respiration rates, reduce photosynthate production, reduce leaf area, and reduce energy reserves by diverting them to current-year growth (e.g., Fritts 1976). Previous-

year summer temperature can also affect current-year growth through its effect on reproductive resources. Production of a large cone crop drains resources that would otherwise be used for radial growth. Previous-year July or August temperature was positively related to current-year cone production for mountain hemlock trees in northern Oregon, and radial growth of these trees was reduced in years with large cone crops (Woodward et al. 1994).

The positive correlation between growth and winter temperature and the negative relationship with spring snowpack differ from some previous studies in dry locations (Kusnierczyk and Ettl 2002; Peterson et al. 2002). Warmer winter temperatures tend to decrease snowpack, and a reduced snowpack

Fig. 7. Summary of growth limiting factors identified in this study, and expected growth in a warmer climate for different forest types in the Hoh and Dungeness watersheds.
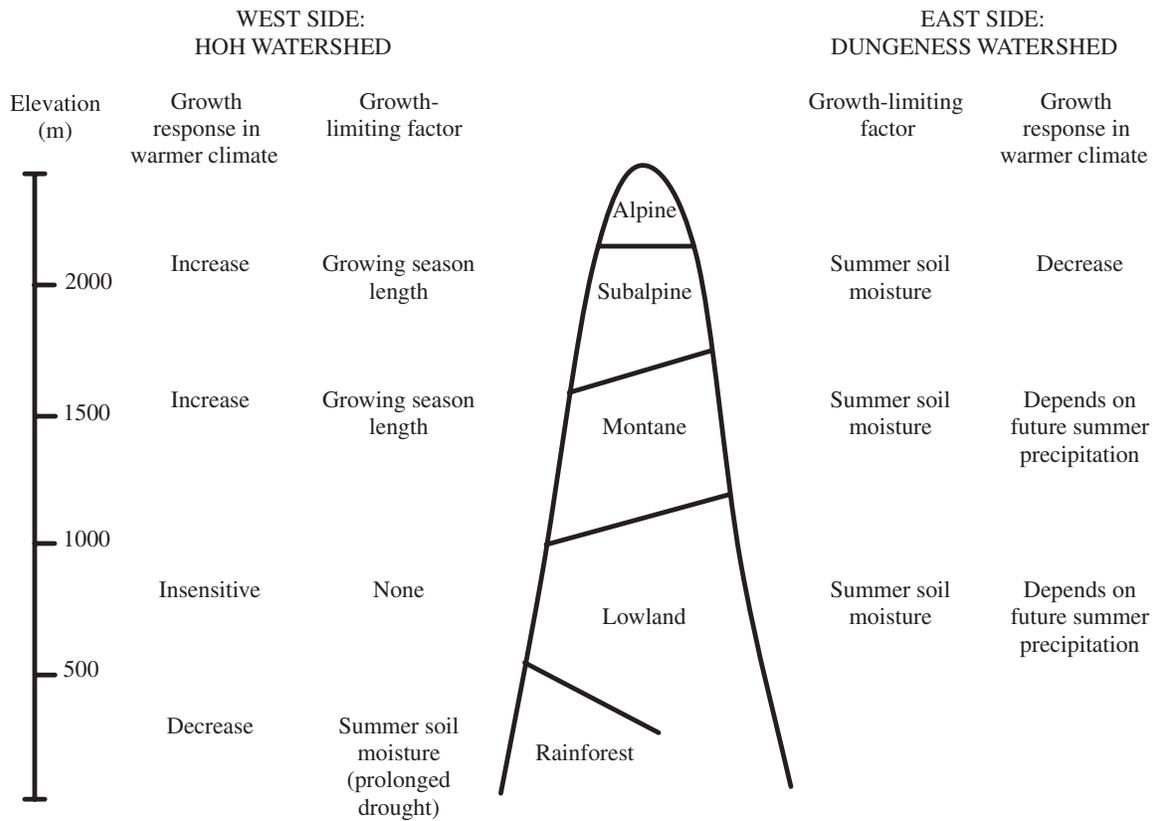
would reduce soil moisture. Although one might expect this to reduce summer soil moisture and reduce tree growth, the relationship of snowpack to the onset of the growing season may also affect growth in the Dungeness watershed. Cooler temperatures, higher precipitation, and more cloud cover would increase water availability and extend the overall period of water availability during the growing season (Peterson and Peterson 2001), although more cloud cover could also reduce photosynthetic activity.

Winter temperature and summer precipitation interact to affect growth in the Dungeness watershed (Holman and Peterson 2006). Above-average growth coincides with above-average winter temperatures. Growth is above average when winter temperatures exceed approximately 7 °C, which would normally enhance growth during spring and early summer. A similar threshold for snowpack quantity was not evident.

Although growth in high-elevation plots and lower elevation plots share similar responses to climatic variables related to summer moisture, a number of differences in growth responses are also apparent. For example, current-year summer precipitation and PDSI are less important for growth at high elevation, and high-elevation growth is less closely associated than low-elevation growth with the time series of factor scores related to summer soil moisture (factor 1) (Fig. 4). Correlations between high-elevation growth and spring snowpack are also more variable in sign than correlations at lower elevations, which were consistently negative. High-elevation stands in the Dungeness watershed have more precipitation and cooler temperatures than lower elevations, which explains the lower sensitivity to summer precipitation. Because for-

ests at lower elevation occupy a larger area than forests at high elevation, the effect of lower soil moisture at the watershed scale would likely be reduced growth and productivity.

Response to future climate

Trends in temperature and precipitation for the Olympic Peninsula have been similar to regional Pacific Northwest trends over the 20th century (Mote 2003), suggesting that future climate predictions for the Pacific Northwest may be applied to the Olympic Peninsula with some confidence. In the Pacific Northwest, mean annual temperatures are predicted to rise by roughly 1.5 to 3.0 °C by the 2050s in response to an increase in atmospheric CO_2 (JISAO 1999). Winter precipitation is expected to increase by about 5%; however, models are divided over whether summer precipitation will increase or decrease. Higher winter temperatures would lead to reduced snow cover except at the highest elevations (Leung and Ghan 1999). Although winter precipitation is expected to increase, much of this precipitation will fall as rain because of the higher temperatures. Decreased snow cover, higher spring and summer temperatures, and increased rain on snow will lead to earlier snowmelt. At the highest elevations, temperatures may not warm sufficiently to cause more rain events, and snowpack may increase. Higher summer temperatures are also expected to increase summer moisture stress.

Forests of the Dungeness and Hoh watersheds are likely to respond differently in the warmer climate expected in the future (Fig. 7). Growth in high-elevation subalpine fir – mountain hemlock and silver fir – western hemlock forests of the Hoh

watershed, currently limited by heavy snowpack and short growing season, will likely increase as a result of reduced snow cover and earlier snowmelt, thereby increasing net productivity and carbon storage. At the very highest elevations, however, growth may decrease as a result of increased snowpack and shorter growing seasons. An increase in summer temperatures, especially if coupled with a decline in precipitation, would decrease growth and productivity in low-elevation Sitka spruce – western hemlock forests in the Hoh watershed. Mid-elevation Douglas-fir and western hemlock forests in the Hoh watershed have lower sensitivity to climate, although these forests could also be affected if temperature continues to increase.

Higher summer temperature would reduce growth across the Dungeness watershed. Growth in high-elevation subalpine fir – lodgepole pine forests will likely be the most affected, because growth here shows strong, negative correlation with current- and previous-year summer temperature. The effect of future climate on growth in the Dungeness watershed will likely depend on whether summer precipitation increases or decreases. Growth in low- to mid-elevation Douglas-fir and western hemlock forests would benefit from an increase in summer precipitation, because their growth shows strong, positive correlation to current- and previous-year precipitation. If summer precipitation increases, growth at low to mid elevations may decline, remain unchanged, or increase, depending on the combined effect of increased summer temperature and precipitation. If summer precipitation remains at current levels or decreases, growth at low elevations will likely decline.

The effects of interactions between temperature and precipitation on growth make it difficult to predict how growth in low- to mid-elevation forests will respond to future climate. Growth in high-elevation subalpine fir – lodgepole pine forests will benefit to a lesser degree from an increase in summer precipitation, because growth correlates only to previous-year summer precipitation, and these correlations, though predominantly positive, are somewhat variable in sign. Increased summer precipitation may partially counter the effects of warmer temperature, but not completely compensate for them. Therefore, we expect growth in high-elevation forests in the Dungeness watershed to decline under future climatic scenarios.

The negative correlation between growth and spring snowpack and the positive correlation with winter temperature add further complexity to growth–climate relationships in the Dungeness watershed. Based on these correlations alone, one would expect growth to increase in the future because of reduced snowpack and warmer winter temperatures. Growth would benefit from an earlier growing season with favourable growing conditions. However, the combined decrease in snowpack and increase in summer temperature may be detrimental to growth in moisture-limited forests. A reduction in snowpack may increase moisture stress, because subsurface recharge from snowmelt is a major source of summer soil moisture.

Changes in disturbance regimes (Peterson et al. 1997) may also play a key role in forest response to future climatic conditions and may be more important than the direct effects of future climate on tree growth. Increased summer temperatures and moisture deficits would increase the amplitude and length of extreme fire weather, leading to more frequent severe fires and changes in the distribution and abundance of plant species (McKenzie et al. 2004). At regional scales, these changes in fire weather may be the most important factor affecting forests in the future. Changes in other disturbances, such as insects, pathogens, and wind, may also affect future forest productivity and distribution at various spatial scales (JISAO 1999).

If climate continues to warm during the next several decades, patterns of forest productivity in the Pacific Northwest could be affected (Case and Peterson 2005; Holman and Peterson 2006). Adaptive management strategies in the face of an altered climate often focus on large spatial scales. However, because forest growth responds differently to climatic variability in different bioclimatic environments, management of forest ecosystems will need to consider growth response at local to watershed scales. Data on which specific forests are sensitive to climatic change will be particularly valuable. The results of this study are relevant for the Olympic Peninsula and are probably applicable to other mountain ecosystems of the Pacific Northwest where the same species occur.

Downscaling of existing vegetation models to smaller spatial scales (Zolbrod and Peterson 1999) will also help develop more accurate predictions at spatial scales at which management actions typically occur.

Acknowledgements

References

Boer, G.J., Flato, G.M., and Ramsden, D. 1999. A transient climate change simulation with historical and projected greenhouse gas and aerosol forcing: projected climate for the 21st century. Clim. Dynam. **16**: 405–425.

Bormann, B.T. 1990. Diameter-based biomass regression models ignore large sapwood-related variation in Sitka spruce. Can. J. For. Res. **20**: 1098–1104.

Bozdogan, H. 1987. Model selection and Akaike's information criterion (AIC): the general theory and its analytical extensions. Psychometrika, **52**: 345–370.

Briffa, K.R. 1998. Trees tell of past climates: but are they speaking less clearly today? Phil. Trans. R. Soc. Lond. **353**: 65–73

Brubaker, L.B. 1980. Spatial patterns of tree growth anomalies in the Pacific Northwest. Ecology, **61**: 798–807.

Buckingham, N.M., Schreiner, E.G., Kaye, T.N., Burger, J.E., and Tisch, E.L. 1995. Flora of the Olympic Peninsula. Northwest Interpretive Association, Seattle, Wash.

Buckley, B.M., Cook, E.R., Peterson, M.J., and Barbetti, M. 1997. A changing temperature response with elevation for

Lagarostrobos franklinii in Tasmania, Australia. Clim. Change **36**: 477–498.

Case, M.J., and Peterson, D.L. 2005. Fine-scale variability in growth–climate relationships of Douglas-fir, North Cascade Range, Washington. Can. J. For. Res. **35**: 2743–2755.

Cayan, D.R. 1996. Interannual climate variability and snowpack in the western United States. J. Clim. **9**: 928–948.

Colenutt, M.E., and Luckman, B.H. 1991. Dendrochronological investigation of *Larix lyallii* at Larch Valley, Alberta. Can. J. For. Res. **21**: 1222–1233.

Cook, E.R., Meko, D.M., Stahle, D.W., and Cleveland, M.K. 1999. Drought reconstructions for the continental United States. J. Clim. **4**: 1145–1162.

Ettl, G.J., and Peterson, D.L. 1995. Growth response of subalpine fir (*Abies lasiocarpa*) to climate in the Olympic Mountains, Washington, USA. Global Change Biol. **1**: 213–230.

Fagre, D.B., Peterson, D.L., and Hessl, A.E. 2003. Taking the pulse of mountains: ecosystem responses to climatic variability. Clim. Change, **59**: 263–282.

Finch, T.L. 1948. Effect of bark growth in measurement of periodic growth of individual trees. USDA For. Serv. North. Rocky Mt. Res. For. Range Exp. Stn. Note 60.

Fritts, H.C. 1976. Tree rings and climate. Academic Press, New York.

Graumlich, L.J. 1993. Response of tree growth to climatic variation in the mixed conifer and deciduous forests of the upper Great Lakes region. Can. J. For. Res. **23**: 133–143.

Graumlich, L.J., and Brubaker, L.B. 1986. Reconstruction of annual temperature (1590–1979) for Longmire, Washington derived from tree rings. Quat. Res. **25**: 223–234.

Grissino-Mayer, H.D. 2001. Evaluating crossdating accuracy: a manual and tutorial for the computer program COFECHA. Tree-Ring Res. **57**: 205–221.

Hansen-Bristow, K.J. 1986. Influence of increasing elevation on growth characteristics at timberline. Can. J. Bot. **64**: 2517–2523.

Henderson, J.A., Peter, D.H., Lesher, R.D., and Shaw, D.C. 1989. Forested plant associations of the Olympic National Forest. USDA For. Serv. Reg. 6 Ecol. Tech. Pap. 001-88.

Hessl, A.E., McKenzie, D., and Schellhaas, R. 2003. Drought and Pacific Decadal Oscillation linked to fire occurrence in the inland Pacific Northwest. Ecol. Appl. **14**: 425–422.

Holman, M.L., and Peterson, D.L. 2006. Sensitivity of forest growth to climatic variability in the Olympic Mountains, Washington. Can. J. For. Res. **36**: 92–104.

Holmes, R.L. 1983. Computer-assisted quality control in tree-ring dating and measurement. Tree-Ring Bull. **43**: 69–75.

Johns, T.C., Carnell, R.E., Crossley, J.F., Gregory, J.M., Mitchell, J.F.B., Senior, C.A., Tett, S.F.B., and Wood, R.A. 1997. The Second Hadley Centre coupled ocean–atmosphere GCM: model description, spinup and validation. Clim. Dynam. **13**: 103–134.

JISAO. 1999. Impacts of climate variability and change in the Pacific Northwest. National Oceanic and Atmospheric Administration, Office of Global Programs, and Joint Institute for the Study of Atmosphere and Oceans – School of Marine Affairs, Climate Impacts Group, University of Washington, Seattle, Wash.

JISAO. 2003. PDO index. Available from http://tao.atmos. washington.edu/PNWimpacts/Download.htm#pdo [cited 1 December 2002].

Körner, C. 1995. Arctic and alpine biodiversity: patterns, causes, and ecosystem consequences. Springer-Verlag, Berlin, Germany.

Körner, C. 1998. A re-assessment of high elevation treeline positions and their explanation. Oecologia, **115**: 445–459.

Kramer, P.J., and Kozlowski, T.T. 1979. Physiology of woody plants. Academic Press, New York.

Kusnierczyk, E.R., and Ettl, G.J. 2002. Growth response of ponderosa pine (*Pinus ponderosa*) to climate in the eastern Cascade Mountains, Washington, USA: implications for climatic change. Ecoscience, **9**: 544–551.

Lenihan, J.M., and Neilson, R.P. 1995. Canadian vegetation sensitivity to projected climatic change at three organizational levels. Clim. Change, **30**: 27–56.

Leung, L.R., and Ghan, S.J. 1999. Pacific Northwest climate sensitivity simulated by a regional climate model driven by a GCM. Part II: $2 \times CO_2$ simulations. J. Clim. **12**: 2031–2053.

Mantua, N.J., Hare, S.R., Zhang, Y., Wallace, J.M., and Francis, R.C. 1997. A Pacific interdecadal climate oscillation with impacts on salmon production. Bull. Am. Meteorol. Soc. **78**: 1069–1079.

McKenzie, D., Hessl, A.E., and Peterson, D.L. 2001. Recent growth of conifer species of western North America: assessing spatial patterns of radial growth trends. Can. J. For. Res. **31**: 526–538.

McKenzie, D., Gedalof, Z.M., Peterson, D.L., and Mote, P. 2004. Climatic change, wildfire, and conservation. Conserv. Biol. **19**: 890–902.

Mote, P.W. 2003. Trends in temperature and precipitation in the Pacific Northwest. Northwest Sci. **77**: 271–282.

Mote, P.W., Parson, E.A., Hamlet, A.F., Ideker, K.G., Keeton, W.S., Lettenmaier, D., Mantua, N., Miles, E.L., Peterson, D.W., Peterson, D.L., Slaughter, R., and Snover, A.K. 2003. Preparing for climate change: the water, salmon, and forests of the Pacific Northwest. Clim. Change, **61**: 45–88.

Nakawatase, J. 2003. Spatial and temporal variability in tree growth–climate relationships in the Olympic Mountains, Washington. Master's thesis, University of Washington, Seattle, Wash.

National Climatic Data Center. 2003. Locate weather observation station record [online]. Available from http://www.ncdc.noaa.gov/oa/climate/stationlocator.html [updated 11 December 2003; cited 15 October 2003].

Natural Resources Conservation Service. 2003. Snow course and monthly SNOTEL data tables [online]. Available from http://www.wcc.nrcs.usda.gov/cgibin/state-site.pl?state = WA&report = snowcourse [updated 26 August 2003; cited 15 October 2003].

Peterson, D.L., Schreiner, E.G., and Buckingham, N.M. 1997. Gradients, vegetation and climate: spatial and temporal dynamics in the Olympic Mountains, U.S.A. Global Ecol. Biogeogr. Lett. **6**: 7–17.

Peterson, D.W., and Peterson, D.L. 1994. Effects of climate on radial growth of subalpine conifers in the North Cascade Mountains. Can. J. For. Res. **24**: 1921–1932.

Peterson, D.W., and Peterson, D.L. 2001. Mountain hemlock growth responds to climatic variability at annual and decadal time scales. Ecology, **82**: 3330–3345.

Peterson, D.W., Peterson, D.L., and Ettl, G.J. 2002. Growth responses of subalpine fir to climatic variability in the Pacific Northwest. Can. J. For. Res. **32**: 1503–1517.

Rencher, A.C. 1995. Factor analysis. *In* Methods of multivariate analysis. Wiley and Sons, New York. pp. 445–488.

Smith, J.H.G., and Kozak, A. 1967. Thickness and percentage of bark of the commercial trees of British Columbia. Faculty of Forestry, The University of British Columbia, Vancouver, B.C.

Smith, B.G., and Henderson, J.A. 1986. Baseline vegetation survey of the Hoh and Dosewallips drainages, Olympic National Park, Washington. Unpublished National Park Service report on file at Olympic National Park, Port Angeles, Wash.

Solberg, B.O., Hofgaard, A., and Hytteborn, H. 2002. Shifts in radial growth responses of coastal *Picea abies* induced by climate

change during the 20th century, central Norway. Ecoscience, **9**: 79–88.

Stephenson, N.L. 1998. Actual evapotranspiration and deficit: biologically meaningful correlates of vegetation distribution across spatial scales. J. Biogeogr. **25**: 855–870.

Villalba, R., Veblen, T.T., and Ogden, J. 1994. Climatic influences on the growth of subalpine trees in the Colorado Front Range. Ecology, **75**: 1450–1462.

Waring, R.H. 1991. Responses of evergreen trees to multiple stresses. *In* Response of plants to multiple stresses. Academic Press, San Diego, Calif. pp. 371–390.

Waring, R.H., and Pitman, G.B. 1985. Modifying lodgepole pine stands to change susceptibility to mountain pine beetle attack. Ecology, **66**: 889–897.

Woodward, A., Silsbee, D.G., Schreiner, E.G., and Means, J.E. 1994. Influence of climate on radial growth and cone production in subalpine fir (*Abies lasiocarpa*) and mountain hemlock (*Tsuga mertensiana*). Can. J. For. Res. **24**: 1133–1143.

Woodward, A., Schreiner, E.G., and Silsbee, D.G. 1995. Climate, geography, and tree establishment in subalpine meadows of the Olympic Mountains, Washington, U.S.A. Arct. Alp. Res. **27**: 217–255.

Worrall, J. 1983. Temperature–bud-burst relationships in amabilis and subalpine fir provenance tests replicated at different elevations. Silvae Genet. **32**: 203–209.

Zhang, Y., Wallace, J.M., and Battisti, D.S. 1997. ENSO-like interdecadal variability: 1900–93. J. Clim. **10**: 1004–1020.

Zolbrod, A.N., and Peterson, D.L. 1999. Response of high-elevation forests in the Olympic Mountains to climatic change. Can. J. For. Res. **29**: 1966–1978.