

Spatial and temporal variability in forest growth in the Olympic Mountains, Washington: sensitivity to climatic variability

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Abstract: We compared annual basal area increment (BAI) at different spatial scales among all size classes and species at diverse locations in the wet western and dry northeastern Olympic Mountains. Weak growth correlations at small spatial scales (average $R = 0.084\text{--}0.406$) suggest that trees are responding to local growth conditions. However, significant positive growth correlations between geographically adjacent forest types ($R = 0.440\text{--}0.852$) and between watersheds ($R = 0.430$) indicate that there is a common overarching growth-limiting factor (e.g., climate) that affects tree growth over large areas. The Sitka spruce (*Picea sitchensis* (Bong.) Carrière) forest type is the most sensitive to environmental change with the highest mean sensitivity (0.345), the highest potential for annual growth change (mean BAI = 0.0047 m^2), and the highest growth variability (coefficient of variation = 0.498). In addition, this forest type is most likely to exhibit extreme positive growth responses (4.2% of years have BAI values 2 standard deviations above the mean). Low-elevation coniferous forests are relatively sensitive to changes in growth-limiting factors (in contrast to the traditional view) and may play an important role in storing carbon in a warmer climate.

Résumé : Les auteurs ont comparé l'accroissement annuel en surface terrière à différentes échelles spatiales pour toutes les classes de dimension et toutes les espèces à divers endroits dans les parties ouest, une région humide, et nord-est, une région sèche, des Montagnes Olympiques. De faibles corrélations de croissance à de grandes échelles spatiales (R moyen de 0,084 à 0,406) indiquent que les arbres réagissent à des conditions locales de croissance. Cependant, des corrélations de croissance positives et significatives entre des types de forêts géographiquement adjacentes ($R = 0,440\text{--}0,852$) et entre des bassins versants ($R = 0,430$) indiquent qu'un facteur prédominant commun limite la croissance (p. ex. le climat) des arbres sur de grandes superficies. Le type de forêt dominé par l'épinette de Sitka (*Picea sitchensis* (Bong.) Carrière) est le plus sensible aux changements environnementaux avec la sensibilité moyenne la plus élevée (0,345), le plus grand potentiel de modification de la croissance annuelle (accroissement moyen en surface terrière de $0,0047\text{ m}^2$) et la plus grande variabilité de la croissance (coefficient de variation de 0,498). De plus, ce type de forêt est le plus sujet à montrer des réactions extrêmes de croissance positive (4,2 % des années montrent des accroissements en surface terrière dépassant la moyenne de deux écart-types). Les forêts de conifères à faible altitude sont relativement sensibles aux modifications des facteurs qui limitent la croissance (contrairement au point de vue traditionnel) et peuvent jouer un rôle important pour entreposer le carbone sous un climat plus chaud.

[Traduit par la Rédaction]

Introduction

Global climatic change will likely alter tree growth rates in some areas of the Pacific Northwest and the productivity of some Pacific Northwest forests (Kirschbaum and Fischlin 1996; Hessel and Peterson 2004). Individual-tree growth patterns and aboveground net primary productivity are sensitive to these annual changes in climate, as demonstrated in several locations in the Pacific Northwest (Brubaker 1980; Graumlich et al. 1989; Ettl and Peterson 1995; D'Arrigo and Jacoby 1996; Peterson and Peterson 2001; Hessel and Peterson 2004; Nakawatase and Peterson 2006). Changes in forest productivity in the Pacific Northwest could substantially affect global

carbon budgets as Pacific Northwest forests store more carbon per unit area ($33\text{ kg}\cdot\text{m}^{-2}$) and have higher net productivity ($1.74\text{ kg}\cdot\text{m}^{-2}\cdot\text{year}^{-1}$) than any other region of the United States (Turner et al. 1995).

Effects of climatic variability on growth and forest productivity will vary by forest type and species according to characteristics such as elevation and topography and species physiologies and allocation patterns. These characteristics vary along steep environmental gradients in mountainous ecosystems and can be directly associated with critical growth-limiting factors (McKenzie et al. 2003). Changes in combinations of these factors will drive local-scale changes in growth (Kirschbaum 2000; Körner 2003). For example, one of the most important

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influences of climatic change on mountainous ecosystems may be the effects of changes in temperature and precipitation on snowpack amount and duration (Cayan 1996), which then influence growth in some areas via changes in growing season length (Peterson 1998; Peterson and Peterson 2001; Peterson et al. 2002) and soil moisture recharge (Keeton et al.³).

Tree growth patterns may also be affected by longer term climatic variability. The Pacific Decadal Oscillation (PDO) is a system of quasiperiodic interdecadal variability in sea surface temperatures, sea level pressures, and wind patterns dominant in the Pacific Northwest (Mantua and Hare 2002). Each phase lasts about 20 to 30 years and is characterized as either warm (and dry) or cool (and wet). Growth patterns of some Pacific Northwest species in different environments are correlated with PDO phases (Peterson and Peterson 2001; Nakawatase and Peterson 2006).

Climate-induced changes in the growth and productivity of a sensitive forest type will have greater relative impacts (e.g., for carbon budgets) if that forest is also very productive. For example, climate – growth response data collected in conifer forests of the Stehekin River watershed of the North Cascade Range, Washington, indicate that mid-elevation forests dominated by Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) are both productive and responsive to climatic variability (Hessl and Peterson 2004). This means that growth of Douglas-fir forests is a potential bioindicator of the effects of a directional change in climate.

Growth responses are often measured at the tree scale via tree-ring analyses. However, if the goal is to develop a comprehensive understanding of growth responses to climate within a large geographic area, several tree species in a variety of forest types and growth environments must be measured to capture the range of spatial variability. Although it is difficult, tree-scale measurements can be scaled up to larger scales. Scaling up of growth measurement involves extrapolation of growth patterns to unmeasured trees (of similar species, size, and growth environment), but it can provide insight into the dominant factors contributing to growth variability at a variety of spatial scales (Hinckley et al. 1998).

There is considerable uncertainty regarding the future magnitude and direction of climatic change, particularly with respect to regional and local precipitation. Furthermore, the effects of single climatic variables on growth are only part of the picture of overall impacts of climatic change on forest ecosystems. Multiple direct and indirect environmental and disturbance factors will interact to influence future changes in forest growth and productivity (Peterson 1998; Kirschbaum 2000; Aber et al. 2001; Dale et al. 2001). Given this complexity and uncertainty, measures of the relative sensitivity of forest assemblages (i.e., potential degree of response) to environmental change can provide a focus for management and policy responses (Leovy and Sarachik 1991; Keeton et al.³).

In this study, we quantified variation in tree growth in the Olympic Mountains over the past 54 years (a period of significant temperature increase in the Pacific Northwest (Mote

2003)) and assessed the sensitivity of Olympic forests (in terms of aboveground tree growth) to climatic variability and change. We examined growth patterns for trees spanning a broad range of biophysical environments and possible climatic influences in the Olympics. We analyzed these growth patterns at multiple spatial scales (plot, forest type, watershed, subregion) to determine the scale at which trees in the Olympic Mountains have similar growth responses and the scale at which growth-limiting factors assert their strongest influence. In addition, we compared growth patterns between the two most recent phases of the PDO to examine the effects of multidecadal climatic influences. We measured trees of all ages and species to fully evaluate growth quantity and pattern at large spatial scales. Finally, we quantified the sensitivity of these forests to environmental variability to inform ecosystem-based management in the face of predicted changes in climate and associated growth-limiting factors.

Materials and methods

Study site

The Olympic Mountains encompass heterogeneous growth environments at small spatial scales resulting from dissected topography and steep temperature and precipitation gradients (Peterson et al. 1997). Precipitation in Olympic National Park reaches values as high as 600 cm·year⁻¹ on Mount Olympus and declines to only 40 cm·year⁻¹ on the east side of the mountains (Henderson et al. 1989). Because of these characteristics, there are many different forest types within the watersheds of the Olympic Mountains, representing distinct species compositions and containing diverse growing conditions. This diversity of forest environments provides a framework for evaluating differences in forest growth patterns.

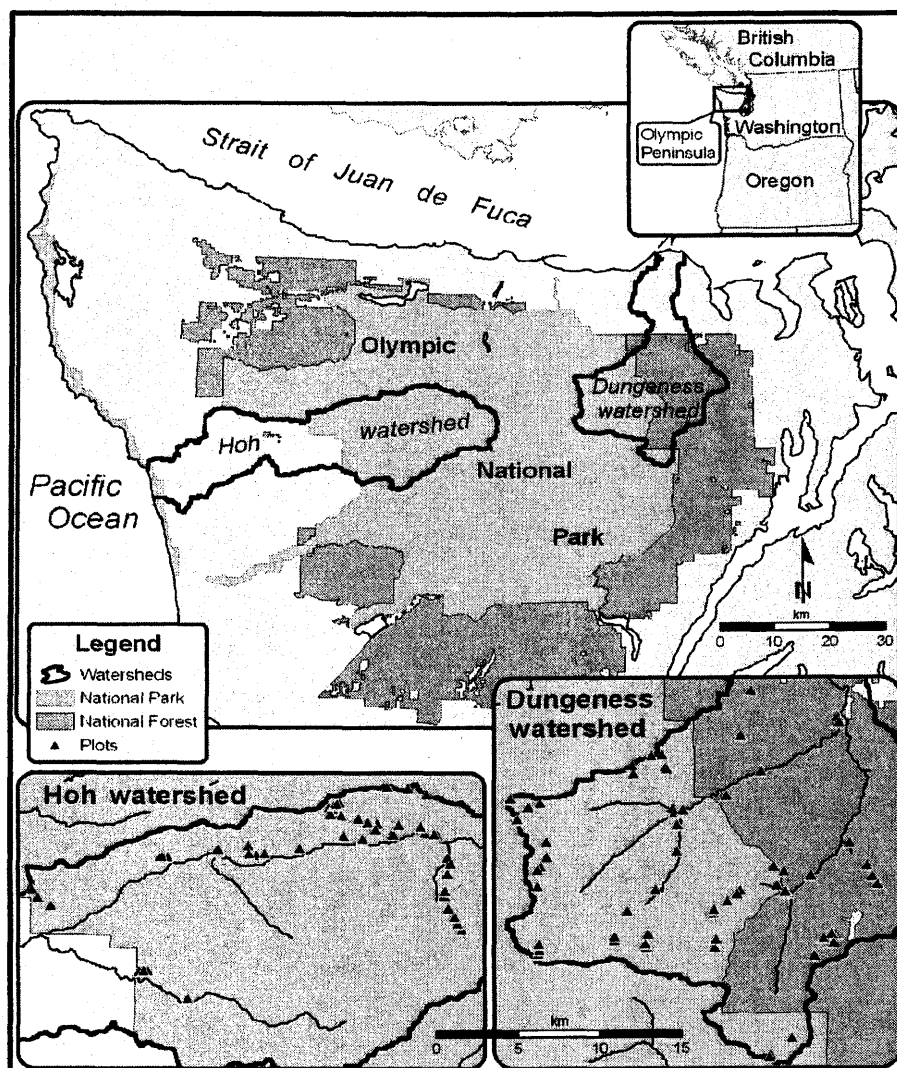
We collected data in the Hoh River watershed, in the wet western Olympics, and the Dungeness River watershed, in the dry eastern Olympics (Fig. 1). The climate throughout the Hoh watershed is mild and extremely wet. Mean annual precipitation ranges from 250 to over 500 cm, and mean monthly temperatures across the watershed range from 1.4 to 26 °C (Harmon and Franklin 1989; Henderson et al. 1989). The Dungeness River watershed approximates a continental climate; it is substantially drier than the Hoh River watershed. Mean annual precipitation ranges from 50 to 200 cm, and mean monthly temperatures range from -0.4 to 24 °C in the lower watershed (Henderson et al. 1989).

Hoh River watershed

Lowland vegetation in the Hoh watershed exhibits temperate rainforest qualities. This lowland area (0–350 m) is dominated by western hemlock (*Tsuga heterophylla* (Raf.) Sarg.), western redcedar (*Thuja plicata* Donn ex D. Don), and Sitka spruce (*Picea sitchensis* (Bong.) Carrière), sometimes with major contributions from red alder (*Alnus rubra* Bong.) and bigleaf maple (*Acer macrophylla* Pursh). As elevation increases, Sitka spruce, red alder, and bigleaf maple are less common, and Douglas-fir becomes the dominant overstory

³ W.S. Keeton, J.F. Franklin, and P.W. Mote. Climate variability, climate change, and forest ecosystems in the Pacific Northwest. Chap. 8. 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. Map of study and plot locations.



species (350 m). At around 600 m, silver fir (*Abies amabilis* (Dougl. ex Loud.) Dougl. ex J. Forbes) enters as a major overstory species and shares dominance in some areas with Douglas-fir and western hemlock. Above 1100 m, the overstory can be composed of yellow-cedar (*Chamaecyparis nootkatensis* (D. Don) Spach) and mountain hemlock as well as silver fir, which disappears as subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.) begins to dominate the overstory (1250 m). At the high elevations, where snowpack and the length of the growing season often determine growth, local variations in temperature and precipitation strongly affect the spatial heterogeneity of vegetation characteristics.

Dungeness River watershed

In the Dungeness watershed, variations in summer moisture stress create distinct vegetation compositions along moisture gradients. The lowland vegetation (0 to about 500 m) is characterized by an abundance of western hemlock and Douglas-fir in the overstory. Above 500 m, overstory species such as grand fir (*Abies grandis* (Dougl. ex D. Don) Lindl.), western redcedar, and silver fir share dominance with Douglas-fir

and western hemlock. Above 1100 to 1300 m, subalpine fir becomes a major overstory species, with some inclusions of mountain hemlock and lodgepole pine (*Pinus contorta* Dougl. ex Loud. var. *latifolia* Engelm.) as silver fir abundance declines. This area then grades into higher elevation (1700 m) tree groups interspersed with shrubby or herbaceous subalpine communities. These higher elevations are the wettest and coolest in the eastern Olympics, and as in the higher elevations of the Hoh watershed, plant communities differ along steep environmental gradients.

An ecological study design

Our objective was to capture the full range of tree and forest growth patterns and to retain as much of the natural growth variation as possible. Therefore, we extensively sampled forest environments, including all tree species and size classes. We used unstandardized basal area increment values to retain variance in growth data and to preserve the natural unbalanced weighting of trees of different sizes and species. The changes in growth patterns of dominant trees will, of course, contribute more to overall changes in forest produc-

tivity and carbon cycling. Results are also reported for prewhitened time series, which have had growth removed that resulted from a lag in growth response to a previous year's growth conditions. Prewhitening allows more accurate comparisons of annual growth patterns for different forests, but it may remove low-frequency variation in growth that may be of interest for some analyses.

Data collection

We collected data in the Hoh (37 plots) and Dungeness (39 plots) watersheds during the summers of 2001 and 2002, as part of the CLIMET (Climate–Landscape Interactions on a Mountain Ecosystem Transect) research program (Fagre et al. 2003). We selected plot access points (mostly along national park trails) prior to sampling using vegetation classifications based on Landsat Thematic Mapper imagery and topographic maps. We chose exact plot locations in the field, with the goal of sampling a comprehensive range of the vegetation assemblages and physiographic environments of each watershed (Fig. 1).

Plots (0.05 ha) ranged in elevation from near sea level to tree line and were located on various aspects and on slopes of varying steepness. Plots were located in mature stands with no obvious evidence of disturbance. This procedure of sampling a small subset of geographic locations and species is a rapid and cost-effective method of estimating trends in productivity as they relate to climate and other factors (Hessl and Peterson 2004). Within each plot, we noted the location coordinates using a GPS unit and the physical characteristics of elevation, slope, and aspect. We recorded species, diameter at breast height (DBH), and height of all trees greater than 10 cm DBH. We took two increment cores from each of two live individuals representing each 10 cm diameter class for all tree species present on the plot. We collected a total of 532 tree cores in the Hoh watershed and 547 tree cores in the Dungeness watershed.

Core processing

We cross-dated and measured ring widths of all tree cores, for the last 100 years when possible, following the procedures of Stokes and Smiley (1968) and Fritts (1976). We did not measure cores that did not cross-date well visually (but these trees were included in the overall analysis, as described in the Plot-scale calculations section). Following cross-dating, we measured ring widths for each core to the nearest 0.001 mm using a Velmex measuring system. We remeasured a randomly selected 10-year segment of each core for quality control. If the standard deviation of the difference (absolute value) between measured and remeasured sections was greater than 0.05, we remeasured the entire core. We verified cross-dating using the COFECHA program (Holmes 1999).

Data analysis

Time periods of analysis

We chose to restrict the length of the time period to the past half century both so as not to underestimate total plot productivity through successive losses due to mortality, and to focus the analysis and conclusions on the recent period of growth that may have been affected by increasing temperatures (e.g., Peterson 1991, 1994; Innes 1998; McKenzie et al. 2001). In addition, we divided the analysis into two sec-

tions: 1947–1976 and 1977–2000. These time periods approximate the two most recent phases of the PDO (the cool, wet (negative) phase of the PDO lasted from 1947–1976, and the warm, dry (positive) phase started in 1977 and may have ended in 1998, although this has not been confirmed (Mantua and Hare 2002; N. Mantua, personal communication, 2004), so we included growth up until the last year measured). Based on previous analysis in the Pacific Northwest, tree growth patterns might be affected differently by climate during each phase (Peterson and Peterson 2001; Peterson et al. 2002).

Plot-scale calculations

We converted ring widths and DBH measurements into annual diameter increments with the following equation used to back calculate diameter without bark (which considers the species-specific increase in bark thickness as a tree grows):

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

where D_{t-1} is the diameter at breast height at year $t - 1$ (diameter inside bark), D_t is the diameter at breast height at year t (diameter outside bark), B_s is the bark coefficient for species s , and R_t is $2 \times$ ring width during year t .

Bark coefficients are derived from Finch (1948), Smith and Kozak (1967), and Bormann (1990). The diameter equation above introduces a small amount of error into the growth time series. However, because we are comparing relative growth patterns, this error should not affect interpretation of the results.

We then converted these values into annual basal area increments:

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

Unlike ring widths, BAI is not subject to decreasing trends as a tree grows, and therefore no detrending is necessary (although the effects of local stand competition on growth trends may still be evident). In addition, BAI serves as a more accurate measure of tree growth than ring widths (Visser 1995). Complete measures of forest net primary production are difficult to obtain because they must also include belowground productivity, mortality, litterfall, and grazing — factors that were not quantified in this study. We attempted to minimize the loss of previous years' BAI due to mortality by restricting the time period of analysis. However, the results from the analysis of the earlier time period (1947–1976) should be interpreted with caution because they may more seriously underestimate plot or forest growth amounts. While we expect that BAI measurements underestimate actual forest net primary productivity, they are an effective means of detecting responses to environmental conditions (Hessl and Peterson 2004).

Plots had an average of eight tree cores of sufficient quality. We assigned uncored (and cored but unmeasured) individuals in the plot (>54 years) with BAI time series for cored (and measured) individuals of the same species and size class within that plot or (infrequently) from a plot in the same forest type with similar physical characteristics. The local error inherent in this process is necessary to improve data representation of physical and ecological gradients in

each watershed and improve conclusions at larger scales. We summed the tree BAI values for every tree within the plot (including uncored trees, which were assigned BAI series) to establish total plot BAI time series and calculate total plot basal area. In addition, we averaged BAI time series and basal areas for the entire plot. There was an average of 24 trees per plot. We prewhitened average plot BAI time series by fitting autoregressive models, using the first-minimum Akaike information criteria to select the model order (number of autocorrelated years (Insightful, Inc., Seattle, Washington, 2002)). Prewhitening removes autocorrelation trends due to lag effects of growth influences on subsequent years' growth. Resulting time series are more statistically robust for year-to-year comparisons, but may lack a significant portion of the actual growth amount. Therefore, we report results for multiple growth measures: each plot is represented by total plot basal area and three growth time series, or chronologies, which are (1) sums of the BAI time series for every individual in the plot, (2) arithmetic averages of the BAI time series for every individual in the plot, and (3) the prewhitened plot-average time series.

Forest-type calculations

We partitioned 76 plots into eight forest types according to biotic zones and major tree species, as delineated by Buckingham et al. (1995), in relation to aspect and elevation within the Olympic Peninsula. These forest types were named Hoh Sitka spruce (14 plots), Hoh low (7 plots), Hoh mid (8 plots), Hoh high (8 plots), Dungeness grand fir (5 plots), Dungeness low (10 plots), Dungeness mid (9 plots), and Dungeness high (15 plots). There were an average of 10 plots per forest type.

We expanded the plot measurements to forest types by summing plot BAI and total basal area for all the plots within a forest type (to obtain a measure of total growth amount per forest type), resulting in a single time series of basal area per hectare for each forest type, as well as values of total basal area per hectare. We also calculated averages of prewhitened, averaged plot BAI time series within each forest type. We then similarly expanded these forest-type values to obtain overall growth time series for each watershed.

Correlation analysis

We calculated mean interseries correlation to assess the degree of similarity among individual BAI time series within each plot (average of 24 BAI time series per plot) as well as among total plot BAI time series within each forest type (average of 10 plots per forest type). Mean interseries correlation calculations present the average of all pairwise Pearson product-moment correlation coefficients for each BAI series within a plot. Similarly, mean "interplot" correlations represent the overall degree of correspondence in growth patterns between plots within a forest type. We also evaluated Pearson's correlation coefficients of all possible forest-type pairs, as well as between watershed BAI time series, to see if growth patterns are statistically similar between certain forest types; this provides information on the scope of growth influences. We also evaluated mean interseries correlation strength among plots grouped by aspect and slope, and by species, size class, and sample size. Because this correlation analysis encompasses multiple scales, we can examine the correlation strength of growth patterns at these different scales (i.e., plot, forest

type, watershed) as an indication of the scale of the dominant growth influences.

Sensitivity analysis

We chose the following measures of tree growth and growth variability to provide a comprehensive view of the relative sensitivity of trees and forests to changes in growth-limiting factors:

- (1) Mean sensitivity — Difference between adjacent BAIs within an individual time series divided by the mean of the two increments, averaged over the entire series. This is a measure of the year-to-year variability in growth. A tree with a high mean sensitivity usually has experienced more growth limitation due to environmental factors, such as climate (Fritts 1976).
- (2) Standard error — Amount of variation in BAI relative to growth amount, taking sample size into consideration.
- (3) Coefficient of variation — Measure of relative variability in BAI, taking growth amount into consideration.
- (4) Growth variability versus growth amount — Forest types that grow more (average BAI) and have high growth variability (mean sensitivity and coefficient of variation) are more sensitive because they may have more dramatic swings in growth and productivity from year to year in response to environmental variability (Hessl and Peterson 2004).
- (5) Extreme growth — Number of years for which growth exceeds a threshold value (1 and 2 times the standard deviation above and below the mean).

Unless noted above, we calculated these sensitivity measures using individual BAI time series and then averaged the calculated values to obtain relative plot and forest-type sensitivity estimates. All of these measures were considered in making a final estimation and comparison of forest sensitivity.

Results

Descriptive statistics

The eight forest types in the Hoh and Dungeness watersheds have significantly different average and total basal areas (Table 1, $p < 0.0001$). These values also differ between time periods for each forest type ($p < 0.0001$). In general, basal areas and average BAI are higher for the Hoh forest types than for the Dungeness forest types, with the Hoh Sitka spruce and Hoh low forest types having the highest values. Total BAI, however, is highest in the Dungeness grand fir forest type (Table 1). Forest-type growth patterns (average and total BAI per hectare) differ between the two time periods, with most displaying higher growth during 1977–2000 ($p < 0.01$).

Correlation analysis

Plot

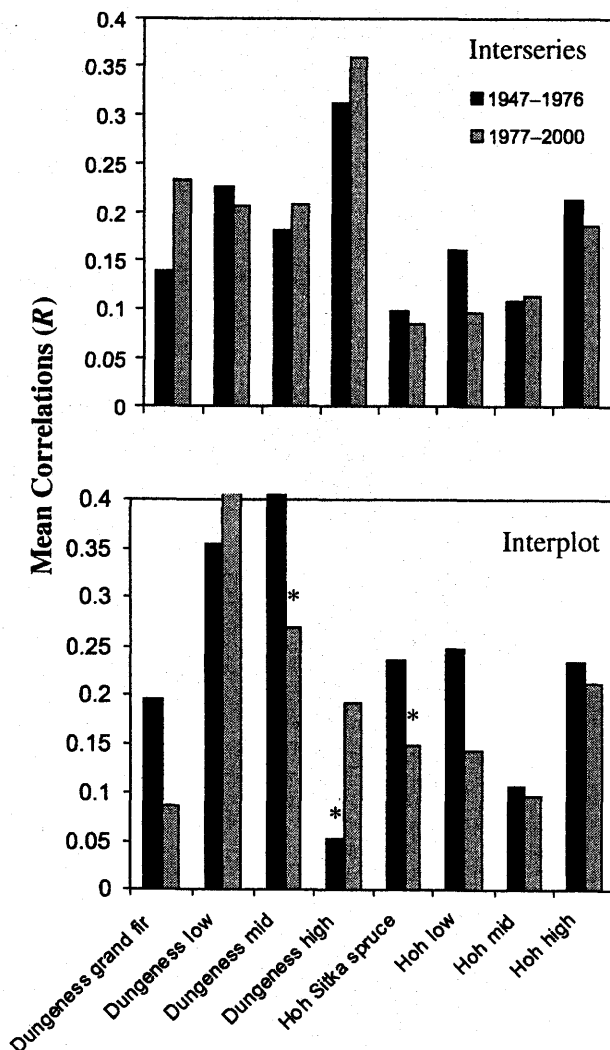
In general, tree BAI series within plots do not exhibit significant mean interseries correlations (Fig. 2). The strength of the within-plot correlation does not depend on the number of trees in the plot, aspect, or slope of the plot. During 1947–1976, plot mean interseries correlations differ by forest type ($p < 0.05$), but this is not the case during 1977–2000. Within-plot mean interseries correlations are stronger in the Dungeness watershed (1977–2000: $R = 0.251$, 1947–

Table 1. Comparison of different growth measures for the eight Olympic forest types during both time periods.

Forest type	2000		1977–2000			1947–1976		
	Average BA (m ²)	Total BA (m ² ·ha ⁻¹)	Average BAI (m ²)	Total BAI (m ² ·ha ⁻¹)	PW average BAI (m ²)	Average BAI (m ²)	Total BAI (m ² ·ha ⁻¹)	PW average BAI (m ²)
Dungeness grand fir	0.137	76.3	0.00163	0.871	-0.0150	0.00137	0.654	0.0704
Dungeness low	0.195	77.7	0.00140	0.370	0.136	0.00121	0.274	0.0450
Dungeness mid	0.195	74.0	0.00144	0.543	0.116	0.00129	0.496	0.105
Dungeness high	0.046	34.6	0.000549	0.286	0.122	0.000445	0.250	0.107
Hoh Sitka spruce	0.807	128	0.00471	0.652	0.0567	0.00451	0.582	0.148
Hoh low	0.818	158	0.00266	0.492	-0.0069	0.00257	0.419	0.114
Hoh mid	0.396	104	0.00160	0.385	0.157	0.00165	0.449	0.102
Hoh high	0.174	88.1	0.000859	0.423	0.120	0.000798	0.380	0.0745

Note: Average BA is the average basal area per plot within a forest type; average BAI is the average basal area increment per tree within a forest type. PW, prewhitened.

Fig. 2. Average plot mean interseries correlations for each forest type (top panel) and average forest type mean interplot correlations (bottom panel) for both time periods. Forest types that have significantly different mean interplot correlations between time periods are indicated by an asterisk.



1976: $R = 0.233$) than in the Hoh watershed (1977–2000: $R = 0.120$, 1947–1976: $R = 0.139$) ($p < 0.001$).

Forest type

Plot growth patterns within a forest type do not correlate well with each other (Fig. 2). During both time periods, the highest mean interplot correlations are for the Dungeness low and mid forest types. The Dungeness mid and Hoh Sitka spruce forest types have significantly stronger mean interplot correlations during the 1947–1976 time period than during the later period, and the reverse is true for the Dungeness high forest type.

Watershed

Within each watershed, BAI growth patterns for each forest type correlate significantly between all bordering forest types during both time periods of analysis (Table 2). In addition, there are some correlations between nonbordering forest types both within and across watersheds, and the strength of these correlations varies depending on time period or on the method of combination of individual BAI series. For example, within the Dungeness watershed, the low- and high-elevation forest types are significantly correlated during both time periods, but only for the total BAI measure. In addition, the Dungeness grand fir forest type correlates negatively with the Dungeness high forest type for some of the measures. Looking across watersheds, the average and total BAI growth patterns in the Hoh high and Dungeness mid forest types are significantly correlated during both time periods.

Overall, significant correlations between forest types are mostly positive, and few plots respond in opposite directions. The grand fir forest type in the Dungeness is the only forest type with very few positive correlations and with two significant negative correlations. Most positive correlations within and between watersheds do not include the two high-elevation forest types. Also, there are more significant correlations during 1947–1976 (53) than during 1977–2000 (35).

Subregional

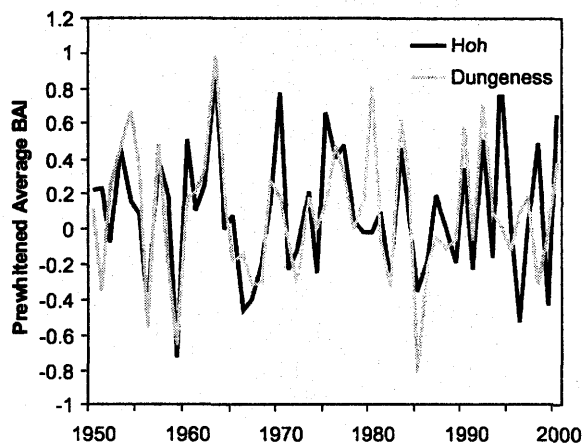
In addition to the positive correlations between bordering (and other) forest types, there is also a positive correlation between the combined BAI growth patterns for the Dungeness and the Hoh watersheds (Table 2, Fig. 3).

Table 2. Pearson's correlation coefficients (R ; $p < 0.05$) from correlation analysis of growth parameters by forest-type pairs, including various methods of compiling basal area increment (BAI) series for each time period.

Forest-type pairs	1977–2000			1947–1976		
	Total BAI (m ² ·ha ⁻¹)	Average BAI (m ²)	PW average BAI (m ²)	Total BAI (m ² ·ha ⁻¹)	Average BAI (m ²)	PW average BAI (m ²)
DU grand fir and DU low		0.80	0.44		0.72	0.37
DU grand fir and DU high	-0.47	-0.63			-0.41	
DU low and DU mid	0.85		0.69	0.80	0.39	0.82
DU low and DU high	0.44			0.55		0.38
DU mid and DU high	0.52	0.60		0.45	0.48	0.56
HO Sitka spruce and HO low	0.45		0.66	0.81	0.77	0.57
HO Sitka spruce and HO mid		0.46		0.31		0.39
HO Sitka spruce and HO high				-0.31		
HO low and HO mid	0.72		0.43	0.56	0.38	0.59
HO low and HO high						0.38
HO mid and HO high	0.48		0.74	0.50	0.38	0.51
HO Sitka spruce and DU grand fir				0.68	0.49	0.48
HO Sitka spruce and DU low	0.42				0.60	0.49
HO Sitka spruce and DU mid					0.40	0.50
HO Sitka spruce and DU high		0.48				
HO low and DU grand fir		0.42		0.74	0.57	0.52
HO low and DU low			0.41		0.75	0.71
HO low and DU mid				0.48	0.53	0.70
HO mid and DU ABGR				0.41		
HO mid and DU low			0.69	0.37	0.40	0.62
HO mid and DU mid		0.50	0.50	0.63	0.54	0.66
HO mid and DU high		0.42				
HO high and DU grand fir			-0.41			
HO high and DU mid	0.64	0.59	0.62	0.52	0.50	0.41
HO high and DU high					0.32	
HO and DU	0.43		0.43	0.87	0.82	0.73

Note: PW, prewhitened; DU, Dungeness; HO, Hoh.

Fig. 3. Prewhitened average watershed growth patterns for the Dungeness and Hoh watersheds. BAI, basal area increment.



Sensitivity analysis

Mean sensitivity

Mean sensitivities of BAI growth for forest types within the Dungeness and Hoh watersheds are significantly different ($p < 0.0001$). Mean sensitivities are not significantly dif-

ferent between time periods. For both time periods, the forest types of the Hoh watershed have significantly higher mean sensitivities than the forest types of the Dungeness watershed.

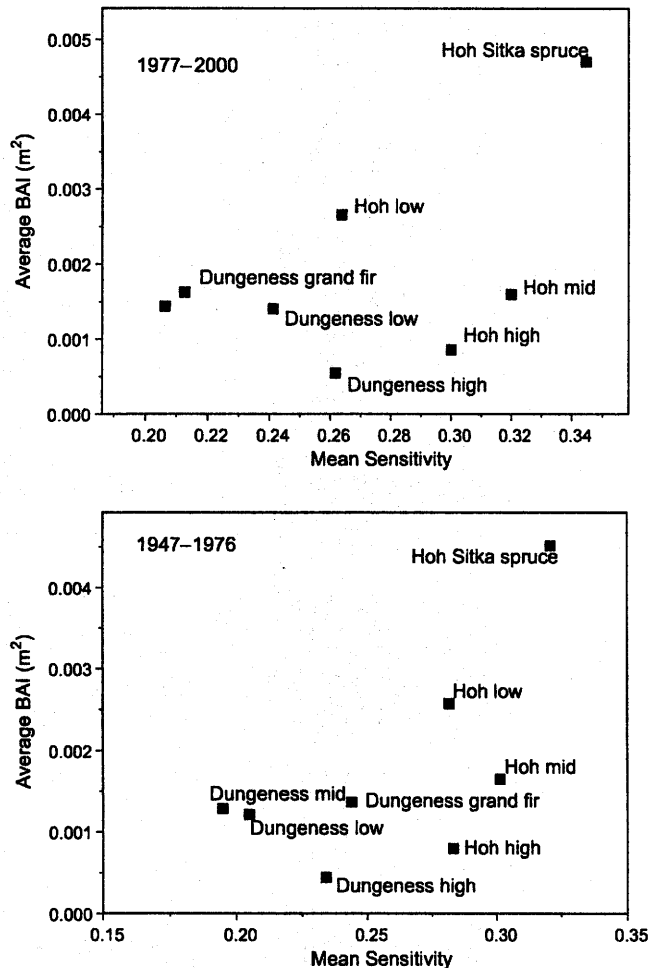
Standard error and coefficient of variation

For both time periods, standard errors are significantly different among forest types ($p < 0.00001$) and between watersheds ($p < 0.01$). The Hoh Sitka spruce forest type has the highest standard error, and the high-elevation forest types in both watersheds have the lowest standard errors, with similar values for the Dungeness low and mid forest types. In addition, the average standard error for the Hoh watershed is greater than that of the Dungeness watershed.

During the 1977–2000 time period, coefficients of variation for the forest types in the Hoh watershed are significantly different from each other, with the Hoh Sitka spruce forest type having the highest value ($p < 0.05$), and, on average, they are higher than those in the Dungeness watershed (Hoh average CV = 0.439, Dungeness average CV = 0.346; but significant at only $p < 0.10$).

During 1947–1976, the average coefficient of variation for the Hoh forest types is greater than that of the Dungeness forest types (Hoh average CV = 0.454, Dungeness average CV = 0.375; $p < 0.01$). In addition, coefficients of variation are significantly different among forest types within both the Hoh and Dungeness watersheds ($p < 0.05$), with the Dungeness

Fig. 4. Assessment of the sensitivity of the Olympic forest types to environmental change based on the characteristics of mean sensitivity and average basal area increment (BAI, m^2/plot) during the time periods 1977–2000 (top panel) and 1947–1976 (bottom panel).

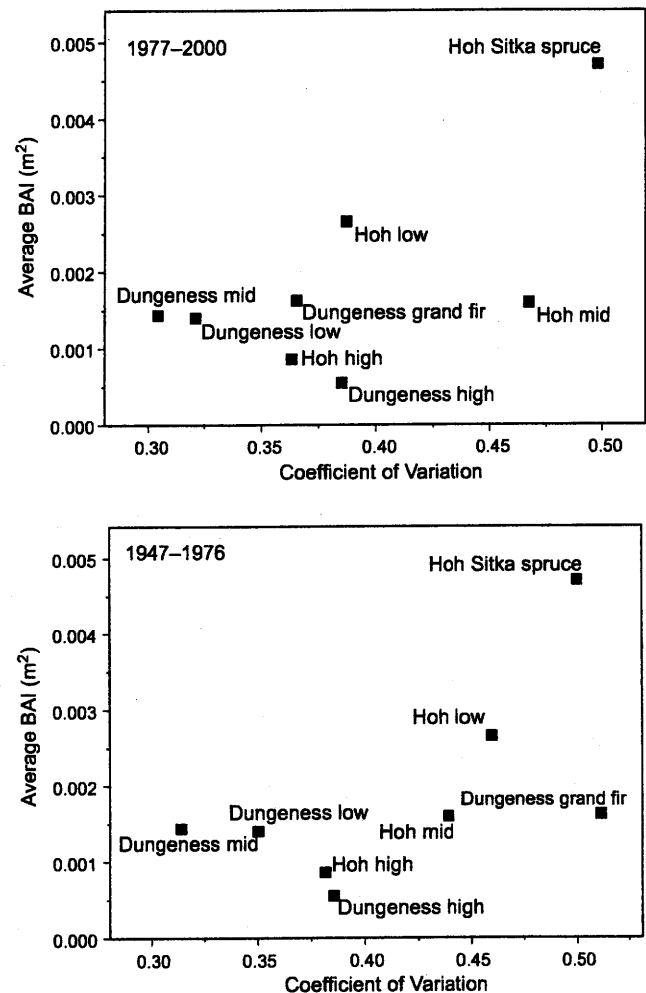


grand fir forest type having the highest average coefficient of variation followed closely by the Hoh Sitka spruce forest type.

Growth variability (mean sensitivity) versus growth amount

The Hoh Sitka spruce forest type has both the highest mean sensitivity (growth variability) and the highest average BAI (growth amount), and Hoh forest types had higher combinations of these two values than Dungeness forest types (Fig. 4). During 1977–2000, the Hoh mid and Hoh low forest types have less sensitivity than the Hoh Sitka spruce forest type, followed by the Hoh high, Dungeness high, Dungeness low, Dungeness grand fir, and Dungeness mid forest types. This ranking is similar during the 1947–1976 time period: Hoh Sitka spruce is followed by Hoh low and Hoh mid, then Dungeness grand fir, Hoh high, Dungeness high, Dungeness mid, and Dungeness low. In general, the Hoh forest types have higher rankings than the Dungeness forest types in comparing growth variability and growth amount.

Fig. 5. Assessment of the sensitivity of the Olympic forest types to environmental change based on the characteristics of coefficient of variation and average basal area increment (BAI, m^2/plot) during the time periods 1977–2000 (top panel) and 1947–1976 (bottom panel).



Growth variability (coefficient of variation) versus growth amount

Similarly, the Hoh forest types had higher combinations of coefficients of variation and average BAI than the Dungeness forest types during both time periods. When looking at this measure of growth variability compared with growth amount, the Hoh Sitka spruce forest type is still the leader in this sensitivity measure (Fig. 5).

Extreme growth

The Dungeness forest types and the Hoh Sitka spruce forest type have more years with BAI growth amounts greater than 1 standard deviation (SD) above the mean ($p = 0.05$) during 1977–2000 than 1947–1976, and the Hoh Sitka spruce and Hoh low forest types have more years with BAI growth greater than 2 SD above the mean (Table 3; $p < 0.05$). During this more recent time period, the Dungeness forest types have more years with BAI growth greater than 2 SD below the mean. During 1947–1976, forest types have similar num-

Table 3. Average number of years for each forest type with extreme growth responses (thresholds of one and two standard deviations (SD)) during both time periods.

Forest types	1977–2000				1947–1976			
	>1 SD above*	>1 SD below	>2 SD above*	>2 SD below*	>1 SD above	>1 SD below	>2 SD above	>2 SD below
Dungeness grand fir	4.2	2.9	0.9	0.0	4.4	4.2	1.4	0.2
Dungeness low	3.1	3.4	1.0	0.0	4.8	4.9	1.3	0.0
Dungeness mid	3.0	3.5	0.5	0.1	4.8	4.6	1.0	0.2
Dungeness high	3.6	4.0	0.3	0.3	4.8	4.3	0.9	0.3
Hoh Sitka spruce	4.4	3.2	0.0	0.4	4.5	4	1.2	0.2
Hoh low	4.2	4.0	0.2	0.4	4.3	3.9	1.4	0.1
Hoh mid	4.1	3.6	0.6	0.0	4.1	4.8	1.3	0.0
Hoh high	3.9	3.6	0.5	0.3	4.6	3.1	1.1	0.3

*Forest types differ significantly ($p < 0.05$) within the column.

bers of years with extreme growth above and below the mean.

During the earlier time period, more plots have average growth responses 1 SD above and below the mean than during the later time period ($p < 0.01$), whereas more trees during the later time period have extreme growth responses 2 SD above the mean ($p < 0.01$).

Discussion

Tree growth in the Olympic Mountains

Basal areas of Olympic mountain forest types as measured in this study (35 to 159 $\text{m}^2\text{-ha}^{-1}$) are comparable to those of other Pacific Northwest forest types (57 to 118 $\text{m}^2\text{-ha}^{-1}$ (Gholz 1982)). Relative to other Pacific Northwest forests, low-elevation Hoh forests (159 $\text{m}^2\text{-ha}^{-1}$) likely make substantial contributions to local and regional carbon budgets and to the annual variability in these budgets over time. In addition, while tree growth patterns do differ across the Olympic Mountains, they do not appear to be responding in opposite directions to the same climatic variations in west-side versus east-side forests, such as has been found for tree growth patterns between the west and east sides of the Cascade Range (Brubaker 1980).

Scale of growth responses to limiting factors

Heterogeneity in growth patterns at small scales (low mean interseries correlations within plots and forest types) suggests local growth-limiting factors affect tree growth and forest productivity in the Olympic Mountains. Microsite variability has been shown to be an important factor in annual tree growth in diverse geographic locations (Kienast et al. 1987). More trees could be experiencing a common growth-limiting factor at the plot scale, resulting in higher mean interseries correlations (at the plot and forest-type scales) in the Dungeness watershed than in the Hoh watershed. Based on climate-growth correlations performed by Nakawatase and Peterson (2006), it is likely that this common growth-limiting factor is summer moisture availability (tree growth in the Dungeness watershed is negatively correlated with summer temperature and positively correlated with summer precipitation and other measures of site water availability).

Diverse biophysical variables at both the plot and forest-type scales create disparate growth patterns. This study indi-

cates that at the plot scale, heterogeneous compositions in terms of species, size, and age of trees may produce multiple growth responses, even if plot environmental conditions are similar. In addition, previous research suggests that within forest types, steep environmental gradients may result in a variety of growth-limiting factors and growth patterns. For example, subalpine fir growth correlates with different climatic patterns in the Olympic Mountains, depending on its specific location (Ettl and Peterson 1995). Growth of subalpine fir in higher elevation, wet sites is limited by snowpack depth and length of growing season, but growth of subalpine fir in lower elevation, dry sites is primarily limited by summer soil moisture. Most sites evaluated by Ettl and Peterson (1995) would have fallen within an eastside high-elevation forest type similar to the Dungeness high forest type.

At large spatial scales (watershed and subregion), forest-type growth patterns show coherence (significantly positively correlated BAI growth patterns), which implies the top-down influence of climate as a growth-limiting factor on dominant growth responses of bordering forest types. Research by Nakawatase and Peterson (2006) suggests that tree growth at the mid and high elevations of the Hoh is limited by growing season length (via snowpack and winter precipitation), and growth of most trees in the Dungeness forests is limited by summer soil moisture, although less so at higher elevations.

Within the Dungeness watershed, growth of low- and high-elevation forest types is significantly correlated, but the Dungeness grand fir forest type correlates negatively with the Dungeness high forest type in half of the possible correlations. This could indicate that grand fir trees are responding with opposite growth trends to an overarching watershed scale climate-growth signal. For example, lower summer precipitation appears to result in lower tree growth in the moisture-limited Dungeness watershed (Nakawatase and Peterson 2006), but the same climatic variation (in the form of lower cloud cover and higher light availability) may have caused tree growth to increase in the Dungeness grand fir forest type, particularly because grand fir is restricted to sites with higher soil moisture (Henderson et al. 1989). Other studies have indicated that light is potentially a strong growth-limiting factor during Pacific Northwest winters (Winner and Thomas 1997).

In addition to the positive correlations between bordering (and other) forest types, there is also a positive correlation

between the overall BAI growth patterns for the Dungeness and Hoh watersheds. This subregional-scale correlation further demonstrates the effect of overarching climatic patterns on tree growth in the Olympic Mountains. Because the data were analyzed for the last part of the 20th century, this could indicate a dominant pattern of increasing growth during a period of increasing temperatures (this pattern in the Hoh watershed is driven by the Hoh Sitka spruce forest type); however, the slopes of the growth trends of these sites do not exceed 0.02 (Nakawatase and Peterson 2006), demonstrating a lack of longer term growth increases. Furthermore, McKenzie et al. (2001) caution against inferring the mechanisms responsible for growth patterns because tree growth response to climate might be delayed (Fritts 1976), and patterns of increasing growth that might be affected by increasing temperatures and CO₂ concentrations may eventually become limited by other factors (Briffa 1998; Vaganov et al. 1999).

The combination of difference in pattern at a relatively small scale and coherence of pattern at a larger scale is not uncommon. Different mechanisms may control growth variability according to the spatial scale of analysis (Innes 1998), and processes acting at one scale have lessening effects as one increases or decreases the spatial scale (Sheriff et al. 1995). However, McKenzie et al. (2003) found that models predicting individual species distributions with respect to climatic and biophysical variables are consistent across spatial scales, the largest scale containing two widely different physiographic locations (the steep North Cascade Range and the rolling Okanogan Highlands of Washington State) and multiple vegetation types. In this study, growth coherence at larger scales likely results from the majority of individual trees in a forest type responding similarly to climate conditions, whereas at smaller scales individual trees responding to more local growth signals lower the correlation strength. It is possible that larger sample sizes at larger scales (watershed, subregion) result in inflated correlations (at the plot scale, sample size does not affect correlation strength).

Forest sensitivity to environmental change

Tree growth in the Hoh watershed appears to be more sensitive to environmental variability than tree growth in the Dungeness watershed, with higher mean sensitivities, standard errors, and coefficients of variation. Correlation analysis suggests that most trees in the Hoh watershed are responding to an overarching growth signal, such as interannual variability in climate. Tree growth in the upper elevations of the Hoh watershed is tied to growing season length; however, tree growth in the lower elevations of the Hoh watershed was not directly related to changes in annual climatic variables (Nakawatase and Peterson 2006). Tree growth in the lower Hoh watershed may be affected by variables that are difficult to measure, such as interannual variation in light availability. This seems likely given the high variability of the Hoh Sitka spruce and Hoh low forest types. It is also possible that higher growth variability in the Hoh watershed is related to higher climatic variability (rather than higher sensitivity to climate).

Lower growth variability in the Dungeness watershed could indicate that growth is less tied to climate, or that most trees in this watershed experience consistent moisture limitations on growth. Zobel et al. (1976) found that grand fir saplings

in the eastern Cascade Range exhibited lower moisture stress than saplings in the western Cascades, despite being subjected to greater evaporative stresses. In this study, we speculate that most trees in the Dungeness watershed experience moisture stress (particularly in mid and low elevations), and that low growth variability is a result of consistently low soil moisture levels and high evaporative demands.

High-elevation plots are also sensitive to annual and interdecadal climatic variability. During the warm phase of the PDO, high-elevation subalpine fir stands in the Dungeness watershed and high-elevation Hoh plots have high mean sensitivities. Lower snowpacks and longer growing seasons may allow greater positive growth responses and higher variability in tree growth from year to year (Nakawatase and Peterson 2006). If future climate results in increased duration of snowpack, tree growth may be substantially reduced throughout higher elevation forest types.

The Hoh Sitka spruce forest type may be the most sensitive to environmental variability of all the Hoh and Dungeness forest types. It has the highest mean sensitivity, highest absolute growth amount (basal area and BAI), and highest growth variability (independent of growth amount), and is most likely to have extreme positive growth responses. Therefore, tree growth in the Hoh Sitka spruce forest type may be most likely to increase if annual climatic conditions are favorable (the range of this forest type is not likely to increase, as it has remained stable throughout the Holocene (L.B. Brubaker, personal communication, 2004)). Favorable conditions could include an increase in light availability, which may accompany increasing temperatures and (or) decreasing precipitation, because interannual variability is highest in the wettest plots during the wettest decades. The absorption of photosynthetically active radiation in Sitka spruce appears to be linearly related to the production of dry biomass (Wang et al. 1991). While Warkentin et al. (1992) noted that Sitka spruce trees in inland plantations in the Olympic Peninsula experienced increased water stress and decreased photosynthesis with increased vapor pressure deficits, which were related to decreased cloud cover, coastal Sitka spruce, such as those measured in this study, did not show this relationship. Therefore, possible increases in growth with increased light availability are not likely to be maintained beyond a certain threshold, as moisture availability becomes limiting.

Because trees in the Hoh Sitka spruce forest type also have the highest annual growth amounts, this forest type has the potential to act as a substantial carbon sink. This conclusion corroborates other empirical evidence that high-latitude, low-elevation maritime sites have experienced increased growth during the 20th century (McKenzie et al. 2001). In addition, Hessl and Peterson (2004) found that highly productive Douglas-fir forests in the Stehekin River watershed of the North Cascade Range are more sensitive to environmental change than any other forest type, suggesting the potential for substantial regional-scale impacts of climatic change on carbon storage. As the Pacific Northwest climate continues to warm (Mote 2003), the potential of these forests (and other lower elevation, highly productive forests, such as in the western Cascades, the Coastal Range of British Columbia, and southern Alaska) to be carbon sinks or sources is important for large-scale carbon assessment, management, and policy.

Effects of decadal-scale climatic variability on growth

While interdecadal climatic variability does not affect plot-scale growth variability, it does appear to influence growth at the forest-type and watershed scales. The Dungeness mid and Hoh Sitka spruce forest types had significantly higher mean interplot correlations during the cool phase of the PDO (1947–1976), suggesting these forest types have greater coherence of growth–climate relationships during this time period. Growth in these forest types may be limited by low temperature, high precipitation, and (or) low light availability, and during the warm phase, reductions in one or more of these growth-limiting factors result in decreased coherence of tree growth patterns. In contrast, the Dungeness high forest type had higher mean interplot correlations during the warm phase of the PDO (1977–2000), suggesting growth is more limited by summer soil moisture availability. Tree growth in the higher elevations of the Dungeness is less sensitive to summer precipitation than tree growth at lower elevations (Nakawatase and Peterson 2006). These results suggest that as summer soil moisture deficits are alleviated during the cool phase of the PDO, growth in the high elevations becomes less sensitive, while growth in the more moisture sensitive lower elevations remains tied to changes in summer precipitation and other summer moisture-related climatic variables during both phases of the PDO.

There were more significant correlations between forest type growth patterns at the watershed scale during the earlier cool phase of the PDO, suggesting that large-scale climatic regimes limit growth throughout the Olympic Mountains. Trees in all forest types (except the Hoh mid forest type) grew more during the warm phase of the PDO than during the cool phase. However, higher unmeasured mortality as a result of the longer length of time from the point of measurement to the cool phase could have affected plot-average BAI during this phase. Nevertheless, in the Olympic Mountains low temperatures, precipitation, and (or) light availability may be significant common growth-limiting factors. If future climate becomes warmer, growth-limiting factors in many Olympic forests may be alleviated, leading to increased growth. However, this pattern would likely cease beyond some threshold, and different growth factors would become limiting in some forest types (e.g., soil moisture availability in the Dungeness watershed (Briffa 1998; Vaganov et al. 1999)).

Interdecadal climatic variability also affects the frequency of annual extreme growth responses in both the Hoh and Dungeness watersheds. Climate during the cool phase of the PDO resulted in more extreme growth years above and below the mean in the Dungeness forest types. This may be an indication of the positive influence of increased moisture availability on tree growth in the Dungeness watershed. In addition, climate during the warm phase of the PDO has greater effects on extreme tree growth above the mean in the lower elevation Hoh forest types. This suggests that warmer temperatures and increased light availability may facilitate growth increases in these forests. This is further indication that a warmer climate may increase growth and carbon storage in low-elevation, wet forest types in the Olympic Mountains.

Examination of study methods

The growth measurements in this study likely underestimate actual forest growth amounts because we cannot ac-

count for belowground growth, shoot extension, branch and needle growth and production, reproduction, decomposition, or mortality. In addition, differences in these components may have affected the comparison of growth values among plots, forest types, and watersheds. However, our representation of growth patterns and connections to productivity are more complete than in typical dendrochronological studies because we analyzed all tree species and size classes and sampled a range of growth environments. A tradeoff of the extensive sampling approach is the small sample size of cores combined to create a given plot BAI series. Because of this, we were unable to analyze other aspects of the effects of climatic variability and change on forest ecosystems, such as the contribution of individual species to variability in growth patterns. Furthermore, the effects of climatic variability and change on species composition, a component this study did not address, is an integral piece in the overall understanding of the effects of climate on long-term changes in forest ecosystems.

The effects of climatic change on disturbance and biotic factors will also influence tree growth patterns. This limits our ability to predict tree growth response to climatic variability and change. Forests that are sensitive in this study will also be sensitive to changes in factors such as competitive regimes and disease and insect pressures. Similarly, because this study took place within relatively undisturbed forests, caution should be applied when extrapolating to intensively managed forests that may have younger trees and experience different magnitudes and frequencies of disturbance.

Although our methods are not direct indicators of forest productivity, they are unbiased surrogates for productivity and are time and cost efficient (Hessl and Peterson 2004). Accurate information on the location and extent of sensitive forests, which will likely have altered productivity in a greenhouse climate with warmer temperatures and altered precipitation, could help to determine changes in carbon dynamics throughout the region and allow resource managers to monitor and possibly mitigate for changes in sensitive forests (Hansen and Weltzin 2000; Aber et al. 2001).

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