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DOUGLAS-FIR GROWTH IN MOUNTAIN ECOSYSTEMS: WATER LIMITS TREE GROWTH FROM STAND TO REGION

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Abstract. The purpose of this work is to understand the nature of growth–climate relationships for Douglas-fir (*Pseudotsuga menziesii*) across the climatic dimensions of its niche. We used a combination of biophysically informed sampling (to identify sample sites) and dendroclimatology (to identify growth–climate relationships) along a climate gradient in northwestern United States mountain ecosystems from the western Olympic Peninsula, Washington to the eastern Rocky Mountain Front, Montana. We used a multi-scale sampling strategy that accounted for continentality, physiography, and topography as non-climatic factors that could influence climate and alter tree growth. We developed a network of 124 Douglas-fir tree-ring chronologies and explored growth–climate correlations across the sampled gradients. We considered two different spatial scales of monthly and seasonal climate variables as potential controlling factors on tree growth. Annual radial growth in 60–65% of the plots across the region is significantly correlated with precipitation, drought, or water balance during the late summer prior to growth and the early summer the year of growth. In a few plots, growth is positively correlated with cool-season temperature or negatively correlated with snowpack. Water availability is therefore more commonly limiting to Douglas-fir growth than energy limitations on growing season length. The first principal component derived from the chronologies is significantly correlated with independent drought reconstructions. The sensitivity of Douglas-fir to summer water balance deficit (potential evapotranspiration minus actual evapotranspiration) indicates that increases in April to September temperature without increases in summer precipitation or soil moisture reserves are likely to cause decreases in growth over much of the sampled area, especially east of the Cascade crest. In contrast, Douglas-fir may exhibit growth increases at some higher elevation sites where seasonal photosynthesis is currently limited by growing-season length or low growing-season temperature. Life-history processes such as establishment, growth, and mortality are precursors to changes in biogeography, and measurements of climate effects on those processes can provide early indications of climate-change effects on ecosystems.

Key words: climate change; climate effects; dendrochronology; Douglas-fir; ecological amplitude; ecophysiology; limiting factors; niche; Pseudotsuga menziesii; *tree growth; water balance deficit.*

INTRODUCTION

Tree species sensitivity to climate at continental scales is usually described in terms of biogeographic distribution; the factors limiting species ranges are often at least partially climatic (e.g., Thompson et al. 2000). Range limits for long-lived trees represent the integration of limitations on establishment, growth, and reproduction at time scales of several decades or longer. Effects of climate, therefore, influence life-history processes such as growth (Peterson and Peterson 2001) and seedling establishment (Daniels and Veblen 2004) well before noticeable biogeographic changes occur. Extreme events, such as multiyear droughts or large fires, can produce broad-scale, temporally coherent pulses of mortality that lead to rapid ecological changes (Allen and Breshears 1998). However, climate can also lead to gradual shifts in population or community processes such as differential species growth, turnover, or establishment, which play a role in biogeographical changes by altering community composition over large areas. Changes in growth and establishment (Stephenson and van Mantgem 2005) may presage measurable mortality in established trees. Understanding climate-mediated population processes, especially their underlying mechanisms and geographic distribution, is a key step to better prediction of climate-change impacts to forest ecosystems. For example, to model the future response of forest vegetation, quantitative relationships derived from long-term climate data and observed population processes at multiple scales can be efficiently extrapolated across mountainous terrain where such data are generally lacking. In this paper, we describe the application of hierarchical sampling, dendroecological

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methods, and gradient analysis to improve understanding of the climate mechanisms limiting growth of Douglas-fir [*Pseudotsuga menziesii* var. *menziesii* (Mirb.) Franco and *P. menziesii* var. *glauca* (Beissn.) Franco] in montane forests of the northwestern United States.

Growth–climate relationships derived from dendrochronological data represent one metric of temporal variation in climate-mediated ecosystem processes (Graumlich et al. 1989, Graumlich and Brubaker 1995). Variance in tree rings is typically controlled by the factors most influencing growth (Fritts 1976), and tree-ring evidence from a wide variety of biophysical settings supports the idea that tree growth is limited by water in some ecosystems and by energy (growing season length, degree days, or mean temperature) in other ecosystems (Waring and Running 1998). In arid ecosystems (usually montane to lower tree line), the interannual variability in tree rings is primarily related to factors affecting water supply, especially precipitation (Douglass 1919, Fritts 1974) or water balance deficit (Pederson et al. 2006). In ecosystems where precipitation is more abundant or energy is more limiting (usually subalpine or high latitude), factors affecting the length of the growing season (e.g., growing season temperature or snowpack) explain most of the variability in tree growth (Graumlich and Brubaker 1986, Peterson and Peterson 1994, 2001, Peterson et al. 2002, Nakawatase and Peterson 2006).

Ecological amplitudes of species are expected to be unimodal with respect to a single biotic or climatic gradient (Whittaker 1956), but can be shown to have nonnormal distributions in practice when multivariate climate relationships are considered (McKenzie et al. 2003). Some research indicates that tree growth can also be expected to follow modal distributions relative to climate, probably because the influence of limiting factors on ecophysiology and growth parallels limits on species distributions. For example, growth rates of mountain hemlock (*Tsuga mertensiana* (Bong.) Carr.) exhibit complex relationships in response to summer temperature (positive) and winter snowpack (negative) (Graumlich and Brubaker 1986, Peterson and Peterson 2001). At the scale of a stand, mountain hemlock growth might be controlled primarily by snowpack duration, but at regional scales, mountain hemlock can be either limited or facilitated by snowpack depending on its abiotic context (Peterson and Peterson 2001). Understanding the distribution of tree growth relative to climate across wide ranges of biophysical conditions requires surveying growth–climate relationships for stands and scales traditionally not sampled in dendroclimatic studies (Littell and Peterson 2005).

For such a survey to successfully compare stands across a species' niche, it is necessary to consider multiple scales of factors affecting the local climate to which such stands are subjected. For example, local topography can mediate the climate of a forest stand and moderate or exacerbate the influences of regional climate (Bunn et al. 2005, Holman and Peterson 2006). At larger scales, physiographic and topographic variability in the mountainous western North America leads to two extremes within forest ecosystems: (1) those that are characteristically water limited in places where annual precipitation is much less than potential evapotranspiration, and (2) those that are energy limited where potential evapotranspiration is much less than precipitation (Stephenson 1990). This contrast occurs because of the water and energy limits on photosynthesis. When more water can be evaporated and transpired than falls as precipitation, plant photosynthesis is water limited. In contrast, when more precipitation falls than can be evaporated or transpired, thermal or light energy tends to be limiting. Water balance variables are more "plant relevant" because they explicitly link climate and plant processes (Lookingbill and Urban 2005). They should therefore improve understanding of plant–climate relationships compared to temperature and precipitation alone (Stephenson 1998).

Hemispheric patterns of ocean–atmosphere interactions affect regional and subregional climate variability on time scales of years to several decades (e.g., Wang and Schimel 2003, McCabe et al. 2004). These patterns affect regional climate and can temporarily override conditions usually determined by local topography or physiography. Significant progress in understanding current and future climatic limitations on growth (and by proxy, other ecological processes such as productivity and ecosystem carbon balance) will be achieved if the mechanisms of such limitations are quantified across important climatic dimensions of a species' niche (i.e., a realized Hutchinsonian hypervolume [Hutchinson 1957] with some dimensions principally defined by climate).

To understand the climatic limitations on tree growth across a species' range, sampling methods must consider all climatic conditions in that range as well as the factors (e.g., topography) influencing growth–climate relationships at multiple scales (Littell and Peterson 2005). Networks of precipitation-sensitive (Watson and Luckman 2001, 2002) or temperature-sensitive (e.g., Wilson and Luckman 2003, Pederson et al. 2004) trees have been developed for climate reconstruction, but networks to examine variability in climate sensitivity across the biophysical niche of a species have not been established. Such a network would be an important step towards estimating the effects of climate change on growth and would be more informative than one based on only a fraction of regional tree populations with known sensitivity (Littell and Peterson 2005).

Prior research on growth–climate relationships of northwest Douglas-fir has focused on evaluating the role of climate in tree growth (Brubaker 1980, Case and Peterson 2005) and productivity (Hessl and Peterson 2004, Nigh et al. 2004) or on reconstructing climate from tree-ring sequences (e.g., Biondi 1999, Watson and Luckman 2002, Pederson et al. 2006). Brubaker (1980) described a dominant pattern of positive correlation

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between spring–summer precipitation and Douglas-fir growth, with a secondary contrast between the negative (west of the Cascade Range crest) and positive (east of the Cascade crest) correlations with winter precipitation and summer temperature. Short-term growth variability was predominantly related to growing season precipitation in several lower-elevation Cascades sites (Brubaker et al. 1992). Little et al. (1995) related low-elevation Douglas-fir growth to climate in the Siskiyou Mountains of Oregon and found moderate influences of temperature (negative) and precipitation (positive) on growth. Watson and Luckman (2002) found regionally coherent patterns of significant climate correlations with Douglas-fir growth in British Columbia and Alberta. Precipitation was positively correlated with growth in some chronologies in all months between April of the year prior to growth and August the year of growth, with highest sensitivity to prior July–August and current May–June precipitation. Temperature relationships with growth were negative during the growing season and weakly positive in winter, with the largest number of chronologies responding negatively to prior July and current June temperature. Pederson et al. (2006) found similar relationships for Douglas-fir in the Rocky Mountains of Montana and inferred that summer water deficit and Palmer drought severity index (PDSI) best described patterns of growth–climate correlations.

Recent studies of Douglas-fir and other species have examined growth–climate relationships across a range of environmental conditions (Littell and Peterson 2005), with a focus on controls of tree growth rather than on dendrochronological interpretation (Case and Peterson 2005, Holman and Peterson 2006, Nakawatase and Peterson 2006). Case and Peterson (2005) conducted an intensive dendroecological census of Douglas-fir in a north Cascade Range (Washington, USA) watershed and found both precipitation facilitation (lower elevation stands) and snowpack and temperature limitation (higher elevation stands) along a 1000-m elevation gradient. Two studies of growth–climate relationships in the Olympic Mountains of Washington showed that growth in multi-species stands was buffered from regional climate variability by local conditions (Holman and Peterson 2006), while the same climate variability clearly influenced growth at subregional scales in forest types limited by summer drought or snow (Nakawatase and Peterson 2006).

In this study, we use radial growth data from a network of Douglas-fir stands (coast Douglas-fir [*P. menziesii* (Mirb.) Franco var. *menziesii*]; Rocky Mountain Douglas-fir [*P. menziesii* var. *glauca* (Beissn.) Franco]) to develop growth–climate relationships along a gradient of maritime-to-continental climate in the northwestern United States. The distribution of Douglas-fir covers a large range of climatic (Thompson et al. 2000) and ecological (Franklin and Dyrness 1988, Hermann and Lavender 1990) conditions. We use and extend dendroecological principles to establish growth–climate relationships along abiotic gradients that encompass the range of environments inhabited by Douglas-fir in Washington (WA), Idaho (ID), and Montana (MT). Our objective is to describe correlations between Douglas-fir growth and climate across a significant portion of its range in this region and outline some likely physiological bases for these relationships. Our working hypothesis is that growth–climate relationships for Douglas-fir are structured along a gradient of water-balance deficit that integrates limiting and facilitating components of temperature and precipitation. Specifically, the climate variables most limiting to growth are spatially variable (e.g., Brubaker 1980, Case and Peterson 2005) but consistent with local ecohydrological regime; at some threshold, water ceases to be the most limiting factor, and energy begins to be more limiting.

Methods

Study area

This study focuses on mountain ecosystems between the maritime western Olympic Peninsula in western Washington and the continental eastern slope of the Rocky Mountains in northwestern Montana. A longitudinal transect from 124° to 113°18′ W between 47°30′ and 49° N latitude passes through four targeted sampling areas: Olympic National Park (ONP), North Cascades National Park (NCNP), the Selkirk Mountains in the Idaho Panhandle National Forest (IPNF), and Glacier National Park (GNP) (Fig. 1).

Mean climate varies from maritime ONP (warm, wet winters and cool, dry summers) to continental GNP (cold, dry winters and warm, dry summers) (Table 1). Estimates for mean climate used to target sample areas are in Table 1; modeled climate variables for each sample watershed are in the Appendix, see *Climate data* section below for details. Mean January temperature varies by 14°C between warmer sites in the ONP (4°C) lowlands and colder sites in GNP (−10°C; Fig. 2A); mean July temperature ranges from ~10°C in GNP to ~19°C in NCNP and IPNF (Fig. 2A). Mean January precipitation is highest in the maritime half of the gradient (Fig. 2B), and annual precipitation decreases from west to east along the transect (>500 cm at highest plot elevations in ONP to ~70 cm at lowest plot elevations in IPNF and GNP; Fig. 2C). Growing season energy/water ratios (Fig. 2D) indicate that strong gradients were sampled for GNP, IPNF, and ONP with more variability evident in NCNP.

Dominant parent materials in the study region are marine sandstone with valley-bottom Quaternary glacial deposits in ONP; metamorphosed gneiss, orthogneiss, and granodiorite (with other intrusions and Quaternary deposits) in NCNP; metamorphosed granite in IPNF; and metamorphosed sedimentary rock in GNP. Soils are generally rocky and skeletal (Appendix).

The composition of forest with canopy Douglas-fir varies with elevation, aspect, and location. Pure or

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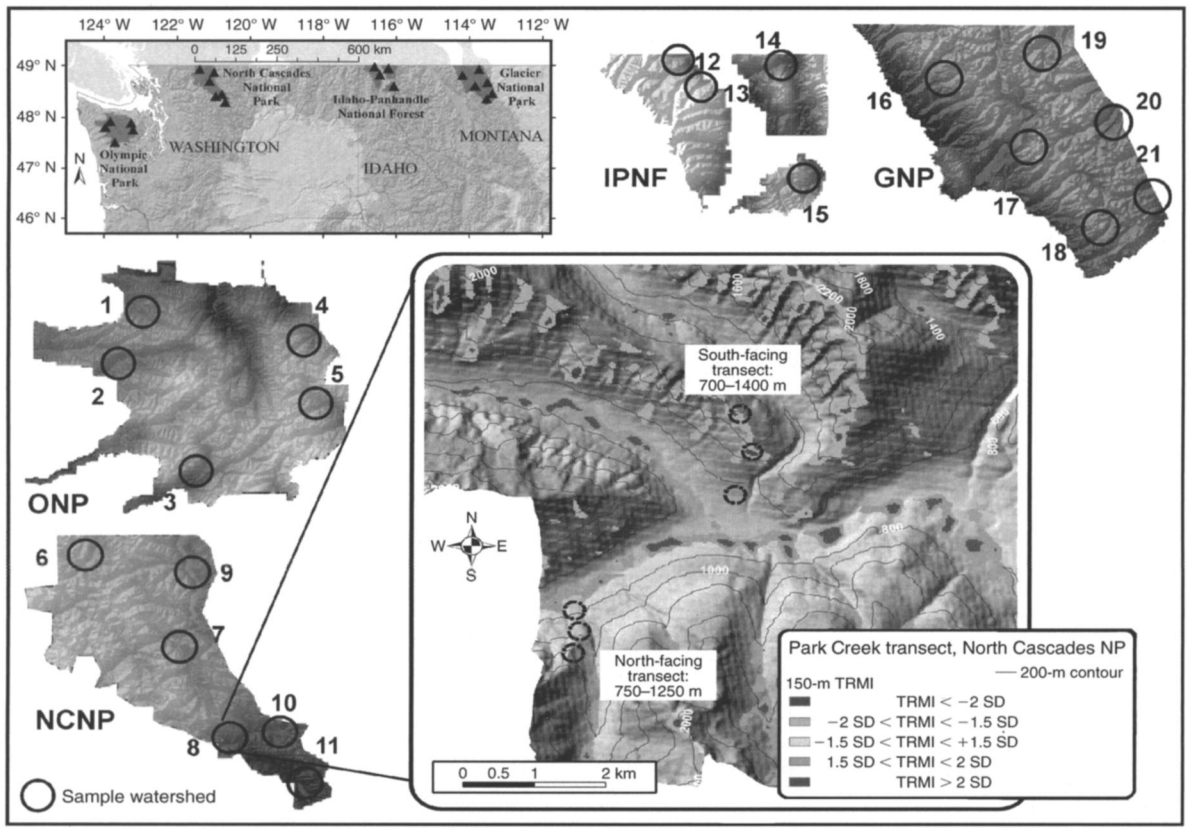

FIG. 1. Multi-scale sampling locations for Douglas-fir chronologies. Sample sites in three national parks and one national forest comprise the network of tree-ring sites describing the range of Douglas-fir in the northwestern United States. Sample watershed numbers refer to site numbers in the Appendix. Dark gray, solid shading in the upper left inset indicates the range of Douglas-fir; solid triangles are the sample watersheds, corresponding to the circles in the separate national park or forest maps. Shading in maps of individual sample areas indicates mean June–August DAYMET (modeled) precipitation: darker watersheds represent less precipitation; lighter areas represent more precipitation. The enlarged map of sample site 8 in North Cascades National Park (NCNP) shows TRMI (topographic relative moisture index, a proxy metric of relative moisture) and location of plots (circles) in one sampled watershed as an example.

TABLE 1. Hierarchical sampling strategy for evaluating Douglas-fir growth responses to climate.

Hierarchy level and location	Range of DAYMET targeted climate	
	Annual precipitation range (cm)	July temperature range (°C)
Physiography†		
Olympic Mountains: Olympic National Park (ONP)	244–533	11.6–16.1
Cascade Range: North Cascades National Park (NCNP)	92–219	12.4–19.8
Selkirk Mountains: Idaho Panhandle National Forest (IPNF)	71–128	14.0–18.6
Northern Rocky Mountains: Glacier National Park (GNP)	68–190	9.2–17.5
Watershed topography: two aspects and three elevations		
North and south aspects	approximately the same	less north, more south
Lowest, mid, and highest local elevation	decreasing from high to low elevation	decreasing from low to high elevation
Stand‡		
Sampling unit	approximately the same	approximately the same

Notes: This maritime to continental climate transect spans 47°30′ to 49° N, 124° to 113°18′ W, after Littell and Peterson (2005).
† Four mountain ranges, each with west–east rain shadow.
‡ There were 10–15 trees within each plot, one core per tree.

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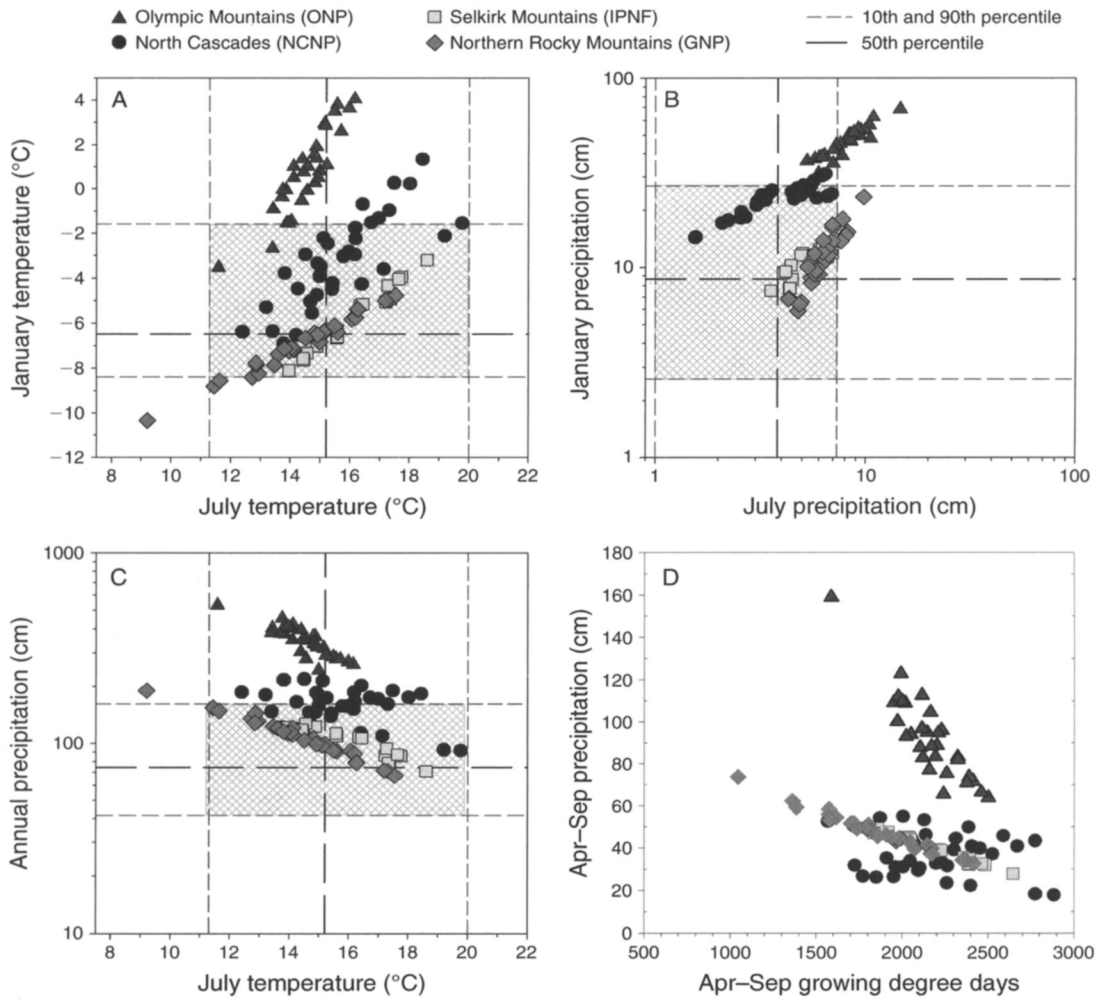

FIG. 2. Climate sampling space for Douglas-fir. Cross-hatched boxes indicate the two-dimensional climate niche for Douglas-fir for the North American continent. Values of plot locator points were determined from DAYMET maps of the indicated climate variables for the period 1980–1997. Sampled plots are depicted in two-dimensional climate space for 10th and 90th percentile limits (light dashed lines); the 50th percentile median (bold dashed lines) indicates continent-wide climatic limits for Douglas-fir described in Thompson et al. (2000). After Littell and Peterson (2005), by permission of *The Forestry Chronicle*. Note the log scales in panels (B) and (C).

nearly pure stands of Douglas-fir occur in all four areas, but are most common in eastern ONP and NCNP. In western ONP, lowland forests are dominated by Sitka spruce (*Picea sitchensis* (Bong.) Carr.), western hemlock (*Tsuga heterophylla* (Raf.) Sarg.), and western redcedar (*Thuja plicata* Donn ex D. Don). At higher elevations, Douglas-fir grows with Pacific silver fir (*Abies amabilis* Dougl. ex Forbes), western hemlock, mountain hemlock, and subalpine fir (*Abies lasiocarpa* var. *lasiocarpa* (Hook.) Nutt.). In eastern ONP and northwestern NCNP, Douglas-fir and western hemlock are often dominant at low elevations, with components of western redcedar, grand fir (*Abies grandis* (Dougl. ex D. Don) Lindl.), or in drier sites, lodgepole pine (*Pinus contorta* Dougl. ex Loud. var. *latifolia* Engelm.). In southeastern NCNP, Douglas-fir, ponderosa pine (*Pinus ponderosa* Dougl. ex Laws), and lodgepole pine are common low-elevation species. High elevations in eastern ONP and NCNP are similar to those in western ONP, including western hemlock, mountain hemlock, and Pacific silver fir; in more continental areas, lodgepole pine, subalpine fir, and Engelmann spruce (*Picea engelmannii* Parry ex Engelm.) are dominant or codominant on dry high-elevation sites. In IPNF and western GNP, western larch (*Larix occidentalis* Nutt.), western hemlock, Douglas-fir, and ponderosa pine, with occasional western redcedar, are common at low elevations. High elevations in IPNF include western white pine (*Pinus monticola* Dougl. ex D. Don), subalpine fir, western hemlock, and western larch. High elevations in GNP include lodgepole pine,

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subalpine fir, Engelmann spruce, and occasionally whitebark pine (*Pinus albicaulis* Engelm.).

Site selection and sampling

We used a combination of geospatial analysis and sampling theory to identify sampling locations in each of the four targeted areas (Fig. 1). The sampling design was informed by four nested factors that bracket variability in growth as a function of climate (Table 1). First, the location of a stand along the maritime-to-continental gradient influences the amount and seasonality of temperature and precipitation. The CLIMET project transect (Fagre et al. 2003), from the maritime Olympic Peninsula in Washington to the continental eastern slope of the central Rocky Mountains in Montana, provided a prototype for this gradient. Second, mountainous terrain in western North America influences precipitation via orographic effects (e.g., Loik et al. 2004). We focused on a few watersheds on each side of the Olympics, Cascades, Selkirks, and northern U.S. Rockies to bracket this physiographic variability (Fig. 1). Third, within a watershed, aspect influences local climate by modulating daily and seasonal distribution of light and temperature, and as a consequence, moisture through evapotranspiration. We sampled north-facing and south-facing slopes within each watershed to provide maximum contrast in topographic influence on climate. Finally, elevation within an aspect determines the seasonal distribution of degree-days, precipitation, and snowpack duration (e.g., Running et al. 1987). We bracketed local Douglas-fir elevation ranges from valley floors to its local maximum elevation to sample a broad range of biophysical conditions.

We used geostatistical analysis of the watershed topography (slope, aspect, and elevation from USGS 10-m digital elevation models [DEM]) and local climate to stratify plot locations. From the USGS DEM, we derived a soil moisture proxy, topographic relative moisture index (TRMI; Parker 1982). Low values of TRMI indicate higher runoff, more sunlight, and longer days due to steeper slopes, convex terrain, and/or south aspect; high values of TRMI indicate low runoff and ambient energy due to shallower slopes, concave terrain, and/or north aspect. TRMI provides a useful means of comparing local ($\sim$100 $\times$ 100 m) topographically influenced water availability. We also used elevation-specific modeled 1980–1997 climate averages (DAYMET, 1-km resolution [Thornton et al. 1997]) to select target watersheds (Fig. 1) across a range of mean precipitation. At the time of writing, DAYMET was the most appropriate climate product because it allowed us to distinguish between relatively local changes in mean climate that other datasets could not. The sampling strategy outlined in Table 1 produced gradients of DAYMET climate parameters that bracket a substantial fraction of the range of Douglas-fir in the western United States (Fig. 2).

Tree-growth data

In 2003 and 2004, we located each plot with a global positioning system and sampled a single increment core from 10–15 canopy-dominant Douglas-fir trees in each plot (variable density plots). Each plot was defined a priori as relatively homogeneous in aspect, slope, and TRMI. Minimum sample size was determined by comparing published estimates of the mean number of trees required to achieve an appropriate signal quality in Douglas-fir dendroclimatic reconstructions (Mäkinen and Vanninen 1999, Watson and Luckman 2002). In practice, some plots had higher sample numbers than others because the number of sound trees and the number of successfully cross-dated samples varied. To minimize the influence of disturbance on growth–climate relationships, we avoided plots with obvious signs of recent disturbance by fire, insects, or windthrow; in some cases this criterion required that we locate substitute plots in comparable landscape facets.

Using standard dendrochronological techniques (Stokes and Smiley 1968, Fritts 1976, Pilcher 1990), we prepared all samples and measured tree-ring widths to the nearest 0.001 mm. All samples were visually crossdated and checked for missing rings or other cross-dating errors with the program COFECHA (Holmes 1999). We produced standardized residual tree-ring chronologies for each elevation and both aspects within each watershed for six plot chronologies per watershed.

A double detrending (standardization) method was employed (Fritts 1976) to remove biological growth trends and minimize the influence of unidentified stand disturbances or inter-tree competition. The first detrending was intended to remove the age-related growth trend using a negative exponential curve or linear trend line of negative or zero slope (Cook and Holmes 1999). In 10 younger ($<$100 yr) plots, the linear alternative occasionally resulted in predicted values less than 0, and in these cases we employed Hugershoff growth curves (e.g., Briffa et al. 2001) to simultaneously include the earliest portion of the tree's growth and still retain a reasonable detrending fit to the rest of the time series. The second detrending was intended to remove residual stochastic (with respect to climate) age trends induced by stand dynamics, and we used a cubic smoothing spline (CSS) that preserved 50% of the variance at 128-yr wavelength. We opted to stabilize the variance using a hybrid method that accounts for changing sample size and other sources of heteroscedasticity, such as a strong relationship between variance and mean ring width over the span of a tree's life. We used both the rbar method (mean correlation of all tree-ring series within a population, independent of sample size; Briffa 1995) and a CSS equal to 67% chronology length because sample size changed appreciably through time in many plots. Finally, the residual chronology was developed using autoregressive modeling tailored to the autoregressive order of each tree to account for the autocor-

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relation that can be imparted by climatological, ecophysiological, and morphological influences on tree growth. The bi-weight robust mean of all series (Cook and Holmes 1999) was calculated to reduce error attributable to nonsynchronous disturbances in the final mean chronology (Cook 1985). This procedure produces a time series with uncorrelated temporal error for each plot that can be statistically compared to climatic time series without artificially inflating correlation measures of linear association.

For each chronology, we calculated mean sensitivity (MS; Fritts 1976), first-order autocorrelation, expressed population signal (EPS; Wigley et al. 1984), and number of trees required to exceed an EPS value of 0.85. These parameters describe the nature of the variability in the chronologies.

Climate data

Long records of mountain climate are not available or suffer from inconsistent observation, especially for higher elevation locations. To achieve good comparison with tree-growth data, we sought long, consistent records of observed climate variables that met two basic criteria. First, we required records that preserved both interannual variability and mean climatic conditions in sample plots. We obtained monthly state climate-division total precipitation (PPT), average temperature (T), and PDSI data for 1895–2002 from the National Climatic Data Center (Karl et al. 1986; data *available online*).[5] Climate divisions containing sample plots include Washington divisions 1, 4, 5, and 6, Idaho division 1, and Montana divisions 1 and 3. We also used the program AET (Gavin and Hu 2006) to develop estimates of water-balance deficit from the divisional precipitation and temperature records. For this calculation, we assumed a field capacity of 100 mm, which is generally conservative for skeletal mountain soils (Stephenson 1988) and is corroborated by gridded field capacity data (Webb et al. 2000). We also assumed a nonlinear declining availability function for plant-available water in the rooting zone (Willmott 1985).

Although divisional climatic data satisfied the observed interannual variability criterion, plot climate, especially temperature and winter precipitation, varies with elevation across climate divisions. We therefore obtained more specific $0.125° \times 0.125°$ gridded climate data from the input (developed from NCDC data) and output data sets for the variable infiltration capacity hydrological model (VIC; Hamlet and Lettenmaier 2005). VIC uses interpolations of weather station precipitation and temperature data, as well as estimates of soil and vegetation properties, to estimate daily and monthly climate variables in places where minimal climate data exist. It is parameterized specifically to estimate hydrological variables such as evapotranspiration, snow water equivalent (SWE), and soil moisture. VIC driving data and modeled output variables therefore have the potential to provide estimates of climate at scales more appropriate to the sampled watersheds than can be achieved with divisional climate. Variables included were 1915–2002 monthly mean temperature, maximum temperature, and minimum temperature; monthly total precipitation and evapotranspiration; and first-of-the-month soil moisture and SWE. All VIC variables except SWE were calculated for the mean elevation in the VIC cell; SWE was specific to four elevation bands within each VIC cell.

[5] ⟨http://www1.ncdc.noaa.gov/pub/data/cirs/⟩

Analysis

We used Pearson product-moment correlations to compare each plot residual chronology to the full monthly and seasonal climate time series from the climate division (1895–2002) and VIC cell (1915–2002) containing the plot. The sheer number of growth–climate correlations guarantees some spurious significant relationships. Rather than imparting an overly restrictive correction (e.g., Bonferroni) that could mask patterns of low but significant correlations, we assumed that consistent patterns (across adjacent months and between sites) in the sign and magnitude of significant growth–climate correlations ($P \leq 0.01$) indicated a pattern worth investigating further. Seasonal aggregations of monthly climate variables are sometimes better than monthly approximations of the actual ecophysiological mechanisms leading to annual growth–climate correlations (e.g., Fritts 1976, Watson and Luckman 2002). When several months exhibited similar correlations for a climate variable, we pooled the monthly values and tested the correlation between the composite seasonal variable and the tree-ring chronologies. For divisional climate, we chose to retain the same seasonal groupings for all variables: Annual (Jan–Dec), water year (Sep–Oct), spring (Apr–Jun), growing season (May–Sep), summer (Jun–Aug) and July–August for total PPT, mean T, mean PDSI, and total deficit. Due to the larger number of VIC climate variables, we used only specific groups of months with similarly high numbers of growth–climate correlations to develop seasonal climate variables.

We conducted a principal components analysis (PCA, e.g., Preisendorfer 1988) on the residual chronology covariance matrix. When applied to a matrix of time series covariances, PCA solves for uncorrelated linear combinations of time series that explain the maximum amount of variance in the multidimensional space described by all the constituent time series. To assess the influence of a declining number of constituent chronologies and to determine the robustness of the PCA variance explained through time, we conducted six different PCA analyses on arbitrary centennial time periods: 1917–2002 (all 124 sampled chronologies), 1900–2002 (117 chronologies), 1800–2002 (71 chronologies), and 1700–2002 (22 chronologies), as well as the

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TABLE 2. Selected chronology summary statistics.

Area	Mean sensitivity	First-order autocorrelation	EPS	Trees to EPS 0.85†
GNP	0.20 ± 0.04	0.52 ± 0.11	0.87 ± 0.06	6.8 ± 2.0
IPNF	0.21 ± 0.03	0.56 ± 0.08	0.89 ± 0.05	5.9 ± 1.6
NCNP	0.15 ± 0.03	0.55 ± 0.12	0.89 ± 0.03	7.1 ± 1.5
ONP	0.13 ± 0.01	0.54 ± 0.08	0.87 ± 0.04	8.3 ± 2.2

Notes: Values (mean ± SD) were calculated over all sample chronologies within targeted sampling areas. EPS stands for expressed population signal.

† The number of trees required to obtain expressed population signal equal to 0.85.

1800–1900 and 1700–1900 portions of the latter two periods.

Given the repeated importance of summer water-balance deficit, precipitation, and temperature in prior results as well as our own analyses, we compared the first PC of the study network to instrumental (1900–2002) and reconstructed (1800–2002) PDSI grid point time series (Cook et al. 2004) for the study region. We conducted two separate PCAs on the instrumental and reconstructed covariance matrices of PDSI grid points 25, 32, 43, 55, 68, and 83 to develop regional PDSI time series.

It is unlikely that a pure drought signal would be the driving factor in growth in all plots in this study. We therefore sought to understand the role of mean site water supply in mediating the relationship between tree growth and climate. Following Milne et al. (2002), we constructed an estimate of water surplus (precipitation minus evapotranspiration divided by precipitation) in the environment for each of the VIC cells used in the study and arrayed the correlation coefficients for two of the most important variables from the seasonal climate analysis above along the resulting gradient.

RESULTS

We sampled trees in 21 watersheds (Fig. 1, Table 2, Appendix), for a total of 124 chronologies (1388 trees; mean plot chronology $n = 11.2$ trees). When arrayed in climate spaces described by Thompson et al. (2000), the sample plots describe a significant fraction of the climatic range of Douglas-fir (Fig. 2). Our transects failed to capture the coldest January/warmest July (Fig. 2A) and driest January/driest July (Fig. 2B) quadrants of the range of Douglas-fir, which lie in the most continental (e.g., interior British Columbia, Alberta, and Wyoming) and arid (e.g., southwestern United States) portions of the species range.

Mean sensitivity was on average higher in GNP and IPNF than in NCNP and ONP, and the number of trees required to achieve an EPS of 0.85 was highest in ONP and lowest in IPNF (Table 2). Mean first-order autocorrelation was ~0.55 in all four areas. EPS in most plots exceeded 0.85, although in about 15% of the plots, the entire 1900–2003 common period was not present in enough trees to estimate the number of trees required to reach the 0.85 value. Relaxing the common period to 1925–2003 generally alleviated the problem. The mean length of the chronologies was 260 yr (range 91–689 yr).

Growth–climate correlations

Divisional and VIC precipitation were similarly correlated with tree growth across the entire geographic range sampled. July, August, and September in the year prior to measured growth and May, June, and July in the year of growth had the largest number of significant positive correlations with tree-ring time series (Fig. 3A, B). Divisional lag 1 July, August, and September precipitation were significantly correlated with more chronologies in IPNF than GNP, NCNP, and especially ONP. VIC precipitation correlations were more consistent among sample areas across the months. VIC climate-growth correlations were much stronger than divisional climate-growth correlations for ONP.

Temperature variables were generally less frequently important than precipitation variables (Fig. 3C, D). July and August precipitation in the year prior to growth, as well as June and July precipitation the year of growth, were positively correlated with Douglas-fir growth in more plots than temperature variables for the same periods. Lag 1 (year prior to growth) April and November divisional temperatures were positively correlated with growth at a number of plots in ONP and NCNP (Fig. 3C). A similar pattern is evident in the VIC relationships except that some plots in IPNF and GNP also had a positive lag 1 November temperature relationship (Fig. 3D). VIC lag 1 October and November average minimum temperatures were positively correlated with tree growth in a few plots, especially in ONP and IPNF (Fig. 4A). Lag 1 November maximum temperature was also positively correlated with tree growth in some plots (Fig. 4B). Lag 1 July and August average maximum temperatures (as well as average minimum July temperature in IPNF) were negatively correlated with growth (Fig. 4A, B), and year of growth June and July maximum temperature exhibited a similar pattern, but more correlations occurred in GNP (Fig. 4B). Warmer late fall temperatures are generally associated with increased growth (Figs. 3C, D and 4A, B), but this relationship is not as common as the negative association with maximum temperature in the previous summer.

VIC soil moisture in the year prior to growth was significant for most months in most plots, but relatively

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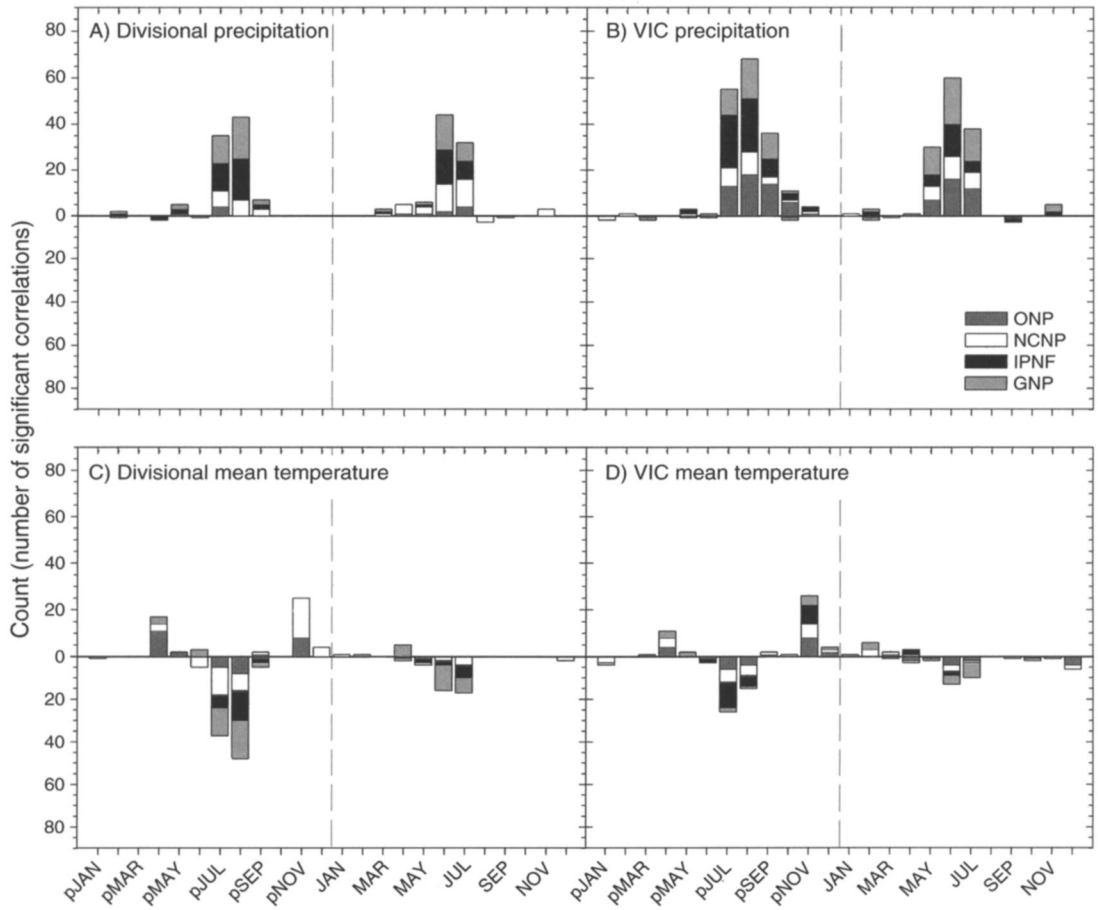

FIG. 3. Monthly divisional (left-hand panels) and variable infiltration capacity (VIC; right-hand panels) hydrological models for (A, B) precipitation and (C, D) mean temperature relationships with growth. Bars indicate the number of significant ($P < 0.01$) correlations between lag-1 (e.g., pJAN) or year-of-growth (e.g., JAN) precipitation and tree-ring time series from all watersheds. In this and all subsequent correlation plots, positive counts are above the line, and negative counts are below. Counts have been weighted such that the different numbers of sample chronologies in Olympic National Park (ONP), North Cascades National Park (NCNP), Idaho Panhandle National Forest (IPNF), and Glacier National Park (GNP) have the potential to contribute equally to the total count and area in each bar. The maximum number of significant correlations is therefore 144, not 124, so that the area in the bars is directly comparable.

unimportant (except in October) during the year of growth (Fig. 4C). Tree growth is frequently correlated with soil moisture between January and April in the year prior to growth, less frequently in May to July, and increasingly frequently from July to December (Fig. 4C). Evapotranspiration has a weaker year-prior pattern of correlations than soil moisture, and it also has a complex pattern of both positive and negative correlations from June to September in the year prior to growth (Fig. 4D). SWE (not shown) had few significant monthly relationships, although ONP, NCNP, and GNP had a few positive correlations with January–May SWE.

Divisional water-balance deficit (negative) and PDSI (positive) (Fig. 4E, F) were consistently correlated with tree-ring time series. Significant relationships with water-balance deficit were primarily lag 1 July, August, and September and year of growth June and July. Significant correlations were most numerous in IPNF in all but lag 1 July. ONP had few year-of-growth correlations with water-balance deficit. Significant correlations were common in lag 1 August, September, October and May, June, July, and August PDSI in the year of growth, but PDSI was significantly correlated with plot chronologies in most months, except in ONP (Fig. 4F).

Seasonal aggregations of divisional precipitation and temperature were more frequently correlated with tree growth than monthly time series (Fig. 5A, B). Lag 1 July–August precipitation was positively correlated with growth in most plots (Fig. 5B), and temperature for the same months exhibited negative correlations with tree-growth Fig. 5A). Correlations with July–August precipitation/temperature variables were significant more frequently than extended summer variables derived from

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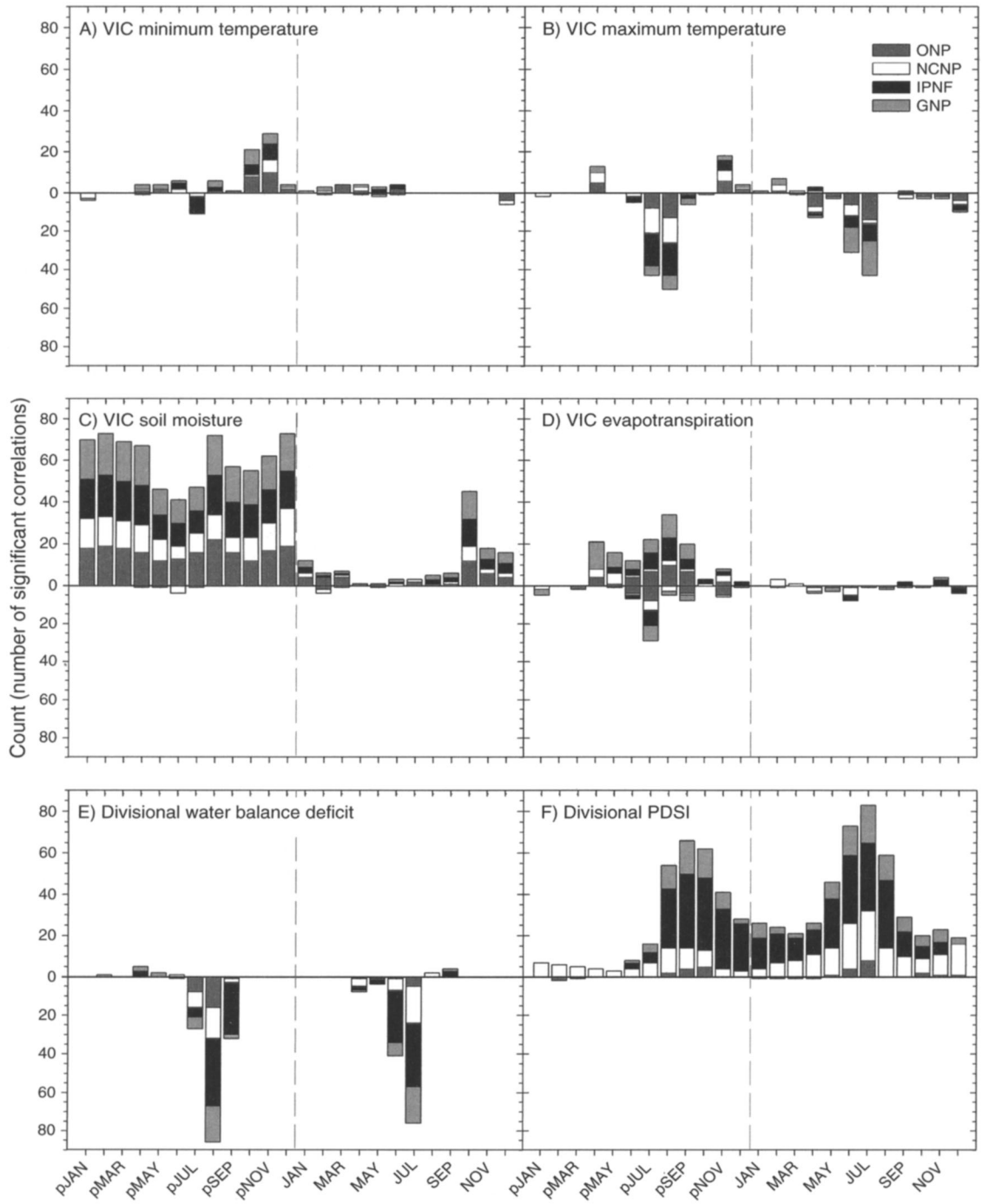

FIG. 4. Monthly VIC and divisional climate relationships with growth: (A) VIC minimum temperature, (B) VIC maximum temperature, (C) VIC soil moisture, (D) VIC evapotranspiration, (E) divisional water balance deficit, and (F) divisional Palmer drought severity index (PDSI). The summary count of significant correlations between monthly temperature (divisional and VIC climate) and tree-ring chronologies is indicated.

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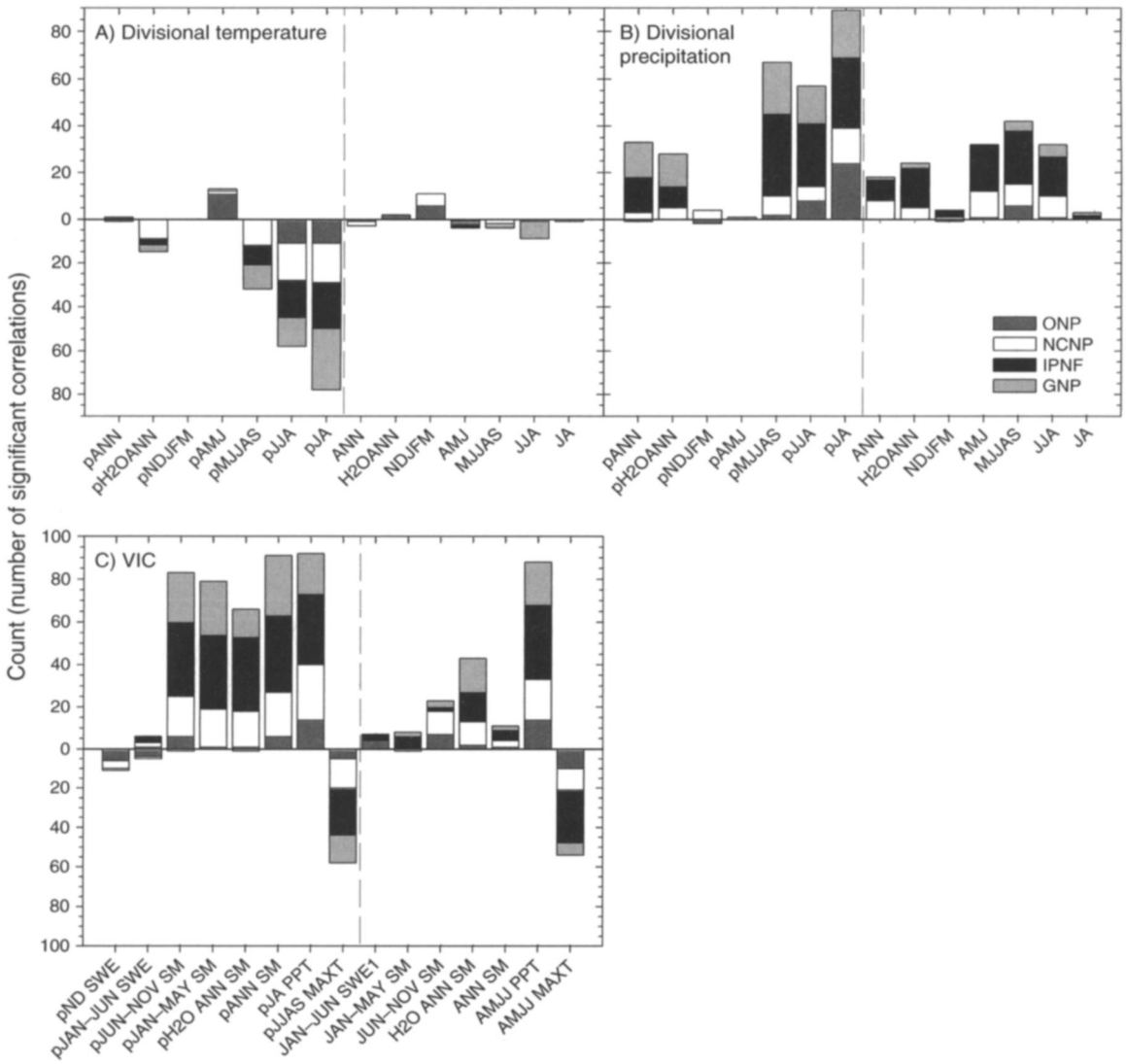

FIG. 5. Summary counts of seasonal (A, B) divisional and (C) VIC climate correlations with growth. Seasonal variables are listed by consecutive months (e.g., AMJJ, Apr–Jul; JJA, Jun–Aug; NDJFM, Nov–Mar; H2O ANN, water year). Abbreviations are: SM, soil moisture; SWE, snow water equivalent; ANN, annual; PPT, precipitation; MAXT, maximum temperature.

July–September or June–August data (Fig. 5A, B). GNP and IPNF plots were most often correlated with precipitation in the water year prior to growth, and IPNF and NCNP plots were most frequently related to year-of-growth water-year precipitation (Fig. 5B).

VIC seasonal climate variables were also more often significantly correlated with tree growth than were monthly variables. Seasonal soil moisture was important in IPNF, NCNP, and GNP and relatively unimportant in ONP (Fig. 5C). Lag 1 annual average soil moisture and lag 1 July–August precipitation were positively correlated with growth in most plots, while lag 1 June–September average maximum temperature was negatively correlated with growth in half the plots. April–July precipitation (positive) and April–July average maximum temperature (negative) in the year of growth were most often correlated with tree growth (Fig. 5C). In some plots, November–December SWE in the year prior to growth (winter prior to growth) was negatively correlated with tree growth, while January–June SWE the year of growth was occasionally positively correlated (Fig. 5C).

In summary, the most important relationships across the different sample areas in the transect are negative temperature (especially maximum temperature) and positive precipitation correlations in the late spring/early summer the year of growth and the mid-to-late summer the year prior to growth. These relationships are

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TABLE 3. Principal components analysis (PCA) results for different time periods.

Period	Number of chronologies	Variance explained		
		PC1	PC2	PC3
1917–2002	124	0.34	0.13	0.06
1900–2002	113	0.37	0.11	0.09
1800–2002	71	0.35	0.12	0.08
1700–2002	22	0.38	0.11	0.10
1800–1900	71	0.37	0.11	0.07
1700–1900	22	0.37	0.11	0.09

corroborated by plant-relevant variables including water balance deficit, soil moisture, and PDSI. However, seasonal soil moisture and precipitation are important in a maximum of 65% of the plots (Fig. 5C).

Principal components analysis

PCA of the residual chronologies for the common period (1917–2002) explained 53% of the total variance in the data set in three principal components (Table 3). PC1 (34%) is positively correlated with all residual chronologies (Fig. 6, mean $r = 0.55$, range 0.17–0.87). The strongest relationships occur in IPNF and western GNP, and the weakest occur in western ONP and NCNP (Fig. 6). PC2 (13%) represents a west–east contrast between ONP and NCNP on one hand (negative correlations) and IPNF and GNP (positive in correlations) on the other (Fig. 6). The variance explained by PCA is not sensitive to the time domain chosen for analysis (Table 3), and much of the common information is preserved during the 1800–2002 period. The 1700–2002 period consists primarily of chronologies in ONP and NCNP, so we eliminated it from further analysis because it is likely that the patterns are not comparable with the other periods given the obvious west–east split indicated by PC2 in the other time periods. The third and fourth PC time series were not interpretable in terms of elevation, aspect, or park/forest. PCA results indicate that the common signal among all plot chronologies is strongly related to reconstructed summer PDSI (Fig. 7), and that the variance explained by the three leading PCs does not change appreciably during the last 300 years (Table 3).

Tree-growth sensitivity to climate along a surplus water gradient

At a particular point along the surplus water gradient, there is a considerable range of correlation coefficients between tree growth and hydroclimate variables (Fig. 8). However, the correlation between lagged water year soil moisture and tree growth declines toward zero as surplus water increases, while the correlation between tree growth and June–July water balance deficit in the year of growth increases linearly toward zero with the same increase (Fig. 8).

DISCUSSION

Hierarchical sampling to assess tree growth

Bracketing the likely determinants (topography, physiography) of mountain biophysical gradients (Fig. 2) and using two different scales of climate variables allowed us to contrast the effects of local biophysical and climatological variables on tree growth. While inferences in this study depend primarily on correlations, the significance of (physically focused) divisional climate variables and (biologically focused) VIC variables indicate the potential to interpret climate–growth relationships over broad geographic areas. The primary response in tree growth was a similar pattern of correlations with monthly and seasonal climatic variables across most sites, and there is little evidence of important, widespread topographic and physiographic differences in growth response to climate. The main differences are in the mean sensitivity of tree growth in different sample units (Table 2) and the decreasing importance of summer water balance and precipitation variables in the wettest plots (Fig. 8). This study focuses on *variability* in tree growth through time; it is possible that the primary influence of topography for montane Douglas-fir is in *mean* growth related to site constraints on productivity. Our sampling methods could have demonstrated patterns of contrasting climate sensitivities (e.g., Case and Peterson 2005), but the most important limiting factor across the sample transect appears to be the common influence of regional climate.

The possibility that fine-scale factors (such as competition or microclimate) are commonly limiting and "scale up" to the regional relationships we observed

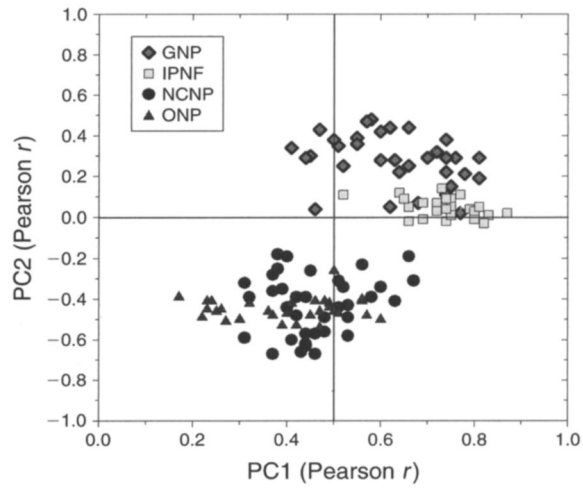

FIG. 6. PCA scores: Pearson correlations between plot time series and the first two principal components of the 1917–2002 PCA. PCA (see *Methods: Analysis*) includes all residual chronologies during the common period (1917–2002). There are no factors on the axes; this is an EOF/PC analysis, so what is expressed is the site loadings on the first and second PCs, and the values are correlation coefficients.

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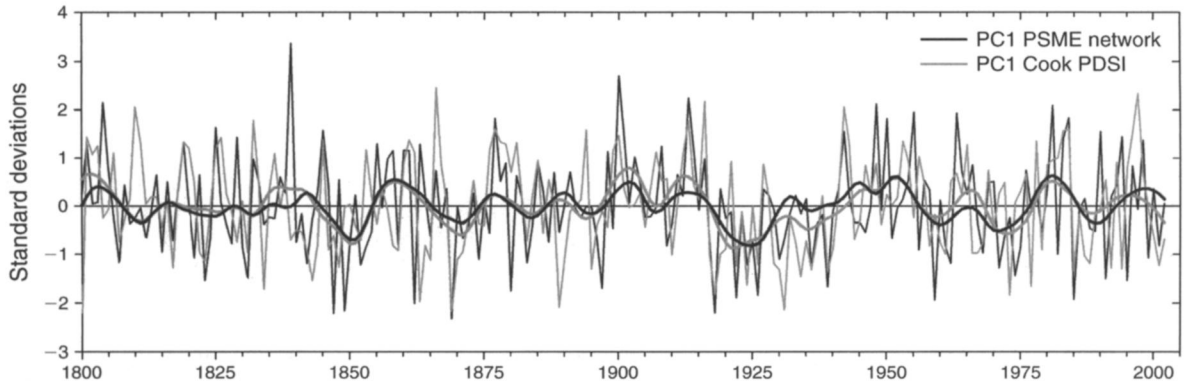

FIG. 7. Douglas-fir ("PSME") network PC1 time series and PC1 of regional reconstructed ("Cook") PDSI. PCA comparison of the 1800–2002 common signal from this study and the common signal from six PDSI (Palmer drought severity index) grid point reconstructions over the same region is shown. Bold lines indicate 21-yr lowess-smoothed time series (PSME, black; PDSI, gray).

exists, though given the range of plot climates inferred from VIC (Appendix), it is unlikely. A logical follow-up to this study would be to examine the within-stand and within-watershed differences in growth/climate relationships, both for the variability in growth and the mean growth rate, but such analysis is beyond the scope of this study.

Growth–climate relationships

Sampling along the full climatic range of Douglas-fir in northwestern mountain ecosystems allowed us to quantify growth–climate correlations in a wide variety of climatic settings. Groundwater and summer precipitation are the main sources of water for tree growth at most locations once snowpack has melted, and the widespread importance of hydroclimatic variables such as precipitation, water balance deficit, and PDSI indicate that water supply is often the most limiting factor.

In contrast, Douglas-fir growth in high-elevation plots was sometimes more limited by factors usually associated with subalpine tree growth (e.g., Graumlich and Brubaker 1986, Peterson et al. 2002, Case and Peterson 2005), where warmer growing seasons and shorter winters with less snowpack cause increased growth. Positive correlations of growth with average and minimum temperatures in April and November the year prior to growth (Fig. 3C, D) indicate that growth in the coolest, wettest end of the transect (Fig. 2) are at least partially limited by shorter growing seasons. We did not find a strong positive role of winter temperature as described in prior studies (Brubaker 1980, Brubaker et al. 1992), perhaps because we sampled Douglas-fir at higher elevations where warm winters would be unlikely to have a positive effect on growth. All mid-to-late summer average and maximum temperature correlations were negative (Figs. 3C, D and 4B), indicating high temperatures are limiting in summer.

Water-balance deficit and PDSI correlations (Fig. 4E, F) corroborate both the positive summer precipitation (Fig. 3A, B) and negative summer temperature (Fig. 3C, D) correlations. Once soil moisture is relatively low, precipitation represents the water available for plant growth and temperature represents an estimate of the atmosphere's ability to draw moisture out of plants (e.g., Stephenson 1990). An important unknown is the quantity and importance of water deep in the substrate. While other factors (such as soil or wind) play a role in site water balance, precipitation and temperature, integrated over a season, appear to be well correlated with Douglas-fir growth.

Seasonal integration of the factors limiting and facilitating tree growth increases confidence in significant monthly relationships, and suggests the importance of ecophysiological mechanisms that operate across several months or seasons. Seasonal growth–climate correlations produced more significant relationships than monthly growth–climate correlations (Fig. 5A, B) for the most important relationships identified in the monthly analysis. Variables that are important at more than half the sample plots indicate that the most proximate climate control on growth is a combination of temperature-driven water demand and precipitation-driven water supply in the year prior to and year of growth.

At the limits of Douglas-fir distribution, the strength of the relationships between growth and the most important climate variables either intensifies or erodes. In ONP, for example, fewer plots are significantly correlated with climate variables related to water supply, because soil water does not limit growth in this maritime environment. At some of the highest elevation plots in all sample areas, early winter precipitation falling as snow is a limiting variable (Fig. 5C), probably because higher snowpacks are more likely to persist into early summer, thus decreasing the length of the growing season (Graumlich and Brubaker 1986, Peterson et al. 2002). Case and Peterson (2005) documented this relationship for Douglas-fir in NCNP, and the same pattern occasionally emerges in this study at high-

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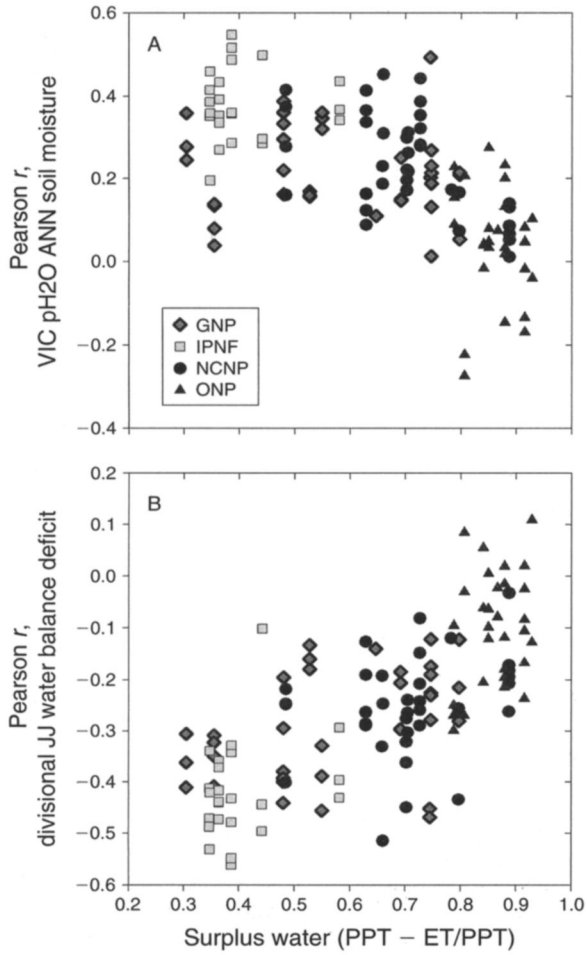

FIG. 8. Surplus water gradients and growth sensitivity to moisture variables. Relationships between mean annual surplus water at sample locations and climate-growth coefficients. (A) Correlations between lag 1 hydrological year (Oct–Sep) soil moisture and tree growth decline along a gradient of surplus water, while (B) correlations between year-of-growth June–July water-balance deficit increase along the gradients. PPT, precipitation; ET, evapotranspiration.

elevation sites where abundant snowpack accumulates or persists. However, the negative influence appears confined to early winter (Nov–Dec); snowfall after January appears to have a positive influence, presumably through its effect on growing-season water supply.

A common growth signal

A moderately strong correlation exists between the dominant signal in our chronology network and independently reconstructed PDSI at annual to decadal time scales. This implies that the climate regime to which most of the trees respond is driven by larger scale influences, perhaps modes of coupled ocean–atmosphere variability. The relationship between this regional PDSI time series (Fig. 7) and the common signal in the 1900–2002 and 1800–2002 study network is significant (1900–2002, $r = 0.46$; 1800–2002, $r = 0.37$). The main difference between the study network PC1 and reconstructed PDSI PC1 for the period 1800–2002 is the failure of the network to capture the full range of precipitation sensitivity captured by the PDSI network (Fig. 7). For example, the wet period between 1900 and 1915, and the 1930s drought, are known periods of above and below average precipitation, respectively, but the network PC exhibits less variance during these periods than the Cook et al. PDSI reconstruction (Fig. 7). Another explanation is that the mountain soil profiles in which the sampled trees for this study are rooted are frequently well drained and skeletal, accentuating sensitivity in locations where climate alone may not produce high variability in radial growth given adequate soil water holding capacity.

The ubiquity of relationships indicating water limitation underscores the need to understand growth–climate relationships across broad ranges of biophysical conditions; the tree species assemblage alone would not have led us to believe growth in many stands was usually water limited. For example, in IPNF, we sampled plots in which Douglas-fir is sympatric with western hemlock and western redcedar (species that are considered less tolerant of low soil moisture), but Douglas-fir growth was still negatively correlated with water balance deficit. Meinzer et al. (2007) showed that Douglas-fir had a higher rate of water extraction than western hemlock and a subsequently higher rate of hydraulic redistribution during dry periods, which could explain such sympatry. PCA indicates that the factors most limiting to growth are similar over a wide variety of ecological locations, and that the influence of local factors should be detectable as departures from the regional pattern of climate influences on growth.

Physiological explanation of growth–climate relationships

The most important relationship between Douglas-fir growth and climate along this study transect is water limitation. Ultimately, mechanistic understanding of the role of climate in physiological relationships that cause increment growth variations along the transect depends upon quantification of local soil–plant–water relationships and ecophysiological responses that are beyond the scope of this study. However, the frequency of correlations between Douglas-fir growth and ecohydrological variables points to water-limited physiological processes. Net photosynthesis in Douglas-fir is known to decrease with increasing vapor pressure deficit (Grieu et al. 1988) and water stress (McMurtrie et al. 1990), which explains the direct negative effects of temperature and positive effects of precipitation on growth during the warmest months. It is important to note that the growth–climate relationships observed in this study likely result from the weekly to seasonal cumulative effects of physiological mechanisms that have time scales of days or less. More explicit physiological mechanisms are implicated, however, and there is a need to

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understand the different roles of carbon assimilation, photosynthesis, and/or respiration, that underlie growth–climate relationships. In terms of plant–water relations at seasonal to annual time scales, individual trees employ two important mechanisms to limit the negative effects of weather and seasonal climate on growth. These are regulation of (1) transpiration (by altering stomatal conductance and leaf area) and (2) the distribution of roots and water in the soil profile (hydraulic redistribution). Regulation of transpiration via stomatal closure or decreases in leaf area will potentially have negative impacts on carbon balance, the latter especially when drought is followed by periods of adequate soil moisture. Loss of leaf area likely represents an important long-term impact on stem growth because carbon will be allocated to increasing foliage area during either seasonal or inter-annual periods of adequate moisture. Prolonged droughts result in stomatal closure, loss of foliage area, and increased allocation of carbon to roots. The latter comes at the expense of carbon for either foliage/crown development or, more likely, aboveground cambial growth.

Regulation of transpiration limits water loss per unit carbon assimilation and is achieved by limiting the conductance of water through the stomata. Decreased stomatal conductance can result in increased water use efficiency because stomatal closure limits transpiration relatively more than photosynthesis. However, under sustained water stress, stomatal restriction on carbon assimilation reduces net photosynthesis; as water-balance deficit increases and a minimum threshold soil water potential is approached, stomata close, foliar water potential declines, and photosynthetic capacity in Douglas-fir declines (Teskey et al. 1995). The importance of one or more direct mechanisms may depend on the severity of water stress; Warren et al. (2004) suggest that for conifers, the diffusional limitation of transfer conductance (the ratio of photosynthesis to the difference between intercellular and chloroplast CO_2) is implicated during low to moderate water stress, whereas decreased conductance of CO_2 across the mesophyll (Evans et al. 1986) is also implicated during severe water stress. Regardless of the mechanism, a limitation on assimilation likely explains the relationship between evapotranspiration and/or water balance deficit and growth in the year of growth. The strength of the correlation between growth and soil moisture (positive, Fig. 4C) and water balance deficit (negative, Fig. 4E) in the year prior are more challenging to interpret in terms of tree regulation of transpiration. The abrupt change in the magnitude of the correlation between growth and soil moisture suggests that an irreversible ecophysiological process that influences subsequent assimilation or photosynthetic capacity (such as bud set, e.g., in coastal Douglas-fir [Lavender et al. 1968]) must also be affected. It is possible, for example, that low soil moisture during the growing season prior, particularly in late July through early September, may have consequences on foliage expansion during the following year by affecting the number of buds developed and the number of needles developed per bud.

Growth does not respond the same way to summer AET (actual evapotranspiration, evapotranspiration in VIC) across the transect. It is likely that the mixed signal in July (Fig. 4D) the year prior to growth represents a divide between plots that are (1) sensitive to increased water (positive growth correlations) and (2) those that are sensitive to higher temperatures (negative growth correlations). AET can represent either abundant water supply that meets environmental demand, or it may indicate that all available water is evaporated or transpired (Stephenson 1990); the interpretation rests on potential evapotranspiration (PET). The nature of the evapotranspiration relationship could be affected by species, age, size, growth conditions, and genotype, all of which vary across the sample transect. However, the common growth response to annual drought suggests that if these variables are important factors, they are influencing the unexplained residual, not the dominant, observed relationships which are consistent with water-balance deficit limitation. For example, net carbon assimilation and transpiration appear to be differentially limited by hydraulic capacity of different sized Douglas-fir, but these differences were evident in wetter sites (Moore et al. 2004) or during wet and mild conditions (McDowell et al. 2005). Moore et al. (2004) observed higher transpiration rates in young (40 yr) vs. old (450 yr) riparian Douglas-fir stands but these differences were not observed during drought (McDowell et al. 2005).

Another mechanism which could affect growth–climate relationships in Douglas-fir is hydraulic redistribution (e.g., Domec et al. 2004, Warren et al. 2005, 2007, Meinzer et al. 2007), which refers to the capacity for trees to uptake water from deep soil layers and release it into the upper layers of the soil profile during periods of low transpiration (e.g., Warren et al. 2005, Meinzer et al. 2007). Hydraulic redistribution allows trees to minimize changes in stomatal conductance in response to drying in the upper soil layers in which water is depleted first during short term drying events and is driven either hydraulically or chemically, i.e., abscisic acid (Warren et al. 2005). In sites where deep soils are rarely depleted, this strategy may reduce the negative impacts of seasonal low precipitation such as suboptimal photosynthetic efficiency in moderately dry sites or loss of hydraulic conductivity due to xylem embolism in the driest sites (e.g., Domec et al. 2004). However, in sites where deep soils are depleted frequently or where poor soils result in low field capacity, it is possible that hydraulic redistribution could result in the lagged growth correlations observed for soil moisture (Fig. 4C) due to soil water recharge in the deepest layers that is subsequently redistributed to shallow soils. This could be indirectly important because of its influence on the maintenance and longevity of fine roots. The capacity for hydraulic redistribution in Douglas-fir stands

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indicates that the effects of climate on tree-growth can be contingent on stand or watershed characteristics (soil depth and field capacity, stand position within the watershed) that interact with climate to determine local water limitations. This may explain some of the variation in growth sensitivity to hydroclimatic variables at a given point on the water limitation gradient (Fig. 8) because hydraulic redistribution can vary substantially within stands and across ecosystems (Warren et al. 2007).

While the dominant growth–climate relationships are consistent with water limitation, some high elevation stands have growth–climate relationships more consistent with energy-limited environments. The few observed negative correlations between Douglas-fir growth and snowpack are probably due to growth reductions caused by low soil temperatures and delayed cambial expansion in spring (Graumlich and Brubaker 1986, Peterson and Peterson 2001, Peterson et al. 2002). This inference is corroborated by observations of soil temperature controls on photosynthesis at upper tree line (Day et al. 1989). In addition, Douglas-fir branch and crown morphology is less resistant to heavy snowfall than most subalpine species and is therefore susceptible to snow damage, although this might manifest as a persistent response over many years. In years when growth continues into late summer due to adequate water supply, a warm autumn can increase annual net photosynthesis. Positive correlations between growth and autumn temperatures may also be the result of fewer nighttime freezes (Hällgren et al. 1990). Similarly, warm spring temperatures can increase cambial expansion at the beginning of the growing season and increase the rate of repair to frost damage occurring in chloroplasts over the winter (Lundmark et al. 1988).

We focus primarily on seasonal to interannual growth–climate relationships, but physiologically speaking, it is also possible that there are climate-driven carbon allocation feedbacks to growth that occur on interannual to longer time scales. Because many of the important growth–climate correlations are lagged as much as 18 months, storage or coupled source–sink relationships (e.g., both photosynthesis and respiration) may explain some of the variation in growth. Lags could also result from delays in opportunities to use stored resources for growth, much as in trees at tree line (Körner 2003). Needle longevity or other long-term impacts to photosynthesis (Reich et al. 1992) might affect the growth signal for seasons or years following the direct climatic conditions resulting in changes in LAI. Gower et al. (1992) observed significantly longer leaf longevity for Rocky Mountain Douglas-fir in central New Mexico (7–9 yr, with a maximum of 20 yr) than for lowland Douglas-fir in Washington (4–5 yr [Turner 1975]). The role of increased water availability observed in a multi-year manipulation of water (double ambient precipitation) in Rocky Mountain Douglas-fir (Gower et al. 1992) shows large shifts in carbon allocation, from belowground net primary production to aboveground net primary production and from emphasis on large roots and fine roots (the latter also have much reduced mortality) to small roots. These responses can occur fast enough to explain the lagged relationships often observed in tree-growth time series, and may indicate that the role of interannual climate variability in tree growth is a combination of source and sink feedbacks rather than a straightforward climate limitation on photosynthesis. A similar mechanism relates increases in leaf area index (LAI) to increased stem volume increment in Douglas-fir (Schroeder et al. 1983), but Gower et al. (1992) note that it is particularly difficult to separate the influence of increased water availability from increased nutrient availability because the two are positively correlated.

The fact that the most frequent growth-limiting factors appear to be water supply and temperature-driven evaporative demand during the growing season, even in relatively mesic sites, points to growing season water balance deficit and its associated ecophysiological impacts. Stephenson (1990) has shown empirically that water balance deficit limits the distribution of biomes in the western United States, and Waring and Franklin (1979) suggested that the primary factor explaining the dominance of conifers in the Pacific Northwest is low summer precipitation and high evaporative demand. Others have shown that growth can be theoretically asymptotic (Loehle 2000) with temperature and/or growing degree days, and that range limits of tree species should change relatively slowly due to temperature limits alone. If growth is a proxy for other life history processes underpinning biogeography, our results indicate that it is unlikely that Douglas-fir in the PNW will exhibit substantial range contractions unless water balance deficit increases substantially. It is possible, however, that the species northern and high elevation range limits could increase if the climatic limitations to growth are relaxed and minimize the growth tradeoffs associated with these environments (Loehle 1998).

Climate change and implications for ecosystem management

Increased April to September temperature (expected to be +3.2°C by 2080 [Mote et al. 2005]) without increases in precipitation, soil moisture reserves, or CO_2-induced increases in water use efficiency is likely to cause decreased growth of Douglas-fir over much of the mountainous northwestern United States, especially in eastern NCNP, IPNF, and western GNP. Evapotranspirative demand on plants increases sharply with small increases in maximum temperature (McCabe and Wolock 2002), and summer precipitation in the study region is projected to remain constant or decrease slightly (Mote et al. 2005). In contrast, Douglas-fir at some higher elevation sites where water is not limiting (ONP,

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western NCNP, northeastern GNP), and net photosynthesis is currently limited by growing season length or low growing season temperature, may exhibit increased growth. If climatically driven source–sink tradeoffs are an important response in Douglas-fir, increased temperature without a concurrent increase in precipitation may result in increased growth variability (Hessl and Peterson 2004) at regional scales; more stands (at least temporarily) would be closer to climatic thresholds at which tradeoffs between aboveground and belowground net primary productivity are more pronounced. Decadal-scale climate variability may serve to mediate or accentuate such variability via plant morphological controls on growth responses.

Increased evaporative demand may accentuate stress complexes by increasing tree vulnerability to climate-mediated disturbances such as fire and insect outbreaks. Planning for these changes can be improved by using a hierarchical sampling design along biophysical gradients to inform predictions about the effects of climate variation and change on ecological processes. Such sampling designs have the capability to bracket the range of climate-mediated responses at a variety of scales and, if appropriate climate data can be measured or modeled, specify the direct climatic mechanisms responsible for variation in the process of interest. Although the degree to which radial tree growth can be used as a proxy for other life-history components is unknown, reconciling the mechanisms by which climate mediates population processes could lead to inexpensive monitoring efforts. For example, to fully understand the response of forested ecosystems to climate change, it is necessary to understand the climatic mediation of establishment, growth, and mortality. The approach used in this study could therefore complement other approaches to quantifying the impacts of climate change, such as bioclimatic models of species distributions, by linking temporal variation in growth with species distributions and the controls on establishment. This approach could also help to identify stands that are near the climatic thresholds where water limitation no longer drives growth variation and other models of forest dynamics (e.g., gap models) might be more appropriate.

Genetic and climatic variability could play important roles in observed growth differences along a transect encompassing so many populations. Elevation differences of 200 m between stands in the same watershed are sufficient to produce genetically determined differences in growth in provenance trials (Rehfeldt 1983). However, the time scale associated with climatic variability recorded in tree rings is probably higher frequency than the time scale associated with selective pressures producing potential between-plot differences, so mean growth (or growth in extreme years) rather than mean sensitivity or variance would likely be more affected. We did not consider the potential for differential influences of coupled ocean-atmosphere variability on growth at these sites, although with reasonable estimates of the actual climate at most sites, such an analysis should be tractable.

Adapting management strategies to climate change will be a critical management and policy issue in Western forests over the next several decades. Decreased Douglas-fir growth rates in mountain protected areas would have fewer direct implications than in adjacent areas where timber production is a primary management objective. However, tree responses to increasing evapotranspiration may lead to increased susceptibility to drought, insects, and fire, which may in turn have greater ecological impacts than decreased growth. Growth changes additionally imply the potential for carbon dynamics to change over very large areas, given the natural range of Douglas-fir in Western forests (Bachelet et al. 2001, Hessl and Peterson 2004). If the results from our transect approach are more widely applicable, most of the lower and mid-elevation Douglas-fir east of the Cascade Crest will be less resistant to interannual variability in summer drought than it is currently, and growth is likely to be more variable (Hessl and Peterson 2004). Although few plots exhibit strong positive correlations with SWE, if winter temperatures increase enough to alter snowpack dynamics (e.g., Hamlet et al. 2005), any influence of prior year snow on soil moisture and thus growth (Fig. 5C) will likely be lost as well, and managers will be faced with a decline in productivity. On the other hand, warmer winters with a greater percentage of precipitation falling as rain could lead to earlier onset of spring growth and compensate for the loss of summer growth. Only the coldest and wettest locations have the potential for carbon gain through relaxation of growth-limiting climate factors.

In actively managed forests where trees are planted, disturbances (timber harvest, fire, insect outbreaks) provide an opportunity for managers to speed mitigation of climate impacts by using provenances better adapted to the ecophysiological stressors associated with warmer climates. Nursery stock from seed sources outside the currently recommended seed zone may be better suited to future conditions, especially if there is not an increase in summer precipitation to offset evapotranspirative demand associated with increasing temperature. For a given location, Douglas-fir populations from a warmer and drier location (typically lower elevation or farther south) may produce seedlings that are more tolerant of drier soil conditions. The expected growth rates for a given climate, which may vary for different regional populations, are typically needed to plan for ecological and silvicultural objectives. Data on forest growth and establishment, from the maximum observable range of the process of interest and obtained across relevant biophysical gradients, can provide the scientific basis for adaptive decision making in a warmer climate.

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APPENDIX

A table showing transect characteristics including mean climate, substrate, and soil type for sample watersheds (*Ecological Archives* M078-013-A1).

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