

MOUNTAIN HEMLOCK GROWTH RESPONDS TO CLIMATIC VARIABILITY AT ANNUAL AND DECADAL TIME SCALES

DAVID W. PETERSON^{1,3} AND DAVID L. PETERSON²

¹College of Forest Resources, University of Washington, Box 352100, Seattle, Washington 98195-2100 USA

²USGS Forest and Rangeland Ecosystem Science Center, Cascadia Field Station, Box 352100, Seattle, Washington 98195-2100 USA

Abstract. Improved understanding of tree growth responses to climate is needed to model and predict forest ecosystem responses to current and future climatic variability. We used dendroecological methods to study the effects of climatic variability on radial growth of a subalpine conifer, mountain hemlock (*Tsuga mertensiana*). Tree-ring chronologies were developed for 31 sites, spanning the latitudinal and elevational ranges of mountain hemlock in the Pacific Northwest. Factor analysis was used to identify common patterns of inter-annual growth variability among the chronologies, and correlation and regression analyses were used to identify climatic factors associated with that variability.

Factor analysis identified three common growth patterns, representing groups of sites with different climate–growth relationships. At high-elevation and midrange sites in Washington and northern Oregon, growth was negatively correlated with spring snowpack depth, and positively correlated with growth-year summer temperature and the winter Pacific Decadal Oscillation index (PDO). In southern Oregon, growth was negatively correlated with spring snowpack depth and previous summer temperature, and positively correlated with previous summer precipitation. At the low-elevation sites, growth was mostly insensitive to annual climatic variability but displayed sensitivity to decadal variability in the PDO opposite to that found at high-elevation sites.

Mountain hemlock growth appears to be limited by late snowmelt, short growing seasons, and cool summer temperatures throughout much of its range in the Pacific Northwest. Earlier snowmelt, higher summer temperatures, and lower summer precipitation in southern Oregon produce conditions under which growth is limited by summer temperature and/or soil water availability.

Increasing atmospheric CO₂ concentrations could produce warmer temperatures and reduced snowpack depths in the next century. Such changes would likely increase mountain hemlock growth and productivity throughout much of its range in Washington and northern Oregon. Increased summer drought stress and reduced productivity would be likely, however, in mountain hemlock forests of southern Oregon and near the species lower elevation limit at some sites.

Key words: Cascade Mountains, Pacific Northwest (USA); climatic variability; dendroecology; elevation; gradients; mountain hemlock; Pacific Decadal Oscillation; snowpack; subalpine forests; temperature; tree growth; *Tsuga mertensiana*.

INTRODUCTION

Global mean temperatures may rise 1°–3°C over the next century in response to a doubling of atmospheric CO₂ concentrations (Watson et al. 1996). Changes in precipitation patterns are also possible, although there is great uncertainty regarding the magnitude, seasonality, and spatial patterns of precipitation changes. Given such changes in climate, biogeographic models predict that some plant and animal species would have to shift their ranges hundreds of kilometers toward the poles or hundreds of meters upward in elevation to stay

within the range of climatic conditions under which they currently exist (Peters and Darling 1985, Leverenz and Lev 1987, Overpeck et al. 1991, Davis and Zabin-ski 1992, Urban et al. 1993, Lenihan and Neilson 1995).

Predicting transient responses of extant forests to future climatic variability or change may be of more immediate importance for scientists, natural resource managers, and policy makers than predicting long-term equilibrium changes in forest composition. Paleoecological studies have shown that plant species are capable of rapid migration in response to climate change (Gear and Huntley 1991, Pitelka et al. 1997, Clark et al. 1998). However, expansion of tree populations into newly suitable habitats will be slowed by seed dispersal limitations, landscape fragmentation, long juvenile periods, and competition from resident populations (Brubaker 1986, Davis 1989, Pitelka et al. 1997). Local extinction of extant tree populations will be slowed by

Manuscript received 26 October 2000; revised and accepted 8 January 2001.

³ Present address: David W. Peterson, Civil and Environmental Engineering, University of Washington, Box 352700, Seattle, Washington 98195-2700 USA.
E-mail: larix@u.washington.edu

long life-spans, the ability of mature trees to endure a wide range of environmental conditions, and the potential for periodic regeneration during periods when climatic variability produces favorable conditions (Davis and Botkin 1985, Brubaker 1986, Davis 1989, Woodward et al. 1995, Swetnam et al. 1999). Forest community change may be especially slow in areas with very low frequency of severe wildfire, timber harvesting, or other major disturbances.

Subalpine forests are particularly sensitive to climatic variability. High-elevation tree lines occur where harsh environmental conditions limit the establishment, growth, and survival of trees in upright form, producing a transition from forest to alpine meadow communities (Wardle 1974, Tranquillini 1979, Körner 1998). Although the specific mechanisms controlling alpine timberlines are often poorly understood, direct or indirect negative influences of declining air temperature with increasing elevation are considered the primary influences in most mountainous regions (Tranquillini 1979, Körner 1998).

In the coastal mountains of the Pacific Northwest, winter snowpack is often the major determinant of tree line (Shaw 1909, Taylor 1922, Brink 1959, Peterson 1998). Heavy winter precipitation combines with cold temperatures at high elevations to produce deep snowpacks that persist well into the summer months. Subalpine tree growth in this region often responds to variations in winter precipitation, spring snowpack depth, summer temperature, and annual temperature (Heikininen 1985, Graumlich and Brubaker 1986, Peterson and Peterson 1994, Ettl and Peterson 1995).

Climatic factors limiting growth and productivity can vary at broad spatial scales in response to regional variations in temperature and precipitation patterns (Fritts 1974, Brubaker 1980, Cook and Cole 1991). At finer spatial scales, climatic limiting factors and climate-growth relationships vary with differences in topographic position and soil properties (Keen 1937, Fritts 1974, Villalba et al. 1994, Ettl and Peterson 1995, Buckley et al. 1997). Different species may respond differently to climate, even when growing together on a common site (Colenutt and Luckman 1991, Graumlich 1993, Peterson and Peterson 1994, Villalba et al. 1994). Identification of regional variations in climate-growth relationships therefore requires careful sampling, including limitations on the species sampled, consideration of topographic variability, and large sample sizes.

We used dendroecological methods with a structured sampling approach to study relationships between climatic variability and tree growth in mountain hemlock (*Tsuga mertensiana*) forests of the Cascade and Olympic Mountains of Washington and Oregon. To identify spatial patterns in interannual growth patterns and climate-growth relationships caused by spatial variations in climate, we sampled mountain hemlock stands at regular intervals along a latitudinal transect from north-

ern Washington to southern Oregon and along elevational transects from the species' lower elevational limit to its upper elevational limit at each latitude. We used dendroecological methods to assess the sensitivity of mountain hemlock to climatic variability at annual and decadal time scales and to identify the major climate-related environmental factors influencing growth and productivity in mountain hemlock forests.

Mountain hemlock was chosen as the target species for this study because it is a common subalpine conifer in the coastal mountain ranges of western North America between southwestern Alaska and central California (Brooke et al. 1970, Parsons 1972, Means 1990). Mountain hemlock is highly shade tolerant and is considered a climax species throughout much of its range. It is also one of the most long-lived species in subalpine forests of this region, with a maximum life-span of 700 yr or more. Wildfires are rare, but timber harvesting has become increasingly common. As a long-lived, late-successional conifer, mountain hemlock is a good example of a species that might be slow to retreat from its current habitat, and for which growth responses to climatic variability are of particular interest.

STUDY AREA

The coastal mountains of the Pacific Northwest have a maritime climate that is strongly influenced by air masses from the Pacific Ocean. Winters are cool and wet. Orographic effects produce heavy precipitation on the west-facing slopes of the mountains. At elevations >1000 m, most winter precipitation falls as snow and is stored in the snowpack until snowmelt begins in the spring. Summers are warm and relatively dry.

Ring-width chronologies were developed from mountain hemlock trees at 31 sites in the Cascade and Olympic Mountains of Washington and Oregon. Sites were chosen to span the latitudinal and elevation range of the species in Washington and Oregon (Fig. 1). Sampling locations were selected along a latitudinal transect that extends from North Cascades National Park (Thornton Lakes, 49°25' N) in northern Washington to Crater Lake National Park (42°50' N) in southern Oregon (Table 1). At each location, we selected three sites for sampling mountain hemlocks: a high-elevation site near the upper tree line, a low-elevation site near the lower species range limit, and a midrange site. A single site was sampled on Wizard Island in Crater Lake.

Elevations of sampled sites ranged between 1100 and 2300 m above sea level (Table 1). The mean elevation difference between the high- and low-elevation sites was 365 m (range 245–610 m). Mean elevation increased by ~700 m from north to south (Table 1).

METHODS

Tree-ring chronology development

Tree-ring chronologies were developed from 10–20 dominant and codominant mountain hemlock trees at

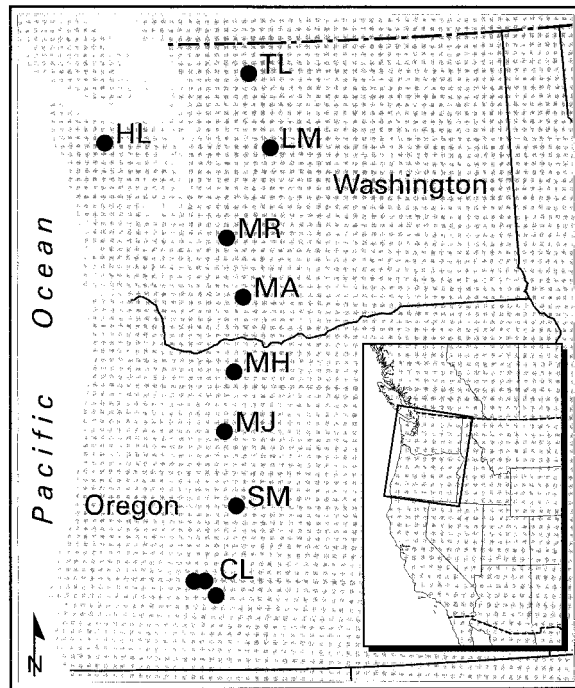


FIG. 1. Locations of mountain hemlock sampling sites along a latitudinal transect.

each site (Table 1). Trees with obvious structural damage were excluded from sampling. Two increment cores were removed from the cross-slope sides of each tree and stored in paper straws for transport. In the laboratory, cores were mounted on grooved boards and sanded with progressively finer grades of sandpaper to produce flat surfaces on which ring boundaries were clearly defined under magnification. One core from each tree was selected for ring-width measurements, with preference given to cores with longer tree-ring records. Rings were crossdated using standard procedures (Stokes and Smiley 1968) and measured to the nearest 0.01 mm. Crossdating of measured tree-ring series was verified using the program COFECHA (Holmes 1983).

Mean growth chronologies were developed from the crossdated ring-width series using the program ARSTAN (Cook and Holmes 1996). Individual ring-width measurement series were standardized to remove trends in mean ring width that typically occur due to increasing circumference of the tree. Cubic spline curves with a 50% cutoff frequency of 100 yr were fit to each ring-width series. Growth index series were then created for each tree by dividing the ring-width measurement for each year by the spline curve value for that year. Mean site growth chronologies were then created by averaging the detrended series together by year using a biweight robust mean (Cook and Briffa 1990).

Descriptive statistics were calculated for each site chronology, including mean sensitivity (Fritts 1976), mean interseries correlation, the order of autoregres-

sive model required to remove serial autocorrelation from the chronology, and the amount of chronology variance explained by the required autoregressive model. Mean sensitivity (MS) describes interannual variability in ring widths as a proportion of local mean ring width. The mean interseries correlation is the average of all pairwise correlations for detrended tree-ring series within a chronology over a common time period of 1895–1991. Higher values indicate greater similarity in annual growth patterns among sampled trees and better representation of overall stand growth by the mean growth chronologies. Autoregressive models were developed using the SAS statistical software (SAS Institute 1989, version 6.12, PROC AUTOREG).

Spatial variability in tree growth patterns

Factor analysis (Johnson and Wichern 1992) with oblique rotation of eigenvectors (SAS Institute 1989, version 6.12, PROC FACTOR) was used as a data reduction technique to identify and extract common patterns of growth variability among the 31 ring-width chronologies. Oblique (Promax) rotation of eigenvectors was chosen over orthogonal rotation because the resulting factor variables better represented actual growth patterns in the ring-width chronologies. Coefficients of variation (r^2) were used to describe associations between the original ring-width chronologies and each of the three new variables produced by the factor analysis (hereafter, factor chronologies). The coefficient of multiple variation (R^2) was used to describe the total variance in each ring-width chronology that could be explained by the three factor chronologies.

Climate data

Climate-growth relationships were investigated by comparing mean ring-width chronologies with monthly temperature and precipitation records for the period 1895–1991. We obtained divisional temperature and precipitation data (National Climate Data Center, Asheville, North Carolina) from three climatic divisions, including the western Washington Cascades (WA-5), northern Oregon Cascades (OR-4), and the high plateau region of southern Oregon (OR-5). Chronologies were matched with climatic divisions as indicated in Table 1. Divisional records were used instead of individual station data, because most sampling sites had no local long-term weather recording station, divisional data better represent regional climatic conditions, and divisional data provide a longer climatic record than is available for most individual stations.

Snowpack depth measurements and snowmelt dates were obtained from long-term monitoring stations at Mount Rainier and Crater Lake. Daily measurements of snowpack depth were taken for several decades at both parks, prior to installation of automated snowpack monitoring equipment in the 1980s. Snowpack depth measurements on 15 May were used for this study as a combined measure of winter snowpack accumulation

TABLE 1. Site descriptions and descriptive statistics for mountain hemlock tree-ring chronologies.

Site name	Latitude (°N)	Longitude (°W)	Climate division	Chron. code	Elevation (m)	Aspect	Mean tree age				AR model order	AR model R^2
							No. trees	(yr)	MS	r_{avg}		
Thornton Lakes	48°40'	121°20'	WA-5	TL-H	1525	S	18	184	0.15	0.34	1	0.17
				TL-M	1370	S	14	206	0.15	0.42	1	0.22
				TL-L	1220	S	16	216	0.17	0.56	1	0.49
Hoh Lake	47°54'	123°45'	WA-5	HL-H	1465	SW	17	313	0.20	0.38	0	0.00
				HL-M	1315	SW	16	157	0.17	0.43	1	0.05
				HL-L	1220	SW	16	268	0.16	0.35	3	0.21
Lake Minotaur	47°50'	121°00'	WA-5	LM-H	1740	S	14	276	0.15	0.39	1	0.08
				LM-M	1465	SE	11	208	0.14	0.36	1	0.31
				LM-L	1130	SE	14	223	0.18	0.29	1	0.08
Mount Rainier	46°50'	121°45'	WA-5	MR-H	1830	W	15	210	0.19	0.33	1	0.06
				MR-M	1654	W	10	194	0.21	0.34	1	0.09
				MR-L	1425	N	12	274	0.13	0.25	1	0.28
Mount Adams	46°10'	121°30'	WA-5	MA-H	1890	W	19	216	0.20	0.43	0	0.00
				MA-M	1735	SW	19	222	0.21	0.40	1	0.03
				MA-L	1495	SW	19	238	0.20	0.40	1	0.04
Mount Hood	45°20'	121°40'	OR-4	MH-H	1920	NW	19	197	0.20	0.39	5	0.07
				MH-M	1790	NW	17	256	0.20	0.31	0	0.00
				MH-L	1585	NW	19	243	0.16	0.35	2	0.19
Mount Jefferson	44°40'	121°50'	OR-4	MJ-H	1950	W	15	248	0.19	0.33	1	0.08
				MJ-M	1785	W	18	233	0.33	0.55	0	0.00
				MJ-L	1585	S	16	243	0.16	0.29	1	0.11
Sheridan Mountain	43°50'	121°40'	OR-5	SM-H	2090	W	19	311	0.15	0.33	1	0.05
				SM-M	1920	W	19	283	0.17	0.38	1	0.04
				SM-L	1755	W	18	321	0.16	0.40	1	0.07
Crater Lake, East	42°50'	122°00'	OR-5	CE-H	2300	S	19	226	0.20	0.46	0	0.00
				CE-M	2075	E	20	196	0.19	0.54	1	0.04
				CE-L	1910	SE	16	251	0.14	0.37	1	0.05
Crater Lake, West	43°00'	122°20'	OR-5	CW-H	2210	SW	19	279	0.20	0.49	0	0.00
				CW-M	2075	W	19	248	0.23	0.47	0	0.00
				CW-L	1950	SW	19	229	0.17	0.40	1	0.04
Wizard Island	43°00'	122°10'	OR-5	WI	2015	NW	13	266	0.19	0.35	0	0.00

Notes: Chronology statistics include mean sensitivity (MS), mean interseries correlation (r_{avg}), the order of autoregressive function required to remove autocorrelation in the mean chronology (AR model order), and the variance explained by the AR model. The chronology code ("Chron. code") is based on the site name and elevation.

and spring snowmelt rates. Snowmelt dates were defined as the first date on which a snowpack measurement of 0.0 cm was recorded.

Historic snow depth and snowpack water equivalent (SWE) data were also available for many snow course survey sites in the Cascade Mountains of Washington and Oregon. We used only the records from the Mount Rainier and Crater Lake sites for this study because they had the longest, most detailed records, they represented temporal variations in snowpack at sites closely associated with two of the three factor chronologies, and they were highly correlated with snowpack records from neighboring stations. There is generally good spatial coherence in snowpack data among historic snow course sites in the Pacific Northwest, with two distinct temporal patterns, one associated with sites in Washington, Idaho, and Montana, and the other associated with sites in Oregon (Cayan 1996).

Recent studies have found close associations between climatic variability in the Pacific Northwest and atmospheric circulation patterns, sea-surface temperatures, and sea-level pressure anomalies in the Pacific Ocean that influence regional weather patterns at annual to decadal time scales (Cayan 1996, Mantua et al. 1997, Zhang et al. 1997). The Southern Oscillation

Index (SOI) describes variations in tropical sea-level pressure measurements associated with El Niño and La Niña events. El Niño and La Niña events occur at intervals of 2–7 yr and are associated with warmer and cooler winter temperatures, respectively.

The Pacific Decadal Oscillation Index (PDO) is similar to the SOI, but describes spatial patterns of sea-surface temperatures in the northern Pacific (Mantua et al. 1997). Negative values of the PDO are associated with cooler winter temperatures, higher precipitation, and increased snowpack accumulations, and vice versa. Unlike the SOI, the PDO appears to shift between warm and cool phases at 20–30 yr intervals. Time series of mean winter (November to March) and summer (June to September) indices were calculated for both the SOI and PDO for the period 1921–1991.

Climatic influences on tree growth

To identify the climatic factors most closely associated with variations in tree growth, product-moment correlations (r) were calculated for relationships between climatic variables and the factor chronologies over the period 1921–1991. Correlation coefficients and coefficients of variation (r^2) were also calculated for relationships between selected climatic variables

TABLE 2. Principal components (PC) and factor analysis of 31 mountain hemlock chronologies for the period 1895–1991.

PC or factor	Principal components			Factors, Promax rotation†	
	Eigenvalue	Variance explained (%)	Cumulative variance (%)	Eigenvalue	Variance explained (%)
1	15.2	49.2	49.2	11.6	37.6
2	3.4	11.0	60.2	11.0	35.5
3	2.5	8.0	68.2	7.8	25.3
4	1.3	4.1	72.3		
5	1.1	3.4	75.7		
6	0.9	2.9	78.6		

† See *Methods: Spatial variability in tree growth patterns*.

and the site chronologies. Climatic variables used in the correlation analysis included mean monthly temperature and total monthly precipitation for 24 mo prior to the end of the growing season in which the ring was formed (two hydrological years, October–September). Additional climatic variables included spring snowpack depth, snowmelt date, winter (November–March) PDO, winter SOI, summer (May–September) PDO and summer SOI for both the growth year and the previous year. Seasonal climatic variables (means of sequential monthly temperature and precipitation variables) were also constructed based on observed sequences of strong positive or negative correlations and prior knowledge about seasonal weather patterns in the mountains.

Monthly and seasonal climatic variables showing strong correlations with tree growth were used as candidate predictor variables in multiple regression models of annual growth for each of the factor chronologies. Final regression models included one or more autoregressive terms as needed to remove autocorrelation from model residuals (SAS Institute 1989, version 6.12, PROC AUTOREG).

RESULTS

Chronology descriptive statistics

Thirty-one site growth chronologies were developed from mature mountain hemlock trees, with estimated mean tree ages (at coring height) of 157–321 yr (Table 1). Mean sensitivity was 0.183 ± 0.037 (mean \pm 1 sd) (Table 1), and mean interseries correlations ranged between 0.249 and 0.559 (0.384 ± 0.076). Neither of these statistics displayed a clear trend with respect to elevation or latitude.

Autoregressive models of null or first order were sufficient to describe the autoregressive structure for 28 of the 31 site chronologies (Table 1). The variance explained by the autoregressive models was <10% for most (23 of 31) chronologies, but ranged as high as 49% for the low-elevation chronology at Thornton Lakes. First-order autocorrelation coefficients for the site chronologies were highly variable, ranging between -0.061 and 0.701 . Autocorrelation coefficients

were highest at the lowest elevation sites and declined with increasing elevation ($r = -0.66$, $P < 0.001$). Autocorrelation coefficients were also correlated with latitude, increasing from south to north ($r = 0.57$, $P < 0.001$).

Spatial variability in tree growth patterns

Factor analysis produced three factor variables, each accounting for 25–38% of the total variance within and among the site chronologies (Table 2). These factor variables can be interpreted as summary growth chronologies (hereafter “factor chronologies”), each containing a common pattern of interannual and interdecadal growth variability that is shared by several site chronologies. Three factors were chosen because principal components analysis showed that three eigenvectors explained 68% of the variance in the 31 mean site chronologies, and that additional eigenvectors accounted for <5% additional variance (Table 2). The three factor chronologies were positively correlated with one another, with correlations ranging from 0.28 to 0.49 (Table 3). Combined, the three factor chronologies explain 33–86% of the variance in the original site chronologies (Table 4). In general, the factor chronologies capture most of the variability in chronologies from high- and middle-elevation sites, but do not represent chronologies from low-elevation sites as well.

Correlations between site chronologies and factor chronologies over the period 1895–1991 showed distinct spatial coherence (Table 4). Site chronologies from high- and middle-elevation sites in Washington and northern Oregon were most closely correlated with the first factor chronology. We therefore call this factor chronology the “high-elevation FC.” Site chronologies from southern Oregon were most closely correlated with the second factor chronology, which is hereafter called the “southern FC.” Several site chronologies from low- and middle-elevation sites were closely correlated with the third factor chronology, which is hereafter called the “low-elevation FC.” Repeating the factor analysis for the periods 1800–1895 and 1850–1945 produced very similar regional groupings of chronologies, indicating temporal stability for these geographical groupings over the past two centuries.

Time plots of the three factor chronologies showed that they contained a combination of high-frequency annual growth variations and lower frequency decadal

TABLE 3. Correlations (r) among factor variables (chronologies) following Promax rotation.

Factor variables	Northern	Southern	Low elevation
Northern factor chronology	1.00	0.49	0.28
Southern factor chronology	0.49	1.00	0.37
Low-elevation factor chronology	0.28	0.37	1.00

Note: See *Methods: Spatial variability in tree growth patterns*.

TABLE 4. Associations between factor chronologies and site chronologies as measured by coefficients of variation (r^2).

Factor chronology	Elevation	←North				Site			South→			
		TL	HL	LM	MR	MA	MH	MJ	SM	CE	CW	CI
a) Northern	High	0.53	0.72	0.58	0.69	0.64	0.45	0.62	0.32	0.40	0.41	
	Middle	0.30	0.45	0.09	0.59	0.52	0.52	0.74	0.21	0.16	0.35	0.18
	Low	0.01	0.27	0.49	0.48	0.55	0.06	0.06	0.05	0.01	0.15	
b) Southern	High	0.22	0.19	0.15	0.08	0.38	0.41	0.29	0.67	0.69	0.77	
	Middle	0.17	0.18	0.18	0.13	0.28	0.41	0.37	0.66	0.72	0.81	0.76
	Low	0.07	0.11	0.09	0.10	0.19	0.10	0.24	0.32	0.53	0.72	
c) Low elevation	High	0.36	0.20	0.09	0.00	0.34	0.00	0.00	0.12	0.05	0.10	
	Middle	0.56	0.30	0.56	0.12	0.32	0.28	0.04	0.40	0.20	0.23	0.09
	Low	0.59	0.44	0.04	0.29	0.19	0.49	0.20	0.52	0.28	0.42	
d) Combined	High	0.70	0.78	0.59	0.77	0.80	0.71	0.74	0.72	0.77	0.84	
	Middle	0.69	0.58	0.59	0.62	0.68	0.70	0.80	0.78	0.74	0.86	0.75
	Low	0.61	0.57	0.49	0.62	0.61	0.50	0.33	0.64	0.73	0.85	

Notes: Values indicate variance in site chronologies that is explained by individual factor chronologies (a–c) and all three factor chronologies combined (d). Numbers in boldface indicate the factor chronology with which each site chronology is most closely associated. For site codes, see Table 1.

growth variations (Fig. 2). The high-elevation and southern FC's were dominated by high-frequency growth variations. The high-elevation FC showed a period of above-average growth during the 1930s, and two periods of reduced growth in the 1950s and early 1970s (Fig. 2a). The southern FC showed a sharp decline in growth between 1915 and 1920, followed by a gradual growth increase during 1920–1945 and decadal oscillations in the running means after 1945 (Fig. 2c).

In contrast, the low-elevation FC captured a common pattern of low-frequency growth variations shared by several sites. The low-elevation FC had a first-order autocorrelation coefficient of 0.62, which was much higher than for the high-elevation ($r = 0.22$, $P = 0.06$) and southern ($r = 0.09$, $P > 0.20$) FC's. The low-elevation FC showed a long period of below-average growth from 1925 to 1948 and several short periods of fast growth (Fig. 2b).

Climatic variability—spatial and temporal

Climate data from high-elevation weather stations at Mount Rainier National Park (1654 m elevation, 1948–1996) and Crater Lake National Park (1974 m, 1931–1996) provided information about differences in mean daily temperatures and mean monthly precipitation along our latitudinal transect (Fig. 3). The Paradise station on Mount Rainier receives $\approx 70\%$ more precipitation per year than Crater Lake (297 and 174 cm/yr), and almost three times as much precipitation during the warmest months, July and August (12.1 vs. 4.4 cm/yr). Climate maps indicated that annual mean precipitation is greatest in the western Olympic Mountains and Mount Rainier areas, and least in southern Oregon (Franklin and Dyrness 1973), so these two stations may provide a reasonable estimate of latitudinal variation in climate. The Stevens Pass station (1240 m, 1948–1996, located near the Lake Minotaur site) receives an intermediate amount of precipitation, and may be rep-

resentative of climate at low-elevation sites in the Washington Cascades.

Mean temperatures vary with both latitude and elevation. Mean daily temperatures at Mount Rainier and Crater Lake are very similar in the winter, but are about $\approx 1.5^\circ\text{C}$ warmer at Crater Lake during July and August (Fig. 2a,c). Daily temperature ranges (maximum minus minimum) are greater at Crater Lake than at Mount Rainier by $\approx 3^\circ\text{C}$ on an annual basis, and by $>5^\circ\text{C}$ in July and August, perhaps because lower mean cloud cover at Crater Lake permits more radiative cooling at night. Assuming a standard lapse rate of 6°C per 1000 m, mean monthly and annual temperatures should be $1.5\text{--}2.5^\circ\text{C}$ warmer at low-elevation sites than at high-elevation sites.

Mount Rainier averaged more snow than Crater Lake (1725 and 1367 cm/yr), and the average snowmelt date at Mount Rainier (12 July) was >3 wk later than at Crater Lake (17 June) (Fig. 4). For the period 1951–1981, mean 15 May snow depth was 399 cm at Mount Rainier. During the same period, mean 15 May snow depths at Crater Lake and Stevens Pass were very similar, at 222 cm and 231 cm, respectively.

Spring snowpack depths at Mount Rainier varied with winter index values of the PDO and SOI. Spring snowpack depth was negatively correlated with the winter PDO (Fig. 5). The warm (El Niño) phase of the SOI significantly reduced spring snowpack depth compared to cool and neutral phases of the SOI. Effects of PDO and SOI were additive, so the greatest reductions in snowpack were found in years when both the PDO and SOI were in their warm phases. PDO and SOI effects on spring snowpack at Crater Lake were statistically insignificant, but followed a similar pattern (Fig. 5).

Time plots of the winter PDO and snowpack depths at Mount Rainier showed obvious low-frequency variability at decadal time scales (Fig. 6a,b). Decadal variations in Mount Rainier snowpack were less pro-

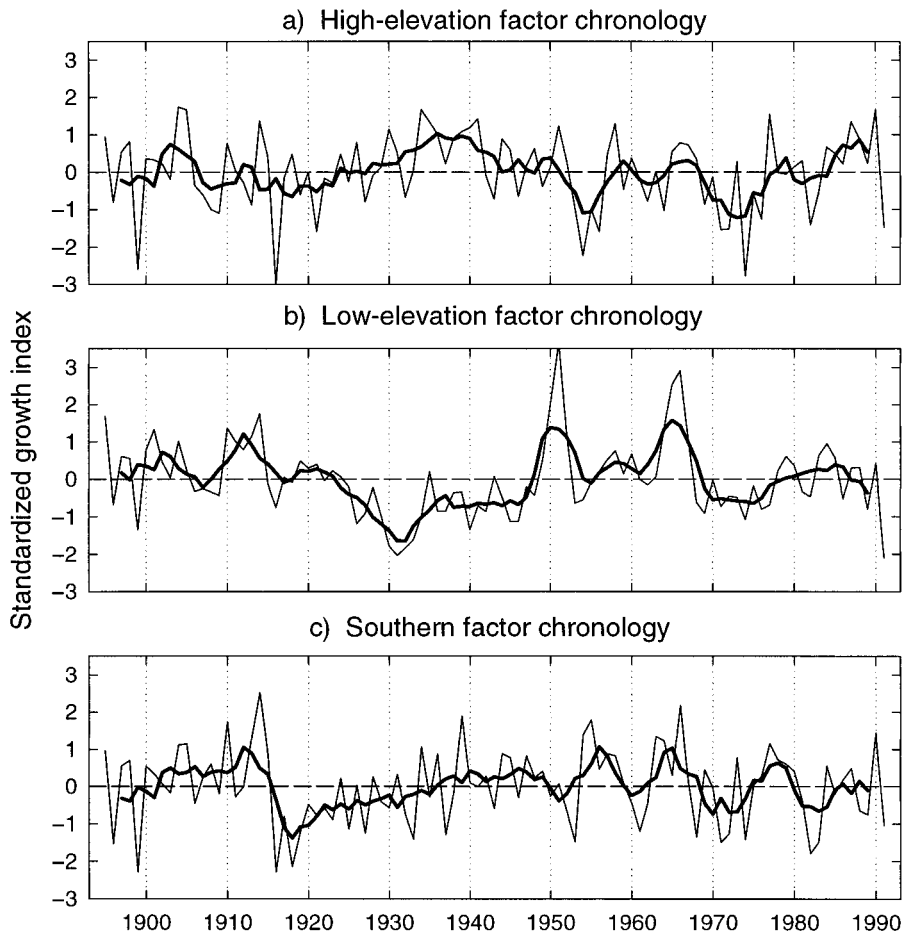


FIG. 2. Time-series plots showing temporal variability in mountain hemlock growth. Variables plotted include (a) the high-elevation factor chronology, (b) the low-elevation factor chronology, and (c) the southern factor chronology. Each time plot includes annual values (thin lines) and 5-yr running averages (thick lines).

nounced than those of the PDO, but still consistent with the negative correlation between snowpack and PDO. In southern Oregon, summer mean temperatures showed significant decadal variability, with a cool period during 1932–1957 (Fig. 6c).

Climatic influences on tree growth

Spring snowpack depth and snow meltout date were the best predictors of mountain hemlock growth throughout most of the study region. Growth was negatively correlated with spring snowpack depth for both the high-elevation and southern FC's (Table 5, Fig. 7). Radial growth was least in years with a deep, late-melting snowpack, and greatest in years with a shallow early-melting snowpack. The high-elevation and southern FC's were also highly correlated with winter precipitation and spring temperature, two variables associated with snowpack formation and persistence. The significant relationship between the high-elevation FC and winter PDO is also consistent with the sensitivity of growth to snowpack depth (Table 5).

Correlations between the high-elevation FC and

monthly climatic variables showed a pattern of negative correlations with precipitation in the fall and winter months and positive correlations with fall, winter, and spring temperatures (Fig. 8a,b). The high-elevation FC was also positively correlated with summer temperatures during the growth year (Table 5, Fig. 8b). A significant negative correlation between growth and July temperature in the summer prior to ring formation was also observed after the effects of spring snowpack were removed (partial correlation). A multiple regression model including spring snowpack depth, growth-year summer temperature, and previous July temperature as predictors explained 67% of the variance in the high-elevation factor chronology (Table 6).

The relationship between mountain hemlock growth and summer temperature was different in southern Oregon. The southern FC was negatively correlated with previous summer temperature and positively correlated with previous August precipitation (Table 5, Fig. 8e,f). Correlations between the southern FC and growth year summer temperatures were statistically insignificant, but also negative (Fig. 8f). A multiple re-

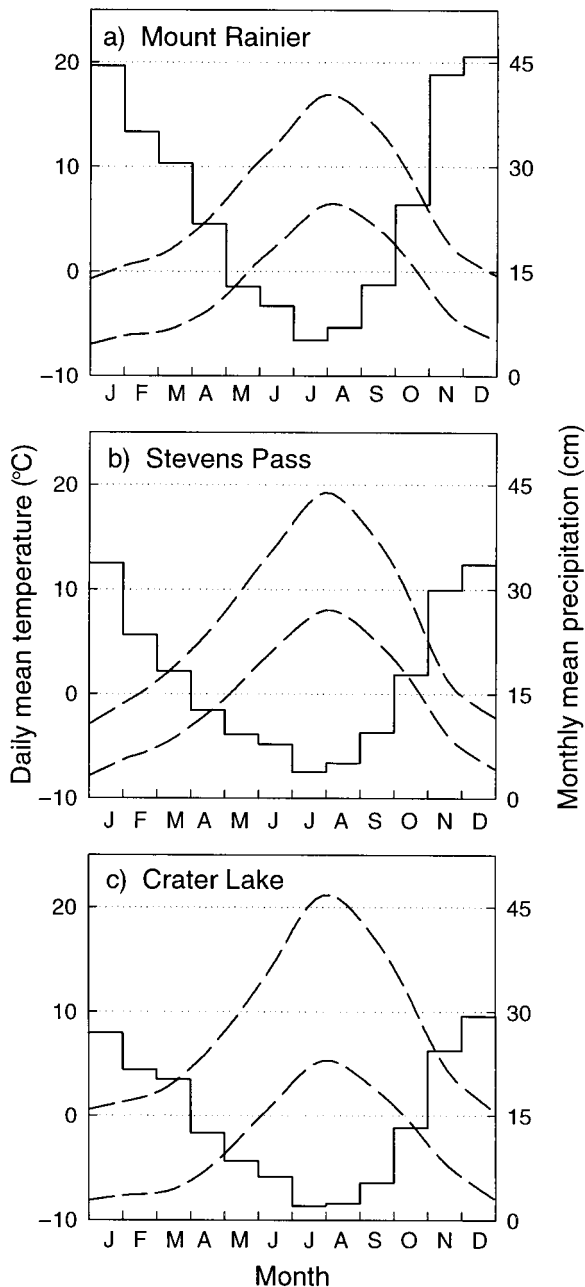


FIG. 3. Climate summaries for (a) Mount Rainier (46°47' N, 1654 m elevation), (b) Stevens Pass (47°44' N, 1240 m), and (c) Crater Lake (42°54' N, 1974 m). Solid lines indicate mean monthly precipitation totals. Dashed lines indicate smoothed mean daily maximum and minimum temperatures.

gression model that included spring snowpack depth, previous summer temperature (July–August), and previous August precipitation as predictor variables accounted for 64% of the variance in the southern growth chronology (Table 6).

The common growth pattern represented by the low-elevation factor chronology was generally insensitive to interannual climatic variability as measured by

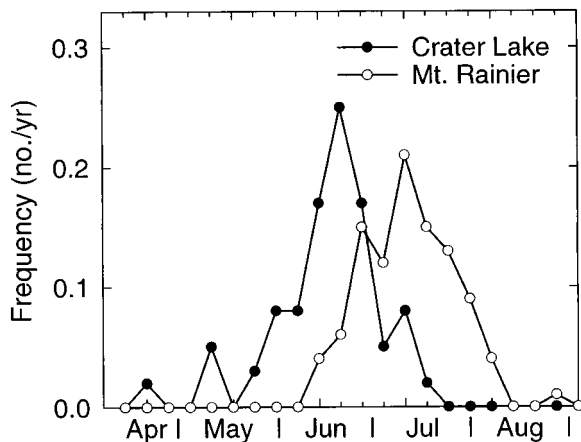


FIG. 4. Histogram of snowmelt dates, by week, for Mount Rainier (open symbols) and Crater Lake (solid symbols).

monthly and seasonal temperature and precipitation. The only significant correlations were with prior July temperature and precipitation, previous year winter PDO, and fall/winter (October–January) precipitation (Table 5, Fig. 8c,d). A multiple regression model that included previous July temperature, previous winter PDO, and first- and second-order autoregressive error terms explained 50% of the variance in the low-elevation growth pattern, with the autoregressive error terms accounting for most of the explained variance.

The strong autocorrelation structure in the low-elevation FC and the obvious growth trends in the high-elevation and southern FC's led us to ask whether these trends might be growth responses to decadal variability in one or more climatic variables. To address this, we used 5-yr running averages with equal weights to filter out high-frequency growth variability and highlight

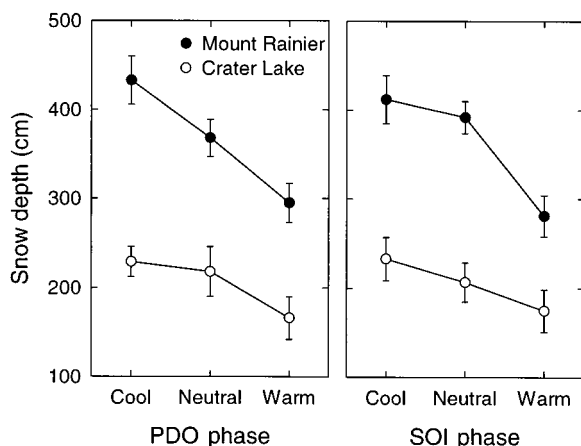


FIG. 5. Effects of Pacific Decadal Oscillation (PDO) and Southern Oscillation Index (SOI) on 15 May snowpack depths at Mount Rainier (solid symbols) and Crater Lake (open symbols). Error bars indicate ± 1 SE. Neutral years had index values (PDO or SOI) within 0.5 standard deviations of the overall mean.

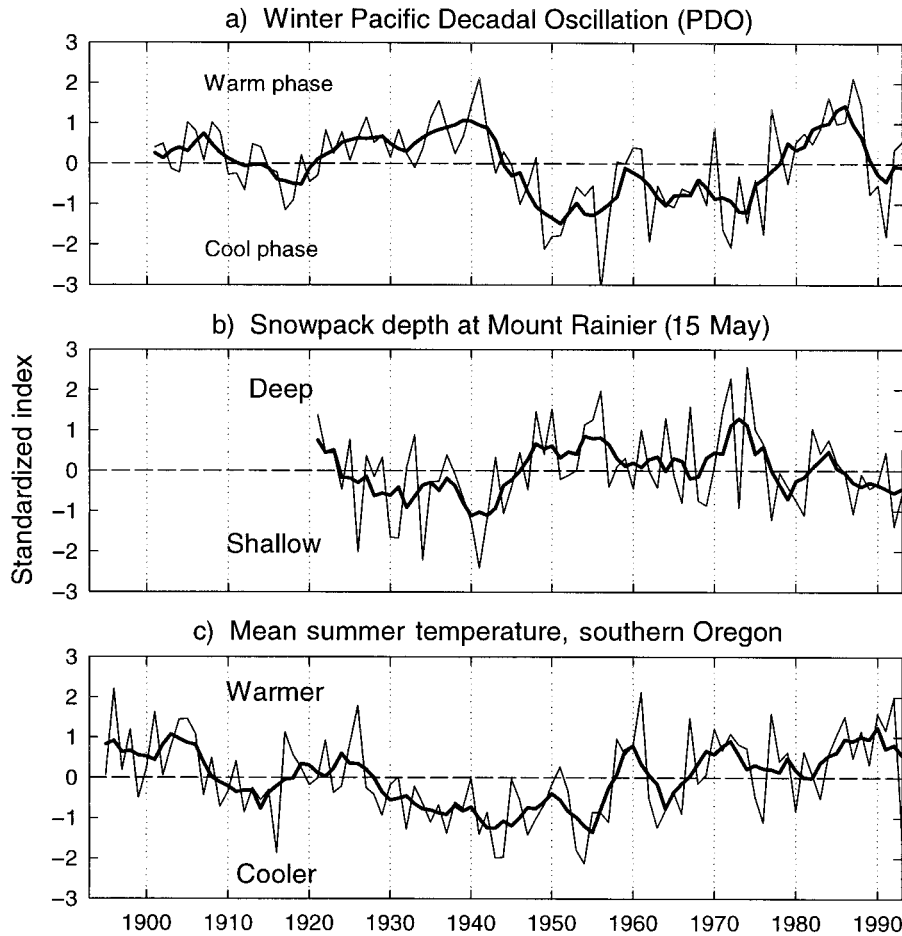


FIG. 6. Time-series plots showing temporal variability in key climate variables. Climate variables include (a) the mean Pacific Decadal Oscillation (PDO) index for winter months (November–March), (b) snowpack depth at Paradise on Mount Rainier (15 May), and (c) mean summer (June–August) temperature in southern Oregon. Each time plot includes annual values (thin lines) and 5-yr running averages (thick lines).

TABLE 5. Coefficients of determination (r^2) between factor chronologies and seasonal climatic variables.

Climatic variable	Sign	Factor chronology		
		Northern	Southern	Low elevation
Spring snowpack depth (15 May)	–	0.48	0.26	...
Snow meltout date (days after 1 Jan)	–	0.52	0.29	...
Winter precipitation (Nov–Mar)	–	0.22	0.11	...
Spring temperature (Apr–May)	+	0.20	0.09	...
Summer temperature, growth year (Jun–Aug)	+	0.12
Summer temperature, prior year (Jul–Aug)	–	...	0.19	...
Summer precipitation, prior year (Jul–Aug)	+	...	0.14	...
Annual temperature, growth year (Oct–Sep)	+	0.26
Annual precipitation, growth year (Oct–Sep)	–	0.23	0.07	...
Winter PDO, growth year	+	0.28
Winter PDO, previous year	–	...	0.08	0.12
Winter SOI, growth year	–	0.08

Notes: Signs (+/–) indicate positive or negative correlations. PDO = Pacific Decadal Oscillation; SOI = Southern Oscillation Index. All values shown are statistically significant ($P < 0.05$).

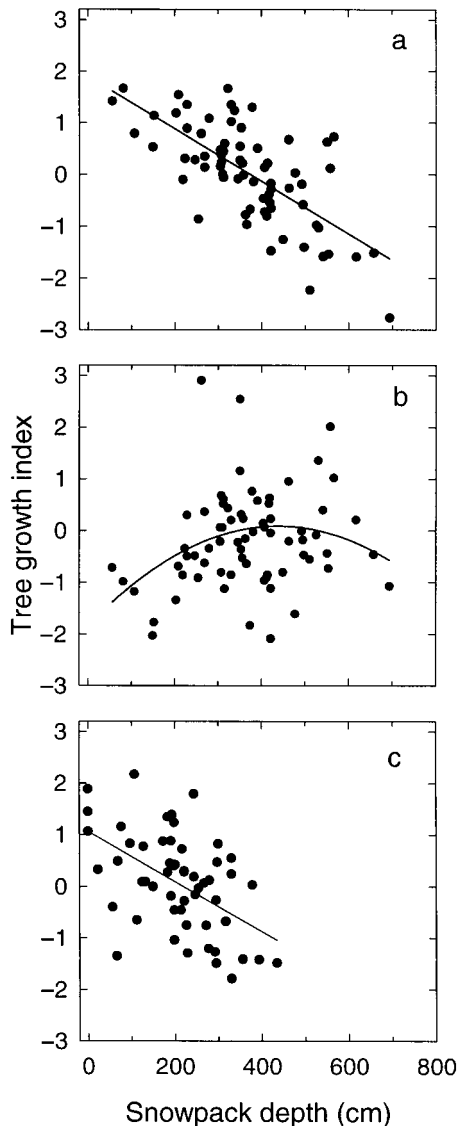


FIG. 7. Relationships between spring snowpack depth and mountain hemlock growth. (a) High-elevation factor chronology plotted against 15 May snowpack depths at Mount Rainier ($y = 1.90 - 5.09x$, $r^2 = 0.47$). (b) Low-elevation factor chronology plotted against 15 May snowpack depths at Mount Rainier ($y = -1.85 + 8.85x - 1.01x^2$, $r^2 = 0.08$). (c) Southern factor chronology plotted against 15 May snowpack depths at Crater Lake ($y = 1.06 - 4.85x$, $r^2 = 0.26$).

lower frequency trends in the three factor chronologies (Fig. 2a–c). The same 5-yr filter was applied to three key climate variables: winter PDO, spring snowpack depth at Mount Rainier, and mean summer temperatures in southern Oregon (Fig. 6a–c). The smoothed growth and climate time series were plotted together on time plots (Fig. 9).

A surprising result was an apparent negative relationship between low-frequency growth variations in the low-elevation FC and low-frequency variations in the winter PDO (Fig. 9c). The smoothed growth index

was below average while the PDO was in its warm phase during 1925–1947. Growth was higher than average during 1948–1968, while the PDO was in its cool phase. Relationships between the low-elevation FC and PDO are less clear after 1970, however.

Low-frequency growth variations in the high-elevation FC tracked low-frequency variations in spring snowpack depth, consistent with our other analyses (Fig. 9a). The high-elevation FC also appeared to track long-term shifts in the PDO (Fig. 9b). Growth trends in the southern FC tracked low-frequency variations in summer temperature (Fig. 9d); again, this result was consistent with results of the correlation and regression analyses.

DISCUSSION

Climatic influences on mountain hemlock growth

The strong negative correlation between spring snowpack depth and the high-elevation FC suggests that mountain hemlock growth is limited by growing season length throughout much of its range in the Pacific Northwest. Snowpack influences the start of the growing season, largely through its effects on soil temperature (Worrall 1983, Hansen-Bristow 1986). Soils in the upper rooting zone remain near freezing while the ground is covered by snow, warm rapidly following snowmelt, and then tend to track mean daily temperatures throughout the remainder of the summer and fall (Brooke et al. 1970, Ballard 1972, Evans and Fonda 1990, Woodward 1998). Little information is available about the phenology of mountain hemlocks, but field observations suggest that it is similar to that of two co-occurring true firs, subalpine fir (*Abies lasiocarpa*) and Pacific silver fir (*A. amabilis*), which initiate leaf and shoot expansion shortly after snowmelt (Worrall 1983, Hansen-Bristow 1986). If so, snowmelt dates are probably good indicators of the start and overall length of the growing season for mountain hemlock.

The positive correlation between the high-elevation FC and summer temperature also supports the hypothesis of growing season length as the major factor limiting growth. Warm summer temperatures at these sites promote earlier snowmelt and more rapid warming of soils, thereby increasing growing season length. Warmer summer temperatures may also promote faster leaf, shoot, and stem growth (Körner 1998). Warmer summer temperatures may also be correlated with higher levels of solar radiation (fewer cloudy days) and reduced frequency of photoinhibition following cold nighttime temperatures (DeLucia and Smith 1987).

Given the positive relationship between growth and summer temperature for the high-elevation FC, it seems strange that growth would also be negatively correlated with previous July temperature. A possible explanation is that July temperatures are associated with cone crop size the following year. Production of a large cone crop can drain resources that would otherwise support radial

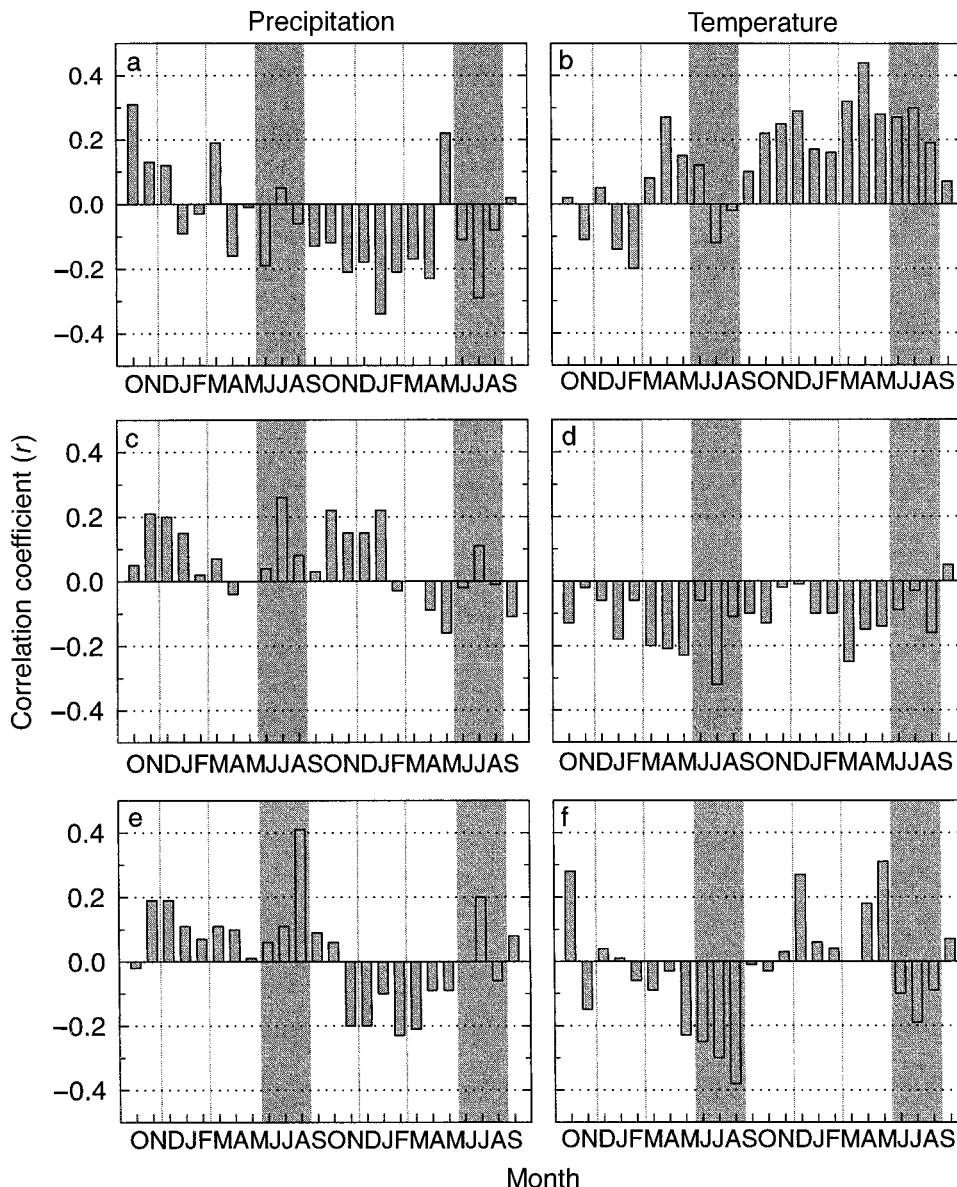


FIG. 8. Correlations (r) between mountain hemlock growth and monthly climate variables for the period 1921–1991. Climate variables include total monthly precipitation (a,c,e) and mean monthly temperatures (b,d,f) for 24 mo (two hydrologic years, October–September) prior to the end of ring formation. Growth variables include the high-elevation factor chronology (a,b), the low-elevation factor chronology (c,d), and the southern factor chronology (e,f). Threshold values for statistical significance of individual correlations are $r = 0.24$ ($P < 0.05$) and $r = 0.30$ ($P < 0.01$). Shaded areas indicate summer growth periods (June–August).

growth (Eis et al. 1965, Tappeiner 1969). Woodward et al. (1994) found that July temperature was a good predictor of cone production the following year for mountain hemlock trees in northern Oregon, and that radial growth was often reduced in years with large cone crops.

In southern Oregon, a different set of climatic factors appears to limit tree growth. Sites there have earlier snowmelt, coarser textured soils, lower mean summer precipitation, higher mean summer temperature, and less summer cloud cover than the sites in Washington

and northern Oregon. Instead of enhancing growth, warm, dry summers in southern Oregon reduce growth the following year.

Lagged effects of summer temperature and precipitation on growth in the following year are commonly observed in tree-ring studies of subalpine conifers, particularly those from lower elevations and drier sites (Peterson and Peterson 1994, Villalba et al. 1994, Ettl and Peterson 1995, Buckley et al. 1997). Climate can influence growth the following year by altering energy reserves used for early growth the following year or

TABLE 6. Multiple-regression models of climate–growth relationships for the northern, southern, and low-elevation factor chronologies.

Factor	Model R^2	Predictor variables	Coefficient	P
Northern	0.67	15 May snowpack depth	−0.0051	<0.001
		Current summer temperature	0.1560	<0.001
		Previous July temperature	−0.1170	<0.001
		Autocorrelation, lag 1	−0.2546	<0.05
Southern	0.64	15 May snowpack depth	−0.0048	<0.001
		Previous summer temperature	−0.2394	<0.001
		Previous August precipitation	0.4741	<0.001
		Previous fall precipitation (Sep–Oct)	0.1177	<0.02
Low elevation	0.50	Previous July temperature	−0.1157	<0.01
		Previous winter PDO†	−0.2333	<0.05
		Autocorrelation, lag 1	−0.7091	<0.001
		Autocorrelation, lag 2	0.2559	<0.05

† PDO = Pacific Decadal Oscillation.

by altering canopy leaf area (Fritts 1976). Specifically, warm, dry summers can reduce energy reserves by limiting photosynthesis through increased drought stress, by increasing maintenance respiration rates, or by diverting energy reserves to current-year growth. Drought stress is the likely explanation in southern Oregon, because our model shows that growth was sensitive to both temperature and precipitation the previous August. Increased respiration and changes in leaf area could also be important, however.

If summer drought limits mountain hemlock growth in southern Oregon, why is growth negatively correlated with spring snowpack, the major source of soil water recharge? The answer is unclear. A possible explanation is that early snowmelt lengthens the effective growing season by initiating growth earlier in the summer, when temperatures are cooler, cloud cover is more frequent, vapor pressure deficits are lower, and occasional rainfall events recharge water supplies near the soil surface. Such conditions would extend the period of water availability during the growing season and might improve water use efficiency.

The insensitivity of the low-elevation FC to annual climatic variability was unexpected, but could be the result of environmental limitations on seedling establishment and survival that exclude the species from more extreme sites. Mountain hemlock seedlings have shallow roots, are drought sensitive, and can require >30 yr to reach a height of 1 m (Lowery 1972, Taylor 1995), so mountain hemlocks are typically found on sites with adequate soil water throughout the year (Habeck 1967, Means 1990). In the Olympic Mountains, establishment of mountain hemlock seedlings requires multiyear periods with mesic conditions; on wet sites, seedlings have established successfully during warm, dry periods (Woodward et al. 1995), while on warmer, more mesic sites, seedlings have established successfully during wet periods (Agee and Smith 1984).

Our climate–growth model for the high-elevation FC is similar to one developed by Graumlich and Brubaker (1986) for mountain hemlock chronologies from western Washington. Both models feature the negative ef-

fects of snowpack and the positive effects of summer temperature on mountain hemlock growth. Correlations between growth and monthly climate similar to those in Fig. 8a have been reported for mountain hemlock chronologies from British Columbia and Alaska (Wiles et al. 1996), suggesting that the snowpack and summer temperature currently limit mountain hemlock growth throughout much of its geographic range. The same basic climate–growth relationship has been reported for subalpine fir chronologies from wet, high-elevation sites in Washington (Peterson and Peterson 1994, Ettl and Peterson 1995).

Response of mountain hemlock forests to future climatic change

Doubling of atmospheric CO₂ levels could produce increases in mean annual temperature of 1.0–2.5°C over the next century, with the largest temperature increases during the winter months (Leung and Ghan 1999a, b). Such changes would alter the fraction of winter precipitation that falls as snow and reduce spring snowpack depth. The mean temperature increase in this scenario is similar to spatial differences in mean temperature between high- and low-elevation sites in our study and to temporal differences in temperature associated with extreme phase combinations for the PDO and SOI (warm PDO/El Niño vs. cool PDO/La Niña). Therefore, our results provide useful predictions of mountain hemlock responses to such a scenario.

For mountain hemlock sites currently associated with the high-elevation FC, a combination of lower spring snowpack depths and warmer summer temperatures would likely reduce growth limitations caused by late snowmelt and increase forest productivity. New pulses of seedling establishment in wet subalpine and alpine meadows and upward movement of the alpine tree line would also be likely, as these have occurred during warm periods of the past century (Rocheffort et al. 1994, Rocheffort and Peterson 1996).

In mountain hemlock forests of southern Oregon, warmer summers would likely reduce growth rates, particularly if summer precipitation remained at current

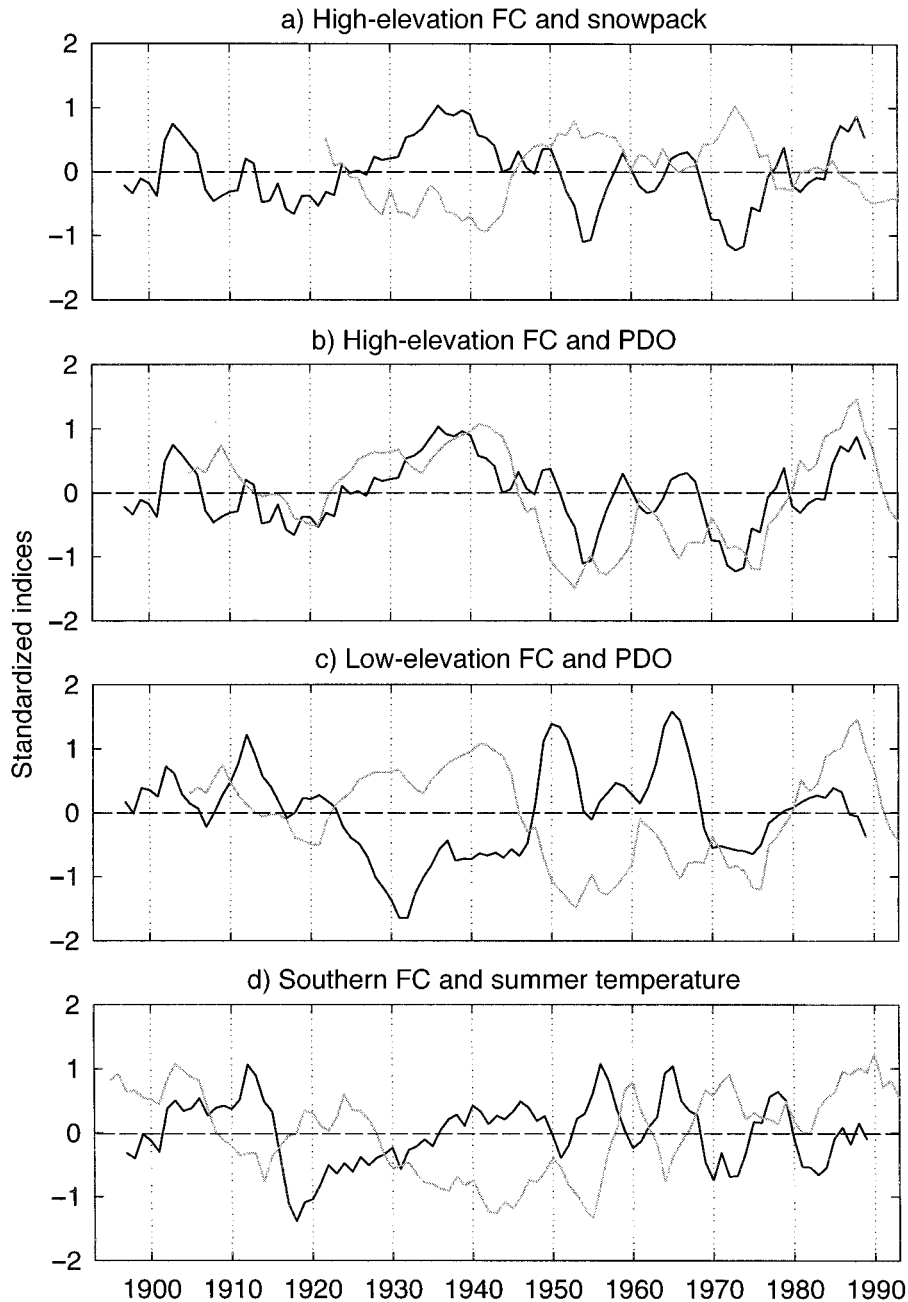


FIG. 9. Time plots comparing low-frequency variations in mountain hemlock growth with low-frequency variations in climate. Plotted values are 5-yr running averages of normalized growth indices (black lines) and climate variables (gray lines): (a) high-elevation factor chronology (FC) and 15 May snowpack depths at Mount Rainier; (b) high-elevation FC and winter Pacific Decadal Oscillation (PDO); (c) low-elevation FC and winter PDO; (d) southern FC and mean summer temperature in southern Oregon.

levels or declined. There could also be increased risk of frost damage if earlier snowmelt causes shoot growth to commence earlier in the spring (Cannell and Smith 1986). Regeneration could be increasingly limited to periods when decadal variability in climate produces a series of summers with reduced temperature and moisture stress.

The possible effects of future climate scenarios on mountain hemlock growth at sites associated with the low-elevation FC are harder to predict. The apparent low-frequency response to variations in the PDO suggests that future warming would reduce growth rates at these sites. The lack of a common, high-frequency growth pattern suggests, however, that there is cur-

rently no single climatic factor consistently limiting growth.

Shifts in the lower elevation limits of mountain hemlock are more likely to be affected by climatic influences on disturbance regimes (Franklin et al. 1991), human disturbance, and increased competition from species currently restricted to lower elevations by snowpack or temperature. Established mountain hemlocks can live for several centuries, providing a long-term seed source and the potential for understory regeneration whenever climatic variability produces conditions favorable for establishment. The biggest threats to these populations are large-scale disturbances, especially severe fires and logging, which kill overstory trees, eliminate seed sources, and alter the regeneration environment by removing the ameliorating effects of tree canopy cover on understory air temperature, humidity, and soil-surface moisture.

Future directions

The structured sampling method used in this study proved valuable for detecting common patterns of annual and decadal variability in mountain hemlock growth, for identifying the spatial extent of those common growth patterns in the region, and for identifying the climatic factors most likely to be limiting growth of mountain hemlocks throughout the region. Regional tree-ring studies have often been used by dendroclimatologists to reconstruct climate and to investigate tree growth patterns over large areas (Fritts et al. 1979, Brubaker 1980, Briffa et al. 1992, Meko et al. 1993; review in Hirschboeck et al. 1996). There have been only a few regional studies of climate-growth relationships for a single species, however (Cook and Cole 1991, Mäkinen et al. 2000). Spatial variations in species climate-growth relationships have been studied with respect to elevation (Norton 1984, Ettl and Peterson 1995, Buckley et al. 1997), aspect (Villalba et al. 1994), and precipitation gradients (Ettl and Peterson 1995). This study may be unique, however, in studying climate-growth relationships for a species at regional spatial scales, with nested sampling to account for local topographic variability.

We encourage future studies of this type because we believe they provide valuable insight about species responses to climatic variability. These studies need not be confined to latitude and elevation transects, however. In mountainous areas, topographic position (slope, aspect), soil properties, and orographic effects on climate all produce spatial patterns in the biophysical environment that may influence tree growth. The increased availability of GIS-based climate data makes it possible to study tree growth responses across predefined climatic gradients. Climate extrapolation models (e.g., MT-CLIM, Running et al. 1987) can further refine estimates of climatic conditions to account for topographic effects in complex terrain. Ecosystem models may also be useful for predicting growth re-

sponse patterns at selected sites prior to field sampling; the chronologies then serve dual purposes of identifying climate-growth relationships and validating (or refuting) model predictions.

One limitation of this study was that we were able to examine only relative growth variations. Field observations and previous studies in subalpine ecosystems suggest that absolute tree growth and total forest productivity is probably highest at the low-elevation sites (Tranquillini 1979), and that environmental stress is least at the lower elevation limit of the species' distribution. Comparison of forest productivity between sites requires additional stand data, however, including stand densities and tree heights, which were not collected for this study. In the future, researchers should consider collecting this data. The required fieldwork would be minimal compared to the time and effort required to process tree cores and develop the tree-ring chronologies, and the potential benefits are significant.

CONCLUSIONS

Growth of mountain hemlocks varied significantly at annual and decadal time scales, and these variations in growth appeared to be largely driven by climatic variability. Snowpack and summer temperatures influenced hemlock growth throughout the region through their influence on growing-season length and site water-balance. Specific limiting factors varied spatially along our latitudinal gradient, apparently in response to latitudinal variations in climate. This was seen most clearly in differences in interannual growth patterns and climate-growth relationships between chronologies from northern and southern Oregon. Climate-growth relationships also vary with elevation, most likely in response to differences in snowpack accumulation and duration.

Dendroecological studies can be useful for identifying climatic factors limiting growth throughout a species' latitudinal and elevation range. Such information should improve our ability to accurately represent species growth responses to climate in forest simulation models and better predict community and ecosystem responses to future climatic variability. Future studies should consider sampling multiple species at each site and collect the additional stand-level data, especially stand density and tree heights, required to compare aboveground productivity among sampling sites. This would help to distinguish between climatic and competitive constraints on species ranges, particularly within the forest zone.

Climatic variation associated with shifts between the cool and warm phases of the PDO is similar to the magnitude of predicted climatic responses to elevated atmospheric CO₂ levels in the Pacific Northwest. At decadal time scales, trees have sufficient time to adjust physiologically and morphologically to altered climatic conditions. Past growth responses to climatic variability at decadal time scales may, therefore, provide the

best indication of potential productivity responses to future climatic change.

ACKNOWLEDGMENTS

Support for this project was provided by the U.S. Geological Survey Global Research Change Program and by the Joint Institute for the Study of the Atmosphere and Ocean (JISAO) under NOAA Cooperative Agreement No. NA67RJ0155 (contribution no. 810). We thank D. Horner, D. Veale, M. Balick, W. Jackman, S. Prichard, S. Brace, N. Zolbrod, E. Schreiner, and A. Woodward for their assistance in collecting and processing tree cores. D. Silsbee contributed to chronology development and statistical analysis. R. Norheim assisted with figures. We thank D. McKenzie, S. T. Jackson, and two anonymous reviewers for helpful manuscript reviews.

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