Spatial Patterns of Tree Growth Anomalies in the Pacific Northwest

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SPATIAL PATTERNS OF TREE GROWTH ANOMALIES IN THE PACIFIC NORTHWEST[1]

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Abstract. Regional patterns of ring width anomalies in Washington, Oregon, and Idaho, USA forests are examined using eigenvector (principal component) techniques. The first two eigenvectors, accounting for nearly 50% of the total variance, represent large-scale spatial patterns. Eigenvector I represents a pattern in which growth anomalies are positively correlated among all sites, and Eigenvector II one in which growth anomalies are negatively correlated between sites located on opposite sides of the Cascade Mountain crest.

These patterns most likely result from two types of tree growth responses to climate variations that extend uniformly across the study area. Common responses to spring–summer rainfall probably cause the positive, region-wide correlations identified by Eigenvector I, and opposite east–west responses to summer temperature and winter precipitation may account for the negative correlations identified by Eigenvector II. No evidence supports the idea that the tree growth eigenvectors directly reflect two distinctive patterns of climate anomalies.

The spatial patterns of these tree growth anomalies have remained essentially constant during the past 300 (possibly 400) yr.

Key words: dendrochronology; limiting factors; Pacific Northwest; principal components; tree growth, tree rings.

INTRODUCTION

Large-scale weather systems affect tree growth by modifying the microenvironment of individual trees. Although the elevation, slope, aspect, and exposure of a site can mitigate the influence of macroclimatic factors, regional weather conditions often play a very important role in determining tree growth rates within individual stands. Studies in a wide range of forest environments, for example, have shown that variations in tree ring widths are well correlated with variations in macroclimatic factors (Giddings 1943, Zahner and Stage 1966, LaMarche 1973, Serre 1973, Fritts 1976, Cook and Jacoby 1978, Kay 1978).

If the response of tree growth to climate-related variables is sufficiently strong, there should be predictable relationships of annual growth among stands which are influenced by the same regional weather systems, even though local site conditions vary greatly. Pacific Northwest forests offer a good opportunity to look for such relationships because numerous mountain ranges in the area create strong temperature and precipitation gradients across very short distances. As a result, sites with contrasting microclimates experience the same relative changes as each new weather system crosses the area.

The purpose of this study is to (1) examine large-scale, spatial patterns of radial growth among 38 forest stands in Washington and adjacent portions of Oregon and Idaho, and (2) investigate the role of macroclimatic factors in determining such patterns. Eigenvec-

tor (principal component) techniques are used to identify and display characteristic spatial patterns of growth anomalies, i.e., repeated ways that tree growth has deviated from long-term average values. To investigate the role of climate, tree growth eigenvector patterns are visually compared to eigenvector patterns of climate variables, and climate-growth relationships are examined for individual sites using multivariate regression techniques.

STUDY AREA

Mountain ranges

Forest stands were sampled in each of four major mountain systems: (1) the Olympic Mountains along the west coast of Washington, (2) the Cascade Mountains which run north-south through the central portion of Washington and Oregon, (3) the Rocky Mountains along the northern and eastern border of the interior Columbia Plateau, and (4) the Blue Mountains bordering the Plateau on the south (Fig. 1).

Climate

The climate of this region is complex, primarily due to the interaction of Pacific air masses with the mountain ranges (Phillips 1972). While the Olympic Mountains cause some orographic lifting and release of moisture from ocean air moving inland, the Cascade Range is the major climatic barrier of the state. Heavy orographic precipitation occurs along the western slopes of these mountains, and the drier air becomes warm as it descends along the eastern slopes, creating near desert conditions in some portions of the Columbia Plateau. Orographic lifting also occurs as air flows
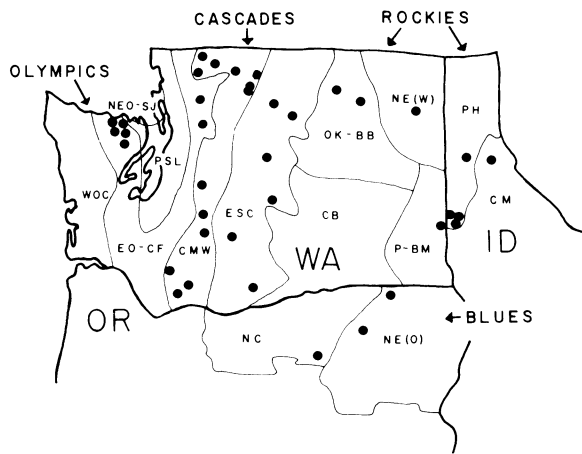
FIG. 1. Climatic divisions of Washington State. WOC = West Olympic Coastal, EO-CF = East Olympic-Cascade Foothills, NEO-SJ = Northeast Olympic-San Juan, PSL = Puget Sound Lowlands, CMW = Cascade Mountains West, ESC = East Slope Cascades, OK-BB = Okanogan-Big Bend, CB = Central Basin, NE(W) = Northeastern (Washington), P-BM = Palouse-Blue Mountains, NE(O) = Northeastern (Oregon), PH = Panhandle, NC = North Central, CM = Central Mountains. Dots indicate study sites.

from the Columbia Plateau toward the Rocky Mountains of Idaho, causing a gradual increase in precipitation from low to high elevations along the eastern border of the state. Likewise, precipitation increases with elevation in the Rocky Mountains to the north and in the Blue Mountains to the south.

Pacific air dominates the area in all months of the year. During the wet season, which extends from October through May, air masses approach from the southwest. Condensation occurs as the moist, relatively warm air moves over the cooler land and rises along the mountain slopes. During the dry summer season, prevailing winds from the northwest bring in dry, cool, and stable air which becomes warmer and drier as it moves across the land.

Forests

Forests in the study area have been described by Franklin and Dyrness (1973). They recognize 10 forest zones in this area, all dominated by coniferous species and distributed primarily according to macroclimatic gradients of temperature and moisture. Summarizing the forests briefly, most of the lower elevation forests in the western portion of the area are dominated by Douglas-fir (*Pseudotsuga menziesii* [Mirb.] Franco), western hemlock (*Tsuga heterophylla* [Raf.] Sarg.), and/or western redcedar (*Thuja plicata* Donn). These species are replaced at higher elevations by Pacific silver fir (*Abies amabilis* [Doug.] Forbes) and mountain hemlock (*Tsuga mertensiana* [Bong.] Carr.). East of the mountains, ponderosa pine (*Pinus ponderosa* Laws), Douglas-fir, grand fir (*Abies grandis* [Dougl.] Lindl.), western larch (*Larix occidentalis* Nutt.), and

lodgepole pine (*Pinus contorta* Dougl.) are common at low to middle elevations, while Engelmann spruce (*Picea engelmannii* Parry), and subalpine fir (*Abies lasiocarpa* [Hook.] Nutt.) occur in high mountain areas.

METHODS

Four criteria were used to select stands for this study. The stands should be (1) slow growing, (2) older than 100 yr, (3) on well-drained sites, and (4) relatively free of disturbance by logging, fire, or insects. This method of site selection tends to minimize the influence of nonclimatic factors which can obscure the climatic information in growth ring sequences (Fritts 1976). An attempt was made to sample several sites at different elevations from each of the major mountain areas, but coverage is not uniform throughout all forested areas (Fig. 1). Low-elevation areas were not sampled because they are treeless in the east and are nearly always covered by young, second-growth forests in the west.

Field collections were made during the summers of 1975 and 1976. At each site, two breast height cores were collected from each of 10–15 trees of the dominant species in the stand. Ponderosa pine was sampled at all sites east of the Cascade crest. The western sites are predominantly Douglas-fir, but also include Engelmann spruce, subalpine fir, noble fir, western hemlock, mountain hemlock, and whitebark pine (*Pinus albicaulis* Engelm.). Cores were mounted in permanent holders and sanded to a high polish. All rings were dated by cross-dating methods (Stokes and Smiley 1968) and measured to the nearest ±0.01 mm with a Bannister's incremental measuring machine.

The ring measurements of each core were standardized to remove inherent trends of decreasing width from pith to bark. This was done by fitting a polynomial, exponential, or linear curve to the measurements from each core, and dividing the width for each ring by the corresponding curve value. The resulting values, called ring width indices, reflect yearly growth variations around the long-term trends removed by the standardization procedure. Site growth chronologies were created by averaging together the index values of the cores according to year (Fritts et al. 1969, Fritts 1976).

The climatic data used for comparison with site chronologies were total monthly precipitation and average monthly temperature (1931–1974) from the climatic division within which each site was located (Fig. 1). The climatic divisions are those taken by National Oceanic and Atmospheric Administration (United States Environmental Data Service 1930–1974) to represent areas of relatively uniform climate. Records from each division are mean values from several climatic stations. The division data were used because they reflect regional climatic variations better than do records from individual climatic stations (Fritts 1976).
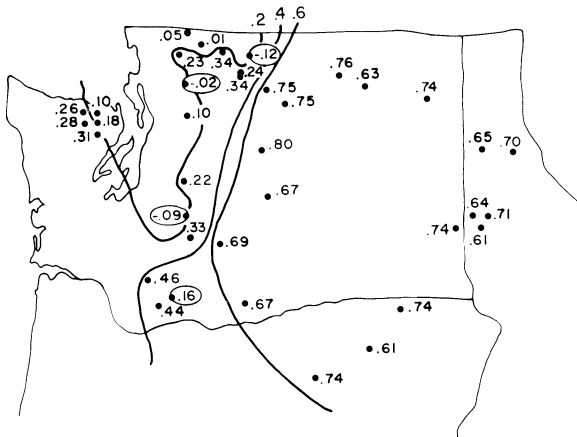
FIG. 2. Component values of tree growth Eigenvector I. Circles values do not correspond with the contour interval.
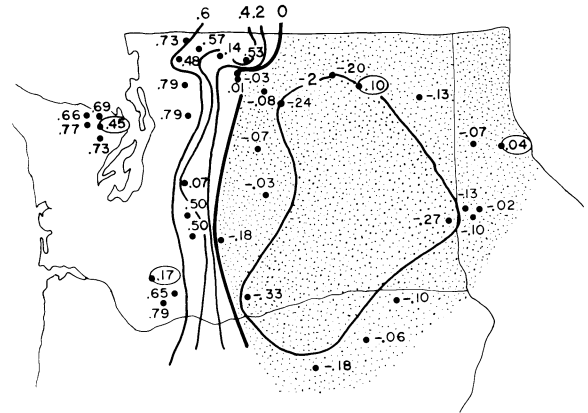

FIG. 3. Component values of tree growth Eigenvector II. Stippling indicates areas with predominantly negative value. Circled values do not correspond with the contour interval.

NUMERICAL ANALYSES

The following sections discuss several analyses of ring width indices and climatic data. The section entitled "Eigenvector analyses" describes ways that growth indices are correlated among the 38 sites, "Climate-growth relationships" examines two hypotheses to explain the role of climate in determining such growth correlations, and "History of growth anomalies" examines the consistency of the growth correlations among sites during the past 400 yr.

Eigenvector analyses

Growth correlations among the 38 sites were identified using eigenvector (principal component) analyses according to procedures described by LaMarche and Fritts (1971), and Blasing and Fritts (1976). The terminology in the present study is consistent with that used by Blasing and Fritts (1976). In each of the analyses of tree ring data, the data set consists of standardized ring width indices for n years (observations) at m sites (variables). Each analysis results in m eigenvectors (e.g., $m = 38$ if all sites are included in the analysis), but only the first few of these describe the major variance relationships among the sites. These lower order eigenvectors represent the most important large-scale anomaly patterns within the ring width data, i.e., characteristic ways that indices at the m sites have varied from their mean values during the n years. Higher order eigenvectors reflect small-scale, growth anomaly relationships and can be discarded from further anlayses as noise.

Each eigenvector consists of m components corresponding to the m sites. These values convey information about characteristic growth correlations among the sites. For example, if the components for several sites have the same sign, the eigenvector reflects a tendency for growth variations at those sites to be positively correlated. If the component value of a site

is near zero, growth at that site has no relationship to the characteristic anomaly pattern represented by that eigenvector. The components of an eigenvector can be plotted on a map of the sites, as shown in Figs. 2 and 3, to display the pattern of growth anomaly which it represents.

Tree ring eigenvectors were derived for each of four different periods: (1) 1875–1974 (38 sites), (2) 1775–1974 (33 sites), (3) 1675–1974 (22 sites), and (4) 1575–1974 (10 sites). The shortest period gives the best spatial coverage of sites (38), but cannot be used to describe growth anomaly patterns before 1875. Data from the longest period can reveal patterns that occurred long ago (400 yr) but may not include enough sites to identify spatial patterns across the entire study area.

For each of the four periods only the first two tree ring eigenvectors produced easily interpretable patterns. In these analyses (Table 1a) the first eigenvector accounted for from 24.7 to 30.8% of the variance ($\bar{x} = 26.9\%$), while the second eigenvector accounted for from 15.4 to 20.8% of the variance ($\bar{x} = 17.6\%$). The 100-yr data set is used in the following discussion of eigenvector patterns, because the inclusion of all 38 sites produces eigenvector maps with greatest spatial resolution. The eigenvector patterns for this data set are representative of those for longer periods, as will be described in "History of growth anomalies."

Eigenvector I for the 100-yr period accounts for 26.2% of the total variance. Its components exhibit positive values at 35 of the 38 sites (Fig. 2). Since similar signs indicate positive correlations, this eigenvector reflects the tendency for annual growth to be positively correlated among sites throughout the study area. Component values are highest at sites east of the crest of the Cascades, indicating that growth is more highly correlated between stands in the Idaho Rockies and east-slope Cascades (300–400 km apart) than it is

TABLE 1. Tree ring and climate eigenvectors: percent variance explained.

a. Tree ring eigenvectors

	I	II
1875–1974	26.2	17.1
1775–1874	24.7	17.0
1675–1774	26.0	15.4
1575–1674	30.8	20.8
$\bar{x}$	26.9	17.6

b. Climate eigenvectors

		J	F	M	A	M	J	J	A	S	O	N	D
Temperature	I	95.0	94.1	91.3	92.7	91.3	87.1	83.9	87.1	90.2	88.3	91.1	90.1
	II	3.3	3.3	4.5	3.6	5.0	7.8	9.3	7.0	5.8	5.1	4.7	5.4
Precipitation	I	75.1	71.0	71.4	67.5	66.3	64.5	67.5	77.4	72.0	79.8	81.9	67.2
	II	14.1	19.3	13.0	16.5	18.8	21.4	18.3	10.2	15.6	10.4	8.4	17.3

between stands only 80–90 km apart on opposite sides of the Cascade crest.

Eigenvector II accounts for 17.1% of the total variance. It represents a growth anomaly pattern in which western and eastern areas are negatively correlated, because the component values of western and eastern sites are opposite in sign (Fig. 3). The strongest gradient in the component values corresponds closely to the crest of the Cascade Range. In certain years, therefore, growth in western areas tends to be high (or low) relative to growth in eastern areas. As a whole, however, western growth anomalies are more important than eastern anomalies in establishing this pattern, because western components values are very large in comparison to eastern values.

Since these eigenvectors represent correlated growth anomalies across several hundred kilometres, they are best explained in terms of responses to variations in regional climatic conditions. Climate is the only agent which can simultaneously and repeatedly affect tree growth over such wide areas.

Climate-growth relationships

Two hypotheses have been developed in an attempt to identify the role of climate in determining these growth anomaly patterns. The first one, called the similar-response hypothesis, implies that a given climatic variation will affect tree growth in the same way everywhere. According to this hypothesis, the tree ring eigenvector patterns reflect the direct effects of two types of climate variations, one in which conditions vary uniformly across the study area and another in which contrasting climate anomalies occur in eastern and western areas. The alternative hypothesis, the mixed-response hypothesis, is that trees in different regions will respond differently to the same climate variation. According to this hypothesis, the pattern of Eigenvector I results from a common growth response at all sites to regionally uniform weather variations, and Eigenvector II results from differential east-west growth responses to regionally uniform weather variations.

Similar-response hypothesis.—To test this hypothesis, climatic data from the 10 Washington climatic divisions were examined by eigenvector techniques. Twenty-four separate analyses were performed: one for each month's mean temperature and total precipitation (1931–1974). These analyses were structured like those of tree ring data, so that the components of each eigenvector reflect a characteristic spatial pattern of climate anomaly. This hypothesis is supported if climate eigenvectors exhibit spatial patterns similar to tree ring eigenvector patterns.

In these analyses, the first eigenvector accounts for 65–95% of the variance (Table 1b). In all cases, the distribution of eigenvector components is similar to that of tree ring Eigenvector I components, indicating that most precipitation and temperature anomalies extend uniformly across the entire region. Common tree growth responses to these anomalies, therefore, could account for the pattern of tree ring Eigenvector I. For this hypothesis also to explain tree ring Eigenvector II, however, there should be a climate eigenvector exhibiting opposite east-west relationships between sites. While none of the monthly temperature eigenvectors show such a pattern, each of the second eigenvector patterns for monthly precipitation show distinct east-west trends. Only the patterns for April through October, however, are identical to tree ring Eigenvector II, showing the Cascade Mountain crest as the transition between positive and negative component values. For other months, the match is poor because the east-west transition in component values is 120 km farther east in the climatic data than in the tree ring data.

These findings provide only weak support for the similar-response hypothesis, because only 7 of the 24 precipitation and temperature variables exhibit eigenvector patterns similar to tree ring Eigenvector II, and these (i.e., second eigenvectors for April through Oc-
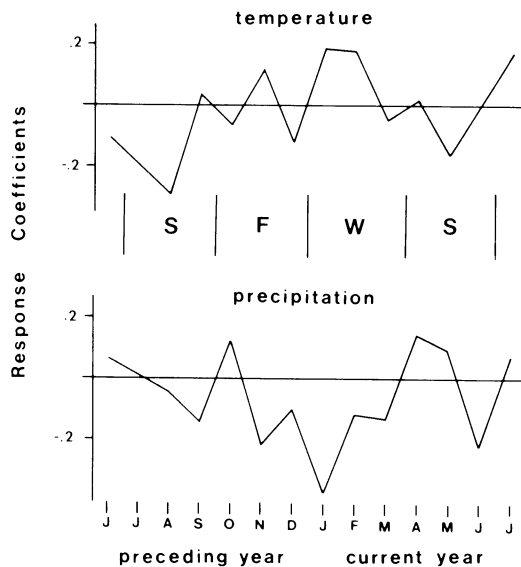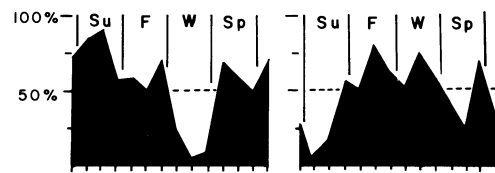
FIG. 4. Response function for a western Washington site. The response function includes 14 coefficients for average monthly temperature and 14 coefficients for total monthly precipitation from June of the year prior to the season of growth through the July concurrent with growth. A positive value indicates a positive correlation between growth and the climatic variable, a negative value indicates a negative correlation. S, F, W, S = summer, fall, winter, spring.
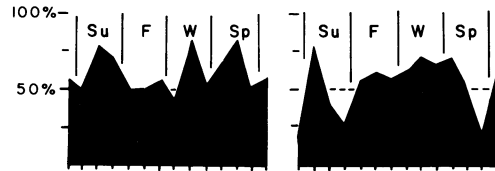

FIG. 5. Summary of response functions from western and eastern areas. For each area, the percentage of sites showing a positive response to the climatic variable is plotted according to month. Months are arranged as indicated in Fig. 4. Su, F, W, Sp = summer, fall, winter, spring.

tober precipitation, Table 1b) account for a relatively small ($\bar{x}$ = 15.9%) portion of the respective total variance. It seems unlikely that such a minor component of the overall temperature and precipitation variation could cause major regional patterns in tree growth. A later section, "Evidence for climatic hypotheses," presents more rigorous evidence for rejecting this hypothesis.

Mixed-response hypothesis.—This hypothesis requires that eastern and western sites exhibit common responses to some regionally uniform climate anomalies, but opposite responses to others. In an attempt to identify such responses, ring width indices at all sites were compared to temperature and precipitation records using a modified multiple regression analysis designed by Fritts et al. (1971). In these analyses, the climatic data consist of monthly total precipitation and average temperature for a 14-mo period starting with June of the previous growth season and ending with July of the current season, 1931–1974. Before regressing indices against climatic data, intercorrelations among the climatic variables were eliminated by transforming the original climatic variables into orthogonal variables by principal component analysis. Nongrowth season conditions were included because conditions prior to cambial activity influence the amount of wood produced while the cambium is active (Helms 1963, Fritts 1976, Waring and Franklin 1979). A 14-mo period was chosen because it generally resulted in highest correlations between growth and climatic vari-

ables. Index values for one, two, and three preceding years were also included in the regression equation to account for the lagging effect of the growth in one season on growth during following seasons (Fritts 1976).

Climate-growth relationships identified by these procedures are expressed as a response function vector, whose entries (analogous to partial regression coefficients) indicate the contribution of variations in each month's temperature and precipitation to variations in ring width indices. A response function for a Douglas-fir site in the Olympic Mountains is shown in Fig. 4. The plotted values show the statistical association between growth and monthly precipitation and temperature. A positive value indicates that above-average growth is associated with an above-average value of the climatic variable and a negative value indicates that above-average growth is associated with a below-average value of the variable.

To test the mixed-response hypothesis, response functions from sites on either side of the Cascade crest were summarized and visually compared. For each area the number of sites exhibiting a positive response to a given climatic factor was determined for each month and expressed as a percentage of the total number of sites (Fig. 5). The following discussion is based on comparisons between the graphs shown in Fig. 5.

The majority of both eastern and western sites show positive growth responses to above-average fall/winter temperatures and spring/summer rainfall. The positive response to preceding summer rainfall is the strongest common behavior among all sites. This type of response to climate could cause growth to be positively

TABLE 2. Regression correlation coefficients of tree ring eigenvector amplitudes.

a. Correlation of amplitudes of Eigenvectors I and II for 100-, 200-, 300-, and 400-yr data sets.*

Eigenvector I	r	Eigenvector II	r
300 vs. 400	.5137	300 vs. 400	.5811
200 vs. 300	.9656	200 vs. 300	.9109
200 vs. 400	.6459	200 vs. 400	.6387
100 vs. 200	.9917	100 vs. 200	.9673
100 vs. 300	.9780	100 vs. 300	.9465
100 vs. 400	.5600	100 vs. 400	.5422
400 with all others	$\bar{r} = .57$	400 with all others	$\bar{r} = .59$
100–300 with each other	$\bar{r} = .98$	100–300 with each other	$\bar{r} = .94$

b. Correlation of amplitudes of tree ring Eigenvector I (1930–1974) with average Palmer Drought Index for prior July–August–September.

Climatic Division	r
East Olympics-Cascade Foothills	.3710 ($P = .008$)
West Cascade Mountains	.2501 ($P = .057$)
East Slope Cascades	.3262 ($P = .019$)
Okanagan-Big Bend	.4538 ($P = .001$)

c. Partial regression coefficients for amplitudes of tree ring Eigenvector II against July temperature and winter (December, January, February) precipitation (temperature lagged 1 yr).

Climatic Division	Temperature coefficient	Precipitation coefficient	Constant
East-Olympics Cascade Foothills	−0.0293 ($P = .001$)	−0.006285 ($P = .035$)	2.04 ($P = .000$)
West Cascade Mountains	−0.0234 ($P = .000$)	−0.002291 ($P = .198$)	1.51 ($P = .000$)
East Slope Cascades	−0.02898 ($P = .000$)	−0.007241 ($P = .118$)	2.00 ($P = .000$)
Okanagan-Big Bend	−0.01675 ($P = .040$)	−0.03483 ($P = .028$)	1.34 ($P = .015$)

* $P = .001$ in all cases.

correlated throughout the study area, as identified in tree ring Eigenvector I.

According to this hypothesis eastern and western sites must also respond differently to some region-wide weather anomalies. Strikingly different responses do occur to winter precipitation and preceding summer (July) temperature. At western sites, growth is negatively correlated with both winter precipitation and prior July temperature; at eastern sites it is positively correlated with these variables. This strongly supports the mixed-response hypothesis, because differential east-west responses to winter precipitation and July temperature could account for the reciprocal behavior of these sites as identified by Eigenvector II.

History of growth anomalies

The history of tree growth anomalies was investigated by examining the eigenvector amplitudes (factor scores) over time. An eigenvector amplitude for a given year is calculated by multiplying the m eigenvector components with the corresponding tree ring indices (expressed as departures from average) for the m sites and summing across all sites. This calculation produces large positive values if the observed growth

anomaly pattern coincides with the anomaly pattern of that eigenvector. Large negative amplitude values occur when the observed growth pattern resembles the eigenvector pattern but is opposite in sign. Amplitudes are near zero if the observed pattern does not resemble the eigenvector pattern.

To examine the consistency of eigenvector patterns through time, amplitude records of the 100-, 200-, 300-, and 400-yr data sets were correlated with each other during their common period, 1875–1974. High correlations between two amplitude records indicate that the respective eigenvectors exhibit the same basic spatial pattern. Correlations were very high among the 100-, 200-, and 300-yr data sets for both eigenvectors ($\bar{r} = .98$, $\bar{r} = .94$), but relatively low for the 400-yr set with the others ($\bar{r} = .57$, $\bar{r} = .59$) (Table 2). These results suggest that tree growth anomaly patterns have not changed greatly during the past 300 yr. The low correlations of the 400-yr data set probably reflect inadequate sample sizes because only 10 sites reached 400 yr and relatively few cores at any one of these sites spanned the entire 400 yr.

Amplitudes of Eigenvector I.—Fig. 6 shows the 300-yr amplitude record for Eigenvector I. Positive values
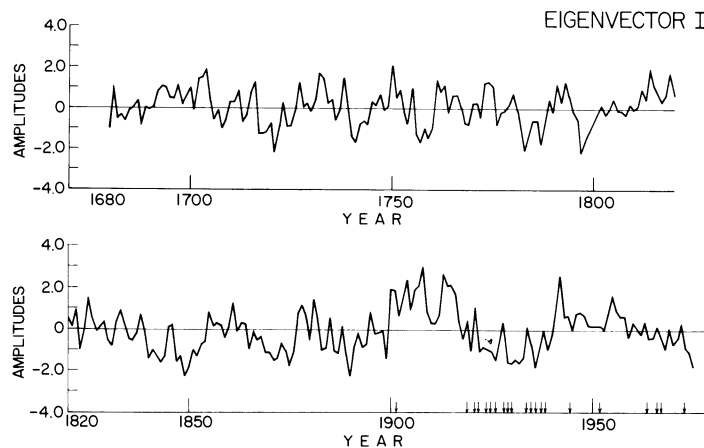
FIG. 6. Amplitudes of tree growth Eigenvector I (1675–1974). Arrows indicate years of regional drought in Washington (Lasher 1977).

indicate that above-average growth occurred throughout the study area, negative values indicate below-average growth, and zero values indicate no uniform growth anomaly in the study area. The most striking features in this record are the high values from 1900 to 1918 and low values from 1919 to 1940. Several factors indicate that this record reflects the effect of regional droughts:

(1) According to response function results (Fig. 5), growth throughout the study area is positively correlated with spring/summer rainfall.

(2) The arrows in Fig. 6 indicate drought years in the state of Washington (Lasher 1977). Though low amplitudes do not always coincide with individual drought years, there is a strong correspondence between frequent droughts and negative values during 1919–1940.

(3) Amplitudes for 1931–1974 are positively correlated ($P = .01$) with average Palmer Drought Index (Palmer 1965) values for prior July–September for selected climatic divisions in both eastern and western Washington (Table 2).

(4) The positive amplitudes during 1900–1919 correspond to a well-documented period of abundant rainfall in western North America (Lamb 1963).

The amplitudes of Eigenvector I, therefore, can be interpreted in terms of drought-related factors. According to this record, droughts are common in the Pacific Northwest. The most prolonged dry period during the past 300 yr occurred between 1920–1940. Prior to 1900, droughts tended to persist only 5–10 yr. These general results agree with recent findings by Fritts et al. (1979).

Furthermore, since Eigenvector I is the most important anomaly pattern of tree growth, another important conclusion is that drought factors (especially spring/summer precipitation) are the most important

factors limiting tree growth in Pacific Northwestern forests.

Amplitudes of Eigenvector II.—The amplitudes of Eigenvector II (Fig. 7) indicate east-vs.-west growth anomalies. Positive values mean that growth anomalies were similar in sign to Eigenvector II, and thus growth was greater in the west than in the east. Likewise, negative values indicate that growth anomalies were opposite in sign to Eigenvector II. Since winter precipitation and summer temperature variations cause different growth responses between eastern and western sites, this record should reflect the history of these variables. To identify such relationships, the amplitude record of Eigenvector II was compared, by multiple regression, to winter (December–February) precipitation and prior July temperature for selected climatic divisions in eastern and western Washington (1931–1974). In both areas the amplitude values are negatively correlated with winter precipitation and prior July temperature (Table 2), which is consistent with response function results. It is difficult, however, to interpret directly this amplitude record in terms of climate variation, because it reflects the combined effects of two different climatic variables.

DISCUSSION

Evidence for climatic hypotheses

The nature of climate variations and tree growth responses to climate support the mixed-response hypothesis because (1) eigenvector analyses of climatic data indicate that most of the variation in temperature and precipitation can be explained by anomalies extending uniformly across the study area, and (2) response function analyses identify certain variables (winter temperature and summer precipitation) which affect growth in the same way everywhere, and others (winter precipitation and prior July temperatures)
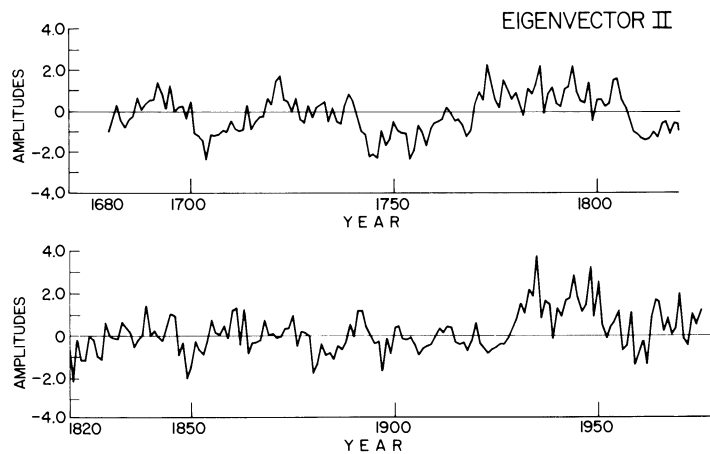
FIG. 7.   Amplitudes of tree growth Eigenvector II (1675–1974).

which affect growth differently in eastern and western areas.

Further support for this hypothesis comes from comparisons between climatic variables and the amplitudes of tree ring eigenvectors. For example, the amplitudes of tree ring Eigenvector I are significantly correlated with indices of summer drought, which has the same growth effect throughout the study area, and amplitudes of Eigenvector II are significantly correlated with winter precipitation and July temperature, both of which have opposite east-west effects on growth. These relationships are in agreement with the mixed-response but not the similar-response hypothesis. According to the similar-response hypothesis, amplitudes of tree ring Eigenvector II should be related to climatic variables having similar east-west growth effects. Furthermore, if this hypothesis were correct, tree ring Eigenvector II would directly reflect precipitation anomalies during April–October, since these are the only variables showing the correct east-west anomaly pattern. Accordingly, one would expect that the amplitudes of this eigenvector should be significantly correlated with the amplitudes of April–October precipitation Eigenvector II. These comparisons were made but no significant correlations were found for any of the months.

Considering the above results in total, it seems reasonable to conclude that the regional differences in ring width anomalies are caused by regional differences in tree growth responses to climate rather than by differences in climate behavior itself.

Comparisons with other studies

Recent coniferous forest biome studies of photosynthesis and forest productivity agree with an important conclusion of this study—that water stress during warm seasons is the primary factor limiting tree growth in the Pacific Northwest. For example, along a transect of mature coniferous communities from the Pacific coast to the Interior Plateau of Oregon, Grier and Running (1977) found strong positive correlations between the availability of water during the growing season and community leaf area index, a measure of net primary productivity. According to them, Pacific Northwest forest trees usually experience water stress during mid- to late summer, because the water required during summer is provided mainly by water stored in the soil at the beginning of the growing season.

In support of this idea, experimental (Helms 1963, Salo 1974) and simulation (Emmingham and Waring 1977) studies of photosynthesis in western Cascade forests have shown that water deficits often greatly reduce net photosynthesis during summer and early fall months. Emmingham and Waring (1977) estimate that summer photosynthesis losses due to drought range from 30 to 55% in four coniferous forest communities in western Oregon. Lopushinski and Klock (1974) have found that transpiration rates of ponderosa pine, Douglas-fir, and Engelmann spruce decrease sharply in response to water deficits.

Nongrowth season photosynthesis is an important part of annual production in the Pacific Northwest (Helms 1963, Salo 1974, Emmingham and Waring 1977). Light is the most important factor limiting winter photosynthesis at low elevations in the west Cascades (Salo 1974). This suggests that the negative responses to winter precipitation exhibited by western sites (Fig. 5) occurs because the cloudiness accompanying precipitation reduces the light available for photosynthesis. At the higher elevation of most of the study sites, however, the negative effect is probably due to increased snowpack. Snow which remains into late spring and summer can reduce photosynthesis and cambial growth by lowering soil temperatures and consequently root growth and water uptake (Emmingham and Waring 1977).

In contrast to the west, eastern sites respond favor-

ably to winter precipitation (Fig. 5). Although no winter measurements of photosynthesis have been made in eastern Washington forests, it is unlikely that significant photosynthesis occurs during winter because the soil is continuously frozen and because daily air temperatures seldom rise above freezing. Since these areas are relatively dry even during the winter, winter precipitation probably favors annual production by recharging soil water, which subsequently allows higher rates of photosynthesis during spring and summer.

Eastern and western sites also exhibit different responses to prior summer (July) temperature. Low summer temperatures are favorable at western sites, but unfavorable at eastern sites. This result is reasonable for western sites (predominantly Douglas-fir) since high summer temperatures decrease photosynthesis of Douglas-fir in the west Cascades (Salo 1974). One would expect, however, that cool summer conditions should also favor photosynthesis and growth at the eastern sites (all ponderosa pine), where summer temperatures are much higher.

Results of two experimental studies (Hadley 1969, Salo 1974) suggest that the surprising differences in response to July temperatures may occur because Douglas-fir and ponderosa pine have very different temperature optima for photosynthesis. According to Salo (1974), the photosynthesis of Douglas-fir in western Washington is highest between 10°–20°C. Unfortunately, no comparable data are available for ponderosa pine in eastern Washington. The most useful data come from a study by Hadley (1969), who measured photosynthesis of field-grown ponderosa pine in southwestern North Dakota. He found that maximum photosynthesis occurs at 25°–35°. Fig. 8 shows Salo's and Hadley's photosynthesis curves in comparison to the average maximum July temperature for the Douglas-fir (western) sites and the ponderosa pine (eastern) sites. The maximum July temperature at western sites is above the optimum for photosynthesis in Douglas-fir, suggesting that increased temperatures should reduce net photosynthesis at these sites. In contrast, the average July temperature maximum at eastern sites is below the optimum for ponderosa pine, suggesting that high temperatures could increase net photosynthesis at these sites. Admittedly, it is hazardous to extrapolate results from South Dakota to explain the behavior of ponderosa pine in eastern Washington because of differences in ecotype, climate, and site factors. Nevertheless, these results suggest the interesting possibility that unique temperature-photosynthesis relationships of Douglas-fir and ponderosa pine explain the opposite responses of western and eastern sites to summer temperature.

CONCLUSIONS

Regional weather systems influence tree growth in a variety of forests on mesic and semi-arid sites in the Pacific Northwest. The patterns of tree growth anom-
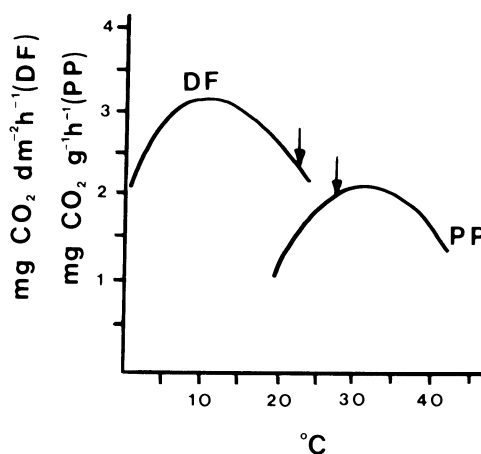

FIG. 8. Net photosynthesis-temperature curves for DF, Douglas-fir (from Salo 1975), and PP, ponderosa pine (from Hadley 1972). Arrows indicate mean maximum July temperature at Douglas-fir and ponderosa pine sites.

alies are most reasonably explained by the nature of growth responses to climate anomalies that extend uniformly across the study area.

Late-spring and summer droughts are probably most important in limiting growth on a regional basis and result in positive correlations among radial growth anomalies of forest stands throughout the study area. This type of growth variation accounts for $\approx 25\%$ of the variability among the stands sampled in this study. Superimposed on the influence of drought is the effect of winter precipitation and summer temperatures. High winter precipitation and high summer temperatures reduce growth in western portions of the study area but increase growth in eastern regions. This reciprocal behavior at eastern and western sites accounts for $\approx 16\%$ of the growth variability in this study. The spatial patterns of growth anomalies identified in this study have existed during the past 300, possibly 400 yr.

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