FREQUENCY-DEPENDENT RELATIONSHIPS BETWEEN TREE-RING SERIES ALONG AN ECOLOGICAL GRADIENT AND SOME DENDROCLIMATIC IMPLICATIONS

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ABSTRACT

Bristlecone pines were sampled at four sites ranging from the arid lower forest border to the upper treeline in the Snake Range of eastern Nevada. Maximum ring-width response to environmental variation is found at the upper and lower forest limits. Ring-width index series from individual trees, as well as the mean site chronologies, were compared by cross-correlation analysis and principal component analysis, combined with digital filtering to emphasize variations in different frequency ranges. Positive correlation exists between the high-frequency variations at all sites, but the longer term trends and fluctuations at the upper treeline are negatively correlated with fluctuations at the lower altitude sites. Cross- spectral analysis substantiates the results of cross-correlation analysis and indicates that the associated variations in the upper treeline and lower forest border chronologies are concentrated in certain frequency ranges that may have climatic significance. From examination of the climatic response functions, the negatively correlated low frequency variations are tentatively judged to be related to warm-season temperature fluctuations, whereas the positively correlated high frequency variations may be related to precipitation. Frequency-dependent relationships between tree-ring chronologies, or between tree-rings and climate should be considered in the analysis of large arrays of tree-ring chronologies representing a broad range of species and ecological situations.

INTRODUCTION

Study of the annual rings along a tree's radius produces a sequence of observations that are fixed in their relative occurrence in time. Statistical methods exist for the investigation of such time series. These time series techniques have been widely applied in meteorology, hydrology, and geology, but many of them have had only limited applications in dendrochronology. Because tree-ring data are gaining importance as proxy records of hydrometeorological variables, their characteristics as time series need to be better known. Furthermore, time series analysis can lend insight into the relationships between tree-ring variations, biological processes, and climatic or other controlling factors.

The importance of time series considerations became evident during an investigation of the paleoclimatic "information" that might be contained in ring-width data from bristlecone pines at upper treeline (LaMarche and Stockton 1974). It appeared that trees of this species on nearby but ecologically contrasting sites were responding to climatic variability in ways that were related to the frequency range considered. In this report some of these relationships are explored and tentatively explained in terms of biological processes and climatic variations.

STUDY AREA AND PROCEDURE

The study area is in the Snake Range of east-central Nevada (Figure 1). This region is fairly dry, with mean annual precipitation ranging from 250 mm in the valleys at 1800 m altitude to an estimated 860 mm at 3000 m altitude in the mountains (LaMarche and Mooney 1972). The vegetation shows a pronounced altitudinal zonation (Billings 1951); the major tree species at lower altitudes are pinyon (*Pinus monophylla*) and juniper (*Juniperus osteosperma*). At intermediate altitudes are white fir (*Abies concolor*), Douglas-fir (*Pseudotsuga menziesii*) and ponderosa pine (*Pinus ponderosa*). The subalpine conifers, extending from an altitude of about 2900 m to the upper treeline at 3400 m, are Englemann spruce (*Picea engelmannii*), bristlecone pine (*Pinus longaeva* D.K. Bailey), and limber pine (*Pinus flexilis*).

Bristlecone pine at four sites over a large altitudinal range were selected for tree-ring study. Site *D* at the lower altitudinal limit of bristlecone pine is judged to be the most xeric site on the basis of its low altitude, steep slope and southerly slope direction (Table 1A), as well as coarse soil texture and shallow depth, low stand density, the gnarled appearance of individual trees, and associated low altitude species. Site *C*, although at a comparable altitude, was judged to be more mesic due to the much gentler slope and the deeper and finer-textured soil. Site *B* is physiographically comparable to *C*

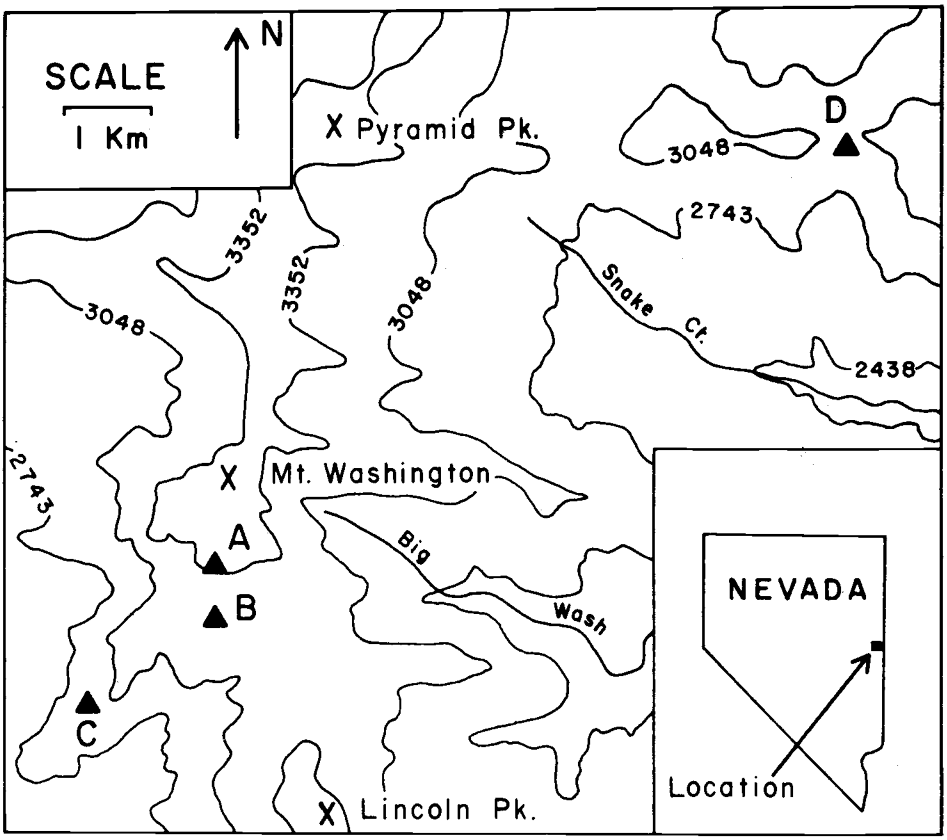

Figure 1. Index map. *X* indicates peak; solid triangles show tree-ring sites.

TABLE 1. Site characteristics and sample statistics.

	A	*B*	*C*	*D*
A. SITE CHARACTERISTICS				
Altitude (m)	3380	3250	2960	2960
Slope Angle	15°	15°	10°	25°
Slope Direction	S 25° W	S 55° W	S 25° W	S 5° E
B. SAMPLE STATISTICS – TOTAL PERIOD				
No. of Trees	10	9	9	9
No. of Radii	15	18	18	14
Period (A.D.)	737-1965	1850-1965	1850-1965	1-1967
C. SAMPLE STATISTICS – CORRELATION AND ANOVA PERIOD				
No. of Trees	5	9	9	3
No. of Radii	10	18	18	6
Period (A.D.)	1860-1965	1850-1965	1850-1965	1840-1939
Mean Ring Width	0.52	0.57	0.37	0.39
Correlation Analysis				
Radii within trees	.70	.58	.48	.55
Radii between trees	.45	.35	.40	.61
Between tree means	.53	.44	.53	.78
Percentage of Chronology Variance				
Common variation	43	35	37	-
Differences between trees	26	22	8	-
Unexplained	31	43	55	-

but is at a higher altitude. Site *A* is at the upper treeline just below the zone of dwarf and krummholz trees (LaMarche and Mooney 1972).

Increment cores were taken from trees on these four sites during the period 1966 through 1968. Within-tree replication (two cores per tree) was obtained on sites *B* and *C*, but only one usable core was obtained from many of the trees at sites *A* and *D*. After mounting and surfacing, the annual rings were dated by crossdating techniques (Stokes and Smiley 1968), and the ring widths were measured to the nearest 0.01 mm. Ring-width indices were then derived for each measured radius using standard techniques (Fritts and others 1969), and a set of sample statistics was calculated for each site (Table 1B). Chronology statistics (Table 2) were also calculated for the mean ring-width index series for each site for the total length of each series.

INTERSITE COMPARISON

Statistical Trends

The maximum ring-width response to variations in climate is normally found in trees near climatically determined limits of distribution. In a study in northern Arizona, Fritts and his co-workers (1965) investigated ring-width characteristics in trees of woodland and montane forest species growing in sites that ranged from the xeric lower forest border to the more mesic forest interior. Among the trends they observed in moving away from the forest border were decreased correlation of ring-width series

TABLE 2. Properties of mean ring-width index chronologies.

	A	*B*	*C*	*D*
CHRONOLOGY STATISTICS (TOTAL PERIOD)				
Site				
Period (A.D.)	737-1965	1850-1965	1850-1965	1-1967
Mean Sensitivity	.230	.117	.157	.269
Standard Deviation	.345	.150	.166	.285
First Order Autocorrelation	.683	.509	.336	.374
CHRONOLOGY STATISTICS (Correlation and ANOVA Period)				
Mean Sensitivity	.145	.121	.162	.202
Standard Deviation	.230	.152	.170	.261
First Order Autocorrelation	.611	.505	.344	.403

within and between trees, decreased standard deviation of the mean site chronologies, and decreased mean sensitivity. The trends reflect a decrease in the frequency of drought conditions which are limiting to the trees' growth processes in this environment, and they parallel the gradients of increasing average precipitation and decreasing average temperature. In Figure 2, these statistics are shown for the four Snake Range sites. They show a pronounced decrease between the lower forest border and the forest interior sites, similar to that found in the Arizona study. However, there is a reversal of trends at the upper treeline. Correlation of radii within (Table 1C) and between trees, and the

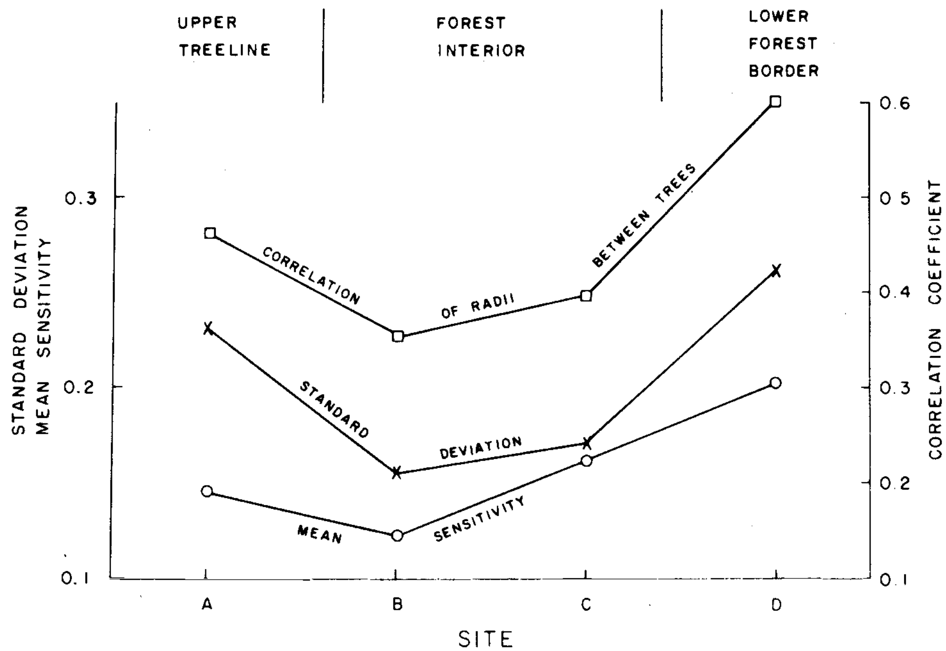

Figure 2. Statistical properties of ring-width index data along an ecological gradient from upper treeline (A) to lower forest border (D). Standard deviation and mean sensitivity are calculated for the mean site chronology.

TABLE 3. Correlation coefficients between chronologies before and after filtering. Period of analysis 1850 to 1959.

		B	C	D
		A. UNFILTERED		
		B	*C*	*D*
	A	−0.01	−0.10	−0.10
Site	*B*		+0.61	+0.46
	C			+0.58
		B. HIGH FREQUENCY		
		B	*C*	*D*
	A	+0.56	+0.28	+0.33
Site	*B*		+0.68	+0.52
	C			+0.51
		C. LOW FREQUENCY		
		B	*C*	*D*
	A	−0.42	−0.42	−0.42
Site	*B*		+0.58	+0.44
	C			+0.68

chronology standard deviation are higher at upper treeline than in the forest interior. Mean sensitivity also shows an increase at upper treeline. These results are interpreted as meaning that ring-width variation in trees in the two extreme habitats – upper treeline and lower forest border – show the greatest response to climatic variation.

Filtering and Cross-Correlation

The mean ring-width index chronologies for the four sites were compared using cross-correlation analysis. The results (Table 3A) show that the three lower altitude chronologies (sites *B, C, D*) are positively correlated with each other, but that all three are uncorrelated or weakly, negatively correlated with the upper treeline chronology (site *A*). This result was interesting because the statistical trends were inferred to mean that the common response of tree-ring growth to climatic factors was greatest at upper treeline and lower forest border. There are at least three possible explanations for the lack of correlation, particularly between sites *A* and *D*. This could be interpreted as meaning that 1) non-climatic environmental factors were influencing ring growth differently on the different sites; 2) ring growth was responding to different climatic factors, or to the same factors operating in different seasons of the year; or 3) trees at the upper and lower forest margins were responding to the same climatic factors, but in different ways.

Examination of the plotted chronologies provides some insight into the relationships that exist among the series. Comparison of the plots showed that crossdating is present. That is, rings that are narrow in relation to the immediately preceding and following rings could be recognized in the same years in all four series. However, the long-term fluctuations (departures from the mean that persist for several years or more) in the chronologies appear to be different. Certain smoothing and filtering techniques can be used to separate these long-term and short-term variations and to study the relationships among the series at different frequency ranges of variation.

A digital filter is a set of numerical weights by which successive values in a time series are multiplied to produce a new, filtered time series. A filter is normally used to accentuate certain variations in a series that lie in a particular frequency range of interest (Mitchell and others 1966). In effect, the series is portrayed as it might appear if variations at other frequencies had not occurred. Different filters can be used to decompose a set of time series into several new sets of series, representing variations in different frequency ranges. Graphical or numerical comparisons between the series can then be made.

Filters that smooth a time series by removing the higher frequency variations are called "low-pass" digital filters. The simple running mean is an example of a type of filter with a long history of application to tree-ring data. However, weighted rather than simple running means are now widely used because they better preserve the phase (placement of peaks and troughs) and amplitude of variations present in the original series. Filters that remove the smooth, lower frequency fluctuations and emphasize the year-to-year variations in a tree-ring series can also be designed and are called "high-pass" digital filters.

A frequency response curve is used to evaluate the effect of filtering on the variations present in the original time series. The curve shows what percentage of the original variance at a particular frequency will be "passed" by the filter, and thus will appear in the resultant filtered series.

A reciprocal pair of digital filters can be used to decompose a time series into its high frequency and low frequency variations. The filter weights, methods of calculation, and frequency response curves for such a pair of filters are given by LaMarche and Fritts (1972). Each of the two filters has a 50 percent response at a frequency of 1/8 cycles per year (cpy). The high-pass filter will produce a series containing no long-term fluctuations, but one which retains nearly all of the original variations at frequencies of 1/2 to 1/4 cpy. The low-pass filter will pass nearly all the original variations at frequencies of 1/16 cpy or less. The result is a smoothed series containing long-term fluctuations and trends. Because the filters are reciprocal, the original series can be almost exactly reconstructed simply by adding together the high-pass and low-pass filtered values for each year.

The four Snake Range bristlecone pine chronologies were filtered with both the high-pass and low-pass digital filters. Similarities or differences between the series in each set (high-pass and low-pass) were then measured by means of the linear product-moment correlation coefficients.

The series obtained by high-pass filtering are shown in Figure 3, *upper*. The positive correlations (Table 3B) indicate a high degree of similarity of the short term or high frequency variations in all four site chronologies. The results of low-pass filtering are shown in Figure 3, *lower*. The long-term or low frequency fluctuations in the three lower altitude chronologies are similar, and the smoothed series are positively correlated (Table 3C). However, the low frequency fluctuations at upper treeline are generally opposite those at lower altitudes, so they are negatively correlated. The lack of significant correlation between the original, unfiltered series clearly results from the combined, opposing effects of the large positive high frequency correlation and the large negative low frequency correlation. It is thus evident that the series are related differently depending on the frequency of variation considered.

Principal Component Analysis

The correlation analysis of the filtered chronologies dealt only with those properties which are found in the mean ring-width index series for each site. A further

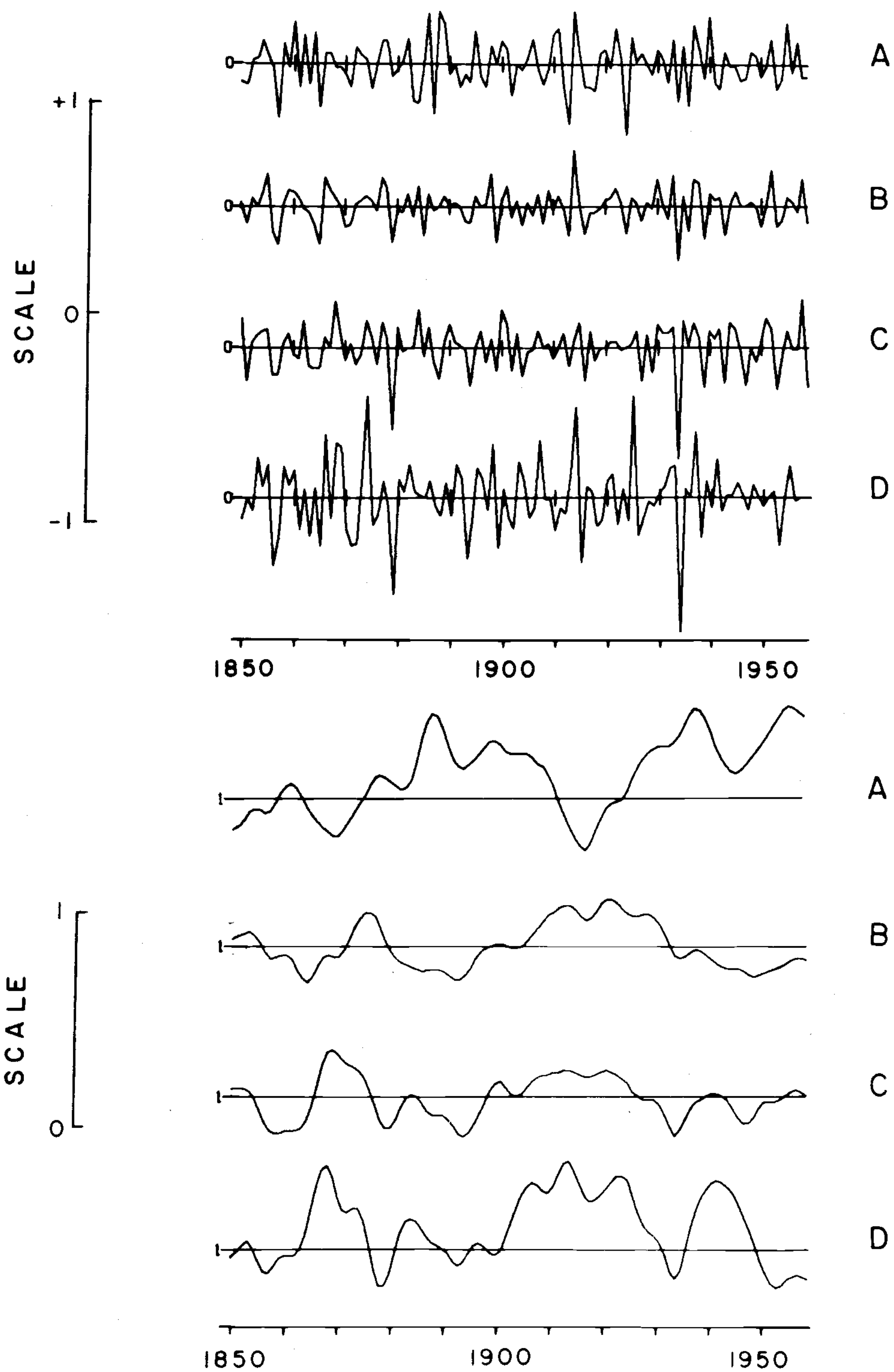

Figure 3. Site chronologies after filtering with *upper*, high-pass digital filter; *lower*, low-pass digital filter.

test was carried out to study the differences among ring-width index series of individual trees on the different sites. Principal component analysis was used to characterize the growth anomaly patterns. In most previous tree-ring applications, a spatial array of mean site chronologies has been used as a starting point in the analysis (LaMarche and Fritts 1971; Fritts and others 1971; Stockton 1971). The sites were considered as variables, and the annual tree-ring indices as observations. This study differs from most previous ones in that the individual trees, rather than the sites, are treated as separate variables. This approach permits us to test the assumption that the mean site chronology truly reflects a response to environmental variation that is common to most or all of the trees on a particular site. Data from 38 trees on the four Snake Range sites were used. Each series represents either the ring-width index series from a single radius, or the mean of two or more radial series from the same tree. Two principal component analyses were performed. In the first analysis, the high frequency series, obtained using the high-pass digital filter, were used. In the second, the low frequency series were used.

In principal component analysis, the eigenvectors representing characteristic anomaly patterns (which are orthogonal or uncorrelated) are extracted in order of decreasing importance, and each can be regarded as "explaining" a certain percentage of the total variance present in the original data. In both the high frequency and low frequency analyses, only the first three eigenvectors were found to show systematic differences between sites. The first three eigenvectors explain 55 percent of the variance in the high frequency data and 64 percent of the variance in the low frequency data. In each case, the remaining eigenvectors are not only small in value, but are difficult to interpret physically, and may represent only random variation.

The elements of the first three eigenvectors of the high frequency data, grouped by site, are plotted in Figure 4, *upper*. It should be noted that the signs are arbitrary. Each eigenvector represents either the response shown or the exact opposite, in which case the signs of all the elements of that eigenvector are reversed. The first high frequency eigenvector (H1) has large negative weights for all trees, and clearly shows the similarity in short-term variations in growth at all four sites. The second eigenvector (H2) shows a contrast in response between the upper treeline (*A*), where all the weights are negative, and the two lowest sites (*C, D*), where most of the weights are positive. The third eigenvector (H3) contrasts the lower forest border site (*D*) with the two forest interior sites (*B, C*). The weights for trees at upper treeline (*A*) are close to zero.

The principal components of the low frequency data (Figure 4, *lower*) are quite different from those of the high frequency data. The most important eigenvector (L1) associates positive anomalies at the three lower sites (*B, C, D*) with negative anomalies at the upper treeline (*A*). The second eigenvector (L2) associates positive anomalies in the two highest sites (*A, B*). The third eigenvector (L3) shows a tendency for negative anomalies at the higher of the forest interior sites (*B*) to be associated with positive anomalies at the other three sites.

The results of the principal component analysis clearly demonstrate the grouping of growth anomaly patterns by individual sites, suggesting a fairly uniform site-wide response to environmental variability. The results confirm that there are frequency-dependent differences in tree-growth variation common to all the trees on a site, as suggested by correlation analysis of the mean site chronologies. The analysis lends additional insight into details of anomaly patterns that cannot be gained from comparison of the site chronologies. Such information is lost if only the mean site chronology is analyzed, yet the inter-tree variability within a given site could be worth further study

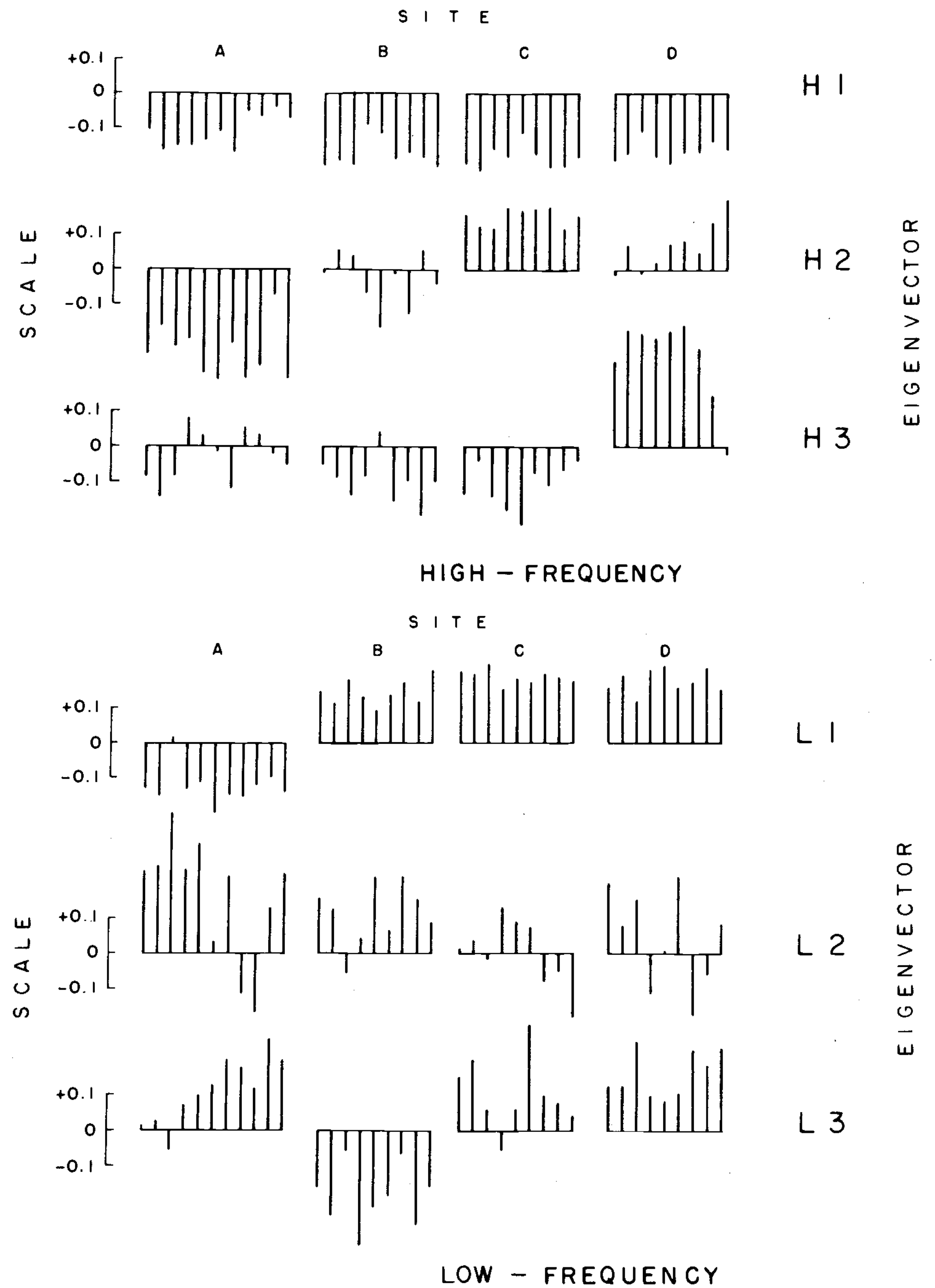

Figure 4. Eigenvectors of filtered ring-width indices from individual trees on four sites.

Each line on the bar graph represents the value of the element of a particular eigenvector for one tree. These can be interpreted as characteristic growth anomaly patterns. *Upper* High-pass data; eigenvectors H1, H2, and H3 account for 34%, 12%, and 9%, respectively, of the variance. *Lower* Low-pass data; eigenvectors L1, L2, and L3 account for 39%, 14%, and 11%, respectively, of the variance. Similarity in response on all sites is indicated by H1. A contrast in response at the upper treeline (A) and three lower forest border sites (B, C, D) is shown by L1.

and analysis. Study of details of the anomaly patterns of individual trees could lead to further stratification of data by tree age, microsite, or other variables.

Spectral Analysis

Although filtering followed by cross-correlation analysis can indicate the general nature of frequency-dependent relationships between time series, as in the case of the four Snake Range chronologies, an arbitrarily selected pair of filters may not split the series into "natural" frequency bands. Spectral analysis is a more powerful tool for investigation of time series. It is based on classic harmonic analysis, but has distinct advantages for study of time series showing only random variation, persistence, or weak, oscillatory behavior. Direct harmonic analysis of a time series results in estimates of the amount of variance at each of several frequencies, corresponding to cosine waves with periods of from twice the record length down to twice the sampling interval that was used to obtain the observations in the time series (two years for annual ring series). A major disadvantage of simple harmonic analysis is that estimates of the variance are centered at frequencies determined in advance by the length of the record studied.

In spectral analysis, the autocorrelation (or autocovariance) function is first computed from the time series. That is, the correlation coefficient (or autocovariance) is first calculated using as joint observations the values for the same year (lag 0), then with values for each year compared with those for the previous year (lag 1), then the values for each year compared with those for two years previous (lag 2), and so forth, up to a maximum number of lags that is ultimately limited by record length, but is usually determined by the need for spectral estimates at particular frequencies or by the requirements for statistical stability of the estimates. A harmonic analysis is then performed on the autocorrelation (or autocovariance) function. The spectral estimates are smoothed, and the results plotted as a function of frequency.

Spectral analysis of a purely random time series will produce spectral estimates (plotted on the ordinate) clustered about a horizontal line. The variance in the time series is thus about equally distributed at all frequencies, and the spectrum is called a "white noise" spectrum by analogy with the properties of white light. Persistence in a time series (the tendency for large values to follow large values or small values to follow small values) causes a "reddening" of the spectrum; again, the term is used by analogy with light. A "red noise" spectrum has high spectral densities at low frequencies. Such persistence in a time series may reflect very low frequency oscillations, trend, or the influence of autoregressive or moving-average mechanisms that introduce a dependency on previous values in the series. The spectrum of a time series containing a strong sinusoidal periodic component will show a sharp peak at the frequency of the basic wave. A broader and less pronounced peak in the spectrum indicates the presence of a rhythmic or oscillatory component that is not exactly periodic, or of a periodic component showing phase shifts. Basic concepts of spectral analysis are lucidly discussed by Mitchell and others (1966) and Kisiel (1969). The underlying theory, procedural steps, and practical considerations are well covered by Jenkins and Watts (1968).

The two longest Snake Range chronologies, from the upper treeline (site *A*) and lower forest border (site *D*), were used in spectral analyses in order to more fully characterize their frequency-dependent properties. Data for the period A.D. 1480 to A.D. 1965 were used, giving a record length of 486 years. The maximum number of lags used to compute the spectra was 80 years. Both spectra (Figure 5) show "reddening" at low frequencies, but the forest border series (dashed line) contains somewhat less low frequency variance than the series from the upper treeline. The biggest difference between the two spectra is at higher frequencies, ranging from about 1/10 cpy to 1/2 cpy. There is more variance in the lower forest border chronology in this high frequency band (a feature also shown in Figure 3, *upper*). Strong periodicities are evidently absent from both series, because neither spectrum shows a strong peak at any particular frequency. However, the small peak in each spectrum corresponding to a period of about 27 years may be important, as will appear from later results.

Cross-spectral analysis is a generalization of spectral analysis used to study relationships between two or more time series over a range of frequencies. Cross-spectral analysis was used to further investigate the frequency-dependent relationships between the upper treeline (site *A*) and lower forest border (site *D*) chronologies. The starting point for cross-spectral analysis is the cross-correlation (or cross-covariance) function rather than the autocorrelation function. Cross-correlation coefficients are calculated at zero lag, at plus and minus one lag, plus and minus two lags, and so forth, up to some chosen maximum number of lags. Correlation coefficients must be calculated in the positive sense (when the first series is lagged with respect to the second) as well as the negative sense (when the second series is lagged with respect to the first) because, in general, the correlation coefficients are not symmetrical about lag 0.

Cross-correlation coefficients between series *D* and series *A*, up to a maximum of 80 lags, are plotted in Figure 6. The cross-correlation function is nearly symmetrical,

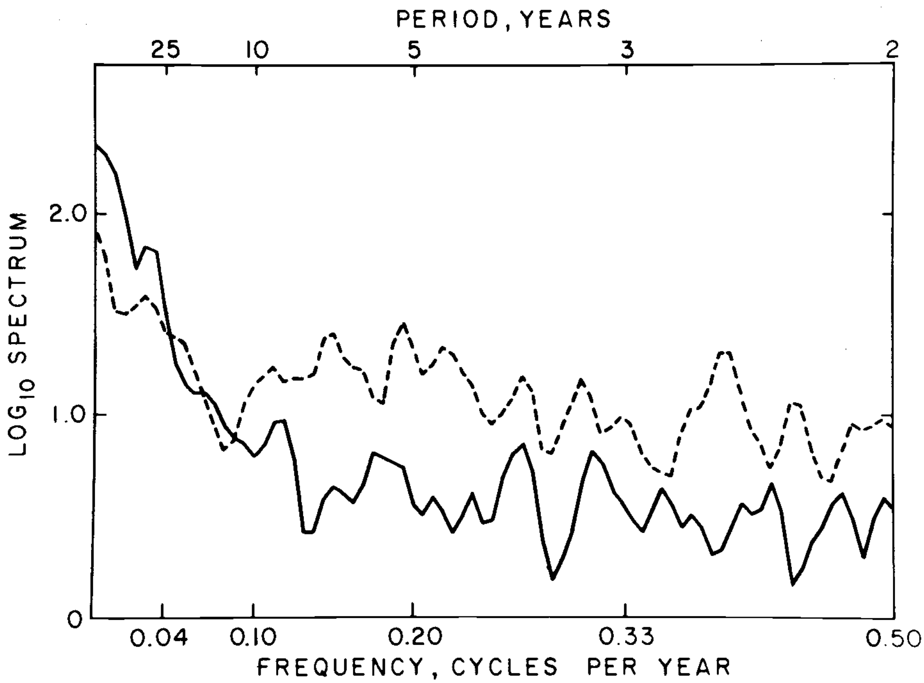

Figure 5. Power spectra of upper treeline (site A, solid) and lower forest border (site D, dashed) chronologies. Period of analysis 1480-1965. Analysis carried out to 80 lags.

except for values of opposite sign at very large lags. This feature is due to trend in series D, as demonstrated by the fact that the autocorrelation function for this series (not shown) does not drop to zero at high lags. Another important feature is the correlation minimum at a lag of +3. This means that maxima in series D are followed three years later by minima in series A. This is apparently a real feature, and not due to a misdating of the rings in either chronology, as shown by the positive correlation at zero lag between the high-pass filtered series (Table 3B).

Cross-spectral parameters are obtained by harmonic analysis of the cross-correlation (or cross-covariance) function. The basic results are expressed in two sets of spectral estimates. First, the cospectral estimates express the amplitude of those components of two time series that are in phase. That is, variations that go in the same directions at the same time in both series will be expressed as positive values in the cospectrum. Negative values of the cospectrum reflect a relationship in which variations in the two series are exactly out of phase, going in opposite directions. The quadrature spectrum measures the amplitude of variations that are of intermediate phase, that is, the variations in one series which tend to precede or to lag behind similar variations in the other series.

Cross-spectral analysis of series A and D produced the cospectrum shown in Figure 7 (solid line). The values are positive in the frequency band between 0.50 and 0.10 cpy (periods of between 2 and 10 years), meaning that a positive, in-phase relationship exists at high frequencies. This is consistent with the positive zero-lag correlation of the high-pass filtered series (Table 3B). The cospectrum is negative for frequencies of between 0.10 and about 0.01 cpy (periods of between 10 and 100 years). The quadrature spectrum (dashed line) has values around zero except in the 0.10 to 0.01 cpy range, where values are also strongly negative. The results show that there is a strong negative association between the lower frequency variation in two tree-ring chronologies, part of

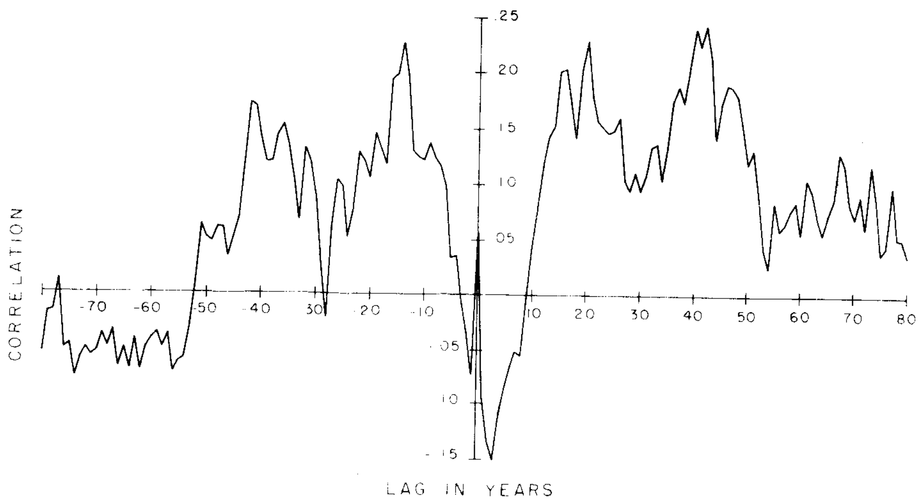

Figure 6. Cross-correlogram showing correlation coefficients between lower forest border and upper treeline chronologies lagged up to 80 years. Maximum negative correlation occurs at a lag of three years.

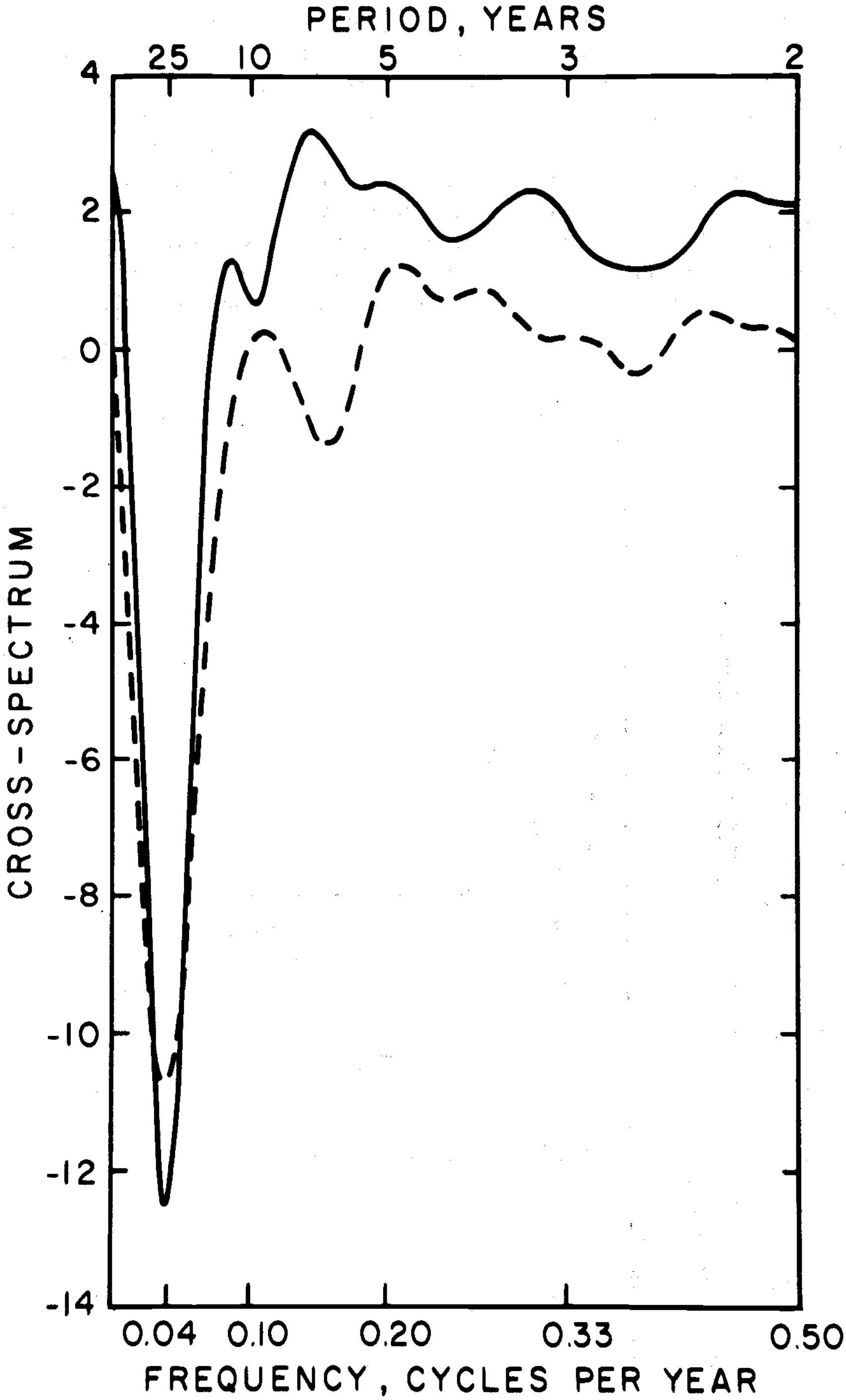

Figure 7. Cospectrum (solid) and quadrature spectrum (dashed) from cross-spectral analysis of lower forest border and upper treeline chronologies. Note negative values at about 1/27 cpy. 20-lag analysis.

which is in phase (cospectrum) and part out of phase (quadrature spectrum). The large negative values occur in the cross-spectrum only in the relatively low frequency range of 0.10 to 0.01 cpy, and are consistent with the negative correlation obtained between the low-pass filtered series (Table 3C). Of particular interest is the occurrence of the cospectral minimum at a frequency of 0.037 cpy (period of 27 years). There are minor peaks in the spectra of both series at this frequency. The negative quadrature spectrum at this frequency shows the effect of the slight lag between the series, noted from inspection of the cross-correlogram (Figure 6). Careful study of the low-pass filtered data shows the tendency for minima (maxima) in series D to occur about three years earlier than maxima (minima) in series A. The phase diagram (Figure 8) confirms this interpretation. The

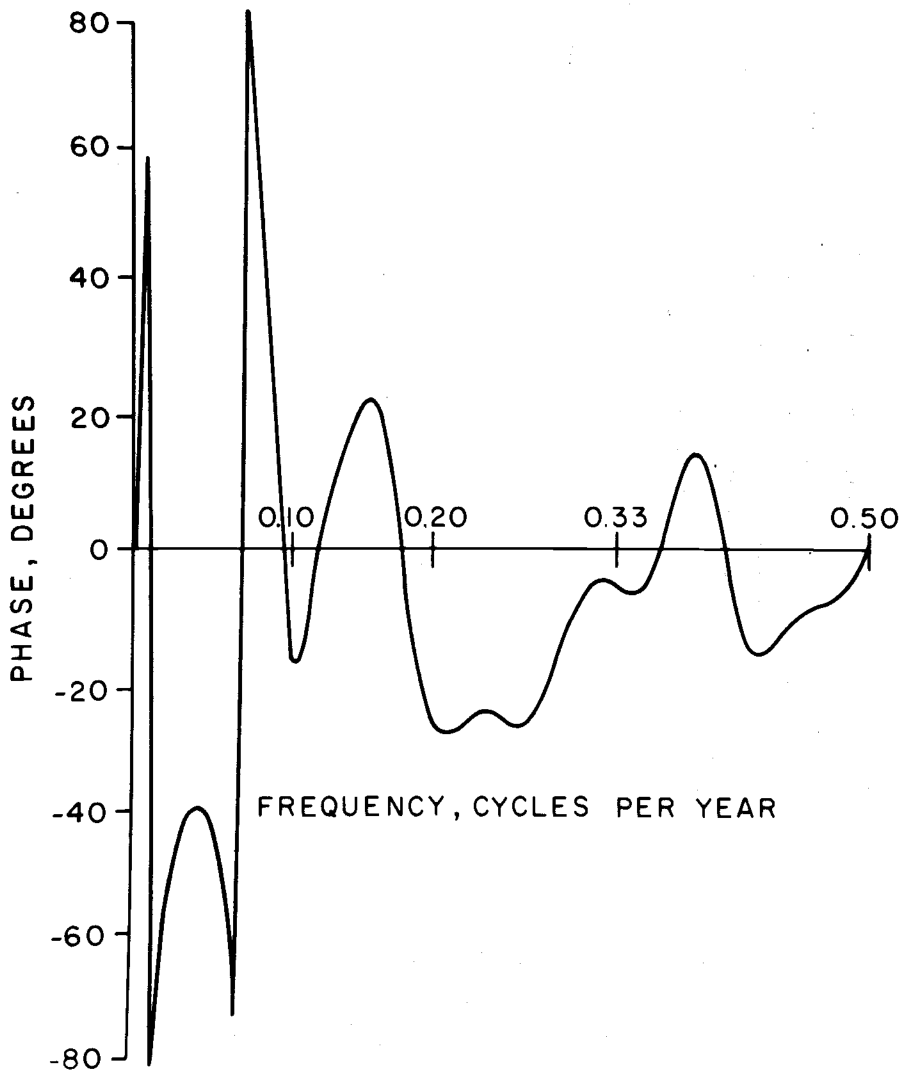

Figure 8. Phase diagram from cross-spectral analysis showing phase relationship between lower forest border and upper treeline chronologies. Negative phase angle at about 1/27 cpy corresponds to 3 years lag shown by cross-correlogram. 20-lag analysis.

phase angle is computed from the cospectrum and quadrature spectrum and measures the lag between out-of-phase components in two series at a particular frequency. The phase angle of -40° at 0.037 cpy corresponds to a lag of three years, because 40° is one-ninth of complete cycle of 27 years.

A single measure of the degree of association between the series is provided by the coherence (or coherency squared). It is computed from the cospectrum and quadrature spectrum, and thus incorporates both in-phase and out-of-phase relationships. The coherence has a range of positive values between 0 and 1, with a value of 0 indicating complete lack of association. It is the cross-spectral analog of the squared cross-correlation coefficient (Koopmans 1967), and thus measures the percentage of covariance between the series, whether the variation is similar or opposite in sign.

The coherence between series *A* and *D* is shown in Figure 9. Values are given for analyses carried out to two different values of maximum lag. This is done because using a large number of lage increases the resolution of individual cross-spectral peaks, but also increases the statistical variability of the estimates. Using a small number of lags gives more reliable estimates, but smooths out the cross-spectrum, so that peaks indicating covariance at one particular frequency may be overlooked. Examining the difference in coherence estimated using two or more values of maximum lag is a useful technique for deciding whether individual peaks represent "real" association between the series. Based on this criterion, the coherency peaks at about 0.45, 0.30, 0.14, and 0.037 cpy may represent real relationships at these frequencies, corresponding to variations with periods of 2.2, 3.3, 7, and 27 years, respectively.

CLIMATIC RELATIONSHIPS

The common year-to-year variations in ring-widths of trees on a given site presumably reflect the response of these trees to some set of common environmental factors, including climatic factors. A method for modelling the response of ring growth to climatic variation has been developed by Fritts and other (1971). The tree-ring chronologies from sites *A* and *D* were modelled in this fashion, using monthly weather data from Fillmore, Utah. The period of analysis was 1897-1965, the period of concurrent tree-ring and climatic data. Although regionally-averaged weather data would probably be more representative of monthly departures in precipitation and temperature in the Snake Range, these are not available prior to 1931. It was felt that the longer climatic series from Fillmore could better resolve the lower frequency variation in growth that is so prominent in tree-ring series. A total of 28 variables was used in the modelling analysis, including mean monthly temperature and total monthly precipitation for the 14-month period beginning in July the previous year, and ending in August of the current growing season.

The response functions (Figure 10) show some important differences in the response of ring growth to climate at different elevations. At the lower forest border (site *D*), precipitation in nearly all months is positively associated with subsequent growth. Precipitation in the previous late summer and autumn is more important than in current spring. Temperature in most months is negatively associated with growth, except for previous August. At upper treeline (site *A*), the response to precipitation is similar to that at the lower forest border in previous fall, late winter, and current spring through summer. However, precipitation during previous late summer and autumn is relatively unimportant, and precipitation in previous December is apparently negatively related to growth at upper treeline. At the upper treeline temperature in previous late summer and

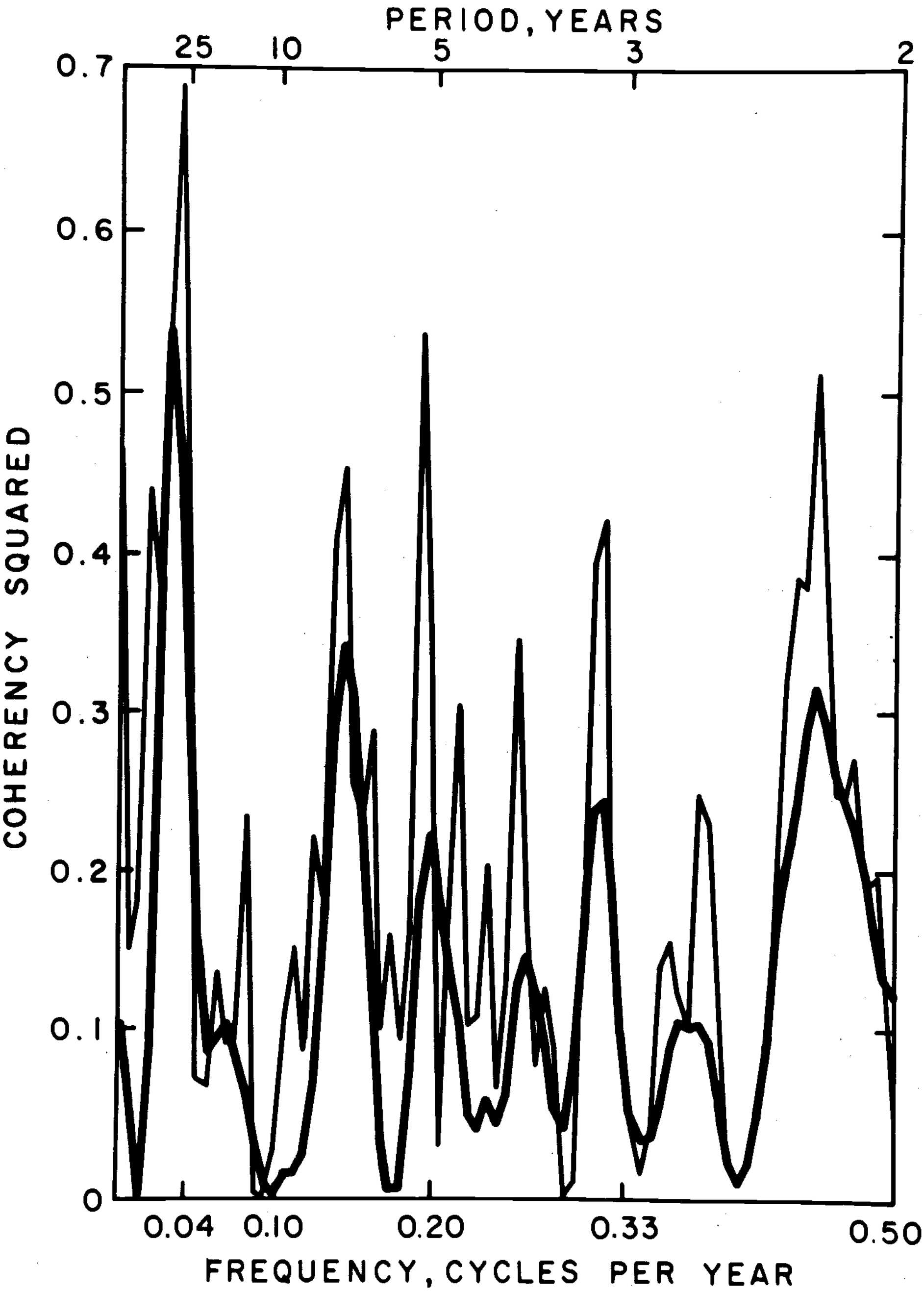

Figure 9. Coherence between lower forest border and upper treeline chronologies. Peak coherence occurs at a frequency of 1/27 cpy. Analyses at 40 (heavy line) and 80 (light line) lags.

fall are positively associated with growth. However, there is a pronounced negative association of temperature in December through April with subsequent growth. Temperature of the current growing season (June, July, August) are positively related to growth at upper treeline, but negatively related to growth at the lower forest border.

Based on the signs of the response functions, the negatively correlated low frequency components of the upper treeline and lower forest border tree-ring chronologies are tentatively judged to be related to fluctuations in current summer temperatures. The high frequency variation, which is positively correlated, may be related to precipitation amounts, particularly in late spring and early summer. Other possible factors producing a common high frequency response are temperature and precipitation of the previous August and September.

DISCUSSION

Some aspects of the relationships between climate and the biological processes affecting tree-ring growth may not be adequately represented by the kind of multivariate modelling scheme used. Needle-length variation linked to climatic variation may be very important in explaining the lower frequency relationships between ring-width index series from lower forest border and upper treeline sites. Such variations may involve

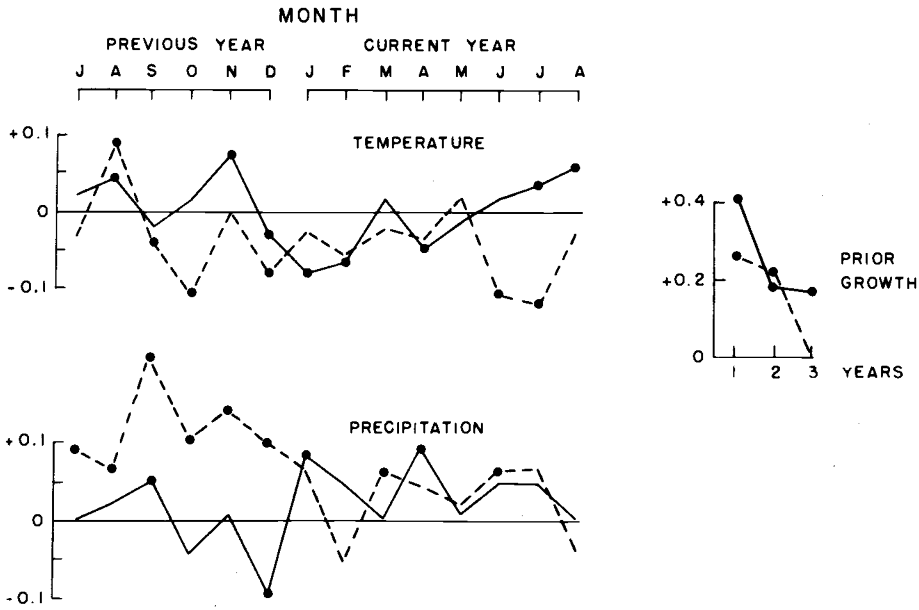

Figure 10. Response functions expressing the effects of prior growth and of temperature and precipitation during a 14-month period on ring-width index of the annual ring formed during the current growing season (June, July, August).

Solid circles indicate that the response is significant at the 95% confidence level. Data for the upper treeline site (A), linked by solid line, data for the lower forest border (D) by dashed line. Units are normalized index values. For the upper treeline (A), total variance explained is 48%; 42% explained by prior growth. For the lower forest border (D), total variance explained is 55%; 17% explained by prior growth.

relationships lagging by several years or more; whereas in the above model, climate is lagged only up to about one year, and prior ring growth up to three years.

It is well known (Fritts and others 1965; Fritts 1969) that the length of needles formed by arid-site trees is directly related to the width of the annual ring formed in the same year. Near the lower forest border, short needles and narrow rings are both formed in years of high moisture stress, related to low precipitation and high temperatures, especially when these conditions occur in the period just prior to the growing season. At the upper treeline, in contrast, needle length of bristlecone pine is highly positively correlated with temperature during the growing season (LaMarche and Stockton 1974), but less well correlated with ring-width. These observations are important because bristlecone pines normally retain needles for 10 to 15 years or more. Therefore, the total needle area available for photosynthesis at any time will reflect climatic conditions influencing needle elongation (as well as shoot growth, number of fascicles, etc.) throughout the previous decade or more. The probable effects of this phenomenon will be a smoothing of the climatic "signal" in the tree-ring data by means of a moving average process, and a lag in response of ring-width fluctuations to variations in climate. Because needle-length variation at upper treeline appear more pronounced than those at lower elevations, this phenomenon may in part explain the much higher autocorrelation found in upper treeline ring-width data (Table 2). Furthermore, the opposite response of needle elongation to temperature in these environments could be partly responsible for the negative low frequency association between series from upper treeline and the lower forest border.

The relatively high coherence between tree-ring series from lower forest border and upper treeline at certain frequencies may reflect climatic oscillations. A well known rhythmic variation is found in wind and pressure data from equatorial regions and in temperature data from many parts of the world (Landsberg and others 1963). This is the "biennial pulse" or "quasi-biennial oscillation" which has a period of 26 to 27 months, or about 2.2 years. Its presence in tree-ring chronologies has been previously suggested from the results of spectral analysis (Bryson and Dutton 1961), and may explain the coherence peak at 0.45 cpy (2.2 years) between the Snake Range chronologies. The positively correlated high frequency variation in the Snake Range sites was interpreted as a response to precipitation variation. Much of this common variation is contained in the frequency band between 0.4 and 0.5 cpy (Figure 9). It is interesting to note, therefore, that Sellers (1960) found evidence for a biennial pulse in summer precipitation amounts in southwestern United States.

Another climatic periodicity is suggested by the work of Brier (1968), who found that soli-lunar tidal influences in the atmosphere could explain certain features of the zonal index record – a measure of the strength of the mid-latitude westerlies. Maximum tidal forces should recur at about the same day of the year at 27 year intervals, so it is reasonable to suppose that any climatic cycle associated with such tidal influences would show a 27-year repeat period. The greatest coherence between the upper treeline and lower forest border chronologies from the Snake Range is centered at 0.037 cpy. That is, there is considerable common variation associated with an oscillation having a period of 27 years. Based on the interpretation of this variation as temperature-dependent phenomenon, it may be that warm season temperatures in the central Great Basin reflect atmospheric tidal effects.

Consideration of frequency-dependent relationships might prove important in certain types of multivariate analyses. Principal component analysis and canonical analysis are being applied increasingly in efforts to relate regional tree-growth anomaly patterns to climatic anomalies and to reconstruct past climates. The starting point in such analyses is a cross-correlation (or covariance) matrix representing the cross-correlation (at zero lag) among a spatial array of tree-ring chronologies, or of tree-ring chronologies and climatic time series. Had the upper treeline chronology from the Snake Range been included in this kind of analysis in the original, unfiltered form, it would have contributed little or nothing to the results because of the absence of correlation with the nearby lower forest border series. However, tree-ring data from upper treeline could contribute greatly if only the low-pass filtered tree-ring series were used. Pre-filtering might also be useful for study of tree-ring variations linked to quasi-periodic variations in climate. For example, a band-pass filter with a maximum response at 1/27 cpy might be used to emphasize variations that could result from soli-lunar tidal oscillations. Analysis of an array of such filtered tree-ring and climatic data series could produce evidence for spatial patterns of climatic anomalies produced by such a mechanism.

ACKNOWLEDGEMENTS

Advice and criticism by Harold C. Fritts and Charles W. Stockton are gratefully acknowledged. The computer programs for the spectral and cross-spectral analyses were obtained from the University of Wisconsin Computing Center, through the courtesy of Donald G. Watts. The analyses were performed at The University of Arizona Computing Center. The research was supported by the Atmospheric Sciences Section, National Science Foundation, NSF Grant GA-4128.

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