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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*

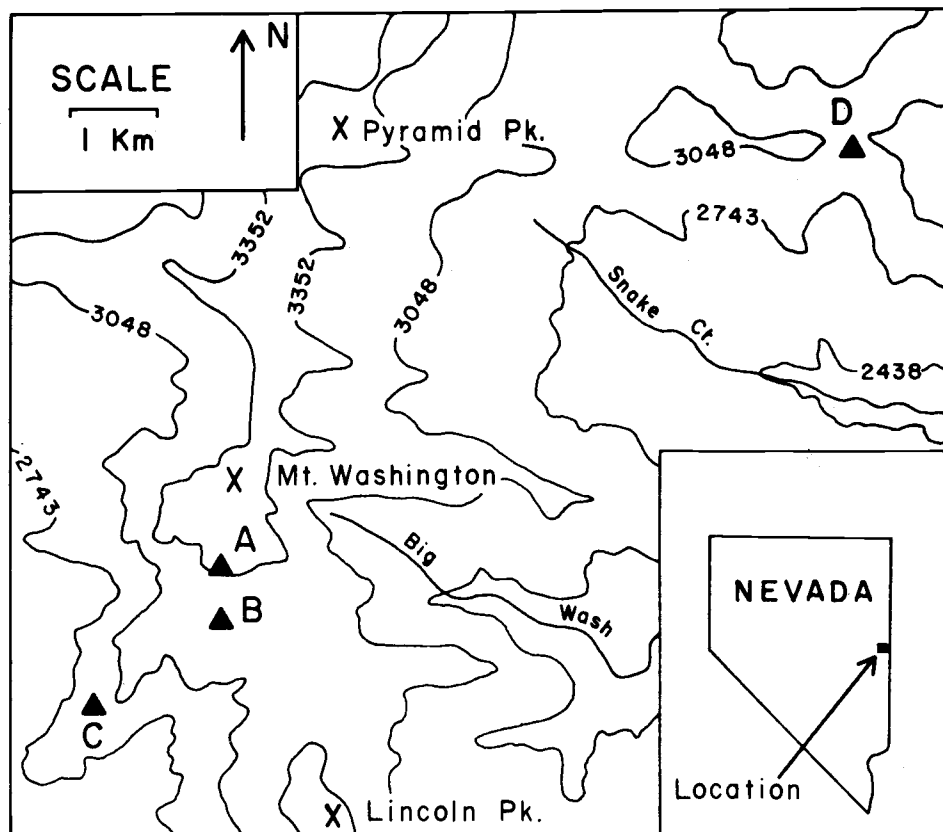


Figure 1. Index map. X indicates peak; solid triangles show tree-ring sites.

TABLE 1. Site characteristics and sample statistics.

	<i>A</i>	<i>B</i>	<i>C</i>	<i>D</i>
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

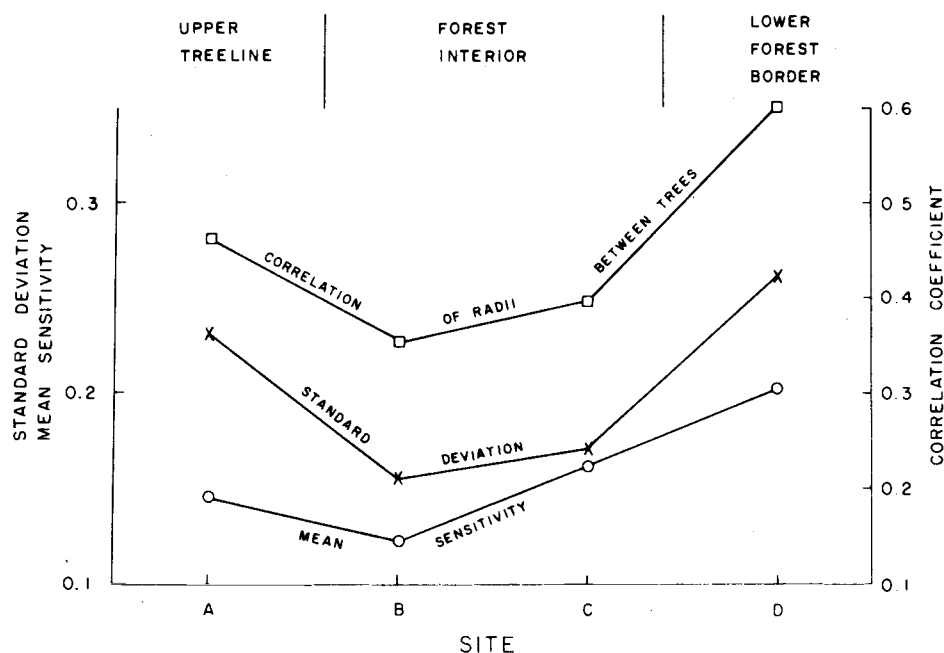


Figure 2. Statistical properties of ring-width index data along an ecological gradient from upper treeline (A) to lower forest border (D). Standard deviation and mean sensitivity are calculated for the mean site chronology.

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

A. UNFILTERED				
Site	<i>A</i>	<i>B</i>	<i>C</i>	<i>D</i>
		-0.01	-0.10	-0.10
	<i>B</i>		+0.61	+0.46
	<i>C</i>			+0.58
B. HIGH FREQUENCY				
Site	<i>A</i>	<i>B</i>	<i>C</i>	<i>D</i>
		+0.56	+0.28	+0.33
	<i>B</i>		+0.68	+0.52
	<i>C</i>			+0.51
C. LOW FREQUENCY				
Site	<i>A</i>	<i>B</i>	<i>C</i>	<i>D</i>
		-0.42	-0.42	-0.42
	<i>B</i>		+0.58	+0.44
	<i>C</i>			+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

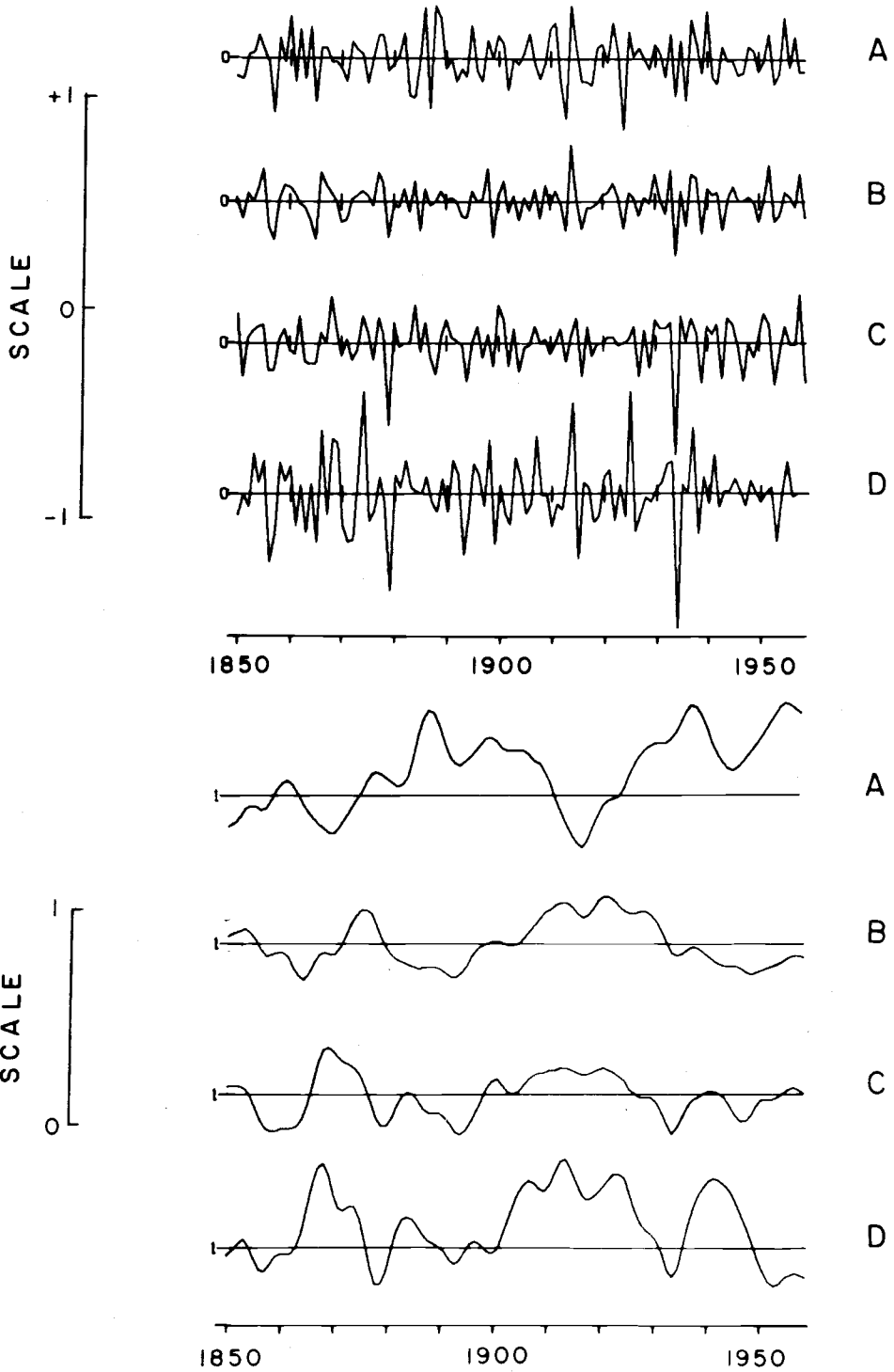


Figure 3. Site chronologies after filtering with *upper*, high-pass digital filter; *lower*, low-pass digital filter.

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

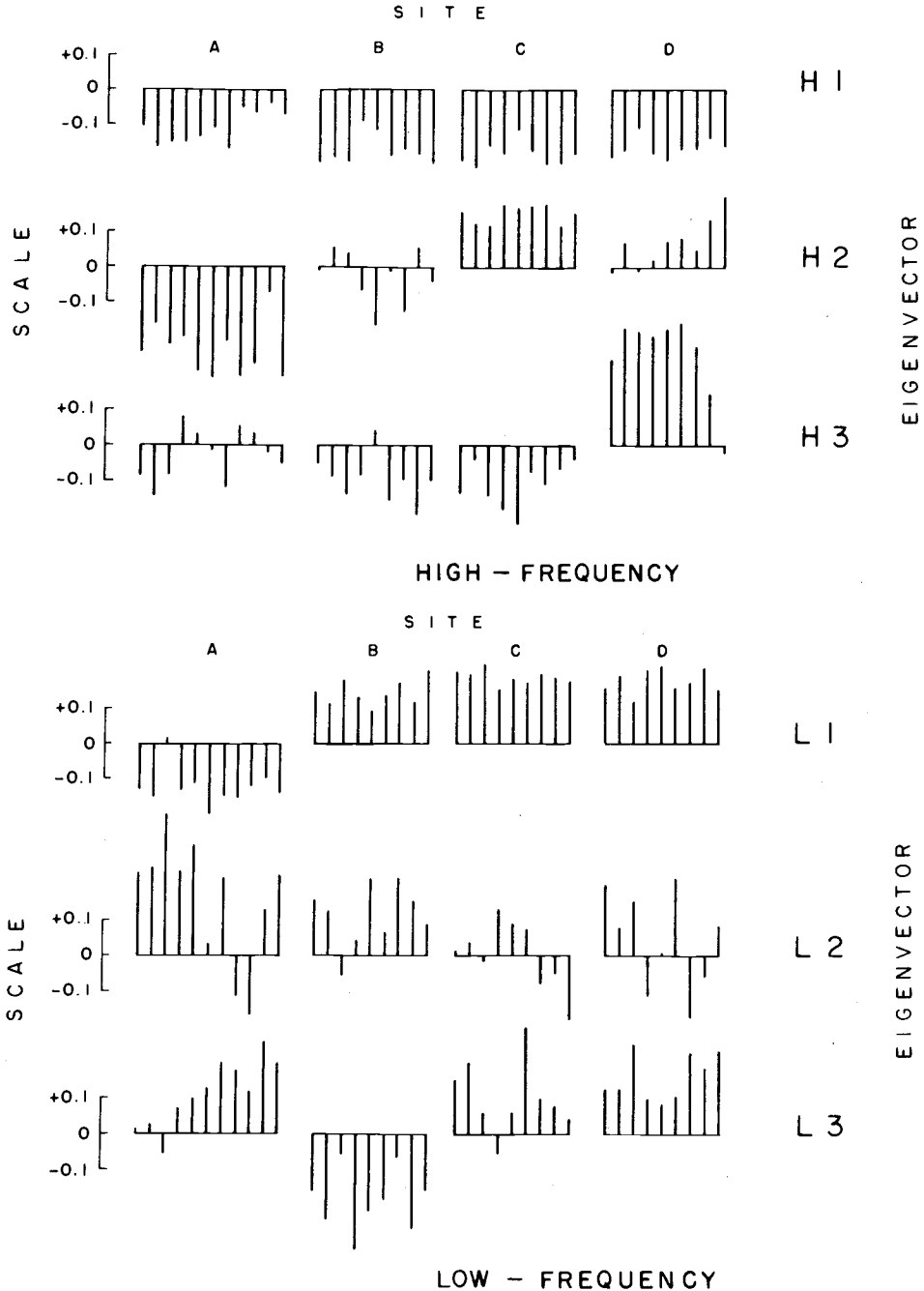


Figure 4. Eigenvectors of filtered ring-width indices from individual trees on four sites.

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,

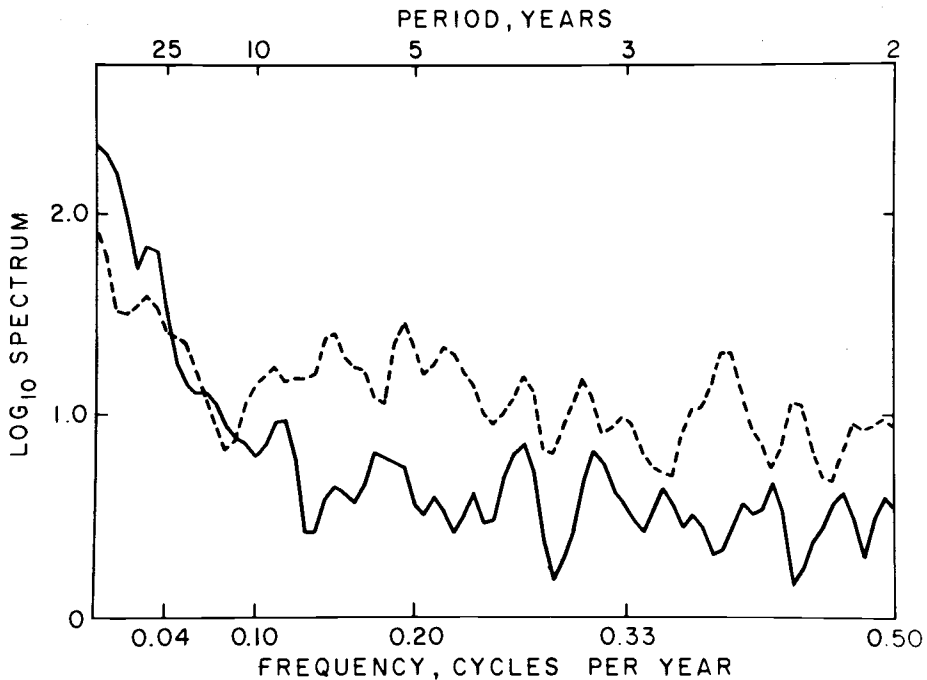


Figure 5. Power spectra of upper treeline (site *A*, solid) and lower forest border (site *D*, dashed) chronologies. Period of analysis 1480-1965. Analysis carried out to 80 lags.

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 cospectrum 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

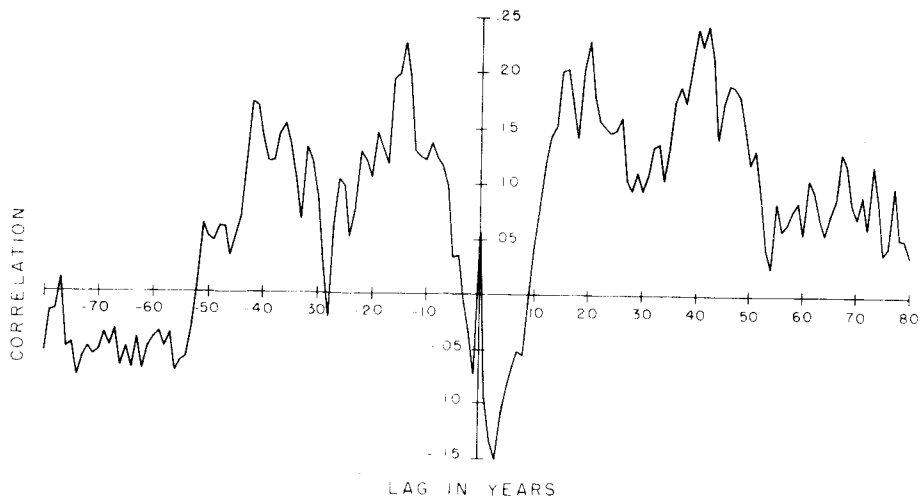


Figure 6. Cross-correlogram showing correlation coefficients between lower forest border and upper treeline chronologies lagged up to 80 years. Maximum negative correlation occurs at a lag of three years.

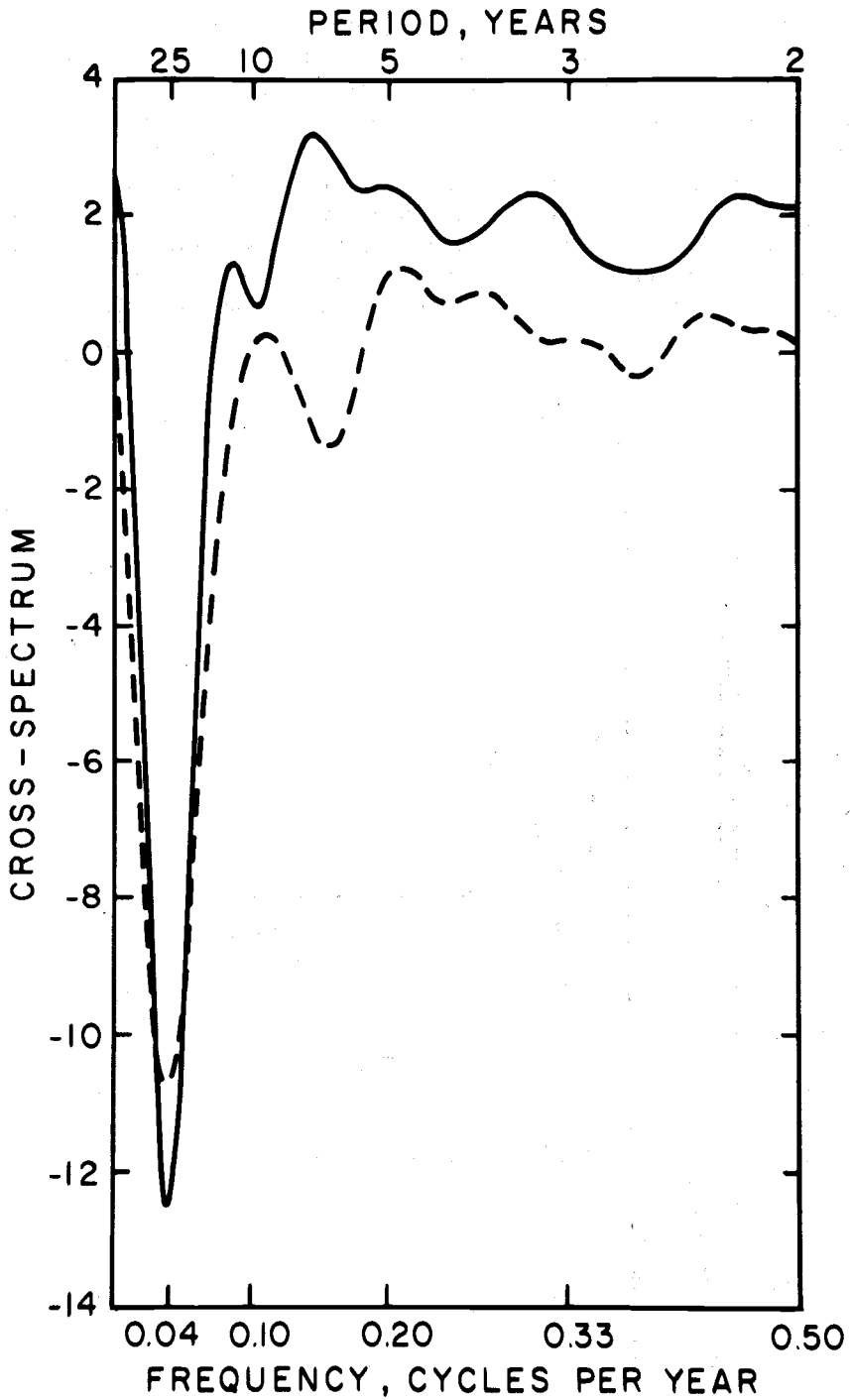


Figure 7. Cospectrum (solid) and quadrature spectrum (dashed) from cross-spectral analysis of lower forest border and upper treeline chronologies. Note negative values at about 1/27 cpy. 20-lag analysis.

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

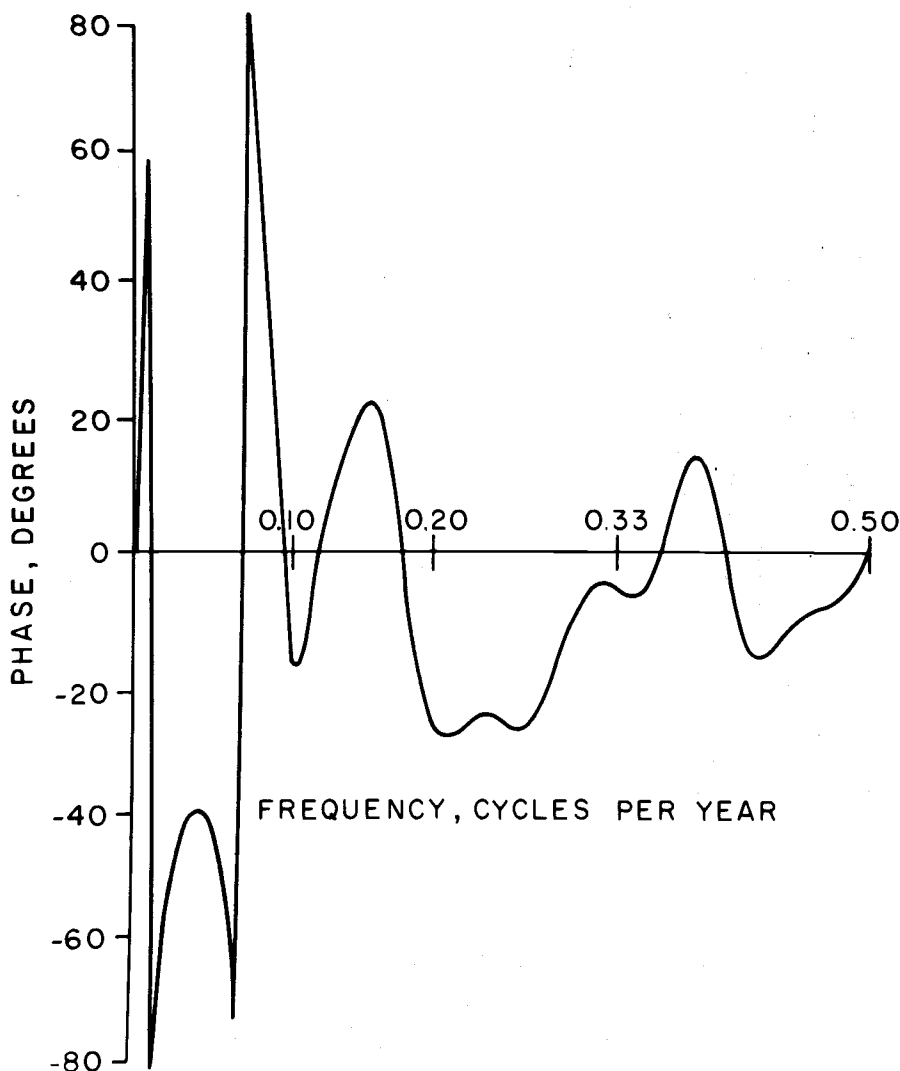


Figure 8. Phase diagram from cross-spectral analysis showing phase relationship between lower forest border and upper treeline chronologies. Negative phase angle at about 1/27 cpy corresponds to 3 years lag shown by cross-correlogram. 20-lag analysis.

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 lags 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

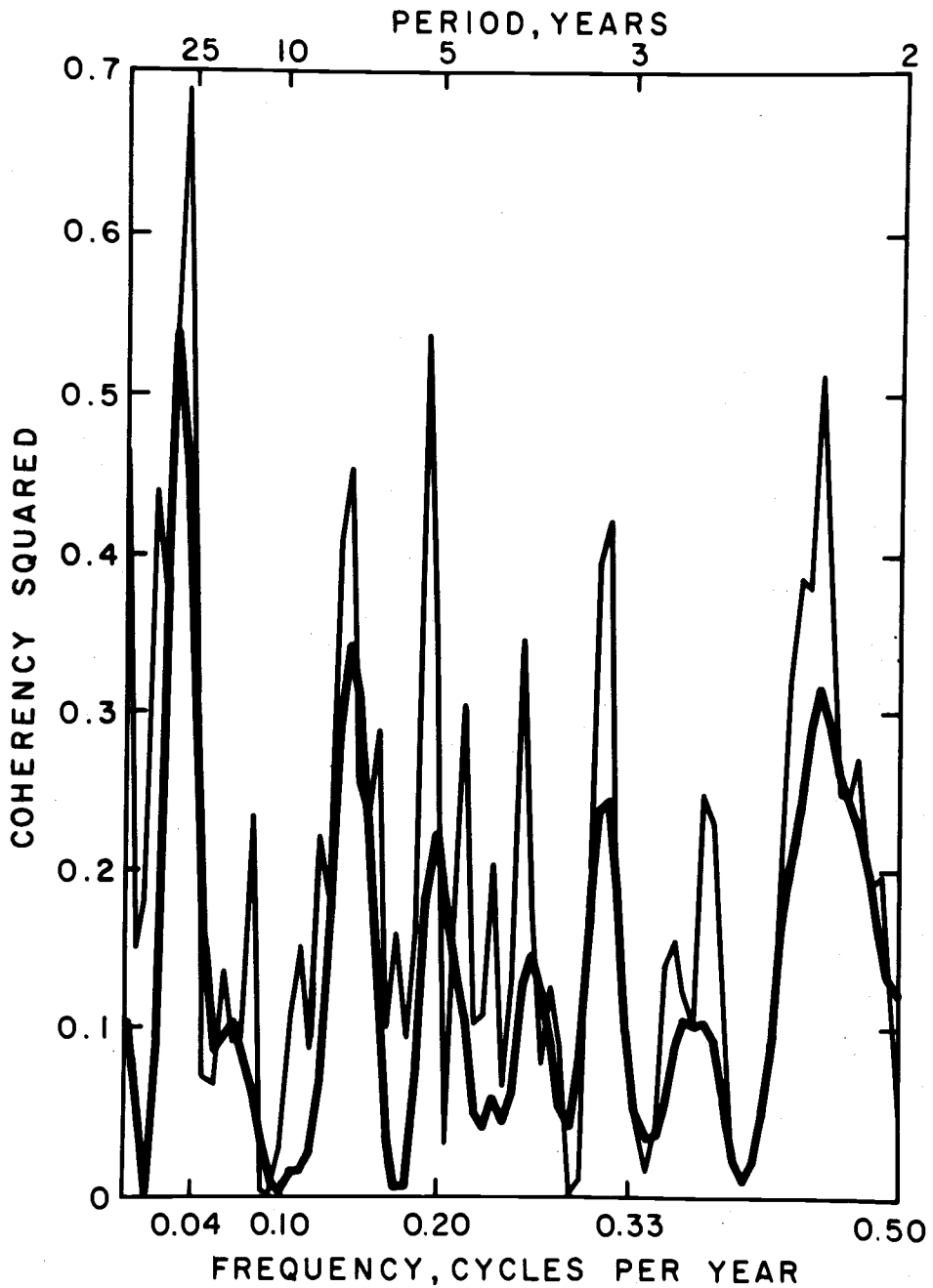


Figure 9. Coherence between lower forest border and upper treeline chronologies. Peak coherence occurs at a frequency of $1/27$ cpy. Analyses at 40 (heavy line) and 80 (light line) lags.

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

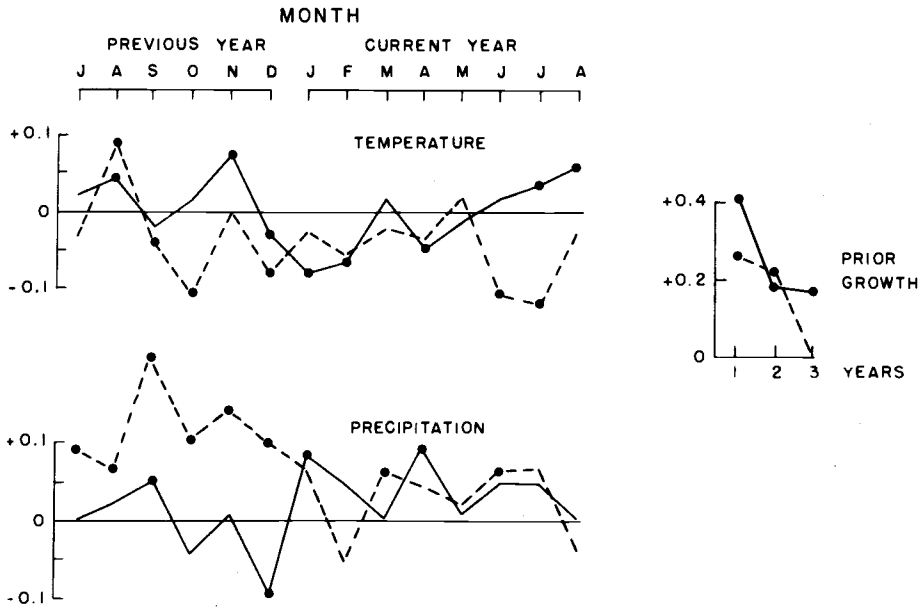


Figure 10. Response functions expressing the effects of prior growth and of temperature and precipitation during a 14-month period on ring-width index of the annual ring formed during the current growing season (June, July, August).

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.

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CHRONOLOGIES FROM TEMPERATURE-SENSITIVE BRISTLECONE PINES AT UPPER TREELINE IN WESTERN UNITED STATES

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ABSTRACT

Ring-width variation in trees at upper treeline in the high mountains of temperate latitudes is a potentially important indicator of past climatic variations, especially temperature variations. Bristlecone pines (*Pinus longaeva* D.K. Bailey and *P. aristata* Engelm.) were sampled at nine sites in western United States. Plotted annual ring-width indices are given for chronologies that range in length from 532 years in New Mexico, 1409 years in Colorado, and 1239 years in Nevada to 1501 years in eastern California. Possibilities for increasing the length of these chronologies by incorporating tree-ring data from logs and remnants are good in several of the areas, and a 5405-year upper treeline chronology has been developed in California.

Tree-ring statistics show that crossdating is poorer, the climatic response is smaller, and the autocorrelation (a measure of year-to-year persistence) is greater in trees at upper treeline sites than at sites near the arid lower forest border. Climatic response functions differ in many details, but generally indicate a positive response of ring growth to warm temperatures in the previous late summer and autumn and current spring and summer. There is a negative response to warm temperatures during some winter and early spring months at several of the sites. The effect of precipitation varies greatly, but a positive response to precipitation during the previous summer or autumn, and during the current spring or summer is indicated. Variations in needle length are related to summer temperature, and may be important in explaining the high autocorrelation of upper treeline ring-width series.

Ring-width departures from the long-term mean during the past 500 years were calculated from upper treeline data for 30-year subperiods. The departures are in the same direction over the whole region during many of these subperiods, indicating that climate, rather than local ecological factors, is responsible for the ring-width variations. Comparison of tree-growth fluctuations with meteorological observations at selected stations shows that a general warming trend between the periods 1901-1930 and 1931-1960 is reflected by an upward trend in tree growth. However, low rates of tree growth during an earlier warm period (1850-1869) may be due to a lag in the response of ring-width growth to climatic changes at upper treeline.

INTRODUCTION

The best correlations between variations in width of annual rings of trees and meteorological records have generally been obtained near climatically determined forest limits, such as the arid lower forest border and the sub-Arctic treeline. In these extreme environments, even small departures from the climatic norm may directly or indirectly limit growth processes within a tree.

In arid regions, decreasing precipitation and increasing temperatures cause a rapid drop in soil moisture available for growth at progressively lower altitudes, and thus are major factors in determining the lower limit of distribution of a given tree species (Shreve 1915). There are changes in tree-ring characteristics that parallel these environmental changes along a gradient from the forest interior to the lower forest border (Fritts and others 1965). Trees closest to their arid lower limits show the greatest year-to-year differences and the highest common variation in ring widths. Furthermore, their growth records yield the highest correlations with concurrent meteorological records. In this environment, narrow rings are associated with low precipitation and high temperatures (Schulman 1956; Fritts 1966).

In the sub-Arctic, the northern forest limits are determined mainly by the length of the warm season and by the daily maximum temperatures, both of which decrease with increasing latitude. Here, as in the arid regions, the trees nearest the forest border are most responsive to year-to-year departures from the climatic norm (Mikola 1962). However, the meteorological element most strongly influencing tree-ring growth is low temperature rather than low precipitation. At the northern treeline, the temperature of the warmest months, or some measure of the heat sum for the warm period, are the only factors significantly correlated with tree-ring growth (Eklund 1957; Giddings 1943; Hustich 1945, 1948; Mikola 1962).

Another important forest boundary is the alpine treeline of the mountains of temperate regions. The climatic information that may be contained in long tree-ring records from this environment is little known, but the possibility of relating ring-width variation in trees at the alpine treeline to meteorological records is suggested by several lines of evidence. The role of temperature in setting the upper altitudinal limits for tree growth has been described (Daubenmire 1954) as "a major autecological principle." Of particular significance are the results of physiological experiments involving high-altitude pines (Tranquillini 1964, 1967; Schulze and others 1968; Mooney and others 1966). These results indicate that the upper treeline marks a critical altitude, above which annual net photosynthesis is insufficient for tree growth because of the short warm season and the low daily maximum temperatures. An important corollary is that at the treeline, successive annual rings would be expected to differ in width as a result of year-to-year differences in the temperature regime. The few studies that have been made, relating high-altitude tree growth to climate, lend support to this hypothesis (Artmann 1949; Brehme 1951; Leopold 1953).

In this report, tree-ring chronologies for bristlecone pines (*Pinus aristata* Engelm. and *P. longaeva* D.K. Bailey) at upper treeline sites in several western states are presented, and some relationships between climate and tree-ring growth in this environment are described. The bristlecone pine was chosen for this study because of the long tree-ring records that can be developed for these species, owing to the unusual longevity of individual trees (LaMarche 1969) as well as the possibility of incorporating data from logs and wood remnants to extend chronologies back thousands of years prior to the establishment of even the oldest living trees (Ferguson 1968).

Dendrochronological applications in western United States have traditionally relied on conifers of the woodland and montane forest zones. Interest in higher altitude species has developed since the 1950's, when Edmund Schulman discovered that certain subalpine conifers, notably the limber pine (*Pinus flexilis* James) and the bristlecone pine could provide climatically sensitive records thousands of years in length. However, after

some initial sampling of relatively high elevation trees (Schulman 1956; Schulman and Ferguson 1956), subsequent dendrochronological studies of bristlecone pine were limited mainly to trees on xeric sites near its lower altitudinal limits, particularly in the White Mountains of eastern California. These "drought-sensitive" trees appeared to offer the best possibilities for climatic reconstruction and for development of chronologies of maximum possible length. However, the dendroclimatic potential of higher altitude trees should not be neglected, because they may contain paleoclimatic information that complements that obtained from trees at lower altitudes in the same area (LaMarche 1974).

Tree-Ring Sites

Bristlecone pines were sampled at nine upper treeline sites in four western States (Figure 1). The Rocky Mountain bristlecone pine (*P. aristata* Engelm.) is represented by three sites in the Sangre de Cristo Range of northern New Mexico and southern Colorado and by two sites in the Colorado Front Range. The Great Basin bristlecone pine (*P. longaeva* D. K. Bailey) was sampled on Mount Washington in the Snake Range of east central Nevada and at three sites in the White Mountains, California. In each area, an attempt was made to locate and sample the highest full-sized erect trees. Krummholz forms, which are developed in all areas but the White Mountains (LaMarche and Mooney 1972), were not sampled because of their distorted radial growth patterns and apparent low ages. Table 1 gives information of each site.

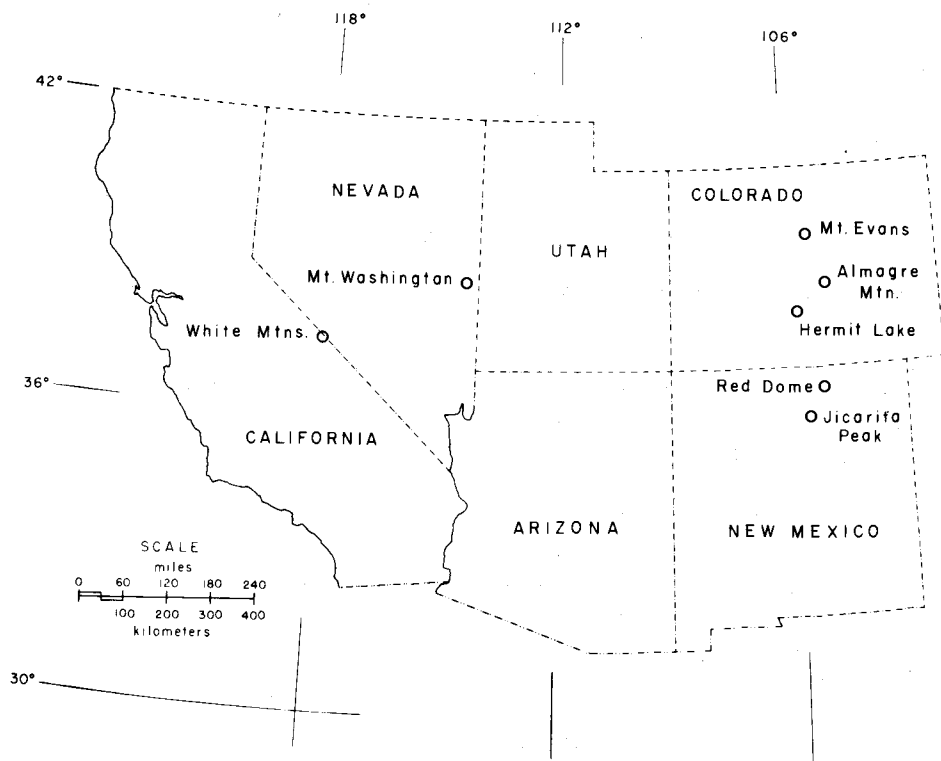


Figure 1. Location of upper treeline samples.

Table 1. Site characteristics.

Sangre de Cristo Range				
	Jicarita Peak, N.M.	Red Dome, N.M.	Hermit Lake, Colo.	
Latitude	36° 03'	36° 33'	38° 06'	
Longitude	105° 32'	105° 23'	105° 37'	
Altitude, m	3718	3695	3718	
Slope Direction	S	SE	S	
Slope Angle	35°	25°	35°	
Substrate	sandstone	sandstone	sandstone	
Front Range				
	Almagne Mtn., Colo.	Mt. Evans, Colo.		
Latitude	38° 46'	39° 38'		
Longitude	104° 59'	105° 35'		
Altitude, m	3535	3535		
Slope Direction	W	S		
Slope Angle	30°	15°		
Substrate	granite	granite		
Great Basin Ranges				
	Mt. Washington Nev.	Cottonwood Calif.	Sheep Mtn. Calif.	Campito Mtn. Calif.
Latitude	38° 54'	37° 33'	37° 32'	37° 30'
Longitude	114° 18'	118° 13'	118° 13'	118° 12'
Altitude, m	3383	3474	3505	3383
Slope Direction	S	N	E	NW
Slope Angle	10°	30°	20°	25°
Substrate	limestone	dolomite	dolomite	sandstone

Processing

Increment cores obtained in field sampling operations were mounted, surfaced, and dated using standard techniques (Stokes and Smiley 1968). Because crossdating with available low-altitude chronologies was poor or nonexistent in many cases, chronology development was carried out independently at each site. Frost rings were used as a supplementary dating aid (LaMarche 1970).

Ring widths on selected radii were measured to the nearest 0.01 mm, tabulated and punched on cards. The ring widths for each measured radius were then transformed to ring-width indices using either an exponential curve or straight line of zero or negative slope (Fritts and others 1969). This transformation is designed to remove the effects of differences in average growth rates between trees, as well as biological age trends.

Two mean index chronologies were developed for most sites. One of these contains ring-width indices for all of the well-dated and continuously measured radii. The other represents a smaller subsample of trees for which measurements along two radii were

available. Such replicated subsamples are required for analysis of variance and for evaluation of correlation between radii within trees.

A set of sample statistics was calculated for the total period covered by each chronology (Table 2) including sample size, mean ring width and the percentage of locally absent rings. The first-order autocorrelation coefficient, standard deviation and mean sensitivity of the mean site chronology are also given. Statistics similar to those in Table 2 are presented for the replicated subsamples (Table 3) based on a period encompassing only the past 100 to 110 years. Results of analysis of variance and cross-correlation for the replicated subsamples for the same period are given in Table 4.

Chronologies representing the maximum length of record obtained at each site are shown in Figures 2 through 5. These indices are being published in tabular form in the Laboratory of Tree-Ring Research Chronology Series (Drew 1972).

Colorado – New Mexico Chronologies

The Front Range chronologies (Almagre Mountain and Mount Evans) are longer and of better quality than those obtained from sites in the Sangre de Cristo Range to the south (Jicarita Peak, Red Dome, and Hermit Lake). A notable feature of all but the Mount Evans record is a pronounced upward trend in ring width since the mid 1800's. Another common feature, particularly pronounced in the New Mexico sites, is an interval of extremely low growth rates during the late 1830's and 1840's. Although some crossdating is apparent, most of the common variance is accounted for by longer-term growth fluctuations. The high autocorrelation coefficients in all the chronologies (Table 2) is a reflection of the large long-term variations.

Possibilities exist for chronology extension in time prior to the records contained in the oldest living trees. This is demonstrated by radiocarbon-based dates for large remnants at and above present treeline on Almagre Mountain that range back to 1300 B.C., whereas the modern chronology from living trees begins only in A.D. 560.

Great Basin Chronologies

The upper treeline chronologies from Mount Washington, Nevada, and from sites in the White Mountains, California, show many of the characteristics of chronologies from the Rocky Mountains. Autocorrelation is high, low frequency fluctuations are dominant, and there has been a pronounced increase in growth rates since about 1850.

The Mount Washington chronology could be extended through use of wood from standing dead snags and remnants, some of which date back to about 2000 B.C. (LaMarche and Mooney 1972). However, crossdating is relatively poor.

The Cottonwood chronology from the White Mountains was obtained from sampling a small stand of old trees on a high-altitude site that is less than 100 m below treeline. The Sheep Mountain samples come from trees at the present upper treeline. Although remnants nearly 6000 years old are found on Sheep Mountain (La Marche 1973), they contain relatively short records and have poor crossdating qualities, so that it would be difficult to extend this chronology back in time.

The Campito Mountain chronology represents a site quite different from Cottonwood and Sheep Mountain. It is at a somewhat lower altitude and is on a sandstone rather than dolomite substrate. Crossdating is good, and the presence of

Table 2. Chronology statistics — Total period.

Site	I.D. No.	No. Trees	No. Radii	Interval Years A.D.	Mean Ring Width, mm	% Locally Absent	First Order Autocorrelation	Standard Deviation	Mean Sensitivity
Jicarita Peak, N.M.	091519	6	13	1436-1968	0.63	0.50	0.87	0.40	0.19
Red Dome, N.M.	092519	7	14	1535-1968	0.63	0.27	0.88	0.31	0.12
Hermit Lake, Colo.	093519	11	17	1259-1968	0.64	0.07	0.82	0.31	0.15
Almagne Mtn., Colo.	095519	13	25	560-1968	—	—	0.70	0.26	0.17
Mt. Evans, Colo.	096510	5	10	977-1968	0.39	0.06	0.66	0.24	0.16
Mt. Washington, Nev.	076519	10	15	737-1965	0.49	0.10	0.68	0.34	0.22
Cottonwood, Calif.	002515	13	23	590-1969	—	—	0.58	0.31	0.26
Sheep Mtn., Calif.	002519	10	21	470-1970	—	—	0.77	0.31	0.17
Campito Mtn., Calif.	001510	10	20	1170-1970	0.38	1.28	0.62	0.33	0.26
Schulman Grove Crest, Calif.*	—	10	20	1860-1962	0.26	3.75	0.21	0.37	0.43

*lower forest border

Table 3. Sample statistics — ANOVA period.

Mean Index Chronology								
Period of Analysis	I.D. No.	No. Trees	No. Radii	Mean Ring Width	% Absent	Mean Standard Error		
UPPER TREELINE								
Jicarita Peak, N.M.	1860-1968	6	12	0.74	0.0	0.14		
Red Dome, N.M.	1860-1967	5	10	0.63	0.0	0.12		
Hermit Lake, Colo.	1860-1968	6	12	0.56	0.3	0.13		
Almagre Mtn., Colo.	1860-1968	8	16	0.47	0.0	0.10		
Mt. Evans, Colo.	1864-1964	5	10	0.50	0.0	0.11		
Mt. Washington, Nev.	1860-1965	5	10	0.52	0.0	0.11		
Cottonwood, Calif.			no analysis					
Sheep Mtn., Calif.	1860-1963	9	18	0.80	0.1	0.07		
Campito Mtn., Calif.	1960-1970	10	20	0.43	0.9	0.08		
LOWER FOREST BORDER								
Schulman Grove Crest, Calif.	1860-1962	10	20	0.26	3.8	0.07		

Table 4. ANOVA and cross-correlation data.

	Analysis of Variance			Cross-Correlation Analysis		
	% of chronology variance related to:			Mean correlation coefficient between:		
	common variation	differences between trees	unexplained	radii within trees	radii between trees	mean tree chronologies
UPPER TREELINE						
Jicarita Peak, N.M.	51	27	22		0.51	0.59
Red Dome, N.M.	30	25	45		0.30	0.38
Hermit Lake, Colo.	38	30	32		0.40	0.45
Almagre Mtn., Colo.	28	23	49		0.31	0.41
Mt. Evans, Colo.	20	49	31		0.23	0.29
Mt. Washington, Nev.	43	26	31		0.45	0.53
Cottonwood, Calif.	33	15	52	no analysis	0.33	0.47
Sheep Mtn., Calif.	37	12	51		0.39	0.51
LOWER FOREST BORDER						
Schulman Grove Crest, Calif.	67	17	16		0.68	0.74

abundant, large remnants has permitted development of a 5405-year chronology (LaMarche and Harlan 1973).

Tree-Ring Response to Climate at Upper Treeline

The usefulness of long tree-ring records for paleoclimatic inference basically depends on the degree to which climate influences ring width. The strength of the climatic "signal" in tree-ring records can often be indirectly inferred from their statistical properties, or more directly by comparison of tree-ring and climatic data.

The statistical properties of ring-width data from the upper treeline sites (Tables 2, 3, and 4) permits evaluation of relative "quality" for dendroclimatic purposes. In Tables 2, 3 and 4, data from bristlecone pines on a superior lower forest border site in the White Mountains (Fritts 1969) are given for comparative purposes. The chronology standard deviation (Table 2) is a measure of the total amount of ring-width variation through time, and thus the magnitude of the environmental "signal" (not necessarily climatic) present in the mean record. Values range from 0.24 to 0.40 (relative to a mean of 1.00 in all cases), with most values from upper treeline falling below that for the lower forest border sites (0.37). The first-order autocorrelation coefficient (r_1) (Table 2) describes the average dependence of the ring-width value for a given year on the value for

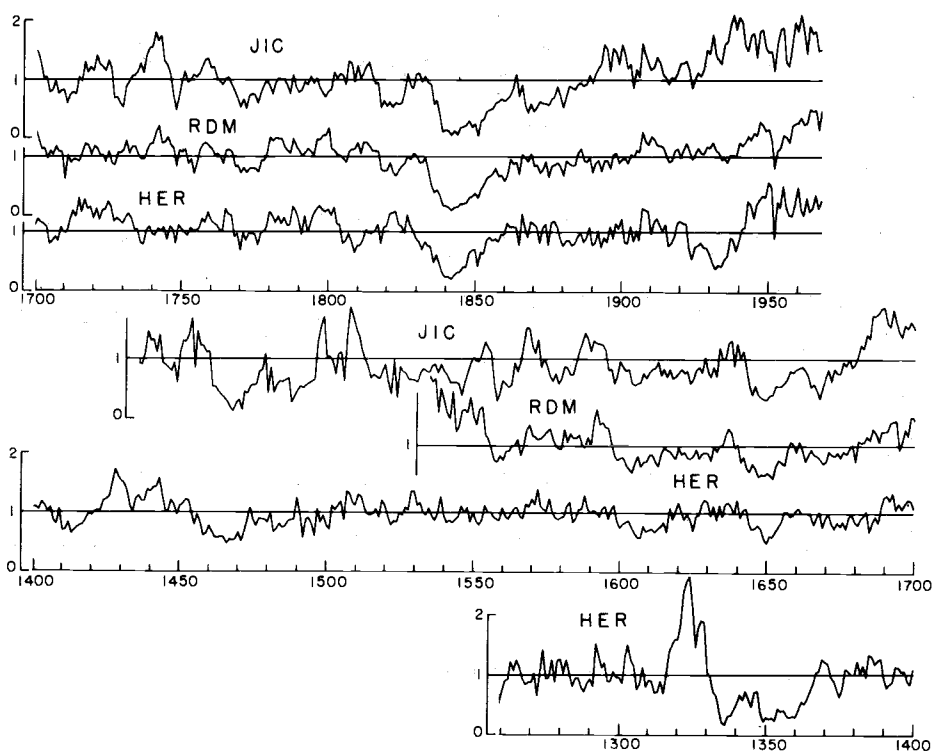


Figure 2. Ring-width indices for localities in the Sangre de Cristo Range: Jicarita Peak (JIC) and Red Dome (RDM), New Mexico; Hermit Lake (HER), Colorado.

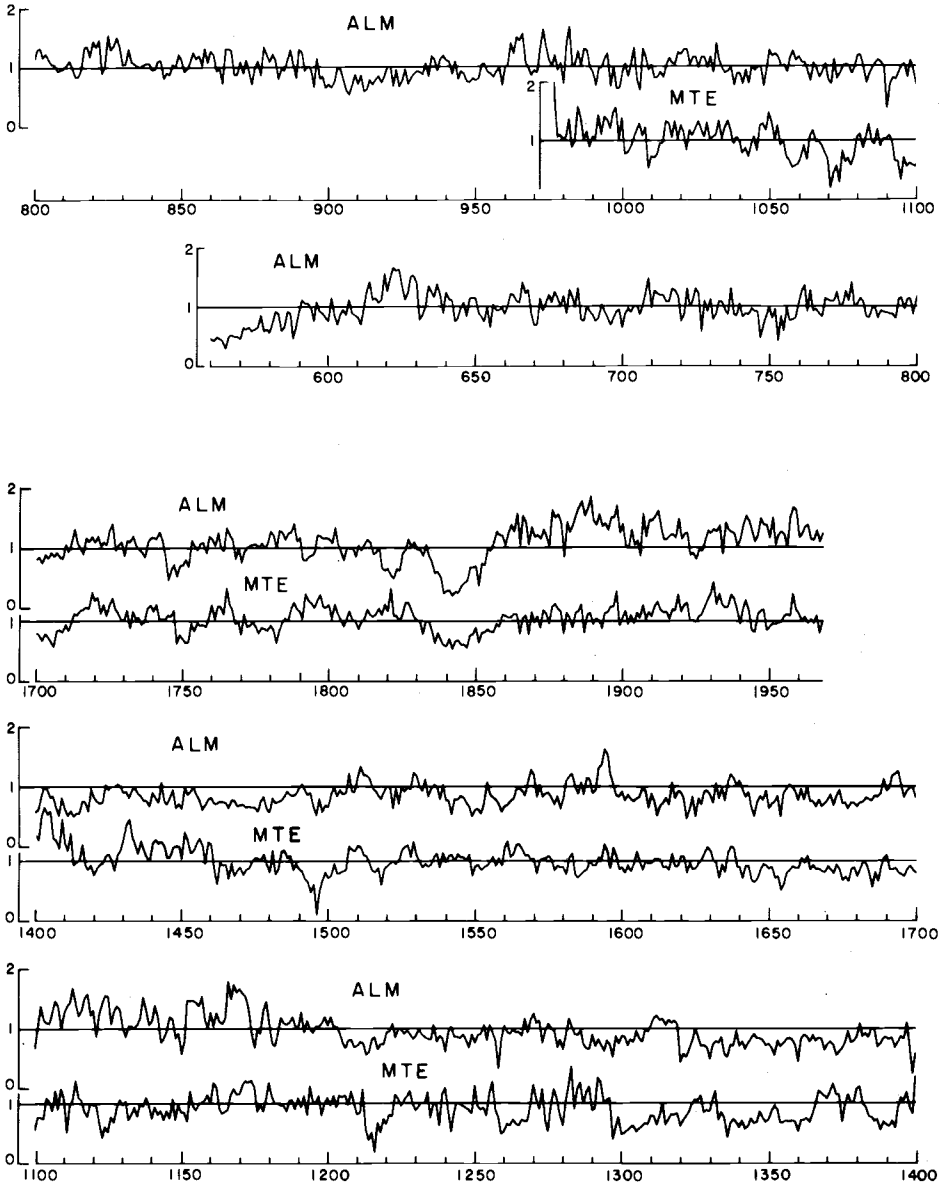


Figure 3. Ring-width indices for Front Range localities: Almagre Mountain (ALM) and Mount Evans (MTE), Colorado.

the year previous. It is thus a measure of the importance of persistent trends or fluctuations in the record or of the influence of moving-average or autoregressive processes. Values of r_1 at upper treeline range from 0.58 to 0.88, and are much higher than values typical of the lower forest border (0.2-0.3). The autocorrelation in upper treeline ring-width chronologies is also much larger than autocorrelation in such climatic variables as seasonal mean temperature and precipitation, suggesting that biological sources of persistence are operating to produce persistence in the tree-ring series. The mean sensitivity (Table 2) is the average absolute difference between two successive ring-width values divided by their mean value. A high mean sensitivity characterizes a series with large year-to-year differences in ring width. Thus, it is directly proportional to standard deviation, but inversely proportional to r_1 . It is the width of an annual ring relative to width of the immediately preceding and following rings that provides the basis for crossdating of ring sequences. Therefore, the relatively low mean sensitivities (0.12 to 0.26) of the upper treeline series compared to those near the lower forest border (0.43) in part explain the generally poorer crossdating qualities of upper treeline material (Schulman and Ferguson 1956).

Another measure of dendroclimatic potential is provided by the degree of common variability present in ring-width series from different radii and from different trees on the same site. Table 4 gives results of analysis of variance (ANOVA) and cross-correlation

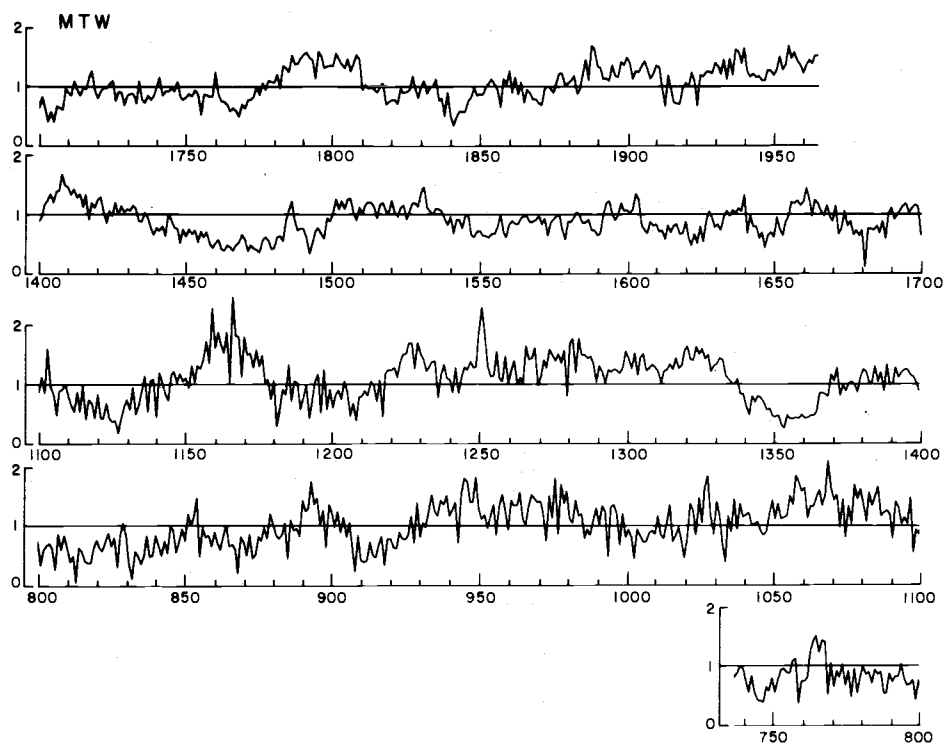


Figure 4. Ring-width indices for Mount Washington (MTW), Nevada.

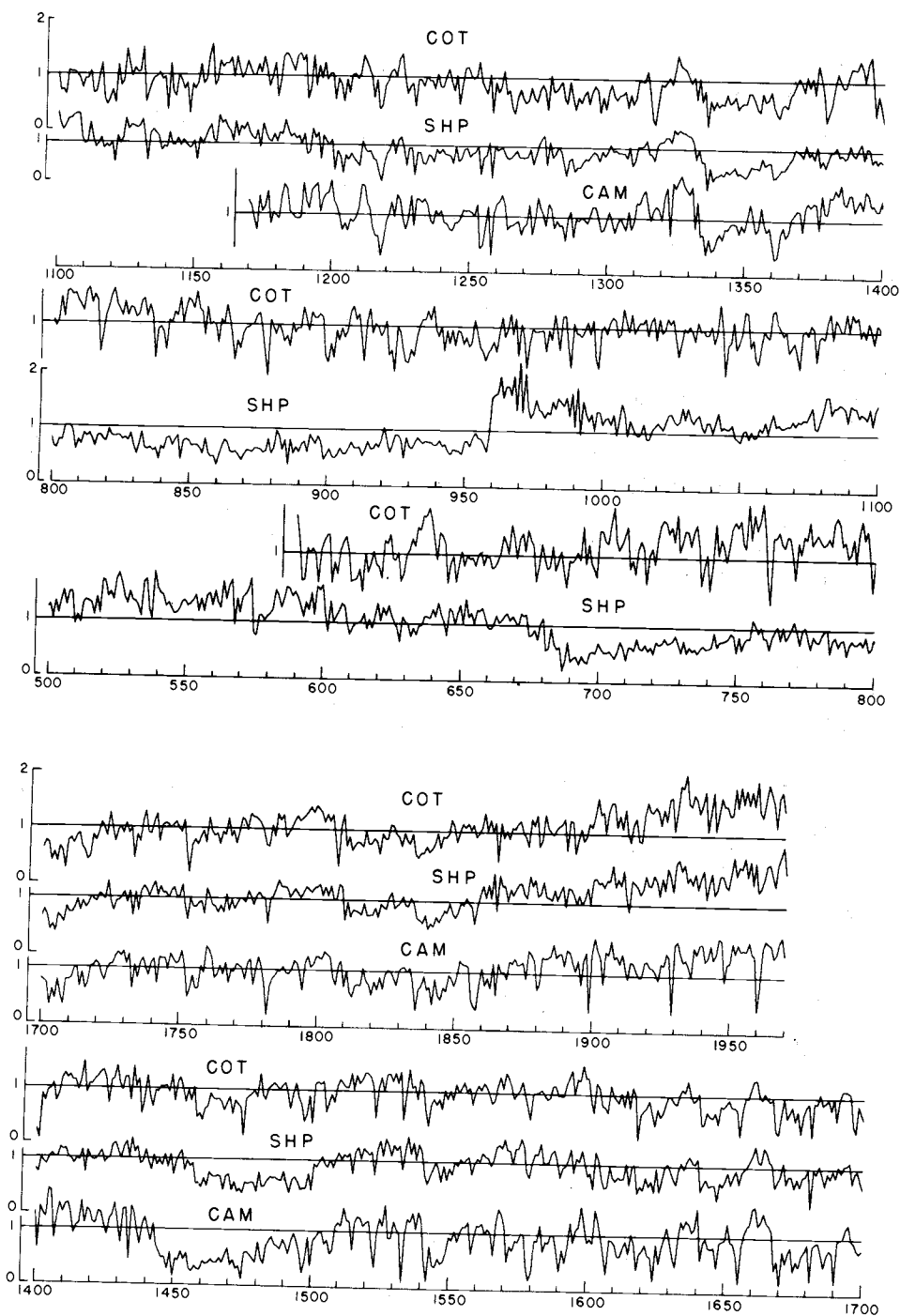


Figure 5. Ring-width indices for localities in the White Mountains, California: Cottonwood (COT), Sheep Mountain (SHP), and Campito Mountain (CAM).

Table 5. Response function parameters.

Chronology	Climatic Station	Data Period	Percent Variance Explained		Step ¹	F-Level ²
			Total	Prior Growth		
NNM	Taos, N.M.	1903-1968	72	59	12	1.09
HER	Cañon City, Colo.	1897-1968	70	56	9	1.11
ALM	Lake Moraine, Colo.	1897-1959	48	25	11	1.42
MTE	Idaho Springs, Colo.	1905-1968	45	20	8	1.30
MTW	Fillmore, Utah	1900-1965	48	42	7	1.03
CAM	Mina, Nev.	1908-1969	27	12	7	1.12
SHP	Mina, Nev.	1908-1969	41	11	10	1.70
COT	Mina, Nev.	1908-1969	40	22	9	1.04

¹ Number of independent variables used in regression.

² F-level at which last independent variable entered regression.

analyses. The first column of the ANOVA results is most important, because it gives the percentage of total variance that is retained by the mean chronology. It ranges from 20 to 51 percent for upper treeline sites, which compare poorly with the lower forest border site (67 percent). Differences between trees account for more variance in the Rocky Mountain and Nevada sites than in the White Mountains. The outstanding result of the correlation analysis is the much poorer degree of correlation within trees and between average records from individual trees at upper treeline (0.29-0.59), as compared with the lower forest border (0.74). The results of these analyses must be viewed with caution, however, because the period of analysis coincides with a period of major growth trend in many of the upper treeline records. The trend dominates the analyses and obscures the relatively poor correspondence of the year-to-year variations on many of these sites.

Empirical comparison of series of ring-width indices with meteorological records is a way of directly evaluating the degree and kind of climatic influence on tree-ring growth. Multiple linear regression analysis using monthly temperature and precipitation as independent variables (Fritts 1962) was initially used in this work, but was unsatisfactory, at least in part because of the intercorrelation of the temperature and precipitation variables. More success was achieved using a more recently developed modelling procedure (Fritts and others 1971). This procedure involves stepwise multiple linear regression, but the climatic variables used in the regression analysis are first transformed into a new set of uncorrelated variables using principal component analysis. The advantages are first, that the new independent variables are uncorrelated, and second, that the number of independent variables can be reduced, yielding additional degrees of freedom for statistical tests of significance of the regression coefficients.

The response functions obtained (Table 5) from the results of the regression analyses show how normalized precipitation and temperature departures influence tree-ring width during the following or current growing season. Average monthly mean temperatures and total monthly precipitation recorded at the nearest station with a relatively long record were used in the analyses (U.S. Government, 1896-1970). Meteorological data for a 14-month period were used, beginning with the July prior to the growing season in which the annual ring is formed and ending with August of the

growing season concurrent with formation of the annual ring. Phenological evidence shows that in at least some years, ring growth in upper treeline bristlecone pines continues into late August or even early September. The widths of the annual rings formed one, two, and three years prior to the current growing season are also included as variables in the regression analysis, to help account for direct and indirect lagged effects. Inclusion of these prior growth variables helps to reduce the influence of biological persistence on the climatic model.

The results of climatic modelling are shown in Figure 6. The two northern New Mexico chronologies (Jicarita Peak and Red Dome) were combined into a single regional chronology (NNM) for purpose of this analysis. Three of the Rocky Mountain chronologies (all except Mount Evans) show qualitatively similar response functions (Figure 6, *upper*). Temperatures during the previous late summer and autumn and current summer are positively correlated with ring width, while temperature during May and June is negatively correlated with growth. The effect of precipitation seems most important at the Almagre Mountain site, where it is positively associated with growth except during the previous July and August, during mid winter and in the current August. At the northern New Mexico sites (NNM) precipitation during the previous autumn and current spring and summer is positively correlated with growth, but inversely correlated during most winter months. The response function for Mount Evans is quite different from those found at other Rocky Mountain sites. Here, temperature is negatively correlated with growth in all but the late spring and summer months in the year concurrent with growth. Precipitation in most months is negatively correlated with ring width. This response function should be viewed with caution, because of the anomalous behavior of the Mount Evans chronology within the period of weather records. Based on the total number of significant response function weights, the Almagre Mountain chronology appears to present the best basis for paleoclimatic estimation.

Response functions for the Great Basin bristlecone pine sites are shown in Figure 6, *lower*. Temperature responses are generally similar, with temperatures of the previous autumn and current summer being positively correlated with growth. Temperature in the late winter and spring is generally negatively correlated with growth in the following summer. The high-altitude Sheep Mountain site yielded the chronology with the greatest temperature response. Precipitation in the previous summer and in mid-winter is positively correlated with growth; late autumn and early winter precipitation are negatively correlated with growth. The lower-altitude and generally more xeric Campito Mountain site has trees showing the greatest precipitation response.

The temperature response functions for most of the upper treeline sites are broadly similar, and can be partly explained by the results of physiological experiments on high altitude pines (LaMarche 1973). First, rates of net photosynthesis at upper treeline are directly proportional to air temperature, so that more photosynthates will be produced during a warm summer than a cool one. Second, because the photosynthetic "mechanism" is in part controlled by the temperature regime, a late occurrence of spring warming and early onset of winter cold restrict the period during which the trees are capable of photosynthesis. Finally, bristlecone pines can lose important amounts of stored photosynthates by respiration on warm days during the winter period of photosynthetic dormancy. To the extent to which production and storage of the products of photosynthesis affect subsequent and current ring growth, these temperature effects provide a basis for explaining some major features of the temperature response functions.

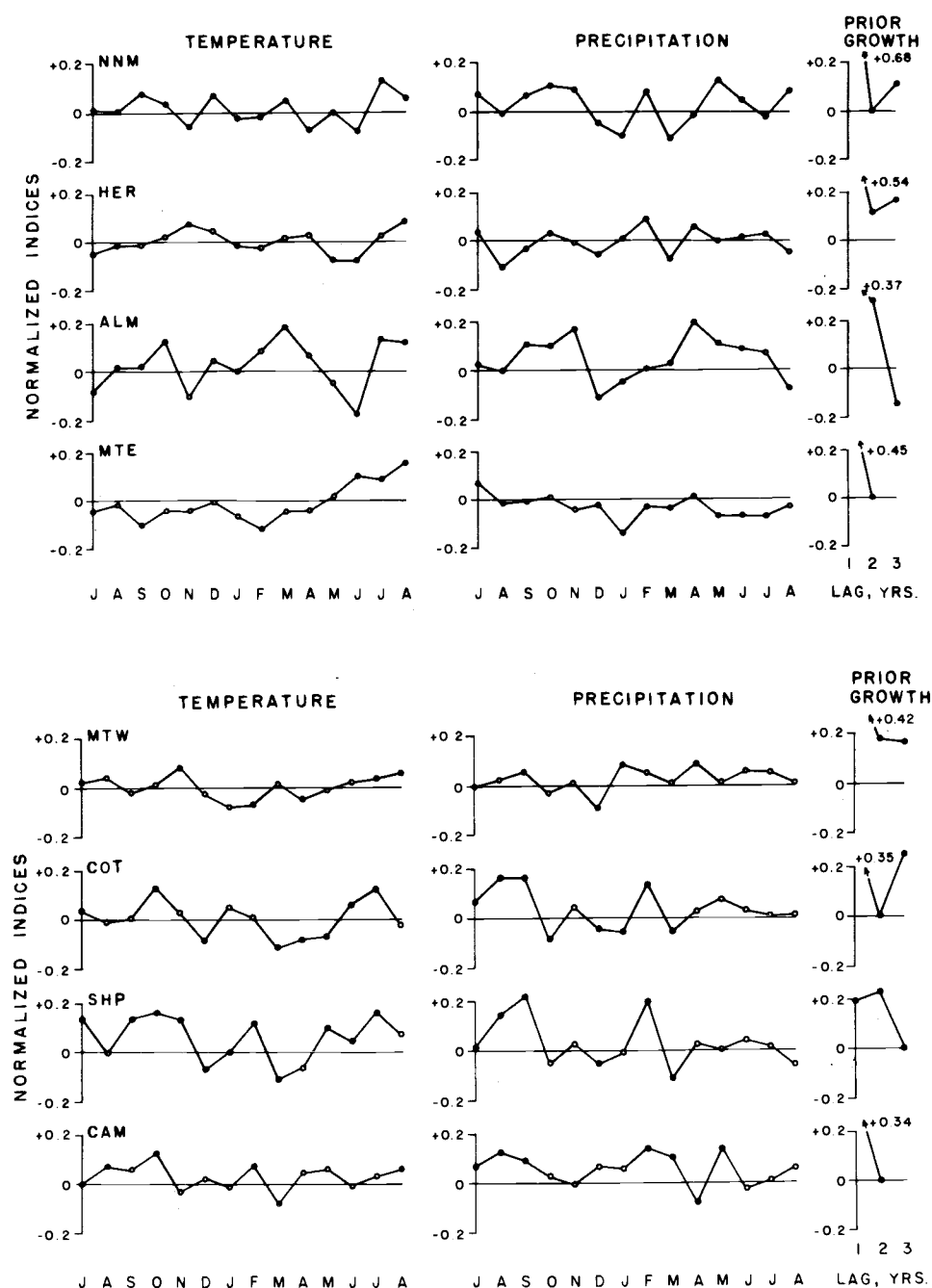


Figure 6. Response functions showing effects of precipitation, temperature, and ring widths in previous years on ring-width indices in upper treeline bristlecone pines. *Upper*, Rocky Mountain localities — NNM represents the mean Jicarita Peak-Red Dome chronology. *Lower*, Great Basin localities.

The positive response to warm, prior autumn (after the end of the previous growing season) may reflect increased net photosynthesis, the products of which are stored and utilized for ring growth the following summer. The negative response to temperature in late winter could be due to the loss of stored photosynthates on warm days during the dormant season. The generally positive response to warmth during the growing season may be attributed to the contribution of current photosynthetic production to annual ring growth, although direct temperature effects on cell division and enlargement are also possible.

Study of another phenomenon suggests that empirical modelling of the type used to obtain the response functions does not adequately portray the role of temperature on tree-ring growth at upper treeline. Bristlecone pines retain their needles for at least ten years; retention for thirty years or more is not uncommon, and as many as 58 successive annual needle clusters have been counted (Bailey 1970). There are large year-to-year variations in needle length that are closely related to summer temperature (Figure 7). Comparison with weather data shows that low temperatures in the summer during which needle elongation takes place result in formation of very short needles. Although the older needles decrease in photosynthetic efficiency, they still represent a major part of the total photosynthetic area of a bristlecone pine. Clearly, a succession of unusually cool or unusually warm summers would result in large changes in photosynthetic area, and consequently, large changes in total net photosynthesis that should be reflected in ring widths. Ring-width variation could be affected in two ways. First, the affect of a few cool summers would be spread out over several subsequent years, a phenomenon that might explain the unusually high autocorrelation coefficients that characterize the upper treeline chronologies. Second, the tree-ring response to a fluctuation in climate would lag behind the climatic event, because several years must elapse before the foliage area can reflect the influence of the changed conditions.

UPPER TREELINE CHRONOLOGIES AS PALEOTEMPERATURE INDICATORS

Physiological considerations and the results of empirical modelling indicate that ring-width chronologies from upper treeline bristlecone pines contain at least some paleoclimatic "information." However, the high degree of persistence in these series suggest that one or more biological smoothing mechanism is operating. One such possible mechanism is the slow response of foliage area to summer temperature changes.

Another approach to the evaluation of the climatic significance of long-term tree growth fluctuations is the consistency of such fluctuations over broad geographic areas. If such consistency is found, it strongly suggests that climate rather than local disturbances, ecological changes, insects, or disease is responsible. The upper treeline chronologies do show broad general agreement in trends over large areas. The upper treeline records can be compared in several ways. The plotted data in Figures 3, 4 and 5 show that there is agreement of the long-term fluctuations in tree-ring width between areas more than 1000 km apart. These relationships are summarized in Figure 8, where the normalized departures of successive 30 year mean ring-width indices are presented for the period of record common to all series (A.D. 1541-1965).

There is a tendency for tree growth to be above (below) normal in the Great Basin and central Rocky Mountains when it is below (above) normal in the southern Rocky Mountains (1661-1690, 1691-1720, 1871-1900). During some subperiods, there is poor

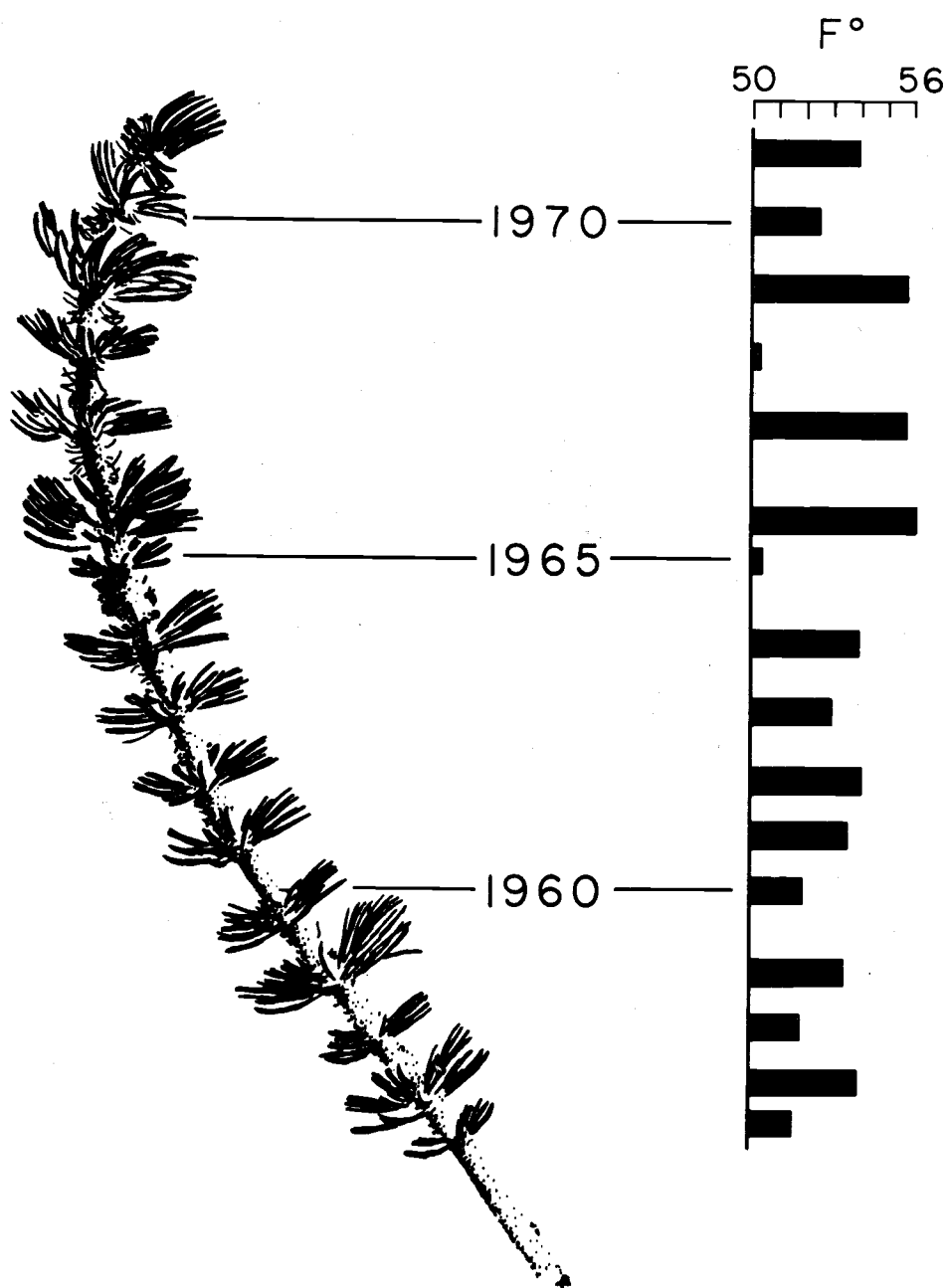
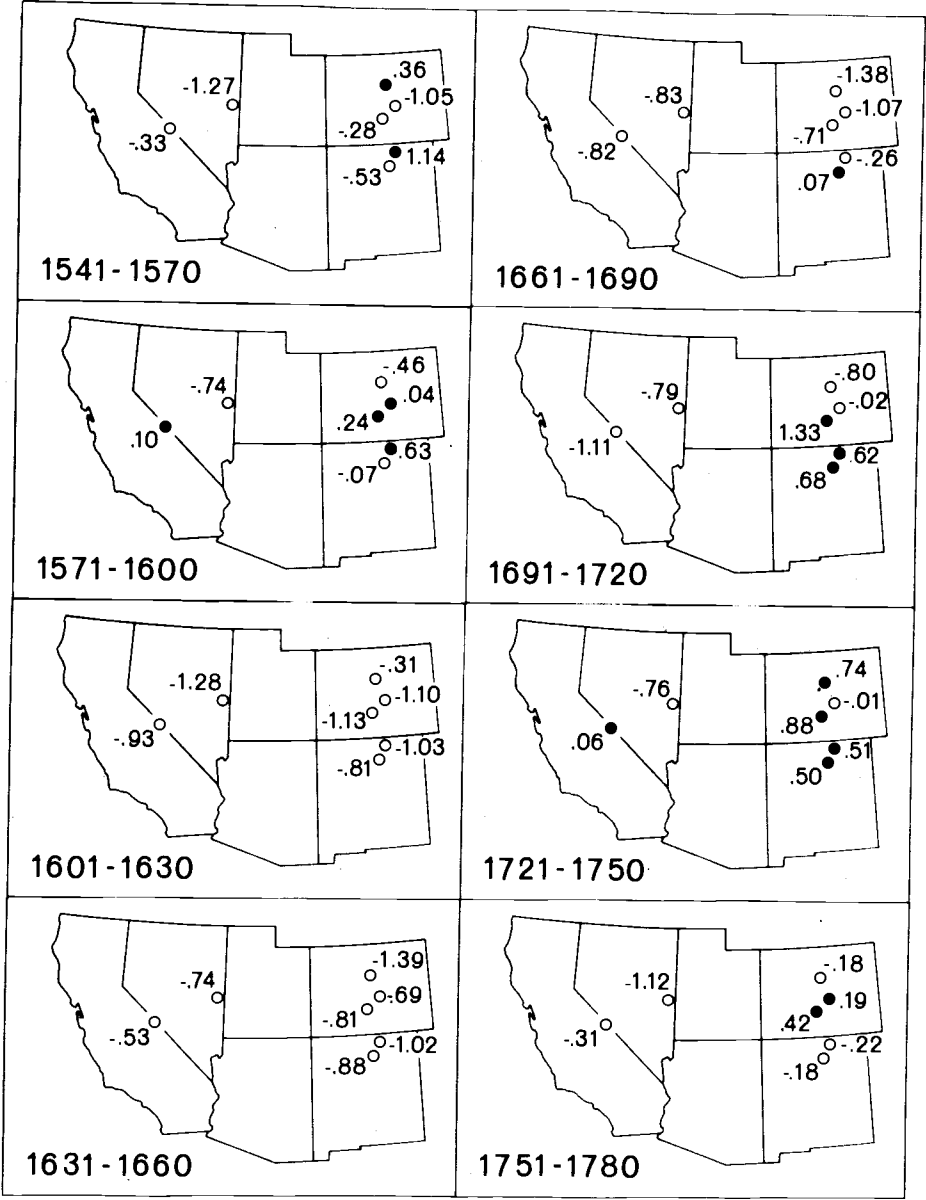


Figure 7. Needle length compared with summer (J, J, A) temperature.



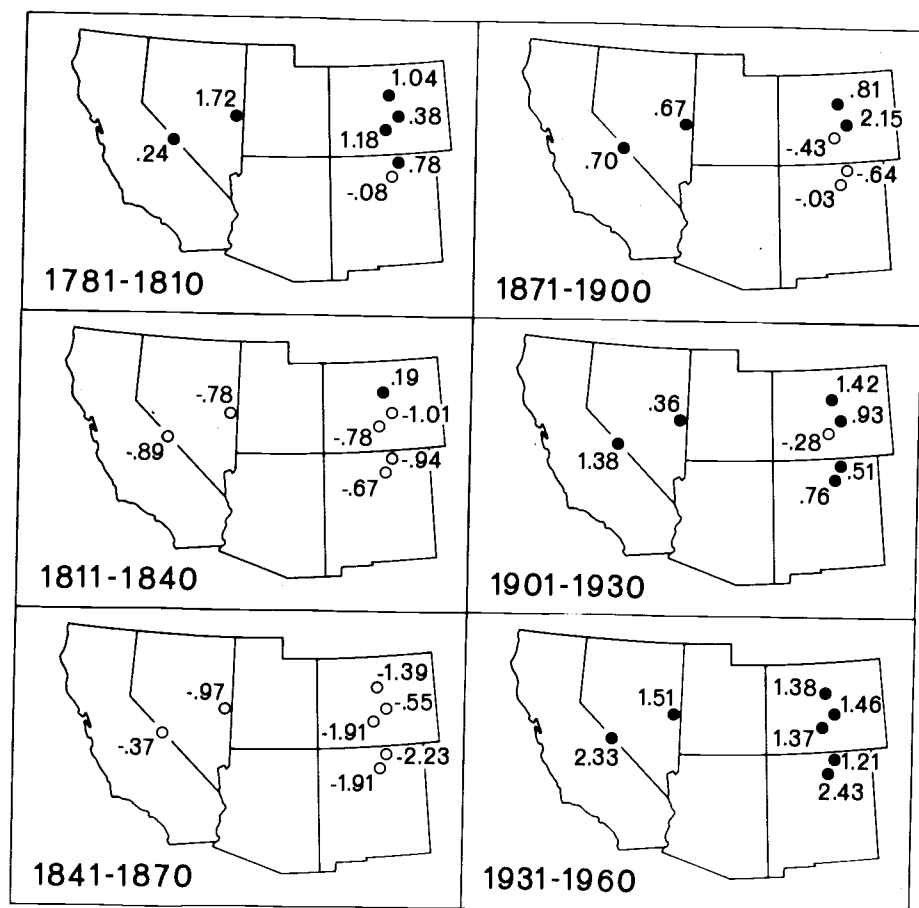


Figure 8. Patterns of tree-growth departures in bristlecone pine at upper treeline. Values are normalized departures of consecutive 30-year mean indices from the long-term (1541-1965) mean at each site.

agreement in the signs of tree-growth departures at sites in the same region (1541-1570, 1721-1750, 1751-1780). However, in most of the 30-year subperiods, the sign and magnitude of the growth departure are similar at nearly all the sites. Thus, it appears that long-term fluctuations in tree growth at upper treeline in southwestern United States do reflect regional trends in climate. Anomalous departures at some of the sites may represent non-climatic effects or real climatic anomaly patterns on a smaller spatial scale.

The broad pattern of tree-ring width departures in western United States also agrees with observed patterns of seasonal temperature departures based on meteorological records during the first 60 years of the twentieth century. In Figure 9, generalized contours show departures of the 1901-1930 mean from the 1931-1960 mean at selected stations in southwestern United States in spring (A), summer (B) and autumn (C). They indicate a trend toward warmer conditions between 1901-1930 and 1931-1960 in the warm season (April-October) over most of this region. Normalized ring-width index departures between the same periods are also shown. The increase in average ring width between 1901-1930 and 1931-1960 at most sites is consistent with the conclusion from biological evidence, that increased warm-season temperatures should result in wider

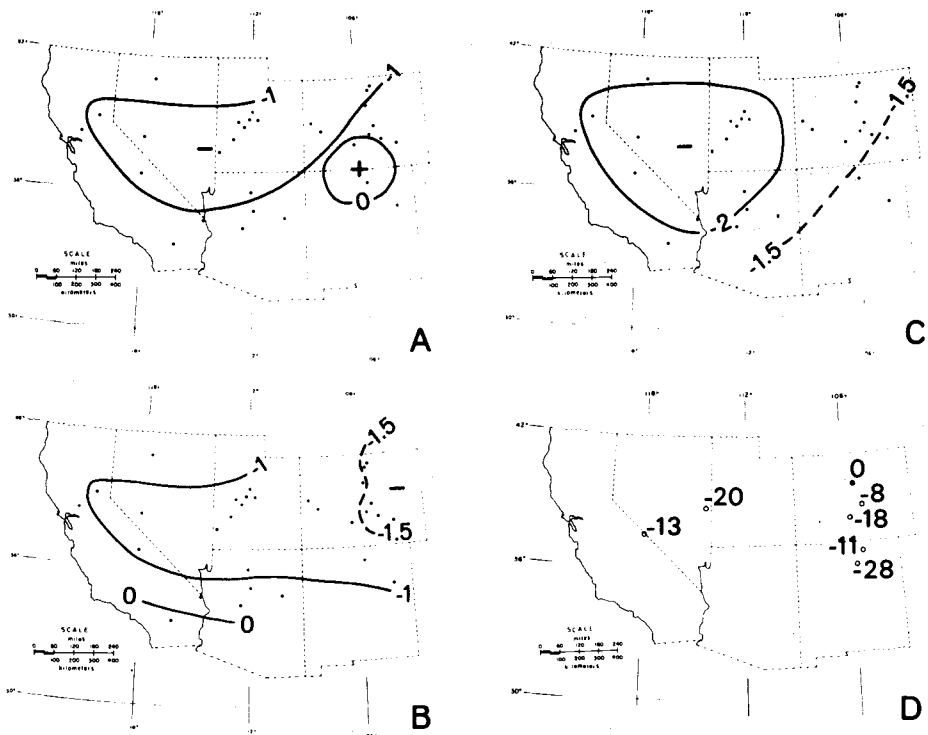


Figure 9. Trends in temperature and in tree growth at upper treeline in southwestern United States since 1901.

Contours show departures of 1901-1930 mean temperatures (F°) from 1931-1960 normals at selected stations for: A. spring (M, A, M) B. summer (J, J, A) and C. autumn (S, O). Mean ring-width indices for 1901-1930 are shown as percentage departures from the 1931-1960 mean at each locality (the White Mountains, California, chronologies were averaged for this analysis).

annual rings at upper treeline. However, the tree-ring records are not in agreement with other evidence for secular climatic changes in western U.S. between 1850 and 1900. Comparison of the tree-ring records for upper treeline sites with meteorological records does show some inconsistencies. Wahl and Lawson (1970) concluded, from a study of early meteorological records, that seasonal temperatures during the period 1850-1869 were higher than those of the 1931-1960 normal period in interior western United States. Bradley and Barry (1973) found much the same results in a study of data for southwestern Colorado. In contrast, nearly all the tree-ring series show higher average growth rates for 1931-1960 than 1850-1869 (Figures 3, 4, 5, 7). The explanation for this discrepancy may lie in the lag in tree-growth response to climatic change postulated from observations of needle length variations. At all the sites, tree growth was much below normal in the 1830's and 1840's, but especially so in southern Colorado and northern New Mexico. Bradley and Barry (1973) note that temperatures rose rapidly in the 1850's in Colorado, but if photosynthetic mass had been reduced by adverse conditions in the immediately preceding decades, then the potential for rapid growth in bristlecone pine at upper treeline sites in this region would remain correspondingly low, until photosynthetic mass had sufficient time to accumulate. In contrast, the unusually warm temperatures and high tree-growth rates of the 1960's (Wahl and Lawson 1970: 264; Namias 1970) followed a long period of relatively high temperatures. With a correspondingly large foliage volume, the trees could fully respond to a favorable temperature regime.

CLIMATIC DATA COLLECTION AND ANALYSIS FOR SOUTHWESTERN UNITED STATES

The primary purpose for collection of the climatic data was calibration with tree-ring data that had already been collected. Therefore, our initial selection of stations was based on proximity to the tree-ring data sites and length of record. Our objective was a grid of reasonably homogenous climatic records representative of climate in southwestern United States over the past 70 years. We initially limited our selection to those stations not situated in large urban centers and to those whose records were approximately 70 years (1900-1969) in length. As a result, our initial selection included about 50 stations.

The monthly data for the precipitation and temperature records from these stations were collected and tabulated from the *Annual Summaries of Climatological Data* published by ESSA. For those months in which there were occasionally missing values, estimates were used. For missing precipitation data, we used the estimation technique as outlined by McDonald (1957), and at least two nearby estimation stations records were used. For missing monthly temperature values, we used a simple linear regression technique. For the estimator station, we used a nearby station of comparable elevation and only then if the correlation coefficient for approximately 30 years of simultaneous record was equal to or greater than 0.70.

After tabulation of the data, the data were keypunched onto computer cards and verified. The data for each station were then seasonalized according to the following monthly distribution: winter – November, December, January, and February; spring – March, April, and May; summer – June, July, and August; autumn – September and October. These so-called "natural" seasons were selected based on known or suspected seasonal distributions affecting high elevation tree growth and inter-monthly correlation within the climatic data themselves.

Following seasonalization, each seasonal record for each station was analyzed for homogeneity. This included the following approach. Each seasonal record was first plotted by the computer, and the plot was scrutinized for anomalous trends and values. Any records with unique trends were eliminated at this point or at least placed in a suspect category. Each seasonal precipitation record was checked for homogeneity by use of the double-mass analysis approach as outlined by Kohler (1949). The technique has been programmed for the CDC 6400, so that the evaluation of each seasonal record involved visually analyzing the double-mass diagrams plotted by the computer for linearity. By necessity, this analysis involves a certain amount of subjectivity, as the tendency is for the double-mass diagrams to oscillate about a straight line. For our purposes, we considered the double-mass diagram to indicate inhomogeneity only if a definite and continuous change in slope could be detected.

The seasonal temperature records were also analyzed for inhomogeneities. the technique we used is partly fashioned after that of Mitchell (1961). The series of annual values from a particular station for one season was transformed to a first-difference series. An unusually large first difference between years bracketing a stations move or observer change is indicative of a non-climatic effect on the record. The cumulative first differences were also calculated and plotted to emphasize the effect of a permanent shift of mean values in the temperature record that might be related to non-climatic influences.

Our final selection of stations chosen for the climatic calibration network is listed in Table 6 and shown on the map of Figure 10. In many cases we were not entirely

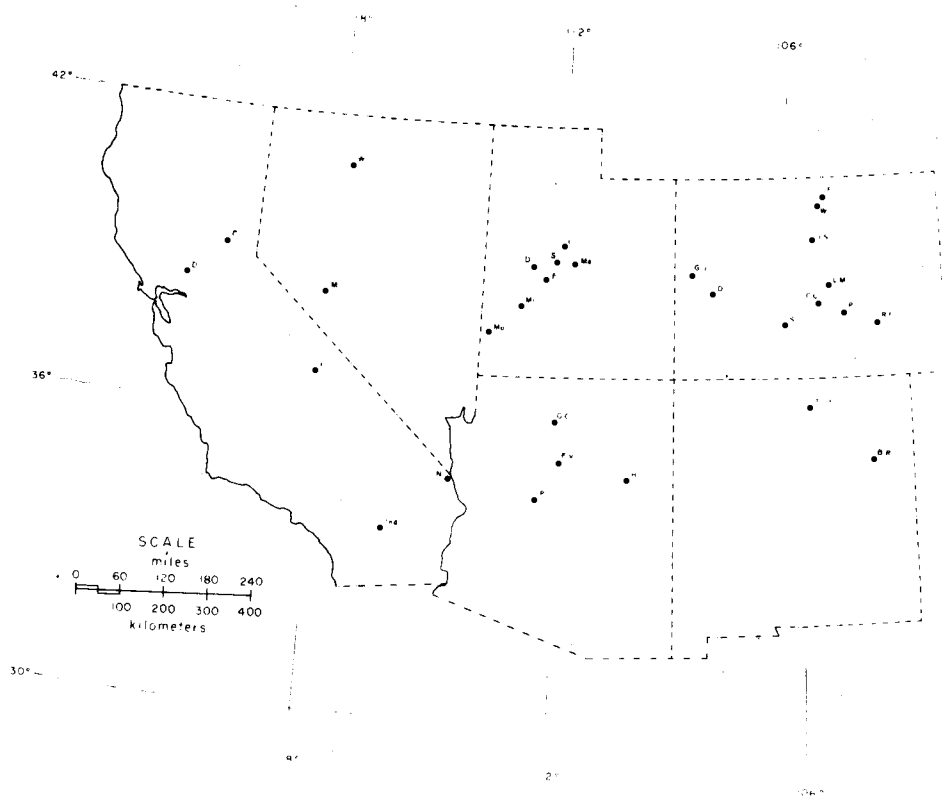


Figure 10. Location of meteorological stations.

Table 6. Meteorological data network.

Station	Map Symbol ¹	Degrees North Latitude	Degrees West Longitude	Elevation In Feet A.M.S.L.	Period of Record	Moves ²
Colfax, Calif.	C	39.06	120.57	2418	1898-1969	None
Davis, Calif.	D	38.32	121.46	60	1899-1969	5
Independence, Calif.	I	36.48	118.12	3950	1899-1969	11
Needles, Calif.	N	34.46	114.37	913	1898-1969	5
Indio, Calif.	Ind.	33.44	116.15	11	1898-1969	3
Winnemucca, Nev.	W	40.54	117.48	4301	1901-1969	8
Mina, Nev. ³	Mi	38.23	118.06	4552	1907-1969	2
Modena, Utah	Mo	37.48	113.55	5460	1902-1969	3
Milford, Utah	Mi	38.26	113.01	5018	1909-1969	11
Fillmore, Utah ³	F	38.57	112.19	5160	1898-1969	3
Deseret, Utah	D	39.17	112.39	4585	1900-1969	5
Scipio, Utah	S	39.15	112.06	5306	1899-1969	3
Levan, Utah	L	39.33	111.52	5300	1900-1969	6
Manti, Utah	Ma	39.15	111.38	5740	1900-1969	7
Grand Canyon, Ariz.	GC	36.03	112.08	6950	1904-1969	1
Fort Valley, Ariz.	FV	35.16	111.44	7347	1910-1969	3
Prescott, Ariz.	P	34.34	112.28	5510	1899-1969	6
Holbrook, Ariz.	H	34.54	110.10	5069	1894-1969	5
Taos, N.M. ³	T	36.22	105.37	6945	1903-1969	4
Bell Ranch, N.M.	BR	35.32	104.06	4500	1906-1969	None
Grand Canyon, Colo.	GJ	39.07	108.32	4855	1987-1969	7
Delta, Colo.	D	38.46	108.07	5055	1897-1969	5
Saguache, Colo.	S	38.05	106.09	7697	1897-1969	3
Canon City, Colo. ³	CC	38.26	105.16	5343	1897-1969	9
Pueblo, Colo.	P	38.17	104.31	4639	1898-1969	1
Rocky Ford, Colo.	RF	38.02	103.42	4178	1897-1969	None
Lake Moraine, Colo.	LM	38.49	105.01	10265	1897-1969	None
Idaho Springs, Colo.	IS	39.45	105.31	7555	1896-1969	4
Waterdale, Colo.	W	40.25	105.12	5260	1903-1969	None
Fort Collins, Colo.	FC	40.35	105.051	5001	1896-1969	2

¹ See Figure 10² This column contains the number of documented moves the station has undergone during the period of record.³ Meteorological data used in modelling response function at nearby tree-ring site

satisfied that we were selecting ideally homogeneous records, but based on proximity to our tree-ring data sites and length of record, we considered this network as being the best available.

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