CHANGES IN THE RELATIONSHIP BETWEEN ANNUAL TREE GROWTH AND CLIMATIC VARIABLES FOR FOUR HARDWOOD SPECIES

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Abstract: A study was conducted to characterize temporal and spatial variability in the growth response of four major hardwood species (white oak, chestnut oak, northern red oak, and yellow-poplar) to climatic fluctuations, and to evaluate the role of environmental factors associated with differences in response among individuals. The study incorporated tree-ring data collected by the Tennessee Valley Authority from a system of permanent forest inventory plots. Results of the dendroclimatic modelling indicated that there is a great deal of temporal variability in the climate/growth relationship for the species and sites included in this study. Statistically significant trends in growth showed a decrease in sensitivity to climate occurring in the tree-ring series. Changes in tree sensitivity did not appear to coincide with changes in climate. Environmental factors were effective in explaining groupings of tree core series as long as interactions between variables were considered. These factors indicate that differences in growth response to climate may be a function of changes in stand structure, competitive interactions and soil moisture holding capacity.

INTRODUCTION

Climate is often considered one of the most prominent and consistent factors affecting year to year variability in tree growth and, depending on the existence of other growth limiting factors, may be one of the most difficult to understand (Fritts 1976). In areas such as the arid southwest United States where moisture is the limiting growth factor, response to rainfall fluctuations is strong and predictable, especially at the forest - desert interface where conditions are marginal for tree survival (Fritts et al. 1965, Stahle 1987). However, moving towards more mesic sites, where moisture is less limiting, response to climate becomes less predictable due to the effects of factors such as nutrient availability and stand competition and their interactions with climate. The dynamic nature of these factors along with their inherent variability further obscures direct climatic effects resulting in a great deal of temporal and spatial variability in tree growth response. As these relationships increase in complexity from the moisture limited "sensitive" trees of the arid southwest to the "complacent" trees growing on more mesic sites, the level of detail of investigation of other factors and the sophistication of analytical techniques must also increase if tree growth response to climate is to be understood.

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As moisture becomes less limiting, other growth-limiting factors increase in relative importance, particularly in that stress due to some other factor may predispose a tree to injury attributable to climate. Site quality changes over time as a result of the natural aging processes of ecosystems, as well as stochastic events that cause significant disturbances. These changes bring about both abrupt and gradual changes in soil properties and species composition before a constant vegetation composition associated with a mature soil is reached (Pritchett and Fisher 1987). Over the life of a forest stand, changes occur in 1) soil physical and chemical properties as well as soil biota (Carmean et al. 1976, Whittaker and Woodwell 1972); 2) the physiology of individual trees and their sensitivity to stresses (Boyce 1961, Daubenmire 1974, Kim and Siccama 1987, Kozlowski 1979, Waring and Cleary 1967); and 3) stand structure and competition among trees (Haines and Cleveland 1981, Hornbeck et al. 1986, Van Deusen 1987, 1988). In addition, microsite differences within a stand modify individual tree response to various stresses.

Variability in tree growth response to climate across geographical gradients can be anticipated due to: 1) varying site requirements for different species (Fowells 1965); 2) differences in soils reflected in moisture availability and nutrient content (Bassett 1964, Kim and Siccama 1986, Pritchett and Fisher 1987); 3) local fluctuations in climate not accounted for in available data (Daubenmire 1974, Haines and Cleveland 1981); 4) intraspecific genetic variability as a result of species adaptation to a particular site; and 5) interactions with other trees (Doyle 1983). Spatial variability is, of course, a function of scale. However, variability in forest ecosystems can be extreme, as conditions influencing tree growth can change substantially over a small area.

The objective of this study was to characterize temporal and spatial variability in tree growth response to climate for four major hardwood species that occur within the Tennessee Valley region: white oak (*Quercus alba*), chestnut oak (*Q. prinus*), northern red oak (*Q. rubra*), and yellow-poplar (*Liriodendron tulipifera*). Temporal variability was examined using a time-variant response function, the Kalman filter (Kalman 1960), to model the relationship between climatic variables and annual increment. The hypothesis that environmental factors could explain differences in growth response in terms of spatial variability was tested using corollary site information and multivariate statistics.

METHODS

In 1986 the Tennessee Valley Authority (TVA) initiated a study to assess factors contributing to forest condition with regard to the possible impact of atmospheric deposition. The research described here utilizes data collected in that study. The study was designed to determine growth trends in uneven-aged, mixed species, second-growth natural hardwood stands occurring in the Tennessee Valley region and was built on an existing framework of permanent forest inventory plots. Since the objectives of the study were to determine the effects of natural factors on growth, plots were selected to represent a variety of sites and stocking levels. Three study sites (figure 1) were selected based on geographic distribution, spatial distribution of plots, and number of remeasurements: 1) the Emory River Land

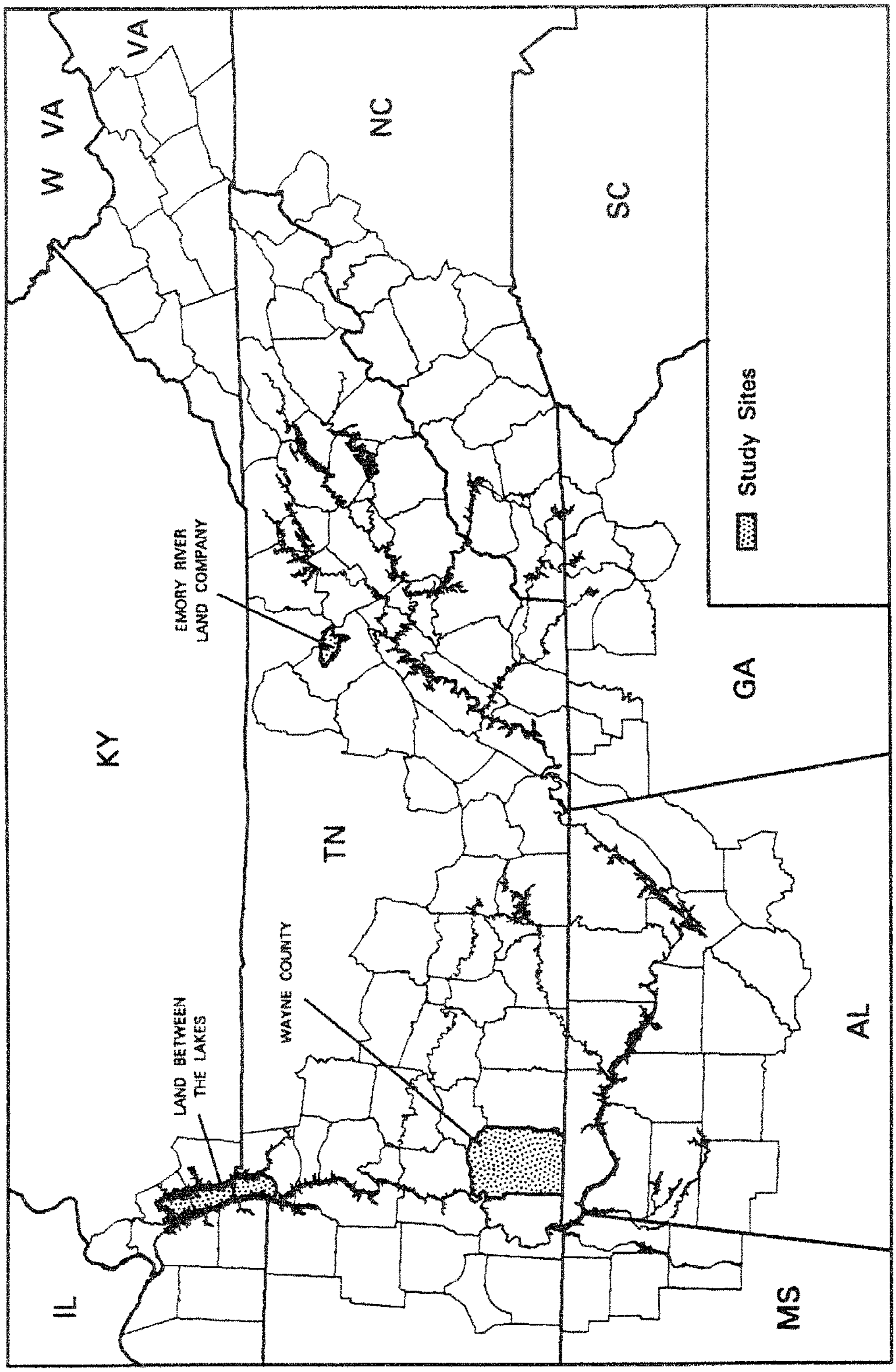

Figure 1. Map showing location of study sites.

Company, a 14,770 ha private land ownership located in Morgan County in northeast Tennessee; 2) "Land Between The Lakes" (LBL), a 68,797 ha national demonstration area managed by TVA and located in northwest Tennessee and southwest Kentucky; and, 3) Wayne County, located in southwest Tennessee, encompassing a total area of 191,903 ha. Together, these sites are considered representative of the forests of the Tennessee Valley region. Plots included in the study were selected from the total inventory based on forest type (white oak--black oak--northern red oak forest cover type and variants, Eyre 1980), size of trees (predominantly large sawtimber size trees -- greater than or equal to 28 cm dbh), and lack of substantial recent disturbance. A total of 267 0.08 ha plots were actually remeasured in the spring and summer of 1987 after preliminary screening.

Increment cores were collected from every living dominant and codominant tree on the plot (regardless of health). Core trees were not selected to represent site condition strata as the intention was to assess growth for a population and the relative importance of each of the many candidate site descriptors was unknown. Additional cores were collected from trees off the plot but in the immediate vicinity to increase core tree sample size. Ideally, five samples per species were collected but because of time constraints the total number of cored trees did not exceed 15 (unless more than 15 dominant and codominant trees occurred on the plot). Diameter at breast height (dbh) was recorded for all core trees to facilitate later age estimation. A prism count was made around every cored tree as a measure of individual competitive pressure. Notes regarding injury or other conditions affecting growth were also recorded for each core tree.

Tree cores were mounted according to the procedures described by Phipps (1985) and sorted by species. Crossdating was done by standard dendrochronological technique and was verified by a computer program COFECHA (Holmes 1985). Measurement of annual radial increment from individual trees was done using a Bannister incremental measuring device linked to an IBM-XT microcomputer. Tree-ring series from a total of 1843 trees were analyzed in this study (table 1). A wide range of ages was represented in each species sample with the youngest tree being a yellow-poplar at LBL with an estimated age of 34 years up to a total estimated age of 319 years for an individual chestnut oak at Emory River.

In complacent species growing in closed-canopy forests, the natural growth trend is often confounded with stand dynamics such as competition. This can complicate standardization of tree-ring series as it is difficult to determine what portion of the year-to-year variation in growth is due to climate and what portion is due to other factors. Therefore, in this study tree-ring series were standardized using first differences of natural logarithms, resulting in values that represent relative annual growth rates (Van Deusen 1990a). This technique avoids subjective decisions about what type of growth curve to use to remove the natural growth trend, or how stiff a spline is necessary to remove the low frequency variation due to endogenous disturbances while maintaining the high frequency variance associated with exogenous disturbances or climate.

Next, series from each species-site combination were scanned to identify a period for which there were measurements in common (table 2). A cluster analysis was run on standardized data for this common period to identify trees that had similar growth patterns. The

Table 1.--Number of trees and range of ages by site and species.

	White oaks	Chestnut oaks	Northern red oaks	Yellow-poplar
Emory River	229 trees (48-206 yrs.)	276 trees (49-319 yrs.)	143 trees (48-185 yrs.)	237 trees (34-161 yrs.)
LBL	384 trees (39-214 yrs.)	123 trees (51-267 yrs.)	15 trees (65-136 yrs.)	26 trees (34-130 yrs.)
Wayne County	193 trees (47-256 yrs.)	106 trees (42-157 yrs.)	62 trees (60-151 yrs.)	49 trees (42-127 yrs.)
Total trees:	806	505	220	312

Table 2.--Common measurement period used for clustering tree-ring data.

Site and Species	measurement period	number of years
Emory River white oak	1949 - 1983	35
LBL white oak	1952 - 1986	35
Wayne Co. white oak	1956 - 1986	31
Emory River chestnut oak	1951 - 1986	36
LBL chestnut oak	1947 - 1986	40
Wayne Co. chestnut oak	1955 - 1986	32
Emory River northern red oak	1956 - 1986	31
LBL northern red oak	1942 - 1986	45
Wayne Co. northern red oak	1948 - 1986	39
Emory River yellow-poplar	1968 - 1986	19
LBL yellow-poplar	1968 - 1986	19
Wayne County yellow-poplar	1960 - 1986	27

FASTCLUS procedure in SAS was run iteratively to group tree-ring series in clusters with high within-cluster correlation. FASTCLUS performs a disjoint cluster analysis on the basis of Euclidean distances computed from one or more variables, which in this case were individual measures of annual increment for the common measurement period. FASTCLUS utilizes *nearest centroid sorting* (SAS 1985). In this procedure, *n* clusters are specified and a set of *n* points known as *cluster seeds* are selected as a first guess of means of the clusters. Each observation is then assigned to the nearest cluster and the cluster seeds are updated according to these temporary cluster groupings. The process is repeated until no further changes occur in the clusters.

Initial sizes of clusters were determined based on the computer memory limitations of the software used in the following analyses; each cluster could have a maximum of 87 series with 91 years of data per series (to be used with climate data available from 1895-1986 minus one year for the differencing). After working with the white oak data, a criterion was established of cluster sizes having a maximum distance from seed to observation equal to or less than approximately 2.5. The initialization method used by FASTCLUS makes it sensitive to outliers; clusters that contained four or less series were discarded as outliers. The resulting number of clusters and associated statistics are given in table 3.

Table 3.--Cluster statistics for each species at the three study sites.

Species/ Site		Percent of Plots with Species	Number of Resulting Clusters	Mean Cluster Size (trees)	Coefficient of Variation for Cluster Size
White oaks					
	ER[1]	68	9	24.3	96%
	LBL	63	9	42.7	48%
	WC	75	6	32.2	67%
Chestnut oaks					
	ER	75	7	39.4	64%
	LBL	17	4	30.8	55%
	WC	42	3	35.3	71%
Northern red oaks					
	ER	58	2	71.5	13%
	LBL	6	2	7.5	47%
	WC	35	3	20.7	44%
Yellow-poplars					
	ER	48	4	59.3	41%
	LBL	6	1	23.0	-
	WC	28	4	12.3	52%

[1] ER = Emory River, LBL = Land Between the Lakes, and WC = Wayne County.

Climate data, consisting of monthly averages of temperature and monthly totals for precipitation, for the period 1895 through 1986 were made available from Oak Ridge National

Laboratory (ORNL) for state climatic divisions in which the study sites occurred. These data were also standardized using the first differences of the natural logarithm so that subsequent analyses would assess the relationship between rates of change in tree growth and rates of change in the climate data. Due to the large amount of data processed in this study, climate variables were selected for each cluster using multiple regression techniques rather than fitting a Kalman filter model one parameter at a time because the latter is a very time-intensive technique.

A stepwise regression was performed using annual values from a cluster mean chronology as the dependent variable with climatic variables for the current year through the end of the growing season and variables lagged one year as independent variables. To enter the model, variables had to be significant at the 0.15 level, and to remain in the model the parameter had to be significant at the 0.05 level. Coincident with fitting the regression, tolerance values were calculated for the variables used in each of the models to determine if there was a potential problem with collinearity. Tolerance values are defined as $1-R^2$ for a variable with respect to all other regressor variables in the model (SAS 1985). Collinearity did not appear to be a problem with the selected variables.

Once climate variables were selected from the stepwise regression, dendroclimatic modelling using the Kalman filter proceeded using the software package DYNACLIM (Van Deusen and Koretz 1988). The Kalman filter has been proposed to address problems in tree-ring analysis arising from temporal nonstationarity in the relationship between annual increment and climate (Van Deusen 1987, 1988; Visser 1986; Visser and Molenaar 1987, 1988). The formulation used here, described by Van Deusen and Koretz (1988), is a generalization of an ordinary regression equation that allows for dynamic parameters which are estimated using maximum likelihood. Models were specified using a non-varying intercept while regression coefficients for all climate variables were allowed to vary through time. DYNACLIM software produced smoothed parameter estimates for each of the climate variables for every year and their associated variances.

Verification of dendroclimatic models traditionally involves demonstration of time stability by comparing a model developed from data from one time period (known as the calibration period) with data from another (known as the verification period). By using the Kalman filter to develop dendroclimatic models we are allowing the relationship between climatic variables and tree growth to be non-stable through time because of the dynamic nature of the trees' growing environment. Therefore, other means of verification must be used. Van Deusen (1990b) suggests a number of statistical tests to assess the possibility of model misspecification or the absence of a systematic component in the resulting model. These include observation of the cumulative sum of the prediction errors and their confidence intervals according to Brown et al. (1975), assessment of recursive residuals using the modified Von Neumann ratio (Harvey 1981), and use of the C^* statistic calculated from the cumulative sum of prediction errors for time t (Harvey 1981). Each of these tests were applied to the models produced using DYNACLIM and no evidence was found of either model misspecification or missing components. Additionally, each tree-ring data set was tested for remaining autocorrelation up to a five-year lag. Although there was evidence of some autocorrelation, it occurred in amounts small enough (generally less than 0.10) to be considered unimportant. Verification was also provided through replication of results. Models developed for clusters within a species generally consisted of the same climatic parameters, although coefficient values differed. Once model testing was completed, a normal distribution for the variance among individual trees was assumed and ninety-five percent confidence intervals were calculated for each of the climate parameters to assess if these values were significantly different from zero.

Observed trends in parameter coefficients were tested using a *runs* test (Draper and Smith 1981) to determine if changes in coefficient values followed a pattern that might be associated with a change in sensitivity to climate or if they occurred randomly and therefore did not reflect true changes in sensitivity. The runs test was performed for individual clusters by calculating a mean coefficient over time for specific climate parameters that were common to a large proportion of the clusters over each site. Deviations from the mean were calculated on a year by year basis and assigned a value of "+" if they were greater than zero and "-" if less than zero. Changes in sign within a sequence of pluses and minuses denote the beginning of a new run. The Z statistic described in Draper and Smith (1981) was used to determine if the number of runs is an "extreme" arrangement as opposed to one which would occur randomly. A small number of runs (the minimum would be 2) indicates a trend in coefficient value, while a large number of runs indicates lack of a trend or a random pattern similar to white noise. The climate data, standardized and non-standardized, were also tested for trends using the runs test.

The last part of the analysis was to determine which environmental factors could be associated with different clusterings and might therefore affect differences in response to climatic fluctuations. This was accomplished using a discriminant analysis on a set of environmental factors that was associated with each individual increment core tree. Each tree was identified with a cluster number and the environmental factors (quantitative variables) were used to discriminate the trees into cluster groupings (classification variables).

Environmental factors consisted of variables associated with individual trees and site variables determined for each plot. Individual tree data consisted of the dbh of the core tree, an estimated age based on average annual increment and tree radius, and the prism count collected for each tree. Site information included descriptive variables such as elevation, slope percent, topographic classification, aspect, and fire and grazing codes. Information calculated from the inventory data included: 1) a productivity index calculated as average annual basal area increment for the plot; 2) relative frequency of each of the four core tree species; 3) an importance value for each of the core tree species calculated as that species' basal area per acre divided by total basal area per acre; 4) mean age of all cored trees; 5) basal area of mortality trees; 6) basal area of cut trees; and 7) percent of trees in the stand affected by the different injury classifications. Soils data consisted of horizon depth and texture for each plot. Horizons were aggregated into an A and E horizon and a B horizon -- deeper horizon data were not included. Soil textures were assigned a categorical name in the field. These data were ranked according to a gradient reflecting change in texture from fine to coarse and assigned a numerical value representative of this gradient. Presence of an argillic zone (Bt horizon) or a fragipan (Bx horizon) was indicated with a presence code of 1 or an absence code of 0 for a variable representing each type of horizon.

Canonical discriminant analysis was applied to the data using the SAS procedure CANDISC. This procedure is a dimension-reduction technique related to PCA and canonical correlation. CANDISC calculates linear combinations of the quantitative variables (known as *canonical variables*) that summarize between-class variations and that have the highest possible multiple correlation with the groups, then tests the hypothesis that resulting canonical correlations are zero in the population. A variable's importance in determining groupings can be evaluated by observing the value of the standardized canonical coefficients associated with it. In conjunction with CANDISC, univariate statistics in the form of one-way analyses of variance were calculated for each environmental variable.

A classificatory discriminant analysis was also performed on the data using the SAS procedure DISCRIM. This procedure generates a linear discriminant function for each group of data as well as probabilities of misclassification (error rates). This provided an evaluation of how well the environmental factors explained the cluster groupings of tree growth.

RESULTS

Clustering of tree-ring series by species and sites resulted in a total of 54 groups. All clusters incorporated trees of different ages and sizes. Series from trees in close proximity to one another sometimes grouped in the same cluster but often did not. Cluster groupings were observed on a plot-by-plot basis to determine the degree of spatial heterogeneity that occurred for each species-site combination. A count was made of the number of plots with more than one sample tree on which all of the trees of a species were grouped into a single cluster. This revealed a great deal of spatial variability with a range of values showing plot homogeneity on only 2% of the plots with chestnut oak at Emory River, up to a high of 39% for northern red oak at Emory River (table 4). Plots with many cluster groupings were compared to those with a single cluster grouping to see if any differences were apparent to explain the degree of heterogeneity. Examination of soils diagrams made in the field showed that the number of cluster groupings could not be explained by differences in soils. Disturbance history accounts were also compared. Plots that were very homogeneous in tree growth response included histories that indicated no apparent disturbance, disturbance by Timber Stand Improvement (TSI), insects, disease, fire and widespread adjacent mortality. Spatial homogeneity did appear to relate to the percent of the stand that was occupied by the individual species. Plots that consisted of only one species generally had core trees that clustered together, while plots with a number of species often exhibited heterogeneity in growth response for each species.

For white oaks, June temperature was overall the most important variable selected in the stepwise regression, exhibiting a negative relationship with growth. Later variables that entered the climate models differed somewhat by site -- at Emory River, generally past August rainfall (a positive relationship) was the next most important variable, while at LBL past December rain (a positive relationship) usually entered the model second, and at Wayne County, each cluster had a different variable entering in the second place position.

Table 4.--Percent of plots in which all trees of one species clustered into the same group.

	White oaks	Chestnut oaks	Northern red oaks	Yellow-poplar
Emory River	5%	2%	39%	24%
LBL	29%	29%	14%	-
Wayne County	24%	16%	33%	18%

June temperature was also the most important variable for chestnut oak, although at Emory River, May rain was a close competitor for first place. June rain was also important, especially at LBL. Northern red oaks behaved similarly, with June temperature the unanimous choice for first entry. Past August rain was important at Emory River, showing similar associations as the white oaks. Summer rains were important to Emory River yellow-poplar, especially June rain. No other clear relationships were apparent for a species or site.

Kalman filter estimates of parameter values for each of the 54 tree-ring clusters indicated some interesting differences and similarities between species and overall time trends in the climate/growth relationship. Changes in parameter coefficients over time were compared with graphs of monthly climatic data over time to determine if changes were coincident with trends in climate. No associations were determined. Additionally, the runs test indicated that the number of runs was not significantly different than random (i.e. no trends) for both standardized and non-standardized climate data. For the most part, each cluster model revealed that through time, these trees become less sensitive (i.e. coefficient values for these parameters approached zero over time) to climate variables such as summer temperature and rainfall.

Trends in coefficient values for June temperature and past August rain were assessed for all clusters which incorporated these parameters in the dendroclimatic model. These variables were not always the most significant for each cluster, however, they were the most prevalent overall and therefore were used to gain insight into the general relationship between climate and tree growth. Figures 2-7 show the percentage of clusters that had a coefficient that was significantly different from zero by year. This graphical display provides an overview of what appears to be a general trend towards decreasing sensitivity to climate. In each graph except for past August rain in Wayne County (figure 7), there is first a trend towards increasing significance in coefficient values, followed by a drop in the percent of clusters which included values that were significantly different from zero. The early low values reflect relatively wide confidence intervals for each coefficient value resulting from a large amount of variation between individuals and small sample sizes for older trees. Later decreases in the percentages of significant values are associated with coefficient values that approach zero over time, reflecting a decreasing sensitivity to these climate variables for most trees.

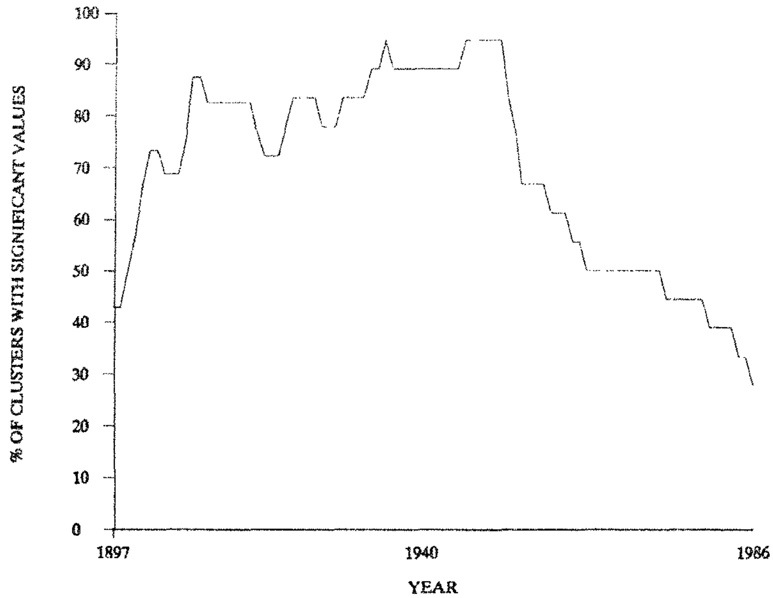

Figure 2. Percent of Emory River clusters with June temperature coefficients that are significantly different than zero by year.

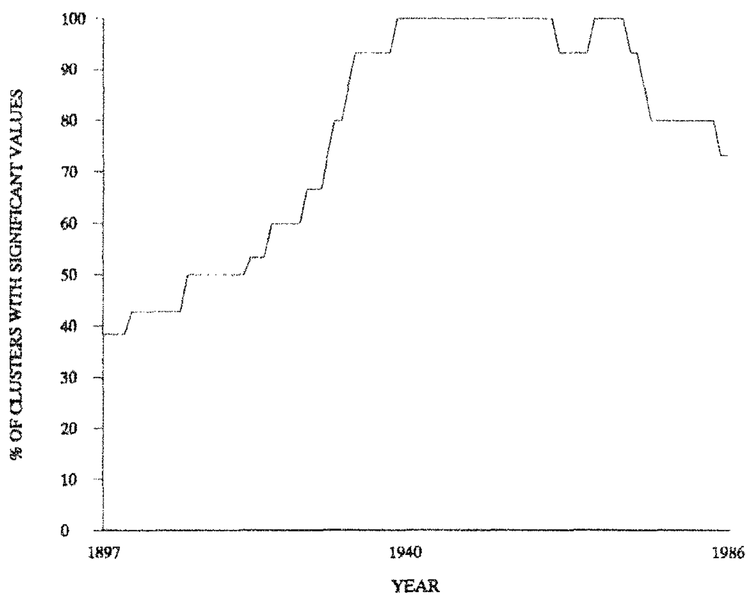

Figure 3. Percent of Emory River clusters with past August rain coefficients that are significantly different than zero by year.

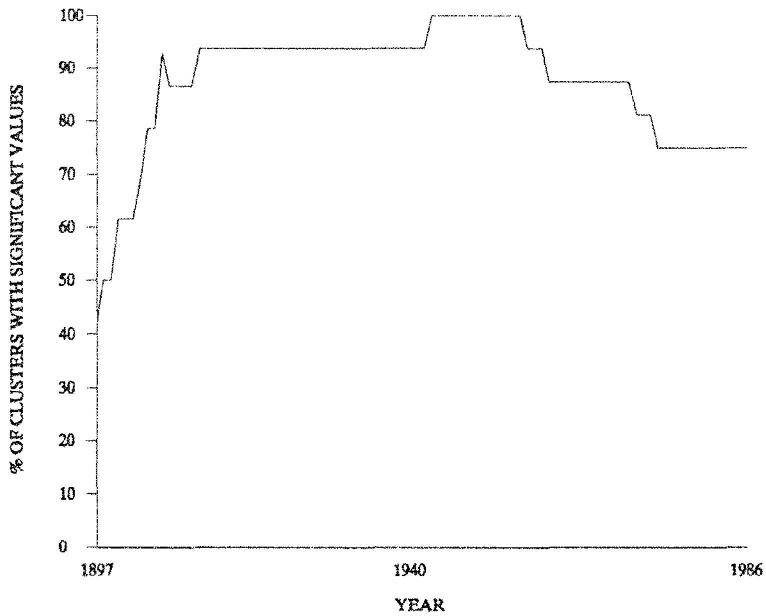

Figure 4. Percent of Land Between the Lakes clusters with June temperature coefficients that are significantly different than zero by year.

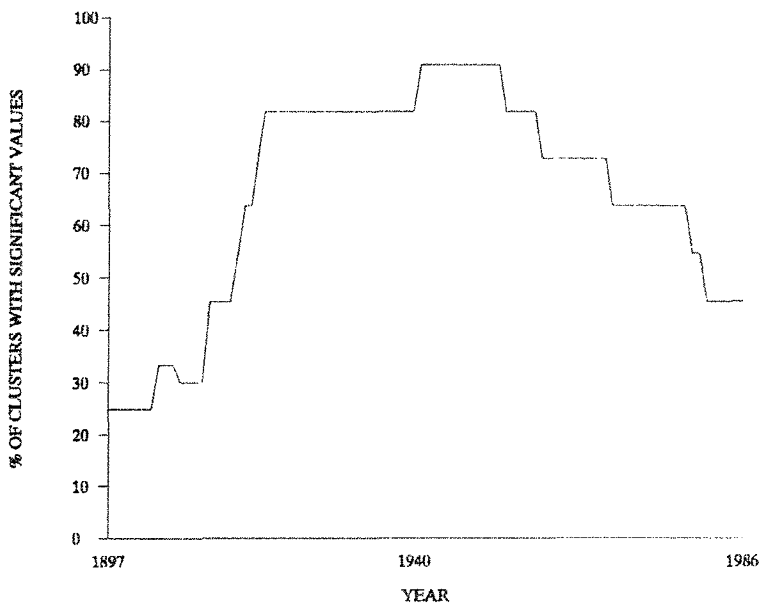

Figure 5. Percent of Land Between the Lakes clusters with past August rain coefficients that are significantly different than zero by year.

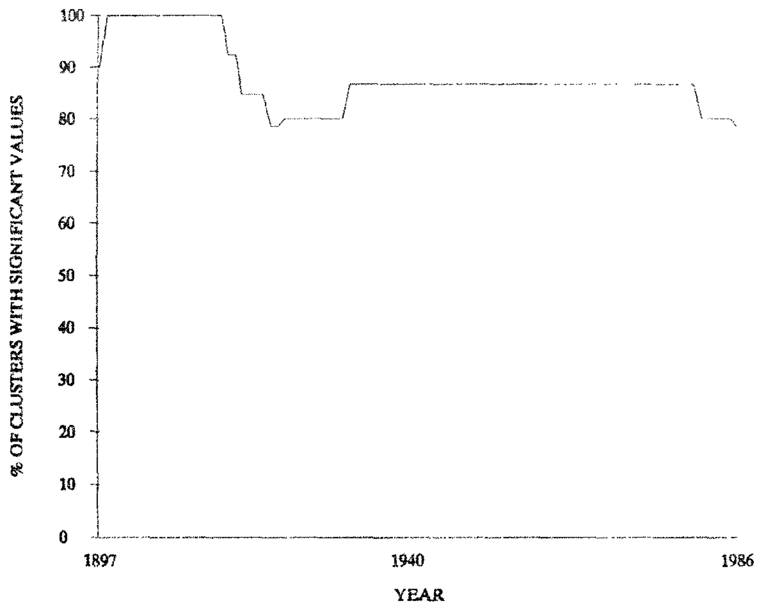

Figure 6. Percent of Wayne County clusters with June temperature coefficients that are significantly different than zero by year.

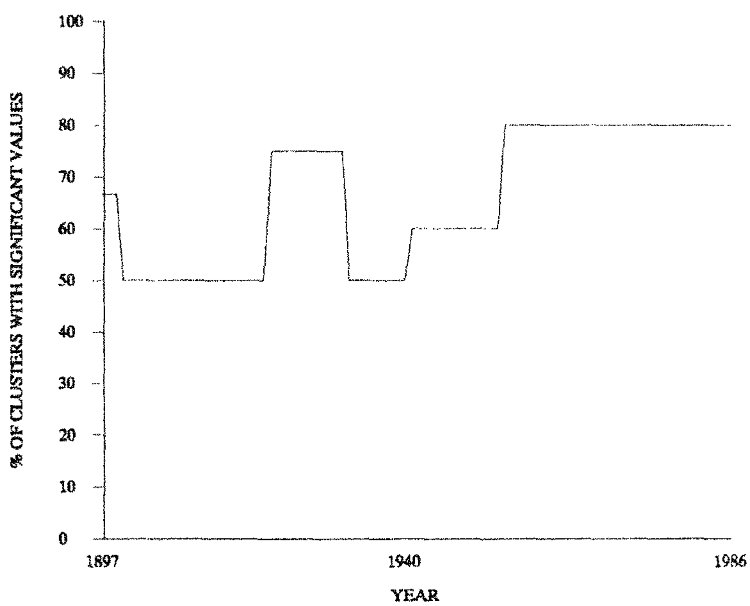

Figure 7. Percent of Wayne County clusters with past August rain coefficients that are significantly different than zero by year.

A runs test was done on June temperature and past August rain for those clusters in which these variables contributed to the explanation of variation in growth. Decreased sensitivity to June temperature is indicated by a change towards less negative coefficients (denoted by a plus sign), while a change towards more negative coefficients (denoted by a minus sign) indicates increased sensitivity. At Emory River, all clusters that exhibit temporal variation in coefficient value showed a trend towards decreasing sensitivity to June temperature that was significantly different than random changes in the relationship (figure 8). One yellow-poplar cluster (number 1) showed a reversal in this trend, towards increased sensitivity. Similar trends were observed for all species at LBL, except where there was no temporal variability in June temperature coefficients. At Wayne County, the pattern was more confused. All white oaks again showed a trend towards decreased sensitivity. Two clusters, chestnut oak number 1 and northern red oak number 1, showed a reversed trend, towards increased sensitivity.

Changes in sensitivity to past August rainfall were not as apparent, although general patterns did exist (figure 9). Decreased sensitivity to past August rain was signified by a less positive coefficient (denoted by a minus). A more positive coefficient (denoted by a plus sign) indicated increased sensitivity. No temporal variation was represented by zeros. Of the 16 clusters at Emory River, four showed no temporal variation, five showed a significant trend towards decreased sensitivity, and seven showed a trend towards increased sensitivity. At LBL, all clusters except white oak number 9 showed a significant trend towards decreased sensitivity. In white oak number 5 there was a recent change towards increased sensitivity. Of the five clusters incorporating past August rain at Wayne County, two showed no temporal variability, and the remaining three showed increased sensitivity to this variable.

Analyses of variance provided little insight into which environmental factors were important in differentiating growth responses to climatic variables. Although a number of environmental variables were significant ($P<0.01$) in explaining differences among groupings, the amount of variation explained by individual factors was very low (table 5). This result was expected because of the nature of the data and its collection. The data base consisting of tree-ring series from 1843 individual trees selected from 267 sites located over a large geographic area was created to represent the forests of the Tennessee Valley and therefore incorporates a wide variety of site conditions and potential stresses. Trees were not selected to represent a specific suite of environmental variables, but rather to represent the population of each of these species within the region.

Discriminant analysis based on environmental variables collected in the study was generally successful in reclassifying tree-ring clusters. Total error count estimates ranged from 0% for northern red oaks at LBL, up to 75% for chestnut oaks at Emory River (table 6). Overall, site statistics outperformed individual tree statistics in discriminatory power, and when analyzed as multivariate data, presence and predominance of competing species was the most important factor influencing tree-ring groupings (table 7). Other factors that commonly had high canonical coefficient values included variables related to soil moisture conditions such as soil depths and textures, topographic position, and aspect; and variables related to changes in stand density, including current basal area, and basal areas of cut and mortality trees.

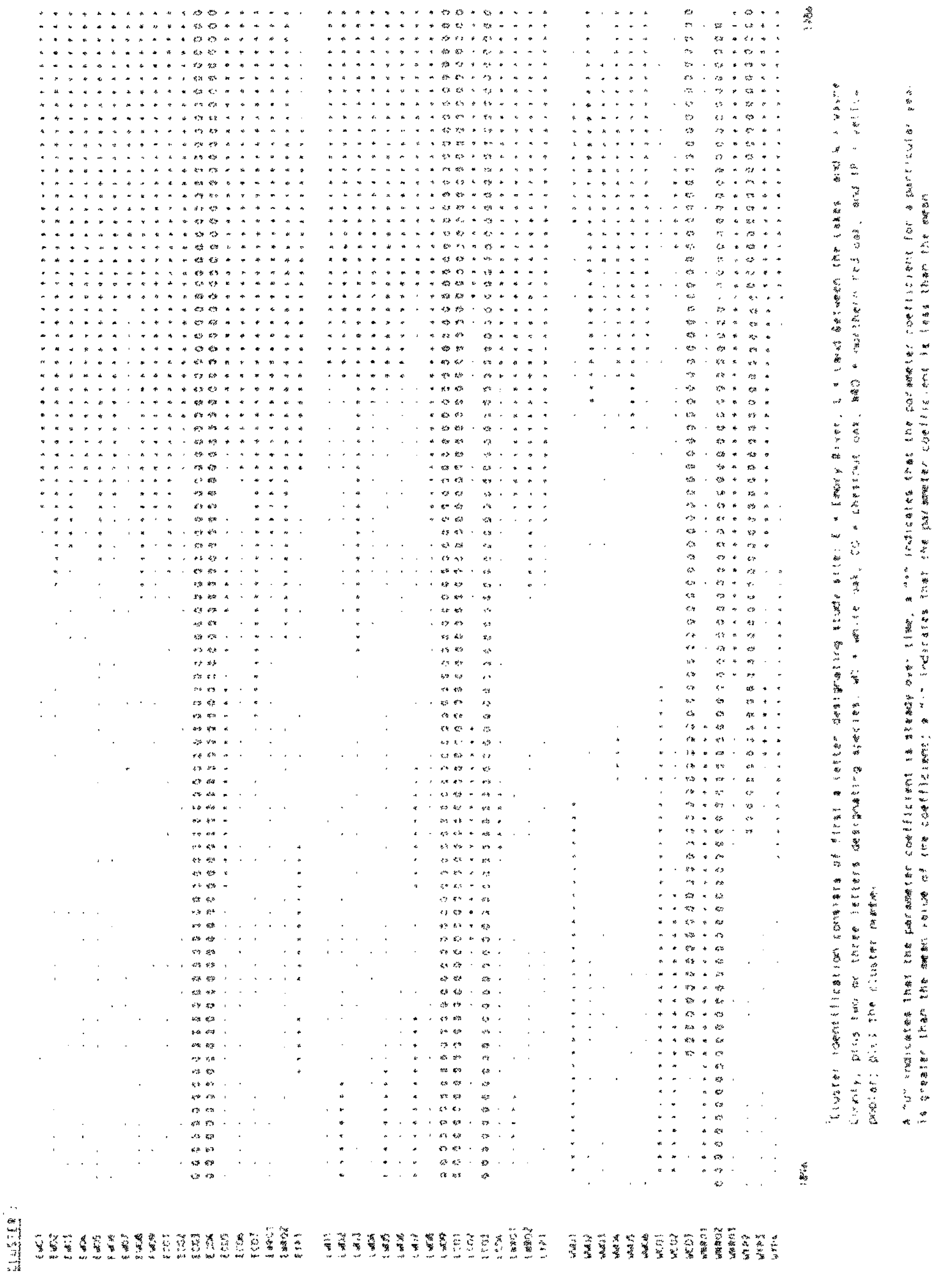

Figure 8. Runs in the time sequence of deviations from the mean for June temperature coefficients.

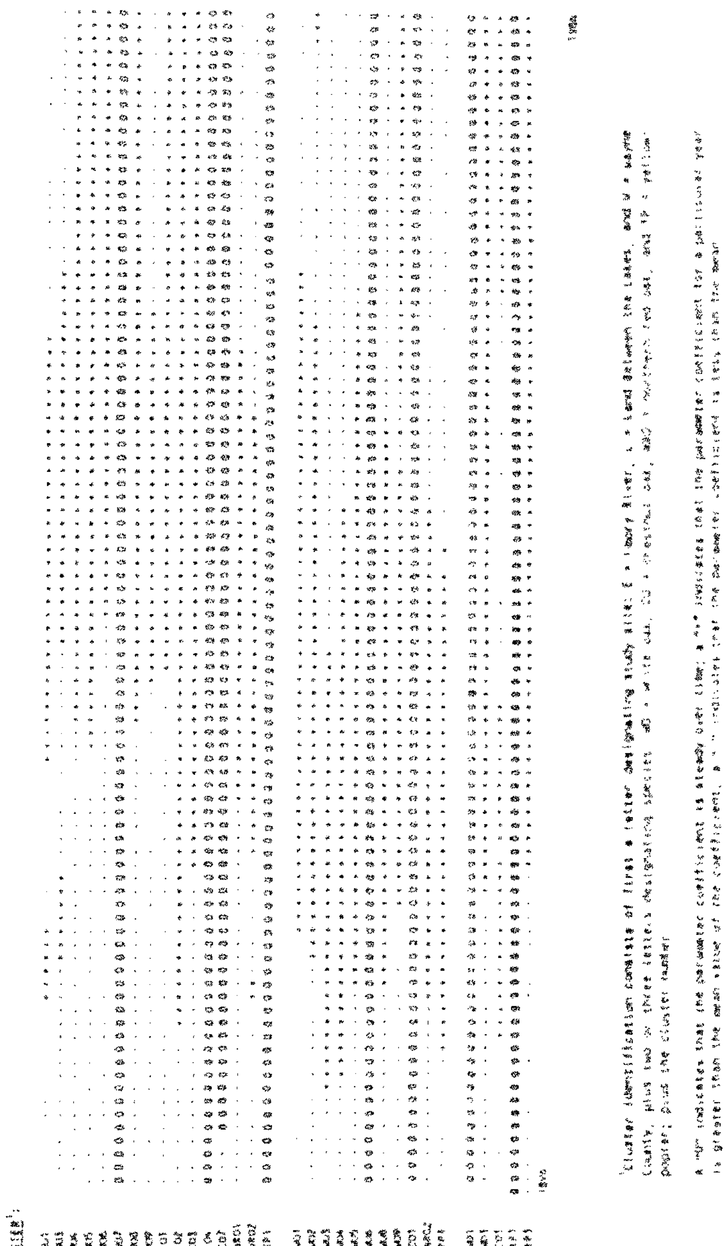

Figure 9. Runs in the time sequence of deviations from the mean for past August rain coefficients.

Table 5.--Results of one-way analyses of variance - average R^2s weighted by variance for environmental variables, by site and species.

Site/Species	R^2
ERWO[1]	0.10
LBLWO	0.16
WCWO	0.16
ERCO	0.01
LBLCO	0.08
WCCO	0.12
ERNRO	0.15
LBLNRO	0.01
WCNRO	0.11
ERYP	0.07
LBLYP[2]	-
WCYP	0.04

[1]Site/Species identification consists of a combination of letters designating site: ER = Emory River, LBL = Land Between the Lakes, WC = Wayne County; followed by letters designating species: WO = white oak, CO = chestnut oak, NRO = northern red oak, and YP = yellow-poplar.
[2]LBL had only one grouping of yellow-poplar series.

Individual tree age was only important for Wayne County yellow-poplar, indicating that variability in growth response was not strongly influenced by changes in tree physiology.

DISCUSSION AND CONCLUSIONS

The results of this study indicate that, for the 4 hardwood species studied within the Tennessee Valley region, relationships between climatic variables and tree growth change over time. Maximum sensitivity to monthly values of temperature and precipitation did not coincide with extreme values of these variables. Instead, maximum sensitivity generally occurred at the beginning of the time series and decreased over time. Patterns of change in sensitivity (parameter coefficient values) were significantly different ($P<0.001$) from random indicating a trend in the relationship. However, statistical tests indicated only random variation in the climatic data. This implies that tree growth sensitivity to climate is not merely a function of climate, or that other factors work to modify the influence of climate. In natural, mixed-species hardwood stands in the Tennessee Valley, these factors are apparently dynamic.

Table 6.--Error count estimates (percent) for linear discriminant functions on non-transformed data.

Species/Site	Cluster # 1	2	3	4	5	6	7	8	9	Total
White oaks										
ER[1]	50	25	29	41	60	50	0	26	33	42
LBL	15	56	11	44	33	35	53	32	28	36
WC	23	26	30	26	40	24				27
Chestnut oaks										
ER	54	63	60	52	63	53	75			57
LBL	50	47	11	23						28
WC	7	27	22							14
Northern red oaks										
ER	21	20								21
LBL	0	0								0
WC	6	8	22							10
Yellow-poplars										
ER	25	32	37	32						30
LBL	-									-
WC	0	11	43	27						20

[1]ER = Emory River; LBL = Land Between the Lakes; WC = Wayne County.

Table 7.--Environmental factors determined important in producing differences in tree growth response to climate from canonical discriminant analysis, by site and species.

Site/Species	Important Environmental Factors
ERWO[1]	Relative frequency and importance values for core tree species, presence of a fragipan
LBLWO	Relative frequency and importance values for core tree species, soil texture
WCWO	Relative frequency and importance values for core tree species, current basal area, elevation
ERCO	Relative frequency and importance values for core tree species, topographic position, presence of an argillic horizon
LBLCO	Relative frequency and importance values for core tree species, aspect
WCCO	Relative frequency and importance values for core tree species, aspect, topographic position, presence of insect damage
ERNRO	Relative frequency and importance values for core tree species, elevation, soil depth and texture
LBLNRO	Current basal area, size distribution of trees, basal area of mortality trees, slope, topographic position, aspect
WCNRO	Relative frequency and importance values for core tree species, grazing damage, aspect
ERYP	Relative frequency and importance values for core tree species, aspect, basal area of mortality trees, soil depth and texture
WCYP	Relative frequency and importance values for core tree species, slope, current basal area, basal area of cut trees, basal area of mortality trees, individual tree age

[1]Site/Species identification consists of a combination of letters designating site: ER = Emory River, LBL = Land Between the Lakes, WC = Wayne County; followed by letters designating species: WO = white oak, CO = chestnut oak, NRO = northern red oak, and YP = yellow-poplar.

Factors that could modify climatic effects include those related to changes that occur within the individual or within the forest stand. Individual or physiological changes occurring within a single tree should be highly correlated with age or size. However, except for yellow-poplar at Wayne County, both of these variables lacked statistical significance in differentiating growth response patterns when analyzed as either univariate or multivariate data. However, factors representing changes in stand density were important for some clusters. Changes that occur within the forest stand may affect attributes associated with climate such as moisture availability which would appear as a change in sensitivity to climate in this analysis. It is well known that climatic extremes are buffered within a fully-developed forest stand through shading and the wind-breaking effect of stand structure (Daubenmire 1974, Haines and Cleveland 1981). Site conditions have also been shown to improve over time with stand development (Whittaker and Woodwell 1972, Carmean et al. 1976). The trend towards decreased growth sensitivity to climatic variables over time is synchronous with a period of increased forest protection and improved forest management within the Tennessee Valley. In general, this has resulted in a transition from poorly-stocked, cutover stands to more productive forests with increased stocking levels. Thus, it appears that decreases in individual tree sensitivity to climate are associated with stand development as the changes in stand structure and site quality buffer climatic variation.

Spatial variation in tree growth response to climate is more difficult to characterize. Univariate statistical analyses (one-way analyses of variance) were ineffective in identifying environmental factors important in producing the different patterns of growth response identified through cluster analysis. However, multivariate analyses of environmental factors were, in most cases, very effective in discriminating differences in patterns of annual increment. Unfortunately, these results are more difficult to interpret, as they indicate that interactions between environmental factors can significantly alter a tree's growth response.

Standardized coefficient values for canonical components indicate the relative importance of each environmental factor as it impacts the relationship between climate and growth. Overall, the most important factors were relative frequency and importance values for the predominant species. This indicates that differences in size and species composition of neighboring trees is associated with differences in pattern of growth response. This could reflect competitive interactions, signifying that trees behave differently according to the company they are in, or it may denote a difference in site quality or some type of ecological gradient. Ermich et al. (1976) suggested that homogeneity of tree growth patterns was related to site quality. Their premise was that low site quality results in increased susceptibility to additional stresses that increase the variability in annual increment among individuals. The results of the current study indicate that spatial heterogeneity increases as the predominance of a species on a site decreases, a fact that may be due to site quality, competitive interactions, or both.

Factors typically associated with soil moisture conditions were also identified as relatively important in producing differences in growth. As expected, there were identifiable differences in growth pattern between mesic and xeric sites. Trees on drier sites generally appeared more sensitive to climate (i.e. coefficient values were of greater magnitude). However, interactions with other, often more subtle, environmental factors exhibited the potential to alter characteristic growth patterns. For example, insect infestation on a mesic site was observed to increase tree sensitivity to climate producing a response more typical of a tree located at a drier site.

The literature on forest tree growth indicates that there is a great deal of both temporal and spatial variability in tree growth response to climate, and that reasons for the variability are not obvious. The results of this study were similar to those reported in the literature. Temporal variability in growth response to climate can be characterized as a trend towards decreased sensitivity to climate that apparently occurs primarily as a result of stand development rather than as a function of changes in individual trees. Spatial variability was profound, occurring in part as a result of changes in site conditions and potentially as a function of competitive interactions among individual trees of different species. Environmental factors were generally useful in explaining similarities in growth response to climate among individual trees, as long as interactions between factors were incorporated into the analysis. Use of additional site variables, information specific to individual trees, and more detailed climate data might provide a better understanding of what response to climate might be expected under various combinations of environmental factors.

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