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TREE-RING CHARACTERISTICS ALONG A VEGETATION GRADIENT IN NORTHERN ARIZONA

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Abstract. Tree-ring samples of *Pseudotsuga menziesii* (Mirb.) Franco, *Pinus ponderosa* Laws., and *Pinus edulis* Engelm. for 1860 through 1962 were obtained from sites along a vegetational gradient, ranging from forest interior sites to semiarid lower forest border sites. Samples were analyzed using a stratified nested plot design. Near the lower forest border tree rings are narrowest, the variability in the relative ring-width response from year to year is greatest, and the variance in common or the correlation between radii and between trees is highest. This variability is more highly related to climatic fluctuations than the variability in forest interior trees and may be attributed to longer and more frequent periods during which water stress is limiting to physiological processes in the trees. Hence, at the arid forest border tree-ring chronologies contain the most consistent, but variable, growth responses and provide the best record of climatic fluctuations. The semiarid lower forest border trees exhibit a high frequency of partial growth layers. Chronologies from the forest interior exhibit very few partial growth layers. Crossdating between both types of sites and among many individuals of different species makes absolute dating not only possible but exceedingly reliable. Such tree-ring analyses may have considerable application to the evaluation of ecological forest gradients.

INTRODUCTION

Dendrochronology, the study of tree rings, has found wide application as a dating technique (Banister 1963, McGinnies 1963) and is a valuable tool for reconstructing climatic variations of the past (Schulman 1953, 1956, Fritts 1962*b*, 1963*a*, 1965). Certain techniques of dendrochronology which were developed by Douglass (1919, 1928) and his colleagues, Schulman (1941, 1956) and Glock (1937), are used to maximize and insure a high degree of relationship among tree-ring chronologies in different geographical areas and between tree-ring chronologies and climatic variation. A basic proposition of dendrochronology in the arid southwest is that the most variable chronologies, which exhibit the best crossdating with one another and which relate most closely to the variability in the year-to-year climatic regime, are obtained by using tree-ring series from marginal semiarid sites near the lower forest border (Schulman 1941). The purpose of this study is to test this proposition by quantitatively evaluating the tree-ring characteristics along a vegetational gradient from relatively moist forest interior sites to the semiarid and lower forest border in the San Francisco Mountains of Arizona. Such an analy-

sis also provides an evaluation of the tree-ring method as a tool for examining ecological gradients.

METHODS

The study area

The forest vegetation of the San Francisco Mountains of Arizona (Fig. 1) which was originally studied by Merriam (1890) represents four major forest types or life zones grading from the high elevation and moist forests of Engelmann spruce (*Picea engelmannii* Parry) and Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco), Merriam's Hudsonian and Canadian zones, to the lower elevation and more arid forests dominated by ponderosa pine (*Pinus ponderosa* Laws.) and by pinyon pine (*P. edulis* Engelm.) and Utah juniper (*Juniperus osteosperma* (Torr.) Little), Merriam's Transition and Upper Sonoran zones. The lower two forest types occur as a vegetation gradient from dense ponderosa pine forests near the base of Humphrey's Peak to the open ponderosa pine and pinyon pine and juniper forests which occur at greater distances from the main mountain mass.

Colton (1958) analyzed the precipitation regimes in the area for the period 1932-56. Precipi-

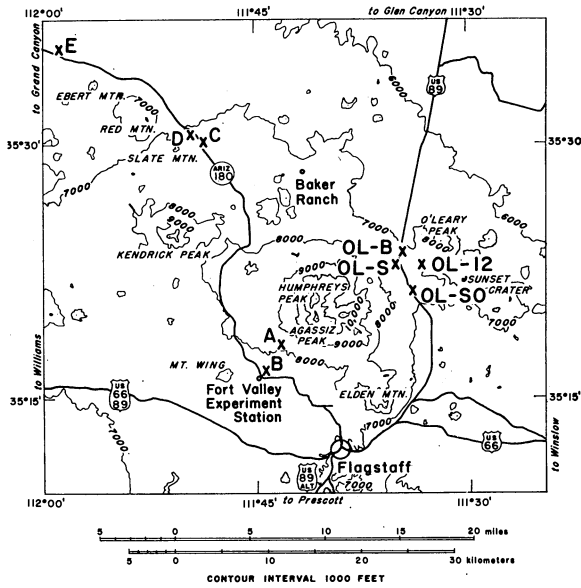


FIG. 1. Topographic map of the study area, San Francisco Mountains, Arizona. Douglas-fir sampled at A. Ponderosa pine sampled at A, B, C, and D. Pinyon pine sampled at D and E. Stations OL are reported by Glock, Germann, and Agerter (1963).

tation from five stations within the ponderosa pine forest type ranged from an annual average of 15.77 inches at Baker Ranch, which is 3 miles north of the San Francisco Peaks, to 22.55 inches at Fort Valley, which is at the base and southwest of the Peaks (Fig. 1). Annual precipitation within the pinyon-juniper forest ranged from 11.40 to 12.48 inches. The lowest and highest amounts of annual precipitation reported by Colton were 10.54 and 31.67 inches in the ponderosa pine forest and 4.66 and 23.15 inches in the pinyon pine-juniper forest.

There were greater differences in winter than in summer precipitation at Colton's stations. Precipitation during December through February at Fort Valley averaged 6.92 inches but at Baker Ranch it averaged 3.22 inches. Precipitation during June through August was 7.09 inches at Fort Valley and 5.86 inches at Baker Ranch. Winter

precipitation in the pinyon-juniper forest ranged from 1.99 to 2.58 inches, and summer precipitation ranged from 3.78 to 5.19 inches.

Collection of study materials

Five areas, designated A through E in Fig. 1, were selected to represent the vegetational gradient. Area A is located at the lower limits of Douglas-fir, and area B represents a mesic forest interior site for ponderosa pine found around the moist Fort Valley weather station. Area C includes semiarid sites comparable to the Baker Ranch weather station. Area D is located at the border between the ponderosa pine and pinyon pine and juniper forests, and Area E represents a relatively semiarid pinyon pine-juniper site.

Seven stands were sampled from the five areas (Table I). Five mature trees were chosen in each stand, and four increment cores were extracted from each tree at breast height along cardinal directions. The trees were selected from a small homogeneous group to minimize variability arising from diverse soil and topographic factors. The only restriction on tree selection was that the ring patterns must exhibit sufficient variability to be dated by means of the Flagstaff master chronology. Such restriction eliminated a few sampled trees which possessed extremely uniform, undatable ring patterns or showed effects of catastrophic influence, such as lightning strike or pronounced release or suppression.

Area A is on the southwestern slope of Humphrey's Peak at an elevation of 8,500 feet. Two stands were sampled, one a Douglas-fir stand on an east-facing slope, and the other a ponderosa pine stand on a southeast-facing slope. Five ponderosa pines were sampled in area B at an elevation of 7,500 feet and within several hundred yards of the Fort Valley weather station. Cores from areas A and B were collected in March 1962.

Area C is located along State Highway 180 at an elevation of 7,300 feet, 20 miles north of the Fort Valley Experiment Station and 7 miles northwest of Baker Ranch. Five ponderosa pines along an arroyo were sampled. Numerous ponderosa

TABLE I. Characteristics associated with trees from each of the sampled stands

Area	Stand	Altitude (feet)	Slope (degrees)	Exposures	Tree height (feet)	Mean dbh (inches)	Average length clear bole (feet)
A	Douglas-fir	8,500	6-30	NE - ENE	80-90	34.2	10
A	Ponderosa pine	8,500	10-25	E - SSE	75-85	24.6	18
B	Ponderosa pine	7,500	3-10	E - S	65-80	26.8	17
C	Ponderosa pine	7,300	1-12	SW - W	65-75	32.9	17
D	Ponderosa pine	7,300	5-10	N - NNE	50-55	25.0	19
D	Pinyon pine	7,300	0-5	S	20-25	20.4	<1
E	Pinyon pine	6,360	0-2	—	20	15.0	2

pine saplings were noted in the area along with occasional seedlings of pinyon pine and juniper. Area D is at approximately the same elevation and three-tenths of a mile farther northwest of area C along State Highway 180. Samples were taken from five ponderosa pines in a stand which is restricted to the north-facing slope and an arroyo, and from five pinyon pines in a well-developed pinyon-juniper stand on a south-facing slope. Area E, at an elevation of 6,360 feet, is located 10 miles farther northwest of area D along State Highway 180. Five pinyon pines in an open pinyon-juniper stand were sampled. Cores from areas C, D, and E were collected in October 1962.

The point-quarter method (Curtis 1956) was used to measure stand characteristics at each site. The measurements were limited to trees of 6 inches dbh or greater, and 24-40 trees were included in each sample, depending on the size of the stand. Dominance was calculated from basal area for each species.

Preparation and treatment of study materials

All cores were mounted, surfaced, and cross-dated both among themselves and with the Flagstaff master chronology. The ring widths for the years 1860 to 1962 were measured parallel to the xylem rays. The numbers of both locally absent and intra-annual rings were tabulated for each core.

The measurements of ring widths were processed by computer techniques. In this procedure ring widths are converted to standardized indices which represent relative departures from a growth curve mathematically fitted to each ring-width series by least squares technique (Fritts 1963*b*). These standardized indices were used to calculate all parameters in this analysis except for mean ring width, percentage of absent rings, and percentage of intra-annual rings. The indices from each of the four cores were averaged to construct the chronology for individual trees, and these indices were further averaged to obtain the chronology for each group of five trees.

Mean sensitivity is a measure of the relative change in ring index from year to year and is calculated as the absolute difference between adjacent indices divided by the mean of the two indices. The individual yearly mean sensitivity values are averaged to obtain the mean of the entire series. Serial correlation, or autocorrelation (Quenouille 1952), measures what Douglas (1919) called the conservation factor, or the tendency for larger than average rings to be followed by large rings and smaller than average rings to be followed by small rings. Standard deviation, which includes components measured by both

mean sensitivity and serial correlation, is calculated in the usual manner (Snedecor 1956). Inter-correlation is the mean of all possible linear correlations between tree chronologies within a group of trees. Intra-correlation is calculated as the mean of all possible correlations among the different radii within the same trees. The percentage variation is calculated from a variance analysis described by Snedecor (1956) and Fritts (1963*b*).

RESULTS AND DISCUSSION

Dominance values (basal area per acre) for each sampled stand are plotted as a histogram in Fig. 2. Where more than one species occurs in

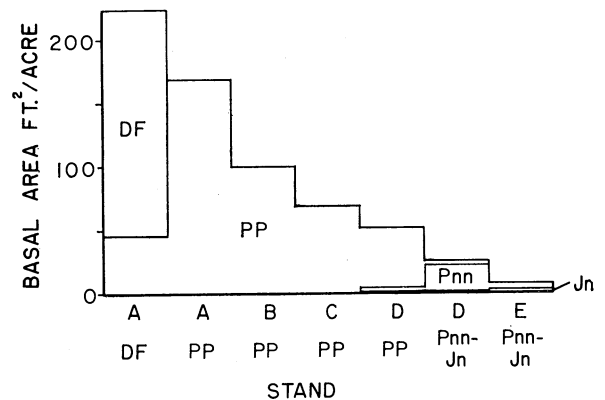


FIG. 2. Dominance (basal area per acre) for sampled stands in the San Francisco Mountains. Top line is total stand dominance and vertical distance is relative to values of individual species. DF = Douglas-fir, PP = ponderosa pine, Pnn = pinyon pine, and Jn = Utah juniper.

the sample the top line represents the total stand dominance, and the vertical distance is partitioned relative to the dominance value for each species in that sample. The decrease in stand dominance along the sampled gradient shows the vegetational changes from a forest interior or mesic environment to the semiarid forest border. This decrease in dominance reflects the decrease in precipitation which is especially marked during the winter months, with increasing distance from the San Francisco peaks. Temperature probably also increases with a corresponding increase in evapotranspiration deficits along the gradient toward the lower forest border.

The yearly mean indices for the chronology of each stand are plotted in Fig. 3, and the tree-ring parameters associated with each chronology are presented in Table II. The data are arranged in order of decreasing stand dominance and of increasing distance from the San Francisco peaks (Fig. 1). Although areas A through E form a single vegetation and environmental gradient from the lower forest border of the Douglas-fir forest

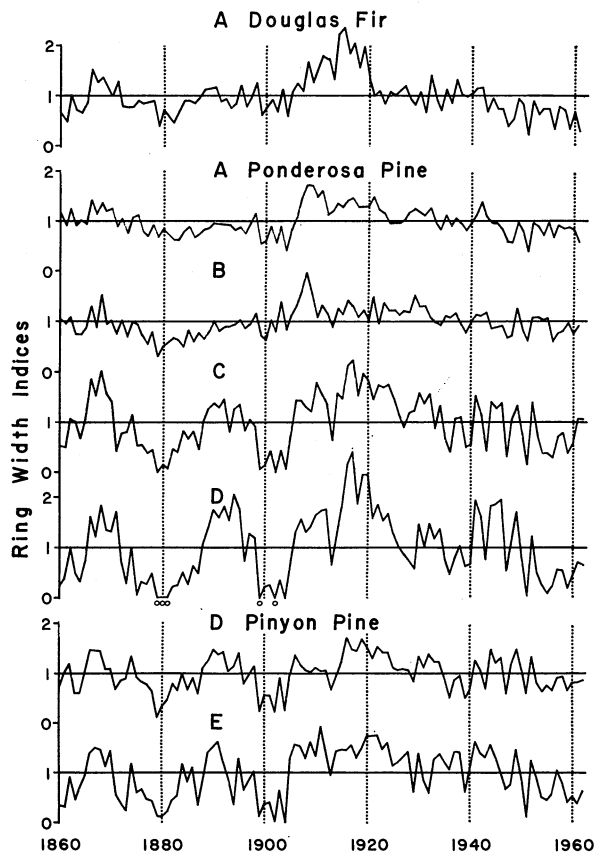


FIG. 3. Tree-ring chronologies for the seven samples arranged in order along the vegetational gradient from the forest interior to the forest border.

to the lower border of the pinyon pine-juniper forest, it is more meaningful to consider the results in terms of the ecological amplitudes and distributions of the individual species. Each species reaches its lower forest border in different areas along this gradient. The Douglas-fir stand at A, the ponderosa pine stand at D, and the pinyon pine stand at E are all growing near the lower forest border for that particular species.

In general, the average ring widths decrease toward the lower forest border of a species (Table II). Pinyon pine appears to be an exception. However, the stem diameters and tree heights for the sampled pinyon pine at area E (Table I) are significantly less than for pinyon pine at area D. The wide rings and smaller size indicate that the forest border trees at E are considerably younger than the trees in the other stand, so that ring-width comparisons reflect differences in age as well as site.

Locally absent rings do not occur often in the cores from the trees in forest interior sites. But in areas C and D, which are separated by a distance of only three-tenths of a mile, the frequency of absent rings in ponderosa pine increases from 4.0% to 7.8%. Several ponderosa pines which were sampled beyond area D could not be dated with certainty without more extensive sampling because the frequencies of absent rings were too high. The index values of zero for ponderosa pine at area D during the 3 years 1879-81 indicate the severity of climatic conditions during this period (Fig. 3). None of the 20 cores sampled from the stand exhibited a ring during these years. Yet in most of the adjacent pinyon pines, as well as in the other ponderosa pine samples, the years 1879-81 are represented by clearly defined, though small, annual rings. Glock, Germann, and Agerter (1963) report a similar high frequency of absent rings for the same period throughout the stem of a single pine (OL-B, Fig. 1) near the semiarid lower forest border. A much lower frequency of absent rings is reported for two other trees growing on more mesic sites (OL-S and OL-SO, Fig. 1).

These results also show that among the three sampled species lower forest border ponderosa pines are most likely to contain locally absent rings, while lower forest border Douglas-fir are least likely to contain locally absent rings. A simi-

TABLE II. Tree-ring characteristics from seven stands in the San Francisco Mountains

Item	Douglas-fir	Ponderosa pine				Pinyon pine	
	A	A	B	C	D	D	E
Mean ring width (mm)	1.50	1.33	.99	.86	.84	.68	.81
Percentage of absent rings	0.0	0.1	0.0	4.0	7.8	0.7	3.5
Percentage of rings with intra-annual bands	1.2	4.3	4.2	4.1	4.1	0.1	0.6
Standard deviation	.396	.273	.276	.531	.679	.343	.484
Mean sensitivity	.29	.20	.22	.49	.58	.31	.44
Inter-correlation between trees	.86	.70	.67	.88	.84	.77	.82
Intra-correlation within trees	.76	.69	.72	.90	.89	.82	.86
Serial correlation	.66	.65	.54	.63	.70	.53	.59
Percentage variation							
Retained by group chronology	71	51	51	80	76	64	72
Due to tree differences	7	18	22	9	12	16	13
Due to radial differences	22	31	27	11	12	20	15

lar relationship in the frequency of absent rings in these three species was reported by Douglass (1946).

In contrast to the marked increase of missing rings toward the forest border, the frequency of intra-annual latewood bands at different sites essentially remains constant for a given species. In fact, the variability from tree to tree and from radius to radius in the same trees is much greater than the variability from site to site. The data also confirm the fact that intra-annual rings occur more frequently in ponderosa pine than in either pinyon pine or Douglas-fir (Douglass 1946). None of the intra-annual bands in any of the cores exhibited a sufficiently sharp boundary so as to be confused with annual rings, though specific cases are known to occur (Schulman 1941, Glock et al. 1963).

Statistical characteristics of tree-ring series change rather abruptly near the forest border. Measures of relative ring-width variability, standard deviation, and mean sensitivity exhibit a marked rise near the lower forest border. The inter-correlation between trees and intra-correlation among the four radii within each tree (Table II) are lowest in the forest interior and highest at the lower forest border. However, a comparison of statistical measures for the ponderosa pine samples at sites C and D indicates that even though the variability continues to rise towards the extreme lower forest margin, the correlation among and within trees reaches a maximum and then appears to decrease at the most extreme sites. Analyses of variance show the same trend. While 51% of the variation in all cores is retained in the group chronologies for ponderosa pine at areas A and B, 80% is retained at area C, and only 76% is retained at area D. The decrease in group chronology variation in ponderosa pine from area C to D is accompanied by a relative increase in variation primarily due to differences among trees (Table II). In areas A and D, where two species occur together, the species closest to its lower forest border exhibits the most variation and also the highest inter-correlation and intra-correlation, indicating a greater uniformity of growth responses among and within trees. Serial correlation shows no clear relationship among the stands, but it is generally highest in the most extreme sites for each species.

Year-to-year variation in the tree-ring chronologies (Table II, Fig. 3) increases toward the lower forest border. This increased variability may be the result of increasing climatic control over processes in the tree which ultimately influence tree growth. To obtain some measure of the relative climatic control, the individual chronologies for

each sample were correlated with quarterly and monthly precipitation data for the years 1909 through 1962 from the Fort Valley weather records (Table III). A stepwise multiple correlation analysis was used to measure the total relationship between all intervals of precipitation data and tree-ring variation (Fritts 1962a). All intervals of precipitation data employed in the analysis are shown in Table IV. The simple correlations between tree-ring indices and precipitation data of the current season are included in the first six columns of Table III. The multiple correlation for the best predicting relationship is given in the seventh column of Table III.

The simple correlations between tree-ring indices and winter and spring precipitation, as well as the multiple correlations, increase from the forest interior to the lower forest border sites. Only July precipitation exhibits the highest correlation with the chronologies of the forest interior samples. The higher multiple correlations for the forest border samples, even though they are further from the weather station, are evidence that climate is more frequently limiting to growth of the lower forest border stands, and that the most variable tree-ring series is also the best climatic indicator.

Tree-ring indices are not independent variables through time but frequently exhibit serial correlation, that is, a dependency upon the amount of growth during the several preceding years. In order to measure the total predictability of tree-ring indices using precipitation, including the serial correlation between indices, a second stepwise multiple correlation analysis was made in which the tree-ring indices for the 3 previous years were added as three additional variables. The simple correlations between index values and those of the first, second, and third previous years are presented on the right of Table III, along with multiple correlations. The significant standardized partial regression weights for these analyses are presented in Table IV. These data also show that precipitation during autumn, winter, and spring is a primary control of ring width. They indicate that not only are all tree-ring series serially correlated with the previous ring, but also that area A Douglas-fir, area D ponderosa pine, and area E pinyon pine, the lower forest border environment for each species, exhibit a high third-order correlation with the index of the third preceding ring. When serial correlation between indices is accounted for, considerably higher multiple correlations are obtained for all series. Similar analyses were run using precipitation and mean temperature, but temperature exhibited lower correlations with ring-width values and did not markedly im-

TABLE III. Simple correlations, serial correlations, and multiple correlations for Fort Valley precipitation data and tree-ring indices

Site	Sample	Correlation between ring indices and precipitation using:						Multiple R	Serial correlation			Multiple R
		Previous autumn	Previous winter	Current spring	June	July	August	Using only precipitation data *	First order	Second order	Third order	Including serial correlation *
A.....	Douglas-fir	.04	.23	.36	-.07	.30	-.34	.56	.69	.68	.65	.89
A.....	Ponderosa	.19	.24	.27	-.05	.30	-.06	.54	.58	.34	.29	.82
B.....	Ponderosa	.15	.15	.23	.03	.37	.08	.51	.51	.47	.39	.78
C.....	Ponderosa	.20	.23	.42	-.26	.27	-.35	.61	.51	.35	.47	.76
D.....	Ponderosa	.15	.27	.49	-.30	.19	-.39	.68	.63	.46	.51	.87
D.....	Pinyon	.11	.30	.42	-.20	.25	-.29	.56	.49	.32	.40	.79
E.....	Pinyon	.19	.39	.49	-.13	.14	-.30	.72	.52	.39	.52	.86

*Stepwise analysis terminating at an F level of 2.5

TABLE IV. Variables and significant standardized regression weights ($P < .05$) for stepwise multiple regression analyses of the seven tree-ring chronologies

Independent variable	Douglas-fir	Ponderosa pine				Pinyon pine	
	A	A	B	C	D	D	E
Total precipitation for:							
August.....				-.212	-.167	-.202	-.216
July.....			.417**				
June.....							
Spring.....	-.258*			.235	.311**	.328*	.298*
Winter.....	.209*	.419**	.237	.239	.331**	.383**	.380**
Previous autumn.....		.432**	.331*				
Previous summer.....			-.216				
Previous spring.....							
Winter 2 previous years.....							
Autumn 2 previous years.....					-.164		
Summer 2 previous years.....							
Spring 2 previous years.....							
Winter 3 previous years.....	-.347**					-.242	-.312*
Autumn 3 previous years.....							
Summer 3 previous years.....							
Spring 3 previous years.....							
Winter 4 previous years.....							
Previous index.....	.334*	.695**	.288	.320*	.635**	.450**	.353**
Index 2 previous years.....	.497**		.340*				.226
Index 3 previous years.....				.290			

*Significant at $P < .01$
 **Significant at $P < .001$

prove the multiple regression relationships (Fritts 1965).

Tree-ring chronologies near the lower forest border exhibit more variability associated with precipitation variation preceding the growing period, and they may exhibit a high first- and third-order serial correlation, indicating a pronounced carry-over effect in growth from year to year. Therefore, the widest or narrowest rings from trees near the lower forest border generally follow a several-year period of favorable or unfavorable conditions; or in other words, the influence of a favorable or unfavorable year may be observed in not only the current tree-ring width, but also in the ring widths for the 3 following years. For example, in the ponderosa pine sample at area D during the unfavorable years of 1879-81 there

were no growth layers formed (Fig. 2), and the indices were low until 1888. The favorable growth period starting in 1890 is represented by high index values until 1896. This serial correlation is less pronounced in pinyon pine and in ponderosa pine from areas C, B, and A. Further discussion of climatic inference from tree-ring series on different sites is presented by Fritts (1965) and Fritts, Smith, and Stokes (1965).

CONCLUSIONS

From observations of tree-ring characteristics early workers in dendrochronology recognized the importance of site selection to insure high ring-width variability and high cross-correlation, which they called "sensitivity" and "dateability." The great number of locally absent rings in "sensitive"

chronologies made it necessary, however, to cross-date the series with the more reliable but less variable chronologies from less extreme sites. This assures the assignment of the correct date of formation for all individual tree rings. Crossdating, therefore, became the control of dendrochronology, while site selection and recognition of "sensitive" chronologies became guiding principles for accepting or rejecting the inclusion of a given tree-ring series as part of a master chronology.

This study provides a quantitative measure of "dateability" and "sensitivity" associated with site differences along a vegetational and precipitation gradient from the mesic forest interior to the semi-arid lower forest border. Certain new relationships are evident from the data, and no major contradictions of existing principles and their underlying assumptions can be found. A schematic representation of some of the relationships is presented in Fig. 4. The gradient from the forest

arboreal dominance exhibit a linear decrease along this gradient, with dominance dropping to zero beyond the last forest stand. Tree-ring dating can be applied in the area between J (Fig. 4), where tree growth is not highly related to climatic variation, and M, where climate is so limiting that a large number of the diagnostic or narrow tree rings are absent from most series. Beyond M so many rings are locally absent that dating is impossible. The chronologies obtained from trees in sites J to K are referred to as "complacent" and from K to M as "sensitive" by the dendrochronologist.

Two measures of variability, mean sensitivity and standard deviation, increase along the entire vegetational gradient of dateable series, but they exhibit the most marked increase nearest the lower forest border. There are almost no absent rings in the forest interior trees, but the frequency of absent rings increases near the lower forest border. The correlations among trees, as well as the correlations within trees, are greatest near the lower forest border (K-M, Fig. 4), but appear to decrease at the extreme lower border (L-M) where trees begin to exhibit more individualistic responses to climatic stresses and their ring-width sequences contain more serial correlation. Therefore, the inter-tree variation increases. Not only is ring-width variability in the area K to M highest and the most similar among trees, but these sites can also be shown to yield the most reliable tree-ring records of climatic fluctuations. Fig. 4 is diagrammatic, and the absolute relationships will vary from species to species and from area to area. The actual boundaries of dateable versus non-dateable series are largely dependent upon the frequency of missing rings at the lower forest border and the correlation or degree of crossdating among trees in the forest interior. The success of dating in marginal sites will also depend upon the sample size used as the crossdating control and the skill of the worker.

The presence of intra-annual growth bands appears to bear no relation to the severity of the site environment. Certain causes of intra-annual growth bands are suggested by Larson (1962), and a more detailed analysis of this phenomenon in ponderosa pine is presented by Fritts et al. (1965).

The correlation and regression analysis represents only a beginning in the evaluation of the influence of climate on tree growth. For the sake of simplicity, the influence of temperature on evapotranspiration stress was ignored, but more exhaustive analysis shows that a somewhat higher predictability can sometimes be achieved by including temperature (Fritts 1965).

The physiological causes for the growth-climatic

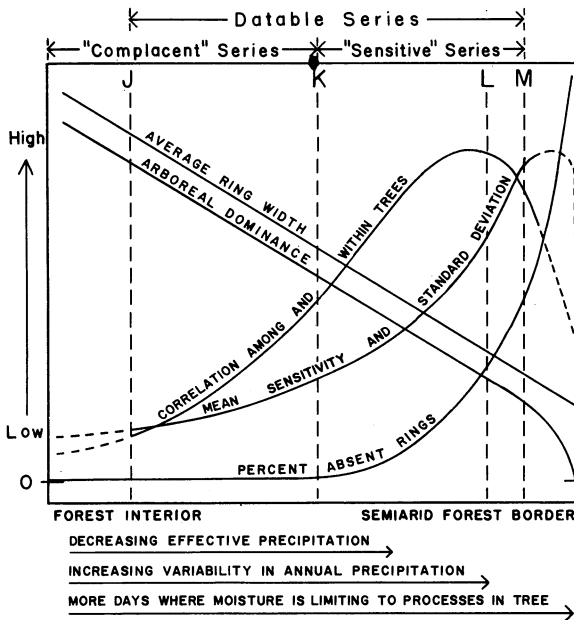


FIG. 4. Diagram of changes in tree-ring characteristics along a transect from the forest interior to the semi-arid forest border.

interior to the lower forest border is represented along the abscissa. Annual precipitation decreases and potential evaporation increases along this gradient so that the effective precipitation, or that precipitation which influences the plant processes, markedly decreases. The coefficient of variation in annual precipitation also increases. As a result of these conditions there are more days throughout the year when moisture is limiting to processes in trees near the semi-arid forest border.

Both the average annual tree-ring width and

relationship are now under intensive investigation. Much evidence is already accumulated which indicates that the climate during the autumn, winter, and spring directly influences net photosynthesis and the accumulation of food reserves in semiarid site trees. Therefore, when radial growth occurs in the late spring and early summer, the ring width is frequently more influenced by the amount of stored food reserve than by the current soil moisture regime (Fritts 1965, Fritts, Smith, and Stokes 1965). Consequently precipitation and temperature prior to the growing season may have a pronounced but indirect influence on the width of the annual ring.

We can conclude that near the lower forest border in northern Arizona the higher degree of variability and similarity in tree-growth responses appears to be directly related to moisture stresses during the autumn, winter, and spring prior to the growth period. Thus the physiological processes, such as photosynthesis, respiration, assimilation, and cambial activity, are largely a function of favorable or unfavorable climatic regimes, and hence the trees exhibit a high amount of similar variation in relative year-to-year fluctuations of their ring widths. In the more mesic forest interior sites, the physiological processes are not as frequently limited by climate and therefore the tree-ring widths are less variable from year to year. Also, individual biotic and edaphic factors are more important and they produce differences among trees so that correlation and crossdating within the stand are not as apparent.

The results demonstrate that tree-ring characteristics can be used as a basis for evaluating the growth response of a species to its environment. Analyses of ring-width correlation and variation can be used to measure the degree of stress exerted by the environment on radial growth. The technique was applied in the recent work of Dodge (1963) and Fritts (1963*b*), where a direct comparison was made between the ring-width responses of two apparently different phenotypes of ponderosa pine in the Santa Catalina Mountains of southern Arizona.

In the seven northern Arizona stands the common variance of tree-ring widths shared by trees within a site is proportional to the influence of yearly climatic variation on growth. In addition, relative ring-width variability and the frequency of locally absent rings are indicative of environmental stress. Thus, tree-ring analysis of selected but comparable forest stands with different heredities or on sites differing in exposure, slope, or soil type can be a useful tool in ecological research, and differences among stands along an ecological gradient such as the semiarid forest border may be

used to measure the degree of water stress which directly or indirectly limits the growth of trees.

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GROWTH PATTERNS OF SOME NATIVE ANNUAL AND PERENNIAL HERBS IN SOUTHERN WISCONSIN

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Abstract. Temporal growth patterns and adaptive characters were studied in 17 perennial, 16 annual, and 4 biennial native herbs for one to three growing seasons in dry-mesic, mesic, and wet-mesic forest and in open barrens in southern Wisconsin. In annuals almost all dry matter produced was retained in aerial organs following the initial growth period. Below-ground weight increased rapidly in early season and then slowly increased or declined. In perennials there was a predominantly upward weight movement during growth initiation and during flowering and fruiting and a downward movement between growth initiation and flowering and preceding aboveground senescence or death. Between autumn and spring, all perennials, including wintergreens, lost weight. Most winter annuals increased in both above- and below-ground dry weight over winter, demonstrating maintenance above the compensation point. Growth patterns of biennials in their first year were similar to perennials and in their second year were similar to annuals.

Forest herbs lost less water before wilting, were more succulent, wilted in a shorter time, and had heavier seeds than herbs of open habitats. The seeds of the forest annuals were heavier and germinated more readily than seeds of forest perennials. Although most annuals are pioneer, drought-resistant plants, forest annuals wilted easily and were very succulent. This suggests that stems and leaves of the annuals apparently are supported more by turgor pressure, while the perennial plants are supported more by cell wall thickening. This special dependence of annuals on water correlates with their greater numbers in wet-mesic and mesic forests compared with drier forests. Growth characteristics are discussed for eight forest annuals: *Amphicarpa bracteata*, *Ellisia nyctelea*, *Floerkea proserpinacoides*, *Galium aparine*, *Impatiens pallida*, *Parietaria pennsylvanica*, and *Pilea pumila*.

INTRODUCTION

Quantitative studies of the temporal weight and growth patterns of herbs usually have been limited to cultivated species grown singly or in pure stands in greenhouses or managed fields (for example, Kreuzler 1877, Hornberger 1882, Reed 1920, Murneek 1926, Graber et al. 1927, Martin 1934, Anderson 1944, Kiesselbach 1950, Ruelke and Smith 1956). The results of studies using artificial plant communities or artificial habitats are inconclusive in understanding growth patterns of plants growing in natural communities. Likewise, many growth-pattern studies have viewed growth as a series of internal, autocatalytic reactions with little relationship to environmental conditions or have used special treatments or highly modified environments in order to understand growth for

agricultural purposes. Weight and growth measurements of native herbs in natural habitats have been made by Salisbury (1942), Tamm (1948, 1956), Randall (1953), and Kieckhefer (1962). In these studies such properties as water balance, chlorophyll content, caloric content, and reproductive potential are related to environment and community type.

In the present study, temporal growth patterns of selected annual, biennial, and perennial herbs were measured in one open habitat and in three forest habitats. Forest annuals were given special attention since they inhabit plant communities characterized mainly by perennial plants, whereas annuals are usually associated with open habitats (Raunkiaer 1934, Tamm 1948) and are considered "indicators" of disturbance (Clements 1949). Sea-