THE VARIABILITY OF RING CHARACTERISTICS WITHIN TREES AS SHOWN BY A REANALYSIS OF FOUR PONDEROSA PINE

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ABSTRACT

Tree-ring characteristics are studied within and among stems of four *Pinus ponderosa* Laws. located at several semiarid sites in northern Arizona. Analyses are made of changes associated with certain physiological, height, and age gradients within the tree. Rings are grouped into twenty or forty-year intervals, are classified in four different arrangements, and the characteristics for the intervals are averaged and plotted to represent the gradients within the tree stem. Tree-rings are widest near the base and central portions of the stem. Ring width decreases with increasing age of the cambium, with increasing height within the young stem, with decreasing terminal growth, and with increasing environmental stress. Double (false or intra-annual) rings occur most frequently in the wide rings near the base and in the younger portions of the stem, or in the upper stem and branches of older trees. The frequency of rings which are locally absent (partial rings) is inversely related to ring width, and directly related to the potentiality for water stress conditions in the site or within the tree. Correlations among the year-to-year ring-width patterns throughout the tree generally increase with increasing tree age and frequency of water stress. They are high within the lower and central bole portions of older trees, but in the upper stem, in lateral branches, and in trees on the most extreme sites correlations among ring-width patterns are somewhat lower. Relative variability in widths of adjacent rings increases with decreasing ring width, increasing age, increasing height in the stem, and increasing environmental stress. First order serial correlation is frequently highest in older trees on semiarid sites. Many of these changes in ring characteristics within the tree are attributed to specific gradients or changes in auxin, food, and water supplies. A wide sampling of annual rings from the base of many semiarid site trees appears more appropriate for evaluating past fluctuations in climatic factors than an intensive sampling of rings at several heights in only a few trees.

In another study (Fritts *et al.* 1965) the writers analyzed the variability of certain tree-ring characteristics along an environmental gradient from the moist sites of the forest interior to the drier sites of the semiarid lower forest border. It was demonstrated that mean ring width and dominance of arboreal species decrease towards the forest border and these are accompanied by an increase in year-to-year ring-width variation, an increase in correlations of ring widths among and within trees, an increase in the frequency of locally absent rings, and an increase in serial correlation of ring widths. The ring-width chronology from lower forest border trees was shown to more accurately reflect annual variations in precipitation than the chronology from forest interior trees (Fritts 1965, Fritts *et al.* 1965), but there was little difference in the frequency of intra-annual latewood bands between the two environmental extremes. However, pronounced differences in the frequency of latewood bands were found among species, between trees on identical sites, and between radii within trees.

This paper represents a study of the same ring characteristics as they vary within the tree along gradients related to ring age and height. Further consideration is given to differences among the trees which are related to their proximity to the semiarid lower forest border. The study is based upon cross sections from four felled ponderosa pine (*Pinus ponderosa* Laws.). One tree, designated as OL-12, was previously collected and described by Glock (1937). The other three ponderosa pine were more recently sectioned and reported by Glock *et al.* (1963). Our study is a reanalysis and reinterpretation of this material. It differs from the earlier work in that (1) a system of classification patterned after the tree-ring studies of Duff and Nolan (1953) is employed, (2) certain statistical measures are used to evaluate relationships, and (3) an attempt is made to discuss the physiological bases for the relationships.

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METHODS

The tree OL-12 was cut in December, 1934, cross sections were obtained, and after study (Glock 1937, p. 34; Schulman and Baldwin, 1939) the materials were deposited at the Laboratory of Tree-Ring Research. Eight of the eleven original cross sections were chosen so that the beginning dates (pith dates) of the sections were approximately 20 years apart (Table 1). The ring series were dated and measured along radii that represent the four cardinal directions, and the ring characteristics were tabulated for each twenty-year period. Tree-ring analyses of the lowest section were made along each radius starting with the ring for the year 1655. On each successively higher section, four radii were analyzed beginning with the ring formed 20 years later than the beginning ring on the next lowest section. Analyses of each section ended with the ring formed in 1934. Thus, each successively higher section contained one less twenty-year period (Table 1).

Data for individual sections were averaged for each twenty-year period. The bottom section included 14 periods while the top section included only 7 periods. Tree-ring characteristics and parameters equivalent to those described by Fritts *et al.* (1965) were calculated and averaged for each of the twenty-year periods. Tree-ring characteristics which were analyzed include (1) ring width, (2) percentage of double (intra-annual or false) rings, and (3) percentage of partial or missing rings. These three characteristics were tabulated for rings along each of the four radii on each section. Ring widths were converted to tree-ring indices (Fritts 1963b) and these data were used to calculate certain parameters for each twenty-year period. These parameters include (1) intra-correlation which is the mean of all possible correlations among the indices for the four radii within each period on each section, (2) inter-correlation which is the mean correlation of the period indices from any one section with the indices for all other sections formed during the same twenty-year period, (3) mean sensitivity which is calculated as the average of the differences between adjacent indices divided by the mean of each pair of indices, and (4) serial correlation and standard deviation which are calculated in the usual manner from the means of the twenty indices for each section in each period (Fritts *et al.* 1965). The data summarized for each twenty-year period on each section were classified, averaged, and plotted according to a modified system similar to the one described by Duff and Nolan (1953).

Tree-ring width data for the other three ponderosa pines used in this study came from Tables 42, 57, and 62 of Glock *et al.* (1963). Since different numbers of radii were measured on the sections from these trees, only the average ring widths for each section were used. However, the percentages of absent rings are based upon data for individual radii of each section. In order to make a continuous systematic analysis, sections were chosen which

TABLE 1. Sections used in the analysis of OL-12 reconstructed from materials and records at the Laboratory of Tree-Ring Research.

New Section Designation	*Original Designation (by Glock)*	*Height in Meters*	*Pith Date*	*New Analysis Started*
8	J	13.4	1795	1795
7	I	12.3	1770	1775
6	H	11.3	1754	1755
5	G	9.8	1731	1735
4	E	8.2	1707	1715
3	D	6.0	1693	1695
2	B	2.3	1664	1675
1	A	0.5	1640	1655

had pith dates approximating forty-year intervals up the stem (Table 2). The rings formed during the period 1660 through 1939 were studied as they provided a comparative analysis of from one to seven forty-year periods within each section. The data for the lowest sections were divided into seven forty-year periods for OL-B-42 and six forty-year periods for the other two younger trees (Table 2). Terminal growth was calculated from height data and pith dates provided by Glock *et al.* (1963, Table 4). All other data processing and analysis schemes were comparable to those described for OL-12.

SITE DESCRIPTION

The study areas are located within a few miles of the semiarid lower forest border in the area of the San Francisco Mountains of northern Arizona, two to four miles southwest of O'Leary Peak at elevations between 7100 and 7300 feet (see Fritts *et al.* 1965, Fig. 1; or Glock *et al.* 1963, Fig. 4). The four trees had full crowns, measured from 22 to 24 inches dbh, and grew on well-drained sites in volcanic soils. Glock (1937) described one site as follows: "OL-12 was part of a nearly pure stand of ponderosa pine possessing its characteristic feature of wide spacing of individual mature trees. It was sufficiently well-isolated and so situated as to avoid effective competition." Numerous ponderosa pine seedlings and saplings were reported in the area.

The trees on the three other sites are described in detail by Glock *et al.* (1963). The tree OL-B-42 was nearest the lower forest border along U. S. Route 89. It grew on a forested spur just above the pinyon-juniper and desert grassland zones. "Ground litter is extremely sparse or absent over large areas." Several young junipers and pinyon pines were noted at this site. Tree OL-SO-57 grew at a slightly higher elevation than OL-B-42. It was part of a pure stand of ponderosa pine, with numerous seedlings and saplings present. The soil was described as being better developed with a higher organic content than under OL-B-42. The tree OL-S-62 was part of a pure stand of widely scattered ponderosa pine with many seedlings and pole-size saplings present. The reproduction at this last site is reported to surpass that of any other site, and the ground litter is described as noticeably more plentiful. All trees were generally free from competition.

It may be in inferred from these descriptions that site OL-B is the most arid site, while site OL-S is the most mesic or most forest interior site. The sites OL-SO and OL-12 appear to be intermediate between OL-B and OL-S. For brevity in the text that follows, the site symbol above stands for the specimen from that site.

TABLE 2. Data used in analysis of trees OL-B-42, OL-SO-53, and OL-S-62.

TREE:	*OL-B-42*			*OL-SO-57*			*OL-S-62*		
New Stem Sections	*Table*[1]	*Pith Date*	*New Analysis Started*	*Table*[1]	*Pith Date*	*New Analysis Started*	*Table*[1]	*Pith Date*	*New Analysis Started*
7	42-11	1898	1900	57-10	1887	1900	62-13	1898	1900
6	42-10	1843	1860	57-9	1853	1860	62-10	1838	1860
5	42-9	1801	1820	57-7	1797	1820	62-9	1814	1820
4	42-8	1769	1780	57-6	1772	1780	62-6	1758	1780
3	42-6	1727	1740	57-4	1726	1740	62-5	1740	1740
2	42-3	1693	1700	57-2	1692	1700	62-2	1695	1700
1	42-1	1645	1660						
New Branch Sections									
A4				57-1-E	1871	1900	62-1-H	1893	1900
A3				57-1-D	1851	1860	62-1-F	1854	1860
A2				57-1-A	1783	1820	62-1-D	1808	1820
A1							62-1-A	1780	1780
B2				57-2-B	1895	1900	62-2-D	1897	1900
B1							62-2-A	1860	1860

[1] Numbers in Glock, *et al.* (1963).

Analysis and Results

Tree-ring characteristics and index parameters for the twenty-year intervals were classified and summarized in four schemes which represent different gradients within the main stem of the tree. The classification schemes are illustrated in the diagrams at the top of Figure 1. These diagrams show only four sections and accent every other twenty-year interval. The heavy lines on the right half of each diagram connect the portions in each section from which data were obtained and averaged to construct the plots located below the diagram.

In classification A (Figure 1) the twenty-year periods which are nearest the pith are averaged in a vertical direction to calculate the value corresponding to a mean age of 10. Those periods approximately 21-40 years from the pith are averaged to calculate the value for mean age of 30, and the next 20 years for mean age of 50. The resulting seven averages represent a gradient of increasing cambium age (ring age starting at the pith). In classification B (Figure 1), the same groups of rings are used but are averaged in a horizontal direction so the resulting values represent averages for the first 140 rings along each section in the tree. The resulting gradient represents increasing height in the tree but the age of the cambium and number of rings counting from the pith in each section is approximately the same. Classifications C and D (Figure 1) incorporate all rings within

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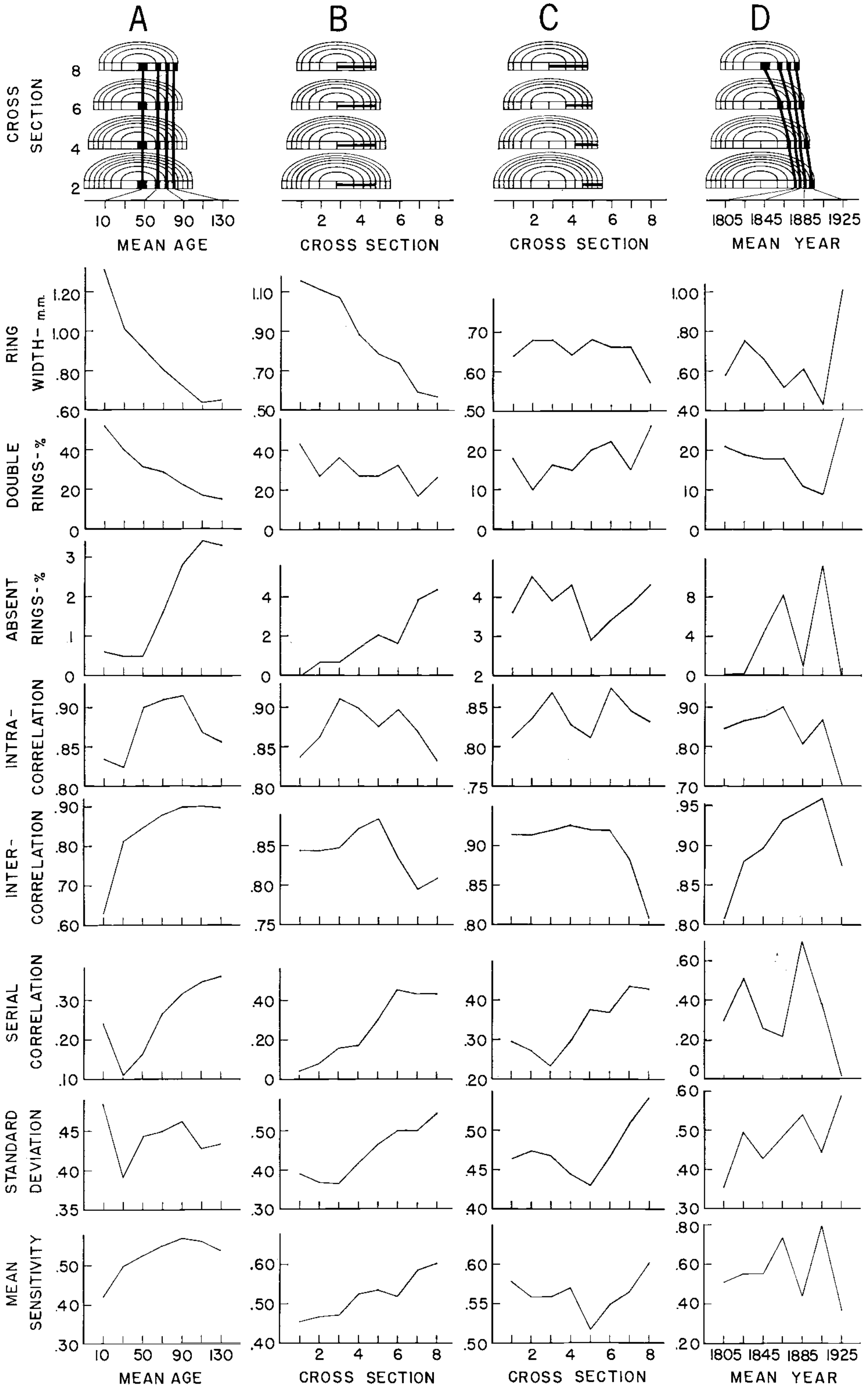
FIG. 1. The average change in tree-ring characteristics for twenty-year groups of rings on eight sections from OL-12. The data are classified, averaged, and plotted in four different arrangements (A-D). Heavy lines in each sketch connect portions in sections from which data were averaged to construct the plots shown below.

In classification A the data for periods arranged in a vertical direction parallel to the pith are averaged. The plots show changes associated with cambium age (number of rings from the pith), while height in the tree is constant. In classification B the data from the inner 140 rings are averaged for each section. The plots show changes associated with section height with cambium age constant.

In classification C the data from the outer 140 rings are averaged for each section. The plots show changes associated with section height. Actual years of formation (1795-1934) are constant.

In classification D the data are averaged for each twenty-year period lying along the diagonal parallel to the cambium. The plots show changes within the tree associated with each period, while height in the tree is constant.


A
B
C
D
CROSS SECTION
8
6
4
2
10 50 90 130
MEAN AGE
2 4 6 8
CROSS SECTION
1805 1845 1885 1925
MEAN YEAR
RING WIDTH- m.m.
1.20
1.00
.80
.60
1.10
.90
.70
.50
.40
1.00
DOUBLE RINGS-%
40
20
10
0
ABSENT RINGS-%
3
2
1
4
8
INTRA-CORRELATION
.90
.85
.80
.75
.70
INTER-CORRELATION
.95
.90
.80
.70
.60
SERIAL CORRELATION
.60
.40
.30
.20
.10
0
STANDARD DEVIATION
.60
.50
.45
.40
.35
.30
MEAN SENSITIVITY
.80
.60
.55
.50
.40
.30
.20

the tree formed from 1795 to 1934 A.D. or in the seven outer twenty-year periods of each section. Classification C is similar to B in that averages are made horizontally along each section. The gradient in C represents increasing height in the tree but the year of formation, not the cambium age (number of rings from the pith), is constant. In classification D averages are made diagonally so that all rings formed within the same twenty-year interval are included. The resulting gradient represents the average twenty-year changes occurring throughout the entire stem during the 140 years of growth prior to cutting in 1934.

The plot of ring width in column A of Figure 1 exhibits the usual logarithmic dieaway curve which is characteristic of ring series in many coniferous trees from southwestern North America (Fritts 1963a). The frequency of intra-annual or double rings, as plotted in column A of Figure 1, decreases with increasing distance from the pith, and is apparently related to the decreasing ring width. The next plot in column A, percentage of absent rings, shows that an annual ring is formed more than 99% of the time during the first 60 years of growth, but as the cambium age approaches 100 years the probability that a ring will be present becomes less than 97%.

The plot of intra-correlation which measures agreement among radii in the same section shows that the amount of agreement is lowest during the first 40 years, highest from 40 to 100 years, and then decreases as the cambial tissues become older. Inter-correlation, which measures vertical consistency of the ring width variation, is quite low during the first 20 years of growth, increases considerably in the second twenty-year period, and approaches a correlation of 0.90 when the cambium age exceeds 100 years.

The plots in column A also show that nearest the center of the sections the tree-ring series in OL-12 exhibit generally decreasing serial correlation and decreasing standard deviation, but mean sensitivity increases. Serial correlation and standard deviation reach a minimum at a mean age of 30, but at ages of 50 to 130 years all three parameters generally increase.

The plots under column B (Figure 1) show changes associated with increasing height in the tree when the cambium age (number of the rings starting at the pith) is held constant. In this classification ring width decreases with height. As is evident in column A, the percentage of double rings in classification B appears to be directly related to ring width, while the frequency of absent rings appears to be inversely related to ring width.

The plot of intra-correlation in column B indicates that in the young, maturing tree circuit uniformity is highest in the middle sections of the bole. Inter-correlation, the average agreement between sections, is also highest in the middle portions but lowest in the upper portions of the tree. Serial correlation, standard deviation and mean sensitivity of OL-12 increase with both increasing height and tree age, along with decreasing mean ring width.

The classification in column C of Figure 1 differs from the classification of B in that, instead of the cambium ages and number of rings from the pith being the same for each average, the years of formation and growing period are the same. This classification excludes all growth for the first 140 years in the life of the tree and includes all growth during the last 140 years. The mean ring widths in column C show little variation between sections 1-7 but in section 8 rings are narrower. The plot of percent of double rings shows a slight increase with height.

The plot in column C for the frequency of absent or partial rings shows that the basal trunk portions and middle-crown portions of the OL-12 stem (sections 1, 5, and 6) exhibit lower frequencies of locally absent rings than in the clear bole and upper crown portions of the stem. Intra-correlation is low in the basal, middle-crown and top portions of the stem, and inter-correlation is high throughout all but the top sections of the stem. Serial correlation, standard deviation, and mean sensitivity are all highest in the upper sections, reach their lowest values in the mid-portions, and exhibit somewhat higher values near the base.

The fourth scheme of classification (column D in Figure 1), summarizes tree-ring characteristics and parameters in OL-12 representing the mean growth responses for the entire tree at twenty-year intervals within the last 140 years of growth. The plot of mean ring width exhibits a slow decline from 1795 to 1914 associated with the effect of tree age. The periods from 1855 through 1874, and 1895 through 1914, show the greatest reduction in ring width. This reduction is probably related to unfavorable environmental conditions which are thought to occur during the two periods (Fritts 1965). Wide tree-rings from 1915 to 1934 are related to favorable climatic conditions; namely, greater precipitation and lower temperatures (Schulman, 1956; Fritts 1965; Fritts *et al.* 1965).

The percentage of double or intra-annual rings in column D parallels mean ring width. Inter-correlation appears inversely related as it increases with increasing age and decreasing ring width, but it declines markedly during the growth surge centering in 1925. The percentage of absent rings, intra-correlation, and mean sensitivity all exhibit their highest values during the two periods of lowest ring width; and their lowest values occur during the periods when ring width is greatest. The lack of agreement of both serial correlation and standard deviation with trends in other parameters suggests that changes in these parameters are not simply related to other measures of trends within the tree. Thus, the plots of serial correlation and standard deviation in column D appear of little significance to the present analysis.

Classifications A and D show gradients associated with age and time. The vertical distribution in each of these gradients is shown in B and C. Differences between the plots in A and B and the plots in D and C (Figure 1) provide a two dimensional picture of ring characteristics in OL-12, while differences between the plots in A and D and the plots in B and C may be used to evaluate changes associated with tree age and time. In making evaluations, it must be kept in mind that the data used from section 1 for A and B is completely different from the data used for C and D, but in section 2 the outer 20 rings included in A and B are also included in C and D. In each successive section 20 additional rings are common to all four classifications so in the 8th section all data are common to all classifications.

The plots for ring width under A and B indicate that the dieaway curve is not equally manifest throughout the entire stem. In fact, plots of data from individual sections show a very pronounced decrease in ring width with age at the base of the stem, but these changes become less pronounced with height, and in sections 7 and 8 no significant decrease in ring width with age is evident.

In Table 3 the rates of terminal growth in OL-12 are tabulated for each twenty-year period along with the mean ring widths formed in the two sections closest to the stem apex. These data show that the widest rings are formed when terminal growth is most rapid. During the first 80 years of growth the increase in height was very rapid, reaching its maximum rate during the period 1695-1714, and the widest rings were formed nearest the apex. By the end of this period the tree was two-thirds its mature size (9.8 m, Table 1). During the following 80 years, except for the period 1755-1774, rates of terminal and radial growth declined and ring widths on the section nearest the apex were less than those on the next lower section. The plots of ring width in classifications C and D show that from 1795 through 1934 after the tree had exceeded a height of 13.4 m (Table 1) no

TABLE 3. Terminal and radial growth occurring near the stem apex of OL-12 as measured from the distance between cross sections and the dates and widths of the inner 40 rings on each section (Table 1).

Growth Interval	*Average Terminal Growth (mm/year)*	*Average Ring Width (mm)*		
		Sections	*First 20 yrs. in Upper Section*	*Second 20 yrs. in Next Lower Section*
1655-1674	79	1	1.64	......
1675-1694	125	2, 1	1.82	1.33
1695-1714	155	3, 2	2.23	1.66
1715-1734	64	4, 3	1.58	1.50
1735-1754	67	5, 4	0.99	1.07
1755-1774	67	6, 5	1.23	1.00
1775-1794	43	7, 6	0.55	0.64
1795-1814	43	8, 7	0.45	0.46

marked dieaway curve is evident and the uppermost section continues to exhibit the narrowest rings.

The plots of percent of double rings show that double rings are most likely to occur near the apex of the stem under conditions of rapid growth. Therefore, the wide inner rings in the lower sections exhibit the most double rings, but as the tree approaches maturity and growth rates decline, there are fewer double rings formed, especially in those sections farthest from the stem apex.

By their very nature, absent rings are inversely related to mean ring width, but the infrequency of missing rings during the first 60 years of growth on a section (classification A in Figure 1) is evidence that the proximity of the stem apex and cambium age may be controlling factors. Classification C shows higher percentages of absent rings in the clear bole sections 2 through 4 than in sections 5 through 7 which are in the crown, yet mean ring widths are about the same. This indicates that the widest rings must be somewhat larger in the lower sections which would inflate standard deviation and especially mean sensitivity.

A comparison of the plots of intra-correlation in columns B and C show that, as the circumference of the section increases, radial uniformity decreases especially in the lower crown or mid-portions of the stem; but plots for inter-correlation show that vertical uniformity in the clear bole or lower portions of the stem increases. Near the base and central portions of the tree the values for serial correlation, standard deviation, and mean sensitivity are markedly higher for the outer rings than for the inner rings of the stem (columns B and C, Figure 1).

The rapid radial and terminal growth, low frequency of locally absent rings, low intra- and inter-correlations, and low mean sensitivity in the younger portions of OL-12 suggest that when the tree was a young, fast-growing sapling, it exhibited a tree growth response more typical of forest interior sites (Fritts *et al.* 1965). As the terminal and radial growth rates decrease with increasing age, the ring patterns formed throughout the entire tree become more typical of trees in semiarid forest border sites.

The results from analyses of the data published by Glock *et al.* (1963) are plotted for each section in Figures 2, 3, and 4. The graphs on the left of each figure are for OL-B, described as having grown on a site which is nearest the lower forest border. The graphs on the right are for OL-S which grew in the most forest interior environment for the trees. Tree OL-SO grew on an intermediate site. The figures represent a scheme similar to the plots in column D of Figure 1, but they differ in that the data for each individual section are plotted at the mid-date of a forty-year, rather than a twenty-year, period.

TABLE 4. The average correlation coefficient among all ring width indices for forty-year periods from 1700 to 1939 A.D. within and among the three trees. N is number of correlations averaged.

	Study Trees					
Comparisons	*OL-B-42*	*N*	*OL-SO-57*	*N*	*OL-S-62*	*N*
Within main stem	0.89	56	0.93	35	0.84	35
Within branches	......	....	0.82	3	0.78	11
Between branches of same tree	......	....	0.82	3	0.47	11
Between branches and main stem of same tree	......	....	0.84	38	0.53	67
Stem of OL-B-42 with other stems	......	....	0.63	112	0.60	91
Stem of OL-SO-57 with stem of OL-S-62	......	....	......	....	0.65	112

Terminal growth rates calculated from the distances between sections are plotted at the top of Figure 2. The corresponding average ring widths and percentage of absent rings are plotted in the middle and lower parts of the figure. Tree OL-B exhibits high rates of both terminal growth and radial growth early in the 18th century followed by a marked decline in terminal and radial growth in the latter part of the 18th century. The ring widths in all sections of OL-B exhibit a steep dieaway growth curve reaching a minimum during the 19th century. During that time, the first 40 rings on the 4th and 5th sections were in the top of the tree, and they produced rings which were markedly below the average width for rings formed in lower portions of the stem. The low growth rate of the 19th century is followed by a marked rise in both terminal and radial growth during the moist period early in the 20th century.

Terminal growth and tree-ring widths of the more forest interior OL-SO and OL-S ponderosa pines exhibit similar but less marked changes through time than those in OL-B. Comparisons among the three trees show that ring width differences among individual sections increase with increasing distance of the tree site from the more arid lower forest border. In more moist sites the upper sections are more likely to exhibit higher rates of growth than the lower sections; although during the last forty-year period, 1900 to 1939, the top sections in all three trees, represented by points in the figures, contain markedly narrower rings. The ring widths of the branches show trends similar to those of the bole, although they are generally narrower.

As was found in OL-12, the percentage of locally absent rings for the three trees exhibits an inverse relationship to ring width. The pattern and frequency of absent rings in OL-12 most resembles the intermediate tree, OL-SO. Tree OL-S has the lowest frequency of locally absent rings, while OL-B has the highest. The tree OL-B also shows a greater frequency of locally absent rings in the early growth periods of each section. Glock *et al.* (1963) report that the branches of this tree have such high frequencies of locally absent rings that they were unable to date the ring patterns.

Measurements of serial correlation, standard deviation, and mean sensitivity for each forty-year period of each section are plotted in Figure 3. As was noted for OL-12, in trees OL-B and OL-SO, on the more arid sites, serial correlation of the indices decreases after the first 40 years of growth and then increases with increasing tree age and decreasing ring width. Serial correlation declines more slowly with the age of OL-S and then rises. The increase in serial correlation with increasing height within the stem which was noted in OL-12 cannot be found in these three trees. The standard devia-

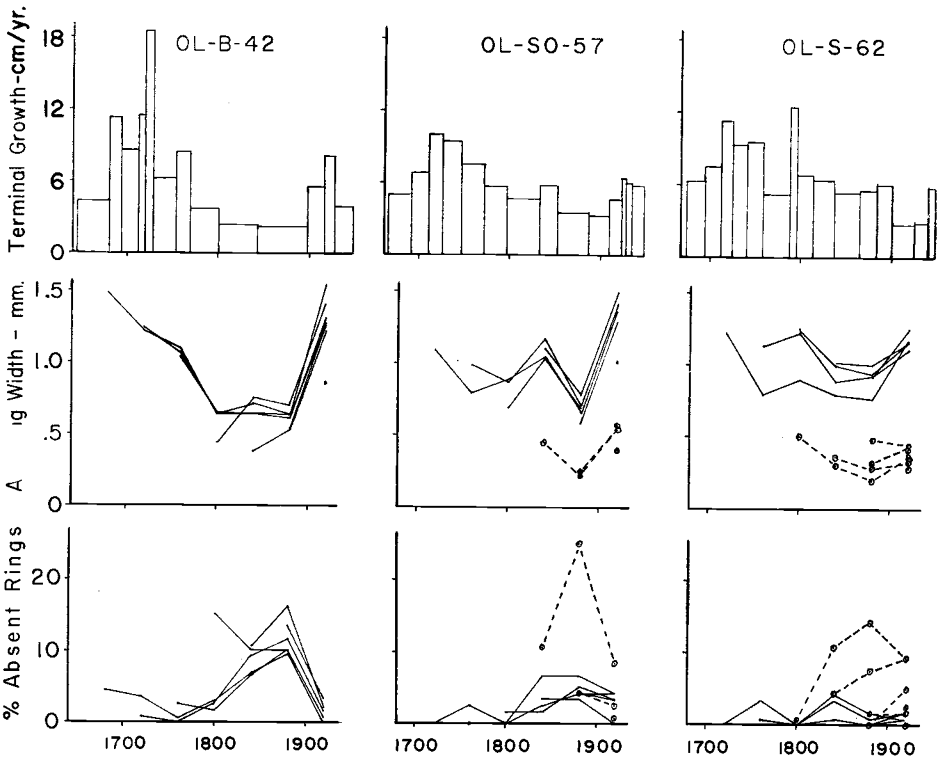


FIG. 2. Terminal growth, average ring width, and percentage of missings rings for forty-year periods on successive sections in the main stem (lines) and branches (dashed lines and circled points) of three ponderosa pine.

tion relates about as poorly to other parameters as it did for OL-12, though it frequently follows the trend in ring width within a tree. On the other hand, the mean of the standard deviations for all sections in the trees decreases from sites OL-B to OL-S, while the average ring width increases.

Mean sensitivity exhibits a consistent, similar relationship throughout all three trees. Mean sensitivity is highest both in the branches and near the top of the main stem of the trees as well as in trees nearest the lower forest border. This measure of tree-ring variability is generally inversely related to mean ring width and directly related to the percentage of absent rings. A major exception is found in the lower forest border tree, OL-B, in the period 1860 to 1899 when rings failed to form throughout a large part of the tree during the three successive years, 1879 to 1881. In this particular case, adjacent tree-ring variation for these three years is zero. This unusual occurrence can account for the reduction in mean sensitivity during the period on this extremely marginal site (see Figure 4 in Fritts *et al.* 1965).

The rings of branches generally exhibit lower serial correlation, a higher standard deviation, and a higher mean sensitivity than do the rings of main stems. Tree OL-SO shows a greater uniformity in serial correlation, standard deviation, and mean sensitivity among its different sections than do the other two trees, OL-S and OL-B. With respect to the majority of characteristics, OL-SO most resembles OL-12.

Linear correlations were calculated for all possible combinations among ring-width indices of stems, branches, and among the three trees for each forty-year interval. The correlations were classified, summed, and averaged

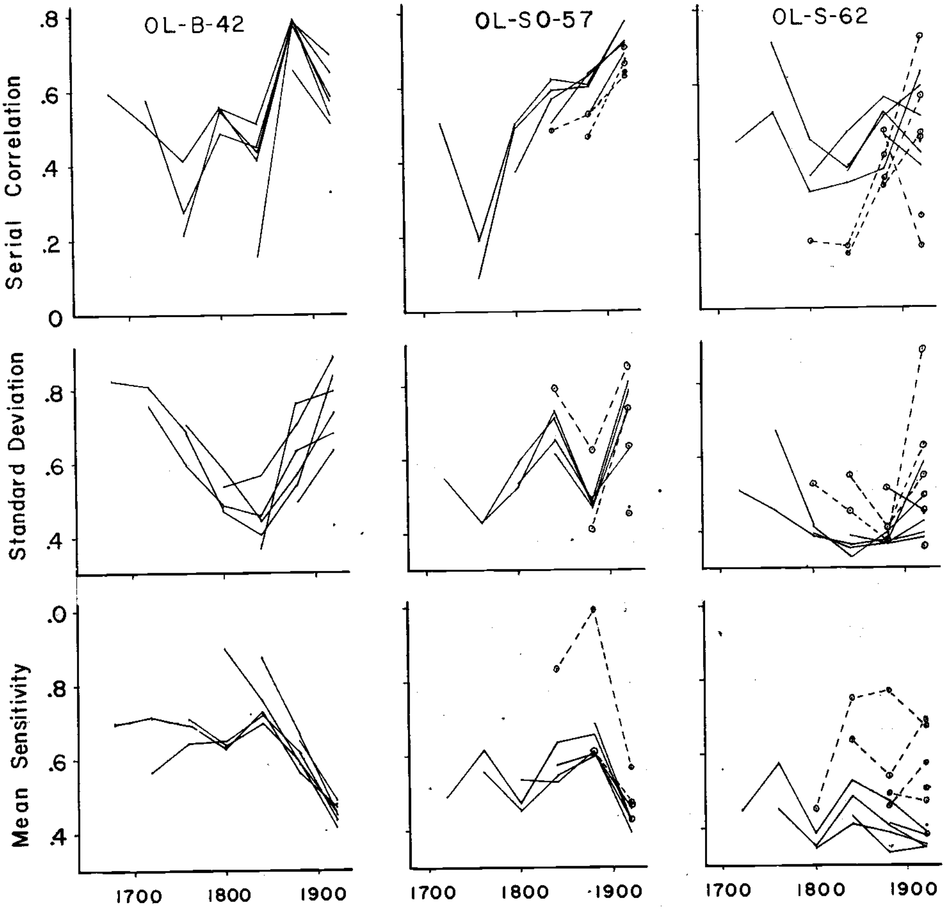


FIG. 3. Serial correlation, standard deviation, and mean sensitivity of tree-ring chronologies for forty-year periods on successive sections in the main stem (lines) and branches (dashed lines and circled points) of three ponderosa pine.

to provide a measure of the average correlations of indices among and between branches and stems (Table 4). The tree OL-SO, which grew on the intermediate site, exhibits the highest average correlation within the main stem, while OL-S, the most forest interior tree, exhibits the lowest average correlation within the main stem. Branch correlations within OL-SO are much higher than within OL-S. However, branches exhibit generally lower correlations with each other than with the main stem. The average of all correlations among the three stems range between 0.60 and 0.65. The lowest correlation occurs between the forest border tree, OL-B, and the most forest interior tree, OL-S. Figure 4 represents the average correlation of each section with the other sections of the main stem for the interval 1860-1899, a generally dry period with small, variable rings, and for the interval 1900-1939, a more moist period with wide, less variable rings. The correlations exceed 0.90 in all sections during the 1860 to 1899 interval, but during the following more moist period, 1900 to 1939, the correlations average below 0.90 in OL-B and OL-S. In all three trees, the top sections exhibit the lowest

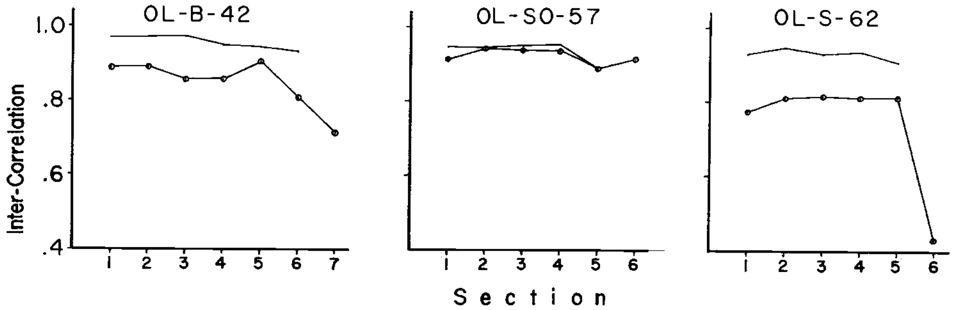


FIG. 4. The average correlation of chronologies at each section with all other sections in each of three ponderosa pine during the years 1860-1899 (upper line) and 1900-1939 (lower line with circled points).

correlations with the other sections of the tree, while no important differences can be noted in the inter-correlations for the sections of the middle and lower portions of the stem.

GENERAL DISCUSSION AND CONCLUSIONS

On the basis of the results of the analyses of terminal growth and ring-width values obtained from all four trees (Figures 1-4, Table 3), it is evident that ring widths and ring-width patterns throughout the tree are not only associated with age of the cambium and distance from the growing tip, but also with the rate of terminal growth. Rapid terminal growth of a young tree is accompanied by wide rings, especially in sections near the apical meristem, while the slow terminal growth of old trees is accompanied by narrow rings. Similarly, an increase in terminal growth associated with favorable climatic conditions is accompanied by an increase in ring width.

It appears that the gradual decrease in ring width, described as the dieaway growth curve characteristic of southwestern, semiarid lower forest border trees, may be attributed to changes in terminal growth as well as to increasing distance from the crown, increasing circumference of the ring, and increasing age of cambium. The relationship may be entirely induced by auxin, may result from changes in carbohydrate production and consumption due to growth and death of branches and to increasing volume of the ring, or more likely, may be a combination of these factors.

Duff and Nolan (1953) recognized a similar relationship in red pine. They were able to relate terminal and radial growth, year by year, when they separated conditions that affect bud formation from conditions that control axial extension. Kramer and Kozlowski (1960) suggest two major types of internal correlation systems, where "one mechanism operates through the action of hormones, the other through modification of the supplies of food, water, and minerals to the various organs." Larson (1963a) relates radial growth of red pine to changes in auxin produced in the stem tips. Mirov (1941) reports that auxin content is higher in shoots of rapidly growing ponderosa pine than in slow growing trees. Rapidly growing stem tips of relatively young trees would be accompanied by greater needle production and a large photosynthetic area producing large amounts of available carbohydrates within the young tree, resulting in wide rings. The proportion of carbohydrates used in respiration increases with increasing age of the tree. This is due both to the increased proportion of non-green living tissues and to the lower photosynthetic efficiency of the older branches (Kramer and Kozlowski, 1960). An increase in the rate of carbohydrates utilized for basic metabolic processes with increasing age may result in a gradually decreasing amount of carbohydrates available for terminal and radial growth. Also, a decrease in terminal growth would result in the formation of fewer leaves, or a decrease in new photosynthetic area, a lower rate of carbohydrate accumulation, and ultimately, less ring growth.

The low intra-correlation and inter-correlation among the first formed rings of each section and the low inter-correlation of the top portions of the tree imply that a closer proximity to the growing tip is accompanied by greater divergence in tree-ring characteristics from the response of the tree as a whole (Figures 1-4). This response divergency may be attributed to auxin gradients where short flushes of terminal growth, associated with favorable growing periods during the summer rainy season, may exert control over radial growth of stem portions which are closest to the auxin source (Larson 1962). It may be further inferred that ring widths in the very young, upper portions of lower forest border trees reflect differences in summer as well as winter and spring climate, while the older, basal portions, including the greater bulk of the tree, are more likely to provide a record of only winter and spring variations in climate (Douglass 1919; Glock 1937, and Fritts *et al.* 1965).

The intra-correlation (uniformity around the circuit) of OL-12 exhibits an apparent decrease at a cambium age of 100 to 120 years and is low in the middle sections located at heights from 55% to about 65% of the final height of the stem tip (see columns B and C in Figure 1). At this cambium age and at this height, major branches are developing and dying. This undoubtedly introduces differences in food and auxin supplies and causes circuit variability in the growth rings below the point of branch attachment (Larson 1962, 1963b). Low intra-correlations are noted near the base of OL-12. These may be associated with butt swell and the growth of major roots. Swelling in the tree butt is associated with the change in direction of the conducting elements at the root level which may impede the flow of growth substances and affect the cell geometry which ultimately influences ring growth (Farrar 1961). The somewhat high serial correlation at the basal sections shown in column C of Figure 1 suggests that in this region ring widths are increasingly serially related with greater age. This may arise in part from a gradual enlargement and increase of growth rate in the butt portion of stems.

The location of double rings within the tree also relates to auxin control of earlywood and latewood formation (Larson 1962, 1963a). Doubling or intra-annual ring formation (false ring) in the younger portions of OL-12 occurs more frequently near the base of the tree and in the earlywood portion of the tree-ring, but as the tree becomes older, the area of most frequent intra-annual rings shifts to the upper regions of the stem and to the outer portions of the ring. Schulman and Baldwin (1939) suggested that the doubling of rings in OL-12 may be related to mean ring width, rate of terminal growth and height in the tree. Larson (1962) states that "false rings occur in nature under a variety of conditions, but all can be associated with a temporary cessation of terminal growth followed by growth resumption as in the case of second flushes. First, the growth suspension must be of sufficient duration so that the diminishing auxin gradient can bring about production of cells with narrow diameters." This growth suspension usually starts at the base of the stem and progresses toward the top of the tree. Larson (1962) states that "the growth resumption must be sufficiently intense that a high auxin gradient can stimulate production of cells with large diameters. As in the case of second flushes, the auxin gradient originating from any slight growth resumption may produce new earlywood cells visible only in the upper reaches of the crown . . ."

In the typical northern Arizona climate with two maxima in precipitation during the winter and summer and drought during the spring and autumn, growth of young trees may start during the spring and terminate sometime during or after the summer rainy period. In years of below normal spring precipitation, latewood cells might be initiated before the summer rains start, and the latewood would probably be formed first near the base of the tree, progressing upward toward the tip. Summer precipitation would initiate a second flush of growth in young trees, and a second band of earlywood would be formed first in the upper part of the trunk, moving down to the base of the tree. In older trees, the initiation of latewood cells is likely to occur earlier in the season and may progress further up the stem before summer rains commence. In addition, the second flush of growth may be weaker and the auxin must travel a greater distance from the step tip to the base, so earlywood re-initiation is less likely to occur and even less likely to reach the base. As a result of these relationships, double rings in basal cross sections will most frequently occur in the central portions of the stem and in the inner portion of the ring. Double rings in the older portions of trees are more likely to be found near the stem tip and in the outer portion of the ring because the growing season is shorter and cambial activity is least likely to be reinitiated by summer rains in the lower stem.

The high frequency of partial or locally absent rings in the lower and older portions of conifers growing on marginal sites may be attributed to the failure of the cambial stimulus originating in the crown to reach the basal portions during years when the environment is particularly unfavorable. However, the high frequency of absent rings in the very young portions of OL-B, the tree closest to the forest border, and the abundance of absent rings near the top of both OL-B and OL-12 suggest that water deficits in he crown may be directly responsible for the failure of cambial initiation in the spring. Baker (1950) reports examples where water seems to become limiting in the tops of tall trees, resulting in decreased growth.

A number of differences among the studied trees may be related to differences in their respective sites. Tree OL-B, which grew in the most arid site, showed the greatest reduction of both terminal and radial growth as the tree matured. Ring width is relatively uniform vertically in the tree throughout the length of the growth layer except at the very top. The percentage of locally absent rings and the variation in width from ring to ring are high, especially near the top. The trees growing on more forest interior sites have both higher growth rates, especially in the crown portions of the stem, and lower variability from ring to ring. The forest border tree, OL-B, exhibited the highest serial correlation, while the intermediate site tree, OL-SO, exhibited the highest internal correlation and greatest consistency or ring-width variation within the stem.

Larson (1963b) and Farrar (1961) review the literature on ring growth and site as it relates to stem form and development of forest trees. Low taper in tree stems is common on optimum forest sites such as might be found at site OL-S, as the radial growth rate is higher in the upper crown portions of the main stem than in the lower branchless portions (Figure 2). On more marginal sites, perhaps similar to OL-B and OL-SO, stem taper is usually more pronounced because height growth is less and the ring increments are more uniformly distributed throughout the upper and lower portions of the stem.

The commonly used statistical parameters, standard deviation and serial correlation, do not clearly describe tree-ring index characteristics that relate to physiological or environmental gradients (Fritts *et al.* 1965). The standard deviations of tree-ring indices, as well as being measures of variability in the populations of indices, can be shown to be directly related to the mean of the population of indices (Fritts and Smith 1962). Similarly, serial correlation is a function of covariance, variance, and the standard deviation so when this parameter is used in tree-ring analysis, it may be dependent upon both serially related variation and the population mean. Conversely, when trends occur in tree-ring series and covariation between adjacent rings is high, the standard deviation, calculated from the total deviation of the population from its mean, will be a poor estimate of the amount of variation between adjacent rings.

In this analysis of the four trees, when the mean ring width varies inversely with the variability in ring widths (column B in Figure 1), standard deviation and serial correlation exhibit clear gradients. But when the mean ring width is independent of the variability (column D of Figure 1), the standard deviation and serial correlation do not exhibit consistent relationships.

Mean sensitivity, on the other hand, is a proportional measurement of adjacent ring-width variability and therefore is independent of the sample mean. Because of this property it provides a more suitable measure of ring width variability than the standard deviation and it exhibits more clearly defined patterns associated with gradients within and between trees (Fritts *et al.* 1965). Although serial correlation and standard deviation appear to be of limited value in evaluating certain tree-ring relationships, these measures should not be ignored as they do provide an estimate of degrees of freedom and confidence limits so that statements concerning probabilities may be made.

Although the early-formed central portions of basal cross sections of tree stems may contain wide rings which vary greatly around the circumference and longitudinally within the tree, these ring widths represent the early growth of the tree and are not found in the upper portions of the stem. When we compare characteristics of later-formed rings which are present in both the upper and lower portions of the stem in a semiarid site tree (column C in Figure 1; Figure 4), there are few differences in the chronologies at the different levels except for the sections nearest the top of the crown. These results indicate that not only do tree-ring samples taken at breast height from semiarid forest border trees provide the longest ring records, but also the relative fluctuations in growth patterns which can be measured from these samples are reliable estimates of ring variation throughout a large portion of the tree stem.

Differences in ring characteristics within the stem are less significant for trees in sites near the arid forest border than for trees in sites of the moist forest interior. Field selection of trees near the arid forest border not only enhances the relationships between growth and climate, but it assures that samples of ring series from lower portions in the stem are valid estimates of the ring chronology formed throughout the entire tree. Rather than making an intensive study using many samples from a few trees, a wider sampling of several basal radii from a large number of trees would seem necessary to provide the best sample for estimating regional climate. Nevertheless, intensive studies on a few trees can make important contributions to the understanding of the processes that govern tree growth.

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