

Annual Growth of Suppressed Chestnut Oak and Red Maple, A Basis for Hydrologic Inference

GEOLOGICAL SURVEY PROFESSIONAL PAPER 485-C

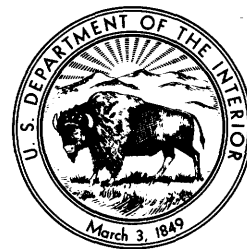


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By RICHARD L. PHIPPS

VEGETATION AND HYDROLOGIC PHENOMENA

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GLOSSARY

Annual increment.—The three-dimensional sheath of xylem added to stems and secondary roots each year. The annual increment has the appearance of a ring (annual ring) when viewed in cross section.

Auxins.—Growth regulators, such as hormones, affecting cell enlargement.

Basipetal.—Proceeding from the top toward the base.

Cambial activity.—The process by which cambial initials divide and form derivatives which differentiate into phloem cells outward from the cambium or xylem cells inward from the cambium.

Cambium.—A tissue in many higher plants, including trees, in which cells divide and form new tissues. The cambium is located in stems and woody roots (not in stem tips and root tips) between the wood (xylem) and inner bark (phloem).

Canopy.—The uppermost level of tree crowns in a forest. All tree crowns in the canopy level are exposed, at least in part, to direct sunlight.

Conifer.—Any cone-bearing tree (most of which trees retain their leaves, or needles, throughout the year) such as pine and hemlock.

Crown.—The part of a tree that includes leaf-bearing branches. There may or may not be a distinct branch-free trunk below the crown and a single main stem which may or may not be distinguishable in the crown (of deciduous trees).

Dbh.—Diameter at breast height. The approximate height (4½ ft above the ground) which is standard for diameter measurements of tree trunks.

Deciduous tree.—Tree, such as oak and hickory, which normally produces new leaves every spring, loses them in the fall of the same year, and overwinters in a leafless condition.

Dendrograph.—Instrument attached to a tree to obtain continuous records of radial growth (actually, radial change) and to record the measurements on a chart automatically.

Dendrometer.—A nonrecording instrument used to obtain periodic measurements of change in a radius of a tree trunk.

Diffuse-porous wood.—Wood in which the vessels are of fairly uniform size and distributed throughout each annual increment, as in red maple and birch.

Earlywood.—Inner part of an annual ring which, in a ring-porous species, contains much larger vessels than are in the outer, or latewood, part of the ring. Earlywood is recognized in diffuse-porous and nonporous woods by density, cell size, cell-wall thickness, and color variations.

Growth.—Increase in size by addition of new cells or cellular material.

Growth regulators.—Organic compounds produced by the tree, which increase and (or) decrease growth rates by affecting physiological processes which control cell division, enlargement, and differentiation. Auxins and hormones are examples of growth regulators.

Internode.—That part of a stem between nodes.

Latewood.—The outer part of an annual ring. See "earlywood."

Main stem.—The stem along the main axis of a tree which is or may become part of the tree trunk.

Node.—The point on a stem at which leaves and (or) branches arise or have arisen.

Nonporous wood.—Wood of conifers which does not contain vessels, as in pine or hemlock.

Phloem.—Food-conducting tissue which constitutes most of the inner bark and is located between the cambium and the outer bark.

Radial growth.—Increase in radius at a given height. Total radial-growth increment of a given year (minus bark increment) is ring width of that year.

Release.—A change in the external environment of a tree that reduces competition with other trees, as would result if the surrounding trees were removed. Decrease in suppression.

Ring.—Two-dimensional cross section of an annual increment.

Ring-porous wood.—Wood in which the vessels are of two distinct sizes, the larger being only in the inner (early-wood) part of the annual increment, as in oaks and hickories.

Stem.—Any of the above-ground parts of a tree which bear or have borne buds and leaves. The trunk and all branches are stems.

Subcanopy.—The lower part of the forest canopy. Trees located in the subcanopy are those whose crowns reach the lower level of the forest canopy.

Suppression.—A condition of growth retardation usually associated with competition.

Terminal growth increment.—An annual increment of longitudinal growth of the main stem.

Trunk.—The main stem of a tree; generally the branch-free part below the crown.

Xylem.—Water-conducting tissue of most plants and supporting tissue (wood) of trees. Develops inward from the cambium.

VEGETATION AND HYDROLOGIC PHENOMENA

ANNUAL GROWTH OF SUPPRESSED CHESTNUT OAK AND RED MAPLE, A BASIS FOR HYDROLOGIC INFERENCE

By RICHARD L. PHIPPS

ABSTRACT

Three-dimensional shape of individual annual xylem growth increments was ascertained from dissected ring-porous chestnut oak and diffuse-porous red maple trees from a native forest in southeastern Ohio. The increments are near paraboloidal, local deviations from true paraboloid shape being characteristic. The red maple rings (in transverse cross section) are widest near the base of the crown, but display only a slight basipetal increase in cross-sectional area. An entire ring of red maple appears somewhat analogous to the latewood of chestnut oak, the earlywood of chestnut oak being unlike that of red maple. The width of earlywood of chestnut oak does not decrease, or decreases only slightly basipetally, and is thus associated with a pronounced basipetal increase in total ring cross-sectional area.

Chestnut oak earlywood cells are hypothesized to have originated prior to the current growth season. Earlywood growth thus appears to be affected by an entirely different set of hydrologic conditions than red maple ring growth and chestnut oak latewood growth, which occur in late spring and early summer.

Annual ring growth of red maple and latewood growth of chestnut oak appear to occur at a successively later time in the growth season with distance from the top of the tree. Since water, probably the most limiting factor to growth, is apparently not typically in limiting supply during the early part of the growth season, little or no growth reduction occurs in the upper part of the tree during even extreme drought years. However, growth reduction throughout the tree may occur during the year after a drought, as a result of the physiological damage caused by the drought. Suppression, such as is induced by encroachment by surrounding trees, results in a similar decrease in growth at all heights which may be erroneously interpreted as resulting from several successive years of drought if rings from only one trunk level are examined. Release from suppression by surrounding trees and release from drought may possibly be distinguishable if ring patterns from more than one level in the trunk are examined. The interrelationships between earlywood and latewood formation in chestnut oak and the causal factors pursuant to variations in size of earlywood are not understood.

Discontinuous or missing rings are noted in annual rings of red maple and in the latewood of chestnut oak, primarily in the lower parts of the trunk during years of less than typical amounts of growth. Trees not severely suppressed would be expected to contain few ring discontinuities, and thus would contain rings more suitable for analysis in regard to climatic

conditions. It is botanically impossible for an annual ring to be missing throughout the entire length of the tree, and no evidence was found to indicate discontinuous earlywood growth of chestnut oak.

INTRODUCTION

A thorough understanding of the relationships between the growth of trees and their hydrologic environment is necessary before tree rings may be utilized with any degree of reliability to infer hydrologic conditions. The achievement of such an understanding is far from simple. Dobbs (1951) stated that, in general, botanists and foresters " * * * have shown the least interest in the remarkable record which the tree leaves behind it in the wood. This is understandable because it is they who are most likely to realize the complexity of that record." Glock (1955) in a review on the subject, stated that " * * * more and more * * * all workers have become impressed with the multiplicity of factors, the complexity of their interactions, and their detailed areal variability."

The purpose of this report is to describe ring growth of two deciduous tree species from measurements at several positions along the trunks. From these descriptions, several hypotheses will be presented concerning various influences of the hydrologic environment on ring form and size. This report is of a very limited and generalized study, which serves as the foundation of a more extensive and intensive research program. The ultimate objective of the program is the accurate estimation of hydrologic conditions from tree-growth records (rings). If successful, long-term ring records can be used to extend hydrologic histories in time prior to current records wherever trees of sufficient age still exist. Short-term ring records, which are readily available, may be used to estimate recent environmental conditions in areas where no hydrologic or climatologic data are available, such as in most first- and second-order stream valleys. Analysis of tree rings can also

be used in studies of changes in environmental conditions other than hydrologic, such as are brought about by acid mine drainage and changes in land usage.

ACKNOWLEDGMENTS

The study was conducted through the facilities of the Neotoma Ecological and Bioclimatic Laboratory of The Ohio State University. During the study, the laboratory was supported by the U.S. Atomic Energy Commission (contract No. AT(11-1)-552) through the Ohio Agricultural Experiment Station. Appreciation is expressed to the director of the laboratory, Dr. Gareth E. Gilbert, for his support and encouragement. Appreciation is expressed also to the owner of Neotoma valley, Dr. Edward S. Thomas, for the use of his land and for permission to remove the four trees utilized in these studies.

This report is based on parts of a thesis presented in partial fulfillment of the requirements for the degree, Doctor of Philosophy, at The Ohio State University. Several members of the Department of Botany and Plant Pathology of The Ohio State University contributed helpful criticisms and suggestions at various stages in the research. Jerry A. Koch, Ronald L. Laughlin, and Victor L. Riemenschneider, of the Neotoma Laboratory, were particularly helpful in interpretations of related studies.

Without the special interest and support of Robert S. Sigafos in all phases of the study, the expeditious completion of the work would not have been possible.

THE STUDY AREA

These studies were conducted in southeastern Ohio in a small valley named Neotoma, located in NE $\frac{1}{4}$ sec. 16, Good Hope Township, Hocking County (long. 82°33'18" W.; lat. 39°35'55" E.). The valley has been the location of ecological studies since the purchase of

the land by Edward S. Thomas in 1922. Extensive microclimatic studies were begun by Wolfe and associates in the late 1930's (Wolfe and others, 1949). More recent ecological and bioenvironmental studies (Wolfe and Gilbert, 1956; Gilbert, 1961, 1964) have been primarily concerned with the central part of Neotoma, but have also resulted in detailed descriptions of bedrock, soils, glacial deposits, and vegetation of the entire valley.

Neotoma lies just inside the western escarpment of the dissected Appalachian Plateau in southeastern Ohio. Bedrock of the Neotoma area is of two formations of Mississippian age, Logan and Cuyahoga (Wolfe and others, 1962). At Neotoma the sandstone of the Logan caps the underlying Black Hand Sandstone, but little of the Logan remains. Slight eastward dipping of all strata has affected the soil-moisture distribution (Laughlin, 1964) and the vegetation distribution in the valley (Koch, 1964).

Vegetation and distribution of soil types illustrate the diversity of habitats on the opposing slopes (figs. 1, 2). Generally, the upper slopes are dryer and contain coarser soils than the lower slopes, and the southwest-facing slope is dryer and has a somewhat more shallow soil than the northeast-facing slope (Riemenschneider, 1964).

A forest in which more than a third of the canopy-sized trees are chestnut oak occupies the upper fourth of the southwest-facing slope, the driest site below the rock cliffs. (Nomenclature of trees follows that used by Little (1953).) The soils of the chestnut oak area are a stony phase of DeKalb sandy loam, having internal drainage probably faster than in the DeKalb soils downslope.

Below the chestnut oak on the southwest-facing slope is a forest of mixed oak trees. American chestnut was an important member of the forest until its death in



FIGURE 1.—Lower northeast-facing slope vegetation (looking northward) through which cross-valley transect passes. Photograph by Alan Heilman, Ohio State University, October 1958.



FIGURE 2.—Middle southwest-facing slope vegetation looking northwest from area through which cross-valley transect passes. Photograph by Alan Hellman, Ohio State University, October 1958.

the late 1930's and early 1940's. Dominant canopy members now include scarlet oak, black oak, white oak, chestnut oak, and red maple—trees that were already present in the forest.

The upper northeast-facing slope is occupied by a forest consisting mostly of chestnut oak, yellow poplar, and red maple. This forest grows on a Neotoma sandy-loam soil which is typically wetter than the DeKalb soil of the oak forest of the opposite slope and dryer than the Neotoma sandy loam of the lower northeast-facing slope. Neotoma is a name recently proposed as a new soil series for which Neotoma valley is the type location (Finney, 1959). The forest growing on the lower northeast-facing slope is the most luxuriant forest type of the area. Canopy dominants include red oak, red maple, chestnut oak, American beech, white ash, butternut, white oak, sweet birch, black cherry, and yellow poplar. Canopy associates include eastern hemlock, mockernut hickory, black gum, sassafras, sugar maple, and black walnut.

THE STUDY TREES

DESCRIPTION OF TREES

A 20-meter-wide transect was established across the valley from the southwest-facing cliff to the northeast-facing cliff. The transect was established for several uses in the overall tree-growth research program, a part of which is described in this report. All the trees of 1-inch dbh (diameter at breast height) and larger along a 20-meter segment of the transect near the middle of the southwest-facing slope are represented diagrammatically in figure 3. The figure illustrates the relative

density of tree stems and layering and overlapping of crowns. The crown density was greater on the opposite slope. Across the entire transect, chestnut oak and red maple are the most numerous trees. Red maple, in 23 of the 34 plots of the transect, and chestnut oak, in 18 of the 34 plots, were chosen as the species for study.

Red maple is a fast-growing deciduous species typically associated with moist habitats, such as flood-plain forests, but capable of reproducing in a wide range of habitats in southeastern Ohio. Chestnut oak is the major tree species in forests on most dry ridges in sandstone areas of southeastern Ohio. Chestnut oak is not found on flood plains, as red maple is, but grows in many valley-slope forests. Red maple is a diffuse-porous species; chestnut oak is ring porous (see glossary).

A red maple and a chestnut oak were felled on each of two opposing slopes of Neotoma valley. Three of the trees were felled in September 1962. The fourth tree, a chestnut oak growing on the northeast-facing slope, was felled in February 1964. The four felled trees were subcanopy size and thus were expected to be characterized by a greater degree of suppression than canopy-sized trees. It was hypothesized that trees subjected to a high degree of suppression would be most likely to yield climatically "sensitive" rings, assuming that growth response to change in climatic factors would be magnified under conditions of growth stress. Thus, it was hoped that suppressed trees growing in the center of their range might be somewhat analogous to "sensitive" trees growing near the limits of their range.

Red maple RM-18 was in the subcanopy level of the lower northeast-facing slope of the sampling transect.

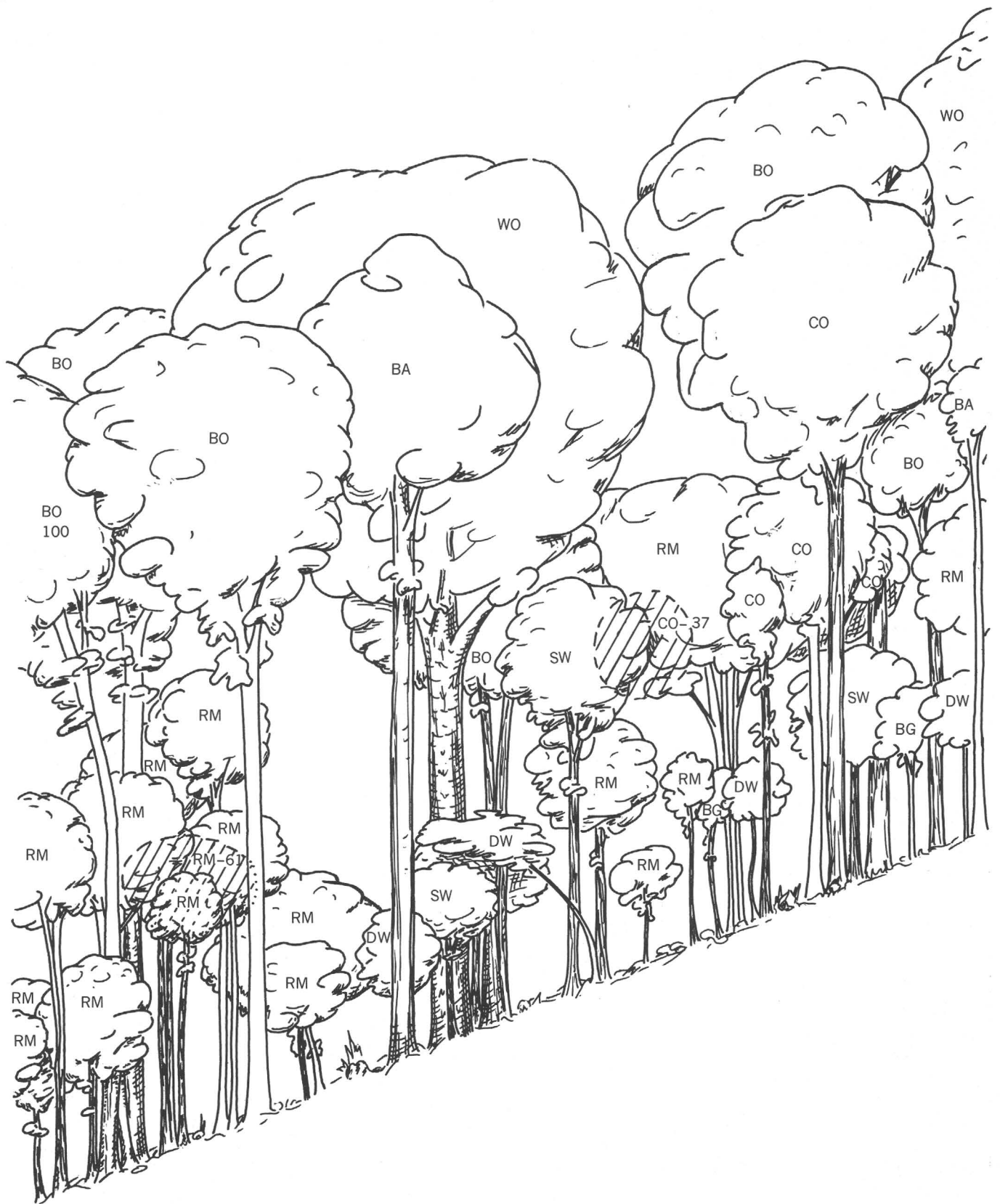


FIGURE 3.—Part of cross-valley transect on southwest-facing slope which included two of the trees felled for dissection. The felled trees were a red maple (RM-61) and a chestnut oak (CO-37), shown with a dashed outline. Other trees are indicated as follows: CO, chestnut oak; RM, red maple; BO, black oak; WO, white oak; BA, bigtooth aspen; SW, sourwood; DW, dogwood; BG, black gum.

RM-18 was overtopped by, and leaning slightly away from, a 16-inch dbh white oak canopy tree about 11 feet upslope and to the northwest. Two other canopy trees, a 10-inch mockernut hickory and a 9-inch white oak, partially overtopped RM-18. Removal of RM-18 made no hole in the canopy—evidence that all of the crown was overtopped. The main stem was forked at about 10 feet from the live top. One branch, about 16 feet in length, was dead. Death of the branch may have been attributable to overtopping by surrounding trees. The live branch may not have begun growth until after death of the other branch. Probably at least as ecologically significant in reducing soil moisture as the shading of RM-18 was the indirect effect of the large white oak upslope.

Red maple RM-61 was a subcanopy tree near the upper limit of the mixed oak forest of the southwest-facing slope (fig. 3). Like its counterpart (RM-18) on the opposite slope, RM-61 leaned slightly away from a large 16-inch dbh white oak canopy tree about 15 feet upslope. Also within 15 feet were two canopy-sized black oaks, but most overtopping was by the white oak with a spreading crown more than 30 feet in diameter. Unlike RM-18, it appeared that at least part of the RM-61 crown was exposed to direct sunlight, and no death of major branches was noted.

Chestnut oak CO-58 was a subcanopy tree on the upper northeast-facing slope. It leaned away from, and was overtopped by, a double-trunked canopy-sized chestnut oak about 20 feet upslope. It leaned into the lower part of the crown of an 8-inch dbh canopy-sized black oak about 8 feet away. Some of the terminal branches of CO-58 that were enmeshed in the black oak crown were dead, and lateral branches had become terminal leaders. The height of the dead branches was just above 30 feet. No samples were taken above this height.

Chestnut oak CO-37 was a subcanopy tree on the southwest-facing slope (fig. 3). It leaned slightly away from, and was only partially overtopped by, the same large white oak tree that almost completely overtopped RM-61. Other than the white oak, the closest tree of any size was an 8-inch canopy-sized black oak about 16 feet upslope. The crown of CO-37 was probably more directly exposed to solar radiation than the crowns of any of the other three sample trees.

A brief comparison of the four study trees follows:

	Red maple		Chestnut oak	
	RM-18	RM-61	CO-58	CO-37
dbh.....inches.....	4	3	5	4
Branch-free height.....feet.....	33	24	33	27
Total height.....do.....	45	32	51	43
Estimated crown diameter.....do.....	10	10	12	6
Age.....years.....	67	49	53	44

Average height growth for the entire life of the trees was about 1 foot per year for chestnut oak on both slopes and about $\frac{2}{3}$ foot per year for red maple on both slopes. Average yearly cross-sectional area increment at breast height was greater in the northeast-facing-slope study trees than in their southwest-facing-slope counterparts. However, inasmuch as such yearly averages of the trees are based on totals of all past main-stem growth, they are of value only in comparing present size of the trees. If, on the other hand, closeness of other trees, degree of overtopping, and death of major branches give some indication of present relative suppression of the trees, then, at the time of cutting, the study trees RM-18 and CO-58 on the moist northeast-facing slope were more suppressed than RM-61 and CO-37 on the opposite slope.

MEASUREMENT METHODS

The trees were cut as close to ground level as practicable, and cross sections 1–2 inches thick were removed at 3-foot intervals from the base to above the lowest major branching of the crown. Each cross section was marked upon removal to show the north side of the standing tree and the top side of the section. The sections were air dried, sanded, and polished. A reference line was inscribed with a knife along each radius to be measured.

Recent studies of rings at more than one sample height have been performed with red and loblolly pines (Duff and Nolan, 1953, 1957; Smith and Wilsie, 1961) from which cross sections were taken along the main stem halfway between each set of annual branch whorls. Because annual terminal-growth increments are distinguishable only near the ends of branches on deciduous trees such as red maple and chestnut oak, sampling of every annual terminal-growth increment is not practicable. It was believed that sampling at equidistant intervals might provide a means of analyzing growth allegedly induced as a result of nutrient or growth regulator gradients or both.

Ring width of RM-18 was measured along the north- and upslope-facing radii (approximately 135° apart). Annual-ring width measurements along the two radii were of sufficient difference that two additional radii were measured. Measurements of sections of the three remaining trees were taken along radii of the four major compass directions.

The width of the annual rings in the cross sections was measured to the nearest thousandth of an inch by the use of a mechanical stage equipped with a dial indicator. Parts of some cross sections were remeasured from time to time and at various positions in the range of the micrometer, and were always within 0.002 inch of the original reading. This slight range indicated

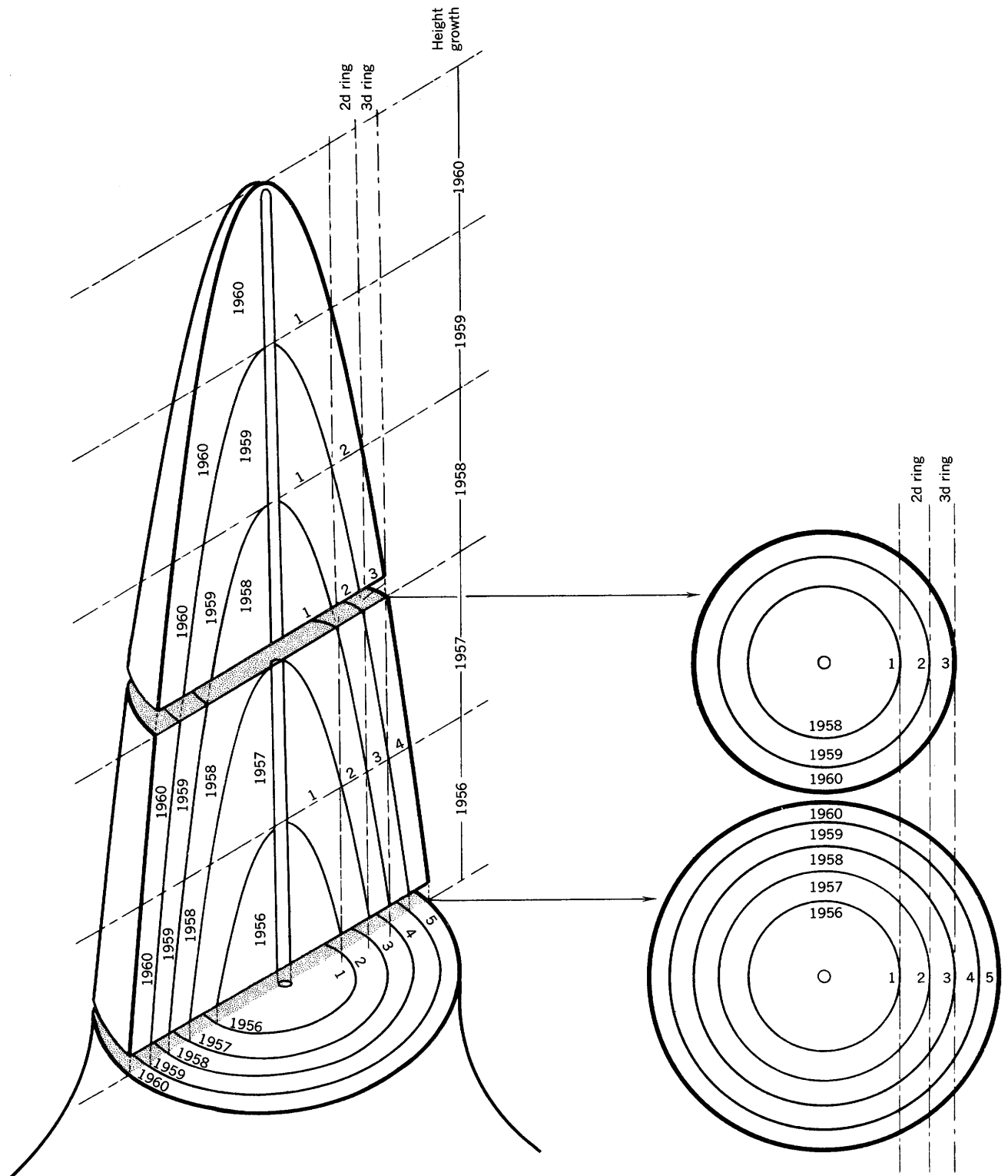


FIGURE 4.—Tree stem illustrating hypothesized three-dimensional relationships between rings and annual increments.

that (1) the accuracy of readings was consistent throughout the range of the micrometer, (2) the measurement cut provided a sufficiently distinct reference to allow repetition of measurements, and (3) the shrinking and swelling of the dried sections during the period of measurements were insignificant.

GROWTH FORM

Metzger (1893), according to Larson (1963) and Büsgen and Münch (1929), described tree-stem form as virtually that of a beam of uniform resistance to bending by wind. The beam thus described is a cubic paraboloid whose cubed diameter at any level is proportional to the distance from that level to the center of the tree crown. More recently, Gray (1956) suggested that the main stem of a tree may be described by a quadratic paraboloid. It should be noted that these workers did not describe individual annual increments as paraboloidal. Duff and Nolan (1953) described the characteristic patterns of annual rings in red pine and demonstrated that the general pattern from center outward at any given height progresses from wide rings to gradually narrower rings, and virtually the same pattern is found in any given annual increment progressing from the apex of the tree to the base. These findings were confirmed by Smith and Wilsie (1961) in work with loblolly pine. Neither Duff and Nolan nor Smith and Wilsie discussed the possibility of the paraboloid shape of individual annual increments or of the entire trunk, even though their descriptions satisfy the geometry of paraboloids.

If it is assumed (1) that the first few rings near the top of a small tree are the same shape as the first few rings near the top of a canopy-sized tree, that is, that the twigs are the same size and (2) that the annual increments are paraboloid, then it follows that all rings in a tree are of the same paraboloid shape. These assumptions, of course, presuppose that environmental conditions, and thus total annual growth, are the same from year to year. Under the above assumptions, the paraboloid patterns of annual increments of a stem grown under constant environmental conditions would be as illustrated in figure 4. Ring width of any given annual increment would be greatest near the apex of the annual increment and would become increasingly narrow with distance from the apex. Ring width of the centermost annual increment at any height would be the same as the width of the centermost annual increment of any other height at the same vertical distance from the apex of that annual increment, the second ring from the center at any height would be the same width as the second ring from the center at any other height, and so forth. Thus, as illustrated in the two cross sections of

figure 4, the third ring of the upper cross section is the same width as the third ring of the lower cross section, even though they were not formed during the same year.

According to the conditions of the hypothesis, the outer surface of any given annual increment would be the same shape as that of any other annual increment, and growth in length each year, by addition of a new annual increment, would be constant. In longitudinal section, the parabola shape of the outside of an annual increment may be described by the standard parabola equation

$$(2r)^2 = 4ay,$$

where $2r$ = parabola width, y = parabola length, and a = the constant, focal length. It follows that

$$\frac{(2r)^2}{y} = 4a,$$

which satisfies the conditions of a quadratic paraboloid as applied to tree stems by Gray (1956). The transverse cross-sectional area of a paraboloid segment defined by the parabola of equations above is obtained by the use of the standard equation for the area of a circle, $A = \pi r^2$.

In cross section, ring area of a given ring, n , becomes the difference in area between the cross section of the base of a paraboloid segment delimiting the outer surface of the n th annual increment and the cross section of the base of a paraboloid segment delimiting the outer surface of the preceding annual increment, $n-1$. According to the hypothesis, the two segments are of the same paraboloid. If growth in length is a constant, s , from year to year, then sn = length of the paraboloid segment delimiting the outer surface of n th annual increment and $s(n-1)$ = length of a paraboloid segment delimiting surface of $n-1$ annual increment, and

$$A_n = \pi r_n^2, \text{ where } r_n^2 = asn,$$

and

$$A_{n-1} = \pi r_{n-1}^2, \text{ where } r_{n-1}^2 = as(n-1).$$

Therefore, the cross-sectional area of the n th ring, R_n , is

$$\begin{aligned} R_n &= A_n - A_{n-1} \\ &= (\pi r_n^2) - (\pi r_{n-1}^2) = \pi(r_n^2 - r_{n-1}^2) \\ &= \pi[asn - as(n-1)] = \pi(asn - asn + as) \\ &= \pi as. \end{aligned}$$

Repeating the procedure for the area of the $n-1$ ring yields

$$\begin{aligned} R_{n-1} &= A_{n-1} - A_{n-2} \\ &= \pi(r_{n-1}^2 - r_{n-2}^2) \\ &= \pi[as(n-1) - as(n-2)] \\ &= \pi as. \end{aligned}$$

Thus, the cross-sectional area of any ring, R_n , is equal to the cross-sectional area of the preceding ring at the same height, R_{n-1} , providing that the annual increment of growth in length, s , remains constant. The same type of reasoning further indicates that the cross-sectional area of any ring at any height in the trunk should be the same as the cross-sectional area at any other height or in any other annual increment. This pattern is in agreement with the general statement of Pressler (1864) as noted by Larson (1963) that "*** in all parts of the branch-free stem, ring area growth will be the same." Pressler apparently did not suggest a paraboloid shape of individual annual increments. Jaccard (1912) assumed that a constant cross-sectional area of a given annual increment at all heights was necessary so water conduction along the stem would not be impeded. It is doubtful that Jaccard considered a constant cross-sectional area between rings at the same height. The equations above show that annual incre-

ment volume of any segment would be equal to the volume of any other annual increment segment of equal length. If the basic annual increment pattern can be shown to be paraboloidal, then the paraboloid could be a useful tool as a mathematical model in analyses of tree rings and annual increments.

ANNUAL INCREMENTS IN RED MAPLES RM-18 AND RM-61

Examination of the ring width sequence of a cross section of any level in the trunk of a tree reveals a time trend in ring width from wider rings near the center to narrower rings with increasing distance from the center (Douglass, 1936). If sequences of trees of various ages are plotted together by year of ring formation, interpretation of data of individual years is confounded because the center rings of one tree (inherently wide) may have been formed during the same years that the outer rings (inherently narrow) of another tree were

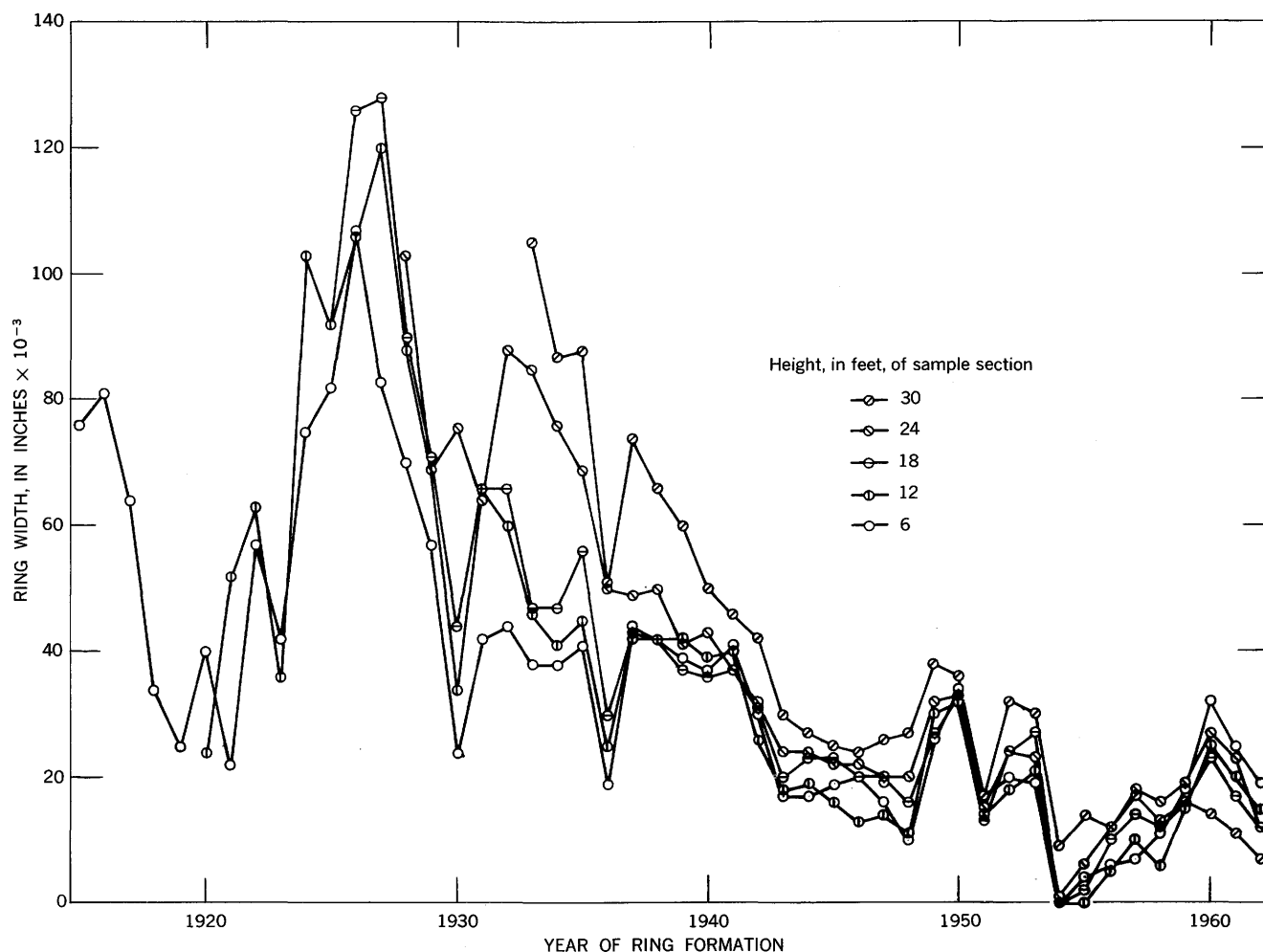


FIGURE 5.—Ring-width sequences of red maple RM-18 plotted by year of ring formation from cross sections at 6-foot intervals. Data are averages of measurements along four radii: north-facing, 112°, 225° (upslope-facing), and 337°. Date of center ring at each measurement: 1914 (6 ft), 1919 (12 ft), 1924 (18 ft), 1927 (24 ft), and 1932 (30 ft).

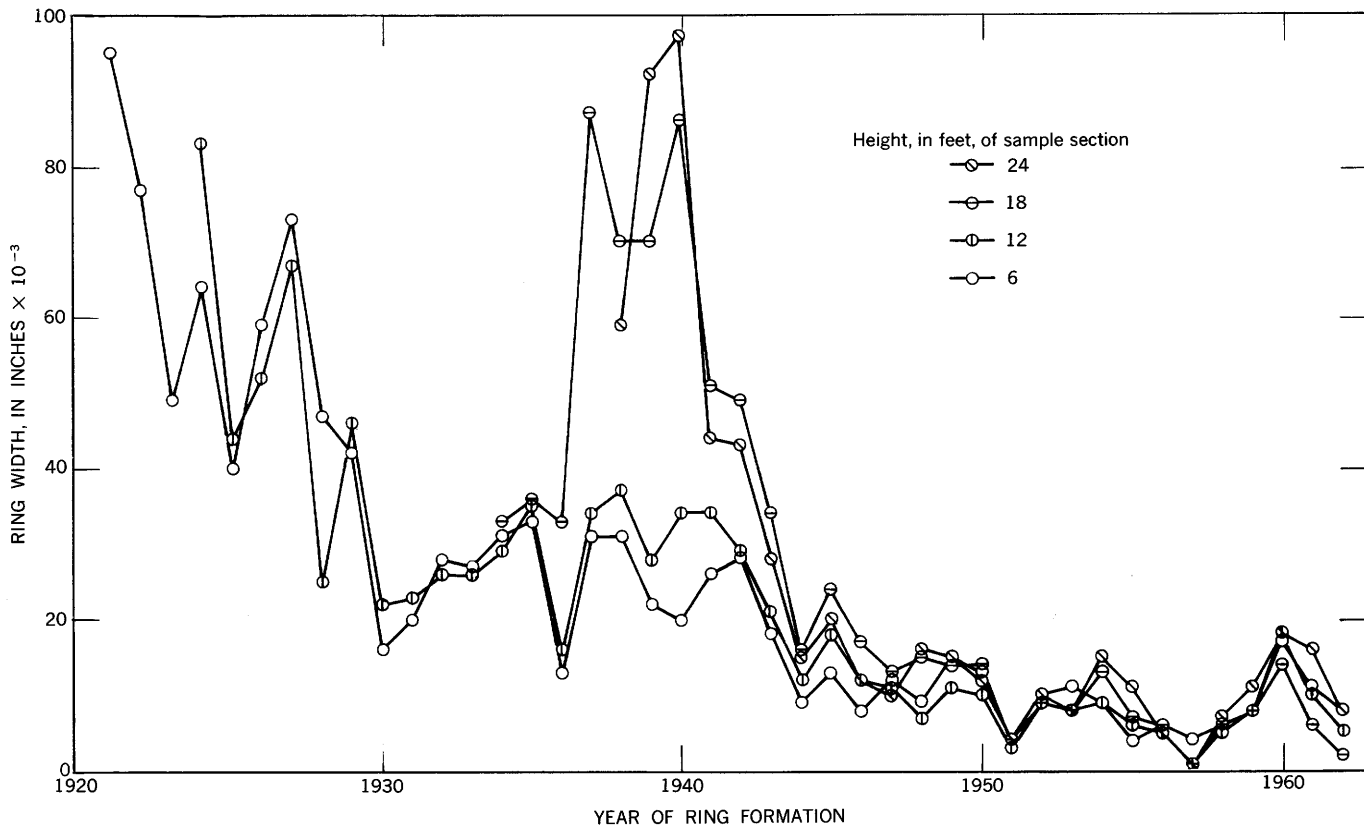


FIGURE 6.—Ring-width sequences of red maple RM-61 plotted by year of ring formation from cross sections at 6-foot intervals. Data are averages of measurements along radii of four major compass points. Date of second ring from center at each measurement height: 1921 (6 ft), 1924 (12 ft), 1934 (19½ ft), and 1938 (24 ft).

formed. The same confusion is observed if ring sequences from several heights in a tree are plotted together (figs. 5, 6), because since center rings at an upper level were formed during the same years as outer rings in the lower levels. Further complications arise if the inner rings at the upper levels are not inherently wide, as is apparently true of trees of the southwestern States (H. C. Fritts, written commun., December 1965).

Alinement of sequences from a single tree by ring number from the center of each cross section superimposes the time-trend curves. Such an alinement for red maple RM-18 is presented in figure 7 from sequences of figure 5. Alinement would permit examination of the shape of the time-trend curve, if the curve is approximately the same shape at all stem heights. Superimposed on the sequence graphs of figure 7 is a smooth curve representing ring widths determined from a series of perfect quadratic paraboloids of the shape delimited by the height and basal diameter of red maple RM-18. The smoothed curve thus represents the ring width sequence that RM-18 would have had if (1) the annual increment of height and of cross-sectional area from year to year had been constant during all of the 50 years represented, if (2) annual incre-

ment form were perfectly parabolic, and thus if (3) the time-trend curves were the same shape for cross sections at all stem heights. The greatest deviations from the smooth curve are the three peaks at rings 4, 9, and 13, and the apparent absence of growth at rings 28, 31, 36, and 41. Figure 5 indicates that the three peaks of figure 7 all occurred between 1925 and 1927 when growth at all levels was great. Figure 5 also indicates that all four growth minima occurred during 1954. If these instances of extreme growth were removed from figure 7, the rest of the data would approximate the smooth curve closely enough to suggest that, notwithstanding environmentally induced yearly variations in height and radial growth, annual growth increment may be somewhat parabolic.

Data from red maple RM-61 (fig. 6) were also replotted by ring number from the center of each cross-section and are presented in figure 8 along with a smooth curve from data of a series of perfect paraboloids. Again, the ring-width data have some correspondence to the smooth curve. The most striking deviations occur after the 23d ring. After that point, growth is consistently below the smooth curve, but reference to figure 6 indicates that all the rings formed after 1943

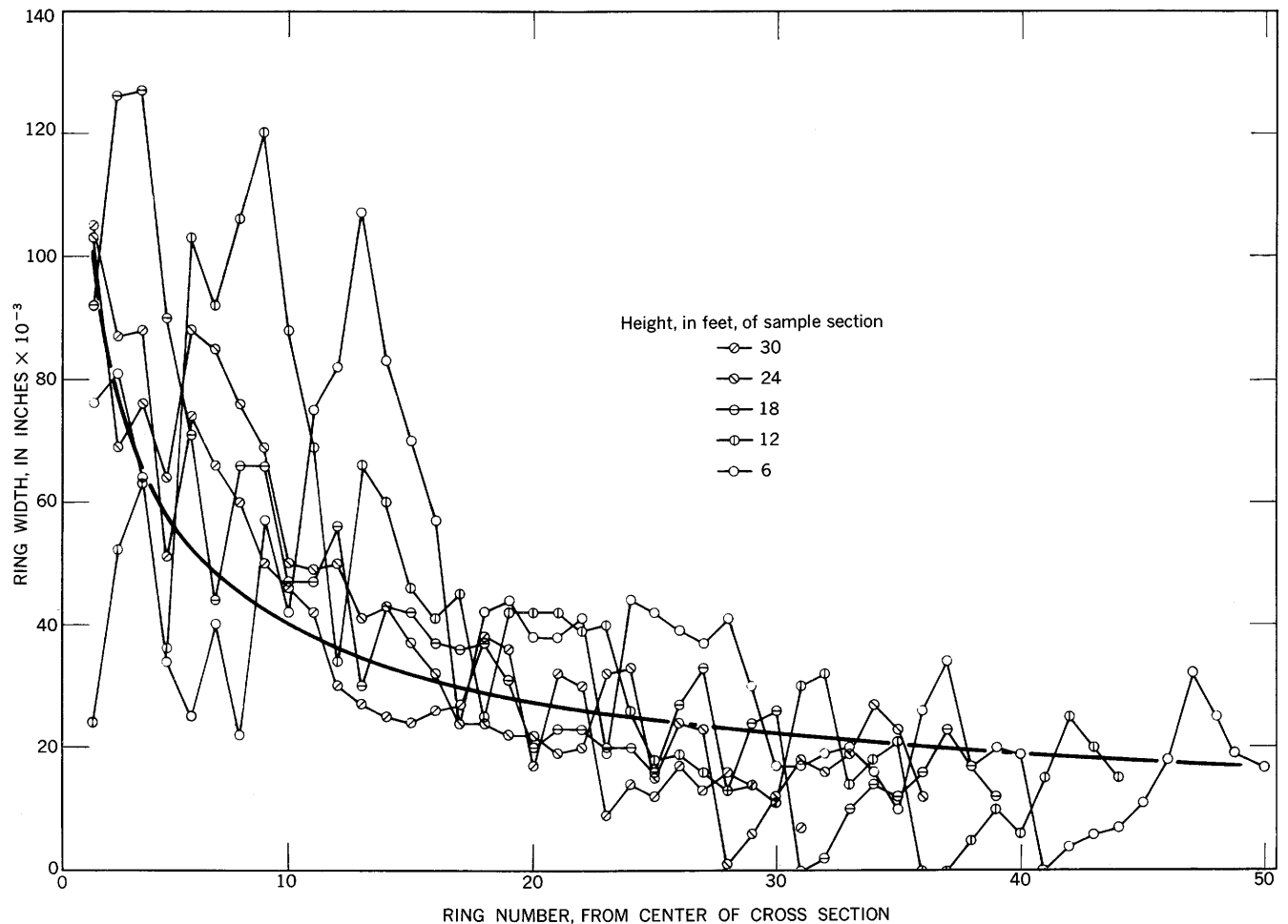


FIGURE 7.—Ring-width sequences of red maple RM-18 plotted by ring number from center of cross section. The sequences are identical to those of figure 5 plotted by year of ring formation. The smooth curve represents a ring width-sequence determined from a series of parabolooids.

were restricted in size. Something happened during or after 1943 which subsequently suppressed growth.

An indication of the general stem shape or form of the two red maples is presented in figure 9. Average radius at each sample height is plotted for 10-year intervals, and the date of the center ring at each sample height is also included. Horizontal exaggeration of the figure is 36 times and consideration of stem form as anything other than cone-shaped seems unjustifiable. However, other than the 0- and 3-foot levels of RM-61 which are considered as butt swell, width of the 10-year increments is generally greatest at the top—a feature that supports the paraboloid hypothesis.

An indication of changes in the rate of yearly height growth was obtained by noting the date of the center ring at each sample height in the study trees (fig. 10). All four trees were apparently growing rapidly in height by the time each was 6 feet tall, but the maples took considerably longer to reach this height than did the oaks. RM-18 appears to have remained in the for-

est understory for at least 20 years before commencing rapid height growth. Rate of height growth of all four trees appears to have declined at about the time the trees reached the lower part of the forest canopy (approximately 25 feet). Death of uppermost branches of RM-18 and CO-58 occurred above the 25-foot height.

According to the hypothesis of paraboloid shape, if yearly growth rate of a tree is constant, then the cross-sectional area of all rings (ring-area growth, R) is a constant, the time trend being a straight line parallel to the abscissa. Early workers who described trunk shape as parabolic agreed that within the crown the form of the main stem probably more closely approximates that of a cone than a paraboloid (Büsgen and Münch, 1929). Larson (1963), citing Pressler (1864), stated “* * * ring area growth (cross-sectional area of a single annual increment) at any given point on the stem is proportional to the quantity of foliage above this point.” Thus, the point of maximum ring width would not be at the top of the tree as suggested in figure 4, but near the

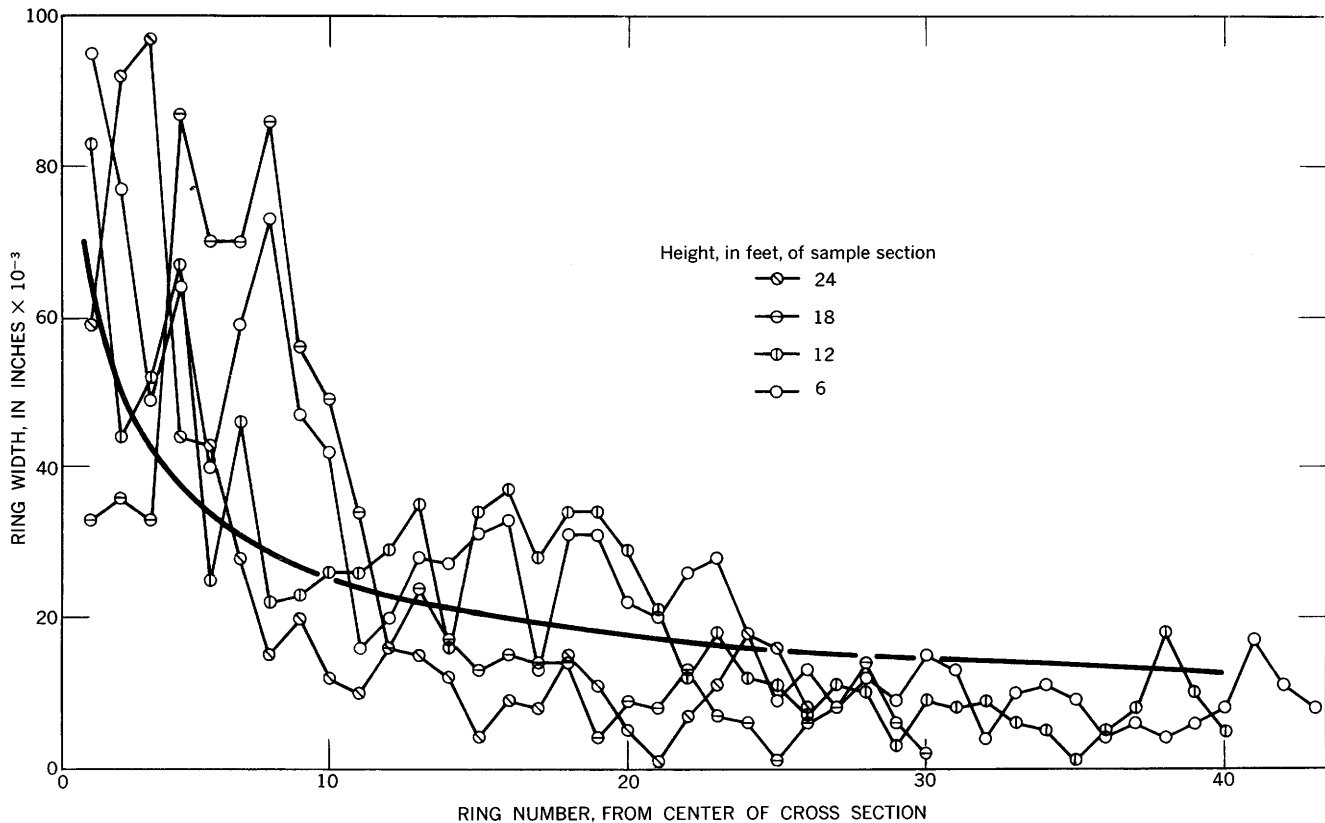


FIGURE 8.—Ring-width sequences of red maple RM-61 plotted by ring number from center of cross section. The sequences are identical to those of figure 6 plotted by year of ring formation. The smooth curve represents a ring width sequence from a series of paraboloids.

base of the crown. Duff and Nolan (1957) found that the point of maximum ring width was in the region of the crown base but that the exact position varied slightly from year to year; it was lower in years of accelerated radial growth and higher in years of restricted radial growth.

Ring-area growth, calculated from data of figures 7 and 8, are presented in figures 11 and 12. Ring-area growth from a series of perfect paraboloids defined by the height and basal diameter of the tree is included in each figure as a dotted line. Each dot thus represents ring-area growth of a single ring at any height and is equal to the average yearly ring-area growth at basal diameter height. Ring-area growth of the two red maples is indicated as consistently below hypothetical values for the first 4-6 rings. The combined data of the center six rings of figures 11 and 12 include rings representing all years from 1914 through 1942. It seems improbable that reduced growth of the first 6 rings at each level is the result of environment only. The first few rings at the center of each section would have been near the top of the tree when they were formed. Thus, in the upper levels of each annual increment, growth apparently is reduced from that of the hypothetical paraboloid shape. It could not be determined if stem

shape in the crown were cone shaped as suggested by earlier workers, but the growth curves indicate crown shapes more conelike than parabolic. The outer rings of the maples (figs. 11, 12) also appear to be reduced somewhat from the hypothetical paraboloid shape. Restricted growth in red maple RM-61 is probably associated with a change in the immediate environment of the tree during or shortly after 1943. In red maple RM-18, some of the outer rings appear to have been restricted but other outer rings were considerably greater than average size. In general, though, both the upper (lower ring numbers) and lower (higher ring numbers) parts of the stem appear to be somewhat constricted, relative to a perfect parabolic shape. The constrictions are in the tree crown at and above center of photosynthetic activity, and at the base of the tree, the stem part farthest from the photosynthetic source. Or, in other terms, the upper constriction is in the proximity of only a fraction of the stem tips where growth regulators presumably are formed. The upper central part is at or near the base of the crown (approximately equidistant from all stem tips) where the highest concentration of growth regulators might be expected, and the lower constriction is farthest from all the stem tips.

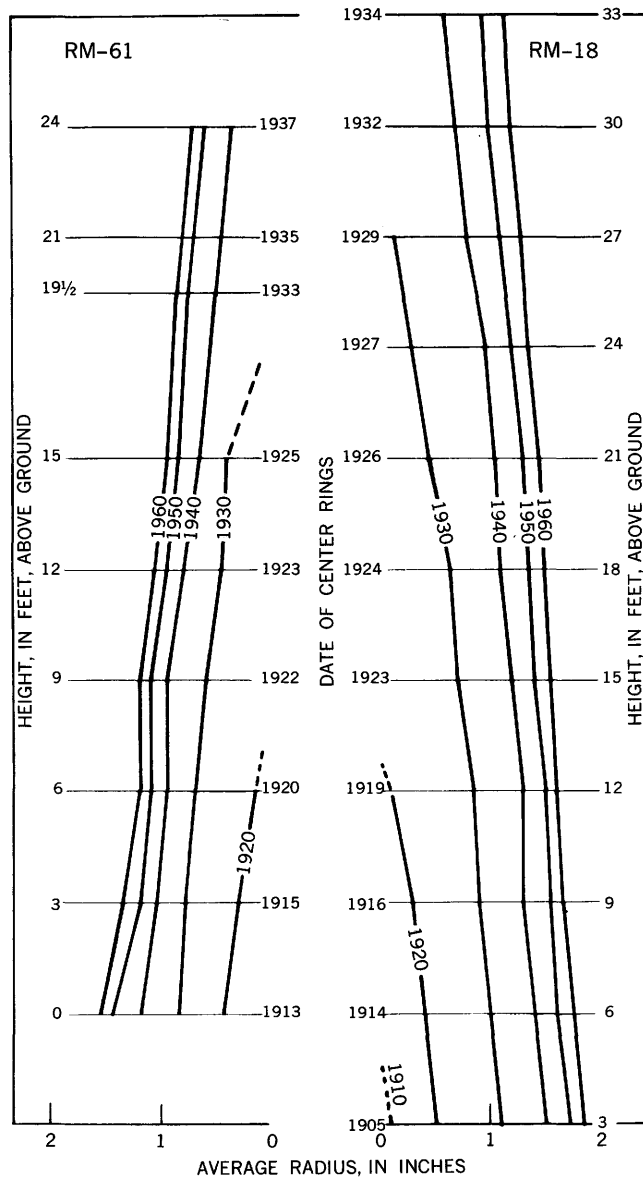


FIGURE 9.—Stem shape of red maples RM-18 and RM-61 at 10-year intervals.

Area increments of individual rings of the two maples are presented in figure 13 for the years 1927–32. Also included in the figure is a bar graph of evapotranspiration deficit for the late spring, early summer, and mid-summer seasons of the same years. The greater the water deficit, as indicated by the evapotranspiration deficit, the more reduced the growth near the bottom of the tree. Water deficit appears related to the basipetal ring-area trend. This relationship in turn suggests either that growth occurs later in the lower part of the tree than in the upper, or that growth stops first in the lower part. Most of the outer rings (higher ring numbers) of the two maples (figs. 11, 12) were smaller than the hypothetical situation.

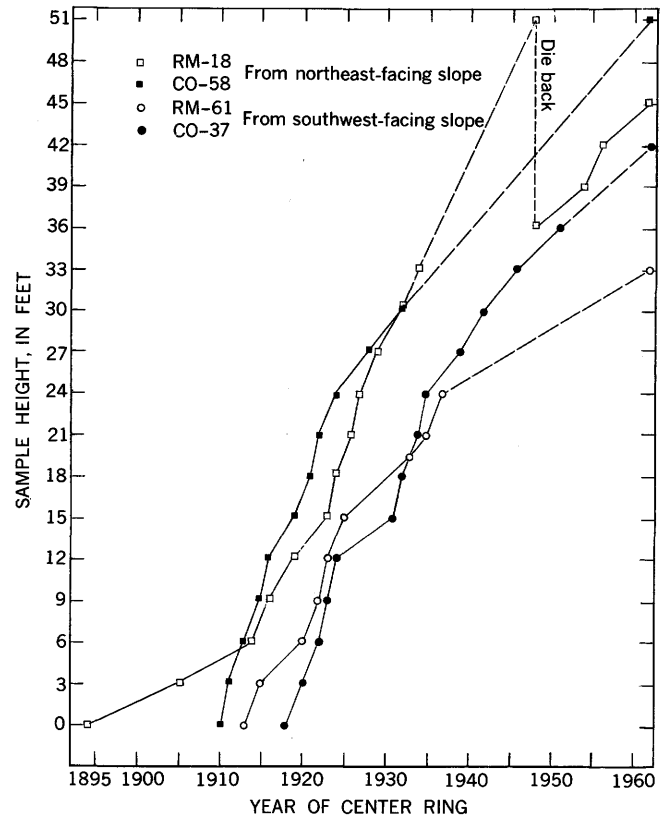


FIGURE 10.—Height growth of the four sample trees, plotted as year of center ring at each sample height.

Ring growth is the result of successful cambial-cell divisions and enlargement and differentiation of the cells thus derived. Growth is initiated each spring at or just beneath the actively developing buds at the branch tips, and progresses basipetally throughout the tree. It is generally agreed that the basipetal "wave" of initial cambial divisions progresses slowly in diffuse-porous species (3–4 weeks from buds to base, according to Wilcox, 1962) such as red maple. The bulk of the growth near the base of a tree occurs within about 10 weeks after initiation (Phipps, 1961). If it is assumed that growth at other heights in the tree occurs within about 10 weeks of the time it is initiated, then it can be calculated at least half of the growth at any height is occurring at the same time that growth is occurring at all heights. However, regardless of the time during which growth occurs simultaneously at all levels, growth at any given height may be affected by a somewhat different set of environmental conditions representing a different part of the growing season from those that affect growth at any other height. Each of the three cell-growth processes—division, enlargement, and differentiation—is probably controlled by availability of carbohydrates and growth regulators in specific quantities. However, as pointed out by Kozlowski (1962),

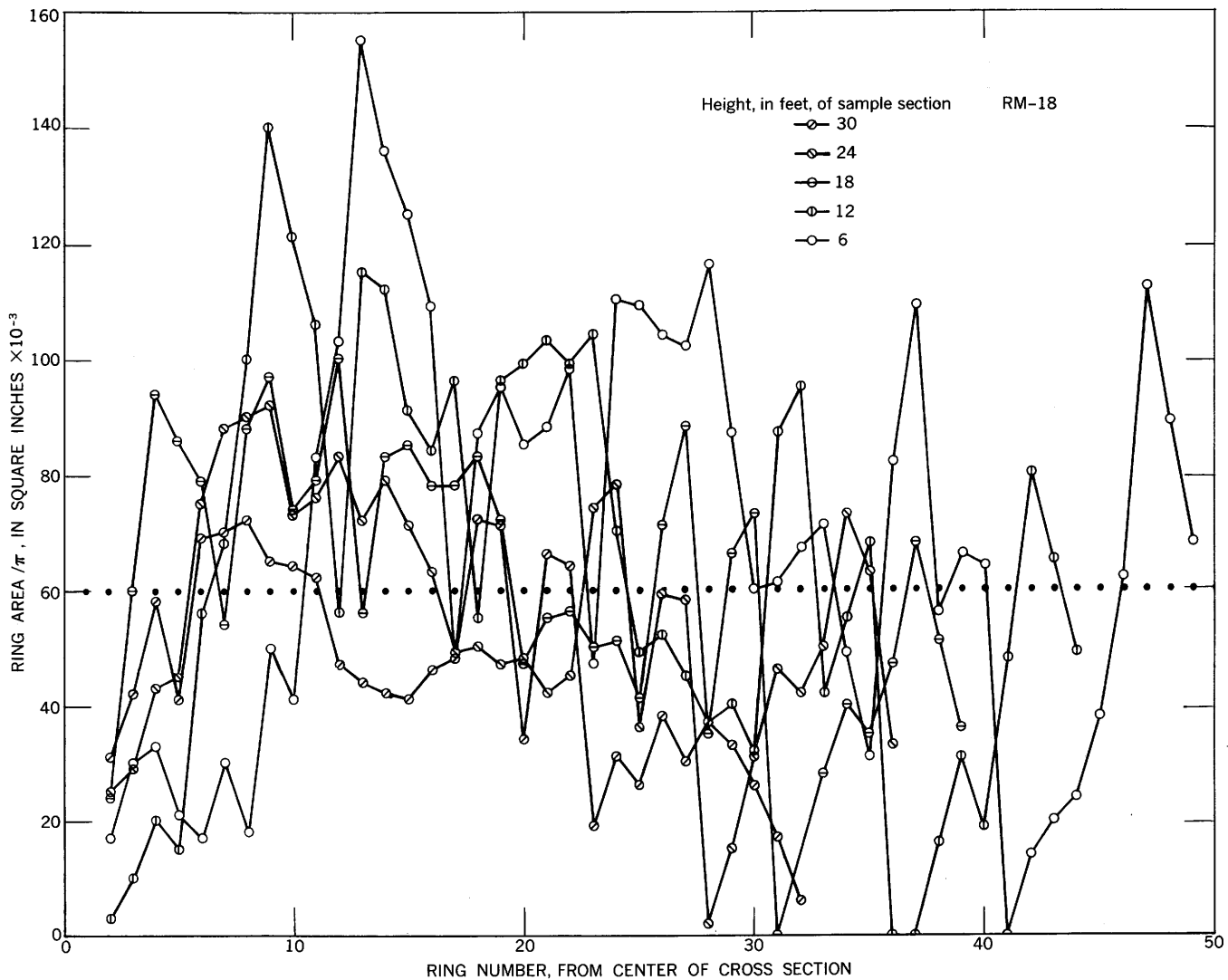


FIGURE 11.—Ring-area growth by ring number from section center of red maple RM-18 plotted by cross-sectional sequences at 6-foot intervals as was figure 5. Solid dots represent ring-area growth of a single ring at any height.

a correlation between carbohydrate and auxin levels complicates a separation of these two as distinct casual factors in growth determinations. For simplification, then, growth is regarded as the result of a complex of interrelated physiological processes, each of which may be varied by any of several environmental conditions. By further simplification, growth at any particular level in the tree is regarded as an expression of surplus photosynthates of the tree at the time growth at that level occurred, and is in turn conditioned by the environmental conditions of the tree at that time. Investigations concerning the time and rate of growth at various levels in the tree are being conducted, and are part of the larger tree-growth research program.

Ten-year ring-area increments calculated from data of figure 9 are given in figure 14. As suggested above (figs. 11, 12), ring increment is somewhat less at the

upper than at the middle trunk heights. A regression fitted to the average annual ring-area-per-year data of RM-18 (fig. 14) appears to be straight line, contrary to the implications of figures 11 and 12, and does not indicate a decrease at the lower trunk heights. If it is assumed that growth occurs at different times at different levels in the tree, then growth of a single ring would not be expected to be constant at all levels because environmental conditions do not remain constant. The data to which the regression line (fig. 14) was fitted represent average annual ring-area growth ($\times 10$) during a 30-year period. How different the slope of this line would be if it represented data for more than 30 years is not known. Because the ring-area (abscissa scale) exaggeration of figure 14 is 240 times, it might be assumed that ring area is virtually constant at all levels. However, the increase in ring area with decreas-

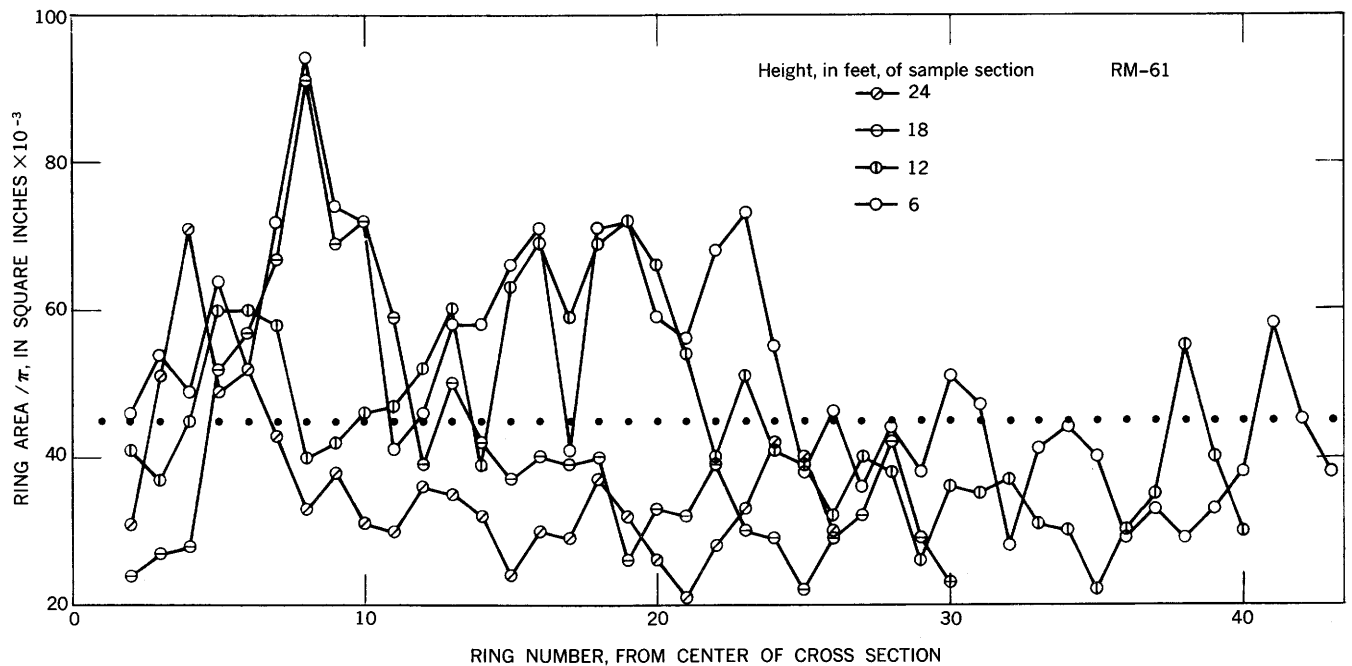


FIGURE 12.—Ring area growth by ring number from section center of red maple RM-61 plotted by cross-sectional sequences at 6-foot intervals as was figure 6. Solid dots represent ring-area growth of a single ring at any height.

ing height is significant. For example, average ring-area growth (1930–60) of RM-18 is one-third again as great at the 3-foot level as at the 27-foot level. Thus, though ring-area growth apparently is nearly constant throughout the tree, a linear increase with distance from the top is suggested strongly enough that it can be assumed that the shape of the plotted ring-area growth only approaches a paraboloid.

Figure 14 indicates a decrease in growth with time in both trees, that is, growth was greatest during the first 10-year interval, 1931–40, and least during the last 10-year interval, 1951–60. This trend seems in agreement with the same general trend of a decreasing rate of height growth during the same period (fig. 10). It might be suspected that as the trees became subjected to increased suppression beneath the forest canopy, growth in height and growth in diameter would decrease. Because of both the decrease in total incremental growth and the basipetal increase in growth of given increments, the general trend in ring area at any given height decreases (figs. 11, 12, and 14). Therefore, decreasing size of the total xylem increments was the factor controlling the time trend of decreasing ring area at any given height in the two suppressed red maples. If the trees had not been suppressed, perhaps the total xylem increments would not have decreased in successive years, and the basipetal trend of increasing ring area could have become the controlling influence of the time trend at any given height. In such conditions, the time trend would have indicated increasing ring area. Further,

if the trees had been released, the same time trend of increasing ring area would have been expected to follow. The change from narrow to wide rings might be indistinguishable from the change resulting when an extended drought is broken, if rings from only one height in the tree were examined.

General overall shape of the main stem of each of the red maples indicated stem form to be somewhat parabolic. Ring-area distribution in individual xylem increments of the stem deviates strongly from the paraboloid pattern. In general, the upper part of each increment was smaller than that explained as paraboloid, and is believed to have been in the crown of the tree at the time of formation. The lower part of most increments is also somewhat reduced from that of the perfect paraboloid. This reduction is inferred to be the result of the conditions of suppression under which the trees grew; such a reduction probably would not be apparent in trees not severely suppressed. A basipetal trend of increasing ring area was noted in most increments, but the lower parts of increments formed during marked drought years were greatly reduced in size. Decreasing rates of height growth were associated with increasing suppression because such decreases apparently did not occur until tree height reached the proximity of the lower part of the forest canopy. Concurrent with decreasing rates of height growth was a general decrease in total annual increment, also thought to be a result of increasing suppression.

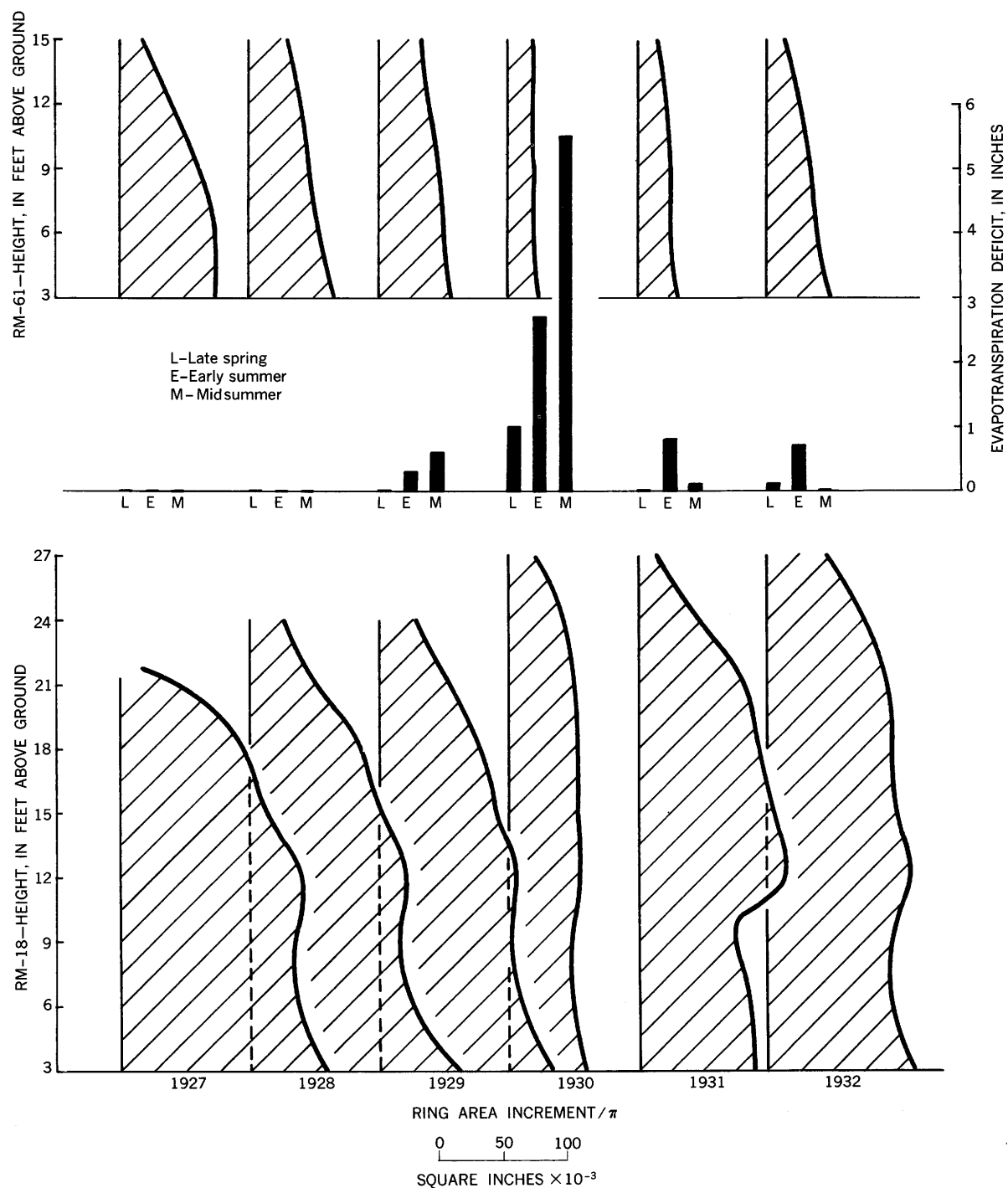


FIGURE 13.—Vertical distribution of annual ring-area increment in RM-61 and RM-18 for 1927-32, and evapotranspiration deficit of late spring, early summer, and midsummer seasons.

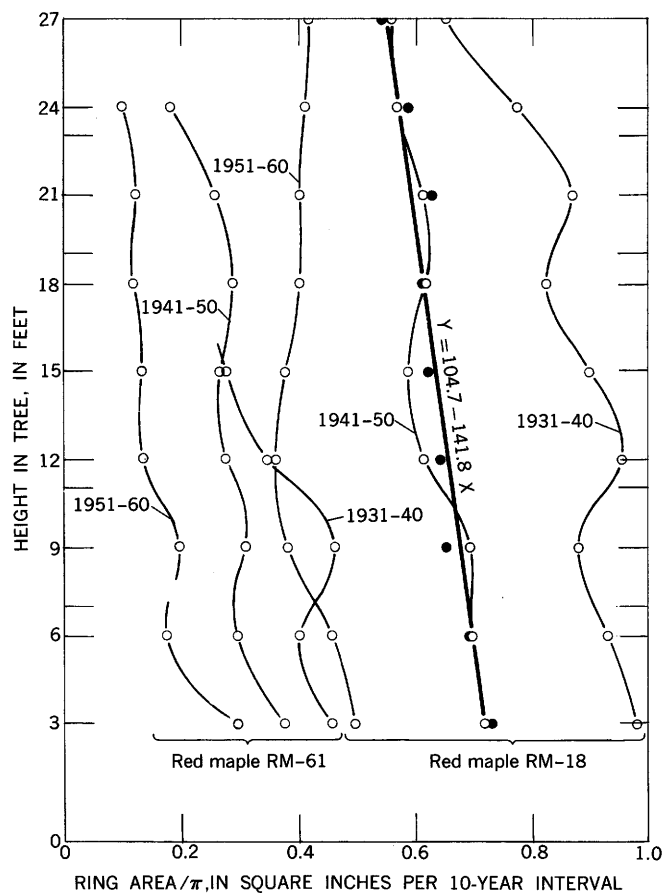


FIGURE 14.—Ten-year ring-area growth increments of red maples RM-18 and RM-61. A regression line has been fitted to the points representing average yearly ring area ($\times 10$) of RM-18 during the years 1931-60.

Trends in changes of the total size of xylem increments possibly are descriptive of general conditions of the tree as influenced by slowly changing factors of environment such as would affect suppression. The basipetal trend of ring areas appears to be an expression of climatic conditions at the time of increment formation. Thus, the radial time trend at any given height apparently is an integrated expression of both the total size trend and the basipetal trend of the increment; therefore, exclusive examination of a radial series of ring areas such as obtained from an increment core probably could not be used to decipher the separate influences of changing suppression by surrounding vegetation and of changing climatic conditions. In theory, a master chronology could be used to remove the effects of age and suppression from a given radial series of ring widths. This procedure presupposes that the series can be cross dated with the master chronology and that the master chronology was synthesized from a sufficiently great number of series to insure that the effects of age and suppression have been completely removed. On

the other hand, the effects of age and suppression probably could be removed subsequent to examination of radial ring series from more than one height in the same tree. This method would be contingent only on successful cross dating between heights.

EARLYWOOD GROWTH OF CHESTNUT OAKS CO-58 AND CO-37

The terms "earlywood" or "spring wood" and "latewood" or "summer wood" have been extensively used in tree-growth literature and have been applied to non-porous, diffuse-porous, and ring-porous woods. Earlywood and latewood were measured separately in the chestnut oak study trees, but no attempt was made to separate the two in the red maple. Even though earlywood and latewood may be easily distinguishable in diffuse-porous xylem, Chalk (1937) appears to have considered the entire diffuse-porous ring as analagous to the latewood part of the ring-porous ring. The daily radial-growth rate of red maple for a single year may be represented by a single peaked curve characteristic of diffuse-porous species; that of chestnut oak is a double peaked curve characteristic of ring-porous species (fig. 15). Fritts (1962) has demonstrated with dendrographs that the first peak of growth of ring-porous white oak corresponds to the growth of the pore zone, or earlywood, of the ring. Dendrometer investigation of Phipps (1961) indicated that the second-growth peak of white oak and chestnut oak roughly corresponds in time with the single peak of red maple and beech (also diffuse porous).

Earlywood growth is apparently initiated almost simultaneously at all levels in the trunk in ring-porous species at about the beginning of bud activity in the spring (Priestly and Scott, 1936). It is not known if initiation of latewood growth proceeds in a slow basipetal fashion in chestnut oak as the increment growth of red maple characteristically does. If this type of growth occurs, then it might take 3-4 weeks for latewood growth initiation to move down the tree. Thus, if earlywood growth, which starts simultaneously throughout the tree, begins 4-5 weeks earlier at the base than latewood, then latewood growth is initiated in the crown at about the same time that earlywood growth is beginning. This relationship, of course, is impossible unless the cells comprising the earlywood layer are already present in the cambial layer as derivatives at the beginning of the growth season. If this hypothesis is correct, then the first growth-rate peak indicated by dendrometer measurements at breast height (fig. 15) is not a reflection of cambial-cell divisions, but of cell enlargement.

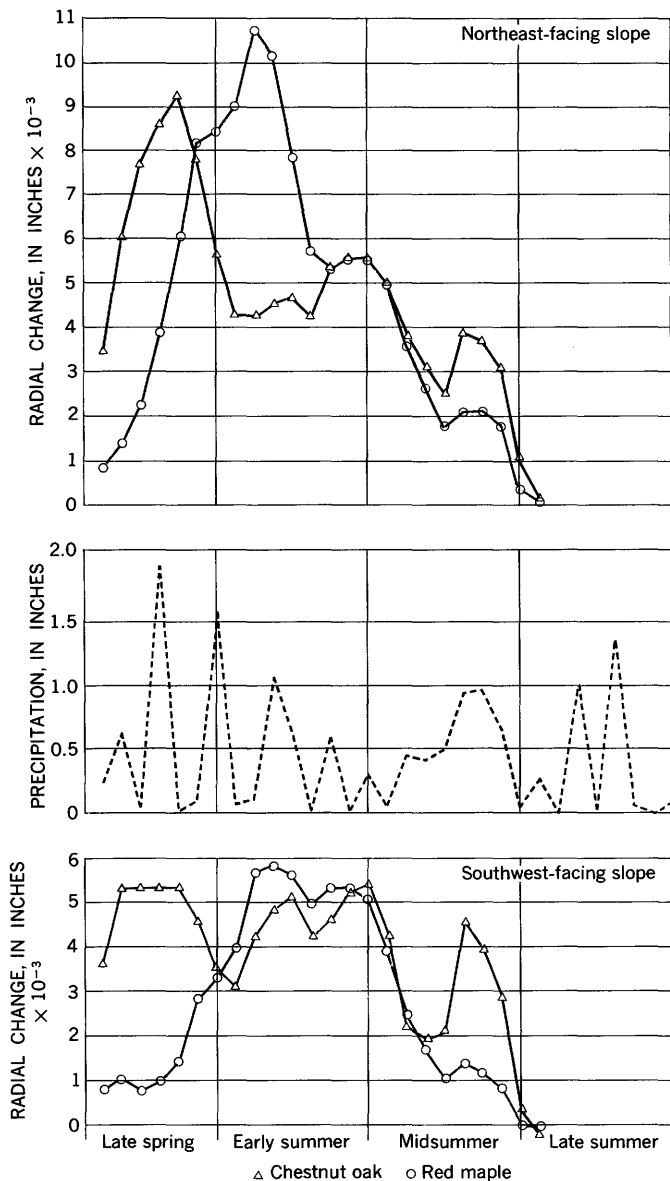


FIGURE 15.—Growth rates (as radial change) of a chestnut oak and a red maple on each slope, and precipitation during spring and summer, 1959. Growth data from Phipps and Gilbert (1961).

Examination of the dissected chestnut oaks revealed no earlywood in the centermost ring of any cross section. The centermost ring at any level was, during the year of its formation, part of the terminal leader. When growth in length occurs in spring, the first secondary xylem to develop (as a result of cambial activity) appears to be only latewood. Formation of latewood associated with growth in length thus occurs before full leaf expansion, which is at the time that earlywood growth occurs at all levels simultaneously. Thus, earlywood growth must be in progress near the top of the tree at the time that cambial activity in the terminal leaders is producing latewood initials.

The effects of wounding on growth, as described by Phipps (1961), may be explained on the basis of this hypothesis, if it is assumed that the wound hormone stimulates cell divisions. Dendrometer screws installed in chestnut oaks during the winter dormant period had no apparent effect on earlywood growth of the first year. Excessive radial growth attributable to wounding was noted only for the latewood of the first year and the earlywood of the second year after installation of the screws. Excessive growth associated with wounding apparently may result from a concentration of growth regulators which induce cell division. Thus, in accordance with the hypothesis outlined above, excessive cell divisions of earlywood initials would affect growth of the second year after wounding, not the first.

Wareing (1951) debudded ring-porous and diffuse-porous trees as a check of the contention that growth-initiating substances originate in the buds. He noted no ring formation in debudded diffuse-porous trees except for a short distance below "strong adventitious buds." In ring-porous species, new annual-ring formation occurred in both control and debudded trees. Wareing (1951) suggested that a reserve of an auxin-precursor was present in the cambium of the ring-porous species prior to the growth season and that some environmental condition triggered the conversion of precursor to auxin throughout the tree. This conversion, he reasoned, would explain simultaneous growth initiation throughout the tree, even when the tree is debudded. The new annual ring formation in debudded ring-porous species referred to by Wareing probably was only earlywood. Earlywood would be expected to form in debudded ring-porous species if, as hypothesized above, undifferentiated earlywood cells are present in the cambial layer before growth initiation in the spring.

Latewood growth of ring-porous species may be similar to the entire growth ring of diffuse-porous species. Further, a number of cambial derivatives may remain undeveloped at the end of the growth season. When triggered by some environmental stimulus in the spring, these derivatives simultaneously begin to develop into earlywood tissue throughout the tree. The first cambial divisions in the spring thus result in latewood initials. Near the branch tips, just below the current year's growth in length, earlywood and latewood growth is occurring simultaneously, and with increasing distance down the trunk, latewood growth is occurring increasingly later relative to the time of earlywood growth.

The ring-width sequences for both earlywood and latewood of CO-58 and CO-37 are presented in figures 16 and 17. The similarity between the curve for chestnut oak latewood (figs. 16, 17) and the curve for the

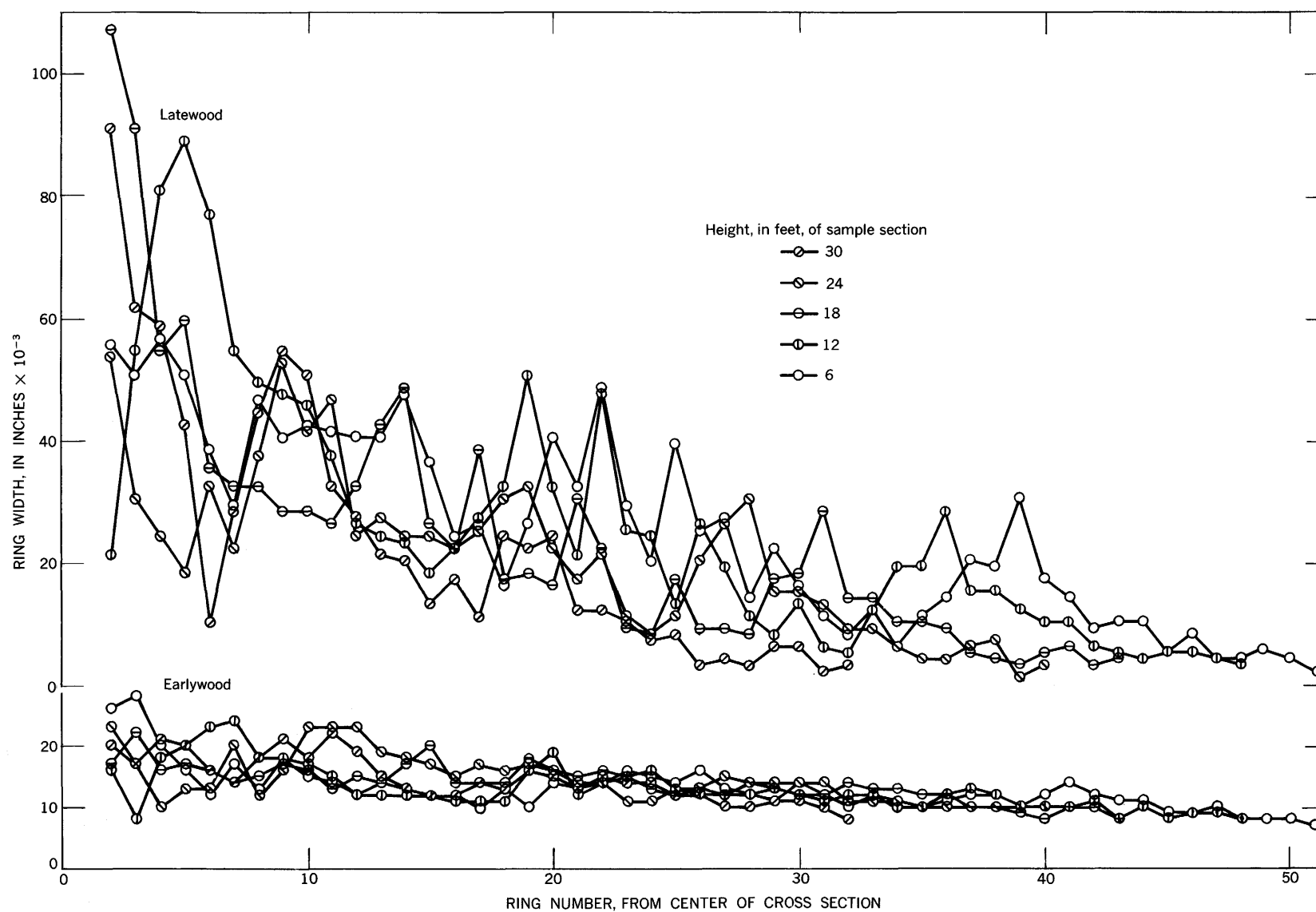


FIGURE 16.—Annual ring-width sequences of earlywood and latewood of chestnut oak CO-58 by ring number from cross section center. Data are from cross sections at 6-foot intervals along the trunk.

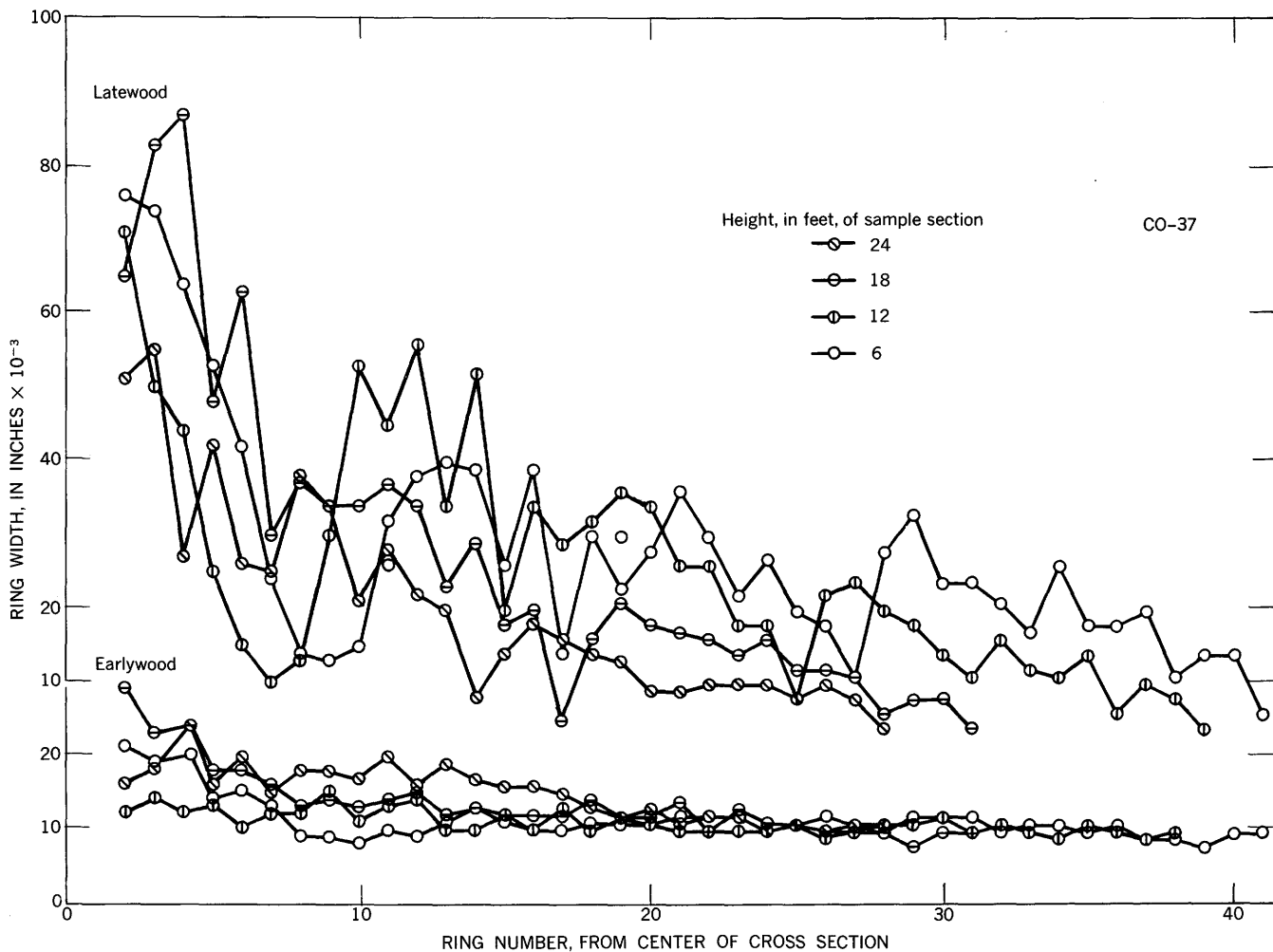


FIGURE 17.—Annual ring-width sequences of earlywood and latewood of chestnut oak CO-37 by ring number from cross section center. Data are from cross sections at 6-foot intervals along the trunk.

total ring width of red maple (fig. 7) is obvious. The major difference between the two is in the first few rings, red maple characteristically beginning with narrow rings and the first rings of a given sample height of chestnut oak characteristically being the widest.

The earlywood data presented in figures 16 and 17 suggest characteristics quite unlike either total ring growth of red maple or latewood growth of chestnut oak. Earlywood growth generally accounts for considerably less of the total ring width than does latewood, but with increasing age (at any given level) the relationship may be occasionally reversed because of the greater variability of latewood growth. Indeed, lack of variability between levels or between adjacent rings of a given level is a pronounced characteristic of earlywood growth. This characteristic is enhanced by the fact that earlywood growth was always greater than a minimum value (4×10^{-3} in. for oak of fig. 18), while latewood may even be discontinuous.

Ring-area growth of chestnut oak latewood (fig. 19) is geometrically similar to the total ring growth of red maple (fig. 11). However, the addition of earlywood (fig. 19) results in a slightly different total ring shape. The generalized curve for total ring area (fig. 19) does not indicate a significant decrease in area with age (of a given level), and the parabolic stem shape thus was not as constricted at the base as was that of the red maples. It might be expected, then, that suppressed subcanopy chestnut oaks could be characterized by a stem with a greater degree of taper than those of suppressed subcanopy red maples.

DISCONTINUOUS RINGS

Since the advent of ring-chronology work as a tool in recent archeological dating, the occurrence of multiple annual rings (more than one apparent ring per year) and the absence of some rings have been widely known and extensively documented in the literature.

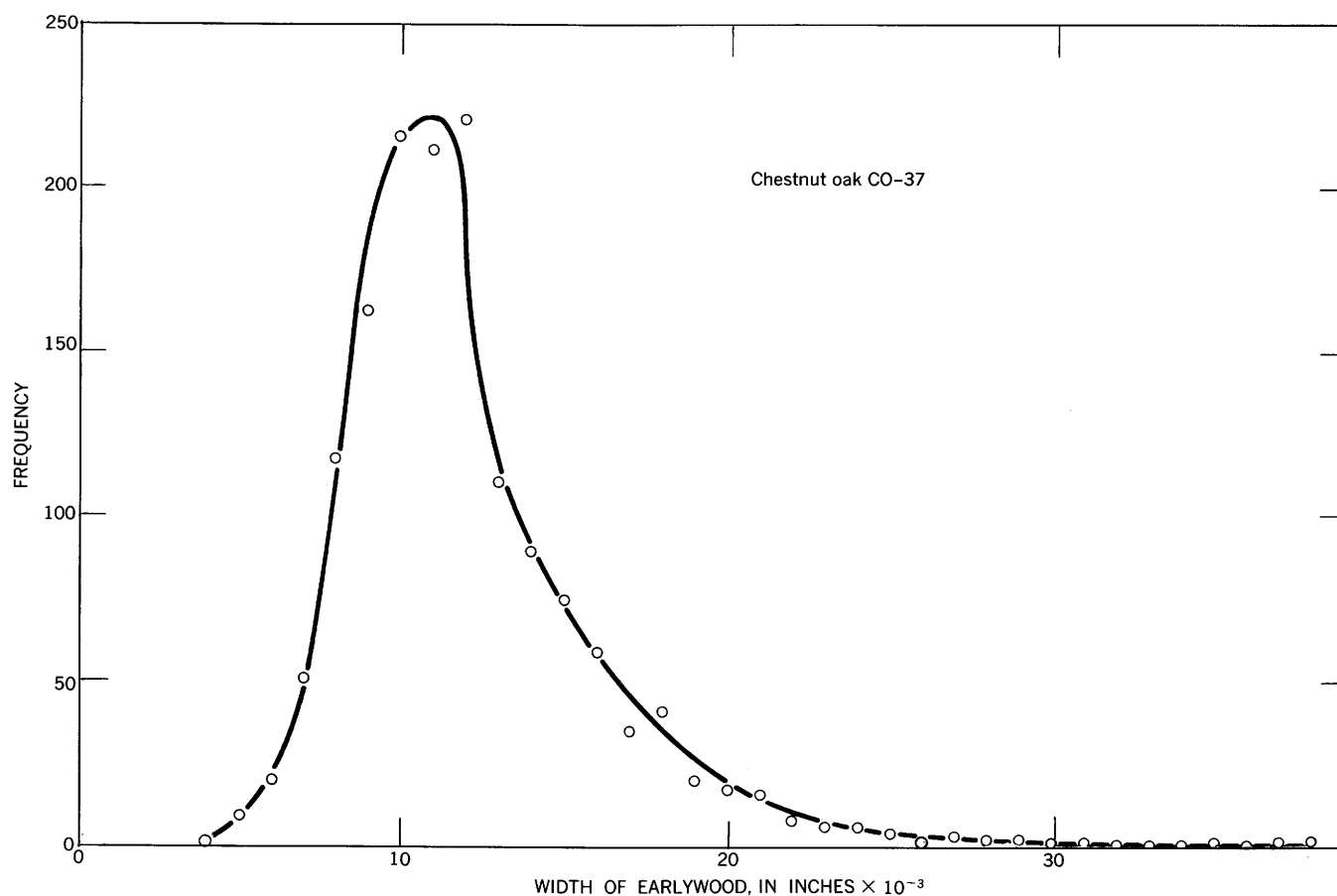


FIGURE 18.—Frequency distribution of earlywood width measurements taken from 1512 locations in chestnut oak CO-37.

It is generally agreed that dating errors incurred by the presence of such irregularities may be eliminated by the application of cross-dating techniques to ring sequences of many trees from the general geographic area of study. In theory, these trees represent growth in a wide range of habitats, and not all the trees would be expected to develop irregular rings during the same years. Thus, by examination of enough trees from enough habitats, all ring irregularities could be identified. However, if even one missing ring of a ring record is not accounted for, the correlation of that ring record with any given climatic parameter is in jeopardy. Because of the inherent serial correlation of rings, failure to recognize the absence of a ring would probably not destroy a correlation between rings and climate, but it would decrease the accuracy of the correlation. In studies involving a limited number of trees in an area for which a master chronology is not available, other methods of identification of ring irregularities must be employed.

Larson (1962) has demonstrated that the occurrence of multiple rings in red pine is caused by variation in auxin concentrations associated with terminal-growth

activity. Thus, if terminal growth were stimulated by some environmental condition such as drought break-age after the typical growth peak, tissue would be formed in the annual ring which would resemble that found in the early part of the ring when terminal growth is typically quite active. No distinct examples of false, or multiple, rings were found at any height in the trunks in any of the four study trees from Neotoma. Though variations within the rings of the four study trees were not distinct enough to be considered as multiple rings, subtle variations in cell size, shape, and number were noted. Anatomical variations within a ring might provide growth parameters correlative with environmental conditions based on time intervals much shorter than phenological seasons or calendar months. Circumferentially oriented bands of parenchyma in the latewood of white and chestnut oak may be an example of such an anatomical variation. Preliminary examination of parenchyma bands in one of the dissected chestnut oaks (CO-58) revealed that the number of bands per ring and the distance between bands were quite variable, but tended to decrease toward the outside of the ring, and the number and distribution of bands ap-

peared to be unrelated to ring width. If production of these parenchyma bands is environmentally controlled, then their occurrence would be expected to correlate with environmental conditions of periods of much less than a phenological season, even at a single sample height.

The upper part of the xylem increments of the four study trees was never discontinuous. Though environmentally induced variation in size from ring to ring was more or less random, there was, as described above, a tendency for all rings to become increasingly narrow with increasing distance from the apex. Some red maple xylem increments, which were narrow near their apices, tapered down the trunk to the point where they completely disappeared on one or more sides of the trunk. Rarely was a ring missing on all sides of the trunk at any given height, and the ring usually reappeared on all sides of the trunk near the base in the region of butt swell.

Data of discontinuous rings at the 6-foot level of RM-18 for the years 1953-62 are presented diagrammatically in figure 20. The data illustrate only the order in which the rings occurred; no attempt was made to present ring width to scale. In the actual section, the two radii "a" and "b" were of a single diameter bisecting the angle of the other two radii "north" and "upslope," which were about 135° apart. The four radii in figure 20 were those used for ring measurement with the mechanical stage. If the four radii only had been used, as would have been done had increment cores instead of cross sections been used, the rings could not have been dated by a simple ring count. If, by chance, the number of rings in each radius had been the same, the rings would have been incorrectly dated.

Even with the entire cross section available for inspection, it is sometimes not possible to ascertain the years represented by all rings. For example, in figure 20, note the discontinuous ring indicated as "unknown" through which radius "b" passes. As illustrated, the "unknown" ring could have been formed during 1954, 1955, or 1956. Determination of the actual year of formation requires examination of the cross sections above and below, and is based not only on the positions of discontinuous rings in adjacent cross sections, but also on the ring widths. For this example, the year of ring formation was determined as being 1955. By this method, it was possible to date all such "unknown" rings.

To illustrate the pattern of discontinuous rings along the trunk, figure 21 was prepared from RM-18 data for the 6-foot height up through the 33-foot height. Presence or absence of rings was determined at 3-foot intervals, and determination of pattern between heights was

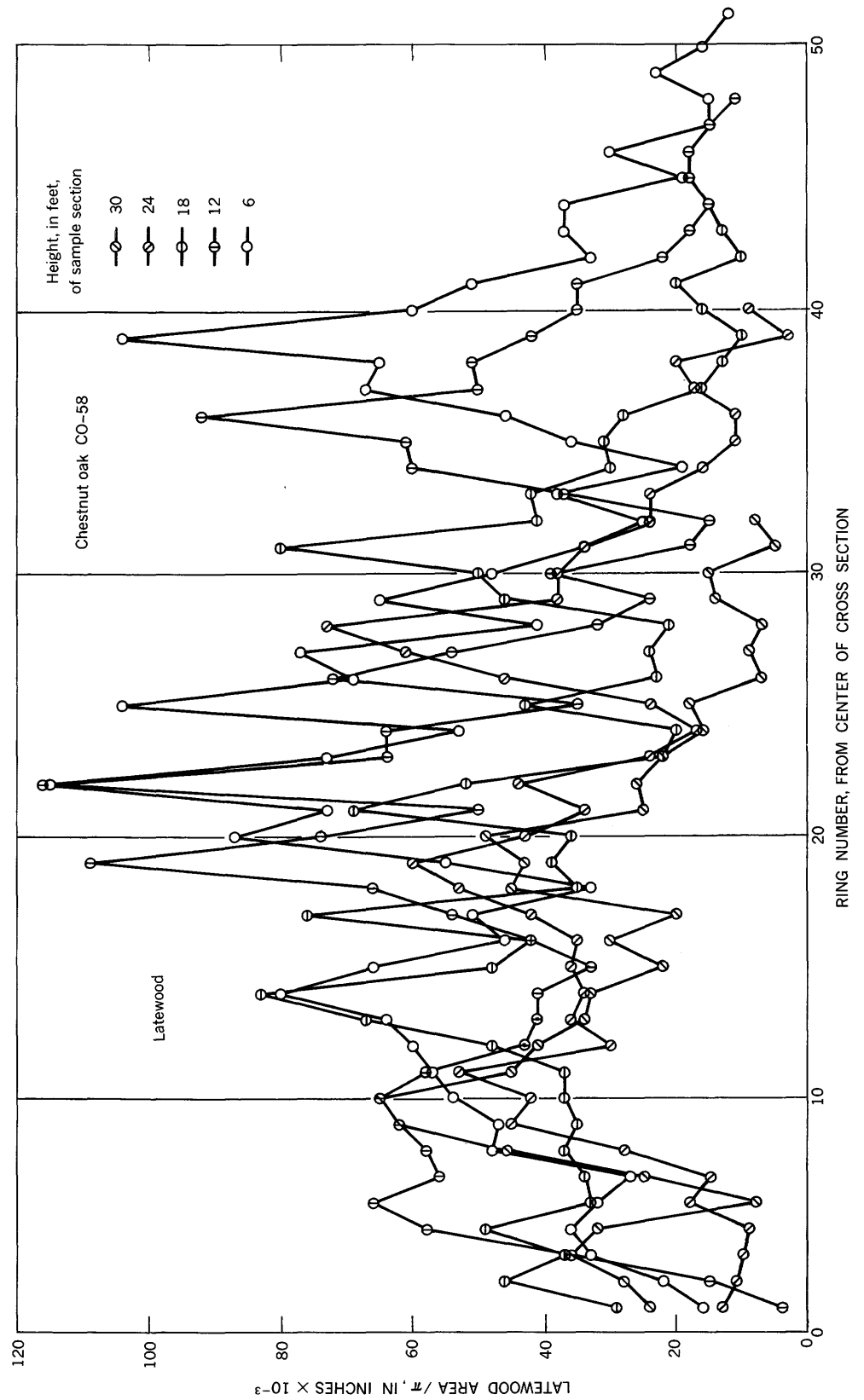
by interpolation. Isolated patches or islands of growth may have been associated with local wounding. If the interpretation of the patterns is correct, several questions are posed. What, for example, is the explanation of the apparent spiralling of the growth layers? Horizontal exaggeration of the illustrations is about 35 times, so it is at least possible that spiralling is not real. If the spiralling does exist, are the tracheae (water tubes) oriented similarly? It is possible that the angle of spiralling is induced by some factor such as water stress, and that the angle may change from ring to ring, or even from level to level in the same ring.

The amounts of early and midsummer precipitation, as shown by U.S. Weather Bureau records from Lancaster, Ohio (9 miles from Neotoma), were below average during 1954 and 1955; rings for these years were absent in the middle and lower trunk levels (fig. 21). During 1956 when growth was discontinuous in local areas of the lower trunk, precipitation was about average in late spring, above average in early summer, but below average in midsummer. These results suggest correlation between precipitation on a seasonal basis and growth at various levels in the tree.

During 1959, precipitation was below average in late spring, greatly above average in early summer, and below average in midsummer. Growth was essentially continuous throughout the tree, and thus did not correlate with precipitation in the same manner as growth during 1956. The tree was growing on a silt loam which could act as a partial dam to internal soil drainage from the sandy loam soil immediately upslope. Thus, during 1957, early summer precipitation may have been great enough that a considerable amount of water was stored above the silt loam and continued to drain into it during midsummer when precipitation was low. If this condition did prevail, growth and precipitation would appear to be correlative only if precipitation and soil moisture are correlative.

During 1958, precipitation at Lancaster was about average during late spring, about 2½ inches above average in early summer, and about 5½ inches above (or twice) average in midsummer. Growth in the lower part of the tree was discontinuous (fig. 21). This reduced growth was probably the result of physiological drought caused by reduced soil aeration associated with high water content of the soil. Again growth at different levels in the tree was indicated as expressions of water conditions of different seasons, but the correlation between growth and precipitation is negative during part of the year.

Precipitation during late spring 1962, which was 2½ inches below (or less than 40 percent of) average, may have been low enough to affect discontinuous growth in



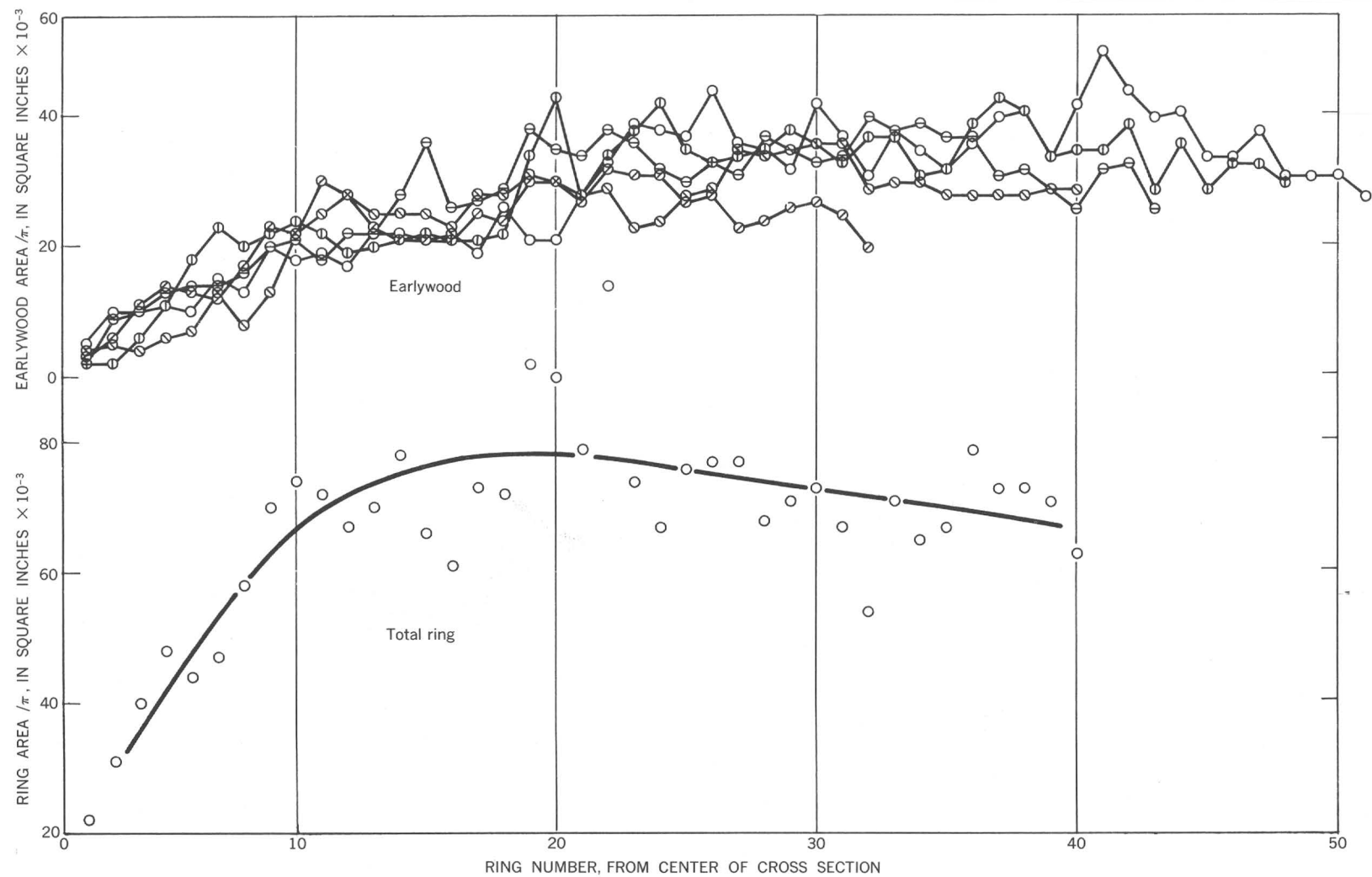


FIGURE 19.—Ring-area growth sequences of earlywood and latewood, and generalized curve of total ring-area growth of chestnut oak CO-58.

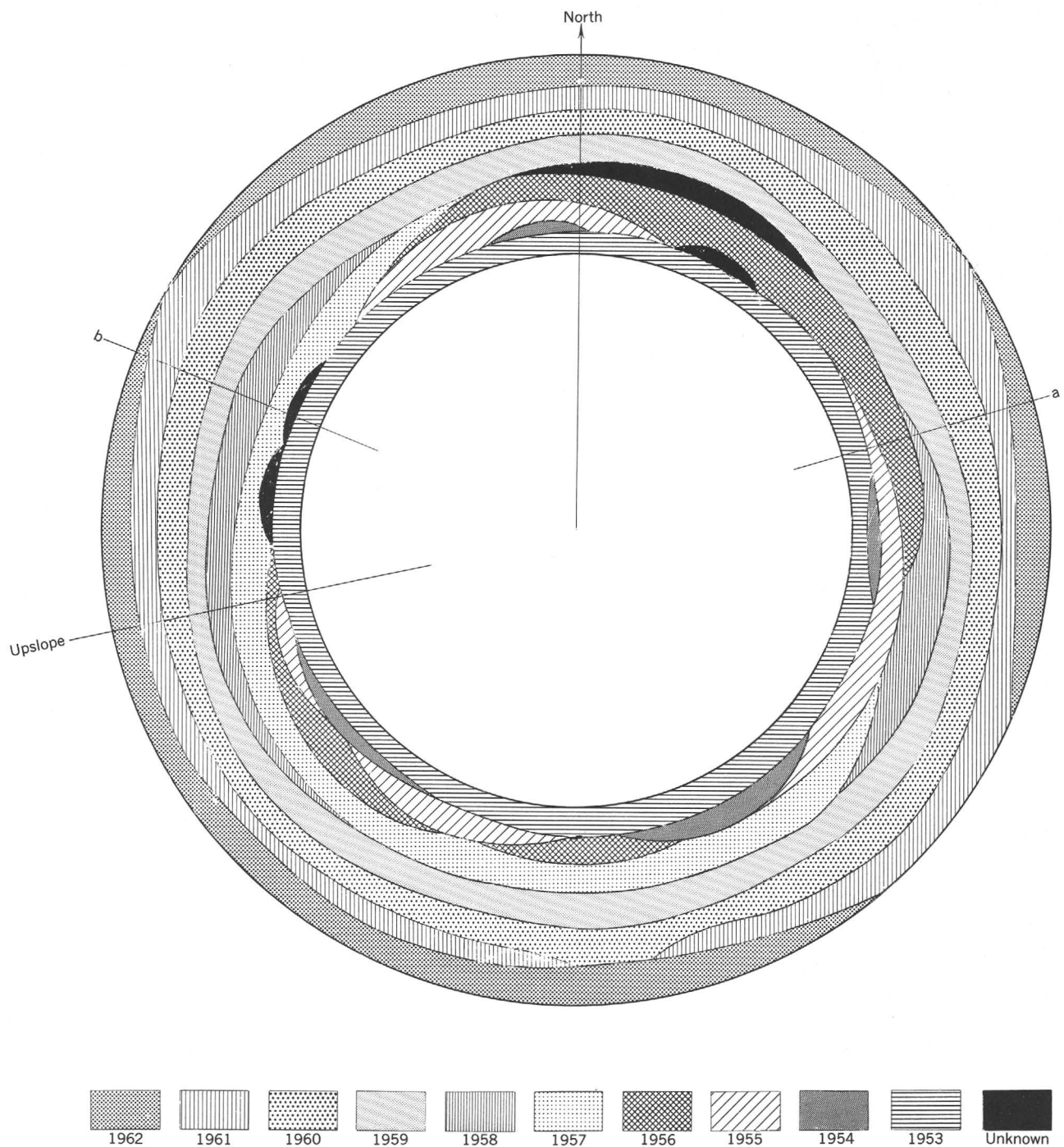


FIGURE 20.—Diagrammatic representation of discontinuity of outer 10 rings at 6-foot level of red maple RM-18.

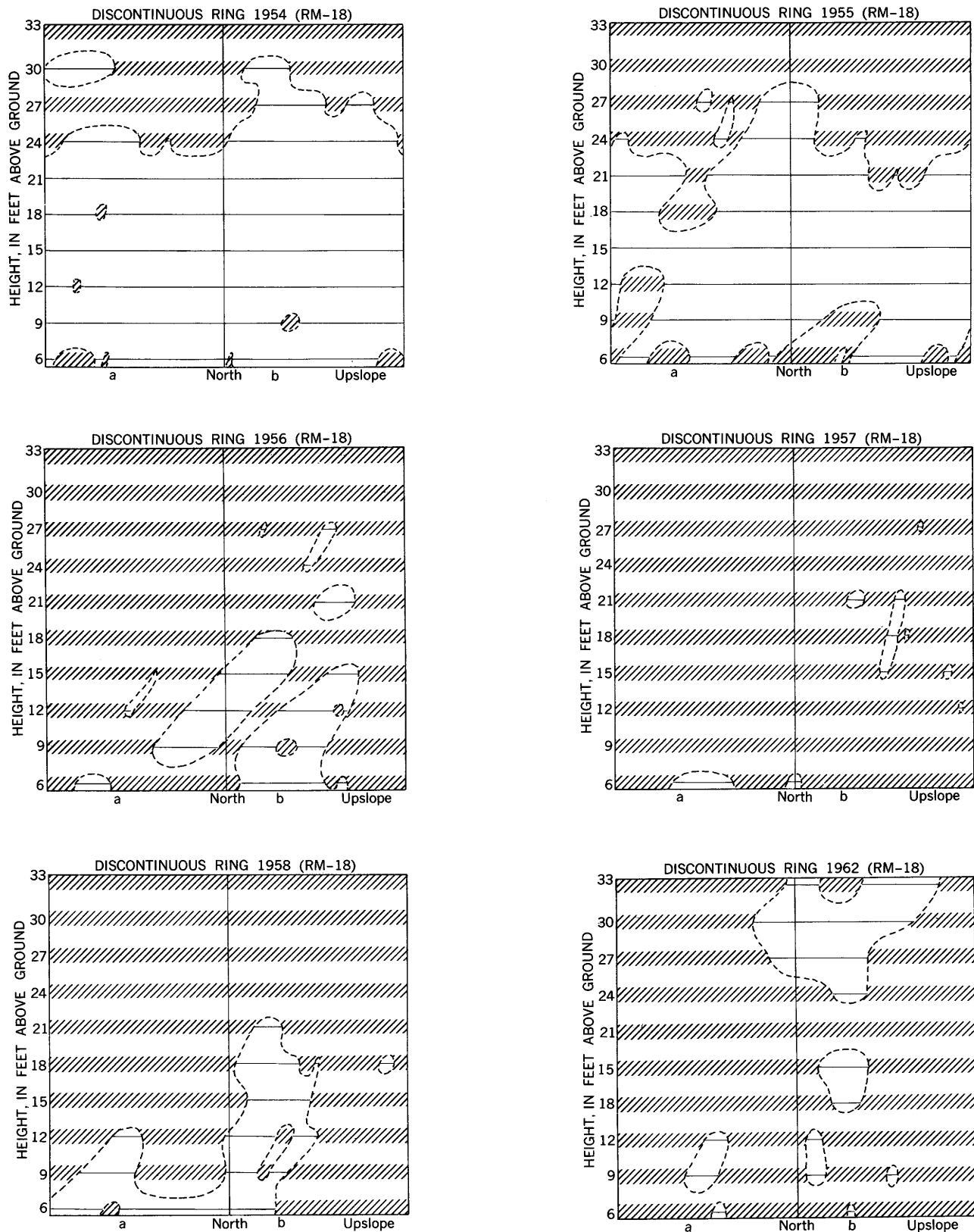


FIGURE 21.—Diagrams of discontinuous growth of individual rings of red maple RM-18. Each diagram is of a single ring as would be obtained if the ring were split along the south side and laid out flat. Shaded parts represent areas of growth of each sample height. Dashed lines are estimations of boundaries between growth and no growth.

the upper trunk levels (fig. 21). Early and midsummer precipitation reception of 1962 was similar to that of 1956 in that early summer was above average and midsummer was below. About $\frac{1}{2}$ inch more precipitation was received in midsummer 1962 than in midsummer 1956; this increase appears correlated with somewhat less discontinuous growth in the lower trunk in 1962 than in 1956. These suggested correlations cannot be regarded as conclusive, but they strongly imply that by sampling rings at more than one trunk level a more reliable growth measurement for correlation with water parameters may be obtained.

Ring discontinuities were found in both red maples and in the latewood of the two chestnut oaks. Generally, discontinuous rings occurred at the lower levels of the trunks during years when the growth increment was small. The number of discontinuous rings in each tree was related to the degree to which each was suppressed by surrounding trees. The greatest amount of discontinuous growth was noted in red maple RM-18, the most suppressed of the four trees, and the least discontinuous growth was in chestnut oak CO-37, the least suppressed. Growth seemed more limited by the immediate environment of each tree (such as implied by suppression from surrounding trees) than by factors relating to slope exposure or direction of the sun. In other words, there was no distinguishable difference between the growth on the north-facing and south-facing sides or between the upslope and downslope sides of the trees. All four trees were overtopped to some degree by canopy-sized trees, and radial growth of the trunks seemed most limited (discontinuous) on the side(s) of greatest suppression. Comparisons of vertical distribution patterns of discontinuous rings with precipitation data strongly suggest growth does not occur at the same time throughout the trunk, but at an increasingly later time with distance from the top of the tree.

SUMMARY

A suppressed chestnut oak and a red maple were felled on each of opposing slopes of a small southern Ohio valley. Cross sections were obtained at 3-foot intervals along the trunks, ring-width measurements were taken from each, and growth increments were subsequently described.

The widest ring at any given height was typically within the centermost 4-5 rings in red maple and was typically the center ring in chestnut oak. Ring width was typically greatest near the apex of any given increment and decreased with increasing distance from the

apex. During periods of suppressed growth from drought or other causes, ring width was often restricted to the point of absence at the lower trunk heights.

Earlywood width in chestnut oak remained relatively constant in all rings at all trunk heights. Earlywood area at any height was thus largely a function of ring diameter. Latewood of chestnut oak appeared similar to the entire ring of red maple.

Ring area (cross-sectional area at given height) increased from increment apex to about the lower level of the tree crown. Generally, ring area decreased with increasing distance downward from the crown during drought years, but continued to increase downward from crown during nondrought years. Earlywood growth of chestnut oak was not necessarily restricted in size during drought years.

Growth seemed to have occurred earlier at the upper levels of any given increment than at the lower levels. Water apparently was not a limiting factor in the early part of any growth season, with the result that growth did not appear restricted in the upper levels of the trees even during more extreme drought years.

Because ring growth during successive years at any given level becomes increasingly distant from the tree top (as the tree grows in height), each successive ring in a given cross section presumably was formed at a later time in growth season. Thus, it would not be expected that all rings in a given cross section could be closely and directly correlated with environmental conditions during the same part of the growing season. On the other hand, it would be expected that systematic analysis of ring data from several cross sections at as many heights could yield accurate correlations with environmental conditions during several parts or short periods of a single growing season.

The earlywood cells of chestnut oak may have been cut off from the cambium at some time prior to the current growth season. The earlywood cells appear to have then enlarged and differentiated simultaneously throughout the tree at the beginning of the growth season. Earlywood thus is suggested to be reflective of an entirely different set of environmental conditions than is latewood. Earlywood cell number possibly reflects certain conditions of the previous season and cell size certain conditions of the current season.

The basic growth characteristics of chestnut oak and red maple indicate that ring measurements of individual species must be treated independently. But, inasmuch as each species reflects somewhat different environmental conditions, a more complete picture is expected from examination of ring growth of several species.

LIST OF TREES

[Nomenclature after that of Little (1953)]

Ash, white	<i>Fraxinus americana</i> L.
Beech, American	<i>Fagus grandifolia</i> Ehrh.
Birch, sweet	<i>Betula lenta</i> L.
Butternut	<i>Juglans cinerea</i> L.
Cherry, black	<i>Prunus serotina</i> Ehrh.
Chestnut, American	<i>Castanea dentata</i> (Marsh.) Borkh.
Gum, black	<i>Nyssa sylvatica</i> Marsh.
Hemlock, eastern	<i>Tsuga canadensis</i> (L.) Carr.
Hickory, mockernut	<i>Carya tomentosa</i> Nutt.
Maple, red	<i>Acer rubrum</i> L.
Maple, sugar	<i>A. saccharum</i> Marsh.
Oak, black	<i>Quercus velutina</i> Lam.
Oak, chestnut	<i>Q. prinus</i> L.
Oak, red	<i>Q. rubra</i> L.
Oak, scarlet	<i>Q. coccinea</i> Muenchh.
Oak, white	<i>Q. alba</i> L.
Pine, loblolly	<i>Pinus taeda</i> L.
Pine, red	<i>P. resinosa</i> Ait.
Poplar, yellow	<i>Liriodendron tulipifera</i> L.
Sassafras	<i>Sassafras albidum</i> (Nutt.) Nees
Walnut, black	<i>Juglans nigra</i> L.

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