RESEARCH CIRCULAR 105 JUNE 1961

The NEOTOMA ECOLOGICAL and BIOCLIMATIC LABORATORY

Special Report No. 3

ANALYSIS OF FIVE YEARS DENDROMETER DATA OBTAINED WITHIN THREE DECIDUOUS FOREST COMMUNITIES OF NEOTOMA

by

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NEOTOMA ECOLOGICAL AND BIOCLIMATIC LABORATORY SPECIAL REPORTS

Gilbert, Gareth E. 1961. The Neotoma ecological and bioclimatic research program as of 1961. Special Report No. 1.

Phipps, Richard L. and Gareth E. Gilbert. 1961. A preliminary report concerning radial growth of selected trees at Neotoma. Special Report No. 2.

Phipps, Richard L. 1961. Analysis of five years dendrometer data obtained within three deciduous forest communities of Neotoma. Special Report No. 3.

ANALYSIS OF FIVE YEARS DENDROMETER DATA OBTAINED WITHIN THREE DECIDUOUS FOREST COMMUNITIES OF NEOTOMA[1]

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Wolfe, Wareham, and Scofield (1949) pioneered an extensive microclimatic study in a small south-central Ohio valley named Neotoma. Recently the investigations at Neotoma have been greatly expanded (Wolfe and Gilbert, 1956; Gilbert and Wolfe, 1959; Gilbert, 1959, 1960, and 1961) to include extensive bioclimatic studies in opposing slope and ridgetop communities. Concurrently, radial growth of selected trees has been measured within these communities by use of dendrometers (Daubenmire, 1945), and more recently with Fritts dendrographs (Fritts and Fritts, 1955) and electric dendrographs (Phipps and Gilbert, 1960). The purpose of this investigation is to correlate selected growth data obtained with dendrometers since the initiation of growth measurements at Neotoma in 1955 with some of the more pertinent environmental data obtained during the same period.

LITERATURE REVIEW

Radial growth of forest trees has received considerable attention during the past 50 years. Many of the early workers concerned themselves with measurements of total yearly increments of xylem and probable relationships with certain climatic variables measured by local Weather Bureaus. Robbins (1921) noted a correlation between increase or decrease in rainfall from March to June and an increase or decrease in width of annual rings of oaks at Columbia, Missouri. He asserted that a dry spring affected growth of that year, but not the following year. Diller (1935), whose work concerned measurements of yearly increments of beech in northern Indiana, pointed out that distribution of precipitation throughout the growing season, not total seasonal amount, is most important in affecting amount of radial

1 Contribution No. 653 of the Dept. of Botany and Plant Pathology of The Ohio State University. A cooperative project of the Ohio Agricultural Experiment Station, The Ohio State University, and the United States Atomic Energy Commission [Contract No. AT(11-1)-552].

growth. He obtained better correlations between seasonal increment and total precipitation for the month of June than with total seasonal precipitation or precipitation of any other month. Also, he concluded that excessive droughts tend to decrease growth of the following year more than the present year, but that unusually wet years show up as an increase in growth of the present year. He reasoned that soil moisture might have been more closely correlated with growth than was precipitation with growth.

Another environmental factor with which most of the earlier students of tree growth were concerned was temperature. Brown (1915), working with *Pinus strobus* L.[2] at Cornell University, stated "The awakening and rapidity of growth is dependent on three factors, moisture, available food (reserve), and temperature. The first two are at an optimum in the spring; the amount of growth therefore is directly proportional to the prevailing temperatures." Robbins (1921) found that the annual radial growth increment of oaks in Missouri varied inversely as the mean monthly temperature for May and June. This was in agreement with the work of Diller (1935), who determined linear regressions between growth and average June temperatures and between growth and total June precipitation. He obtained regressions suggesting better negative correlations for growth-temperature regressions than positive correlations for growth-precipitation, explaining that "Temperature . . . does not show such wide local variations as are exhibited by precipitation."

With the development of instruments capable of measuring radial change (Reineke, 1932; MacDougal, 1938; Daubenmire, 1945), it was possible to study cause and effect relationships responsible for variations in growth rates occurring throughout a given growth season, not only between species, but between members of the same species. Considerable attention has been paid to the comparison of growth patterns of ring-porous and diffuse-porous trees and causes for the initiation and cessation of radial growth of these two types. Friesner (1941), in a paper concerning the study of beech, cited several references substantiating the initiation of growth of ring-porous woods as consistently occurring earlier in the spring than initiation of growth of diffuse-porous woods. Friesner (1942) reported that radial growth of beech commenced within one to two weeks after the leaves had reached maximum size in the spring, increased rapidly to a

2 Nomenclature that of Fernald, 1950 (Gray's Manual of Botany, 8th ed.) except for capitalization of specific epithets.

growth rate peak six to seven weeks later (around the end of June), followed by a decrease in growth rate until the latter part of the season at which time radial growth was characterized by small fluctuations corresponding to rains.

Daubenmire and Deters (1947), working with planted deciduous species within the prairie climate of Moscow, Idaho, stated "... the dates of growth initiation are almost identical for the ring-porous *Ulmus* and *Quercus* and the diffuse-porous *Fagus*." These results do not appear to apply to work concerning trees growing in their native environment. Friesner (1942) stated that growth initiation of *Ulmus* and *Quercus* occurred on approximately April 21 in 1941, which closely corresponded to the time at which vegetative buds of the two species began to swell, and that during the same year growth initiation of *Fagus* occurred on approximately May 12, approximately one week after the leaves had reached maximum size. Fritts (1956), working with radial growth of beech near Columbus, Ohio, during the 1952 growing season, found that breaking of cambium dormancy occurred on approximately April 20, the "grand period" of growth beginning between May 17 and 27, which corresponds favorably with the observations of Friesner (1942). In a later paper concerning radial growth of six beech trees during 1954 and 1955, Fritts (1958) stated, "In all but the number 2 tree, radial growth started after the leaves unfolded and before they were fully expanded." He further stated, "... that the initiation of radial growth may be associated with, but is not dependent on, a certain stage in phenological development."

Fraser (1952), in an intensive study of initiation of cambial activity, cited Wareing (1951) as having observed that, in general, cambial activity of ring-porous trees is initiated rapidly throughout the tree, while a much slower basipetal movement of cambial activity characterized the diffuse-porous trees. Fraser (1952) compared growth measurements as obtained by dendrometers with measurements obtained from sectioned wood samples, and stated that "... the march of initiation of cambial activity proceeded from the apex to the base..." He further concluded that the stimulus responsible for initiation was probably produced by a hormone proceeding from the buds and developing leaves in the spring. Koch (1960), working with chestnut oak and tulip-tree at Neotoma, found that diurnal fluctuations in radius of tree trunks is more closely correlated with changes in internal water content than any environmental factor. It is thus possible that water uptake by trees during the spring period may be confused with growth initiation.

Fritts (1956) reported the growth of three beech trees near Columbus, Ohio, for the 1952 growing season. One tree was located in a depression, another on a gentle rise, and the third on a better-drained site in a mature Beech-Maple community. In summarizing comparisons of the growth curves for the latter part of the season — when soil moisture was low — he stated, "These curves appear to be coincident with the moisture regimes. The growth of the tree near the depression which had a shallow root system was steady while the soil contained a high percent moisture. But the growth abruptly stopped when the soil moisture began to rapidly decrease in the A horizon in early July." Fritts (1958) conducted an intensive study concerning radial growth of beech in the same study area as used in his earlier study. Six trees were measured with the Fritts dendrograph and statistically analyzed with several environmental variables. He concluded that "In early season, maximum daily temperature is more influential than soil moisture; but in late season, this relationship is reversed." This is contrary to earlier studies by other workers who felt that growth varied inversely with temperature. However, these earlier studies were concerned only with seasonal trends and average temperature, whereas Fritts was working with many variables on a daily basis. Fritts was unable to obtain a significant partial regression coefficient between growth and minimum temperature. However, in a recent study of white oak and sugar maple in east-central Illinois (1957 growing season), Fritts (1959) showed high maximum daily temperature to be more limiting to the growth of sugar maple and low maximum daily temperatures to be more limiting to growth of white oak.

METHODS AND RESULTS

Weekly radial growth data were obtained from 41 individuals representing 20 species within the Mixed Mesophytic, Mixed Oak, and Chestnut Oak forest communities of Neotoma (Figs. 1, 2, and 3) during the period 1955-1959 and reported within Neotoma Special Report No. 2 (Phipps and Gilbert, 1961). Spring and summer growth data for chestnut oak (*Quercus prinus* L.), white oak (*Q. alba* L.), beech (*Fagus grandifolia* Ehrh.), and red maple (*Acer rubrum* L.) were selected from data presented within this report for the analysis presented herein. Growth rate data (thousandths-of-an-inch change in radius over the previous measurement reading) for each growing season are included in Tables 1, 2, and 3. Tables 5 and 6 include dates of initiation and cessation, total amount, and duration of growth of each tree. Since weekly growth measurements were taken throughout the year it was possible to delimit growth initiation as the time at which definite increases over the maximum of the previous growth season occurred. The time of radial growth cessation was arbitrarily determined as the time at which maximum size was attained which was not followed by a further increase for at least two weeks. Dates of growth cessation are difficult to determine since, as stated by Fraser (1952), in the "... phloem where there is a gradual transition from mature, undistorted tissue to cells crushed by radial pressure...", it is not uncommon to obtain measurement increase several weeks after the arbitrarily chosen cessation date. Perhaps, however, such fluctuations at the end of the season did not indicate growth, but

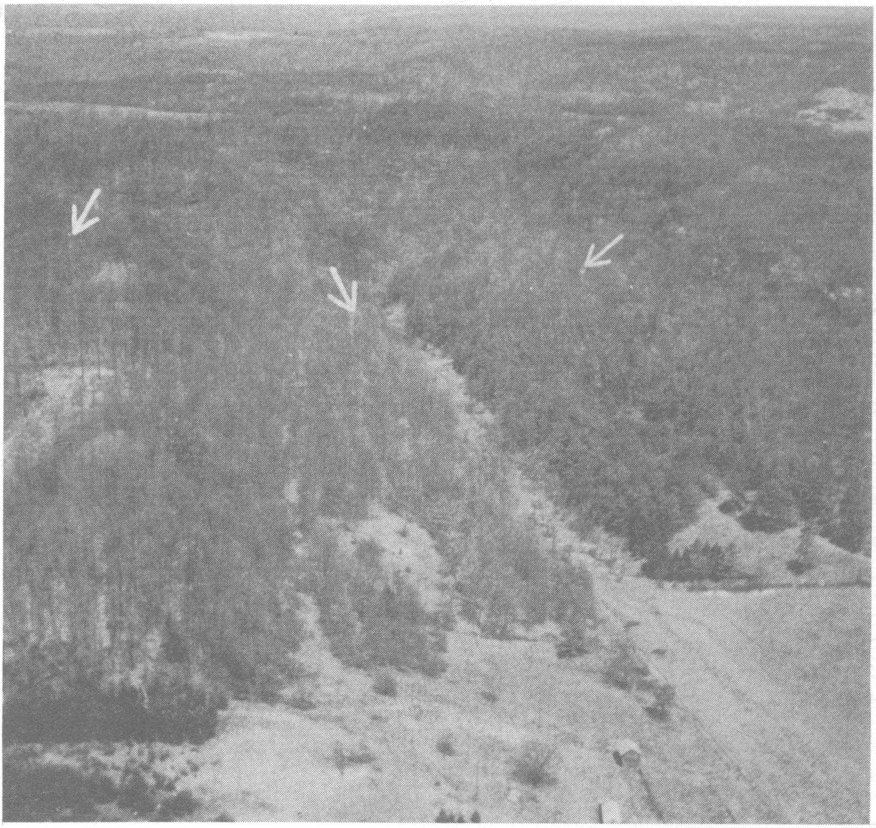

Fig. 1. Aerial view of Neotoma looking near due north during winter season. Instrument towers (arrows) identify location of the three forest community study areas.

merely rehydration of the tissues as soil moisture was replenished in late summer. It might be noted that occasionally such an increase over the previous maximum occurred in December or January when the trees were obviously dormant.

Data included in Tables 1, 2, and 3 were adjusted, where necessary, so that all data represented seven-day measurement periods. Five-week successive averages were then calculated and plotted, and growth-rate curves fitted to the points. These curves are presented in Figures 4, 5, and 6 and are assumed to indicate general seasonal

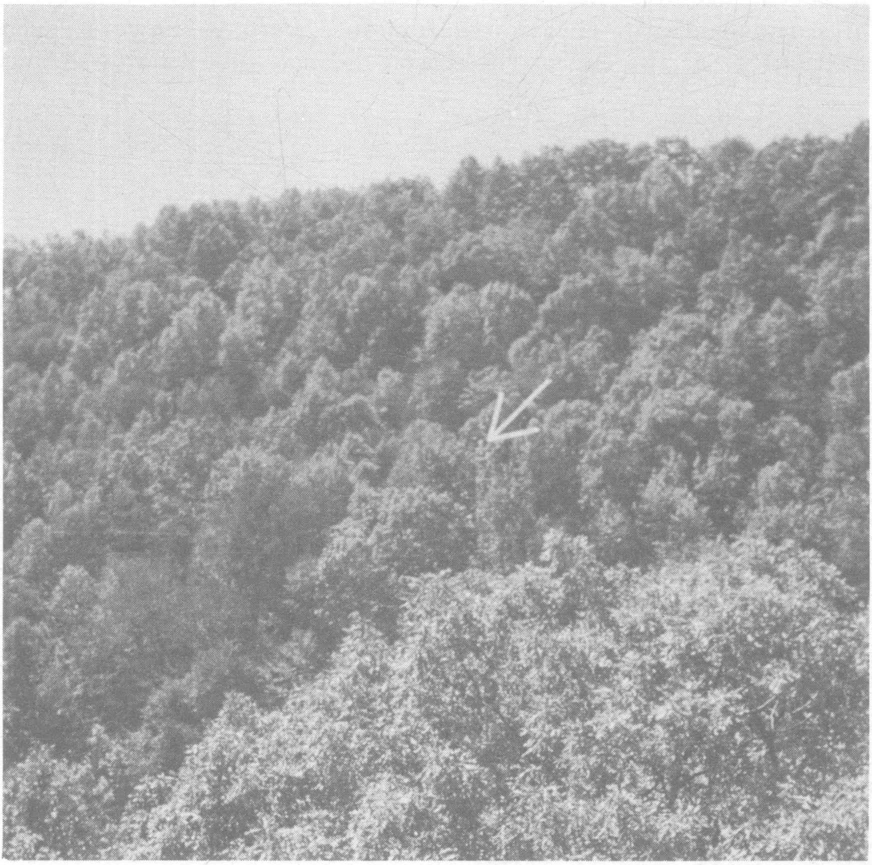

Fig. 2. Mixed Mesophytic (lower slope) and Chestnut Oak-Tuliptree vegetation (upper slope) of northeast-facing slope. Note instrument tower located at approximate center of study area within Mixed Mesophytic vegetation.

trends of growth with elimination of short-term fluctuations. Thus, the curves represent more pronounced trends such as drought or extended extreme temperatures and make for an easier comparison of growth rates, duration of growth, and relative occurrence of peak growth rates of different trees, and the same tree for different years.

Bioclimatic data of Neotoma used in conjunction with this study were obtained from studies initiated by Wolfe and Gilbert (1956), Gilbert and Wolfe (1959), and Gilbert (1959, 1960, 1961, and 1961a).

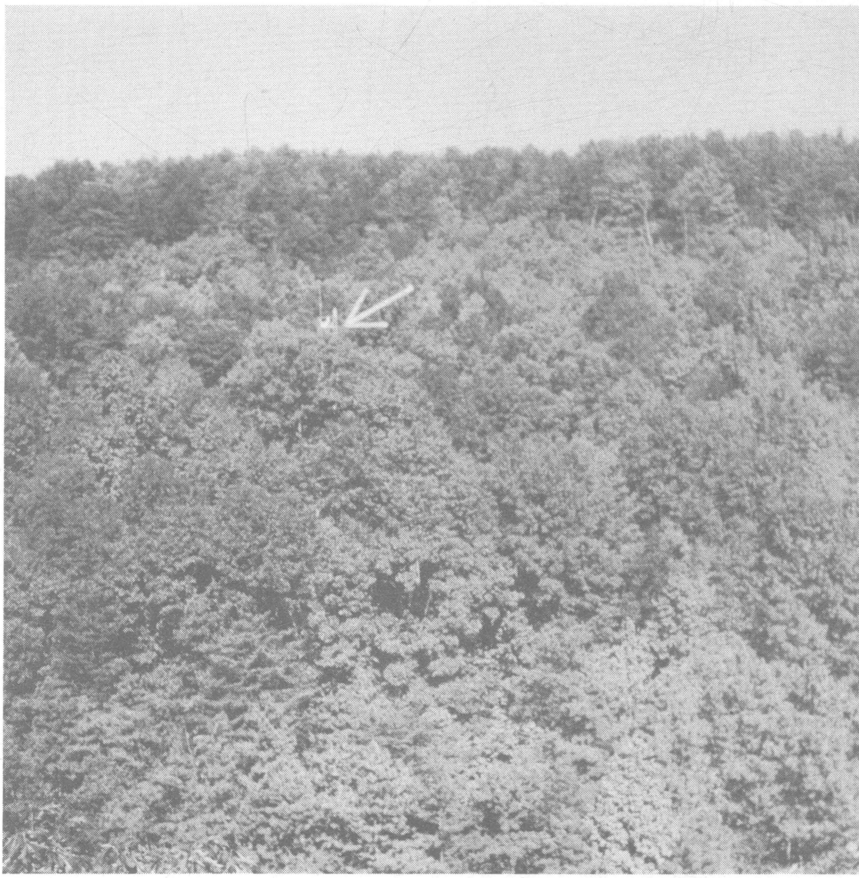

Fig. 3. Mixed Oak vegetation of southwest-facing slope. Note instrument tower located at approximate center of study area within Mixed Oak vegetation.

ANALYSIS

Graphed curves of radial growth rate of typical diffuse-porous species are single peaked while rate curves of ring-porous individuals correspond in time to the second peak of the ring-porous individuals (Phipps and Gilbert, 1961). Table 4 indicates weeks during which

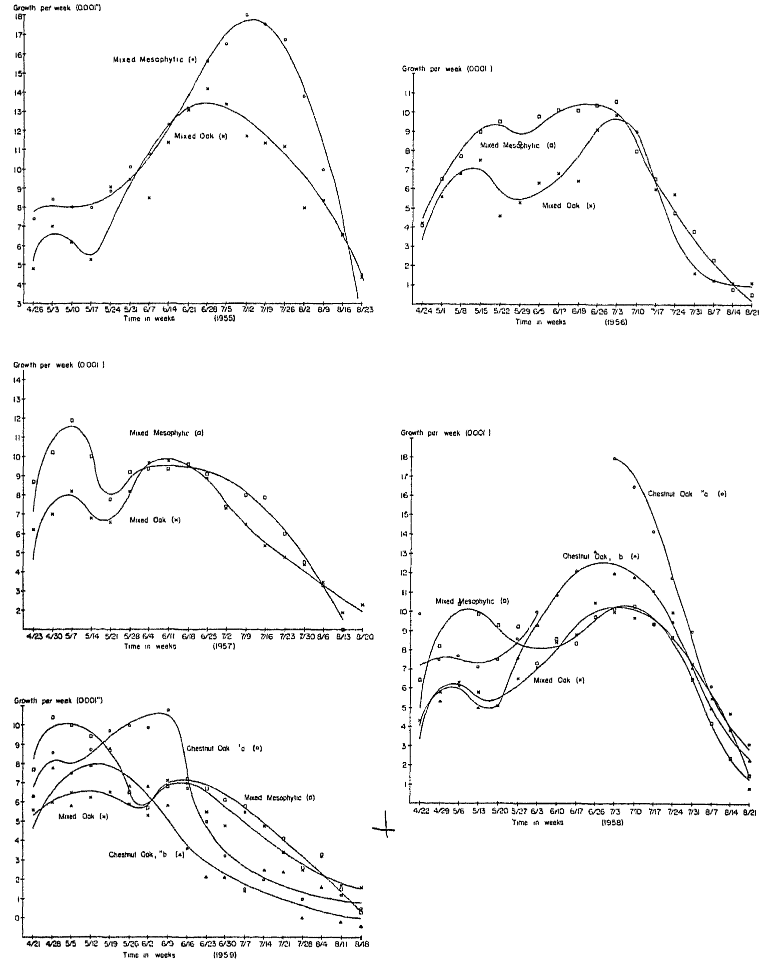

Fig. 4. Smoothed curves of weekly radial growth rates of Chestnut Oak in the Mixed Mesophytic, Mixed Oak, and Chestnut Oak forest communities at Neotoma, 1955 through 1959.

marked bud swelling, leaf unfolding, and mature leaf size were first noted of chestnut oak, white oak, beech, and red maple during 1957, 1958, and 1959 at each of the three study communities at Neotoma. The dates of growth initiation of the specific study trees are listed in Tables 5 and 6. Even though initiation dates varied between communities for a given year as well between years for a given community, they were within one week of the date of first noted bud swelling of chestnut oak and white oak (ring-porous), and within one week of initiation of leaf unfolding of beech (diffuse-porous). Growth initiation of ring-porous species usually occurs earlier than in diffuse-

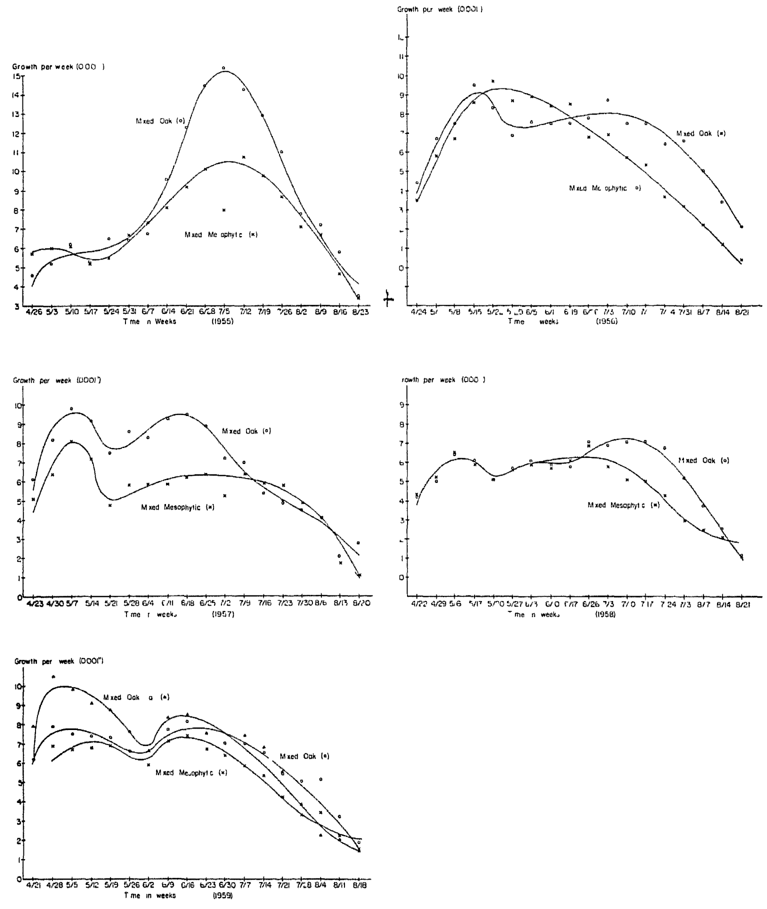

Fig. 5. Smoothed curves of weekly radial growth rates of White Oak in the Mixed Mesophytic and Mixed Oak forest communities at Neotoma, 1955 through 1959.

porous species, and in both cases are from year to year associated with a particular stage in phenological development, but not with a particular calendar date.

Table 7 contains data representing maximum weekly growth rate and approximate amount of growth of the spring and summer growth periods of white oak for 1955-1959. Also included is the width of increment of the early- and latewood of white oak as obtained from dried increment borings. Fritts has suggested that width of earlywood increment in ring-porous species appears to correspond with the amount of growth during the spring growth period.[3] In general, this appears to be true in white oak at Neotoma. However, growth measured by dendrometer during summer radial growth periods was occa-

3 Personal communication.

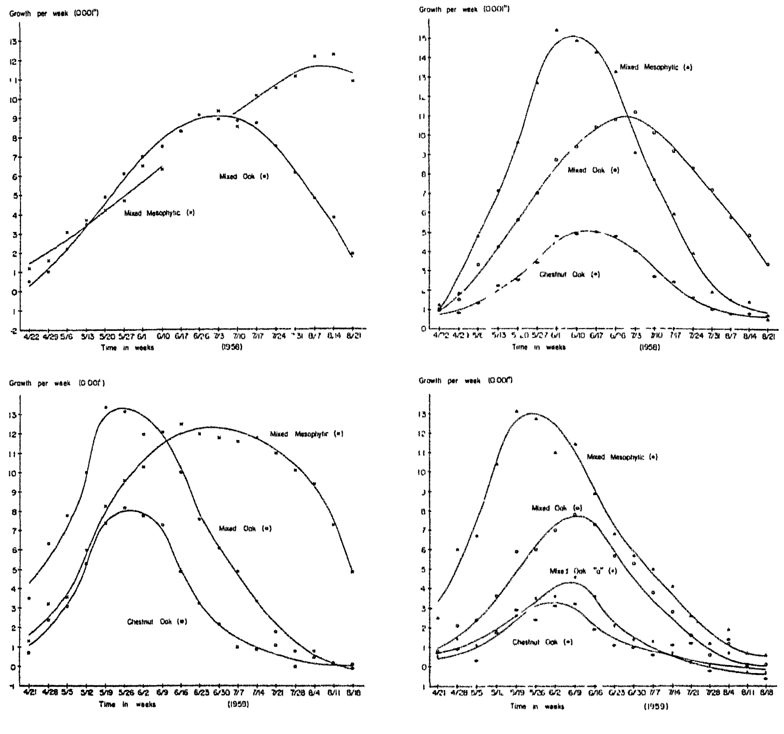

Fig. 6. Smoothed curves of weekly radial growth rates of Beech (left, upper and lower) and Red Maple (right, upper and lower) in the Mixed Mesophytic, Mixed Oak, and Chestnut Oak forest communities at Neotoma, 1958 and 1959.

sionally as much as twice the amount of latewood of increment borings. According to Kramer and Koslowski (1960), "Some of the phloem cells cut off during one season mature before the onset of dormancy, while the remainder mature the following year." This, they point out, seems correlated with the two peaks in starch accumulation (Siminovich, *et al.,* 1953), and suggests that this starch reserve is used in phloem differentiation. It is possible that temperatures low enough to be inhibitory to the maturation of phloem cells does not occur at Neotoma until late fall, thus leaving only a small fraction to mature the following spring. Occurrence of most of the phloem growth in summer and fall would account for the difference between dendrometer and boring data since dendrometer data is a measure of both xylem and phloem growth but boring data is a measure of xylem growth only.

There appears to be similarity between the maximum growth rate of the summer growth period and the maximum growth rate of the spring growth period of the following season (Table 7 and Figs. 4, 5, and 6). Regardless of the number of phloem cells formed during the latter part of the season the rate and degree to which these cells enlarge and differentiate is no doubt influenced by the prevailing environmental conditions of both late summer and the following spring; however, phloem growth accounts for only a part of the apparent growth measured by the dendrometers before the leaves have expanded.

Data representing deviations of maximum and minimum temperature, precipitation, and soil moisture are presented in Tables 8, 9, and 10, respectively. During the 1958 summer growth period, temperatures were below the 1955-1959 average, precipitation was above average, and growth of white oak and chestnut oak during the same period (Figs. 4 and 5) was above average for that part of the season. Growth during the spring period of 1959 was also above average even though precipitation was below the five year average. Above average growth rates during the spring period of 1957 correspond with a large amount of summer growth during 1956. While radial growth occurring after leaf expansion and active production of photosynthates has begun is probably largely dependent upon current environmental conditions, growth during the spring period before the leaves are expanded must of necessity be greatly dependent upon photosynthate reserves. The greatest amount of spring period growth of white oak occurred in 1957 and 1959. Both of these seasons were preceded by above average rainfall and soil moisture in July of the previous season (Tables 9 and 10) which might have been conducive to accumulation of carbohydrate reserves. Maximum and minimum temperatures were below the five year average in April, 1959, and not significantly above average in April, 1957, so that amount of reserve carbohydrates used for respiration process would have been relatively low. May temperatures in 1957 were considerably below average and soil moisture was not low, which appears to have been favorable to high growth rate during spring. During May, 1959, when minimum temperatures, and thus respiration rates were considerably above average, growth rates were below those of May, 1957. High values of total spring growth in 1959 appear due to the extended spring growth period probably induced by water stresses from lower than average soil moisture during latter May and June, and thus belated initiation of summer growth.

Correlations of 1955 data. – Since 1955 marks the beginning of growth measurements at Neotoma, data is not available concerning growth of the previous season which might have affected spring period growth of that year. During spring, 1955, maximum and minimum temperatures were considerably above average in April (Table 8) and soil moisture was above average (Table 10) even though precipitation was below average (Table 9). Average daily maximum temperature during the month of April was particularly high on the Mixed Oak slope, which is correlated with low growth rate of the Mixed Oak white oak. Amount of spring period growth of both chestnut oak and white oak appears small, even though growth rate was just as low in 1958 for all but the Mixed Mesophytic chestnut oak. Growth rate of the 1955 summer period was the greatest achieved by any of the chestnut and white oaks measured during the entire five years. The only time that any ring-porous tree surpassed the growth rate attained by the white oaks and chestnut oaks measured in 1955 was in 1958 when the growth rates of two chestnut oaks on the Chestnut Oak ridge top surpassed 12 and 18 thousandths inch per week. In this case, as with the four trees in 1955, it was the first year that dendrometer measurements were taken on the respective trees. If these results can be termed as greater growth rates than may be accounted for by climatic conditions, then they seem in agreement with earlier workers who attributed excessive growth the first season after initiation of dendrometer studies to excessive hormone accumulation in the region of wounding by the dendrometer screws. The ratio of growth of the Mixed Oak individuals to the growth of the

Mixed Mesophytic individuals was somewhat below the five year average. Precipitation was only slightly below average, soil moisture did not appear to deviate significantly from average, and only on the Mixed Oak slope did June and July temperatures deviate significantly from the average. Maximum temperature averaged about 5°F above average and minimum temperature averaged about 3½°F above average on the Mixed Oak slope. Greater than average air temperatures in the Mixed Oak community may have caused higher respiration rates, accounting for the greater than average difference in growth between the Mixed Oak and Mixed Mesophytic communities.

Correlations of 1956 data. – Radial growth during the spring period of 1956 of all four trees, while not initiated particularly later than usual (Table 5), was greater, the result being that an appreciable increase in summer growth rate over that attained during the spring period was attained by none of the trees. Lateness of the spring growth peak was so apparent for the white oak within the Mixed Mesophytic community that spring and summer peaks did not differentiate. The maximum radial growth rate attained during the spring period by chestnut oak and white oak of the Mixed Oak community occurred during mid-May, the same species of the opposing slope not reaching a peak until approximately one week later. These dates represent the latest dates of maximum spring radial growth of the entire five year period. Soil moisture and precipitation did not vary considerably from average, and May temperatures, during which maximum growth rate occurred, were close to average. Effects of wounding were still apparent during the spring period, but it is inferred that hormone concentration dropped off during the summer period since growth rates more nearly approximated those of subsequent years. During the summer growth period soil moisture on the Mixed Oak slope was below average in July. This appears correlated with the more rapid decrease in growth rate of chestnut oak and white oak within the Mixed Oak community than within the Mixed Mesophytic community of the opposing slope.

Correlations of 1957 data. – Initiation of radial growth during spring of 1957 occurred approximately one week later than in 1956. Following initiation growth rate increased relatively rapidly, culminating in a spring maximum weekly rate in all four trees during the first two weeks of May (Table 5 and Figs. 4 and 5). In all except the Mixed Mesophytic chestnut oak, growth continued into September. Environmental conditions – temperature, soil moisture, and precipitation—were not markedly different from the five year average and the effects of hormone concentration no longer seemed apparent. Summer growth of the two oaks on the Mixed Oak slope increased rapidly during the latter part of May and early June reaching a peak in mid-June. The Mixed Mesophytic chestnut oak also reached a summer peak in mid-June, but by early July growth rate was decreasing rapidly and continued decreasing until cessation in late July or early August. The pronounced peak in growth rate of the two Mixed Oak individuals appears correlated with high minimum temperature and thus less extreme temperature. Neither less extreme temperature nor pronounced growth peak in June were associated with growth of the Mixed Mesophytic individuals. The curves of both Mixed Oak individuals did not decrease as rapidly near the end of the season as the growth rates of the Mixed Mesophytic individuals. Soil moisture was relatively low in August (Gilbert and Wolfe, 1959), but much closer to wilting percentage within the Mixed Oak habitat than within the Mixed Mesophytic environment of the opposing slope. Thus, relief of moisture stresses was much more pronounced on the Mixed Oak slope when soil moisture was partially replenished in early September. With reduction of water stresses in early September, xylem tissue, particularly in the Mixed Oak trees, expanded. Since the curves were calculated from five week averages the last two points on the curves would include data taken in early September when expansion had occurred. Increase in radius continued after the replenishment of soil moisture in early September. Whether or not increase measured by the dendrometers actually represented growth or, as was suspected, just rehydration of the tissue was not determined. Total increases of 3, 4, 8, and 8½ thousandths of an inch were measured in September for Mixed Mesophytic chestnut oak and white oak, and for Mixed Oak chestnut oak and white oak individuals respectively. Radial increase in the Mixed Mesophytic individuals may well have been due only to rehydration of the tissue, but the values measured on the Mixed Oak individuals seem rather large to be due solely to rehydration. It thus appears possible that when soil moisture is replenished at the end of a dry period occurring near the end of the growing season the period of radial growth may be extended.

Correlations of 1958 data. — In addition to the two chestnut oaks and two white oaks previously discussed, radial growth data and curves of seven additional trees are included for the 1958 growing season (Table 2 and Figs. 4, 5, and 6). Maximum and minimum temperatures were generally below the five year average in April and above average during latter June and in July when precipitation was considerably above the five year average (Tables 2, 9, and 10). Spring period growth of chestnut oak was comparable in magnitude to that of the previous year for the same individuals, but growth of white oak was somewhat less than the previous year.

Both trees decreased in growth rate as early as late May or early June, but with continued below average temperatures and much greater than average rainfall, both trees increased in growth rate and growth continued to the latter part of August. Soil moisture of the Mixed Oak habitat was not as low as within the Mixed Mesophytic community before the occurrence of heavy summer rains, with the result that the Mixed Mesophytic white oak responded more quickly to soil moisture replenishment than did the Mixed Oak white oak. Total summer period growth of the Mixed Mesophytic white oak was therefore somewhat higher than that of the previous year, while the 1958 summer period growth of the Mixed Oak white oak was somewhat less than during the previous year (Table 7).

Radial growth data was also obtained during 1958 of two additional chestnut oak individuals occurring within the Chestnut Oak community of the western ridge. Radial growth of these individuals did not appear excessive during the spring period, but was relatively great during the summer period (Table 6 and Fig. 4). This agrees closely with the pattern for the initial measurement year of the other two chestnut oaks (1955) even though climatic conditions were considerably different. Radial growth data of a beech in each of the opposing slope communities and a red maple in each of the three communities are also here included. The growth patterns of both of these species are single peaked, characteristic of diffuse-porous trees in general. The Mixed Mesophytic beech grew almost half again as much as the Mixed Oak beech, which may be largely attributed to a longer growing period. Total growth of the Mixed Mesophytic and Mixed Oak red maples was approximately the same even though the maximum growth rate of the former exceeded that of the latter.

Correlations of 1959 data. — Temperatures were below average within both the Mixed Mesophytic and Mixed Oak communities during April. Precipitation was near average, but soil moisture was considerably below average on the Mixed Oak slope. Spring growth rates were relatively great for all ring-porous species suggesting that even though soil moisture was below average it was great enough in the spring that it was not appreciably limiting to growth. Precipitation remained near average during May but was below average during June. Even though July precipitation was near average, the deficit incurred in June was sufficient to cause soil moisture to remain below average on both slopes during June and July (Tables 9 and 10). Temperatures generally averaged at or above average on both slopes during May and June. July temperatures were near average except on the Mixed Oak slope where maximum monthly temperature was about 3½°F below the five year average (Table 8). The years 1955 and 1959 were the only years of the five year period in which late spring and summer temperatures were consistently above average and precipitation below average. However, in 1955 unusually high soil moisture in the early spring carried over through most of the season in contrast to the low moisture values of the 1959 season. Growth rate and total amount of growth during the summer period of 1959 were both the lowest encountered during the five years for the ring-porous species.

The unusual curves of the two chestnut oak individuals on the ridgetop are worthy of note (Fig. 4). During the summer period of 1958 and the spring period of 1959 growth of these two trees appeared appreciably high. This is similar to the pattern of the other chestnut oaks during 1955 and 1956, and thus also appears due to high concentrations of hormones in the area of wounding by dendrometer screws.

The growth peaks and growth cessation dates of the red maples and beeches occurred earlier in 1959 than in 1958, which is a characteristic of hormone action in the oaks. However, since soil moisture was low and temperatures were relatively high during 1959, which conceivably also could produce these results, it is impossible to determine if wounding did effect the growth of these species. The same sharp distinctions between individuals of different sites occurred in 1959 as in 1958. The Mixed Mesophytic beech reached peak growth later than the other individuals and continued growth much longer. Of the beech measured in three communities, growth was greatest in the Mixed Mesophytic beech and least in the erratic on the ridge top (Table 6). Even though red maple is a more common associate on the Mixed Oak slope than is beech, differences in amount of growth of individuals of the opposing slopes was more pronounced than in the case of beech. It is possible that once established, growth of beech will actually be greater on the Mixed Oak slope than will red maple, relative to the growth of these two species within the Mixed Mesophytic community. This being the case, the abundance of red maple and beech within the Mixed Oak community may be dependent upon the relative ability of the two species to survive the critical germination and seedling stages.

SUMMARY AND CONCLUSIONS

A five year study concerning radial growth of chestnut oak, white oak, beech, and red maple individuals occurring within opposing slope and ridge top forest communities of Neotoma is here reported.

Initiation of radial growth of all individuals was found to be correlated with, but not necessarily dependent upon, a certain stage in phenological development. Initiation of ring-porous species was correlated with time of bud swelling, and initiation of diffuse-porous species with time of leaf unfolding.

Rate and total amount of growth of earlywood of ring-porous species appears to be determined largely by amounts of carbohydrate reserves of the previous season and to a lesser degree by current environmental conditions since most of the earlywood growth occurs before leaf expansion. Of the two, a closer correlation was observed between maximum weekly growth rate of spring and maximum weekly growth rate of previous summer periods than between total amount of growth of the spring period and total amount of summer period.

Increment borings of white oak were measured and a close correlation was found between width of earlywood and amount of growth during the spring period as measured by dendrometers. Dendrometer measurements of total summer period growth were significantly greater than latewood measurements from borings, perhaps due to late summer phloem growth indicated by dendrometer data but not boring data.

Abnormally high growth rates occurred during the summer growth period of the first year and the spring growth period of the second year following installation of dendrometer screws during the winter dormant period. Abnormally high growth rates were not evident during the spring period of the first year or after the beginning of the summer period of the second year.

Successive averages of weekly growth data were determined, plotted, and generalized curves drawn for each year of the trees included in the study. The curves, representing seasonal trends, were correlated with deviations from the five year average of average daily maximum and minimum air temperature per month, monthly gross precipitation, and average weekly soil moisture per month.

High air temperatures (average maximum and/or minimum) were associated with lower growth rates for all species studied. It is concluded that these low growth rates were mainly due to increased respiration rates and, since higher temperatures were usually associated with periods of low soil moisture, to water stresses developing from low soil moisture and high transpiration.

It is concluded that below average soil moisture was never sufficiently low during spring growth periods to be appreciably limiting to growth of earlywood.

Soil moisture appears most limiting to growth in the latter part of the season when the presence of low amounts of soil moisture may be associated with temporary or complete stoppage of growth.

Replenishment of soil moisture during the latter part of a summer growth period characterized by low soil moisture may extend the growth period longer than during periods when soil moisture is not low.

Response of chestnut oak and white oak to environmental variables appeared similar in magnitude between individuals occurring in opposing slope habitats.

Total growth of white oak on the Mixed Oak slope exceeded that on the Mixed Mesophytic and the reverse was true of chestnut oak. However these differences may be due to size, age, and competition differences rather than hereditary differences between species.

Beech had appreciably longer growing seasons in the Mixed Mesophytic community during the five year period than within the Mixed Oak and Chestnut Oak communities of the southwest-facing slope and ridge top habitats respectively.

Maximum growth rate of the Mixed Mesophytic red maple was as much as twice as great as the Mixed Oak individuals and three times as great as those occurring within the Chestnut Oak community.

Relative to the growth rates of beech and red maple occurring within the Mixed Mesophytic community, growth of beech is greater than red maple within both the Mixed Oak and ridge top habitats, suggesting that paucity of beech in these two sites may be due to inability to germinate and survive the seedling stage rather than to growth after these stages.

ACKNOWLEDGMENTS

Sincere appreciation is hereby expressed to Dr. Edward S. Thomas for use of his land, to Mr. John Freeman for use of his land and power equipment for haulage of heavy equipment, to the Ohio Power Company for extension of electrical service into the study area, and to the United States Atomic Energy Commission for financial support of the Neotoma basic ecological and bioclimatic research program.

Table 1.
Weekly radial change (thousandths of an inch) of white oak and chestnut oak in the Mixed Mesophytic community (M.M.) and the Mixed Oak community (M.O.) during 1955, 1956, and 1957.

	1955					1956					1957			
	Chestnut Oak		White Oak			Chestnut Oak		White Oak			Chestnut Oak		White Oak	
Trees/ Dates	M.M.	M.O.	M.M.	M.O.	Trees/ Dates	M.M.	M.O.	M.M.	M.O.	Trees/ Dates	M.M.	M.O.	M.M.	M.O.
4/5-4/12	3	3	3	2	4/3-4/10	0	1	—2	—1½	4/2-4/9	2½	1	0	1
4/13-4/19	11	8	5	1	4/11-4/17	3	2	3½	3½	4/10-4/16	—½	2½	—1½	—2½
4/20-4/26	10½	9	10	8	4/18-4/24	3	1½	—1	—1	4/17-4/23	15½	14	6½	7½
4/27-5/3	4½	4½	4	3½	4/25-5/1	13	16	7	9½	4/24-4/30	20½	10½	16½	18
5/4-5/10	8½		7	8½	5/2-5/5	5	—3	5½	6	5/1-5/7	5½	3	4	6½
5/11-5/17	7½	13½	4	5	5/6-5/12	15	8½	11	12½	5/8-5/14	18	5	13½	11½
5/18-5/24	9	4	5½	6	5/13-5/21	11	10½	9½	9	5/15-5/21		8½		5½
5/25-6/1	12	5	6½	4	5/22-5/30	12½	6	11½	12	5/22-5/29	7	8	2	5
6/2-6/7	23½	14	17½	9	5/31-6/5	4	1	11	2	5/30-6/4	8½	8½	4½	9
6/8-6/14		11		8	6/6-6/12	6	4	5	4½	6/5-6/11	12½	11	9	12
6/15-6/21	27½	27	16½	27	6/13-6/19	19	13½	10½	13½	6/12-6/18	9½	12½	8	10
6/22-6/28					6/20-6/26	10½	10	5½	7	6/19-6/25	—	9	—	10½
6/29-7/5	15	13	11	17	6/27-7/3	9½	3	9	9	6/26-7/2	7	5½	3½	5½
7/6-7/12	20	20	13	20½	7/4-7/10	7	15	4	5	7/3-7/9	7½	6½	5	6½
7/13-7/19	20	7	9½	12½	7/11-7/17	7	8	5½	9	7/10-7/16	5½	3	4½	3½
7/20-7/26	17	7	9½	7	7/18-7/24	6	—	4½	7½	7/17-7/23	12	8½	12½	9
7/27-8/2	15½	10	6	7½	7/25-7/31	3	—2	3½	7	7/24-7/30	7½	3½	4	2½
8/3-8/9	11	12	5½	7½	8/1-8/7	1	2	1	3½	7/31-8/6	—2½	2½	3	3
8/10-8/16	5½	4	5	4½	8/8-8/14	2	—1½	1½	6	8/7-8/13	0	4½	½	4½
8/17-8/23	1	9	7½	9½	8/15-8/21	—½	6½	½	1	8/14-8/20	0	—1½	½	1½
8/24-8/30	0	—2	—½	0	8/22-8/28	—1½	½	—½	—½	8/21-8/27	0	½	½	—1
8/31-9/5	5	—5	—½	—4	8/29-9/4	1½	—2	—½	½	8/28-9/3	3	4½	1	6

Table 2.

Weekly radial change (thousandths of an inch) of chestnut oak, beech, white oak, and red maple in the Mixed Mesophytic (M.M.), Mixed Oak (M.O.), and Chestnut Oak (C.O.) community during 1958. The suffix "a" refers to an additional tree within the Chestnut Oak community.

Dates	Chestnut Oak				Beech		White Oak		Red Maple		
Trees/	M.M.	M.O.	C.O.	C.O. "a"	M.M.	C.O.	M.M.	M.O.	M.M.	M.O.	C.O.
4/2-4/8	0	—½	2	16½	1	—	½	½	—1	0	1
4/9-4/15	½	½	0	6	—½	½	0	0	0	0	0
4/16-4/22	10	6½	8½	11	2	—½	6	6	1½	1½	0
4/23-4/29	12	10	10	13	1½	—½	9	9½	3	2½	2
4/30-5/8	12	6½	6	4	2½	3	7½	6½	3½	1½	2
5/9-5/13	6½	5½	2	3½	2½	2½	3½	3	1	2	0
5/14-5/20	11½	3	4	7	7	6½	6½	7	15	9	2½
5/21-5/27	7½	4	3	8	5	6	3	4½	13	6	4½
5/28-6/3	9	6½	10½	15	4	6½	5	4½	15½	9½	3½
6/4-6/10	—	12	17	—	—	8½	8½	8	18	8	6
6/11-6/17	8½	10	12	—	10	7½	6½	6½	4	11	7½
6/18-6/26	12½	12	15½	—	—	11½	7	8	16½	16	4
6/27-7/3	6½	6	10	16	—	12	5	4	10½	11	5½
7/4-7/10	14½	15	15	21	10	8½	9	11	11½	11½	2
7/11-7/17	12	9½	11	17	8	7½	3	7	1½	10	2
7/18-7/24	9	8½	11	12	7½	7	3	7½	2	5½	1
7/25-7/31	5	8	7½	5	15	8½	5	6	4	8	1½
8/1-8/7	3	10½	2	2	12	4	1½	2½	½	6½	1
8/8-8/14	3½		4	—	13	3½	2½	3	1½	6	—½
8/15-8/21	½	½	½	5½	13	1	½	0	—½	3	1
8/22-8/28	0	{2	5½	3	8	2	1	1½	1½	1	1
8/29-9/4	1		—½	2	8	—1	0	—1	—½	½	½

Table 3.

Weekly radial change (thousandths of an inch) of chestnut oak, beech, white oak, and red maple in the Mixed Mesophytic (M.M.), Mixed Oak (M.O.), and Chestnut Oak (C.O.) communities during 1959. The suffix "a" refers to additional measurement trees within the same communities.

Trees/	Chestnut Oak				Beech		
Dates	M.M.	M.O.	C.O.	C.O. "a"	M.M.	M.O.	C.O.
3/31-4/7	0	0	1	½	—½	½	0
4/8-4/14	4	5	15	5	½	1	½
4/15-4/21	9	8½	—2	10	1	2½	½
4/22-4/28	11½	7½	9	10	2	3½	1
4/29-5/5	14	7	8½	6	3½	10	1½
5/6-5/12	13½	9	9	12	9	14½	8½
5/13-5/19	2	½	3½	—½	3	8½	4
5/20-5/28	7½	9	13	20½	16	23½	15
5/29-6/2	6½	7	10	10½	10	10½	8
6/3-6/9	3	4	—1½	7½	10	9	5½
6/10-6/16	9½	6	8	11½	12½	8½	6½
6/17-6/23	7½	9½	—½	4	12	9	1½
6/24-6/30	8	6½	—1	—4½	14½	8	—½
7/1-7/7	5½	1½	5½	6½	11	3½	3½
7/8-7/14	0	½	—1½	—1½	9	1½	0
7/15-7/21	8	9½	4½	3	11½	2½	½
7/22-7/28	6	6	5	6½	13	1½	1
7/29-8/4	1	—½	—1½	2½	10½	0	½
8/5-8/11	—2	—3	—6½	—5½	6½	—1½	—2
8/12-8/18	3½	4	6½	9½	5½	1½	2½
8/19-8/26	—1	2½	—5	—8	1	—½	—1½
8/27-9/3	0	6½	6	5½	1	0	1

Table 3. (Continued)

Weekly radial change (thousandths of an inch) of chestnut oak, beech, white oak, and red maple in the Mixed Mesophytic (M.M.), Mixed Oak (M.O.), and Chestnut Oak (C.O.) communities during 1959. The suffix "a" refers to additional measurement trees within the same communities.

Trees/	White Oak			Red Maple			
Dates	M.M.	M.O.	M.O. "a"	M.M.	M.O.	M.O. "a"	C.O.
3/31-4/7	½	½	—1	—½	—½	—1	—½
4/8-4/14	1½	2½	4½	2	1	1	4
4/15-4/21	4½	6½	10½	1½	2½	2	—2½
4/22-4/28	7	8	11½	2½	—½	1½	1
4/29-5/5	16½	8½	9	7	1½	—1	1½
5/6-5/12		9	12	17	6	3½	½
5/13-5/19	½	½	1	5½	2½	—½	1
5/20-5/28	6½	7½	9	26	11	7	5½
5/29-6/2	6	6	7½	10	8½	5	6
6/3-6/9	3½	5	3½	5	2	2½	—1
6/10-6/16	8	5½	7	8½	11	4	4
6/17-6/23	6½	9½	9½	7½	6½	4½	1½
6/24-6/30	6½	8	8	7½	6	½	—2
7/1-7/7	4	2	4½	5½	3	—1	3
7/8-7/14	2	1½	1	—½	0	—1	—1½
7/15-7/21	5	9	9	5	3½	3½	2
7/22-7/28	4	7	6½	3	1½	1½	4
7/29-8/4	1	2½	1½	0	0	—2	—1½
8/5-8/11	—½	0	—4	—1½	—2	—1½	—4
8/12-8/18	2½	2	—7	3	3	2	6½
8/19-8/26	—1	—½	9	—1	—2½	—1½	—6
8/27-9/3	0	½	2½	3½	3	2	3

Table 4.

Weeks during 1957, 1958, and 1959 when bud swelling, leaf unfolding, and mature leaf size of chestnut oak, white oak, beech, and red maple were first noted within the Mixed Mesophytic, Mixed Oak, and Chestnut Oak communities at Neotoma.

	Bud Swelling			Leaf Unfolding			Mature Leaf Size		
	Mixed Mesophytic	Mixed Oak	Chestnut Oak	Mixed Mesophytic	Mixed Oak	Chestnut Oak	Mixed Mesophytic	Mixed Oak	Chestnut Oak
Chestnut Oak									
1957		4/17-24			4/25-30			5/9-16	
1958	4/17-24	4/9-16	4/9-16	4/25-30	4/25-30	4/17-24	5/17-24	6/1-8	5/17-24
1959	4/17-24	4/17-24	4/17-24		5/1-8	4/25-30	5/9-16	5/9-16	5/9-16
White Oak									
1957		4/9-16		3/17-24	4/17-24			5/25-31	
1958	4/9-16	4/9-16		5/1-8	4/25-30		5/25-31	6/1-8	
1959	4/17-24	4/17-24			5/1-8		5/25-31	5/17-24	
Beech									
1958	3/25-31		4/1-8	4/17-24		5/1-8	5/9-16		5/25-31
1959	3/25-31		4/17-24	4/25-30		4/25-30	5/9-16		5/9-16
Red Maple									
1958	3/25-31	4/1-8	4/1-8	4/17-24	4/17-24	4/17-24	5/9-16	6/1-8	5/17-24
1959	3/17-24	3/25-31		5/1-8	4/17-24	4/9-16	5/17-24	5/17-24	5/9-16

Table 5.

Dates of initiation (I), cessation (C), total amount (A) in thousandths of an inch, and duration (D) of radial growth in weeks during 1955, 1956, and 1957 of chestnut and white oak within Mixed Mesophytic and Mixed Oak communities of Neotoma. Items in ( ) are in doubt.

Species and Community	1955				1956				1957			
	I.	C.	A.	D.	I.	C.	A.	D.	I.	C.	A.	D.
Chestnut Oak, M.M.	4/5- 4/12	8/17 8/23	222	20	4/11- 4/17	8/8- 8/14	137½	18	4/17- 4/23	7/24- 7/30	170½*	15
Chestnut Oak, M.O.	(4/5- 4/12)	8/17- 8/23	(181)	(20)	4/11- 4/17	8/22- 8/28	101½*	20	4/17- 4/23	9/11- 9/17	131	22
White Oak, M.M.	4/13- 4/19	8/17- 8/23	143	19	4/11- 4/17	8/15- 8/21	108½	19	4/17- 4/23	9/17- 9/24	98*	23
White Oak, M.O.	4/13- 4/19	8/17- 8/23	166	19	4/11- 4/17	8/15- 8/21	126½	19	4/17- 4/23	9/17- 9/24	139	23

*One wk. absent.

Table 6.

Dates of initiation (I), cessation (C), total amount (A) in thousandths of an inch, and duration (D) of growth in weeks of chestnut oak, white oak, red maple, and beech within the Mixed Mesophytic (M.M.), Mixed Oak (M.O.), and Chestnut Oak (C.O.) communities at Neotoma during 1958 and 1959. Items in ( ) are in doubt. The suffix "a" refers to additional individuals within the same communities.

Species and Community	1958 I.	1958 C.	1958 A.	1958 D.	1959 I.	1959 C.	1959 A.	1959 D.
Chestnut Oak, M.M.	4/9-4/15	(8/15-8/21)	(144)	(19)	4/8-4/14	8/12-8/18	118	19
Chestnut Oak, M.O.	4/9-4/15	(8/15-8/21)	(134½)	(19)	4/8-4/14	(8/27-9/3)	(111)	(21)
Chestnut Oak, C.O.	4/16-4/22	8/22-8/28	155	19	3/24-3/31	(7/22-7/28)	(98)	(19)
Chestnut Oak, C.O. "a"	4/2-4/8	(9/12-9/18)	(172½)*	(24)	4/8-4/14	(8/12-8/18)	(113)	(19)
White Oak, M.M.	4/16-4/22	8/22-8/28	93	19	4/8-4/14	8/19-8/26	85	19
White Oak, M.O.	4/16-4/22	8/22-8/28	106	19	4/8-4/14	8/19-8/26	100½	19
White Oak, M.O. "a"					4/8-4/14	8/5-8/11	115½	17
Red Maple, M.M.	4/23-4/29	8/22-8/28	123½	19	4/28-5/5	(8/27-9/3)	(116)	(17)
Red Maple, M.O.	4/16-4/22	9/12-9/18	132	22	4/15-4/21	8/19-8/26	66	18

*Four weeks not included.

Table 6. (contd.).

Species and Community	1958 I.	1958 C.	1958 A.	1958 D.	1959 I.	1959 C.	1959 A.	1959 D.
Red Maple, M.O. "a"					4/15- 4/21	7/29- 8/4	32	15
Red Maple, C.O.	4/23- 4/29	9/12- 9/18	48½	21	4/8- 4/14	7/29- 8/4	27	16
Beech, M.M.	(4/16- 4/22)	9/12- 9/18	(132½)**	(22)	4/15- 4/21	9/4- 9/8	162½	20
Beech, M.O.	4/30- 5/8	8/22- 8/28	106	17	4/15- 4/21	7/29- 8/4	116½	15
Beech, C.O.					4/15- 4/21	—	(57)	(20)

**Data of three weeks not available. Estimated correction of +25 was used.

Table 7.

Amount of growth of white oak in the Mixed Mesophytic and Mixed Oak communities at Neotoma in thousandths of an inch of earlywood and latewood as obtained from dried increment borings (I); amount of growth during the spring growth period and during the summer growth period from dendrometer data (D); and maximum weekly growth rate.

	Mixed Oak			Mixed Mesophytic		
	I.	D.	Max. Rate	I.	D.	Max. Rate
1955						
spring	28	21	—	26	26	6
summer	73	145	15½	65	117	10½
1956						
spring	32	30½	9	32	26	9½
summer	36	96	8	36	82½	—
1957						
spring	34	43½	9½	30	40½	8
summer	46	95½	9½	40	57½*	6½
1958						
spring	30	22	6½	21	22½	6½
summer	38	84	7½	26	70½	6½
1959						
spring	25	48½	7½	19	42½	7
summer	42	52	8	20	42½	7½

*Data of one week not available.

Table 8.

Deviations from five year average of the daily maximum and minimum temperatures per month at the Mixed Mesophytic and Mi·.ed Oak stations during April, May, June, and July of 1955 through 1959.

Mixed Meso-phytic		Ave. of 1955-1959	1955	1956	1957	1958	1959
April	(Max.)	64.4	+5.8	−3.4	+0.6	−1.9	−1.1
	(Min.)	38.5	+4.0	−2.5	+1.3	−2.3	−0.4
May	(Max.)	72.5	+2.8	+1.3	−4.3	−1.2	+1.4
	(Min.)	47.4	+3.1	−0.4	−3.2	−3.4	+3.9
June	(Max.)	74.7	+1.6	+1.6	−1.2	−3.0	+0.8
	(Min.)	54.3	+0.4	−1.3	+0.5	−1.3	+1.7
July	(Max.)	78.4	—	−0.4	+0.1	—	+0.4
	(Min.)	59.3	—	+2.2	−2.3	—	0.0
Mixed Oak							
April	(Max.)	64.4	+7.6	−2.4	+2.4	−5.9	−1.7
	(Min.)	39.9	+2.1	−1.2	+1.9	−1.4	−1.4
May	(Max.)	74.2	+2.0	0.0	−0.4	−3.2	+1.6
	(Min.)	48.4	+0.1	−1.2	+0.4	−4.6	+5.5
June	(Max.)	77.3	+0.2	+0.9	+1.7	−2.0	−0.9
	(Min.)	55.6	−3.6	+1.2	+3.2	−2.6	+1.8
July	(Max.)	80.7	+4.6	−2.7	+1.5	—	−3.4
	(Min.)	61.8	+3.5	−1.3	−2.0	—	−0.3

Table 9.

Deviations from the five year average of monthly gross precipitation (inches) in the open valley for the months April, May, June, and July during 1955 through 1959.

Mixed Meso-phytic	Ave. of 1955-1959	1955	1956	1957	1958	1959
April	4.1	−0.7	+0.5	−0.3	+0.9	−0.2
May	3.8	−0.7	+0.5	+0.1	0.0	−0.1
June	3.5	−0.4	−0.3	−0.1	+3.0	−1.9
July	4.4	−1.2	+1.5	−1.1	+4.3	−0.4

Table 10.

Deviations from the five year average of monthly soil moisture in percent dry weight obtained weekly at the 1-3 inch depth in the Mixed Mesophytic and Mixed Oak habitats at Neotoma during 1955 through 1959. Field capacity (1/3 atm) is 15.5% in the Mixed Mesophytic and 21.0% in the Mixed Oak soils at 1-3 inch depth.

Mixed Mesophytic	Ave. of 1955-1959	1955	1956	1957	1958	1959
April	33	+6	–3	0	–4	0
May	29	+1	0	–1	0	–1
June	27	+1	0	+1	+1	–3
July	21	–1	+2	0	+5	–4
Mixed Oak						
April	30	+5	+3	+1	–3	–5
May	28	+4	0	–1	+1	–2
June	23	+2	0	+1	+3	–8
July	16	–2	+1	–2	+7	–6

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