Some Aspects of Tree Growth

RAY C. FRIESNER, Butler University

Interest in the general subject of tree growth is by no means recent. According to Glock (11) the literature of the nineteenth century contains many references bearing in one way or another upon the matter of growth in trees. Apparently the earliest, as well as the most sustained interest, has been displayed with regard to the nature and significance of growth rings. But in spite of this long period of interest and its consequent stimulus to study, there still remain today a number of important unsolved problems—such problems, for example, as: (1) the relation of growth to total rainfall; (2) the rainfall period showing highest degree of correlation with growth; (3) relation to temperature; (4) relation of vertical growth to diametral growth; (5) relation of vertical growth to environmental factors; (6) correspondence of elongation both as to initiation and duration in different parts of the same tree.

In the development of my subject I should like to treat it under three main subdivisions, viz. (1) Elongation; (2) Diametral growth during the current season; (3) Annual ring studies of past years.

Elongation

Time of Initiation. The time of awakening of bud activity is a direct response of the individual to factors of the environment, the most important of which, insofar as any particular species, in successive years, is concerned, is temperature. Each species shows its own specific relation to temperature. Apparently, pines initiate vegetative bud-activity about one to three weeks earlier than some of our hardwoods. In 1941 (8) *Pinus resinosa*, *P. sylvestris* and *P. banksiana* began activity in Brown County, Indiana, during the week ending April 13, and *P. strobus* during the following week while during the same year, in Marion County, activity began in *Fagus grandifolia* and *Quercus alba* during the week ending April 21, in *Ulmus americana* and *U. fulva*, April 28 and in *Fraxinus americana*, May 5. Other broad-leaf trees, however, are as early in growth initiation as the pines, e.g. *Acer saccharum* in 1941 began during the same week as the pines.

In 1942 *Fagus grandifolia* and *Quercus alba* showed initiation of bud activity during the week ending April 20, *Fraxinus americana* during the week ending May 4, while *Pinus strobus* began April 15 and *P. resinosa*, April 6.

In more northern latitudes initiation comes later but the relationship in times of initiation between conifers and broadleaf species remains about the same. Thus, in *Pinus resinosa* elongation began at Ithaca, N. Y., May 7 (1), at Stephentown, N. Y., April 27 to May 12 (3), at Keene, N. H., May 15 (13), and in northwestern Connecticut (14) the 4-year average in 23 individuals was April 27. The broadleaf species, *Fraxinus* *americana*, *Quercus rubra* (probably *Q. borealis* var. *maxima*), *Acer rubrum*, *Betula populifolia* and *B. papyrifera* all began at about the same time as that for *P. resinosa*.

Behavior and Duration of the Growth Curve. The elongation growth curve for every species of tree studied exhibits essentially a grand-period type of behavior wherein activity begins slowly, accelerates with increasing rate to a maximum and decelerates in much the same, except inverse order to a dragging minimum followed by complete cessation. Published data of this type includes *Pinus strobus* (8) (3) (24), *P. resinosa* (8) (1) (3) (13) (14) (26), *P. sylvestris* (8), *P. banksiana* (8), *Larix laricina* (3), *L. decidua* (3) (14), *Picea abies* (3), *P. canadensis* (3), *P. rubra* (3), *Tsuga canadensis* (3), *Fraxinus americana* (14), *Quercus borealis* var. *maxima* (14), *Acer rubrum* (14), *Betula papyrifera* (14), and *B. Populifolia* (14). Various modifications of the symmetrical grand-period curve are found, e.g. either the accelerating or the decelerating side may be much longer drawn-out than the other side; either side may have flat or nearly flat places; double peaks may occur and they may be either essentially equal or they may be quite unequal with the secondary peak coming on either the accelerating or the decelerating side.

Apparently the essential character of these curves is little modified by external conditions. The time when elongation begins, the height of its peak, and the total amount of elongation are affected to some extent by external factors of both the present season and the past season. The height of the curve and total elongation are especially influenced by both available reserves constructed and stored during the past season and by available moisture during the present season.

Modifications of the symmetrical grand-period curve are probably largely due to internal factors such as availability and activity of enzymes and growth hormones, and conduction problems of water, minerals, and food reserves.

The duration of the growth curve varies with different species and also with different individuals of the same species. In *Pinus strobus* the total range for all individuals is 49-84 days with 81% of the individuals showing 56-70 days, (8). In *P. resinosa* the total range is 45-70 days. In Brown County, Indiana, (8) 76% of the individuals showed 63 days; at Keene, N. H., and in northwestern Connecticut Kienholz (13, 14) found the average to be 60 days; at Ithaca, N. Y., Baldwin (1) found it to be 69 days, while at Stephentown, N. Y., Cook (3) found it to vary over a five-year period from 45-63 days. In *P. sylvestris* the range (8) is 56-84 days with 78% of the individuals showing 56-63 days. In *P. banksiana* (8) the range is 49-84 days with 90% of the individuals showing 56-70 days. Apparently, there is no correlation between time of initiation and length of duration, nor is there any correlation with initial height of the individual.

Kienholz (14) found that broadleaf species fall into 2 groups on the basis of height growth behavior. In the first group height growth rises rapidly to a climax in late May (in Connecticut) and falls off to zero by late June with a total growth period of about 60 days. Of this growth 90% occurred in the 30 days beginning within 1 or 2 weeks after initiation of activity. Species belonging to this group are *Quercus borealis* var. *maxima*, *Acer saccharum*, *A. rubrum*, *Fraxinus americana*, and *Fagus grandifolia*.

In the second group growth begins about the same time but rises more gradually to a climax which was reached in Connecticut in mid-June and then falls off to zero by mid-August with a total growth period of 110 days. In this group 90% of the growth occurred in the 60 days beginning 3-4 weeks after initiation of activity. *Betula populifolia*, *B. papyrifera* and probably *Liriodendron tulipifera*, *Populus grandidentata* and *P. tremuloides* belong to this second group.

There is a remarkable similarity in the behavior of the growth curve in the same species in successive years. Tryon and Finn (26) found that the peak of growth came in *Pinus resinosa* and *Picea glauca* at the same time for each of 3 years and in *Larix decidua* it came at nearly the same time for each of these years. Stevens (24) and Kienholz (13) found similar results in *Pinus resinosa* and *P. strobus* and Kienholz (14) found nearly similar results for *Fraxinus americana*, *Quercus borealis* var. *maxima*, and *Acer rubrum* over a 4-year period. Species with longer growing period showed greater variation in this regard.

In every individual the midsummer zero-point is followed by some further elongation, varying from zero to a few mm per week. In a few individuals (approximately 10%) this post-midsummer elongation is true stem elongation but in the greater majority (approximately 80%) of the individuals, it is probably confined to elongation incident to bud formation because the total amount of elongation does not exceed the original length of the winter buds. Of the individuals showing true post-midsummer stem elongation, 80% were *Pinus banksiana*.

In young trees the total amount of seasonal elongation of the primary axis shows a relation to the initial height of the trees. Taller size-classes show greater average elongation than shorter size-classes. This would undoubtedly find a limit in height-class beyond which it would not hold, but no data are at present available on this point.

When elongation of different axes of the same tree is considered it is found that the primary axis initiates growth earlier, continues longer and attains greater total elongation than axes of secondary or lesser rank. Secondary axes average greater elongation than tertiary and those nearer the top of the tree begin earlier and attain greater total growth than those farther from the top.

Diametral Enlargement

Initiation of growth. Diametral increase in trunks of most deciduous trees depends for its initiation upon the beginning of bud activity in the spring but this is not true of evergreen species, at least not in coniferous evergreens. The time of initiation of cambial growth in coniferous evergreens is more closely dependent upon temperature than any other factor of the usual environment. MacDougal (20, 21) has shown this to be true in *Pinus radiata* in California and my own unpublished data obtained by Mr. Gershom Walden show it to be true in *Pinus strobus* in Maine.

In most deciduous trees initiation of cambial activity occurs with or follows at some little time after the initiation of bud activity. A striking exception to this is found in Fraxinus. Chalk (2) working with *F. excelsior* and *F. oxycarpa* and MacDougal (21) working with *F. velutina* have shown that diametral enlargement begins as much as three weeks before vegetative buds begin to show activity. My own unpublished data show that it begins in *F. americana* at least a full week ahead of vegetative bud activity. In *Fagus grandifolia* (6, 9), *Acer saccharum* (21, 9) and *A. macrophyllum* (21) initiation of cambial activity ranges from just prior to shortly after the leaves have attained full size. In *Ulmus americana* (9, 16) and *U. fulva* (9), initiation ranges from just before to shortly after the beginning of vegetative bud activity but does not reach any considerable amount until leaves are nearly full size. In *Quercus velutina* (21), *Q. borealis* var. *maxima* (21) and *Q. alba* (9) initiation essentially coincides with beginning of vegetative bud activity.

Behavior of Growth Curve and Its Duration. Above we have shown that, in deciduous trees, the initiation of the growth curve is definitely related to time of awakening of bud activity. This, in turn, of course, is related to both external and internal environmental conditions, the most obvious and readily measurable of which, is temperature. The behavior of the growth curve, once it has started, is quite variable in different species and shows varying degrees of relation to measurable environmental conditions. In *Fagus grandifolia* (6, 9), the curve appears always to show a grand-period type of behavior. Environmental conditions, especially the temperature-available moisture-transpiration complex, play a prominent part in the time of initiation, the amplitude of the curve, and the time of its cessation, but not in the type of curve. That is to say, environment controls the quantitative but not the qualitative aspects of the behavior.

In other species, *Ulmus americana*, for example, the curve of growth rate has practically no resemblance to a grand-period type of curve. Successive weeks show almost continuous alternation of greater and lesser diametral increments (9) with no very definite relation either to amount of rainfall, average daily temperature or evaporating power of the atmosphere. In still other species, *Ulmus fulva*, *Acer saccharum* and *Quercus alba*, for example, the growth curve, while not illustrating the clean-cut grand-period type found in Fagus, approximates this type.

It must be remembered that diametral changes are a combination of the addition of wood and bark cells on the one hand and turgidity changes on the other. This is clearly shown by the fact that net diametral losses are encountered when available water falls below transpiration demands and by the presence of daily reversible variations to be discussed below. How much of the autumnal changes are true growth additions and how much are mere turgidity changes cannot be differentiated precisely, but it is certain that they are mostly turgidity changes, especially when the autumn is mild and dry, because the final diameter measurements in late December are never (in deciduous species) much more, and more often considerably less, than at the late summer zero-point.

Daily Reversible Variations. Hourly variations in diameter are recorded by the dendrograph during some parts of the vegetative season for all species studied. These daily reversible variations are entirely due to turgidity changes and set in whenever the transpiration loss exceeds the ability of the absorbing and conducting organs to supply water. The amplitude of these reversible changes is directly proportional to this net difference and amounts in concrete measurements to as much as 0.3 mm. The fact that these daily losses and recoveries continue for some little time after all leaves are either dead or fallen indicates that even twigs and buds, especially in mild rainless periods, may lose water during the light period of the day faster than it can be absorbed and conveyed past the point of diametral measurement.

MacDougal (21) has shown that there is a very close relation between the diameter of trees and available moisture in his irrigation experiments. Irrigation of a specimen of *Quercus agrifolia* (an evergreen oak) which had shown no growth increase for 3 weeks resulted in diametral increase within 2 hours after application of water.

For more detailed and thorough treatment of diametral growth changes the student is referred to MacDougal's "Tree Growth" (21).

Annual Ring Studies

In the preceding 2 subdivisions of this discussion attention was focussed upon current-season growth. In this final subdivision I should like to summarize some of the more important data dealing with growth during past years as revealed in a study of growth rings. For an exhaustive resume of the relation of such data to climate the student is referred to Glock's (11) able treatment in Botanical Reviews. If one is interested in a still broader consideration of the entire field of growth rings there is available a bibliography by Schulman (23) published in "Tree-Ring Bulletin" in April, 1940. The former of these articles contains a bibliography of 203 references and the latter, 412.

Relation to Rainfall. The problem of sorting out the different factors of the environment and determining just what role each plays in the matter of growth is well nigh unsolvable because the behavior of the individual is its response to its total environment.

Nevertheless, some of the factors of the environment are much more nearly uniform for any particular individual from year to year than others and hence wide variations in growth from year to year may reasonably be concluded to be due to those factors of the environment which also have a wide variation during the same time interval (15). Thus, of all the factors of the external environment, rainfall, amount of sunlight and temperature are probably the most variable from year to year. These three factors have a definite inter-relationship to each other. Any one of them may become a limiting factor.

Rainfall becomes more important during periods when available moisture is near the critical point. It has been shown (7) that there is a much closer correspondence between width of year-rings and rainfall when there is a considerable decrease following a year of average rainfall than when the same amount of decrease follows a year when rainfall was well above the average. The converse is also true, viz. a considerable increase in rainfall in one year is accompanied by greater increase in growth when it follows a year deficient in available moisture than when it follows a year of nearly average rainfall. Thus it is apparent that tree growth reflects rainfall only when the latter is such as to influence the physiological processes of the tree. It must, therefore, be obvious that rainfall during some rainfall periods will be far more critical than that during others. These rainfall periods which are most critical will vary with different species of trees, with different types of topography and to a less extent in the same species and on the same site with different years depending upon rainfall in other rainfall periods.

In New England, Lyon (19, 17) finds no consistent correlation between any rainfall period and growth rings in *Pinus nigra* var. *austriaca*, *Picea excelsa* and *Larix decidua* while there was significant correlation in the case of *Pinus strobus*, *Pinus sylvestris*, *Tsuga canadensis* and *Quercus borealis* with rainfall during April-August and a number of combinations of months between these. In an earlier study Goldthwait and Lyon (12) found *Pinus strobus* (also in New England) to show closest correlation between year-ring width and rainfall during the months of May-July.

In northern Indiana Diller (4) found growth in *Fagus grandifolia* to show closest correlation with rainfall during the month of June while in the Knobs area of southern Indiana, Kleine, Potzger and Friesner (15) found annual-ring width in *Quercus alba*, *Q. borealis* var. *maxima*, *Q. montana* and *Q. velutina* to correlate with rainfall for June-August in 19 out of 24 years, with April-May in 4 of the remaining 5 years and with annual rainfall in the other year.

Rainfall for the calendar year as a whole has been found to show significant correlation in some studies, e.g. in the case of oak in Illinois (10), *Juniperus virginiana* in Nebraska (27). Rainfall periods consisting of many other combinations of months have been found significant for different species and in different areas, e.g. the vegetative year, i.e. November to and including the following October; the water year, i.e. October to the following September; September-August; August-July; 15-month period, June of one year to and including August of the following year; January-August; January-July; January-May; March-June; March-May; April-May.

The differences in rainfall periods correlating best in different areas and in different species are partly explainable on such bases as differences in time of most active growth in different species; differences in topography; differences in time of growth season in different geographical areas and differences in rainfall of past periods.

The correlation in *Fagus grandifolia* for the month of June is significant in view of the fact that dendrometer studies have shown (6, 9) that 70% of the annual diametral increase in this species occurs during this month and an additional 10% during the following month. The correlation in Quercus with rainfall for the June-August period is significant from two standpoints. Dendrometer studies (9) show that 62.5% of the diametral enlargement occurs during this same period and the studies were made in a region with such high relief that run-off is always high, this offering little opportunity for much moisture carry-over from previous periods. The fact that 4 of the 5 years showing no correlation with June-August rainfall showed correlation with April-May rainfall is also significant in view of the fact that the remaining 37.5% of growth occurs during April and May.

The fact that the same species may show best correlation with different rainfall periods in different geographical areas and under different topographical conditions is well illustrated by the differences shown by oaks in different areas. In the Knobs of Indiana where relief is high the most significant correlation (15) was with rainfall for June-August. In Marshall County, Indiana (7), on a site where relief is very little, the most significant correlation in *Quercus alba* was with rainfall for the 12-month period November-October, but in *Q. borealis* var. *maxima* it was with rainfall for June-August. In Illinois, Fuller (10) found the calendar year most significant while in Missouri, Robbins (22) found rainfall for March-June most significant and in New York, Stewart (25) found June-July to correlate best.

The same rainfall-period does not always necessarily have equal significance in any two successive years, especially when topographic conditions are such that there is opportunity for sufficient water to soak in and be held as a carry-over from a previous rainfall-period. This is well illustrated when we consider the June-August rainfall-period for Indianapolis for the years 1940 and 1941 (9). In 1941 the June-August rainfall was 93.86% of normal while in 1940 it was only 55.4% of normal. However, diametral increase in *Fagus grandifolia* (6, 9) was 17.9% greater in 1940 when June-August rainfall was 55.4% of normal than in 1941 when rainfall was 93.86% of normal. This is correlated with the fact that the lower rainfall in June-August 1940 followed a January-May rainfall which was 87.73% of normal while the higher rainfall in June-August 1941 followed a January-May rainfall which was only 37.9% of normal.

Relation to Temperature. Temperature probably plays its most significant role in determining the time of initiation of growth but shows only an obscure and indirect relation to the quantity of growth. Of course, it must be remembered that the response of the organism is to the sum total of its environmental conditions and that temperature is a part of this total. On the other hand, other factors which enter into this total, more particularly available water, are more likely to constitute the "bottle-neck" in the factor complex. If all factors exclusive of temperature were at their optimum, then a definite relation between growth and temperature would be readily demonstrated, but in nature this probably seldom occurs except at the beginning and end of the vegetative season or in higher latitudes.

Significantly enough the relation between temperature and growth, to the degree to which it can be established, is mostly inverse in lower latitudes and direct in higher latitudes.

In Finland and northern Sweden, Erlandsson (5) found a direct relationship between July temperature and growth but the curves show agreement in only about ⅔ of the years. In New England Goldthwait and Lyon (12) found the relation between growth in *Pinus strobus* and temperature to be direct for April-May and inverse for June, while Lyon (18) found in *Tsuga canadensis* a positive relation to March-April temperature but no consistent relation to that occurring during the growing season.

In almost all cases in warmer latitudes, summer relationships, if detectable at all, have been of an inverse character but that relationship has often been weak and the two curves may parallel or oppose each other in different years. Diller (4) found that the relationship is inverse for *Fagus grandifolia* with June temperature for northern Indiana in 19 out of 20 years. Kleine, Potzger and Friesner (15) found best correlation for four species of Quercus to be inverse with June-August temperature but there were numerous exceptions.

The fact that the effects of temperature upon tree growth are both direct and indirect is understandable when we recall that while increase in temperature up to its optimum will speed up the physiological processes concerned in growth it will also result in greater demands upon the water supply to replace that lost through increasing transpiration rate. When water is abundant an increase in loss through transpiration may even help growth through aiding in transport of mineral salts but on most sites water supply is more apt to be a limiting factor during the growing season and hence increased temperature resulting in increased transpiration causes a reduction in growth rate.

The fact that the inverse relationship is for different periods in different species of trees is, in part, at least, correlated with differences in times when the larger percentage of growth occurs. Thus, the inverse relation between growth in *Fagus grandifolia* and June temperature (Diller, 4) is correlated with the fact that 70% of the growth in this species occurs in that month (14, 15); while the inverse correlation between growth in Quercus and temperature during June-August is correlated with the fact (15) that 62.5% of the growth occurs during this period.

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