SIZE AND SHOOT GROWTH PATTERNS IN BROADLEAVED TREES

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ABSTRACT

Under identical climatic conditions, shoot growth in large, older broadleaf trees is generally less vigorous than in young trees, as reflected in shorter periods of indeterminate growth, fewer recurrent flushes, a higher fraction of short shoots, etc. Based on model considerations and experimental results, it is suggested that both the internal controls of shoot growth and the interaction of a tree with its environment are altered as a function of tree size and complexity, resulting in observable changes in shoot growth patterns.

INTRODUCTION

For many years, experimental work with trees was largely restricted to the use of seedlings, and application of the results to large trees was often difficult. Recently, significant progress has been made in the analysis of the interaction of large trees with their environment. Based on data obtained with new and improved ecophysiological research methods, water relations and primary productivity of entire trees are now being assessed with the help of mathematical methods developed for ecosystems analysis (Hinckley *et al*. 1975; Shugart *et al*. 1974).

Application of these methods to the analysis of growth and development of trees has progressed slowly (Murphy *et al*. 1972), although there can be little doubt that many characteristic aspects of tree development are the direct consequence of the nature of trees as complex systems of large size and long life. For example, under a variety of different environmental conditions shoot growth patterns of broadleaf trees change with age. These alterations suggest that changing shoot growth patterns might be the consequence of age-dependent modifications in the system structure of trees.

Age-related Changes in Shoot Growth Patterns in Broad-leaved Trees

That juvenile trees differ from adult ones by their inability to flower and by a high capacity to form adventitious roots in cuttings is common knowledge and has received considerable attention among foresters and horticulturists because of the practical significance of these properties (Doorenbos 1965). However, numerous other aspects of tree growth

and development change markedly as a tree ages and increases in size and complexity (Borchert 1976). Since many of these changes can be reversed by severe pruning of a tree and are observed only in aging trees but not shrubs, it is likely that they are the consequence of the age-related increase in size and complexity of a tree, rather than of "age" per se (Borchert 1976).

With respect to primary shoot growth, the following age-related changes have been observed:

Seasonal duration of indeterminate shoot growth: If watered and fertilized well, many seedlings of temperate zone trees will grow throughout the growing season. Shoot growth is terminated in fall, often in response to declining photoperiods, by formation of a resting bud or shoot tip abortion (e.g. Betula, Liriodendron, Populus, Robinia and others). In several species of the genera Acer, Fraxinus, and Prunus, seedlings will grow continuously for long periods, but saplings may grow rapidly for awhile, then undergo a marked decline in shoot growth rate accompanied by a partial or complete transformation of leaves into cataphylls (Späth 1912), resume rapid growth again, and finally form a resting bud. Shoot elongation in adult trees of all these genera usually ceases earlier in the season than shoot growth in seedlings, i.e., at a time when environmental conditions permit continued growth of seedlings (Kozlowski 1971).

Recurrent shoot growth: In Quercus, seedlings may undergo 3 or 4 annual flushes of determinate growth, while a maximum of 2 flushes occurs in older trees, and these second flushes are mostly confined to vigorous terminal shoots (Longman and Coutts 1974). A similar reduction in the number of annual flushes has been observed in pines of recurrent shoot growth (Kozlowski 1971).

Sylleptic shoots: In many trees characterized by indeterminate shoot growth, lateral buds may escape correlative inhibition and develop during the same growth cycle as the shoot that bears them, thus forming so-called "sylleptic shoots" ("sylleptische Triebe", "rameaux anticipés" e.g. in Ulmus, Salix, Liriodendron, Betula and others). Champagnat (1965) demonstrated that this escape from correlative inhibition occurs only when the growth rate of the main shoot exceeds a certain threshold value and is usually confined to vigorous shoots on juvenile trees. Similarly, Brown et al. (1967) reported that in Liriodendron and Liquidambar the phenomenon occurs only in vigorous terminal shoots and not in suppressed ones or in small trees of the forest understory. Thorns are sylleptic lateral shoots undergoing early lignification and death, and thorniness of juvenile shoots in Malus, Citrus, Gleditsia triacanthos L., Maclura pomifera (Raf.) Schn. and others is thus another aspect of the same phenomenon.

Long vs. short shoots: In all trees the fraction of vigorous terminal shoots showing indeterminate or recurrent growth declines

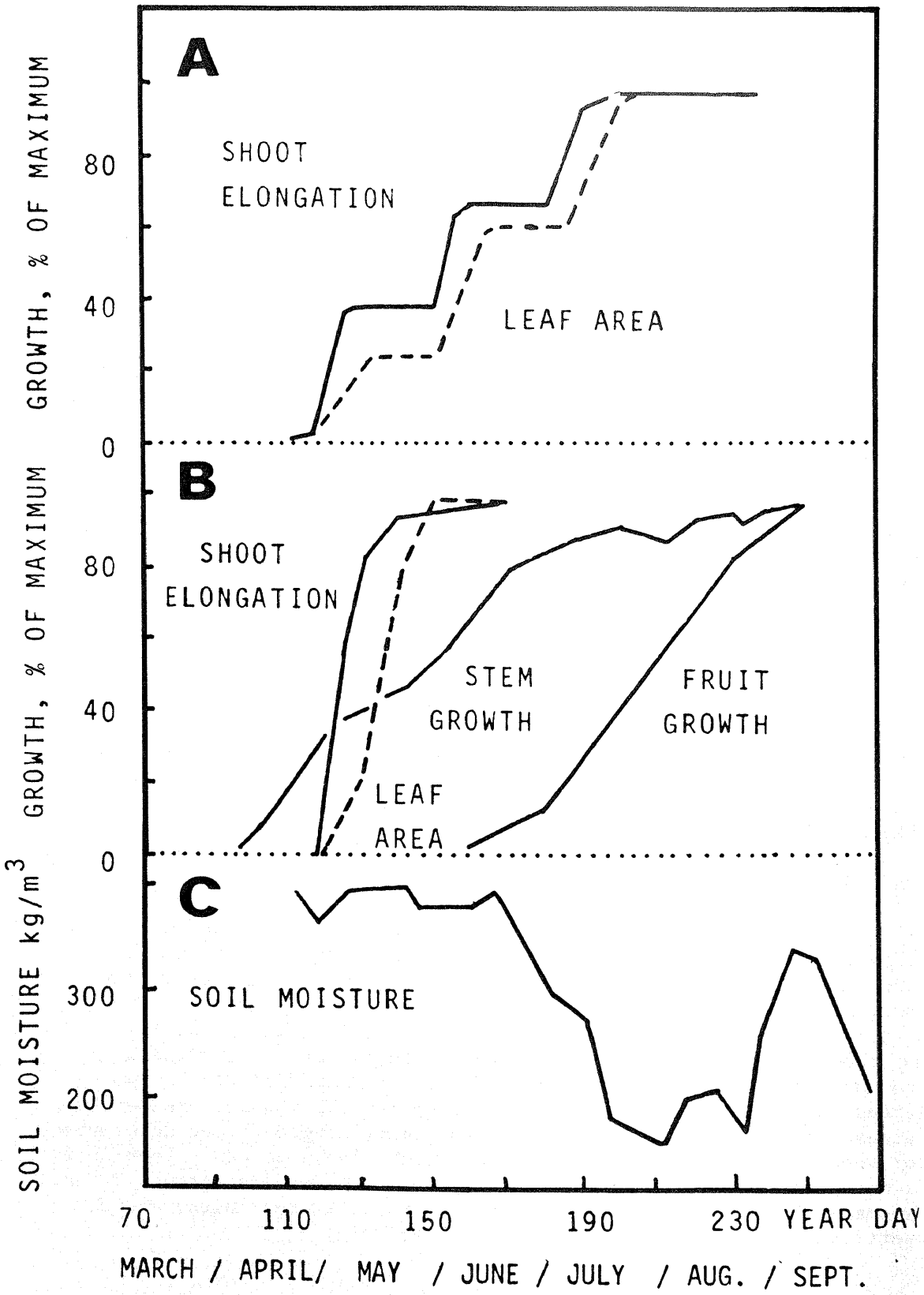
significantly with age, and short shoots may constitute more than 90% of all shoots in older trees (e.g. in Acer: Wilson 1966). Short shoots are usually lateral shoots subject to correlative inhibition by the terminal bud. They display determinate growth, and in each season only the leaves contained in the resting bud are expanded.

In general terms, all these changes reflect an overall decline in the vigor of individual shoots as a function of age. Paradoxically, this decline in growth vigor occurs already in rather young trees, which considered as a whole grow vigorously and are in the midst of their logarithmic increase in biomass.

More specifically, the age-dependent increase in the fraction of short shoots and the loss of the tendency to form sylleptic shoots imply that lateral shoots become increasingly more subject to inhibition by the terminal bud. The reduction in the duration of indeterminate growth and in the number of recurrent flushes would mean that the physiological condition responsible for the arrest of growth in terminal shoots manifests itself earlier in the season in old than in young trees. All these age-dependent changes point to significant shifts in the internal mechanisms that control shoot growth.

Seasonal patterns of primary shoot growth are intimately related to the overall seasonal development of a tree and to its pattern of resource allocation. In young trees, primary shoot growth occurs only in part at the expense of reserve materials and constitutes a sink for currently produced assimilates throughout much of the growing season. Primary shoot growth will thus compete with secondary growth and the formation of reserves (Figure 1A). In large trees, on the other hand, primary shoot growth occurs mostly at the expense of reserve materials and, because of its short duration, will compete with the more extended secondary growth only to a limited degree, and not at all with fruit setting and establishment of reserves (Figure 1A, B).

As a consequence of the changes in shoot growth patterns discussed above, the temporal pattern of seasonal leaf growth changes with age. Since most leaves of older trees are born on shoots of determinate growth, they will expand within a relatively short period after bud break (Figure 1B). This means that in old trees all or the major part of the assimilatory surface is established rather quickly and early in the season and is thus functional for a longer period than in young trees, where leaves may be formed throughout the season. These observations should be considered in the assessment of growth and development of vegetation in models of primary productivity of trees. They indicate a mechanism which might determine the cessation of leaf growth in early summer, the total leaf area of a tree, its leaf area index, and other pertinent variables (Shugart et al. 1974).


A
SHOOT
ELONGATION
LEAF AREA
GROWTH, % OF MAXIMUM
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GROWTH
LEAF
AREA
GROWTH, % OF MAXIMUM
80
40
0
C
SOIL MOISTURE
SOIL MOISTURE kg/m3
300
200
70
110
150
190
230
YEAR DAY
MARCH / APRIL/ MAY / JUNE / JULY / AUG. / SEPT.

Two basic questions are central to the observations reviewed here: (1) Why do shoot growth patterns of broadleaved trees change as trees get older and larger and (2) Why do growth patterns of old trees converge in such a remarkable way when seedlings show much more variety in growth patterns? Or, to put it differently, why is the range of shoot growth patterns well adapted to the seasonal climate of the temperate zone apparently much more limited in old than in young trees?

The phenotype of a plant is usually considered to be the product of the interaction between the set of environmental factors under which a plant is growing and the internal factors controlling growth and development. Obviously, the seasonal changes in environmental conditions encountered by large and small trees are the same. If nevertheless under the same environmental conditions such profound differences in growth patterns are observed, either the internal controls of shoot growth, or the interaction of the tree with its environment, or both, must change as a function of tree size. Any investigation of the questions raised above must therefore consider the size-dependent changes in the internal controls of shoot growth, as well as the consequences of these changes for the tree's interaction with its environment.

Interaction Between Internal and Environmental Control of Shoot Growth

In an earlier study, the possible interaction between internal and environmental factors in the control of rhythmic shoot growth under constant environmental conditions was simulated in a mathematical model (Borchert 1973). In this model of rhythmic growth, the tree was considered as a system consisting of two major subsystems, root and shoot, the latter being in turn composed of stems and leaves. In view of the interdependence of these subsystems, it was assumed that continuous growth of the entire tree is possible only if all its subsystems are in a functional equilibrium. If the latter is disturbed, growth of some subsystem must be temporarily inhibited until a functional balance is restored. For instance, if the shoot system of a tree grows faster than its root system for any length of time, transpiration will increase faster than the capacity to absorb water, and a water deficit will arise in the shoot. This water deficit might slow down and stop shoot growth until a functional equilibrium between root and shoot (a favorable root/shoot ratio) has been restored. Such a feedback system in which one subsystem is rate-limiting for another one can cause endogenous growth rhythms under constant environmental conditions and has been considered the basis for rhythmic growth (Borchert 1973). Although the inhibition of shoot growth by temporary internal water deficits, as assumed in the model, has not been proven experimentally, strong indirect support for

Figure 1. A. Seasonal time course of shoot elongation and leaf growth in a 3-year old, well-watered, potted sapling of pin oak growing in a greenhouse (from Borchert 1975). B. Seasonal time course of shoot elongation, leaf growth, stem growth in girth, and growth of acorns in a 19 m tall, mature *Quercus alba* L. as observed near Columbia, Missouri, in summer 1974. C. Soil moisture for the same site and period (Data in B and C were kindly supplied by Dr. T. M. Hinckley, School of Forestry, Fisheries and Wildlife, University of Missouri, Columbia).

this idea has been presented with respect to rhythmic growth in oak (Borchert 1975). The period length of the rhythms will depend on the quantitative genetic characters determining the growth rates of the various subsystems and on the particular set of environmental conditions under which a tree is growing. Logically, if any of these parameters is changed, the growth pattern must change as well. For example, according to the model, a reduction in the root/shoot ratio as well as a decrease in relative humidity should shift the rhythmic growth pattern towards shorter flushes of shoot growth separated by longer rest periods.

Shoot growth patterns predicted by the model agree well with those observed in oak (Borchert 1975) and in several tropical trees (Borchert 1973).

Effect of Increasing Complexity

As discussed so far, the model applies to a small, single-shoot tree growing under constant and optimum environmental conditions. How, then, will an increase in size and complexity affect the growth patterns predicted by the model? Let us assume that we have two sets of identical trees. At a certain time, in one set several axillary buds are released from inhibition by the apical bud and form lateral shoots. There will be now several growing shoots as compared to only one in the control group. Consequently, the total leaf area and thus transpiration will increase much faster in the multiple-shoot trees than in the control group. Hence, assuming that root growth rate remains the same, the functional balance between root and shoot system will be lost faster, and it will take longer to restore it after shoot growth has been arrested. In trees of rhythmic growth, growth flushes would thus become shorter and less frequent with increasing complexity. In trees of continuous growth, growth flushes of limited duration would result even under constant environmental conditions. Both predictions agree with the age-related changes in shoot growth patterns described above and have been confirmed in comparisons between shoot growth in single-shoot and multiple-shoot *Quercus palustris* Muenchh. saplings (Table 1A, B; Borchert 1975). Inversely, when the rate of growth in leaf area was experimentally reduced, the duration of shoot growth and the number of flushes increased correspondingly (Table 1C).

These data also illustrate the relations between the structure of the shoot system and hormonal control of shoot growth. There can be little doubt that on the molecular level the arrest of shoot growth is caused by a change from a stimulatory to an inhibitory combination of growth regulators. However, this change in the physiological state of every growing meristem is itself the consequence of the dynamics of the entire growing system. In multiple-shoot trees, shoot growth inhibition occurs soon after the initiation of shoot growth and persists for the rest of the growing season. In single-shoot trees it is induced at a later time and, before becoming permanent, is reversed permitting a second flush of growth. Also, the same terminal bud may produce a shoot growing for 10 or 30 days depending only on the number of competing shoots.

Table 1. Means of selected variables characterizing seasonal shoot growth in potted saplings of *Quercus palustris*. Experimental treatments: A - One shoot per tree allowed to grow. B - All shoots allowed to grow. C - Each leaf reduced to about 1/5 its normal length. In treatment B, total shoot growth and maximum shoot growth rate data obtained from one vigorous shoot per plant.

Variable	Experimental group		
	A	B	C
Number of flushes	1.9	1.0	2.9
Days of active shoot growth	25.4	8.0	48.2
Total leaf area, dm^2	10.5	12.9	0.9
Number of leaves	26.7	64.4	46.0
(% of leaves in first flush)	(66)	(97)	(60)
Area/leaf, cm^2	39.4	20.0	2.0
Total shoot growth, cm	33.7	16.3	30.2
Maximum shoot growth rate, cm/day	2.7	1.9	1.7
Number of shoots per tree	1	7.3	1
Number of trees per group	7	7	9

Limitations to Root Growth

According to the model, long term rhythmic growth of constant period length or continuous growth is possible only if environmental conditions remain constant. Whereas a growing shoot system is not subject to any significant limitations imposed by its environment (the atmosphere), the expanding root system will necessarily be faced with progressively deteriorating growing conditions which are the direct consequence of the physical nature of the soil system. With increasing depth, soil structure usually becomes less favorable for root growth, and inefficient gas exchange may restrict root metabolism. Consequently, in most trees the great majority of absorbing roots are found in the upper 60 to at most 100 cm of the soil. Lateral expansion of the root system will be often limited by competing root systems of neighboring trees. Thus, sooner or later in the life of a tree, the root system will approach its physical limits, root growth must slow down, and in the absence of comparable restrictions to shoot growth, the root/shoot ratio will decline. Such a reduction in the ratio between belowground and aboveground biomass due to increasing age has indeed been observed in a mixed deciduous forest (Harris *et al.* 1973). Even under optimum environmental conditions, as they might exist in the humid tropics, the limitations imposed on root growth should cause at least a temporary cessation of shoot growth, and truly continuous shoot growth of large trees should never occur. Indeed, many authors describing the growth of tropical trees concur in stating that the majority of these trees show intermittent growth and even trees

without clear morphological differences between consecutive growth flushes pass through prolonged periods of rest (Koriba 1958).

The effect of restricted root growth on shoot growth patterns can be assessed experimentally in container-grown plants. The size of the container will determine the maximum extension and functional capacity of the root system and thus, indirectly, the maximum size of the shoot. Seasonal shoot growth of potted, well-watered trees should end whenever they have attained maximum size (leaf area). In agreement with these considerations, mean total leaf area per tree among different groups of pin oak saplings was found to be in the same range, whereas other components of the shoot growth pattern varied widely. Mean leaf area was 12.9 dm^2 in multi-shoot trees (Table 1B), 10.5 dm^2 in single-shoot trees having passed through 2 consecutive flushes (Table 1A), and 9.5 cm^2 in less vigorous single-shoot trees having completed 3 growth flushes (Borchert 1975). Finally, if multi-shoot trees were grown in or transplanted to larger containers, many second flushes were observed as compared to only a few in trees growing in smaller containers.

Determination of Shoot Growth Patterns in Seasonal Climates

The observed seasonal shoot growth patterns in young and old trees might result from the following interactions between endogenous and environmental controls. In deciduous trees of the temperate zone, functional relationships between root and shoot systems change dramatically in the course of the year. Leaves are shed in the fall, but functional roots may persist throughout the winter. In spring, root growth usually starts before bud-break, thereby establishing a higher root/shoot ratio favorable for the initiation of shoot growth. During early shoot growth in spring, leaves are expanding rapidly, the root/shoot ratio declines correspondingly and causes eventually a slowdown or termination of shoot growth. The faster shoot growth and leaf expansion occur, the earlier shoot growth will come to an end (see approx. day 130 in Figure 1A, B).

If recurrent flushing or continued indeterminate growth is to occur a favorable root/shoot ratio must be maintained throughout late spring and early summer. At this time soil moisture is usually high, but temperature rises and hence transpiration and the need for water absorption by the root system increase. For instance, within a period of 8 weeks from early May to July, the leaf area of a young citrus tree increased by 68%, the rate of transpiration (water loss per unit leaf area) by 45%, and the total water loss of the entire tree by 142% (Chapman and Parker 1942). Small trees are apparently capable of restoring their functional balance under these circumstances and resume or continue shoot growth. Large trees seem to be unable to fully regain this functional equilibrium and continued shoot growth occurs only in vigorous branches or not at all (Figure 1, days 150-180). Two abnormal growth patterns are in agreement with this interpretation: (1) if large trees are defoliated early in the season by drought or insect attack, they may produce a second flush of shoot growth later, provided that the soil moisture is adequate;

(2) well watered multi-shoot oak saplings growing in small pots will flush only once (Table 1B), but will reflush if transplanted to larger containers.

During the summer, soil water losses due to evapotranspiration are, in most areas, not completely replaced by precipitation, and the soil water reservoir is gradually depleted. Consequently, trees are subject to increasingly greater water stress, which will not only prevent recurrent flushing and arrest indeterminate growth, but will eventually inhibit secondary shoot growth as well (Figure 1B, C). If small trees can draw on a relatively larger soil water reservoir, they should suffer from drought later in the season than large ones.

In conclusion, it appears that early in the season, when favorable environmental conditions prevail, differences in shoot growth patterns between small and large trees result mainly from variations in internal controls and correlations. As environmental stress increases during the growing season, modifications in the interaction with and dependence on environmental conditions become more and more responsible for the observed differences in growth patterns. Apparently there is only a limited range of solutions to the functional problems faced by a mature broadleaf tree growing in a strongly seasonal climate which imposes a prolonged annual rest period and causes an annual turnover of the entire photosynthetic surface. This limited range of solutions is reflected in the similarity of annual patterns of primary shoot growth observed among mature broadleaf trees in the temperate zone and other areas with seasonal climates.

To put the proposed model on a firm experimental base, future studies of shoot growth patterns should be designed to yield data in the following areas: (1) quantitative descriptions of the structure of the tree under study, permitting an assessment of tree size and complexity; (2) precise measurements of seasonal shoot growth patterns and reasonably good estimates of root growth; (3) precise monitoring of environmental variables; (4) ecophysiological measurements which assess daily and seasonal changes in the water status of the tree; (5) physiological studies concerning the mechanism which causes the arrest of shoot growth under favorable environmental conditions as observed during rhythmic shoot growth or summer dormancy.

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