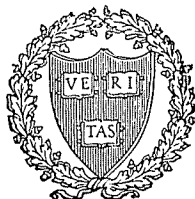


1966

HARVARD FOREST PAPER No. 14

DEVELOPMENT OF THE SHOOT SYSTEM OF ACER RUBRUM L

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ABSTRACT

The shoot system of red maple (*Acer rubrum* L.) is made up of a framework of long-shoots, each bearing leaves, flower buds, and short-shoots. The short-shoots, in turn, bear leaves and flower buds, but no lateral shoots. Quantitative data on lateral shoot production by each order of long-shoots were used to estimate the total number of shoots in a shoot system as it develops over a 70-year period. Eighty-five to 95% of all branches are short-shoots, mostly fourth and fifth order. Most long-shoots are third or fourth order. The estimates for shoot number and the values for leaf number, leaf area, and flower bud number per shoot were multiplied to estimate changes in developing shoot systems. The roles of apical dominance and shoot vigor in determining the course of lateral bud development are discussed briefly.

INTRODUCTION

Red maple (*Acer rubrum* L.) is a common tree on all parts of the Harvard Forest, occurring as single stems scattered among other species, as multiple stems of stump-sprout origin, and as dense thickets in wet swales. Growth of red maple on the Harvard Forest was first investigated by Carter (1913). More recent papers have treated the root system (Lyford and Wilson, 1964; Wilson, 1964). This paper describes the pattern of branching, leaf, and flower bud production during development of the shoot system.

The shoot system of a large red maple tree is complex because it consists of so many individual shoots. This complexity develops from the relatively simple and orderly annual production of long-shoots bearing numerous short-shoots. The purpose of this paper is to describe quantitatively the pattern of organ proliferation as the shoot system develops, and to investigate the interactions among individual shoots that influence this pattern.

Most quantitative studies take a statistical approach for describing the shoot system. Estimates of leaf number, etc., are usually based on correlations between tree or branch dimensions and organ number or size, with no attempt to describe the process of crown development. At the level of the interaction among individual shoots, Brown, McAlpine and Kormanik (1966) have recently concluded that little is known about the basic mechanisms of apical dominance and bud inhibition in woody plants, because the sequence of lateral bud formation and periods of dormancy present problems uncommon to herbaceous plants.

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MATERIALS AND METHODS

Special terms used in this paper are defined below, and illustrated diagrammatically in Figure 1:

Long-shoots: Branches that elongate more than 2 cm per year and normally bear lateral branches if more than one year old.

Short-shoots: Branches that elongate less than 2 cm per year and do not bear lateral branches. N.B. The growth rate and branching characteristics of a shoot may change if the local environment of the shoot changes; thus, short-shoots occasionally change to long-shoots and vice versa.

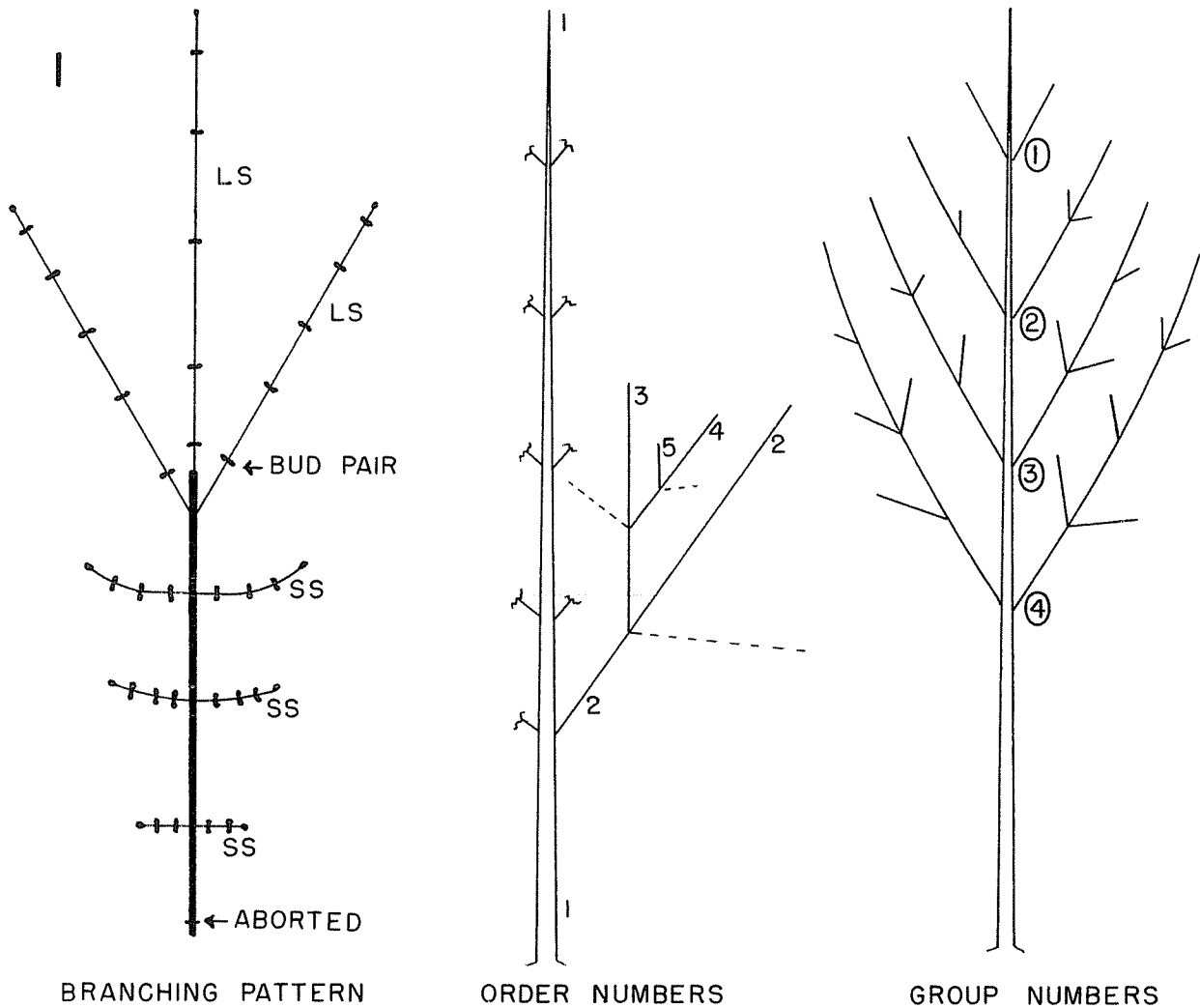


Figure 1. Diagram showing the terminology of branching. Branching pattern: a two-year-old long-shoot and its laterals. The one-year-old portions are drawn in thin lines with the position of the lateral buds shown. On the two-year-old portion of the parent long-shoot (thick line) the upper pair of buds has developed into lateral long-shoots, the three middle pairs into lateral short-shoots, and the lowest pair has aborted. Order number: Each lateral branch has an order number one greater than its parent branch. Group number: Compare this diagram showing groups of second order long-shoots with the photographs in Figs. 2, 3.

Order number: All shoots have been assigned an order number based on their relation to the main stem. The main stem is called the first order. Shoots lateral to it are second order, those lateral to the second order are third order, and so forth. If a terminal bud is injured and a lateral branch changes orientation in replacing the injured shoot, the replacement shoot then acquires the order number of the injured, parent shoot.

Group number: A group of second order long-shoots is analogous to a whorl of branches in a pine tree. The groups are numbered from the top of the tree down. Red maple in the winter characteristically bears 5 or more pairs of lateral buds on the one-year-old terminal portion of the main stem (Fig. 1). When these buds elongate in the spring the uppermost pairs develop into long-shoots, the middle pairs into short-shoots, and the lowest pair may abort. Thus, second order long-shoots develop in groups at the top of each annual increment (Fig. 1-3). Second order short-shoots are lateral to the main stem between successive groups of long-shoots. They are given the number of the group just above them. All third and higher order shoots are given the group number of the second order long-shoot to which they are related.

Node, leaf-pair and bud number: For each annual increment, nodes and lateral organs (leaves or buds) arising from them are numbered starting at the base of the increment at the terminal bud scale scars. Internodes are given the number of the node at their upper end.

Early and late leaves: Following the terminology of Critchfield (1960), early leaves are those present and partially developed in the overwintering buds (usually 3 pairs in red maple at the Harvard Forest); long-shoots produce late-leaves after the buds open in the spring.

Net increment (per shoot per group): The groups of second order branches can be interpreted as a time sequence of branch development, with the youngest group at the top of the tree and each successive lower group at least a year older. Each long-shoot adds new lateral shoots at the tip and may lose old lateral shoots at the base. Thus, the difference in total number of lateral shoots present on a parent shoot from one group to the next lower group is the net increment. The net increment can be estimated by comparing the number of lateral shoots per parent shoot from group to group.

The red maple trees studied were of varying ages growing on well-drained Gloucester soils in the Prospect Hill and Tom Swamp tracts of the Harvard Forest, Petersham, Massachusetts. Thirty-eight trees were felled for analysis of various aspects of branching and leaf production. These trees were all single stems at the time of cutting but they may have originated as stump-sprouts. Ten trees were cut for analysis of flower production. Two trees were observed from a 10 m tower for measurement of leaf growth from 20 buds (Figs. 3, 4). About 75 stumps bearing sprouts 1-6 years old were observed and measured.

For branch counting, one second order long-shoot was taken from each group on the felled tree. All the branches on these second order long-shoots were counted and classified by shoot type, order number and group number. These data were then expressed as the ratio

$$\frac{\text{Total number of lateral shoots}}{\text{Total number of parent shoots}}$$

The ratios were averaged for each group number. Few trees had more than 20 groups, therefore at high group numbers ratios from successive groups were lumped so that at



Figures 2-4. Figure 2, a red maple shoot system showing branching in the upper 12 groups of a tree with 15 groups. Figure 3, two red maple trees in flower beside a 10 m tower (May 4, 1963). Figure 4, as in Figure 3, leaves well developed (June 13, 1963).

least 3 sample branches were included in the average. The average ratios, multiplied together, gave an estimate of the number of shoots in each group (e.g., number of third order shoots per group = $\frac{\text{third order}}{\text{second order}} \times \text{number of second order per group}$). The estimates of the total for each group were summed cumulatively from group 1 on down the main stem to give estimates of the number of shoots in a tree with any given number of groups. Thus, tree size is determined by the number of groups alone rather than the traditional height and diameter dimensions.

It is important to realize that a given increase in the ratio of lateral to parent shoots from one group to the next may not be equal to the net increment per long-shoot. For second order shoots per first order and for third order shoots per second order they are the same, but for fourth order per third order shoots and all higher order shoots they are not. In these higher order shoots an increase in the ratio from one group to the next is less than the net increment. This relationship is illustrated in the algebraic model of these types of data in Table 1.

Estimates of leaf number, leaf area and flower bud number were made for the different orders and types of shoots. The estimates for leaves and flowers of whole trees were then calculated by multiplying the number or area per shoot by the number of shoots.

Group	Total number of shoots per 2nd order long-shoot			Ratio of lateral to parent shoots		
	3rd order	4th order	5th order	3rd/2nd order	4th/3rd order	5th/4th order
1						
2	a			a		
3	2a	ab		2a	b/2	
4	3a	3ab	abc	3a	b	c/3
5	4a	6ab	4abc	4a	3b/2	2c/3
6	5a	10ab	10abc	5a	2b	c
7	6a	15ab	20abc	6a	5b/2	4c/3
8	7a	21ab	35abc	7a	3b	5c/3
9	8a	28ab	56abc	8a	7b/2	2c
10	9a	36ab	84abc	9a	4b	7c/3

Table 1. Sample of calculation form for total shoots per group, assuming constant net increments per long-shoot (a = third/second, b = fourth/third, c = fifth/fourth). See text for discussion of net increments. Total number of shoots of order X + 1 at group Y = total number at group Y - 1 + (total number of order X at group Y - 1)(net increment per long-shoot). Net increment/group = (total of order X + 1 at group Y) ÷ (total of order X at group Y).

Because leaf areas are so time consuming to measure, the correlation between leaf blade area (one side only) and leaf length was established from 220 leaves and then all leaf areas were calculated from leaf lengths. Despite the great variation in mature leaf size, there was a high correlation between log of leaf area and log of leaf length ($\log \text{ area} = 0.0898 + 1.81 \log \text{ length}$, $r = 0.997$). Comparable allometric relationships between log leaf length and log area have been found for other species (e.g., Turrell, 1961).

RESULTS

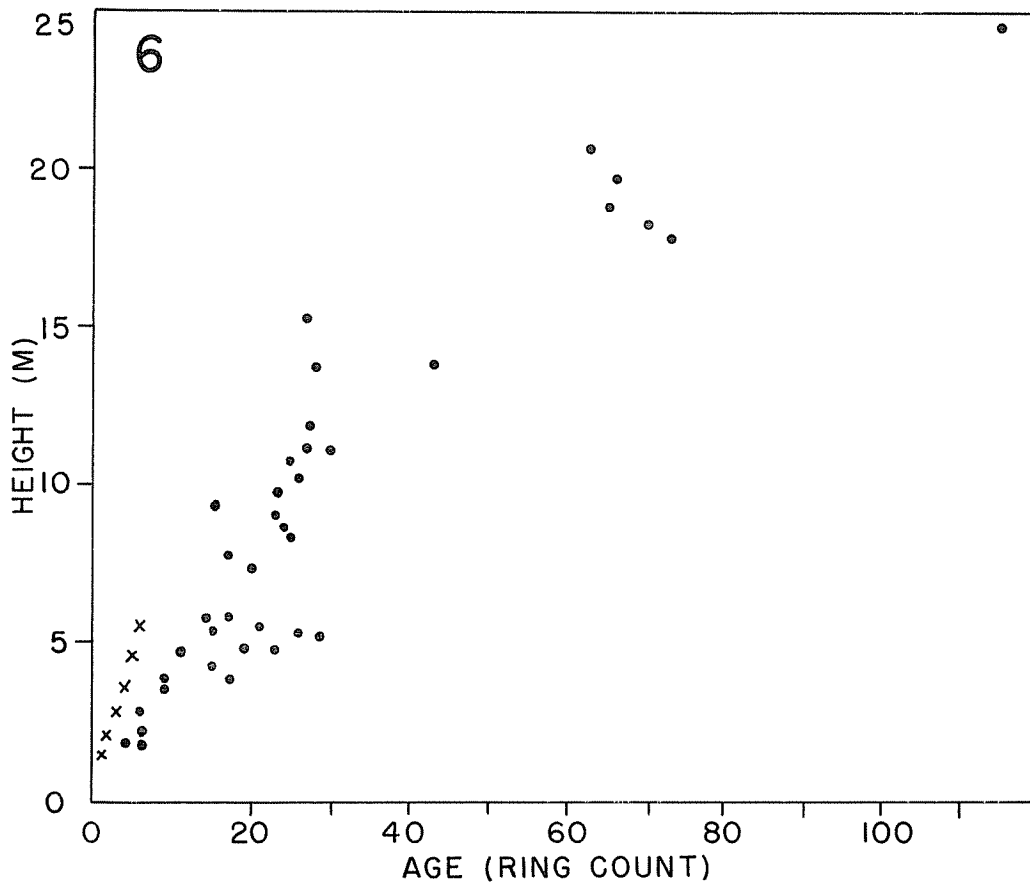
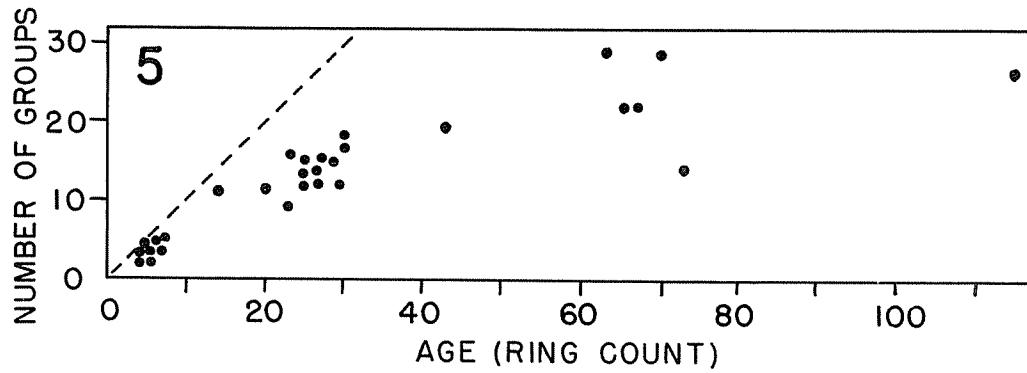
BRANCHING

Branch groups are usually produced annually at the top of the main stem. However, due both to loss of groups from death of the older long-shoots and to occasional years when no long-shoots develop, the number of groups is always less than the age of the tree (Fig. 5). As the tree grows older the loss of branch groups toward the base of the crown equals, or exceeds, the addition of groups at the top of the crown. Thus, the maximum number of groups of live branches observed in this study was 29. Growth rings in the branches were too ill-defined to determine the age of the second order branches directly, but when estimated indirectly (by dividing the distance of the base of the branch from the top of the tree by the height increment per year of that tree) the second order branches of the 29th group were about 45 years old. The upper groups were spaced about one year apart, by group 20 they were spaced an average of 1.5 years apart, and by the oldest group 3-4 years apart.

Height growth of the sample trees was about 30 cm/yr for 40 years, whereas the stump sprouts measured (the fastest growing stem from each stump) had grown at about 85 cm/yr for 6 years (Fig. 6). On the Prospect Hill tract, trees about 20 m high seemed to have reached their maximum height. These trees had partially dead tops where the first order shoot had died back for a distance of a meter or so, and had been replaced by a second order long-shoot. This process could have occurred several times and, although the replacement shoots still showed growth increments of about 30 cm/yr, there was no net height increment. The tallest tree, cut on the Tom Swamp tract, had a single first order shoot that had grown at only 10 cm/yr for the previous 15 years and had produced no second order long-shoots during these years (thus, the first group of second order branches in this tree was 15 years old). Second order long-shoots in the first group grew almost as much as the first order, but the annual increment decreased in lower whorls where the branches were older. The average of 50 annual length increments from several old branches was, from second to sixth order respectively; 8.8, 4.5, 3.6, 3.4, and 2.7 cm. These relative amounts of growth were also characteristic of younger branches.

The number of live second order long-shoots per group varied from 1 to 6 with an over-all average of 2 (Fig. 7). In general, the number of long-shoots per group was less in groups lower in the crown. The decrease was due both to death of individual long-shoots and to conversion of long-shoots to short-shoots. In groups with more than 4 second order long-shoots there is competition between the branches so that the lower long-shoots in a group grow more slowly and are converted to short-shoots after a few years.

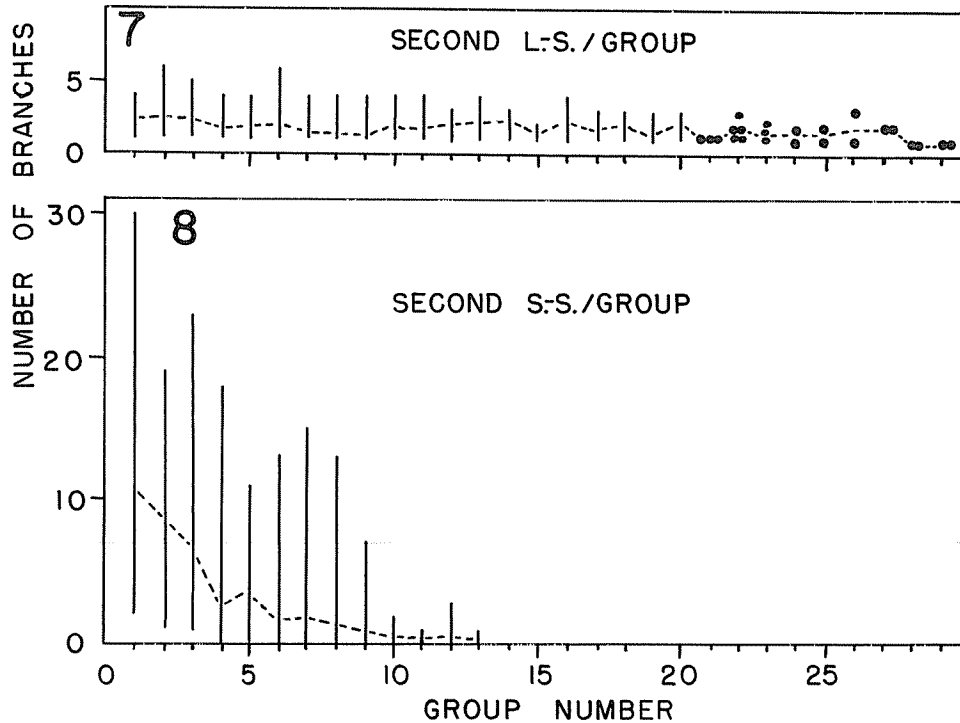
Second order short-shoots are relatively short-lived. None were found below the fourteenth group of long-shoots. As a result, the main stem toward the bottom of the crown bears only long-shoots, and the maximum number of second order short-shoots (41) is reached in trees having 13 groups of branches (Fig. 8).



Figures 5, 6. Figure 5, relation between sample tree age and the number of groups of second order long-shoots on the main stem. The dotted line shows values where age = number of groups. Figure 6, relation between tree age and height for the trees sampled (dots) and for stump sprouts (x's).

The ratios of related orders in each group show that in general there are far more short-shoots than long-shoots, and there is a dramatic decrease in the number of long-shoots higher than third order (note differences of scale in Fig. 9). The ratios are highly variable within any one group, and the variability is greater in the higher group numbers, i.e., those lower in the crown. The variability reflects differences in size of second order branches because of competition among branches, competition that is most intense in the lower groups of the crown. Despite the variability, the general trend is for the ratios to increase for the first 10-15 groups, then the ratios may continue to increase, but in most orders the ratios stay about the same or even decrease, from groups 15 to 29.

During the period when the ratios are increasing, the net increment per long-shoot per group may be estimated (Table 2). The net increment of second order shoots during



Figures 7, 8. Numbers of second order long-shoots and short-shoots per group. Each dot is the value for one sample branch, vertical bars show the range where there were more than 10 values, dotted lines connect the averages for each group.

<u>Order number</u>	<u>Long-shoots</u>	<u>Short-shoots</u>
3rd/2nd	1.5	4
4th/3rd	0.1	4
5th/4th	0.03	4

Table 2. Net increment per long-shoot per group, estimated from Fig. 9, for whorls 1-15. There were not enough data for sixth order long-shoots and sixth and seventh order short-shoots to make an estimate.

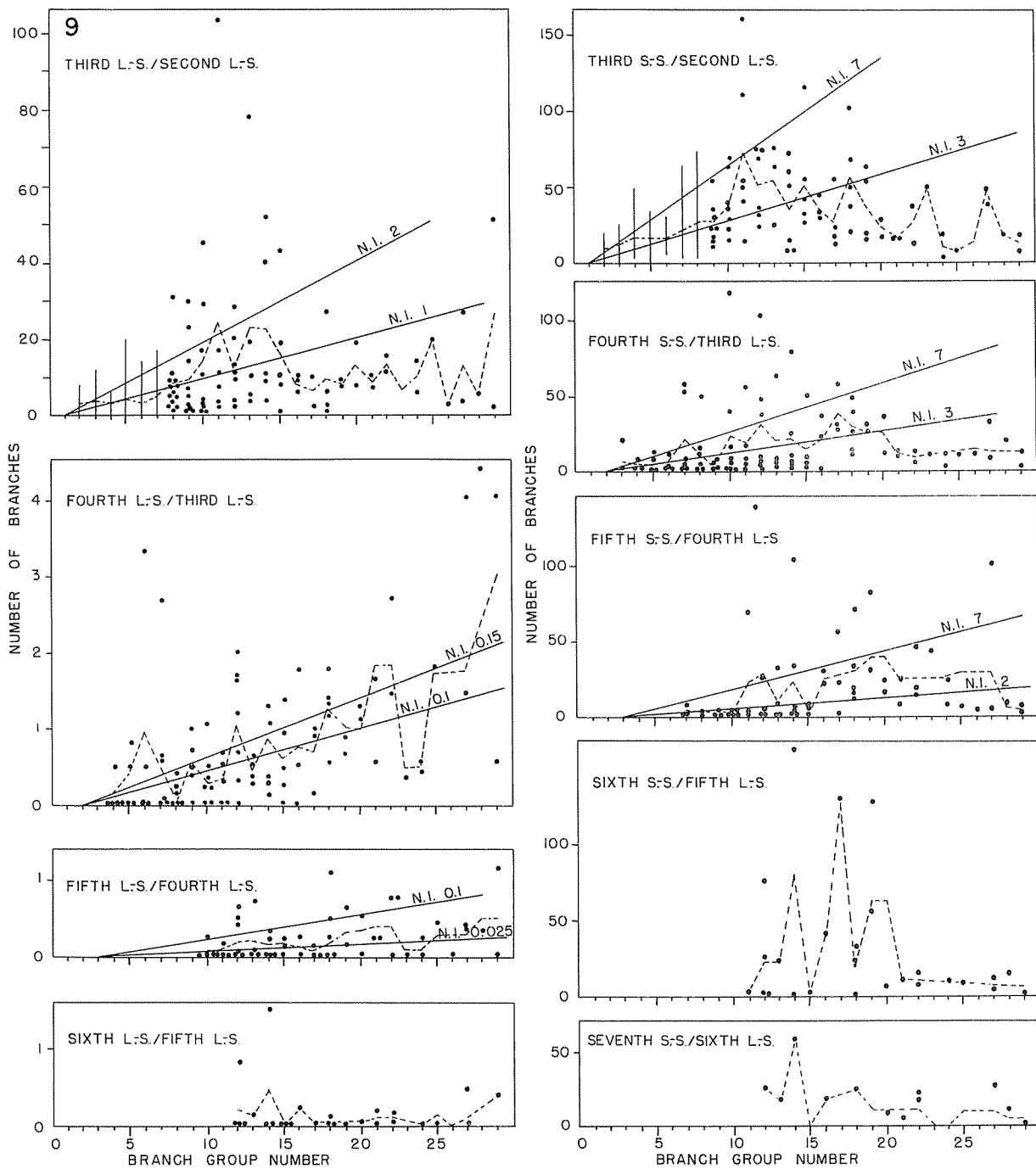


Figure 9. Ratios for the number of lateral shoots to the number of parent long-shoots for each group number, L:-S. = long-shoot, S:-S. , short-shoot, N. I. = net increment. Note differences in vertical scale. Each dot is the value for one sample branch, vertical bars show the range where there were more than 10 values, dotted lines connect the averages for each group. The lines showing the ratios that would result from given net increments were derived from a table like table 1. The 2 net increment lines show the general range of probable net increments and indicate the extent to which a change in net increment changes the slope at different order numbers.

the same period was approximately 1.8 long-shoots and 4 short-shoots. The net increment of third order shoots was about the same, but third and higher order long-shoots produce fewer lateral shoots, most of which are short-shoots. In groups 15 to 29, the net increment may stay at zero, or even decrease. In these cases either the rate of lateral production decreases, the rate of loss of old laterals increases, or both. The two possibilities cannot be separated in these data.

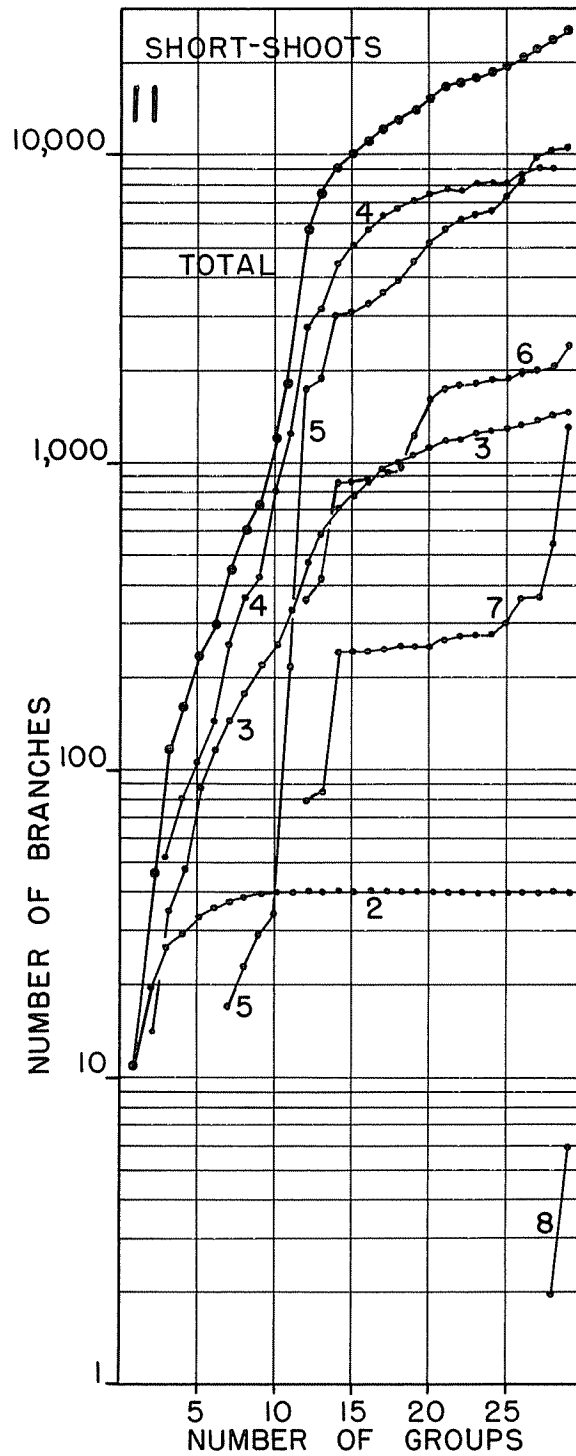
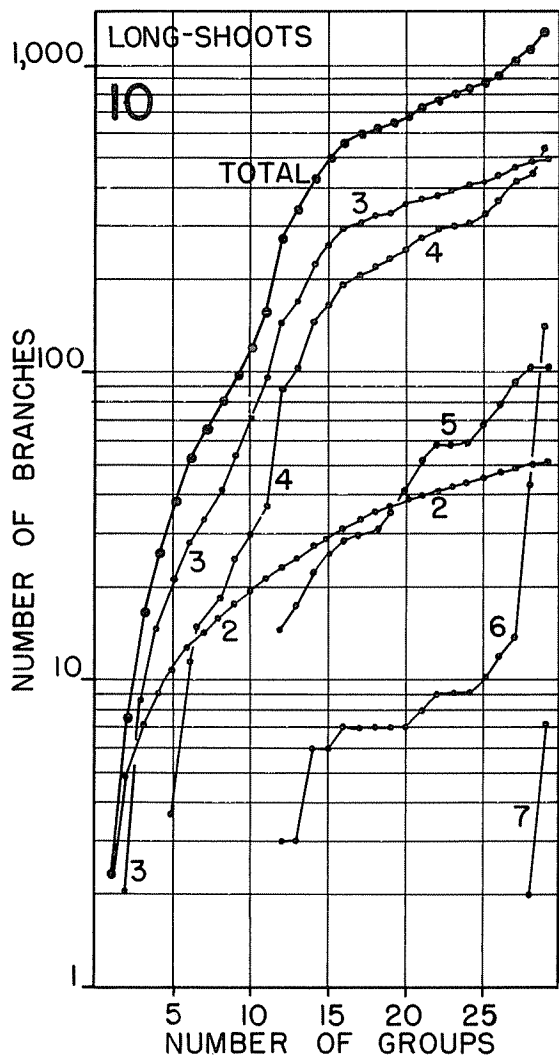
The data on ratios of shoot orders were used to estimate the number of shoots on whole trees (Figs. 10, 11). These estimates show several points about shoot systems. (1) There are far more short-shoots than long-shoots on most trees; in fact, 85-95% of the shoots on a tree are short-shoots. (2) Although the relative numerical importance of the different orders changes with the number of groups present, in most trees third and fourth order long-shoots and fourth and fifth order short-shoots constitute the bulk of the shoots in the shoot system. In trees with 29 groups, 75% of all the branches in the crown are fourth and fifth order short-shoots. (3) Because all the orders are related, the drop in number of third order long-shoots above group 15 affects the total number of all higher orders. The drop is reinforced by the decrease in production of other orders. Thus, the rate of increase of the total number of shoots slows markedly at about group 15.

There is no provision in these estimates for forking of the main stem, although forked branches have been included in the averaged data for higher orders. Forking of the main stem was frequently observed and may be important in crown development. A forked stem would essentially double the number of organs above the point of forking if each of the two stems grew as much as a single stem. If, however, the two stems compete strongly, then together they would grow less, perhaps only as much as a single stem.

One experiment was made to see if the pattern of lateral shoot production by the main stem (see diagram, Fig. 1) was related to inherent differences among buds due to position on the annual increment. Six different bud removal treatments, each replicated 6 times, were made in the winter on 8-10 year old field-grown trees. The terminal bud and/or upper lateral buds were removed. The following summer, after the remaining buds had grown out, the measurement of lateral shoot lengths showed that there were no inherent differences in bud growth due to position, rather that all the lateral buds were potentially long-shoots. It seemed that the pattern of shoot development resulted from a type of bud inhibition where the terminal bud and uppermost laterals developed into long-shoots; these long-shoots then inhibited the development of the lower lateral buds so that they only developed into short-shoots (Table 3).

LEAVES AND INTERNODES

Bud break in Petersham occurs during the first week in May. The three pairs of early leaves grow rapidly and simultaneously for about a month (Fig. 12). Some suppressed short-shoots have only 1 or 2 pairs of early leaves, occasional long-shoots have 4 pairs. The curves for early leaf development are qualitatively the same for both long-shoots and short-shoots. Most long-shoots produce late leaves with differently shaped lobes than the early leaves (Fig. 13). The first late leaves, pair 4, are measurable 10 to 14 days after bud break, and successive pairs of late leaves become measurable at intervals of several days to a week. Total growth of the last late leaves is not finished until the first week in July (Fig. 12).



Figures 10, 11. Estimated values for the total number of long-shoots and short-shoots of different orders for trees with from 1 to 29 groups of second order long-shoots.

Table 3. Growth of lateral second order buds after experimental removal of inhibiting buds on the same shoot. Each value is the average from 12 different buds.

Terminal bud	Bud pair number (from terminal)												
	1	2	3	4	5	6	7	8	9	10	11	12	13
18	14	10	7	2	2	2	1	1	1	0	0		
15	- ^a	-	17	7	5	2	1	1	0				
21	-	-	-	-	13	10	2	2	1	1	1		
-	-	-	-	19	20	8	8	1	1	1	1	1	
-	-	-	-	-	18	20	13	3	2	2			
-	-	-	-	-	-	-	-	-	-	-	20	20	9

^a A dash indicates where a bud was removed the preceding winter.

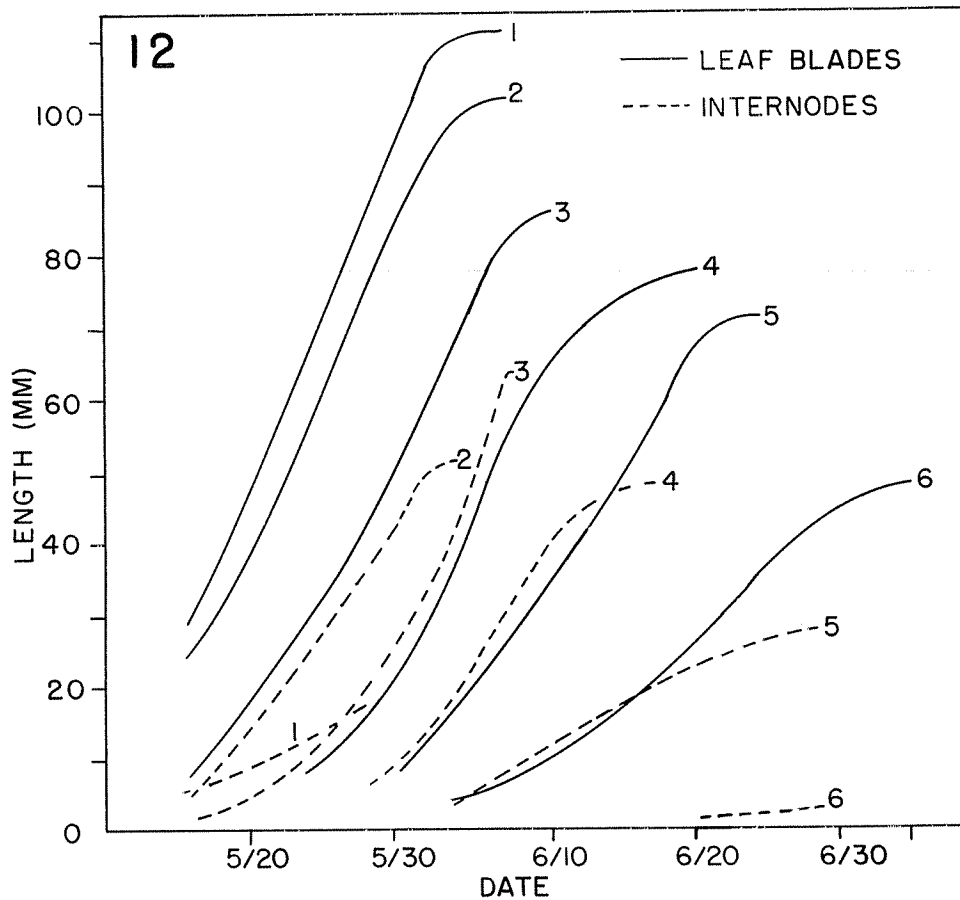


Figure 12. Growth in length of the leaf blades and internodes on a typical long-shoot in Spring, 1963. Numbers on the curves are the leaf pair or internode number.

Internode elongation starts slightly after the initiation of leaf growth (Fig. 12), and bursting of the buds results from elongation of the early leaves. The relation of leaf growth to internode growth is comparable to that described by Critchfield (1960) for *Populus*. Marked internode elongation occurs only if late leaves are produced, although there is some elongation in all shoots, even those with only early leaves. Thus, shoots which produce only early leaves are short-shoots or partially suppressed long-shoots, and those that produce both late and early leaves are typical long-shoots. In long-shoots the third or fourth internode is usually the longest, in short-shoots the second internode is the longest.

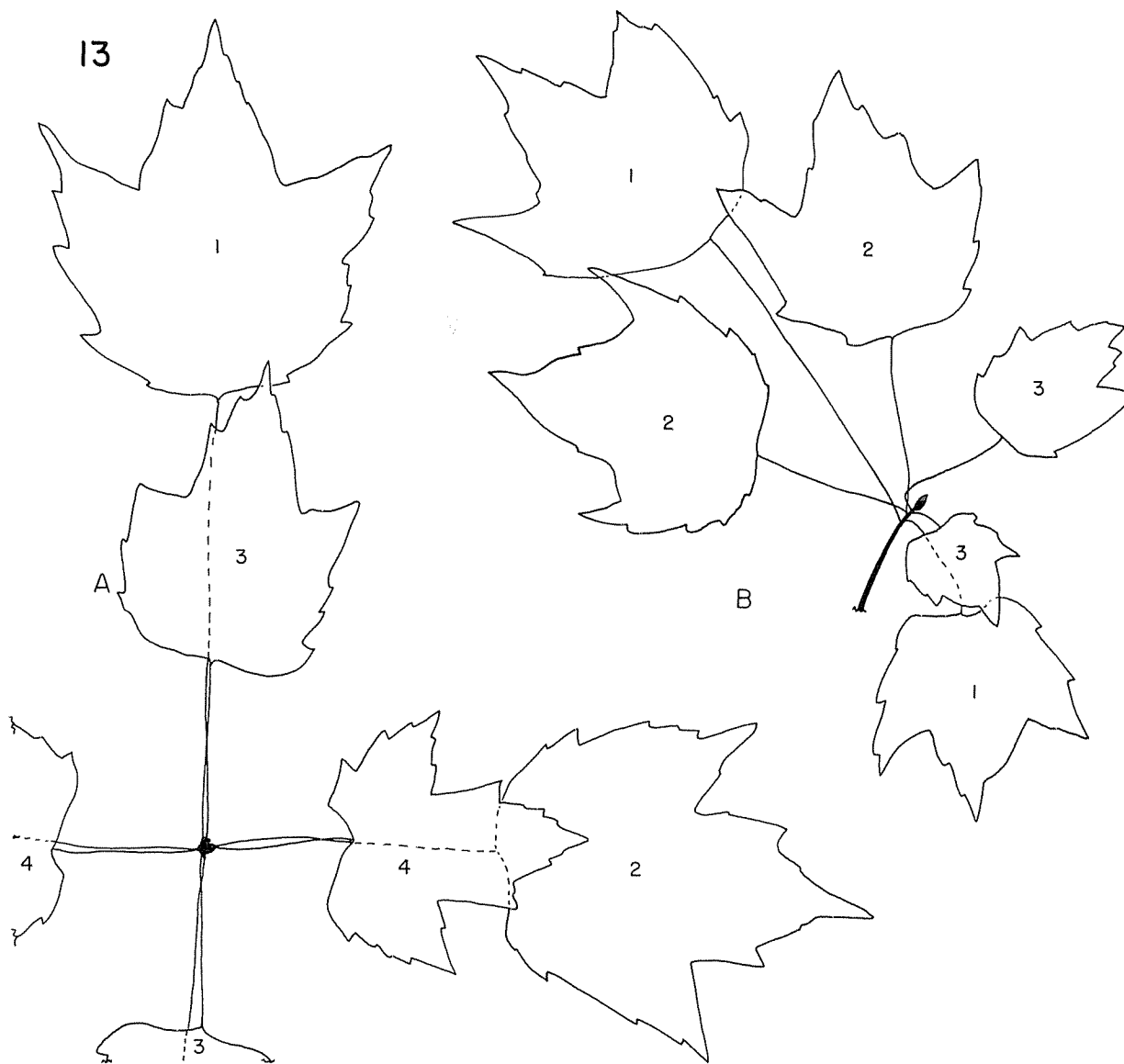


Figure 13. Aerial views of the leaf arrangement on a vertical long-shoot (A) and a horizontal short-shoot (B). Each leaf is numbered according to the node of origin. The petioles of the horizontal shoot (B) have twisted so that the leaf blades are all in a horizontal plane. Pairs 1 and 3 were oriented vertically so that the leaves on the lower right originally grew up and the ones in the upper left grew down.

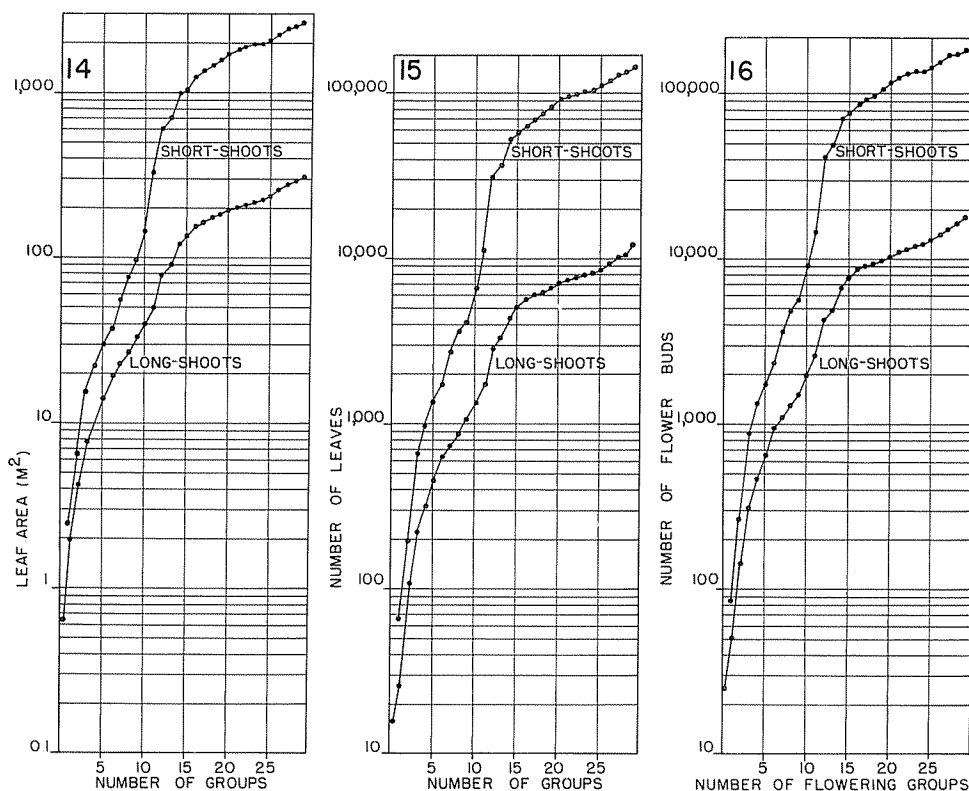
LONG-SHOOTS			SHORT-SHOOTS		
Order	Leaf Pair	Area/leaf (cm ²)	Order	Leaf Pair	Area/leaf (cm ²)
1	1	58	2	1	44
	2	64		2	42
	3	44		3	25
		4	28	Leaf area/shoot	222
		5	36	Flower buds/shoot	8
		6	36	Leaf number/shoot	6
		7	31		
		8	14		
	Leaf area/shoot	622	3	1	19
	Flower buds/shoot	25		2	22
	Leaf number/shoot	16		3	10
2	1	52	Leaf area/shoot	102	
	2	54	Flower buds/shoot	8	
	3	37	Leaf number/shoot	6	
	4	32	4	1	22
	5	22		2	26
	6	20		3	13
	7	17		Leaf area/shoot	122
	Leaf area/shoot	468	Flower buds/shoot	8	
	Flower buds/shoot	22	Leaf number/shoot	6	
	Leaf number/shoot	14	5	1	22
3	1	34		2	21
	2	40		3	13
	3	29		Leaf area/shoot	112
	4	17		Flower buds/shoot	8
	5	13		Leaf number/shoot	6
	6	8	6	1	15
	Leaf area/shoot	282		2	10
	Flower buds/shoot	18	Leaf area/shoot	50	
	Leaf number/shoot	12	Flower buds/shoot	5	
4	1	37	Leaf number/shoot	4	
	2	43	7	1	10
	3	30		Leaf area/shoot	20
	4	13		Flower buds/shoot	2
	Leaf area/shoot	246		Leaf number/shoot	2
	Flower buds/shoot	12			
	Leaf number/shoot	8			
5	1	30			
	2	32			
	3	15			
	Leaf area/shoot	154			
	Flower buds/shoot	8			
	Leaf number/shoot	6			

Table 4: Data used in calculating leaf area, leaf and flower bud number in Fig.14-16.

To a large extent, variation in mature leaf size is related to leaf position (Table 4). Usually leaves of pair 1, and less frequently pair 2, are the largest on a shoot and each successive leaf is smaller. When leaves of the same relative position are compared, leaf size decreases with increasing order number of the shoot and leaves are bigger on long-shoots than on short-shoots of the same order. Due to differences in both size and number of leaves, the total leaf area on each shoot decreases with increasing order number and is greater on long-shoots than on short-shoots of the same order.

Using data on leaf number and size per shoot (Table 4) and the estimate of the number of branches on a tree (Figs. 10, 11), the leaf number and total leaf area of different size trees can be calculated (Figs. 14, 15). The general distribution of leaf number and size among the various orders was about the same as for the branches, but the lower orders carried a slightly higher proportion of the leaves because they had relatively more and larger leaves. Because the quantity of foliage is directly proportional to the number of branches that can bear leaves, the curves for total branch number (Figs. 10, 11), leaf number and leaf area (Figs. 14, 15) have the same shapes. The relationships among the different orders are also the same.

There may be large size differences between the two leaves of a pair due to the phenomenon of anisophylly. When a pair of leaves is oriented so that one is on the upper side of a branch and the other on the lower side of a branch, the leaf that initially grows downward is the larger (Fig. 13). Anisophylly in *Acer platinoides* has been discussed by White (1957).



Figures 14-16. Estimates of leaf area, leaf number and flower bud number on trees with 1 to 29 groups of second order long-shoots. Values for the different orders of shoots are in the same relation to each other and to the totals shown here as in the number of long-shoots and short-shoots (Figs. 10, 11).

The disposition and orientation of mature leaves on a shoot minimizes shading effects. In vertical shoots differences in petiole length result in almost no shading (Fig. 13). In horizontal shoots, differences in leaf blade size and petiole length plus differential growth of the petiole result in a distribution of leaves with the blades essentially in one plane and with little mutual shading (Fig. 13).

Some sample branches from trees had leaves in whorls of three rather than in pairs. By tracing the leaf scars back along the branch it could be seen that the apex had changed from producing pairs of leaves to producing whorls and would have, perhaps, eventually reverted to producing pairs. Occasional stump sprouts were observed with leaves in whorls of three leaves. Several hundred seeds were germinated and of these 6% had 3 cotyledons rather than 2. Some of these seedlings continued to produce leaves in whorls; however, most of them reverted to producing pairs of leaves before the end of the first growing season. The change from producing leaf pairs to producing whorls appeared to be normal, but infrequent.

FLOWERING

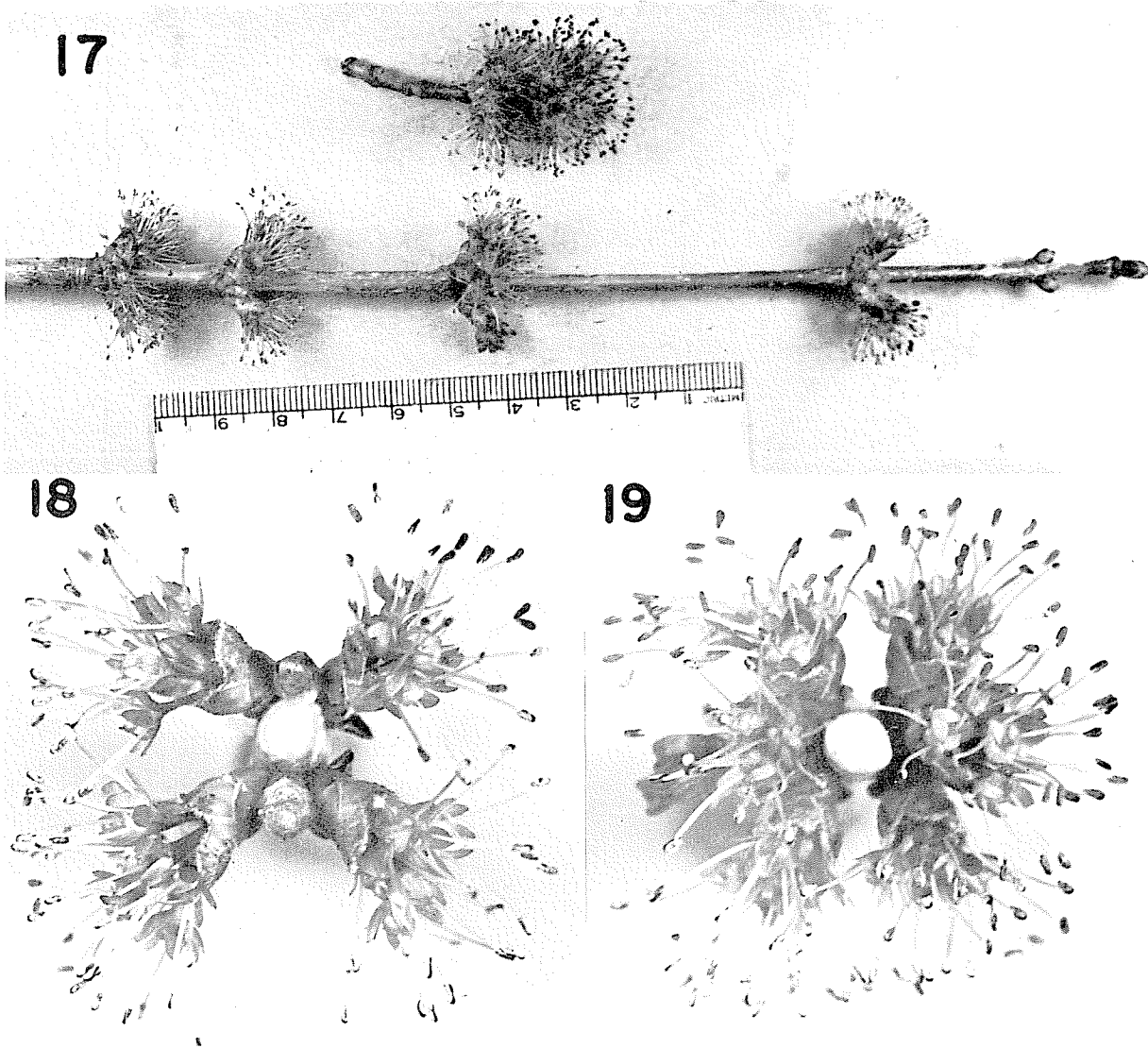
Red maple trees in the Petersham area flower about the last week in April, several weeks before vegetative bud break. Some trees flower when only 2-3 m tall if they are growing in the open, but heavily shaded trees generally do not flower. Likewise, flowering occurs on all the branches within the upper, well-lit portion of the crown, but there is no flowering below the point of interlocking in the crown canopy. Non-flowering portions of the crown are characteristically slow growing and lack vigor.

Flower buds are produced laterally in the axils of leaves, in many cases along with vegetative buds. Every combination of vegetative and flower buds was observed, with from 0 to 2 vegetative buds and from 0 to 6 flower buds per node (Figs. 17-19). Although more than 6 flower buds at a node was uncommon, up to 12 were observed. Each flower bud usually contains 4 to 7 flowers, with 5 being the most common.

There were no obvious differences in the distribution of flower buds in male, female, hermaphroditic, fast or slow growing trees. Thus, data for all trees were lumped to illustrate the distribution of bud types shown in Figure 20. Short-shoots with 1-3 nodes had no lateral vegetative buds. Shoots with one node usually had a pair of flower buds, shoots with two nodes either had two pairs of flower buds or a pair at the upper node and four at the lower node. Long-shoots with 3 nodes had a pair of lateral vegetative buds at the uppermost node. Both long-shoots and short-shoots with 3 nodes usually had a pair of flower buds at the upper node, four at the middle and lower nodes. Branches with four or more nodes were long-shoots. In general the uppermost node had a pair of vegetative buds and no flower buds, the middle nodes had a pair of vegetative buds plus four flower buds, and the lowermost node had no vegetative buds but four, or often six, flower buds. The slope of the regression lines in Figure 20 shows the number of buds with each additional node, usually two for vegetative buds and four for flower buds.

The number of flowers on different type shoots has been summarized in Table 4, and used to estimate the number of flowers on whole trees (Fig. 16). As in quantitative data on the foliage, the curves for flower number have the same shape and relation between orders as those for branch number.

A problem in the estimation of the total number of flowers is that below the point of crown interlocking there are no flowers. Because the older second order branches tend to curve up at the ends, the tip portion of a group might be flowering while the base was not. Therefore the estimate of flower number is certain to be high for larger trees if all groups are included. It should be fairly accurate, however, if only those groups that are actually flowering are included in the estimate. For example, a tree with 27 whorls might have only 20 that were flowering.



Figures 17-19. Figure 17, a short-shoot on the left and a long-shoot on the right, both with male flowers. Figs. 18, 19, aerial view of the arrangement of flower buds. The typical arrangement for the middle nodes of a long-shoot is 2 vegetative buds and 4 flower buds (Fig. 18). The lowest node usually has no vegetative buds and 6 flower buds (Fig. 19).

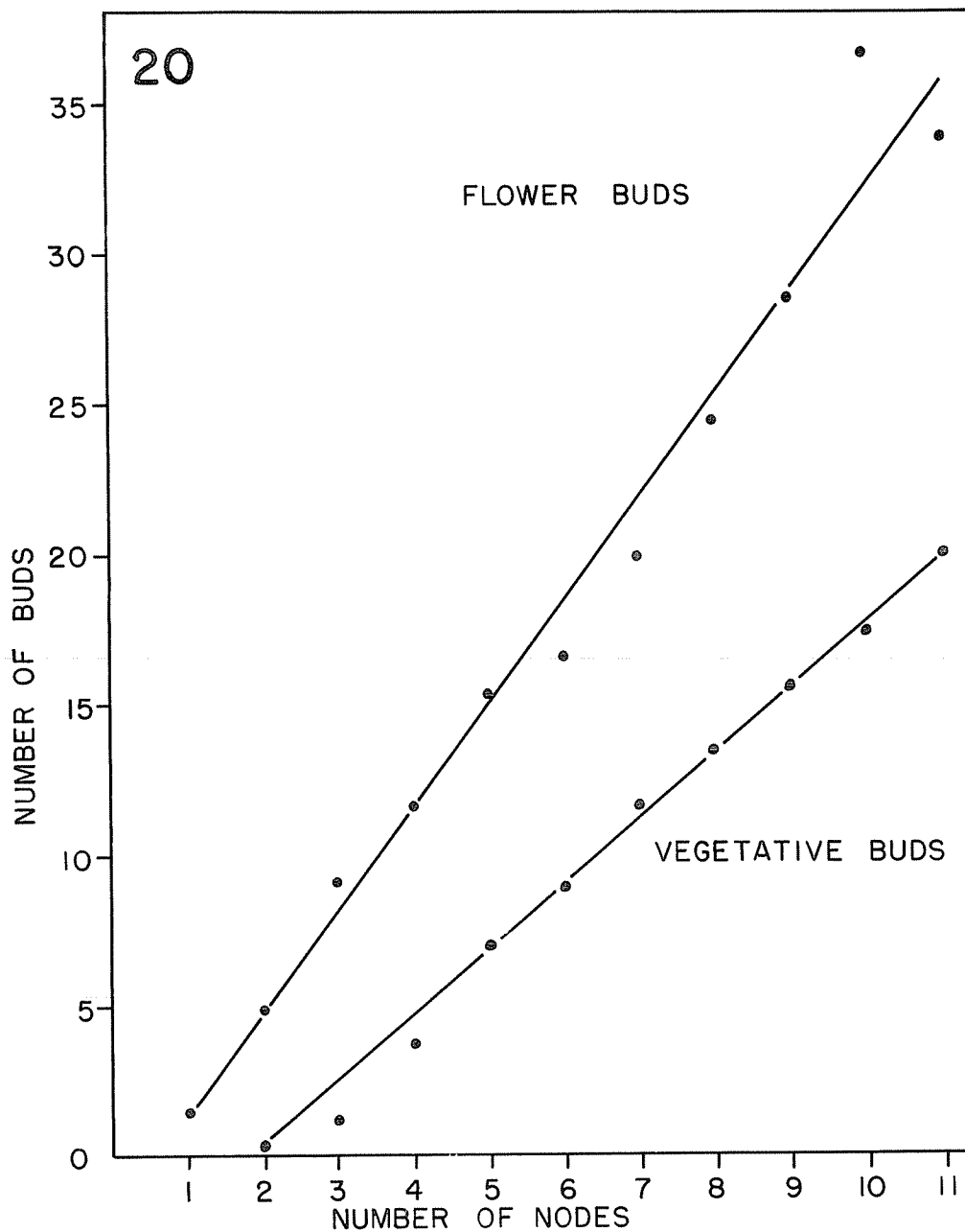


Figure 20. Relation between the number of nodes on the year-old portion of a shoot and the number of flower and vegetative buds on the shoot. Each point is the average for all shoots with a particular number of nodes from all 9 trees studied.

DISCUSSION

In this study the numbers of organs on trees were estimated on the basis of quantitative developmental relationships within the shoot system. Most other estimates have been based on samples of the branches in the crown from which correlations between branch dimensions and leaf number and area per branch were determined (Büsgen and Münch, 1929; Cummings, 1941; Turrell, 1934, 1961). It is difficult and unrewarding to compare the accuracy of these two approaches because they have not been used on comparable trees. A technique based on sampling and correlations is probably most satisfactory for production studies, but it obscures the developmental relationships between the parts of the shoot system, the subject of the present study. It is probable that sampling techniques could be improved if they were based on these relationships, because the shoot system of a tree is certainly not just a random collection of branches, leaves and flowers.

The process of shoot development in red maple can be interpreted as a mechanism for the efficient disposition of leaves for light absorption. Second order long-shoots grow rapidly from the main stem at an angle that decreases with time. The main stem and second order long-shoots, therefore, outline an ever increasing volume for crown development (Figs. 2, 3). The limits of the crown expand both out and up in young trees, but when the tips of older second order long-shoots are growing vertically the expansion is predominantly upwards. Third and fourth order long-shoots, growing more slowly at angles to the parent long-shoots, build up a framework of long-shoots within the volume of the crown. This framework bears the slow growing short-shoots that occupy most of the volume of the crown and bear most of the leaves and flowers (Figs. 2-4). Higher orders of long-shoots produce progressively fewer lateral long-shoots. Thus, as only long-shoots bear lateral branches, by the eighth order the few shoots present are all short-shoots.

Shaded branches, presumably near the compensation point for photosynthesis, die, so the photosynthetic leaf surface always tends to be peripheral in the crown. Different leaf blade and petiole sizes and petiole orientation ensure optimum disposition of leaf blades for absorption of sunlight. Thus, there is a division of labor between long-shoots that grow relatively rapidly, extending and penetrating the volume of the crown, and the essentially sessile short-shoots that bear the leaves. This situation is comparable to the division of labor between woody and non-woody roots in the soil (Lyford and Wilson, 1964).

There is a definite correlation between the position of buds and their pattern of development. The position of a bud results, in effect, from the interaction of its relation to other buds, through apical dominance and bud inhibition, and its vigor, as determined by the local environment of the shoot. From information available on apical dominance in trees (Critchfield, 1960; Gunckel and Thimann, 1949; Titman and Wetmore, 1955), it seems logical to assume that in red maple the relatively high auxin production by the terminal and uppermost lateral buds as they develop late leaves causes the elongation of their internodes so that they form long-shoots, and the high auxin production also causes the inhibition of late leaf development by the lower buds. An anomaly is that the upper lateral buds are not inhibited by the terminal. One would expect that, as in peas (Went and Thimann, 1937), the lowermost buds would be least inhibited, and therefore form long-shoots, because they are farthest from the source of inhibiting auxin. Sachs (1965) has suggested that the upper laterals start growing at the same time as the terminal which permits them to escape inhibition. Presumably the uppermost, vigorous laterals produce late leaves and high auxin before they are inhibited, whereas the lower buds are inhibited before they can produce late leaves. The question then becomes, why are the uppermost buds more fast growing and vigorous than the lower ones.

In general, the growth rate of a red maple shoot is related to the number of lateral long-shoots that develop, as in other species (Gunckel, Thimann and Wetmore, 1949; Titman and Wetmore, 1955). In red maple, the net increment of long-shoots decreases with increasing order number of the parent shoot, yet both growth rate and net increment of long-shoots can be increased in any order by a more favorable environment in the crown. It seems likely that the potential for growth of the lateral buds decreases as growth rate of the shoot as a whole decreases. In the case of extremely slow-growing short-shoots, all lateral buds become flower buds with no potential for elongation and the terminal buds cannot produce late leaves. The only legitimate conclusion is that of Brown *et al.* (1966), that we know little about some of the basic mechanisms controlling but inhibition in woody plants.

It seems that the factors favoring long-shoot production are the ones that inhibit the production of flower buds. The distribution of flower buds is almost the opposite of the distribution of long-shoots. Short-shoots produce only flower buds; on long-shoots the lowest node usually produces only flower buds and the uppermost node produces only vegetative buds that usually develop into long-shoots. The formation of flower buds occurs during the same time when the relative vigor of the lateral vegetative buds is determined. Possibly the high auxin production associated with long-shoot formation is one of the factors required for the differentiation of lateral vegetative buds.

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