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THE FORMATION, GROWTH, AND FATE OF BUDS OF FRAXINUS AMERICANA L. IN CENTRAL MASSACHUSETTS

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ABSTRACT

The morphology and growth of shoots of trees and saplings of Fraxinus americana has been studied in Central Massachusetts. During the winter the current increments of shoots have large terminal and decreasingly smaller lateral buds at successively lower nodes. The buds in the axils of the scale scars at the base of each increment are the smallest. However, within the short length of shoot which bears scale scars the lowest buds are largest. Number of leaf primordia in a bud and the size of the bud are correlated; large buds have many, small buds have few primordia. After bud burst and shoot elongation, axillary bud size is correlated in a limited way with the size of the subtending leaf, so that large leaves subtend large buds. After elongation of the parent shoot ends, daughter buds continue to develop, the terminal and upper buds growing most, thus re-establishing the winter pattern. In trees and saplings, all leaves on the current increments result from the expansion of overwintering primordia but in stump sprouts this is not so. Overwintering buds may or may not form shoots in the subsequent spring. The ultimate behavior of various kinds of bud is described. Many of the observed phenomena are intimately related to bud dormancy, the causes of which are discussed.

Introduction

A physiological understanding of the growth and reproduction of a tree can only follow from a thorough knowledge of its morphology and development. It is obviously more difficult to experiment with large trees than small seedlings, and observations made on seedlings may not be valid for large trees. The few studies that have been made with mature trees are described in the review by Romberger (1963).

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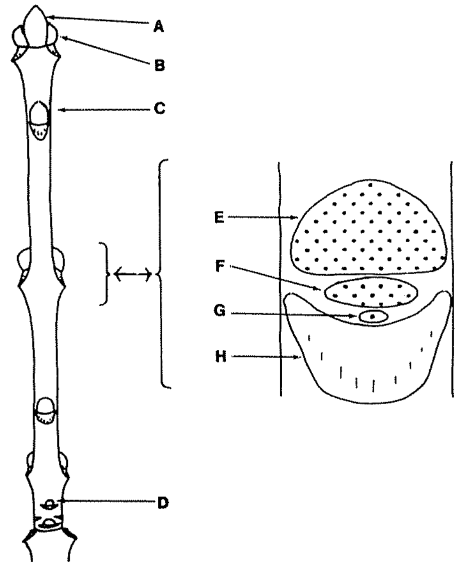

Fig. 1. The current increment of a shoot of Fraxinus americana as it appears in winter.

Left: photograph - compare this with central diagram.

Center: a 15 cm long increment. "A" is the terminal bud, "B" is the uppermost axillary bud in the axil of a leaf scar, "C" is an axillary bud in the axil of a leaf scar, "D" is a bud in the axil of the scar left by a scale.

Right: diagram of a nodal area greatly enlarged. "E" is the major bud in the axil while "F" and "G" are minor buds. "H" depicts the scar left by a foliage leaf.

It was the aim of this study to investigate in the field, some aspects of the behavior of mature trees, saplings, and sprouts. The shoot system arises from the outgrowth of buds. Hence the origin, development, and fate of buds was studied. Fraxinus americana L. was chosen for the investigation because it is widely distributed in the eastern United States. The species is known to be composed of a number of morphologically and physiologically distinct races or ecotypes (Wright, 1944 a). Plants studied at the Harvard Forest in Central Massachusetts belong to the northern ecotype.

There is no elongation of shoots during winter. The leafless shoot shows a series of well-defined growth increments each delimited by the scars of bud scales and the youngest of these increments are the major sites of regrowth in spring. On the subsequent pages, the structure and arrangement of the buds on the current overwintering shoot is first described, followed by observations on the re-establishment of the winter pattern during spring and summer. Some buds on the winter shoot form reproductive structures, others form vegetative branches, and some do not expand. The structure and fate of these long-dormant buds is examined.

THE VEGETATIVE WINTER SHOOT

(i) Types of bud

The current growth increment is delimited from the previous one by a series of closely-spaced scars left by the scales which had enclosed a former terminal bud (Fig. 1D, see also photograph on left). The terminal bud (Fig. 1A) is flanked by a pair of lateral buds (Fig. 1B) which were formed in the axils of the uppermost leaves of the shoot. Leaves are decussate, so buds are correspondingly in pairs at each node. Buds in the axils of bud-scale scars (Fig. 1D) are solitary, but in the axil of a foliage leaf there can be a vertical series of 2 - 3 buds. Of these, the uppermost (major) bud is largest, the lower (minor) buds are smaller (Fig. 1E-G). These axillary buds and the terminal bud on the current increment are here called first-order buds. Within these first-order buds dissection may reveal second-order buds in the axils of the bud scales. Table 1 summarizes, in the form of a dichotomous key, the nomenclature used to distinguish the kinds of bud on one increment.

The number of buds on current increments varies widely (Table 2). The variation in total number is due to variation in the numbers of both second-order and first-order buds.

Table 1. Nomenclature for buds on the current increments of winter shoots.

1. Buds obviously not enclosed within another bud..... First-order buds
   - A. Buds apical, not subtended by a leaf scar.... Terminal buds
   - B. Buds axillary, subtended by a scar of a scale or foliage leaf...................... Axillary buds
     - (a) Largest bud in an axil............. Major bud
     - (b) Smaller buds in the same axil as (a)..................... Minor buds
2. Buds not obvious, enclosed within another bud...... Second-order buds

Table 2. Numbers of buds of different categories on the current increments of selected shoots.

Length of current increment (cm).	First-order				Second-order	Total
	Terminal	Axillary				
		Leaf		Scale		
		Major	Minor			
1	1	6	0	6	28	41
16	1	10	6	6	40	63
76	1	10	8	8	44	71
89	1	16	26	8	54	105

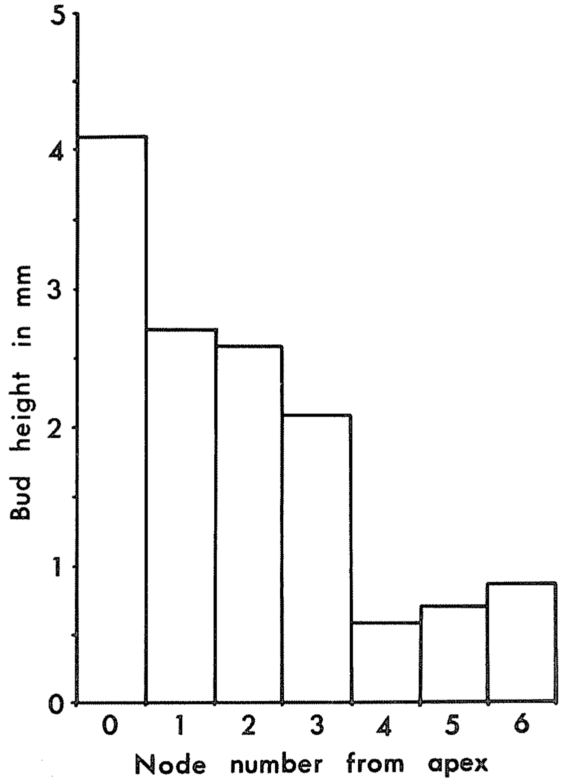

Fig. 2. Bud height in relation to position on a vertical shoot (current increment only). Node "0" is the terminal bud, nodes 4 - 6 are defined by bud-scale scars.

(ii) <u>Bud size and position</u>

The terminal bud is the largest on any current increment regardless of whether this is horizontal or vertical. Axillary buds show a constant size relationship along the increment influenced partly by shoot orientation.

In vertical shoots the largest axillary buds are found either at the first or second node from the apex (Fig. 2). Further below the apex, major buds are progressively smaller. The progression is interrupted by buds in the axils of the scale scars. Here, in the zone of bud-scale scars, distal scale buds are smaller than tne proximal ones, so that the previous trend is reversed. This local pattern in the scale zone reflects the situation which existed when these scale buds were themselves second-order buds within a parental terminal bud.

Buds on horizontal shoots show the same distribution as those on vertical shoots except that those on the lower side of the shoot are larger than those of the same node in the upper position. Horizontal shoots are short and have few nodes.

Buds vary in length from 0.2 to 6 mm. The smallest buds may contain only one pair of primordia while the largest have up to 11 pairs. Figure 3 shows that size of bud and the total number of primordia in the bud are always related regardless of age or position. When data from more than one current increment are plotted the overall relation is the same, but the scatter of points on the graph is increased.

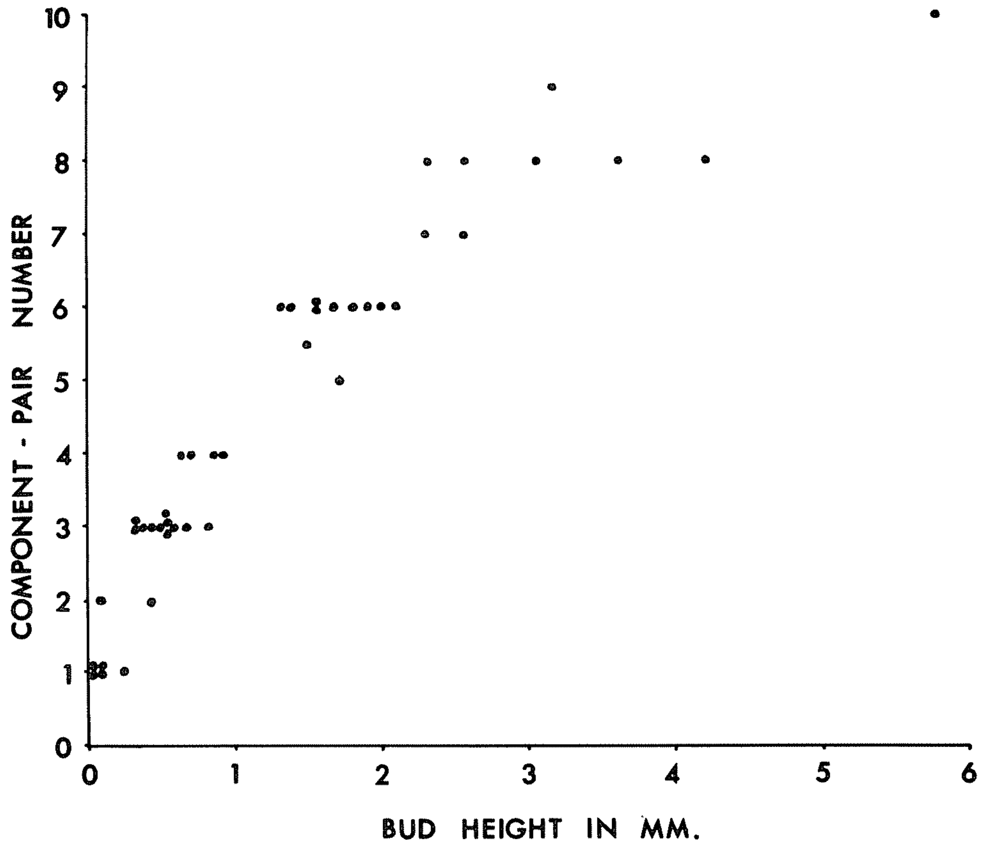

Fig. 3. Number of primordial pairs in relation to bud height for the buds of a single, current, winter increment.

(iii) Bud structure

Many primordia in the bud may be recognized as the primordia of scales or foliage leaves depending on whether they have less or more than half the axis differentiated as a leaflet-bearing rachis (Fig. 4). Otherwise the youngest primordia, closest to the apex, remain undetermined. The ultimate expression of a primordium is determined by environment during bud expansion. For example, a terminal bud induced artificially to grow out soon after its formation can have one pair of scales and several pairs of leaves. If the same terminal bud had been allowed to overwinter and grow out normally in the following spring it would have 3 to 5 pairs of scales as well as several pairs of leaves. Hence, the same primordium might become either a scale or a foliage leaf.

The numbers of these different kinds of primordia in a bud varies according to the type of bud (Table 3). Terminal buds usually contain 3 - 5 pairs of scale primordia surrounding 3 - 6 pairs of leaf primordia and a pair of undetermined primordia. These are all symmetrically and decussately arranged about the morphological apex of the shoot. The outermost scale primordia are often tough and leathery and covered with small hairs. They may be topped by a small rachis bearing leaflet primordia, showing that the bulk of the scale is morphologically a petiole. Primordia nearer the center are progressively

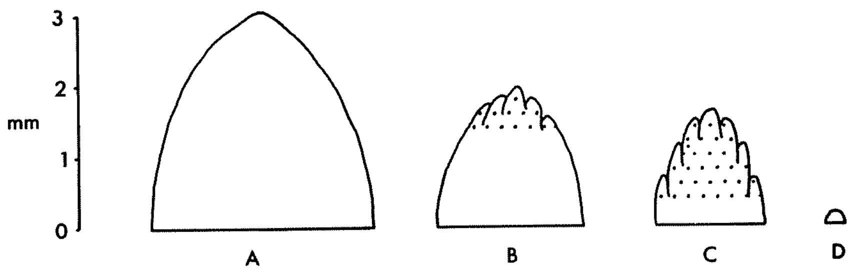

Fig. 4. Components of buds of Fraxinus americana: "A" and "B" are scale primordia, "C" is a leaf primordium, "D" is undetermined.

Table 3. The structure of the buds of the current increment.

Bud type	Pairs of primordia. Total	Pairs of scale primordia	Pairs of leaf primordia	Pairs of second-order buds	First-order buds per node	Number of samples
Terminal	6 - 11	3 - 5	3 - 6	1 - 5		18
Major (leaf) axillary	4 - 10	2 - 4	2 - 5	1 - 2	1 - 3	21
Minor (leaf) axillary	3 - 6	1 - 3	0 - 4	0		17
Second-order	1 - 5	0 - 2	0 - 4	0		54
Axillary (scale)	3 - 6	1 - 4	0 - 4	0	1	20

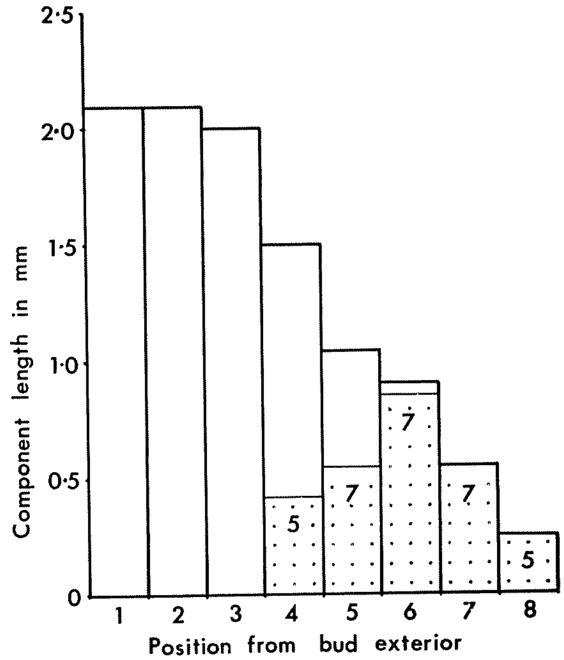

Fig. 5. Length of leaf and scale primordia as they come off upon dissection. Position 1 represents the outermost scale pair, position 8 is innermost. Zones occupied by leaflet primordia are stippled while the remainders of the primordia are shown blank. The number of leaflet primordia at each position is shown within the body of each column.

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more succulent and the length of the leaflet-bearing rachis is proportionately greater while the indumentum is less conspicuous (Fig. 5). Undetermined primordia close to the apex are usually less than 0.2 mm high, glabrous and succulent. Each major axillary bud has 2 - 4 pairs of scale primordia and 2 - 5 pairs of foliage leaf primordia. The outermost pairs of scales may subtend second-order buds. Minor axillary buds have 3 - 6 pairs of primordia of which 2 - 4 pairs are scale primordia and 2 - 5 are pairs of leaf primordia. In these buds, second-order buds are absent. Buds in the axils of scales are smaller and simpler. Of the 3 - 6 primordial pairs there may be 4 pairs of leaf primordia or there may be none. These buds, now first-order, were originally second-order buds of the previous increment.

The second-order buds in turn can be dissected and analyzed. They have 1 - 5 pairs of primordia consisting of up to 2 pairs of scale primordia and up to 4 pairs of leaf primordia. Scale primordia are usually present and in the simplest case they may merely enclose a further pair of undetermined primordia. Rarely the whole bud may consist solely of a pair of undetermined primordia.

Buds of different types but with the same number of primordia also have the same number of scale, leaf and undetermined primordia, with the exception of the second-order buds which tend to have one or two pairs of scale primordia fewer than other kinds of bud.

THE VEGETATIVE SPRING SHOOT

(i) Bud swell and burst

Under natural conditions between the middle of April and the middle of May the inner bud scales and the bud axis begin to elongate (bud swell). Previously enclosed parts of inner bud scales become exposed in such a way that a pattern of contrasting light (previously enclosed) and darker brown (previously exposed) surfaces appears. As the bud continues to grow the outermost scales gradually become reflexed, and the inner scales become greener.

Two to three weeks after bud swell the tips of the compound leaves appear above the scales (bud burst). Internodes between foliage leaves elongate more than those between the scales, leaflets expand, leaves and scales are reflexed.

The terminal bud and the axillary buds in the upper or middle parts of the current increment are usually the first to swell and burst in the spring. Lateral buds closest to the terminal bud often do not grow out whereas those at the second node often do and form persistent lateral branches. Buds at lower nodes may or may not develop into branches depending on the vigor of the parent shoot.

Second-order buds do not usually form shoots but remain dormant. Similarly, the minor buds in the axils of leaf scars and buds in the axils of scale scars rarely produce shoots at this time.

(ii) Branch development

During shoot elongation the scales at the base of the increment turn yellow and fall, as may also the uppermost leaf pair next to the developing terminal bud. In shoots of very low vigor the yellowing and loss of leaves is quite common. The small shoot to which they are attached is also often lost subsequently.

Branching of any increment in its second year is restricted because buds have differing potential. Axillary buds may or may not grow out. Those that do not produce a vegetative branch either abort, produce a flowering shoot, or persist to the second year. The fate of the major buds at each node on shoots produced in 1967 was examined on July 1, 1968.

On shoots from the mature trees most of the lateral buds were absent from the axils of both leaves and scales (Table 4). Few branches were observed. In the sapling shoots, on the other hand, there were more branches and fewer aborted buds even in increments with the same number of nodes as those from trees.

Persistent branches are formed from the larger buds of the winter shoot. Minor axillary buds very rarely form branches except on shoots of unusual vigor. The total number of branches produced depends on the vigor of the shoot as measured by its length, diameter, and number of nodes. An axis of very low vigor may produce a flowering rather than a vegetative branch. The period of elongation of the main axis and branches is also related to the inherent vigor of the shoot system. Elongation in shoots of poor vigor may cease in May whereas very vigorous shoots will continue their growth into June, July or even early August. When elongation ceases the terminal bud begins to form.

Table 4. Fate of buds produced on the 1967 shoots of mature trees and saplings as observed on July 1, 1968. Each figure in the table is the average of 20 observations.

Plant size	Group	Characteristics of 1967 increments			Fates of axillary buds		
		Pairs of scales	Pairs of leaves	Total nodes	Pairs of branches	Pairs aborted (major buds)	Pairs of major buds remaining
Mature	1	3.6	3.75	7.35	0.42	3.3	0.03
"	2	3.85	4.0	7.85	0.85	3.15	0.0
Sapling	1	3.1	5.05	8.15	1.65	1.85	1.55
"	2	3.0	4.6	7.6	1.3	1.23	2.07

(iii) Leaf production

Leaves of temperate woody plants arise either from overwintering primordia alone, or from these and from additional new primordia formed and expanded during the current period of growth. In the latter case the different morphology of early and late leaves may reflect the two origins (Critchfield 1960). Late-leaf development is associated with continued elongation, and the growth of the shoot may be said to be indeterminate. Where leaf number and elongation are limited by the number of primordia in the overwintering bud, growth may be said to be determinate. An experiment was carried out to ascertain whether the elongation of the shoots of vigorous saplings of *Fraxinus* is determinate or indeterminate. Opposed terminal buds of opposite branches and opposite lateral buds in symmetrical vertical shoots were used in the experiment. One of each pair of opposed buds was removed and dissected in the winter of 1966. The following summer the number of leaves formed from the second bud of each pair was counted.

There were 3 - 6 pairs of leaf primordia in the dissected buds and usually one pair of undetermined primordia. From 3 - 7 leaf pairs were produced in the opposite branch or bud. For the 15 comparisons that were made, the chi-square value was 3.78 which is not statistically significant. Thus the number of leaves arising from the bud is equal to the number of overwintering primordial leaves: growth is determinate.

(iv) Axillary and terminal bud development

When the terminal bud grows out in spring its outermost second-order buds fail to develop. The smaller buds in the axils of inner scales of this same terminal bud, however, do increase in size and produce further primordia as their subtending scales grow. Nevertheless, these buds rarely achieve the size of the outermost second-order buds. The terminal bud contains no second-order bud in the axils of the leaf primordia during the winter but these develop as the bud grows out to form a shoot. The first sign of the axillary bud can be detected under the dissecting microscope when its associated leaf reaches a length of from 3 - 6 mm.

At this stage the axillary bud consists merely of a pair of undetermined primordia enclosing the bud apex. These and several subsequent pairs form scale primordia while later primordia are foliar. When this major axillary bud has developed to a stage where it consists of approximately three pairs of primordia, a minor bud may form below it. Subsequently, when the major bud has approximately 4 pairs of primordia and the minor two, a third first-order bud may form. Whether these minor axillary buds develop or not seems to depend on the vigor of the shoot (see Table 2).

Axillary buds on actively elongating shoots are simpler than those on winter shoots. In the elongating shoot the number of primordia within a bud increases in a basal direction. Buds near the apex have fewest, those in the axils of fully expanded leaves have most, primordia. After leaf expansion, axillary buds do not differ much in size initially, although the size of leaves may vary widely. In other words, there is only a limited correlation between the size of a bud and the size of its subtending leaf at this stage.

The terminal bud begins to form as shoot elongation ceases. It develops in the same way as axillary buds except that the inner primordia of its predecessor may now be incorporated as outer primordia. Thus former leaf primordia may comprise the outer covering of the terminal bud in the form of scale primordia. This is indicated by the leaflet primordia which are sometimes apparent at the apices of outer bud scales. The outer scales of axillary buds lack leaflet primordia.

As the terminal bud adds new primordia and increases in size during summer the pattern of relative bud size to be observed in winter is gradually established on the current increment. Lower buds change little in size whereas upper buds enlarge.

THE FLOWERING SHOOT

Trees of _Fraxinus americana_ are usually dioecious but sometimes they are monoecious according to Fernald (1950). Flower buds are produced on the terminal increment of the shoot, mainly on mature trees. They are found not only on very short (e.g. 2 cm) branches but also on longer branches (e.g. up to 45 cm) on any one tree in one year. The buds that become reproductive are those in the axils of foliage leaves (cf. staminate catkins of _Carya_, _Quercus_). Within these buds male or female flowers occur in the axils of every bract and also terminate each reduced axis. The arrangement of bracts exactly parallels the arrangement of scales in the vegetative bud including that of the second-order buds. Morphologically, the outer bracts are indistinguishable from the scales of a vegetative bud whereas inner primordia look more like scale primordia than leaf primordia. Up to five small "leaflet" primordia may be present on these inner bract primordia.

Outgrowth of the flowering shoot differs from its vegetative counterpart in that little growth of bract primordia occurs and elongation of both first and second-order axes takes place. Female flowers usually appear either before or simultaneously with the first leaves but are preceded by male flowers.

Fertilization varies widely from year to year and in 1967 and 1968 little seed was set. However, the distribution of persistent fruiting peduncles on previous growth increments suggests that 1963 was a good seed year. The 1969 crop was also prolific. Rare trees flower and fruit each year with apparent regularity. Trees in the Boston area have similar behavior to those studied here (Anderson and Wheldon, 1936).

PERSISTENT BUDS

Buds on an increment which do not grow out in the second year may or may not persist. Many are either lost by abortion, or eaten or become diseased. The persistent remainder (Table 4) may still grow out in a subsequent year. These persistent buds widen tangentially because of the overall increase in the circumference of the stem and they become embedded in the bark. Outer bud scales may die and fall off but they are replaced by newly-developed ones.

Because of the articulate growth of shoots, with annual increments clearly indicated by bud-scale scars, it is possible to measure changes in persistent buds with age, by comparing them with buds in equivalent positions on other increments. Information from a shoot examined in the winter of 1967-8 is shown in Table 5. This allows buds on the increments formed from 1964-7 to be compared. It includes bud height, total number of primordial pairs, and the number of these pairs which were scale primordia, for up to 6 equivalent nodes on each increment. These data show that there is little change in bud height but the total number of primordia in the bud may increase. Most of these new primordia are scales (primordia with little development of the rachis).

Persistent buds may eventually grow out if apical dominance is lost or if the environment is changed, for example as a result of forest thinning.

The relation between "normal" second-order branches (produced in the second year of growth of an increment) and those produced on older increments is shown in Fig. 6. Buds may grow out over a period of several years in no apparent order.

Buds may also grow out from the stump of a felled tree to produce the familiar stump sprouts. Growth of these may be rapid, up to 230 cm in the first year if they are protected from browsing deer. Up to 16 nodes may be developed and first-order branches are not uncommon. These arise from axillary buds 5-11 nodes below the apex of the sprout.

In order to investigate the growth and development of stump sprouts new active sprouts up to 6 cm long were dissected in June 1968. These had grown from stumps of trees felled the previous winter and spring. The young shoots had 7-16 nodes, enough to account for the number of nodes on sprouts with fully expanded leaves. This suggests that the sprouts are determinate or that primordia are generated very early in the growth of the sprout. However, the growth of any lateral branch on these sprouts in this first season, must be due to the outgrowth of a recently formed bud, not an overwintered bud.

Morphologically, the branches on one year old sprouts are exceptional because they

Table 5. Axillary (scale) bud dissection. The figures in the body of the table represent bud height (mm), total number of primordial pairs (in parentheses) and number of pairs of scale primordia. The terminal bud represents the 1968 increment.

Node number from base of increment	Year of bud formation			
	1967	1966	1965	1964
1	1.7(5)2	1.7(6)4	1.5(9)5	2.1(11)8
2	1.7(5)1	1.8(7)2	1.3(8)4	1.8(10)7
3	1.2(3)1	1.5(6)3	1.3(7)4	1.3(10)8.5
4	0.5(2)1	1.1(6)3.5	0.9(7)3	1.1(9)5.5
5	0.1(1)0	-	-	1.1(9)6
6	-	-	-	0.7(9)6

have a long naked segment of stem below the first leaf pair, unlike the more usual branches of this species which have basal bud-scales separated by congested internodes. This also occurs in stump sprouts of other species in the same area such as Acer rubrum L. This kind of branch is common in tropical trees but is also found in a few temperate species which regularly branch within the current growth-increment e.g. Sassafras albidum (Nutt.) and Cornus alternifolia L.

Basal leaves of the sprouts are usually simple but leaflet number increases in distal leaves. Basal leaves probably arise from scale primordia whereas distal ones originate from leaf primordia. We have already seen that scale primordia have fewer leaflet primordia than do leaf primordia.

DORMANCY IN BUDS

"Dormant" is a general term used to describe an organ which is disposed to elongate but does not do so. Various types of dormancy can be distinguished and those defined by Romberger (1963) are used here. "Quiescence" is a dormancy imposed by the external environment; "correlated inhibition" is a dormancy imposed by one organ on another; "rest" is a dormancy maintained by agents or conditions within the organ itself.

Although the buds on the current summer increment do not normally grow out until the following spring they may be induced to do so within a few weeks by defoliation during the period June through July. The resulting apical shoots are usually of low vigor but

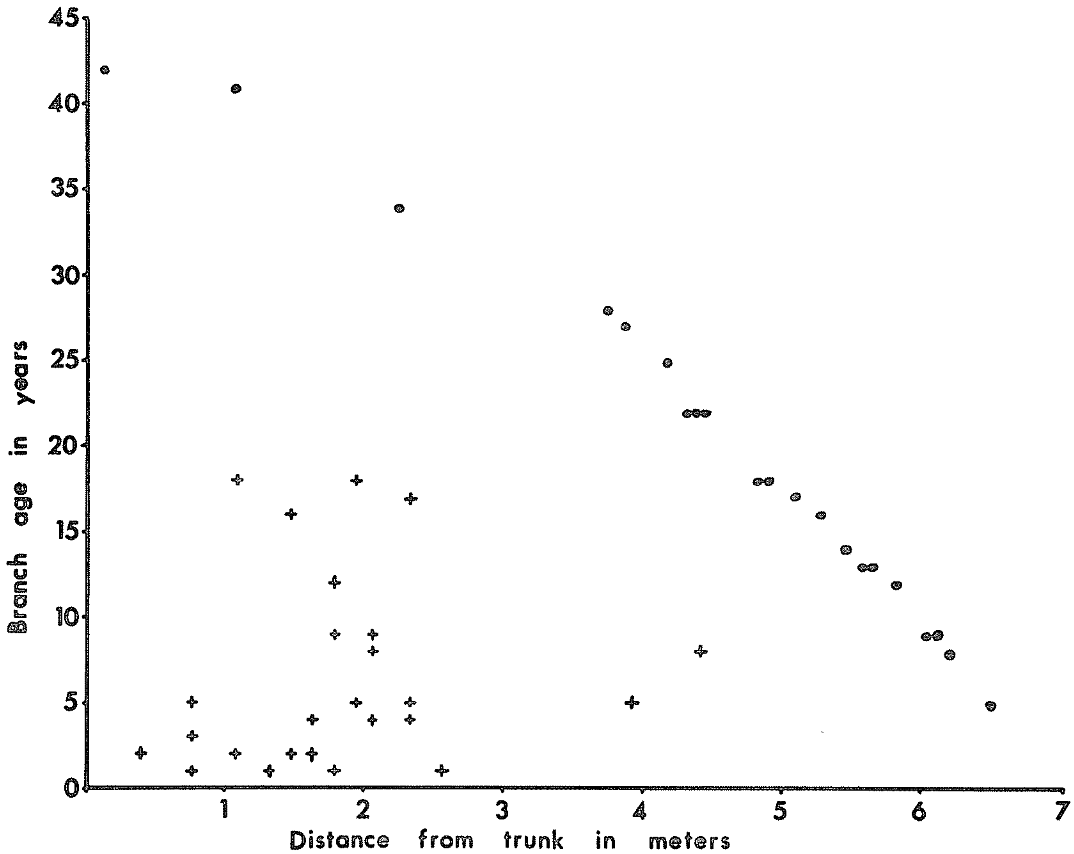

Fig. 6. Age of second-order branches in relation to position on a horizontal first-order branch. The dots represent branches formed on current overwintering increments while the crosses represent branches formed later from persistent buds.

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resemble stump sprouts in that basal leaves are often simple, more distal leaves compound, and only one or two pairs of scales are present. Removal of the terminal bud during this period fails to affect dormancy of axillary buds in saplings but may be effective in sprouts.

Defoliation of saplings during August or September has no effect on the dormancy of the terminal bud. However, similar terminal buds of defoliated cuttings taken before mid-August will burst when placed in a warm room (18^o - 24^o C) with a 16 hour photoperiod. Cuttings taken after mid-August or later could not be induced to respond. This showed that rest, as defined above, had begun. Rest was broken by about mid-December. Modal response was 37 days for a collection made in mid-December 1966 and 30 days for one made in the last week of 1967. Subsequently, as the time for bud burst in the field approached i.e. early May in 1967 and mid April 1968, the time for the same response in the cuttings declined.

Attempts were made to influence the response of the cuttings. From a collection made on November 22, 1967, one set of twigs was placed in the dark at 20°C and another set in the dark at 5°C. After one month the cuttings showed no visible response to this pre-treatment. When they were placed in a warm room under lights, those pre-treated at 20°C failed to respond whereas 9 of the 11 shoots treated at 5°C responded by bud swell after one month. Thus it appears that rest in ash can be broken by chilling.

In the period following the break of rest, but preceding bud swell in the field, the effect of long photoperiod on bud response was investigated. Cuttings placed in the dark were compared with cuttings under a 16 hour photoperiod. Since both groups showed bud burst it was obvious that photoperiod had no effect.

DISCUSSION

Height-growth patterns of North Temperate hardwoods fall into two categories, determinate and indeterminate. In the determinate type described, buds grow out in the spring and leaves expand until all the primordia have differentiated. A new terminal bud then forms with new primordia arising continually until late summer or fall. In the following year the cycle is repeated, the amount of elongation being correlated to some extent with the number of primordia in the bud.

The other type of height-growth pattern has been described by Critchfield (1960) for Populus trichocarpa. Here, growth is not limited by the number of primordia in the overwintering bud as new ones are formed which subsequently expand in the same season. Apparently use of available photosynthates for late leaf expansion precludes extensive investment in primordia, and thus relatively few are formed in terminal buds.

Elongation in seedlings of Fraxinus americana seems to be under different controls than that in more mature plants. In the latter, internal control is suggested by the association between cessation of elongation and the expansion of all available overwintering primordia - from late May to early August. In seedlings, however, environmental control by photoperiod seems likely. Thus Wright (1944 a, b) using white ash (F. americana) in Central Massachusetts and ecotypes of the closely related red ash (F. pennsylvanica) found continuous growth until October when "terminal buds" were formed. These resembled the apical buds of actively elongating shoots, however, rather than the scale-covered terminal buds of their long-inactive counterparts on trees. Vaartaja (1959), using red-ash ecotypes, found that elongation was stopped and "terminal bud" formation was induced by a 14 hour photoperiod while longer photoperiods were not effective. Thus growth of seedlings, in contrast to that of trees of the same species, seems indeterminate.

While photoperiod may have no role in the control of shoot elongation in ash, its importance in other processes is not precluded. It probably induces rest as it does in many northern populations of trees (Romberger, 1963). In the trees studied here, rest began about late August following a period of correlative inhibition (imposed by mature leaves) and quiescence. Thus from this time (late August) the importance of the leaves in preventing the outgrowth of buds has been eliminated and natural defoliation follows.

In spring, many species require a long photoperiod for bud swell and outgrowth but in ash there is no such requirement (see also Pauley, 1958). Rest is broken by about mid-December after a chilling requirement has been satisfied. The declining time for bud burst on successive collections of cuttings kept in a warm room suggests that field populations may need exposure to a certain quantity of heat before bud swell will begin. In *F. excelsior* Hemberg (1949) has shown that an inhibitor of an anti-auxin type decreases in activity as the time for bud break approaches, but the role of auxin in bud outgrowth has yet to be demonstrated.

Correlative inhibition is established soon after buds have begun their growth. In most cases it is only the larger buds of the current increments which form branches despite the fact that the multitude of buds elsewhere on the trees have been exposed to the same environmental stimuli. If these larger buds are removed outgrowth of smaller buds occurs. Thus the smaller are correlatively inhibited. Large buds may exert their control through the quantities of certain growth substances they produce. There is a great amount of evidence to suggest that cambial activity is stimulated by growth substances from these large buds (Wareing *et al.*, 1964) and these substances may be involved in establishing this early correlative inhibition between buds.

Among current increments in spring more branches are formed on the more vigorous axes but on the new shoots no branch is usually formed. However, in vigorous stump sprouts branches may form near the mid-section of the axis, probably arising while the apex is growing at its maximum rate. In this regard Sachs and Thimann (1967) surmise that sensitivity to inhibition decreases as growth rate increases. The release of lateral buds of stump sprouts upon apical decapitation, in addition to branching behavior, supports this. In most species of this region, however, vigor rarely reaches the level necessary for branch formation on the current increment. Where it does occur naturally and often in this area, viz. in *Cornus alternifolia* and *Sassafras albidum*, such a relationship between vigor and branching is less clear and accurate measurement would be helpful in its interpretation.

Literature Cited

ANDERSON, E. and C. M. WHELDON. 1936. Studies in the genus *Fraxinus* II. Data on the flowering and fruiting habits of three American species of ash - of possible economic importance in the production of rapid growing forest trees. J. Hered. 27:473-474.

CRITCHFIELD, W. B. 1960. Leaf dimorphism in *Populus trichocarpa*. Amer. J. Bot. 47: 699-711.

FERNALD, M. L. 1950. "Gray's Manual of Botany", 8th edition. American Book Co., New York.

HEMBERG, T. 1949. Growth inhibiting substances in terminal buds of *Fraxinus*. Physiol. Plant 2:37-44.

PAULEY, S. S. 1958. Photoperiodism in relation to tree improvement. In: "The Physiology of Forest Trees" edited by K V. Thimann, pp. 557-571. Ronald Press, New York.

ROMBERGER, J. A. 1963. Meristems, growth and development in woody plants. U.S.D.A. Tech. Bull. 1293.

SACHS, T. and K. V. THIMANN. 1967. The role of auxins and cytokinins in the release of buds from dominance. Amer. J. Bot. 54:136-144.

VAARTAJA, O. 1959. Evidence of photoperiodic ecotypes in trees. Ecol. Monog. 29:91-111.

WAREING, P. F., C. E. A. HANNEY and J. DIGBY. 1964. The role of endogenous hormones in cambial activity and xylem differentiation. In: "The Formation of Wood in Forest Trees", edited by M. H. ZIMMERMANN. pp. 323-344. Academic Press, New York.

WRIGHT, J. W. 1944a. Genotypic variation in white ash. J. For. 42:489-495.

_____________ 1944b. Ecotypic variation in red ash. J. For. 42:591-597.