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SHOOT GROWTH AND HETEROPHYLLY IN ACER[1]

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IN *Acer* and many other woody genera, leaf form changes drastically and often abruptly during the life of the plant. Heterophylly is of two principal kinds in these woody plants: (1) changes during seedling and post-seedling stages, and (2) changes during the development of single annual shoots of adult plants. Type (1) is ubiquitous in *Acer*; type (2) is a regular feature of some species but uncommon or poorly expressed in others. These two types of heterophylly tend to converge; deviations in leaf shape on adult plants are often in the direction of seedling leaves. This tendency of woody plants to produce reversions, among other aspects of heterophylly, attracted a great deal of attention around the end of the 19th century, and much of our knowledge of these phenomena derives from that period. The principle that ontogeny tends to recapitulate phylogeny (Haeckel's biogenetic "law") was widely accepted by biologists at the time, and variations in leaf form during development offered many apparent illustrations.

Partly in reaction to such phylogenetic interpretations of variation in plant form, Goebel (1900) formulated the concept of heteroblastic development, which dealt with the same kinds of variations in ontogenetic and physiological terms. In plants exhibiting heteroblastic development, the juvenile and adult stages are markedly different, and the adult sometimes produces reversions to the juvenile state. Both features are illustrated by several common maples (Jackson, 1899). Their seedling leaves are either unlobed or slightly lobed, in contrast to the pronounced lobing of most adult leaves. In older plants, Jackson noted, a tendency toward reduced lobing reappears on sprouts and in leaves produced toward the tips of vigorous shoots; the latter is a regular feature of elongate shoots of *Acer pseudoplatanus* L. Schüepp (1929) established that these differences in leaf shape on a single shoot originate at an early stage of leaf ontogeny. His work is among the very few ontogenetic approaches to the neglected problem of heterophylly in woody plants.

The incidence of heterophylly in *Acer* and several other woody genera of temperate regions is closely associated with the specialization of the shoot system into long and short shoots. *Populus trichocarpa* (Critchfield, 1960) exemplifies this heterogeneous group, which includes *Ginkgo*

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biloba and representatives of *Betula, Cercidiphyllum, Liquidambar,* and *Parthenocissus* (Clausen & Kozlowski, 1965; Critchfield 1970a, 1970b; Smith, 1967; Titman & Wetmore, 1955). This link between heterophylly and shoot specialization is conspicuous in two maples of eastern North America: *Acer rubrum* L. (red maple) and *A. pensylvanicum* L. (striped maple). This paper describes shoot development in these species, surveys the patterns of shoot growth and incidence of heterophylly in other members of this genus, and compares *Acer* to other groups with similar patterns of shoot development and leaf variation.

MATERIALS AND TERMINOLOGY

The growth of leaves and internodes was measured at 4-day to 4-week intervals on long and short shoots of red and striped maples. Total leaf length was measured in 1957–58; in 1959 blades and petioles were measured separately. Observations of red maple were made on 5- to 10-year-old trees growing in natural stands on the Harvard Forest at Petersham, Massachusetts (1957, 1959) or in a plantation of Harvard Forest and other Massachusetts origins on the Case Estates of the Arnold Arboretum at Weston, Mass. (1958). Shoot growth of striped maple was measured in 1958–59 on young trees in two stands on the Harvard Forest. Sprouts were induced to develop by partial stripping of the buds and branches from small trees.

Other species of *Acer* were observed mostly in the Arnold Arboretum. Illustrated shoots and leaves are from Arboretum trees except *Acer orientale* L. (*A. creticum* L.), which I collected in the mountains of western Crete. Dried specimens were examined in the Gray Herbarium and the herbarium of the Arnold Arboretum.

Terminology follows that of an earlier paper (Critchfield, 1960). The *early leaves* expand when the buds open in the spring; the *late leaves* are produced subsequently. *Transitional leaves,* present on some annual shoots, are intermediate between early and late leaves in time of appearance, position on the shoot, and form. Leaves are numbered from the base of the annual shoot, and an internode has the same number as the leaf at its upper end. The *phyllochron* (Bond, 1945) is the time interval between corresponding developmental stages of successive leaves, excluding initiation (to which *plastochron* refers). The stage on which the phyllochrons are based here is leaf maturation, defined as 90 percent of final leaf or blade length. Blade length was preferred because of the great variation in growth duration and final length of petioles, particularly in red maple.

The term *epigenetic* is applied to the ontogeny of all leaves that are not preformed in winter buds. In contrast to the distinctly two-stage growth of preformed leaves, epigenetic development is continuous from initiation (or a very early stage of ontogeny) to maturation.

ORGANIZATION OF THE SHOOT SYSTEM

Acer pensylvanicum. — The long and short shoots produced by striped maple during a single season are distinct from each other in both stem length and leaf production. Short shoots greatly outnumber long shoots after the first few years of growth, and suppressed understory trees may not produce any long shoots. The short shoots almost invariably bear a single pair of the large leaves which typify this species, and terminate in a bud or inflorescence.

The stem of the short shoot rarely exceeds 5 cm. in length, and consists mostly of the internode below the single leaf-node. In a sample of 40 short shoots on herbarium specimens from widely scattered localities, the stems had a mean length of 2.0 cm. (range 0.3 to 4.6). An exceptional short shoot from Quebec had two similar pairs of leaves and a length of 2.0 cm., but all others had only one pair.

Long shoots of striped maple have more leaves (two or more pairs) and much longer stems than short shoots, and the length of the stem is roughly proportional to the number of leaf pairs. In a sample of 37 long shoots from six trees used for growth observations, 27 shoots had 2 to 4 leaf pairs and the others had 5 to 9. The stems ranged in length from 10.7 to 102.6 cm. Shoots with only two pairs of leaves averaged 18 cm. in stem length (range 10.7 to 28.4). The shortest long-shoot stem observed (on a herbarium specimen from Pennsylvania) had two leaf-nodes and was 7.4 cm. long. No shoots between 5.3 and 7.4 cm. were encountered.

Individual internodes are exceptionally long in this species. Many long shoots had at least one internode between 20 and 25 cm.; the longest observed was 28.5 cm.

Acer rubrum. — The annual shoots of red maple have smaller, more numerous leaves and shorter internodes than striped maple shoots. They terminate in vegetative buds; inflorescences are borne on separate non-leafy shoots in this species. As in striped maple, the long shoots are outnumbered by short shoots early in the life of the tree, and in the crowns of older trees they make up only 4 to 5 percent of the annual shoots (Wilson, 1966).

The long and short shoots produced in a single season are not as sharply distinct as in striped maple, but the great majority are readily classifiable as short (less than 2.5 cm.) or long (more than 3.0 cm.). Shoots with one or two pairs of leaves are nearly always short, and shoots with four or more pairs (ranging up to at least 16) are nearly always long. Shoots with three leaf pairs are extremely variable; those developing from terminal buds are usually short, but axillary buds sometimes produce long shoots with only three leaf-nodes. In a sample of 48 long shoots from six trees, the longest were 50 to 54 cm. and bore 12 to 16 pairs of leaves.

THE WINTER BUD AND ITS CONTENTS

Acer pensylvanicum. — The dormant vegetative buds of striped maple are remarkably uniform in construction and contents, and they offer no indications of the type of shoot they will produce the following spring. Nearly all have two pairs of bud scales, with only the outer pair exposed. As in other maples, the scales are modified leaf bases. The terminal buds are 6 to 10 mm. long; axillary buds are smaller (2 to 5 mm.), and some are rudimentary. In both this species and red maple, the envelope formed by the bud scales is much larger than the embryonic shoot it covers, leaving considerable space for the shoot to enlarge before the bud begins to expand.

With rare exceptions, the buds contain a single pair of embryonic leaves and a pair of primordia. In terminal buds collected at the end of the growing season, the embryonic leaves were 13 to 40 times as long as the primordia (TABLE 1). They were far advanced in development, having a short petiole and a blade with three nearly equal lobes and many teeth (FIGURE 1). The primordia were either undifferentiated in shape, as in FIGURE 1, or showed the beginnings of two lateral lobes. If a bud subsequently produces a short shoot, the embryonic leaves expand into the single pair of leaves on the shoot, and the primordia develop into the outer scales of the new winter bud. If the bud produces a long shoot, the primordia develop into the second pair of foliage leaves.

During bud expansion in the spring, the outer scales separate and the inner scales elongate. They form a loose envelope around the growing shoot, held tightly together along their margins by abundant tangled hairs. By the time they separate, both pairs of leaves have increased greatly in size (TABLE 1) and are densely pubescent. A new pair of primordia is initiated at the apex of most embryonic shoots during bud enlargement (TABLE 1).

The distinction between future long and short shoots was usually apparent during the later stages of bud enlargement. The primordia at the second node of future short shoots began to develop into bud scales. They grew at a relatively slow rate, and the leaf bases increased disproportionately in size. The first leaf pair was 16 to 38 times as long as the second in putative short-shoot buds. In this category were most axillary buds and the terminal buds of all short shoots and a few (3 of 20) long shoots. In buds that produce long shoots, the growth rate of the second pair of leaves was much faster, and by the time the buds opened pair 1 was only 3.3 to 16 times as long as pair 2. Most long-shoot terminal buds (17 of 20) and a few axillary buds were in this category.

A single terminal bud sampled at this stage (omitted from TABLE 1) differed from all others in having two pairs of well-developed embryonic leaves. The second pair was 40 percent as long as the first and 19 times as long as the pair of primordia at the apex. On the same tree, a bud like

TABLE 1. — **Bud contents and previous season's leaf production of Acer pensylvanicum and A. rubrum**

	A. PENSYLVANICUM			A. RUBRUM		
	Terminal buds			Terminal buds		
	Long shoots	Short shoots	Axil. buds	Long shoots	Short shoots	Axil. buds
BUDS DORMANT [1]						
No. of buds	15		5	9	14	1
No. leaf-nodes on previous season's shoot:						
Mean	4.1		–	7.8	2.0	–
Range	2–8		–	4–11	1–3	–
No. lf. pairs in bud:						
Mean	2		2	3	2.4	2
Range	–		–	–	2–3	–
Range in lf. length (mm.) at node:						
1	2.6–4.3		1.3–3.1	.80–1.2	.60–.90	.60
2	.05–.30		.02–.11	.50–.85	.25–.70	.30
3	–		–	.10–.35	.04–.20	–
BUDS SWELLING [2]						
No. of buds	20	3	41	33	20	14
No. leaf-nodes on previous season's shoot:						
Mean	4.0	1	–	7.9	2.0	–
Range	2–8	–	–	4–16	1–3	–
No. lf. pairs in bud:						
Mean	2.8	2.6	2.7	4.0	3.6	3.3
Range	2–3	2–3	2–3	3–5	3–4	2–4
Range in lf. length (mm.) at node:						
1	5.5–27	7.0–24	2.5–28	2.5–8.0	1.5–6.0	.60–5.7
2	.30–3.1	.40–1.0	.07–2.6	2.0–6.5	1.2–5.0	.37–3.5
3	.01–.15	.01–.10	.01–.15	.45–5.0	.15–2.2	.05–.70
4				.01–1.5	.01–.55	.01–.10
5				.01–.35	–	–

[1] *A. pensylvanicum* collected late Sept. and mid-Oct. from 2 trees. *A. rubrum* collected mid-Feb. from 1 tree.

[2] *A. pensylvanicum* collected mid- to late April from 4 trees; a few buds opening. *A. rubrum* collected same period from 6 trees.

this one apparently produced a single long shoot with two pairs of early leaves during the ensuing growing season (*see* next section).

Acer rubrum. — The dormant buds of red maple are much smaller (2.5 to 5.0 mm.) than those of striped maple, but they have more bud scales (6 to 12) and usually contain more leaves. The terminal buds of long shoots and some short shoots sampled in mid-winter had three pairs of leaves (TABLE 1), and the same number was reported by Wilson (1966). The other buds contained two leaf pairs. In buds with three pairs, pairs 2 and 3 were 67 and 22 percent as long as was pair 1 (ranges

60 to 78, 11 to 30). The embryonic leaves at nodes 1 and 2, despite their small size, had well developed, mostly glabrous blades with three nearly equal lobes and several marginal teeth, but only the largest had distinct petioles. The leaves at node 3 were unlobed if they were less than .15 to .20 mm. long, but above this size they had the beginnings of two lateral lobes.

In red maple, bud enlargement and the growth of the embryonic shoot was a gradual process that began long before the buds opened at the beginning of May. By mid-April, long-shoot terminal buds from the same tree sampled in February had nearly doubled in length, and the first pair of leaves had more than tripled (from 1.0 to 3.5 mm.). Pairs 2 and 3 had grown even faster, and were 79 and 37 percent as long as pair 1 (ranges 73 to 82, 28 to 42). Most red maple buds initiated an additional pair of primordia during enlargement (TABLE 1). A few

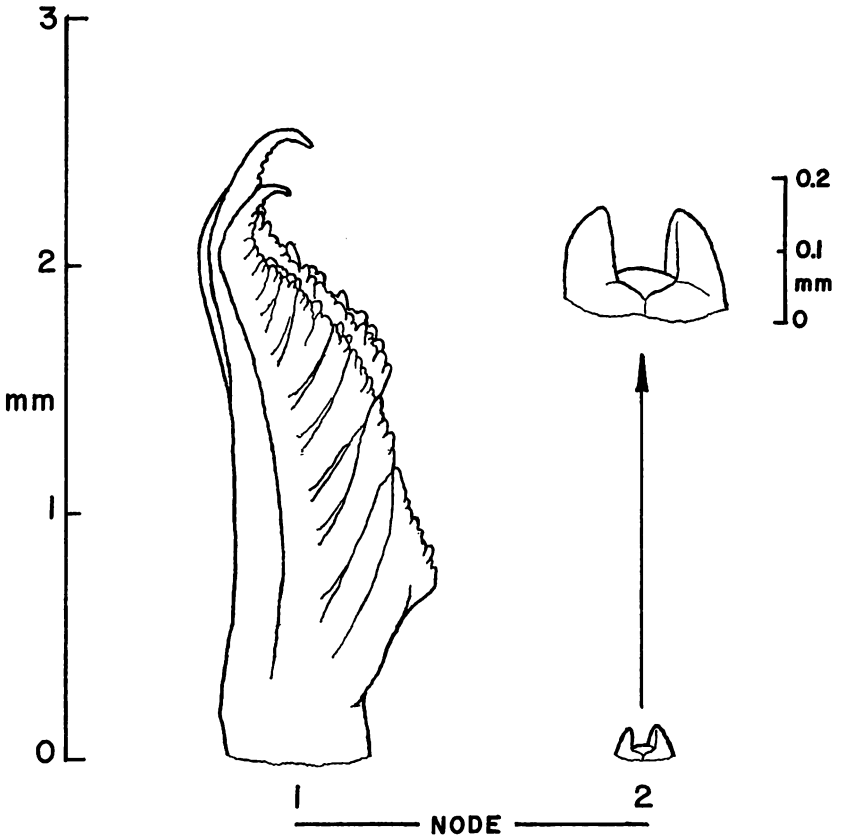

FIGURE 1. Contents of a winter bud of *A. pensylvanicum*. Collected in mid-October, this bud terminated a long shoot with seven pairs of leaves. One of the embryonic leaves at node 1 is omitted. The primordia at node 2 flank the dome-shaped apical meristem.

expanding terminal buds of long shoots (3 of 33) had five pairs of leaves (TABLE 1), but it is uncertain whether they had four pairs in the dormant bud or initiated two pairs during bud swelling.

Other species. — Expanding buds were collected in late April, a few days before bud opening, from a single tree of *Acer saccharum* Marsh. (sugar maple). This species lacks the specialized long and short shoots of red and striped maples. The buds were terminal or axillary on annual shoots 1.0 to 21.8 cm. long with 2 to 3 pairs of leaf scars. The nine buds in the sample had 8 to 10 pairs of scales and contained 3 to 6 pairs of leaves, the uppermost a pair of primordia. If the latter were initiated during bud expansion, as in red and striped maples, the dormant buds contained 2 to 5 pairs of leaves.

In *Acer platanoides* L., according to Moore (1909), the entire leaf complement of the next season's shoot is present in the winter bud. She found 3 to 4 pairs of leaves, the uppermost pair small and morphologically undifferentiated. Küster (1898) also reported three leaf pairs in the buds of this maple. The winter buds of another European species, *A. pseudoplatanus*, have 6 to 8 pairs of scales and 2 to 4 pairs of leaves (Schüepp, 1929).

GROWTH OF THE SHOOT

Red and striped maples are among the many temperate woody plants in which the principal shoots elongate until midsummer or later. Stem extension of red maple has been reported to continue until late June to late August in the northern U.S. (Kienholz, 1941; Jacobs, 1965).

Other maples belong to another large group of woody plants in which shoot elongation of plants past the juvenile stage is confined to a short period in the spring and early summer. *Acer saccharum* completes 90 to 100 percent of its stem extension in 17 to 35 days (Cook, 1941; Kienholz, 1941; Jacobs, 1965). It is widely assumed that shoot growth in this group, unlike the first, is restricted to leaves and internodes laid down in the bud. The evidence supporting this reasonable assumption is sparse, however, since few of the many investigations of stem extension in trees have paid much attention to bud contents or leaf production.

Acer pensylvanicum. — The inner bud scales separated at the end of April, when the buds were 2 to 5 cm. long, and were shed within a few weeks. The expansion of the embryonic leaves of the winter bud into the early leaves of the shoot was well under way by the time the bud opened.

The rapid growth of the early leaves continued through most of May. The blades reflexed and unfolded soon after emergence. The first pair of leaves on all measured shoots (14 shoots on 5 trees) reached 90 percent of their final length between May 28 and June 8 (FIGURE 2). A second pair of early leaves produced by a single long shoot matured 11.5

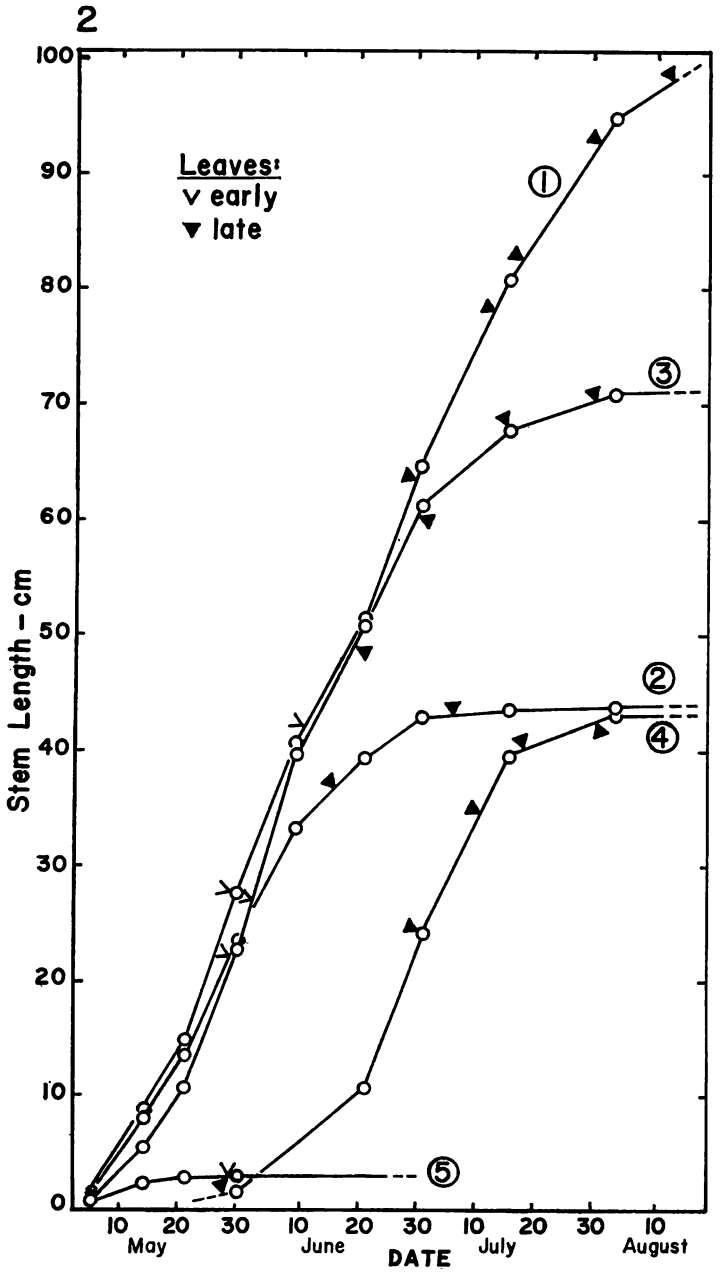

FIGURE 2. The timing of stem elongation and leaf maturation on *A. pensylvanicum* shoots. Triangles and V's indicate dates on which leaves reached 90 percent of their final length on three long shoots (1–3), one short shoot (5), and one sprout (4). Two additional pairs of leaves matured on shoot 1 before growth stopped.

days after the first pair (FIGURE 2: shoot 1). The petioles of the early leaves lagged behind the blades, reaching 90 percent of their final length an average of 11.1 days later (range 7 to 16).

The first internode, already 2 to 6 mm. long in elongating buds, grew rapidly after the shoot emerged. On both long and short shoots, it reached 90 percent of its final length in the latter half of May, 7.5 to 13 days before the pair of early leaves at its upper end. This internode elongated faster and reached much greater final lengths on long shoots: 5.2 to 14.5 cm. in the 37-shoot sample.

The expansion of the leaves at the first node, the extension of the stem below the node, and the development of a new winter bud completes the growth of non-flowering short shoots. The bud and the short internode separating it from the leaf-node developed slowly throughout the summer. The internode below the bud ultimately reached a length of 2.5 to 8 mm. The "stalked" bud, with its single pair of exposed scales, is a characteristic feature of the subdivision of *Acer* to which *A. pensylvanicum* belongs (section MACRANTHA PAX).

On long shoots, the first pair of late leaves began its most rapid growth in length in the third week of May, when the early leaves were about two-thirds of their final size. The phyllochron of the first late leaves was the longest on most shoots, averaging 18.3 days (range 16 to 21). Succeeding pairs of late leaves, all initiated during the growing season, developed at intervals of 14.1 days (range 4.5 to 20). The petioles matured after the blades, but the lag was shorter (mean 7.6 days) and more variable (range 0 to 21) than in early leaves.

The long internodes of the late leaves matured well before the corresponding leaves. They reached 90 percent of their final length 11.5 days earlier (range 6.5 to 17).

At the completion of extension growth, internode 2 was usually the longest on the shoot (FIGURE 12c). The only exceptions in the 37-shoot sample were three 2-node shoots, each with a longer basal internode, and three shoots with 5 to 9 leaf-nodes, on which internode 3 was the longest. One of the latter was the only shoot with two pairs of early leaves (FIGURE 2: shoot 1).

The final length of internodes decreased steadily from the longest internode to the shoot tip on long shoots with six or fewer leaf-nodes, but shoots with seven or more nodes had a second peak in internode length higher on the shoot, 3 to 5 internodes above the first. Most long shoots of *Populus trichocarpa* (Critchfield, 1960) and *Ginkgo biloba* (Critchfield, 1970a) also have two peaks in internode length, but the hormonal or other basis of this characteristic feature of long shoots is unknown.

Sprouts were produced by stripping branch systems of all vegetative buds in mid-April. The growth of one sprout was followed in detail (FIGURE 2: shoot 4). It appeared to originate from one of the rudimentary accessory buds which are sometimes present in the leaf axils of striped maple. The first small pair of leaves (FIGURE 6) matured in late May, when the sprout was only 1 cm. long; the second pair, much larger than

the first, did not reach 90 percent of their final length until more than a month later (FIGURE 2). By the time shoot growth stopped at the end of July, three more pairs of leaves had matured at intervals averaging 10 days (range 7.5 to 12.5). Leaf pairs 2 to 5 were like the late leaves of long shoots in all respects.

In a small defoliation experiment, the removal of the late leaves at an early stage of development drastically reduced the elongation of long-shoot stems. Three shoots on the same sprout clump were treated. Beginning in mid-May, leaf pairs 2 to 5 were cut off when they reached lengths of 1.2 to 3.0 cm. (FIGURE 3), and the cut surfaces were covered with lanolin. Stem extension, which is largely concentrated in internode 2 during late May and early June, continued almost normally for about 3 weeks. On two of the three shoots (FIGURE 3: B, C) the elongation of this internode was hardly affected by the treatment; its final length was 83 to 84 percent of the control. On the third treated shoot (A), the final length of internode 2 was only 38 percent of the control.

In early June, stem extension of all three treated shoots declined abruptly and permanently (FIGURE 3). Later-formed internodes were only 8 to 12 percent as long as corresponding internodes of the control shoot. Two shoots (B, C) began to die back from the tip in early July, after elongation had almost stopped. Shoot A subsequently produced a sixth pair of leaves, but by the end of the season all three treated shoots had died back to the first node.

Acer rubrum. — The buds opened in early May when they were 8 to 11 mm. long. The 2 to 3 pairs of early leaves on each shoot expanded rapidly through most of May. Early in development, the unfolding blade reflexed, forming an acute angle with the petiole.

The expansion of the first two leaf pairs was almost simultaneous. The phyllochron of pair 2 averaged only 1.0 days, ranging from −2.5 to + 4 days. (Negative phyllochrons were due to the maturation of pair 2 out of sequence.) If a third pair of early leaves was produced, it matured 2.5 to 5.5 days later, with a mean phyllochron of 3.4 days. All early leaves on a total of 17 shoots measured in three seasons reached 90 percent of their final length between May 25 and June 13. The petioles of the early leaves matured a mean of 10.1 days after the blades, and their variation in final length was reflected in the range of this interval: 5 to 20 days.

The internodes of the early leaves matured a week or more before the corresponding leaves. This interval could not be accurately estimated on short shoots, which rarely produce internodes more than 1 cm. long, but the longer internodes of early leaves on long shoots reached 90 percent of their final length 8.5 days before the leaves (range 5 to 13).

The growth of most short shoots of red maple was almost completed by early June (FIGURE 4: shoots 3, 6; FIGURE 9). Some short shoots later produced a pair of small transitional or late leaves, but their expansion was not accompanied by appreciable stem elongation. The new

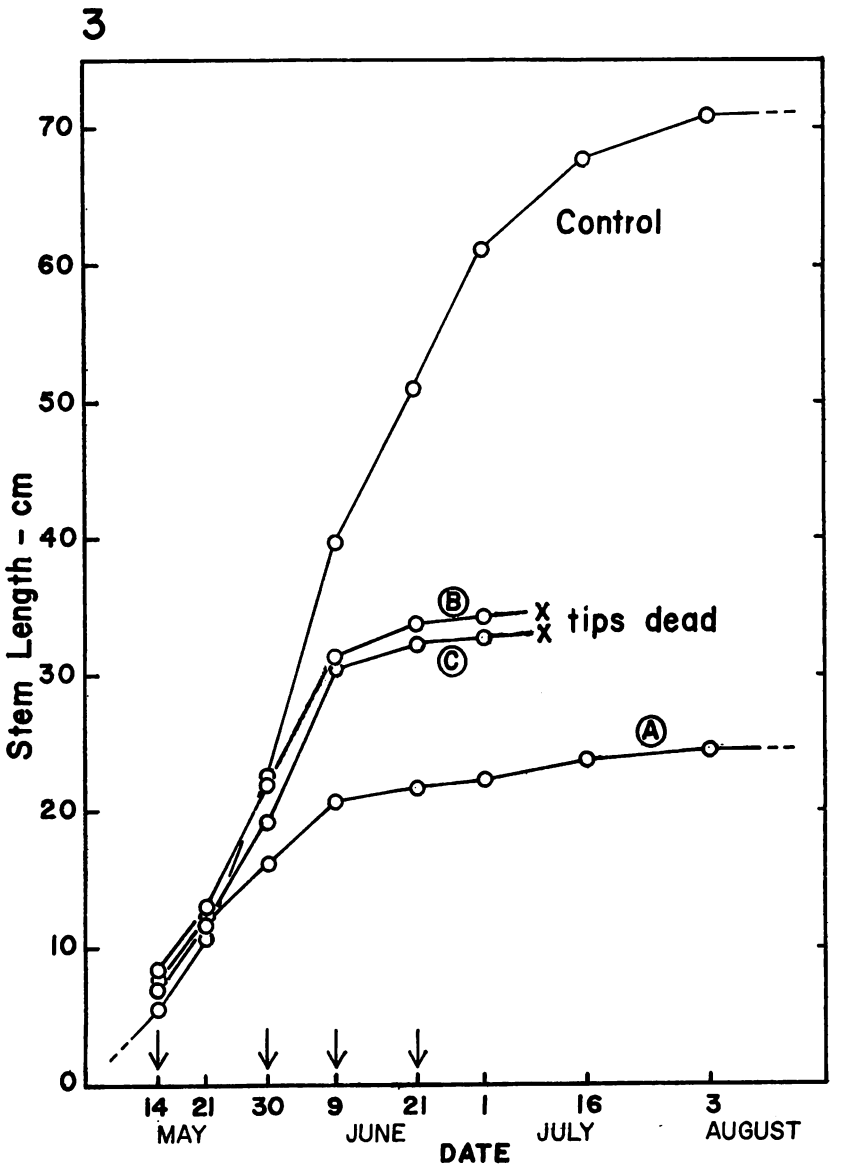

FIGURE 3. The effect of late-leaf removal on stem extension in *A. pensylvanicum*. A pair of developing late leaves was removed from each treated shoot (A–C) on dates indicated by arrows. Control is shoot 3 of FIGURE 2.

terminal buds of the short shoots developed slowly, reaching their final size in August.

The production of a second set of leaves on long shoots began after

a distinct hiatus in the continuity of leaf production. At this stage the early leaves and their internodes had nearly completed their growth, but the first pair of late leaves was only a fraction of its final size and its internode was still elongating (FIGURE 8). On the long shoots measured in 1957–58, the phyllochron of total length for the first pair of late leaves averaged 12.9 days (range 7.5 to 19); in 1959 the phyllochron of blade length for this pair averaged 8.8 days (FIGURE 4). On all shoots, this interval was 5 to 16 days longer than the preceding phyllochron and 1 to 9 days longer than the next.

Successive pairs of late leaves matured at intervals averaging 6.9 days (range 2 to 16). Their petioles tended to be relatively shorter than those of early leaves, and the interval between blade and petiole maturation was slightly less (mean 8.2 days, range 2 to 16).

The interval between internode and leaf maturation was also somewhat shortened on the late-leaf part of the shoot, and tended to decrease toward the shoot tip. Internodes matured an average of 5.7 days before the corresponding late leaves (range 0 to 12).

In their early stages the blades of late leaves are red-pigmented and strongly reflexed. This gives the crowns of actively growing red maples a characteristic appearance in early summer, when late-leaf production is at its height. Each of the principal branch systems, comprising a perennial long shoot covered with short shoots of various ages, terminates in a distinct reddish cone of developing late leaves.

When stem extension is completed, the internode separating the early and late leaves is usually the longest on the shoot. Most shoots from terminal buds have three pairs of early leaves, and internode 4 is usually the longest. On long shoots maturing from axillary buds, which more commonly have only two early-leaf nodes, internode 3 is usually the longest. In the 48-shoot sample, internode 4 was longest on 23 of 32 shoots from terminal buds, and internode 3 was longest on 12 of 16 shoots from axillary buds. Most of the exceptions were shoots with two peaks of internode length, on which internode 3 or 4 was the first peak and the second peak was the longest internode on the shoot.

As in striped maple, the incidence of two peaks in the final length of internodes along the shoot depends partly on number of internodes. In red maple it also varies from tree to tree, with two-peaked shoots uncommon or absent on some trees. In the 48-shoot sample, few (3 of 29) shoots with 4 to 8 internodes had two peaks, but 9 of 17 shoots with more than 8 internodes had two peaks 2 to 5 internodes apart (mean 3.5).

Other species. — The timing of leaf expansion was measured on five shoots of a single sugar maple growing at the Harvard Forest. The shoots developed from terminal buds of shoots that had produced 2 to 5 pairs of leaves the previous year. The buds opened in late April, and 2 to 4 pairs of leaves reached 90 percent of their final length during the last half of May at mean phyllochrons of 1.0, 1.2, and 5.8 days. One

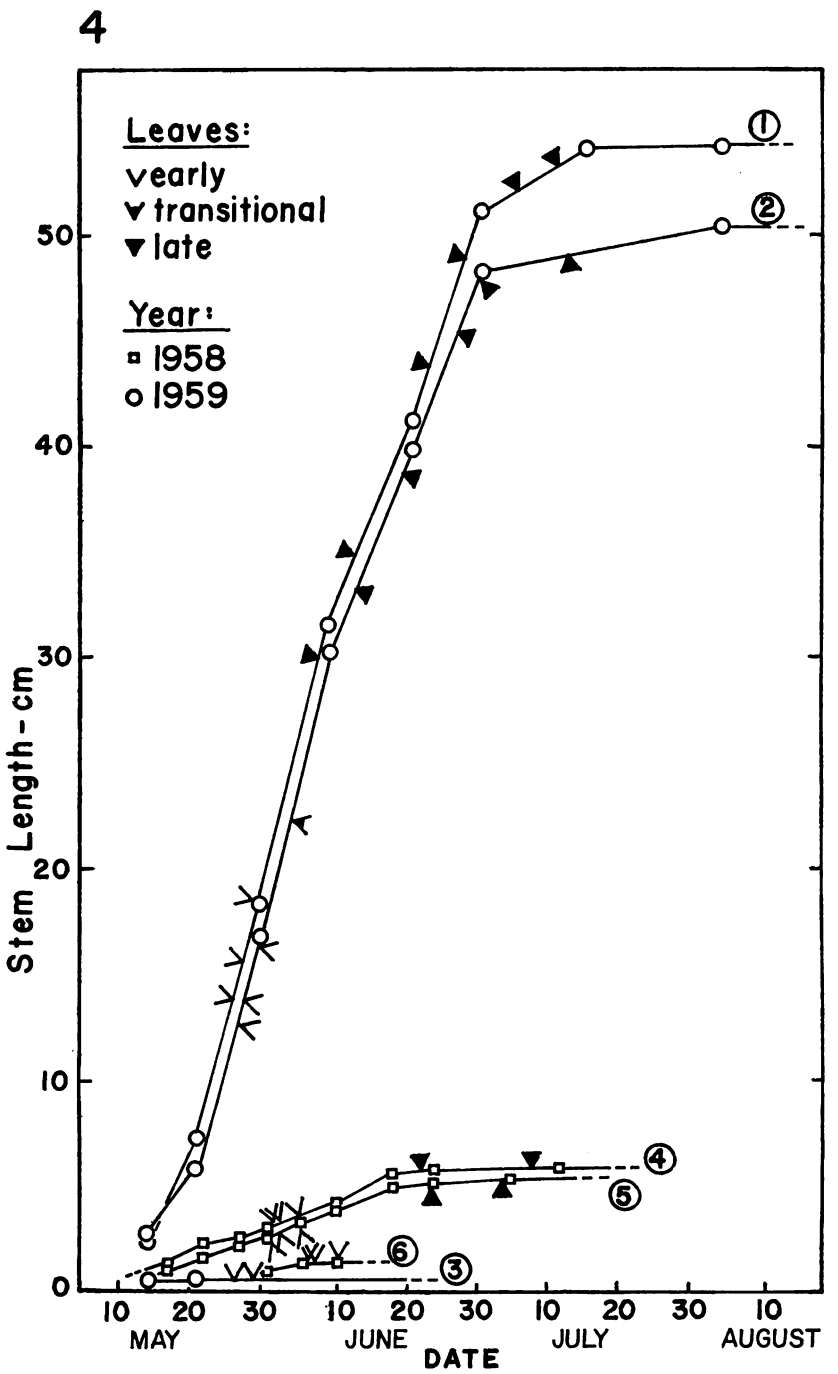

FIGURE 4. The timing of stem elongation and leaf maturation on *A. rubrum*

shoot produced a fifth and smaller pair of leaves which matured about 2 weeks after pair 4.

The development of a single heterophyllous long shoot of *A. pseudoplatanus* was described in detail by Schüepp (1929). The rapid expansion of the first three pairs of leaves after the bud opened was followed by a long pause before the second set of leaves began to mature. Phyllochrons of blade length (estimated from Schüepp's *Figure 4*) were 1 and 3.5 days for pairs 2 and 3, but pair 4 (the first late leaves, in the terminology used here) did not mature until 20.5 days later. Blades of the next six pairs of leaves matured at intervals of 7 to 12.5 days (mean 8.7). The petioles of all leaves matured 14 to 27 days after the blades. Stem elongation was continuous, and by the time it ceased in early August the shoot had 14 pairs of leaves. Its development differed from that of a comparable red maple shoot primarily in the longer interval between blade and petiole maturation, and the much longer phyllochron separating the early and late leaves.

VARIATION IN LEAF FORM

The early leaves of red and striped maples, developing from embryonic leaves in the winter bud, predominate in the crowns of all but the youngest trees. From the data of Wilson (1966) on red maple, it is estimated that they make up about 83 percent of the photosynthetic area of the crown of 5-year-old trees, and this proportion increases to 97 percent in trees 60 years old or more. The early leaves are usually the only leaves associated with the reproductive structures of maples. These are the leaves that have been utilized in the classification of the maples, since most plant collections sample parts of the shoot system bearing flowers and fruits. In taxonomic descriptions the early leaves are sometimes referred to as "typical," "ordinary," or "adult" leaves.

Leaves that are not preformed in buds are produced throughout the life of red and striped maple trees, although their relative number diminishes with age. In this category are such diverse types as the small leaves of first-year seedlings, the large leaves of vigorous sprouts, and the late leaves of long shoots. Also included are leaves of the lammas and disguised lammas shoots [2] regularly produced by young trees of *Acer platanoides*, *A. pseudoplatanus*, and other maples (Späth, 1912; Burger,

[2] Lammas shoots originate from partly developed buds during the summer, after the spring flush of growth is completed. Disguised lammas shoots ("Verkappter Johannistriebe": Späth, 1912) of maples differ in that the leaves whose enlarged bases function as bud scales also have expanded blades. These two intergrading shoot types may be most common in species that do not routinely produce long and short shoots; I have not encountered them in red or striped maple.

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shoots. Triangles and V's indicate dates on which leaves (1958) or blades (1959) reached 90 percent of final length. Shoots 3 and 6 are short shoots, the others long shoots. Three additional pairs of leaves on shoots 1 and 2 were too badly damaged by insects for growth measurements.

1926). All of these kinds of leaves develop epigenetically, and this common mode of ontogeny appears to be responsible for the tendency of leaves on these otherwise dissimilar kinds of shoots to resemble each other in shape.

In species with lobed leaves, including red and striped maples and many others, the lateral lobes of epigenetic leaves tend to be displaced downward on the blade, to project outward from the midrib at a greater angle, and often to be reduced in size. These leaves, borne mostly on "sterile" shoots, are poorly represented in herbaria. In taxonomic accounts they are sometimes referred to as "atypical," "extraordinary," or "juvenile" leaves.

Acer pensylvanicum. — The early leaves of striped maple are among the largest in the genus. They are bigger than any of the late leaves on the same shoot, but the two kinds of leaves overlap in size on different shoots. In a sample of both shoot types, the blade area of early leaves was 87–388 cm.^{2}; that of late leaves 14–179 cm.^{2} On the most vigorous long shoots (5 to 9 leaf-nodes) the biggest late leaves were 46 to 64 percent as large as the early leaves, but on long shoots with only two nodes the late leaves were much smaller (9 to 35 percent).

The two kinds of leaves also differ in shape. The more uniform early leaves terminate in three nearly equal lobes (FIGURE 5). The principal lateral lobes of the late leaves are shorter than the middle lobe and displaced basally (FIGURE 12a, e). The veins forming the axes of the lateral lobes were 79 to 98 percent as long as the midrib in the early leaves of the sampled shoots, 49 to 76 percent in the late leaves. The middle lobe of early leaves was 35 to 45 percent of the blade length; that of late leaves was 49 to 62 percent.

The lateral lobes are most conspicuously reduced at the first late-leaf node (FIGURE 5), and sometimes are no larger than the marginal teeth. Succeeding pairs of late leaves nearly always have reduced but definable lobes. The first pair of late leaves also tends to be narrower than the others, with relatively shorter petioles.

The first leaves of sprouts are small, unlobed, and coarsely toothed, but above the first node the leaves are indistinguishable from late leaves of long shoots in size and shape (FIGURE 6). This sequence in leaf shape is also followed on elongate sylleptic shoots — branches that develop directly from axillary meristems during the same season as the parent axis (Späth, 1912).

The first, and often the only, pair of leaves on first-year seedlings of striped maple are serrate but not lobed. Their similarity in shape to the unlobed leaves of older trees was pointed out by Deane (1896). They are much smaller, however, a few measured seedling leaves having blade areas of only 2.6–6.7 cm.^{2}

Acer rubrum. — Although red maple has an extensive infraspecific nomenclature based primarily on its variability in leaf shape, the differences

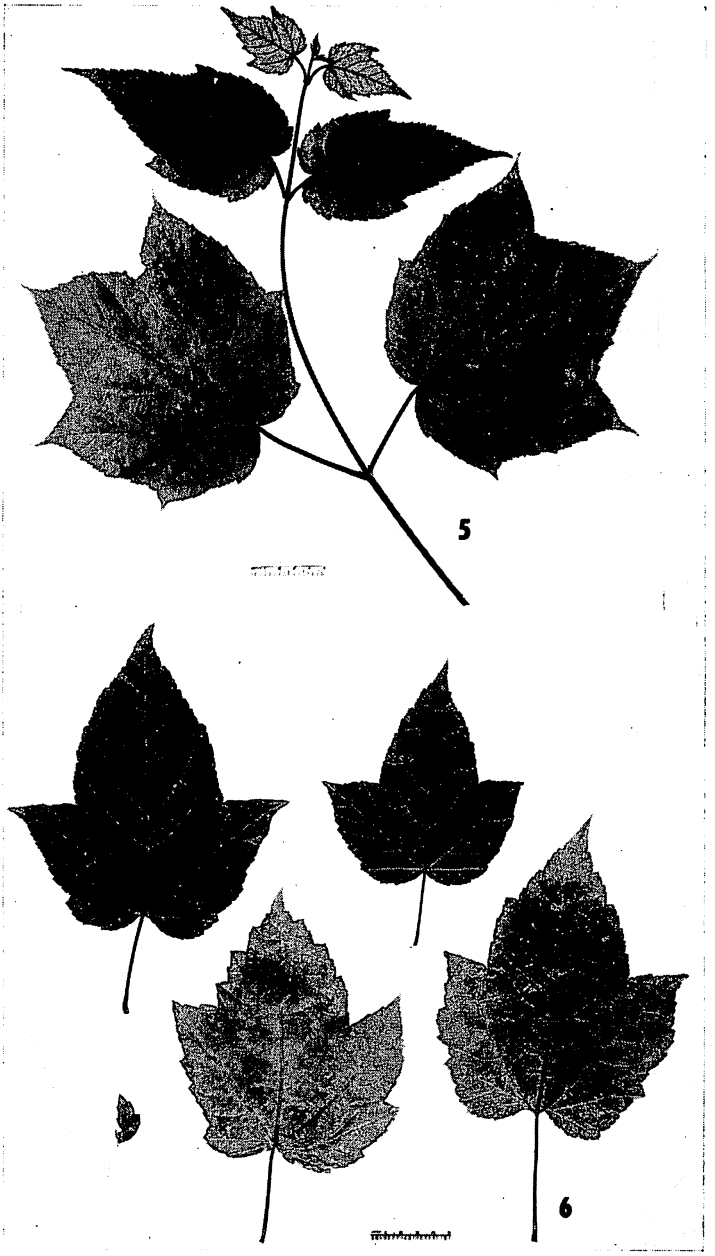

FIGURE 5. A developing long shoot of *A. pensylvanicum*. Collected at the Harvard Forest in early June, this shoot has one pair of nearly mature early leaves and two unfolded pairs of late leaves.

FIGURE 6. Mature leaves of a sprout of *A. pensylvanicum* (1 leaf per node). Except for leaf at node 1 (lower left), they are indistinguishable from late leaves of long shoots. Growth of this sprout is shown in FIGURE 2 (shoot 4).

between early and late leaves of the same shoot are not as pronounced as in striped maple, and transitions are common. The early leaves, like those of striped maple, generally have larger blades (Wilson, 1966).

Differences in leaf shape also parallel those of striped maple (FIGURE 12a, e). Early-leaf blades have three subequal lobes (FIGURES 8–10), in contrast to the elongate median lobe of late leaves (FIGURE 10). In a sample of long shoots, the midlobe was 46 to 56 percent of the blade length in early leaves, 60 to 70 percent in late leaves. The main lateral veins of the first two pairs of early leaves were 82 to 91 percent as long as the blade, but the third pair, which often has narrower blades (FIGURES 8, 10), sometimes fell within the range of the late leaves (65 to 79 percent).

The basally displaced and shortened lateral lobes of the late leaves tend to project outward from the midrib. The angle formed by their axes was 95–117°, compared to 73–86° in early leaves. This feature provided a consistent distinction between the two kinds of leaves in this species but not in striped maple.

The relative length of petioles tends to decrease from node to node, stabilizing somewhat in the late-leaf series (FIGURES 10, 12b). The petioles of early leaves were 60 to 114 percent as long as the blades; late-leaf petioles were 30 to 80 percent. As Wilson (1966) has pointed out, variations along the shoot in petiole length, together with changes in blade size and internode length, tend to minimize the mutual shading of leaves.

The leaves of red maple sprouts and sylleptic shoots resemble the late leaves of long shoots in their elongate median lobes, shortened and projecting lateral lobes, and short petioles (Jackson, 1899: pp. 99, 100, *Figure 27*). These tendencies reach their extreme expression in the leaves of first-year seedlings. The lateral lobes of seedling leaves are usually much smaller than the elongate median lobe (FIGURE 7; Jackson's *Figure 28*), and are sometimes reduced to teeth (Brayshaw, 1959: *photo.* on p. 28).

Other species. — This survey was largely restricted to maples with medium-sized or small leaves. Herbarium specimens of species with large simple leaves (e.g. *A. macrophyllum* Pursh) or compound leaves (sections TRIFOLIATA Pax and NEGUNDO (Boehm.) Maxim.) usually include only short stem segments and are not suitable for observations of shoot organization. The available specimens of first-year seedlings were supplemented by published accounts (Brayshaw, 1959; Elwes and Henry, 1908; Kondrat'eva-Melville, 1965). *Acer* has not been comprehensively monographed in this century, and the partial classification of Rehder (1940), slightly modified by Brizicky (1963), is followed here.

Despite the limitations of herbarium specimens for observations of shoot organization, it was evident from this survey that the maples can be conveniently grouped into four categories based on shoot growth and heterophylly:

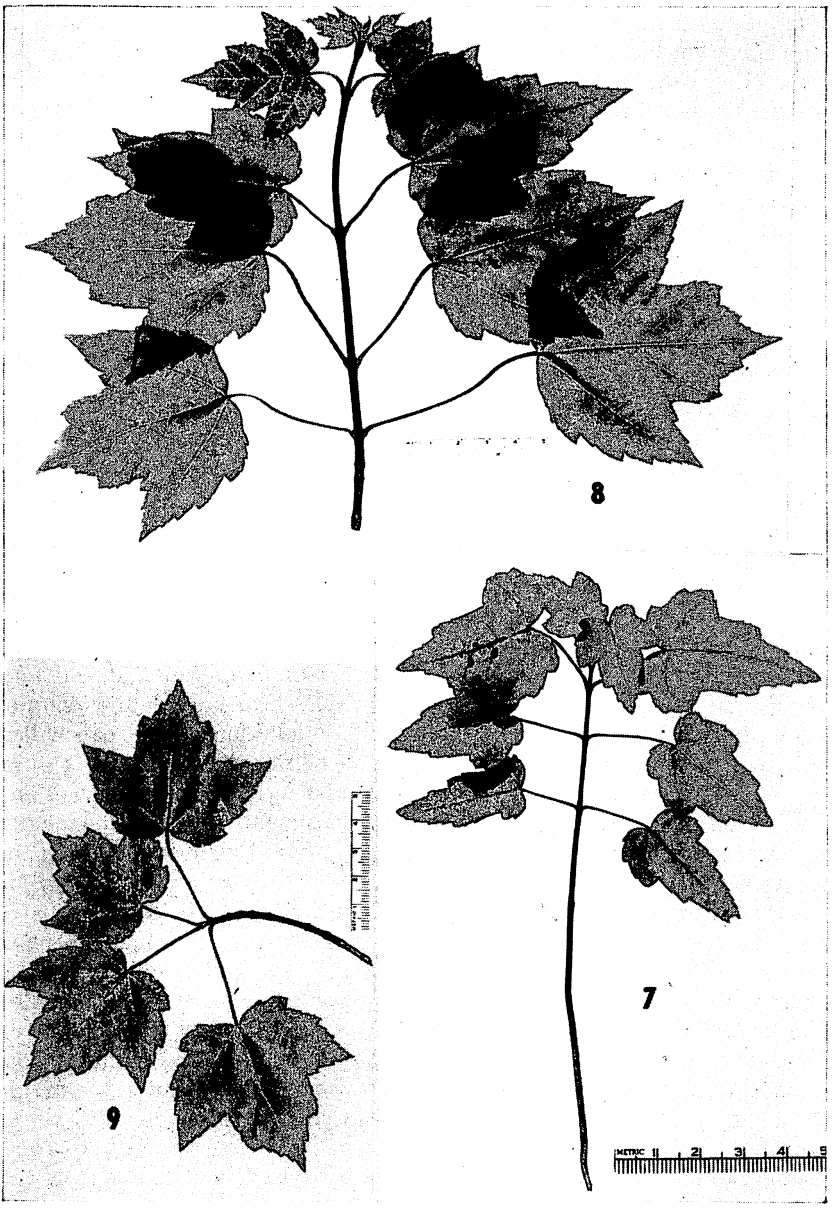

FIGURE 7. First-year seedling of *A. rubrum* collected at Harvard Forest in late August.

FIGURES 8, 9. Developing long and short shoots of *A. rubrum* collected on same date (late May) from same tree. On the long shoot (FIGURE 8) three pairs of early leaves are nearly mature and two pairs of late leaves have unfolded. The growth of the short shoot (FIGURE 9), with two pairs of early leaves, is nearly complete.

(1) Species in this category, which possibly includes the majority in the genus, are like red or striped maple in the organization of the shoot system and the regular production of two kinds of leaves. Included here are the other species in sect. MACRANTHA, all closely similar to striped maple. More widespread in the genus is the red maple pattern: less sharply distinct long and short shoots, more than one early-leaf node on most shoots, and less abrupt changes in leaf shape on long shoots. This pattern is represented in sections CAMPESTRIA Pax, ARGUTA Rehd., and ACER (*Spicata* Pax). It is also present in *A. pycnanthum* K. Koch, a Japanese maple in sect. RUBRA which closely resembles red maple in most of its characteristics. Members of group (1) are considered in more detail below.

(2) This group has the same kind of shoot organization as (1), but epigenetic leaves of long and other types of shoots do not differ as consistently in size and shape from leaves preformed in buds. Included here are maples in sections RUBRA (*A. saccharinum* L.) and ACER (*A. spicatum* Lam., *A. caudatum* Wall.).

(3) In this group the shoot system is not organized into long and short shoots, and the elongate shoots of the crown are known or inferred to be mostly preformed in the bud. But leaves that develop epigenetically, when they are produced at all, differ in form and size from preformed leaves. All of the species in section PLATANOIDEA Pax are included here.

Representative of this group are *Acer platanoides* and *A. miyabei* Maxim. Many elongate shoots of these maples bear only 3 to 4 pairs of leaves, but the most vigorous produce 1 to 3 additional pairs of smaller, differently shaped leaves crowded at the shoot tip. On such shoots of *A. miyabei* there was a distinct break in size and form between nodes 4 and 5 (FIGURE 12d, e). The upper leaves were smaller, with an elongate median lobe and reduced lateral lobes projecting at right angles from the midrib.

Acer platanoides shows the same tendencies in leaves at the tips of elongate shoots in the crown, on sprouts, on lammas and disguised lammas shoots of young trees, and on the weak sylleptic shoots that often develop at the upper leaf-node of flowering shoots in this and other maples. The first seedling leaves are usually unlobed or obscurely lobed, but on many first-year seedlings they are followed by a disguised lammas shoot (Kondrat'eva-Melville, 1965: *Figure 3*), with small leaves which are similar in shape to epigenetic leaves produced at later stages of development.

(4) The shoot system of this group is organized like that of (3), but the differences in size and shape between preformed and other leaves are less consistent. Sections SACCHARINA Pax (including *A. saccharum*) and PALMATA Pax are in this category. The leaves of individual sugar maples are fairly uniform in shape, and even sprout leaves are not always markedly different. The first pair of leaves of *A. saccharum* seedlings are unlobed or nearly so, but additional leaves produced during the first season may be shaped much like leaves produced at later stages.

Of the many maples in category (1), the largest aggregation of related species is sect. MACRANTHA, which includes 15 to 20 Asian species in addition to *Acer pensylvanicum*. Their classification is based almost entirely on differences in size and shape of early leaves; the reproductive structures are rather uniform and do not provide many useful distinctions (Rehder, 1933).

The Asian species are nearly identical to striped maple in the organization of their shoot systems. Throughout the section, the short shoots have a single pair of early leaves which vary in shape from 3- or 5-lobed to unlobed in different species. The long shoots bear, in addition, one or more pairs of smaller late leaves, and internode 2 is the longest on most shoots (FIGURE 12c). In species with lobed leaves, the differences in shape between the two kinds of leaves are much like those in striped maple: the late leaves have relatively elongate median lobes and shortened, basally displaced lateral lobes (FIGURE 11b: *A. rufinerve* Sieb. & Zucc.; FIGURE 12a, e: *A. tegmentosum* Maxim., *A. capillipes* Maxim.). In some species the angle formed by the lateral veins is consistently larger in late leaves (e.g., *A. grosseri* Pax: 65–82° in early leaves *vs.* 92–106° in late leaves). The trend toward reduced lobing is sometimes reversed in species with unlobed or obscurely lobed early leaves, and the late leaves may have small lateral lobes at the base of the blade. Throughout this section, the marginal serrations of late leaves tend to be fewer, coarser, and blunter.

Apart from leaf shape, the other maples in section MACRANTHA differ from striped maple primarily in their smaller vegetative structures. Only *A. tegmentosum* approaches it in leaf, internode, and bud size. In the other species, both kinds of leaves are smaller, the vegetative short shoots average 1 to 1.5 cm. and rarely exceed 3 cm. in length, and the longest internodes of most long shoots are only 8 to 12 cm.

Also included in group (1) are most or all of the maples in sect. CAMPESTRIA Pax. (Possible exceptions are *A. opalus* Mill. and *A. hyrcanum* Fisch. & Mey., for which adequate material was not available). The organization of the shoot system is much like that of red maple, with 1 to 3 pairs of early leaves on all shoots originating from buds. Long shoots are regularly produced, and heterophylly is pronounced (FIGURE 11c, e, f), but the differences between early and late leaves vary greatly between species. *Acer campestre* L., like many other maples, has late leaves with short petioles (FIGURE 12b) and basally displaced lateral lobes (12e) which project from the midrib at large angles (12d). Unlike the late leaves of most other maples, however, they often have more lobes and blunt teeth than the early leaves. This tendency is more conspicuous in *A. monspessulanum* L., in which the more numerous lobes and teeth of the late leaves are the most reliable distinction between the two kinds of leaves (FIGURE 11e). The opposite is true of *A. orientale*, a Mediterranean species with small leathery leaves. The lateral lobes of its late leaves are much reduced in size (FIGURE 11f), and the first pair on long shoots may lack lobes or teeth.

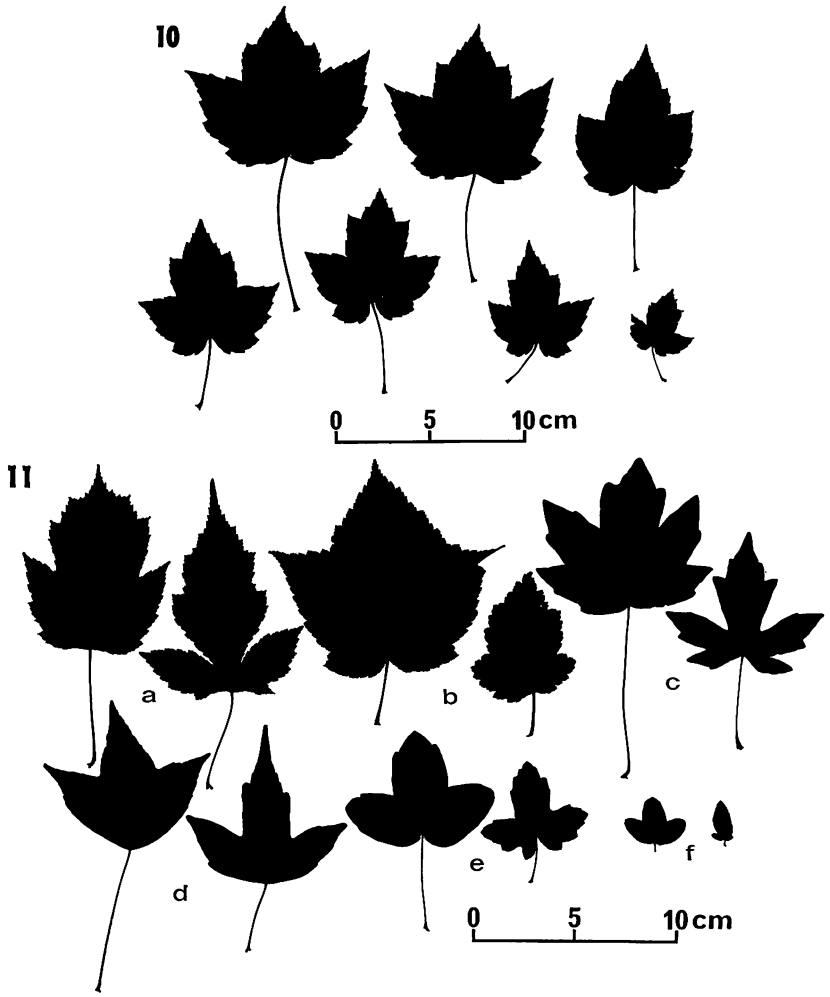

FIGURE 10. Mature leaves of a long shoot of *A. rubrum* (one leaf per node). Early leaves in upper row, node 1 at left.

FIGURE 11. Early and late leaves of *Acer* species: a. *A. tataricum* (nodes 2, 5), b. *A. rufinerve* (1, 3), c. *A. campestre* var. *leiocarpum* (2, 5), d. *A. buergerianum* (2, 7), e. *A. monspessulanum* (1, 8), f. *A. orientale* (1, 4). Leaves in a, c, and d from shoots illustrated in FIGURE 12.

The species in section ARGUTA also conform closely to the red maple pattern of shoot organization. They have a maximum of two or three early leaves per shoot, depending on the species. The expression of heterophylly in *A. barbinerve* Maxim. is typical of this section and similar to many other maples. Its late leaves have shorter petioles (FIGURE 12b) and smaller, basally displaced, projecting lateral lobes (FIGURE 12a, d, e).

Acer section ACER (*Spicata*), the most heterogeneous of Rehder's sec-

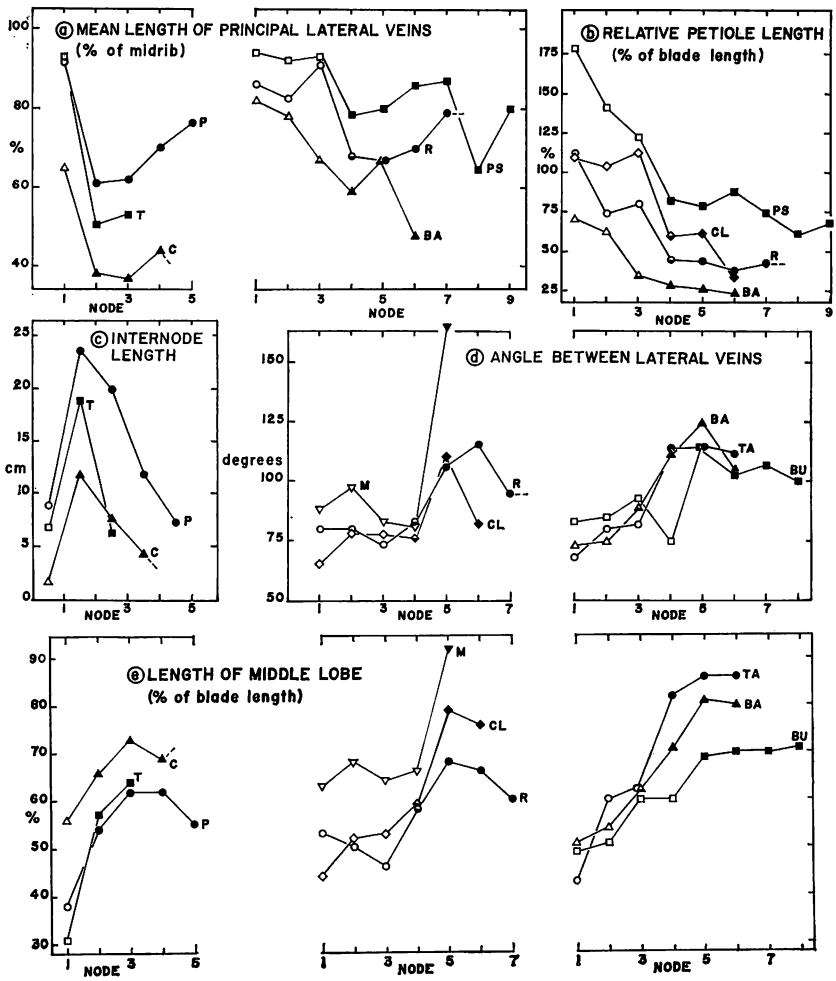

FIGURE 12. Variation in leaves and internodes on long shoots of *Acer* species: *A. barbinerve* (BA), *A. buergerianum* (BU), *A. campestre* var. *leiocarpum* (CL), *A. capillipes* (C), *A. miyabei* (M), *A. pensylvanicum* (P), *A. pseudoplatanus* (PS; data from Schüepp, 1929), *A. rubrum* (R), *A. tataricum* (TA), and *A. tegmentosum* (T). Transitional and late leaves shown by half-black and all-black symbols. Uppermost leaf-nodes (not shown) were immature in *A. capillipes*, damaged by insects in *A. rubrum*.

tions, includes several taxa that conform in varying degrees to the red maple pattern: *A. pseudoplatanus*, *A. buergerianum* Miq., and the shrubby species-complex made up of *A. tataricum* L. and *A. ginnala* Maxim. Of these, *A. pseudoplatanus* appears to be least regular in the production of long shoots; extension growth of young trees is commonly prolonged by lammas and disguised lammas shoots (Späth, 1912; Burger, 1926). Long

shoots are most abundantly produced by the *A. tataricum-A. ginnala* complex, and this abundance is a factor in their shrubby habit.

The expression of heterophylly in these members of section SPICATA follows the familiar maple pattern. Pearsall and Hanby (1926) observed that *A. pseudoplatanus* leaves produced during the summer were smaller and more dissected, with reduced basal lobes. They associated these morphological differences with increased water stresses. In the same species, the reduced lateral lobes of a long-shoot late leaf and a leaf of a sylleptic shoot were illustrated by Schüepp (1929: *Figure 16*). His data on a single long shoot shows a pronounced break between nodes 3 and 4 in the relative length of lateral lobes and petioles (FIGURE 12a, b). Schüepp's comparative observations of preformed and epigenetic leaf ontogeny make it clear that the lateral lobes of the preformed leaves appear earlier and are more nearly equal in size to the median lobe at subsequent stages of development. First-year seedling leaves of *A. pseudoplatanus* are either unlobed or have reduced lateral lobes (Elwes & Henry, 1908: p. 642).

Heterophylly is more pronounced in *A. buergerianum* and *A. tataricum* (FIGURE 11a, d). Both have late leaves with elongate median lobes and projecting lateral lobes (FIGURE 12d, e). One feature of *Acer tataricum* and its close relatives is unusual in this genus; the leaves at the first node are smaller than succeeding leaves, often unlobed, and occasionally almost devoid of serrations (Jackson, 1899: *Figure 33*).

DISCUSSION

The genus *Acer* is far more diverse than most woody genera in the organization of the shoot system and in the ways in which extension growth is prolonged after the expansion of the leaves and internodes laid down in the winter bud. In the many maples with some variation of long- and short-shoot organization, extension growth is ordinarily prolonged by the continued elongation of the long shoots after the spring flush of growth. Other maples, such as *A. saccharum* and to a large extent the species of section PLATANOIDEA, are much closer to the *Quercus-Fagus* type of shoot development. In these woody plants elongation stops, at least temporarily, after the expansion of the embryonic shoot in the winter bud. Prolonged extension growth of young trees tends to be discontinuous, through the repeated formation of lammas and (in maples) disguised lammas shoots (Späth, 1912).

The long shoots of red and striped maples, and by inference other maples with specialized shoots, originate in much the same way as those of *Populus trichocarpa* (Critchfield, 1960) and other woody plants of this type. Stem elongation is negligible if leaf production is confined to the relatively well-developed leaves of the winter bud. Only if additional leaves expand does appreciable elongation occur. The first of these added leaves may be present as primordia in the winter bud; in striped maple

the second set of leaves on long shoots sometimes consists solely of a single pair of late leaves originating from such primordia. More commonly, most of the leaves produced during the second phase of long-shoot development are initiated and expand during the same season.

In some woody plants with long and short shoots, this causal relationship between the production of a second set of leaves by some shoots and the elongation of those shoots appears to be mediated by auxin or auxin precursors produced by the developing leaves. The evidence for this interpretation, including the relative auxin production of long and short shoots in *Ginkgo biloba* (Gunckel & Thimann, 1949) and *Cercidiphyllum japonicum* (Titman & Wetmore, 1955), has been reviewed elsewhere (Critchfield, 1960). The work of Zimmermann (1936) on the production of auxin by *Acer pseudoplatanus* shoots supports the extension of this interpretation to maples with specialized shoot systems. Zimmermann did not discriminate between long and short shoots, but his data and photographs show that long shoots with about eight leaf-nodes, sampled in late June, had much higher levels of auxin than any shoots sampled earlier in the season. Zimmermann also found a fairly close relationship between internode length and auxin content in developing long shoots of this maple.

The stems of maple short shoots usually exhibit a limited but measurable amount of elongation, unlike those of some woody plants with specialized shoots. *Ginkgo biloba*, for example, produces short shoots only 1 to 2 mm. long. The leaf complement of red maple short shoots ranges from one to three pairs, and the presence of each additional pair is associated with small but consistent increases in stem length. These increments of stem growth are of a different order of magnitude, however, than those associated with late-leaf production. This is best illustrated by striped maple, in which the distinction between short and long shoots is reduced to the simplest possible terms. If a shoot produces only a single leaf-node it elongates an average of only 2 cm., despite the large size of the leaves. But the expansion of a single pair of late leaves, although they are only 1/10 to 1/3 the size of the early leaves, produces a stem averaging nine times as long. This great discrepancy between leaf size and stem length — 30- to 90-fold — illustrates one of the principal questions concerning plants with specialized shoot systems: why the elongation of short-shoot internodes is either limited (striped maple) or nonexistent (*Ginkgo*).

Red and striped maples, despite their similarity in shoot organization, differ greatly in potential leaf production per shoot. The greater potential of red maple is due partly to the nearly synchronous expansion of 2 to 3 pairs of preformed leaves, but a more important factor is its short late-leaf phyllochron — less than half of the 2-week interval of striped maple growing in the same environment. At an average rate of leaf development, a long shoot of red maple in the Harvard Forest could produce 17 leaf pairs by mid-September. An average shoot of striped maple could produce only eight pairs in the same period. However, because striped maple has larger leaves and longer internodes, it is estimated that its 8-

node shoot would exceed the 17-node shoot of red maple by at least 50 percent in both stem length and photosynthetic area.

In addition to the foliage leaves, maple shoots periodically produce another type of appendage, the bud scales. From comparisons of foliage-leaf and bud-scale ontogeny in *Acer platanoides* and other woody plants Goebel (1905) concluded ". . . the path of development is originally the same for all leaves, but in many leaves at an earlier or later period the development may proceed along different paths." His interpretation is equally applicable to the early divergence in development of preformed and epigenetic leaves of *Acer*, as Schüepp (1929) showed in *A. pseudoplatanus*.

Of the ontogenetic alternatives represented by early and late leaves, the development of leaves at the tip of a growing shoot is much more general. Leaves preformed in winter buds are produced only during the post-seedling growth of perennial plants. They develop in the very different microenvironment of the enclosed bud, and their ontogeny is sharply discontinuous, unlike that of epigenetic leaves. The first phase is a prolonged, well-defined period of what Sachs (1893) called "morphologische Ausgestaltung" (putting-into-shape), during which the form of the leaf is determined. The shape of the first leaves in the winter buds of *Acer palmatum* Thunb. is fully blocked out by the time they are 0.5 mm. long, and undergoes little change during later development (Meijknecht, 1955). The embryonic phase of preformed leaves, as Sachs pointed out, is separated from their expansion phase by a sharp boundary imposed by winter dormancy.

The degree of heterophylly associated with these two developmental patterns varies greatly between species of *Acer*, although the same morphological trends are present throughout the genus. *Acer saccharinum*, a close relative of red maple, regularly produces long shoots with late leaves that differ only subtly from the early leaves at the base of the same shoot. In most maples, however, the two kinds of leaves are distinct in size and shape, and maples with specialized shoot systems have both kinds present in the crowns of most trees.

The prevalence of this type of heterophylly in *Acer* has caused fewer taxonomic difficulties than might be expected. The main reason for this appears to be the sampling bias mentioned earlier. The great majority of herbarium specimens are flowering or fruiting shoots associated with only preformed leaves; foliage of elongate vegetative axes is under-represented or absent. Some taxonomic descriptions and keys are based explicitly on the leaves of fertile shoots only. Despite their limitations, they are probably more useful than those diffuse descriptions which attempt to encompass the range of nongenetic variation in leaf characters without recognizing its nature.

This failure to recognize and deal with heterophylly in woody plants has imposed unnecessary restrictions on the scope and usefulness of classification. Even in the context of the herbarium, it is often difficult or impossible to identify the occasional vegetative specimen lacking early

leaves, usually a segment of a long shoot or sprout. Yet the characteristics of other leaf types, and the organization of the shoot system itself, could be of considerable intrinsic value in classification. One of the most distinctive and unifying features of section MACRANTHA, for example, is the presence of a single pair of leaves on all short shoots. The regular production of heterophyllous long shoots by *Acer campestre* argues against its proposed transfer to section PLATANOIDEA (Brizicky, 1963), which lacks this type of shoot organization. Apart from this taxonomic potential, the recognition and exploitation of heterophylly and shoot characteristics in the classification of such woody genera as *Acer* would increase the value of taxonomic information in such related fields as ecology and paleobotany, which necessarily deal with whole-plant variability.

LITERATURE CITED

BOND, T. E. T. Studies in the vegetative growth and anatomy of the tea plant (*Camellia thea* Link.) with special reference to the phloem II. Further analysis of flushing behaviour. Ann. Bot. II. **9**: 183–216. 1945.

BRAYSHAW, T. C. Tree seedlings of eastern Canada. Canada Forestry Branch Bull. 122. 38 pp. 1959.

BRIZICKY, G. K. The genera of Sapindales in the southeastern United States. Jour. Arnold Arb. **44**: 462–501. 1963.

BURGER, H. Untersuchungen über das Höhenwachstum verschiedener Holzarten. Mitt. Schweiz. Centralanst. Forstl. Versuchswesen. **14**: 29–158. 1926.

CLAUSEN, J. J., & T. T. KOZLOWSKI. Heterophyllous shoots in *Betula papyrifera*. Nature **205**: 1030–31. 1965.

COOK, D. B. The period of growth in some northeastern trees. Jour. Forest. **39**: 956–959. 1941.

CRITCHFIELD, W. B. Leaf dimorphism in *Populus trichocarpa*. Am. Jour. Bot. **47**: 699–711. 1960.

———. Shoot growth and heterophylly in *Ginkgo biloba*. Bot. Gaz. **131**: 150–162. 1970a.

———. Shoot growth and leaf dimorphism in Boston ivy (*Parthenocissus tricuspidata*). Am. Jour. Bot. **57**: 535–542. 1970b.

DEANE, W. Notes from my herbarium V. My seedling collection. Bot. Gaz. **21**: 210–214. 1896.

ELWES, H. J., & A. HENRY. The trees of Great Britain and Ireland, vol. 3. Privately printed, Edinburgh. 1908.

GOEBEL, K. Organography of plants, Parts I & II. English ed. Clarendon Press, Oxford. 270 & 707 pp. 1900 & 1905.

GUNCKEL, J. E., & K. V. THIMANN. Studies of development in long shoots and short shoots of *Ginkgo biloba* L. III. Auxin production in shoot growth. Am. Jour. Bot. **36**: 145–151. 1949.

JACKSON, R. T. Localized stages in development in plants and animals. Mem. Boston Soc. Nat. Hist. **5**: 89–153. 1899.

JACOBS, R. D. Seasonal height growth patterns of sugar maple, yellow birch, and red maple seedlings in Upper Michigan. U.S. Dep. Agr. Forest Serv. Lake States Forest Exp. Sta. Res. Note LS–57. 4 pp. 1965.

KIENHOLZ, R. Seasonal course of height growth in some hardwoods in Connecticut. Ecology **22**: 249–258. 1941.

KONDRAT'EVA-MELVILLE, H. A. On the heterophylly in the seedlings of some woody plants. (In Russian; English summary) Bot. Zhur. **50:** 605–613. 1965.

KÜSTER, E. Über das Wachstum der Knospen während des Winters. Beitr. Wiss. Bot. **2:** 401–413. 1898.

MEIJKNECHT, J. G. On the ideal value of varying characters. Acta Bot. Neerl. **4:** 273–320. 1955.

MOORE, E. The study of winter buds with reference to their growth and leaf content. Bull. Torrey Bot. Club **36:** 117–145. 1909.

PEARSALL, W. H., & A. M. HANBY. Growth studies V. Factors affecting the development and form of leaves. Ann. Bot. **40:** 85–103. 1926.

REHDER, A. New species, varieties and combinations from the herbarium and the collections of the Arnold Arboretum. Jour. Arnold Arb. **14:** 200–222. 1933.

———. Manual of cultivated trees and shrubs. ed. 2. 996 pp. New York. 1940.

SACHS, J. Physiologische Notizen VII. Ueber Wachstumsperioden und Bildungsreize. Flora **77:** 217–253. 1893.

SCHÜEPP, O. Untersuchungen zur beschreibenden und experimentellen Entwicklungsgeschichte von *Acer Pseudoplatanus* L. Jahrb. Wiss. Bot. **70:** 743–804. 1929.

SMITH, R. F. The leaf dimorphism of *Liquidambar styraciflua*. Am. Midl. Nat. **77:** 42–50. 1967.

SPÄTH, H. L. Der Johannistrieb. 91 pp. Paul Parey Verlags. Berlin. 1912.

TITMAN, P. W., & R. H. WETMORE. The growth of long and short shoots in *Cercidiphyllum*. Am. Jour. Bot. **42:** 364–372. 1955.

WILSON, B. F. Development of the shoot system of *Acer rubrum* L. Harvard Forest Pap. 14. 21 pp. Harvard Forest, Petersham, Massachusetts. 1966.

ZIMMERMANN, W. A. Untersuchungen über die räumliche und zeitliche Verteilung des Wuchsstoffes bei Bäumen. Zeitschr. Bot. **30:** 209–252. 1936.

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