

Annual cycle of shoot development in sugar maple¹

ROBERT A. GREGORY

United States Department of Agriculture, Forest Service, Northeastern Forest Experiment Station, Burlington, VT, U.S.A.
05402

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Cytology and the development and morphogenesis of sugar maple (*Acer saccharum* Marsh.) shoots were studied. Three types were recognized: short shoots, long shoots entirely preformed in the bud (Epf long), and long shoots partially preformed in the bud (heterophyllous). The three shoot types varied not only in the size and number of internodes and leaves but also in the development of terminal buds. Terminal bud formation was delayed in heterophyllous shoots but because of a shorter plastochron, which extended later into the growing season, the terminal apices of these shoots were able to annually produce more primordia than in other shoot types. The beginning of embryonic shoot formation, however, began about the same time (late July) for all shoot types.

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La cytohistologie, le développement et la morphogénèse de pousses d'érable à sucre (*Acer saccharum* Marsh.) ont été étudiés. Trois types ont été reconnus: pousses courtes, pousses longues entièrement préformées dans le bourgeon (Epf long) et pousses longues partiellement préformées dans le bourgeon (hétérophylles). Les trois types de pousses variaient non seulement quant à la dimension et le nombre des entre-nœuds et des feuilles mais aussi dans le développement des bourgeons terminaux. La formation du bourgeon terminal était retardée chez les pousses hétérophylles mais, à cause d'une plus brève plastochrone qui s'est amplifiée plus tard dans la saison de croissance, l'apex terminal de ces pousses était capable de produire annuellement plus de primordiums que chez les autres types de pousses. L'amorce de la formation embryonnaire de la pousse s'est toutefois effectuée au même moment (fin juillet) chez tous les types de pousses.

[Traduit par le journal]

Introduction

Few detailed studies have been made of the morphogenesis and anatomical development of shoots of arborescent dicotyledons although considerable attention has been given recently to detecting the presence of hormones that control these events. Yet the sequence, and presumably the hormonal physiology, of annual shoot development is not uniform among shoots of a tree crown. The vegetative development of annual shoots varies appreciably with position in the crown, and with age and vigor of the tree. A better understanding of this variation during the seasonal course of development would be helpful for investigating and understanding the physiological processes involved.

Studies preliminary to the one reported here indicated that most shoots of sugar maple (*Acer saccharum* Marsh.) are preformed entirely in the bud: that is, an embryonic shoot, consisting of all of the next year's leaf primordia in various stages of differentiation and the unextended internodes, is enclosed, along with the apical dome, within 8 to 12 pairs of bud scales. After overwintering in the bud the embryonic shoot emerges early in the next growing season, and the apical dome begins immediately that spring to initiate primordia that develop into bud scales, the first step in formation of

a new bud. However, at the terminal apex of young, vigorous first- and second-order branches, the shoots are often not entirely preformed; instead of beginning to form a new bud in the spring, the primordia pairs produced by the apical dome develop into foliage leaves rather than bud scales, and this may continue for several weeks before bud formation begins. These shoots, called heterophyllous (Critchfield 1960), reflect the vigor of their progenitors. The preformed part of the shoots have large leaves and unusually long internodes.

Among those sugar maple shoots that are entirely preformed, one can usually recognize two types primarily on the basis of internode length. Most, especially in older, less vigorous trees, are what are commonly referred to as short shoots. These usually have two to three leaf pairs, internodes less than 10 mm, and no lateral branches. Entirely preformed (Epf) long shoots, however, have three to five leaf pairs and internodes much longer than 10 mm, and they normally bear lateral branches.

The development of these three shoot types, short, Epf long, and heterophyllous, is reported in this paper and is related to some of the existing information on hormonal physiology.

Materials and methods

All material was from 20- to 25-year-old trees growing in the vicinity of the University of Vermont Proctor Maple Research

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Farm, Underhill, Vermont, U.S.A. Terminal apices of Epf and heterophyllous long shoots were prepared for microscopic study in 1975. From March 16 through August 6 collections were made at weekly intervals and then at biweekly intervals through October 1. After excising the outer bud scales, the apices were fixed in Navashin's fluid (Jensen 1962) and embedded in paraffin. Serial longitudinal and transverse sections, 5 to 8 μm thick, were cut with a rotary microtome, mounted on slides, stained by the periodic acid - Schiff (PAS) reaction, and counterstained with Heidenhain's iron hematoxylin.

Twenty apices each of short, Epf long, and heterophyllous shoots were collected at biweekly intervals from August 24 through October 5, 1977. On March 15, 1978, sampling was resumed at weekly intervals through August 23 and then at biweekly intervals through October 4. In 1978 the number of samples was reduced to 10 per sample date for each shoot type. To facilitate quantitative expression of development, sampling was confined to those fully developed or elongating shoots that were most abundant and typical of each shoot type: all selected short shoots had two nodes; Epf long shoots had four nodes; and heterophyllous shoots had seven or more nodes. The pairs of primordia that had been produced during the growing season when sampling occurred were identified and recorded as scales, embryonic leaves, or undifferentiated. As soon as the 1977 embryonic shoots began to extend out of the bud scales in May 1978, the samples were made to include all of the extending shoots as well as the developing bud. From then on the lengths of each internode and leaf midrib in the extending shoots were measured and recorded along with the data from the terminal bud. Also in 1978, transections were removed from the middle of the oldest internode (IN 1) of the 1978 Epf long shoots and 10 μm thick sections were prepared for light microscopy as described previously.

Following bud opening in the spring of 1978, internodal elongation was monitored in two Epf long shoots on each of five trees. The distance from a fixed point on the previous year's shoot to each of the nodes of the developing 1978 shoot was recorded weekly and subsequently expressed as a percentage of the total 1978 elongation of each internode.

Mean values and sampling errors at $P = 0.05$ were calculated for the data measured at each sampling date. Seasonal curves were fitted mathematically to some of the data as will be explained later.

Mitotic activity was used to detect the beginning of growth of the embryonic shoots in 1975 and 1978. Additional shoot apices were collected for this purpose from each shoot type in the spring of 1978. Microsections were prepared as described previously.

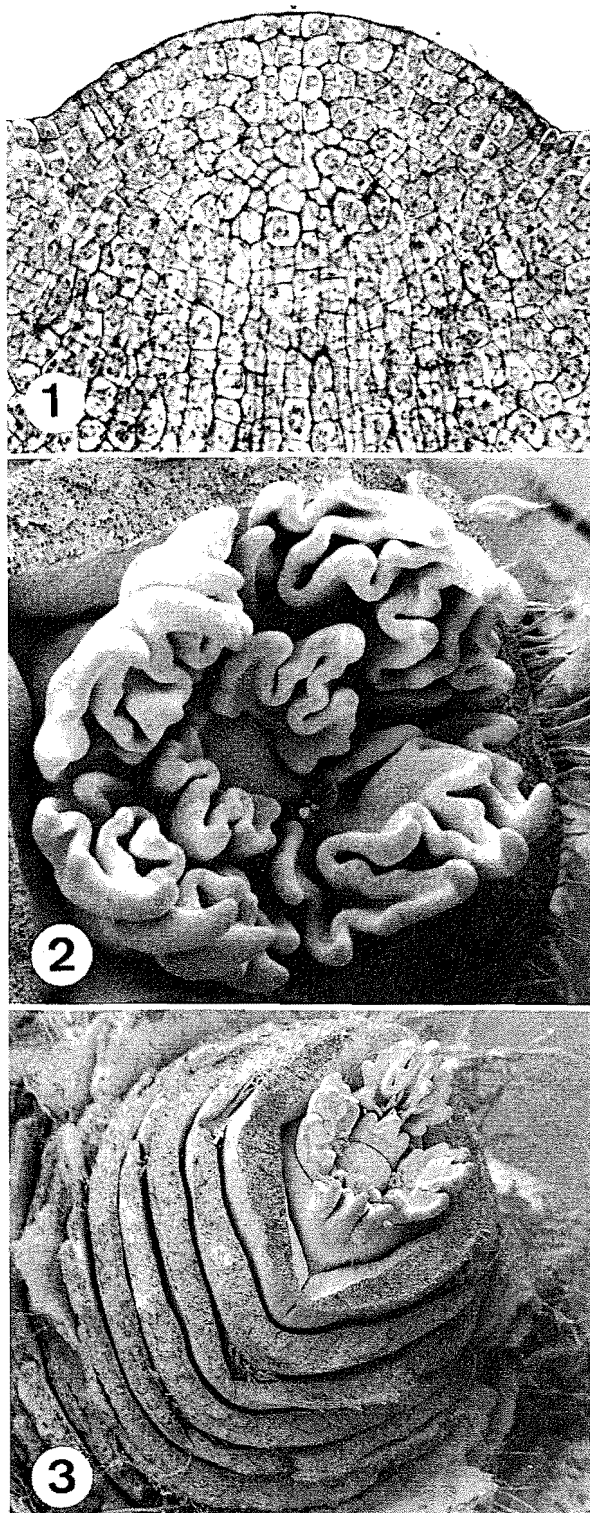
A few 1978 samples of shoot apices were prepared for viewing with scanning electron microscopes (SEM). These were dehydrated in ethanol, dried by the critical point method using CO_2 as the transitional fluid, and coated with gold-palladium for SEM viewing.

Results

Apex anatomy

Cytohistological zonation is readily apparent in the terminal apices of sugar maple shoots (Fig. 1).

FIGS. 1-3. Terminal shoot apices of sugar maple in 1978. Fig. 1. Median longisection showing cytohistological zonation of the apical dome. Mid-April. $\times 320$. Fig. 2. A quiescent embryonic shoot with three pairs of embryonic leaves and one pair of undifferentiated primordia. Early October. $\times 59$. Fig. 3. A bud with scales removed exposing the developing embryonic shoot. August 24. $\times 24$.



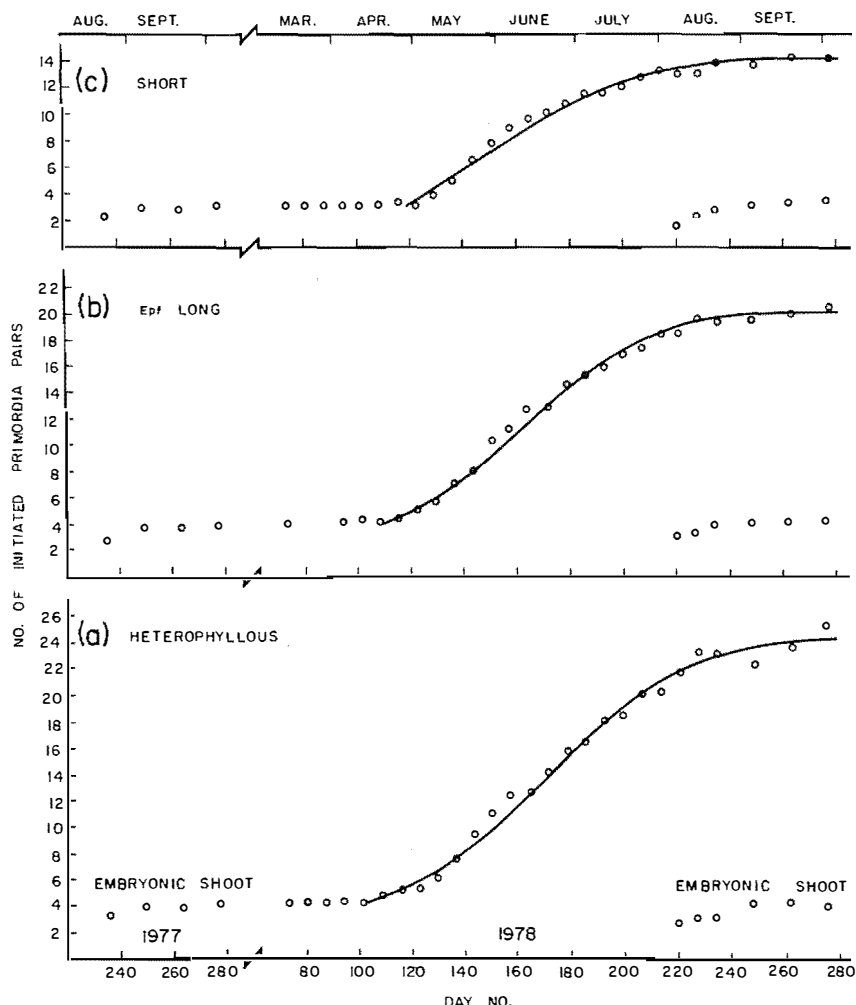


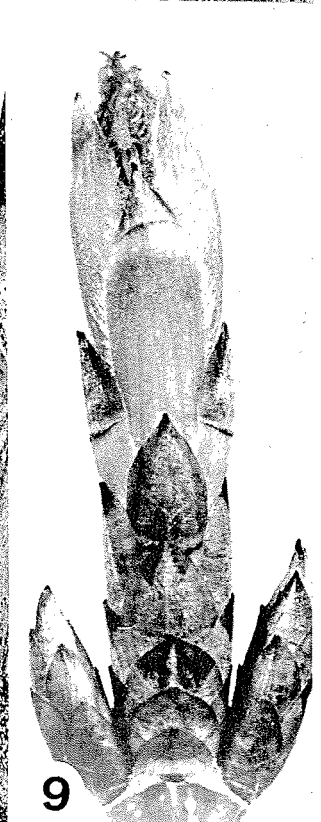
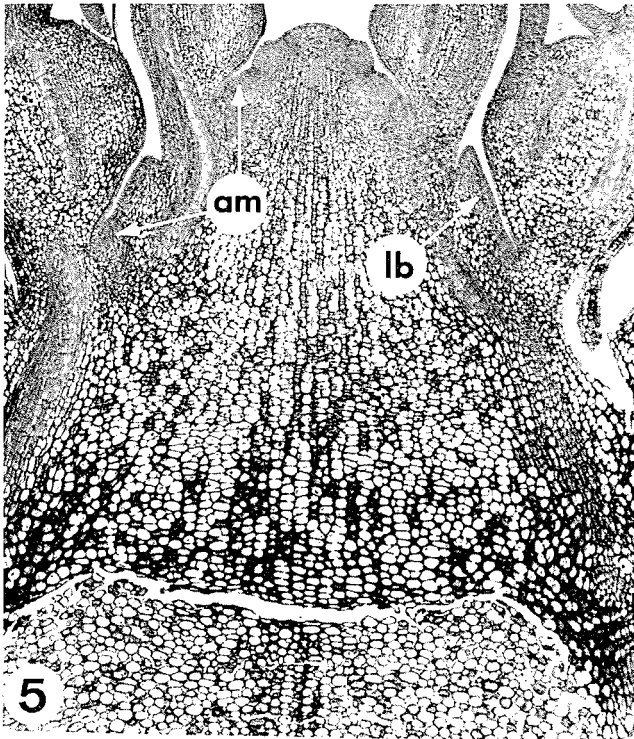
FIG. 4. Number of primordia pairs initiated by the apical domes of heterophyllous (a), Epf long (b), and short (c) shoots as a function of time (day number or calendar date). Circles represent mean values. Sampling errors at $P = 0.05$ were too small to illustrate.

There is a central zone consisting of large cells with thickened primary walls and protoplasts that are highly vacuolate during the growing season. The central zone is bordered peripherally by a region of smaller, cytoplasmically dense cells which give rise to successive pairs of primordia that alternate with one another at right angles (decussate phyllotaxy). A pith rib meristem at the base of the central zone gives rise to longitudinal files of cells extending into the subapical region.

Whether a tunica, which in the strict sense would consist of surface layers having only anticlinal divisions, occurs in the apical dome was not determined. Judging by the usual disordered arrangement of cells below the surface layer, especially in the central zone, it seems unlikely that a tunica with more than a single layer of cells could exist.

The shape of the apical dome varies, being relatively low and narrow early, and high and broad late in the plastochron. Basal diameters and heights

FIGS. 5-9. Terminal shoot apices of sugar maple. Fig. 5. Same section as Fig. 1 showing internal anatomy of the embryonic shoot including the crown region at its base. $\times 50$. Fig. 6. Median longisection from a developing bud with all but the last (youngest) pair of scales removed. Note crown areas (arrows) just below embryonic shoot and at the base of the bud. Early August. $\times 20$. Fig. 7. The youngest, trichome-covered pair of bud scales on a fully developed bud. Early October. $\times 38$. Fig. 8. Median longisection from an enlarging bud in early May. The lowest of the developing axillary buds (arrows) is at the node of the next to youngest pair of scales. $\times 20$. Fig. 9. An enlarged opening bud. $\times 4$. *am*, axillary meristematic region; *lb*, leaf base encircling shoot; *s*, scale.



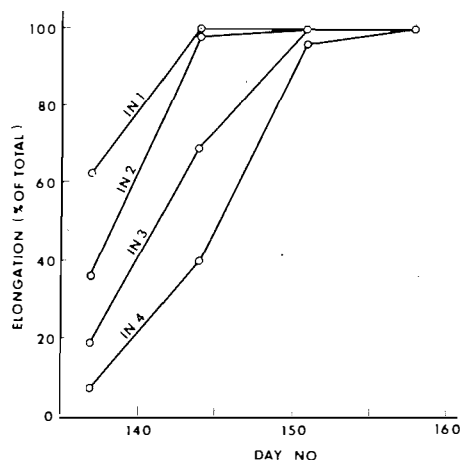


FIG. 10. Internodal elongation in 1978 long shoots as a function of time. Vertical bars depict sampling errors of the mean where $P = 0.05$ and $n = 10$ except for IN 4 where $n = 6$.

of the domes of long shoots ranged from 140 to 240 μm and from 25 to 80 μm , respectively.

Shoots with three equidistantly spaced primordia per node (60° rather than 180° horizontal divergence angle) were observed occasionally. This apparently unstable departure from the normal paired configuration never occurred throughout an entire crown or even persisted in an entire branch.

Mature terminal bud

Embryonic shoots, as they appear in overwintering terminal buds, typically have an undifferentiated pair of primordia that were produced at the end of the previous growing season (Figs. 2, 5). In addition, embryonic long shoots usually have three to four pairs of embryonic foliage leaves enclosed in 8 to 12 pairs of scales (Figs. 2-4) while short shoots usually have two pairs of leaves enclosed in 8 to 9 pairs of scales (Fig. 4).

The medullary region of embryonic shoots is separated from that of the rest of the bud by a plate of thick-walled cells similar to what has been referred to in other species as the "crown" (Fig. 5). According to Romberger (1963) this feature was observed by Schröder in buds of *Acer platanoides* L., and was first described by him in 1869. A second similar platelike region delimits the entire terminal bud from subjacent regions (Fig. 6).

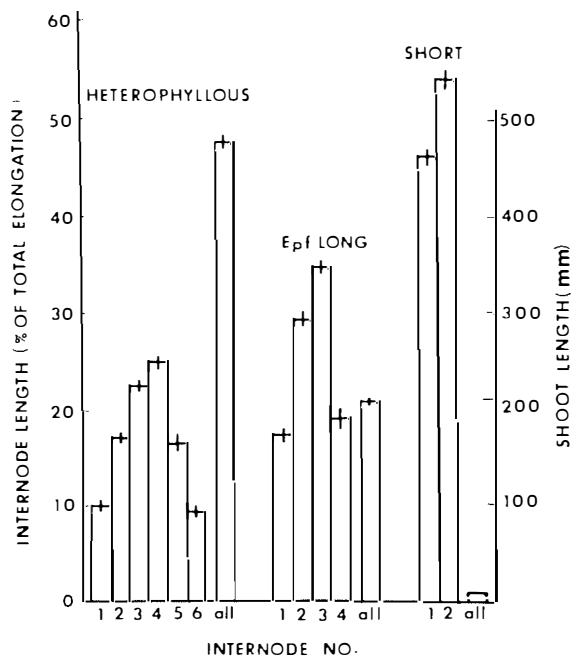


FIG. 11. Internode length and total shoot length (all) in 1978 heterophyllous, Epf long, and short shoots. Vertical bars depict sampling errors of the mean where $P = 0.05$ and $n = 230$.

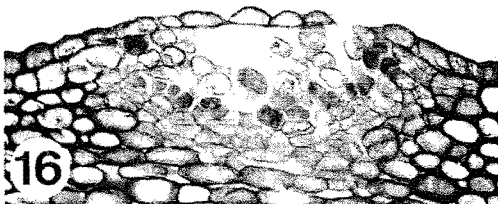
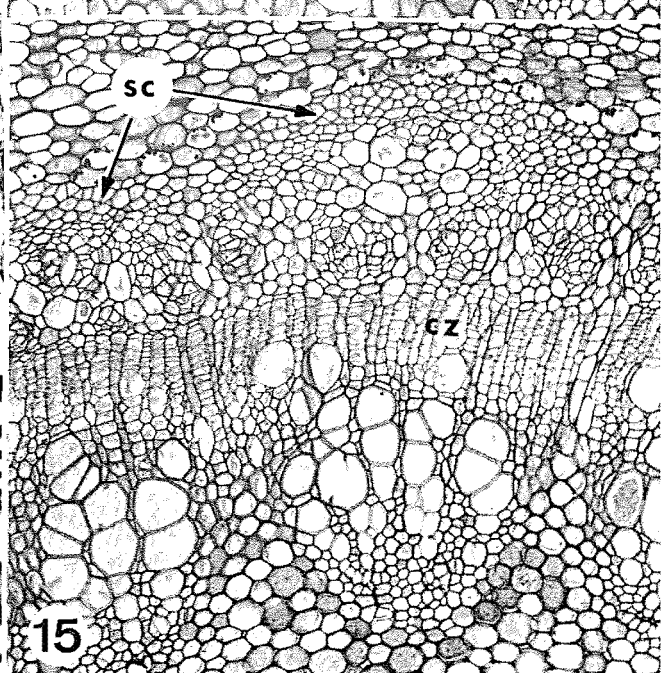
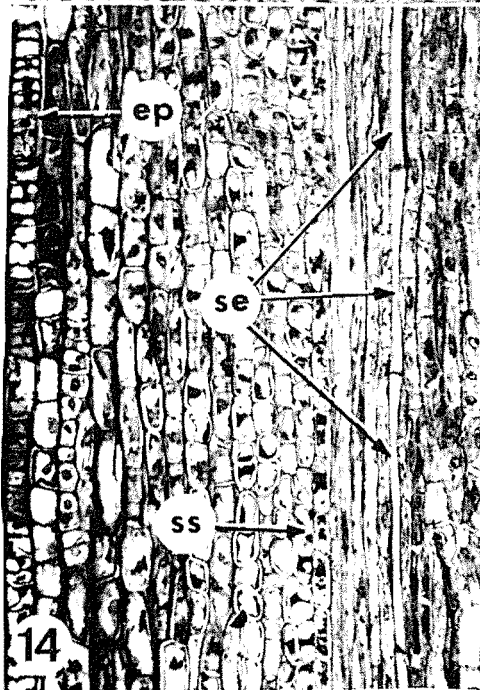
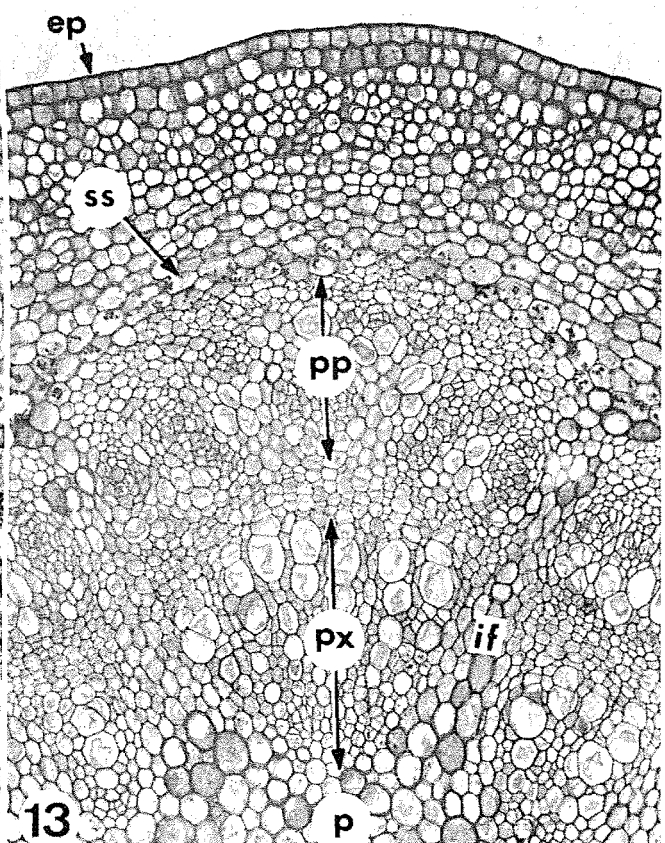
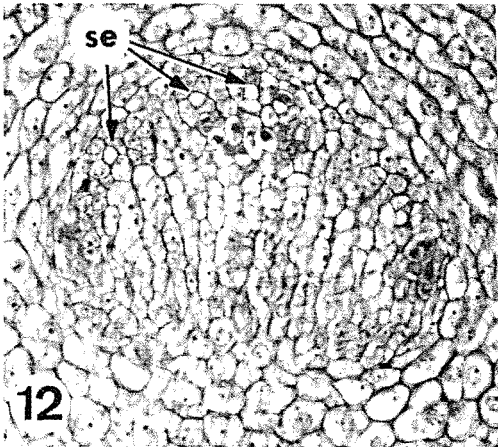
The older, first-formed scales (prophylls) differ from the younger, last-formed scales, although the differences are not nearly as great as between scales and embryonic leaves. The prophylls undergo more marginal and less adaxial growth than the younger scales. The latter are densely covered with trichomes on both surfaces (Figs. 6, 7).

Meristematic regions in the axils of the leaves and younger scales (Fig. 5) subsequently give rise to lateral buds that develop concurrently with the next terminal bud (Fig. 8).

Vernal reactivation

Mitotic activity in the embryonic shoots resumed in mid-April in both 1975 and 1978. In 1978, mitoses were first observed in sections of some of the buds from both short and long shoots collected April 19 (day 109). A week later, mitoses were abundant in all of the sectioned embryonic shoots and in the younger scales. By May 3 (day 123), considerable development had occurred in the leaves and younger scales, internodes had begun to elongate

FIGS. 12-17. Internode 1 in the 1978 developing Epf long shoots of sugar maple. Fig. 12. Transection of a sympodia of leaf traces in a mature embryonic shoot in early October. $\times 210$. Fig. 13. Transection taken from a shoot sampled shortly before completion of extension of IN 1. May 17. $\times 150$. Fig. 14. Radial section from the same shoot as in Fig. 13. $\times 220$. Fig. 15. Transection taken from a shoot sampled shortly after completion of extension of IN 1. May 14. $\times 128$. Fig. 16. Transection through a recently developed lenticel. May 31. $\times 200$. Fig. 17. Transection showing recent periclinal divisions in the subepidermal layer marking the initiation of a phellogen. May 31. $\times 200$. *cz*, cambial zone; *ep*, epidermis; *if*, interfascicular area; *p*, pith; *pp*, primary phloem; *px*, primary xylem; *se*, sieve element; *ss*, starch sheath; *sc*, sclerenchyma cylinder.



(Fig. 8), new primordia were being initiated at the terminal apex (Fig. 4), and apical domes had developed in the axils of leaves and younger scales (Fig. 8). By May 10 (day 130) the buds were swollen, younger scales had elongated noticeably (Fig. 9), and the developing shoots emerged from the buds within the next few days.

Internode development

Internodal elongation proceeded rapidly after emergence of the shoots from the buds. Mean values from the measured Epf long shoots (Fig. 10) showed that almost all internodal growth outside of the bud occurred in about 22 days. On the average, extension of IN 1 was complete in 12 days (May 24, day 144); IN 2 in 15 days; IN 3 in 20 days; and IN 4, when present, in 22 days (June 7, day 158).

The heterophyllous shoots had the longest internodes (Fig. 11). Although there was very little elongation of short shoots, their internodes were of nearly equal length whereas in long shoots the middle internodes were significantly longer than others.

Anatomical development of IN 1 in Epf long shoots was observed in transections made from the weekly and biweekly samples. By early October various tissues had become differentiated in IN 1 of the mature embryonic shoot. Most prominent were the leaf trace sympodia which contained differentiated primary sieve elements but no xylem elements (Fig. 12). There was no discernible change in IN 1 overwinter. Further vascularization occurred shortly after vernal reactivation. By the end of April, well differentiated primary xylem elements were observed. Primary vascularization was completed by May 17, shortly before completion of internodal extension. At that time, xylem and phloem were separated by an incipient cambial zone which had not yet bridged the interfascicular areas connecting the pith and cortex (Fig. 13). The outer regions of the vascular bundles were capped by the early primary phloem which, in addition to a few sieve elements, consisted of axially elongated parenchyma cells (Figs. 13, 14). A starch sheath demarcated the inner cortex (Fig. 13).

By May 24, after completion of internodal extension, there was a well developed cambial zone and the first elements of the secondary vascular tissues, including rays, were differentiating (Fig. 15). At that time, cells of the cortex had undergone tangential enlargement and the walls of the early phloem that capped the vascular bundles had thickened, thus creating an almost continuous cylinder of sclerenchyma bounded by the still-apparent starch sheath. The early sieve elements had ap-

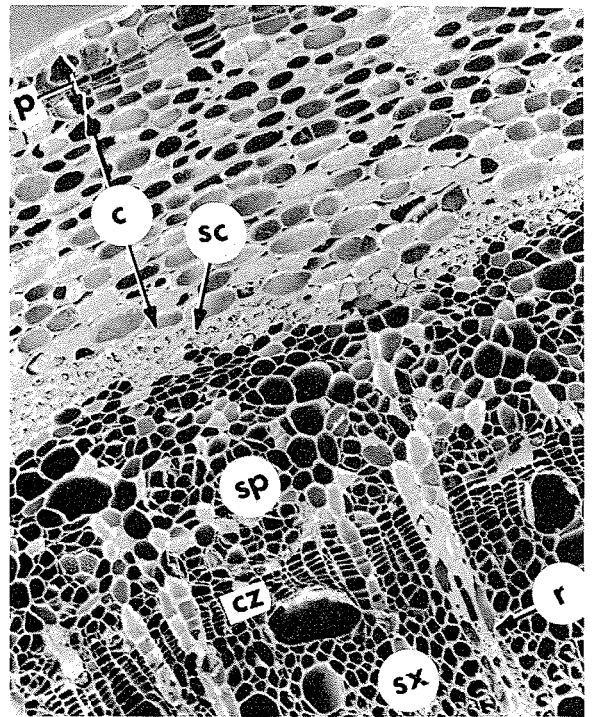


FIG. 18. Transection, through internode 1 of a mid-June sample. $\times 250$. c, cortex; cz, cambial zone; e, epidermis; p, periderm; sc, sclerenchyma cylinder; sp, secondary phloem; sx, secondary xylem; r, ray.

parently stretched and collapsed. A week later (May 31) considerable secondary vascular tissue had been produced and the outer stele was delimited by a well defined sclerenchyma cylinder. Lenticels with prominent periderms had appeared (Fig. 16) and elsewhere around the circumference of the internode periclinal divisions in the subepidermal layer marked the initiation of a phellogen (Fig. 17). Within 2 weeks the periderm was well developed over the entire internode (Fig. 18) and from then to the end of the growing season little anatomical change occurred other than continued production, principally by the vascular cambium, of secondary tissues. Thus by the 2nd week in June, IN 1 of the developing long shoots had reached the relatively stable anatomical configuration illustrated in Fig. 18.

Leaf enlargement

The enlargement of preformed leaves, as indicated by midrib length, proceeded rapidly after bud opening (Fig. 19). Leaf pairs preformed in the buds (early leaves), including those that developed from the last primordia produced the previous year,

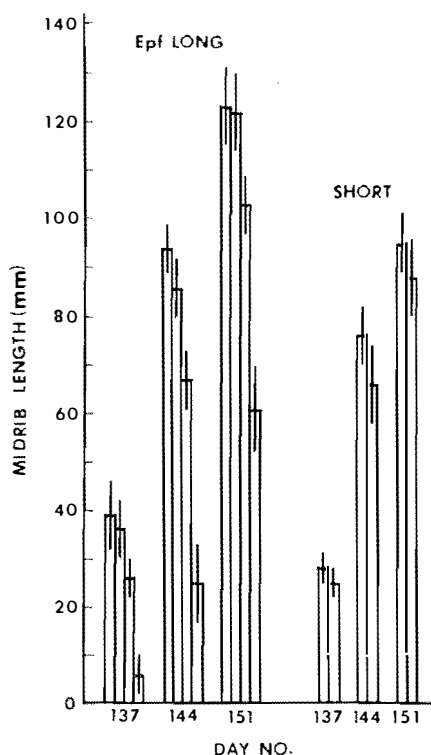


FIG. 19. Length of leaf midribs at nodes 1, 2, 3, 4 (left to right) in Epf long shoots and at nodes 1 and 2 in short shoots. Vertical bars depict sampling errors of the mean where $P = 0.05$ and $n = 20$.

were fully enlarged by May 31 (day 151), less than 20 days after bud opening. On heterophyllous shoots additional leaf pairs (late leaves) were produced for variable periods into the 1978 season and these, of course, enlarged later than preformed leaves. The smallest early leaves were on short shoots and the largest on heterophyllous shoots. There was, however, little difference in the size of leaves on short shoots. On long shoots, the first two leaf pairs, at nodes 1 and 2, were about equal in size, those at the third node were significantly smaller, and those at node 4 smaller yet, even smaller than those on short shoots. The late leaves on heterophyllous shoots were smaller than any of the early leaves, successive pairs decreasing in size. They were often malformed because of insect injury sustained during their development.

Bud development

The initiation of new primordia by the apical domes of terminal buds occurred in mid-April in heterophyllous shoots, late April in Epf long shoots, and early May in short shoots (Fig. 4), in most cases considerably earlier than bud opening. In the short and Epf long shoots, this marked the

beginning of bud formation; those early primordia developed into the first scales of the 1978 bud. In heterophyllous shoots, primordia that were clearly developing into scales were not observed at the shoot apices until day 158 (June 7) and were observed in only 1 of 10 shoots at that time. Not until 3 weeks later (day 179) were scales observed on all of the terminal buds of the heterophyllous shoots. Thus the apical domes of terminal buds in heterophyllous shoots were not covered by scales for about 1 month at the beginning of the growing season.

Curves were fitted mathematically to the data points representing the primordia initiated for the 1977 embryonic shoot and 1978 buds (Fig. 4). This was to facilitate computation of the seasonal course of plastochron duration (PD), the interval between initiation of successive scale or leaf primordia pairs, in 1978. The data points suggested a sigmoid curve for the number of primordia as a function of time. Upper asymptotes were graphically estimated for each of the three curves (24.4, 20.2, and 14.2 for heterophyllous, Epf long, and short shoots, respectively) and a computer program was used to fit logistic equations of the form

$$y = k [1.0 + \exp(a + bx + cx^2)]^{-1}$$

where k = the upper asymptote, y = the number of initiated primordia, x = day number, and a , b , c , etc., of the polynomial exponent, are the computed constants giving the curve of best fit. The resulting equations were

$$y = 24.4[1.0 + \exp(2.76 - 0.2356 \times 10^{-2}x - 0.687 \times 10^{-4}x^2 - 0.8 \times 10^{-7}x^3)]^{-1}$$

$$y = 20.2[1.0 + \exp(1.11 + 0.328 \times 10^{-1}x - 0.325 \times 10^{-3}x^2 + 0.437 \times 10^{-6}x^3)]^{-1}$$

$$y = 14.2[1.0 + \exp(14.5 - 0.204x + 0.2103 \times 10^{-2}x^2 - 0.212 \times 10^{-5}x^3)]^{-1}$$

PD duration in days was then expressed as the reciprocal of the first derivative of these equations (Fig. 20).

There seemed to be little difference in PD between the different shoot types early in the season. By early June, however, the difference between long and short shoots was about 2 days, and PD was increasing for short shoots. The minimum PD for Epf long shoots (a little over 5 days) was reached about mid-June and for heterophyllous shoots (a little less than 5 days) toward the end of June. PD exceeded 20 days by the end of July for short shoots, by early August for Epf long shoots, but not until late August for heterophyllous shoots. Thus, because of a shorter PD, especially later in

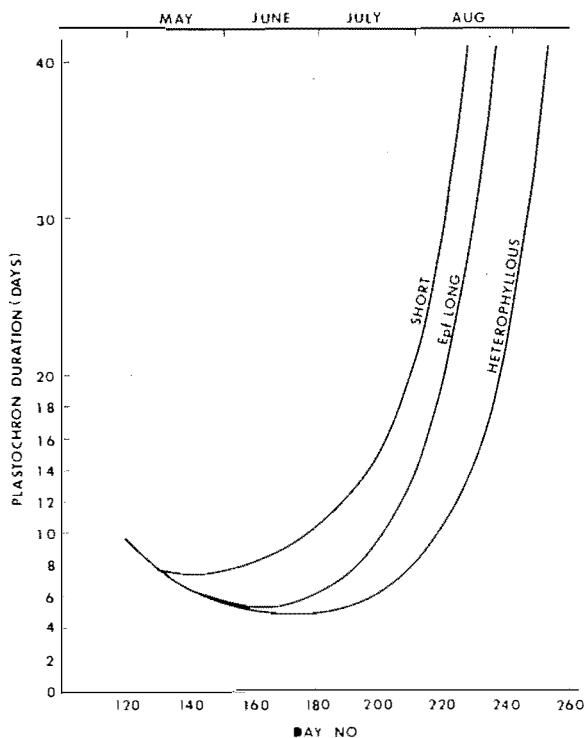


FIG. 20. Plastochron duration as a function of time.

the season, heterophyllous shoots were able to exceed the other shoot types in total bud primordia despite a delay in the beginning of bud formation of about a month early in the season.

The first primordia that were clearly differentiated into embryonic foliage leaves were observed on all shoot types in the August 9 (day 221) collection (Fig. 21). These had been initiated two or three plastochrons previously. They were deeply lobed in contrast to scale primordia where growth had occurred mostly from the activity of the basal and marginal meristems. It appears, therefore, that the morphological switchover from scale to leaf differentiation occurred in late July or early August for all shoot types, and that this switchover was independent of plastochronic age.

There were usually three leaf pairs and one undifferentiated pair of primordia in long shoots in late August (Fig. 3). By mid-September the embryonic shoots were fully developed (Fig. 2).

Discussion

Although heterophyllous shoots have been described for several *Acer* species (Wilson 1966; Critchfield 1971), they have not been reported previously in sugar maple. As in other *Acer* species these shoots are fairly abundant in the crowns of

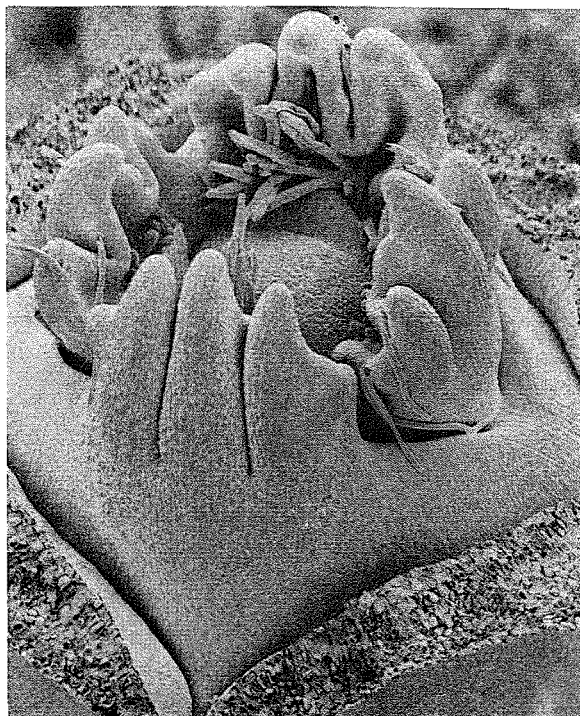


FIG. 21. Developing embryonic shoot in early August. Extensive lobing of the primordia identify them as developing embryonic leaves. $\times 108$.

young vigorous trees and rare in slower growing mature trees. Short shoots seem to be the predominant type in older trees. As in *Acer rubrum* L. (Wilson 1966) there is a marked decrease in the number of long shoots, and hence a concomitant decrease in leaf size, as the branching order increases.

The continuous decline in the size of late leaves and in the length of associated internodes in heterophyllous shoots may reflect the exhaustion of carbohydrate reserves from source tissues of the stem and roots in late May and early June. Starch accumulation, as indicated by the PAS reaction, was not observed in the transections of IN 1 of the 1978 Epf long shoots until mid-June. By late June starch was fairly abundant in the living cells of IN 1 (mostly pith and ray cells), but by then bud formation had begun in all of the sampled heterophyllous shoots.

The growth and development of sugar maple shoots and buds is from about mid-April to early fall at the latitude ($44^{\circ}32' \text{ N}$) where this study was conducted. During the intervening period the buds are either quiescent or dormant. It has been reported that sugar maple seedlings growing in southern Ontario do not fulfill their chilling require-

ments until mid-March or late March (Taylor and Dumbroff 1975). Root growth and rehydration of the buds showed an upward trend beginning in late winter. Cytokinin activity was observed in the buds simultaneously, attaining a peak in early April. Subsequently, Dumbroff *et al.* (1979) found that abscissic acid (ABA) level in buds of sugar maple saplings was high during summer, fall, and winter, then fell sharply in late winter reaching a nadir in early spring. Thus the lowest level of ABA and the highest level of cytokinin, both of which were coincident with maximum bud succulence, occurred about the time when mitoses were first observed in embryonic shoots in this study, several weeks before bud opening.

There is evidence that the leaves of *Acer pseudoplatanus* L. produce an inhibitor that accumulates in the apex (Phillips and Wareing 1958), and there is also evidence that the site of inhibitor accumulation in some species is in the bud scales (Schneider 1968; Tinklin and Schwabe 1970). There is little other information for any species, however, on the exact sites of the production and accumulation of growth-inhibiting substances with respect to different shoot types, PD, or the switchover from production of scales to embryonic leaves.

The role of bud scales in shoot development is also unreported. In sugar maple, the distal scales remain succulent and undergo considerable vernal enlargement before they abscise (Fig. 9). Yet, there is no information on their metabolic activity and its correlative effect, if any, in the developing shoot.

The presence of leaves apparently promotes bud formation in most sugar maple shoots. If the leaves are removed, as in insect defoliation, bud development stops and newly initiated primordia and internodes begin to develop immediately into extended shoots with foliage leaves. It has been reported that such reflushing of sugar maple declines steadily with later defoliation and that no reflushing occurs after late July (Giese *et al.* 1964), the approximate time of switchover from scale to leaf production noted in this study. After this, from late July to the period of leaf abscission, Dumbroff *et al.* (1979) observed a decline in the concentration of free ABA in sugar maple buds, although late summer concentrations remained well above that which was measured during vernal reactivation. Whether these events are correlated or simply unrelated and coincidental is unknown. The late summer decline in ABA does not, by itself, help to explain the switchover to embryonic shoot formation nor the lack of response to late defoliation. Events

associated with the beginning of embryonic shoot formation seem to, in some way, prevent full development of new tissue until chilling requirements are fulfilled.

The effect of reflushing at successively later dates in the growing season on survival of the apices of the reflushing shoots is not known. Reflushing interrupts the normal cycle of events in the apex. The later the occurrence of reflushing, the less time there is for bud formation. The plastochron duration also begins to lengthen fairly early in the season (Fig. 20), further limiting, it would seem, the possibility for complete bud development, especially on short shoots.

Sugar maple, like many other woody species, produces many surplus buds that never develop into shoots. These are buds, often referred to as epicormic, that develop in the axils of scales. They remain alive for many years but are inhibited from progressing further than the embryonic stage, presumably by auxin produced in the leaves of developing shoots. Wilson (1979) found that this bud type in *Acer pensylvanicum* L. could be released, after either normal chilling or treatment with gibberellic acid, by removing the terminal bud. He speculated that substances from the terminal shoot may inhibit the small and relatively undeveloped epicormic buds at concentrations too low to affect the larger lateral buds. Perhaps the situation is similar in sugar maple. Giese *et al.* (1964) observed prolific flushing of epicormic buds on sugar maple shoots whose terminal bud had died after defoliation the previous year.

The shoot system of sugar maple, like that of other tree species, is a complex and flexible integrated unit of apical meristems whose behavior, about which we know little, varies significantly with age and position in the crown. Effective silvicultural manipulation, insect and disease control, and genetic selection all require a much better understanding of the mechanisms that regulate this system.

Acknowledgments

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