Amer. J. Bot. 57(5): 535–542. 1970.

SHOOT GROWTH AND LEAF DIMORPHISM IN BOSTON IVY (PARTHENOCISSUS TRICUSPIDATA)[1]

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A B S T R A C T

Boston ivy, a common ornamental vine in the grape family, successively produces two kinds of leaves during the growing season. The two "early leaves" at the base of each shoot are preformed in the winter bud, and their expansion in the spring is accompanied by little stem elongation. At maturity they have large three-lobed blades and long petioles. Most short shoots produce no more leaves, but "late leaves" develop on all long shoots at intervals of less than 2 days. All but the first few undergo their entire development during the growing season. They are much smaller than early leaves, and the lateral lobes of their blades are reduced or eliminated. They are separated from the early leaves and from each other by long internodes. The early and late leaves differ in the circumstances and continuity of ontogeny, and diverge in form at an early stage. This vine and its relatives are unique in their three-node cyclical pattern of organ occurrence and internode length along the shoot. Lateral shoots and buds are present at every third node, with tendrils at intervening nodes. The long shoots branch freely and repeatedly, and the production of late leaves and new shoot axes by vigorous compound shoots is limited only by the growing season. Despite its specialized organization, Boston ivy resembles several tree species in its association between a seasonal type of leaf dimorphism and a shoot system constructed of long and short shoots.

BOSTON OR JAPANESE IVY (*Parthenocissus tricuspidata* (S. & Z.) Planch.), a native of Asia, is a common ornamental vine of temperate regions. Widely used as a wall cover because of its holdfast tendrils and attractive foliage, it is popularly identified with academic institutions, and is the common ivy of the "Ivy League" colleges in the eastern United States.

Most descriptions of Boston ivy mention the conspicuous dimorphism of its leaves, which differ in size, shape, and position on the shoot (e.g., Sprague, 1909). A similar type of heterophylly is present in other deciduous woody genera of the temperate flora, including *Acer*, *Betula*, *Cercidiphyllum*, *Liquidambar*, and *Populus* (Schüepp, 1929; Titman and Wetmore, 1955; Critchfield, 1960; Clausen and Kozlowski, 1965; Smith, 1967). In many of these trees and in Boston ivy, the permanent shoot system is made up of long and short shoots, and the dimorphism of the leaves is closely related to this type of shoot architecture.

These parallels with other woody plants are partly obscured by the morphological complexities that Boston ivy shares with other members of the Vitaceae. The nature of the vitaceous tendril has been debated for more than a century (for divergent recent views see Bugnon, 1953; Millington, 1966; Shah and Dave, 1966), but the tendril will be mentioned here only incidentally. This paper is primarily concerned with (1) those aspects of shoot organization and development related to the seasonal type of leaf dimorphism in this vine, and (2) the similarities and differences between Boston ivy and other woody plants exhibiting this kind of heterophylly.

MATERIALS AND TERMINOLOGY—Observations were made in Cambridge, Massachusetts, and in Berkeley and near Placerville, California. Periodic growth measurements of eight compound shoots on a single flowering vine were made at Placerville in 1967. The shoots developed on a wide range of older shoot types, including perennial short shoots and vigorous, much-branched long shoots. Descriptions of leaf characteristics are based on these shoots.

Terminology follows that of an earlier paper (Critchfield, 1960). The "early leaves" expand when the winter buds open; the "late leaves" develop subsequently. Leaves and internodes are numbered from the base of the annual shoot, and an internode has the same number as the leaf at its upper end. Boston ivy leaves have stipules, and are alternate and sub-distichous.

[1] Received for publication 8 October 1969.

This study was begun while the author was on the staff of the Maria Moors Cabot Foundation for Botanical Research at Harvard University, and completed during a Charles Bullard Forest Research Fellowship at the same institution. The leaf silhouettes were photographed by Mr. L. C. Johnson. Drs. A. R. Berg and J. A. Romberger made helpful criticisms of the manuscript.

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The terms "embryonic leaf" and "leaf primordium" designate two categories of leaves in the winter bud. The embryonic leaves are much larger, and have distinct blades and petioles (Fig. 2: 1, 2).

The "phyllochron" (Bond, 1945) is the time interval between corresponding developmental stages of successive leaves. Phyllochrons are based here on leaf maturation, defined as 90% of final blade length. Negative phyllochrons are due to the maturation of leaves out of sequence.

ORGANIZATION OF THE SHOOT SYSTEM—The shoot system of Boston ivy has several unusual features, some of them unique to the Vitaceae: (1) Terminal buds are not produced at any stage of development, so growth from year to year is strictly sympodial. (2) The development of a single shoot axis is interpreted as monopodial, following the nearly unanimous view of recent observers of the vitaceous shoot (but see Bugnon, 1953, for a review of the once-prevalent hypothesis that tendril-bearing vitaceous shoots develop sympodially). (3) Except in the seedling stage, all annual shoots are compound. The meristems axillary to the foliage leaves of older plants always produce extended shoots without any intervening bud stage, although these lateral shoots may abort and abscise early in development. Only seedlings produce buds axillary to foliage leaves. (4) Each shoot axis produces a single axillary bud. It is always located in the axil of the shoot's basal appendage, a scale-leaf. (5) All winter buds are compound. Each comprises several embryonic axes, and each axis is a separate bud. The largest component bud is axillary to the basal appendage of an elongate shoot of the previous season, but each of the others is axillary to the basal appendage of the preceding embryonic shoot. Only the largest—the primary bud—ordinarily expands and produces a shoot during the season after the compound bud is laid down. (6) As a rule, two of three successive leaves have no axillary structures of any kind. Tendrils or inflorescences are present at these nodes, opposite the leaves.

During the winter, few of these complexities are apparent except the absence of buds at many nodes. The most conspicuous feature of the leafless vine is the sharp demarcation between the short and long shoots produced the previous season. They differ in stem length and number of nodes, with no overlapping. The cumulative annual increments of these two shoot types make up the permanent woody skeleton of Boston ivy. Short shoots predominate on older parts of the vine, long shoots at the periphery.

The short shoots are usually less than 1 cm long, and terminate in shoot scars. Each short shoot has two leaf scars separated by an internode 2–5 mm long. The upper node has a tendril or tendril scar but no axillary structures. The only

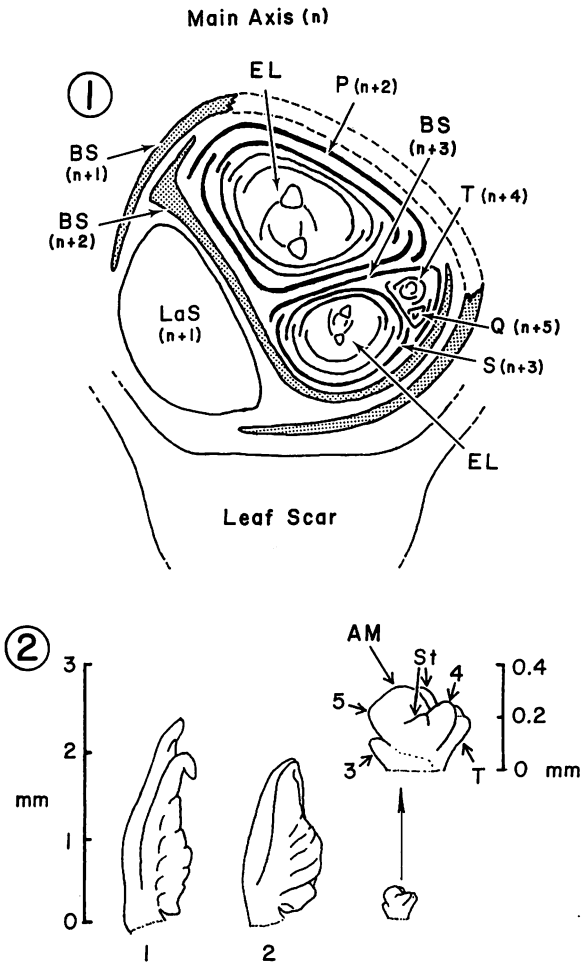

Fig. 1–2. The winter bud of Boston ivy.—Fig. 1. Diagram of the axillary complex at node 1 of a representative short shoot, showing lateral-shoot scar (*LaS*); primary (*P*), secondary (*S*), tertiary (*T*), and quaternary (*Q*) buds; embryonic leaves with stipules in *P* and *S* buds (*EL*); branch orders n to n + 5; and basal scales (*BS*) of axes n + 1 to n + 3.—Fig. 2. Contents of a primary bud with two embryonic leaves (1, 2) and three leaf primordia (3–5), showing tendril opposite leaf 3 (*T*), stipules of leaf 4 (*St*), and apical meristem (*AM*). Tendril opposite leaf 2 and stipules of 1–3 are omitted.

winter bud on the short shoot is at the lower node, topographically in the axil of the leaf scar (Fig. 1). This compound bud, 1–2 mm high, is flanked by the scar of a lateral shoot (Fig. 1: *LaS*). The basal appendage of this lateral remains attached to the parent shoot, subtending the entire bud and forming its outermost scale (Fig. 1, *BS*, n + 1). By winter it is often represented by two widely separated fragments which appear to be distinct bud scales.

Following usage in *Vitis*, the components of the winter bud are referred to as primary, secondary, tertiary, . . . buds, although the two genera differ in the origin and structure of the bud. The

compound bud of Boston ivy has 3–5 nested components (four in Fig. 1), each with its own bud scales. If the axis of the short shoot is designated n, the axis of the lateral shoot at node 1 is n + 1, and a compound bud with four embryonic shoots comprises axes n + 2 (primary bud) to n + 5 (quaternary bud) (Fig. 1).

The long shoots of the previous season are highly variable in length, branching, and number of nodes. The first-order laterals of the main axis may themselves have permanent branches, but third- and higher-order laterals usually abscise by the end of the growing season.

Despite the variability of the long shoots, the basal portion of each duplicates the short shoot. The lowermost internodes are usually longer, but the structures at nodes 1 and 2 are identical to those of the short shoot. Node 3, separated from 2 by a long internode, is like node 2 except that the positions of leaf and tendril scars are reversed (Fig. 3, shoot 5).

This three-node sequence of axillary complex-tendril-tendril is repeated along all axes of vegetative long shoots. The compound winter buds at nodes 4, 7, 10, . . . are identical to the bud at node 1, although they decrease in size and complexity as stem diameter decreases. Variations of the three-node cycle are characteristic of many genera of Vitaceae (Bugnon, 1953; Suessenguth, 1953), but Boston ivy is exceptional in exhibiting this sequence from the base of each shoot.

CONTENTS OF THE WINTER BUD—The primary buds of Boston ivy are similar in structure and contents, and during the winter it is impossible to predict what type of shoot a bud will produce. The seven or eight bud scales (eight in Fig. 1) are equivalent to leaves in arrangement, and appear to consist mostly of modified, fused stipules.

Each primary bud contains two kinds of foliar appendages: two embryonic leaves and 1–3 leaf primordia. The embryonic leaves are 8–30 times as long as the largest primordia on the same axis, and much of the principal venation and marginal toothing of their three-lobed blades is evident. The leaf at node 1 is usually the larger. In 17 buds collected from November to February, the mean lengths of leaves 1 and 2 were 1.32 and 1.16 mm (ranges 1.00–1.85 and 0.70–1.68). These features are illustrated in Fig. 2 by leaves at a slightly later stage, just before bud opening in late April.

In the axil of leaf 1 are the apical meristem and first appendage of the next season's lateral shoot. During the ensuing growing season a new compound bud will develop in the axil of this appendage. Opposite leaf 2 is a once- or twice-branched embryonic tendril enveloped by a bract.

The leaf primordia of the primary bud are morphologically undifferentiated, with no indications of a lamina or petiole (Fig. 2). In the same sample of winter buds, the primordia at node 3 were 0.03–0.19 mm long. The buds contained no leaves between 0.70 mm (the smallest embryonic leaf) and 0.19 mm (the largest leaf primordium). Opposite the leaf at node 3 is a primordium that can develop into either a tendril or inflorescence (Fig. 2, *T*). Most buds have one or two additional leaf primordia. Four or more have been observed only in late winter, in buds that may have resumed leaf initiation.

Secondary buds differ from primary buds in their smaller size, fewer scales (6–7), smaller embryonic leaves (40–70% as long as those of the primary bud), and fewer leaf primordia (0–2). Tertiary buds are still smaller, with 4–5 bud scales and 0–3 leaves. These higher-order buds usually remain quiescent during the season after their formation, and the majority never open.

GROWTH OF THE SHOOT—At Placerville a single vine may exhibit a range of 4–6 weeks in the timing of bud expansion due to differences in exposure. Most buds start to elongate by the end of April, and the leaves emerge when the buds are 10–15 mm long.

The embryonic leaves of the bud expand into two early leaves, which differ in size and shape from the late leaves that succeed them on the shoot. The one to three leaf primordia of the winter bud give rise to the first late leaves, but these leaves do not differ in any way from succeeding late leaves initiated during the growing season.

The initiation of new leaves began during bud elongation. By the time the early leaves were half-emerged from the bud, the total number of foliar appendages per embryonic shoot had increased from 3–5 to an average of eight. The tendril at node 2 had produced its full complement of 6–9 branches, and the lateral shoot at node 1 had produced two or three leaf primordia and begun to elongate above its basal scale. In the axil of this scale was the apical meristem of the new primary bud. It had produced its first appendage, the scale that ultimately subtends the secondary bud.

The blades of the two early leaves on each shoot expanded rapidly and almost synchronously. They reached 90% of their final length 3–4 weeks after the bud opened. The phyllochron of leaf 2 averaged only 1.4 days (range −1 to +5). The petioles of the early leaves (and all subsequent leaves) grew much more slowly, and did not reach 90% of their final length until 2–5 weeks after the blades. The short internodes of the early leaves reached their final length before or soon after the bud scales were shed.

This first phase of growth is common to all shoots, but further development varies greatly from shoot to shoot. All long shoots continue leaf production, but many future short shoots produce no more mature leaves. If the main

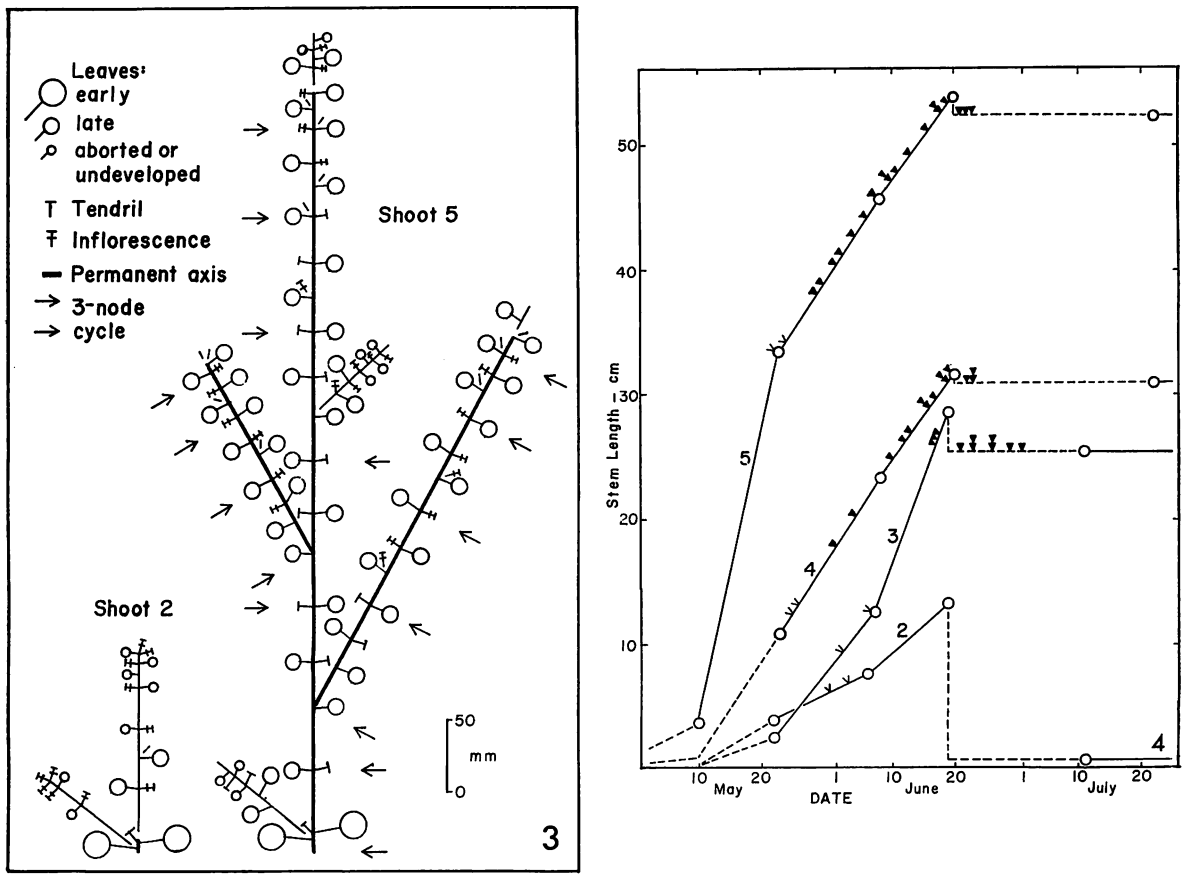

Fig. 3–4. The development of Boston ivy shoots.—Fig. 3. Diagram of a short and a long shoot. Internodes of permanent axes (broad lines) are drawn to scale. All shoots and portions of shoots which eventually abscised are shown detached from the permanent axes. Short detached lines in leaf axils are lateral shoots which abscised very early in development—Fig. 4. The growth of shoots 2–5. Stem length measurements are indicated by circles and blade maturation dates by V's (early leaves) or triangles (late leaves). All shoot tips abscised in late June or early July (dashed lines), and shoot 3 abscised at node 2 later in the season.

axis and the lateral shoot at node 1 shift immediately to flowering, additional leaves abort when they are only a few mm long. Or the axes may remain vegetative but abscise (the main axis at node 2) before any late leaves reach maturity. Most short shoots are of these two types, but a few produce mature late leaves before they are finally pruned back to a two-node permanent stem.

The rapid expansion of the preformed early leaves is followed by a definite pause before the first late leaf reaches maturity. This hiatus in leaf production is measured by the phyllochron of leaf 3. At Placerville this interval averaged 9.6 days, ranging from 6–18 days (Fig. 4, shoots 3–5). Successive late leaves unfold when they are 1–2 cm long, and the blades mature at short but irregular intervals. Their phyllochrons ranged from −8 to +8 days, averaging +1.6 days. The placement of tendrils and lateral shoots was a factor in this variation. The leaves slowest to mature were at tendril nodes. They may have been retarded by the opposing tendril or by a lateral shoot at an adjacent node; in their early stages both structures are active sinks for photosynthate in *Vitis vinifera* (Hale and Weaver, 1962).

The most vigorous shoots of Boston ivy continue leaf production until late in the growing season, and the number of leaf-producing shoot tips is multiplied by repeated branching. By autumn a single compound shoot, originating from a winter bud containing only three to five foliar appendages, may bear several hundred leaves. A representative shoot collected in Cambridge in late September had 12 axes, including the main axis and three orders of laterals. It totalled 7.7 m in length, and had produced two early leaves and 350 late leaves. Four of the axes still had growing tips. The shoots measured at Placerville stopped growing much earlier and produced fewer leaves, however. By the time growth ceased in late June, the longest had produced 41 mature late leaves: 18 on the main

axis and 23 on two permanent first-order laterals (Fig. 3, 4, shoot 5).

The long internodes of the late leaves elongated very rapidly, reaching 90% of their final length much sooner than the corresponding leaves. Internodes of the first late leaves matured an average of two weeks earlier, but this difference later decreased to 3–5 days.

The sequence of internodal maturation along the shoot was as irregular as that of the leaves, and part of this variation was definitely associated with the three-node cycle. The internode between two tendril-nodes, usually longer at maturity than either adjacent internode, tended to prolong its growth and mature out of sequence.

The rate and timing of stem elongation may have been influenced by the growth of lateral shoots. Shoot 4, with no vigorous laterals, grew at a uniform rate of 0.75 cm per day for several weeks (Fig. 4). Shoot 5 elongated 2.3 cm per day at first, but its growth rate decreased in late May, coincident with the accelerating growth of laterals at nodes 4 and 7. Their aggregate length was 23% of the main axis on 23 May, 48% on 8 June, and 83% at the end of extension growth (Fig. 3).

The tip of an elongating shoot appears to exert no control over the development of lateral shoots above the basal node, and each shoot ultimately produces approximately one-third as many laterals as leaves. An axillary meristem is visible soon after the subtending leaf is initiated, and five or six plastochrons below the parent-shoot apex it has initiated its basal scale and first leaf primordium. During the early stages of elongation, the lateral shoot is partly covered by its basal scale and the stipules of the subtending leaf. At Placerville, the blade of leaf 1 on first-order laterals matured 17–33 days after the subtending leaf. Leaf 1 is offset from the parent shoot by a long internode (Fig. 3). Subsequent development of lateral shoots of all orders does not differ from the development of the main axis.

Each lateral shoot produces a compound winter bud in the axil of its basal scale. The primary bud lags two to three plastochrons behind its parent shoot in the production of appendages. By the time it has produced its second appendage, the apical meristem of the secondary bud is visible in the axil of the first appendage. At Placerville, the first embryonic leaf was initiated in the most advanced primary buds by late May.

Inflorescences occupy the same positions on the shoot as tendrils. They may replace tendrils at any node except the second, which has a predetermined tendril opposite the early leaf. Flowering is restricted to short shoots on most vines. The organization of the flowering axes is highly modified above the lowermost nodes, and each axis appears to terminate in a complex of reproductive structures (Fig. 3, shoot 2; Fig. 8). Long-shoot axes do not ordinarily produce inflorescences, but the vines at Placerville were atypical in this respect. Inflorescences eventually replaced tendrils on all shoots under observation, and newly initiated laterals often had the appearance of single much-branched inflorescences (Fig. 3, shoot 5).

Although the repeated ramification of a shoot is limited only by the length of the growing season, many axes are eliminated by abscission early in development. Abscission is also responsible for establishing the ultimately sharp distinction between long and short shoots.

Shoot abscission began on a large scale in late June and early July at Placerville, and the final length of most shoots was established at this time (Fig. 3, 4). Shoot 5 was reduced from at least 16 axes with growing tips to three woody axes terminating in shoot scars. Shoot 2 was cut back from two long flowering axes which failed to produce fruit, to a short shoot 7 mm long.

On many stems abscission was foreshadowed by the absence of appreciable secondary thickening above the node where the abscission zone formed (Fig. 8). Woody stems were not necessarily permanent, however. The main axis of shoot 3, woody up to node 10, abscised at node 12 between 19 June and 11 July (Fig. 4), but by early November it had been further pruned back to a two-node short shoot.

Several kinds of observations suggest that the actively growing tip of a shoot controls the development of the axillary bud at its first node, in contrast to the uninhibited production of lateral shoots above this node. In these instances, the cessation of growth or complete elimination of the parent shoot was followed by the expansion of the axillary bud.

(1) In late April 1967, many expanding primary buds were killed by low temperatures. They were replaced by the adjacent secondary buds, which were visibly elongating within 2 weeks. These secondary buds had originated, the season before, in the axils of the basal scales of the primary buds. They would ordinarily not have expanded until the following season, if ever.

(2) Secondary buds also sometimes expanded after the elongate parent shoot, originating from the primary bud, had been heavily pruned back by abscission. After the tip and lateral branches of shoot 3 had abscised in early summer, the secondary bud at the base of the shoot produced a permanent, ramified long shoot.

(3) Partly developed primary buds sometimes expanded and produced lammas shoots during the season in which the buds were initiated. Lammas shoots, common on many vines (Fig. 7), are distinguishable from ordinary lateral shoots by the bud-scale scars at their base. In late summer, lammas shoots developed at nodes 7 and 10 of shoot 3 after the abscission of their parent shoots, the lateral branches at these nodes. The

branched, woody lammas shoots were eventually shed, together with the rest of shoot 3 above node 2.

(4) The delayed expansion of secondary and higher order buds also suggests release from apical control by the parent shoot. Secondary buds, especially on perennial short shoots, often open the second season after their formation. Tertiary and higher-order buds, in turn, occasionally open a year or two after the buds to which they are axillary.

CYCLICAL VARIATION ALONG THE SHOOT—The three-node cycle of axillary complex-tendril-tendril underlies many of the unusual features of vegetative shoot growth in this vine. It is partly responsible for the erratic timing of successive growth events, and is influential in determining the relative amounts of elongation in the internodes comprising the stem.

Cyclical variation appears early in the life of the plant. First-year seedlings produced only two or three closely spaced leaves with true axillary buds, but on the long shoots of the next season there were no deviations from the three-node sequence above nodes 2–4 (Fig. 5d).

On adult vines this sequence is repeated on all shoot axes, beginning with a lateral-shoot/compound-bud complex at the first leaf-node. Extra shoot/bud nodes and missing tendril-nodes have been observed, but deviations are not common.

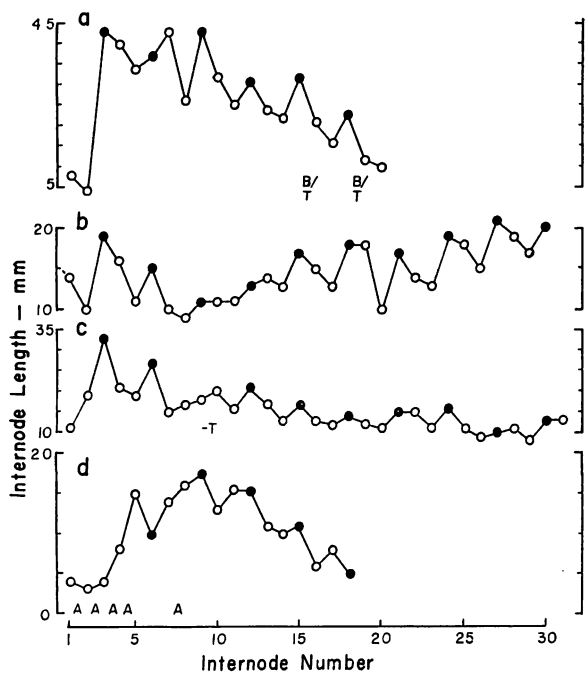

Fig. 5. Cyclical variation along the shoot. Solid black circles are tendril-tendril internodes. Variations and deviations from the three-node cycle include: true axillary buds (*A*), axillary complex at tendril node (*B/T*), and missing tendril (*−T*). 5*a*, long shoot (shoot 5); *b*, terminal portion of lateral shoot; *c*, lammas shoot; *d*, shoot of second-year seedling.

One standard variation of this pattern is the addition of a shoot/bud complex at the upper tendril node. This sequence was found only in cycles 2–6 (Fig. 3, shoot 5, cycles 5, 6), and reached a peak frequency of about 50% in cycle 5. This is the standard pattern on shoots of *Parthenocissus inserta* (= *P. vitacea*), according to Millington (1966). Much less common variations observed in Boston ivy were the absence of a tendril at a tendril-node (Fig. 5c) and the absence of a shoot/bud complex at the first node of lateral shoots (Fig. 3, shoot 5).

The tendril-tendril internode is the longest in about 75% of the three-node sequences of adult vines. It is usually preceded by the shortest internode in the sequence (Fig. 5a–c). Variants of this internodal pattern are common in the Vitaceae (see Bugnon, 1953, and Suessenguth, 1953, for earlier references).

MORPHOLOGY OF EARLY AND LATE LEAVES—In Boston ivy the two kinds of leaves are discontinuously different in size and shape (Fig. 6–8; Sprague, 1909). Transitional forms are mostly confined to shoots of aberrant ontogeny, including a minority of lammas shoots and shoots from poorly developed secondary buds which expand prematurely.

The early leaves have much bigger blades and proportionally longer petioles. Their mean surface area was 6.7 times that of the late leaves on the measured shoots (means 79.6 and 11.9 cm^2). Collectively the two kinds of leaves overlapped slightly in blade area (ranges 38.4–137.6 and 2.6–40.0 cm^2), but on individual shoots the smaller early leaf was 2.6–15.6 times the size of the largest late leaf. The petioles of the early leaves averaged 1.1 times the blade length (range of petiole/blade 0.7–1.8); those of late leaves averaged only half the blade length (mean 0.5, range 0.3–0.8).

Most Boston ivy leaves are three-lobed, and the lobes of early leaves are nearly equal in length[3]. The midlobe of the early leaves sampled averaged only 13% longer (range 5–22) than the mean lateral lobe, and had fewer spine-tipped marginal teeth (mean 81%, range 61–100). The midlobe of late leaves averaged 62% longer (range 35–109) than the mean lateral lobe, and had more teeth (mean 130%, range 67–200). The lateral

[3] On branches near the base of some vines the early leaves are compound, with three leaflets. Since the leaves of seedlings are also compound, this type of heterophylly can be interpreted as the topographic retention of a juvenile condition. This phenomenon approaches the "phase changes" of plants like *Hedera* (see Allsopp, 1965, for review), although short shoots with compound leaves sometimes produce inflorescences. This topographic type of heterophylly appears to be independent of the seasonally repeated type described here, except that it is restricted on older plants to preformed early leaves.

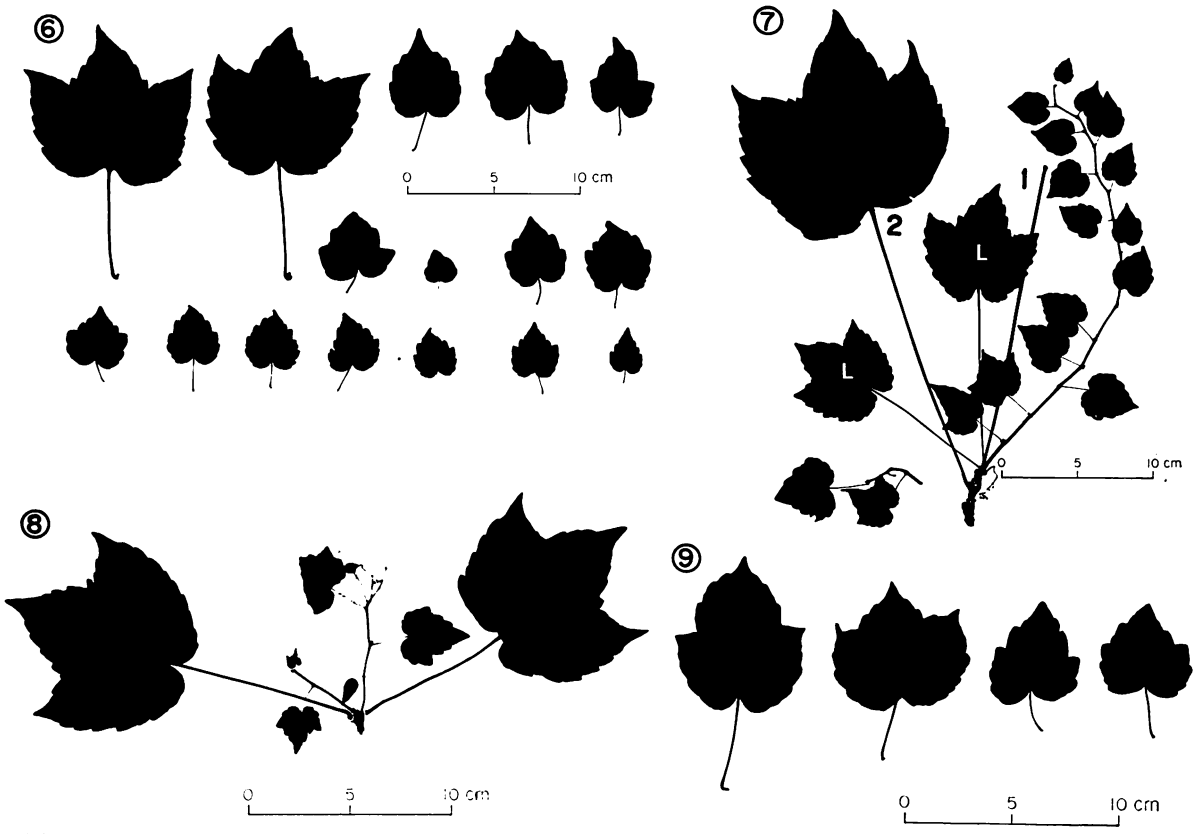

Fig. 6–9. Boston ivy shoots and leaves.—Fig. 6. The leaves of long shoot 4. Leaf 1 in upper left, 16 in lower right.—Fig. 7. A lammas shoot produced by an immature primary bud at the first node of a short shoot. Short-shoot leaves are numbered 1 and 2 (blade of 1 omitted). The two-leaf shoot axillary to leaf 1 is detached at lower left. The first two leaves (*L*) of the lammas shoot are shaped like early leaves.—Fig. 8. A fruiting short shoot. The main axis, with its single berry, will eventually abscise at node 2. The terminal part of the lateral shoot at node 1 has already abscised, and the rest of the shoot is about to.—Fig. 9. Leaves 1–4 of a shoot from a poorly developed secondary bud. The first two leaves are intermediate between early and late leaves in size, shape, and petiole length.

lobes of late leaves are sometimes reduced to the size of other marginal teeth (Fig. 6).

These differences in leaf shape originate early in ontogeny. The early leaves are three-lobed by the time they are 250–300 μ long. The lateral lobes of late leaves do not appear until the primordia are 350–500 μ long. The lobes arise low on the flanks of the late-leaf primordia, and are much smaller than the middle lobe throughout subsequent development.

Discussion—The shoot system of Boston ivy illustrates the primary functional distinction between long and short shoots, first pointed out by Goebel (1905): "... the long shoots are instruments of the special branching of the plant; the short shoots are chiefly organs of assimilation." The principal foliage leaves of Boston ivy short shoots are well developed before winter dormancy and able to expand very rapidly when growth is renewed in the spring. They probably begin to export photosynthate soon after bud opening; the preformed leaves of *Vitis vinifera* are active exporters within a few weeks of bud expansion (Hale and Weaver, 1962), and leaves of herbaceous plants begin exporting when they are one-third to one-half of their final area (Wardlaw, 1968). Flowering is also a specialized function of the short shoots of Boston ivy, but they play no significant part in extending the woody skeleton of the vine.

The long shoots have a dual role. The basal part of each duplicates the short shoot, and the early leaves make up a sizeable fraction of the shoot's photosynthetic area. The blade area of the 2 early leaves on shoot 4 was nearly as great (92.3%) as the area of all 14 late leaves. The early leaves of shoot 5 were 48.2% the size of the 41 late leaves on this branched shoot. The existence at the base of each long shoot of an early-maturing region chiefly concerned with assimilation must enable the rest of the shoot to fulfill more effectively its special function of extending the permanent shoot system.

In the specialization of its shoots, Boston ivy resembles a heterogeneous group of woody plants exemplified by *Populus trichocarpa* (Critchfield, 1960). This poplar also has dimorphic leaves,

and both kinds are present on long shoots. The heterophyllous long shoots of *P. trichocarpa* are remarkably like those of Boston ivy in some respects. In both, the separation of photosynthetic surfaces is maximized by an inverse relationship between petiole and internode length. The early leaves, crowded at the base of the shoot, have long petioles, and the widely spaced late leaves have short petioles. In both the poplar and Boston ivy, the internode separating the two sets of leaves is often the longest on the shoot.

Apart from its vitaceous specializations, Boston ivy differs most strikingly from woody plants like *Populus trichocarpa* in the origin of short shoots. Only early leaves are produced on short shoots of this poplar, and when the supply of preformed leaves is exhausted the shoot forms a new bud without elongating. Future short shoots of Boston ivy, by contrast, always produce at least two elongate axes, and their status as short shoots may be finally determined only by abscission late in the growing season.

The early and late leaves of Boston ivy and other woody plants of this type differ in the circumstances and continuity of early ontogeny. The late leaves of Boston ivy develop at the tip of a growing shoot, like seedling leaves and the leaves of annual plants. The development of all but the first late leaves is continuous from initiation to maturation. The early leaves, on the contrary, undergo embryonic development in the very different microenvironment of a closed bud. Their ontogeny includes a distinct and prolonged period of what Sachs (1893) called "morphologische Ausgestaltung" (putting-into-shape). As Sachs pointed out, nature has imposed a sharp boundary between the embryonic and expansion phases of leaves preformed in winter buds.

All leaf primordia less than 190–200 μ long are relatively undifferentiated in Boston ivy. Primordia that ultimately develop into early leaves have three nearly equal lobes by the time they are 250–300 μ. Thus the critical threshold in the determination of leaf form is in the range of 200–250 μ. Leaves of this size are nonexistent in dormant primary buds, but they may occur in immature or poorly developed buds. When such buds expand under circumstances described above, the leaves at the first two nodes are often intermediate between early and late leaves in size and form (Fig. 9, leaves 1, 2).

Heterophylly is a descriptive term applied to a group of diverse phenomena. Recent attempts to formulate a unifying explanation of these phenomena have emphasized the size and nutritional levels of the apical meristem and subapical regions of the stem (see Allsopp, 1965, for review). A nutritional explanation hardly seems applicable to the problem of leaf dimorphism in Boston ivy, however. By early summer, and until late in the growing season, early and late leaves in all stages of embryonic development are diffused throughout an actively growing, ramified shoot of this vine, the early leaves in developing buds and the late leaves at the shoot tips. Both embryonic regions are active sinks for photosynthate in the grapevine (Hale and Weaver, 1962).

The type of dimorphism in Boston ivy and other woody plants like it, appears to originate in a fundamental difference in the continuity and circumstances of the early ontogeny of the leaf itself. The sequence of leaf shapes on shoots of aberrant ontogeny suggests that if a future early leaf is diverted from its usual ontogenetic pathway at a sufficiently early stage and forced into the continuous developmental pattern of the late leaf, it tends to resemble the late leaf in its final form. This ontogenetic interpretation of leaf dimorphism offers no clues to the factors that are ultimately responsible for this difference in form, but it provides a context in which the experimental manipulation of leaf form might provide such clues.

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