Growth Patterns in Woody Plants with Examples from the Genus *Viburnum*

by Michael Donoghue

Scientific journals are full of information obtained at the current limits of human perception. Using instruments like the electron microscope, biologists examine the structure of very small objects while astronomers, using extraordinarily complicated technology, can tell us details about the structure of the universe. All of this may give the impression that scientists have already observed and understood everything that can be seen with the naked eye. In botany, at least, nothing could be further from the truth. As Peter Raven (1976) has made painfully clear, we know virtually nothing about most plants, especially those that grow in the tropics. There are still many things we can learn just by *looking* at plants closely (Tomlinson, 1964).

One thing that botanists know surprisingly little about is why and how it is that woody plants (trees and shrubs) come in so many different shapes and sizes. We are all aware that elms, firs and oaks (Fig. 1), to choose only a few examples, have characteristic forms that differ radically from one another, but we seldom stop to consider what accounts for this. There are several kinds of explanations for these differences in form. One kind of explanation concerns the evolutionary causes of the differences. For example someone might "explain" that woody plants occupy a wide variety of habitats, that in

Figure 1. *These three photographs by E. H. Wilson serve as a reminder that trees come in a wide variety of shapes and sizes. The American elm* (upper left), *fir* (upper right), *and white oak* (bottom) *each has its characteristic shape, and these differ markedly from one another. These differences in shape are related to differences in growth pattern.*

different habitats particular dispositions of the leaves confer a selective advantage, and that therefore, plants with a wide variety of sizes and shapes have evolved. Another kind of explanation concerns the actual mechanisms whereby plants attain their characteristic statures. Differences in form could be "explained" solely in terms of the differing physiologies of plants, that is, in terms of hormones and their effects throughout the life of the plant. This sort of explanation is certainly not incompatible with the first kind; they are simply two ways of looking at the same problem.

In this article I want to focus attention on yet another level of explanation for plant form: growth patterns. Growth patterns of different kinds of plants vary and, at least on one level, this can account for the diversity of plant forms that we see. The study of growth patterns consists of the analysis of the number and position of a plant's meristems ("growing points") and the kinds of stems produced by them as the plant develops. New portions of stem (which bear the leaves) are added to a plant each year by the activity of its meristems which are present inside of the buds. Different kinds and amounts of new stem can be produced by such meristems. The study of growth patterns is the search for regularities in the construction of plants and the analysis of how such regularities are related to plant form.

A few botanists (DuRietz, 1931; Raunkiaer, 1934) have categorized plants according to their form or physiognomy but very little is known about the range of growth patterns in plants. This is somewhat puzzling because plant construction is relatively easy to study and one might suppose that an understanding of growth patterns would precede studies of the comparative physiology of growth or of the evolution of plant form. The reasons are in part historical. First, botanists have concentrated their efforts primarily in temperate areas and therefore have failed to see the tremendous diversity of distinctive growth patterns that occur only in the tropics. Secondly, many plants, especially those from the tropics, are known from only a handful of herbarium specimens, which may retain little information about the way that the plants were growing. A third reason is that from very early on in the study of flowering plants, interest has focused on the organs of reproduction, especially the flowers. Linnaeus' admittedly artificial classification was based on floral characters, but even in more recent systems these organs seemed to best indicate the natural relationships among plants. Finally, it has never been clear just how information about plant construction once recorded would be useful. When we have considered in more detail what a study of growth patterns involves and the kinds of information it yields, then we can consider how such studies might be of interest to plant anatomists, physiologists, ecologists, taxonomists and horticulturalists.

In 1970 Francis Hallé, a French botanist, and Roelof Oldeman, a Dutchman, introduced the idea of analyzing the form of woody plants in terms of yearly growth in their book *Essai sur l'Architecture et la*

Dynamique de Croissance des Arbres Tropicaux (not available in English until 1975). More recently, Hallé and Oldeman, along with P. B. Tomlinson of Harvard University have tried to provide a framework for the analysis of plant construction (1978). They categorized the different ways that plants grow, referring them to a number of "architectural models." Their analysis concentrates on the growth of woody plants from the time of germination to the inception of sexual reproduction, at which point a plant can be assigned to its "model." However, one need not have access to populations of seedlings and saplings to determine many things about how a plant is growing. In particular, if only mature plants are available, it is still possible to analyze the method of growth from year to year after the plants have entered their reproductive phase.

An arboretum is one of the best places to begin a study of growth patterns, especially when the living collections are sufficiently diverse and if the plants have been left relatively undisturbed so that they can exhibit their characteristic methods of growth. A study of growth patterns requires only a willingness to look closely at (sometimes with the aid of a hand lens) and accurately record (by means of line drawings and/or photographs) the growth of particular study plants throughout the year. But to do this requires a familiarity with the basic ways that plants are constructed and some understanding of what to look for. I have outlined below the sorts of features that should be examined in any study of growth patterns. I have not attempted to describe all of the ways that plants grow, but instead I've tried to introduce the basic morphological concepts that are needed in examining the growth of whole plants. For more detailed information about these concepts and for an analysis of the diversity of plant architecture, Hallé, Oldeman, and Tomlinson (1978) should be consulted.

In order to provide concrete examples of growth patterns I have included information on the growth of some viburnums. *Viburnum* is a genus of about 125 species of shrubs and trees, many of which are horticulturally important. Most of my examples concern just a few *Viburnum* species that are frequently cultivated and therefore readily available for study. The information that pertains solely to *Viburnum* is set off with smaller type. By reading the offset portion of the text, and referring to the illustrations, it should be possible to piece together the complete growth patterns for a few *Viburnum* species. These examples should make it easier to understand the study of growth patterns, while illustrating the extent to which growth pattern can vary within a group of closely related plants.

THE ELEMENTS OF GROWTH PATTERN IN WOODY PLANTS

Leaf Arrangement

One of the first things to look at when examining a woody plant is the arrangement of the leaves on the stem, that is, its **phyllotaxis.** The point of attachment of a leaf is called a **node** and the area of stem

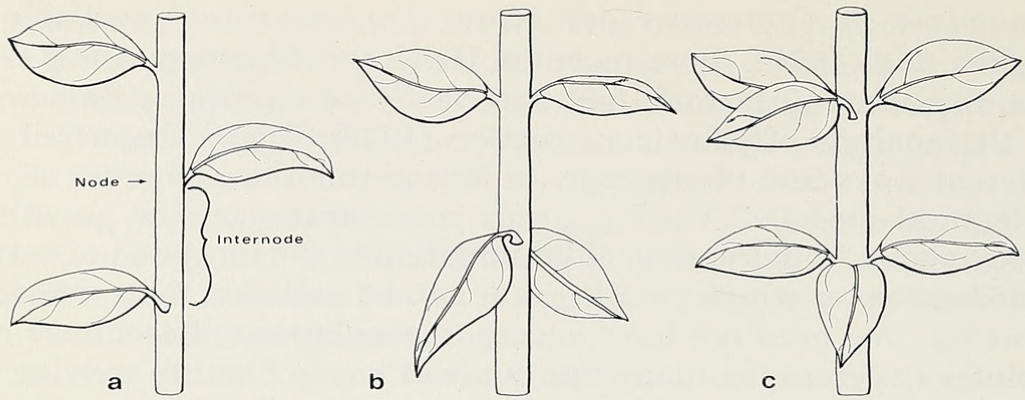

Figure 2. *Leaf arrangements in side view.* (a) *alternate leaves (one leaf at each node);* (b) *opposite leaves (two leaves at each node);* (c) *whorled leaves (more than two leaves at each node).*

between points of leaf attachment is known as an **internode** (Fig. 2a). If there is only one leaf at each area of leaf attachment, the leaves are **alternate** (Fig. 2a). If there are two leaves at each node, then the leaves are **opposite** one another on the stem (Fig. 2b), and if more than two leaves are attached at the same point along the stem, we say the leaves are **whorled** (Fig. 2c).

Another important aspect of phyllotaxis is the arrangement of the leaves around the stem when a branch is viewed end-on. In many plants with alternate leaves, the leaves are **spirally** arranged around the stem, each succeeding leaf being displaced around the stem by some relatively constant angle (Fig. 3a; Stevens, 1974). In plants with opposite leaves the leaves are often **decussate,** that is, each pair of leaves is at right angles (rotated 90°) to the pair above and below it (Fig. 3b). Some plants produce branches along which the leaves are arranged in just one plane (Fig. 3c). This so-called **distichous** arrangement can occur in plants with alternate or opposite leaves; it is most common on branches which are borne horizontally.

The arrangement of the leaves can be determined even when they are absent, such as during the winter. This can be done because when a leaf falls off, or abscises, it leaves a characteristic scar on the twig; by examining the arrangement of leaf scars, the arrangement of the leaves can be inferred.

In the genus *Viburnum* the leaves are opposite or rarely (in some Latin American species) in whorls of three. They are decussately arranged when they are first initiated but in one species, *V. plicatum* (the "double-file viburnum"), they become more or less distichous Fig. 9 due to a twisting of the internodal areas as a young horizontal branch develops.

Buds

Buds are embryonic shoots which are commonly dormant for some period of time. In the Northeast (U.S.) they are often most evident and easy to observe in the winter when they appear as "bumps" along the

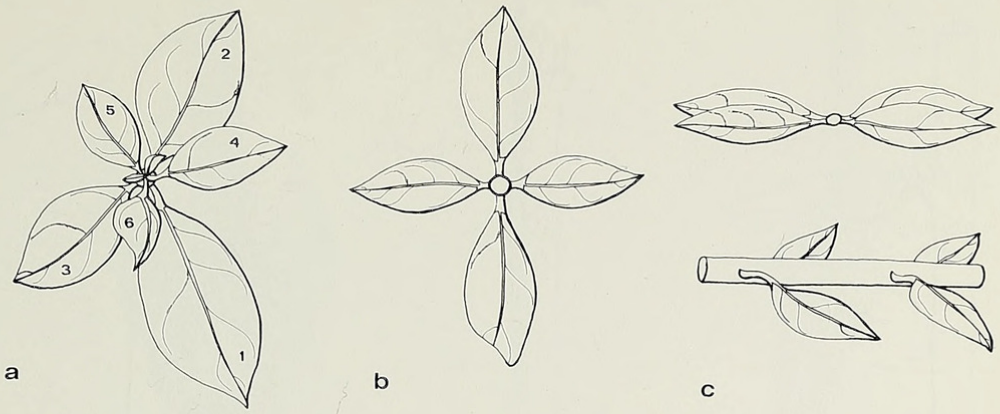

Figure 3. *Leaf arrangements viewed end-on.* (a) *spiral arrangement (the numbers indicate the relative ages of the leaves; number 1 was expanded first and number 6 was the most recent leaf to begin its growth);* (b) *decussate arrangement of opposite leaves;* (c) *distichous arrangement, the leaves borne in one plane.*

twig. A bud is commonly located in the **axil** of the leaf (or its scar), that is, on the stem just above (distal to) the point of attachment of a leaf (Fig. 4a). Such buds are called **axillary** or lateral. A bud that terminates a portion of stem and that was not produced in the axil of a leaf is said to be **terminal** (Fig. 4b). Sometimes the bud at the tip of a stem will appear to be a terminal bud. However, what actually has happened is that the apex of the stem aborted (leaving a tiny "branch" or "stem scar") and the bud was produced in the axil of the last leaf of the season (Fig. 4c). These so-called **pseudoterminal** buds can be deceptive (as in the elms, for example), so twigs must be examined very carefully to determine the exact positions of the buds.

Sometimes buds are produced in the axil of every leaf while in other cases buds may be produced only in the axils of certain leaves (e.g. the first two leaves below the shoot apex) and not in others. In some cases buds will be produced but will regularly abort in the axils of certain leaves, or buds may develop but not function (expand or produce a mature shoot) for many years. These so-called reserve buds may be released if the plant is damaged in some way.

Some plants regularly produce more than one bud in the axil of each leaf. These so-called accessory buds can be on either side of the principal axillary bud (**collateral** bud), or above it (**superposed** bud), or both (Fig. 4d, e). When this occurs, it is very important to determine the fate of the different buds. Some of the buds may produce short shoots with flowers while others produce longer vegetative shoots, and still others may remain as reserve buds.

Buds come in many shapes and sizes and are constructed in a variety of ways. In order to interpret the growth pattern of a plant it is important to understand not only the locations but also the structure of its buds. In our area many woody plants produce buds with a series of tiny leaf primordia on a shortened axis enclosed by one or a number of specialized bud scales. When these buds "break" in the spring, the scales simply fall off but their presence and position is marked on the

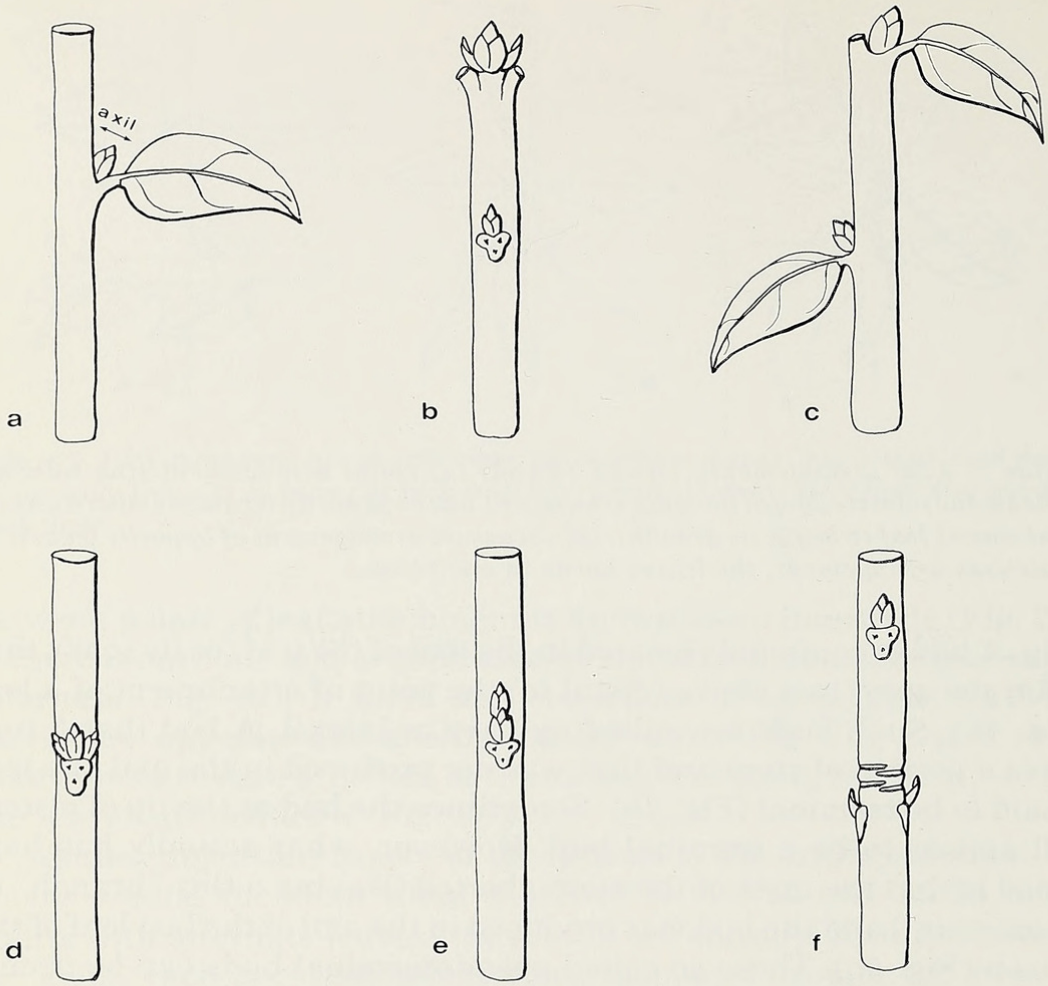

Figure 4. *Buds.* (a) *axillary or lateral buds are those produced in the axil of a leaf;* (b) *a terminal bud flanked by two lateral buds;* (c) *a pseudoterminal bud; the uppermost lateral bud appears to be terminal but the apex aborted and died back, leaving a small "branch" or "stem scar";* (d) *colateral buds flank the principal axillary bud;* (e) *a superposed bud above the principal axillary bud;* (f) *bud scale scars indicate the former presence of a bud, in this case, a terminal bud.*

twig by tiny bud scale scars (Fig. 4f). Such scars are very evident on the large twigs of the horsechestnut. This is handy for determining growth pattern because a segment of a branch can be examined and the extent and nature of the growth of each season can in most cases be assessed readily by noting the positions of the bud scale scars.

Some plants produce so-called "naked buds" which lack specialized protective scales. Instead, the outer envelopes of the bud are simply small, often very hairy, leaf primordia that will expand into the first leaves of the next season. The growth pattern of plants with naked buds is not as easy to determine as it is for those with scaly buds; it is harder to accurately assess what growth occurred during each season since the position of buds is not marked by scale scars. However, other clues, such as color and hairyness differences between the growth of different seasons, can often be used to infer the extent of a season's growth.

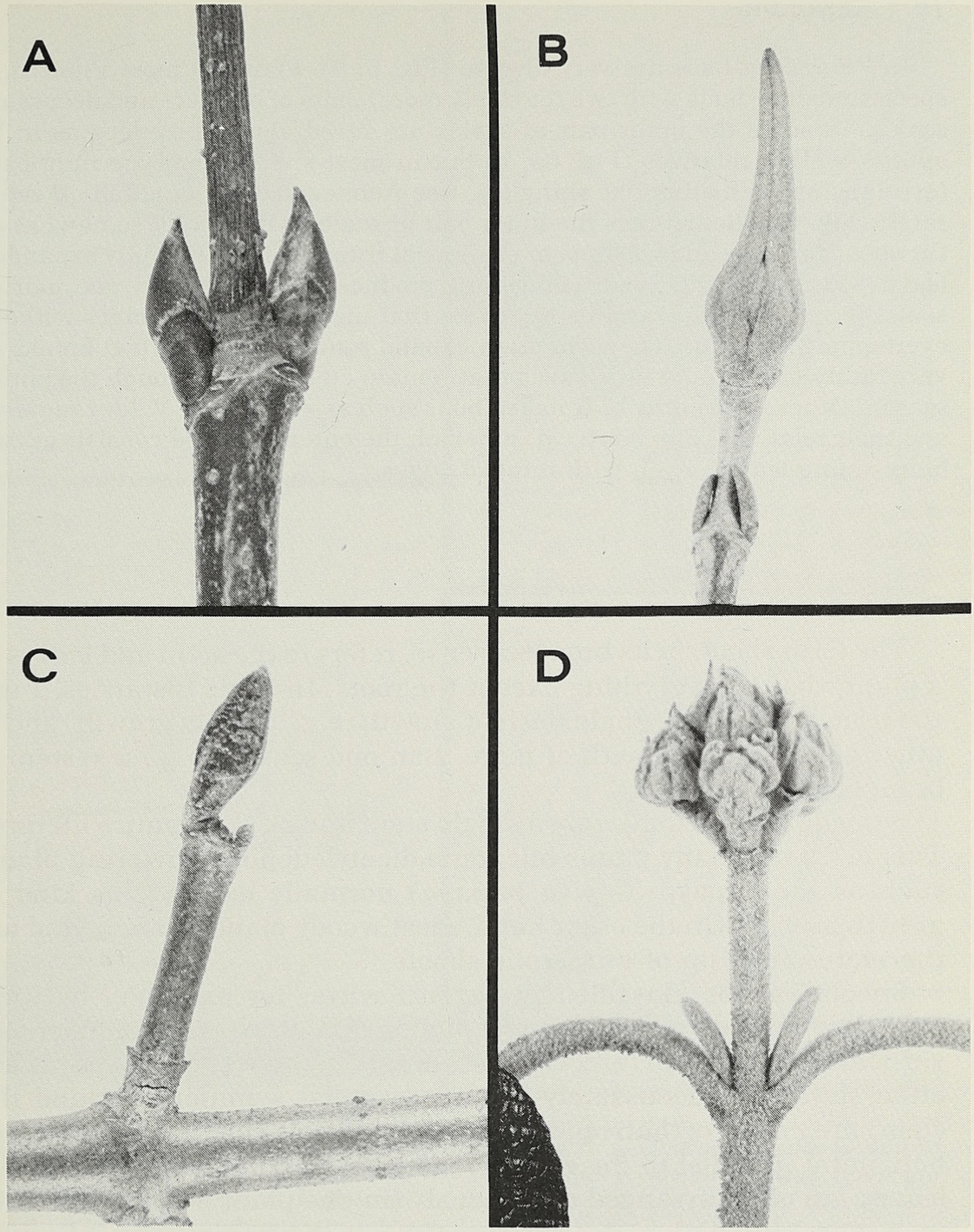

Figure 5. *This figure and Figure 6 illustrate the diversity of buds that occur in the genus* Viburnum. Viburnum molle (A) *and its relatives (section* Odontotinus) *have two pairs of opposite and decussate bud scales that are imbricate.* Viburnum lentago (B) *and its relatives (section* Lentago) *have only one pair of bud scales. These come together along their margins (valvate arrangement). The large, pointed terminal bud encloses the primordia of next year's leaves, inflorescence, and branches. Two lateral buds are also visible.* Viburnum plicatum (C) *likewise has only one pair of bud scales that are valvate. Pictured here is a single short shoot in winter. Note that the bud on the left (which was closest to the center of the plant) is much larger than the bud on the right. In the next season the larger one expands and repeats the growth of the previous season. In* V. × rhytidophylloides (D) *and its relatives (section* Lantana) *the buds are naked and the inflorescence is exposed during the winter. When it opens during the next season the two lateral buds will be expanding (see* Figure 15). *This plant is evergreen in our area and a small portion of a leaf blade is visible in the lower left hand corner.*

In *Viburnum* buds are very diverse (Fig. 5; 6). Plants of most *Viburnum* species produce buds with two (or rarely more) pairs of opposite and decussate scales. In some the outer pair of scales are fused along the edges as in *V. opulus* and its relatives (Fig. 6a, b) but in most species they are imbricate (overlapping each other like shingles), free from each other, and fall off separately (Fig. 5a). Sometimes the inner pair of scales will expand somewhat as the shoot develops and will appear somewhat transitional to the fully expanded leaves (Fig. 15, left). Some viburnums produce buds with only one pair of scales (e.g., *V. lentago* and its relatives) that meet along their edges without overlapping (Fig. 5b). They will often expand somewhat as the bud breaks or very rarely will expand into leaves that remain on the twig through the entire season. Other viburnums bear naked buds such as *V. lantana, V. lantanoides*, and their relatives (Fig. 5d; 6 c,d) in which the outer envelope consists of two hairy young leaves, each with inrolled edges.

Shoots

The term shoot, in its broadest sense, refers to the stem and leaves of a plant, that is, everything except the roots. In some instances, I use the term to refer to a single flush of growth (e.g., a years growth) and in other cases to the growth of more than one season (e.g., a system of branches).

Some plants produce only a single stem during their entire lifetime. This is true of many palms but some dicotyledonous flowering plants such as the papaya (*Carica papaya*) normally exhibit this kind of growth as well. On the other hand, most woody plants branch, and are therefore made up of numerous shoots.

Shoots can be classified in several ways; for example, by their orientation, relative size, and/or function. Shoots that are more or less vertical in orientation (erect or upright) and upon which the leaves are often spirally or decussately arranged (radial symmetry around the stem) are called **orthotropic.** In contrast, shoots that are more or less horizontal (parallel to the ground) in orientation and upon which the leaves are often arranged distichously (in one plane — bilateral symmetry) are called **plagiotropic.** Some shoots seem from their initiation to be intermediate in orientation, others are orthotropic but bend over or sag as the shoot system elongates with age and therefore may appear to be plagiotropic. Others, known as **mixed shoots,** begin as orthotropic and then bend over and actually become plagiotropic shoots or vice versa. All of these phenomena present problems in classifying shoots by their orientation but nevertheless, in many groups of plants, it is very helpful to consider shoots in this way. Some plants are constructed entirely of orthotropic shoots, others produce plagiotropic shoots in addition to orthotropic shoots, and still others are made up entirely of mixed shoots.

Plants of most *Viburnum* species are constructed of essentially equivalent orthotropic shoots, though these can vary in length and in whether they are

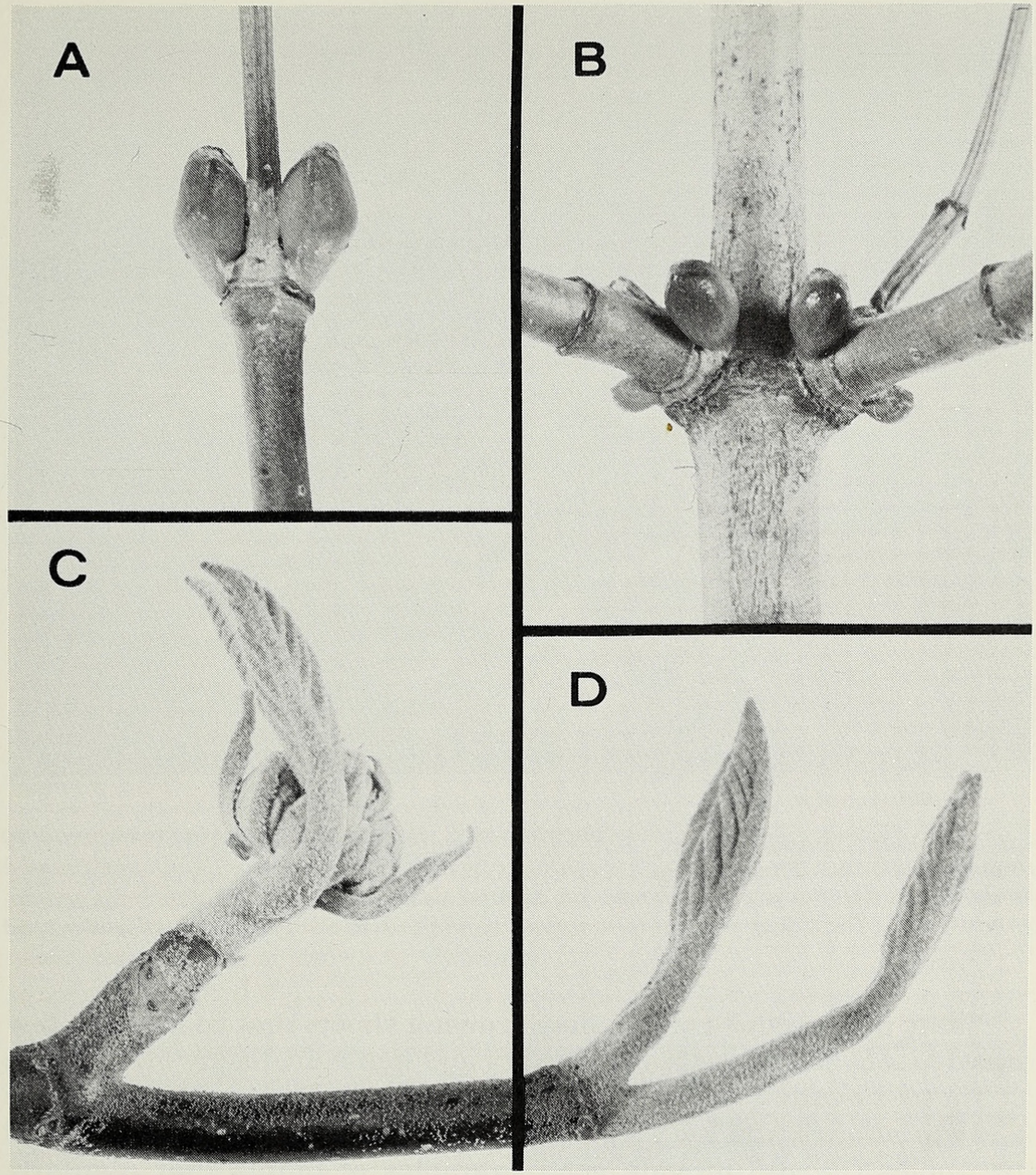

Figure 6. *More* Viburnum *buds. The highbush cranberries,* Viburnum opulus (A *and* B) *and its relatives (section* Opulus*), have two pairs of bud scales but the outer pair are fused along their margins so it appears that there is just a single envelope. The Asian* V. furcatum (C *and* D) *and its eastern North American counterpart.* V. lantanoides *have naked buds. As in the section* Lantana *the well developed inflorescences are exposed during the winter* (C).

reproductive (bear an inflorescence) in a particular year. A few *Viburnum* species (*V. plicatum; V. lantanoides* (the hobblebush, formerly *V. alnifolium*) and its Asian relative *V. furcatum*) produce an orthotropic trunk axis and plagiotropic lateral branches. The plagiotropic shoots result in plants with a very distinctive appearance, even from a distance. Egolf (1962) noted of *V. plicatum* that its "superimposed tiered horizontal branches extended to 15 feet or more" and that this results in "a spectacular pyramid shaped shrub" (Fig. 7). The growth of the plagiotropic shoots of *V. plicatum* differs from the growth of those of *V. lantanoides* and *V. furcatum* as I will detail below under a discussion of shoot growth and branching.

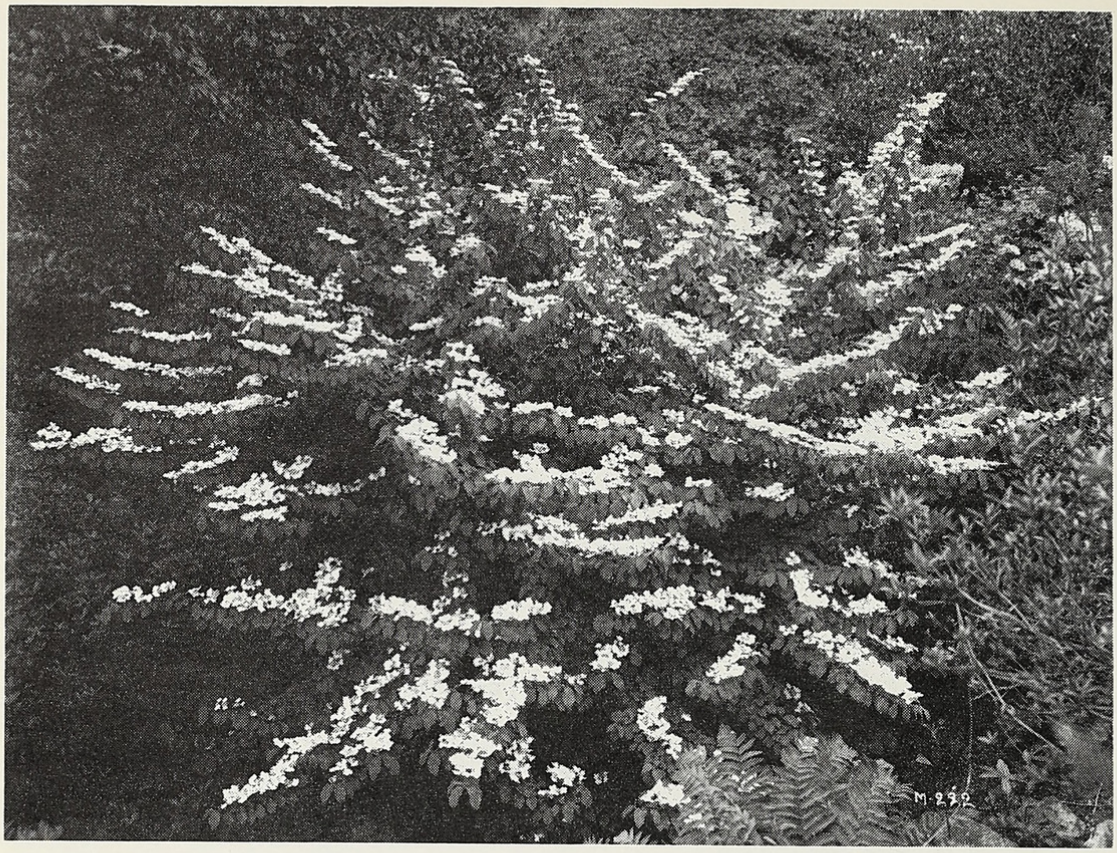

Figure 7. *Photograph of* Viburnum plicatum *by E. H. Wilson illustrating the spreading form of a mature, open grown plant of this species. The inflorescences, each one rimmed by large sterile flowers, are borne on shoots along both sides of the long plagiotropic shoots. The inflorescences turn upward and the distichously arranged leaves tend to droop.*

Plants may produce short, slow growing shoots that bear only a few crowded leaves each season. Flowers and hence fruits are often borne on these so-called "spur" or "short shoots." The maidenhair tree (*Ginkgo biloba*), the katsura tree (*Cercidophyllum japonicum*), and the apples (*Pyrus*) provide good examples of plants that regularly produce short shoots. Such shoots are usually borne laterally along a "long shoot" which has elongate internodes and a greater number of leaves per season. Sometimes a short shoot can be "released" and become a long shoot in subsequent seasons.

Most viburnums do not produce short shoots though sometimes a vegetative branch will grow very slowly and this results in crowded nodes. However, a few viburnums regularly bear their inflorescences on short lateral shoots. In *V. plicatum* the inflorescences terminate short shoots produced by lateral buds at many nodes along both sides of each plagiotropic shoot (see Fig. 9). It is because of this characteristic arrangement that *V. plicatum* is called the "double-file viburnum." A season's growth results in short shoots consisting of a pair of bud scale scars, a relatively short internode, a pair of leaves, and a stalked, terminal inflorescence that turns upwards (Fig. 5c). These short shoots can continue to grow and bear flowers in subsequent seasons. This occurs because one of the lateral buds (usually the bud closest to the center of the plant) below the inflorescence expands and produces another short shoot constructed just like the first one (Figs. 9, 10). *Viburnum farreri* (often called

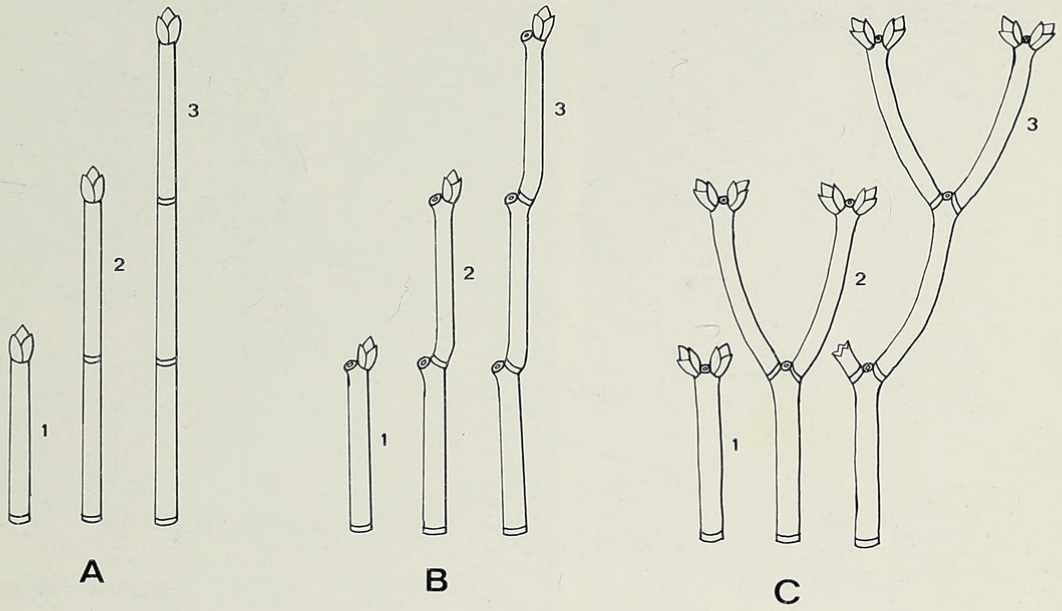

Figure 8. *Monopodial and sympodial growth.* (A) *monopodial growth (renewed growth from a terminal bud); the numbers refer to seasons of growth;* (B) *sympodial growth; successive replacement of the main axis by a pseudoterminal lateral bud;* (C) *sympodial growth; replacement of the main axis each season by two lateral buds. The latter is the most common mode of growth in* Viburnum.

V. fragrans) also produces short shoots. In our area this is the first *Viburnum* to flower in the spring and the flowers open while the plant is nearly leafless (Donoghue, 1980). Its inflorescences terminate very short, lateral segments of stem which bear two pairs of bud scales and usually a pair of leaves.

The growth of a shoot from one year to the next can occur in one of two ways. If a terminal bud is produced from which growth continues during the next season, the growth is said to be **monopodial** (Fig. 8a). If the shoot terminates in a flower or inflorescence, or if its apex aborts, or if it becomes a short shoot, then continued extension growth is possible only if one or more lateral buds grow out and replace the main axis. Successive replacement of the main axis by a lateral branch is called **sympodial** growth (Fig. 8 b,c). In some cases it may not be easy to tell whether growth is monopodial or sympodial. It is very important in this regard to determine if a bud at the tip of a branch is truly terminal or if the apex has aborted and it is a pseudoterminal lateral bud. It is also necessary to determine exactly where the flowers are produced. If a flower or inflorescence truly terminates a portion of stem (i.e., the apical meristem is completely converted into the production of flowers) then continued extension growth of the shoot is only possible if one or more lateral branches are produced. If the

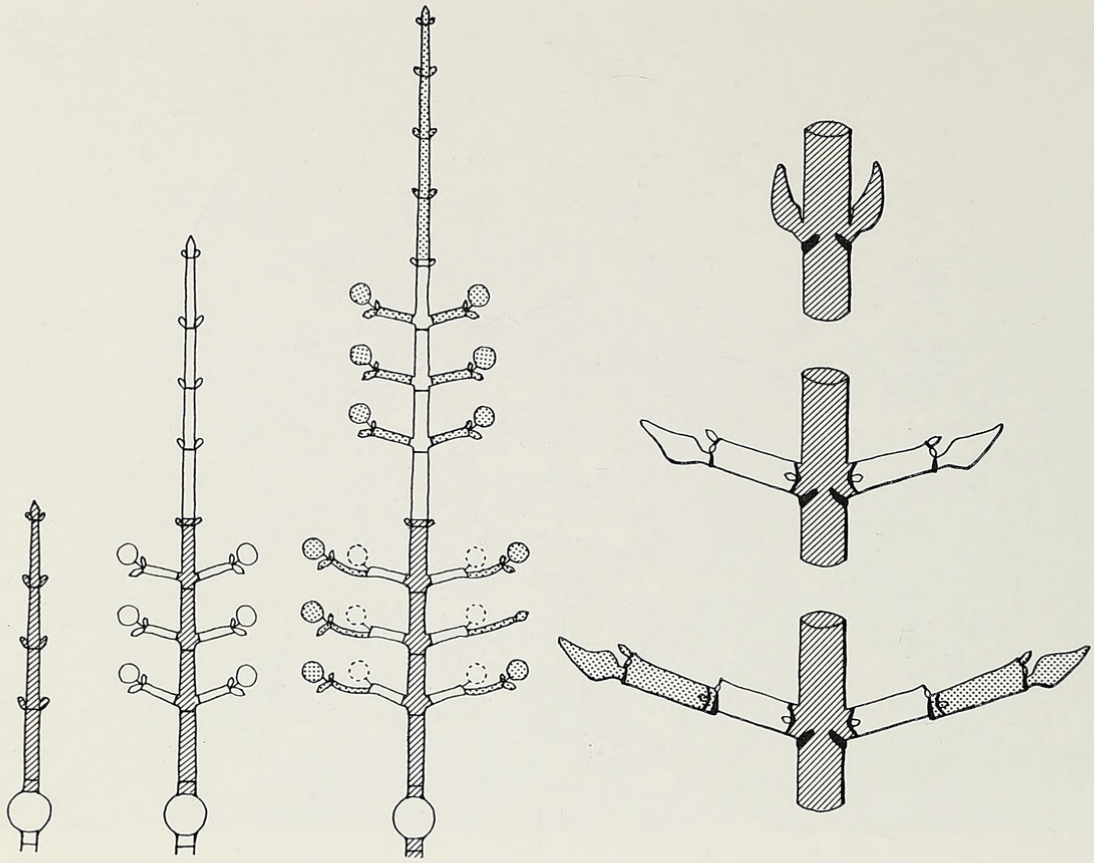

Figure 9. *The growth of a plagiotropic shoots of* Viburnum plicatum. *In this and subsequent growth pattern diagrams, the dotted portions represent the most recent flush of growth, the blank portions represent the growth of the season previous to that, and the slashed areas show the growth of three seasons past.* Right: *looking down on a plagiotropic branch, you should notice that its growth is monopodial, the buds are distichously arranged, and that the short shoots (that bear the inflorescences) are produced along each side of the main axis.* Left: *a closer look at the structure and sympodial growth of the short shoots.*

flowers are borne laterally in the axils of leaves or on short shoots, then monopodial growth of the shoot is possible.

All of the shoots of a plant need not grow in the same way. In fact, it is not uncommon for a central orthotropic trunk to exhibit monopodial growth while lateral orthotropic or plagiotropic shoots may grow sympodially. Sometimes a given axis will alternate between monopodial and sympodial growth. For instance, a shoot can grow monopodially for several years and then terminate in an inflorescence. The growth of the following season will by sympodial. Subsequent growth may be monopodial or sympodial depending on whether a terminal inflorescence is produced in a particular season.

In *Viburnum* the inflorescences are always terminal though in the few cases discussed above they are borne on short lateral shoots. This means that once a particular shoot ends in an inflorescence there must be sympodial growth for the shoot to continue to extend. However, a given shoot can extend monopodially for many seasons before entering a reproductive phase.

Viburnum plicatum and *V. lantanoides* produce both orthotropic and plagiotropic shoots. In both species the growth of the orthotropic trunk axis is

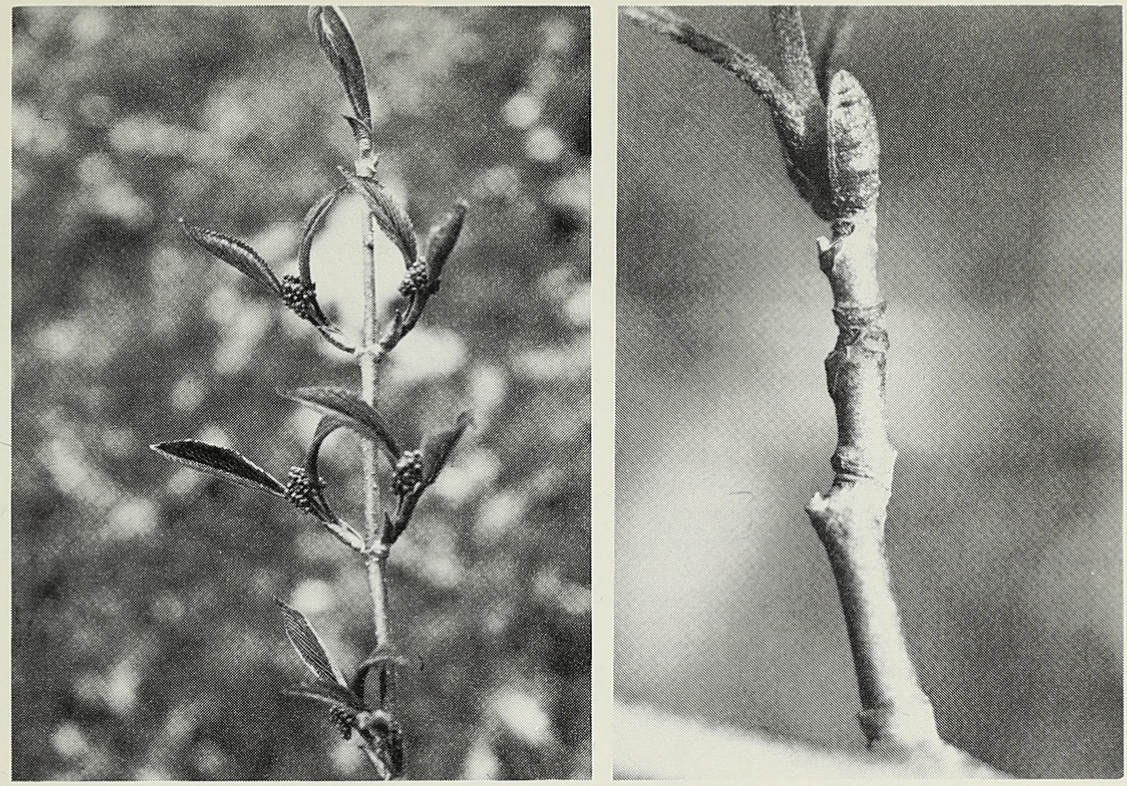

Figure 10. *The growth of* Viburnum plicatum. Left: *a terminal portion of a plagiotropic shoot from above. This picture was taken in the early spring as the buds were breaking and the new shoots were emerging. A new portion of plagiotropic shoot will be produced by the expanding terminal bud at the top of the picture. The lateral buds are developing into short shoots, each with an expanding pair of leaves and a terminal inflorescence.* Right: *A close up picture of a single short shoot that is entering its fourth season of growth. Each season the growth was terminated by an inflorescence and subsequent growth was from one of the lateral buds.*

monopodial for many years but the plagiotropic shoots of the two species differ markedly in growth. In *V. plicatum* the plagiotropic shoots grow monopodially for many years and the inflorescences are borne on the short lateral branches which are, of necessity, sympodial in growth. The tip of the plagiotropic shoot turns upwards towards the end of each season and a long-stalked lateral bud is produced which will continue the growth of the plagiotropic shoot system in the next season. The short upturned axis will bear inflorescences in subsequent seasons (Fig. 11 and Fig. 6 c,d.)

The growth of *V. opulus* (the highbush cranberry or guelder rose, including the American *V. trilobum*) is very unusual in *Viburnum* in that terminal buds are almost never produced and growth is, therefore, always sympodial. Long vegetative shoots are produced that do not end in inflorescences or in terminal buds. Instead, these shoots continue to grow well into the summer until eventually the apex of the shoot aborts and the twig dies back to the last pair of leaves that were produced. The uppermost pairs of lateral buds that were produced grow, during the next season, into shoots that terminate in inflorescences. These reproductive shoots generally die back at the end of the season and in the following year new long vegetative shoots arise from buds in the axils of the first pair of bud scales for each reproductive shoot. This method of growth is illustrated in Fig. 12 and Fig. 6 a,b.

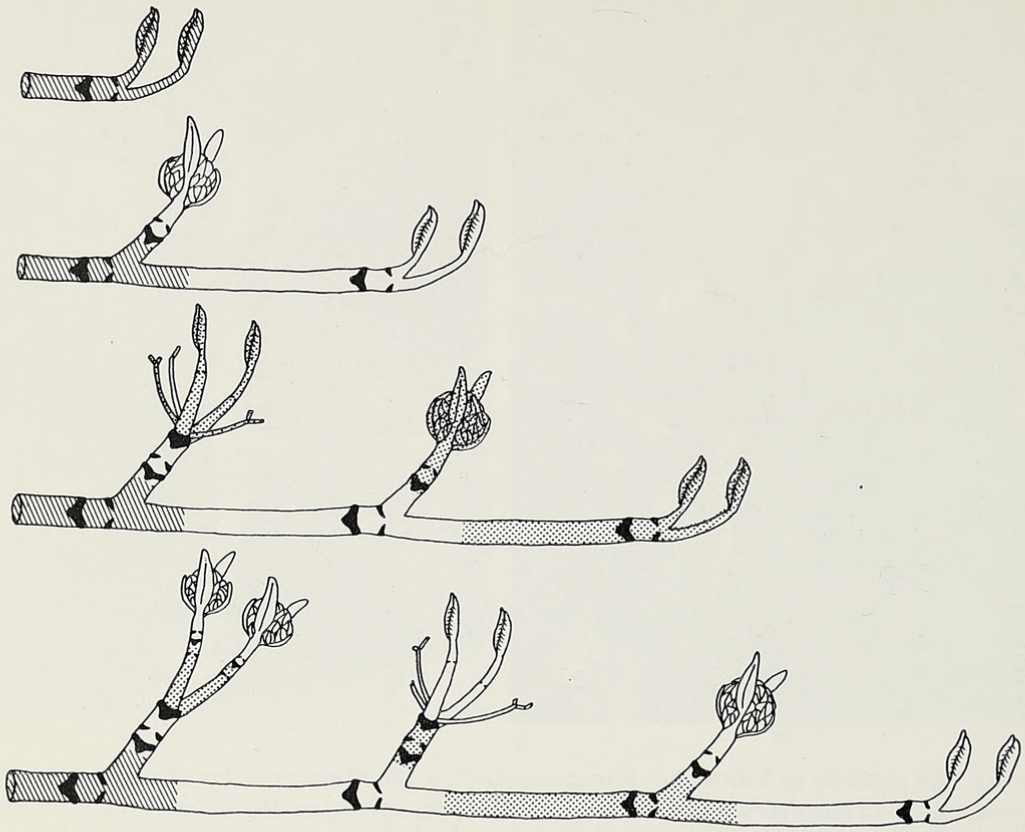

Figure 11. *The growth of a plagiotropic shoot of* Viburnum furcatum. *Four seasons of growth are shown in this diagram. The growth is sympodial; the main axis turns upward at the end of each season and it is replaced by the growth of a lateral bud, which overwinters as a stalked structure (see* Figure 6D*). Inflorescences are produced along the plagiotropic shoot on the upturned portions, which can continue to grow for many seasons. The inflorescences are well developed and exposed during the winter (see* Figure 6C*).*

The Timing of Growth

Some tropical plants seem to grow continuously. They exhibit no morphological evidence of dormancy in that their stems are not obviously segmented and their buds always seem to contain the same number and kinds of parts (e.g., primordial leaves). Some palms provide examples of plants that are "ever-growing" and produce leaves at a continuous rate.

Most woody plants, including all of the trees and shrubs in temperate and boreal regions, exhibit rhythmic growth, that is, periods of dormancy alternate with periods of extension growth in plants with scaly buds. The morphological indication of rhythmic growth is a more or less pronounced segmentation of the mature shoot system. In plants with naked buds it can be difficult to assess the periodicity or growth but a series of shortened internodes or smaller leaves usually indicates a slowdown or cessation of growth.

Growth in *Viburnum* is always rhythmic. In our area viburnums are dormant during the fall and winter and there is a single episode of extension

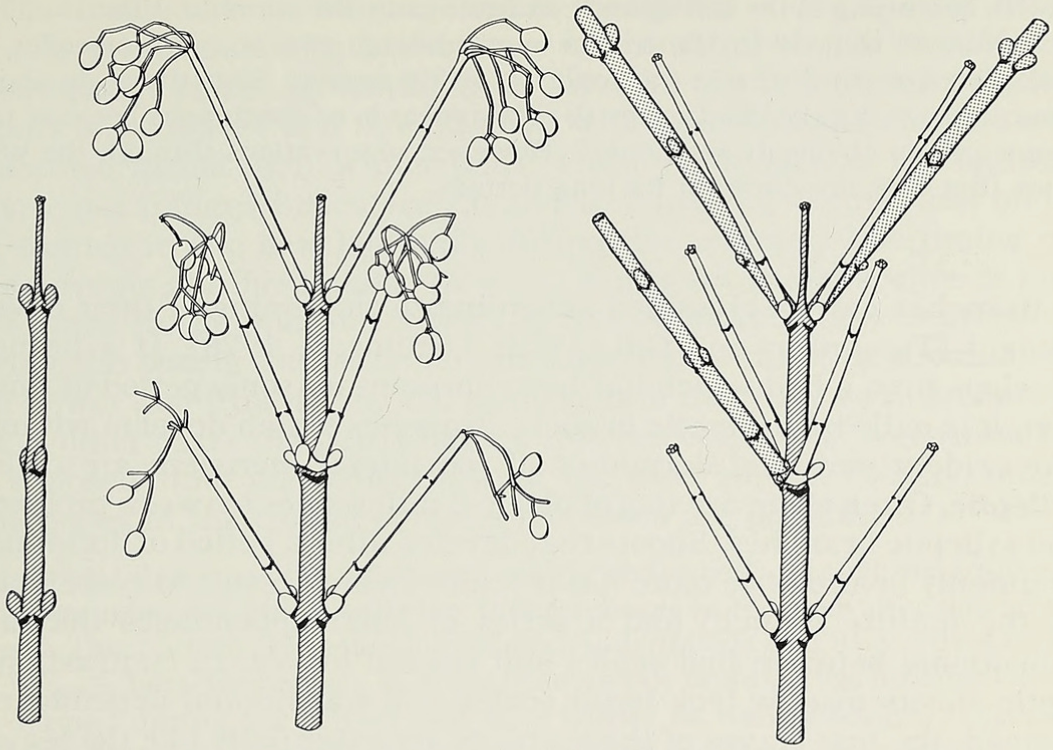

Figure 12. *The growth of* Viburnum opulus. *In this species and its relatives terminal buds are almost never produced. Long vegetative shoots abort at the apex and die back to the first pair of lateral buds (see* Figure 6A). *These buds expand to produce ephemeral shoots that bear the inflorescences. New vegetative shoots are produced from buds at the bases of these reproductive shoots (see* Figures 6B *and* 13).

Figure 13. *The growth of* Viburnum sargentii. *Plants of this species grow like* V. opulus *plants. Here, new vegetative shoots are beginning to grow from buds at the bases of last years reproductive shoots, which have persisted as dead twigs.*

growth beginning in the spring and continuing into the summer. Viburnums of mountainous regions in the tropics may undergo two or more episodes of extension growth during a particular growing season. Sometimes, in those viburnums with naked buds, growth may appear to be continuous because the stems are not obviously segmented. However, observations through the year show that they are dormant for long periods.

Branches can be classified according to the timing of their development (Tomlinson and Gill, 1973; Tomlinson, 1978). If a branch develops from a bud which has been dormant for some period of time, then it is called a **proleptic** branch. Branches which develop without any evident period of dormancy of the lateral meristem are called **sylleptic.** Often there are morphological differences between proleptic and sylleptic branches. Shoots that develop after a period of dormancy commonly bear one or more basal scales (which result in scale scars on the mature branch) and a series of foliar appendages that are transitional between bud scales and normal leaves. In contrast, sylleptic shoots usually lack basal scales and transitional appendages. Instead, the first leaves of these shoots are essentially like the leaves produced later and they are separated from the point of branch insertion by a long internode which has been called a hypopodium. Occasionally, branch morphology can be very misleading about the timing of events. A branch can have developed after dormancy but exhibit the usual morphology of sylleptic branches. This is often true of plants with naked buds because there are no bud scale scars to mark the site of a dormant bud. In some of these cases the first leaves of a branch will be small or differ in shape from subsequent leaves, or the first internodes will be shorter, but this is not always true. It is important to realize that branch morphology can provide clues to the timing of branching but to be certain, plants have to be carefully observed throughout the year.

Branching in most viburnums is strictly proleptic and usually this is clearly reflected in branch morphology. In those species with bud scales, bud scale scars make it very easy to tell when and where there was a period of dormancy. In some cases an inner pair of bud scales may be transitional in appearance to normal leaves but in most cases there is a sharp distinction and sudden change between bud scales and foliage leaves. In most of the viburnums with naked buds, branching follows a period of dormancy but the resulting shoots appear to be sylleptic on morphological grounds.

Sylleptic branching occurs sporadically in many viburnums. It is not uncommon for very vigorous, rapidly growing shoots to produce lateral branches which do not undergo an evident dormancy. In some of the viburnums with naked buds, such as *V. furcatum* (Fig. 6D), conspicuous lateral portions of stem are regularly produced without any evident period of dormancy. These do not bear any expanded leaves during the season in which they are produced and are therefore probably best considered stalked buds rather than sylleptic branches.

The timing of branching relative to the timing of flowering is often of interest and should be noted in any study of growth patterns. Many woody plants of the temperate zone have all of the primordia of the organs (e.g., leaves and flowers) that will expand in the next season preformed inside their winter buds. These buds open in the spring, leaves and inflorescences are expanded, flowering occurs, and buds are formed in the new leaf axils during the summer. The timing of these events can be shifted. In some plants the inflorescence is not preformed in the bud, but rather, is formed as the shoot is growing during the spring and summer. In some cases these inflorescences will flower and fruit during the same season that they were produced but in other cases the newly formed inflorescences will overwinter in an exposed state and flower during the next spring. Clearly, other differences in the timing of these processes are possible.

In most viburnums the inflorescences are preformed and enclosed inside of buds; branches are produced below inflorescences in the year after flowering occurs. This pattern characterizes *Viburnum dentatum* and its relatives (Fig. 14, left; 15, left). In contrast, in *V. lantana* and its relatives the inflorescences are formed during the season and over winter as well developed, exposed primordia (Fig. 5D). Then in the following spring the flowers open while at the same time proleptic branches are produced below the inflorescence (Fig. 14, right; 15, right).

One final, very important consideration is the absolute length of time that a shoot grows in a particular way, because this largely accounts for size and shape in woody plants. For example, if an orthotropic shoot continues monopodial growth for many years, a tall plant with a trunk-like axis will result. If on the other hand, the period of monopodial growth is short and is followed by the production of lateral plagiotropic shoots then the overall stature of the plant will be very different. The number of possible combinations of different amounts of different kinds of growth of different shoots is almost unlimited. There are at least as many combinations as there are differently shaped plants.

THE IMPORTANCE OF UNDERSTANDING GROWTH PATTERNS

Analyzing patterns of growth requires very little in the way of equipment or technical expertise but can provide many valuable insights. Findings in the study of growth patterns will help in assessing the overall diversity of plant morphologies and thus will clarify morphological categories such as the kinds of shoots or the types of branching in plants. This, in turn, will be of interest to anatomists studying the structure of branching points (Wheat, 1980) and to physiologists investigating the flow of water and nutrients in plants (Zimmermann, 1978).

Growth patterns can also be of interest to ecologists and evolutionary biologists since certain kinds of growth may be limited to

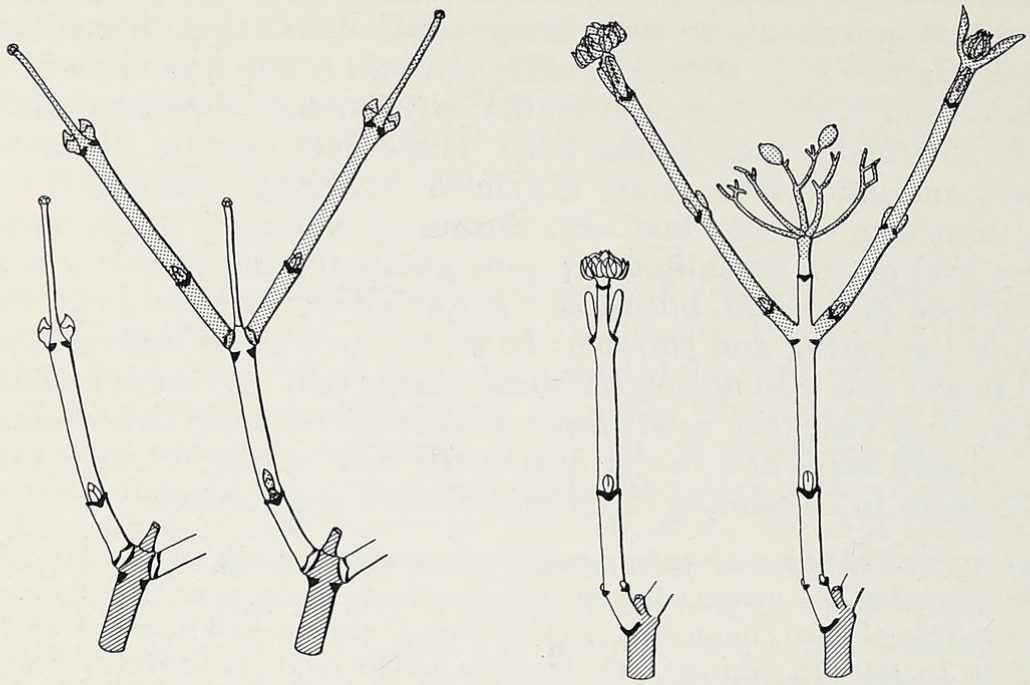

Figure 14. *Differences in the timing of inflorescence development and branch production are illustrated by the growth patterns of* Viburnum dentatum *and its relatives* (left) *and* V. lantana *and its relatives* (right).

particular habitats or certain stages in vegetational succession (Ashton, 1978; Oldeman, 1978). In addition, branching patterns, when correlated with other features such as leaf size and shape, will help us to understand the ways that plants are adapted to different light regimes (Horn, 1971; Fisher & Honda, 1979a,b). Simply understanding how plants grow from year to year may make it possible to quickly age plants and determine the extent of vegetative and reproductive effort over a number of years. A good example of this use of growth patterns is provided by the studies of Sohn and Policansky (1977) on populations of the mayapple (*Podophyllum peltatum*).

An understanding of growth patterns can be useful in agriculture and horticulture as well. It is especially important to know when and where on the plant flowers and hence fruits are produced. This knowledge along with an understanding of the physiology of growth may make it possible for plant breeders to significantly alter growth patterns so as to increase flower production and fruit yields. Landscape architects interested in plants of a certain form for particular settings should understand growth patterns and the extent to which they can vary and be altered. A clear understanding of growth pattern is required before pruning a plant to achieve a desired effect.

Finally, studies of growth pattern, in providing a variety of characters, can be of value to systematists trying to understand the relationships among plants. As Hallé, Oldeman and Tomlinson (1978) pointed out, "clouds of leaves, flowers, fruits, trichomes, and other diagnostically useful characters do not hang somewhere in the air but form part of whole organisms." However, with only a few exceptions (Fagerlind,

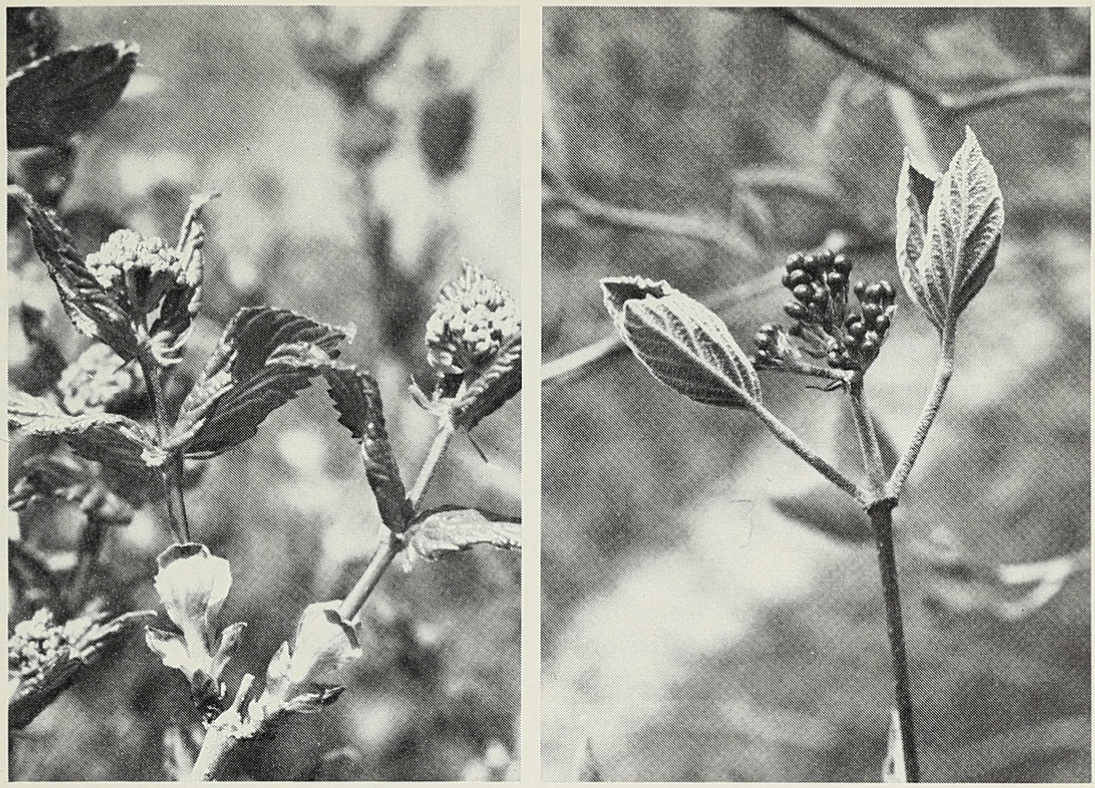

Figure 15. Viburnum rafinesquianum (left) *is a relative of* V. dentatum (*see* Figure 14). *Notice that the new shoots are produced in the axils of the first leaves below last years inflorescence. The buds open and the shoots expand rapidly. The inflorescences, which are still young, will open their flowers within a few weeks.* Viburnum carlesii (right) *is a relative of* V. lantana (*see* Figure 14). *Plants of these species have naked buds and they expand their lateral branches at the same time that the inflorescence on the parent axis continues its development and eventually flowers.*

1943; Lems, 1962; Petit, 1964), taxonomists have made little use of growth characters. Perhaps this is because they often work primarily with herbarium specimens and have field experience with only a few of the species that they treat. But it should be noted that it is often possible to extend an analysis of growth patterns to species that have not been studied in the field. Once some familiarity with growth patterns has been obtained with living plants, it is possible to decipher a great deal about growth by looking at herbarium specimens alone, especially when ample material is available and in groups in which the leaves and flowers are not overly large. If plant collectors were to pay more attention to growth characters the value of herbarium specimens for these purposes could be greatly increased (Ridsdale, 1975). An understanding of the diversity of growth patterns in *Viburnum* is helping me to make sense of the relationships of the species to one another. Along with other kinds of evidence growth patterns provide valuable insights into the evolution of the genus.

The elements of growth discussed above (and some that I have not discussed) can occur together in many different combinations and this results in a great diversity of growth patterns. An extensive terminology has been developed to try to encompass all of the ways that plants can grow. But nature is sufficiently complex that some situations cannot be accurately described with existing terms (Sattler, 1966).

Forcing plant growth into rigidly defined categories would only distort our perceptions of the many different ways that plants are constructed. For the present it is most important to carefully observe and accurately document the ways that plants actually grow.

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