CHAPTER III

GROWTH AND FORM

Claud L. Brown

INTRODUCTION

Trees, because of their perennial habit, massive size, and morphological diversity, present many intriguing problems of growth and development. They are of special interest to the physiologist due to the many correlations existing between leaves and buds, buds and stems, and stems and roots. From an organizational and functional viewpoint, trees must be considered as much more than an aggregate of twigs and branches attached to a common axis. No one cell, tissue, or organ can influence another without in some way having influenced itself. Such physiological "feed-back" is inherent in the organization of multicellular plants; and trees, because of their continued growth in height and breadth, have been the subject of many interesting morphogenetic studies.

Growth, as we have seen in the previous chapters, does not proceed equally in all directions. Beginning with the very first divisions of the fertilized egg, a specific, inherent polarity is established which leads to continued organized development throughout the life of the plant. Thus, the vascular plant becomes an axiate bipolar structure, with the shoot apex at one end giving rise to leaves and buds in an inherent phyllotaxic pattern, and the root apex at the other producing lateral roots in a manner often peculiar to the species. In this chapter we will look at the many ramifications of growth and form in woody plants in an attempt to gain a better insight into the physiological processes controlling these developmental responses.

1. INHERENT PATTERNS OF GROWTH AND FORM

a. Trees and shrubs

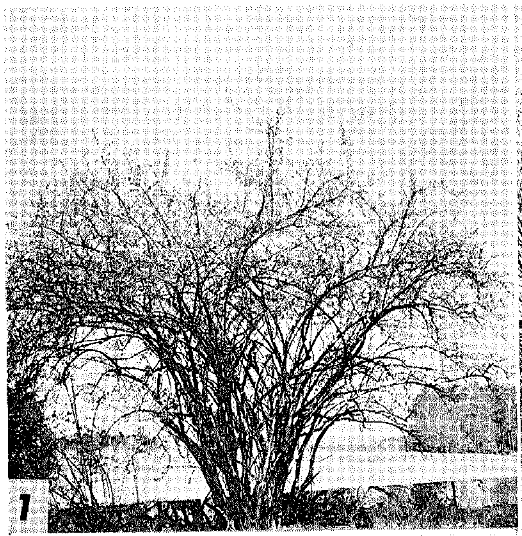
The easily recognized differences between redwoods and mesquite or live oaks and blueberries are so apparent to the casual observer that a discussion of what constitutes a tree or shrub may at first seem pedantic. Yet, there are several distinctions of physiological importance to be made concerning basic differences between these two patterns of growth habit.

Theophrastus, a student of Aristotle, in the third century B.C. attempted a natural system of plant classification based upon trees, shrubs, and herbs. Since that time botanists and foresters have arbitrarily separated trees from shrubs by assigning certain sizes and dimensions to each. In the discussion to follow, we are more concerned with the physiological and morphological relationships resulting in a particular form than we are in establishing criteria to delineate one from the other.

To say that the main differences between trees and shrubs is genetic does not explain the physiological basis for these differences. When one looks at the many different types of woody shrubs, it becomes apparent that their ultimate size and habit of growth may be controlled or modified by vastly different physiological processes or environmental conditions. One cannot generalize by stating that shrubs are smaller than trees because of an initially slower growth rate. In fact, some species of short-lived woody shrubs can successfully compete with, and even outgrow, certain tree species at an early age only to become subordinate a few years later because of a rapid decline in growth rates. In distinct contrast, other shrubs initially possess an extremely slow rate of growth which is maintained throughout their life span.

The shrubby habit of growth has arisen in various ways and may be associated with different physiological mechanisms. Conceivably, either an initially slow rate of growth or a decline in growth at an early age may in some way be linked to fundamental problems of transport in either xylem or phloem, or in both. For example, transport in either tissue could be seriously impaired by the hormonal control of cambial activity resulting in a reduction of xylem and phloem formation. A reduction in phloem transport capacity from leaf to root could limit root extension causing a decrease in water and nutrient uptake with a concomitant reduction in photosynthate so that the potential for height growth is reached at a very early age. One can also think of specific factors that might lead to the shrubby habit in other species. For example, the timing between extension growth and the formation of adequately lignified secondary xylem for mechanical support may result in the formation of drooping or semi-prostrate forms (Fig. III-1). Once a terminal or upright shoot bends out of the vertical, the influence of gravity on rates of transport of growth factors and food is changed. This in turn affects the release of buds from apical dominance (see Section 5b). A continued repetition of this growth pattern causes a sprawling shrubby appearance rather than the upright tree habit.

Other woody plants become shrubby early in life because they sprout profusely near the root collar or produce root suckers at closely spaced intervals along their lateral roots (Figs. III-2, III-3). In these species not only does the genetic potential exist for the formation of numerous adventitious buds, but also the shoot apex loses control over these buds at an early age releasing them from inhibition to form numerous upright stems which successfully competes with the



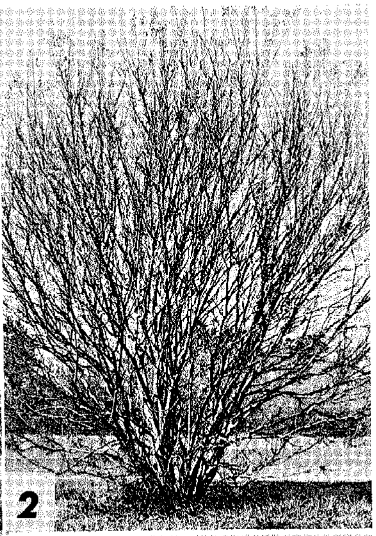


Fig. III–1. Drooping habit of winter honeysuckle (*Lonicera fragrantissima* Lind. and Paxt.) common to many woody shrubs.

Fig. III–2. Crepe myrtle (*Lagerstroemia indica* L.), a woody ornamental which sprouts profusely from the root collar.

Fig. III–3. A clone of sassafras (*Sassafras albidum* (Nutt.) Nees) formed by the growth of root suckers from lateral roots.

original mother shoot. In due time the later formed shoots give rise to additional sprouts until sizable clumps or clones of woody shrubs are established.

Occasionally the shrubby habit arises by mutation among our common forest trees. A typical example of reversion to a dwarf shrubby habit is shown by the mutant form of sweetgum (*Liquidambar styraciflua* L.) in Fig. III-4a. In this particular case the base of the young plant branched profusely near the root collar giving rise to a network of predominately short shoots comprising most of the crown. Occasionally a short shoot reverts to an intermediate long shoot which grows several inches during one season, then reverts again to the typical short shoot habit. Some of the lateral twigs may extend to a length of only 10–15 cm in 6–8 years (Fig. III-4b). Of particular interest in such mutant forms is the physiological mechanism causing this reversion to the short shoot habit. The physiology of short shoots is eminently associated with auxin and other growth factors; in addition, inhibitors are probably involved. The balance of growth factors and inhibitors at any given locus determines whether a short shoot will remain a short shoot that season or revert to a long shoot for one or more seasons. Dwarf varieties such as the sweetgum shown above should prove very valuable in making comparative studies to determine what histological and physiological differences might account for this expression of form.

Many types of woody shrubs near the timber line are adapted to protection by snow cover in the severe winter months, so that their ultimate size is limited by the depth of snow and severity of winter winds.

Before leaving the subject of trees and shrubs, one can recall that the growth habit of some shrubs can be readily altered by judicious pruning and training of the stems so that small trees or tree-like forms can be maintained for long periods

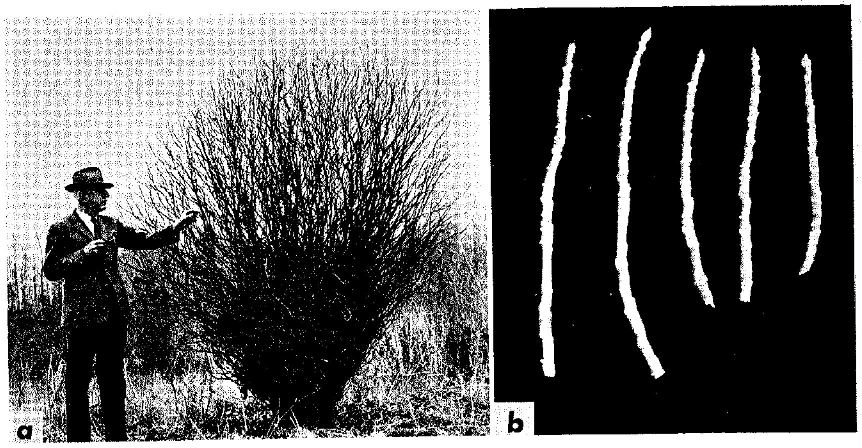


Fig. III–4a, b. Dwarf mutant form of sweetgum (*Liquidambar styraciflua* L.). (a) Propagule from the original parent tree less than 9 feet tall at 25 years of age. (b) Twigs 10–15 cm in length ranging from 3–8 years of age possessing varying degrees of the short shoot growth habit.

of time. The limitation imposed here is one of genetic potential, because it is obvious that growth can only be enhanced to a certain level even under the most optimal environment. The opposite condition can be environmentally induced by dwarfing normal tree species through repeated pruning, or growing them under severe environmental stress. Many examples can be cited in which trees, when grown out of their normal geographic range or ecological niche, acquire a shrubby or semi-dwarf habit because their genetic potential is limited by the new environment. White spruce (*Picea glauca* L.) that makes a well-formed, valuable timber tree in New Hampshire may well become a shrub at the timber line in northern Canada; whereas, wild cotton (*Gossypium* spp.) which grows as a woody perennial in South America can exist only as a semi-woody annual in the southern United States.

The most vivid examples of induced dwarfism in woody plants is the age-old practice of culturing the Bonsai trees of China and Japan. In such practice an extreme reduction of shoot growth is induced by the careful restriction and confinement of the root systems. Of practical commercial importance, many fruit trees including apples, peaches, pears, and plums, are now dwarfed to varying degrees by grafting or budding the desired variety onto genetically dwarfed rootstocks inducing a shrub-like appearance. This practice restricts vegetative growth and promotes the production of flowers and fruits apparently by holding high reserves of carbohydrates in the above-ground portion of the small trees (Sax, 1962).

b. Leaf arrangement and crown form

The origin of leaves and axillary buds and their arrangement into alternate, opposite, and whorled patterns has been discussed in Chapter I. We mention bud arrangement again at this point because it may significantly contribute to the pattern of growth and form of individual branches and the overall appearance o the tree crown. For example, the repeated forking or false dichotomy of maple and ash crowns usually has a diagnostic value in species recognition because it i at once associated with the opposite arrangement of leaves and buds (Fig. III-5a) Many botanists and foresters are unaware, however, that an almost identica crown appearance can also arise from alternately arranged leaves and buds i certain species (Fig. III-5b). Another anomaly is the distinguishing whorled ap pearance of the branches in many gymnosperms which nevertheless arise in very precise alternate pattern (cf. Fig. III-13). Therefore, it is important to recog nize that the final form and shape of tree crowns result from many inherent an environmental influences, and similar forms can develop in more than one wa by modification of the initial branching habit. This enormous range in the r sponse of trees to their environment makes it difficult to classify or categoriz each species on the basis of overall crown appearance, although the growth hab of some trees is so rigidly controlled genetically that they always possess a cha acteristic shape and form.

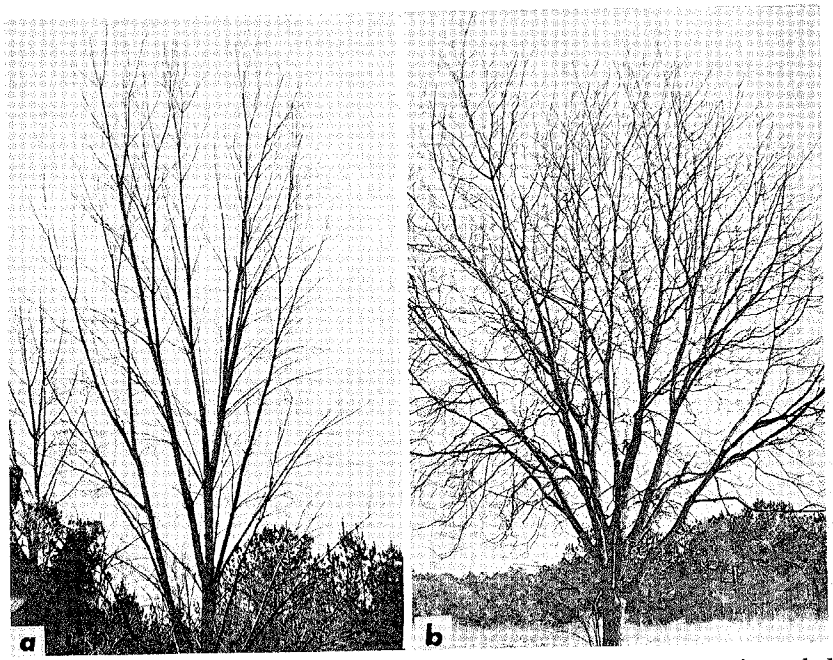


Fig. III–5a, b. Similarity in crown form between certain trees with opposite and alternately arranged leaves and buds. (a) Crown of green ash (*Fraxinus pennsylvanica* Marsh.) showing repeated forking associated with the opposite arrangement of branches. (b) Repeated forking in the crown of pecan (*Carya illinoensis* cv. *Stuart* (Wangenh.) K. Koch) caused by the inhibition and frequent dieback of terminal shoots releasing the alternately arranged branch buds.

2. APICAL CONTROL OF GROWTH AND FORM

a. Columnar, excurrent, and decurrent forms

The form of woody plants is determined by the differential elongation of buds and branches, and the expression of a particular growth habit is commonly associated with the phenomenon of apical dominance. For example, the absence of vegetative lateral buds in most arborescent monocotyledons leads to the columnar growth habit where unbranched stems simply terminate in a tuft of leaves (Fig. III-6a). In most coniferous species and in some dicotyledons the main stem or leader outgrows the lateral branches beneath giving rise to cone-shaped crowns and a clearly defined central bole (Fig. III-6b). This pattern of branching is termed excurrent. In the majority of dicotyledonous trees, notably the oaks, hickories, maples, elms, and many others, the lateral branches grow as fast as, or faster than, the terminal shoot, giving rise to the decurrent or deliquescent growth habit where the central stem eventually disappears from repeated forking to form a large spreading crown (Fig. III-6c).

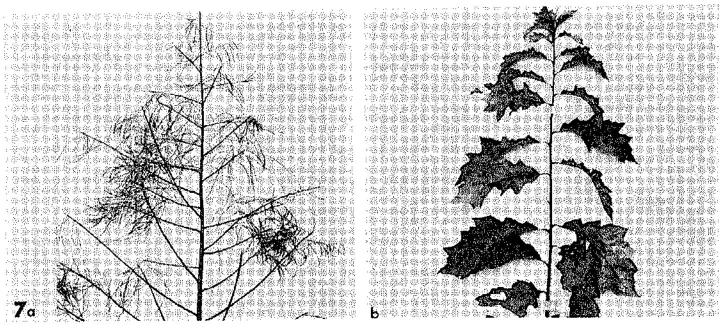
Fig. III–6a, b, c. The columnar, excurrent, and decurrent growth habit of trees illustrated by (a) the royal palm [*Roystonea alata* (Bartr.) Harper], (b) loblolly pine (*P. taeda* L.) and (c) black walnut (*Juglans nigra* L.)

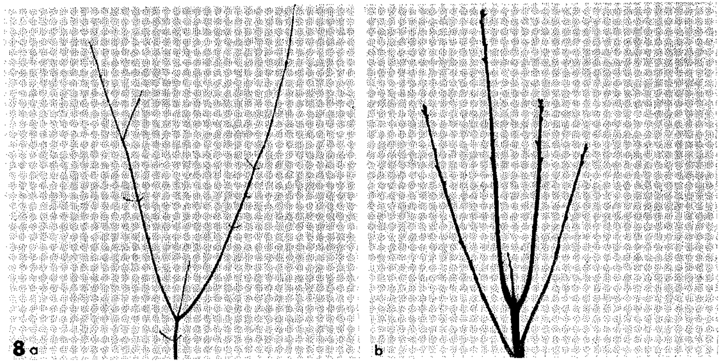
Most foresters and botanists assume the excurrent branching habit to be an expression of strong apical dominance because the terminal leader maintains control over the branches beneath. Likewise, the decurrent or deliquescent branching habit is usually explained on the basis of weak apical dominance because of the profusely branched crown. Brown *et al.* (1967) pointed out that the physiological mechanism controlling these patterns of growth is more complex than formerly realized, and cannot be simply explained in terms of strong or weak apical dominance as in herbaceous plants. For example, in the excurrent forms most of the uppermost lateral buds on the current year terminal leader are only partially inhibited by the actively growing apex (Fig. III-7a), whereas, in the profusely branched decurrent forms almost all of the lateral buds on the current year shoots are completely inhibited (Fig. III-7b). In the decurrent and deliquescent forms during the second season, after a period of dormancy or occasionally during the current season if lammas shoots are formed, one or more of the uppermost lateral buds elongate as rapidly as, or more rapidly than, the terminal bud giving rise to repeatedly branched stems (Fig. III-8a, b).

The interpretation of crown form on the basis of apical dominance undoubtedly came about by attempting to relate the classical work of Thimann and Skoog (1933, 1934) with *Vicia faba* L. to woody plants without having studied the patterns of bud inhibition on individual tree branches. Because decapitation of bean seedlings leads to branching and the bushy habit of growth, it was assumed that trees with the decurrent or deliquescent branching habit must have lost apical dominance. The disparity between the release of lateral buds on herbaceous plants following decapitation and the natural release of inhibited lateral buds on twigs after over-wintering or following periods of drought is obvious, so the relationship between bud inhibition and form in woody plants is not nearly as simple as it might first appear.

The problem of crown form is confounded because of the time sequence involved in the formation and release of lateral buds. For example, we have recently observed that most axillary buds which undergo a period of winter dormancy in the terminal bud fail to elongate during the following growing season. Usually they remain completely inhibited on the current year's shoot, and it is not until the second spring, following another period of winter dormancy, that some of the most vigorous buds in the uppermost position of the shoot elongate. This observation seems to hold true for all decurrent trees in the temperate zones making one rapid flush of growth early in the growing season and forming new terminal buds which become dormant even under the most optimal external conditions for growth. It is of interest that even in the excurrent angiosperms, such as sweetgum (*Liquidambar styraciflua* L.) and yellow poplar (*Liriodendron tulipifera* L.), the preformed lateral buds overwintering in the terminal bud remain completely inhibited during leader extension the following spring. It is those buds laid down by the apical meristem during the current growing season (late leaves and buds, see Chapter I, Section 2) that elongate immediately beneath the active shoot apex.

There are also decurrent species which grow late into the season producing





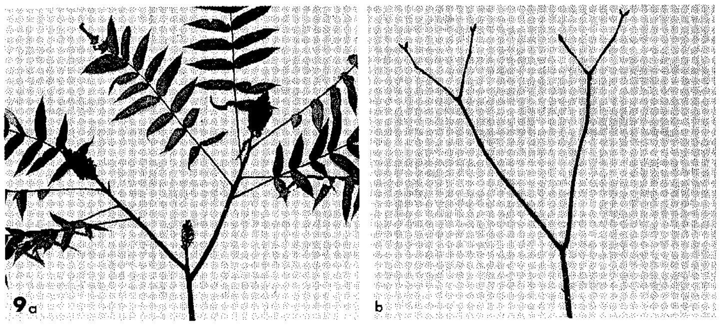


Fig. III–7a, b. Terminal leader of current year's growth in (a) an excurrent conifer, *Taxiodium distichum* var. *nutans* (Ait.) Sweet, and (b) a decurrent dicotyledon, *Quercus rubra* L. Note the extension of almost all lateral buds in the former and the complete inhibition of lateral buds in the latter.

Fig. III–8a, b. Branched stems of (a) red maple (*Acer rubrum* L.) and (b) pecan (*Carya illinoensis* (Wangenh.) K. Koch) due to the release of the uppermost lateral buds in spring. Note inhibition and suppression of vegetative terminal shoots.

Fig. III–9a, b. Repeated forking of (a) *Rhus glabra* L. and (b) *Aesculus georgiana* Sarg. due to formation of terminal infloresenses at an early age.

new leaves and lateral buds which fail to elongate, so that all lateral buds formed during the current and previous season remain completely inhibited. All ring-porous hardwoods we have observed in the temperate zones possess the decurrent branching habit because all of their lateral buds are completely inhibited during shoot extension and leaf development. If growth of these trees occurs late into the season it is by repeated flushes, i.e., the extension of newly formed terminal buds (Lammas shoots), rather than by the continuous formation of late leaves and axillary buds. In contrast, diffuse-porous hardwoods may possess either the excurrent or decurrent branching habit, but the excurrent habit appears to be restricted to those species producing late leaves and buds.

We may briefly summarize our concepts of apical dominance and form in woody plants by stating that the term apical dominance is misleading when applied to tree crowns and that its usage should be restricted to the pattern of bud inhibition on currently elongating individual shoots as originally applied to herbaceous plants. If by definition, the term apical dominance connotes bud inhibition by an active apex on currently elongating shoots, then form in trees must be explained in a manner that will be consistent with the original meaning of the term. Another term, *apical control,* seems better suited for describing the physiological condition governing the excurrent or decurrent pattern of growth. One could then explain the excurrent pattern of growth in terms of strong *apical control* made possible by the initial expression of weak apical dominance or incomplete bud inhibition, so that the terminal leader always maintains complete control over the partially suppressed branches below. Only by this pattern can truly conical shaped crowns arise and be indefinitely maintained. Conversely, strong apical dominance resulting in the complete inhibition of lateral buds on the current year's shoots gives rise to the decurrent habit of growth. The release and rapid growth of two or more uppermost lateral buds the following spring tends to suppress the terminal leader so that apical control is lost and repeated forking occurs in the crown. Although this terminology, viz., *strong apical control* versus *weak apical dominance* and vice versa, may at first seem contradictory, it is consistent with our observations and the general pattern of growth and form in woody plants.

3. MODIFICATION OF FORM WITH AGE

In the preceding section we discussed the general branching habits of trees, i.e., excurrent versus decurrent forms, and their relationship to the phenomenon of apical dominance and the sequence of lateral bud release on individual branches. Although these basic patterns of growth and stem form are inherently controlled by the tree's genetic potential, one must realize that trees are continually exposed to a wide range of environmental conditions during phasic development from juvenility to maturity, modifying crown form in various ways during different stages of development.

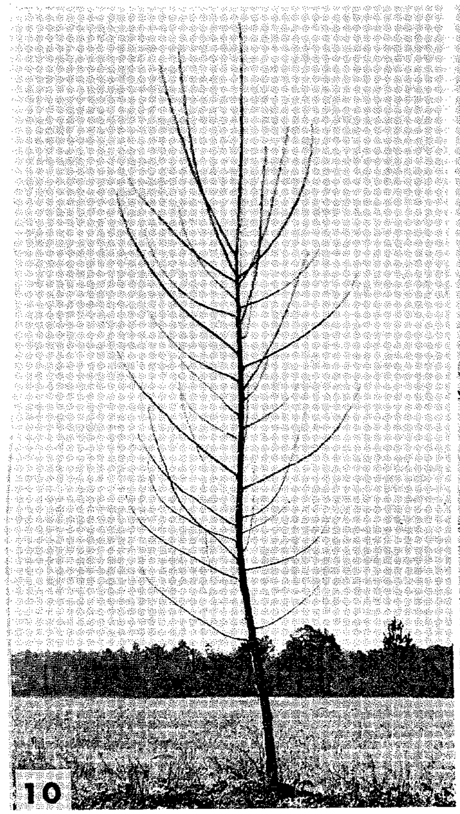
For example, *all* forest trees initially possess the excurrent habit of growth for some period during their early development, otherwise none would exist with an unbranched bole for any period of time. The shift from the excurrent to the decurrent form varies in time with species; nevertheless, vigor, competition (open-grown versus densely-grown), and reproductive patterns play important roles in determining at what time the uppermost lateral buds will develop rapidly enough to suppress or outgrow the terminal leader. In some species the shift comes early and abruptly because of the formation of terminal inflorescenses as in sumac (*Rhus glabra* L. and *Aesculus georgiana* Sarg.) (Fig. III-9a and b); whereas, in other species there appears to be a gradual shift in declining vigor of the terminal leader accompanied by a gradual yearly increase in the vigor of the uppermost competing lateral buds as shown in young cottonwood trees (*Populus deltoides* Bartr.) (Fig. III-10).

The shift of excurrent trees to a decurrent form, can also be brought about at an early age whenever such trees are grown on service sites, especially where available moisture becomes limiting for tree growth (Fig. III-11). Also, in overmature conifers, especially in some species of *Pinus*, the crowns become flat-topped and decurrent because of an apparent loss in vigor associated with their massive size, increased competition among branches, and stresses in long range transport of water, nutrients, and food (Fig. III-12). Twigs from the crowns of old trees grafted onto young rootstocks usually "rejuvenate" rapidly with respect to increased growth and vigor, however, they retain the morphological features of old trees with respect to stem size, coarseness of foliage, and reproductive habits (Fig. III-13).

a. Branch angles and crown form

One of the most striking features of tree crowns is the change in orientation of individual branches from the apex toward the base. With few exceptions, one may observe progressive changes in branch angles and position from acutely oriented branches in the upper crown, through horizontally oriented ones near mid-crown, to the lower, less vigorous, drooping branches at the base. Thus, it is seen that the position of individual branches may change considerably during ontogeny, especially during the early stages of rapid growth, so that during the course of tree development a given branch occupies different angles with the vertical axis. If one follows these changes from the beginning of lateral-branch formation, the initial angle of divergence may be rather acute, even in excurrent species where a strong epinastic response is usually operative (see Section 5a). As the branch extends in length it bends downward so that the angle becomes less acute, while the ends being more responsive to light and gravity tend to turn upward again in many species. Burtt (1899) termed the angle produced during the middle course of growth "angle of inclination" and the angle formed by the turned up tip of the branch "geotropic angle."

Büsgen and Münch (1929) discuss the importance of crown from in the distribution of run-off water from precipitation in and around individual trees. Trees having branches with acute angles of inclination collect run-off water toward the center of the crown and near the main bole; those with more horizontal branches favor the movement of water toward the outside of the crown. There-



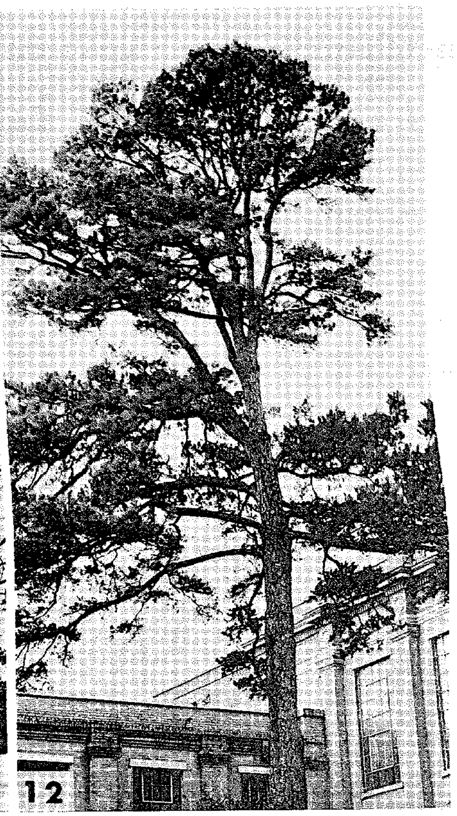


Fig. III–10. Gradual shift to the decurrent growth habit by a young cottonwood tree (*Populus deltoides* Bartr.) growing in an open field. Note uppermost lateral branches strongly competing with terminal leader which will result in early forking of the main bole.

Fig. III–11. A 35-year-old tulip poplar (*Liriodendron tulipifera* L.) growing on a dry, severe site. Note the early shift to the decurrent growth habit and the repeated forking of lateral branches.

Fig. III–12. Shift from the excurrent to decurrent growth habit of shortleaf pine (*P. echinata* Mill.) associated with age and site limitations.

Fig. III–13. Eight-year-old slash pine *(P. elliottii* Engelm.) clonal seed orchard established by grafting scions from older trees onto two-year-old seedling root stock. Note swelling or over-growth of the root stock at the point of graft union. (Photograph courtesy James Wynens, Georgia Forestry Commission).

fore, in young, small trees with acute angles of inclination much of the intercepted water would stay near the developing root system; whereas, in older trees with spreading crowns the water would be channeled further outward to the zone of finer, absorbing roots.

In excurrent species, branch angles are usually less acute than in decurrent forms. This tendency toward horizontal positioning of lateral branches can be interpreted in terms of strong apical control whereby the terminal leader exerts a pronounced epinastic response to counteract the negative geotropic response of the branch. For this reason the lateral branches of most coniferous species tend to develop perpendicular to the vertical axis (cf. Fig. III-7a).

In decurrent trees where the terminal leader is often suppressed, its epinastic effect is lost and the lateral branches tend to grow upward at more acute angles (see Figs. III-8a, b). Two co-dominant lateral branches growing upward at acute angles tend to exert a mutual epinastic effect on each other. If either is removed by pruning, the remaining leader will assume the vertical position (Fig. III-14).

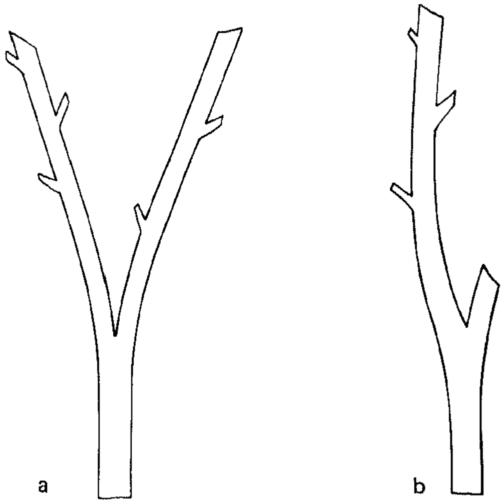


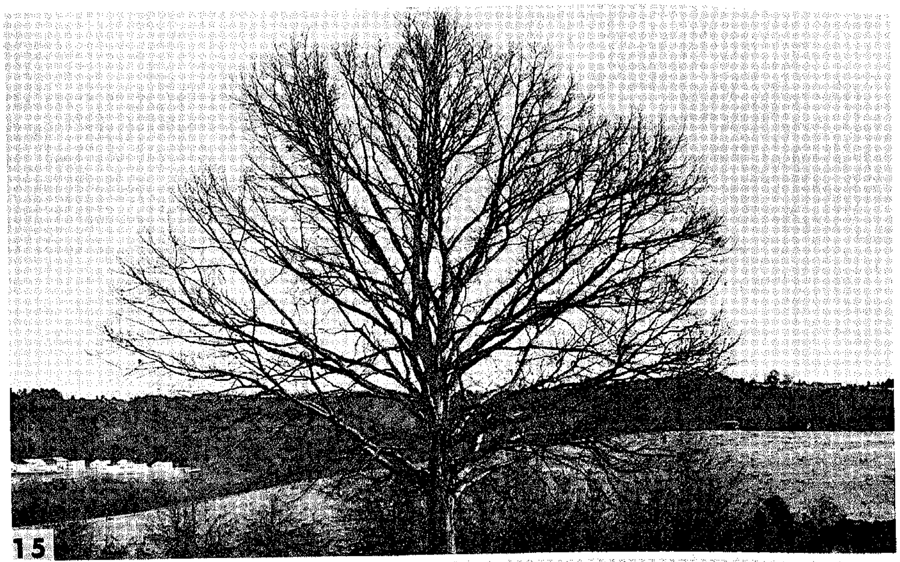
Fig. III–14. Diagram of the mutual epinastic effect exerted by lateral branches (a) and the loss of this effect upon removal of one of the branches (b).

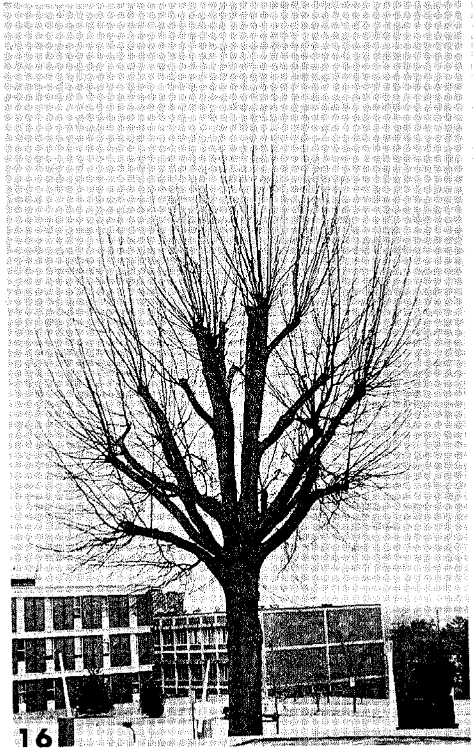
In the profusely branched decurrent trees, many of the uppermost branches, long free from apical control of the main stem at an earlier age, compete with each other for light and growing space and tend to become vertically oriented across the summit of the crown (Fig. III-15). A somewhat exaggerated expression of this condition may be seen in older trees that have been severely pruned (pollarded) which causes the simultaneous release of numerous suppressed or adventitious buds to form an array of upright shoots (Fig. III-16).

Occasionally genetic variants known as fastigiate forms arise in various species in which all branches are formed and tend to persist at acute angles to the vertical axis (Fig. III-17). Such fastigiate variants show a high degree of genetic control over this trait and these forms are often prized as ornamental. However, in selecting superior coniferous phenotypes forest geneticists prefer trees with wide, rather than narrow, branch angles because of the relationships between branch angle and wood quality. Conifers with narrow or acute branch angles are inclined to prune less readily, produce larger knots, and result in greater formation of reaction wood.

b. Juvenile versus adult forms

Many morphological and physiological changes occur in trees during their ontogeny. Plants undergo phasic development in essentially the same way as animals; i.e., they pass through stages of embryonic growth, juvenility, adolescence and maturity, followed by senescence and death. In woody plants these stages are often very pronounced because of their long life cycle. The juvenile stage in trees has received much attention in the past because of the many distinct morphological and physiological changes which occur in the transition from juvenility to sexual maturity. Schaffalitzky de Muckadell (1959) has described





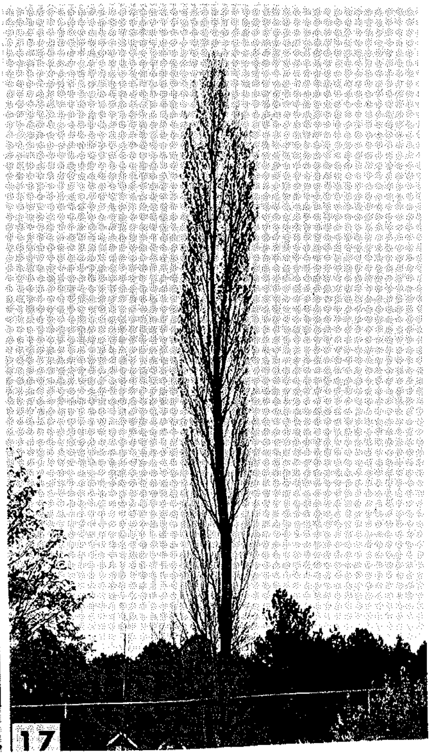


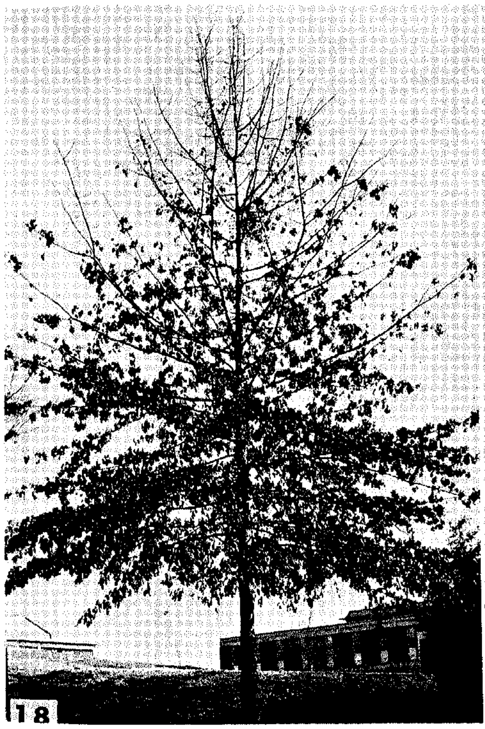
Fig. III–15. Open-grown tree of white oak (*Quercus alba* L.) illustrating the strong negative geotropic response of individual twigs in becoming vertically oriented across the summit of the crown.

Fig. III–16. The release of numerous buds following pruning of a 65-year-old red oak (*Quercus falcata* Michx.). Not how each shoot tends to express dominance and essentially functions as a young individual tree on a common root stock.

Fig. III–17. The Lombardy poplar (*Populus nigra* var. *italica* Muenchh.) with its fastigiate, columnar form is cultivated widely as an ornamental tree.

many of the morphological traits associated with the juvenile habit such as differences in leaf shape and phyllotaxy, growth habit, bark appearance, production of spines or thorns, and retention of leaves by the lower and inner portion of tree crowns Fig. III-18).

Two of the more common physiological traits associated with juvenility are the non-flowering response and rootability of cuttings. Of particular interest is the general observation that each of the traits mentioned so far may be transmitted by vegetative propagation. Although vegetatively propagated offspring from the juvenile stage normally proceed to the adult stage in their normal ontogeny, the duration of the juvenile stage in some trees may persist for 50 years or more (Sax, 1962). Apparently some conifers remain in the juvenile stage for



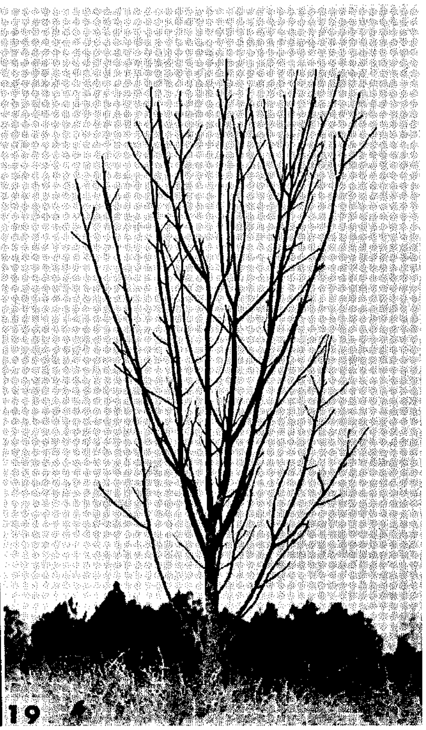


Fig. III–18. Retention of leaves during the winter months on lower branches of scarlet oak (*Quercus coccinea* Muenchh.), a juvenile trait common to many deciduous hardwoods.

Fig. III–19. A five-year-old tulip poplar (*Liriodendron tulipifera* L.) growing on a dry, severe site in the Georgia Piedmont. This species normally makes strong excurrent growth up until 35–50 years of age on average to better than average sites even in open-grown situations. Note the shift to the decurrent habit during its second and third growing season.

their entire life, such as the "Retinospora" forms of *Thuja* (Beissner, 1930). Woyciki (1954), however, in attempting to produce the "Retinospora" forms from cuttings taken from the juvenile portion of *Thuja, Chamaecyparis,* and *Biota,* found that the juvenile foliage did not persist. He concluded that the "Retinospora" forms arose by somatic mutations in the seedlings or young shoots. Although some controversy may exist over the duration of the juvenile period in these forms, the juvenile condition can be maintained for long periods of time in several plants by vegetative propagation.

Molisch (1930) used the term *topophysis* in describing those cases in which cuttings taken from a certain part of the tree retain the characteristics of that portion of the tree for extended periods of time but which do not involve a genetic change. Thus, in the strictest sense, any juvenile trait which persists for any length of time after grafting or propagation that happens to be related to position, can be termed a topophysis phenomenon. One of the often used examples of a true topophysis effect, not necessarily related to a juvenile characteristic, is the persistence of the flattened, dorsiventral habit of lateral branches from *Araucaria* trees (see Fig. III-26) when grafted into a terminal position. Such branches fail to gain apical control and continue to grow in a horizontal position with respect to gravity. This example is rather atypical, however, because the lateral branches of most trees when grafted onto young rootstock do develop as normal plants.

To foresters the physiological aspects of aging in trees often become of more interest than morphological ones because they directly involve sexual reproduction and rootability. Although it has been claimed by Braddick (1822) that scions from seedling trees can be induced to flower early by grafting them onto older flower bearing branches, many attempts to hasten flowering in fruit trees and forest species have failed (Sax, 1962). The reverse effect has been claimed by Michurin (1949); i.e., that adult flowering branches when grafted onto seedlings promote earlier flowering. These observations have not been widely observed, however, and they remain controversial for the present.

The rooting response of woody plants in relation to juvenility was noted by Goebel (1898) in conifers and has since been confirmed by numerous workers. Most woody plants can be rooted from seedlings, but the ability to form roots seems to decrease rapidly with increasing age. In fact, it is almost impossible to root some conifers even at five years of age, and some fail to root at all even with the application of so-called "rooting hormones" under optimal conditions for propagation where light, humidity, and temperature are controlled.

In some species, cuttings from lateral branches root more easily than those from the upper part of the tree (Thimann and Delisle, 1939); however, this generalization cannot be applied to most adult trees. In young trees the lower branches may retain some degree of physiological juvenility, but in older trees they usually lose vigor and root with difficulty or not at all. The early observations of Knight (1795) that the basal part of the tree retains its juvenility appears, in general, to hold true, and numerous trees that cannot be propagated from the lower lateral or terminal branches can be perpetuated by using stump or root sprouts. In many species these sprouts can be induced to form by partial or complete girdling of the main stem near the ground. There is also some indication that suppressed buds along the lower portion of the bole, when released by girdling to form epicormic branches, retain their juvenile condition with respect to ease of rooting (Kormanik and Porterfield, 1966).

Moorby and Wareing (1963), in reviewing certain aspects of aging in woody plants, referred to these relatively stable (graft transferable) morphological and physiological characteristics as *maturation,* whereas they used the term *aging* in a more restricted sense to describe certain reversible physiological changes occurring during the life of the tree. Some of the changes they studied were reduced annual growth increment, decrease in geotropic responses, and loss of apical dominance. All of these conditions are easily reversible by grafting older scions onto young seedlings.

The results of various pruning experiments conducted on young trees of Scots pine (*Pinus sylvestris* L.) and Japanese larch (*Larix leptolepis,* Sieb. and Zucc.) led Moorby and Wareing (1963) to conclude that these aging processes were directly related to competition for nutrients among individual branches and that apical dominance played an important role in the distribution of available nutrients. Their conclusions were supported by tracing the accumulation of ^{32}P in different aged twigs on 3-year-old branches in association with the pruning treatments.

Although competition for available nutrients is involved in loss of vigor of subordinate twigs and branches, the distribution and availability of water may be just as important in large trees growing under natural conditions. In fact, each of the physiological traits studied by Moorby and Wareing is easily induced even in young plants grown under high soil-moisture stress (Fig. III-19). As mentioned in our discussion on apical control of growth and form, the shift from the excurrent to decurrent branching habit in older trees is associated with massive increases in size; therefore, competition for water and nutrients, coupled with problems of long-distance transport in both directions, undoubtedly influences the vigor and growth patterns of individual shoots. The fact that competition among branches is a significant factor in determining crown form is clearly shown by the higher ratio of short shoots to long shoots with increasing age in tree crowns. Wilson (1966), in a quantitative study of bud and branch distribution in red maple (*Acer rubrum* L.), found that over 90 per cent of the buds in older trees developed as short shoots.

Hence, aging in woody plants involves both permanent and temporary changes in relation to time and position, and these changes can ultimately be traced to the cells of the meristems. What causes these changes in apical and lateral meristems? Some support the viewpoint that the aging of meristems is determined by the materials supplied to it by the rest of the plant. That is, the cells of the meristem themselves do not change or age during the life of the plant, rather the morphological and physiological differences observed between juvenile and adult stages, or in different locations, result from the quality and quantity of the substances reaching the different meristems as the tree grows older and more massive. The distribution of inorganic nutrients, carbohydrates, amino acids, and various growth substances, are known to be influenced by water stress and competition, and some researchers maintain that it is the balance of these factors which determines the various aging phenomena.

Other workers assume that the meristems themselves age; i.e., they undergo change during the life of the plant so that there are young meristems and adult meristems on the same plant. The response of each meristem is still affected by the substances brought to it from the other part of the plant, but the response to any substance may differ because the meristems themselves are different. Evidence can be presented to support either of these viewpoints because some aging traits are readily reversible when the meristems are treated in certain ways, whereas others are stable.

The latter viewpoint appears to be more consistent with the concept of phasic development of plants in which different genes are turned "on" and "off" with varying degrees of difficulty or ease. In adult meristems, the genes controlling form seem more stable than those controlling certain physiological mechanisms, and once "turned on" cannot be reversed to the perhaps less stable juvenile condition. Even some physiologically controlled processes, such as the flowering response, a typical adult trait, are exceedingly stable. Once the genes for the production of "florigen" are turned on, they apparently are difficult to reverse.

The problems of aging in trees are complex and much remains to be learned about the causal mechanisms involved. One might ask, why some cells remain functional for years; whereas others, even in the same plant, exist for only a few hours. Or why the seeds of some trees such as the poplars and willows are short-lived, while those of certain legumes may remain viable for a hundred years or more? The biochemical processes associated with aging, senescense, and death constitute one of the many fascinating areas of biology today.

4. GROWTH CORRELATIONS AND FORM

a. Types of stimulatory and inhibitory responses

The massive size obtained by woody plants is made possible by correlations between extension and radial growth. Extensive shoot and root development can only occur in gymnosperms and dicotyledons if secondary tissue is formed to give mechanical support while providing a bi-directional pathway for long-distance transport of water, nutrients, and foods.

It is clear that growth in one part of a plant affects what occurs in another part and that each must in some way be integrated into an organized whole. This integration is accompanied by various types of physiological correlations in higher plants. Some correlations may be purely nutritional, in which the growth of one part is dependent upon food produced in another. For example, root growth is completely dependent upon food and certain growth factors (vitamins and hormones) produced by the leaves. Similar nutritional correlations are readily observed between leaf area and fruit size, or crown size and stem growth.

Another type of nutritional correlation which involves more than just the transfer of foods and nutrients from one part to the other, can be shown by the removal of mobilization centers. Goebel (1928) described growing organs (shoots, leaves, fruits, etc.) as "attraction centers," which under normal conditions draw to them ions, carbohydrates, and nitrogenous compounds needed for synthesis. If such centers are removed, the growth of remaining meristematic centers is enhanced. This response is referred to as a *compensatory correlation* because of the compensatory increase in the growth of the remaining structures. Horticulturists often take advantage of this compensatory response by mechanically or chemically thinning young fruits so that the remaining ones will grow larger. *Topiary,* the art of training shrubs and trees into unnatural shapes by removal of certain buds to stimulate the growth of others, utilizes compensatory correlations.

Other growth correlations are of a more humoral nature and result in promoting or inhibiting a certain response. For example, growth factors such as auxins, cytokinins, and gibberellins interact with natural inhibitors or with themselves in such a way that the balance of these substances may cause either *stimulatory* or *inhibitory* responses. Young leaf primordia and immature leaves may exert a pronounced stimulatory effect on the elongating internodes beneath apparently through the growth-promoting activity of auxin and auxin precursors they produce. In other cases, leaves are known to exert inhibitory effects on axillary buds, or even the terminal bud of the main shoot (see Chapter I, Section 4c).

One of the best examples of a stimulatory effect of one structure on another is the effect of young, developing ovules on fruit set and size. Nitsch (1950) has clearly shown that the presence of young developing achenes promote the growth of the receptacle in strawberries, and the natural stimulatory effect can be replaced by the application of synthetic auxin to receptacles where the achenes are artificially removed.

Many growth relationships may be traced to inhibitory correlations, i.e., one part inhibits the growth of another by some means other than competition for food. A classical example is the phenomenon of apical dominance in which auxin produced by the actively growing apex or expanding terminal bud inhibits the growth of the lateral buds beneath. In other cases, natural inhibitors produced in one place may also exert their inhibitory effect in another (see Chapter I, Section 8b).

Our present concepts of growth correlations in woody plants are constantly changing by the discovery of additional naturally occurring growth promotors and inhibitors. A few years ago almost all humoral responses were explained solely on the action of naturally occurring auxin, i.e. indole-3-acetic acid; whereas, today workers are beginning to think in terms of growth hormone interactions and levels of different substances in controlling the biochemical machinery of cells and tissues. This should in no way be interpreted to mean that auxin is indirectly involved in correlation phenomena; rather, it points out that growth factors other than auxin are also important in determining what process(es) can proceed at any given time.