b. Relationship between extension growth and radial growth

Some of the early observations on the relationship of stem growth to diameter growth were made by Theodor Hartig (1862) who showed a causal relationship between shoot growth and cambial activity. Later, Jost (1891, 1893) revealed that an ample supply of nutrients did not cause diameter growth unless the cambium was first activated by some stimulus coming from the young growing shoot. Jost demonstrated this by debudding shoots of *Pinus* and *Rhododendron* and observed that even in the presence of leaves the stems did not grow. He also showed that the stimulus was not transmitted below a girdle and that it was always basipetal in nature, being transported through the bark. Coster (1927) confirmed the findings of Jost and interpreted them in terms of a hormonal stimulus. Since this time numerous workers have contributed to our knowledge of cambium activation, yet there are still many questions to be answered about the physiology of cambial activity (see Chapter II, Section 1g).

Münch (1938) extended some of the earlier work on debudding and girdling of young seedlings to older trees and added considerably to our knowledge of the relationships between stem and branch diameter growth at various points along the bole. When Münch began his work in the mid-thirties the general concepts of cambial growth at that time could be summarized as follows: (1) growth hormones were produced in expanding buds and young leaves which not only stimulated growth of the shoot, but also stimulated the cambium into activity in the stem beneath, (2) the movement of the growth hormone(s) occurred in the bark in a basipetal manner, and (3) assimilates moving in the bark could move equally well in both directions and normally to the places where growth was stimulated by the growth hormone itself (Chapter V, Section 2c).

In his early experiments, Münch completely debudded young white pine (*Pinus strobus* L.) trees before the initiation of spring growth and carefully followed the activity of the cambium in the branches and stem beneath. To his surprise, and in contrast to the experiments of earlier workers with angiosperms, the suppression of extension growth by debudding inhibited cambial activity in the young branches and stems but promoted it in the older portion of the tree. A decrease in cambial activity was found only near the shoot tips in the first- and second-year portion; the third-year portion of branches and the main stem was normal or above, and in older portions of the tree bole further down cambial growth was greatly increased over the controls. The effect of debudding caused a downward shift of diameter growth in both stem and branches (Fig. III-20).

In additional experiments, all twigs on another group of white pines were debudded except the weakest twig in the uppermost whorl which quickly became the dominant leader. The former debudded leader grew very little in diameter, whereas the main stem grew equally well and there was no downward shift of cambial activity as in the first experiment. Growth of the stem immediately adjacent to the new leader was quite eccentric however, but a short distance below the eccentricity completely disappeared.

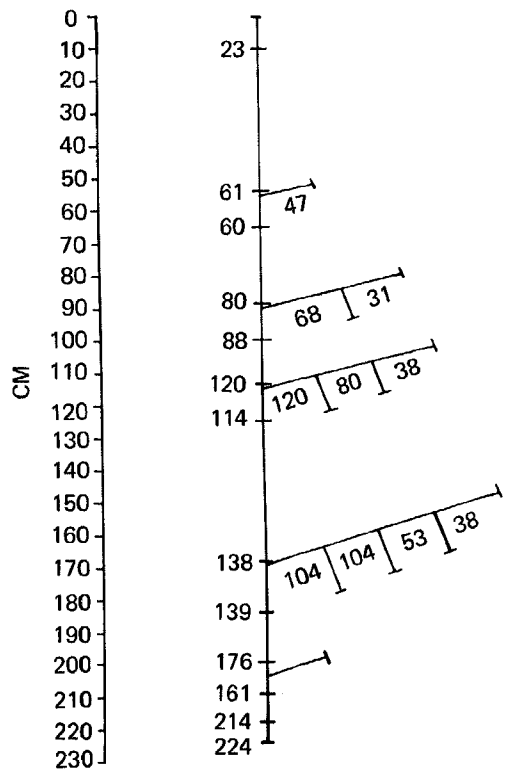


Fig. III–20. Diagram showing the effect of debudding young white pine (*P. strobus* L.) trees on the growth of the main axis and lateral branches. Figures to the left of the stem and beneath the branches indicate diameter increment during the year of debudding as percentage of the previous year's increment (after Münch, 1938).

In other experiments, Münch studied the effects of defoliation alone, as well as defoliation and debudding together, on cambial activity and distribution of growth along the stem. In the completely defoliated trees the buds grew out very slowly to form "brush shoots," and cambial activity was greatly reduced. Apparently the new needles and reserve materials were insufficient to supply the cambium with ample food in these young trees. In trees which were defoliated and debudded at the same time, the cambium failed to become active and no increment was added. This confirmed the observations of Th. Hartig (1862) that completely defoliated and debudded young white pines failed to grow in diameter, although Münch mentioned that Robert Hartig did obtain some diameter growth in older trees following the same treatment.

Because debudding without defoliation in the earlier experiments of Münch caused a downward shift in the amount of diameter growth, additional trees

were debudded and girdled near the base to determine if some stimulus were moving upward from the roots through the bark. This treatment had no apparent effect, however, on the downward increase in diameter growth. If such a stimulus came from the roots, it was transported in the xylem.

Also, in the debudding experiments it was noted that the lower lateral branches possessed most of the tree's foliage. The question was raised if the abundance of foliage on the lateral branches directly contributed to the increased growth toward the base following debudding. Pruning of the lower branches of debudded trees did reduce diameter growth all along the bole, but the basal portion still added more increment than the upper part nearest the debudded shoots. In distinct contract, when the lower branches were debudded and the terminals left intact, there was an upward shift in the pattern of growth. The uppermost portion of the bole grew more than the lower, indicating the mobilizing effect of the upper growing shoots on diameter growth in the upper portion of the main stem.

In studying the time course of cambial activity in the control and treated trees, Münch found that the debudded trees stopped growing considerably earlier in the upper portion, but the lower part of the bole grew as late as the controls and even at a greater rate. Thus, not only was the pattern of growth shifted downward by debudding, but the debudded trees had a greater total volume than the controls.

Münch (1938) explained the results of these experiments in terms of both stimulatory and compensatory correlations. Debudding caused a pronounced decrease in the level of auxin in the upper portion of that shoot and a concomitant decrease in diameter growth at that point. The older needles apparently contributed enough auxin to stimulate the cambium into activity beneath. With the mobilizing effect of the uppermost debudded branches removed, the carbohydrate normally attracted to them was free to go elsewhere; hence, the cambium beneath was stimulated into greater activity because of increased nutrition. Some may object to Münch's conclusion that the older needles on debudded twigs of white pine stimulated diameter growth beneath on the assumption that the debudding created a wound response and therefore the formation of auxin; however, Münch pointed out that the cambium of white pine becomes active in early spring long before the buds show any growth. We now know this condition also occurs in ring-porous but not diffuse-porous hardwoods (see Chapter II, Section 1f).

Thus, in looking at growth correlations between extension and radial growth, there is ample evidence that growing shoots have a definite influence on the amount and distribution of growth in the stem beneath. This effect is more noticeable in young trees than in older ones because of problems relating to transport and competition among different branches of massive tree crowns. Although growth factors are produced in copious quantities in young extending shoots, they are also produced in older shoots and leaves and undoubtedly in the cambium itself. The pattern of cambial activity and distribution of growth differs, as we have seen in Chapter II, between ring- and diffuse-porous hard-

woods and gymnosperms, the latter being more like the ring-porous hardwoods so that rapid extension growth has less effect on diameter growth in this group than others. Nevertheless extension growth and cambial activity interact to produce the final form of the tree. It is significant that shoot extension has such a direct pronounced effect on secondary activity whereas the cambium has virtually no effect on shoot elongation. This difference in response is only natural because the initiation of secondary activity evolved from, and under, control of the primary plant body.

5. EFFECT OF GRAVITY ON FORM

Gravity, because it is continuous, uniform in intensity, and constant in direction, is one of the most important formative factors in plants. Land plants must constantly regulate their growth with respect to gravity because they are restricted to the site in which they develop. The physiological mechanisms for adapting plants to respond to gravity are relatively simple in some instances but unusually subtle in others. For example, the well known opposite geotropic response of roots and shoots in the young developing plant is attributed to the unilateral displacement of auxin on the lower sides of these organs which causes a rapid differential growth response. Auxin accumulation on the underside of the young epicotyl stimulated the cells to elongate more rapidly in this region thereby causing the stem to turn upward; whereas, in the primary root the cells on the lower side are inhibited resulting in the downward curvature of the young root. This explanation of the geotropic response in young plants has not gone unchallenged by plant physiologists, and the question is often raised as to how auxin (indole-3-acetic acid), in such low physiological concentrations and even in adjacent tissues, can promote growth in one instance and inhibit it in another. The most plausible explanation is that the sensitivity of cells in different tissues differs markedly in respect to auxin action, and one can readily show in the laboratory that the level of auxin which inhibits root growth greatly enhances the growth of shoots. This principle, in fact, has been the basis for developing very sensitive auxin bioassays using excised roots of different species.

Rigid geotropic responses in early life usually become modified as trees become older and more massive in size. One should recognize that a wide range of differences exists in species response; for example, some trees such as the spruces and firs are more responsive to geotropic effects at maturity than many broad-leaved trees at a much younger age. The shape or form of the tree crown as already shown is associated with inherent branching patterns which permit an optimal utilization of space and light. Branches do not grow randomly in various directions, but are regulated in their direction of growth by the interaction of gravity and light on internal hormonal mechanisms. Trees with excurrent form exert a high degree of apical control over the direction of growth of the lateral branches beneath. One would expect this condition because strong terminal leaders are more geotropically active or sensitive than first-order branches; and the latter, more responsive to gravity than third- or lower-order branches. In

decurrent species with tree crowns consisting of myriads of separate shoots which occupy different angles with the vertical, strong apical control is lacking. In both forms, however, there is a constant regulation of branch angle with respect to gravity and the position of other branches. This regulation and positioning of lateral organs (shoots and roots) in space is termed *plagiotropism.*

a. Plagiotropism

Since the middle of the 19th century, many workers have attempted to answer the questions of why lateral branches grow in a certain direction or in a characteristic pattern in different species, and why branches displaced from their position in respect to gravity respond in a specific way to regain their original position. During the late 1800's numerous observations were made on the responses of lateral branches to decapitation of the terminal leader, and the subsequent growth of such branches when placed in different positions with respect to gravity. From such studies DeVries came to the conclusion that the inclined position of lateral branches was the result of two opposing forces: (1) negative geotropism which tends to erect a twig, and (2) epinasty which tends to depress it.

Following the isolation of the native hormone in plants in the early 1930's, interest was renewed on the mechanism of control of plagiotropic growth in woody plants. Münch (1938), in a series of experiments with several coniferous species (mostly spruces and firs), repeated and confirmed many of the earlier observations of DeVries and extended these observations to different-aged branches along the stem of young trees.

As pointed out by Münch, species differ in their plagiotropic responses. In spruce, fir and other conifers the new extension growth exerts a continuous epinastic effect; i.e., the geotropic response is counteracted from the very beginning of shoot elongation so that the new growth on lateral branches is outward. In the branches of pines the new extending twigs are vertically oriented indicating a strong negative geotropic response and the initial lack of counteracting epinastic response (Fig. III-21a, b). However, in pine, during the growing season, the new extension growth gradually moves downward to the normal position of the branch. This response is referred to by Münch as an example of "delayed epinasty" because the terminal leader or main stem still exerts control over this later movement.

Prior to Münch's published work in 1938, the majority of observations on plagiotropic growth were made on young extending twigs rather than older branches containing secondary xylem. It is important to make this distinction because plagiotropic movements in older branches are controlled by the unilateral formation of reaction wood rather than by the differential elongation of cells in the tropic responses of primary shoots.

From the many experiments conducted by Münch, consistent observations were made that girdling at the base of the leader, as well as debudding, or removal of the leader caused the erection of the lower branches one to two meters below, the degree of erection decreasing with distance from the apex

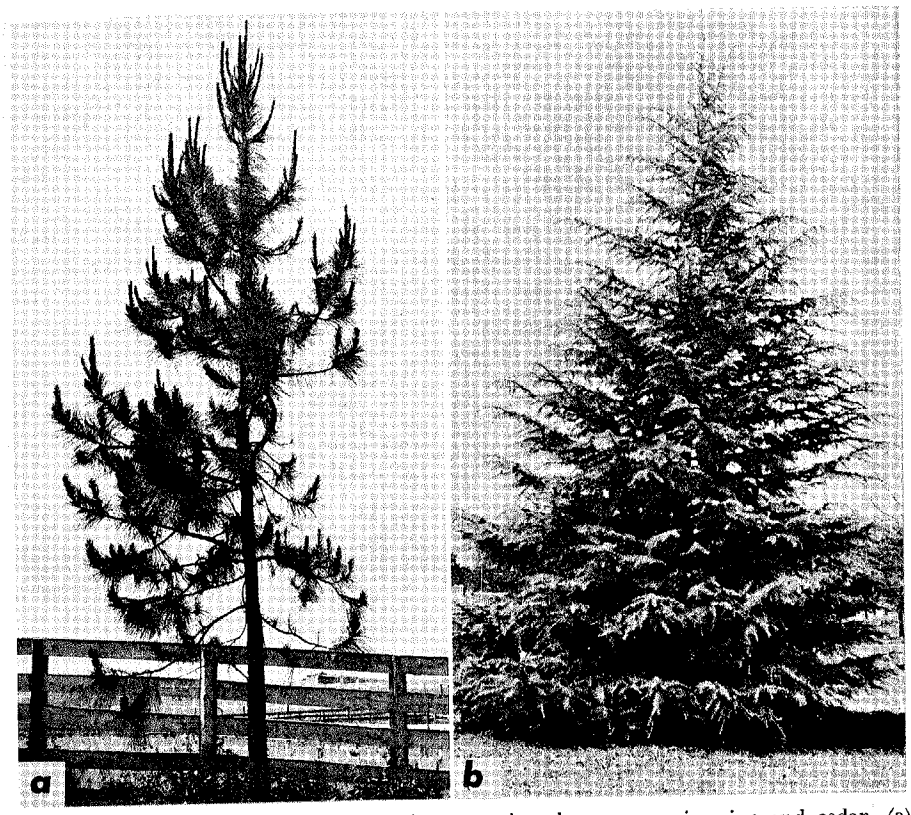


Fig. III–21a, b. Delayed and continuous epinastic responses in pine and cedar. (a) Strong negative geotropic response of lateral branches in slash pine (*P. elliottii* Engelm.) during extension growth in spring, and (b) continuous outward growth of lateral branches in deodar cedar (*Cedrus deodara* (Roxb.) Loud.).

(Fig. III-22). Following any of the above treatments, an auxillary leader soon forms which in turn epinastically depresses the branches beneath. Thus, Münch concludes that the terminal shoot not only prevents the lower branches from erection, but in effect pushes them down. The epinastic effect coming from the terminal shoot is still effective even when it is covered for an entire season with a black cloth. The girdling experiments performed at different places along the main stem further indicated that the hormonal stimulus controlling epinastic movements is transported downward through the bark, but never upward. This observation led Münch to suggest that the hormone is probably identical to that produced by the young leaves.

As pointed out by Münch, the terminal leader not only affects radial growth on the underside of the stem (i.e., inhibition of excessive compression wood formation), it can also actively depress the branch by promoting the formation of compression wood on the upper side of the branch. Hartmann (1942, 1943) and

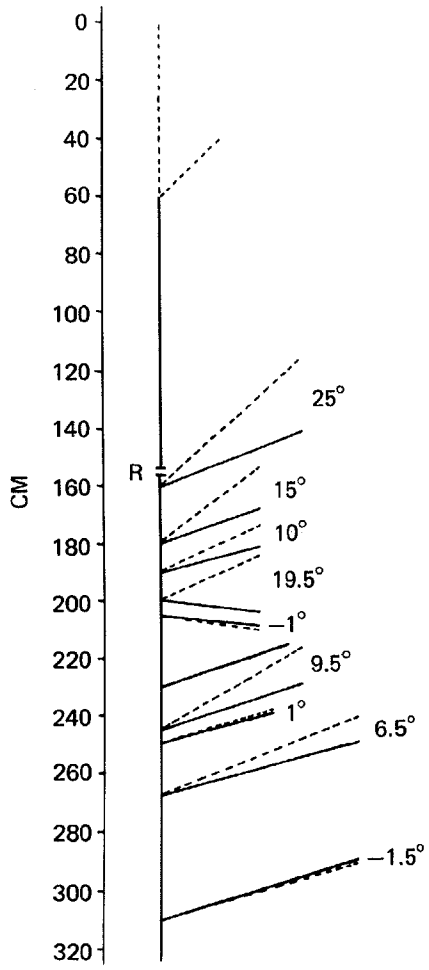


Fig. III–22. Diagram showing the effect of ringing (R) on the erection of lateral branches in young spruce trees. Changes in branch positions at the end of one growing season are indicated with dashed lines (after Münch, 1938).

Sinnott (1952) demonstrated this effect by bending and holding lateral branches out of their normal position. In every case, reaction wood formed on the upperside of the lateral branches bent upward, and on the lower side of those bent downward, thereby the branch is returned to its normal position (see Fig. II-19).

These epinastic responses, at least in conifers, have been either directly or indirectly attributed to the stimulatory effect of auxin which comes from the terminal leader and regulates in some way the amount of reaction wood needed to position the branch in its normal direction with respect to gravity. The manner

in which the basipetally transported auxin of the main leader counteracts the endogenously and polarly transported auxin of the lateral branch to check the negative geotropic response of the latter is not easily explained.

Several important questions arise as to the actual pathway of auxin movement into and out of lateral branches. Because the phloem is continuous from the main stem with that of the branches in a manner comparable to the fitting of a glove over the hand and fingers, certain problems of polar auxin transport are encountered. Auxin produced by the young expanding leaves and rib meristems of the extending lateral twig is polarly transported in a proximal direction in primary tissues of the cortex, phloem parenchyma, and pith. In the secondary phloem, polar transport from cell to cell would have to be via the vertical phloem parenchyma, whereas non-polar transport could occur in the sieve elements along with other materials in mass transport. From a histogenic standpoint there seems to be no reason for a disruption of polar transport in the phloem parenchyma from the underside of the branch, but on the upper side two opposing polar systems appear to meet with respect to the phloem parenchyma, the polarity of each tissue being previously determined by their respective shoot axis. This obviously would not prevent the transport of exogenous auxin from the leader or main stem into the upper side of the lateral branch by mass flow in the phloem, but it could logically impede or block the transport of endogenous auxin out of the upper side of the branch. Perhaps only a slight difference in threshold levels of auxin between upper and lower sides is needed to inhibit or promote the formation of compression wood in conifers, and this difference could result from a lateral redistribution of auxin in the phloem parenchyma under the influence of gravity. The explanation of the formation of tension wood in the angiosperms in terms of an auxin-gravity response can also be explained by a similar mechanism (see Chapter II, Section 4b).

b. Gravimorphism

In the previous section we focused our discussion upon geotropic and epinastic responses. These are primarily curvature responses brought about by the unilateral or unequal growth of young twigs or older branches. Gravity, however, is known to have many other formative effects on vegetative growth, and the term *gravimorphism* has been used by Wareing and Nasr (1961) to describe these causal relationships.

Horticulturists have known for a long time that bending the upright shoots of fruit trees out of the vertical and training them in a horizontal or pendent position will promote earlier and heavier flowering and fruiting (Sax, 1962). Foresters and others have also observed for many years the release of buds from inhibition along the uppermost side of wind or ice-thrown trees in the forest. In more recent studies, Wareing and Nasr (1958, 1961) and Wareing and Longman (1958) explored in considerable detail the effects of gravity on extension growth, apical dominance, and flowering in several fruit trees and a conifer, Japanese larch (*Larix leptolepis,* Murr.). When young clonal varieties of apple, plum, and cherry trees were grown in pots in a horizontal position, the total

amount of extension growth was considerably less than that of the vertically grown controls. The effect was even greater when the horizontally placed plants were rotated twice daily. Reduction in total length in some species was due to a reduction in both number and length of internodes; in other species it was mainly due to internode length. Flowering was also greatly increased in the clonal varieties of cherry, plum, and apple, and strobili production was much greater in the young Japanese larch trees when grown in a horizontal position.

In these same experiments, Wareing and his co-workers found that apical dominance (apical control) was exerted by the terminal leader only when it occupied its normal vertical position. Placing the terminal leader in an horizontal position had essentially the same effect as decapitation in that the uppermost lateral branch assumed dominance in the vertical position. In addition, there was a marked tendency for lateral buds to extend on the upperside of horizontally placed plants. One can observe the same naturally occurring phenomena in different species of "weeping" woody shrubs and trees. For example, the annual height increment of the weeping willow (*Salix babylonica* L.) is added in a "stair-step" fashion by the release of one or more lateral buds on the summit of the uppermost shoot as it bends over under the influence of gravity (Fig. III-23).

Some interesting observations were made by Wareing and Nasr (1961) on the pattern of bud release in horizontally placed cherry trees when the proximal and distal portions of the main stem were oriented in different positions with respect to gravity. In these experiments none of the current year's lateral buds were released from inhibition in any of the treated trees or controls; rather, two or more buds on the 2-year-old proximal portion of the horizontally placed stems normally extended. From these various treatments it appears that the outgrowth of lateral shoots at the proximal end of the stem is very little affected by the orientation of the distal portion of the main shoot, instead the outgrowth seems to be concentrated in any proximal portion of the shoot deviating from the normal vertical position.

To learn more about this pattern of bud release, Wareing and Nasr (1961) placed complete stem girdles on arched seedlings (i.e., stems of vertically growing seedlings bent over to form an arch) in the following ways: (1) below the summit of the arch, (2) above the summit, but only a few centimeters below the terminal bud, and (3) in both positions. In treatment 1, the laterals grew out below the girdle in about the same way as in non-girdled trees, but the uppermost branch was always the most vigorous, which was not always the case in the non-girdled trees. In treatment 2, the pattern was similar to the non-girdled controls, except a few weak lateral shoots did extend at the distal end just beneath the girdle. When the double girdle was applied in treatment 3, the pattern of bud release was essentially the same as in treatment 2, the upper distal branches being even weaker. It is seen, therefore, that girdling horizontally arched stems had little effect on the basic pattern of bud release.

We have observed similar patterns of bud release along the main bole of older sweetgum trees (*Liquidambar styraciflua* L.) i.e., trees from 10–20 inches in

Fig. III-23. Growth habit of weeping willow (*Salix babylonica* L.) showing release of lateral buds near the summit of the arch in the uppermost pendant branches.

Fig. III-24. Release of suppressed buds all along the bole of a horizontally displaced sweetgum (*Liquidambar styraciflua* L.). Note larger size of branches at the summit of the arch near the ground, the largest of which will remain dominant and develop into an upright tree.

diameter and 40–80 feet tall. Sweetgum trees inherently possess innumerable suppressed buds embedded in the periderm all along the main bole (see Chapter I, Section 7) which can readily be released just below a girdle in upright stems (Kormanik and Brown, 1967). In this species, however, girdling only releases the inhibited buds for a distance of 1–2 feet below the girdle and successive girdles spaced about two feet apart are required to release the majority of inhibited buds. In distinct contrast, similar sized trees when wind or ice-thrown to a near horizontal position release numerous buds and form epicormic branches for some distance along the uppermost side of the main bole (Fig. III-24).

Wareing, in interpreting the results of his experiments on gravimorphism, points out that none of the present day concepts of the mechanism of auxin action in correlative inhibition fully satisfy the patterns of bud release in horizontally placed stems. For example, the hypothesis that buds grow out on the upper side of horizontally placed shoots because of reduced auxin levels does not explain why bud release is primarily restricted to the proximal portion of the stem. Furthermore, the placing of a complete girdle near the distal end of the shoot has little effect on the release of proximal buds; i.e., whether or not

basipetally transported auxin from the apex is blocked has little effect on the pattern of bud release on the basal portion of the stem. If the "direct" theory of auxin inhibition of buds (Thimann, 1937) is applied, those buds just beneath the girdle should show optimal vigorous growth. The "indirect" theory of auxin inhibition as proposed by Went (1939) suggests that the topmost bud, because of its higher auxin content, attracts or mobilizes nutrients and food factors to it. This hypothesis is also difficult to reconcile with the fact that there is initially *less* auxin in the buds on the upper side of horizontal shoots. Neither does the nutritional hypothesis proposed by Gregory and Veale (1957) adequately explain the pattern of bud release in these studies.

Wareing and Nasr (1961) were led to the conclusion that the outgrowth of buds in young trees occurs at the point nearest the roots at which the shoot is diverted from the vertical. This indicates, as he suggested, that position effect, itself, is involved in the release of lateral buds from inhibition. Nutrients seem to be diverted into the highest buds on arched stems, and proximity of these buds to the roots appears to be favorable to their release.

We agree with Wareing's conclusion that it is difficult to explain these correlative inhibitions solely in terms of basipetally transported auxin coming from the shoot apex. Perhaps some of the apparent discrepancies relating to apical dominance and bud inhibition in woody plants lie in the fact that we have always attempted to explain correlative growth promotion or inhibition in these plants in precisely the same manner as in herbaceous annuals, failing to realize, however, that the sites of auxin production, type of transport, age of tissues, presence of dormancy periods, and interaction of growth inhibitors are obviously quite different in secondary tissues. For example, in the past some physiologists have indiscriminately used the term apical dominance to include everything from currently inhibited lateral buds by actively growing apices in herbaceous annuals to lateral buds all along the bole of woody stems. Some of the latter have undergone several periods of dormancy and have long been free of the influence of apical dominance, i.e. auxin produced by an actively growing apex during shoot extension. It is surprising how many physiologists still think that all the auxin produced in massive tree trunks can be traced back to the shoot apex in young leaves and elongating twigs. One should realize that actively dividing cells in the cambial zone can produce auxin and other growth factors autonomously, and any metabolically active parenchyma cell may likewise function in this respect but at a much lower level of production. Münch (1938) came to this conclusion over 30 years ago.

In the experiments of Wareing and Nasr (1961) one could hypothesize that gravity caused a shift in the balance of growth factors at the point where the vertically oriented shoot meets the horizontally displaced portion (summit of the arch). As a result, the internal conditions are more favorable for the initial *in situ* production of cytokinins releasing these buds from their inhibition. Once such buds are released from inhibition, synthesis of other growth factors in the rib-meristem of the bud stimulates additional cell division and elongation resulting in rapid shoot extension.

c. Dorsiventral symmetry

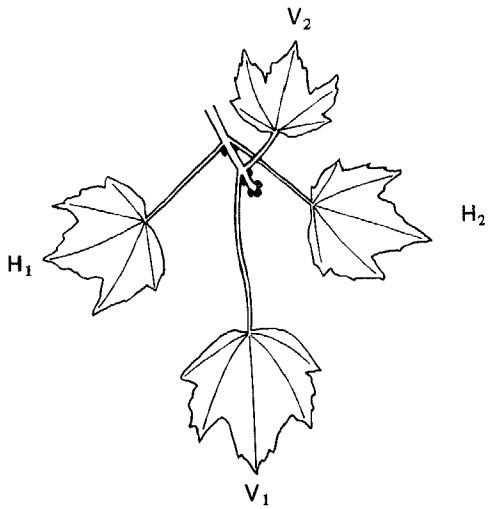
In addition to the gravimorphic effects already discussed, gravity also has marked formative effects on the growth and development of radially symmetrical twigs and branches when these are displaced from the vertical in plagiotropic growth. Such twigs tend to assume a dorsiventral symmetry by the secondary twisting or alignment of buds and leaves into a two-ranked position. This condition is very pronounced in such broadleaved trees as beech (*Fagus grandifolia* Ehrh.) (Fig. III-25a,b), alder (*Alnus serrulata* (Ait.) Willd.) mimosa (*Albizia julibrissin,* Durazz.), and other species. The two-ranked habit of lateral branches becomes most pronounced in different genera of the *Coniferae,* viz. *Taxus, Cephalotaxus, Tsuga, Taxodium, Abies, Picea, Araucaria, Cunninghamia,* and *Cedrus* because of the compact arrangement of their twigs and foliage (Figure III-26).

Aside from the tendency of lateral branches to become flattened or two-ranked, the dorsiventrality of shoots may lead to a conspicuous dissimilarity of the leaves borne on the two sides. These differences to which Wiesner (1895) gave the term *anisophylly* are common in many plants and are discussed in length by Goebel (1928). In woody plants, anisophylly is induced by the interaction of gravity and light, and is especially noticeable in many opposite-leaved trees such

Fig. III–25a, b. Dorsiventrality of lateral branches in beech (*Fagus grandifolia* Ehrh.). (a) Horizontal view of lateral branch, (b) view of same branch from above.

Fig. III–26. The perfect dorsiventral symmetry of *Araucaria excelsa* L. branches.

as the maple (Fig.III-27.) In maple the upper leaf of a vertically oriented pair is small, and the lower portion of horizontally oriented leaves is large. Differences in petiole length are very noticeable, and usually attributed more to a light response than to gravity. In many trees with alternately arranged buds and leaves anisophylly exists by the formation of asymmetric leaves in a regular and predictable pattern. For example, in horizontal branches of elms (Ulmus spp.) the



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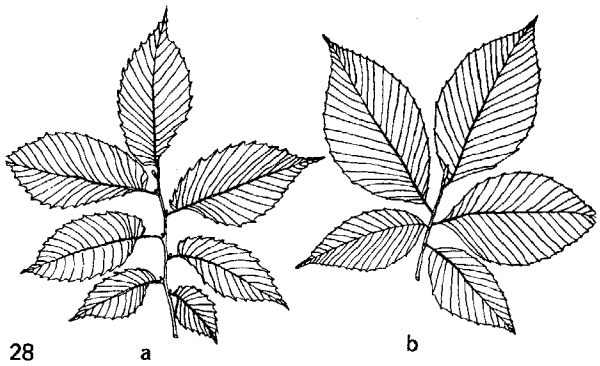

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Fig. III–27. Diagram of lateral twig of red maple (*Acer rubrum* L.) showing anisophylly. The vertically oriented pair of leaves (V_1 and V_2) are symmetrical but differ greatly in size. The horizontally oriented pair of leaves (H_1 and H_2) are similar in size, but asymmetrical, the lower half of each leaf is larger than the upper.

Fig. III–28a, b. Differences in asymmetry of leaves in various species. (a) Asymmetric leaves in elm (*Ulmus* spp.) where the inner half of the leaf blade toward the shoot apex is larger and extends further down the midrib. (b) In beech (*Fagus grandifolia* Ehrh.) the outer portion of the blade away from the apex is often larger.

inner half of the leaf directed toward the apex of the branch is larger than the outer portion, and the blade extends further down the mid-rib. In beech, the reverse asymmetry occurs, with the outer part of the leaf being larger (Fig. III-28a, b).

Asymmetric patterns of branch development are also observed in many trees. Commonly, the second-order branches are larger on the outer side away from the apex of the lateral branch. Wiesner (1895) termed this condition *exotrophy* and explained it on the basis of better nutrition. These patterns of asymmetry seem to be induced by shifting a radial system to a dorsiventral one. The actual mechanism through which gravity works appears to involve both hormonal and nutritional growth responses.

The leaves of trees, with a few exceptions, are typically dorsiventral structures because they have evolved in the seed plants to become best adapted for the absorption of light and exchange of gases; i.e., they function best in the production of photosynthate as broad, thin structures oriented at right angles toward incident light. The dorsiventrality of angiosperm leaves is particularly evident in their internal structure, not only in the arrangement of the palisade cells and spongy parenchyma cells but also in the dorsiventral nature of the xylem and phloem. The vascular supply to each leaf passes outward from the primary vascular ring, and in this pattern of differentiation the phloem must necessarily occupy the lower portion of the veins while the xylem occupies the uppermost part in a typical dorsiventral pattern from the very beginning of leaf differentiation.

Roots of trees, even though they develop extensive lateral systems, fail to show distinct dorsiventrality in either external or internal structure. The primary root emerging from the seed, almost without exception, possesses a strong positive geotropic response; however, the lateral roots as they become older and further removed from the primary root system become much less reactive to the effects of gravity. In fact, the direction of growth of roots depends primarily upon the environment to which they are subjected; i.e., they grow into soil areas where water and nutrient availability are highest whenever temperatures are favorable. Hence, their direction of growth may be upward, downward, horizontally, or somewhere in between these extremes (see Chapter I, Section 11a).

6. ENVIRONMENTAL INFLUENCES AND FORM

a. Mechanical forces

During their life history trees are constantly subjected to stresses such as compression and tension brought about by differential rates of growth in the secondary plant body, annual increases in total mass, and the mechanical effects of bending and swaying under the influence of wind. Differential warming and cooling of various tissues and parts of the tree also have a pronounced mechanical effect on expansion and shrinking of tissues.

Numerous studies have been conducted in the past on the effects of longitudinal tension (pulling) and compression (weighting down) of stems in herbaceous

plants and, to a lesser extent, in woody plants (Sinnott, 1960). Most of the effects of induced traction and compression are indecisive and contradictory, mainly because researchers used different species in various stages of growth and development where sensitivity to response was neglected. The effects of bending and swaying on the form of plants is more definitive than those of applied tension or compression. Various workers have subjected herbaceous and woody plants to continuous swaying by mechanical devices and found that, in general, the stem axis tends to be elliptical with its wider dimension in the plane of sway (Knight, 1811; Burns, 1920). In these instances, more mechanical tissue, especially secondary xylem, is developed in the treated plants than in the controls.

Jacobs (1954) used a different approach in studying the effects of bending and swaying on the growth of trees by guying the trunk of young Monterey pines (*Pinus radiata* Don.) with wires about 20 feet from the ground so that they could only sway above this point. The portion of the stem above the guy wires which was permitted to sway grew much more rapidly than the portion beneath. When the guy wires were removed, the lower portion of the bole again grew in a normal manner. Swaying, therefore, may in some way stimulate the cambium to divide more, and movement could have an appreciable effect on the bole form of open- versus densely-grown trees. The increased activity of the cambium at the base of the stem resulting in prominent butt swell of many trees is, in part, influenced by mechanical forces such as compression and swaying (see Chapter II, Section 6b).

b. Light

Light, together with gravity, is one of the most important constituents of the environment in determining the course of development in woody plants. The growth and form of trees from the time of seed germination to maturity is directly affected by light intensity, quality and duration. One of the most commonly described effects of high on the direction of growth is the general phenomenon of phototropism. Phototropic responses of individual twigs play an important role in the positioning of branches in the much-branched crowns of decurrent species. Light, gravity, and competition for growing space interact to determine the overall size and shape of tree crowns. That light has a direct formative effect on tree crowns is readily seen by the unilateral growth of branches into openings in the forest canopy created by partial cutting or natural causes.

The direct formative effects of light on leaf and stem structure are well known. Light intensity has much influence on the general structure and morphology of leaves, stems, and roots. Tree seedlings grown in weak light in contrast to full sunlight usually possesses longer internodes; thinner stems; broader, thinner leaves; and poorly developed root systems. Internally, such plants have longer and thinner-walled parenchyma cells, reduced vascular tissues, and weakly lignified tracheary elements.

Thomson's (1954) opinion is that increasing amounts of light accelerates whatever growth processes are taking place. Thus, if rapidly-growing stems are exposed to high light intensity, the light will effect a quicker cessation of cell

division and/or cellular elongation, resulting in both a decrease in cell number and size and shorter internodes. Leaves, however, respond differently to stems in these respects and much significance has been attached to the physiological and structural qualities of shade versus sun leaves. The latter are more xerophytic in nature, possess thicker cuticles, more and longer palisade cells, and well-developed vascular tissues (Fig. III-29a, b).

Light quality, i.e. the various wave lengths of light, has been shown to affect these same morphogenetic processes quantitatively. In general, it seems that

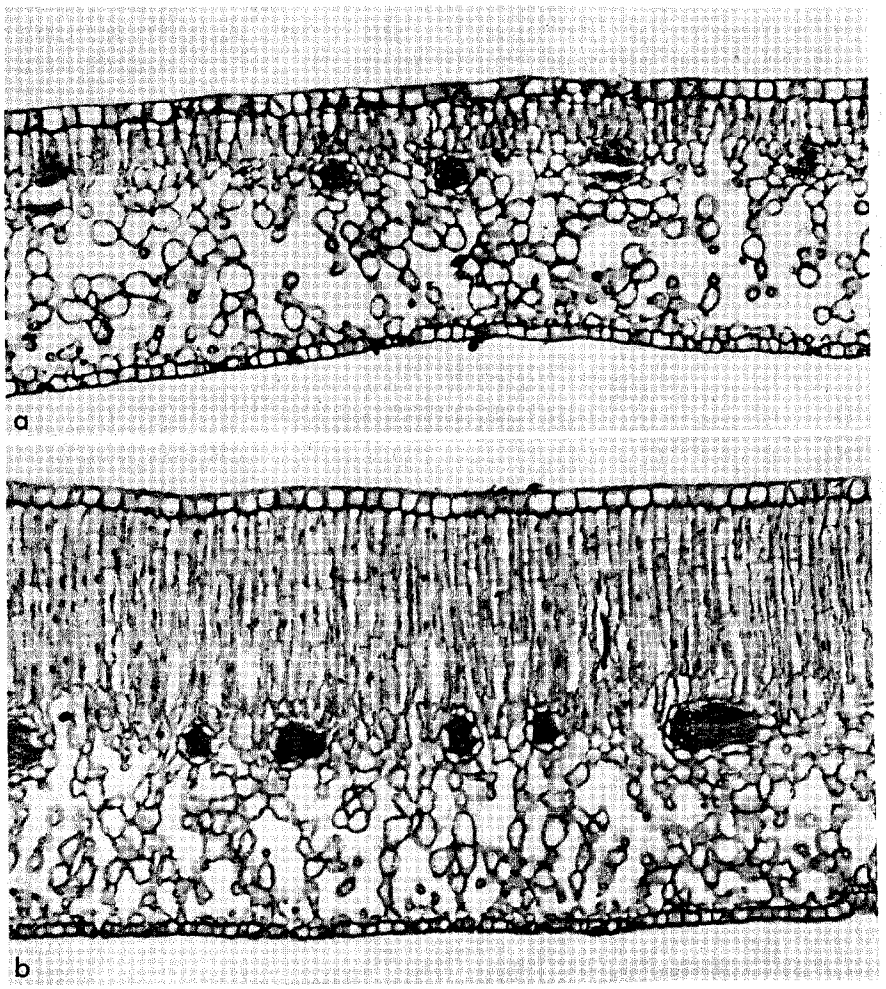

Fig. III–29a, b. Differences in internal structure of (a) shade and (b) sun leaves of cherry laurel (*Prunus caroliniana* (Mill.) Ait.) Note extensive development of palisade layer and vascular tissue in latter. Both 150 x.

blue light hastens the cessation of cell division and elongation to a greater degree than red light, and red light is more effective than far-red; whereas, the greatest cell numbers and lengths are obtained in complete darkness (Theodoresco, 1929; Vince, 1956; LeNoir, 1967). Hence, plants growing in blue light of sufficient energy tend to develop in essentially the same way as those grown in white light, while those grown under red or far-red light tend to develop etiolated characteristics. The morphogenetic effects of light quality have been reviewed by Parker and Borthwick (1950) and Wassink and Stolwijk (1956).

The effect of the daily duration of light, or *photoperiod,* on growth and development in woody plants has been studied extensively in recent years. Because the length of day varies considerably from the tropics to the higher latitudes, it has had a significant adaptative influence on the growth habit of plants. Although there are wide differences among woody plants in their reaction to photoperiod, even among species growing together at the same latitude, photoperiodism has been demonstrated to have a marked effect on many physiological processes involving growth and development. Among these are rate and duration of shoot and diameter growth, breaking of dormancy, cessation of growth, seed germination, leaf abscission, frost resistance, and the flowering response. Although an experimentally imposed photoperiod may have a distinct effect on one or more of the above processes, the same process(es) may not be controlled by photoperiod under natural conditions. Whereas, the cessation of growth of many species in the north temperate zones may be brought about by the shortening day lengths in late summer, the growth of numerous species in the south temperate zones stops long before day length becomes a limiting factor. Likewise, many tropical species respond favorably to long photoperiods even though they have evolved and thrive under a natural short day.

These differences in response to photoperiod may have much practical application to foresters, horticulturists, and others in moving species outside their geographic range. North temperate zoned species whose cessation of growth is controlled by photoperiod cease growth much earlier in the season when moved southward, resulting in an adverse affect on growth rates, vigor, and possible susceptibility to insects and disease (Pauley and Perry, 1954). Conversely, species from the south temperate zones moved northward may likely continue growth under the longer photoperiods of summer and fail to harden off in time to resist injury or death from winter cold.

From a morphogenetic viewpoint, photoperiod becomes important because it affects the total amount of growth through its effects on rates and duration of growth. In the initial epicotyl growth of one-year-old conifers and in those species of angiosperms which grow late into the season by the continued activity of the apical meristem, the increased total amount of extension growth under long photoperiods results from an increased number of nodes as well as greater elongation of internodes. In those species containing all of their preformed nodes in the winter bud, long photoperiods only influence the length of the internodes (Wareing, 1950a, 1950b, 1956). In this latter group, however, long days may bring about continued growth for extended periods in some species by promoting

the formation of recurrent flushes of growth. Although this may occur, there is a gradual inhibition of growth in that each successive flush of activity is shorter than the previous one until growth finally ceases even under continuous light. For a more detailed account of these photoperiodic growth responses the reader is referred to the observations of Downs and Borthwick (1956) and Downs (1958, 1962).

In concluding this brief discussion on some of the effects of photoperiod on tree growth, we would like to point out that virtually nothing is known concerning the histogenetic effects of long and short photoperiods on the rates and duration of cell division and elongation in the various internodes of extending shoots.

c. Water stress

The availability of water is the most singly important environmental factor limiting growth and distribution of trees. Almost every physiological process occurring in trees is in some way affected or limited by the availability of water at some critical time during development. Because water relationships and tree growth encompass such a broad field of study, we will of necessity limit our discussion to some of the more important morphogenetic aspects of water on growth and form.

Anyone who has observed trees growing under moisture stress in semi-arid regions or on locally severe sites such as dry ridges, deep sands, or precipitous slopes, has noticed their unusual shrubby appearance due to reduced growth and early loss of apical control. In many cases the tree crowns become knarled and grotesque because of repeated dieback of terminal and lateral branches during recurrent years of severe moisture stress. Tree species that occupy such sites commonly possess structural characteristics collectively referred to as *xeromorphy*. For example, xeromorphic plants tend to have reduced leaf surfaces, heavy cuticles, small and thick-walled cells, increased mechanical tissues, high stomatal frequency, and large root systems. The question often arises as to the adaptive significance of xeromorphic traits because many plants possessing such traits transpire more water than do mesophytes when water is readily available. Likewise, most mesophytes will develop various xerophytic traits, not as an adaptation to drought, but because water is limiting during certain stages of development. Such structural changes occurring during ontogeny are obviously the result of the environment and not an adaptation to conserve moisture. Many studies have been conducted with both herbaceous and woody plants showing that the upper leaves in the crown are more xeromorphic than lower ones even under favorable water regimes, and that these differences become even greater under moisture stress (Zalenski, 1904; Maximov, 1931 and Shields, 1950).

Some of the morphological differences mentioned earlier between sun and shade leaves may also be enhanced by water stress. Leaves on the outside of tree crowns, especially those on the south side in the north temperate zone, are normally more xerophytic in that they are smaller, thicker, and transpire more per unit area than shade leaves from the interior of the crown (Hanson, 1917). Huber

(1926) is inclined to agree that the structure of sun leaves is due, at least in part, to water deficits as well as higher light intensity. Söding (1934) grew tree seedlings under conditions of physiological drought by adding salt to the soil and found that the plants produced leaves very similar to sun leaves.

Another interesting aspect of developmental effects of water on higher plants is the relationship between rate of transpiration and the development of vascular tissues. Because plants grown under high light intensity normally transpire much more and possess considerably more xylem than those grown in shade, the role of transpiration in stimulating xylem development is sometimes raised. Huber (1924), in comparing the amount of water transpired from oak branches growing in the sun with those growing in the shade on the basis of leaf area and cross-sectional area of the stems, found a correlation between the amount of water transpired and size of the vascular system. Huber points out, however, that the rate of water transported through stems is a function of physical forces established in the leaves and resistance to flow in the xylem elements themselves and not simply a function of size (see Chapter IV). It is a well known fact that one may drastically reduce the volume of conducting xylem elements by wounding and not seriously affect the growth and development of the crown. The fallacy of proposing a causal relationship between the amount of water transpired and the cross-sectional area of stems because the two are correlated is comparable to attributing the increased growth of trees on moist versus dry sites to increased rates of transpiration or the total amount of water transpired.

d. Temperature

Temperature, like light, is an important factor in tree growth and development because it influences many physiological activities through its affect on rates of metabolism. Although temperature does have a direct and pronounced effect on the form of trees in certain localities, e.g., on tree growth at the timber line, its formative effects are usually less direct than those of light and water. Our discussion, therefore, will be restricted to a few of the most obvious effects of temperature on development.

Numerous studies of tree growth have been conducted in the higher latitudes of the Scandinavian countries since the turn of the century, and a considerable amount of data is available correlating height and diameter growth of several conifers with mean temperatures during the four summer months (Mikola, 1962).

Hesselman (1904) in Sweden showed over 50 years ago that an excellent correlation existed between the length of the terminal shoot of Scots Pine (*Pinus silvestris* L.) and the mean July and August temperatures of the preceding year. This correlation exists because the total length of shoots in coniferous species is largely dependent upon the number of needles (nodes) it contains in the preformed terminal bud. Therefore, the temperatures during the time of bud formation, i.e. July and August of the previous year, become considerably important. Needle length, in contrast, depends on the climatic conditions existing during their growth, temperature being the most important or limiting factor at or near the timber line. Similar relationships have been found in other tem-

perate zone forest trees that normally make only one rapid flush of terminal growth in spring and early summer (Büsgen and Münch, 1929).

Another aspect of temperature in relation to development in trees is the effect of different day and night temperatures on patterns of shoot growth. The term *thermoperiodism* was used by Went (1948) to describe the reaction of herbaceous plants to different combinations of day and night temperatures.

Kramer (1957, 1958), in studying the response of loblolly pine (*Pinus taeda* L.) and northern red oak (*Quercus rubra* L.) seedlings to different combinations of day and night temperatures, found both species grew best when night temperatures were 6° to 12° C lower than day temperatures. The least shoot growth was made when the seedlings were grown under the same day and night temperature (23°C).

In a similar study, Hellmers (1962) observed that the recurrent flushing of loblolly pine seedlings was closely related to temperature. Increased temperatures, either day or night, caused an increase in the number of flushes (Table III-1).

TABLE III-1

Height Growth of Loblolly Pine Seedlings Grown 64 Weeks from Cotyledon Stage Under Different Day and Night Temperature Combinations. (after Hellmers, 1962).

Day Temperature	Night Temperature 7°C.	17°C.	26°C.
	Height in Centimeters		
30°C.	——	52 (6.4)	29 (6.6)
23°C.	60 (4.2)[a]	50 (5.6)	35 (7.0)
17°C.	43 (3.0)	38 (4.1)	——

[a] Numbers in parentheses are the average numbers of flushes of growth produced.

As Hellmers pointed out, while there was a reduction in total height growth with increasing night temperatures, there was also a tendency to form more terminal buds. It has been suggested by Vegis (1956) that high temperatures may induce dormancy or rest in tree buds; but in Hellmer's studies, the highest day and night temperatures (30° and 26° respectively), although reducing total growth significantly, failed to induce dormancy in the buds of loblolly pine.

Hellmers (1962) also found that some forest species were less sensitive to differences in day and night temperatures than they were to a specific day or night temperature regime. For example, redwood seedlings (*Sequoia sempervirens* (D. Don) Endl.) responded significantly to increasing day temperatures up to 23° C, whereas the day-night temperature differential appeared to have little or no effect on top growth. In Digger pine (*Pinus sabiniana* Dougl.) a night temperature of 17° C was more effective on height growth than were increasing day temperatures. In still other species, Hellmers found that the daily heat sum (total daily temperatures) irrespective of application time was more important for total shoot growth.

Thus, it is seen that considerable variation exists in species response to thermoperiodism and considerably more research must be done before its role in nature can be clearly evaluated. Kramer (1958) suggests the possibility that thermoperiodism through its effect on growth, vigor, and competition could have an important influence on the range and distribution of certain species. Although the suggestion is quite plausible, one also must take into consideration the effect of temperature on daily and seasonal CO_2 fixation and rates of respiration in studying growth, reproduction, and distribution of forest trees. The problem is also complicated by interactions between temperature and photoperiodic effects on both vegetative and reproductive development.

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