THE INDIVIDUAL ROOT and shoot axes grow by additive processes. New cells are added to make them thicker or longer so the total size is the sum of all the additions. The growth in total number of axes each year is multiplicative because the rate is determined by the number of parent axes multiplied by the branching rate per axis. Later in the book we will look at how tree axes are connected together in a structure with regular patterns; this chapter will describe how additive and multiplicative growth of the population of root and shoot axes occurs in the tree.

Both additive and multiplicative growth in trees is from meristems. Meristems are localized areas of axes that act as cell-producing factories. They cause elongation, thickening, and branching. Meristems produce new cells by division, the cells then enlarge and subsequently differentiate into one of the many cell types that make up a tree. Apical meristems at the tip of each growing root and shoot produce cells for elongation of axes, and they also produce the cells that form new meristems. There are lateral meristems—the cambium between the wood and bark and the cork cambium within the bark—that produce cells for the thickening of axes and also produce more meristem cells to increase the size of the lateral meristem, which is a parallel to branching in apical meristems.

Elongation and thickening occur through the production of files of cells—longitudinal files in apical meristems and radial files in cambia (fig. 4). As the files get longer through the addition of new cells by the meristem, the axis elongates or thickens. The increase in length of files of cells to produce elongation and thickening is a result of both cell division to produce new cells in a file and the subsequent enlargement of each new cell. Although cell

Shoot tip

Root tip
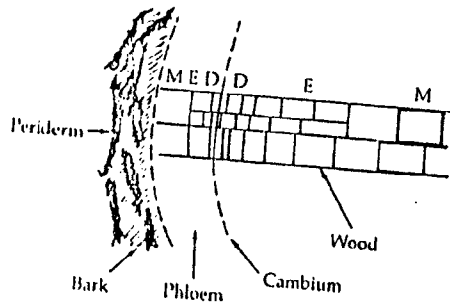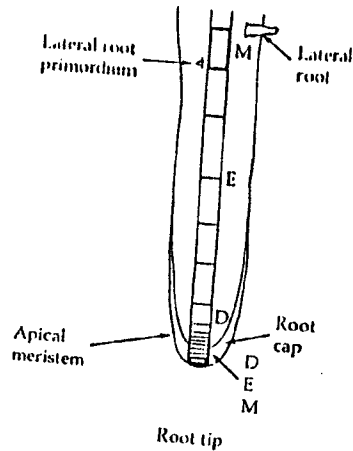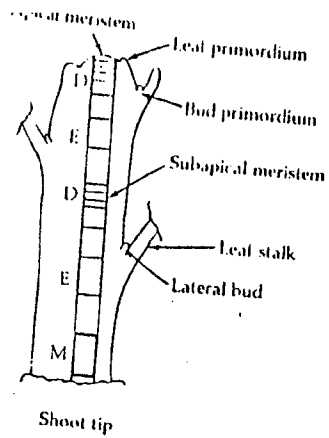
4 FILES FROM MERISTEMS
Diagrams of sample radial files produced by meristems. Each file has zones of cell division (D), enlargement (E), and maturation or wall differentiation (M). Shoot and root apical meristems form lateral buds or roots. The cambium forms new files of cells.

size may vary throughout a year in a file of cells, there is surprisingly little difference between cell size in a fast- or slow-growing file. The major differences in the amount of elongation or thickening are due to the number of cells in a file. The number of cells is determined by the number of cell divisions that create the new cells. Therefore, differences in amounts of growth are due primarily to differences in the numbers of cell divisions in meristems.

Because of the additive nature of tree growth the youngest cells in a file are in the meristems where cell divisions occur. Therefore, distance from a meristem is related to the time since a cell, or tissue, was formed. The youngest leaves are nearest the apical meristem that formed them and the oldest the furthest away. Wood is youngest at the outside of the tree near the cambial meristem and oldest on the inside. A sequence of cells, tissues, or organs at increasing distances from the meristem that formed them also represents a developmental sequence in time. Scientists studying development in trees, or in any plants that grow from meristems, often use the technique of substituting space for time. For example, it is easier to study a sequence of branches from the top to the bottom of a tree, each branch a year older, than to wait while a particular branch grows over the years. Because a record of cambial activity is stored in the wood and a record of annual elongation in the shoot and root systems, it is also possible to work backward through space and time to see how a particular shoot or root has developed over the years. One problem with this technique is that it is not possible to reconstruct the whole history of a tree because many shoots and roots, and of course the leaves, have died and disappeared over the years.

Meristems also produce new meristems. The shoot apical meristem produces lateral leaves that grow by short-lived meristems. The shoot or root apical meristems also produce lateral shoot or root meristems that grow into lateral branches each with its own apical meristem. New cambial meristem, to accommodate

... ...creasing girth of the cambium as an axis thickens, is produced from existing cambial meristem by special cell divisions. New cambial meristem is also formed in axes created by shoot and root elongation. It arises from undifferentiated cells produced by the apical meristems. Later the cambial meristem expands circumferentially by producing new meristem cells of its own.

Division and cell enlargement are localized near the meristem. Therefore growth only occurs immediately adjacent to meristems. The tissue that has been formed in the past is stored as the bulk of the tree, except for leaves and other parts that die and are lost. Most of the tree, once formed, stays the same. A wire fence nailed to a tree is an example of the stability of nonmeristematic parts of trees. As the years pass, the fence stays at the same height on the tree, because elongation occurs only near apical meristems at the tip of the tree and at the end of each branch. As the tree grows in diameter, wood grows over the nail and the wire. The wire does not move and new wood is added outside the old wood. Therefore, the wire is buried in the tree marking the height and year it was first put up. Once buried, cambial activity and radial enlargement occur on the outside of the tree, beyond the wire.

This localization of current growth and storing up of previous growth permits some detective work to measure growth from previous years. It is easiest to measure previous growth in temperate trees that have annual seasons of growth and nongrowth. In many of these trees the annual elongation of each shoot is marked by successive groups of bud-scale scars on the surface of the bark and the annual thickening of the wood is marked by annual rings (fig. 5). Detective work on previous growth is not always easy. Not all trees have bud-scale scars and some produce more than one set of bud-scale scars per year, but in these cases there may be other clues to the amount of elongation. For instance, the pattern of branching often is annual. Many trees

Hardwood branch

Pine tree
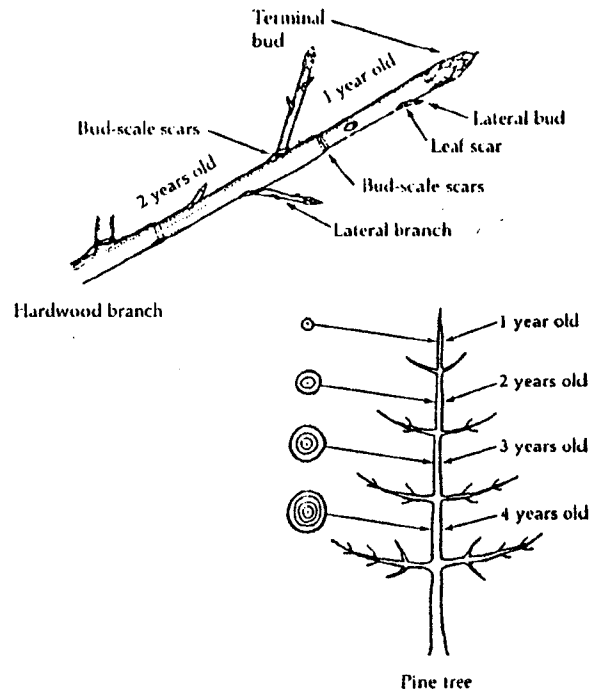
5   ANNUAL DIVISIONS OF SHOOTS
Divisions are marked on the outside of shoots by bud-scale scars or groups of long branches and in the wood by the number of annual rings.

growing in the tropics produce no rings in the wood at all. Some trees may produce more than one ring each year, either because of injury or because of distinct flushes of growth. In general, it is difficult to work out previous growth rates in the root system. There are no bud scales, there is usually no annual pattern of branching, and growth rings in the wood are difficult to see and frequently do not go all the way around the root.

The files of cells that meristems produce arise because cells divide and redivide in the same plane, perpendicular to the axis

(see fig. 4). As cells from a meristem are added to the file, they pass through phases of division, enlargement, and differentiation. Because adjacent cells tend to be in the same phase of development, there are zones of division, enlargement, and differentiation in the files. This process of cell production and file development is easiest to visualize in cambial activity. The general processes are similar in longitudinal files from apical meristems, but there may be major differences between files from the center to the outside of the root or shoot axes. In shoot apical meristems a few cells in each file may begin to divide again after the rest have stopped. These bands, or slices, of dividing cells form subapical meristems that are important in producing new cells in files. Both root apical meristems and cambial meristems actually produce radial files in two directions. In roots, the root cap is produced outward and the bulk of the root, inward. In the cambium, the wood is produced to the inside and phloem to the outside, while the cork cambium produces cork to the outside and thin-walled cells to the inside.

New leaves and buds are produced from localized divisions in surface layers of the shoot apical meristems, essentially areas where meristematic activity continues, as is shown in figure 4. These new meristems are called *primordia* when they are very small. Tiny protrusions from the surface of the meristem, the leaf primordia, form first. They are produced in regular sequences, either in spirals in alternate-leaved plants, or in successive opposite pairs in opposite-leaved plants. These primordia eventually develop into leaves through the activity of short-lived terminal and marginal meristems found only in leaves. Soon after the leaves begin to develop, bud primordia form associated with each leaf, usually on the stem just above the leaf base. The bud primordia soon differentiate to form new shoot apical meristems that can form new lateral shoots when branching occurs.
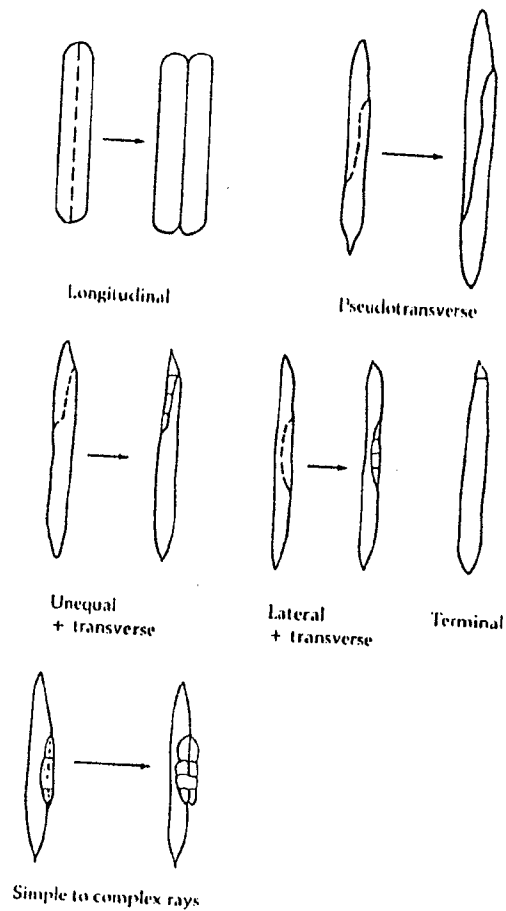
New lateral root primordia form inside roots in a tissue that has remained undifferentiated (see fig. 4). These primordia form by localized divisions to develop a small cluster of meristematic cells. The root primordium soon differentiates into a root apical meristem, which later grows out through the side of the root. Lateral root primordia are not formed in regular sequences as are leaf and bud primordia, but they usually develop in several lines along the root.

The cambium does not produce lateral appendages, but it does enlarge as the tree grows by adding new meristem that forms new files. As apical meristems elongate, the cambium is extended into the new axes by cells in an inner cylinder of tissue that have already elongated but that begin to redivide to form new cambium and new radial files of wood and phloem cells. This formation of new meristem by redivision of cells from the apical meristems is somewhat comparable to the formation of lateral leaf, shoot, and root primordia by redivision of cells in special areas, except that in the cambium the new meristem forms a complete cylinder rather than discrete clusters of cells as it does in the primordia.

There are two basic cell types in the cambium. Fusiform cells are long, needle-shaped cells oriented longitudinally. Ray cells are rectangular, relatively short, and radially oriented. Each cell type produces files of cells of its own type. Fusiform cells ultimately constitute 60 to 80 percent of the wood and function primarily in water transport and mechanical support. Ray cells make up the rest of the wood and function primarily in transporting materials from the outside to the inside of the tree. Ray cells are usually aggregated into units called *rays*. Rays are large enough to see in many hardwoods, particularly in oak. They appear as lines or stripes across the annual rings.

New cambial meristem is also formed by occasional special cell divisions within existing cambium (fig. 6). Most divisions are oriented so that the new walls are perpendicular to the axis of the radial files. These divisions increase cell numbers in the files. Sometimes, however, a division will occur so that the new wall is

Longitudinal

Pseudotransverse

Unequal
+ transverse

Lateral
+ transverse

Terminal

Simple to complex rays

6 CAMBIAL DIVISIONS
Types of divisions producing new fusiform and ray cambial cells.

parallel to the radial axis and a new meristematic cell is produced. This new meristematic cell can then produce a new radial file. This mechanism increases the number of both fusiform and ray files as the cambium increases in girth.

There are a number of types of divisions that produce new cambial cells from parent fusiform cambial cells. The parent cell may be divided by a straight wall from end-to-end of the cell to produce two daughter cells the same length as the parent. The new dividing wall is, however, frequently not straight. It may be S-shaped and not run the length of the cell (a pseudotransverse division);[1] it may cut out one side of the cell (a lateral division); it may just cut off the tip of the cell. Divisions that produce daughter cells of about equal size usually produce new fusiform cells. Where divisions produce daughter cells markedly unequal in size the smaller cell either becomes directly a ray cell or becomes, through subsequent redivisions, a series of ray cells.[2] Thus, fusiform parent cells can produce either new fusiform or new ray cells in the cambium.

Cork cambium produces most of the hard part of the bark in trees. It produces cork to the outside of the tree and, in most cases, just a few cells to the inside. The general operation of a cork cambium is similar to the cambium, but there are no ray cells. Cork cells are in radial files produced by oriented divisions in the meristem, just like wood cells. There is a tremendous variation in the extent and longevity of cork cambia in different tree species. Trees with thin, smooth bark, like beech, have a long-lived cork cambium that forms a sheath around the tree stem just as the cambium does and expands as the stem thickens. Trees with rough bark, however, have many cork cambia, each of small area and relatively short-lived. New cork cambia keep forming under the old ones in these trees.

Cork cambia form in a process analogous to the formation of cambium in new root and shoot axes. The first cambia form in tissue produced by the apical meristem. Adjacent cells just under

the outer surface of the stem begin to divide to produce a sheet of meristem that then forms radial files. In trees where the cork cambia are short-lived, successive cambia are formed by similar processes of localized sheets of division underneath the old cork cambia. After a while new cork cambia begin to form in old phloem tissue produced by the cambium. As these successive cambia form underneath each other and the tree expands in girth the bark develops ridges or plates of dead corky tissue to the outside. Bark may peel, or separate and fall off, through layers of weak, thin-walled cells in the cork or between successive cork cambia. Some birches have bark that peels off in strips. In some trees, like sycamore or, most spectacularly, in some eucalypt species, the older layers of bark fall off the tree, leaving the younger, lighter-colored layers exposed. I have seen eucalypt trees where the dark gray outer bark is shed to reveal a creamy white layer of bark, which gradually turns pink and then gray. The change of bark colors is as dramatic as the autumn coloring in leaves of deciduous trees.

The growth and proliferation of root and shoot axes in a tree is entirely from meristematic activity. Meristems are tiny, but they are absolutely vital to trees. As a result they are protected, by leaves or bud scales, the root cap, or the bark. There are also mechanisms by which new meristems can be regenerated in undifferentiated tissue if the old meristems are destroyed. Meristems may be easy to overlook in a tree, but their importance cannot be overemphasized.

BRANCHES IN THE shoot or root system develop in patterns with different levels of organization. The simplest level is determined by the nature of lateral formation in apical meristems. Branches grow from the sides of a parent axis. Therefore, it is convenient to classify branches by order, with orders being comparable to generations in populations. The main axis is called the first order, all branches off the first order are called the second order, all branches off the second order are called the third order, and so on (fig. 7).

Branches are not formed randomly. In the shoot system they are in successive pairs (opposite), or in a spiral (alternate), in a regular pattern called *phyllotaxy* that is determined in the apical meristem. In the root system, laterals are usually in rows along the parent root, with successive laterals somewhat evenly spaced, but not as completely regular as they are in the shoot system.

Another level of complexity is that each higher order usually elongates more slowly than the parent order. Root systems have a relatively simple basic pattern resulting from the fairly regular spacing of laterals and the slower growth of each higher order (fig. 8). The pattern becomes more complex because successive branches may not elongate at the same rate. Many shoot systems have annually repeating patterns where the uppermost, youngest lateral branches on each annual shoot increment are the longest, with a decrease in length of laterals down to the lowermost, oldest lateral of that year, which is the shortest (fig. 9).

CAMBIAL ACTIVITY THICKENS the framework produced by elongation and lateral formation. The products of cambial activity—wood and phloem—are most of the tree's bulk. The products of apical meristems are only a millimeter or two in diameter, but the trunk of a large tree may be several meters thick. Most of the biomass in a forest is wood that accumulates from cambial activity. The phloem is just as necessary as wood in the function of a tree, but because there is not nearly so much of it and because its cell walls are relatively thin and unlignified, phloem does not accumulate a tremendous amount of biomass.
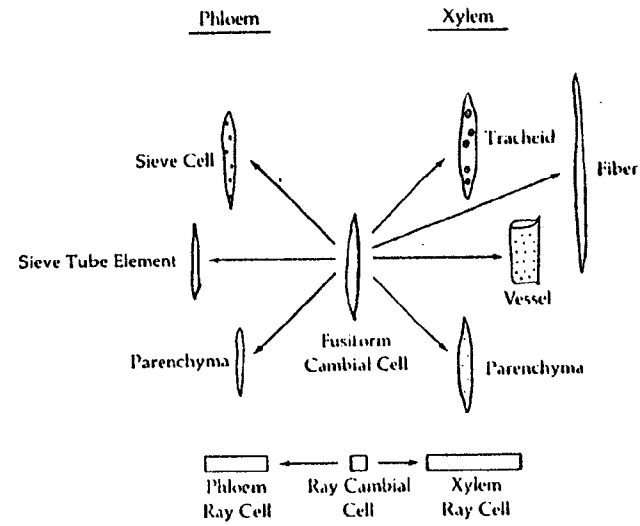
Wood is added to the framework of the tree in sheaths just underneath the bark. The sheaths are added as if the tree were putting on successive pairs of long underwear—adding each layer on top of the last and getting fatter and fatter as each new sheath is produced. Usually we see these sheaths in a tree only from cross sections of branches, stem, or roots. In cross section each layer looks like a ring. In temperate areas, rings are usually annual, but in other areas there may be more than one growth ring in a year or, in many tropical trees, there may be no distinguishable rings at all.

There are three common types of wood: coniferous wood (softwood), ring-porous wood, and diffuse-porous wood (both hardwoods) (fig. 23). All wood is made mostly of vertically oriented cells for strength, water conduction, and, perhaps, some storage. There are also horizontally oriented cells, the ray cells, that conduct materials radially into the wood from the outer parts of the

White Oak
Ring Porous

Red Maple
Diffuse Porous

Hemlock
Coniferous
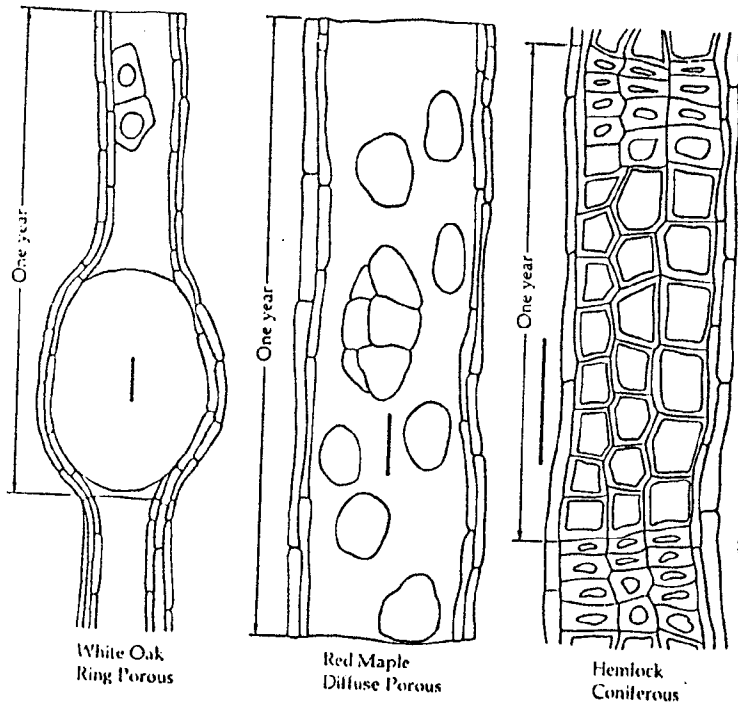
23   WOOD TYPES

A portion of cross sections of annual rings showing rays and the water-conducting cells (vessels in oak and maple, tracheids in hemlock). The hemlock drawing is magnified twice as much as the other types (the bar in each drawing is 0.1 mm long).

Phloem   Xylem

Sieve Cell

Sieve Tube Element

Parenchyma

Tracheid

Fiber

Vessel

Parenchyma

Fusiform
Cambial Cell

Phloem   Ray Cambial   Xylem
Ray Cell   Cell   Ray Cell

24   DIFFERENTIATION OF CAMBIAL CELLS

Sieve cells and sieve tube members are specialized for phloem transport; vessels are specialized for water transport, as fibers are for strength; tracheids combine specialization for both strength and water transport; parenchyma often store materials; ray cells transport materials radially (e.g., from the phloem into the wood).

tree (fig. 24). Ray cells are aggregated into the rays that are often visible as lines on the surface of finished wood, particularly oak. Individual ray cells are somewhat similar in different wood types, but rays are smaller in softwoods than in hardwoods. Generally rays constitute 10–20 percent of the wood volume. The vertical cells of different wood types are quite different, one from another. Coniferous wood is made almost entirely of tracheids, small needle-shaped (fusiform) cells a few millimeters long and twenty to forty microns wide (1,000 microns equal 1 millimeter). Tracheids serve both to strengthen the wood with their thick walls and to conduct water through their hollow interiors. Water
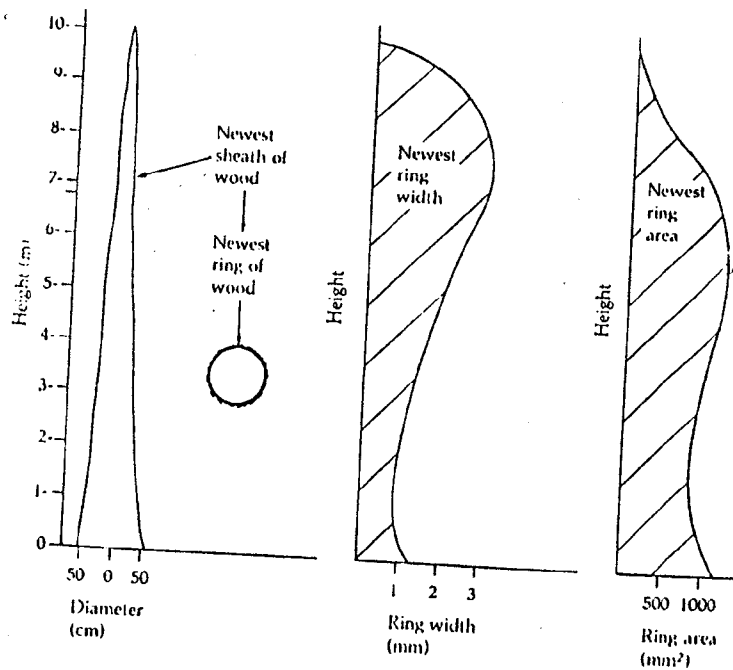
25 WOOD DISTRIBUTION
Distribution of an annual sheath of wood on a tree stem.

passes from tracheid to tracheid through holes in the walls called *pits*. There may also be occasional fusiform parenchyma in coniferous wood to store materials. Hardwoods have developed a division of labor in vertical wood cells. Cells vary in shape, yet they all were derived from similar fusiform cambial cells. Vessels are made of tubelike elements lined up vertically to provide efficient channels for water transport. Thick-walled fibers are specialized for strength and thin-walled parenchyma for storage. Diffuse-porous wood has vessels forty to sixty microns wide scattered throughout the wood. Ring-porous wood has a ring of very large vessels produced at the beginning of each annual ring and a few

small vessels in the rest of the ring. These large vessels may be over 300 microns wide and just visible to the unaided eye. Ring-porous wood represents the ultimate in specialization of cell types. The large vessels are very efficient in water transport, but there are relatively few of these vessels so the system is risky if the large vessels become nonfunctional.

The ring width of the annual sheath of cambial activity varies from the top to the bottom of the tree.[1] The ring width changes according to the position of the ring in relation to the crown of the tree. The most-recent annual ring in a tree, the ring at the outside just under the bark, is smallest near the top of the tree, largest toward the base of the crown where the most productive branches are, and gradually smaller going down the tree below the live crown (fig. 25). Usually the ring width increases right at the base of the tree where the major lateral roots are attached to the stem. There are differences in distribution of ring width according to the size and distribution of the live crown. Very suppressed trees with very short crowns may not even grow near the base of the tree, although they cannot survive long if they grow that slowly. Open-grown trees with live crowns nearly to the bottom may have increasing ring width right to the base of the stem.

The inherent pattern of ring width within any annual sheath is determined by the position and vigor of the crown. This pattern of cambial activity is reflected in an inherent pattern of ring widths in any given cross section going from the pith in the center to the bark on the outside. The ring next to the pith was formed at the top of the tree, the part of the tree that is only one year old. The next ring was formed in the two-year-old portion of the top of the tree, the third ring from the pith in the three-year-old portion of the top, and so forth. Any one cross section stays in the same place relative to the ground, but every year as the terminal shoots elongate, the section gets further and further away from the top of the tree. Eventually it will be where the most productive branches are and then later it will be below the crown. Thus,

the pattern from pith to bark in a section reflects the pattern from tip to base of the tree within any one sheath of wood.

The sum of all the annual sheaths of wood determines the form of the stem of the tree. Open-grown trees have ring widths increasing from top to bottom, so when they are added together the stem tapers all the way from top to bottom. Forest-grown trees, where ring width decreases below the crown, have stems that taper within the crown, but that may be almost cylindrical below the crown.

In the root system, ring widths decrease exponentially with distance from the stem in mature trees.[2] This decrease produces a zone of rapid taper within one to two meters (three to six feet) of the stem. In that zone, ring widths are much greater on the top of the root than on the underside. Beyond the zone of rapid taper, ring widths are narrow all around the root and decrease very slightly with increasing distance from the stem. The roots stay about the same diameter and are almost ropelike until there is a major fork in the root. The annual rings in these roots are frequently discontinuous and they do not extend all the way around the root. Discontinuities make it difficult to determine the age of roots by counting rings.

We frequently make judgments about the rate of cambial activity based on the ring width. For instance, if the rings are wider inside the tree than at the outside it seems that the tree is slowing in growth. However, the actual amount of cambial activity, the total area of wood produced each year, may be increasing even though the ring width is decreasing (see fig. 25). The area of a ring of constant width increases with distance from the center of the tree because the circumference of the tree increases. The influence of the increasing circumference can offset the effect of decreasing ring widths. If a tree is maintaining a constant ring width at a cross section then it must actually be producing more wood at that section each year.

Cambial activity starts at about the same time in all the trees of a species in a stand whether they are fast- or slow-growing. The stimulus is the combination of the longer days and warmer temperatures of spring. All indications are that cambial activity is controlled primarily by growth regulators coming from leaves and growing buds. The initiation of cambial activity starts below newly active buds in diffuse-porous and coniferous trees. Cambial activity then spreads down the trunk at five to ten cm per hour, which is approximately the rate of polar auxin transport. If the stem is girdled by removing a band of bark and phloem below the expanding buds then the wave of initiation is stopped and there is no cambial activity below the girdle. Experiments with isolated stem segments from which the buds were removed show that adding auxin and gibberellin to the top end of the section initiates almost normal cambial activity.[3] Auxin alone causes a few cells to differentiate and gibberellin alone causes the production of cells which do not differentiate. Together the two regulators stimulate both division and differentiation.

Ring-porous trees start cambial activity before the buds grow and activity starts all over the tree at about the same time. It is important for cambial activity to proceed before the leaves grow out in ring-porous trees because the new leaves depend on the new vessels for water. Apparently cambial activity starts in ring-porous trees because an auxin precursor from the leaves was stored in the cambial zone the previous autumn.[4] In the spring, according to the theory, the precursor is converted to auxin and the auxin initiates cambial activity, but there is no wave of initiation because the precursor is distributed throughout the tree and is converted at about the same time throughout the tree.

Once cambial activity has been initiated it still needs regulators from above to continue. The rate of activity may vary and the rate can be measured by the rate of cell production. The rate of cell production is determined by the number of dividing cells in each file and the rate at which they divide. In white spruce the rate is determined primarily by the number of dividing cells and the rate

of division is similar for fast- and slow-growing trees.[5] In other species both the number of dividing cells and the rate of division may vary. It is not known which regulators determine either the rate of division or the number of dividing cells.

* Cessation of cambial activity seems to occur as the production of regulators by leaves slows and stops, although there is always the possibility of inhibitors building up in the cambial zone toward the end of the season. In pines, cambial activity stops shortly after needle elongation stops, but needle elongation proceeds long after the cessation of shoot elongation. In diffuse-porous trees, which are usually indeterminate so that their shoot growth may continue for some time, cambial activity also stops shortly after the leaves stop growing. In ring-porous trees, which are usually determinate species whose leaves stop growing early in the season, cambial activity continues after leaf growth in fast-growing trees, presumably because the mature leaves continue to produce growth regulators. In general, cambial activity stops first at the base of the tree, then up the stem, and finally in the crown.

Although initiation of cambial activity occurs at about the same time in trees of different growth rates, cessation usually occurs earlier in slow-growing, suppressed trees than in fast-growing, dominant trees. Variation in ring width between trees is, therefore, due both to differences in rate of cell production during cambial activity and to the length of time that the cambium is active during a season. The same factors that produce different ring widths between trees probably also determine the different ring widths up and down an annual sheath of wood in any one tree. Cambial activity goes on for a longer time in the crown, because it starts in the crown and stops first toward the base, but the rate of cell production may also be faster in the crown because there is a higher concentration of growth regulators there.

It is clear that the position of the cambium relative to the crown, which is the source of both growth regulators and photosynthate, is a major determinant of annual ring width. The nearer the cambium to the most active leaves, the wider the annual ring. The swaying of the stem in the wind is another important factor in regulating ring width. If a tree sways back and forth so that the stem is bent frequently, then wood is added to the stem to keep the actual bending at the surface of the cambium the same along the whole length of the stem.[6] If a particular part of the stem bends more, then it will have more cambial activity and, as a result, the amount of bending will be reduced because the stem becomes stronger. This sort of feedback between bending and cambial activity occurs constantly along the whole stem as it sways. If a stem is stopped from swaying by guying it with wires, cambial activity is reduced even though photosynthesis is unaffected in the short term by the guying.[7] There are some practical effects of the stimulation of cambial activity by stem sway. If newly planted street trees are supported by guy wires for too long, the stem below the wires will not thicken enough to support the tree when the wires are finally removed and it will break in the wind. Trees in dense plantations are restricted from swaying because the crowns are in such close contact. As a result the lower stems are relatively thin. When the stand is thinned the trees are suddenly exposed to the wind. Many of them break if there is a wind storm before the stems have had time to respond to the increased amount of sway by thickening the lower portion of the stem.

Growth rings in the wood are marked by differences in cell size and cell-wall thickness. In conifers the first-formed tracheids (the *earlywood*) have relatively large diameters and thin walls, and the last-formed tracheids (the *latewood*) have relatively small diameters and thick walls. In Douglas-fir the actual amount of wall produced in each cell is the same in both early and late wood, but, because the cells are smaller in late wood, the walls are thicker.[8] Most conifers have rings that are easily seen and counted, primarily because the dense latewood is darker brown as a result of its high lignin content. It can be shown experimentally in pines

that cell size (radial diameter) and cell-wall thickness are under separate controls. Trees grown under artificial long days can produce "long-day latewood," large-diameter cells with thick walls. Under drought conditions trees may produce drought rings, with small-diameter, thin-walled cells in the latewood.[9] One theory is that auxin concentration regulates tracheid diameter. Auxin concentration is high in the spring and summer so diameters are large, but auxin decreases later in the year and thus the cells are smaller in diameter. Recent careful measurements have shown that auxin concentration is higher in the spring in the cambial zone of pine,[10] but other regulators are probably also involved. Wall thickness largely reflects the amount of available photosynthate. Trees grown under high night temperatures have high levels of respiration at night, high use of photosynthate, and thus produce thin-walled cells. Trees grown under low night temperatures have lower respiration rates, more available photosynthate, and thicker walls.[11] Another factor in wall thickness may be that latewood cells stay alive longer and therefore have more time to synthesize new walls.

Diffuse-porous wood has rings that are hard to see. The latewood is only marked by a few small fibers that are not highly lignified. If you are trying to determine the age of trees by counting rings, avoid diffuse-porous species like maple, cherry, and birch because the rings are so hard to count. Instead, select either a conifer (hemlock is easy to count) or a ring-porous tree like an oak. Ring-porous trees have very obvious rings because of the large vessels in the first-formed earlywood. These vessels are presumably so large because they form during the initial period when there is a high level of auxin present following conversion of the auxin precursor. After this first band of wood with large cells the rest of the earlywood has very few vessels and the latewood is no more distinguishable than in diffuse-porous trees.

Cell types in diffuse-porous and ring-porous woods are distributed in a regular pattern for each species. The pattern is so characteristic that it is a major feature in identifying wood. Vessels, or groups of vessels, are spaced fairly regularly within the matrix of fibers. Parenchyma are usually in some predictable position relative to the vessels, often just around them. Not only are the cell types in a regular pattern in cross sections, but there also is vertical continuity of development so that vessel elements are lined up to make the vertical, continuous files that form the vessels.

These complex geometric patterns of cell distribution are probably determined by growth regulators. The pattern of cell formation can be totally changed by applying growth regulators. High auxin concentrations can produce wood that is almost all vessels, high gibberellin can produce wood that is mostly parenchyma. In experiments with ash, a ring-porous wood, the number of sites that form the large vessels in the spring can be modified by changing the gibberellin concentration, but the number of vessels formed at each site is controlled by auxin.[12] The vertical control of vessel development seems to be from auxin moving down from the leaves. Once a vessel has started to differentiate it appears to interact with the adjoining cells to maintain spacing between vessels and to cause parenchyma to develop in predictable positions relative to the vessels. The enlarging vessels either could be producing substances that regulate differentiation of the other cells or could be using up some factor required for vessel differentiation. The whole process of regulation of wood development is complex because it occurs in four dimensions, the three spatial dimensions and the time dimension. All this takes place in a narrow layer just outside the cambial zone.

Dead trees, where the bark has fallen off, often show spiral grain. The cells, and the cracks that form between the cells as wood dries or is split, actually run at an angle to the stem and spiral around it. The grain angle often changes over time and even may change from spiraling to the left to spiraling to the right. An elegant way to demonstrate these changes in grain angle is with
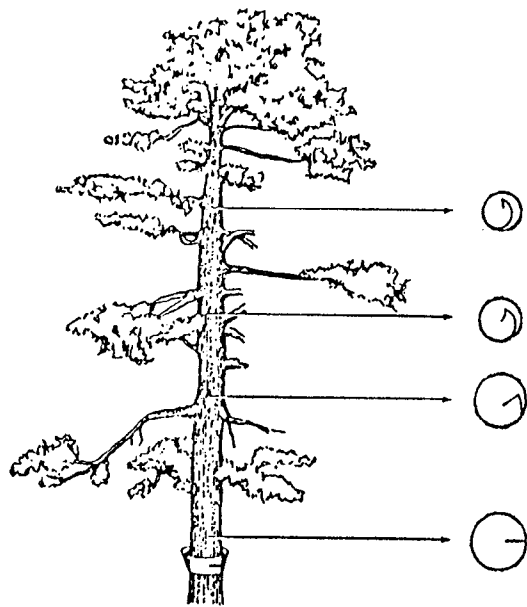
26 DYE ASCENT
The dye is put in a collar around the stem and the leaves pull it into a hole drilled in the wood. As the dye moves up the stem it follows the path of spiral grain and the movement to the side is shown in cross sections taken at different heights.

a dye ascent.[13] In this process, a hole is drilled deep into the wood at the base of a transpiring tree and dye from a reservoir is pulled into the wood and up the tree. At each point along the length of the hole the dye moves up in the direction of the grain. If the grain spirals to the right the dye will be displaced to the right, and vice versa for a left-handed spiral. The path of movement of the dye can be followed by cutting the tree down and taking out disks at intervals up the stem (fig. 26). The history of the changes in orientation of the grain from the inside, the past, to the outside, the present, is revealed by the relative displacement around the stem. In trees with interlocked grain where the wood is hard to split, like elm, the grain may change from a right- to a left-handed spiral each year. In many trees the grain angle reverses after a few years and gradually increases over the years so that spiral grain angle is greater in older than younger trees. One of the best ways to become interested in grain angle and to study it first hand is to split firewood. Working with firewood makes one really appreciate straight-grained wood that splits with a touch of an axe as opposed to interlocked grain, as in elm, where it is possible to bury a wedge in the wood and hardly split it at all. Another subject of practical study is the distortions of grain around knots or at branches, which makes splitting difficult.

Spiral grain originates in the cambial zone. It has to be formed there because wood cells cannot change orientation once they have developed thick walls. The probable cause is that when fusiform initial cells divide perpendicularly to form new files of cells (a *pseudotransverse division*) the new cell wall is slanted across the parent fusiform initial. Whole areas of cambium may have the new slanted walls predominantly in one direction.[14] After the pseudotransverse divisions the daughter cambial cells slowly elongate at the tips. If the direction of the new walls is random then the direction of the grain stays the same, but if the direction of the new walls is predominantly one way, the grain angle will gradually change. In some trees the areas where divisions are predominantly in one direction slowly move over the surface of the cambium so that the grain changes irregularly; in others the change is more regular. Changes in grain angle are not clearly related to structural demands of the stem.

Once wood is formed, the water-transporting cells die quite rapidly, but parenchyma cells and ray cells may live for decades. Younger wood toward the outside of the tree is functional in water transport. This light-colored wood is called *sapwood*. Older wood, the *heartwood*, becomes nonfunctional in water transport. The vessels are filled with air and may then be blocked by in-

growths (*tyloses*) from parenchyma cells. As the vessels and tra-
cheids become nonfunctional, materials are transported down
the rays and stored in the heartwood. These materials often com-
bine to form the dark-colored substances that make it easy to dif-
ferentiate heartwood. It seems likely that the heartwood is being
used as a chemical dump for the excretion of unwanted sub-
stances. One of the results is our finest cabinet woods, which in
fact are the attractively colored heartwoods from the tree's waste
disposal system.

THE PRECEDING CHAPTERS have discussed how
the framework of the tree is built by apical meristems producing
new axes in regular patterns and how the framework is then
thickened by cambial activity. This information, along with the
information on how the different axes are attached to each other,
is almost sufficient to describe the structure of a tree. What is
needed to complete the description is information about the ori-
entation of each axis and how that orientation changes over time
if an axis moves. The orientation of apical growth determines the
initial position of axes. There may be later movements due to
bending from self-weight or bending from special wood called
reaction wood.

Orientation of an axis can be described in relation to the verti-
cal, using angles and a three-dimensional coordinate system, or
in relation to the parent axis from which it was derived, using an-
gles alone. Both methods have some virtue. Axes oriented with
respect to gravity (vertical) are best described in a coordinate sys-
tem because to some extent the axes orient independently of each
other. On the other hand, many aspects of axis orientation are not
independent. For instance, if a tree is tipped over or swayed in
the wind, the same basic orientation is kept between axes, but
every axis changes orientation within a coordinate system.

The first axes of a tree are the primary root and shoot growing
out of the seed. The root grows down and the shoot grows up. All
the rest of the axes of a tree originate laterally as lateral meri-
stems. The initial orientation of each lateral is determined by its

Just as in shoots, when a root tip is injured the lateral roots just behind the injury bend from their usual orientation at right angles toward the direction of the parent shoot. The mechanism of this apical control in roots has not been studied. Root tips do not produce much, if any, auxin, so the mechanisms are presumably different in roots than in shoots even though the result is the same.

THE INITIAL ORIENTATION of a shoot is established by primary growth, but the orientation can be changed later. Although the emphasis of this chapter will be on reorientation of a woody stem or branch from active bending, it is important to realize that when a woody shoot bends, all the higher order branches off the shoot are passively reoriented. The same thing happens if a shoot is tipped or broken. The most dramatic example is when a tree is tipped over by a storm. Then the stem and each branch in the crown is reoriented. Another example is when a branch bends up at the base. The outer parts of the branch, and all higher order branches along with it, rotate around the branch base. The further a shoot is from the bending base the more it is moved, even though the shoot itself does not bend at all.

A shoot can be bent by external forces like wind, snow, rain, and self-weight or by internal forces generated by differentiating wood cells. The amount of bending of an axis is determined by the amount of force acting on it and by its resistance to bending. If a shoot bends too far, it breaks. If a bending main stem puts too much stress on the roots that hold the stem in the ground then the roots break and the stem tips over.

Resistance to bending is a function of the stiffness of the wood and the cross-sectional radius of the shoot axis (fig. 29). Stiffness varies between species. Generally hardwoods like oak are stiffer than softwoods like pine. If an oak and a pine branch of the same size are bent with the same force, the pine bends more than the oak. For each species, a thicker branch bends less with a given
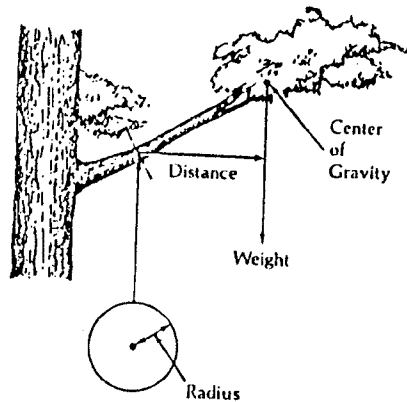
29 BRANCH BENDING
Factors determining bending force and resistance to bending in a branch.

force than a thinner branch. The stiffness of wood within an individual tree does vary with the age of the wood and the percentage of latewood, but the major variable in resistance to bending within a particular tree is the radius of the shoot. Resistance to bending of a branch that is circular in cross section is a function of the fourth power of the radius. Therefore, small growth in the radius produces big increases in stiffness. For example, if the radius increases from two to three, a 50 percent increase, the stiffness increases 500 percent, from sixteen to eighty-one. Thus, as a stem or branch thickens from cambial activity it gets much stiffer and much harder to bend.

The actual force acting to bend a shoot at any particular cross section is called the *bending moment*. The bending moment is the force acting multiplied by the distance from its plane of action (see fig. 29). To appreciate the effect of distance, hold a moderately heavy weight in your hand with your hand near your shoulder and then move your hand out until your arm is extended. As the weight moves further from your shoulder, the bending moment increases and it is harder and harder to hold the weight. For bending by self-weight the distance is measured to the center of gravity of the weight beyond the cross section. For bending by wind the distance is measured to the center of where the force is applied, essentially to the center of the sail-like structure created by the crown or branch.

Bending moments can also be generated by internal growth stresses. Growth stresses develop when fusiform wood cells tend to lengthen or shorten as the thick secondary walls differentiate. These stresses are normal by-products of cell-wall differentiation. Most cells tend to shrink as they differentiate (fig. 30), so they develop tensile stresses.[1] Each sheath of new wood that is added to the tree tends to shrink longitudinally. This tendency to shrink, and the resulting tensile stress, is resisted by the older core of wood. As more and more sheaths of wood are added in tensile stress the central core is actually compressed. In extreme cases the core is compressed so much that there are many compression failures in the wood. Eucalypts in Australia develop brittle heart in the center where the wood has so many compression failures that large beams can break under light loads because of the internal failures. Many tropical trees develop such high growth stresses that when the tree is cut the trunk splits apart. Loggers cutting such trees are in danger because if a tall tree splits up the trunk as it is being cut, the split half may suddenly move out a meter or more and kill anyone in the way.

If growth stresses are evenly distributed around the trunk then no bending force develops, but if there is an uneven distribution of stresses then there is a bending force. The bending moment is the difference in force between the opposite sides of the stem multiplied by the distance of the sheath from the center of the stem. More precisely, the distance is from the neutral plane of bending. When a branch bends, one side gets longer and the other side gets shorter. Near the center is a plane where no change in length occurs, called the *neutral plane of bending*.

In ——→ Out   In ——→ Out   In ——→ Out

Tension   Normal   Compression
Wood   Wood   Wood
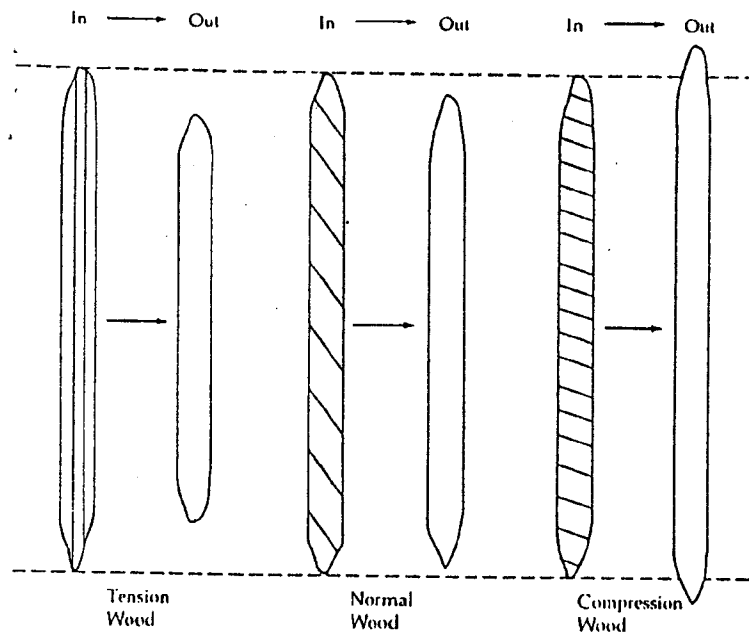
30   WOOD GROWTH STRAINS
Diagrams of the change in length of wood cells when the growth stresses
are released by taking the cells out of the wood. The orientation of the
microfibrils is shown in the "in" drawing.

After a tree stem is tilted over by the wind, new wood cells
change their secondary wall differentiation to produce different
levels of growth stresses. The upper side produces wood with
higher tensile stress (it tries to shrink) and the lower side pro-
duces wood with lower tensile stress or even with compressive
stress (it tries to expand). The result is an uneven distribution of
growth stresses that tend to bend the stem toward vertical.

This tendency to produce differential growth stresses reaches
its maximum expression when reaction wood is formed. In soft-
woods, like pines, the underside of a leaning stem develops com-

pression wood. Compression wood cells have extra thick walls
and are dark because they have a high lignin content. These
compression wood cells actually develop compressive growth
stresses. Because they are on the underside of the stem they act
to bend it up by pushing. In hardwoods, like oak or maple, the
upper side of a leaning stem develops tension wood. The tension
wood cells have an extra cell wall layer and they develop very
high tensile stresses, much greater than in cells with normal
walls. Therefore, in hardwoods the tension wood tends to pull
the branch up. The action is opposite to compression wood action
in softwoods, but they both tend to bend leaning stems upward
because the tension wood forms on the top and pulls, while the
compression wood forms on the bottom and pushes. (Compres-
sion wood forms only in softwoods and tension wood only in
hardwoods. Normal cells of both types develop tensile growth
stresses.)

Reaction wood, to a large extent, is just a specialized version of
normal wood that produces unusual levels of stress.[2] The excep-
tion to that conclusion is the special layer of cell wall that de-
velops in tension wood and which is limited to tension wood
cells. There seem to be two types of mechanisms responsible for
growth stresses. The first mechanism is responsible for develop-
ment of stresses in most cell walls (see fig. 30). Cell walls of
wood are formed by cellulose strands, called *microfibrils*, that
form a framework on which lignin is deposited. As the lignin is
deposited it swells and pushes the microfibrils apart. The micro-
fibrils are oriented in regular helices around the cell and the angle
of the helix to the axis of the cell is critical to the amount and type
of stress that develops. In normal cell walls, the angle of the mi-
crofibrils to the axis of the cells is small. As the lignin forces the
microfibrils apart the cell tends to shrink and therefore develops
tensile stress. The microfibril angle of cells is smallest on the up-
per side of leaning trees so the tensile stress is greatest. On the
sides of a leaning tree the microfibril angle is almost unchanged

so the tensile stress is about the same as in normal wood. On the underside, the angle is even greater and the tension is reduced even further. In conifers, the microfibril angle can increase so much that as the lignin pushes the microfibrils apart the cell actually tends to increase in length and a compressive stress develops. Compression wood is in this sense just an extension of normal wood with a larger microfibril angle and more lignin. The high lignin content in compression wood presumably increases the tendency to push the microfibrils apart and produces even higher compressive stresses. The second mechanism appears to be peculiar to the special layer of tension wood cells. This layer does not have much lignin, although other compounds are deposited on the cellulose framework. The cellulose microfibrils are oriented nearly parallel to the axis of the cells. It seems likely that in this layer the tension is generated because the cellulose microfibrils actually shrink as they are formed. The outer layers of tension wood cells behave like normal wood cell walls and the stress they develop is determined by the microfibril angle; only the extra inside layer is special.

Reaction wood forms under several different circumstances. Each stem and branch has an angle, the preferred angle, at which it does not form reaction wood. If the stem or branch is moved out of this angle it forms reaction wood to bend the axis back to the preferred angle. For example, if a vertical stem is tipped over by a wind storm it develops reaction wood to bend it back to vertical. Softwoods develop compression wood on the underside and hardwoods develop tension wood on the upperside. Horizontal branches tend to sag under their own weight so they form reaction wood to bend them back toward the horizontal. If branches are artificially bent up and tied in position they form reaction wood to force them back down to horizontal. In this example the "normal" positions are reversed, hardwoods make tension wood on the underside and softwoods make compression wood on the upperside. This induction of reaction wood because of changed orientation presumably is a response to gravitational stimulus. Somehow each axis can detect when it is out of its preferred orientation to gravity.

Reaction wood can also be induced in branches without any change in orientation, or gravitational stimulus, by removing apical control. Injuring the terminal causes reaction wood to form that will bend the branch to the orientation of the parent axis so that the branch becomes a replacement shoot. Apical control can be removed by cutting off the stem above the branch or by removing a strip of bark and phloem all the way around the stem above the branch. Many branches do form some reaction wood even though they are under apical control. Generally they do not form enough reaction wood to counterbalance the downward-bending moment from the self-weight of the branch. These branches form more reaction wood when apical control is removed and the branch bends up. A few species, like ash, do not normally form reaction wood in branches, but when apical control is removed ash does form tension wood and the branch bends up. Essentially, when apical control is removed, the preferred angle of the branch changes to the angle of the parent axis and it forms reaction wood to bend to its new preferred angle.

Reaction wood formation seems to be regulated by auxin. When a stem is tipped over there is a higher auxin concentration on the underside than on the upperside. Moving the stem out of its preferred angle stimulates some mechanism, perhaps lateral auxin transport from one side of the stem to the other, that leads to differential auxin distribution. In softwoods the high concentration on the underside stimulates compression wood formation and in hardwoods the low concentration on the upperside stimulates tension wood formation. This difference in response to auxin concentration can also be shown in vertical stems that do not normally form reaction wood. If auxin is added to such a softwood stem it forms compression wood below the point of application. If auxin is reduced in a hardwood stem by adding triiodo-
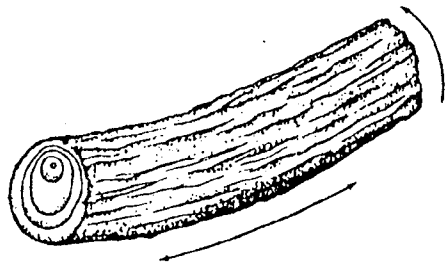
Compression wood
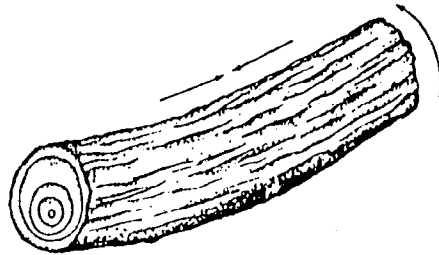
Tension wood

31 REACTION WOOD

Location and action of the two types of reaction wood in tilted stems.

benzoic acid, which stops auxin movement down the stem from the leaves, then the stem below forms tension wood.

Thus, if a vertical stem is tipped, auxin concentration is reduced on the upperside and increased on the underside. As a result, the microfibril angle of the wood produced after tipping changes and reaction wood is formed. Compression wood forms on the underside in softwoods and tension wood forms on the upperside in hardwoods (fig. 31). Compression wood tends to expand and tension wood tends to contract so both of them act to

bend the stem up toward vertical. Compression wood pushes it up and tension wood pulls it up.

Reaction wood formation is usually associated with increased ring width. In a tipped stem the widest part of the ring is usually on the side where the reaction wood forms so that if it forms for some time the stem becomes eccentric with growth mostly on the top in hardwoods and on the bottom in softwoods. This correlation of increased ring width with reaction-wood formation is characteristic, but it does not always happen. The fact that reaction-wood formation and increased ring width can be separated shows that they are not controlled by the same regulators. In any case, it seems unlikely that high auxin would increase growth in softwoods and decrease it in hardwoods. It is probable that some other regulator is responsible for increasing ring width, perhaps gibberellin, but it is not clear why the regulator concentration might be higher on the top of tipped hardwood stems and on the bottom of tipped softwood stems.

When apical control is removed, a branch responds by growing faster all around, but the growth increase is greatest on the side where reaction wood forms. The location of the major increase in growth is presumably due to the same mechanism responsible for increased ring width where reaction wood forms in tipped stems. The explanation for the general increase seems to be that when the branch is under apical control most of the photosynthate it produces moves out of the branch and is used in stem growth. Essentially the branch and the stem compete for the branch photosynthate and the success of the stem in the competition depends on regulators moving down the stem from above. The most important regulator seems to be auxin because auxin can replace apical control and keep the branch from growing faster. When apical control is removed by cutting off the stem above the branch, then the branch can retain more of its photosynthate and grow more because the stem cannot compete successfully with the branch.

The angles of old branches reflect the balance between bending down by self-weight and bending up by reaction wood. Many softwoods that have a central stem much larger than the branches, like pines, show a clear sequence of branch angles from the young branches at the top to the older branches at the bottom. Young branches grow at about a forty-five-degree angle. As the branches elongate, most of the photosynthate either goes into making more needles and elongating the branch or is transported out of the branch to the stem. There is some cambial activity to thicken the branch, but not enough to keep it from sagging from the increased bending moment of its own weight. Toward the tip the branch usually bends up slightly because the tip elongates somewhat upward and it takes several years of loading from increased branch weight before the old tip portion is bent down. Therefore, at the bottom of a pine tree the branches are near horizontal except toward the tip. In a maple grown in the open, however, the main stem is quite short and there are many large branches. The lower branches grow rapidly and sweep up until the tips are nearly vertical. Enough photosynthate is retained by the branches so that they thicken and are not bent down very much by the increasing self-weight.

TREES IN MOST regions need to survive occasional hard times. For a large part of the world, the hard times are the cold winters. In other parts there are droughts (although trees do not grow at all in the driest parts of the world) and floods. Most of these hard times occur annually at fairly regular seasons. Trees usually start preparations before the hard times actually arrive. If a tree were still growing when there was a freeze it might be killed, so there is a tremendous advantage for it to be dormant and frost-hardy well before the dangers of winter arrive. To prepare ahead of time trees have to use environmental cues. Trees, like most organisms, are sensitive to day length. They can essentially tell what time of year it is by the length of the day. Many of the preparations for winter start as the days begin to get shorter in the summer. If days are extended with artificial light, the trees just keep on growing as if it were early summer.

Along rivers, trees are flooded regularly, usually in the spring before the leaves grow out and when the trees are most resistant to flooding. Trees that are regularly flooded for long periods have special mechanisms to survive the problem of insufficient root aeration.[1] Other trees are killed by extended flooding when they are in leaf.

Droughts that are not seasonal cannot be cued by day length, but they develop slowly as the soil dries out, so the decreased water availability is another kind of environmental cue. When the water potential in the leaf drops, the leaf begins to form abscisic acid. The abscisic acid stimulates the stomata to close. Abscisic