Forest Products and Wood Science
An Introduction

Fifth Edition

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CHAPTER

1

Tree Growth and Production of Woody Tissue

Trees are complex organisms. Originating through vegetative propagation or from sexually fertilized eggs that become tiny seed-encased embryos, trees grow to be one of nature's largest living organisms.

Like humans, trees are delicate when young and typically grow vigorously when given proper nutrition and a suitable environment. As juveniles, they form tissues that differ from those formed in mature trees. They respire. They require a balanced intake of minerals to maintain health. They metabolize food, but unlike humans they also synthesize their own foods. If wounded, they react quickly to effect healing. As age progresses, vigor is maintained for a lengthy period but then begins to wane. Life processes eventually slow to the point that the tree has difficulty healing wounds and warding off disease. Finally, the tree dies.

The focus of this book is not on the growth process but on an important product of growth: wood. However, a brief study of the process of wood formation provides a useful basis for a study of wood itself.

Wood is formed by a variety of plants, including many that do not attain tree stature. A *tree* is generally defined as a woody plant 4–6 m (15–20 ft) or more in height and characterized by a single trunk rather than several stems. Plants of smaller size are called shrubs or bushes. Species that normally grow to tree size may occasionally develop as shrubs, especially where growth conditions are adverse. Because of the size attained, wood produced by plants of tree stature is useful for a wider range of products than wood from shrubs and bushes. For this reason, wood produced by trees is emphasized.

Classification of Woody Plants

Woods, and the trees that produce them, are divided into two categories: hardwoods and softwoods. Hardwood and softwood trees are botanically quite different. Both are included in the botanical division spermatophytes (Table 1.1), meaning they produce seeds. They are, however, in different botanical subdivisions. Hardwoods are in the subdivision angiospermae and softwoods are in the gymnospermae subdivision. *Angio-*

TABLE 1.1. Trees in the Plant Kingdom.

Divisions:	Thallophytes Algae Fungi	Bryophytes Mosses Liverworts	Pteridophytes Ferns Horsetails Rushes	Spermatophytes (seed plants)	
Subdivisions:	Gymnosperms (naked seed)			Angiosperms (seed in fruit)	
Orders:	Cycadales (palmlike)	Ginkgoales (rare)	Gnetales	Coniferales	Classes: Monocots Yucca — Dicots
Families:	Cupressaceae Cedar Juniper Cypress	Taxaceae Yew	Pinaceae Fir Hemlock Pine Spruce Larch	Taxodiaceae Redwood Baldcypress	25 families in the United States

sperms are characterized by production of seeds within ovaries, whereas *gymnosperms* produce seeds that lack a covering layer.

Needlelike leaves characterize *softwood* trees. Such trees are commonly known as evergreens, because most remain green the year around, annually losing only a portion of their needles. Most softwoods also bear scaly cones (inside which seeds are produced) and are therefore often referred to as *conifers*. Included in the softwood group in the Northern Hemisphere are the genera *Pinus* (pine), *Picea* (spruce), *Larix* (larch), *Abies* (fir), *Tsuga* (hemlock), *Sequoia* (redwood), *Taxus* (yew), *Taxodium* (cypress), *Pseudotsuga* (Douglas-fir), and the genera of those woods known commonly as cedars (*Juniperus, Thuja, Chamaecyparis,* and *Calocedrus*).

In contrast to softwoods, *hardwoods* are angiosperms that bear broad leaves (which generally change color and drop in the autumn in temperate zones) and produce seeds within acorns, pods, or other fruiting bodies. Referring again to Table 1.1, note that angiosperms are subdivided into monocotyledons and dicotyledons. Hardwood-producing species fall within the dicotyledon class. Hardwood genera of the Northern Hemisphere include *Quercus* (oak), *Fraxinus* (ash), *Ulmus* (elm), *Acer* (maple), *Betula* (birch), *Fagus* (beech), and *Populus* (cottonwood, aspen) and others. Included in the monocotyledon class are the palms and yuccas. Many of the roughly 2,500 species of palms produce relatively large-diameter fibrous stems, which are strong if left in the round condition but tend to fall apart when cut into lumber; some species of palm, however, produce stems suitable for production of local use construction "lumber." Composite panels and flooring can be made from partially refined stems and paper can be made from the fiber.

Not only do hardwood and softwood trees differ in external appearance, but the wood formed by them differs structurally or morphologically. The types of cells, their relative numbers, and their arrangements are different, the fundamental difference being that hardwoods contain a type of cell called a *vessel element*. This cell type occurs in most hardwoods but very seldom in softwoods. Hardwoods are classified as ring- or diffuse-porous, depending upon the size and distribution of vessels in a cross section. Woods that form very large-diameter vessels part of a year and smaller ones thereafter are called ring-porous. Woods that form vessels of the same size throughout the year are classified as diffuse-porous.

All hardwoods do not, incidentally, always produce hard, dense wood. Despite the implication in the names *hardwood* and *softwood,* many softwoods produce wood that is harder and more dense than wood produced by some hardwoods. Balsa wood, for example, is from a hardwood species.

Distribution of Hardwoods and Softwoods

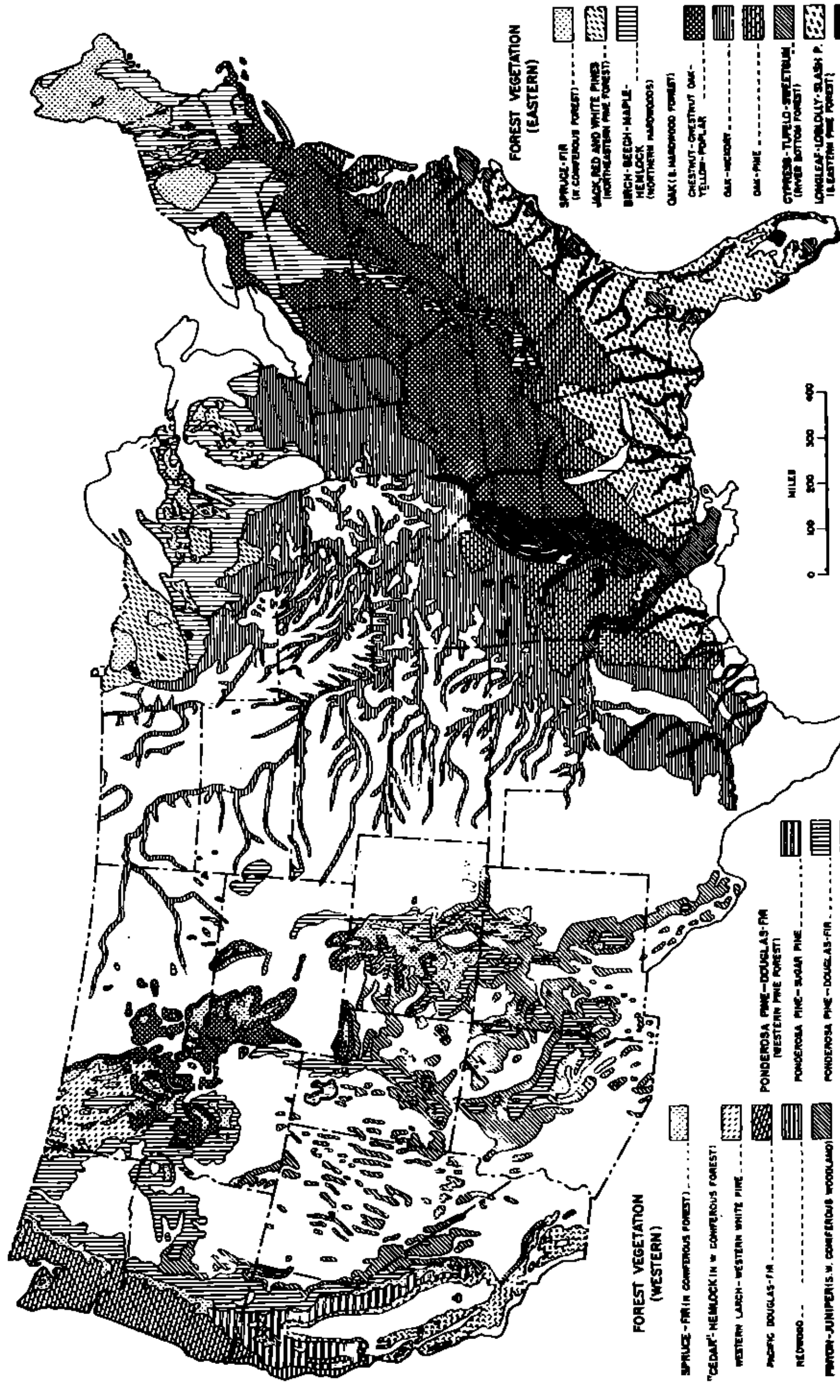
Hardwood species occur in every major region of the United States. They predominate in the East, forming an almost unbroken forest from the Appalachians westward to the Great Plains. Across the Plains, the trees that line rivers, streams, and ponds and form windbreaks along agricultural fields are hardwoods. Farther west, the perpetually green softwoods that cover the Rocky Mountains are frequently interrupted by patches of white-stemmed aspen and other hardwoods. In the far West, hardwoods grow in valleys below softwood-covered mountains. Softwoods dominate forests of the deep South, the far North, the mountainous West, and the extreme Northwest (Fig. 1.1). Softwoods also are predominant in the mountains and coastal regions of Alaska.

Hardwood growing stock globally has been estimated to exist in volumes almost double that of softwoods. The area covered by hardwood forests is greater as well. Sedjo and Lyon (1990) noted that hardwoods predominate in 57 percent of the area covered by closed-canopy forests and that softwoods predominate in the remaining 43 percent. North America, Russia, and Europe account for over 92 percent of the world's softwood forests. Hardwoods, on the other hand, are more widely distributed than softwoods. Natural forests of the tropics are almost totally hardwood. South America alone contains about one-third of the world's hardwood forests and South America and Asia account for over one-half of hardwood forests worldwide. In addition, Africa's forests are 99 percent hardwood. The hardwood forests of North America, Russia, and Europe together comprise about one-third of the world's hardwood forests. Overall, forests cover some 3,869 million hectares (9,556 million acres) worldwide, of which just over 95 percent are natural forests (Table 1.2).

In the United States about one hundred wood-producing and commercially important species reach tree size; only about thirty-five of these are softwoods. Roughly the same is true of Europe. However, throughout the world, and particularly the tropical regions, the number of wood-producing species of tree size exceeds ten thousand. Of these, the number of softwoods is small—only about five hundred. The wet tropics are particularly rich in species; several hectares may contain several hundred species. The large number of species complicates efforts to fully utilize the tropical rain forest. Despite considerable research to determine properties, use potential, and processing technology, work has been completed on only a relatively small number of species. Today, approximately twenty-five hundred tree species have commercial importance.

Wood—A Collection of Small Cells

A close look at wood shows it to be made up of tiny cells or fibers that are so small they generally cannot be seen without a magnifying glass or microscope. Illustrated in Figure



(Courtesy USDA Forest Service)

FIGURE 1.1. Forest vegetation of the continental United States.

TABLE 1.2. Forest area by region and type.

Region	Land Area (million ha)	Total Forest (natural forests and forest plantations) area (million ha)	% of land area	% of world's forests	Natural Forest (million ha)	Forest Plantation (million ha)
Africa	2978	650	22	17	642	8
Asia	3085	548	18	14	432	116
Europe	2260	1039	46	27	1007	32
N. and Central America	2137	549	26	14	532	18
Oceania	849	198	23	5	194	3
South America	1755	886	51	23	875	10
World total	13064	3869	30	100	3682	187

Source: FAO (2005).

1.2 is a type of cell that makes up most of the volume of a softwood such as white fir; the cell has a hollow center (*lumen*), is closed at the ends, and is perforated with openings known as pits in the sidewall.

Figure 1.3 shows how a tiny block of white fir would look if magnified. Unmagnified, this block would occupy only about 1/50,000 cm^3. Rays, which are composed of a number of individual ray cells and provide for horizontal movement of substances in a standing tree, can be seen cutting across the near left (radial) surface; rays in an end view can be seen on the right vertical (tangential) surface.

In Figure 1.3, note that the three different surfaces of the block—labeled transverse (cross section), radial, and tangential—look quite different (see also Fig. 2.1). A cross-sectional or *transverse* surface is formed by cutting a log or piece of lumber to length; radial and tangential surfaces result from cutting along the grain. A *radial* surface is made by cutting longitudinally along the radius of a round cross section. Tangential surfaces result from cutting perpendicular to a radius or a tangent to the growth rings. The names *transverse*, *radial*, and *tangential* are frequently encountered in the study of wood science.

Basic Processes in Tree Growth

The mechanisms that result in tree growth are remarkably complex, a reality that is becoming more and more evident with advances in science. In the following section, tree growth is discussed in rather general terms to provide a basic understanding of the processes involved.

Production of Wood and Bark

Wood (*xylem*) is found inside a covering of bark, which is composed of an inner layer (*phloem*) and an outer protective layer (*outer bark*). As a tree grows, it adds new wood,

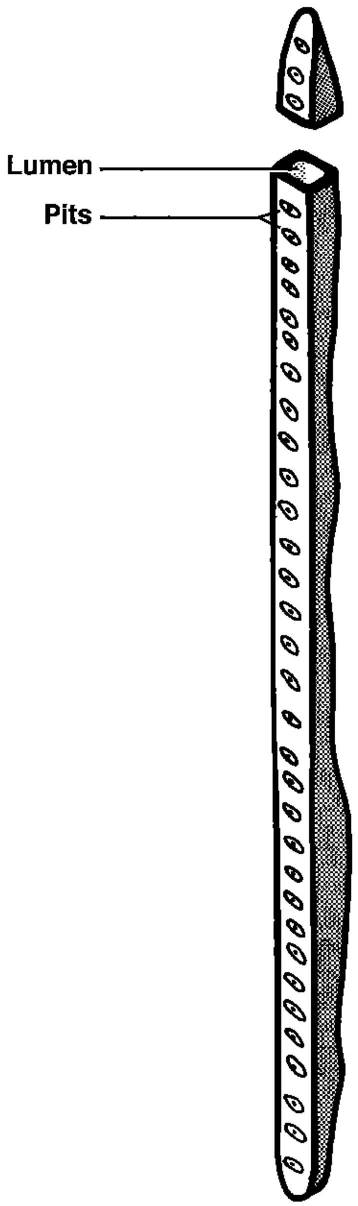


FIGURE 1.2. Typical longitudinal tracheid of softwood.

increasing the diameter of its main stem and branches. Bark is also added in the process of growth to replace that which cracks and flakes off as the stem grows larger.

Like all green plants, a tree can manufacture its own food through the process of photosynthesis, which takes place in the leaves. It needs only water (from the soil), carbon dioxide (from the atmosphere), and light (from the sun) to do this. Water, along with nutrients, is taken up by the roots and moved through the outer part of the xylem up to the leaves. The wood cells provide pathways for unbroken fluid columns that link the roots to the leaves. Note that in physics, capillary action is influenced by pore diam-

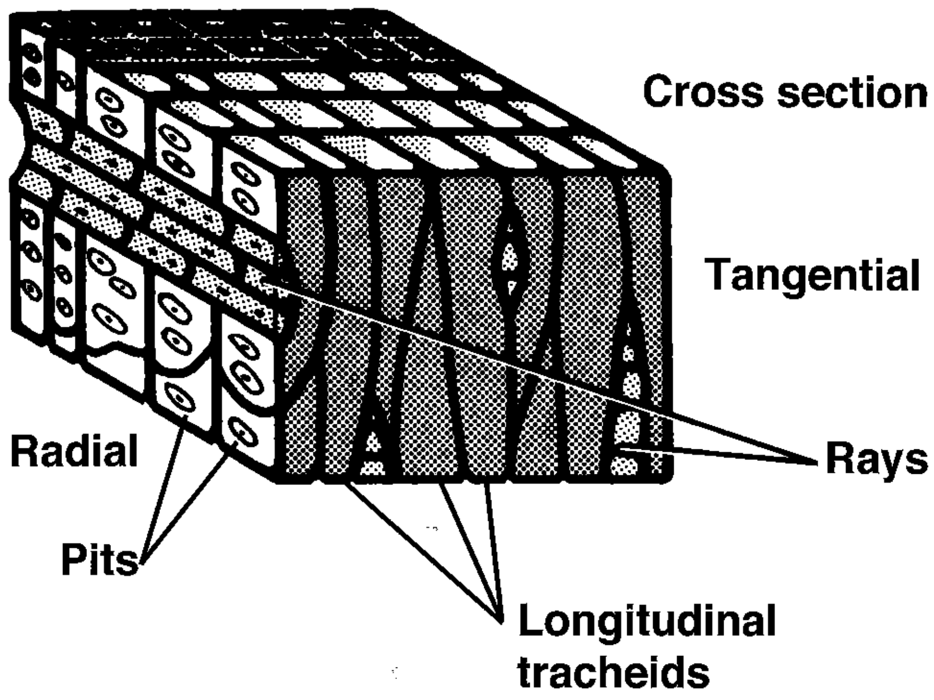


FIGURE 1.3. Three-dimensional drawing of softwood block.

eter and surface tension; in trees the combination of these suggests that the maximum column height is about 100 m (330 ft), the height of the tallest trees. Carbon dioxide is taken in through tiny openings in leaf surfaces. With the help of the sun, water and air are combined in the presence of chlorophyll to make sugars that provide energy to the growing tree. Some sugars are used in making new leaves, some in making new shoots, and some in making new wood. A part of the sugar moves to special locations in the wood or to the roots where it is stored for later use; a part is consumed through respiration. Sugars used in making new wood move down a tree through the phloem.

Sugar is transported throughout the tree in the form of *sap*, a solution containing various sugars and water as well as growth regulators and other substances. The term *sap* is also used to refer to the mineral-rich water that is taken up by roots and moved upward through the outer portion of the xylem.

A thin layer between the xylem and phloem produces new xylem and phloem tissue. This layer, called the *cambium*, completely sheaths the twigs, branches, trunk, and roots, meaning that a season of growth results in a new continuous layer of wood throughout the tree (Fig. 1.4).

Because sap moves down the tree through the phloem but is necessary for food in the cambium, a way is needed for it to travel horizontally toward the center of the tree. *Wood rays* provide for this horizontal movement. Rays also function in storing carbohydrates and may serve as avenues of horizontal transport for stored materials from near the center of the tree outward following periods of dormancy.

Figure 1.5 illustrates the relative position of various portions of a tree stem. Careful

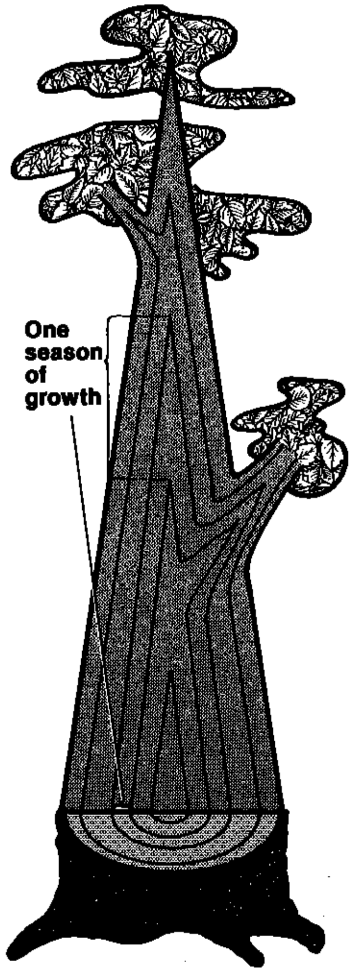


FIGURE 1.4. New growth occurs as a sheath covering the main stem, branches, and twigs.

examination should help in gaining an understanding of the relationship between various layers of tissue.

Development of a Young Stem

To begin a study of the development process, growth of a young pine seedling will be considered (Fig. 1.6). The seedling shown has a well-developed root system and crown typical of a 1- to 2-year-old tree. With the beginning of growth in early spring, buds at the tip of each branch swell as tissue expands through formation and growth of cells. These regions in which cells divide repeatedly to form new cells are called *meristematic regions.* Highlighted in Figure 1.6 is an expanding bud at the apex of a young pine. Buds of similar appearance occur at the tip of each branch. The meristematic zone at the apex of the main stem is of special significance because it controls, to some extent, the development of branches and shoots; it is called the *apical meristem.*

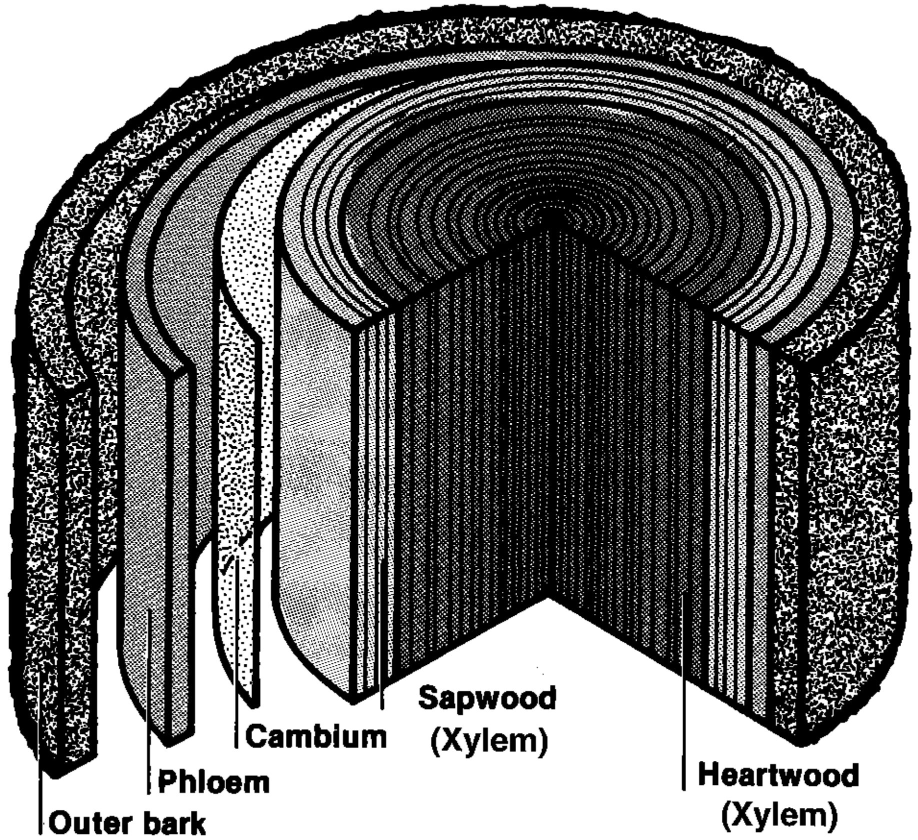


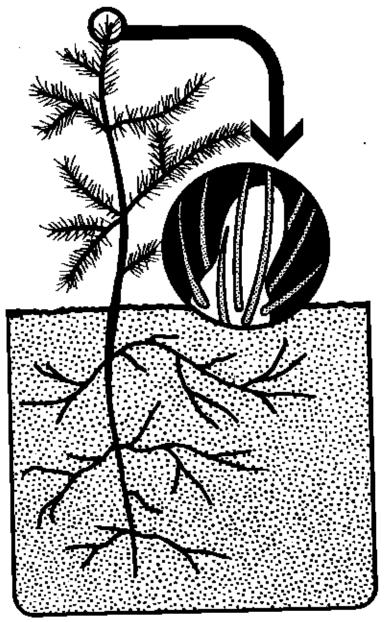
FIGURE 1.5. Parts of a mature tree stem.

Cell division at the apical meristem serves to lengthen the main stem. New cell production at this location is followed by cell elongation resulting in height growth. As the stem is built through production of new cells during growth periods, the terminal bud moves upward, leaving new and expanding cells behind. Because trees grow in height from the apex rather than from the base, initials carved into a tree at, for example, 2 m above ground level will remain 2 m off the ground regardless of the height to which the tree grows.

Cell production at the stem tip and subsequent cell lengthening are followed by a sequence of changes as newly formed cells mature. We explain this entire process using a representation of a section of a growing stem tip that shows various tissue layers (Fig. 1.7). The student should be cautioned that Figure 1.7 and the accompanying discussion present a greatly simplified picture of the actual growth process.

New cells are produced in the several layers of cells in the area designated as section I. Soon after formation, these newly formed cells begin to differentiate with changes in size, shape, and function. Tissue at the outer edge of the young stem forms an *epidermis* composed of one layer of cells, which have thick, wax (cutin)-covered outer walls serving as protection from moisture loss. Nearer the center of the stem, cells undergo a de-

FIGURE 1.6. Pine seedling.



velopmental process, changing size and shape to eventually form an unbroken ring about the stem center. This region is called the *procambium* and is the precursor of a new meristematic region that develops a bit later. At the very center of the stem, cells develop differently yet, forming a layer dissimilar to the wood that will later surround it. This is the *pith*. The pith, procambium, and epidermis can be seen in section II of Figure 1.7.

The process of change continues. The procambium reaches a maximum size (lower edge of section II); then cells that make it up undergo further differentiation. As depicted in section III, inner cells of the procambium continue to undergo change to become similar to xylem, which will form later. Cells of the outer portion of the procambium assume characteristics similar to phloem, formation of which will also follow. These two new tissue layers are called *primary xylem* and *primary phloem*. The transformation to primary xylem or primary phloem continues until eventually a ring of procambium tissue only one to several cells in width remains (sections IV–V).

As a final step in the developmental process that began at the stem apex, the remaining ring of procambial tissue becomes active, its cells dividing repeatedly to form xylem and phloem. Vascular cambium (or simply cambium) is the name given to this meristematic layer.

The new lateral meristem, the vascular cambium, is considered of secondary origin because it forms after the terminal meristem. Xylem and phloem cells produced in this new meristem are thus correctly called *secondary xylem* and *secondary phloem*, respectively. It is interesting to note that in monocotyledons (such as palms) all procambial cells typically differentiate into primary xylem or phloem, leaving no vascular cambium. These plants, therefore, do not produce secondary xylem and phloem.

After being formed at a given location in the tree, the vascular cambium remains active throughout the life of the tree (or tree part). Because new cell formation in the cam-

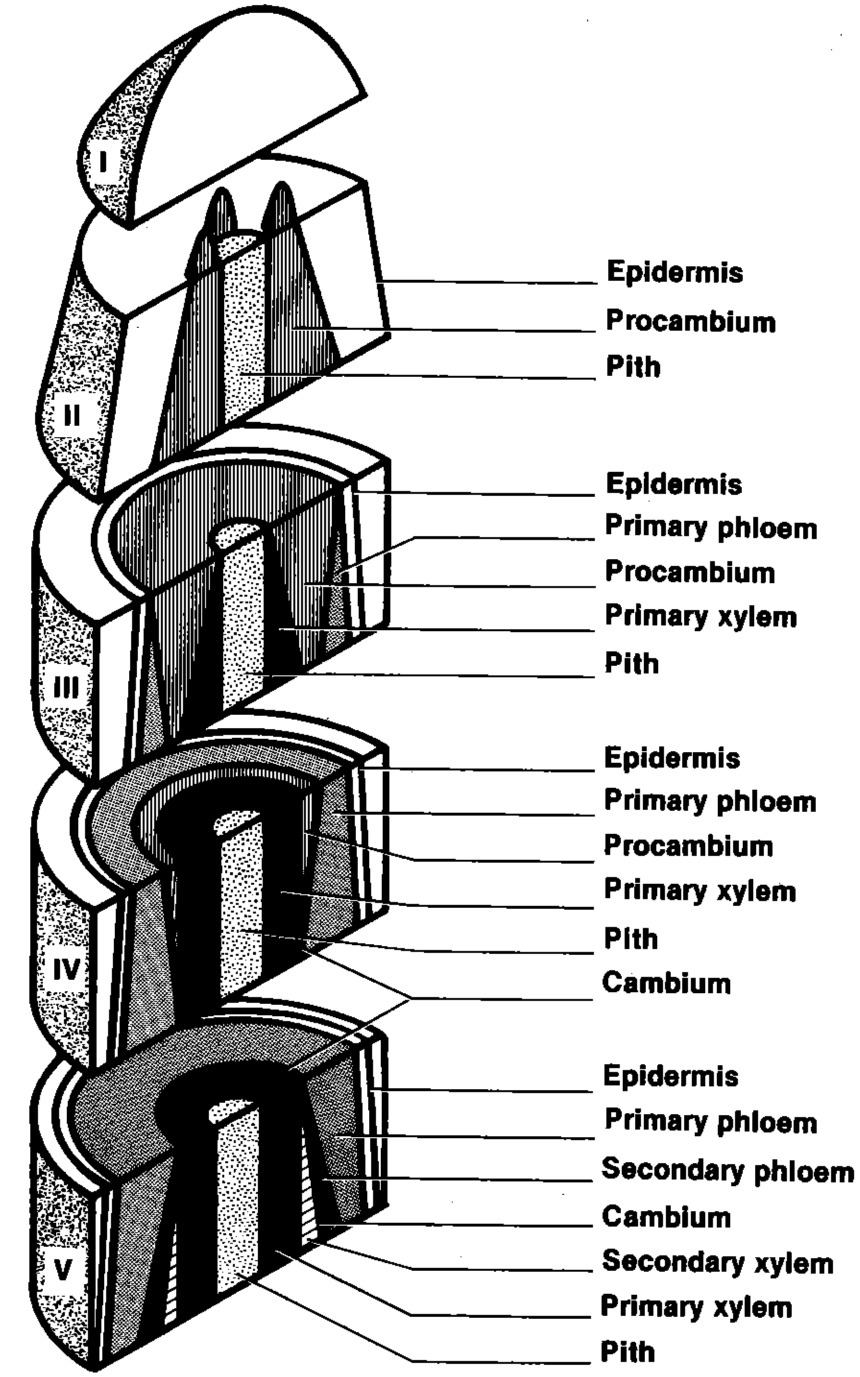


FIGURE 1.7. Representation of a developing stem.

bium serves to increase stem diameter, the very large stature attained by mature trees is traceable to cell division in the cambium.

The stem depicted in section V of Figure 1.7 would be about 1 year old. Note that the tissue layers that sheathed the woody stem soon after its formation have become thinner; this is because of compression forces resulting from diameter expansion. The same is true of the primary phloem. At this stage of stem development, no cell division occurs in any of the layers outside the secondary phloem. Because of this, the circumference of these layers cannot keep pace with the expanding stem diameter. As explained in more detail in Chapter 7, the epidermal layer fractures with stem expansion and flakes off, giving way to a new outer bark layer. A new cell-producing layer forms outside the secondary phloem, and eventually (normally within the second growing season) all tissue originally formed outside the secondary phloem is shed.

Vascular Cambium

Because the cells that compose wood are formed in the vascular cambium, growth processes in this part of the tree are examined more closely. As before, what are in reality very complex processes are summarized in simplified terms.

Composition

In the previous section, the vascular cambium was described as consisting of a one- to several-cell–width ring of meristematic cells. An artist's conception of a cambium layer that has been isolated from surrounding wood and bark tissue is shown in Figure 1.8. Two kinds of cells can be seen to make up the cambium layer. The long, slender cells are called *fusiform initials;* these divide repeatedly to form either new *cambial initials* or new xylem and phloem cells (Fig. 1.9). The short, rounded cells shown in Figure 1.8 are *ray initials;* division of these creates either new xylem or phloem rays or new ray initials. Division parallel to the stem surface in a tangential plane that results in formation of either xylem or phloem cells is called *periclinal division.* Production of new initials by radial partitioning is termed *anticlinal division.*

Development and Growth of Xylem and Phloem

Periclinal division of a fusiform initial results in formation of two cells, one of which remains meristematic and a part of the cambium. The other cell becomes either a xylem or phloem *mother cell.* The mother cell immediately begins to expand radially and may itself divide one or more times before developing into a mature xylem or phloem element. Maturation of new xylem cells involves growth in diameter and length, with growth accompanied by thickening of the cell walls and finally lignification.

Note that not all types of cells grow in both diameter and length. For example, longitudinal cells formed in late summer by pines, spruces, and other softwoods grow considerably in length but little in diameter. Vessel elements that characterize hardwood (*broadleaf*) species grow little or may even shrink slightly in length but may expand up to fifty times in diameter.

Two consecutive periclinal divisions of a fusiform initial are illustrated in Figure 1.10. Beginning at (a), a fusiform initial prepares to divide, as chromosomes split, and

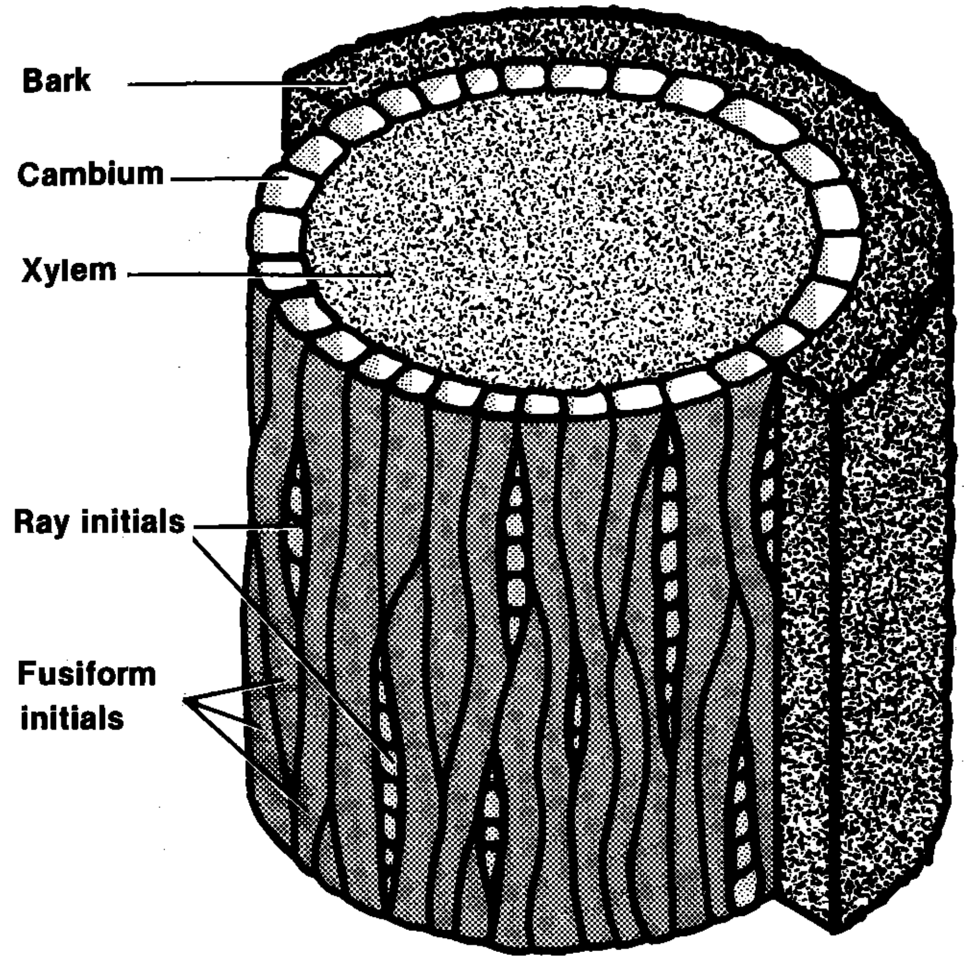
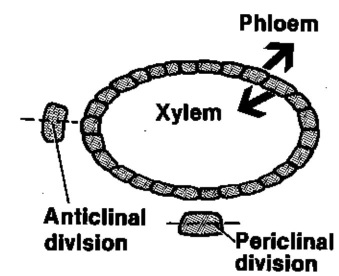


FIGURE 1.8. Three-dimensional representation of the vascular cambium.

FIGURE 1.9. Cambial cell division.



then separate. In (b), a cell plate begins to form and becomes a new cell wall at (c). Both cells begin to grow in diameter (d) and length (e). The innermost cell becomes part of the xylem, pushing outward the other portion that remains part of the cambium. In (f), the cycle begins again.

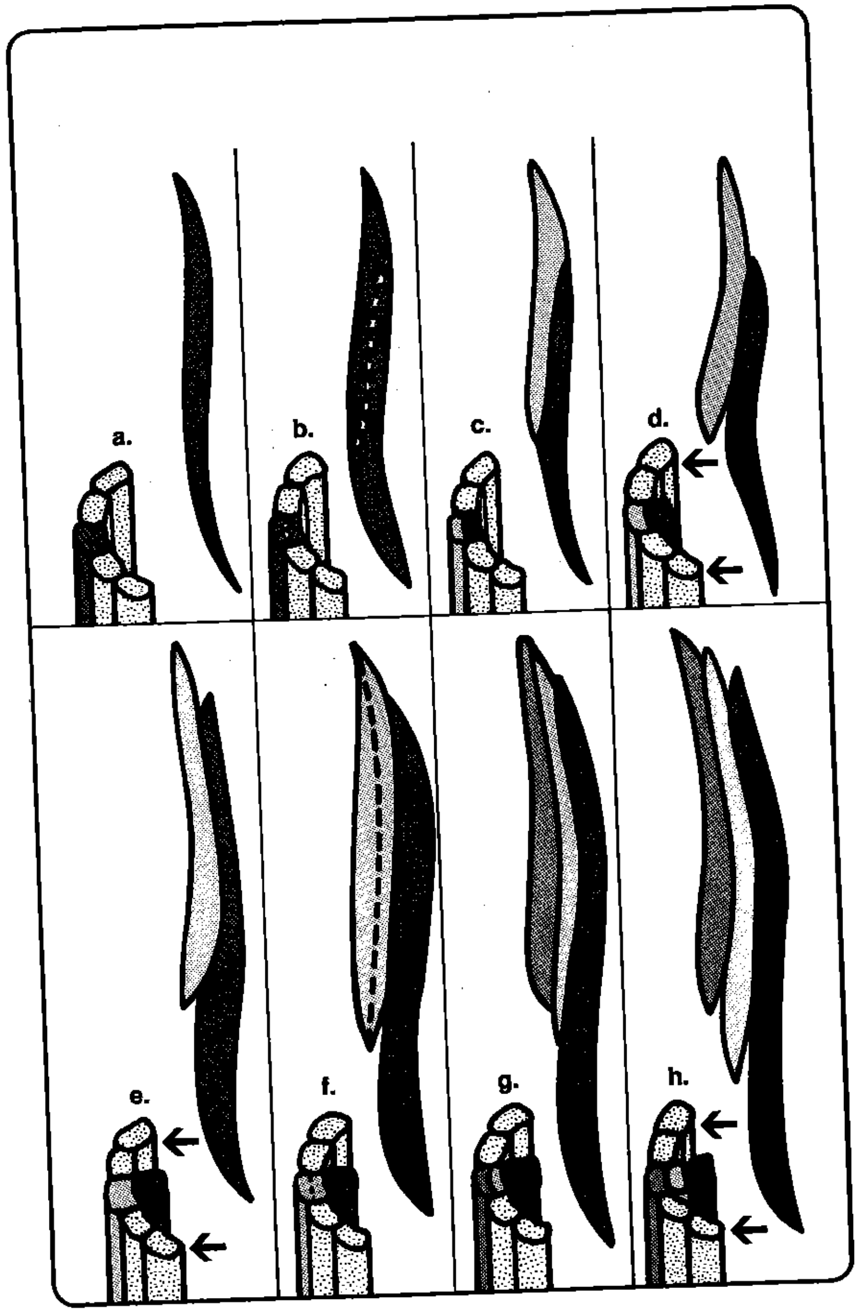


FIGURE 1.10. Periclinal division of fusiform initials. **a, b.** A fusiform initial of the vascular cambium prepares to divide. **c.** The initial divides, forming two new cells, one of which remains in the cambium (shaded), the other becoming a xylem mother cell (black). **d,e.** Both cells begin to increase in diameter and length, increasing the diameter of the stem and pushing the vascular cambium outward. **f,g.** After a period of rest, the initial once again divides, resulting as before in a fusiform initial and a new xylem mother cell. **h.** As both the new initial and mother cell increase in diameter and length, the vascular cambium is again pushed outward.

Early in the growing season, new cell production in primary meristems at stem tips occurs rapidly. Intervals of only eight to eighteen hours between successive divisions in the primary meristems of white cedar (*Thuja*) have been reported (Zimmermann and Brown 1971, 78). This rate diminishes as the season progresses. Cambial initial division typically commences later than division at the apical meristems, and once initiated, division occurs relatively slowly. (See the section "Duration of Cambial Activity in Temperate Regions" later in this chapter for an explanation of this phenomenon.) Bannan (1955) found in experiments with northern white cedar (*Thuja occidentalis*) that successive cambial divisions occurred about once weekly (each seven days) in the early spring. Zimmermann and Brown (1971), after working with the same species, agreed with the finding of a seven-day interval. They found, however, that the rate of division increased several weeks into the growing season. Only three to four cambial initial divisions were noted in the first few weeks of activity, after which the rate increased to one division per four- to six-day interval during the period of most-rapid earlywood formation. Wilson (1964), on the other hand, found a ten-day interval between successive divisions of cambial initials during earlywood formation in white pine. These rates of cell division translate to production of about 30 to 50 divisions of each cambial initial during each growing season. This total meshes with the findings of Deslauriers and Morin (2005) who tracked longitudinal tracheid production in balsam fir; they found the average number of cells produced each year to be rather uniform, varying from 37 to 41 over a 3-year period.

The process of periclinal division of cambial initials is again illustrated in Figure 1.11; subsequent development of new cells is also depicted. In 1.11A, the one-cell-wide cambium (C), with mother cells (M) adjacent on either side, can be seen sandwiched between the xylem (X) and phloem (P). Line 1 of 1.11B shows the appearance of cells in and near the cambial zone during a period of cambial activity. To the left of the cambial initial are two xylem mother cells and one cell of mature secondary xylem. To the right of the cambial initial is one phloem mother cell and a secondary phloem cell. Line 2, which represents the cambial zone a short time later, shows that the xylem mother cell nearest the cambium has divided to form two mother cells. The xylem mother cell farthest from the cambium has begun to enlarge (E). No activity is noted on the phloem side of the cambium or in the cambium itself. By line 3, one of the xylem mother cells formed in the previous period has divided again. The other has begun to enlarge. Although no cambial activity is noted in this period, outward movement of the cambium and phloem cells has occurred as the result of new cell formation through division of a xylem mother cell. At the stage of activity illustrated by line 4, the cambial initial has divided; a portion of the initial remains in the cambium, and the other half becomes a xylem mother cell. Enlargement of yet another xylem mother cell has begun. Growth of the innermost mother cell has ceased and cell wall thickening has begun. This cell (X_1) is mature and cannot divide further. To the outside of the cambium, the phloem mother cell seen earlier has divided into two cells, one of which has begun to enlarge. This sequence of events is repeated again and again as growth continues.

Figure 1.11 and the previous discussion describe the cambium as being one cell in width. However, the research of Catesson (1984) suggests that any of the cells in the cambial zone can, given the proper stimulus, either divide to form new cells or differentiate into vascular tissue. This raises the possibility that specific initials may be frequently replaced as the initials themselves differentiate to become cells of the xylem or phloem. Kozlowski and Pallardy (1997b) recognize the likelihood of a single-layer of cambial ini-

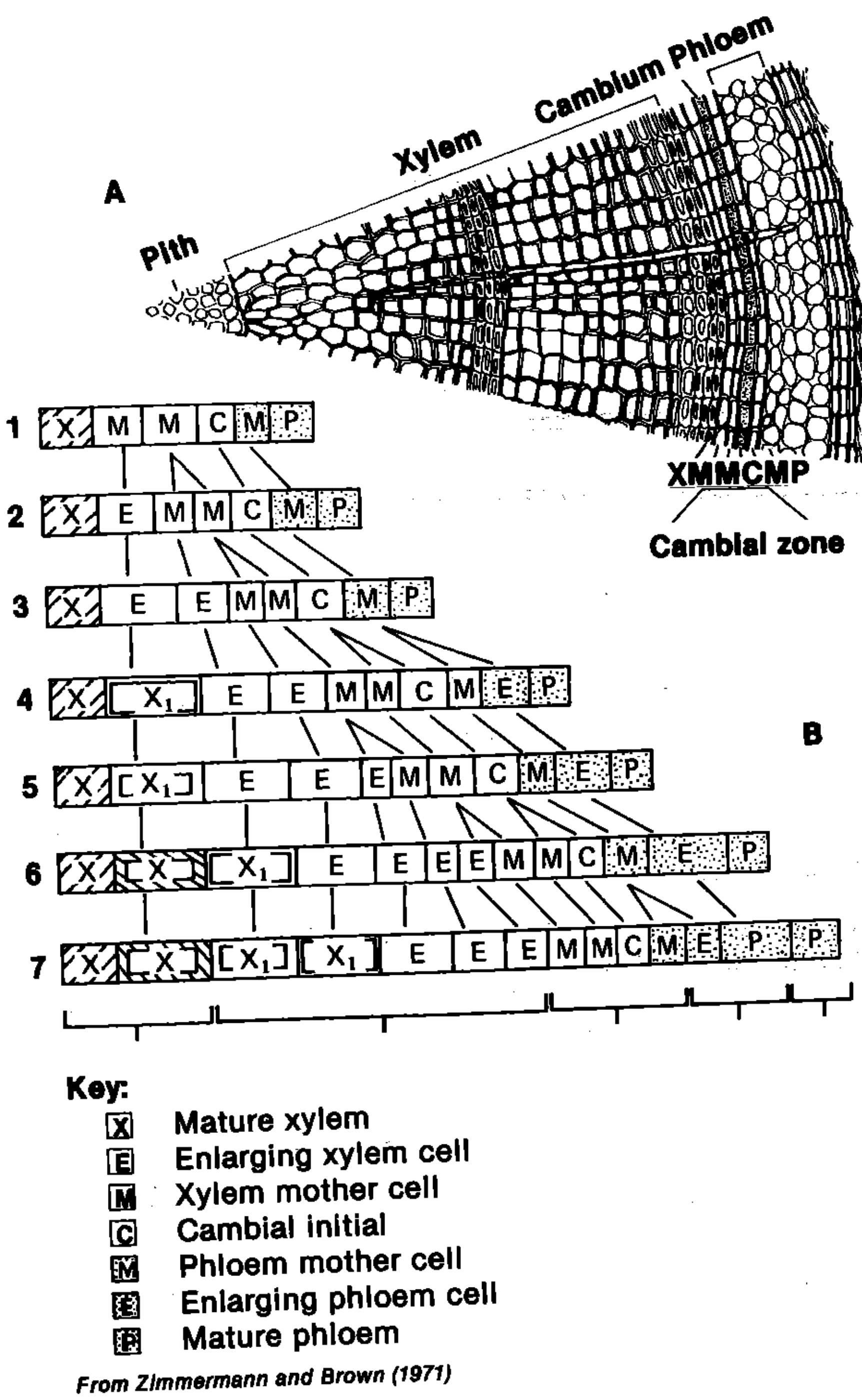


FIGURE 1.11. The cambial zone and cambial activity.

tials, but acknowledge that it is difficult to conclusively identify such a layer. They suggest use of the term *cambial zone* to refer to the entire zone of cambial initials and xylem and phloem mother cells.

Expansion of the Cambial Layer

As a tree expands in diameter, the cambium is pushed progressively outward. Thus the cambium must expand in circumference to remain an unbroken layer around the stem. Such growth of the cambium is achieved in several ways, the most important of which is anticlinal division of fusiform initials.

Anticlinal division of a fusiform initial (see Fig. 1.9) results in two cells, both of which remain in the cambium. Assuming that the new cells survive, they begin to grow in length almost immediately. After a short rest, the new meristematic cells may divide again, either periclinally or anticlinally.

As with new initials that result from periclinal division, survival of new fusiform initials formed anticlinally is dependent upon availability of adequate nutrition. Availability of nutrition is, in turn, dependent upon proximity to rays. A fusiform initial without sufficient ray contact may die or further divide to form one or more ray initials (Zimmermann and Brown 1971, 74). Initials in the process of failing in this manner have been called *declining initials* (Philipson et al. 1971, 26). Kozlowski and Pallardy (1997b) report that survival of new cells produced through anticlinal division is high in rapidly growing trees, and that new fusiform initials and cambial deriviatives are short. In older trees the rate of anticlinal division is said to be slower and the survival rate lower, giving rise to longer fusiform initials and derivatives. This contrasts with the findings of Bannan (1960) who reported that only 20 percent of new cambial initials formed in rapidly growing northern white cedar remained as part of the cambium. The figure was 50 percent for slower-growing trees. The fact that ray contact is needed for survival and normal development means that long cells, which nearly always have adequate contact, survive while very short cells nearly always decline. There is evidence that very small fusiform initials usually decline even where ray contact is extensive (Philipson et al. 1971). This mechanism ensures that fusiform initials will maintain a long average length, even in periods of rapid growth (Panshin and de Zeeuw 1980).

In addition to expansion through an increase in the number of fusiform initials, the cambium also expands through an increase in the length of these cells. The length of initials progressively increases over time so that the length of functioning initials in a mature tree is much greater than those present at the seedling to sapling stage. In one study of white pine, initials at the age of 60 years were found to be four to five times longer than those present in the first year of growth. Kozlowski and Pallardy (1997b) note that this occurs in part because the rate of survival of newly formed cambial initials declines in older trees. This, in turn, means that surviving initials have more room in which to expand, translating to longer fusiform initials and cambial derivatives.

Other factors leading to circumferential expansion of a cambium are diameter growth of fusiform and ray initials and increases in the number of ray initials (Bailey 1923).

Duration of Cambial Activity in Temperate Regions

During cold winter months the vascular cambium is inactive. In the spring, reactivation occurs, apparently in response to hormonal signals at the stem tips and possibly in the roots as well. An increase in average temperature to about 7°C (44°F) (the precise temperature varying by species) or higher is apparently the most important of several factors leading to the onset of cell division.

Initiation of growth means production of new cells at the stem apices and, in addition, growth stimulators or *auxins* such as indole-3-acetic acid (IAA). IAA plays an important role in reinitiating activity in the cambium as it travels downward (with sap) to growth sites (Avery et al. 1937; Wareing 1951, 1958; Wareing et al. 1964; Digby and Wareing 1966; Thimann 1972; Little and Savidge 1987). Kozlowski and Pallardy (1997a) describe the role of auxins in regulating cambial activity as predominant. Other compounds linked to growth stimulation are gibberellic acid (GA)—at least in hardwoods—and ethylene. Some have suggested that growth stimulating compounds may have direct and specific roles in the process of cambial cell division, with IAA or closely related compounds linked to stimulation of cambial cell replication and xylem production, and gibberellin linked to production of phloem (Roberts et al. 1988).

Because IAA is produced in the buds, developing shoots, and leaves—and movement is downward from that point—cambial growth begins in the spring at the top of a stem and moves toward the base (Little and Savidge 1987). In a large softwood, cambial activity may begin at the top of the tree two to six weeks before the cambium is reactivated at the base of the trunk (Digby and Wareing 1966; Zimmermann and Brown 1971, 75–76). Much the same is true in diffuse-porous hardwoods (Eames and MacDaniels 1947, 155–156). However, in ring-porous hardwoods, cambial activity may begin almost simultaneously throughout a tree (Priestley 1930; Priestley and Scott 1933; Zimmerman and Brown 1971).

Shoot extension, which normally begins earlier than diameter growth, typically ceases earlier. In fact, height growth often occurs rapidly in the spring over a period of only 7–10 weeks and then ceases altogether (Kozlowski et al. 1991), whereas in some temperate species such as loblolly and Monterey (radiata) pine, as well as many tropical species, height growth occurs in a series of waves or flushes through the growing season (Kozlowski and Pallardy 1997b). Cambial growth, on the other hand, ordinarily continues more slowly and over a much longer period, sometimes extending into the early fall (Kienholz 1934; Reimer 1949).

As the latter part of the growing season approaches (mid-July to October, depending upon latitude) the rate of cell division in the cambium slows and then ceases as cells again become dormant. The precise mechanisms causing the onset of dormancy are not known, but as noted by Kozlowski et al. (1991), the decreasing *photoperiod* (length of day) in late summer in middle to high latitudes is a certain indicator of the coming of autumn and winter, and many species cease shoot growth and develop resting buds in response to short days. Freezing and near-freezing temperatures have also been reported to induce dormancy. However, shoots of many woody plants stop growing before seasonal temperatures are low enough to stop growth and days are short enough to promote dormancy (Kramer and Kozlowski 1979). Moreover, experiments in which trees are artificially exposed to long days have shown that shoot growth in some species can be prolonged, but not indefinitely. Wareing (1956) found, for example, that Scots pine (*Pinus sylvestris*) and sycamore maple (*Acer pseudoplatanus*) eventually reached a dormant state even in the presence of continuous light.

The fact that many tree species reach a dormant state even in the absence of photoperiod or temperature variation indicates that other, perhaps more complex mechanisms play a role in cessation of growth. There is some evidence that development and subsequent breaking of dormancy are related to the presence of relative quantities of growth stimulators, or auxins, and growth inhibitors such as abscisic acid, especially under low stem moisture conditions (Nitsch 1957; Larson 1964; Kramer and Kozlowski 1979; Creelman et al. 1990; Leitch and Savidge 1995). Experimentation has shown high concentrations of growth inhibitors in terminal meristems during periods of dormancy and much lower concentrations during initiation of growth (Wareing 1958; Wareing and Phillips 1970; Borchert 1991). Borchert (1991) noted that this relationship "suggests that the ratio between ABA [abscisic acid] and growth-producing hormones might control the induction and breaking of dormancy or rest." However, Little and Savidge (1987) question earlier suggestions of an influence of growth promoter/growth inhibitor ratios on shoot dormancy, pointing out that research findings to that point were far from conclusive. Further research is needed to resolve the question.

The ages of both the tree part and the tree itself have been noted to have an effect upon the duration of seasonal growth activity. It has been reported that in both cases, the greater the age, the shorter the duration of cambial activity (Eames and MacDaniels 1947; Kozlowski and Pallardy 1997b). Shoot growth has been reported to occur over a longer period in young trees than in older ones (Kozlowski 1971).

Duration of Cambial Activity in Tropical Regions

In the tropics, cambial activity in trees may be continuous (Oppenheimer 1945; Lanner 1964; Kozlowski et al. 1991; Kozlowski and Pallardy 1997b); such trees are often characterized by a lack of distinct growth rings (Jacoby 1989). However, intermittent cambial activity is more common, leading to periodic or annual growth rings (Kozlowski and Pallardy 1997b; Kramer and Kozlowski 1979; Worbes 1989, 1995; Zimmerman and Brown 1971). From one to five growth/dormancy cycles annually were reported by Tomlinson and Longman (1981), whereas Bauch and Dünish (2000) found as many as eleven to fifteen such cycles annually in very young trees. The same growth pattern has been found in trees from temperate zones that have been transplanted in the tropics (Romberger 1963). Formation of well-defined growth rings appears to be most closely associated with seasonal variation in rainfall (Ogden 1981), although moderate seasonality of temperature can also induce dormancy and growth ring formation (Jacoby 1989).

Review

A. Terms to define or explain:
1. Tree
2. Xylem
3. Phloem
4. Sap
5. Angiosperm
6. Gymnosperm
7. Pith
8. Meristematic
9. Mother cell

B. Questions or concepts to explain:
1. Explain the difference between the origin of primary and secondary xylem.
2. Know the sequence of events leading up to development of the vascular cambium.

3. Understand the difference between periclinal and anticlinal division of fusiform initials. Know the products of each type of division.
4. Explain the stages of development of a xylem mother cell from the time of formation to maturity.
5. Draw a cross section of a woody stem that is several years old, indicating the various layers of tissue that would be present. Be able to explain why some layers that were present in the first year are missing.
6. Know the means by which a cambium can increase in diameter and understand why diameter expansion is necessary.
7. Understand the basic function of rays. Know the primary direction of flow along the rays.
8. Given the fact that long fibers are preferred for manufacture of high-strength papers, explain why a mill manufacturing such paper would be more interested in chips obtained from outer slabs of a log (from a sawmill) than from the portion of the log near the pith.

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