2nd Edition

ANATOMY OF SEED PLANTS

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Xylem: Variations in Wood Structure

Woods are usually classified in two main groups, the softwoods and the hardwoods. The term softwood is applied to gymnosperm wood, that of hardwood to the dicotyledon wood. The two kinds of wood show basic structural differences, but they are not necessarily distinct in degree of density and hardness. The gymnosperm wood is homogeneous in structure—with long straight elements predominating—and is, therefore, easily workable. It is highly suitable for papermaking. Many commercially used dicotyledon woods are especially strong, dense, and heavy because of high proportion of fiber tracheids and libriform fibers (*Quercus, Carya, Eucalyptus, Acacia*), but some are light and soft (the lightest and softest is balsa, *Ochroma*). The main sources of commercial timbers are the conifers among the gymnosperms and the dicotyledons among the angiosperms. The monocotyledons having secondary growth do not produce a commercially important homogeneous body of secondary xylem.

CONIFER WOOD

The secondary xylem of conifers is relatively simple in structure[17] (figs. 9.1 and 9.2), simpler than that of most of the dicotyledons. One of its outstanding features is the lack of vessels. The tracheary elements are imperforate and are mainly tracheids. Fiber-tracheids may occur in the late wood, but libriform fibers are absent. The tracheids are narrow elongated cells averaging 2 to 5 millimeters in length (fig. 8.3,*A*). Their overlapping ends may be curved and branched because of intrusive growth. Basically, the ends are wedge shaped, with the approximately truncated end of the wedge exposed in the radial section (fig. 9.1).

The early wood tracheids have circular bordered pits with circular inner apertures (fig. 8.5). The late wood tracheids (or fiber-tracheids) have somewhat reduced borders with oval inner apertures. This difference in pit structure is a concomitant of the increase in wall thickness in the late wood cells. The

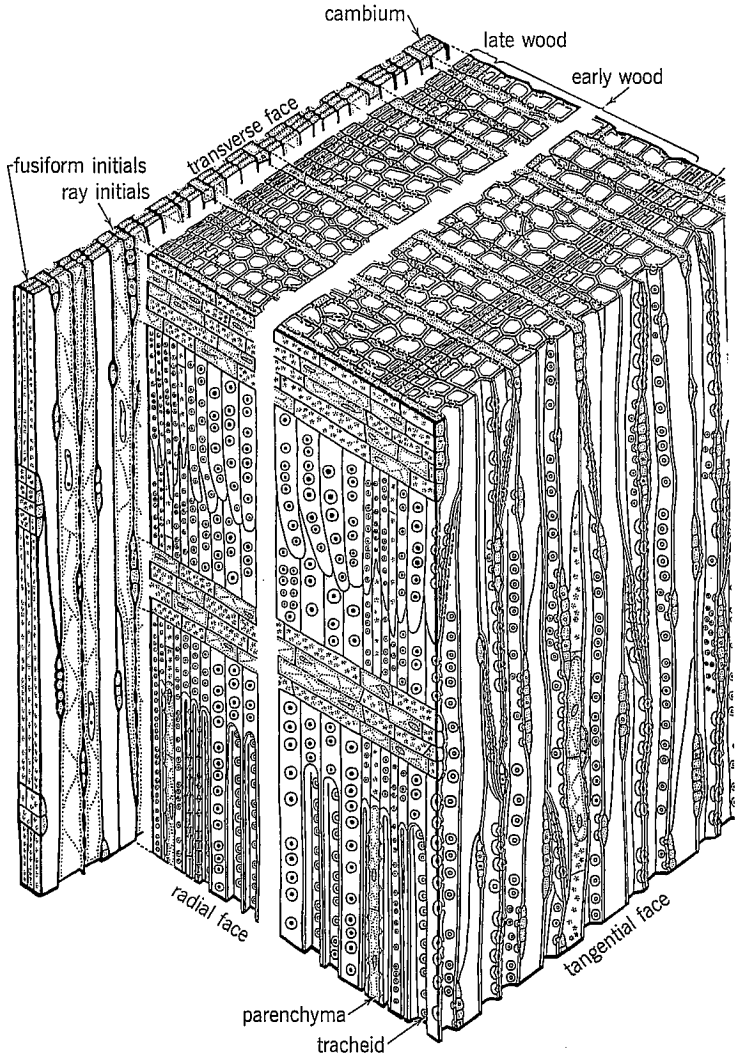

Figure 9.1 Block diagram of vascular cambium and wood of *Thuja occidentalis* (wh cedar), a conifer. The axial system consists of tracheids and some parenchyma cells. T rays contain only parenchyma cells. (From Esau, *Plant Anatomy,* 2nd ed. John Wiley Sons, 1965.)

pit-pairs between tracheids usually have tori. Throughout most of a growth layer the pits are restricted to the radial walls (fig. 9.1); the tangential walls may bear pits in the late wood. The pit-pairs are abundant on the overlapping ends of tracheids. The pits are typ cally in one row. In Taxodiaceae and Pin ceae some wide early wood tracheids m have two or more rows of pits in oppos arrangement. Conifer tracheids may ha

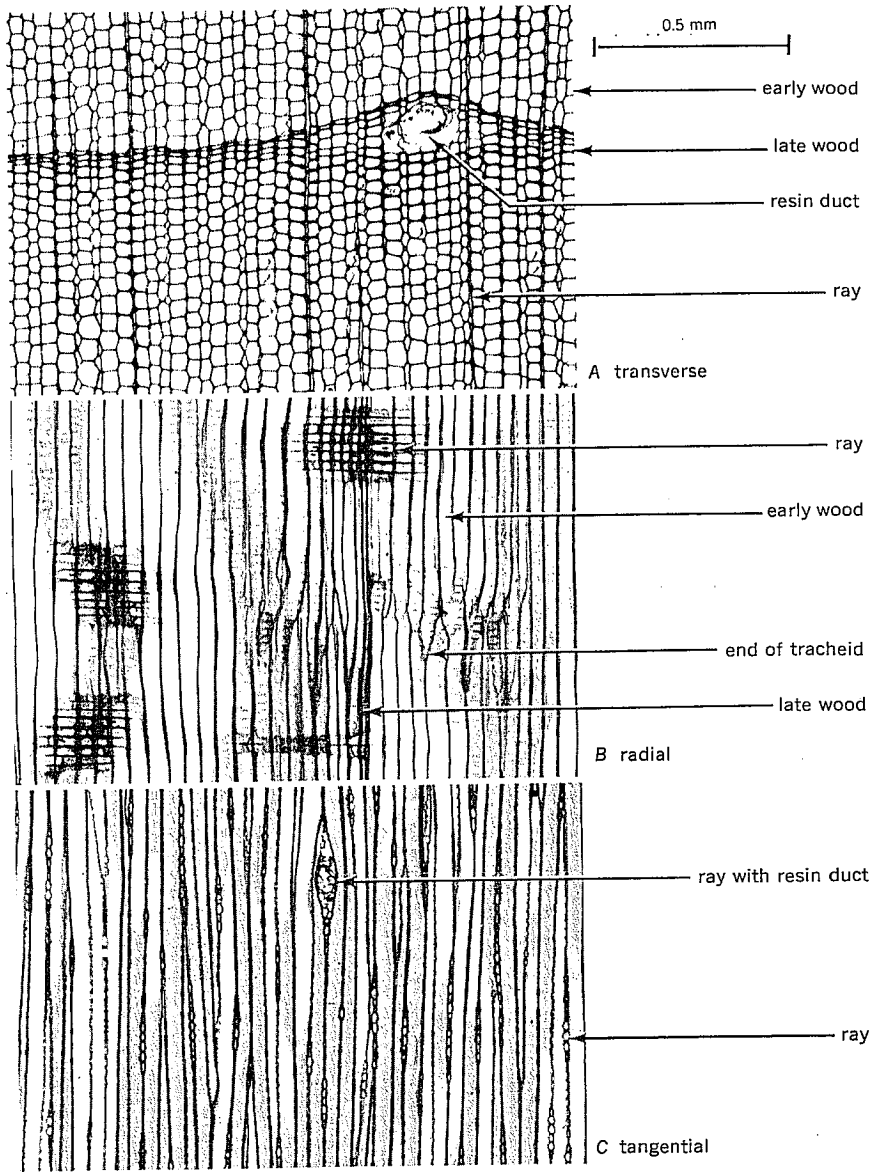

Figure 9.2 Wood of pine (*Pinus strobus*), a conifer in three kinds of sections.

helical thickenings in addition to the pitted secondary wall.

Axial parenchyma may or may not be present in conifer wood. In Podocarpaceae, Taxodiaceae, and Cupressaceae parenchyma is prominent in the wood (fig 9.1). It is scantily developed or absent in Araucariaceae, Pinaceae, and Taxaceae. In some genera, axial parenchyma is restricted to that associated with resin ducts (*Pinus, Picea,*

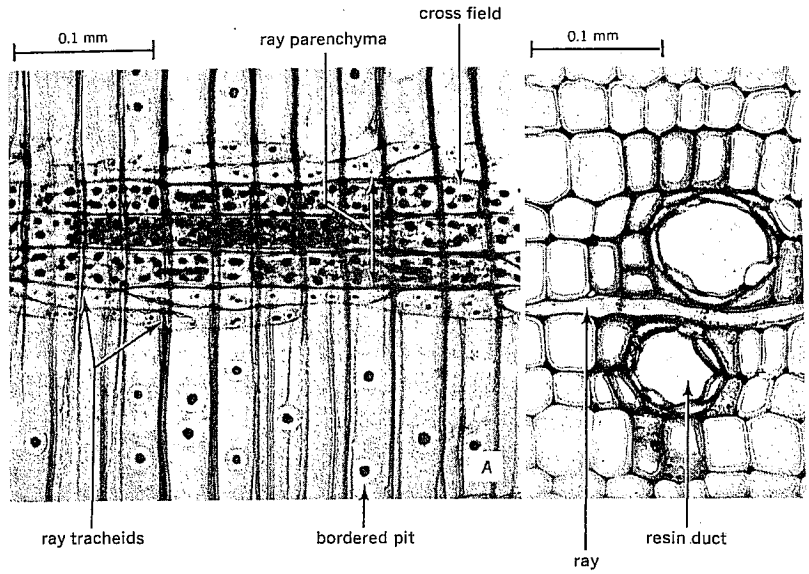

Figure 9.3 Details of conifer wood. *A*, radial section of *Larix laricina* wood sh parts of axial tracheids with bordered pits and of a ray consisting of parenchyma c the middle and of ray tracheids at the margins. The ray parenchyma cells show accu tions of stained cytoplasm in the pits in the cross fields. The ray tracheids have bor pits and no cytoplasm. *B*, transverse section of wood of *Pseudotsuga taxifolia* showir resin ducts with thick-walled epithelial cells.

Larix, Pseudotsuga). Resin ducts (figs. 9.2 and 9.3,*B*) appear as a constant feature of some woods (Pinaceae), but they also develop as a result of injury (traumatic resin ducts.[9]) Resin ducts occur in the axial and in the radial systems.

The rays of conifers are mostly one cell wide (figs. 9.1 and 9.2), occasionally biseriate and from one to twenty or even to fifty cells high. Presence of resin ducts makes the normally uniseriate rays appear multiseriate (fig. 9.2,*C*). The rays consist of parenchyma cells or may also contain ray tracheids. These tracheids resemble parenchyma cells in shape but are devoid of protoplasts at maturity and have secondary walls with bordered pits (fig 9.3,*A*). Ray tracheids are normally present in most Pinaceae, occasionally in *Sequoia* and the Cupressaceae. The ray tracheids commonly occur along the margins of rays, one or more cells in depth.

Each axial tracheid is in contact with or more rays (fig. 9.1). The pit-pairs betwee axial tracheids and ray parenchyma cell half-bordered, with the border on the sic the tracheid (chapter 4); those betwee axial and the ray tracheids are fully borde The pitting between ray parenchyma and axial tracheids form such character patterns in radial sections that the cross-f that is, the rectangle formed by the radial of a ray cell against an axial tracheid 9.3,*A*), is utilized in classification and in onomic studies of conifer woods.

DICOTYLEDON WOOD

The wood of dicotyledons is more va than that of gymnosperms. The wood of primitively vesselless dicotyledons is r tively simple, but that of the vessel-contair

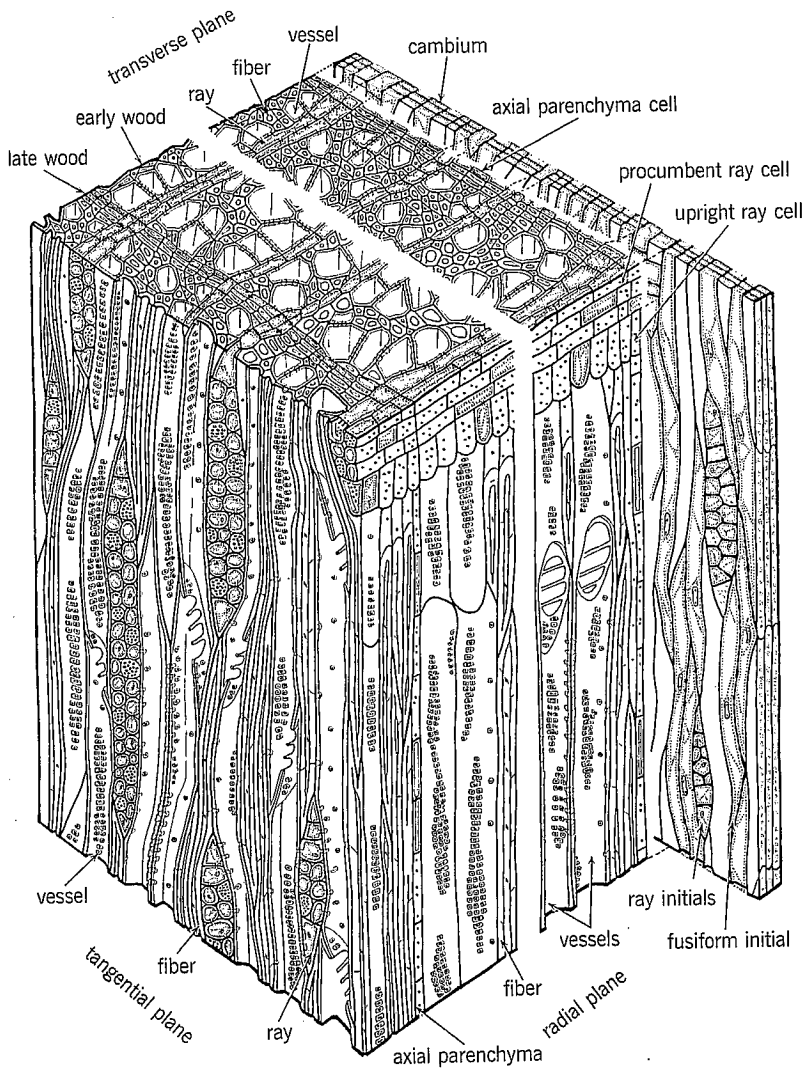

Figure 9.4 Block diagram of vascular cambium and wood of *Liriodendron tulipifera* (tulip tree), a dicotyledon. The axial system consists of vessel members with scalariform perforation plates, fiber-tracheids, and axial xylem parenchyma strands in terminal position. (From Esau, *Plant Anatomy,* 2nd ed. John Wiley & Sons, 1965.)

species is usually complex. Wood of the latter species may have both vessels and tracheids, one or more categories of fibers (chapter 8), axial parenchyma, and rays of one or more kinds (figs. 9.4–9.6).

Storied and nonstoried wood

In transverse sections the secondary xylem shows more or less orderly radial seriation of cells—a result of the origin of cells from

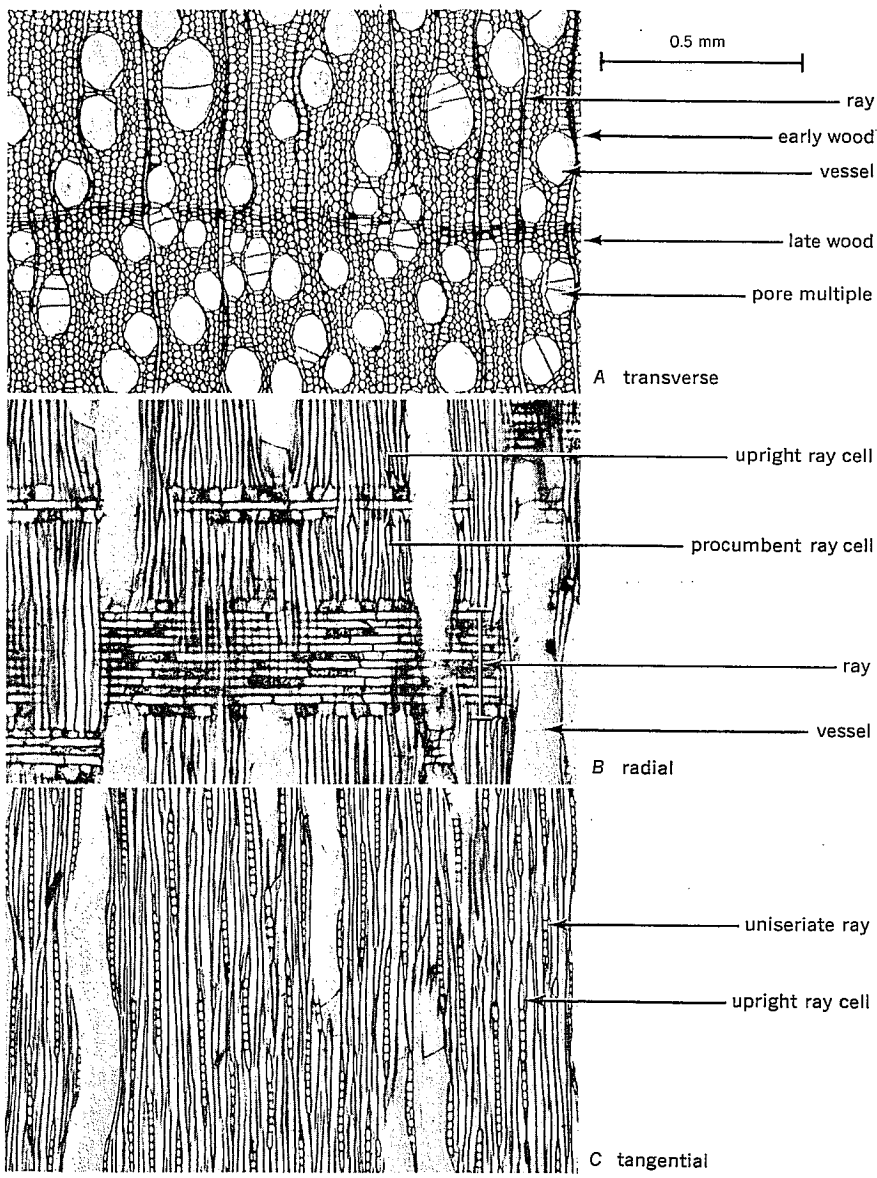

Figure 9.5 Wood of willow (*Salix nigra*), a dicotyledon, in three kinds of sections. Diffuse-porous nonstoried wood with uniseriate heterocellular rays.

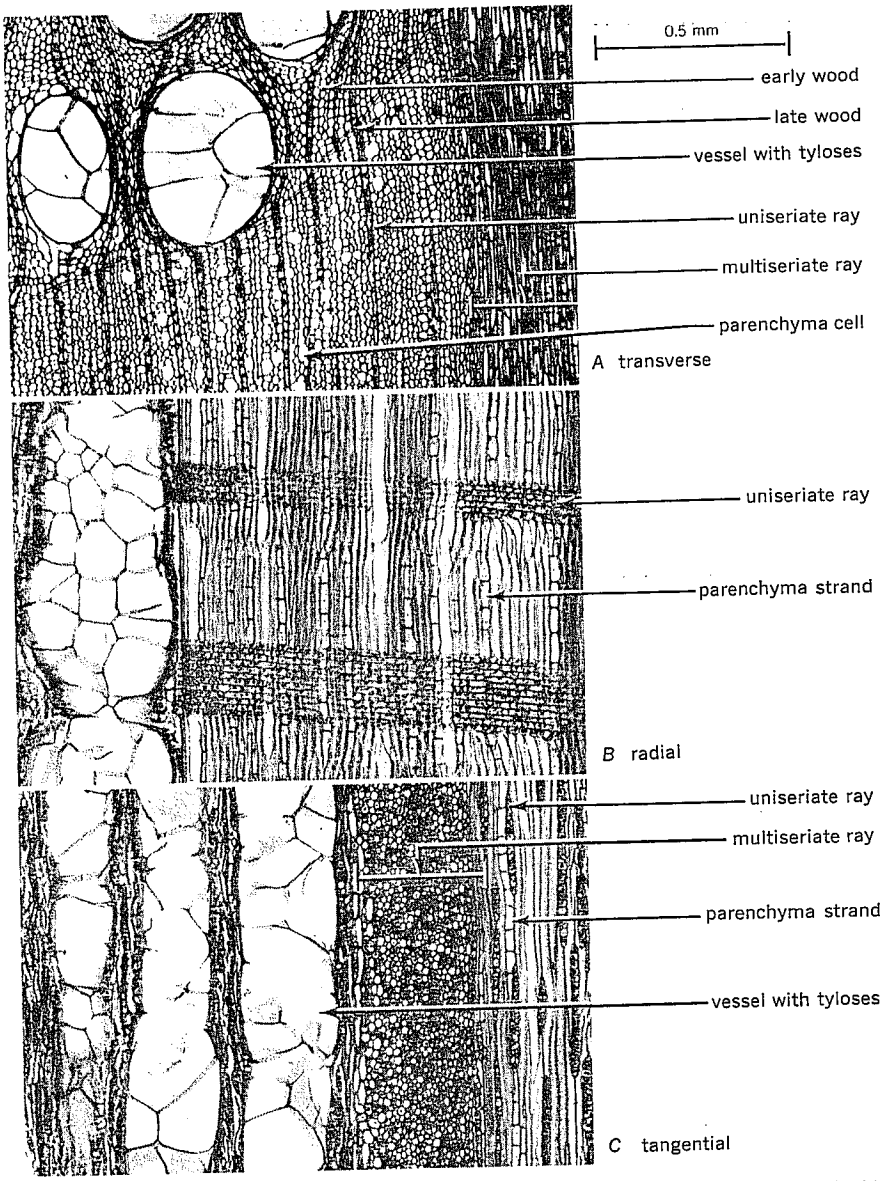

Figure 9.6 Wood of oak (*Quercus alba*), a dicotyledon, in three kinds of sections. Ring-porous nonstoried wood with high multiseriate and low uniseriate rays. The large vessels are occluded by tyloses.

tangentially dividing cambial cells. In the homogeneous conifer wood this seriation is pronounced (fig. 9.2); in vessel-containing dicotyledons it may be somewhat obscured by the ontogenetic enlargement of the vessel members and the consequent displacement of adjacent cells (figs. 9.5 and 9.6). Radial sections also reveal the radial seriation, and they indicate that the radial series of the axial system are superimposed one upon the other in horizontal layers, or tiers (fig 9.6). The tangential sections are varied in their appearance in different woods. In some, the cells of one tier unevenly overlap those of another; in others the horizontal layers are clearly displayed in tangential sections. Thus, some woods are nonstratified, or nonstoried, in tangential sections (fig. 9.7,*A; Castanea, Fraxinus, Juglans, Quercus*), others stratified, or storied (fig. 9.7,*B; Aesculus, Cryptocarya, Ficus, Tilia,* numerous Fabales). The storied condition is especially pronounced when the height of the ray matches that of a horizontal layer of the axial system. From the evolutionary aspect the storied woods are more highly specialized than the nonstoried. They are derived from vascular cambia with short fusiform initials. Many intermediate patterns are found between the strictly storied woods and the strictly nonstoried woods derived from cambia with long fusiform initials.

Distribution of vessels

The wood anatomist refers to a vessel in cross section as a pore. Two principal types of woods are recognized on the basis of distribution of pores in a growth layer: diffuse-porous wood with pores rather uniform in size and distribution throughout a growth ring (figs. 9.5 and 9.8,*A,B*; species in *Acer, Betula, Carpinus, Fagus, Juglans, Liriodendron, Platanus, Populus, Pyrus*); ring-porous wood with pores distinctly larger in the early wood than in the late wood (figs. 8.1, 9.6, and 9.8,*D*; species in *Castanea, Catalpa, Celtis, Fraxinus, Gleditsia, Morus, Quercus, Robinia, Ulmus*). Intergrading patterns occur between the two types of pattern. The ring-porous condition appears to be an indication of evolutionary specialization and occurs in comparatively few species, nearly all characteristic of the north temperate zone. A ring-

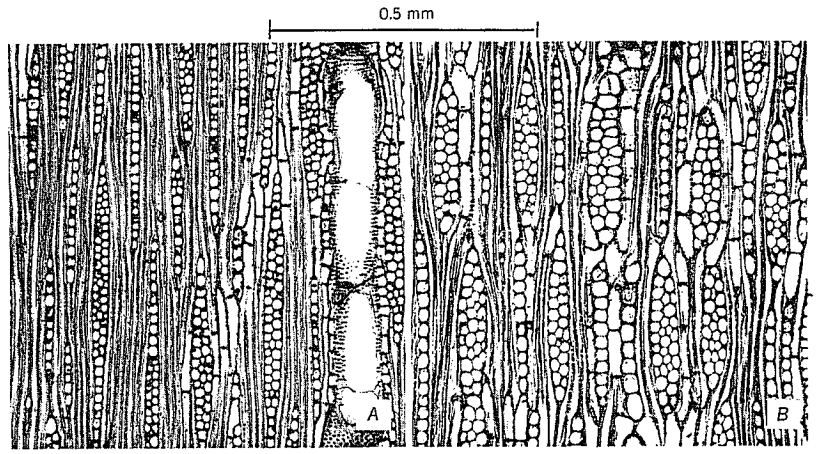

Figure 9.7 *A*, nonstoried wood of pecan (*Carya pecan*). *B*, storied wood of persimmon (*Diospyros virginiana*). Both tangential sections.

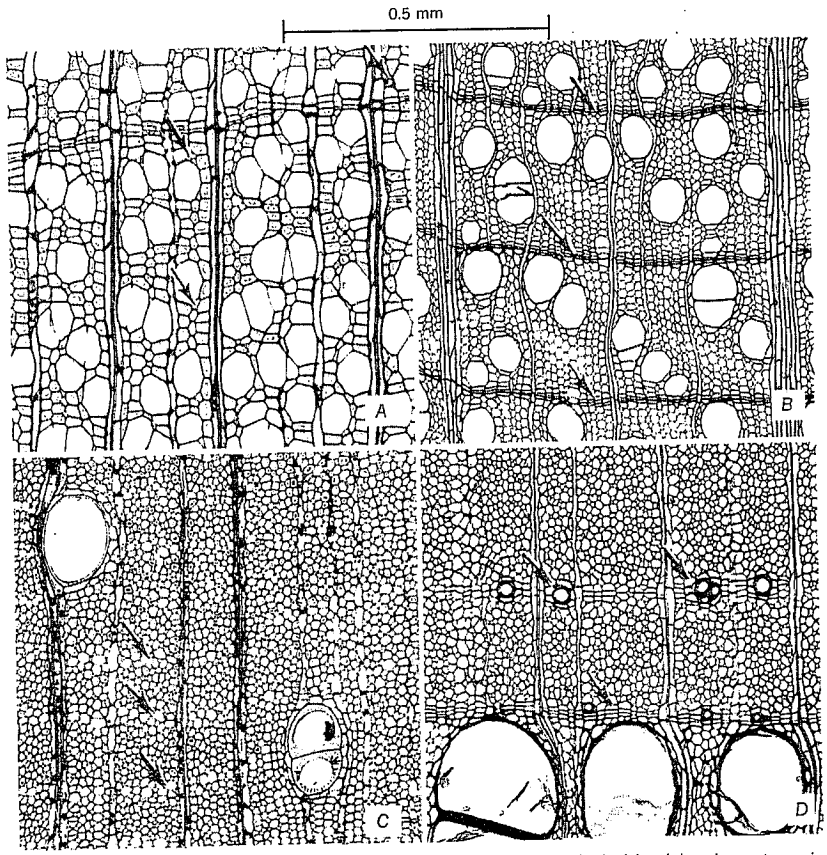

Figure 9.8 Distribution of axial parenchyma (arrows) in wood. *A, Liquidambar styraciflua,* parenchyma very sparse. *B, Acer saccharum,* boundary parenchyma. *C, Carya pecan,* apotracheal banded parenchyma. *D, Fraxinus* sp., paratracheal and boundary parenchyma. All cross sections.

porous wood conducts water almost entirely in the outermost growth increment, at a speed that is about ten times greater than is recorded for diffuse-porous woods.

Within the main distributional patterns of vessels, minor variations occur in the spatial relation of the pores to each other. A pore is called solitary when the vessel is completely surrounded by other types of cells (figs. 9.6 and 9.8,*C*). A group of two or more pores appearing together form a pore multiple (fig. 9.5,*A*). This may be a radial pore multiple, with pores in a radial file, or a pore cluster, with an irregular grouping of pores. Although vessels or vessel groups may appear isolated in wood transections, in the three-dimensional space the vessels are interconnected in various planes. In some species the vessels are interconnected only within individual growth increments, in others connections occur across the boundaries of growth increments.[1]

Distribution of axial parenchyma

The distribution of the axial xylem parenchyma shows many intergrading patterns. The spatial relation to vessels, as seen in transec-

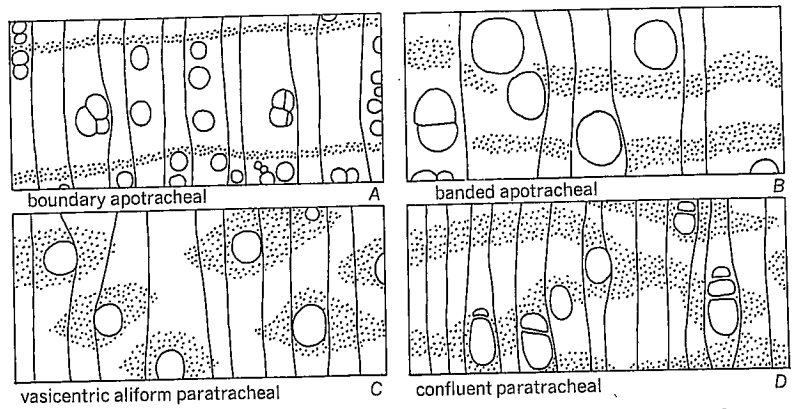

Figure 9.9 Distribution of axial parenchyma (stipples) in wood of *A*, *Michelia*; *B*, *Saccopetalum*; *C*, a leguminous species; *D*, *Terminalia*. (Drawn from photographs in S. J. Record, *Timbers of North America*, John Wiley & Sons, 1934.)

tions, serves for the division in two main patterns: *apotracheal*, parenchyma not definitely associated with the vessels (fig. 9.9,*A*,*B*); *paratracheal*, parenchyma consistently associated with the vessels (fig. 9.9,*C*,*D*). The apotracheal parenchyma is further subdivided into: *diffuse*, single parenchyma cells or parenchyma strands scattered among fibers (fig. 9.6); apotracheal *banded* (figs. 9.8,*C* and 9.9,*B*); boundary[12] or *marginal*[2] parenchyma, with single cells or a band at the end (terminal) or at the beginning (initial) of a growth layer (figs. 9.8,*B*,*D*, and 9.9, *A*). Diffuse apotracheal parenchyma may be sparse (fig. 9.8,*A*). The paratracheal parenchyma appears in the following forms: *scanty vasicentric*, forming complete sheaths around vessels; *aliform* vasicentric with wing-like tangential extensions (fig. 9.9,*C*); and *confluent*, coalesced aliform forming irregular tangential or diagonal bands (fig. 9.9,*D*). If septate fibers instead of axial parenchyma occur in the xylem, they show distributional patterns similar to those assumed by the axial xylem parenchyma. From the evolutionary aspect the apotracheal and diffuse patterns are primitive.[14]

The paratracheal parenchyma shows physiologic differences from parenchyma scattered among fibers.[1,5] During the mobilization of stored carbohydrates in the spring, starch dissolves earlier in paratracheal cells than in the scattered ones. Paratracheal cells also show a high phosphatase activity. They release sugar into the vessels for rapid transport to the buds and appear to participate in refilling with water those vessels that have accumulated gases during dormancy. Parenchyma cells having the distinct physiologic relation to the vessels have been named *contact cells*.[18] They are analogous to the companion cells that serve in the sugar exchange with the sieve elements in the phloem (chapter 11).

Structure of rays

In contrast to the predominantly uniseriate rays of conifers, those of the dicotyledons may be one to many cells wide, that is, they may be uniseriate (fig. 9.5) or multiseriate (figs. 9.4, 9.6, and 9.7), and range in height from one to many cells (from a few mm to 3 cm or more).

The multiseriate rays frequently have uniseriate margins (fig. 9.7,*A*). Small rays may be grouped so as to appear to be one large ray. Such groups are called aggregate rays (*Carpinus*).

The appearance of rays in radial and tangential sections can be used as a basis for their classification. Individual rays may be homocellular, that is, composed of cells of one form only (figs. 8.6,*C*,*D*, and 9.6), either procumbent or upright, or heterocellular, that is, having two morphological cell types, procumbent and upright (figs. 8.6,*A*,*B*,9.4, and 9.5). The entire ray system of a wood may consist of either homocellular or heterocellular rays or of combinations of the two types of rays. On this basis the ray tissue system is classified into homogeneous, rays all homocellular (procumbent cells only), or heterogeneous, rays all heterocellular or combinations of homocellular and heterocellular.[12] Further variations between homogeneous and heterogeneous ray tissues result from combinations of uniseriate and multiseriate rays or absence of multiseriate rays.

The different ray combinations have a phylogenetic significance. The primitive ray tissue may be exemplified by that of the Winteraceae (*Drimys*). The rays are of two kinds: one homocellular—uniseriate composed of upright cells; the other heterocellular—multiseriate composed of radially elongated or nearly isodiametric cells in the multiseriate part and upright cells in the uniseriate marginal parts. Both kinds of ray are many cells in height. From such primitive ray structure other ray systems, more specialized, have been derived. For example, multiseriate rays may be eliminated (*Aesculus hippocastanum*) or increased in size (*Quercus*), or both multiseriate and uniseriate rays may be decreased in size (*Fraxinus*).

The evolution of rays strikingly illustrates the maxim that phylogenetic changes depend on successively modified ontogenies. In a given wood the specialized ray structure may appear gradually. The earlier growth layers may have a more primitive ray structure than the later because the vascular cambium commonly undergoes successive changes before it begins to produce a ray pattern of a more specialized type.

The ray cells share some functions with the axial parenchyma cells and are also concerned with radial transport of assimilates.[1] Ray cells that are connected through pits with tracheary elements (illustrated for a conifer wood in fig. 9.3,*A*) function as contact cells in delivering carbohydrates to the vessels.[18] They mobilize their stored starch precociously in the spring, show a periodic high phosphatase activity and a periodic increase in size of nucleoli, and have a high fat content. Contact ray cells may be upright or procumbent but they always show prominent pit connections with vessels. Ray cells that have no contacts with vessels—such cells are particularly numerous in multiseriate rays—deposit starch in the early summer and mobilize it in the early spring. The cells are mainly procumbent and show polarized phosphatase activity in the spring; in a given cell, the activity is concentrated next to the periclinal wall that is facing the cambium. The cells appear to be concerned with periodic radial transport of mobilized carbohydrate toward the reactivated cambium.

Tyloses

In many species, axial and ray parenchyma cells located next to the vessels form outgrowths through the pit cavities into the lumina of the vessels when the latter become inactive (fig. 9.6). These outgrowths are called tyloses. The membranes of the pits from which tyloses issue are modified by deposition of a so-

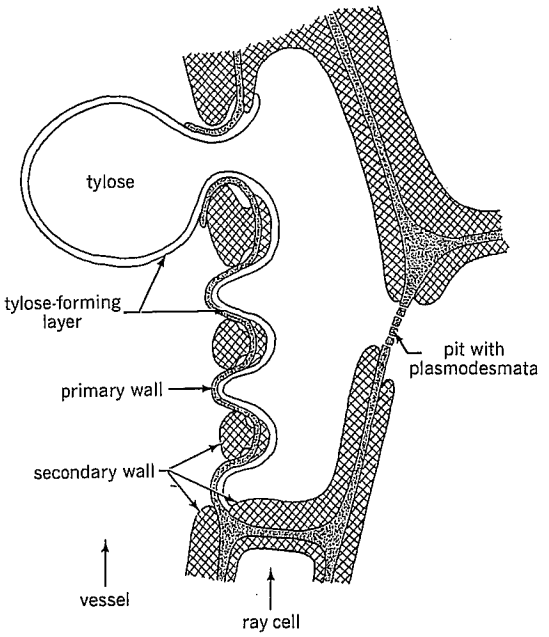

Figure 9.10 Diagram of ray cell that has formed a tylose protruding through a pit into the lumen of a vessel. The tylose-forming layer is also called protective layer. (Constructed from data in Foster[10] and Meyer and Côté.[13])

called protective layer on the side of the parenchyma cell.[13] This layer has a loose fibrillar structure and consists of polysaccharides and pectins.[6] The deposition occurs toward the end of tissue differentiation and seals off the parenchyma cell from the mature vessel element. The additional wall is laid down not only on the pit membranes but on the entire wall facing the vessel member[10] (fig. 9.10), and may occur as a thin layer on walls between contiguous parenchyma cells. The pit membrane becomes degraded enzymically whereas the unlignified protective layer undergoes surface growth and baloons out as a tylose into the vessel lumen. The nucleus and part of the cytoplasm of the parenchyma cell commonly migrate into the tylose. Tyloses store ergastic substances and may develop secondary walls, or even differentiate into sclereids. It seems that tylose development is possible only if the pit aperture on the vesse side is no less than 10 microns wide. Examples of woods with abundant develop ment of tyloses are those of *Quercus* (white oak species), *Robinia, Vitis, Morus, Catalpa Juglans nigra, Maclura.* Tyloses occur ir primary xylem also and, as observed in oa coleoptiles and bean leaves, originate from a wall enriched with acidic polyuronides.[1]

Tyloses block the lumina of vessels and re duce the permeability of the wood. Techni cally this phenomenon is important in the treatment of wood with preservatives and ir its selection for tight coopering. With regarc to conduction in the xylem, the significance o tyloses is not clearly understood. They are known to block vessels during the formatior of heartwood and, in the sapwood, ir response to wounding and infection with dis eases.

Intercellular canals and cavities

Intercellular canals similar to the resir ducts of gymnosperms occur in the dicotyledon woods. They are often called gum ducts although they may contain resins. They occur in both the axial and the radial systems and may be normal or traumatic. Intercellular canals vary in extent, and some are more appropriately called intercellular cavities. Intercellular canals and cavities may be schizogenous, but gummosis of surrounding cells may also occur. Canals associated with gummosis are well known in such genera as *Amygdalus* and *Prunus.*

SOME FACTORS IN DEVELOPMENT OF SECONDARY XYLEM

The secondary xylem is produced by the vascular cambium (chapter 10) and consequently its development is greatly affected by

factors controlling cambial activity. The intermittent functioning of the cambium, which is mainly seasonal in the temperate regions, is reflected in the production of growth increments in the wood. The increments, or rings in transections, are delimited from one another by anatomic differences between early wood and late wood (chapter 8). The causes of these differences have not been fully revealed, and most of the pertinent studies were conducted on coniferous seedlings.[25]

According to a common concept, auxin attains high levels under conditions promoting shoot growth and continued leaf development. The cells produced in the xylem at this time are wide and thus of the early wood type. Conversely, conditions adversely affecting shoot growth lower the level of diffusible auxin and induce the formation of narrow flattened cells of the late wood type. It should be stressed, however, that the auxin involved in secondary growth is only partly derived from the growing shoots. The differentiating vascular tissues, and specifically xylem, appear to be important sources of auxin that maintains cambial activity after its initial reactivation under the influence of expanding buds.[20] The increase in cell wall thickness in late wood cells, which is causally unrelated to cell diameter, is usually explained in terms of promotion of synthesis of cell wall material by seasonal assimilation.

This brief summary does not do justice to the complexity of the phenomenon of annual growth, for, undoubtedly, several types of growth promoting substances and some natural inhibitors are involved in secondary development, and the activity of the substances is modified by nutritional conditions and availability of water. Many variations in width of wood rings within a tree may be attributed to changing supplies of food. The nutritional factors in turn are affected by the climate. Recognition of these relations has led to the development of dendrochronology, that is, study of yearly growth patterns in trees and use of the information for evaluating past fluctuations in climate and dating past events.[11]

Sometimes individual factors can be related to specific aspects of xylem differentiation. When *Xanthium* seedlings were decapitated cambial activity continued but fibers failed to differentiate in the secondary xylem.[21] Fiber differentiation could be induced by applying naphthaleneacetic acid to the decapitated plants, a result suggesting that auxin directly affects differentiation of xylem cells[22] rather than indirectly through induction of cell division (chapter 8). Detached *Fraxinus* stems, grown in a culture medium, in which the water potential (controlled by addition of polyethylene glycol) and the concentration of growth substances were varied, showed that the width of new tissue produced was influenced more by the water potential than by the concentrations of indoleacetic and gibberellic acids.[8] Growth relations in the wound callus formed on the detached *Fraxinus* stems provided the additional evidence that, besides a certain concentration of auxin, xylem differentiation requires physical pressure.[8] The importance of mechanical pressure in secondary tissue development was demonstrated also by manipulating longitudinal strips of bark partly separated along the differentiating xylem from stems of *Populus* and *Pinus*.[25] A strip of bark attached to the bole above but left suspended below formed callus on its inner side. Later, a cambium developed in the callus in continuity with the existing cambium in the strip converting the latter into a stemlike structure. In about three weeks after the strip was isolated orderly formation of xylem and phloem was in progress. In a strip of bark that was not left suspended but placed back against the wood of the bole (with a plastic film separating the two) and subjected to

some pressure, callus formation was very restricted and normal production of xylem and phloem was shortly restored.

Differentiation of specific cell types of xylem and their distribution in the tissue might also lend itself to analyses in terms of indentifiable factors. The previously mentioned experiments with *Fraxinus*[8] indicate that vessel development is particularly sensitive to indoleacetic acid supply. Increase of this supply results in the formation of wider vessels but the effect diminishes when the water potential is reduced. The authors suggest that the nonuniform distribution of vessels may be the result of differential distribution of the necessary growth factors among xylem mother cells. Possibly individual cells or cell groups form metabolic sinks and, by sequestering growth factors, increase solute concentration and take up water preferentially in competition with neighboring cells. The successfully competing cells expand rapidly and differentiate into vessel members.

The developmental effects of vessels upon contiguous cells at the histological level clearly indicate the presence of a competitive factor in cell adjustments during vessel differentiation. When a future vessel element begins to expand in the cambial mother cell zone, production of cells ceases in one or more rows adjacent to the row containing the expanding cell. Divisions are resumed in these rows after the vessel has expanded and the cambium has been displaced outward. If the space thus provided does not suffice to accommodate the expanding vessel, the latter forces adjacent cells apart. The separating cells often assume irregular shapes and, at maturity, are called *disjunctive parenchyma cells* or *disjunctive tracheids* depending on their final differentiation.

The recognition of specific relations between availability of auxins and water and the differentiation of vessels is just a begi ning in analyses of factors that bring abo the profound differences among cells derive from apparently identical cambial pr cursors. The intrusive elongation of fibe (chapter 6), the idioblastic behavior of cel accumulating specific ergastic substances differentiating into sclereids, the physiolog specializations of the parenchymatic mer bers of the xylem are some examples of pr grammed developments that await interpr tation with reference to controlling factor

Reaction wood

The reaction type of wood is formed on th lower sides of branches and leaning crooked stems of conifer trees, and on th upper sides of similar structures in dicot ledon trees. This wood is called reactic wood (compression wood in conifers and te sion wood in dicotyledons) because i development is assumed to result from th tendency of the branch or stem to countera the force inducing the inclined position. Reaction wood occurs in roots also.[24]

Research involving experimental modific tions in position of plant axes has provide evidence that the stimulus of gravity and th distribution of endogenous growth sul stances are important factors in evoking th development of reaction wood.[3,24] Expe ments with auxins and anti-auxins indica that the tension wood of dicotyledons formed where auxin concentration is low.[15] contrast, the compression wood of gymn sperms is formed in regions of high auxin co centration.[24] As to the force counteracting th inclined position, it is thought to reside in th region where the differentiating reactic wood cells are undergoing lignification ar to arise from the swelling of cell walls as a r sult of the lignification.[19]

The reaction wood differs from the normal in both anatomy and chemistry.[7] The compression wood of conifers is typically denser and darker than the surrounding tissue, and its tracheids are shorter than those in normal wood. The cell walls appear rounded in transections and contain more or less strongly lignified layers. The inner layer of the usually three-layered secondary wall is missing. In the tension wood of dicotyledons the vessels are reduced in width and number and the fibers have a thick highly refractive inner layer—the so-called gelatinous layer—consisting largely of cellulose. The walls of these fibers may be two to four layered; the gelatinous layer is usually the innermost (chapter 8).

IDENTIFICATION OF WOOD

The use of wood for purposes of identification requires a very sound knowledge of wood structure and of factors modifying that structure. The search for diagnostic features is best based on an examination of collections from more than one tree of the same species, made with proper attention to the location of the sample on the tree. The wood acquires its mature character not at the beginning of cambial activity but in the later growth increments. Thus, the wood of a twig would be of a different ontogenetic age than that of a trunk of the same tree. Furthermore, in certain sites, the wood has reaction wood properties that deviate more or less strongly from features considered to be typical of the taxon in question. Adverse or unusual environmental conditions and improper methods of preparation of sample for microscopy also may obscure the diagnostic features.

A further complicating aspect of wood identification is that the anatomical characteristics of woods are often less differentiated than the external features of the taxa involved. Although woods of large taxa differ considerably from one another, within groups of closely related taxa, such as species, or even genera, the wood may be so uniform that no consistent differences are detectable. Under such circumstances, it is imperative to use aggregates of macroscopic and microscopic characters of woods, as well as odor and taste.

Characters used in identification of woods

The two large taxa that yield commercial timber and the wood anatomy of which is well known are the conifers (softwoods) and the dicotyledons (hardwoods). In keys for wood identification these two taxa are invariably separated on the basis of absence or presence of vessels: nonporous wood (vessels absent), conifers; porous wood (vessels present), dicotyledons. The exceptional vesselless lower dicotyledons (*Drimys*, *Zygogynum*, etc.) can be identified by their ray structure, which is more varied than in the conifers. In the following, the important diagnostic features of softwoods and hardwoods are summarized with reference to examples of genera and species showing these features.

CONIFERS.

Several genera (*Pinus*, *Picea*, *Larix*, and *Pseudotsuga*) have normal resin canals in axial and ray systems, although in *Picea* the canals are often less abundant than in the other three genera. Other conifers (*Abies*, *Sequoia*, *Taxodium*) may have traumatically induced resin canals, but these are recognizable in the axial system by their alignment in tangential groups or rows. The epithelial cells of the resin canals have thin walls in *Pinus*, thick walls in *Picea*, *Larix*, and *Pseudotsuga*.

The thin-walled cells may be collapsed in sectioned wood, particularly in the axial system; their identification is more certain in rays.

Ray tracheids are present in *Pinus, Picea, Larix, Pseudotsuga, Cedrus, Tsuga, Chamaecyparis nootkatensis,* and sporadically in *Abies balsamea.* The ray tracheids have dentate wall ornamentations in some pines (*Pinus strobus,* white pine, *P. lambertiana,* sugar pine), smooth walls in others (*P. ponderosa,* western yellow pine).

Ray parenchyma cells also have diagnostic characteristics. Their tangential walls (end walls), as seen in radial sections, may be smooth (*Thuja plicata, Chamaecyparis lawsoniana, Araucaria, Podocarpus chilinus, Sequoia sempervirens, Taxodium distichum, Taxus baccata*) or they may appear beaded because of deep pitting (species of *Cedrus, Tsuga, Abies pectinata, Pseudotsuga, Picea, Larix*). The pits on the radial walls of ray parenchyma cells visible within the confines of a cross-field vary in size, number, arrangement, and degree of development of the border in the contiguous axial tracheid. The pines have either one or two large pits to a cross-field (*Pinus lambertiana*) or several smaller ones (*P. ponderosa*), all with none or barely perceptible borders in the adjacent tracheids. Most other conifers have one to several pits with borders in the adjoining axial tracheids (half-bordered pit-pairs). The pits in a cross field may be in one or two rows or rather irregularly arranged.

Helical thickenings deposited over the secondary walls are normally present in axial tracheids of *Pseudotsuga,* being especially well developed in the early wood. Helical thickenings are found occasionally in late wood tracheids of *Larix* and some species of *Picea,* but not in *Pinus. Taxus* has helices in all axial tracheids but differs from *Pseudotsuga* in having no normal resin canals and no ray tracheids. *Agathis* and *Araucaria* differ from other conifers in having arrangement of pits on the axial tr the pits are in two or more rows. A st ture of the axial tracheids of *Cedr* crenulated edge in the torus of the pit.

The size and shape of rays, as tangential sections, may be useful i wood identification. In *Pinus, Picea,* the resin canal region in the fusi (resin canal-containing ray in tange tion) bulges abruptly and often has u extensions above and below. In *tsuga,* the ray outline is commonly m larly fusiform. The rays in *Sequoia virens* have rather large cells and a biseriate. In the closely related *Taxoc tichum* the rays have smaller cells a contain biseriate portions. Rays in o may be markedly higher than in *Cedrus,* for example, has higher ray times exceeding 40 cells) than *Ts Chamaecyparis nootkatensis,* both otherwise have wood rather similar t *Cedrus.* Presence of axial parenchyn *Sequoia* and *Taxodium,* may be a diagnostic feature.

DICOTYLEDONS.

The hardwoods are usually subdivi two major groups on the basis of pres absence of rings of pores (early vessels) in cross sections: ring porou wood vessels appreciably larger tha of the late wood; diffuse porous, earl vessels not larger or only slightly larg those of the late wood. Ring porous visible with a hand lens on a clean su a piece of timber. The choice between alternatives in identifying a wood n made difficult by the following conditi Early wood vessels are much large others but grade into those of the late (*Carya*). (2) Early wood vessels are onl erately larger than the late wood v

and intergrade with them; this condition is sometimes classified as semi-ring porous or semi-diffuse porous, and the same species may fit into the ring-porous or one of the intermediate categories (*Carya, Catalpa, Robinia*). (3) Vessels predominate in the early wood but are not appreciably larger than those of the late wood; this condition is classified as diffuse porous (*Juglans, Tilia*).

Ring-porous woods are distinguished from one another by the degree of expression of ring porousness and other characters. In *Fraxinus, Quercus,* and *Ulmus* the change from early wood to late wood is abrupt, in *Castanea* and *Paulownia* it is gradual. In *Ulmus* and *Celtis,* the late wood vessels, vascular tracheids, and paratracheal parenchyma are aggregated into undulating tangential bands as seen in cross sections. The deciduous oaks may be separated from other ring-porous woods by the combination of very broad high rays visible with the unaided eye and narrow, mostly uniseriate, low rays. These oaks are divisible in two groups: red oaks (*Quercus borealis, Q. palustris, Q. velutina*) in which the early wood vessels are usually free of tyloses in the heartwood, the late wood vessels are rounded in transections and have thick walls, and the large rays average 6 to 12 mm in height; white oaks (*Q. alba, Q. bicolor, Q. macrocarpa*) in which the early wood vessels become occluded with tyloses, the late wood vessels are not rounded in transections and have thin walls, and the large rays average 12 to 32 mm in height. Tyloses are common also in *Carya, Maclura, Morus,* and *Robinia.*

A number of ring-porous woods have helical thickenings in the narrow late wood vessels, for example *Catalpa, Celtis,* and *Gymnocladus. Sassafras* has occasional scalariform perforation plates in late wood vessels, thin-walled fibers, and oil cells in the 1–4 seriate rays. The representatives of the

Table 9.1 EXAMPLES OF WOODS WITH DIFFERENT DISTRIBUTIONS OF VESSELS

Ring Porous

Carya pecan (pecan)
Castanea dentata (American chestnut)
Catalpa speciosa
Celtis occidentalis (hackberry)
Fraxinus americana (white ash)
Gleditsia triacanthos (honey locust)
Gymnocladus dioicus (Kentucky coffee tree)
Maclura pomifera (Osage orange)
Morus rubra (red mulberry)
Paulownia tomentosa
Quercus spp. (deciduous oaks)
Robinia pseudoacacia (black locust)
Sassafras albidum
Ulmus americana (American elm)

Semi-Ring Porous or Semi-Diffuse Porous

Diospyros virginiana (persimmon)
Juglans cinerea (butternut)
Juglans nigra (black walnut)
Lithocarpus densiflora (tanbark oak)
Populus deltoides (cottonwood)
Prunus serotina (black cherry)
Quercus virginiana (live oak)
Salix nigra (black willow)

Diffuse Porous

Acer saccharinum (silver maple)
Acer saccharum (sugar maple)
Aesculus glabra (buckeye)
Aesculus hippocastanum (horse chestnut)
Alnus rubra (red alder)
Betula nigra (red birch)
Carpinus caroliniana (blue beech)
Cornus florida (dogwood)
Fagus grandifolia (American beech)
Ilex opaca (holly)
Liquidambar styraciflua (American sweet gum)
Liriodendron tulipifera (tulip tree)
Magnolia grandiflora (evergreen magnolia)
Nyssa sylvatica (black gum)
Platanus occidentalis (American plane tree)
Tilia americana (basswood)
Umbellularia californica (California laurel)

Fabales, *Cercis, Gleditsia, Gymnocladus,* and *Robinia* have vestured bordered pits (see Glossary).

The distribution of axial parenchyma and character of rays can be usefully combined with other characters. The rays are seldom uniformly homocellular or heterocellular. Uniseriate homocellular rays occur in *Castanea,* and multicellular, essentially homocellular rays are found in *Fraxinus, Gymnocladus, Paulownia,* and *Ulmus. Fraxinus* has conspicuous vasicentric parenchyma. The apotracheal parenchyma forms 1–4 seriate tangential bands in cross sections of *Carya* wood.

Among the taxa with semi-ring porous wood, *Diospyros* is distinguished by an essentially storied wood. It also has minute intervessel pitting and thick vessel walls. *Prunus* shows helices in vessels and has very sparse axial parenchyma. *Salix* has uniseriate, heterocellular rays, *Populus* uniseriate, homocellular rays. *Quercus virginiana* and *Lithocarpus* resemble the deciduous oaks in having rays of two sizes numerous low uniseriate rays and high, broad multiseriate rays. The latter may be simple or aggregate. The aggregate condition is more distinct in *Lithocarpus.* In both genera, vasicentric tracheids and sparse paratracheal parenchyma form sheaths about the vessels.

In the taxa with diffuse-porous woods, a number of genera typically have scalariform perforation plates: *Alnus, Betula, Cornus, Ilex, Liriodendron, Liquidambar, Nyssa;* mostly scalariform, some simple: *Magnolia;* simple, occasionally scalariform: *Carpinus, Fagus, Platanus.* Intervessel pitting may be a helpful diagnostic feature. It is commonly scalariform in *Cornus* and *Magnolia,* opposite in *Liriodendron* and *Nyssa,* opposite or linear in *Liquidambar.* The pitting is minute in *Betula,* crowded in *Carpinus* and *Fagus,* not crowded in *Alnus* and *Platanus.* Helical thickenings are typical in *Ilex, Magnolia,* and *Tilia;* may be present, sometimes only in the taper ends of vessel members, in *Aesculus, Li dendron,* and *Nyssa.*

Some characteristic ray structures are: mocellular 1-3 seriate rays in *Betula;* narr simple rays and wide aggregate rays in *Alr* and *Carpinus;* 3-14 seriate homocellular ra up to 3 mm in height, in *Platanus.* Rays of t distinct sizes occur in *Fagus,* narrow, mos uniseriate low rays and broad multiseri high rays, a combination similar to that in t oaks. Two sizes of rays are found also in *Ac* (intergrading in some species) and *Tilia. Cornus* and *Ilex,* the uniseriate rays are co posed entirely or largely of upright cells, t multiseriate rays contain procumbent cells the middle portions and upright cells in t uniseriate margins. *Liquidambar* has a sir lar ray system except that the proportions upright cells are relatively small. *Liquida bar* may have traumatic gum canals. *U bellularia* has oil cells in the rays.

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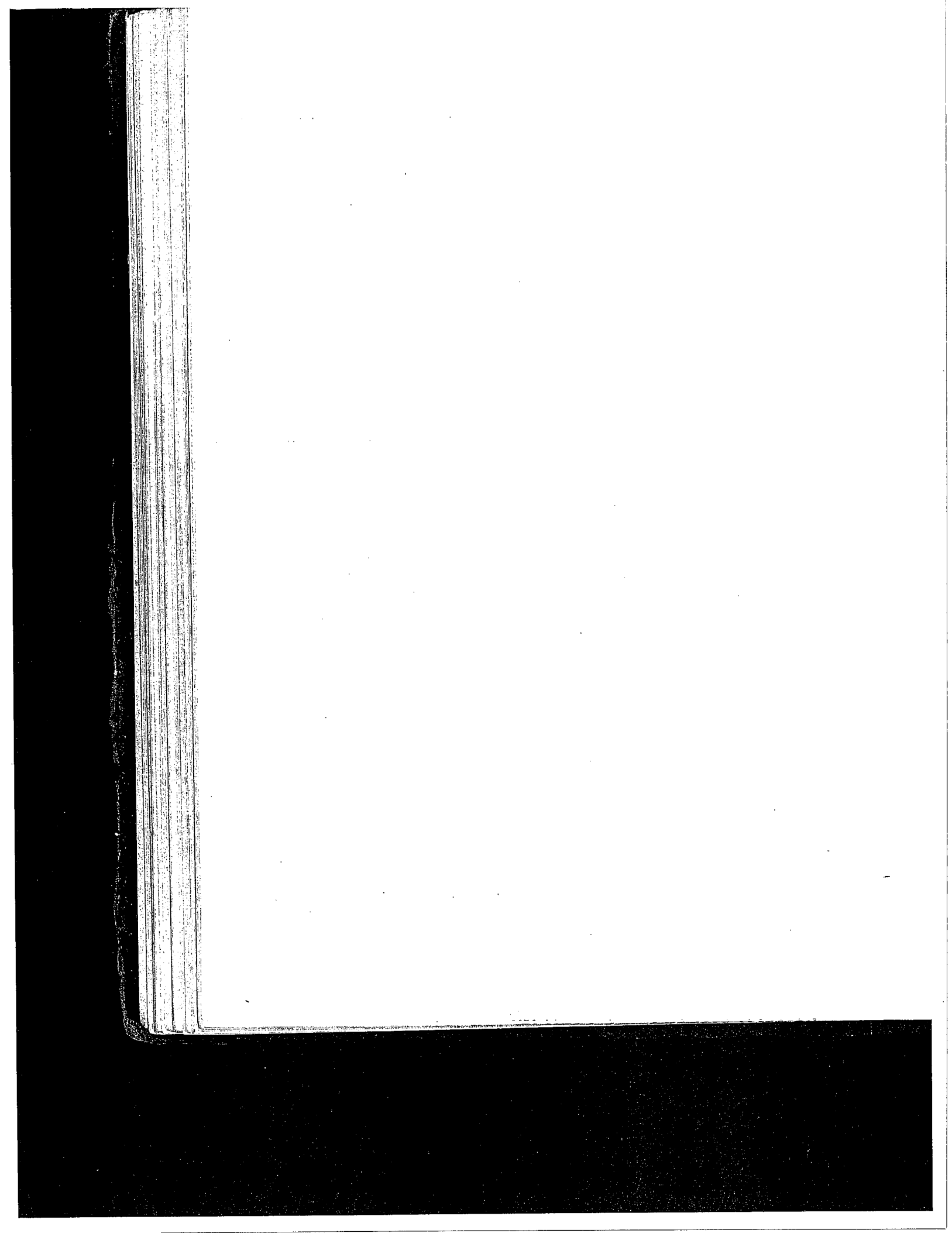

10

Vascular Cambium

The vascular cambium is the meristem that produces the secondary vascular tissues. It is a lateral meristem, for in contrast to the apical meristem it occupies a lateral position in stem and root. In the three-dimensional aspect, the cambium is a continuous sheath about the xylem of stem and root and their branches, and it extends in the form of strips into the leaves if the latter have secondary growth.

ORGANIZATION OF CAMBIUM

The cells of the vascular cambium do not fit the usual descriptions of meristematic cells, as those that have dense cytoplasm, large nuclei, and are approximately isodiametric in shape. Although the resting cambial cells have relatively few small vacuoles, the active cambial cells are highly vacuolated.[18] Morphologically, cambial cells occur in two forms. One type of cell, the *fusiform initial* (fig. 10.1,*A*), is several to many times longer than wide; the other, the *ray initial* (fig. 10.1,*B*), is slightly elongated to nearly isodiametric. The term fusiform implies that the cell is shaped like a spindle. A fusiform initial, however, is an approximately prismatic cell in its middle part and wedge shaped at the ends. The pointed end of the wedge is seen in tangential sections, the truncated end in radial sections (fig. 10.1,*A*). The tangential sides of the cell are wider than the radial.

In the cambial zone, the fusiform initials and their derivatives constitute the axial system, the ray initials the radial system. The cambium may be storied or nonstoried depending on whether or not, as seen in tangential sections, the cells are arranged in horizontal tiers (fig. 10.2). In a storied cambium the fusiform initials are shorter and less strongly overlapping than in a nonstoried cambium. The arrangement of the cambial initials determines the organization of the secondary vascular tissues. The cells of the axial systems in these tissues are derived from the similarly arranged fusiform initials

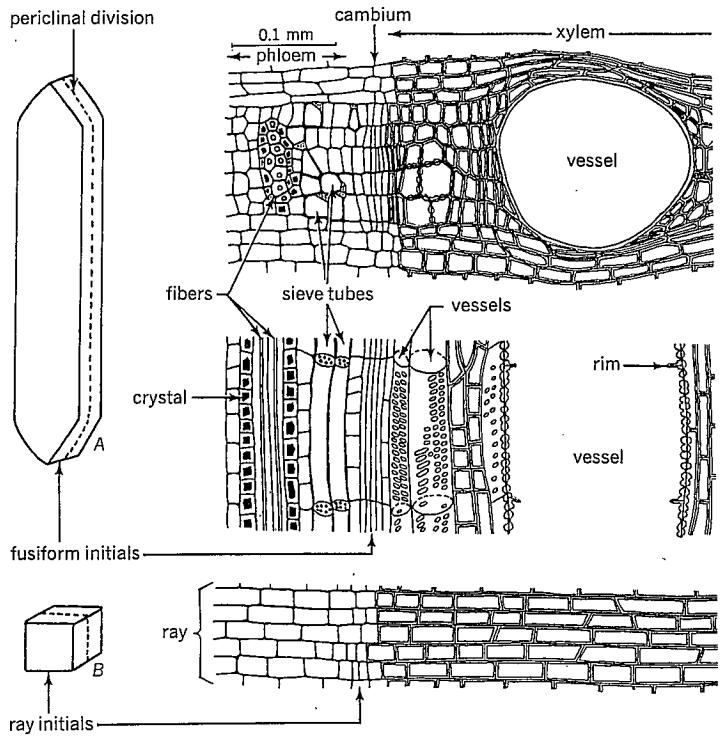

Figure 10.1 Vascular cambium in relation to derivative tissues. *A*, diagram of fu initial; *B*, of ray initial. In both, orientation of division concerned with formation of pl and xylem cells (periclinal division) is indicated by broken lines. *C*, *D*, *E*, *Robinia doacacia;* sections of stem include phloem, cambium, and xylem. *C*, transverse; *D*, (axial system only); *E*, radial (ray only).

and the ray systems from the ray initials; the storied and nonstoried cambia give rise to storied and nonstoried woods, respectively.

When the cambial initials produce secondary xylem and phloem cells they divide periclinally (fig. 10.1,*A*,*B*). At one time a derivative cell is produced toward the xylem, at another time toward the phloem, although not necessarily in alternation. Thus, each cambial initial produces radial files of cells, one toward the outside, the other toward the inside, and the two files meet at the cambial initial (figs. 10.1,*C*, and 10.3). Cambial divisions that add cells to the secondary vascular tissues are called *additive divisions*.[2]

During the height of cambial activity, addition occurs so rapidly that older cells still meristematic when new cells are duced by the initials. Thus, a wide zon more or less undifferentiated cells accu lates. Within this zone, the *cambial zone,* one cell in a given radial file is considere be an initial in the sense that after it div periclinally, one of the two resulting cells mains as the initial and the other is give toward the differentiating phloem or xyl The initials are difficult to distinguish f their recent derivatives because these der tives divide periclinally one or more times fore they begin to differentiate into xyler

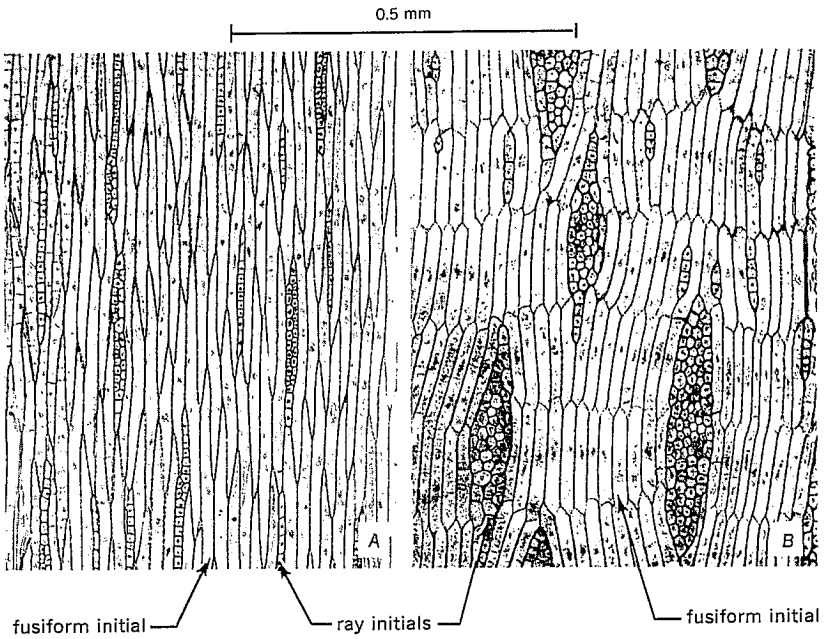

Figure 10.2 Arrangement of cells in vascular cambium as seen in tangential sections. *A*, nonstoried cambium of *Rhus typhina*. *B*, storied cambium of Wisteria sp.

phloem cells. Some workers, therefore, prefer to use the word cambium to designate the entire cambial zone.[7]

The cambial zone thus constitutes a more or less wide stratum of periclinally dividing cells organized into axial and ray systems. In the approximately median plane (it is more often an off-median plane) of this stratum one commonly visualizes a single layer of cambial initials flanked along their two tangential walls by initials of the vascular tissues, the phloem initials (or phloem mother cells) toward the periphery, the xylem initials (or xylem mother cells) toward the inside (fig. 10.4). The initial of a given radial file of cells in the cambial zone does not necessarily have an accurate tangential alignment with the initials in neighboring radial files.[3] In one radial file, the initial may be located closer to the xylem or the phloem than in another file. Moreover, a given initial may cease to participate in additive divisions and be displaced by its derivative which then assumes the role of a cambial initial.

DEVELOPMENTAL CHANGES IN THE INITIAL LAYER

As the core of secondary xylem increases in thickness, the cambium is displaced outward and its circumference increases. This increase is accomplished by division of cells, but in arborescent species it also involves complex phenomena of intrusive growth, elimination of initials, and formation of ray initials from fusiform initials. The changes in the cambium are reflected in cell relationships of the derivative tissues so that serial transverse and tangential sections, particularly of the xylem, may be used to analyze the behavior of the cambium in the past.

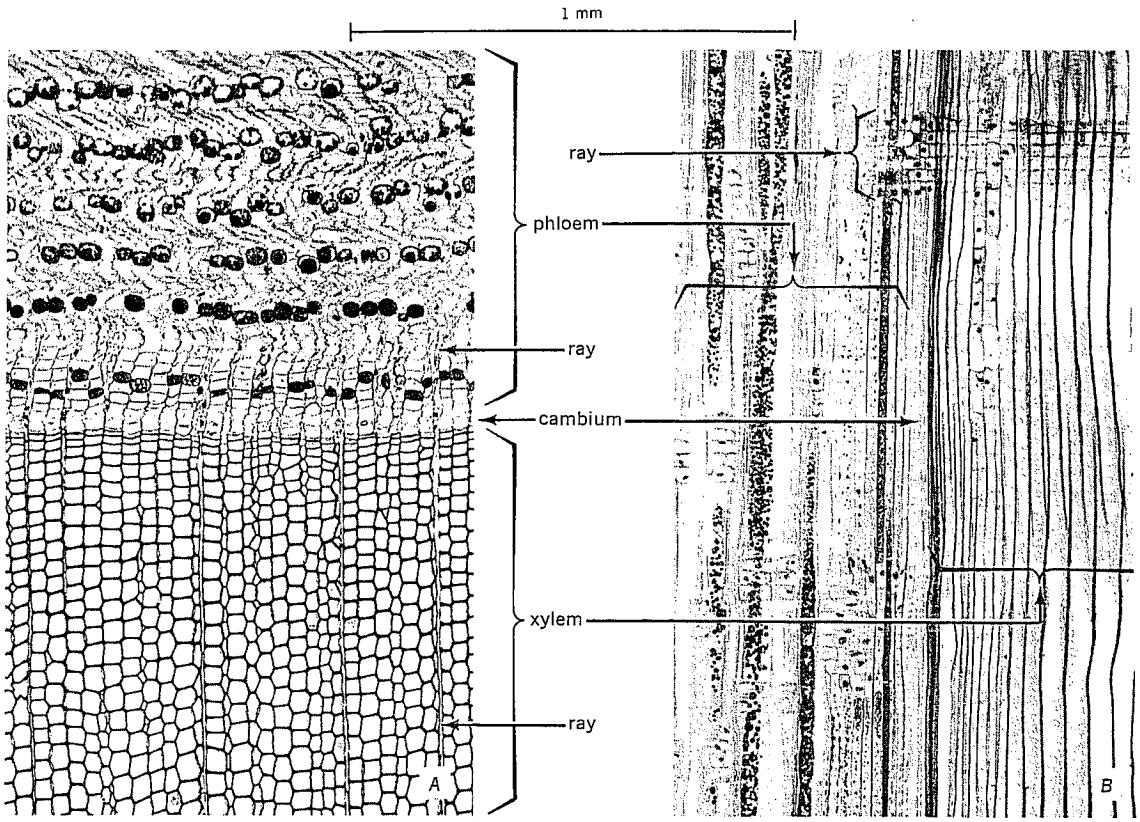

Figure 10.3 Vascular tissues and cambium in stem of pine (*Pinus* sp., a conifer) in cross (*A*) and radial (*B*) sections

The divisions increasing the number of initials are called *multiplicative divisions.*[2] In cambia with short fusiform initials, the multiplicative divisions are mostly *radial anticlinal*[6] (fig. 10.5,*A*). Thus, two cells appear side by side where one was present formerly, and each enlarges tangentially. In herbaceous and shrubby dicotyledons the anticlinal divisions are frequently *lateral;* that is, they intersect twice the same mother cell wall[10] (fig. 10.5,*B*). Long fusiform initials divide by more or less inclined anticlinal walls[3] (*pseudotransverse divisions;* figs. 10.5,*C–E*, and 10.6,*A*), and each new cell elongates by apical intrusive growth (fig. 10.5,*F,G*). As a result of this growth the new sister cells come to lie side by side in the tangential plane (fig 10.5,*G*), and they thus increase the circumfer ence of the cambium. During the intrusive growth the ends of the cells may fork (fig 10.5,*H,I*). The ray initials also divide radially anticlinally if the plant has biseriate or multiseriate rays.

The formation of ray initials from fusiform initials, or their segments, is a common phenomenon. If one compares growth layers in the xylem near the pith with those farther outward, a relative constancy in the ratio between the rays and the axial components may be observed.[5] This constancy results from the addition of new rays as the column of xylem increases in girth; that is, new ray ini-

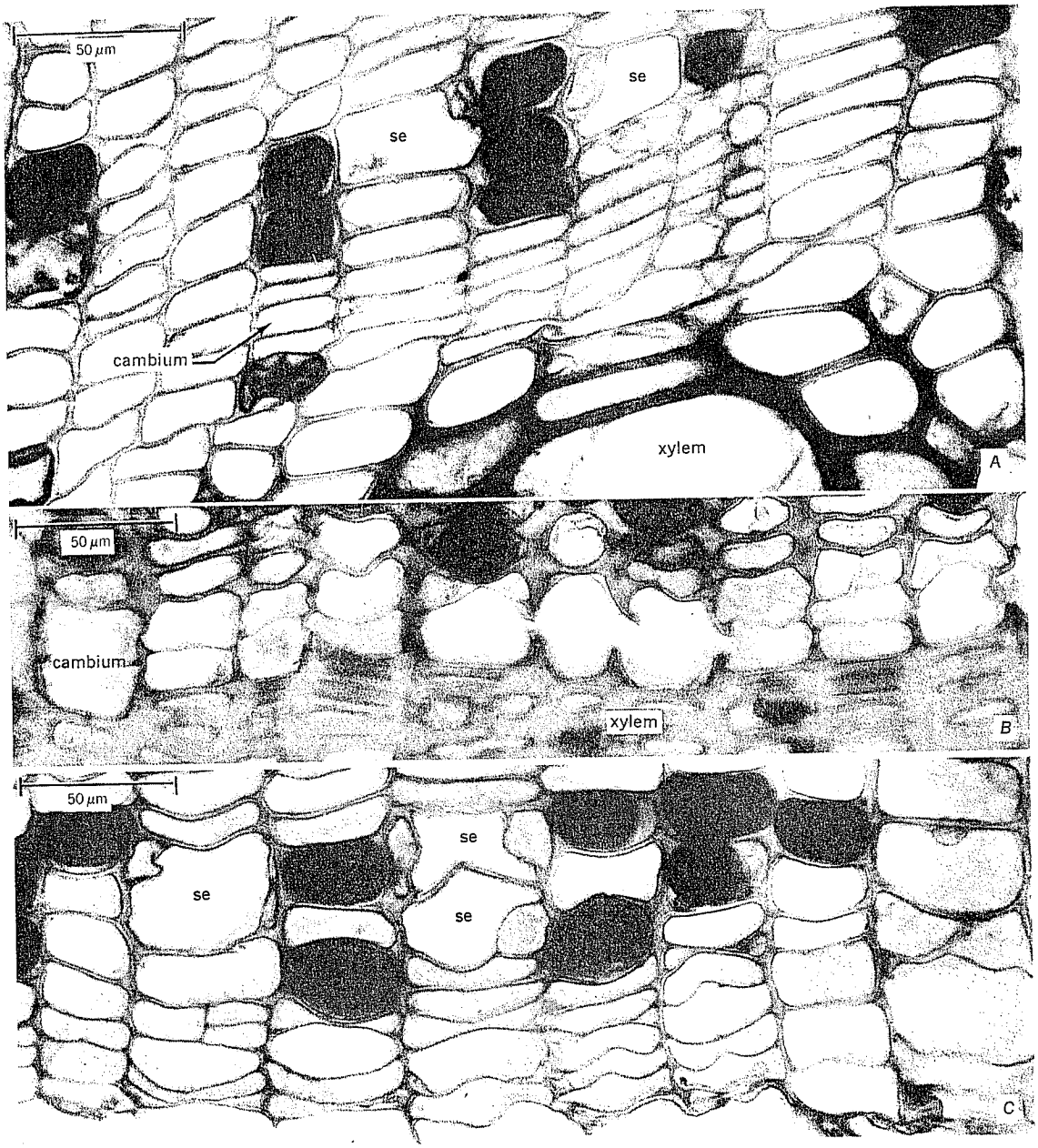

Figure 10.4 Vascular cambium from stem of grapevine (*Vitis vinifera*) in cross sections. *A*, active cambium late in the season. *B*, cambium at beginning of reactivation with first tangential walls of the season and some ruptures in anticlinal walls. *C*, active cambium at later stage than in *B*; breakage occurred through the youngest cambial cells and caused the bark to slip, that is, to separate from the xylem. Detail: *se*, sieve elements, each with one or two companion cells. (From K. Esau, *Hilgardia* 18:217–296, 1948.)

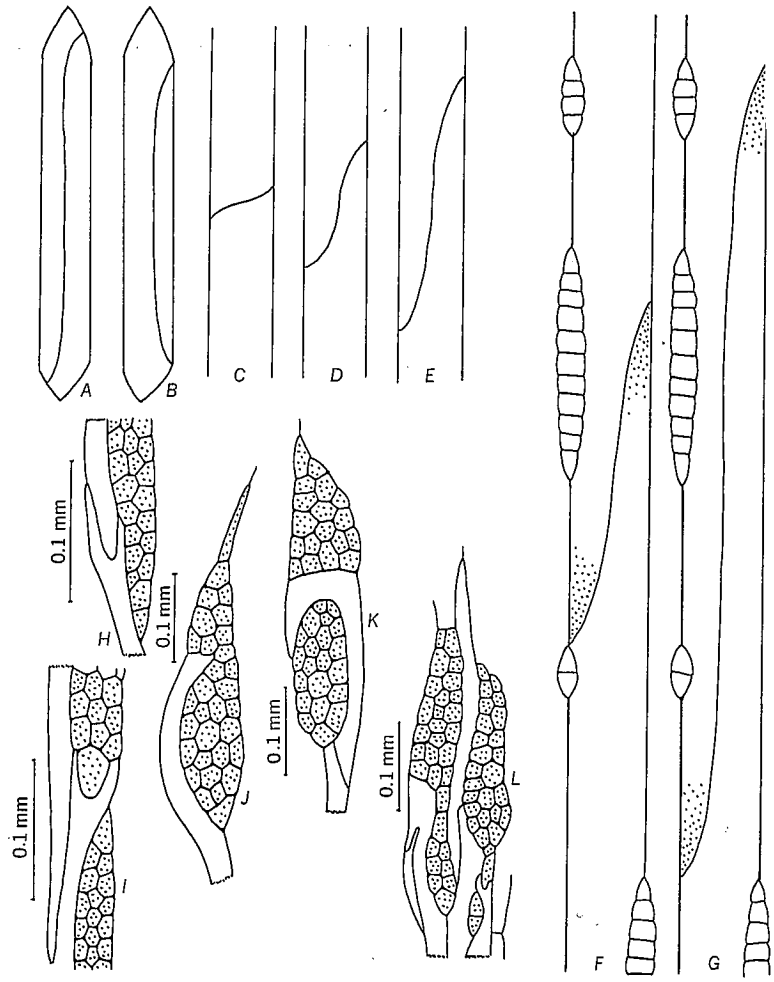

Figure 10.5 Division and growth of fusiform initials. Initial divided: *A*, by radial anticlinal wall; *B*, by lateral anticlinal wall; *C–E*, by various oblique anticlinal walls. *F*, *G*, oblique anticlinal division is followed by apical intrusive growth (growing apices are stippled). *H*, *I*, forking of fusiform initials during intrusive growth (*Juglans*). *J–L*, intrusion of fusiform initials into rays (*Liriodendron*). (All tangential views.)

tials appear in the cambium. These new ray initials are derived from fusiform initials.

The initials of new uniseriate rays may arise as unicellular segments cut out from fusiform initials at their apices or in the middle parts (conifers[5]) or by transverse divisions of such initials (herbaceous and shrubby dicotyledons[8–10]). The origin of rays, however, may be a highly complicated process involving a transverse subdivision of fusiform initials into several cells, loss of some of the products of these divisions, and the transformation of others into ray initials.[2] The loss, or elimination, of an initial is a displacement of this cell

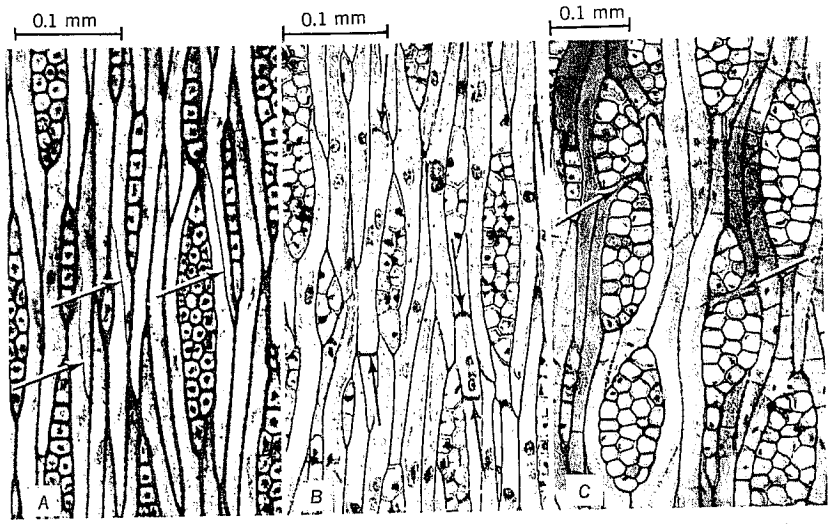

Figure 10.6 Division and growth of fusiform initials. *A*, cambium of *Juglans* with three fusiform initials recently divided by oblique anticlinal walls (arrows). *B*, cambium of *Cryptocarya;* two periclinally dividing fusiform initials with phragmoplasts (arrows), which indicate extent of cell plates. *C*, phloem of *Liriodendron* with two rays penetrated by axial cells, as a result of intrusive growth, while the tissue was still in cambial state. All, tangential sections.

toward the xylem or the phloem and eventual maturation into a xylem or a phloem cell, often after a gradual reduction in size while the cell is still in the initial layer.[1]

In conifers and dicotyledons new uniseriate rays begin as rays one or two cells high and only gradually attain the height typical for the species.[5] The increase in height occurs through transverse divisions of the established ray initials and through fusion of rays located one above the other. In the formation of multiseriate rays radial anticlinal divisions and fusions of laterally approximated rays are involved. Indications are that in the process of fusion some fusiform initials intervening between rays are converted into ray initials by transverse divisions; others are displaced toward the xylem or the phloem and are thus lost from the initial zone. The reverse process, a splitting of rays, also occurs. A common method of such splitting is a breaking up of a panel of ray initials by a fusiform initial that intrudes among the ray initials (figs. 10.5,*I–L*, and 10.6,*C*).

The multiplicative and additive divisions commonly occur toward the end of the maximal growth concerned with the seasonal production of xylem and phloem.[3,5] In plants with nonstoried cambia this timing in divisions means that the cambium contains, on the average, shorter fusiform initials at the end of the season than earlier. Subsequently the new cells elongate so that the average length of the initials increases until a new period of divisions ensues at the end of the growth season.

The periodic changes in length of the fusiform initials are reflected in the variation in length in the resulting xylem cells. In both gymnosperms and angiosperms the length of the elongated types of cells (tracheids, fibers) rises from the first-formed early wood to the last formed late wood.[4] There is also an overall increase in the length of the fusiform

initials from the beginning of secondary growth and through the successive years until the length is more or less stabilized or perhaps reduced.[12]

In some conifers, the anticlinal divisions of fusiform initials occur according to a precise pattern.[14] The inclined walls formed during the multiplicative divisions are tilted in one direction through panels ("domains") of cambium of considerable size. The panels vary in size, and the orientation of new walls changes periodically throughout a given panel. The unidirectional orientation of anticlinal walls and of the intrusively growing tips of the new cells, combined with a frequent loss of initials, appears to be causally related to the development of spiral grain in the wood.

The foregoing discussion of developmental transformations in the initial region of the cambium clearly indicates that this meristem is in continuous state of change. The concept of cambial initials must take into account this lack of stability. Elimination of initials is a particularly significant feature in this regard. The initials have no continuing individuality, but the function of initiation of new cells is sustained; it is "inherited" by one cell after another.[16] Recognition of the impermanence of cellular composition of the cambium also affects the concept of the uniseriate cambial initial layer. The assumption that only one specific layer in the cambium merits the name of initial layer has frequently been questioned.[17] Studies on conifer cambium have demonstrated, however, that the multiplicative divisions, which establish new patterns of cell alignment in xylem and phloem, occur mainly in one specific layer.[3] Thus, the several layers of a cambial zone, which are similar cytologically and are undergoing divisions, are not equivalent in the degree of their impact upon the architecture of the secondary vascular tissues. At a given time, a single layer functions as the initial layer by perpet ating bidirectionally the pattern of its cellul arrangement.

Cytokinesis, or formation of new cells, the cambium is of special interest when th cells divide longitudinally and the new wall formed along the long diameter of the cell. such a division, the diameter of the initi phragmoplast originating during telophas (fig. 10.7,*A*) is very much shorter than the lor diameter of the cell. The phragmoplast ar the cell plate reach the longitudinal walls the cambial cell soon after nuclear divisic (fig. 10.7,*E*), but the progress of the cell pla toward the ends of the cell is an extende process (fig. 10.7,*A–C*). Before the side wal are reached the phragmoplast appears as circular halo in front view (fig. 10.7,*D*). Aft those walls are intersected by the ce plate—but before the ends of cells ai

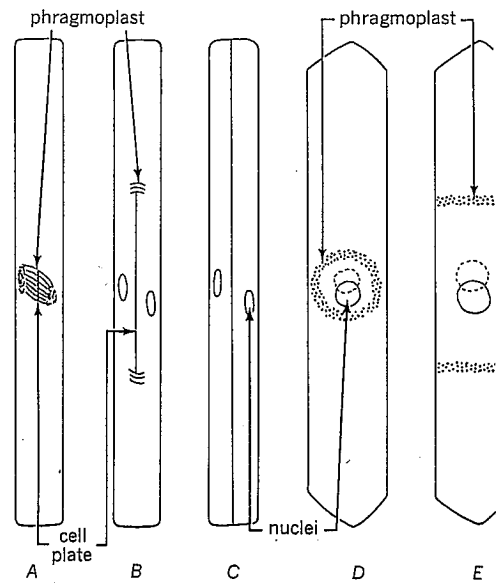

Figure 10.7 Cell division in fusiform initials. *A–C*, thre stages in formation of cell plate as seen in radial se tions. *D*, *E*, two stages of cell-plate formation as seen tangential sections. The cell plate has extended throug about one-third of the cell in *B* and *E*. All views illustra tangential divisions.

reached—the phragmoplast in the front view forms two bars intersecting the side walls (figs. 10.6,*B*, and 10.7,*E*).

The ultrastructural features of cytokinesis of the long cambial cells dividing longitudinally are similar to those observed during the division of shorter cells (chapter 4). Since the dividing cambial cells are considerably vacuolated, the formation of a cytoplasmic layer, the phragmosome, bridging the vacuole would seem to be a particularly important prerequisite for the progress of the phragmoplast and the cell plate from the site of the nucleus to the ends of the cell. A phragmosome has been recognized in transections of dividing fusiform initials,[13] but remains to be demonstrated in longitudinal views. It may not appear as a continuous layer at once but be formed successively in advance of the progressing phragmoplast in continuity with the parietal cytoplasm.

PATTERNS AND CAUSAL RELATIONS IN CAMBIAL ACTIVITY

The seasonal changes in the activity of vascular cambium is a much explored topic but continues to reveal new aspects as the causal relations in growth and differentiation are elucidated.[15] In the temperate regions, winter rest is succeeded by reactivation of the vascular cambium. Cambial cells take up water, enlarge radially, and divide periclinally (fig. 10.4,*B*). While the cells enlarge, their radial walls become thinner and, as a result, the bark (phloem and tissues outside of it; chapter 12) may be easily peeled off, that is, "the bark slips" (fig. 10.4,*C*). Cell division does not necessarily start in the initial layer. The first divisions may appear in the overwintering mother cells of the xylem or the phloem, followed later by additive divisions in the initial layer. The slippage of bark occurs not only through this layer but often also through the differentiating xylem. In dicotyledons, the expanding vessels constitute a particularly weak connection between bark and wood during cambial growth. The maximum of additive divisions is reached a few weeks after the cambium is reactivated. Periodicity in cambial activity occurs in both deciduous and evergreen species and is not confined to the temperate regions. In the tropics, however, the periodicity is less clearly related to seasonal changes in environmental conditions and may be weakly expressed or absent.

The first additions from the initial layer may be made toward either the xylem or the phloem, the variation depending on plant species. Generally, however, more cells are added to the xylem than to the phloem. This well-known pattern of cell addition has been confirmed by the use of radioactively labeled CO_2 and the resulting ^{14}C marking of the walls in new secondary tissue in a *Eucalyptus*.[23] Cell production toward the xylem was about four times that toward the phloem. A greater difference was observed in a conifer.[1] In a vigorously growing *Thuja occidentalis,* 12 to 16 new cells were formed on the phloem side and 100 or more on the xylem side.

Initiation of cambial activity in the spring is often clearly related to resumption of bud growth. The relation is somewhat variable but is well expressed in dicotyledons with diffuse-porous wood. Cambial activity, as determined by bark slippage, begins beneath the emerging new shoots and proceeds basipetally toward the trunk and root. Many weeks may pass between the time of cambial reactivation under the buds and that in the roots. The relationship is less clear in dicotyledons with ring-porous woods and in conifers, but experimental work involving removal of buds and leaves indicates that primary growth in the shoot generally provides the stimulus for

the inception of secondary growth in the axis below. Correspondingly, the cessation of cambial activity at the end of the growth season may be correlated with the completion of shoot extension.[11]

The hormonal nature of the stimulus inducing cambial activity was postulated by some of the earliest students of secondary growth. Subsequent intensive research has repeatedly associated the initial stimulation of cambial activity with the downward movement of growth substances from the expanding buds.[19] This movement establishes gradients of hormones to which the spread of cambial activity is clearly related.[11] Although the growing buds provide the initial hormonal stimulus for the resumption of cambial activity, the maintenance of that activity appears to be independent of the auxin from the shoots. The continued cambial growth has a local source of auxin as is evidenced by studies on secondary growth in excised internodes.[21] Analysis of auxin content in the three layers of the cambial region, the differentiating xylem, the differentiating phloem, and the cambium, indicates that the differentiating xylem may be the main source of this locally supplied auxin. It is proposed[20] that this auxin is released by the autolysing tracheary cells as they mature into nonliving conducting cells.

Auxin appears to be one of the most important growth substances associated with cambial growth but other substances, such as cytokinins and gibberellic acid, may interact with auxins in activating the cambium and affecting the pattern of differentiation of derivatives. Moreover, the growth-regulating substances act in conjunction with other growth factors, namely, availability of food (especially sugar[22]) and water, appropriate temperature and photoperiod, and the endogenously determined rhythm of growth characteristic of a given species.

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