

Structure and Function of Wood

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Wood is a complex biological structure, a composite of many chemistries and cell types acting together to serve the needs of a living plant. Attempting to understand wood in the context of wood technology, we have often overlooked the key and basic fact that wood evolved over the course of millions of years to serve three main functions in plants: conduction of water from the roots to the leaves, mechanical support of the plant body, and storage of biochemicals. There is no property of wood—physical, mechanical, chemical, biological, or technological—that is not fundamentally derived from the fact that wood is formed to meet the needs of the living tree. To accomplish any of these functions, wood must have cells that are designed and interconnected in ways sufficient to perform these functions. These three functions have influenced the evolution of approximately 150,000 different species of woody plants (FitzJohn and others 2014), each with unique properties, uses, and capabilities, in both plant and human contexts. Understanding the basic requirements dictated by these three functions and identifying the structures in wood that perform them allow insight to the realm of wood as an engineering material (Hoadley 2000). A scientist who understands the interrelationships between form and function can predict the utility of a specific wood in a new context. The objective of this chapter is to review the basic biological structure of wood and provide a basis for interpreting its properties in an engineering context. By understanding the function of wood in the living tree, we can better understand the strengths and limitations it presents as a material.

The component parts of wood must be defined and delimited at a variety of scales. The wood anatomical expertise necessary for a researcher who is using a solid wood beam is different from that necessary for an engineer designing a glued-laminated beam, which in turn is different from that required for making a wood–resin composite with wood flour. Differences in the kinds of knowledge required in these three cases are related to the scale at which one intends to interact with wood, and in all three cases the properties of these materials are derived from the biological needs of the living tree. For this reason, this chapter explains the structure of wood at decreasing scales and in ways that demonstrate the biological rationale for a plant to produce wood with such features. This background will permit the reader to understand the biological bases for the properties presented in subsequent chapters.

Although shrubs and many vines form wood, the remainder of this chapter will focus on wood from trees, which are the predominant source of wood for commercial and engineering applications and provide examples of virtually all features that merit discussion.

Biological Structure of Wood at Decreasing Scales

The Tree

A living, growing tree has two main domains, the shoot and the roots. Roots are the subterranean structures responsible for water and mineral nutrient uptake, mechanical anchoring of the shoot, and storage of biochemicals. The shoot is made up of the trunk or bole, branches, and leaves (Raven and others 1999). The remainder of the chapter will be concerned with the trunk of the tree.

If one cuts down a tree and looks at the stump, several gross observations can be made. The trunk is composed of various materials present in concentric bands. From the outside of the tree to the inside are outer bark, inner bark, vascular cambium, sapwood, heartwood, and the pith (Fig. 3–1). Outer bark provides mechanical protection to the softer inner bark and also helps to limit evaporative water loss. Inner bark is the tissue through which sugars (food) produced by photosynthesis are translocated from the leaves to the roots or growing portions of the tree. The vascular cambium is the layer between the inner bark and the wood that produces both these tissues each year. The sapwood is the active, “living” wood that conducts the water (or sap) from the roots to the leaves. It has not yet accumulated the often-colored chemicals that set apart the non-conductive heartwood found as a core of darker-colored wood in the middle of most trees. The pith at the very center of the trunk is the remnant of the early growth of the trunk, before wood was formed.

Softwoods and Hardwoods

Despite what one might think based on the terminology, not all softwoods have soft, lightweight wood, nor do all hardwoods have hard, heavy wood. To define them botanically, softwoods are those woods that come from gymnosperms (mostly conifers), and hardwoods are woods that come from angiosperms (flowering plants). In the temperate portion of the northern hemisphere, softwoods are generally needle-leaved evergreen trees such as pine (*Pinus*) and spruce (*Picea*), whereas hardwoods are typically broadleaf, deciduous trees such as maple (*Acer*), birch (*Betula*), and oak (*Quercus*). Softwoods and hardwoods not only differ in terms of the types of trees from which they are derived, but they also differ in terms of their component cells. Softwoods have a simpler basic structure than do hardwoods because they have only two cell types and relatively little variation in structure within these cell types.

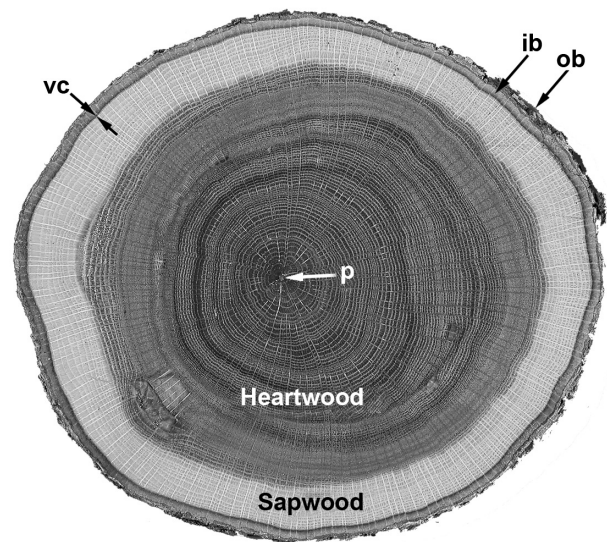


Figure 3–1. Macroscopic view of a transverse section of a *Quercus alba* trunk. Beginning at the outside of the tree is the outer bark (ob). Next is the inner bark (ib) and then the vascular cambium (vc), which is too narrow to see at this magnification. Interior toward the vascular cambium is the sapwood, which is easily differentiated from the heartwood that lies toward the interior. At the center of the trunk is the pith (p), which is barely discernible in the center of the heartwood.

Hardwoods have greater structural complexity because they have both a greater number of basic cell types and a far greater degree of variability within the cell types. The single most important distinction between the two general kinds of wood is that hardwoods have a characteristic type of cell called a vessel element (or pore) whereas softwoods lack these (Fig. 3–2). An important cellular similarity between softwoods and hardwoods is that in both kinds of wood, most of the cells are dead at maturity, even in the sapwood. The cells that are alive at maturity are known as parenchyma cells and can be found in both softwoods and hardwoods.

Sapwood and Heartwood

In both softwoods and hardwoods, the wood in the trunk of the tree is typically divided into two zones, each of which serves an important function distinct from the other. The actively conducting portion of the stem in which parenchyma cells are still alive and metabolically active is referred to as sapwood. A looser, more broadly applied definition is that sapwood is the band of lighter colored wood adjacent to the bark. Heartwood is the darker colored wood found to the interior of the sapwood (Fig. 3–1).

In the living tree, sapwood is responsible not only for conduction of sap but also for storage and synthesis of biochemicals. An important storage function is the long-term storage of photosynthate. Carbon that must be expended to form a new flush of leaves or needles must be stored somewhere in the tree, and parenchyma cells of the sapwood are often where this material is stored. The primary

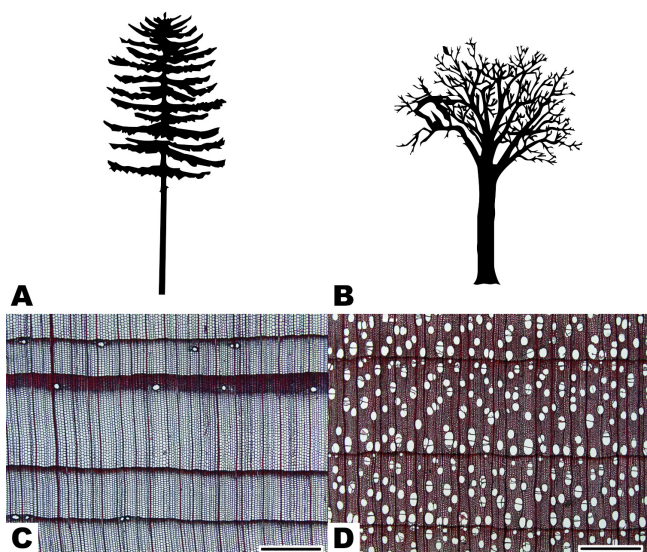


Figure 3–2. A, the general form of a generic softwood tree. B, the general form of a generic hardwood tree. C, transverse section of *Pseudotsuga mensiezii*, a typical softwood; the thirteen round white spaces are resin canals. D, transverse section of *Betula allegheniensis*, a typical hardwood; the many large, round white structures are vessels or pores, the characteristic feature of a hardwood. Scale bars = 780 μm .

storage forms of photosynthate are starch and lipids. Starch grains are stored in the parenchyma cells and can be easily seen with a microscope. The starch content of sapwood can have important ramifications in the wood industry. For example, in the tropical tree ceiba (*Ceiba pentandra*), an abundance of starch can lead to growth of anaerobic bacteria that produce ill-smelling compounds that can make the wood commercially unusable (Chudnoff 1984). In southern yellow pines of the United States, a high starch content encourages growth of sap-stain fungi that, though they do not affect the strength of the wood, can nonetheless decrease the lumber value for aesthetic reasons (Simpson 1991).

Living cells of the sapwood are also the agents of heartwood formation. Biochemicals must be actively synthesized and translocated by living cells. For this reason, living cells at the border between heartwood and sapwood are responsible for the formation and deposition of heartwood chemicals, one important step leading to heartwood formation (Hillis 1996). Heartwood functions in long-term storage of biochemicals of many varieties depending on the species in question. These chemicals are known collectively as extractives. In the past, heartwood was thought to be a disposal site for harmful byproducts of cellular metabolism, the so-called secondary metabolites. This led to the concept of the heartwood as a dumping ground for chemicals that, to a greater or lesser degree, would harm living cells if not sequestered in a safe place. We now know that extractives are a normal part of the plant's system of protecting its wood. Extractives are formed by parenchyma cells at the heartwood–sapwood boundary and are then exuded through

pits into adjacent cells (Hillis 1996). In this way, dead cells can become occluded or infiltrated with extractives despite the fact that these cells lack the ability to synthesize or accumulate these compounds on their own.

Extractives are responsible for imparting several larger-scale characteristics to wood. For example, extractives provide natural durability to timbers that have a resistance to decay fungi. In the case of a wood like teak (*Tectona grandis*), known for its stability and water resistance, these properties are conferred in large part by the waxes and oils formed and deposited in the heartwood. Many woods valued for their colors, such as mahogany (*Swietenia mahagoni*), African blackwood (*Diospyros melanoxylon*), Brazilian rosewood (*Dalbergia nigra*), and others, owe their value to the type and quantity of extractives in the heartwood. For these species, the sapwood has little or no value, because the desirable properties are imparted by heartwood extractives. Gharu wood, or eagle wood (*Aquilaria malaccensis*), has been driven to endangered status due to human harvest of the wood to extract valuable resins used in perfume making (Lagenheim 2003). Sandalwood (*Santalum spicatum*), a wood famed for its use in incenses and perfumes, is valuable only if the heartwood is rich with the desired scented extractives. The utility of a wood for a technological application can be directly affected by extractives. For example, if a wood like western redcedar, high in hydrophilic extractives, is finished with a water-based paint without a stain blocker, extractives may bleed through the paint, ruining the product (Chap. 16).

Axial and Radial Systems

The distinction between sapwood and heartwood, though important, is a gross feature that is often fairly easily observed. More detailed inquiry into the structure of wood shows that wood is composed of discrete cells connected and interconnected in an intricate and predictable fashion to form an integrated system that is continuous from root to twig. The cells of wood are typically many times longer than wide and are specifically oriented in two separate systems of cells: the axial system and the radial system. Cells of the axial system have their long axes running parallel to the long axis of the organ (up and down the trunk). Cells of the radial system are elongated perpendicularly to the long axis of the organ and are oriented like radii in a circle or spokes in a bicycle wheel, from the pith to the bark. In the trunk of a tree, the axial system runs up and down, functions in long-distance water movement, and provides the bulk of the mechanical strength of the tree. The radial system runs in a pith to bark direction, provides lateral transport for biochemicals, and in many cases performs a large fraction of the storage function in wood. These two systems are interpenetrating and interconnected, and their presence is a defining characteristic of wood as a tissue.

Planes of Section

Although wood can be cut in any direction for examination, the organization and interrelationship between the axial and radial systems give rise to three main perspectives from which they can be viewed to glean the most information. These three perspectives are the transverse plane of section (the cross section), the radial plane of section, and the tangential plane of section. Radial and tangential sections are referred to as longitudinal sections because they extend parallel to the axial system (along the grain).

The transverse plane of section is the face that is exposed when a tree is cut down. Looking down at the stump one sees the transverse section (as in Fig. 3–3H); cutting a board across the grain exposes the transverse section. The transverse plane of section provides information about features that vary both in the pith to bark direction (called the radial direction) and also those that vary in the circumferential direction (called the tangential direction). It does not provide information about variations up and down the trunk.

The radial plane of section runs in a pith-to-bark direction (Fig. 3–3A, top), and it is parallel to the axial system, so it provides information about longitudinal changes in the stem and from pith to bark along the radial system. To describe it geometrically, it is parallel to the radius of a cylinder, and extending up and down the length of the cylinder. In a practical sense, it is the face or plane that is exposed when a log is split exactly from pith to bark. It does not provide any information about features that vary in a tangential direction.

The tangential plane is at a right angle to the radial plane (Fig. 3–3A, top). Geometrically, it is parallel to any tangent line that would touch the cylinder, and it extends along the length of the cylinder. One way in which the tangential plane would be exposed is if the bark were peeled from a log; the exposed face is the tangential plane. The tangential plane of section does not provide any information about features that vary in the radial direction, but it does provide information about the tangential dimensions of features.

All three planes of section are important to the proper observation of wood, and only by looking at each can a holistic and accurate understanding of the three-dimensional structure of wood be gleaned. The three planes of section are determined by the structure of wood and the way in which the cells in wood are arrayed. The topology of wood and the distribution of the cells are accomplished by a specific part of the tree stem.

Vascular Cambium

The axial and radial systems and their component cells are derived from a part of the tree called the vascular cambium. The vascular cambium is a thin layer of cells that exists between the inner bark and the wood (Figs. 3–1, 3–4)

that produces, by means of many cell divisions, wood (or secondary xylem) to the inside and bark (or secondary phloem) to the outside, both of which are vascular conducting tissues (Larson 1994). As the vascular cambium adds cells to the layers of wood and bark around a tree, the girth of the tree increases, and thus the total surface area of the vascular cambium itself must increase, and this is accomplished by cell division as well.

The axial and radial systems are generated in the vascular cambium by two component cells: fusiform initials and ray initials. Fusiform initials, named to describe their long, slender shape, give rise to cells of the axial system, and ray initials give rise to the radial system. For this reason, there is a direct and continuous link between the most recently formed wood, the vascular cambium, and the inner bark. In most cases, the radial system in the wood is continuous into the inner bark, through the vascular cambium. In this way wood, the water-conducting tissue, stays connected to the inner bark, the photosynthate-conducting tissue. They are interdependent tissues because the living cells in wood require photosynthate for respiration and cell growth and the inner bark requires water in which to dissolve and transport the photosynthate. Outer bark is formed in part by a separate cambium not involved in the formation of wood, and in part by the maturation and death of the inner bark from prior years.

Growth Rings

Wood is produced by the vascular cambium one layer of cell divisions at a time, but we know from general experience that in many woods large groups of cells are produced more or less together in time, and these groups act together to serve the tree. These collections of cells produced together over a discrete time interval are known as growth increments or growth rings. Cells formed at the beginning of the growth increment are called earlywood cells, and cells formed in the latter portion of the growth increment are called latewood cells (Fig. 3–3D,E). Springwood and summerwood were terms formerly used to refer to earlywood and latewood, respectively, but their use is no longer recommended (IAWA 1989).

In temperate portions of the world and anywhere else with distinct, regular seasonality, trees form their wood in annual growth increments; that is, all the wood produced in one growing season is organized together into a recognizable, functional entity that many sources refer to as annual rings. Such terminology reflects this temperate bias, so a preferred term is growth increment, or growth ring (IAWA 1989). In many woods in the tropics, growth rings are not evident. However, continuing research in this area has uncovered several characteristics whereby growth rings can be correlated with seasonality changes in some tropical species (Worbes 1995, 1999; Callado and others 2001).

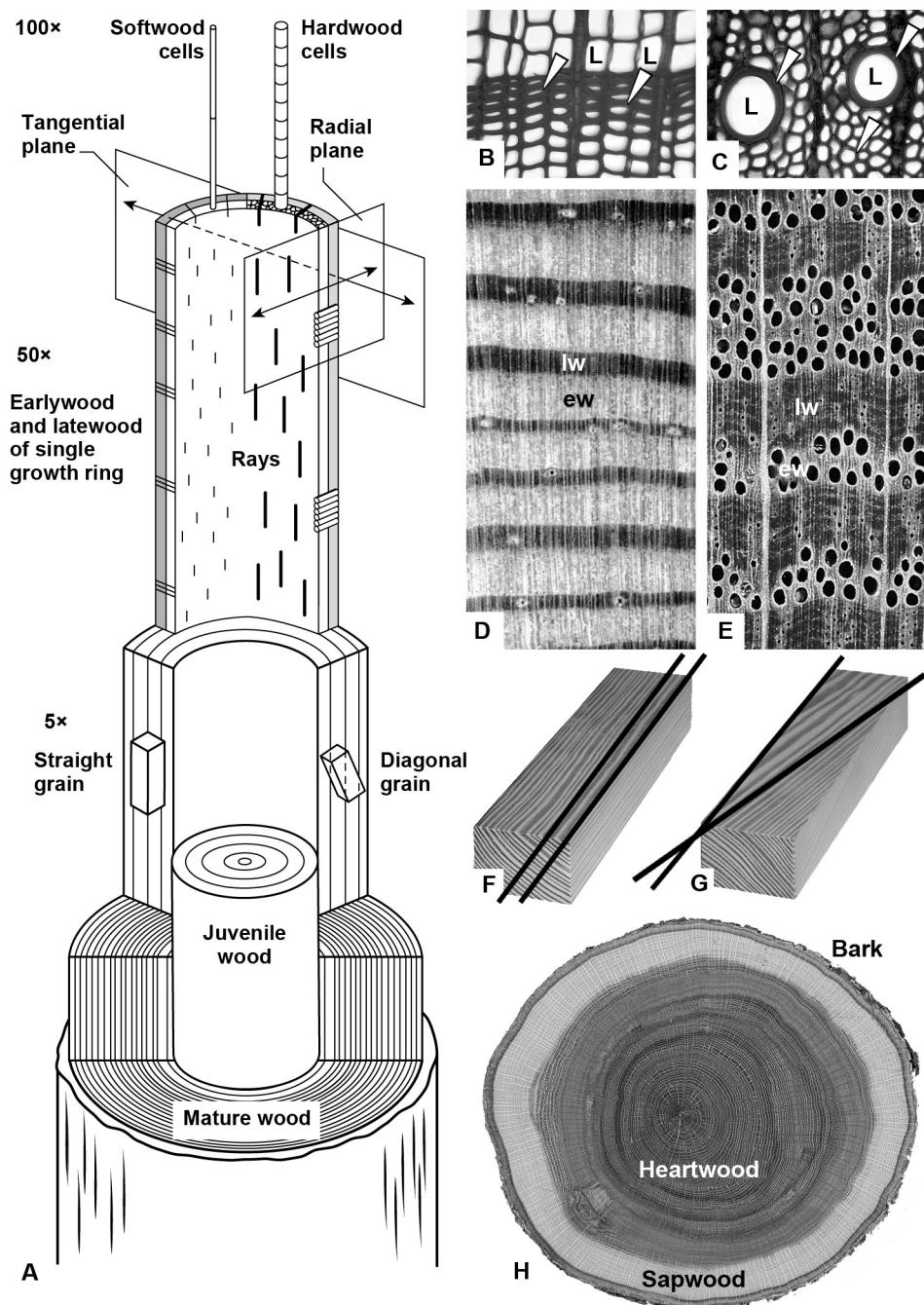


Figure 3-3. A, illustration of a cut-away tree at various magnifications, corresponding roughly with the images to its right; at the top, at an approximate magnification of 100 $\times$, a softwood cell and several hardwood cells are illustrated, to give a sense of scale between the two; one tier lower, at an approximate magnification of 50 $\times$, is a single growth ring of a softwood (left) and a hardwood (right), and an indication of the radial and tangential planes; the next tier, at approximately 5 $\times$ magnification, illustrates many growth rings together and how one might produce a straight-grained rather than a diagonal-grained board; the lowest tier includes an illustration of the relative position of juvenile and mature wood in the tree, at 1 $\times$ magnification. B,C, light microscopic views of the lumina (L) and cell walls (arrowheads) of a softwood (B) and a hardwood (C). D,E, hand-lens views of growth rings, each composed of earlywood (ew) and latewood (lw), in a softwood (D) and a hardwood (E). F, a straight-grained board; note that the line along the edge of the board is parallel to the line along the grain of the board. G, a diagonal-grained board; note that the two lines are markedly not parallel; this board has a slope of grain of about 1 in 7. H, the gross anatomy of a tree trunk, showing bark, sapwood, and heartwood.

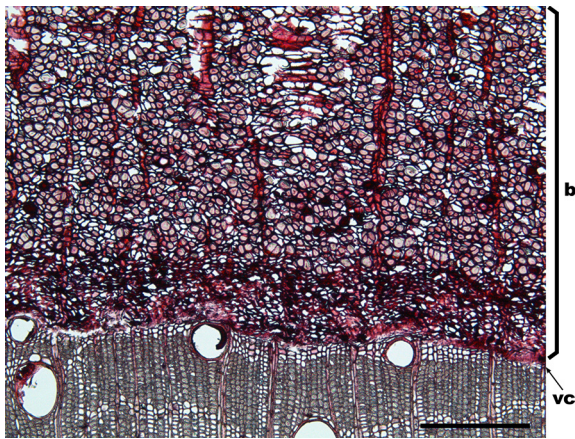


Figure 3–4. Light microscopic view of the vascular cambium. Transverse section showing vascular cambium (vc) and bark (b) in *Croton macrobothrys*. The tissue below the vascular cambium is wood. Scale bar = 390 μm .

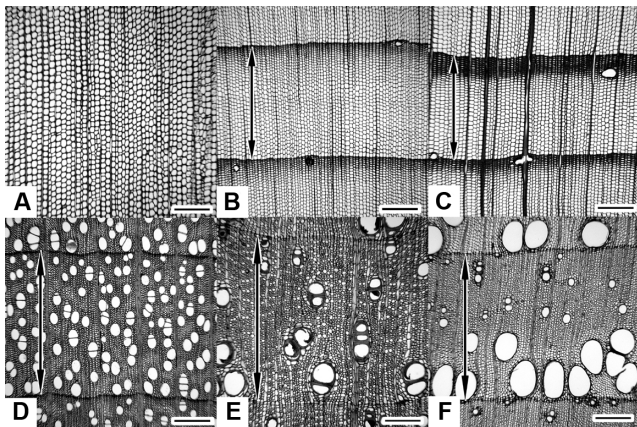


Figure 3–5. Transverse sections of woods showing types of growth rings. Arrows delimit growth rings, when present. A–C, softwoods. A, no transition within the growth ring (growth ring absent) in *Podocarpus imbricata*. B, gradual transition from earlywood to latewood in *Picea glauca*. C, abrupt transition from earlywood to latewood in *Pseudotsuga menziesii*. D–F, hardwoods. D, diffuse-porous wood (no transition) in *Acer saccharum*. E, semi-ring-porous wood (gradual transition) in *Diospyros virginiana*. F, ring-porous wood (abrupt transition) in *Fraxinus americana*. Scale bars = 300 μm .

Woods that form distinct growth rings, and this includes most woods that are likely to be used as engineering materials in North America, show three fundamental patterns within a growth ring: no change in cell pattern across the ring; a gradual reduction of the inner diameter of conducting elements from the earlywood to the latewood; and a sudden and distinct change in the inner diameter of the conducting elements across the ring (Fig. 3–5). These patterns appear in both softwoods and hardwoods but differ in each because of the distinct anatomical differences between the two.

Non-porous woods (or softwoods, woods without vessels) can exhibit any of these three general patterns. Some softwoods such as Western redcedar (*Thuja plicata*), northern white-cedar (*Thuja occidentalis*), and species of spruce (*Picea*) and true fir (*Abies*) have growth increments that undergo a gradual transition from the thin-walled wide-lumined earlywood cells to the thicker-walled, narrower-lumined latewood cells (Fig. 3–5B). Other woods undergo an abrupt transition from earlywood to latewood, such as southern yellow pine (*Pinus*), larch (*Larix*), Douglas-fir (*Pseudotsuga menziesii*), baldcypress (*Taxodium disticum*), and redwood (*Sequoia sempervirens*) (Fig. 3–5C). Because most softwoods are native to the north temperate regions, growth rings are clearly evident. Only in species such as araucaria (*Araucaria*) and some podocarps (*Podocarpus*) does one find no transition within the growth ring (Fig. 3–5A). Some authors report this state as growth rings being absent or only barely evident (Phillips 1948, Kukachka 1960).

Porous woods (or hardwoods, woods with vessels) have two main types of growth rings and one intermediate form. In diffuse-porous woods, vessels either do not markedly differ in size and distribution from the earlywood to the latewood, or the change in size and distribution is gradual and no clear distinction between earlywood and latewood can be found (Fig. 3–5D). Maple (*Acer*), birch (*Betula*), aspen/cottonwood (*Populus*), and yellow-poplar (*Liriodendron tulipifera*) are examples of diffuse porous species.

This pattern is in contrast to ring-porous woods wherein the transition from earlywood to latewood is abrupt, with vessel diameters decreasing substantially (often by an order or magnitude or more); this change in vessel size is often accompanied by a change in the pattern of vessel distribution as well. This creates a ring pattern of large earlywood vessels around the inner portion of the growth increment, and then denser, more fibrous tissue in the latewood, as is found in hackberry (*Celtis occidentalis*), white ash (*Fraxinus americana*), shagbark hickory (*Carya ovata*), and northern red oak (*Quercus rubra*) (Fig. 3–5F).

Sometimes the vessel size and distribution pattern falls more or less between these two definitions, and this condition is referred to as semi-ring-porous (Fig. 3–5E). Black walnut (*Juglans nigra*) is a temperate-zone semi-ring-porous wood. Most tropical hardwoods are diffuse-porous; the best-known commercial exceptions to this are the Spanish cedars (*Cedrela* spp.) and teak (*Tectona grandis*), which are generally semi-ring-porous and ring-porous, respectively.

Few distinctly ring-porous species grow in the tropics and comparatively few grow in the southern hemisphere. In genera that span temperate and tropical zones, it is common to have ring-porous species in the temperate zone and diffuse-porous species in the tropics. The oaks (*Quercus*), ashes (*Fraxinus*), and hackberries (*Celtis*) native to the tropics are diffuse-porous, whereas their temperate

congeners are ring-porous. Numerous detailed texts provide more information on growth increments in wood, a few of which are of particular note (Panshin and deZeeuw 1980, Dickison 2000, Carlquist 2001).

Cells in Wood

Understanding a growth ring in greater detail requires some familiarity with the structure, function, and variability of cells that make up the ring. A living plant cell consists of two primary domains: the protoplast and the cell wall. The protoplast is the sum of the living contents that are bounded by the cell membrane. The cell wall is a non-living, largely carbohydrate matrix extruded by the protoplast to the exterior of the cell membrane. The plant cell wall protects the protoplast from osmotic lysis and often provides mechanical support to the plant at large (Esau 1977, Raven and others 1999, Dickison 2000).

For cells in wood, the situation is somewhat more complicated than this highly generalized case. In many cases in wood, the ultimate function of the cell is borne solely by the cell wall. This means that many mature wood cells not only do not require their protoplasts, but indeed must completely remove their protoplasts prior to achieving functional maturity. For this reason, a common convention in wood literature is to refer to a cell wall without a protoplast as a cell. Although this is technically incorrect from a cell biological standpoint, this convention is common in the literature and will be observed throughout the remainder of the chapter.

In the case of a mature cell in wood in which there is no protoplast, the open portion of the cell where the protoplast would have existed is known as the lumen (plural: lumina). Thus, in most cells in wood there are two domains; the cell wall and the lumen (Fig. 3–3B,C). The lumen is a critical component of many cells, whether in the context of the amount of space available for water conduction or in the context of a ratio between the width of the lumen and the thickness of the cell wall. The lumen has no structure per se, as it is the void space in the interior of the cell. Thus, wood is a substance that has two basic domains; air space (mostly in the lumina of the cells) and the cell walls of the component cells.

Cell Walls

Cell walls in wood give wood the majority of its properties discussed in later chapters. Unlike the lumen, which is a void space, the cell wall itself is a highly regular structure, from one cell type to another, between species, and even when comparing softwoods and hardwoods. The cell wall consists of three main regions: the middle lamella, the primary wall, and the secondary wall (Fig. 3–6). In each region, the cell wall has three major components: cellulose microfibrils (with characteristic distributions and organization), hemicelluloses, and a matrix or

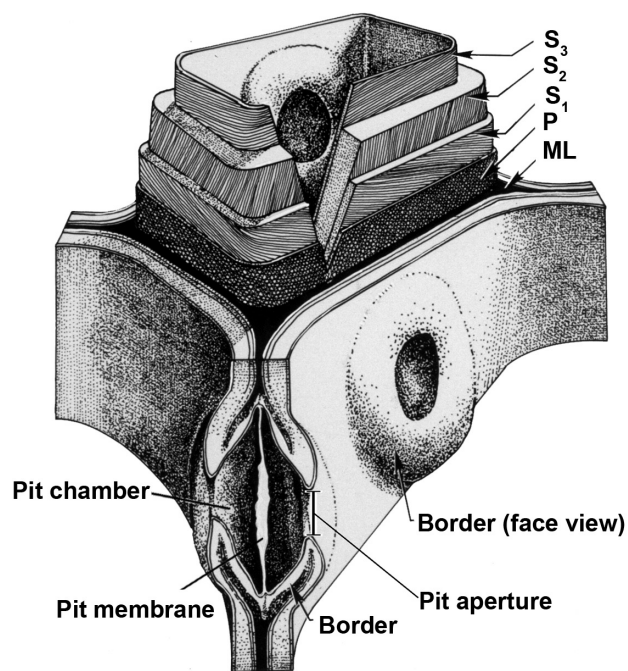


Figure 3–6. Cut-away drawing of the cell wall, including the structural details of a bordered pit. The various layers of the cell wall are detailed at the top of the drawing, beginning with the middle lamella (ML). The next layer is the primary wall (P), and on the surface of this layer the random orientation of the cellulose microfibrils is detailed. Interior to the primary wall is the secondary wall in its three layers: S₁, S₂, and S₃. The microfibril angle of each layer is illustrated, as well as the relative thickness of the layers. The lower portion of the illustration shows bordered pits in both sectional and face view.

encrusting material, typically pectin in primary walls and lignin in secondary walls (Panshin and deZeeuw 1980). In a general sense, cellulose can be understood as a long string-like molecule with high tensile strength; microfibrils are collections of cellulose molecules into even longer, stronger thread-like macromolecules. Lignin is a brittle matrix material. The hemicelluloses are smaller, branched molecules thought to help link the lignin and cellulose into a unified whole in each layer of the cell wall.

To understand these wall layers and their interrelationships, it is necessary to remember that plant cells generally do not exist singly in nature; instead they are adjacent to many other cells, and this association of thousands of cells, taken together, forms an organ, such as a leaf. Each of the individual cells must adhere to one another in a coherent way to ensure that the cells can act as a unified whole. This means they must be interconnected to permit the movement of biochemicals (such as photosynthate, hormones, cell-signaling agents) and water. This adhesion is provided by the middle lamella, the layer of cell wall material between two or more cells, a part of which is contributed by each of the individual cells (Fig. 3–6). This layer is the outermost layer of the cell wall continuum and in a non-woody organ

is pectin rich. In the case of wood, the middle lamella is lignified.

The next layer formed by the protoplast just interior to the middle lamella is the primary wall (Fig. 3–6). The primary wall is characterized by a largely random orientation of cellulose microfibrils; like thin threads wound round and round a balloon in no particular order, where any microfibril angle from 0° to 90° relative to the long axis of the cell may be present. In cells in wood, the primary wall is thin and is generally indistinguishable from the middle lamella. For this reason, the term compound middle lamella is used to denote the primary cell wall of a cell, the middle lamella, and the primary cell wall of the adjacent cell. Even when viewed with transmission electron microscopy, the compound middle lamella often cannot be separated unequivocally into its component layers.

The remaining cell wall domain, found in virtually all cells in wood (and in many cells in non-woody plants or plant parts), is the secondary cell wall. The secondary cell wall is composed of three layers (Fig. 3–6). As the protoplast lays down the cell wall layers, it progressively reduces the lumen volume. The first-formed secondary cell wall layer is the S_1 (Fig. 3–6), which is adjacent to compound middle lamella (or technically, the primary wall). This layer is a thin layer and is characterized by a large microfibril angle. That is to say, the cellulose microfibrils are laid down in a helical fashion, and the angle between the mean microfibril direction and the long axis of the cell is large (50° to 70°).

The next wall layer is arguably the most important cell wall layer in determining the properties of the cell and, thus, the wood properties at a macroscopic level (Panshin and deZeeuw 1980). This layer, formed interior to the S_1 layer, is the S_2 layer (Fig. 3–6). This is the thickest secondary cell wall layer and it makes the greatest contribution to the overall properties of the cell wall. It is characterized by a lower lignin percentage and a low microfibril angle (5° to 30°). The microfibril angle of the S_2 layer of the wall has a strong but not fully understood relationship with wood properties at a macroscopic level (Kretschmann and others 1998), and this is an area of active research.

Interior to the S_2 layer is the S_3 layer, a relatively thin wall layer (Fig. 3–6). The microfibril angle of this layer is relatively high and similar to the S_1 (>70°). This layer has the lowest percentage of lignin of any of the secondary wall layers. The explanation of this phenomenon is related directly to the physiology of the living tree. In brief, for water to move up the plant (transpiration), there must be adhesion between the water molecules and the cell walls of the water conduits. Lignin is a hydrophobic macromolecule, so it must be in low concentration in the S_3 to permit adhesion of water to the cell wall and thus facilitate transpiration. For more detail on these wall components and information on transpiration and the role of the cell wall, see

any college-level plant physiology textbook (for example, Kozlowski and Pallardy 1997, Taiz and Zeiger 1991).

Pits

Any discussion of cell walls in wood must be accompanied by a discussion of the ways in which cell walls are modified to allow communication and transport between the cells in the living plant. These wall modifications, called pit-pairs (or more commonly just pits), are thin areas in the cell walls between two cells and are a critical aspect of wood structure too often overlooked in wood technological treatments. Pits have three domains: the pit membrane, the pit aperture, and the pit chamber. The pit membrane (Fig. 3–6) is the thin semi-porous remnant of the primary wall; it is a carbohydrate and not a phospholipid membrane. The pit aperture is the opening or hole leading into the open area of the pit, which is called the pit chamber (Fig. 3–6). The type, number, size, and relative proportion of pits can be characteristic of certain types of wood and furthermore can directly affect how wood behaves in a variety of situations, such as how wood interacts with surface coatings (DeMeijer and others 1998, Rijkaert and others 2001).

Pits of predictable types occur between different types of cells. In the cell walls of two adjacent cells, pits will form in the wall of each cell separately but in a coordinated location so that the pitting of one cell will match up with the pitting of the adjacent cell (thus a pit-pair). When this coordination is lacking and a pit is formed only in one of the two cells, it is called a blind pit. Blind pits are fairly rare in wood. Understanding the type of pit can permit one to determine what type of cell is being examined in the absence of other information. It can also allow one to make a prediction about how the cell might behave, particularly in contexts that involve fluid flow. Pits occur in three varieties: bordered, simple, and half-bordered (Esau 1977, Raven and others 1999).

Bordered pits are thus named because the secondary wall overarches the pit chamber and the aperture is generally smaller or differently shaped than the pit chamber, or both. The portion of the cell wall that is overarched the pit chamber is called the border (Figs. 3–6, 3–7A,D). When seen in face view, bordered pits often are round in appearance and look somewhat like a doughnut (Fig. 3–6). When seen in sectional view, the pit often looks like a pair of V's with the open ends of the V's facing each other (Fig. 3–7A,D). In this case, the long stems of the V represent the borders, the secondary walls that are overarched the pit chamber. Bordered pits always occur between two conducting cells, and sometimes between other cells, typically those with thick cell walls. The structure and function of bordered pits, particularly those in softwoods (see following section), are much-studied and considered to be well-suited to the safe and efficient conduction of sap. The status of the bordered pit (whether it is open or closed)

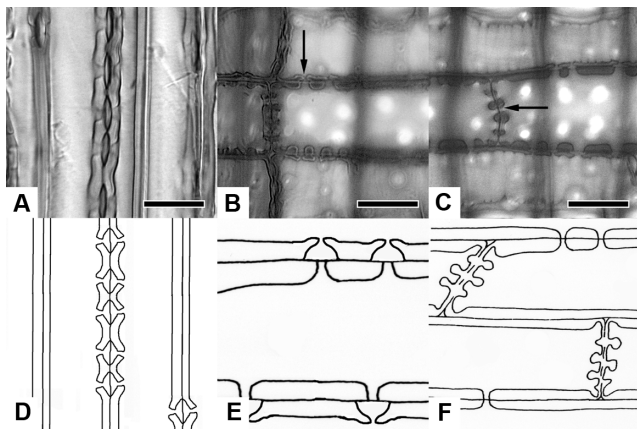


Figure 3-7. Light micrographs and sketches of the three types of pits. A,D, longitudinal section of bordered pits in *Xanthocyparis vietnamensis*; the pits look like a vertical stack of thick-walled letter Vs. B,E, half-bordered pits in *Pseudotsuga mensiezii*; the arrow shows one half-bordered pit. C,F, simple pits on an end-wall in *Pseudotsuga mensiezii*; the arrow indicates one of five simple pits on the end wall. Scale bars = 20 μ m.

has great importance in the field of wood preservation and can affect wood finishing and adhesive bonding.

Simple pits lack any sort of border (Fig. 3-7C,F). The pit chamber is straight-walled, and the pits are uniform in size and shape in each of the partner cells. Simple pits are typical between parenchyma cells and in face view merely look like clear areas in the walls.

Half-bordered pits occur between a conducting cell and a parenchyma cell. In this case, each cell forms the kind of pit that would be typical of its type (bordered in the case of a conducting cell and simple in the case of a parenchyma cell) and thus half of the pit pair is simple and half is bordered (Fig. 3-7B,E). In the living tree, these pits are of great importance because they represent the communication between conducting cells and biochemically active parenchyma cells.

Wood Chemistry

The final scale at which we will address wood structure is that of the chemistry of wood. The three main chemical components of cell walls—cellulose, hemicelluloses, and lignin—were previously introduced as having different structural features that work together to impart physical integrity of the cell wall. With respect to their elemental compositions, each of these is made up of only carbon (C), oxygen (O), and hydrogen (H) atoms. All are polymers, or larger molecules formed by linking together numerous smaller molecules, called monomers. They differentiate from each other at the molecular level. Cellulose is formed from a single sugar monomer, or monosaccharide, whereas the hemicelluloses are composed of different monosaccharides. Because both cellulose and the hemicelluloses are composed of

numerous monosaccharides, they together are classified as polysaccharides. Lignin is composed of chemically different monomers, the monolignols, which are formed by different biosynthetic pathways than those of the monosaccharides. In addition to cell wall components, wood accumulates and stores nonstructural biochemicals (extractives) and also has inorganic chemical constituents.

Polysaccharides

Cellulose is the main chemical component of wood, being 40% to 50% of the dry substance of wood, and is often stated to be the most abundant organic substance found in nature (Fengel and Wegener 1983). Glucose (β -D-glucopyranose) is the monosaccharide, linked together by (1 $\rightarrow$ 4)-glycosidic bonds to form a completely linear polymer that aggregates with other cellulose molecules through so-called hydrogen bonds, whereby the hydroxyl (–OH) groups along the polymer are attracted to each other. Although a single hydrogen bond may be relatively weak, innumerable hydrogen bonds between cellulose molecules results in the formation of compact microfibrils that provide the framework of high tensile strength to the main axis of the wood cell.

The hemicelluloses, being smaller in molecular size, were once thought to be precursors of cellulose. The hemicelluloses are now known to form by different biosynthetic pathways. Hemicelluloses comprise 20% to 30% of the dry substance of wood (Sjöström 1981). Although the singular term hemicellulose is often used, the plural is preferred because the hemicelluloses are made up of several molecular structures, differing in monosaccharide compositions, linkages between those monosaccharides, and total polymer size. Indeed, the hemicelluloses present in softwoods and hardwoods are quite different. Whereas the main hemicelluloses in softwoods are the galactoglucomannans, composed of galactose, glucose, and mannose, the main hemicelluloses in hardwoods are xylans, composed of a backbone chain of xylose with pendant sugars of glucose and arabinose. Hydrogen bonding occurs between the hemicelluloses; however, given their branched structures, they do not compact into microfibrils, but instead impart a means to fill between the microfibrils and associate with the encrusting cell wall polymer, lignin.

Lignins

Lignin is a phenylpropanoid polymer composed of up to three monomers, the so-called monolignols—*p*-coumaryl, coniferyl, and sinapyl alcohols. The term phenylpropanoid is derived from the monolignols sharing a common chemical skeleton of a phenol with a three-carbon side chain; the monomeric units differing from each other by the number of methoxyl groups (–OCH₃) on the aromatic ring of the phenol, either none, one, or two. Lignins comprise 26% to 32% of the dry substance of wood for softwoods, and lower amounts (20% to 28%) for hardwoods (Sjöström

1981). Aside from different proportions in wood, the lignins are distinctly different in the monolignols comprising them. Softwood lignins are primarily composed of coniferyl alcohol and small amounts of *p*-coumaryl alcohol (5% to 10%). Hardwood lignins have a proportion of sinapyl alcohol that approaches the proportion of coniferyl alcohol, with the amount of *p*-coumaryl being similar to that in softwood lignins. Through a dehydrogenative polymerization process, the monolignols combine to form a three-dimensional network polymer that encrusts the cell wall, and in high concentrations between individual wood fibers, binds them together in wood.

Extractives and Inorganics

Compounds that can be removed from wood by extraction with neutral solvents are collectively called extractives. The amounts found in wood can vary from almost none to as high as 50% in extreme cases; typical contents for woods from the temperate zone are up to 5% to 10% (Hon and Shiraishi 2001). As with two of the cell wall polymers, hemicelluloses and lignin, the chemical composition of extractives can be distinctly different between the softwoods and hardwoods. For softwoods, the extractives are generally nonpolar resinous materials rich in fatty acids and diterpene ($C_{20}H_{32}$) resin acids. The resin solids flow in the living tree by the presence of the smaller and chemically related monoterpenes ($C_{10}H_{16}$) serving as a solvent. A monoterpene mixture distilled from the resin or wood of pines is commonly known as turpentine, which has long been used as water-immiscible solvent in paints and varnishes. Although hardwoods also contain similarly nonpolar extractives, the predominant group of extractive compounds in the heartwood is a series of polyphenols known collectively as tannins. Heartwood tannins, and those obtained from tree bark, have long been used in tanning, the process used to make leather from animal hides.

Wood also contains inorganic elements, with calcium, potassium, and magnesium being the most prevalent. These and other inorganic elements contribute to the ash remaining after wood combustion. The ash content of wood is normally low, typically being less than 1% of the dry weight of wood (Pettersen 1984).

Microscopic Structure of Softwoods and Hardwoods

As discussed previously, the fundamental differences between woods are founded on the types, sizes, proportions, pits, and arrangements of different cells that comprise the wood. These fine details of structure can affect the use of a wood.

Softwoods

The structure of a typical softwood is relatively simple. The axial or vertical system is composed mostly of axial

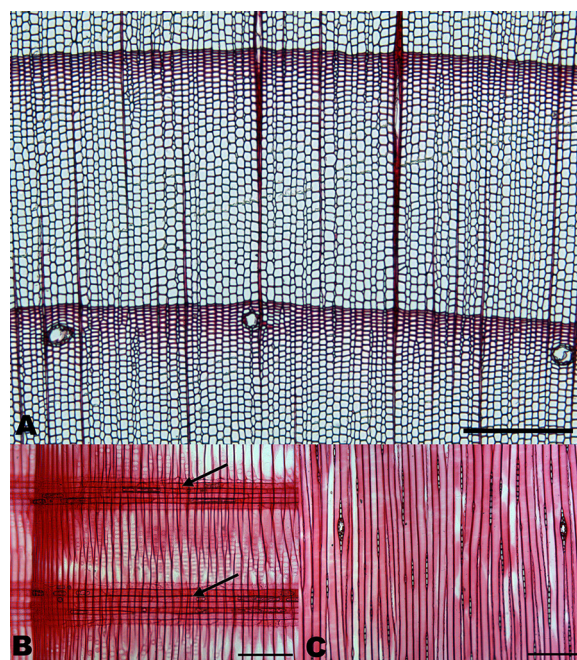


Figure 3–8. Microscopic structure of *Picea glauca*, a typical softwood. A, transverse section, scale bar = 390 μ m; the bulk of the wood is made of tracheids, the small rectangles of various thicknesses; the three large, round structures are resin canals and their associated cells; the dark lines running from the top to the bottom of the photo are the ray cells of the rays. B, radial section showing two rays (arrows) running from left to right; each cell in the ray is a ray cell, and they are low, rectangular cells; the rays begin on the right in the earlywood (thin-walled tracheids) and continue into and through the latewood (thick-walled tracheids) and into the earlywood of the next growth ring, on the left side of the photo; scale bar = 195 μ m. C, tangential section; rays seen in end-view, mostly only one cell wide; two rays are fusiform rays; there are radial resin canals embedded in the rays, causing them to bulge; scale bar = 195 μ m.

tracheids, and the radial or horizontal system is the rays, which are composed mostly of ray parenchyma cells.

Tracheids

Tracheids are long cells that are often more than 100 times longer (1 to 10 mm) than wide and they are the major component of softwoods, making up over 90% of the volume of the wood. They serve both the conductive and mechanical needs of softwoods. On the transverse view or section (Fig. 3–8A), tracheids appear as square or slightly rectangular cells in radial rows. Within one growth ring they are typically thin-walled in the earlywood and thicker-walled in the latewood. For water to flow between tracheids, it must pass through circular bordered pits that are concentrated in the long, tapered ends of the cells. Tracheids overlap with adjacent cells across both the top and bottom 20% to 30% of their length. Water flow thus must take a slightly zigzag path as it goes from one cell to the next

CHAPTER 3 | Structure and Function of Wood

through the pits. Because the pits have a pit membrane, resistance to flow is substantial. The resistance of the pit membrane coupled with the narrow diameter of the lumina makes tracheids relatively inefficient conduits compared with the conducting cells of hardwoods. Detailed treatments of the structure of wood in relation to its conductive functions can be found in the literature (Zimmermann 1983, Kozlowski and Pallardy 1997).

Axial Parenchyma and Resin Canal Complexes

Another cell type that is sometimes present in softwoods is axial parenchyma. Axial parenchyma cells are similar in size and shape to ray parenchyma cells, but they are vertically oriented and stacked one on top of the other to form a parenchyma strand. In transverse section they often look like axial tracheids but can be differentiated when they contain dark colored organic substances in the lumina of the cells. In the radial or tangential section they appear as long strands of cells generally containing dark-colored substances. Axial parenchyma is most common in redwood, juniper, cypress, baldcypress, and some species of *Podocarpus* but never makes up even 1% of the volume of a block of wood. Axial parenchyma is generally absent in pine, spruce, larch, hemlock, and species of *Araucaria* and *Agathis*.

In species of pine, spruce, Douglas-fir, and larch, structures commonly called resin ducts or resin canals are present axially (Fig. 3–9) and radially (Fig. 3–9C). These structures are voids or spaces in the wood and are not cells. Specialized parenchyma cells that function in resin production surround resin canals. When referring to the resin canal and all the associated parenchyma cells, the correct term is axial or radial resin canal complex (Wiedenhoef and Miller 2002). In pine, resin canal complexes are often visible on the transverse section to the naked eye, but they are much smaller in spruce, larch, and Douglas-fir, and a hand lens is needed to see them. Radial resin canal complexes are embedded in specialized rays called fusiform rays (Figs. 3–8C, 3–9C). These rays are typically taller and wider than normal rays. Resin canal complexes are absent in the normal wood of other softwoods, but some species can form large tangential clusters of traumatic axial resin canals in response to substantial injury.

Rays

The other cells in Figure 3–8A are ray parenchyma cells that are barely visible and appear as dark lines running in a top-to-bottom direction. Ray parenchyma cells are rectangular prisms or brick-shaped cells. Typically they are approximately 15 μm high by 10 μm wide by 150 to 250 μm long in the radial or horizontal direction (Fig. 3–8B). These brick-like cells form the rays, which function primarily in synthesis, storage, and lateral transport of biochemicals and, to a lesser degree, water. In radial view

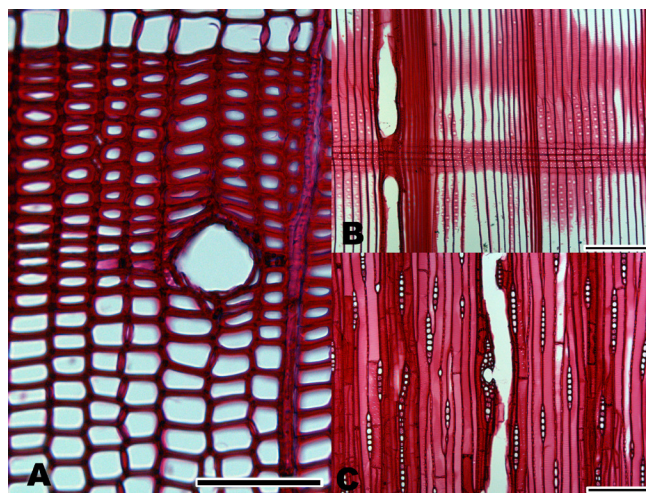


Figure 3–9. Resin canal complexes in *Pseudotsuga menziesii*. A, transverse section showing a single axial resin canal complex. In this view the tangential and radial diameters of the canal can be measured accurately. Scale bar = 100 μm . B, radial section showing an axial resin canal complex embedded in the latewood. It is crossed by a ray that also extends into the earlywood on either side of the latewood. Scale bar = 195 μm . C, tangential section showing the anastomosis between an axial and a radial resin canal complex. The fusiform ray bearing the radial resin canal complex is in contact with the axial resin canal complex. Scale bar = 195 μm .

or section (Fig. 3–8B), the rays look like brick walls and the ray parenchyma cells are sometimes filled with dark-colored substances. In tangential section (Fig. 3–8C), the rays are stacks of ray parenchyma cells one on top of the other forming a ray that is only one cell in width, called a uniseriate ray.

When ray parenchyma cells intersect with axial tracheids, specialized pits are formed to connect the axial and radial systems. The area of contact between the tracheid wall and the wall of the ray parenchyma cells is called a cross-field. The type, shape, and size and number of pits in the cross-field are generally consistent within a species and can be diagnostic for wood identification.

Species that have resin canal complexes also have ray tracheids, which are specialized horizontal tracheids that normally are situated at the margins of the rays. These ray tracheids have bordered pits like axial tracheids but are much shorter and narrower. Ray tracheids also occur in a few species that do not have resin canals. Alaska yellow-cedar, (*Chamaecyparis nootkatensis*), hemlock (*Tsuga*), and rarely some species of true fir (*Abies*) have ray tracheids. Additional detail regarding the microscopic structure of softwoods can be found in the literature (Phillips 1948, Kukachka 1960, Panshin and deZeeuw 1980, IAWA 2004).

Hardwoods

The structure of a typical hardwood is much more complicated than that of a softwood. The axial system is composed of fibrous elements of various kinds, vessel elements in various sizes and arrangements, and axial parenchyma in various patterns and abundance. As in softwoods, rays comprise the radial system and are composed of ray parenchyma cells, but hardwoods show greater variety in cell sizes and shapes.

Vessels

Vessel elements are the specialized water-conducting cells of hardwoods. They are stacked one on top of the other to form vessels. Where the ends of the vessel elements come in contact with one another, a hole is formed called a perforation plate. Thus hardwoods have perforated tracheary elements (vessels elements) for water conduction, whereas softwoods have imperforate tracheary elements (tracheids). On the transverse section, vessels appear as large openings and are often referred to as pores (Fig. 3–2D).

Vessel diameters may be small ($<30\text{ }\mu\text{m}$) or quite large ($>300\text{ }\mu\text{m}$), but typically range from 50 to 200 μm . They are much shorter than tracheids and range from 100 to 1,200 μm , or 0.1 to 1.2 mm. Vessels can be arranged in various patterns. If all the vessels are the same size and more or less scattered throughout the growth ring, the wood is diffuse-porous (Fig. 3–5D). If the earlywood vessels are much larger than the latewood vessels, the wood is ring-porous (Fig. 3–5F). Vessels can also be arranged in a tangential or oblique arrangement in a radial arrangement, in clusters, or in many combinations of these types (IAWA 1989). In addition, individual vessels may occur alone (solitary arrangement) or in pairs or radial multiples of up to five or more vessels in a row. At the end of the vessel element is a hole or perforation plate. If there are no obstructions across the perforation plate, it is called a simple perforation plate. If bars are present, the perforation plate is called a scalariform perforation plate.

Where vessel elements come in contact with each other tangentially, intervessel or intervascular bordered pits are formed. These pits range in size from 2 to $>16\text{ }\mu\text{m}$ in height and are arranged on the vessel walls in three basic ways. The most common arrangement is alternate, where the pits are offset by half the diameter of a pit from one row to the next. In the opposite arrangement, the pits are in files with their apertures aligned vertically and horizontally. In the scalariform arrangement, the pits are much wider than high. Combinations of these arrangements can also be observed in some species. Where vessel elements come in contact with ray cells, often half-bordered pits are formed called vessel–ray pits. These pits can be the same size and shape as the intervessel pits or much larger.

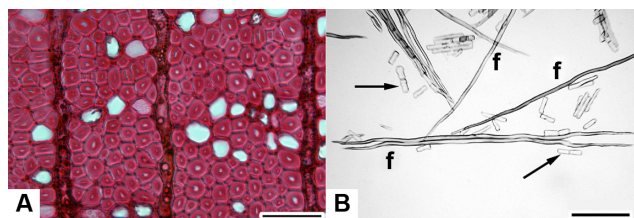


Figure 3–10. Fibers in *Quercus rubra*. A, transverse section showing thick-walled, narrow-lumined fibers; three rays are passing vertically through the photo, and there are a number of axial parenchyma cells, the thin-walled, wide-lumined cells, in the photo; scale bar = 50 μm . B, macerated wood; there are several fibers (f), two of which are marked; also easily observed are parenchyma cells (arrows), both individually and in small groups; note the thin walls and small rectangular shape compared to the fibers; scale bar = 300 μm .

Fibers

Fibers in hardwoods function almost exclusively as mechanical supporting cells. They are shorter than softwood tracheids (0.2 to 1.2 mm), average about half the width of softwood tracheids, but are usually two to ten times longer than vessel elements (Fig. 3–10B). The thickness of the fiber cell wall is the major factor governing density and mechanical strength of hardwood timbers. Species with thin-walled fibers, such as cottonwood (*Populus deltoides*), basswood (*Tilia americana*), ceiba, and balsa (*Ochroma pyramidale*), have low density and strength; species with thick-walled fibers, such as hard maple, black locust (*Robinia pseudoacacia*), ipe (*Tabebuia serratifolia*), and bulletwood (*Manilkara bidentata*), have high density and strength. Pits between fibers are generally inconspicuous and may be simple or bordered. In some woods such as oak (*Quercus*) and meranti/lauan (*Shorea*), vascular or vascentric tracheids are present, especially near or surrounding the vessels. These specialized fibrous elements in hardwoods typically have bordered pits, are thin-walled, and are shorter than the fibers of the species; they should not be confused with the tracheids in softwoods, which are much longer than hardwood fibers.

Axial Parenchyma

Axial parenchyma in softwoods is absent or only occasionally present as scattered cells, but hardwoods have a wide variety of axial parenchyma patterns (Fig. 3–11). The axial parenchyma cells in hardwoods and softwoods are roughly the same size and shape, and they also function in the same manner. The difference comes in the abundance and specific patterns in hardwoods. Two major types of axial parenchyma are found in hardwoods. Paratracheal parenchyma is associated with the vessels, and apotracheal parenchyma is not associated with the vessels. Paratracheal parenchyma is further divided into vascentric (surrounding the vessels, Fig. 3–11A), aliform (surrounding the vessel and with wing-like extensions, Fig. 3–11C), and confluent (several connecting patches of paratracheal parenchyma

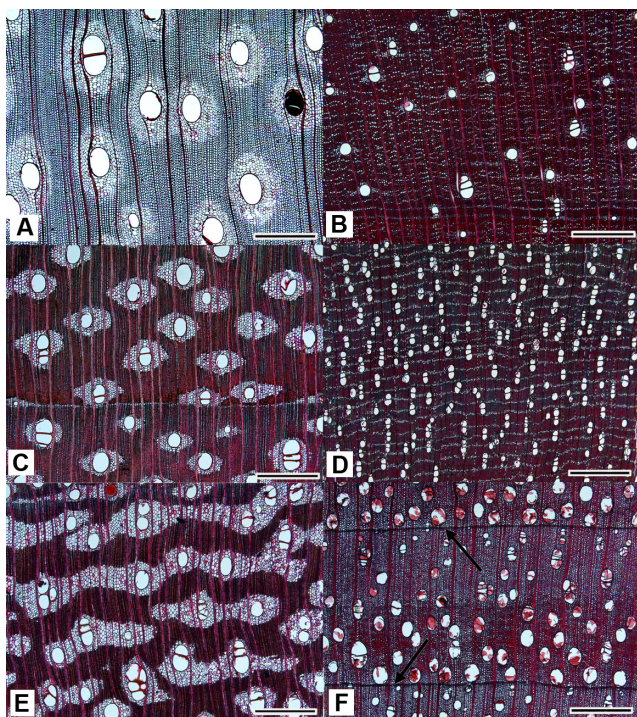


Figure 3–11. Transverse sections of various woods showing a range of hardwood axial parenchyma patterns. A, C, and E are woods with paratracheal types of parenchyma. A, vasicentric parenchyma in *Enterolobium maximum*; note that two vessels in the middle of the view are connected by parenchyma, which is the feature also shown in E; the other vessels in the image present vasicentric parenchyma only. C, aliform parenchyma in *Afzelia africana*; the parenchyma cells are the light-colored, thin-walled cells, and are easily visible. E, confluent parenchyma in *Afzelia cuazensis*. B, D, and F are woods with apotracheal types of parenchyma. B, diffuse-in-aggregate parenchyma in *Dalbergia stevensonii*. D, banded parenchyma in *Micropholis guyanensis*. F, marginal parenchyma in *Juglans nigra*; in this case, the parenchyma cells are darker in color, and they delimit the growth rings (arrows). Scale bars = 780 μm .

sometimes forming a band, Fig. 3–11E). Apotracheal parenchyma is divided into diffuse (scattered), diffuse-in-aggregate (short bands, Fig. 3–11B), and banded, whether at the beginning or end of the growth ring (marginal, Fig. 3–11F) or within a growth ring (Fig. 3–11D). Each species has a particular pattern of axial parenchyma, which is more or less consistent from specimen to specimen, and these cell patterns are important in wood identification.

Rays

The rays in hardwoods are structurally more diverse than those found in softwoods. In some species such as willow (*Salix*), cottonwood, and koa (*Acacia koa*), the rays are exclusively uniseriate and are much like softwood rays. In hardwoods, most species have rays that are more than one cell wide. In oak and hard maple, the rays are two-sized, uniseriate and more than eight cells wide and in oak several centimeters high (Fig. 3–12A). In most species the rays

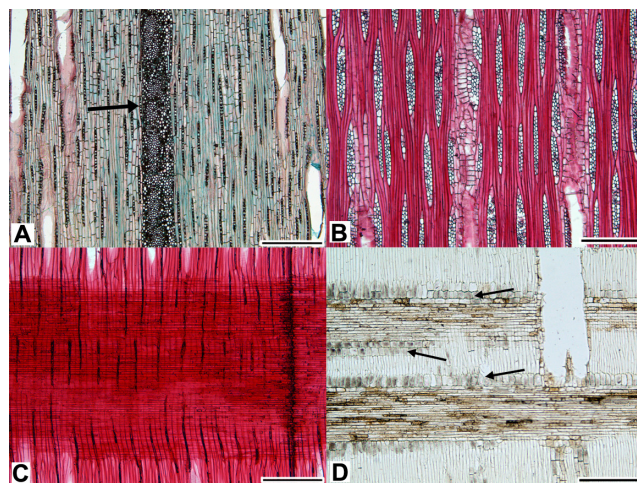


Figure 3–12. Rays in longitudinal sections. A and B show tangential sections, scale bars = 300 μm . A, *Quercus falcata* showing a wide multiseriate ray (arrow) and many uniseriate rays. B, *Swietenia macrophylla* showing numerous rays ranging from 1 to 4 cells wide; note that in this wood the rays are arranged roughly in rows from side to side. C and D show radial sections, scale bars = 200 μm . C, homocellular ray in *Tilia americana*; all cells in the ray are procumbent cells; they are longer radially than they are tall. D, two heterocellular rays in *Khaya ivorensis*; the central portion of the ray is composed of procumbent cells, but the margins of the ray, both top and bottom, have two rows of upright cells (arrows), which are as tall as or taller than they are wide.

are one to five cells wide and <1 mm high (Fig. 3–12B). Rays in hardwoods are composed of ray parenchyma cells that are either procumbent or upright. As the name implies, procumbent ray cells are horizontal and are similar in shape and size to the softwood ray parenchyma cells (Fig. 3–12C). Upright ray cells have their long axis oriented axially (Fig. 3–12D). Upright ray cells are generally shorter than procumbent cells are long, and sometimes they are nearly square. Rays that have only one type of ray cell, typically only procumbent cells, are called homocellular rays. Those that have procumbent and upright cells are called heterocellular rays. The number of rows of upright ray cells, when present, varies from one to many and can be diagnostic in wood identification.

The great diversity of hardwood anatomy is treated in many sources throughout the literature (Metcalf and Chalk 1950, 1979, 1987; Panshin and deZeeuw 1980; IAWA 1989; Gregory 1994; Cutler and Gregory 1998; Dickison 2000; Carlquist 2001).

Wood Technology

Though briefly discussing each kind of cell in isolation is necessary, the beauty and complexity of wood are found in the interrelationship between many cells at a much larger scale. The macroscopic properties of wood such as density, hardness, bending strength, and others are properties derived

from the cells that make up the wood. Such larger-scale properties are based on chemical and anatomical details of wood structure (Panshin and deZeeuw 1980).

Moisture Relations

The cell wall is largely made up of cellulose and hemicellulose, and the hydroxyl groups on these chemicals make the cell wall hygroscopic. Lignin, the agent cementing cells together, is a comparatively hydrophobic molecule. This means that the cell walls in wood have a great affinity for water, but the ability of the walls to take up water is limited in part by the presence of lignin. Water in wood has a strong effect on wood properties, and wood–water relations greatly affect the industrial use of wood in wood products. Additional information regarding dimensional changes of wood with changing moisture content can be found in Chapters 4 and 13.

Density

Density (or specific gravity) is one of the most important physical properties of wood (Desch and Dinwoodie 1996, Bowyer and others 2003). Density is the weight or mass of wood divided by the volume of the specimen at a given moisture content. Thus, units for density are typically expressed as pounds per cubic foot (lb ft^{-3}) or kilograms per cubic meter (kg m^{-3}). When density values are reported in the literature, the moisture content of the wood must also be given. Specific gravity is the density of the sample normalized to the density of water. (This topic is addressed in greater detail in Chap. 4, including a detailed explanation of wood specific gravity.)

Wood structure determines wood density; in softwoods where latewood is abundant (Fig. 3–3D) in proportion to earlywood, density is higher (for example, 0.59 specific gravity in longleaf pine, *Pinus palustris*). The reverse is true when there is much more earlywood than latewood (Fig. 3–5B) (for example, 0.35 specific gravity in eastern white pine, *Pinus strobus*). To say it another way, density increases as the proportion of cells with thick cell walls increases. In hardwoods, density is dependent not only on fiber wall thickness, but also on the amount of void space occupied by vessels and parenchyma. In balsa, vessels are large (typically $>250\ \mu\text{m}$ in tangential diameter) and there is an abundance of axial and ray parenchyma. Fibers that are present are thin walled, and the specific gravity may be <0.20 . In dense woods, the fibers are thick walled, lumina are virtually absent, and fibers are abundant in relation to vessels and parenchyma. Some tropical hardwoods have specific gravities >1.0 . In all woods, density is related to the proportion of the volume of cell wall material to the volume of lumina of those cells in a given bulk volume.

Juvenile Wood and Reaction Wood

Two key examples of the biology of the tree affecting the quality of wood can be seen in the formation of juvenile wood and reaction wood. They are grouped together because they share several common cellular, chemical, and tree physiological characteristics, and each may or may not be present in a certain piece of wood.

Juvenile wood is the first-formed wood of the young tree—the rings closest to the pith (Fig. 3–3A, bottom). Juvenile wood in softwoods is in part characterized by the production of axial tracheids that have a higher microfibril angle in the S_2 wall layer (Larson and others 2001). A higher microfibril angle in the S_2 is correlated with drastic longitudinal shrinkage of the cells when the wood is dried for human use, resulting in a piece of wood that has a tendency to warp, cup, and check. The morphology of the cells themselves is often altered so that the cells, instead of being long and straight, are often shorter and angled, twisted, or bent. The precise functions of juvenile wood in the living tree are not fully understood but are thought to confer little-understood mechanical advantages.

Reaction wood is similar to juvenile wood in several respects but is formed by the tree for different reasons. Most any tree of any age will form reaction wood when the woody organ (whether a twig, branch, or the trunk) is deflected from the vertical by more than one or two degrees. This means that all non-vertical branches form considerable quantities of reaction wood. The type of reaction wood formed by a tree differs in softwoods and hardwoods. In softwoods, the reaction wood is formed on the underside of the leaning organ and is called compression wood (Fig. 3–13A) (Timmel 1986). In hardwoods, the reaction wood forms on the top side of the leaning organ and is called tension wood (Fig. 3–13B) (Desch and Dinwoodie 1996, Bowyer and others 2003). As mentioned above, the various features of juvenile wood and reaction wood are similar. In compression wood, the tracheids are shorter, misshapen cells with a large S_2 microfibril angle, a high degree of longitudinal shrinkage, and high lignin content (Timmel 1986). They also take on a distinctly rounded outline (Fig. 3–13C). In tension wood, the fibers fail to form a proper secondary wall and instead form a highly cellulosic wall layer called the G layer, or gelatinous layer (Fig. 3–13D).

Appearance of Wood as Sawn Lumber

Color and Luster

As mentioned previously when discussing heartwood and sapwood, the sapwood color of most species is in the white

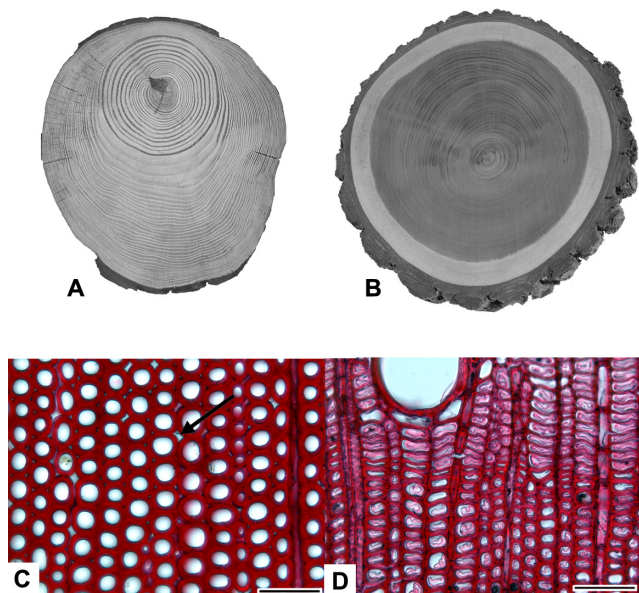


Figure 3–13. Macroscopic and microscopic views of reaction wood in a softwood and a hardwood. A, compression wood in *Pinus* sp.; note that the pith is not in the center of the trunk, and the growth rings are much wider in the compression wood zone. B, tension wood in *Juglans nigra*; the pith is nearly centered in the trunk, but the growth rings are wider in the tension wood zone. C, transverse section of compression wood in *Picea engelmannii*; the tracheids are thick-walled and round in outline, giving rise to prominent intercellular spaces in the cell corners (arrow). D, tension wood fibers showing prominent gelatinous layers in *Croton gossypifolius*; the gelatinous layers in the fibers are most pronounced across the top of the image on either side of and just below the vessel; the fibers in the lower half of the image show thinner gelatinous layers. Scale bars = 50 μ m.

range. The color of heartwood depends on the presence, characteristics, and concentrations of extractives in the wood. The heartwood color of a given species can vary greatly, depending on growth history and health of the tree, genetic differences between trees, and other factors. Heartwood formation, particularly as it relates to final timber color, is not fully understood. Description of color in wood is highly dependent on the particular author; assertions that a particular wood is exactly one color are spurious.

Luster is a somewhat subjective characteristic of some woods and refers to the way in which light reflecting from the wood appears to penetrate into and then shine from the surface of the board. Genuine mahogany (*Swietenia* sp.) is one of the better-known woods with distinct luster.

Grain and Texture

The terms grain and texture are commonly used rather loosely in connection with wood. Grain is often used in reference to the relative sizes and distributions of cells, as in fine grain and coarse grain; this use of grain is roughly synonymous with texture (below). Grain is also used to

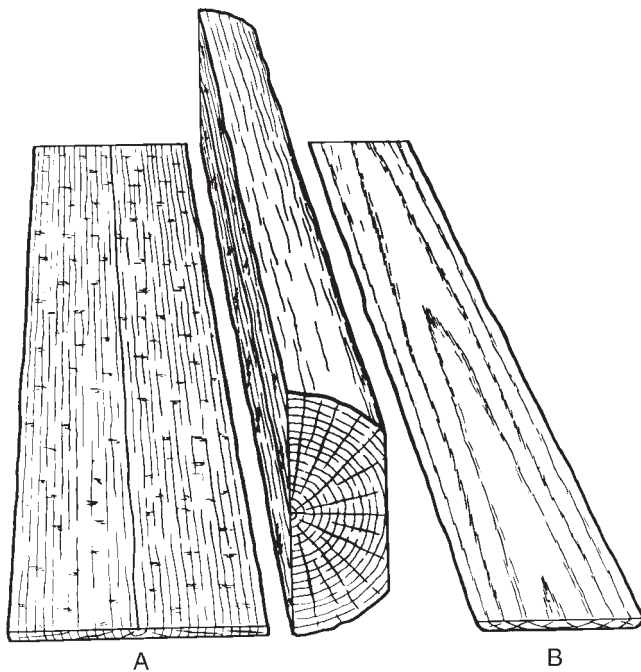
indicate the orientation of the cells of the axial system (“fiber direction”), as in “along the grain,” straight grain, spiral grain, and interlocked grain, and this use of the term is preferred. Grain, as a synonym for fiber direction, is discussed in detail relative to mechanical properties in Chapter 5. Wood finishers refer to wood as open grained and close (or closed) grained, which are terms reflecting the relative size of the cells and the need for fillers prior to finishing. Texture is another word used to describe a macroscopic summary of the relative sizes of cells in wood. Fine-textured woods have uniform structure with typically small cells. Coarse-textured woods generally have structure with concentrations of large diameter cells (such as the earlywood in ring porous hardwoods, Fig. 3–5F) that produce areas of clearly different appearance to the naked eye. Even-textured woods may have uniformly large or small cells, but their distribution is not concentrated in particular areas, such as in diffuse porous hardwoods. Even if terms used for describing the appearance of wood were universally agreed upon (and they are not), variations in wood structure within a tree, between trees of the same species, and between two or more species would defy complete characterization using these terms. For this reason, when discussing wood, reference should be made to specific properties when possible. At a minimum, it is desirable to ensure that the same operating definitions of terms like “open grained” or “coarse textured” are used by all parties.

Plainsawn and Quartersawn

When boards are cut from logs, a sawyer makes decisions about how to orient to the log with respect to the saw blade and in this way produces boards with different cuts. Specific nomenclature for these angles of cutting exists but is not precisely the same for hardwood lumber and softwood lumber; this unfortunate fact results in a parallel set of terms for hardwoods and softwoods. The sawyer can cut boards from a log in two distinct ways: (a) tangential to the growth rings, producing flatsawn or plainsawn lumber in hardwoods and flatsawn or slash-grained lumber in softwoods, and (b) radially from the pith or parallel to the rays, producing quartersawn lumber in hardwoods and edge-grained or vertical-grained lumber in softwoods (Fig. 3–14). In plainsawn boards, the surfaces next to the edges are often far from tangential to the rings, and quartersawn lumber is not usually cut strictly parallel with the rays. In commercial practice, lumber with rings at angles of 0° to 45° to the wide surface is called plainsawn and lumber with rings at angles of 45° to 90° to the wide surface is called quartersawn. Hardwood lumber in which annual rings form angles of 30° to 60° to the wide face is sometimes called bastard sawn. For many purposes, either plainsawn or quartersawn lumber is satisfactory, but each type has certain advantages that can be important for a particular use. Some advantages of plainsawn and quartersawn lumber are given in Table 3–1.

Table 3–1. Some advantages of plainsawn and quartersawn lumber

Plainsawn	Quartersawn
Shrinks and swells less in thickness	Shrinks and swells less in width
Surface appearance less affected by round or oval knots compared to effect of spike knots in quartersawn boards; boards with round or oval knots not as weak as boards with spike knots	Cups, surface-checks, and splits less in seasoning and in use
Shakes and pitch pockets, when present, extend through fewer boards	Raised grain caused by separation in annual rings does not become as pronounced
Figure patterns resulting from annual rings and some other types of figure brought out more conspicuously	Figure patterns resulting from pronounced rays, interlocked grain, and wavy grain are brought out more conspicuously
Is less susceptible to collapse in drying	Does not allow liquids to pass through readily in some species
Costs less because it is easy to obtain	Holds paint better in some species
	Sapwood appears in boards at edges and its width is limited by the width of the log

**Figure 3–14. Quartersawn (A) and plainsawn (B) boards cut from a log.**

Slope of Grain: Straight, Diagonal, Spiral, and Interlocked Grain

The slope of grain of a board is determined by the way in which the sawyer cuts the board and the basic biological characteristics of the log from which the board is cut, but it is distinct from the type of cut (plainsawn or quartersawn). In an idealized saw log, the cells of the axial system in the wood are parallel to the length of the log; they run straight up and down the trunk. When this is the case, the grain angle of a board cut from the log is wholly a function of how the sawyer cuts the board. It is assumed that when a board is cut from the log, the long edge of the board will be parallel (or nearly so) with the cells of the axial system, or parallel with the grain (middle of Fig. 3–3A, 3–3F). Boards prepared in this way are straight-grained boards.

When the long edge of the board is not parallel with the grain, the board has what is called diagonal grain (middle of Fig. 3–3A, 3–3F). Boards with diagonal grain will show atypical shrinking and swelling with changes in moisture content (Chap. 4), and altered mechanical properties (Chap. 5) depending on the slope of grain. The degree to which the long edge of a board is not parallel to the grain is referred to as slope of grain and is addressed in Chapter 5.

Not all logs have grain that runs perfectly straight up and down the length of the log. In some logs, the grain runs in a helical manner up the trunk, like the stripes on a barber pole or the lines on a candy cane. Such logs produce boards with spiral grain, and there is no way to cut long boards from such a log to produce straight-grained lumber. In other logs, the angle of helical growth of the wood cells will change over time, such that the grain may curve in a right-handed helix (e.g., 5°) for a few years and then over the course of a few years change to a left-handed 5° helix, and so on over the life of the tree. This growth produces wood with interlocked grain. There is no way to saw a board from such a log to produce uniformly straight grain. Therefore, a straight-grained board can be cut only from a straight-grained log; a log with spiral or interlocked grain can never produce truly straight-grained lumber, regardless of the skill of the sawyer.

Knots

Knots are remnants of branches in the tree appearing in a board. In a flatwsawn board, knots appear as round and typically brown pieces of wood perpendicular to the grain of the board. In a quartersawn board, knots can be cut along their length and are referred to as spike knots. Independent of the cut of the board, knots occur in two basic varieties: intergrown knots and encased knots. These terms refer to the continuity, or lack thereof, of stem wood with wood of the branch. If the branch was alive at the time when the growth rings making up the board were formed, the wood of the trunk of the tree and that branch is continuous; the growth rings continue uninterrupted out along the branch,

forming an intergrown knot. If the branch was dead at the time when growth rings of the board were formed, the stem wood curves around the branch without continuing up the branch, giving rise to a knot that is not continuous with the stem wood; this produces an encased knot. With intergrown knots, the grain angle of the trunk wood in the vicinity of the knot is typically more disturbed than in encased knots, and this influences wood properties (Chap. 5). Encased knots generally disturb the grain angle less than intergrown knots.

Decorative Features

The decorative value of wood depends upon its color, figure, luster, and the way in which it bleaches or takes fillers, stains, and transparent finishes. In addition to quantifiable or explicable characteristics, decorative value is also determined by the individual preferences of the end user.

The structure of a given wood, in conjunction with how the final wood product was cut from a log, gives rise to the majority of the patterns seen in wood. A general term for the pattern of wood is figure, which can refer to mundane features, such as the appearance of growth rings in a plainsawn board or the appearance of ray fleck on a quartersawn board, or more exotic patterns determined by anomalous growth, such as birdseye, wavy grain, or wood burls.

Wood Identification

The identification of wood can be of critical importance to the primary and secondary wood using industry, government agencies, museums, law enforcement, and scientists in the fields of botany, ecology, anthropology, forestry, and wood technology. Wood identification is the recognition of characteristic cell patterns and wood features and is generally accurate only to the generic level. Because woods of different species from the same genus often have different properties and perform differently under various conditions, serious problems can develop if species or genera are mixed during the manufacturing process and in use. Because foreign woods are imported to the U.S. market, both buyers and sellers must have access to correct identifications and information about properties and uses.

Lumber graders, furniture workers, those working in the industry, and hobbyists often identify wood without laboratory tools. Features often used are color, odor, grain patterns, density, and hardness. With experience, these features can be used to identify many different woods, but the accuracy of the identification is dependent on the experience of the person and the quality of the unknown wood. If the unknown wood specimen is atypical, decayed, or small, often the identification is incorrect. Examining woods, especially hardwoods, with a 10 to 20 hand lens, greatly improves the accuracy of the identification (Panshin and deZeeuw 1980, Hoadley 1990, Brunner and others

1994). Some foresters and wood technologists armed with a hand lens and sharp knife can accurately identify lumber in the field. They make a cut on the transverse surface and examine all patterns to make an identification.

Interest in forensic identification of wood has exploded over the past decade, especially in the context of endangered species protection and combatting illegal logging and fraud (Wiedenhoeft and others 2019). International prescriptive manuals (UNODC 2016), scholarly publications (Dormontt and others 2015), and international expert consortia (Schmitz and others 2019) have surveyed and updated the state of the science in wood identification, so we do not treat it in detail here. The primary techniques are hand lens identification (for example, Ruffinatto and others 2015, Wiedenhoeft 2011), computer-vision-based identification (Rosa and others 2017; Ravindran and others 2018, 2019, 2020; Ravindran and Wiedenhoeft 2020), traditional light microscopic identification (Wheeler and Baas 1998, Miles 1978, Schweingruber 1978, Core and others 1979, Gregory 1980, Ilic 1991, Miller and Détienne 2001) (also see North Carolina State University InsideWood database at <http://insidewood.lib.ncsu.edu/>), near-infrared spectroscopic approaches (Pastore and others 2010, Bergo and others 2016, Snel and others 2018), mass spectroscopic techniques (Espinoza and others 2014), and DNA-based approaches (Yu and others 2017, Jiao and others 2018, Hassold and others 2016, He and others 2019). The principal conclusion about wood identification in the context of the range of available techniques is that by cooperatively applying the relevant techniques in a sensible sequence, we can best take advantage of the strengths and minimize the weaknesses of each approach (Lowe and others 2016).

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Wood Handbook

Wood as an Engineering Material

Abstract

Summarizes information on wood as an engineering material. Presents properties of wood and wood-based products of particular concern to the architect and engineer. Includes discussion of designing with wood and wood-based products along with some pertinent uses.

Keywords: wood structure, physical properties (wood), mechanical properties (wood), lumber, wood-based composites, plywood, panel products, design, fastenings, wood moisture, drying, gluing, fire resistance, finishing, decay, preservation, wood-based products, heat sterilization, sustainable use

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