
2 Structure and Function of Wood

Alex C. Wiedenhoef

CONTENTS

2.1	Introduction	9
2.2	The Tree.....	10
2.3	Softwoods and Hardwoods	11
2.4	Sapwood and Heartwood	11
2.5	Axial and Radial Systems	13
2.6	Planes of Section.....	13
2.7	Vascular Cambium	15
2.8	Growth Rings.....	16
2.9	Cells in Wood	17
2.10	Cell Walls	18
2.11	Pits	19
2.12	Microscopic Structure of Softwoods and Hardwoods	21
2.12.1	Softwoods.....	21
2.12.1.1	Tracheids.....	21
2.12.1.2	Axial Parenchyma and Resin Canal Complexes	22
2.12.1.3	Rays.....	23
2.12.2	Hardwoods	23
2.12.2.1	Vessels.....	23
2.12.2.2	Fibers.....	24
2.12.2.3	Axial Parenchyma	24
2.12.2.4	Rays.....	25
2.13	Wood Technology	26
2.14	Moisture Relations	26
2.15	Density	27
2.16	Juvenile Wood and Reaction Wood	28
2.17	Wood Identification	28
	References	30

2.1 INTRODUCTION

Wood is a complex biological structure, a composite of many cell types and chemistries acting together to serve the needs of living plant. Attempting to understand wood in the context of wood technology, we have often overlooked the 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 and synthesis of biochemicals. There is no property of wood—physical, mechanical, chemical, biological, or technological—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 them. These three functions have influenced the evolution of approximately 20,000 different species of woody plants, 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 a composite material itself, and as a component of composite wood products (Hoadley 2000, Barnett and Jeronimidis 2003). 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 spatial scales, and those parts related to the form and function of the plant. 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, and to access directly the primary literature in wood structure.

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.

2.2 THE TREE

A 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 the storage of biochemicals. The shoot is made up of the trunk or bole, branches, and leaves (Raven et al. 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 (Figure 2.1).

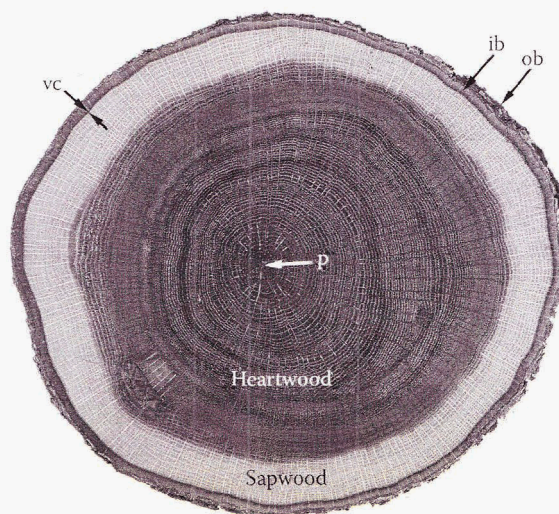


FIGURE 2.1 Macroscopic view of a transverse section of a *Quercus alba* trunk. Beginning at the outside of the tree is the outer bark (ob). Next is the inner bark (ib) and then the vascular cambium (vc), which is too narrow to be seen at this magnification. Interior toward the vascular cambium is the 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.

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 produced by photosynthesis (photosynthate) are translocated within the tree. The vascular cambium is the layer between the 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 nonconductive heartwood found as a core of darker-colored wood in the middle of most trees. The pith, at the center of the trunk, is the remnant of early growth before wood was formed.

2.3 SOFTWOODS AND HARDWOODS

Despite what one might think based on the names, 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. 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 most important distinction between softwoods and hardwoods is that hardwoods have a characteristic type of cell called a vessel element (or pore) which softwoods lack (Figure 2.2). An important cellular similarity between softwoods and hardwoods is most cells are dead at maturity, even in the sapwood. Cells alive at functional maturity in wood are typically limited to the sapwood, are known as parenchyma cells, and can be found in both softwoods and hardwoods.

2.4 SAPWOOD AND HEARTWOOD

In both softwoods and hardwoods, the wood in the trunk of the tree is typically divided into two functionally distinct zones, sapwood and heartwood. Sapwood is located adjacent to the bark and represents the actively conducting portion of the stem, in which parenchyma cells are still alive and metabolically active. Heartwood is found to the interior of the sapwood, is decommissioned sapwood, and in many species, can be easily distinguished thanks to its darker color (Figure 2.1).

In the living tree, sapwood is responsible not only for the conduction of sap but also for storage and synthesis of biochemicals. An important storage function is the long-term storage of photosynthate. Carbon necessary 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 storage forms of photosynthate are starch and lipids. Starch grains are stored in parenchyma cells and can be easily seen with a microscope (Figure 2.2a). 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, making the wood commercially unusable (Chudnoff 1984). In southern yellow pines of the United States, and in other softwood timbers, a high starch content encourages growth of sap-stain fungi (Figure 2.2b) that, though they do not affect the strength of the wood, can nonetheless decrease the lumber value for aesthetic reasons (Simpson 1991).

Parenchyma cells of the sapwood are also the agents of heartwood formation, as biochemicals must be actively synthesized and translocated by living cells (Hillis 1996). Heartwood functions in long-term storage of biochemicals of many varieties depending on the species in question, and these chemicals are what impart color to the heartwood. Heartwood chemicals are known collectively as

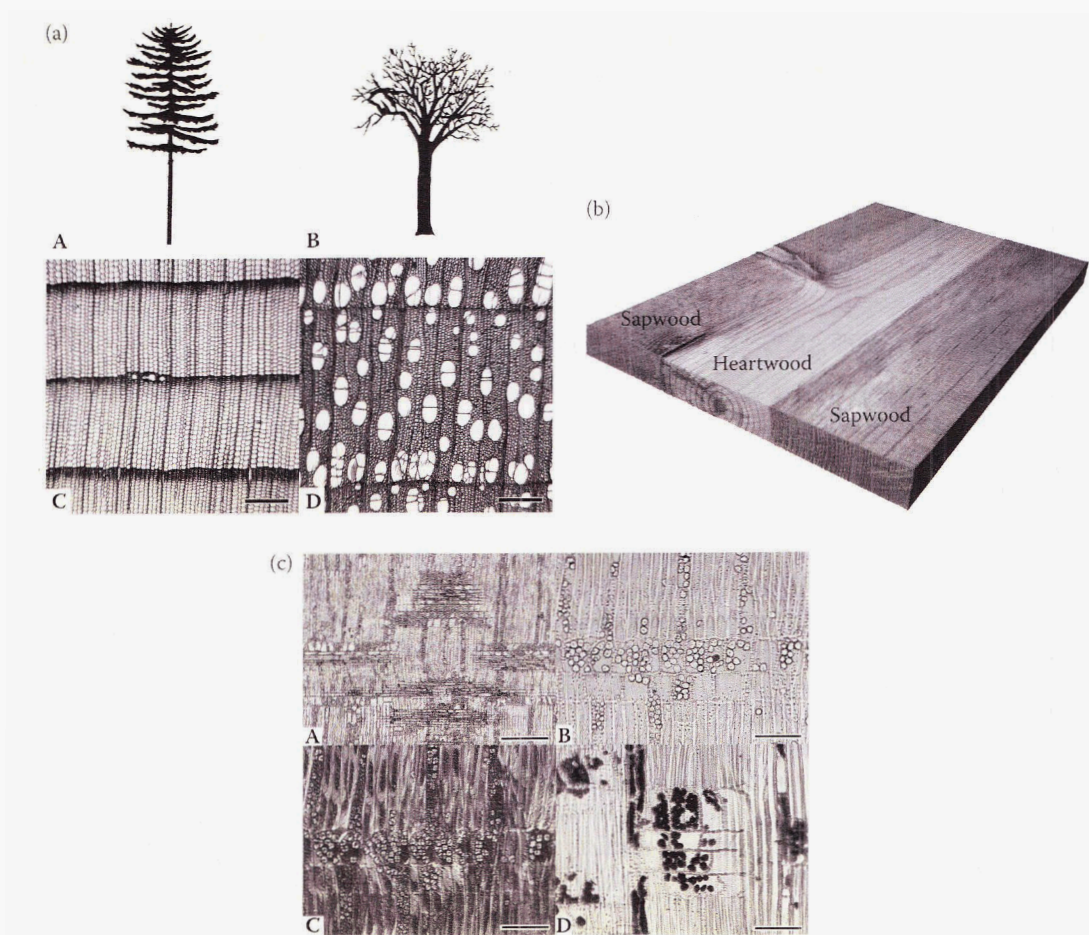


FIGURE 2.2 (a) (A) The general form of a generic softwood tree. (B) The general form of a generic hardwood tree. (C) Transverse section of *Pseudotsuga menziesii*, a typical softwood; the 13 round white spaces are resin canals. (D) Transverse section of *Betula Allegheniensis*, a typical hardwood; the many large, round white structures are vessels or pores, the characteristic feature of a hardwood. Scale bars = 780 μm . (b) Blue stain in the sapwood of a softwood. Note that the heartwood does not exhibit the darker color of the fungal stain, but the sapwood does. This is a dramatic demonstration of the storage function in wood, as the sapwood contents encourage fungal growth, and the heartwood contents prevent it. Blue stain does not alter the mechanical properties of wood, but can be considered a defect in some products. (c) Light micrographs of starch grains in the parenchyma cells of *Hevea brasiliensis*. (A) Transmitted light microscopy of unstained wood, radial section. The many small spherical objects are starch grains. (B) same as (A), but at higher magnification. Individual starch grains can easily be resolved. (C) same image as (B), but illuminated with polarized light. The cell walls and starch grains are birefringent. The cross-shaped pattern of light in the starch grains are characteristic of amylose. (D) Another radial section, stained with I_2KI ; the starch grains are dark brown or purple and contrast strongly with the background. Scale bars = (A) 390 μm , (B)-(D) 98 μm .

extractives because they are not structural components of the wood itself, and can be extracted from the wood using solvents (Hillis 1987). 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 accumulated by parenchyma cells either

at a distinct heartwood–sapwood boundary (Type 1 or *Robinia*-type heartwood formation) or in the aging sapwood tissue (Type 2 or *Juglans*-type heartwood formation) (Magel 2000) 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 (Hillis 1987). 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.

2.5 AXIAL AND RADIAL SYSTEMS

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 continuous from root to twig. The cells of wood are typically many times longer than wide and are specifically oriented in two separate systems: 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 sap 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.

2.6 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 wood should 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 exposed when a tree is cut down. Looking down at the stump one sees the transverse section (as in Figure 2.3h); 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 (Figure 2.3a, top), and is parallel to the axial system, thus 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,

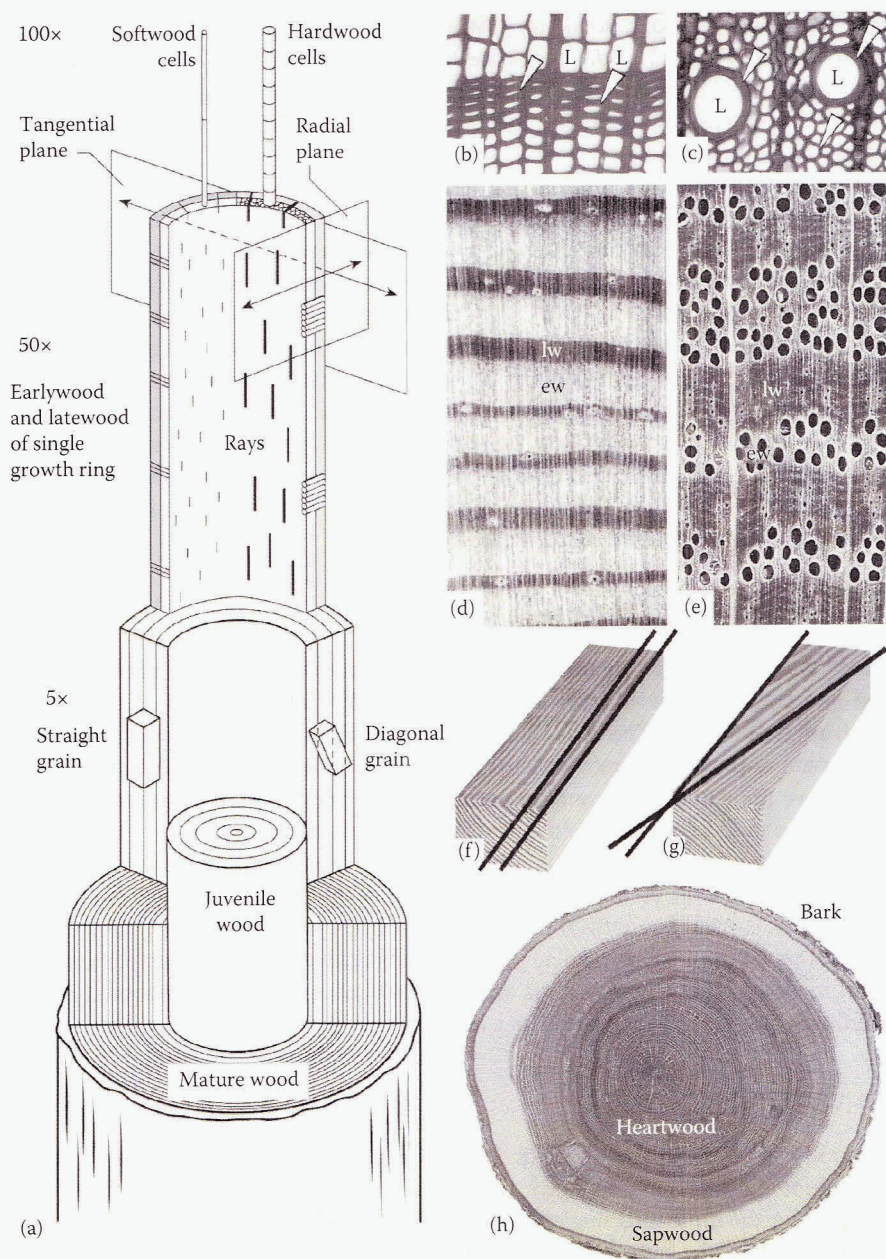


FIGURE 2.3 (a) Illustration of a cut-away tree at various magnifications, corresponding roughly with the images to its right; at the top, at an approximate magnification of 100 $\times$, a softwood cell and several hardwood cells are illustrated, to give a sense of scale between the two; one tier lower, 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 early wood (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.

and extending up and down the length of the cylinder. In a practical sense, it is the face or plane exposed when a log is split exactly from pith to bark. It does not provide any information about features that vary in the tangential direction.

The tangential plane is at a right angle to the radial plane (Figure 2.3a, top). Geometrically, it is parallel to any tangential 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.

2.7 VASCULAR CAMBIUM

The axial and radial systems and their component cells are derived from the vascular cambium, which is a thin layer of cells between the inner bark and the wood (Figures 3.1, 3.4). It 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; this is accomplished by cell division as well. Q3

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. In most cases, the radial system in the wood is continuous into the inner bark, through the vascular cambium (Sauter 2000). In this way wood, the water-conducting tissue, remains connected to the inner bark, the photosynthate-conducting tissue. They are interdependent tissues because 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. The vascular cambium is an integral feature that not only gives rise to these tissue systems but also links them so that they may function in the living tree.

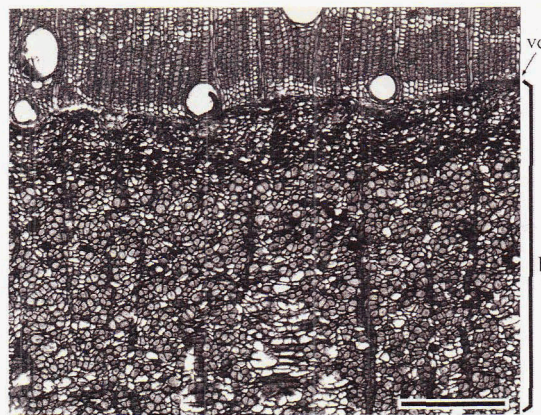


FIGURE 2.4 Light microscopic view of the vascular cambium. Transverse section showing vascular cambium (vc) and bark (b) in *Croton macrobothrys*. The tissue above the vascular cambium is wood. Scale bar = 390 μm .

2.8 GROWTH RINGS

Wood is produced by the vascular cambium, one layer of cell division 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 cohorts 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 (Figure 2.3d,e). Springwood and summerwood were terms formerly used to refer earlywood and latewood, respectively, but their use is no longer recommended (IAWA 1989).

In parts of the world with annual seasonality in temperature and/or precipitation, or in trees with annual cycles in growth, the growth increments are often called annual rings. In parts of the world without such seasonality, and in many evergreen plants (e.g., many trees in the tropics), growth rings are not distinct in the wood. The absence of obvious growth increments does not necessarily imply continuous cambial growth; research has uncovered several characteristics whereby wood structure can be correlated with seasonality changes in some tropical species (Worbes 1995, 1999; Callado et al. 2001).

Woods that form distinct growth rings show one of 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 earlywood to latewood; and a sudden and distinct change in the inner diameter of the conducting elements across the ring (Figure 2.5). These patterns appear in both softwoods and hardwoods but differ in each because of the distinct anatomical differences between the two.

Softwoods (nonporous woods, woods without vessels) can exhibit any of these three general patterns. Some softwoods such as western red-cedar (*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 (Figure 2.5b). Other woods undergo an abrupt transition

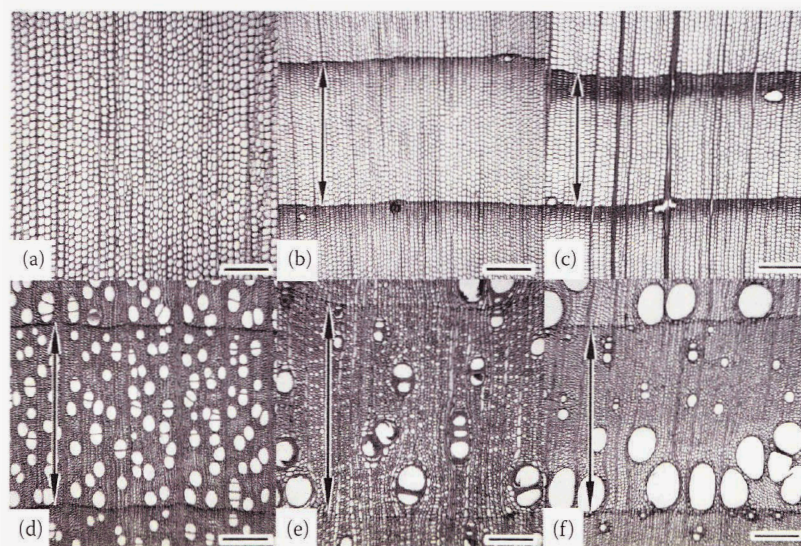


FIGURE 2.5 Transverse sections of woods showing types of growth rings. Arrows delimit growth rings, when present. (a)–(c) Softwoods. (a) No transition within the growth ring (growth ring absent) in *Podocarpus imbricata*. (b) Gradual transition from earlywood to latewood in *Picea glauca*. (c) Abrupt transition from earlywood to latewood in *Pseudotsuga menziesii 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 μ m.

from earlywood to latewood, such as southern yellow pine (*Pinus*), larch (*Larix*), Douglas-fir (*Pseudotsuga menziesii*), baldcypress (*Taxodium distichum*), and redwood (*Sequoia sempervirens*) (Figure 2.5c). 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 (Figure 2.5a). Some authors report this state as growth rings being absent or only barely evident (Phillips 1948, Kukachka 1960).

Hardwoods (porous woods, woods with vessels) also exhibit the three patterns of change within a growth ring, and this is referred to as porosity. In diffuse-porous woods, vessels either do not markedly differ in size and distribution from earlywood to latewood, or the change in size and distribution is gradual and no clear distinction between earlywood and latewood can be found (Figure 2.5d). Maple (*Acer*), birch (*Betula*), aspen/cottonwood (*Populus*), and yellow-poplar (*Liriodendron tulipifera*) are 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 of 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*), and northern red oak (*Quercus rubra*) (Figure 2.5f).

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 (Figure 2.5e). Black walnut (*Juglans nigra*) is a temperate-zone semi-ring-porous wood. Although 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, Schweingruber 2007).

2.9 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 nonliving, 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 (Raven et al. 1999, Dickison 2000, Evert 2006).

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, and it 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 (Figure 2.3b,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, a fact that will be discussed later when speaking of wood technology.

2.10 CELL WALLS

Cell walls in wood impart the majority of the 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 (Figure 2.6). In each region, the cell wall has three major components: cellulose microfibrils (with characteristic distributions and organization), hemicelluloses, and a matrix or 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

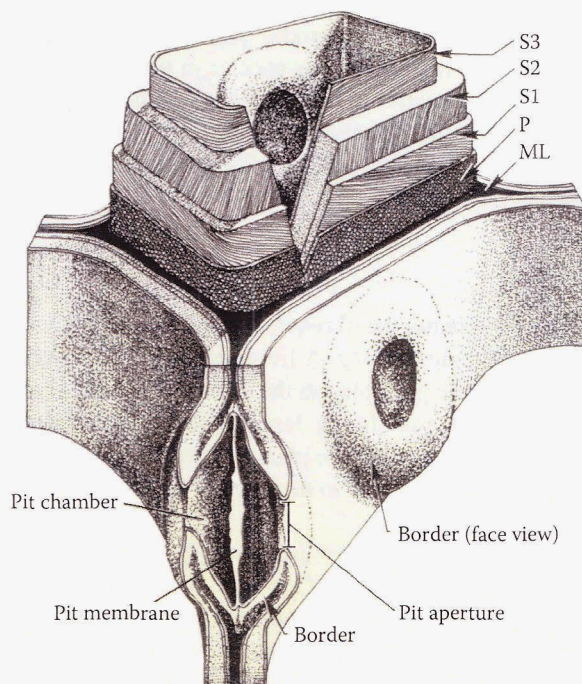


FIGURE 2.6 Cut-away drawing of the cell wall, including the structural details of a bordered pit. The various layers of the cell wall are detailed at the top of the drawing, beginning with the middle lamella (ML). The next layer is the primary wall (P), and on the surface of this layer the random orientation 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.

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 (Figure 2.6). This layer is the outermost layer of the cell wall continuum and in a nonwoody organ, is rich in pectin. In the case of wood, the middle lamella is lignified.

The layer interior to the middle lamella is the primary wall (Figure 2.6). The primary wall is characterized by a largely random orientation of cellulose microfibrils; like thin threads wound 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 of 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 (Kerr and Bailey 1934). 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 nonwoody plants or plant parts), is the secondary cell wall. The secondary cell wall is composed of three layers (Figure 2.6), distinguished mainly on the basis of the different angle that the helically oriented microfibrils make with the long axis of the cell (Frey-Wyssling 1975, Abe and Funada 2005). As cell wall layers are deposited, the lumen volume is progressively reduced. The first-formed secondary cell wall layer is the S_1 (Figure 2.6), which is adjacent to the compound middle lamella (or technically, the primary wall). This layer is thin and characterized by a large microfibril angle. That is to say, the angle between the mean microfibril direction and the long axis of the cell is large ($50\text{--}70^\circ$).

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 (Figure 2.6). As the thickest secondary cell wall layer 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 ($5\text{--}30^\circ$). 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 et al. 1998, Sheng-zuo et al. 2006), and this is an area of active research.

Interior to the S_2 layer is the relatively thin S_3 layer (Figure 2.6). The microfibril angle of the S_3 layer is relatively high and similar to the S_1 ($>70^\circ$). The S_3 layer has the lowest percentage of lignin of any of the secondary wall layers, which is likely in part related to the movement of sap within the tree. 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 (e.g., Kozlowski and Pallardy 1997, Taiz Q4 and Zeiger 2010).

2.11 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 intercellular communication and transport 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 (Figure 2.6) is the thin semi-porous remnant of the primary wall; it is a carbohydrate, a critical fact for biologists accustomed to thinking of phospholipid cell or organelle membranes. The pit aperture is the opening or hole leading into the open area of the pit, which is called the pit chamber (Figure 2.6). 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 et al. 1998, Rijkaert et al. 2001).

Pits of predictable types occur between different types of cells. For 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 (Raven et al. 1999, Evert 2006).

Q5 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 overarched by the pit chamber is called the border (Figures 3.6, 3.7a,d). When seen in face view, bordered pits often are round in appearance and look somewhat like a doughnut (Figure 2.6). 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 (Figure 2.7a,d). In this case, the long stems of the V represent the borders, the secondary walls that are overarched by 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) has great importance in the field of wood preservation and can affect wood finishing and adhesive bonding.

Simple pits lack any sort of border (Figure 2.7c,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 (Figure 2.7b,e). In the living tree, these pits are of great importance because they represent the communication between conducting cells and biochemically active parenchyma cells.

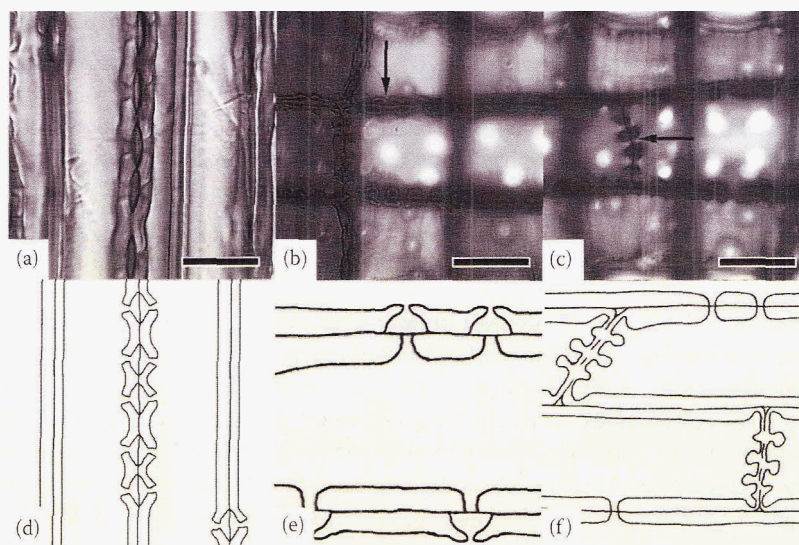


FIGURE 2.7 Light micrographs and sketches of the three types of pits. (a,d) Longitudinal section of bordered pits in *Xanthocyparis vietnamensis*; the pits look like a vertical stack of thick-walled letter 'v's (b,e) Half-bordered pits in *Pseudotsuga menziesii*; the arrow shows one half bordered pit. (c,f) Simple pits on an end wall in *Pseudotsuga menziesii*; the arrow indicates one of the simple pits on the endwall. Scale bars = 20 μm .

2.12 MICROSCOPIC STRUCTURE OF SOFTWOODS AND HARDWOODS

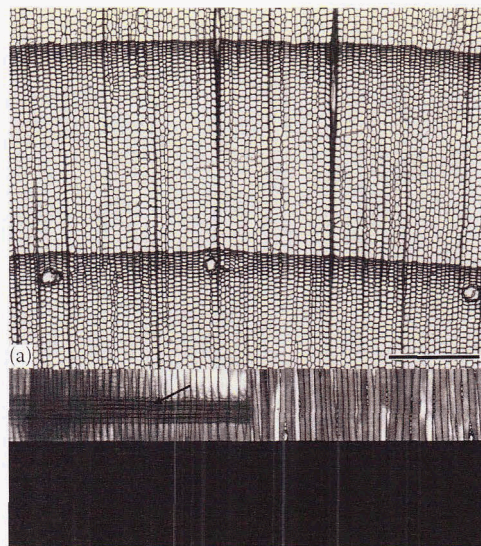
As discussed previously, the fundamental differences between woods are founded on the types, sizes, proportions, pits, and arrangements of different cells that comprise the wood. These fine details of structure can affect the use of a wood.

2.12.1 SOFTWOODS

The structure of a typical softwood is relatively simple. The axial or vertical system is composed mostly of axial tracheids, and the radial or horizontal system is made of rays, which are composed mostly of ray parenchyma cells.

2.12.1.1 Tracheids

Tracheids are long cells, often more than 100 times longer (1–10 mm) than wide, and comprise over 90% of the volume of softwoods. They serve both the conductive and mechanical needs of softwoods. On the transverse view (Figure 2.8a), tracheids appear as square or slightly rectangular cells in radial rows. Within one growth ring they are typically thin-walled in the earlywood and thick-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 20–30% of their length. Water flow thus must take a slightly zigzag path as it goes from one cell to the next 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



Q13

FIGURE 2.8 Microscopic structure of *Picea glauca*, a typical softwood. (a) Transverse section, scale bar = 390 μm ; 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 μm . (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 μm .

of hardwoods. Detailed treatments of the structure of wood in relation to its conductive functions can be found in the literature (Zimmermann 1983, Pallardy 2008).

2.12.1.2 Axial Parenchyma and Resin Canal Complexes

Another cell type 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 their lumina. 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 rarely, if ever, makes up even 1% of the volume of a block of wood. Axial parenchyma strands are 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 (Figure 2.9) and radially (Figure 2.9c). 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 (Figures 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.

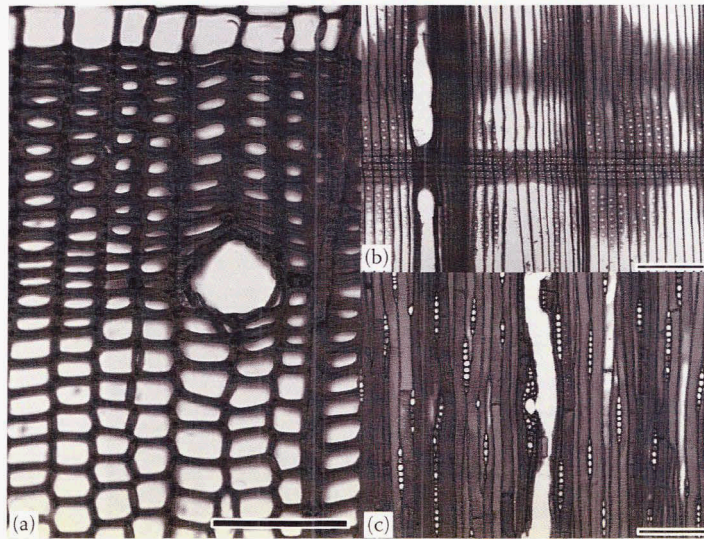


FIGURE 2.9 Resin canal complexes in *Pseudotsuga menziesii*. (a) Transverse section showing a single axial resin canal complex. In this view the tangential and radial diameters of the canal can be measured accurately. Scale bar = 100 μm . (b) Radial section showing an axial resin canal complex embedded 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 .

2.12.1.3 Rays

The other cells in Figure 3.8a that are barely visible and appear as dark lines running in a top-to-bottom direction are ray parenchyma cells. Ray parenchyma cells are rectangular prisms or brick-shaped cells. Typically they are approximately 15–20 µm high × 10–20 µm wide × 150–250 µm long in the radial or horizontal direction (Figure 2.8b). 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 or section (Figure 2.8b), the rays look like brick walls and the ray parenchyma cells are sometimes filled with dark-colored substances. In tangential section (Figure 2.8c), the rays are stacks of ray parenchyma cells one on top of the other forming a ray 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, 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 axial and radial resin canal complexes also have ray tracheids, which are specialized tracheids that normally are situated at the margins of the rays. 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 details regarding the microscopic structure of softwoods can be found in the literature (Phillips 1948, Kukachka 1960, Panshin and deZeeuw 1980, IAWA 2004).

2.12.2 HARDWOODS

The structure of a typical hardwood is 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.

2.12.2.1 Vessels

Vessel elements are the specialized water-conducting cells of hardwoods. They are stacked one on top of another to form vessels. Where the ends of the vessel elements come in contact with one another, a hole (with no membrane; it is not a pit) is formed called a 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. 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 (Figure 2.2d).

Vessel diameters may be small (<30 µm) or quite large (>300 µm), but typically range from 50 to 200 µm. They are much shorter than tracheids and range from 100 to 1200 µm (0.1–1.2 mm). Vessels can be arranged in various patterns. As mentioned under the discussion of growth rings, if the vessels are of the same size and more or less scattered throughout the growth ring, the wood is called diffuse-porous (Figure 2.5d). If the earlywood vessels are much larger than the latewood vessels, the wood is called ring porous (Figure 2.5f). Vessels can also be arranged in a tangential or oblique arrangement, in radial arrangement, in clusters, or in many combinations of these types (IAWA 1989). In addition, individual vessels may occur alone (solitary) or in pairs or radial multiples of up to five or more vessels in a row.

Where vessel elements come in contact with each other, intervessel pits are formed. These pits are bordered, range in size from 2 to >16 µm 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.

2.12.2.2 Fibers

Fibers in hardwoods provide mechanical support to the wood. They are shorter than softwood tracheids (0.2–1.2mm), average about half the width of softwood tracheids, but are usually 2–10times longer than vessel elements of the same wood (Figure 2.10b). The thickness of the fiber cell wall is a 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 (*Tabeuia 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 vasicentric 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.

2.12.2.3 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 (Figure 2.11). 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, whereas apotracheal parenchyma is not associated with the vessels. Paratracheal parenchyma is further divided into vasicentric (surrounding the vessels, Figure 2.11a), aliform (surrounding the vessel and with wing-like extensions, Figure 2.11c), and confluent (several connecting patches of paratracheal parenchyma sometimes forming a band, Figure 2.11e). Apotracheal parenchyma is divided into diffuse (scattered), diffuse-in-aggregate (short bands, Figure 2.11b), and banded, whether at the beginning or end of the growth ring (marginal, Figure 2.11f) or within a growth ring (Figure 2.11d). Every wood has a particular pattern of axial parenchyma, which is more or less consistent from specimen to specimen, and these cell patterns are important in traditional hardwood identification.

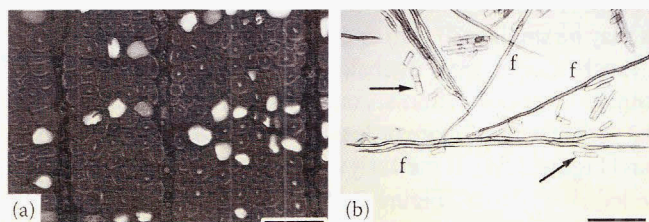


FIGURE 2.10 Fibers in *Quercus rubra*. (a) Transverse section showing thick-walled, narrow-lumined fibers; three rays are passing vertically through the photo, and there are a number of axial parenchyma cells, the thin-walled, wide-lumined cells, in the photo; scale bar = 50 μm (b) Macerated wood; there 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 .

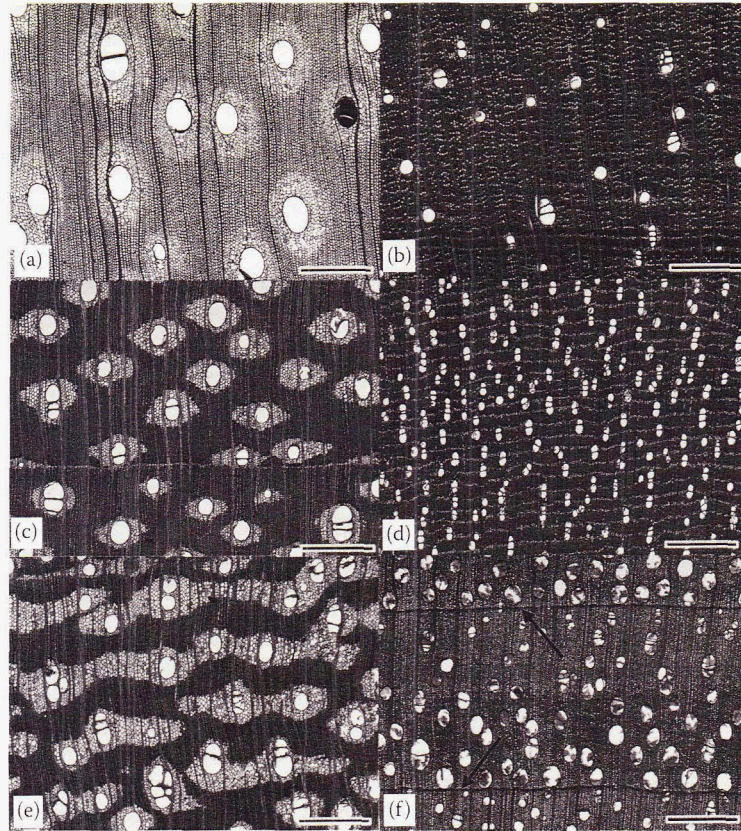


FIGURE 2.11 Transverse sections of various woods showing a range of hardwood axial parenchyma patterns. (a, c, e) Are woods with paratracheal types of parenchyma. (a) Vasicentric parenchyma in *Enterolobium maximum*; note that two vessels in the middle of the view are connected by parenchyma, which is 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, 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 .

2.12.2.4 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 more than one cell wide. In oak and hard maple, the rays are two-sized, uniseriate and more than eight cells wide (Figure 2.12a). In most species, rays are 1–5 cells wide and <1 mm high (Figure 2.12b). Rays in hardwoods are composed of ray parenchyma cells that are either procumbent or upright. As the name implies, procumbent ray cells are horizontally elongated and are similar in shape and size to softwood ray parenchyma cells (Figure 2.12c). Upright ray cells have their long axis oriented axially (Figure 2.12d). Upright ray cells are generally shorter than procumbent cells, and sometimes 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.

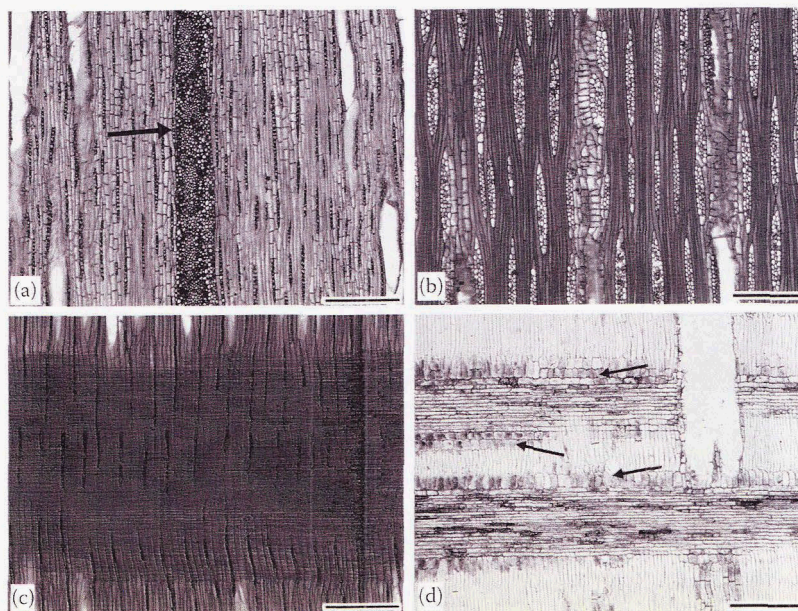


FIGURE 2.12 Rays in longitudinal sections. (a) and (b) Show tangential sections, scale bars = 300 μm . (a) *Quercus falcata* showing a wide multiseriate ray (arrow) and many uniseriate rays. (b) *Swietenia macrophylla* showing numerous rays ranging from 1 to 4 cells wide; note that in this wood the rays 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.

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, Dickinson 2000, Carlquist 2001, Schweingruber et al. 2006).

2.13 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, Barnett and Jeronimidis 2003).

2.14 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 and rigidifying the cell wall, 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. Moisture in wood has a strong effect on wood properties, and wood–water relations greatly affect the industrial use of wood in wood products.

Often it is useful to know how much water is contained in the tree or a piece of wood. This relationship is called moisture content and is the weight of water in the wood expressed as a percentage of the weight of wood with no water (oven-dry weight). Although it is somewhat oversimplified, water exists in wood in two forms, free water and bound water. Free water is the liquid water within

the lumina of the cells. Bound water is the water that is adsorbed to the cellulose and hemicellulose in the cell wall. Free water is only found when all sites for the adsorption of water in the cell wall are filled; this point is called the fiber saturation point (FSP). All water added to wood after the FSP has been reached exists as free water.

Wood of a freshly cut tree is said to be green and the moisture content of green wood can be over 100%; in such cases the mass of water in the wood is greater than the mass of the dried cells. In softwoods the moisture content of the sapwood is typically much higher than that of the heartwood, but in hardwoods, the difference may not be as great and in a few cases the heartwood has a higher moisture content than the sapwood.

When drying from the green condition to FSP (commonly reported as 25–30% moisture content for many species) only free water is lost, and thus no change in the cell-wall volumes has occurred. Once the wood is dried below the FSP, bound water is removed from the cell walls and shrinkage of the wood begins. Some of the shrinkage that occurs from green to dry is irreversible; no amount of rewetting can swell the wood back to its original dimensions. After this process of irreversible shrinkage has occurred, however, shrinkage and swelling is reversible from 0% moisture content up to FSP. Controlling the rate at which bound water is removed from green wood is the subject of entire fields of research. By properly controlling the rate at which wood dries, drying defects such as cracking, checking, honeycombing, and collapse can be minimized (Hillis 1996).

2.15 DENSITY

Density (or specific gravity) is one of the most important physical properties of wood (Desch and Dinwoodie 1996, Bowyer et al. 2003). Density is the mass of wood divided by the volume of wood at a given moisture content. Thus, units for density are typically expressed as grams per cubic centimeter (g cm^{-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. Usually density values are listed as air-dry, which means 12% moisture content in North America and Europe, but sometimes means 15% moisture content in tropical countries. Specific gravity is the density of the sample normalized to the density of water—the ratio of the density of wood to the density of water. Since 1 cm^3 of water weighs 1 g, density in g/cm^3 is numerically equivalent to specific gravity. Density in kg/m^3 must be divided by 1000 to get the same numerical value as specific gravity. Because specific gravity is a ratio, it does not have units.

Basic specific gravity = density of wood (oven-dry wt/volume when green) $\div$ density of water

Specific gravity can be determined at any moisture content, but typically it is based on mass when oven-dry and volume when green; this known as the basic specific gravity, and is generally the standard used throughout the world. The most important reason for measuring basic specific gravity is repeatability. The mass of wood (and the moisture therein) can be determined at any moisture content, but conditioning the wood to a given moisture content consistently is difficult. The oven-dry mass (0% moisture content) is easy to obtain on a consistent basis. Green volume is also relatively easy to determine using water displacement method, as a sample can be large or small and nearly any shape. Thus basic specific gravity can be determined as follows:

Basic specific gravity = oven-dry mass $\div$ mass of displaced water

Basic specific gravity is the scientifically preferred metric for comparing between woods, it is the oven-dry mass of the wood divided by the volume of the wood at the time the tree was felled. This basis for comparison avoids the changes in volume associated with wood drying. When consulting the literature or reporting wood density or specific gravity, it is necessary to establish under what conditions the values were obtained.

Wood structure determines the wood specific gravity; softwoods in which latewood is abundant (Figure 2.3d) in proportion to earlywood have higher specific gravity (e.g., 0.59 specific gravity in longleaf pine, *Pinus palustris*). The reverse is true when there is more earlywood than latewood

(Figure 2.5b) (e.g., 0.35 specific gravity in eastern white pine, *Pinus strobus*). To say it another way, specific gravity increases as the proportion of cells with thick cell walls increases. In hardwoods, specific gravity 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 μm 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.

2.16 JUVENILE WOOD AND REACTION WOOD

Q6 Two key examples of the biology of the tree affecting wood quality can be seen in the formation of juvenile wood and reaction wood (Barnett 2003). 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—things closest to the pith (Figure 2.3a, bottom). Juvenile wood in softwoods is in part characterized by the production of axial tracheids that have a higher microfibril angle in the S2 wall layer (Larson et al. 2001). A higher microfibril angle in the S2 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 exhibit normal deformations, such as cup and radial checks, and develop anomalous ones, like bow, spring, and cross-grain checking. 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. Juvenile wood is thought to afford the young tree mechanical advantages in that stage of growth, but the mechanism of formation is still not fully understood (Barnett and Bonham 2004).

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 1° or 2°. This means that all nonvertical branches form considerable quantities of reaction wood. The type of reaction wood formed by a tree differs in softwoods and hardwoods. In softwoods, reaction wood is formed on the underside of the leaning organ and is called compression wood (Figure 2.13a) (Timmel 1986). In hardwoods, reaction wood forms on the top side of the leaning organ and is called tension wood (Figure 2.13b) (Desch and Dinwoodie 1996, Bowyer et al. 2003). In compression wood, tracheids are shorter, misshapened cells with a large S, microfibril angle and high lignin content (Timmel 1986). They also take on a distinctly rounded outline (Figure 2.13c). 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 (Figure 2.13d). As mentioned earlier, many features of juvenile wood and reaction wood are similar and analogies and differences between the two are being explored (Xu et al. 2011).

2.17 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, and to ensure compliance with laws governing timber imports.

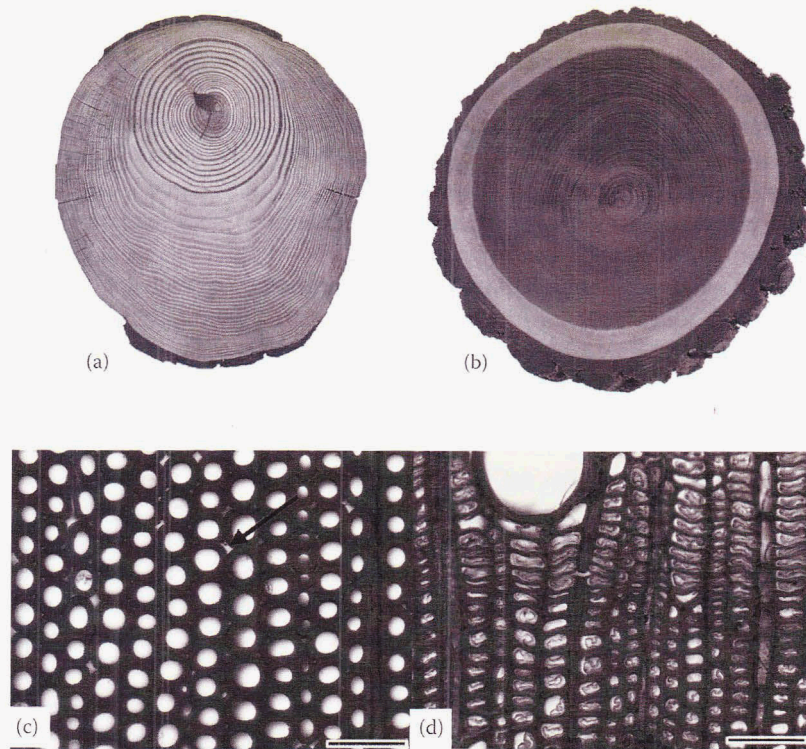


FIGURE 2.13 Macroscopic and microscopic views of reaction wood in a softwood and a hardwood. (a) Compression wood in *Pinus* sp.; note that the pith is not in the center of the trunk, and the growth rings are much wider in the compression wood zone. (b) Tension wood in *Juglans nigra*; the pith is nearly 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 μm .

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 $\times$ to 20 $\times$ hand lens, greatly improves the accuracy of the identification (Panshin and deZeeuw 1980, Hoadley 1990, Brunner et al. 1994, CITES 2002, Richter and Oelker 2002, Wiedenhoef 2011). Some foresters and wood technologists armed with a hand lens and sharp knife can accurately identify lumber in the field by examining cell patterns on the transverse surface.

The accepted technique for scientifically rigorous, accurate identifications requires that wood be sectioned and examined with a light microscope. With the light microscope, even with only a 10 $\times$ objective, many more features are available for use in making a determination. Equally important as the light microscope in wood identification is the reference collection of correctly identified specimens to which unknown samples can be compared (Wheeler and Baas 1998). If a reference collection is not available, books of photomicrographs or books or journal articles with anatomical descriptions and dichotomous keys can be used (Miles 1978, Schweingruber 1978, Core et al. 1979,

Gregory 1980, Ilic 1991, Miller and Détienné 2001, Ogata et al. 2008). In addition to these resources, several computer-assisted wood identification packages are available and are suitable for people with a robust wood anatomical background, such as the on-line searchable resource InsideWood (<http://insidewood.lib.ncsu.edu/>) or Richter and Dallwitz (2000).

Wood identification by means of molecular biological techniques is an active and promising field of research (Lowe and Cross 2011). Depending on the scale of the question being asked, various molecular techniques can be applied to determine the species (DNA barcoding), the region or stand of origin (phylogeographic methods), or even the individual tree (DNA fingerprinting) from which a wood was derived. With increased research, public databasing of results, and advanced analytical methods, the substantial population-biological effects previously expected to limit the statistical likelihood of a robust identification for routine work (Canadian Forest Service 1999) may well be overcome. One limit to the DNA-based identification of wood is the difficulty in extracting high-quality DNA from wood. This limit is based in part on the structure of wood itself; only cells alive at functional maturity, parenchyma cells, are expected to have DNA. The effects of standard wood processing (e.g., kiln-drying) on DNA extractability for wood is unknown even in a general sense, and on a species-by-species basis has not yet been explored. As technological advances improve the quality, quantity, and speed with which molecular data can be collected, the difficulty and cost of molecular wood identification will decrease. We can reasonably expect that at some point in the future molecular tools will be employed in routine identification of wood and that such techniques will greatly increase the specificity and accuracy of identification. For the present, routine scientific wood identification still depends on microscopic evaluation of wood anatomical features.

REFERENCES

- Abe, H. and Funada, R. 2005. Review: The orientation of cellulose microfibrils in the cell walls of tracheids in conifers. *IAWA Journal*. 26(2): 161–174.
- Barnett, J.R. and Bonham, V.A. 2004. Cellulose microfibril angle in the cell wall of wood fibres. *Biological Reviews*. 79: 461–472.
- Q7** Barnett, J.R. and Jeronimidis, G. 2003. *Wood Quality and Its Biological Basis*. Blackwell Publishing Ltd. 225pp.
- Bowyer, J., Shmulsky, R., and Haygreen, J.G. 2003. *Forest Products and Wood Science: An Introduction*. 4th ed. Iowa City, IA: Iowa State Press. 554pp.
- Brunner, M., Kucera, L.J., and Zürcher, E. 1994. Major timber trees of Guyana: A lens key. *Tropenbos Series* 10. Wageningen, The Netherlands: The Tropenbos Foundation. 224pp.
- Burtin, P., Jay-Allemand, C., Charpentier, J., and Janin, G. 1998. Natural wood colouring process in *Juglans* sp. (*J. nigra*, *J. regia*, and hybrid *J. nigra* 23 × *J. regia*) depends on native phenolic compounds accumulated in the transition zone between sapwood and heartwood. *Trees*. 12(5): 258–264.
- Q8** Callado, C.H., da Silva Neto, S.J., Scarano, F.R., and Costa, C.G. 2001. Periodicity of growth rings in some flood-prone trees of the Atlantic rain forest in Rio de Janeiro. *Brazil. Trees*. 15: 492–497.
- Canadian Forest Service, Pacific Forestry Centre. 1999. Combating tree theft using DNA technology. *Breakout Session Consensus*. Victoria, BC.
- Carlquist, S. 2001. *Comparative Wood Anatomy*. 2nd ed. Berlin: Springer. 448pp.
- Chudnoff, M. 1984. Tropical timbers of the world. *Agric. Handb.* 607. Madison, WI: U.S. Department of Agriculture, Forest Service, Forest Products Laboratory. 464pp.
- CITES. 2002. *CITES Identification Guide—Tropical Woods*. Wildlife Enforcement and Intelligence Division, Enforcement Branch, Environment Canada.
- Core, H.A., Côte, W.A., and Day, A.C. 1979. *Wood Structure and Identification*. 2nd ed. Syracuse, NY: Syracuse University Press. 182pp.
- Cutler, D.F. and Gregory, M. 1998. *Anatomy of the Dicotyledons*. 2nd ed. New York, NY: Oxford University Press. 304pp. Vol. IV.
- DeMeijer, M., Thurich, K., and Militz, H. 1998. Comparative study on penetration characteristics of modern wood coatings. *Wood Science and Technology*. 32: 347–365.
- Desch, H.E. and Dinwoodie, J.M. 1996. *Timber Structure, Properties, Conversion and Use*. 7th ed. London, UK: Macmillan Press. 306pp.
- Dickison, W. 2000. *Integrative Plant Anatomy*. New York, NY: Academic Press. 533pp.

- Evert, R.F. 2006. *Esau's Plant Anatomy: Meristems, Cells, and Tissues of the Plant Body: Their Structure, Function, and Development*. 3rd ed. John Wiley & Sons, Inc., Hoboken, New Jersey. 601pp.
- Frey-Wyssling, A. 1976. The plant cell wall. In: *Handbuch der Pflanzenanatomie*, Band 3, Teil 4. Abt. Cytologie, 3rd rev. ed. Gebrüder Borntraeger, Berlin.
- Gregory, M. 1980. Wood identification: An annotated bibliography. *IAWA Bull.* 1. ISSN: New Series. 1(1): 3–41.
- Gregory, M. 1994. Bibliography of systematic wood anatomy of dicotyledons. *IAWA Journal*. Supplement 1. **Q9**
- Hillis, W.E. 1987. *Heartwood and Tree Exudates*. Springer-Verlag, Berlin. 240pp.
- Hillis, W.E. 1996. Formation of robinetin crystals in vessels of *Intsia* species. *IAWA Journal*. 17(4): 405–419.
- Hoadley, R.B. 1990 *Identifying Wood: Accurate Results with Simple Tools*. Newtown, CT: Taunton Press. 223pp.
- Hoadley, R.B. 2000. *Understanding Wood: A Craftsman's Guide to Wood Technology*. 2nd ed. Newtown, CT: Taunton Press. 280pp.
- IAWA Committee. 1989. IAWA list of microscopic features for hardwood identification. In: Wheeler, E.A.; Baas, P.; Gasson, P., eds. *IAWA Bull.* 10. ISSN: New Series 10(3): 219–332.
- IAWA Committee. 2004. IAWA list of microscopic features of softwood identification. In: Richter, H.G.; Grosser, D.; Heinz, I.; Gasson, P., eds. *IAWA Journal*. 25(1): 1–70.
- Ilic, J. 1991. *CSIRO Atlas of Hardwoods*. Bathurst, Australia: Crawford House Press. 525pp.
- Ishiguri, F., Maruyama, S., Takahashi, K., Abe, Z., Yokota, S., Andoh, M., and Yoshizawa, N. 2003. Extractives relating to heartwood color changes in sugi (*Cryptomeria japonica*) by a combination of smoke-heating and UV radiation exposure. *Journal of Wood Science*. 49: 135–139. **Q10**
- Kerr, T. and Bailey, W. 1934. The cambium and its derivative tissues. X. Structure, optical properties and chemical composition of the so-called middle lamella. *J. Arnold Arb.* 15: 327–349.
- Kretschmann, D.E., Alden, H.A., and Verrill, S. 1998. Variations of microfibril angle in loblolly pine: Comparison of iodine crystallization and X-ray diffraction techniques. In: Butterfield, B.G., ed. *Microfibril Angle in Wood*. New Zealand: University of Canterbury. 157–176.
- Kukachka, B.F. 1960. Identification of coniferous woods. *Tappi Journal*. 43(11): 887–896.
- Lagenheim, J.H. 2003. *Plant Resins: Chemistry, Evolution, Ecology, and Ethnobotany*. Portland, OR: Timber Press. 448pp.
- Larson, P.R. 1994. *The Vascular Cambium, Development and Structure*. Berlin: Springer-Verlag. 725pp.
- Larson, P.R., Kretschmann, D.E., Clark, A., III and Isenbrands, J.G. 2001. Formation and properties of juvenile wood in southern pines: A synopsis. Gen. Tech. Rep. FPL–GTR–129. Madison, WI: U.S. Department of Agriculture, Forest Service, Forest Products Laboratory.
- Lowe, A.J. and Cross, H.B. 2011. The application of DNA methods to timber tracking and origin verification. *IAWA Journal*. 32(2): 251–262.
- Magel, E.A. 2000. Biochemistry and physiology of heartwood formation. In: Savidge, R.A., Barnett, J.R., Napier, R. Cell and Molecular Biology of Wood Formation. Eds. *BIOS Scientific*, Oxford. 363–376.
- Marschner, S.R., Westin, S.H., Arbree, A., and Moon, J.T. 2000. Measuring and modelling the appearance of finished wood. *ACM Transactions on Graphics (SIGGRAPH 2005 Proceedings)* 24: 727–734. **Q10**
- Metcalfe, C.R. and Chalk, L. 1950. *Anatomy of the Dicotyledons*. Oxford, UK: Clarendon Press. 2 vols. 1,500pp.
- Metcalfe, C.R. and Chalk, L. 1979. *Anatomy of the Dicotyledons*. 2nd ed. New York: Oxford University Press. Vol. I. 276pp.
- Metcalfe, C.R. and Chalk, L. 1987. *Anatomy of the Dicotyledons*. 2nd ed. New York: Oxford University Press. Vol. III. 224pp.
- Miles, A. 1978. *Photomicrographs of world woods. Building Research Establishment*. Princes Risborough Laboratory; London: Her Majesty's Stationery Office. 233pp.
- Miller, R.B. and Détienne, P. 2001. Major timber trees of Guyana: Wood anatomy. *Tropenbos Series* 20. Wageningen, The Netherlands: The Tropenbos Foundation. 218pp.
- Ogata, K., Fujii T., Abe, H., and Baas, P. 2008. *Identification of the Timbers of Southeast Asia and the Western Pacific*. Kaiseisha Press. 400pp. **Q11**
- Pallardy, S.G. 2008. *Physiology of Woody Plants*. Third edition. Elsevier. Chapters 11, 12. **Q11**
- Panshin, A.J. and deZeeuw, C. 1980. *Textbook of Wood Technology*. 4th ed. New York: McGraw-Hill. 722pp.
- Phillips, E.W.J. 1948. Identification of softwoods by microscopic structure. *Forest Products Res. Bull.* 22. **Q12**
- Raven, P., Evert, R., and Eichhorn, S. 1999. *Biology of Plants*. 6th ed. New York, NY: W.H. Freeman & Company. 944pp.
- Richter, H.G. and Dallwitz, M.J. 2000 onwards. Commercial timbers: Descriptions, illustrations, identification, and information retrieval. In English, French, German, Portuguese, and Spanish. Version: 16th April 2006. <http://delta-intkey.com>.
- Richter, H.G. and Oelker, M. 2002 onwards. MacroHOLZdata Commercial timbers: Descriptions, illustrations, identification, and information retrieval. In English and German. Version: October 2002.

- Rijkaert, V., Stevens, M., de Meijer, M., and Militz, H. 2001. Quantitative assessment of the penetration of water-borne and solvent-borne wood coatings in Scots pine sapwood. *Holz als Roh-und Werkstoff*. 59: 278–287.
- Sauter, J.J. 2000. Photosynthate allocation to the vascular cambium: facts and problems. In: Savidge, R.A., Barnett, J.R., and Napier, R. *Cell and Molecular Biology of Wood Formation*. Eds. BIOS Scientific, Oxford. 71–83.
- Sheng-zuo, F., Wen-zhong, Y., and Xiang-xiang, F. 2006. Variation of microfibril angle and its correlation to wood properties in poplars. *Journal of Forestry Research*. 15(4): 261–267.
- Schweingruber, F. 1978. Microscopic wood anatomy. *Birmensdorf*: Swiss Federal Institute for Foreign Research. 800pp.
- Schweingruber, F.H., Borner A., and Schulze E.-D. 2006. *Atlas of Woody Plant Stems. Evolution, Structure, and Environmental Modifications*. Berlin: Springer-Verlag. 229pp.
- Schweingruber, F.H. 2007. *Wood Structure and Environment*. Berlin: Springer-Verlag. 279pp.
- Simpson, W.T., ed. 1991. Dry kiln operator's manual. *Agric. Handb.* AH-188. Madison, WI: U.S. Department of Agriculture, Forest Service, Forest Products Laboratory. 274pp.
- Taiz, L. and Zeiger, E. 2010. *Plant Physiology*, Fifth Edition. Sunderland, MA: Sinauer. 782pp.
- Timmel, T.E. (1986). *Compression Wood in Gymnosperms*. Heidelberg: Springer. 2,150pp.
- Wheeler, E.A. and Baas, P. 1998. Wood identification: A review. *IAWA Journal*. 19(3): 241–264.
- Wiedenhoef, A.C. and Miller, R.B. 2002. Brief comments on the nomenclature of softwood axial resin canals and their associated cells. *IAWA Journal*. 23(3): 299–303.
- Wiedenhoef, A.C. (2011). *Identification of Central American Woods. Identificación de las Especies Maderables de Centroamérica*. Madison, WI: Forest Products Society. 167pp.
- Worbes, M. 1995. How to measure growth dynamics in tropical trees: A review. *IAWA Journal*. 16(4): 337–351.
- Worbes, M. 1999. Annual growth rings, rainfall-dependent growth and long-term growth patterns of tropical trees in the Capar Forest Reserve in Venezuela. *Journal of Ecology*. 87: 391–403.
- Xu, P., Liu, H., Donaldson, L.A., and Zhang, Y. 2011. Mechanical performance and cellulose microfibrils in wood with high S₂ microfibril angles. *Journal of Materials Science*. 46(2): 534–540.
- Zimmermann, M.H. 1983. *Xylem Structure and the Ascent of Sap*. New York: Springer-Verlag. 143pp.

Handbook of Wood Chemistry and Wood Composites

SECOND EDITION

Edited by Roger M. Rowell



CRC Press

Taylor & Francis Group

Boca Raton London New York

CRC Press is an imprint of the
Taylor & Francis Group, an informa business

CRC Press
Taylor & Francis Group
6000 Broken Sound Parkway NW, Suite 300
Boca Raton, FL 33487-2742

© 2013 by Taylor & Francis Group, LLC
CRC Press is an imprint of Taylor & Francis Group, an Informa business

No claim to original U.S. Government works

Printed in the United States of America on acid-free paper
Version Date: 20120725

International Standard Book Number: 978-1-4398-5380-1 (Hardback)

This book contains information obtained from authentic and highly regarded sources. Reasonable efforts have been made to publish reliable data and information, but the author and publisher cannot assume responsibility for the validity of all materials or the consequences of their use. The authors and publishers have attempted to trace the copyright holders of all material reproduced in this publication and apologize to copyright holders if permission to publish in this form has not been obtained. If any copyright material has not been acknowledged please write and let us know so we may rectify in any future reprint.

Except as permitted under U.S. Copyright Law, no part of this book may be reprinted, reproduced, transmitted, or utilized in any form by any electronic, mechanical, or other means, now known or hereafter invented, including photocopying, microfilming, and recording, or in any information storage or retrieval system, without written permission from the publishers.

For permission to photocopy or use material electronically from this work, please access www.copyright.com (<http://www.copyright.com/>) or contact the Copyright Clearance Center, Inc. (CCC), 222 Rosewood Drive, Danvers, MA 01923, 978-750-8400. CCC is a not-for-profit organization that provides licenses and registration for a variety of users. For organizations that have been granted a photocopy license by the CCC, a separate system of payment has been arranged.

Trademark Notice: Product or corporate names may be trademarks or registered trademarks, and are used only for identification and explanation without intent to infringe.

Visit the Taylor & Francis Web site at
<http://www.taylorandfrancis.com>

and the CRC Press Web site at
<http://www.crcpress.com>