2 Structure and Function of Wood

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Despite the many human uses to which various woods are suited, at a fundamental level wood is a complex biological structure, itself a composite of many chemistries and cell types acting together to serve the needs of the plant. Although humans have striven 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: the conduction of water from the roots to the leaves, the mechanical support of the plant body, and the storage of biochemicals. The need for these three functions has driven the evolution of approximately 20,000 different extant 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 allows insights into the realm of human wood use

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(Hoadley 2000). A scientist with a robust understanding of the interrelationships between form and function can predict the usefulness of a specific wood in a new context.

To begin, it is necessary to define and delimit the component parts of wood at a variety of scales. There is a significant difference in the quality and quantity of wood anatomical expertise necessary for a researcher who is using a solid wood beam compared to the knowledge necessary for an engineer designing a glued-laminated beam, and these are in turn different compared to the knowledge required for making a wood-resin composite with wood flour. In the first case, a large-scale anatomical understanding may help to explain and quantify the mechanical properties of the beam. In the second case, an understanding of anatomical effects on mechanical properties must be coupled with chemical knowledge about the efficacy of various adhesives. In the third case, an understanding of particle size distribution and wood cell wall chemistry will be key pieces of knowledge. The differences in the kinds of knowledge in these three cases are related to the scale at which one intends to interact with wood, and in all three cases the technologically different properties are derived from the biological needs of the living tree. For this reason, the structure of wood will be explained in this chapter at decreasing scales, and in ways that demonstrate the biological rationale for a plant to produce wood with such features. Such background will permit the reader to access primary literature related to wood structure with greater ease.

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

2.1 THE TREE

The general body plan of a tree must be briefly outlined so that all subsequent information can be understood in its proper context within the living organism. A living, growing tree has two main domains, the shoot and the roots. The roots are the subterranean structures responsible for water uptake, mechanical support of the shoot, and storage of biochemicals. The shoot comprises the

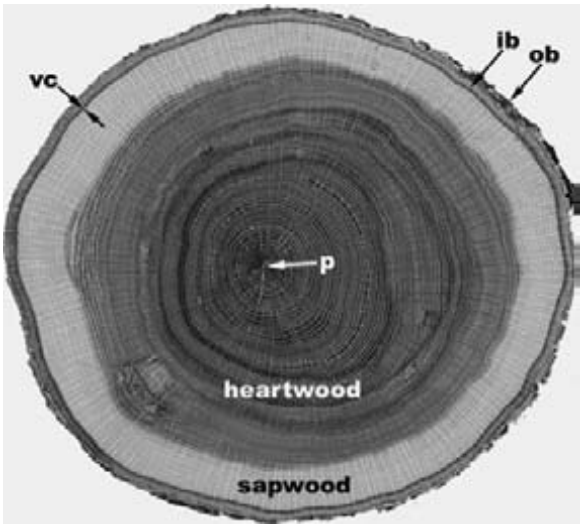

FIGURE 2.1 Macroscopic view of a transverse section of a *Quercus alba* trunk. Beginning at the outside of the tree, there is the outer bark (ob), the inner bark (ib), and then the vascular cambium (vc), which is too narrow to see at this magnification. Interior to the vascular cambium is the sapwood, which is easily differentiated from the heartwood that lies to the interior. At the center of the trunk is the pith (p), which is barely discernible in the center of the heartwood.

trunk or bole of the tree, the branches, and the leaves (Raven et al. 1999). It is with the trunk of the tree that the remainder of the chapter will be concerned.

If one cuts down a tree and looks at the stump, there are several gross observations that can be easily made. The trunk is composed of various materials present in concentric bands. From the outside of the tree to the inside there are six layers: outer bark, inner bark, vascular cambium, sapwood, heartwood, and the pith (Figure 2.1). Outer bark provides mechanical protection to the softer inner bark, and also helps to limit evaporative water loss. Inner bark (phloem) is the tissue through which sugars produced by photosynthesis (photosynthate or "food") are translocated from the leaves to the roots or growing portions of the tree. The vascular cambium is the layer between the bark and the wood that is responsible for producing both these tissues. The sapwood is the active, "living" wood that is responsible for conducting 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 very center of the trunk is the remnants of the early growth of the trunk, before wood was formed.

2.2 SOFTWOODS AND HARDWOODS

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*) and birch (*Betula*). Not only do softwoods and hardwoods differ in terms of the types of trees from which they are derived, but they also differ in terms of their component cells. 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 (Figure 2.2). An important cellular similarity between softwoods and hardwoods is that

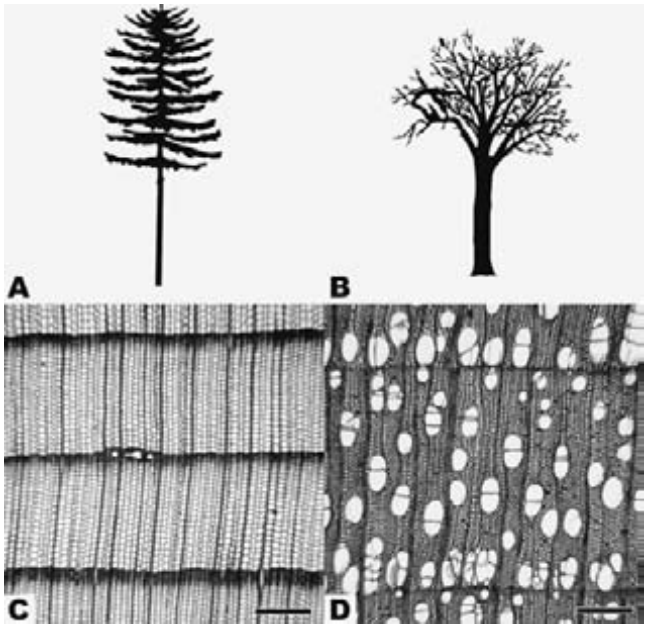

FIGURE 2.2 Softwood and hardwood. (A) The general form of a generic softwood tree. (B) The general form of a generic hardwood tree. (C) Transverse section of *Pseudotsuga mensiezii*, a typical softwood. The three round white spaces are resin canals. (D) Transverse section of *Betula allegheniensis*, a typical hardwood. The many large, round white structures are vessels or pores, the characteristic feature of a hardwood. Scale bars = 300 μm.

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. Additionally, despite what one might conclude based on the names, not all softwoods have soft, lightweight wood, nor do all hardwoods have hard, heavy wood.

2.3 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 the parenchyma cells are still alive and metabolically active, is referred to as the sapwood. A looser definition that is more broadly applied is that the sapwood is the band of lighter-colored wood adjacent to the bark. The heartwood is the darker-colored wood found to the interior of the sapwood (Figure 2.1).

In the living tree, the sapwood is responsible not only for the conduction of sap, but also for the storage and synthesis of biochemicals. This function is often underappreciated in wood technological discourse. An important storage function is the long-term storage of photosynthate. The carbon that must be expended to form a new flush of leaves or needles must be stored somewhere in the tree, and it is often in the parenchyma cells of the sapwood that this material is stored. The primary storage forms of photosynthate are starch and lipids. Starch grains are stored in the parenchyma cells, and can be easily seen using 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 the growth of anaerobic bacteria that produce ill-smelling compounds that can make the wood unusable (Chudnoff 1984). In the southern yellow pines of the United States, a high starch content encourages the growth of sap-stain fungi that, though they do not effect the strength of the wood, can nonetheless cause a significant decrease in lumber value for aesthetic reasons (Simpson 1991).

The living cells of the sapwood are also the agents of heartwood formation. In order for the tree to accumulate biochemicals, they must be actively synthesized and translocated by living cells. For this reason, living cells at the border between the heartwood and sapwood are responsible for the formation and deposition of heartwood chemicals, one of the important steps leading to heartwood formation (Hillis 1996).

Heartwood functions in the long-term storage of biochemicals of many varieties depending on the species in question. These chemicals are known collectively as extractives. In the past it was thought that the heartwood was a disposal site for harmful by-products 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 the living cells if not sequestered in a safe place. A more modern understanding of extractives indicates that they are a normal and intentional part of the plant's efforts to protect 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 it is possible for dead cells to 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 such as teak (*Tectona grandis*), famed for its stability and water resistance, these properties are conferred 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

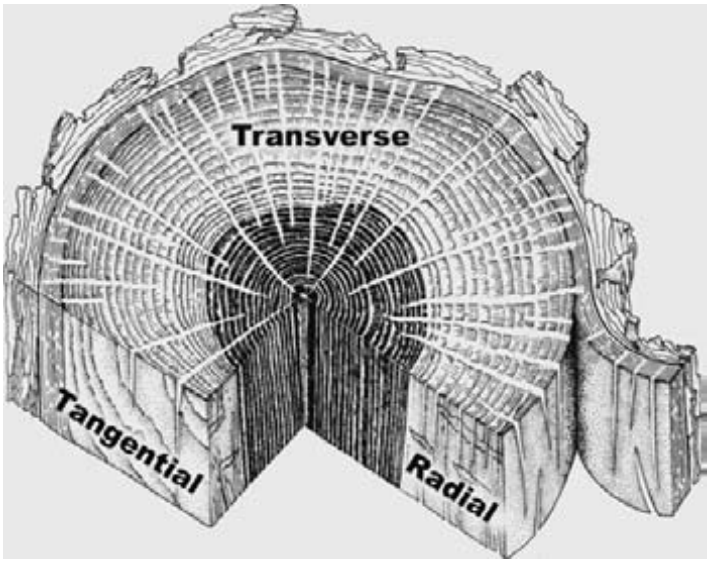

FIGURE 2.3 Illustration of the three planes of section. Note that for the tangential plane of section, only the right-hand portion of the cut is perpendicular to the rays; due to the curvature of the rings, the left portion of the cut is out of plane. From *Biology of Plants*, 4/e, by Peter H. Raven, et. al. © 1971, 1976, 1986 Worth Publishers. Used with permission.

extract valuable resins used in perfume making (Lagenheim 2003). Sandalwood (*Santalum spicatum*), a wood famed for its use in incenses and perfumes, is only valuable if the heartwood is rich with the desired aromatic extractives. The utility of a wood for a technological application can be directly affected by extractives. For example, if a wood high in hydrophobic extractives is used in a composite bonded with a water-based adhesive, weak or incomplete bonding can result.

2.4 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 that are 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. The cells of the axial system have their long axes running parallel to the long axis of the organ (e.g., up and down the trunk). The 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 (Figure 2.3). 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.

2.5 PLANES OF SECTION

Though one could cut wood in any direction and then look at it, such an approach would, in the vast majority of cases, result in perspectives that can provide only a small proportion of the information

that could be gleaned if the wood were properly examined. The organization and interrelationship between the axial and radial systems give rise to three main perspectives from which they can be viewed (Figure 2.3). These three perspectives are the transverse plane of section (the cross-section), the radial plane of section, and the tangential plane of section. The latter planes of section 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. 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 (call 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, and it is parallel to the axial system, so it provides information about longitudinal changes in the stem and from the 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. 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 in turn can a holistic and accurate understanding of the three-dimensional structure of wood be gained. The three planes of section are determined by the structure of wood, and the way in which the cells in wood are arrayed. The cells are laid down in these special arrangements by a special part of the trunk.

2.6 VASCULAR CAMBIUM

The axial and radial systems and their component cells are derived from a special 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 (Figure 2.1, Figure 2.4A), and is responsible for forming, by means of

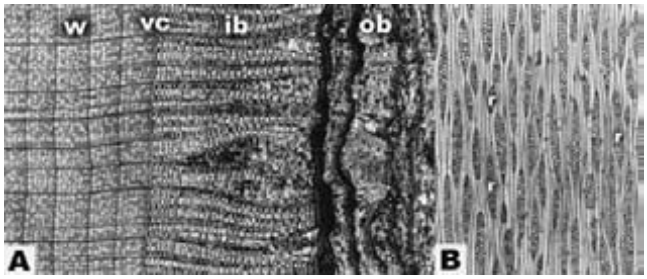

FIGURE 2.4 Light microscopic views of the vascular cambium. (A) Transverse section showing wood (w), vascular cambium (vc), inner bark (ib), and outer bark (ob) in *Tilia americana*. (B) Tangential section through the vascular cambium of *Malus sylvestris*. Ray initials (r) occur in groups that will give rise to the rays. The vertically oriented cells are fusiform initials, which will give rise to the axial system. Scale bars not available. From *Biology of Plants*, 4/e, by Peter H. Raven, et. al. © 1971, 1976, 1986 Worth Publishers. Used with permission.

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 diameter and 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: the fusiform initials and the ray initials (Figure 2.4B). The fusiform initials, named to describe their long, slender shape, give rise to the cells of the axial system, and the 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 the wood, a water-conducting tissue, stays connected to the photosynthate-conducting tissue, the inner bark. 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. 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.

In the opening paragraph of this chapter, reference was made to the three functions of wood in the living tree. It is worth reiterating them and their relevance at this point. 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. A complementary view is that any anatomical feature of wood can be assessed in the context of the tree's need for water conduction, mechanical support, and storage of biochemicals. To accomplish any of these functions, wood must have cells that are designed and interconnected in ways suitable to perform these functions.

2.7 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 there are large cohorts of cells produced more or less together in time, and these cohorts 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. The cells formed at the beginning of the growth increment are called earlywood cells and the cells formed in the latter portion of the growth increment are called latewood cells (Figure 2.5). Springwood and summerwood were terms formerly used to refer to earlywood and latewood, respectively, but their use is anachronistic and not recommended (IAWA Committee1989).

In the temperate portions of the world and anywhere else where there is a 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 Committee 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 (Worbes 1995, Worbes 1999, Callado et al. 2001).

When one looks at woods that form distinct growth rings, and this includes most woods that are likely to be used for wood composites, there are 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 (Figure 2.6). These patterns appear in both softwoods and hardwoods, but differ in each due to the distinct anatomical structural differences between the two. Many authors use the general term porosity to describe growth rings (recall that vessels and pores are synonymous.)

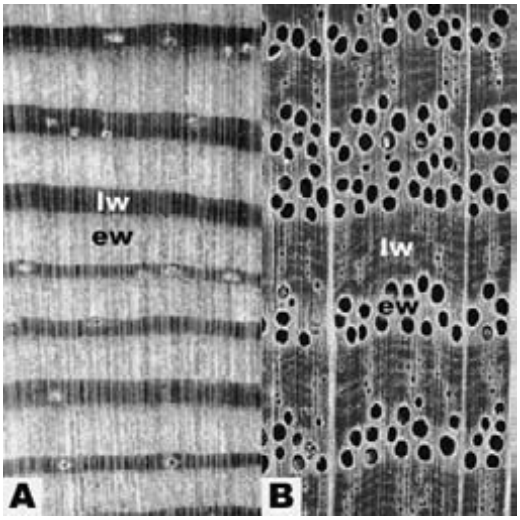

FIGURE 2.5 Hand-lens views (approximately 14x magnification) of the transverse section showing earlywood and latewood. (A) Distinction in a softwood growth ring between earlywood (ew) and latewood (lw) in *Pinus resinosa*. (B) Distinction in a hardwood growth ring between earlywood (ew) and latewood (lw) in *Quercus rubra.*

Nonporous woods (woods without vessels) are softwoods. Softwoods can exhibit any of the three general patterns noted above. 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 2.6B). Other woods undergo an abrupt transition from earlywood to latewood, including Southern yellow pine (*Pinus*), larch

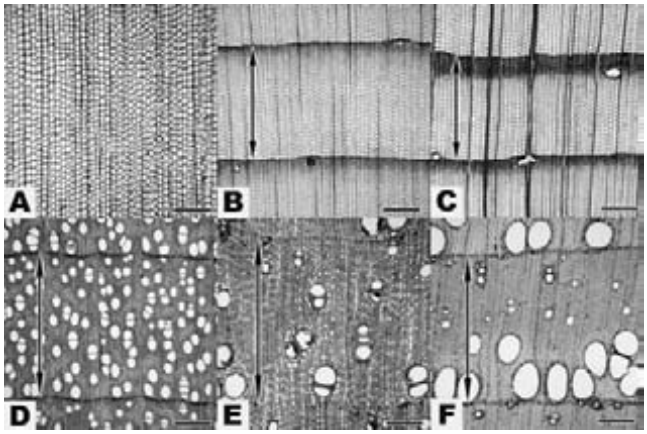

FIGURE 2.6 Transverse sections of woods showing types of growth rings. Arrows delimit growth rings, when present. (A–C) Softwoods: (A) No transition within the growth ring (growth ring absent) in *Podocarpus imbricata*. (B) Gradual transition from earlywood to latewood in *Picea glauca*. (C) Abrupt transition from earlywood to latewood in *Pseudotsuga mensiezii*. (D–F) Hardwoods: (D) Diffuse porous wood (no transition) in *Acer saccharum*. (E) Semi-diffuse porous wood (gradual transition) in *Diospyros virginiana*. (F) Ring porous wood (abrupt transition) in *Fraxinus americana*. Scale bars = 300 μm.

(*Larix*), Douglas fir (*Pseudotsuga menziesii*), bald cypress (*Taxodium disticum*), and redwood (*Sequoia sempervirens*) (Figure 2.6C). Since 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*) do you find no transition within the growth ring (Figure 2.6A). Many authors have reported this state as growth rings being absent or only barely evident (Phillips 1948, Kukachka 1960).

Porous woods (woods with vessels) are hardwoods, which have two main types of growth rings, and one intermediate form. In diffuse porous woods, the vessels either do not significantly change 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 (Figure 2.6D). 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 in which the transition from earlywood to latewood is abrupt, i.e., the vessels reduce significantly (often by an order or magnitude or more) in diameter and often change their distribution as well. This creates a ring pattern of large, earlywood vessels around the inner portion of the growth increment, alternating with 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*) (Figure 2.6F).

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 2.6E). Black walnut (*Juglans nigra*) and black cherry (*Prunus serotina*) are temperate-zone semi-ring porous woods. Most tropical hardwoods are diffuse porous except for Spanish cedar (*Cedrela*) and teak (*Tectona grandis*), which are generally semi-ring porous.

There are no distinctly ring porous species in the tropics and only a very few in the Southern Hemisphere. It is interesting that in genera that span temperate and tropical zones, it is common to have ring porous representatives in the temperate zone and diffuse porous species in the tropics. The oaks (*Quercus*), ashes (*Fraxinus*), and hackberries (*Celtis*) that are native to the tropics are diffuse porous, while their temperate relatives are ring porous. There are numerous detailed texts with more information on growth increments in wood, a few of which are of particular note (Panshin and deZeeuw 1980, Dickison 2000, Carlquist 2001).

2.8 CELLS IN WOOD

To understand a growth ring in greater detail, it is essential to begin with an understanding of the structure, function, and variability of the cells that compose the ring. A single 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 can provide significant mechanical support to the plant at large (Esau 1977, Raven et al. 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, it is a common convention in wood literature to refer to a cell wall without a protoplast as a cell. Although this is technically incorrect from a cell biological standpoint, it is a convention 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. Thus, in most cells in wood there are two domains: the cell wall and the cell lumen (Figure 2.7). The lumen is a critical component of many cells, whether in the context of the amount of space available for water conduction or in

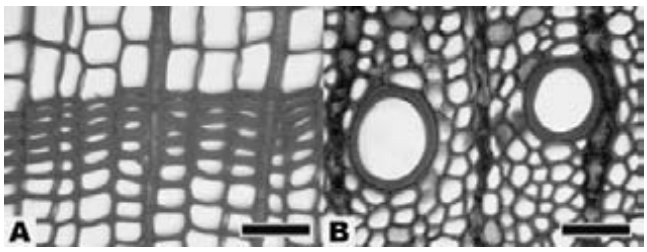

FIGURE 2.7 Transverse sections of wood showing cell walls and lumina. (A) Softwood: All the rectangular cells are of the same type, some with thicker cell walls and narrower lumina, and others with thinner walls and wider lumina in *Pseudotsuga mensiezii.* (B) Hardwood: The large round cells have thick cell walls and very large lumina. Other cells have thinner walls and narrower lumina in *Quercus rubra*. Scale bars = 50 μm.

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 really the void space in the interior of the cell. The relevance of the lumen to the formation of wood composites is the subject of Chapter 15.

2.9 CELL WALLS

The cell walls in wood are important structures. 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 2.8). 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).

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 others in a coherent way to ensure that the cells can act as a unified whole. This means that they must be interconnected with one another to permit the movement of biochemicals (e.g., photosynthate, hormones, cell signaling agents, etc.) 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 2.8). 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 (Figure 2.8). 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 degrees relative to the long axis of the cell may be present. In cells in wood, the primary wall is very 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 with transmission electron microscopy, the compound middle lamella often cannot be separated unequivocally into its component layers. The compound middle lamella in wood is almost invariably lignified.

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 (Figure 2.8). 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 layer (Figure 2.8), which is adjacent to compound middle lamella (or technically the primary wall). This layer is a thin layer

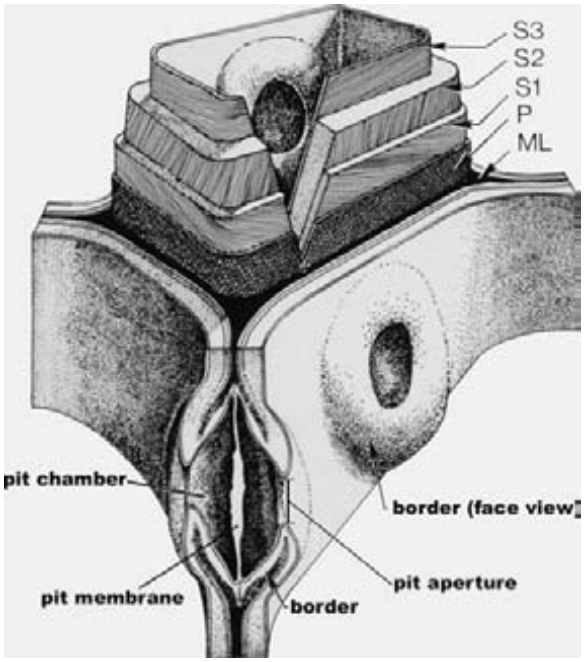

FIGURE 2.8 A cut-away drawing of the cell wall including the structural details of a bordered pit. The various layers of the cell wall are detailed at the top of the drawing, beginning with the middle lamella (ML). The next layer is the primary wall (P), and on the surface of this layer the random orientation 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. The four domains of the pit are illustrated: the pit aperture (pa), the pit chamber (pc), the pit membrane (pm) and the border (b).

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 degrees.

The next wall layer is arguably the most important 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 2.8). 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 degrees. There is a strong but not fully understood relationship between the microfibril angle of the S_2 layer of the wall and the wood properties at a macroscopic level (Kretschmann et al. 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 (Figure 2.8). The microfibril angle of this layer is relatively high and similar to that of S_1: 70+ degrees. 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 a significant 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 layer to permit adhesion of water to the cell wall and thus facilitate transpiration. For more detail regarding these wall components and information regarding transpiration and the role of the cell wall, see Chapter 3 or any college-level plant physiology textbook (Kozlowski and Pallardy 1997, Taiz and Zeiger 1991).

2.10 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 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 (Figure 2.8). Pits have three domains: the pit membrane, the pit aperture, and the pit chamber. The pit membrane (Figure 2.8) is the thin semiporous 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 (Figure 2.8). 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. 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 et al. 1999).

Bordered pits are thus called because the secondary wall overarches the pit chamber and the aperture is generally smaller and/or of a different shape than the pit chamber. The portion of the cell wall that is overarching the pit chamber is called the border (Figure 2.8, Figure 2.9A, and Figure 2.9D). When seen in face view, bordered pits often are round in appearance and look somewhat like a doughnut, with a small round or almond-shaped hole, the pit aperture, in the middle of the pit (Figure 2.9). 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 2.9A and Figure 2.9D). In this case, the long stems of the V represent the borders, the secondary walls that are overarching the pit chamber. Bordered pits always occur between two conducting cells, and sometimes between other cells,

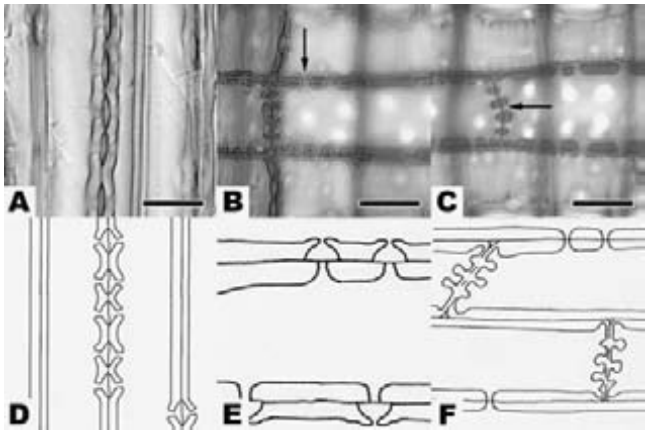

FIGURE 2.9 Light micrographs and sketches of the three types of pits. (A) Longitudinal section of bordered pits in *Xanthocyparis vietnamensis*. The pits look like a vertical stack of thick-walled letter V's. (B) Half-bordered pits in *Pseudotsuga mensiezii*. The arrow shows one half-bordered pit. (C) Simple pits on an end wall in *Pseudotsuga mensiezii*. The arrow indicates one of five simple pits on the end wall. Scale bars = 20 μm. (D–F) Sketches of the pits shown in A–C.

typically those with thick cell walls. The structure and function of bordered pits, particularly those in softwoods (see next section), are much studied and known 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 fields of wood preservation, wood finishing, and bonding.

Simple pits are so called because they lack any sort of border (Figure 2.9C and Figure 2.9F). 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 one half of the pit pair is simple and one half is bordered (Figure 2.9B and Figure 2.9E). In the living tree, these pits are of great importance, as they represent the communication link between the conducting cells and the biochemically active cells.

2.11 THE MICROSCOPIC STRUCTURE OF SOFTWOODS AND HARDWOODS

As is no doubt clear by now, the fundamental differences between different kinds of woods are founded on the types, sizes, proportions, pits, and arrangements of different cells that compose the wood. Softwoods have a simpler basic structure than do hardwoods due to the presence of 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. In each case, however, there are fine details of structure that could affect the use of a wood, and elucidating these details is the subject of the next portion of this chapter.

2.11.1 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, the rays, are composed mostly of ray parenchyma cells.

2.11.1.1 Tracheids

Tracheids are very long cells, often more than 100 times longer than wide, and they are the major component of softwoods, making up over 90% of the volume of the wood. They provide both conductive and mechanical functions to softwoods. In the transverse view or section (Figure 2.10A), tracheids appear as square or slightly rectangular cells in radial rows. Within one growth ring they can be thin-walled in the earlywood and thicker-walled in the latewood. In order 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, there is a significant resistance to flow. The resistance of the pit membrane coupled with the narrow diameter of the lumina makes tracheids relatively inefficient conduits, compared to 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).

2.11.1.2 Axial Parenchyma and Resin Canal Complexes

Another cell type that is sometimes present 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

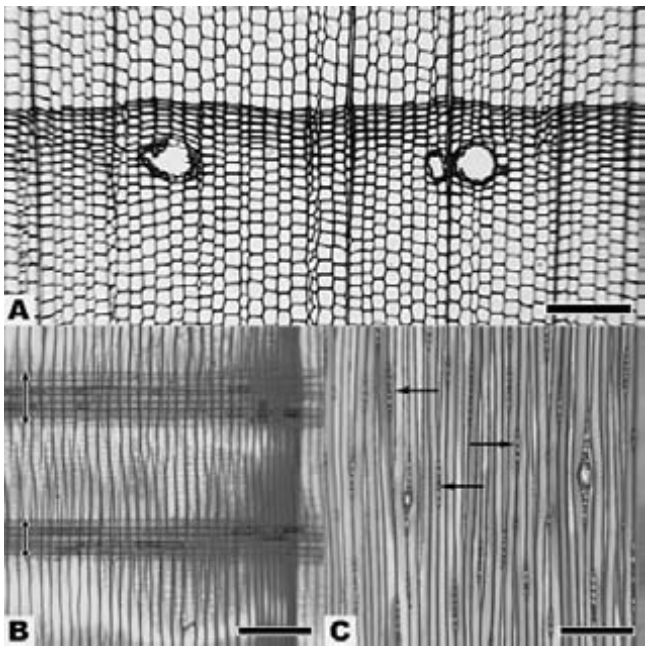

FIGURE 2.10 The microscopic structure of *Picea glauca*, a typical softwood. (A) Transverse section, scale bar = 150 μm. The bulk of the wood is made of tracheids, the small rectangles of various thicknesses. The three large, round structures are resin canals and their associated cells. The dark lines 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 left in the earlywood (thin-walled tracheids) and continue into and through the latewood (thick-walled tracheids), and into the next growth ring, on the right side of the photo. Scale bar = 200 μm. (C) Tangential section. Rays seen in end-view; they are 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 = 200 μm.

of the other to form a parenchyma strand. In transverse section (Figure 2.11A) they often look like an axial tracheid, but can be differentiated when they contain dark-colored organic substances in the lumen of the cell. In the radial or tangential section (Figure 2.11B) they appear as long strands of cells generally containing dark-colored substances. Axial parenchyma is most common in redwood, juniper, cypress, bald cypress, and some species of *Podocarpus*, but never makes up even 1% of the cells. 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 vertically (Figure 2.12) and horizontally (Figure 2.12C). These structures are voids or spaces in the wood and are not cells. However, 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 (Wiedenhoeft 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 (Figure 2.10C and Figure 2.12C). These rays are much higher 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 resin canals in response to significant injury.

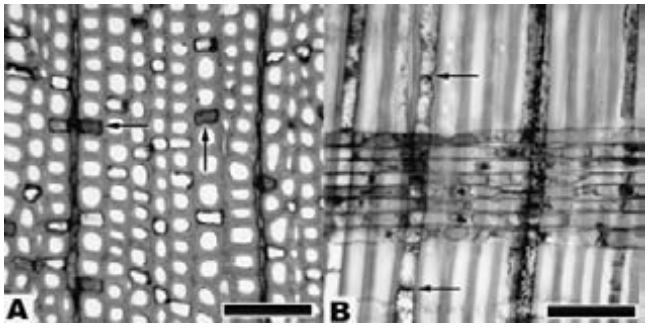

FIGURE 2.11 Axial parenchyma in *Podocarpus madagascarensis*. (A) Transverse section showing individual axial parenchyma cells. They are the dark-staining rectangular cells. Two are denoted by arrows, but many more can be seen. (B) Radial section showing axial parenchyma in longitundinal view. The parenchyma cells can be differentiated from the tracheids by the presence of end walls (arrows) in addition to the dark-staining contents. Scale bars = 100 μm.

2.11.1.3 Rays

The other cells in Figure 2.10A 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 150–250 μm long in the radial or horizontal direction (Figure 2.10B). These brick-like cells form the rays, which function primarily in the synthesis, storage, and lateral transport of biochemicals and, to a lesser degree, water. In radial view or section (Figure 2.10B), the rays look like a brick wall and the ray parenchyma cells are sometimes filled with dark-colored substances. In tangential section (Figure 2.10C), 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 vertical 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 is generally consistent within a species and very diagnostic. Figure 2.13 illustrates several types of cross-field pitting.

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 vertical tracheids, but are much shorter and narrower. Ray tracheids also occur in a few

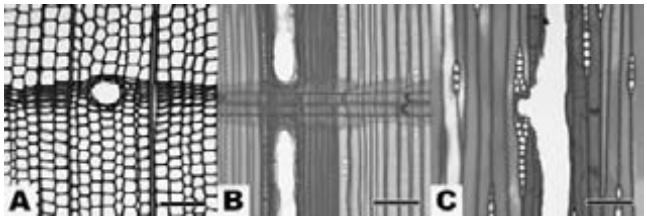

FIGURE 2.12 Resin canal complexes in *Pseudotsuga mensiezii*. (A) Transverse section showing a single axial resin canal complex. In this view the tangential and radial diameters of the canal can be measured accurately. (B) Radial section showing an axial resin canal complex embedded in the latewood. It is crossed by a ray that also extends into the earlywood on either side of the latewood. (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 bars = 100 μm.

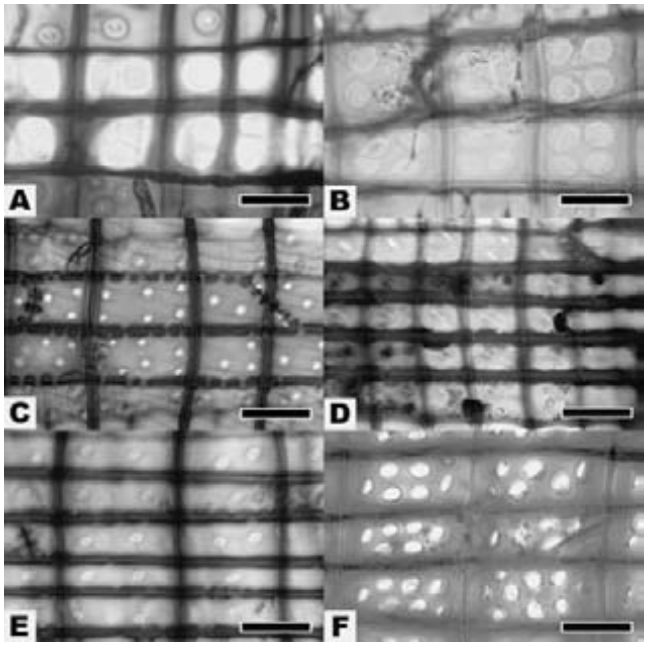

FIGURE 2.13 Radial sections showing a variety of types of cross-field pitting. All the pits are half-bordered pits, but in some cases the borders are difficult to see. (A) Fenestriform pitting in *Pinus strobus*. (B) Pinoid pitting in *Pinus elliottii*. (C) Piceoid pitting in *Pseudotsuga mensiezii*. (D) Cuppressoid pitting in *Juniperus virginiana*. (E) Taxodioid pitting in *Abies concolor.* (F) Araucarioid pitting in *Araucaria angustifolia*. Scale bars = 30 μm.

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 Committee 2004).

2.11.2 Hardwoods

The structure of a typical hardwood is much more complicated than that of a softwood. The axial or vertical system is composed of fibrous elements of various kinds, vessel elements in various sizes and arrangements, and axial parenchyma cells in various patterns and abundance. Like softwoods, the radial or horizontal system are the rays, which are composed of ray parenchyma cells, but unlike softwoods, hardwood rays are much more diverse in size and shape.

2.11.2.1 Vessels

The unique feature that separates hardwoods from softwoods is the presence of specialized conducting cells in hardwoods called vessels elements (Figure 2.14A). These cells 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 (vessel 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 quite small (<30 μm) or quite large (>300 μm), but typically range from 50–200 μm. Their length is much shorter than tracheids and range from 100–1200 μm or

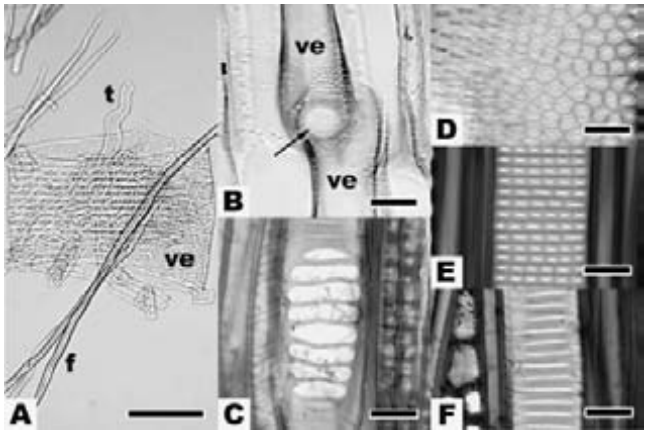

FIGURE 2.14 Vessel elements and vessel features. (A) Macerated cells of *Quercus rubra*. There are three types of cells labeled. There is a single vessel element (ve); note that it is wider than it is tall, and it is open on both ends. The fiber (f) is long, narrow, and thick-walled. The hardwood tracheid (t) is shorter than a fiber but longer than a vessel element, and it is contorted in shape. Scale bar = 200 μm. (B) A simple perforation plate in *Malouetia virescens*. There are two vessel elements (ve), and where they overlap there is an open hole between the cells, the perforation plate (arrow). As the perforation is completely open, it is called a simple perforation plate. (C) A scalariform perforation plate in *Magnolia grandiflora*. This perforation plate has eight bars crossing it (the eighth is very small), and it is the presence of bars that distinguishes this type of perforation plate from a simple plate. (D) Alternate intervessel pitting in *Hevea microphylla*. (E) Opposite intervessel pitting in *Liriodendron tulipifera*. (F) Linear (scalariform) intervessel pitting in *Magnolia grandiflora*. Note that these intervessel pits are not the same structures as the scalariform perforation plate seen in C. Scale bars in B–F = 30 μm.

0.1–1.2 mm. Vessels are 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 (Figure 2.6D). If the earlywood vessels are much larger than the latewood vessels, the wood is ring porous (Figure 2.6F). 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 Committee 1989). In addition, the 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 (Figure 2.14B). If bars are present, the perforation plate is called a scalariform perforation plate (Figure 2.14C).

Where the vessels elements come in contact with each other tangentially, intervessel or intervascular bordered pits are formed (Figure 2.14D, Figure 2.14E, and Figure 2.14F). These pits range in size from 2–16 μm in height and are arranged on the vessels walls in threes basic ways. The most common arrangement is alternate, in which the pits are more or less staggered (Figure 2.14D). In the opposite arrangement the pits are opposite each other (Figure 2.14E), and in the scalariform arrangement the pits are much wider than high (Figure 2.14F). Combinations of these can also be observed in some species. Where vessel elements come in contact with ray cells, often simple or bordered pits called vessel-ray pits are formed. These pits can be the same size and shape and the intervessel pits or much larger.

2.11.2.2 Fibers

Fibers in hardwoods function solely as support. They are shorter than softwood tracheids (200–1200 μm) and average about half the width of softwood tracheids, but are usually 2–10 times longer than vessel elements (Figure 2.15). The thickness of the fiber cell wall is the major factor governing

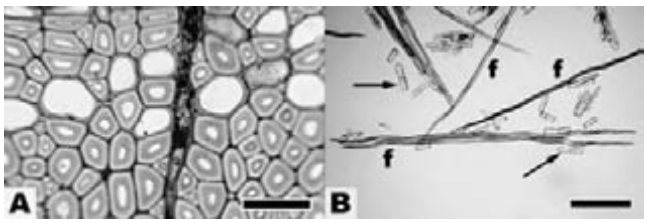

FIGURE 2.15 Fibers in *Quercus rubra*. (A) Transverse section showing thick-walled, narrow-lumined fibers. A ray is passing vertically through the photo, and there are nine axial parenchyma cells, the thin-walled, wide-lumined cells, in the photo. Scale bar = 30 μm. (B) Macerated wood. There are several 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.

density and strength. Species with thin-walled fibers such as cottonwood (*Populus deltoides*), basswood (*Tilia americana*), ceiba (*Ceiba pentandra*), and balsa (*Ochroma pyramidale*) have a low density and strength, whereas species with thick-walled fibers such as hard maple (*Acer saccharum* and *Acer nigrum*), black locust (*Robinia pseudoacacia*), ipe (*Tabebuia serratifolia*), and bulletwood (*Manilkara bidentata*) have a high density and strength. The air-dry (12% moisture content) density of hardwoods varies from 100–1400 kg/m^3. The air-dry density of typical softwoods varies from 300–800 kg/m^3. Fiber pits are generally inconspicuous and may be simple or bordered. In some woods like oak (*Quercus*) and meranti/lauan (*Shorea*), vascular or vasicentric tracheids are present especially near or surrounding the vessels (Figure 2.14A). These specialized fibrous elements in hardwoods typically have bordered pits, are thin-walled, and are shorter than the fibers of the species. The tracheids in hardwoods function in both support and transport.

2.11.2.3 Axial Parenchyma

In softwoods, axial parenchyma is absent or only occasionally present as scattered cells, but in hardwoods there is a wide variety of axial parenchyma patterns (Figure 2.16). The axial parenchyma cells in hardwoods and softwoods is essentially the same size and shape, and they also function in the same manner. The difference comes in the abundance and specific patterns in hardwoods. There are two major types of axial parenchyma in hardwoods. Paratracheal parenchyma is associated with the vessels and apotracheal is not associated with the vessels. Paratracheal parenchyma is further divided into vasicentric (surrounding the vessels, Figure 2.16A), aliform (surrounding the vessel and with wing-like extensions, Figure 2.16C), and confluent (several connecting patches of paratracheal parenchyma sometimes forming a band, Figure 2.16E). Apotracheal parenchyma is also divided into diffuse (scattered), diffuse in aggregate (short bands, Figure 2.16B), and banded whether at the beginning or end of the growth ring (marginal, Figure 2.16F) or within a growth ring (Figure 2.16D). Each species has a particular pattern of axial parenchyma, which is more or less consistent from specimen to specimen, and these cell patterns are very important in wood identification.

2.11.2.4 Rays

The rays in hardwoods are much more diverse than those found in softwood. In some species, including willow (*Salix*), cottonwood, and koa (*Acacia koa*), the rays are exclusively uniseriate and are much like the 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 over eight cells wide, and in oak several centimeters high (Figure 2.17A). In most species the rays are 1–5 cells wide and less than 1 mm high (Figure 2.17B) 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

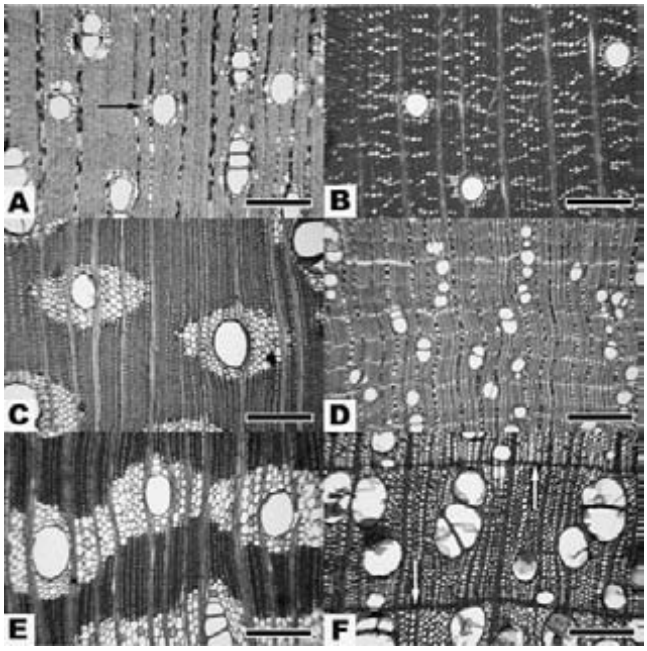

FIGURE 2.16 Transverse sections of various woods showing a range of hardwood axial parenchyma patterns. A, C, and E show woods with paratracheal types of parenchyma. (A) Vasicentric parenchyma (arrow) in *Licaria excelsa*. (C) Aliform parenchyma in *Afzelia africana*. The parenchyma cells are the light-colored, thin-walled cells, and are easily visible. (E) Confluent parenchyma in *Afzelia cuazensis*. B, D, and F show 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 = 300 μm.

similar in shape and size to the softwood ray parenchyma cells (Figure 2.17C). The upright ray cells are ray parenchyma cells turned on end so that their long axis is vertical (Figure 2.17D). Upright ray cells are generally shorter and sometimes 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 varies from one to more than five.

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

2.12 WOOD TECHNOLOGY

Though it is necessary to speak briefly of each kind of cell in isolation, 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, and bending strength, among others, are properties derived from the cells that compose wood. Such larger-scale properties are really the product of a synergy in which the whole is indeed greater than the sum of its parts, but are nonetheless based on chemical and anatomical details of wood structure (Panshin and deZeeuw 1980).

The cell wall is largely made up of cellulose and hemicellulose, and the hydroxyl groups on these chemicals make the cell wall very hygroscopic. Lignin, the agent cementing cells together,

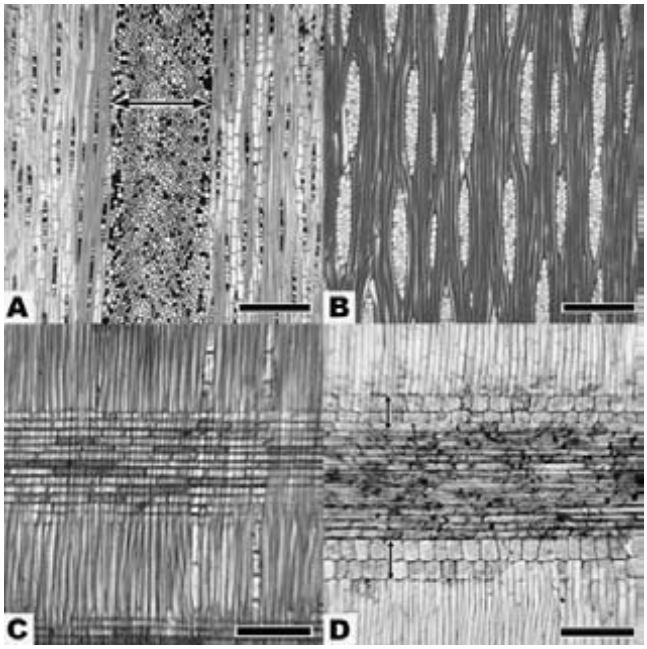

FIGURE 2.17 Rays in longitudinal sections. A and B show tangential sections, scale bars = 300 μm. (A) *Quercus rubra* showing very wide multiseriate ray (arrow) and many uniseriate rays. (B) *Swietenia macrophylla* showing numerous rays ranging from one to four cells wide. Note that in this wood the rays are arranged roughly in rows from side to side. C and D show radial sections, scale bars = 200 μm. (C) Homocellular ray in *Fraxinus americana.* All the cells in the ray are procumbent cells; they are longer radially than they are tall. (D) A heterocellular ray 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.

is a generally 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 great effect on wood properties, and wood-water interactions greatly affect the industrial use of wood in wood products.

Often it is useful to know how much water is contained in a tree or a piece of wood. This relationship is called moisture content and is the weight of water in the cell walls and lumina expressed as a percentage of the weight of wood with no water (oven-dry weight). Water exists in wood in two forms: free water and bound water. Free water is the liquid water that exists 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; the moisture content of green wood can be over 100%, meaning that the weight of water in the wood is more than the weight of the dried cells. In softwoods the moisture content of the sapwood is 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 the FSP (approximately 25–30% moisture content), only free water is lost, and thus no change in the cell wall volumes occurs. However, when the wood is dried further, 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 and essentially linear from 0% moisture content up to the 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).

Density or specific gravity is one of the most important physical properties of wood (Desch and Dinwoodie 1996, Forest Products Laboratory 1999, Bowyer et al. 2003). Density is the weight of wood divided by the volume at a given moisture content. Thus the units for density are typically expressed as pounds per cubic foot (lbs/ft^3) or kilograms per cubic meter (kg/m^3). When density values are reported in the literature it is critical that the moisture content of the wood is also given. Often density values are listed as air-dry, which means 12% moisture content in North America and Europe, but air-dry sometimes means 15% moisture content in tropical countries.

Specific gravity is similar to density and is defined as 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 the same as specific gravity. Density in kg/m^3 must be divided by 1000 to get the same numerical number as specific gravity. Since specific gravity is a ratio, it does not have units. The term basic specific gravity (sometimes referred to as basic density) is defined as the oven-dry weight of wood divided by the volume of the wood when green (no shrinkage).

$$\text{Basic specific gravity} = \frac{\text{Density of wood (oven-dry weight/volume when green)}}{\text{Density of water}}$$

Specific gravity can be determined at any moisture content, but typically it is based on weight when oven-dry and when the volume is green or at 12% moisture content (Forest Products Laboratory 1999). However, basic specific gravity is generally the standard used throughout the world. The most important reason for measuring basic specific gravity is repeatability. The weight of wood can be determined at any moisture content, but conditioning the wood to a given moisture content consistently is difficult. The oven-dry weight (at 0% moisture content) is relatively easy to obtain on a consistent basis. Green volume is also relatively easy to determine using the water displacement method (ref). The sample can be large or small and nearly any shape. Thus basic specific gravity can be determined as follows:

$$\text{Basic specific gravity} = \frac{\text{Oven-dry weight}}{\text{Weight of displaced water}}$$

Specific gravity and density are strongly dependent on the weight of the cell wall material in the bulk volume of the wood specimen. In softwoods where the latewood is abundant (Figure 2.5A) in proportion to the earlywood, the specific gravity is high (e.g., 0.54 in longleaf pine, *Pinus palustris*). The reverse is true when there is much more earlywood than latewood (Figure 2.6B) (e.g., 0.34 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 not only dependent on fiber wall thickness, but also on the amount of void space occupied by the vessels and parenchyma. In balsa the vessels are large (typically >250 μm in tangential diameter), and there is an abundance of axial and ray parenchyma. The fibers that are present are very-thin-walled and the basic specific gravity may be less than 0.20. In very dense woods the fibers are very-thick-walled, the lumina are virtually absent, and the fibers are abundant in relation to the vessels and parenchyma. Some tropical hardwoods have a basic specific gravity of greater than 1.0. In a general sense in all woods, the specific gravity is the relation between the volume of cell wall material to the volume of the lumina of those cells in a given bulk volume.

2.13 JUVENILE WOOD AND REACTION WOOD

Two key examples of the biology of the tree affecting the quality of the 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. If one looks at the growth form of a tree, based on the derivation of wood from the vascular cambium, it quickly becomes evident that the layers of wood in a tree are concentric cones. In a tree of large diameter, the deflection of the long edge of the cone from vertical may be very close to zero, but in narrower-diameter trees, or narrower-diameter portions of a large tree, the angle of deflection is considerably greater. These areas of narrower diameter are typically chronologically younger portions of the tree, for example, the first 15–20 years of growth in softwoods are the areas where juvenile wood may form. 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 et al. 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 shorter and angled, twisted, or bent. The precise functions of juvenile wood in the living tree are not fully understood, but it must confer certain little-understood advantages.

Reaction wood is similar to juvenile wood in several respects, but is formed by the tree for different reasons. Almost any tree of any age will form reaction wood when the woody organ

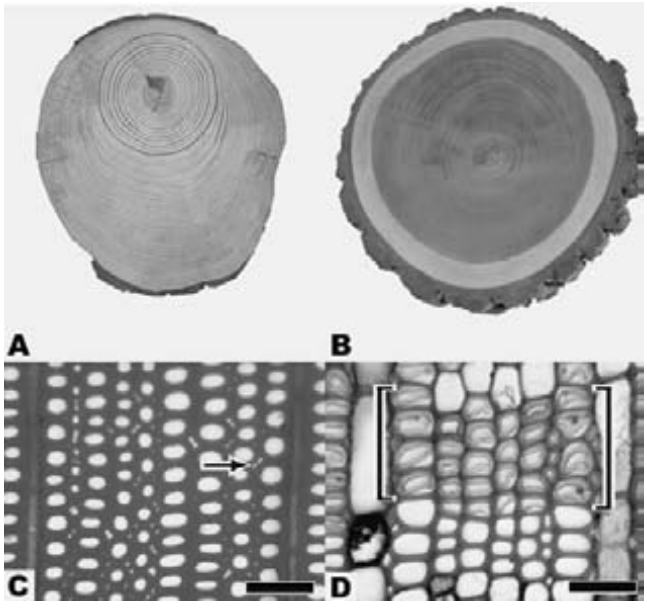

FIGURE 2.18 Macroscopic and microscopic views of reaction wood in a softwood and a hardwood. (A) Compression wood in *Pinus* sp. Note that the pith is not in the center of the trunk, and the growth rings are much wider in the compression wood zone. (B) Tension wood in *Juglans nigra*. The is nearly centered 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 (between the brackets) showing prominent gelatinous layers in *Hevea microphylla*. Rays run from top to bottom on either side of the tension wood fibers, and below them is a band of normal fibers with thinner walls. Scale bars (in C and D) = 50 μm.

(whether a twig, a branch, or the trunk) is deflected from the vertical by more than one or two degrees. 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, the reaction wood is formed on the underside of the leaning organ, and is called compression wood (Figure 2.18A) (Timmel 1986). In hardwoods, the reaction wood forms on the top side of the leaning organ, and is called tension wood (Figure 2.18B) (Desch and Dinwoodie 1996, Bowyer et al. 2003). As just mentioned, 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 (Figure 2.18C). 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 2.18D).

2.14 WOOD IDENTIFICATION

The identification of wood can be of critical importance to primary and secondary industrial users of wood, government agencies, and museums, as well as to 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. Since 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. Since foreign woods are imported into the U.S. market, it is imperative that both buyers and sellers have access to correct identifications and information about their properties and uses.

Lumber graders, furniture workers, and those working in the industry, as well as hobbyists, often identify wood with their naked eye. 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 is atypical, decayed, or small, often the identification is incorrect. Examining woods, especially hardwoods, with a 10–20X hand lens greatly improves the accuracy of the identification (Panshin and deZeeuw 1980, Hoadley 1990, Brunner et al. 1994). 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 the vessel and parenchyma patterns to make an identification.

Scientifically rigorous accurate identifications require that the wood be sectioned and examined with a light microscope. With the light microscope even with only a 10X objective, many more features are available for use in making the determination. Equally as 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 Détienne 2001). In addition to these resources, several computer-assisted wood identification packages are available and are suitable for people with a robust wood anatomical background.

Wood identification by means of molecular biological techniques is a field that is still in its infancy. Though technically feasible, there are significant population-biological limits to the statistical likelihood of a robust and certain identification for routine work (Canadian Forest Service 1999). In highly limited cases of great financial or criminal import and a narrowly defined context, the cost and labor associated with rigorous evaluation of DNA from wood can be warranted (Hipkins 2001). For example, if the question were, “Did this piece of wood come from this individual tree?” or, “Of the 15 species present in this limited geographical area, which one

produced this root?" it is feasible to analyze the specimens with molecular techniques (Brunner et al. 2001). If, however, the question were, "What kind of wood is this, and from which forest did it come?" it would not be feasible at this point in time to analyze the specimen. Workers have shown that specific identification among six species of Japanese white oak can be accomplished using DNA (Ohyama et al. 2001), but the broad application of their methods is not likely for some time. 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. At some point in the indefinite future it is reasonable to expect that molecular tools will be employed in the routine identification of wood, and that such techniques will greatly increase the specificity and accuracy of identification, but until that day comes, scientific wood identifications will rely on microscopic evaluation of wood anatomical features.

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HANDBOOK OF
WOOD CHEMISTRY AND WOOD COMPOSITES

Edited by
Roger M. Rowell

CRC PRESS

Boca Raton London New York Washington, D.C.

Library of Congress Cataloging-in-Publication Data

Handbook of wood chemistry and wood composites / edited by Roger M. Rowell.
p. cm.
Includes bibliographical references and index.
ISBN 0-8493-1588-3 (alk. paper)
1. Wood—Chemistry—Handbooks, manuals, etc. 2. Engineered wood—Handbooks, manuals, etc.
I. Rowell, Roger M.

TS932.H36
620.1'2—dc22 2004057915

Visit the CRC Press Web site at www.crcpress.com

International Standard Book Number 0-8493-1588-3
Library of Congress Card Number 2004057915
Printed in the United States of America 1 2 3 4 5 6 7 8 9 0
Printed on acid-free paper