CHAPTER

3

Composition and Structure of Wood Cells

As a building material, wood is one of the simplest, most easily used products; it can be cut and shaped with ease and fastened readily. At the same time, wood is one of our most complex materials. It is made up of tiny cells, each of which has a precise structure of tiny openings, membranes, and intricately layered walls. The ease with which wood is converted to a product and maintained depends upon practical knowledge of its structure. The cellular nature of wood was introduced in Chapters 1 and 2. In this chapter the molecular composition of wood cells is discussed.

Chemical Components

Wood is composed principally of carbon, hydrogen, and oxygen. Table 3.1 details the chemical composition of a typical North American wood and shows carbon to be the dominant element on a weight basis. In addition, wood contains inorganic compounds that remain after high-temperature combustion in the presence of abundant oxygen; such residues are known as *ash*. Ash is traceable to the occurrence of incombustible compounds containing elements such as calcium, potassium, magnesium, manganese, and silicon. The fact that domestic woods have a very low ash content, particularly a low silica content, is important from the standpoint of utilization; woods having a silica content of greater than about 0.3 percent (on a dry weight basis) dull cutting tools excessively. Silica contents exceeding 0.5 percent are relatively common in tropical hardwoods and in some species may exceed 2 percent by weight.

The elemental constituents of wood are combined into a number of organic *polymers* (from Greek, *poly* plus *metros*, meaning "many parts") (Brown 1997): cellulose, hemicellulose, and lignin. Table 3.2 shows the approximate percentage of dry weight of each in hardwood and softwood. Cellulose, perhaps the most important component of wood, constitutes slightly less than one-half the weight of both hardwoods and softwoods. The proportion of lignin and hemicellulose varies widely among species and between the hardwood and softwood groups.

TABLE 3.1. Elemental composition of wood.

Element	% dry weight
Carbon	49
Hydrogen	6
Oxygen	44
Nitrogen	0.1
Ash	0.2–0.5*

*As high as 3.0–3.5 in some tropical species.
Source: Fengel and Wegner (1984).

TABLE 3.2. Organic constituents of wood.

Type	Cellulose	Hemicellulose	Lignin
		% dry weight	
Hardwood	40–44	15–35	18–25
Softwood	40–44	20–32	25–35

Source: Kollmann and Côté (1968), 57, 65.
Note: Pectins and starch commonly compose approximately 6% of the dry weight.

Cellulose

Photosynthesis is the process by which water and carbon dioxide are combined in the leaves of green plants, employing the energy from sunlight to form glucose and other simple sugars, with oxygen as a by-product (Fig. 3.1). Following its formation, glucose may be converted to starch, or to other sugars such as glucose 6-phosphate or fructose 6-phosphate and then to sucrose ($C_{12}H_{22}O_{11}$) (Kozlowski and Pallardy 1997). Sucrose and other sugars are then transported in the form of sap to processing centers located at branch tips (apical meristems) and through the inner bark to meristems at the root tips and to the cambial region that sheaths the main bole, branches, and roots. Upon reaching the cytoplasm of individual cells in these various regions, sucrose is hydrolyzed (combined with water) to form glucose and fructose (both $C_6H_{12}O_6$). As indicated in Chapter 1, trees use these sugars to make leaves, wood, and bark.

Cellulose is synthesized within living cells from a glucose-based sugar nucleotide. A nucleotide is a compound derived from combining a sugar with a phosphate group and a base that is a constituent of RNA or DNA. Complex and separate mechanisms are thought to control initiation of cellulose-chain formation, chain elongation, and termination of the synthesis process (Peng at al. 2002). The net effect of these processes is that glucose molecules are joined together end to end, with elimination of a water molecule for each chemical linkage formed between neighboring units. The ensuing linear long-chain polymer, cellulose $(C_6H_{10}O_5)n$, has a degree of polymerization, n, which may be as large as 10,000. The structural relationship between glucose and cellulose is formally depicted in Figure 3.2. Hemicelluloses are synthesized in a sequence similar to that outlined above, but they start from a different nucleotide. It is important to note that fructose may convert to glucose for use in synthesis of cellulose, or to mannose, or to other sugars used in making hemicellulose or other compounds.

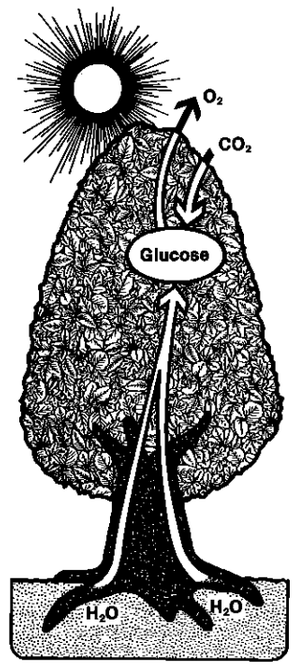

FIGURE 3.1. The process of photosynthesis.

Cellulose is a material with which people are somewhat familiar. Cotton, for example, is 99 percent pure cellulose. Fine writing papers are also manufactured largely from the cellulosic fraction of wood. Although it is a carbohydrate, cellulose is not a source of food for humans or most animals. In cellulose, the glucose units are interconnected through ß linkages, where the ß designation refers to a specific spatial configuration of the glucosidic bond connecting successive sugar units. As a point of interest, the glucose residues of the *polysaccharide* (saccharide meaning *sugar unit*) starch are identical in every respect except one: They incorporate an α glucosidic bond (actually, the mirror image of ß) between glucose units. Though cellulose in the form of wood or cotton has as much food value as sucrose, cellulose cannot be digested by humans because the enzymes in body fluids can hydrolyze ß but not α linkages. However, certain animals (ruminants) are able to utilize cellulose as food because they maintain intestinal colonies of microorganisms that produce enzymes known as cellulases, which convert cellulose to metabolically useful glucose. Termites have similar internal microflora.

At this point it is important that the reader have an idea of the size of the material being discussed. After reading about a cellulose molecule made of up to 10,000 glucose units, a very large structure might be envisioned. Although large from a molecular viewpoint, the longest cellulose molecules are about 10 microns (μm) (1/1000 cm) in length and about 8 angstroms (Å) in diameter (1 Å = 1/10,000,000 cm), too small to be seen even with the use of an electron microscope.

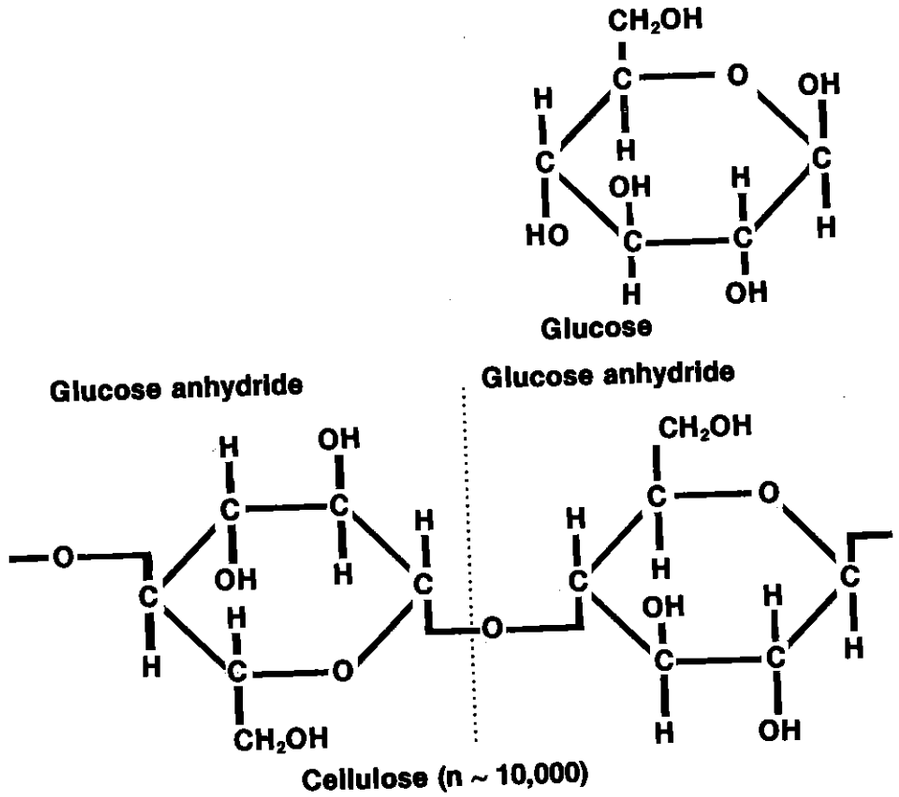

FIGURE 3.2A. Glucose to cellulose.

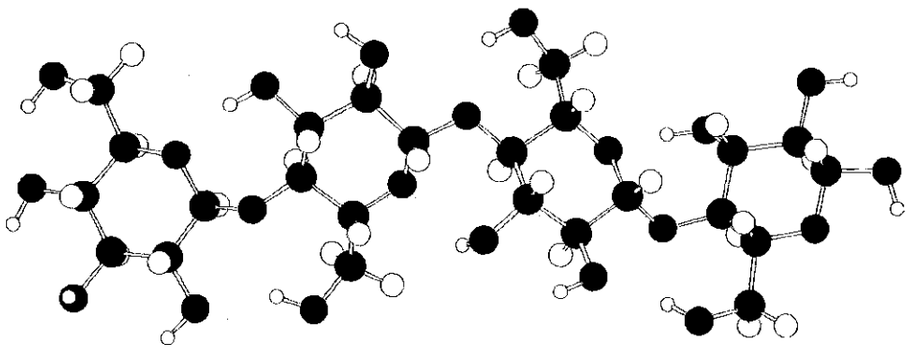

FIGURE 3.2B. Stereo view of a portion of cellulose molecule. (Drawing by Charles Frazier, using ChambridgeSoft, Chem3D, v. 4.0.)

Hemicellulose

Although glucose is the primary sugar produced in the process of photosynthesis, it is not the only one. Other six-carbon sugars, such as galactose and mannose, and five-carbon sugars, such as xylose and arabinose, are also manufactured in the leaves. These and other sugar derivatives such as glucuronic acid, along with glucose, are used within developing cells in synthesizing lower molecular weight polysaccharides called *hemicelluloses*. Most of the hemicelluloses are branched-chain polymers, in contrast to the straight-chain polymer cellulose, and generally are made up of sugar units numbering only in the hundreds (that is, the degrees of polymerization are in the hundreds rather than thousands or tens of thousands).

Lignin

Lignin is a complex and high molecular weight polymer built upon phenylpropane units (Fig. 3.3). Although composed of carbon, hydrogen, and oxygen, lignin is not a carbohydrate nor even related to this class of compound. It is, instead, essentially phenolic in nature. Lignin is quite stable and difficult to isolate and occurs, moreover, in a variety of forms; because of this, the exact configuration of lignin within wood remains uncertain. One view is that lignin consists of a group of aromatic polymers, predominantly glycolignin—an ordered polymer made up of multiples of a repeating unit consisting of 18 phenylpropane units (Forss and Fremer 2003).

Lignin occurs between individual cells and within the cell walls. Between cells, it serves as a binding agent to hold the cells together. Within cell walls, lignin is very intimately associated with cellulose and the hemicelluloses, and it gives rigidity to the cell. Lignin is also credited with reducing dimensional change with moisture content fluctuation and has been said to add to wood's toxicity, thus making it resistant to decay and insect attack. The rigidity provided by lignin is an important determinant of wood properties. Recollection of the very soft nature of cotton (almost pure cellulose) and the com-

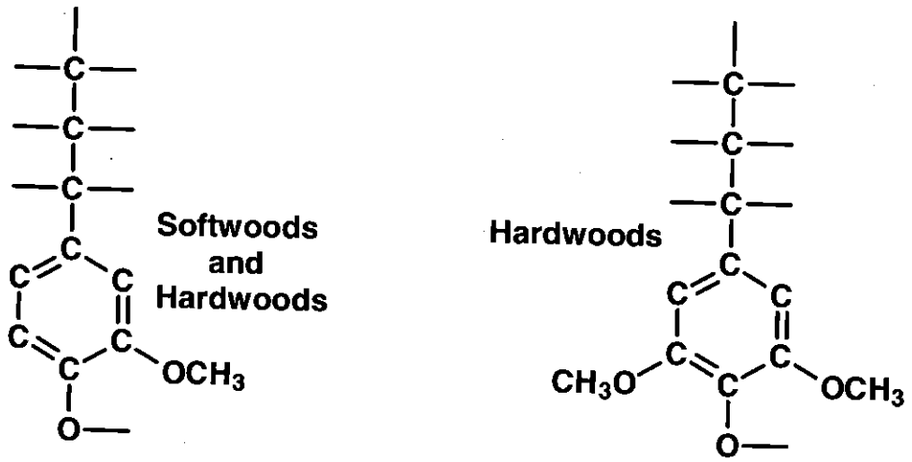

FIGURE 3.3. Building blocks of lignin.

pliant nature of seaweed (which has very little lignin) are indications of how nonrigid wood would be without a stiffening ingredient.

In its native form, lignin is only very lightly colored. However, even the mildest treatments available for removing lignin from wood cause appreciable degradation of its structure, resulting in a deepening of its color. Thus, chemical pulps (see Chapter 17) that contain residual lignin require considerable bleaching to make them white in color. Because the pulping process used in making newsprint involves mechanical separation of fibers and not lignin removal, only a light brown color develops, which is readily removed by chemical bleaching. However, when the lignin present in newsprint is exposed to air, particularly in the presence of sunlight, the resulting lignin derivatives tend to become yellow or brown with age; a small part of yellowing with age is also traceable to the hemicelluloses. Because of the lignin in mechanical pulp, newsprint has a notoriously short longevity due to its high lignin content; it is also coarse, bulky, and of low strength because the fibers are difficult to bond to one another because of their inherent stiffness.

Cell Wall

Recall that a tree is sheathed by a thin cambial layer, which is composed of cells capable of repeated division. New cells produced to the inside of this sheath become new wood, and those moved to the outside become part of the bark. In this section, the chemical configuration of woody cell walls is examined, as are steps in the development of new cells.

Chemical Structure

A newly formed wood cell is encased in a thin, membranelike and pectin-rich wall called a *primary wall,* and the cell is filled with fluid. *Pectins* are complex colloidal substances of high molecular weight that, upon hydrolysis, usually yield galacturonic acid and small amounts of arabinose and galactose. The precise structure of pectin is not completely understood. In a process that may take several days to several weeks to complete, the cell enlarges and the cell wall gradually thickens as biopolymers produced within the cells are progressively added to the inside (lumen side) of the wall (Fig. 3.4). Eventually, the protoplasm that fills the cell is lost and the cell has a thickened wall, consisting of primary and secondary wall layers, and a hollow center (Fig. 3.4d). Successive arrangements of biopolymer assemblies are responsible for the gradual thickening of a cell wall. But what are these *biopolymers*? They are the three distinct types of macromolecule described earlier: cellulose, hemicellulose, and lignin.

The buildup of biopolymers on the inner surfaces of the cell wall is not haphazard; it occurs in a very precise fashion. Cellulose, for example, is not incorporated into the cell wall as individual molecules but rather as intricately arranged clusters of molecules. The long-chain cellulose molecules are synthesized from anhydroglucose (actually glucose attached to a mononucleotide) in many specific locations at the inner surface of the cell wall itself. As these chains lengthen, they aggregate laterally in a well-defined way with their immediate neighbors, which are also growing, to form crystalline domains in a unit cell configuration (Fig. 3.5). The cellulose crystal lattice is held together by intermolecular and dipolar interactions primarily in the form of hydrogen bonds; this arrangement is so stable that the individual chains cannot be dissolved in common sol-

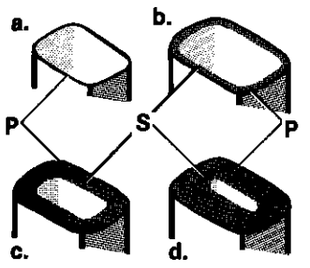

FIGURE 3.4. Stages in development of a wood cell. Longitudinal cells in cross section: (a) new cell has only ultrathin primary wall (P); (b,c) cell enlarges and then wall thickens as secondary wall (S) forms to inside of primary wall; (d) wall continues to thicken with buildup of deposits.

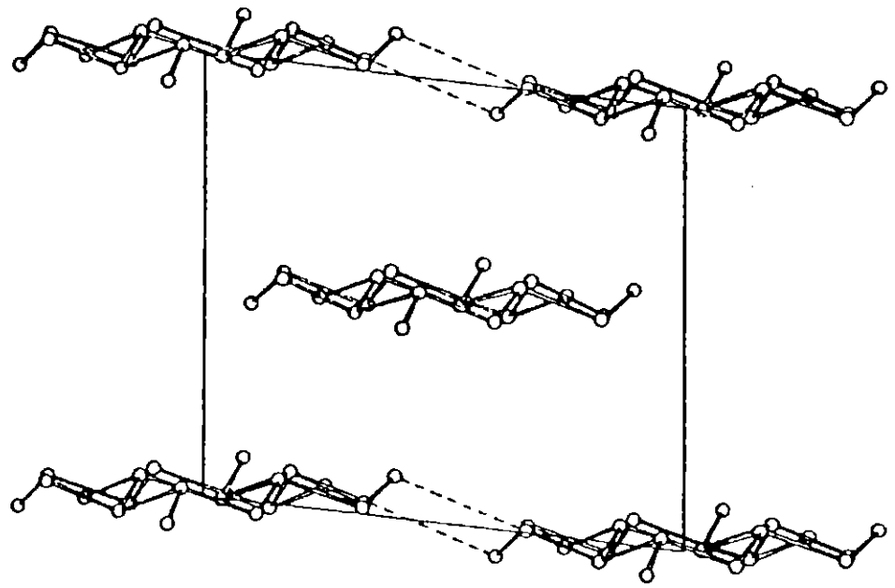

FIGURE 3.5. Unit cell configuration of cellulose. Source: Woodcock (1979).

vents such as water or acetone. Cellulose can be dissolved in very exotic, highly polar solvents capable of disrupting hydrogen bonds (Heinze and Liebert 2001).

A number of studies of wood, with some dating back three decades, have determined that the highly crystalline networks of cellulose are united into larger structures within the wood cell wall. These structures are known as *microfibrils.*

As noted by Preston (1986), studies of cellulose in the late 1940s and early 1950s soon after introduction of the electron microscope showed the cell wall to be composed of long, thin strands. These strands, or microfibrils, were later shown to be cellulosic and composed of bundles of cellulose chains lying parallel to the microfibril length. Subsequent research in the mid-1950s through early 1970s, in which isolated microfibrils were subjected to chemical extraction, showed microfibrils to consist of an inner core consisting almost entirely of glucose constituent sugars (suggesting a cellulose core) and an outer core composed of 15 percent or more nonglucose sugars (Stamm 1964;

Jane et al. 1970). These findings led to the conclusion that cellulose bundles are covered or sheathed in strongly adsorbed chains of sugars other than glucose (such as hemicellulose). Research also points to crystalline (highly ordered) and amorphous (less ordered) regions within microfibrils, with individual cellulose molecules running through several crystalline and amorphous regions (Kollmann and Côté 1968; Tsuchikawa and Siesler 2006).

Because of the difficulty of isolating cellulose that is part of a heavily lignified woody cell wall, researchers have focused on cells that can be more easily studied. One such kind of cell is that of the green algae, valonia, that has unlignified cell walls in which cellulose is organized into microfibrils. Other work has been done with the bacterium *Acetobacter xylinum* and the primary walls of tobacco leaf epidermal cells. Findings have been correlated with measured sizes of wood microfibrils to develop models of the cellulose structure in wood.

Fujita and Harada (1991) described cellulose microfibrils in a very straightforward manner, describing them as consisting of a "core crystalline region of cellulose surrounded by the paracrystalline [less highly ordered] cellulose and short chain hemicellulose." Ruben et al. (1989) proposed a more specific structure based on their studies of tobacco leaf cells and *A. xylinum*. Their work indicates that the extent of each crystalline domain is confined to just nine cellulose chains, which together may be viewed as a *subelementary fibril* 18Å in width. Three such subelementary fibrils are wound in a left-handed triple-helical fashion around one another to form an *elementary fibril* that is 37Å wide. These elementary fibrils then aggregate into microfibrillar bundles with some assistance from hydrogen bonding in which hemicellulose plays a role. A proposed model of the arrangement of elementary fibrils (Fig. 3.6) shows crystalline and amorphous regions and variations in spacing between elementary fibrils in hardwoods and softwoods.

Later work led to the observation that electron micrograph analyses of microfibrils of valonia showed cellulose to be highly crystalline; furthermore, there did not appear to be any subunits in these microfibrils corresponding to elementary or subelementary fibrils (Fujita and Harada 1991). There is some speculation that the triple-stranded structures typify microfibrils in the primary cell wall, whereas microfibrils in the *secondary cell wall* are highly crystalline arrays of straight cellulose chains (Ruben et al. 1989). There is also now strong evidence that each microfibril in a woody cell wall is composed of thirty-six glucan chains (Dellmer and Armor 1995). In any case, it is clear that long-chain cellulose molecules are arranged within the cell wall in a rather precise fashion and are combined into larger structures, the microfibrils.

What, then, of the hemicellulose and lignin? The hemicelluloses, probably somewhat selectively, interact through hydrogen bonding with the cellulose and have been implicated in the aggregation of elementary fibrils into microfibrils. Hemicelluloses, as noted earlier, are known to sheath the microfibrillar bundles. Moreover, the hemicelluloses are chemically linked to lignin *macromolecules* and thus fulfill a particularly important function in maintaining cohesion between the architectural building materials of the wood cell wall. The way in which lignin is incorporated into the cell wall represents another area of disagreement among scientists. The longstanding view is that lignin is deposited between microfibrils during and after the wall thickening process. Another view (Goring 1977) is that lignin is placed in a lamellar configuration between the microfibrils (Fig. 3.7): it appears to occupy its allocated space in the form of undulating two-dimensional sheets with thicknesses of 16–20Å. Although the precise nature of

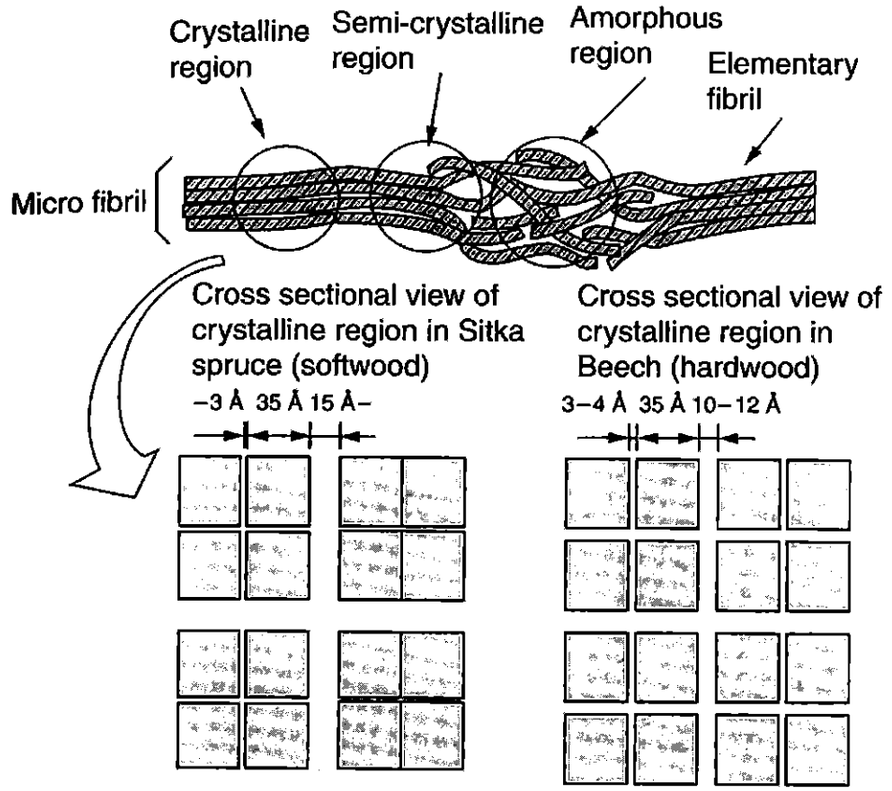

FIGURE 3.6. Crystalline and amorphous regions within a microfibril. Source: Tsuchikawa and Siesler (2006).

lignin continues to elude researchers, it is known that the aromatic rings tend to lie parallel to one another within the wood cell wall. Yet neither lignin nor its chemical derivatives have ever been coaxed into a crystalline form from solution, whereas cellulose and many of the hemicelluloses crystallize quite readily.

In summary, the secondary layer of the wood cell wall can be viewed as a laminated filamentary composite. The cellulose molecules provide the structurally reinforcing network. These are embedded in a matrix composed also of hemicelluloses and lamellar lignin "sheets" that are partly bound to one another through chemical bonds. There is, however, more to the story, and the part to come is no less important.

Layering

The primary wall, described previously as being pectin rich, later becomes heavily lignified. The primary wall is also reinforced with a more-or-less random network of microfibrils. This random arrangement contrasts with the very organized microfibril pattern in the secondary wall.

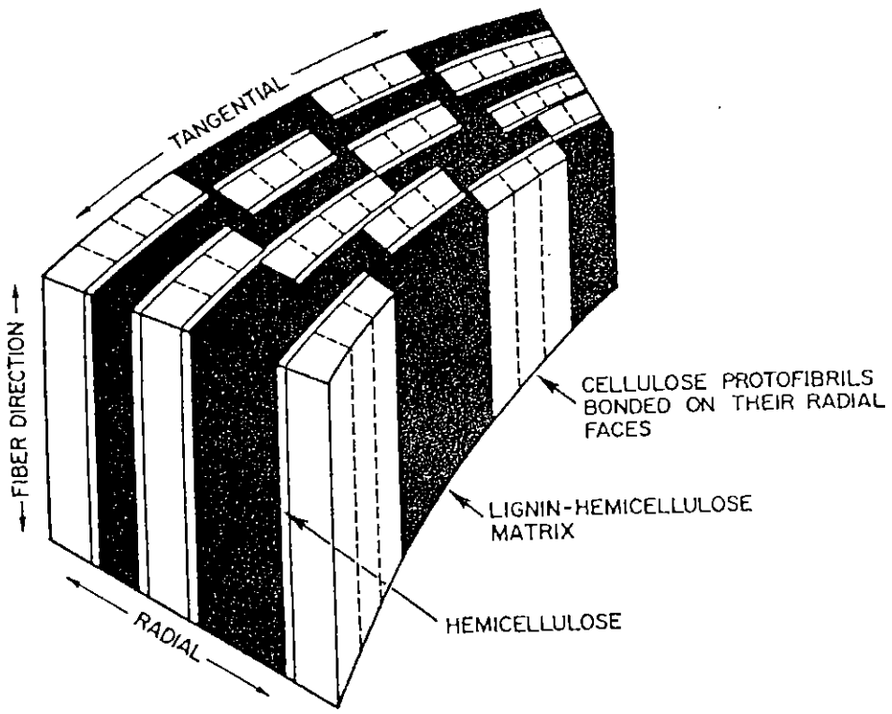

FIGURE 3.7. Ultrastructural arrangement of lignin and polysaccharides in wood cell wall.

The first few microfibrils that are synthesized as the secondary wall starts to form are laid down in a particular way; they are spiraled around the cell interior, with the long axes of the microfibrils nearly perpendicular to the long axis of the cell. After a few layers form in this way, the orientation begins to change; microfibrils spiral about the cell at a much smaller angle to the cell axis. Just prior to final development of the cell, a change in orientation again occurs, with the last several layers arranged similarly to the first few layers. Thus the secondary part of a cell wall has three more-or-less distinct layers (Fig. 3.8). For purposes of discussion, these layers are numbered according to the order in which they are formed: S-1, S-2, S-3. Study Figure 3.8 carefully. This intricate structure of the cell wall is the key to the behavior of wood. Note that the S-2 layer is much thicker than the others. The S-1 and S-3 layers in a softwood are on the order of four to six layers of clustered microfibrils, or *lamellae,* thick; the number of lamellae comprising the S-2 may vary from 30 to 40 in thin-walled earlywood cells to 150 or more in latewood cells (Kollmann and Côté 1968, 26). In an earlywood cell, these proportions would translate to thicknesses of about 0.1 μm for S-1 and S-3 layers and 0.6 μm for the S-2. Because the S-2 layer is much thicker, this wall layer has the greatest effect on how the cell behaves.

As various layers of the secondary wall are built up as a series of uniformly thick sublayers or lamellae, microfibril angles in the cell wall change gradually from lamella to lamella, rather than abruptly as might be inferred from Figure 3.8. As described by

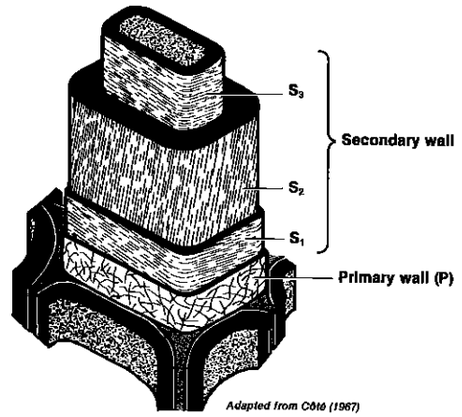

FIGURE 3.8. Layering of a mature cell wall.

Abe et al. (1995, 1997) and Abe and Funada (2005), the orientation of microfibrils in the S-1 layer of conifers shifts gradually in a clockwise direction from an S-helix (>90°) to a Z-helix (<90°) from the outer to the inner layer in the S-1 layer. In the S-2 layer the Z-helix is maintained, although the microfibril angle is much smaller than in the S-1 layer. In the S-3 layer the microfibril orientation again gradually shifts clockwise from a Z-helix to an S-helix at the innermost surface. An example of microfibril orientation is provided by radiata pine; in this species microfibril angles in the S-1, S-2, and S-3 layers have been measured at 79–113 degrees, 1–59 degrees, and 50–113 degrees, respectively (Donaldson and Xu 2005).

It is known that a high microfibril angle significantly affects both strength and directional shrinkage properties of wood, thus creating concerns about the presence of juvenile wood in lumber and other structural and nonstructural wood products. Courchene et al. (2006) demonstrated that microfibril angle is equally important in raw material used in making paper, with test results showing paper tensile strength, stretch, modulus of elasticity, stiffness, and moisture-induced expansion in refined and unrefined pulps also significantly impacted by microfibril angle.

A look at the distribution of biopolymeric components in the various wall layers concludes this discussion of cell wall organization. It is important to recognize that cellulose, hemicellulose, and lignin all occur in each layer of the cell wall. This is illustrated in Figure 3.9, which was derived from chemical analysis of various cell wall layers of coniferous woods. Note that cellulose is present in only small amounts in the compound middle lamella, increasing as a proportion of the dry weight of the cell wall through the center portion of the S-2 layer. Lignin, on the other hand, is the dominant component between cells, with the concentration as a proportion of the cell wall decreasing as the lumen is approached. Considerable disagreement exists as to the proportion of lignin in the compound middle lamella. Figure 3.9 shows that although the largest concentration of lignin is in the middle lamella, the extreme thinness of this layer means that most of the overall quantity of lignin is found in the secondary wall.

The intricate structure of the woody cell wall that defines many of the physical and mechanical properties of wood and the fact that this intricacy develops within living cells have not escaped the attention of wood scientists. Relatively recent development of

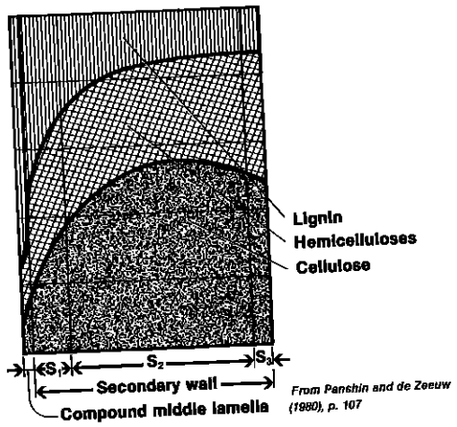

FIGURE 3.9. Distribution of organic compounds within various cell wall layers of a softwood.

scientific tools that allow measurement and imaging of extremely small structures laid the foundation for a new field of scientific inquiry and development known as *nanotechnology*. Most early work in this area has focused on carbon and the use of carbon *nanotubes* (perfectly straight tubules with diameters of nanometer size, and properties close to that of an ideal graphite fiber) for applications ranging from microelectrodes in electrochemical reactions to mechanical reinforcement of a range of products (Ajayan and Zhou 2001). For purposes of reference, a nanometer is one billionth of a meter, and a sheet of paper is about 100,000 nanometers thick.

Now, scientists are beginning to look at wood and the possibility of working at the nanoscale to create new, lighter, stronger, more absorptive products. A commentary about cellulose nanofibrils (cellulose molecules and microfibrils) as compared to carbon nanotubes included the observation that "cellulose nanofibrils exhibit a modulus roughly one-quarter to one-fifth that of carbon nanotubes, yet they are produced naturally without the need for energy consuming, high-temperature processing." (Atalla et al. 2006).

The potential gains from application of nanotechnology to wood science are large. If scientists were, for example, able to understand the intricate mechanisms that control formation of cellulose, hemicellulose, microfibrils, and lignin within the cytoplasm of developing cells under the guidance of genetic encoding, that might enable them to develop new materials that self-assemble from molecular building blocks. Or, it might be possible to insert nonwood materials with some precision into the cellular structure of wood for the purpose of developing or enhancing specific properties, or to create molecular scale holes or punctures in cell walls to enhance wood densification, wood chemical modification, and surface adhesion (Moon et al. 2006, Atalla et al. 2006). Considerable research into nanotechnology applications in wood science is likely in coming years.

Cell Wall Sculpturing

Wood cells that function primarily in the storage and conduction of food materials are known as *parenchyma*. These cells typically form thin secondary walls and are the last to remain functional prior to heartwood formation. Other kinds of cells, in contrast, serve principally as avenues of fluid conduction in the living tree; these often form thick

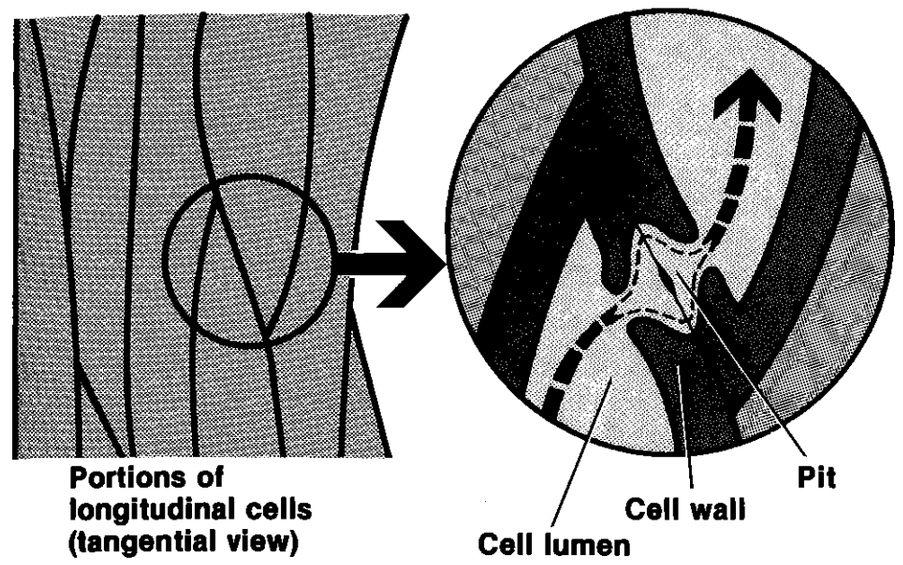

FIGURE 3.10. Pits provide tiny passageways for flow.

secondary walls and thus are important in providing mechanical support to stems in which they occur.

Pitting. All types of cells are characterized by secondary wall layers that are not continuous. Instead, walls are interrupted by regions in which the secondary portion of the wall is lacking. Known as *pits*, these regions generally appear quite different in parenchyma as compared to other kinds of cells.

Normally, pit placement in one cell is exactly matched by the position of pits in adjoining cells. Pits thus tend to occur as matched pairs.

Because pit regions are areas of the cell wall that lack secondary thickening, they are, in effect, thin spots in the cell wall. As such, these areas are much more readily penetrated by fluids and gases than are unpitted zones; thus *pit pairs* are the primary avenues of cell lumen-to-lumen transport (Fig. 3.10).

Pits that mark the walls of parenchyma cells are called *simple pits*. Pitting between two ray parenchyma cells is illustrated in Figure 3.11. Because both cells in this figure are of the parenchyma type, the pits shown form a simple pit pair. Note that whereas secondary wall material is lacking in the pit zone, the primary walls of the two adjacent cells remain. The primary walls and the thin layer of intercellular material that separates them form the *pit membrane*.

The type of pit typifying nonparenchyma cells is shown in Figures 3.12 and 3.13. This is called a *bordered pit*, so named because the pit aperture appears to be surrounded by a border when viewed frontally. Rather than consisting of a simple gap in the secondary part of the wall, a bordered pit is a conical depression in the secondary wall that is concave toward the middle lamella and has an opening leading to the cell lumen at the depth of the depression. A pair of this kind of pit, typical of those connecting two con-

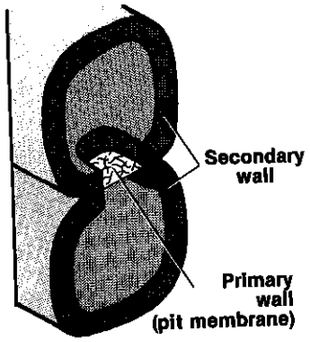

FIGURE 3.11. Simple pitting in adjoining ray parenchyma cells (tangential view).

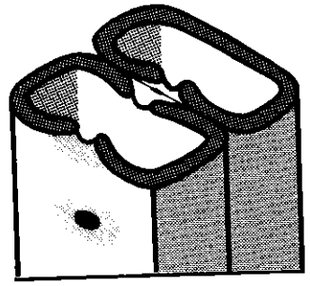

FIGURE 3.12. Bordered pitting in softwood longitudinal tracheids.

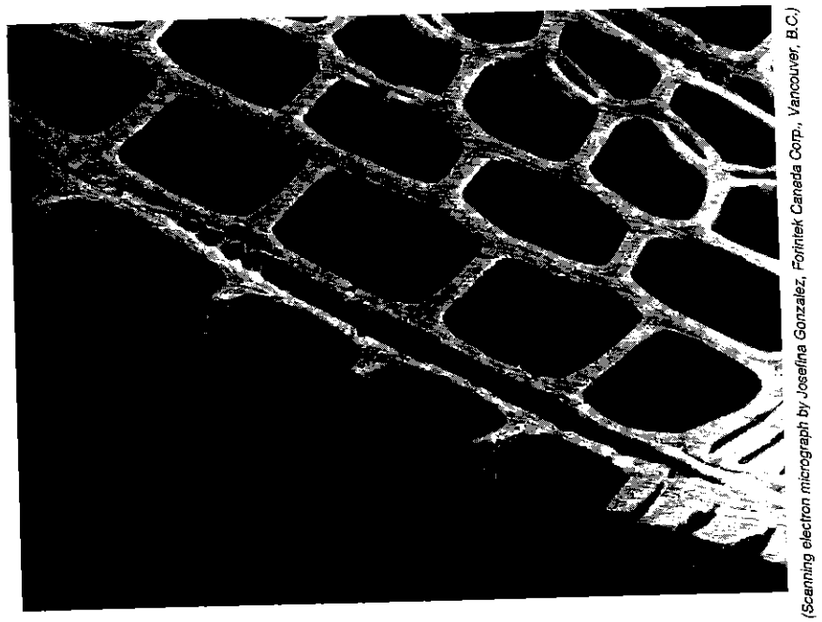

FIGURE 3.13. Bordered pitting in longitudinal tracheids. Radial/transverse view of Sitka spruce (*Picea sitchensis*). ×400.

ductive cells, is shown in highly magnified profile view in Figure 3.14B. In this view, secondary walls are seen to overarch the primary wall, forming a pit cavity. As in simple pits, the primary walls of adjacent cells form a pit membrane. When storage (parenchyma) and conductive cells are in contact, each cell usually forms simple and bordered pits, respectively. The resulting pit pair is termed *half-bordered* (Fig. 3.14C).

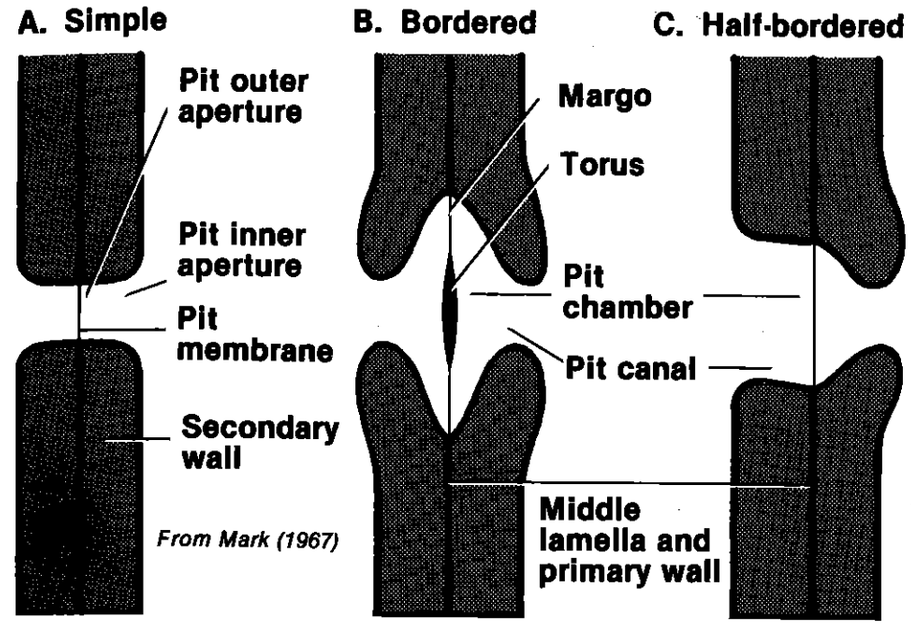

FIGURE 3.14. Profile of various types of pit pairs.

In softwoods, the pit membrane between two bordered pits differs from that separating a simple or half-bordered pit pair. In the latter two kinds, the pectin-rich and microfibril-reinforced primary wall remains unmodified within the pit zone. The common primary walls separating two softwood bordered pits are, however, changed considerably as pits are formed.

Bordered pit formation apparently begins prior to the start of S-1 layer formation with the development of a ring of cellulose on the primary wall. This ring defines the outer boundary of the pit. Then, as secondary wall formation commences, the pit membrane undergoes modification. The membrane center becomes thickened through accumulation of densely packed and sometimes circularly arranged microfibrils. This thickening is called the *torus*. The area surrounding the torus is named the *margo*, and it too becomes different from the normal primary wall. A net of radially arranged microfibrils may form over the existing primary wall, connecting the torus to the pit exterior. At about the same time, the pectin-rich matrix of the compound middle lamella enzymatically decomposes, leaving a more or less open network (Fig. 3.15). In at least one species, Ginko biloba, torus thickening of the pit membrane is the first step in bordered pit formation, occurring during the process of radial expansion of the longitudinal tracheid (Dute 1994). Finally, secondary wall thickening is completed through successive development of microfibrillar layers, thus forming the arch or conically shaped wall structure (Wardrop 1964).

Bordered pits are structurally similar in hardwood and softwood species except that the membranes are quite different. Membranes of all pit combinations in hardwoods are similar to those characterizing simple and half-bordered pit pairs in softwoods. Hence,

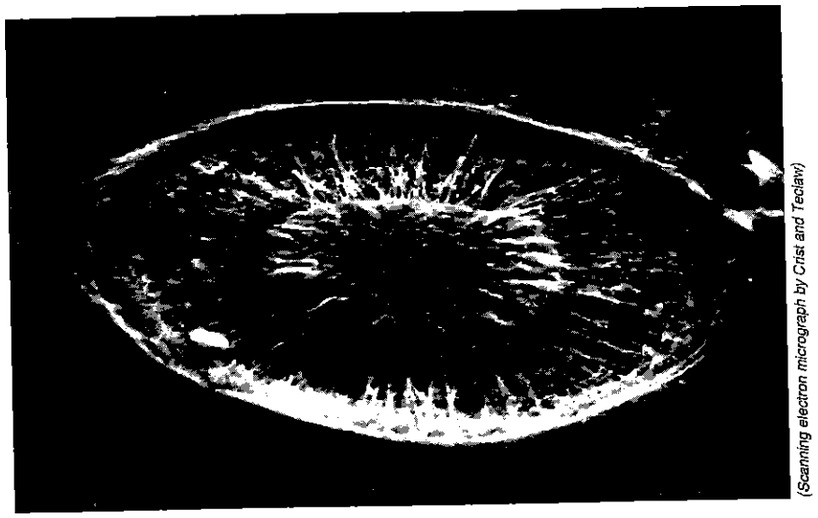

FIGURE 3.15. Bordered pit membrane. Red pine (*Pinus resinosa*). ×3400.

no torus develops and there is no dissolution of portions of the primary wall. In such an unmodified wall, it has been reported that no openings are visible, even at magnifications of ×100,000 (Kollmann and Côté 1968, 31). In comparison, filtration experiments with softwood bordered pit membranes have shown openings approximating 0.2 μm in size in the reinforced microfibril network (Liese 1954).

It has long been conjectured that pit regions substantially reduce fiber strength, a notion that is not generally substantiated by scientific observation (Mark 1967, 47). Bailey (1958) noted that bordered pits, which characterize stem-strengthening and fluid-conducting cells, appear to be configured to provide the maximum exposure of thin, readily penetrable wall area, with only minimal reduction in secondary wall reinforcement. Microfibril buildup around pit areas may also help to reduce the effect of pits upon wall strength.

The pits dotting the cell wall cause local variation in the normal S-1, S-2, and S-3 microfibril orientation discussed earlier. Sedighi-Gilani et al. (2006) used confocal laser scanning microscopy to study microfibril angles in spruce, showing clear evidence of microfibril angle disruption around large bordered pits on radial cell walls of earlywood, but little disruption on tangential cell walls and in cell walls of latewood. Figure 3.16 illustrates how microfibrils curve around the pit regions (Mark 1967, 13; Anagnost et al. 2002).

Spiral Thickening. In some woods, formation of the S-3 layer is followed by development of spirally arranged ridges of microfibril bundles on the lumen side of the secondary wall. Such ridges are distinctly separate from the S-3 layer, as evidenced by the fact that they are relatively easily detached from it (Wardrop 1964), and they only rarely parallel the S-3 microfibril orientation. These ridges are termed *spiral thickenings* (Fig. 3.17).

Spiral thickenings occur in cells of relatively few softwoods and thus, when present, are a valuable clue to a wood's identity. In hardwoods, spiral thickening is relatively

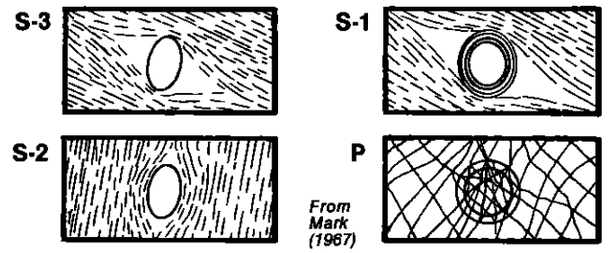

FIGURE 3.16. Pits disrupt regular microfibril angles.

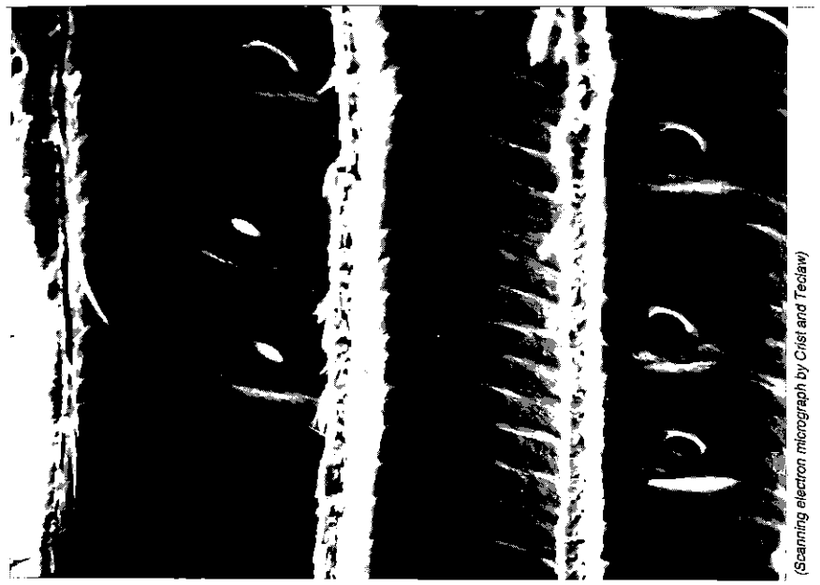

FIGURE 3.17. Spiral thickening in longitudinal tracheids. Douglas-fir (*Pseudotsuga menziesii*). ×830.

common. Although helically arranged thickenings may form throughout the length of a cell, this feature in other cells may be restricted to only the tips or center portions. Because location of thickenings is often consistent within a given species of wood, this factor can also be of diagnostic significance.

Review

A. Terms to define or explain:
   1. Carbohydrate
   2. Micron
   3. Nanometer
   4. Crystallites
   5. Parenchyma
   6. Torus

7. Simple pit
8. Bordered pit
9. Spiral thickening
10. Primary wall
11. Secondary wall
12. Microfibril
13. Elementary fibril
14. Subelementary fibril
15. Polymerization

B. Questions or concepts to explain:
1. What are the principal biopolymeric components in wood and the approximate proportions of wood made up of each? How do softwoods and hardwoods differ in this regard?
2. Describe the essential characteristics of cellulose, hemicellulose, and lignin.
3. How are the biopolymeric components structurally incorporated into the cell wall?
4. What is the function of pit pairs in adjacent wood cells? Which kinds of pitting connect different types of cells?
5. What are pit membranes? What is the nature of such membranes?

C. Food for thought:
1. Knowing the orientation of microfibrils in the S-2 layer of a cell, what would be the effect on cell dimensions if these microfibrils were somehow to move more closely together?
2. Assuming that water molecules could gain access to sites between microfibrils in the S-2 layer of the cell wall and cause them to move farther apart, what might happen if this process were not restrained? Along these lines, what might be one function of the S-1 and S-3 layers of the cell wall?

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