Cell Walls

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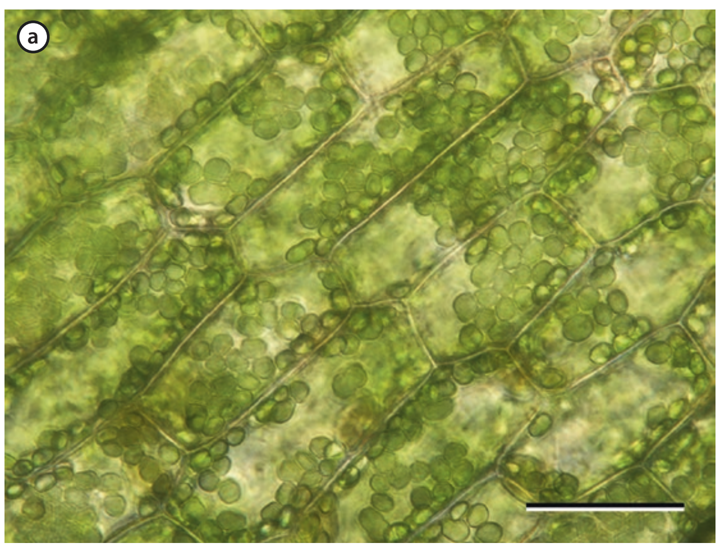
Introduction

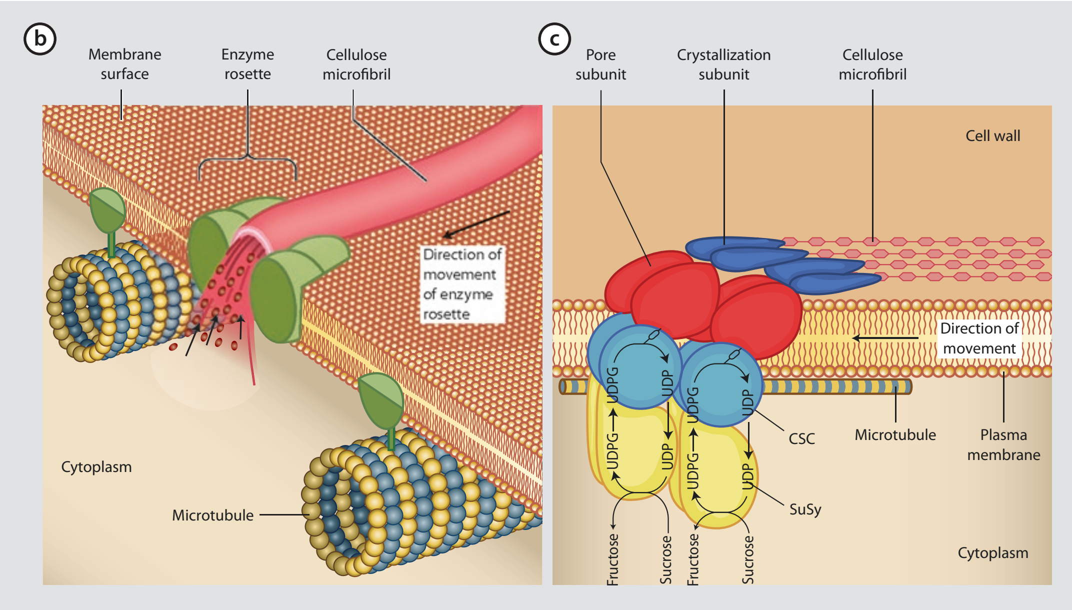
The cell wall is unique to higher plant cells. Due to their reliance on hydraulics for growth, expansion, and transport, plant cells develop tremendous internal pressures. Without walls, they would rupture due to the high osmotic pressures from within. There are two basic types of cell walls. Primary cell walls surround living cells and are made of a loose, and "loosenable," matrix of cellulose, **cross-linking glycans**, and structural proteins and contain enzymes capable of loosening and strengthening the wall. The primary wall offers physical support during the time of growth and in herbaceous tissues. Secondary cell walls are greatly stiffened by the deposition of lignin, are rigid, and are found in tissues or organs that require great strength and support, such as tracheary elements and wood. Typically, those cells are dead at maturity. Cell-to-cell communication and transport, which are of vital importance, occur via plasmodesmata in the primary cell wall or pits in the secondary cell wall.

5.1 Transparent Plant Cell Walls Contain Cellulose and Are Synthesized to the Exterior of the Protoplast

Although most plant cells are highly colored (▶ Chap. 1), **cell walls**, the main structural component of plants, rarely contain pigments. Light needs to penetrate many plant tissues; therefore, most cell walls, especially primary walls, are typically transparent or translucent (◘ Fig. 5.1a).



◘ **Fig. 5.1** **a** Chloroplast-containing elodea (*Elodea canadensis*) leaf cells separated by translucent primary cell walls. Scale bar = 50 µm (RR Wise)



◘ **Fig. 5.1** **b**, **c** Diagrammatic representation of portion of a plasma membrane with islands of cellulose synthase complexes (aka rosettes). These enzyme complexes generate the cellulose microfilaments on the outer surface of the membrane but are oriented by the positioning of cytoplasmic microtubules on the inner surface of the membrane. They are mobile and can move throughout the membrane. *CSC* cellulose synthase complexes, *PM* plasma membrane, *CSI1 CSC* associated proteins, *MT* microtubule. (Figure redrawn from John Tiftickjian (Delta State University))

All plant cell walls contain the polysaccharide cellulose, a polymer of ß-glucose units, arranged in crystalline structures only a few nanometers in diameter called microfibrils. Cellulose microfibrils are synthesized to the cell surface by large enzyme **cellulose synthase complexes** having hexagonal symmetry, sometimes called "rosettes" (Lei et al. 2012). Underlying microtubules in the cytoplasm guide the direction of the rosettes as they circle the cell by means of the action of motor proteins (◘ Fig. 5.1b, c, Wightman and Turner 2010). This results in the cell becoming wrapped in layers of cellulose **microfibrils**, which become the early primary cell wall (◘ Fig. 5.1d). Different layers of the cell wall may have different patterns since microtubules can depolymerize and re-polymerize in multiple orientations. The assembly and orientation of cellulose are connected, as several cellulose synthase mutants have phenotypes defective in cellulose orientation and plant structure as well as being depleted in cellulose content.

Not only cellulosic microfibrils but other polysaccharides are exported to the cell wall region either as a part of a permanent wall or as part of temporary secretions that play a significant role in lubricating for the growth of root structures through soil particles, harboring symbiotic and mutualistic microorganisms, and enveloping enzymes for extracellular degradation and transport. Within the cytoplasm, numerous Golgi bodies secrete vesicles that deliver components to the external cell wall either directly or through the endoplasmic reticulum (◘ Fig. 5.1e).

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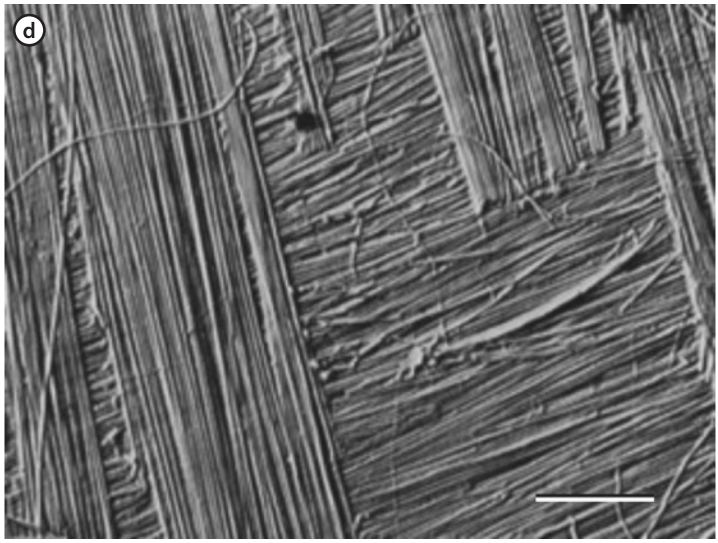


Fig. 5.1 **d** Orientation of numerous cellulosic microfibrils as shown by scanning electron microscopy that are enveloping the protoplasmic cell surface of a plant. The microfibrils shown here are firmly held to the adjacent fibrils by hydrogen bonds between their –OH groups. Scale bar = 1 µm (Crang and Vassilyev 2003)

5.2 Primary Cell Walls Are a Structural Matrix of Cellulose and Several Other Components

The wall of a dividing and growing cell is called the **primary cell wall** (Fig. 5.2a, Cosgrove 2005). This early wall is composed of multiple compounds formed in complex assemblages from within the cytoplasm of the cell, and transported across the cell (plasma) membrane (a.k.a. plasma lemma), which is a semifluid barrier of the early living cell (refer to ► Sect. 3.3). In addition to the carbohydrate cellulose (Fig. 5.2b), the main component of most cell walls, the primary cell walls also contain a matrix of polysaccharides in the form of amorphous substances (e.g., pectic and cross-linking glycans; Fig. 5.2c, d). Pectic substances are composed of polymers of galacturonic acid in which some of the carboxyl groups are esterified with methanol. **Pectins** act as a glue to hold adjacent cells together and are a main component of the **middle lamella** (see below). The pectic substances that are extracted from plants are commonly called pectins, and their sticky nature makes them an ideal choice for making jams and jellies. Cross-linking glycans (which used to be called hemicelluloses) bind to cellulose molecules to provide a strong but flexible web-like complex. They are composed of several different sugar monomers including glucose, arabinose, galactose, rhamnose, mannose, and xylose. The next most abundant component usually is water that is followed by a wide variety of compounds such as lignin, proteins, and mineral ions. Cell walls of some cell types may also contain polymeric lipids such as **waxes**, **cutins**, and **suberins** (Fig. 5.2e) which form hydrophobic deposits on hydrophilic walls, particularly conspicuous on the surface of the epidermis, in the **Casparian strip** of the endodermis and in the walls of **cork**.

Fig. 5.1 **e** A portion of a developing root cell from maize (*Zea mays*) showing many dictyosomes with swollen trans vesicles containing polysaccharides that are emptying their contents at the site of the cell wall (CW). Scale bar = 1 μm. (Micrograph courtesy of Hilton H. Mollenhauer; HH Mollenhauer, Texas A&M University)

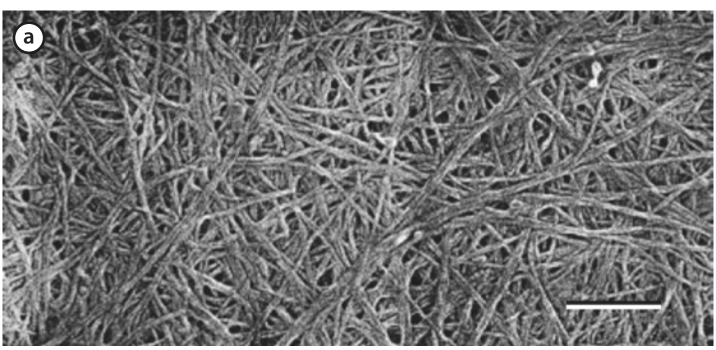
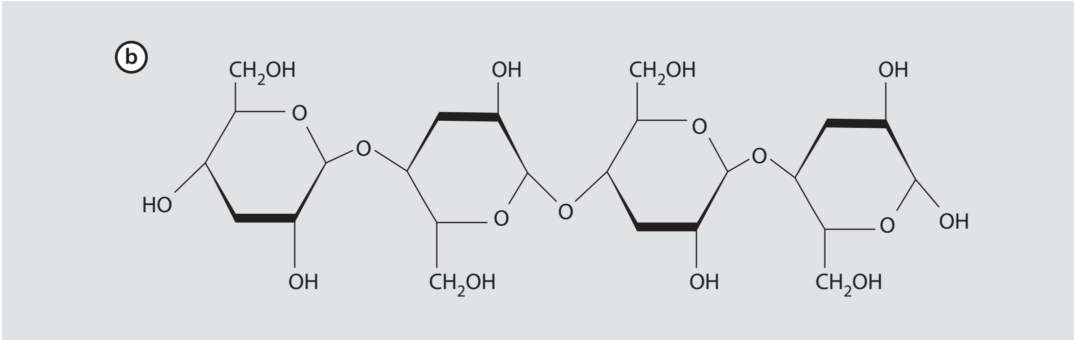
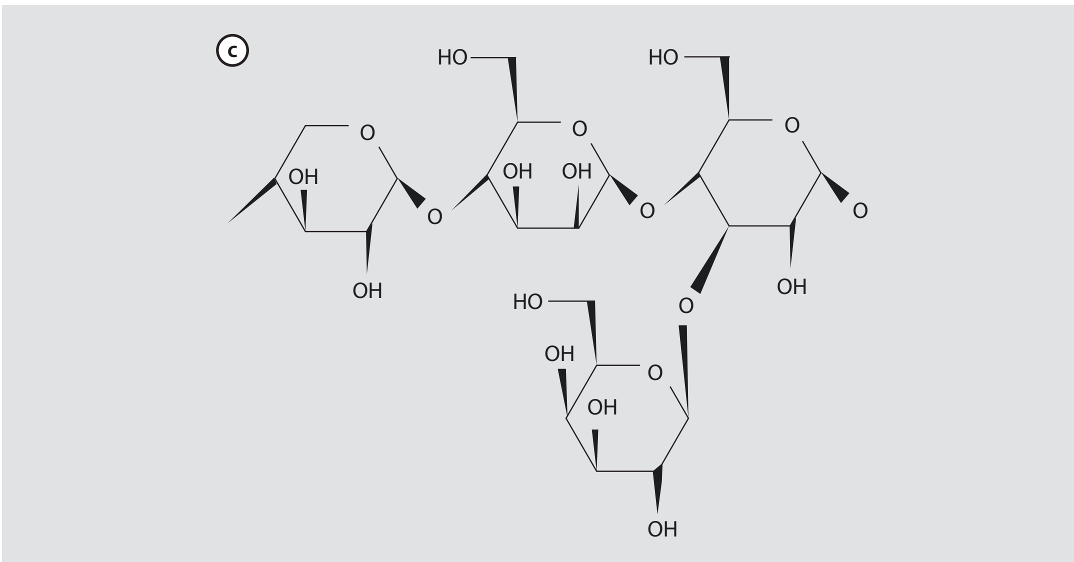


Fig. 5.2 **a** This transmission electron micrograph shows the primary cell wall of an onion (*Allium cepa*) parenchyma cell from a bulb after the extraction of noncellulosic polysaccharides. Although the extraction process enhances the cellulose microfibrils, it has altered their parallel orientation from that in the intact cell wall. Scale bar = 0.2 μm (Crang and Vassilyev 2003)



■ **Fig. 5.2** **b** The basic structure of cellulose, a linear polysaccharide with glucose units connected by a beta-acetyl linkage (Public domain)



■ **Fig. 5.2** **c** A common molecular orientation of a cross-linking glycan that contains several sugars including glucose, galactose, mannose and xylose (Public domain)

Each plant cell develops its own cell wall, and neighboring cells in the plant body are held together by the middle lamella (Zamil and Geitmann 2017), which originates as a pectic cell plate formed at telophase. The middle lamella is very thin and often indistinguishable from the developing primary cell wall (■ Fig. 5.2f). When two adjacent primary walls are cemented together with a middle lamella, the combination is designated as a **compound middle lamella** (■ Fig. 5.2g).

If chemical agents or enzymes are used to dissolve the middle lamella, the cell walls become separated from each other. Such an artificial process of cell separation is called **maceration** and is achieved in the laboratory by treatment with enzymes, acid, and/or alkaline solutions. However, a more common event is natural maceration when pectins of the middle lamella are enzymatically dissolved as during the process of leaf loss (e.g., **abscission**). Very often, partial maceration occurs when the middle lamella is solubilized only at certain sites, primarily at the cell corners. Cells round off due to turgor pressure,

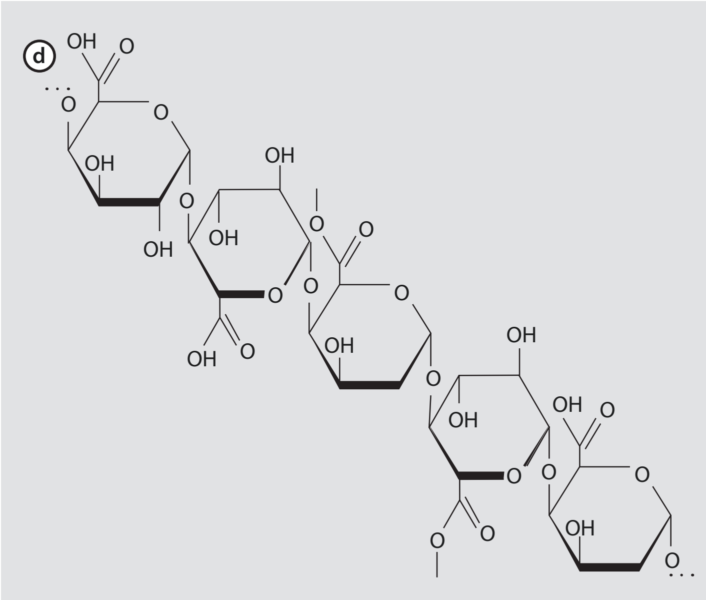


Fig. 5.2 **d** Chemical structure of a pectin which may contain a variety of sugars as well as being rich in galacturonic acid (Public domain)

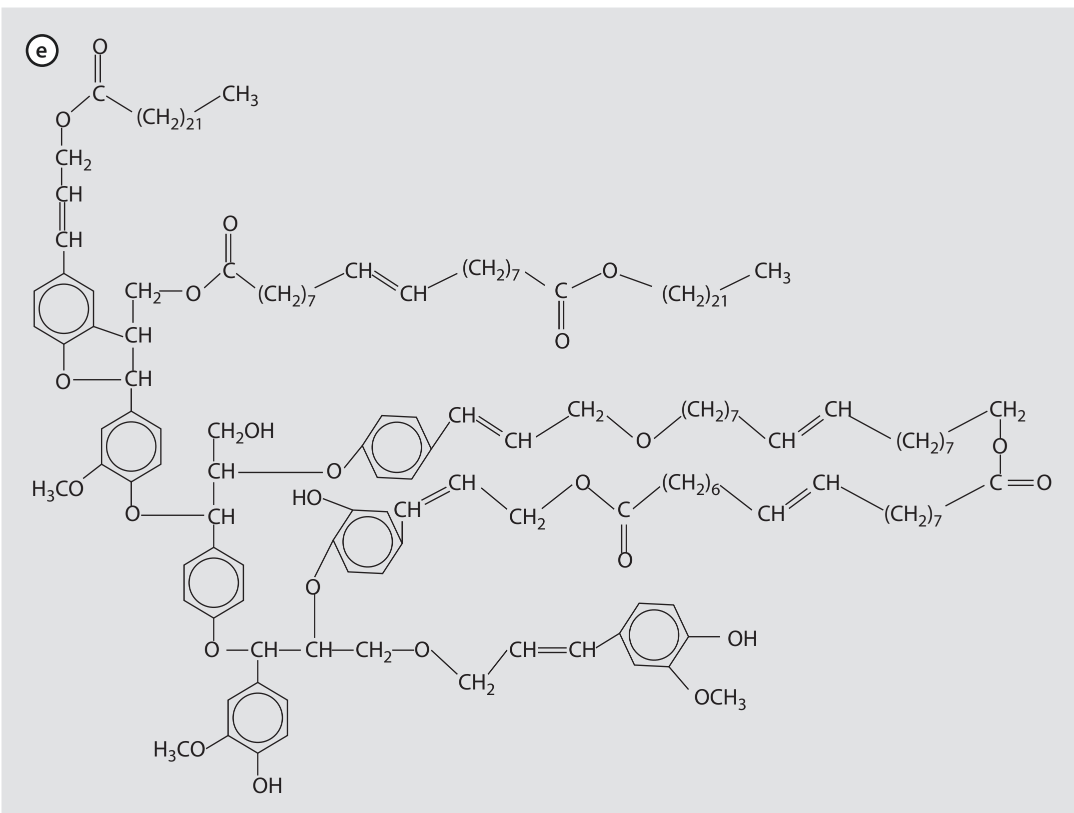


Fig. 5.2 **e** A hypothetical structure of a suberin polymer. Such glycerolipid polymers are specific to plants. Cutin is responsible for the composition of the cuticle on the aerial epidermis. Suberin is mostly present in the bark and underground organs of plants (Public domain)

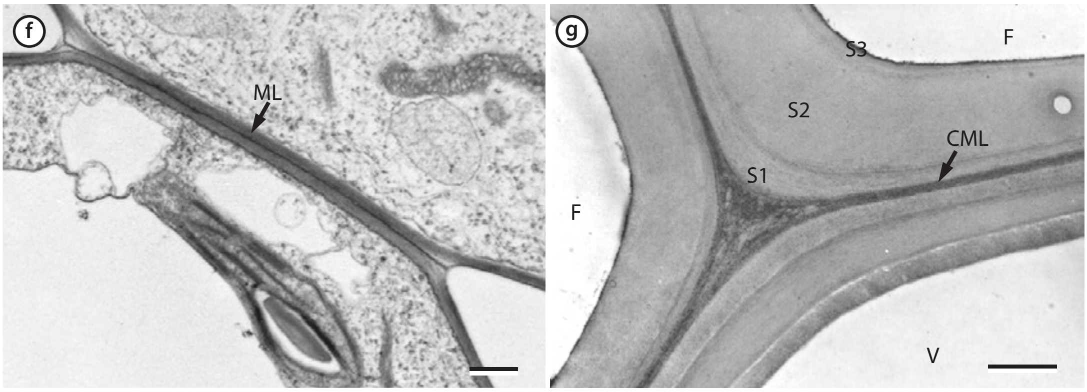


Fig. 5.2 **f** Middle lamella (ML) between adjacent cells in water lettuce (*Pistia stratiotes*). (GM Volk and VR Franceschi, Washington State University). **g** Compound middle lamella between three adjacent cells in developing poplar (*Populus* sp.) wood, two fibers (F) and one vessel element (V). The middle lamella and the two primary walls in **apposition** have fused to form the compound middle lamella (CML), and three layers of secondary wall have developed (S1, S2, and S3). (K Ruel, CNRS, France). Scale bars = 5 µm in **f** and 1 µm in **g**

and intercellular air spaces appear at these sites. These spaces enlarge and fuse with each other as cells grow, and a single-branched system may appear which is filled with gases and water vapor. Therefore, intercellular spaces facilitate exchange into and out of plant cells for gases such as oxygen, water vapor, and carbon dioxide.

Box 5.1 Using Plant Cells for the Oral Delivery of Protein Drugs

Protein drugs include compounds such as hormones, vaccines, and enzymes. They are expensive to manufacture and require cold storage. Because these drugs can be degraded by proteases and acids if ingested and have difficulty crossing intestinal barriers, they are typically administered by injection, often by medical professionals that further increases costs.

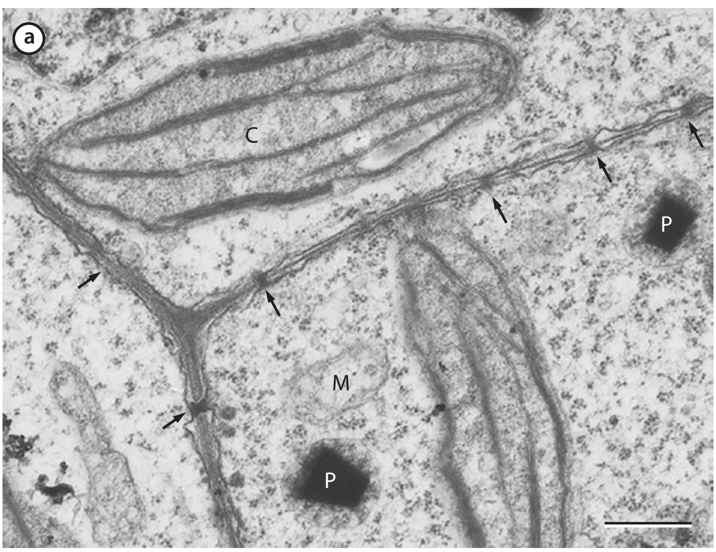
The use of plant cells to manufacture and store protein drugs could provide both convenience of oral delivery and economic relief for patients. Here is the basic concept of drug production and delivery using plant cells: drug companies engineer chloroplasts to express genes of medicinal interest. The plant leaves are harvested, freeze-dried, and placed in a capsule. Envision a patient orally ingesting the capsule containing a gene product, such as insulin, instead of administering the hormone via self-injection. Since the human body does not produce cellulases, enzymes that break down plant cell walls, the drug would not be dispensed until encountering gut bacteria in the intestines can denature the walls, releasing the drug. Within the intestines, the drug can be integrated into the body. Freeze-drying allows these protein drugs to remain stable at room temperature, keeping storage costs down. Since these drugs may not require purification or professional administration, costs to patients would be reduced. This research of drug bioencapsulation within plant cell walls may lead to increased efficiency in treating metabolic disorders and diseases such as diabetes, hypertension, and Alzheimer's. While oral delivery of drugs is still in its experimental stages, it shows much promise.

Reference: Xiao et al. 2016

5.3 Plasmodesmata Connect Adjacent Cells Via Holes in the Primary Cell Wall

Plasmodesmata are tiny (30–60 nm), intercellular, cytoplasmic extensions between adjacent cells and are lined with the plasma membrane of the two adjacent cells (◘ Fig. 5.3a). They are dynamic structures that control the passage of large molecules between cells and also in cell-to-cell communication (Overall and Blackman 1996; Maule 2008).

Practically all living cells of the plant body are interconnected by plasmodesmata. An exception is the subsidiary cells surrounding guard cells found in epidermal layers (refer to ► Sect. 9.3). There are numerous plasmodesmatal connections between the subsidiary cells and guard cells but none between the subsidiary cells and adjacent pavement cells of the epidermis. With that exception, plasmodesmatal connections between adjacent cells link the cytoplasm of practically every cell in the plant into a **symplastic** whole. Due to the presence of multiple plasmodesmata, plant cells can be considered to form a **syncytium** or multinucleate mass with cytoplasmic



◘ **Fig. 5.3** **a** Newly formed cell walls in water lettuce (*Pistia stratiotes*) containing numerous plasmodesmata (arrows). Note also the chloroplasts (C), mitochondrion (M), and two peroxisomes (P) containing darkly stained catalase crystals. Scale bar = 0.5 µm. (Image courtesy of Gayle Volk and Vincent Franceschi; Washington State University) continuity (in contrast to a **coenocyte** which can result from multiple nuclear divisions without accompanying cytokinesis). Accordingly, the tiny channels have caused a significant amount of debate among scientists regarding cell theory, some suggesting that the cells of higher plants are not cells at all since they are not physically separated or structurally independent from one another.

There are two forms of plasmodesmata: primary and secondary (Ehlers and Kollmann 2001). Primary are formed from the sites where strands of endoplasmic reticulum were trapped in the developing cell plate during cytokinesis. Secondary plasmodesmata are formed by insertion into existing cell walls between nondividing cells. Secondary plasmodesmata are a much less common occurrence than primary plasmodesmata.

Areas in the primary cell wall that have a concentration of plasmodesmata are called **primary pit fields**, and in cells that form a secondary wall, the primary wall's pit fields are left exposed. This creates large perforations in the secondary wall called **pits** (refer to ► Sect. 5.5, below). Secondary cell wall pits of adjacent cells are usually aligned with each other so that the two primary cell walls and middle lamella form a selectively permeable pit membrane, pierced by multiple plasmodesmata. Going from one cell to the adjacent one, the sequence of structures is as follows: pit-primary wall-middle lamella-primary wall-pit. Such a secondary wall pit pair can transmit water, nutrients, plant growth regulators (hormones), etc. between adjacent cells.

Plasmodesmata may be straight or branched, and plasmodesmatal diameter varies across the length (◘ Fig. 5.3b, c). They are 30–40 nm at the wall surface and approximately 50–60 nm in diameter at the midpoint. Note the plasmodesmata in ◘ Fig. 5.3c that are closer to the cytoplasmic surface of the cell wall are smaller than the plasmodesmata further from the cytoplasm and thus deeper in the wall.

Plasmodesmatal internal structure is delimited by a plasma membrane encircling a solid-looking core (or **desmotubule**) and an intervening layer known as the **cytoplasmic annulus** (◘ Fig. 5.3d). The cytoplasmic annulus is the space between the desmotubule and the plasma membrane. Around the desmotubule and the plasma membrane, areas of an electron-dense material have been observed with the aid of the transmission electron microscope and often joined together by spoke-like structures that seem to split the plasmodesmata into smaller channels. In this case, these proteins may be used in the selective transport of relatively large molecules between adjacent cells. It has been found that a typical plant cell may have between 10^3 and 10^5 plasmodesmata connecting adjacent cells, which may equate to between 1 and 10 per μm^2.

Plasmodesmata are more than merely passive holes connecting adjacent cells (Ehlers and Kollmann 2001). Plants may regulate plasmodesmatal transport by the accumulation of callose around the end regions of plasmodesmata to form a restriction, which may reduce the diameter of the plasmodesmata at those sites and thereby control the passage of substances through the plasmodesmata. Through the action of ATP, proteins associated with the desmotubule can expand the radius of the plasmodesmata, allowing larger unfolded proteins to pass through from one cell to the next. Also,

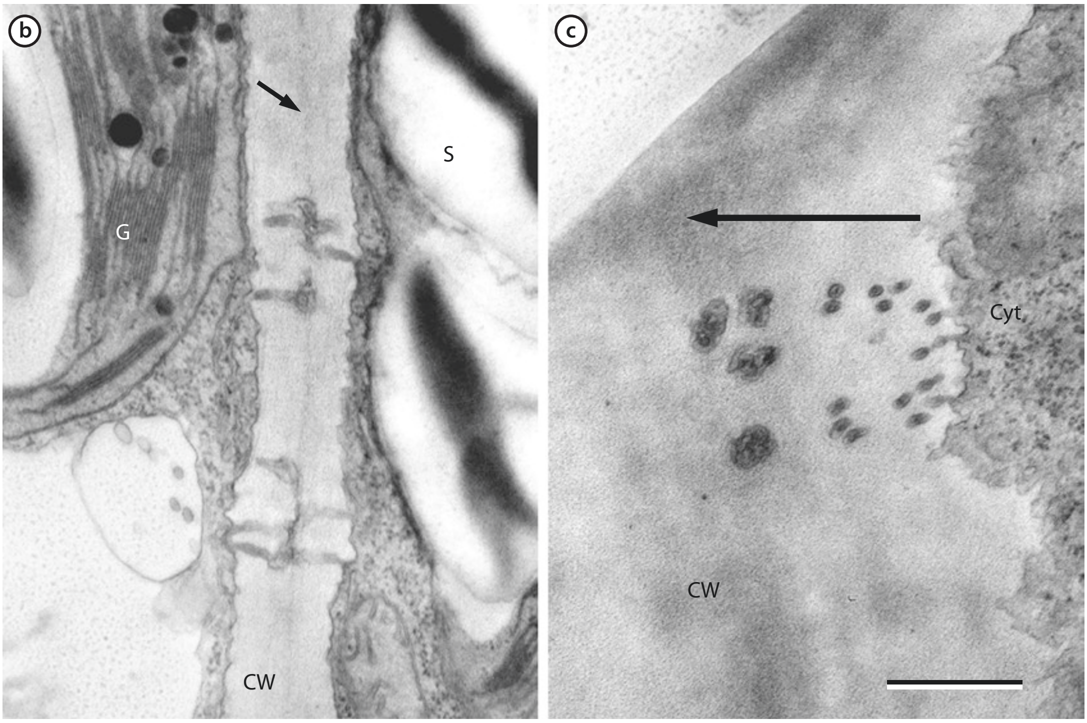


Fig. 5.3 **b** Branched plasmodesmata seen in cross-section traversing the two primary cell walls (CW) separating two leaf cells. The middle lamella is indicated with an arrow. Chloroplasts with grana (G) and starch (S) are also indicated. **c** Plasmodesmata seen in face view in an oblique section of a primary cell wall (CW). Cytoplasm (Cyt) is to the right in the image, and the arrow indicates increasing depth into the cell wall. Both images are from the leaf of the lyre-leaved sand cress (*Arabidopsis lyrata*). Scale bar = 0.1 µm for both panels (**b**, **c** RR Wise)

cells can utilize both passive and active transport to move molecules and ions through the plasmodesmata.

Numerous large molecules have been shown to traffic from cell to cell via plasmodesmata. Studies have tracked cell-to-cell movement of proteins, transcription factors, messenger RNA, and even entire viral genomes. The latter is mediated by proteins encoded by the virus called "movement proteins." The ability of a virus to make movement proteins is key to its virulence because it allows the virus to spread throughout the plant (Heinlein 2015). Tobacco mosaic virus encodes MP-30, a 30 kDa movement protein that binds to and traffics the entire viral genome through the plasmodesmata, thus spreading the infection.

Finally, the plant cell membrane typically has a rather large electrical potential, in the range of −150 mV (negative on the inside) as compared to the −40 to −60 mV potentials found in most animal cells (Flickinger et al. 2010). Because plasmodesmata allow for ion (electrolyte) transport between cells, uniform membrane potentials across a plant organ can be maintained.

Persimmon fruit contains cells with extremely thick primary cell walls (Fig. 5.3e) and is a common specimen for classroom study of bundles of plasmodesmata as the long channels are easily seen with the light microscope. This allowed early microscopists to visualize plasmodesmata long before the development of the transmission electron microscope permitted high-resolution studies, ones that continue to this day.

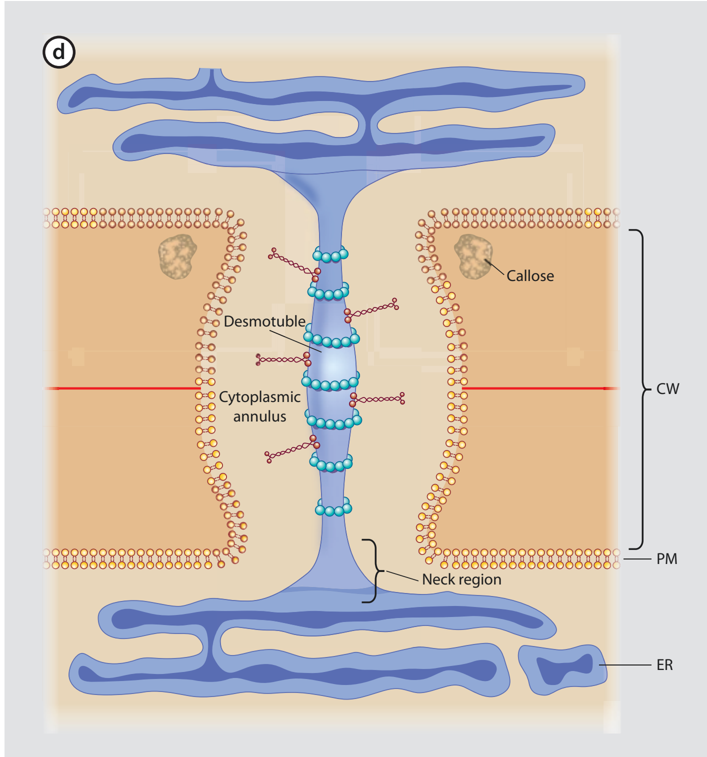


Fig. 5.3 **d** The structure of an unbranched plasmodesmata. Light green area cytoplasmic sleeve; *CW* cell wall, *CA* callose, *PM* plasma membrane, *ER* endoplasmic reticulum, *DM* desmotubule, purple circles and spokes – other agents such as ATP and proteins within the cytoplasmic sleeve that may include myosin. The combination of actin and myosin may be in the selective transport of large molecules between two cells through the plasmodesmata and along the desmotubule. (Figure modified from Sevilem et al. (2015))

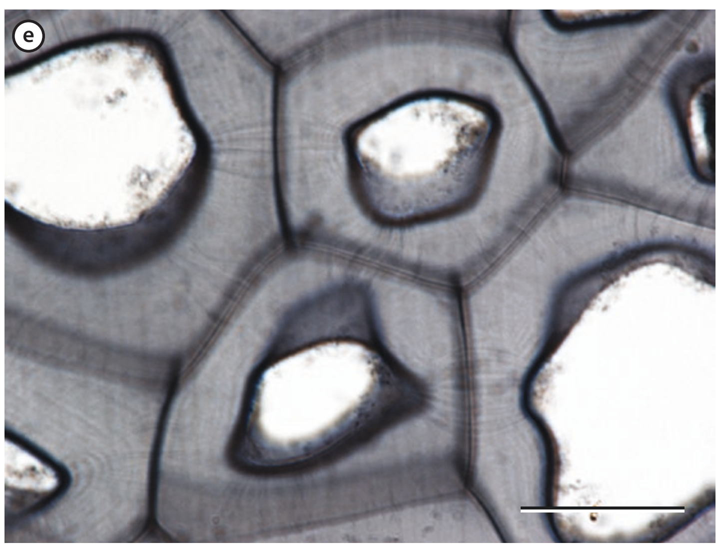
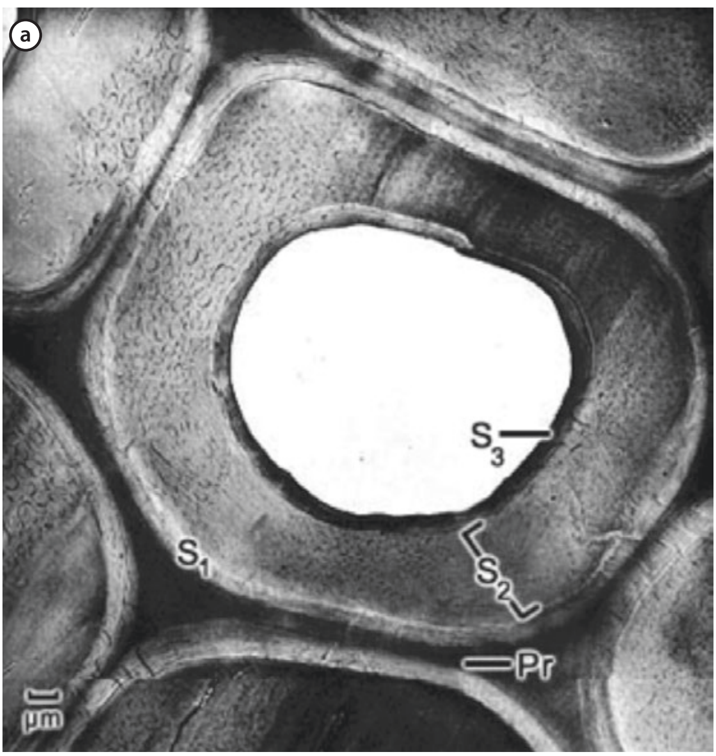


Fig. 5.3 **e** Cell walls of persimmon (*Diospyros* sp.) in cross-section showing fine bundles of plasmodesmata traversing the walls, through the middle lamella, and interconnecting every cell in the field of view. Scale bar = 25 µm (RR Wise)

5.4 Secondary Cell Walls Are Rigid, Thick, and Lignified

For many cell types, wall formation ends with the cessation of cell growth. Such cells remain surrounded by a thin primary wall during their whole life. But in other cell types, the deposition of wall material continues. The wall layers deposited after cell enlargement ceases are collectively termed the **secondary cell wall**. Because of secondary wall growth, the thickness of the wall increases, at the expense of the volume of the living cell cavity (◘ Fig. 5.4a).

Primary cell walls of different tissues and plant species will vary in their composition and function. Likewise, secondary walls will also vary in that regard for the different layers that can be established. For some cell types, such as tracheids, vessel members, cork cells, and some sclereids and fibers, the formation of the secondary wall is the main function of their **protoplasts**, and the cells eventually die because of fulfilling that principal function. In such a case, the secondary wall mainly provides mechanical support and is responsible for the specific structural features of wood, textile fiber, and paper.



◘ **Fig. 5.4** **a** Cross-section of late-wood tracheids of longleaf pine (*Pinus palustris*) showing the layers of the secondary wall (S_1, S_2, and S_3), the thin primary wall (Pr), and the true middle lamella, which is markedly thickened at the cell corners. The combination of the primary cell walls and the middle lamella is often termed a compound middle lamella. Scale bar = 1 µm (Crang and Vassilyev 2003)

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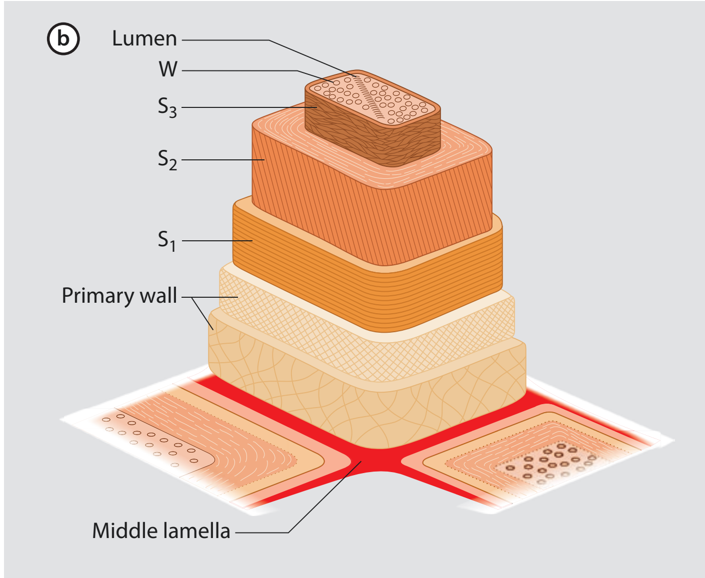


Fig. 5.4 **b** This diagram shows the order of wall layers for a cell with secondary wall development. The middle lamella is amorphous in organization. The primary wall typically shows a nonlinear pattern of cellulose microfibril deposition. The orientation of fibrils may determine the direction of cell elongation. Fibril patterns that are nonlinear cause the walls to undergo minimal expansion. Note, however, that the three layers of secondary wall material (labeled, S_1, S_2, and S_3) have distinct orientations of the cellulose microfibrils. A "warty" layer (possibly representing the remaining nonliving cell contents) may also be found as a lining to the S_3 layer. Not all cells that form secondary wall material will result in all the layers. (Figure modified from Esau (1977))

In cells with well-developed secondary walls (S), up to three concentric wall layers may be distinguished: an outer narrow S_1 layer adjacent to the primary wall, a thicker middle S_2 layer, and a thin inner layer bordering on the cell cavity (S_3, Fig. 5.4b). The layers differ not only in thickness but also in chemical composition and in the angle of cellulose microfibril orientation in relation to the cell axis (Richter et al. 2011). The three-layered structure of secondary walls is characteristic of wood elements of conifers and some angiosperms, but in some cells the S_3 is lacking. The S_2 layer is the richest in cellulose and is responsible for most of the properties of secondary walls. **Lignification** results in the substantial modification of cell wall properties, e.g., the loss of elasticity, a drastic increase in hardness and tensile compression, and a decrease in the permeability of water as the lignin polymerizes within the cell walls. Lignin is found in many or all the secondary wall layers.

In some specialized cells (mainly those engaged in water conduction, called xylem tracheary elements), the secondary wall is not deposited over the entire inner surface of primary wall but appears as individual rings, continuous helices, or net-like arrangements (Fig. 5.4c). Xylem tracheary element structure will be covered in more detail in ► Chap. 7.

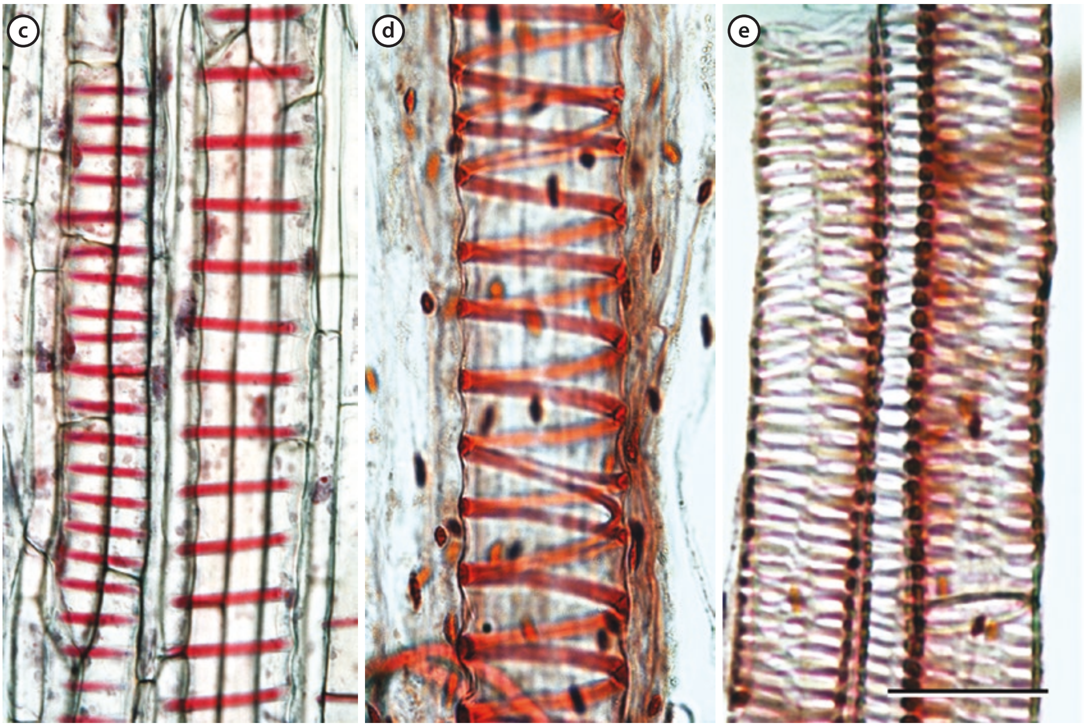


Fig. 5.4 Variations in secondary cell wall thickening patterns in protoxylem tracheary elements from celery (*Apium* sp.) petiole. **c** Annular thickenings, **d** helical thickenings, **e** reticulate thickenings. Scale bar in e = 50 µm for all three panels (**c**–**e** RR Wise)

The different compositions of cell walls in plants allow for a variety of economic and practical uses of the materials. For example, an obvious and vastly important product is lumber, used as a building product. Also, other products that derive value from the cell wall include the following: paper products, fibers for weaving and as dietary supplements, extracts for textiles, ink products, food thickening and flavor products, oils, as well as cellulosic materials for hydrolysis and fermentation into biofuels.

5.5 Pits Are Holes in the Secondary Cell Wall

In secondary walls of all types of cells, areas remain where secondary wall material is not deposited. Such interruptions in the secondary wall (Fig. 5.5a) are called pits due to their appearance in the light microscope. Three main types of pits are recognized: **simple pits** (Fig. 5.5b, c), **bordered pits** (Fig. 5.5d, e), and **half-bordered pits**. In simple pits, the canal typically has a cylindrical form, whereas in bordered pits, the canal becomes much narrower in the process of secondary wall deposition and consequently, the diameter of the **pit aperture** facing the cell cavity is significantly less than the diameter of the so-called pit membrane. In adjacent cells, pits arise opposite

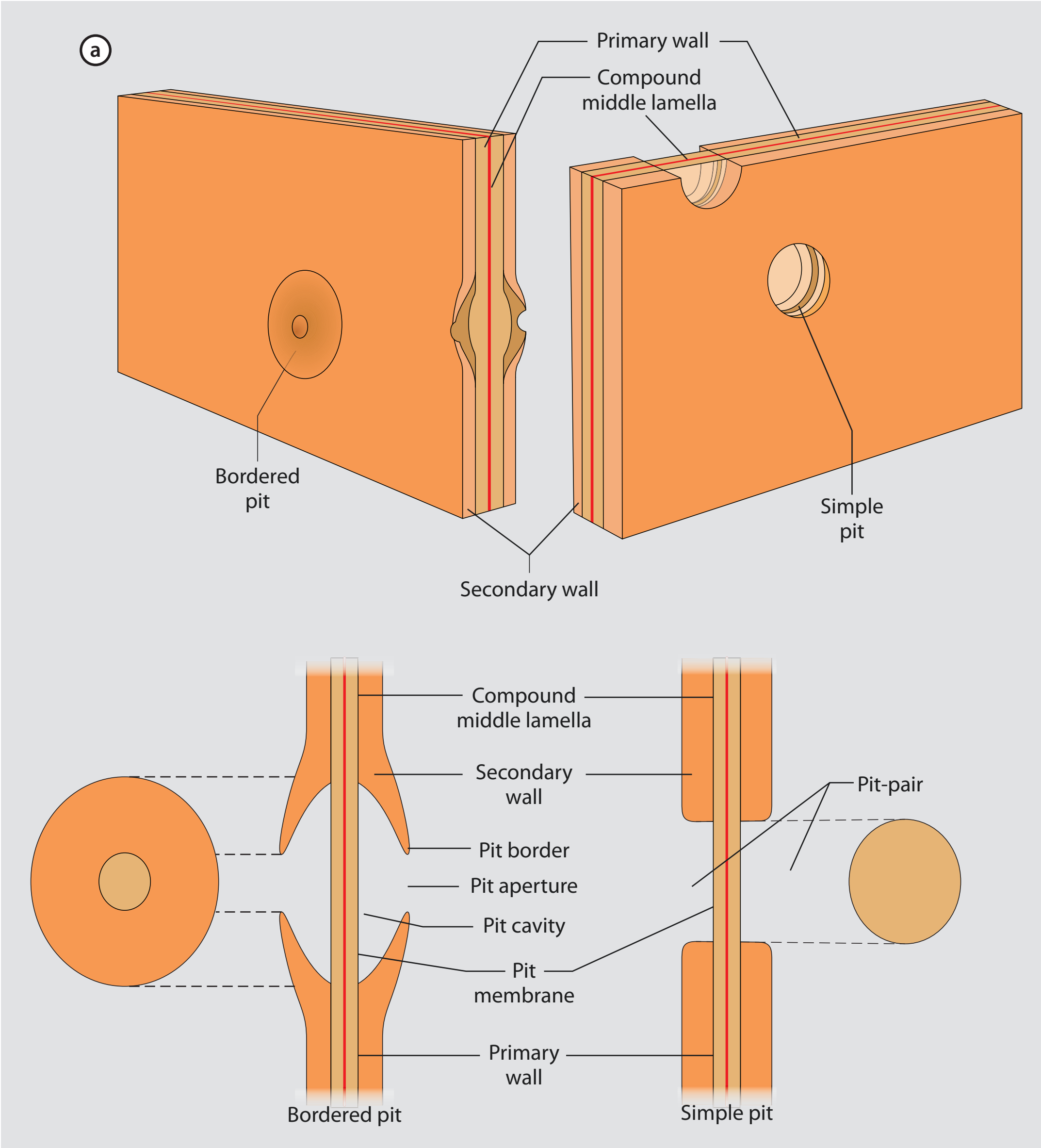
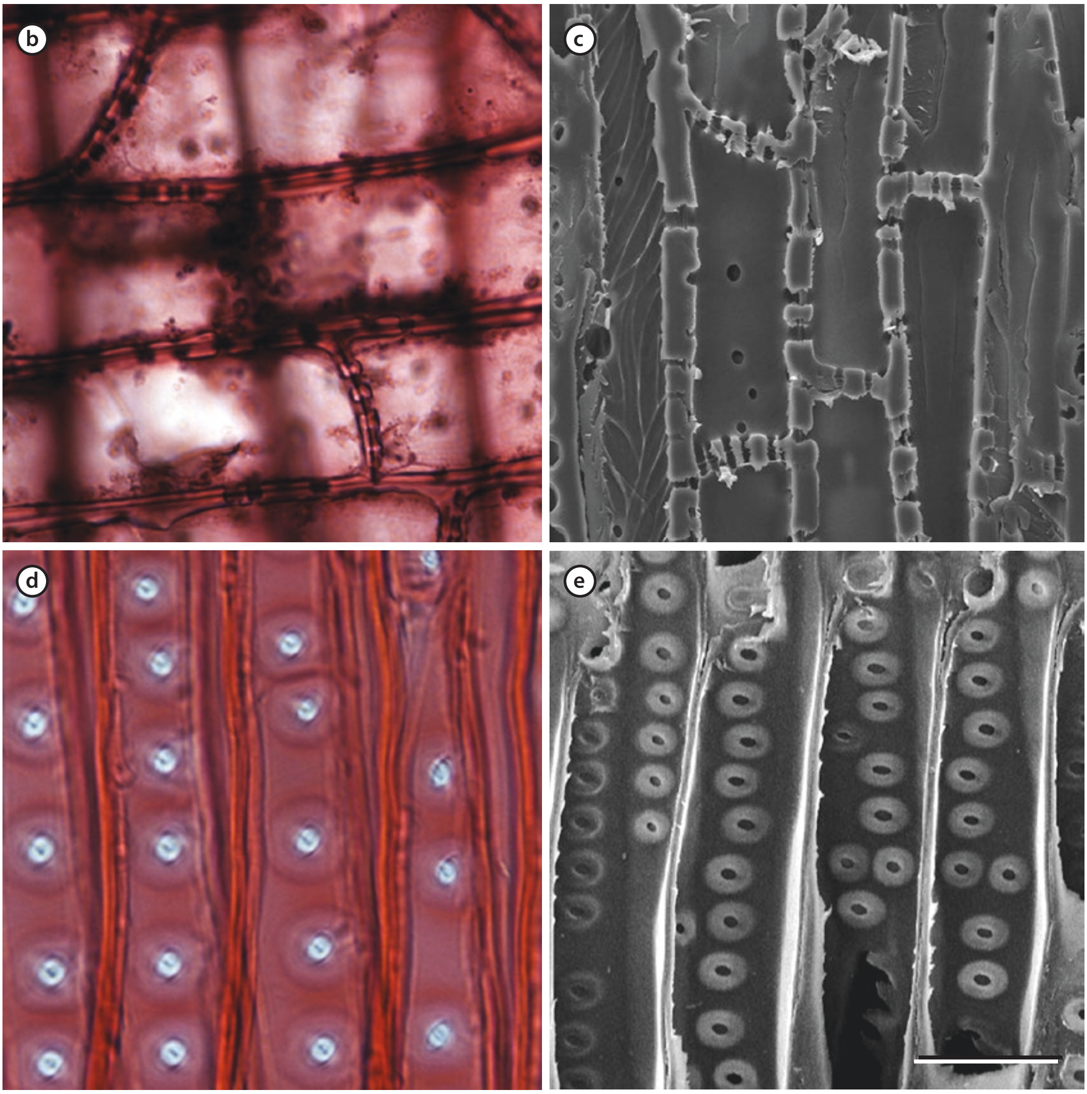


Fig. 5.5 **a** A diagrammatic representation of two segments of cell walls, with the orientation of middle lamella, primary and secondary layers shown. Each represents a model of adjacent cell walls appressed to each other. On the left are shown bordered pits in which the secondary wall material forms an overlaying circular rim over the compound middle lamella. On the right, the simple pits have only the compound middle lamella extending across the pit opening, and the primary and secondary layers of the cell wall are of common dimension (Redrawn from Crang and Vassilyev 2003)

each other and have a common pit membrane. Such a configuration is said to be a **pit pair**. While the two pits of a pit pair are usually of the same type – i.e., simple or bordered – half-bordered pits are a combination of a simple pit and a bordered pit. Simple pits are found in cell walls of living cells such as cells of parenchyma and some fibers. Bordered pits are characteristic of water-conducting cells of wood, which are dead at maturity (tracheids and vessel members). Pits facilitate the intercellular transport of water and solutes.



◘ **Fig. 5.5** **b** Simple pits seen in cross-section from radial parenchyma in catalpa (*Catalpa speciosa* and **c** honey locust (*Gleditsia triacanthos*) wood. **d** Bordered pits seen face-on in **d** tracheids of white cedar (*Thuja occidentalis*) and **e** pine (*Pinus* sp.). Scale bar in **e** = 20 µm and applies to all panels (**b**–**e** RR Wise)

The portion of the primary cell walls and middle lamella that traverses the pit is called the **pit membrane** (◘ Fig. 5.5f). Despite its name, there is no living membrane present, the "membrane" being the original primary cell wall. The primary cell wall is modified from that of a living cell to increase its permeability for water transport.

In cells with very thick secondary walls, pits can be very long indeed. For instance, in brachysclereids of pear fruit (e.g., stone cells; refer to ► Sect. 6.7), pits appear in sectional view as long radial canals through the secondary cell wall, extending from one cell to another (◘ Fig. 5.5g). The scanning electron microscope allows visualization of the inner cytoplasmic surface of secondary cell wall and shows the density of pits (◘ Fig. 5.5h).

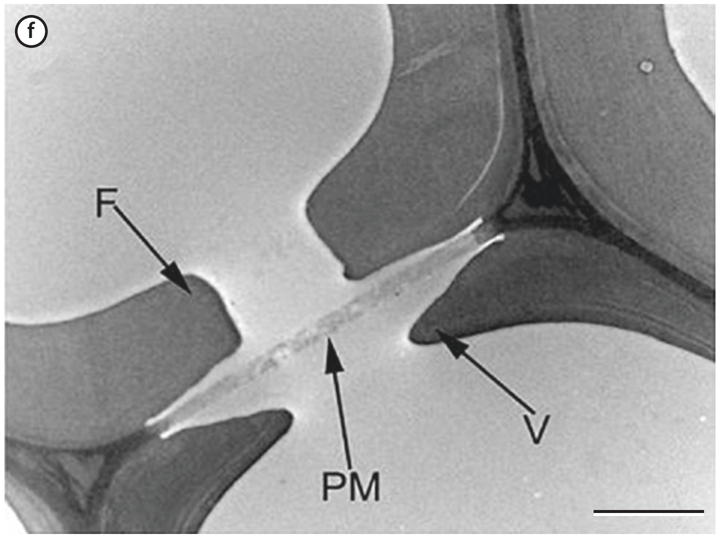


Fig. 5.5 **f** A pit membrane (PM) between a fiber (F) and a vessel (V) in Tatarian dogwood (*Cornus alba*). Note that the fiber has a simple pit, while the vessel has a bordered pit. Scale bar = 1.0 µm. (Image courtesy of Feng Xu; Beijing Forestry University)

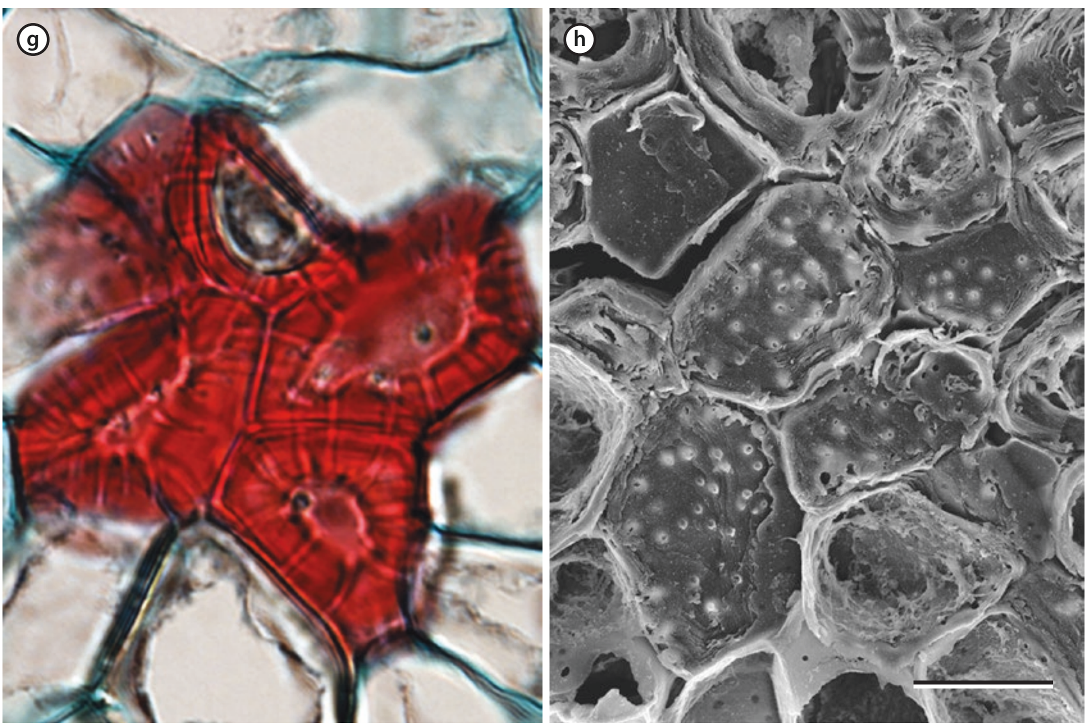


Fig. 5.5 Simple pits in the brachysclereids of pear (*Pyrus communis*) fruit. **g** Pits are shown in cross-sectional view in the light microscope. The thick secondary cell walls are stained red. **h** Pits are shown in face view in the scanning electron microscope. Scale bar in **h** = 20 µm for both panels (**g**, **h** RR Wise)

5.6 Transfer Cells Have Elaborated Primary Cell Walls for High Rates of Transport

Transfer cells are characterized by extensive ingrowths of the primary cell wall (Gunning and Pate 1969). Such ingrowths function by greatly enlarging the surface area of the plasma membrane, thereby facilitating the absorption or secretion of ions, products, metabolites, etc. They are usually confined to only one area of a cell, and are often found in tissues, which sustain large amounts of metabolite transport such as the "stem" (pedicel and/or suspensor) that attaches a developing fruit to the parent plant (McCurdy and Hueros 2014).

Mangrove is also a unique example in that it is a viviparous plant, meaning that seeds germinate while still in the fruit and the seedling remains attached to the mother plant for the first several weeks of development (◘ Fig. 5.6a). The entire surface of the developing seedling that remains in contact with the fruit develops into transfer cells (◘ Fig. 5.6b, c, Wise and Juncosa 1989). Some recent evidence suggests that a small amount of secondary wall deposition may be present in certain plant species.

◘ **Fig. 5.6** **a** Developing seedling (S) of red mangrove (*Rhizophora mangle*) emerging from the fruit (F). The top end of the seedling and the zone of transfer cells are indicated by the dashed line. Scale bar = 5 cm (RR Wise)

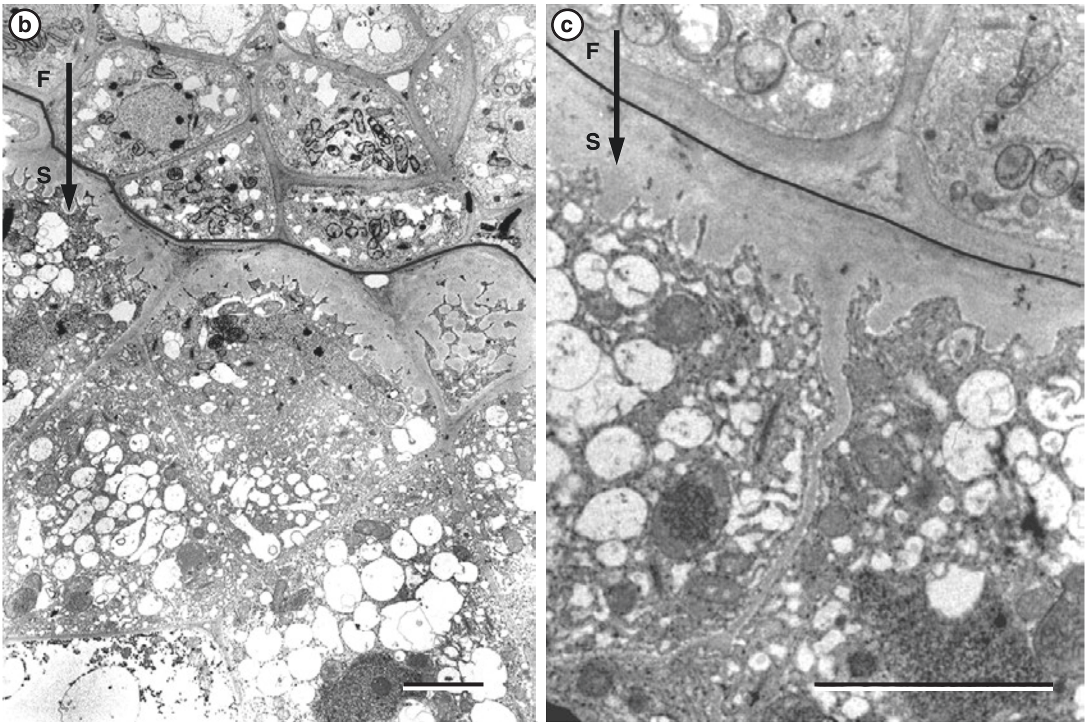


Fig. 5.6 Two views of transfer cells in a mangrove (*Rhizophora mangle*) embryo. **b** Note the substantial protrusions of the primary cell wall that increases the surface area for molecular exchange. Mangrove seeds germinate while still in the fruit (F, above the black lines in both panels), and the seedling (S, below the black lines) stays attached to the mother plant for the first several weeks of development. **c** All water and nutrients are transported from the fruit to the seedling across the transfer cell zone in the direction indicated by the arrows. Scale bars = 10 μm in both panels (**b**, **c** RR Wise)

Box 5.2 Understanding Gene Control of Transfer Cell Development and Function May Lead to Increases in Crop Yield

The elaborate and characteristic cell wall ingrowths of transfer cells, and their location at critical plant exchange surfaces, have confirmed their roles in nutrient and solute transport. They play a role in phloem loading/unloading, providing nutrition to the developing embryo in viviparous plants, and for the transfer of nutrients into the endosperm during seed development. In the latter two cases, the transfer process is between different generations and genetically distinct individuals, thus requiring coordinated communication between the individuals during transfer cell development and functioning. Lopata et al. (2014) reviewed the recent literature on the expression of genes during endosperm transfer cell (ETC) development of cereal crops. ETC-specific genes were placed in five categories: (1) Signal reception and transduction proteins that form the basis of a two-component signaling system between maternal tissue and developing grain (this communication is important for ETC differentiation and development), (2) transcriptional regulators and cofactors which also play a role in ETC differentiation, (3) genes responsible for sugar conversion and transport from the maternal vascular system into the developing endosperm, (4) genes that code for lipid transfer proteins found in the cell membrane, and (5) a group of genes with unknown functions. The authors make particular note of the potential application of this knowledge to the manipulation of seed filling rates, and increased plant yield, which has been a goal of agronomists for roughly the past 10,000 years.

Reference: Lopata et al. (2014)

5.7 Chapter Review

Concept Review

5.1 *Transparent plant cell walls contain cellulose and are synthesized to the exterior of the protoplast*. The plant cell wall is a major structural component of the plant body. Cell walls are mostly transparent; therefore light can penetrate the plant body and be absorbed by a variety of plant pigments. The building blocks of the primary wall are synthesized in the cell cytoplasm but exported to the exterior where they are assembled into the structural components in the wall.

5.2 *Primary cell walls are a structural matrix of cellulose and several other components*. The primary cell wall is composed of several complex carbohydrate molecules such as cellulose, cross-linking glycans, and pectic substances in addition to numerous proteins and ions. Individual cells secrete a cell wall to the exterior of the plasma membrane. The middle lamella glues the cell to the wall of the adjacent cell.

5.3 *Plasmodesmata connect adjacent cells via holes in the primary cell wall*. Plasmodesmata are membrane-lined passages linking adjoining living cells. Primary plasmodesmata develop during cytokinesis to connect daughter cells and secondary plasmodesmata form between existing cells. Plasmodesmata are a tube of a plasma membrane containing a cytoplasmic sleeve and a desmotubule. Proteins, mRNA, and viral genomes are known to be passed through plasmodesmata.

5.4 *Secondary cell walls are rigid, thick, and lignified*. Secondary cell walls are laid down between the plasma membrane and the existing primary cell wall. Thus, they push inward against the cytoplasm and reduce protoplasmic volume. The secondary cell wall may cover the entire cell surface or be deposited in a helical or spiral fashion depending on cell function. The secondary cell wall has multiple layers of different orientation and chemical composition. The deposition of lignin provides significant strength.

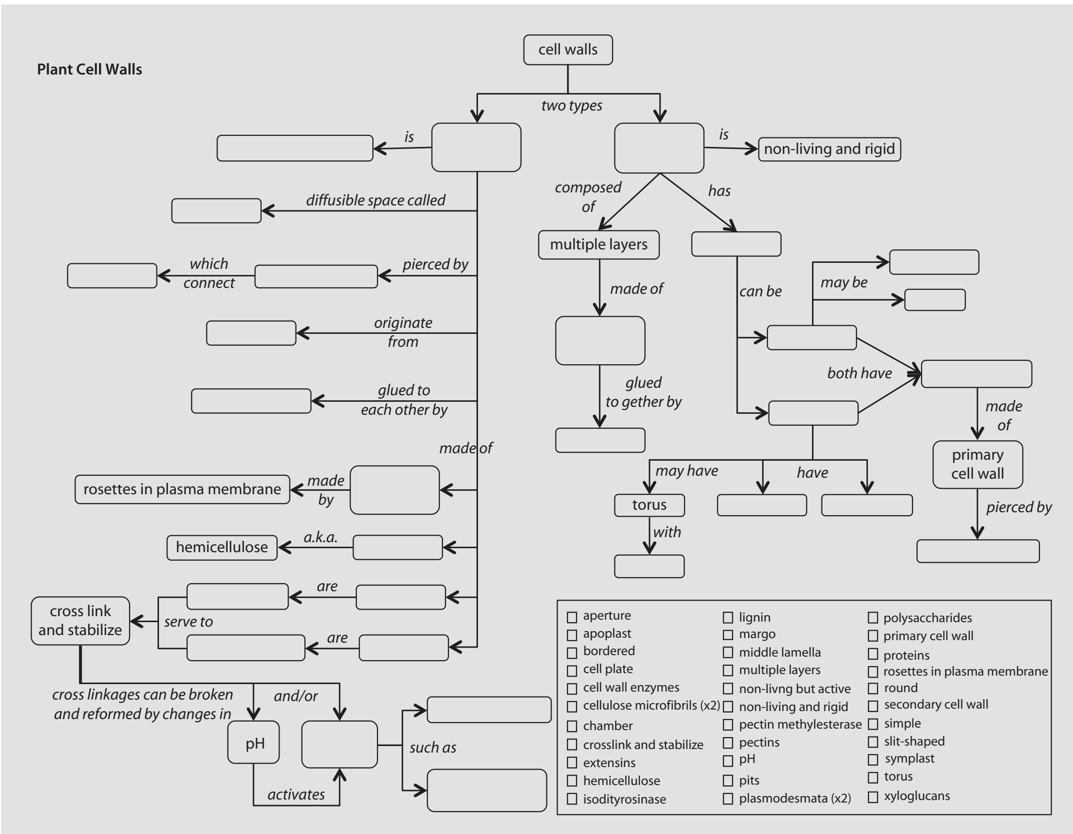
5.5 Pits are holes in the secondary wall. Pits represent a secondary cell wall gap in adjacent cells that allows for the high rate of water movement from cell to cell. Both simple and bordered pits exist in pit pairs—one pit for each of the two adjacent cells.

5.6. *Transfer cells have elaborated primary cell walls for high rates of transport*. The highly folded cell walls of transfer cells increase the surface area available for membrane transport. Accordingly, transfer cells are found in tissues that engage in higher than normal rates of metabolite transport. While normally having primary cell walls, some plants may also possess secondary thickenings to their infolded walls.

5

■ Concept Connections

1. Fill in the concept map below.



■ Concept Assessment

2. The primary function of intercellular spaces in most plant tissues is to
   a. allow for the movement of organic compounds.
   b. provide space for the addition of secondary wall materials to cells.
   c. facilitate gaseous exchange of cells.
   d. maintain turgor pressure.
   e. provide a site of extracellular storage.

3. Where may lignin be found?
   a. secondary walls only.
   b. compound middle lamella.
   c. s_3 layer only.
   d. primary walls only.
   e. all cell wall layers.

4. The S_2 layer of a cell wall is found
   a. adjacent to the cell membrane.
   b. inside of the S_3 layer.
   c. adjacent to vacuolar membrane (tonoplast).
   d. outside of the S_1 layer.
   e. inside of the S_1 layer.

5. Pectic substances are polymers of
   a. galacturonic acid.
   b. lipids.
   c. glucose residues.
   d. amino acids.
   e. calloses.

6. Cellulose is a polymer of
   a. galactose.
   b. glucose.
   c. mannose.
   d. rhamnose.
   e. xylose.

7. The role of pectin in the primary cell **wall is to**
   a. reinforce the cellulose in the wall.
   b. make the wall transparent.
   c. transport precursors to the developing cell wall.
   d. glue adjacent cells together.
   e. cross link the cross-linking glycans.

8. Viruses can spread throughout the cell via
   a. the vacuole.
   b. the cell wall.
   c. secondary cell wall.
   d. pits.
   e. plasmodesmata.

9. Compared to primary cell walls, secondary cell walls are typically
   a. thicker.
   b. stronger.
   c. less active.
   d. more lignified.
   e. all of the above.

10. The elaborate cell walls of transfer cells allow for
    a. the movement of viruses from one cell to the next.
    b. the formation of pits and pit membranes.
    c. the deposition of multiple secondary cell wall layers.
    d. high rates of metabolite transport.
    e. both straight and branched plasmodesmata.

11. Plant cell walls are the basis of which of the following industries?
    a. paper, fiber, and pulp.
    b. lumber, timber, resins, and tars.
    c. textiles, inks, and biofuels.
    d. food thickening and flavor products.
    e. all of the above.

- **Concept Applications**

12. Global climate change is being driven largely by an increase in atmospheric CO_2 levels. Plants take CO_2 out of the atmosphere via photosynthesis and use it to make, among other things, cell walls. Herbaceous plants contain mostly primary cell walls, while woody plants contain mostly secondary cell walls. If you were to plant a garden of plants to sequester CO_2 from the atmosphere, would you use herbaceous or woody plants, and why?

13. A class of enzymes called pectin methyl esterases (PMEs) degrade pectin molecules (by breaking methyl ester bridges between pectin molecules). Why would PMEs be most active in ripening fruit?

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