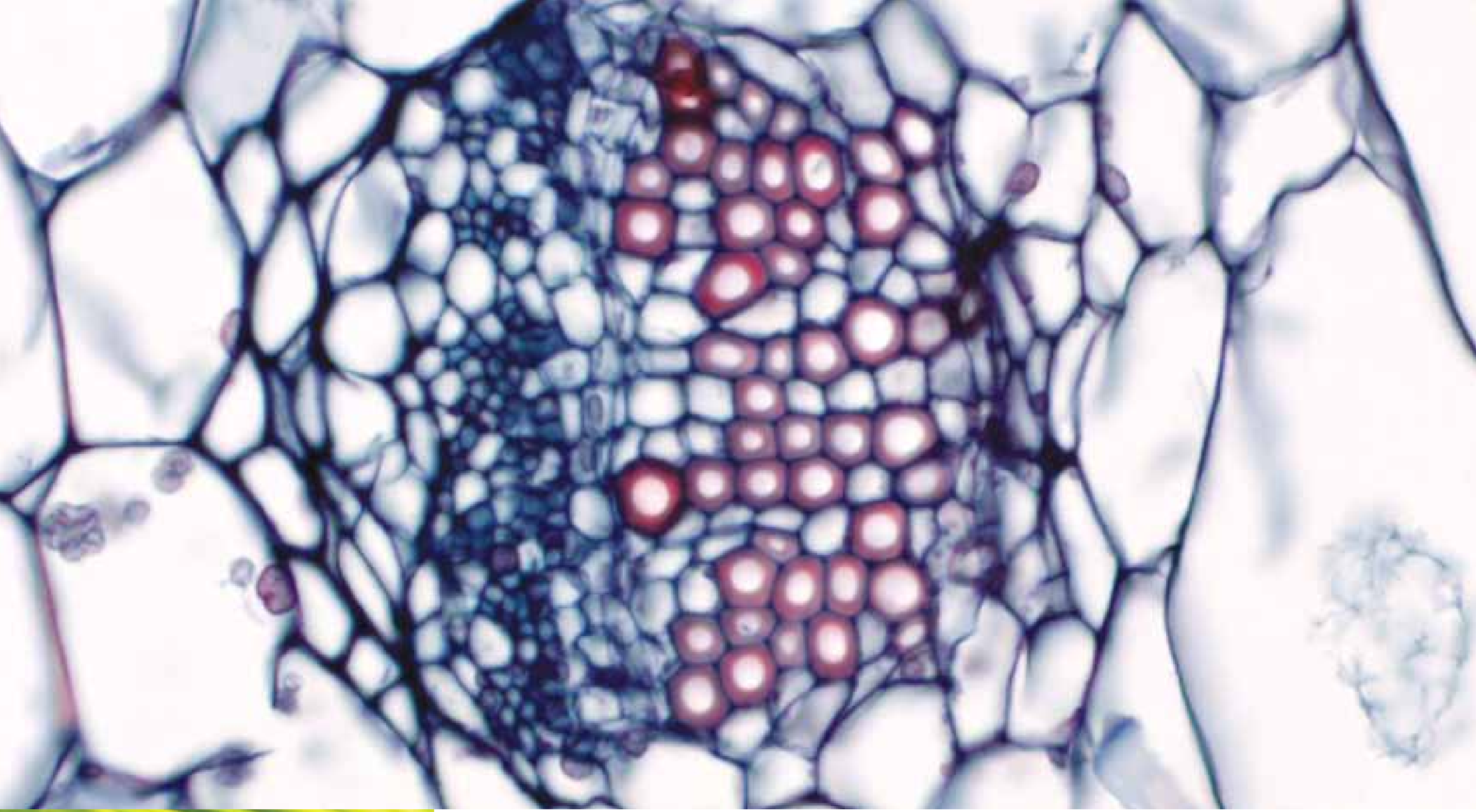


3

Cells, Tissues, and Organs: The Microscopic Components of Plant Structure

Plants are composed of a variety of cells and tissues that must work together in a coordinated fashion if the plants are to survive. These are cells that conduct water (red) and sugars (blue) in the veins of a leaf.

All organisms contain a material called **protoplasm**, which is composed of water, numerous organic compounds, and mineral nutrients. The nature of protoplasm was not well understood until the early 1900s. For hundreds of years it was thought to be a unique substance with an extraordinary property not found in other substances such as rock, water, air, iron, and so on: protoplasm could be alive. One of the first experiments to actually analyze protoplasm was reported in 1644 by Jean-Baptiste van Helmont. He carefully weighed a small willow plant and a pot of soil. After planting the willow in the soil, he cultivated it for 5 years, then unpotted it, washed the roots to obtain all remaining soil, and discovered that the plant had increased in weight by 164 pounds (73 kg [kilograms]) and the soil had lost only 2 ounces (57 g [grams]). He concluded that the plant and its protoplasm must be composed mostly of altered water and a small amount of minerals. He concluded that protoplasm might be special, but it was composed of ordinary chemical compounds.

Other chemists confirmed that protoplasm is indeed composed of water, organic compounds, and mineral nutrients, but the belief still persisted that protoplasm must differ from other substances by having a component called "vital force," which if present allowed it to be alive and if absent caused it to be dead. Only in the late 1800s did Louis Pasteur and others prove that vital force does not exist: protoplasm is alive when its many complex chemical reactions are running properly, it dies if some of these reactions fail.

The protoplasm of all organisms is divided into small bodies called cells, but our understanding of cells was also slow to develop. Early Greek philosophers knew that living creatures have organs: plants have roots, stems, and leaves; animals have hearts, stomachs, and so on. But even with the best eyesight, organs looked merely homogeneous or at most mealy or fibrous. After the first microscopes were invented, in 1665 Robert Hooke discovered that plant organs are composed of small boxes, which he named cells. Plant cells were easy to study even with crude early microscopes because plant cells are large and each is surrounded by a cell wall that appears as a fine line when viewed by a microscope. It was quickly realized that all parts of a plant's body are composed of cells. Also, early plant microscopists realized that plant cells are composed of small units (**organelles**): all green cells in leaves, stems, and unripe fruits hold their green photosynthetic pigment chlorophyll in small, bright green dots named chloroplasts (**FIGURE 3.1**). Starchy foods like potatoes have starch grains in their cells, and colorful petals and fruits display their pigments as particles or droplets in the cells.

Progress was much slower in the study of animal cells. They lack cell walls, and neighboring cells fit together so tightly that even today it is almost impossible to identify individual animal cells with even the best modern light microscopes. Furthermore, most organelles within both plant and animal cells have no natural color, so they remained unseen until microscopists began experimenting with artificial dyes and stains.

We now know that all organisms are composed of cells, and that in plants, each cell consists of a cell wall surrounding a small bit of protoplasm. The protoplasm itself contains many diverse organelles, and cells specialize for particular tasks by adjusting the number and metabolic activity of their organelles. Cells that specialize for photosynthesis develop large numbers of chloroplasts whereas flower petal cells develop various pigments. The same is true of us: our skin cells produce large amounts of the pigment melanin whereas our red blood cells fill themselves with hemoglobin instead; our liver cells have an abundance of organelles that break down toxins whereas muscle cells can contract because of the proteins they contain.

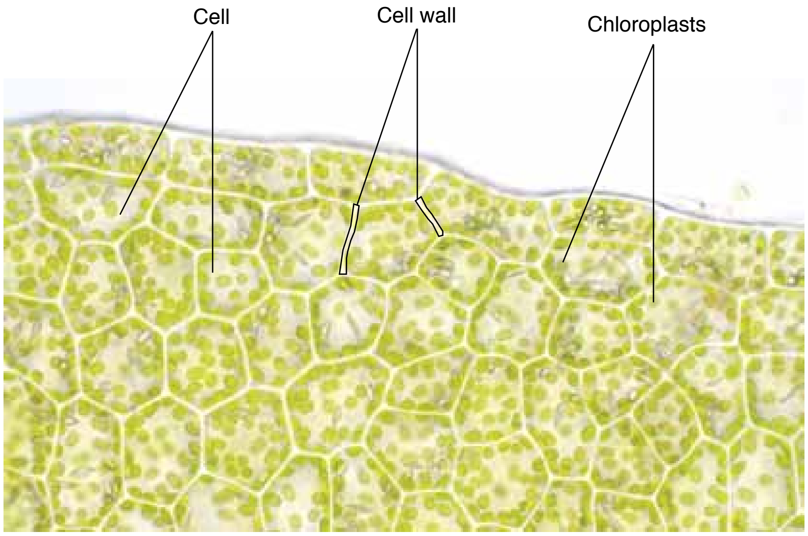


FIGURE 3.1. This is a view of a liverwort, *Pallavicinia*, a plant that has a body only one or two cells thick, thus allowing us to see details that are difficult to view in thicker plants. The white lines are cell walls, and each space enclosed by walls is a distinct cell. Each cell has numerous green spots, organelles called chloroplasts that contain chlorophyll and carry out photosynthesis (×200) (each cell is about 40μm wide; a strip of tissue 1 inch long would have about 625 cells side by side).

The body of every large organism, whether tree or human, is composed of organs that are in turn composed of cells. It is possible to imagine a bit of protoplasm or a single cell growing to the size of a tree or a human but it is difficult to imagine it being able to form specialized parts, each with a particular structure and function. Because organisms are composed of cells and because cells can specialize as they grow and develop, organisms can become both large and complex.

Cells

It is important to ask ourselves "Where do cells come from?" "How do cells grow and develop?" "Do cells die?" All cells originate in just one of two ways: either by (1) cell fusion or by (2) cell division. Cell fusion is the rarer type, occurring when one sperm cell fuses with one egg cell, resulting in one zygote (a fertilized egg). The zygote then grows and develops and at some point it will divide into two new daughter cells. These in turn grow then divide, and the process is repeated many times. Every cell in a plant's body and in our own bodies can be traced to its parental cell and the one that preceded that and so on back to the zygote. None of our cells is ever produced in any other way.

Because we animals have diffuse growth, most of our cells retain this capacity to grow and divide, thus allowing us to grow to adult size (our brain cells are exceptional and stop dividing while we are very young). Plants are different though, and have localized growth. While a plant embryo is still tiny inside an immature seed, cells in the center stop dividing and instead grow and differentiate into mature cells of shoot and root; these cells almost never divide again and do not contribute any further to the growth of the plant. Cells at the shoot and root tip, however, organize themselves into the root apical meristem and shoot apical meristem, and it is these cells that will continue to divide and produce new cells for the plant for the rest of its life (**FIGURES** 2.2 and **3.2**). All plants therefore have some small dividing cells, some developing cells, and some full-sized, fully mature cells. This is important to remember because plant cells usually change dramatically as they mature. Think of a flower's apical meristem, that of a cherry for example: while a flower bud is still tiny all its cells are small, soft, and some are dividing. The cells produced by the meristematic cells develop in various ways. Those that will be part of the sepals produce large numbers of chloroplasts and turn green; others produce a delicate pink pigment and become petals; still others will become enormous, filling themselves with sugar and red pigment and becoming the fruit we eat; and finally those that will make up the pit grow to their adult size, then alter their walls to become rock hard, then they die. These last cells, just like those of our own hair, nails, and skin, perform their protective function while dead.

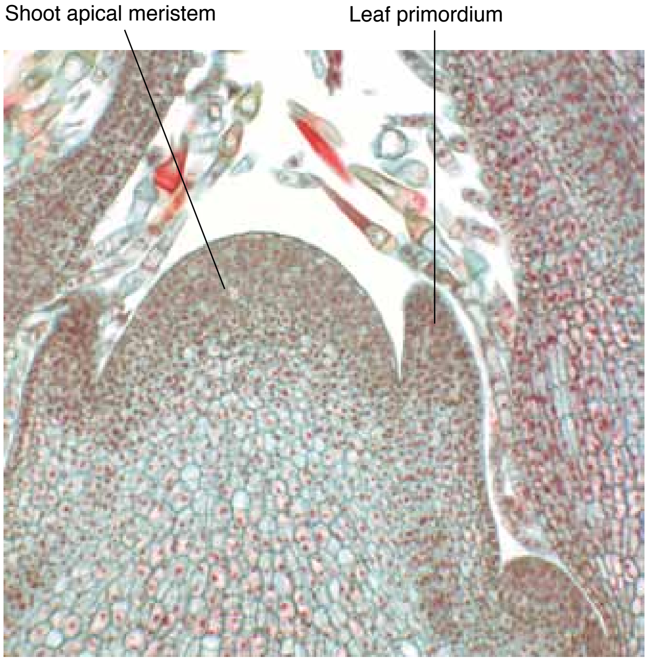


FIGURE 3.2. This shoot apex has been cut vertically down its center (a longitudinal section) and magnified enough to see its very small cells. Each cell divides into two new cells, then both grow back to their original size then divide again, thus producing new cells for the shoot. Along the sides of the meristem, some cells grow more rapidly than others, producing bulges that develop into leaves (×100).

Organelles

The **cell wall** is the outermost organelle; it surrounds and protects the rest of the cell (**TABLE 3.1**). All plant cells have a **primary cell wall** that is thin and flexible but strong enough to give the cell its shape and to control its size

TABLE 3.1. Organelles of a Plant Cell

Cell Part	Function
Cell wall	Provides strength.
Plasma membrane	Controls which chemicals enter or leave the cell.
Central vacuole	Storage, recycling, part of turgor pressure system of support.
Plastids	
Chloroplasts	Perform photosynthesis.
Chromoplasts	Store pigments other than chlorophyll.
Amyloplasts	Store starch.
Proplastids	These are plastids in meristematic cells; they differentiate into the other types.
Mitochondria	Carry out respiration.
Endoplasmic reticulum	A set of tubular membranes involved in moving material throughout the cell; ER also synthesizes certain lipids.
Dictyosomes	Package material into vesicles.
Ribosomes	Carry out protein synthesis.
Microtubules	Provide a framework inside the cell; involved in moving organelles through the cell.
Cytosol	The liquid (nonmembranous, nonparticulate) part of cytoplasm.

(**FIGURE 3.3**). Most of a wall's strength comes from one of its components, **cellulose**, which is a long, chain-like carbohydrate molecule. Cellulose molecules aggregate side by side into fibrils that wrap around the cell, reminiscent of the bandages wrapped around a broken arm to make a cast. Also, just like a cast, the cellulose must be held in place, and a plant uses other carbohydrates called **hemicelluloses** for this. Cell walls also contain proteins, pectin, and water (**TABLE 3.2**). Primary cell walls are extremely permeable, that is, water and small molecules like sugars, vitamins, and amino acids pass through them easily, allowing cells to obtain needed materials from neighboring cells.

When a cell divides, two new cell walls form in its center, separating one new cell from the other. These two new walls must adhere to each other and to the preexisting wall of the parent cell; otherwise the plant would fall apart into many single cells. The adhesive plants use to glue one cell to another is surprising—jelly, or more exactly, pectin (calcium pectate). Where two cells adjoin each other, a thin layer of pectin, called the **middle lamella**, holds the cells to each other. All the cells of the wood in a baseball bat or a piano or a giant redwood tree are held in place by the principle ingredient of jelly.

Where neighboring cells meet, primary cell walls have thin areas, called **primary pit fields**, and these in turn have extremely fine holes (**plasmodesmata**; singular: plasmodesma) that allow the protoplasm of one cell to actually be in contact with that of the neighboring cells (**FIGURE 3.4**). All cells of a plant are interconnected by plasmodesmata. **Secondary walls** are produced in sclerenchyma cells after the cell has grown to its proper size and shape; these are discussed below.

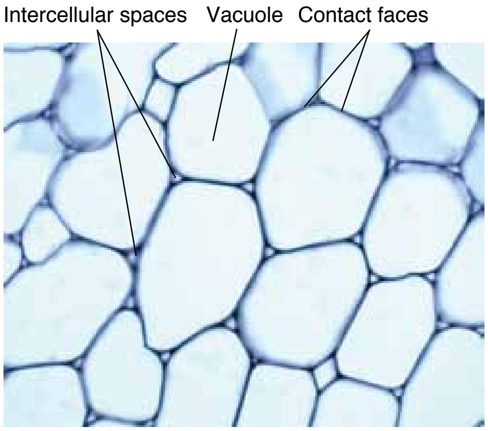


FIGURE 3.3. Each line here is a cell wall, and where cells touch each other, there are two walls pressed against each other. The region where cells touch is called a contact face, and it is where the cells are glued together by a middle lamella. Although it appears as if each cell is empty, each actually has a thin layer of organelles too small and sparse to see with a light microscope (these cells do not have chloroplasts that are easy to see as in Figure 3.1). The large white center of each cell is its central vacuole. The small spaces between adjacent cells are intercellular spaces. These are mature cells in the center of a sunflower stem (×300).

TABLE 3.2. Components of Cell Walls

Basic components found in all cell walls	Components found in specialized walls
Cellulose	Casparian strips: lignin and suberin
Hemicellulose	Cork: suberin
Cell wall proteins	Epidermis: cutin and wax
Pectins	Sclerenchyma: lignin
Water	

The small mass of protoplasm surrounded by a cell wall is called the cell's **protoplast**, and its outermost layer is a membrane, the **plasma membrane** (sometimes called the plasmalemma). Like all cell membranes, this is composed of lipids and proteins, and is **selectively permeable**; it controls which molecules pass through it and which do not. The plasma membrane then determines which molecules are allowed into the cell (usually nutrients) and which are not (usually toxic substances).

Each cell, at least while young, has a single **nucleus** that contains genetic material (DNA) that stores most of the information needed for plants to grow, develop, and reproduce (**FIGURE 3.5**). The nuclear DNA guides the synthesis of enzymes that carry out the cell's metabolism. There is a limit to the rate at which one nucleus and its DNA can guide a cell's metabolism; consequently, a cell must not grow so large that the nucleus can no longer control it. Rarely, some cells allow their nuclei to divide such that the cell is binucleate or tetranucleate (or more), and this allows the cell to become larger or have a more rapid metabolism. Certain phloem cells (sieve tube members) destroy their nucleus as part of their development, and then must function while being enucleate.

Each nucleus is surrounded by two selectively permeable membranes, the **nuclear envelope**, which keeps the nuclear material separate from the rest of the cell. The nuclear envelope allows the cell to have two distinct compartments, each with a specialized metabolic environment: one inside the nucleus and adjusted for the type of chemical reactions that must occur there, and a second environment suitable for the rest of the protoplasm (the portion of the protoplasm that is not nucleus is called **cytoplasm**). This is called **compartmentation**. Nuclear pores control passage of material between the nucleus and cytoplasm.

The **central vacuole** is an organelle that occurs in plants, algae, and fungi but never in animals, and it affects many aspects of plant biology. It is surrounded by a selectively permeable membrane (the **vacuole membrane** or tonoplast), so it is a compartment distinct from that inside the nucleus and in the rest of the cytoplasm. The vacuole membrane is able to forcefully pump certain molecules—for example waste products, sugars, and potassium—into the central vacuole. Unlike animals, plants do not dump their wastes outside their bodies (they have no kidneys or colon) but instead store them in their central vacuole (**FIGURE 3.6**). Storing waste inside your own body seems counterintuitive but waste products have little nutritional value for animals or fungi, so as they accumulate inside the central vacuole, the cell's value as food decreases. Animals prefer to eat young, nutritious leaves and stems rather than old, mature waste-filled ones.

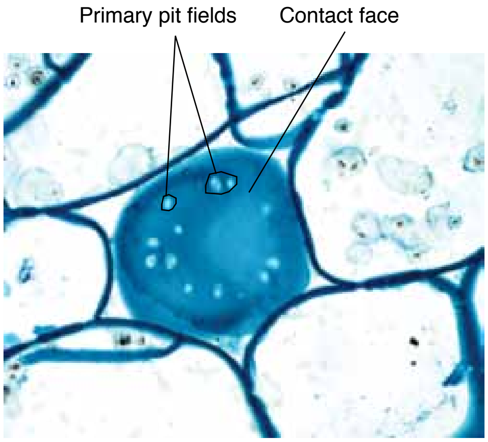


FIGURE 3.4. The dark blue area is a contact face (two cell walls glued together) seen in face view (contact faces are in side view in Figure 3.3). The white areas in the contact face are primary pit fields, areas where the two walls are exceptionally thin. Each contains many plasmodesmata, but they are too narrow to be visible with a light microscope (×200).

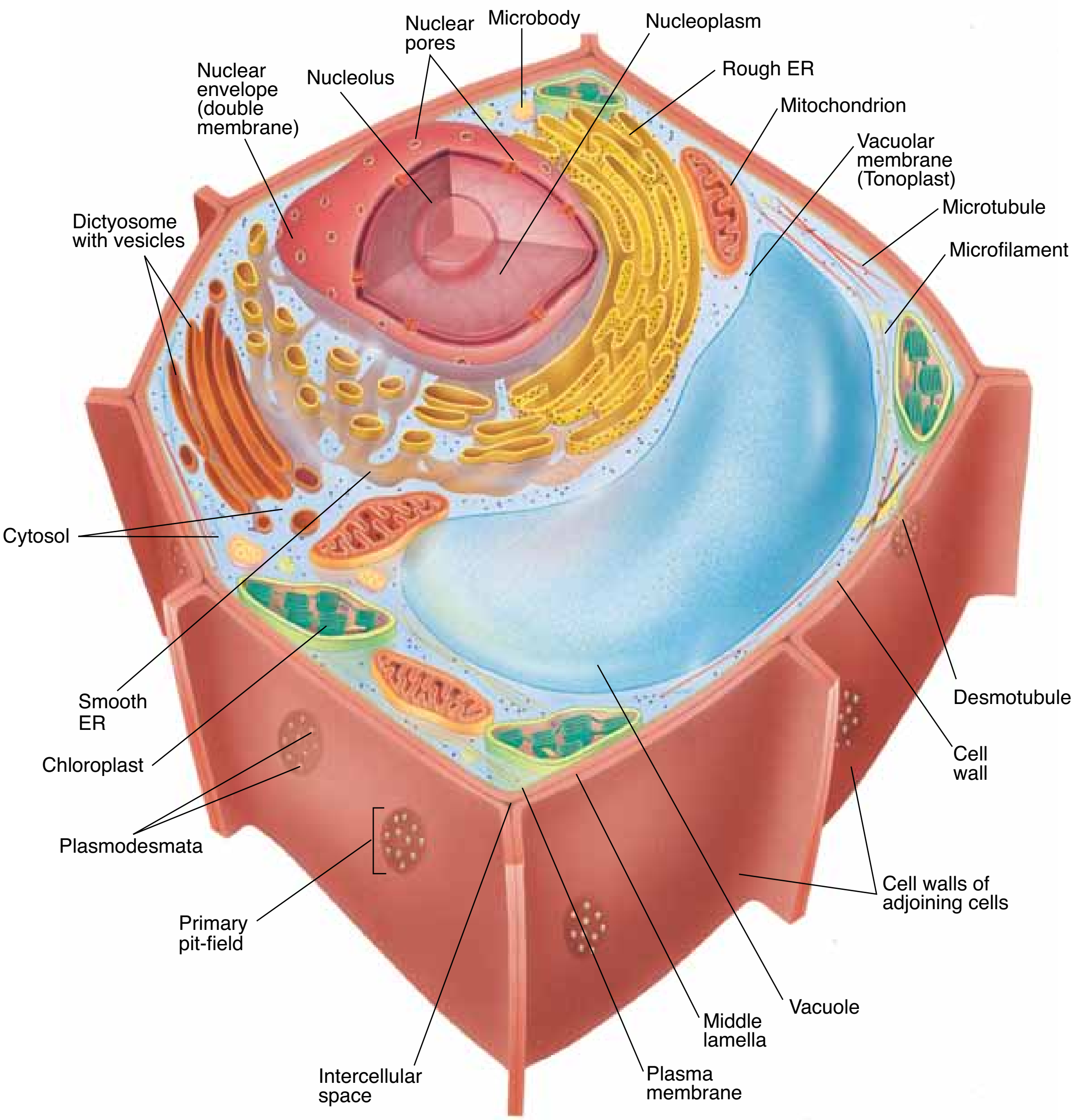


FIGURE 3.5. Diagram of a generalized plant cell. The vacuole has been drawn exceptionally small here to save space, otherwise the diagram would occupy several pages and be mostly vacuole.

Plants obtain defense against predators merely by storing their waste rather than throwing it away. This defense mechanism would not work for us: we generate such a large quantity of waste that if we tried to store even one month's worth, we would be too heavy to move. In addition to wastes, central vacuoles are used to display pigments in flower petals and fruits in many plants (**FIGURE 3.7**).

Plant cells contain small **plastids**, a type of organelle that can change its structure and metabolism, thus allowing cells to also alter their physiology. In shoot and root apical meristems, plastids are small, nondescript **proplastids**, bodies with an outer and inner membrane; some plastid DNA; and a small amount of water, chemicals, and other components. As meristem cells grow and divide, their proplastids also grow and divide such that each new daughter cell receives an adequate supply of proplastids. If some of the meristem cells become part of a leaf primordium, their

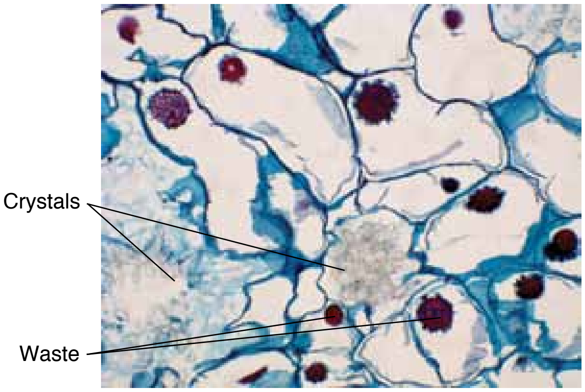


FIGURE 3.6. The dark red materials in these very old cells are accumulated waste products. Many crystals are also present, and in general these cells appear old (×300).

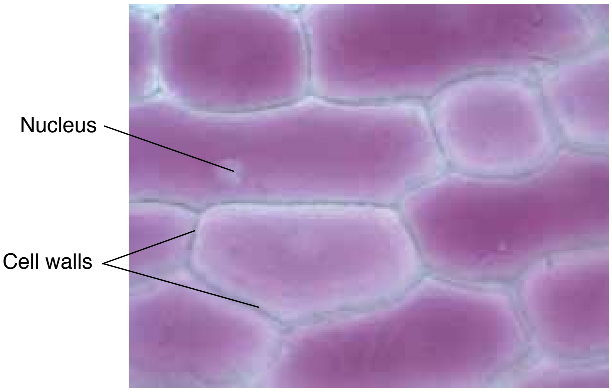


FIGURE 3.7. These are fresh cells from the skin of a purple onion. The color is pigment stored in each cell's central vacuole, and we can see that the vacuole occupies almost the entire volume of each cell. The dark lines are cell walls and clear areas are nuclei. These cells fit together tightly with no intercellular spaces (×200).

proplastids convert themselves into **chloroplasts** by synthesizing chlorophyll along with other factors needed for photosynthesis (Figure 3.1). Each chloroplast enlarges and its inner membrane folds into a complex three-dimensional shape. Once fully differentiated, carbon dioxide can pass through the outer chloroplast membrane and be converted into sugar by the chloroplast's enzymes and the light energy captured by chlorophyll. Chloroplasts are abundant in cells of dark green leaves, like those of spinach, but are more sparse in leaves, stems, and fruits that are pale green.

Many flowers and fruits are green while immature but change to some other color when mature. In many cases, this color change is caused by chloroplasts converting themselves to **chromoplasts** as they dismantle their chlorophyll and replace it with some other pigment (**FIGURE 3.8**). As starchy organs like potato


(a) (b)

FIGURE 3.8. **(a)**The red color of these peppers (*Capsicum*) is due to pigments in chromoplasts whereas the stalks are green because they contain chloroplasts. **(b)** Each orange particle is a chromoplast in cells of red pepper; although they look orange here, altogether they produce the red color of the peppers in part a (×80).

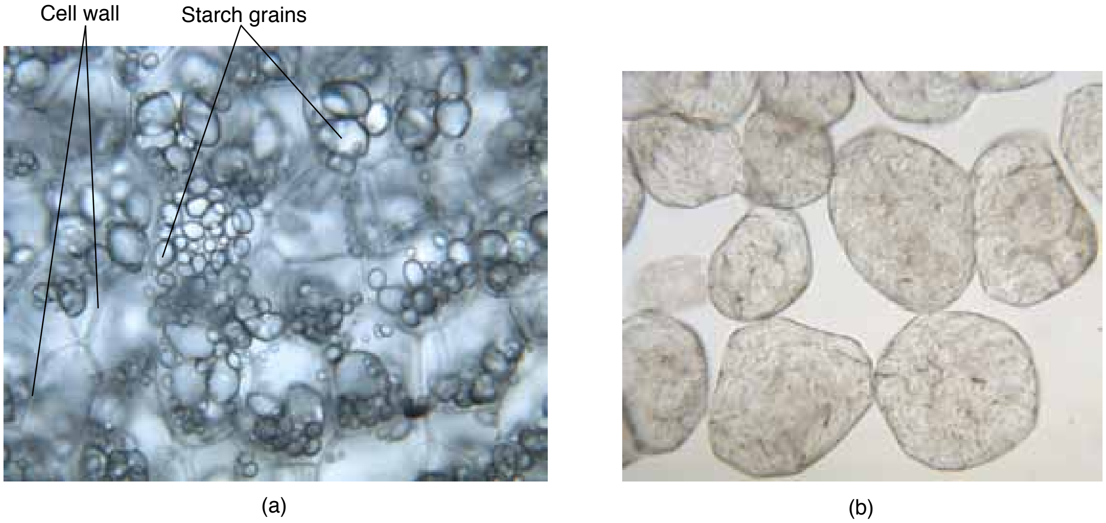


FIGURE 3.9. **(a)** This is a view of living potato cells, each of which contains many oval amyloplasts (starch grains). Cell walls are so thin they are just barely visible. Most cells are about half filled with amyloplasts, most of which are so heavy they have settled to the bottom of the cell (×80). **(b)** These are boiled potato cells: the only thing visible is greatly swollen starch grains (same magnification as part a. Boiling has caused the starch grains to absorb water and swell, making them more digestible for us (×80).

tubers, yams, and rice grains develop, their proplastids turn into **amyloplasts** (starch grains) (**FIGURE 3.9**). Amyloplasts absorb sugars and polymerize them into starch, which is so stable it can be stored in the cells for months or years. Most plant cells have at least a few amyloplasts at some point in their life, but starchy cells have numerous amyloplasts and develop in roots, stems, wood, bark, fruits, and especially seeds. When the plant needs the energy stored in the starch, the amyloplast breaks it back down into sugars, then loads them into phloem where they can be transported to tissues and organs that need them. As a seed germinates, starch is broken down and sugars are moved to the root and shoot apical meristems. Similarly, when a century plant finally blooms, amyloplasts in cells throughout all its massive leaves release sugar that is used to build its giant flower stalks (see Figure 2.22). Some of the cells and their amyloplasts may be more than 20 years old. We animals never store starch; we use fats in our adipose cells for long-term energy storage.

Two other critical roles of plastids are that they synthesize certain lipids and amino acids that no other organelle can make. Only algae and plants have plastids; no other organisms do.

Starch, sugar, and fats are energy-rich molecules, but that energy must be transferred to a smaller molecule, called ATP, by the process of respiration (see Chapter 5). Some steps of respiration occur in cytoplasm but the last steps, which involve oxygen, occur in **mitochondria** (singular: mitochondrion) (**FIGURE 3.10**). All cells of all organisms (except bacteria and archaeans) have mitochondria, and cells that require large amounts of energy (rapidly growing meristems, germinating seeds, muscles, liver) have large numbers of mitochondria. Like plastids, mitochondria have an outer and inner membrane, their own mitochondrial DNA, and they can divide to produce more mitochondria.

Within the cytoplasm are many other small organelles, composed mostly of membranes, that are involved in moving materials from place to place within the

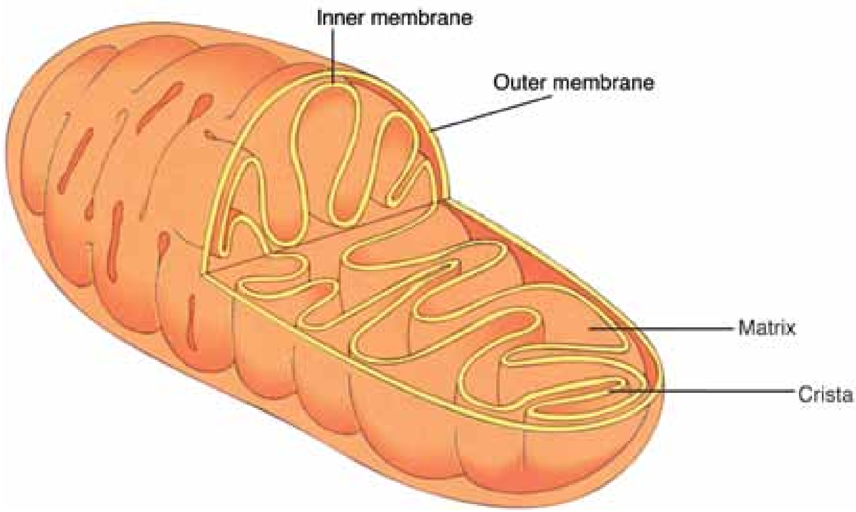


FIGURE 3.10. Diagram of a mitochondrion showing the smooth outer membrane and highly folded inner membrane.

cell. The **endoplasmic reticulum** is a network of tubes and sacs that extends throughout the cytoplasm. Like the plastids, it also synthesizes certain lipids that are made nowhere else. **Dictyosomes** are sets of flattened sacs that process materials that will be exported from the cell. Raw materials are absorbed by the dictyosomes, converted to finished products, then are packaged into a vesicle (a small bag composed of membrane), which moves through the cell. When a vesicle touches the cell membrane, the two fuse and the vesicle's contents are released to the exterior of the cell. This is especially common in us, and is the method by which we secrete our digestive enzymes into our stomach. Carnivorous plants like Venus's flytraps and sundews also secrete digestive enzymes by means of dictyosome vesicles. In plants that are slimy (okra, prickly pears), the slimy mucilage is synthesized in dictyosomes and then stored in the central vacuole.

Many of the membranes mentioned above are interconnected, at least from time to time. The outer envelope of the nucleus connects to the endoplasmic reticulum, which in turn can form vesicles that accumulate to produce a dictyosome. Dictyosome vesicles can fuse with plasma membrane or vacuole membrane. When plastids and mitochondria wear out and stop functioning, they enter the central vacuole by fusing with the vacuole membrane; once inside they are digested into individual molecules that can be re-used to build new organelles. Membranes, vesicles, and organelles are constantly moving in plant cells; a plant may stand still but its protoplasm is in constant motion. This set of interconnected membranes is called the endomembrane system.

Finally, plant cells contain several organelles that are not composed of membranes. **Ribosomes** are small particles that construct proteins from amino acids, guided by molecules produced by DNA. **Microtubules** and microfilaments are linear aggregates of proteins that act like a scaffold (the **cytoskeleton**) and give the cytoplasm structure, while at the same time being responsible for pulling organelles from site to site within the cell. Finally, many plant cells contain crystals of calcium salts; these may be spiky balls (druses), a single large spear-like crystal (styloids), tiny needles that occur in bundles (raphides), or numerous tiny cubic crystals (crystal sand). The liquid portion of cytoplasm, the part not composed of membranes or particles, is **cytosol**.

Intercellular Spaces

In addition to cells, plants are also composed of **intercellular spaces**. Imagine filling a room with beach balls that are so fully inflated they are almost inflexible. Once the room contains as many balls as possible, there will still be a great deal of empty space between the balls. Also, each ball will touch its neighbors in just a small area (called a **contact face**) (**FIGURE 3.11**). Now imagine filling the room with balls that are just a little underinflated. You can pack more balls into the room, there is less space between them, and each ball has a greater contact area with its neighbors. Now imagine using balls that contain so little air that each is extremely flexible; the room can be completely filled with balls because each can bend and flex to match the contours of its neighbors. There is no longer any air space left in the room, and the entire surface of each ball contacts one neighbor or another. Animal cells and plant meristematic cells are like the last group: their surfaces are so delicate the cells mostly fit snuggly together. But as plant cells grow, the pressure of the central vacuoles often causes them to be more rounded and they push away from their neighbors, partially tearing the middle lamella, and creating intercellular spaces at their corners. If they expand more, the cells become almost spherical and the intercellular spaces become larger.

Intercellular spaces allow oxygen and carbon dioxide to diffuse quickly throughout a plant. Because plants have no lungs, gills, or circulatory system, they cannot move these gases forcefully through their bodies the way we animals do, and plants must rely on diffusion. Gases diffuse thousands of times more rapidly through intercellular spaces than through cells, and without intercellular spaces, the innermost cells of thick plant parts would suffocate.

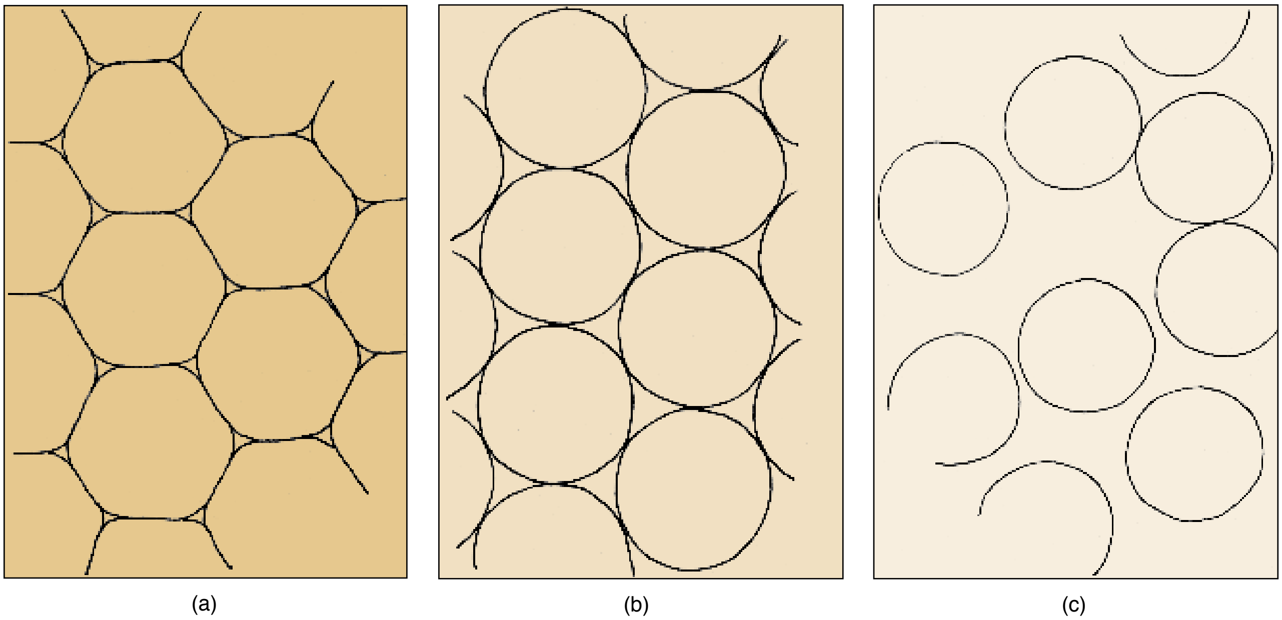


FIGURE 3.11. If plant cells are not very turgid, or if they are glued together strongly by their middle lamellas, then each has extensive contact with adjacent cells and intercellular spaces between them are small **(a)**. But if cells are very turgid, they swell and pull away from each other **(b)**, causing the intercellular spaces to expand, which permits air to diffuse more rapidly through the tissue. With even more expansion **(c)**, some cells pull completely away from some of their neighbors.

Tissues

There are just three types of plant cells: parenchyma, collenchyma, and sclerenchyma, and they never occur in a disorderly jumble (**TABLE 3.3**). Instead numerous cells develop in groups that allow them to perform certain functions. For example, certain cells work together as the epidermis (or skin) of the plant, others function in water conduction, and so on. If all the cells of a tissue are similar, the tissue is a simple tissue, but if several different types of cells work together, they are called a complex tissue.

Simple Tissues

Parenchyma is a simple tissue composed of just parenchyma cells, and these are defined as cells that have a uniformly thin primary wall and also lack a secondary wall (**FIGURE 3.12**, and see Figures 3.1 and 3.3). Because primary walls are permeable to small molecules, parenchyma cells are well adapted for many metabolic functions: material can be moved easily into parenchyma cells, chemically altered, and then be moved back out to other parts of the plant. Photosynthetic cells are parenchyma (often called chlorenchyma): carbon dioxide, water, and light enter the cells easily and newly synthesized sugars leave easily. Similarly, starch storage cells in tubers and seeds are parenchyma cells, as are cells that store oils (avocado, sunflower seeds), pigments (petals, fruits), or water (cacti and other succulents). Meristematic cells are also parenchyma; their thin walls allow the cells to grow.

Collenchyma and **sclerenchyma** are both cells that are specialized such that they provide much more strength and support than can be offered by the thin walls of parenchyma cells. Collenchyma cells are defined by having primary walls that are especially thick at each corner of the cell (Figure 3.12), whereas sclerenchyma cells have a secondary wall that lies just interior to its primary wall (**FIGURE 3.13**). More importantly, these two cell and tissue types provide different types of strength. Collenchyma provides **plastic strength**: it can be forced into a new shape and it will then maintain that new shape. Think of clay, which can be pushed and pulled to make a bowl or cup and it holds that shape once we stop working with it. Similarly, collenchyma can grow into a new shape or size and then maintain it, so collenchyma can be used to strengthen long, thin organs *while they are growing*, such as the young internodes of vines or the midribs of large leaves for example. These organs would be too fragile if they were composed only of parenchyma.

TABLE 3.3. Basic Types of Plant Cells

Parenchyma cells have thin, permeable primary cell walls; cells are metabolically active.

Collenchyma cells have primary cell walls thickened at corners; plastic strength (strength that permits growth).

Sclerenchyma cells have both primary and secondary cell walls; elastic strength (strength that restores mature size and shape).

- Fibers provide flexible elasticity.
- Sclereids provide inflexible elasticity.

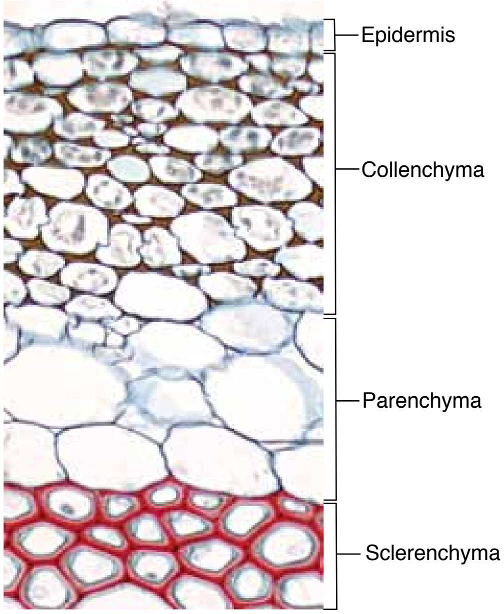


FIGURE 3.12. A stem of cucumber has been cut in transverse section and the outer part photographed. The uppermost layer of cells is the epidermis, and just below it is a band of collenchyma about eight to ten cells thick. The corners of collenchyma cells are thickened. The large cells with thin walls in the center are parenchyma, and the cells at the bottom are sclerenchyma: they have secondary walls (×150).

BOX 3.1. Parenchyma, Sclerenchyma, and Food

Most of the fruits, vegetables, and other plant parts we eat as food consist of almost pure parenchyma. With their thin walls, parenchyma cells are soft and easy for us to chew if eating our food fresh or cooked, and they can be ground, mashed, and sliced for processed food. Whereas collenchyma and sclerenchyma are used for strength, parenchyma cells are the sites for synthesis and storage of an amazing variety of organic compounds: carbohydrates, fats, proteins, vitamins, pigments, flavors, and other nutritious materials essential to our health.

Parenchymatous foods are easy to recognize because we can bite through them easily: apples, pears, strawberries, blueberries, potatoes, lettuce, spinach, and so on. All seeds such as popcorn, beans, rice, and wheat are parenchyma as well, but in their dry, ungerminated, uncooked condition, they are too hard to be edible, despite having thin cell walls. Boiling allows water to loosen hard starch grains and protein bodies, and to soften the walls.

Collenchyma is not present in all plants, and is never really abundant. It is almost always just a minor fraction of all the cells in leaves and stems, and virtually never occurs in roots. The most familiar collenchymatous food is celery: we eat the petioles of leaves, and each ridge along the surface is a mass of collenchyma cells. Also, each vascular bundle inside the petiole has a cap of collenchyma along one side; these bundles cause celery's stringiness. Other leafy vegetables with thick petioles, like rhubarb and bok choy, also have abundant collenchyma. Most of us eat these for their flavor and nutrients, not for the pleasure of chewing endlessly on collenchyma strands.

Plants can store starch and proteins in fibers, but they do so only rarely. With the low nutrition and difficulty in chewing, we never use truly fibrous material like mature bamboo shoots and wood for food. However, many vascular bundles contain fiber cells, so even when eating parenchymatous foods we still consume some sclerenchyma. The fibers may be very noticeable, as in asparagus that is a bit too old, green beans, snow peas, artichokes, pineapples, and mangoes. In others, the fibers are a bit softer, especially after being cooked, but you may still notice them in things like squash, pumpkin, and zucchini. You have probably noticed when carving jack-o-lanterns that cleaning a pumpkin is really just a matter of removing seeds and fibers.

Sclereids also occur in some of our foods. Clusters of them cause the grittiness in pears. The seed coats of beans, peas, and most other seeds are also made up of sclereids, as is the covering on seeds of corn. The pieces that get stuck in our teeth while eating corn on the cob are composed of sclereids (and the inedible cob is mostly fibers). In small seeds that are ground into flour (wheat, rye, barley), the sclereid-rich seed coats are broken down into small pieces (the bran) that are easy to eat. Sclereids also make up the brown covering of unpopped popcorn, and popping breaks up the covering. In all cases, we do not digest any part of the secondary walls of sclerenchyma cells; all the walls simply pass right through us.

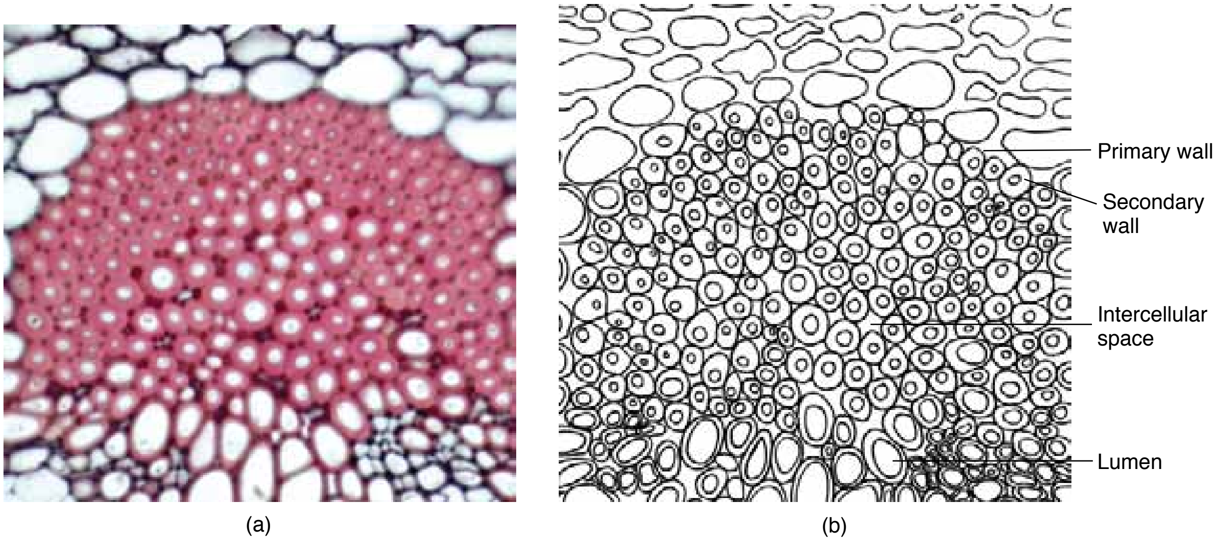


FIGURE 3.13. Sclerenchyma cells are recognizable because they have a thick secondary wall just inside their primary wall. The secondary wall is so thick in each cell that it occupies most of the cell's volume: by the time each cell had finished constructing its secondary wall, the cell's protoplasm had been squeezed down to fit inside the white area (the lumen) in the center of each cell. These cells appear round, but they are very long fiber cells that have been cut in transverse section. It is unusual to have such large intercellular spaces in a mass of fibers (×200).

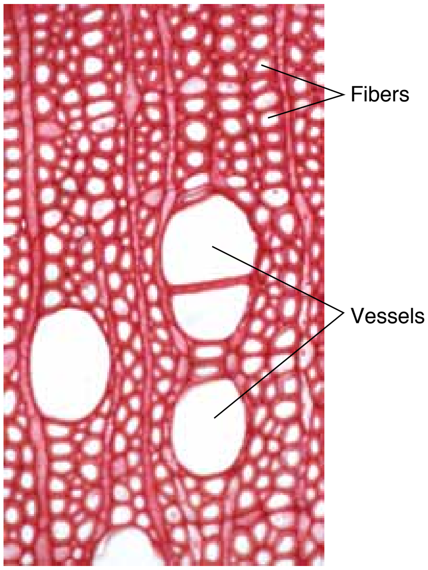
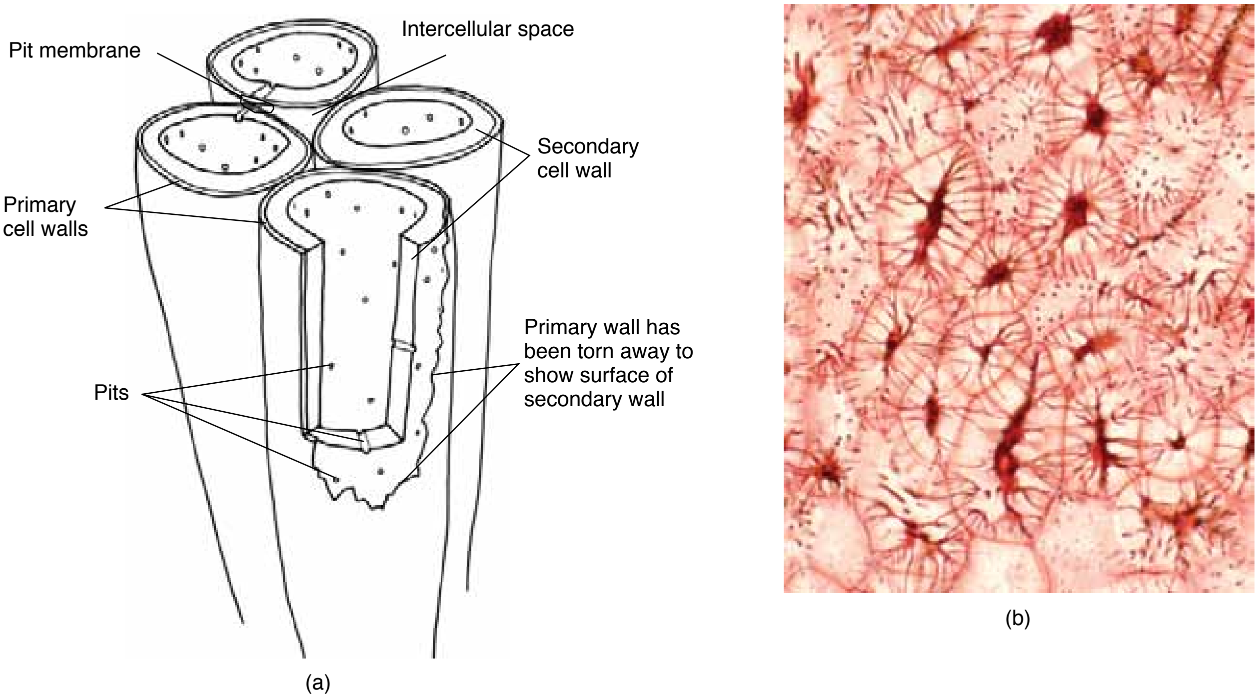


FIGURE 3.14. This is a transverse section of wood of American hornbeam (*Carpinus caroliniana*), showing that almost all the cells are fibers (all the cells with small white centers). Fibers give the wood both strength and flexible elasticity. The several wider cells are vessel elements, which conduct water through the wood (×200).

Collenchyma cells occur together as bands with no other types of cells mixed in with them (Figure 3.12). This is collenchyma tissue, a simple tissue. Collenchyma does not occur in all plants, but in those that have it, it usually occurs as a band several cells thick located just interior to the epidermis of stems, and just below or above the largest veins of leaves. Our most familiar example is celery: its stringy masses are whole vascular bundles, each of which has a mass of collenchyma alongside it. Each ridge on the surface of a celery stalk is a bundle of just collenchyma cells.

In contrast, sclerenchyma provides **elastic strength**. Like an elastic waistband in clothing, it can be pulled to a new shape but once we stop pulling, it returns to its original size and shape. Sclerenchyma differentiates in large organs *after they have already grown* to their proper size and shape. Woody branches are good examples of sclerenchyma's elasticity: the branch grows to a particular form and then is occasionally bent by wind or snow or even heavy fruit or birds (**FIGURE 3.14**). The branch should not stay in the new shape; it should spring back to its original shape once the wind has stopped. The secondary wall is so strong it cannot be stretched by the central vacuole, so a fully differentiated sclerenchyma cell cannot grow; instead, it begins its life as a parenchyma cell, grows to its proper size and shape, and only then can it build its secondary wall. If you have cleaned and cut asparagus for cooking, you know that the top green young part is soft and edible; the basal white part is old, tough and fibrous. The green part is still growing longer and all its cells have just thin primary walls. The lower white part has finished elongating, all its cells have reached their proper length, and some have deposited a secondary wall and transformed themselves from parenchyma cells into sclerenchyma cells.

The secondary wall is made of the same components as the primary wall, but it is much thicker and stronger. Also, sclerenchyma cells add another component, **lignin**, which hardens into a solid matrix around all the other wall components, making the secondary wall extremely tough and resistant to decay. Lignin also makes the wall impermeable to water and almost everything else, so if a cell encased itself completely in a secondary wall, it would soon die of starvation or asphyxiation. Instead the secondary wall has small tunnels (called **pits**) that provide a passageway for nutrients (**FIGURE 3.15**). In sclerenchyma tissue, in which all cells have secondary walls (for example the shells of nuts, the masses of fibers in bamboo, or the spines of cacti), the pits of neighboring cells must interconnect.



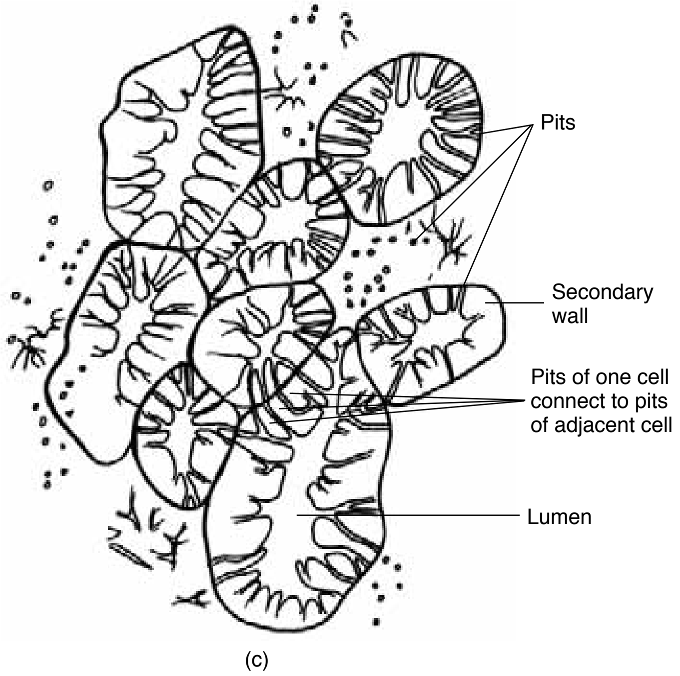


FIGURE 3.15. Sclerenchyma cells, both fibers **(a)** and sclereids (**b, c**) are interconnected by pits. A pit is an area where there is no secondary wall, but the primary walls of each cell are still present (**a**), so particles cannot pass from one cell to another through pits. Fibers are usually interconnected by very few pits whereas sclereids have many. (**b**) is a section through the pit of a peach (×250).

Sclerenchyma provides plants with two types of elastic support: flexible and inflexible. Flexible support is provided by long sclerenchyma cells called **fibers**. These allow woody stems and fibrous leaves to bend and flex without breaking. If the fiber cell walls are extremely thick and heavily lignified, as in wood of oak or hickory, it may take a great deal of force to flex the wood, but with thinner walls and less lignin, as in willow wood, the fibers are more supple. Inflexible support results from spherical or cube-shaped sclerenchyma cells called **sclereids**. Sclereids make up the shells of seeds like walnuts, pecans, coconut, and so on; inside each shell is a delicate seed and its embryo, both made of fragile parenchyma cells. A shell made of fibers might flex without breaking, but the embryo inside would be crushed; inflexible sclereids are needed. We have bones with these same properties: our long bones provide flexible elasticity (our ribs are more flexible than our leg bones) whereas our skull must provide inflexible elasticity if it is to protect our brain.

Many sclerenchyma cells die after they make and lignify their secondary wall. The strength is provided just by the wall, a living protoplast is not needed. In fact, keeping the sclerenchyma cells alive after they have completed their secondary wall would be an unnecessary metabolic expense.

Sclerenchyma cells often occur as large groups of just fibers or just sclereids, with no other cells mixed in (**FIGURE 3.16**). This is sclerenchyma tissue, a simple tissue. The majority of sclerenchyma in most plants occurs as part of complex tissues, mixed together with parenchyma cells. Wood and bark are good examples of complex tissue that contain sclerenchyma and parenchyma together. Fibers are used to make cloth, fabrics, and paper, and are discussed in Chapter 16.

Complex Tissues

Meristems are small discrete groups of parenchyma cells that do at least two things: they divide to make new cells, and they make those cells in specific layers and patterns (Figure 3.2). Their thin walls allow these cells to easily absorb nutrients that have been transported to them by xylem and phloem from the rest of the plant. The nutrients are converted into more complex compounds such as carbohydrates, lipids, proteins, DNA, and these in turn are assembled into microtubules, membranes, proplastids, and all the other organelles that make up protoplasm. The accumulation of newly synthesized protoplasm causes the cells to enlarge, then the cells divide, producing new, smaller cells which repeat the process. If all new cells continued to act as meristematic cells, then the meristems would become larger, but instead, some of the cells are pushed out of the meristem and begin to differentiate such that they can carry out specialized tasks. For example, cells on the surface of the shoot apical meristem form a single layer located on the surface of stems and leaves; these cells differentiate into epidermis. Other cells, located deeper in the shoot apical meristem will also be deeper in the stem, and some will mature as xylem, others as phloem, and so on. In each case, the cells enlarge as they differentiate, and some produce chloroplasts, others amyloplasts, some make secondary walls, and so on.

The **epidermis** is a complex tissue that forms the outermost surface of young plant organs (**FIGURE 3.17**). If an organ, such as woody stems and roots, becomes old, the epidermis will be replaced by bark. The word “epidermis” is used for both plants and animals but a plant epidermis differs greatly from an animal one. Our epidermis is thick, consisting of many layers of dead and dying cells, we have sweat glands, hair follicles, nerves, and numerous other features. In plants, the epidermis is almost always just one single layer of parenchyma cells.

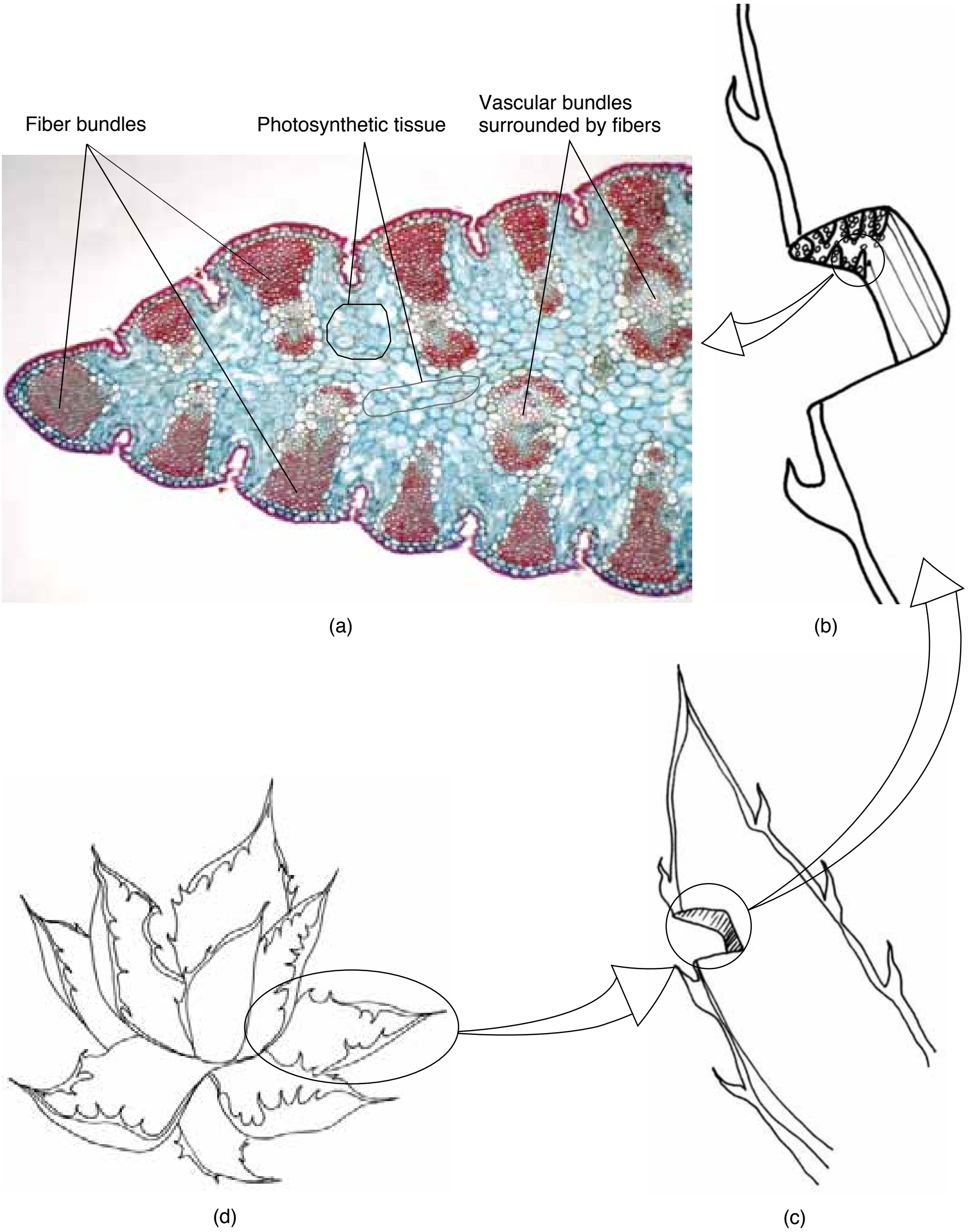


FIGURE 3.16. The long strap-shaped leaves of many monocots such as yuccas and agaves often have bundles of fibers along each surface, making the leaves tough, flexible, and resistant to being torn by wind and eaten by animals. The fiber bundles are often extracted and used for rope or weaving coarse cloth. Some of the bundles shown in transverse section in the micrograph would be as long as the entire leaf shown in the drawing (×70).

As epidermis cells differentiate, the endoplasmic reticulum produces several kinds of fatty acids that are transferred across the plasma membrane and into the cell wall that is exposed to the plant's environment. The fatty acids accumulate in and on the wall, and polymerize into an impermeable substance called **cutin**; a layer of cutin is called the **cuticle**. Wax is also present in the cuticle of most plants. Being impermeable, the cuticle prevents water from evaporating rapidly out of the plant on dry days.

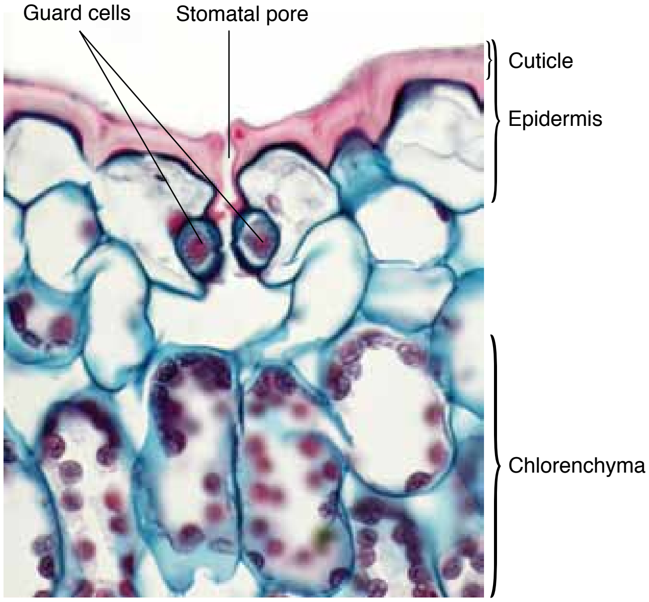


FIGURE 3.17. This is a transverse section of a leaf, showing the epidermis on its upper surface, as well as a few internal photosynthetic cells. The pink layer is the cuticle, which makes the outer layer of the epidermis both waterproof and resistant to attack by fungi and insects. The space between the two dark cells (the guard cells) allows carbon dioxide to diffuse into the leaf where it is used by the chloroplasts in the parenchyma cells at the bottom of the image (×200).

It also greatly hinders the movement of oxygen and carbon dioxide. Certain organs, such as petals and roots, do not carry out photosynthesis, do not need carbon dioxide, and their metabolism is so low they need little oxygen. Organs like this can have an epidermis in which the cuticle is uninterrupted and has no holes in it.

Foliage leaves have a more complex epidermis. Leaves must allow large amounts of carbon dioxide to pass from the air across the epidermis and into their photosynthetic cells while simultaneously allowing oxygen to escape. Consequently, foliage leaf epidermis has numerous small holes, called **stomatal pores**, that are not blocked by cuticle and that allow the plant to exchange gases with the air (**FIGURE 3.18**). There is a problem however: water vapor can also escape through the pores, and this could dehydrate the plant. While the plant is photosynthesizing during sunlight hours, there is little that can be done, and if the soil is moist enough the roots absorb adequate water to compensate for the water lost by leaves. But at night, when photosynthesis is not possible, water would still be lost even though the plant would not need to absorb carbon dioxide. This problem was solved when guard cells evolved. **Guard cells** are curved cells that occur in pairs, one on either side of a stomatal pore (**FIGURE 3.19**). At sunrise they increase their turgor pressure, swell and bend slightly more, opening the stomatal pore. At sunset, they lose turgor pressure, shrink and close the pore, preventing water loss at night. The term **"stoma"** (plural: stomata) is often used to refer to either the pore or both the guard cells and the pore (for example, an epidermis might have 100 stomata per square millimeter [an area about the size of the period at the end of this sentence]).

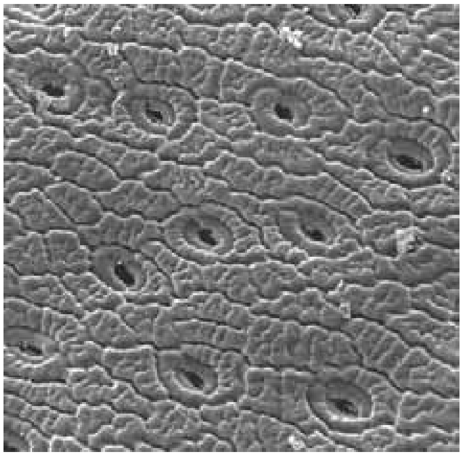


FIGURE 3.18. A scanning electron micrograph of the outer surface of an epidermis, showing the numerous stomata. Every photosynthetic cell (out of view on the other side of the epidermis) is close to a source of carbon dioxide (×50). (Courtesy of Urs Eggli.)

The epidermis of at least some parts of plants may produce **hairs (trichomes)** (**FIGURE 3.20**). Plant hairs may be as simple as just a single epidermis cell growing outward as a long cylinder (a unicellular trichome), or the cell may subdivide such that it is several cells long or wide (multicellular trichomes). They may be unbranched or branched, and most are parenchyma, but some hairs build a secondary wall and become sclerenchyma. In many cases, plant hairs die immediately after reaching their full size.

FIGURE 3.19. Each stomatal pore is surrounded by two guard cells and then by other epidermis cells. This specimen was prepared while the guard cells were swollen and pushed apart, opening the pore (×800). (Courtesy of Urs Eggli.)

FIGURE 3.20. The hairs on this leaf of lambs ear (*Stachys byzantina*) affect its biology in many ways: they make it difficult for insects to walk on the leaf, they keep dirt and dust away from the stomata, they reflect excess sunlight away from chloroplasts, and, when dew forms, the droplets form on the tip of the hairs where they will not block stomatal pores.

Hairs affect plant biology in many ways. Bright habitats like deserts, seashores, and high alpine areas may have too much sunlight, and a layer of dead hairs prevents the leaves from being sunburned and having their chlorophyll damaged. A thick layer of hairs, especially if they are curly or sharp, make it difficult for animals to walk around on a plant's surface, so they are less likely to eat the plant or lay eggs in it. Also, a layer of hairs creates a zone of calm air near the leaf's surface, which reduces the rate at which wind draws water out of the leaf through open stomatal pores.

Glandular hairs secrete substances, almost always defensive compounds. Those of stinging nettle secrete the irritating compounds formic acid and histamine, those of mala mujer have toxins that will blister the skin. Glandular hairs on *Pavonia odorata* secrete such sticky compounds that they entangle insects on the plants where they starve to death without getting a chance to harm the plant. These plants have been planted in gardens and plantations as a natural way to control insect pests.

Phloem is a complex tissue that conducts sugars throughout the plant (**TABLE 3.4**). In many plants, it also has cells that store sugars and other compounds, and has fibers that strengthen the vascular bundles in stems and leaves. The conducting cells of phloem in flowering plants are called **sieve tube members**, and they are basically parenchyma cells that have grown to be long, slender tubes (**FIGURES 3.21** and **3.22**). When young, they have plasmodesmata in primary pit fields, but as the cells mature, their plasmodesmata become wider (about 2.0 µm in diameter) and we call them **sieve pores**. The primary pit fields are also given a new name, **sieve areas**. Sieve tube members are aligned end to end with their sieve pores interconnected.

TABLE 3.4. Vascular Tissues

Phloem: conducts water, minerals, sugars, and other organic material; conducting cells are living parenchyma cells but they destroy their nuclei before they begin to conduct.

Sieve cells have small sieve areas and narrow sieve pores only; they do not have sieve plates with a large sieve area and especially wide sieve pores.

Sieve tube members have small sieve areas and narrow sieve pores on their side walls, but their end walls are sieve plates with a large sieve area and especially wide sieve pores.

Xylem: conducts water, minerals (and rarely sugars); conducting cells are sclerenchyma cells and must digest their protoplasm and die before water can be pulled through them.

Tracheids have no perforations; all water must enter or leave through pits and must cross pit membranes. Tracheids provide a very safe method of conduction, but cause high friction.

Vessel members have perforations; water moves from member to member within a vessel by passing through perforations. Water passes from one vessel to another through pits and pit membranes. Vessels provide low-friction conduction, but when an air bubble forms, it incapacitates many vessel members.

A long series of sieve tube members is a **sieve tube**. The nuclei break down during development, so sieve tube members lack a nucleus, and instead their metabolism is controlled by the nucleus of an adjacent cell, a **companion cell**. The vacuole membrane also breaks down, causing most of the cytoplasm to become a watery solution called **phloem sap**.

Technically, the terms "sieve tube member" and "companion cell" should be used only for angiosperms. For all other vascular plants, the terms "sieve cell" and "albuminous cell" should be used.

Xylem is a complex tissue that conducts water and dissolved mineral nutrients, usually upward from roots, through stems and into leaves and flowers (Figure 3.21). Like phloem, it has conducting cells as well as storage cells and fiber cells. There are two types of xylem conducting cell: tracheids and vessel members.

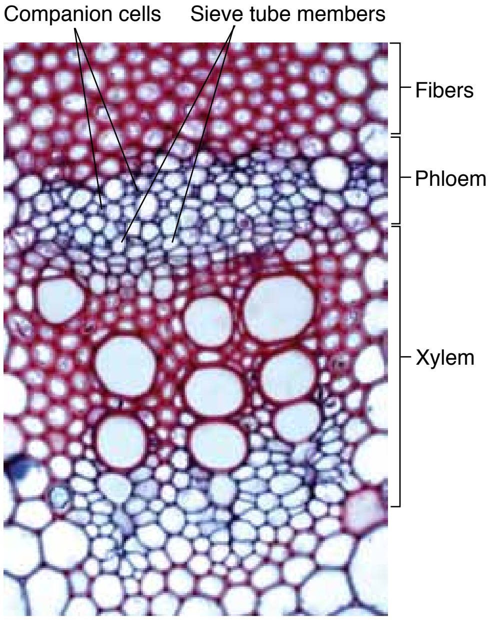


FIGURE 3.21. Vascular bundles have both xylem and phloem running side by side, parallel to each other. The xylem in this vascular bundle contains both narrow fibers and wide vessel elements; the phloem consists of sieve tube members and companion cells. A large mass of fibers protects the outer side of the bundle. This is from a stem of sunflower (×220).

Tracheids begin life as small parenchyma cells and they grow to be long, narrow cells with tapered ends; they resemble very long fibers (**FIGURE 3.23**). At maturity, they deposit a lignified secondary wall that has many broad pits; water flows from one tracheid to the next through the interconnected pits. Once the wall is complete, the tracheids die and digest all their protoplasm: when functional, a tracheid consists only of a cell wall. It is important that tracheids occur in groups, with many tracheids side by side and with their tapered ends interdigitating, so any mature tracheid is surrounded by many others; they do not function by themselves.

The pits that interconnect tracheids are like the pits of fibers and sclereids, but much wider and more numerous. An important point about pits is that each is a tunnel just through a secondary wall of a cell, not through the primary wall. Thus, a set of two aligned pits is not a completely open passage between two tracheids: there are two primary walls (called the **pit membrane**). Even though pit membranes are permeable, water moves more slowly when it has to cross the pit membrane as opposed to when it is merely being pulled through the pit or through the tracheid lumen. Thus, as water is pulled upward it passes from one

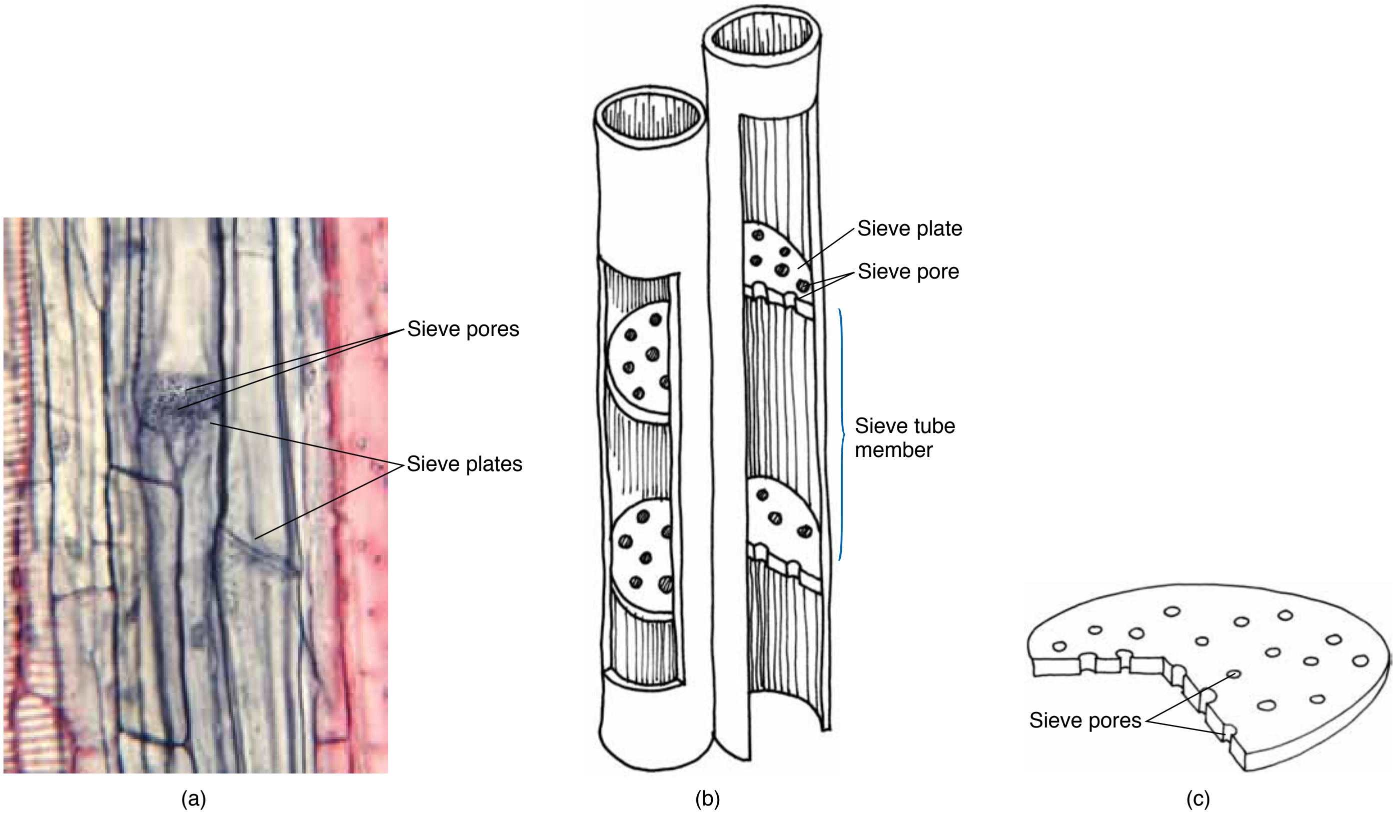


FIGURE 3.22. **(a)** Sieve tube members are long, slender, and delicate, and consequently are difficult to photograph and difficult for students to see in lab. Two sieve tubes are visible here, both with tilted sieve plates. **(b)** One sieve plate is in side view, the other is in face view such that **(c)** its sieve pores (white dots) are visible (×300).

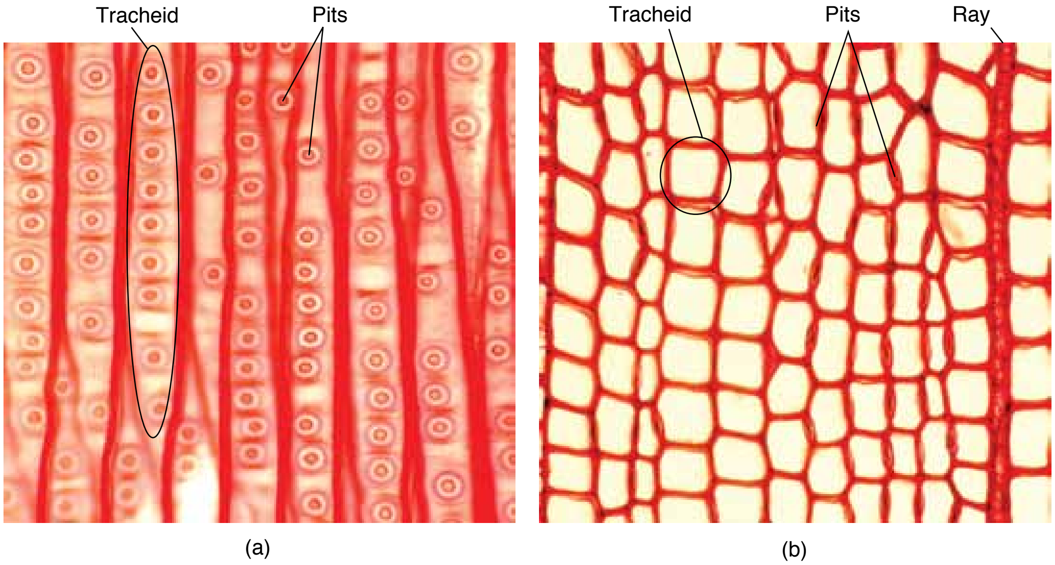


FIGURE 3.23. Tracheids are long, slender conducting cells that occur in masses, each interconnected to its neighbors by many broad pits. As water passes from one tracheid to another, it must pass through the narrow pits as well as the pit membranes. In **(a)**, the tracheids were cut lengthwise so that we could see their side walls; the pits are visible in face view; in **(b)**, the tracheids were cut in transverse section and we see the pits in side view (×300).

tracheid to another going through the pits of both. Tracheids are exceptionally long cells, but none is as long as an entire plant. If a plant is 1.0 m tall (about 3 feet) and its tracheids are each about 1 cm long (about 2.5 inches), each water molecule would need to be pulled through at least 100 tracheids and pit membranes. Because tracheids are narrow and each pit is even narrower, transporting water through tracheids involves a lot of friction (imagine drinking a milkshake through a narrow straw rather than a wide one).

Vessel members provide an alternative, low-friction method of conducting water in xylem. As a young parenchyma cell grows to be a vessel member, it becomes a very wide, short cylinder (**FIGURE 3.24**). Like a tracheid, it deposits a lignified secondary wall that has numerous wide pits aligned with the pits of vessel members lying alongside it. Just before dying and degrading away all its protoplasm, it completely digests its two end walls: it produces two large holes, called **perforations**,

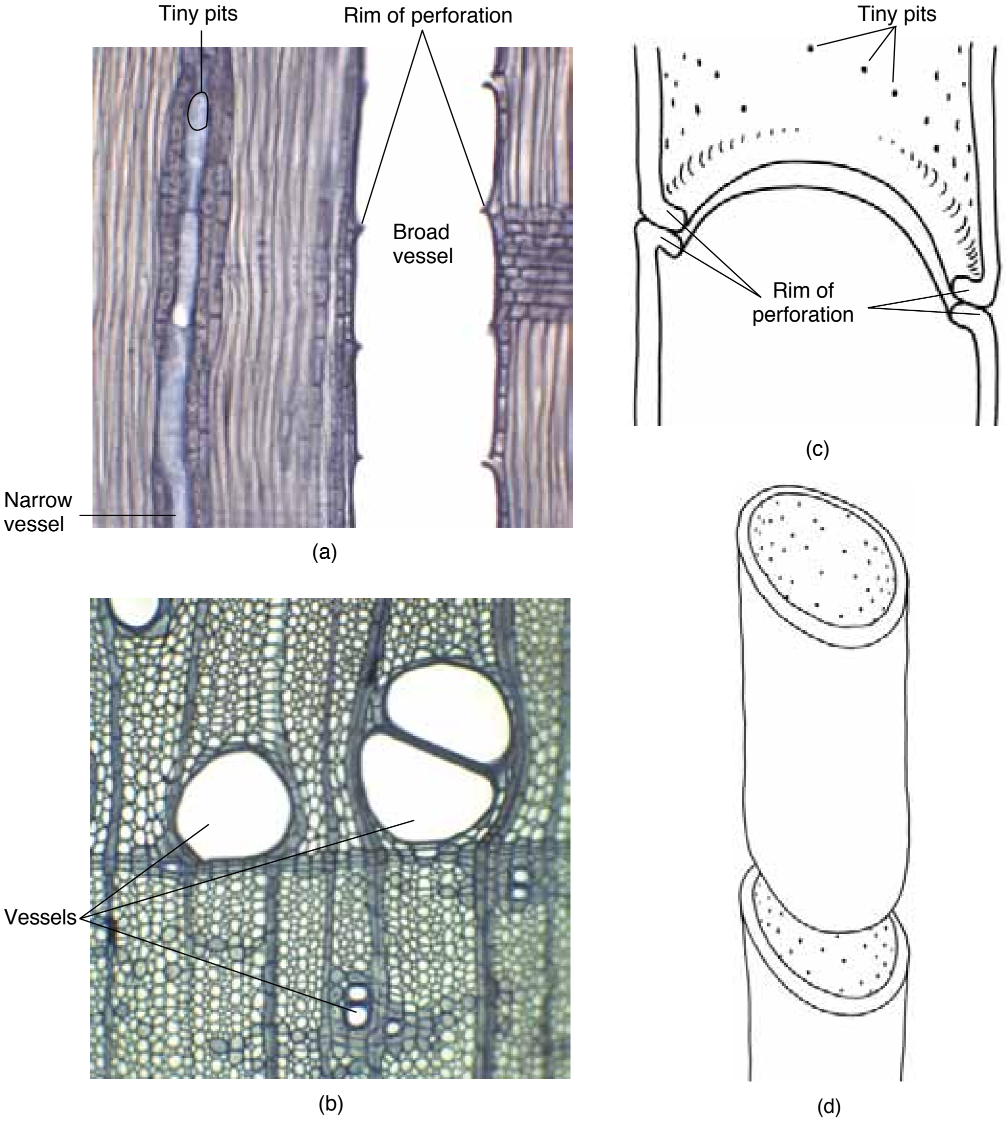


FIGURE 3.24. Vessel members are usually broader and shorter than tracheids, and each has a large hole (a perforation) on each end where it connects to the adjacent members of the same vessel. Pits along the sides of vessel members allow water to transfer from one vessel to another. **(c)** and **(d)** show how two vessel elements fit together.

one on each end of the vessel member. Once mature, it looks basically like the cement pipes used to build sewer lines, and indeed vessel members fit together the same way: the perforation on each of its ends is aligned with those on the vessel members above and below it. Hundreds or thousands of vessel members become interconnected this way, forming a long tube called a **vessel**. As water is pulled through vessels, it moves from one member to another through perforations—wide, open holes—rather than through narrow pits with pit membranes. Water moves much more easily and with less friction through a set of vessels as compared to a set of tracheids. Although vessels are often very long (often more than a meter [3 feet]), each does have a top and bottom end where the terminal vessel member has only one perforation, not two. Water must enter and leave a vessel through the pits on the sides of the vessel members.

The Internal Organization of the Primary Plant Body

Individual organs such as roots, stems, leaves, and flower parts are each composed of distinctive arrangements of tissues. Stems vary from bulbs to rhizomes to tendrils and others (see Box 2.1), but as mentioned before, they all have the same stereotyped parts: internodes, nodes, axillary buds, and so on. The same is usually true of the internal organization of plant organs: despite an outward appearance of diversity, internally, most stems are remarkably similar in the organization and patterns of their tissues, and the same is true of roots, leaves and flower parts.

Stems

If we cut across the internode of a young stem and examine it in transverse section, the pattern of tissues will be the same for almost all species. The outermost layer will be epidermis, followed by cortex, a set of vascular bundles, and then pith in the very center (**FIGURE 3.25**). The epidermis of a stem varies from one species to another, but it always is similar to the epidermis described above. The cuticle and waxes may be especially thick in plants of desert regions and rainforests; in deserts, the extra cuticle helps to keep water in the plant, but in rainforests it helps to keep all that rain from leaching chemicals and nutrients out of the plant. Stomata may be abundant in the stem epidermis of some species but completely absent from that of others.

Interior to the epidermis is the **cortex**, by definition the entire region between epidermis and the vascular bundles. In many species, the cortex is only about a millimeter or two thick (less than one-quarter inch) but in cacti and other succulents, the cortex may be several centimeters thick (from one to several inches) and consist of many layers of giant parenchyma cells that store water in their exceptionally large central vacuoles. The outermost layers of cortex are often a band of collenchyma cells that provide plastic strength to the internode; in other plants, this region remains parenchymatic while the internode grows, but once it reaches its full length, the cells differentiate into a band of fibers that provide elastic strength. Any band of specialized cells just below the epidermis is called a **hypodermis**. Cortex is usually green because at least some cells have chloroplasts. It is not unusual to find various types of defensive cells in the cortex: cells filled with poisons, irritating compounds or crystals, all of which make the stem less palatable to animals. In milkweeds and spurges, the milky sap that exudes when the plant is cut is produced in cortex cells (**FIGURE 3.26**).

In the center of the stem of most plants is the **pith**, which is similar to cortex. It is very narrow and almost always consists of just parenchyma cells, some with crystals

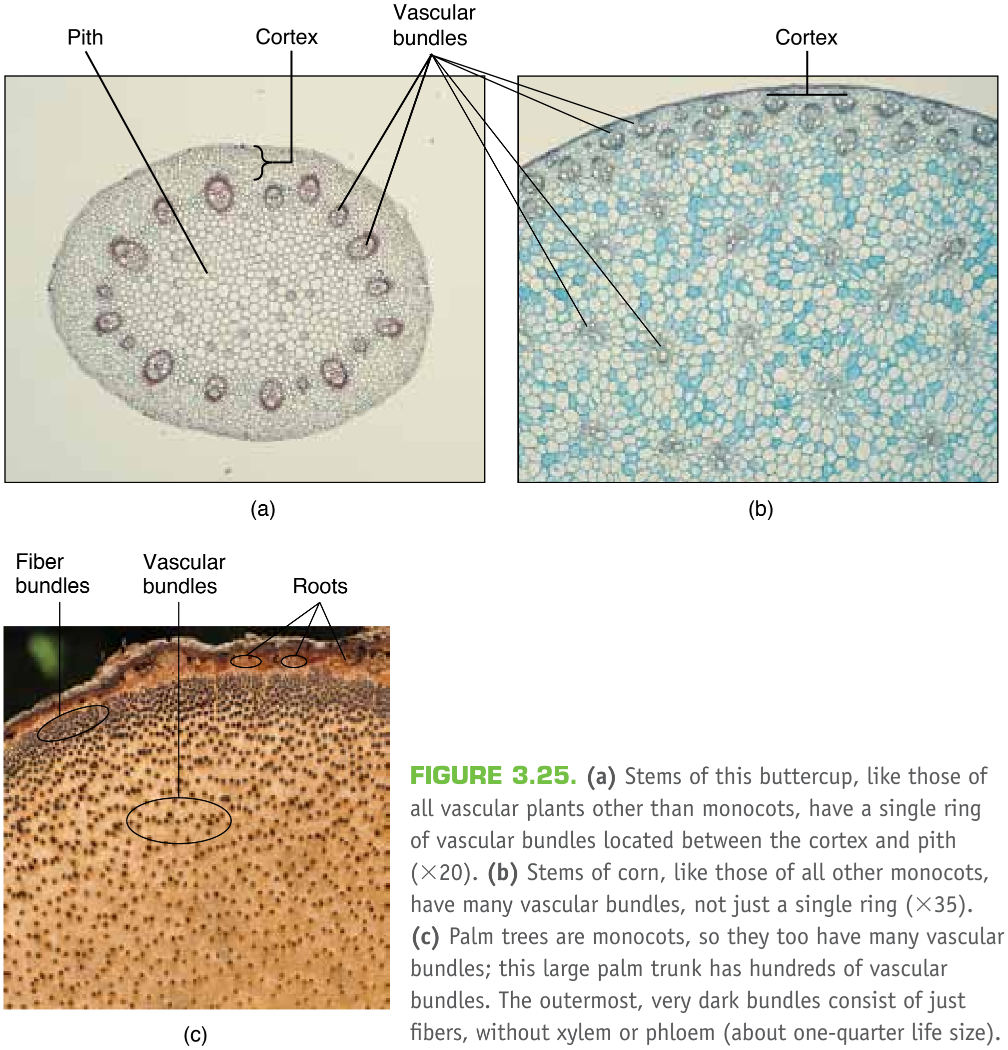


FIGURE 3.25. **(a)** Stems of this buttercup, like those of all vascular plants other than monocots, have a single ring of vascular bundles located between the cortex and pith (×20). **(b)** Stems of corn, like those of all other monocots, have many vascular bundles, not just a single ring (×35). **(c)** Palm trees are monocots, so they too have many vascular bundles; this large palm trunk has hundreds of vascular bundles. The outermost, very dark bundles consist of just fibers, without xylem or phloem (about one-quarter life size).

or defensive compounds. Starch grains may be present, but the pith is so slender it contains too few cells to provide much storage volume.

Between the cortex and pith is a ring of closely spaced **vascular bundles**, each having phloem on the outer side and xylem on the inner side (Figure 3.25a). When viewed in an internode cut in transverse section, as few as 20 or 30 vascular bundles might be visible in narrow stems, but there can be hundreds in wider stems. The phloem and xylem in these bundles is like that described above. Phloem contains sieve tubes and companion cells as well as other parenchyma cells that store material. Fibers may be mixed in as well, but it is most common for the outer margin of each bundle to have a cap of fibers or collenchyma cells running upward parallel to the bundle. This cap not only strengthens the bundles and the stem, it protects the phloem from animals like aphids that suck sap from sieve tubes (**FIGURE 3.27**).

The xylem of each bundle usually has 10 or more (maybe many more) vessels accompanied by parenchyma cells and fibers (**FIGURE 3.28**). Even a very small plant with narrow stems might have 20 vascular bundles each with about 20 vessels; thus there would be at least 400 vessels visible anywhere the stem is cut in transverse section. Each vascular bundle usually runs straight up the stem from one node to the next, but at the nodes, most bundles will merge with one or more of their neighbors, then continue up into the next internode. The separate bundles visible in internodes are really

FIGURE 3.26. A leaf was pulled off this milkweed (*Asclepias tuberosa*, also known as butterfly bush) causing milky sap to flow out of secretory cells in its cortex. Milky sap is often poisonous and can cause serious harm if it contacts your eyes.

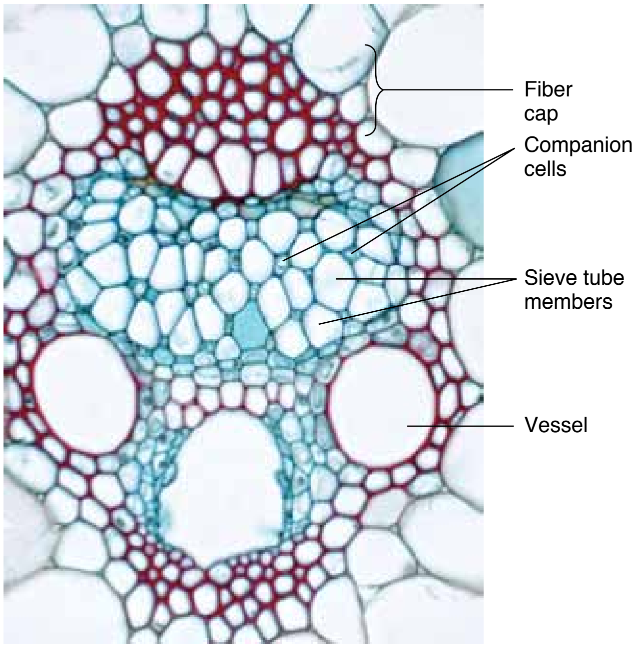


FIGURE 3.27. This vascular bundle of corn is protected by a cap of fibers between the phloem and the cortex. Companion cells and sieve tube members are especially easy to identify in this specimen (×200).

parts of an interconnected network of bundles whose vessels can exchange water with each other, just as their sieve tubes can exchange sugars.

Having a single ring of vascular bundles is by far the most common pattern; it occurs in ferns, conifers, and broadleaf plants (dicots). In monocots, there are numerous vascular bundles distributed throughout the center of the stem, not just in one ring (Figure 3.25b, c). Also, in most monocots, rather than just having a cap of fibers protecting the phloem, each vascular bundle may be completely encased in a **bundle sheath** composed of many fibers.

At nodes, where leaves and axillary buds are attached to stems, are sets of vascular bundles called **leaf traces** and **bud traces**. They are attached to the stem bundles at one end, cross the cortex and enter the leaf and axillary bud at the other: typically, several leaf trace vessels run side by side with several stem vascular bundle vessels, picking up water through the pits that interconnect the two. Then the leaf trace vessels carry the water out to the leaves. Similarly sieve tubes carry phloem sap from leaves into the stem then they transfer the sugars to the stem vascular bundle sieve tubes.

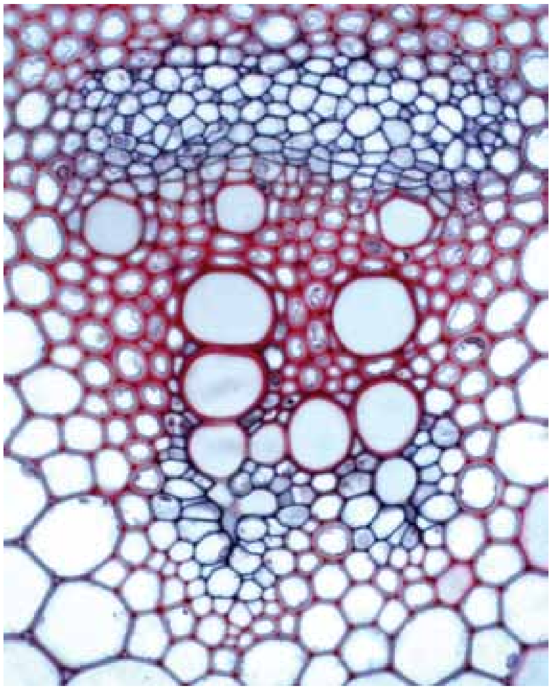


FIGURE 3.28. This is a very young vascular bundle, near the shoot tip of a sunflower. It has not yet formed all its xylem, but already almost a dozen vessels are present. The stem had many more vascular bundles: even at the shoot tip where leaves are young and small, about 100 vessels are mature and conducting water (×200).

Leaves

The internal structure of the blade of a foliage leaf facilitates photosynthesis. It has adaptations that maximize the absorption of light and carbon dioxide and a dense array of vascular bundles (often called leaf veins) that distribute water to all parts of the leaf while exporting sugars. The epidermis on the lower side of a foliage leaf (the lower epidermis) has numerous stomata, permitting rapid absorption of carbon dioxide. Hairs are often present, keeping the air calm around the stomata and thus increasing the likelihood that water that escapes out of the stomata may remain long enough that it will, by chance, reenter the leaf. The upper epidermis usually has many fewer stomata or none at all. Sunlight warms leaves, so air rises off them just as it rises from any warm surface. If the upper epidermis has stomata, any water that diffuses out is immediately swept away and has no chance to form a humid layer that would protect the leaf. Also, when dew forms, it covers the upper leaf surface, and even a fine film of water would block a stomatal pore, preventing the absorption of carbon dioxide.

The interior of a leaf is called **mesophyll**. Leaves sometimes have a hypodermis below the upper epidermis, but this would block light and is not very common. Instead, it is most typical to have one or two layers of columnar cells that project downward, like the bristles of a brush from the upper epidermis (**FIGURE 3.29**). This is **palisade mesophyll** and it is always photosynthetic parenchyma, with each cell having numerous chloroplasts. Palisade mesophyll cells lie close together but only rarely touch each other; instead of being glued tightly together by middle lamellas, almost every part of the cell wall faces intercellular space, from which it can absorb carbon dioxide. The lower portion of foliage leaves is occupied by **spongy mesophyll**, a tissue in which cells are widely separated, touching only one or two neighbors; intercellular spaces make up more than half the volume. The arrangement of foliage leaf mesophyll thus allows carbon dioxide to enter through numerous stomata in the lower epidermis, diffuse rapidly throughout the spongy mesophyll, quickly reaching all parts of the leaf, then diffusing up and around all sides of the palisade

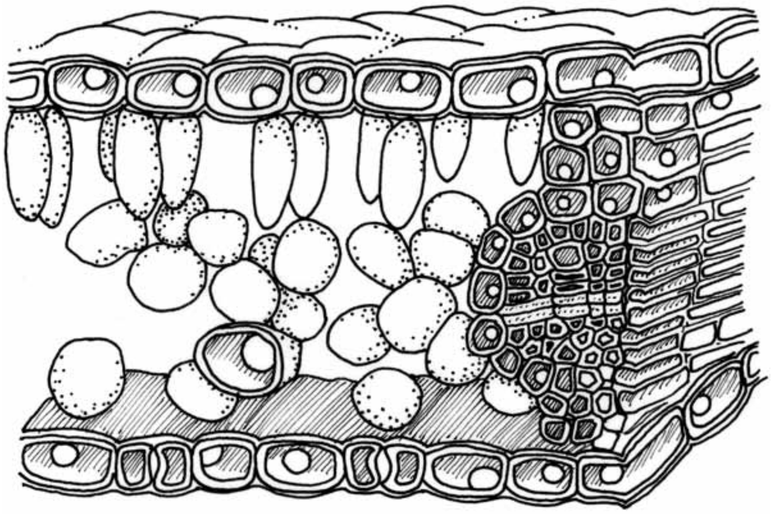


FIGURE 3.29. The interior of a leaf has many air spaces that allow carbon dioxide to diffuse from the stomata in the lower epidermis up to the photosynthetic cells of the palisade parenchyma. Xylem in the vascular bundle carries water to leaf cells; phloem brings sugar out of the leaf to the stem.

mesophyll cells. At the same time, light is passing through the upper epidermis and being captured by palisade cell chloroplasts where it powers the conversion of carbon dioxide into sugar.

Vascular bundles run in a single layer between the palisade and spongy mesophyll. Each has phloem on its lower side, xylem on the upper side (**FIGURE 3.30** and see Figures 2.5 and 2.6). In transverse section, the midrib and larger vascular bundles have relatively large amounts of xylem and phloem, and typically also have caps of collenchyma or fibers. The smallest, finest bundles may have only one or two vessels and sieve tubes, and no caps.

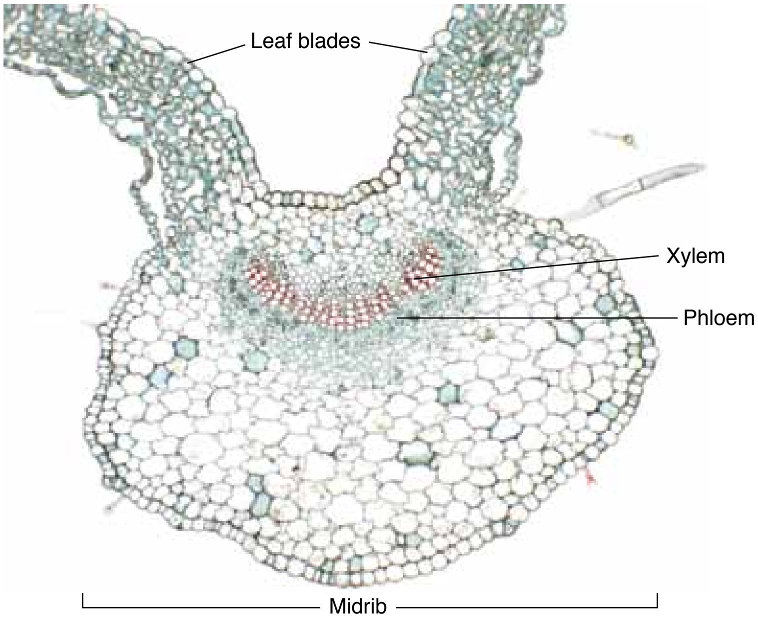


FIGURE 3.30. The midrib of this foxglove leaf contains a large amount of phloem and xylem. Whereas the leaf blade is thin, the midrib is thick and provides strength that holds the leaf into the sunlight (×50).

Roots

Roots evolved from stems and still resemble them in many ways, but several internal features are adaptations that increase a root's ability to absorb water and minerals (Figures 2.13 and 2.14). Because roots are subterranean and do not photosynthesize, stomata are not necessary in their epidermis. Instead, root epidermis produces thousands of special unicellular hairs, **root hairs**, that greatly increase the root's absorptive surface area and that are narrow enough to enter very tiny soil spaces where water and minerals are most likely to be found. Root cortex is typically narrow, just a few layers of rounded parenchyma cells. Intercellular spaces are prominent at their corners; roots need to allow oxygen to diffuse through them so that they don't suffocate. Some root cortex cells may contain crystals or defensive compounds, but typically a root's cortex lives only briefly. In many plants, it dies not long after the root hairs have stopped absorbing material.

The **endodermis** is a cylinder of parenchyma cells that lie between the cortex and vascular tissues in roots (**FIGURE 3.31**). It is a critically important barrier between the outside world and the plant. Because cell walls are permeable, any minerals dissolved in the soil water can diffuse through the root epidermis and cortex, just by moving through walls and intercellular spaces, without ever actually entering a cell's protoplasm. This is true both for beneficial minerals as well as harmful ones like lead and other toxic metals. But the radial walls (the sides, top, and bottom walls) of endodermis cells have a **Casparian strip**, a band where the walls are incrusted with waterproof chemicals. Nothing can diffuse past the Casparian strip; at this point, water and anything else must be accepted by a plasma membrane, enter an endodermis cell and then be released on the inner side of the endodermis. The plasma membrane allows beneficial elements in but blocks harmful ones.

Root vascular tissues do not occur in bundles. Instead xylem occurs in the center as a star-shaped column, the star having three or four arms in most roots (**FIGURE 3.32**). Alternating with the xylem arms are columns of phloem. Between the xylem, phloem, and endodermis are parenchyma cells called **pericycle**. Some pericycle cells divide and form the primordia of lateral roots, most simply store a little starch. Monocot roots are typically much wider than those of dicots and all other plants. The central column of xylem in monocot roots is exceptionally wide and may have dozens of arms alternating with an equal number of phloem columns. Roots never have pith.

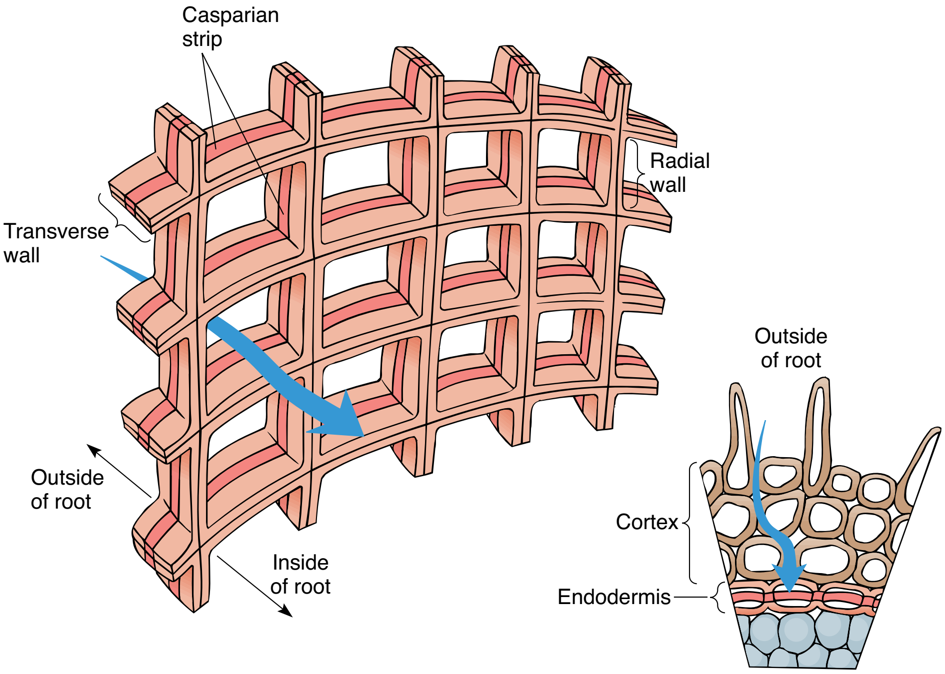


FIGURE 3.31. The endodermis is a cylinder, one cell thick, with Casparian strips on the radial walls of all cells. Chemicals dissolved in soil water cannot get past the endodermis by simply moving through the walls. Any chemical that is not accepted by a cell plasma membrane cannot get into the xylem.

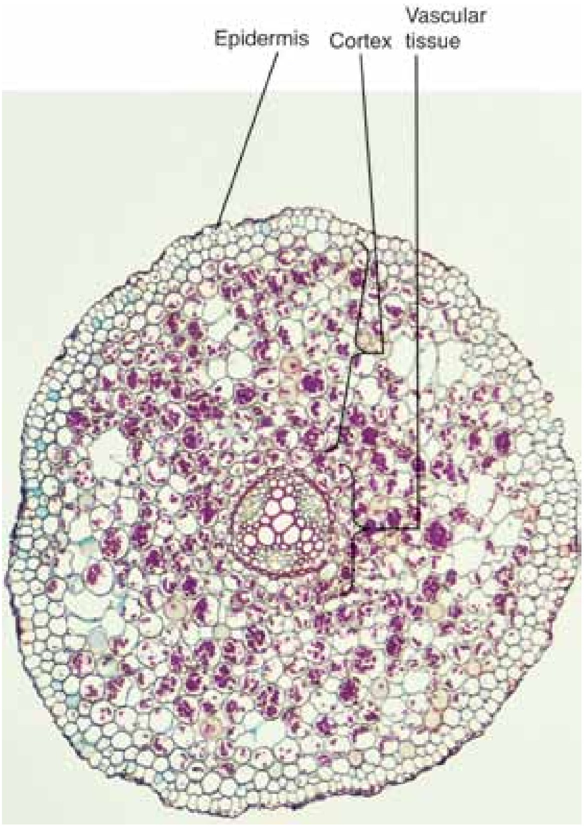


FIGURE 3.32. Transverse section of a root of buttercup. The cortex is broad, and the xylem in the center is shaped like a star rather than being part of vascular bundles as in stems. Columns of phloem are located between the arms of the xylem star (×50).

The Internal Organization of the Secondary Plant Body

In stems and roots of an herb, all cells of epidermis, cortex, xylem, phloem, and pith stop dividing, then they differentiate and mature within a few hours or days after having been produced by an apical meristem. But in woody plants, some cells located between the xylem and phloem do not stop dividing, instead they continue to act as meristematic cells and they constitute the vascular cambium. Vascular cambia produce cells to both the interior and exterior of the cambial cylinder. Cells on the inner side develop into **wood** (**secondary xylem**); those on the outer side become **secondary phloem** (see Figure 2.24). These are complex tissues, each containing several types of cells, but wood, being a type of xylem, will have tracheids or vessels or both, and secondary phloem will have sieve tubes in angiosperms, sieve cells in other types of plants. Both secondary xylem and phloem in angiosperms usually have fibers, which give wood and bark their strength. Because fibers are present, angiosperm wood is called **hardwood** (**FIGURE 3.33**). In contrast, wood of conifers, even giant Douglas firs and coastal redwoods, have no fibers and so are called **softwoods** (**FIGURE 3.34**). In some cases, the tracheids of conifers have such thick, heavily lignified walls they constitute a stronger wood than the fibrous wood of some angiosperms. Wood of the conifer bald cypress (a softwood) is much harder and more rot-resistant than is wood of the angiosperm balsa (a hardwood).

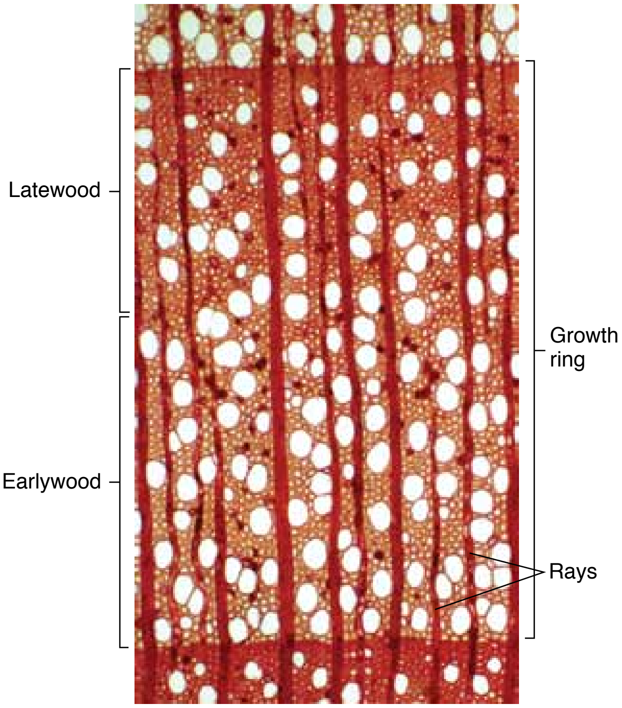


FIGURE 3.33. This is a transverse section of wood from an apple tree (*Pyrus malus*). Vessels are abundant but not very wide, and most of the cells between the vessels are fibers: because this has fibers, it is a hardwood. Rays are abundant, and one entire growth ring is visible, along with the latewood of the previous year and the earlywood of the following year. The vascular cambium and bark would be located above the top of the image (×50).

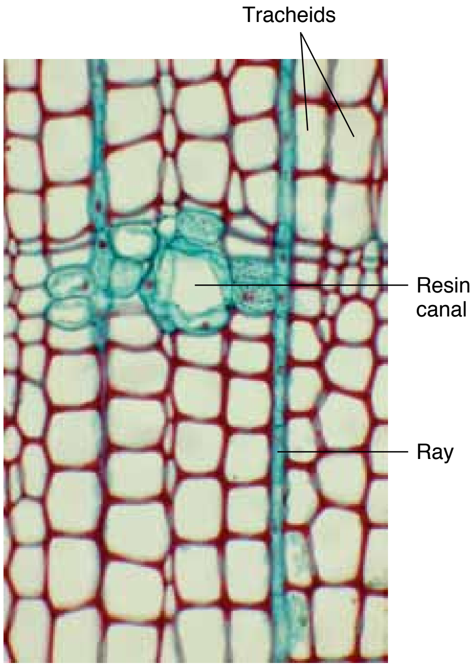


FIGURE 3.34. This is a transverse section of wood from a pine tree (*Pinus*). No fibers are present, so this is a softwood. All the cells with red-stained walls are tracheids. A resin canal is present, and several rays are visible (×200).

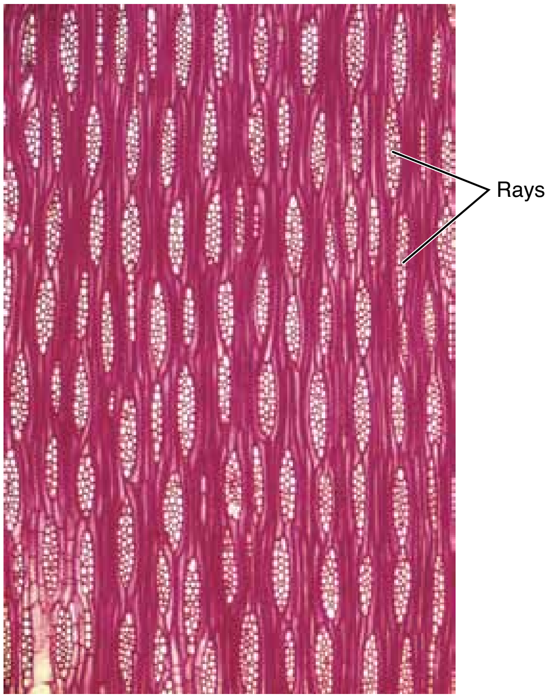


FIGURE 3.35. This is a tangential section of wood, cut near the surface of the tree trunk, parallel to the surface. The rays are masses of living parenchyma cells that store water, minerals, and starches in the wood. While they are alive, ray cells help resist fungi and insects that invade the wood (×40).

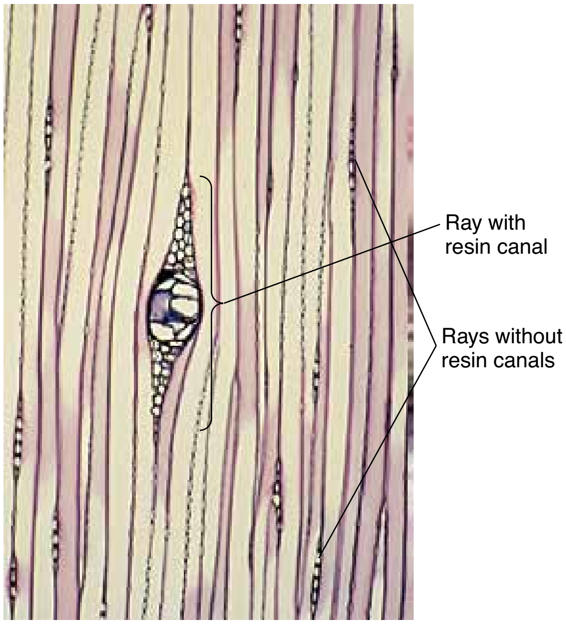


FIGURE 3.36. Tangential section of pinewood, showing that most rays are tall and narrow, but one has a resin canal in it. All the elongate, vertical cells are tracheids (×40).

Wood and secondary phloem have many parenchyma cells that store water and starch during winter when trees are leafless. Wood parenchyma cells also defend the rest of the wood from boring insects and wood-rotting fungi. All these are elongate cells produced by long, slender vascular cambium cells called fusiform initials. Both wood and secondary phloem have **rays** (**FIGURES 3.35** and **3.36**), groups of short parenchyma cells that store starch and water and that also help protect wood from invasive organisms. Ray cells are produced by short ray initials in the vascular cambium.

Vascular cambia are another example of localized, indeterminate growth. A vascular cambium can remain active for hundreds, even thousands of years, causing the trunk, branches, and roots to become wider each year. The most spectacular examples of this are the giant redwood trees of California, some of which have trunks 17 meters (57 feet) thick. Some trees become wide very quickly because their vascular cambia produce large numbers of wood cells each year, whereas in others, the vascular cambia are less active and even very old tree trunks are slender.

In springtime, vascular cambia usually produce wood with a high percentage of wide vessels. This provides high-volume conduction while soil is moist and leaves are young; also many trees flower in spring, and flowers need water. In summer, cambia usually produce wood that has a greater abundance of fibers and only a few, narrow vessels; this wood provides extra strength. The two types of wood are called **earlywood** (or springwood) and **latewood** (or summerwood). All the wood produced in a single year is called a **growth ring** (or an annual ring). The outermost growth ring (nearest to the vascular cambium and bark) is the newest one, and each one deeper in is 1 year older (**FIGURE 3.37**).

While wood is young, it contains living cells. All the tracheids and vessel elements are alive while growing and differentiating. It is only when they are mature that they must be dead and devoid of protoplasm so that they can conduct. In addition, most wood fiber cells die once their secondary wall is formed and lignified. But cells of the wood rays are living parenchyma cells, and often there are living cells next to vessels or mixed in with fibers. Also, when first formed by the cambium, all tracheids and vessels are filled with water and are conducting, but during dry seasons, some cells accidentally fill with air bubbles and stop conducting. Over the course of several years, more and more cells fill with air until finally all the tracheids or vessels of a growth ring are useless for conduction. But during this time, the vascular cambium will have made more wood with functional conducting cells. In many species, after vessels fill with air, the parenchyma cells next to them fill them with plugs called **tyloses** (singular: tylosis), which prevent fungi from growing in them. Once a growth ring stops conducting, its parenchyma cells synthesize numerous compounds that are antimicrobial and rot-resistant, then the cells die. At this point, all cells in the wood are dead, but it is still strong and helps hold up the trunk, branches, and roots. The outermost wood, that which has living cells and some conduction, is **sapwood**, whereas the inner wood that is not conductive and not alive is **heartwood** (see Figure 2.24c).

Although secondary phloem is also produced annually and cyclically, it typically does not have recognizable growth rings. Also, because it is produced to the outside of the wood and vascular cambium, it is pushed outward every time a new ring of wood is added. This causes the secondary phloem to be stretched and to crack, and bits and pieces of it fall off the tree. Whereas wood remains permanently on the tree (unless a branch falls off), secondary phloem remains attached only temporarily.

When a young woody stem or root sheds its first bark, the epidermis is shed with it, and the plant needs a new protective layer. Within the secondary phloem, band-like regions of parenchyma cells begin to divide and produce new parenchyma cells to their outer side. The dividing cells are the cork cambium. The cells they produce differentiate into **cork cells** by enlarging, putting a chemical called suberin into their walls, then dying. Suberin not only makes cork cells waterproof, they become resistant to fungi, bacteria, and other microbes. Cork is also indigestible, and because it is dead, it has no nutritional value, so animals do not seek it as food. The mixture of secondary phloem and cork is **bark**. Bark may be hard if the secondary phloem is very fibrous and the layers of cork are thin, or bark can be soft and spongy if cork is abundant

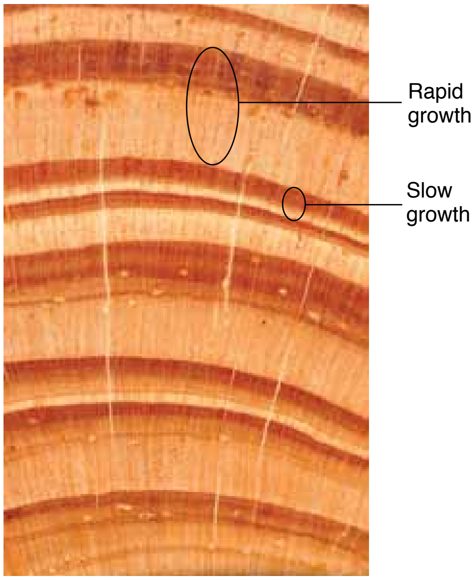


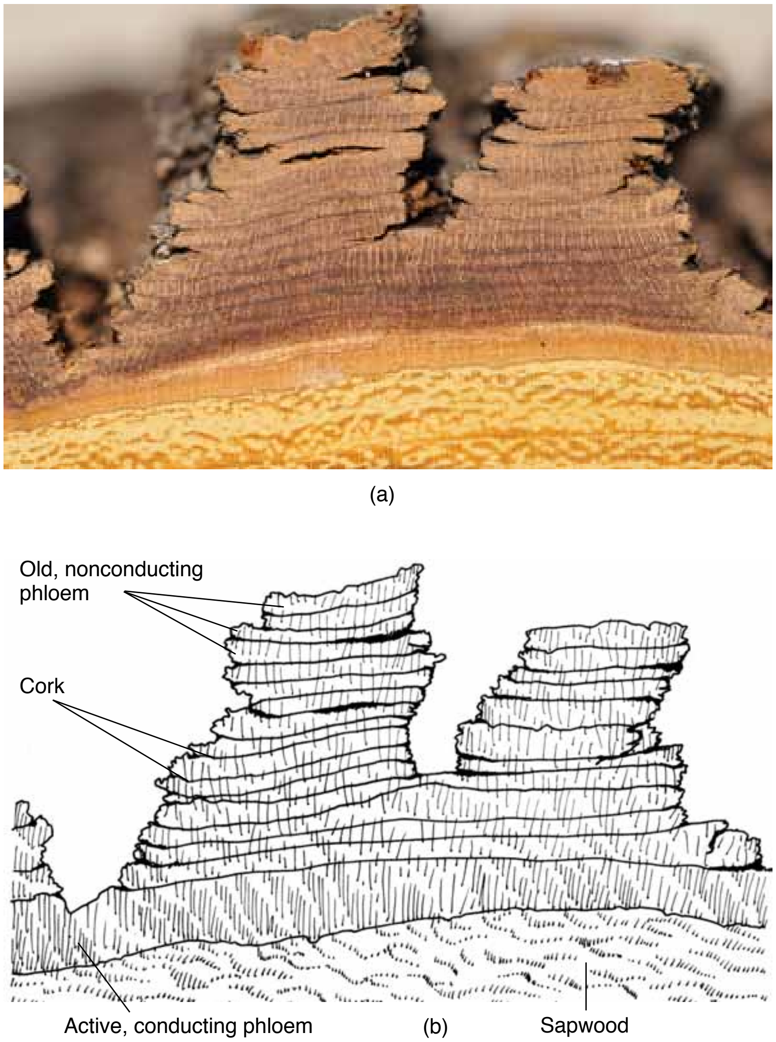
FIGURE 3.37. Growth rings are easy to see in this transverse section of a limb from a pine tree. Each growth ring consists of a light-colored band of earlywood and a darker band of latewood. Thick rings were formed when the tree (or at least the limb) was growing vigorously, thin rings indicate years when the limb's vascular cambium made only a few cells. White streaks are rays; dots are resin canals (about twice life size).

BOX 3.2. Dendrochronology: Analyzing Past Events with Tree Rings

The growth rings in wood carry information about a plant's past environment. Each year, a vascular cambium produces a new growth ring, and if the tree is healthy and vigorous, if it has enough rain, sunlight, and warmth, the cambium will produce many xylem cells and make a thick ring. On the other hand, if the summer is cool, dry, or cloudy, the plant will not photosynthesize well and there will be few resources for the cambium, and it might make only a thin ring. By examining a tree trunk cut in transverse section, we can usually see, even without a microscope, that some rings are thick, others are thin. By cutting or sanding the surface carefully, and then using a microscope, we can actually count the number of cells produced each year. If the wood was taken from a living tree, we know that the outermost ring is this year's growth, the next one deeper in is last year's and so on. Many trees live to be 500 or more years old, and we can identify which ring corresponds to each year for several centuries into the past.

Identifying good years (with wide rings) and bad years (narrow ones) is only the beginning. A single narrow ring surrounded by ones of ordinary size would indicate that just a single poor year occurred. However, if several narrow rings occur together, that would indicate many years of poor conditions for the tree. Perhaps there was an exceptional drought that lasted for many years, or a prolonged cool period. Long periods of bad weather in the tree's past might indicate that conditions were so poor that people in the region would have had poor crops and may have faced starvation. In contrast, a large number of wide rings together might indicate that weather was good for the region and any people there would have been prosperous. In areas where people have kept no written history, such as the American Southwest during the time of cliff dwellings, the dendrochronology record is invaluable.

Tree rings record more than just weather. If the tree survived a forest fire, one of its rings should show a scar and charcoal. Similarly, signs of unseasonal freezes, volcanic eruptions, and floods can be detected in tree rings, and from the age of the ring, we know when those events occurred.


(a)

(b)

FIGURE 3.38. It is rare for bark to stay on a sample of wood; usually the weak cells in the region of the vascular cambium break and the bark separates from the wood. **(a)** The bark of this sample of honey mesquite (*Prosopis gladulosa*) contains many small patches of cork, each produced by a cork cambium that produced only a few cells then stopped functioning. **(b)** Because the bark does not stretch, it forms fissures as the tree forms more wood and pushes the bark outward.

and the secondary phloem has few or no fibers. Because bark is constantly being pushed outward and shed, new cork cambia must be produced periodically, each one deeper in the secondary phloem than the previous one (**FIGURE 3.38**).

Bark has **lenticels**, small regions of loose cork cells with intercellular spaces that allow oxygen to diffuse into the plant (**FIGURE 3.39**). Ordinary regions of cork are impermeable to gases because their cells fit together tightly, but in lenticels, cork cells are rounded just enough to create intercellular spaces at their corners, permitting oxygen to diffuse into the inner regions of phloem, cambium, and sapwood, all of which have living cells that need oxygen for respiration. This does increase the risk of invasion by bacteria, but passageways for oxygen are essential.

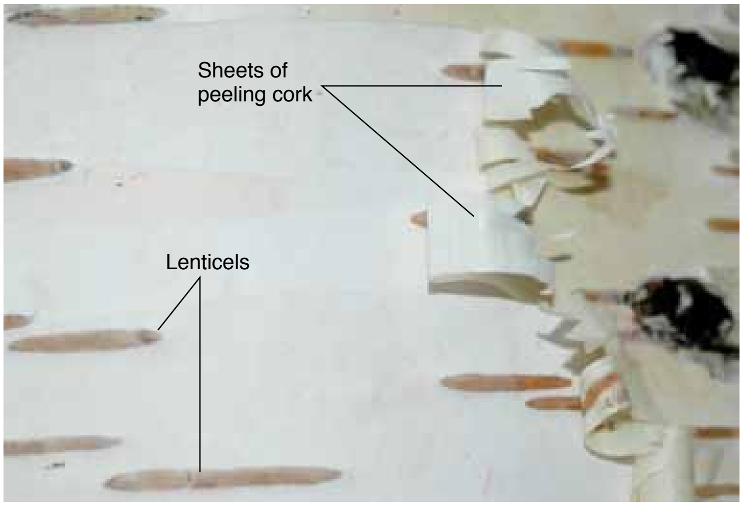


FIGURE 3.39. Unlike the bark of mesquite in Figure 3.38, birch bark (*Betula*) is very smooth and peels off in thin sheets. Its smoothness makes its wide, short lenticels visible. Oxygen diffuses through intercellular spaces in the lenticels and permits the living cells inside the phloem, cambium, and sapwood to respire.

Important Terms

amyloplast
bark
bud trace
bundle sheath
Casparian strip
cell wall
cellulose
central vacuole
chloroplast
chromoplast
collenchyma
companion cell
compartmentation
contact face
cork cell
cortex
cuticle
cutin
cytoplasm
cytoskeleton
cytosol
dictyosome
earlywood
elastic strength
endodermis
endoplasmic reticulum
epidermis
fiber
growth ring
guard cell
hair
hardwood
heartwood
hemicellulose
hypodermis
intercellular space
latewood
leaf trace
lenticel
lignin
mesophyll
microtubule
middle lamella
mitochondrion
nuclear envelope
nucleus
organelle
palisade mesophyll
parenchyma
perforation
pericycle
phloem sap
pit
pit membrane
pith
plasma membrane
plasmodesma
plastic strength
plastid
primary cell wall
primary pit field
proplastid
protoplasm
protoplast
ray
ribosome
root hair
sapwood
sclereid
sclerenchyma
secondary phloem
secondary wall
secondary xylem
selectively permeable
sieve area
sieve pore
sieve tube member
sieve tube
softwood
spongy mesophyll
stoma
stomatal pore
tracheid
trichome
tylosis
vacuole membrane
vascular bundle
vessel
vessel member
wood

Concepts

- All organisms are composed of cells that contain protoplasm.
- Protoplasm consists of ordinary chemical compounds and has no special properties, no vital force.
- Each cell consists of numerous compartments, bounded by selectively permeable membranes, and each specialized for a particular metabolism.
- There are three basic types of plant cell: parenchyma, collenchyma, and sclerenchyma.
- Almost all herbaceous stems have the same internal organization: epidermis, cortex, vascular bundles (each with phloem and xylem), and pith.
- Some terms, such as epidermis and hair, are used for both plants and animals but may refer to very different structures in each.