

**University of Anbar**

**1<sup>st</sup> lecture**

**College of science**



# **BOTANY**

**BIOLOGY DEPARTMENT**

**1<sup>st</sup> stage**

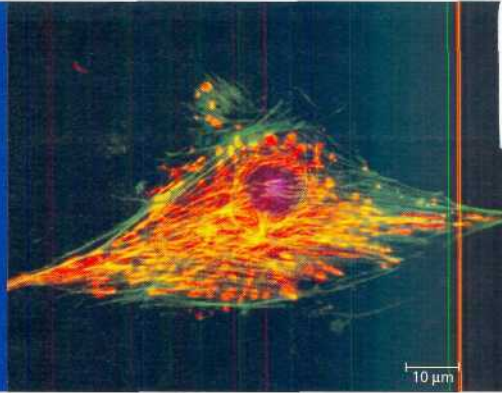
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**2021**

# 6

## A Tour of the Cell



4 Figure 6.1 A cell and its skeleton viewed by fluorescence microscopy.

### Key Concepts

- 8.1 To study cells, biologists use microscopes and the tools of biochemistry
- 6.2 Eukaryotic cells have internal membranes that compartmentalize their functions
- 6.3 The eukaryotic cell's genetic instructions are housed in the nucleus and carried out by the ribosomes
- 6.4 The endomembrane system regulates protein traffic and performs metabolic functions in the cell
- 6.5 Mitochondria and chloroplasts change energy from one form to another
- 6.6 The cytoskeleton is a network of fibers that organizes structures and activities in the cell
- 6.7 Extracellular components and connections between cells help coordinate cellular activities

### Overview

#### The Importance of Cells

The cell is as fundamental to biology as the atom is to chemistry: All organisms are made of cells. In the hierarchy of biological organization, the cell is the simplest collection of matter that can live. Indeed, there are diverse forms of life existing as single-celled organisms. More complex organisms, including plants and animals, are multicellular; their bodies are cooperatives of many kinds of specialized cells that could not survive for long on their own. However, even when they are arranged into higher levels of organization, such as tissues and organs, cells can be singled out as the organisms basic units of structure and function. The contraction of muscle cells moves your eyes as you read this sentence; when you decide to turn the

next page, nerve cells will transmit that decision from your brain to the muscle cells of your hand. Everything an organism does occurs fundamentally at the cellular level.

The cell is a microcosm that demonstrates most of the themes introduced in Chapter 1. Life at the cellular level arises from structural order, reinforcing the themes of emergent properties and the correlation between structure and function. For example, the movement of an animal cell depends on an intricate interplay of the structures that make up a cellular skeleton (green and red in the micrograph in **Figure 6.1**). Another recurring theme in biology is the interaction of organisms with their environment. Cells sense and respond to environmental fluctuations. And keep in mind the one biological theme that unifies all others: evolution. All cells are related by their descent from earlier cells. However, they have been modified in many different ways during the long evolutionary history of life on Earth.

Although cells can differ substantially from each other, they share certain common characteristics. In this chapter, we'll first learn about the tools and experimental approaches that have allowed us to understand subcellular details; then we'll tour the cell and become acquainted with its components.

### Concept 1

#### To study cells, biologists use microscopes and the tools of biochemistry

It can be difficult to understand how a cell, usually too small to be seen by the unaided eye, can be so complex. How can cell biologists possibly investigate the inner workings of such tiny entities? Before we actually tour the cell, it will be helpful to learn how cells are studied.

## Concept 6.2

### Eukaryotic cells have internal membranes that compartmentalize their functions

The basic structural and functional unit of every organism is one of two types of cells—prokaryotic or eukaryotic. Only organisms of the domains Bacteria and Archaea consist of prokaryotic cells. Protists, fungi, animals, and plants all consist of eukaryotic cells. This chapter focuses on generalized animal and plant cells, after first comparing them with prokaryotic cells.

#### Comparing Prokaryotic and Eukaryotic Cells

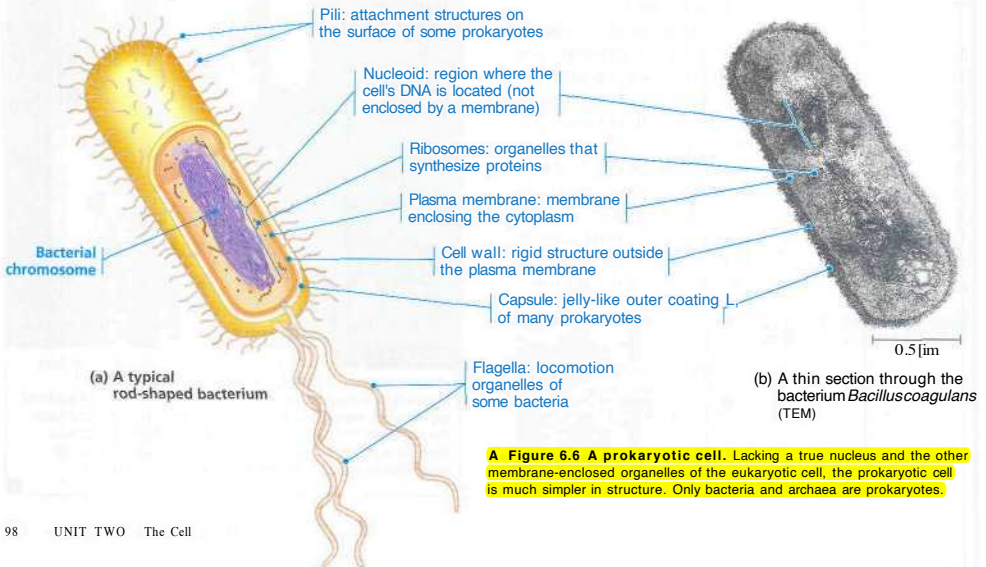
All cells have several basic features in common: They are all bounded by a membrane, called a *plasma membrane*. Within the membrane is a semifluid substance, *cytosol*, in which organelles are found. All cells contain *chromosomes*, carrying genes in the form of DNA. And all cells have *ribosomes*, tiny organelles that make proteins according to instructions from the genes.

A major difference between prokaryotic and eukaryotic cells, indicated by their names, is that the chromosomes of a eukaryotic cell are located in a membrane-enclosed organelle called the *nucleus*. The word *prokaryotic* is from the Greek *pro*, meaning "before," and *karyon*, meaning "kernel," referring here to the nucleus. In a *prokaryotic cell* (Figure 6.6), the DNA is concentrated in a region called the *nucleoid*, but no membrane

separates this region from the rest of the cell. In contrast, the *eukaryotic cell* (Greek *eu*, true, and *karyon*) has a *true nucleus*, bounded by a membranous nuclear envelope (see Figure 6.Q, pp. 100–101). The entire region between the nucleus and the plasma membrane is called the *cytoplasm*, a term also used for the interior of a prokaryotic cell. Within the cytoplasm of a eukaryotic cell, suspended in cytosol, are a variety of membrane-bounded organelles of specialized form and function. These are absent in prokaryotic cells. Thus, the presence or absence of a true nucleus is just one example of the disparity in structural complexity between the two types of cells.

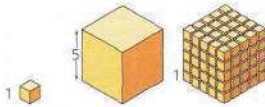
Eukaryotic cells are generally quite a bit bigger than prokaryotic cells (see Figure 6.2). Size is a general aspect of cell structure that relates to function. The logistics of carrying out cellular metabolism sets limits on cell size. At the lower limit, the smallest cells known are bacteria called mycoplasmas, which have diameters between 0.1 and 1.0  $\mu\text{m}$ . These are perhaps the smallest packages with enough DNA to program metabolism and enough enzymes and other cellular equipment to carry out the activities necessary for a cell to sustain itself and reproduce. Most bacteria are 1–10  $\mu\text{m}$  in diameter, a dimension about ten times greater than that of mycoplasmas. Eukaryotic cells are typically 10–100  $\mu\text{m}$  in diameter.

Metabolic requirements also impose theoretical upper limits on the size that is practical for a single cell. As an object of a particular shape increases in size, its volume grows proportionately more than its surface area. (Area is proportional to a linear dimension squared, whereas volume is proportional to the linear dimension cubed.) Thus, the smaller the object, the greater its ratio of surface area to volume (Figure 6.7).



**Figure 6.6 A prokaryotic cell.** Lacking a true nucleus and the other membrane-enclosed organelles of the eukaryotic cell, the prokaryotic cell is much simpler in structure. Only bacteria and archaea are prokaryotes.

Surface area increases while total volume remains constant



|   |   |     |     |
|---|---|-----|-----|
| Total surface area (height x width x number of sides x number of boxes) | 6 | 150 | 750 |
| Total volume (height x width x length x number of boxes)                | 1 | 125 | 125 |
| Surface-to-volume ratio (surface area ÷ volume)                         | 6 | U   | 6   |

**A Figure 6.7 Geometric relationships between surface area and volume.** In this diagram, cells are represented as boxes. Using arbitrary units of length, we can calculate the cell's surface area (in square units), volume (in cubic units), and ratio of surface area to volume. The smaller the cell, the higher the surface-to-volume ratio. A high surface-to-volume ratio facilitates the exchange of materials between a cell and its environment.

At the boundary of every cell, the **plasma membrane** functions as a selective barrier that allows sufficient passage of oxygen, nutrients, and wastes to service the entire volume of the cell (**Figure 6.8**). For each square micrometer of membrane, only so much of a particular substance can cross per second. Rates of chemical exchange with the extracellular environment might be inadequate to maintain a cell with a very large cytoplasm. The need for a surface area sufficiently large to accommodate the volume helps explain the microscopic size of most cells. Larger organisms do not generally have larger cells than smaller organisms—simply *more* cells. A sufficiently high ratio of surface area to volume is especially important in cells that exchange a lot of material with their surroundings, such as

intestinal cells. Such cells may have many long, thin projections from their surface called microvilli, which increase surface area without an appreciable increase in volume.

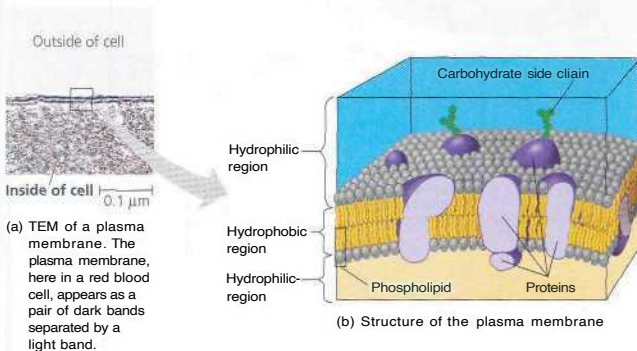
Prokaryotic cells will be described in detail in Chapters 18 and 27 (see Table 27.2 for a comparison of prokaryotes and eukaryotes), and the possible evolutionary relationships between prokaryotic and eukaryotic cells will be discussed in Chapter 28. Most of the discussion of cell structure that follows in this chapter applies to eukaryotic cells.

## A Panoramic View of the Eukaryotic Cell

In addition to the plasma membrane at its outer surface, a eukaryotic cell has extensive and elaborately arranged internal membranes, which partition the cell into compartments—the membranous organelles mentioned earlier. These membranes also participate directly in the cell's metabolism, because many enzymes are built right into the membranes. Furthermore, the cell's compartments provide different local environments that facilitate specific metabolic functions, so incompatible processes can go on simultaneously inside the same cell.

Membranes of various kinds are fundamental to the organization of the cell. In general, biological membranes consist of a double layer of phospholipids and other lipids. Embedded in this lipid bilayer or attached to its surfaces are diverse proteins (see **Figure 6.8**). However, each type of membrane has a unique composition of lipids and proteins suited to that membrane's specific functions. For example, enzymes embedded in the membranes of the organelles called mitochondria function in cellular respiration.

Before continuing with this chapter, examine the overviews of eukaryotic cells in **Figure 6.9** on the next two pages. These generalized cell diagrams introduce the various organelles and provide a map of the cell for the detailed tour upon which we will now embark. **Figure 6.9** also contrasts animal and plant cells. As eukaryotic cells, they have much more in common than either has with any prokaryotic cell. As you will see, however, there are important differences between animal and plant cells.

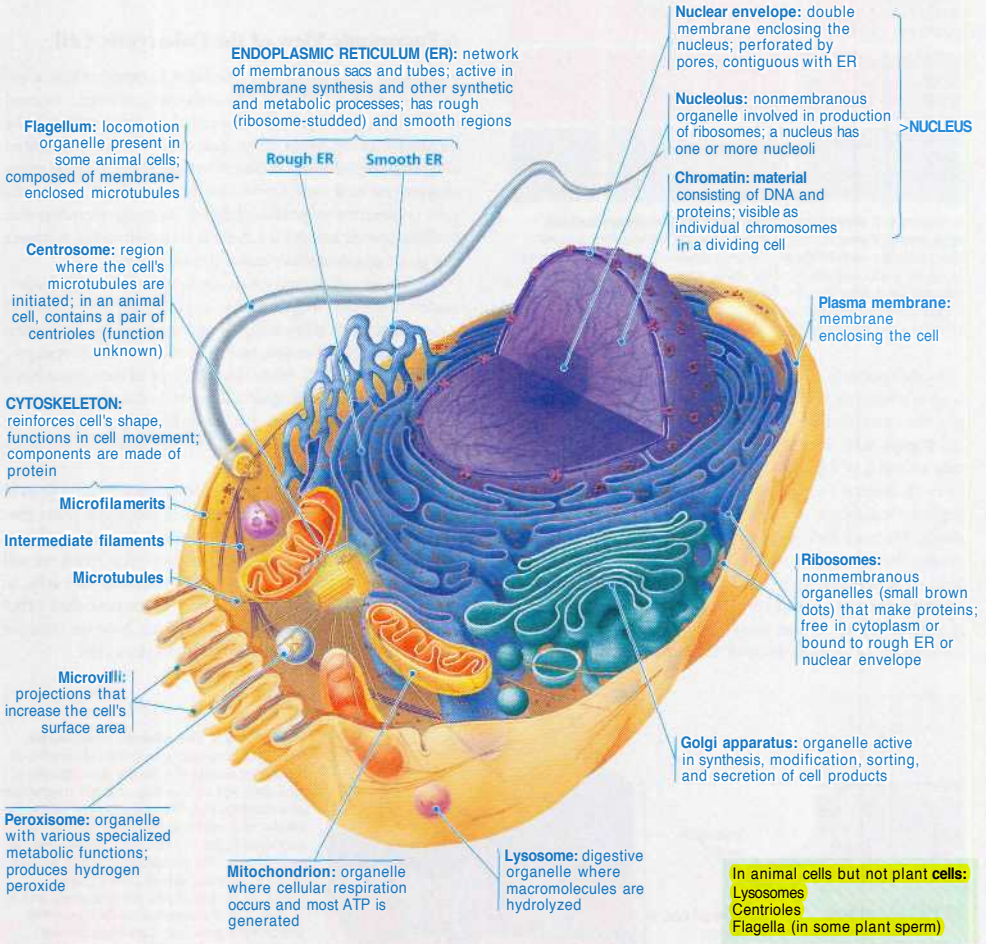


**4 Figure 6.8 The plasma membrane.**

The plasma membrane and the membranes of organelles consist of a double layer (bilayer) of phospholipids with various proteins attached to or embedded in it. The phospholipid tails in the interior of a membrane are hydrophobic; the interior portions of membrane proteins are also hydrophobic. The phospholipid heads, exterior proteins, exterior parts of proteins, and carbohydrate side chains are hydrophilic and in contact with the aqueous solution on either side of the membrane. Carbohydrate side chains are found only on the outer surface of the plasma membrane. The specific functions of a membrane depend on the kinds of phospholipids and proteins present.

This drawing of a generalized animal cell incorporates the most common structures of animal cells (no cell actually looks just like this). As shown by this cutaway view, the cell has a variety of organelles ("little organs"), many of which are bounded by membranes. The most prominent organelle in an animal cell is usually the nucleus.

Most of the cell's metabolic activities occur in the cytoplasm, the entire region between the nucleus and the plasma membrane. The cytoplasm contains many organelles suspended in a semifluid medium, the cytosol. Pervading much of the cytoplasm is a labyrinth of membranes called the endoplasmic reticulum (ER).

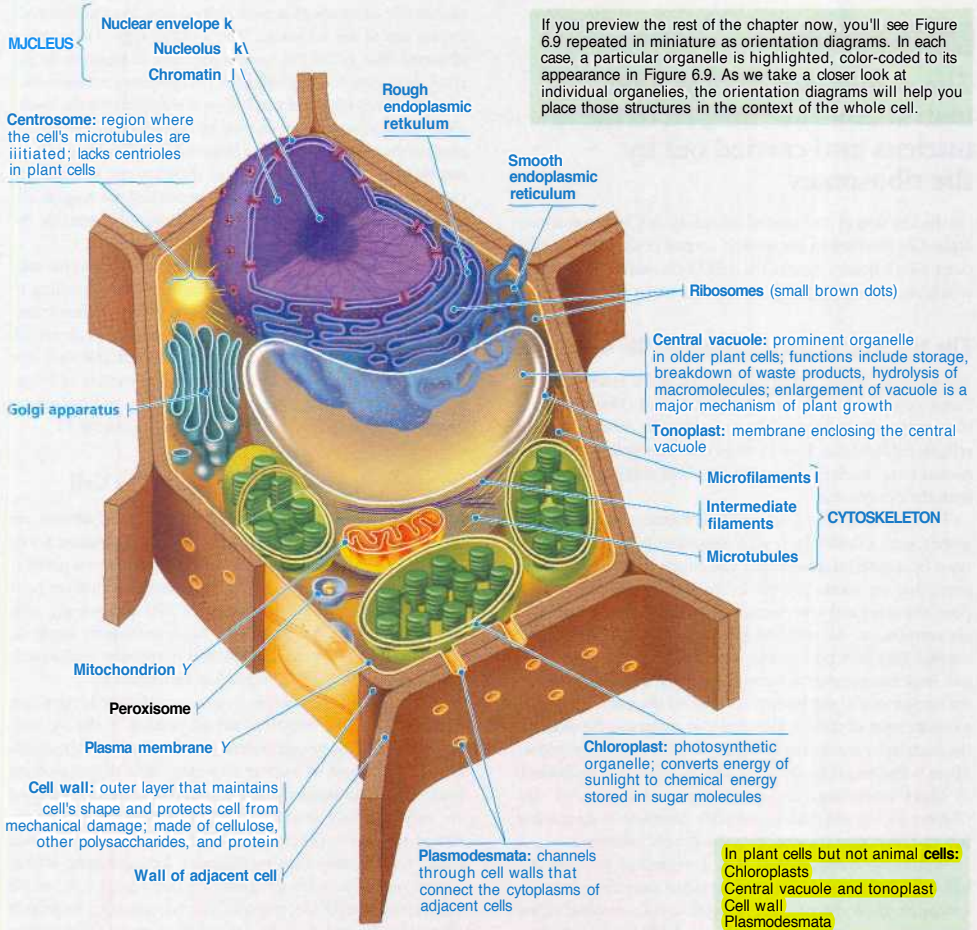


## PLANT CELL

This drawing of a generalized plant cell reveals the similarities and differences between an animal cell and a plant cell. In addition to most of the features seen in an animal cell, a plant cell has membrane-enclosed organelles called plastids. The most important

type of plastid is the chloroplast, which carries out photosynthesis. Many plant cells have a large central vacuole; some may have one or more smaller vacuoles. Outside a plant cell's plasma membrane is a thick cell wall, perforated by channels called plasmodesmata.

If you preview the rest of the chapter now, you'll see Figure 6.9 repeated in miniature as orientation diagrams. In each case, a particular organelle is highlighted, color-coded to its appearance in Figure 6.9. As we take a closer look at individual organelles, the orientation diagrams will help you place those structures in the context of the whole cell.



becomes surrounded by a membrane, and a lysosome fuses with this vesicle (Figure 6.14b). The lysosomal enzymes dismantle the enclosed material, and the organic monomers are returned to the cytosol for reuse. With the help of lysosomes, the cell continually renews itself. A human liver cell, for example, recycles half of its macromolecules each week.

The cells of people with inherited lysosomal storage diseases lack a functioning hydrolytic enzyme normally present in lysosomes. The lysosomes become engorged with indigestible substrates, which begin to interfere with other cellular activities. In Tay-Sachs disease, for example, a lipid-digesting enzyme is missing or inactive, and the brain becomes impaired by an accumulation of lipids in the cells. Fortunately lysosomal storage diseases are rare in the general population.

### Vacuoles: Diverse Maintenance Compartments

A plant or fungal cell may have one or several vacuoles. While vacuoles carry out hydrolysis and are thus similar to lysosomes, they carry out other functions as well. Food vacuoles, formed by phagocytosis, have already been mentioned (see Figure 6.14a). Many freshwater protists have contractile vacuoles that pump excess water out of the cell, thereby maintaining the appropriate concentration of salts and other molecules (see Figure 7.14). Mature plant cells generally contain a large central vacuole (Figure 6.15) enclosed by a membrane called the tonoplast. The central vacuole develops by the

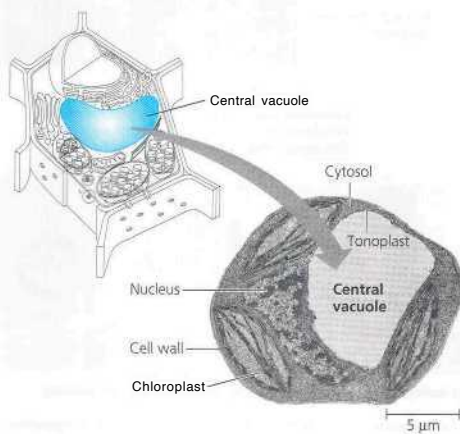
coalescence of smaller vacuoles, themselves derived from the endoplasmic reticulum and Golgi apparatus. The vacuole is in this way an integral part of a plant cell's endomembrane system. Like all cellular membranes, the tonoplast is selective in transporting solutes; as a result, the solution inside the vacuole, called cell sap, differs in composition from the cytosol.

The plant cell's central vacuole is a versatile compartment. It can hold reserves of important organic compounds, such as the proteins stockpiled in the vacuoles of storage cells in seeds. It is also the plant cell's main repository of inorganic ions, such as potassium and chloride. Many plant cells use their vacuoles as disposal sites for metabolic by-products that would endanger the cell if they accumulated in the cytosol. Some vacuoles contain pigments that color the cells, such as the red and blue pigments of petals that help attract pollinating insects to flowers. Vacuoles may also help protect the plant against predators by containing compounds that are poisonous or unpalatable to animals. The vacuole has a major role in the growth of plant cells, which enlarge as their vacuoles absorb water, enabling the cell to become larger with a minimal investment in new cytoplasm. And because of the large vacuole, the cytosol often occupies only a thin layer between the plasma membrane and the tonoplast, so the ratio of membrane surface to cytosolic volume is great, even for a large plant cell.

### The Endomembrane System: A Review

Figure 6.16 reviews the endomembrane system, showing the flow of membrane lipids and proteins through the various organelles. As the membrane moves from the ER to the Golgi and then elsewhere, its molecular composition and metabolic functions are modified, along with those of its contents. The endomembrane system is a complex and dynamic player in the cell's compartmental organization.

We'll continue our tour of the cell with some membranous organelles that are *not* closely related to the endomembrane system, but play crucial roles in the energy transformations carried out by cells.

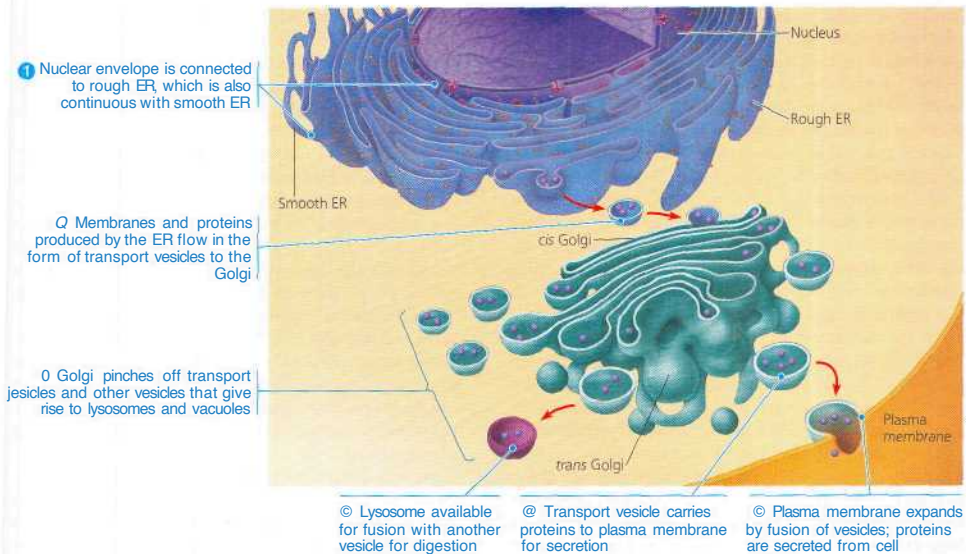


**Figure 6.15** The plant cell vacuole. The central vacuole is usually the largest compartment in a plant cell; the rest of the cytoplasm is generally confined to a narrow zone between the vacuolar membrane (tonoplast) and the plasma membrane (TEM).

### Concept Check 6.4

1. Describe the structural and functional distinctions between rough and smooth ER.
2. Imagine a protein that functions in the ER, but requires modification in the Golgi apparatus before it can achieve that function. Describe the protein's path through the cell, starting with the mRNA molecule that specifies the protein.
3. How do transport vesicles serve to integrate the endomembrane system?

For suggested answers, see Appendix A.



**A Figure 6.16 Review: relationships among organelles of the endomembrane system.** The red arrows show some of the migration pathways for membranes and the materials they enclose.

## Concept 6.5

### Mitochondria and chloroplasts change energy from one form to another

Organisms transform energy they acquire from their surroundings. In eukaryotic cells, mitochondria and chloroplasts are the organelles that convert energy to forms that cells can use for work. Mitochondria (singular, *mitochondrion*) are the sites of cellular respiration, the metabolic process that generates ATP by extracting energy from sugars, fats, and other fuels with the help of oxygen. Chloroplasts, found only in plants and algae, are the sites of photosynthesis. They convert solar energy to chemical energy by absorbing sunlight and using it to drive the synthesis of organic compounds such as sugars from carbon dioxide and water.

Although mitochondria and chloroplasts are enclosed by membranes, they are not part of the endomembrane system. In contrast to organelles of the endomembrane system, each of these organelles has at least two membranes separating the innermost space from the cytosol. Their membrane proteins

are made not by the ER, but by free ribosomes in the cytosol and by ribosomes contained within these organelles themselves. Not only do these organelles have ribosomes, but they also contain a small amount of DNA. It is this DNA that programs the synthesis of the proteins made on the organelles' own ribosomes. (Proteins imported from the cytosol—constituting most of the organelles' proteins—are programmed by nuclear DNA.) Mitochondria and chloroplasts are semi-autonomous organelles that grow and reproduce within the cell. In Chapters 9 and 10, we will focus on how mitochondria and chloroplasts function. We will consider the evolution of these organelles in Chapter 28. Here we are concerned mainly with the structure of these energy transformers.

In this section, we will also consider the peroxisome, an oxidative organelle that is not part of the endomembrane system. Like mitochondria and chloroplasts, the peroxisome imports its proteins primarily from the cytosol.

### Mitochondria: Chemical Energy Conversion

Mitochondria are found in nearly all eukaryotic cells, including those of plants, animals, fungi, and protists. Some cells have a single large mitochondrion, but more often a cell has



hundreds or even thousands of mitochondria; the number is correlated with the cell's level of metabolic activity. For example, motile or contractile cells have proportionally more mitochondria per volume than less active cells. Mitochondria are about 1–10  $\mu\text{m}$  long. Time-lapse films of living cells reveal mitochondria moving around, changing their shapes, and dividing in two, unlike the static cylinders seen in electron micrographs of dead cells.

The mitochondrion is enclosed by two membranes, each a phospholipid bilayer with a unique collection of embedded proteins (Figure 6.17). The outer membrane is smooth, but the inner membrane is convoluted, with infoldings called cristae. The inner membrane divides the mitochondrion into two internal compartments. The first is the intermembrane space, the narrow region between the inner and outer membranes. The second compartment, the mitochondrial matrix, is enclosed by the inner membrane. The matrix contains many different enzymes as well as the mitochondrial DNA and ribosomes. Some of the metabolic steps of cellular respiration are catalyzed by enzymes in the matrix. Other proteins that function in respiration, including the enzyme that makes ATP, are built into the inner membrane. As highly folded surfaces, the cristae give the inner mitochondrial membrane a large surface area for these proteins, thus enhancing the productivity of cellular respiration. This is another example of structure fitting function.

### Chloroplasts: Capture of Light Energy

The chloroplast is a specialized member of a family of closely related plant organelles called plastids. *Amyloplasts* are colorless plastids that store starch (amylose), particularly in roots and tubers. *Ochromoplasts* have pigments that give fruits and

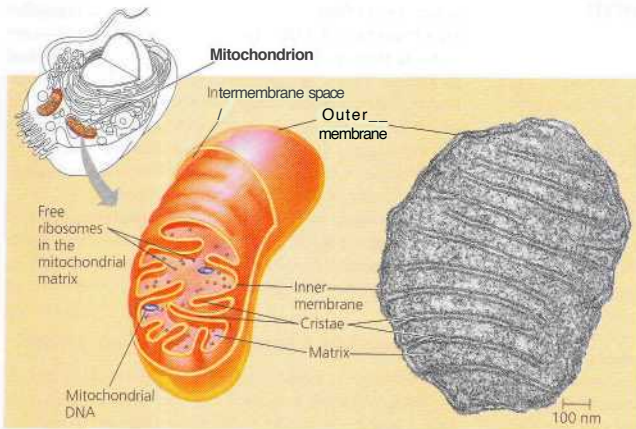
flowers their orange and yellow hues. *Chloroplasts* contain the green pigment chlorophyll, along with enzymes and other molecules that function in the photosynthetic production of sugar. These lens-shaped organelles, measuring about 2  $\mu\text{m}$  by 5  $\mu\text{m}$ , are found in leaves and other green organs of plants and in algae (Figure 6.18).

The contents of a chloroplast are partitioned from the cytosol by an envelope consisting of two membranes separated by a very narrow intermembrane space. Inside the chloroplast is another membranous system in the form of flattened, interconnected sacs called thylakoids. In some regions, thylakoids are stacked like poker chips; each stack is called a granum (plural, *grana*). The fluid outside the thylakoids is the stroma, which contains the chloroplast DNA and ribosomes as well as many enzymes. The membranes of the chloroplast divide the chloroplast space into three compartments: the intermembrane space, the stroma, and the thylakoid space. In Chapter 10, you will learn how this compartmental organization enables the chloroplast to convert light energy to chemical energy during photosynthesis.

As with mitochondria, the static and rigid appearance of chloroplasts in micrographs or schematic diagrams is not true to their dynamic behavior in the living cell. Their shapes are changeable, and they grow and occasionally pinch in two, reproducing themselves. They are mobile and move around the cell with mitochondria and other organelles along tracks of the cytoskeleton, a structural network we will consider later in this chapter.

### Peroxisomes: Oxidation

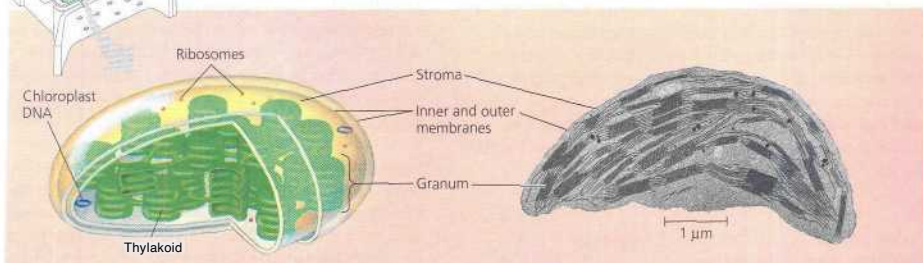
The peroxisome is a specialized metabolic compartment bounded by a single membrane (Figure 6.19). Peroxisomes



^ **Figure 6.17** The mitochondrion, site of cellular respiration. The inner and outer membranes of the mitochondrion are evident in the drawing and micrograph (TEM). The cristae are infoldings of the inner membrane. The cutaway drawing shows the two compartments bounded by the membranes: the intermembrane space and the mitochondrial matrix. Free ribosomes are seen in the matrix, along with one to several copies of the mitochondrial genome (DNA). The DNA molecules are usually circular and are attached to the inner mitochondrial membrane.

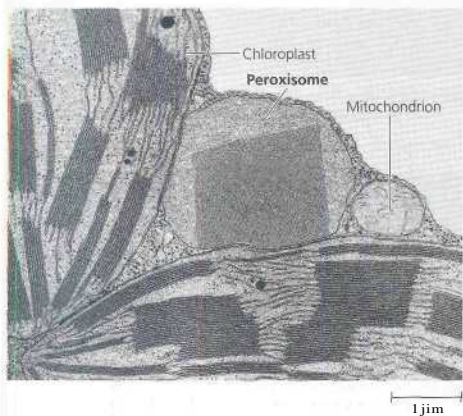


**f Figure 6.18 The chloroplast, site of photosynthesis.** A chloroplast is enclosed by two membranes separated by a narrow intermembrane space that constitutes an outer compartment. The inner membrane encloses a second compartment containing the fluid called stroma. Free ribosomes and copies of the chloroplast genome (DNA) are present in the stroma. The stroma surrounds a third compartment, the thylakoid space, delineated by the thylakoid membrane. Interconnected thylakoid sacs (thylakoids) are stacked to form structures called grana (singular, granum), which are further connected by thin tubules between individual thylakoids (TEM).



contain enzymes that transfer hydrogen from various substrates to oxygen, producing hydrogen peroxide ( $H_2O_2$ ) as a by-product, from which the organelle derives its name. These reactions may have many different functions. Some peroxisomes use oxygen to break fatty acids down into smaller molecules that can then be transported to mitochondria,

where they are used as fuel for cellular respiration. Peroxisomes in the liver detoxify alcohol and other harmful compounds by transferring hydrogen from the poisons to oxygen. The  $H_2O_2$  formed by peroxisome metabolism is itself toxic, but the organelle contains an enzyme that converts the  $H_2O_2$  to water. Enclosing in the same space both the enzymes that produce hydrogen peroxide and those that dispose of this toxic compound is another example of how the cell's compartmental structure is crucial to its functions.



**A▶ Figure 6.19 Peroxisomes.** Peroxisomes are roughly spherical and often have a granular or crystalline core that is thought to be a dense collection of enzyme molecules. This peroxisome is in a leaf cell. Notice its proximity to two chloroplasts and a mitochondrion. These organelles cooperate with peroxisomes in certain metabolic functions (TEM).

Specialized peroxisomes called **glyoxysomes** are found in the fat-storing tissues of plant seeds. These organelles contain enzymes that initiate the conversion of fatty acids to sugar, which the emerging seedling can use as a source of energy and carbon until it is able to produce its own sugar by photosynthesis.

Unlike lysosomes, peroxisomes do not bud from the endomembrane system. They grow larger by incorporating proteins made primarily in the cytosol, lipids made in the ER, and lipids synthesized within the peroxisome itself. Peroxisomes may increase in number by splitting in two when they reach a certain size.

### Concept Check 6.5

1. Describe at least two common characteristics of chloroplasts and mitochondria.
2. Explain the characteristics of mitochondria and chloroplasts that place them in a separate category from organelles in the endomembrane system.

For suggested answers, see *Appendix A*.

the actin reassembles into a network. Amoebas are not the only cells that move by crawling; so do many cells in the animal body, including some white blood cells.

In plant cells, both actin-myosin interactions and sol-gel transformations brought about by actin may be involved in cytoplasmic streaming, a circular flow of cytoplasm within cells (Figure 6.27c). This movement, which is especially common in large plant cells, speeds the distribution of materials within the cell.

### Intermediate Filaments

Intermediate filaments are named for their diameter, which, at 8–12 nm, is larger than the diameter of microfilaments but smaller than that of microtubules (see Table 6.1, p. 113). Specialized for bearing tension (like microfilaments), intermediate filaments are a diverse class of cytoskeletal elements. Each type is constructed from a different molecular subunit belonging to a family of proteins whose members include the keratins. Microtubules and microfilaments, in contrast, are consistent in diameter and composition in all eukaryotic cells.

Intermediate filaments are more permanent fixtures of cells than are microfilaments and microtubules, which are often disassembled and reassembled in various parts of a cell. Even after cells die, intermediate filament networks often persist; for example, the outer layer of our skin consists of dead skin cells full of keratin proteins. Chemical treatments that remove microfilaments and microtubules from the cytoplasm of living cells leave a web of intermediate filaments that retains its original shape. Such experiments suggest that intermediate filaments are especially important in reinforcing the shape of a cell and fixing the position of certain organelles. For example, the nucleus commonly sits within a cage made of intermediate filaments, fixed in location by branches of the filaments that extend into the cytoplasm. Other intermediate filaments make up the nuclear lamina that lines the interior of the nuclear envelope (see Figure 6.10). In cases where the shape of the entire cell is correlated with function, intermediate filaments support that shape. For instance, the long extensions (axons) of nerve cells that transmit impulses are strengthened by one class of intermediate filament. Thus, the various kinds of intermediate filaments may function as the framework of the entire cytoskeleton.

### Concept Check 6.6

1. Describe how the properties of microtubules, microfilaments, and intermediate filaments allow them to determine cell shape.
2. How do cilia and flagella bend?

*For suggested answers, see Appendix A.*

## Concept 6.7

### Extracellular components and connections between cells help coordinate cellular activities

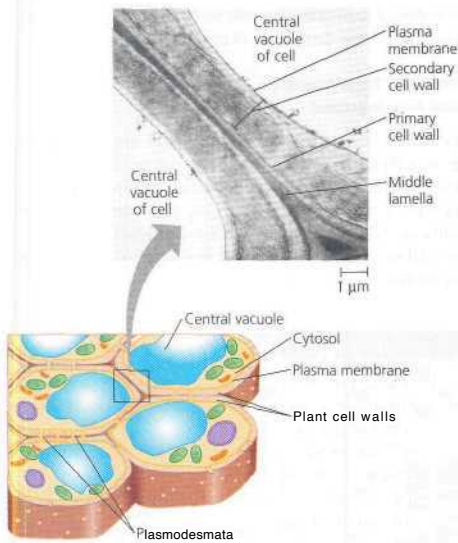
Having crisscrossed the interior of the cell to explore various organelles, we complete our tour of the cell by returning to the surface of this microscopic world, where there are additional structures with important functions. The plasma membrane is usually regarded as the boundary of the living cell, but most cells synthesize and secrete materials of one kind or another that are external to the plasma membrane. Although they are outside the cell, the study of these extracellular structures is central to cell biology because they are involved in so many cellular functions.

### Cell Walls of Plants

The cell wall is an extracellular structure of plant cells that distinguishes them from animal cells. The wall protects the plant cell, maintains its shape, and prevents excessive uptake of water. On the level of the whole plant, the strong walls of specialized cells hold the plant up against the force of gravity. Prokaryotes, fungi, and some protists also have cell walls, but we will postpone discussion of them until Unit Five.

Plant cell walls are much thicker than the plasma membrane, ranging from 0.1  $\mu\text{m}$  to several micrometers. The exact chemical composition of the wall varies from species to species and even from one cell type to another in the same plant, but the basic design of the wall is consistent. Microfibrils made of the polysaccharide cellulose (see Figure 5.8) are embedded in a matrix of other polysaccharides and protein. This combination of materials, strong fibers in a "ground substance" (matrix), is the same basic architectural design found in steel-reinforced concrete and in fiberglass.

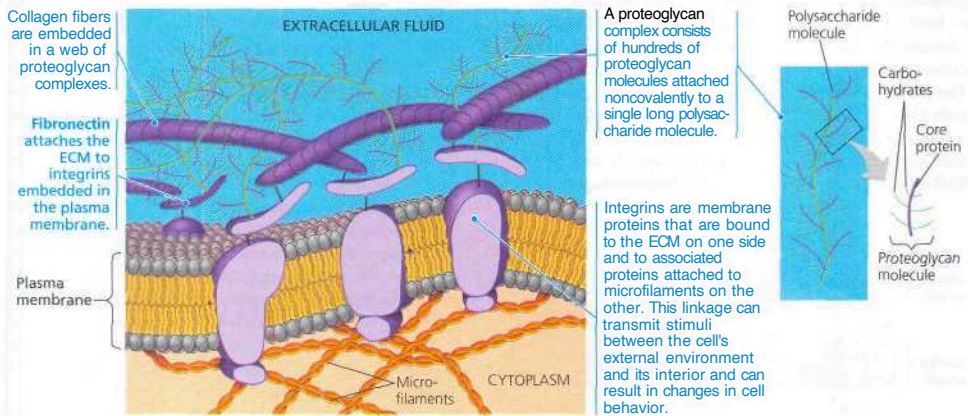
A young plant cell first secretes a relatively thin and flexible wall called the primary cell wall (Figure 6.28). Between primary walls of adjacent cells is the middle lamella, a thin layer rich in sticky polysaccharides called pectins. The middle lamella glues adjacent cells together (pectin is used as a thickening agent in jams and jellies). When the cell matures and stops growing, it strengthens its wall. Some plant cells do this simply by secreting hardening substances into the primary wall. Other cells add a secondary cell wall between the plasma membrane and the primary wall. The secondary wall, often deposited in several laminated layers, has a strong and durable matrix that affords the cell protection and support. Wood, for example, consists mainly of secondary walls. Plant cell walls are commonly perforated by channels between adjacent cells called plasmodesmata (see Figure 6.28), which will be discussed shortly.



iii **Figure 6.28 Plant cell walls.** The orientation drawing shows several cells, each with a large vacuole, a nucleus, and several chloroplasts and mitochondria. The transmission electron micrograph (TEM) shows the cell walls where two cells come together. The multilayered partition between plant cells consists of adjoining walls individually secreted by the cells.

## The Extracellular Matrix (ECM) of Animal Cells

Although animal cells lack walls akin to those of plant cells, they do have an elaborate **extracellular matrix (ECM)** (Figure 6.29). The main ingredients of the ECM are glycoproteins secreted by the cells. (Recall that glycoproteins are proteins with covalently bonded carbohydrate, usually short chains of sugars.) The most abundant glycoprotein in the ECM of most animal cells is **collagen**, which forms strong fibers outside the cells. In fact, collagen accounts for about half of the total protein in the human body. The collagen fibers are embedded in a network woven from proteoglycans, which are glycoproteins of another class. A proteoglycan molecule consists of a small core protein with many carbohydrate chains covalently attached, so that it may be up to 95% carbohydrate. Large proteoglycan complexes can form when hundreds of proteoglycans become noncovalently attached to a single long polysaccharide molecule, as shown in Figure 6.29. Some cells are attached to the ECM by still other ECM glycoproteins, including **fibronectin**. Fibronectin and other ECM proteins bind to cell surface receptor proteins called **integrins** that are built into the plasma membrane. Integrins span the membrane and bind on their cytoplasmic side to associated proteins attached to microfilaments of the cytoskeleton. The name integrin is based on the word *integrate*: Integrins are in a position to transmit changes between the ECM and the cytoskeleton and thus to integrate changes occurring outside and inside the cell.



**A. Figure 6.29 Extracellular matrix (ECM) of an animal cell.** The molecular composition and structure of the ECM varies from one cell type to another. In this example, three different types of glycoproteins are present: proteoglycans, collagen, and fibronectin.

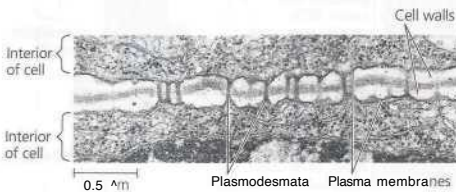
Current research on fibronectin, other ECM molecules, and integrins is revealing the influential role of the extracellular matrix in the lives of cells. By communicating with a cell through integrins, the ECM can regulate a cell's behavior. For example, some cells in a developing **embryo** migrate along specific pathways by matching the orientation of their microfilaments to the "grain" of fibers in the extracellular matrix. Researchers are also learning that the extracellular matrix around a cell can influence the activity of genes in the nucleus. Information about the ECM probably reaches the nucleus by a combination of mechanical and chemical signaling pathways. Mechanical signaling involves fibronectin, integrins, and microfilaments of the cytoskeleton. Changes in the cytoskeleton may in turn trigger chemical signaling pathways inside the cell, leading to changes in the set of proteins being made by the cell and therefore changes in the cell's function. In this way, the extracellular matrix of a particular tissue may help coordinate the behavior of all the cells within that tissue. Direct connections between cells also function in this coordination, as we discuss next.

## Intercellular Junctions

The many cells of an animal or plant are organized into tissues, organs, and organ systems. Neighboring cells often adhere, interact, and communicate through special patches of direct physical contact.

### Plants: *Plasmodesmata*

It might seem that the nonliving cell walls of plants would isolate cells from one another. But in fact, as shown in **Figure 6.30**, plant cell walls are perforated with channels called *plasmodesmata* (singular, *plasmodesma*; from the Greek *desmos*, to bind). Cytosol passes through the *plasmodesmata* and connects the chemical environments of adjacent cells. These connections unify most of the plant into one living continuum. The plasma membranes of adjacent cells line the channel of each *plasmodesma* and thus are continuous. Water and small solutes can pass freely from cell to cell, and recent experiments have shown that in certain circumstances, specific proteins and RNA molecules can also do this. The macromolecules to be



**A Figure 6.30 Plasmodesmata between plant cells.** The cytoplasm of one plant cell is continuous with the cytoplasm of its neighbors via *plasmodesmata*, channels through the cell walls (TEM).

transported to neighboring cells seem to reach the *plasmodesmata* by moving along fibers of the cytoskeleton.

### Animals: *Tight Junctions, Desmosomes, and Gap Junctions*

In animals, there are three main types of intercellular junctions: *tight junctions*, *desmosomes*, and *gap junctions* (which are most like the *plasmodesmata* of plants). All three types are especially common in epithelial tissue, which lines the internal surfaces of the body. **Figure 6.31** uses epithelial cells of the intestinal lining to illustrate these junctions; please study this figure before moving on.

### Concept Check 6.7

1. In what ways are the cells of multicellular plants and animals structurally different from single-celled plants or animals?
2. What characteristics of the plant cell wall and animal cell extracellular matrix allow the cells to fulfill their need to exchange matter and information with their external environment?

For suggested answers, see Appendix A.

## The Cell: A Living Unit Greater Than the Sum of Its Parts

From our panoramic view of the cells overall compartmental organization to our close-up inspection of each organelle's architecture, this tour of the cell has provided many opportunities to correlate structure with function. (This would be a good time to review cell structure by returning to Figure 6.9, pp. 100 and 101.) But even as we dissect the cell, remember that none of its organelles works alone. As an example of cellular integration, consider the microscopic scene in **Figure 6.32**. The large cell is a macrophage (see Figure 6.14a). It helps defend the body against infections by ingesting bacteria (the smaller cells) into phagocytic vesicles. The macrophage crawls along a surface and reaches out to the bacteria with thin pseudopodia (called filopodia). Actin filaments interact with other elements of the cytoskeleton in these movements. After the macrophage engulfs the bacteria, they are destroyed by lysosomes. The elaborate endomembrane system produces the lysosomes. The digestive enzymes of the lysosomes and the proteins of the cytoskeleton are all made on ribosomes. And the synthesis of these proteins is programmed by genetic messages dispatched from the DNA in the nucleus. All these processes require energy, which mitochondria supply in the form of ATP. Cellular functions arise from cellular order: The cell is a living unit greater than the sum of its parts.

**University of Anbar**

**2<sup>nd</sup> lecture**

**College of science**



# **BOTANY**

**BIOLOGY DEPARTMENT**

**1<sup>st</sup> stage**

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**2021**

# 35 Plant Structure, Growth, and Development



▲ Figure 35.1 Fanwort (*Cabomba caroliniana*).

## Key Concepts

- 35.1 The plant body has a hierarchy of organs, tissues, and cells
- 35.2 Meristems generate cells for new organs
- 35.3 Primary growth lengthens roots and shoots
- 35.4 Secondary growth adds girth to stems and roots in woody plants
- 35.5 Growth, morphogenesis, and differentiation produce the plant body

## Overview

### No Two Plants Are Alike

To some people, the plant in **Figure 35.1** is an intrusive aquatic weed that clogs streams, rivers, and lakes. Others consider it an attractive addition to an aquarium. Whatever else the fanwort (*Cabomba caroliniana*) may be, it is a striking example of **plasticity**—an organism's ability to alter or "mold" itself in response to local environmental conditions. The underwater leaves have a feathery appearance, an adaptation that may provide protection from the stress of moving water. In contrast, the surface leaves are pads that aid in flotation. Both leaf types have genetically identical cells, but the dissimilar environments cause different genes involved in leaf formation to be turned on or off. Such extreme developmental plasticity is much more common in plants than in animals and may help compensate for their lack of mobility. As Natasha Raikhel puts it in the interview preceding this chapter, "Plants have to be exquisite to survive because they can't run." Also, since the form of any plant is controlled by environmental as well as genetic factors, no two plants are exactly alike.

In addition to plastic structural responses by individual plants to specific environments, entire species have by natu-

ral selection accumulated characteristics of morphology, size, and external form, that vary little among plants within the species. For example, some species of desert plants, such as cacti, have leaves that are so highly reduced as spines that the stem is actually the primary photosynthetic organ. This reduction in leaf size, and thus in surface area, results in reduced water loss. These leaf adaptations have enhanced survival and reproductive success in the desert environment.

This chapter focuses on how the body of a plant is formed, setting the stage for the rest of this unit on plant biology. Chapters 29 and 30 described the evolution and characteristics of bryophytes, seedless vascular plants, gymnosperms, and angiosperms. This chapter and Unit Six in general focus mainly on vascular plants—especially angiosperms because flowering plants comprise about 90% of plant species and are the base of nearly every terrestrial food web. As the world's population increases, the need for plants to supply food, fuel, fiber, medicine, lumber, and paper has never been greater, heightening the importance of understanding how plants grow and develop.

## Concept 35.1

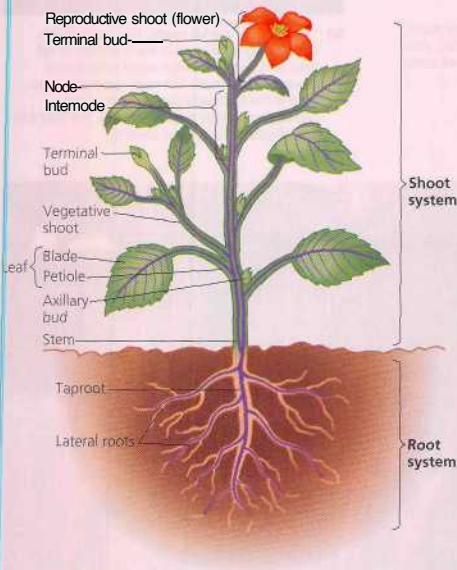
### The plant body has a hierarchy of organs, tissues, and cells

Plants, like multicellular animals, have organs composed of different tissues, and these tissues are composed of cells. A tissue is a group of cells with a common function, structure, or both. An organ consists of several types of tissues that together carry out particular functions. In looking at the hierarchy of plant organs, tissues, and cells, we will focus first on organs as the most readily observable features of plant structure.

## Title Three Basic Plant Organs: Roots, Stems, and Leaves

The basic morphology of vascular plants reflects their evolutionary history as terrestrial organisms that inhabit and draw resources from two very different environments—below-ground and above-ground. Plants must absorb water and minerals from below the ground and CO<sub>2</sub> and light from above the ground. The evolutionary solution to this separation of resources was the development of three basic organs: roots, stems, and leaves. They are organized into a root system and a shoot system, the latter consisting of stems and leaves (Figure 35.2). With few exceptions, angiosperms and other vascular plants rely completely on both systems for survival. Roots are typically photosynthetic and would starve without the organic nutrients imported from the shoot system. Conversely, the shoot system depends on the water and minerals that roots absorb from the soil.

Later in the chapter, we will discuss the transition from vegetative shoots (shoots that are nonreproductive) to reproductive shoots. In angiosperms, the reproductive shoots are flowers, which are composed of leaves that are highly modified for sexual reproduction.



▲ **Figure 35.2** An overview of a flowering plant. The plant body is divided into a root system and a shoot system, connected by vascular tissue (purple strands in this diagram) that is continuous throughout the plant. The plant shown is an idealized eudicot.

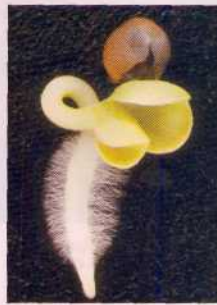
As we take a closer look at roots, stems, and leaves, try to view these organs from the evolutionary perspective of adaptations to living on land, by identifying some variations in these organs, we will focus mainly on the two major groups of angiosperms: monocots and eudicots (see Figure 30.12).

### Roots

A root is an organ that anchors a vascular plant (usually in the soil), absorbs minerals and water, and often stores organic nutrients. Most eudicots and gymnosperms have a taproot system, consisting of one main vertical root (the taproot) that develops from an embryonic root. The taproot gives rise to lateral roots, also called branch roots (see Figure 35.2). In angiosperms, the taproot often stores organic nutrients that the plant consumes during flowering and fruit production. For this reason, root crops such as carrots, turnips, and sugar beets are harvested before they flower. Taproot systems generally penetrate deeply into the ground.

In seedless vascular plants and in most monocots, such as grasses, the embryonic root dies and does not give rise to a main root. Instead, many small roots grow from the stem, with each small root forming its own lateral roots. The result is a fibrous root system—a mat of generally thin roots spreading out below the soil surface, with no root standing out as the main one (see Figure 30.12). Roots arising from the stem are said to be adventitious (from the Latin *adventitus*, extraneous), a term describing any plant part that grows in an unusual location. A fibrous root system is usually shallower than a taproot system. Grass roots are particularly shallow, being concentrated in the upper few centimeters of the soil. Because grass roots hold the topsoil in place, they make excellent ground cover for preventing erosion. Large monocots, such as palms and bamboo, are mainly anchored by sturdy rhizomes, which are horizontal underground stems.

The entire root system helps anchor a plant, but in most plants the absorption of water and minerals occurs primarily near the root tips, where vast numbers of tiny root hairs increase the surface area of the root enormously (Figure 35.3). A



▲ **Figure 35.3** Root hairs and root tip. Growing by the thousands just behind each root tip, root hairs increase the surface area for the absorption of water and minerals by the roots.



**root hair** is an extension of a root epidermal cell (protective cell on a plant surface). Root hairs are not to be confused with lateral roots, which are multicellular organs. Absorption is often enhanced by symbiotic relationships between plant roots and fungi and bacteria, as you will see in Chapters 36 and 37.

**Figure 35.4 Modified roots.**

Environmental adaptations may result in roots being modified for a variety of functions. Many modified roots are aerial roots that are above the ground during normal development.

Many plants have modified roots. Some of these arise from roots, and others are adventitious, developing from stems and, in rare cases, leaves. Some modified roots provide more support and anchorage, while others store water and nutrients or absorb oxygen or water from the air (Figure 35.4).



(a) **Prop roots.** The aerial roots shown here in maize are examples of prop roots, so named because they support tall, top-heavy plants. All roots of a mature maize plant are adventitious after the original roots die. The emerging roots shown here will eventually penetrate the soil.



(b) **Storage roots.** Many plants, such as sweet potatoes, store food and water in their roots.



(c) **"Strangling" aerial roots.** The seeds of this strangler fig germinate in the branches of tall trees and send numerous aerial roots to the ground. These snake-like roots gradually wrap around the hosts and objects such as this Cambodian temple ruin. Eventually, the host tree dies of strangulation and shading.



(d) **Buttress roots.** Aerial roots that look like buttresses support the tall trunks of some tropical trees, such as this ceiba tree in Central America.



(e) **Pneumatophores.** Also known as air roots, pneumatophores are produced by trees such as mangroves that inhabit tidal swamps. By projecting above the surface, they enable the root system to obtain oxygen, which is lacking in the thick, waterlogged mud.

## Stems

A **stem** is an organ consisting of an alternating system of **nodes**, ME points at which leaves are attached, and **internodes**, the stem segments between nodes (see Figure 35.2). In the angle (axil) formed by each leaf and the stem is an **axillary bud**, a structure that has the potential to form a lateral shoot, commonly called a branch. Most axillary buds of a young shoot are dormant (not growing). Thus, elongation of a young shoot is usually concentrated near the shoot apex (tip), which consists of: a **terminal bud** with developing leaves and a compact series of nodes and internodes.

The proximity of the terminal bud is partly responsible for inhibiting the growth of axillary buds, a phenomenon called **apical dominance**. By concentrating resources toward elongation, apical dominance is an evolutionary adaptation that increases the plant's exposure to light. But what if an animal eats the end of the shoot? Or what if, because of obstructions, light is more intense to the side of a plant than directly above it? Under such conditions, axillary buds break dormancy; that is, they start growing. A growing axillary bud gives rise to a lateral shoot, complete with its own terminal bud, leaves, and

axillary buds. Removing the terminal bud usually stimulates the growth of axillary buds, resulting in more lateral shoots. That is why pruning trees and shrubs and "pinching back" houseplants will make them "bushier."

Modified stems with diverse functions have evolved in many plants as environmental adaptations. These modified stems, which include stolons, rhizomes, tubers, and bulbs, are often mistaken for roots (Figure 35.5).

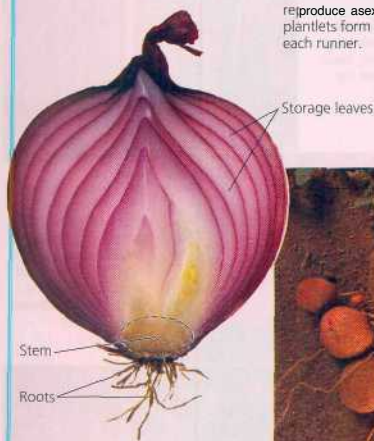
## Leaves

The **leaf** is the main photosynthetic organ of most vascular plants, although green stems also perform photosynthesis. Leaves vary extensively in form but generally consist of a flattened **blade** and a stalk, the **petiole**, which joins the leaf to a node of the stem (see Figure 35.2). Among angiosperms, grasses and many other monocots lack petioles; instead, the base of the leaf forms a sheath that envelops the stem. Some monocots, including palm trees, do have petioles.

Monocots and eudicots differ in the arrangement of veins, the vascular tissue of leaves. Most monocots have parallel major veins that run the length of the leaf blade. In contrast,

► **Figure 35.5 Modified stems.**

(a) **Stolons.** Shown here on a strawberry plant, stolons are horizontal stems that grow along the surface. These "runners" enable a plant to reproduce asexually, as plantlets form at nodes along each runner.

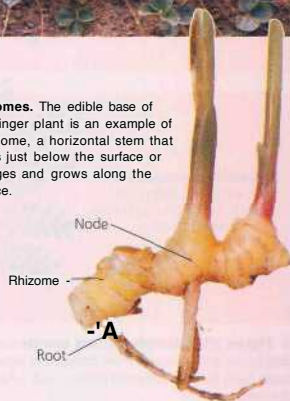


(b) **Bulbs.** Bulbs are vertical, underground shoots consisting mostly of the enlarged bases of leaves that store food. You can see the many layers of modified leaves attached to the short stem by slicing an onion bulb lengthwise.



(c) **Tubers.** Tubers, such as these red potatoes, are enlarged ends of rhizomes specialized for storing food. The "eyes" arranged in a spiral pattern around a potato are clusters of axillary buds that mark the nodes.

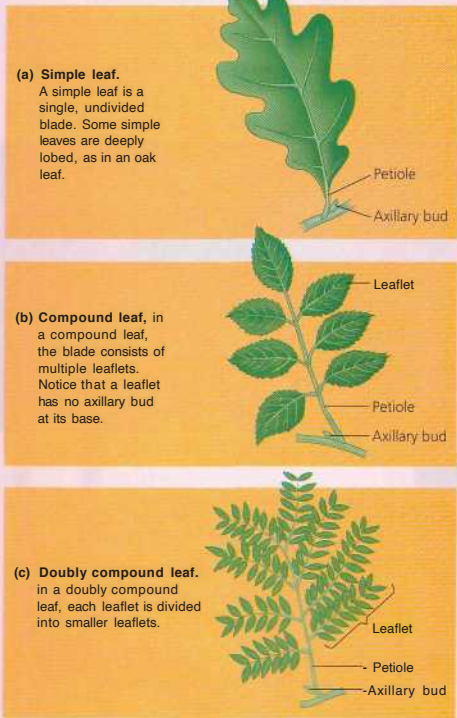
(d) **Rhizomes.** The edible base of this ginger plant is an example of a rhizome, a horizontal stem that grows just below the surface or emerges and grows along the surface.



eudicot leaves generally have a multibranched network of major veins (see Figure 30.12).

In identifying and classifying angiosperms, taxonomists rely mainly on floral morphology, but they also use variations in leaf morphology, such as leaf shape, spatial arrangement of leaves, and the pattern of a leaf's veins. **Figure 35.6 illustrates a difference in leaf shape: simple versus compound leaves. Most very large leaves are compound or doubly compound.** This structural adaptation may enable large leaves to withstand strong wind with less tearing and also confine some pathogens that invade the leaf to a single leaflet, rather than allowing them to spread to the entire leaf.

**Most leaves are specialized for photosynthesis. However, some plant species have leaves that have become adapted by evolution for other functions, such as support, protection, storage, or reproduction (Figure 35.7).**



**A Figure 35.6 Simple versus compound leaves.** You can distinguish simple leaves from compound leaves by looking for axillary buds. Each leaf has only one axillary bud, where the petiole attaches to the stem.

**• Figure 35.7 Modified leaves.**

**(a) Tendrils.** The tendrils by which this pea plant clings to a support are modified leaves. After it has "lassoed" a support, a tendrill forms a coil that brings the plant closer to the support. Tendrils are typically modified leaves, but some tendrils are modified stems, as in grapevines.



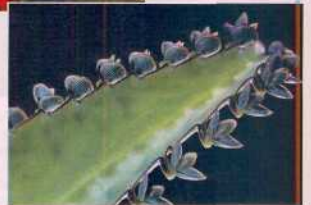
**(b) Spines.** The spines of cacti, such as this prickly pear, are actually leaves, and photosynthesis is carried out mainly by the fleshy green stems.

**(c) Storage leaves.** Most succulents, such as this ice plant, have leaves modified for storing water.



**(d) Bracts.** Red parts of the poinsettia are often mistaken for petals but are actually modified leaves called bracts that surround a group of flowers. Such brightly colored leaves attract pollinators.

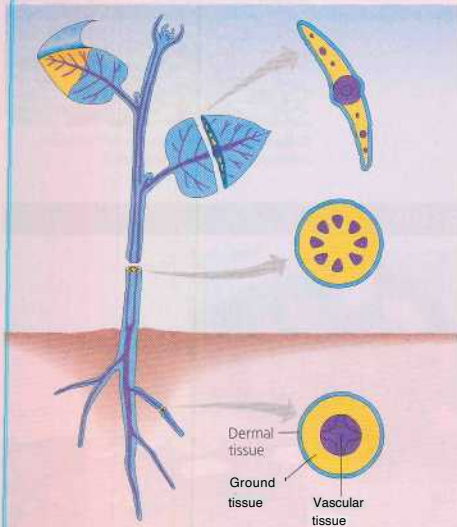
**(e) Reproductive leaves.** The leaves of some succulents, such as *Kalanchoe daigremontiana*, produce adventitious plantlets, which fall off the leaf and take root in the soil.



## The Three Tissue Systems: Dermal, Vascular, and Ground

Each plant organ—root, stem, or leaf—has dermal, vascular, and ground tissues. A tissue system consists of one or more tissues organized into a functional unit connecting the organs of a plant. Each tissue system is continuous throughout the entire plant body, but specific characteristics of the tissues and their spatial relationships to one another vary in different organs (Figure 35.8).

The dermal tissue system is the outer protective covering. Like our skin, it forms the first line of defense against physical damage and pathogenic organisms. In nonwoody plants, the dermal tissue usually consists of a single layer of tightly packed cells called the epidermis. In woody plants, protective tissues known as periderm replace the epidermis in older regions of stems and roots by a process discussed later in the chapter. In addition to protecting the plant from water loss and disease, the epidermis has specialized characteristics in each organ. For example, the root hairs so important in the absorption of water and mineral ions are extensions of epidermal cells near root tips. In the epidermis of leaves and most stems, a wax coating called the cuticle helps prevent water loss—an important adaptation



**▲ Figure 35.8 The three tissue systems.** The dermal tissue system (blue) covers the entire body of a plant. The vascular tissue system (purple) is also continuous throughout the plant, but is arranged differently in each organ. The ground tissue system (yellow), responsible for most of the plant's metabolic functions, is located between the dermal tissue and the vascular tissue in each organ.

to living on land. Later we will look at specialized leaf cells that regulate CO<sub>2</sub> exchange. Leaf trichomes, which are outgrowths of the epidermis, are yet another example of specialization. For instance, trichomes in aromatic leaves such as mint secrete oils that protect plants from herbivores and disease.

The vascular tissue system carries out long-distance transport of materials between roots and shoots. The two vascular tissues are xylem and phloem. Xylem conveys water and dissolved minerals upward from roots into the shoots. Phloem transports organic nutrients such as sugars from where they are made (usually the leaves) to where they are needed—usually roots and sites of growth, such as developing leaves and fruits. The vascular tissue of a root or stem is collectively called the stele (the Greek word for "pillar"). The arrangement of the stele varies, depending on species and organ. In angiosperms, the stele of the root is in the form of a solid central vascular cylinder. In contrast, the stele of stems and leaves is divided into vascular bundles, strands consisting of xylem and phloem. Both xylem and phloem are composed of a variety of cell types, including cells highly specialized for transport.

Tissues that are neither dermal nor vascular are part of the ground tissue system. Ground tissue that is internal to the vascular tissue is called pith, and ground tissue that is external to the vascular tissue is called cortex. The ground tissue system is more than just filler. It includes various cells specialized for functions such as storage, photosynthesis, and support.

## Common Types of Plant Cells

Like any multicellular organism, a plant is characterized by cellular differentiation, the specialization of cells in structure and function. In plant cells, differentiation is sometimes evident within the protoplast, the cell contents exclusive of the cell wall. For example, the protoplasts of some plant cells have chloroplasts, whereas other types of plant cells lack functional chloroplasts. Cell wall modifications also play a role in plant cell differentiation. Figure 35.9, on the next two pages, focuses on some major types of plant cells: parenchyma, collenchyma, sclerenchyma, the water-conducting cells of the xylem, and the sugar-conducting cells of the phloem. Notice the structural adaptations that make specific functions possible. You may wish to review Figures 6.9 and 6.28, which show basic plant cell structure.

## Concept Check 35.1

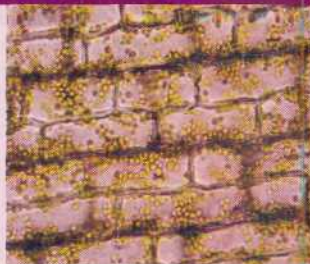
1. How does the vascular tissue system enable leaves and roots to combine functions to support growth and development of the whole plant?
2. Describe at least three specializations in plant organs and plant cells that are adaptations to life on land.
3. Describe the role of each tissue system in a leaf.

For suggested answers, see Appendix A.

## Exploring Examples of Differentiated Plant Cells

## PARENCHYMA CELLS

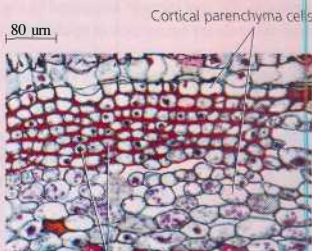
Mature parenchyma cells have primary walls that are relatively thin and flexible, and most lack secondary walls. (See Figure 6.28 to review primary and secondary layers of cell walls.) The protoplast generally has a large central vacuole. Parenchyma cells are often depicted as "typical" plant cells because they appear to be the least specialized structurally. Parenchyma cells perform most of the metabolic functions of the plant, synthesizing and storing various organic products. For example, photosynthesis occurs within the chloroplasts of parenchyma cells in the leaf. Some parenchyma cells in stems and roots have colorless plastids that store starch. The fleshy tissue of a typical fruit is composed mainly of parenchyma cells. Most parenchyma cells retain the ability to divide and differentiate into other types of plant cells under special conditions—during the repair and replacement of organs after injury to the plant, for example. It is even possible in the laboratory to regenerate an entire plant from a single parenchyma cell.



Parenchyma cells in *Echinacea* leaf, with chloroplasts  
50  $\mu\text{m}$

## COLLENGYMA CELLS

Grouped in strands or cylinders, collenchyma cells help support young parts of the plant shoot. Collenchyma cells have thicker primary walls than parenchyma cells, though the walls are unevenly thickened. Young stems and petioles often have strands of collenchyma cells just below their epidermis (the "strings" of a celery stalk, for example). Collenchyma cells lack secondary walls, and the hardening agent lignin is absent in their primary walls. Therefore, they provide flexible support without restraining growth. At functional maturity, collenchyma cells are living and flexible, elongating with the stems and leaves they support—unlike sclerenchyma cells, which we discuss next.

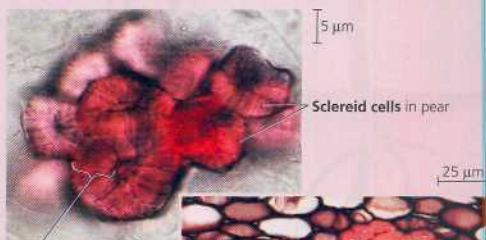


Collenchyma cells (in cortex of *Sambucus*, elderberry, cell walls stained red)  
80  $\mu\text{m}$

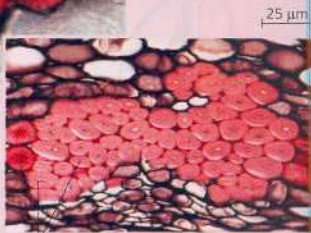
## SCLERENCHYMA CELLS

Also functioning as supporting elements in the plant, but with thick secondary walls usually strengthened by lignin, sclerenchyma cells are much more rigid than collenchyma cells. Mature sclerenchyma cells cannot elongate, and they occur in regions of the plant that have stopped growing in length. Sclerenchyma cells are so specialized for support that many are dead at functional maturity, but they produce secondary walls before the protoplast dies. The rigid walls remain as a "skeleton" that supports the plant, in some cases for hundreds of years. In parts of the plant that are still elongating, the secondary walls of immature sclerenchyma are deposited unevenly in spiral or ring patterns. These forms of cell wall thickenings enable the cell wall to stretch like a spring as the cell elongates.

Two types of sclerenchyma cells called sclereids and fibers are specialized entirely for support and strengthening. Sclereids, which are shorter than fibers and irregular in shape, have very thick, lignified secondary walls. Sclereids impart the hardness to nutshells and seed coats and the gritty texture to pear fruits. Fibers, which are usually arranged in threads, are long, slender, and tapered. Some are used commercially, such as hemp fibers for making rope and flax fibers for weaving into linen.



Sclereid cells in pear  
5  $\mu\text{m}$



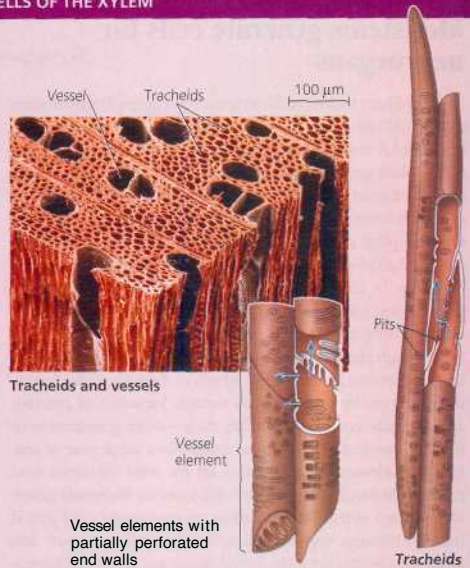
Fiber cells (transverse section from ash tree)  
25  $\mu\text{m}$

## WATER-CONDUCTING CELLS OF THE XYLEM

The two types of water-conducting cells, tracheids and vessel elements, are tubular, elongated cells that are dead at functional maturity. Tracheids are found in the xylem of all vascular plants. In addition to tracheids, most angiosperms, as well as a few gymnosperms and a few seedless vascular plants, have vessel elements. When the protoplast of a tracheid or vessel element disintegrates, the cells thicken cell walls remain behind, forming a nonliving conduit through, which water can flow. The secondary walls of tracheids and vessel elements are often interrupted by pits, thinner regions where only primary walls are present (see Figure 6.18 to review primary and secondary walls). Water can migrate laterally between neighboring cells through pits.

Tracheids are long, thin cells with tapered ends. Water moves from cell to cell mainly through the pits, where it does not have to cross thick secondary walls. The secondary walls of tracheids are hardened with lignin, which prevents collapse under the tensions of water transport and also provides support.

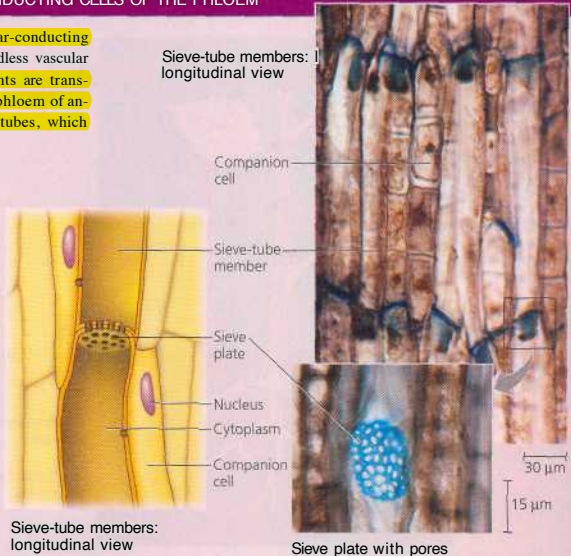
Vessel elements are generally wider, shorter, thinner walled, and less tapered than tracheids. They are aligned end to end, forming long micro-pipes known as vessels. The end walls of vessel elements have perforations, enabling water to flow freely through, the vessels.



## SUGAR-CONDUCTING CELLS OF THE PHLOEM

Unlike the water-conducting cells of the xylem, the sugar-conducting cells of the phloem are alive at functional maturity. In seedless vascular plants and gymnosperms, sugars and other organic nutrients are transported through long, narrow cells called sieve cells. In the phloem of angiosperms, these nutrients are transported through, sieve tubes, which consist of chains of cells called sieve-tube members.

Though alive, sieve-tube members lack such organelles as the nucleus, ribosomes, and a distinct vacuole. This reduction in cell contents enables nutrients to pass more easily through the cell. The end walls between sieve-tube members, called sieve plates, have pores that facilitate the flow of fluid from cell to cell along the sieve tube. Alongside each sieve-tube member is a nonconducting cell called a companion cell, which is connected to the sieve-tube member by numerous channels, the plasmodesmata (see Figure 6.8). The nucleus and ribosomes of the companion cell may serve not only that cell itself but also the adjacent sieve-tube member. In some plants, companion cells in leaves also help load sugars into the sieve-tube members, which then transport the sugars to other parts of the plant.



**University of Anbar**

**3<sup>rd</sup> lecture**

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# **BOTANY**

**BIOLOGY DEPARTMENT**

**1<sup>st</sup> stage**

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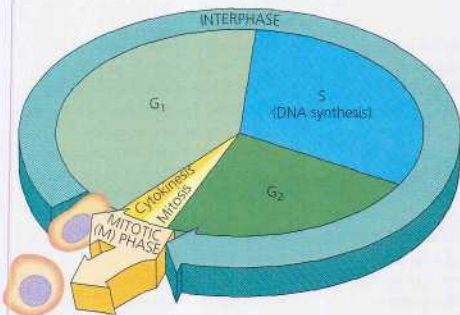
**2021**

## The mitotic phase alternates with interphase in the cell cycle

In 1882, a German anatomist named Walther Flemming developed dyes that allowed him to observe, for the first time, the behavior of chromosomes during mitosis and cytokinesis. (In fact, Flemming coined the terms *mitosis* and *chromatin*.) During the period between one cell division and the next, it appeared to Flemming that the cell was simply growing larger. But we now know that many critical events occur during this stage in the life of a cell.

### Phases of the Cell Cycle

Mitosis is just one part of the cell cycle (Figure 12.5). In fact, the mitotic (M) phase, which includes both mitosis and cytokinesis, is usually the shortest part of the cell cycle. Mitotic cell division alternates with a much longer stage called interphase, which often accounts for about 90% of the cycle. During interphase the cell grows and copies its chromosomes in preparation for cell division. Interphase can be divided into subphases: the G<sub>1</sub> phase ("first gap"), the S phase ("synthesis"), and the G<sub>2</sub> phase ("second gap"). During all three subphases, the cell grows by producing proteins and cytoplasmic organelles such as mitochondria and endoplasmic reticulum. However, chromosomes are duplicated only during the S phase (we discuss synthesis of DNA in Chapter 16). Thus, a cell grows (G<sub>1</sub>), continues to grow as it copies its chromosomes (S), grows more as it completes preparations for cell division (G<sub>2</sub>), and divides (M). The daughter cells may then repeat the cycle.



**Figure 12.5 The cell cycle.** In a dividing cell, the mitotic (M) phase alternates with interphase, a growth period. The first part of interphase, called G<sub>1</sub>, is followed by the S phase, when the chromosomes replicate; the last part of interphase is called G<sub>2</sub>. In the M phase, mitosis divides the nucleus and distributes its chromosomes to the daughter nuclei, and cytokinesis divides the cytoplasm, producing two daughter cells.

A typical human cell might undergo one division in 24 hours. Of this time, the M phase would occupy less than 1 hour, while the S phase might occupy about 10–12 hours, or about half the cycle. The rest of the time would be apportioned between the G<sub>1</sub> and G<sub>2</sub> phases. The G<sub>2</sub> phase usually takes 4–6 hours; in our example, G<sub>1</sub> would occupy about 5–6 hours. G<sub>1</sub> is the most variable in length in different types of cells.

Time-lapse films of living, dividing cells reveal the dynamics of mitosis as a continuum of changes. For purposes of description, however, mitosis is conventionally broken down into five stages: prophase, prometaphase, metaphase, anaphase, and telophase. Overlapping with the latter stages of mitosis, cytokinesis completes the mitotic phase. Figure 12.6, on the next two pages, describes these stages in an animal cell. Be sure to study this figure thoroughly before progressing to the next two sections, which examine mitosis and cytokinesis more closely.

### The Mitotic Spindle: A Closer Look

Many of the events of mitosis depend on the mitotic spindle, which begins to form in the cytoplasm during prophase. This structure consists of fibers made of microtubules and associated proteins. While the mitotic spindle assembles, the other microtubules of the cytoskeleton partially disassemble, probably providing the material used to construct the spindle. The spindle microtubules elongate by incorporating more subunits of the protein tubulin (see Table 6.1).

The assembly of spindle microtubules starts at the centrosome, a nonmembranous organelle that functions throughout the cell cycle to organize the cell's microtubules (it is also called the *microtubule-organizing center*). In animal cells, a pair of centrioles is located at the center of the centrosome, but the centrioles are not essential for cell division, in fact, the centrosomes of most plants lack centrioles, and if the centrioles of an animal cell are destroyed with a laser microbeam, a spindle nevertheless forms during mitosis.

During interphase, the single centrosome replicates, forming two centrosomes, which remain together near the nucleus (see Figure 12.6). The two centrosomes move apart from each other during prophase and prometaphase of mitosis, as spindle microtubules grow out from them. By the end of prometaphase, the two centrosomes, one at each pole of the spindle, are at opposite ends of the cell. An aster, a radial array of short microtubules, extends from each centrosome. The spindle includes the centrosomes, the spindle microtubules, and the asters.

Each of the two sister chromatids of a chromosome has a kinetochore, a structure of proteins associated with specific sections of chromosomal DNA at the centromere. The chromosome's two kinetochores face in opposite directions. During prometaphase, some of the spindle microtubules attach to the kinetochores; these are called kinetochore microtubules. (The number of microtubules attached to a kinetochore varies

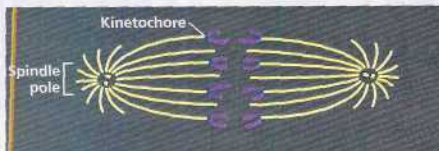


Figure 12.8

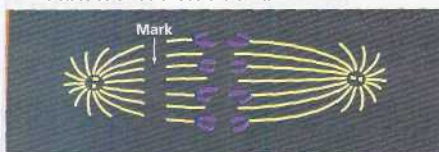
**Inquiry v** During anaphase, do kinetochore microtubules shorten at their spindle pole ends or their kinetochore ends?

**EXPERIMENT**

O The microtubules of a cell in early anaphase were labeled with a fluorescent dye that glows in the microscope (yellow).

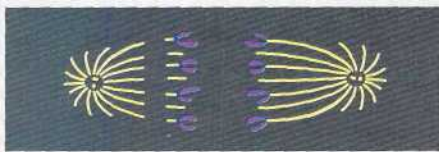


2 (A laser was used to mark the kinetochore microtubules by eliminating the fluorescence in a region between one spindle pole and the chromosomes. As anaphase proceeded, researchers monitored the changes in the lengths of the microtubules on either side of the mark.



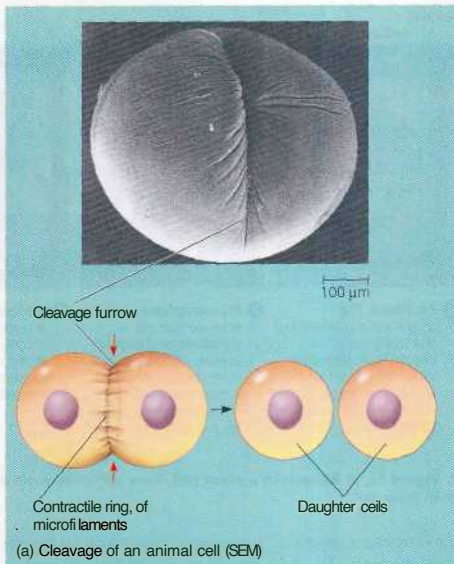
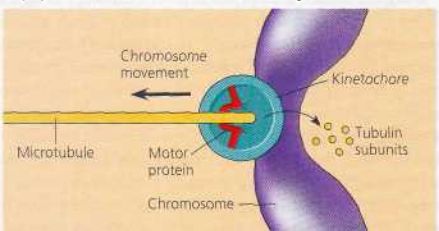
**RESULTS**

As the chromosomes moved toward the poles, the microtubule segments on the kinetochore side of the laser mark shortened, while those on the spindle pole side stayed the same length.

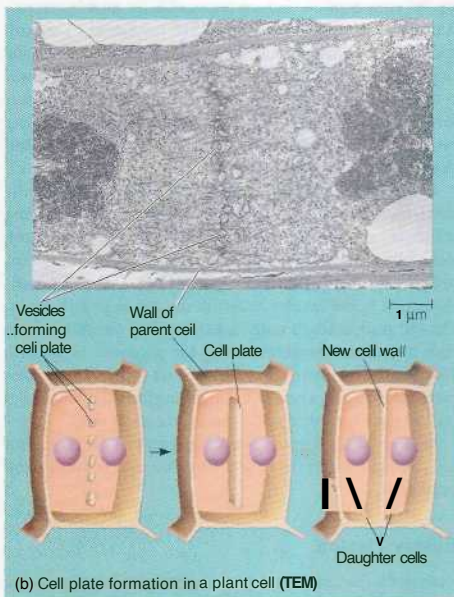


**CONCLUSION**

This experiment demonstrated that during anaphase, kinetochore microtubules shorten at their kinetochore ends, not at their spindle pole ends. This is just one of the experiments supporting the hypothesis that during anaphase, a chromosome tracks along a microtubule as the microtubule depolymerizes at its kinetochore end, releasing tubulin subunits.



(a) Cleavage of an animal cell (SEM)



(b) Cell plate formation in a plant cell (TEM)

▲ Figure 12.9 Cytokinesis in animal and plant cells.



**0 Prophase.** The chromatin is condensing. The nucleolus is beginning to disappear. Although not yet visible in the micrograph, the mitotic spindle is starting to form.

**2 Prometaphase.** We now see discrete chromosomes; each consists of two identical sister chromatids. Later in prometaphase, the nuclear envelope will fragment.

**0 Metaphase.** The spindle is complete, and the chromosomes, attached to microtubules at their kinetochores, are all at the metaphase plate.

**© Anaphase.** The chromatids of each chromosome have separated, and the daughter chromosomes are moving to the ends of the cell as their kinetochore microtubules shorten.

**0 Telophase.** Daughter nuclei are forming. Meanwhile, cytokinesis has started; The cell plate, which will divide the cytoplasm in two, is growing toward the perimeter of the parent cell.

**A Figure 12.10 Mitosis in a plant cell.** These light micrographs show mitosis in cells of an onion root.

the furrow is a contractile ring of actin microfilaments associated with molecules of the protein myosin. (Actin and myosin are the same proteins that are responsible for muscle contraction as well as many other kinds of cell movement.) The actin microfilaments interact with the myosin molecules, causing the ring to contract. The contraction of the dividing cells ring of microfilaments is like the pulling of drawstrings. The cleavage furrow deepens until the parent cell is pinched in two, producing two completely separated cells, each with its own nucleus and share of cytosol and organelles.

Cytokinesis in plant cells, which have cell walls, is markedly different. There is no cleavage furrow. Instead, during telophase, vesicles derived from the Golgi apparatus move along microtubules to the middle of the cell, where they coalesce, producing a cell plate (Figure 12.9b). Cell wall materials carried in the vesicles collect in the cell plate as it grows. The cell plate enlarges until its surrounding membrane fuses with the plasma membrane along the perimeter of the cell. Two daughter cells result, each with its own plasma membrane. Meanwhile, a new cell wall arising from the contents of the cell plate has formed between the daughter cells.

Figure 12.10 is a series of micrographs of a dividing plant cell. Examining this figure will help you review mitosis and cytokinesis.

## Binary Fission

Prokaryotes (bacteria) reproduce by a type of cell division called binary fission, meaning literally "division in half." Most bacterial genes are carried on a single *bacterial chromosome* that consists

of a circular DNA molecule and associated proteins. Although bacteria are smaller and simpler than eukaryotic cells, the problem of replicating their genomes in an orderly fashion and distributing the copies equally to two daughter cells is still formidable. The chromosome of the bacterium *Escherichia coli*, for example, when it is fully stretched out, is about 500 times longer than the length of the cell. Clearly, such a long chromosome must be highly coiled and folded within the cell—and it is.

In *E. coli*, the process of cell division begins when the DNA of the bacterial chromosome begins to replicate at a specific place on the chromosome called the origin of replication, producing two origins. As the chromosome continues to replicate, one origin moves rapidly toward the opposite end of the cell (Figure 12.11). While the chromosome is replicating, the cell elongates. When replication is complete and the bacterium has reached about twice its initial size, its plasma membrane grows inward, dividing the parent *E. coli* cell into two daughter cells. Each cell inherits a complete genome.

Using the techniques of modern DNA technology to tag the origins of replication with molecules that glow green in fluorescence microscopy (see Figure 6.3), researchers have directly observed the movement of bacterial chromosomes. This movement is reminiscent of the poleward movements of the centromere regions of eukaryotic chromosomes during anaphase of mitosis, but bacteria don't have visible mitotic spindles or even microtubules. In most bacterial species studied, the two origins of replication end up at opposite ends of the cell or in some other very specific location, possibly anchored there by one or more proteins. How bacterial chromosomes move and how their specific location is established and maintained are

result: Each cycle of chromosome halving and doubling contributes to genetic variation among offspring. A closer look at meiosis will reveal the sources of this variation.

### Concept Check 13.2

1. How does the karyotype of a human female differ from that of a human male?
2. How does the alternation of meiosis and fertilization in the life cycles of sexually reproducing organisms maintain the normal chromosome count for each species?
2. Dog sperm contain 39 chromosomes. What are the haploid number and diploid number for dogs?
4. What process (meiosis or mitosis) is more directly involved in the production of gametes in animals? In plants and most fungi?

For suggested answers, see Appendix A.

### Concept 13.3

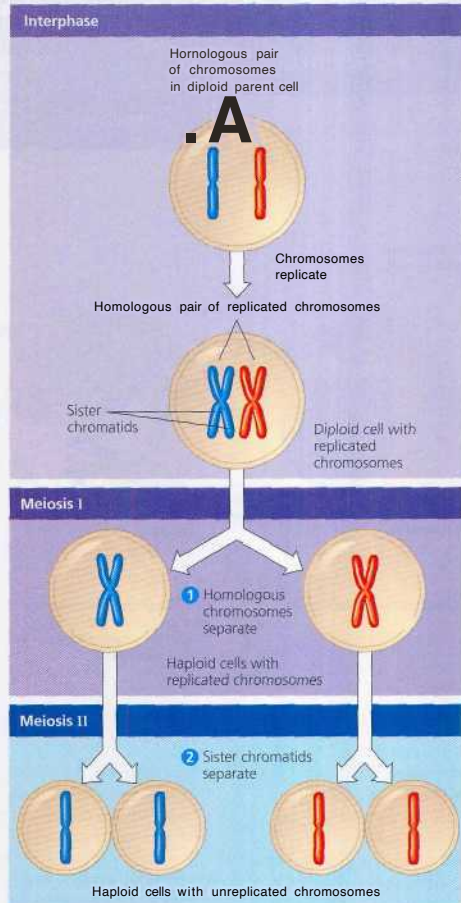
## Meiosis reduces the number of dirosome sets from diploid to haploid

Many of the steps of meiosis closely resemble corresponding steps in mitosis. Meiosis, like mitosis, is preceded by the replication of chromosomes. However, this single replication is followed by two consecutive cell divisions, called meiosis I and meiosis II. These divisions result in four daughter cells (rather than the two daughter cells of mitosis), each with only half as many chromosomes as the parent cell.

### The Stages of Meiosis

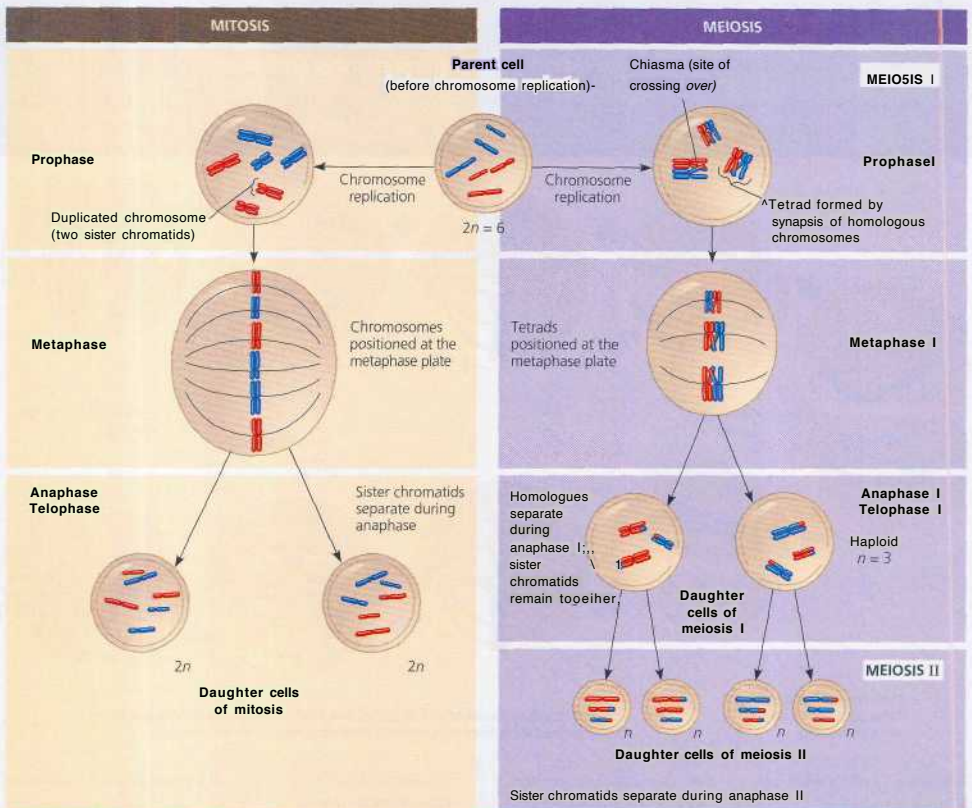
The overview of meiosis in Figure 13.7 shows how both members of a single homologous pair of chromosomes in a diploid cell are replicated and the copies then sorted into four haploid daughter cells. Recall that sister chromatids are two copies of one chromosome, attached at the centromere; together they make up one duplicated chromosome (see Figure 13.4). In contrast, the two chromosomes of a homologous pair are individual chromosomes that were inherited from different parents; they are not usually connected to each other. Homologues appear alike in the microscope, but they may have different versions of genes at corresponding loci (for example, a gene for freckles on one chromosome and a gene for the absence of freckles at the same locus on the homologue).

Figure 13.8, on the next two pages, describes in detail the stages of the two divisions of meiosis for an animal cell whose diploid number is 6. Meiosis halves the total number of chromosomes



**A Figure 13.7 Overview of meiosis: how meiosis reduces chromosome number.** After the chromosomes replicate in interphase, the diploid cell divides twice, yielding four haploid daughter cells. This overview tracks just one pair of homologous chromosomes, which for the sake of simplicity are drawn in the condensed state throughout (they would not normally be condensed during interphase). The red chromosome was inherited from the female parent, the blue chromosome from the male parent.

in a very specific way reducing the number of sets from two to one, with each daughter cell receiving one set of chromosomes. Study Figure 13.8 thoroughly before going on to the next section.



**SUMMARY**

| Property   | Mitosis   | Meiosis  |
|--|---|--|
| DNA replication                                  | Occurs during interphase before mitosis begins  | Occurs during interphase before meiosis I begins   |
| Number of divisions                              | One, including prophase, metaphase, anaphase, and telophase                                   | Two, each including prophase, metaphase, anaphase, and telophase   |
| Synapsis of homologous chromosomes               | Does not occur  | Occurs during prophase I, forming tetrads (groups of four chromatids); is associated with crossing over between non-sister chromatids              |
| Number of daughter cells and genetic composition | Two, each diploid ( $2n$ ) and genetically identical to the parent cell                       | Four, each haploid ( $n$ ), containing half as many chromosomes as the parent cell; genetically different from the parent cell and from each other |
| Role in the animal body                          | Enables multicellular adult to arise from zygote; produces cells for growth and tissue repair | Produces gametes; reduces number of chromosomes by half and introduces genetic variability among the gametes                                       |

**Hi HH**  
 A Figure 13.9 A comparison of mitosis and meiosis.

## Meristems generate cells for new organs

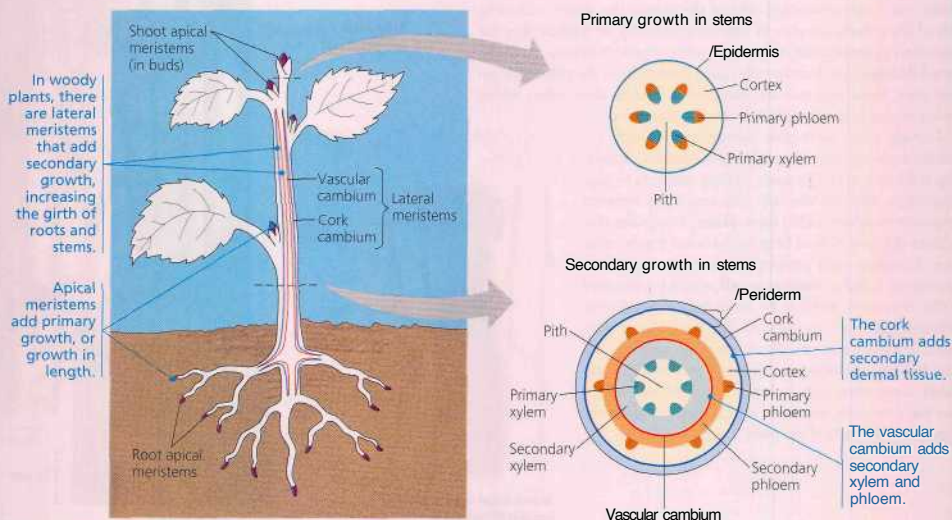
So far, we have looked at the structure and arrangement of plant tissues and cells in mature organs. But how does this organization arise? A major difference between plants and most animals is that plant growth is not limited to an embryonic or juvenile period. Instead, growth occurs throughout the plant's life, a condition known as **indeterminate growth**. At any given time, a typical plant consists of embryonic, developing, and mature organs. Except for periods of dormancy, most plants grow continuously. In contrast, most animals and some plant organs, such as most leaves, undergo **determinate growth**; that is, they cease growing after reaching a certain size.

Although plants continue to grow throughout their lives, they do die, of course. Based on the length of their life cycle, flowering plants can be categorized as annuals, biennials, or perennials. **Annuals** complete their life cycle—from germination to flowering to seed production to death—in a single year or less. Many wildflowers are annuals, as are the most important food crops, including the cereal grains and legumes. **Biennials** generally live two years, often including an intervening cold period (winter) between vegetative growth (first spring/summer) and flowering (second spring/summer). Beets and carrots are bienni-

als but are rarely left in the ground long enough to flower. **Perennials** live many years and include trees, shrubs, and some grasses. Some buffalo grass of the North American plains is believed to have been growing for 10,000 years from seeds that sprouted at the close of the last ice age. When a perennial dies it is not usually from old age, but from an infection or some environmental trauma, such as fire or severe drought.

Plants are capable of indeterminate growth because they have perpetually embryonic tissues called meristems. There are two main types; apical meristems and lateral meristems. **Apical meristems**, located at the tips of roots and in the buds of shoots, provide additional cells that enable the plant to grow in length, a process known as **primary growth**. Primary growth allows roots to extend throughout the soil and shoots to increase exposure to light and CO<sub>2</sub>. In herbaceous (nonwoody) plants, primary growth produces all, or almost all, of the plant body. Woody plants, however, grow in girth in the parts of stems and roots where primary growth has ceased. This growth in thickness, known as **secondary growth**, is caused by the activity of **lateral meristems** called the **vascular cambium** and **cork cambium**. These cylinders of dividing cells extend along the length of roots and stems (Figure 35.10). The **vascular cambium** adds layers of vascular tissue called secondary xylem (wood) and secondary phloem. The **cork cambium** replaces the epidermis with periderm, which is thicker and tougher.

The cells within meristems divide relatively frequently, generating additional cells. Some products of this division



**A Figure 35.10** An overview of primary and secondary growth.

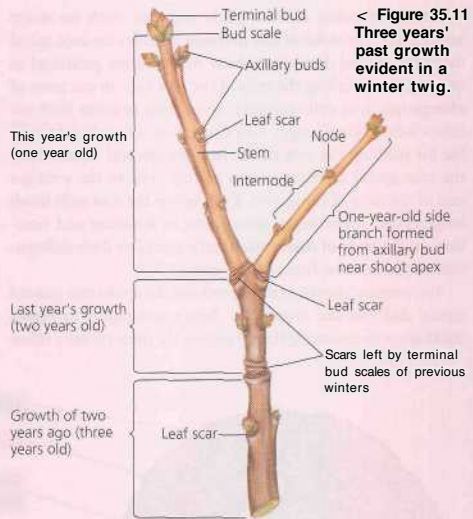
remain in the meristem and produce more cells, while others differentiate and are incorporated into tissues and organs of the growing plant. Cells that remain as sources of new cells are called initials. The new cells displaced from the meristem, called derivatives, continue to divide until the cells they produce become specialized within developing tissues.

In woody plants, primary and secondary growth occur simultaneously but in different locations. Each growing season, primary growth near the apical meristem produces young extensions of roots and shoots, while lateral meristems produce secondary growth that thickens and strengthens other parts of the plant (Figure 35.11). The oldest regions, such as a tree trunk base, have the most accumulation of tissues produced by secondary growth.

### Concept Check 35.2

1. Cells in lower layers of your skin divide and replace dead cells sloughed from the surface. Why is it inaccurate to compare such regions of cell division to a plant meristem?
2. Contrast the types of growth arising from apical and lateral meristems.

For suggested answers, see Appendix A.



< Figure 35.11  
Three years' past growth evident in a winter twig.

### Concept 35.3

## Primary growth lengthens roots and shoots

Primary growth produces the primary plant body, the parts of the root and shoot systems produced by apical meristems. In herbaceous plants, the primary plant body is usually the entire plant. In woody plants, it consists only of the youngest parts, which have not yet become woody. Although apical meristems lengthen both roots and shoots, there are differences in the primary growth of these two systems.

### Primary Growth of Roots

The root tip is covered by a thimble-like root cap, which protects the delicate apical meristem as the root pushes through the abrasive soil during primary growth. The root cap also secretes a polysaccharide slime that lubricates the soil around the root. Growth occurs just behind the root tip, in three zones of cells at successive stages of primary growth. Moving away from the root tip, they are the zones of cell division, elongation, and maturation (Figure 35.12).

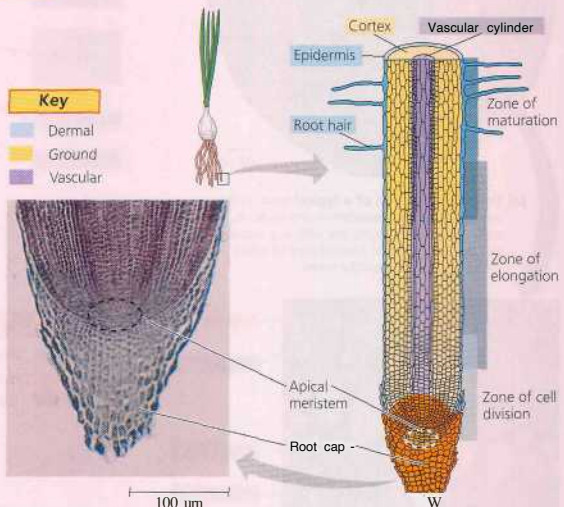


Figure 35.12 Primary growth of a root. The diagram and light micrograph take us into the tip of an onion root. Mitosis is concentrated in the zone of cell division, where the apical meristem and its immediate products are located. The apical meristem also maintains the root cap by generating new cells that replace those that are sloughed off. Most lengthening of the root is concentrated in the zone of elongation. Cells become functionally mature in the zone of maturation. The zones grade into one another without sharp boundaries.

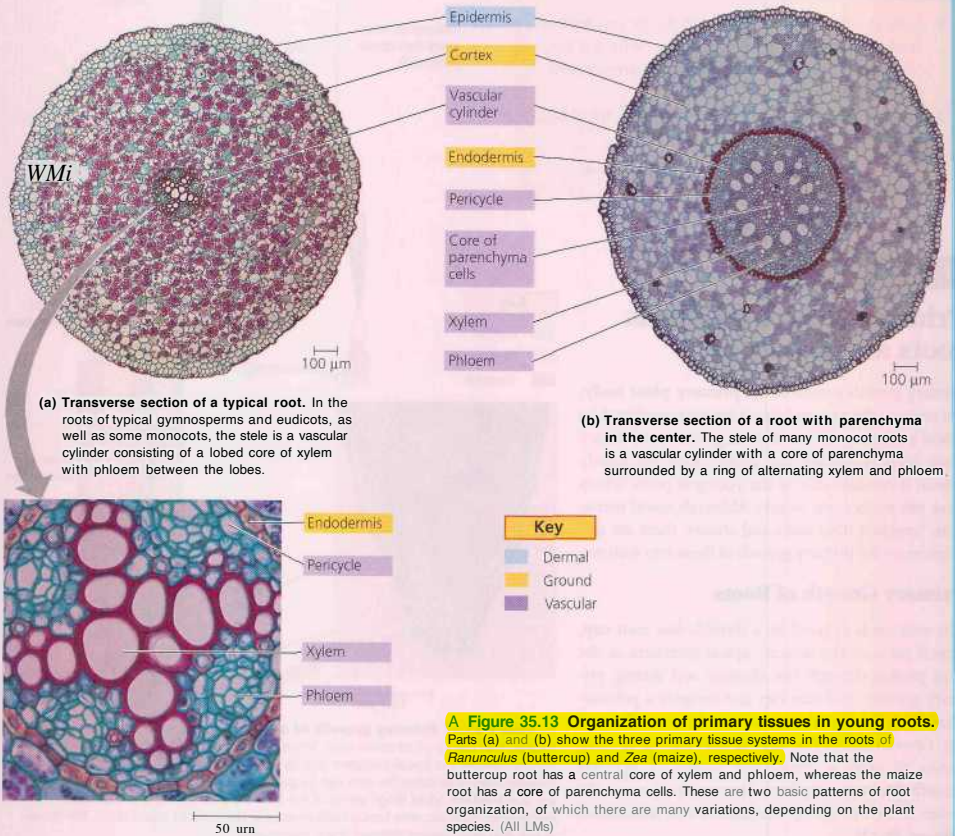
The three zones of cells grade together, with no sharp boundaries. The **zone of cell division** includes the root apical meristem and its derivatives. New root cells are produced in this region, including the cells of the root cap. In the **zone of elongation**, root cells elongate, sometimes to more than ten times their original length. Cell elongation is mainly responsible for pushing the root tip farther into the soil. Meanwhile, the root apical meristem keeps adding cells to the younger end of the zone of elongation. Even before the root cells finish lengthening, many begin specializing in structure and function. In the **zone of maturation**, cells complete their differentiation and become functionally mature.

The primary growth of roots produces the epidermis, ground tissue, and vascular tissue. The light micrographs in Figure 35.13 show in transverse (cross) section the three primary tissue

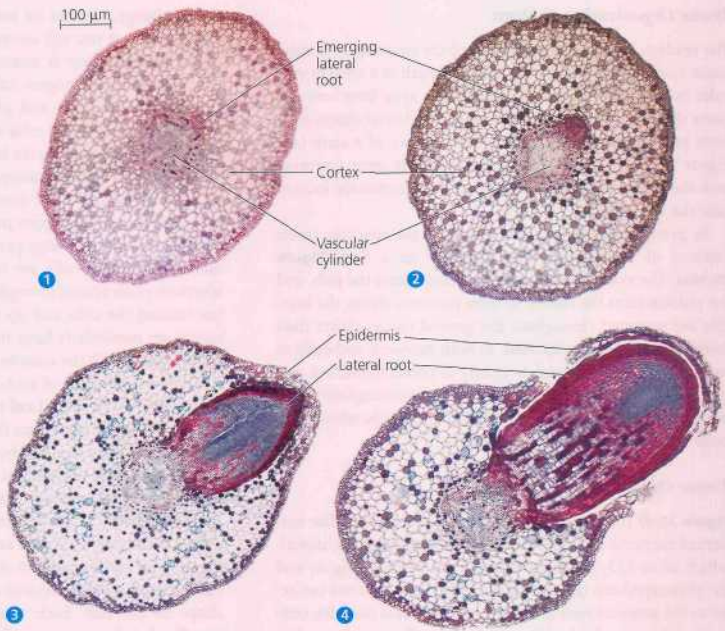
systems in the young roots of a eudicot (*Ranunculus*, buttercup) and a monocot (*Zea*, maize). Water and minerals absorbed from the soil must enter through the epidermis, a single layer of cells covering the root. Root hairs enhance this process by greatly increasing the surface area of epidermal cells.

In most roots, the stele is a vascular cylinder, a solid core of xylem and phloem (see Figure 35.13a). The xylem radiates from the center in two or more spokes, with phloem developing in the wedges between the spokes. In many monocot roots, the vascular tissue consists of a central core of parenchyma cells surrounded by alternating rings of xylem and phloem (see Figure 35.13b). The central region is often called pith but should not be confused with stem pith, which is ground tissue.

The ground tissue of roots, consisting mostly of parenchyma cells, fills the cortex, the region between the vascular cylinder



► **Figure 35.14** The formation of a lateral root. A lateral root originates in the pericycle, the outermost layer of the vascular cylinder of a root, and grows out through the cortex and epidermis, in this series of micrographs, the view of the original root is a transverse section, while the view of the lateral root is a longitudinal section.



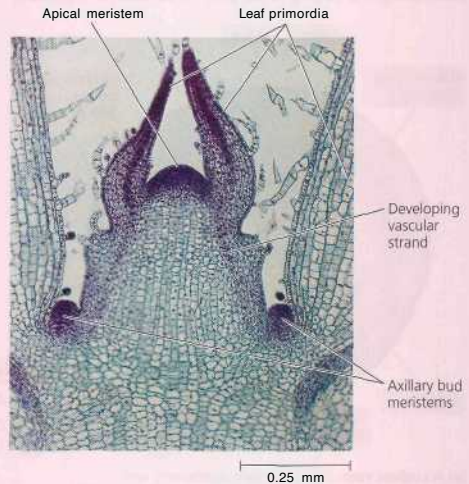
and epidermis. Cells within the ground tissue store organic nutrients, and their plasma membranes absorb minerals from the soil solution. The innermost layer of the cortex is called the endodermis, a cylinder one cell thick that forms the boundary with the vascular cylinder. You will learn in Chapter 36 how the endodermis is a selective barrier regulating passage of substances from the soil solution into the vascular cylinder.

Lateral roots arise from within the pericycle, the outermost cell layer in the vascular cylinder (see Figure 35.13). A lateral root elongates and pushes through the cortex and epidermis until it emerges from the established root (Figure 35.14). It cannot originate near the root's surface because it must remain connected with the vascular cylinder of the established root as part of the continuous vascular tissue system.

### Primary Growth of Shoots

A shoot apical meristem is a dome-shaped mass of dividing cells at the tip of the terminal bud (Figure 35.15). Leaves arise as leaf primordia (singular, *primordium*), finger-like projections along the flanks of the apical meristem. Axillary buds develop from islands of meristematic cells left by the apical meristem at the bases of the leaf primordia. Axillary buds can form lateral shoots at some later time (see Figure 35.2).

Within a bud, leaf primordia are crowded close together because internodes are very short. Most of the actual elongation of the shoot occurs by the growth in length of slightly longer internodes below the shoot apex. This growth is due to cell division and cell elongation within the internode. The plants, including grasses, elongate all along the shoot because there are meristematic regions called intercalary meristems at the base of each leaf. That is why grass continues to grow after being mowed.



► **Figure 35.15** The terminal bud and primary growth of a shoot. Leaf primordia arise from the flanks of the apical dome. This is a longitudinal section of the shoot tip of *Coleus* (LM).



## Tissue Organization of Stems

The epidermis covers stems as part of the continuous dermal tissue system. Vascular tissue runs the length of a stem in vascular bundles. Unlike lateral roots, which arise from vascular tissue deep within a root (see Figure 35.14), lateral shoots arise from preexisting axillary buds on the surface of a stem (see Figure 35.15). The vascular bundles of the stem converge with the roots vascular cylinder in a zone of transition located near the soil surface.

In gymnosperms and most eudicots, the vascular tissue consists of vascular bundles arranged in a ring (Figure 35.16a). The xylem in each vascular bundle faces the pith, and the phloem faces the cortex. In most monocot stems, the bundles are scattered throughout the ground tissue, rather than forming a ring (Figure 35.16b). In both monocot and eudicot stems, ground tissue consists mostly of parenchyma, but collenchyma cells just beneath the epidermis strengthen many stems. Sclerenchyma cells, specifically fiber cells within vascular bundles, also provide support.

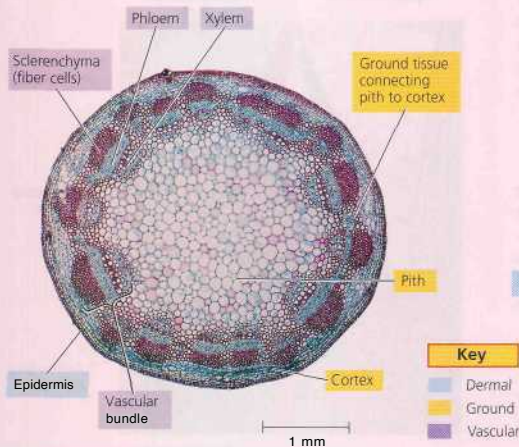
## Tissue Organization of Leaves

Figure 35.17 provides an overview of leaf structure. The epidermal barrier is interrupted by the stomata (singular, *stoma*), which allow CO<sub>2</sub> exchange between the surrounding air and the photosynthetic cells inside the leaf. The term *stoma* can refer to the stomatal pore or to the entire stomatal complex consisting of a pore flanked by two guard cells, which regulate the opening and closing of the pore. In addition to regulating

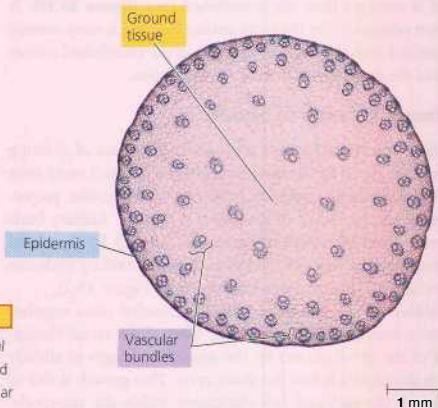
CO<sub>2</sub> exchange, stomata are major avenues for the evaporation of water, as you will see in Chapter 36.

The ground tissue is sandwiched between the upper and lower epidermis, a region called the **mesophyll** (from the Greek *mesos*, middle, and *phyll*, leaf). **Mesophyll** consists mainly of parenchyma cells specialized for photosynthesis. The leaves of many eudicots have two distinct areas: palisade mesophyll and spongy mesophyll. The palisade mesophyll, or palisade parenchyma, consists of one or more layers of elongated cells on the upper part of the leaf. The spongy mesophyll, also called spongy parenchyma, is below the palisade mesophyll. These cells are more loosely arranged, with a labyrinth of air spaces through which CO<sub>2</sub> and oxygen circulate around the cells and up to the palisade region. The air spaces are particularly large in the vicinity of stomata, where gas exchange with the outside air occurs.

The vascular tissue of each leaf is continuous with the vascular tissue of the stem. Leaf traces, connections from vascular bundles in the stem, pass through petioles and into leaves. Veins are the leaf's vascular bundles, which subdivide repeatedly and branch throughout the mesophyll. This network brings xylem and phloem into close contact with the photosynthetic tissue, which obtains water and minerals from the xylem and loads its sugars and other organic products into the phloem for shipment to other parts of the plant. The vascular structure also functions as a skeleton that reinforces the shape of the leaf. Each vein is enclosed by a protective bundle sheath, consisting of one or more cell layers, usually consisting of parenchyma.



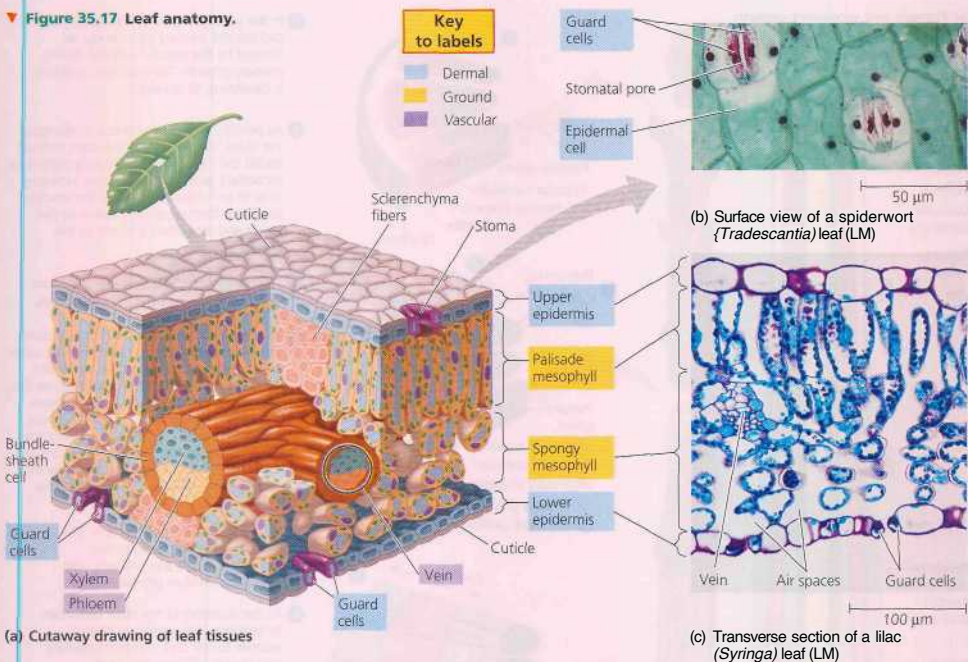
**(a) A eudicot stem.** A eudicot stem (sunflower), with vascular bundles forming a ring. Ground tissue toward the inside is called pith, and ground tissue toward the outside is called cortex. (LM of transverse section)



**(b) A monocot stem.** A monocot stem (maize) with vascular bundles scattered throughout the ground tissue. In such an arrangement, ground tissue is not partitioned into pith and cortex. (LM of transverse section)

## A Figure 35.16 Organization of primary tissues in young stems.

▼ **Figure 35.17 Leaf anatomy.**



### Concept Check 35.3

1. Describe how roots and shoots differ in their branching.
2. Contrast primary growth in roots and shoots.
3. Describe the functions of leaf veins.

For suggested answers, see Appendix A.

### Concept 35.4

## Secondary growth adds girth to stems and roots in woody plants

Secondary growth, the growth in thickness produced by lateral meristems, occurs in stems and roots of woody plants, but rarely in leaves. The secondary plant body consists of the tissues produced by the vascular cambium and cork cambium. The vascular cambium adds secondary xylem (wood) and secondary phloem. Cork cambium produces a tough, thick covering consisting mainly of cork cells.

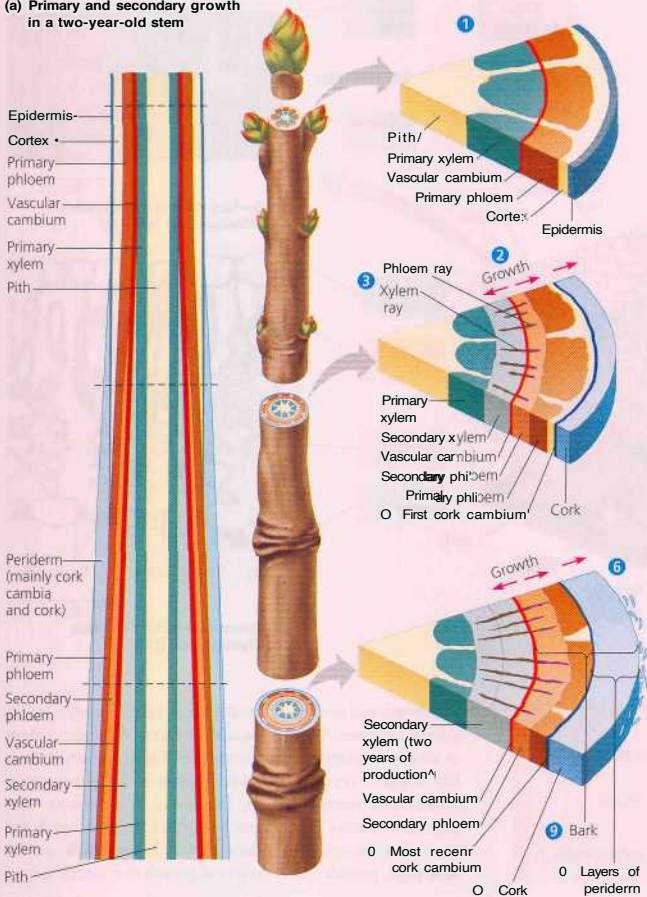
Primary and secondary growth occur simultaneously but in different regions. While an apical meristem elongates a stem or root, secondary growth commences where primary growth has stopped, occurring in older regions of all gymnosperm species and many eudicots, but rarely in monocots. The process is similar in stems and roots, which look much the same after extensive secondary growth. **Figure 35.18, on the next page, provides an overview of growth in a woody stem.**

### The Vascular Cambium and Secondary Vascular Tissue

The vascular cambium is a cylinder of meristematic cells one cell thick. It increases in circumference and also lays down successive layers of secondary xylem to its interior and secondary phloem to its exterior, each layer with a larger diameter than the previous layer (see Figure 35.18). In this way, it is primarily responsible for the thickening of a root or stem.

The vascular cambium develops from undifferentiated cells and parenchyma cells that regain the capacity to divide. In a typical gymnosperm or woody eudicot stem, the vascular cambium forms in a layer between the primary xylem and primary phloem of each vascular bundle and in the ground tissue between the bundles. The meristematic bands within and between the

**(a) Primary and secondary growth in a two-year-old stem**



Q In the youngest part of the stem, you can see the primary plant body, as formed by the apical meristem during primary growth. The vascular cambium is beginning to **tear**.

Q As primary growth continues to elongate the stem, the portion of the stem formed earlier the same year has already started its secondary growth. This portion increases in girth as fusiform initials of the vascular cambium form secondary xylem to the inside and secondary phloem to the outside.

O The ray initials of the vascular cambium give rise to the xylem and phloem rays.

O As the diameter of the vascular cambium increases, the secondary phloem and other tissues external to the cambium cannot keep pace with the expansion because the cells no longer divide. As a result, these tissues, including the epidermis, rupture. A second lateral meristem, the cork cambium, develops from parenchyma cells in the cortex. The cork cambium produces cork cells, which replace the epidermis.

O In year 2 of secondary growth, the vascular cambium adds to the secondary xylem and phloem, and the cork cambium produces cork.

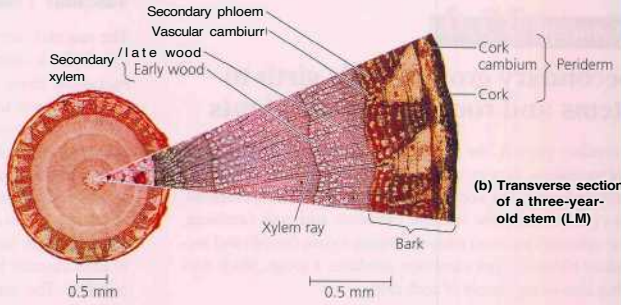
O As the diameter of the stem continues to increase, the outermost tissues exterior to the cork cambium rupture and slough off from the stem.

O Cork cambium re-forms in progressively deeper layers of the cortex. When none of the original cortex is left, the cork cambium develops from parenchyma cells in the secondary phloem.

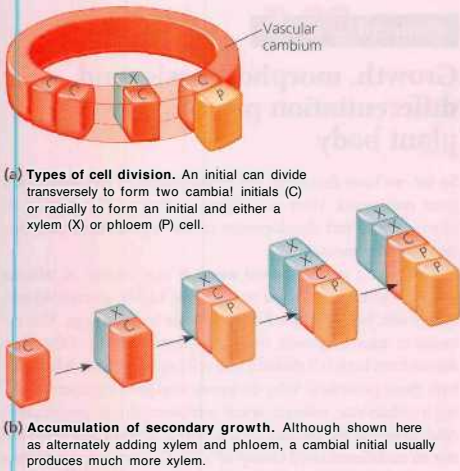
O Each cork cambium and the tissues it produces form a layer of periderm.

O Bark consists of all tissues exterior to the vascular cambium.

**A Figure 35,18 Primary and secondary growth of a stem.** You can track the progress of secondary growth by examining the sections through sequentially older parts of the stem. (You would observe the same changes if you could follow the youngest region, near the apex, for the next three years.)



**(b) Transverse section of a three-year-old stem (LM)**



**Figure 35.19** Cell division in the vascular cambium.

Vascular bundles unite to become a continuous cylinder of dividing cells. In a typical gymnosperm or woody eudicot root, the vascular cambium forms in segments between the primary phloem, the lobes of primary xylem, and the pericycle, eventually becoming a cylinder.

Viewed in transverse section, the vascular cambium appears as a ring, with interspersed regions of cells called fusiform initials and ray initials. When these initials divide, they increase the circumference of the cambium itself and add secondary xylem to the inside of the cambium and secondary phloem to the outside (Figure 35.19). Fusiform initials produce elongated cells such as the tracheids, vessel elements, and fibers of the xylem, as well as the sieve-tube members, companion cells, parenchyma, and fibers of the phloem. They have tapered (fusiform) ends and are oriented parallel to the axis of a stem or root. Ray initials, which are shorter and oriented perpendicular to the stem or root axis, produce vascular rays—radial files consisting mainly of parenchyma cells. Vascular rays are living avenues that move water and nutrients between the secondary xylem and secondary phloem. They also store starch and other organic nutrients. The portion of a vascular ray tested in the secondary xylem is known as a xylem ray. The portion located in the secondary phloem is called a phloem ray.

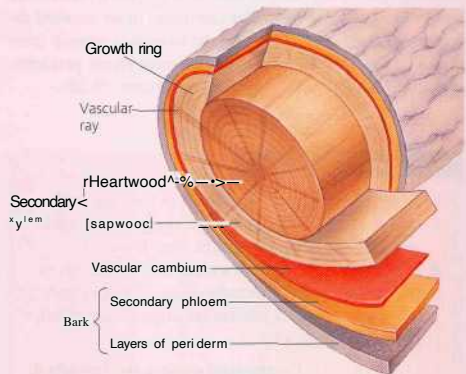
As secondary growth continues over the years, layers of secondary xylem (wood) accumulate, consisting mainly of tracheids, vessel elements, and fibers (see Figure 35.9). Gymnosperms have tracheids, whereas angiosperms have both tracheids and vessel elements. Dead at functional maturity, both types of cells have thick, lignified walls that give wood its hardness and strength. Tracheids and vessel elements that develop

early in the growing season, typically in early spring, are known as early wood and usually have relatively large diameters and thin cell walls (see Figure 35.18b). This structure maximizes delivery of water to new, expanding leaves. Tracheids and vessel elements produced later in the growing season, during late summer or early fall, are known as late wood. They are thick-walled cells that do not transport as much water but do add more support than do the thinner-walled cells of early wood.

In temperate regions, secondary growth in perennial plants is interrupted each year when the vascular cambium becomes dormant during winter. When growth resumes the next spring, the boundary between the large cells of the new early wood and the smaller cells of the late wood produced during the previous growing season is usually a distinct ring in the transverse sections of most tree trunks and roots. Therefore, a tree's age can be estimated by counting its annual rings. The rings can have varying thicknesses, reflecting the amount of seasonal growth.

As a tree or woody shrub ages, the older layers of secondary xylem no longer transport water and minerals (xylem sap). These layers are called heartwood because they are closer to the center of a stem or root (Figure 35.20). The outer layers still transport xylem sap and are therefore known as sapwood. That is why a large tree can still survive even if the center of its trunk is hollow. Because each new layer of secondary xylem has a larger circumference, secondary growth enables the xylem to transport more sap each year, supplying an increasing number of leaves. Heartwood is generally darker than sapwood because of resins and other compounds that clog the cell cavities and help protect the core of the tree from fungi and wood-boring insects.

Only the youngest secondary phloem, closest to the vascular cambium, functions in sugar transport. As a stem or root increases in circumference, the older secondary phloem is sloughed off, which is why secondary phloem does not accumulate as extensively as does secondary xylem.



**Figure 35.20** Anatomy of a tree trunk.

# 36

## Transport in Vascular Plants



A Figure 36.1 Coast redwoods (*Sequoia sempervirens*).

### Key Concepts

- 36.1 Physical processes drive the transport of materials in plants over a range of distances
- 36.2 Roots absorb water and minerals from the soil
- 36.3 Water and minerals ascend from roots to shoots through the xylem
- 36.4 Stomata help regulate the rate of transpiration
- 36.5 Organic nutrients are translocated through the phloem

### Overview

#### Pathways for Survival

The algal ancestors of plants absorbed water, minerals, and  $CO_2$  directly from the water in which they were immersed; none of their cells were far from these ingredients. Bryophytes also lack an extensive transport system and are confined to living in very moist environments. For vascular plants, in contrast, the evolutionary journey onto land involved the differentiation of the plant body into roots and shoots. **Roots absorb water and minerals from the soil, and shoots absorb light and atmospheric  $CO_2$  for photosynthesis.**

**Xylem transports water and minerals from roots to shoots. Phloem transports sugars from where they are produced or stored to where they are needed for growth and metabolism.** Such transport, which is necessary for a plant to function as a whole, may occur over long distances. For example, the highest leaves of some coast redwoods are more than 100 m (over 300 feet) from the roots (Figure 36.1). What enables a vascular plant to conduct water, minerals, and organic nutrients over such long distances? The mechanisms responsible for internal transport are the subject of this chapter.

### Concept 36.1

#### Physical forces drive the transport of materials in plants over a range of distances

Transport in vascular plants occurs on three scales: (1) transport of water and solutes by individual cells, such as root hairs; (2) short-distance transport of substances from cell to cell at the levels of tissues and organs, such as the loading of sugar from photosynthetic leaf cells into the sieve tubes of the phloem; and (3) long-distance transport within xylem or phloem at the level of the whole plant. A variety of physical processes are involved in these different types of transport. **Figure 36.2** provides an overview of long-distance transport in a vascular plant.

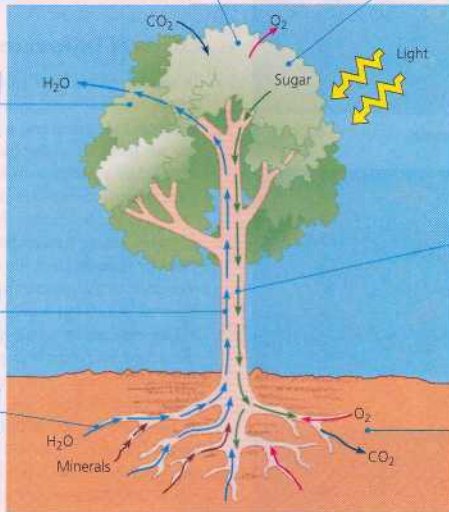
#### Selective Permeability of Membranes: A Review

We covered the transport of solutes and water across biological membranes in detail in Chapter 7. Here we reexamine a few of these transport processes in the specific context of plant cells. The selective permeability of a plant cell's plasma membrane controls the movement of solutes into and out of the cell. Recall from Chapter 7 that solutes tend to diffuse down their gradients and that diffusion across a membrane is called passive transport because it happens without the cell directly using metabolic energy. Active transport is the pumping of solutes across membranes against their electrochemical gradients, the combined effects of the concentration gradient of the solute and the voltage (charge difference) across the membrane. It is called "active" because the cell must expend energy.

0 Through stomata, leaves take in  $\text{CO}_2$  and expel  $\text{O}_2$ . The  $\text{CO}_2$  provides carbon for photosynthesis. Some  $\text{O}_2$  produced by photosynthesis is used in cellular respiration.

0 Sugars are produced by photosynthesis in the leaves.

3 Transpiration, the loss of water from leaves (mostly through stomata), creates a force within leaves that pulls xylem sap upward.



0 Sugars are transported as phloem sap to roots and other parts of the plant.

0 Water and minerals are transported upward from roots to shoots as xylem sap.

0 Roots absorb water and dissolved minerals from the soil.

0 Roots exchange gases with the air spaces of soil, taking in  $\text{O}_2$  and discharging  $\text{CO}_2$ . In cellular respiration,  $\text{O}_2$  supports the breakdown of sugars.

▲ **Figure 36.2 An overview of transport in a vascular plant.**

energy, usually in the form of ATP, to transport a solute "uphill" — counter to the net direction in which the solute diffuses.

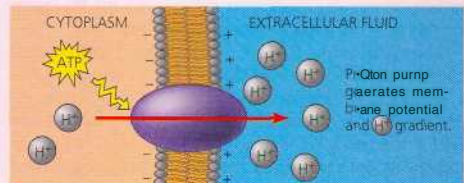
Most solutes cannot cross the lipid bilayer of the membrane; they must pass through **transport proteins** embedded in the membrane. Some transport proteins bind selectively to a solute on one side of the membrane and release the solute on the opposite side. Other transport proteins provide selective channels across the membrane. For example, membranes of most plant cells have potassium channels that allow potassium ions ( $\text{K}^+$ ) to pass, but not other ions, such as sodium ( $\text{Na}^+$ ). Later in this chapter, we will discuss how  $\text{K}^+$  channels in guard cells function in the opening and closing of stomata. Some channels are gated, opening or closing in response to certain stimuli.

## The Central Role of Proton Pumps

The most important active transport protein in the plasma membranes of plant cells is the **proton pump**, which uses energy from ATP to pump hydrogen ions ( $\text{H}^+$ ) out of the cell. This results in a proton gradient with a higher  $\text{H}^+$  concentration outside the cell than inside (Figure 36.3). The gradient is a form of potential (stored) energy because the hydrogen ions tend to diffuse "downhill" back into the cell, and this "flow" of  $\text{H}^+$  can be harnessed to do work. And because the proton

pump moves positive charge, in the form of  $\text{H}^+$ , out of the cell, the pump also contributes to a voltage known as a membrane potential, a separation of opposite charges across a membrane. Proton pumping makes the inside of a plant cell negative in charge relative to the outside. This voltage is called a membrane potential because the charge separation is a form of potential energy that can be harnessed to perform cellular work.

Plant cells use energy stored in the proton gradient and membrane potential to drive the transport of many different solutes. For example, the membrane potential generated by proton pumps contributes to the uptake of  $\text{K}^+$  by root cells



▲ **Figure 36.3 Proton pumps provide energy for solute transport.** By pumping  $\text{H}^+$  out of the cell, proton pumps produce an  $\text{H}^+$  gradient and a charge separation called a membrane potential. These two forms of potential energy can be used to drive the transport of solutes.

long-distance transport. Transpiration, the evaporation of water from a leaf, reduces pressure in the leaf xylem. This creates a tension that pulls xylem sap upward from the roots.

If you have ever dealt with a partially clogged drain, you know that the volume of flow through a pipe depends on the pipe's internal diameter. Clogs reduce flow because they reduce the effective diameter of the drainpipe. Such household experiences help us understand how the unusual structures of plant cells specialized for bulk flow—the sieve-tube members of the phloem and the tracheids and vessel elements of the xylem—fit their function. Recall from Chapter 35 that the cytoplasm of sieve-tube members is almost devoid of internal organelles and that mature tracheids and vessel elements, being dead cells, have no cytoplasm. Like unplugging a kitchen drain, loss of cytoplasm in a plants "plumbing" allows for efficient bulk flow through the xylem and phloem. Bulk flow is also enhanced by the perforated end walls of vessel elements and the porous plates connecting sieve-tube members (see Figure 35.9).

Now that we have an overview of the basic mechanisms of transport at the cellular, tissue, and whole-plant levels, we will look more closely at how these mechanisms work together. For example, bulk flow due to a pressure difference is the mechanism of long-distance transport of phloem sap, but it is active transport of sugar at the cellular level that maintains this pressure difference. The four transport functions we will examine in more detail are the absorption of water and minerals by roots, the ascent of xylem sap, the control of transpiration, and the transport of organic nutrients within phloem.

### Concept Check 36.1

1. Some farmers throughout the world irrigate crops using groundwater, which has a relatively high content of dissolved salts. How might this practice affect water potential in crops?
2. If a plant cell immersed in distilled water has a  $\Psi$  of  $-0.7$  MPa and a  $\Psi_s$  of  $0$  MPa, what is the cell's  $\Psi_w$ ? If you put the same cell in an open beaker of solution that has a  $\Psi_r$  of  $-0.4$  MPa, what would be the cell's  $\Psi_p$  at equilibrium?

*For suggested answers, see Appendix A.*

### Concept 36.2

## Roots absorb water and minerals from the soil

Water and mineral salts from the soil enter the plant through the epidermis of roots, cross the root cortex, pass into the vascular cylinder, and then flow up tracheids and vessels to the

shoot system. This section focuses on short-distance transport between cells in the soil-to-xylem pathway. As you read, use Figure 36.9 to reinforce your understanding.

## The Roles of Root Hairs, Mycorrhizae, and Cortical Cells

Much of the absorption of water and minerals occurs near root tips, where the epidermis is permeable to water and where root hairs are located. Root hairs, which are extensions of epidermal cells, account for much of the surface area of roots (see Figure 35.12). Soil particles, usually coated with water and dissolved minerals, adhere tightly to the root hairs. The soil solution flows into the hydrophilic walls of epidermal cells and passes freely along the apoplast into the root cortex. This exposes the symplast of all the cells of the cortex to the soil solution, providing a much greater surface area of membrane than the surface area of the epidermis alone.

As the soil solution moves along the apoplast into the roots, cells of the epidermis and cortex take up water and certain solutes into the symplast. Although the soil solution is usually very dilute, active transport enables roots to accumulate essential minerals, such as  $K^+$ , to concentrations hundreds of times higher than in the soil.

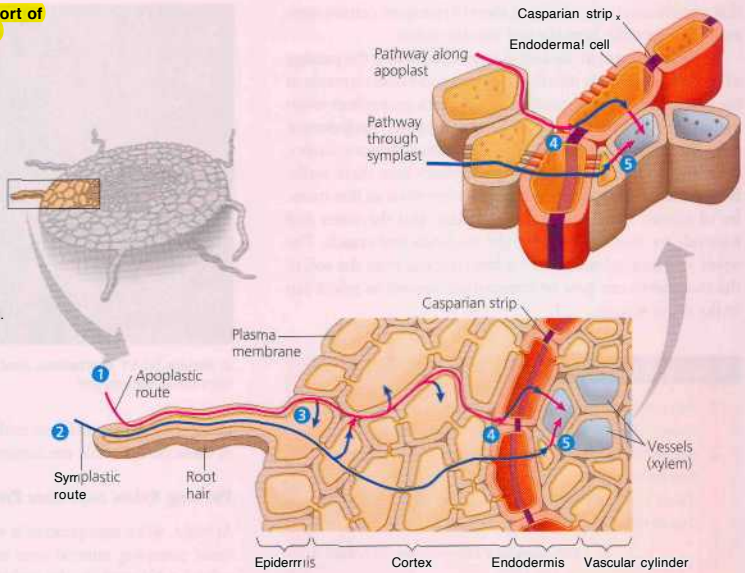
Most plants form mutually beneficial relationships with fungi, which facilitate the absorption of water and minerals from the soil. Roots and fungi form mycorrhizae, symbiotic structures consisting of plant roots united with fungal hyphae (filaments) (Figure 36.10). The hyphae absorb water and selected minerals, transferring much of these resources to the host plant. Chapter 37 highlights the role of mycorrhizae in plant nutrition, and Chapter 31 features the fungal partners in these mutualistic relationships. What is important to understand here is that the mycelium (network of hyphae) of the fungus endows mycorrhizae, and thus the plant roots, with an enormous surface area for absorption. As much as 3 m of hyphae can extend from each centimeter along a root's length, reaching a far greater volume of soil than the root alone could penetrate. Mycorrhizae enable even older regions of roots, kilometers from the root tips, to supply water and minerals to the plant.

## The Endodermis: A Selective Sentry

Water and minerals that pass from the soil into the root cortex cannot be transported to the rest of the plant until they enter the xylem of the vascular cylinder. The endodermis, the innermost layer of cells in the root cortex, surrounds the vascular cylinder and functions as a last checkpoint for the selective passage of minerals from the cortex into the vascular tissue (see Figure 36.9). Minerals already in the symplast when they reach the endodermis continue through the plasmodesmata of endodermal cells and pass into the vascular cylinder. These minerals were already screened by the selective membranes they had to cross to enter the symplast in the epidermis c

**Figure 36.9 Lateral transport of minerals and water in roots.**

- Uptake of soil solution by the hydrophilic walls of root hairs provides access to the apoplast. Water and minerals can then soak into the cortex along this matrix of walls.
- Minerals and water that cross the plasma membranes of root hairs enter the symplast.
- As soil solution moves along the apoplast, some water and minerals are transported into the protoplasts of cells of the epidermis and cortex and then move inward via the symplast.
- Within the transverse and radial walls of each endodermal cell is the Casparian strip, a belt of waxy material (purple band) that blocks the passage of water and dissolved minerals. Only minerals already in the symplast or entering that pathway by crossing the plasma membrane of an endodermal cell can detour around the Casparian strip and pass into the vascular cylinder.



- Endodermal cells and also parenchyma cells within the vascular cylinder discharge water and minerals into their walls (apoplast). The xylem vessels transport the water and minerals upward into the shoot system.

cortex- Those minerals that reach the endodermis via the apoplast encounter a dead end that, blocks their passage into the vascular cylinder: In the transverse and radial walls of each endodermal cell is the Casparian strip, a belt made of suberin, a waxy material impervious to water and dissolved minerals. Thus, water and minerals cannot cross the endodermis and enter vascular tissue via the apoplast. The only way past this barrier is for the water and minerals to cross the plasma membrane of an endodermal cell and enter the vascular cylinder via the symplast.

The endodermis, with its Casparian strip, ensures that no minerals can reach the vascular tissue of the root without crossing a selectively permeable plasma membrane. If minerals do not enter the symplast of cells in the epidermis or cortex, they must enter endodermal cells or be excluded from the vascular tissue. The endodermis also prevents solutes that have been accumulated in the xylem sap from leaking back into the soil solution. The structure of the endodermis and its strategic location in the root fit its function as sentry of the border between the cortex and the vascular cylinder, a function



**A Figure 36.10 Mycorrhizae, symbiotic associations of fungi and roots.** The white mycelium of the fungus ensheathes these roots of a pine tree. The fungal hyphae provide an extensive surface area for the absorption of water and minerals.



that contributes to the ability of roots to transport certain minerals preferentially from the soil into the xylem.

The last segment in the soil-to-xylem pathway is the passage of water and minerals into the tracheids and vessel elements of the xylem. These water-conducting cells lack protoplasts when mature and are therefore part of the apoplast. Endodermal cells, as well as parenchyma cells within the vascular cylinder, discharge minerals from their protoplasts into their walls. Both diffusion and active transport are involved in this transfer of solutes from symplast to apoplast, and the water and minerals are now free to enter the tracheids and vessels. The water and mineral nutrients we have tracked from the soil to the root xylem can now be transported upward as xylem sap to the shoot system.

### Concept Check 36.2

1. Why might a crop develop a severe phosphate deficiency after being sprayed with a fungicide?
2. A scientist adds a water-soluble inhibitor of photosynthesis to the roots of a plant. However, photosynthesis is not affected by addition of the inhibitor in this manner. Why?

For suggested answers, see Appendix A.

### Concept 36.3

## Water and minerals ascend from roots to shoots through the xylem

Here we will focus on the long-distance transport of xylem sap. The sap flows upward from roots throughout the shoot system to veins that branch throughout each leaf. Leaves depend on this efficient delivery system for their supply of water. Plants lose an astonishing amount of water by transpiration, the loss of water vapor from leaves and other aerial parts of the plant. Consider the example of maize (commonly called corn in the U.S.). A single plant transpires 125 L of water during a growing season. A maize crop growing at a typical density of 75,000 plants per hectare transpires almost 10 million L (10 million kg) of water per hectare every growing season (equivalent to about 1.25 million gallons of water per acre per growing season). Unless the transpired water is replaced by water transported up from the roots, the leaves will wilt and the plants will eventually die. The upward flow of xylem sap also brings mineral nutrients to the shoot system.

### Factors Affecting the Ascent of Xylem Sap

Xylem sap rises to heights of more than 100 m in the tallest trees. Is the sap *pushed* upward from the roots, or is it *pulled*



**Figure 36.11 Guttation.** Root pressure is forcing excess water from this strawberry leaf.

upward by the leaves? Let's evaluate the relative contributions of these two possible mechanisms.

#### Pushing Xylem Sap: Root Pressure

At night, when transpiration is very low or zero, root cells continue pumping mineral ions into the xylem of the vascular cylinder. Meanwhile, the endodermis helps prevent the ions from leaking out. The resulting accumulation of minerals lowers the water potential within the vascular cylinder. Water flows in from the root cortex, generating root pressure, an upward push of xylem sap. The root pressure sometimes helps cause more water to enter the leaves than is transpired, resulting in guttation, the exudation of water droplets that can be seen in the morning on tips of grass blades or the leaf margins of some small, herbaceous eudicots (Figure 36.11). Guttation fluid differs from dew, which is condensed moisture produced during transpiration.

In most plants, root pressure is a minor mechanism driving the ascent of xylem sap, at most forcing water upward only a few meters. Many plants do not generate any root pressure. Even in plants that display guttation, root pressure cannot keep pace with transpiration after sunrise. For the most part, xylem sap is not pushed from below by root pressure but pulled upward by the leaves themselves.

#### Pulling Xylem Sap: The Transpiration-Cohesion-Tension Mechanism

To move material upward, we can apply positive pressure from below or negative pressure from above (as when sucking liquid through a straw). Here we will focus on the process by which water is pulled upward by negative pressure in the xylem. As we investigate this mechanism of transport, we will see that transpiration provides the pull, and the cohesion of water due to hydrogen bonding transmits the upward pull along the entire length of the xylem to the roots.

## Stomata: Major Pathways for Water Loss

About 90% of the water a plant loses escapes through stomata, though these pores account for only 1-2% of the external leaf surface. The waxy cuticle limits water loss through the remaining surface of the leaf. Each stoma is flanked by a pair of guard cells, which are kidney-shaped in eudicots and dumb-bell-shaped in many monocots. Guard cells control the diameter of the stoma by changing shape, thereby widening or narrowing the gap between the two cells (Figure 36.15a). The amount of water lost by a leaf depends on the number of stomata and the average size of their apertures.

The stomatal density of a leaf, which may be as high as 20,000 per square centimeter, is under both genetic and environmental control. For example, as a result of evolution by natural selection, desert plants have lower stomatal densities than do marsh plants. Stomatal density, however, is also a developmentally plastic feature of many plants. High light intensities and low carbon dioxide levels during leaf development tend to increase stomatal density in many plant species. By measuring the stomatal density of leaf fossils, scientists have been able to gain insight into the levels of atmospheric  $\text{CO}_2$  in past climates. A recent British survey found that the stomatal density of many woodland species has decreased since 1927, when a similar survey was made. This survey is consistent with the finding that atmospheric  $\text{CO}_2$  levels increased dramatically during the 20th century as a result of the increased burning of fossil fuels.

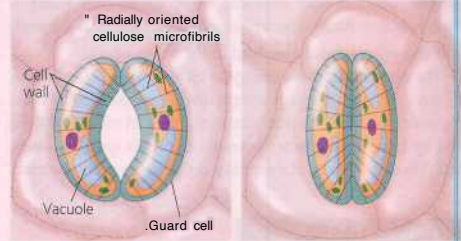
When guard cells take in water from neighboring cells by osmosis, they become more turgid and bowed. In most angiosperm species, the cell walls of guard cells are uneven in thickness, and the cellulose microfibrils are oriented in a direction that causes the guard cells to buckle outward when they are turgid, as you can see in Figure 36.15a. This buckling increases the size of the pore between the guard cells. When the cells lose water and become flaccid, they become less bowed and close the pore.

The changes in turgor pressure that open and close stomata result primarily from the reversible uptake and loss of potassium ions ( $\text{K}^+$ ) by the guard cells. Stomata open when guard cells actively accumulate  $\text{K}^+$  from neighboring epidermal cells (Figure 36.15b). This uptake of solute causes the water potential to become more negative within the guard cells, and the cells become more turgid as water enters by osmosis. Most of the  $\text{K}^+$  and water are stored in the vacuole, and thus the vacuolar membrane also plays a role in regulating the water potential of guard cells. Stomatal closing results from an exit of  $\text{K}^+$  from guard cells to neighboring cells, which leads to an osmotic loss of water. Regulation of aquaporins may also be involved in the swelling and shrinking of guard cells by varying the permeability of the membranes to water.

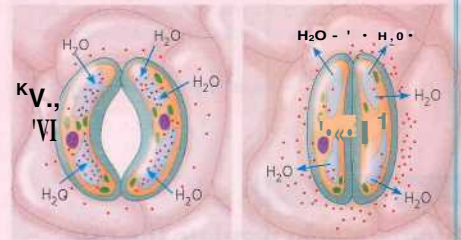
The  $\text{K}^+$  fluxes across the guard cell membrane are coupled to the generation of membrane potentials by proton pumps.

Cells turgid/Stoma open

Cells flaccid/Stoma closed



(a) Changes in guard cell shape and stomatal opening and closing (surface view). Guard cells of a typical angiosperm are illustrated in their turgid (stoma open) and flaccid (stoma closed) states. The pair of guard cells buckle outward when turgid. Cellulose microfibrils in the walls resist stretching and compression in the direction parallel to the microfibrils. Thus, the radial orientation of the microfibrils causes the cells to increase in length more than width when turgor increases. The two guard cells are attached at their tips, so the increase in length causes buckling.



(b) Role of potassium in stomatal opening and closing. The transport of  $\text{K}^+$  (potassium ions, symbolized here as red dots) across the plasma membrane and vacuolar membrane causes the turgor changes of guard cells.

### A Figure 36.15 The mechanism of stomatal opening and closing.

Stomatal opening correlates with active transport of  $\text{H}^+$  out of the guard cell. The resulting voltage (membrane potential) drives  $\text{K}^+$  into the cell through specific membrane channels (see Figure 36.4a).

In general, stomata are open during the day and closed at night. This prevents the plant from losing water when it is too dark for photosynthesis. At least three cues contribute to stomatal opening at dawn. First, light itself stimulates guard cells to accumulate  $\text{K}^+$  and become turgid. This response is triggered by the illumination of a blue-light receptor in the plasma membrane of guard cells. Activation of these blue-light receptors stimulates the activity of ATP-powered proton pumps in the plasma membrane of the guard cells, in turn promoting the uptake of  $\text{K}^+$ .

A second stimulus causing stomata to open is depletion of  $\text{CO}_2$  within air spaces of the leaf, which occurs when photosynthesis begins in the mesophyll. A plant will actually open its stomata at night if it is placed in a chamber devoid of  $\text{CO}_2$ .

A third cue causing stomatal opening is an internal "clock" in the guard cells. Even if you keep a plant in a dark closet, stomata will continue their daily rhythm of opening and closing. All eukaryotic organisms have internal clocks that regulate cyclic processes. Cycles that have intervals of approximately 24 hours are called circadian rhythms. You will learn more about circadian rhythms and the biological clocks that control them in Chapter 39.

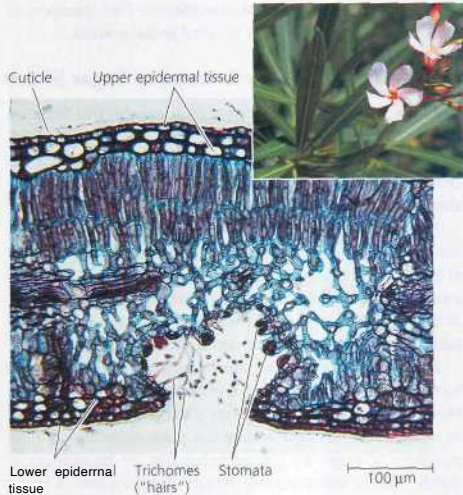
Environmental stresses can cause stomata to close during the daytime. When the plant suffers a water deficiency, guard cells may lose turgor and close stomata. In addition, a hormone called abscisic acid, which is produced in the roots in response to water deficiency, signals guard cells to close stomata. This response reduces further wilting but also restricts intake of  $\text{CO}_2$  and thereby slows photosynthesis. This is one reason why droughts reduce crop yields.

Guard cells arbitrate the photosynthesis-transpiration compromise on a moment-to-moment basis by integrating a variety of internal and external stimuli. Even the passage of a cloud or a transient shaft of sunlight through a forest canopy can affect the rate of transpiration.

## Xerophyte Adaptations That Reduce Transpiration

Plants adapted to arid climates, called xerophytes, have various leaf modifications that reduce the rate of transpiration. Many xerophytes have small, thick leaves, an adaptation that limits water loss by reducing surface area relative to leaf volume. A thick cuticle gives some of these leaves a leathery consistency. Some other xerophyte adaptations are highly reflective leaves and hairy leaves that trap a boundary layer of water. The stomata of xerophytes are concentrated on the lower (shady) leaf surface, and they are often located in depressions that shelter the pores from the dry wind (Figure 36.16). During the driest months, some desert plants shed their leaves. Others, such as cacti, subsist on water the plant stores in fleshy stems during the rainy season.

An elegant adaptation to arid habitats is found in succulents of the family Crassulaceae, in ice plants, and in many other plant families. These plants assimilate  $\text{CO}_2$  by an alternative photosynthetic pathway known as CAM, for crassulacean acid metabolism (see Figure 10.20). Mesophyll cells in a CAM plant have enzymes that can incorporate  $\text{CO}_2$  into organic acids during the night. During the daytime, the organic acids are broken down to release  $\text{CO}_2$  in the same cells, and sugars are synthesized by the conventional ( $\text{C}_3$ ) photosynthetic pathway. Because the leaf takes in  $\text{CO}_2$  at night, the stomata can close during the day, when transpiration would be greatest.



**Figure 36.16 Structural adaptations of a xerophyte leaf.** Oleander (*Nerium oleander*), shown in the inset, is commonly found in arid climates. The leaves have a thick cuticle and multiple-layered epidermal tissue that reduce water loss. Stomata are recessed in "crypts," an adaptation that reduces the rate of transpiration by protecting the stomata from hot, dry wind. The trichomes ("hairs") also help minimize transpiration by breaking up the flow of air, allowing the chamber of the crypt to have a higher humidity than the surrounding atmosphere (LM).

### Concept Check 36.4

1. Some leaf molds, which are fungi that parasitize plants, secrete a chemical that causes guard cells to accumulate potassium ions. How does this adaptation enable the leaf mold to infect the plant?
2. Describe the environmental conditions that would minimize the transpiration-to-photosynthesis ratio for a  $\text{C}_3$  plant, such as an oak tree.

For suggested answers, see Appendix A.

### Concept 36.5

## Organic nutrients are translocated through the phloem

Xylem sap flows from roots to leaves, in a direction opposite to that necessary to transport sugars from leaves to other parts of the plant. It is a second vascular tissue, the phloem, that

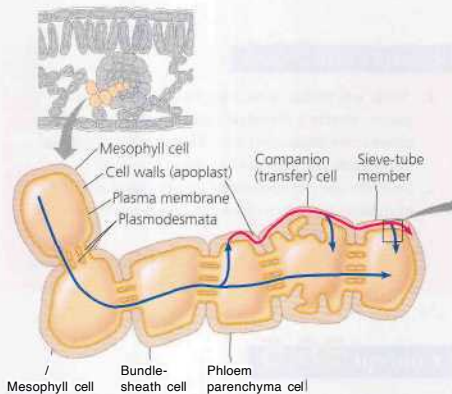
transports the products of photosynthesis. This transport of organic nutrients in the plant is called **translocation**.

## Movement from Sugar Sources to Sugar Sinks

In angiosperms, the specialized cells of phloem that function as the conduits for translocation are the sieve-tube members, arranged end to end to form long sieve tubes. Between the cells are sieve plates, structures that allow the flow of sap along the sieve tube (see Figure 35.9).

Phloem sap is an aqueous solution that differs markedly in composition from xylem sap. By far the most prevalent solute in phloem sap is sugar, primarily the disaccharide sucrose in most species. The sucrose concentration may be as high as 30% by weight, giving the sap a syrupy thickness. Phloem sap may also contain minerals, amino acids, and hormones.

In contrast to the unidirectional transport of xylem sap from roots to leaves, the direction that phloem sap travels is variable. However, sieve tubes always carry sugars from a sugar source to a sugar sink. A **sugar source** is a plant organ that is a net producer of sugar, by photosynthesis or by breakdown of starch. Mature leaves are the primary sugar sources. A **sugar sink** is an organ that is a net consumer or storer of sugar. Growing roots, buds, stems, and fruits are sugar sinks. A storage organ, such as a tuber or a bulb, may be a source or a sink, depending on the season. When stockpiling carbohydrates in the summer, it is a sugar sink. After breaking dormancy in the spring, it is a source as its starch is broken down to sugar, which is carried to the growing tips of the plant.



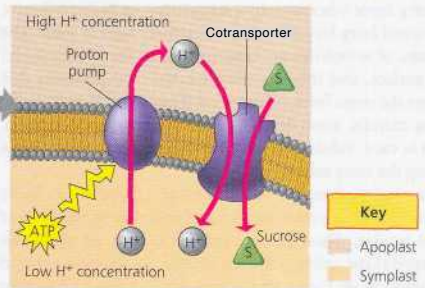
(a) Sucrose manufactured in mesophyll cells can travel via the symplast (blue arrows) to sieve-tube members. In some species, sucrose exits the symplast (red arrow) near sieve tubes and is actively accumulated from the apoplast by sieve-tube members and their companion cells.

A sugar sink usually receives sugar from the nearest source. Upper leaves on a branch may send sugar to the growing shoot tip, whereas lower leaves export sugar to roots. A growing fruit may monopolize sugar sources around it. For each sieve tube, the direction of transport depends on the locations of the source and sink connected by that tube. Therefore, neighboring tubes may carry sap in opposite directions. Direction of flow may also vary by season or developmental stage of the plant.

Sugar must be loaded into sieve-tube members before being exported to sinks. In some species, it moves from mesophyll cells to sieve-tube members via the symplast, passing through plasmodesmata. In other species, it moves by symplastic and apoplastic pathways (Figure 36.17a). In maize leaves, for example, sucrose diffuses through the symplast from chloroplast-containing mesophyll cells into small veins. Much of it then moves into the apoplast and is accumulated by nearby sieve-tube members, either directly or through companion cells, in some plants, companion cells have many ingrowths of their walls, enhancing transfer of solutes between apoplast and symplast. Such modified cells are called transfer cells (see Figure 29.5).

In maize and many other plants, phloem loading requires active transport because sucrose concentrations in sieve-tube members are two to three times higher than in mesophyll. Proton pumping and cotransport of sucrose and  $H^+$  enable the cells to accumulate sucrose (Figure 36.17b).

Phloem unloads sucrose at the sink end of a sieve tube. The process varies by plant species and type of organ. However, the concentration of free sugar in the sink is always lower than in the sieve tube because the unloaded sugar is either consumed during growth and metabolism of the sink cells or converted into insoluble polymers such as starch. As a result of this sugar concentration gradient, sugar molecules diffuse from the phloem into the sink tissues, and water follows by osmosis.



(b) A chemiosmotic mechanism is responsible for the active transport of sucrose into companion cells and sieve-tube members. Proton pumps generate an  $H^+$  gradient, which drives sucrose accumulation with the help of a cotransport protein that couples sucrose transport to the diffusion of  $H^+$  back into the cell.

**A** Figure 36.17 Loading of sucrose into phloem.

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# **BOTANY**

**BIOLOGY DEPARTMENT**

**1<sup>st</sup> stage**

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**2021**

# 10

## Photosynthesis



A Figure 10.1 Sunlight consists of a spectrum of colors, visible here in a rainbow.

### Key Concepts

- 13.1 Photosynthesis converts light energy to the chemical energy of food
- 13.2 The light reactions convert solar energy to the chemical energy of ATP and NADPH
- 10.3 The Calvin cycle uses ATP and NADPH to convert  $\text{CO}_2$  to sugar
- 10.4 Alternative mechanisms of carbon fixation have evolved in hot, arid climates

### Overview

## The Process That Feeds the Biosphere

Life on Earth is solar powered. The chloroplasts of plants capture light energy that has traveled 150 million kilometers from the sun and convert it to chemical energy stored in sugar and other organic molecules. This conversion process is called photosynthesis. Lets begin by placing photosynthesis in its ecological context.

Photosynthesis nourishes almost the entire living world directly or indirectly. An organism acquires the organic compounds it uses for energy and carbon skeletons by one of two major modes: autotrophic nutrition or heterotrophic nutrition. Autotrophs are "self-feeders" (auto means "self," and *trophos* means "feed"); they sustain themselves without eating anything derived from other organisms. Autotrophs produce their organic molecules from  $\text{CO}_2$  and other inorganic raw materials obtained from the environment. They are the ultimate sources of organic compounds for all nonautotrophic

organisms, and for this reason, biologists refer to autotrophs as the *producers* of the biosphere.

Almost all plants are autotrophs; the only nutrients they require are water and minerals from the soil and carbon dioxide from the air. Specifically, plants are photoautotrophs, organisms that use light as a source of energy to synthesize organic substances (Figure 10.1). Photosynthesis also occurs in algae, certain other protists, and some prokaryotes (Figure 10.2, on the next page). In this chapter, our emphasis will be on plants; variations in autotrophic nutrition that occur in prokaryotes and algae will be discussed in Chapters 27 and 28.

Heterotrophs obtain their organic material by the second major mode of nutrition. Unable to make their own food, they live on compounds produced by other organisms (*hetero* means "other"). Heterotrophs are the biosphere's *consumers*. The most obvious form of this "other-feeding" occurs when an animal eats plants or other animals. But heterotrophic nutrition may be more subtle. Some heterotrophs consume the remains of dead organisms by decomposing and feeding on organic litter such as carcasses, feces, and fallen leaves; they are known as decomposers. Most fungi and many types of prokaryotes get their nourishment this way. Almost all heterotrophs, including humans, are completely dependent on photoautotrophs for food—and also for oxygen, a by-product of photosynthesis.

In this chapter, you will learn how photosynthesis works. After a discussion of the general principles of photosynthesis, we will consider the two stages of photosynthesis: the light reactions, in which solar energy is captured and transformed into chemical energy; and the Calvin cycle, in which the chemical energy is used to make organic molecules of food. Finally, we will consider photosynthesis from an evolutionary perspective.

• **Figure 10.2 Photoautotrophs.** These organisms use light energy to drive the synthesis of organic molecules from carbon dioxide and (in most cases) water. They feed not only themselves, but the entire living world. (a) On land, plants are the predominant producers of food. In aquatic environments, photosynthetic organisms include (b) multicellular algae, such as this kelp; (c) some unicellular protists, such as *Euglena*; (d) the prokaryotes called cyanobacteria; and (e) other photosynthetic prokaryotes, such as these purple sulfur bacteria, which produce sulfur (spherical globules) (c, d, e: LMs).



(a) Plants

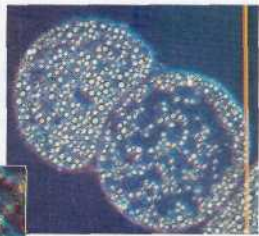


(b) Multicellular algae



(c) Unicellular protist

1  $\mu\text{m}$



(e) Purple sulfur bacteria

15  $\mu\text{m}$



(d) Cyanobacteria

40  $\mu\text{m}$

## Concept 10.1

### Photosynthesis converts light energy to the chemical energy of food

You were introduced to the chloroplast in Chapter 6. This remarkable organelle is responsible for feeding the vast majority of organisms on our planet. Chloroplasts are present in a variety of photosynthesizing organisms (see Figure 10.2), but here we will focus on plants.

#### Chloroplasts: The Sites of Photosynthesis in Plants

All green parts of a plant, including green stems and un-fipened fruit, have chloroplasts, but the leaves are the major sites of photosynthesis in most plants (Figure 10.3). There are

about half a million chloroplasts per square millimeter of leaf surface. The color of the leaf is from **chlorophyll**, the green pigment located within chloroplasts. It is the light energy absorbed by chlorophyll that drives the synthesis of organic molecules in the chloroplast. Chloroplasts are found mainly in the cells of the **mesophyll**, the tissue in the interior of the leaf. Carbon dioxide enters the leaf, and oxygen exits, by way of microscopic pores called **stomata** (singular, *stoma*; from the Greek, meaning "mouth"). Water absorbed by the roots is delivered to the leaves in veins. Leaves also use veins to export sugar to roots and other nonphotosynthetic parts of the plant.

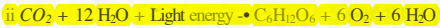
A typical mesophyll cell has about 30 to 40 chloroplasts each organelle measuring about 2-4  $\mu\text{m}$  by 4-7  $\mu\text{m}$ . An envelope of two membranes encloses the **stroma**, the dense fluid within the chloroplast. An elaborate system of interconnected membranous sacs called **thylakoids** segregates the stroma from another compartment, the interior of the thylakoids, or **thylakoid space**. In some places, thylakoid sacs are stacked in columns called **grana** (singular, *granum*). Chlorophyll resides

• **Figure 10.3 Focusing in on the location of photosynthesis in a plant.** Leaves are the major organs of photosynthesis in plants. These pictures take you into a leaf, then into a cell, and finally into a chloroplast, the organelle where photosynthesis occurs (middle, LM; bottom, TEM).

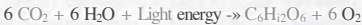
in the thylakoid membranes. (Photosynthetic prokaryotes lack chloroplasts, but they do have photosynthetic membranes arising from infolded regions of the plasma membrane that function in a manner similar to the thylakoid membranes of chloroplasts; see Figure 27.7b.) Now that we have looked at the sites of photosynthesis in plants, we are ready to look more closely at the process of photosynthesis.

**Tracking Atoms Through Photosynthesis: Scientific Inquiry**

Scientists have tried for centuries to piece together the process by which plants make food. Although some of the steps are still not completely understood, the overall photosynthetic equation has been known since the 1800s: In the presence of light, the green parts of plants produce organic compounds and oxygen from carbon dioxide and water. Using molecular formulas, we can summarize photosynthesis with this chemical equation:

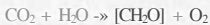


The carbohydrate  $\text{C}_6\text{H}_{12}\text{O}_6$  is glucose.\* Water appears on both sides of the equation because 12 molecules are consumed and 6 molecules are newly formed during photosynthesis. We can simplify the equation by indicating only the net consumption of water:



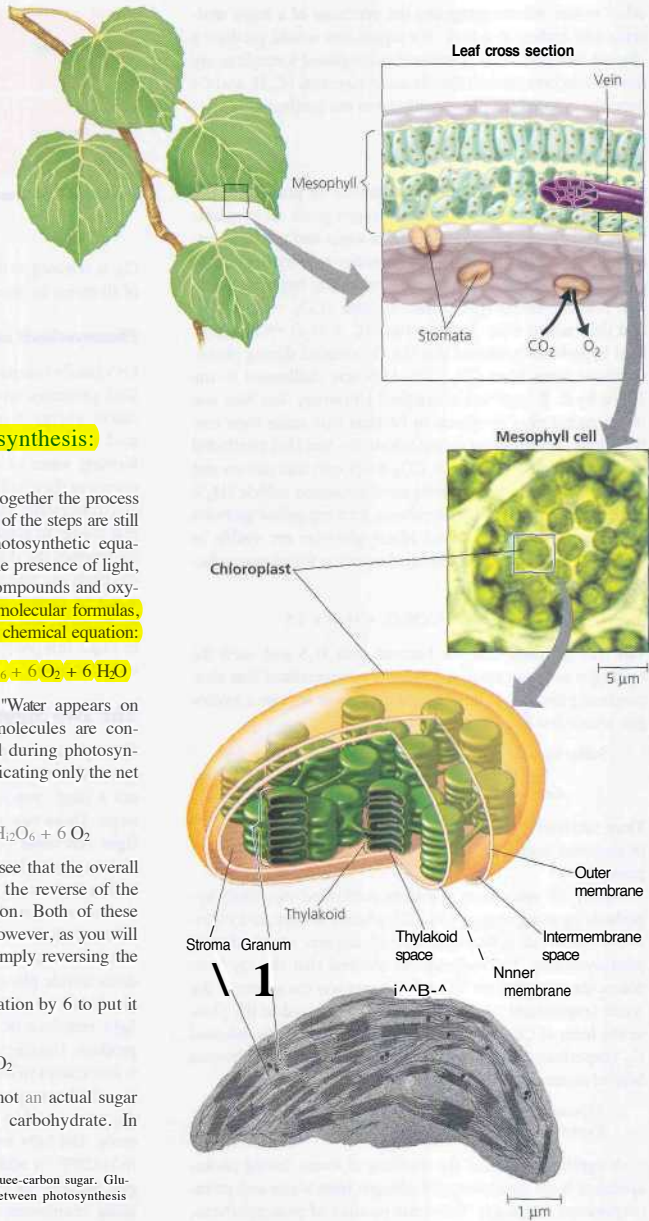
Writing the equation in this form, we can see that the overall chemical change during photosynthesis is the reverse of the *oae* that occurs during cellular respiration. Both of these metabolic processes occur in plant cells. However, as you will soon learn, plants do not make food by simply reversing the steps of respiration.

Now let's divide the photosynthetic equation by 6 to put it in its simplest possible form:



Here, the brackets indicate that  $\text{CH}_2\text{O}$  is not an actual sugar but represents the general formula for a carbohydrate. In

\* The direct product of photosynthesis is actually a three-carbon sugar. Glucose is used here only to simplify the relationship between photosynthesis and respiration.





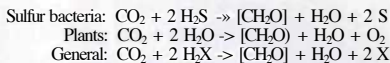
other words, we are imagining the synthesis of a sugar molecule one carbon at a time. Six repetitions would produce a glucose molecule. Let's now use this simplified formula to see how researchers tracked the chemical elements (C, H, and O) from the reactants of photosynthesis to the products.

### The Splitting of Water

One of the first clues to the mechanism of photosynthesis came from the discovery that the oxygen given off by plants through their stomata is derived from water and not from carbon dioxide. The chloroplast splits water into hydrogen and oxygen. Before this discovery, the prevailing hypothesis was that photosynthesis split carbon dioxide ( $\text{CO}_2 \rightarrow \text{C} + \text{O}_2$ ) and then added water to the carbon ( $\text{C} + \text{H}_2\text{O} \rightarrow [\text{CH}_2\text{O}]$ ). This hypothesis predicted that the  $\text{O}_2$  released during photosynthesis came from  $\text{CO}_2$ . This idea was challenged in the 1930s by C. B. van Niel of Stanford University. Van Niel was investigating photosynthesis in bacteria that make their carbohydrate from  $\text{CO}_2$  but do not release  $\text{O}_2$ . Van Niel concluded that, at least in these bacteria,  $\text{CO}_2$  is not split into carbon and oxygen. One group of bacteria used hydrogen sulfide ( $\text{H}_2\text{S}$ ) rather than water for photosynthesis, forming yellow globules of sulfur as a waste product (these globules are visible in Figure 10.2e). Here is the chemical equation for photosynthesis in these sulfur bacteria:

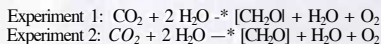


Van Niel reasoned that the bacteria split  $\text{H}_2\text{S}$  and used the hydrogen atoms to make sugar. He then generalized that idea, proposing that all photosynthetic organisms require a hydrogen source but that the source varies:

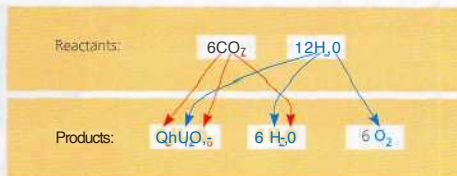


Thus, van Niel hypothesized that plants split water as a source of electrons from hydrogen atoms, releasing oxygen as a by-product.

Nearly 20 years later, scientists confirmed van Niel's hypothesis by using oxygen-18 ( $^{18}\text{O}$ ), a heavy isotope, as a radioactive tracer to follow the fate of oxygen atoms during photosynthesis. The experiments showed that the  $\text{O}_2$  from plants was labeled with  $^{18}\text{O}$  only if water was the source of the tracer (experiment 1). If the  $^{18}\text{O}$  was introduced to the plant in the form of  $\text{CO}_2$ , the label did not turn up in the released  $\text{O}_2$  (experiment 2). In the following summary red denotes labeled atoms of oxygen ( $^{18}\text{O}$ ):



A significant result of the shuffling of atoms during photosynthesis is the extraction of hydrogen from water and its incorporation into sugar. The waste product of photosynthesis,



**A Figure 10.4** Tracking atoms through photosynthesis.

$\text{O}_2$ , is released to the atmosphere. **Figure 10.4** shows the fates of all atoms in photosynthesis.

### Photosynthesis as a Redox Process

Let's briefly compare photosynthesis with cellular respiration. Both processes involve redox reactions. During cellular respiration, energy is released from sugar when electrons associated with hydrogen are transported by carriers to oxygen, forming water as a by-product. The electrons lose potential energy as they "fall" down the electron transport chain toward electronegative oxygen, and the mitochondrion harnesses that energy to synthesize ATP (see Figure 9.15). Photosynthesis reverses the direction of electron flow. Water is split, and electrons are transferred along with hydrogen ions from the water to carbon dioxide, reducing it to sugar. Because the electrons increase in potential energy as they move from water to sugar, this process requires energy. This energy boost is provided by light.

### The Two Stages of Photosynthesis: A Preview

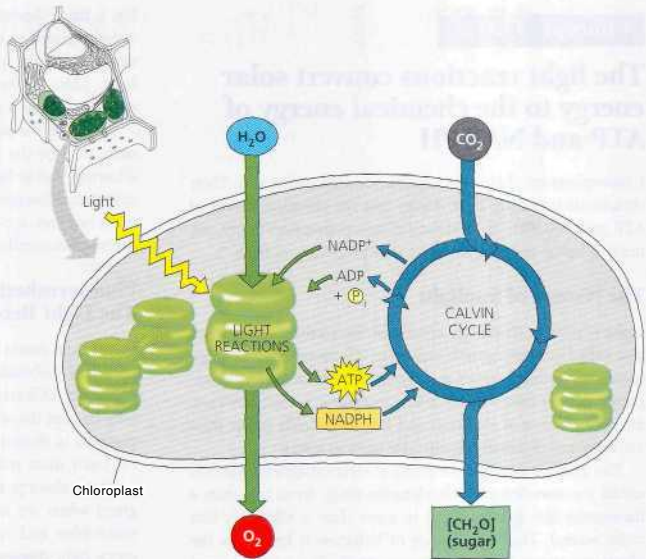
The equation for photosynthesis is a deceptively simple summary of a very complex process. **Actually, photosynthesis is not a single process, but two processes, each with multiple steps.** These two stages of photosynthesis are known as the light reactions (the *photo* part of photosynthesis) and the Calvin cycle (the *synthesis* part) (**Figure 10.5**).

**The light reactions are the steps of photosynthesis that convert solar energy to chemical energy.** Light absorbed by chlorophyll drives a transfer of electrons and hydrogen from water to an acceptor called  $\text{NADP}^+$  (nicotinamide adenine dinucleotide phosphate), which temporarily stores the **energized electrons**. Water is split in the process, and thus it is the light reactions of photosynthesis that give off  $\text{O}_2$  as a by-product. The electron acceptor of the light reactions,  $\text{NADP}^+$ , is first cousin to  $\text{NAD}^+$ , which functions as an electron carrier in cellular respiration; the two molecules differ only by the presence of an extra phosphate group in the  $\text{NADP}^+$  molecule. **The light reactions use solar power to reduce  $\text{NADP}^+$  to  $\text{NADPH}$  by adding a pair of electrons along with a hydrogen nucleus, or  $\text{H}^+$ .** The light reactions also generate ATP, using chemiosmosis to power the addition of a phosphate

**Figure 10.5 An overview of photosynthesis: cooperation of the light reactions and the Calvin cycle.**

In the chloroplast, the thylakoid membranes are the sites of the light reactions, whereas the Calvin cycle occurs in the stroma. The light reactions use solar energy to make ATP and NADPH, which function as chemical energy and reducing power, respectively, in the Calvin cycle. The Calvin cycle incorporates  $\text{CO}_2$  into organic molecules, which are converted to sugar (Recall from Chapter 5 that most simple sugars have formulas that are some multiple of  $[\text{CH}_2\text{O}]$ .)

A smaller version of this diagram will reappear in several subsequent figures as a reminder of whether the events being described occur in the light reactions or in the Calvin cycle.



group to  $\text{ADP}$ , a process called **photophosphorylation**. Thus, light energy is initially converted to chemical energy in the form of two compounds:  $\text{NADPH}$ , a source of energized electrons ("reducing power"), and  $\text{ATP}$ , the versatile energy currency of cells. Notice that the light reactions produce no sugar; that happens in the second stage of photosynthesis, the Calvin cycle.

The Calvin cycle is named for Melvin Calvin, who, along with his colleagues, began to elucidate its steps in the late 1940s. The cycle begins by incorporating  $\text{CO}_2$  from the air into organic molecules already present in the chloroplast. This initial incorporation of carbon into organic compounds is known as **carbon fixation**. The Calvin cycle then reduces the fixed carbon to carbohydrate by the addition of electrons. The reducing power is provided by  $\text{NADPH}$ , which acquired energized electrons in the light reactions. To convert  $\text{CO}_2$  to carbohydrate, the Calvin cycle also requires chemical energy in the form of  $\text{ATP}$ , which is also generated by the light reactions. Thus, it is the Calvin cycle that makes sugar, but it can do so only with the help of the  $\text{NADPH}$  and  $\text{ATP}$  produced by the light reactions. The metabolic steps of the Calvin cycle are sometimes referred to as the dark reactions, or light-independent reactions, because none of the steps requires light *directly*. Nevertheless, the Calvin cycle in most plants occurs during daylight, for only then can the light reactions provide the  $\text{NADPH}$  and

$\text{ATP}$  that the Calvin cycle requires. In essence, the chloroplast uses light energy to make sugar by coordinating the two stages of photosynthesis.

As Figure 10.5 indicates, the thylakoids of the chloroplast are the sites of the light reactions, while the Calvin cycle occurs in the stroma. In the thylakoids, molecules of  $\text{NADP}^+$  and  $\text{ADP}$  pick up electrons and phosphate, respectively, and then are released to the stroma, where they transfer their high-energy cargo to the Calvin cycle. The two stages of photosynthesis are treated in this figure as metabolic modules that take in ingredients and crank out products. Our next step toward understanding photosynthesis is to look more closely at how the two stages work, beginning with the light reactions.

**Concept Check 10.1**

1. How do the reactant molecules of photosynthesis reach the chloroplasts in leaves?
2. How did the use of an oxygen isotope help elucidate the chemistry of photosynthesis?
3. Describe how the two stages of photosynthesis are dependent on each other.

For suggested answers, see Appendix A.

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# **BOTANY**

**BIOLOGY DEPARTMENT**

**1<sup>st</sup> stage**

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**2021**

# 9

## Cellular Respiration Harvesting Chemical Energy



**A Figure 9.1** This giant panda is consuming fuel to power the work of life.

### Key Concepts

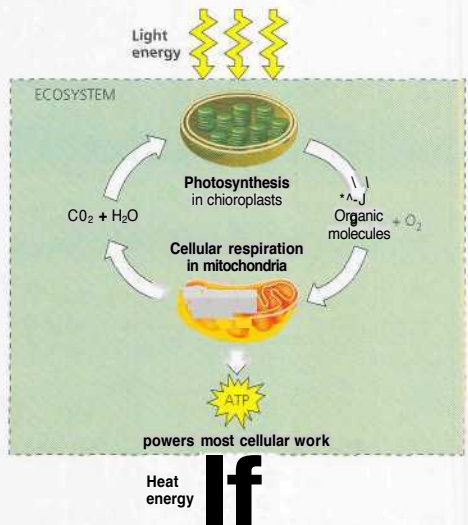
- 9.1 Catabolic pathways yield energy by oxidizing organic fuels
- 9.2 Glycolysis harvests chemical energy by oxidizing glucose to pyruvate
- 9.3 The citric acid cycle completes the energy-yielding oxidation of organic molecules
- 9.4 During oxidative phosphorylation, chemiosmosis couples electron transport to ATP synthesis
- 9.5 Fermentation enables some cells to produce ATP without the use of oxygen
- 9.6 Glycolysis and the citric acid cycle connect to many other metabolic pathways

### Overview

#### Life Is Work

Living cells require transfusions of energy from outside sources to perform their many tasks—for example, assembling polymers, pumping substances across membranes, moving, and reproducing. The giant panda in **Figure 9.1** obtains energy for its cells by eating plants; some animals feed on other organisms that eat plants. The energy stored in the organic molecules of food ultimately comes from the sun. Energy flows into an ecosystem as sunlight and leaves as heat (**Figure 9.2**). In contrast, the chemical elements essential to life are recycled. Photosynthesis generates oxygen and organic molecules used by the mitochondria of eukaryotes (including plants and algae) as fuel for cellular respiration. Respiration breaks this fuel down, generating ATP. The waste products of respiration, carbon dioxide and water, are the raw materials for photosynthesis. In this chapter, we con-

sider how cells harvest the chemical energy stored in organic molecules and use it to generate ATP, the molecule that drives most cellular work. After presenting some basics about respiration, we will focus on the three key pathways of respiration: glycolysis, the citric acid cycle, and oxidative phosphorylation.



**A Figure 9.2** Energy flow and chemical recycling in ecosystems. Energy flows into an ecosystem as sunlight and ultimately leaves as heat, while the chemical elements essential to life are recycled.

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# **BOTANY**

**BIOLOGY DEPARTMENT**

**1<sup>st</sup> stage**

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# 37

## Plant Nutrition



A Figure 37.1 Root and shoot systems of a pea seedling.

### Key Concepts

- 37.1 Plants require certain chemical elements to complete their life cycle
- 37.2 Soil quality is a major determinant of plant distribution and growth
- 37.3 Nitrogen is often the mineral that has the greatest effect on plant growth
- 37.4 Plant nutritional adaptations often involve relationships with other organisms

### Overview

## A Nutritional Network

Every organism continuously exchanges energy and materials with its environment. At the level of the ecosystem, plants and other photosynthetic autotrophs perform the key step of transforming inorganic compounds into organic compounds. Autotrophic, however, does not mean autonomous. Plants need light as the energy source for photosynthesis. In order to synthesize organic matter, plants also require raw materials in the form of inorganic nutrients: water, minerals, and carbon dioxide. For a typical plant, water and minerals come from the soil, while carbon dioxide comes from the air. The branching root system and the shoot system of a vascular plant (Figure 37.1) ensure extensive networking with both of these reservoirs of inorganic nutrients.

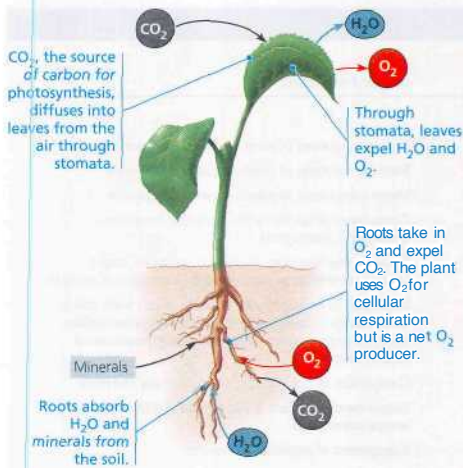
In Chapter 36, you studied the mechanisms by which vascular plants transport water, minerals, and organic nutrients. Here you will learn more about nutritional requirements and examine some nutritional adaptations that have evolved in plants, often in relationship with other organisms.

### Concept 37.1

## Plants require certain chemical elements to complete their life cycle

Watch a large plant grow from a tiny seed, and you cannot help wondering where all the mass comes from. Aristotle thought that soil provided the substance for plant growth because plants seemed to spring from the ground. He believed that leaves of flowering plants simply shaded developing fruit. In the 17th century, Jan Baptista van Helmont performed an experiment to test the hypothesis that plants grow by consuming soil. He planted a small willow in a pot that contained 90.9 kg of soil. After five years, the willow had grown into a tree weighing 76.8 kg, but only 0.06 kg of soil had disappeared from the pot. He concluded that the willow had grown mainly from the water he had added regularly. A century later, in English physiologist named Stephen Hales postulated that plants are nourished mostly by air.

There is some truth to all three hypotheses because so 1, water, and air all contribute to plant growth (Figure 37.2). Plants extract mineral nutrients, essential chemical elements, from the soil in the form of inorganic ions. Plants acquire nitrogen, for example, in the form of nitrate ions ( $\text{NO}_3^-$ ). However, mineral nutrients add little to the plants overall mass. Typically, 80-90% of a plant is water, and plants grow mainly by accumulating water in the central vacuoles of their cells. Water is also a nutrient that supplies most of the hydrogen atoms and some of the oxygen atoms incorporated into organic compounds by photosynthesis (see Figure 10.4). Still, only a small fraction of the water that enters a plant contributes atoms to organic molecules. For example, it has been estimated that more than 90% of



**Figure 37.2 The uptake of nutrients by a plant:** a review. From CO<sub>2</sub>, O<sub>2</sub>, H<sub>2</sub>O, and minerals, the plant produces all of its own organic material. See also Figure 36.2.

the water absorbed by maize plants is lost by transpiration. The water retained by a plant serves three main functions: It acts as a solvent, provides most of the volume for cell elongation, and helps maintain the form of soft tissue by keeping cells turgid. By weight, the bulk of a plant's organic material is derived not from water or soil minerals, but from the CO<sub>2</sub> that is assimilated from the air.

We can measure water content by comparing the weight of plant material before and after it is dried. We can then analyze the chemical composition of the dry residue. Organic substances account for about 96% of the dry weight, with inorganic substances making up the remaining 4%. Most of the organic material is carbohydrate, including the cellulose of cell walls. Thus, the components of carbohydrates—carbon, oxygen, and hydrogen—are the most abundant elements in the dry weight of a plant. Because some organic molecules contain nitrogen, sulfur, or phosphorus, these elements are also relatively abundant in plants.

## Macronutrients and Micronutrients

More than 50 chemical elements have been identified among the inorganic substances in plants, but not all of these elements are essential. A chemical element is considered an essential element if it is required for a plant to complete a life cycle and produce another generation. In studying the chemical composition of plants, we must distinguish elements that are essential from those that are merely present in the plant. To some extent, the chemical elements in a plant reflect the soil composition.

Plants growing on mine tailings, for instance, may contain gold or silver, but these minerals have no nutritional function.

To determine which chemical elements are essential elements, researchers use hydroponic culture, in which plants are grown without soil by using mineral solutions (Figure 37.3). Such studies have helped identify 17 essential elements that are needed by all plants (Table 37.1, on the next page).

Nine of the essential elements are called macronutrients because plants require them in relatively large amounts. Six of these are the major components of organic compounds forming the structure of a plant: carbon, oxygen, hydrogen, nitrogen, phosphorus, and sulfur. The other three macronutrients are potassium, calcium, and magnesium.

The remaining eight essential elements are known as micronutrients because plants need them in very small amounts. They are chlorine, iron, manganese, boron, zinc, copper, nickel, and molybdenum. Micronutrients function in plants mainly as cofactors, non-protein helpers in enzymatic reactions (see Chapter 8). Iron, for example, is a metallic component of cytochromes, the proteins in the electron transport

**Figure 37.3**  
**Research Method Hydroponic Culture**

**APPLICATION** In hydroponic culture, plants are grown in mineral solutions without soil. One use of hydroponic culture is to identify essential elements in plants.

**TECHNIQUE** Plant roots are bathed in aerated solutions of known mineral composition. Aerating the water provides the roots with oxygen for cellular respiration. A particular mineral, such as potassium, can be omitted to test whether it is essential.



**RESULTS** If the omitted mineral is essential, mineral deficiency symptoms occur, such as stunted growth and discolored leaves. Deficiencies of different elements may have different symptoms, which can aid in diagnosing mineral deficiencies in soil.

**Table 37.1 Essential Elements in Plants**

| Element               | Form Available to Plants   | % Mass in Dry Tissue | Major Functions  |
|-----------------------|--|----------------------|--|
| <b>Macronutrients</b> |  |                      |  |
| Carbon                | CO <sub>2</sub>  | 45%                  | Major component of plant's organic compounds   |
| Oxygen                | CO <sub>2</sub>  | 45%                  | Major component of plant's organic compounds   |
| Hydrogen              | H <sub>2</sub> O   | 6%                   | Major component of plant's organic compounds   |
| Nitrogen              | NO <sub>3</sub> <sup>-</sup> , NH <sub>4</sub> <sup>+</sup> *                | 1.5%                 | Component of nucleic acids, proteins, hormones, chlorophyll, coenzymes   |
| Potassium             | K <sup>+</sup>   | 1.0%                 | Cofactor that functions in protein synthesis; major solute functioning in water balance; operation of stomata  |
| Calcium               | Ca <sup>2+</sup> *   | 0.5%                 | Important in formation and stability of cell walls and in maintenance of membrane structure and permeability; activates some enzymes; regulates many responses of cells to stimuli |
| Magnesium             | Mg <sup>2+</sup>   | 0.2%                 | Component of chlorophyll; activates many enzymes   |
| Phosphorus            | H <sub>2</sub> PO <sub>4</sub> <sup>-</sup> , HPO <sub>4</sub> <sup>2-</sup> | <b>0.2%</b>          | Component of nucleic acids, phospholipids, ATP, several coenzymes  |
| Sulfur                | SO <sub>4</sub> <sup>2-</sup>  | 0.1%                 | Component of proteins, coenzymes   |
| <b>Micronutrients</b> |  |                      |  |
| Chlorine              | Cl <sup>-</sup>  | 0.01%                | Required for water-splitting step of photosynthesis; functions in water balance  |
| Iron                  | Fe <sup>3+</sup> , Fe <sup>2+</sup>  | 0.01%                | Component of cytochromes; activates some enzymes   |
| Manganese             | Mn <sup>2+</sup>   | 0.005%               | Active in formation of amino acids; activates some enzymes; required for water-splitting step of photosynthesis  |
| Boron                 | H <sub>2</sub> BO <sub>3</sub> <sup>-</sup>                                  | 0.002%               | Cofactor in chlorophyll synthesis; may be involved in carbohydrate transport and nucleic acid synthesis; role in cell wall function  |
| Zinc                  | Zn <sup>2+</sup>   | 0.002%               | Active in formation of chlorophyll; activates some enzymes   |
| Copper                | Cu <sup>+</sup> , Cu <sup>2+</sup>   | < 0.001%             | Component of many redox and lignin-biosynthetic enzymes  |
| Nickel                | Ni <sup>2+</sup>   | < 0.001%             | Cofactor for an enzyme functioning in nitrogen metabolism  |
| Molybdenum            | MoO <sub>4</sub> <sup>2-</sup>   | < 0.0001%            | Essential for symbiotic relationship with nitrogen-fixing bacteria; cofactor that functions in nitrate reduction   |

chains of chloroplasts and mitochondria. It is because micronutrients generally play catalytic roles that plants need only minute quantities. The requirement for molybdenum, for instance, is so modest that there is only one atom of this rare element for every 60 million atoms of hydrogen in dried plant material. Yet a deficiency of molybdenum or any other micronutrient can weaken or kill a plant.

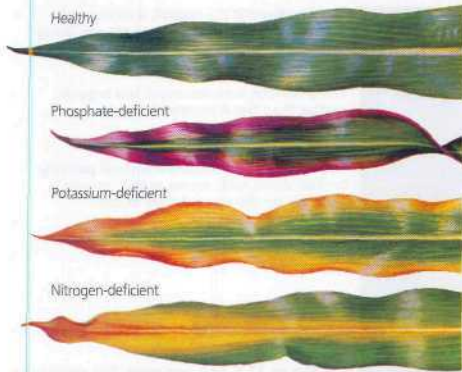
### Symptoms of Mineral Deficiency

The symptoms of a mineral deficiency depend partly on the nutrient's function. For example, a deficiency of magnesium, a component of chlorophyll, causes yellowing of the leaves, known as chlorosis. In some cases, the relationship between a mineral deficiency and its symptoms is less direct. For instance, iron deficiency can cause chlorosis even though chloro-

phyll contains no iron, because iron ions are required as a cofactor in one of the enzymatic steps of chlorophyll synthesis.

Mineral deficiency symptoms depend not only on the role of the nutrient but also on its mobility within the plant. If a nutrient moves about freely, symptoms will show up first in older organs because young, growing tissues have more "drawing power" for nutrients in short supply. For example, magnesium is relatively mobile and is shunted preferentially to young leaves. Therefore, a plant starved for magnesium will show signs of chlorosis first in its older leaves. The mechanism for preferential routing is the source-to-sink translocation in phloem as minerals move along with the sugars to the growing tissues (see Figure 36.18). In contrast, a deficiency of a mineral that is relatively immobile will affect young parts of the plant first. Older tissues may have adequate amounts, which they are able to retain during periods of short supply. For example, iron does not mole-





**Figure 37.4** The most common mineral deficiencies, as seen in maize leaves. Phosphate-deficient plants have reddish purple margins, particularly in young leaves. Potassium-deficient plants exhibit "firing," or drying, along tips and margins of older leaves. Nitrogen deficiency is evident in a yellowing that starts at the tip and moves along the center (midrib) of older leaves.

freely within a plant, and an iron deficiency will cause yellowing of young leaves before any effect on older leaves is visible.

Deficiencies of nitrogen, phosphorus, and potassium are most common. Shortages of micronutrients are less common and tend to occur in certain geographic regions because of differences in soil composition. The symptoms of a mineral deficiency are often distinctive enough for a plant physiologist or farmer to diagnose its cause (Figure 37.4). One way to confirm a diagnosis is to analyze the mineral content of the plant and soil. The amount of a micronutrient needed to correct a deficiency is usually quite small. For example, a zinc deficiency in fruit trees can usually be cured by hammering a few zinc nails into each tree trunk. Moderation is important because overdoses of many nutrients can be toxic to plants. Hydroponic culture can ensure optimal mineral nutrition by using nutrient solutions that can be precisely regulated. However, this method is not used widely in agriculture because it is relatively expensive compared with growing crops in soil.

### IConcept Check 37.1

1. Explain how Table 37.1 can be used to support Hales' hypothesis, yet does not refute van Helmont's hypothesis.
2. Are some essential elements more important than others? Explain.
3. Can a single leaf be used to diagnose all of a plant's mineral deficiencies? Explain.

For suggested answers, see Appendix A.

## Concept 37.2

### Soil quality is a major determinant of plant distribution and growth

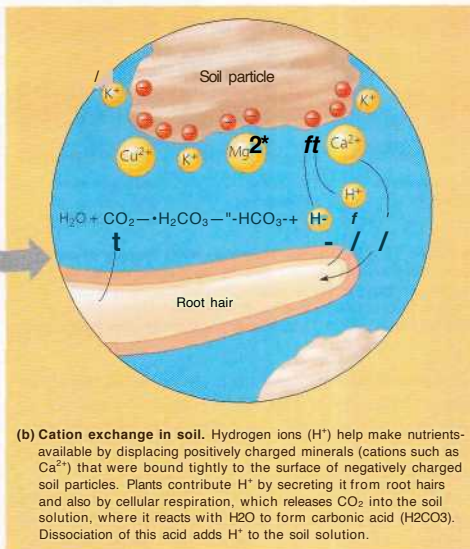
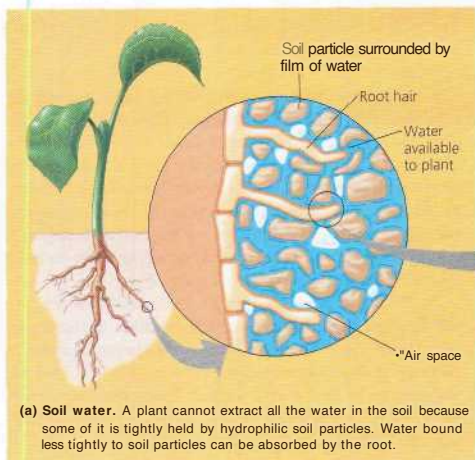
Along with climate, the major factors determining whether particular plants can grow well in a certain location are the texture and composition of the soil. Texture is the soil's general structure, referring to the relative amounts of various sizes of soil particles. Composition refers to the soil's organic and inorganic chemical components. Plants that grow naturally in a certain type of soil are adapted to its texture and composition and can absorb water and extract essential mineral nutrients. In turn, plants affect the soil, as you will soon see. The soil-plant interface is a critical part of the chemical cycles that sustain terrestrial ecosystems.

#### Texture and Composition of Soils

Soil has its origin in the weathering of solid rock. The freezing of water that has seeped into crevices can mechanically fracture rocks. Acids dissolved in the water can also help break rocks down chemically. When organisms are able to invade the rock, they accelerate breakdown by chemical and mechanical means. Some organisms, for example, secrete acids that dissolve the rock. Roots that grow in fissures lead to mechanical fracturing. The eventual result of all this activity is topsoil, a mixture of particles derived from rock, living organisms, and humus, the remains of partially decayed organic material. The topsoil and other distinct soil layers, or horizons, are often visible in vertical profile where there is a road cut or deep hole (Figure 37.5, on the next page). The topsoil, also known as the A horizon, is the richest in organic material and is therefore most important for plant growth.

The texture of topsoil depends on the sizes of its particles, which are classified in a range from coarse sand to microscopic clay particles. The most fertile soils are usually loams, made up of roughly equal amounts of sand, silt (particles of intermediate size), and clay. Loamy soils have enough fine particles to provide a large surface area for retaining minerals and water, which adhere to the particles. But loams also have enough coarse particles to provide air spaces containing oxygen that can be used by roots for cellular respiration. If soil does not drain adequately, roots suffocate because the air spaces are replaced by water; the roots may also be attacked by molds that favor soaked soil. These are common hazards for houseplants that are overwatered in pots with poor drainage.

Soil composition includes organic components as well as minerals. Topsoil is home to an astonishing number and variety of organisms. A teaspoon of topsoil has about 5 billion



▲ **Figure 37.6** The availability of soil water and minerals.

farmland useless and forcing hundreds of thousands of people to abandon homes and land, a plight immortalized in John Steinbeck's *The Grapes of Wrath*. Better soil conservation practices could have preserved soil fertility and sustained agricultural productivity.

To understand soil conservation, we must first remember that agriculture can only be sustained by human intervention. In forests, grasslands, and other natural ecosystems, mineral nutrients are usually recycled by the decomposition of dead organic material in the soil. In contrast, when farmers harvest a crop, essential elements are diverted from the chemical cycles going on in that location. In general, agriculture depletes the mineral content of the soil. To grow 1,000 kg of wheat grain, the soil gives up 20 kg of nitrogen, 4 kg of phosphorus, and 4.5 kg of potassium. Each year, the soil fertility diminishes unless fertilizers replace lost minerals such as nitrogen, phosphorus, and potassium. Many crops also use far more water than the vegetation that once grew naturally on that land, forcing farmers to irrigate. Prudent fertilization, thoughtful irrigation, and the prevention of erosion are three of the most important goals of soil conservation. Complementing soil conservation is soil reclamation, the goal of returning agricultural productivity to exhausted or damaged soil. More than 30% of the world's farmland suffers from low productivity stemming from poor

soil conditions such as chemical contamination, mineral deficiencies, acidity, salinity and poor drainage.

### Fertilizers

Prehistoric farmers may have started fertilizing their fields after noticing that grass grew faster and greener where animals had defecated. In developed nations today, most farmers use commercially produced fertilizers containing minerals that are either mined or prepared by industrial processes. These fertilizers are usually enriched in nitrogen, phosphorus, and potassium, the macro nutrients most commonly deficient in farm and garden soils. Fertilizers are labeled with a three-number code called the N-P-K ratio, indicating the content of these minerals. A fertilizer marked "15-10-5," for instance, is 15% nitrogen (as ammonium or nitrate), 10% phosphorus (as phosphoric acid), and 5% potassium (as the mineral potash).

Manure, fishmeal, and compost are called "organic" fertilizers because they are of biological origin and contain decomposing organic material. Before plants can use organic material, however, it must be decomposed into the inorganic nutrients that roots can absorb. Whether from organic fertilizer or a chemical factory, the minerals a plant extracts are in the same form, but organic fertilizers release minerals gradually whereas minerals in

# C38 Angiosperm Reproduction and Biotechnology



A Figure 38.1 *Rafflesia arnoldii*, "monster flower" of Indonesia.

## Key Concepts

- 38.1 Pollination enables gametes to come together within a flower
- 38.2 After fertilization, ovules develop into seeds and ovaries into fruits
- 3B3 Many flowering plants clone themselves by asexual reproduction
- 3i8.4 Plant biotechnology is transforming agriculture

## Overview

### To Seed or Not to Seed

The parasitic plant *Rafflesia arnoldii*, found only in Southeast Asia, spends most of its life invisible to passersby, growing within the woody tissue of a host vine. The plant makes its presence known in a spectacular fashion by producing a cabbage-sized floral bud that eventually develops into a gigantic (lower the size of an automobile tire (Figure 38.1). With an odor reminiscent of a decaying corpse, the flower attracts carrion flies that shuttle the pollen from one flower to another. A few days after opening, the flower collapses and shrivels, its function completed. A single female flower may produce up to 4 million seeds. However, sexual reproduction, as in *Rafflesia*, is not the only means by which flowering plants (angiosperms) reproduce. Many species also reproduce asexually, creating offspring that are genetically identical to the parent.

The propagation of flowering plants by sexual and asexual reproduction forms the basis of agriculture. Since the dawn of agriculture about 10,000 years ago, plant breeders have genetically manipulated the traits of a few hundred wild angiosperm

species by artificial selection, transforming them into the crops we cultivate today. The speed and extent of plant modification have increased dramatically in recent decades with the advent of genetic engineering.

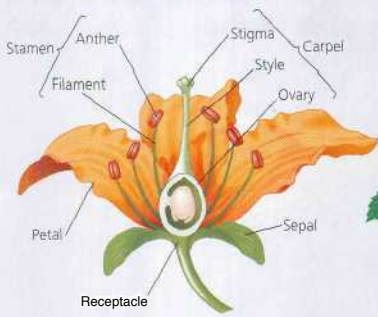
In Chapters 29 and 30, we approached plant reproduction from an evolutionary perspective, tracing the descent of angiosperms and other land plants from their algal ancestors, in this chapter, we will explore the reproductive biology of flowering plants in much greater detail because they are the most important group of plants in most terrestrial ecosystems and in agriculture. After discussing the sexual and asexual reproduction of angiosperms, we will then examine modern plant biotechnology and the role of humans in the genetic alteration of crop species.

## Concept 38.1

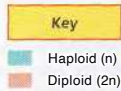
### Pollination enables gametes to come together within a flower

Recall from Chapters 29 and 30 that the life cycles of plants are characterized by an alternation of generations, in which haploid ( $n$ ) and diploid ( $2n$ ) generations take turns producing each other (see Figures 29.5 and 30.10). The diploid plant, which is the sporophyte, produces haploid spores by meiosis. These spores divide by mitosis, giving rise to the gametophytes, the small male and female haploid plants that produce gametes (sperm and eggs). Fertilization results in diploid zygotes, which divide by mitosis and form new sporophytes.

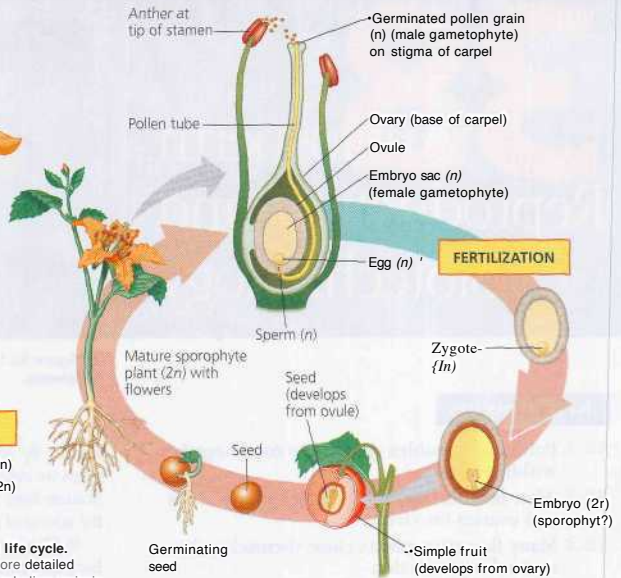
In angiosperms, the sporophyte is the dominant generation in the sense that it is the largest, most conspicuous, and longest-living plant we see. Over the course of seed plant



(a) An idealized flower.



(b) Simplified angiosperm life cycle. See Figure 30.10 for a more detailed version of the life cycle, including meiosis.



### A Figure 38.2 An overview of angiosperm reproduction.

evolution, gametophytes became reduced in size and wholly dependent on the sporophyte generation for nutrients. Angiosperm gametophytes are the most reduced of all plants, consisting of only a few cells. Angiosperm sporophytes develop a unique reproductive structure—the flower.

Figure 38.2 reviews the angiosperm life cycle, which is shown in more detail in Figure 30.10. Male and female gametophytes develop within the anthers and ovules, respectively. Pollination by wind, water, or animals brings a pollen grain containing a male gametophyte to the stigma of a flower. Pollen germination brings sperm produced by the male gametophyte to a female gametophyte contained in an ovule embedded in the ovary of a flower. Union of egg and sperm (fertilization) takes place within each ovule in the ovary. Ovules develop into seeds, while the ovary itself becomes a fruit (another unique structure of the angiosperms). In this section, we will focus on the role of the flower in gametophyte development and the process of pollination.

### Flower Structure

Flowers, the reproductive shoots of the angiosperm sporophyte, are typically composed of four whorls of highly modified leaves called floral organs, which are separated by very short internodes. Unlike vegetative shoots, which grow inde-

terminately, flowers are determinate shoots, meaning that they cease growing after the flower and fruit are formed.

Floral organs—sepals, petals, stamens, and carpels—are attached to a part of the stem called the receptacle. Stamens and carpels are reproductive organs, whereas sepals and petals are sterile. Sepals, which enclose and protect the floral bud before it opens, are usually green and more leaflike in appearance than the other floral organs. In many species, petals are more brightly colored than sepals and advertise the flower to insects and other pollinators.

A stamen consists of a stalk called the filament and a terminal structure called the anther; within the anther are chambers called pollen sacs, in which pollen is produced. A carpel has an ovary at its base and a long, slender neck called the style. At the top of the style is a sticky structure called the stigma that serves as a landing platform for pollen. Within the ovary are one or more ovules, with the number depending on the species. The flower shown in Figure 38.2 has a single carpel, but the flowers of many species have multiple carpels. In most species, two or more carpels are fused into a single structure; the result is an ovary with two or more chambers, each containing one or more ovules. The term pistil is sometimes used to refer to a single carpel or to a group of fused carpels. Figure 38.3 shows examples of variations in floral structure that have evolved during the 140 million years of angiosperm history.

## Gametophyte Development and Pollination

Anthers and ovules bear sporangia, structures where spores are produced by meiosis and gametophytes develop. Pollen grains, each consisting of a mature male gametophyte surrounded by a spore wall, are formed within pollen sacs (microsporangia) of anthers. An egg-producing female gametophyte, or embryo sac, forms within each ovule.

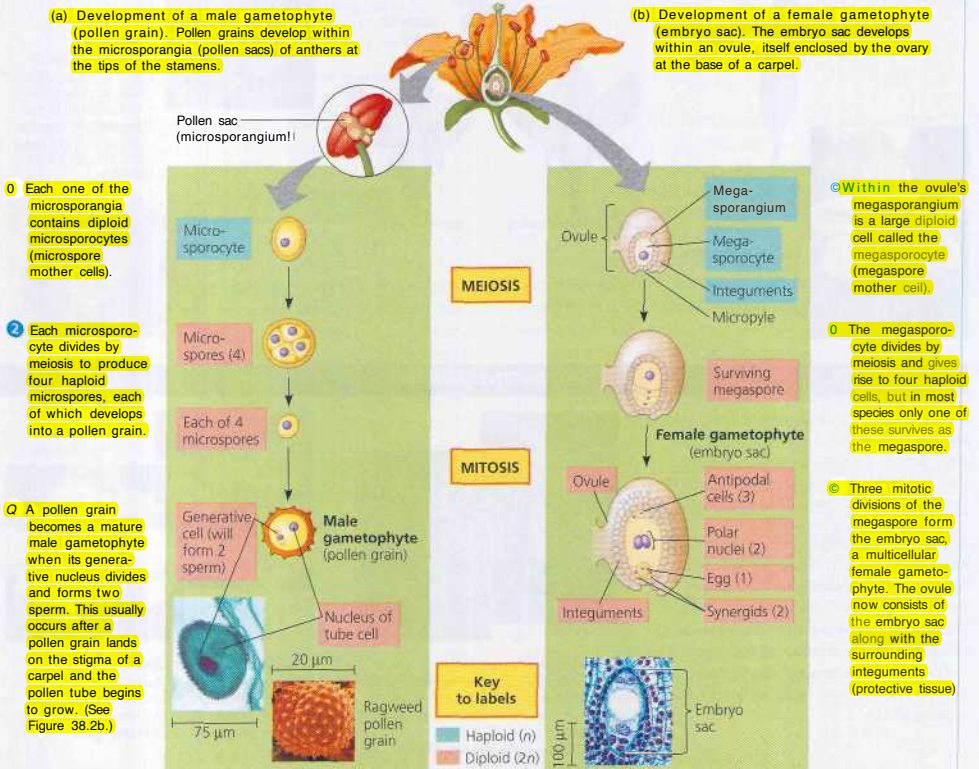
In angiosperms, pollination is the transfer of pollen from an anther to a stigma. If pollination is successful, a pollen grain produces a structure called a pollen tube, which grows and digests its way down into the ovary via the style and discharges sperm in the vicinity of the embryo sac, resulting in fertilization of the egg (see Figure 38.2b). The zygote gives rise to an embryo, and as the embryo grows, the ovule that contains it develops into a seed. The entire ovary,

meanwhile, develops into a fruit containing one or more seeds, depending on the species. Fruits, which disperse by dropping to the ground or being carried by wind or animals, help spread seeds some distance from their source plants. When light, soil, and temperature conditions are suitable, seeds germinate and the embryo carried in the seed grows and develops into a seedling.

We will now look more closely at the development of angiosperm gametophytes and the process of pollination. Keep in mind, however, that there are many variations in the details of these processes, depending on the species.

Within the microsporangia (pollen sacs) of an anther are many diploid cells called microsporocytes, also known as microspore mother cells (Figure 38.4a). Each microsporocyte undergoes meiosis, forming four haploid microspores, each of which can eventually give rise to a haploid male gametophyte

Figure 38.4 The development of angiosperm gametophytes (pollen grains and embryo sacs).



Recognition of "self pollen" is based on genes for self-incompatibility, called S-genes. In the gene pool of a plant population, there can be dozens of alleles of an S-gene. If a pollen grain has an allele that matches an allele of the stigma on which it lands, the pollen tube fails to grow. Depending on the species, self-recognition blocks pollen tube growth by one of two molecular mechanisms: gametophytic self-incompatibility or sporophytic self-incompatibility.

In gametophytic self-incompatibility, the S-allele in the pollen genome governs the blocking of fertilization. For example, an S<sub>1</sub> pollen grain from an S<sub>1</sub>S<sub>2</sub> parental sporophyte will fail to fertilize eggs of an S<sub>1</sub>S<sub>2</sub> flower but will fertilize an S<sub>2</sub>S<sub>3</sub> flower. An S<sub>2</sub> pollen grain would not fertilize either flower. Self-recognition of this kind involves the enzymatic destruction of RNA within a rudimentary pollen tube. RNA-hydrolyzing enzymes in the style of the carpel can enter a pollen tube and attack its RNA only if the pollen is of a "self" type.

In sporophytic self-incompatibility, fertilization is blocked by S-allele gene products in tissues of the parental sporophyte that adhere to the pollen wall. For example, neither an S<sub>1</sub> nor S<sub>2</sub> pollen grain from an S<sub>1</sub>S<sub>2</sub> parental sporophyte will fertilize eggs of an S<sub>1</sub>S<sub>2</sub> flower or S<sub>2</sub>S<sub>3</sub> flower. Sporophytic incompatibility involves a signal transduction pathway in epidermal cells of the stigma that prevents germination of the pollen grain.

Some crops, such as nonhybrid cultivated varieties of peas, maize, and tomatoes, routinely self-pollinate with satisfactory results. However, plant breeders sometimes hybridize different varieties of a crop plant in order to combine the best traits of the varieties and counter the loss of vigor that can result from excessive inbreeding (see Chapter 14). To obtain hybrid seeds, plant breeders currently must prevent self-fertilization either by laboriously removing the anthers from the parent plants that provide the seeds or by developing male sterile plants. The latter option is increasingly important. Eventually, it may also be possible to impose self-incompatibility on crop species that are normally self-compatible. Basic research on mechanisms of self-incompatibility may therefore lead to agricultural applications.

### Concept Check 38.1

1. Give some examples of how form fits function in flower structure.
2. Distinguish pollination from fertilization.
3. Given the seeming disadvantages of selfing as a reproductive "strategy" in nature, it is surprising that about 20% of angiosperm species primarily rely on selfing. Although fairly common in nature, self-fertilization has been called an "evolutionary dead end." Suggest a reason why selfing might be selected for in nature and yet still be an "evolutionary dead end!"

For suggested answers, see Appendix A.

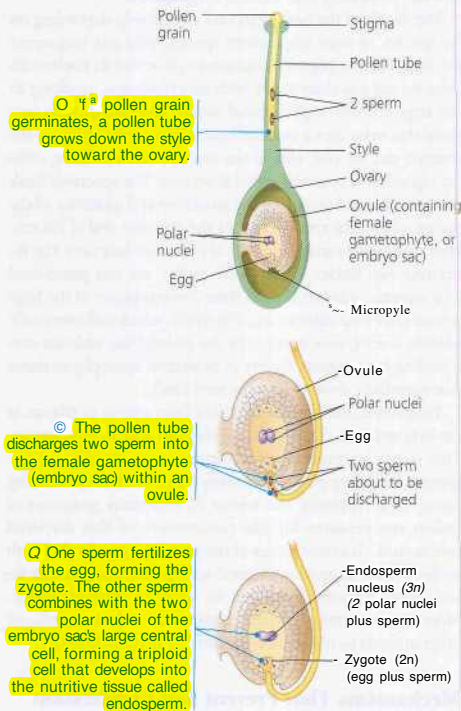
## Concept 38.2

### After fertilization, ovules develop into seeds and ovaries into fruits

We have traced the processes of gametophyte development and pollination. Now we will look at fertilization and its products: seeds and fruits.

#### Double Fertilization

After landing on a receptive stigma, a pollen grain absorbs moisture and germinates; that is, it produces a pollen tube that extends down between the cells of the style toward the ovary (Figure 38.6). The nucleus of the generative cell divides by mitosis and forms two sperm. Directed by a chemical attractant, possibly calcium, the tip of the pollen tube enters the ovary, prob(s



**A Figure 38.6** Growth of the pollen tube and double fertilization.

through the micropyle (a gap in the integuments of the ovule), and discharges its two sperm near or within the embryo sac.

The events that follow are a distinctive feature of the angiosperm life cycle. One sperm fertilizes the egg to form the zygote. The other sperm combines with the two polar nuclei to form a triploid ( $3n$ ) nucleus in the center of the large central cell of the embryo sac. This large cell will give rise to the endosperm, a food-storing tissue of the seed. The union of two sperm cells with different nuclei of the embryo sac is called double fertilization. Double fertilization ensures that the endosperm will develop only in ovules where the egg has been fertilized, thereby preventing angiosperms from squandering nutrients.

The tissues surrounding the embryo sac have prevented researchers from being able to directly observe fertilization in plants grown under normal conditions. Recently, however, scientists have isolated sperm from germinated pollen grains and eggs from embryo sacs and have observed the merging of plant gametes *in vitro* (in an artificial environment). The first cellular event that takes place after gamete fusion is an increase in the cytoplasmic calcium ( $Ca^{2+}$ ) levels of the egg, as also occurs during animal gamete fusion (see Chapter 47). Another similarity to animals is the establishment of a block to polyspermy: the fertilization of an egg by more than one sperm cell. Thus, maize (*Zea mays*) sperm cannot fuse with zygotes *in vitro*. In maize, this barrier to polyspermy is established as early as 45 seconds after the initial sperm fusion with the egg.

### From Ovule to Seed

After double fertilization, each ovule develops into a seed, and the ovary develops into a fruit enclosing the seed(s). As the embryo develops from the zygote, the seed stockpiles proteins, oils, and starch to varying extents, depending on the species.

This is why seeds are such major sugar sinks (see Chapter 36). Initially, these nutrients are stored in the endosperm, but later in seed development in many species, the storage function of the endosperm is more or less taken over by the swelling cotyledons of the embryo.

### Endosperm Development

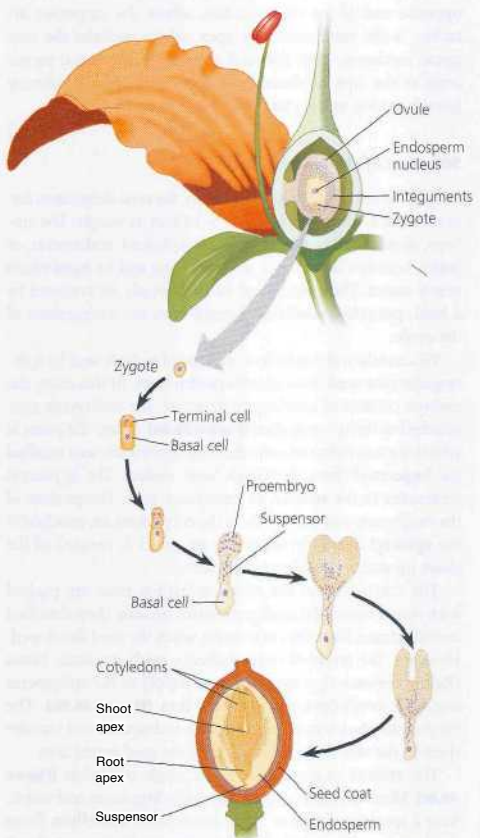
Endosperm development usually precedes embryo development. After double fertilization, the triploid nucleus of the ovule's central cell divides, forming a multinucleate "supercell" having a milky consistency. This liquid mass, the endosperm, becomes multicellular when cytokinesis partitions the cytoplasm by forming membranes between the nuclei. Eventually, these "naked" cells produce cell walls, and the endosperm becomes solid. Coconut "milk" is an example of liquid endosperm; coconut "meat" is an example of solid endosperm. The white fluffy part of popcorn is also solid endosperm.

In grains and most other monocots, as well as many eudicots, the endosperm stores nutrients that can be used by the

seedling after germination. In other eudicots (including bean seeds), the food reserves of the endosperm are completely exported to the cotyledons before the seed completes its development; consequently, the mature seed lacks endosperm.

### Embryo Development

The first mitotic division of the zygote is transverse, splitting the fertilized egg into a basal cell and a terminal cell (Figure 38.7). The terminal cell eventually gives rise to most of the embryo. The basal cell continues to divide transversely, producing a



**Figure 38.7** The development of a eudicot plant embryo. By the time the ovule becomes a mature seed and the integuments harden and thicken to form the seed coat, the zygote has given rise to an embryonic plant with rudimentary organs.

thread of cells called the suspensor, which anchors the embryo to its parent. The suspensor functions in the transfer of nutrients to the embryo from the parent plant and, in some plants, from the endosperm. As the suspensor elongates, it also pushes the embryo deeper into the nutritive and protective tissues. Meanwhile, the terminal cell divides several times and forms a spherical proembryo attached to the suspensor. The cotyledons begin to form as bumps on the proembryo. A eudicot, with its two cotyledons, is heart-shaped at this stage. Only one cotyledon develops in monocots.

Soon after the rudimentary cotyledons appear, the embryo elongates. Cradled between the cotyledons is the embryonic shoot apex, which includes the shoot apical meristem. At the opposite end of the embryo's axis, where the suspensor attaches, is the embryonic root apex, which includes the root apical meristem. After the seed germinates, the apical meristems at the tips of shoots and roots will sustain primary growth as long as the plant lives (see Figure 35.10).

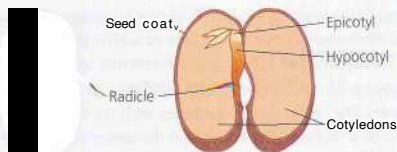
### Structure of the Mature Seed

During the last stages of its maturation, the seed dehydrates until its water content is only about 5-15% of its weight. The embryo, surrounded by a food supply (cotyledons, endosperm, or both), becomes dormant; it stops growing and its metabolism nearly ceases. The embryo and its food supply are enclosed by a hard, protective seed coat formed from the integuments of the ovule.

We can take a closer look at one type of eudicot seed by splitting open the seed of a common garden bean. At this stage, the embryo consists of an elongate structure, the embryonic axis, attached to fleshy cotyledons (Figure 38.8a). Below the point at which the cotyledons are attached, the embryonic axis is called the hypocotyl (from the Greek *hypo*, under). The hypocotyl terminates in the radicle, or embryonic root. The portion of the embryonic axis above where the cotyledons are attached is the epicotyl (from the Greek *epi*, on, over). It consists of the shoot tip with a pair of miniature leaves.

The cotyledons of the common garden bean are packed with starch before the seed germinates because they absorbed carbohydrates from the endosperm when the seed developed. However, the seeds of some eudicots, such as castor beans (*Ricinus communis*), retain their food supply in the endosperm and have cotyledons that are very thin (Figure 38.8b). The cotyledons absorb nutrients from the endosperm and transfer them to the rest of the embryo when the seed germinates.

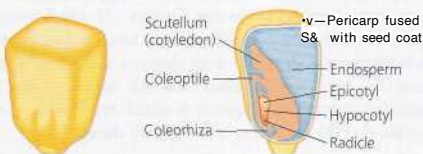
The embryo of a monocot has a single cotyledon (Figure 38.8c). Members of the grass family, including maize and wheat, have a specialized type of cotyledon called a scutellum (from the Latin *scutella*, small shield, a reference to the scutellum's shape). The scutellum is very thin, with a large surface area pressed against the endosperm, from which the scutellum absorbs nutrients during germination. The embryo of a grass seed



(a) Common garden bean, a eudicot with thick cotyledons. The fleshy cotyledons store food absorbed from the endosperm before the seed germinates.



(b) Castor bean, a eudicot with thin cotyledons. The narrow, membranous cotyledons (shown in edge and flat views) absorb food from the endosperm when the seed germinates.



(c) Maize, a monocot. Like all monocots, maize has only one cotyledon. Maize and other grasses have a large cotyledon called a scutellum. The rudimentary shoot is sheathed in a structure called the coleoptile, and the coleorhiza covers the young root.

### A Figure 38.8 Seed structure.

is enclosed by two sheaths: a coleoptile, which covers the young shoot, and a coleorhiza, which covers the young root.

## From Ovary to Fruit

While the seeds are developing from ovules, the ovary of the flower is developing into a fruit, which protects the enclosed seeds and, when mature, aids in their dispersal by wind or animals. Fertilization triggers hormonal changes that cause the ovary to begin its transformation into a fruit. If a flower has not been pollinated, fruit usually does not develop, and the entire flower withers and falls away.

During fruit development, the ovary wall becomes the pericarp, the thickened wall of the fruit. As the ovary grows, the other parts of the flower wither and are shed. For example, the pointed tip of a pea pod is the withered remains of the pea flower's stigma.

Fruits are classified into several types, depending on their developmental origin (Figure 38.9). Most fruits are derived from a single carpel or several fused carpels and are called