

# 28

## Plant Structure and Growth

### KEY CONCEPTS

- 28.1** Plants have a hierarchical organization consisting of organs, tissues, and cells
- 28.2** Meristems generate new cells for growth and control the developmental phases and life spans of plants
- 28.3** Primary growth lengthens roots and shoots
- 28.4** Secondary growth increases the diameter of stems and roots in woody plants

### OVERVIEW

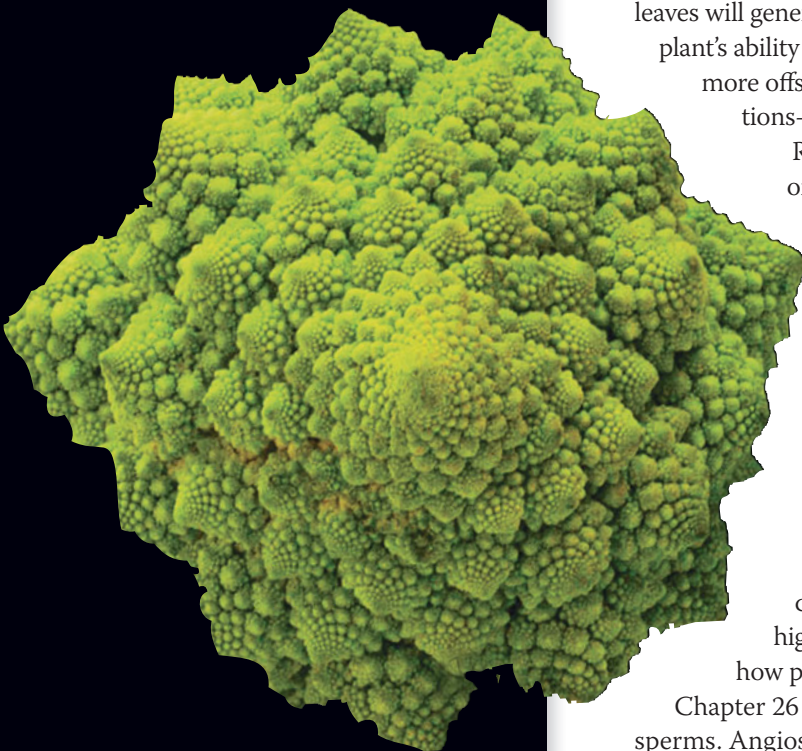
## Are Plants Computers?

The object in **Figure 28.1** is not the creation of a computer genius with a flair for the artistic. It is a head of romanesco, an edible relative of broccoli. Romanesco's mesmerizing beauty is attributable to the fact that each of its smaller buds resembles in miniature the entire vegetable. (Mathematicians refer to such repetitive patterns as *fractals*.) If romanesco looks like it was generated by a computer, it's because its growth pattern follows a repetitive sequence of instructions. As in most plants, the growing shoot tips lay down a pattern of stem . . . leaf . . . bud, over and over again. These repetitive developmental patterns are genetically determined and subject to natural selection. For example, a mutation that shortens the stem segments between leaves will generate a bushier plant. If this altered architecture enhances the plant's ability to access resources such as light and, by doing so, to produce more offspring, then this trait will occur more frequently in later generations—evolution will have occurred.

Romanesco is unusual in adhering so rigidly to its basic body organization. Most plants show much greater diversity in their individual forms because the growth of most plants, much more than in animals, is affected by local environmental conditions. All adult lions, for example, have four legs and are roughly the same size, but oak trees vary in the number and arrangement of their branches. This is because plants respond to challenges and opportunities in their local environment by altering their growth. (In contrast, animals typically respond by movement.) Illumination of a plant from the side, for example, creates asymmetries in its basic body plan. Branches grow more quickly from the illuminated side of a shoot than from the shaded side, an architectural change of obvious benefit for photosynthesis. Recognizing the highly adaptive development of plants is critical for understanding how plants acquire resources from their environment.

Chapter 26 described the evolution of plants from green algae to angiosperms. Angiosperms (flowering plants) are the primary producers in many terrestrial ecosystems and are of great agricultural importance. Taxonomists split the angiosperms into two major clades: *monocots*, named for their single cotyledon (seed leaf), and *eudicots*, which typically have two cotyledons. Monocots and eudicots have several other structural differences as well (**Figure 28.2**). In this chapter, we'll explore the structure and growth of both these types of flowering plants.

▼ **Figure 28.1** Computer art?



## CONCEPT 28.1

### Plants have a hierarchical organization consisting of organs, tissues, and cells

Plants, like most animals, are made up of organs, tissues, and cells. An **organ** consists of several types of tissues that together carry out particular functions. A **tissue** is a group of cells, consisting of one or more cell types, that together perform a specialized function. In looking at the hierarchy of plant organs, tissues, and cells, we begin with organs because they are the most familiar plant structures. As you learn about the hierarchy of plant structure, keep in mind how natural selection has produced plant forms that fit plant function at all levels of organization.





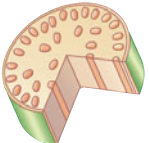
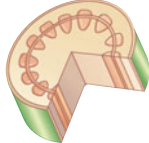






### The Three Basic Plant Organs: Roots, Stems, and Leaves

**EVOLUTION** The basic morphology of vascular plants reflects their evolutionary history as terrestrial organisms that inhabit and draw resources from two very different environments—below the ground and above the ground. They must absorb water and minerals from below the ground surface and CO<sub>2</sub> and light from above. The ability to acquire these resources efficiently is traceable to the evolution of three basic organs—roots, stems, and leaves. These organs form a **root system** and a **shoot system**, the latter consisting of stems and leaves (**Figure 28.3**). Vascular plants rely on both systems for survival. Roots, with few exceptions, are not photosynthetic; they starve unless *photosynthates*, the sugars and other carbohydrates produced during photosynthesis, are imported from the shoot system. Conversely, the shoot system depends on the water and minerals that roots absorb from the soil.

#### Roots

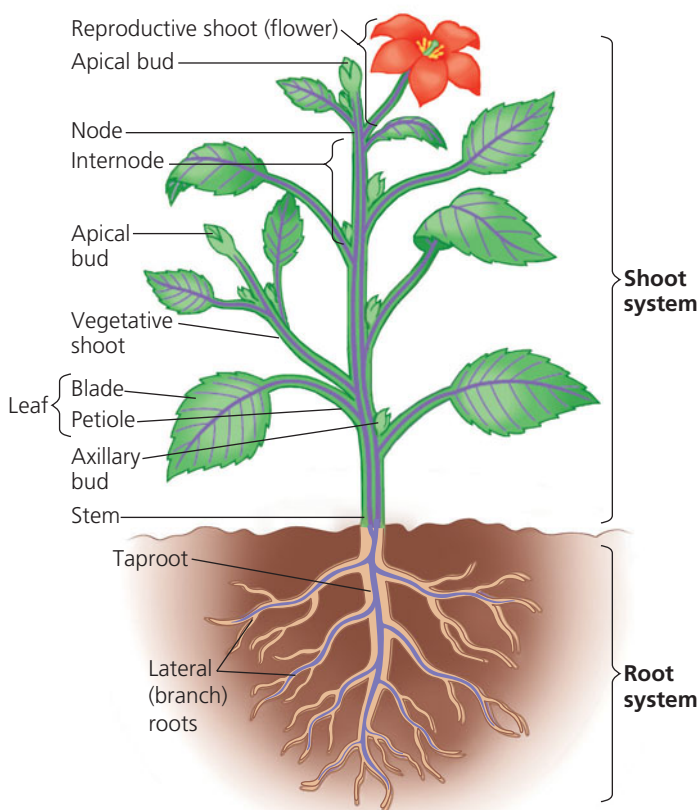
A **root** is an organ that anchors a vascular plant in the soil, absorbs minerals and water, and often stores carbohydrates. Tall, erect plants with large shoot masses generally have a *taproot system*, consisting of one main vertical root, the **taproot**, which penetrates the soil deeply and helps prevent the plant from toppling. In taproot systems, the role of absorption is restricted largely to **lateral roots**, which branch off from the taproot (see Figure 28.3). A taproot, although energetically expensive to make, allows the plant to be taller, thereby giving it access to more favorable light conditions and, in some cases, providing an advantage for pollen and seed dispersal.

Small plants or those that have a trailing growth habit are particularly susceptible to grazing animals that can potentially uproot the plant and kill it. Such plants are most efficiently anchored by a *fibrous root system*, a mat of thin roots spreading out below the soil surface (see Figure 28.2). In plants that have

	Monocots	Eudicots
Embryos	 One cotyledon	 Two cotyledons
Leaf venation	 Veins usually parallel	 Veins usually netlike
Stems	 Vascular tissue scattered	 Vascular tissue usually arranged in ring
Roots	 Root system usually fibrous (no main root)	 Taproot (main root) usually present
Pollen	 Pollen grain with one opening	 Pollen grain with three openings
Flowers	 Floral organs usually in multiples of three	 Floral organs usually in multiples of four or five

▲ **Figure 28.2 A comparison of monocots and eudicots.** These classes of angiosperms are named for the number of cotyledons (seed leaves) they typically possess. Monocots typically have one cotyledon. Eudicots typically have two cotyledons. Monocots include orchids, bamboos, palms, and lilies, as well as grasses, such as wheat, maize, and rice. A few examples of eudicots are beans, sunflowers, maples, and oaks.





▲ **Figure 28.3 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.

fibrous root systems, including most monocots, the embryonic root dies early on and does not form a taproot. Instead, many small roots emerge from the stem. Such roots are said to be *adventitious*, a term describing a plant organ that grows in an unusual location, such as roots arising from stems or leaves. Each root forms its own lateral roots, which in turn form their own lateral roots, thereby creating a thick mat of slender roots. Because these mats of fibrous roots hold the topsoil in place, plants such as grasses that have dense fibrous root systems are especially good for preventing soil erosion.

In most plants, the absorption of water and minerals occurs primarily near the tips of roots, where vast numbers of **root hairs**, thin, finger-like extensions of root epidermal cells, emerge and increase the surface area of the root enormously (**Figure 28.4**). Most terrestrial plant root systems also form



▲ **Figure 28.4 Root hairs of a radish seedling.** Root hairs grow by the thousands near the tip of each root. By increasing the root's surface area, they greatly enhance the absorption of water and minerals from the soil.

*mycorrhizal associations*, symbiotic interactions with soil fungi that increase a plant's ability to absorb minerals (see Figure 29.13).

Many plants have root adaptations with specialized functions (**Figure 28.5**). Some of these arise from the roots, and others are adventitious, developing from stems or, in rare cases, leaves. Some modified roots add support and anchorage. Others store water and nutrients or absorb oxygen from the air.

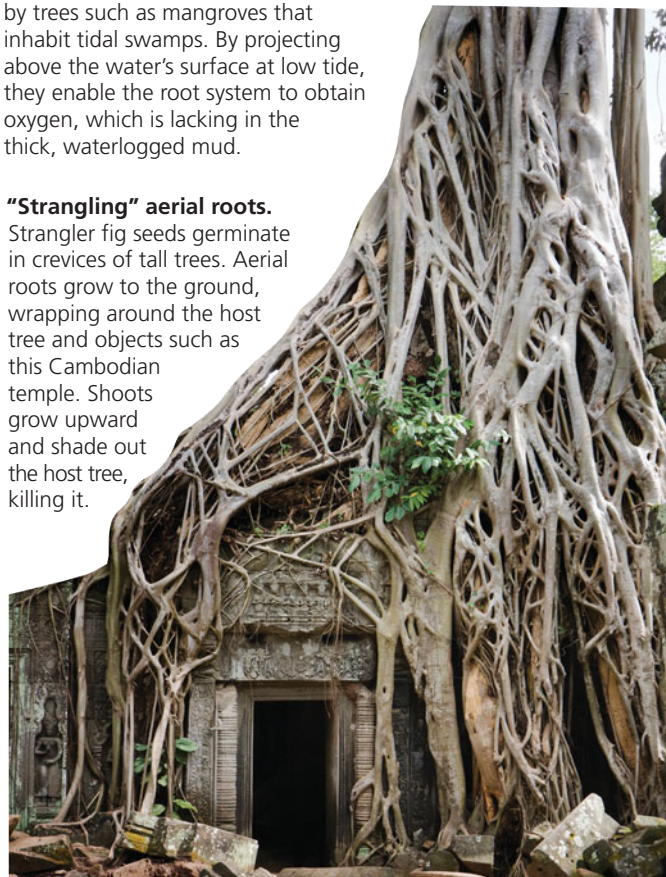


▲ **Pneumatophores.** Also known as air roots, pneumatophores are produced by trees such as mangroves that inhabit tidal swamps. By projecting above the water's surface at low tide, they enable the root system to obtain oxygen, which is lacking in the thick, waterlogged mud.



▲ **Storage roots.** Many plants, such as the common beet, store food and water in their roots.

► **"Strangling" aerial roots.** Strangler fig seeds germinate in crevices of tall trees. Aerial roots grow to the ground, wrapping around the host tree and objects such as this Cambodian temple. Shoots grow upward and shade out the host tree, killing it.



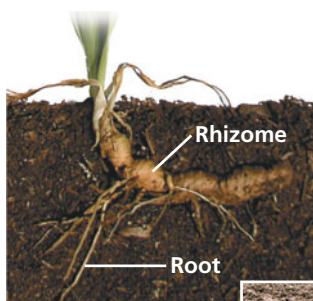
▲ **Figure 28.5 Evolutionary adaptations of roots.**



## Stems

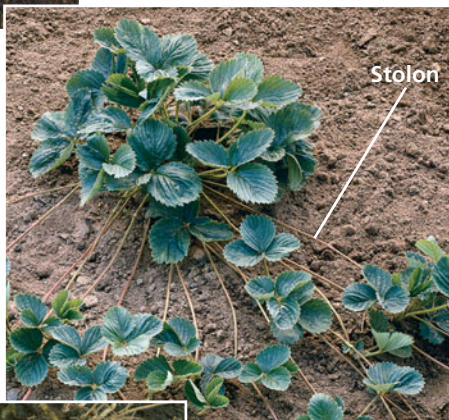
In a typical plant, a **stem** is the organ to which leaves are attached. Its chief function is to elongate and orient the shoot in a way that maximizes photosynthesis by the leaves. Another function of stems is to elevate reproductive structures, thereby facilitating the dispersal of pollen and fruit. Green stems may also perform a limited amount of photosynthesis. Each stem consists of an alternating system of **nodes**, the points at which leaves are attached, and **internodes**, the stem segments between nodes (see Figure 28.3). Most of the growth of a young shoot is concentrated near the shoot tip, which consists of an **apical bud** composed of developing leaves and a compact series of nodes and internodes. Apical buds are not the only types of buds found in shoots. In the upper angle (axil) formed by each leaf and the stem is a dormant **axillary bud**, a structure that can potentially form a lateral branch or, in some cases, a thorn or flower.

Some plants have stems with alternative functions, such as food storage or asexual reproduction. Many of these modified stems, including rhizomes, bulbs, stolons, and tubers, are often mistaken for roots (**Figure 28.6**).



◀ **Rhizomes.** The base of this iris plant is an example of a rhizome, a horizontal shoot that grows just below the surface. Vertical shoots emerge from axillary buds on the rhizome.

▶ **Stolons.** Shown here on a strawberry plant, stolons are horizontal shoots that grow along the surface. These “runners” enable a plant to reproduce asexually, as plantlets form at nodes along each runner.



◀ **Tubers.** Tubers, such as these potatoes, are enlarged ends of rhizomes or stolons specialized for storing food. The “eyes” of a potato are clusters of axillary buds that mark the nodes.

▲ **Figure 28.6** Evolutionary adaptations of stems.

## Leaves

In most vascular plants, the **leaf** is the main photosynthetic organ. In addition to intercepting light, leaves exchange gases with the atmosphere, dissipate heat, and defend themselves from herbivores and pathogens. These functions may have conflicting physiological, anatomical, or morphological requirements. For example, a dense covering of hairs may help repel herbivorous insects but may also trap air near the leaf surface, thereby reducing gas exchange and, consequently, photosynthesis. Because of these conflicting demands and trade-offs, leaves vary extensively in form. In general, however, a leaf consists of a flattened **blade** and a stalk, the **petiole**, which joins the leaf to the stem at a node (see Figure 28.3). Grasses and many other monocots lack petioles; instead, the base of the leaf forms a sheath that envelops the stem. 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 blade. Eudicots generally have a branched network of major veins (see Figure 28.2). The morphological features of leaves are often a product of genetic programs that are tweaked to varying extents by environmental influences. Interpret the data in the **Scientific Skills Exercise** (p. 560) to explore the roles of genetics and the environment in determining the leaf morphology of red maple trees.

Almost all leaves are specialized for photosynthesis. However, some species have leaves with adaptations that enable them to perform additional functions, such as support, protection, storage, or reproduction (**Figure 28.7**).

## Dermal, Vascular, and Ground Tissue Systems

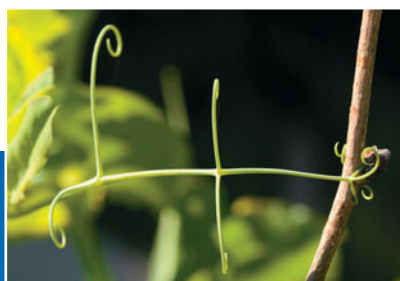
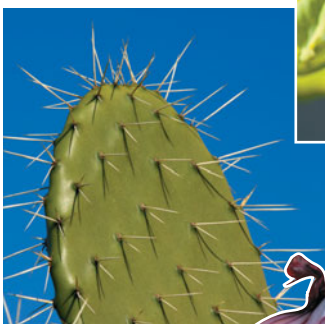
All plant organs—roots, stems, and leaves—are composed of three fundamental tissue systems: dermal, vascular, and ground tissue. These tissue systems are continuous throughout the plant, but their specific characteristics and spatial relationships to one another vary in different organs (**Figure 28.8**).

The **dermal tissue system** is the plant’s outer protective covering. Like our skin, it forms the first line of defense against physical damage and pathogens. In nonwoody plants, it is usually a single tissue called the **epidermis**, a layer of tightly packed cells. In leaves and most stems, the **cuticle**, a waxy coating on the epidermal surface, helps prevent water loss. In woody plants, protective tissues called **periderm** replace the epidermis in older regions of stems and roots. In addition to protecting the plant from water loss and disease, the epidermis has specialized characteristics in each organ. For example, a root hair is an extension of an epidermal cell near the tip of a root. *Trichomes* are hairlike outgrowths of the shoot epidermis. In some desert species, trichomes reduce water loss and reflect excess light, but their most common function is to defend against herbivores and pathogens by forming a mechanical barrier or secreting chemicals.

The chief functions of the **vascular tissue system** are to facilitate the transport of materials through the plant and to



► **Tendrils.** The tendrils by which this pea plant clings to a support are modified leaves. After it has “lassoed” a support, a tendril 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.



◀ **Spines.** The spines of cacti, such as this prickly pear, are actually leaves; photosynthesis is carried out by the fleshy green stems.



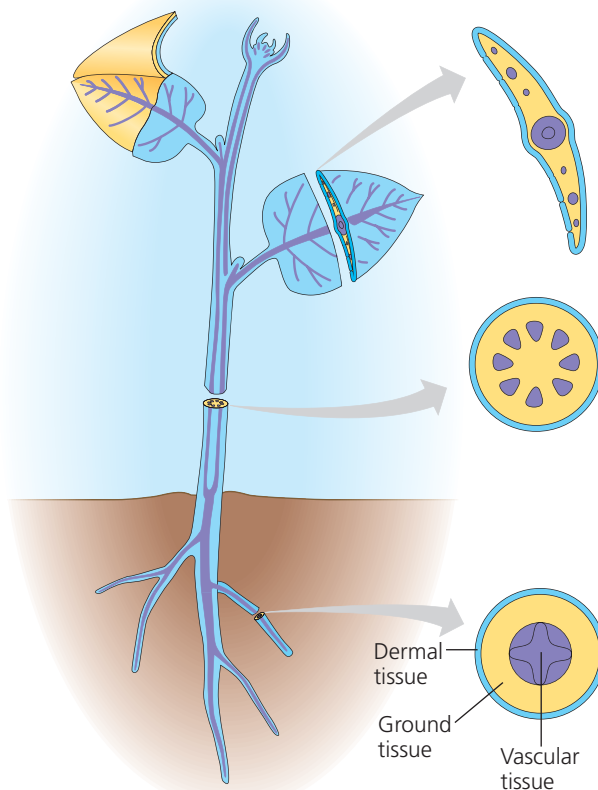
◀ **Storage leaves.** Bulbs, such as this cut onion, have a short underground stem and modified leaves that store food.

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

▲ **Figure 28.7** Evolutionary adaptations of leaves.

provide mechanical support. The two types of vascular tissues are xylem and phloem. **Xylem** conducts water and dissolved minerals upward from roots into the shoots. **Phloem** transports sugars, the products of photosynthesis, 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 the species and organ. In angiosperms, for example, the root stele is a solid central *vascular cylinder* of xylem and phloem, whereas the stele of stems and leaves consists of *vascular bundles*, separate strands containing xylem and phloem (see Figure 28.8). Both xylem and phloem are composed of a variety of cell types, including cells that are highly specialized for transport or support.

Tissues that are neither dermal nor vascular are part of the **ground tissue system**. Ground tissue that is internal to the vascular tissue is known as **pith**, and ground tissue that is external to the vascular tissue is called **cortex**. The ground tissue system is not just filler. It may include cells specialized for functions such as photosynthesis, short-distance transport, storage, or support.



▲ **Figure 28.8** The three tissue systems. The dermal tissue system (blue) provides a protective cover for the entire body of a plant. The vascular tissue system (purple), which transports materials between the root and shoot systems, is also continuous throughout the plant, but is arranged differently in each organ. The ground tissue system (yellow), which is responsible for most of the plant’s metabolic functions, is located between the dermal tissue and the vascular tissue in each organ.

## Common Types of Plant Cells

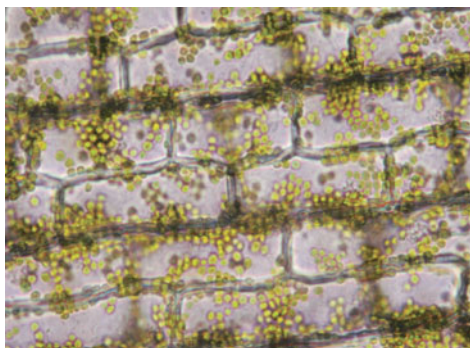
**Figure 28.9** focuses on the major types of plant cells: parenchyma cells, collenchyma cells, sclerenchyma cells, the water-conducting cells of the xylem, and the sugar-conducting cells of the phloem. Notice the structural adaptations in the different cells that make their specific functions possible. You may also wish to review basic plant cell structure (see Figures 4.7 and 4.25).

### CONCEPT CHECK 28.1

1. How does the vascular tissue system enable leaves and roots to function together in supporting growth and development of the whole plant?
2. **WHAT IF?** If humans were photoautotrophs, making food by capturing light energy for photosynthesis, how might our anatomy be different?
3. **MAKE CONNECTIONS** Explain how central vacuoles and cellulose cell walls contribute to plant growth (see Concepts 4.4 and 4.7).

For suggested answers, see Appendix A.

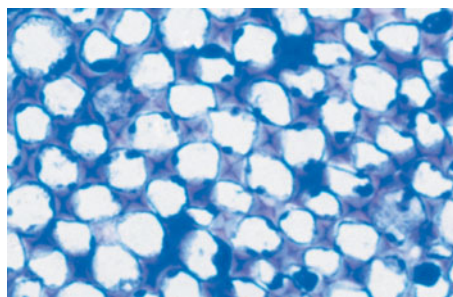
## Parenchyma Cells



**Parenchyma cells** with chloroplasts  
(in *Elodea* leaf) (LM) 60 μm

Mature **parenchyma cells** have primary walls that are relatively thin and flexible, and most lack secondary walls. (See Figure 4.25 to review primary and secondary cell walls.) When mature, parenchyma cells generally have a large central vacuole. 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 many fruits is composed mainly of parenchyma cells. Most parenchyma cells retain the ability to divide and differentiate into other types of plant cells under particular conditions—during wound repair, for example. It is even possible to grow an entire plant from a single parenchyma cell.

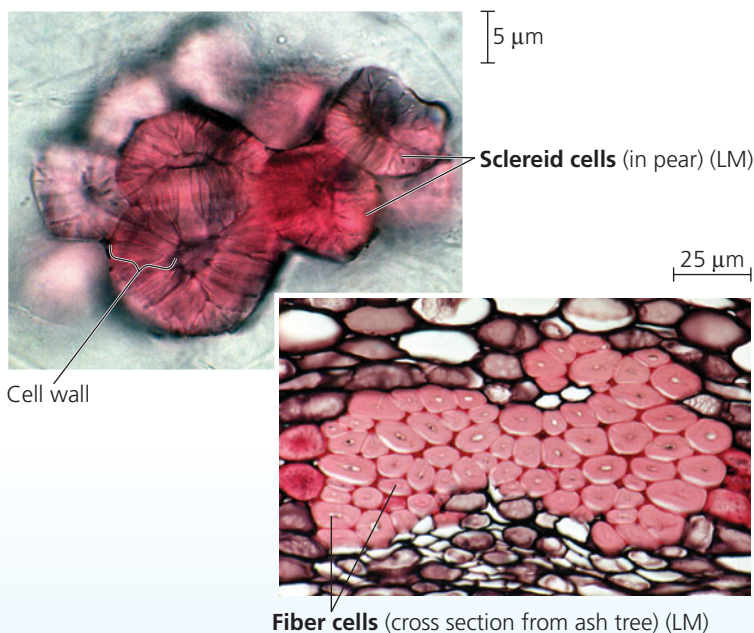
## Collenchyma Cells



**Collenchyma cells**  
(in *Helianthus* stem) (LM) 5 μm

Grouped in strands, **collenchyma cells** (seen here in cross section) help support young parts of the plant shoot. Collenchyma cells are generally elongated cells that 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. Collenchyma cells provide flexible support without restraining growth. At maturity, these cells are living and flexible, elongating with the stems and leaves they support—unlike sclerenchyma cells, which we discuss next.

## Sclerenchyma Cells



**Sclerenchyma cells** also function as supporting elements in the plant but are much more rigid than collenchyma cells. In sclerenchyma cells, the secondary cell wall, produced after cell elongation has ceased, is thick and contains large amounts of **lignin**, a relatively indigestible strengthening polymer that accounts for more than a quarter of the dry mass of wood. Lignin is present in all vascular plants but not in bryophytes. 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 (the living part of the cell) dies. The rigid walls remain as a “skeleton” that supports the plant, in some cases for hundreds of years.

Two types of sclerenchyma cells, known as **sclereids** and **fibers**, are specialized entirely for support and strengthening. Sclereids, which are boxier 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 grouped in strands, are long, slender, and tapered. Some are used commercially, such as hemp fibers for making rope and flax fibers for weaving into linen.



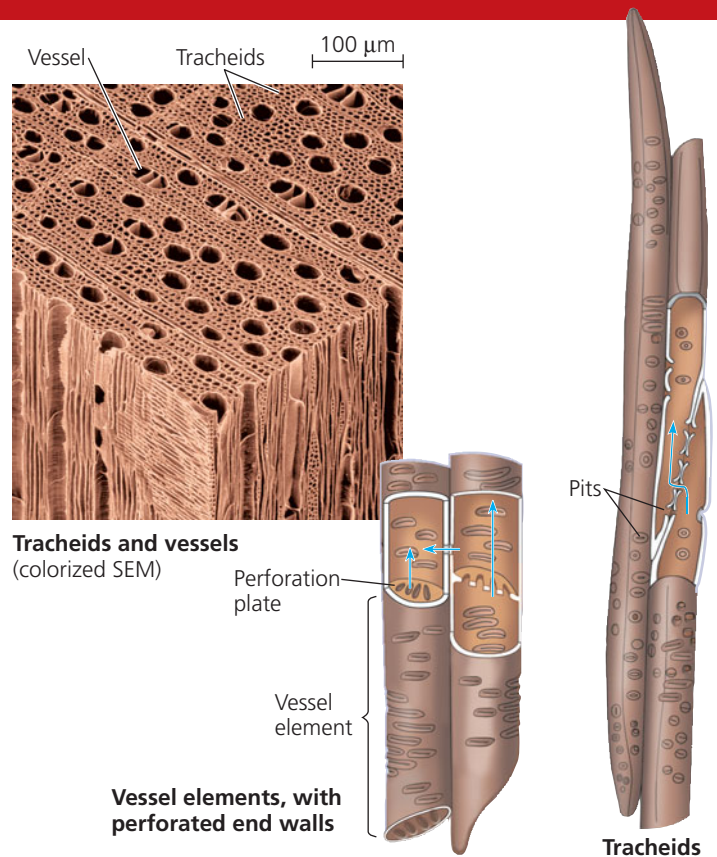
## Water-Conducting Cells of the Xylem

The two types of water-conducting cells, **tracheids** and **vessel elements**, are tubular, elongated cells that are dead at functional maturity. Tracheids occur 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 living cellular contents of a tracheid or vessel element disintegrate, the cell's thickened 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 4.25 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.

Vessel elements are generally wider, shorter, thinner walled, and less tapered than the tracheids. They are aligned end to end, forming long pipes known as **vessels** that in some cases are visible with the naked eye. The end walls of vessel elements have perforation plates that enable water to flow freely through the vessels.

The secondary walls of tracheids and vessel elements are hardened with lignin. This hardening provides support and prevents collapse under the tension of water transport.



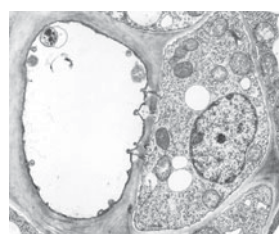
## Sugar-Conducting Cells of the Phloem

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 that are called **sieve-tube elements**, or sieve-tube members.

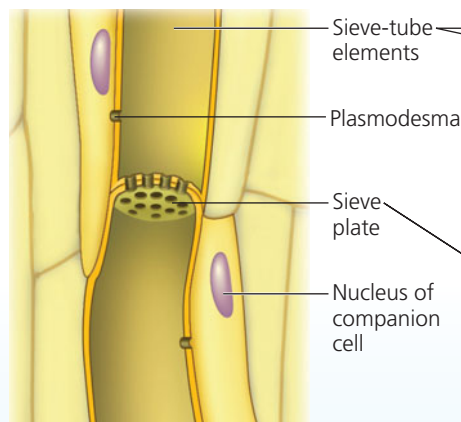
Though alive, sieve-tube elements lack a nucleus, ribosomes, a distinct vacuole, and cytoskeletal elements. This reduction in cell contents enables nutrients to pass more easily through the cell. The end walls between sieve-tube elements, called **sieve plates**, have pores that facilitate the flow of fluid from cell to cell along the sieve tube. Alongside each sieve-tube element is a nonconducting cell called a **companion cell**, which is connected to the sieve-tube element by numerous plasmodesmata (see Figure 4.25). The nucleus and ribosomes of the companion cell serve not only that cell itself but also the adjacent sieve-tube element. In some plants, the companion cells in leaves also help load sugars into the sieve-tube elements, which then transport the sugars to other parts of the plant.



Visit the Study Area in **MasteringBiology** for the BioFlix® 3-D Animation Tour of a Plant Cell.



**Sieve-tube element (left) and companion cell: cross section (TEM)**



**Sieve-tube elements: longitudinal view**

**Sieve-tube elements: longitudinal view (LM)**



**Sieve plate with pores (LM)**

Using Bar Graphs to Interpret Data

Nature versus Nurture: Why Are Leaves from Northern Red Maples “Toothier” Than Leaves from Southern Red Maples?

Not all leaves of red maple (*Acer rubrum*) are the same. The “teeth” along the margins of leaves growing in northern locations differ in size and number compared with their southern counterparts. (The leaf seen here has an intermediate appearance.) Are these morphological differences due to genetic differences between northern and southern *A. rubrum* populations, or do they arise from environmental differences between northern and southern locations, such as average temperature, that affect gene expression?



**How the Experiment Was Done** Seeds of *Acer rubrum* were collected from four latitudinally distinct sites: Ontario (Canada), Pennsylvania, South Carolina, and Florida. The seeds collected from the four locations were then grown in a northern location (Rhode Island) and a southern location (Florida). After a few years of growth, leaves were harvested from the four sets of plants growing in the two locations. The average area of single teeth and the average number of teeth per leaf area were determined.


Data from the Experiment

Seed Collection Site	Average Area of a Single Tooth (cm <sup>2</sup> )		Number of Teeth per cm <sup>2</sup> of Leaf Area	
	Grown in Rhode Island	Grown in Florida	Grown in Rhode Island	Grown in Florida
Ontario 43.32°N	0.017	0.017	3.9	3.2
Pennsylvania 42.12°N	0.020	0.014	3.0	3.5
South Carolina 33.45°N	0.024	0.028	2.3	1.9
Florida 30.65°N	0.027	0.047	2.1	0.9

Interpret the Data

1. Make a bar graph for tooth size and a bar graph for number of teeth. (For additional information about bar graphs, see the Scientific Skills Review in Appendix F and in the Study Area in MasteringBiology.) From north to south, what is the general trend in tooth size and number of teeth in leaves of *Acer rubrum*?
2. Based on the data above, would you estimate that leaf tooth traits in red maple are largely determined by genetic heritage (genotype) or the capacity for responding to environmental change within a single genotype (phenotypic plasticity) or both? Make specific reference to the data in answering the question.
3. The “toothiness” of leaf fossils of known age has been used by paleoclimatologists to estimate past temperatures in a region. If a 10,000-year-old fossilized red maple leaf from South Carolina had an average of 4.2 teeth per square centimeter of leaf area, what could you infer about the relative temperature of South Carolina 10,000 years ago compared with today? Explain your reasoning.

**Data from** D. L. Royer et al., Phenotypic plasticity of leaf shape along a temperature gradient in *Acer rubrum*, *PLoS ONE* 4(10): e7653 (2009).

 A version of this Scientific Skills Exercise can be assigned in MasteringBiology.

Meristems generate new cells for growth and control the developmental phases and life spans of plants

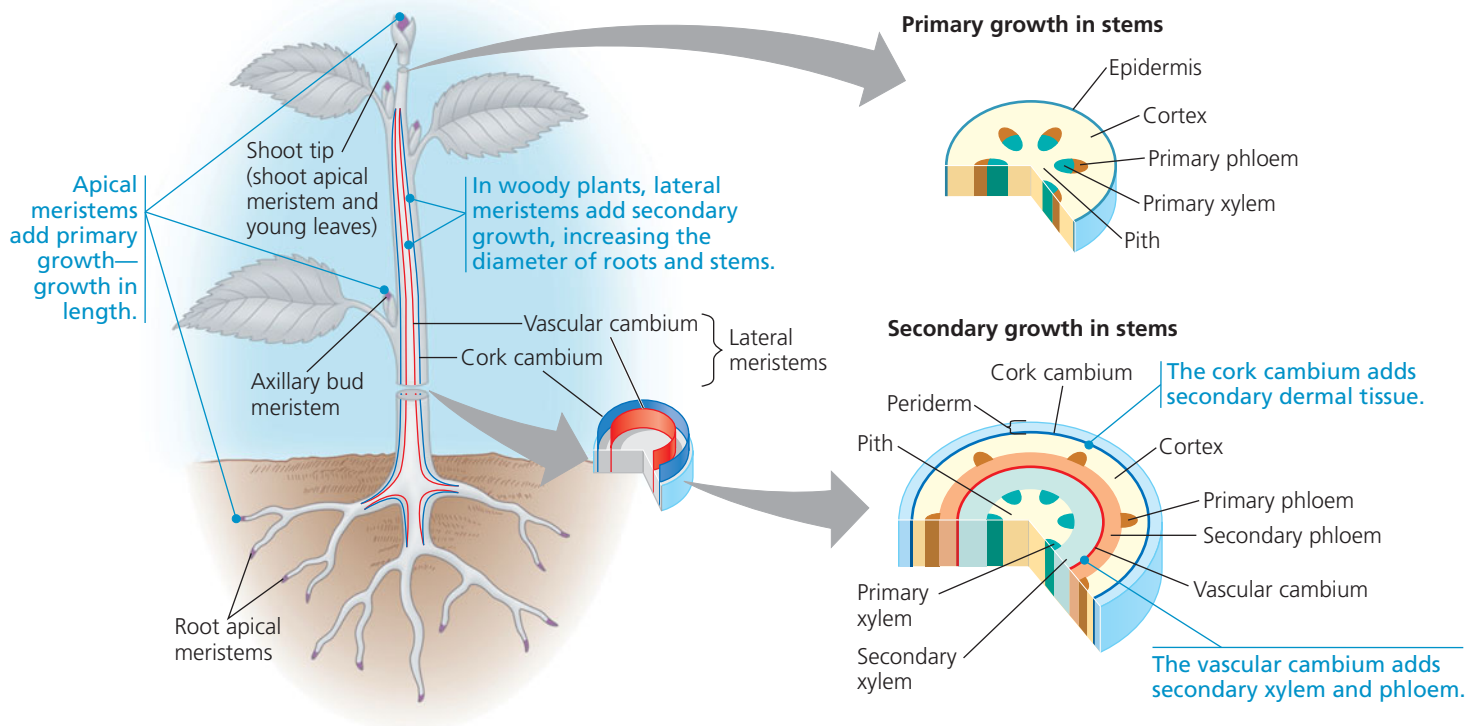
How do plant organs develop? A major difference between plants and most animals is that plant growth is not limited to an embryonic or juvenile period. Instead, growth occurs throughout the plant’s life, a process known as **indeterminate growth**. Plants are capable of indeterminate growth because they have perpetually undifferentiated tissues called **meristems** that divide when conditions permit, leading to new cells that can elongate. At any given time, a typical plant has embryonic, developing, and mature organs. Except for dormant periods, most plants grow continuously. In contrast, most animals and some plant organs—such as leaves, thorns, and flowers—undergo **determinate growth**; that is, they stop growing after reaching a certain size.

Different Meristems Produce Primary and Secondary Growth

There are two main types of meristems: apical meristems and lateral meristems (**Figure 28.10**). **Apical meristems**, located at the tips of roots and shoots and in axillary buds of shoots, provide additional cells that enable growth in length, a process known as **primary growth**. Primary growth allows roots to extend throughout the soil and shoots to increase their exposure to light. In herbaceous (nonwoody) plants, primary growth produces all, or almost all, of the plant body. Woody plants, however, also grow in circumference in the parts of stems and roots that no longer grow in length. This growth in thickness, known as **secondary growth**, is caused by **lateral meristems** called the vascular cambium and cork cambium. These cylinders of dividing cells extend along the length of roots and stems. The **vascular cambium** adds layers of vascular tissue called secondary xylem (wood) and secondary phloem. The **cork cambium** replaces the epidermis with the thicker, tougher periderm.

The relationship between primary and secondary growth is clearly seen in the winter twig of a deciduous tree. At the shoot tip is the dormant apical bud, enclosed by scales that protect its apical meristem (**Figure 28.11**). In spring, the bud sheds its scales and begins a new spurt of primary growth, producing a series of nodes and internodes. Along each growth segment, nodes are marked by scars that were left when leaves fell. Above each leaf scar is an axillary bud or a branch formed by an axillary bud. Farther down the twig are bud scars from the whorls of scales that enclosed the apical bud during the previous winter. During each growing season, primary growth extends the shoots, and secondary growth increases the diameter of the parts that formed in previous years.





▲ **Figure 28.10** An overview of primary and secondary growth.

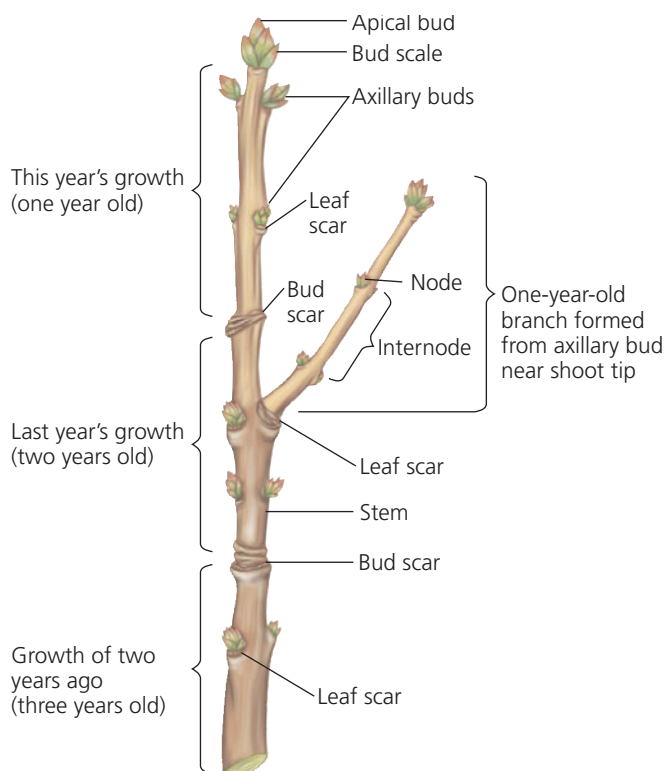
The cells within meristems divide relatively frequently, generating additional cells. Some new cells remain in the meristem and produce more cells, while others differentiate and are incorporated into tissues and organs of the growing plant. Cells

that remain as sources of new cells have traditionally been called *initials* but are increasingly being called *stem cells* to correspond to animal stem cells, which also perpetually divide and remain undifferentiated. The new cells displaced from the meristem, called *derivatives*, divide until the cells they produce become specialized in mature tissues.

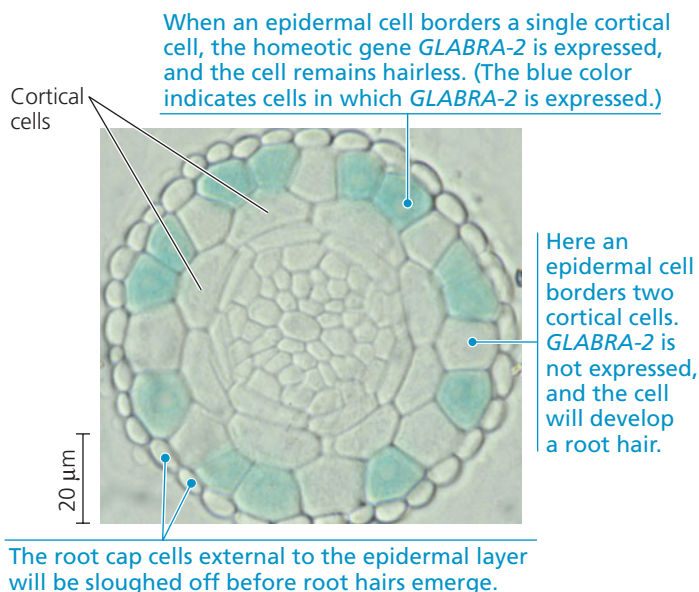
## Gene Expression and Control of Cell Differentiation

Derivative cells can diverge in structure and function even though they share a common genome. Such cell differentiation depends, to a large degree, on the control of gene expression—the regulation of transcription and translation, resulting in the production of specific proteins. Although cell differentiation depends on the control of gene expression, the fate of a plant cell is determined by its final position in the developing organ.

Evidence suggests that the activation or inactivation of specific genes involved in cell differentiation depends largely on cell-to-cell communication. For example, two cell types arise in the root epidermis of the model plant *Arabidopsis thaliana*: root hair cells and hairless epidermal cells. Cell fate is associated with the position of the epidermal cells. The immature epidermal cells that are in contact with two underlying cells of the root cortex differentiate into root hair cells, whereas the immature epidermal cells in contact with only one cortical cell differentiate into mature hairless cells. Differential expression of a gene called *GLABRA-2* (from the Latin *glaber*, bald) is required for appropriate root hair distribution. Researchers have demonstrated this requirement by coupling the *GLABRA-2*



▲ **Figure 28.11** Three years' growth in a winter twig.



▲ **Figure 28.12** Control of root hair differentiation by a master regulatory gene (LM).

**WHAT IF?** What would the roots look like if *GLABRA-2* were rendered dysfunctional by a mutation?

gene to a “reporter gene” that causes every cell expressing *GLABRA-2* in the root to turn pale blue following a certain treatment. The *GLABRA-2* gene is normally expressed only in epidermal cells that will not develop root hairs (**Figure 28.12**).

## Meristematic Control of the Transition to Flowering and the Life Spans of Plants

**Vegetative growth**—the production of leaves, stems, and roots (as well as asexual, or vegetative, reproduction)—is only one phase in a plant’s life. Most angiosperms at some point in their life direct some or all of their shoot apical meristems to undergo a transition from vegetative growth to *reproductive growth*, the production of flowers, fruits, and seeds. This transition is triggered by a combination of environmental cues, such as day length, and internal signals, such as hormones. (You will learn more about the roles of these signals in flowering in Chapter 31.) Unlike vegetative growth, which is indeterminate, reproductive growth is determinate: The production of a flower by a shoot apical meristem stops the primary growth of that shoot. Some plants may also go through a juvenile phase during which they are incapable of reproductive growth.

Based on the timing and completeness of a plant species’ switch from vegetative to reproductive growth, 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 most staple food crops, including legumes and cereal grains such as wheat and rice. *Biennials*, such as turnips, generally require two growing seasons to complete their life cycle, flowering and fruiting only in their second year. *Perennials* live many years and include trees, shrubs, and some grasses.

### CONCEPT CHECK 28.2

1. Distinguish between primary and secondary growth.
2. Roots and stems grow indeterminately, but leaves do not. How might this benefit the plant?
3. **WHAT IF?** A gardener leaves carrots in the ground for two years, thinking their roots will grow larger during the second year since they are biennials. Is this a good idea? Explain.

For suggested answers, see Appendix A.

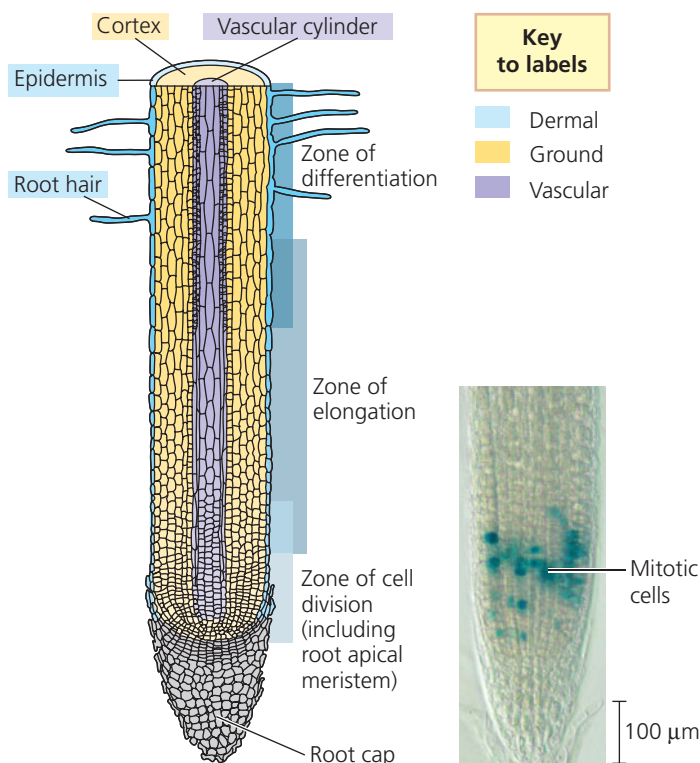
## CONCEPT 28.3

### Primary growth lengthens roots and shoots

Primary growth arises directly from cells produced by apical meristems. In herbaceous plants, the plant is produced almost entirely by primary growth; in woody plants, only the nonwoody, more recently formed parts of the plant represent primary growth. Although the elongation of both roots and shoots arises from cells derived from apical meristems, the primary growth of roots and primary growth of shoots differ in many ways.

#### Primary Growth of Roots

The tip of a root is covered by a thimble-like **root cap** (**Figure 28.13**), which protects the delicate apical meristem as the root



▲ **Figure 28.13** Primary growth of a typical eudicot root. The root apical meristem produces all the cells of the root and the root cap. Most lengthening of the root occurs in the zone of elongation. In the micrograph, cells undergoing mitosis in the apical meristem are revealed by staining for cyclin, a protein that plays an important role in cell division (LM).



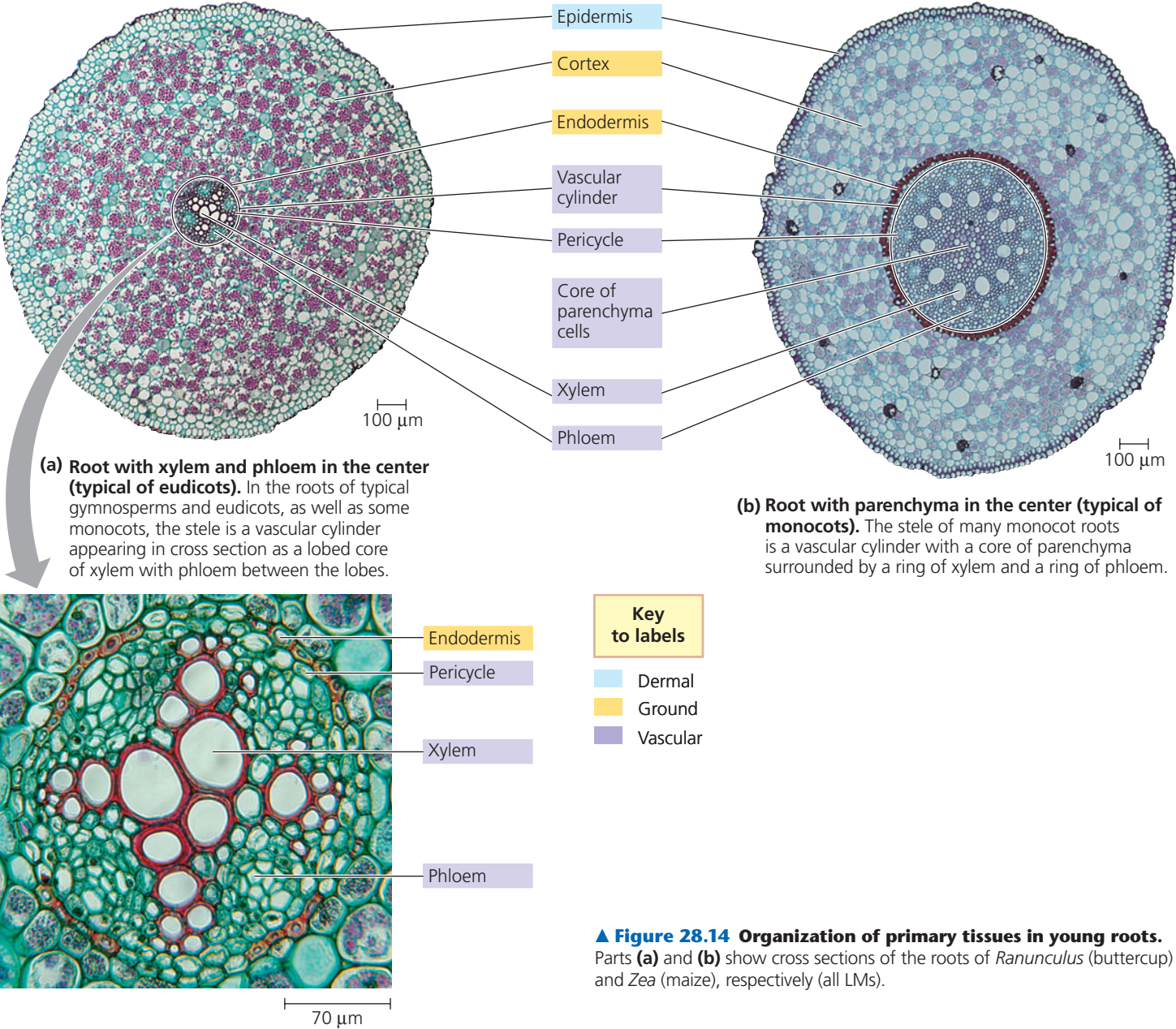
pushes through the abrasive soil during primary growth. The root cap also secretes a polysaccharide slime that lubricates the soil around the tip of the root. Growth occurs just behind the tip in three overlapping zones of cells at successive stages of primary growth. These are the zones of cell division, elongation, and differentiation (see Figure 28.13).

The *zone of cell division* includes the root apical meristem and its derivatives. New root cells are produced in this region, including cells of the root cap. Typically, a few millimeters behind the tip of the root is the *zone of elongation*, where most of the growth occurs as root cells elongate—sometimes to more than ten times their original length. Cell elongation in this zone pushes the 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; for example, roots hairs start to form. In the *zone*

*of differentiation*, or zone of maturation, cells complete their differentiation and become distinct cell types.

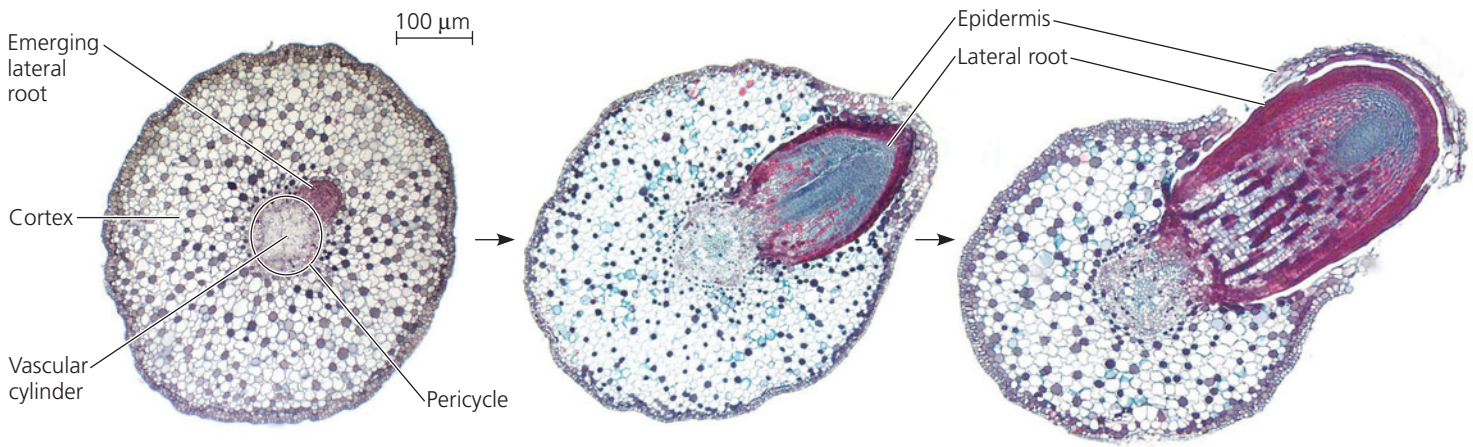
The primary growth of a root produces its epidermis, ground tissue, and vascular tissue. **Figure 28.14** shows in cross section the three primary tissue systems in the young roots of a eudicot (*Ranunculus*, buttercup) and a monocot (*Zea*, maize). These represent two basic patterns of root organization, of which there are many variations, depending on the plant species.

In angiosperm roots, the stele is a vascular cylinder, consisting of a solid core of xylem and phloem tissues (**Figure 28.14a**). In most eudicot roots, the xylem has a starlike appearance in cross section, and the phloem occupies the indentations between the arms of the xylem “star.” In many monocot roots, the vascular tissue consists of a central core of undifferentiated parenchyma cells surrounded by a ring of alternating and differentiated xylem and phloem tissues (**Figure 28.14b**).



**▲ Figure 28.14 Organization of primary tissues in young roots.** Parts (a) and (b) show cross sections of the roots of *Ranunculus* (buttercup) and *Zea* (maize), respectively (all LMIs).





▲ **Figure 28.15 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 light micrographs, the view of the original root is a cross section, while the view of the lateral root is a longitudinal section.

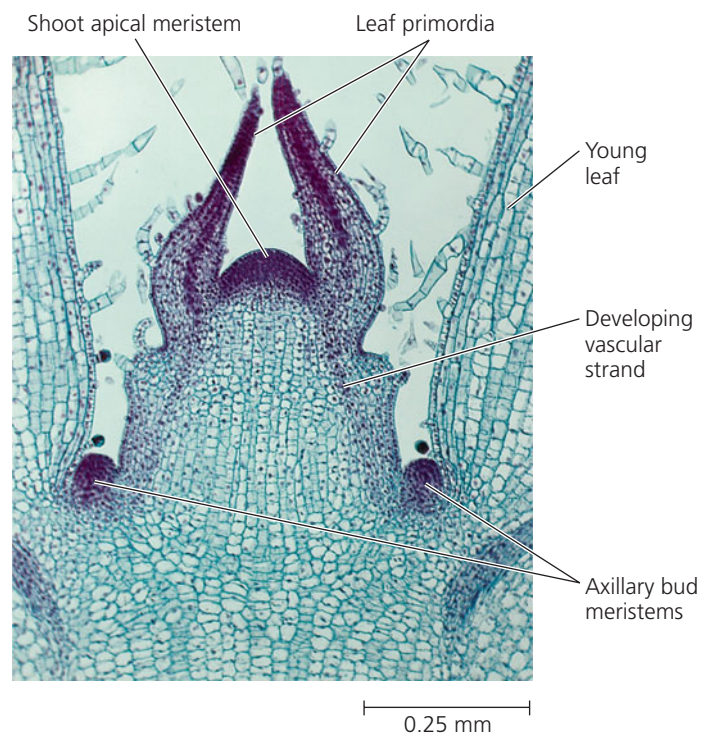
The ground tissue of roots, consisting mostly of parenchyma cells, is found in the cortex, the region between the vascular cylinder and epidermis. In addition to storing carbohydrates, cortical cells transport water and salts from the root hairs to the center of the root. The cortex, because of its large intercellular spaces, also allows for the *extracellular* diffusion of water, minerals, and oxygen from the root hairs inward. The innermost layer of the cortex is called the **endodermis**, a cylinder one cell thick that forms the boundary with the vascular cylinder. The endodermis is a selective barrier that regulates passage of substances from the soil into the vascular cylinder (see Figure 29.16).

Lateral roots arise from the **pericycle**, the outermost cell layer in the vascular cylinder, which is adjacent to and just inside the endodermis (see Figure 28.14). A lateral root pushes through the cortex and epidermis until it emerges from the established root (**Figure 28.15**).

## Primary Growth of Shoots

A shoot apical meristem is a dome-shaped mass of dividing cells at the shoot tip (**Figure 28.16**). Leaves develop from **leaf primordia** (singular, *primordium*), projections shaped like a cow's horn that emerge along the sides of the shoot apical meristem. Within a bud, young leaves are spaced close together because the internodes are very short. Shoot elongation is due to the lengthening of internode cells below the shoot tip.

Branching, which is also part of primary growth, arises from the activation of axillary buds. Within each axillary bud is a shoot apical meristem. Its dormancy results from inhibition by an active apical bud, a phenomenon called **apical dominance**. Generally, the closer an axillary bud is to an active apical bud, the more inhibited it is. If an animal eats the end of the shoot or if shading results in the light being more intense on the side of the shoot, axillary buds break dormancy and start growing. A growing axillary bud gives rise to a lateral shoot, complete with its own apical bud, leaves, and axillary buds. Removing the apical bud stimulates the growth of axillary buds, resulting

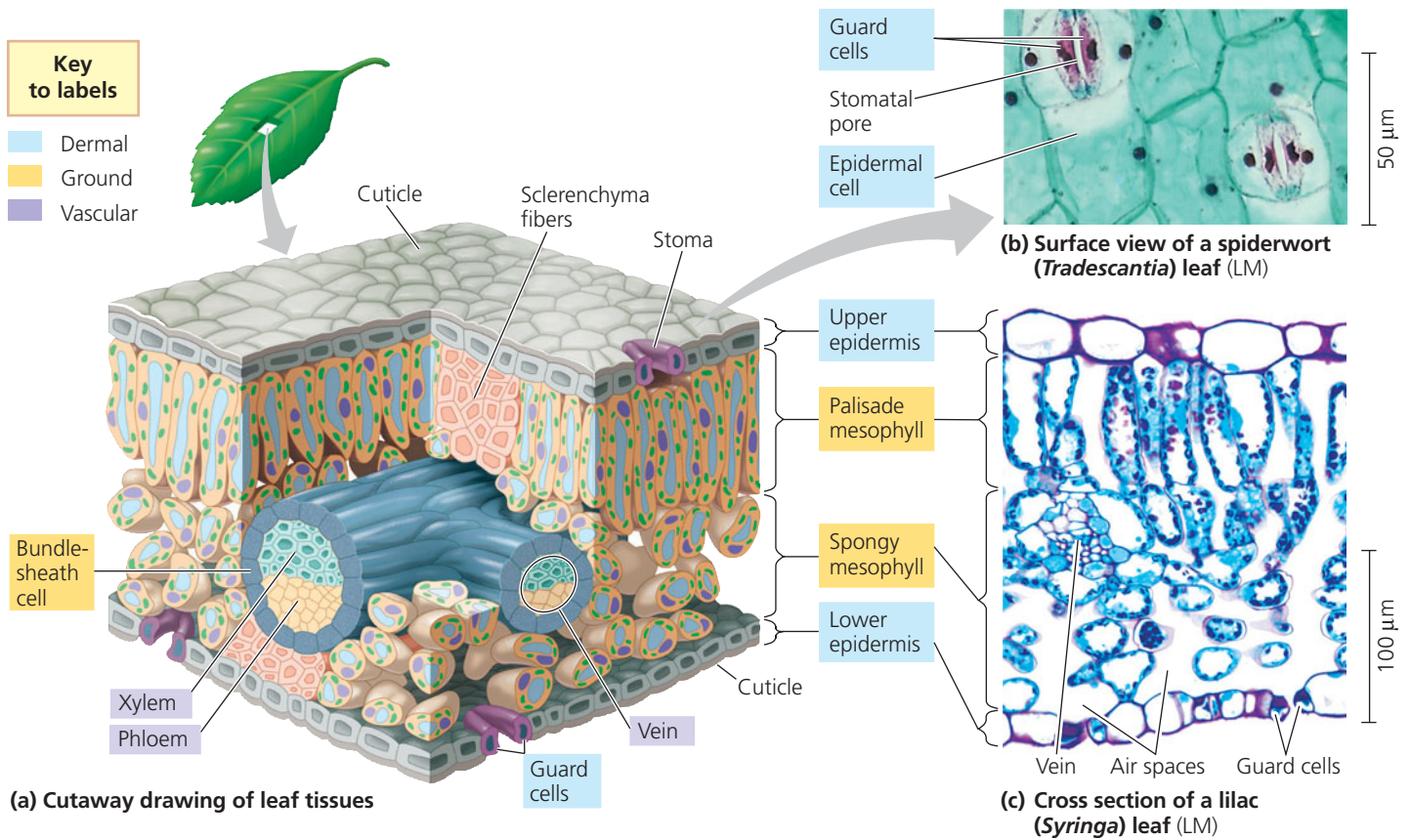


▲ **Figure 28.16 The shoot tip.** Leaf primordia arise from the flanks of the dome of the apical meristem. This is a longitudinal section of the shoot tip of *Coleus* (LM).

in more and longer branches. That is why pruning trees and shrubs and pinching back houseplants will make them bushier. (The hormonal changes underlying apical dominance are discussed in Concept 31.1.)

In some monocots, particularly grasses, meristematic activity occurs at the bases of stems and leaves. These areas, called *intercalary meristems*, allow damaged leaves to rapidly regrow, which accounts for the ability of lawns to grow following mowing. The ability of grasses to regrow leaves by intercalary meristems enables the plant to recover more effectively from damage incurred from grazing herbivores.





▲ **Figure 28.17** Leaf anatomy.

## Tissue Organization of Leaves

**Figure 28.17** provides an overview of leaf structure. The epidermis is interrupted by pores called **stomata** (singular, *stoma*), which allow exchange of  $\text{CO}_2$  and  $\text{O}_2$  between the surrounding air and the photosynthetic cells inside the leaf. In addition to regulating  $\text{CO}_2$  uptake for photosynthesis, stomata are major avenues for the evaporative loss of water. The term *stoma* can refer to the stomatal pore or to the entire stomatal complex consisting of a pore flanked by two specialized epidermal cells called **guard cells**, which regulate the opening and closing of the pore. (We'll discuss stomata in detail in Concept 29.6.)

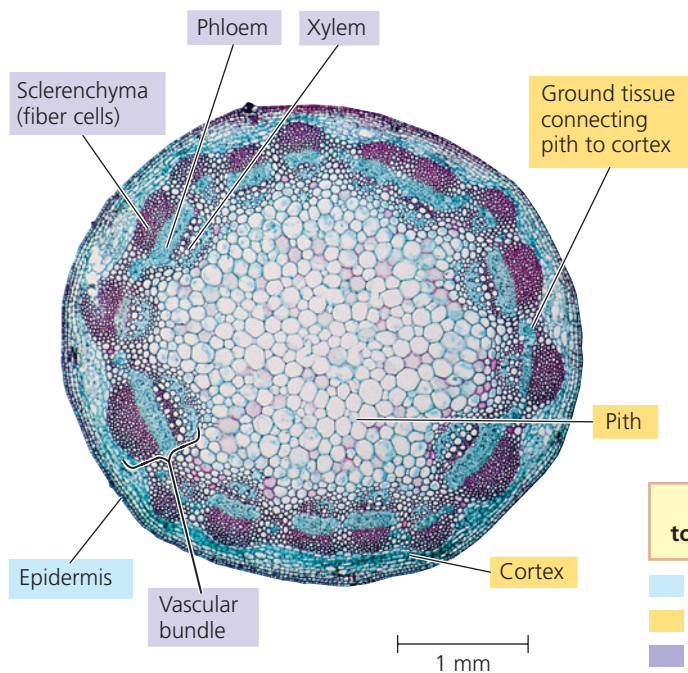
The ground tissue of a leaf, a region called the **mesophyll** (from the Greek *mesos*, middle, and *phyll*, leaf), is sandwiched between the upper and lower epidermal layers. Mesophyll consists mainly of parenchyma cells specialized for photosynthesis. The mesophyll in the leaves of many eudicots has two distinct layers: palisade mesophyll and spongy mesophyll. *Palisade mesophyll* consists of one or more layers of elongated parenchyma cells on the upper part of the leaf. The *spongy mesophyll* is below the palisade mesophyll. These parenchyma cells are more loosely arranged, with a labyrinth of air spaces through which  $\text{CO}_2$  and  $\text{O}_2$  circulate around the cells and up to the palisade region. The air spaces are particularly large in the

vicinity of stomata, where  $\text{CO}_2$  is taken up from the outside air and  $\text{O}_2$  is released.

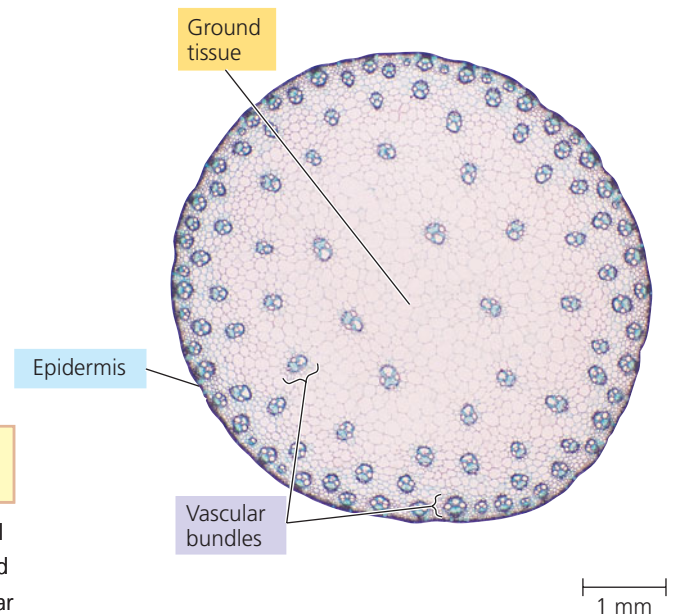
The vascular tissue of each leaf is continuous with the vascular tissue of the stem. Veins subdivide repeatedly and branch throughout the mesophyll. This network brings xylem and phloem into close contact with the photosynthetic tissue, which obtains water and minerals from the xylem and loads its sugars and other organic products into the phloem for transport to other parts of the plant. The vascular structure also functions as a framework that reinforces the leaf. Each vein is enclosed by a protective *bundle sheath*, a layer of cells that regulates the movement of substances between the vascular tissue and the mesophyll. Bundle-sheath cells are particularly prominent in leaves of plant species that carry out  $\text{C}_4$  photosynthesis (see Concept 8.3).

## 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 and disrupt the vascular cylinder, cortex, and epidermis as they emerge (see Figure 28.15), lateral shoots develop from axillary bud meristems on the stem's surface and disrupt no other



**(a) Cross section of stem with vascular bundles forming a ring (typical of eudicots).** Ground tissue toward the inside is called pith, and ground tissue toward the outside is called cortex (LM).



**(b) Cross section of stem with scattered vascular bundles (typical of monocots).** In such an arrangement, ground tissue is not partitioned into pith and cortex (LM).

**▲ Figure 28.18 Organization of primary tissues in young stems.**

**?** Why aren't the terms pith and cortex used to describe the ground tissue of monocot stems?

tissues (see Figure 28.16). The vascular bundles of the stem converge with the root's vascular cylinder in a zone of transition located near the soil surface.

In most eudicot species, the vascular tissue of stems consists of vascular bundles arranged in a ring (**Figure 28.18a**). The xylem in each vascular bundle is adjacent to the pith, and the phloem in each bundle is adjacent to the cortex. In most monocot stems, the vascular bundles are scattered throughout the ground tissue rather than forming a ring (**Figure 28.18b**). In the stems of both monocots and eudicots, the ground tissue consists mostly of parenchyma cells. However, collenchyma cells just beneath the epidermis strengthen many stems. Sclerenchyma cells, especially fiber cells, also provide support in those parts of the stems that are no longer elongating. Many economically important products, such as textiles, rope, and paper are derived from plant fibers. Note that “dietary fiber” derives not from plant fiber cells but from the cellulose cell walls of edible plant tissues.

### CONCEPT CHECK 28.3

1. Contrast primary growth in roots and shoots.
2. **WHAT IF?** If a plant species has vertically oriented leaves, would you expect its mesophyll to be divided into spongy and palisade layers? Explain.
3. **MAKE CONNECTIONS** How are root hairs and microvilli analogous structures? (See Figure 4.7 and the discussion of analogy in Concept 20.2.)

For suggested answers, see Appendix A.

## CONCEPT 28.4

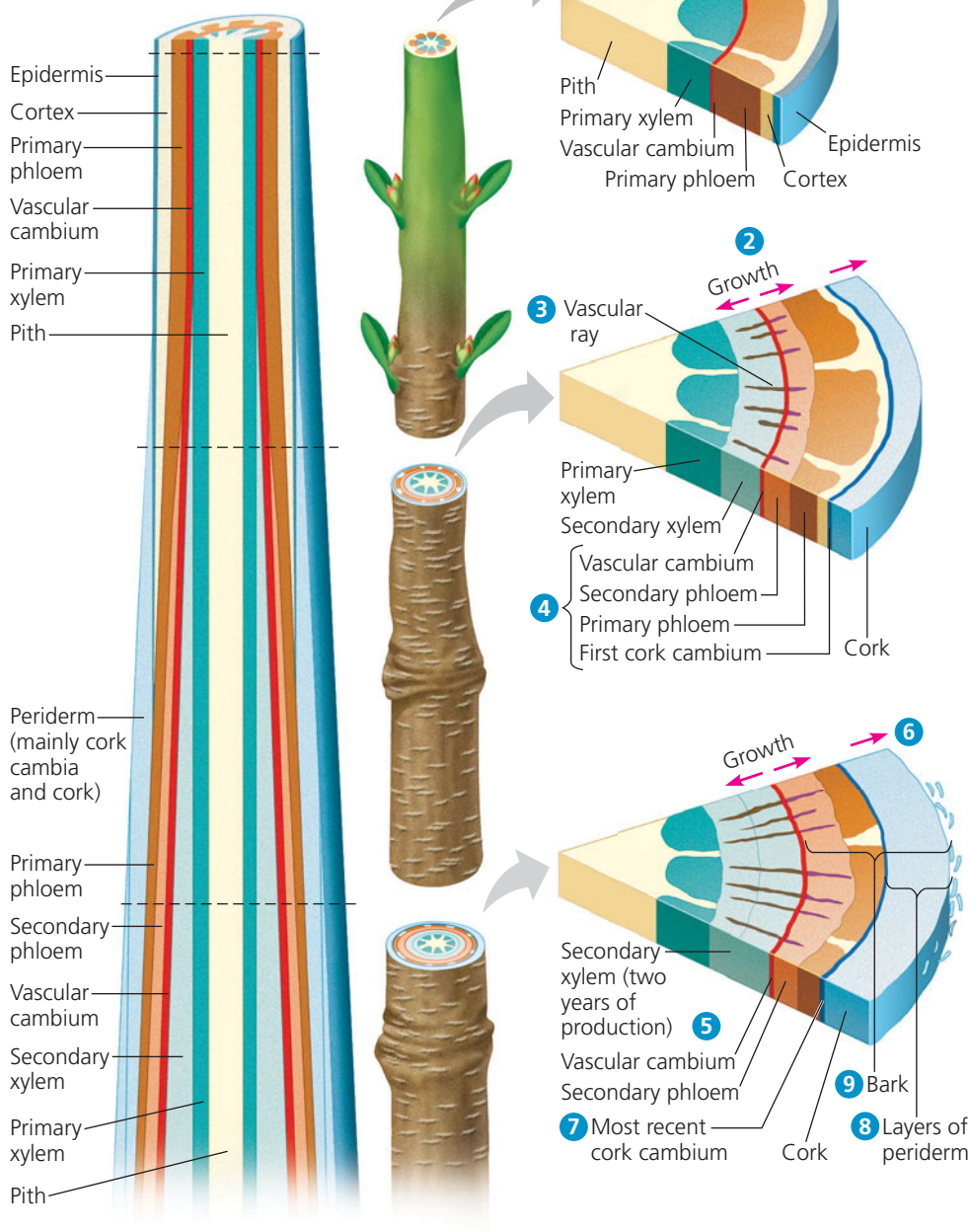
### Secondary growth increases the diameter of stems and roots in woody plants

Many land plants display secondary growth, the growth in thickness produced by lateral meristems. The advent of secondary growth during plant evolution allowed the production of novel plant forms ranging from massive forest trees to woody vines. All gymnosperm species and many eudicot species undergo secondary growth, but it is rare in monocots. Secondary growth occurs in stems and roots of woody plants, but rarely in leaves. Secondary growth consists of the tissues produced by the vascular cambium and cork cambium. The vascular cambium adds secondary xylem (wood) and secondary phloem, thereby increasing vascular flow and support for the shoots. The cork cambium produces a tough, thick covering of waxy cells that protect the stem from water loss and from invasion by insects, bacteria, and fungi.

In woody plants, primary growth and secondary growth occur simultaneously. As primary growth adds leaves and lengthens stems and roots in the younger regions of a plant, secondary growth increases the diameter of stems and roots in older regions where primary growth has ceased. The process is similar in shoots and roots. **Figure 28.19** provides an overview of growth in a woody stem.



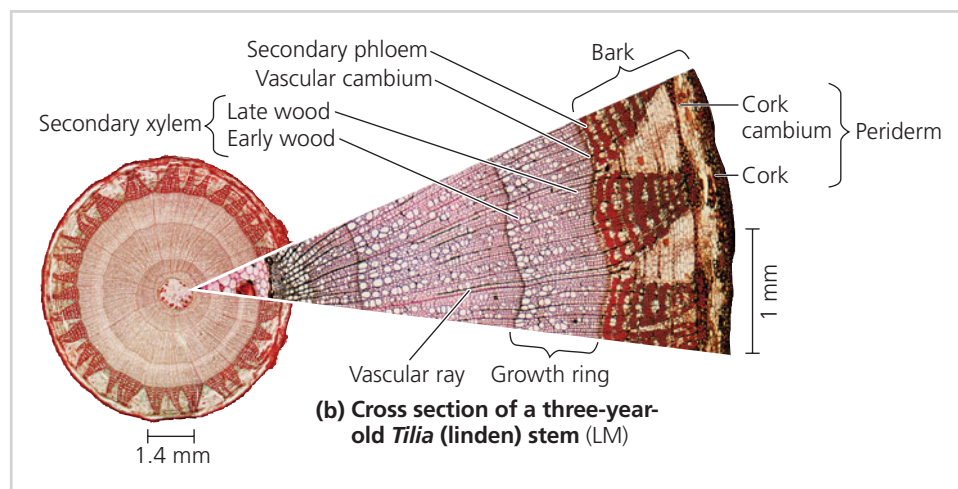
**(a) Primary and secondary growth in a two-year-old woody stem**



- 1 Primary growth from the activity of the apical meristem is nearing completion. The vascular cambium has just formed.
- 2 Although primary growth continues in the apical bud, only secondary growth occurs in this region. The stem thickens as the vascular cambium forms secondary xylem to the inside and secondary phloem to the outside.
- 3 Some initials of the vascular cambium give rise to vascular rays.
- 4 As the vascular cambium's diameter increases, the secondary phloem and other tissues external to the cambium can't keep pace because their cells no longer divide. As a result, these tissues, including the epidermis, will eventually 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.
- 5 In year 2 of secondary growth, the vascular cambium produces more secondary xylem and phloem, and the cork cambium produces more cork.
- 6 As the stem's diameter increases, the outermost tissues exterior to the cork cambium rupture and are sloughed off.
- 7 In many cases, the cork cambium re-forms deeper in the cortex. When none of the cortex is left, the cambium develops from phloem parenchyma cells.
- 8 Each cork cambium and the tissues it produces form a layer of periderm.
- 9 Bark consists of all tissues exterior to the vascular cambium.

**▲ Figure 28.19 Primary and secondary growth of a woody stem.** The progress of secondary growth can be tracked by examining the sections through sequentially older parts of the stem.

**?** How does the vascular cambium cause some tissues to rupture?



## The Vascular Cambium and Secondary Vascular Tissue

The vascular cambium, a cylinder of meristematic cells only one cell thick, is wholly responsible for the production of secondary vascular tissue. In a typical woody stem, the vascular cambium is located outside the pith and primary xylem and to the inside of the primary phloem and cortex. In a typical woody root, the vascular cambium forms to the exterior of the primary xylem and interior to the primary phloem and pericycle.

Viewed in cross section, the vascular cambium appears as a ring of meristematic cells (see Figure 28.19). As these cambial cells divide, they increase the circumference of the vascular cambium and also add secondary xylem to the inside of the cambium and secondary phloem to the outside (Figure 28.20). Each layer has a larger diameter than the previous layer. In this way, the vascular cambium increases the diameter of roots and stems.

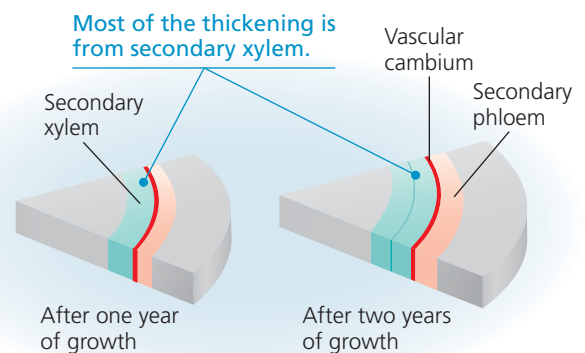
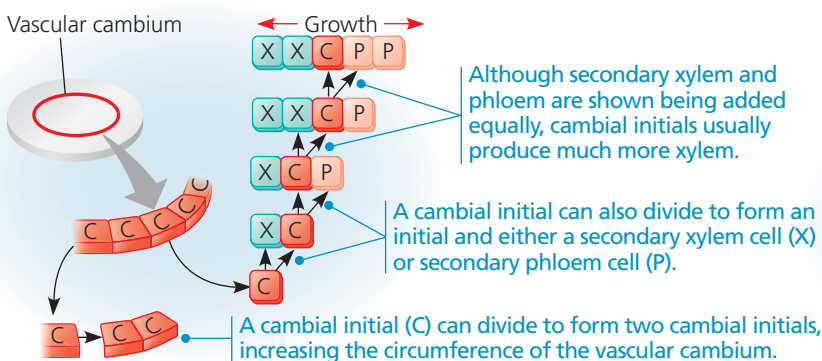
Some of the initials produced by the vascular cambium are elongated and are oriented with their long axis parallel to the axis of the stem or root. They produce cells such as the tracheids, vessel elements, and fibers of the xylem, as well as the sieve-tube elements, companion cells, axially oriented parenchyma, and fibers of the phloem. The other initials are shorter and are oriented perpendicular to the axis of the stem or root. They produce *vascular rays*—radial files of mostly parenchyma cells that connect the secondary xylem and phloem (see Figure 28.19b). The cells of a vascular ray move water and nutrients between the secondary xylem and phloem, store carbohydrates, and aid in wound repair.

As secondary growth continues over many years, layers of secondary xylem (wood) accumulate, consisting mainly of tracheids, vessel elements, and fibers (see Figure 28.9). Tracheids are the only kind of water-conducting cell found in the xylem tissue of most gymnosperms, whereas both tracheids and vessel elements are found in most angiosperms. The walls of secondary xylem cells are heavily lignified and account for the hardness and strength of wood.

In temperate regions, wood that develops early in the spring, known as early (or spring) wood, usually consists of secondary xylem cells with relatively large diameters and thin cell walls (see Figure 28.19b). This structure maximizes delivery of water to new leaves. Wood produced during the rest of the growing season is called late (or summer) wood. It is composed of thick-walled cells that do not transport as much water but provide more support. Because there is a marked contrast between the large cells of the new early wood and the smaller cells of the late wood of the previous growing season, a year's growth appears as a distinct *growth ring* in the cross sections of most tree trunks and roots. Therefore, researchers can estimate a tree's age by counting its growth rings. *Dendrochronology* (from the Greek *dendron*, trees, and *chronos*, time) is the science of analyzing tree growth ring patterns. Growth rings can vary in thickness, depending on seasonal growth. Trees grow well in wet and warm years but may grow hardly at all in cold or dry years. Because a thick ring indicates a warm year and a thin ring indicates a cold or dry one, scientists can use ring patterns to study climate changes.

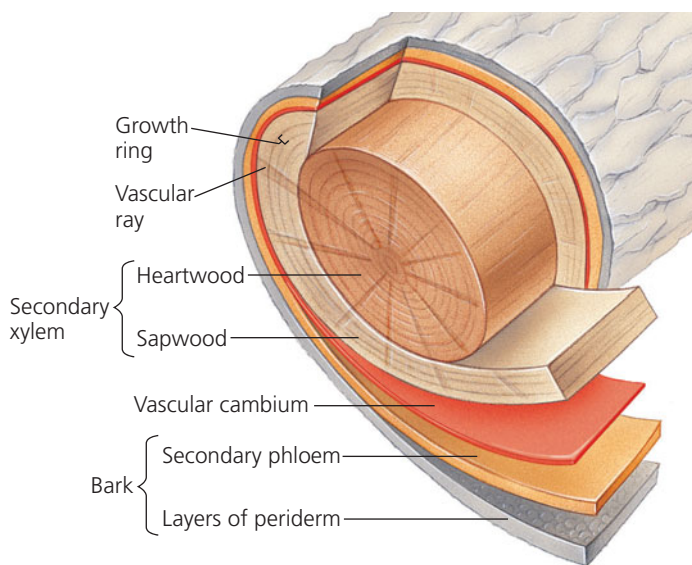
As a tree or woody shrub ages, the older layers of secondary xylem no longer transport water and minerals (a solution called xylem sap). These layers are called *heartwood* because they are closer to the center of a stem or root (Figure 28.21). The newest, outer layers of secondary xylem still transport xylem sap and are therefore known as *sapwood*. Sapwood allows a large tree to 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. The heartwood is generally darker than sapwood because of resins and other compounds that permeate 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



▲ **Figure 28.20** Secondary growth produced by the vascular cambium.





▲ **Figure 28.21** Anatomy of a tree trunk.

sloughed off, which is one reason secondary phloem does not accumulate as extensively as secondary xylem.

## The Cork Cambium and the Production of Periderm

During the early stages of secondary growth, the epidermis is pushed outward, causing it to split, dry, and fall off the stem or root. It is replaced by tissues produced by the first cork cambium, a cylinder of dividing cells that arises in the outer cortex of stems (see Figure 28.19a) and in the outer layer of the pericycle in roots. The cork cambium gives rise to *cork cells* that accumulate to the exterior of the cork cambium. As cork cells mature, they deposit a waxy, hydrophobic material called *suberin* in their walls and then die. Because cork cells have suberin and are usually compacted together, most of the periderm is impermeable to water and gases, unlike the epidermis. Cork

thus functions as a barrier that helps protect the stem or root from water loss, physical damage, and pathogens. “Cork” is commonly and incorrectly referred to as “bark.” In botany, **bark** includes all tissues external to the vascular cambium. Its main components are the secondary phloem (produced by the vascular cambium) and, external to that, the most recent periderm and all the older layers of periderm (see Figure 28.21).

How can living cells in the interior tissues of woody organs absorb oxygen and respire if they are surrounded by a waxy periderm? Dotting the periderm are small, raised areas called **lenticels**, in which there is more space between cork cells, enabling living cells within a woody stem or root to exchange gases with the outside air. Lenticels often appear as horizontal slits, as shown on the stem in Figure 28.19a.

In examining the parts of plants in a dissected fashion as we have done in this chapter, it is important not to lose sight of the fact that the whole plant functions as an integrated organism. In the following chapters, you’ll learn more about how materials are absorbed and transported by vascular plants (Chapter 29), how flowering plants reproduce (Chapter 30), and how plant functions are coordinated (Chapter 31). When thinking about plants, bear in mind that plant structures largely reflect evolutionary adaptations to the challenges of a photoautotrophic existence on land.

### CONCEPT CHECK 28.4

1. A sign is hammered into a tree 2 m from the tree’s base. If the tree is 10 m tall and elongates 1 m each year, how high will the sign be after 10 years?
2. Would you expect a tropical tree to have distinct growth rings? Why or why not?
3. **WHAT IF?** If a complete ring of bark is removed around a tree trunk (a process called girdling), would the tree die slowly (in weeks) or quickly (in days)? Explain why.

For suggested answers, see Appendix A.

# 28 Chapter Review

## SUMMARY OF KEY CONCEPTS

### CONCEPT 28.1

**Plants have a hierarchical organization consisting of organs, tissues, and cells (pp. 554–560)**

- Vascular plants have shoots consisting of **stems**, **leaves**, and, in angiosperms, **flowers**. **Roots** anchor the plant, absorb and conduct water and minerals, and store food. Leaves are attached to stem **nodes** and are the main **organs** of photosynthesis. **Axillary buds**, in axils of leaves and stems, give rise to branches. Plant organs may be adapted for specialized functions.
- Vascular plants have three tissue systems—dermal, vascular, and ground—which are continuous throughout the plant. **Dermal tissue** protects against pathogens, herbivores, and drought and aids in the absorption of water, minerals, and carbon dioxide.

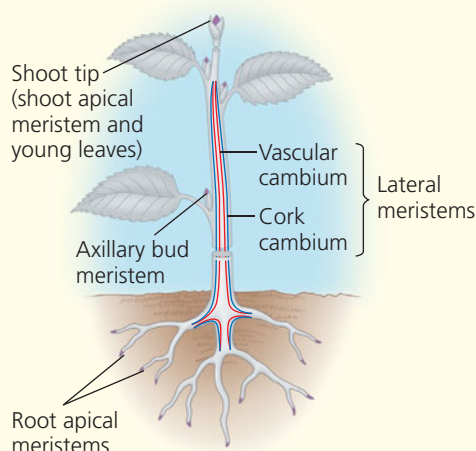
**Vascular tissues** (**xylem** and **phloem**) facilitate the long-distance transport of substances. **Ground tissues** function in storage, metabolism, and regeneration.

- **Parenchyma cells** are relatively unspecialized and thin-walled cells that retain the ability to divide; they perform most of the plant’s metabolic functions of synthesis and storage. **Collenchyma cells** have unevenly thickened walls; they support young, growing parts of the plant. **Sclerenchyma cells**—fibers and sclereids—have thick, lignified walls that help support mature, nongrowing parts of the plant. **Tracheids** and **vessel elements**, the water-conducting cells of xylem, have thick walls and are dead at functional maturity. **Sieve-tube elements** are living but highly modified cells that are largely devoid of internal organelles; they function in the transport of sugars through the phloem of angiosperms.

**?** Describe at least three specializations in plant organs and plant cells that are adaptations to life on land.

## CONCEPT 28.2

**Meristems generate new cells for growth and control the developmental phases and life spans of plants (pp. 560–562)**



? Which plant organs originate from the activity of meristems?

## CONCEPT 28.3

**Primary growth lengthens roots and shoots (pp. 562–566)**

- The root **apical meristem** is located near the tip of the root, where it generates cells for the growing root axis and the **root cap**.
- The apical meristem of a shoot is located in the **apical bud**, where it gives rise to alternating **internodes** and leaf-bearing nodes.

? How does branching differ in roots versus stems?

## CONCEPT 28.4

**Secondary growth increases the diameter of stems and roots in woody plants (pp. 566–569)**

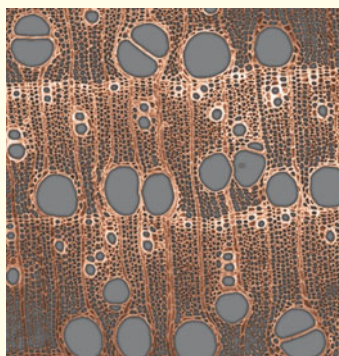
- The **vascular cambium** is a meristematic cylinder that produces secondary xylem and secondary phloem during **secondary growth**. Older layers of secondary xylem (heartwood) become inactive, whereas younger layers (sapwood) still conduct water.
- The **cork cambium** gives rise to a thick protective covering called the **periderm**, which consists of the cork cambium plus the layers of cork cells it produces.

? What advantages did plants gain from the evolution of secondary growth?

3. Lateral roots arise from the
  - a. periderm.
  - b. vascular cambium.
  - c. pericycle.
  - d. root apical meristem.
  - e. root cap.

### Level 2: Application/Analysis

4. Which of the following arise, directly or indirectly, from meristematic activity?
  - a. secondary xylem
  - b. leaves
  - c. dermal tissue
  - d. tubers
  - e. all of the above
5. Which of the following would not be seen in a cross section through the woody part of a root?
  - a. sclerenchyma cells
  - b. parenchyma cells
  - c. sieve-tube elements
  - d. root hairs
  - e. vessel elements
6. **DRAW IT** On this cross section from a woody eudicot, label a growth ring, late wood, early wood, and a vessel element. Then draw an arrow in the pith-to-cork direction.



### Level 3: Synthesis/Evaluation

7. **SCIENTIFIC INQUIRY**

Grasslands typically do not flourish when large herbivores are removed. In fact, they are soon replaced by broad-leaved herbaceous eudicots, shrubs, and trees. Based on your knowledge of the structure and growth habits of monocots versus eudicots, suggest a reason why.
8. **FOCUS ON EVOLUTION**

Evolutionary biologists have coined the term *exaptation* to describe a common occurrence in the evolution of life: A limb or organ evolves in a particular context but over time takes on a new function (see Concept 23.4). What are some examples of exaptations in plant organs?
9. **FOCUS ON ORGANIZATION**

In a short essay (100–150 words), explain how the evolution of lignin affected vascular plant structure and function.

For selected answers, see Appendix A.

## TEST YOUR UNDERSTANDING

### Level 1: Knowledge/Comprehension

1. The innermost layer of the root cortex is the
  - a. core.
  - b. pericycle.
  - c. endodermis.
  - d. pith.
  - e. vascular cambium.
2. Heartwood and sapwood consist of
  - a. bark.
  - b. periderm.
  - c. secondary xylem.
  - d. secondary phloem.
  - e. cork.

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# Resource Acquisition, Nutrition, and Transport in Vascular Plants

## KEY CONCEPTS

- 29.1** Adaptations for acquiring resources were key steps in the evolution of vascular plants
- 29.2** Different mechanisms transport substances over short or long distances
- 29.3** Plant roots absorb essential elements from the soil
- 29.4** Plant nutrition often involves relationships with other organisms
- 29.5** Transpiration drives the transport of water and minerals from roots to shoots via the xylem
- 29.6** The rate of transpiration is regulated by stomata
- 29.7** Sugars are transported from sources to sinks via the phloem

## OVERVIEW

### Underground Plants

**T**he Kalahari Desert of southern Africa receives only about 20 cm of precipitation a year, almost entirely during the summer, when daytime temperatures reach a scorching 35–45°C (95–113°F). Many animals escape the heat by seeking shelter underground. A peculiar genus of perennial plants called stone plants (*Lithops*) has a similar, mostly subterranean lifestyle

(**Figure 29.1**). Except for the tips of two succulent leaves that are exposed to the surface, a stone plant lives entirely below ground. Each leaf tip has a region of clear, lens-like cells that allow light to penetrate to the photosynthetic tissues underground. These adaptations enable stone plants to conserve moisture, hide from grazing tortoises, and avoid the potentially harmful temperatures and high light intensities of the desert.

The remarkable growth habit of *Lithops* reminds us that the success of plants depends largely on their ability to gather and conserve resources from their environment. Through natural selection, many plant species have become highly proficient in acquiring or conserving resources that are especially limited in their environment, but there are often trade-offs in such specializations. For example, the mostly subterranean lifestyle of stone plants reduces water loss from evaporation but also reduces photosynthesis. As a result, stone plants grow very slowly.

The first concept in this chapter examines structural features of shoot and root systems that increase their efficiency in acquiring water, minerals, carbon dioxide, and light. Resource acquisition, however, is not the end of the story but the beginning. Resources must be transported within the plant to where they are needed. Therefore, the rest of the chapter focuses on how water, minerals, and the products of photosynthesis (sugars) are transported in vascular plants.

▼ **Figure 29.1** Plants or pebbles?



## CONCEPT 29.1

### Adaptations for acquiring resources were key steps in the evolution of vascular plants

**EVOLUTION** Land plants typically inhabit two worlds—above ground, where their shoot systems acquire sunlight and  $\text{CO}_2$ , and below ground, where their root systems acquire water and minerals. Without adaptations that allow acquisition of these resources, plants could not have colonized land.

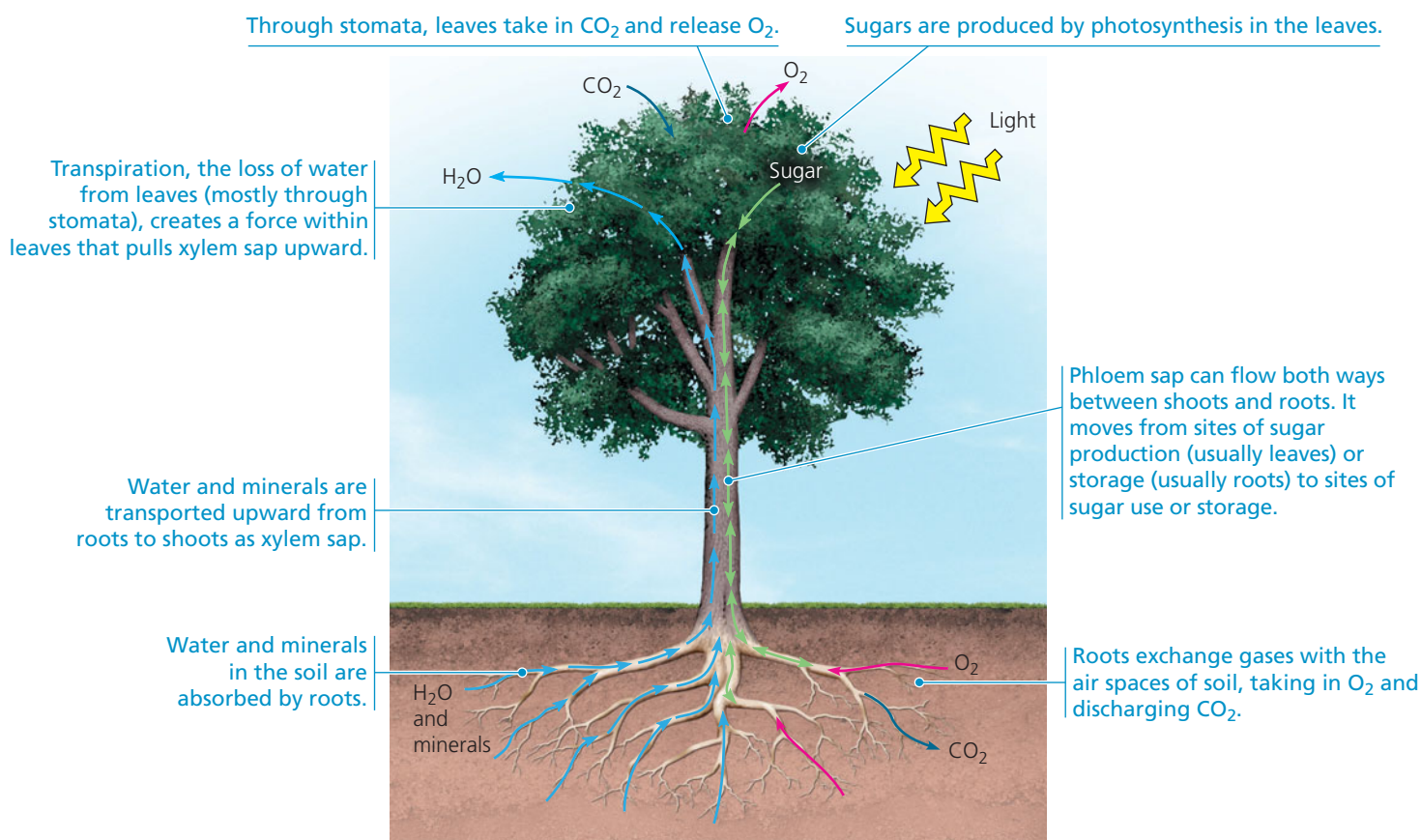
The algal ancestors of land plants absorbed water, minerals, and  $\text{CO}_2$  directly from the water in which they lived. Transport in these algae was relatively simple because every cell was close to the source of these substances. The earliest land plants were nonvascular plants that grew photosynthetic shoots above the shallow fresh water in which they lived. These leafless shoots typically had waxy cuticles and few stomata, which allowed them to avoid excessive water loss while still permitting some exchange of  $\text{CO}_2$  and  $\text{O}_2$  for photosynthesis. The anchoring and absorbing functions of early land plants were assumed by the base of the stem or by threadlike rhizoids.

As land plants evolved and increased in number, competition for light, water, and nutrients intensified. Taller plants

with broad, flat appendages had an advantage in absorbing light. This increase in surface area, however, resulted in more evaporation and therefore a greater need for water. Larger shoots also required more anchorage. These needs favored the production of multicellular, branching roots. Meanwhile, as greater shoot heights further separated the photosynthesizing leaves from the nonphotosynthetic parts below ground, natural selection favored plants capable of efficient long-distance transport of water, minerals, and products of photosynthesis.

The evolution of vascular tissue consisting of xylem and phloem made possible the development of extensive root and shoot systems that carry out long-distance transport (see Figure 28.9). The **xylem** transports water and minerals from roots to shoots. The **phloem** transports products of photosynthesis from where they are made or stored to where they are needed. **Figure 29.2** provides an overview of resource acquisition and transport in a vascular plant.

Because plant success depends on photosynthesis, evolution has resulted in many structural adaptations for efficiently acquiring light from the sun,  $\text{CO}_2$  from the air, and water from the ground. Perhaps just as importantly, land plants must minimize the evaporative loss of water, particularly in environments where water is scarce. The adaptations of each species represent compromises between enhancing photosynthesis and minimizing water loss in the species' particular habitat.



▲ **Figure 29.2** An overview of resource acquisition and transport in a vascular plant.



Later in the chapter, we'll discuss how plants enhance CO<sub>2</sub> uptake and minimize water loss by regulating stomatal pores. Here we examine how the basic architecture of shoots and roots helps plants acquire resources.

## Shoot Architecture and Light Capture

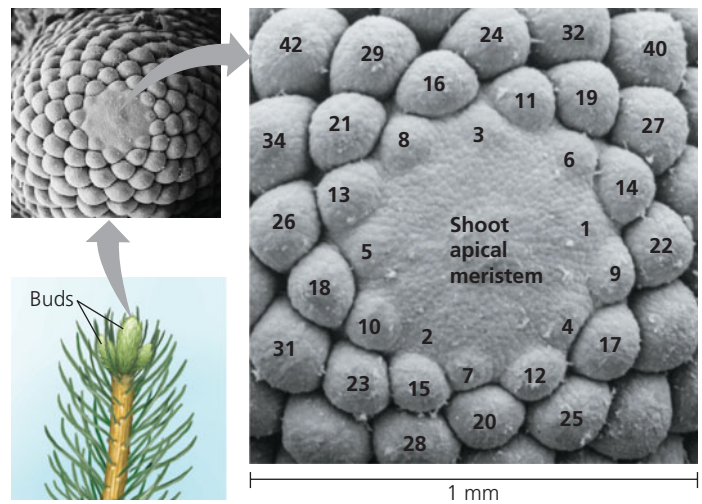
The macroscopic diversity we see in plant species is a reflection of architectural differences in the branching patterns, dimensions, shapes, and orientations of aboveground plant organs—the stems and leaves.

Stems serve as supporting structures for leaves and as conduits for the transport of water and nutrients. The height of the shoots and their branching pattern are two architectural features affecting light capture. Plants that grow tall avoid shading from neighboring plants. Most tall plants require thick stems, which enable greater vascular flow to the leaves and mechanical support for them. Vines are an exception, relying on other structures (usually other plants) to raise their leaves higher. In woody plants, stems become thicker through secondary growth (see Figure 28.10).

Branching generally enables plants to harvest sunlight for photosynthesis more effectively. However, some species, such as the coconut palm, do not branch at all. Why is there so much variation in branching patterns? Plants have only a finite amount of energy to devote to shoot growth. If most of that energy goes into branching, there is less energy to devote toward growing tall, and there is increased risk of being shaded by taller plants. If most of the energy goes into growing tall, the plants are not optimally exploiting the resources above ground. Natural selection has produced a variety of shoot architectures among species, fine-tuning the ability to absorb light in the ecological niche each species occupies.

The arrangement of leaves on a stem, known as **phyllotaxy**, is another architectural feature important in light capture. Phyllotaxy is determined by the shoot apical meristem (see Figure 28.16) and is specific to each species (Figure 29.3). A species may have one leaf per node (alternate, or spiral, phyllotaxy), two leaves per node (opposite phyllotaxy), or more (whorled phyllotaxy). Most angiosperms have alternate phyllotaxy, with leaves arranged in an ascending spiral around the stem, each successive leaf emerging 137.5° from the site of the previous one. Why 137.5°? Mathematical analyses suggest that this angle minimizes shading of the lower leaves by those above. In environments where intense sunlight can harm leaves, the greater shading provided by oppositely arranged leaves may be advantageous.

The **canopy** is the leafy portion of all the plants in a community. The depth of the canopy—how many leaf layers there are from the top of the canopy to the bottom—affects the productivity of each plant. When the canopy is too thick, the shading of the lower leaves on an individual plant may be so great that they photosynthesize less than they respire. When this happens, the nonproductive leaves or branches undergo



**▲ Figure 29.3 Emerging phyllotaxy of Norway spruce.** This SEM, taken from above a shoot tip, shows the pattern of emergence of leaves. The leaves are numbered, with 1 being the youngest. (Some numbered leaves are not visible in the close-up.)

**?** With your finger, trace the progression of leaf emergence, moving from leaf number 29 to 28 and so on. What is the pattern?

programmed cell death and are eventually shed, a process called *self-pruning*.

Another factor affecting light capture is leaf orientation. Some plants have horizontally oriented leaves; others, such as grasses, have leaves that are vertically oriented. In low-light conditions, horizontal leaves capture sunlight much more effectively than vertical leaves. In grasslands or other sunny regions, however, horizontal orientation may expose upper leaves to overly intense light, injuring leaves and reducing photosynthesis. But if a plant's leaves are nearly vertical, light rays are essentially parallel to the leaf surfaces, so no leaf receives too much light, and light penetrates more deeply to the lower leaves.

## Root Architecture and Acquisition of Water and Minerals

Just as carbon dioxide and sunlight are resources exploited by the shoot system, soil contains resources mined by the root system. Plants can rapidly adjust the architecture and physiology of their roots to exploit patches of available nutrients in the soil. The roots of many plants, for example, respond to pockets of low nitrate availability in soils by extending straight through the pockets instead of branching within them. Conversely, when encountering a pocket rich in nitrate, a root will often branch extensively there. Root cells also respond to high soil nitrate levels by synthesizing more proteins involved in nitrate transport and assimilation. Thus, not only does the plant devote more of its mass to exploiting a nitrate-rich patch; the cells also absorb nitrate more efficiently.

Researchers have uncovered a fascinating physiological mechanism that reduces competition within the root system of a plant. Cuttings from the stolons of buffalo grass (*Buchloe dactyloides*) develop fewer and shorter roots in the presence

of cuttings from the same plant than they do in the presence of cuttings from another buffalo grass plant. Although the mechanism underlying this ability to distinguish self from nonself is unknown, avoiding competition between roots of the same plant for the same limited pool of resources certainly seems beneficial.

Plant roots also form mutually beneficial relationships with microorganisms that enable them to exploit soil resources more efficiently. For example, the evolution of mutualistic associations between roots and fungi called mycorrhizae was a critical step in the successful colonization of land by plants (see Figures 26.12 and 26.13). Mycorrhizal hyphae endow the fungus and plant roots with an enormous surface area for absorbing water and minerals. The role of mycorrhizae in plant nutrition will be examined more fully in Concept 29.4.

Once acquired, resources must be transported to other parts of the plant that need them. In the next section, we examine the processes and pathways that enable resources such as water, minerals, and sugars to be transported throughout the plant.

#### CONCEPT CHECK 29.1

1. Why is long-distance transport important for vascular plants?
2. What architectural features influence self-shading?
3. **WHAT IF?** Some plants can detect increased levels of light reflected from leaves of encroaching neighbors. This detection elicits stem elongation, production of erect leaves, and less branching. How do these responses help the plant compete?

For suggested answers, see Appendix A.

## CONCEPT 29.2

### Different mechanisms transport substances over short or long distances

Given the diversity of substances that move through plants and the great range of distances and barriers over which such substances must be transported, it is not surprising that plants employ a variety of transport processes. Before examining

these processes, however, let's consider the two major pathways of transport: the apoplast and the symplast.

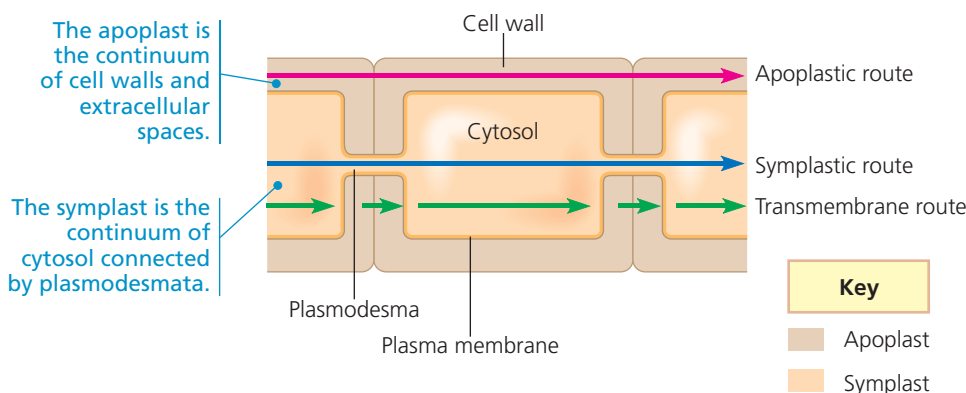
### The Apoplast and Symplast: Transport Continuums

Plant tissues may be viewed as having two major compartments—the apoplast and the symplast. The **apoplast** consists of everything external to the plasma membranes of living cells and includes cell walls, extracellular spaces, and the interior of dead cells such as vessel elements and tracheids (see Figure 28.9). The **symplast** consists of the entire mass of cytosol of all the living cells in a plant, as well as the plasmodesmata, the cytoplasmic channels that interconnect them.

The compartmental structure of plants provides three routes for transport within a plant tissue or organ: the apoplastic, symplastic, and transmembrane routes (**Figure 29.4**). In the *apoplastic route*, water and solutes (dissolved chemicals) move along the continuum of cell walls and extracellular spaces. In the *symplastic route*, water and solutes move along the continuum of cytosol. This route requires substances to cross a plasma membrane once, when they first enter the plant. After entering one cell, substances can move from cell to cell via plasmodesmata. In the *transmembrane route*, water and solutes move out of one cell, across the cell wall, and into the neighboring cell, which may pass them to the next cell in the same way. The transmembrane route requires repeated crossings of plasma membranes as substances exit one cell and enter the next. These three routes are not mutually exclusive, and some substances may use more than one route to varying degrees.

### Short-Distance Transport of Solutes Across Plasma Membranes

In plants, as in any organism, the selective permeability of the plasma membrane controls the short-distance movement of substances into and out of cells (see Chapter 5). Both active and passive transport mechanisms occur in plants, and plant cell membranes are equipped with the same general types of pumps and transport proteins (channel proteins, carrier proteins, and cotransporters) that function in other cells. In



◀ **Figure 29.4** Cell compartments and routes for short-distance transport. Some substances may use more than one transport route.



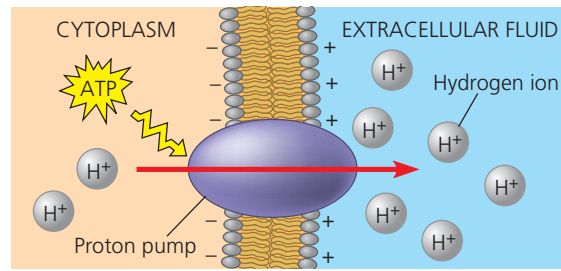
this section, we focus on some ways that plants differ from animals in solute transport across plasma membranes.

Hydrogen ions ( $H^+$ ), rather than sodium ions ( $Na^+$ ), play the primary role in basic transport processes in plant cells. For example, in plant cells the membrane potential (the voltage across the membrane) is established mainly through the pumping of  $H^+$  by proton pumps (Figure 29.5a), rather than the pumping of  $Na^+$  by sodium-potassium pumps. Also,  $H^+$  is most often cotransported in plants, whereas  $Na^+$  is typically cotransported in animals. During cotransport, plant cells use the energy in the  $H^+$  gradient and membrane potential to drive the active transport of many different solutes. For instance, cotransport with  $H^+$  is responsible for absorption of neutral solutes, such as the sugar sucrose, by phloem cells and other plant cells. An  $H^+$ /sucrose cotransporter couples movement of sucrose against its concentration gradient with movement of  $H^+$  down its electrochemical gradient (Figure 29.5b). Cotransport with  $H^+$  also facilitates movement of ions, as in the uptake of nitrate ( $NO_3^-$ ) by root cells (Figure 29.5c).

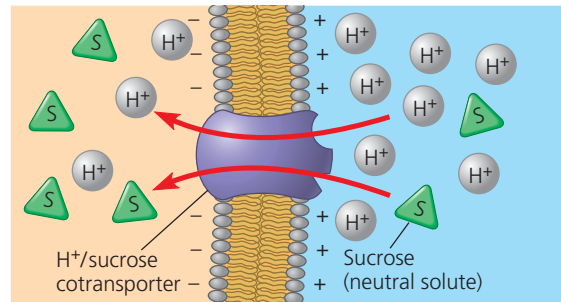
The membranes of plant cells also have ion channels that allow only certain ions to pass (Figure 29.5d). As in animal cells, most channels are gated, opening or closing in response to stimuli such as chemicals, pressure, or voltage. Later in this chapter, we'll discuss how potassium ( $K^+$ ) ion channels in guard cells function in opening and closing stomata. Ion channels are also involved in producing electrical signals analogous to the action potentials of animals (see Chapter 37). For example, the phloem conducts nerve-like electrical signals that help integrate whole-plant function. However, these signals are 1,000 times slower than in animals and employ calcium ( $Ca^{2+}$ ) activated anion channels rather than the sodium ( $Na^+$ ) ion channels used by animal cells.

## Short-Distance Transport of Water Across Plasma Membranes

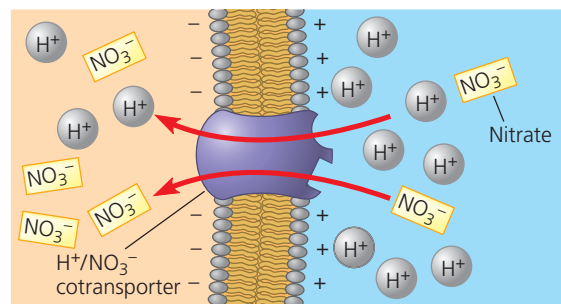
The absorption or loss of water by a cell occurs by **osmosis**, the diffusion of free water—water that is not bound to solutes or surfaces—across a membrane (see Figure 5.10). The physical property that predicts the direction in which water will flow is



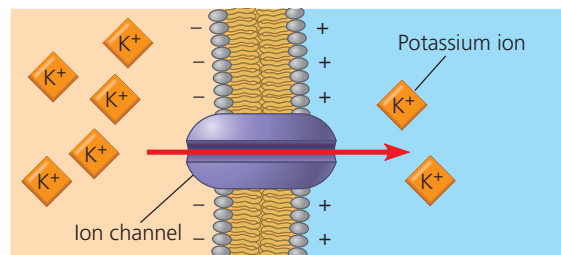
**(a)  $H^+$  and membrane potential.** The plasma membranes of plant cells use ATP-dependent proton pumps to pump  $H^+$  out of the cell. These pumps contribute to the membrane potential and the establishment of a pH gradient across the membrane. These two forms of potential energy can drive the transport of solutes.



**(b)  $H^+$  and cotransport of neutral solutes.** Neutral solutes such as sugars can be loaded into plant cells by cotransport with  $H^+$  ions.  $H^+$ /sucrose cotransporters, for example, play a key role in loading sugar into the phloem prior to its transport throughout the plant.



**(c)  $H^+$  and cotransport of ions.** Cotransport mechanisms involving  $H^+$  also participate in regulating ion fluxes into and out of cells. For example,  $H^+$ / $NO_3^-$  cotransporters in the plasma membranes of root cells are important for the uptake of  $NO_3^-$  by plant roots.



**(d) Ion channels.** Plant ion channels open and close in response to voltage, stretching of the membrane, and chemical factors. When open, ion channels allow specific ions to diffuse across membranes. For example, a  $K^+$  ion channel is involved in the release of  $K^+$  from guard cells when stomata close.

**▲ Figure 29.5 Solute transport across plant cell plasma membranes.**

**?** Assume that a plant cell has all four of the plasma membrane transport proteins shown above. Assume also that you have specific inhibitors for each of the four transport proteins. Predict what effect the individual application of each inhibitor would have on the cell's membrane potential.

called **water potential**, a quantity that includes the effects of solute concentration and physical pressure. Free water moves from regions of higher water potential to regions of lower water potential if there is no barrier to its flow. For example, if a plant cell is immersed in a solution that has a higher water potential than the cell, water will move into the cell. As the cell gains water, its water potential increases until equilibrium is reached between inside and out, and net water movement ceases. The word *potential* in the term *water potential* refers to water's potential energy—water's capacity to perform work when it moves or is absorbed. The growth of a plant cell, for example, is

primarily driven by water uptake. The expansion of plant cells and seeds can be a powerful force: growing tree roots, for example, can break sidewalks, and the swelling of wet grain within the holds of damaged ships has led to complete hull failure resulting in sinking of the ships. Given the strong forces generated by swelling seeds, it is interesting to consider whether metabolism is involved in water uptake by seeds; this question can be explored by analyzing the data in the **Scientific Skills Exercise**.

Water potential is abbreviated by the Greek letter  $\psi$  (psi, pronounced “sigh”). Plant biologists measure  $\psi$  in a unit of pressure called a **megapascal (MPa)**. By definition, the  $\psi$  of pure water in a container open to the atmosphere under standard conditions (at sea level and at room temperature) is 0 MPa.

### How Solutes and Pressure Affect Water Potential

Solute concentration and physical pressure are the major determinants of water potential in hydrated plants, as expressed in the *water potential equation*:

$$\psi = \psi_s + \psi_p$$

where  $\psi$  is the water potential,  $\psi_s$  is the solute potential (osmotic potential), and  $\psi_p$  is the pressure potential. The **solute**

**potential ( $\psi_s$ )** of a solution is directly proportional to its molarity. Solute potential is also called *osmotic potential* because solutes affect the direction of osmosis. The solutes in plants are typically ions and sugars. By definition, the  $\psi_s$  of pure water is 0. When solutes are added, they bind water molecules. As a result, there are fewer free water molecules, reducing the capacity of the water to move and do work. In this way, an increase in solutes has a negative effect on water potential, which is why the  $\psi_s$  of a solution is always expressed as a negative number. For example, a 0.1 M solution of a sugar has a  $\psi_s$  of  $-0.23$  MPa. As the solute concentration increases,  $\psi_s$  becomes more negative.

**Pressure potential ( $\psi_p$ )** is the physical pressure on a solution. Unlike  $\psi_s$ ,  $\psi_p$  can be positive or negative relative to atmospheric pressure. For example, the water in the hollow, nonliving xylem cells (tracheids and vessel elements) of a plant is often under a negative pressure potential (tension) of less than  $-2$  MPa. Conversely, much like the air in a tire’s inner tube, the water in living cells is usually under positive pressure due to the osmotic uptake of water. Specifically, the cell contents press the plasma membrane against the cell wall, and the

## Scientific Skills Exercise

### Calculating and Interpreting Temperature Coefficients

#### Does the Initial Uptake of Water by Seeds Depend on Temperature?

One way to answer this question is to soak seeds in water at different temperatures and measure the rate of water uptake at each temperature. The collected data can be used to calculate the temperature coefficient,  $Q_{10}$ , the factor by which a physiological process or reaction rate increases when the temperature is raised by  $10^\circ\text{C}$ :

$$Q_{10} = \left( \frac{k_2}{k_1} \right)^{\frac{10}{t_2 - t_1}}$$

where  $t_2$  = higher temperature ( $^\circ\text{C}$ ),  $t_1$  = lower temperature,  $k_2$  = reaction rate at  $t_2$ , and  $k_1$  = reaction rate at  $t_1$ . (Note that if  $t_2 - t_1 = 10$ , as in this exercise, the math is simplified.)

$Q_{10}$  values may be used to make inferences about the physiological process under investigation. Chemical (metabolic) processes involving large-scale protein shape changes are highly dependent on temperature and have higher  $Q_{10}$  values, closer to 2 or 3. In contrast, many, but not all, physical parameters are relatively independent of temperature and have  $Q_{10}$  values closer to 1. For example, the  $Q_{10}$  of the change in the viscosity of water is 1.2–1.3. In this exercise, you will calculate  $Q_{10}$  using data for radish seeds (*Raphanus sativus*) to assess whether the initial uptake of water by seeds is more likely to be a physical or a chemical process.

**How the Experiment Was Done** Samples of radish seeds were weighed and placed in water at four different temperatures. After 30 minutes, the seeds were removed, blotted dry, and reweighed. The researchers then calculated the percent increase in mass due to water uptake for each sample.

#### Data from the Experiment

Temperature	% Increase in Mass Due to Water Uptake after 30 Minutes
$5^\circ\text{C}$	18.5%
$15^\circ\text{C}$	26.0%
$25^\circ\text{C}$	31.0%
$35^\circ\text{C}$	36.2%

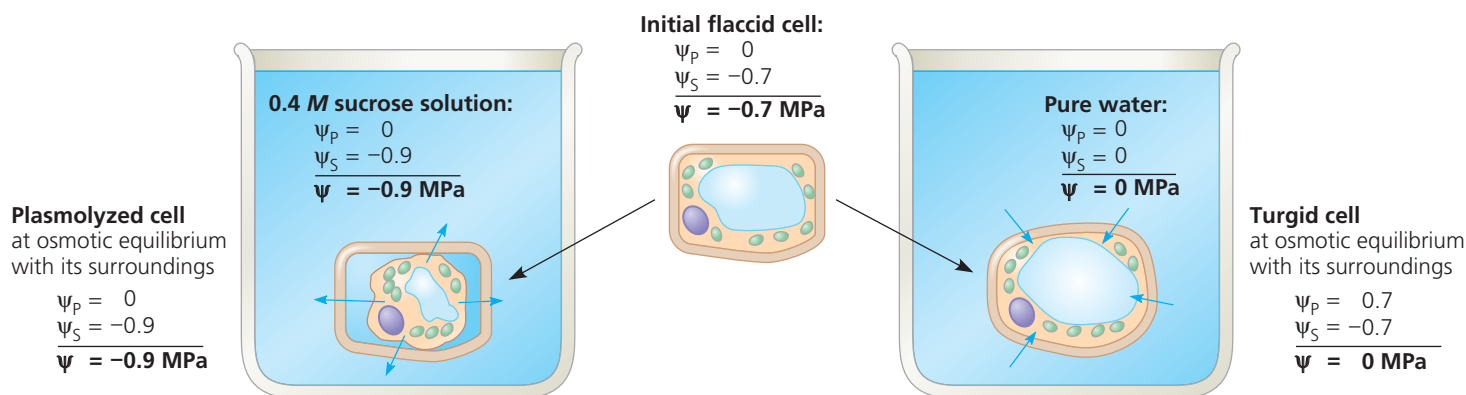
#### Interpret the Data

- Based on the data, does the initial uptake of water by radish seeds vary with temperature? What is the relationship between temperature and water uptake?
- (a) Using the data for  $35^\circ\text{C}$  and  $25^\circ\text{C}$ , calculate  $Q_{10}$  for water uptake by radish seeds. Repeat the calculation using the data for  $25^\circ\text{C}$  and  $15^\circ\text{C}$  and the data for  $15^\circ\text{C}$  and  $5^\circ\text{C}$ . (b) What is the average  $Q_{10}$ ? (c) Do your results imply that the uptake of water by radish seeds is mainly a physical process or a chemical (metabolic) process? (d) Given that the  $Q_{10}$  for the change in the viscosity of water is 1.2–1.3, could the slight temperature dependence of water uptake by seeds be a reflection of the slight temperature dependence of the viscosity of water?
- Besides temperature, what other independent variables could you alter to test whether radish seed swelling is essentially a physical process or a chemical process?
- Would you expect plant growth to have a  $Q_{10}$  closer to 1 or 3? Why?

**Data from** J. D. Murphy and D. L. Noland, Temperature effects on seed imbibition and leakage mediated by viscosity and membranes, *Plant Physiology* 69:428–431 (1982).

 A version of this Scientific Skills Exercise can be assigned in MasteringBiology.





(a) Initial conditions: cellular  $\psi >$  environmental  $\psi$ . The cell loses water and plasmolyzes. After plasmolysis is complete, the water potentials of the cell and its surroundings are the same.

(b) Initial conditions: cellular  $\psi <$  environmental  $\psi$ . There is a net uptake of water by osmosis, causing the cell to become turgid. When this tendency for water to enter is offset by the back pressure of the elastic wall, water potentials are equal for the cell and its surroundings. (The volume change of the cell is exaggerated in this diagram.)

▲ **Figure 29.6 Water relations in plant cells.** In these experiments, flaccid cells (cells in which the protoplast contacts the cell wall but lacks turgor pressure) are placed in two environments. Blue arrows indicate initial net water movement.

cell wall then presses against the **protoplast** (the living part of the cell, which includes the plasma membrane), producing what is called **turgor pressure**. This internal pressure is critical for plant function because it helps maintain the stiffness of plant tissues and also serves as the driving force for cell elongation. The key point to remember as you read about the water relations of plants is that *water moves from regions of higher water potential to regions of lower water potential*.

### Water Movement Across Plant Cell Membranes

Now let's consider how water potential affects absorption and loss of water by a living plant cell. First, imagine a cell that is **flaccid** (limp) as a result of losing water. The cell has a  $\psi_P$  of 0 MPa. Suppose this flaccid cell is bathed in a solution of higher solute concentration (more negative solute potential) than the cell itself (**Figure 29.6a**). Since the external solution has the lower (more negative) water potential, water diffuses out of the cell. The cell's protoplast undergoes **plasmolysis**—that is, it shrinks and pulls away from the cell wall. If we place the same flaccid cell in pure water ( $\psi = 0 \text{ MPa}$ ) (**Figure 29.6b**), the cell, because it contains solutes, has a lower water potential than the water, and water enters the cell by osmosis. The contents of the cell begin to swell and press the plasma membrane against the cell wall. The partially elastic wall, exerting turgor pressure, confines the pressurized protoplast. When this pressure is enough to offset the tendency for water to enter because of the solutes in the cell, then  $\psi_P$  and  $\psi_S$  are equal, and  $\psi = 0$ . This matches the water potential of the extracellular environment—in this example, 0 MPa. A dynamic equilibrium has been reached, and there is no further net movement of water.

In contrast to a flaccid cell, a walled cell with a greater solute concentration than its surroundings is **turgid**, or very firm. When turgid cells push against each other, the tissue stiffens.



▲ **Figure 29.7 A moderately wilted plant can regain its turgor when watered.**

The effects of turgor loss are seen during **wilting**, when leaves and stems droop as a result of cells losing water (**Figure 29.7**).

### Aquaporins: Facilitating Diffusion of Water

A difference in water potential determines the *direction* of water movement across membranes, but how do water molecules actually cross the membranes? The movement of water molecules across biological membranes is too rapid to be explained by unaided diffusion. In most cases, transport proteins called **aquaporins** (see Figure 5.1) facilitate the transmembrane transport of water. By opening and closing, these selective channels affect the *rate* at which water moves osmotically across the membrane.

### Long-Distance Transport: The Role of Bulk Flow

Long-distance transport in plants occurs through **bulk flow**, the movement of liquid in response to a pressure gradient. The bulk flow of material always occurs from higher to lower

pressure. Unlike osmosis, bulk flow is independent of solute concentration. Long-distance bulk flow occurs within the tracheids and vessel elements of the xylem and within the sieve-tube elements of the phloem. The structures of these conducting cells facilitate bulk flow. Mature tracheids and vessel elements are dead cells (see Figure 28.9) and therefore have no cytoplasm, and the cytoplasm of sieve-tube elements is almost devoid of internal organelles. If you have ever dealt with a partially clogged drain, you know that the volume of flow depends on the pipe's diameter. Clogs reduce the effective diameter of the drainpipe. Such experiences help us understand how the structures of plant cells specialized for bulk flow fit their function. Like the unplugging of a kitchen drain, the absence or reduction of cytoplasm in a plant's "plumbing" allows for efficient bulk flow through the xylem and phloem.

Diffusion, active transport, and bulk flow act in concert to transport resources throughout the whole plant. In the following sections, we examine in more detail the transport of water and minerals from roots to shoots, the control of evaporation, and the transport of sugars.

### CONCEPT CHECK 29.2

1. If a plant cell immersed in distilled water has a  $\psi_s$  of  $-0.7$  MPa and a  $\psi$  of  $0$  MPa, what is the cell's  $\psi_p$ ? If you put it in an open beaker of solution that has a  $\psi$  of  $-0.4$  MPa, what would be its  $\psi_p$  at equilibrium?
2. How would a reduction in the number of aquaporin channels affect a plant cell's ability to adjust to new osmotic conditions?
3. **WHAT IF?** What would happen if you put plant protoplasts in pure water? Explain.

For suggested answers, see Appendix A.

## CONCEPT 29.3

### Plant roots absorb essential elements from the soil

Water, air, and soil minerals all contribute to plant growth. The water content of a plant can be measured by comparing the plant's mass before and after drying. Typically, 80–90% of a plant's fresh mass is water. Some 96% of the remaining dry mass consists of carbohydrates such as cellulose that are produced by photosynthesis. Thus, the components of carbohydrates—carbon, oxygen, and hydrogen—are the most abundant elements in dried plant residue. Inorganic substances from the soil, although essential for plant survival, generally account for only about 4% of a plant's dry mass.

### Macronutrients and Micronutrients

The inorganic substances in plants consist of more than 50 chemical elements. In studying the chemical composition of plants, we must distinguish elements that are essential from

those that are merely present in the plant. A chemical element is considered an **essential element** only if it is required for a plant to complete its life cycle and produce another generation.

To determine which chemical elements are essential, researchers often use **hydroponic culture**, in which plants are grown in mineral solutions instead of soil (**Figure 29.8**). Such studies have helped identify 17 essential elements needed by all plants (**Table 29.1**). Hydroponic culture is also used on a small scale to grow some greenhouse crops.

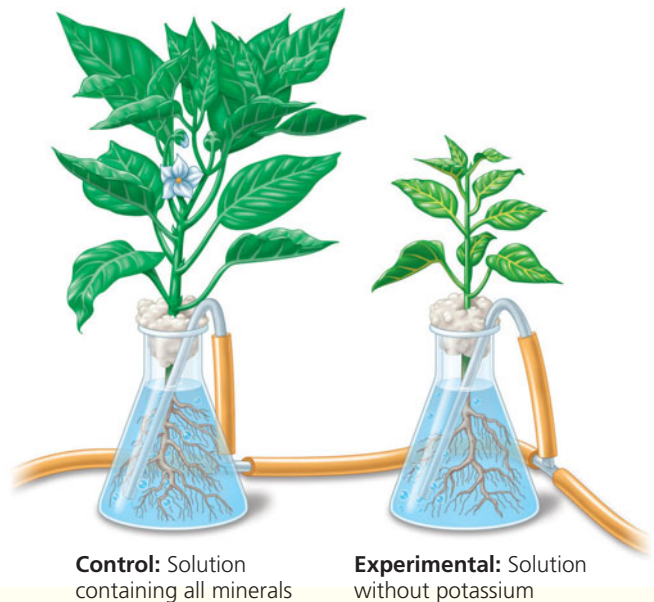
Nine of the essential elements are called **macronutrients** because plants require them in relatively large amounts. Six of these are the major components of organic compounds forming a plant's structure: carbon, oxygen, hydrogen, nitrogen, phosphorus, and sulfur. The other three macronutrients are potassium, calcium, and magnesium. Of all the mineral nutrients, nitrogen contributes the most to plant growth and crop yields. Plants require nitrogen as a component of proteins, nucleic acids, chlorophyll, and other important organic molecules.

### ▼ Figure 29.8 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. (Note: The flasks would normally be opaque to prevent algal growth.) A 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. By definition, the plant would not be able to complete its life cycle. Deficiencies of different elements may have different symptoms, which can aid in diagnosing mineral deficiencies in soil.



**Table 29.1** Essential Elements in Plants

Element	Form Primarily Absorbed by 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%	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; cofactor and activator of many enzymes
Phosphorus	H <sub>2</sub> PO <sub>4</sub> <sup>-</sup> , HPO <sub>4</sub> <sup>2-</sup>	0.2%	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; cofactor of some enzymes; needed for photosynthesis
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; cofactor of some enzymes; needed for DNA transcription
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 mutualistic relationship with nitrogen-fixing bacteria; cofactor in nitrate reduction

**MAKE CONNECTIONS** Humans require the minerals fluorine, selenium, and chromium in their diet (Concept 33.1), and they obtain these minerals from plants. However, these minerals are not essential for plant survival. How can plants be a source of these minerals when they don't need them to complete their life cycle?

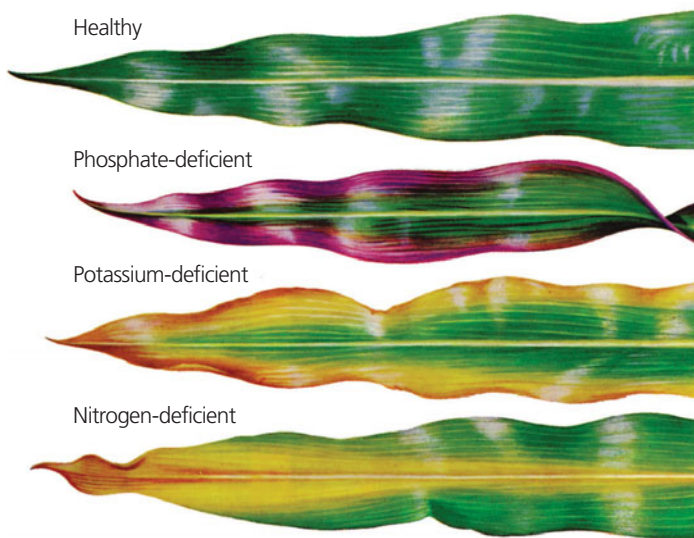
The remaining eight essential elements are known as **micronutrients** because plants need them in only tiny quantities. They are chlorine, iron, manganese, boron, zinc, copper, nickel, and molybdenum. Sodium is a ninth essential micronutrient for plants that use the CAM or C<sub>4</sub> pathway of photosynthesis. Too much of a nutrient can, of course, damage plants.

Micronutrients function in plants mainly as cofactors, non-protein helpers in enzymatic reactions (see Concept 6.4). Iron, for example, is a metallic component of cytochromes, the proteins in the electron transport chains of chloroplasts and mitochondria. It is because micronutrients generally play catalytic roles that plants need only tiny 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 deficiency depend partly on the mineral's function as a nutrient. For example, a deficiency of magnesium, a component of chlorophyll, causes *chlorosis*, yellowing of the leaves. In some cases, the relationship between a mineral deficiency and its symptoms is less direct. For instance, iron deficiency can cause chlorosis even though chlorophyll 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 appear first in older organs, because young, growing tissues are a greater sink for nutrients that are in short supply. For example, magnesium is relatively mobile and is shunted preferentially to young leaves. Therefore, a plant deficient in magnesium first shows signs of chlorosis in its older leaves. In contrast, a deficiency of a mineral that is relatively immobile affects young parts of the plant first. Older tissues may have adequate amounts that they retain during periods of short supply. For example, iron does not move freely within a plant, and an iron deficiency causes yellowing of young



▲ **Figure 29.9 The most common mineral deficiencies, as seen in maize leaves.** Mineral deficiency symptoms may vary in different species. In maize, phosphate-deficient plants have reddish purple margins, particularly in young leaves. Potassium-deficient maize 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.

leaves before any effect on older leaves is visible. The mineral requirements of a plant also change with the age of the plant. Young seedlings, for example, rarely show mineral deficiency symptoms because their mineral needs are met largely by the mineral reserves stored in the seeds themselves.

The symptoms of a mineral deficiency in a given plant species are often distinctive enough to aid in diagnosis (**Figure 29.9**). Deficiencies of phosphorus, potassium, and especially nitrogen are most common. Micronutrient shortages are less common and reflect local differences in soil composition. 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 detrimental or toxic to plants. Too much nitrogen, for example, can lead to excessive vine growth in tomato plants at the expense of good fruit production.

## Soil Management

Ancient farmers recognized that yields on a particular plot of land decreased over the years. Moving to uncultivated areas, they observed the same pattern of reduced yields over time. Eventually, they realized that fertilization could make soil a renewable resource that enabled crops to be cultivated season after season at a fixed location. This sedentary agriculture facilitated a new way of life. People began to build permanent dwellings—the first villages. They also stored food for use between harvests, and food surpluses enabled some members of these early communities to specialize in nonfarming occupations. In short, the early discovery of soil fertilization helped prepare the way for modern societies.

## Fertilization

In natural ecosystems, mineral nutrients are usually recycled by the excretion of animal wastes and the decomposition of **humus**, the remains of dead organisms and other organic matter. Agriculture, however, is not a natural ecosystem. The lettuce you eat, for example, contains minerals extracted from a farmer’s field. As you excrete wastes, these minerals are deposited far from their original source. Over many harvests, the farmer’s field will eventually become depleted of nutrients. Nutrient depletion is a major cause of global soil degradation. Farmers must reverse nutrient depletion by fertilization, the addition of mineral nutrients to the soil.

Today, most farmers in industrialized nations use fertilizers containing minerals that are either mined or prepared by energy-intensive processes. These fertilizers are usually enriched in nitrogen (N), phosphorus (P), and potassium (K)—the nutrients most commonly deficient in depleted soils. You may have seen fertilizers labeled with a three-number code, called the N–P–K ratio. A fertilizer marked “15–10–5,” for instance, is 15% N (as ammonium or nitrate), 10% P (as phosphate), and 5% K (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. However, organic fertilizers release them gradually, whereas minerals in commercial fertilizers are immediately available but may not be retained by the soil for long. A drawback of modern fertilization practices is that minerals not absorbed by roots are often leached from the soil by rainwater or irrigation. To make matters worse, mineral runoff into lakes may lead to explosions in algal populations that can deplete oxygen levels and decimate fish populations.

## Adjusting Soil pH

Soil pH is an important factor that influences mineral availability by its effect on cation exchange and the chemical form of minerals. Depending on the soil pH, a particular mineral may be bound too tightly to soil particles or may be in a chemical form that the plant cannot absorb. Most plants prefer slightly acidic soil because the high  $H^+$  concentrations can displace positively charged minerals from soil particles, making them more available for absorption. Adjusting soil pH for optimal crop growth is tricky because a change in  $H^+$  concentration may make one mineral more available but another less available. At pH 8, for instance, plants can absorb calcium, but iron is almost unavailable. The soil pH should be matched to a crop’s mineral needs. If the soil is too alkaline, adding sulfate will lower the pH. Soil that is too acidic can be adjusted by adding lime (calcium carbonate or calcium hydroxide).



When the soil pH dips to 5 or lower, toxic aluminum ions ( $\text{Al}^{3+}$ ) become more soluble and are absorbed by roots, stunting root growth and preventing the uptake of calcium, a needed plant nutrient. Some plants can cope with high  $\text{Al}^{3+}$  levels by secreting organic anions that bind  $\text{Al}^{3+}$  and render it harmless. However, low soil pH and  $\text{Al}^{3+}$  toxicity continue to pose serious problems, especially in tropical regions, where the pressure of producing food for a growing population is often most acute.

Soil mismanagement is a major problem facing the world. More than 30% of the world's farmland has reduced productivity stemming from poor soil conditions, such as chemical contamination, mineral deficiencies, acidity, salinity, and poor drainage. As the world's population continues to grow, the demand for food increases. Because soil quality is a major determinant of crop yield, the need to manage soil resources prudently has never been greater.

## The Living, Complex Ecosystem of Soil

The successful cultivation of plants in soil-free hydroponic systems demonstrates that plants do not need soil to complete their life cycles. Still, most terrestrial plants do grow in soil, and it is from the topsoil that they usually acquire mineral nutrients. Thus, an understanding of the properties of soil is important for understanding plants and their growth. We begin by discussing the basic physical properties of soil: its texture and composition.

### Soil Texture

The texture of soil depends on the size of its particles. Soil particles can range from coarse sand (0.02–2 mm in diameter) to silt (0.002–0.02 mm) to microscopic clay particles (less than 0.002 mm). These different-sized particles arise ultimately from the weathering of rock. Water freezing in the crevices of rocks causes mechanical fracturing, and weak acids in the soil break rocks down chemically. When organisms penetrate the rock, they accelerate breakdown by chemical and mechanical means. Plant roots, for example, secrete acids that dissolve the rock, and their growth in fissures leads to mechanical fracturing. The mineral particles released by weathering become mixed with living organisms and humus, forming topsoil.

In the topsoil, plants are nourished by the soil solution, the water and dissolved minerals in the pores between soil particles. The pores also contain air pockets. After a heavy rainfall, water drains away from the larger spaces in the soil, but smaller spaces retain water because water molecules are attracted to the negatively charged surfaces of clay and other soil particles.

The most fertile topsoils are **loams**, which are composed of roughly equal amounts of sand, silt, and clay. Loamy soils have enough small silt and clay particles to provide ample surface area for the adhesion and retention of minerals and water. Meanwhile, the large spaces between sand particles enable efficient diffusion of oxygen to the roots. Sandy soils generally don't retain enough water to support vigorous plant growth,

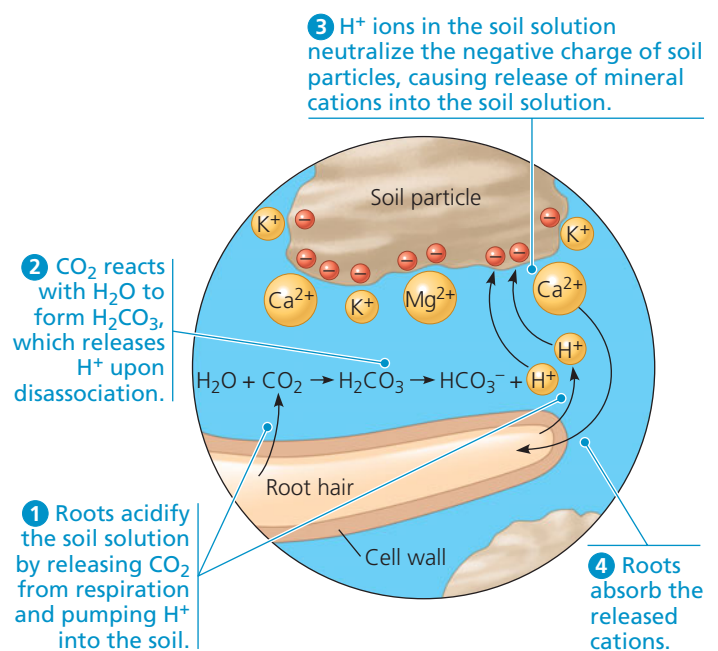
and clayey soils tend to retain too much water. When soil does not drain adequately, the air is replaced by water, and the roots suffocate from lack of oxygen. Typically, the most fertile topsoils have pores that are about half water and half air, providing a good balance between aeration, drainage, and water storage capacity. The physical properties of soils can be adjusted by adding soil amendments, such as peat moss, compost, manure, or sand.

### Topsoil Composition

A topsoil's composition encompasses its inorganic (mineral) and organic chemical components. The organic components include the many life-forms that inhabit the soil.

**Inorganic Components** The surface charges of soil particles determine their ability to bind many nutrients. Most soil particles are negatively charged. Negatively charged ions (anions)—such as the plant nutrients nitrate ( $\text{NO}_3^-$ ), phosphate ( $\text{H}_2\text{PO}_4^-$ ), and sulfate ( $\text{SO}_4^{2-}$ )—do not bind to the negatively charged soil particles and are therefore easily lost by leaching, the percolation of water through the soil. By comparison, positively charged ions (cations)—such as potassium ( $\text{K}^+$ ), calcium ( $\text{Ca}^{2+}$ ), and magnesium ( $\text{Mg}^{2+}$ )—bind more strongly to soil particles and are less easily lost by leaching.

Roots, however, do not absorb mineral cations directly from soil particles; they absorb them from the soil solution. Mineral cations enter the soil solution by **cation exchange**, a process in which cations are displaced from soil particles by other cations, particularly  $\text{H}^+$  (**Figure 29.10**). Therefore, a soil's capacity to exchange cations is determined by the number of cation adhesion sites and by the soil's pH. Soils with higher capacities generally have a larger reserve of mineral nutrients.



▲ **Figure 29.10** Cation exchange in soil.

? Which are more likely to be leached from the soil by heavy rains—cations or anions? Explain.

**Organic Components** Humus, which consists of the organic material produced by decomposition of fallen leaves, feces, dead organisms, and other organic matter by bacteria and fungi, is the major organic component of topsoil. Humus prevents clay particles from packing together and forms a crumbly soil that retains water but is still porous enough to aerate roots adequately. Humus also increases the soil's capacity to exchange cations and serves as a reservoir of mineral nutrients that return gradually to the soil as microorganisms decompose the organic matter.

**Living Components** Topsoil is home to an astonishing number and variety of organisms. A teaspoon of topsoil has about 5 billion bacteria, which cohabit with fungi, algae and other protists, insects, earthworms, nematodes, and plant roots. The activities of all these organisms affect the soil's physical and chemical properties. Earthworms, for example, consume organic matter and derive their nutrition from the bacteria and fungi growing on this material. They excrete wastes and move large amounts of material to the soil surface. In addition, they move organic matter into deeper layers of the soil. In effect, earthworms mix and clump the soil particles, allowing for better gaseous diffusion and retention of water. Plant roots also affect soil texture and composition. For example, by binding the soil, they reduce erosion, and by excreting acids, they lower soil pH.

#### CONCEPT CHECK 29.3

1. Are some essential elements more important than others? Explain.
2. **WHAT IF?** If an element increases the growth rate of a plant, can it be defined as an essential element?
3. **MAKE CONNECTIONS** Based on Figure 7.17, explain why ethanol accumulates in plant roots subjected to waterlogging.

For suggested answers, see Appendix A.

## CONCEPT 29.4

### Plant nutrition often involves relationships with other organisms

To this point, we have portrayed plants as exploiters of soil resources. But plants and soil have a two-way relationship. Dead plants provide much of the energy needed by soil microorganisms. Moreover, secretions from living roots support a wide variety of microbes in the near-root environment. Here we'll focus on some *mutualistic*—mutually beneficial—relationships between plants and soil bacteria or fungi. Then we'll look at some nonmutualistic forms of plant nutrition involving other organisms.

#### Soil Bacteria and Plant Nutrition

Some soil bacteria engage in mutually beneficial chemical exchanges with plant roots. Others enhance the decomposition of organic materials and increase nutrient availability. Some even live inside roots and convert nitrogen from the air.

#### Rhizobacteria

**Rhizobacteria** are soil bacteria with especially large populations in the **rhizosphere**, the soil layer that surrounds the plant's roots. Different soils vary greatly in the types and number of rhizobacteria they harbor. Microbial activity within a plant's rhizosphere is 10 to 100 times higher than in nearby soil because the roots secrete nutrients such as sugars, amino acids, and organic acids. Up to 20% of a plant's photosynthetic production fuels the organisms in this miniature ecosystem. As a result of diverse plant-microbe interactions, the composition of this microbial population often differs greatly from the surrounding soil and the rhizospheres of other plant species. Each rhizosphere contains a unique and complex cocktail of root secretions and microbial products.

Rhizobacteria known as *plant-growth-promoting rhizobacteria* enhance plant growth by a variety of mechanisms. Some produce chemicals that stimulate plant growth. Others produce antibiotics that protect roots from disease. Still others absorb toxic metals or make nutrients more available to roots. Inoculation of seeds with plant-growth-promoting rhizobacteria can increase crop yield and reduce the need for fertilizers and pesticides. How do the bacteria benefit by interacting with plants? Nutrients secreted by roots supply most of the energy in the rhizosphere, so bacterial adaptations that help a plant thrive also help the bacteria.

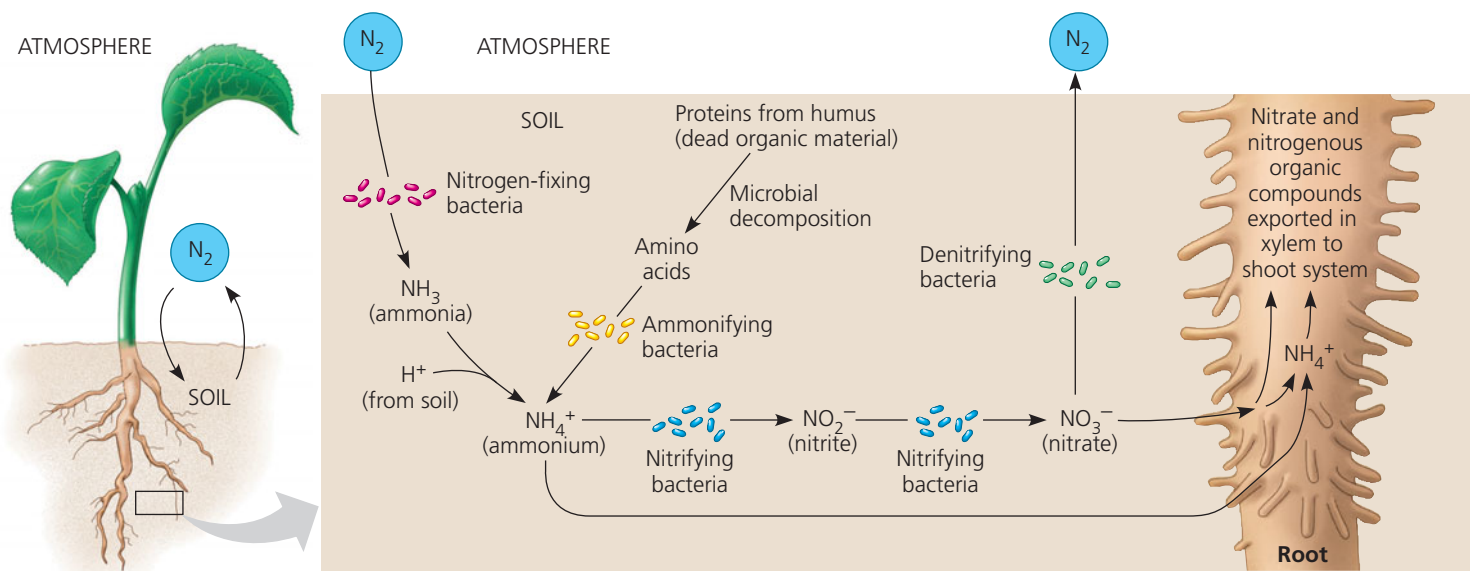
#### Bacteria in the Nitrogen Cycle

Unlike other soil minerals, ammonium ions ( $\text{NH}_4^+$ ) and nitrate ions ( $\text{NO}_3^-$ )—the forms of nitrogen that plants can use—are not derived from the weathering of rocks. Although lightning produces small amounts of  $\text{NO}_3^-$  that get carried to the soil in rain, most soil nitrogen comes from the activity of bacteria (**Figure 29.11**). From a global perspective, no mineral nutrient is more limiting to plant growth than nitrogen, which is required in large amounts for synthesizing proteins and nucleic acids.

The **nitrogen cycle**, also discussed in Figure 42.13, describes transformations of nitrogen and nitrogenous compounds in nature. When a plant or animal dies or an animal expels waste, the initial form of nitrogen is organic. Decomposers called *ammonifying bacteria* convert the organic nitrogen within the remains back to ammonium ( $\text{NH}_4^+$ ), a process called ammonification. Other sources of soil  $\text{NH}_4^+$  are *nitrogen-fixing bacteria*, which convert gaseous nitrogen ( $\text{N}_2$ ) to  $\text{NH}_3$ , which in turn picks up another  $\text{H}^+$  in the soil solution to form  $\text{NH}_4^+$ .

Plants can also acquire nitrogen in the form of  $\text{NO}_3^-$  (nitrate). Soil  $\text{NO}_3^-$  is largely formed by a two-step process called *nitrification*, which consists of the oxidation of  $\text{NH}_4^+$  to nitrite ( $\text{NO}_2^-$ ), followed by the oxidation of nitrite to nitrate ( $\text{NO}_3^-$ ). Different types of *nitrifying bacteria* mediate each step. After the roots absorb  $\text{NO}_3^-$ , a plant enzyme reduces it back to  $\text{NH}_4^+$ , which other enzymes incorporate into amino acids and





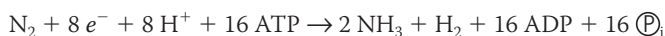
▲ **Figure 29.11 The roles of soil bacteria in the nitrogen nutrition of plants.** Ammonium is made available to plants by two types of soil bacteria: those that fix atmospheric  $N_2$  (nitrogen-fixing bacteria) and those that decompose organic material (ammonifying bacteria). Although plants absorb some ammonium from the soil, they absorb mainly nitrate, which is produced from ammonium by nitrifying bacteria. Plants reduce nitrate back to ammonium before incorporating the nitrogen into organic compounds.

other organic compounds. Most plant species export nitrogen from roots to shoots via the xylem as  $NO_3^-$  or organic compounds synthesized in the roots. Some soil nitrogen is lost, particularly in anaerobic soils, when denitrifying bacteria convert  $NO_3^-$  to  $N_2$ , which diffuses into the atmosphere.

### Nitrogen-Fixing Bacteria: A Closer Look

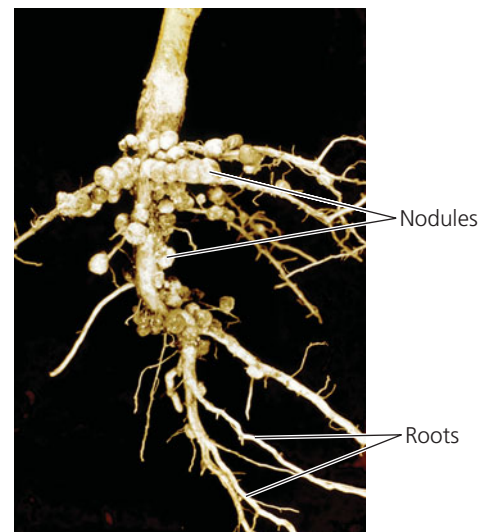
Although Earth's atmosphere is 79% nitrogen ( $N_2$ ), plants cannot use gaseous  $N_2$  directly because there is a triple bond between the two nitrogen atoms, making the molecule almost inert. For  $N_2$  to be of use to plants, it must be reduced to  $NH_3$  by a process called **nitrogen fixation**. All  $N_2$ -fixing organisms are bacteria, and some that carry out this process are free-living (see Figure 29.11). One of the more important bacteria involved in  $N_2$  fixation is the genus *Rhizobium*, which forms intimate associations with the roots of legumes (such as peas and soybeans) and markedly alters their root structure. Although *Rhizobium* can be free-living in the soil, it cannot fix  $N_2$  in its free state, nor can legume roots fix  $N_2$  without the bacteria.

The multistep conversion of  $N_2$  to  $NH_3$  by  $N_2$  fixation can be summarized as follows:



The reaction is driven by the enzyme complex *nitrogenase*. Because the process of  $N_2$  fixation requires 8 ATP molecules for each  $NH_3$  synthesized,  $N_2$ -fixing bacteria require a rich supply of carbohydrates from decaying material, root secretions, or (in the case of *Rhizobium*) the vascular tissue of roots.

The mutualism between *Rhizobium* (“root living”) bacteria and legume roots involves dramatic changes in root structure. Along a legume’s roots are swellings called **nodules**, composed of plant cells that have been “infected” by *Rhizobium* (Figure 29.12). Inside each nodule, *Rhizobium* bacteria assume a form called **bacteroids**, which are contained within vesicles formed in the root cells. Legume-*Rhizobium* relationships generate more usable nitrogen for plants than all industrial fertilizers used today—and at virtually no cost to the farmer.



▲ **Figure 29.12 Soybean root nodules.** The spherical structures along this soybean root system are nodules containing *Rhizobium* bacteria. The bacteria fix nitrogen and obtain photosynthetic products made by the plant.

The location of the bacteroids inside living, nonphotosynthetic cells facilitates  $N_2$  fixation, which requires an anaerobic environment. Lignified external layers of root nodules also limit gas exchange. Some root nodules appear reddish because of a molecule called leghemoglobin (*leg-* for “legume”), an iron-containing protein that binds reversibly to oxygen (similar to the hemoglobin in human red blood cells). This protein is an oxygen “buffer,” reducing the concentration of free oxygen and thereby providing an anaerobic environment for  $N_2$  fixation while regulating the oxygen supply for the intense cellular respiration required to produce ATP for  $N_2$  fixation.

Each legume species is associated with a particular strain of *Rhizobium*. The symbiotic relationship between a legume and  $N_2$ -fixing bacteria is mutualistic in that the bacteria supply the host plant with fixed nitrogen while the plant provides the bacteria with carbohydrates and other organic compounds. The root nodules use most of the ammonium produced to make amino acids, which are then transported up to the shoot through the xylem.

## Fungi and Plant Nutrition

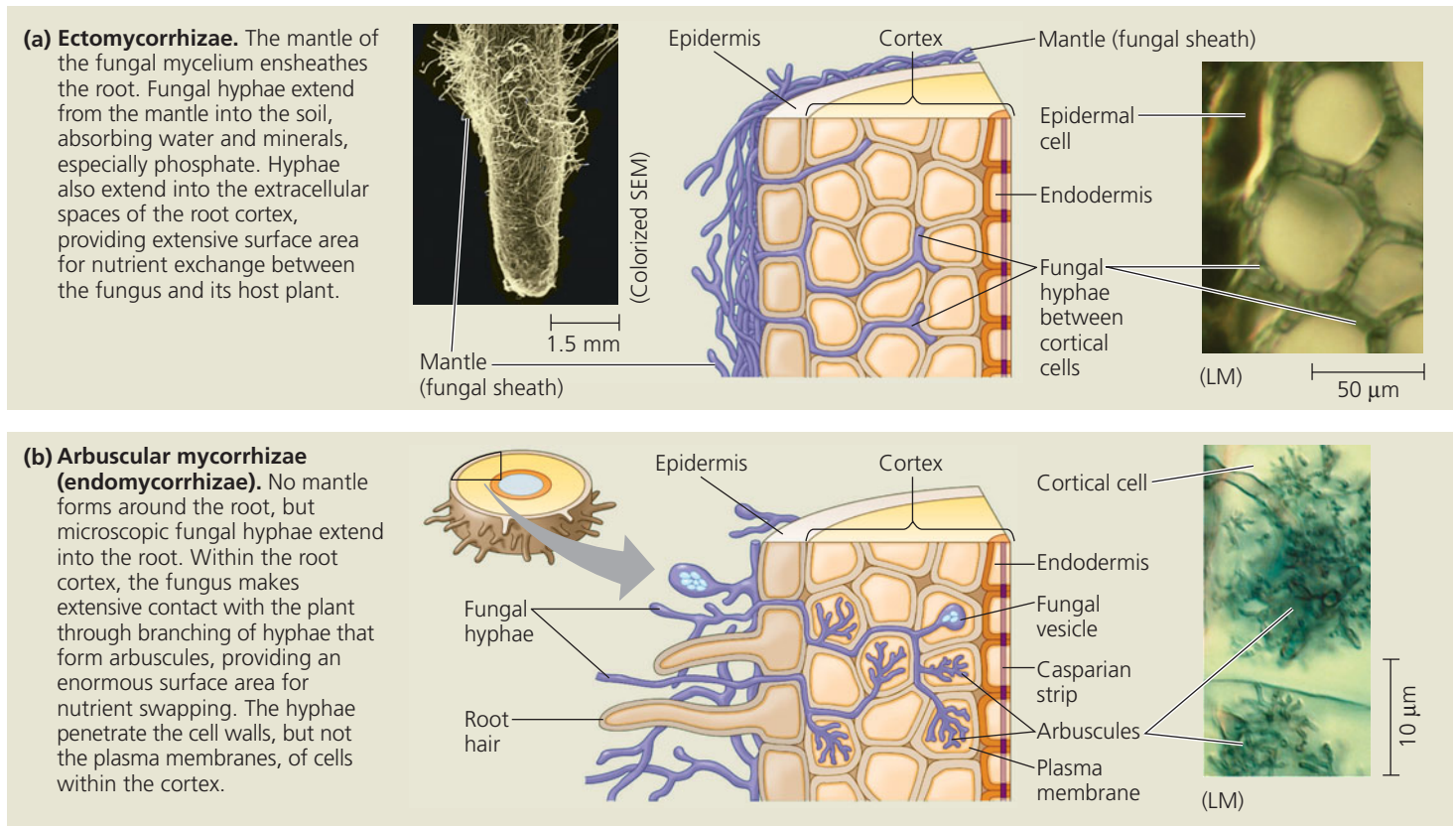
**Mycorrhizae** (“fungus roots”) are mutualistic associations of roots and fungi that play a major role in plant nutrition. The host plant provides the fungus with a steady supply of sugar. Meanwhile, the fungus increases the surface area for water

uptake and also supplies the plant with phosphate and other minerals absorbed from the soil. The fungi of mycorrhizae also secrete growth factors that stimulate roots to grow and branch, as well as antibiotics that help protect the plant from soil pathogens.

### The Two Main Types of Mycorrhizae

One type of mycorrhiza—the **ectomycorrhizae**—forms a dense sheath, or mantle, of mycelia (mass of branching hyphae) over the surface of the root (**Figure 29.13a**). Fungal hyphae extend from the mantle into the soil, greatly increasing the surface area for water and mineral absorption. Hyphae also grow into the root cortex, forming an apoplastic network within the extracellular spaces that facilitates nutrient exchange. Of the 10% of plant families that have species that form ectomycorrhizae, the majority are woody, including members of the pine, birch, and eucalyptus families.

**Arbuscular mycorrhizae** are more common than ectomycorrhizae and are found in over 85% of plant species, including most crops. Unlike ectomycorrhizae, they do not form a dense mantle ensheathing the root (**Figure 29.13b**). Arbuscular mycorrhizal associations start when microscopic soil hyphae respond to the presence of a root by growing toward it, establishing contact, and growing along its surface. Hyphae penetrate between epidermal cells and then enter the root cortex. These hyphae digest small patches of the cortical cell walls, but



▲ **Figure 29.13** Mycorrhizae.



they do not actually pierce the plasma membrane and enter the cytoplasm. Instead, a hypha grows into a tube formed by invagination of the root cell's membrane. The process is analogous to poking a finger gently into a balloon without popping it; your finger is like the fungal hypha, and the balloon skin is like the root cell's membrane. After the fungal hyphae have penetrated in this way, some branch densely, forming structures called arbuscules ("little trees"), which are important sites of nutrient transfer between the fungus and the plant. Within the hyphae themselves, oval vesicles may form, possibly serving as food storage sites for the fungus. To the unaided eye, arbuscular mycorrhizae look like "normal" roots with root hairs, but a microscope reveals the enormous extent of the mutualistic relationship.

### Agricultural and Ecological Importance of Mycorrhizae

Roots can form mycorrhizal symbioses only if exposed to the appropriate species of fungus. In most ecosystems, these fungi are present in the soil, but if seeds are collected in one environment and planted in foreign soil, the plants may show signs of malnutrition (particularly phosphorus deficiency), resulting from the absence of fungal partners. Treating seeds with mycorrhizal fungal spores can help seedlings form mycorrhizae and improve crop yield.

Mycorrhizal associations are also important in understanding ecological relationships. Invasive exotic plants sometimes colonize areas by disrupting interactions between native organisms. For example, garlic mustard (*Alliaria petiolata*), introduced into New England from Europe during the 1800s, has invaded woodlands throughout the eastern and middle United States, suppressing tree seedlings and other native plants. Recent evidence suggests that its invasive properties may stem from its ability to slow the growth of other plant species by preventing the growth of arbuscular mycorrhizal fungi (Figure 29.14).

### Epiphytes, Parasitic Plants, and Carnivorous Plants

Almost all plant species have mutualistic symbiotic relationships with soil fungi or bacteria or both. Though rarer, there are also plant species with nutritional adaptations that use other organisms in nonmutualistic ways. Figure 29.15 provides an overview of three unusual adaptations: epiphytes, parasitic plants, and carnivorous plants.

#### CONCEPT CHECK 29.4

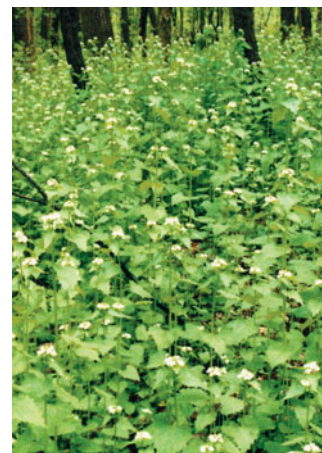
1. Why is the study of the rhizosphere critical to understanding plant nutrition?
2. How do soil bacteria and mycorrhizae contribute to plant nutrition?
3. **WHAT IF?** A soybean farmer finds that the older leaves of his plant are turning yellow following a long period of wet weather. Suggest a reason why.

For suggested answers, see Appendix A.

#### ▼ Figure 29.14 Inquiry

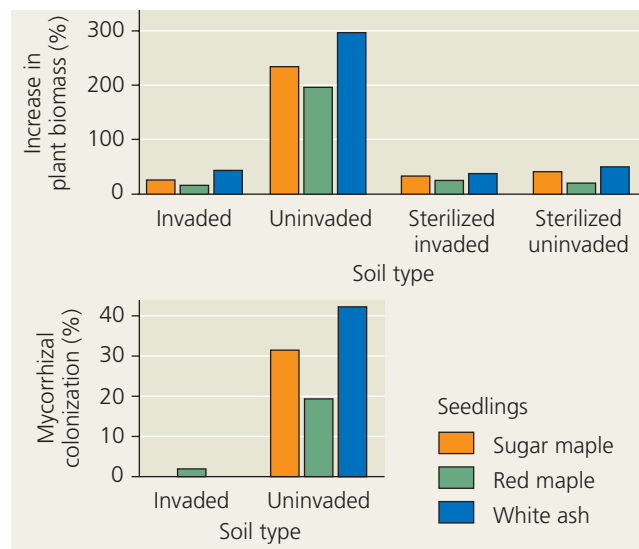
### Does the invasive weed garlic mustard disrupt mutualistic associations between native tree seedlings and arbuscular mycorrhizal fungi?

**Experiment** Kristina Stinson, of Harvard University, and colleagues investigated the effect of invasive garlic mustard (shown in the photo) on the growth of native tree seedlings and associated mycorrhizal fungi. In one experiment, they grew seedlings of three North American trees—sugar maple, red maple, and white ash—in four different soils. Two of the soil samples were collected from a location where garlic mustard was growing, and one of these samples was sterilized. The other two soil samples were collected from a location devoid of garlic mustard, and one of these was sterilized.



After four months of growth, the researchers harvested the shoots and roots and determined the dried biomass. The roots were also analyzed for percent colonization by arbuscular mycorrhizal fungi.

**Results** Native tree seedlings grew more slowly and were less able to form mycorrhizal associations when grown either in sterilized soil or in unsterilized soil collected from a location that had been invaded by garlic mustard.



**Conclusion** The data support the hypothesis that garlic mustard suppresses growth of native trees by affecting the soil in a way that disrupts mutualistic associations between the trees and arbuscular mycorrhizal fungi.

**Source** K. A. Stinson et al., Invasive plant suppresses the growth of native tree seedlings by disrupting belowground mutualisms, *PLoS Biol* (Public Library of Science: Biology) 4(5): e140 (2006).

**Inquiry in Action** Read and analyze the original paper in *Inquiry in Action: Interpreting Scientific Papers*.

**WHAT IF?** What effect would applying inorganic phosphate to soil invaded by garlic mustard have on the plant's ability to outcompete native species?

## Epiphytes

An **epiphyte** (from the Greek *epi*, upon, and *phyton*, plant) is a plant that grows on another plant. Epiphytes produce and gather their own nutrients; they do not tap into their hosts for sustenance. Usually anchored to the branches or trunks of living trees, epiphytes absorb water and minerals from rain, mostly through leaves rather than roots. Some examples are staghorn ferns, bromeliads, and many orchids, including the vanilla plant.

► **Staghorn fern**, an epiphyte



## Parasitic Plants



Unlike epiphytes, parasitic plants absorb water, minerals, and sometimes products of photosynthesis from their living hosts. Many species have roots that function as haustoria, nutrient-absorbing projections that tap into the host plant. Some parasitic species, such as orange-colored, spaghetti-like dodder (genus *Cuscuta*), lack chlorophyll entirely, whereas others, such as mistletoe (genus *Phoradendron*), are photosynthetic. Still others, such as Indian pipe (*Monotropa uniflora*), absorb nutrients from the hyphae of mycorrhizae associated with other plants.

◄ **Mistletoe**, a photosynthetic parasite



▲ **Dodder**, a nonphotosynthetic parasite (orange)



▲ **Indian pipe**, a nonphotosynthetic parasite of mycorrhizae

## Carnivorous Plants

Carnivorous plants are photosynthetic but supplement their mineral diet by capturing insects and other small animals. They live in acid bogs and other habitats where soils are poor in nitrogen and other minerals. Pitcher plants such as *Nepenthes* and *Sarracenia* have water-filled funnels into which prey slip and drown, eventually to be digested by enzymes. Sundews (genus *Drosera*) exude a sticky fluid from tentacle-like glands on highly modified leaves. Stalked glands secrete sweet mucilage that attracts and ensnares insects, and they also release digestive enzymes. Other glands then absorb the nutrient "soup." The highly modified leaves of Venus flytrap (*Dionaea muscipula*) close quickly but partially when a prey hits two trigger hairs in rapid enough succession. Smaller insects can escape, but larger ones are trapped by the teeth lining the margins of the lobes. Excitation by the prey causes the trap to narrow more and digestive enzymes to be released.



◄ **Pitcher plants**



▲ **Sundew**



◄ **Venus flytraps**



## Transpiration drives the transport of water and minerals from roots to shoots via the xylem

An average-sized tree, despite having neither heart nor muscle, transports nearly 800 L of water on a warm, sunny day. How do trees accomplish this feat? To answer this question, we'll follow each step in the journey of water and minerals from the tips of roots to leaves.

### Absorption of Water and Minerals by Root Cells

Although all living plant cells absorb nutrients across their plasma membranes, the cells near the tips of roots are particularly important because most of the absorption of water and minerals occurs there. In this region, the epidermal cells are permeable to water, and many are differentiated into root hairs, modified cells that account for much of the absorption of water by roots (see Figure 28.4). The root hairs absorb the

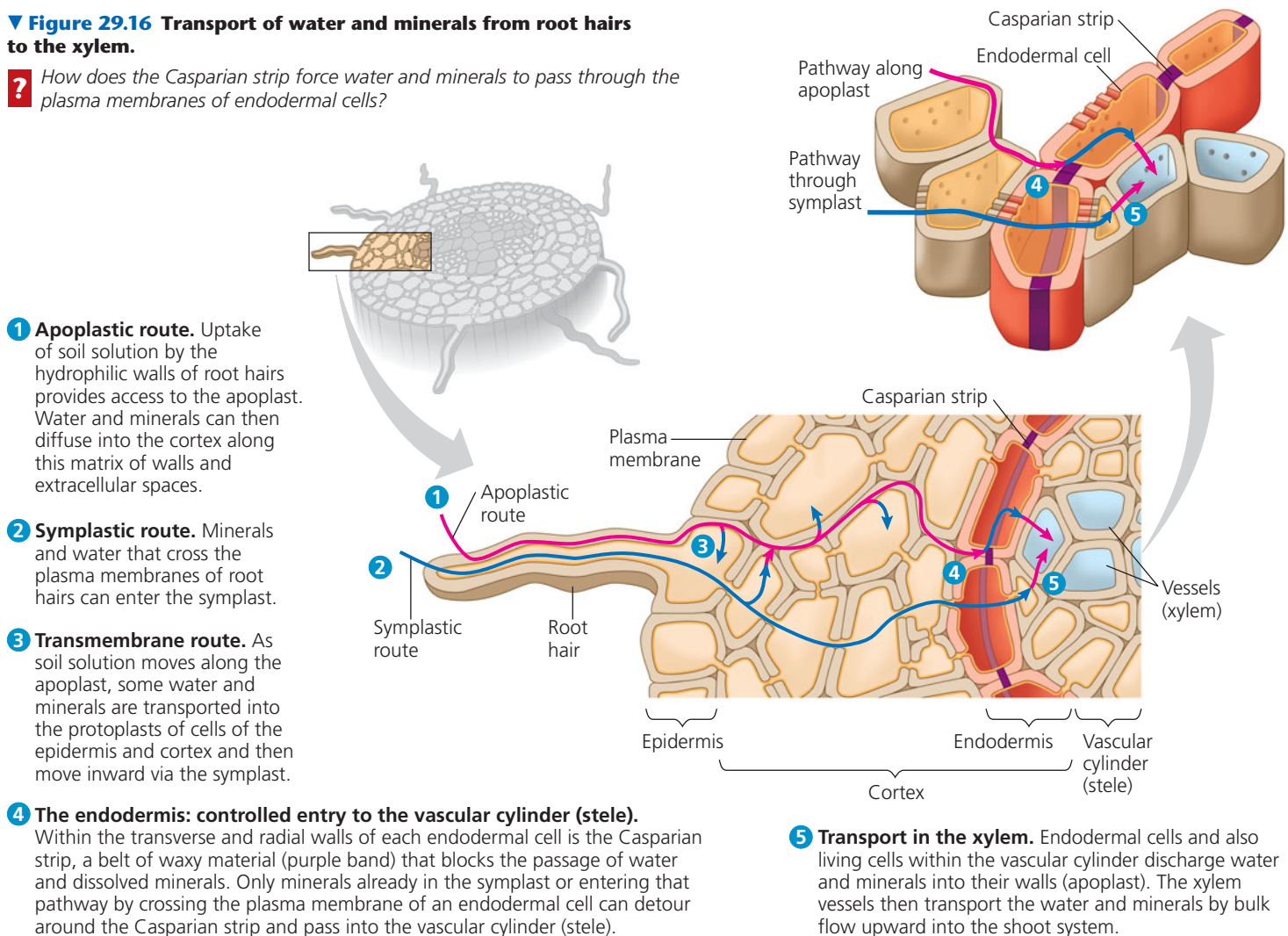
soil solution, which consists of water molecules and dissolved mineral ions that are not bound tightly to soil particles. The soil solution is drawn into the hydrophilic walls of epidermal cells and passes freely along the cell walls and the extracellular spaces into the root cortex. This flow enhances the exposure of the cells of the cortex to the soil solution, providing a much greater membrane surface area for absorption than the surface area of the epidermis alone. Although the soil solution usually has a low mineral concentration, active transport enables roots to accumulate essential minerals to concentrations hundreds of times greater than in the soil.

### Transport of Water and Minerals into the Xylem

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, or stele. The **endodermis**, the innermost layer of the cortex, functions as a last checkpoint for the selective passage of minerals into the vascular cylinder (**Figure 29.16**). Minerals already in the symplast when they reach the endodermis continue through

▼ **Figure 29.16** Transport of water and minerals from root hairs to the xylem.

? How does the Casparian strip force water and minerals to pass through the plasma membranes of endodermal cells?



the plasmodesmata of endodermal cells and pass into the vascular cylinder. These minerals were already screened by the plasma membrane they had to cross to enter the symplast in the epidermis or cortex. Those minerals that reach the endodermis via the apoplast encounter a dead end that blocks their passage into the vascular cylinder. This barrier, located 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 (see Figure 29.16). The Casparian strip forces water and minerals that are passively moving through the apoplast to cross the plasma membrane of an endodermal cell before they can enter the vascular cylinder. 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. The endodermis also prevents solutes that have accumulated in the xylem from leaking back into the soil solution.

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 parts of the apoplast. Endodermal cells, as well as living cells within the vascular cylinder, discharge minerals from their protoplasts into their own cell 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 vessel elements, where they are transported to the shoot system by bulk flow.

## Bulk Flow Transport via the Xylem

Water and minerals from the soil enter the plant through the epidermis of roots, cross the root cortex, and pass into the vascular cylinder. From there the **xylem sap**, the water and dissolved minerals in the xylem, gets transported long distances by bulk flow to the veins that branch throughout each leaf. As noted earlier, bulk flow is much faster than diffusion or active transport. Peak velocities in the transport of xylem sap can range from 15 to 45 m/hr for trees with wide vessel elements. Stems and leaves depend on this efficient delivery system for their supply of water and minerals. Xylem sap rises to heights of more than 120 m in the tallest trees, largely by being pulled upward.

The process of transporting xylem sap involves the loss of an astonishing amount of water by **transpiration**, the loss of water vapor from leaves and other aerial parts of the plant. A single maize plant, for example, transpires 60 L of water (the equivalent of 170 12-ounce bottles) during a growing season. A maize crop growing at a typical density of 60,000 plants per hectare transpires almost 4 million L of water per hectare every growing season (about 400,000 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 may eventually die.

## Pulling Xylem Sap:

### The Cohesion-Tension Hypothesis

The xylem sap that rises through a tree does not require living cells to do so. Early researchers demonstrated that leafy stems with their lower end immersed in toxic solutions of copper sulfate or acid readily draw these poisons up if the stem is cut below the surface of the liquid. As the toxic solutions ascend, they kill all living cells in their path, eventually arriving in the transpiring leaves and killing the leaf cells as well. Nevertheless, the uptake of the toxic solutions and the loss of water from the dead leaves can continue for weeks.

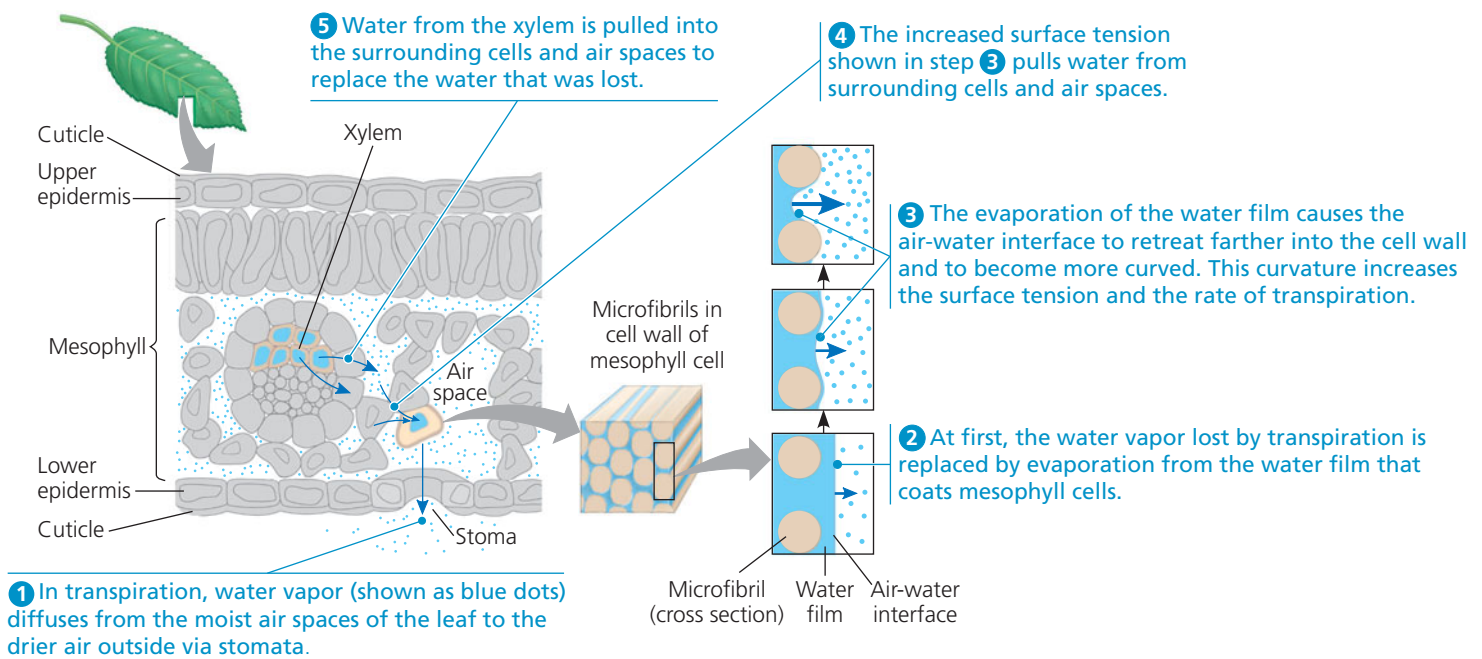
The **cohesion-tension hypothesis** is almost universally accepted by plant biologists as the mechanism underlying the ascent of xylem sap. According to this hypothesis, transpiration provides the pull for the ascent of xylem sap, and the cohesion of water molecules transmits this pull along the entire length of the xylem from shoots to roots. Hence, xylem sap is normally under negative pressure, or tension. Since transpiration is a “pulling” process, our exploration of the rise of xylem sap by the cohesion-tension mechanism begins not with the roots but with the leaves, where the driving force for transpirational pull begins.

**Transpirational Pull** Stomata on a leaf’s surface lead to a maze of internal air spaces that expose the mesophyll cells to the CO<sub>2</sub> required for photosynthesis. The air in these spaces is saturated with water vapor. On most days, the air outside the leaf is drier; that is, it has lower water potential than the air inside the leaf. Therefore, water vapor in the air spaces of a leaf diffuses down its water potential gradient and exits the leaf via the stomata. Transpiration refers to this loss of water vapor from plants by diffusion and evaporation.

But how does loss of water vapor from the leaf translate into a pulling force for upward movement of water through a plant? The negative pressure potential that causes water to move up through the xylem develops at the surface of mesophyll cell walls in the leaf (**Figure 29.17**). The cell wall acts like a very thin capillary network. Water adheres to the cellulose microfibrils and other hydrophilic components of the cell wall. As water evaporates from the water film that covers the cell walls of mesophyll cells, the air-water interface retreats farther into the cell wall. Because of the high surface tension of water, the curvature of the interface induces a tension, or negative pressure potential, in the water. As more water evaporates from the cell wall, the curvature of the air-water interface increases and the pressure of the water becomes more negative. Water molecules from the more hydrated parts of the leaf are then pulled toward this area, reducing the tension. These pulling forces are transferred to the xylem because each water molecule is cohesively bound to the next by hydrogen bonds. Thus, transpirational pull depends on several of the properties of water discussed in Chapter 2: adhesion, cohesion, and surface tension.

The role of negative pressure potential in transpiration is consistent with the water potential equation because negative





**▲ Figure 29.17 Generation of transpirational pull.** Negative pressure (tension) at the air-water interface in the leaf is the basis of transpirational pull, which draws water out of the xylem.

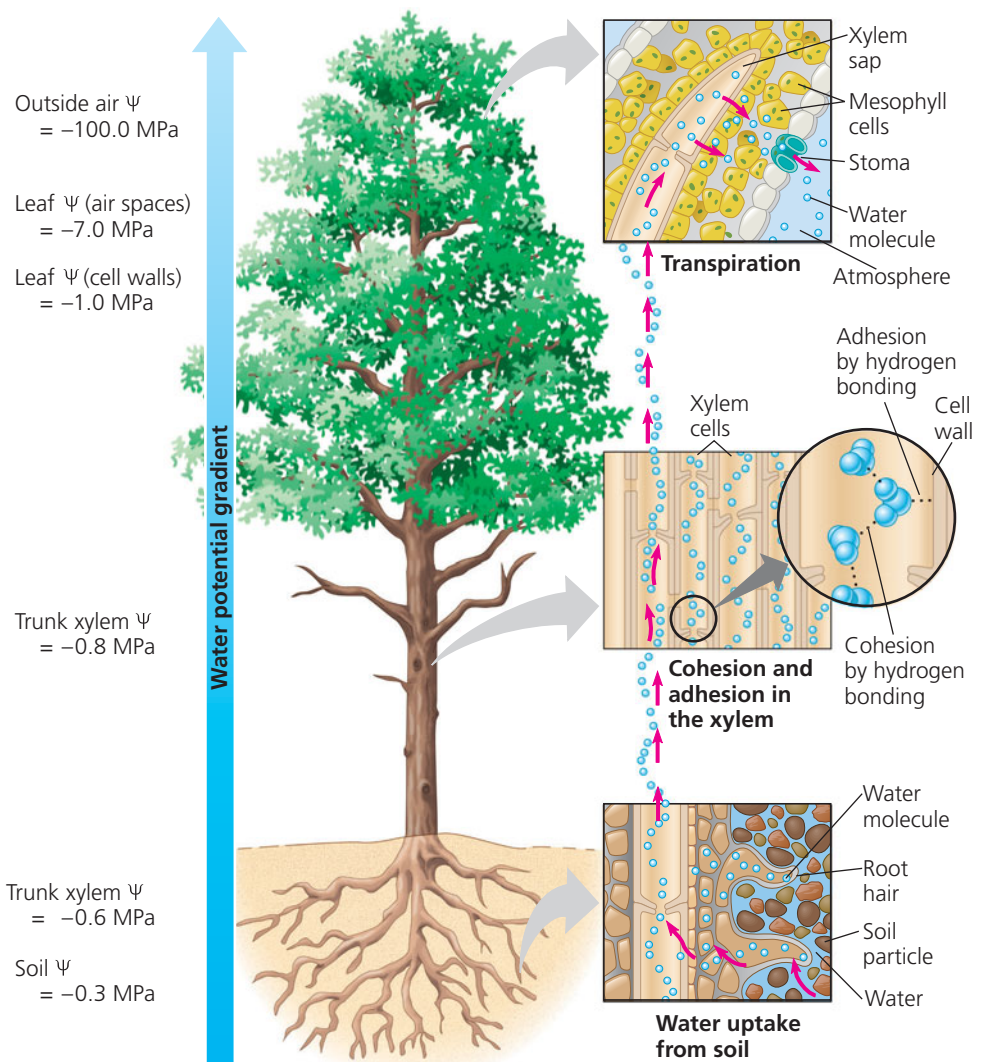
pressure potential (tension) *lowers* water potential (see Figure 29.6). Because water moves from areas of higher water potential to areas of lower water potential, the more negative pressure potential at the air-water interface causes water in xylem cells to be “pulled” into mesophyll cells, which lose water to the air spaces, the water eventually diffusing out through stomata. In this way, the negative water potential of leaves provides the “pull” in transpirational pull. The transpirational pull on xylem sap is transmitted all the way from the leaves to the root tips and even into the soil solution (**Figure 29.18**).

#### ► **Figure 29.18 Ascent of xylem sap.**

Hydrogen bonding forms an unbroken chain of water molecules extending from leaves to the soil. The force driving the ascent of xylem sap is a gradient of water potential ( $\psi$ ). For bulk flow over long distance, the  $\psi$  gradient is due mainly to a gradient of the pressure potential ( $\psi_p$ ). Transpiration results in the  $\psi_p$  at the leaf end of the xylem being lower than the  $\psi_p$  at the root end. The  $\psi$  values shown on the left side of the figure are a “snapshot.” They may vary during daylight, but the direction of the  $\psi$  gradient remains the same.



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**Cohesion and Adhesion in the Ascent of Xylem Sap** Cohesion and adhesion facilitate the transport of water by bulk flow. Cohesion is the attractive force between molecules of the same substance. Water has an unusually high cohesive force due to the hydrogen bonds each water molecule can potentially make with other water molecules. Water's cohesive force within the xylem gives it a tensile strength equivalent to that of a steel wire of similar diameter. The cohesion of water makes it possible to pull a column of xylem sap from above without the water molecules separating. Water molecules exiting the xylem in the leaf tug on adjacent water molecules, and this pull is relayed, molecule by molecule, down the entire column of water in the xylem. Meanwhile, the strong adhesion of water molecules (again by hydrogen bonds) to the hydrophilic walls of xylem cells helps offset the downward force of gravity.

The upward pull on the sap creates tension within the vessel elements and tracheids, which are like elastic pipes. Positive pressure causes an elastic pipe to swell, whereas tension pulls the walls of the pipe inward. On a warm day, a decrease in the diameter of a tree trunk can even be measured. As transpirational pull puts the vessel elements and tracheids under tension, their thick secondary walls prevent them from collapsing, much as wire rings maintain the shape of a vacuum-cleaner hose. The tension produced by transpirational pull lowers water potential in the root xylem to such an extent that water flows passively from the soil, across the root cortex, and into the vascular cylinder.

Transpirational pull can extend down to the roots only through an unbroken chain of water molecules. Cavitation, the formation of a water vapor pocket, breaks the chain. It is more common in wide vessel elements than in tracheids and can occur during drought stress or when xylem sap freezes in winter. The air bubbles resulting from cavitation expand and block the water channels of the xylem. The interruption of xylem sap transport by cavitation is not always permanent. The chain of water molecules can detour around the air bubbles through pits between adjacent tracheids or vessel elements (see Figure 28.9). Moreover, secondary growth adds a layer of new xylem each year, and only the youngest, outermost secondary xylem layers transport water. Finally, an active though minor force called *root pressure* enables some small plants to refill blocked vessel elements.

## Xylem Sap Ascent by Bulk Flow: A Review

In the long-distance transport of water from roots to leaves by bulk flow, the movement of fluid is driven by a water potential difference at opposite ends of xylem tissue. The water potential difference is created at the leaf end of the xylem by the evaporation of water from leaf cells. Evaporation lowers the water potential at the air-water interface, thereby generating the negative pressure (tension) that pulls water through the xylem.

Bulk flow in the xylem differs from diffusion in some key ways. First, it is driven by differences in pressure potential ( $\psi_p$ ); solute potential ( $\psi_s$ ) is not a factor. Therefore, the water

potential gradient within the xylem is essentially a pressure gradient. Also, the flow does not occur across plasma membranes of living cells, but instead within hollow, dead cells. Furthermore, it moves the entire solution together—not just water or solutes—and at much greater speed than diffusion.

The plant expends no energy to lift xylem sap by bulk flow. Instead, the absorption of sunlight drives most of transpiration by causing water to evaporate from the moist walls of mesophyll cells and by lowering the water potential in the air spaces within a leaf. Thus, the ascent of xylem sap, like the process of photosynthesis, is ultimately solar powered.

### CONCEPT CHECK 29.5

1. A scientist adds a water-soluble inhibitor of photosynthesis to roots of a transpiring plant, but photosynthesis is not reduced. Why?
2. **WHAT IF?** Suppose an *Arabidopsis* mutant lacking functional aquaporin proteins has a root mass three times greater than that of wild-type plants. Suggest an explanation.
3. **MAKE CONNECTIONS** How are the Casparian strip and tight junctions similar? See Figure 4.27.

For suggested answers, see Appendix A.

## CONCEPT 29.6

### The rate of transpiration is regulated by stomata

Leaves generally have large surface areas and high surface-to-volume ratios. The large surface area enhances light absorption for photosynthesis. The high surface-to-volume ratio aids in  $\text{CO}_2$  absorption during photosynthesis as well as in the release of  $\text{O}_2$ , a by-product of photosynthesis. Upon diffusing through the stomata,  $\text{CO}_2$  enters a honeycomb of air spaces formed by the spongy mesophyll cells (see Figure 28.17). Because of the irregular shapes of these cells, the leaf's internal surface area may be 10 to 30 times greater than the external surface area.

Although large surface areas and high surface-to-volume ratios increase the rate of photosynthesis, they also increase water loss by way of the stomata. Thus, a plant's tremendous requirement for water is largely a consequence of the shoot system's need for ample exchange of  $\text{CO}_2$  and  $\text{O}_2$  for photosynthesis. By opening and closing the stomata, guard cells help balance the plant's requirement to conserve water with its requirement for photosynthesis.

### Stomata: Major Pathways for Water Loss

About 95% of the water a plant loses escapes through stomata, although 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. Guard cells control the diameter of the stoma by changing shape, thereby widening or narrowing the gap between the



two guard cells. Under the same environmental conditions, the amount of water lost by a leaf depends largely on the number of stomata and the average size of their pores.

The stomatal density of a leaf is under both genetic and environmental control. For example, desert plants are genetically programmed to have lower stomatal densities than do marsh plants. Stomatal density, however, is a developmentally plastic feature of many plants. High light exposures and low  $\text{CO}_2$  levels during leaf development lead to increased density in many species. By measuring the stomatal density of dried herbarium specimens, scientists have gained insight into the levels of atmospheric  $\text{CO}_2$  in the past. A recent British survey found that stomatal density of many woodland species has decreased since 1927, when a similar survey was made. This observation is consistent with other findings that atmospheric  $\text{CO}_2$  levels increased dramatically during the late 20th century.

## Mechanisms of Stomatal Opening and Closing

When guard cells absorb water from neighboring cells, they become more turgid. 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 bow outward when turgid (Figure 29.19a). This bowing outward increases the size of the pore between the guard cells. When the cells lose water and become flaccid, they become less bowed, and the pore closes.

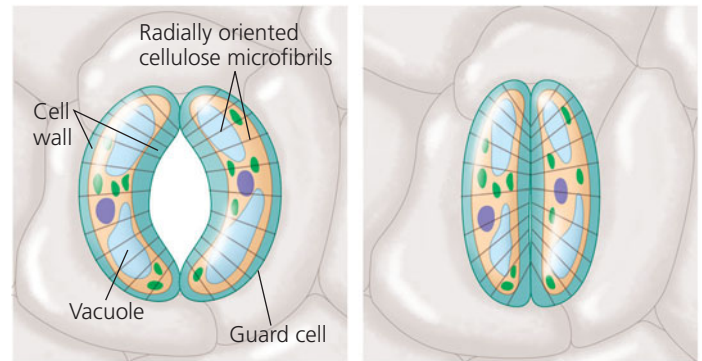
The changes in turgor pressure in guard cells result primarily from the reversible absorption and loss of potassium ions ( $\text{K}^+$ ). Stomata open when guard cells actively accumulate  $\text{K}^+$  from neighboring epidermal cells (Figure 29.19b). The flow of  $\text{K}^+$  across the plasma membrane of the guard cell is coupled to the generation of a membrane potential by proton pumps (see Figure 29.5a). 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. The absorption of  $\text{K}^+$  causes the water potential to become more negative within the guard cells, and the cells become more turgid as water enters by osmosis. Stomatal closing results from a loss of  $\text{K}^+$  from guard cells to neighboring cells, which leads to an osmotic loss of water. Aquaporins also help regulate the osmotic swelling and shrinking of guard cells.

## Stimuli for Stomatal Opening and Closing

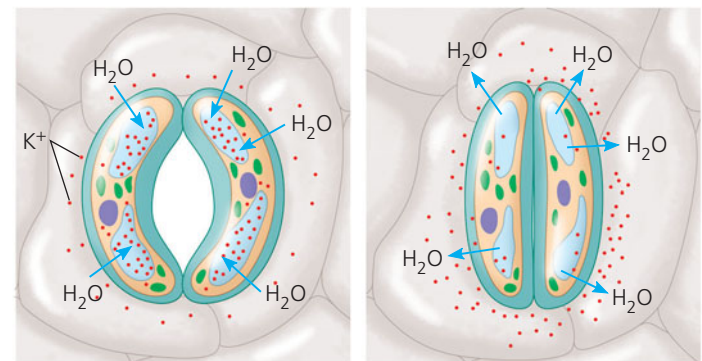
In general, stomata are open during the day and mostly closed at night, preventing the plant from losing water under conditions when photosynthesis cannot occur. At least three cues contribute to stomatal opening at dawn: light,  $\text{CO}_2$  depletion, and an internal “clock” in guard cells.

The light stimulates guard cells to accumulate  $\text{K}^+$  and become turgid. This response is triggered by illumination of blue-light receptors in the plasma membrane of guard cells. Activation of these receptors stimulates the activity of proton

**Guard cells turgid/Stoma open      Guard 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 radial orientation of cellulose microfibrils in the cell walls causes the guard cells to increase more in length than width when turgor increases. Since the two guard cells are tightly joined at their tips, they bow outward when turgid, causing the stomatal pore to open.



**(b) Role of potassium ions ( $\text{K}^+$ ) in stomatal opening and closing.** The transport of  $\text{K}^+$  (symbolized here as red dots) across the plasma membrane and vacuolar membrane causes the turgor changes of guard cells. The uptake of anions, such as malate and chloride ions (not shown), also contributes to guard cell swelling.

**▲ Figure 29.19 Mechanisms of stomatal opening and closing.**

pumps in the plasma membrane of the guard cells, in turn promoting absorption of  $\text{K}^+$ .

The stomata also open in response to depletion of  $\text{CO}_2$  within the leaf’s air spaces as a result of photosynthesis. As  $\text{CO}_2$  concentrations decrease during the day, the stomata progressively open if sufficient water is supplied to the leaf.

A third cue, the internal “clock” in the guard cells, ensures that stomata continue their daily rhythm of opening and closing. This rhythm occurs even if a plant is kept in a dark location. All eukaryotic organisms have internal clocks that regulate cyclic processes. Cycles with intervals of approximately 24 hours are called **circadian rhythms**, which you’ll learn more about in Chapter 31.

Drought stress can also cause stomata to close. A hormone called **abscisic acid (ABA)** is produced in roots and leaves in response to water deficiency and signals guard cells to close stomata. This response reduces wilting but also restricts  $\text{CO}_2$  absorption, thereby slowing photosynthesis. ABA also directly

inhibits photosynthesis. Water availability is so tied to plant productivity not because water is needed as a substrate in photosynthesis but because freely available water allows plants to keep stomata open and take up more  $\text{CO}_2$ .

## Effects of Transpiration on Wilting and Leaf Temperature

As long as most stomata remain open, transpiration is greatest on days that are sunny, warm, dry, and windy because these environmental factors increase evaporation. If transpiration cannot pull sufficient water to the leaves, the shoot becomes slightly wilted as cells lose turgor pressure. Although plants respond to such mild drought stress by rapidly closing stomata, some evaporative water loss still occurs through the cuticle. Under prolonged drought conditions, the leaves can become irreversibly injured.

Transpiration also results in evaporative cooling, which can lower a leaf's temperature by as much as  $10^\circ\text{C}$  compared with the surrounding air. This cooling prevents the leaf from reaching temperatures that could lead to protein denaturation.

► Ocotillo (*Fouquieria splendens*) is common in the southwestern region of the United States and northern Mexico. It is leafless during most of the year, thereby avoiding excessive water loss (right). Immediately after a heavy rainfall, it produces small leaves (below and inset). As the soil dries, the leaves quickly shrivel and die.

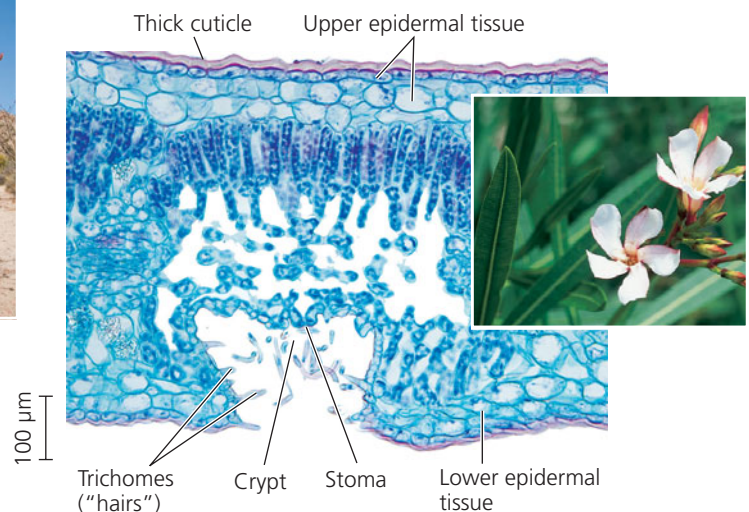


## Adaptations That Reduce Evaporative Water Loss

Many species of desert plants avoid drying out by completing their short life cycles during the brief rainy seasons. Rain comes infrequently in deserts, but when it arrives, the vegetation is transformed as dormant seeds of annual species quickly germinate and bloom, completing their life cycle before dry conditions return. Longer-lived species have unusual physiological or morphological adaptations that enable them to withstand the harsh desert conditions. Plants adapted to arid environments, such as the stone plants (see Figure 29.1), are called **xerophytes** (from the Greek *xero*, dry). **Figure 29.20** shows other examples. Many xerophytes, such as cacti, have highly reduced leaves that resist excessive water loss; they carry out photosynthesis mainly in their stems. The stems of many xerophytes are fleshy because they store water for use during long dry periods.

Another adaptation to arid habitats is **crassulacean acid metabolism (CAM)**, a specialized form of photosynthesis found in succulents of the family Crassulaceae and several

▼ Oleander (*Nerium oleander*), shown in the inset, is commonly found in arid climates. Its leaves have a thick cuticle and multiple-layered epidermal tissue that reduce water loss. Stomata are recessed in cavities called "crypts," an adaptation that reduces the rate of transpiration by protecting the stomata from hot, dry wind. Trichomes 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).



► The long, white hairlike bristles along the stem of the old man cactus (*Cephalocereus senilis*) help reflect the intense sunlight of the Mexican desert.



▲ **Figure 29.20** Some xerophytic adaptations.



other families. Because the leaves of CAM plants take in  $\text{CO}_2$  at night, the stomata can remain closed during the day, when evaporative stresses are greater.

### CONCEPT CHECK 29.6

1. The pathogenic fungus *Fusicoccum amygdali* secretes a toxin called fusicoccin that activates the plasma membrane proton pumps of plant cells and leads to uncontrolled water loss. Suggest a mechanism by which the activation of proton pumps could lead to severe wilting.
2. **WHAT IF?** If you buy cut flowers, why might the florist recommend cutting the stems underwater and then transferring the flowers to a vase while the cut ends are still wet?
3. **MAKE CONNECTIONS** Explain why the evaporation of water from leaves lowers their temperature. See Concept 2.5.

For suggested answers, see Appendix A.

## CONCEPT 29.7

### Sugars are transported from sources to sinks via the phloem

The unidirectional flow of water and minerals from soil to roots to leaves through the xylem is largely in an upward direction. In contrast, the movement of photosynthates often runs in the opposite direction, transporting sugars from mature leaves to lower parts of the plant, such as root tips that require large amounts of sugars for energy and growth. The transport of the products of photosynthesis, known as **translocation**, is carried out by another tissue, the phloem.

#### Movement from Sugar Sources to Sugar Sinks

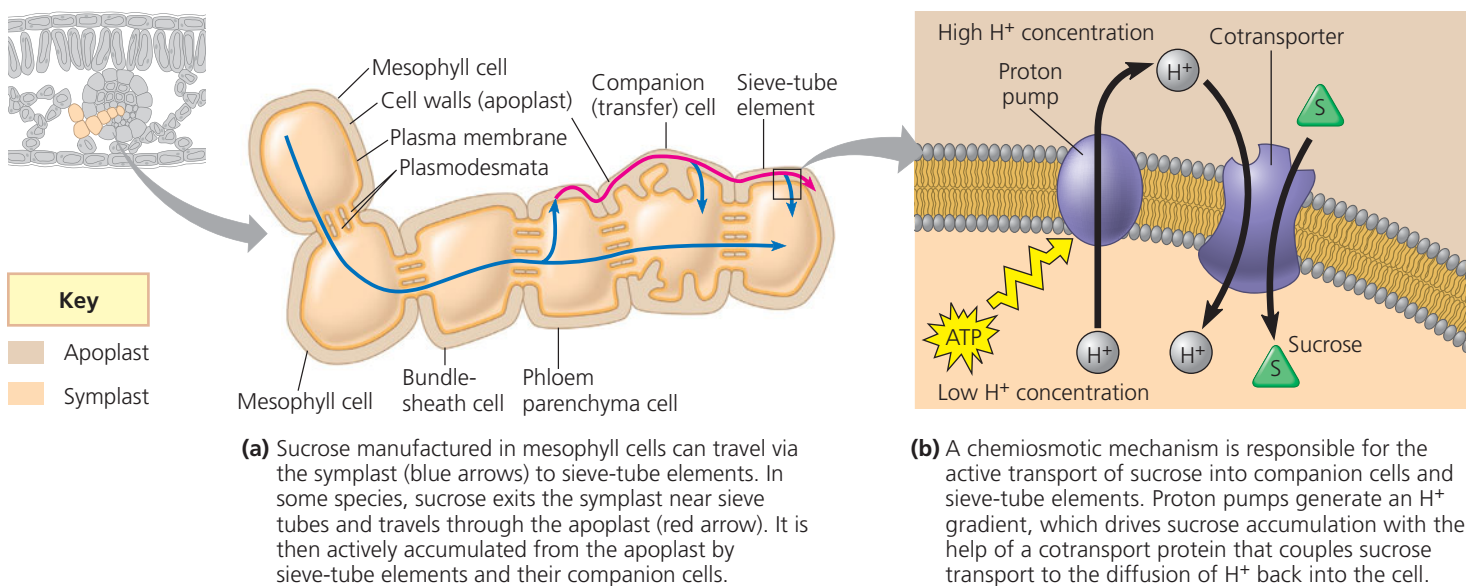
Sieve-tube elements are specialized cells in angiosperms that serve as conduits for translocation. Arranged end to end, they form long sieve tubes (see Figure 28.9). Between these cells are sieve plates, structures that allow the flow of sap along the

sieve tube. **Phloem sap**, the solution that flows through sieve tubes, differs markedly from the xylem sap that is transported by tracheids and vessel elements. By far the most prevalent solute in phloem sap is sugar, typically 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 amino acids, hormones, and minerals.

In contrast to the unidirectional transport of xylem sap from roots to leaves, phloem sap moves from sites of sugar production to sites of sugar use or storage (see Figure 29.2). A **sugar source** is a plant organ that is a net producer of sugar, by photosynthesis or by breakdown of starch. A **sugar sink** is an organ that is a net consumer or depository of sugar. Growing roots, buds, stems, and fruits are sugar sinks. Although expanding leaves are sugar sinks, mature leaves, if well illuminated, are sugar sources. 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 becomes a sugar source because its starch is broken down to sugar, which is carried to the growing shoot tips.

Sinks usually receive sugar from the nearest sugar sources. For each sieve tube, the direction of transport depends on the locations of the sugar source and sugar sink that are connected by that tube. Therefore, neighboring sieve tubes may carry sap in opposite directions if they originate and end in different locations.

Sugar must be transported, or loaded, into sieve-tube elements before being exported to sugar sinks. In some species, it moves from mesophyll cells to sieve-tube elements via the symplast, passing through plasmodesmata. In other species, it moves by symplastic and apoplastic pathways. During apoplastic loading, sugar is accumulated by nearby sieve-tube elements, either directly or through the companion cells (**Figure 29.21a**). In some plants, the walls of the companion



▲ **Figure 29.21** Loading of sucrose into phloem.

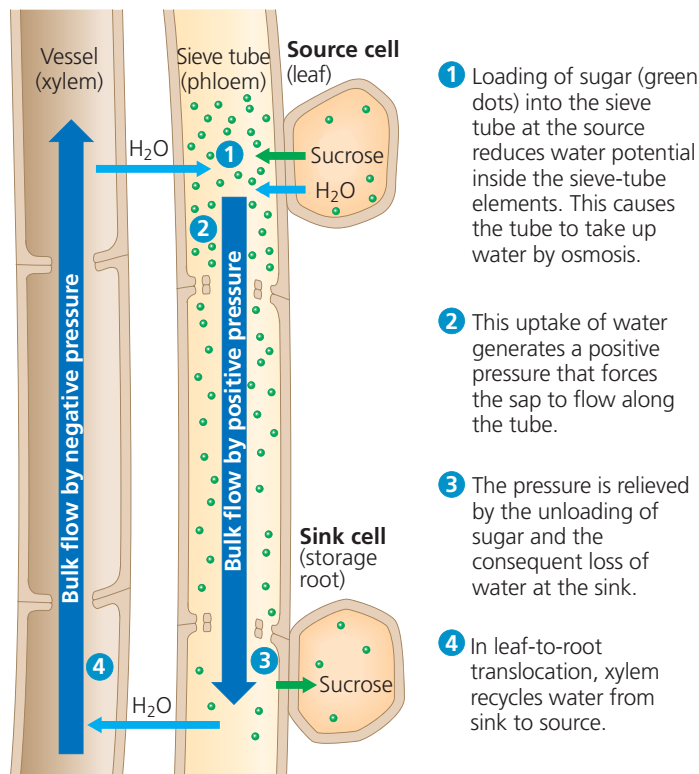
cells feature many ingrowths, enhancing solute transfer between apoplast and symplast.

In most plants, sugar movement into the phloem requires active transport because sucrose is more concentrated in sieve-tube elements and companion cells than in mesophyll. Proton pumping and  $H^+$ /sucrose cotransport enable sucrose to move from mesophyll cells to sieve-tube elements or companion cells (Figure 29.21b).

Sucrose is unloaded at the sink end of a sieve tube. The process varies by species and organ. However, the concentration of free sugar in the sink is always lower than in the sieve tube because the unloaded sugar is consumed during growth and metabolism of the cells of the sink or converted to 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.

### Bulk Flow by Positive Pressure: The Mechanism of Translocation in Angiosperms

Phloem sap flows from source to sink at rates as great as 1 m/hr, much faster than diffusion or cytoplasmic streaming. The translocation of phloem sap through sieve tubes by bulk flow is driven by positive pressure, or *pressure flow* (Figure 29.22). The building of pressure at the source and reduction of that pressure at the sink cause sap to flow from source to sink. Sinks vary in energy demands and capacity to unload sugars. Sometimes there are more sinks than can be supported by sources. In such cases, a plant might abort some flowers, seeds, or fruits—a phenomenon called *self-thinning*. Removing sinks can also be a horticulturally useful practice. For example, since large apples command a much better price than small ones, growers sometimes remove flowers or young fruits so that their trees produce fewer but larger apples.



▲ Figure 29.22 Bulk flow by positive pressure (pressure flow) in a sieve tube.

#### CONCEPT CHECK 29.7

1. Identify plant organs that are sugar sources, organs that are sugar sinks, and organs that might be either. Explain.
2. Why can xylem transport water and minerals using dead cells, whereas phloem requires living cells?
3. **WHAT IF?** Apple growers in Japan sometimes make a nonlethal spiral slash around the bark of trees that will be removed after the growing season. This makes the apples sweeter. Why?

For suggested answers, see Appendix A.

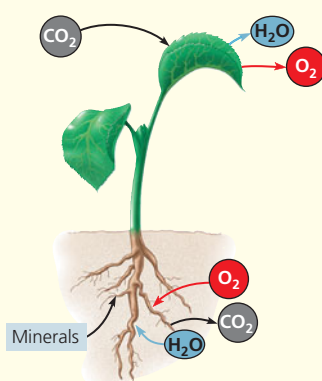
## 29 Chapter Review

### SUMMARY OF KEY CONCEPTS

#### CONCEPT 29.1

**Adaptations for acquiring resources were key steps in the evolution of vascular plants (pp. 572–574)**

- Leaves typically function in gathering sunlight and  $CO_2$ . Stems serve as supporting structures for leaves and as conduits for the long-distance transport of water and nutrients. Roots mine the soil for water and minerals and anchor the whole plant.



- Natural selection has produced plant architectures that fine-tune resource acquisition in the ecological niche in which the plant species naturally exists.

**?** How did the evolution of xylem and phloem contribute to the successful colonization of land by vascular plants?

#### CONCEPT 29.2

**Different mechanisms transport substances over short or long distances (pp. 574–578)**

- The selective permeability of the plasma membrane controls the movement of substances into and out of cells. Both active and passive transport mechanisms occur in plants.
- Plant tissues have two major compartments: the **apoplast** (everything outside the cells' plasma membranes) and the **symplast** (the cytosol and connecting plasmodesmata).



- The direction of water movement depends on the **water potential**, a quantity incorporating solute concentration and physical pressure. The osmotic uptake of water by plant cells and the resulting internal pressure that builds up make plant cells **turgid**.
- Long-distance transport occurs through **bulk flow**, the movement of liquid in response to a pressure gradient. Bulk flow occurs within the tracheids and vessel elements of the xylem and within the sieve-tube elements of the phloem.

**?** *Is xylem sap usually pulled or pushed up the plant?*

## CONCEPT 29.3

### Plant roots absorb essential elements from the soil (pp. 578–582)

- **Macronutrients**, elements required in relatively large amounts, include carbon, oxygen, hydrogen, nitrogen, and other major ingredients of organic compounds. **Micronutrients**, elements required in very small amounts, typically have catalytic functions as cofactors of enzymes.
- Deficiency of a mobile nutrient usually affects older organs more than younger ones; the reverse is true for nutrients that are less mobile within a plant. Macronutrient deficiencies are most common, particularly deficiencies of nitrogen, phosphorus, and potassium.
- Soil particles of various sizes derived from the breakdown of rock are found in soil. Soil particle size affects the availability of water, oxygen, and minerals in the soil.
- A soil's composition refers to its inorganic and organic components. Topsoil is a complex ecosystem teeming with bacteria, fungi, protists, animals, and the roots of plants.

**?** *Do plants need soil to grow? Explain.*

## CONCEPT 29.4

### Plant nutrition often involves relationships with other organisms (pp. 582–586)

- **Rhizobacteria** derive their energy from the **rhizosphere**, a microbe-enriched ecosystem intimately associated with roots. Plant secretions support the energy needs of the rhizosphere. Some rhizobacteria produce antibiotics, whereas others make nutrients more available for plants. Most are free-living, but some live inside plants. Plants satisfy most of their huge needs for nitrogen from the bacterial decomposition of humus and the fixation of gaseous  $N_2$ .
- $N_2$ -fixing bacteria convert atmospheric  $N_2$  to nitrogenous minerals that plants can absorb as a nitrogen source for organic synthesis. The most efficient mutualism between plants and nitrogen-fixing bacteria occurs in the nodules formed by *Rhizobium* bacteria growing in the roots of legumes. These bacteria obtain sugar from the plant and supply the plant with fixed nitrogen.
- **Mycorrhizae** are mutualistic associations formed between roots and certain soil fungi that aid in the absorption of minerals and water.
- **Epiphytes** grow on the surfaces of other plants but acquire water and minerals from rain. Parasitic plants absorb nutrients from host plants. Carnivorous plants supplement their mineral nutrition by digesting animals.

**?** *Do all plants gain their energy directly from photosynthesis? Explain.*

## CONCEPT 29.5

### Transpiration drives the transport of water and minerals from roots to shoots via the xylem (pp. 587–590)

- Water and minerals from the soil enter the plant through the epidermis of roots, cross the root cortex, and then pass into the vascular cylinder by way of the selectively permeable cells of the **endodermis**. From the vascular cylinder, the **xylem sap** is transported long distances by bulk flow to the veins that branch throughout each leaf.
- The **cohesion-tension hypothesis** proposes that the movement of xylem sap is driven by a water potential difference created at the leaf end of the xylem by the evaporation of water from leaf cells. Evaporation lowers the water potential at the air-water interface, thereby generating the negative pressure that pulls water through the xylem.

**?** *Why is the ability of water molecules to form hydrogen bonds important for the movement of xylem sap?*

## CONCEPT 29.6

### The rate of transpiration is regulated by stomata (pp. 590–593)

- **Transpiration** is the loss of water vapor from plants. **Wilting** occurs when the water lost by transpiration is not replaced by absorption from roots.
- Stomata are the major pathway for water loss from plants. Guard cells widen or narrow the stomatal pores. When guard cells take up  $K^+$ , the pore widens. The opening and closing of stomata are controlled by light,  $CO_2$ , the drought hormone **abscisic acid**, and a **circadian rhythm**.
- Reduced leaves and CAM photosynthesis are examples of adaptations to arid environments.

**?** *Why are stomata necessary?*

## CONCEPT 29.7

### Sugars are transported from sources to sinks via the phloem (pp. 593–594)

- Mature leaves are the main **sugar sources**, although storage organs can be seasonal sources. Growing organs such as roots, stems, and fruits are the main **sugar sinks**.
- Phloem loading depends on the active transport of sucrose. Sucrose is cotransported with  $H^+$ , which diffuses down a gradient generated by proton pumps. Loading of sugar at the source and unloading at the sink maintain a pressure difference that keeps sap flowing through a sieve tube.

**?** *Why is phloem transport considered an active process?*

## TEST YOUR UNDERSTANDING

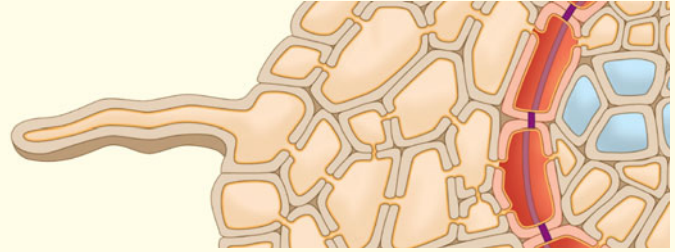
### Level 1: Knowledge/Comprehension

- Which structure or compartment is part of the symplast?
  - the interior of a vessel element
  - the interior of a sieve tube
  - the cell wall of a mesophyll cell
  - an extracellular air space
  - a Casparian strip

2. Which of the following is an adaptation that enhances the uptake of water and minerals by roots?
  - a. mycorrhizae
  - b. cavitation
  - c. active uptake by vessel elements
  - d. rhythmic contractions by cortical cells
  - e. pumping through plasmodesmata
3. The inorganic nutrient most often lacking in plants is
  - a. carbon.
  - b. nitrogen.
  - c. phosphorus.
  - d. potassium.
  - e. molybdenum.
4. Movement of xylem sap from roots to leaves
  - a. occurs through the apoplast of sieve-tube elements.
  - b. usually depends on tension, or negative pressure potential.
  - c. depends on active transport.
  - d. depends on the pumping of water through aquaporins.
  - e. results mainly from diffusion.

### Level 2: Application/Analysis

5. What would enhance water uptake by a plant cell?
  - a. decreasing the  $\psi$  of the surrounding solution
  - b. increasing the pressure exerted by the cell wall
  - c. the loss of solutes from the cell
  - d. increasing the  $\psi$  of the cytoplasm
  - e. positive pressure on the surrounding solution
6. A plant cell with a  $\psi_s$  of  $-0.65$  MPa maintains a constant volume when bathed in a solution that has a  $\psi_s$  of  $-0.30$  MPa and is in an open container. The cell has a
  - a.  $\psi_p$  of  $+0.65$  MPa.
  - b.  $\psi$  of  $-0.65$  MPa.
  - c.  $\psi_p$  of  $+0.35$  MPa.
  - d.  $\psi_p$  of  $+0.30$  MPa.
  - e.  $\psi$  of  $0$  MPa.
7. Compared with a cell with few aquaporin proteins in its membrane, a cell containing many aquaporin proteins will
  - a. have a faster rate of osmosis.
  - b. have a lower water potential.
  - c. have a higher water potential.
  - d. have a faster rate of active transport.
  - e. accumulate water by active transport.
8. A mineral deficiency is likely to affect older leaves more than younger leaves if
  - a. the mineral is a micronutrient.
  - b. the mineral is very mobile within the plant.
  - c. the mineral is required for chlorophyll synthesis.
  - d. the mineral is a macronutrient.
  - e. the older leaves are in direct sunlight.
9. Two groups of tomatoes were grown in the laboratory, one with humus added to the soil and the other a control without humus. The leaves of the plants grown without humus were yellowish (less green) compared with those of the plants grown in humus-enriched soil. The best explanation for this difference is that
  - a. the healthy plants used carbohydrates in the decomposing leaves of the humus for energy to make chlorophyll.
  - b. the humus made the soil more loosely packed, so water penetrated more easily to the roots.
  - c. the humus contained minerals such as magnesium and iron, needed for the synthesis of chlorophyll.
  - d. the heat released by the decomposing leaves of the humus caused more rapid growth and chlorophyll synthesis.
  - e. the healthy plants absorbed chlorophyll from the humus.
10. **DRAW IT** Trace the uptake of water and minerals from root hairs to the endodermis in a root, following a symplastic route and an apoplastic route. Label the routes on the diagram below.



### Level 3: Synthesis/Evaluation

#### 11. SCIENTIFIC INQUIRY

Acid precipitation has an abnormally high concentration of hydrogen ions ( $H^+$ ). One effect of acid precipitation is to deplete the soil of nutrients such as calcium ( $Ca^{2+}$ ), potassium ( $K^+$ ), and magnesium ( $Mg^{2+}$ ). Suggest a hypothesis to explain how acid precipitation washes the nutrients from the soil. How might you test your hypothesis?

#### 12. SCIENTIFIC INQUIRY

A Minnesota gardener notes that the plants immediately bordering a walkway are stunted compared with those farther away. Suspecting that the soil near the walkway may be contaminated from salt added to the walkway in winter, the gardener tests the soil. The composition of the soil near the walkway is identical to that farther away except that it contains an additional  $50$  mM NaCl. Assuming that the NaCl is completely ionized, calculate how much it will lower the solute potential of the soil at  $20^\circ\text{C}$  using the *solute potential equation*:

$$\psi_s = -iCRT$$

where  $i$  = the ionization constant ( $2$  for NaCl);  $C$  = the molar concentration (in moles/liter);  $R$  = the pressure constant ( $R = 0.00831$  liter MPa/mole K); and  $T$  = temperature in Kelvin ( $273 + ^\circ\text{C}$ ). How would this change in the solute potential of the soil affect the water potential of the soil? In what way would the change in the water potential of the soil affect the movement of water in or out of the roots?

#### 13. FOCUS ON EVOLUTION

Large brown algae called kelps can grow as tall as  $25$  m. Kelps consist of a holdfast anchored to the ocean floor, blades that float at the surface and collect light, and a long stalk connecting the blades to the holdfast (see Figure 25.14). Specialized cells in the stalk, although nonvascular, can transport sugar. Suggest a reason why these structures analogous to sieve-tube elements might have evolved in kelps.

#### 14. FOCUS ON INTERACTIONS

The soil in which plants grow teems with organisms from every taxonomic kingdom. In a short essay ( $100$ – $150$  words), discuss examples of how the mutualistic interactions of plants with bacteria, fungi, and animals improve plant nutrition.

For selected answers, see Appendix A.

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# Reproduction and Domestication of Flowering Plants

▼ **Figure 30.1** Why is this bee trying to mate with this flower?



## KEY CONCEPTS

- 30.1** Flowers, double fertilization, and fruits are unique features of the angiosperm life cycle
- 30.2** Flowering plants reproduce sexually, asexually, or both
- 30.3** People modify crops through breeding and genetic engineering

## OVERVIEW

### Flowers of Deceit

**M**ale long-horned bees (*Eucera longicornis*) often attempt to copulate with flowers of the Mediterranean orchid *Ophrys scolopax* (**Figure 30.1**). During this encounter, a yellow sac of pollen becomes glued to the insect's body. Eventually frustrated, the bee flies off and deposits the pollen onto another *Ophrys* flower that has become the object of his misplaced ardor. *Ophrys* flowers offer no reward such as nectar to the male bees, only sexual frustration. So what makes the male bees so enamored of this orchid? The traditional answer has been that the shape and color of the orchid's largest petal and its bristles vaguely resemble the female bee. These

visual cues, however, are only part of the deception: some *Ophrys* orchids also emit chemicals with a scent similar to that produced by sexually receptive female bees.

This orchid and its bee pollinators are one example of the amazing ways in which angiosperms (flowering plants) reproduce sexually with spatially distant members of their own species. Sex, however, is not their only means of reproduction. Many species also reproduce asexually, creating offspring that are genetically identical to the parent.

An unusual aspect of the orchid and bee example is that the insect does not profit from interacting with the flower. In fact, by wasting time and energy, the bee is probably rendered less fit. More typically, a plant lures an animal pollinator to its flowers not with offers of sex but with rewards of energy-rich nectar or pollen. Thus, both plant and pollinator benefit. Participating in such mutually beneficial relationships with other organisms is common in the plant kingdom. In fact, in recent evolutionary times, some flowering plants have formed relationships with an animal that not only disperses their seeds but also provides the plants with water and mineral nutrients and vigorously protects them from encroaching competitors, pathogens, and predators.

In return for these favors, the animal typically gets to eat a fraction of some part of the plants, such as their seeds or fruits. The plants involved in these relationships are called crops; the animals are humans.

Since the origins of crop domestication over 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 grow today. Genetic engineering has dramatically increased the variety of ways and the speed with which we can now modify plants.

In Chapter 26, we approached plant reproduction from an evolutionary perspective, tracing the descent of land plants from algal ancestors. Because

angiosperms are the most important group of plants in agriculture and in most terrestrial ecosystems, we'll explore their reproductive biology in detail in this chapter. After discussing the sexual and asexual reproduction of angiosperms, we'll examine the role that people have played in domesticating crop species, as well as the controversies surrounding modern plant biotechnology.

## CONCEPT 30.1

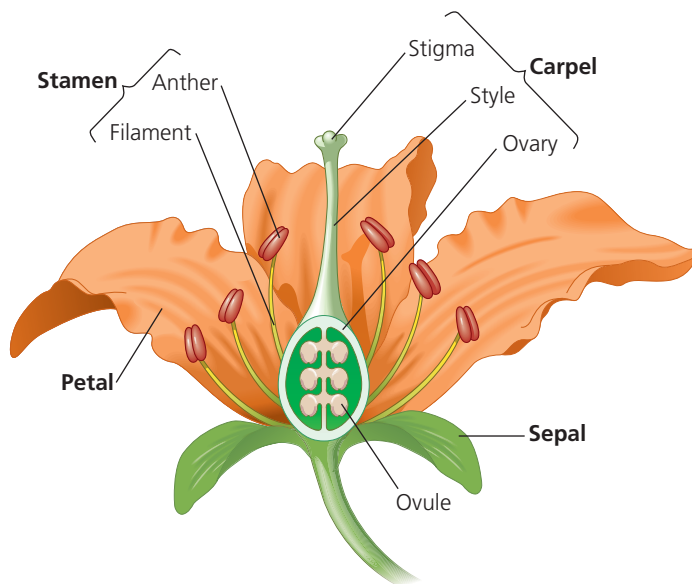
### Flowers, double fertilization, and fruits are unique features of the angiosperm life cycle

The life cycles of plants are characterized by an alternation of generations, in which multicellular haploid ( $n$ ) and multicellular diploid ( $2n$ ) generations alternate, producing each other (see Figures 10.6b and 26.6). The diploid plant, the sporophyte, produces haploid spores by meiosis. These spores divide by mitosis, giving rise to the multicellular gametophytes, the male and female haploid plants that produce gametes (sperm and eggs). **Fertilization**, the fusion of gametes, results in diploid zygotes, which divide by mitosis and form new sporophytes. In angiosperms, the sporophyte is the dominant generation: It is larger, more conspicuous, and longer-lived than the gametophyte. Over the course of seed plant evolution, gametophytes became reduced in size and wholly dependent on the sporophyte for nutrients. Angiosperm gametophytes are the most reduced of all plants, consisting of only a few cells. The key traits of the angiosperm life cycle can be remembered as the “three Fs”—flowers, double fertilization, and fruits.

#### Flower Structure and Function

Flowers, the reproductive shoots of angiosperm sporophytes, are typically composed of four types of floral organs: **carpels**, **stamens**, **petals**, and **sepals** (Figure 30.2). When viewed from above, these organs appear as concentric whorls. Carpels form the first (innermost) whorl, stamens form the second, petals form the third, and sepals form the fourth (outermost) whorl. All four types of floral organs are attached to a part of the stem called the **receptacle**. Unlike vegetative shoots, flowers are determinate shoots; they cease growing after the flower and fruit are formed.

Carpels and stamens are reproductive organs; sepals and petals are sterile. 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 captures pollen. Within the ovary are one or more **ovules**; the number of ovules depends on the species. The flower shown in Figure 30.2 has a single carpel, but 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 two or more fused carpels. A stamen consists of a stalk called the *filament* and a terminal structure



▲ Figure 30.2 The structure of an idealized flower.

called the **anther**; within the anther are chambers called microsporangia (pollen sacs) that produce pollen. Petals are typically more brightly colored than sepals and advertise the flower to insects and other animal pollinators. Sepals, which enclose and protect unopened floral buds, usually resemble leaves more than the other floral organs do.

**Complete flowers** have all four basic floral organs (see Figure 30.2). Some species have **incomplete flowers**, lacking sepals, petals, stamens, or carpels. For example, most grass flowers lack petals. Some incomplete flowers are sterile, lacking functional stamens and carpels; others are *unisexual*, lacking either stamens or carpels. Flowers also vary in size, shape, color, odor, organ arrangement, and time of opening. Some are borne singly, while others are arranged in showy clusters called **inflorescences**. For example, a daisy is actually an inflorescence consisting of a central disk composed of hundreds of tiny complete flowers surrounded by sterile, incomplete flowers that look like white petals. Much of floral diversity represents adaptations to specific pollinators.

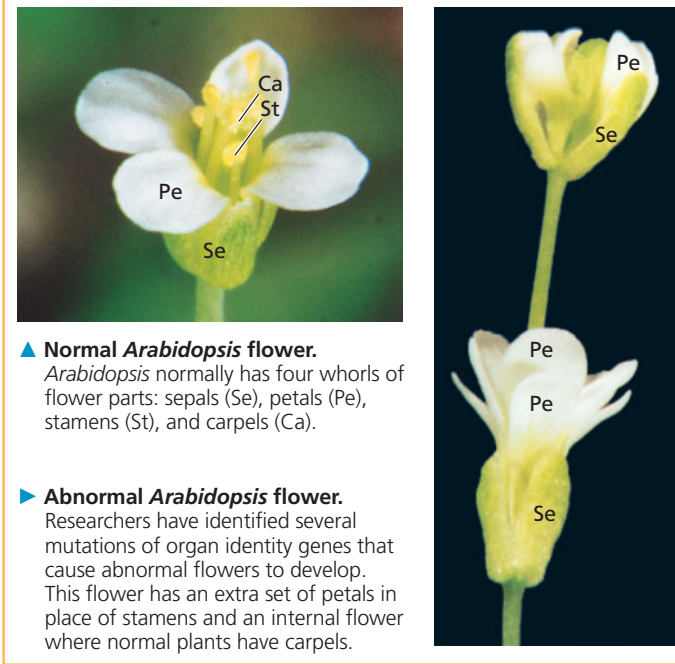
#### Flower Formation

The flowers of a given plant species typically appear suddenly at a specific time of year. Such synchrony promotes outbreeding, the main advantage of sexual reproduction. Flower formation involves a developmental switch in the shoot apical meristem from a vegetative to a reproductive growth mode. This transition into a *floral meristem* is triggered by a combination of environmental cues, such as day length, and internal signals. (You'll learn more about the roles of these signals in flowering in Chapter 31.) Once the transition to flowering has begun, the order of each organ's emergence from the floral meristem determines whether it will develop into a sepal, petal, stamen, or carpel. Several organ identity genes have been identified that encode transcription factors that regulate the development of this floral organization. A mutation in one of these genes can



cause abnormal floral development, such as petals growing in place of stamens (**Figure 30.3**).

By studying flower mutants, researchers have developed a model called the **ABC hypothesis** to explain how three floral organ identity genes direct the formation of the four types of floral organs. According to the slightly simplified version of the ABC hypothesis presented in **Figure 30.4a**, each class of organ identity genes is switched on in two specific whorls of the floral meristem. Normally, *A* genes are switched on in the two outer whorls (sepals and petals), *B* genes are switched on in the two middle whorls (petals and stamens), and *C* genes are switched on in the two inner whorls (stamens and carpels). Sepals arise from those parts of the floral meristems in which only *A* genes are active, petals where *A* and *B* genes are active,

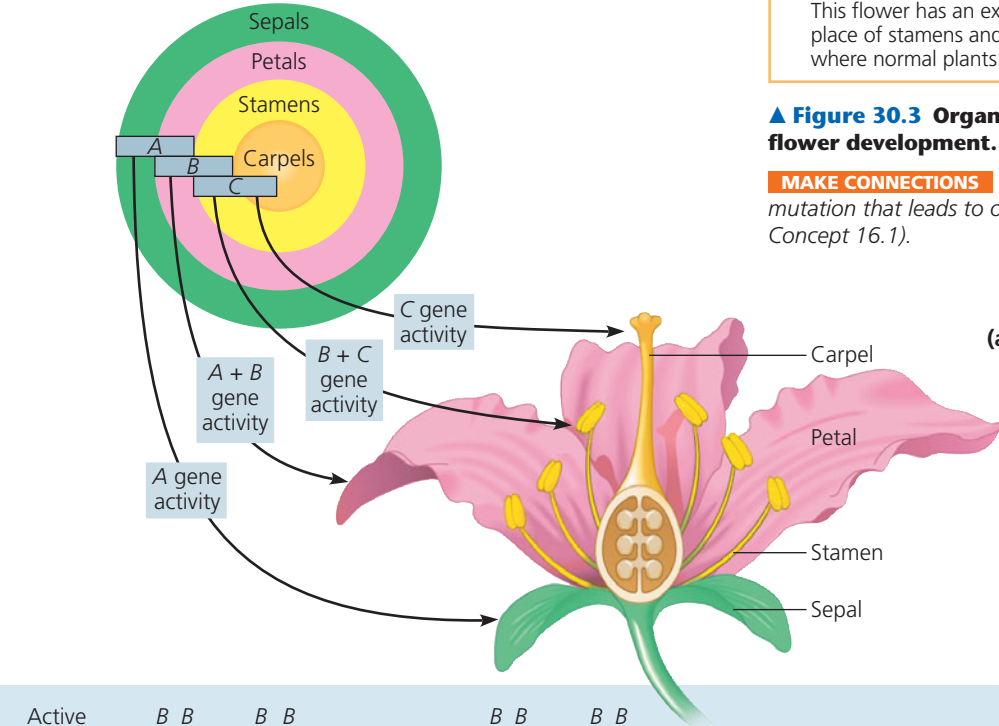


**▲ Normal *Arabidopsis* flower.** *Arabidopsis* normally has four whorls of flower parts: sepals (Se), petals (Pe), stamens (St), and carpels (Ca).

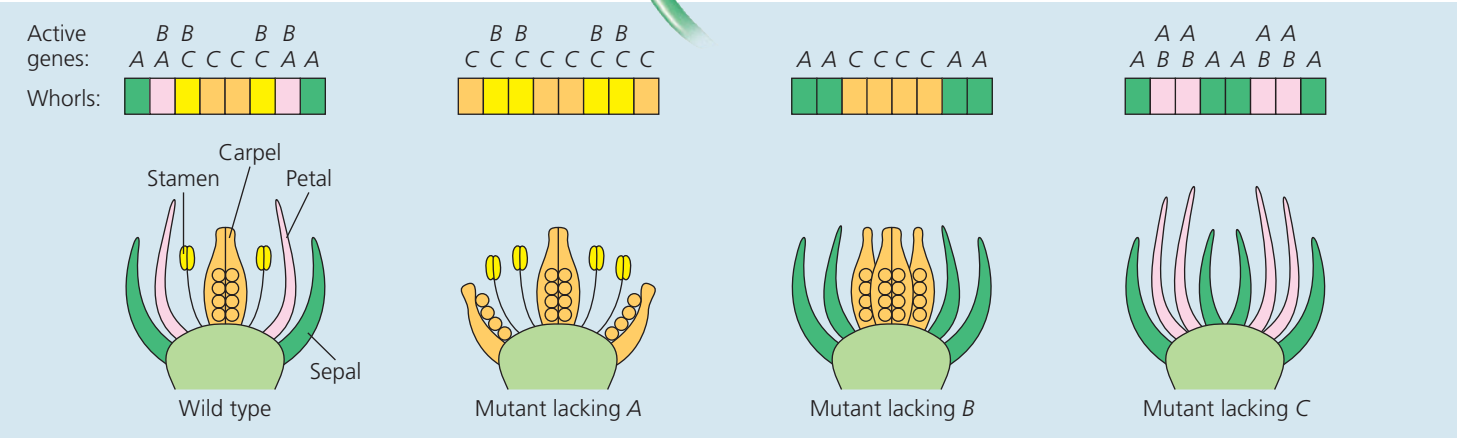
**► Abnormal *Arabidopsis* flower.** Researchers have identified several mutations of organ identity genes that cause abnormal flowers to develop. This flower has an extra set of petals in place of stamens and an internal flower where normal plants have carpels.

**▲ Figure 30.3 Organ identity genes and pattern formation in flower development.**

**MAKE CONNECTIONS** Provide another example of a homeotic gene mutation that leads to organs being produced in the wrong place (see Concept 16.1).



**(a) A schematic diagram of the ABC hypothesis.** Studies of plant mutations reveal that three classes of organ identity genes are responsible for the spatial pattern of floral parts. These genes, designated *A*, *B*, and *C*, regulate expression of other genes responsible for development of sepals, petals, stamens, and carpels. Sepals develop from the meristematic region where only *A* genes are active. Petals develop where both *A* and *B* genes are expressed. Stamens arise where *B* and *C* genes are active. Carpels arise where only *C* genes are expressed.



**(b) Side view of flowers with organ identity mutations.** The phenotype of mutants lacking a functional *A*, *B*, or *C* organ identity gene can be explained by combining the model in part (a) with the rule that if *A* or *C* activity is missing, the other activity occurs through all four whorls.

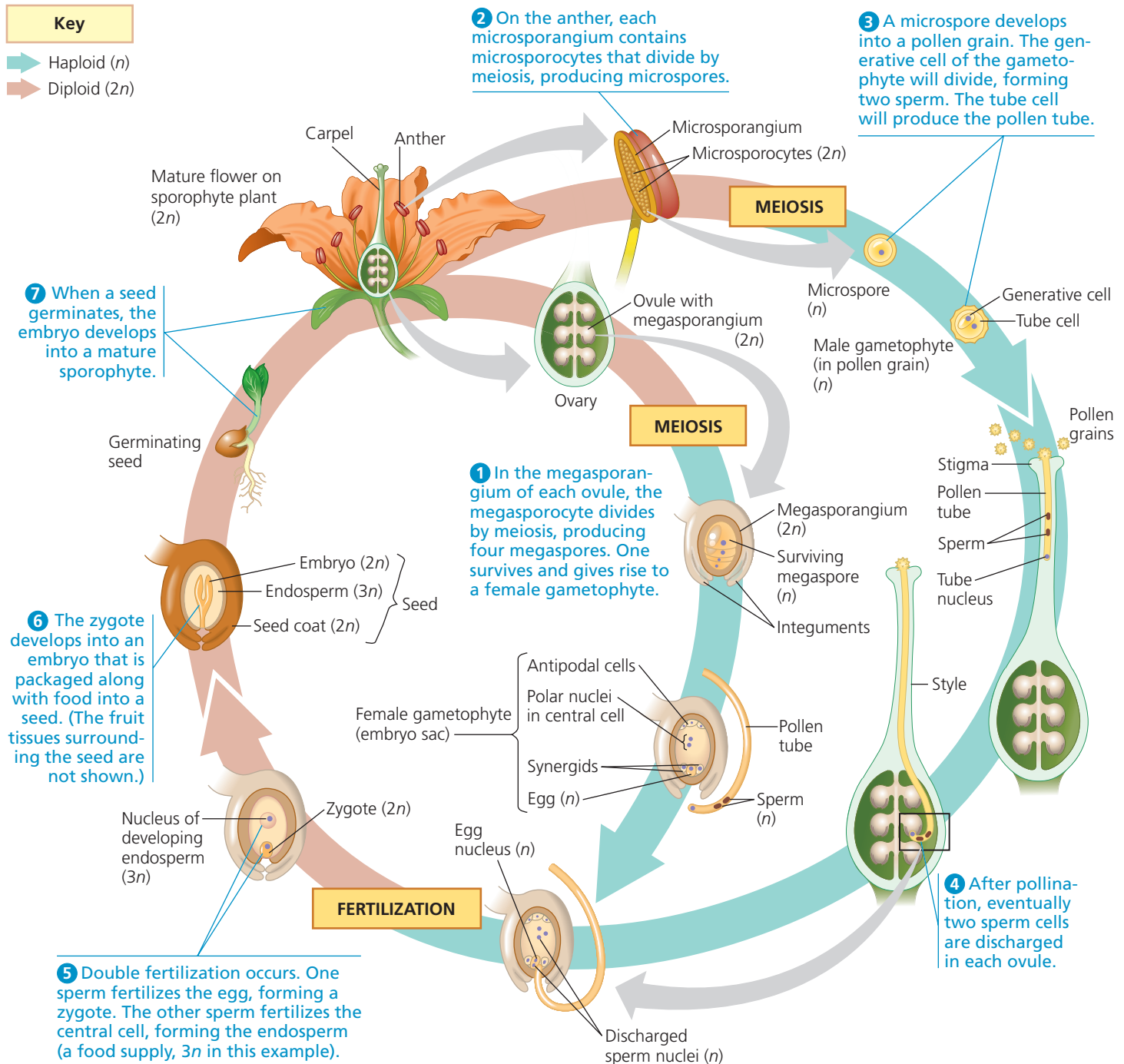
**▲ Figure 30.4 The ABC hypothesis for the functioning of organ identity genes in flower development.**

**WHAT IF?** What would a flower look like if the *A* genes and *B* genes were inactivated?

stamens where *B* and *C* genes are active, and carpels where only *C* genes are active. The ABC hypothesis can account for the phenotypes of mutants lacking *A*, *B*, or *C* gene activity, with one addition: Where gene *A* activity is present, it inhibits *C*, and vice versa. If either *A* or *C* is missing, the other takes its place. **Figure 30.4b** shows the floral patterns of mutants lacking each of the three classes of organ identity genes and depicts how the hypothesis accounts for their floral phenotypes.

## Development of Female Gametophytes (Embryo Sacs)

**Figure 30.5** shows the angiosperm life cycle. We will start with the development of a female gametophyte **1**. As a carpel develops, one or more immature seeds (ovules) form deep within its ovary, its swollen base. A female gametophyte, also known as an **embryo sac**, develops inside each ovule. The process of embryo



▲ **Figure 30.5** The life cycle of an angiosperm.



sac formation—one variation of which we'll discuss here—occurs in a tissue called the megasporangium within each ovule. Two *integuments* (layers of protective sporophytic tissue that will develop into the seed coat) surround each megasporangium except at a gap called the *micropyle*. Female gametophyte development begins when one cell in the megasporangium of each ovule, the *megasporeocyte* (or megaspore mother cell), enlarges and undergoes meiosis, producing four haploid **megaspores**. Only one megaspore survives; the others degenerate.

The nucleus of the surviving megaspore divides by mitosis three times without cytokinesis, resulting in one large cell with eight haploid nuclei. This multinucleate mass is then divided by membranes to form an embryo sac. At the micropylar end of the embryo sac, two cells called synergids flank the egg and help attract and guide the pollen tube to the embryo sac. At the opposite end of the embryo sac are three antipodal cells of unknown function. The other two nuclei, called polar nuclei, are not partitioned into separate cells but share the cytoplasm of the large central cell of the embryo sac. The ovule, which will become a seed, now consists of the embryo sac, surrounded by the megasporangium (which eventually withers) and two surrounding integuments.

### Development of Male Gametophytes in Pollen Grains

As stamens are produced, each anther develops four microsporangia, also called pollen sacs. Within the microsporangia are many diploid cells called *microsporocytes*, or microspore mother cells (see Figure 30.5, ②). Each microsporocyte undergoes meiosis, forming four haploid **microspores**. Each microspore then undergoes mitosis, producing a haploid male gametophyte consisting of only two cells: the *generative cell* and the *tube cell*. Together, these two cells *and* the spore wall constitute a **pollen grain**. The spore wall, which consists of material produced by both the microspore and the anther, usually exhibits an elaborate pattern unique to the species. During maturation of the male gametophyte, the generative cell passes into the tube cell: The tube cell now has a completely free-standing cell inside it. After the microsporangium breaks open and releases its pollen, a pollen grain may be transferred to a receptive surface of a stigma—the act of pollination. There, the tube cell produces the **pollen tube**, a long cellular protuberance that delivers sperm to the female gametophyte. Pollen tubes can grow very quickly, at rates of 1 cm/hr or more. As a pollen tube elongates through the style, the generative cell usually divides and produces two sperm cells, which remain inside the tube cell. The pollen tube grows through the style and into the ovary, where it releases the sperm cells in the vicinity of the female gametophyte.

### Pollination

In angiosperms, **pollination** is the transfer of pollen from an anther to a stigma. It is accomplished by wind or animals

(**Figure 30.6**). In wind-pollinated species, including grasses and many trees, the release of enormous quantities of smaller-sized pollen compensates for the randomness of dispersal by the wind. At certain times of the year, the air is loaded with pollen grains, as anyone who has a pollen allergy can attest. Some species of aquatic plants rely on water to disperse pollen. Most angiosperm species, however, depend on insects, birds, or other animal pollinators to transfer pollen directly from one flower to another. If pollination is successful, a pollen grain produces a pollen tube, which then grows down into the ovary via the style.

### Double Fertilization

At the time of pollination, the pollen grain typically consists of only the tube cell and the generative cell. After a pollen grain lands on a suitable stigma, it absorbs water and germinates by producing a pollen tube, which grows between the cells of the style toward the ovary (**Figure 30.7**). The nucleus of the generative cell divides by mitosis and forms two sperm. In response to chemical attractants produced by the synergids, the tip of the pollen tube grows toward the micropyle. Its arrival initiates the death of one of the two synergids, thereby providing a passageway into the embryo sac for the two sperm that are discharged from the pollen tube.

Upon reaching the female gametophyte, one sperm fertilizes the egg, forming the zygote. The other sperm combines with the two polar nuclei, forming a triploid ( $3n$ ) nucleus in the center of the large central cell of the female gametophyte. 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 female gametophyte is called **double fertilization**. Double fertilization ensures that endosperm develops only in ovules where the egg has been fertilized, thereby preventing angiosperms from squandering nutrients on infertile ovules.

### Seed Development, Form, and Function

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 degrees, depending on the species. Initially, carbohydrates and other nutrients are stored in the seed's endosperm, but later the swelling cotyledons (seed leaves) of the embryo take over this function in some species.

### Endosperm Development

Endosperm usually develops before the embryo does. After double fertilization, the triploid nucleus of the ovule's central cell divides, forming a multinucleate "supercell" that has 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" and "meat" are examples of liquid and

Most angiosperm species rely on a living (biotic) or nonliving (abiotic) pollinating agent that can move pollen from the anther of a flower on one plant to the stigma of a flower on another plant. Approximately 80% of all angiosperm pollination is biotic, employing animal go-betweens. Among abiotically pollinated species, 98% rely on wind and 2% on water.

## Abiotic Pollination by Wind

Since the reproductive success of wind-pollinated angiosperms does not depend on attracting pollinators, there has been no selective pressure favoring colorful or scented flowers. Accordingly, the flowers of wind-pollinated species are often small, green, and inconspicuous, and they produce neither nectar nor scent. Most temperate trees and grasses are wind-pollinated. The flowers of hazel (*Corylus avellana*) and many other temperate, wind-pollinated trees appear in early spring, when leaves are not present to interfere with pollen movement. The relative inefficiency of wind pollination is compensated for by production of enormous numbers of pollen grains.



▲ Hazel carpellate flower (carpels only)



▲ Hazel staminate flower (stamens only)

## Pollination by Insects



▲ Common dandelion under normal light



▲ Common dandelion under ultraviolet light

About 65% of all flowering plants require insects for pollination; the percentage is even greater for major crops. Pollinating insects include bees, moths, butterflies, flies, and beetles. Bees are the most important, and there is great concern that honeybee populations are in decline. Pollinating bees depend on pollen and the sugary solution called nectar for food. The main function of nectar, which is produced by nectaries at the base of many flowers, is to “reward” the pollinator. Typically, bee-pollinated flowers have a delicate, sweet fragrance. Bees are attracted to bright colors, primarily yellow and blue. Red appears dull to them, but they can see ultraviolet radiation. Many bee-pollinated flowers, such as the common dandelion (*Taraxacum officinale*), have markings called “nectar guides” that help insects locate the nectaries (nectar-producing glands); some of these markings are visible to human eyes only under ultraviolet light.

## Pollination by Bats

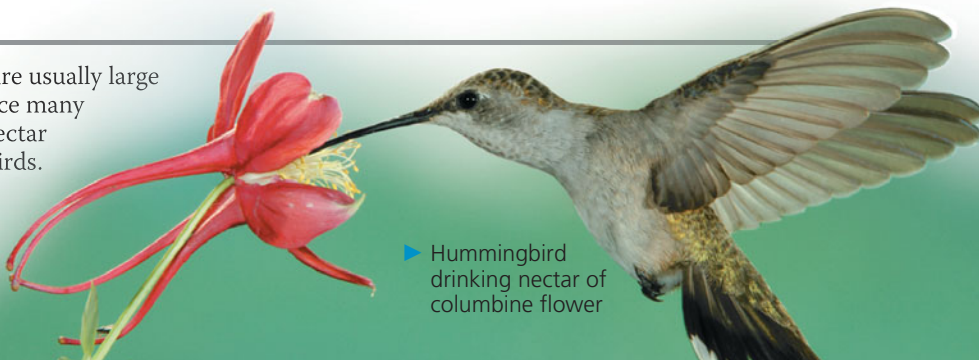
Bat-pollinated flowers are light-colored and aromatic, attracting their nocturnal pollinators. The lesser long-nosed bat (*Leptonycteris curasoae yerbabuenae*) pollinates agave and cactus flowers in the southwestern United States and Mexico as it feeds on their nectar and pollen.

▶ Long-nosed bat feeding on cactus flower at night



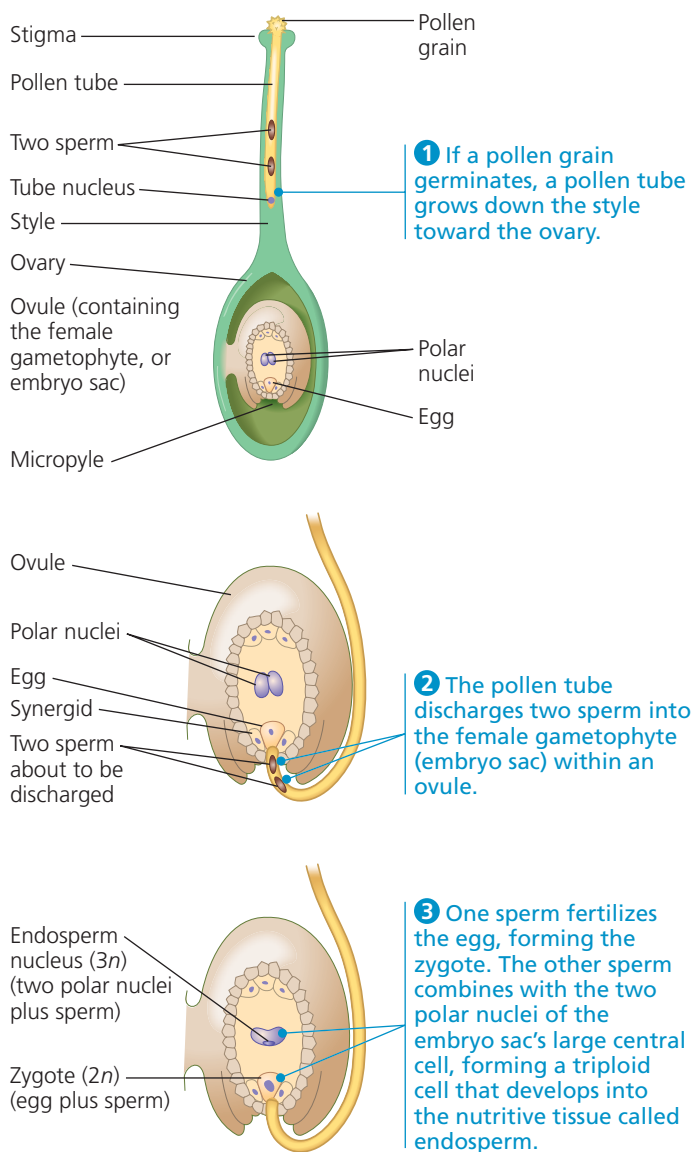
## Pollination by Birds

Bird-pollinated flowers, such as columbine flowers, are usually large and bright red or yellow, but they have little odor since many birds do not have a well-developed sense of smell. Nectar helps meet the high energy demands of pollinating birds. The petals of bird-pollinated flowers are often fused, forming a bent floral tube that fits the curved beak of the bird.



▶ Hummingbird drinking nectar of columbine flower





▲ **Figure 30.7** Growth of the pollen tube and double fertilization.

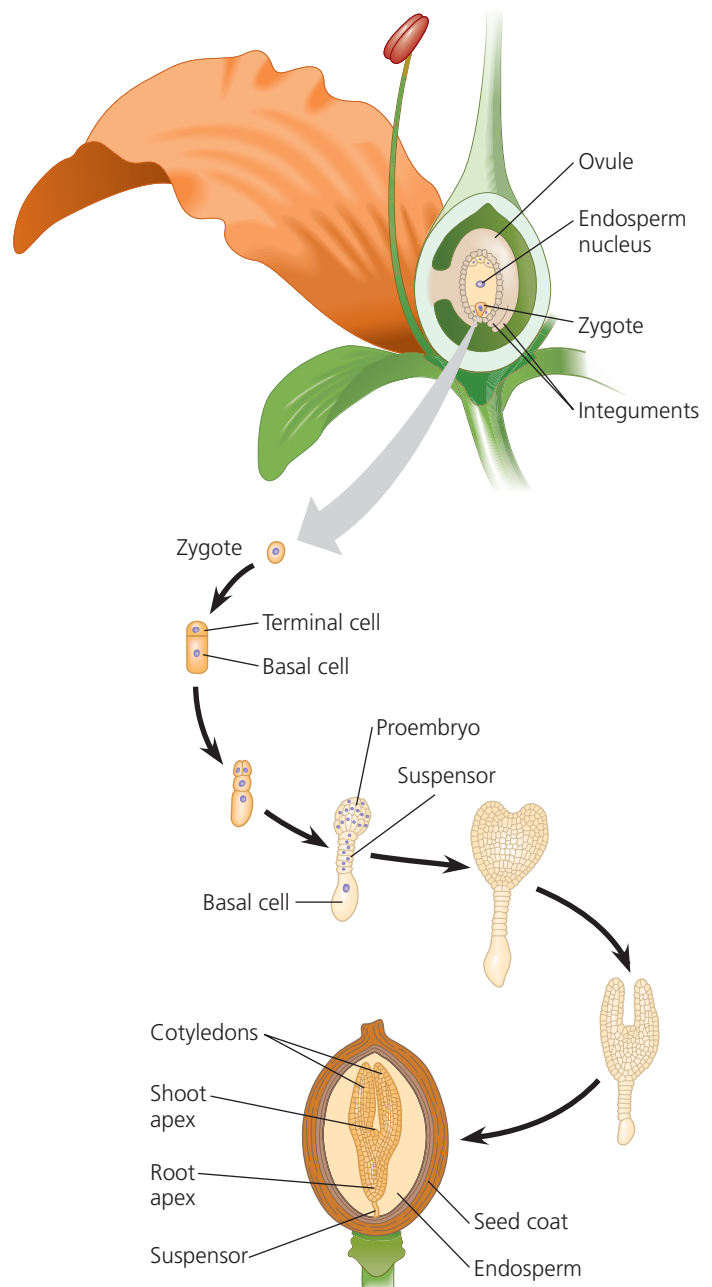
solid endosperm, respectively. The white fluffy part of popcorn is also endosperm.

In grains and most other species of monocots, as well as many eudicots, the endosperm stores nutrients that can be used by the seedling after germination. In other eudicot 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 splits the fertilized egg into a basal cell and a terminal cell (**Figure 30.8**). The terminal cell eventually gives rise to most of the embryo. The basal cell continues to divide, producing a thread of cells called the *suspensor*, which anchors the embryo to the parent plant. The

suspensor helps in transferring nutrients to the embryo from the parent plant and, in some species, from the endosperm. As the suspensor elongates, it pushes the embryo deeper into the nutritive and protective tissues. Meanwhile, the terminal cell divides several times and forms a spherical proembryo (early embryo) attached to the suspensor. The cotyledons begin to form as bumps on the proembryo. A eudicot, which typically has two cotyledons, is heart-shaped at this stage. Only one cotyledon develops in monocots.



▲ **Figure 30.8** The development of a eudicot plant embryo.

By the time the ovule becomes a mature seed and the integuments harden and thicken into the seed coat, the zygote has given rise to an embryonic plant with rudimentary organs.

Soon after the rudimentary cotyledons appear, the embryo elongates. Cradled between the two cotyledons is the embryonic shoot apex. At the opposite end of the embryo's axis, where the suspensor attaches, an embryonic root apex forms. After the seed germinates—indeed, for the rest of the plant's life—the apical meristems at the apices of shoots and roots sustain primary growth (see Figure 28.10).

### Structure of the Mature Seed

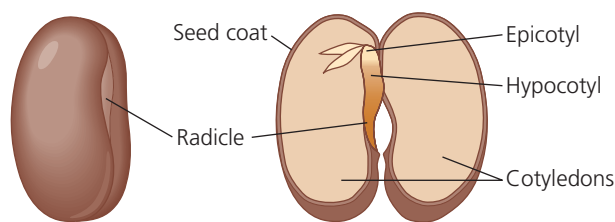
During the last stages of its maturation, the seed dehydrates until its water content is only about 5–15% of its weight. The embryo, which is surrounded by a food supply (cotyledons, endosperm, or both), enters **dormancy**; that is, it stops growing and its metabolism nearly ceases. The embryo and its food supply are enclosed by a hard, protective **seed coat** formed from the integuments of the ovule. In some species, dormancy is imposed by the presence of an intact seed coat rather than by the embryo itself.

You can take a closer look at one type of eudicot seed by splitting open the seed of a common garden bean. The embryo consists of an elongate structure, the embryonic axis, attached to two large cotyledons (**Figure 30.9a**). Below where 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 and below the first pair of miniature leaves is the **epicotyl** (from the Greek *epi*, on, over). The epicotyl, young leaves, and shoot apical meristem are collectively called the *plumule*.

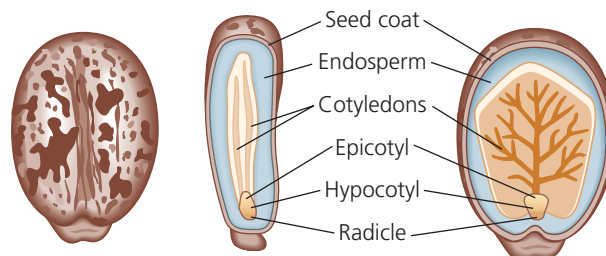
The cotyledons of the common garden bean are packed with starch before the seed germinates because they absorbed carbohydrates from the endosperm when the seed was developing. However, the seeds of some eudicot species, such as castor beans (*Ricinus communis*), retain their food supply in the endosperm and have very thin cotyledons (**Figure 30.9b**). The cotyledons absorb nutrients from the endosperm and transfer them to the rest of the embryo when the seed germinates.

The embryos of monocots possess only a single cotyledon (**Figure 30.9c**). Grasses, including maize and wheat, have a specialized cotyledon called a *scutellum* (from the Latin *scutella*, small shield, a reference to its shape). The scutellum, which has a large surface area, is pressed against the endosperm, from which it absorbs nutrients during germination. The embryo of a grass seed is enclosed within two protective sheathes: a **coleoptile**, which covers the young shoot, and a **coleorhiza**, which covers the young root. Both structures aid in soil penetration after germination.

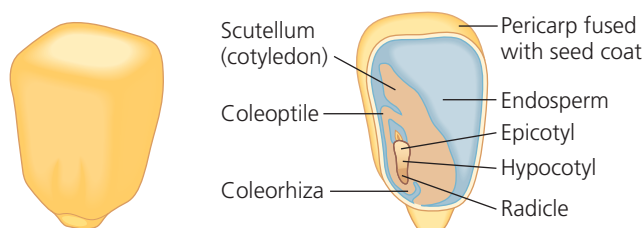
Seed weights range from less than 1  $\mu\text{g}$  for some orchids to 20 kg for coco-de-mer palms. Orchid seeds have almost no food reserves and must bond symbiotically with mycorrhizae prior to germination. Large, endosperm-rich palm seeds are an adaptation for seedling establishment on nutrient-poor beaches.



(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.

### ▲ Figure 30.9 Seed structure.

**MAKE CONNECTIONS** In addition to cotyledon number, what are some other ways that the structures of monocots and eudicots differ? (See Figure 28.2.)

### Seed Dormancy: An Adaptation for Tough Times

Environmental conditions required to break seed dormancy vary among species. Seeds of some species germinate as soon as they are in a suitable environment. Others remain dormant, even if sown in a favorable place, until a specific environmental cue causes them to break dormancy.

The requirement for specific cues to break seed dormancy increases the chances that germination will occur at a time and place most advantageous to the seedling. Seeds of many desert plants, for instance, germinate only after a substantial rainfall. If they were to germinate after a mild drizzle, the soil might soon become too dry to support the seedlings. Where natural fires are common, many seeds require intense heat or smoke to break dormancy; seedlings are therefore most abundant after fire has cleared away competing vegetation. Where winters are



harsh, seeds may require extended exposure to cold before they germinate; seeds sown during summer or fall will therefore not germinate until the following spring, ensuring a long growth season before the next winter. Certain small seeds, such as those of some lettuce varieties, require light for germination and will break dormancy only if buried shallow enough for the seedlings to poke through the soil surface. Some seeds have coats that must be weakened by chemical attack as they pass through an animal's digestive tract and thus are usually carried a considerable distance before germinating from dropped feces.

The length of time a dormant seed remains viable and capable of germinating varies from a few days to decades or even longer, depending on the plant species and environmental conditions. The oldest carbon-14–dated seed that has grown into a viable plant was a 2,000-year-old date palm seed recovered from excavations of Herod's palace in Israel. Most seeds are durable enough to last a year or two until conditions are favorable for germinating. Thus, the soil has a bank of ungerminated seeds that may have accumulated for several years. This is one reason vegetation reappears so rapidly after an environmental disruption such as fire.

### Seed Germination and Seedling Development

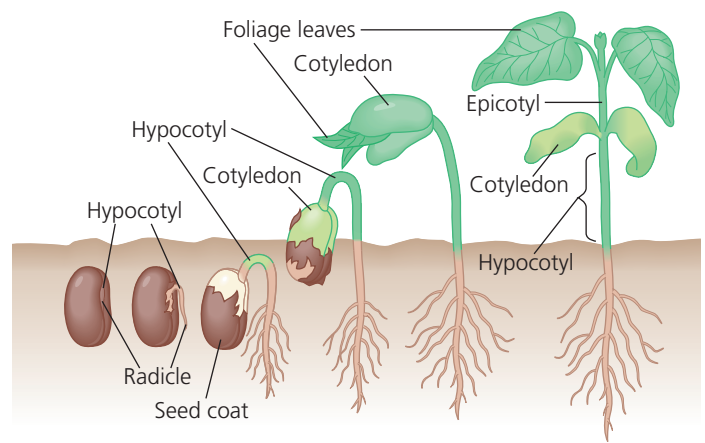
Seed germination depends on **imbibition**, the uptake of water due to the low water potential of the dry seed. Imbibing water causes the seed to expand and rupture its coat and also triggers metabolic changes in the embryo that enable it to resume growth. Following hydration, enzymes begin digesting the storage materials of the endosperm or cotyledons, and the nutrients are transferred to the growing regions of the embryo.

The first organ to emerge from the germinating seed is the radicle, the embryonic root. Next, the shoot tip must break through the soil surface. In garden beans and many other eudicots, a hook forms in the hypocotyl, and growth pushes the hook above ground (**Figure 30.10a**). In response to light, the hypocotyl straightens, the cotyledons separate, and the delicate epicotyl, now exposed, spreads its first true leaves (as distinct from the cotyledons, or seed leaves). These leaves expand, become green, and begin making food by photosynthesis. The cotyledons shrivel and fall away from the seedling, their food reserves having been exhausted by the germinating embryo.

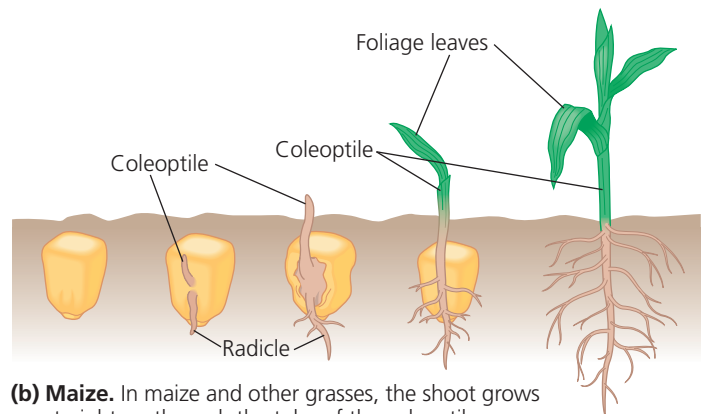
Some monocots, such as maize and other grasses, use a different method for breaking ground when they germinate (**Figure 30.10b**). The coleoptile, the sheath enclosing and protecting the embryonic shoot, pushes upward through the soil and into the air. The shoot tip then grows straight up through the tunnel provided by the tubular coleoptile and eventually breaks out through the coleoptile's tip.

### Fruit Form and Function

While the seeds are developing from ovules, the ovary of the flower is developing into a **fruit**, which protects the enclosed



(a) **Common garden bean.** In common garden beans, straightening of a hook in the hypocotyl pulls the cotyledons from the soil.



(b) **Maize.** In maize and other grasses, the shoot grows straight up through the tube of the coleoptile.

### ▲ Figure 30.10 Two common types of seed germination.

**?** How do bean and maize seedlings protect their shoot systems as they push through the soil?

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 typically does not develop, and the entire flower usually withers and falls away.

During fruit development, the ovary wall becomes the *pericarp*, the thickened wall of the fruit. In some fruits, such as soybean pods, the ovary wall dries out completely at maturity, whereas in other fruits, such as grapes, it remains fleshy. In still others, such as peaches, the inner part of the ovary becomes stony (the pit) while the outer parts stay fleshy. As the ovary grows, the other parts of the flower usually wither and are shed. For example, the pointed tip of a pea pod is the shriveled remains of the pea flower's stigma.

Fruits are classified into several types based on their developmental origins. A fruit that is derived from a single

carpel or several fused carpels is called a **simple fruit** (Figure 30.11a). An **aggregate fruit** results from a single flower that has more than one separate carpel, each forming a small fruit (Figure 30.11b). These “fruitlets” are clustered together on a single receptacle, as in a raspberry. A **multiple fruit** develops from an inflorescence, a group of flowers tightly clustered together. When the walls of the many ovaries start to thicken, they fuse together and become incorporated into one fruit, as in a pineapple (Figure 30.11c).

In some angiosperms, other floral parts contribute to what we commonly call the fruit. Such fruits are called **accessory fruits**. In apple flowers, the ovary is embedded in the receptacle, and the fleshy part of this simple fruit is derived mainly from the enlarged receptacle; only the apple core develops from the ovary (Figure 30.11d).

A fruit usually ripens about the same time that its seeds complete their development. Whereas the ripening of a dry fruit, such as a soybean pod, involves the aging and drying out of fruit tissues, the process in a fleshy fruit is more elaborate. Complex interactions of hormones result in an edible fruit that entices animals that help disperse the seeds. The fruit’s “pulp” becomes softer as a result of enzymes digesting components of

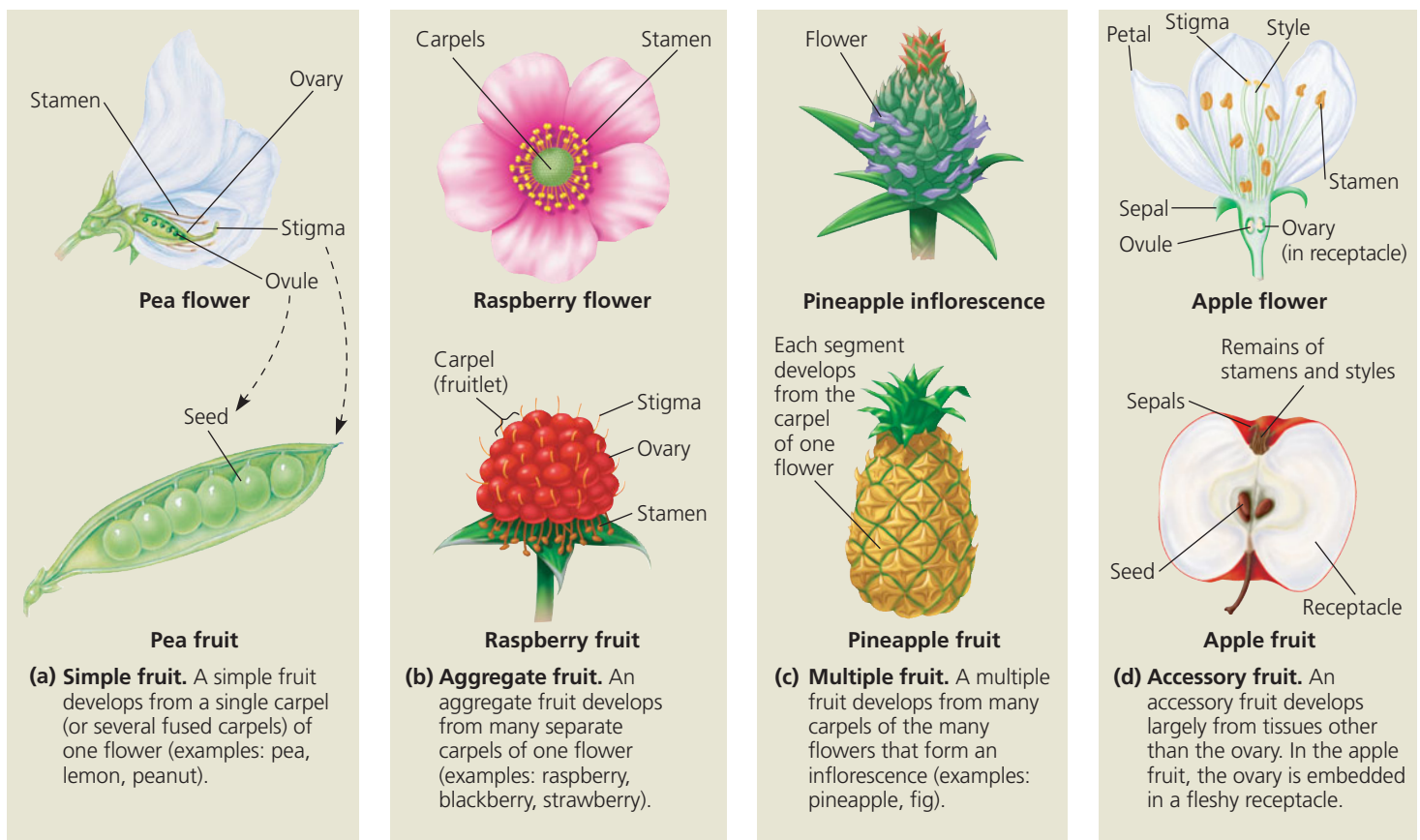
the cell walls. The color usually changes from green to a more overt color, such as red, orange, or yellow. The fruit becomes sweeter as organic acids or starch molecules are converted to sugar, which may reach a concentration of as much as 20% in a ripe fruit. Figure 30.12 examines some mechanisms of fruit dispersal in more detail.

In this section, you have learned about the unique features of sexual reproduction in angiosperms—flowers, fruits, and double fertilization. Next, we’ll examine asexual reproduction.

### CONCEPT CHECK 30.1

- WHAT IF?** If flowers had shorter styles, pollen tubes would more easily reach the embryo sac. Suggest an explanation for why very long styles have evolved in most flowering plants.
- WHAT IF?** In some species, sepals look like petals, and both are collectively called “tepals.” Suggest a possible extension to the ABC hypothesis that could account for the origin of tepals.
- MAKE CONNECTIONS** Does the life cycle of animals have any structures analogous to plant gametophytes? Explain your answer (see Figure 10.6).

For suggested answers, see Appendix A.



▲ **Figure 30.11** Developmental origins of fruits.



## ▼ Figure 30.12 Exploring Fruit and Seed Dispersal

A plant's life depends on finding fertile ground. But a seed that falls and sprouts beneath the parent plant will stand little chance of competing successfully for nutrients. To prosper, seeds must be widely dispersed. Plants use biotic dispersal agents as well as abiotic agents such as water and wind.

### Dispersal by Water

► Some buoyant seeds and fruits can survive months or years at sea. In coconut, the seed embryo and fleshy white "meat" (endosperm) are within a hard layer (endocarp) surrounded by a thick and buoyant fibrous husk.



### Dispersal by Wind

► With a wingspan of 12 cm, the giant seed of the tropical Asian climbing gourd *Alsomitra macrocarpa* glides through the air of the rain forest in wide circles when released.



▼ The winged fruit of a maple spins like a helicopter blade, slowing descent and increasing the chance of being carried farther by horizontal winds.



► Tumbleweeds break off at the ground and tumble across the terrain, scattering their seeds.



▲ Some seeds and fruits are attached to umbrella-like "parachutes" that are made of intricately branched hairs and often produced in puffy clusters. These dandelion "seeds" (actually one-seeded fruits) are carried aloft by the slightest gust of wind.

### Dispersal by Animals



◀ The sharp, tack-like spines on the fruits of puncture vine (*Tribulus terrestris*) can pierce bicycle tires and injure animals, including humans. When these painful "tacks" are removed and discarded, the seeds are dispersed.

► Seeds in edible fruits are often dispersed in feces, such as the black bear feces shown here. Such dispersal may carry seeds far from the parent plant.



◀ Some animals, such as squirrels, hoard seeds or fruits in underground caches. If the animal dies or forgets the cache's location, the buried seeds are well positioned to germinate.

► Ants are chemically attracted to seeds with "food bodies" rich in fatty acids, amino acids, and sugars. The ants carry the seed to their underground nest, where the food body (the lighter-colored portion shown here) is removed and fed to larvae. Due to the seed's size, unwieldy shape, or hard coating, the remainder is usually left intact in the nest, where it germinates.





## Flowering plants reproduce sexually, asexually, or both

Imagine chopping off your finger and watching it develop into an exact copy of you. If this could actually occur, it would be an example of **asexual reproduction**, in which offspring are derived from a single parent without fusion of egg and sperm. The result would be a clone, an asexually produced, genetically identical organism. Asexual reproduction is common in angiosperms, as well as in other plants, and for some plant species it is the predominant mode of reproduction.

### Mechanisms of Asexual Reproduction

Asexual reproduction in plants is typically an extension of the capacity for indeterminate growth. Plant growth can be sustained or renewed indefinitely by meristems, regions of undifferentiated, dividing cells (see Concept 28.2). In addition, parenchyma cells throughout the plant can divide and differentiate into more specialized types of cells, enabling plants to regenerate lost parts. Detached vegetative fragments of some plants can develop into whole offspring; for example, pieces of a potato with an “eye” (vegetative bud) can each regenerate a whole plant. Such **fragmentation**, the separation of a parent plant into parts that develop into whole plants, is one of the most common modes of asexual reproduction. The adventitious plantlets on *Kalanchoë* leaves exemplify an unusual type of fragmentation (see Figure 28.7). In other cases, the root system of a single parent, such as an aspen tree, can give rise to many adventitious shoots that become separate shoot systems (**Figure 30.13**). One aspen clone in Utah has been estimated to be composed of 47,000 stems of genetically identical trees. Although it is likely that some of the root system connections



▲ **Figure 30.13 Asexual reproduction in aspen trees.** Some aspen groves, such as those shown here, consist of thousands of trees descended by asexual reproduction. Each grove of trees derives from the root system of one parent. Thus, the grove is a clone. Notice that genetic differences between groves descended from different parents result in different timing for the development of fall color.

have been severed, making some of the trees isolated from the rest of the clone, each tree still shares a common genome.

An entirely different mechanism of asexual reproduction has evolved in dandelions and some other plants. These plants can sometimes produce seeds without pollination or fertilization. This asexual production of seeds is called **apomixis** (from the Greek words meaning “away from the act of mixing”) because there is no joining or, indeed, production of sperm and egg. Instead, a diploid cell in the ovule gives rise to the embryo, and the ovules mature into seeds, which in the dandelion are dispersed by windblown fruits. Thus, these plants clone themselves by an asexual process but have the advantage of seed dispersal, usually associated with sexual reproduction. Introducing apomixis into hybrid crops is of great interest to plant breeders because apomixis would allow hybrid plants to pass on their desirable genomes intact to their offspring.

### Advantages and Disadvantages of Asexual Versus Sexual Reproduction

**EVOLUTION** An advantage of asexual reproduction is that there is no need for a pollinator. This may be beneficial if plants of the same species are sparsely distributed and unlikely to be visited by the same pollinator. Asexual reproduction also allows the plant to pass on all of its genetic legacy intact to its progeny. In contrast, when reproducing sexually, a plant passes on only half of its alleles. If a plant is superbly suited to its environment, asexual reproduction can be advantageous. A vigorous plant can potentially clone many copies of itself, and if the environmental circumstances remain stable, these offspring will also be genetically well adapted to the same environmental conditions under which the parent flourished.

Generally, the progeny produced by asexual reproduction are stronger than seedlings produced by sexual reproduction. The offspring usually arise from mature vegetative fragments from the parent plant, which is why asexual reproduction in plants is also known as **vegetative reproduction**. In contrast, seed germination is a precarious stage in a plant’s life. The tough seed gives rise to a fragile seedling that may face exposure to predation, competition, and other hazards. In the wild, only a small fraction of seedlings survive to become parents themselves. Production of enormous numbers of seeds compensates for the odds against individual survival and gives natural selection ample genetic variations to screen. However, this is an expensive means of reproduction in terms of the resources consumed in flowering and fruiting.

Because sexual reproduction generates variation in offspring and populations, it can be advantageous in unstable environments where evolving pathogens and other fluctuating conditions affect survival and reproductive success. In contrast, the genotypic uniformity of asexually produced plants puts them at great risk of local extinction if there is a catastrophic environmental change, such as a new strain of disease. Moreover, seeds (which are almost always produced sexually)

facilitate the dispersal of offspring to more distant locations. Finally, seed dormancy allows growth to be suspended until environmental conditions become more favorable. In the **Scientific Skills Exercise**, you can use data to determine which species of monkey flower are mainly asexual reproducers and which are mainly sexual reproducers.

Although sexual reproduction involving two genetically different plants has the benefit of producing the most genetically diverse offspring, some plants, such as garden peas, usually self-fertilize. This process, called “selfing,” is a desirable attribute in some crop plants because it ensures that every ovule will develop into a seed. In many angiosperm species, however, mechanisms have evolved that make it difficult or impossible for a flower to fertilize itself, as we’ll discuss next.

## Mechanisms That Prevent Self-Fertilization

The various mechanisms that prevent self-fertilization contribute to genetic variety by ensuring that the sperm and egg come from different parents. In the case of **dioecious** species, plants cannot self-fertilize because different individuals have either staminate flowers (lacking carpels) or carpellate flowers (lacking stamens) (**Figure 30.14a**). Other plants have flowers with functional stamens and carpels that mature at different times or are structurally arranged in such a way that it is unlikely that an animal pollinator could transfer pollen from an anther to a stigma of the same flower (**Figure 30.14b**). However, the most common anti-selfing mechanism in flowering plants is **self-incompatibility**, the ability of a plant to reject its own pollen and the pollen of closely related individuals. If a pollen grain lands on a stigma of a flower of the same or a closely related individual, a biochemical block prevents the pollen from completing its development and fertilizing an egg.

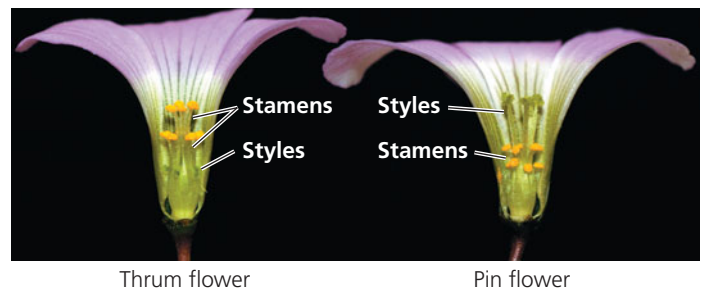
Researchers are unraveling the molecular mechanisms involved in self-incompatibility. Recognition of “self” pollen is based on genes for self-incompatibility, called *S*-genes. In the gene pool of a plant population, there can be dozens of alleles of an *S*-gene. If a pollen grain has an allele that matches an allele of the stigma on which it lands, either the pollen fails to germinate or it germinates but its tube fails to grow through the style to the ovary.

There are two types of self-incompatibility—gametophytic and sporophytic. In gametophytic self-incompatibility, the *S*-allele in the pollen genome governs the blocking of fertilization. For example, an  $S_1$  pollen grain from an  $S_1S_2$  parental sporophyte cannot fertilize eggs of an  $S_1S_2$  flower but can fertilize an  $S_2S_3$  flower. An  $S_2$  pollen grain cannot fertilize either flower. In some plant families, self-incompatibility of this kind involves the enzymatic destruction of RNA within a pollen tube. RNA-hydrolyzing enzymes are produced by the style and enter the pollen tube. If the pollen tube is a “self” type, these enzymes destroy its RNA.

In sporophytic self-incompatibility, fertilization is blocked by *S*-allele gene products in tissues of the parental sporophyte that adhere to the pollen grain wall. For example, neither an  $S_1$



(a) Some species, such as *Sagittaria latifolia* (common arrowhead), are dioecious, having plants that produce only staminate flowers (left) or carpellate flowers (right).



(b) Some species, such as *Oxalis alpina* (alpine woodsorrel), produce two types of flowers on different individuals: “thrums,” which have short styles and long stamens, and “pins,” which have long styles and short stamens. An insect foraging for nectar would collect pollen on different parts of its body; thrum pollen would be deposited on pin stigmas, and vice versa.

▲ **Figure 30.14** Some floral adaptations that prevent self-fertilization.

nor  $S_2$  pollen grain from an  $S_1S_2$  parental sporophyte can fertilize eggs of an  $S_1S_2$  flower or  $S_2S_3$  flower due to the  $S_1S_2$  parental tissue attached to the pollen wall. Sporophytic incompatibility involves a signal transduction pathway in epidermal cells of the stigma that prevents germination of the pollen grain.

Plant breeders frequently hybridize different varieties of a crop plant to combine the best traits of the varieties and counter the loss of vigor that can often result from excessive inbreeding. To obtain hybrid seeds, plant breeders prevent self-fertilization either by laboriously removing the anthers from the parent plants that provide the seeds (as Mendel did) or by developing male-sterile plants. The latter option is increasingly common. Eventually, it may also be possible to impose self-incompatibility genetically on crop species that are normally self-compatible. Basic research on the mechanisms of self-incompatibility may thus have agricultural applications.

## Totipotency, Vegetative Reproduction, and Tissue Culture

In a multicellular organism, any cell that can divide and asexually generate a clone of the original organism is said to be **totipotent**. Totipotency is found to a high degree in many plants and is generally associated with meristematic tissues. In some plants, however, even differentiated cells can dedifferentiate and become meristematic.

## Using Positive and Negative Correlations to Interpret Data

### Do Monkey Flower Species Differ in Allocating Energy to Sexual Versus Asexual Reproduction?

Over the course of its lifespan, a plant captures only a finite amount of resources and energy, which must be allocated to best meet the plant's individual requirements for maintenance, growth, defense, and reproduction. Researchers examined how five species of monkey flower (genus *Mimulus*) use their resources for sexual and asexual reproduction.

#### How the Experiment Was Done

After growing specimens of each species in separate pots in the open, the researchers determined averages for nectar volume, nectar concentration, seeds produced per flower, and the number of times the plants were visited by broad-tailed hummingbirds (*Selasphorus platycircus*, shown above). Using greenhouse-grown specimens, they determined the average number of rooted branches per gram fresh shoot weight for each species. The phrase *rooted branches* refers to asexual reproduction through horizontal shoots that develop roots.



#### Data from the Experiment

Species	Nectar Volume (μL)	Nectar Concentration (% wt of sucrose/total wt)	Seeds per Flower	Visits per Flower	Rooted Branches per Gram Shoot Weight
<i>M. rupestris</i>	4.93	16.6	2.2	0.22	0.673
<i>M. eastwoodiae</i>	4.94	19.8	25.0	0.74	0.488
<i>M. nelsonii</i>	20.25	17.1	102.5	1.08	0.139
<i>M. verbenaceus</i>	38.96	16.9	155.1	1.26	0.091
<i>M. cardinalis</i>	50.00	19.9	283.7	1.75	0.069

### Interpret the Data

- A correlation is a way to describe the relationship between two variables. In a positive correlation, as the values of one of the variables increase, the values of the second variable also increase. In a negative correlation, as the values of one of the variables increase, the values of the second variable decrease. Or there may be no correlation between two variables. If researchers know how two variables are correlated, they can make a prediction about one variable based on what they know about the other variable. (a) Which variable(s) is (are) positively correlated with the volume of nectar production in this genus? (b) Which is (are) negatively correlated? (c) Which show(s) no clear relationship?
- (a) Which *Mimulus* species would you categorize as mainly asexual reproducers? Why? (b) Which species would you categorize as mainly sexual reproducers? Why?
- (a) Which species would probably fare better in response to a pathogen that infects all *Mimulus* species? (b) Which species would fare better if a pathogen were to cause hummingbird populations to dwindle? Explain.

**Data from** S. Sutherland and R. K. Vickery, Jr., Trade-offs between sexual and asexual reproduction in the genus *Mimulus*. *Oecologia*, 76:330–335 (1988).

 A version of this Scientific Skills Exercise can be assigned in MasteringBiology.

## Vegetative Propagation and Grafting

Vegetative reproduction occurs naturally in many plants, but it can often be facilitated or induced by humans, in which case it is called **vegetative propagation**. Most houseplants, woody ornamentals, and orchard trees, for example, are asexually reproduced from plant fragments called cuttings. In most cases, shoot cuttings are used. At the cut end of the shoot, a mass of dividing, undifferentiated cells called a **callus** forms, and adventitious roots then develop from the callus. If the shoot fragment includes a node, then adventitious roots form without a callus stage.

In a modification of vegetative reproduction from cuttings, a twig or bud from one plant can be grafted onto a plant of a closely related species or a different variety of the same species. Grafting makes it possible to combine the best qualities of different species or varieties into a single plant. The plant that provides the root system is called the **stock**; the twig grafted onto the stock is referred to as the **scion**. For example, scions from French varieties of vines that produce superior wine

grapes are grafted onto rootstocks of American varieties that produce inferior grapes but are more resistant to certain soil pathogens. The genes of the scion determine the quality of the fruit. During grafting, a callus first forms between the adjoining cut ends of the scion and stock; cell differentiation then completes the functional unification of the grafted individuals.

## Test-Tube Cloning and Related Techniques

Plant biologists have adopted *in vitro* methods to clone plants for research or horticulture. Whole plants can be obtained by culturing small pieces of tissue from the parent plant on an artificial medium containing nutrients and hormones. The cells or tissues can come from any part of a plant, but growth may vary depending on the plant part, species, and artificial medium. In some media, the cultured cells divide and form a callus of undifferentiated cells (**Figure 30.15a**). When the concentrations of hormones and nutrients are manipulated appropriately, a callus can sprout shoots and roots with fully differentiated cells (**Figure 30.15b** and **c**). If desired, the plantlets



## CONCEPT 30.3

### People modify crops through breeding and genetic engineering

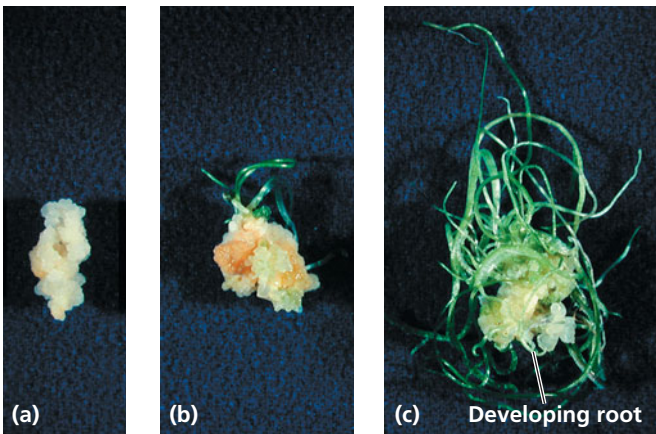
People have intervened in the reproduction and genetic makeup of plants since the dawn of agriculture. Maize, for example, owes its existence to humans. Left on its own in nature, maize would soon become extinct for the simple reason that it cannot spread its seeds. Maize kernels are not only permanently attached to the central axis (the “cob”) but also permanently protected by tough, overlapping leaf sheathes (the “husk”) (**Figure 30.16**). These attributes arose by artificial selection by humans. (See Chapter 19 to review the basic concept of artificial selection.) Despite having no understanding of the scientific principles underlying plant breeding, early farmers domesticated most of our crop species over a relatively short period about 10,000 years ago. But genetic modification began long before people started altering crops by artificial selection. For example, the wheat species we rely on for much of our food evolved by the natural hybridization between different species of grasses. Such hybridization is common in plants and has long been exploited by breeders to introduce genetic variation for artificial selection and crop improvement.

#### Plant Breeding

The art of recognizing valuable traits is important in plant breeding. Breeders scrutinize their fields carefully and travel far and wide searching for domesticated varieties or wild relatives with desirable traits. Such traits occasionally arise spontaneously through mutation, but the natural rate of mutation is too slow and unreliable to produce all the mutations that breeders would like to study. Breeders sometimes hasten mutations by treating large batches of seeds or seedlings with radiation or chemicals.



▲ **Figure 30.16 Maize: a product of artificial selection.** Modern maize (bottom) was derived from teosinte (top). Teosinte kernels are tiny, and each row has a husk that must be removed to get at the kernel. The seeds are loose at maturity, allowing dispersal, which probably made harvesting difficult for early farmers. Ancient farmers selected seeds from plants with larger cob and kernel size as well as the permanent attachment of seeds to the cob and the encasing of the entire cob by a tough husk.



▲ **Figure 30.15 Laboratory cloning of a garlic plant.**

(a) A root from a garlic clove gave rise to this callus culture, a mass of undifferentiated cells. (b and c) The differentiation of a callus into a plantlet depends on the nutrient levels and hormone concentrations in the artificial medium, as can be seen in these cultures grown for different lengths of time.

can then be transferred to soil, where they continue their growth. A single plant can be cloned into thousands of copies by dividing calluses as they grow.

Plant tissue culture is important in eliminating weakly pathogenic viruses from vegetatively propagated varieties. Although the presence of weak viruses may not be obvious, yield or quality may be substantially reduced as a result of infection. Strawberry plants, for example, are susceptible to more than 60 viruses, and typically the plants must be replaced each year because of viral infection. However, the distribution of viruses in a plant is not uniform, and the apical meristems are sometimes virus-free. Therefore, apical meristems can be excised and used to produce virus-free material for tissue culture.

Plant tissue culture also facilitates genetic engineering. Most techniques for the introduction of foreign genes into plants require small pieces of plant tissue or single plant cells as the starting material. Test-tube culture makes it possible to regenerate genetically modified (GM) plants from a single plant cell into which the foreign DNA has been incorporated. In the next section, we’ll take a closer look at some of the promises and challenges surrounding the use of GM plants in agriculture.

#### CONCEPT CHECK 30.2

1. What are three ways that flowering plants avoid self-fertilization?
2. The seedless banana, the world’s most popular fruit, is losing the battle against two fungal epidemics. Why do such epidemics generally pose a greater risk to asexually propagated crops?
3. Self-fertilization, or selfing, seems to have obvious disadvantages as a reproductive “strategy” in nature, and it has even been called an “evolutionary dead end.” So it is surprising that about 20% of angiosperm species primarily rely on selfing. Suggest a reason why selfing might be advantageous and still be an evolutionary dead end.

For suggested answers, see Appendix A.

When a desirable trait is identified in a wild species, the wild species is crossed with a domesticated variety. Generally, those progeny that have inherited the desirable trait from the wild parent have also inherited many traits that are not desirable for agriculture, such as small fruits or low yields. The progeny that express the desired trait are again crossed with members of the domesticated species and their progeny examined for the desired trait. This process is continued until the progeny with the desired wild trait resemble the original domesticated parent in their other agricultural attributes.

While most breeders cross-pollinate plants of a single species, some breeding methods rely on hybridization between two distant species of the same genus. Such crosses sometimes result in the abortion of the hybrid seed during development. Often in these cases, the embryo begins to develop, but the endosperm does not. Hybrid embryos are sometimes rescued by surgically removing them from the ovule and culturing them *in vitro*.

## Plant Biotechnology and Genetic Engineering

Plant biotechnology has two meanings. In the general sense, it refers to innovations in the use of plants (or substances obtained from plants) to make products of use to people—an endeavor that began in prehistory. In a more specific sense, biotechnology refers to the use of GM organisms in agriculture and industry. Indeed, in the last two decades, genetic engineering has become such a powerful force that the terms *genetic engineering* and *biotechnology* have become synonymous in the media.

Unlike traditional plant breeders, modern plant biotechnologists, using techniques of genetic engineering, are not limited to the transfer of genes between closely related species or genera. For example, traditional breeding techniques could not be used to insert a desired gene from daffodil into rice because the many intermediate species between rice and daffodil and their common ancestor are extinct. In theory, if breeders had the intermediate species, over the course of several centuries they could probably introduce a daffodil gene into rice by traditional hybridization and breeding methods. With genetic engineering, however, such gene transfers can be done more quickly, more specifically, and without the need for intermediate species. The term **transgenic** is used to describe organisms that have been engineered to express a gene from another species.

In the remainder of this chapter, we examine the prospects and controversies surrounding the use of GM crops. The advocates of plant biotechnology contend that the genetic engineering of crop plants is the key to overcoming some of the most pressing problems of the 21st century, including world hunger and fossil fuel dependency.

### Reducing World Hunger and Malnutrition

Currently, 800 million people suffer from nutritional deficiencies, with 40,000 dying each day of malnutrition, half of them children. There is much disagreement about the causes of such

hunger. Some argue that food shortages arise from inequities in distribution and that the dire poor simply cannot afford food. Others regard food shortages as evidence that the world is overpopulated—that the human species has exceeded the carrying capacity of the planet (see Chapter 40). Whatever the social and demographic causes of malnutrition, increasing food production is a humane objective. Because land and water are the most limiting resources, the best option is to increase yields on already existing farmland. Indeed, there is very little “extra” land that can be farmed, especially if the few remaining pockets of wilderness are to be preserved. Based on conservative estimates of population growth, farmers will have to produce 40% more grain per hectare to feed the human population in 2030. Plant biotechnology can help make these crop yields possible.

The commercial use of transgenic crops has been one of the most dramatic examples of rapid technology adoption in the history of agriculture. These crops include varieties and hybrids of cotton, maize, and potatoes that contain genes from the bacterium *Bacillus thuringiensis*. These “transgenes” encode a protein (*Bt* toxin) that is toxic to insect pests. The use of such plant varieties greatly reduces the need for chemical insecticides. The *Bt* toxin used in crops is produced in the plant as a harmless protoxin that only becomes toxic if activated by alkaline conditions, such as occur in the guts of insects. Because vertebrates have highly acidic stomachs, protoxin consumed by humans or farm animals is rendered harmless by denaturation.

Considerable progress has also been made in developing transgenic crops that tolerate certain herbicides. The cultivation of these plants may reduce production costs by enabling farmers to “weed” crops with herbicides that do not damage the transgenic crop plants, instead of using heavy tillage, which can cause soil erosion. Researchers are also engineering plants with enhanced resistance to disease. In one case, a transgenic papaya that is resistant to a ring spot virus was introduced into Hawaii, thereby saving its papaya industry.

The nutritional quality of plants is also being improved. For example, some 250,000 to 500,000 children go blind each year because of vitamin A deficiencies. More than half of these children die within a year of becoming blind. In response to this crisis, genetic engineers have created “Golden Rice,” a transgenic variety supplemented with two daffodil genes that enable it to produce grain with increased levels of beta-carotene, a precursor of vitamin A. Another target for improvement by genetic engineering is cassava, a staple for 800 million of the poorest people on our planet (**Figure 30.17**).

### Reducing Fossil Fuel Dependency

Global sources of inexpensive fossil fuels, particularly oil, are rapidly being depleted. Moreover, most climatologists attribute global warming mainly to the rampant burning of fossil fuels, such as coal and oil, and the resulting release of the greenhouse gas CO<sub>2</sub>. How can the world meet its energy demands in the 21st century in an economical and nonpolluting way? In certain

► **Figure 30.17 Fighting world hunger with transgenic cassava (*Manihot esculenta*).** This starchy root crop is the primary food for 800 million of the world's poor, but it does not provide a balanced diet. Moreover, it must be processed to remove chemicals that release cyanide, a toxin. Transgenic cassava plants have been developed with greatly increased levels of iron and beta-carotene (a vitamin A precursor). Researchers have also created cassava plants with root masses twice the normal size that contain almost no cyanide-producing chemicals.



localities, wind or solar power may become economically viable, but such alternative energy sources are unlikely to fill the global energy demands completely. Many scientists predict that **biofuels**—fuels derived from living biomass—could produce a sizable fraction of the world's energy needs in the not-too-distant future. **Biomass** is the total mass of organic matter in a group of organisms in a particular habitat. The use of biofuels from plant biomass would reduce the net emission of CO<sub>2</sub>. Whereas burning fossil fuels increases atmospheric CO<sub>2</sub> concentrations, biofuel crops reabsorb by photosynthesis the CO<sub>2</sub> emitted when biofuels are burned, creating a cycle that is carbon neutral.

In working to create biofuel crops from wild precursors, scientists are focusing their domestication efforts on fast-growing plants, such as switchgrass (*Panicum virgatum*) and poplar (*Populus trichocarpa*), that can grow on soil that is too poor for food production. Scientists do not envisage the plant biomass being burned directly. Instead, the polymers in cell walls, such as cellulose and hemicellulose, which constitute the most abundant organic compounds on Earth, would be broken down into sugars by enzymatic reactions. These sugars, in turn, would be fermented into alcohol, which would be distilled to yield biofuels. Currently, the enzymes and pretreatment processes involved in converting cellulosic biomass to ethanol are very expensive. In addition to increasing plant polysaccharide content and overall biomass, researchers are trying to genetically engineer plants with cell wall properties, such as reduced lignin content, that will lower the costs of biofuel production.

## The Debate over Plant Biotechnology

Much of the debate about GM organisms (GMOs) in agriculture is political, social, economic, or ethical and therefore outside the scope of this book. But we *should* consider the biological concerns about GM crops. Some biologists, particularly ecologists, are concerned about the unknown risks associated with the release of GMOs into the environment. The debate centers on the extent to which GMOs could harm the environment or human health. Those who want to proceed more slowly with agricultural biotechnology (or end it) are

concerned about the unstoppable nature of the “experiment.” If a drug trial produces unanticipated harmful results, the trial is stopped. But we may not be able to stop the “trial” of introducing novel organisms into the biosphere. Here, we examine some of the proposed negative consequences of using GM crops, including their effects on human health and nontarget organisms and the potential for transgene escape.

## Issues of Human Health

Many GMO opponents worry that genetic engineering may inadvertently transfer allergens, molecules to which some people are allergic, from a species that produces an allergen to a plant used for food. However, biotechnologists are already engaged in removing genes that encode allergenic proteins from soybeans and other crops. So far, there is no credible evidence that GM plants specifically designed for human consumption have adverse effects on human health. In fact, some GM foods are potentially healthier than non-GM foods. For example, *Bt* maize (the transgenic variety with the *Bt* toxin) contains 90% less of a fungal toxin that causes cancer and birth defects than non-*Bt* maize. Called fumonisin, this toxin is highly resistant to degradation and has been found in alarmingly high concentrations in some batches of processed maize products, ranging from cornflakes to beer. Fumonisin is produced by a fungus (*Fusarium*) that infects insect-damaged maize. Because *Bt* maize generally suffers less insect damage than non-GM maize, it contains much less fumonisin.

Nevertheless, because of health concerns, GMO opponents lobby for the clear labeling of all foods containing products of GMOs. Some also argue for strict regulations against the mixing of GM foods with non-GM foods during food transport, storage, and processing. Biotechnology advocates, however, note that similar demands were not made when “transgenic” crops produced by traditional plant-breeding techniques were put on the market. There are, for example, some commercially grown varieties of wheat derived by traditional plant-breeding techniques that contain entire chromosomes (and thousands of genes) from rye.

## Possible Effects on Nontarget Organisms

Many ecologists are concerned that the growing of GM crops might have unforeseen effects on nontarget organisms. One laboratory study indicated that the larvae (caterpillars) of monarch butterflies responded adversely and even died after eating milkweed leaves (their preferred food) heavily dusted with pollen from transgenic *Bt* maize. This study has since been discredited, affording a good example of the self-correcting nature of science. As it turns out, when the original researcher shook the male maize inflorescences onto the milkweed leaves in the laboratory, the filaments of stamens, opened microsporangia, and other floral parts also rained onto the leaves. Subsequent research found that it was these other floral parts, *not* the pollen, that contained *Bt* toxin in high concentrations.



Unlike pollen, these floral parts would not be carried by the wind to neighboring milkweed plants when shed under natural field conditions. Only one *Bt* maize line, accounting for less than 2% of commercial *Bt* maize production (and now discontinued), produced pollen with high *Bt* toxin concentrations.

In considering the negative effects of *Bt* pollen on monarch butterflies, we must also weigh the effects of an alternative to the cultivation of *Bt* maize—the spraying of non-*Bt* maize with chemical pesticides. Recent studies have shown that such spraying is much more harmful to nearby monarch populations than is *Bt* maize production. Although the effects of *Bt* maize pollen on monarch butterfly larvae appear to be minor, the controversy has emphasized the need for accurate field testing of all GM crops and the importance of targeting gene expression to specific tissues to improve safety.

### Addressing the Problem of Transgene Escape

Perhaps the most serious concern raised about GM crops is the possibility of the introduced genes escaping from a transgenic crop into related weeds through crop-to-weed hybridization. The fear is that the spontaneous hybridization between a crop engineered for herbicide resistance and a wild relative might give rise to a “superweed” that would have a selective advantage over other weeds in the wild and would be much more difficult to control in the field. GMO advocates point out that the likelihood of transgene escape depends on the ability of the crop and weed to hybridize and on how the transgenes affect the overall fitness of the hybrids. A desirable crop trait—a dwarf phenotype, for example—might be disadvantageous to a weed growing in the wild. In other instances, there are no weedy relatives nearby with which to hybridize; soybean, for example, has no wild relatives in the United States. However, canola, sorghum, and many other crops do hybridize readily with weeds, and crop-to-weed transgene escape has occurred. In 2003 a transgenic variety of creeping bentgrass (*Agrostis stolonifera*) genetically engineered to resist the herbicide glyphosate escaped from an experimental plot in Oregon following a windstorm. Despite efforts to eradicate the escapee, 62% of the *Agrostis* plants found in the vicinity three years later were glyphosate resistant. So far, the ecological impact of this event appears to be minor, but that not may be the case with future transgenic escapes.

Many different strategies are being pursued with the goal of preventing transgene escape. For example, if male sterility could be engineered into plants, these plants would still produce seeds and fruit if pollinated by nearby nontransgenic plants, but they would produce no viable pollen. A second approach involves genetically engineering apomixis into transgenic crops. When a seed is produced by apomixis, the embryo and endosperm develop without fertilization. The transfer of this trait to transgenic crops would therefore minimize the possibility of transgene escape via pollen because plants could be male-sterile without compromising seed or fruit production. A third approach is to engineer the transgene into the chloroplast DNA of the crop. Chloroplast DNA in many plant species is inherited strictly from the egg, so transgenes in the chloroplast cannot be transferred by pollen. A fourth approach for preventing transgene escape is to genetically engineer flowers that develop normally but fail to open. Consequently, self-pollination would occur, but pollen would be unlikely to escape from the flower. This solution would require modifications to flower design. Several floral genes have been identified that could be manipulated to this end.

The continuing debate about GMOs in agriculture exemplifies one of this textbook’s recurring ideas: the relationship of science and technology to society. Technological advances almost always involve some risk of unintended outcomes. In plant biotechnology, zero risk is probably unattainable. Therefore, scientists and the public must assess on a case-by-case basis the possible benefits of transgenic products versus the risks that society is willing to take. The best scenario is for these discussions and decisions to be based on sound scientific information and rigorous testing rather than on reflexive fear or blind optimism.

#### CONCEPT CHECK 30.3

1. Compare traditional plant-breeding methods with genetic engineering.
2. Why does *Bt* maize have less fumonisin than non-GM maize?
3. **WHAT IF?** In a few species, chloroplast genes are inherited only from sperm. How might this influence efforts to prevent transgene escape?

For suggested answers, see Appendix A.

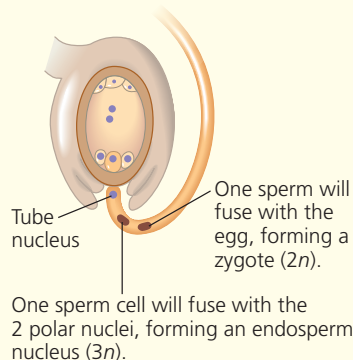
# 30 Chapter Review

## SUMMARY OF KEY CONCEPTS

### CONCEPT 30.1

#### Flowers, double fertilization, and fruits are unique features of the angiosperm life cycle (pp. 598–607)

- Angiosperm reproduction involves an alternation of generations between a multicellular diploid sporophyte generation and multicellular haploid gametophyte generation. Flowers, produced by the sporophyte, function in sexual reproduction.
- The four floral organs are sepals, petals, stamens, and carpels. **Sepals** protect the floral bud. **Petals** help attract pollinators. **Stamens** bear **anthers** in which haploid **microspores** develop into **pollen grains** containing a male gametophyte. **Carpels** contain **ovules** (immature seeds) in their swollen bases. Within the ovules, **embryos sacs** (female gametophytes) develop from **megaspores**.
- **Pollination**, which precedes **fertilization**, is the placing of pollen on the **stigma** of a carpel. After pollination, the **pollen tube** discharges two sperm into the female gametophyte. Two sperm are needed for **double fertilization**, a process in which one sperm fertilizes the egg, forming a zygote and eventually an embryo, while the other sperm combines with the polar nuclei, giving rise to food-storing **endosperm**.
- The **seed coat** encloses the embryo along with a food supply stocked in either the endosperm or the **cotyledons**. Seed **dormancy** ensures that seeds germinate only when conditions for seedling survival are optimal. The breaking of dormancy often requires environmental cues, such as temperature or lighting changes.
- The **fruit** protects the enclosed seeds and aids in wind dispersal or in the attraction of seed-dispersing animals.



? *What changes occur to the four types of floral parts as a flower changes into a fruit?*

### CONCEPT 30.2

#### Flowering plants reproduce sexually, asexually, or both (pp. 608–611)

- **Asexual reproduction** enables successful plants to proliferate quickly. Sexual reproduction generates most of the genetic variation that makes evolutionary adaptation possible.
- Plants have evolved many mechanisms to avoid self-fertilization, including having male and female flowers on different individuals (**dioecious** species), asynchronous production of male and female parts within a single flower, and **self-incompatibility**, in which pollen grains that bear an allele identical to one in the female are rejected.
- Plants can be cloned from single cells, which can be genetically manipulated before being allowed to develop into a plant.

? *What are the advantages of asexual and sexual reproduction?*

### CONCEPT 30.3

#### People modify crops through breeding and genetic engineering (pp. 611–614)

- Hybridization of different varieties and even species of plants is common in nature and has been used by breeders, ancient and modern, to introduce new genes into crops. After two plants are successfully hybridized, plant breeders select those progeny that have the desired traits.
- In genetic engineering, genes from unrelated organisms are incorporated into plants. Genetically modified (GM) plants have the potential of increasing the quality and quantity of food worldwide and may also become increasingly important as biofuels.
- Two important GM crops are Golden Rice, which provides more vitamin A, and *Bt* maize, which is insect resistant.
- There are concerns about the unknown risks of releasing GM organisms into the environment, but the potential benefits of **transgenic** crops need to be considered.

? *Give three examples of how genetic engineering has improved food quality or agricultural productivity.*

## TEST YOUR UNDERSTANDING

### Level 1: Knowledge/Comprehension

1. A seed develops from
  - a. an ovum.
  - b. a pollen grain.
  - c. an ovule.
  - d. an ovary.
  - e. an embryo.
2. A fruit is
  - a. a mature ovary.
  - b. a mature ovule.
  - c. a seed plus its integuments.
  - d. a fused carpel.
  - e. an enlarged embryo sac.
3. Double fertilization means that
  - a. flowers must be pollinated twice to yield fruits and seeds.
  - b. every egg must receive two sperm to produce an embryo.
  - c. one sperm is needed to fertilize the egg, and a second sperm is needed to fertilize the polar nuclei.
  - d. the egg of the embryo sac is diploid.
  - e. every sperm has two nuclei.
4. “Golden Rice”
  - a. is resistant to various herbicides, making it practical to weed rice fields with those herbicides.
  - b. is resistant to a virus that commonly attacks rice fields.
  - c. includes bacterial genes that produce a toxin that reduces damage from insect pests.
  - d. produces larger, golden grains that increase crop yields.
  - e. contains daffodil genes that increase vitamin A content.
5. Which statement concerning grafting is correct?
  - a. Stocks and scions refer to twigs of different species.
  - b. Stocks come from vines, but scions come from trees.
  - c. Stocks provide root systems for grafting.
  - d. Grafting creates new species.
  - e. Stocks and scions must come from unrelated species.

## Level 2: Application/Analysis

6. Some dioecious species have the XY genotype for male and XX for female. After double fertilization, what would be the genotypes of the embryos and endosperm nuclei?
  - a. embryo X/endosperm XX or embryo Y/endosperm XY
  - b. embryo XX/endosperm XX or embryo XY/endosperm XY
  - c. embryo XX/endosperm XXX or embryo XY/endosperm XYY
  - d. embryo XX/endosperm XXX or embryo XY/endosperm XXY
  - e. embryo XY/endosperm XXX or embryo XX/endosperm XXY
7. A small flower with green petals is most likely
  - a. bee-pollinated.
  - b. bird-pollinated.
  - c. bat-pollinated.
  - d. wind-pollinated.
  - e. moth-pollinated.
8. The pollen produced by wind-pollinated plants is often smaller than the pollen produced by animal-pollinated plants. A reason for this might be that
  - a. wind-pollinated plants, in general, are smaller than animal-pollinated plants.
  - b. wind-pollinated plants release pollen in the spring, before the plant has stored enough energy to make large pollen grains.
  - c. small pollen grains can be carried farther by the wind.
  - d. animal pollinators are more facile at picking up large pollen grains.
  - e. wind-pollinated flowers don't need large pollen grains because they don't have to attract animal pollinators.
9. The black dots that cover strawberries are actually individual fruits from a flower with multiple carpels. The fleshy and tasty portion of a strawberry derives from the receptacle of the flower. Therefore, a strawberry is
  - a. both a multiple fruit and an aggregate fruit.
  - b. both a multiple fruit and an accessory fruit.
  - c. both a simple fruit and an aggregate fruit.
  - d. both an aggregate fruit and an accessory fruit.
  - e. a simple fruit with many seeds.
10. **DRAW IT** Draw and label the parts of a flower.

## Level 3: Synthesis/Evaluation

### 11. SCIENTIFIC INQUIRY

Critics of GM foods have argued that foreign genes may disturb normal cellular functioning, causing unexpected and potentially harmful substances to appear inside cells. Toxic intermediary substances that normally occur in very small amounts may arise in larger amounts, or new substances may appear. The disruption may also lead to loss of substances that help maintain normal metabolism. If you were your nation's chief scientific advisor, how would you respond to these criticisms?

### 12. SCIENCE, TECHNOLOGY, AND SOCIETY

People have engaged in genetic manipulation for millennia, producing plant and animal varieties through selective breeding and hybridization processes that significantly modify the genomes of organisms. Why do you think modern genetic engineering, which often entails introducing or modifying only one or a few genes, has met with so much public opposition? Should some forms of genetic engineering be of greater concern than others? Explain.

### 13. FOCUS ON EVOLUTION

With respect to sexual reproduction, some plant species are fully self-fertile, others are fully self-incompatible, and some exhibit a "mixed strategy" with partial self-incompatibility. These reproductive strategies differ in their implications for evolutionary potential. How might these three strategies fare in a small founder population (see Chapter 21)?

### 14. FOCUS ON ORGANIZATION

In a short essay (100–150 words), discuss how the ability of a flower to reproduce with other flowers of the same species is an emergent property that arises from its floral parts and their organization.

*For selected answers, see Appendix A.*

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# Plant Responses to Internal and External Signals

▼ **Figure 31.1** How do plants detect light?



## KEY CONCEPTS

- 31.1** Plant hormones help coordinate growth, development, and responses to stimuli
- 31.2** Responses to light are critical for plant success
- 31.3** Plants respond to a wide variety of stimuli other than light
- 31.4** Plants respond to attacks by herbivores and pathogens

## OVERVIEW

### The Race to Live

**T**hese tender barley seedlings, their stored seed reserves nearing exhaustion, have reached a critical point in their lives (**Figure 31.1**). If they fail to attain sufficient light, they will not be able to outcompete their neighbors in the race for resources, and they will perish. It is not surprising, therefore, that mechanisms have evolved in plants that enable them to adjust their growth and development according to the spectral composition of the light available. But how are differences in light quality detected? The sensing of light by plants

involves the activation of signal transduction pathways that, in the big picture, are not too far removed from some of the pathways that you use to interact with your environment. In effect, at the levels of signal *reception* and signal *transduction*, your cells are not all that different from those of a barley seedling—certainly the similarities far outweigh the differences. As an animal, however, your *responses* to environmental stimuli are generally quite different from those of plants. Animals commonly respond to environmental challenges and opportunities by movement; plants, such as these young barley seedlings, by altering their growth and development.

Architectural modifications due to altered growth are essentially changes in spatial orientation, but plants must also adjust themselves according to changes in time. The passage of seasons is an example of a temporal variable that plants need to measure to compete successfully. Plants also do not exist in isolation: They interact positively or negatively with a wide range of organisms. All of these physical and chemical interactions

and all of the internal chemical changes they initiate involve signal transduction pathways of comparable complexity. In this chapter, first we'll discuss the internal chemicals (hormones) that regulate plant growth and development; then we'll explore how plants perceive and respond to light and other environmental signals.

## CONCEPT 31.1

### Plant hormones help coordinate growth, development, and responses to stimuli

A **hormone**, in the original meaning of the term, is a signaling molecule that is produced in tiny amounts by one part of an organism's body and transported to other parts, where it binds to a specific receptor and triggers responses

in target cells and tissues. In animals, hormones are usually transported through the circulatory system, a criterion often included in definitions of the term. Many plant biologists, however, argue that the hormone concept, which originated from studies of animals, is too limiting to describe plant physiological processes. For example, plants don't have circulating blood to transport hormone-like signaling molecules. Moreover, some signaling molecules that are considered plant hormones act only locally. Finally, some signaling molecules in plants, such as sucrose, typically occur at concentrations hundreds of thousands times greater than that of a typical hormone. Nevertheless, they are transported through plants and activate signal transduction pathways that greatly alter the functioning of plants in a manner similar to a hormone. Thus, many plant biologists prefer the broader term *plant growth regulator* to describe organic compounds, whether natural or synthetic, that modify or control one or more specific physiological processes within a plant. Currently, the terms *plant hormone* and *plant growth regulator* are used about equally, but for historical continuity we will use the term *plant hormone* and adhere to the criterion that plant hormones are active at very low concentrations.

Plant hormones are produced in very low concentrations, but a tiny amount of hormone can have a profound effect on plant growth and development. Virtually every aspect of plant growth and development is under hormonal control to some degree. Each hormone has multiple effects, depending on its site of action, its concentration, and the developmental stage of the plant. Conversely, multiple hormones can influence a single process. Response to a hormone usually depends not so much on the amount of that hormone as on its relative concentration compared with other hormones. It is often the interactions between different hormones, rather than hormones acting in isolation, that control growth and development. These interactions will become apparent in the following survey of hormone function.

## The Discovery of Plant Hormones

The idea that chemical messengers exist in plants emerged from a series of classic experiments on how stems respond to light. As you know, the shoots of plants grow toward light (see Figure 31.1). Any growth response that results in plant organs curving toward or away from stimuli is called a **tropism** (from the Greek *tropos*, turn). The growth of a plant organ toward light or away from it is called **phototropism**; shoots generally exhibit positive phototropism, whereas roots exhibit negative phototropism. In nature, positive phototropism directs shoot growth toward the sunlight that powers photosynthesis. This response involves cells on the darker side elongating faster than the cells on the brighter side.

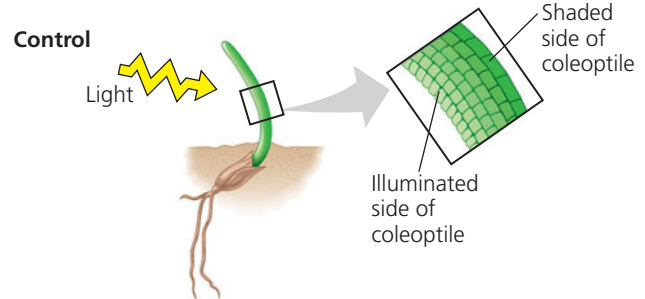
Charles Darwin and his son Francis conducted some of the earliest experiments on phototropism (Figure 31.2). They observed that a grass seedling ensheathed in its coleoptile

### ▼ Figure 31.2 Inquiry

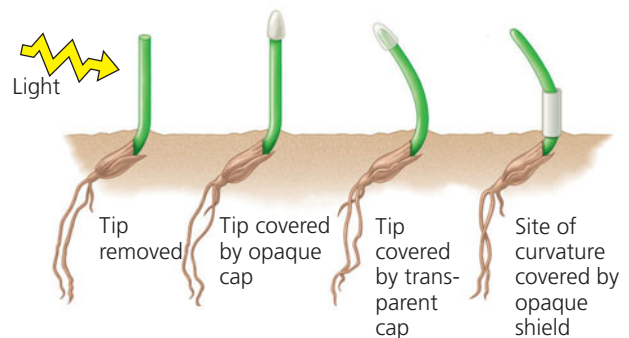
#### What part of a grass coleoptile senses light, and how is the signal transmitted?

**Experiment** In 1880, Charles and Francis Darwin removed and covered parts of grass coleoptiles to determine what part senses light. In 1913, Peter Boysen-Jensen separated coleoptiles with different materials to determine how the signal for phototropism is transmitted.

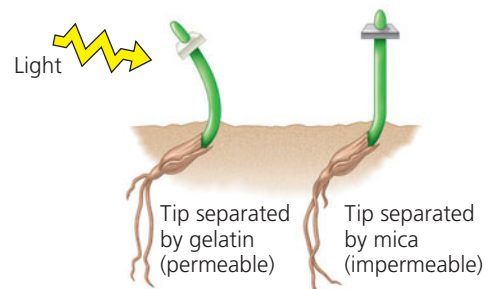
#### Results



#### Darwin and Darwin: Phototropism occurs only when the tip is illuminated.



#### Boysen-Jensen: Phototropism occurs when the tip is separated by a permeable barrier but not an impermeable barrier.



**Conclusion** The Darwins' experiment suggested that only the tip of the coleoptile senses light. The phototropic bending, however, occurred at a distance from the site of light perception (the tip). Boysen-Jensen's results suggested that the signal for the bending is a light-activated mobile chemical.

**Sources** C. R. Darwin, *The power of movement in plants*, John Murray, London (1880). P. Boysen-Jensen, *Concerning the performance of phototropic stimuli on the Avena coleoptile*, *Berichte der Deutschen Botanischen Gesellschaft (Reports of the German Botanical Society)* 31:559–566 (1913).

**WHAT IF?** How could you experimentally determine which colors of light cause the most phototropic bending?

(see Figure 30.10b) could bend toward light only if the tip of the coleoptile was present. If the tip was removed, the coleoptile did not curve. The seedling also failed to grow toward light if the tip was covered with an opaque cap; but neither a transparent cap over the tip nor an opaque shield placed below the coleoptile tip prevented the phototropic response. It was the tip of the coleoptile, the Darwins concluded, that was responsible for sensing light. However, they noted that the differential growth response that led to curvature of the coleoptile occurred some distance below the tip. The Darwins postulated that some signal was transmitted downward from the tip to the elongating region of the coleoptile. A few decades later, the Danish scientist Peter Boysen-Jensen demonstrated that the signal was a mobile chemical substance. He separated the tip from the remainder of the coleoptile by a cube of gelatin, which prevented cellular contact but allowed chemicals to pass through. These seedlings responded normally, bending toward light. However, if the tip was experimentally separated from the lower coleoptile by an impermeable barrier, such as the mineral mica, no phototropic response occurred.

In 1926, Frits Went extracted the chemical messenger for phototropism by modifying the experiments of Boysen-Jensen (**Figure 31.3**). Went removed the coleoptile tip and placed it on a cube of agar, a gelatinous material. The chemical messenger moving from the tip, Went reasoned, should diffuse into the agar, and the agar block should then be able to substitute for the coleoptile tip. Went placed the agar blocks on decapitated coleoptiles that were kept in the dark. A block that was centered on top of the coleoptile caused the stem to grow straight upward. However, when the block was placed off center, the coleoptile began to bend away from the side with the agar block, as though growing toward light. Went concluded that the agar block contained a chemical produced in the coleoptile tip, that this chemical stimulated growth as it passed down the coleoptile, and that a coleoptile curved toward light because of a higher concentration of the growth-promoting chemical on the darker side of the coleoptile. For this chemical messenger, or hormone, Went chose the name auxin (from the Greek *auxein*, to increase). The major type of auxin was later purified, and its chemical structure was then determined to be indoleacetic acid (IAA).

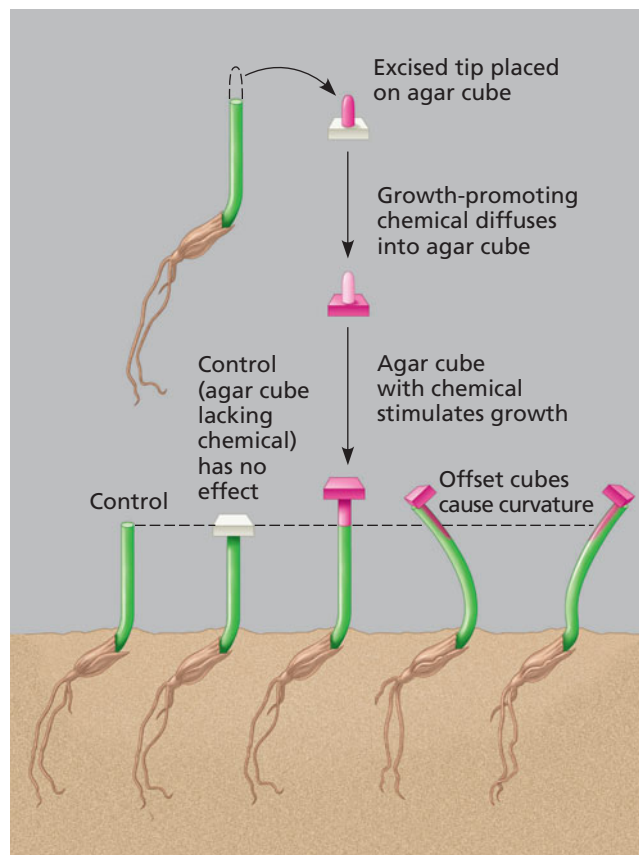
These classic experiments involving grass coleoptiles support the idea that an asymmetric distribution of auxin moving down from the coleoptile tip causes cells on the darker side to elongate faster than cells on the brighter side. But studies of phototropism in organs other than grass coleoptiles provide less support for this idea. There is no evidence that illumination from one side causes asymmetric distribution of auxin in stems of sunflowers or other eudicots. There *is*, however, asymmetric distribution of certain substances that may act as growth *inhibitors*, and these substances are more concentrated on the lighted side of a stem.

### ▼ Figure 31.3 Inquiry

#### Does asymmetric distribution of a growth-promoting chemical cause a coleoptile to grow toward the light?

**Experiment** In 1926, Frits Went's experiment identified how a growth-promoting chemical causes a coleoptile to grow toward light. He placed coleoptiles in the dark and removed their tips, putting some tips on agar cubes that he predicted would absorb the growth-promoting chemical. On a control coleoptile, he placed a cube that lacked the chemical. On others, he placed cubes containing the chemical, either centered on top of the coleoptile to distribute the chemical evenly or offset to increase the concentration on one side.

**Results** The coleoptile grew straight if the growth-promoting chemical was distributed evenly. If the chemical was distributed unevenly, the coleoptile curved away from the side with the cube, as if growing toward light, even though it was grown in the dark.



**Conclusion** Went concluded that a coleoptile curves toward light because its dark side has a higher concentration of the growth-promoting chemical, which he named auxin.

**Source** F. Went, A growth substance and growth, *Recueils des Travaux Botaniques Néerlandais (Collections of Dutch Botanical Works)* 25:1–116 (1928).



A related Experimental Inquiry Tutorial can be assigned in MasteringBiology.

**WHAT IF?** Triiodobenzoic acid (TIBA) inhibits auxin transport. If a tiny agar bead containing TIBA were placed off center on the tip of an intact coleoptile, which way would the coleoptile bend: toward the side with the bead or away from it? Explain.



## A Survey of Plant Hormones

The discovery of auxin stimulated the search for other plant hormones. **Table 31.1** previews some major classes of plant hormones: auxin, cytokinins, gibberellins, brassinosteroids, abscisic acid, and ethylene (this list is by no means exhaustive).

### Auxin

The term **auxin** is used for any chemical substance that promotes elongation of coleoptiles, although auxins have multiple functions in flowering plants. The major natural auxin in plants is indoleacetic acid (IAA), although several other compounds, including some synthetic ones, have auxin activity. (Unless mentioned otherwise, we will use the term *auxin* synonymously with IAA.)

Auxin is produced predominantly in shoot tips and is transported from cell to cell down the stem at a rate of about 1 cm/hr. It moves only from tip to base, not in the reverse direction. This unidirectional transport of auxin is called *polar transport*. Polar transport is unrelated to gravity; experiments have shown that auxin travels upward when a stem or coleoptile segment is placed upside down. Rather, the polarity of auxin movement is attributable to the polar distribution of auxin transport protein in the cells. Concentrated at the basal end of a cell, the auxin transporters move the hormone out of the cell.

The auxin can then enter the apical end of the neighboring cell (**Figure 31.4**). Auxin has a variety of effects, including stimulating cell elongation and regulating plant architecture.

**The Role of Auxin in Cell Elongation** One of auxin’s chief functions is to stimulate elongation of cells within young developing shoots. As auxin from the shoot tip (see Figure 28.16) moves down to the region of cell elongation, the hormone stimulates cell growth, probably by binding to a receptor in the plasma membrane. Auxin stimulates growth only over a certain concentration range, from about  $10^{-8}$  to  $10^{-4}$  M. At higher concentrations, auxin may inhibit cell elongation by inducing the production of ethylene, a hormone that generally hinders growth. We’ll return to this hormonal interaction when we discuss ethylene.

According to a model called the *acid growth hypothesis*, proton pumps play a major role in the growth response of cells to auxin. In a shoot’s region of elongation, auxin stimulates the plasma membrane’s proton (H<sup>+</sup>) pumps. This pumping of H<sup>+</sup> increases the voltage across the membrane (membrane potential) and lowers the pH in the cell wall within minutes (**Figure 31.5**). Acidification of the wall activates enzymes called **expansins** that break the cross-links (hydrogen bonds) between cellulose microfibrils and other cell wall constituents,

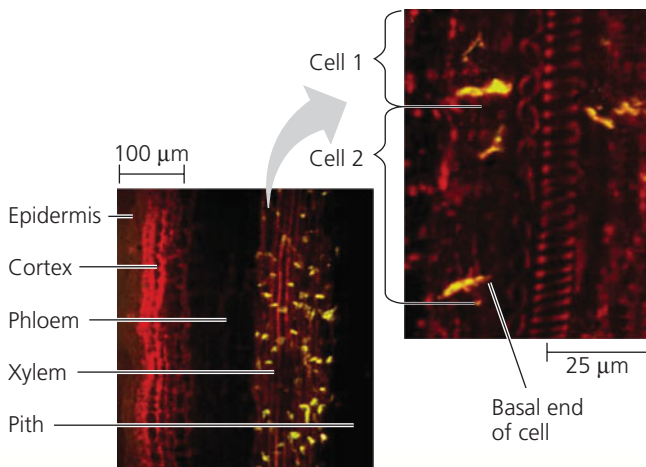
Table 31.1 Overview of Plant Hormones		
Hormone	Where Produced or Found in Plant	Major Functions
Auxin (IAA)	Shoot apical meristems and young leaves are the primary sites of auxin synthesis. Root apical meristems also produce auxin, although the root depends on the shoot for much of its auxin. Developing seeds and fruits contain high levels of auxin, but it is unclear whether it is newly synthesized or transported from maternal tissues.	Stimulates stem elongation (low concentration only); promotes the formation of lateral and adventitious roots; regulates development of fruit; enhances apical dominance; functions in phototropism and gravitropism; promotes vascular differentiation; retards leaf abscission.
Cytokinins	These are synthesized primarily in roots and transported to other organs, although there are many minor sites of production as well.	Regulate cell division in shoots and roots; modify apical dominance and promote lateral bud growth; promote movement of nutrients into sink tissues; stimulate seed germination; delay leaf senescence.
Gibberellins	Meristems of apical buds and roots, young leaves, and developing seeds are the primary sites of production.	Stimulate stem elongation, pollen development, pollen tube growth, fruit growth, and seed development and germination; regulate sex determination and the transition from juvenile to adult phases.
Brassinosteroids	These compounds are present in all plant tissues, although different intermediates predominate in different organs. Internally produced brassinosteroids act near the site of synthesis.	Promote cell expansion and cell division in shoots; promote root growth at low concentrations; inhibit root growth at high concentrations; promote xylem differentiation and inhibit phloem differentiation; promote seed germination and pollen tube elongation.
Abscisic acid (ABA)	Almost all plant cells have the ability to synthesize abscisic acid, and its presence has been detected in every major organ and living tissue; may be transported in the phloem or xylem.	Inhibits growth; promotes stomatal closure during drought stress; promotes seed dormancy and inhibits early germination; promotes leaf senescence; promotes desiccation tolerance.
Ethylene	This gaseous hormone can be produced by most parts of the plant. It is produced in high concentrations during senescence, leaf abscission, and the ripening of some types of fruit. Synthesis is also stimulated by wounding and stress.	Promotes ripening of many types of fruit, leaf abscission, and the triple response in seedlings (inhibition of stem elongation, promotion of lateral expansion, and horizontal growth); enhances the rate of senescence; promotes root and root hair formation; promotes flowering in the pineapple family.

## ▼ Figure 31.4 Inquiry

### What causes polar movement of auxin from shoot tip to base?

**Experiment** To investigate how auxin is transported unidirectionally, Leo Gälweiler and colleagues designed an experiment to identify the location of the auxin transport protein. They used a greenish yellow fluorescent molecule to label antibodies that bind to the auxin transport protein. Then they applied the antibodies to longitudinally sectioned *Arabidopsis* stems.

**Results** The light micrograph on the left shows that auxin transport proteins are not found in all stem tissues, but only in the xylem parenchyma. In the light micrograph on the right, a higher magnification reveals that these proteins are primarily localized at the basal ends of the cells.



**Conclusion** The results support the hypothesis that concentration of the auxin transport protein at the basal ends of cells mediates the polar transport of auxin.

**Source** L. Gälweiler et al., Regulation of polar auxin transport by At-PIN1 in *Arabidopsis* vascular tissue, *Science* 282:2226–2230 (1998).

**WHAT IF?** If auxin transport proteins were equally distributed at both ends of the cells, would polar auxin still be possible? Explain.

loosening the wall's fabric. Increasing the membrane potential enhances ion uptake into the cell, which causes osmotic uptake of water and increased turgor. Increased turgor and increased cell wall plasticity enable the cell to elongate.

Auxin also rapidly alters gene expression, causing cells in the region of elongation to produce new proteins within minutes. Some of these proteins are short-lived transcription factors that repress or activate the expression of other genes. For sustained growth after this initial spurt, cells must make more cytoplasm and wall material. Auxin also stimulates this sustained growth response.

**Auxin's Role in Plant Development** The polar transport of auxin is a central element controlling the spatial organization, or *pattern formation*, of the developing plant. Auxin is synthesized in shoot tips, and it carries integrated information about the development, size, and environment of individual branches. This flow of information controls branching patterns. A reduced flow of auxin from a branch, for example, indicates that the branch is not being sufficiently productive: New branches are needed elsewhere. Thus, lateral buds below the branch are released from dormancy and begin to grow.

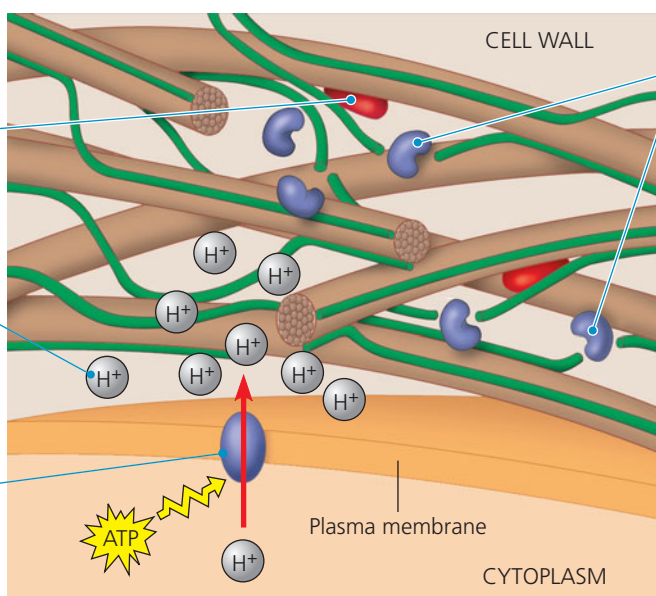
The transport of auxin also plays a key role in establishing *phyllotaxy* (see Figure 29.3), the arrangement of leaves on the stem. A leading model proposes that polar auxin transport in the shoot tip generates local peaks in auxin concentration that determine the site of leaf primordium formation and thereby the different phyllotaxies found in nature.

Auxin, cytokinins, and newly discovered plant hormones called strigolactones interact in the control of apical dominance, the ability of the apical bud to suppress the development of axillary buds. If the apical bud, the primary source of auxin, is removed, the inhibition of axillary buds is removed and the plant becomes bushier. Applying auxin to the cut

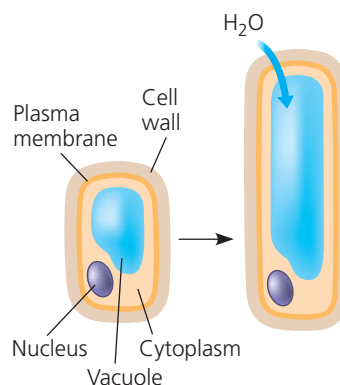
**3** Wedge-shaped expansins (red), activated by low pH, separate cellulose microfibrils (brown) from cross-linking polysaccharides (green). The exposed cross-linking polysaccharides are now more accessible to cell wall-loosening enzymes (purple).

**2** The cell wall becomes more acidic.

**1** Auxin increases the activity of proton pumps.



**4** Cell wall-loosening enzymes (purple) cleave cross-linking polysaccharides (green), allowing cellulose microfibrils to slide. The extensibility of the cell wall is increased. Turgor causes the cell to expand.



**5** With the cellulose loosened, the cell can elongate.

▲ Figure 31.5 Cell elongation in response to auxin: the acid growth hypothesis.

surface of the decapitated shoot resuppresses the growth of the lateral buds.

**Practical Uses for Auxins** Auxins, both natural and synthetic, have many commercial applications. For example, the natural auxin indolebutyric acid (IBA) is used in the vegetative propagation of plants by cuttings. (The formation of lateral roots in intact plants is one case where IBA seems to be a more important auxin than IAA.) Treating a detached leaf or stem with powder containing IBA often causes adventitious roots to form near the cut surface.

Certain synthetic auxins, including 2,4-dichlorophenoxyacetic acid (2,4-D), are widely used as herbicides. Monocots, such as maize and turfgrass, can rapidly inactivate such synthetic auxins. However, eudicots cannot and therefore die from hormonal overdose. Spraying cereal fields or turf with 2,4-D eliminates eudicot (broadleaf) weeds.

Developing seeds produce auxin, which promotes fruit growth. In tomato plants grown in greenhouses, often fewer seeds are produced, resulting in poorly developed tomato fruits. However, spraying synthetic auxins on greenhouse-grown tomato vines induces normal fruit development, making the greenhouse-cultivated tomatoes commercially viable.

## Cytokinins

Trial-and-error attempts to find chemical additives that would enhance the growth and development of plant cells in tissue culture led to the discovery of **cytokinins**. In the 1940s, researchers stimulated the growth of plant embryos in culture by adding coconut milk, the liquid endosperm of a coconut's giant seed. Subsequent researchers found that they could induce cultured tobacco cells to divide by adding degraded DNA samples. The active ingredients of both experimental additives turned out to be modified forms of adenine, a component of nucleic acids. These growth regulators were named cytokinins because they stimulate cytokinesis, or cell division. The most common natural cytokinin is zeatin, so named because it was discovered first in maize (*Zea mays*). The effects of cytokinins on cell division and differentiation, apical dominance, and aging are well documented.

**Control of Cell Division and Differentiation** Cytokinins are produced in actively growing tissues, particularly in roots, embryos, and fruits. Cytokinins produced in roots reach their target tissues by moving up the plant in the xylem sap. Acting in concert with auxin, cytokinins stimulate cell division and influence the pathway of differentiation. The effects of cytokinins on cells growing in tissue culture provide clues about how this class of hormones may function in an intact plant. When a piece of parenchyma tissue from a stem is cultured in the absence of cytokinins, the cells grow very large but do not divide. But if cytokinins are added along with auxin, the cells divide. Cytokinins alone have no effect. The ratio of cytokinins to auxin

controls cell differentiation. When the concentrations of these two hormones are at certain levels, the mass of cells continues to grow, but it remains a cluster of undifferentiated cells called a callus (see Figure 30.15). If cytokinin levels increase, shoot buds develop from the callus. If auxin levels increase, roots form.

**Anti-Aging Effects** Cytokinins slow the aging of certain plant organs by inhibiting protein breakdown, stimulating RNA and protein synthesis, and mobilizing nutrients from surrounding tissues. If leaves removed from a plant are dipped in a cytokinin solution, they stay green much longer than otherwise.

## Gibberellins

In the early 1900s, farmers in Asia noticed that some rice seedlings in their paddies grew so tall and spindly that they toppled over before they could mature. In 1926, it was discovered that a fungus of the genus *Gibberella* causes this “foolish seedling disease.” By the 1930s, it was determined that the fungus causes hyperelongation of rice stems by secreting a chemical, which was given the name **gibberellin**. In the 1950s, researchers determined that plants also produce gibberellins (GAs). Since that time, scientists have identified more than 100 different gibberellins that occur naturally in plants, although a much smaller number occur in each plant species. “Foolish rice” seedlings, it seems, suffer from too much gibberellin. Gibberellins have a variety of effects, such as stem elongation, fruit growth, and seed germination.

**Stem Elongation** The major sites of gibberellin production are young roots and leaves. Gibberellins are best known for stimulating stem and leaf growth by enhancing cell elongation *and* cell division. One hypothesis proposes that they activate enzymes that loosen cell walls, facilitating entry of expansin proteins. Thus, gibberellins act in concert with auxin to promote stem elongation.

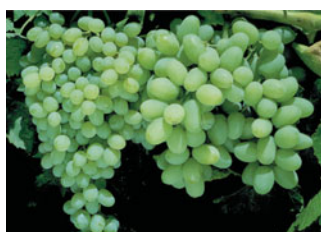
The effects of gibberellins in enhancing stem elongation are evident when certain dwarf (mutant) varieties of plants are treated with gibberellins. For instance, some dwarf pea plants grow tall if treated with gibberellins. But there is often no response if the gibberellins are applied to wild-type plants. Apparently, these plants already produce an optimal dose of the hormone. The most dramatic example of gibberellin-induced stem elongation is *bolting*, rapid growth of the floral stalk (**Figure 31.6a**).

**Fruit Growth** In many plants, both auxin and gibberellins must be present for fruit to develop. The most important commercial application of gibberellins is in the spraying of Thompson seedless grapes (**Figure 31.6b**). The hormone makes the individual grapes grow larger, a trait valued by the consumer. The gibberellin sprays also make the internodes of the grape bunch elongate, allowing more space for the individual grapes. By enhancing air circulation between the grapes, this increase in space also makes it harder for yeasts and other microorganisms to infect the fruit.





(a) Some plants develop in a rosette form, low to the ground with very short internodes, as in the *Arabidopsis* plant shown at the left. As the plant switches to reproductive growth, a surge of gibberellins induces bolting: Internodes elongate rapidly, elevating floral buds that develop at stem tips (right).



(b) The Thompson seedless grape bunch on the left is from an untreated control vine. The bunch on the right is growing from a vine that was sprayed with gibberellin during fruit development.

▲ **Figure 31.6** Effects of gibberellins on stem elongation and fruit growth.

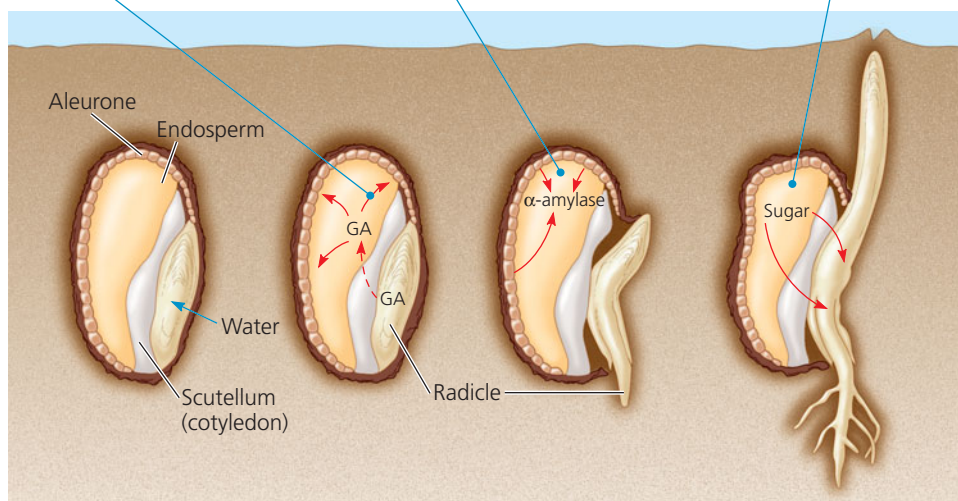
**Germination** The embryo of a seed is a rich source of gibberellins. After water is imbibed, the release of gibberellins from the embryo signals the seed to break dormancy and germinate. Some seeds that normally require particular environmental conditions to germinate, such as exposure to light or low temperatures, break dormancy if they are treated with gibberellins. Gibberellins support the growth of cereal seedlings by stimulating the synthesis of digestive enzymes such as  $\alpha$ -amylase that mobilize stored nutrients (**Figure 31.7**).

► **Figure 31.7** Mobilization of nutrients by gibberellins during the germination of grain seeds such as barley.

1 After a seed imbibes water, the embryo releases gibberellin (GA), which sends a signal to the aleurone, the thin outer layer of the endosperm.

2 The aleurone responds to GA by synthesizing and secreting digestive enzymes that hydrolyze nutrients stored in the endosperm. One example is  $\alpha$ -amylase, which hydrolyzes starch.

3 Sugars and other nutrients absorbed from the endosperm by the scutellum (cotyledon) are consumed during growth of the embryo into a seedling.



## Brassinosteroids

**Brassinosteroids** are steroids similar to cholesterol and the sex hormones of animals. They induce cell elongation and division in stem segments and seedlings at concentrations as low as  $10^{-12}$  M. They also slow leaf abscission (leaf drop) and promote xylem differentiation. These effects are so qualitatively similar to those of auxin that it took years for plant physiologists to determine that brassinosteroids were not types of auxins.

The identification of brassinosteroids as plant hormones arose from studies of an *Arabidopsis* mutant that exhibited morphological features similar to those of light-grown plants even when grown in the dark. The researchers discovered that the mutation affects a gene that normally codes for an enzyme similar to one involved in steroid synthesis in mammals. They also found that this brassinosteroid-deficient mutant could be restored to the wild-type phenotype by applying brassinosteroids.

## Abscisic Acid

In the 1960s, one research group studying the chemical changes that precede bud dormancy and leaf abscission in deciduous trees and another team investigating chemical changes preceding abscission of cotton fruits isolated the same compound, **abscisic acid (ABA)**. Ironically, ABA is no longer thought to play a primary role in bud dormancy or leaf abscission, but it is very important in other functions. Unlike the growth-stimulating hormones we have discussed so far—auxin, cytokinins, gibberellins, and brassinosteroids—ABA *slows* growth. ABA often antagonizes the actions of growth hormones, and the ratio of ABA to one or more growth hormones determines the

final physiological outcome. We will consider here two of ABA's many effects: seed dormancy and drought tolerance.

**Seed Dormancy** Seed dormancy increases the likelihood that seeds will germinate only when there are sufficient amounts of light, temperature, and moisture for the seedlings to survive (see Chapter 30). What prevents seeds dispersed in autumn from germinating immediately, only to die in winter? What mechanisms ensure that such seeds do not germinate until spring? For that matter, what prevents seeds from germinating in the dark, moist interior of the fruit? The answer to these questions is ABA. The levels of ABA may increase 100-fold during seed maturation. The high levels of ABA in maturing seeds inhibit germination and induce the production of proteins that help the seeds withstand the extreme dehydration that accompanies maturation.

Many types of dormant seeds germinate when ABA is removed or inactivated. The seeds of some desert plants break dormancy only when heavy rains wash ABA out of them. Other seeds require light or prolonged exposure to cold to inactivate ABA. Often, the ratio of ABA to gibberellins determines whether seeds remain dormant or germinate, and adding ABA to seeds that are primed to germinate makes them dormant again. Low levels of ABA or ABA sensitivity can lead to precocious (early) germination (**Figure 31.8**). Precocious germination of red mangrove seeds, due to low ABA levels, is actually an adaptation that helps the young seedlings to plant themselves like darts in the soft mud below the parent tree.

**Drought Tolerance** ABA plays a major role in drought signaling. When a plant begins to wilt, ABA accumulates in the leaves and causes stomata to close rapidly, reducing transpiration and preventing further water loss. By affecting second messengers such as calcium, ABA causes potassium channels in the plasma membrane of guard cells to open, leading to a massive loss of potassium ions from the cells. The accompanying osmotic loss of water reduces guard cell turgor and leads to closing of the stomatal pores (see Figure 29.19). In some cases, water shortage stresses the root system before the shoot system, and ABA transported from roots to leaves may function as an “early warning system.”

## Ethylene

During the 1800s, when coal gas was used as fuel for streetlights, leakage from gas pipes caused nearby trees to drop leaves prematurely. In 1901, the gas **ethylene** was demonstrated to be the active factor in coal gas. But the idea that it is a plant hormone was not widely accepted until the advent of a technique called gas chromatography simplified its identification.

Plants produce ethylene in response to stresses such as drought, flooding, mechanical pressure, injury, and infection. Ethylene is also produced during fruit ripening and programmed cell death and in response to high concentrations



◀ Red mangrove (*Rhizophora mangle*) seeds produce only low levels of ABA, and their seeds germinate while still on the tree. In this case, early germination is a useful adaptation. When released, the radicle of the dart-like seedling deeply penetrates the soft mudflats in which the mangroves grow.



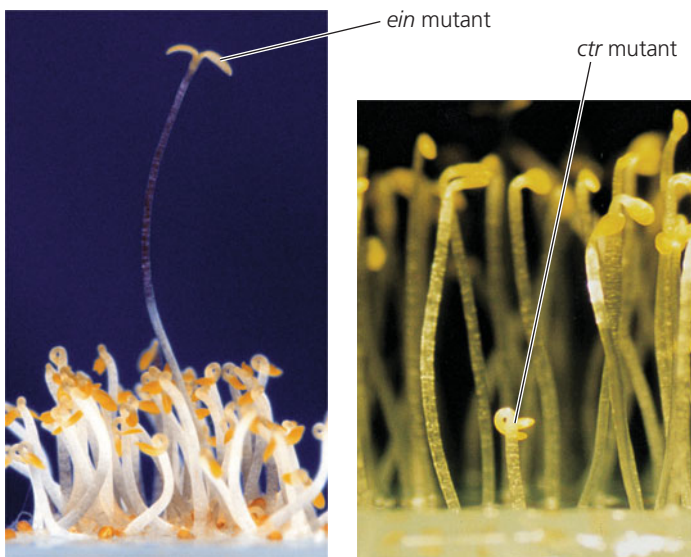
▲ Precocious germination in this maize mutant is caused by lack of a functional transcription factor required for ABA action.

▲ **Figure 31.8** Precocious germination of wild-type mangrove and mutant maize seeds.

of externally applied auxin. Indeed, many effects previously ascribed to auxin, such as inhibition of root elongation, may be due to auxin-induced ethylene production. We will focus here on four of ethylene's many effects: response to mechanical stress, senescence, leaf abscission, and fruit ripening.

**The Triple Response to Mechanical Stress** Imagine a pea seedling pushing upward through the soil, only to come up against a stone. As it pushes against the obstacle, the stress in its delicate tip induces the seedling to produce ethylene. The hormone then instigates a growth maneuver known as the **triple response** that enables the shoot to avoid the obstacle. The three parts of this response are a slowing of stem elongation, a thickening of the stem (which makes it stronger), and a curvature that causes the stem to start growing horizontally. As the effects of the initial ethylene pulse lessen, the stem resumes vertical growth. If it again contacts a barrier, another burst of ethylene is released, and horizontal growth resumes. However, if the upward touch detects no solid object, then ethylene production decreases, and the stem, now clear of the obstacle, resumes its normal upward growth. It is ethylene that induces the stem to grow horizontally rather than the physical obstruction itself; when ethylene is applied to normal seedlings growing free of physical impediments, they still undergo the triple response.





(a) ***ein* mutant.** An ethylene-insensitive (*ein*) mutant fails to undergo the triple response in the presence of ethylene. (b) ***ctr* mutant.** A constitutive triple-response (*ctr*) mutant undergoes the triple response even in the absence of ethylene.

▲ **Figure 31.9 Ethylene triple-response *Arabidopsis* mutants.**

Studies of *Arabidopsis* mutants with abnormal triple responses are an example of how biologists identify a signal transduction pathway. Scientists isolated ethylene-insensitive (*ein*) mutants, which fail to undergo the triple response after exposure to ethylene (Figure 31.9a). Some types of *ein* mutants are insensitive to ethylene because they lack a functional ethylene receptor. Mutants of a different sort undergo the triple response even out of soil, in the air, where there are no physical obstacles. Some of these mutants have a regulatory defect that causes them to produce ethylene at rates 20 times normal. The phenotype of such ethylene-overproducing (*eto*) mutants can be restored to wild-type by treating the seedlings with inhibitors of ethylene synthesis. Other mutants, called constitutive triple-response (*ctr*) mutants, undergo the triple response in air but do not respond to inhibitors of ethylene synthesis (Figure 31.9b). (Constitutive genes are genes that are continually expressed in all cells of an organism.) In *ctr* mutants, ethylene signal transduction is permanently turned on, even though ethylene is not present.

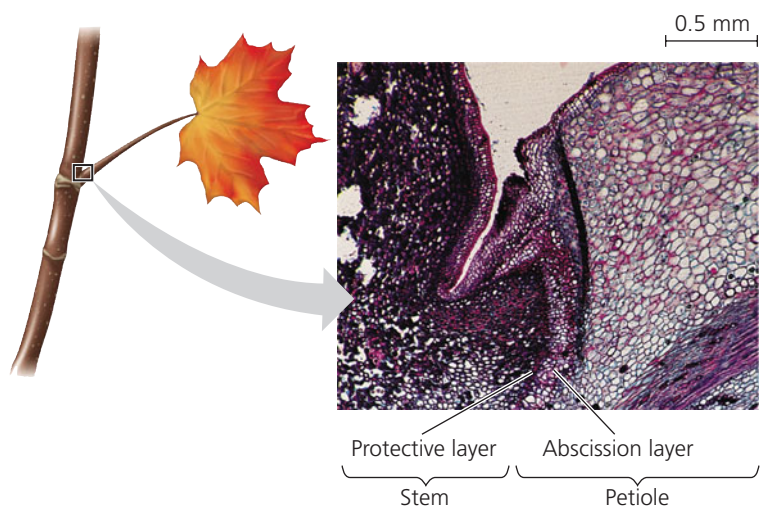
The affected gene in *ctr* mutants codes for a protein kinase. The fact that this mutation *activates* the ethylene response suggests that the normal kinase product of the wild-type allele is a *negative* regulator of ethylene signal transduction. Thus, binding of the hormone ethylene to the ethylene receptor normally leads to inactivation of the kinase; and the inactivation of this negative regulator allows synthesis of the proteins required for the triple response.

**Senescence** Consider the shedding of a leaf in autumn or the death of an annual after flowering. Or think about the final step in differentiation of a vessel element, when its living contents

are destroyed, leaving a hollow tube behind. Such events involve **senescence**—the programmed death of certain cells or organs or the entire plant. Cells, organs, and plants genetically programmed to die on a schedule do not simply shut down cellular machinery and await death. Instead, at the molecular level, the onset of the programmed cell death called *apoptosis* is a very busy time in a cell's life, requiring new gene expression. During apoptosis, newly formed enzymes break down many chemical components, including chlorophyll, DNA, RNA, proteins, and membrane lipids. The plant salvages many of the breakdown products. A burst of ethylene is almost always associated with the apoptosis of cells during senescence.

**Leaf Abscission** The loss of leaves from deciduous trees helps prevent desiccation during seasonal periods when the availability of water to the roots is severely limited. Before dying leaves abscise, many essential elements are salvaged from them and stored in stem parenchyma cells. These nutrients are recycled back to developing leaves the following spring. Autumn leaf color is due to newly made red pigments as well as yellow and orange carotenoids (see Concept 8.2) that were already present in the leaf and are rendered visible by the breakdown of the dark green chlorophyll in autumn.

When an autumn leaf falls, it detaches from the stem at an abscission layer that develops near the base of the petiole (Figure 31.10). The small parenchyma cells of this layer have very thin walls, and there are no fiber cells around the vascular tissue. The abscission layer is further weakened when enzymes hydrolyze polysaccharides in the cell walls. Finally, the weight of the leaf, with the help of the wind, causes a separation within the abscission layer. Even before the leaf falls, a layer of cork forms a protective scar on the twig side of the abscission layer, preventing pathogens from invading the plant.



▲ **Figure 31.10 Abscission of a maple leaf.** Abscission is controlled by a change in the ratio of ethylene to auxin. The abscission layer is seen in this longitudinal section as a vertical band at the base of the petiole. After the leaf falls, a protective layer of cork becomes the leaf scar that helps prevent pathogens from invading the plant (LM).



A change in the ratio of ethylene to auxin controls abscission. An aging leaf produces less and less auxin, rendering the cells of the abscission layer more sensitive to ethylene. As the influence of ethylene on the abscission layer prevails, the cells produce enzymes that digest the cellulose and other components of cell walls.

**Fruit Ripening** Immature fleshy fruits are generally tart, hard, and green—features that help protect the developing seeds from herbivores. After ripening, the mature fruits help *attract* animals that disperse the seeds (see Figure 30.12). In many cases, a burst of ethylene production in the fruit triggers the ripening process. The enzymatic breakdown of cell wall components softens the fruit, and the conversion of starches and acids to sugars makes the fruit sweet. The production of new scents and colors helps advertise ripeness to animals, which eat the fruits and disperse the seeds.

A chain reaction occurs during ripening: Ethylene triggers ripening, and ripening triggers more ethylene production. The result is a huge burst in ethylene production. Because ethylene is a gas, the signal to ripen spreads from fruit to fruit. If you pick or buy green fruit, you may be able to speed ripening by storing the fruit in a paper bag, allowing ethylene to accumulate. On a commercial scale, many kinds of fruits are ripened in huge storage containers in which ethylene levels are enhanced. In other cases, fruit producers take measures to slow ripening caused by natural ethylene. Apples, for instance, are stored in bins flushed with carbon dioxide. Circulating the air prevents ethylene from accumulating, and carbon dioxide inhibits synthesis of new ethylene. Stored in this way, apples picked in autumn can still be shipped to grocery stores the following summer.

#### CONCEPT CHECK 31.1

1. Fusicoccin is a fungal toxin that stimulates the plasma membrane  $H^+$  pumps of plant cells. How would it affect the growth of isolated stem sections?
2. **WHAT IF?** If a plant has the double mutation *ctr* and *ein*, what is its triple-response phenotype? Explain your answer.
3. **MAKE CONNECTIONS** What type of feedback process is exemplified by the production of ethylene during fruit ripening? Explain. (See Concept 32.2.)

For suggested answers, see Appendix A.

## CONCEPT 31.2

### Responses to light are critical for plant success

Light is an especially important environmental factor in the lives of plants. In addition to being required for photosynthesis, light triggers many key events in plant growth and development, collectively known as **photomorphogenesis**. Light reception also allows plants to measure the passage of days and seasons.

### Photomorphogenesis

As an example of photomorphogenesis, consider a sprouting potato (**Figure 31.11a**). This modified underground stem, or tuber, has sprouted shoots from its “eyes” (axillary buds). These shoots, however, scarcely resemble those of a typical plant. Instead of sturdy stems and broad green leaves, this plant has ghostly pale stems and unexpanded leaves, as well as short, stubby roots. These morphological adaptations for growing in darkness, collectively referred to as **etiolation**, make sense if we consider that a young potato plant in nature usually encounters continuous darkness when sprouting underground. Under these circumstances, expanded leaves would be a hindrance to soil penetration and would be damaged as the shoots pushed through the soil. Because the leaves are unexpanded and underground, there is little evaporative loss of water and little requirement for an extensive root system to replace the water lost by transpiration. Moreover, the energy expended in producing green chlorophyll would be wasted because there is no light for photosynthesis. Instead, a potato plant growing in the dark allocates as much energy as possible to elongating its stems. This adaptation enables the shoots to break ground before the nutrient reserves in the tuber are exhausted.

When a shoot reaches light, the plant undergoes profound changes, collectively called **de-etiolation** (informally known as greening). Stem elongation slows; leaves expand; roots elongate; and the shoot produces chlorophyll. In short, it begins to resemble a typical plant (**Figure 31.11b**). How do light signals initiate this remarkable change in form? As in all signal transduction processes, the signal must first be detected by a receptor protein.

Plants detect not only the presence of light signals but also their direction, intensity, and wavelength (color). A graph called an **action spectrum** depicts the relative effectiveness

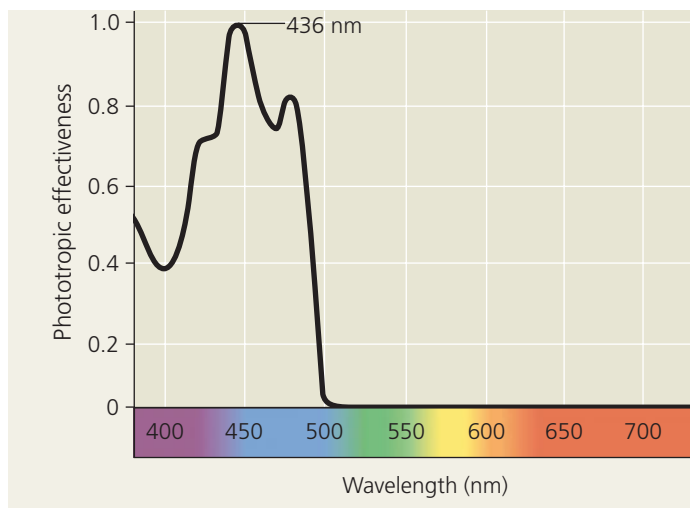


**(a) Before exposure to light.** A dark-grown potato has tall, spindly stems and nonexpanded leaves—morphological adaptations that enable the shoots to penetrate the soil. The roots are short, but there is little need for water absorption because little water is lost by the shoots.

**(b) After a week's exposure to natural daylight.** The potato plant begins to resemble a typical plant with broad green leaves, short sturdy stems, and long roots. This transformation begins with the reception of light by a specific pigment, phytochrome.

▲ **Figure 31.11** Light-induced de-etiolation (greening) of dark-grown potatoes.

of different wavelengths of radiation in driving a particular process, such as photosynthesis (see Figure 8.9b). Action spectra are useful in studying *any* process that depends on light, including phototropism (**Figure 31.12**). By comparing action spectra of various plant responses, researchers determine which responses are mediated by the same photoreceptor (pigment). They also compare action spectra with absorption spectra of pigments; a close correspondence for a given pigment suggests that the pigment is the photoreceptor mediating the response. In the case of photomorphogenesis, action spectra reveal that red and blue light are the most important colors. In



(a) This action spectrum illustrates that only light wavelengths below 500 nm (blue and violet light) induce curvature.



(b) When coleoptiles are exposed to light of various wavelengths as shown here, violet light induces slight curvature toward the light and blue light induces the most curvature. The other colors do not induce any curvature.

▲ **Figure 31.12** Action spectrum for blue-light-stimulated phototropism in maize coleoptiles. Phototropic bending toward light is controlled by phototropin, a photoreceptor sensitive to blue and violet light, particularly blue light.

fact, there are two major classes of photoreceptors in plants: **blue-light photoreceptors** and **phytochromes**, photoreceptors that absorb mostly red light.

### Blue-Light Photoreceptors

Blue light initiates a variety of responses in plants, including phototropism, the light-induced opening of stomata (see Figure 29.19), and the light-induced slowing of hypocotyl elongation that occurs when a seedling breaks ground. The biochemical identity of the blue-light photoreceptor was so elusive that in the 1970s, plant physiologists began to call this receptor “cryptochrome” (from the Greek *kryptos*, hidden, and *chrom*, pigment). In the 1990s, molecular biologists analyzing *Arabidopsis* mutants found that plants use different types of pigments to detect blue light. *Cryptochromes*, molecular relatives of DNA repair enzymes, are involved in the blue-light-induced inhibition of stem elongation that occurs, for example, when a seedling first emerges from the soil. *Phototropin* is a protein kinase involved in mediating blue-light-mediated stomatal opening, chloroplast movements in response to light, and phototropic curvatures, such as those studied by the Darwins.

### Phytochrome Photoreceptors

Phytochromes, another class of photoreceptors, regulate many plant responses to light, including seed germination and shade avoidance.

**Phytochromes and Seed Germination** Studies of seed germination led to the discovery of phytochromes. Because of limited nutrient reserves, many types of seeds, especially small ones, germinate only when the light environment and other conditions are near optimal. Such seeds often remain dormant for years until light conditions change. For example, the death of a shading tree or the plowing of a field may create a favorable light environment.

In the 1930s, scientists determined the action spectrum for light-induced germination of lettuce seeds. They exposed water-swollen seeds to a few minutes of single-colored light of various wavelengths and then stored the seeds in the dark. After two days, the researchers counted the number of seeds that had germinated under each light regimen. They found that red light of wavelength 660 nm increased the germination percentage of lettuce seeds maximally, whereas far-red light—that is, light of wavelengths near the upper edge of human visibility (730 nm)—*inhibited* germination compared with dark controls (**Figure 31.13**). What happens when the lettuce seeds are subjected to a flash of red light followed by a flash of far-red light or, conversely, to far-red light followed by red light? The *last* flash of light determines the seeds’ response: The effects of red and far-red light are reversible.

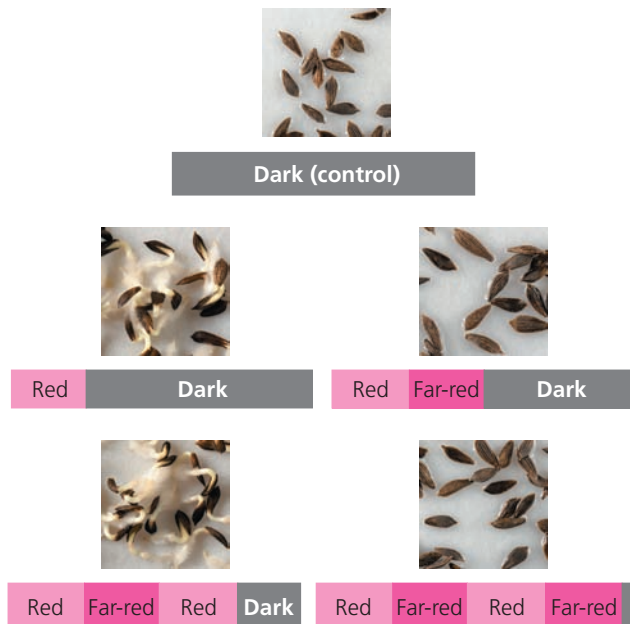
The photoreceptors responsible for the opposing effects of red and far-red light are phytochromes. So far, researchers have identified five phytochromes in *Arabidopsis*, each with a slightly

## ▼ Figure 31.13 Inquiry

### How does the order of red and far-red illumination affect seed germination?

**Experiment** Scientists at the U.S. Department of Agriculture briefly exposed batches of lettuce seeds to red light or far-red light to test the effects on germination. After the light exposure, the seeds were placed in the dark, and the results were compared with control seeds that were not exposed to light.

**Results** The bar below each photo indicates the sequence of red light exposure, far-red light exposure, and darkness. The germination rate increased greatly in groups of seeds that were last exposed to red light (left). Germination was inhibited in groups of seeds that were last exposed to far-red light (right).

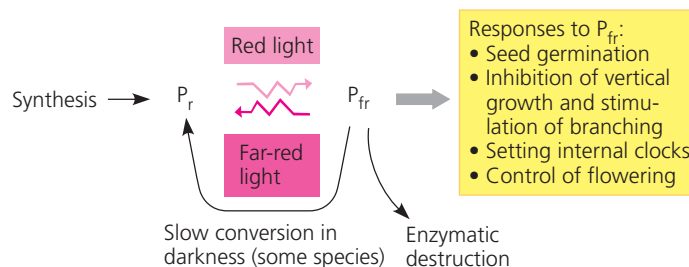


**Conclusion** Red light stimulates germination, and far-red light inhibits germination. The final light exposure is the determining factor. The effects of red and far-red light are reversible.

**Source** H. Borthwick et al., A reversible photoreaction controlling seed germination, *Proceedings of the National Academy of Sciences, USA* 38:662–666 (1952).

**WHAT IF?** Phytochrome responds faster to red light than to far-red light. If the seeds had been placed in white light instead of the dark after their red and far-red light treatments, would the results have been different? Explain.

different polypeptide component. In most phytochromes, the light-absorbing portion is photoreversible, converting back and forth between two forms, depending on the color of light it is exposed to. In its  $P_r$  form, a phytochrome absorbs red (r) light maximally and is converted to the  $P_{fr}$  form; in its  $P_{fr}$  form, it absorbs far-red (fr) light and is converted to its  $P_r$  form (Figure 31.14). This  $P_r \leftrightarrow P_{fr}$  interconversion is a switching mechanism that controls various light-induced events in the life of the plant.  $P_{fr}$  is the form of phytochrome that triggers many of a plant's developmental responses to light. For example,  $P_r$  in lettuce seeds exposed to red light is converted to  $P_{fr}$ ,



▲ **Figure 31.14 Phytochrome: a molecular switching mechanism.** Absorption of red light causes  $P_r$  to change to  $P_{fr}$ . Far-red light reverses this conversion.

stimulating the cellular responses that lead to germination. When red-illuminated seeds are then exposed to far-red light,  $P_{fr}$  is converted back to  $P_r$ , inhibiting the germination response.

How does phytochrome switching explain light-induced germination in nature? Plants synthesize phytochrome as  $P_r$ , and if seeds are kept in the dark, the pigment remains almost entirely in the  $P_r$  form (see Figure 31.14). Sunlight contains both red light and far-red light, but the conversion to  $P_{fr}$  is faster than the conversion to  $P_r$ . Therefore, the ratio of  $P_{fr}$  to  $P_r$  increases in sunlight. When seeds are exposed to adequate sunlight, the production and accumulation of  $P_{fr}$  will trigger their germination.

**Phytochromes and Shade Avoidance** The phytochrome system also provides the plant with information about the *quality* of light. Because sunlight includes both red and far-red radiation, during the day the  $P_r \leftrightarrow P_{fr}$  interconversion reaches a dynamic equilibrium, with the ratio of the two phytochrome forms indicating the relative amounts of red and far-red light. This sensing mechanism enables plants to adapt to changes in light conditions. Consider, for example, the “shade avoidance” response of a tree that requires relatively high light intensity. If other trees in a forest shade this tree, the phytochrome ratio shifts in favor of  $P_r$  because the forest canopy screens out more red light than far-red light. This is because the chlorophyll pigments in the leaves of the canopy absorb red light and allow far-red light to pass through. The shift in the ratio of red to far-red light induces the tree to allocate more of its resources to growing taller. In contrast, direct sunlight increases the proportion of  $P_{fr}$ , which stimulates branching and inhibits vertical growth.

In addition to helping plants detect light, phytochrome helps a plant keep track of the passage of days and seasons. To understand phytochrome's role in these timekeeping processes, we must first examine the nature of the plant's internal clock.

## Biological Clocks and Circadian Rhythms

Many plant processes, such as transpiration and the synthesis of certain enzymes, undergo a daily oscillation. Some of these cyclic variations are responses to the changes in light levels and temperature that accompany the 24-hour cycle of day and night. We can control these external factors by growing plants





▲ **Figure 31.15** Sleep movements of a bean plant (*Phaseolus vulgaris*). The movements are caused by reversible changes in the turgor pressure of cells on opposing sides of the pulvini, motor organs of the leaf.

in growth chambers under rigidly maintained conditions of light and temperature. But even under artificially constant conditions, many physiological processes in plants, such as the opening and closing of stomata and the production of photosynthetic enzymes, continue to oscillate with a frequency of about 24 hours. For example, many legumes lower their leaves in the evening and raise them in the morning (**Figure 31.15**). A bean plant continues these “sleep movements” even if kept in constant light or constant darkness; the leaves are not simply responding to sunrise and sunset. Such cycles, with a frequency of about 24 hours and not directly controlled by any known environmental variable, are called **circadian rhythms** (from the Latin *circa*, approximately, and *dies*, day).

Recent research supports the idea that the molecular “gears” of the circadian clock really are internal and not a daily response to some subtle but pervasive environmental cycle, such as geomagnetism or cosmic radiation. Organisms, including plants and people, continue their rhythms even after being placed in deep mine shafts or orbiting in spacecraft, conditions that alter these subtle geophysical periodicities. However, daily signals from the environment can entrain (set) the circadian clock to a period of precisely 24 hours.

If an organism is kept in a constant environment, its circadian rhythms deviate from a 24-hour period (a period is the duration of one cycle). These free-running periods, as they are called, vary from about 21 to 27 hours, depending on the particular rhythmic response. The sleep movements of bean plants, for instance, have a period of 26 hours when the plants are kept in the free-running condition of constant darkness. Deviation of the free-running period from exactly 24 hours does not mean that biological clocks drift erratically. Free-running clocks are still keeping perfect time, but they are not synchronized with the outside world. To understand the mechanisms underlying circadian rhythms, we must distinguish between the clock and the rhythmic processes it controls. For example, the leaves of the bean plant in Figure 31.15 are the clock’s “hands” but are not the essence of the clock itself. If bean leaves are restrained for several hours and then

released, they will reestablish the position appropriate for the time of day. We can interfere with a biological rhythm, but the underlying clockwork continues to tick.

At the heart of the molecular mechanisms underlying circadian rhythms are oscillations in the transcription of certain genes. Mathematical models propose that the 24-hour period arises from negative-feedback loops involving the transcription of a few central “clock genes.” Some clock genes may encode transcription factors that inhibit, after a time delay, the transcription of the gene that encodes the transcription factor itself. Such negative-feedback loops, together with a time delay, are enough to produce oscillations.

### The Effect of Light on the Biological Clock

As we have discussed, the free-running period of the circadian rhythm of bean leaf movements is 26 hours. Consider a bean plant placed at dawn in a dark cabinet for 72 hours: Its leaves would not rise again until 2 hours after natural dawn on the second day, 4 hours after natural dawn on the third day, and so on. Shut off from environmental cues, the plant becomes desynchronized. Desynchronization happens to humans when we fly across time zones; when we reach our destination, the clocks on the wall are not synchronized with our internal clocks. Most organisms are probably prone to jet lag.

The factor that entrains the biological clock to precisely 24 hours every day is light. Both phytochromes and blue-light photoreceptors can entrain circadian rhythms in plants, but our understanding of how phytochromes do this is more complete. The mechanism involves turning cellular responses on and off by means of the  $P_r \leftrightarrow P_{fr}$  switch.

Consider again the photoreversible system in Figure 31.14. In darkness, the phytochrome ratio shifts gradually in favor of the  $P_r$  form, partly as a result of turnover in the overall phytochrome pool. The pigment is synthesized in the  $P_r$  form, and enzymes destroy more  $P_{fr}$  than  $P_r$ . In some plant species,  $P_{fr}$  present at sundown slowly converts to  $P_r$ . In darkness, there is no means for the  $P_r$  to be reconverted to  $P_{fr}$ , but upon illumination, the  $P_{fr}$  level suddenly increases again as  $P_r$  is rapidly converted. This increase in  $P_{fr}$  each day at dawn resets the biological clock: Bean leaves reach their most extreme night position 16 hours after dawn.

In nature, interactions between phytochrome and the biological clock enable plants to measure the passage of night and day. The relative lengths of night and day, however, change over the course of the year (except at the equator). Plants use this change to adjust their activities in synchrony with the seasons.

### Photoperiodism and Responses to Seasons

Imagine the consequences if a plant produced flowers when pollinators were not present or if a deciduous tree produced leaves in the middle of winter. Seasonal events are of critical importance in the life cycles of most plants. Seed germination, flowering, and the onset and breaking of bud dormancy are

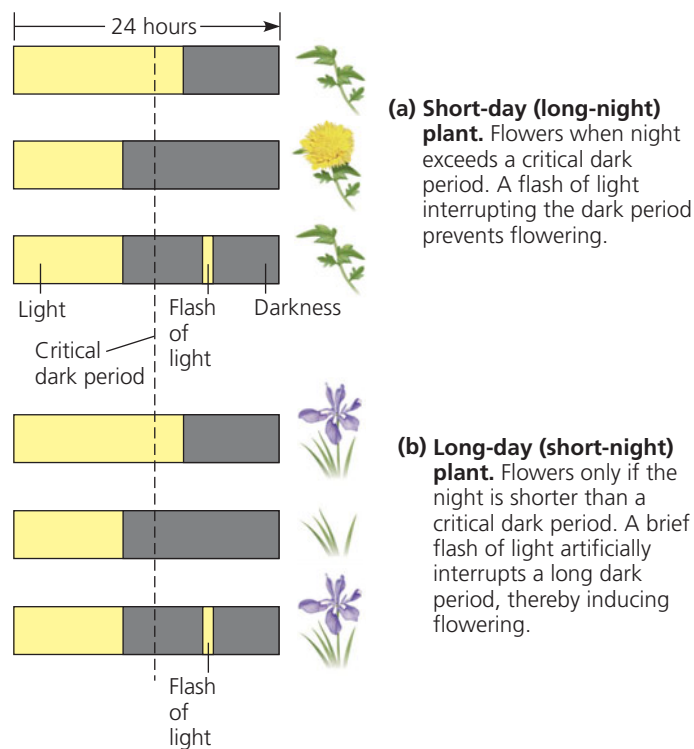
all stages that usually occur at specific times of the year. The environmental stimulus that plants use most often to detect the time of year is the photoperiod, the relative lengths of night and day. A physiological response to photoperiod, such as flowering, is called **photoperiodism**.

### Photoperiodism and Control of Flowering

An early clue to how plants detect seasons came from a mutant variety of tobacco, Maryland Mammoth, that grew tall but failed to flower during summer. It finally bloomed in a greenhouse in December. Researchers determined that the shortening days of winter stimulated this variety to flower. If the plants were kept in light-tight boxes so that lamps could manipulate “day” and “night,” flowering occurred only if the day length was 14 hours or shorter. It did not flower during summer because at Maryland’s latitude, the summer days were too long.

The researchers called Maryland Mammoth a **short-day plant** because it apparently required a light period *shorter* than a critical length to flower. Chrysanthemums, poinsettias, and some soybean varieties are also short-day plants, which generally flower in late summer, fall, or winter. Another group of plants flower only when the light period is *longer* than a certain number of hours. These **long-day plants** generally flower in late spring or early summer. Spinach, for example, flowers when days are 14 hours or longer. Radishes, lettuce, irises, and many cereal varieties are also long-day plants. **Day-neutral plants**, such as tomatoes, rice, and dandelions, are unaffected by photoperiod and flower when they reach a certain stage of maturity, regardless of day length.

**Critical Night Length** In the 1940s, researchers learned that flowering and other responses to photoperiod are actually controlled by night length, not day length. Many of these scientists worked with cocklebur (*Xanthium strumarium*), a short-day plant that flowers only when days are 16 hours or shorter (and nights are at least 8 hours long). These researchers found that if the light portion of the photoperiod is broken by a brief exposure to darkness, flowering proceeds. However, if the dark part of the photoperiod is interrupted by even a few minutes of dim light, cocklebur will not flower, and this turned out to be true for other short-day plants as well (**Figure 31.16a**). Cocklebur is unresponsive to day length, but it requires at least 8 hours of continuous darkness to flower. Short-day plants are really long-night plants, but the older term is embedded firmly in the lexicon of plant physiology. Similarly, long-day plants are actually short-night plants. A long-day plant grown on photoperiods of long nights that would not normally induce flowering will flower if the period of continuous darkness is interrupted by a few minutes of light (**Figure 31.16b**). Notice that we distinguish long-day from short-day plants *not* by an absolute night length but by whether the critical night length sets a maximum (long-day plants) or minimum (short-day plants) number of hours of darkness required for flowering. In both cases, the



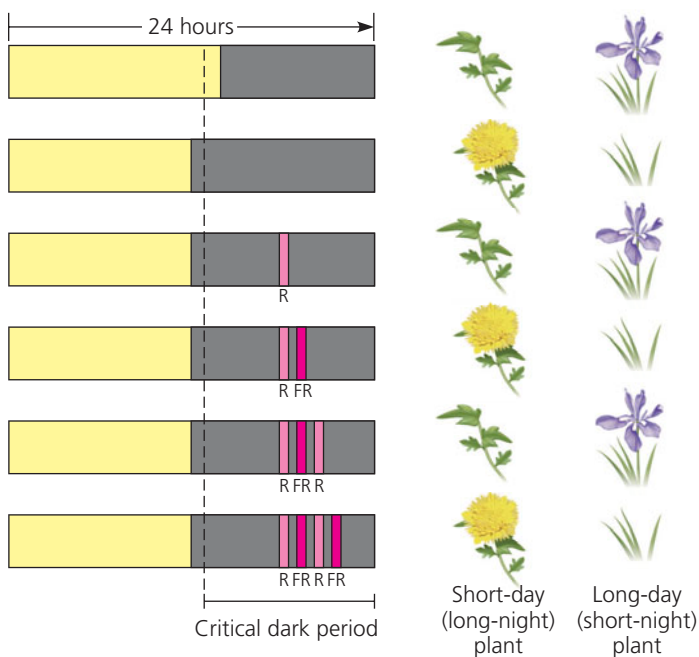
▲ **Figure 31.16** Photoperiodic control of flowering.

actual number of hours in the critical night length is specific to each species of plant.

Red light is the most effective color in interrupting the nighttime portion of the photoperiod. Action spectra and photoreversibility experiments show that phytochrome is the pigment that detects the red light (**Figure 31.17**). For example, if a flash of red (R) light during the dark period is followed by a flash of far-red (FR) light, then the plant detects no interruption of night length. As in the case of phytochrome-mediated seed germination, red/far-red photoreversibility occurs.

Plants detect night length very precisely; some short-day plants will not flower if night is even 1 minute shorter than the critical length. Some plant species always flower on the same day each year. It appears that plants use their biological clock, entrained by night length with the help of phytochrome, to tell the season of the year. The floriculture (flower-growing) industry applies this knowledge to produce flowers out of season. Chrysanthemums, for instance, are short-day plants that normally bloom in fall, but their blooming can be stalled until Mother’s Day in May by punctuating each long night with a flash of light, thus turning one long night into two short nights.

Some plants bloom after a single exposure to the photoperiod required for flowering. Other species need several successive days of the appropriate photoperiod. Still others respond to a photoperiod only if they have been previously exposed to some other environmental stimulus, such as a period of cold. Winter wheat, for example, will not flower unless it has been exposed to several weeks of temperatures below 10°C. The use of pretreatment with cold to induce flowering is called



▲ **Figure 31.17 Reversible effects of red and far-red light on photoperiodic response.** A flash of red (R) light shortens the dark period. A subsequent flash of far-red (FR) light cancels the red flash's effect.

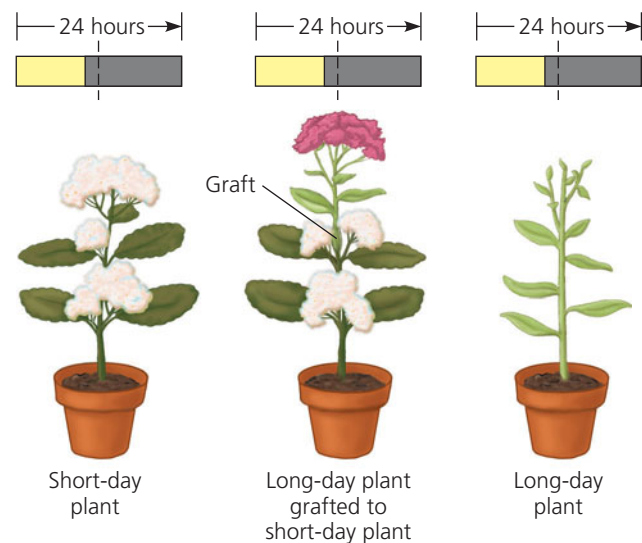
? How would a single flash of full-spectrum light affect each plant?

**vernalization** (from the Latin for “spring”). Several weeks after winter wheat is vernalized, a photoperiod with long days (short nights) induces flowering.

### A Flowering Hormone?

Although flowers form from apical or axillary bud meristems, it is leaves that detect changes in photoperiod and produce signaling molecules that cue buds to develop as flowers. In many short-day and long-day plants, exposing just one leaf to the appropriate photoperiod is enough to induce flowering. Indeed, as long as one leaf is left on the plant, photoperiod is detected and floral buds are induced. If all leaves are removed, the plant is insensitive to photoperiod.

Classic experiments revealed that the floral stimulus could move across a graft from an induced plant to a noninduced plant and trigger flowering in the latter. Moreover, the flowering stimulus appears to be the same for short-day and long-day plants, despite the different photoperiodic conditions required for leaves to send this signal (**Figure 31.18**). The hypothetical signaling molecule for flowering, called **florigen**, remained unidentified for over 70 years as scientists focused on small hormone-like molecules. However, large macromolecules, such as mRNA and proteins, can move by the symplastic route via plasmodesmata and regulate plant development. It now appears that florigen is a protein. A gene called *FLOWERING LOCUS T (FT)* is activated in leaf cells during conditions favoring flowering, and the FT protein travels through the



▲ **Figure 31.18 Experimental evidence for a flowering hormone.** If grown individually under short-day conditions, a short-day plant will flower and a long-day plant will not. However, both will flower if grafted together and exposed to short days. This result indicates that a flower-inducing substance (florigen) is transmitted across grafts and induces flowering in both short-day and long-day plants.

**WHAT IF?** If flowering were inhibited in both parts of the grafted plants, what would you conclude?

sympasm to the shoot apical meristem and initiates the transition of a bud's meristem from a vegetative to a flowering state.

### CONCEPT CHECK 31.2

1. If an enzyme in field-grown soybean leaves is most active at noon and least active at midnight, is its activity under circadian regulation?
2. **WHAT IF?** If a plant flowers in a controlled chamber with a daily cycle of 10 hours of light and 14 hours of darkness, is it a short-day plant? Explain.
3. **MAKE CONNECTIONS** Plants detect the quality of their light environment by using blue-light photoreceptors and red-light-absorbing phytochromes. Suggest a reason why plants are so sensitive to these colors of light. (See Figure 8.9.)

For suggested answers, see Appendix A.

## CONCEPT 31.3

### Plants respond to a wide variety of stimuli other than light

Plants are immobile, but mechanisms have evolved by natural selection that enable them to adjust to a wide range of environmental circumstances by developmental or physiological means. Light is so important in the life of a plant that we devoted the entire previous section to a plant's reception of and response to this one environmental factor. In this section, we examine responses to some of the other environmental stimuli that a plant commonly encounters.

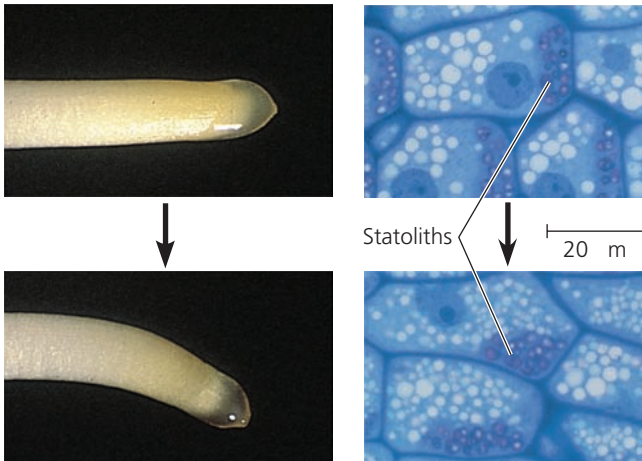


## Gravity

Because plants are photoautotrophs, it is not surprising that mechanisms for growing toward sunlight have evolved. But what environmental cue does the shoot of a young seedling use to grow upward when it is completely underground and there is no light for it to detect? Similarly, what environmental factor prompts the young root to grow downward? The answer to both questions is gravity.

Place a plant on its side, and it adjusts its growth so that the shoot bends upward and the root curves downward. In their responses to gravity, or **gravitropism**, roots display positive gravitropism (**Figure 31.19a**) and shoots exhibit negative gravitropism. Gravitropism occurs as soon as a seed germinates, ensuring that the root grows into the soil and the shoot grows toward sunlight, regardless of how the seed is oriented when it lands.

Plants may detect gravity by the settling of **statoliths**, dense cytoplasmic components that settle under the influence of gravity to the lower portions of the cell. The statoliths of vascular plants are specialized plastids containing dense starch grains (**Figure 31.19b**). In roots, statoliths are located in certain cells of the root cap. According to one hypothesis, the aggregation of statoliths at the low points of these cells triggers a redistribution of calcium, which causes lateral transport of auxin within the root. The calcium and auxin accumulate on the lower side of the root's zone of elongation. At high concentration, auxin inhibits cell elongation, an effect that slows growth on the root's lower side. The more rapid elongation of cells on the upper side eventually causes the root to grow straight downward.



**(a)** Over the course of hours, a horizontally oriented primary root of maize bends gravitropically until its growing tip becomes vertically oriented (LMs).

**(b)** Within minutes after the root is placed horizontally, plastids called statoliths begin settling to the lowest sides of root cap cells. This settling may be the gravity-sensing mechanism that leads to redistribution of auxin and differing rates of elongation by cells on opposite sides of the root (LMs).

▲ **Figure 31.19 Positive gravitropism in roots: the statolith hypothesis.**

Falling statoliths, however, may not be indispensable for gravitropism. For example, there are mutants of *Arabidopsis* and tobacco that lack statoliths but are still capable of gravitropism, though the response is slower than in wild-type plants. It could be that the entire cell helps the root sense gravity by mechanically pulling on proteins that tether the protoplast to the cell wall, stretching the proteins on the “up” side and compressing the proteins on the “down” side of the root cells. Dense organelles, in addition to starch granules, may also contribute by distorting the cytoskeleton as they are pulled by gravity. Statoliths, because of their density, may enhance gravitational sensing by a mechanism that simply works more slowly in their absence.

## Mechanical Stimuli

Trees in windy environments usually have shorter, stockier trunks than trees of the same species growing in more sheltered locations. The advantage of this stunted morphology is that it enables the plant to resist strong gusts of wind. The term **thigmomorphogenesis** (from the Greek *thigma*, touch) refers to the changes in form that result from mechanical perturbation. Plants are very sensitive to mechanical stress: Even the act of measuring the length of a leaf with a ruler alters its subsequent growth. Rubbing the stems of a young plant a couple of times daily results in plants that are shorter than controls (**Figure 31.20**).

Some plant species have become, over the course of their evolution, “touch specialists.” Acute responsiveness to mechanical stimuli is an integral part of these plants’ “life strategies.” Most vines and other climbing plants have tendrils that coil rapidly around supports (see Figure 28.7). These grasping organs usually grow straight until they touch something; the contact stimulates a coiling response caused by differential growth of cells on opposite sides of the tendril. This directional growth in response to



▲ **Figure 31.20 Thigmomorphogenesis in *Arabidopsis*.** The shorter plant on the left was rubbed twice a day. The untouched plant (right) grew much taller.

touch is called **thigmotropism**, and it allows the vine to take advantage of whatever mechanical supports it comes across as it climbs upward toward a forest canopy.

Other examples of touch specialists are plants that undergo rapid leaf movements in response to mechanical stimulation. For example, when the compound leaf of the sensitive plant *Mimosa pudica* is gently touched, its leaflets fold together

(Figure 31.21). This response, which takes only a second or two, results from a rapid loss of turgor in specialized motor cells

located at the base of each leaflet. The motor cells suddenly become flaccid after stimulation because they lose potassium ions, causing water to leave the cells by osmosis. It takes about 10 minutes for the cells to regain their turgor and restore the “unstimulated” form of the leaf. The function of the sensitive plant’s behavior invites speculation. Perhaps by folding its leaves and reducing its surface area when jostled, the plant appears less leafy and appetizing to herbivores.

A remarkable feature of rapid leaf movements is the mode of transmission of the stimulus through the plant. If one leaflet on a sensitive plant is touched, first that leaflet responds, then the adjacent leaflet responds, and so on, until all the leaflet pairs have folded together. From the point of stimulation, the signal that produces this response travels at a speed of about 1 cm/sec. An electrical impulse traveling at the same rate can be detected when electrodes are attached to the leaf. These impulses, called **action potentials**, resemble nerve impulses in animals, though the action potentials of plants are thousands of times slower. Action potentials have been discovered in many species of algae and plants and may be used as a form of internal communication. For example, in the Venus flytrap (*Dionaea muscipula*), action potentials are transmitted from sensory hairs in the trap to the cells that respond by closing the trap (see Figure 29.15). In the case of *Mimosa pudica*, more violent stimuli, such as touching a leaf with a hot needle, causes *all* the leaves and leaflets on a plant to droop, but this whole-plant response involves the spread of signaling molecules released from the injured area to other parts of the shoot.

## Environmental Stresses

Certain factors in the environment may change severely enough to have a potentially adverse effect on a plant’s survival, growth, and reproduction. Environmental stresses, such as flooding, drought, or extreme temperatures, can have a devastating impact on crop yields in agriculture. In natural ecosystems, plants that cannot tolerate an environmental stress will either succumb or be outcompeted by other plants. Thus, environmental stresses are an important factor in determining the geographic ranges of plants. Here we’ll consider some



(a) Unstimulated state (leaflets spread apart)



(b) Stimulated state (leaflets folded)

▲ **Figure 31.21** Rapid turgor movements by the sensitive plant (*Mimosa pudica*).

of the more common **abiotic** (nonliving) stresses that plants encounter. In the last section of this chapter, we’ll examine the defensive responses of plants to common **biotic** (living) stresses, such as herbivores and pathogens.

### Drought

On a dry, sunny day, a plant may wilt because its water loss by transpiration exceeds water absorption from the soil. Prolonged drought, of course, will kill a plant, but plants have control systems that enable them to cope with less extreme water deficits.

Many of a plant’s responses to water deficit help the plant conserve water by reducing the rate of transpiration. Water deficit in a leaf causes stomata to close, thereby slowing transpiration dramatically (see Figure 29.19). Water deficit stimulates increased synthesis and release of ABA in the leaves and roots; this hormone helps keep stomata closed by acting on guard cell membranes. Leaves respond to water deficit in several other ways. For example, when the leaves of grasses wilt, they roll into a tubelike shape that reduces transpiration by exposing less leaf surface to dry air and wind. Other plants, such as ocotillo (see Figure 29.20), shed their leaves in response to seasonal drought. Although these leaf responses conserve water, they also reduce photosynthesis, which is one reason why a drought diminishes crop yield. Plants can even take advantage of “early warnings” in the form of chemical signals from wilting neighbors and prime themselves to respond more readily and intensely to impending drought stress—a phenomenon you’ll explore in the **Scientific Skills Exercise**.

### Flooding

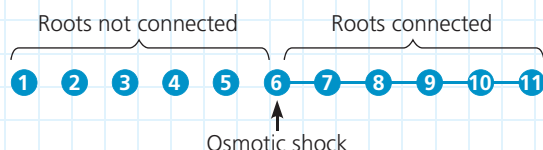
Too much water is also problematic for plants. An overwatered houseplant may suffocate because the soil lacks the air spaces that provide oxygen for cellular respiration in the roots. Some plants are structurally adapted to very wet habitats. For example, the submerged roots of mangroves, which inhabit coastal marshes, are continuous with aerial roots exposed to oxygen (see Figure 28.5). But how do less specialized plants cope with oxygen deprivation in waterlogged soils? Oxygen deprivation stimulates the production of ethylene, which

# Interpreting Experimental Results from a Bar Graph

**Do Drought-Stressed Plants Communicate Their Condition to Their Neighbors?** Researchers wanted to learn if plants can communicate drought-induced stress to neighboring plants and, if so, whether they use aboveground or belowground signals.

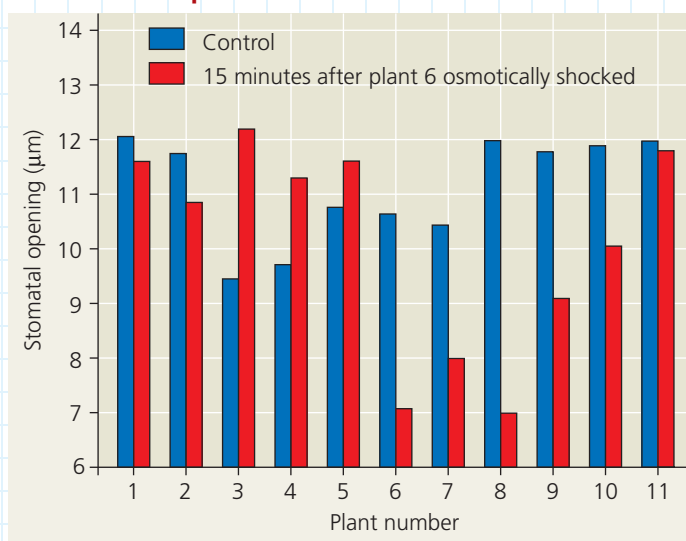
## How the Experiment Was Done

Eleven potted pea plants (*Pisum sativum*) were placed equidistantly in a row. The root systems of plants 6–11 were connected to their immediate neighbors by tubes, which allowed chemicals to move from the roots of one plant to the roots of the next plant without moving through the soil. The root systems of plants 1–6 were not connected. Osmotic shock was inflicted on plant 6 using a highly concentrated solution of mannitol, a natural sugar commonly used to mimic drought stress in vascular plants.



Fifteen minutes following the osmotic shock to plant 6, researchers measured the width of stomatal openings in leaves from all the plants. A control experiment was also done in which water was added to plant 6 instead of mannitol.

## Data from the Experiment



► Pea plant (*Pisum sativum*)



## Interpret the Data

1. How do the widths of the stomatal openings of plants 6–8 and plants 9 and 10 compare with those of the other plants in the experiment? What does this indicate about the state of plants 6–8 and 9 and 10? (For information about reading graphs, see the Scientific Skills Review in Appendix F and in the Study Area in MasteringBiology.)
2. Do the data support the idea that plants can communicate their drought-stressed condition to their neighbors? If so, do the data indicate that the communication is via the shoot system or the root system? Make specific reference to the data in answering both questions.
3. Why was it necessary to make sure that chemicals could not move through the soil from one plant to the next?
4. When the experiment was run for 1 hour rather than 15 minutes, the results were about the same except that the stomatal openings of plants 9–11 were comparable to those of plants 6–8. Suggest a reason why.
5. Why was water added to plant 6 instead of mannitol in the control experiment? What do the results of the control experiment indicate?

**Data from** O. Falik et al., Rumor has it...: Relay communication of stress cues in plants, *PLoS ONE* 6(11): e23625 (2011).

**MB** A version of this Scientific Skills Exercise can be assigned in MasteringBiology.

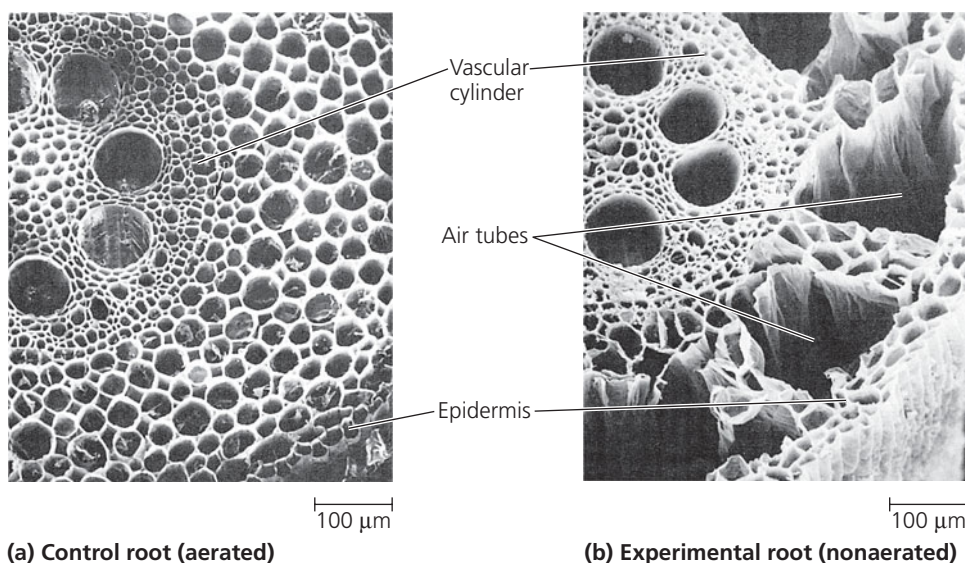
causes some cells in the root cortex to die. The destruction of these cells creates air tubes that function as “snorkels,” providing oxygen to the submerged roots (**Figure 31.22**).

## Salt Stress

An excess of sodium chloride or other salts in the soil threatens plants for two reasons. First, by lowering the water potential of the soil solution, salt can cause a water deficit in plants even though the soil has plenty of water. As the water potential of the soil solution becomes more negative, the water potential gradient from soil to roots is lowered, thereby reducing

water uptake (see Chapter 29). Another problem with saline soil is that sodium and certain other ions are toxic to plants when their concentrations are too high. Many plants can respond to moderate soil salinity by producing solutes that are well tolerated at high concentrations: These mostly organic compounds keep the water potential of cells more negative than that of the soil solution without admitting toxic quantities of salt. However, most plants cannot survive salt stress for long. The exceptions are *halophytes*, salt-tolerant plants with adaptations such as salt glands that pump salts out across the leaf epidermis.





**▲ Figure 31.22 A developmental response of maize roots to flooding and oxygen deprivation.** (a) A cross section of a control root grown in an aerated hydroponic medium. (b) A root grown in a nonaerated hydroponic medium. Ethylene-stimulated apoptosis (programmed cell death) creates the air tubes (SEMs).

### Heat Stress

Excessive heat may harm and even kill a plant by denaturing its enzymes. Transpiration helps cool leaves by evaporative cooling. On a warm day, for example, the temperature of a leaf may be 3–10°C below the ambient air temperature. Hot, dry weather also tends to dehydrate many plants; the closing of stomata in response to this stress conserves water but then sacrifices evaporative cooling. This dilemma is one reason why very hot, dry days take a toll on most plants. Most plants have a backup response that enables them to survive heat stress. Above a certain temperature—about 40°C for most plants in temperate regions—plant cells begin synthesizing **heat-shock proteins**, which help protect other proteins from denaturing.

### Cold Stress

One problem plants face when the temperature of the environment falls is a change in the fluidity of cell membranes. When a membrane cools below a critical point, membranes lose their fluidity as the lipids become locked into crystalline structures. This alters solute transport across the membrane and also adversely affects the functions of membrane proteins. Plants respond to cold stress by altering the lipid composition of their membranes. For example, membrane lipids increase in their proportion of unsaturated fatty acids, which have shapes that help keep membranes more fluid at low temperatures. Such membrane modification requires from several hours to days, which is one reason why unseasonably cold temperatures are generally more stressful to plants than the more gradual seasonal drop in air temperature.

Freezing is another type of cold stress. At subfreezing temperatures, ice forms in the cell walls and intercellular spaces of most plants. The cytosol generally does not freeze at the cooling rates encountered in nature because it contains more solutes than

the very dilute solution found in the cell wall, and solutes lower the freezing point of a solution. The reduction in liquid water in the cell wall caused by ice formation lowers the extracellular water potential, causing water to leave the cytoplasm. The resulting increase in the concentration of ions in the cytoplasm is harmful and can lead to cell death. Whether the cell survives depends largely on how well it resists dehydration. In regions with cold winters, native plants are adapted to cope with freezing stress. For example, before the onset of winter, the cells of many frost-tolerant species increase cytoplasmic levels of specific solutes, such as sugars, that are well tolerated at high concentrations and that help reduce the loss of water from the cell during extracellular freezing. The unsaturation of membrane lipids also increases, thereby maintaining proper levels of membrane fluidity.

**EVOLUTION** Many organisms, including certain vertebrates, fungi, bacteria, and many species of plants, have special proteins that hinder ice crystals from growing, helping the organism escape freezing damage. First described in Arctic fish in the 1950s, these *antifreeze proteins* permit survival at temperatures below 0°C. Antifreeze proteins bind to small ice crystals and inhibit their growth or, in the case of plants, prevent the crystallization of ice. The five major classes of antifreeze proteins differ markedly in their amino acid sequences but have a similar three-dimensional structure, suggesting convergent evolution. Surprisingly, antifreeze proteins from winter rye are homologous to antifungal proteins called PR proteins that you'll learn about later in the chapter, but they are produced in response to cold temperatures and shorter days, not fungal pathogens. Progress is being made in increasing the freezing tolerance of crop plants by genetically engineering antifreeze protein genes into their genomes.

### CONCEPT CHECK 31.3

1. Thermal images are photographs of the heat emitted by an object. Researchers have used thermal imaging of plants to isolate mutants that overproduce abscisic acid. Suggest a reason why these mutants are warmer than wild-type plants under conditions that are normally nonstressful.
2. A greenhouse worker finds that potted chrysanthemums nearest to the aisles are often shorter than those in the middle of the bench. Explain this "edge effect," a common problem in horticulture.
3. **WHAT IF?** If you removed the root cap from a root, would the root still respond to gravity? Explain.

For suggested answers, see Appendix A.

## Plants respond to attacks by herbivores and pathogens

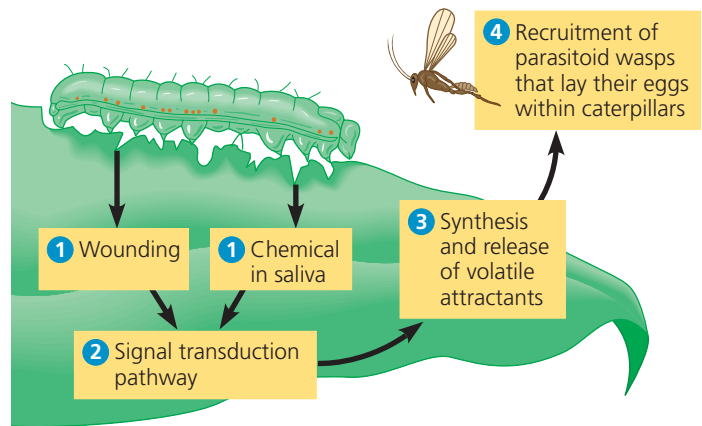
**EVOLUTION** Through natural selection, plants have evolved many types of interactions with other species in their communities. Some interspecific interactions are mutually beneficial, such as the associations of plants with mycorrhizal fungi (see Figure 29.13) or with pollinators (see Figure 30.6). Many plant interactions with other organisms, however, do not benefit the plant. As primary producers, plants are at the base of most food webs and are subject to attack by a wide range of plant-eating (herbivorous) animals. A plant is also subject to infection by diverse pathogens that can damage tissues or even kill the plant. Plants counter these threats with defense systems that deter herbivory and prevent infection or combat pathogens that infect the plant.

### Defenses Against Herbivores

Herbivory—animals eating plants—is a stress that plants face in any ecosystem. Plants prevent excessive herbivory by using both physical defenses, such as thorns and trichomes, and chemical defenses, such as the production of distasteful or toxic compounds.

Some plants even “recruit” predatory animals that help defend the plant against specific herbivores. Consider the insects called parasitoid wasps, which inject their eggs into caterpillars feeding on plants. The eggs hatch within the caterpillars, and the larvae eat through their organic containers from the inside out. The plant, which benefits from the destruction of the herbivorous caterpillars, has an active role in this drama. A leaf damaged by caterpillars releases volatile compounds that attract parasitoid wasps. The stimulus for this response is a combination of physical damage to the leaf caused by the munching caterpillar and a specific compound in the caterpillar’s saliva (**Figure 31.23**).

The volatile molecules a plant releases in response to herbivore damage can also function as an early warning system for nearby plants of the same species. For example, lima bean plants infested with spider mites release a cocktail of volatile chemicals that signal “news” of the attack to neighboring, noninfested lima bean plants. In response to these volatile compounds, the neighbors instigate biochemical changes that make themselves less susceptible, including the release of volatile chemicals that attract another predatory mite species that feeds on spider mites. Researchers have even transgenically engineered *Arabidopsis* plants to produce two volatile chemicals that normally are not made by *Arabidopsis* but which have been found to attract carnivorous predatory mites in other plants. The predatory mites become attracted to the genetically modified *Arabidopsis*, a finding that could have implications for the genetic engineering of insect resistance in crop plants.



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▲ **Figure 31.23** A maize leaf “recruiting” a parasitoid wasp as a defensive response to an armyworm caterpillar, an herbivore.

### Defenses Against Pathogens

A plant’s first line of defense against infection is the physical barrier presented by the epidermis and periderm of the plant body (see Figure 28.19). This first defense system, however, is not impenetrable. The mechanical wounding of leaves by herbivores, for example, opens up portals for invasion by pathogens. Even when plant tissues are intact, viruses, bacteria, and the spores and hyphae of fungi can still enter the plant through natural openings in the epidermis, such as stomata.

When a pathogen invades a plant, the plant mounts a second line of defense, a chemical attack that destroys the pathogen and prevents its spread from the site of infection. This second defense system is enhanced by the plant’s ability to recognize certain pathogens. Successful pathogens cause disease because they evade recognition or suppress the host’s defense mechanisms.

### Host-Pathogen Coevolution

Pathogens against which a plant has little specific defense are **virulent** pathogens. Strains of pathogens that mildly harm but do not kill the host plant are said to be **avirulent** pathogens. Virulent pathogens are the exceptions. If they were not, hosts and pathogens would soon perish together. Complete resistance to a pathogen often comes at an energetic cost to the plant, however, and in the absence of the pathogen, resistant plants are outcompeted by those with less resistance. Of course, plants with no resistance will succumb to a pathogen outbreak. Thus, a “compromise” has evolved between plants and most of their pathogens: The pathogen gains enough access to its host to enable it to perpetuate itself without severely damaging or killing the plant.

**Gene-for-gene recognition** is a form of plant disease resistance in which pathogen-derived molecules called *effectors* are recognized by one of the hundreds of resistance (R) proteins encoded by resistance genes in a plant’s genome. Protein effectors, encoded by the pathogen’s avirulence (*Avr*) genes, can facilitate infection in plants that lack the appropriate R protein

by redirecting the host's metabolism to the pathogen's advantage. In plants that do have the appropriate R protein, however, effector proteins can directly trigger a suite of strong defense responses. The recognition of effectors by R proteins triggers signal transduction pathways that activate an arsenal of defense responses, including a local defense called the hypersensitive response and a general defense called systemic acquired resistance. Local and systemic responses to pathogens require extensive genetic reprogramming and commitment of cellular resources. Therefore, a plant activates these defenses only after detecting an invading pathogen.

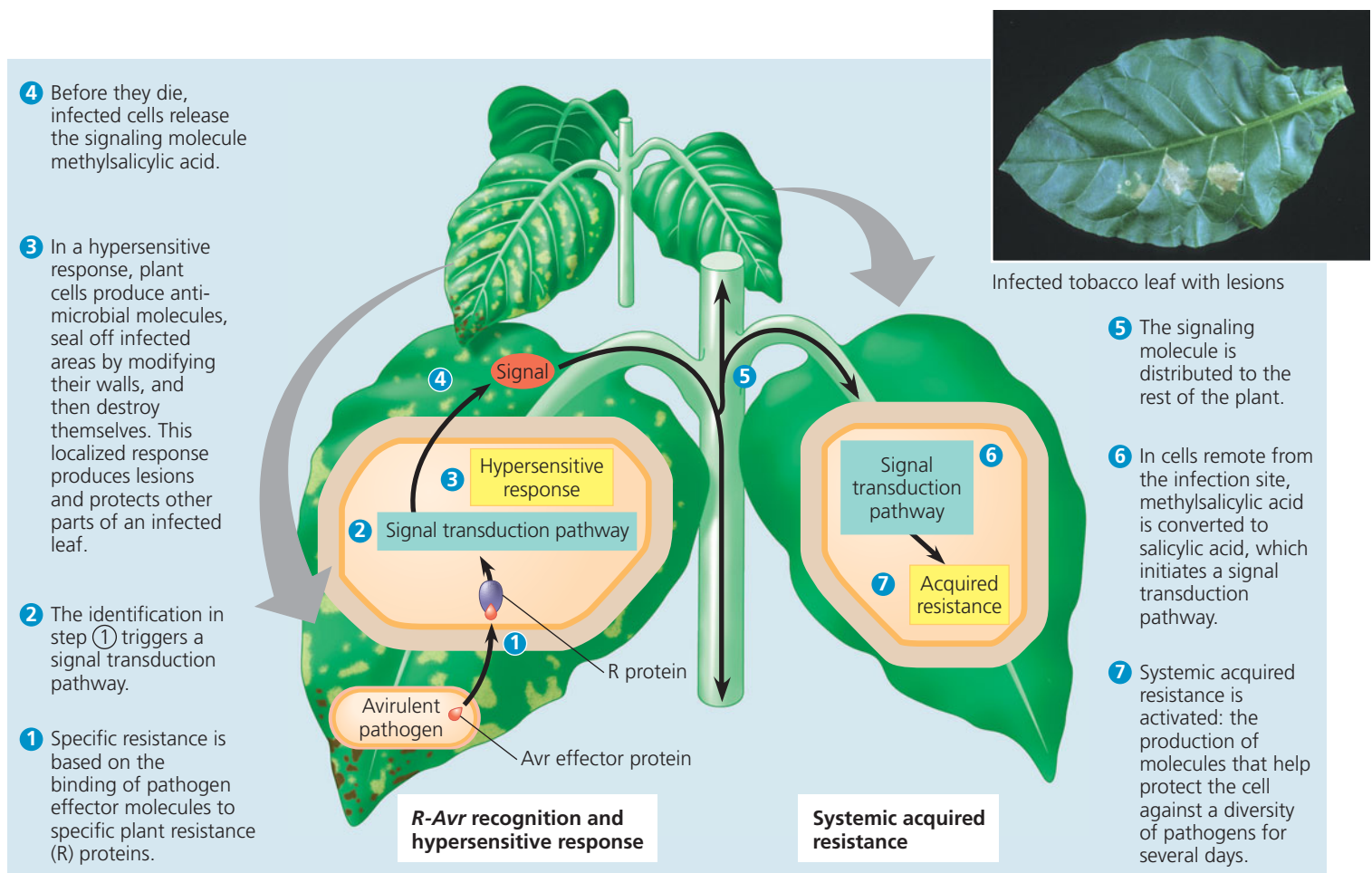
### The Hypersensitive Response

The **hypersensitive response** is a defense response that causes cell and tissue death near the infection site, thereby restricting the spread of a pathogen. After the cells at the infection site mount a chemical defense and seal off the area, they destroy themselves. As indicated in **Figure 31.24**, the hypersensitive response is initiated when pathogen effectors bind to R proteins and stimulate the production of phytoalexins, which are compounds having fungicidal and bactericidal properties. The hypersensitive response also induces production of *PR*

*proteins* (pathogenesis-related proteins), many of which are enzymes that hydrolyze components in the cell walls of pathogens. Infection also stimulates the formation of lignin and the cross-linking of molecules within the plant cell wall, responses that hinder the spread of the pathogen to other parts of the plant. We can see the result of a hypersensitive response as lesions on a leaf, as shown at the upper right in the figure. As “sick” as such a leaf appears, it will still survive, and its defensive response will help protect the rest of the plant.

### Systemic Acquired Resistance

The hypersensitive response is localized and specific. However, as noted previously, pathogen invasions can also produce signaling molecules that “sound the alarm” of infection to the whole plant. The resulting **systemic acquired resistance** arises from the plant-wide expression of defense genes. It is nonspecific, providing protection against a diversity of pathogens that lasts for days. The search for a signaling molecule that moves from the infection site to elicit systemic acquired resistance led to the identification of *methylsalicylic acid* as the most likely candidate. Methylsalicylic acid is produced around the infection site and carried by the phloem throughout the



▲ **Figure 31.24** Defense responses against an avirulent pathogen. Plants can often prevent the systemic spread of infection by instigating a hypersensitive response. This response helps isolate the pathogen by producing lesions that form “rings of death” around the sites of infection.



plant, where it is converted to **salicylic acid** in areas remote from the sites of infection. Salicylic acid activates a signal transduction pathway that induces the production of PR proteins and resistance to pathogen attack (see Figure 31.24).

Plant disease epidemics, such as potato late blight, which caused the Irish potato famine of the 1840s, can lead to incalculable human misery (see Concept 25.4). Other diseases, such as chestnut blight (see Concept 26.5) and sudden oak death (see Concept 41.5), can dramatically alter community structures. Plant epidemics are often the result of infected plants or timber being inadvertently transported around the world. As global commerce increases, such epidemics will become increasingly common. To prepare for such outbreaks, plant biologists are stockpiling the seeds of wild relatives of crop plants in special storage facilities. Scientists hope that undomesticated relatives may have genes that will be able to curb the next plant epidemic. These scientists, along with thousands

of other plant biologists, are extending an age-old tradition of curiosity about the green organisms that feed our species and the biosphere.

CONCEPT CHECK 31.4

- 1. What are some drawbacks of spraying fields with general-purpose insecticides?
- 2. Chewing insects mechanically damage plants and lessen the surface area of leaves for photosynthesis. In addition, these insects make plants more vulnerable to pathogen attack. Suggest a reason why.
- 3. **WHAT IF?** Suppose a scientist finds that a population of plants growing in a breezy location is more prone to herbivory by insects than a population of the same species growing in a sheltered area. Suggest a hypothesis to account for this observation.

For suggested answers, see Appendix A.

# 31 Chapter Review

## SUMMARY OF KEY CONCEPTS

CONCEPT 31.1

Plant hormones help coordinate growth, development, and responses to stimuli (pp. 617–626)

- Hormones control plant growth and development by affecting the division, elongation, and differentiation of cells. Some hormones also mediate the responses of plants to environmental stimuli.

Plant Hormone	Major Responses
Auxin	Stimulates cell elongation; regulates branching and organ bending
Cytokinins	Stimulate plant cell division; promote later bud growth; slow organ death
Gibberellins	Promote stem elongation; help seeds break dormancy and use stored reserves
Brassinosteroids	Chemically similar to the sex hormones of animals; induce cell elongation and division
Absciscic acid	Promotes stomatal closure in response to drought; promotes seed dormancy
Ethylene	Mediates fruit ripening

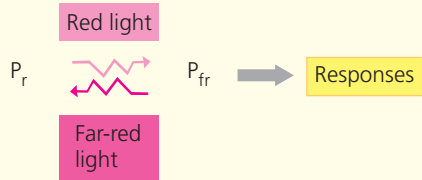
**?** Is there any truth to the old adage “One bad apple spoils the whole bunch”? Explain.

CONCEPT 31.2

Responses to light are critical for plant success (pp. 626–631)

- **Blue-light photoreceptors** control hypocotyl elongation, stomatal opening, and phototropism.

- **Phytochromes** act like molecular “on-off” switches. Red light turns phytochrome “on,” and far-red light turns it “off”:



Phytochrome regulates shade avoidance and the germination of many seed types.

- Many daily rhythms in plant behavior are controlled by an internal circadian clock. Free-running circadian cycles are approximately 24 hours long but are entrained to exactly 24 hours by dawn and dusk effects on phytochrome form.
- Phytochrome conversion also provides information about the relative lengths of day and night (photoperiod) and hence the time of year. Photoperiodism regulates the time of flowering in many species. **Short-day plants** require a night longer than a critical length to flower. **Long-day plants** need a night length shorter than a critical period to flower.

**?** Why did plant physiologists propose the existence of a mobile molecule (florigen) that triggers flowering?

CONCEPT 31.3

Plants respond to a wide variety of stimuli other than light (pp. 631–635)

- **Gravitropism** is the bending of an organ in response to gravity. Roots show positive gravitropism, and stems show negative gravitropism. **Statoliths**, starch-filled plastids, enable plant roots to detect gravity.
- Plants are highly sensitive to touch. **Thigmotropism** is a growth response to touch. Rapid leaf movements involve transmission of electrical impulses called action potentials.

- Plants are sensitive to environmental stresses, including drought, flooding, high salinity, and extremes of temperature.

Environmental Stress	Major Response
Drought	ABA production, reducing water loss by closing stomata
Flooding	Formation of air tubes that help roots survive oxygen deprivation
Salt	Avoiding osmotic water loss by producing solutes tolerated at high concentrations
Heat	Synthesis of heat-shock proteins, which reduce protein denaturation at high temperatures
Cold	Adjusting membrane fluidity; avoiding osmotic water loss; producing antifreeze proteins

**?** *Plants that have acclimated to drought stress are often more resistant to freezing stress as well. Suggest a reason why.*

## CONCEPT 31.4

### Plants respond to attacks by herbivores and pathogens (pp. 636–638)

- In addition to physical defenses such as thorns and trichomes, plants produce distasteful or toxic chemicals, as well as attractants that recruit animals that destroy herbivores.
- The **hypersensitive response** seals off an infection and destroys both pathogen and host cells in the region. **Systemic acquired resistance** is a generalized defense response in organs distant from the infection site.

**?** *How do chewing insects make plants more susceptible to pathogens?*

## TEST YOUR UNDERSTANDING

### Level 1: Knowledge/Comprehension

- The hormone that helps plants respond to drought is
  - auxin.
  - gibberellin.
  - cytokinin.
  - ethylene.
  - abscisic acid.
- Auxin enhances cell elongation in all of these ways *except*
  - increased uptake of solutes.
  - gene activation.
  - acid-induced denaturation of cell wall proteins.
  - increased activity of plasma membrane proton pumps.
  - cell wall loosening.
- Charles and Francis Darwin discovered that
  - auxin is responsible for phototropic curvature.
  - auxin can pass through agar.
  - light destroys auxin.
  - light is perceived by the tips of coleoptiles.
  - red light is most effective in shoot phototropism.

### Level 2: Application/Analysis

- The signaling molecule for flowering might be released earlier than usual in a long-day plant exposed to flashes of
  - far-red light during the night.
  - red light during the night.
  - red light followed by far-red light during the night.
  - far-red light during the day.
  - red light during the day.

- If a long-day plant has a critical night length of 9 hours, which 24-hour cycle would prevent flowering?
  - 16 hours light/8 hours dark
  - 14 hours light/10 hours dark
  - 15.5 hours light/8.5 hours dark
  - 4 hours light/8 hours dark/4 hours light/8 hours dark
  - 8 hours light/8 hours dark/light flash/8 hours dark
- A plant mutant that showed normal gravitropic bending but did not store starch in its plastids would require a reevaluation of the role of \_\_\_\_\_ in gravitropism.
  - auxin
  - calcium
  - statoliths
  - light
  - differential growth
- DRAW IT** Indicate the response to each condition by drawing a straight seedling or one with the triple response.

	Control	Ethylene added	Ethylene synthesis inhibitor
Wild-type			
Ethylene insensitive ( <i>ein</i> )			
Ethylene overproducing ( <i>eto</i> )			
Constitutive triple response ( <i>ctr</i> )			

### Level 3: Synthesis/Evaluation

#### 8. SCIENTIFIC INQUIRY

A field biologist notes that a caterpillar quits feeding on a certain plant after a while, rejects nearby uneaten plants, and begins feeding anew on plants some distance away from the original. The biologist hypothesizes that insect-damaged leaves emit volatile “alarm” chemicals that signal nearby plants to initiate plant defense responses. Suggest a test of this hypothesis.

#### 9. FOCUS ON EVOLUTION

As a general rule, light-sensitive germination is more pronounced in small seeds compared with large seeds. Suggest a reason why.

#### 10. FOCUS ON INTERACTIONS

In a short essay (100–150 words), summarize phytochrome’s role in altering shoot growth for the enhancement of light capture.

For selected answers, see Appendix A.

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