

# 35

## Plant Structure, Growth, and Development



▲ Figure 35.1 Computer art?

### KEY CONCEPTS

- 35.1 Plants have a hierarchical organization consisting of organs, tissues, and cells
- 35.2 Meristems generate cells for primary and secondary growth
- 35.3 Primary growth lengthens roots and shoots
- 35.4 Secondary growth increases the diameter of stems and roots in woody plants
- 35.5 Growth, morphogenesis, and cell differentiation produce the plant body

### OVERVIEW

#### Are Plants Computers?

The object in **Figure 35.1** 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*.) Romanesco looks as if it were generated by a computer because its growth pattern follows a repetitive sequence of instructions. As in most plants, the growing shoot tips lay down a pattern of leaf . . . bud . . . stem, 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 leave 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 lions, for example, have four legs and are of roughly the same size, but oak trees vary in the number and arrangement of their branches. This is because lions and other animals respond to challenges and opportunities in their local environment by movement, whereas plants respond by altering their growth. 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 interact with their environment.

Chapters 29 and 30 described the evolution of plants from green algae to angiosperms (flowering plants). In Unit Six, we focus primarily on angiosperms because they serve as the primary producers in many ecosystems and are of great agricultural importance. We begin by discussing the structure of flowering plants and how these plants develop.

### CONCEPT 35.1

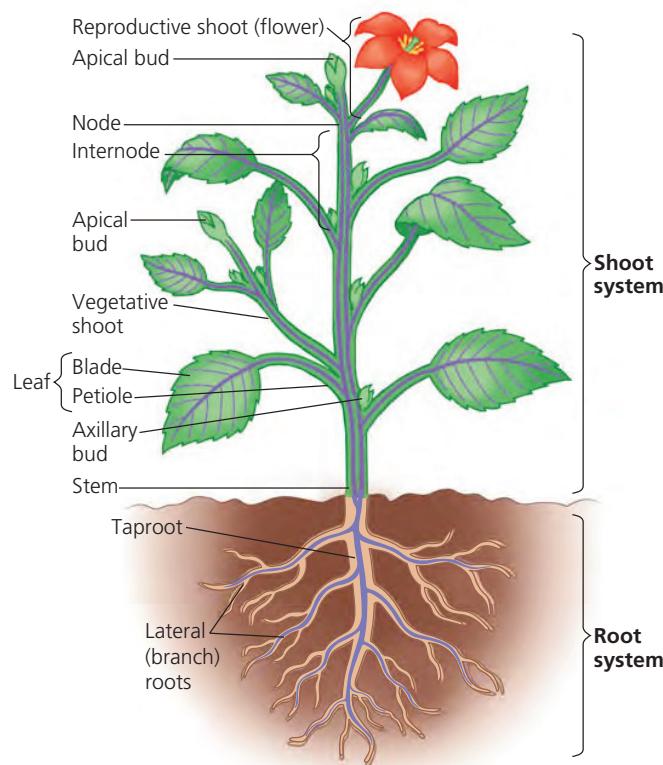
#### Plants have a hierarchical organization consisting of organs, tissues, and cells

Plants, like most animals, have organs composed of different tissues, which in turn are composed of different cell types. A **tissue** is a group of cells, consisting of one or more cell types, that together perform a specialized function. An **organ** consists of several types of tissues that together carry out particular functions. In looking at the hierarchy of plant organs, tissues, and cells, we begin with organs because they are the most familiar and easily observed 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

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 ground surface. 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 35.2). With few exceptions, vascular plants rely completely on both systems for survival. Roots typically 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.

Vegetative growth—production of nonreproductive leaves, stems, and roots—is only one stage in a plant’s life. Most plants also undergo growth relating to sexual reproduction. In angiosperms, reproductive shoots bear flowers, which consist of leaves that are highly modified for sexual reproduction.



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

Later in this chapter, we’ll discuss the transition from vegetative shoot formation to reproductive shoot formation.

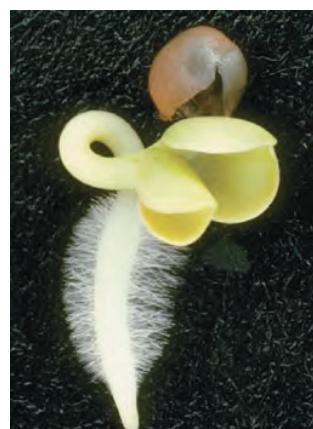
In describing plant organs, we’ll draw examples mainly from the two major groups of angiosperms: monocots and eudicots (see Figure 30.13).

### Roots

A **root** is an organ that anchors a vascular plant in the soil, absorbs minerals and water, and often stores carbohydrates. Most eudicots and gymnosperms have a *taproot system*, consisting of one main vertical root, the **taproot**, which develops from an embryonic root. The taproot gives rise to **lateral roots**, also called branch roots (see Figure 35.2). Taproot systems generally penetrate deeply and are therefore well adapted to deep soils, where the groundwater is not close to the surface.

In most monocots, such as grasses, 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* (from the Latin *adventicus*, extraneous), a term describing a plant organ that grows in an unusual location, such as roots arising from stems or leaves. Each small root forms its own lateral roots. The result is a *fibrous root system*—a mat of generally thin roots spreading out below the soil surface (see Figure 30.13). Fibrous root systems usually do not penetrate deeply and are therefore best adapted to shallow soils or regions where rainfall is light and does not moisten the soil much below the surface layer. Most grasses have shallow roots, concentrated in the upper few centimeters of the soil. Because these shallow roots hold the topsoil in place, grass makes excellent ground cover for preventing erosion.

Although the entire root system helps anchor a plant, in most plants the absorption of water and minerals occurs primarily near the tips of roots, where vast numbers of **root hairs** emerge and increase the surface area of the root enormously (Figure 35.3). A root hair is a thin, tubular extension of a root epidermal cell. It should not be confused with a lateral root, which is an organ. Despite their great surface



◀ **Figure 35.3 Root hairs of a radish seedling.** Root hairs grow by the thousands just behind the tip of each root. By increasing the root’s surface area, they greatly enhance the absorption of water and minerals from the soil.

area, root hairs, unlike lateral roots, contribute little to plant anchorage. Their main function is absorption.

Many plants have root adaptations with specialized functions (**Figure 35.4**). 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.

▼ **Figure 35.4** Evolutionary adaptations of roots.



▲ **Prop roots.** The aerial roots of hala trees are examples of prop roots, so named because they support the tall, top-heavy trees. Hala trees grow along coastal areas in the South Pacific where the sandy soils are shallow and unstable.



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



▲ **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, they enable the root system to obtain oxygen, which is lacking in the thick, waterlogged mud.

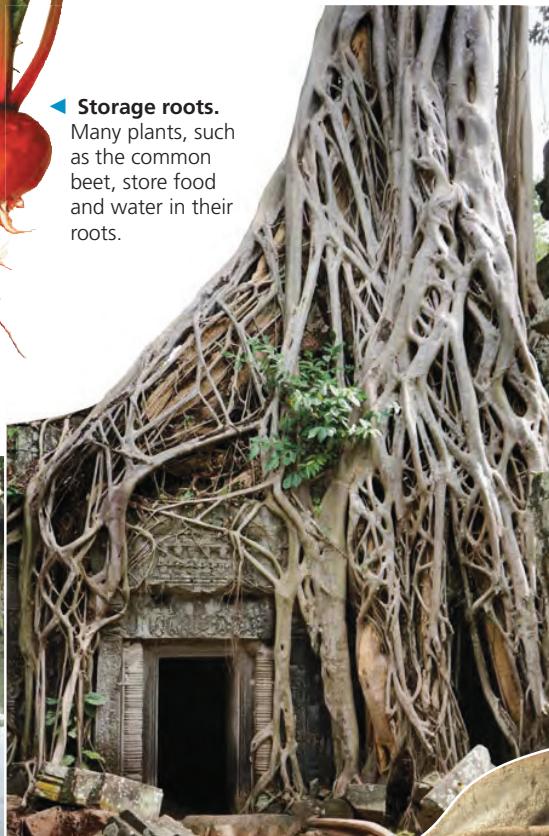
## Stems

A **stem** is an organ that raises or separates leaves, exposing them to sunlight. Stems also raise reproductive structures, facilitating dispersal of pollen and fruit. 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 35.2). In the upper angle (axil) formed by each leaf and the stem is an **axillary bud**, a structure that can form a lateral shoot, commonly called a branch. Young axillary buds typically grow very slowly: Most of the growth of a young shoot is concentrated near the shoot tip, which consists of an **apical bud**, or terminal bud, that is composed of developing leaves and a compact series of nodes and internodes.

The proximity of the axillary buds to the apical bud is partly responsible for their dormancy. The inhibition of axillary buds by an apical bud is called **apical dominance**. If an animal eats the end of the shoot or if shading results in

### “Strangling” aerial roots.

The seeds of this strangler fig germinate in the branches of tall trees of other species and send numerous aerial roots to the ground. These snakelike roots gradually wrap around the host tree and objects such as this Cambodian temple ruin. Eventually, the host tree dies of shading by the fig leaves.



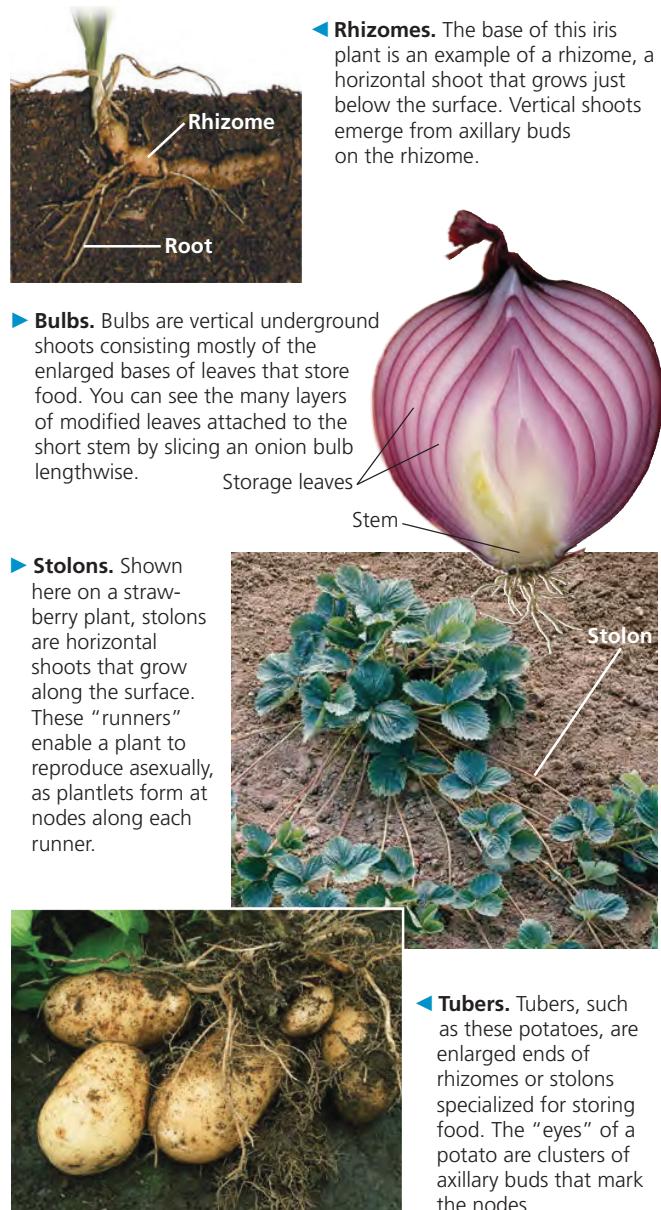
▼ **Buttress roots.** Because of moist conditions in the tropics, root systems of many of the tallest trees are surprisingly shallow. Aerial roots that look like buttresses, such as seen in this ceiba tree in Central America, give architectural support to the trunks of such trees.



the light being more intense to the side of the shoot, axillary buds break dormancy; that is, they 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 in more lateral shoots. That is why pruning trees and shrubs and pinching back houseplants will make them bushier. The hormonal changes underlying apical dominance are discussed in Chapter 39.

Some plants have stems with additional functions, such as food storage and asexual reproduction. These modified stems, which include rhizomes, bulbs, stolons, and tubers, are often mistaken for roots (**Figure 35.5**).

▼ **Figure 35.5 Evolutionary adaptations of stems.**



## Leaves

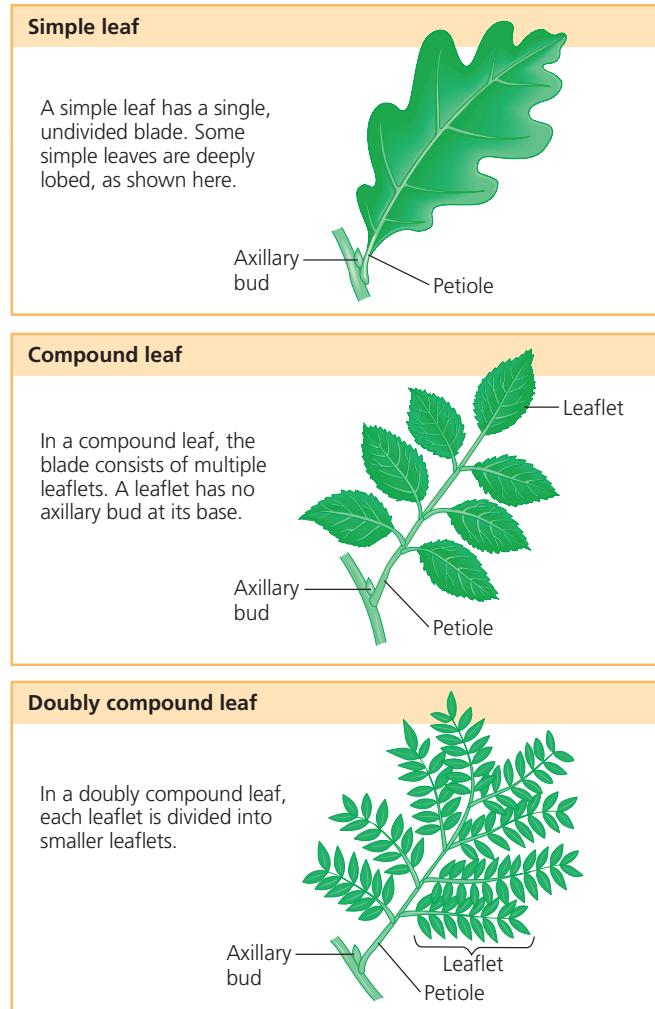
In most vascular plants, the **leaf** is the main photosynthetic organ, although green stems also perform photosynthesis. Leaves vary extensively in form but generally consist of a flattened **blade** and a stalk, the **petiole**, which joins the leaf to the stem at a node (see Figure 35.2). Grasses 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 30.13).

In identifying angiosperms according to structure, taxonomists rely mainly on floral morphology, but they also use variations in leaf morphology, such as leaf shape, the branching pattern of veins, and the spatial arrangement of leaves.

**Figure 35.6** illustrates a difference in leaf shape: simple versus compound. Many leaves, such as those of poison ivy, are

▼ **Figure 35.6 Simple versus compound leaves.**

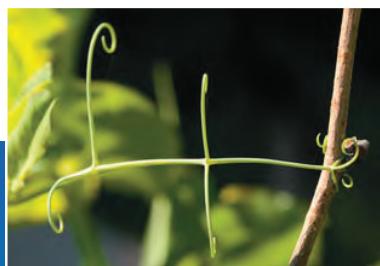


compound or doubly compound. This structural adaptation may enable leaves to withstand strong wind with less tearing. It may also confine some pathogens (disease-causing organisms and viruses) that invade the leaf to a single leaflet, rather than allowing them to spread to the entire leaf.

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 35.7).

#### ▼ Figure 35.7 Evolutionary adaptations of leaves.

► **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.** Most succulents, such as this ice plant, have leaves adapted for storing water.



► **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.



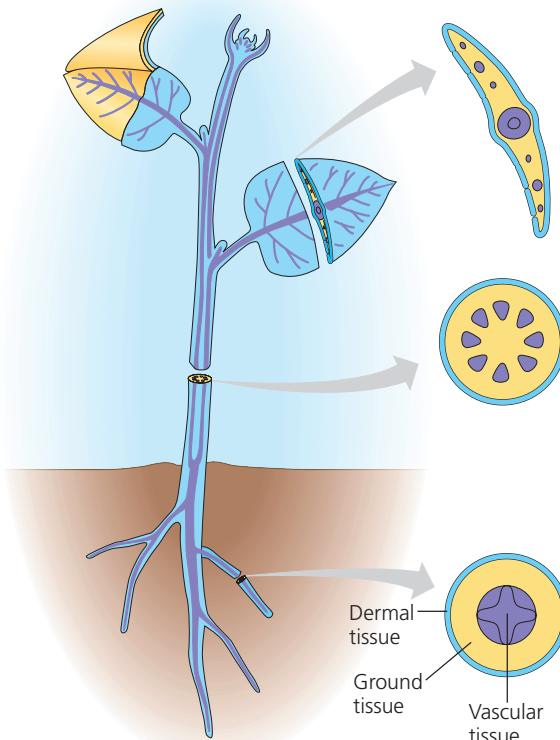
► **Bracts.** Often mistaken for petals, the red parts of the poinsettia are actually modified leaves called bracts that surround a group of flowers. Such brightly colored leaves attract pollinators.



## Dermal, Vascular, and Ground Tissues

Each plant organ—root, stem, or leaf—has dermal, vascular, and ground tissues. Each of these three categories forms a **tissue system**, a functional unit connecting all of the plant's organs. Although each tissue system is continuous throughout the plant, specific characteristics of the tissues and their spatial relationships to one another vary in different organs (Figure 35.8).

The **dermal tissue system** is the 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, they reduce water loss and reflect excess light, but their most common function



▲ **Figure 35.8 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.

is to provide defense against insects by forming a barrier or by secreting sticky fluids or toxic compounds. For instance, the trichomes on aromatic leaves such as mint secrete oils that protect the plants from herbivores and disease. **Figure 35.9** describes an investigation of the relationship between trichome density on soybean pods and damage by beetles.

▼ **Figure 35.9**

## INQUIRY

### Do soybean pod trichomes deter herbivores?

**EXPERIMENT** Bean leaf beetles (*Cerotoma trifurcata*) feed on developing legume pods, causing pod scarring and decreased seed quality. W. F. Lam and L. P. Pedigo, of Purdue University, investigated whether the stiff trichomes on soybean pods (*Glycine max*) physically deter these beetles. The researchers placed hungry beetles in muslin bags and sealed the bags around the pods of adjacent plants expressing different pod hairiness. The amount of damage to the pods was assessed after 24 hours.



**RESULTS** Beetle damage to very hairy soybean pods was much lower than damage to the other pod types.



**CONCLUSION** Soybean pod trichomes protect against beetle damage.

**SOURCE** W. F. Lam and L. P. Pedigo, Effect of trichome density on soybean pod feeding by adult bean leaf beetles (Coleoptera: Chrysomelidae), *Journal of Economic Entomology* 94:1459–1463 (2001).

**WHAT IF?** The pod trichomes of most soybean varieties are white, but some varieties have tan-colored trichomes. Suppose that the effects of trichome density on beetle feeding were observed only in tan-haired varieties. What might this finding suggest about how these trichomes deter beetles?

The **vascular tissue system** carries out long-distance transport of materials between the root and shoot systems. 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 35.8). 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 includes various cells specialized for functions such as storage, photosynthesis, and support.

### Common Types of Plant Cells

Like any multicellular organism, a plant is characterized by cell differentiation, the specialization of cells in structure and function. Cell differentiation may involve changes both in the cytoplasm and its organelles and in the cell wall. **Figure 35.10**, on the next two pages, 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 Figures 6.9 and 6.28, which show basic plant cell structure.

### CONCEPT CHECK 35.1

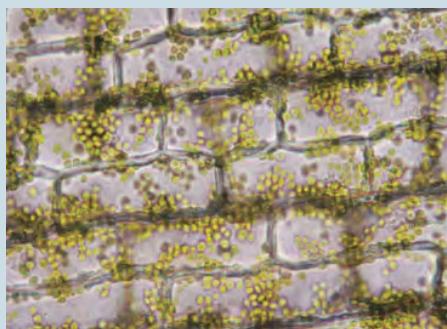
- How does the vascular tissue system enable leaves and roots to function together in supporting growth and development of the whole plant?
- What plant structure is each of the following? (a) brussels sprouts; (b) celery; (c) onions; (d) carrots
- WHAT IF?** If humans were photoautotrophs, making food by capturing light energy for photosynthesis, how might our anatomy be different?
- MAKE CONNECTIONS** Explain how central vacuoles and cellulose cell walls contribute to plant growth (see Chapter 6, pp. 108 and 118–119).

For suggested answers, see Appendix A.

▼ Figure 35.10

## Exploring Examples of Differentiated Plant Cells

### Parenchyma Cells

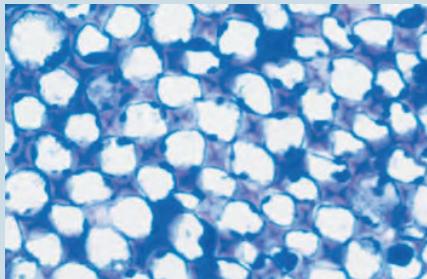


Parenchyma cells in *Elodea* leaf,  
with chloroplasts (LM)

60 μm

Mature **parenchyma cells** have primary walls that are relatively thin and flexible, and most lack secondary walls. (See Figure 6.28 to review primary and secondary 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

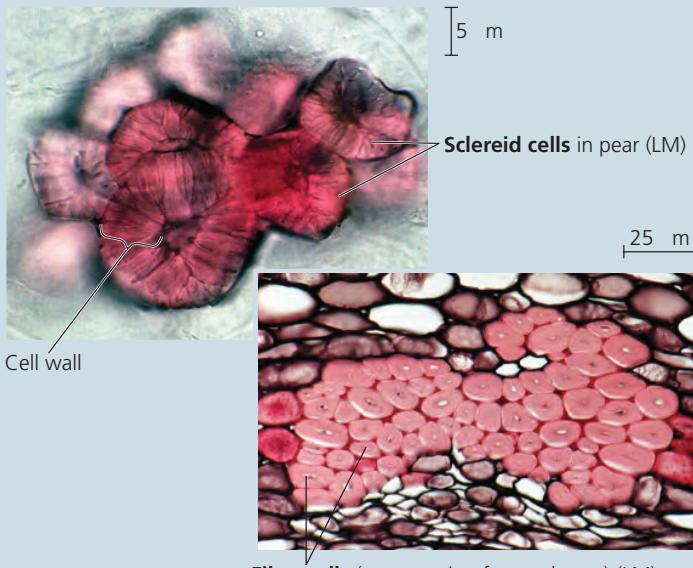


Collenchyma cells  
(in *Helianthus* stem) (LM)

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 (for example, the “strings” of a celery stalk, which is a petiole). 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. The secondary walls of sclerenchyma cells are thick and contain large amounts of lignin. This relatively indigestible strengthening polymer 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.

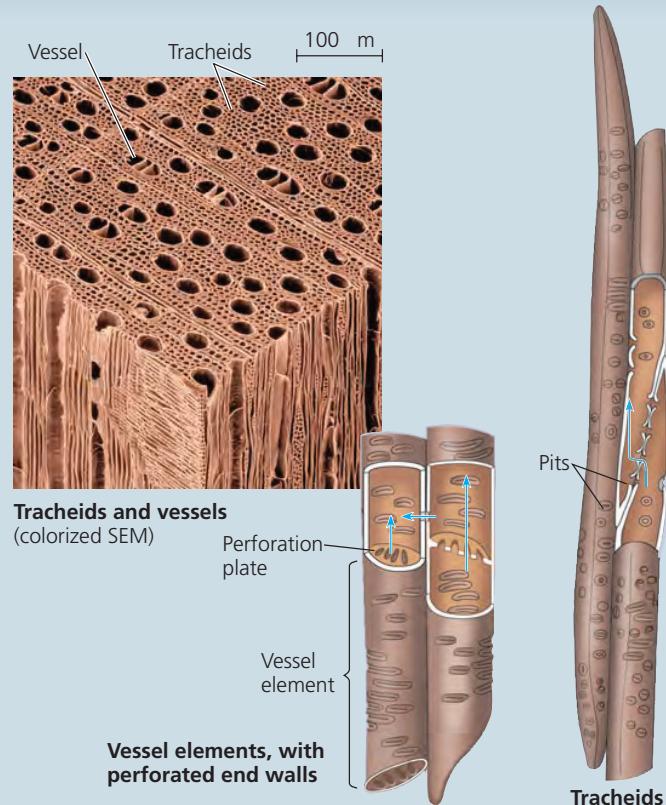
## Water-Conducting Cells of the Xylem

The two types of water-conducting cells, **tracheids** and **vessel elements**, are tubular, elongated cells that are dead at functional maturity. Tracheids are in the xylem of nearly 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 non-living conduit through which water can flow. The secondary walls of tracheids and vessel elements are often interrupted by pits, thinner regions where only primary walls are present (see Figure 6.28 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 micropipes known as **vessels**. The end walls of vessel elements have perforation plates that enable water to flow freely through the vessels.

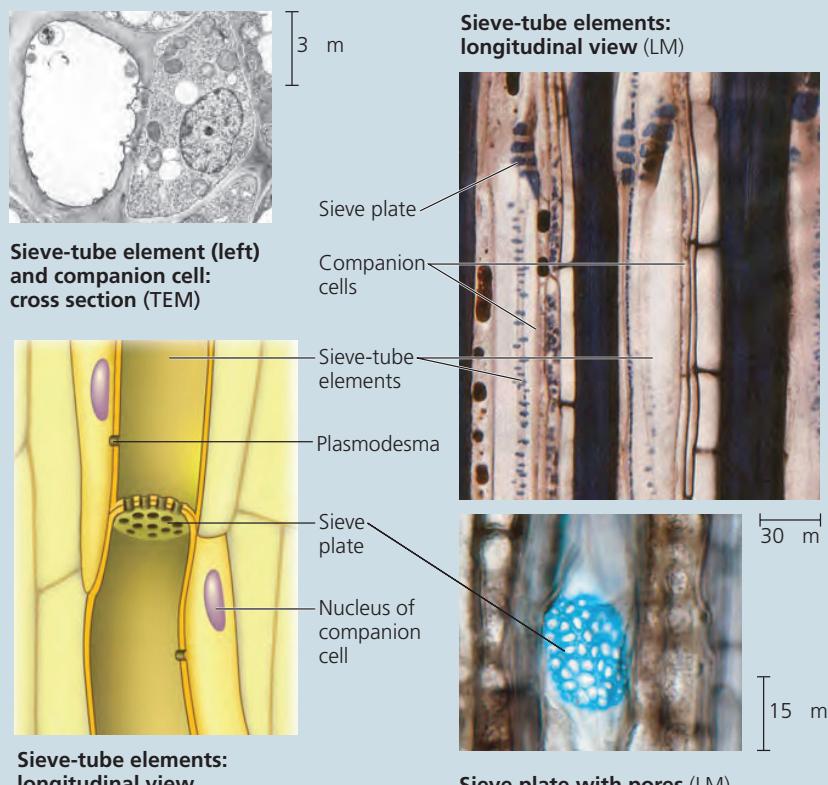
The secondary walls of tracheids and vessel elements are hardened with lignin. This hardening prevents collapse under the tensions of water transport and also provides support.



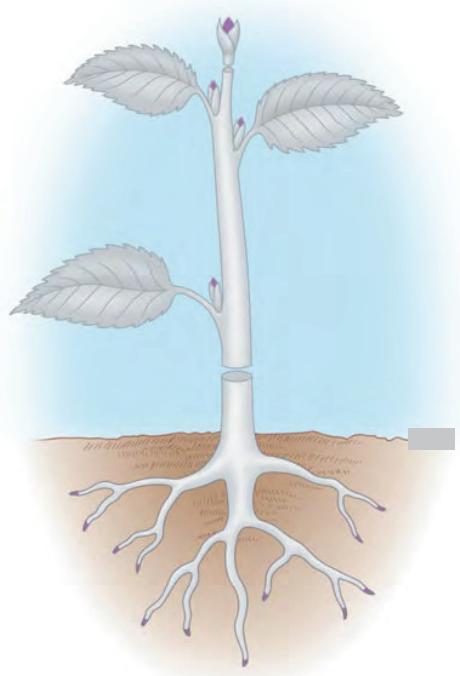
## Sugar-Conducting Cells of the Phloem

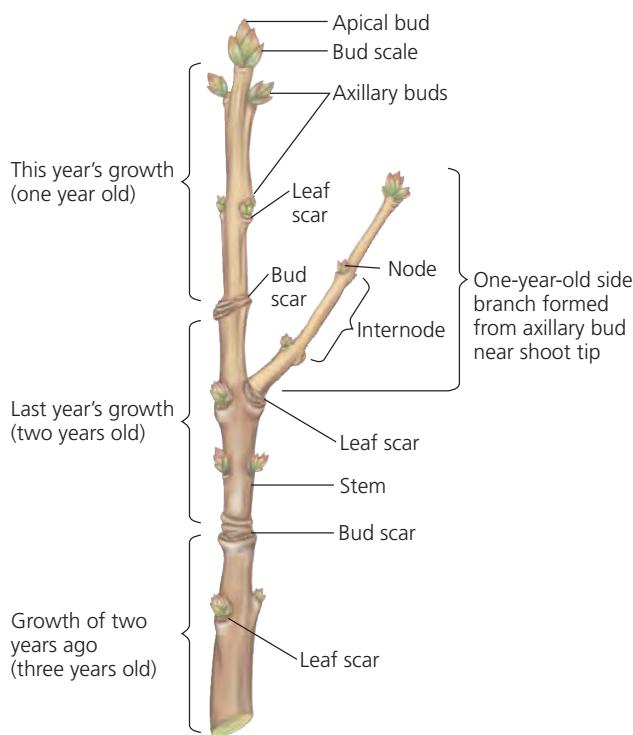
Unlike the water-conducting cells of the xylem, the sugar-conducting cells of the phloem are alive at functional maturity. In seedless vascular plants and gymnosperms, sugars and other organic nutrients are transported through long, narrow cells called sieve cells. In the phloem of angiosperms, these nutrients are transported through sieve tubes, which consist of chains of cells called **sieve-tube 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 channels called plasmodesma (see Figure 6.28). 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.



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for the BioFlix® 3-D Animation called  
Tour of a Plant Cell.





▲ Figure 35.12 Three years' growth in a winter twig.

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. Some buffalo grass of the North American plains is thought to have been growing for 10,000 years from seeds that sprouted at the close of the last ice age.

## CONCEPT CHECK 35.2

1. Distinguish between primary and secondary growth.
2. Cells in lower layers of your skin divide and replace dead cells sloughed from the surface. Are such regions of cell division comparable to a plant meristem? Explain your answer.
3. Roots and stems grow indeterminately, but leaves do not. How might this benefit the plant?
4. **WHAT IF?** Suppose a gardener uproots some carrots after one season and sees they are too small. Carrots are biennials, and so the gardener leaves the remaining plants in the ground, thinking their roots will grow larger during their second year. Is this a good idea? Explain.

For suggested answers, see Appendix A.

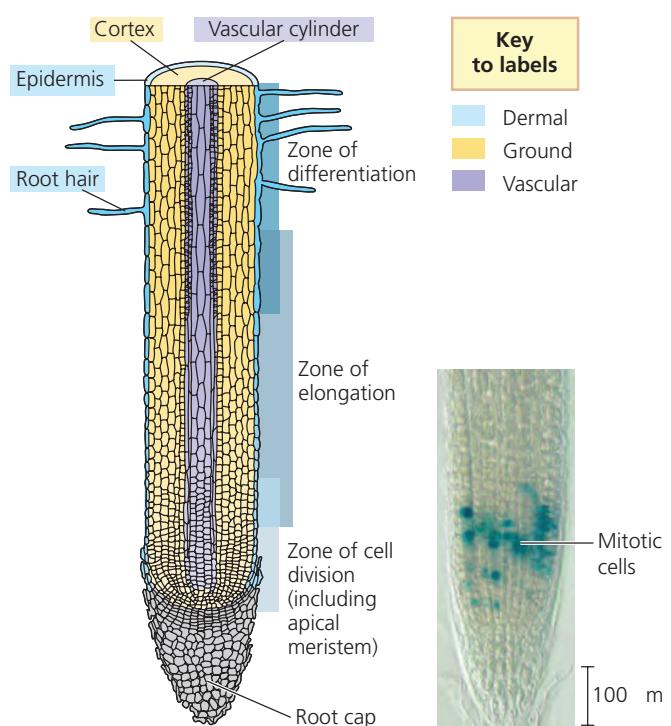
## CONCEPT 35.3

### Primary growth lengthens roots and shoots

As you have learned, primary growth arises directly from cells produced by apical meristems. In herbaceous plants, the entire plant consists of primary growth, whereas in woody plants, only the nonwoody, more recently formed parts of the plant are 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**, which protects the delicate apical meristem as the root pushes through the abrasive soil during primary growth. The root cap also secretes a polysaccharide slime that lubricates the soil around the 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 (Figure 35.13).



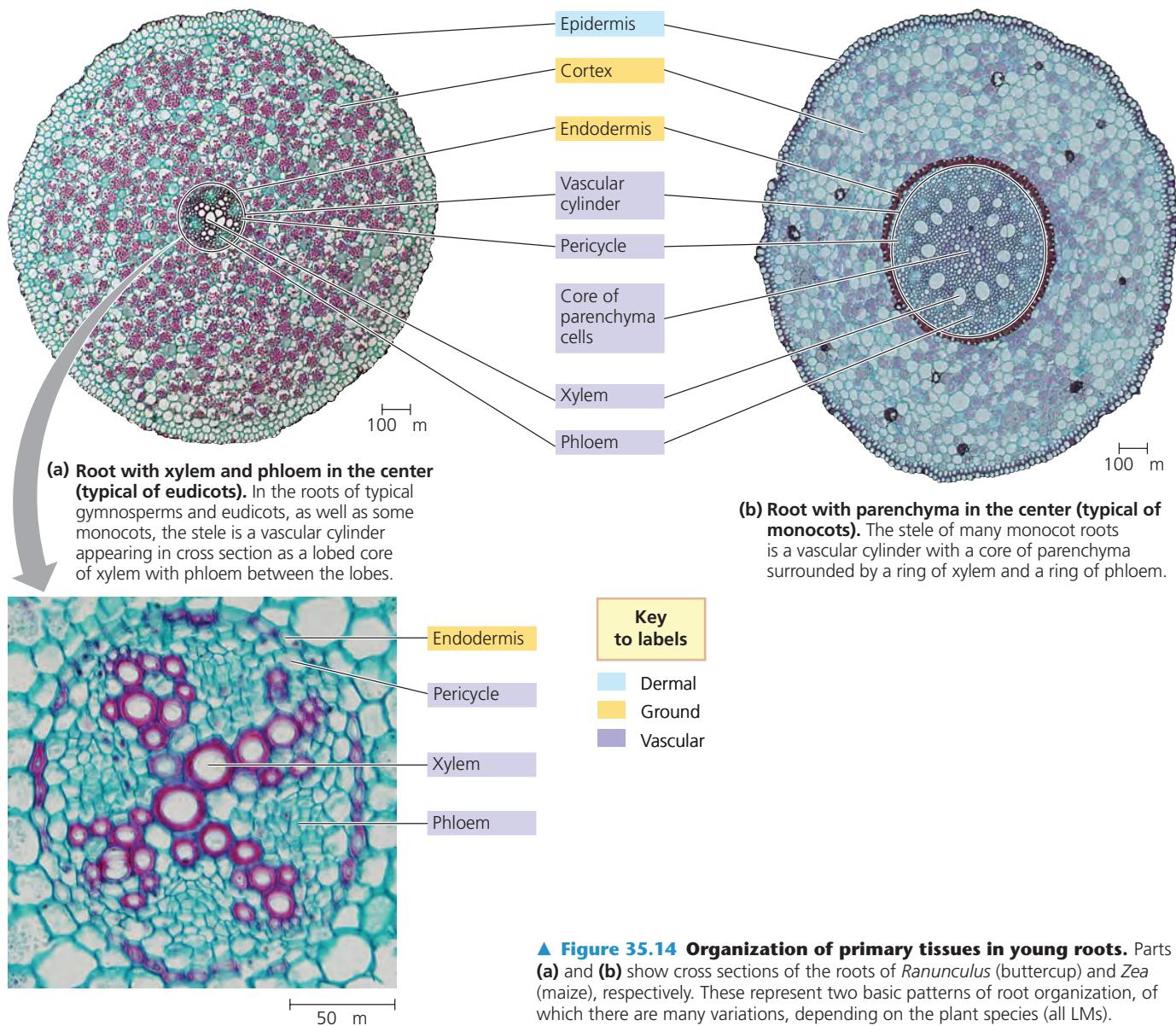
▲ Figure 35.13 Primary growth of a root. The diagram depicts the anatomical features of the tip of a typical eudicot root. The apical meristem produces all the cells of the root and the root cap. Most lengthening of the root occurs in the zone of elongation. In the micrograph, cells undergoing mitosis in the apical meristem are revealed by staining for cyclin, a protein that plays an important role in cell division (LM).

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

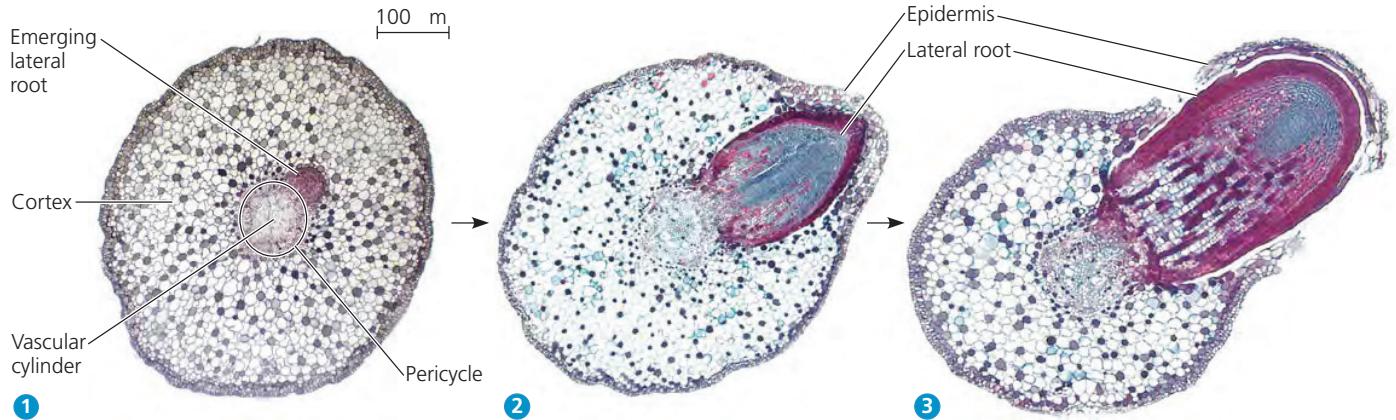
The primary growth of a root produces its epidermis, ground tissue, and vascular tissue. **Figure 35.14** shows in

cross section the three primary tissue systems in the young roots of a eudicot (*Ranunculus*, buttercup) and a monocot (*Zea*, maize). Water and minerals absorbed from the soil must enter through the root's epidermis. Root hairs, which account for much of this absorption, enhance this process by greatly increasing the surface area of the epidermis.

In angiosperm roots, the stele is a vascular cylinder, consisting of a solid core of xylem and phloem (**Figure 35.14a**). 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 parenchyma cells surrounded by a ring of xylem and a ring of phloem (**Figure 35.14b**).



▲ **Figure 35.14 Organization of primary tissues in young roots.** Parts (a) and (b) show cross sections of the roots of *Ranunculus* (buttercup) and *Zea* (maize), respectively. These represent two basic patterns of root organization, of which there are many variations, depending on the plant species (all LMs).



**▲ Figure 35.15 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, fills the cortex, the region between the vascular cylinder and epidermis. Cells within the ground tissue store carbohydrates and absorb water and minerals from the soil. The innermost layer of the cortex is called the **endodermis**, a cylinder one cell thick that forms the boundary with the vascular cylinder. As you will see in Chapter 36, the endodermis is a selective barrier that regulates passage of substances from the soil into the vascular cylinder.

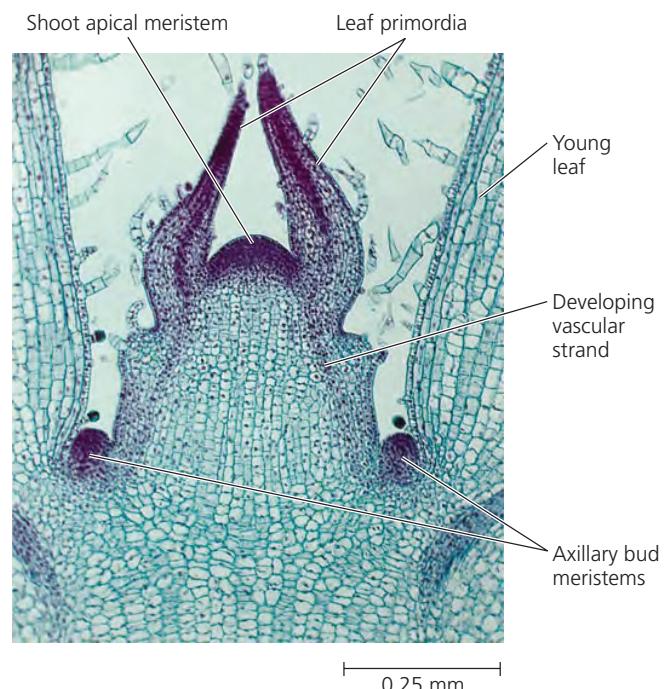
Lateral roots arise from the **pericycle**, the outermost cell layer in the vascular cylinder, which is adjacent to and just inside the endodermis (see Figure 35.14). A lateral root pushes through the cortex and epidermis until it emerges from the established root (**Figure 35.15**).

### Primary Growth of Shoots

A shoot apical meristem is a dome-shaped mass of dividing cells at the shoot tip (**Figure 35.16**). Leaves develop from **leaf primordia** (singular, *primordium*), finger-like projections along the sides of the 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 depends mainly on its proximity to an active apical bud. Generally, the closer an axillary bud is to an active apical bud, the more inhibited it is.

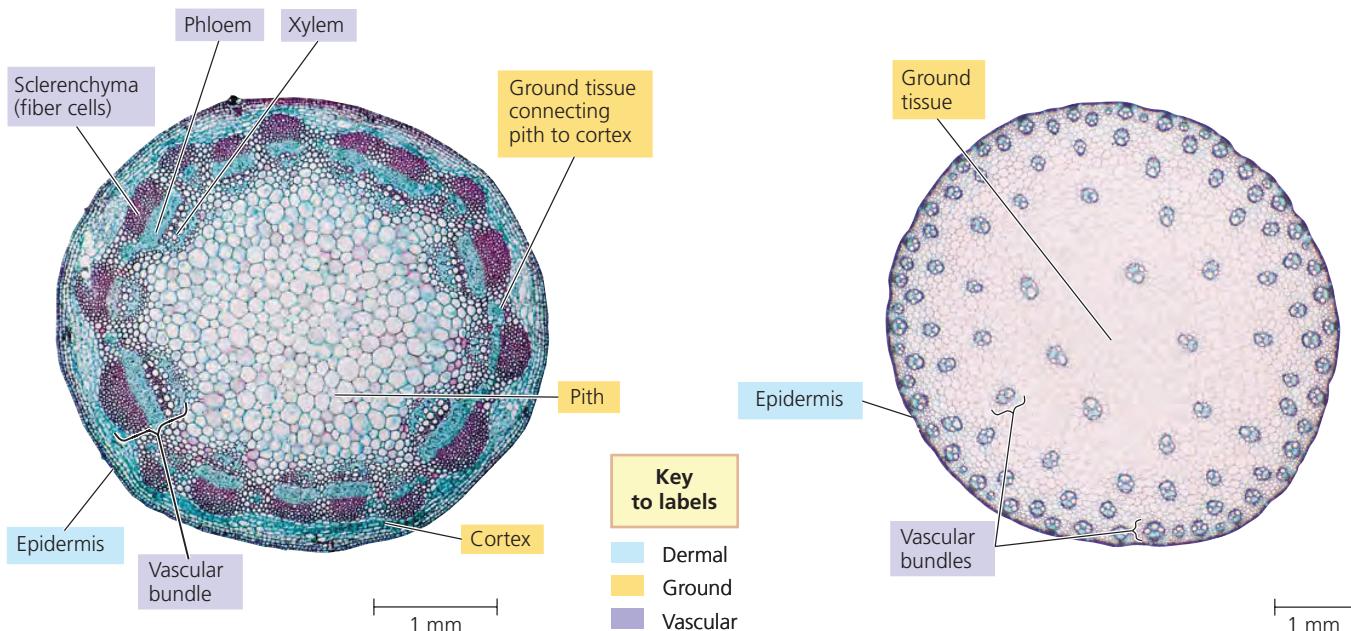
In some monocots, particularly grasses, meristematic activity occurs at the bases of stems and leaves. These areas, called *intercalary meristems*, allow damaged leaves to rapidly regrow, which accounts for the ability of lawns to grow following mowing. The ability of grasses to regrow leaves by intercalary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



**▲ Figure 35.16 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).

### 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 35.15), lateral shoots develop from axillary bud meristems on the stem's surface and disrupt no other tissues (see Figure 35.16). The vascular bundles of the stem converge with the root's vascular cylinder in a zone of transition located near the soil surface.



**(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 35.17 Organization of primary tissues in young stems.

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

In most eudicot species, the vascular tissue consists of vascular bundles arranged in a ring (Figure 35.17a). 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 35.17b). 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.

### Tissue Organization of Leaves

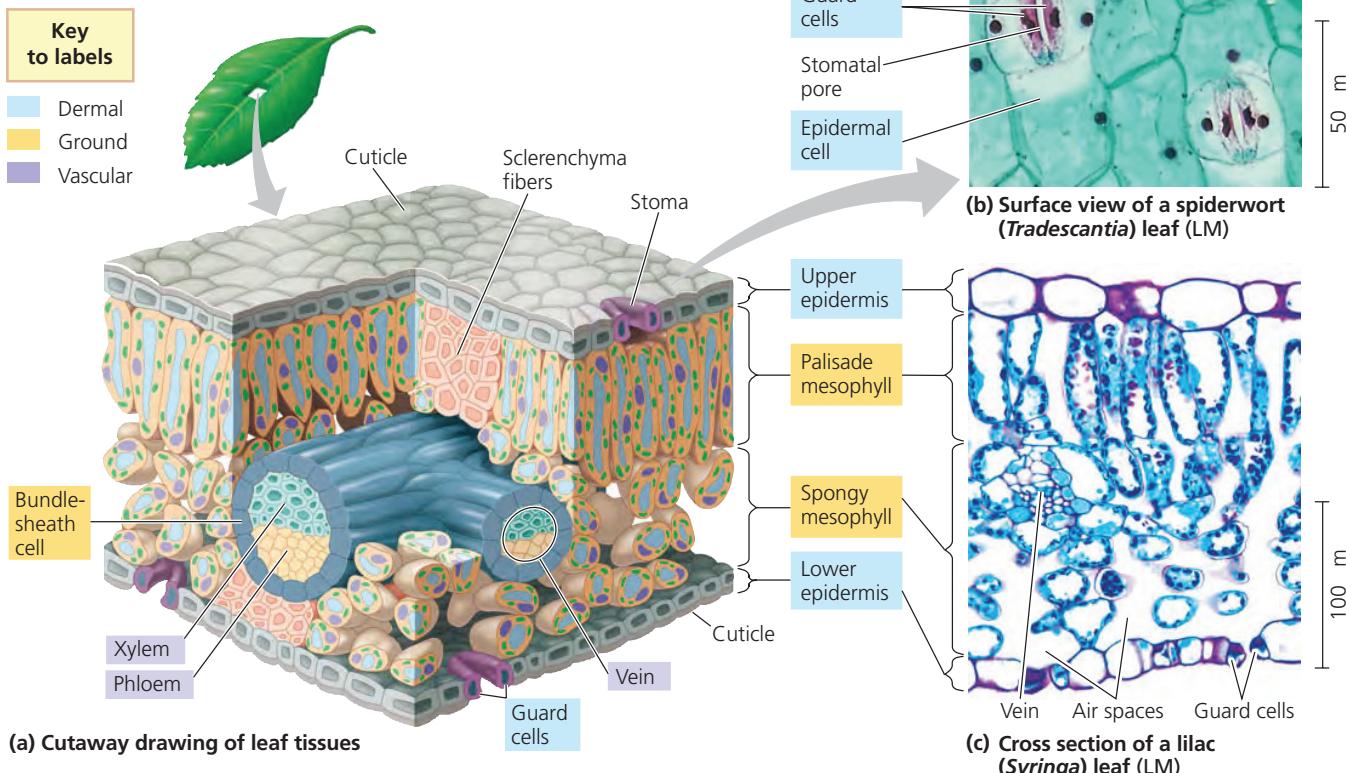
Figure 35.18 provides an overview of leaf structure. The epidermis is interrupted by pores called **stomata** (singular, *stoma*), which allow exchange of CO<sub>2</sub> and O<sub>2</sub> between the surrounding air and the photosynthetic cells inside the leaf. In addition to regulating CO<sub>2</sub> 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 **guard cells**, which regulate the opening and closing of the pore. We'll discuss stomata in detail in Chapter 36.

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 mesophylls of many eudicots have 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. *Spongy mesophyll* is below the palisade mesophyll. These parenchyma cells are more loosely arranged, with a labyrinth of air spaces through which CO<sub>2</sub> and oxygen circulate around the cells and up to the palisade region. The air spaces are particularly large in the vicinity of stomata, where CO<sub>2</sub> is taken up from the outside air and O<sub>2</sub> is discharged.

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 shape of the leaf. Each vein is enclosed by a protective *bundle sheath*, consisting of one or more layers of cells, usually parenchyma cells. Bundle sheath cells are particularly prominent in leaves of plant species that undergo C<sub>4</sub> photosynthesis (see Chapter 10).

▼ Figure 35.18 Leaf anatomy.



### CONCEPT CHECK 35.3

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 6.8 on p. 100 and the discussion of analogy on p. 540 of Concept 26.2.)

For suggested answers, see Appendix A.

produces a tough, thick covering consisting mainly of wax-impregnated cells that protect the stem from water loss and from invasion by insects, bacteria, and fungi. All gymnosperm species and many eudicot species undergo secondary growth, but it is rare in monocots.

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 thickens stems and roots in older regions where primary growth has stopped. The process is similar in shoots and roots. **Figure 35.19**, on the next page, provides an overview of growth in a woody stem.

### The Vascular Cambium and Secondary Vascular Tissue

The vascular cambium is a cylinder of meristematic cells, often only one cell thick. It increases in circumference and also adds layers of secondary xylem to its interior and secondary phloem to its exterior. Each layer has a larger diameter than the previous layer (see Figure 35.19). In this way, the vascular cambium thickens roots and stems.

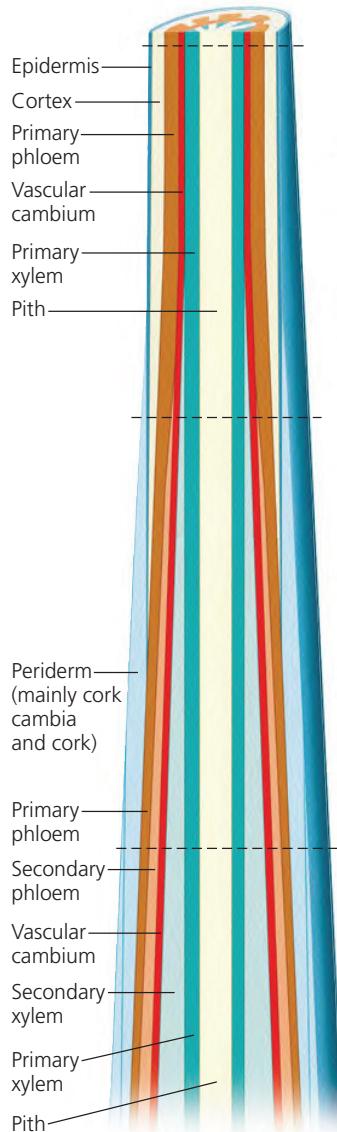
In a typical woody stem, the vascular cambium consists of a continuous cylinder of undifferentiated parenchyma cells, located outside the pith and primary xylem and to the inside of the cortex and primary phloem. In a typical woody root, the vascular cambium forms to the exterior of the primary xylem and interior to the primary phloem and pericycle.

### CONCEPT 35.4

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

As you have seen, primary growth arises from apical meristems and involves the production and elongation of roots, stems, and leaves. In contrast, secondary growth, the growth in thickness produced by lateral meristems, 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

**(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 (see next page).

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.

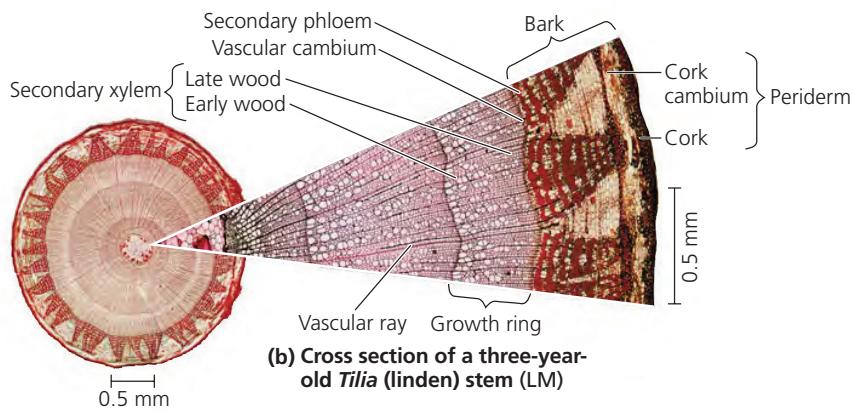
5 In year 2 of secondary growth, the vascular cambium produces more secondary xylem and phloem, and the cork cambium produces more cork.

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.

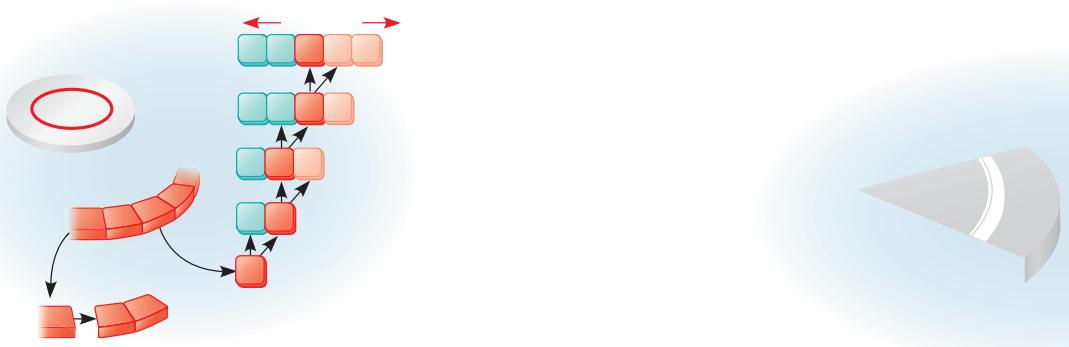
8 Each cork cambium and the tissues it produces form a layer of periderm.

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



**▲ Figure 35.19 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?



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 35.22). The newest, outer layers of secondary xylem still transport xylem sap and are therefore known as *sapwood*. That is why a large tree can survive even if the center of its trunk is hollow (Figure 35.23). 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 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 two tissues produced by the first cork cambium, a cylinder of dividing cells that arises in the outer cortex of stems (see Figure 35.19a) and in the outer layer of the pericycle in roots. One tissue, called *phellogen*, is a thin layer of parenchyma cells that forms to the interior of the cork cambium. The other tissue consists of 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. The cork tissue then functions as a barrier that helps protect the stem or root from water loss, physical damage, and pathogens. Each cork cambium and the tissues it produces comprise a layer of periderm.

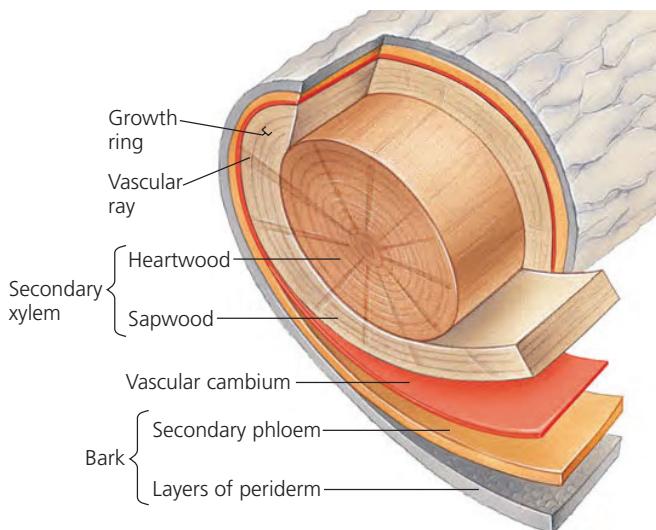
Because cork cells have suberin and are usually compacted together, most of the periderm is impermeable to water and gases, unlike the epidermis. In most plants, therefore, water and minerals are absorbed primarily in the youngest parts of roots. The older parts of roots anchor the plant and transport water and solutes between the soil and shoots. 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 35.19a.

The thickening of a stem or root often splits the first cork cambium, which loses its meristematic activity and differentiates into cork cells. A new cork cambium forms to the inside, resulting in another layer of periderm. As this process continues, older layers of periderm are sloughed off, as you can see in the cracked, peeling bark of many tree trunks.

There is a popular misconception that bark consists only of the protective outer covering of a woody stem or root. Actually, **bark** includes all tissues external to the vascular cambium. Moving outward, its main components are the secondary phloem (produced by the vascular cambium), the most recent periderm, and all the older layers of periderm (see Figure 35.22).

### Evolution of Secondary Growth

**EVOLUTION** Although the genome of one tree species, the poplar (*Populus trichocarpa*), has been sequenced, studying the molecular biology of secondary growth is difficult



▲ Figure 35.22 Anatomy of a tree trunk.



◀ Figure 35.23 Is this tree living or dead? The Wawona Sequoia tunnel in Yosemite National Park in California was cut in 1881 as a tourist attraction. This giant sequoia (*Sequoiadendron giganteum*) lived for another 88 years before falling during a severe winter. It was 71.3 m tall and estimated to be 2,100 years old. Though conservation policies today would forbid the mutilation of such an important specimen, the Wawona Sequoia did teach a valuable botanical lesson: Trees can survive the excision of large portions of their heartwood.

because woody plants take years to develop and require large areas to grow. Surprisingly, some insights into the evolution of secondary growth have been achieved by studying the herbaceous plant *Arabidopsis thaliana*. Researchers have found that they can stimulate some secondary growth in *Arabidopsis* stems by adding weights to the plant. These findings suggest that weight carried by the stem activates a developmental program leading to wood formation. Moreover, several developmental genes that regulate shoot apical meristems in *Arabidopsis* have been found to regulate vascular cambium activity in *Populus*. This suggests that the processes of primary and secondary growth are evolutionarily more closely related than previously thought.

### CONCEPT CHECK 35.4

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. Stomata and lenticels are both involved in exchange of CO<sub>2</sub> and O<sub>2</sub>. Why do stomata need to be able to close, but lenticels do not?
3. Would you expect a tropical tree to have distinct growth rings? Why or why not?
4. **WHAT IF?** If a complete ring of bark is removed around a tree trunk (a process called girdling), the tree usually dies. Explain why.

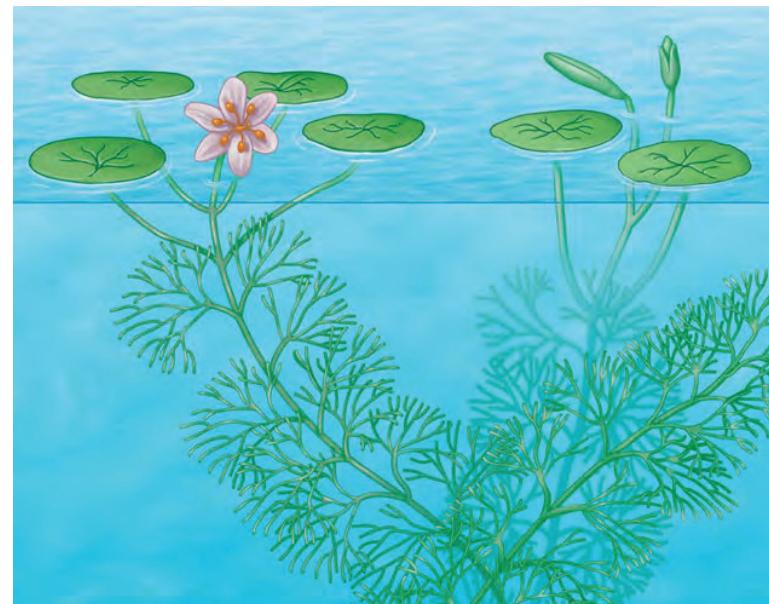
For suggested answers, see Appendix A.

### CONCEPT 35.5

## Growth, morphogenesis, and cell differentiation produce the plant body

As you'll recall, the specific series of changes by which cells form tissues, organs, and organisms is called **development**. Development unfolds according to the genetic information that an organism inherits from its parents but is also influenced by the external environment. A single genotype can produce different phenotypes in different environments. For example, the aquatic plant called the fanwort (*Cabomba caroliniana*) forms two very different types of leaves, depending on whether or not the shoot apical meristem is submerged (**Figure 35.24**). This ability to alter form in response to local environmental conditions is called *developmental plasticity*. Dramatic examples of plasticity, as in *Cabomba*, are much more common in plants than in animals and may help compensate for plants' inability to escape adverse conditions by moving.

Let's briefly review the three overlapping processes in development: growth, morphogenesis, and cell differentiation. **Growth** is an irreversible increase in size. **Morphogenesis** (from the Greek *morphe*, shape, and *genesis*, creation) is the



▲ **Figure 35.24** **Developmental plasticity in the aquatic plant *Cabomba caroliniana*.** The underwater leaves of *Cabomba* are feathery, an adaptation that protects them from damage by lessening their resistance to moving water. In contrast, the surface leaves are pads that aid in flotation. Both leaf types have genetically identical cells, but their different environments result in the turning on or off of different genes during leaf development.

process that gives a tissue, organ, or organism its shape and determines the positions of cell types. Cell **differentiation** is the process by which cells with the same genes become different from one another. We'll examine these three processes in turn, but first we'll discuss how applying techniques of modern molecular biology to model organisms, particularly *Arabidopsis thaliana*, has revolutionized the study of plant development.

### Model Organisms: Revolutionizing the Study of Plants

As in other branches of biology, molecular biological techniques and a focus on model organisms such as *Arabidopsis thaliana* have catalyzed a research explosion in the last two decades. *Arabidopsis*, a tiny weed in the mustard family, has no inherent agricultural value but is a favored model organism of plant geneticists and molecular biologists for many reasons. It is so small that thousands of plants can be cultivated in a few square meters of lab space. It also has a short generation time, taking about six weeks for a seed to grow into a mature plant that produces more seeds. This rapid maturation enables biologists to conduct genetic cross experiments in a relatively short time frame. One plant can produce over 5,000 seeds, another property that makes *Arabidopsis* useful for genetic analysis.

Beyond these basic traits, the plant's genome makes it particularly well suited for analysis by molecular genetic methods. The *Arabidopsis* genome, which includes about 27,400 protein-encoding genes, is among the smallest known in plants. Furthermore, the plant has only five pairs



**Table 35.1** *Arabidopsis thaliana* Gene Functions

Gene Function	Number of Genes	Percent of Total*
Unknown function	9,967	36%
Protein metabolism	3,204	12%
Transport	2,253	8%
Transcription	2,039	7%
Response to stress	1,811	7%
Development	1,627	6%
Environmental sensing	1,627	6%
Cell division and organization	1,201	4%
Signal transduction	1,097	4%
Nucleic acid metabolism	333	1%
Energy pathways	304	1%
Other cellular processes	8,959	33%
Other metabolic processes	8,476	31%
Other biological processes	1,592	6%

Source: The *Arabidopsis* Information Resource, 2010

\*The percentages total more than 100% because some genes are listed in more than one category.

of chromosomes, making it easier for geneticists to locate specific genes. Because *Arabidopsis* has such a small genome, it was the first plant to have its entire genome sequenced—a six-year, multinational effort (Table 35.1).

Another property that makes *Arabidopsis* attractive to molecular biologists is that the plant's cells are easy to transform with foreign DNA. The transformation of *Arabidopsis* cells is useful for studying how genes function and interact with other genes. Biologists usually transform plant cells by infecting them with genetically altered varieties of the bacterium *Agrobacterium tumefaciens* (see Figure 20.26). *Arabidopsis* researchers also use a variation of this technique to create a plant with a particular mutation. Studying the effect of a mutation in a gene often yields important information about the gene's normal function. Because *Agrobacterium* inserts its transforming DNA randomly into the genome, the DNA may be inserted in the middle of a gene. Such an insertion usually destroys the function of the disrupted gene, resulting in a "knock-out mutant."

Large-scale projects using this technique are under way to determine the function of every gene in *Arabidopsis*. By identifying each gene's function and tracking every biochemical pathway, researchers aim to determine the blueprints for plant development, a major goal of systems biology. It may one day be possible to create a computer-generated "virtual plant" that enables researchers to visualize which genes are activated in different parts of the plant as the plant develops.

Basic research involving model organisms such as *Arabidopsis* has accelerated the pace of discovery in the plant

sciences, including the identification of the complex genetic pathways underlying plant structure. As you read more about this, you'll be able to appreciate not just the power of studying model organisms but also the rich history of plant investigation that underpins all modern plant research.

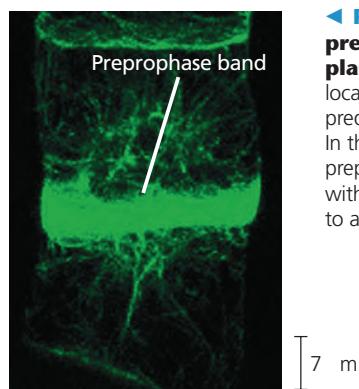
## Growth: Cell Division and Cell Expansion

Cell division enhances the potential for growth by increasing the number of cells, but plant growth itself is brought about by cell enlargement. The process of plant cell division is described more fully in Chapter 12 (see Figure 12.10), and Chapter 39 discusses the process of cell elongation (see Figure 39.8). Here we are more concerned with how these processes contribute to plant form.

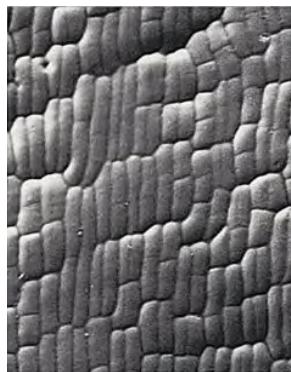
### The Plane and Symmetry of Cell Division

The new cell walls that bisect plant cells during cytokinesis develop from the cell plate (see Figure 12.10). The precise plane of cell division, determined during late interphase, usually corresponds to the shortest path that will halve the volume of the parent cell. The first sign of this spatial orientation is rearrangement of the cytoskeleton. Microtubules in the cytoplasm become concentrated into a ring called the *preprophase band* (Figure 35.25). The band disappears before metaphase but predicts the future plane of cell division.

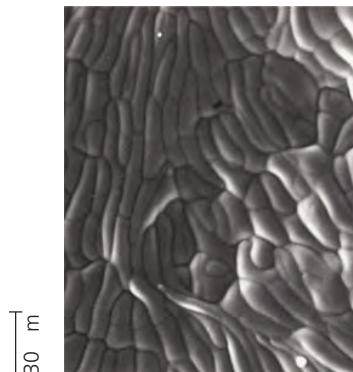
It has long been thought that the plane of cell division provides the foundation for the forms of plant organs, but studies of an internally disorganized maize mutant called *tangled-1* have led researchers to question that view. In wild-type maize plants, leaf cells divide either transversely (crosswise) or longitudinally relative to the axis of the parent cell. Transverse divisions are associated with leaf elongation, and longitudinal divisions are associated with leaf broadening. In *tangled-1* leaves, transverse divisions are normal, but most longitudinal divisions are oriented abnormally, leading to cells that are crooked or curved (Figure 35.26). However, these abnormal cell divisions do not affect leaf shape. Mutant leaves grow more slowly than wild-type leaves, but their overall shapes remain normal, indicating that leaf shape does not depend solely on precise spatial control of cell division. In addition,



**◀ Figure 35.25** The preprophase band and the plane of cell division. The location of the preprophase band predicts the plane of cell division. In this light micrograph, the preprophase band has been stained with green fluorescent protein bound to a microtubule-associated protein.



Leaf epidermal cells of wild-type maize



Leaf epidermal cells of *tangled-1* maize mutant

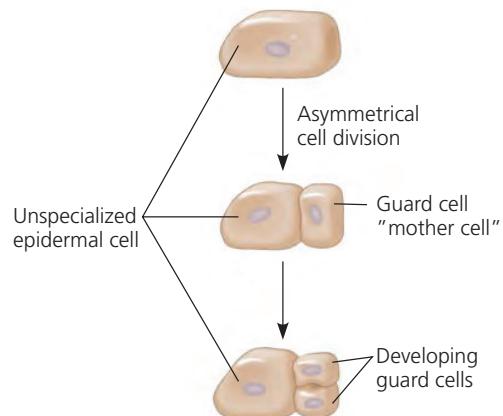
**▲ Figure 35.26 Cell division patterns in wild-type versus mutant maize plants.** Compared with the epidermal cells of wild-type maize plants (left), the epidermal cells of the *tangled-1* mutant of maize (right) are highly disordered. Nevertheless, *tangled-1* maize plants produce normal-looking leaves.

recent evidence suggests that the shape of the shoot apex in *Arabidopsis* depends not on the plane of cell division but on microtubule-dependent mechanical stresses stemming from the “crowding” associated with cell proliferation and growth.

Although the *plane* of cell division does not determine the shape of plant organs, the *symmetry* of cell division—the distribution of cytoplasm between daughter cells—is important in determining cell fate. Not all plant cells divide into two equal halves during mitosis. Although chromosomes are allocated to daughter cells equally during mitosis, the cytoplasm may sometimes divide asymmetrically. *Asymmetrical cell division*, in which one daughter cell receives more cytoplasm than the other during mitosis, usually signals a key event in development. For example, the formation of guard cells typically involves both an asymmetrical cell division and a change in the plane of cell division. An epidermal cell divides asymmetrically, forming a large cell that remains an unspecialized epidermal cell and a small cell that becomes the guard cell “mother cell.” Guard cells form when this small mother cell divides in a plane perpendicular to the first cell division (Figure 35.27). Thus, asymmetrical cell division generates cells with different fates—that is, cells that mature into different types.

Asymmetrical cell divisions also play a role in the establishment of **polarity**, the condition of having structural or chemical differences at opposite ends of an organism. Plants typically have an axis, with a root end and a shoot end. Such polarity is most obvious in morphological differences, but it is also apparent in physiological properties, including the movement of the hormone auxin in a single direction and the emergence of adventitious roots and shoots from “cuttings.” Adventitious roots form within the root end of a stem cutting, and adventitious shoots arise from the shoot end of a root cutting.

The first division of a plant zygote is normally asymmetrical, initiating polarization of the plant body into shoot



**▲ Figure 35.27 Asymmetrical cell division and stomatal development.** An asymmetrical cell division precedes the development of epidermal guard cells, the cells that border stomata (see Figure 35.18).

and root. This polarity is difficult to reverse experimentally, indicating that the proper establishment of axial polarity is a critical step in a plant’s morphogenesis. In the *gnom* (from the German for a dwarf and misshapen creature) mutant of *Arabidopsis*, the establishment of polarity is defective. The first cell division of the zygote is abnormal because it is symmetrical, and the resulting ball-shaped plant has neither roots nor leaves (Figure 35.28).

### Orientation of Cell Expansion

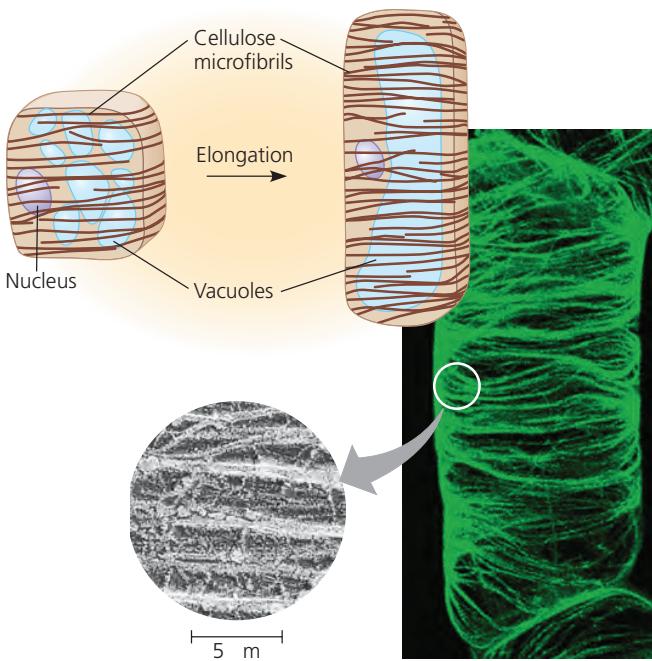
Before discussing how cell expansion contributes to plant form, it is useful to consider the difference in cell expansion between plants and animals. Animal cells grow mainly by synthesizing protein-rich cytoplasm, a metabolically expensive process. Growing plant cells also produce additional protein-rich material in their cytoplasm, but water uptake typically accounts for about 90% of expansion. Most of this



**▲ Figure 35.28 Establishment of axial polarity.** The normal *Arabidopsis* seedling (left) has a shoot end and a root end. In the *gnom* mutant (right), the first division of the zygote was not asymmetrical; as a result, the plant is ball-shaped and lacks leaves and roots. The defect in *gnom* mutants has been traced to an inability to transport the hormone auxin in a polar manner.

water is packaged in the large central vacuole. Vacuolar sap is very dilute and nearly devoid of the energetically expensive macromolecules that are found in great abundance in the rest of the cytoplasm. Large vacuoles are therefore a “cheap” way of filling space, enabling a plant to grow rapidly and economically. Bamboo shoots, for instance, can elongate more than 2 m per week. Rapid and efficient extensibility of shoots and roots was an important evolutionary adaptation that increased their exposure to light and soil.

Plant cells rarely expand equally in all directions. Their greatest expansion is usually oriented along the plant’s main axis. For example, cells near the tip of the root may elongate up to 20 times their original length, with relatively little increase in width. The orientation of cellulose microfibrils in the innermost layers of the cell wall causes this differential growth. The microfibrils do not stretch, so the cell expands mainly perpendicular to the main orientation of the microfibrils, as shown in **Figure 35.29**. As with the plane of cell division, microtubules play a key role in regulating the plane of cell expansion. It is the orientation of microtubules in the cell’s outermost cytoplasm that determines the orientation of cellulose microfibrils, the basic structural units of the cell wall.



**▲ Figure 35.29 The orientation of plant cell expansion.** Growing plant cells expand mainly through water uptake. In a growing cell, enzymes weaken cross-links in the cell wall, allowing it to expand as water diffuses into the vacuole by osmosis; at the same time, more microfibrils are made. The orientation of cell growth is mainly in the plane perpendicular to the orientation of cellulose microfibrils in the wall. The orientation of microtubules in the cell’s outermost cytoplasm determines the orientation of the cellulose microfibrils (fluorescent LM). The microfibrils are embedded in a matrix of other (noncellulose) polysaccharides, some of which form the cross-links visible in the TEM.

## Morphogenesis and Pattern Formation

A plant’s body is more than a collection of dividing and expanding cells. During morphogenesis, cells acquire different identities in an ordered spatial arrangement. For example, dermal tissue forms on the exterior, and vascular tissue in the interior—never the other way around. The development of specific structures in specific locations is called **pattern formation**.

Two types of hypotheses have been put forward to explain how the fate of plant cells is determined during pattern formation. Hypotheses based on *lineage-based mechanisms* propose that cell fate is determined early in development and that cells pass on this destiny to their progeny. According to this view, the basic pattern of cell differentiation is mapped out according to the directions in which meristematic cells divide and expand. On the other hand, hypotheses based on *position-based mechanisms* propose that the cell’s final position in an emerging organ determines what kind of cell it will become. In support of this view, experimental manipulations of cell positions by surgically destroying certain cells with lasers have demonstrated that a plant cell’s fate is established late in development and largely depends on signaling from neighboring cells.

In contrast, cell fate in animals is largely determined by lineage-dependent mechanisms involving transcription factors. The homeotic (*Hox*) genes that encode such transcription factors are critical for the proper number and placement of embryonic structures, such as legs and antennae, in the fruit fly *Drosophila* (see Figure 18.19). Interestingly, maize has a homolog of *Hox* genes called *KNOTTED-1*, but unlike its counterparts in the animal world, *KNOTTED-1* does not affect the proper number or placement of plant organs. As you will see, an unrelated class of transcription factors called *MADS-box* proteins plays that role in plants. *KNOTTED-1* is, however, important in the development of leaf morphology, including the production of compound leaves. If the *KNOTTED-1* gene is expressed in greater quantity than normal in the genome of tomato plants, the normally compound leaves become “super-compound” (**Figure 35.30**).



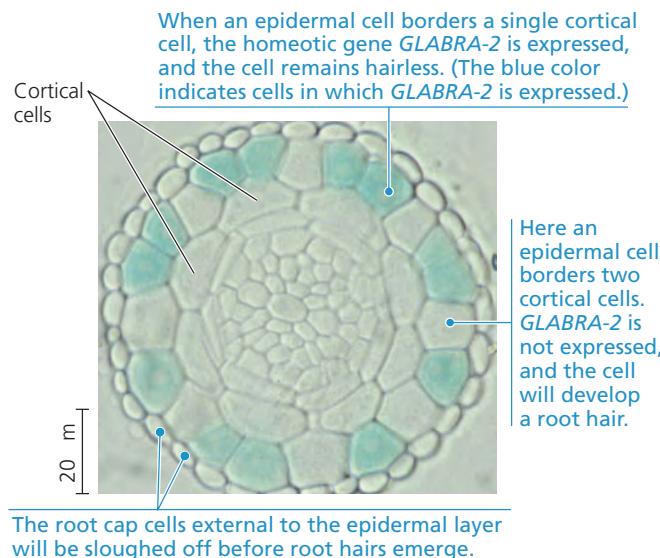
**▲ Figure 35.30 Overexpression of a *Hox*-like gene in leaf formation.** *KNOTTED-1* is a gene involved in leaf and leaflet formation. An increase in its expression in tomato plants results in leaves that are “super-compound” (right) compared with normal leaves (left).

## Gene Expression and Control of Cell Differentiation

Cells of a developing organism can synthesize different proteins and diverge in structure and function even though they share a common genome. If a mature cell removed from a root or leaf can dedifferentiate in tissue culture and give rise to the diverse cell types of a plant, then it must possess all the genes necessary to make any kind of plant cell (see Figure 20.17). Therefore, 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, not by cell lineage. If an undifferentiated cell is displaced, it will differentiate into a cell type appropriate to its new position. One aspect of plant cell interaction is the communication of positional information from one cell to another.

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 *Arabidopsis*: 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 homeotic gene called *GLABRA-2* (from the Latin *glaber*, bald) is required for appropriate root hair distribution (Figure 35.31). Researchers have



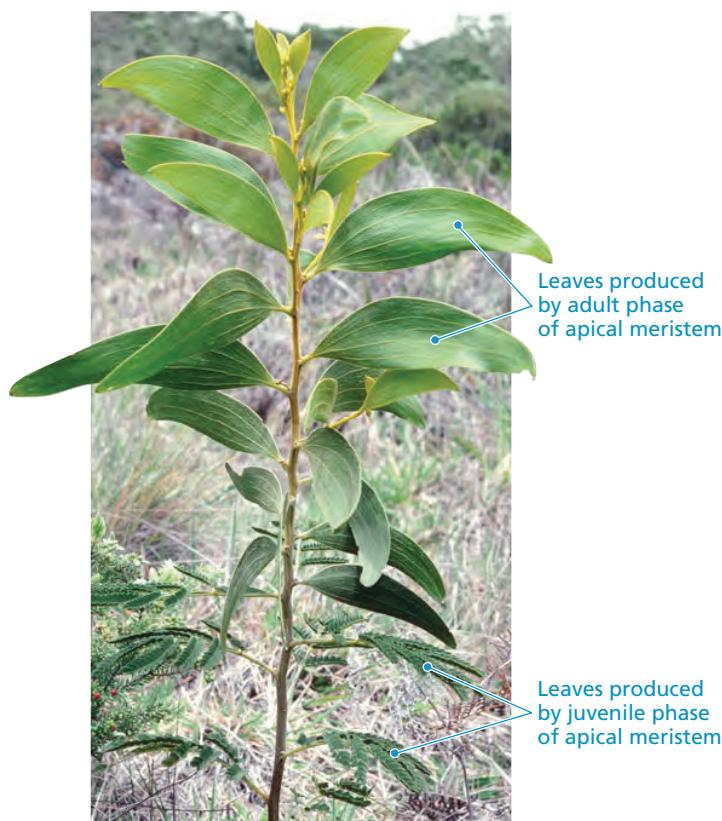
▲ **Figure 35.31** Control of root hair differentiation by a homeotic gene (LM).

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

demonstrated this by coupling the *GLABRA-2* 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.

## Shifts in Development: Phase Changes

Multicellular organisms generally pass through developmental stages. In humans, these are infancy, childhood, adolescence, and adulthood, with puberty as the dividing line between the nonreproductive and reproductive stages. Plants also pass through stages, developing from a juvenile stage to an adult vegetative stage to an adult reproductive stage. In animals, the developmental changes take place throughout the entire organism, such as when a larva develops into an adult animal. In contrast, plant developmental stages, called *phases*, occur within a single region, the shoot apical meristem. The morphological changes that arise from these transitions in shoot apical meristem activity are called **phase changes**. During the transition from a juvenile phase to an adult phase, the most obvious morphological changes typically occur in leaf size and shape (Figure 35.32). Juvenile nodes and internodes



▲ **Figure 35.32** Phase change in the shoot system of *Acacia koa*. This native of Hawaii has compound juvenile leaves, consisting of many small leaflets, and simple mature leaves. This dual foliage reflects a phase change in the development of the apical meristem of each shoot. Once a node forms, the developmental phase—juvenile or adult—is fixed; that is, compound leaves do not mature into simple leaves.

retain their juvenile status even after the shoot continues to elongate and the shoot apical meristem has changed to the adult phase. Therefore, any new leaves that develop on branches that emerge from axillary buds at juvenile nodes will also be juvenile, even though the apical meristem of the stem's main axis may have been producing mature nodes for years.

If environmental conditions permit, an adult plant is induced to flower. Biologists have made great progress in explaining the genetic control of floral development—the topic of the next section.

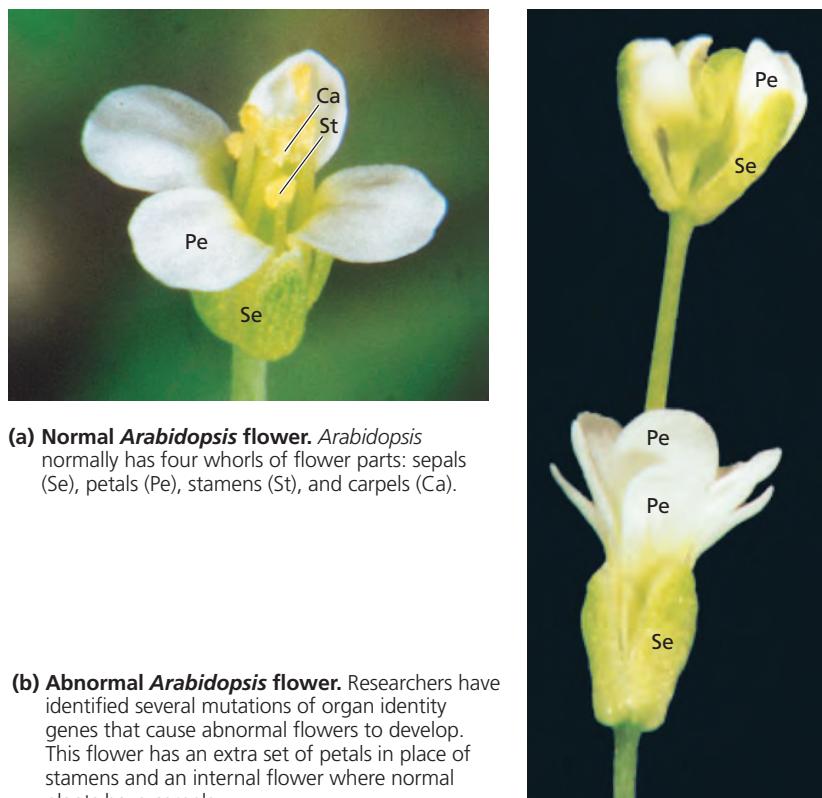
## Genetic Control of Flowering

Flower formation involves a phase change from vegetative growth to reproductive growth. 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 39.) Unlike vegetative growth, which is indeterminate, floral growth is determinate: The production of a flower by a shoot apical meristem stops the primary growth of that shoot. The transition from vegetative growth to flowering is associated with the switching on of floral **meristem identity genes**. The protein products of these genes are transcription factors that regulate the genes required for the conversion of the indeterminate vegetative meristems to determinate floral meristems.

When a shoot apical meristem is induced to flower, the order of each primordium's emergence determines its development into a specific type of floral organ—a sepal, petal, stamen, or carpel (see Figure 30.7 to review basic flower structure). These floral organs form four whorls that can be described roughly as concentric “circles” when viewed from above. Sepals form the first (outermost) whorl; petals form the second; stamens form the third; and carpels form the fourth (innermost) whorl. Plant biologists have identified several **organ identity genes** belonging to the *MADS-box* family that encode transcription factors that regulate the development of this characteristic floral pattern. Positional information determines which organ identity genes are expressed in a particular floral organ primordium. The result is the development of an emerging floral primordium into a specific floral organ. A mutation in a plant organ identity gene can cause abnormal floral development, such as petals growing in place of stamens (**Figure 35.33**). Some homeotic mutants with increased petal numbers produce showier flowers that are prized by gardeners.

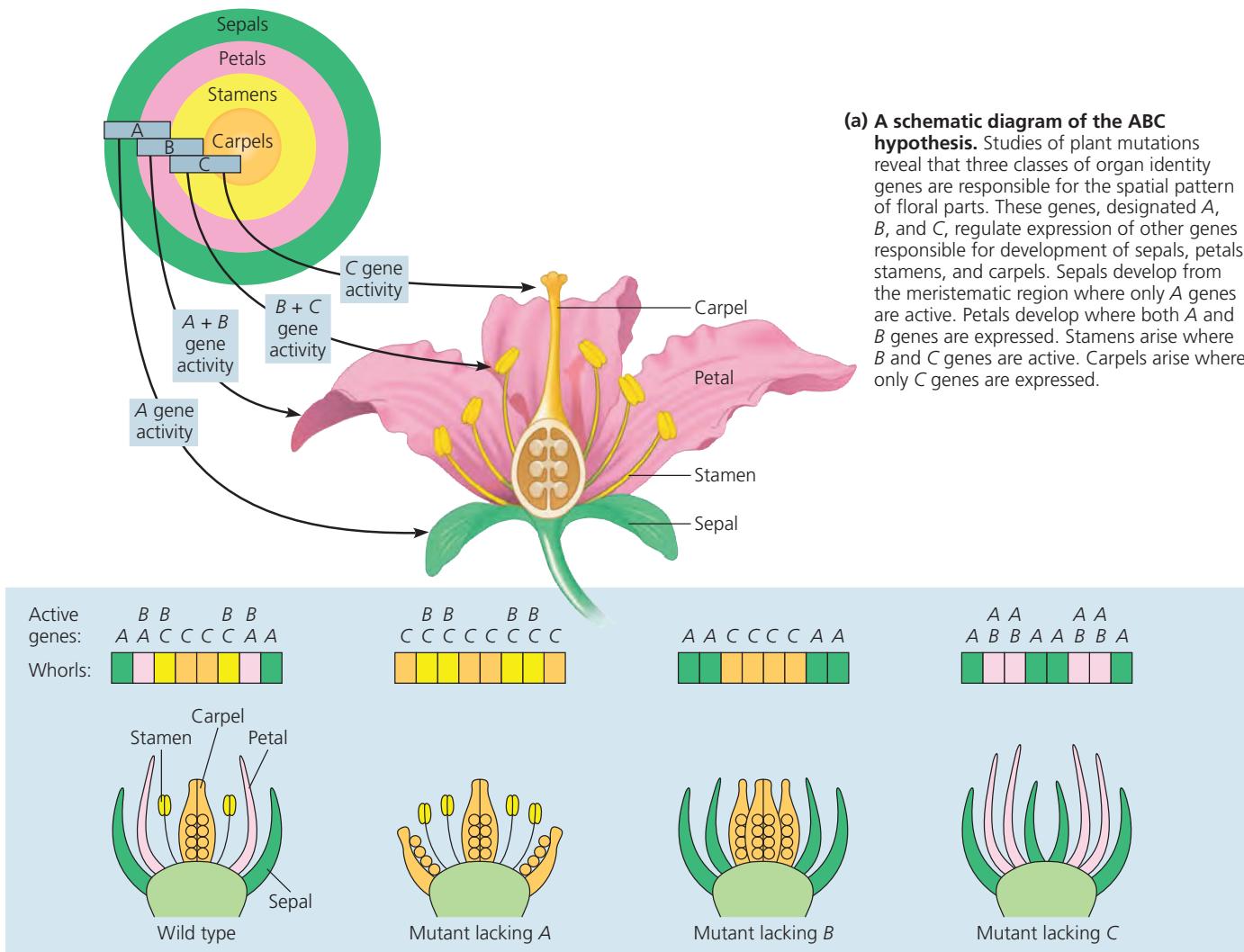
By studying mutants with abnormal flowers, researchers have identified and cloned three

classes of floral organ identity genes, and their studies are beginning to reveal how these genes function. **Figure 35.34a** shows a simplified version of the **ABC hypothesis** of flower formation, which proposes that three classes of genes direct the formation of the four types of floral organs. According to the ABC hypothesis, 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 arise where *A* and *B* genes are active; 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 35.34b** shows the floral patterns of mutants lacking each of the three classes of organ identity genes and depicts how the hypothesis accounts for the floral phenotypes. By constructing such hypotheses and designing experiments to test them, researchers are tracing the genetic basis of plant development.



▲ **Figure 35.33** Organ identity genes and pattern formation in flower development.

**MAKE CONNECTIONS** Review Concept 18.4 on pages 366–373, and provide another example of a homeotic gene mutation that leads to organs being produced in the wrong place.



**(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 35.34 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?

In dissecting the plant to examine its parts, as we have done in this chapter, we must remember that the whole plant functions as an integrated organism. In the following chapters, you'll learn more about how materials are transported within vascular plants (Chapter 36), how plants obtain nutrients (Chapter 37), how plants reproduce (Chapter 38, focusing on flowering plants), and how plant functions are coordinated (Chapter 39). As you read further, your understanding of plants will be enhanced by bearing in mind that the plant structures largely reflect evolutionary adaptations to the challenges of a photoautotrophic existence on land.

### CONCEPT CHECK 35.5

- How can two cells in a plant have vastly different structures even though they have the same genome?
- What are three differences between animal development and plant development?
- WHAT IF?** In some species, sepals look like petals, and both are collectively called “tepals.” Suggest an extension to the ABC hypothesis that could hypothetically account for the origin of tepals.

For suggested answers, see Appendix A.

# 35 CHAPTER REVIEW

## SUMMARY OF KEY CONCEPTS

### CONCEPT 35.1

Plants have a hierarchical organization consisting of organs, tissues, and cells (pp. 738–745)

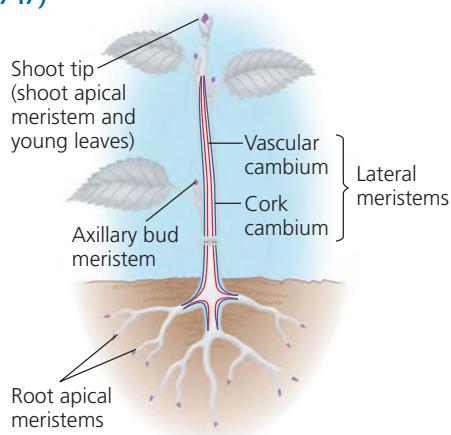
- Vascular plants have shoots consisting of **stems**, **leaves**, and, in angiosperms, flowers. **Roots** anchor the plant, absorb and conduct water and minerals, and store food. Leaves are attached to stem **nodes** and are the main **organs** of photosynthesis.
- Axillary buds**, in axils of leaves 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 35.2

Meristems generate cells for primary and secondary growth (pp. 746–747)



?

Which plant organs originate from the activity of meristems?

### CONCEPT 35.3

Primary growth lengthens roots and shoots (pp. 747–751)

- 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 35.4

Secondary growth increases the diameter of stems and roots in woody plants (pp. 751–755)

- 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?

### CONCEPT 35.5

Growth, morphogenesis, and cell differentiation produce the plant body (pp. 755–761)

- Cell division and cell expansion are the primary determinants of **growth**. A preprophase band of microtubules determines where a cell plate will form in a dividing cell. Microtubule orientation also affects the direction of cell elongation by controlling the orientation of cellulose microfibrils in the cell wall.
- Morphogenesis**, the development of body shape and organization, depends on cells responding to positional information from its neighbors.
- Cell differentiation**, arising from differential gene activation, enables cells within the plant to assume different functions despite having identical genomes. The way in which a plant cell differentiates is determined largely by the cell's position in the developing plant.
- Internal or environmental cues may cause a plant to switch from one developmental stage to another—for example, from developing juvenile leaves to developing mature leaves. Such morphological changes are called **phase changes**.
- Research on **organ identity genes** in developing flowers provides a model system for studying **pattern formation**. The **ABC hypothesis** identifies how three classes of organ identity genes control formation of sepals, petals, stamens, and carpels.

?

By what mechanism do plant cells tend to elongate along one axis instead of expanding like a balloon in all directions?

## TEST YOUR UNDERSTANDING

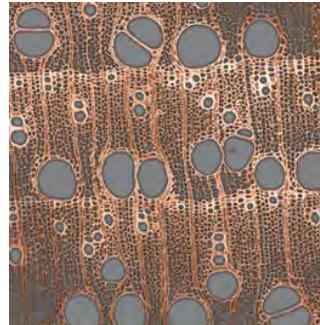
### LEVEL 1: KNOWLEDGE/COMPREHENSION

1. Most of the growth of a plant body is the result of
  - a. cell differentiation.
  - b. morphogenesis.
  - c. cell division.
  - d. cell elongation.
  - e. reproduction.
2. The innermost layer of the root cortex is the
  - a. core.
  - b. pericycle.
  - c. endodermis.
  - d. pith.
  - e. vascular cambium.
3. Heartwood and sapwood consist of
  - a. bark.
  - b. periderm.
  - c. secondary xylem.
  - d. secondary phloem.
  - e. cork.
4. The phase change of an apical meristem from the juvenile to the mature vegetative phase is often revealed by
  - a. a change in the morphology of the leaves produced.
  - b. the initiation of secondary growth.
  - c. the formation of lateral roots.
  - d. a change in the orientation of preprophase bands and cytoplasmic microtubules in lateral meristems.
  - e. the activation of floral meristem identity genes.

### LEVEL 2: APPLICATION/ANALYSIS

5. Based on the ABC hypothesis, what would be the structure of a flower from the outermost whorl that had normal expression of genes A and C and expression of gene B in all four whorls?
  - a. carpel-petal-petal-carpel
  - b. petal-petal-stamen-stamen
  - c. sepal-carpel-carpel-sepal
  - d. sepal-sepal-carpel-carpel
  - e. carpel-carpel-carpel-carpel
6. 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
7. 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

8. **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

#### 9. EVOLUTION CONNECTION

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 Chapter 25). What are some examples of exaptations in plant organs?

#### 10. 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.

#### 11. SCIENCE, TECHNOLOGY, AND SOCIETY

Hunger and malnutrition are urgent problems for many poor countries, and yet plant biologists in wealthy nations have focused most of their research efforts on *Arabidopsis thaliana*. Some people have argued that if plant biologists are truly concerned about fighting world hunger, they should focus their studies on crops such as cassava and plantain because they are staples for many of the world's poor. If you were an *Arabidopsis* researcher, how might you respond to these arguments?

#### 12. WRITE ABOUT A THEME

**Structure and Function** 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.

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