

35

The Plant Body



On November 1, 2002, John Quigley climbed into the branches of a 70-foot-tall oak tree estimated to be 150 to 400 years old. He stayed perched there until he was removed, 71 days later, to allow a housing developer to cut down the tree. That was a short stay, however, compared with Julia Butterfly Hill's sojourn in a 600-year-old redwood. In the year 2000, Hill created a perch 180 feet above ground and didn't come down to Earth until just over 2 years later, when the Pacific Lumber Company agreed to spare that tree and others in its immediate vicinity.

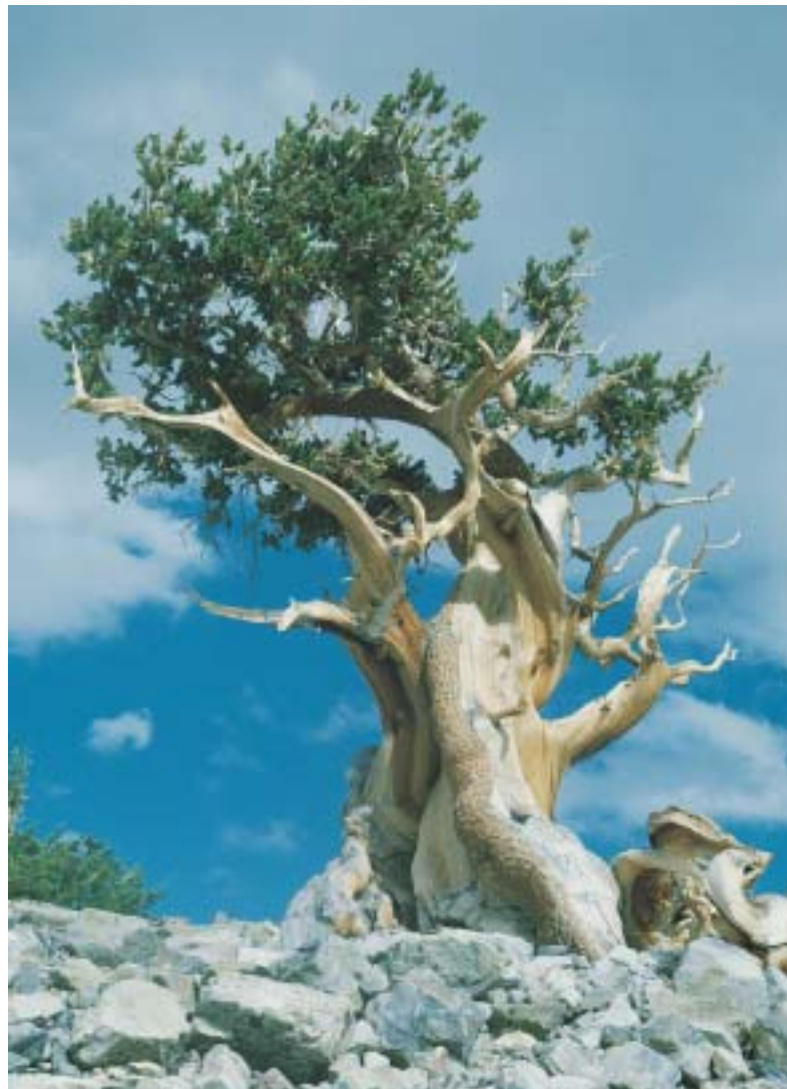
What prompts some people to tree-sit or protest in other ways against the removal of trees? Clearly, one motivation is their admiration for the sheer longevity of these organisms, which have survived in their environments for decades and even centuries, during which a great deal of human history has taken place. The oldest known individual plant is a bristlecone pine that has lived for more than 4,900 years—almost 50 centuries. In contrast, it is doubtful that any animal has ever lived much longer than 2 centuries.

This longevity is even more impressive when it is understood that plants cannot move from site to site to avoid danger or environmental challenges. Even though plants are not motile, the extreme ages achieved by some trees prove that plants can nevertheless cope successfully with their environment. The plant body creates and maintains an internal environment that differs from the external environment.

Plants accomplish through growth some of the same things that animals achieve through mobility. Growing roots, for example, can reach into new supplies of water and nutrients. By growing, stems and leaves rise out of shaded areas into the sun to obtain energy.

Although plants do not need to obtain complex substances like vitamins from their environments as animals do, they must nevertheless obtain nutrients—not only the raw materials of photosynthesis (carbon dioxide and water), but also mineral elements such as nitrogen, potassium, and calcium. Seed plants—even the tallest trees—transport water and minerals from the soil to their tops, and they transport the products of photosynthesis from the leaves to their roots and other parts.

An Ancient Individual Bristlecone pines (*Pinus longaeva*) can live for centuries. The oldest known living organism is a bristlecone pine that has been alive for almost 5,000 years—long enough to have witnessed all of recorded human history.



Plants also interact with their living and nonliving environments. They respond to environmental cues as they grow and develop. Their responses are mediated by chemical signals that move within cells and throughout the plant body. Among the resulting changes are ones that lead to growth, development, and reproduction.

Because we can understand the functioning of plants only in terms of their underlying structure, this chapter focuses on the structure of the plant body, with a primary emphasis on flowering plants. We'll examine plant structure at the levels of organs, cells, tissues, and tissue systems. Then we'll see how organized groups of dividing cells, called meristems, contribute to the growth of the plant body, both in length and, in woody plants, in width. The chapter concludes with a consideration of how leaf structure supports photosynthesis.

Vegetative Organs of the Flowering Plant Body

You will recall from Chapter 30 that flowering plants (angiosperms) are *tracheophytes* that are characterized by double fertilization, a triploid endosperm, and seeds enclosed in modified leaves called carpels. Their xylem contains cells called vessel elements and fibers, and their phloem contains sieve tube elements and companion cells.

Flowering plants possess three kinds of *vegetative* (nonreproductive) organs: roots, stems, and leaves. Flowers, which are the plant's devices for sexual reproduction, consist of modified leaves and stems; flowers will be considered in detail in a later chapter.

Most flowering plants belong to one of two major lineages. **Monocots** are generally narrow-leaved flowering plants such as grasses, lilies, orchids, and palms. **Eudicots** are broad-leaved flowering plants such as soybeans, roses, sunflowers, and maples. These two lineages account for 97 per-

cent of flowering plant species (Figure 35.1). Most of the remaining species (including water lilies and magnoliids) are structurally similar to the eudicots.*

The basic body plans of a generalized monocot and a generalized eudicot are shown in Figure 35.2. In both lineages, the vegetative plant body consists of two systems: the shoot system and the root system.

The **shoot system** of a plant consists of the stems, leaves, and flowers. Broadly speaking, the **leaves** are the chief organs of photosynthesis. The **stems** hold and display the leaves to the sun and provide connections for the transport of materials between roots and leaves. The locations where leaves attach to a stem are called **nodes**, and the stem regions between successive nodes are **internodes**.

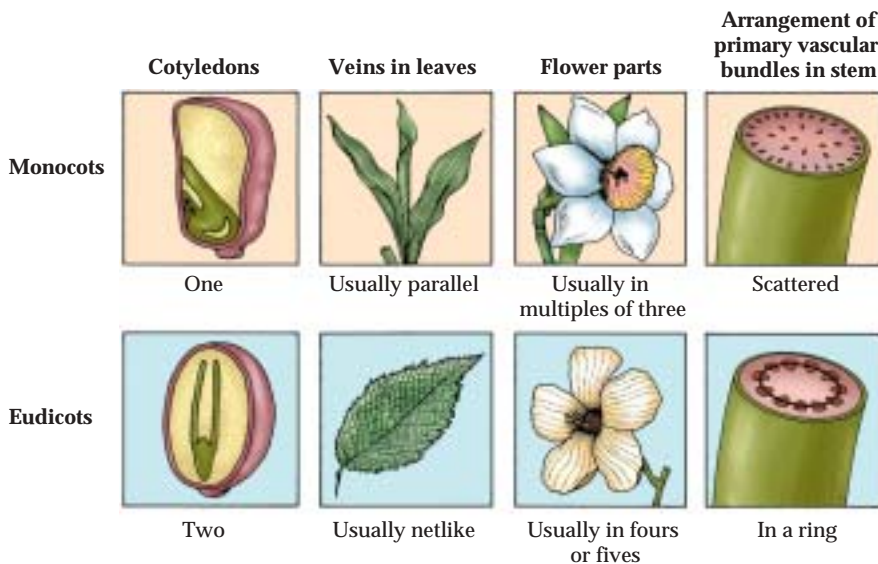
The **root system** anchors the plant in place and provides nutrition. The extreme branching of plant roots and their high surface area-to-volume ratio allow them to absorb water and mineral nutrients from the soil.

Each of the vegetative organs can be understood in terms of its structure. By *structure* we mean both its overall form, called its *morphology*, and its component cells and tissues and their arrangement, called its *anatomy*. Let's first consider the overall forms of roots, stems, and leaves.

Roots anchor the plant and take up water and minerals

Water and minerals usually enter the plant through the root system, which usually lies in the soil, where light does not penetrate. Roots typically lack the capacity for photosynthesis even when removed from the soil and placed in light.

*Botanists traditionally have referred to all flowering plants other than monocots as *dicots*. However, the dicots do not constitute a monophyletic lineage (see Figure 30.13). Because we wish to emphasize lineages, we do not use the term *dicot* here.

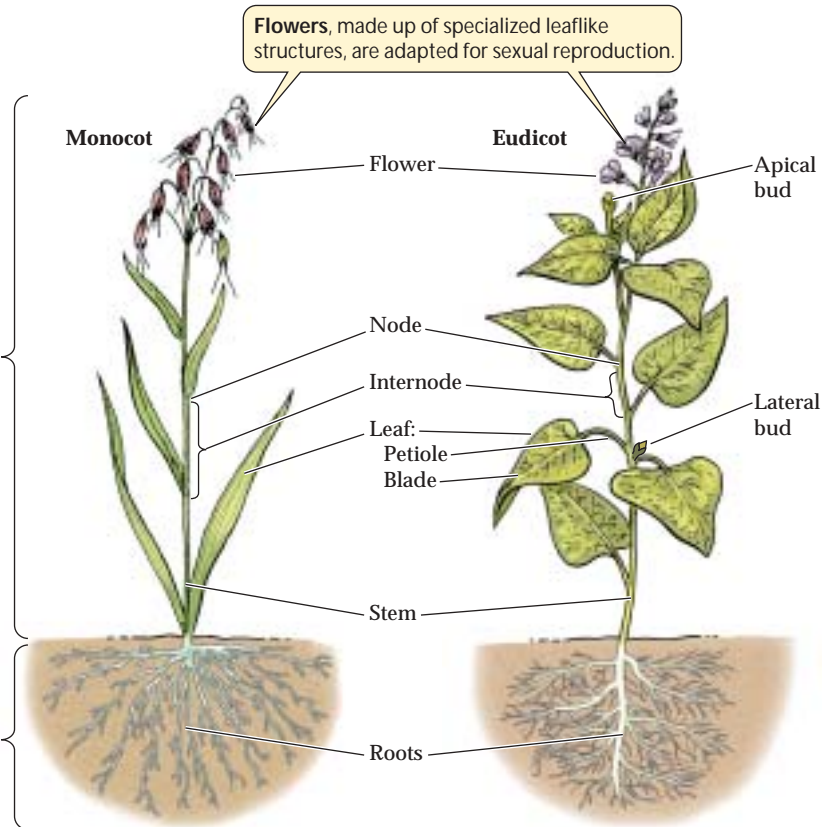


35.1 Monocots versus Eudicots The possession of a single cotyledon clearly distinguishes the monocots from the other angiosperms. Several other anatomical characteristics also differ between the monocots and the eudicots. Most angiosperms that do not belong to either lineage resemble eudicots in the characteristics shown here.

35.2 Vegetative Organs and Systems The basic plant body plan and the principal vegetative organs are similar in monocots and eudicots.

The **shoot system** consists of stems and leaves, in which photosynthesis takes place.

The **root system** anchors and provides nutrients for the shoot system.



There are two principal types of root systems. Many eudicots have a *taproot system*: a single, large, deep-growing primary root accompanied by less prominent lateral roots. The taproot itself often functions as a nutrient storage organ, as in carrots (Figure 35.3a).

By contrast, monocots and some eudicots have a *fibrous root system*, which is composed of numerous thin roots that are all roughly equal in diameter (Figure 35.3b). Many fibrous root systems have a large surface area for the absorption of water and minerals. A fibrous root system clings to soil very well. Grasses with fibrous root systems, for example, may protect steep hillsides where runoff from rain would otherwise cause erosion.

Some plants have *adventitious roots*. These roots arise above ground from points along the stem; some even arise from the leaves. In many species, adventitious roots can form when a piece of shoot is cut from the plant and placed in water or soil. Adventitious rooting enables the cutting to establish itself in the soil as a new plant. Such a cutting is a form of vegetative reproduction, which we will discuss in a later chapter. Some plants—corn, banyan trees, and some palms, for example—use adventitious roots as props to help support the shoot.

Stems bear buds, leaves, and flowers

Unlike roots, stems bear buds of various types. A *bud* is an embryonic shoot. A stem bears leaves at its nodes, and where each leaf meets the stem there is a **lateral bud** (see Figure

35.2). If it becomes active, the lateral bud can develop into a new *branch*, or extension of the shoot system. The branching patterns of plants are highly variable, depending on the species, environmental conditions, and a gardener's pruning activities.



35.3 Root Systems The taproot system of a carrot (a) contrasts with the fibrous root system of a grass (b).

At the tip of each stem or branch is an **apical bud**, which produces the cells for the upward and outward growth and development of that shoot. Under appropriate conditions, other buds form that develop into flowers.

Some stems are highly modified. The *tuber* of a potato, for example—the part of the plant eaten by humans—is an underground stem rather than a root. Its “eyes” contain lateral buds; thus, a sprouting potato is just a branching stem (Figure 35.4a). The *runners* of strawberry plants and Bermuda grass are horizontal stems from which roots grow at frequent intervals (Figure 35.4b). If the links between the rooted portions are broken, independent plants can develop on each side of the break. This phenomenon is a form of vegetative reproduction.

Although stems are usually green and capable of photosynthesis, they usually are not the principal sites of photosynthesis. Most photosynthesis takes place in leaves.

Leaves are the primary sites of photosynthesis

In gymnosperms and most flowering plants, the leaves are responsible for most of the plant’s photosynthesis, producing energy-rich organic molecules and releasing oxygen gas.

In certain plants, the leaves are highly modified for more specialized functions, as we will see below.

As photosynthetic organs, leaves are marvelously adapted for gathering light. Typically, the **blade** of a leaf is a thin, flat structure attached to the stem by a stalk called a **petiole**. During the daytime, the leaf blade is held by its petiole at an angle almost perpendicular to the rays of the sun. This orientation, with the leaf surface facing the sun, maximizes the amount of light available for photosynthesis. Some leaves track the sun, moving so that they constantly face it.

The leaves at different sites on a single plant may have quite different shapes. These shapes result from a combination of genetic, environmental, and developmental influences. Most species, however, bear similar, if not identical, leaves of a particular broadly defined type. A leaf may be *simple*, consisting of a single blade, or *compound*, with blades, or *leaflets*, arranged along an axis or radiating from a central point (Figure 35.5). In a simple leaf, or in a leaflet of a compound leaf, the veins may be parallel to one another, as in monocots, or in a netlike arrangement, as in eudicots.

The general development of a specific leaf pattern is programmed in the plant’s genes and is expressed by differential growth of the leaf veins and of the tissue between the veins. As a result, plant taxonomists have often found leaf forms (outlines, margins, tips, bases, and patterns of arrangement) to be reliable characters for classification and identification. At least some of the forms in Figure 35.5 probably look familiar to you.

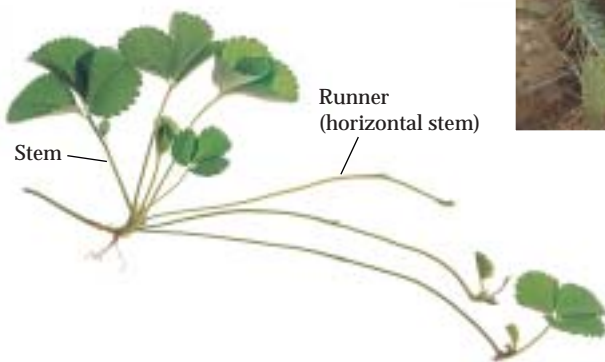
During development in some plant species, leaves are highly modified for special functions. For example, modified leaves serve as storage depots for energy-rich molecules, as in the bulbs of onions. In other species, the leaves store water, as in succulents. The spines of cacti are modified leaves (see Figure 35.4c). Many plants, such as peas, have modified portions of leaves called *tendrils* that support the plant by wrapping around other structures or plants.

Leaves, like all other plant organs, are composed of cells, tissues, and tis-

(a) Tuber (modified stem) Branches



(b) Runner (horizontal stem)

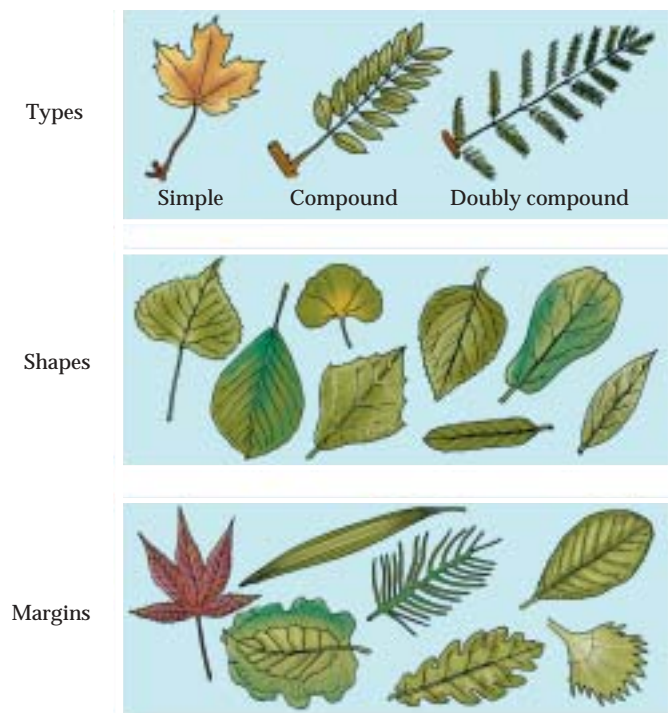


(c)



Stem (enlarged) Spines

35.4 Modified Stems (a) A potato is a modified stem called a tuber; the sprouts that grow from its eyes are shoots, not roots. (b) The runners of this beach strawberry are horizontal stems that produce roots at intervals. Runners provide a local water supply and allow rooted portions of the plant to live independently if the runner is cut. (c) The stem of this barrel cactus is enlarged to store water. Its thorny spines are modified leaves.



35.5 The Diversity of Leaf Forms Simple leaves are those with a single blade. Some compound leaves consist of leaflets arranged along a central axis. Further division of leaflets results in a doubly compound leaf. Other characters of leaf form can also be used to identify a plant's species.

sue systems. Let's now consider plant cells—the basic structural and functional units of plant organs.

Plant Cells

Plant cells have all the essential organelles common to eukaryotes (see Figure 4.7). In addition, they have certain structures and organelles that distinguish them from many other eukaryotes:

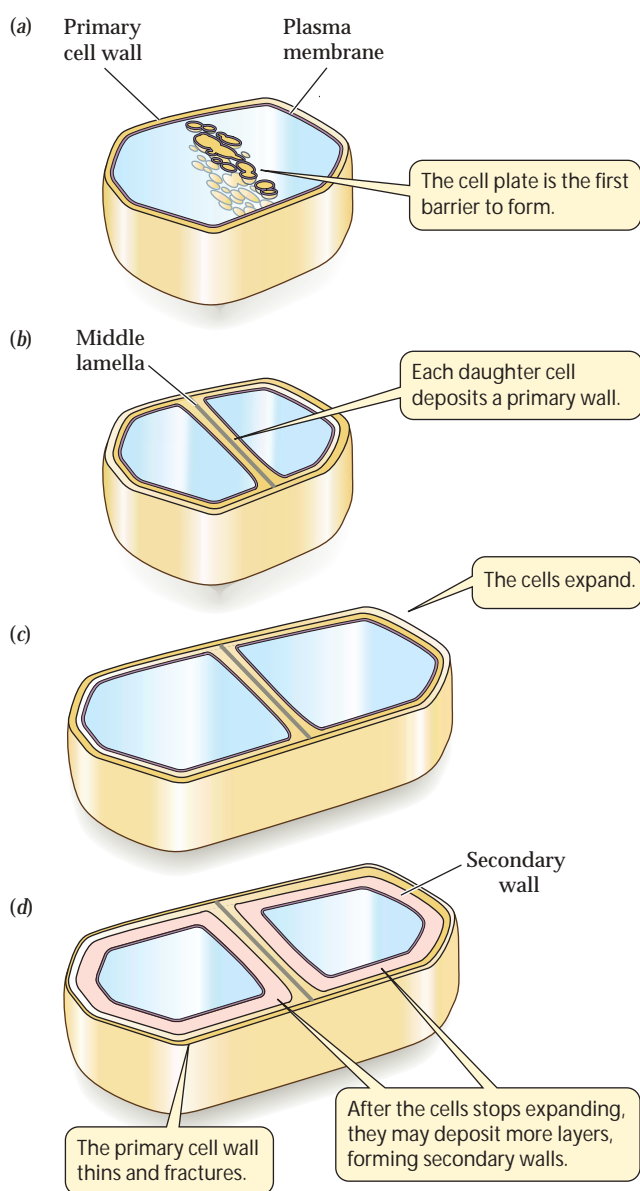
- ▶ They contain *chloroplasts* or other plastids.
- ▶ They contain *vacuoles*.
- ▶ They possess cellulose-containing *cell walls*.

Plant cells are alive when they divide and grow, but certain cells function only after their living parts have died and disintegrated. Other plant cells develop specialized metabolic capabilities; for example, some can perform photosynthesis, and others produce and secrete waterproofing materials. There are several different types of plant cells, which differ dramatically in the composition and structure of their cell walls. The walls of each cell type have a composition and structure that corresponds to its special functions.

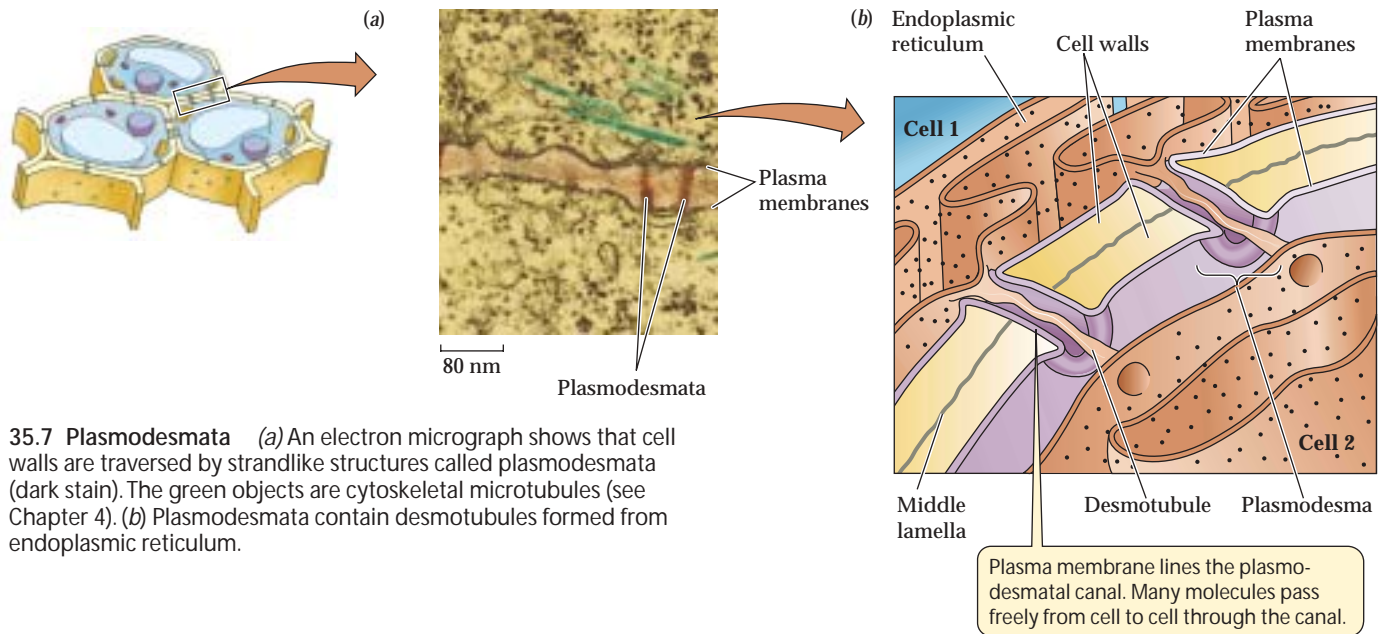
Cell walls may be complex in structure

The cytokinesis of a plant cell is completed when the two daughter cells are separated by a cell plate (see Figure 9.10*b*). The daughter cells then deposit a glue-like substance within the cell plate; this substance constitutes the **middle lamella**. Next, each daughter cell secretes cellulose and other polysaccharides to form a **primary wall**. This deposition and secretion continue as the cell expands to its final size (Figure 35.6).

Once cell expansion stops, a plant cell may deposit one or more additional cellulosic layers to form a **secondary wall** internal to the primary wall (Figure 35.6). Secondary walls



35.6 Cell Wall Formation Plant cell walls form as the final step in cell division.



35.7 Plasmodesmata (a) An electron micrograph shows that cell walls are traversed by strandlike structures called plasmodesmata (dark stain). The green objects are cytoskeletal microtubules (see Chapter 4). (b) Plasmodesmata contain desmotubules formed from endoplasmic reticulum.

are often impregnated with unique substances that give them special properties. Those impregnated with the polymer **lignin** become strong, as in wood cells. Walls to which the complex lipid **suberin** are added become waterproof.

Although it lies outside the plasma membrane, the cell wall is not a chemically inactive region. In addition to cellulose and other polysaccharides, the cell wall contains proteins, some of which are enzymes. Chemical reactions in the wall play important roles in cell expansion and in defense against invading organisms. Cell walls may thicken or be sculpted or perforated as cells differentiate into specialized cell types. Except where the secondary wall is waterproofed, the cell wall is permeable to water, small molecules, and mineral ions.

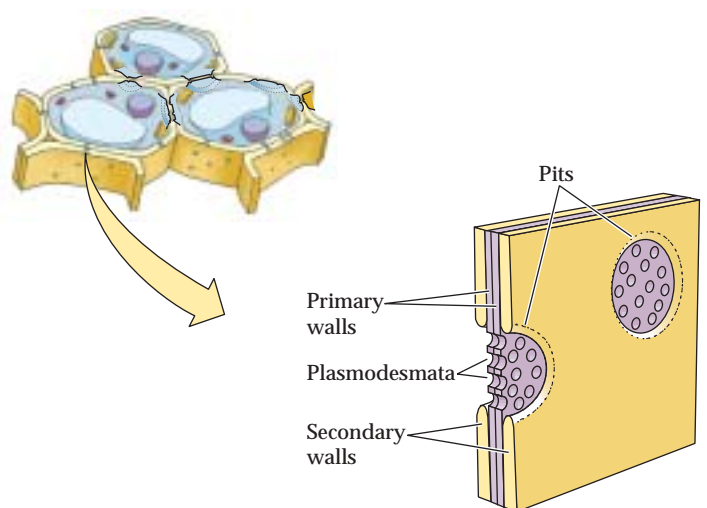
Localized modifications in the walls of adjacent cells allow water and dissolved materials to move easily from cell to cell. The primary wall usually has regions where it becomes quite thin. In these regions, strands of cytoplasm called **plasmodesmata** (singular, plasmodesma) pass through the primary wall, allowing direct communication between plant cells. A plasmodesma is a plasma-membrane lined canal traversed by a strand of endoplasmic reticulum called the **desmotubule** (Figure 35.7). Under certain circumstances, a plasmodesma can enlarge dramatically, allowing even macromolecules and viruses to pass directly between cells (see Chapter 15). Substances can move from cell to cell through plasmodesmata without having to cross a plasma membrane.

Even in cells with a waterproofed secondary wall, water and dissolved materials can pass from cell to cell by way of structures called **pits**. Pits are interruptions in the secondary wall that leave the thin regions of the primary wall, and

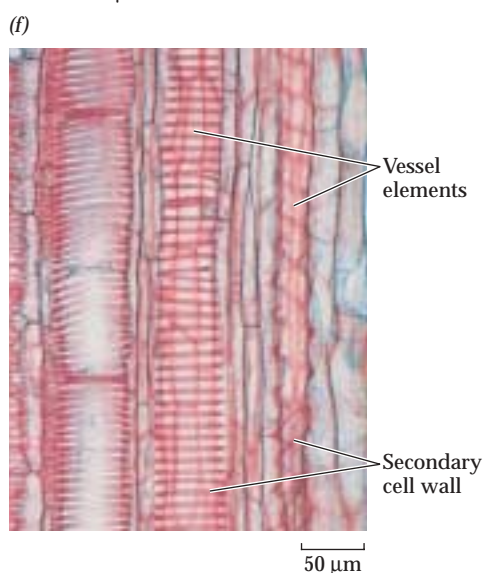
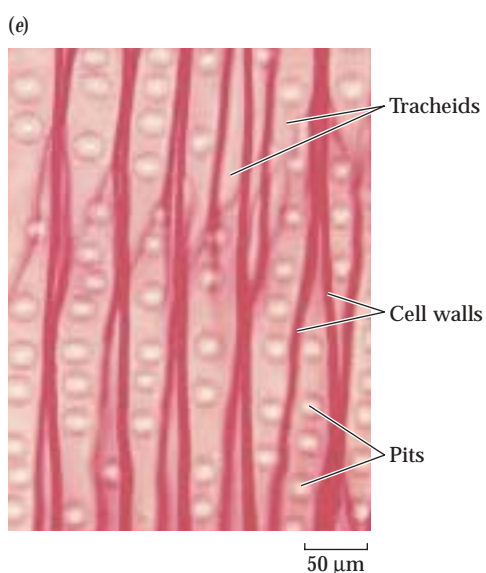
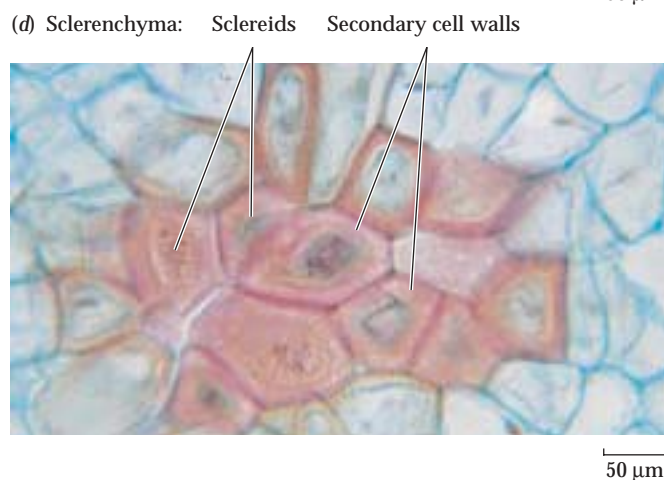
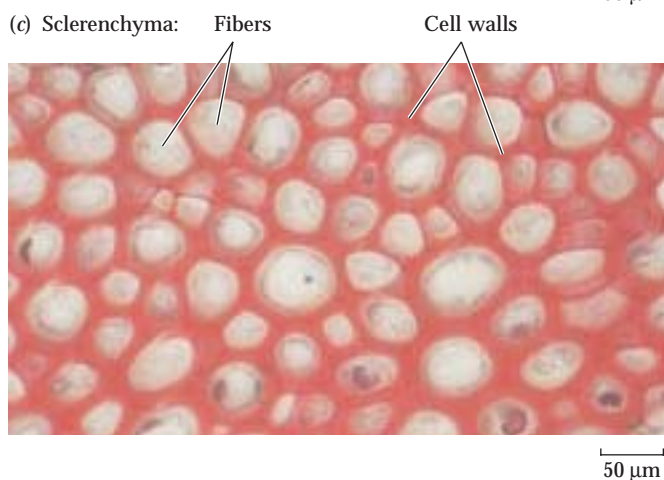
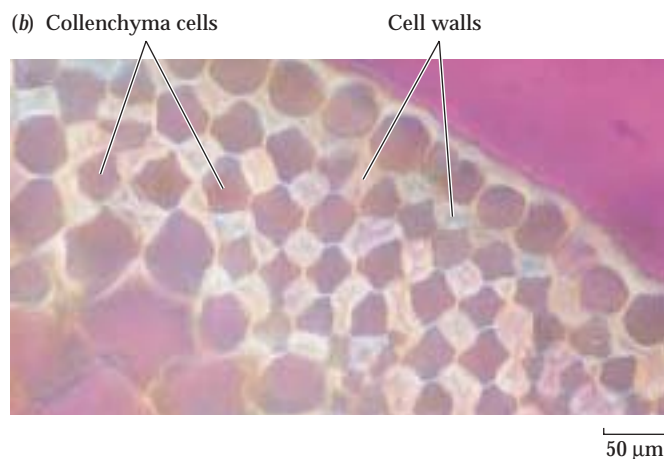
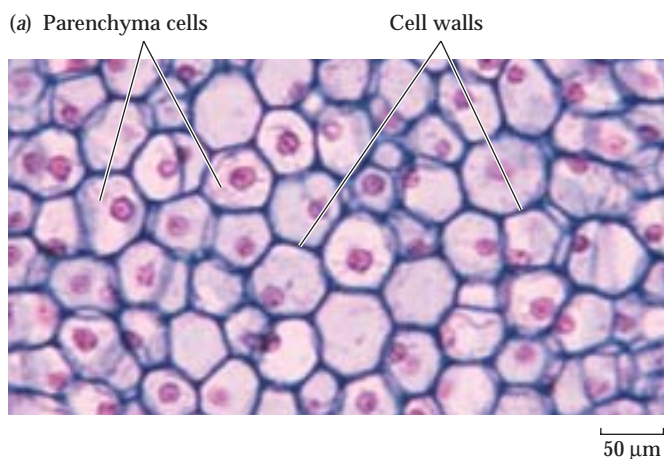
thus any plasmodesmata that are present, unobstructed (Figure 35.8).

Parenchyma cells are alive when they perform their functions

The most numerous cell type in young plants is the **parenchyma cell** (Figure 35.9a). Parenchyma cells usually have thin walls, consisting only of a primary wall and the shared middle lamella. Many parenchyma cells have shapes with multiple faces. Most have large central vacuoles.



35.8 Pits Secondary walls may be interrupted by pits, which allow the passage of water and other materials between cells.



35.9 Plant Cell Types (a) Parenchyma cells in the leaf stem of *Coleus*. Note the thin, uniform cell walls. (b) Collenchyma cells make up the five outer cell layers of this spinach leaf vein. Their cell walls are thick at the corners of the cells and thin elsewhere. (c) Sclerenchyma: Fibers in a sunflower plant (*Helianthus*). The thick secondary walls are stained red. (d) Sclerenchyma: Sclereids. The extremely thick secondary walls of sclereids are laid down in layers. They provide support and a hard texture to structures such as nuts and seeds. (e) Water-conducting tracheids in pine wood. The thick cell walls are stained dark red. (f) Vessel elements in the stem of a squash. The secondary walls are stained red; note the different patterns of thickening, including rings and spirals.

The photosynthetic cells in leaves are parenchyma cells that contain numerous chloroplasts. Some nonphotosynthetic parenchyma cells store substances such as starch or lipids. In the cytoplasm of these cells, starch is often stored in specialized plastids called *leucoplasts* (see Figure 4.17b). Lipids may

be stored as oil droplets, also in the cytoplasm. Some parenchyma cells appear to serve as “packing material” and play a vital role in supporting the stem. Many retain the capacity to divide and hence may give rise to new cells, as when a wound results in cell proliferation.

Collenchyma cells provide flexible support while alive

Collenchyma cells are supporting cells. Their primary walls are characteristically thick at the corners of the cells (Figure 35.9b). Collenchyma cells are generally elongated. In these cells, the primary wall thickens, but no secondary wall forms. Collenchyma provides support to leaf petioles, nonwoody stems, and growing organs. Tissue made of collenchyma cells is flexible, permitting stems and petioles to sway in the wind without snapping. The familiar “strings” in celery consist primarily of collenchyma cells.

Sclerenchyma cells provide rigid support

In contrast to collenchyma cells, **sclerenchyma** cells have a thickened secondary wall that performs their major function: support. Many sclerenchyma cells function when dead. There are two types of sclerenchyma cells: elongated **fibers** and variously shaped **scleireids**. Fibers provide relatively rigid support in wood and other parts of the plant, where they are often organized into bundles (Figure 35.9c). The bark of trees owes much of its mechanical strength to long fibers. Scleireids may pack together densely, as in a nut’s shell or in some seed coats (Figure 35.9d). Isolated clumps of scleireids, called *stone cells*, in pears and some other fruits give them their characteristic gritty texture.

Xylem transports water from roots to stems and leaves

The **xylem** of tracheophytes conducts water from roots to aboveground plant parts. It contains conducting cells called **tracheary elements**, which undergo programmed cell death before they assume their function of transporting water and dissolved minerals. There are two types of tracheary elements. The evolutionarily more ancient tracheary elements, found in gymnosperms and other tracheophytes, are **tracheids**—spindle-shaped cells interconnected by numerous pits in their cell walls (Figure 35.9e). When the cell contents—nucleus and cytoplasm—disintegrate upon cell death, water can move with little resistance from one tracheid to its neighbors by way of the pits.

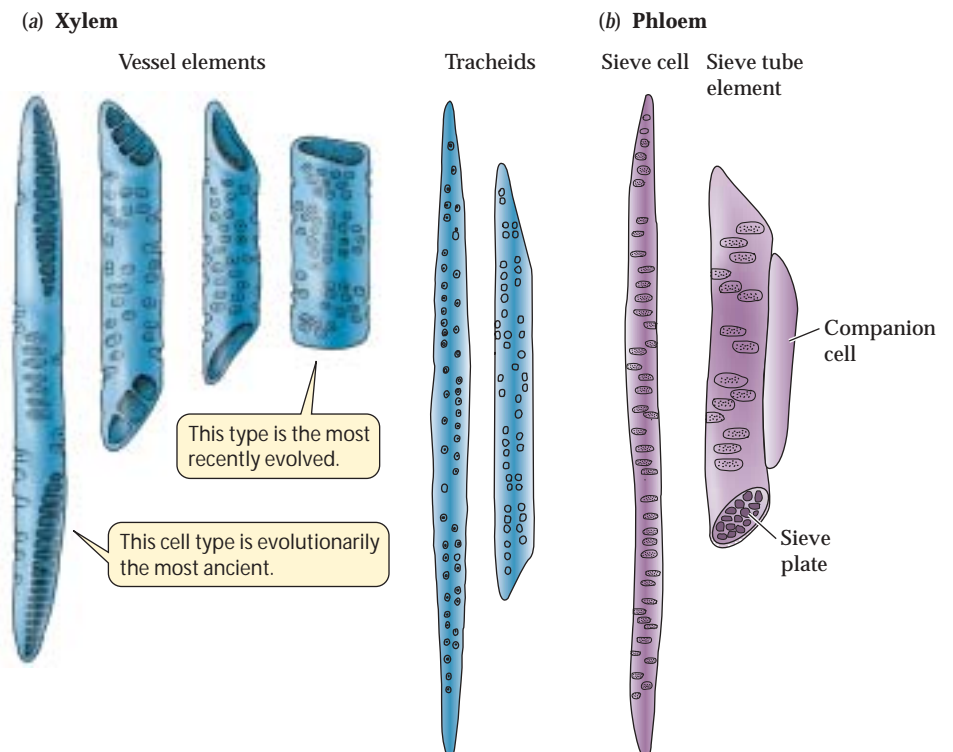
Flowering plants evolved a water-conducting system made up of **vessels**. The individual cells that form vessels, called **vessel elements**, must also die

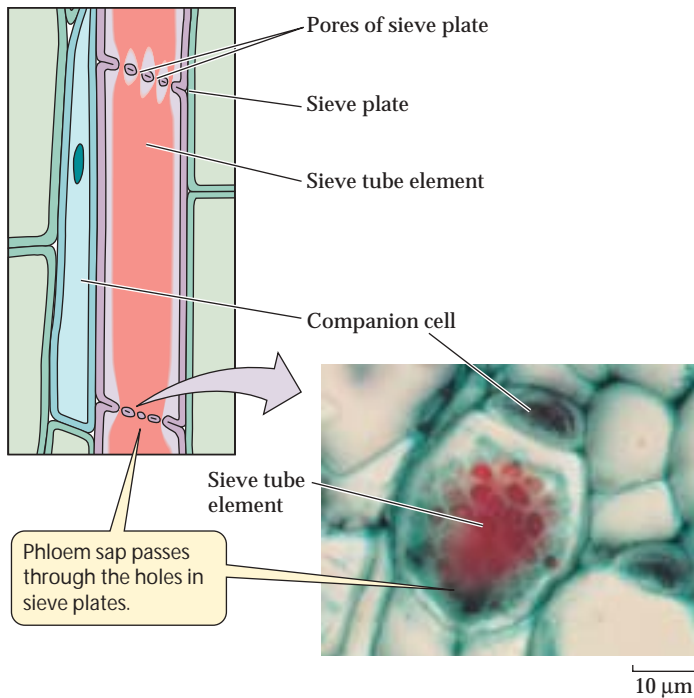
and become empty before they can transport water. These cells secrete lignin into their cell walls, then break down their end walls, and finally die and disintegrate. The result is a hollow tube through which water can flow freely. Vessel elements are generally larger in diameter than tracheids. They are laid down end-to-end, so that each vessel is a continuous hollow tube consisting of many vessel elements, providing an open pipeline for water conduction (Figure 35.9f). In the course of angiosperm evolution, vessel elements have become shorter, and their end walls have become less and less obliquely oriented and less obstructed, presumably increasing the efficiency of water transport through them (Figure 35.10). The xylem of many angiosperms also includes tracheids.

Phloem translocates carbohydrates and other nutrients

The transport cells of the **phloem**, unlike those of the mature xylem, are living cells. In flowering plants, the characteristic cells of the phloem are **sieve tube elements** (Figure 35.11). Like vessel elements, these cells meet end-to-end. They form long *sieve tubes*, which transport carbohydrates and many other materials from their sources to tissues that consume or store them. In plants with mature leaves, for example, products of photosynthesis move from leaves to root tissues.

35.10 Evolution of the Conducting Cells of Vascular Systems
The xylem of angiosperms has changed over time. The cells that conduct water and mineral nutrients have become shorter, and the end walls have become more perpendicular to the side walls.





35.11 Sieve Tubes Individual sieve tube elements join together to form long tubes that transport carbohydrates and other nutrient molecules throughout the plant body. Sieve plates form at the ends of each sieve tube element.

As sieve tube elements mature, plasmodesmata in their end walls enlarge to form pores, enhancing the connection between neighboring cells. The result is end walls that look like sieves, called **sieve plates** (see Figure 35.11). As the holes in the sieve plates expand, the membrane that encloses the central vacuole, called the *tonoplast*, disappears. The nucleus and some cytoplasmic components also break down, and thus do not clog the pores of the sieve.

At functional maturity, a sieve tube element is filled with *sieve tube sap*, consisting of water, dissolved sugars, and other solutes. This solution moves from cell to cell along the sieve tube. The moving sap solution is distinct from the layer of cytoplasm at the periphery of a sieve tube element, next to the cell wall. This stationary layer of cytoplasm contains the organelles remaining in the sieve tube element.

Each sieve tube element has one or more **companion cells** (see Figure 35.11), produced as a daughter cell along with the sieve tube element when a parent cell divides. Numerous plasmodesmata link a companion cell with its sieve tube element. Companion cells retain all their organelles and, through the activities of their nuclei, they may be thought of as the “life-support systems” of the sieve tube elements.

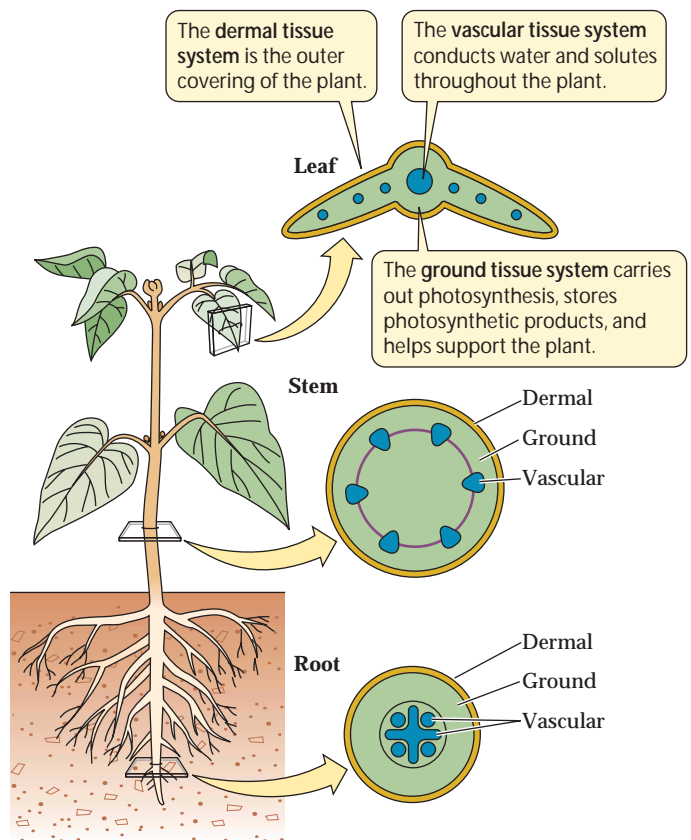
All of these types of plant cells play important roles. Next we’ll see how they are organized into tissues and tissue systems.

Plant Tissues and Tissue Systems

A *tissue*, as we learned in Chapter 1, is an organized group of cells that have features in common and that work together as a structural and functional unit. Parenchyma cells make up parenchyma tissue, a *simple tissue*—that is, a tissue composed of only one type of cell. Sclerenchyma and collenchyma are other simple tissues, composed, respectively, of sclerenchyma and collenchyma cells.

Different cell types combine to form *complex tissues*. Xylem and phloem are complex tissues, each composed of more than one type of cell. As a result of its cellular complexity, xylem can perform a variety of functions, including transport, support, and storage. The xylem of angiosperms contains vessel elements and tracheids for conduction, thick-walled fibers for support, and parenchyma cells that store nutrients. The phloem of angiosperms includes sieve tube elements, companion cells, fibers, sclereids, and parenchyma cells.

Tissues, in turn, are grouped into *tissue systems* that extend throughout the body of the plant, from organ to organ, in a concentric arrangement. Vascular plants have three tissue systems: vascular, dermal, and ground (Figure 35.12).



35.12 Three Tissue Systems Extend throughout the Plant Body The arrangement shown here is typical of eudicots.

The **vascular tissue system**, which includes the xylem and phloem, is the plant's plumbing or transport system. All the living cells of the plant body require a source of energy and chemical building blocks. The phloem transports carbohydrates from sites of production (called *sources*, primarily leaves) to sites of utilization or storage (called *sinks*, such as growing tissue, storage tubers, and developing flowers). The xylem distributes water and mineral ions taken up by the roots to all the cells of the stem and leaves.

The **dermal tissue system** is the outer covering of the plant. All parts of the young plant body are covered by an **epidermis**, which may be a single layer of cells or several layers. The epidermis contains *epidermal cells* and may also include specialized cell types, such as the *guard cells* that form stomata (pores) in leaves. The shoot epidermis secretes a layer of wax-covered cutin, the **cuticle**, that helps retard water loss from stems and leaves. The stems and roots of woody plants have a protective covering called the periderm, which will be discussed later in this chapter.

The **ground tissue system** makes up the rest of the plant. It consists primarily of parenchyma tissue, often supplemented by collenchyma or sclerenchyma. Ground tissue functions primarily in storage, support, photosynthesis, and the production of defensive and attractive substances.

In the discussions that follow, we'll examine how the tissue systems are organized in the different organs of a flowering plant. Let's begin by seeing how this organization develops as the plant grows.

Forming the Plant Body

In its early embryonic stages, a plant establishes the basic body plan for its mature form. Two patterns contribute to the plant body plan:

- ▶ The arrangement of cells and tissues along the main axis from root to shoot
- ▶ The concentric arrangement of the tissue systems

Both patterns arise through orderly development and are best understood in developmental terms.

Plants and animals grow differently

As the plant body grows, it may lose parts, and it forms new parts that may grow at different rates. The growing stem consists of **modules** or **units**, laid down one after another. Each module consists of a node with its attached leaf or leaves, the internode below that node, and the lateral bud or buds at the base of that internode (see Figure 35.2). New modules are formed as long as the stem continues to grow.

Each branch of a plant may be thought of as a unit that is in some ways independent of the other branches. A branch

of a plant does not bear the same relationship to the remainder of the plant body as a limb does to the remainder of an animal body. Among other things, branches form one after another (unlike limbs, which form simultaneously during embryonic development). Also, branches often differ from one another in their number of leaves and in the degree to which they themselves branch.

Leaves are units of another sort. They are usually short-lived, lasting weeks to a few years. Branches and stems are longer-lived, lasting from years to centuries.

Root systems are also branching structures, and lateral roots are semi-independent units. As the root system grows, penetrating and exploring the soil environment, many roots die and are replaced by new ones.

All parts of the animal body grow as an individual develops from embryo to adult, but in most animals, this growth is *determinate*. That is, the growth of the individual and all its parts ceases when the adult state is reached. Determinate growth is also characteristic of some plant parts, such as leaves, flowers, and fruits. The growth of stems and roots, by contrast, is *indeterminate*, and it is generated from specific regions of active cell division and cell expansion.

The localized regions of cell division in plants are called **meristems**. Meristems are forever young, retaining the ability to produce new cells indefinitely. The cells that perpetuate the meristems, called **initials**, are comparable to the stem cells found in animals (discussed in Chapter 19). When an initial divides, one daughter cell develops into another meristem cell the size of its parent, while the other daughter cell differentiates into a more specialized cell.

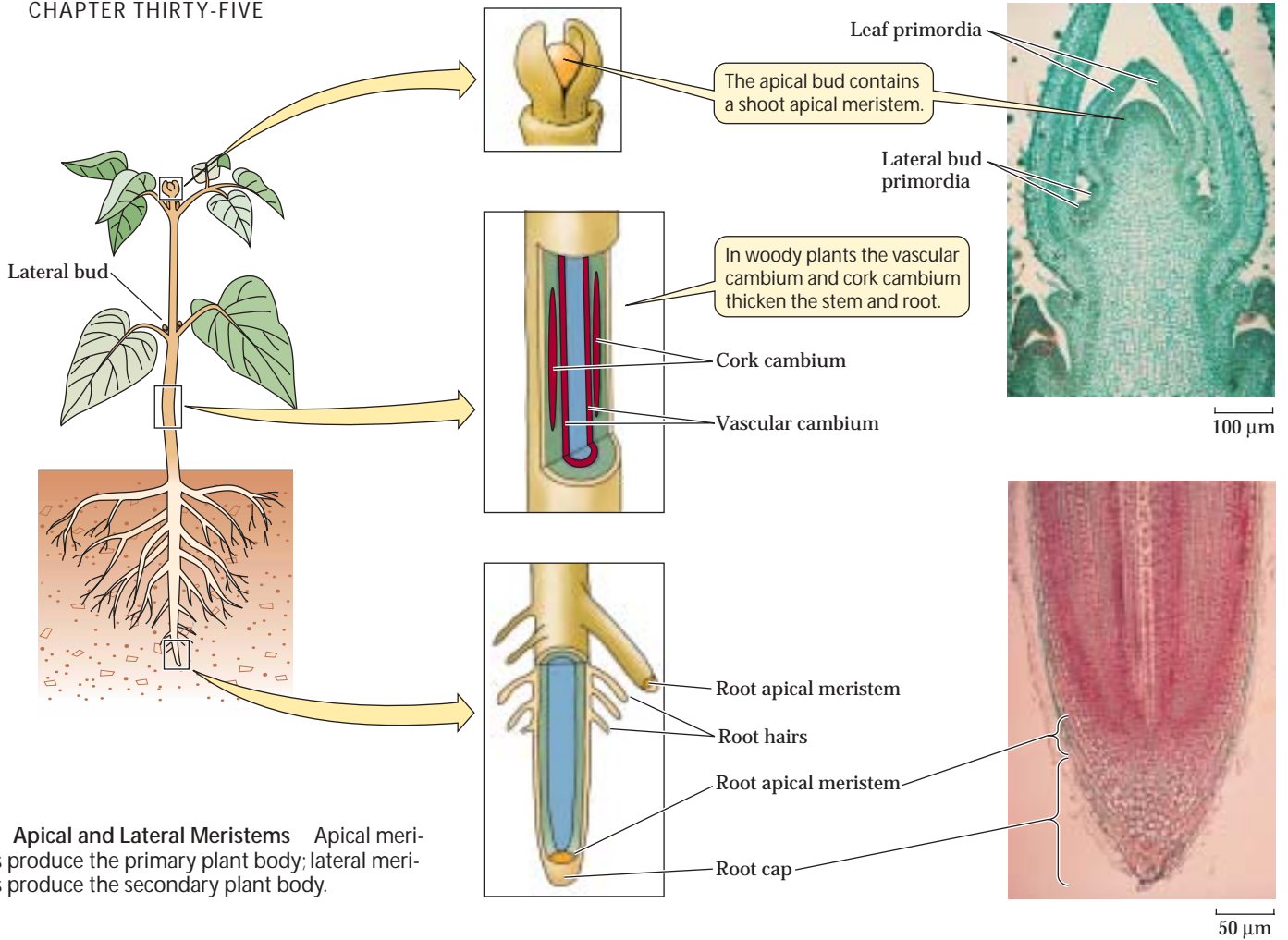
A hierarchy of meristems generates a plant's body

There are two types of meristems:

- ▶ **Apical meristems** give rise to the *primary plant body*, which is the entire body of many plants.
- ▶ **Lateral meristems** give rise to the *secondary plant body*. The stems and roots of some plants (most obviously trees) form wood and become thick; it is the lateral meristems that give rise to the tissues responsible for this thickening.

APICAL MERISTEMS. Apical meristems are located at the tips of roots and stems and in buds. They extend the plant body by producing the cells that subsequently expand and differentiate to form all plant organs (Figure 35.13).

- ▶ *Shoot apical meristems* supply the cells that extend stems and branches, allowing more leaves to form and photosynthesize.
- ▶ *Root apical meristems* supply the cells that extend roots, enabling the plant to "forage" for water and minerals.



35.13 Apical and Lateral Meristems Apical meristems produce the primary plant body; lateral meristems produce the secondary plant body.

Both root and shoot apical meristems give rise to a set of cylindrical *primary meristems* that produce the primary tissues of the plant body. From the outside to the inside of the root or shoot, which are both cylindrical organs, the primary meristems are the **protoderm**, the **ground meristem**, and the **procambium**. These in turn give rise to the three tissue systems:

Apical meristems	→	Primary meristems	→	Tissue systems
Root or shoot apical meristem	↙	Protoderm	→	Dermal tissue system
		Ground meristem	→	Ground tissue system
		Procambium	→	Vascular tissue system

Apical meristems are responsible for **primary growth**, which leads to lengthening of the plant body and organ formation. All plant organs arise ultimately from cell divisions in the apical meristems, followed by cell expansion and differentiation. Primary growth gives rise to the entire body of many plants.

Because meristems can continue to produce new organs throughout the lifetime of the plant, the plant body is much more variable in form than the animal body, whose organs are produced only once.

LATERAL MERISTEMS. Some roots and stems develop a secondary body, the tissues of which we commonly refer to as

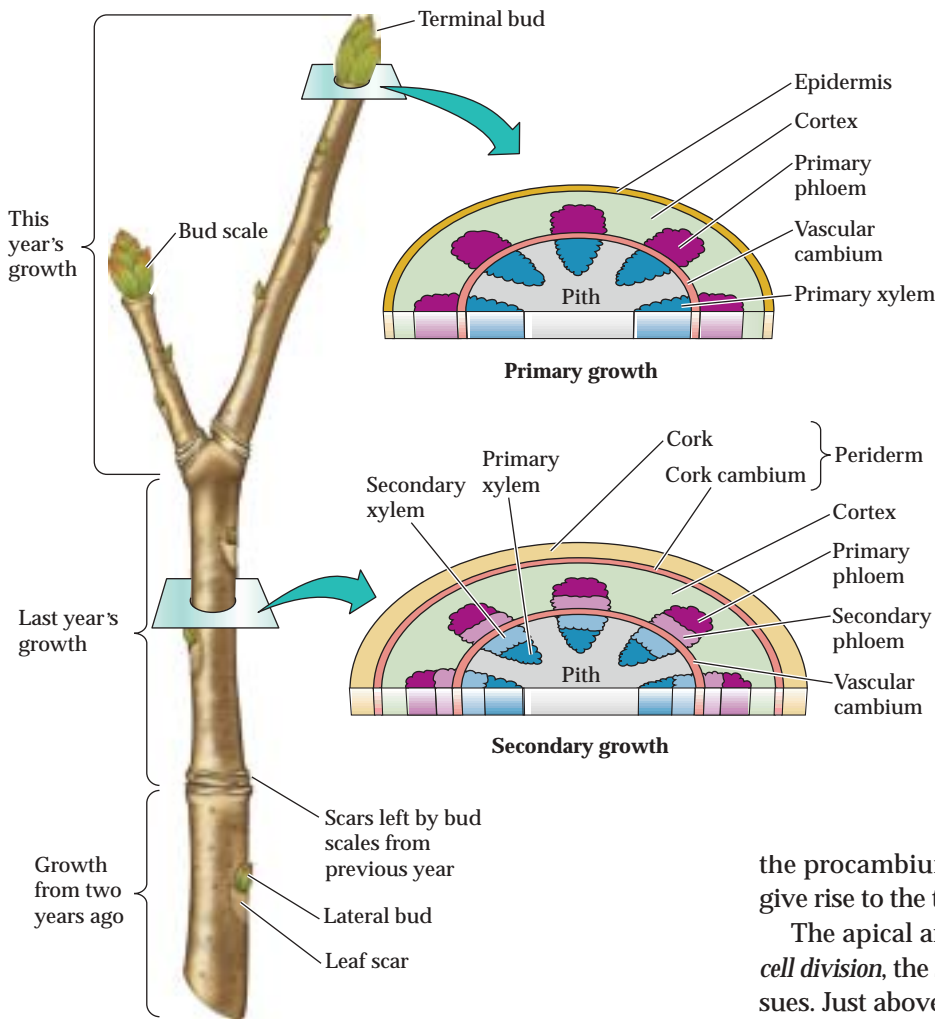
wood and bark. These complex tissues are derived from two lateral meristems: the vascular cambium and the cork cambium (Figure 35.14).

The **vascular cambium** is a cylindrical tissue consisting predominantly of vertically elongated cells that divide frequently. Toward the inside of the stem or root, the dividing cells form new xylem, the *secondary xylem*, and toward the outside they form new phloem, the *secondary phloem*.

As a tree trunk grows in diameter, the outermost layers of the stem crack and fall off. Without the activity of the **cork cambium**, this sloughing off of tissues, including the epidermis, would expose the tree to potential damage, including excessive water loss or invasion by microorganisms. The cork cambium produces new protective cells, primarily in the outward direction. The walls of these cork cells become impregnated with suberin. The mass of waterproofed cells produced by the cork cambium is called the **periderm**.

Growth in the diameter of stems and roots, produced by the vascular and cork cambia, is called **secondary growth**. It is the source of wood and bark. **Wood** is secondary xylem. **Bark** is everything external to the vascular cambium (periderm plus secondary phloem).

Each year, deciduous trees lose their leaves, leaving bare branches and twigs in winter. These twigs illustrate both pri-



35.14 A Woody Twig Apical meristems produce primary growth. Lateral meristems produce secondary growth.

mary and secondary growth (Figure 35.14). The apical meristems of the twigs and their branches are enclosed in buds protected by bud scales. When the buds begin to grow in the spring, the scales fall away, leaving scars that show us where the bud was and identifying each year's growth. The dormant twig shown in Figure 35.14 is the product of primary and secondary growth. Only the buds consist entirely of primary tissues.

In some plants, meristems may remain active for years—even centuries. The bristlecone pine mentioned at the beginning of this chapter provides a dramatic example. Such plants grow in size, or at least in diameter, throughout their lives. In the sections that follow, we'll examine how the various meristems give rise to the plant body.

The root apical meristem gives rise to the root cap and the primary meristems

The root apical meristem produces all the cells that contribute to growth in the length of the root. Some of the daughter cells from the apical (tip) end of the root apical meristem con-

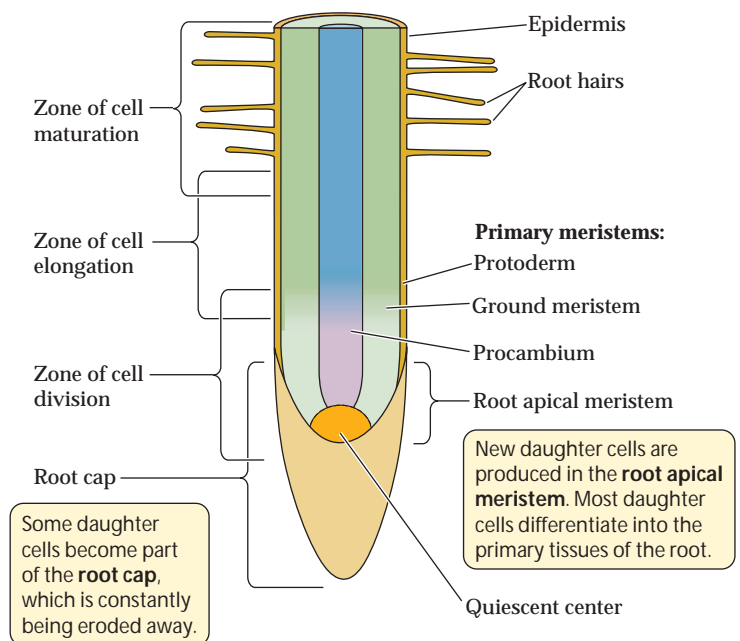
tribute to a **root cap**, which protects the delicate growing region of the root as it pushes through the soil. The cells of the root cap are often damaged or scraped away and must therefore be replaced constantly. The root cap is also the structure that detects the pull of gravity and thus controls the downward growth of roots.

Part of the root apical meristem nearest the tip of the root forms a **quiescent center**, in which cell divisions are rare. The quiescent center can become more active when needed—following injury, for example.

The daughter cells that are produced at the basal end of the apical meristem (away from the root cap) elongate and lengthen the root. Following elongation, these cells differentiate, giving rise to the various tissues of the mature root. The growing region above the apical meristem comprises the three cylindrical primary meristems: the protoderm, the ground meristem, and

the procambium (Figure 35.15). These primary meristems give rise to the three tissue systems of the root.

The apical and primary meristems constitute the *zone of cell division*, the source of all the cells of the root's primary tissues. Just above this zone is the *zone of cell elongation*, where the newly formed cells are elongating and thus causing the root to reach farther into the soil. Above this is the *zone of mat-*



35.15 Tissues and Regions of the Root Tip Extensive cell division creates the complex structure of the root.

uration, where the cells are differentiating, taking on specialized forms and functions such as water transport or mineral uptake. These three zones grade imperceptibly into one another; there is no abrupt line of demarcation.

The products of the root's primary meristems become root tissues

What are the products of the three primary meristems? The protoderm gives rise to the outer layer of cells—the epidermis—which is adapted for protection of the root and for the absorption of mineral ions and water (Figure 35.16). In the zone of maturation, many of the epidermal cells produce amazingly long, delicate **root hairs**, which vastly increase the surface area of the root (Figure 35.16*b*). It has been estimated that the root system of a mature rye plant has a total absorptive surface of more than 600 square meters (almost half again the area of a basketball court). Root hairs grow out among the soil particles, probing nooks and crannies and taking up water and minerals.

Internal to the epidermis, the ground meristem gives rise to a region of ground tissue that is many cells thick, called the **cortex**. The cells of the cortex are relatively unspecialized and often function in nutrient storage.

In the great majority of plants, especially in trees, a fungus is closely associated with the root tips. This association, called a *mycorrhiza*, increases the plant's absorption of minerals and water (see Figure 31.16). Such roots have poorly developed

or no root hairs. These plants cannot survive without the mycorrhizae that help them absorb minerals.

Proceeding inward, we come to the **endodermis** of the root, a single cylindrical layer of cells that is the innermost cell layer of the cortex. Unlike those of other cortical cells, the cell walls of the endodermal cells contain suberin. The placement of this waterproofing substance in only certain parts of the cell wall enables the cylindrical ring of endodermal cells to control the access of water and dissolved ions to the vascular tissues.

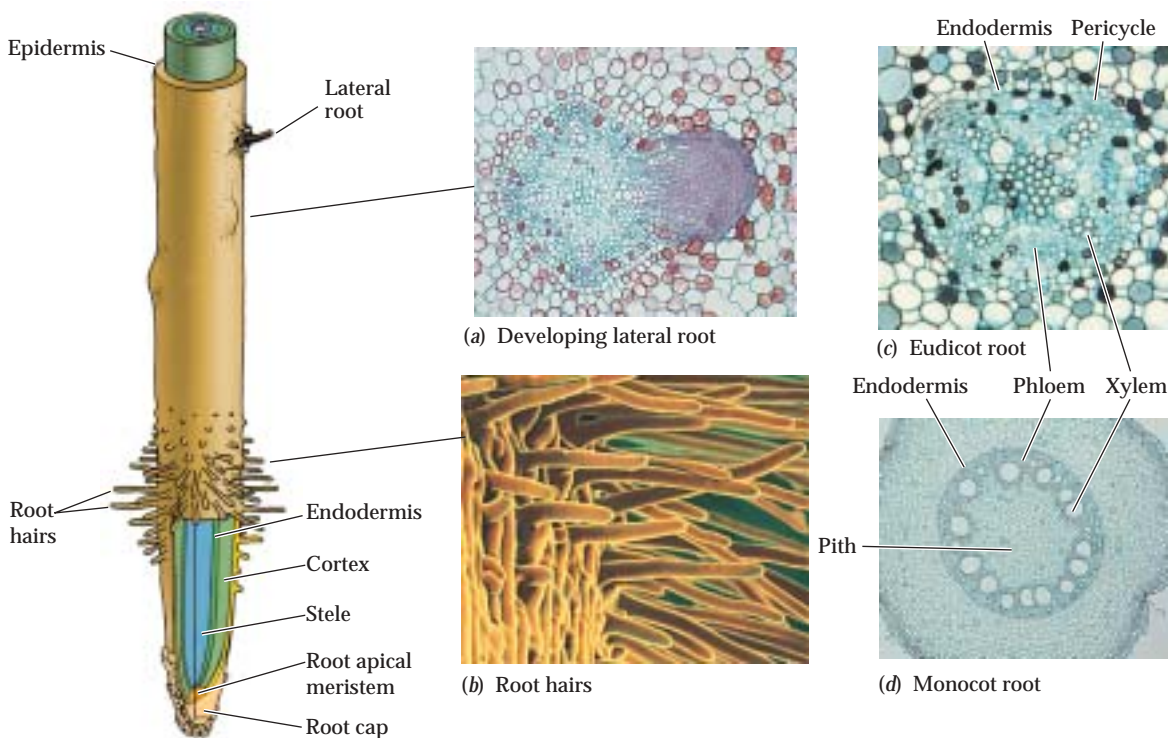
Moving inward past the endodermis, we enter the vascular cylinder, or **stele**, produced by the procambium. The stele consists of three tissues: pericycle, xylem, and phloem (Figure 35.17).

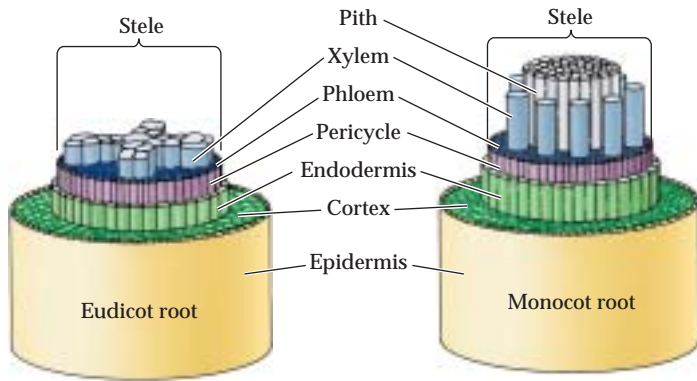
The **pericycle** consists of one or more layers of relatively undifferentiated cells. It has three important functions:

- ▶ It is the tissue within which lateral roots arise (see Figure 35.16*a*).
- ▶ It can contribute to secondary growth by giving rise to lateral meristems that thicken the root.
- ▶ Its cells contain membrane transport proteins that export nutrient ions into the cells of the xylem.



35.16 Root Anatomy The drawing at the left shows a generalized root structure. (a) Cross section through the tip of a lateral root. Cells in the pericycle divide and the products differentiate, forming the tissues of a lateral root. (b) Root hairs, seen with a scanning electron microscope. (c, d) Cross sections showing the primary root tissues of (c) a eudicot and (d) a monocot. The monocot has a central pith region; the eudicot does not.





35.17 The Stele The arrangement of tissues in the stele—the region internal to the endodermis—differs in the roots of eudicots and monocots.

At the very center of the root of a eudicot lies the xylem—seen in cross section in the shape of a star with a variable number of points. Between the points are bundles of phloem. In monocots, a region of parenchyma cells, called the **pith**, lies in the center of the root. The pith often stores carbohydrate reserves.

The products of the stem's primary meristems become stem tissues

The shoot apical meristem, like the root apical meristem, forms three primary meristems: the protoderm, the ground meristem, and the procambium. These primary meristems, in turn, give rise to the three tissue systems. The shoot apical meristem also repetitively lays down the beginnings of leaves and lateral buds. Leaves arise from bulges called **leaf primordia**, which form as cells divide on the sides of shoot apical meristems (see Figure 35.13). **Bud primordia** form at the bases of the leaf primordia. The growing stem has no protective structure analogous to the root cap, but the leaf primordia can act as a protective covering for the shoot apical meristem.

The plumbing of angiosperm stems differs from that of roots. In a root, the vascular tissue lies deep in the interior, with the xylem at or near the very center

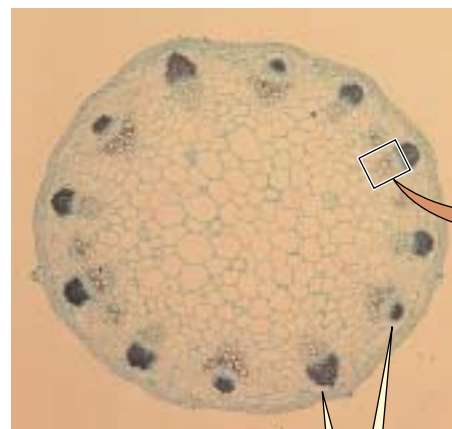
(see Figure 35.16). The vascular tissue of a young stem, however, is divided into discrete **vascular bundles**. Each vascular bundle contains both xylem and phloem. In eudicots, the vascular bundles generally form a cylinder, but in monocots, they are seemingly scattered throughout the stem (Figure 35.18).

In addition to the vascular tissues, the stem contains other important storage and supportive tissues. Internal to the ring of vascular bundles in eudicots is a storage tissue, the pith, and to the outside lies a similar storage tissue, the cortex. The cortex may contain supportive collenchyma cells with thickened walls. The pith, the cortex, and the regions between the vascular bundles in eudicots—called *pith rays*—constitute the ground tissue system of the stem. The outermost cell layer of the young stem is the epidermis, the primary function of which is to minimize the loss of water from the tissues within.



35.18 Vascular Bundles in Stems (a) In eudicot stems, the vascular bundles are arranged in a cylinder, with the pith in the center and the cortex outside the cylinder. (b) A scattered arrangement of vascular bundles is typical of monocot stems.

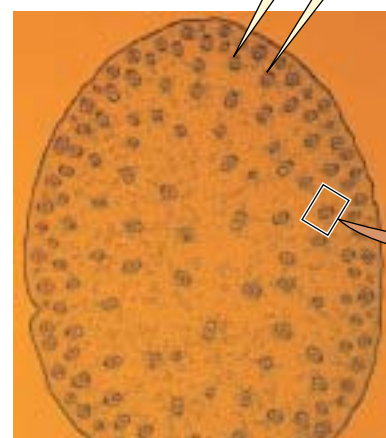
(a) Eudicot



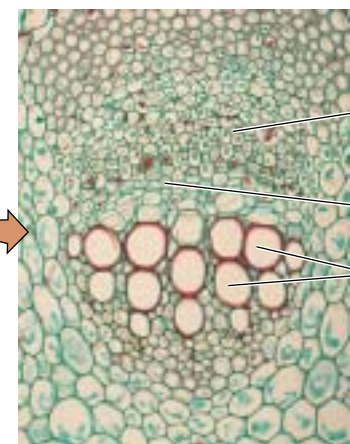
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The vascular tissues in stems are organized into bundles.

(b) Monocot

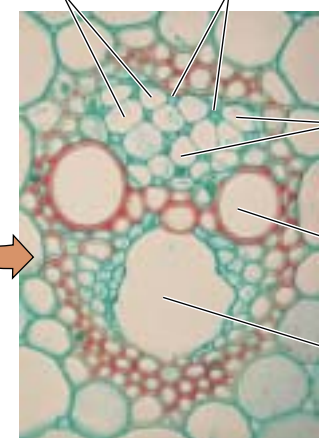


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Eudicot vascular bundle

Sieve tube members Companion cells



Monocot vascular bundle

Many stems and roots undergo secondary growth

Some stems and roots remain slender and show little or no secondary growth. However, in many eudicots, secondary growth thickens stems and roots considerably. This process gives rise to wood and bark, and it makes the support of tall trees possible.

Secondary growth results from the activity of the two lateral meristems: vascular cambium and cork cambium (see Figure 35.13). Vascular cambium consists of cells that divide to produce secondary xylem and phloem cells, while cork cambium produces mainly waxy-walled *cork cells*.

Initially, the vascular cambium is a single layer of cells lying between the primary xylem and the primary phloem (see Figure 35.18a). The root or stem increases in diameter when the cells of the vascular cambium divide, producing secondary xylem cells toward the inside of the root or stem and producing secondary phloem cells toward the outside (Figure 35.19). In the stems of woody plants, cells in the pith rays between the vascular bundles also divide, forming a continuous cylinder of vascular cambium running the length of the stem. This cylinder, in turn, gives rise to complete cylinders of secondary xylem (wood) and secondary phloem, which contributes to the bark.

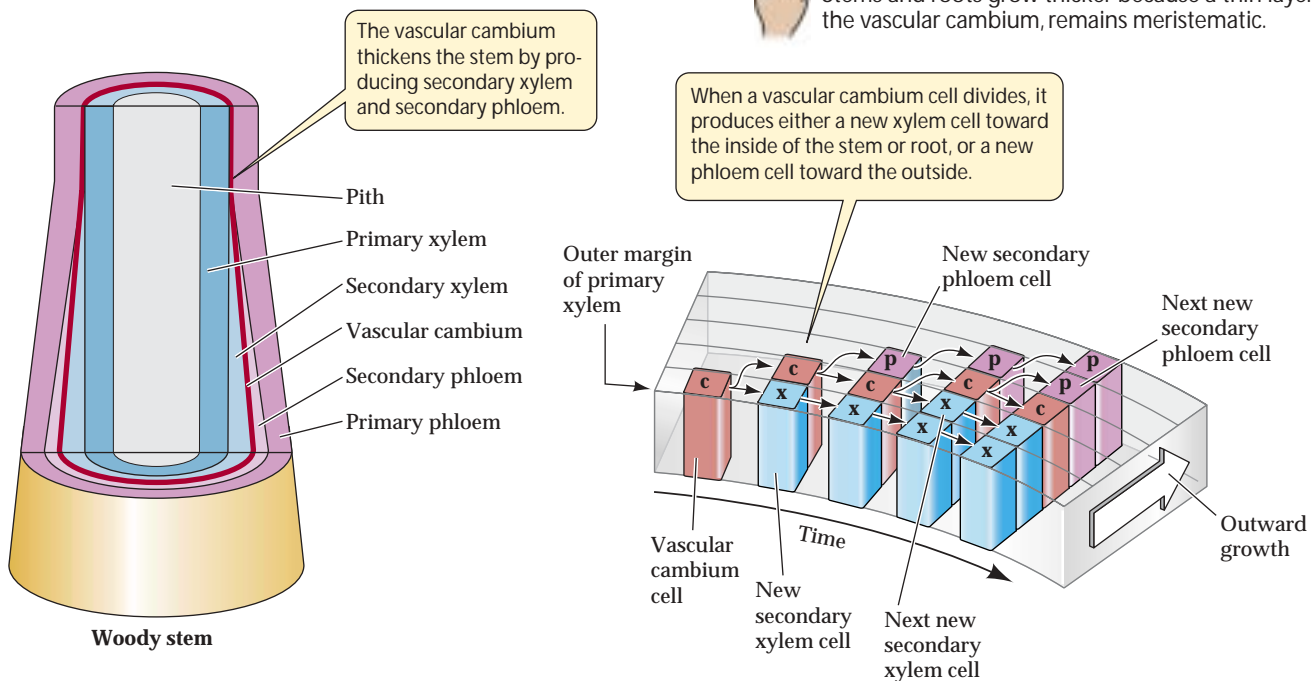
As the vascular cambium produces secondary xylem and phloem, its principal cell products are vessel elements, supportive fibers, and parenchyma cells in the xylem and sieve tube elements, companion cells, fibers, and parenchyma cells in the phloem. The parenchyma cells in the xylem and phloem store carbohydrate reserves in the stem and root.

Living tissues such as this storage parenchyma must be connected to the sieve tubes of the phloem, or they will starve to death. These connections are provided by **vascular rays**, which are composed of cells derived from the vascular cambium. These rays, laid down progressively as the cambium divides, are rows of living parenchyma cells that run perpendicular to the xylem vessels and phloem sieve tubes (Figure 35.20). As the root or stem continues to increase in diameter, new vascular rays are initiated so that this storage and transport tissue continues to meet the needs of both the bark and the living cells in the xylem.

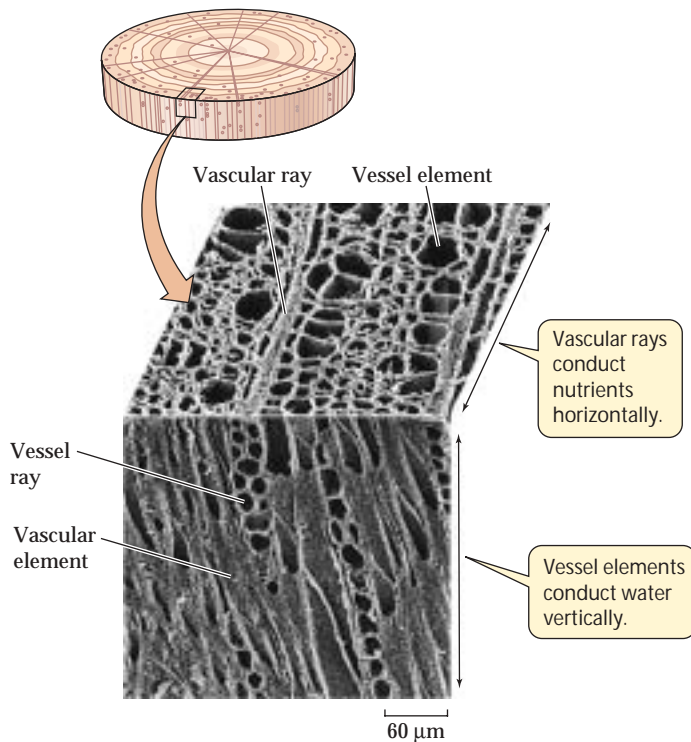
The vascular cambium itself increases in circumference with the growth of the root or stem. To do this, some of its cells divide in a plane at right angles to the plane that gives rise to secondary xylem and phloem. The products of each of these divisions lie within the vascular cambium itself and increase its circumference.

Only eudicots and other non-monocot angiosperms have a vascular cambium and a cork cambium and thus undergo secondary growth. The few monocots that form thickened stems—palm trees, for example—do so without using vascular cambium or cork cambium. Palm trees have a very wide apical meristem that produces a wide stem, and dead leaf bases also add to the diameter of the stem. Basically, monocots grow in the same way as do other angiosperms that lack secondary growth.

Wood and bark, consisting of secondary phloem, are unique to plants showing secondary growth. These tissues have their own patterns of organization and development.



35.19 Vascular Cambium Thickens Stems and Roots
Stems and roots grow thicker because a thin layer of cells, the vascular cambium, remains meristematic.



35.20 Vascular Rays and Vessel Elements In this sample of wood from the tulip poplar, the orientation of vascular rays is perpendicular to that of the vessel elements. The vascular rays transport sieve tube sap horizontally from the phloem to storage parenchyma cells.

WOOD. Cross sections of most tree trunks (mature stems) in temperate-zone forests show *annual rings* (Figure 35.21), which result from seasonal environmental conditions. In spring, when water is relatively plentiful, the tracheids or vessel elements produced by the vascular cambium tend to be large in diameter and thin-walled. Such wood is well adapted for transporting water and minerals. As water becomes less available during the summer, narrower cells with thicker walls are produced, making this summer wood darker and perhaps more dense than the wood formed in spring. Thus each growing season is usually recorded in a tree trunk by a clearly visible annual ring. Trees in the moist Tropics do not undergo seasonal growth, so they do not lay down such obvious regular rings. Variations in temperature or water supply can lead to the formation of more than one “annual” ring in a single year.

The difference between old and new regions of wood also contributes to its appearance. As a tree grows in diameter, the xylem toward the center becomes clogged with water-insoluble substances and ceases to conduct water and minerals; this *heartwood* appears darker in color. The portion of the xylem that is actively conducting water and minerals throughout the tree is called *sapwood* and is lighter in color and more porous than heartwood.

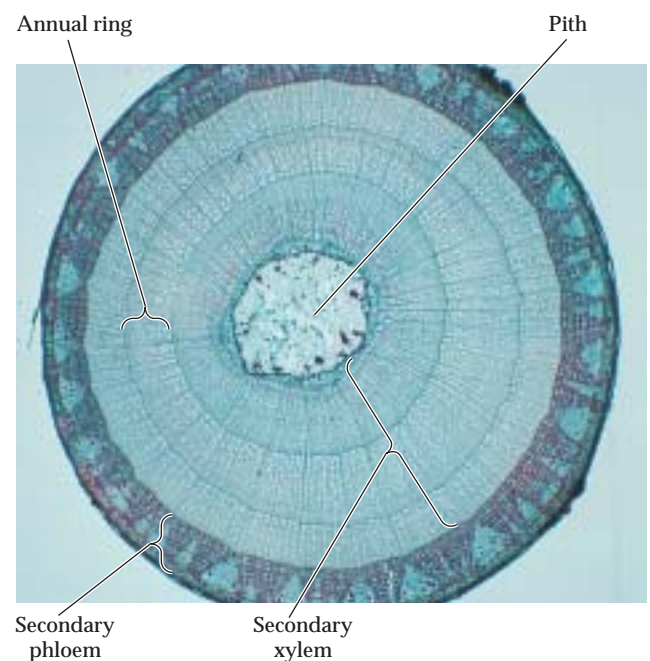
The knots that we find attractive in knotty pine but regard as a defect in structural timbers are cross sections of branches.

As a trunk grows, the bases of branches become buried in the trunk’s new wood and appear as knots when the trunk is cut lengthwise.

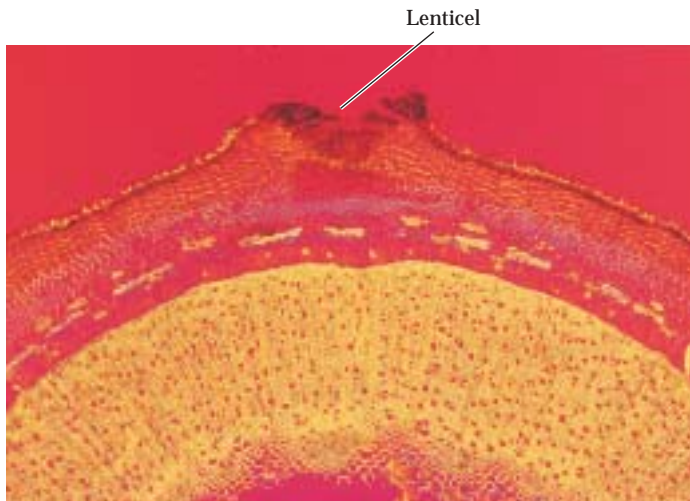
BARK. As secondary growth of stems or roots continues, the expanding vascular tissue stretches and breaks the epidermis and cortex, which ultimately flake away. Tissue derived from the secondary phloem then becomes the outermost part of the stem. Before the dermal tissues are broken away, cells lying near the surface of the secondary phloem begin to divide and produce layers of **cork**, a tissue composed of cells with thick walls, waterproofed with suberin. The cork soon becomes the outermost tissue of the stem or root (see Figure 35.14). The dividing cells, derived from the secondary phloem, form a cork cambium. Sometimes the cork cambium produces cells to the inside as well as to the outside; these cells constitute what is known as the *phelloderm*.

Cork, cork cambium, and phelloderm make up the periderm of the secondary plant body. As the vascular cambium continues to produce secondary vascular tissue, the corky layers are in turn lost, but the continuous formation of new cork cambia in the underlying phloem gives rise to new corky layers.

When periderm forms on stems and roots, the underlying tissues still need to release carbon dioxide and take up oxygen. **Lenticels** are spongy regions in the periderm of stems and roots that allow such gas exchange (Figure 35.22).



35.21 Annual Rings Rings of secondary xylem are the most noticeable feature of this cross section from a 3-year-old basswood stem.



35.22 Lenticels Allow Gas Exchange through the Periderm The region of periderm that appears broken open is a lenticel in a year-old elder twig; note the spongy tissue that constitutes the lenticel.

Leaf Anatomy Supports Photosynthesis

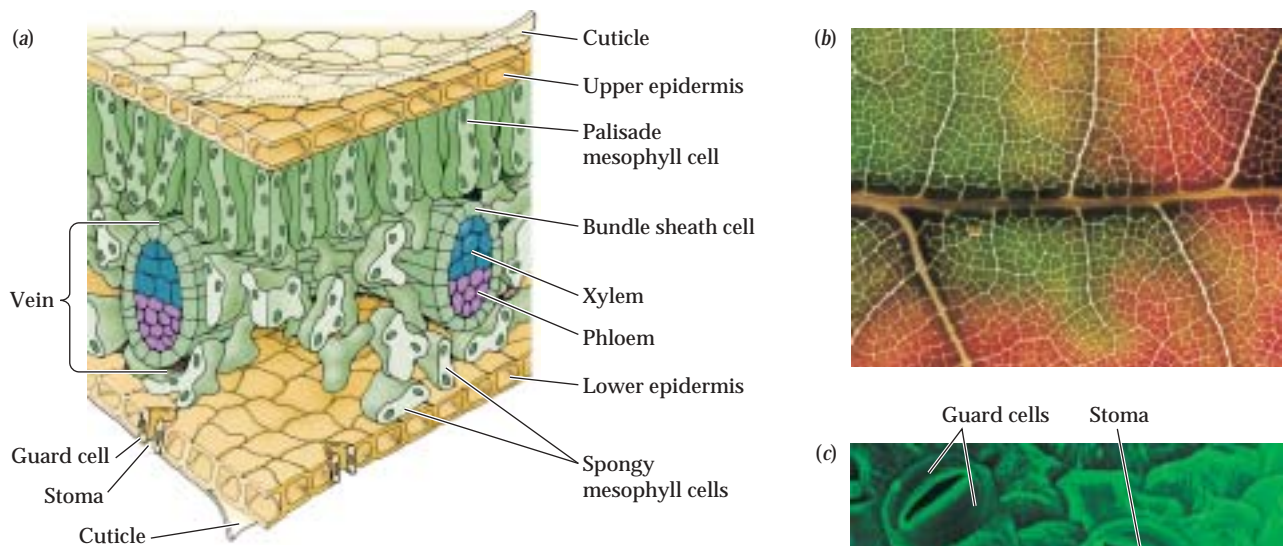
We can think of roots and stems as important supporting actors that sustain the activities of the real stars of the plant body, the leaves—the organs of photosynthesis. Leaf anatomy is beautifully adapted to carry out photosynthesis and to support it by exchanging the gases O_2 and CO_2 with the environment, limiting evaporative water loss, and exporting the products of photosynthesis to the rest of the plant. Figure 35.23a shows a typical eudicot leaf in three dimensions.

Most eudicot leaves have two zones of photosynthetic parenchyma tissue referred to as **mesophyll**, which means “middle of the leaf.” The upper layer or layers of mesophyll consist of elongated cells; this zone is referred to as *palisade mesophyll*. The lower layer or layers consist of irregularly shaped cells; this zone is called *spongy mesophyll*. Within the mesophyll is a great deal of air space through which carbon dioxide can diffuse to reach and be absorbed by photosynthesizing cells.

Vascular tissue branches extensively throughout the leaf, forming a network of **veins** (Figure 35.23b). Veins extend to within a few cell diameters of all the cells of the leaf, ensuring that the mesophyll cells are well supplied with water and minerals. The products of photosynthesis are loaded into the phloem of the veins for export to the rest of the plant.

Covering the entire leaf on both its upper and lower surfaces is a layer of nonphotosynthetic cells, which constitute the epidermis. The epidermal cells have an overlying waxy cuticle that is highly impermeable to water. But this impermeability poses a problem: While keeping water in the leaf, the epidermis also keeps carbon dioxide—the other raw material of photosynthesis—out.

The problem of balancing water retention and carbon dioxide availability is solved by an elegant regulatory system that will be discussed in more detail in the next chapter. *Guard cells* are modified epidermal cells that change their shape, thereby opening or closing pores called *stomata*, which serve as passageways between the environment and the leaf’s interior (Figure 35.23c). When the stomata are open, carbon dioxide can enter and oxygen can leave, but water vapor can also be lost.



35.23 The Eudicot Leaf (a) This three-dimensional diagram shows a eudicot leaf. (b) The network of fine veins in this maple leaf carries water to the mesophyll cells and carries photosynthetic products away from them. (c) These paired cells on the lower epidermis of a eudicot leaf are guard cells; the gaps between them are stomata, through which carbon dioxide enters the leaf.

In Chapter 8 we described C_4 plants, which can fix carbon dioxide efficiently even when the carbon dioxide supply in the leaf decreases to a level at which the photosynthesis of C_3 plants is inefficient. One adaptation that helps C_4 plants do this is their modified leaf anatomy (see Figure 8.16). The photosynthetic cells in the C_4 leaf are grouped around the veins in concentric layers, forming an outer mesophyll layer and an inner *bundle sheath*. These layers each contain different types of chloroplasts, leading to the biochemical division of labor illustrated in Figure 8.17.

Leaves receive water and mineral nutrients from the roots by way of the stems. In return, the leaves export products of photosynthesis, providing a supply of chemical energy to the rest of the plant body. And, as we have just seen, leaves exchange gases, including water vapor, with the environment by way of the stomata. All three of these processes will be considered in detail in the next chapter.

Chapter Summary

Vegetative Organs of the Flowering Plant Body

- ▶ Monocots typically have a single cotyledon, narrow leaves with parallel veins, flower parts in threes or multiples of three, and stems with scattered vascular bundles. **Review Figure 35.1**
- ▶ Eudicots typically have two cotyledons, broad leaves with netlike veins, flower parts in fours or fives, and vascular bundles in a ring. **Review Figure 35.1**
- ▶ Flowering plants that are neither monocots nor eudicots are generally similar in structure to eudicots.
- ▶ The vegetative organs of flowering plants are roots, which form a root system, and stems and leaves, which form a shoot system. **Review Figure 35.2**
- ▶ Roots anchor the plant and take up water and minerals.
- ▶ Stems bear leaves and buds. Lateral buds form branches. Apical buds produce cells that contribute to the elongation of the stem.
- ▶ Leaves are responsible for most photosynthesis, for which their flat blades, held perpendicular to the sun's rays, are well adapted. **Review Figure 35.5**

Plant Cells

- ▶ The walls of plant cells have a structure that often corresponds to the special functions of the cell.
- ▶ The walls of individual cells are separated by a middle lamella common to two neighboring cells; each cell also has its own primary wall. **Review Figure 35.6**
- ▶ Some cells produce a thick secondary wall. Adjacent cells are connected by plasmodesmata. **Review Figures 35.7, 35.8**
- ▶ Parenchyma cells have thin walls. Many parenchyma cells store starch or lipids; some others carry out photosynthesis. **Review Figure 35.9a**
- ▶ Collenchyma cells provide flexible support. **Review Figure 35.9b**
- ▶ Sclerenchyma cells provide strength and often function when dead. **Review Figure 35.9c, d**
- ▶ Tracheids and vessel elements are xylem cells that conduct water and minerals after the cells die. **Review Figures 35.9e, f, 35.10**

- ▶ Sieve tube elements are the conducting cells of the phloem. Their activities are often controlled by companion cells. **Review Figure 35.11**

Plant Tissues and Tissue Systems

- ▶ Three tissue systems extend throughout the plant body.
- ▶ The vascular tissue system, consisting of xylem and phloem, conducts water, minerals, and the products of photosynthesis throughout the plant body.
- ▶ The dermal tissue system protects the body surface.
- ▶ The ground tissue system produces and stores nutrient materials and performs other functions. **Review Figure 35.12**

Forming the Plant Body

- ▶ The pattern of cells and tissues along the long axis and the concentric arrangement of the tissue systems are parts of the plant body plan; they arise through orderly development.
- ▶ The plant body consists of semi-independent modules or units. The growth of stems and roots is indeterminate. Leaves, flowers, and fruits show determinate growth.
- ▶ Meristems are localized regions of cell division. A hierarchy of meristems generates the plant body.
- ▶ Apical meristems at the tips of stems and roots produce the primary tissues of those organs. **Review Figure 35.13**
- ▶ Shoot apical meristems and root apical meristems give rise to primary meristems: the protoderm, the ground meristem, and the procambium. The protoderm produces the dermal tissue system, the ground meristem produces the ground tissue system, and the procambium produces the vascular tissue system.
- ▶ In some plants, the products of primary growth constitute the entire plant body. Many other plants show secondary growth. Two lateral meristems, the vascular cambium and cork cambium, are responsible for secondary growth. **Review Figure 35.13**
- ▶ The structure of a winter woody twig reflects both primary and secondary growth. **Review Figure 35.14**
- ▶ The young root has an apical meristem that gives rise to the root cap and to the three primary meristems, which in turn produce the three tissue systems. Root tips have three overlapping zones: the zone of cell division, the zone of cell elongation, and the zone of maturation. **Review Figure 35.15**
- ▶ The protoderm gives rise to the epidermis, part of which forms the root hairs that are responsible for absorbing water and minerals. **Review Figure 35.16**
- ▶ The ground tissue system of a young root is the cortex, whose innermost cell layer, the endodermis, controls access to the stele.
- ▶ The stele, consisting of the pericycle, xylem, and phloem, is the root's vascular tissue system. Lateral roots arise in the pericycle. **Review Figure 35.17. See Web/CD Activities 35.1 and 35.2**
- ▶ The shoot apical meristem also gives rise to three primary meristems, with roles similar to their counterparts in the root. Leaf primordia on the sides of the apical meristem develop into leaves.
- ▶ The vascular tissue in young stems is divided into vascular bundles, each containing both xylem and phloem. Pith occupies the center of the eudicot stem, and cortex lies outside the ring of vascular bundles, with pith rays lying between the vascular bundles. **Review Figure 35.18. See Web/CD Activities 35.3 and 35.4**
- ▶ Many eudicot stems and roots show secondary growth in which vascular cambia and cork cambia give rise, respectively, to secondary xylem (wood) and secondary phloem and to cork. **Review Figure 35.19. See Web/CD Tutorial 35.1**

- ▶ The vascular cambium lays down layers of secondary xylem and phloem. Living cells within these tissues are nourished by vascular rays. **Review Figure 35.20**
- ▶ The periderm consists of cork, cork cambium, and phellogen, all pierced at intervals by lenticels that allow gas exchange.

Leaf Anatomy Supports Photosynthesis

- ▶ The photosynthetic tissue of a leaf is called mesophyll. Veins bring water and minerals to the mesophyll and carry the products of photosynthesis to other parts of the plant body.
- ▶ A waxy cuticle retards water loss from the leaf and is impermeable to carbon dioxide. Guard cells control the opening of stomata, openings in the leaf that allow CO₂ to enter, but also allow some water to escape. **Review Figure 35.23. See Web/CD Activity 35.5**

Self-Quiz

1. Which of the following is *not* a difference between monocots and eudicots?
 - a. Eudicots more frequently have broad leaves.
 - b. Monocots commonly have flower parts in multiples of three.
 - c. Monocot stems do not generally undergo secondary thickening.
 - d. The vascular bundles of monocots are commonly arranged as a cylinder.
 - e. Eudicot embryos commonly have two cotyledons.
2. Roots
 - a. always form a fibrous root system that holds the soil.
 - b. possess a root cap at their tip.
 - c. form branches from lateral buds.
 - d. are commonly photosynthetic.
 - e. do not show secondary growth.
3. The plant cell wall
 - a. lies immediately inside the plasma membrane.
 - b. is an impermeable barrier between cells.
 - c. is always waterproofed with either lignin or suberin.
 - d. always consists of a primary wall and a secondary wall, separated by a middle lamella.
 - e. contains cellulose and other polysaccharides.
4. Which statement about parenchyma cells is *not* true?
 - a. They are alive when they perform their functions.
 - b. They typically lack a secondary wall.
 - c. They often function as storage depots.
 - d. They are the most numerous cells in the primary plant body.
 - e. They are found only in stems and roots.
5. Tracheids and vessel elements
 - a. die before they become functional.
 - b. are important constituents of all plants.
 - c. have walls consisting of middle lamella and primary wall.
 - d. are always accompanied by companion cells.
 - e. are found only in the secondary plant body.
6. Which statement about sieve tube elements is *not* true?
 - a. Their end walls are called sieve plates.
 - b. They die before they become functional.
 - c. They link end-to-end, forming sieve tubes.
 - d. They form the system for translocation of organic nutrients.
 - e. They lose the membrane that surrounds their central vacuole.
7. The pericycle
 - a. separates the stele from the cortex.
 - b. is the tissue within which branch roots arise.
 - c. consists of highly differentiated cells.
 - d. forms a star-shaped structure at the very center of the root.
 - e. is waterproofed by Casparian strips.
8. Secondary growth of stems and roots
 - a. is brought about by the apical meristems.
 - b. is common in both monocots and eudicots.
 - c. is brought about by vascular and cork cambia.
 - d. produces only xylem and phloem.
 - e. is brought about by vascular rays.
9. Periderm
 - a. contains lenticels that allow for gas exchange.
 - b. is produced during primary growth.
 - c. is permanent; it lasts as long as the plant does.
 - d. is the innermost part of the plant.
 - e. contains vascular bundles.
10. Which statement about leaf anatomy is *not* true?
 - a. Stomata are controlled by paired guard cells.
 - b. The cuticle is secreted by the epidermis.
 - c. The veins contain xylem and phloem.
 - d. The cells of the mesophyll are packed together, minimizing air space.
 - e. C₃ and C₄ plants differ in leaf anatomy.

For Discussion

1. When a young oak was 5 m tall, a thoughtless person carved his initials in its trunk at a height of 1.5 m above the ground. Today that tree is 10 m tall. How high above the ground are those initials? Explain your answer in terms of the manner of plant growth.
2. Consider a newly formed sieve tube element in the secondary phloem of an oak tree. What kind of cell divided to produce the sieve tube element? What kind of cell divided to produce that parent cell? Keep tracing back until you arrive at a cell in the apical meristem.
3. Distinguish between sclerenchyma cells and collenchyma cells in terms of structure and function.
4. Distinguish between primary and secondary growth. Do all angiosperms undergo secondary growth? Explain.
5. What anatomical features make it possible for a plant to retain water as it grows? Describe the plant tissues and how and when they form.