Basic parts of the shoot system of an apple tree *(Malus domestica)*, including leaves, stems, and vividly colored fruits.

31 The Plant Body

Study Plan

Why It Matters

Food, fibers for clothing, wood and other materials for construction, paper and inks, dozens of pharmaceuticals—these and many other essentials of modern human life derive from the parts of plants. In fact, members of the genus *Homo* have been depending on plant parts for their entire history. Fossil teeth discovered in the East African Rift Valley indicate that our early ancestors' diet likely included hard-shelled nuts, dry seeds, soft fruits, and leaves. By about 11,000 years ago humans were domesticating seed plants to provide stable food supplies. Directly or indirectly, leaves, stems, roots, flowers, seeds, and fruits of plants are the basic sources of energy for Earth's human inhabitants and all other animals as well **(Figures 31.1).**

As you saw in Chapter 27, plants that made the transition from aquatic to terrestrial life did so only as adaptations in form and function helped solve problems posed by the terrestrial environment. These evolutionary adaptations included a shoot system that helps support leaves and other body parts in air, a root system that anchors the plant in soil and provides access to soil nutrients and water, tissues for internal transport of nutrients, and specializations for preventing water loss.

Figure 31.1
Examples of plant parts that provide food for animals. **(a)** Mechanized harvesting of *Triticum* seeds, commonly known as wheat grains. **(b)** A pronghorn *(Antilocarpa americana)*, which consumes leaves and grasses. **(c)** Cedar waxwing *(Bombycilla cedrorum)* feeding on plump berries of *Sorbus americana*, the American mountain ash.

This unit surveys the structure and functioning of plants—their morphology, anatomy, and physiology. A plant's *morphology* is its external form, such as the shape of its leaves, and *anatomy* is the structure and arrangement of its internal parts. Plant *physiology* refers to the mechanisms by which the plant's body functions in its environment. Our focus is the plant phylum Anthophyta—angiosperms, or flowering plants—in terms of distribution and sheer numbers of species, the most successful plants on Earth.

31.1 Plant Structure and Growth: An Overview

Plants are photosynthetic autotrophs—"self-feeding" photosynthesizers that need sunlight and the carbon dioxide available in air as well as the water available in soil. In addition, many plants require nutrients that are usually available only in soil, and their aboveground parts may need the physical support of structures anchored in the ground. The evolutionary response to these challenges produced a plant body consisting of two closely linked but quite different components—a photosynthetic *shoot system* extending upward into the air and a nonphotosynthetic *root system* extending downward into the soil. Each system consists of various **organs**—body structures that contain two or more types of tissues and that have a definite form and function. Plant organs include leaves, stems, and roots, among others. A **tissue** is a group of cells and intercellular substances that function together in one or more specialized tasks.

In All Plant Tissues the Cells Share Some General Features

All plant cells share certain features, regardless of the tissue in which they reside. New plant cells develop a primary cell wall around the **protoplast,** the botanical term for the cell's cytoplasm, organelles, and plasma membrane. The primary wall contains cellulose, an insoluble polysaccharide made up of glucose subunits that is embedded in a matrix of other polysaccharides called hemicelluloses. This combination helps make the wall rigid but flexible. Pectin, another polysaccharide, is abundant in the primary wall and in the middle lamella, the layer between the primary walls of neighboring cells that helps bind cells together in tissues. (Plant pectin is often used to congeal jams and jellies.) As a young plant grows, the protoplast of many types of plant cells deposits additional cellulose and other materials inside the primary wall, forming a strong secondary cell wall (see Figure 5.25).

As in animals, all of a plant's cells have the same genes in their nuclei. As each cell matures and *differentiates* (becomes specialized for a particular function), specific genes become active. For the most part, fully differentiated animal cells perform their functions while alive, but some types of plant cells die after differentiating, and their protoplasts disappear. The walls that remain, however, serve key functions, particularly in vascular tissue.

The secondary cell walls of some plants contain lignin, a water-insoluble, inert polymer. **Lignification,** the deposition of lignin in cell walls, anchors the cellulose fibers in the walls, making them stronger and more rigid, and protects the other wall components from physical or chemical damage. Because water cannot penetrate and soften lignified cell walls, lignification also creates a waterproof barrier around the wall's cellulose strands. Many biologists believe that the evolution of large vascular plants became possible when certain cells developed biochemical pathways leading to lignification and could therefore become organized into watertight conducting channels.

Substances pass from one lignified cell to another through various routes. Solutes such as amino acids and sugars move in the plasmodesmata linking adjacent cells (see Figure 5.25). Water moves from cell to cell across *pits,* narrow regions where the secondary wall is absent and the primary wall is thinner and more porous than elsewhere.

Shoot and Root Systems Perform Different but Integrated Functions

A flowering plant's **shoot system** typically consists of stems, leaves, buds, and—during part of the plant's life cycle—reproductive organs known as flowers **(Figure 31.2).** A stem with its attached leaves and buds is a *vegetative* (nonreproductive) shoot; a bud eventually gives rise to an extension of the shoot or to a new, branching shoot. A *reproductive* shoot produces flowers, which later develop fruits containing seeds.

The shoot system is highly adapted for photosynthesis. Leaves greatly increase a plant's surface area and thus its exposure to light. Stems are frameworks for upright growth, which favorably position leaves for light exposure and flowers for pollination. Some parts of the shoot system also store carbohydrates manufactured during photosynthesis.

The **root system** usually grows belowground. It anchors the plant, and sometimes structurally supports its upright parts. It also absorbs water and dissolved minerals from soil and stores carbohydrates. Adaptations in the structure and function of plant cells and tissues were an integral part of the evolution of shoots and roots. For example, vascular tissues specialized to serve as internal pipelines conduct water, minerals, and organic substances throughout the plant. The root hairs sketched in Figure 31.2 are surface cells specialized for absorbing water from soil.

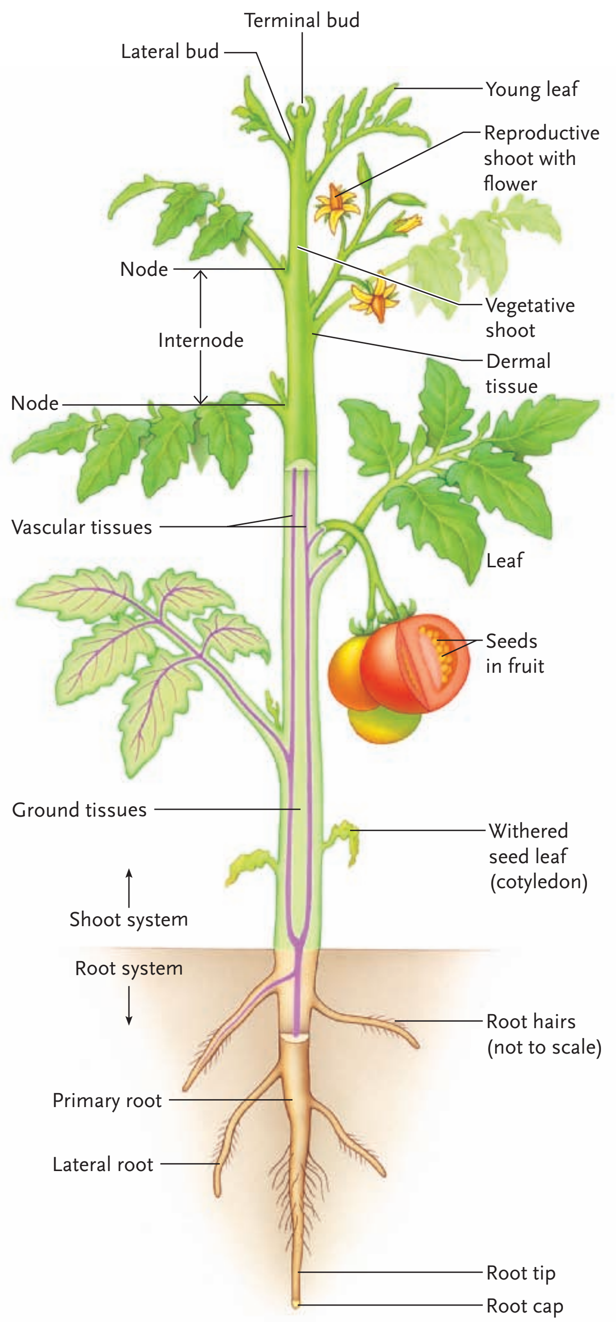


Figure 31.2
Body plan for the commercially grown tomato plant *Solanum lycopersicum*, a typical angiosperm. Vascular tissues (purple) conduct water, dissolved minerals, and organic substances. They thread through ground tissues, which make up most of the plant body. Dermal tissues (epidermis, in this case) cover the surfaces of the root and shoot systems.

Meristems Produce New Tissues Throughout a Plant's Life

As you know from experience, animals generally grow to a certain size, and then their growth slows dramatically or stops. This pattern is called **determinate growth.** In contrast, a plant can grow throughout its life, a pattern called **indeterminate growth.** Individual plant parts such as leaves, flowers, and fruits exhibit determinate growth, but every plant also has self-perpetuating embryonic tissue at the tips of shoots and roots. Under the influence of plant hormones, these **meristems** (*merizein* = to divide) produce new tissues more or less continuously while a plant is alive. A capacity for indeterminate growth gives plants a great deal of flexibility—or what biologists often call *plasticity*—in their possible responses to changes in environmental factors such as light, temperature, water, and nutrients. This plasticity has major adaptive benefits for an organism that cannot move about, as most animals can. For example, if external factors change the direction of incoming light for photosyn-

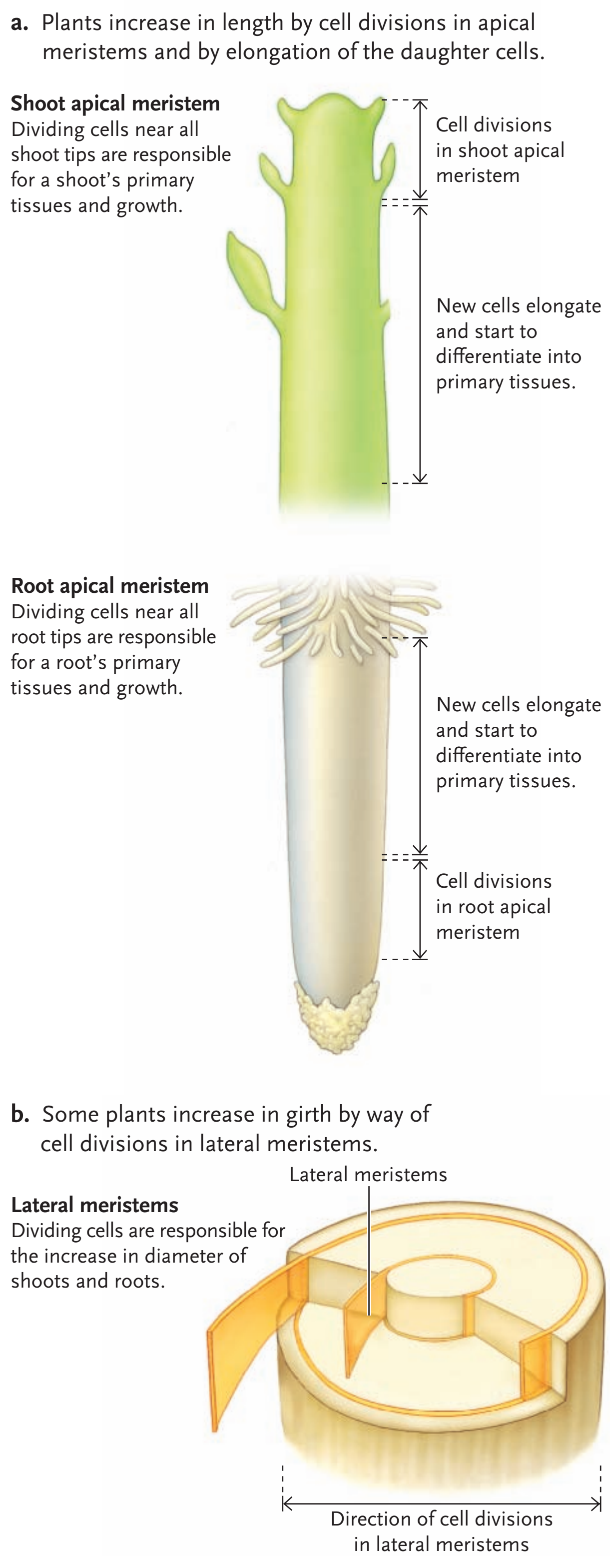


Figure 31.3
Approximate locations of types of meristems that are responsible for increases in the length and diameter of the shoots and roots of a vascular plant.

thesis, stems can "shift gears" and grow in that direction. Likewise, roots can grow outward toward water. These and other plant movements, called tropisms, are a major topic of Chapter 35.

As you know, animals grow mainly by mitosis, which increases the number of body cells. Plants, however, grow by two mechanisms—an increase in the number of cells by mitotic cell division in the meristems, *and* an increase in the size of individual cells. In regions adjacent to the meristems in the tips of shoots and roots, the daughter cells rapidly increase in size—especially in length—for some time after they are produced. In contrast, when animal cells divide mitotically the daughter cells usually increase in size only a little.

Meristems Are Responsible for Growth in Both Height and Girth

Some plants have only one kind of meristem while others have two **(Figure 31.3).** All vascular plants have **apical meristems,** clumps of self-perpetuating tissue at the tips of their buds, stems, and roots (see Figure 31.3a). Tissues that develop from apical meristems are called **primary tissues** and make up the **primary plant body.** Growth of the primary plant body is called **primary growth.**

Some species of plants—grasses and dandelions, for example—show only primary growth, which occurs at the tips of roots and shoots. Others, particularly plants that have a woody body, show **secondary growth,** which originates at self-perpetuating cylinders of tissue called **lateral meristems.** Secondary growth increases the diameter of older roots and stems (see Figure 31.3b). The tissues that develop from lateral meristems, called **secondary tissues,** make up the woody **secondary plant body** we see in trees and shrubs.

Primary and secondary growth can go on simultaneously in a single plant, with primary growth increasing the length of shoot parts and secondary growth adding girth. Each spring, for example, a maple tree undergoes primary growth at each of its root and shoot tips, while secondary growth increases the diameter of its older woody parts. Plant hormones govern these growth processes and other key events that are described in Chapter 35.

Monocots and Eudicots Are the Two General Structural Forms of Flowering Plants

As noted in Chapter 27, several broad categories of body architecture arose as flowering plants evolved. The two major ones are the **monocot** and **eudicot** lineages. Grasses, daylilies, irises, cattails, and palms are examples of monocots. Eudicots include nearly all familiar angiosperm trees and shrubs, as well as many nonwoody (herbaceous) plants. Examples are maples, willows, oaks, cacti, roses, poppies, sunflowers, and garden beans and peas.

Monocots and eudicots, recall, differ in the number of *cotyledons*—the seed leaves associated with plant embryos. Monocot seeds have one cotyledon and eudicot seeds have two. Although monocots and eudicots have similar types of tissues, their body structures differ in distinctive ways **(Table 31.1).** As we discuss the morphology of flowering plants, we will refer frequently to these structural differences.

Flowering Plants Can Be Grouped according to Type of Growth and Lifespan

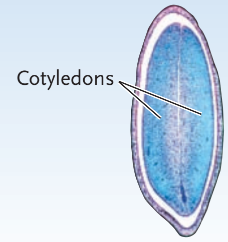
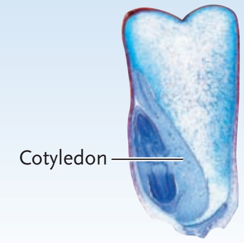
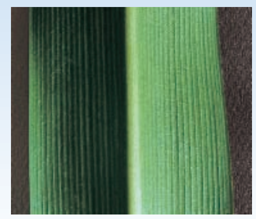
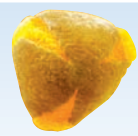
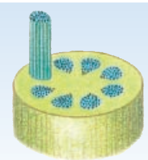
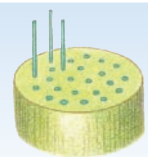
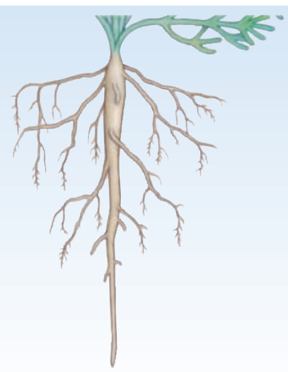
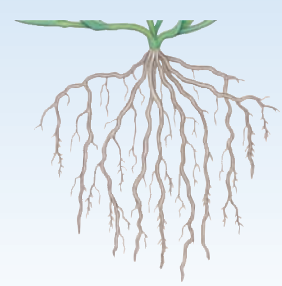
In evolutionary terms, the distinction between monocot and eudicot flowering plants is most important structurally and developmentally. Yet botanists sometimes use other criteria to distinguish between flowering plants—for example, by whether they have secondary growth. Most monocots and some eudicots are *herbaceous* plants, showing little or no secondary growth during their life cycle. In contrast, many eudicots (and all gymnosperms) are *woody* plants, which do have secondary growth.

We can also distinguish plants by lifespan. **Annuals** are herbaceous plants in which the life cycle is completed in one growing season. With minimal or no secondary growth, annuals typically have only apical meristems. Examples are marigolds (a eudicot) and corn (a monocot). **Biennials** complete the life cycle in two growing seasons, and limited secondary growth occurs in some species. Roots, stems, and leaves form in the first season, then the plant flowers, forms seeds, and dies in the second. Examples are carrots and celery (eudicots). In **perennials**, vegetative growth and reproduction continue year after year. Many perennials, such as trees, shrubs, and some vines, have secondary tissues, although others, such as irises and daffodils, do not.

Study Break

1. Compare and contrast the components and functions of a land plant's shoot and root systems.
2. Explain what meristem tissue is, and name and describe the functions of the basic types of meristems.

Table 31.1 Eudicots and Monocots Compared

Character	Eudicots	Monocots
Cotyledons	 © Bruce Iverson Inside seeds, two cotyledons (seed leaves of embryo)	 © Mike Clayton/University of Wisconsin Department of Botany Inside seeds, one cotyledon (seed leaf of embryo)
Floral parts	 © Ernest Manewal/Index Stock Photography Usually four or five floral parts (or multiples of four or five)	 © Darrell Gulin/Corbis Usually three floral parts (or multiples of three)
Leaf veins	 © Simon Fraser/Photo Researchers, Inc. Leaf veins usually in a netlike array	 Gary Head Leaf veins usually running parallel with one another
Pollen pores and furrows	 © Andrew Syred/Photo Researchers, Inc. Three pores or furrows (or furrows with pores) in pollen grains	 © Andrew Syred/Photo Researchers, Inc. One pore or furrow in the pollen grain surface
Location of vascular bundles	 Vascular bundles organized as a ring in ground tissue	 Vascular bundles distributed throughout ground tissue
Root system	 Usually a main taproot with smaller lateral roots	 Usually a branching fibrous root system

31.2 The Three Plant Tissue Systems

Plants develop three tissue systems that provide the foundation for the various plant organs. The **ground tissue system**, which makes up most of the plant body, functions in metabolism, storage, and support. The **vascular tissue system** consists of various tubes that transport water and nutrients throughout the plant. The tubes are organized in bundles that are dispersed through the ground tissues. The **dermal tissue system** serves as a skinlike protective covering for the plant body. Figure 31.2 shows the general location of each system in the shoot and root.

Table 31.2 **Summary of Flowering Plant Tissues and Their Components**

Tissue System	Name of Tissue	Cell Types in Tissue	Tissue Function
Ground tissue	Parenchyma	Parenchyma cells	Photosynthesis, respiration, storage, secretion
	Collenchyma	Collenchyma cells	Flexible strength for growing plant parts
	Sclerenchyma	Fibers or sclereids	Rigid support, deterring herbivores
Vascular tissue	Xylem	Conducting cells (tracheids, vessel members); parenchyma cells; sclerenchyma cells	Transport of water and dissolved minerals
	Phloem	Conducting cells (sieve tube members); parenchyma cells; sclerenchyma cells	Sugar transport
Dermal tissue	Epidermis	Undifferentiated cells; guard cells and other specialized cells	Control of gas exchange, water loss; protection
	Periderm	Cork; cork cambium; secondary cortex	Protection

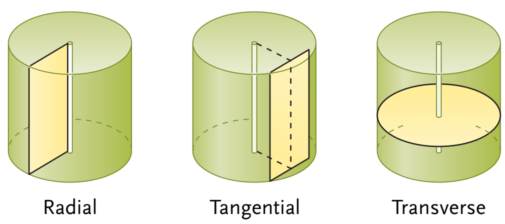


Figure 31.4
Terms that identify how tissue specimens are cut from a plant. Along the radius of a stem or root, longitudinal cuts give radial sections. Cuts at right angles to a root or stem radius give tangential sections. Cuts perpendicular to the long axis of a stem or root give transverse sections (cross sections).

Each tissue system includes several types of tissue, and each tissue is made up of cells with specializations for different functions **(Table 31.2).** *Simple* tissues have only one type of cell. Other tissues are *complex,* with organized arrays of two or more types of cells. **Figure 31.4** will help you interpret micrographs of plant tissues, beginning with the tissues in a transverse section of a stem shown in **Figure 31.5.**

Ground Tissues Are All Structurally Simple, but They Exhibit Important Differences

Plants have three types of ground tissue, each with a distinct structure and function—*parenchyma, collenchyma,* and *sclerenchyma* **(Figure 31.6).** Each type is structurally simple, being composed mainly of one kind of cell. In a very real sense the cells in ground tissues are the "worker bees" of plants, carrying out photosynthesis, storing carbohydrates, providing mechanical support for the plant body, and performing other basic functions. Each kind of cell has a distinctive wall structure, and some have variations in the protoplast as well.

Parenchyma: Soft Primary Tissues. Parenchyma (*para* = around, *chein* = fill in, or pour) makes up the bulk of the soft, moist primary growth of roots, stems, leaves, flowers, and fruits. Most parenchyma cells have only a thin primary wall and so are pliable and permeable to water. Often the cells are spherical or many-sided, although they also can be elongated like a sausage, as in Figure 31.6a. Parenchyma cells sometimes have air spaces between them, especially in leaves (see Figure 31.17). The air spaces may be sizeable in the stems and leaves of aquatic plants, such as water lilies. This adaptation facilitates the movement of oxygen from aerial leaves and stems to submerged parts of the plant, and it also helps the leaves float upward toward the light.

Parenchyma cells may be specialized for tasks as varied as storage, secretion, and photosynthesis. They can occur both as part of parenchyma tissue and as individual cells in other tissues. In many plant species, modified parenchyma cells are specialized for short-distance transport of solutes. Such cells are common in tissues in which water and solutes must be rapidly moved from cell to cell—for example, in vascular tissues and in tissues that secrete nectar. Parenchyma cells usually remain alive and,

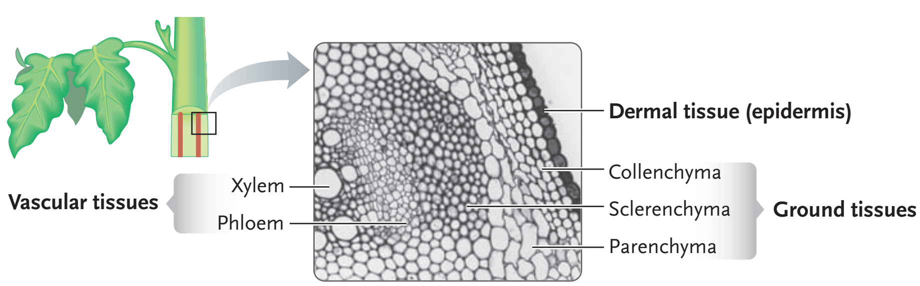
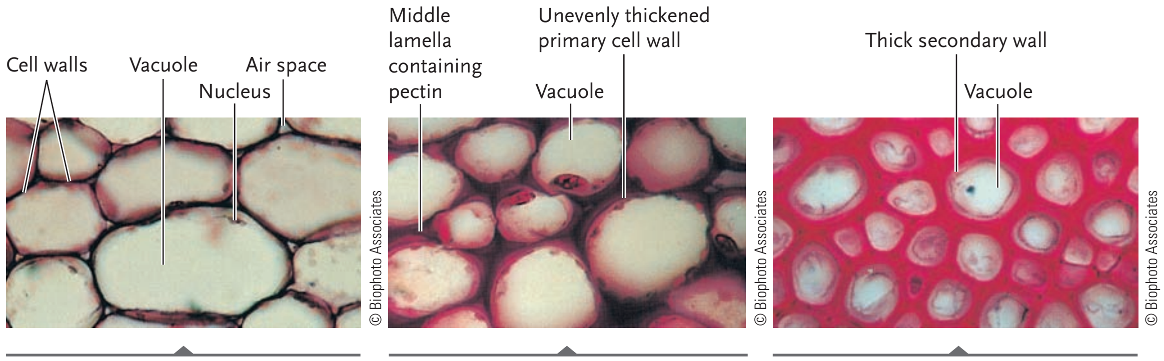


Figure 31.5
Locations of ground, vascular, and dermal tissues in one kind of plant stem, transverse section. Ground tissues are simple tissues while vascular and dermal tissues are complex, containing various types of specialized cells. (Micrograph: James D. Mauseth, Plant Anatomy, Benjamin Cummings, 1988.)



a. Parenchyma tissues consist of soft, living cells specialized for storage, other functions.

b. Collenchyma tissues provide flexible support.

c. Sclerenchyma tissues provide rigid support and protection.

Figure 31.6
Examples of ground tissues from the stem of a sunflower plant *(Helianthus annuus)*.

when mature, retain the capacity to divide; in fact, their mitotic divisions often heal wounds in plant parts.

Collenchyma: Flexible Support. The "strings" in celery are examples of the flexible ground tissue called **collenchyma** (see Figure 31.6b), which helps strengthen plant parts that are still elongating (*kolla* = glue). Collenchyma cells are typically elongated, and collectively they often form strands or a sheathlike cylinder under the dermal tissue of growing shoot regions and the stalklike petioles that attach leaves to stems.

The primary walls of collenchyma cells are built of alternating layers of cellulose and pectin. These walls thicken and stretch as the cell enlarges. Mature collenchyma cells are alive and metabolically active, and they continue to synthesize cellulose and pectin layers as the plant grows.

Sclerenchyma: Rigid Support and Protection. Mature plant parts gain additional mechanical support and protection from **sclerenchyma** (*skleros* = hard). The cells of this ground tissue develop thick secondary walls (see Figure 31.6c), which commonly are lignified and perforated by pits through which water can pass. After mature sclerenchyma cells become encased in lignin, they die because their protoplasts can no longer exchange gases, nutrients, and other materials with the environment. The walls, however, continue to provide protection and support.

The two types of sclerenchyma cells—*sclereids* and *fibers*—differ in their shape and arrangement. Sheetlike arrays of rigid **sclereids** form a protective coat around seeds; examples are the hard casings of a coconut shell or peach pit. Sclereids come in a range of shapes; the gritty texture of a pear comes from the roughly cube-shaped sclereids scattered through its flesh **(Figure 31.7a)**. The long, tapered cells called **fibers** **(Figure 31.7b)** resist stretching, but are more pliable than sclereids. Fibers in the stems of flax plants are massed in parallel; they can flex and twist without stretching and are used to manufacture rope, paper, and linen cloth.

Vascular Tissues Are Specialized for Conducting Fluids

Vascular tissues are complex tissues composed of specialized conducting cells, parenchyma cells, and fibers. *Xylem* and *phloem,* the two kinds of vascular tissues in flowering plants, are organized into bundles of interconnected cells that extend throughout the plant.

Xylem: Transporting Water and Minerals. **Xylem** (*xylon* = wood) conducts water and dissolved minerals absorbed from the soil upward from a plant's roots to the shoot. As you read in Chapter 27, xylem was a key early adaptation allowing plants to make the transition to life on land. Xylem contains two types of conducting cells: *tracheids* and *vessel members*. Both develop thick, lignified secondary cell walls and die at maturity. The empty cell walls of abutting cells serve as pipelines for water and minerals.

Tracheids are elongated, with tapered, overlapping ends **(Figure 31.8a).** In plants adapted to drier soil conditions, they have strong secondary walls that keep them from collapsing when less water is present. As in sclerenchyma, water can move from cell to cell through

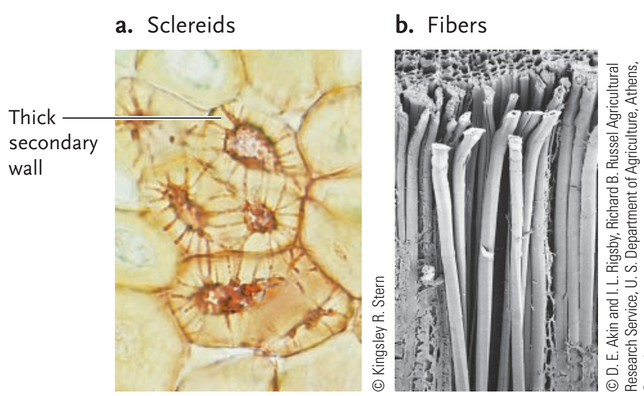


Figure 31.7
Examples of sclerenchyma cells. **(a)** From the flesh of a pear *(Pyrus),* one type of sclereid: stone cells, each with a thick, lignified wall. **(b)** Strong fibers from stems of a flax plant *(Linum)*.

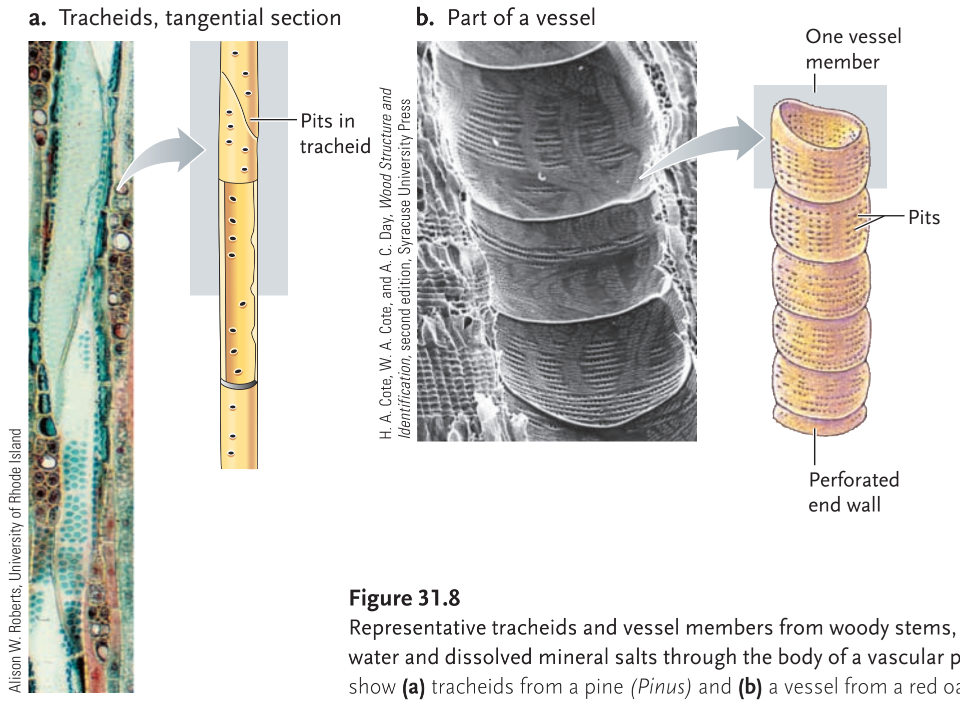


Figure 31.8
Representative tracheids and vessel members from woody stems, elements in xylem that conduct water and dissolved mineral salts through the body of a vascular plant. The electron micrographs show **(a)** tracheids from a pine *(Pinus)* and **(b)** a vessel from a red oak *(Quercus rubra)*.

pits. Usually, a pit in one cell is opposite a pit of an adjacent cell, so water seeps laterally from tracheid to tracheid.

Vessel members (or vessel elements) are shorter cells joined end to end in tubelike columns called vessels **(Figure 31.8b). Vessels** are typically several centimeters long, and in some vines and trees they may be many meters long. Like tracheids, vessel members have pits; however, they also have another adaptation that greatly enhances water flow. As vessel members mature, enzymes break down portions of their end walls, producing perforations. Some vessel members have a single, large perforation, so that the end is completely open (see Figure 31.8b). Others have a cluster of small, round perforations, or ladderlike bars, extending across the open end (see Figure 31.8). The predictability of the perforation patterns suggests that this process is under precise genetic control.

Fossil evidence shows that the forerunners of modern plant species relied solely on tracheids for water transport, and today ferns and most gymnosperms still have only tracheids. Nearly all angiosperms and a few other types of plants have both tracheids and vessel members, however, which confers an adaptive advantage. Flowing water sometimes incorporates air bubbles, which represent a potentially lethal threat to the plant. Water can flow rapidly through vessel members that are linked end to end, but the open channel cannot prevent air bubbles from forming and possibly blocking the flow through the whole vessel. By contrast, even though water moves more slowly in tracheids, the pit membranes are impermeable to air bubbles, and a bubble that forms in one tracheid stays there; water continues to move between other tracheids.

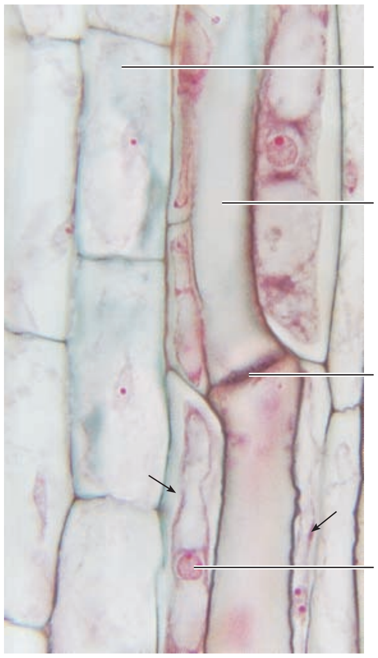
Conducting cells that form after the surrounding tissue has reached its maximum size have complete secondary walls, with pits or perforations. In growing plants, however, only a partial secondary wall forms in cells of xylem, so the cell can elongate as the tissue it services grows. At maturity, tracheids and vessel members die as genetic cues cause their protoplasts to degenerate and lignin to be deposited in cell walls.

Parenchyma cells in xylem participate in the transport of minerals through vessel members and tracheids. Sclerenchyma fibers function like steel cables in concrete, helping keep the tissue fairly rigid and lending structural support to the plant.

Phloem: Transporting Sugars and Other Solutes. The vascular tissue **phloem** (*phloios* = tree bark) transports solutes, notably the sugars made in photosynthesis, throughout the plant body. The main conducting cells of phloem are **sieve tube members (Figure 31.9),** which connect end to end, forming a **sieve tube.** As the name implies, their end walls, called sieve plates, are studded with pores. In flowering plants the phloem is strengthened by fibers and sclereids.

Immature sieve tube members contain the usual plant organelles. Over time, however, the cell nucleus and internal membranes in plastids break down, mitochondria shrink, and the cytoplasm is reduced to a thin layer lining the interior surface of the cell wall. Even without a nucleus, the cell lives up to several years in most plants, and much longer in some trees.

a. Sieve-tube members



b. Sieve plate

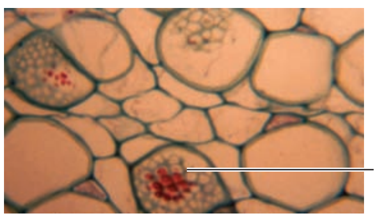


Figure 31.9
Structure of sieve tube members. **(a)** Micrograph showing sieve tube members in longitudinal section. The arrows point to cells that may be companion cells. Long tubes of sieve tube members conduct sugars and other organic compounds. **(b)** Sieve plate in a cell in phloem, cross section.

In many flowering plants, specialized parenchyma cells known as **companion cells** are connected to mature sieve tube members by plasmodesmata. Unlike sieve tube members, companion cells retain their nucleus when mature. They assist sieve tube members both with the uptake of sugars and with the unloading of sugars in tissues engaged in food storage or growth. They may also help regulate the metabolism of mature sieve tube members. We return to the functions of phloem cells in Chapter 32.

Dermal Tissues Protect Plant Surfaces

A complex tissue called **epidermis** covers the primary plant body in a single continuous layer **(Figure 31.10a)** or sometimes in multiple layers of tightly packed cells. The external surface of epidermal cell walls is coated with waxes that are embedded in cutin, a network of chemically linked fats. Epidermal cells secrete this coating, or **cuticle**, which resists water loss and helps fend off attacks by microbes. A cuticle coats all plant parts except the very tips of the shoot and most absorptive parts of roots; other root regions have an extremely thin cuticle.

Most epidermal cells are relatively unspecialized, but some are modified in ways that represent important adaptations for plants. Young stems, leaves, flower parts, and even some roots have pairs of crescent-shaped **guard cells (Figure 31.10b).** Unlike other cells of the epidermis, guard cells contain chloroplasts and so can carry out photosynthesis. The pore between a pair of guard cells is termed a **stoma** (plural, *stomata*). Water vapor, carbon dioxide, and oxygen move across the epidermis through the stomata, which open and close by way of mechanisms we consider in Chapter 32.

With their exact spacing and vital role in regulating the exchange of gases between a plant and its environment, stomata have captured the interest of

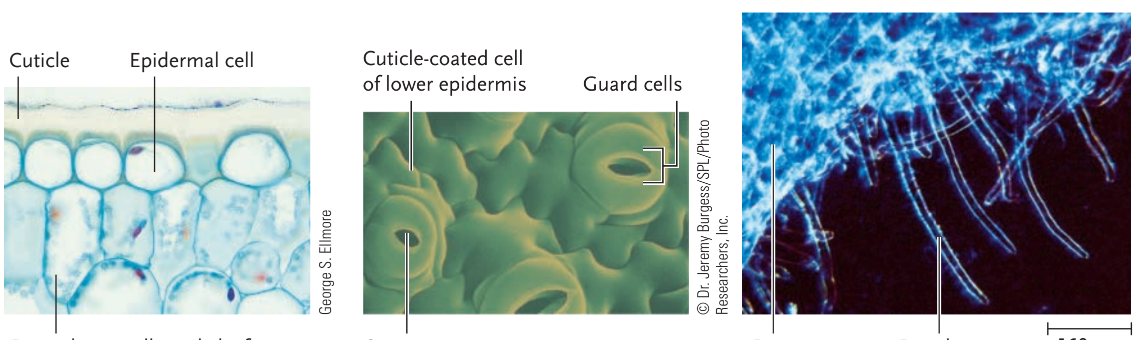


Figure 31.10
Structure and examples of epidermal tissue. **(a)** Cross section of leaf epidermis from a bush lily *(Clivia miniata)*. **(b)** Scanning electron micrograph of a leaf surface, showing cuticle-covered epidermal cells and stomata. **(c)** Root hairs, an epidermal specialization.

Insights from the Molecular Revolution

Shaping up Flower Color

Different pigments in flowers produce different colors, but are pigments the whole story? A molecular study of flower color in snapdragons *(Antirrhinum majus)* provided a surprising answer. Kenichi Noda of the Nippon Oil Company in Japan and Beverly J. Glover and her colleagues at the John Innes Institute in England were interested in a mutant snapdragon called *mixta,* which produces pale red flower petals with a dull, flat surface rather than the deep red, velvety petals of wild-type plants **(Figure a).**

Through a series of steps, the investigators isolated and cloned the *mixta* gene. Sequencing the gene revealed close similarities to a regulatory gene that activates genes in some other plants. The similarities suggested that the normal snapdragon gene also codes for a regulatory protein that produces normal flower color. When the transposable element inserts in the gene, the regulatory protein is lost.

How does the regulatory protein govern flower color? At first Noda and his colleagues thought it regulated production of anthocyanin, a pigment that gives flowers a red color, and that loss of the protein in mutant plants hampered anthocyanin production. They discarded this hypothesis when both the wild-type and *mixta* plants were found to have normal levels of anthocyanin. However, microscopic examination of flower petals revealed that wild-type and *mixta* epidermal cells are shaped differently. Normal plants have conical epidermal cells, with the tip of the cone pointing outward and giving the petals a velvety appearance. Epidermal cells of *mixta* mutants have a flat, irregular surface that produces a dull appearance. **Figure b** shows the surface of a variegated flower petal, which has both conical and flat cells. This structural difference suggested that in wild-type petals, the cone tips act as prisms that make the red pigment clearly visible, while the irregular surface of the mutant cells scatters light and masks the pigment color.

As a test, the research team removed the cell walls from the epidermal petal cells, a step that eliminated differences in cell shape. Both the normal and mutant cells had the same intense, red color. On this basis, the researchers proposed that the regulatory protein encoded in the normal *mixta* gene activates other genes whose protein products in some way produce the conical cell shape.

William E. Ferguson

Figure a
Wild-type snapdragon, which has flowers with deep red petals.

Cathie Martin

Figure b
Scanning electron micrograph of the surface of a variegated snapdragon petal, showing conical cells in the bright red colored areas and flat cells in the pale colored areas. The genetic events that produce variegated petals were clues that helped the research team identify the *mixta* gene.

geneticists probing the molecular underpinnings of plant development. Working with *Arabidopsis thaliana* (thale cress) plants, researchers have identified an enzyme—encoded by the gene *YDA*—that appears to ultimately control where and how many stomata form. In mutant plants with a defective enzyme, the epidermis is blanketed with stomata packed side by side. The plants often die early in development or are stunted and appear fuzzy—hence the enzyme's name, YODA, recalling the short, hairy Star Wars character. In nonmutated wild-type plants, unequal divisions of precursor cells produce one smaller and one larger daughter cell, and the smaller one gives rise to the two guard cells of a stoma. (The larger cell either divides again or becomes an underlying epidermal cell.) YODA comes into play when a series of precursor reactions phosphorylate it. The activated enzyme then triggers a cascade of reactions that, by some as-yet-unknown mechanism, either promote or restrict these asymmetric divisions.

Other epidermal specializations are the single-celled or multicellular outgrowths collectively called **trichomes**, which give the stems or leaves of some plants a hairy appearance. Some trichomes exude sugars that attract insect pollinators. Leaf trichomes of *Urtica,* the stinging nettle, provide protection by injecting an irritating toxin into the skin of animals that brush against the plant or try to eat it. **Root hairs,** which develop as extensions in the outer wall of root epidermal cells **(Figure 31.10c),** are also trichomes. Root hairs absorb much of a plant's water and minerals from the soil.

The epidermal cells of flower petals (which are modified leaves) synthesize pigments that are partly responsible for a blossom's colors. However, molecular studies have revealed that flower colors and their intensity or brightness also depend on the shape of the epidermal cells, as described in *Insights from the Molecular Revolution*.

Study Break

1. Describe the defining features, cellular components, and functions of the ground tissue system.
2. What are the functions of xylem and phloem?
3. What are the cellular components and functions of the dermal tissue system?

31.3 Primary Shoot Systems

A young flowering plant's shoot system consists of the main stem, leaves, and buds as well as flowers and fruits. Chapter 34 looks more closely at flowers and fruits; here we focus on the growth and organization of stems, buds, and leaves of the primary shoot system.

Stems Are Adapted to Provide Support, Routes for Vascular Tissues, Storage, and New Growth

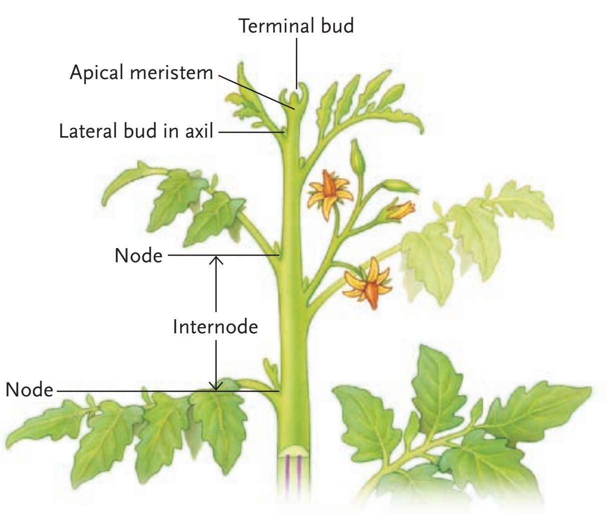
Stems are structurally adapted for four main functions. First, they provide mechanical support, generally along a vertical (upright) axis, for body parts involved in growth, photosynthesis, and reproduction. These parts include meristematic tissues, leaves, and flowers. Second, they house the vascular tissues (xylem and phloem), which transport products of photosynthesis, water and dissolved minerals, hormones, and other substances throughout the plant. Third, they often are modified to store water and food. And finally, buds and specific stem regions contain meristematic tissue that gives rise to new cells of the shoot.

The Modular Organization of a Stem. A plant stem develops in a pattern that divides the stem into modules, each consisting of a *node* and an *internode*. A **node** is a place on the stem where one or more leaves are attached; the area between two nodes is thus an **internode.** The upper angle between the stem and an attached leaf is an **axil.** New primary growth occurs in buds—a **terminal bud** at the apex of the main shoot, and **lateral buds,** which produce branches (lateral shoots), in the leaf axils. Meristematic tissue in buds gives rise to leaves, flowers, or both **(Figure 31.11).**

In eudicots, most growth in a stem's length occurs directly below the apical meristem, as internode cells divide and elongate. Internode cells nearest the apex are most active, so the most visible new growth occurs at the ends of stems. In grasses and some other monocots, by contrast, the upper cells of an internode stop dividing as the internode elongates, and cell divisions are limited to a meristematic region at the base of the internode. The stems of bamboo and other grasses elongate as the internodes are "pushed up" by the growth of such meristems. This adaptation allows grasses to grow back readily after grazing by herbivores (or being chopped off by a lawnmower), because the meristem is not removed.

Terminal buds release a hormone that inhibits the growth of nearby lateral buds, a phenomenon called **apical dominance.** Gardeners who want a bushier plant can stimulate lateral bud growth by periodically cutting off the terminal bud. The flow of hormone signals then dwindles to a level low enough that lateral buds begin to grow. In nature, apical dominance is an adaptation that directs the plant's resources into growing up toward the light.

a. Location of nodes and buds



b. Leaves at a terminal bud

Figure 31.11
Modular structure of a stem. **(a)** The arrangement of nodes and buds on a plant stem. **(b)** Formation of leaves at a terminal bud of a dogwood (genus *Cornus*).

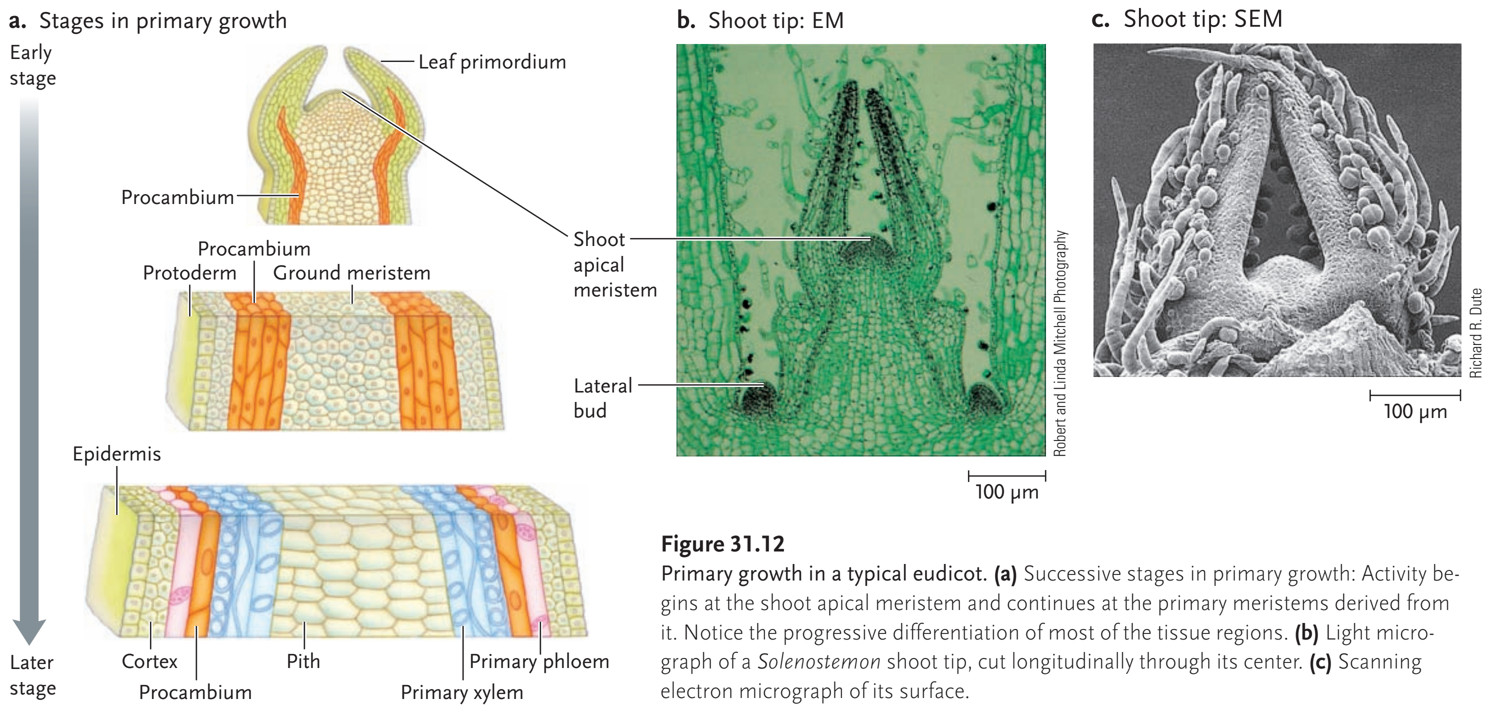


Figure 31.12
Primary growth in a typical eudicot. **(a)** Successive stages in primary growth: Activity begins at the shoot apical meristem and continues at the primary meristems derived from it. Notice the progressive differentiation of most of the tissue regions. **(b)** Light micrograph of a *Solenostemon* shoot tip, cut longitudinally through its center. **(c)** Scanning electron micrograph of its surface.

Primary Growth and Structure of a Stem. Primary growth, the cell divisions and enlargement that produce the primary plant body, begins in the shoot and root apical meristems. The sequence of events is similar in roots and shoots; it is shown for a eudicot shoot in **Figure 31.12.**

The shoot apical meristem is a dome-shaped mass of cells. When one cell divides, one of its daughter cells becomes an **initial,** a cell that remains as part of the meristem. The other daughter cell becomes a **derivative.** The derivative typically divides once or twice and then enters on the path to differentiation. When initials divide, they replenish the supply of derivatives in the meristem.

As derivatives differentiate, they give rise to three **primary meristems:** *protoderm, procambium,* and *ground meristem* (see Figure 31.12). These primary meristems are relatively unspecialized tissues with cells that differentiate in turn into specialized cells and tissues. In eudicots, the primary meristems are also responsible for elongation of the plant body.

How do the genetically identical cells of an apical meristem give rise to three types of primary meristem cells, and ultimately to all the specialized cells of the plant? *Focus on Research* describes some experiments that are probing the genetic mechanisms underlying meristem activity.

Each primary meristem occupies a different position in the shoot tip, as shown in Figure 31.12a. Outermost is **protoderm,** a meristem that will produce the stem's epidermis. While protoderm cells divide and the resulting derivatives are maturing, the shoot tip continues to grow. Eventually, the protoderm cells differentiate into specific types of epidermal cells, including guard cells and trichomes. Some monocots, such as palms, have a primary thickening meristem just under the protoderm; this tissue contributes to both lateral growth and elongation of the stem.

Inward from the protoderm is the **ground meristem,** which will give rise to ground tissue, most of it parenchyma. **Procambium,** which produces the primary vascular tissues, is sandwiched between ground meristem layers. Procambial cells are long and thin, and their spatial orientation foreshadows the future function of the tissues they produce. In most plants, inner procambial cells give rise to xylem and outer procambial cells to phloem. In plants with secondary growth, a thin region of procambium between the primary xylem and phloem remains undifferentiated. Later on it will give rise to the lateral meristems.

The developing vascular tissues become organized into **vascular bundles,** multistranded cords of primary xylem and phloem that are wrapped in sclerenchyma and thread lengthwise through the parenchyma. In the stems and roots of most eudicots and some conifers, the vascular bundles form a **stele** (Greek *stele* = pillar), also known as a *vascular cylinder,* that vertically divides the column of ground tissue into an outer **cortex** and an inner **pith (Figure 31.13a).** Both cortex and pith consist mainly of parenchyma; in some plant species the pith parenchyma stores starch reserves. In the stems of most monocots, vascular bundles are dispersed through the ground tissue **(Figure 31.13b),** so separate cortical and pith regions do not form. In some monocots, including bamboo, the pith breaks down, leaving the stem with a hollow core. The hollow stems of certain hard-walled bamboo species are used to make bamboo flutes.

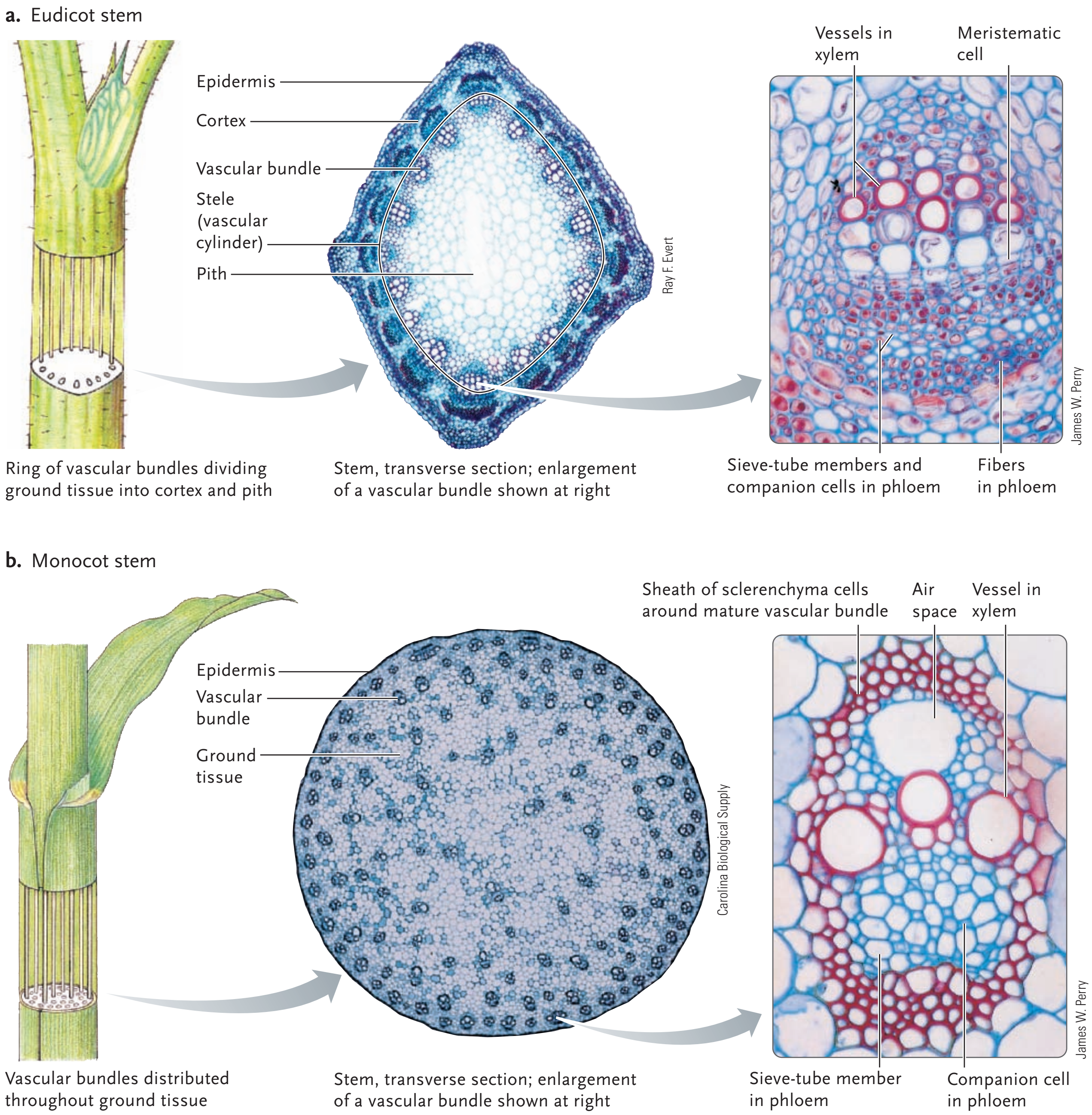


Figure 31.13
Organization of cells and tissues inside the stem of a eudicot and a monocot. **(a)** Part of a stem from alfalfa *(Medicago)*, a eudicot. In many species of eudicots and conifers, the vascular bundles develop in a more or less ringlike array in the ground tissue system, as shown here. **(b)** Part of a stem from corn *(Zea mays)*, a monocot. In most monocots and some herbaceous eudicots, vascular bundles are scattered through the ground tissue, as shown here.

As leaves and buds appear along a stem, some vascular bundles in the stem branch off into these developing tissues. The arrangement of vascular bundles in a plant ultimately depends on the number of branch points to leaves and buds and on the number and distribution of leaves.

Stem Modifications. Evolution has produced a range of stem specializations, including structures modified for reproduction, food storage, or both **(Figure 31.14).** An onion or a garlic head is a *bulb*, a modified shoot that consists of a bud with fleshy leaves. *Tubers* are stem regions enlarged by the presence of starch-storing parenchyma cells; examples of plants that form tubers are the potato and the cassava (the source of tapioca). The “eyes” of a potato are buds at nodes of the modified stem, and the regions between eyes are internodes. Many grasses, such as Bermuda grass, and some weeds are difficult to eradicate because they have *rhizomes*—long underground stems that can

Focus on Research

Basic Research: Homeobox Genes: How the Meristem Gives Its Marching Orders

How do descendents of some dividing cells in a shoot apical meristem (SAM) "know" to become stem tissues, while others embark on the developmental path that produces leaves or other shoot parts? Although the full answer to this question is not yet known, research teams at several laboratories around the world have found evidence of a genetic mechanism in plant meristem cells that appears to guide the process.

Working with SAM tissue from maize (*Zea mays,* generally known in North America as corn), investigators have identified more than a dozen regulatory genes whose protein products activate groups of other genes in differentiating cells. Some genes that act in this way to guide development along a particular path are called *homeotic genes,* because they contain a nucleotide sequence called the homeobox. The homeobox (see Chapter 48) binds to a specific promoter region shared by all of the genes that a homeotic gene controls. Interaction with a homeobox sequence turns the affected genes on or off. Homeobox genes were first discovered in studies of how legs, antennae, and other structures develop in *Drosophila,* the common fruit fly.

Researcher Sarah Hake of the Plant Gene Expression Center (U.S. Department of Agriculture) was curious about the action of a homeotic gene in maize known as *knotted-1 (KN-1)*. Normally the *KN-1* gene is expressed in apical meristems, where it maintains the meristem in an undifferentiated state. When a mutated form, *kn-1,* is expressed, however, the mutation causes abnormal knobby growths on leaves—hence the gene's name. Hake's research helped establish that *KN-1* defines developmental pathways that unfold in meristems. For example, when Hake cloned the *KN-1* gene and inserted it into tobacco leaf cells, the cells *de*differentiated and began acting like meristem cells. As they divided, they produced lines that could differentiate into leaves and stems.

Subsequent studies of *KN-1* in species as diverse as sunflowers and garden peas have led to the identification of the family of what are now called knotted-1-like genes, all of which encode regulatory proteins that influence developmental pathways. As in maize, some are typically expressed in SAM tissue. In sunflower, tomato, and perhaps other species, knotted-1-like genes also appear to be expressed in differentiated plant parts including leaves, flowers, stems, and even roots. The early work on SAM tissue and homeobox genes in maize has blossomed into a wide-ranging investigation of the molecular signals that shape plant architecture.

extend as much as half a meter deep into the soil and rapidly produce new shoots when existing ones are pulled out. The pungent, starchy "root" of ginger is a rhizome also. Crocuses and some other ornamental plants develop elongated, fleshy underground stems called *corms,* another starch-storage adaptation. Tubers, rhizomes, and corms all have meristematic tissue at nodes from which new plants can be propagated—a vegetative (asexual) reproductive mode. Other plants, including the strawberry, reproduce vegetatively via slender stems called *stolons,* which grow along the soil surface. New plants arise at nodes along the stolon.

Leaves Carry Out Photosynthesis and Gas Exchange

Each spring a mature maple tree heralds the new season by unfurling roughly 100,000 leaves. Some other tree species produce leaves by the millions. For these

a. Onion bulb **b.** Potato tuber **c.** Ginger rhizome **d.** Crocus corm **e.** Strawberry stolons

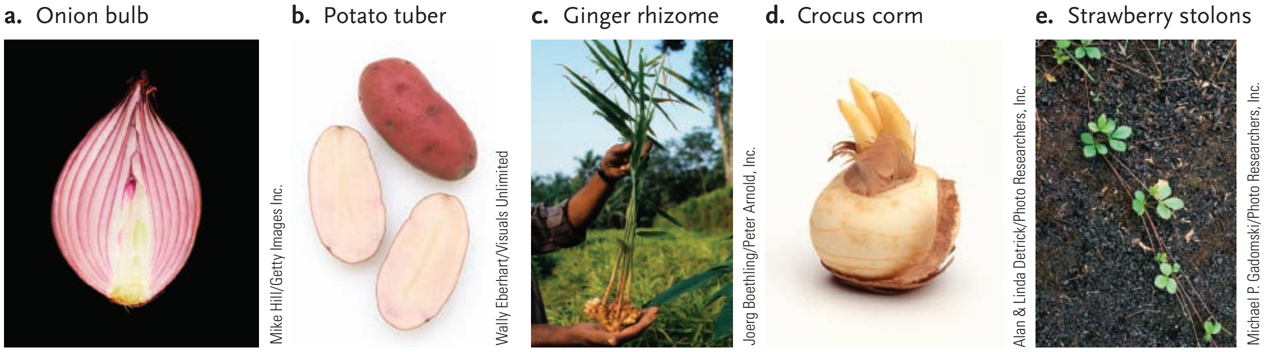


Figure 31.14
A selection of modified stems. **(a)** The fleshy bulbs of onions *(Allium cepa)* are modified shoots in which the plant stores starch. **(b)** A potato *(Solanum tuberosum),* a tuber. **(c)** Ginger "root," the pungent, starchy rhizome of the ginger plant *(Zingiber officinale)*. **(d)** Crocus plants (genus *Crocus*) typically grow from a corm. **(e)** A strawberry plant *(Fragaria ananassa)* and stolon.

and most other plants, leaves are the main organs of photosynthesis and gas exchange.

Leaf Morphology and Anatomy. In both eudicots and monocots, the leaf **blade** provides a large surface area for absorbing sunlight and carbon dioxide **(Figure 31.15a).** Studies show that in general, leaves of flowering plants are oriented on the stem axis so that they can capture the maximum amount of sunlight; the stems and leaves of some plants follow the sun's movement during the course of a day by changing position (this phenomenon is described in Chapter 35).

Many eudicot leaves, such as those of maples, have a broad, flat blade attached to the stem by a stalklike **petiole.** Depending on the species, the petiole can be long, short, or in between. A celery stalk is a fleshy petiole. Unless a petiole is very short, it holds a leaf away from the stem and helps prevent individual leaves from shading one another. In many plant species petioles allow leaves to move in the breeze. This helps circulate air around the leaf, replenishing the supply of carbon dioxide for photosynthesis. In most monocot leaves, such as those of rye grass or corn, the blade is longer and narrower and its base simply forms a sheath around the stem.

Leaf Modifications. Leaf forms are based on two basic patterns: simple leaves, which have a single blade **(Figure 31.15b),** and compound leaves, in which the leaf blade is divided into smaller leaflets **(Figure 31.15c).** As with other plant parts, there is huge variety in the morphology of leaves. For instance, leaf edges or margins may be smooth, toothed, or lobed. Some leaves are modified as spines **(Figure 31.16a),** while others have trichomes that take the form of hairs or hooks—all possibly adaptations for defense against herbivores. Leaves or parts of leaves also may be modified into tendrils, like those of the sweet pea **(Figure 31.16b),** or other structures. Epidermal cells on the leaves of the saltbush *Atriplex spongiosa* form balloonlike structures **(Figure 31.16c)** that contain concentrated Na^+ and Cl^- taken up from the salty soil. Eventually, the salt-filled epidermal cells burst or fall off the leaf, releasing the salt to the outside. This adaptation helps control the salt concentration in the plant's tissues—another example of the link between structure, function, and the environment in which a plant lives.

Leaf Primary Growth and Internal Structure. In both angiosperms and gymnosperms, leaves develop on the sides of the shoot apical meristem. Initially, meristem cells near the apex divide and their derivatives elongate. The resulting bulge enlarges into a thin, rudimentary leaf, or **leaf primordium** (see Figure 31.12). As the plant grows and internodes elongate, the leaves that form from leaf primordia become spaced at intervals along the length of the stem or its branches.

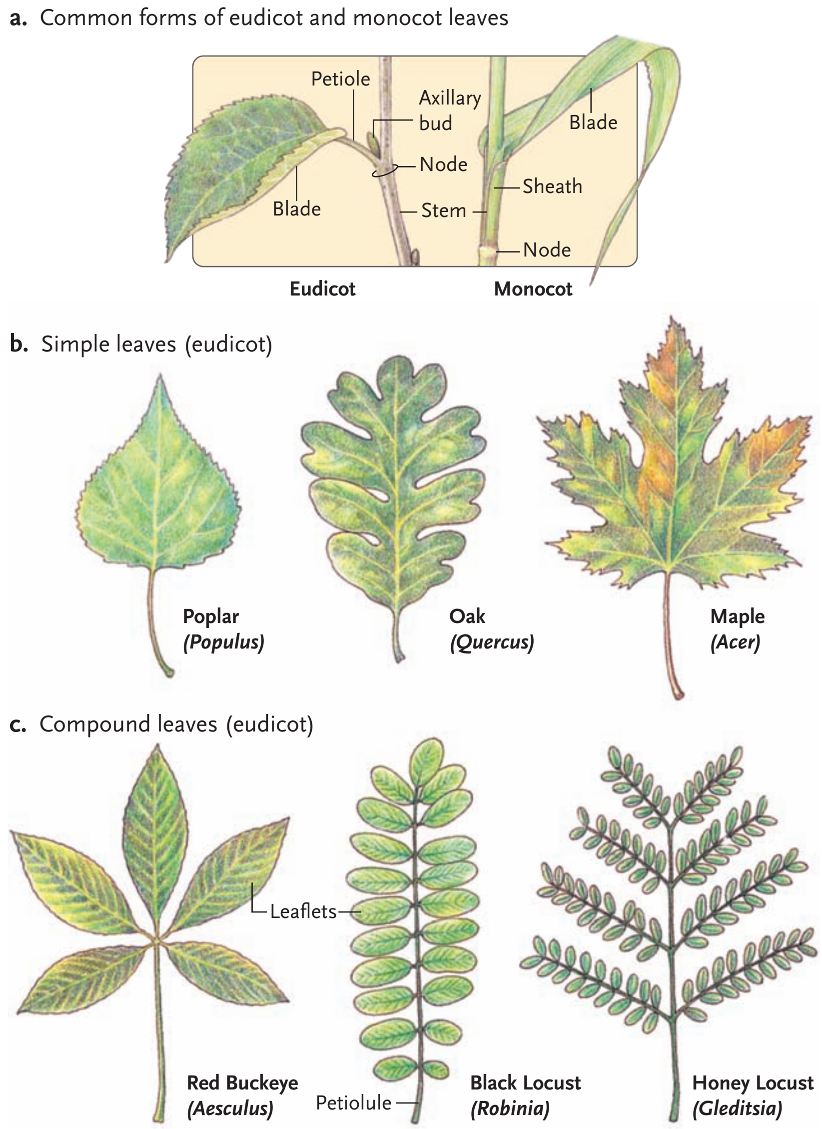


Figure 31.15
Leaf forms.
(a) Common forms of eudicot and monocot leaves. **(b)** Examples of simple eudicot leaves. **(c)** Examples of compound eudicot leaves.

Leaf tissues typically form several layers **(Figure 31.17).** Uppermost is epidermis, with cuticle covering its outer surface. Just beneath the epidermis is **mesophyll** (*mesos* = middle; *phyllon* = leaf), ground tissue composed of loosely packed parenchyma cells that contain chloroplasts. The leaves of many plants, especially eudicots, contain two layers of mesophyll. *Palisade mesophyll* cells contain more chloroplasts and are arranged in compact columns with smaller air spaces between them, typically toward the upper leaf surface. *Spongy mesophyll,* which tends to be located toward the underside of a leaf, consists of irregularly arranged cells with a conspicuous network of air spaces that gives it a spongy appearance. Air spaces between mesophyll cells enhance the uptake of carbon dioxide and release of oxygen during photosynthesis and account for 15% to 50% of a leaf's volume. Mesophyll also contains collenchyma and sclerenchyma cells, which support the photosynthetic cells.

Below the mesophyll is another cuticle-covered epidermal layer. Except in grasses and a few other

a. Cactus spines

b. Tendrils

c. Salt bladders, a form of trichome

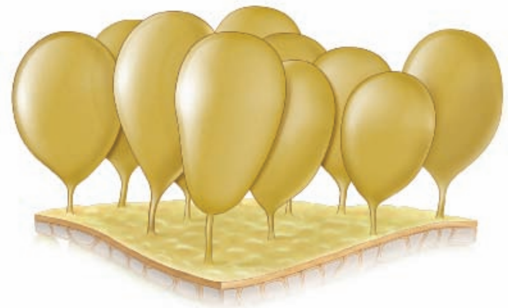
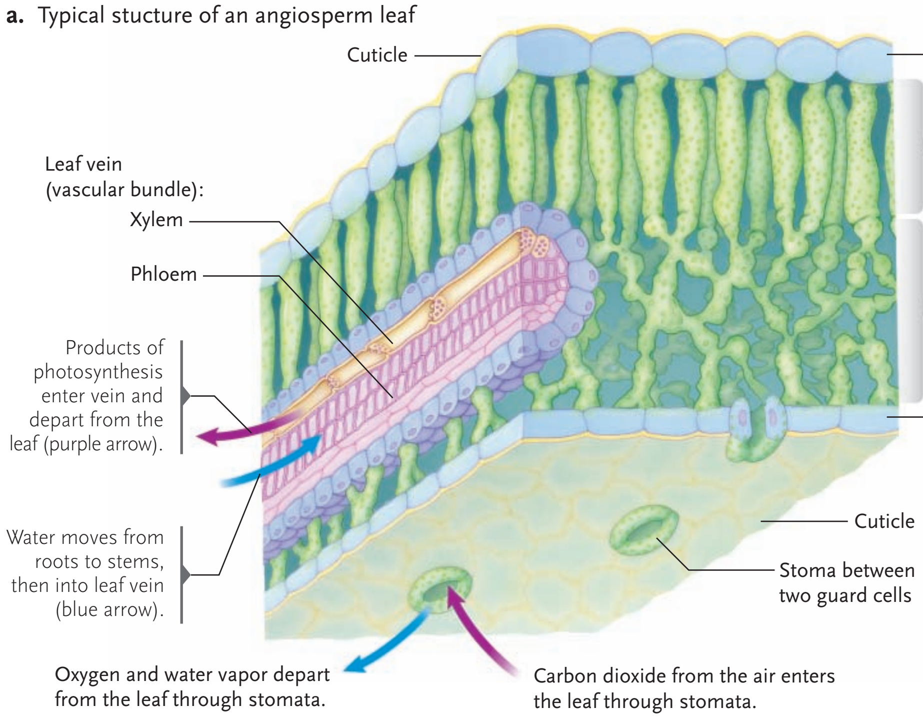


Figure 31.16
A few adaptations of leaves. **(a)** Spines on a barrel cactus *(Ferrocactus covillei)* thwart browsing herbivores and limit the surface area from which water is lost in the plant's arid environment. **(b)** The tendrils of a sweet pea *(Lathyrus odoratus)* help to support the climbing plant's stem. **(c)** SEM of salt bladders on the leaf of a saltbush plant *(Atriplex spongiosa)*. The "bladders" are trichomes, specialized outgrowths of the leaf epidermis in which excess salt from the plant's tissue fluid accumulates. The salt-laden trichomes eventually burst or slough off.

a. Typical stucture of an angiosperm leaf



b. Fine structure of a bean leaf *(Phaseolus)*

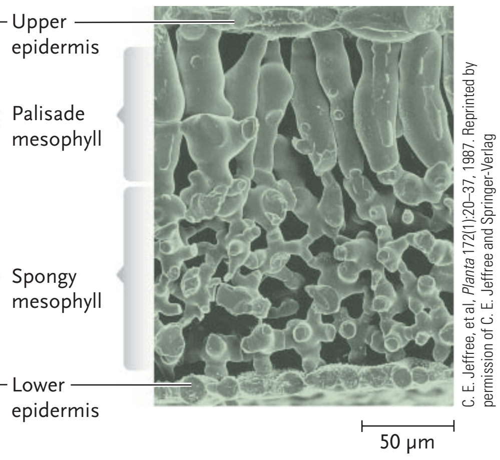


Figure 31.17
Internal structure of a leaf. **(a)** Diagram of typical leaf structure for many kinds of flowering plants. **(b)** Scanning electron micrograph of tissue from the leaf of a kidney bean plant *(Phaseolus)*, transverse section. Notice the compact organization of epidermal cells. See Figure 31.10b for a scanning electron micrograph of stomata.

plants, this layer contains most of the stomata through which water vapor exits the leaf and gas exchange occurs. For example, the upper surface of an apple leaf has no stomata, while a square centimeter of the lower surface has more than 20,000. A square centimeter of the upper epidermis of a tomato leaf has about 1200 stomata, whereas the same area of the lower epidermis has 13,000. The positioning of stomata on the side of the leaf that faces away from the sun may be an adaptation limiting water loss by evaporation through stomatal openings.

Vascular bundles form a lacy network of **veins** throughout the leaf. Eudicot leaves typically have a branching vein pattern; in monocot leaves, veins tend to run in parallel arrays.

In temperate regions, most leaves are temporary structures. In deciduous (*deciduus* = falling off, shedding) species such as birches and maples, hormonal signals cause the leaves to drop from the stem as days shorten in autumn. Other temperate species, such as camellias or hollies, as well as conifers, also drop leaves, but they appear "evergreen" because the leaves may persist for several years and do not all drop at the same time.

Plant Shoots May Have Juvenile and Adult Forms

Leaf shape and other shoot characteristics can mirror the progress of a long-lived plant through its life cycle. Plants that live many years may spend part of their lives in a juvenile phase, then shift to a mature or adult phase. The differences between juveniles and adults often are reflected in leaf size and shape, in the arrangement of leaves on the stem, or in a change from vegetative growth to a reproductive stage—or sometimes all three. For example, oak saplings (genus *Quercus*) have fewer leaves than mature oaks do, but the leaves are considerably larger—an adaptation that probably provides saplings with increased leaf surface area for taking in carbon (in carbon dioxide). Young English ivy plants *(Hedera helix)* grow as vines, have leaves with multiple lobes arranged on the stem in an alternating pattern, and do not flower **(Figure 31.18a).** By contrast, mature English ivy is a flowering shrub with oval leaves that arise on the stem in a spiral pattern **(Figure 31.18b).** A magnolia tree *(Magnolia grandiflora)* doesn't flower until its juvenile phase ends, which can be 20 years or more from the time the *Magnolia* seed sprouts. Most woody plants must attain a certain size before their meristem tissue can respond to the hormonal signals that govern flower development, a topic we consider in Chapter 35.

Phase changes provide more examples of the plasticity that characterizes plant development. They almost certainly are associated with changes in the expression of genes that control the development of stem nodes, leaf and flower buds, and other basic aspects of plant growth.

Study Break

1. Describe the functions of stems and stem structure, and list the basic steps in primary growth of stems.
2. Explain the general function of leaves and how leaf anatomy supports this role in eudicots and monocots.
3. Describe the steps in primary growth of a leaf and the structures that result from the process.
4. Describe two examples of the life phases of long-lived plant species.

31.4 Root Systems

Plants must absorb enough water and dissolved minerals to sustain growth and routine cellular maintenance, a task that requires a tremendous root surface. In one study, measurements of the root system of a rye plant *(Secale cereale)* that have been growing for only 4 months may have a surface area of more than 700 m^2—about 130 times greater than the surface area of its shoot system. The roots of carrots, sugar beets, and most other plants also store nutrients produced in photosynthesis, some to be used by root cells and some to be transported later to cells of the shoot. As a root system penetrates downward and spreads out, it also anchors the aboveground parts.

a. Young English ivy **b.** Mature English ivy

Figure 31.18 Age-related phase changes in English ivy *(Hedera helix)*. **(a)** The juvenile, vine-type growth habit. **(b)** The mature shrub.

Taproot and Fibrous Root Systems Are Specialized for Particular Functions

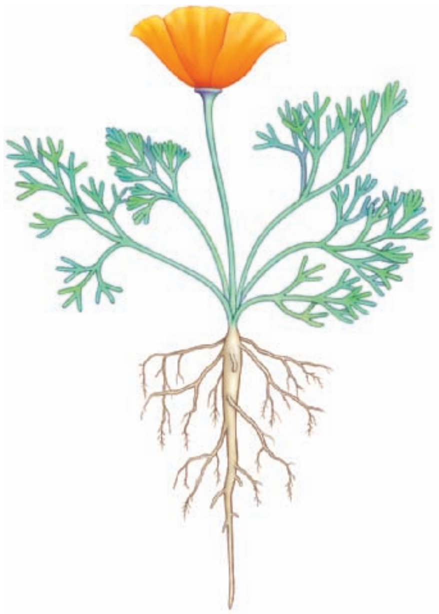
Most eudicots have a **taproot system**—a single main root, or taproot, that is adapted for storage and smaller branching roots called **lateral roots** **(Figure 31.19a).** As the main root grows downward, its diameter increases, and the lateral roots emerge along the length of its older, differentiated regions. The youngest lateral roots are near the root tip. Carrots and dandelions have a taproot system, as do pines and many other conifers. A pine's taproot system can penetrate 6 m or more into the soil.

Grasses and many other monocots develop a **fibrous root system** in which several main roots branch to form a dense mass of smaller roots **(Figure 31.19b).** Fibrous root systems are adapted to absorb water and nutrients from the upper layers of soil, and tend to spread out laterally from the base of the stem. Fibrous roots are important ecologically because dense root networks help hold topsoil in place and prevent erosion. During the 1930s, drought, overgrazing by livestock, and intensive farming in the North American Midwest destroyed hundreds of thousands of acres of native prairie grasses, contributing to soil erosion on a massive scale. Swirling clouds of soil particles prompted journalists to name the area the Dust Bowl.

In some plants, **adventitious roots** arise from the stem of the young plant. "Adventitious" refers to any structure arising at an unusual location, such as roots that grow from stems or leaves. Adventitious roots and their branchings all are about the same length and diameter. Those of English ivy and some other climbing plants produce a gluelike substance (from trichomes) that allows them to cling to vertical surfaces. The *prop roots* of a corn plant are adventitious roots that develop from the shoot node nearest the soil surface; they both support the plant and absorb water and nutrients. Mangroves and other trees that grow in marshy habitats often have huge prop roots, which develop from branches as well as from the main stem **(Figure 31.19c).**

Figure 31.19 Types of roots. **(a)** Taproot system of a California poppy *(Eschscholzia californica)*. **(b)** Fibrous root system of a grass plant. **(c)** The prop roots of red mangrove trees *(Rhizophora)*, examples of adventitious roots.

a. Taproot system



b. Fibrous root system

c. Adventitious roots

Root Structure Is Specialized for Underground Growth

Like shoots, roots have distinct anatomical parts, each with a specific function. In most plants, primary growth of roots begins when an embryonic root (called a *radicle*) emerges from a germinating seed and its meristems become active. **Figure 31.20** shows the structure of a root tip. Notice that the root apical meristem terminates in a dome-shaped cell mass, the **root cap.** The meristem produces the cap, which in turn surrounds and protects the meristem as the root elongates through the soil. Certain cells in the cap respond to gravity, which guides the root tip downward. Cap cells also secrete a polysaccharide-rich substance that lubricates the tip and eases the growing root's passage through the soil. Outer root cap cells are continually abraded off and replaced by new cells at the cap's base.

Zones of Primary Growth in Roots. Primary growth takes place in successive stages, beginning at the root tip and progressing upward. Just inside the root cap some roots have a small clump of apical meristem cells called the **quiescent center.** Unlike other meristematic cells, cells of the quiescent center divide very slowly unless the root cap or the apical meristem is injured; then they become active and can regenerate the damaged part. The quiescent center also may include cells that synthesize plant hormones controlling root development.

The root apical meristem and the actively dividing cells behind it form the **zone of cell division.** As in the stem, cells of the apical meristem segregate into three primary meristems. Cells in the center of the root tip become the procambium; those just outside the procambium become ground meristem; and those on the periphery of the apical meristem become protoderm.

The zone of cell division merges into the **zone of elongation.** Most of the increase in a root's length comes about here as cells become longer as their vacuoles fill with water. This "hydraulic" elongation pushes the root cap and apical meristem through the soil as much as several centimeters a day.

Above the zone of elongation, cells do not increase in length but they may differentiate further and take on specialized roles in the **zone of maturation.** For instance, epidermal cells in this zone give rise to root hairs, and the procambium, ground meristem, and protoderm complete their differentiation in this region.

Tissues of the Root System. Coupled with primary growth of the shoot, primary root growth produces a unified system of vascular pipelines extending from root tip to shoot tip. The root procambium produces cells that mature into the root's xylem and phloem **(Figure 31.21).** Ground meristem gives rise to the root's cortex, its ground tissue of starch-storing parenchyma cells that surround the stele. In eudicots, the stele runs through the center of the root (see Figure 31.21a). In corn and some other monocots, the stele forms a ring that divides the ground tissue into cortex and pith (see Figure 31.21b).

The cortex contains air spaces that allow oxygen to reach all of the living root cells. Numerous plasmodesmata connect the cytoplasm of adjacent cells of the cortex. In many flowering plants, the outer root cortex cells give rise to an **exodermis,** a thin band of cells that, among other functions, may limit water losses from roots and help regulate the absorption of ions. The innermost layer of the root cortex is the **endodermis,** a thin, selectively permeable barrier that helps control the movement of water and dissolved minerals into the stele. We look in more detail at the roles of exodermis and endodermis in Chapter 32.

Between the stele and the endodermis is the **pericycle,** consisting of one or more layers of parenchyma cells that can still function as meristem. The pericycle gives rise to lateral roots **(Figure 31.22).** In response to chemical growth regulators, **root primordia** (rudimentary roots) arise at specific sites in the pericycle. Gradually, the lateral roots emerge and grow out through the cortex and epidermis, aided by enzymes released by the root primordium that help break down the intervening cells. The distribution and frequency of lateral root formation partly control the overall shape of the root system—and the extent of the soil area it can penetrate.

In some cells in the developing root epidermis the outer surface becomes extended into root hairs (see Figure 31.20). Root hairs can be more than a centimeter long and can form in less than a day. Collectively, the thousands or millions of them on a plant's roots greatly increase the plant's absorptive surface. Root hair structure supports this essential function. Each hair is a slender tube with thin walls made sticky on their surface by a coating of pectin. Soil particles tend to adhere to the wall, providing an intimate association between the hair and the surrounding earth, thus facilitating the uptake of water molecules and

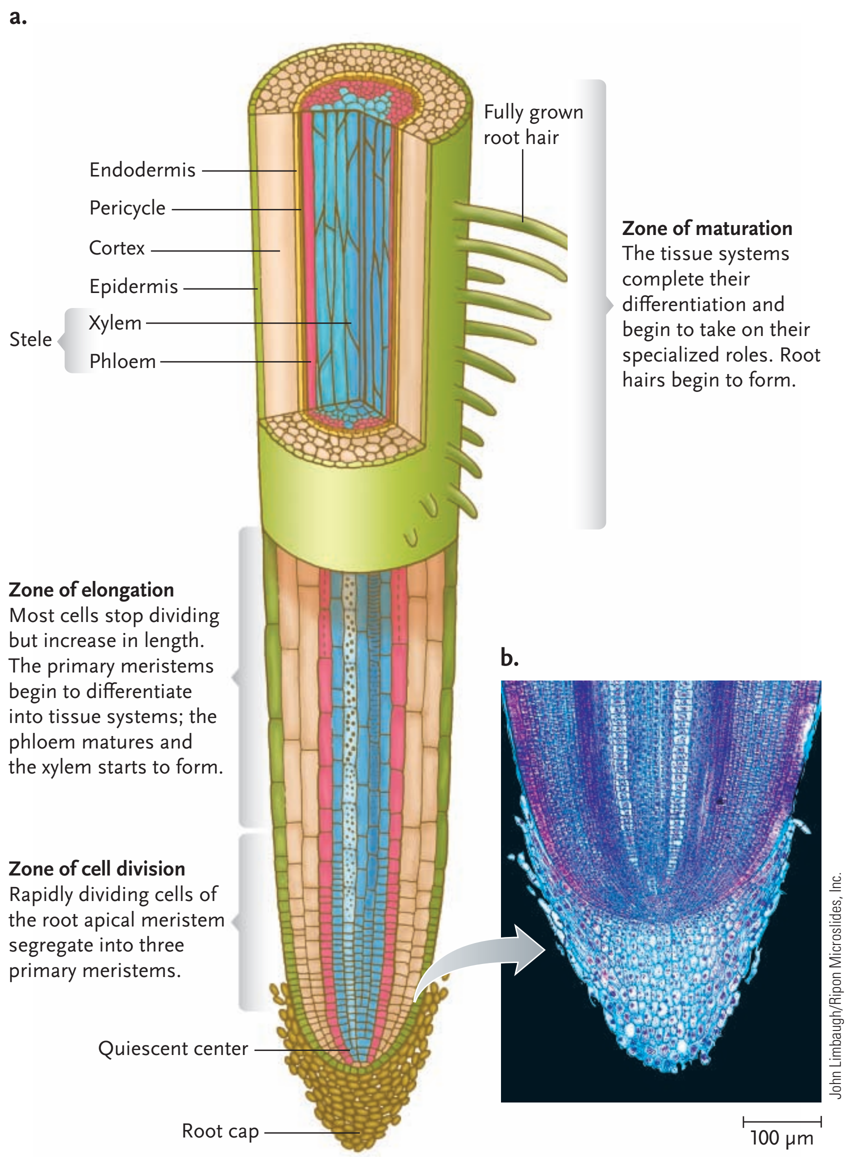


Figure 31.20
Tissues and zones of primary growth in a root tip. **(a)** Generalized root tip, longitudinal section. **(b)** Micrograph of a corn root tip, longitudinal section.

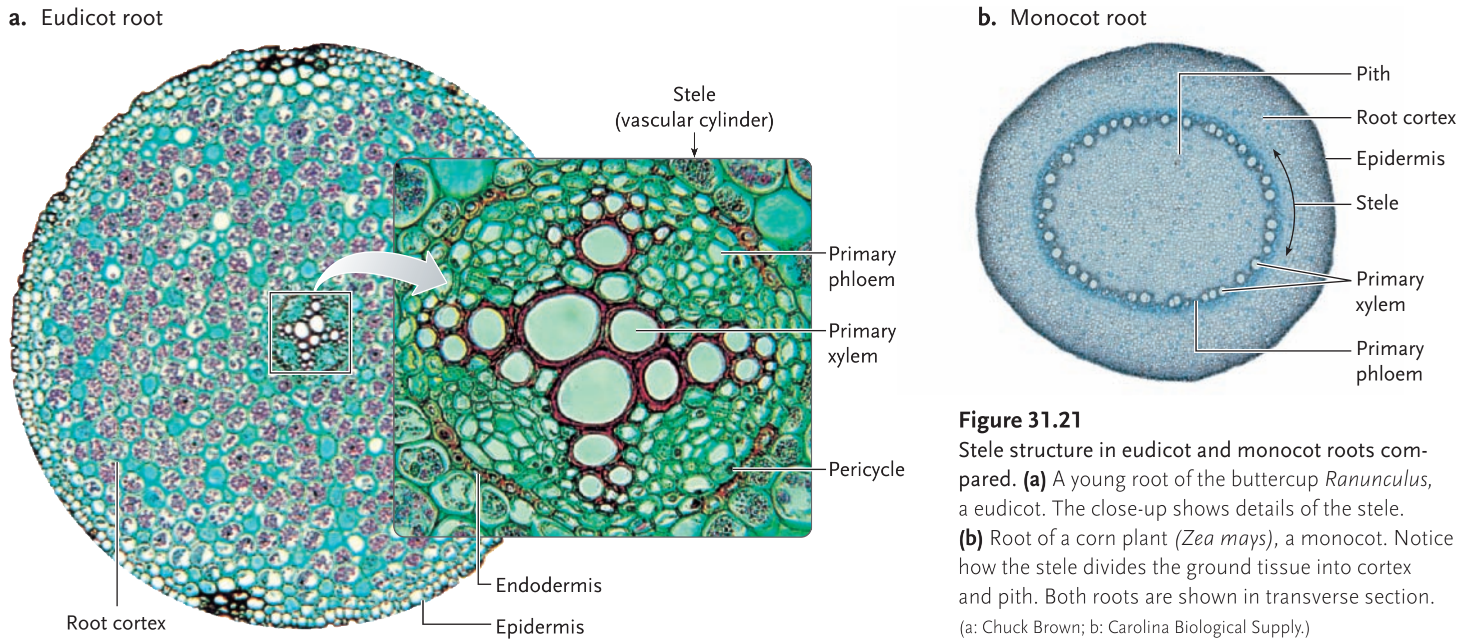


Figure 31.21
Stele structure in eudicot and monocot roots compared. **(a)** A young root of the buttercup *Ranunculus*, a eudicot. The close-up shows details of the stele. **(b)** Root of a corn plant *(Zea mays)*, a monocot. Notice how the stele divides the ground tissue into cortex and pith. Both roots are shown in transverse section. (a: Chuck Brown; b: Carolina Biological Supply.)

mineral ions from soil. When plants are transplanted, rough handling can tear off much of the fragile absorptive surface. Unable to take up enough water and minerals, the transplant may die before new root hairs can form.

Study Break

1. Compare the two general types of root systems.
2. Describe the zones of primary growth in roots.
3. Describe the various tissues that arise in a root system and their functions.

31.5 Secondary Growth

All plants undergo primary growth of the root and stem. In addition, some plants have secondary growth processes that add girth to roots and stems over two or more growing seasons. In plant species that have secondary growth, older stems and roots become more massive and woody through the activity of two types of lateral meristems, or *cambia* (singular, cambium). One of these meristems, the **vascular cambium**, produces secondary xylem and phloem. The other, called the **cork cambium**, produces **cork**, a secondary epidermis that is one element of the multilayered structure known as bark. In cells of these tissues, mitosis is periodically reactivated. Hence secondary growth permits woody plants to grow taller and live longer than herbaceous plants.

Vascular Cambium Gives Rise to Secondary Growth in Stems

Recall that after the stem of a woody plant completes its primary growth, each vascular bundle contains a layer of undifferentiated cells between the primary xylem and the primary phloem. These cells, along with parenchyma cells between the bundles, eventually give rise to a cylinder of vascular cambium that wraps around the xylem and pith of the stem **(Figure 31.23).** Vascular cambium consists of two types of cells—*fusiform initials* and *ray initials*—that have different shapes and functions (see Figure 31.23b). Secondary growth takes place as these cells divide. Initials divide at right angles to the stem surface, so their descendants add girth to the stem instead of length. **Fusiform initials,** which are derived from cambium inside the vascular bundles, give rise to secondary xylem and phloem cells. Secondary xylem forms on the inner face of the vascular cambium, and secondary phloem forms on the outer face. **Ray initials** are derived from the parenchyma cells between vascular bundles. As they divide, their descendants form spokelike *rays.* These

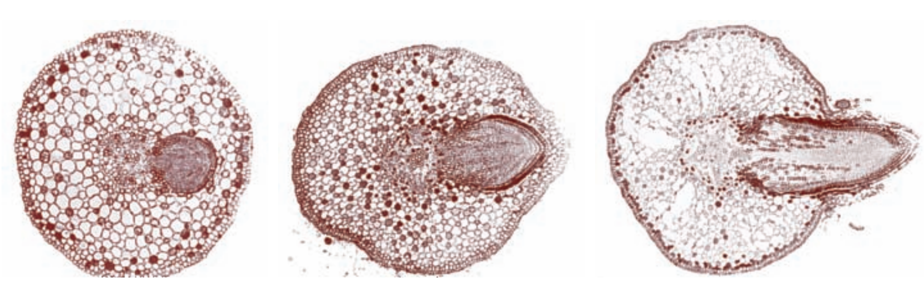
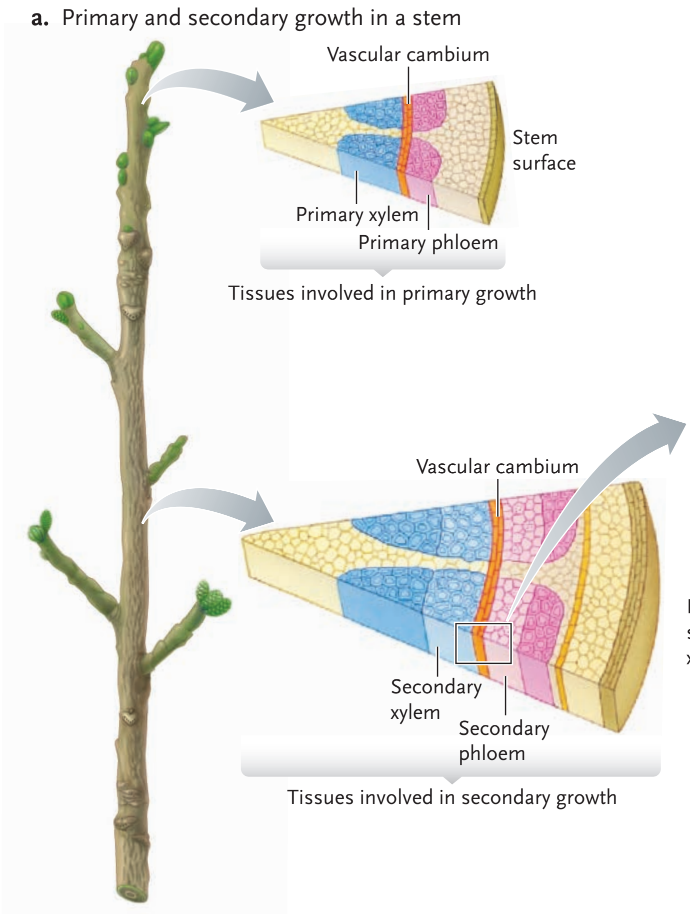


Figure 31.22
Micrographs showing the formation of a lateral root from the pericycle of a willow tree *(Salix)*. These micrographs show transverse sections. (All images: © Omnikron/Photo Researches, Inc.)



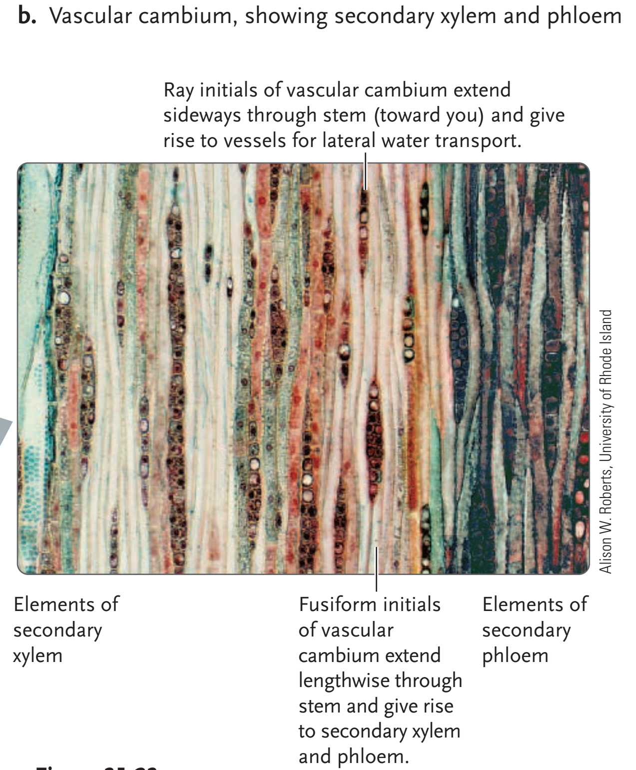


Figure 31.23
Secondary and primary growth compared. **(a)** In a woody plant, primary growth resumes each spring at the terminal and lateral buds. Secondary growth resumes at the vascular cambium inside the stem. **(b)** Fusiform initials and ray initials of the vascular cambium of a walnut tree *(Juglans)*, tangential section.

horizontal channels carry water sideways through the stem, in a radial pattern that resembles a sliced pie. While xylem and phloem mainly conduct fluid lengthwise in the stem, rays ensure that water and solutes also move laterally as stems thicken.

With time, the mass of secondary xylem inside the ring of vascular cambium increases, forming the hard tissue known as **wood.** Outside the vascular cambium, secondary phloem cells also are added each year **(Figure 31.24).** (The primary phloem cells, which have thin walls, are destroyed as they are pushed outward by secondary growth.) As a stem increases in diameter, the growing mass of new tissue eventually causes the cortex, and the secondary phloem beyond

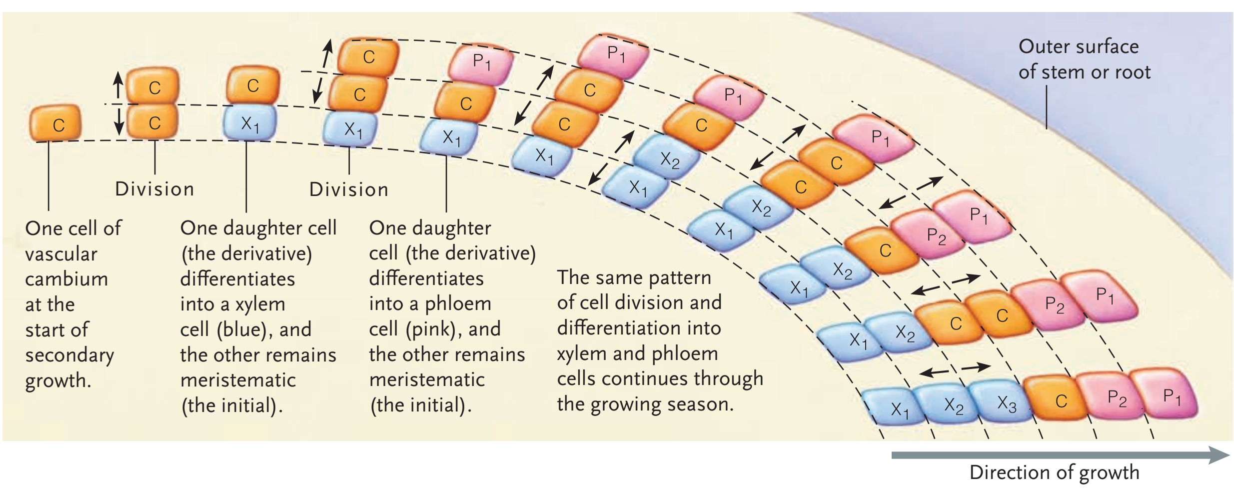


Figure 31.24
Relationship between the vascular cambium and its derivative cells (secondary xylem and phloem). The drawing shows stem growth through successive seasons. Notice how the ongoing divisions displace the cambial cells, moving them steadily outward even as the core of xylem increases the stem or root thickness.

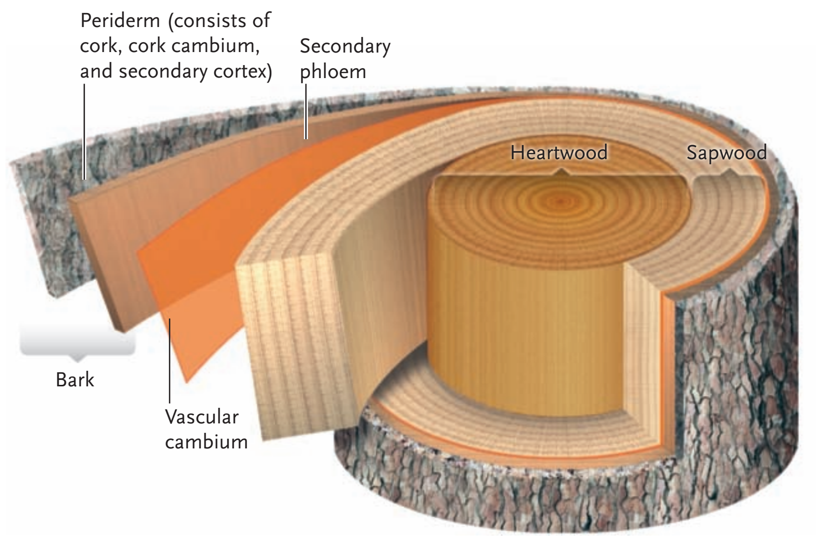


Figure 31.25
Structure of a woody stem showing extensive secondary growth. Heartwood, the mature tree's core, has no living cells. Sapwood, the cylindrical zone of xylem between the heartwood and vascular cambium, contains some living parenchyma cells among the nonliving vessels and tracheids. Everything outside the vascular cambium is bark. Everything inside it is wood.

it, to rupture. Parts of the cortex split away and carry epidermis with them. Cork cambium—produced early in the stem's secondary development by meristem cells in the cortex, epidermis, or secondary phloem—replaces the lost epidermis with cork. The cork cambium produces cork to the outside and secondary cortex to the inside.

Bark encompasses all the living and nonliving tissues between the vascular cambium and the stem surface. It includes the secondary phloem and the **periderm** (*peri* = surrounding; *derma* = skin), the outermost portion of bark that consists of cork, cork cambium, and secondary cortex **(Figure 31.25).** Girdling a tree by removing a belt of bark around the trunk is lethal because it destroys the secondary phloem layer, and so nutrients from photosynthesis in leaves cannot reach the tree's roots. Natural corks used to seal bottles are manufactured from the especially thick outer bark of the cork oak, *Quercus suber*. Tubular openings called *lenticels* develop in the periderm. They function a bit like snorkels, permitting exchanges of oxygen and carbon dioxide between the living tissues and the outside air.

As a tree ages, changes also unfold in the appearance and function of the wood itself. In the center of its older stems and roots is **heartwood,** dry tissue that no longer transports water and solutes and is a storage depot for some defensive compounds. In time, these substances—including resins, oils, gums, and tannins—clog and fill in the oldest xylem pipelines. Typically they darken heartwood, strengthen it, and make it more aromatic and resistant to decay. **Sapwood** is secondary growth located between heartwood and the vascular cambium. Compared with heartwood, it is wet and not as strong.

In temperate climates, trees produce secondary xylem seasonally, with larger-diameter cells produced in spring and smaller-diameter cells in summer. This "spring wood" and "summer wood" reflect light differently, and it is possible to identify them as alternating light and dark bands. The alternating bands represent annual growth layers, or "tree rings" **(Figure 31.26).**

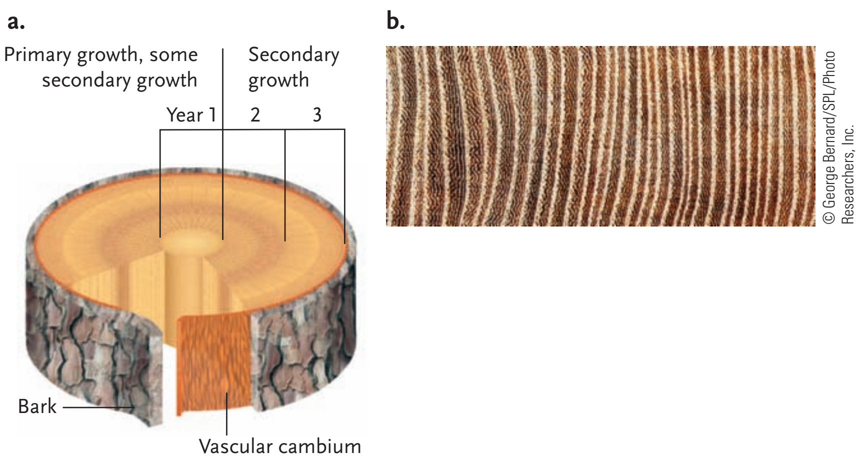
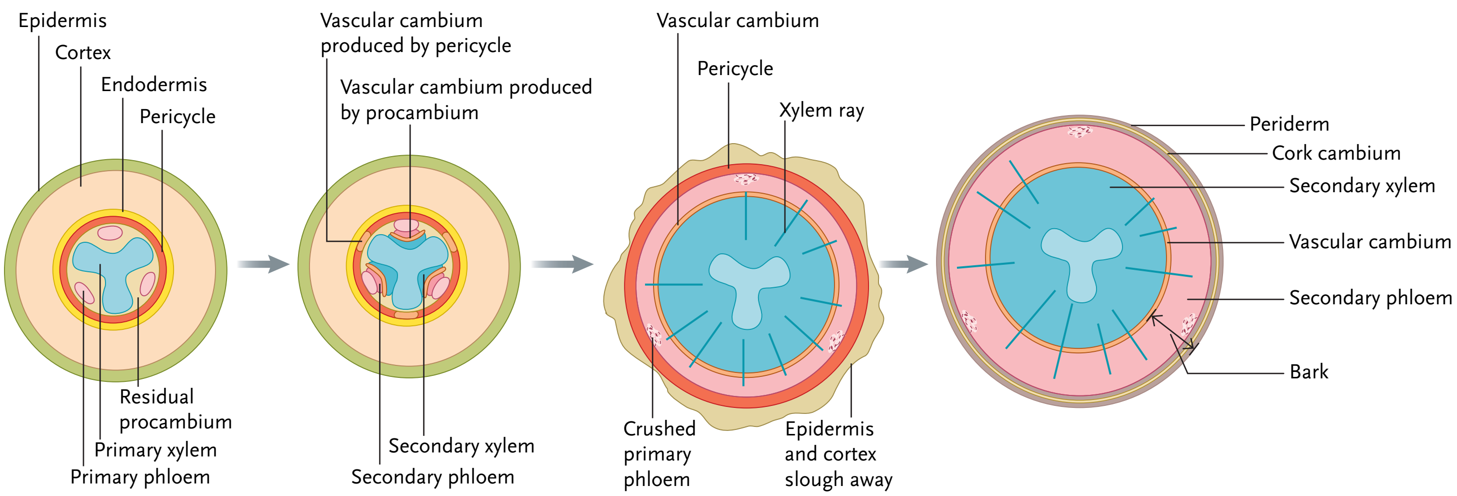


Figure 31.26
Secondary growth and tree ring formation. **(a)** Radial cut through a woody stem that has three annual rings, corresponding to secondary growth in years 2 through 4. **(b)** Tree rings in an elm *(Ulmas)*. Each ring corresponds to one growing season. Differences in the widths of tree rings correspond to shifts in climate, including the availability of water.

Secondary Growth Can Also Occur in Roots

The roots of grasses, palms, and other monocots are almost always the product of primary growth alone. In plants with roots that have secondary growth, the continuous ring of vascular cambium develops differently than it does in stems. When their primary growth is complete, these roots have a layer of residual procambium between the xylem and phloem of the stele (**Figure 31.27,** step 1). The vascular cambium arises in part from this residual cambium, and in part from the pericycle (step 2). Eventually, the cambial tissues arising from the procambium and those arising from the pericycle merge into a complete cylinder of vascular cambium (step 3). The vascular cambium functions in roots as it does in stems, giving rise to secondary xylem to the inside and secondary phloem to the outside. As secondary xylem accumulates, older roots can become extremely thick and woody. Their ongoing secondary growth is powerful enough to break through concrete sidewalks and even dislodge the foundations of homes.

Cork cambium also forms in roots, where it is produced by the pericycle. In many woody eudicots and in all gymnosperms, most of the root epidermis and cortex fall away, and the surface consists entirely of periderm (step 4).



1 At the close of primary growth, the root's procambium has given rise to primary xylem and phloem. Thick root cortex surrounds thin layers of pericycle and endodermis. The epidermis is the outermost layer of the root.

2 Procambium gives rise to the pericycle and distinct regions of vascular cambium. One region gives rise to secondary xylem; the other gives rise to secondary phloem.

3 The mature stele forms as secondary xylem and phloem enlarge and vascular cambium becomes sandwiched between them. The pericycle forms the outer layer of the stele. Xylem rays develop, primary xylem is crushed by the expanding secondary phloem, and the epidermis and underlying root cortex begin to slough away.

4 Outer cells of the pericycle give rise to cork cambium, from which a layered periderm develops. Bark consists of all the tissues outside the vascular cambium, including secondary phloem.

Figure 31.27
Secondary growth in the root of one type of woody plant.

Unanswered Questions

Do plants have a "backup" copy of their genome?

As described at the beginning of this chapter, land plants manifest adaptations that allow them to survive and reproduce in unfavorable or hostile conditions. Adaptations include changes in growth and development reflecting responses to environmental fluctuations that occur naturally during the normal life cycle of plants. Being physically anchored in one place has driven plant adaptation so that changes in the plant body can facilitate survival. It is also possible, however, that the sessile existence of land plants may have selected for unusual adaptive strategies. Might plants have devised a strategy to utilize previously unknown genetic resources and thereby expand their potential repertoire of adaptive responses? Recent findings demonstrating the existence of a previously unknown mechanism of genetic instability suggest that such a strategy may indeed have been in place during the evolution of land plants. These findings suggest that, at least in *Arabidopsis thaliana,* a "backup" copy of the genome exists that can be accessed under unfavorable conditions.

Why have a backup copy of the genome? Simply put, if the system crashes, it can be restored. By analogy, the genome could be considered the "operating system" stored on the "hard drive" of the organism. If that operating system becomes corrupted, for example, by a devastating power surge or a computer virus, a global systems failure might occur. However, if a backup copy were maintained at least in a subset of the population, then, under conditions that might lead to extinction, the backup copy could be used to "restore" the system and increase the chances of survival for that organism or population. In other words, the genome could adapt using the stored information.

An intriguing possibility is that such a backup genome might exist in the form of RNA. The fact that backup copies have not been found using conventional DNA-based detection methods or classical genetic approaches leaves open the exciting possibility that RNA might serve as the storage medium for this information. In a sense, having the information stored in an alternative chemical form (analogous to a different computer language or code) might also make it less susceptible to corruption. Furthermore, it may be that this backup genome is a remnant of an ancestral condition where the genome was RNA-based.

How would you go about testing these different possibilities? First, the findings would have to be independently verified and the existence of a "restoration" mechanism would have to be confirmed by other research groups working on *Arabidopsis* or other plant species. Second, the source and chemical nature of the backup information would need to be identified. Where is it, and is it RNA, DNA, protein, or a combination of these? The question of mechanism would also need to be addressed. How is the system restored, and when does it happen? The question of how global this phenomenon is would also need to be considered. Do all plant species maintain a backup copy and do organisms outside of the plant kingdom have a backup genome?

Susan Lolle is associate professor of biology at the University of Waterloo in Waterloo, Canada. Her research interests include plant development, genetics, and genome biology. To learn more go to http://www.biology.uwaterloo.ca/.

Secondary Growth Is an Adaptive Response

Plants, like all living organisms, compete for resources, and woody stems and roots confer some advantages. Plants with taller stems or wider canopies that defy the pull of gravity can intercept more of the light energy from the sun. With a greater energy supply for photosynthesis, they have the metabolic means to increase their root and shoot systems, and thus are better able to acquire resources—and ultimately to reproduce successfully.

In every stage of a plant's growth cycle, growth maintains a balance between the shoot system and root system. Leaves and other photosynthetic parts of the shoot must supply root cells with enough sugars to support their metabolism, and roots must provide shoot structures with water and minerals. As long as a plant is growing, this balance is maintained, even as the complexity of the root and shoot systems increases, whether the plant lives only a few months or—like some bristlecone pines—for 6000 years.

Study Break

1. Explain the nature of secondary growth and where it typically occurs in plants.
2. Describe the components of vascular cambium and their roles in secondary growth in stems, including the development of tissues such as bark, cork, and wood.
3. Compare secondary growth in stems and in roots.

Review

Go to ThomsonNOW™ at www.thomsonedu.com/login to access quizzing, animations, exercises, articles, and personalized homework help.

31.1 Plant Structure and Growth: An Overview

- The vascular plant body consists of an aboveground shoot system with stems, leaves, and flowers, and an underground root system (Figure 31.2).
- Meristems (Figure 31.3) give rise to the plant body and are responsible for a plant's lifelong growth. Each meristem cell divides to produce an initial, which functions as meristem, and a derivative, which may differentiate into a specialized body cell.
- Primary growth of roots and shoots originates at apical meristems at root and shoot tips. Some plants show secondary growth as lateral meristems increase the diameter of stems and roots.
- The two major classes of flowering plants (angiosperms) are monocots and eudicots (Table 31.1).

31.2 The Three Plant Tissue Systems

- Growing plant cells form secondary walls outside the primary walls. Maturing cells become specialized for specific functions, with some functions accomplished by walls of dead cells.
- Plants have three tissue systems (Figure 31.5). Ground tissues make up most of the plant body, vascular tissues serve in transport, and dermal tissue forms a protective cover.
- Of the three types of ground tissues, parenchyma is active in photosynthesis, storage, and other tasks (Figure 31.6); collenchyma and sclerenchyma provide mechanical support.
- Xylem and phloem are the plant vascular tissues. Xylem conducts water and solutes and consists of conducting cells called tracheids and vessel members (Figure 31.8). Phloem, the food-conducting tissue, contains living cells (sieve tube members) joined end to end in sieve tubes (Figure 31.9).
- The dermal tissue, epidermis (Figure 31.10) is coated with a waxy cuticle that restricts water loss. Water vapor and other gases enter and leave the plant through pores called stomata, which are flanked by specialized epidermal cells called guard cells. Epidermal specializations also include trichomes, such as root hairs.

Animation: Tissue systems of a tomato plant

Animation: Apical meristems

Animation: Shoot differentiation

31.3 Primary Shoot Systems

- The primary shoot system consists of the main stem, leaves, and buds, plus any attached flowers and fruits. Stems provide mechanical support, house vascular tissues, and may store food and fluid.
- Stems are organized into modular segments. Nodes are points where leaves and buds are attached, and internodes fall between nodes (Figure 31.11). The terminal bud at a shoot tip consists of shoot apical meristem (Figure 31.12). Lateral buds occur at intervals along the stem. Meristem tissue in buds gives rise to leaves, flowers, or both.
- Derivatives of the apical meristem produce three primary meristems: protoderm makes the stem's epidermis, procambium gives rise to primary xylem and phloem, and ground meristem gives rise to ground tissue.
- Vascular tissues are organized into vascular bundles, with phloem surrounding xylem in each bundle (Figure 31.13).
- Monocot and eudicot leaves have blades of different forms, all providing a large surface area for absorbing sunlight and carbon dioxide (Figure 31.15). Leaf modifications are adaptive responses to environmental selection pressures (Figure 31.16). Leaf characteristics such as shape or arrangement may change over the life cycle of a long-lived plant (Figure 31.18).

Animation: Ground tissues

Animation: Vascular tissues

Animation: Monocot and dicot leaves

Animation: Simple and compound leaves

Animation: Leaf organization

31.4 Root Systems

- Roots absorb water and dissolved minerals and conduct them to aerial plant parts; they anchor and sometimes support the plant and often store food. Root morphologies include taproot systems, fibrous root systems, and adventitious roots (Figure 31.19).
- During primary growth of a root, the primary meristem and actively dividing cells make up the zone of cell division, which merges into the zone of elongation. Past the zone of elongation, cells may differentiate and perform specialized roles in the zone of cell maturation (Figure 31.20).
- A root's vascular tissues (xylem and phloem) usually are arranged as a central stele (Figure 31.21). Parenchyma around the stele forms the root cortex. The root endodermis also wraps around the stele. Inside it is the pericycle, containing parenchyma that can function as meristem. It gives rise to root primordia from which lateral roots emerge (Figure 31.22). Root hairs greatly increase the surface available for absorbing water and solutes.

  Animation: Root organization

  Animation: Root cross section

  Animation: Root systems

31.5 Secondary Growth

- In plants with secondary growth, older stems and roots become more massive and woody via the activity of vascular cambium and cork cambium.
- Vascular cambium consists of two types of cells: fusiform initials, which generate secondary xylem and phloem, and ray initials, which produce horizontal water transport channels called xylem rays (Figures 31.23 and 31.24). Secondary growth takes place as these cells divide.
- Cork cambium gives rise to cork, which replaces epidermis lost when stems increase in diameter. Together, cork cambium and cork make up the periderm (Figure 31.25), the outer portion of bark.
- In root secondary growth, a thin layer of procambium cells between the xylem and phloem differentiates into vascular cambium (Figure 31.27), which gives rise to secondary xylem and phloem. The pericycle produces root cork cambium.

  Animation: Secondary growth

  Animation: Secondary growth in a root

  Animation: Growth in a walnut twig

  Animation: Layers in a woody stem

  Animation: Annual rings

Questions

Self-Test Questions

1. With respect to growth, plants differ from animals in that:
   a. plant growth involves only an increase in the total number of the organism's cells.
   b. plant cells remain roughly the same size after cell division, whereas animal cells increase in size after they form.
   c. all plants form woody tissues during growth.
   d. plants have indeterminate growth; animals have determinate growth.
   e. plants can grow only when young; animals grow for many years.
2. Identify the correct pairing of a plant tissue and its function.
   a. epidermis: rigid support
   b. xylem: sugar transport
   c. parenchyma: photosynthesis, respiration
   d. phloem: water and mineral transport
   e. periderm: control of gas exchange
3. Identify the correct pairing of a structure and its component(s).
   a. epidermis: companion cells
   b. phloem: sieve tube members
   c. sclerenchyma: nonlignified cell walls
   d. secondary cell wall: cuticle
   e. parenchyma: sclereids
4. Which of the following is *not* part of a stem?
   a. petiole
   b. pith
   c. xylem
   d. procambium
   e. ground meristem
5. Which of the following would be absent in a eudicot leaf?
   a. spongy mesophyll
   b. palisade mesophyll
   c. pericycle
   d. vascular bundles
   e. stoma
6. A student left a carrot in her refrigerator. Three weeks later she noticed slender white fibers growing from its surface. They were not a fungus. Instead they represented:
   a. lateral roots on a taproot.
   b. adventitious roots.
   c. root hairs on a fibrous root.
   d. root hairs on a lateral root.
   e. young prop roots.
7. Which of the following is *not* a structure that results from secondary plant growth?
   a. periderm
   b. sapwood
   c. cork
   d. pith
   e. heartwood
8. Which characteristic do monocots and eudicots share?
   a. the position of the vascular bundles
   b. the pattern of leaf veins
   c. the number of grooves in the pollen grains
   d. the number of cotyledons
   e. the formation of flowers
9. A student forgets to water his plant and the leaves start to droop. The structures first affected by water loss and now not functioning are the:
   a. sieve tubes.
   b. sclereids and fibers.
   c. vessel members and tracheids.
   d. companion cells.
   e. guard cells and stoma.
10. The greatest mitotic activity in a root takes place in the:
   a. zone of maturation.
   b. zone of cell division.
   c. zone of elongation.
   d. root cap.
   e. endodermis.

Questions for Discussion

1. Leaves are modified in diverse ways. Cactus leaves, for example, are transformed into spines. Cacti are adapted to arid habitats in which relatively few other plant species grow. What kinds of selection pressures may have operated to favor the evolution of spinelike cactus leaves?
2. While camping in a national forest you notice a "Do Not Litter" sign nailed onto the trunk of a mature fir tree about 7 feet off the ground. When you return 5 years later, will the sign be at the same height, or will the tree's growth have raised it higher?

3. Peaches, cherries, and other fruits with pits are produced only on secondary branches that are 1 year old. To renew the fruiting wood on a peach tree, how often would you prune it? Where on a branch would you make the cut, and why?
4. African violets and some other flowering plants are propagated commercially using leaf cuttings. Initially, a leaf detached from a parent plant is placed in a growth medium. In time, adventitious shoots and roots develop from the leaf blade, producing a new plant. Which cells in the original leaf tissue are the most likely to give rise to the new structures? What property of the cells makes this propagation method possible?

Experimental Analysis

The sticky cinquefoil *(Potentilla glandulosa)* is a small, deciduous plant with bright yellow flowers that lives in throughout the American West, and its leaf phenotype can vary depending on environmental conditions. Inland, where there are dramatic seasonal temperature swings and unpredictable droughts, plants shed their large "summer leaves" in autumn when the temperature begins to drop. In the spring new leaves are smaller and develop in a compact rosette. This phenotype persists for several months and is thought to be an adaptation that makes the plants less vulnerable to drought (because less water evaporates from reduced leaf surfaces). By contrast, the leaves of *P. glandulosa* plants growing in a coastal climate are always large. In their habitat, seasonal temperature swings are not as great and the annual cycle of winter rain and summer drought is highly predictable. Suppose you decide to explore the hypothesis that the coastal population is genetically capable of exhibiting the same seasonal shift in leaf morphology as the inland plants. Would you need access to a greenhouse where you can control variables, or would it be just as easy to do experiments in the wild? Explain your reasoning and outline your experimental design—including the variable or variables you will test in the first experiment.

Evolution Link

About 90 million years ago flowering plants began their rapid (in a geologic timeframe) rise to dominance in the modern Kingdom Plantae. The first angiosperms may originally have been small, treelike plants in tropical regions, but at some point they began diversifying rapidly into other habitats where early gymnosperms flourished. In the 1990s South African botanist William Bond proposed the "slow seedling" hypothesis to help explain this evolutionary change, and botanists continue to explore and refine it. The hypothesis proposes that angiosperms were able to encroach on and eventually dominate many habitats where ancient gymnosperms lived in part because flowering species increasingly evolved adaptations that made them fast-growing herbaceous plants. Gymnosperms, by contrast grow more slowly. Based on your reading in this chapter and Chapter 27, what are some structural and biochemical features of gymnosperms (such as conifers) that might result in slower growth, putting them at a competitive disadvantage in this scenario?

How Would You Vote?

Large-scale farms and large cities compete for clean, fresh water, which is becoming scarcer as human population growth skyrockets. Should cities restrict urban growth to reduce conflicts over water supplies? Go to www.thomsonedu.com/login to investigate both sides of the issue and then vote.