29 PLANT TISSUES

Droughts Versus Civilization

The more we dig up records of past climates, the more we wonder about what is happening now. In any given year there are bad *droughts*, or significantly less rainfall than we expect in a given region. Drought is a normal climatic cycle, but it has been worse than usual in North America, Australia, Africa, and elsewhere—enough to cause mass starvation, cripple economies, and invite conflicts among people. What is the long-term forecast? More of the same.

Humans built the whole of modern civilization on a vast agricultural base. Today we reel from droughts that last two, five, seven years or so. Imagine a drought lasting *200 years*. It happened. About 3,400 years ago, rainfall dried up and brought an end to the Akkadian civilization in northern Mesopotamia. Samples obtained from drilling in the seafloor, lake bottoms, and ice sheets point to a worldwide change in climate that also brought an end to societies elsewhere.

Look beyond the architectural marvels of the Maya civilization (Figure 29.1). A drought that lasted more than 150 years contributed to its collapse in the ninth century. Or look to Afghanistan, recently scorched by the worst drought in the past 100 years. Subsistence farmers make up 70 percent of Afghan population. Six years of droughts wiped out harvests, dried up wells, and killed livestock. In desperation, the rural families sold their land, their possessions, and their daughters. Despite crop imports, starvation has affected about 37 percent of the population. Can the world's leading exporters of wheat and other

Figure 29.1 Why study plants? We absolutely depend on the adaptations by which they obtain and use environmental resources, which include water. Directly or indirectly, plants make the food that sustains nearly all forms of life on Earth.

(**a**) Mute reminder of the failed Maya civilization. (**b**) Rice crop, which must grow in shallow water of continuously flooded fields. *Facing page*, from a Guatemalan field, an atrophied corncob—one reminder of a prolonged drought and widespread crop failures.

IMPACTS, ISSUES

Watch the video online!

crops help? They cannot do much for others when they themselves experience droughts.

Even brief episodes of drought reduce photosynthesis and crop production. Plants conserve water by closing stomata, which of course also stops carbon dioxide from moving in. No carbon dioxide, no sugars. When stressed, a flowering plant also makes fewer flowers. The flowers that it does make might not open fully, so they may not get pollinated. Even if they do, its seeds and fruits may fall off the plant before they ripen.

This unit focuses on the seed-bearing vascular plants, with emphasis on flowering types that are intimately interconnected with human life. You will be taking a look at how these plants function and consider their patterns of growth, development, and reproduction. Their structure and physiology help them survive short-term droughts and other hostile times—but not long-term water deprivation.

This is a huge question mark for your future. Which nations will stumble during long-term climate change? Which ones will make it through a severe drought that does not end any time soon?

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? See BiologyNow for details, then vote online.

Key Concepts

OVERVIEW OF PLANT TISSUES

Seed-bearing vascular plants have a shoot system, with stems, leaves, and reproductive parts. Most have a root system. Ground tissues make up the bulk of the plant body. Vascular tissues distribute water, nutrients, and products of photosynthesis. Dermal tissues cover exposed surfaces.

Plants put on new growth at meristems, or regions where undifferentiated cells divide rapidly. Shoot and root tips lengthen by activity at their apical meristems, which is called primary growth. Sections 29.1, 29.2

ORGANIZATION OF PRIMARY SHOOTS

Ground, vascular, and dermal tissue systems of monocot and eudicot stems and leaves are organized in distinct patterns. Patterns of leaf growth and internal leaf structure are adaptations that maximize sunlight interception, water conservation, and gas exchange. Sections 29.3, 29.4

ORGANIZATION OF PRIMARY ROOTS

Ground, vascular, and dermal tissue systems of monocot and eudicot roots are organized in distinct patterns. Root systems absorb water and dissolved mineral ions, and many anchor the plant. Section 29.5

THE WOODY PLANTS

Older stems and roots of many plant species thicken over successive growing seasons, which is called secondary growth. Wood forms by activity at lateral meristems inside the stem or root. Sections 29.6, 29.7

Links to Earlier Concepts

In this chapter, you will build on Sections 23.2 and 28.1, which introduced the nature of plant structure and correlated it with present and past functions. You will deepen your understanding of how the fine structure of plant cells (4.9) and photosynthesis (7.3) are adaptations to environmental conditions (7.7).

OVERVIEW OF PLANT TISSUES

29.1 Components of the Plant Body

LINKS TO
SECTIONS
23.2, 28.1

With 260,000 species, flowering plants dominate the plant kingdom, as surveyed in Chapter 23. Its major groups are the magnoliids, eudicots (true dicots), and monocots. We focus here on the eudicots and monocots, many of which have a body plan similar to that shown in Figure 29.2.

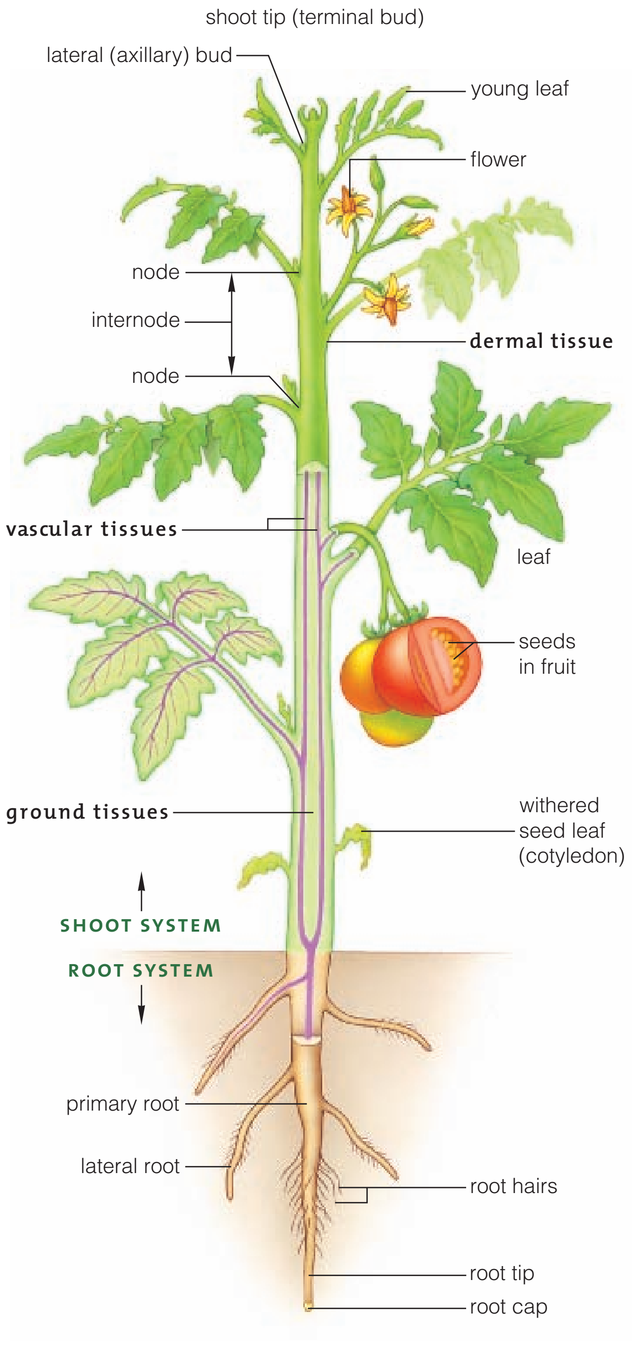
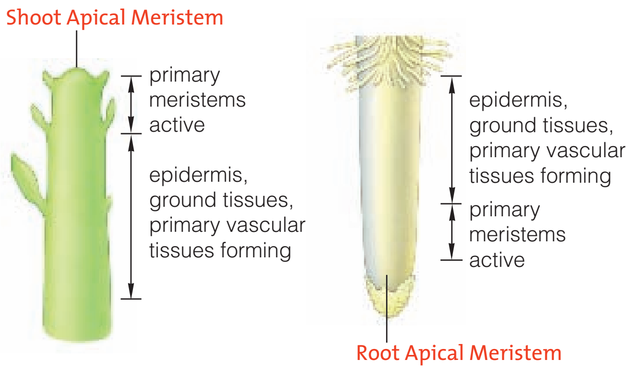


Figure 29.2 ***Animated!*** Body plan for the commercially grown tomato plant (*Lycopersicon esculentum*). Its vascular tissues (*purple*) conduct water, dissolved minerals, and organic substances. They thread through ground tissues that make up most of the plant body. Epidermis, a type of dermal tissue, covers root and shoot surfaces.

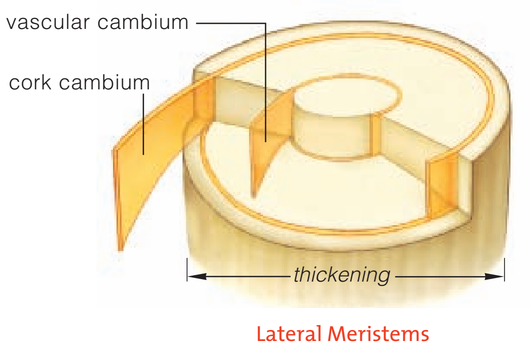
THREE PLANT TISSUE SYSTEMS

Shoots are the aboveground parts of plants, and they include stems, leaves, and flowers. Structurally, stems are frameworks for upright growth, a boon for cells that intercept energy from the sun. For most plants, **roots** are structures that grow downward and outward through soil, where they absorb water and dissolved ions. Often they anchor aboveground parts. Root cells store and release photosynthetically derived food for their own use and often for the rest of the plant body.



a The cellular descendants of *apical meristems* divide, grow, and differentiate. They form three *primary meristems*, the activity of which lengthens shoots and roots:

Protoderm ⟶ epidermis
Ground meristem ⟶ ground tissues
Procambium ⟶ primary vascular tissues



b In woody plants, activity of two *lateral meristems* thickens older stems and roots; they result in secondary growth:

Vascular cambium ⟶ secondary vascular tissues
Cork cambium ⟶ periderm

Figure 29.3 (**a**) Apical meristems, sources of primary growth—that is, a lengthening of shoot and root tissues. (**b**) In many plants, other meristems form in older stems and roots. They are sources of secondary growth, of a thickening of tissues that causes increases in diameter.

Stems, branches, leaves, and roots consist of three major tissue systems (Figure 29.2). The **ground tissue system** serves basic functions, such as photosynthesis and food storage. The **vascular tissue system** moves water and solutes to all plant parts. The **dermal tissue system** covers and protects exposed surfaces.

All three systems incorporate simple tissues, each made of one cell type only. Parenchyma, collenchyma, and sclerenchyma are like this. All three systems have complex tissues, which have two or more cell types. Xylem, phloem, and epidermis are complex tissues.

Most plant growth proceeds at **meristems**, each an embryonic region of undifferentiated cells that retain the capacity to divide. Active meristems give rise to all new cells that mature and differentiate into tissues. A plant lengthens only at its shoot and root tips, which contain *apical* meristem. Populations of cells that form here are immature forerunners of epidermis, ground tissue, and primary vascular tissues. The lengthening of stems and roots during a growing season is called the plant's **primary growth** (Figure 29.3*a*).

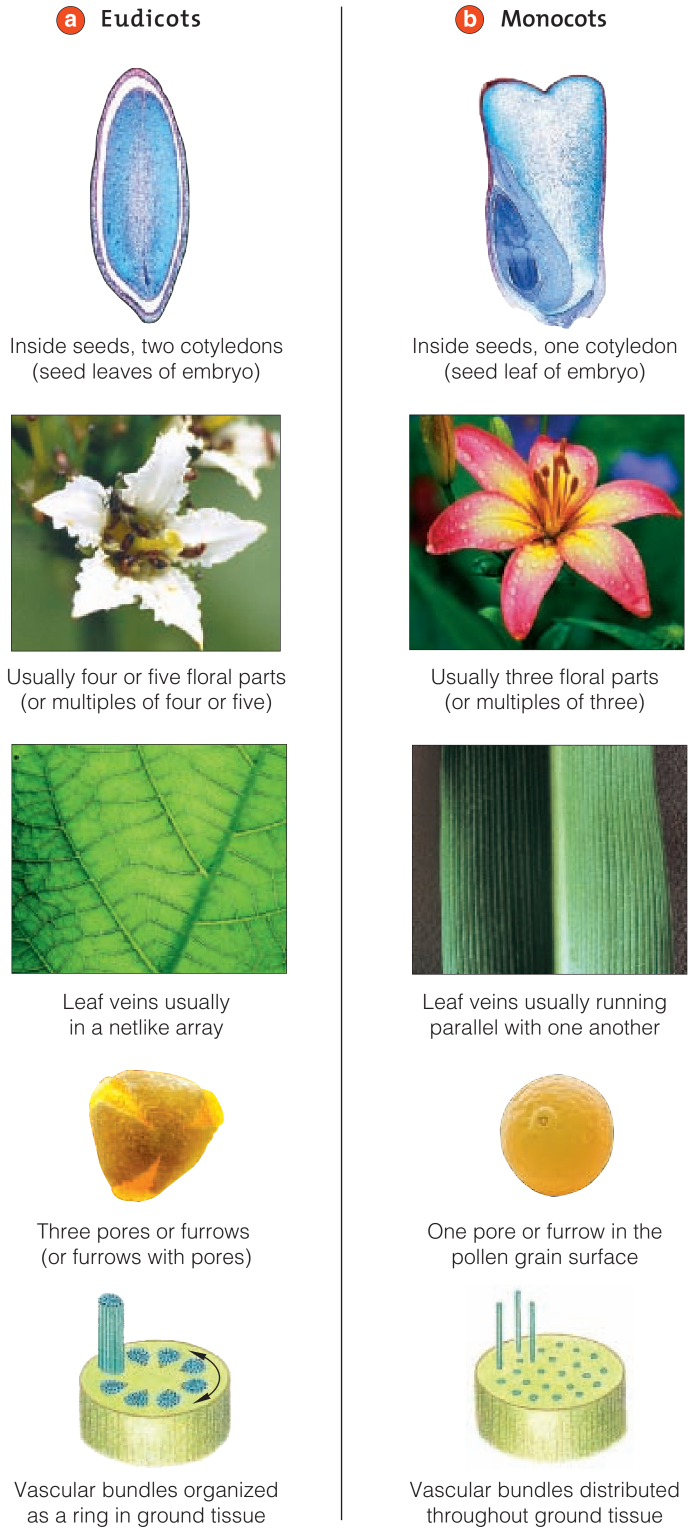
In many plants, activity at *lateral* meristems results in **secondary growth**: a thickening of older stems and roots. Lateral meristems are cylindrical arrays of cells that form inside stems and roots (Figure 29.3*b*).

EUDICOTS AND MONOCOTS—SAME TISSUES, DIFFERENT FEATURES

Eudicots ("true dicots") include most of the familiar trees and shrubs, such as maples, roses, and beans. Lilies, orchids, corn, and wheat are typical monocots. Eudicots and monocots are similar in structure and function but differ in distinctive ways. For instance, eudicot seeds have two cotyledons and monocot seeds have just one. **Cotyledons**, or seed leaves, are leaflike structures that form inside seeds as part of the plant embryo. Their cells store or absorb food for it. After a seed germinates, they wither, and new leaves start to make food by photosynthesis. Figure 29.4 compares other structural features of eudicots and monocots.

Most vascular plants have stems for upright growth, leaves that function in photosynthesis, specialized reproductive shoots called flowers, and roots that absorb water and solutes. Vascular tissue threads through the plant body.

Apical meristems in shoot and root tips are the source of primary growth, or the lengthening of plant parts. In many species, lateral meristems are the source of secondary growth, or a thickening of older stems and roots.



Inside seeds, two cotyledons (seed leaves of embryo)

Inside seeds, one cotyledon (seed leaf of embryo)

Usually four or five floral parts (or multiples of four or five)

Usually three floral parts (or multiples of three)

Leaf veins usually in a netlike array

Leaf veins usually running parallel with one another

Three pores or furrows (or furrows with pores)

One pore or furrow in the pollen grain surface

Vascular bundles organized as a ring in ground tissue

Vascular bundles distributed throughout ground tissue

Figure 29.4 ***Animated!*** Some of the differences among eudicots and monocots. Compare Table 21.1.

29.2 Two Categories of Plant Tissues

LINKS TO SECTIONS 15.3, 28.1

Simple and complex tissues make up the ground, vascular, and dermal tissues of the flowering plant body.

Growth, remember, is an increase in the number, size, and volume of cells in a multicelled body. Plants put on new growth only where descendants of meristems divide, lengthen, and differentiate. This happens just behind shoot and root tips. It also happens when new tissues form in layers over older stem and root parts, which are no longer growing. Before considering the organization of the new tissues, review Figure 29.5. It will help you interpret micrographs of them.

OVERVIEW OF SIMPLE TISSUES

Figures 29.6 and 29.7 show examples of parenchyma, collenchyma, and sclerenchyma, which are all simple tissues. **Parenchyma** makes up most of the soft, moist, primary growth of roots, stems, leaves, and flowers. Its cells tend to be thin-walled, pliable, and many-sided. Parenchyma cells are alive at maturity and can still divide. Their mitotic cell divisions repair plant wounds. Many spaces between cells of photosynthetic parenchyma, or mesophyll, help cells exchange gases with the air inside leaves. Parenchyma also functions in storage, secretion, and other tasks.

Collenchyma is a stretchable tissue that can support rapidly growing plant parts, such as young stems and leaf stalks. Its elongated cells are alive at maturity. Their primary wall is rich in a pliable polysaccharide, pectin. The wall is notably thickened wherever three or more collenchyma cells abut (Figure 29.7*a*).

The cells of **sclerenchyma** are dead at maturity, but this tissue resists compression from lignin in the cell

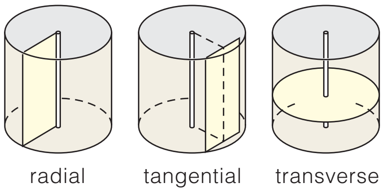


Figure 29.5 Terms that identify how tissue specimens are cut from a plant. Along the radius of a stem or a root, longitudinal cuts give *radial* sections. Cuts at right angles to a root or stem radius give *tangential* sections. Cuts perpendicular to the long axis of a stem or root give *transverse* sections (cross-sections).

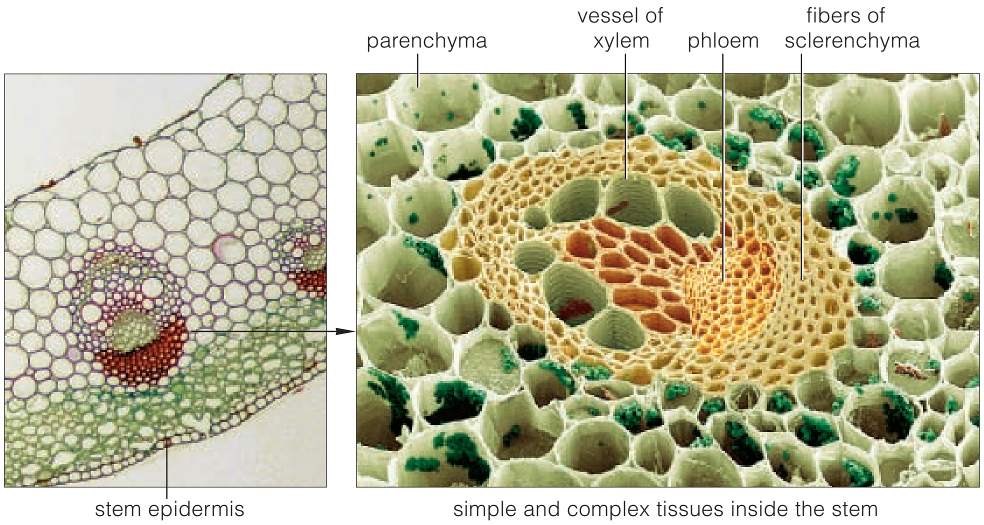


Figure 29.6 Locations of simple and complex tissues inside the stem of a yellow buttercup (*Ranunculus*), transverse sections.

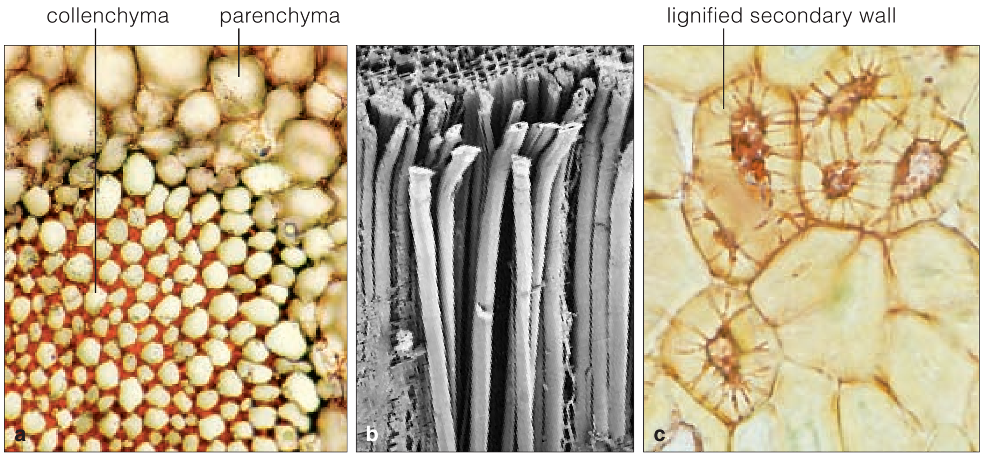


Figure 29.7 More simple tissues. (**a**) Collenchyma from a supporting strand in a celery stem, transverse section. Sclerenchyma: (**b**) fibers of a strong flax stem, tangential view. (**c**) Stone cells, a type of sclereid in pears, transverse section.

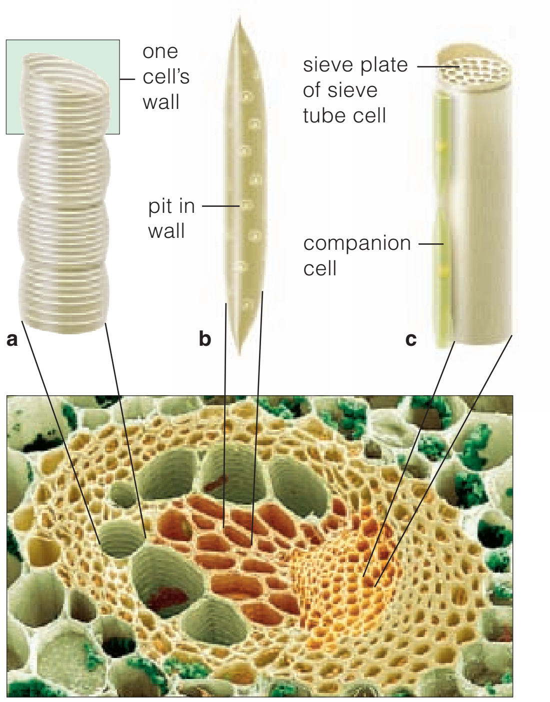


Figure 29.8 From xylem, (**a**) part of a column of vessel members and (**b**) one tracheid. These cells are dead at maturity; only the pitted walls remain as interconnected water-conducting tubes. (**c**) One of the living cells that interconnect as sieve tubes in phloem, which transport sugars and other solutes. You will read more about the structure and function of these cells in the next chapter.

walls that are left behind. Remember, upright plants could not have evolved on land without lignin, which provides mechanical support (Section 23.2). Lignin also deters some fungal attacks.

Fibers and sclereids are typical sclerenchyma cells. *Fibers* are long, tapered cells that structurally support the vascular tissues in some stems and leaves (Figure 29.7*b*). They flex, twist, and resist stretching. We use certain fibers as materials for cloth, rope, paper, and other commercial products. The far stubbier and often branched *sclereids* strengthen hard seed coats, such as peach pits, and make pears gritty (Figure 29.7*c*).

OVERVIEW OF COMPLEX TISSUES

Vascular Tissues Xylem and phloem are vascular tissues. They have elongated conducting cells that are typically sheathed in fibers and parenchyma.

Xylem conducts water and dissolved mineral ions, and structurally supports plants. *Vessel members* and *tracheids* are two cell types that make up conducting tubes (Figure 29.8*a*,*b*). Both are dead at maturity, but their secondary wall acts like a sturdy tube. Lignin stiffens the cell wall and waterproofs it, except at pits across the wall. Many pits in adjoining walls match up, so that water flows laterally beween vessels and tracheids as well as upward through the xylem.

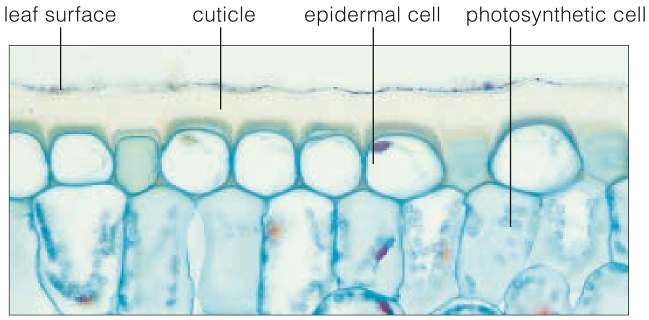


Figure 29.9 A typical plant cuticle, with epidermal cells and photosynthetic cells just beneath it.

Phloem conducts sugars and other organic solutes. Its main cells, *sieve-tube members*, are alive at maturity. They connect end to end, at their sieve plates (Figure 29.8*c*). Special, living parenchyma cells, the *companion cells*, load photosynthetically derived sugars into these transport tubes, which then deliver them to cells in all growing or storage regions.

Dermal Tissues The first dermal tissue to form on a plant is **epidermis**, which is usually a single layer of cells. Epidermal cells secrete cutin, a waxy substance, onto their outward-facing wall. The secretions form a covering, a **cuticle**, that helps the plant conserve water and deflect attacks by some pathogens (Figure 29.9). Periderm, a different tissue, replaces the epidermis in woody stems and roots.

Leaf epidermis and young stems have specialized cells. For instance, a tiny gap across the epidermis, or **stoma** (plural, stomata), forms when a pair of guard cells swell and change shape. Most plants have many stomata, where the diffusion of water vapor, oxygen, and carbon dioxide across epidermis is controlled.

Most of the plant body—the ground tissue system—consists of parenchyma, collenchyma, and sclerenchyma. Each of these simple tissues consists of only a single type of cell.

Xylem and phloem are vascular tissues. In xylem, tubes of interconnected tracheids and vessel members conduct water and dissolved ions. In phloem, sieve-tube members interact with companion cells to distribute organic compounds.

Epidermis covers the surfaces of the primary plant body. Periderm forms on older, woody stems and roots.

29.3 Primary Structure of Shoots

Ground, vascular, and dermal tissues of monocot and dicot stems become organized in characteristic patterns during growth.

BEHIND THE APICAL MERISTEM

The structural organization of a new flowering plant has become mapped out by the time it is an embryo sporophyte inside a seed coat. As you will read later, a tiny primary root and shoot have already formed as part of the embryo. Both are poised to resume growth and development as soon as the seed germinates.

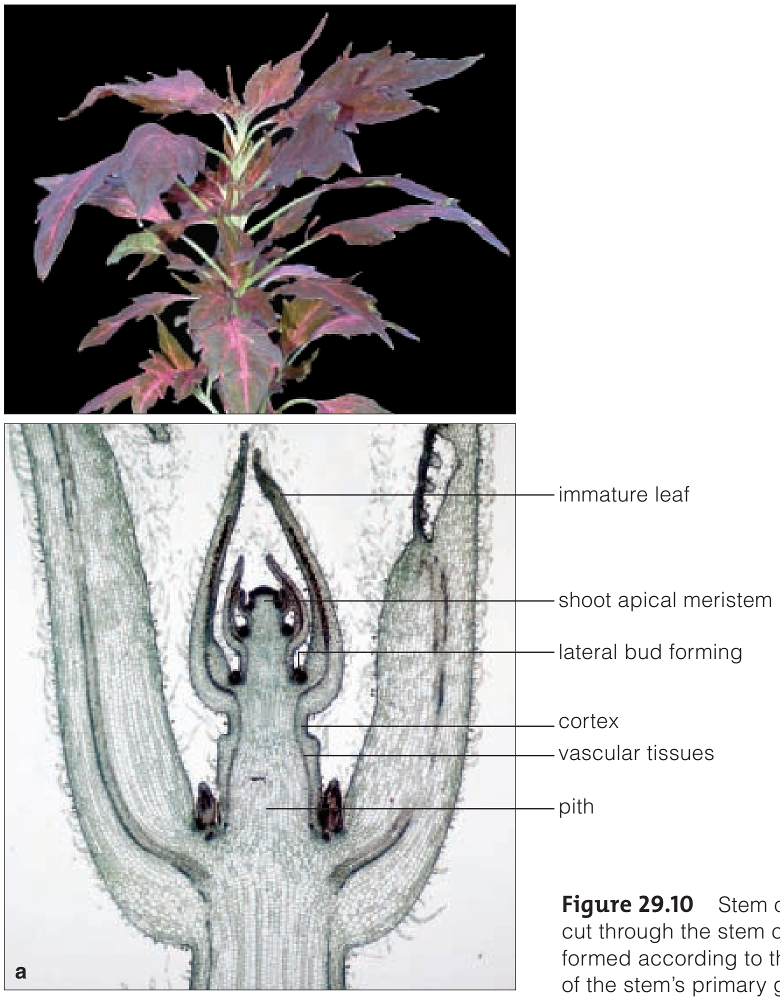
Terminal buds are a shoot's main zone of primary growth. Just beneath a terminal bud's surface, cells of shoot apical meristem divide continuously during the growing season. Some of its descendants divide and differentiate into specialized tissues. Each descendant cell lineage divides in orderly directions, at different rates, and its individual cells go on to differentiate in size, shape, and function (Figure 29.10).

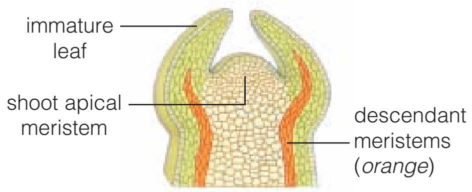
Just below the terminal bud, along the sides of the apical meristem, tiny bulges of tissue develop. Each is the start of a leaf. As the stem continues to lengthen, new leaves form and mature in orderly tiers, one after another. Each stem region where one or more leaves have formed is a node, and the region between two successive nodes is an internode (Figure 29.2).

Lateral buds, or *axillary* buds, are dormant shoots of mostly meristematic tissue. Each forms in a leaf axil, which is just above the petiole's upper surface where the leaf attaches to the stem. Often, protective bud scales, or modified leaves, encase it. Different axillary buds are the start of side branches, leaves, or flowers. As you will read in Section 32.2, a hormone secreted by a terminal bud can keep lateral buds dormant.

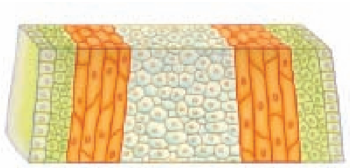
INSIDE THE STEM

In most flowering plants, the cells of primary xylem and phloem form inside the same cylindrical sheath

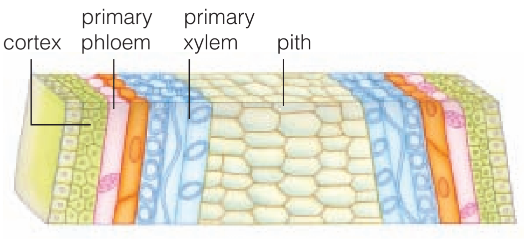




b Sketch of the shoot tip, corresponding to (**a**)



c Same stem region later on, after shoot lengthened above it



d Same stem region, later still

Figure 29.10 Stem of *Coleus*, a eudicot. (**a**) The light micrograph is a tangential cut through the stem center. The top tiers of the plant in the photograph above it formed according to this linear pattern of development. (**b**–**d**) Successive stages of the stem's primary growth, starting at the shoot apical meristem.

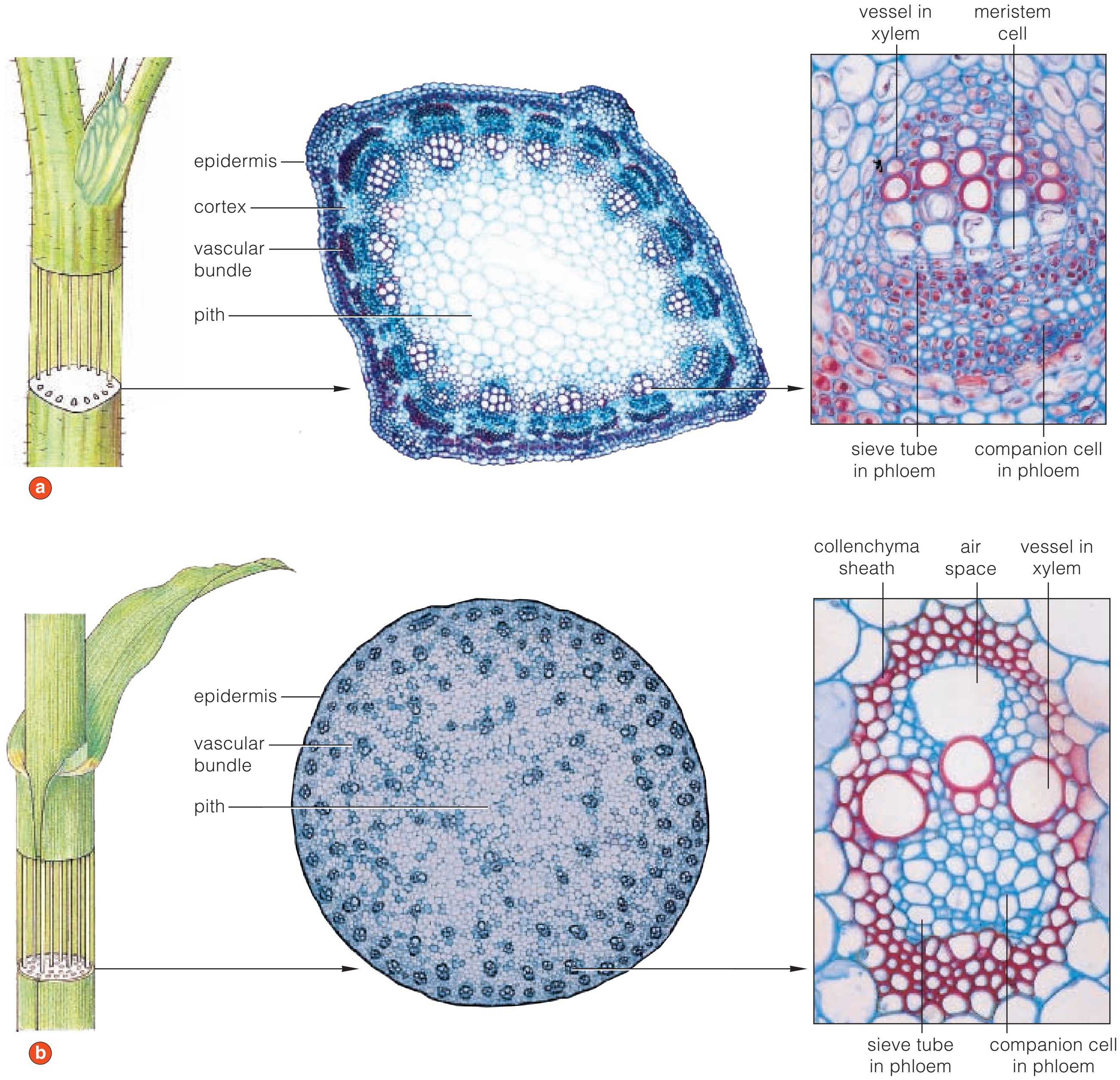


Figure 29.11 ***Animated!*** Internal stem organization. (**a**) Alfalfa (*Medicago*), a eudicot. (**b**) Corn (*Zea mays*), a monocot.

of cells, as distinctively long, **vascular bundles**. These multistranded cords thread lengthwise through every shoot's ground tissue system.

Vascular bundles form in two genetically dictated patterns. In most eudicots, they develop in a ringlike array that runs parallel with the shoot's long axis. The ring divides parenchyma of the ground tissue into a cortex and pith (Figure 29.11*a*). The stem *cortex* is the portion between the ring of vascular bundles and the epidermis. The *pith* is the part inside the ring.

Most monocot and some magnoliid stems have a different arrangement. Their long vascular bundles do not form a ring; rather, they are distributed all through the ground tissue (Figure 29.11*b*). The next chapter explains how these vascular tissues take up, conduct, and give up water and solutes throughout the plant.

Ground, vascular, and dermal tissues of monocot and eudicot stems have distinct organizational patterns. A stem's primary growth starts at apical meristems in terminal and lateral buds.

The meristematic activity gives rise to the primary plant body, which develops a distinctive internal structure, as in the pattern in which its vascular bundles are arranged.

29.4 A Closer Look at Leaves

LINKS TO SECTIONS 4.9, 7.7, 23.2

*Each **leaf** is a metabolic factory with many photosynthetic cells. Even so, leaves vary greatly in size, shape, surface specializations, and internal structure.*

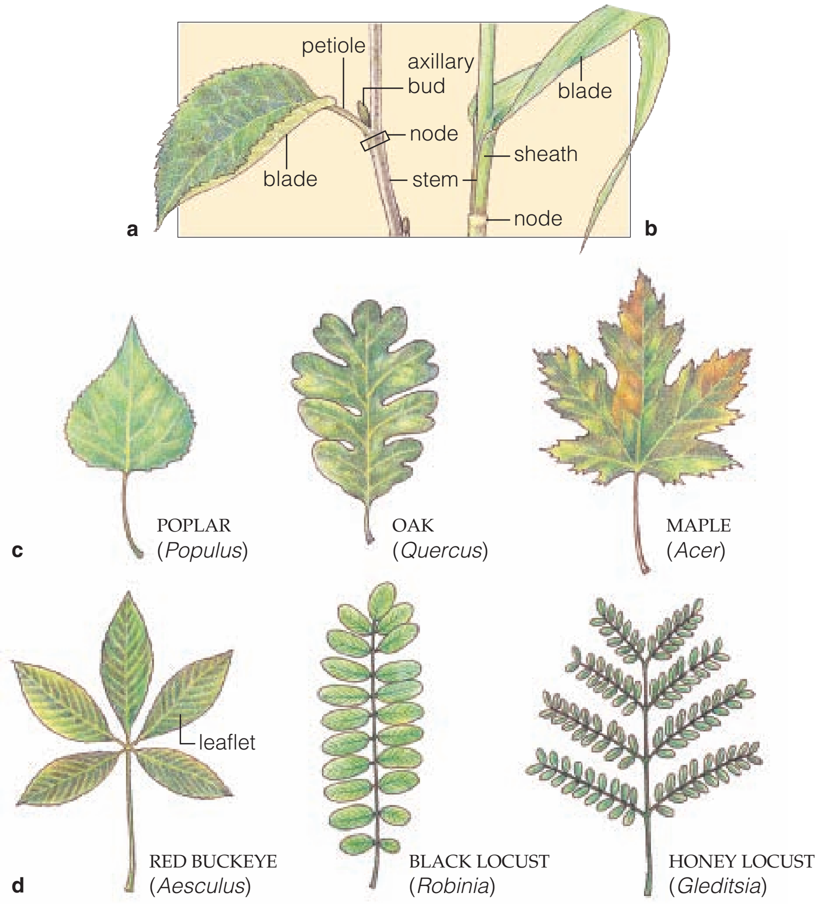


Figure 29.12 Common leaf forms of (**a**) eudicots and (**b**) monocots. Examples of (**c**) simple leaves and (**d**) compound leaves.

Figure 29.13 Example of leaf specializations. Leaves of the cobra lily (*Darlingtonia californica*) form a "pitcher." The pitcher becomes partially filled with plant secretions that hold digestive enzymes. It also gives off chemical odors that some insects find irresistible. Insects lured in often cannot find the way back out; light that is shining through the patterned dome of the pitcher's leaves confuses them. They just wander around and down, adhering to downward-pointing leaf hairs—which are slickened with wax above the potent vat.

LEAF SIMILARITIES AND DIFFERENCES

Figures 29.12 and 29.13 hint at some of the structural and functional variations among leaves, which also differ in size. A duckweed leaf is 1 millimeter (0.04 inch) across; leaves of one palm (*Attalea*) are 12 meters across. Leaves are shaped like needles, blades, spikes, cups, tubes, and feathers. They differ in color, odor, and edibility; many form toxins. Leaves of birches and other *deciduous* species wither and drop from stems as winter nears. Leaves of camellias and other *evergreen* plants also drop but not all at the same time.

A typical leaf has a flat blade and a petiole, or stalk, attached to the stem (Figure 29.12*a*). *Simple* leaves are undivided, although many are lobed. *Compound* leaves have blades divided as leaflets. Most monocots, such as ryegrass and corn, have flat blades, the base of which encircles and sheathes the stem.

Leaf shapes and orientations function to intercept sunlight and to exchange gases. Most leaves are thin, with a high surface-to-volume ratio, and most reorient themselves during the day so that they stay perpendicular to the sun's rays. Leaves often project from the same stem in a pattern that keeps one another in sunlight, as the four-leaf clover at right is doing. In hot, arid places, however, the leaves of many desert plants orient themselves parallel with the sun's rays and so reduce heat absorption. The thick leaves and stems of a cactus and some other plants also help store water.

LEAF FINE STRUCTURE

A leaf's fine structure, too, is adapted to intercept the sun's rays and enhance gas exchange. Many leaves also have surface specializations.

Leaf Epidermis Epidermis covers every leaf surface exposed to the air. This surface tissue may be smooth, sticky, or slimy, with "hairs," scales, spikes, hooks, glands, and other specializations. A cuticle covers the sheetlike, compact array of epidermal cells; it restricts water loss (Figures 29.9 and 29.14). Most leaves have far more stomata on the lower surface. In arid or cold habitats, stomata and thickly coated epidermal hairs often occur in depressions in the leaf surface. Both leaf adaptations help conserve water.

Mesophyll—Photosynthetic Ground Tissue Each leaf holds **mesophyll**, a photosynthetic parenchyma in which the individual cells are exposed to air spaces

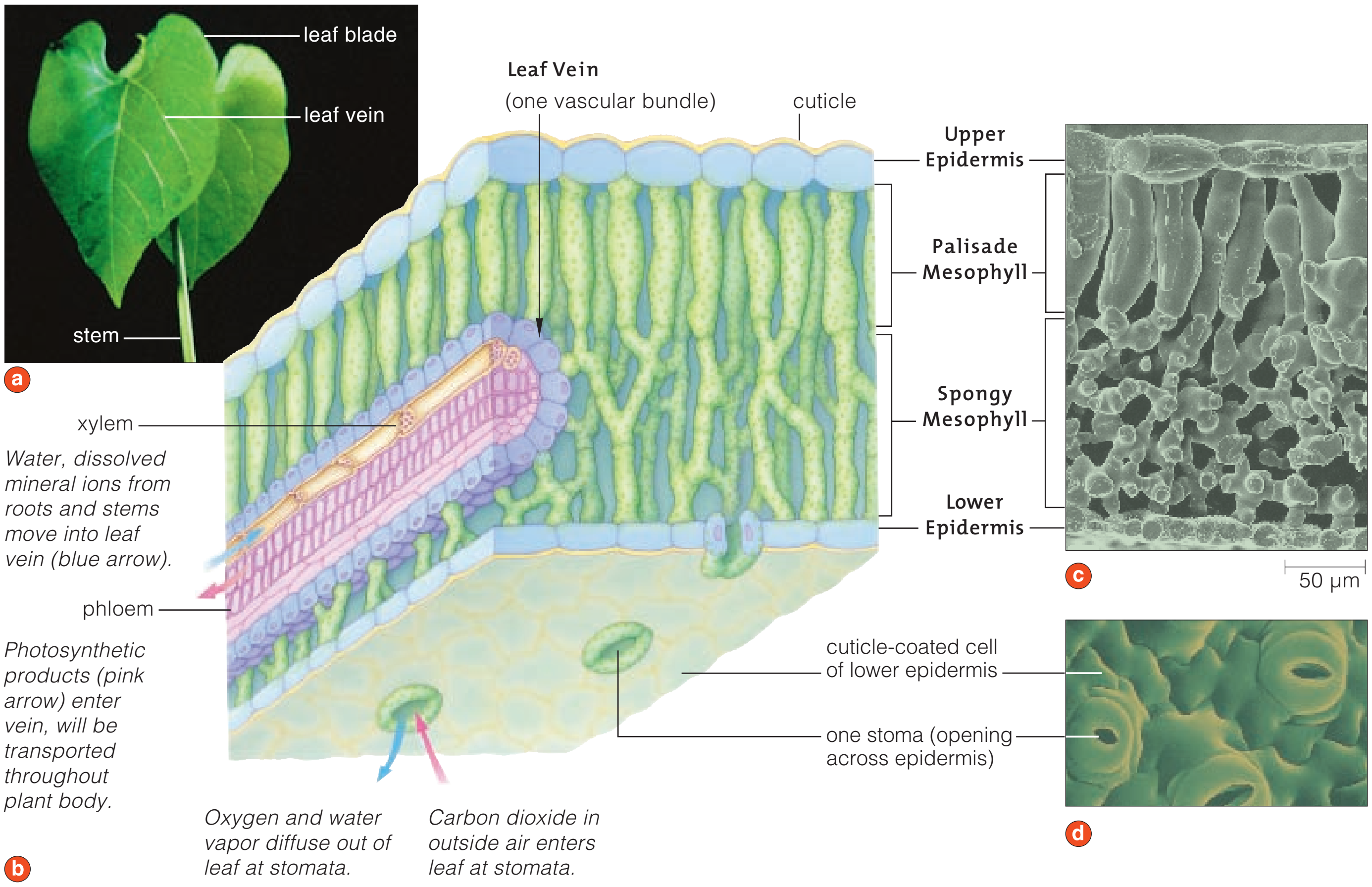


Figure 29.14 ***Animated!*** Leaf organization for *Phaseolus*, a bean plant. (**a**) Foliage leaves. (**b**–**d**) Leaf fine structure.

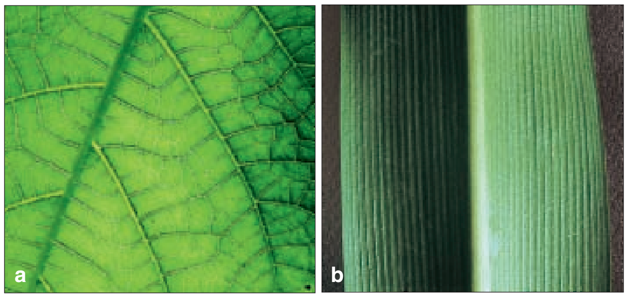


Figure 29.15 Typical vein patterns in flowering plants. (**a**) A netlike array of veins is common among eudicots. A stiffened midrib often runs from the petiole to the leaf tip, and ever smaller veins branch from it. (**b**) A strongly parallel orientation of veins is typical of monocot leaves. Like our blood-transporting veins, leaf veins are conduits for dissolved substances. Like an umbrella's ribs, stiffened veins also help maintain leaf shape.

(Section 7.7 and Figure 29.14). Carbon dioxide reaches these cells by diffusing into the leaf through stomata; oxygen wastes of photosynthesis diffuse out the other way. Plasmodesmata functionally connect these cells. This type of junction aligns across the walls of two adjoining cells and allows substances to flow rapidly into and out of their cytoplasm (Section 4.9).

Leaves oriented perpendicular to the sun have two mesophyll regions. Attached to the upper epidermis is *palisade* mesophyll. These columnar parenchymal cells have more chloroplasts and photosynthetic potential than cells of the *spongy* mesophyll layer below (Figure 29.14). In grass blades and other monocot leaves, the mesophyll is not divided into two layers. Such leaves grow vertically and intercept light from all directions.

Veins—The Leaf's Vascular Bundles Leaf **veins** are vascular bundles, usually strengthened with fibers. Their continuous strands of xylem rapidly move water and dissolved nutrients to all mesophyll cells, and the continuous strands of phloem carry photosynthetic products—especially sugars—away from them. In most eudicots, veins branch lacily into a number of minor veins embedded in the mesophyll. In most monocots, the veins are more or less similar in length and run parallel with the leaf's long axis (Figure 29.15).

A leaf's shape, orientation, and structure typically function in sunlight interception, gas exchange, and distribution of water and solutes to and from its living cells. Its epidermis encloses photosynthetic parenchyma (mesophyll) and veins.

ORGANIZATION OF PRIMARY ROOTS

29.5 Primary Structure of Roots

LINKS TO SECTIONS 23.2, 28.2

Roots function mainly in providing plants with a large surface area for absorbing water and essential mineral ions dissolved in it.

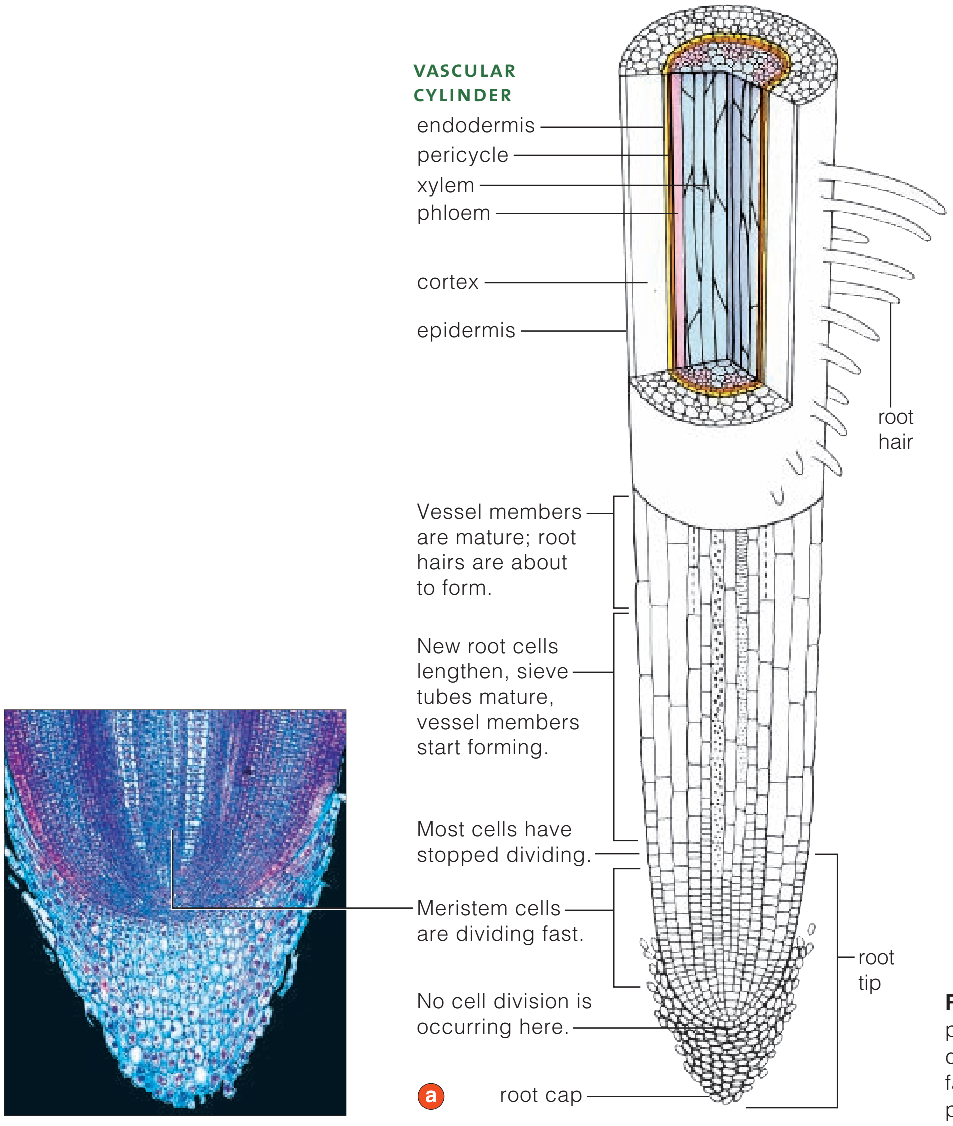
Unless tree roots start to buckle a sidewalk or choke off a sewer line, most of us do not pay much attention to flowering plant root systems. As we are walking above them, roots are busily mining the soil for water and minerals, and most grow no deeper than 2 to 5 meters. In hot deserts, where free water is scarce, one hardy mesquite shrub sent its roots down 53.4 meters (175 feet) near a stream bed. Some cacti have shallow roots radiating outward for 15 meters.

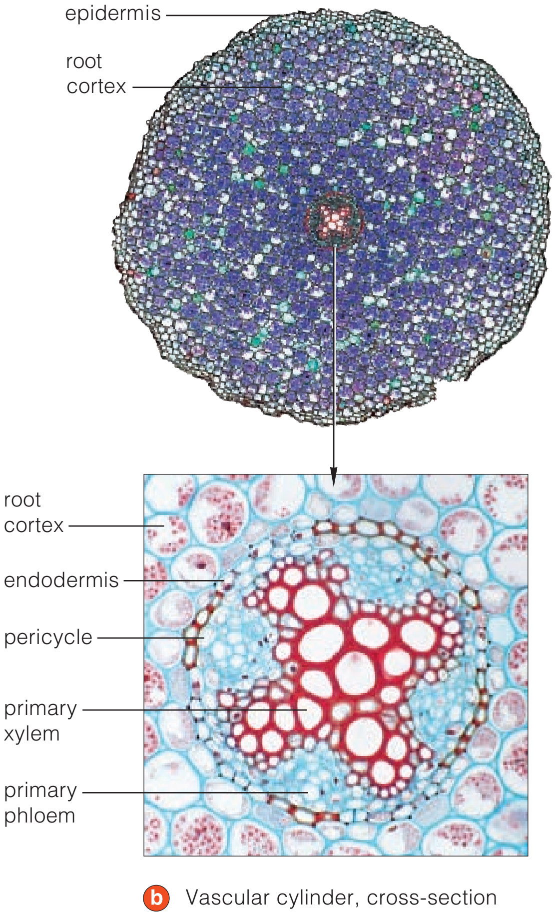
Someone once measured the roots of a young rye plant that had been growing for four months in 6 liters of soil water. If the surface area of that root system were laid out as one sheet, it would occupy more than 600 square meters, or close to 6,500 square feet!

INTERNAL STRUCTURE OF ROOTS

A root's structural organization, recall, is laid out in a seed. When a seed germinates, a primary root is the first structure to poke through the seed coat. In nearly all eudicot seedlings, the primary root thickens.

Look at the Figure 29.16*a* root tip. Some cellular descendants of root apical meristem give rise to a root cap, a dome-shaped mass of cells that helps protect the soft, young root as it grows through soil. Other cells give rise to three primary meristems—which divide, enlarge, elongate, and differentiate into the dermal, ground, and vascular tissue systems.





Vascular cylinder, cross-section

Figure 29.16 ***Animated!*** (**a**) Organization of a typical primary root and zones where cells divide, lengthen, and differentiate into primary tissues. Oldest root cells are farthest from apical meristem at the tip, which a root cap protects. (**b**) *Ranunculus* vascular cylinder.

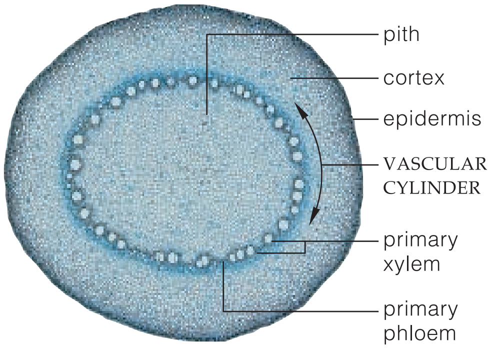


Figure 29.17 Root of corn (*Z. mays*), transverse section. Its vascular cylinder divides the ground tissue into two zones—cortex and pith.

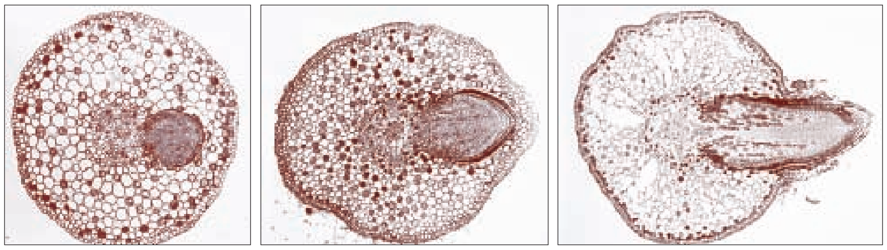


Figure 29.18 Lateral root formation from the pericycle, a cylindrical sheet of cells, one cell thick, inside the endodermis. Transverse sections.

Root epidermis is the plant's absorptive interface with soil. Some epidermal cells send out extensions called **root hairs**. Collectively, root hairs enormously increase the surface area available for taking up water and dissolved oxygen and mineral ions. We consider the nutritional role of root hairs in the next chapter. For now, simply note that an abundance of spaces between the cells of the ground tissue system allows oxygen to diffuse easily through all roots. Like other living cells in the plant, root cells make ATP by aerobic respiration and require oxygen for the reactions.

Root apical meristem also gives rise to the ground tissue system and to the **vascular cylinder**. A vascular cylinder consists of primary xylem and phloem inside a pericycle: one or more layers of parenchyma cells (Figure 29.16*b*). In corn and some other monocots, the vascular cylinder divides the root ground tissue into cortex and pith (Figure 29.17).

Although pericycle cells are differentiated, some retain the capacity to divide. They divide repeatedly in a direction perpendicular to the root axis. Masses of cells erupt through the cortex and epidermis as the start of new, lateral roots (Figure 29.18).

As you will see in the next chapter, water entering a root moves from cell to cell until it reaches the **endodermis**—a layer of cells around the pericycle. Abutting endodermal cells are waterproofed, so water must pass *through* the cytoplasm of these cells to reach the vascular cylinder. Transport proteins built into the plasma membrane exert some control over the uptake of water and dissolved substances.

TAPROOT AND FIBROUS ROOT SYSTEMS

Root primary growth results in one of two kinds of root systems. In eudicots, a **taproot system** consists of a primary root and its lateral branchings. Dandelions, carrots, oak trees, and poppies are among the plants having this system (Figure 29.19*a*). By comparison, the primary root of most monocots, such as grasses, is short-lived. Adventitious roots arise from the stem in its place, and then lateral roots branch from them. (*Adventitious* refers to any plant structure that forms at an unusual place, relative to most species.) Lateral roots are more or less similar in diameter and length. Such roots form a **fibrous root system** (Figure 29.19*b*).

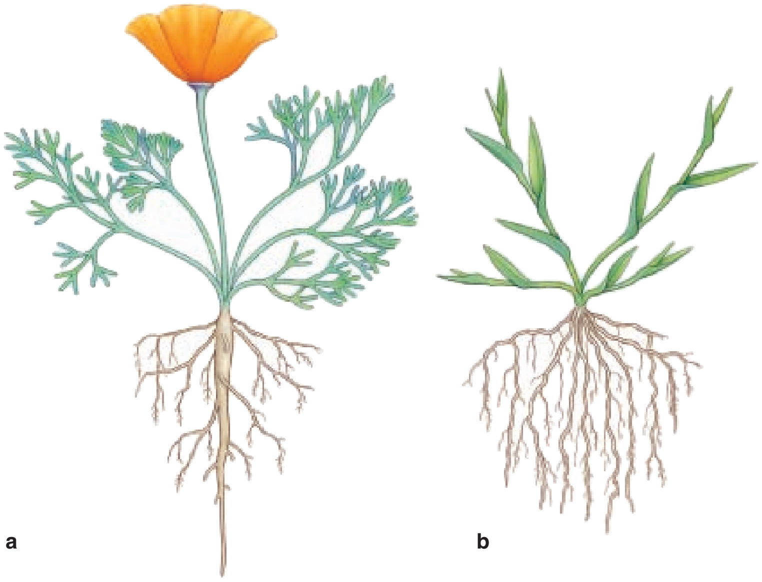


Figure 29.19 (**a**) Taproot system of the eudicot California poppy. (**b**) Fibrous root system of a grass plant, a monocot.

Roots provide a plant with a tremendous surface area for absorbing water and solutes. Inside each is a vascular cylinder, with long strands of primary xylem and phloem.

Taproot systems consist of a primary root and lateral branchings. Fibrous root systems consist of similar roots that replace the primary root.

29.6 Accumulated Secondary Growth—The Woody Plants

LINKS TO SECTIONS 23.2, 28.2

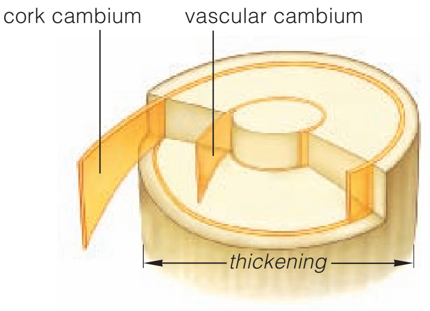
Flowering plant life cycles differ. ***Annuals****, or herbaceous (nonwoody) types, survive for only one growing season.* ***Biennials*** *form roots, stems, and leaves in one season, then flower, make seeds, and die the next.* ***Perennials*** *grow and make seeds year after year. Their roots and stems, like those of some biennials, thicken by way of activity at vascular cambium.*

WHAT HAPPENS AT VASCULAR CAMBIUM?

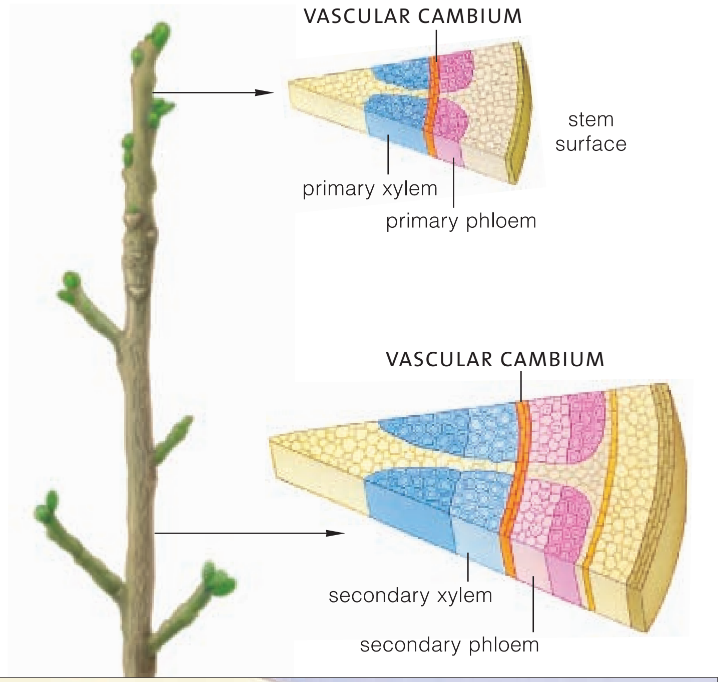
Some monocots, many eudicots, the magnoliids, and most gymnosperms add secondary growth in two or more growing seasons. They are *woody* plants. Early in life, their stems and roots are like those of nonwoody plants. Differences emerge as their lateral meristems become active. These are the meristems that produce secondary xylem and phloem. When roots and stems add secondary growth season after season, periderm eventually replaces the epidermis.

Figure 29.20 shows the growth pattern at vascular cambium. Secondary xylem forms on the *inner* face of this meristem. Secondary phloem forms on its *outer* face. The inner core of xylem thickens and displaces meristematic cells toward the surface of the stem. The displaced cells maintain the ring of vascular cambium by dividing sideways, in a widening circle.

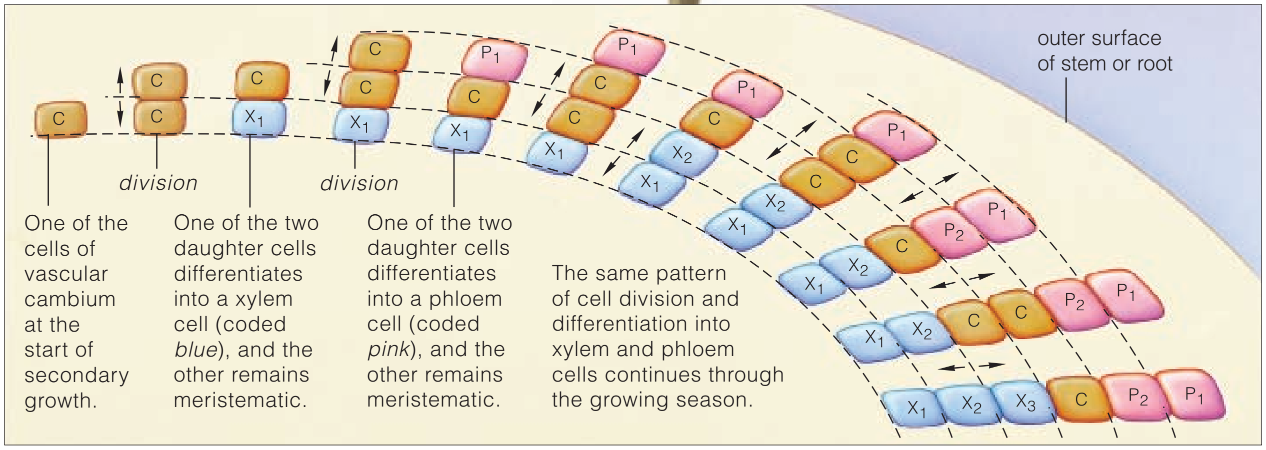
In spring, as primary growth resumes at the stem's buds, secondary growth is added *inside* it. When fully formed, vascular cambium in a stem is like a cylinder, one or a few cells thick. Some cells (fusiform initials) give rise to secondary xylem and phloem that extend *lengthwise* through the stem. Other cells (ray initials)



a Two lateral meristems in older stems and roots of woody plants produce secondary growth, or increases in diameter. *Vascular cambium* gives rise to secondary vascular tissues. *Cork cambium* gives rise to periderm.



b Pattern of activity at vascular cambium. Reading left to right, ongoing cell divisions enlarge the inner core of secondary xylem and displace vascular cambium toward the stem or root surface.



c

Figure 29.20 ***Animated!*** (**a**) Two meristems that become active during secondary growth. (**b**) Twig from a walnut tree in winter, after leaves dropped. In spring, *primary* growth resumes at terminal and lateral buds. *Secondary* growth resumes at vascular cambium. (**c**) The overall pattern of growth at vascular cambium.

form *horizontal* rays of parenchyma, in a pattern that is a bit like the spokes of a bike wheel. Through these secondary vascular tissues, water and solutes travel up, down, and sideways through an ever enlarging woody stem (Figure 29.21).

In different perennials, vascular cambium has been reactivated each growing season for tens, hundreds, or thousands of years. Some individual trees become giants. At last measure, the massive trunk of a coast redwood (a gymnosperm) had grown more than 110 meters (360 feet) above the forest floor. Its secondary growth might weigh close to 120 tons. As another example, the tree having the largest girth is one of the chestnuts (*Castanea*). It is growing in Sicily. To walk completely around the base of it, you would have to pace off 58 meters, or 190 feet.

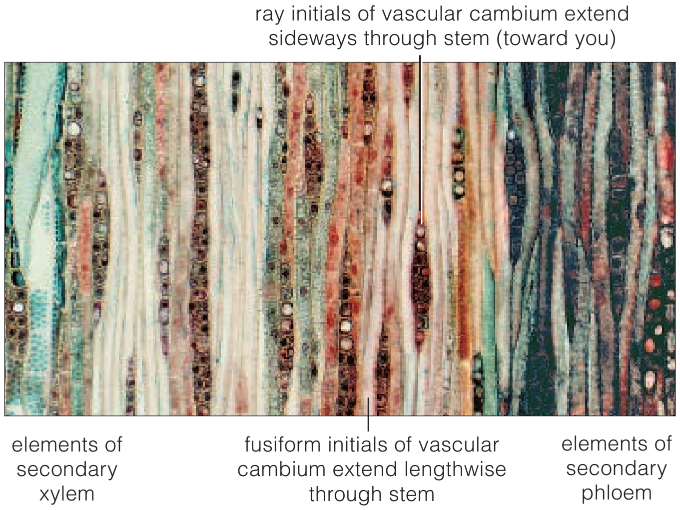


Figure 29.21 Fusiform initials and ray initials of the vascular cambium of a walnut tree, tangential section. Notice the tracheids (*light blue*) at far left.

DON'T FORGET THE WOODY ROOTS

We have been focusing on how stems can thicken year after year through secondary growth. Bear in mind, secondary xylem and phloem also form at vascular cambium in the plant's roots. Figure 29.22 represents the overall pattern of secondary growth at vascular cambium in the root of a typical woody plant.

WOODY AND NONWOODY PLANTS COMPARED

Woody stems and roots have selective advantages. Like other organisms, plants compete for resources. Plants with taller stems or broader canopies that defy the pull of gravity intercept more energy streaming in from the sun. By tapping a greater supply of energy for photosynthesis, they have the metabolic means to form large root and shoot systems. With larger root and shoot systems, they can be more competitive than their neighbors in acquiring resources. Other factors being equal, they ultimately will be more successful, in reproductive terms, in particular habitats.

In woody plants, secondary vascular tissues form at a ring of vascular cambium inside older stems and roots. Wood is an accumulation of secondary xylem especially.

With their sturdier tissues, woody plants defy gravity and grow taller and broader. Where competition for sunlight is intense, the ones that intercept the most sunlight win.

When other factors are equal, plants that can secure more energy than their neighbors to drive photosynthesis have advantages in terms of metabolic capabilities, growth, and reproductive success.

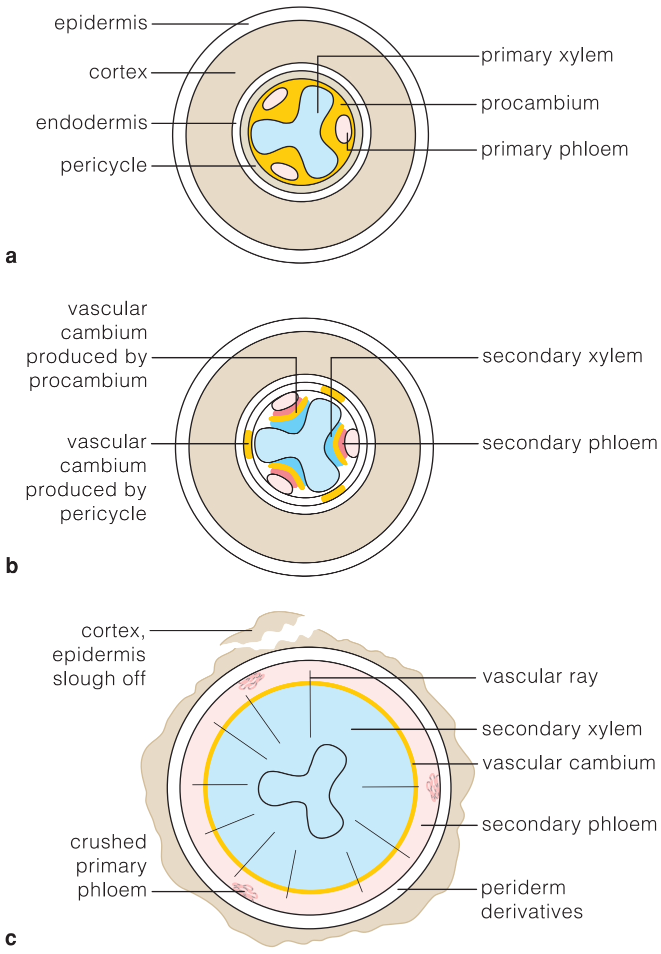


Figure 29.22 Secondary growth in one type of woody root. (**a**) This is how tissues are organized as primary growth ends. (**b**,**c**) A thin cylinder of vascular cambium forms and gives rise to secondary xylem and phloem. Cell divisions are parallel with the vascular cambium. The cortex ruptures as the root thickens.

29.7 A Closer Look At Wood and Bark

LINK TO SECTION 28.4

A core of secondary xylem—wood—makes up 90 percent of the mass of some trees. Secondary phloem, a narrow zone outside the vascular cambium, has thin-walled, living parenchyma cells and sieve tubes, often interspersed between bands of thick-walled reinforcing fibers. The only functioning sieve tubes lie within a centimeter or so of the vascular cambium. The rest died, but they help protect the living cells beneath them.

FORMATION OF BARK

As the seasons pass, a tree ages and the inner core of xylem continues its outward expansion. The resulting pressure is directed toward the stem or root surface. Eventually it ruptures the cortex and the outer part of secondary phloem. When that happens, parenchyma cells in this region start dividing, and they give rise to the cork cambium. Where rupturing causes the cortex and epidermis to split away, ongoing cell divisions at the cork cambium give rise to the **periderm**. This new dermal tissue is composed of parenchyma and cork, as well as the cork cambium that produces it.

Figure 29.23 Thick, fire-resistant bark of a coast redwood. This gymnosperm is a champion of secondary growth.

Collectively, the periderm and secondary phloem constitute **bark**. In other words, *bark consists of living cells and dead tissues on the outside of vascular cambium* (Figures 29.23 and 29.24).

The **cork** component of bark has densely packed rows of cells, each with a wall thickened by a fatty substance called suberin. Only the innermost cells of this tissue are alive, because they alone have access to nourishment from xylem and phloem. With its many suberized layers, cork can protect, insulate, and also waterproof the stem or root surface. Cork also forms over wounded tissues. When leaves are about to drop from the plant, cork forms at the place where petioles attach to stems.

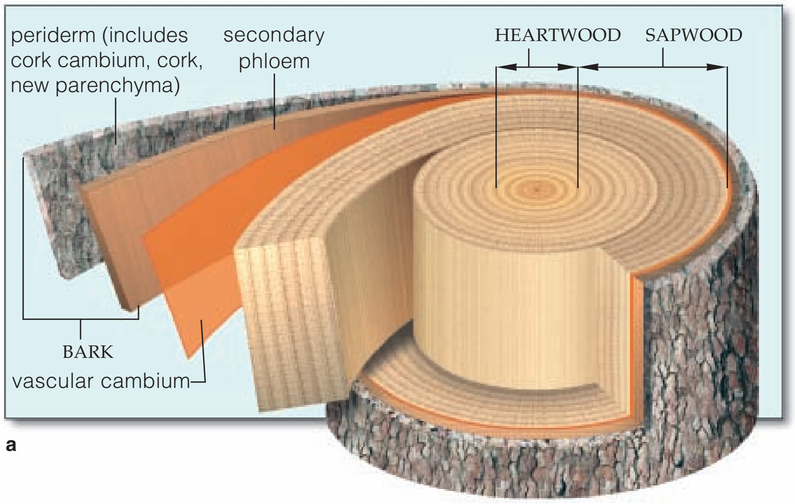
Like all living plant cells, the cells in woody stems and roots require oxygen for aerobic respiration and give off carbon dioxide wastes. So how do these gases get across the suberized, corky surface of bark? They can cross through lenticels, which are localized areas where the packing of cork cells is loosened up a bit. Those dark spots you might have noticed on a wine bottle's cork are all that is left of lenticels.

HEARTWOOD AND SAPWOOD

Wood's appearance and function change as a stem or root ages. The core becomes **heartwood**, a dry tissue that no longer transports water and solutes but helps the tree defy gravity. Metabolic wastes, such as resins, tannins, gums, and oils, collect in heartwood. In time, they fill and clog the oldest xylem pipelines. They often darken the heartwood, which becomes stronger, more aromatic, and prized by furniture builders.

In the early 1900s, when lumbermen were active in California's groves of old-growth redwoods, someone cut a tunnel through heartwood of a few big trees, the better to drive an automobile through them.

Sapwood is all of the secondary growth in between the vascular cambium and heartwood (Figure 29.24*a*). Unlike heartwood, sapwood is wet, usually pale, and not as strong, as in maple trees. Each spring, New Englanders insert tubes into sugar maple sapwood. Sap, a sugar-rich fluid in the secondary xylem, drips through the tubes, into buckets positioned below.



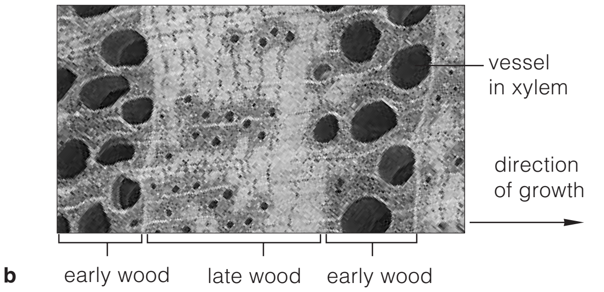


Figure 29.24 *Animated!* (**a**) One type of woody stem. (**b**) Early and late wood cut from red oak. Late wood is evidence that a tree did not waste energy making large-diameter xylem cells for water uptake during a dry summer or drought.

EARLY WOOD, LATE WOOD, AND TREE RINGS

Vascular cambium becomes inactive in cool winters or long dry spells. *Early* wood, with large-diameter, thin-walled cells, starts forming with the first rains of the growing season. *Late* wood forms in dry summers and has small-diameter, thick-walled xylem cells. The two form one annual **growth ring**. A transverse cut from a trunk reveals alternating bands, because early and late wood reflect light differently. The differences are growth rings, which also are known informally as "tree rings" (Figures 29.24 and 29.25).

Seasonal change is predictable in temperate zones, and trees growing there usually add one growth ring per year. In deserts, thunderstorms rumble through at different times of year, and trees respond by adding more than one ring of early wood in the same season. In the tropics, seasonal change is almost nonexistent, so growth rings are not a feature of tropical trees.

Oak, hickory, and other eudicot trees that evolved in temperate and tropical zones are **hardwoods**, with vessels, tracheids, and fibers in their xylem. Pines, redwoods, and the other conifers are **softwood** trees; their xylem has tracheids and rays of parenchyma, but no vessels or fibers. Lacking fibers, the trees are weaker and less dense than hardwoods (Figure 29.25).

LIMITS TO SECONDARY GROWTH

Some species, such as redwoods and bristlecone pines, add secondary growth over centuries. Most die far sooner from old age and environmental assaults. One response, compartmentalization, counters threats but eventually shuts off the flow of essential water and solutes through the vascular system (Section 28.4).

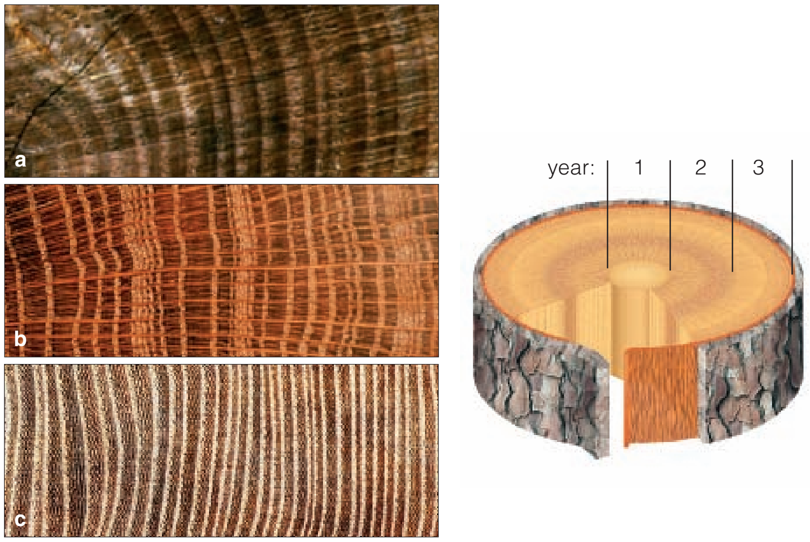


Figure 29.25 Tree rings, each corresponding to one growing season. In its first season, a stem puts on primary and some secondary growth; in later years, it adds secondary growth. Growth layers of (**a**) pine, (**b**) oak, and (**c**) elm. Pine, a softwood, is lightweight, resists warping, and grows faster than hardwoods. It is commercially farmed as a source of relatively inexpensive lumber. Oak and elm are strong, durable hardwoods. The elm made this series between 1911 and 1950. Differences in growth layer widths correspond to shifts in climate, including water availability. Count the rings and you have clues to a tree's age and to climates and life in the past.

Bark consists of all living and nonliving tissues outside the vascular cambium, both secondary phloem and periderm. Periderm consists of cork (the outermost covering of woody stems and roots), cork cambium, and new parenchyma.

Wood may be classified by its location and functions (as in heartwood versus sapwood) and by the type of plant (many dicots produce hardwood, and conifers produce softwood).

Summary

Section 29.1 The aboveground shoot systems of most plants include stems, leaves, and reproductive parts called flowers. Most species have root systems that grow downward and outward through soil.

A vascular tissue system distributes nutrients and water through the plant. A dermal system protects plant surfaces. A ground tissue system makes up the bulk of the plant body. All tissues originate at meristems: regions of cells that are undifferentiated and retain a capacity for division. Primary growth at apical meristems lengthens shoots and roots. Secondary growth thickens older stems and roots, often accumulating as wood.

Monocots and eudicots have the same tissues, but these are organized in somewhat different ways.

Biology Now

Explore the tomato body plan and compare monocot and dicot tissues with the animation on BiologyNow.

Section 29.2 Parenchyma, collenchyma, as well as sclerenchyma are simple tissues. Each consists of one cell type, but these can vary in form and function (Table 29.1). Parenchyma's living, thin-walled cells, the bulk of ground tissue systems, serve in photosynthesis, storage, and other tasks. Collenchyma's living cells have unevenly thickened walls. It elastically supports fast-growing plant parts. Sclerenchyma cells die at maturity; their lignin-reinforced walls remain and support the plant.

Complex plant tissues have two or more cell types. Vascular tissues (xylem and phloem) and dermal tissues (epidermis and periderm) are examples. Xylem's vessel members and tracheids conduct water. They are dead at maturity; their pitted, interconnected walls are pipelines for water and dissolved minerals. Sieve-tube members, phloem's interconnected sugar-conducting cells, are alive at maturity. Companion cells help load sugars into them.

Epidermis covers and protects the outer surfaces of primary plant parts. Periderm replaces epidermis on the woody plants, which show extensive secondary growth.

Section 29.3 Stems of most species serve in upright growth, which favors sunlight interception. Vascular bundles (xylem and phloem) thread through them. In most eudicot stems, a ring of bundles divides ground tissue into cortex and pith. Monocot stems often have vascular bundles distributed through the ground tissue.

Biology Now

Look inside stems with the animation on BiologyNow.

Section 29.4 Leaves are photosynthesis factories. They have veins (vascular bundles) and mesophyll (photosynthetic parenchyma) between upper and lower epidermis. Air spaces around mesophyll cells enhance gas exchange. Water vapor, oxygen, and carbon dioxide cross the cuticle-covered epidermis at stomata.

Biology Now

Explore the structure of a leaf with the animation on BiologyNow.

Section 29.5 Roots absorb water and dissolved mineral ions, which become distributed to aboveground parts. Most anchor plants and store food. Some help support aboveground parts. Eudicots typically have a taproot system, and many monocots have a fibrous root system, with many lateral branchings.

Biology Now

Learn about root structure and function with the animation on BiologyNow.

Sections 29.6, 29.7 Activity at lateral meristems thickens many older stems and roots. Wood is classified by location and function, as in heartwood or sapwood. Bark consists of secondary phloem and periderm.

Biology Now

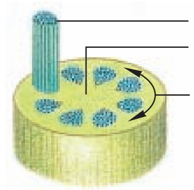
Learn about the structure of wood with the animation on BiologyNow.

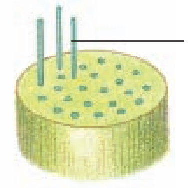
Table 29.1 Flowering Plant Tissues

Simple tissues	
Parenchyma	Parenchyma cells
Collenchyma	Collenchyma cells
Sclerenchyma	Fibers or sclereids
Complex tissues	
Xylem	Conducting cells (tracheids, vessel members); parenchyma cells; sclerenchyma cells
Phloem	Conducting cells (sieve-tube members); parenchyma cells; sclerenchyma cells
Epidermis	Undifferentiated cells; also guard cells (stomata) and other specialized cells
Periderm	Cork; cork cambium; new parenchyma

Self-Quiz

Answers in Appendix II





1. Which of the two stem sections at the *left* is common among eudicots? Which is common among monocots? Label the main tissue regions of both sections.

2. Roots and shoots lengthen through activity at ______ .
   a. apical meristems   c. vascular cambium
   b. lateral meristems   d. cork cambium

3. In many plant species, older roots and stems thicken by activity at ______ .
   a. apical meristems   c. vascular cambium
   b. cork cambium   d. both b and c

4. Is the plant with the yellow flower in Figure 29.26*a* a eudicot or a monocot? What about the plant with the purple flower (Figure 29.26*b*)?

5. ______ conducts water and ions; ______ conducts food.
   a. Phloem; xylem   c. Xylem; phloem
   b. Cambium; phloem   d. Xylem; cambium

6. Mesophyll consists of ______ .
   a. waxes and cutin   c. photosynthetic cells
   b. lignified cell walls   d. cork but not bark

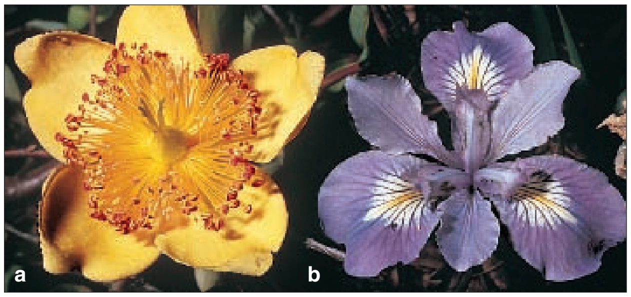


Figure 29.26 Flower of (**a**) St. John's wort (*Hypericum*) and (**b**) an iris (*Iris*).

7. In phloem, organic compounds flow through ________ .
   a. collenchyma cells c. vessels
   b. sieve tubes d. tracheids

8. Xylem and phloem are ________ tissues.
   a. ground b. vascular c. dermal d. both b and c

9. In early wood, cells have ______ diameters, ______ walls.
   a. small; thick c. large; thick
   b. small; thin d. large; thin

10. Match the plant parts with the suitable description.
   _____ apical meristem a. massive secondary growth
   _____ lateral meristem b. source of primary growth
   _____ xylem c. distribution of sugars
   _____ phloem d. source of secondary growth
   _____ vascular cylinder e. distribution of water
   _____ wood f. central column in roots

Additional questions are available on **Biology Now**™

Critical Thinking

1. Think about the conditions that might prevail in a hot desert in New Mexico or Arizona; on the floor of a shady, moist forest in Georgia or Oregon; and in the arctic tundra in Alaska. Then "design" a flowering plant that could do well in one of those places, and explain why.

2. Fitzgerald, widely known for his underdeveloped sense of nature, sneaks into a forest preserve at night and then maliciously girdles an old-growth redwood. *Girdling* a tree means cutting away the bark and cambium in a ring around its girth, and can kill it by interrupting the circulation of water and nutrients. He settles down and watches the tree, waiting for it to die. But the tree will not die that night or any time soon. Explain why.

3. Sylvia lives in Santa Barbara, where droughts are common. She replaced most of her lawn with drought-tolerant plants and waters the remaining lawn twice a week after the sun goes down, soaking it to a depth of several inches. Why is her strategy good for lawn grasses?

4. Oscar and Lucinda meet in a tropical rain forest and fall in love, and he carves their initials into the bark of a tiny tree. They never do get together, though. Ten years later, still heartbroken, Oscar searches for the tree. Given what you know about primary and secondary growth, will he find the carved initials higher relative to ground level? If he goes berserk and chops down the tree, what kinds of growth rings will he see?

5. In 1587, about 150 English settlers arrived at Roanoke Island off the coast of North Carolina. When ships arrived in 1589 to resupply the colony, they found the island had been abandoned. Searches up and down the coast failed to turn up the missing colonists. About twenty years later, the English established a colony at Jamestown, Virginia. Although this colony survived, the initial years were hard. In the summer of 1610 alone, more than 40 percent of the colonists died, many of starvation.

Scientists examined wood cores from bald cypress (*Taxodium distichum*) that had been growing at the time the Roanoke and Jamestown colonies were founded. Growth rings revealed the colonists were in the wrong place at the wrong time (Figure 29.27). They arrived at Roanoke just in time for the worst droughts in eight hundred years. Nearly a decade of severe drought struck Jamestown.

We know the corn crop of the Jamestown colony failed totally. Drought-related crop failures probably occurred at Roanoke. The settlers also had trouble finding fresh water. Jamestown was established at the head of an estuary; when river levels dropped, the water became brackish.

If secrets locked in trees intrigue you, look into a field of study called *dendroclimatology*. For example, find out what growth layers reveal about fluctuations in climate where you live. See if you can correlate them with human events at the time the changes were being recorded.

Figure 29.27 (**a**) Location of two of the early American colonies. (**b**) Bald cypress swamp. (**c**) Bald cypress growth layers, cross-section. This tree was living when English colonists first settled in North America. Narrow annual rings mark severe drought years, which stunted tree growth. Compare Section 29.7.