Root hairs can number over 37,000 cm^2 of root surface and many billions per plant; they greatly increase the surface area and therefore the absorptive capacity of the root. Symbiotic bacteria that fix atmospheric nitrogen into a form usable by legumes enter the plant via root hairs and "instruct" the plant to create a nitrogen-fixing nodule around it (see chapter 39).

Parenchyma cells are produced by the ground meristem immediately to the interior of the epidermis. This tissue, called the **cortex,** may be many cell layers wide and functions in food storage. As just described, the inner boundary of the cortex differentiates into a single-layered cylinder of **endodermis,** after an asymmetrical cell division regulated by *SCR* (see figures 36.16 and 36.17). Endodermal primary walls are impregnated with *suberin,* a fatty substance that is impervious to water. The suberin is produced in bands, called **Casparian strips,** that surround each adjacent endodermal cell wall perpendicular to the root's surface (see figure 36.17). These strips block transport between cells. The two surfaces that are parallel to the root surface are the only way into the vascular tissue of the root, and the plasma membranes control what passes through. Plants with a *scr* mutation lack this waterproof Casparian strip.

All the tissues interior to the endodermis are collectively referred to as the **stele.** Immediately adjacent and interior to the endodermis is a cylinder of parenchyma cells known as the **pericycle.** Pericycle cells divide, even after they mature. They can give rise to lateral (branch) roots or, in eudicots, to the two lateral meristems, the vascular cambium and the cork cambium.

The water-conducting cells of the primary xylem are differentiated as a solid core in the center of young eudicot roots. In a cross section of a eudicot root, the central core of primary xylem often is somewhat star-shaped, having from two to several radiating arms that point toward the pericycle (see figure 36.17). In monocot (and a few eudicot) roots, the primary xylem is in discrete vascular bundles arranged in a ring, which surrounds

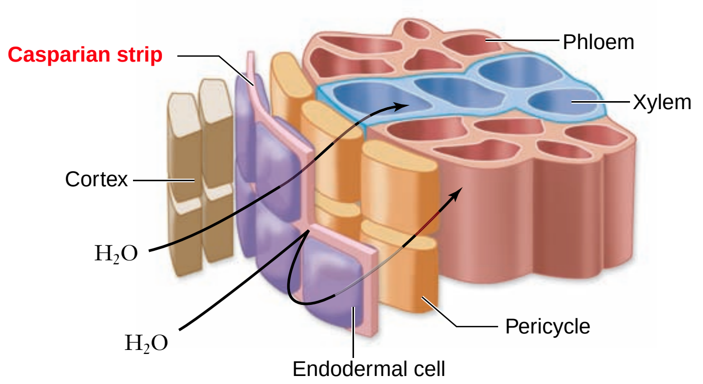
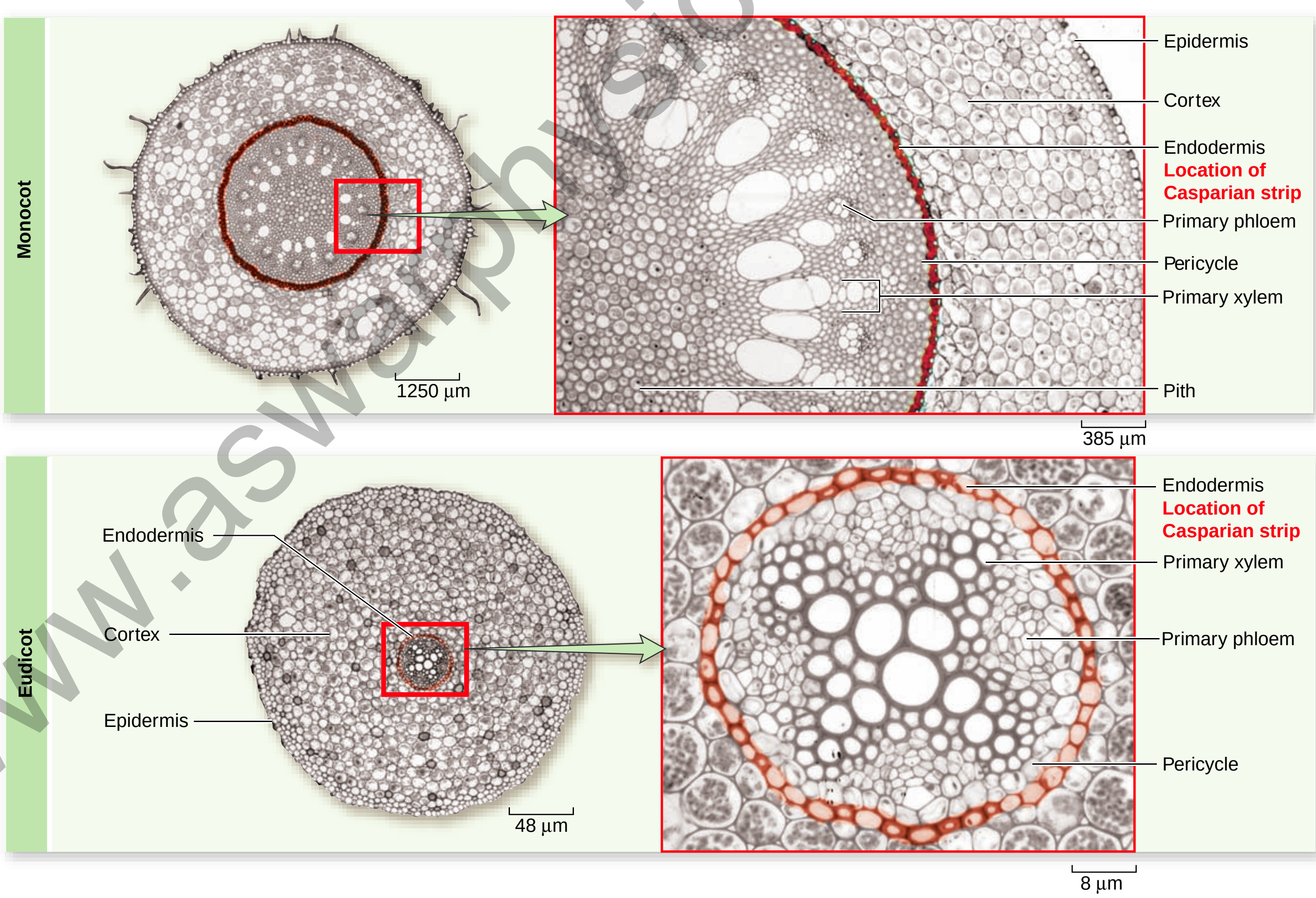


Figure 36.17 Cross sections of the zone of maturation of roots. Both monocot and eudicot roots have a Casparian strip as seen in the cross section of greenbriar *(Smilax)*, a monocot, and buttercup *(Ranunculus)*, a eudicot. The Casparian strip is a waterproofing band that forces water and minerals to pass through the plasma membranes, rather than through the spaces in the cell walls.



parenchyma cells, called *pith*, at the very center of the root (see figure 36.17). Primary phloem, composed of cells involved in food conduction, is differentiated in discrete groups of cells adjacent to the xylem in both eudicot and monocot roots.

In eudicots and other plants with secondary growth, part of the pericycle and the parenchyma cells between the phloem patches and the xylem become the root vascular cambium, which starts producing secondary xylem to the inside and secondary phloem to the outside. Eventually, the secondary tissues acquire the form of concentric cylinders. The primary phloem, cortex, and epidermis become crushed and are sloughed off as more secondary tissues are added.

In the pericycle of woody plants, the cork cambium contributes to the outer bark, which will be discussed in more detail when we look at stems. In the case of secondary growth in eudicot roots, everything outside the stele is lost and replaced with bark. Figure 36.18 summarizes the process of differentiation that occurs in plant tissue.

Modified roots accomplish specialized functions

Most plants produce either a taproot system, characterized by a single large root with smaller branch roots, or a fibrous root system, composed of many smaller roots of similar diameter. Some plants, however, have intriguing root modifications with specific functions in addition to those of anchorage and absorption.

Not all roots are produced by preexisting roots. Any root that arises along a stem or in some place other than the root of the plant is called an **adventitious root.** For example, climbing plants such as ivy produce roots from their stems; these can anchor the stems to tree trunks or to a brick wall. Adventitious root formation in ivy depends on the developmental stage of the shoot. When the shoot enters the adult phase of development, it is no longer capable of initiating these roots. Below we investigate functions of modified roots.

Prop roots. Some monocots, such as corn, produce thick adventitious roots from the lower parts of the stem. These so-called prop roots grow down to the ground and brace the plants against wind (figure 36.19*a*). Adventious roots are common in wetland plants, allowing them to tolerate wet conditions.

Aerial roots. Plants such as epiphytic orchids, which are attached to tree branches and grow unconnected to the ground (but are not parasites), have roots that extend into the air (figure 36.19*b*). Some aerial roots have an epidermis that is several cell layers thick, an adaptation to reduce water loss. These aerial roots may also be green and photosynthetic, as in the vanilla orchid *(Vanilla planifolia)*.

Pneumatophores. Some plants that grow in swamps and other wet places may produce spongy outgrowths called *pneumatophores* from their underwater roots (figure 36.19*c*). The pneumatophores commonly extend several centimeters above water, facilitating oxygen uptake in the roots beneath (figure 36.19*c*).

Contractile roots. The roots from the bulbs of lilies and from several other plants, such as dandelions, contract by spiraling to pull the plant a little deeper into the soil each year, until they reach an area of relatively stable temperature. The roots may contract to one-third their original length as they spiral like a corkscrew due to cellular thickening and constricting.

Parasitic roots. The stems of certain plants that lack chlorophyll, such as dodder (*Cuscuta* spp.), produce peglike roots called *haustoria* that penetrate the host plants around which they are twined. The haustoria establish contact with the conducting tissues of the host and effectively parasitize their host. Dodder not only weakens plants but can also spread disease when it grows and attaches to several plants.

Food storage roots. The xylem of branch roots of sweet potatoes and similar plants produce at intervals many extra parenchyma cells that store large quantities of carbohydrates. Carrots, beets, parsnips, radishes, and turnips have combinations of stem and root that also function in food storage. Cross sections of these roots reveal multiple rings of secondary growth.

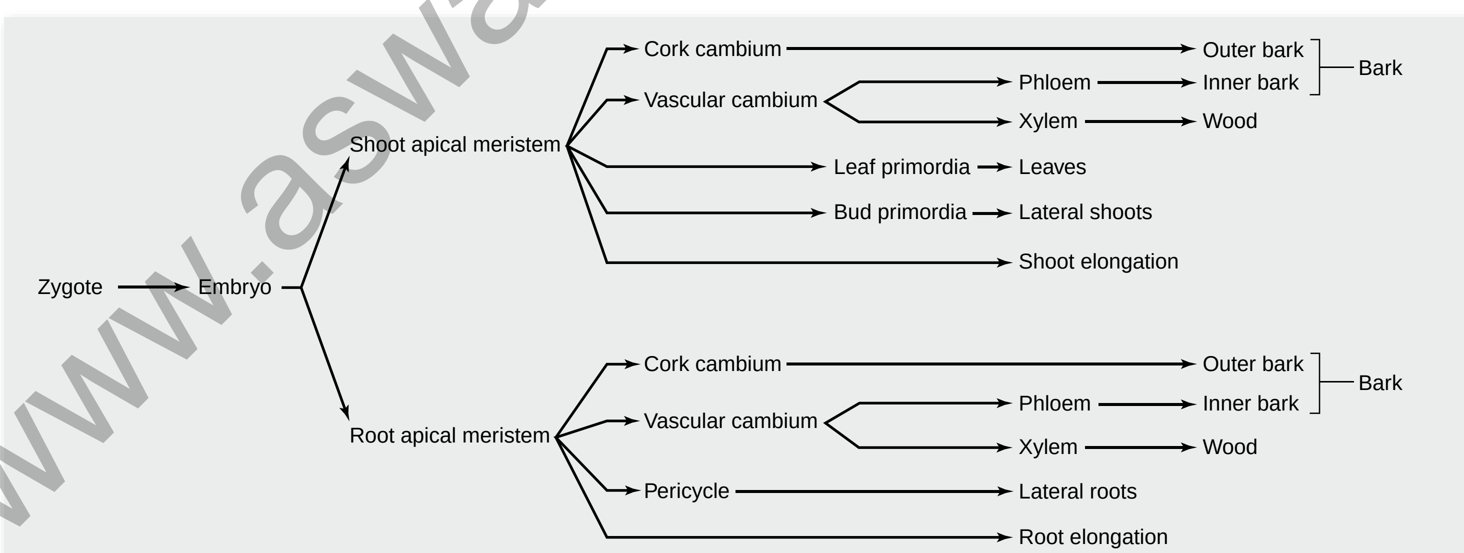


Figure 36.18 Stages in the differentiation of plant tissues.

a.

b.

Figure 36.19 Five types of modified roots. ***a.*** Maize (corn) prop roots originate from the stem and keep the plant upright. ***b.*** Epiphytic orchids attach to trees far above the tropical soil. Their roots are adapted to obtain water from the air rather than the soil. ***c.*** Pneumatophores *(foreground)* are spongy outgrowths from the roots below. ***d.*** A water storage root weighing over 25 kg (60 pounds). ***e.*** Buttress roots of a tropical fig tree.

c.

d.

e.

Water storage roots. Some members of the pumpkin family (Cucurbitaceae), especially those that grow in arid regions, may produce water storage roots weighing 50 kg or more (figure 36.19*d*).

Buttress roots. Certain species of fig and other tropical trees produce huge buttress roots toward the base of the trunk, which provide considerable stability (figure 36.19*e*).

Learning Outcomes Review 36.3

The root cap protects the root apical meristem and helps to sense gravity. New cells formed in the zone of cell division grow in length in the zone of elongation. Cells differentiate in the zone of maturation, and root hairs appear here. Root hairs greatly increase the absorptive surface area of roots. Modified roots allow plants to carry out many additional functions, including bracing, aeration, and storage of nutrients and water.

- ***Why do you suppose root hairs are not formed in the region of elongation?***

36.4 *Stems: Support for Above-Ground Organs*

Learning Outcomes

1. *List the potential products of an axillary bud.*
2. *Differentiate between cross sections of a monocot stem and a eudicot stem.*
3. *Describe three functions of modified stems.*

The supporting structure of a vascular plant's shoot system is the mass of stems that extend from the root system below ground into the air, often reaching great height. Stiff stems capable of rising upward against gravity are an ancient adaptation that allowed plants to move into terrestrial ecosystems.

Stems carry leaves and flowers and support the plant's weight

Like roots, stems contain the three types of plant tissue. Stems also undergo growth from cell division in apical and lateral meristems. The stem may be thought of as an axis from which other stems or organs grow. The shoot apical meristems are capable of producing these new stems and organs.

External stem structure

The shoot apical meristem initiates stem tissue and intermittently produces bulges (primordia) that are capable of developing into leaves, other shoots, or even flowers (figure 36.20).

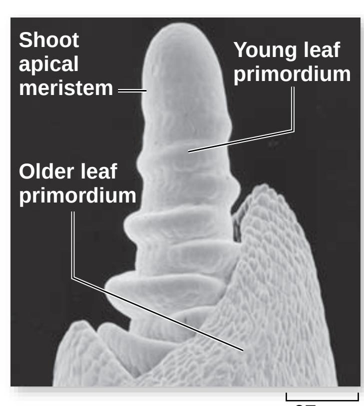


Figure 36.20 A shoot apex. Scanning electron micrograph of the apical meristem of wheat *(Triticum)*.

Leaves may be arranged in a spiral around the stem, or they may be in pairs opposite or alternate to one another; they also may occur in whorls (circles) of three or more (figure 36.21). The spiral arrangement is the most common, and for reasons still not understood, sequential leaves tend to be placed 137.5° apart. This angle relates to the golden mean, a mathematical ratio found in nature. The angle of coiling in shells of some gastropods is the same. The golden mean has been used in classical architecture (the Greek Parthenon wall dimensions), and even in modern art (for example, in paintings by Mondrian). In plants, this pattern of leaf arrangement, called **phyllotaxy,** may optimize the exposure of leaves to the sun.

The region or area of leaf attachment to the stem is called a **node;** the area of stem between two nodes is called an **internode.** A leaf usually has a flattened blade and sometimes a petiole (stalk). The angle between a leaf's petiole (or blade) and the stem is called an **axil.** An **axillary bud** is produced in each axil. This bud is a product of the primary shoot apical meristem, and it is itself a shoot apical meristem. Axillary buds frequently develop into branches with leaves or may form flowers.

Neither monocots nor herbaceous eudicot stems produce a cork cambium. The stems in these plants are usually green and photosynthetic, with at least the outer cells of the cortex containing chloroplasts. Herbaceous stems commonly have stomata, and may have various types of trichomes (hairs).

Woody stems can persist over a number of years and develop distinctive markings in addition to the original organs that form (figure 36.22). Terminal buds usually extend the length of the shoot system during the growing season. Some buds, such as those of geraniums, are unprotected, but most buds of woody plants have protective winter bud scales that drop off, leaving tiny bud scale scars as the buds expand.

Some twigs have tiny scars of a different origin. A pair of butterfly-like appendages called *stipules* (part of the leaf) develop at the base of some leaves. The stipules can fall off and leave stipule *scars.* When the leaves of deciduous trees drop in the fall, they leave leaf scars with tiny bundle scars, marking where vascular connections were. The shapes, sizes, and other features of leaf scars can be distinctive enough to identify deciduous plants in winter, when they lack leaves (see figure 36.22).

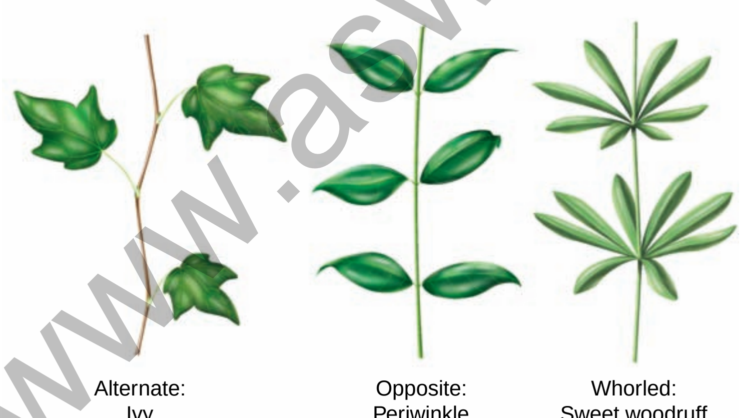


Figure 36.21 Types of leaf arrangements. The three common types of leaf arrangements are alternate, opposite, and whorled.

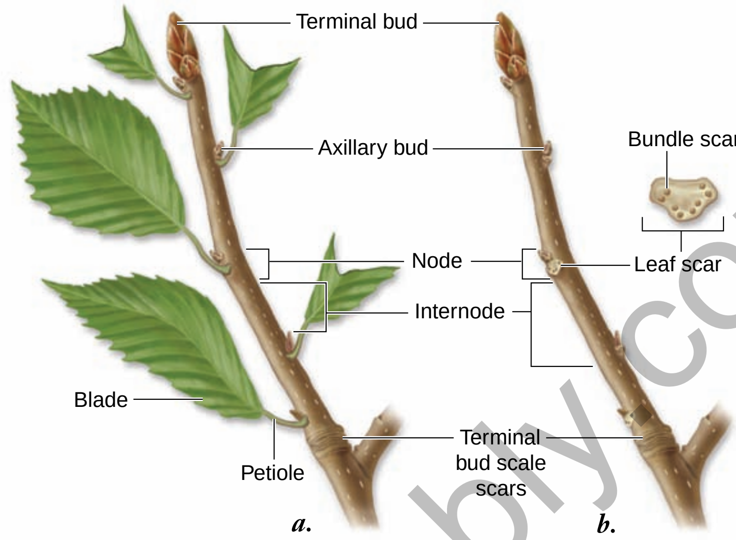


Figure 36.22 A woody twig. ***a.*** In summer. ***b.*** In winter.

Internal stem structure

A major distinguishing feature between monocot and eudicot stems is the organization of the vascular tissue system (figure 36.23). Most monocot vascular bundles are scattered throughout the ground tissue system, whereas eudicot vascular tissue is arranged in a ring with internal ground tissue *(pith)* and external ground tissues *(cortex).* The arrangement of vascular tissue is directly related to the ability of the stem to undergo

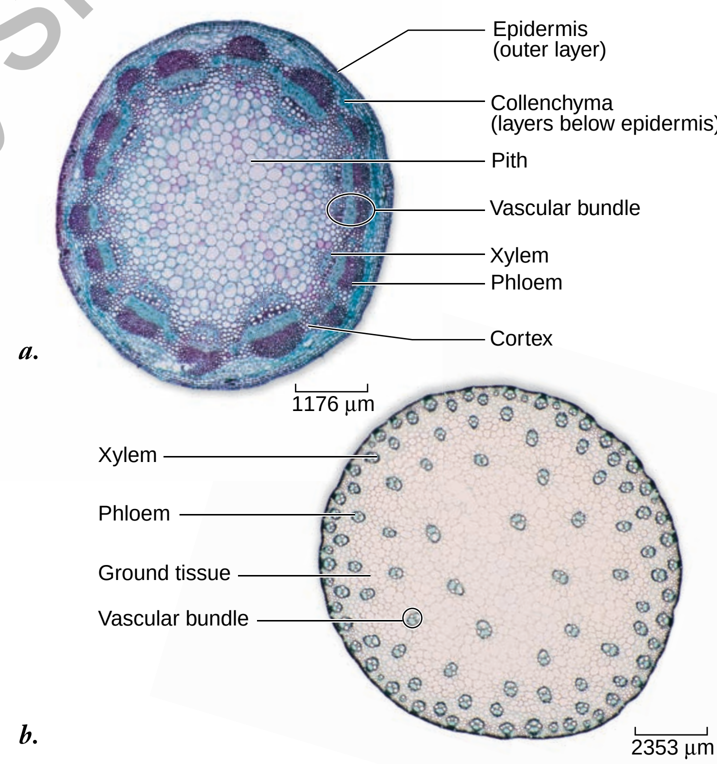


Figure 36.23 Stems. Transverse sections of a young stem in ***(a)*** a eudicot, the common sunflower *(Helianthus annuus),* in which the vascular bundles are arranged around the outside of the stem; and ***(b)*** a monocot, corn *(Zea mays),* with characteristically scattered vascular bundles.

secondary growth. In eudicots, a vascular cambium may develop between the primary xylem and primary phloem (figure 36.24). In many ways, this is a connect-the-dots game in which the vascular cambium connects the ring of primary vascular bundles. There is no logical way to connect primary monocot vascular tissue that would allow a uniform increase in girth. Lacking a vascular cambium, therefore, monocots do not have secondary growth.

Rings in the stump of a tree reveal annual patterns of vascular cambium growth; cell size varies, depending on growth conditions (figure 36.25). Large cells form under favorable conditions such as abundant rainfalls. Rings of smaller cells mark the seasons where growth is limited. In woody eudicots and gymnosperms, a second cambium, the cork cambium, arises in the outer cortex (occasionally in the epidermis or phloem); it produces boxlike cork cells to the outside and also may produce parenchyma-like phelloderm cells to the inside (figure 36.26).

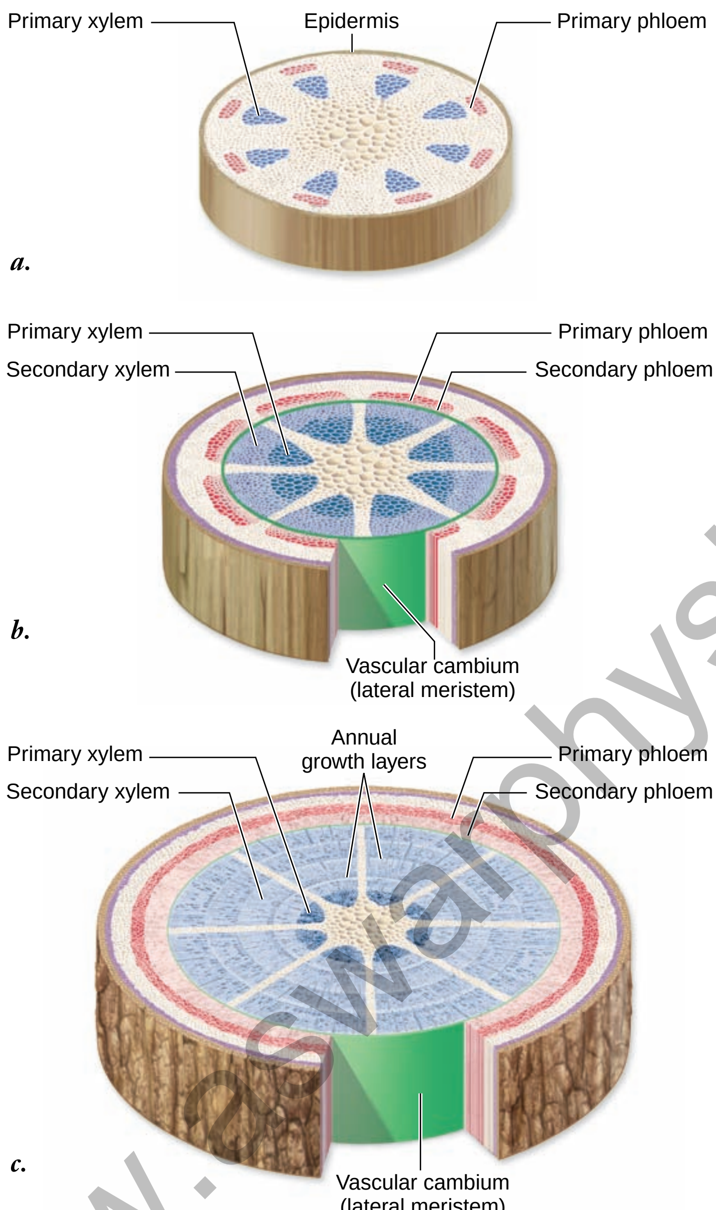


Figure 36.24 Secondary growth. ***a.*** Before secondary growth begins in eudicot stems, primary tissues continue to elongate as the apical meristems produce primary growth. ***b.*** As secondary growth begins, the vascular cambium produces secondary tissues, and the stem's diameter increases. ***c.*** In this four-year-old stem, the secondary tissues continue to widen, and the trunk has become thick and woody. Note that the vascular cambium forms a cylinder that runs axially (up and down) in the roots and shoots that have them.

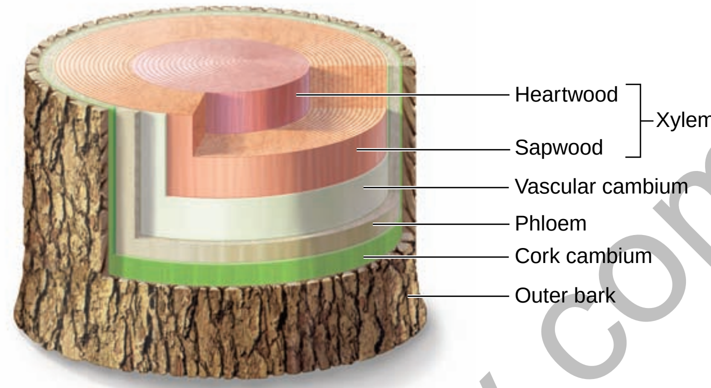


Figure 36.25 Tree stump. The vascular cambium produces rings of xylem (sapwood and nonconducting heartwood) and phloem, and the cork cambium produces the cork.

The cork cambium, cork, and phelloderm are collectively referred to as the *periderm* (see figure 36.26). Cork tissues, the cells of which become impregnated with water-repellent suberin shortly after they are formed and which then die, constitute the *outer bark*. The cork tissue cuts off water and food to the epidermis, which dies and sloughs off. In young stems, gas exchange between stem tissues and the air takes place through stomata, but as the cork cambium produces cork, it also produces patches of unsuberized cells beneath the stomata. These unsuberized cells, which permit gas exchange to continue, are called *lenticels* (figure 36.27).

Modified stems carry out vegetative propagation and store nutrients

Although most stems grow erect, some have modifications that serve special purposes, including natural vegetative propagation. In fact, the widespread artificial vegetative propagation of plants,

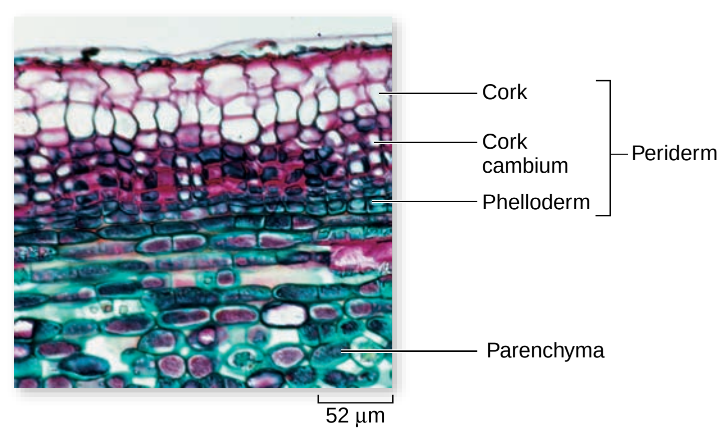


Figure 36.26 Section of periderm. An early stage in the development of periderm in cottonwood, *Populus* sp.

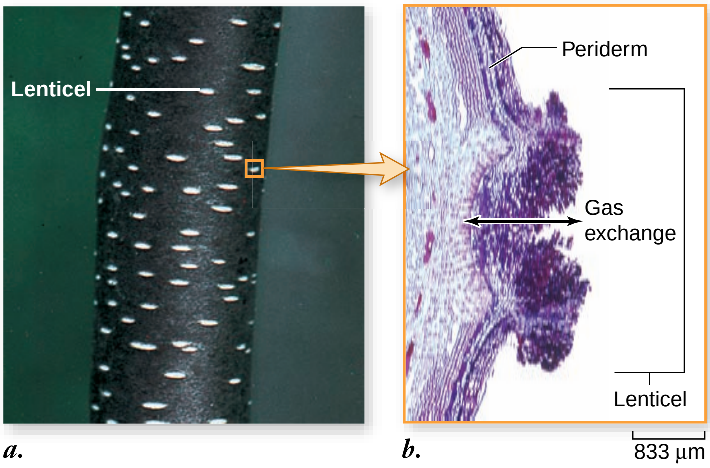


Figure 36.27 Lenticels. ***a.*** Lenticels, the numerous small, pale, raised areas shown here on cherry tree bark *(Prunus cerasifera)*, allow gas exchange between the external atmosphere and the living tissues immediately beneath the bark of woody plants. ***b.*** Transverse section through a lenticel in a stem of elderberry, *Sambucus canadensis*.

both commercial and private, frequently involves cutting modified stems into segments, which are then planted, producing new plants. As you become acquainted with the following modified stems, keep in mind that stems have leaves at nodes, with internodes between the nodes, and buds in the axils of the leaves, whereas roots have no leaves, nodes, or axillary buds.

Bulbs. Onions, lilies, and tulips have swollen underground stems that are really large buds with adventitious roots at the base (figure 36.28*a*). Most of a bulb consists of fleshy leaves attached to a small, knoblike stem. For most bulbs, next year's foliage comes from the tip of the shoot apex, protected by storage leaves from the previous year

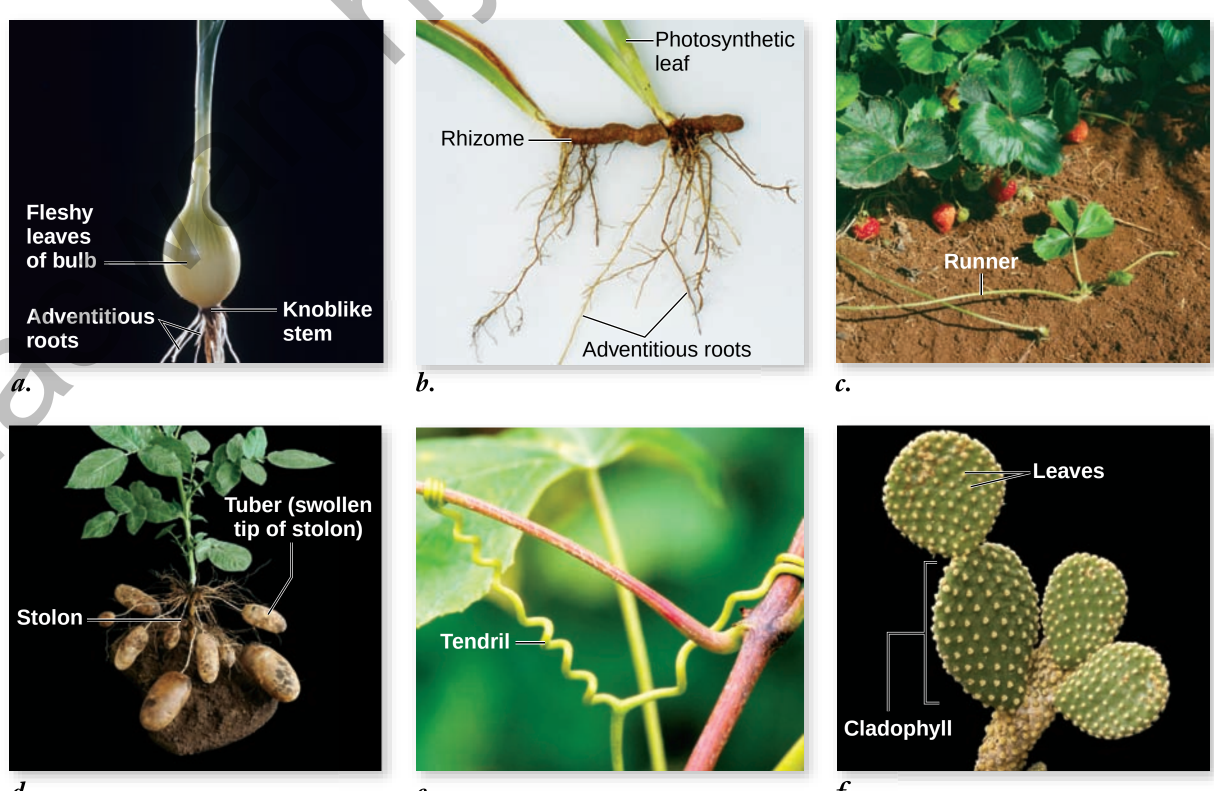
Corms. Crocuses, gladioluses, and other popular garden plants produce corms that superficially resemble bulbs. Cutting a corm in half, however, reveals no fleshy leaves. Instead, almost all of a corm consists of stem, with a few papery, brown nonfunctional leaves on the outside, and adventitious roots below.

Rhizomes. Perennial grasses, ferns, bearded iris, and many other plants produce rhizomes, which typically are horizontal stems that grow underground, often close to the surface (figure 36.28*b*). Each node has an inconspicuous scalelike leaf with an axillary bud; much larger photosynthetic leaves may be produced at the rhizome tip. Adventitious roots are produced throughout the length of the rhizome, mainly on the lower surface.

Runners and stolons. Strawberry plants produce horizontal stems with long internodes that unlike rhizomes, usually grow along the surface of the ground. Several runners may radiate out from a single plant (figure 36.28*c*). Some biologists use the term *stolon* synonymously with runner; others reserve the term *stolon* for a stem with long internodes (but no roots) that grows underground, as seen in potato plants (*Solanum* sp.). A potato itself, however, is another type of modified stem—a tuber.

Tubers. In potato plants, carbohydrates may accumulate at the tips of rhizomes, which swell, becoming tubers; the rhizomes die after the tubers mature (figure 36.28*d*). The "eyes" of a potato are axillary buds formed in the axils of scalelike leaves. These leaves, which are present when the potato is starting to form, soon drop off; the tiny ridge adjacent to each "eye" of a mature potato is a leaf scar.

Figure 36.28
Types of modified stems. ***a.*** Bulb.
b. Adventitious roots.
c. Runner. d. Stolon.
e. Tendril.
f. Cladophyll.



Crop potatoes are not grown from seeds produced by potato flowers, but propagated vegetatively from "seed potatoes." A tuber is cut up into pieces that contain at least one eye, and these pieces are planted. The eye then grows into a new potato plant.

Tendrils. Many climbing plants, such as grapes and English ivy, produce modified stems known as tendrils that twine around supports and aid in climbing (figure 36.28*e*). Some other tendrils, such as those of peas and pumpkins, are actually modified leaves or leaflets.

Cladophylls. Cacti and several other plants produce flattened, photosynthetic stems called cladophylls that resemble leaves (figure 36.28*f*). In cacti, the real leaves are modified as spines (see the following section).

Learning Outcomes Review 36.4

Shoots grow from apical and lateral meristems. Auxilliary buds may develop into branches, flowers, or leaves. In monocots, vascular tissue is evenly spaced throughout the stem ground tissue; in eudicots, vascular tissue is arranged in a ring with inner and outer ground tissues. Some plants produce modified stems for support, vegetative reproduction, or nutrient storage.

- ***Why don't stems produce the equivalent of root caps?***

36.5 *Leaves: Photosynthetic Organs*

Learning Outcomes

1. ***Distinguish between a simple and a compound leaf.***
2. ***Compare the mesophyll of a monocot leaf with that of a eudicot leaf.***

Leaves, which are initiated as primordia by the apical meristems (see figure 36.20), are vital to life as we know it because they are the principal sites of photosynthesis on land, providing the base of the food chain. Leaves expand by cell enlargement and cell division. Like arms and legs in humans, they are determinate structures, which means their growth stops at maturity. Because leaves are crucial to a plant, features such as their arrangement, form, size, and internal structure are highly significant and can differ greatly. Different patterns have adaptive value in different environments.

Leaves are an extension of the shoot apical meristem and stem development. When they first emerge as primordia, they are not committed to being leaves. Experiments in which very young leaf primordia are isolated from fern and coleus plants and grown in culture have demonstrated this feature: If the primordia are young enough, they will form an entire shoot rather than a leaf. The positioning of leaf primordia and the initial cell divisions occur before those cells are committed to the leaf developmental pathway.

External leaf structure reflects vascular morphology

Leaves fall into two different morphological groups, which may reflect differences in evolutionary origin. A **microphyll** is a leaf with one vein branching from the vascular cylinder of the stem and not extending the full length of the leaf; microphylls are mostly small and are associated primarily with the phylum Lycophyta (see chapter 30). Most plants have leaves called **megaphylls,** which have several to many veins.

Most eudicot leaves have a flattened **blade** and a slender stalk, the **petiole.** The flattening of the leaf blade reflects a shift from radial symmetry to dorsal–ventral (top–bottom) symmetry. Leaf flattening increases the photosynthetic surface. Plant biologists are just beginning to understand how this shift occurs by analyzing mutants lacking distinct tops and bottoms (figure 36.29).

In addition, leaves may have a pair of **stipules,** which are outgrowths at the base of the petiole. The stipules, which may be leaflike or modified as spines (as in the black locust, *Robinia pseudo-acacia*) or glands (as in the purple-leaf plum tree *Prunus cerasifera*), vary considerably in size from the microscopic to almost half the size of the leaf blade. Grasses and other monocot leaves usually lack a petiole; these leaves tend to sheathe the stem toward the base.

Veins (a term used for the vascular bundles in leaves) consist of both xylem and phloem and are distributed

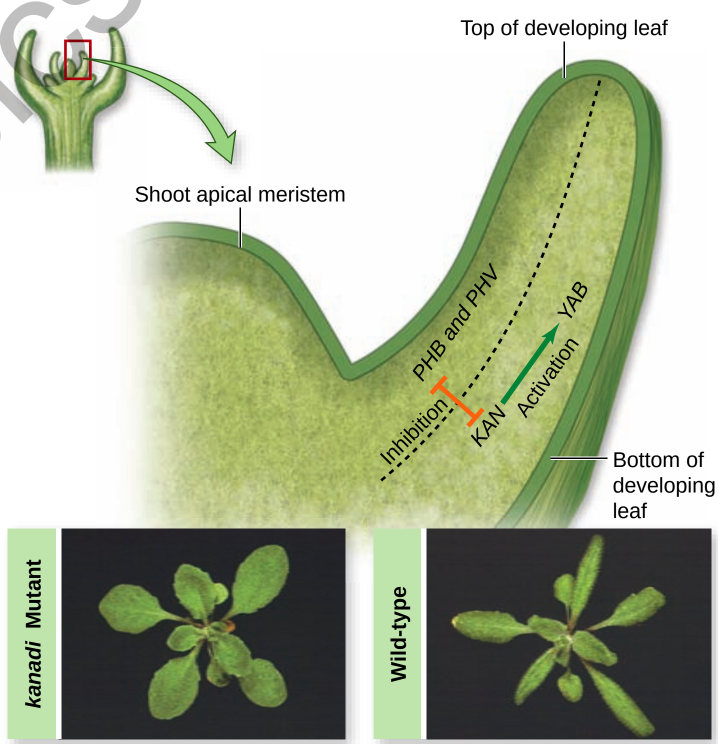
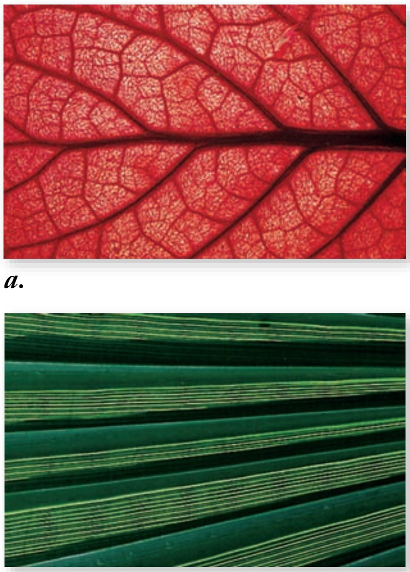


Figure 36.29 Establishing top and bottom in leaves. Several genes, including *PHABULOSA (PHB)*, *PHAVOLUTA (PHV)*, *KANADI (KAN)*, and *YABBY (YAB)* make a flattened *Arabidopsis* leaf with a distinct upper and lower surface. *PHB* and PHV RNAs are restricted to the top; *KAN* and *YAB* are expressed in the bottom cells of a leaf. PHB and KAN have an antagonistic relationship, restricting expression of each to separate leaf regions. *KAN* leads to *YABBY* expression and lower leaf development. Without *KAN*, both sides of the leaf develop like the top portion.



a.

b.

Figure 36.30 Eudicot and monocot leaves. ***a.*** The leaves of eudicots, such as this African violet relative from Sri Lanka, have netted, or reticulate, veins. ***b.*** Those of monocots, such as this cabbage palmetto, have parallel veins. The eudicot leaf has been cleared with chemicals and stained with a red dye to make the veins show more clearly.

throughout the leaf blades. The main veins are parallel in most monocot leaves; the veins of eudicots, on the other hand, form an often intricate network (figure 36.30).

Leaf blades come in a variety of forms, from oval to deeply lobed to having separate leaflets. In **simple leaves** (figure 36.31*a*), such as those of lilacs or birch trees, the blades are undivided, but simple leaves may have teeth, indentations, or lobes of various sizes, as in the leaves of maples and oaks.

In **compound leaves** (figure 36.31*b*), such as those of ashes, box elders, and walnuts, the blade is divided into *leaflets*. The relationship between the development of compound and simple leaves is an open question. Two explanations are being debated: (1) A compound leaf is a highly lobed simple leaf, or (2) a compound leaf utilizes a shoot development program, and each leaflet was once a leaf. To address this question, researchers are using single mutations that are known to convert compound leaves to simple leaves (figure 36.32).

a. *b.*

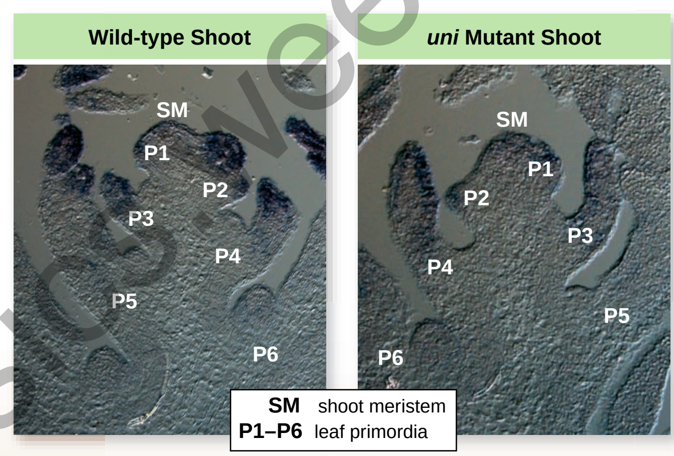
Figure 36.31 Simple versus compound leaves. ***a.*** A simple leaf, its margin deeply lobed, from the oak tree *(Quercus robur)*. ***b.*** A pinnately compound leaf, from a black walnut *(Juglans nigra)*. A compound leaf is associated with a single lateral bud, located where the petiole is attached to the stem.

SCIENTIFIC THINKING

Hypothesis: *The gene* UNIFOLIATA (UNI) *is necessary for compound leaf development in garden pea,* Pisum sativum.

Prediction: *Developing leaf primordia of a wild-type pea plant will express the* UNI *gene while* uni *mutant plants will not express the gene.*

Test: *Cut thin sections of wild-type and mutant pea shoots and place them on a microscope slide. Test for the presence of* UNI *RNA using a color-labeled, single-stranded DNA probe that will hybridize (bind) only the* UNI *RNA. View the labeled sections under a microscope.*



Result: UNI *RNA was found in the wild-type and also in mutant leaves, but at lower levels.*

Conclusion: *The mutant* uni *gene is transcribed but at lower levels than the wild-type gene. Thus the prediction was incorrect.*

Further Experiments: *Although the* uni *gene is expressed, compound leaves do not develop. Refine the hypothesis and propose an experiment to test the revised hypothesis.*

Figure 36.32 Genetic regulation of leaf development.

Internal leaf structure regulates gas exchange and evaporation

The entire surface of a leaf is covered by a transparent epidermis, and most of these epidermal cells have no chloroplasts. As described earlier, the epidermis has a waxy cuticle, and different types of glands and trichomes may be present. Also, the lower epidermis (and occasionally the upper epidermis) of most leaves contains numerous slitlike or mouth-shaped stomata flanked by guard cells (figure 36.33).

The tissue between the upper and lower epidermis is called **mesophyll.** Mesophyll is interspersed with veins of various sizes.

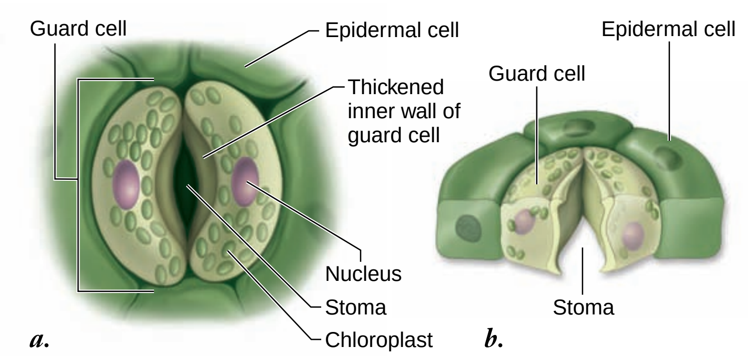


Figure 36.33 A stoma. ***a.*** Surface view. ***b.*** View in cross section.

Most eudicot leaves have two distinct types of mesophyll. Closest to the upper epidermis are one to several (usually two) rows of tightly packed, barrel-shaped to cylindrical chlorenchyma cells (parenchyma with chloroplasts) that constitute the palisade mesophyll (figure 36.34). Some plants, including species of *Eucalyptus*, have leaves that hang down, rather than extend horizontally. They have palisade mesophyll on both sides of the leaf.

Nearly all eudicot leaves have loosely arranged spongy mesophyll cells between the palisade mesophyll and the lower epidermis, with many air spaces throughout the tissue. The interconnected intercellular spaces, along with the stomata, function in gas exchange and the passage of water vapor from the leaves.

The mesophyll of monocot leaves often is not differentiated into palisade and spongy layers, and there is often little distinction between the upper and lower epidermis. Instead, cells surrounding the vascular tissue are distinctive and are the site of carbon fixation. This anatomical difference often correlates with a modified photosynthetic pathway, C_4 *photosynthesis*, that maximizes the amount of CO_2 relative to O_2 to reduce energy loss through photorespiration (see chapter 9). The anatomy of a leaf directly relates to its juggling act of balancing water loss, gas exchange, and transport of photosynthetic products to the rest of the plant.

Modified leaves are highly versatile organs

As plants colonized a wide variety of environments, from deserts to lakes to tropical rain forests, plant organ modifications arose that would adapt the plants to their specific habitats. Leaves, in particular, have evolved some remarkable adaptations. A brief discussion of a few of these modifications follows:

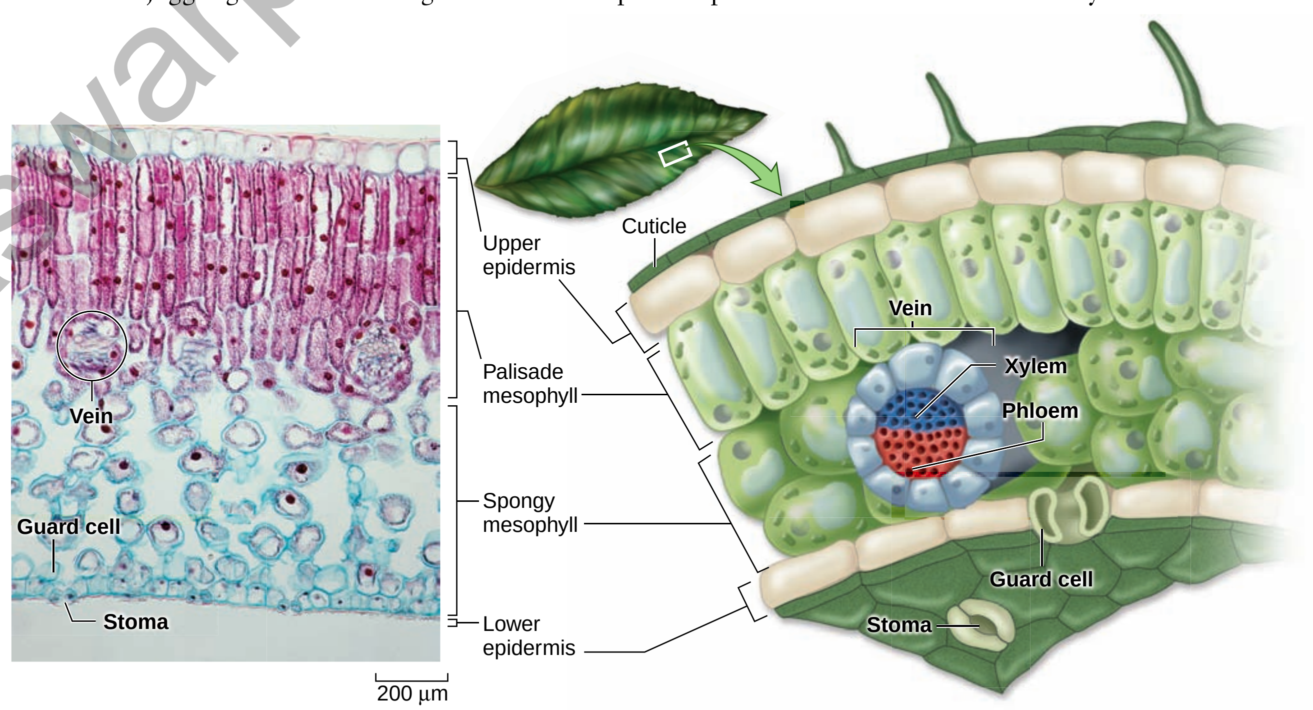
Floral leaves (bracts). Poinsettias and dogwoods have relatively inconspicuous, small, greenish yellow flowers. However, both plants produce large modified leaves called *bracts* (mostly colored red in poinsettias and white or pink in dogwoods). These bracts surround the true flowers and perform the same function as showy petals. In other plants, however, bracts can be quite small and inconspicuous.

Spines. The leaves of many cacti and other plants are modified as *spines* (see figure 36.28*f*). In cacti, having less leaf surface reduces water loss, and the sharp spines also may deter predators. Spines should not be confused with *thorns*, such as those on the honey locust *(Gleditsia triacanthos)*, which are modified stems, or with the prickles on raspberries, which are simply outgrowths from the epidermis or the cortex just beneath it.

Reproductive leaves. Several plants, notably *Kalanchoë*, produce tiny but complete plantlets along their margins. Each plantlet, when separated from the leaf, is capable of growing independently into a full-sized plant. The walking fern *(Asplenium rhizophyllum)* produces new plantlets at the tips of its fronds. Although many species can regenerate a whole plant from isolated leaf tissue, this in vivo regeneration is found among just a few species.

Window leaves. Several genera of plants growing in arid regions produce succulent, cone-shaped leaves with transparent tips. The leaves often become mostly buried

Figure 36.34 A leaf in cross section. Transection of a leaf showing the arrangement of palisade and spongy mesophyll, a vascular bundle or vein, and the epidermis with paired guard cells flanking the stoma.



in sand blown by the wind, but the transparent tips, which have a thick epidermis and cuticle, admit light to the hollow interiors. This strategy allows photosynthesis to take place beneath the surface of the ground.

Shade leaves. Leaves produced in the shade, where they receive little sunlight, tend to be larger in surface area, but thinner and with less mesophyll than leaves on the same tree receiving more direct light. This plasticity in development is remarkable. Environmental signals can have a major effect on development.

Insectivorous leaves. Almost 200 species of flowering plants are known to have leaves that trap insects; some plants digest the insects' soft parts. Plants with insectivorous leaves often grow in acid swamps that are deficient in needed elements or contain elements in forms not readily available to the plants; this inhibits the plants' capacities to maintain metabolic processes needed for their growth and reproduction. Their needs are met, however, by the supplementary absorption of nutrients from the animal kingdom.

Pitcher plants (for example, *Sarracenia*, *Darlingtonia*, or *Nepenthes* spp.) have cone-shaped leaves in which rainwater can accumulate. The insides of the leaves are very smooth, but stiff, downward-pointing hairs line the rim. An insect falling into such a leaf finds it very difficult to escape and eventually drowns. The leaf absorbs the nutrients released when bacteria, and in most species the plant's own digestive enzymes, decompose the insect bodies. Other plants, such as sundews *(Drosera)*, have glands that secrete sticky mucilage that traps insects, which are then digested by enzymes.

The Venus flytrap *(Dionaea muscipula)* produces leaves that look hinged at the midrib. When tiny trigger hairs on the leaf blade are stimulated by a moving insect, the two halves of the leaf snap shut, and digestive enzymes break down the soft parts of the trapped insect into nutrients that can be absorbed through the leaf surface. Nitrogen is the most common nutrient needed. Curiously, the Venus flytrap cannot survive in a nitrogen-rich environment, perhaps as a result of a biochemical trade-off during the intricate evolutionary process that developed its ability to capture and digest insects.

Learning Outcomes Review 36.5

Leaves come in a range of forms. A simple leaf is undivided, whereas a compound leaf has a number of separate leaflets. Pinnate leaves have a central rib like a feather; palmate leaves have several ribs radiating from a central point, like the palm of the hand. Monocots typically produce leaves with parallel veins, while those of eudicots are netted. Mesophyll cells carry out photosynthesis; in monocots, mesophyll is undifferentiated, whereas in eudicots it is divided into palisade and spongy mesophyll. Leaves may be modified for reproduction, protection, water conservation, uptake of nutrients, and even as traps for insects.

- ***Why would a plant with vertically oriented leaves produce palisade, but not spongy mesophyll cells?***

Chapter Review

36.1 Organization of the Plant Body: An Overview

Vascular plants have roots and shoots.

The root system is primarily below ground; roots anchor the plant and take up water and minerals. The shoot system is above ground and provides support for leaves and flowers.

Roots and shoots are composed of three types of tissues.

The three types of tissues are dermal tissue, ground tissue, and vascular tissue.

Meristems elaborate the body plan throughout the plant's life.

Apical meristems are located on the tips of stems and near the tips of roots. Lateral meristems are found in plants that exhibit secondary growth. They add to the diameter of a stem or root.

36.2 Plant Tissues

Dermal tissue forms a protective interface with the environment.

Dermal tissue is primarily the epidermis, which is usually one cell thick and is covered with a fatty or waxy cuticle to retard water loss.

Guard cells in the epidermis control water loss through stomata. Root hairs are epidermal cell structures that help increase the absorptive area of roots.

Ground tissue cells perform many functions, including storage, photosynthesis, and support.

Ground tissue is mainly composed of parenchyma cells, which function in storage, photosynthesis, and secretion. Collenchyma cells provide flexible support, and sclerenchyma cells provide rigid support.

Vascular tissue conducts water and nutrients throughout the plant.

Xylem tissue conducts water through dead cells called tracheids and vessel elements.

Phloem tissue conducts nutrients such as dissolved sucrose through living cells called sieve-tube members and sieve cells.

36.3 Roots: Anchoring and Absorption Structures

Roots evolved after shoots and are a major innovation for terrestrial living.

Roots are adapted for growing underground and absorbing water and solutes.

Developing roots exhibit four regions: (1) the root cap, which protects the root; (2) the zone of cell division, which contains the apical meristem; (3) the zone of elongation, which extends the root through the soil; and (4) the zone of maturation, in which cells become differentiated.

Modified roots accomplish specialized functions.

Most plants produce either a taproot system containing a single large root with smaller branch roots, or a fibrous root system composed of many small roots.

Adventitious roots may be modified for support, stability, acquisition of oxygen, storage of water and food, or parasitism of a host plant.

36.4 Stems: Support for Above-Ground Organs

Stems carry leaves and flowers and support the plant's weight.

Leaves are attached to stems at nodes. The axil is the area between the leaf and stem, and an axillary bud develops in axils of eudicots.

The vascular bundles in stems of monocots are randomly scattered, whereas in eudicots the bundles are arranged in a ring.

Vascular cambium develops between the inner xylem and the outer phloem, allowing for secondary growth.

Modified stems carry out vegetative propagation and store nutrients.

Bulbs, corms, rhizomes, runners and stolons, tubers, tendrils, and cladophylls are examples of modified stems. The tubers of potatoes are both a food source and a means of propagating new plants.

36.5 Leaves: Photosynthetic Organs

Leaves are the principle sites of photosynthesis. Leaf features such as their arrangement, form, size, and internal structure can be highly variable across environments.

External leaf structure reflects vascular morphology.

Vascular bundles are parallel in monocots, but form a network in eudicots. The leaves of most eudicots have a flattened blade and a slender petiole; monocots usually do not have a petiole.

Leaf blades may be simple or compound (divided into leaflets). Leaves may also be pinnate (with a central rib, like a feather) or palmate (with ribs radiating from a central point).

Internal leaf structure regulates gas exchange and evaporation.

The tissues of the leaf include the epidermis with guard cells, vascular tissue, and mesophyll in which photosynthesis takes place.

In eudicot leaves with a horizontal orientation, the mesophyll is partitioned into palisade cells near the upper surface and spongy cells near the lower surface.

The mesophyll of monocot leaves is often not differentiated.

Modified leaves are highly versatile organs.

Leaves are highly variable in form and are adapted to serve many different functions. Leaves may be modified for reproduction, protection, storage, mineral uptake, or even as insect traps in carnivorous plants.

Review Questions

UNDERSTAND

1. Which cells lack living protoplasts at maturity?
   a. Parenchyma
   b. Companion
   c. Collenchyma
   d. Sclerenchyma
2. The food-conducting cells in an oak tree are called
   a. tracheids.
   b. vessels.
   c. companion cells.
   d. sieve-tube members.
3. Root hairs form in the zone of
   a. cell division.
   b. elongation.
   c. maturation.
   d. more than one of the above
4. Roots differ from stems because roots lack
   a. vessel elements.
   b. nodes.
   c. an epidermis.
   d. ground tissue.
5. A plant that produces two axillary buds at a node is said to have what type of leaf arrangement?
   a. Opposite
   b. Alternate
   c. Whorled
   d. Palmate
6. Unlike eudicot stems, monocot stems lack
   a. vascular bundles.
   b. parenchyma.
   c. pith.
   d. epidermis.
7. The function of guard cells is to
   a. allow carbon dioxide uptake.
   b. repel insects and other herbivores.
   c. support leaf tissue.
   d. allow water uptake.
8. Palisade and spongy parenchyma are typically found in the mesophyll of
   a. monocots.
   b. eudicots.
   c. monocots and eudicots.
   d. neither monocots or eudicots
9. In vascular plants, one difference between root and shoot systems is that:
   a. root systems cannot undergo secondary growth.
   b. root systems undergo secondary growth, but do not form bark.
   c. root systems contain pronounced zones of cell elongation, whereas shoot systems do not.
   d. root systems can store food reserves, whereas stem structures do not.
10. Which of the following statements is not true of the stems of vascular plants?
    a. Stems are composed of repeating segments, including nodes and internodes.
    b. Primary growth only occurs at the shoot apical meristem.
    c. Vascular tissues may be arranged on the outside of the stem or scattered throughout the stem.
    d. Stems can contain stomata.
11. Which of the following plant cell type is mismatched to its function?
    a. Xylem—conducts mineral nutrients
    b. Phloem—serves as part of the bark
    c. Trichomes—reduces evaporation
    d. Collenchyma—performs photosynthesis

APPLY

1. Fifteen years ago, your parents hung a swing from the lower branch of a large tree growing in your yard. When you go and sit in it today, you realize it is exactly the same height off the ground as it was when you first sat in it 15 years ago. The reason the swing is not higher off the ground as the tree has grown is that
   a. the tree trunk lacks secondary growth.
   b. the tree trunk is part of the primary growth system of the plant, but elongation is no longer occurring in that part of the tree.
   c. trees lack apical meristems and so do not get taller.
   d. you are hallucinating, because it is impossible for the swing not to have been raised off the ground as the tree grew.
2. A unique feature of plants is indeterminate growth. Indeterminate growth is possible because
   a. meristematic regions for primary growth occur throughout the entire plant body.
   b. all cell types in a plant often give rise to meristematic tissue.
   c. meristematic cells continually replace themselves.
   d. all cells in a plant continue to divide indefinitely.
3. If you were to relocate the pericycle of a plant root to the epidermal layer, how would it affect root growth?
   a. Secondary growth in the mature region of the root would not occur.
   b. The root apical meristem would produce vascular tissue in place of dermal tissue.
   c. Nothing would change because the pericycle is normally located near the epidermal layer of the root.
   d. Lateral roots would grow from the outer region of the root and fail to connect with the vascular tissue.
4. Many vegetables are grown today through hydroponics, in which the plant roots exist primarily in an aqueous solution. Which of the following root structures is no longer beneficial in hydroponics?
   a. Epidermis
   b. Xylem
   c. Root cap
   d. Bark
5. When you peel your potatoes for dinner, you are removing the majority of their
   a. dermal tissue.
   b. vascular tissue.
   c. ground tissue.
   d. Only (a) and (b) are removed with the peel.
   e. All of these are removed with the peel.
6. You can determine the age of an oak tree by counting the annual rings of _____________ formed by the ___________.
   a. primary xylem; apical meristem
   b. secondary phloem; vascular cambium
   c. dermal tissue; cork cambium
   d. secondary xylem; vascular cambium
7. Root hairs and lateral roots are similar in each respect except
   a. both increase the absorptive surface area of the root system.
   b. both are generally long-lived.
   c. both are multicellular.
   d. (b) and (c).
8. Plant organs form by
   a. cell division in gamete tissue.
   b. cell division in meristematic tissue.
   c. cell migration into the appropriate position in the tissue.
   d. eliminating chromosomes in the precursor cells.
9. Which is the correct sequence of cell types encountered in an oak tree, moving from the center of the tree out?
   a. Pith, secondary xylem, primary xylem, vascular cambium, primary phloem, secondary phloem, cork cambium, cork.
   b. Pith, primary xylem, secondary xylem, vascular cambium, secondary phloem, primary phloem, cork cambium, cork
   c. Pith, primary xylem, secondary xylem, vascular cambium, secondary phloem, primary phloem, cork, cork cambium
   d. Pith, primary phloem secondary phloem, vascular cambium, secondary xylem, primary xylem, cork cambium, cork.
10. You've just bought a house with a great view of the mountains, but you have a neighbor who planted a bunch of trees that are now blocking your view. In an attempt to ultimately remove the trees and remain unlinked to the deed, you begin training several porcupines to enter the yard under the cover of night and perform a stealth operation. In order to most effectively kill the trees, you should train the porcupines to completely remove
    a. the vascular cambium.
    b. the cork.
    c. the cork cambium.
    d. the primary phloem.

SYNTHESIZE

1. If you were given an unfamiliar vegetable, how could you tell if it was a root or a stem, based on its external features and a microscopic examination of its cross section?
2. Potato tubers harvested from wet soil often have large lenticels. What is the adaptive significance of this?
3. Plant organs undergo many modifications to deal with environmental challenges. Design an imaginary, modified root, shoot, or leaf, and make a case for why it is the best example of a modified plant organ.
4. You have identified a mutant maize plant that cannot differentiate vessel cells. How would this affect the functioning of the plant?
5. Increasing human population on the planet is stretching our ability to produce sufficient food to support the world's population. If you could engineer the perfect crop plant, what features might it possess?

CHAPTER 37

Chapter 37

Vegetative Plant Development

Chapter Outline

Introduction

How does a fertilized egg develop into a complex adult plant body? Because plant cells cannot move, the timing and directionality of each cell division must be carefully orchestrated. Cells need information about their location relative to other cells so that cell specialization is coordinated. The developing embryo is quite fragile, and numerous protective structures have evolved since plants first colonized land.

Only a portion of the plant has actually formed when its seedling first emerges from the soil. New plant organs develop throughout the plant's life.

37.1 *Embryo Development*

Learning Outcomes

1. *Name the two axes of the plant body that are established during embryonic development.*
2. *List the three tissue systems that develop in an embryo.*
3. *Describe the three critical events that must accompany seed development.*

Embryo development begins once the egg cell is fertilized. As described briefly in chapter 30, the growing pollen tube from a pollen grain enters the angiosperm embryo sac through one of the synergids, releasing two sperm cells (figure 37.1). One sperm cell fertilizes the central cell with its polar nuclei, and the resulting cell division produces a nutrient source, the **endosperm,** for the embryo. The other sperm cell fertilizes the egg to produce a zygote, and cell division soon follows, creating the **embryo.**

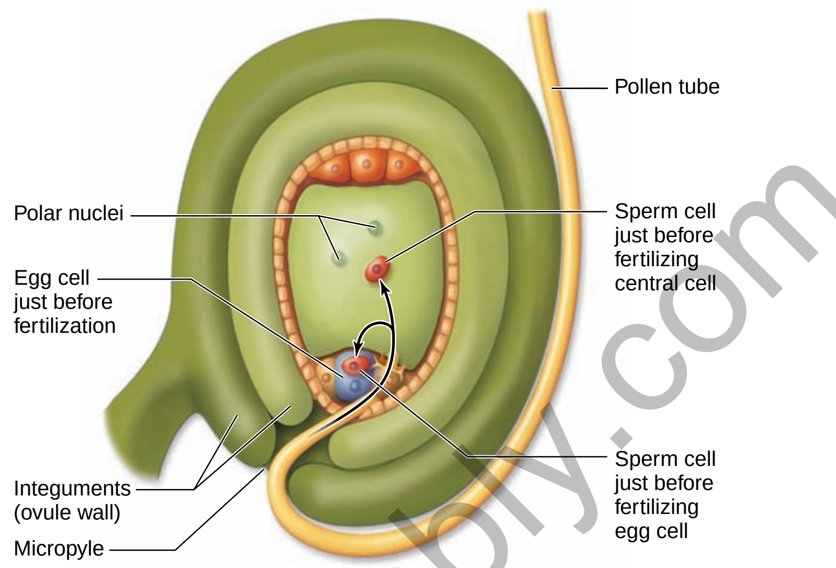


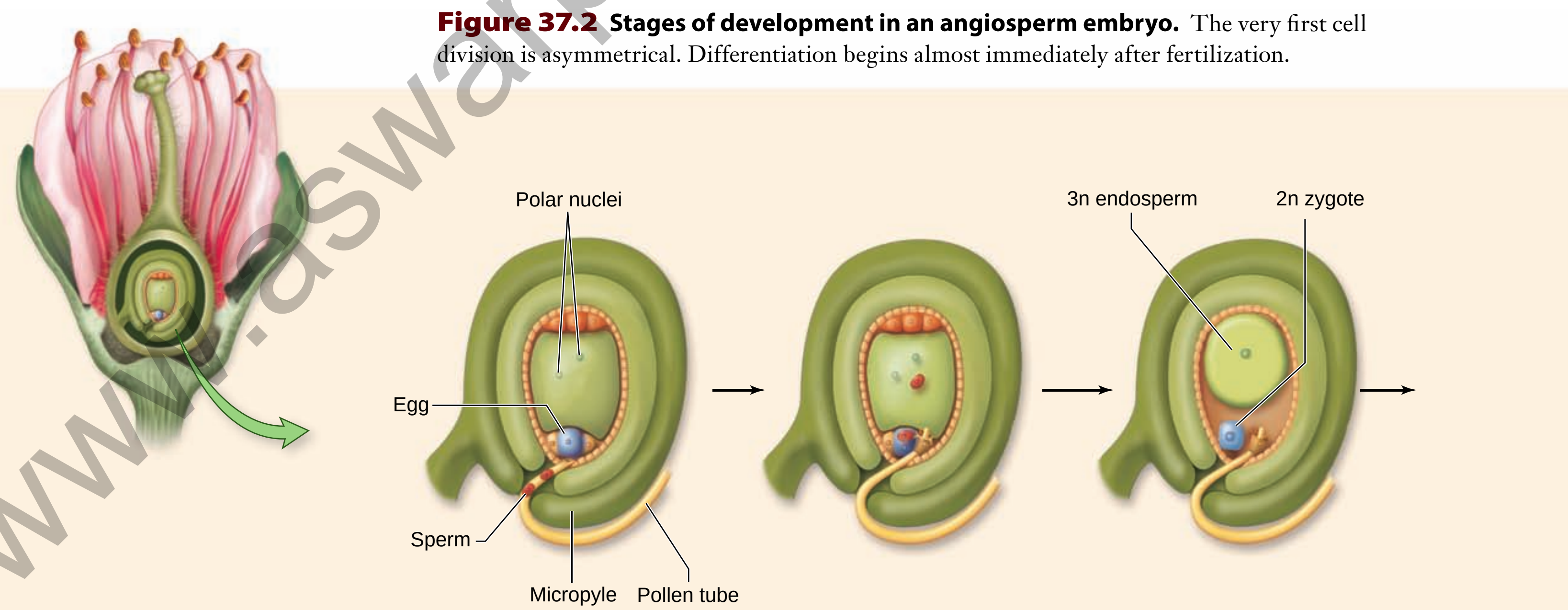
Figure 37.1 Fertilization triggers embryogenesis. The egg cell, within the embryo sac, is fertilized by one sperm cell released from the pollen tube. The second sperm cell fertilizes the central cell and initiates endosperm development. This diagram shows sperm just before fertilization.

A single cell divides to produce a three-dimensional body plan

The first division of the zygote (fertilized egg) in a flowering plant is asymmetrical and generates cells with two different fates (figure 37.2). One daughter cell is small, with dense cytoplasm. That cell, which is destined to become the embryo, begins to divide repeatedly in different planes, forming a ball of cells. The other, larger daughter cell divides repeatedly, forming an elongated structure called a **suspensor,** which links the embryo to the nutrient tissue of the seed. The suspensor also provides a route for nutrients to reach the developing embryo. The root–shoot axis also forms at this time; cells near the suspensor are destined to form a root, while those at the other end of the axis ultimately become a shoot.

Investigating mechanisms for establishing asymmetry in plant embryo development is difficult because the zygote is embedded within the female gametophyte, which is surrounded by sporophyte tissue (ovule and carpel tissue) (see chapter 30). To understand the cell biology of the first asymmetrical division of zygotes, biologists have studied the brown alga *Fucus.* We must be cautious about inferring too much about angiosperm asymmetrical divisions from the brown algae because the last common ancestor of brown algae and the angiosperm line was a single-celled organism. Nevertheless,

Figure 37.2 Stages of development in an angiosperm embryo. The very first cell division is asymmetrical. Differentiation begins almost immediately after fertilization.



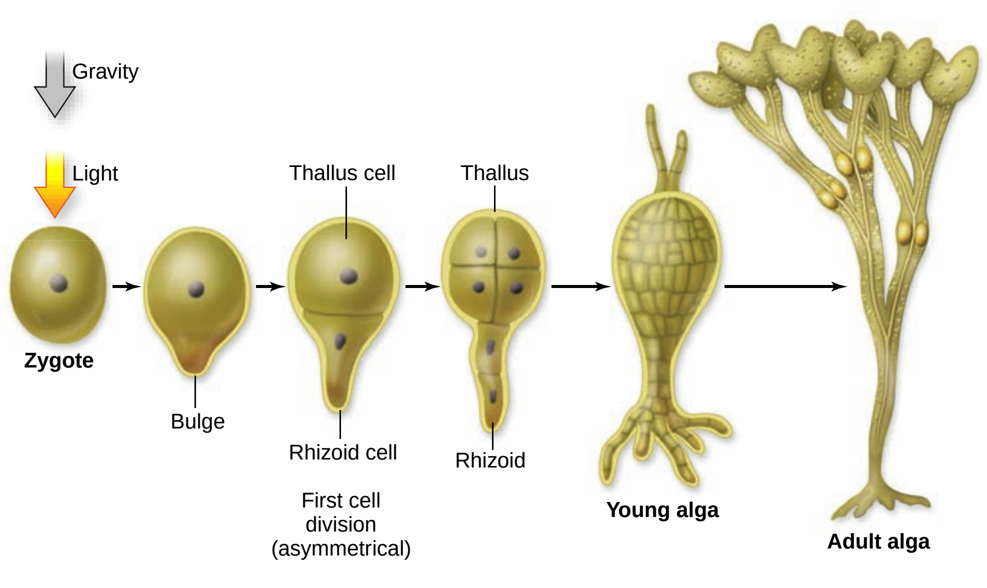


Figure 37.3 Asymmetrical cell division in a *Fucus* zygote. An unequal distribution of material in the zygote leads to a bulge where the first cell division will occur. This division results in a smaller cell that will go on to divide and produce the rhizoid that anchors the alga; the larger cell divides to form the thallus, or main algal body. The point of sperm entry determines where the smaller rhizoid cell will form, but light and gravity can modify this to ensure that the rhizoid will point downward where it can anchor this brown alga. Calcium-mediated currents set up an internal gradient of charged molecules, which leads to a weakening of the cell wall where the rhizoid will form. The fate of the two resulting cells is held "in memory" by cell wall components.

asymmetrical division extends far back in the tree of life. Even prokaryotes can divide asymmetrically

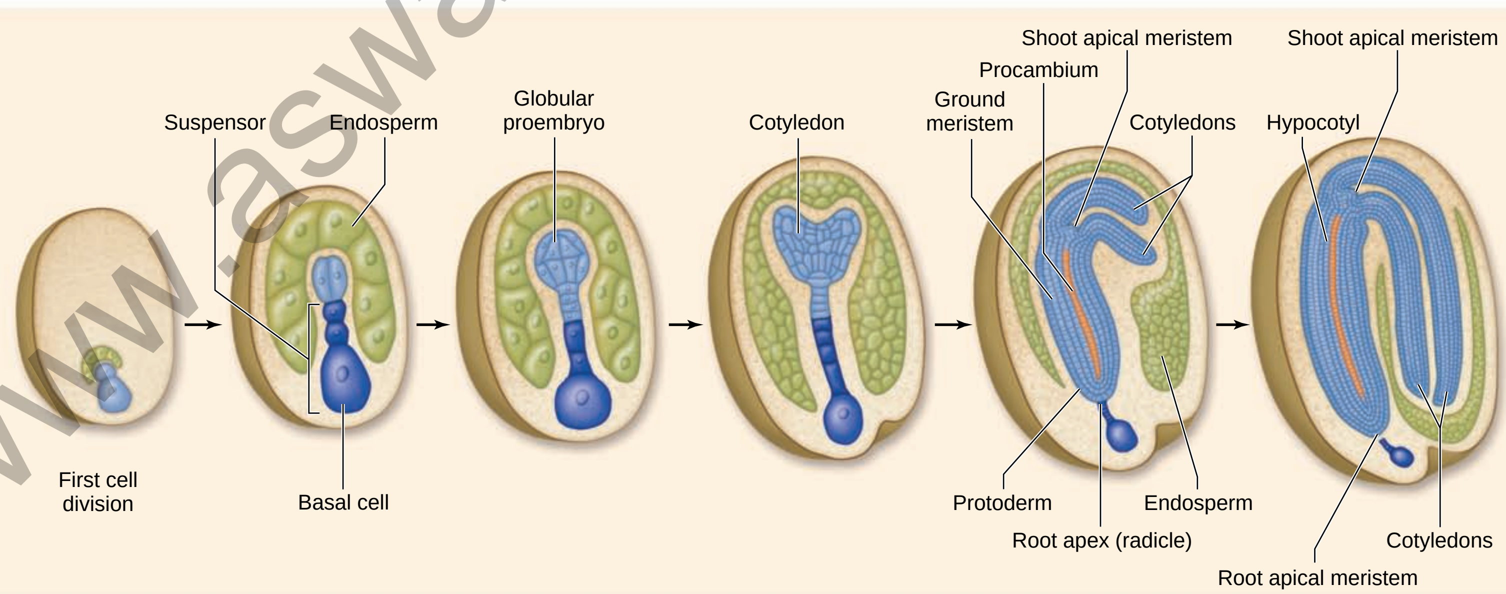
Zygote development in Fucus

In the brown alga *Fucus*, the egg is released prior to fertilization, so no extra tissues surround the zygote, making its development easier to observe. A bulge that develops on one side of the zygote establishes the vertical axis. Cell division occurs, and the original bulge becomes the smaller of the two daughter cells. The smaller cell develops into a rhizoid that anchors the alga, and the larger cell develops into the main body, or thallus, of the sporophyte (figure 37.3).

This axis is first established by the point of sperm entry, but it can be changed by environmental signals, especially light and gravity, which ensure that the rhizoid attaches to a solid base and the thallus is oriented toward a light source. Internal gradients are established that specify where the rhizoid forms in response to environmental signals.

Establishing asymmetry in angiosperms

Genetic approaches make it possible to explore asymmetrical development in angiosperms. Studies of mutants reveal what can go wrong in development, which often makes it possible to infer normal developmental mechanisms. For example, the suspensor mutant in *Arabidopsis thaliana* undergoes aberrant development in the embryo followed by embryo-like development of the suspensor (figure 37.4). Analysis of this mutant led to the conclusion that the presence of the embryo normally prevents the suspensor from developing into a second embryo.



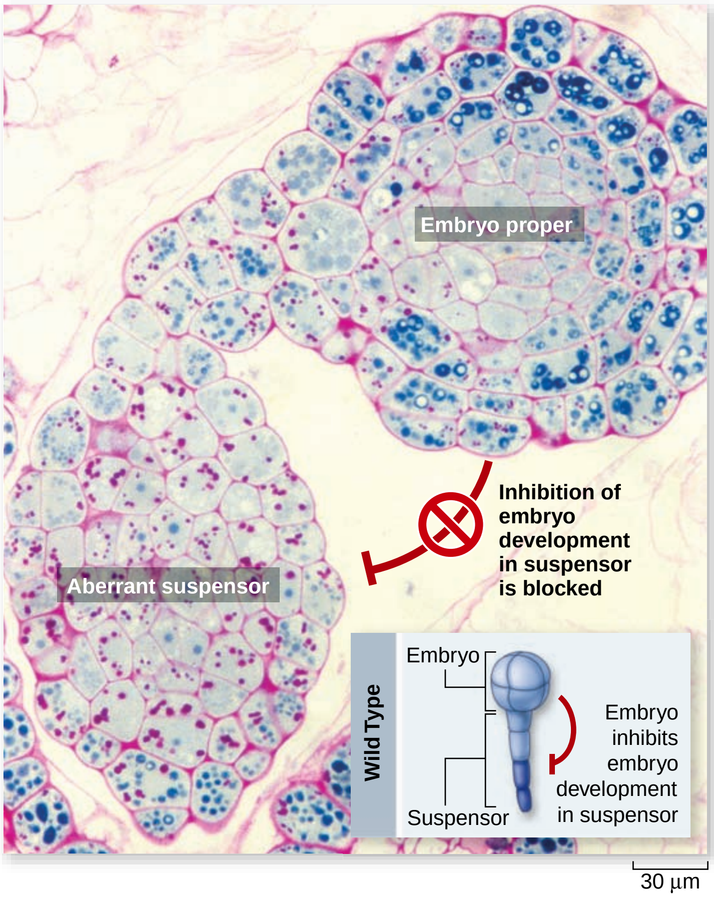


Figure 37.4 The embryo suppresses development of the suspensor as a second embryo. This *suspensor (sus)* mutant of *Arabidopsis* has a defect in embryo development. Aborted embryo development is followed by embryo-like development of the suspensor. *SUS* is required to suppress embryo development in suspensor cells.

A simple body plan emerges during embryogenesis

In plants, three-dimensional shape and form arise by regulating the amount and the pattern of cell division. We have just described how a vertical axis (root–shoot axis) becomes established at a very early stage; the same is true for establishment of a radial axis (inner–outer axis) (figure 37.5). Although the first cell division gives rise to a single row of cells, cells soon begin dividing in different directions, producing a three-dimensional solid ball of cells. The root–shoot axis lengthens as cells divide. New cell walls form perpendicular to the root–shoot axis, stacking new cells along the root–shoot axis.

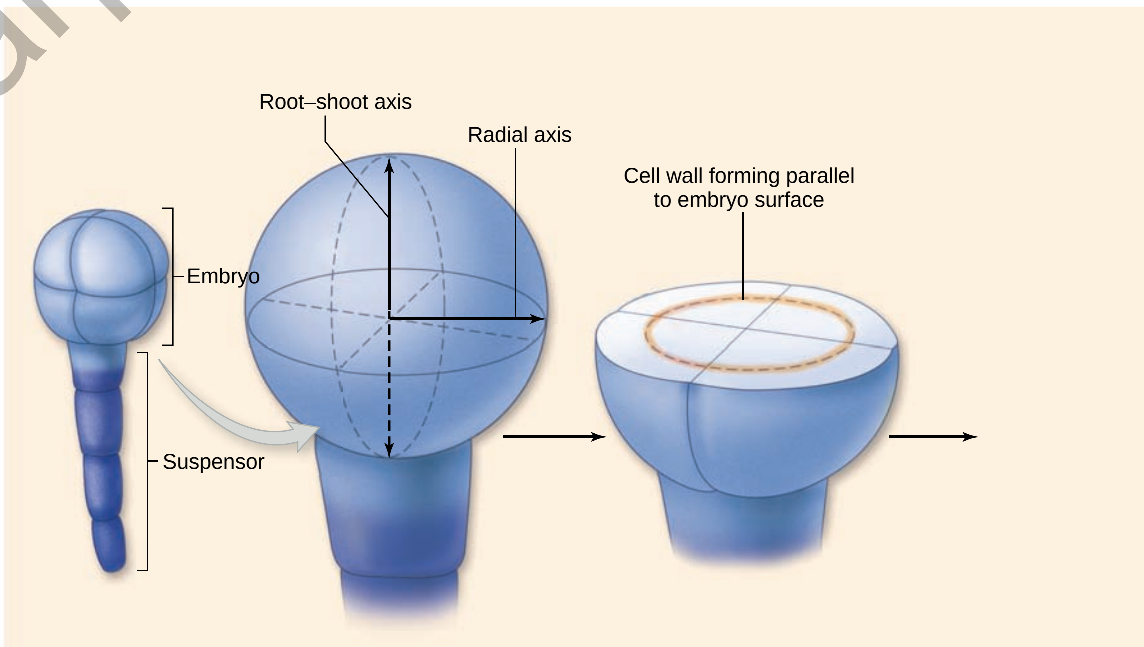
The cells must divide in two directions in the radial plane in order to maintain proper three dimensional shape in early development. The body plan that emerges is shown in figure 37.6. Apical meristems, the actively dividing cell regions at the tips of roots and shoots, establish the root–shoot axis in the globular stage, from which the three basic tissue systems arise: *dermal*, *ground*, and *vascular* tissue (see chapter 36). These tissues are organized radially around the root–shoot axis.

Root and shoot formation

Both the shoot and root meristems are apical meristems, but their formation is controlled independently. Shoot formation requires the *SHOOTMERISTEMLESS (STM)* gene in *Arabidopsis*. Plants that do not make STM protein fail to produce viable shoots, but do produce roots (figure 37.7).

The *STM* gene codes for a transcription factor with a homeobox region, sharing a common evolutionary origin with the *Hox* genes that are important in establishing animal body plans (see chapters 19 and 25). Compared with animals, however, *Hox*-like genes have a more limited role in regulating plant body plans. Other gene families, encoding different transcription factors, also play key roles in patterning in plants.

Figure 37.5 Two axes are established in the developing embryo. The root–shoot axis is vertical, and the radial axis creates a two-dimensional plane perpendicular to the root–shoot axis. The ends of the root–shoot axis become the root and shoot apical meristems. Three tissue systems develop around the radial axis. Embryos form concentric rings of cells around the root–shoot axis by regulating the planes of cell division. Early in embryogenesis cells alternate between coordinated divisions that produce new cell walls parallel to the plane containing the radial axis and cell divisions that produce new cell walls perpendicular to the plane containing the raidal axis. The orange lines show the formation of new cell walls. The diagram shows one plane of cells parallel to the ground. Cell divisions are also adding cells above and below this plane as the root–shoot axis lengthens.



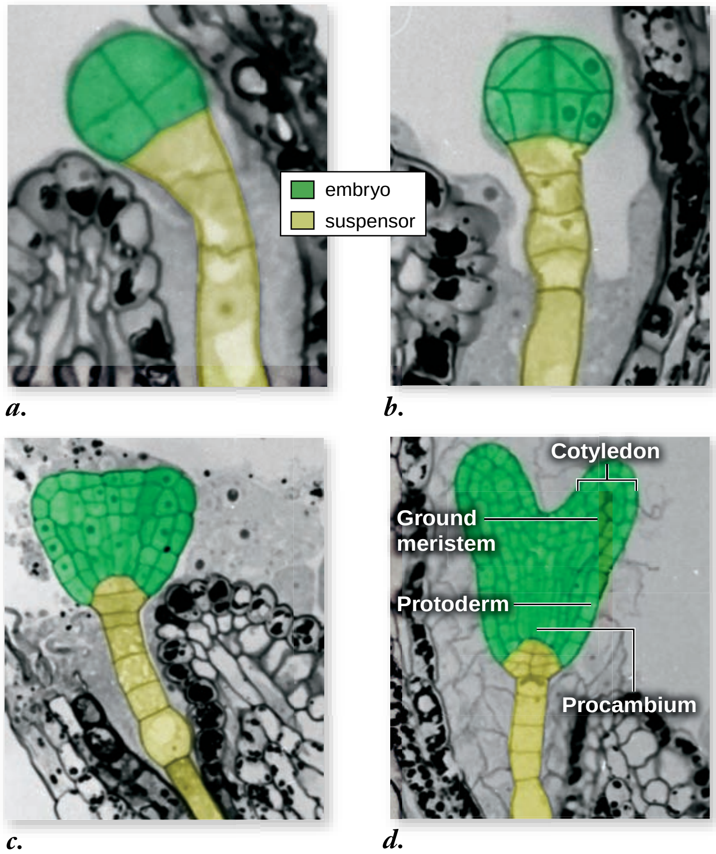


Figure 37.6 Early developmental stages of *Arabidopsis thaliana*. ***a.*** Early cell division has produced the embryo and suspensor. ***b.*** Globular stage results from cell divisions along both the root–shoot and radial axes. Cell differentiation, including establishment of the root and shoot apical meristems occurs at this stage. ***c, d.*** Heart-shaped stage. The cotyledons (seed leaves) are now visible, and the three tissue systems continue to differentiate.

Figure 37.7 *SHOOTMERISTEMLESS* is needed for shoot formation. Shoot-specific genes specify formation of the shoot apical meristem, but are not necessary for root development. The *stm* mutant of *Arabidopsis* (shown on top) has a normal root meristem but fails to produce a shoot meristem between its two cotyledons. The *STM* wild type is shown below the *stm* mutant for comparison.

Root formation requires the *HOBBIT* gene in *Arabidopsis* (figure 37.8). The *hobbit* mutants form shoot meristems, but no root meristems form. Cell divisions in *hobbit* roots occur in the wrong directions. Plants with a *hobbit* mutation accumulate a biochemical repressor of genes that are induced by auxin (a plant hormone). Based on the mutant phenotype, *HOBBIT* appears to repress the production of the repressor of auxin-induced genes. Or, more simply stated, HOBBIT protein allows auxin to induce the expression of a gene or genes needed for correct cell division to make a root meristem. Auxin is one of seven classes of hormones that regulate plant development and

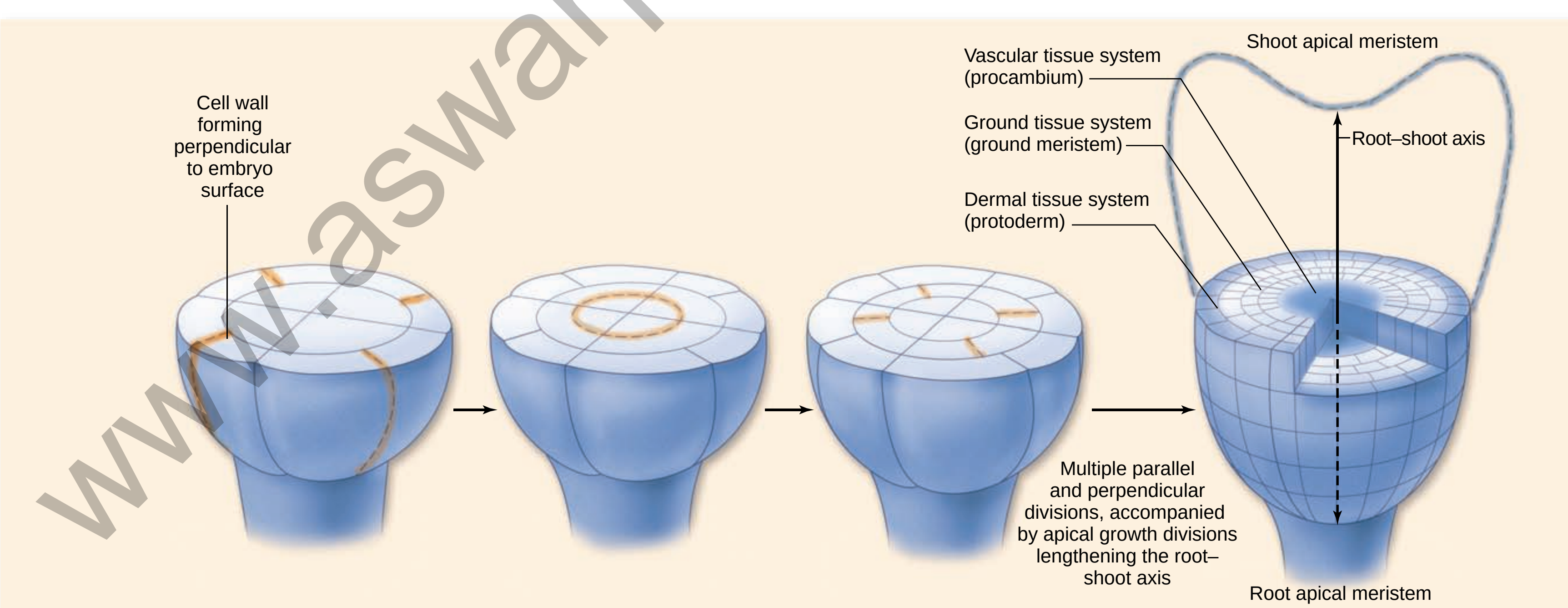
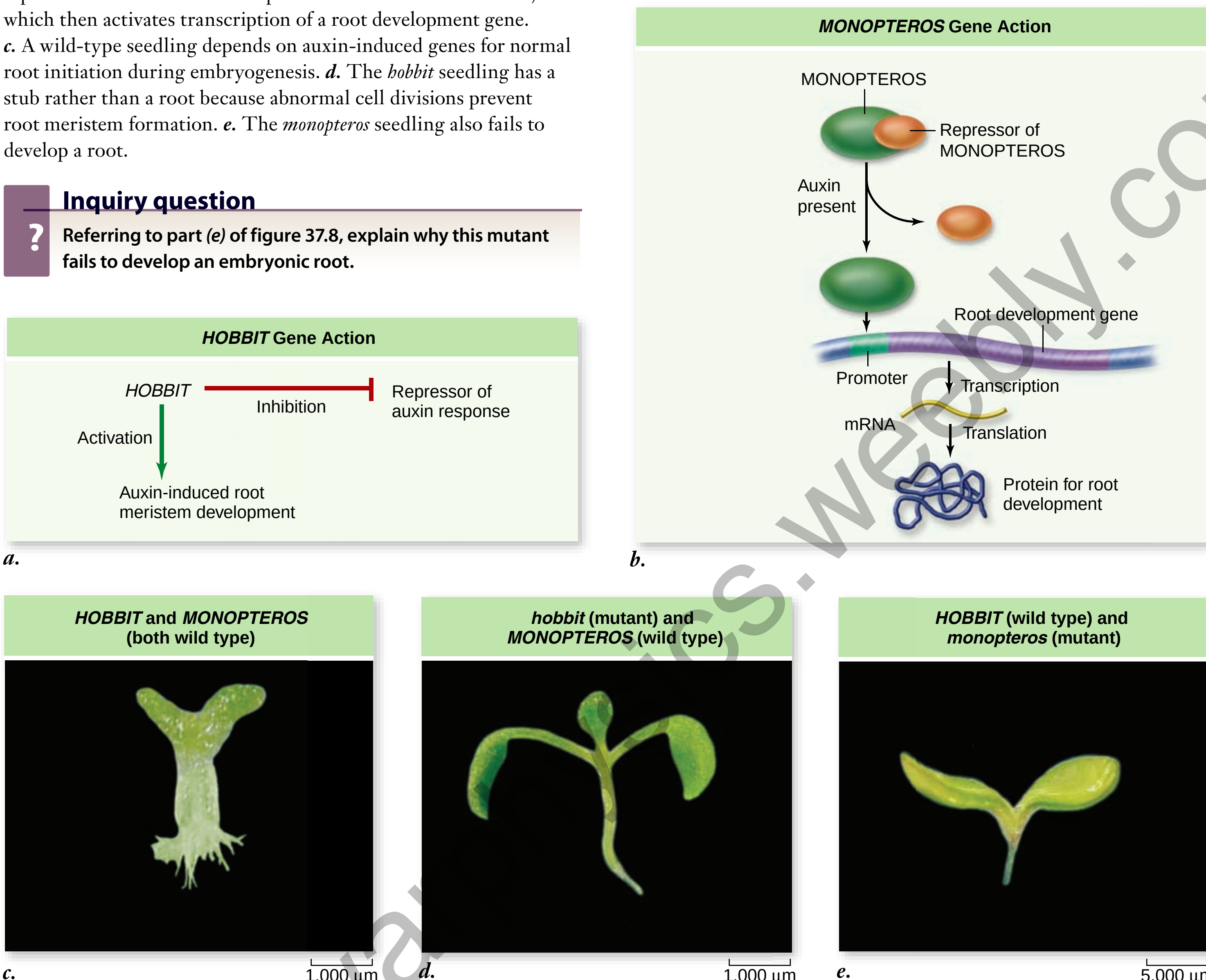


Figure 37.8 Genetic control of embryonic root development in *Arabidopsis*. ***a.*** HOBBIT represses the repression of the auxin response, allowing auxin-induced root development to occur. ***b.*** MONOPTEROS cannot act as a transcription factor when it is bound by a repressor. Auxin releases the repressor from MONOPTEROS, which then activates transcription of a root development gene. ***c.*** A wild-type seedling depends on auxin-induced genes for normal root initiation during embryogenesis. ***d.*** The *hobbit* seedling has a stub rather than a root because abnormal cell divisions prevent root meristem formation. ***e.*** The *monopteros* seedling also fails to develop a root.

Inquiry question

Referring to part *(e)* of figure 37.8, explain why this mutant fails to develop an embryonic root.



function; we will explore each of these classes of hormones in chapter 41.

One way that auxin induces gene expression is by activating a transcription factor. *MONOPTEROS (MP)* is a gene that codes for an auxin-induced transcription factor (see figure 37.8), and like *HOBBIT*, it is necessary for root formation, but not shoot formation, in *Arabidopsis*. Once activated, MP protein binds to the promoter of another gene, leading to transcription of a gene or genes needed for root meristem formation.

Inquiry question

Predict the phenotype of a plant with a mutation in the *MP* gene that results in an MP protein that can no longer bind its repressor.

Formation of the three tissue systems

Three basic tissues, called *primary meristems*, differentiate while the plant embryo is still a ball of cells (called the globular stage; see figure 37.6). No cell movements are involved in plant embryo development. The protoderm consists of the outermost cells in a plant embryo and will become *dermal tissue* (see chapter 36). These cells almost always divide with their cell plate perpendicular to the body surface, thus perpetuating a single outer layer of cells. Dermal tissue protects the plant from desiccation. Stomata that open and close to facilitate gas exchange and minimize water loss are derived dermal tissue.

A ground meristem gives rise to the bulk of the embryonic interior, consisting of *ground tissue* cells that eventually function in food and water storage.

Finally, procambium at the core of the embryo will form the future *vascular tissue*, which is responsible for water and nutrient transport.

Cell fates are generally more limited after embryogenesis, however, when embryo-specific genes are not expressed. For example, the *LEAFY COTYLEDON* gene in *Arabidopsis* is active in early and late embryo development, and it may be responsible for maintaining an embryonic environment. It is possible to turn this gene on later in development using recombinant DNA techniques described in chapter 16. When it is turned on, embryos can form on leaves!

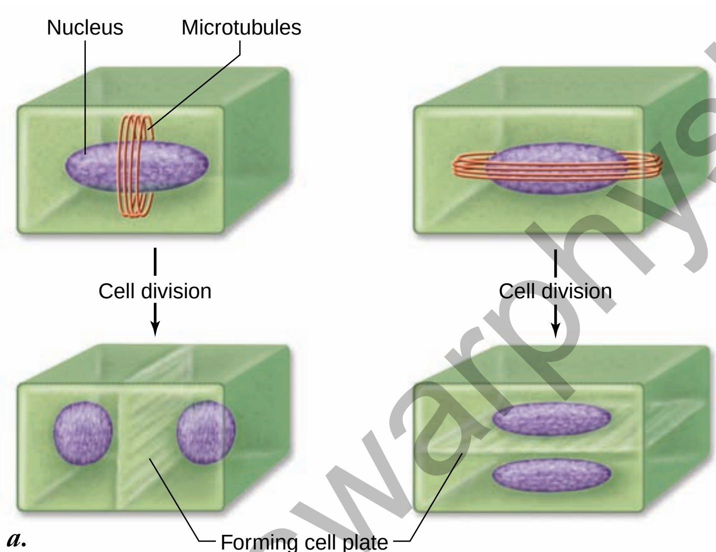
Morphogenesis

The globular stage gives rise to a heart-shaped embryo with two bulges in one group of angiosperms (the eudicots, such as *A. thaliana* in figure 37.6*c*, *d*), and a ball with a bulge on a single side in another group (the monocots). These bulges are **cotyledons** ("first leaves") and are produced by the embryonic cells, and not by the shoot apical meristem that begins forming during the globular stage. This process, called morphogenesis (generation of form), results from changes in planes and rates of cell division (see figure 37.5).

Because plant cells cannot move, the form of a plant body is largely determined by the plane in which its cells divide. It is also controlled by changes in cell shape as cells expand osmotically after they form (figure 37.9). The position of the cell plate determines the direction of division, and both microtubules and actin play a role in establishing the cell plate's position. Plant hormones and other factors influence the orientation of bundles of microtubules on the interior of the plasma membrane. These microtubules also guide cellulose deposition as the cell wall forms around the outside of a new cell (see figure 36.2) where four of the six sides are reinforced more heavily with cellulose; the cell tends to expand and grow in the direction of the two sides having less reinforcement (figure 37.9*b*).

Much is being learned about morphogenesis at the cellular level from mutants that are able to divide, but cannot control their plane of cell division or the direction of cell expansion. The lack of root meristem development in *hobbit* mutants is just one such example. As the procambium begins differentiating in the root, a critical division parallel to the root's surface is regulated by the gene *WOODEN LEG* (*WOL*, figure 37.10). Without that division, the cylinder of cells that would form phloem is missing. Only xylem forms in the vascular tissue system, giving the root a "wooden leg."

Early in embryonic development, most cells can give rise to a wide range of cell and organ types, including leaves. As development proceeds, the cells with multiple potentials are mainly restricted to the meristem regions. Many meristems have been established by the time embryogenesis ends and the seed becomes dormant. After germination, apical meristems continue adding cells to the growing root and shoot tips. Apical meristem cells of corn, for example, divide every 12 hours, producing half a million cells per day in an actively growing corn plant. Lateral meristems can cause an increase in the girth of some plants, while intercalary meristems in the stems of grasses allow for elongation.



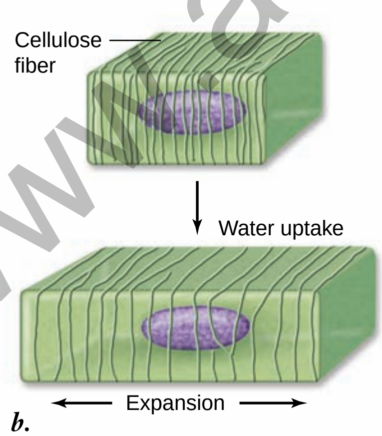


Figure 37.9 Cell division and expansion. ***a.*** Orientation of microtubules determines the orientation of cell plate formation and thus the new cell wall. ***b.*** Not all sides of a plant cell have the same amount of cellulose reinforcement. With water uptake, cells expand in directions that have the least amount of cell wall reinforcement.

Food reserves form during embryogenesis

While the embryo is developing, three other critical events are occurring in angiosperms: (1) development of a food supply, (2) development of the seed coat, and (3) development of the

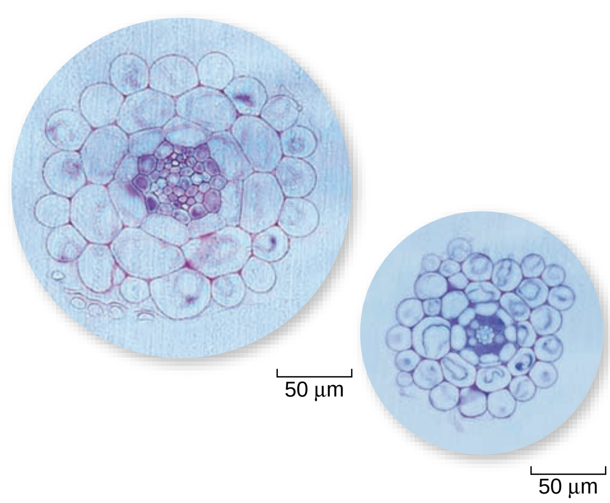


Figure 37.10 *WOODEN LEG* is needed for phloem development. The *wol* mutant (right) has less vascular tissue than wild-type *Arabidopsis* (left), but all of it is xylem.

fruit surrounding the seed. Nutritional reserves support the embryo during germination, while it gains photosynthetic capacity. In angiosperms, double fertilization produces endosperm for nutrition; in gymnosperms, the megagametophyte is the food source (see chapter 30). The seed coat is the result of the differentiation of ovule tissue (from the parental sporophyte) to form a hard, protective covering around the embryo. The seed then enters a dormant phase, signaling the end of embryogenesis. In angiosperms, the fruit develops from the carpel wall surrounding the ovule. Seed development and germination, as well as fruit development, are addressed later in this chapter. In this section, we focus on nutrient reserves.

Throughout embryogenesis, starch, lipids, and proteins are synthesized. The seed storage proteins are so abundant that the genes coding for them were the first cloning targets for plant molecular biologists. Providing nutritional resources is part of the evolutionary trend toward enhancing embryo survival.

The sporophyte transfers nutrients via the suspensor in angiosperms. (In gymnosperms, the suspensor serves only to push the embryo closer to the megagametophytic nutrient source.) This happens concurrently with the development of the endosperm, which is present only in angiosperms (although double fertilization has been observed in the gymnosperm *Ephedra*). Endosperm formation may be extensive or minimal.

Endosperm in coconut includes the "milk," a liquid. In corn, the endosperm is solid. In popping corn it expands with heat to form the white edible part of popped corn. In peas and beans, the endosperm is used up during embryo development, and nutrients are stored in thick, fleshy cotyledons (figure 37.11).

Because the photosynthetic machinery is built in response to light, it is critical that seeds have stored nutrients to aid in germination until the growing sporophyte can photosynthesize. A seed buried too deeply in the soil will use up all its reserves in cellular respiration before reaching the surface and sunlight.

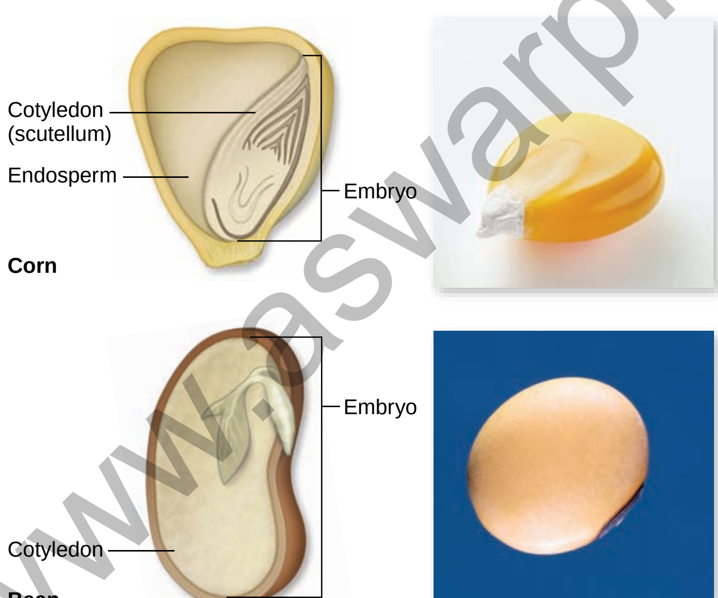


Figure 37.11 Endosperm in maize and bean. The maize kernel has endosperm that is still present at maturity, but the endosperm in the bean has disappeared. The bean embryo's cotyledons take over food storage functions.

Learning Outcomes Review 37.1

The root-shoot axis and the radial axis form during plant embryogenesis. The three tissues formed in an embryo are the protoderm, ground meristem, and procambium, which give rise to the three adults tissues. While the embryo is being formed, a food supply is being established for the embryo in the form of endosperm; a seed coat is forming from ovule tissues; and the fruit is developing from the carpel wall.

- ***How does the nutritive tissue of a gymnosperm seed differ from that of an angiosperm seed?***

37.2 *Seeds*

Learning Outcomes

1. ***Describe four ways in which seeds help to ensure the survival of a plant's offspring.***
2. ***List environmental conditions that can lead to seed germination in some plants.***

Early in the development of an angiosperm embryo, a profoundly important event occurs: The embryo stops developing. In many plants, development of the embryo is arrested soon after the meristems and cotyledons differentiate. The integuments—the outer cell layers of the ovule—develop into a relatively impermeable **seed coat,** which encloses the seed with its dormant embryo and stored food (figure 37.12).

Seeds protect the embryo

The seed is a vehicle for dispersing the embryo to distant sites. Being encased in the protective layers of a seed allows a plant embryo to survive in environments that might kill a mature plant.

Seeds are an important adaptation in at least four ways:

1. Seeds maintain dormancy under unfavorable conditions and postpone development until better conditions arise. If conditions are marginal, a plant can "afford" to have some seeds germinate, because some of those that germinate may survive, while others remain dormant.
2. Seeds afford maximum protection to the young plant at its most vulnerable stage of development.
3. Seeds contain stored food that allows a young plant to grow and develop before photosynthetic activity begins.
4. Perhaps most important, seeds are adapted for dispersal, facilitating the migration of plant genotypes into new habitats.

A mature seed contains only about 5 to 20% water. Under these conditions, the seed and the young plant within it are very stable; its arrested growth is primarily due to the progressive and severe desiccation of the embryo and the associated reduction in metabolic activity. Germination cannot take place until water and oxygen reach the embryo. Seeds of some

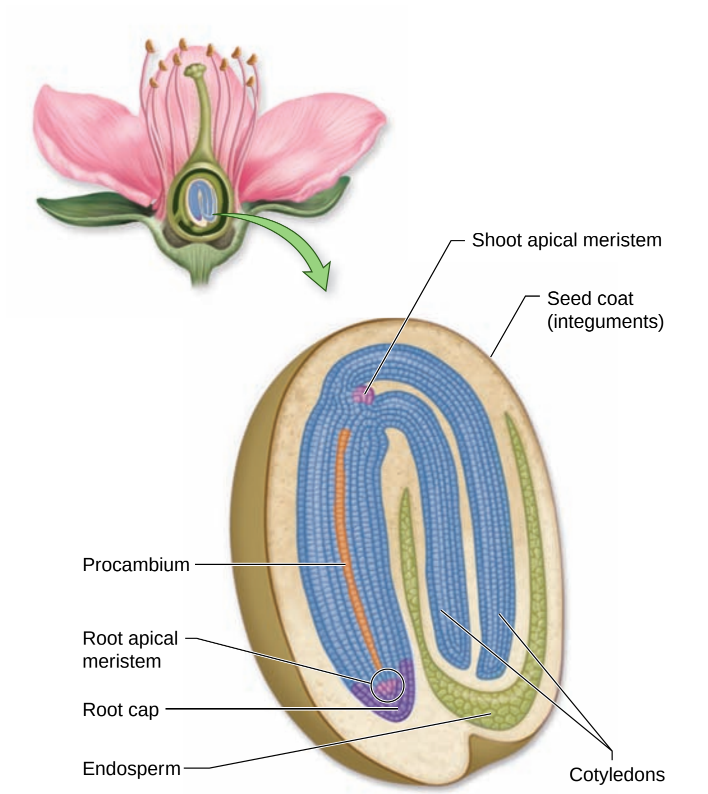


Figure 37.12 Seed development. The integuments of this mature angiosperm ovule are forming the seed coat. Note that the two cotyledons have grown into a bent shape to accommodate the tight confines of the seed. In some embryos, the shoot apical meristem will have already initiated a few leaf primordia as well.

Inquiry question

? Is this embryo a monocot or a eudicot?

plants have been known to remain viable for hundreds and, in rare instances, thousands of years.

Specialized seed adaptations improve survival

Specific adaptations often help ensure that seeds will germinate only under appropriate conditions. Sometimes, seeds lie within tough cones that do not open until they are exposed to the heat of a fire (figure 37.13). This strategy causes the seed to germinate in an open, fire-cleared habitat where nutrients are relatively abundant, having been released from plants burned in the fire.

Seeds of other plants germinate only when inhibitory chemicals leach from their seed coats, thus guaranteeing their germination when sufficient water is available. Still other seeds germinate only after they pass through the intestines of birds or mammals or are regurgitated by them, which both weakens the seed coats and ensures dispersal. Sometimes seeds of plants thought to be extinct in a particular area may germinate under unique or improved environmental circumstances, and the plants may then reestablish themselves.

a.

b.

Figure 37.13 Fire induces seed release in some pines. Fire can destroy adult jack pines, but stimulate growth of the next generation. ***a.*** The cones of a jack pine are tightly sealed and cannot release the seeds protected by the scales. ***b.*** High temperatures lead to the release of the seeds.

Learning Outcomes Review 37.2

The seed coat originates from the integuments and encloses the embryo and stored nutrients. The four advantages conferred by seeds are dormancy, protection of the embryo, nourishment, and a method of dispersal. Fire, heavy rains, or passage through an animal's digestive tract may be required for germination in some species.

- *What type of seed dormancy would you expect to find in trees living in climates with cold winters?*

37.3 *Fruits*

Learning Outcomes

1. *Identify the structures from which fruits develop.*
2. *Distinguish among berries, legumes, drupes, and samaras.*

Survival of angiosperm embryos depends on fruit development as well as seed development. Fruits are most simply defined as mature ovaries (carpels). During seed formation,

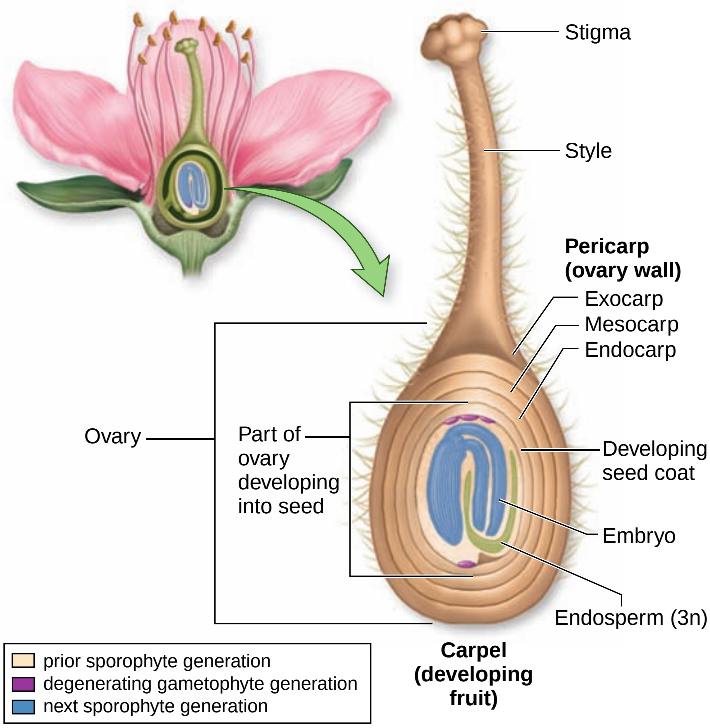


Figure 37.14 Fruit development. The carpel (specifically the ovary) wall is composed of three layers: the exocarp, mesocarp, and endocarp. One, some, or all of these layers develops to contribute to the recognized fruit in different species. The seed matures within this developing fruit.

Inquiry question

? Three generations are represented in this diagram. Label the ploidy levels of the tissues of different generations shown here.

the flower ovary begins to develop into fruit (figure 37.14). In some cases, pollen landing on the stigma can initiate fruit development, but more frequently the coordination of fruit, seed coat, embryo, and endosperm development follow fertilization.

It is possible for fruits to develop without seed development. Commercial bananas for example have aborted seed development, but do produce mature, edible ovaries. Bananas are propagated asexually since no embryo develops.

Fruits are adapted for dispersal

Fruits form in many ways and exhibit a wide array of adaptations for dispersal. Three layers of ovary wall, also called the *pericarp*, can have distinct fates, which account for the diversity of fruit types from fleshy to dry and hard. The differences among some of the fruit types are shown in figure 37.15.

Developmentally, fruits are fascinating organs that contain three genotypes in one package. The fruit and seed coat are from the prior sporophyte generation. Remnants of the gametophyte generation that produced the egg are found in the developing seed, and the embryo represents the next sporophyte generation (see figure 37.14).

Fruits allow angiosperms to colonize large areas

Aside from the many ways fruits can form, they also exhibit a wide array of specialized dispersal methods. Fruits with fleshy coverings, often shiny black or bright blue or red, normally are dispersed by birds or other vertebrates (figure 37.16*a*). Like red flowers, red fruits signal an abundant food supply. By feeding on these fruits, birds and other animals may carry seeds from place to place and thus transfer plants from one suitable habitat to another. Such seeds require a hard seed coat to resist stomach acids and digestive enzymes.

Fruits with hooked spines, such as those of burrs (figure 37.16*b*), are typical of several genera of plants that occur in the northern deciduous forests. Such fruits are often disseminated by mammals, including humans, when they hitch a ride on fur or clothing. Squirrels and similar mammals disperse and bury fruits such as acorns and other nuts. Some of these sprout when conditions become favorable, such as after the spring thaw.

Other fruits, including those of maples, elms, and ashes, have wings that aid in their distribution by the wind. Orchids have minute, dustlike seeds, which are likewise blown away by the wind. The dandelion provides another familiar example of a fruit type that is wind-dispersed (figure 37.16*c*), and the dispersal of seeds from plants such as milkweeds, willows, and cottonwoods is similar. Water dispersal adaptations include air-filled chambers surrounded by impermeable membranes to prevent the entrance of H_2O.

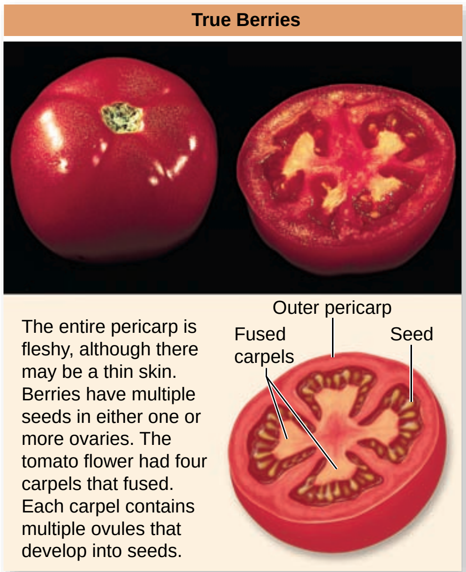
Coconuts and other plants that characteristically occur on or near beaches are regularly spread throughout a region by floating in water (figure 37.16*d*). This sort of dispersal is especially important in the colonization of distant island groups, such as the Hawaiian Islands.

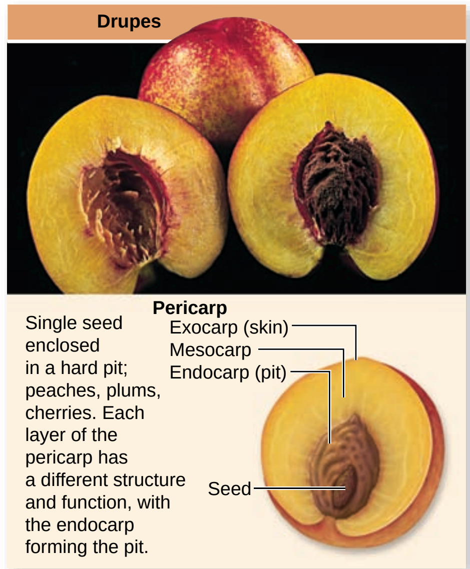
It has been calculated that the seeds of about 175 angiosperms, nearly one-third from North America, must have reached Hawaii to have evolved into the roughly 970 species found there today. Some of these seeds blew through the air, others were transported on the feathers or in the guts of birds, and still others floated across the Pacific. Although the distances are rarely as great as the distance between Hawaii and the mainland, dispersal is just as important for mainland plant species that have discontinuous habitats, such as mountaintops, marshes, or north-facing cliffs.

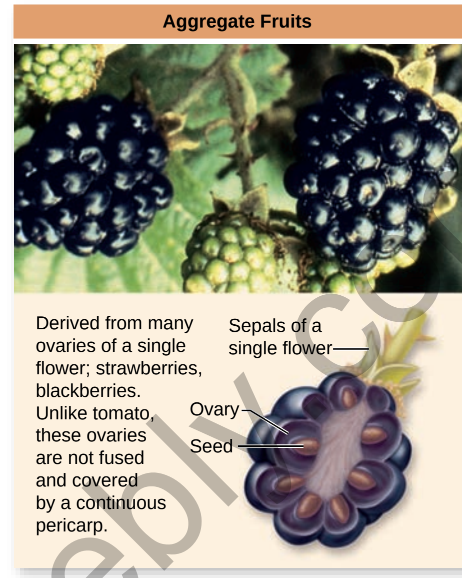
Learning Outcomes Review 37.3

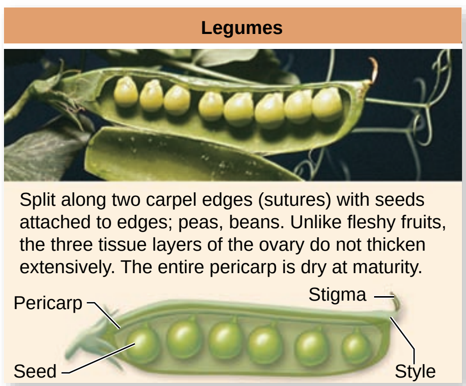
As a seed develops, the pericarp layers of the ovary wall develop into the fruit. A berry has a fleshy pericarp; a legume has a dry pericarp that opens to release seeds; the outer layers of a drupe pericarp are fleshy; and a samara is a dry structure with a wing. Animals often distribute the seeds of fleshy fruits and fruits with spines or hooks. Wind disperses lightweight seeds and samara forms.

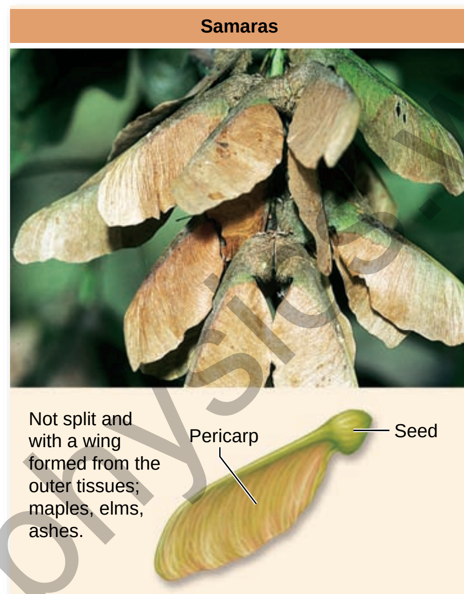
- ***What features of fruits might encourage animals to eat them?***











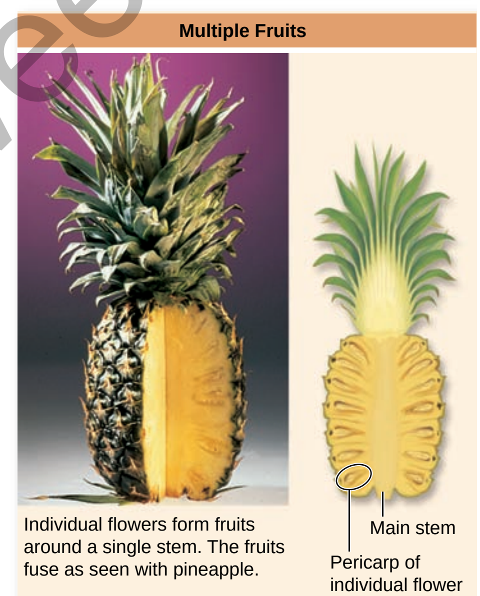
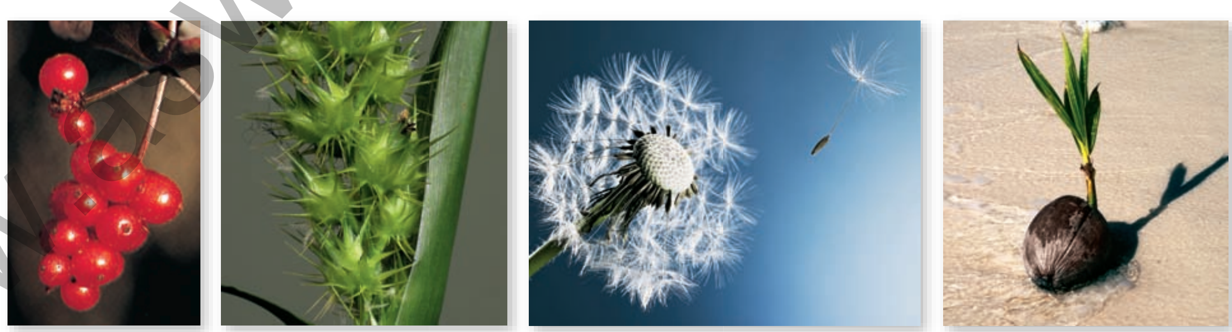


Figure 37.15 Examples of some kinds of fruits. Legumes and samaras are examples of dry fruits. Legumes open to release their seeds, while samara do not. Drupes and true berries are simple fleshy fruits; they develop from a flower with a single pistil composed of one or more carpels. Aggregate and multiple fruits are compound fleshy fruits; they develop from flowers with more than one pistil or from more than one flower.



a. *b.* *c.* *d.*

Figure 37.16 Animal-dispersed fruits. ***a.*** The bright red berries of this honeysuckle, *Lonicera hispidula*, are highly attractive to birds. After eating the fruits, birds may carry the seeds they contain for great distances either internally or, because of their sticky pulp, stuck to their feet or other body parts. ***b.*** You will know if you have ever stepped on the fruits of *Cenchrus incertus*; their spines adhere readily to any passing animal. ***c.*** False dandelion, *Pyrrhopappus carolinianus*, has "parachutes" that widely disperse the fruits in the wind, much to the gardener's despair. ***d.*** This fruit of the coconut palm, *Cocos nucifera*, is sprouting on a sandy beach. Coconuts, one of the most useful fruits for humans in the tropics, have become established on other islands by drifting there on the waves.

37.4 Germination

Learning Outcomes

1. *Describe the events that occur during seed germination.*
2. *Contrast the pattern of shoot emergence in bean (dicot) with that in maize (monocot).*

When conditions are satisfactory, the embryo emerges from its previously desiccated state, utilizes food reserves, and resumes growth. Although **germination** is a process characterized by several stages, it is often defined as the emergence of the **radicle** (first root) through the seed coat.

External signals and conditions trigger germination

Germination begins when a seed absorbs water and its metabolism resumes. The amount of water a seed can absorb is phenomenal, and osmotic pressure creates a force strong enough to break the seed coat. At this point, it is important that oxygen be available to the developing embryo because plants, like animals, require oxygen for cellular respiration. Few plants produce seeds that germinate successfully under water, although some, such as rice, have evolved a tolerance to anaerobic conditions.

Even though a dormant seed may have imbibed a full supply of water and may be respiring, synthesizing proteins and RNA, and apparently carrying on normal metabolism, it may fail to germinate without an additional signal from the environment. This signal may be light of the correct wavelength and intensity, a series of cold days, or simply the passage of time at temperatures appropriate for germination. The seeds of many plants will not germinate unless they have been **stratified**—held for periods of time at low temperatures. This phenomenon prevents the seeds of plants that grow in seasonally cold areas from germinating until they have passed the winter, thus protecting their tender seedlings from harsh, cold conditions.

Germination can occur over a wide temperature range (5° to 30°C), although certain species may have relatively narrow optimum ranges. Some seeds will not germinate even under the best conditions. In some species, a significant fraction of a season's seeds remain dormant for an indeterminate length of time, providing a gene pool of great evolutionary significance to the future plant population. The presence of ungerminated seeds in the soil of an area is referred to as the **seed bank.**

Nutrient reserves sustain the growing seedling

Germination occurs when all internal and external requirements are met. Germination and early seedling growth require the utilization of metabolic reserves stored as starch in amyloplasts (colorless plastids) and protein bodies. Fats and oils, also stored, in some kinds of seeds, can readily be digested during germination to produce glycerol and fatty acids, which yield energy through cellular respiration. They can also be converted to glucose. Depending on the kind of plant, any of these reserves may be stored in the embryo or in the endosperm.

In the kernels of cereal grains, the single cotyledon is modified into a relatively massive structure called the **scutellum** (figure 37.17). The abundant food stored in the scutellum is used up first during germination. Later, while the seedling is

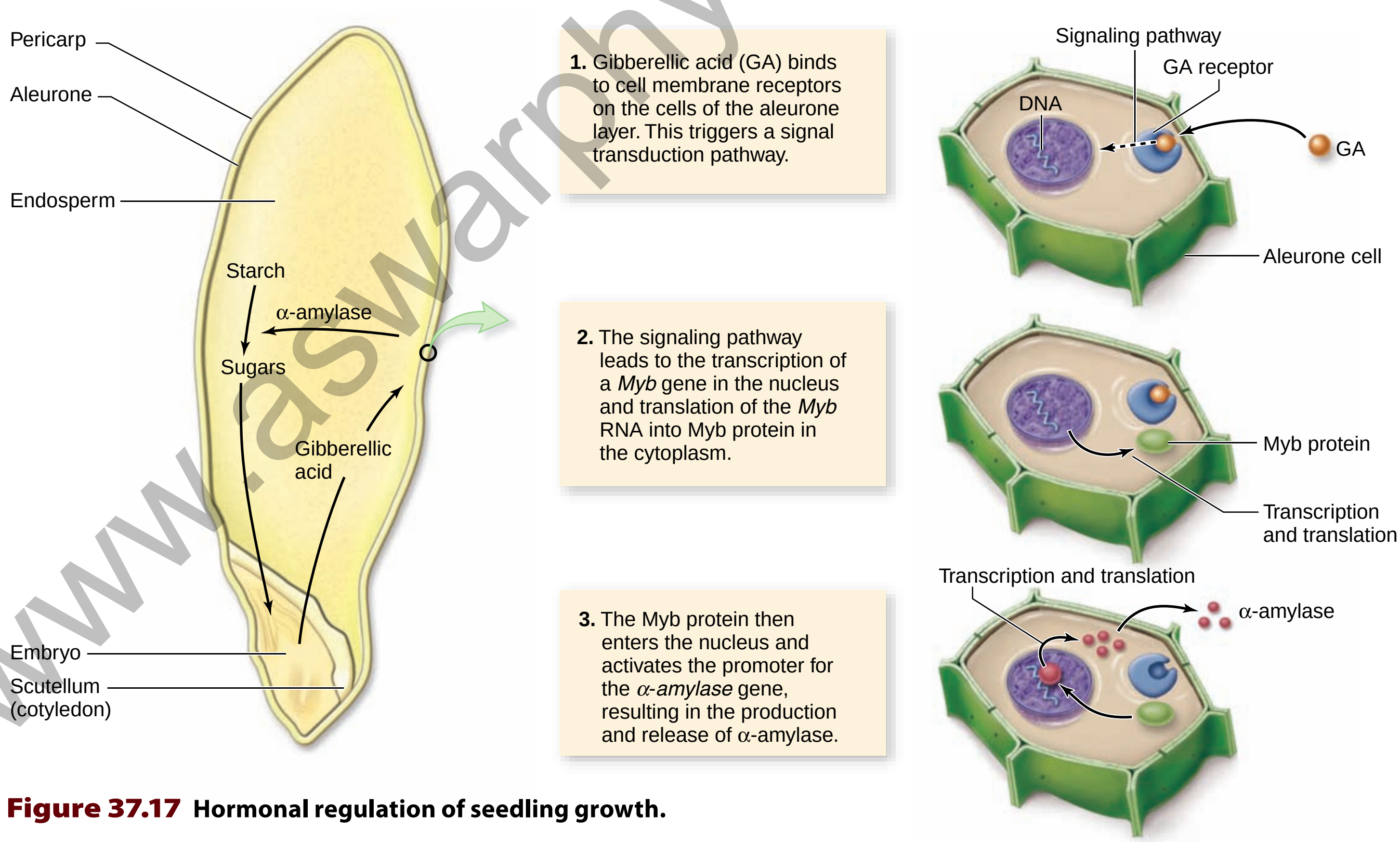


Figure 37.17 Hormonal regulation of seedling growth.

becoming established, the scutellum serves as a nutrient conduit from the endosperm to the rest of the embryo.

The utilization of stored starch by germinating plants is one of the best examples of how hormones modulate plant development (see figure 37.17). The embryo produces gibberellic acid, a hormone, that signals the outer layer of the endosperm, called the **aleurone,** to produce α-amylase. This enzyme is responsible for breaking down the endosperm's starch, primarily amylose, into sugars that are passed by the scutellum to the embryo. Abscisic acid, another plant hormone, which is important in establishing dormancy, can inhibit starch breakdown. Abscisic acid levels may be reduced when a seed beginning to germinate absorbs water. (The action of plant hormones is covered in chapter 41.)

The seedling becomes oriented in the environment, and photosynthesis begins

As the sporophyte pushes through the seed coat, it orients with the environment so that the root grows down and the shoot grows up. New growth comes from delicate meristems that are protected from environmental rigors. The shoot becomes photosynthetic, and the postembryonic phase of growth and development is under way. Figure 37.18 shows the process of germination and subsequent development of the plant body in eudicots and monocots.

The emerging shoot and root tips are protected by additional tissue layers in the monocots—the *coleoptile* surrounding the shoot, and the *coleorhiza* surrounding the radicle. Other protective strategies include having a bent shoot emerge so tissues with more rugged cell walls push through the soil.

The emergence of the embryonic root and shoot from the seed during germination varies widely from species to species. In most plants, the root emerges before the shoot appears and anchors the young seedling in the soil (see figure 37.18). In plants such as peas, the cotyledons may be held below ground; in other plants, such as beans, radishes, and onions, the cotyledons are held above ground. The cotyledons may become green and contribute to the nutrition of the seedling as it becomes established, or they may shrivel relatively quickly. The period from the germination of the seed to the establishment of the young plant is critical for the plant's survival; the seedling is unusually susceptible to disease and drought during this period. Soil composition and pH can also affect the survival of a newly germinated plant (figure 37.19).

Learning Outcomes Review 37.4

During germination, the seed and embryo take up water, increase respiration, and synthesize protein and RNA. Metabolic reserves in seeds include starch, fats, and oils. During seedling emergence, the cotyledons and seed coat may be pulled out of the ground and become photosynthetic, as they do in dicots such as beans. Alternatively, the cotyledon and seed coat may remain in the ground, as they do in monocots such as maize.

- ***What might be an advantage of retaining a seed in the ground during seedling emergence?***

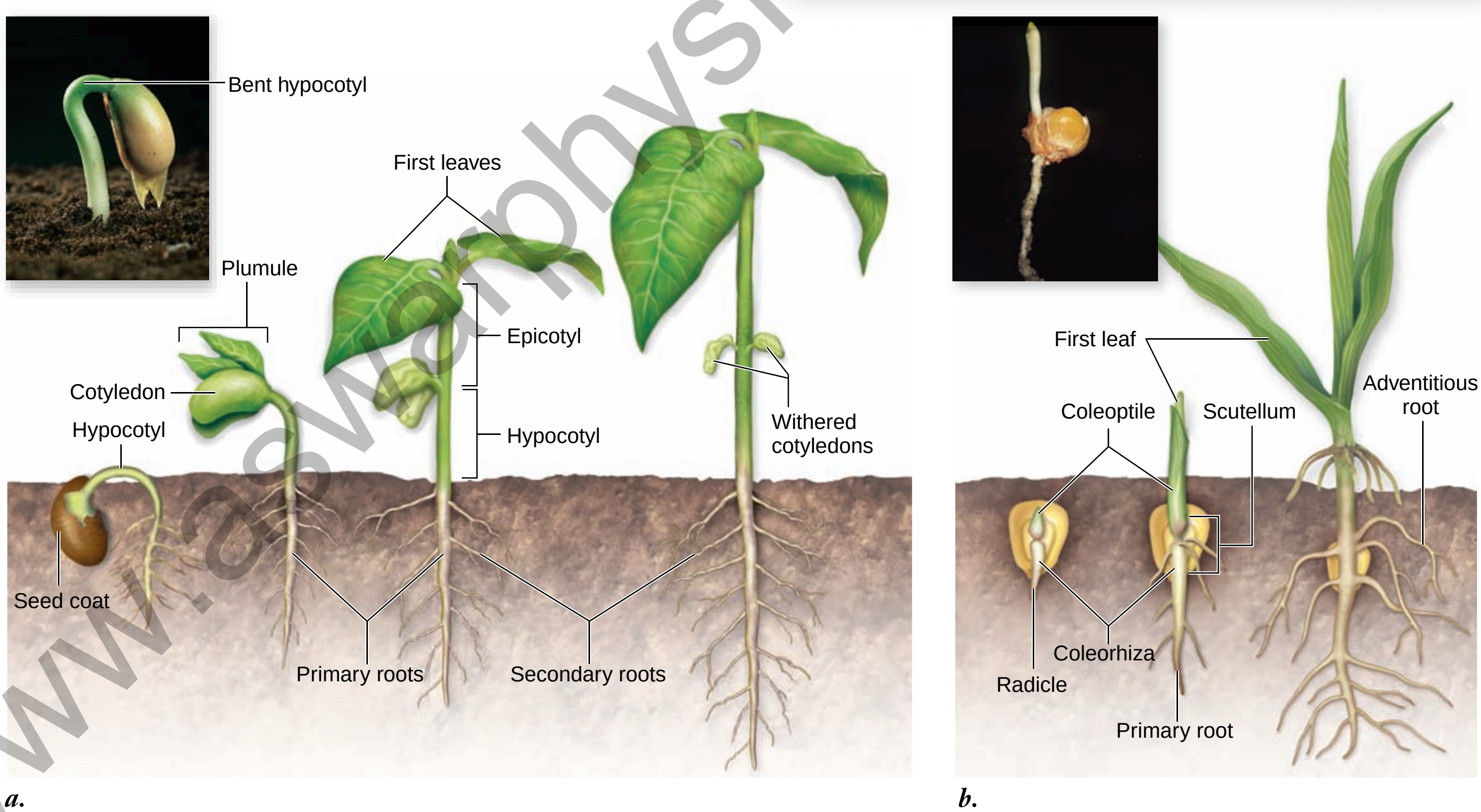


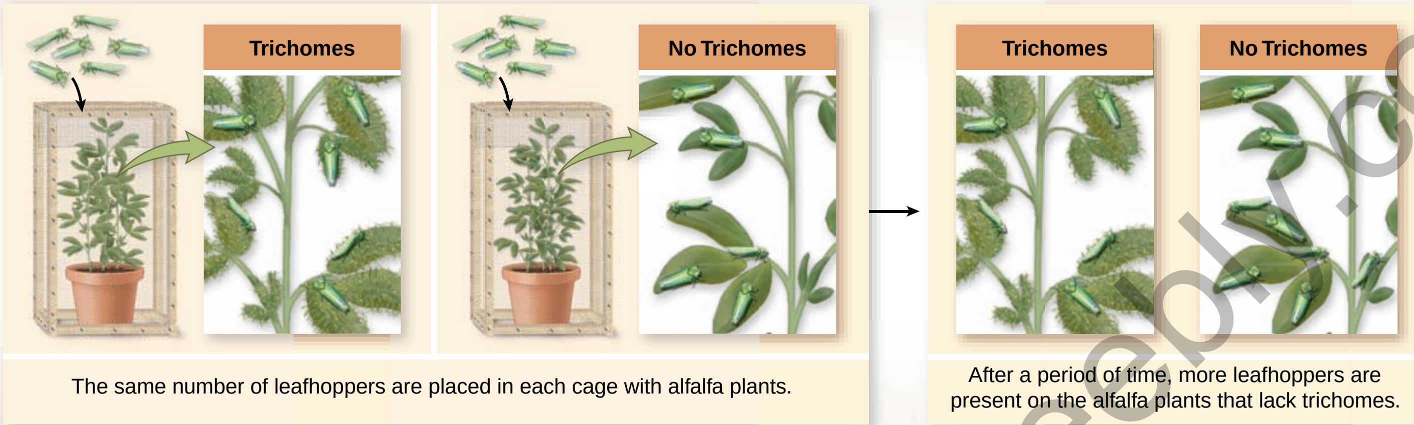
Figure 37.18 Germination. The stages shown are for ***(a)*** a eudicot, the common bean *(Phaseolus vulgaris)*, and ***(b)*** a monocot, maize *(Zea mays)*. Note that the bending of the hypocotyl (region below the cotyledons) protects the delicate bean shoot apex as it emerges through the soil. Maize radicles are protected by a protective layer of tissue called the coleorhiza, in addition to the root cap found in both bean and maize. A sheath of cells called the coleoptile, rather than a hypocotyl tissue, protects the emerging maize shoot tip.

SCIENTIFIC THINKING

Hypothesis: *Glandular trichomes prevent leafhoppers from feeding and reproducing on alfalfa plants.*

Prediction: *Rates of leafhopper survival and reproduction will be lower on plants with glandular trichomes than on those without glandular trichomes.*

Test: *Place alfalfa variety that produces glandular trichomes in a cage and a variety that lacks glandular trichomes in another cage. Place the same number of leafhoppers in each cage. Return after a period of time and count the number of live leafhoppers in each cage.*



Result: *There are fewer live leafhoppers in the cage with the trichome-bearing plant.*

Conclusion: *The hypothesis is supported. The survival and reproduction rate of leafhoppers on plants with trichomes was lower than that on plants lacking trichomes.*

Further Experiments: *Design an experiment to determine if trichomes in general or just glandular trichomes can deter leafhoppers.*

Figure 37.19 **Glandular trichomes can protect plants from insects.**

Chapter Review

37.1 Embryo Development

A single cell divides to produce a three-dimensional body plan.

An angiosperm zygote divides to produce an embryo surrounded by endosperm (see figure 37.1). In early divisions, the root-shoot axis and radial axis become established.

Developmental mutants in model plants reveal what can go wrong, allowing inferences about how development proceeds under normal conditions.

A simple body plan emerges during embryogenesis.

Shoot and root apical meristems develop, and protoderm, ground meristem, and procambium differentiate; these will become the three types of tissue in an adult plant.

Morphogenesis creates a three-dimensional embryo that includes one or two cotyledons.

Food reserves form during embryogenesis.

While the embryo is being formed, a food supply is being established for the embryo. In angiosperms, this consists of the endosperm produced by double fertilization; in gymnosperms, the megagametophyte is the food source. In addition, a seed coat forms, and the fruit develops.

37.2 Seeds (see figure 37.12)

Seeds protect the embryo.

Seeds help to ensure the survival of the next generation by maintaining dormancy during unfavorable conditions, protecting the embryo, providing food for the embryo, and providing a means for dispersal.

Specialized seed adaptations improve survival.

Before a seed germinates, its seed coat must become permeable so that water and oxygen can reach the embryo. Adaptations have evolved to ensure germination under appropriate survival conditions. In certain gymnosperms, seeds may be released from cones after a fire. Alternatively, seeds may require passage through a digestive tract, freeze–thaw cycles, or abundant moisture.

37.3 Fruits (see figure 37.14)

Fruits are adapted for dispersal.

In angiosperms, a fruit is a mature ovary. Fruit development is coordinated with embryo, endosperm, and seed coat development.

Angiosperms produce many types of fruit, which vary depending on the fate of the pericarp (carpel wall). Fruits can be dry or fleshy, and they can be simple (single carpel), aggregate (multiple carpels), or multiple (multiple flowers).

A fruit is genetically unique because it contains tissues from the parent sporophyte (the seed coat and fruit tissue), the gametophyte (remnants in the developing seed) and the offspring sporophyte (the embryo).

Fruits allow angiosperms to colonize large areas.

Fruits exhibit a wide array of dispersal mechanisms. They may be ingested and transported by animals, buried in caches by herbivores, carried away by birds and mammals, blown by the wind, or float away on water.

37.4 Germination

Seed germination is defined as the emergence of the radical through the seed coat.

External signals and conditions trigger germination.

A seed must imbibe water in order to germinate. Abundant oxygen is necessary to support the high metabolic rate of a germinating seed.

Environmental signals are often needed for germination. Examples include light of a certain wavelength, an appropriate temperature, and stratification (a period of chilling).

Nutrient reserves sustain the growing seedling.

Germination is a high-energy process, requiring stored nutrients such as starch, fats, and oils.

The endosperm acts as a starch reserve. Utilization of stored starch begins when the embryo produces the plant hormone gibberellic acid, which in turn stimulates production of an amylase to break down amylose. Starch metabolism can be inhibited by abscisic acid, a plant hormone that has a role in dormancy.

The seedling becomes oriented in the environment, and photosynthesis begins.

In most plants, the root emerges before the shoot appears, anchoring the young seedling.

In many eudicots, the shoot is bent as it emerges from the soil, protecting the growing tip (see figure 37.18). Monocots produce additional tissues to protect emerging shoots and roots.

During seedling emergence in dicots such as beans, the cotyledons are often pulled up with the growing shoot. In monocots such as corn, the cotyledon remains underground.

A seedling enters the postembryonic phase of growth and development when the emerging shoot becomes photosynthetic.

Review Questions

UNDERSTAND

1. After the first mitotic division of the zygote, the larger of the two cells becomes the
   a. embryo.
   b. endosperm.
   c. suspensor.
   d. micropyle.
2. Endosperm is produced by the union of
   a. a central cell with a sperm cell.
   b. a sperm cell with a synergid cell.
   c. an egg cell with a sperm cell.
   d. a suspensor with an egg cell.
3. During the globular stage of embryo development, apical meristems establish the
   a. embryo–suspensor axis.
   b. inner–outer axis.
   c. embryo–endosperm axis.
   d. root–shoot axis.
4. Which of the following is not a primary meristem?
   a. Cork cambium
   b. Ground meristem
   c. Procambium
   d. Protoderm
5. The integuments of an ovule will develop into the
   a. embryo.
   b. endosperm.
   c. fruit.
   d. seed coat.
6. An example of a drupe is a
   a. strawberry.
   b. plum.
   c. bean.
   d. pineapple.
7. The pericarp is the
   a. ovary wall.
   b. developing seed coat.
   c. ovary.
   d. mature endosperm.
8. During seed germination, this hormone produces the signal for the aleurone to begin starch breakdown.
   a. Abscisic acid
   b. Ethylene
   c. Gibberellic acid
   d. Auxin
9. The shoot tip of an emerging maize seedling is protected by
   a. hypocotyl.
   b. epicotyl.
   c. coleoptile.
   d. plumule.

APPLY

1. A plant lacking the *WOODEN LEG* gene will likely
   a. be incapable of transporting water to its leaves.
   b. lack xylem and phloem.
   c. be incapable of transporting photosynthate.
   d. all of the above
2. Explore how plant development changes if the functions of the genes *SHOOTMERISTEMLESS (STM)* and *MONOPTEROUS (MP)* were reversed?
   a. The embryo–suspensor axis would be reversed.
   b. The embryo–suspensor axis would be duplicated.
   c. The root–shoot axis would be reversed.
   d. The root–shoot axis would be duplicated.
3. How would a loss-of-function mutation in the α-amylase gene affect seed germination?
   a. The seed could not imbibe water.
   b. The embryo would starve.
   c. The seed coat would not rupture.
   d. The seed would germinate prematurely.

4. Fruits are complex organs that are specialized for dispersal of seeds. Which of the following plant tissues does *not* contribute to mature fruit?
   a. Sporophytic tissue from the previous generation
   b. Gametophytic tissue from the previous generation
   c. Sporophytic tissue from the next generation
   d. Gametophytic tissue from the next generation
5. Loss-of-function mutations in the *suspensor* gene in *Arabidopsis* lead to the development of two embryos in a seed. After analyzing the expression of this gene in early wild-type embryos, you find high levels of mRNA transcribed from the *suspensor* gene in the developing suspensor cells. What is the likely function of the suspensor protein?
   a. Suspensor protein likely stimulates development of the embryonic tissue.
   b. Suspensor protein likely stimulates development of the suspensor tissue.
   c. Suspensor protein likely inhibits embryonic development in the suspensor.
   d. Suspensor protein likely inhibits suspensor development in the embryo.

SYNTHESIZE

1. Design an experiment to determine whether light or gravity is more important in determining the orientation of the rhizoid during zygote development in *Fucus*.
2. In gymnosperms, the nutritive tissue in the seed is megagametophyte tissue. It is a product of meiosis. A major evolutionary advance in the angiosperms is that the nutritive tissue is endosperm, a triploid product of fertilization. Why do you suppose endosperm is a richer source of nutrition than megagametophyte tissue?
3. As you are eating an apple one day, you decide that you'd like to save the seeds and plant them. You do so, but they fail to germinate. Discuss all possible reasons that the seeds did not germinate and strategies you could try to improve your chances of success.

CHAPTER 38

Chapter 38

Transport in Plants

Chapter Outline

Introduction

Terrestrial plants face two major challenges: maintaining water and nutrient balance, and providing sufficient structural support for upright growth. The vascular system transports water, minerals, and organic molecules over great distances. Whereas the secondary growth of vascular tissue allows trees to achieve great heights, water balance alone keeps herbaceous plants upright. Think of a plant cell as a water balloon pressing against the insides of a soft-sided box, with many other balloon/box cells stacked on top. If the balloon springs a leak, the support is gone, and the box can collapse. How water, minerals, and organic molecules move between the roots and shoots of small and tall plants is the topic of this chapter.

38.1 *Transport Mechanisms*

Learning Outcomes

1. *Define transpiration.*
2. *Explain how to predict the direction of movement of water based on water potential.*
3. *Explain the driving force for transpiration.*

How does water get from the roots to the top of a 10-story-high tree? Throughout human existence, curious people have wondered about this question. Plants lack muscle tissue or a circulatory system like animals have to pump fluid throughout a plant's body. Nevertheless, water moves through the cell wall spaces between the protoplasts of cells, through plasmodesmata (connections between cells), through plasma membranes, and through the interconnected, conducting elements extending throughout a plant (figure 38.1). Water first enters the roots and then moves to the xylem, the innermost vascular tissue of plants. Water rises through the xylem because of a combination of factors, and most of that water exits through the stomata in the leaves (figure 38.2).

Local changes result in long-distance movement of materials

The greatest distances traveled by water molecules and dissolved minerals are in the xylem. Once water enters the xylem of a redwood, for example, it can move upward as much as 100 m. Most of the force is "pulling" caused by transpiration—evaporation from thin films of water in the stomata. This pulling occurs because water molecules stick to each other (cohesion) and to the walls of the tracheid or xylem vessel (adhesion). The result is an unusually stable column of liquid reaching great heights.

The movement of water at the cellular level plays a significant role in bulk water transport in the plant as well, although over much shorter distances. Although water can diffuse through plasma membranes, charged ions and organic compounds, including sucrose, depend on protein transporters to cross membranes through facilitated diffusion or active transport (see figure 38.1 and chapter 5). ATP-dependent hydrogen ion pumps often fuel active transport. They create a hydrogen ion gradient across a membrane. This hydrogen ion gradient can be used in a variety of ways, including transporting sucrose (see figure 38.1). Unequal concentrations of solutes (for example, ions and organic molecules), drive osmosis as you saw in chapter 5. Using a quantitative approach to osmosis you can predict which way water will move.

Water potential regulates movement of water through the plant

Plant biologists explain the forces that act on water within a plant in terms of potentials. *Potentials* are a way of representing free energy (the potential to do work; see chapter 5). **Water potential,** abbreviated by the Greek letter psi with a subscript W (Ψ_w), is used to predict which way water will move. The key is to remember that water will move from a cell or solution with higher water potential to a cell or solution with lower water potential. Water potential is measured in units of pressure called **megapascals (MPa).** If you turn on your kitchen or bathroom faucet full blast, the water pressure should be between 0.2 and 0.3 MPa (30 to 45 psi).

Movement of water by osmosis

If a single plant cell is placed into water, then the concentration of solutes inside the cell is greater than that of the external

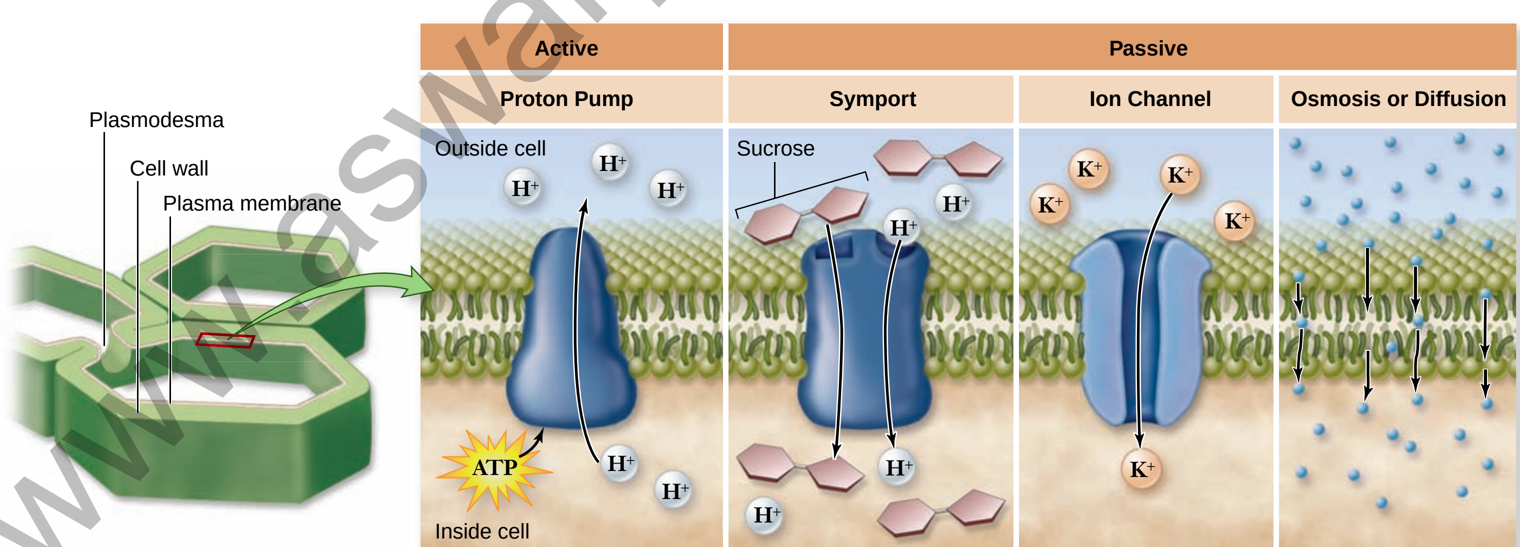
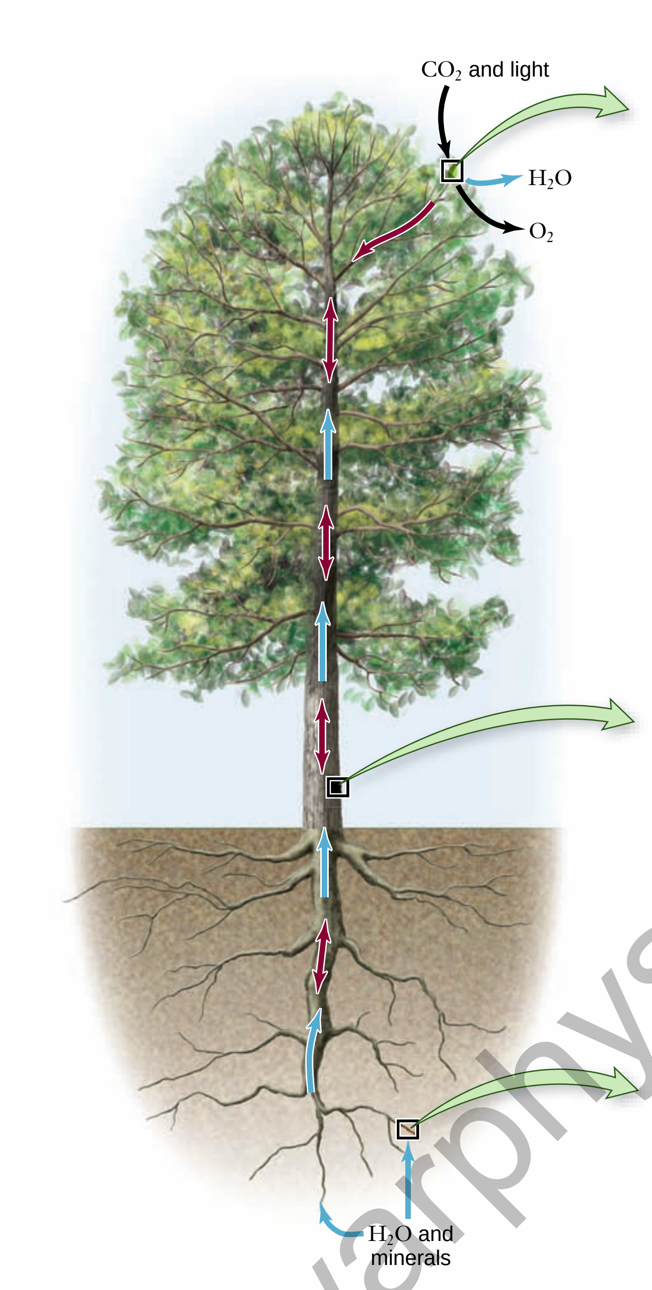


Figure 38.1 Transport between cells. Water, minerals, and organic molecules can diffuse across membranes, be actively or passively transported by membrane-bound transporters, or move through plasmodesmata. Details of membrane transport are found in chapter 5.



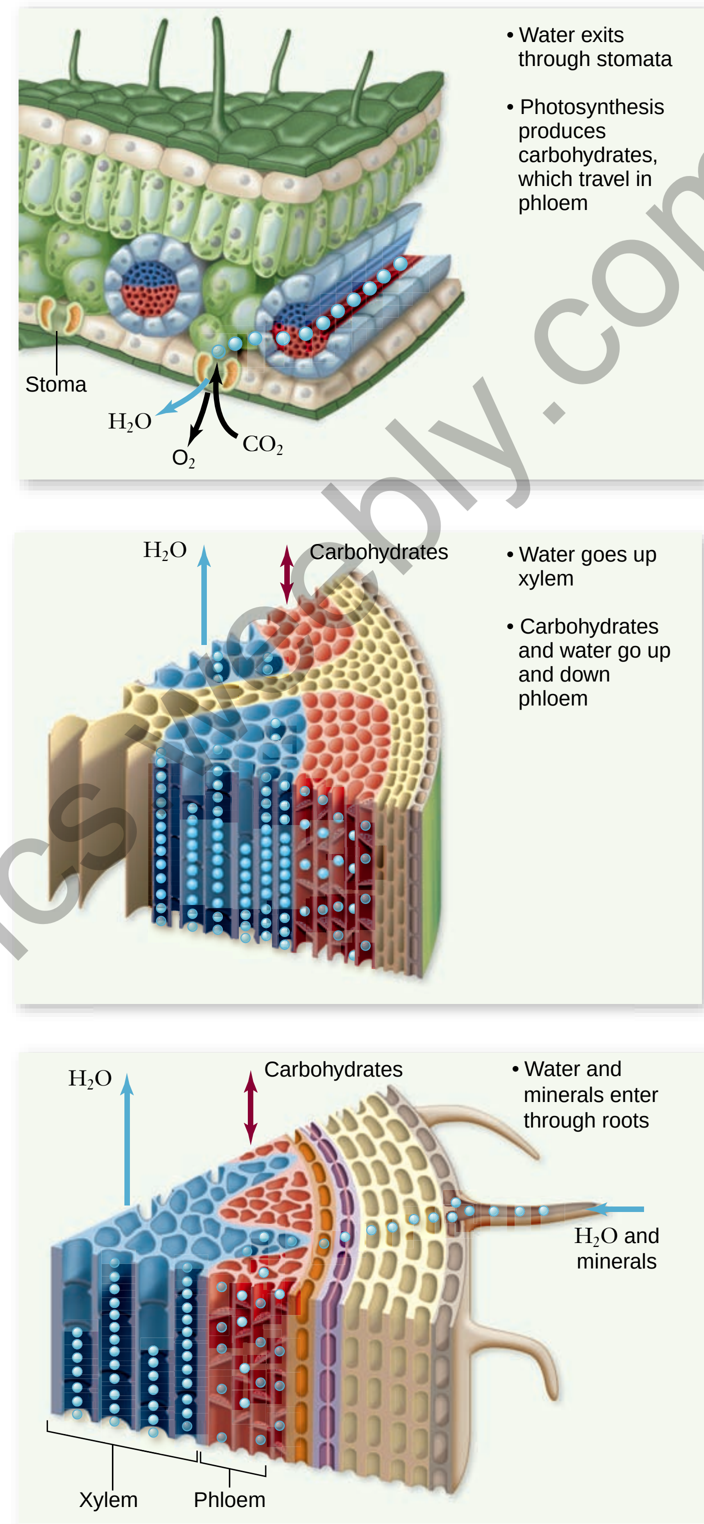


Figure 38.2 Water and mineral movement through a plant. This diagram illustrates the path of water and inorganic materials as they move into, through, and out of the plant body.

solution, and water moves into the cell by the process of **osmosis,** which you may recall from the discussion of membranes in chapter 5. The cell expands and presses against the cell wall, making it *turgid*, or swollen, because of the cell's increased turgor pressure. By contrast, if the cell is placed into a solution with a very high concentration of sucrose, water leaves the cell and turgor pressure drops. The cell membrane pulls away from the cell wall as the volume of the cell shrinks. This process is called **plasmolysis,** and if the cell loses too much water it will die. Even a tiny change in cell volume causes large changes in turgor pressure. When the turgor pressure falls to zero, most plants will wilt.

Calculation of water potential

A change in turgor pressure can be predicted more accurately by calculating the water potential of the cell and the surrounding solution. Water potential has two components: (1) physical forces, such as pressure on a plant cell wall or gravity, and (2) the concentration of solute in each solution.

In terms of physical forces, the contribution of gravity to water potential is so small that it is generally not included in calculations unless you are considering a very tall tree. The turgor pressure, resulting from pressure against the cell wall, is referred to as **pressure potential (Ψ_p)**. As turgor pressure increases, Ψ_p increases. A beaker of water containing dissolved sucrose, however, is not bounded by a cell membrane or a cell wall. Solutions that are not contained within a vessel or membrane cannot have turgor pressure, and they always have a Ψ_p of 0 MPa (figure 38.3*a*).

Water potential also arises from an uneven distribution of a solute on either side of a membrane, which results in osmosis. Applying pressure on the side of the membrane that has the greater concentration of solute prevents osmosis. The smallest amount of pressure needed to stop osmosis is proportional to the osmotic or **solute potential (Ψ_s)** of the solution (figure 38.3*b*). Pure water has a solute potential of zero. As a solution increases in solute concentration, it decreases in Ψ_s (< 0 MPa). A solution with a higher solute concentration has a more negative Ψ_s.

The total water potential (Ψ_w) of a plant cell is the sum of its pressure potential (Ψ_p) and solute potential (Ψ_s); it represents the total potential energy of the water in the cell:

$$\Psi_w = \Psi_p + \Psi_s$$

When the Ψ_w inside the cell equals that of the solution, there is no net movement of water (figure 38.3*c*).

When a cell is placed into a solution with a different Ψ_w, the tendency is for water to move in the direction that eventually results in equilibrium—both the cell and the solution have the same Ψ_w (figure 38.4). The Ψ_p and Ψ_s values may differ for cell and solution, but the sum ($=\Psi_w$) should be the same.

Aquaporins enhance osmosis

For a long time, scientists did not understand how water moved across the lipid bilayer of the plasma membrane. Water, however, was found to move more rapidly than predicted by osmosis alone. We now know that osmosis is enhanced by membrane water channels called aquaporins, which you first encountered in chapter 5 (figure 38.5). These transport channels occur in both plants and animals; in plants, they exist in vacuoles and plasma membranes and also allow for bulk flow across the membrane.

At least 30 different genes code for aquaporin-like proteins in *Arabidopsis*. Aquaporins speed up osmosis, but they do not change the direction of water movement. They are important in maintaining water balance within a cell and in moving water into the xylem.

Water potential and pressure gradients form a foundation for understanding local and long-distance transport in plants. The remaining sections of this chapter explore transport within and among different tissues and organs of the plant in more depth.

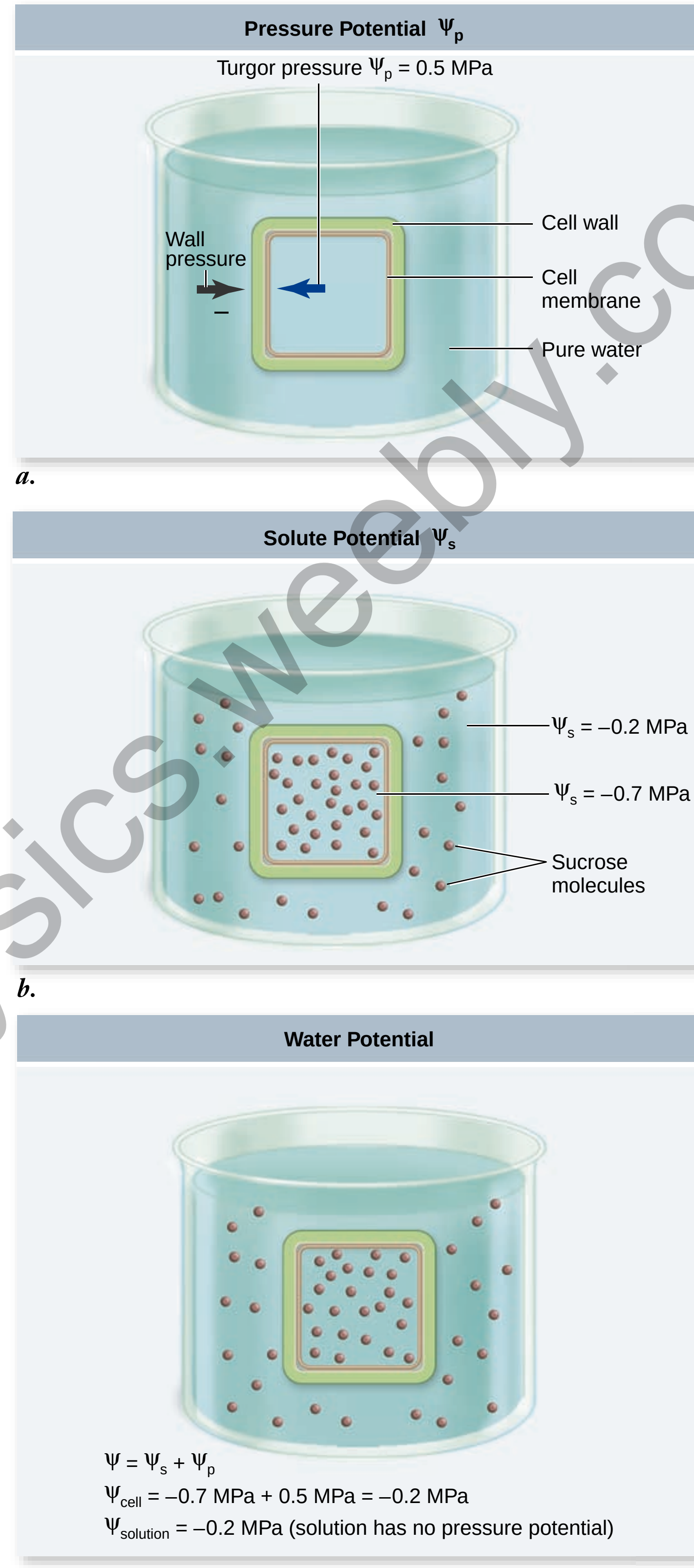


Figure 38.3 Determining water potential. ***a.*** Cell walls exert pressure in the opposite direction of cell turgor pressure. ***b.*** Using the given solute potentials, predict the direction of water movement based only on solute potential. ***c.*** Total water potential is the sum of Ψ_s and Ψ_p. Since the water potential inside the cell equals that of the solution, there is no net movement of water.

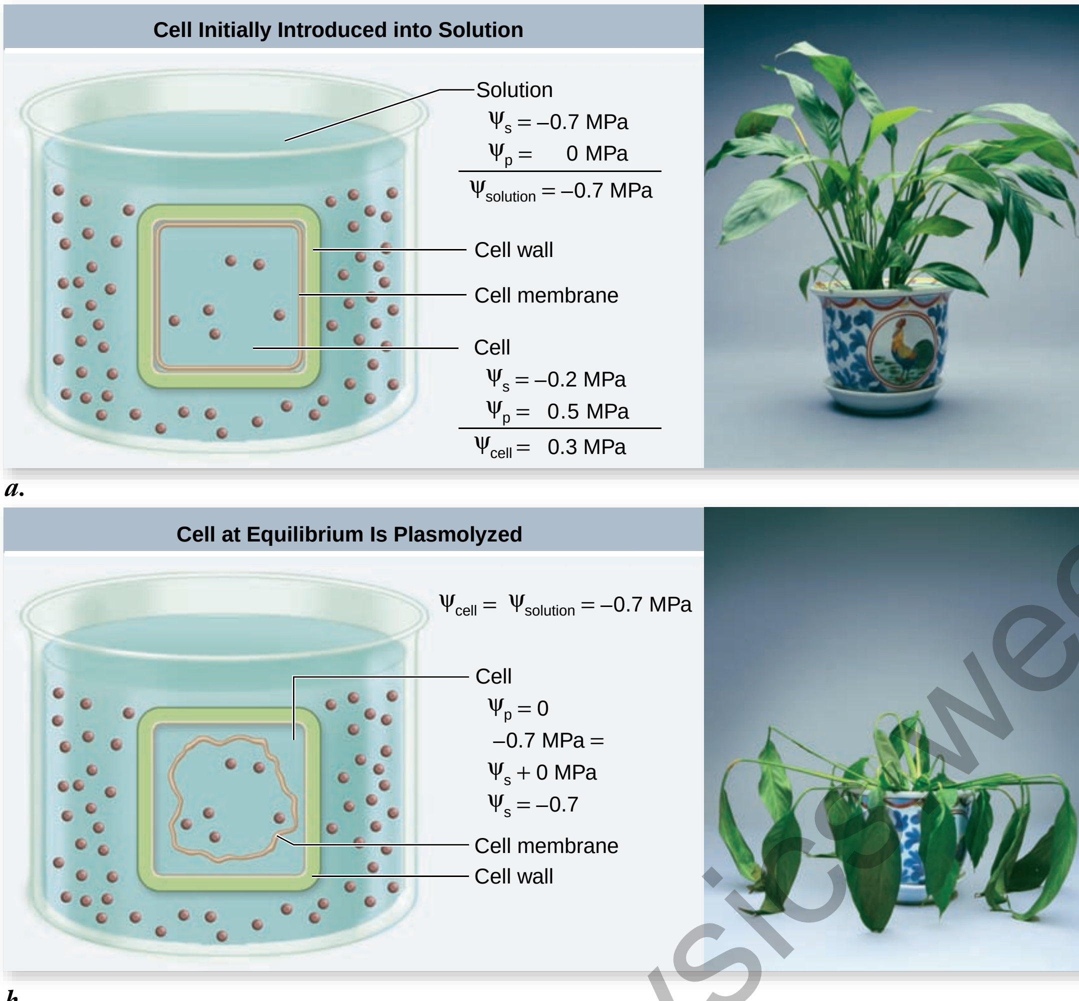


Figure 38.4 Water potential at equilibrium. ***a.*** This cell initially had a larger Ψ_w than the solution surrounding it. ***b.*** At osmotic equilibrium, the Ψ_w of the cell and the solution should be the same. We assume that the cell is in a very large volume of solution of constant concentration. The final Ψ_w of the cell should therefore equal the initial Ψ_w of the solution. When a cell is plasmolyzed, $\Psi_p = 0$. As the cell loses water, the cell's solution becomes concentrated.

? Inquiry question

What would Ψ_w, Ψ_s, and Ψ_p of the cell in (a) be at equilibrium if it had been placed in a solution with a Ψ_s of -0.5?

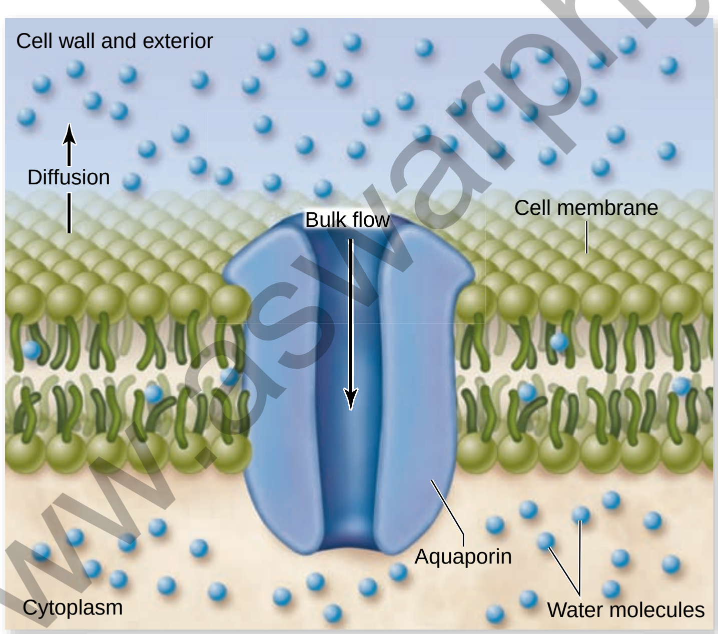


Figure 38.5 Aquaporins. Aquaporins are water-selective pores in the plasma membrane that increase the rate of osmosis because they allow bulk flow across the membrane. They do not alter the direction of water movement, however.

Learning Outcomes Review 38.1

Transpiration is the evaporation of thin films of water from the stomata, exerting a lifting force on water in the xylem. Water potential is the sum of the pressure potential and the solute potential; water moves from an area of high water potential to an area of low water potential. This difference moves water from the soil into roots, and from the roots to the rest of the plant body. The vapor pressure gradient between the inside and the outside of a leaf drives transpiration.

- *Explain how physical pressure and solute concentration contribute to water potential.*

38.2 *Water and Mineral Absorption*

Learning Outcomes

1. *Explain the function of root hairs.*
2. *List the three water transport routes through plants.*
3. *Describe the function of Casparian strips.*

Most of the water absorbed by the plant comes in through the region of the root with root hairs (figures 38.6 and 38.7). As you learned in chapter 36, root hairs are extensions of root epidermal cells located just behind the tips of growing roots.

Surface area for the absorption of water and minerals is further increased in many species of plants by interacting with mycorrhizal fungi. These fungi extend the absorptive net far beyond that of root hairs and are particularly helpful in the uptake of phosphorous in the soil. Mycorrhizae are discussed in detail in chapter 31.

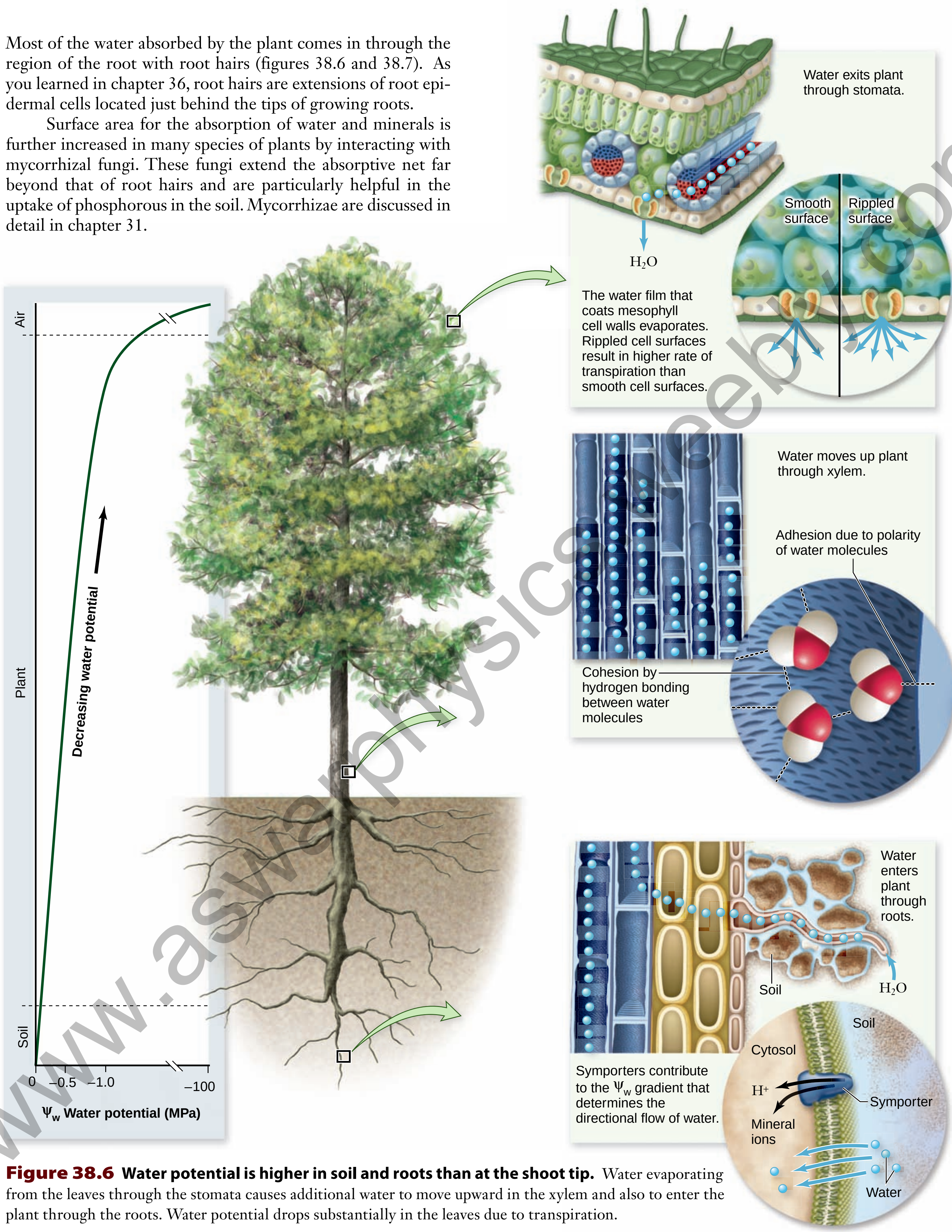


Figure 38.6 Water potential is higher in soil and roots than at the shoot tip. Water evaporating from the leaves through the stomata causes additional water to move upward in the xylem and also to enter the plant through the roots. Water potential drops substantially in the leaves due to transpiration.

cell the greatest amount of control over what substances enter and leave. These three routes are not exclusive, and molecules can change pathways at any time, until reaching the endodermis of the root.

Figure 38.7 **Water and minerals move into roots in regions rich with root hairs.**

Once absorbed through root hairs, water and minerals must move across cell layers until they reach the vascular tissues; water and dissolved ions then enter the xylem and move throughout the plant.

Three transport routes exist through cells

Water and minerals can follow three pathways to the vascular tissue of the root (figure 38.8). The **apoplast route** includes movement through the cell walls and the space between cells. Transport through the apoplast avoids membrane transport. The **symplast route** is the continuum of cytoplasm between cells connected by plasmodesmata. Once molecules are inside a cell, they can move between cells through plasmodesmata without crossing a plasma membrane. The **transmembrane route** involves membrane transport between cells and also across the membranes of vacuoles within cells. This route permits each cell the greatest amount of control over what substances enter and leave. These three routes are not exclusive, and molecules can change pathways at any time, until reaching the endodermis of the root.

Transport through the endodermis is selective

Eventually, on their journey inward, molecules reach the endodermis. Any further passage through the cell walls is blocked by the Casparian strips. As described in chapter 36, all cells in the cylinder of endodermis have connecting walls embedded with the waterproof material suberin (figure 38.9). Molecules must pass through the plasma membranes and protoplasts of the endodermal cells to reach the xylem. The endodermis, with its unique structure, along with the cortex and epidermis, controls water and nutrient flow to the xylem to regulate water potential and helps limit leakage of water out of the root.

Because the mineral ion concentration in the soil water is usually much lower than it is in the plant, an expenditure of energy (supplied by ATP) is required for these ions to accumulate in root cells. The plasma membranes of endodermal cells contain a variety of protein transport channels, through which proton pumps transport specific ions against even larger concentration gradients (refer to figure 38.1). Once inside the vascular stele, the ions, which are plant nutrients, are transported via the xylem throughout the plant.

Learning Outcomes Review 38.2

Water and minerals move into the plant from the soil, particularly in the region rich with root hairs. The three water transport routes are the apoplast route through the cells walls, the symplast route through plasmodesmata, and the transmembrane route across cell and vacuole membranes. Casparian strips force water and nutrients to move through the cell membranes of the endodermis, allowing selective control.

- ***What qualities of the cell membrane allow it to act as a selective barrier?***

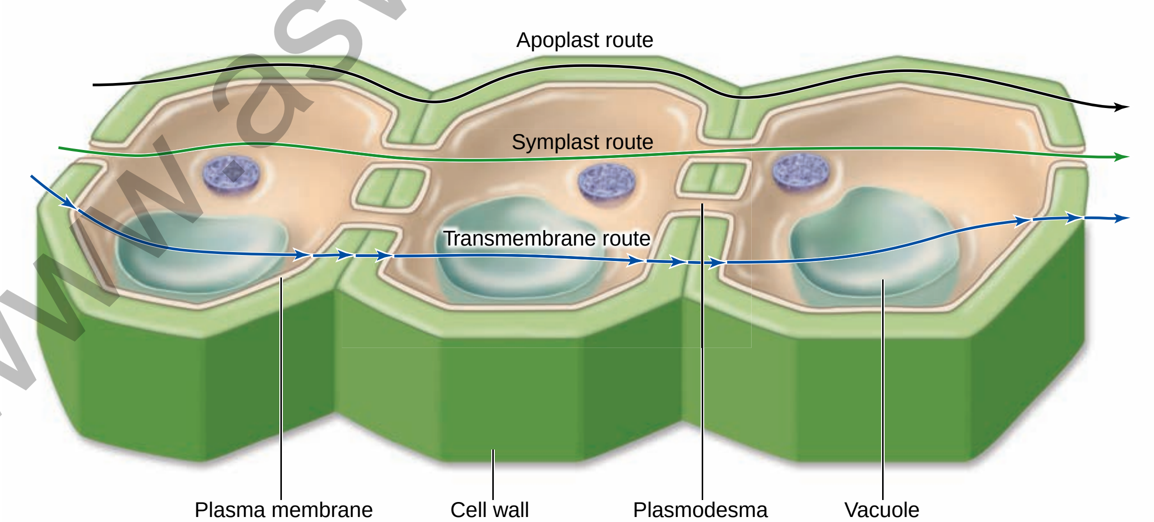


Figure 38.8 **Transport routes between cells.**

Inquiry question

? **Which route would be the fastest for water movement? Would this always be the best way to move nutrients into the plant?**

38.3 Xylem Transport

Learning Outcomes

1. *Describe the environmental conditions in which guttation occurs.*
2. *List the properties of water that cause it to have a high tensile strength.*
3. *Explain how cavitation interrupts water flow.*

The aqueous solution that passes through the membranes of endodermal cells enters the plant's vascular tissues and moves into the tracheids and vessel members of the xylem. As ions are actively pumped into the root or move via facilitated diffusion, their presence increases the water potential and increases turgor pressure in the roots due to osmosis.

Root pressure is present even when transpiration is low or not occurring

Root pressure, which often occurs at night, is caused by the continued accumulation of ions in the roots at times when transpiration from the leaves is very low or absent. This accumulation results in an increasingly high ion concentration within the cells, which in turn causes more water to enter the root hair cells by osmosis. Ion transport further decreases the Ψ_s of the roots. The result is movement of water into the plant and up the xylem columns despite the absence of transpiration.

Under certain circumstances, root pressure is so strong that water will ooze out of a cut plant stem for hours or even days. When root pressure is very high, it can force water up to the leaves, where it may be lost in a liquid form through a process known as **guttation.** Guttation cannot move water up great heights or at rapid speeds. It does not take place through the stomata, but instead occurs through special groups of cells located near the ends of small veins that function only in this process. Guttation produces what is more commonly called dew on leaves.

Root pressure alone, however, is insufficient to explain xylem transport. Transpiration provides the main force for moving water and ionic solutes from roots to leaves.

A water potential gradient from roots to shoots enables transport

Water potential regulates the movement of water through a whole plant, as well as across cell membranes. Roots are the entry point. Water moves from the soil into the plant only if water potential of the soil is greater than in the root. Too much fertilizer or drought conditions lower the Ψ_w of the soil and limit water flow into the plant. Water in a plant moves along a Ψ_w gradient from the soil (where the Ψ_w may be close to zero under wet conditions) to successively more negative water potentials in the roots, stems, leaves, and atmosphere (see figure 38.6).

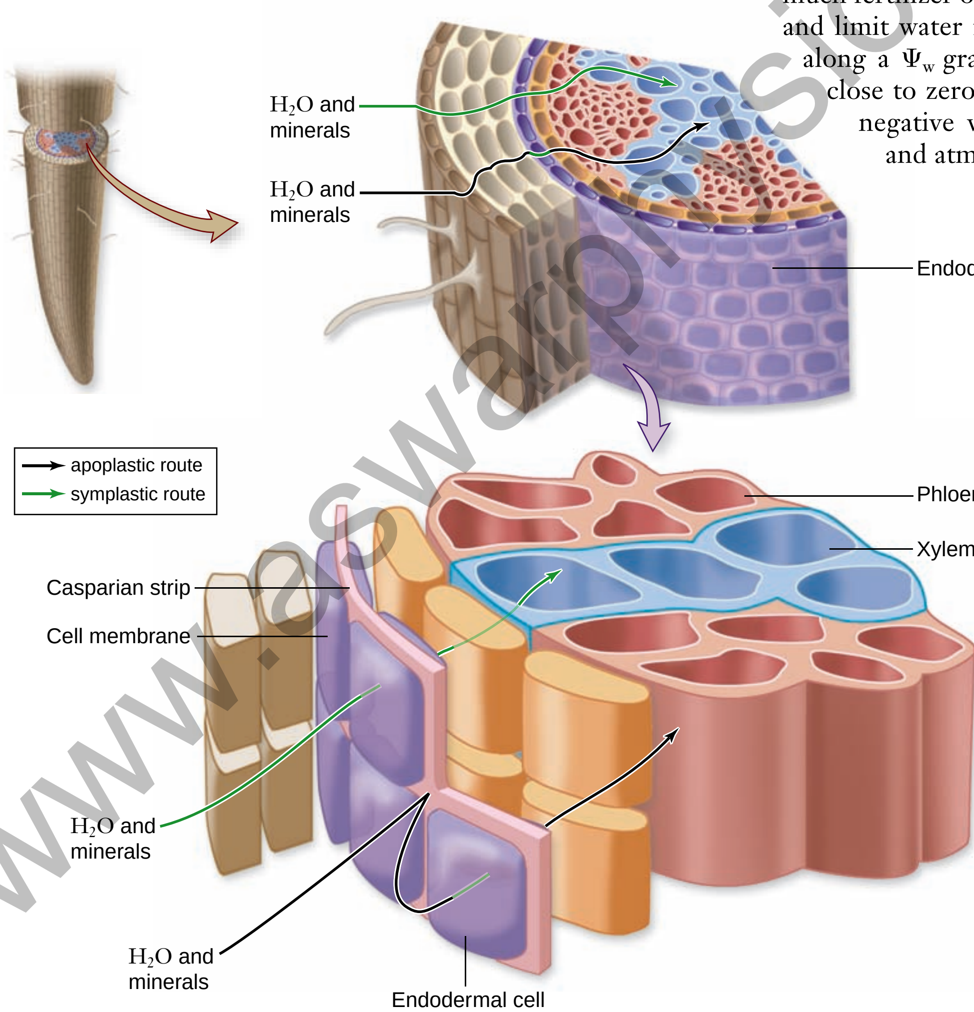


Figure 38.9 The pathways of mineral transport in roots. Minerals are absorbed at the surface of the root. In passing through the cortex, they must either follow the cell walls and the spaces between them or go directly through the plasma membranes and the protoplasts of the cells, passing from one cell to the next by way of the plasmodesmata. When they reach the endodermis, however, their further passage through the cell walls is blocked by the Casparian strips, and they must pass through the membrane and protoplast of an endodermal cell before they can reach the xylem.