38

The Plant Body

Concept Outline

38.1 Meristems elaborate the plant body plan after germination.

Meristems. Growth occurs in the continually dividing cells that function like stem cells in animals.

Organization of the Plant Body. The plant body is a series of iterative units stacked above and below the ground.

Primary and Secondary Growth. Different meristems allow plants to grow in both height and circumference.

38.2 Plants have three basic tissues, each composed of several cell types.

Dermal Tissue. This tissue forms the "skin" of the plant body, protecting it and preventing water loss.

Ground Tissue. Much of a young plant is ground tissue, which supports the plant body and stores food and water.

Vascular Tissue. Special piping tissues conduct water and sugars through the plant body.

38.3 Root cells differentiate as they become distanced from the dividing root apical meristem.

Root Structure. Roots have a durable cap, behind which primary growth occurs.

Modified Roots. Roots can have specialized functions.

38.4 Stems are the backbone of the shoot, transporting nutrients and supporting the aerial plant organs.

Stem Structure. The stem supports the leaves and is anchored by the roots. Vascular tissues are organized within the stem in different ways.

Modified Stems. Specialized stems are adapted for storage and vegetative (asexual) propagation.

38.5 Leaves are adapted to support basic plant functions.

Leaf External Structure. Leaves have flattened blades and slender stalks.

Leaf Internal Structure. Leaves contain cells that carry out photosynthesis, gas exchange, and evaporation.

Modified Leaves. In some plants, leaf development has been modified to provide for a unique need.

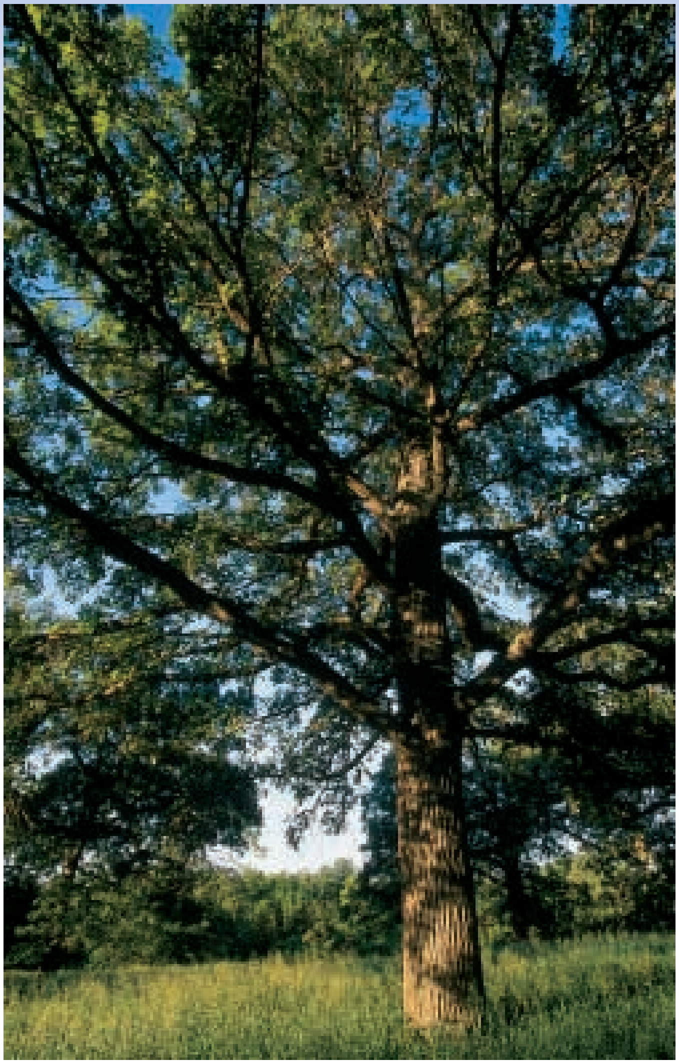


FIGURE 38.1
All vascular plants share certain characteristics. Vascular plants such as this tree require an elaborate system of support and fluid transport to grow this large. Smaller plants have similar (though simpler) structures. Much of this support system is actually underground in the form of extensive branching root systems.

Although the similarities between a cactus, an orchid plant, and a tree might not be obvious at first sight, most plants have a basic unity of structure (figure 38.1). This unity is reflected in how the plants are constructed; in the way they grow, manufacture, and transport their food; and in how their development is regulated. This chapter addresses the question of how a vascular plant is "built." We will focus on the diversity of cell, tissue, and organ types that compose the adult body. The roots and shoots which give the adult plant its distinct above and below ground architecture are the final product of a basic body plan first established during embryogenesis, a process we will explore in detail in chapter 40.

38.1 Meristems elaborate the plant body plan after germination.

Meristems

The plant body that develops after germination depends on the activities of meristematic tissues. Meristematic tissues are lumps of small cells with dense cytoplasm and proportionately large nuclei that act like stem cells in animals. That is, one cell divides to give rise to two cells. One remains meristematic, while the other is free to differentiate and contribute to the plant body. In this way, the population of meristem cells is continually renewed. Molecular genetic evidence supports the hypothesis that stem cells and meristem cells may also share some common molecular mechanisms.

Elongation of both root and shoot takes place as a result of repeated cell divisions and subsequent elongation of the cells produced by the **apical meristems**. In some vascular plants, including shrubs and most trees, **lateral meristems** produce an increase in girth.

Apical Meristems

Apical meristems are located at the tips of stems (figure 38.2) and at the tips of roots (figure 38.3), just behind the root cap. The plant tissues that result from primary growth are called **primary tissues.** During periods of growth, the cells of apical meristems divide and continually add more cells to the tips of a seedling's body. Thus, the seedling lengthens. Primary growth in plants is brought about by the apical meristems. The elongation of the root and stem forms what is known as the **primary plant body,** which is made up of primary tissues. The primary plant body comprises the young, soft shoots and roots of a tree or shrub, or the entire plant body in some herbaceous plants.

Both root and shoot apical meristems are composed of delicate cells that need protection. The root apical meristem is protected from the time it emerges by the root cap. Root cap cells are produced by the root meristem and are sloughed off and replaced as the root moves through the soil. A variety of adaptive mechanisms protect shoot apical meristem during germination (figure 38.4). The epicotyl or hypocotyl ("stemlike" tissue above or below the cotyledons) may bend as the seedling emerges to minimize the force on the shoot tip. In the monocots (a late evolving group of angiosperms) there is often a coleoptile (sheath of tissue) that forms a protective tube around the emerging shoot. Later in development, the leaf primordia cover the shoot apical meristem which is particularly susceptible to desiccation.

The apical meristem gives rise to three types of embryonic tissue systems called **primary meristems.** Cell division continues in these partly differentiated tissues as they develop into the primary tissues of the plant body. The

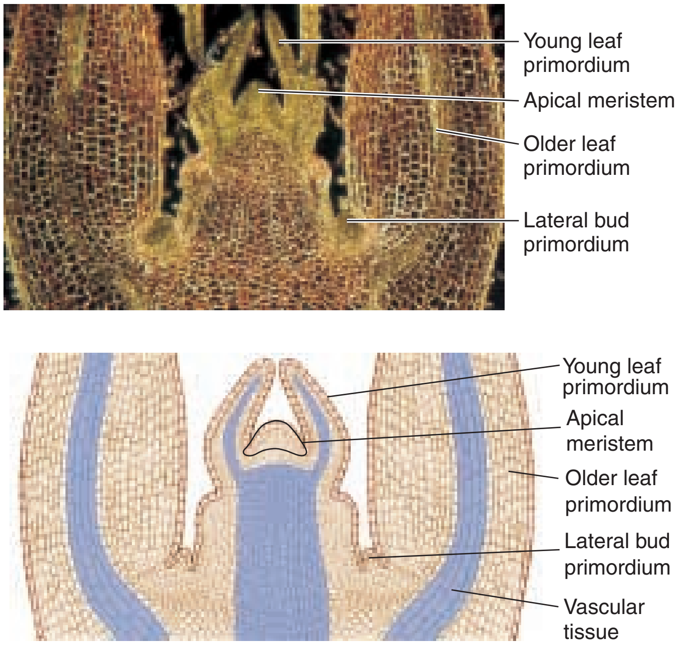


FIGURE 38.2
An apical shoot meristem. This longitudinal section through a shoot apex in *Coleus* shows the tip of a stem. Between the young leaf primordia is the apical meristem.

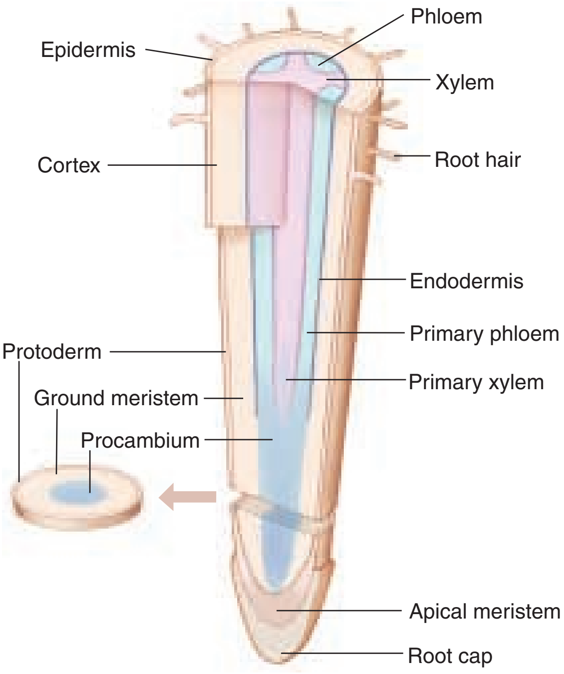
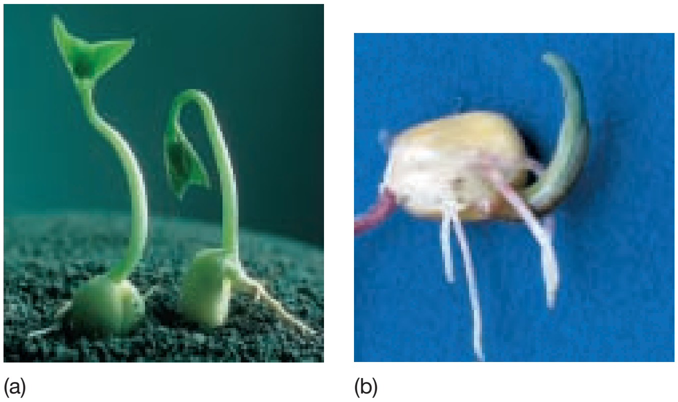


FIGURE 38.3
An apical root meristem. This diagram of meristems in the root shows their relation to the root tip.



(a) (b)

FIGURE 38.4
Developing seedling. Apical meristems are protected early in development. (*a*) In this soybean, a dicot, a bent epicotyl (stem above the cotyledons), rather than the shoot tip, pushes through the soil before straightening. (*b*) In corn, a monocot, a sleeve of tissue called the coleoptile sheaths the shoot tip until it has made it to daylight.

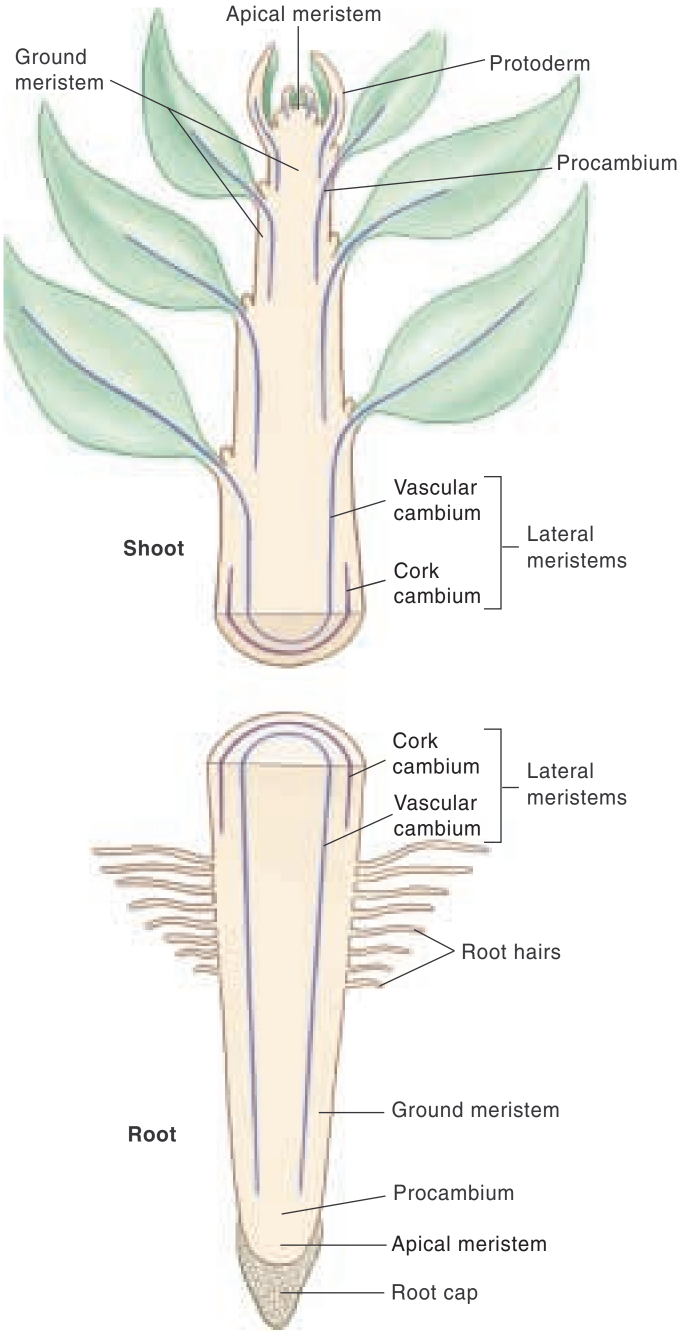


FIGURE 38.5
Apical and lateral meristems. Apical meristems produce primary growth, the elongation of the root and stem. In some plants, the lateral meristems produce an increase in the girth of a plant. This type of growth is secondary because the meristems were not directly produced by apical meristems.

three primary meristems are the **protoderm,** which forms the epidermis; the **procambium,** which produces primary vascular tissues (primary xylem and primary phloem); and the **ground meristem,** which differentiates further into ground tissue, which is composed of parenchyma cells. In some plants, such as horsetails and corn, **intercalary meristems** arise in stem internodes, adding to the internode lengths. If you walk through a corn field (when the corn is about knee high) on a quiet summer night, you may hear a soft popping sound. This is caused by the rapid growth of intercalary meristems. The amount of stem elongation that occurs in a very short time is quite surprising.

Lateral Meristems

Many herbaceous plants exhibit only primary growth, but others also exhibit **secondary growth.** Most trees, shrubs, and some herbs have active **lateral meristems,** which are cylinders of meristematic tissue within the stems and roots (figure 38.5). Although secondary growth increases girth in many nonwoody plants, its effects are most dramatic in woody plants which have two lateral meristems. Within the bark of a woody stem is the **cork cambium,** a lateral meristem that produces the cork cells of the outer bark. Just beneath the bark is the **vascular cambium,** a lateral meristem that produces secondary vascular tissue. The vascular cambium forms between the xylem and phloem in vascular bundles, adding secondary vascular tissue on opposite sides of the vascular cambium. *Secondary xylem* is the main component of wood. *Secondary phloem* is very close to the outer surface of a woody stem. Removing the bark of a tree damages the phloem and may eventually kill the tree. Tissues formed from lateral meristems, which comprise most of the trunk, branches, and older roots of trees and shrubs, are known as **secondary tissues** and are collectively called the secondary plant body.

Meristems are actively dividing, embryonic tissues responsible for both primary and secondary growth.

Organization of the Plant Body

Coordination of primary and secondary meristematic growth produces the body of the adult sporophyte plant. Plant bodies do not have a fixed size. Parts such as leaves, roots, branches, and flowers all vary in size and number from plant to plant—even within a species. The development of the form and structure of plant parts may be relatively rigidly controlled, but some aspects of leaf, stem, and root development are quite flexible. As a plant grows, the number, location, size, and even structure of leaves and roots are often influenced by the environment.

A vascular plant consists of a **root system** and a **shoot system** (figure 38.6). The root system anchors the plant and penetrates the soil, from which it absorbs water and ions crucial to the plant's nutrition. The shoot system consists of the **stems** and their **leaves.** The stem serves as a framework for positioning the leaves, the principal sites of photosynthesis. The arrangement, size, and other features of the leaves are of critical importance in the plant's production of food. Flowers, other reproductive organs, and, ultimately, fruits and seeds are also formed on the shoot (see chapters 40 and 42). The reiterative unit of the vegetative shoot consists of the internode, node, leaf, and axillary buds. Axillary buds are apical meristems derived from the primary apical meristem that allow the plant to branch or replace the main shoot if it is munched by an herbivore. A vegetative axillary bud has the capacity to reiterate the development of the primary shoot. When the plant has transited to the reproductive phase of development (see chapter 41), these axillaries may produce flowers or floral shoots.

Three basic types of tissues exist in plants: *ground tissue*, *dermal*, and *vascular tissue*. Each of the three basic tissues has its own distinctive, functionally related cell types. Some of these cell types will be discussed later in this chapter. In plants limited to primary growth, the dermal system is composed of the **epidermis.** This tissue is one cell thick in most plants, and forms the outer protective covering of the plant. In young exposed parts of the plant, the epidermis is covered with a fatty **cutin** layer constituting the **cuticle;** in plants such as the desert succulents, a layer of wax may be added outside the cuticle. In plants with secondary growth, the bark forms the outer protective layer and is considered a part of the dermal tissue system.

Ground tissue consists primarily of thin-walled **parenchyma** cells that are initially (but briefly) more or less spherical. However, the cells, which have living protoplasts, push up against each other shortly after they are produced and assume other shapes, often ending up with 11 to 17 sides. Parenchyma cells may live for many years; they function in storage, photosynthesis, and secretion.

Vascular tissue includes two kinds of conducting tissues: (1) **xylem,** which conducts water and dissolved minerals; and (2) **phloem,** which conducts carbohydrates—mainly sucrose—used by plants for food. The phloem also transports hormones, amino acids, and other substances that are necessary for plant growth. Xylem and phloem differ in structure as well as in function.

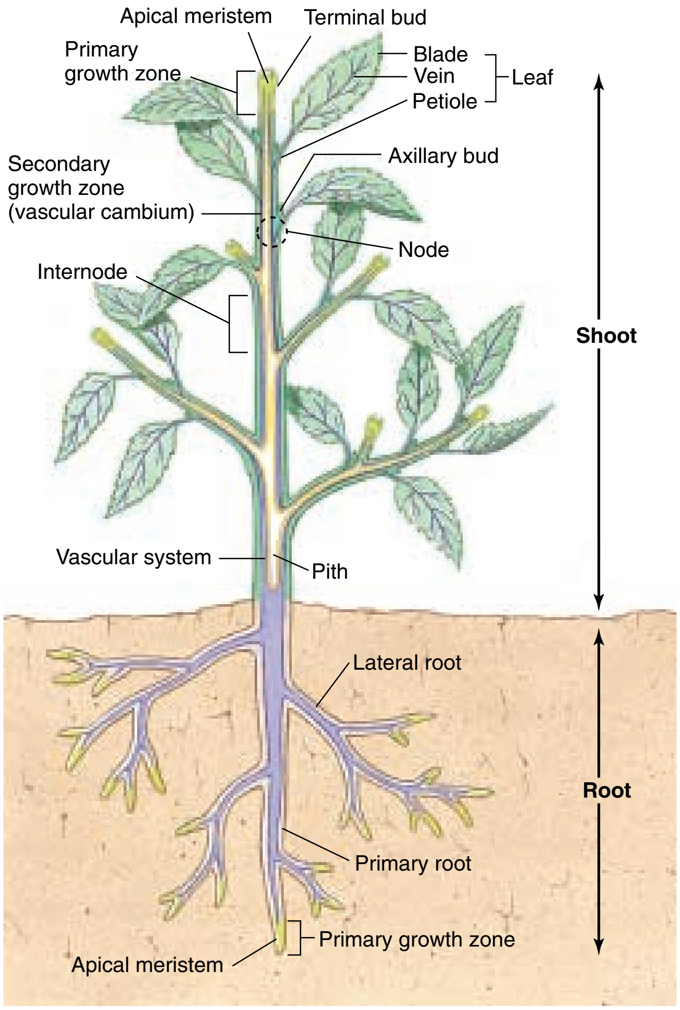


FIGURE 38.6
Diagram of a plant body. Branching in both the root and shoot system increases the number of apical meristems. A significant increase in stem/root circumference and the formation of bark can only occur if there is secondary growth initiated by vascular and cork cambium (secondary meristems). The lime green areas are zones of active elongation; secondary growth occurs in the lavender areas.

Root and shoot meristems give rise to a plant body with an extensive underground, branching root system and aboveground shoot system with reiterative units of advantageously placed leaves joined at the node of the plant, internode, and axillary buds.

Primary and Secondary Growth

Primary and secondary growth play important roles in establishing the basic body plan of the organism. Here we will look at how these meristems give rise to highly differentiated tissues that support the growing plant body. In the earliest vascular plants, the vascular tissues produced by primary meristems played the same conducting roles as they do in contemporary vascular plants. There was no differentiation of the plant body into stems, leaves, and roots. The presence of these three kinds of organs is a property of most modern plants. It reflects increasing specialization in relation to the demands of a terrestrial existence.

With the evolution of secondary growth, vascular plants could develop thick trunks and become treelike (figure 38.7). This evolutionary advance in the sporophyte generation made possible the development of forests and the domination of the land by plants. As discussed in chapter 37, reproductive constraints would have made secondary growth and increased height nonadaptive if it had occurred in the gametophyte generation. Judging from the fossil record, secondary growth evolved independently in several groups of vascular plants by the middle of the Devonian period 380 million years ago.

There were two types of conducting systems in the earliest plants—systems that have become characteristic of vascular plants as a group. *Sieve-tube members* conduct carbohydrates away from areas where they are manufactured or stored. *Vessel members* and *tracheids* are thick-walled cells that transport water and dissolved minerals up from the roots. Both kinds of cells are elongated and occur in linked strands making tubes. Sieve-tube members are characteristic of phloem tissue; vessel members and tracheids are characteristic of xylem tissue. In primary tissues, which result from primary growth, these two types of tissue are typically associated with each other in the same vascular strands. In secondary growth, the phloem is found on the periphery, while a very thick xylem core develops more centrally. You will see that roots and shoots of many vascular plants have different patterns of vascular tissue and secondary growth. Keep in mind that water and nutrients travel between the most distant tip of a redwood root and the tip of the shoot. For the system to work, these tissues connect, which they do in the transition zone between the root and the shoot. In the next section, we will consider the three tissue systems that are present in all plant organs, whether the plant has secondary growth or not.

Plants grow from the division of meristematic tissue. Primary growth results from cell division at the apical meristem at the tip of the plant, making the shoot longer. Secondary growth results from cell division at the lateral meristem in a cylinder encasing the shoot, and increases the shoot's girth.

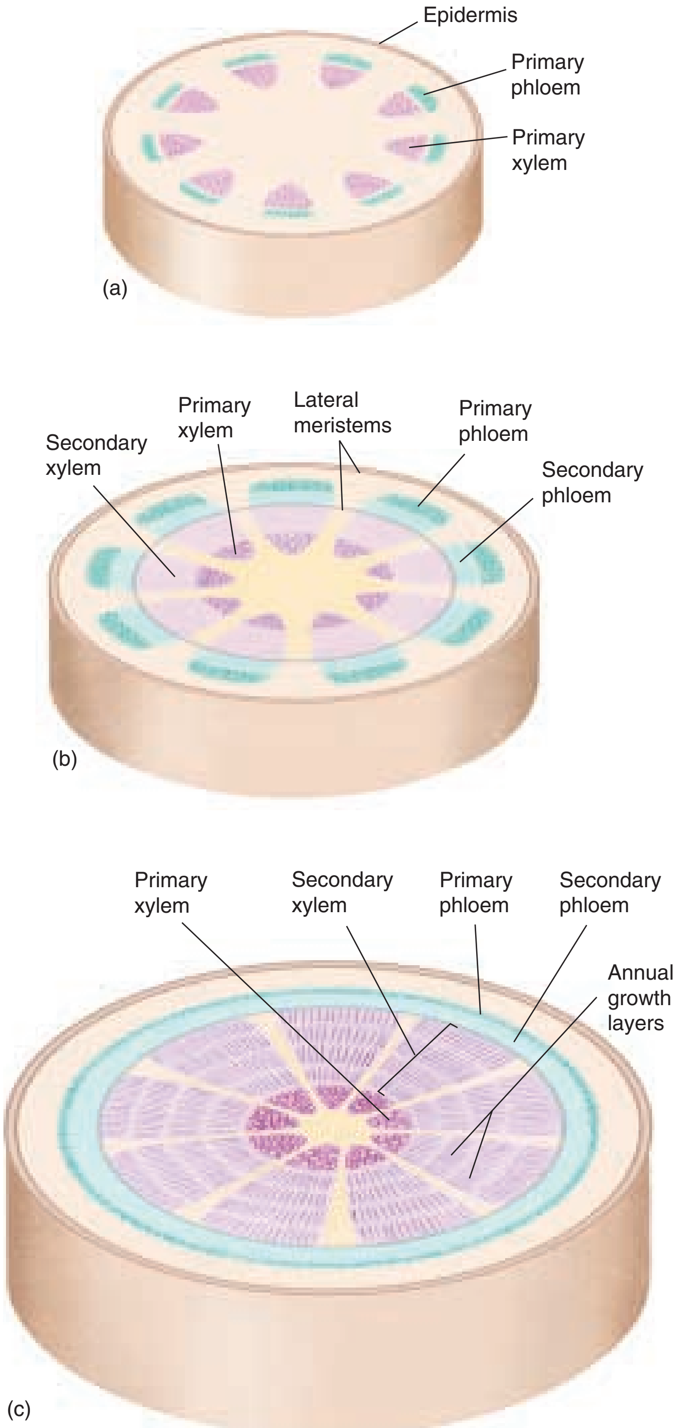


FIGURE 38.7
Secondary growth. (*a*) Before secondary growth begins, primary tissues continue to elongate as the apical meristems produce primary growth. (*b*) As secondary growth begins, the lateral meristems produce secondary tissues, and the stem's girth increases. (*c*) In this three-year-old stem, the secondary tissues continue to widen, and the trunk has become thick and woody. Note that the lateral meristems form cylinders that run axially in roots and shoots that have them.

38.2 Plants have three basic tissues, each composed of several cell types.

Dermal Tissue

Epidermal cells, which originate from the protoderm, cover all parts of the primary plant body. This is probably the earliest tissue system to appear in embryogenesis. The exposed outer walls have a cuticle that varies in thickness, depending on the species and environmental conditions. A number of types of specialized cells occur in the epidermis, including **guard cells, trichomes,** and **root hairs.**

Guard cells are paired sausage- or dumbbell-shaped cells flanking a **stoma** (plural, **stomata**), a mouth-shaped epidermal opening. Guard cells, unlike other epidermal cells, contain chloroplasts. Stomata occur in the epidermis of leaves (figure 38.8), and sometimes on other parts of the plant, such as stems or fruits. The passage of oxygen and carbon dioxide, as well as diffusion of water in vapor form, takes place almost exclusively through the stomata. There are between 1000 to more than 1 million stomata per square centimeter of leaf surface. In many plants, stomata are more numerous on the lower epidermis than on the upper epidermis of the leaf. Some plants have stomata only on the lower epidermis, and a few, such as water lilies, have them only on the upper epidermis.

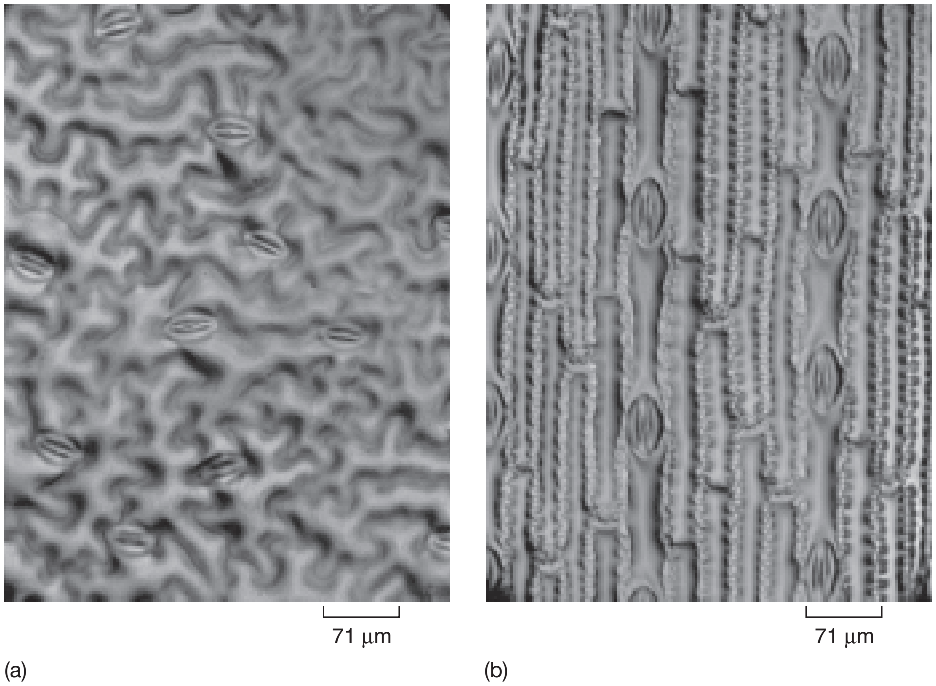


FIGURE 38.8
Epidermis of a dicot and monocot leaf (250×). Stomata are evenly distributed over the epidermis of monocots and dicots, but the patterning is quite different. (*a*) A pea (dicot) leaf with a random arrangement of stomata. (*b*) A corn leaf with stomata evenly spaced in rows. These photos also show the variety of cell shapes in plants. Some plant cells are boxlike, as seen in corn (*b*), while others are irregularly shaped, as seen in peas (*a*).

Guard cell formation is the result of an asymmetrical cell division just like we saw in the first cell division in an algal and angiosperm zygote. The patterning of these asymmetrical divisions resulting in stomatal distribution has intrigued developmental biologists. Research on mutants that get "confused" about where to position stomata are providing information on the timing of stomatal initiation and the kind of intercellular communication that triggers guard cell formation. For example, the *too many mouths* mutation may be caused by a failure of developing stomata to suppress stomatal formation in neighboring cells (figure 38.9).

The stomata open and shut in response to external factors such as light, temperature, and availability of water. During periods of active photosynthesis, the stomata are open, allowing the free passage of carbon dioxide into and oxygen out of the leaf. We will consider the mechanism that governs such movements in chapter 39.

Trichomes are hairlike outgrowths of the epidermis (figure 38.10). They occur frequently on stems, leaves, and reproductive organs. A "fuzzy" or "woolly" leaf is covered with trichomes that can be seen clearly with a microscope

FIGURE 38.9
The *too many mouths* stomatal mutant. This *Arabidopsis* plant lacks an essential signal for spacing guard cells.

under low magnification. Trichomes play an important role in keeping the leaf surface cool and in reducing the rate of evaporation. Trichomes vary greatly in form in different kinds of plants; some consist of a single cell, while others may consist of several cells. Some are glandular, often secreting sticky or toxic substances to deter herbivory.

Trichome development has been investigated extensively in *Arabidopsis*. Four genes are needed to specify the site of trichome formation and initiate it (figure 38.11). Next, eight genes are necessary for extension growth. Loss of function of any one of these genes results in a trichome with a distorted root hair. This is an example of taking a very simple system and trying to genetically dissect all the component parts. Understanding the formation of more complex plant parts is a major challenge.

Root hairs, which are tubular extensions of individual epidermal cells, occur in a zone just behind the tips of young, growing roots (see figure 38.3). Because a root hair is simply an extension and not a separate cell, there is no crosswall isolating it from the epidermal cell. Root hairs keep the root in intimate contact with the surrounding soil particles and greatly increase the root's surface area and the efficiency of absorption. As the root grows, the extent of the root hair zone remains roughly constant as root hairs at the older end slough off while new ones are produced at the other end. Most of the absorption of water and minerals occurs through root hairs, especially in herbaceous plants. Root hairs should not be confused with lateral roots which are multicellular and have their origins deep within the root.

In the case of secondary growth, the cork cambium (discussed in the section on stems in this chapter) produces the bark of a tree trunk or root. This replaces the epidermis which gets stretched and broken with the radial expansion of the axis. Epidermal cells generally lack the plasticity of other cells, but in some cases, they can fuse to the epidermal cells of another organ or organelle and dedifferentiate.

Some epidermal cells are specialized for protection, others for absorption. Spacing of these specialized cells within the epidermis maximizes their function and is an intriguing developmental puzzle.

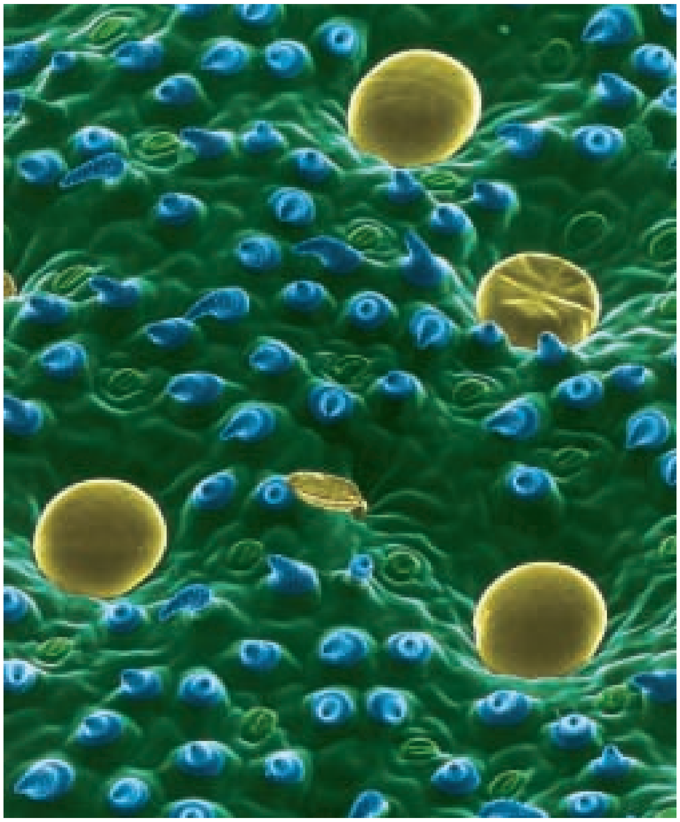


FIGURE 38.10
Trichomes. A covering of trichomes, teardrop-shaped blue structures above, creates a layer of more humid air near the leaf surface, enabling the plant to conserve available water supplies.

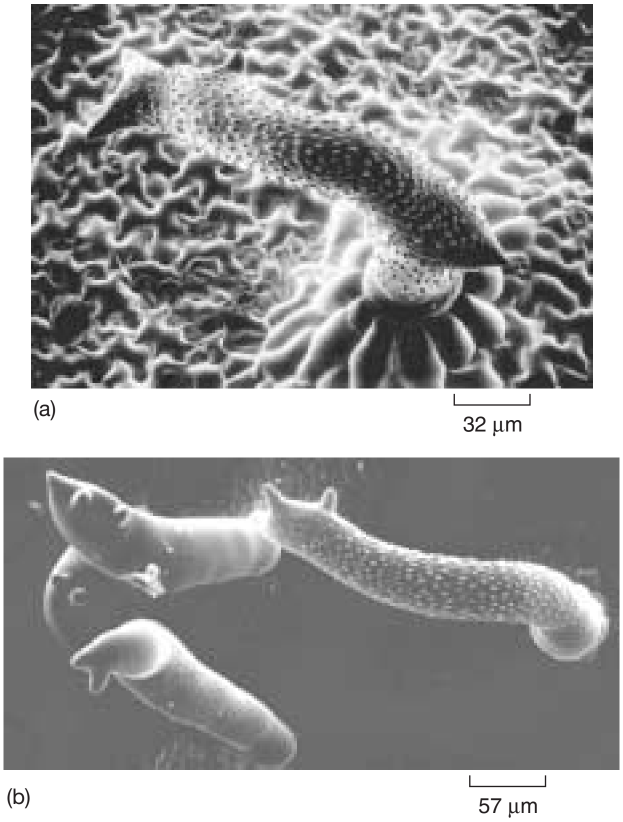


FIGURE 38.11
Trichome mutations. Mutants have revealed genes involved in a signal transduction pathway that regulates the spacing and development of trichomes. These include (*a*) *DISTORTED1* (*DIS1*) and (*b*) *DIS2* mutants in which trichomes are swollen and twisted.

Ground Tissue

Parenchyma

Parenchyma cells, which have large vacuoles, thin walls, and an average of 14 sides at maturity, are the most common type of plant cell. They are the most abundant cells of primary tissues and may also occur, to a much lesser extent, in secondary tissues (figure 38.12*a*). Most parenchyma cells have only primary walls, which are walls laid down while the cells are still maturing. Parenchyma are less specialized than other plant cells, although there are many variations that do have special functions such as nectar and resin secretion, or storage of latex, proteins, and metabolic wastes.

Parenchyma cells, which have functional nuclei and are capable of dividing, commonly also store food and water, and usually remain alive after they mature; in some plants (for example, cacti), they may live to be over 100 years old. The majority of cells in fruits such as apples are parenchyma. Some parenchyma contain chloroplasts, especially in leaves and in the outer parts of herbaceous stems. Such photosynthetic parenchyma tissue is called *chlorenchyma.*

Collenchyma

Collenchyma cells, like parenchyma cells, have living protoplasts and may live for many years. The cells, which are usually a little longer than wide, have walls that vary in thickness (figure 38.12*b*). Collenchyma cells, which are relatively flexible, provide support for plant organs, allowing them to bend without breaking. They often form strands or continuous cylinders beneath the epidermis of stems or leaf petioles (stalks) and along the veins in leaves. Strands of collenchyma provide much of the support for stems in which secondary growth has not taken place. The parts of celery that we eat (petioles, or leaf stalks), have "strings" that consist mainly of collenchyma and vascular bundles (conducting tissues).

Sclerenchyma

Sclerenchyma cells have tough, thick walls; they usually lack living protoplasts when they are mature. Their secondary cell walls are often impregnated with **lignin,** a highly branched polymer that makes cell walls more rigid. Cell walls containing lignin are said to be **lignified.** Lignin is common in the walls of plant cells that have a supporting or mechanical function. Some kinds of cells have lignin deposited in primary as well as secondary cell walls.

There are two types of sclerenchyma: fibers and sclereids. **Fibers** are long, slender cells that are usually grouped together in strands. Linen, for example, is woven from strands of sclerenchyma fibers that occur in the phloem of flax. **Sclereids** are variable in shape but often branched. They may occur singly or in groups; they are not elongated, but may have various forms, including that of a star. The gritty texture of a pear is caused by groups of sclereids that occur throughout the soft flesh of the fruit (figure 38.12*c*). Both of these tough, thick-walled cell types serve to strengthen the tissues in which they occur.

Parenchyma cells are the most common type of plant cells and have various functions. Collenchyma cells provide much of the support in young stems and leaves. Sclerenchyma cells strengthen plant tissues and may be nonliving at maturity.

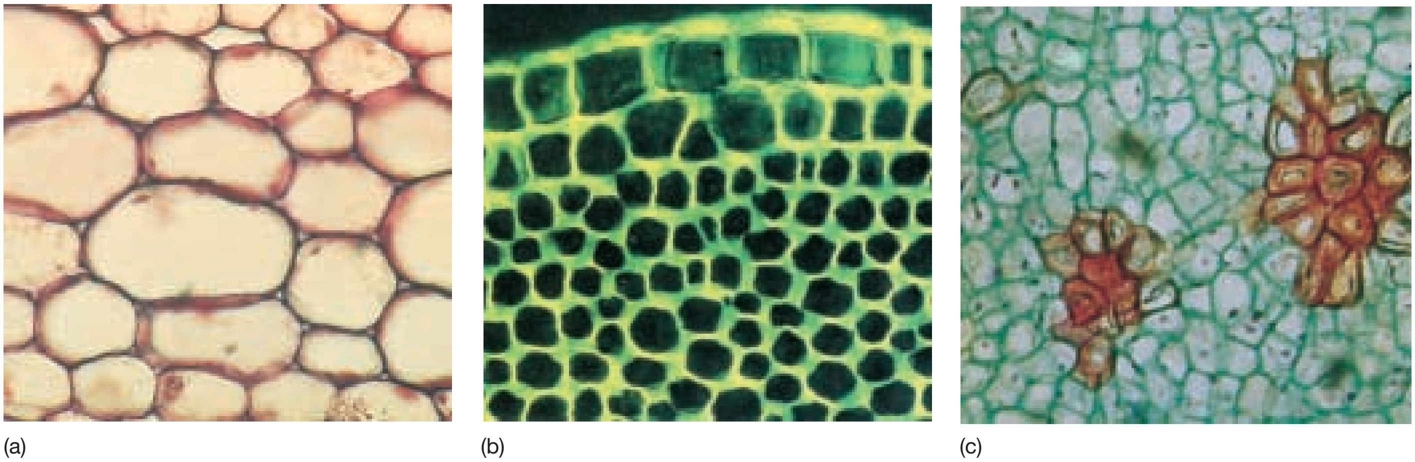

(a) (b) (c)

FIGURE 38.12
The three types of ground tissue. (*a*) Parenchyma cells. Only primary cell walls are seen in this cross-section of parenchyma cells from grass. (*b*) Collenchyma cells. Thickened side walls are seen in this cross-section of collenchyma cells from a young branch of elderberry (*Sambucus*). In other kinds of collenchyma cells, the thickened areas may occur at the corners of the cells or in other kinds of strips. (*c*) Sclereids. Clusters of sclereids ("stone cells"), stained red in this preparation, in the pulp of a pear. The surrounding thin-walled cells, stained light blue, are *parenchyma.* These sclereid clusters give pears their gritty texture.

Vascular Tissue

Xylem

Xylem, the principal water-conducting tissues of plants, usually contains a combination of **vessels,** which are continuous tubes formed from dead, hollow, cylindrical cells **(vessel members)** arranged end to end, and **tracheids,** which are dead cells that taper at the ends and overlap one another (figure 38.13). In some plants, such as gymnosperms, tracheids are the only water-conducting cells present; water passes in an unbroken stream through the xylem from the roots up through the shoot and into the leaves. When the water reaches the leaves, much of it passes into a film of water on the outside of the parenchyma cells, and then it diffuses in the form of water vapor into the intercellular spaces and out of the leaves into the surrounding air, mainly through the stomata. This diffusion of water vapor from a plant is known as **transpiration.** In addition to conducting water, dissolved minerals, and inorganic ions such as nitrates and phosphates throughout the plant, xylem supplies support for the plant body.

Primary xylem is derived from the procambium, which comes from the apical meristem. *Secondary xylem* is formed by the vascular cambium, a lateral meristem that develops later. Wood consists of accumulated secondary xylem.

Vessel members are found almost exclusively in angiosperms. In primitive angiosperms, vessel members tend to resemble fibers and are relatively long. In more advanced angiosperms, vessel members tend to be shorter and wider, resembling microscopic, squat coffee cans with both ends removed. Both vessel members and tracheids have thick, lignified secondary walls and no living protoplasts at maturity. Lignin is produced by the cell and secreted to strengthen the cellulose cell walls before the protoplast dies, leaving only the cell wall. When the continuous stream of water in a plant flows through tracheids, it passes through **pits,** which are small, mostly rounded-to-elliptical areas where no secondary wall material has been deposited. The pits of adjacent cells occur opposite one another. In contrast, vessel members, which are joined end to end, may be almost completely open or may have bars or strips of wall material across the open ends.

Vessels appear to conduct water more efficiently than do the overlapping strands of tracheids. We know this partly because vessel members have evolved from tracheids independently in several groups of plants, suggesting that they are favored by natural selection. It is also probable that some types of fibers have evolved from tracheids, becoming specialized for strengthening rather than conducting. Some ancient flowering plants have only tracheids, but virtually all modern angiosperms have vessels. Plants, with a mutation that prevents the differentiation of xylem, but does not affect tracheids, wilt soon after germination and are unable to transport water efficiently.

In addition to conducting cells, xylem typically includes fibers and parenchyma cells (ground tissue cells). The parenchyma cells, which are usually produced in horizontal rows called **rays** by special *ray initials* of the vascular cambium, function in lateral conduction and food storage. An initial is another term for a meristematic cell. It divides to produce another initial and a cell that differentiates into a ray cell. In cross-sections of woody stems and roots, the rays can be seen radiating out from the center of the xylem like the spokes of a wheel. Fibers are abundant in some kinds of wood, such as oak (*Quercus*), and the wood is correspondingly dense and heavy. The arrangements of these and other kinds of cells in the xylem make it possible to identify most plant genera and many species from their wood alone. These fibers are a major component in modern paper. Earlier paper was made from fibers in phloem.

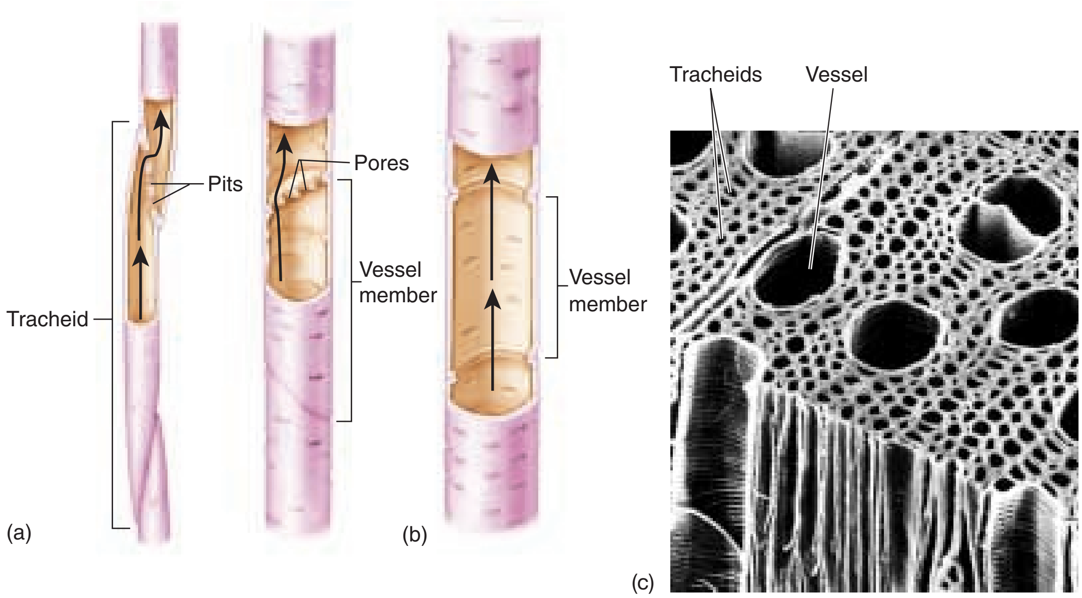


FIGURE 38.13
Comparison between vessel members and tracheids. (*a*) In tracheids, the water passes from cell to cell by means of pits, (*b*) while in vessel members, it moves by way of perforation plates or between bars of wall material. In gymnosperm wood, tracheids both conduct water and provide support; in most kinds of angiosperms, vessels are present in addition to tracheids, or present exclusively. These two types of cells conduct the water, and fibers provide additional support. (*c*) Scanning micrograph of the wood of red maple, *Acer rubrum* (350×).

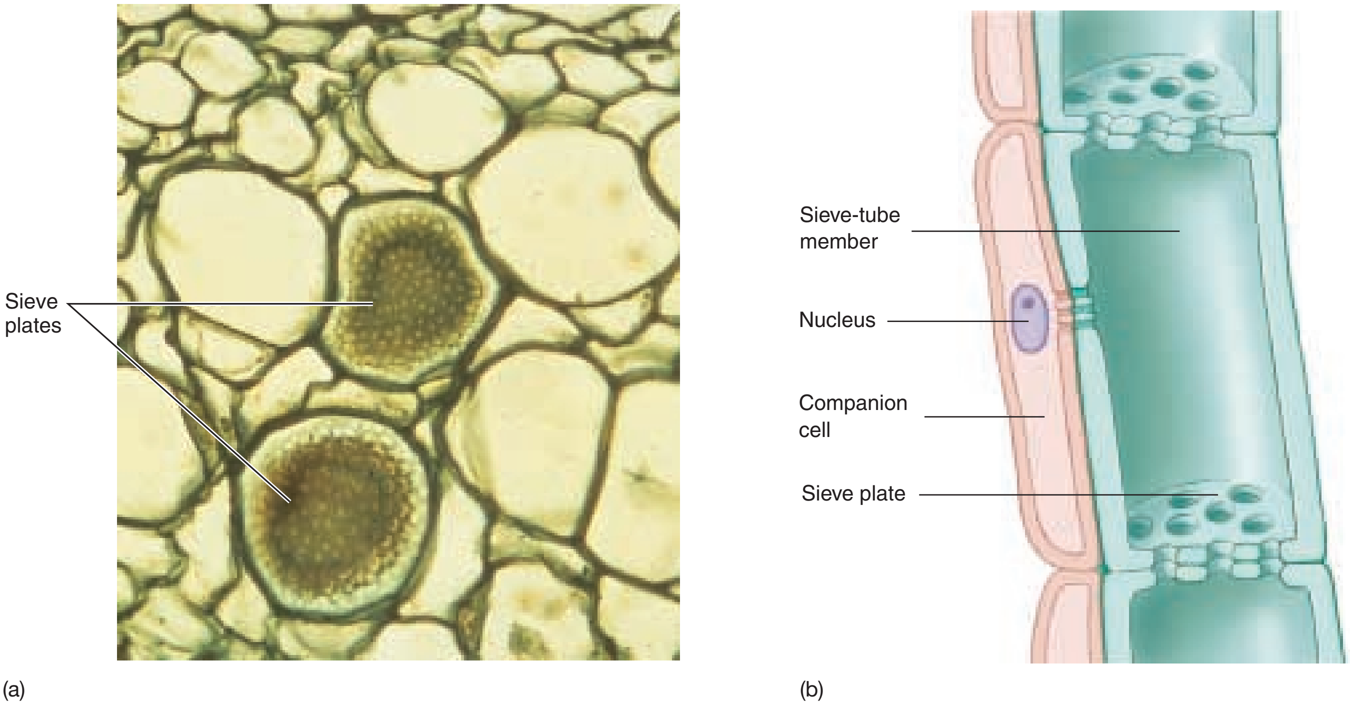


FIGURE 38.14
A sieve-tube member. (*a*) Looking down into sieve plates in squash phloem reveals the perforations sucrose and hormones move through. (*b*) Sieve-tube member cells are stacked with the sieve plates forming the connection. The narrow cell with the nucleus at the left of the sieve-tube member is a companion cell. This cell nourishes the sieve-tube members, which have plasma membranes, but no nuclei.

Phloem

Phloem, which is located toward the outer part of roots and stems, is the principal food-conducting tissue in vascular plants. If a plant is *girdled* (by removing a substantial strip of bark down to the vascular cambium), the plant eventually dies from starvation of the roots.

Food conduction in phloem is carried out through two kinds of elongated cells: **sieve cells** and **sieve-tube members** (figure 38.14). Seedless vascular plants and gymnosperms have only sieve cells; most angiosperms have sieve-tube members. Both types of cells have clusters of pores known as **sieve areas.** Sieve areas are more abundant on the overlapping ends of the cells and connect the protoplasts of adjoining sieve cells and sieve-tube members. Both of these types of cells are living, but most sieve cells and all sieve-tube members lack a nucleus at maturity. This type of cell differentiation has parallels to the differentiation of human red blood cells which also lack a nucleus at maturity.

In sieve-tube members, some sieve areas have larger pores and are called **sieve plates.** Sieve-tube members occur end to end, forming longitudinal series called **sieve tubes.** Sieve cells are less specialized than sieve-tube members, and the pores in all of their sieve areas are roughly of the same diameter. In an evolutionary sense, sieve-tube members are more advanced, more specialized, and, presumably, more efficient.

Each sieve-tube member is associated with an adjacent specialized parenchyma cell known as a **companion cell.** Companion cells apparently carry out some of the metabolic functions that are needed to maintain the associated sieve-tube member. In angiosperms, a common initial cell divides asymmetrically to produce a sieve-tube member cell and its companion cell. Companion cells have all of the components of normal parenchyma cells, including nuclei, and their numerous **plasmodesmata** (cytoplasmic connections between adjacent cells) connect their cytoplasm with that of the associated sieve-tube members. Fibers and parenchyma cells are often abundant in phloem.

Xylem conducts water and dissolved minerals from the roots to the shoots and the leaves. Phloem carries organic materials from one part of the plant to another.

38.3 Root cells differentiate as they become distanced from the dividing root apical meristem.

Root Structure

The three tissue systems are found in the three kinds of vegetative organs in plants: **roots, stems,** and **leaves.** Roots have a simpler pattern of organization and development than stems, and we will consider them first. Four zones or regions are commonly recognized in developing roots. The zones are called the **root cap,** the **zone of cell division,** the **zone of elongation,** and the **zone of maturation** (figure 38.15). In three of the zones, the boundaries are not clearly defined. When apical initials divide, daughter cells that end up on the tip end of the root become root cap cells. Cells that divide in the opposite direction pass through the three other zones before they finish differentiating. As you consider the different zones, visualize the tip of the root moving away from the soil surface by growth. This will counter the static image of a root that diagrams and photos convey.

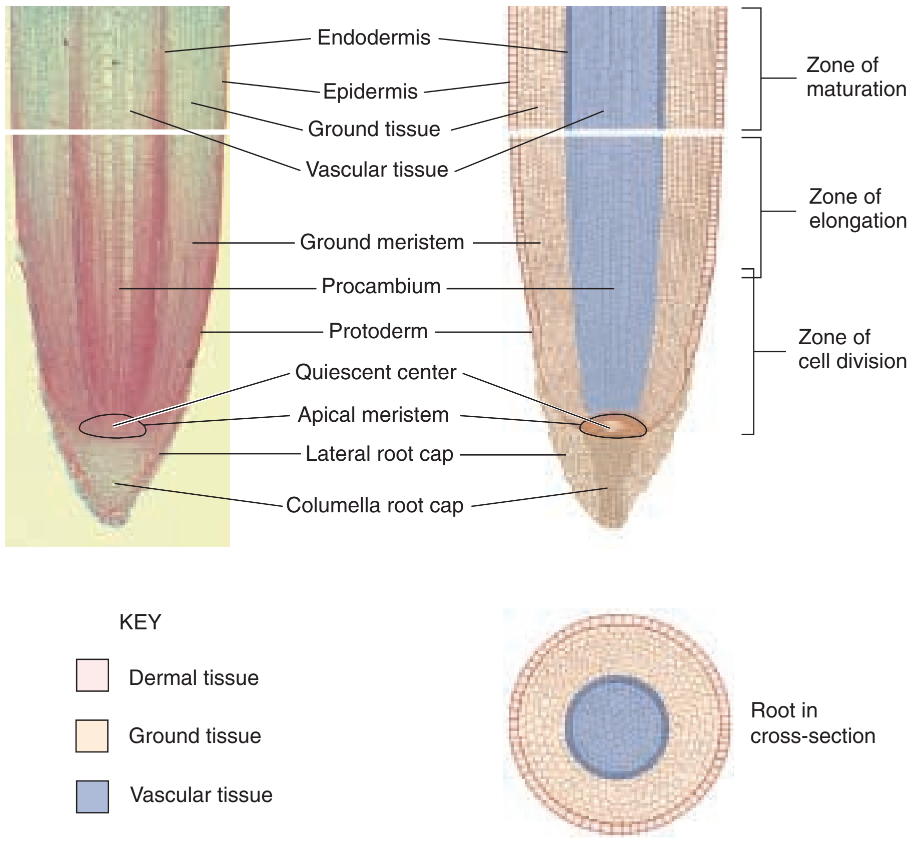


FIGURE 38.15
Root structure. A root tip in corn, *Zea mays.* This longitudinal section of a root shows the root cap, apical meristem, procambium, protoderm, epidermis, and ground meristem.

The Root Cap

The root cap has no equivalent in stems. It is composed of two types of cells, the inner columella (they look like columns) cells and the outer, lateral root cap cells that are continuously replenished by the root apical meristem. In some plants with larger roots it is quite obvious. Its most obvious function is to protect the delicate tissues behind it as growth extends the root through mostly abrasive soil particles. Golgi bodies in the outer root cap cells secrete and release a slimy substance that passes through the cell walls to the outside. The cells, which have an average life of less than a week, are constantly being replaced from the inside, forming a mucilaginous lubricant that eases the root through the soil. The slimy mass also provides a medium for the growth of beneficial nitrogen-fixing bacteria in the roots of some plants such as legumes.

A new root cap is produced when an existing one is artificially or accidentally removed from a root. The root cap also functions in the *perception of gravity.* The columella cells are highly specialized with the endoplasmic reticulum in the periphery and the nucleus located at either the middle or the top of the cell. There are no large vacuoles. Columella cells contain amyloplasts (plastids with starch grains) that collect on the sides of cells facing the pull of gravity. When a potted plant is placed on its side, the amyloplasts drift or tumble down to the side nearest the source of gravity, and the root bends in that direction. Lasers have been used to ablate (kill) individual columella cells in *Arabidopsis.* It turns out that only two of the columella cells are essential for gravity sensing! The precise nature of the gravitational response is not known, but some evidence indicates that calcium ions in the amyloplasts influence the distribution of growth hormones (auxin in this case) in the cells. There may be multiple signaling mechanisms because bending has been observed in the absence of auxin. A current hypothesis is that an electrical signal moves from the columella cell to cells in the distal region of the elongation zone (the region closest to the zone of cell division).

The Zone of Cell Division

The apical meristem is shaped like an inverted, concave dome of cells and is located in the center of the root tip in the area protected by the root cap. Most of the activity in this *zone of cell division* takes place toward the edges of the dome, where the cells divide every 12 to 36 hours, often rhythmically, reaching a peak of division once or twice a day. Most of the cells are essentially cuboidal with small vacuoles and proportionately large, centrally located nuclei. These rapidly dividing cells are daughter cells of the apical meristem. The *quiescent center* is a group of cells in the center of the root apical meristem. They divide very infrequently. This makes sense if you think about a solid ball expanding. The outer surface would have to increase far more rapidly than the very center.

The apical meristem daughter cells soon subdivide into the three primary tissue systems previously discussed: *protoderm*, *procambium*, and *ground meristem*. Genes have been identified in the relatively simple root of *Arabidopsis* that regulate the patterning of these tissue systems. The patterning of these cells begins in this zone, but it is not until the cells reach the zone of maturation that the anatomical and morphological expression of this patterning is fully revealed. *WEREWOLF*, for example, is required for the patterning of the two root epidermal cell types, those with and without root hairs (figure 38.16*a*). The *SCARECROW* gene is important in ground cell differentiation (figure 38.16*b*). It is necessary for an asymmetric cell division that gives rise to two cylinders of cells from one. The outer cell layer becomes ground tissue and serves a storage function. The inner cell layer forms the endodermis which regulates the intercellular flow of water and solutes into the vascular core of the root. Cells in this region develop according to their position. If that position changes because of a mistake in cell division or the ablation of another cell, the cell develops according to its new position.

The Zone of Elongation

In the *zone of elongation*, the cells produced by the primary meristems become several times longer than wide, and their width also increases slightly. The small vacuoles present merge and grow until they occupy 90% or more of the volume of each cell. No further increase in cell size occurs above the zone of elongation, and the mature parts of the root, except for an increase in girth, remain stationary for the life of the plant.

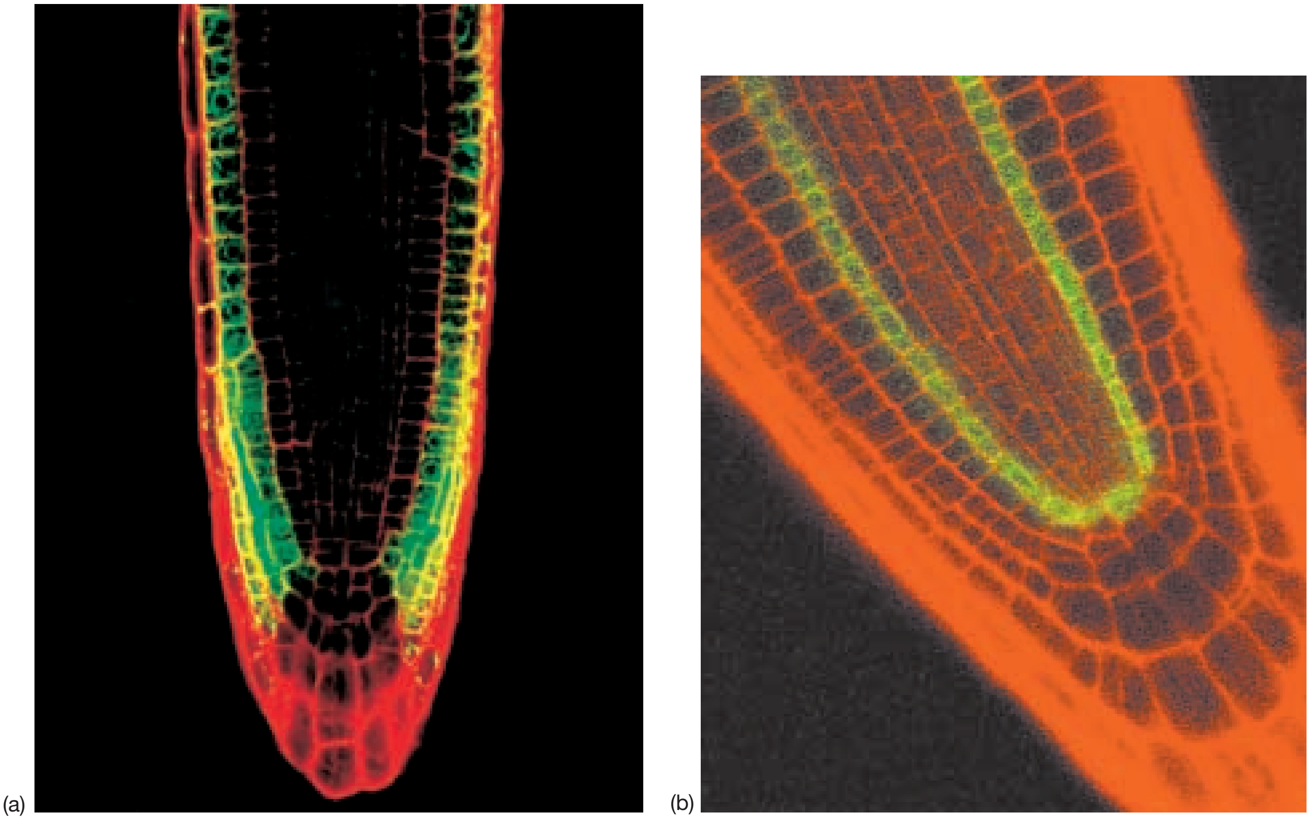


FIGURE 38.16
Tissue-specific gene expression. (*a*) Epidermal-specific gene expression. The promoter of the *WEREWOLF* gene of *Arabidopsis* was attached to a green fluorescent protein and used to make a transgenic plant. The green fluorescence shows the epidermal cells where the gene is expressed. The red was used to visually indicate cell boundaries. (*b*) Ground tissue-specific gene expression. The *SCARECROW* gene is needed for an asymmetric cell division allowing for the formation of side-by-side ground tissue and endodermal cells. These two layers are blue in wild-type, but in the mutant, only one cell layer is blue because the asymmetric cell division does not occur.

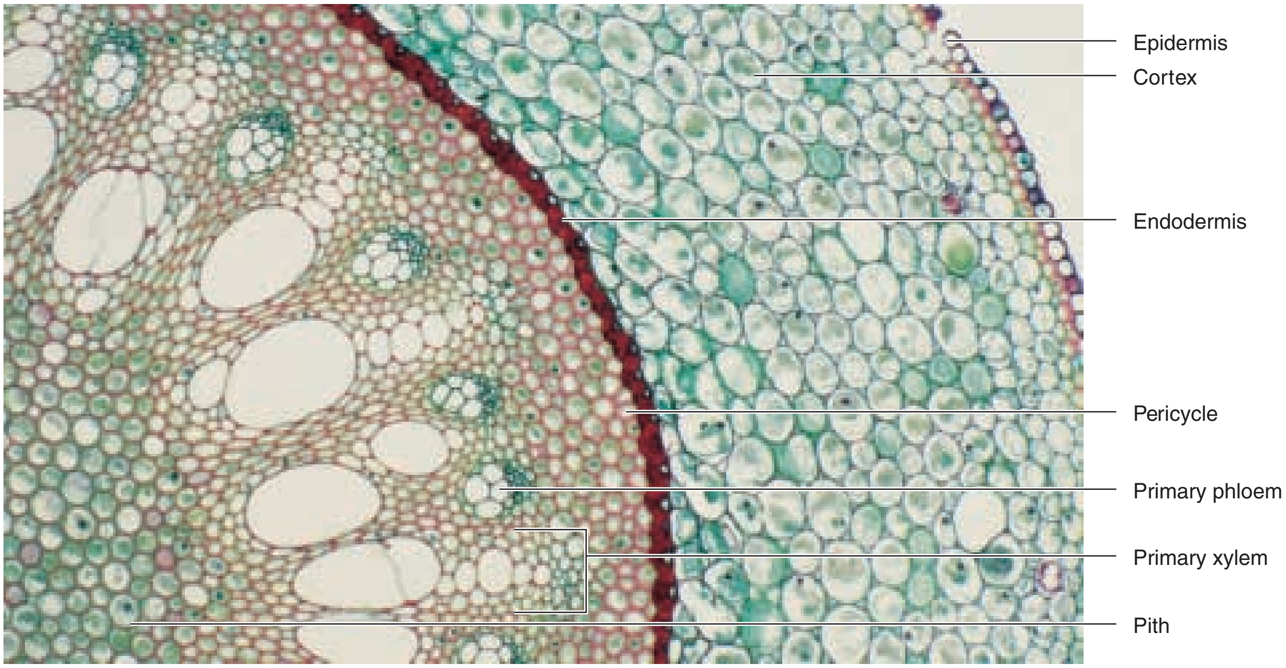


FIGURE 38.17
Cross-section of the zone of maturation of a young monocot root. Greenbrier (*Smilax*), a monocot (100×).

The Zone of Maturation

The cells that have elongated in the zone of elongation become differentiated into specific cell types in the *zone of maturation.* The cells of the root surface cylinder mature into *epidermal cells*, which have a very thin cuticle. Many of the epidermal cells each develop a **root hair;** the protuberance is not separated by a crosswall from the main part of the cell and the nucleus may move into it. Root hairs, which can number over 35,000 per square centimeter of root surface and many billions per plant, greatly increase the surface area and therefore the absorptive capacity of the root. The root hairs usually are alive and functional for only a few days before they are sloughed off at the older part of the zone of maturation, while new ones are being produced toward the zone of elongation. 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 nodule around it.

Parenchyma cells are produced by the ground meristem immediately to the interior of the epidermis. This tissue, called the **cortex,** may be many cells wide and functions in food storage. The inner boundary of the cortex differentiates into a single-layered cylinder of **endodermis** (figure 38.17), whose 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 (figure 38.18). This blocks transport between cells. The two surfaces that are parallel to the root surface are the only way into the core of the root and the cell membranes control what passes through.

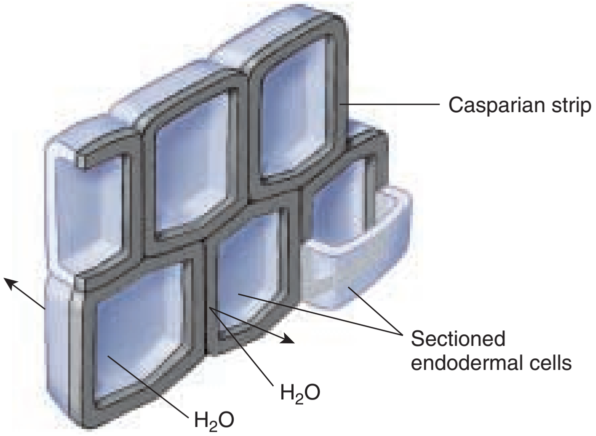


FIGURE 38.18
Casparian strip. The Casparian strip is a water-proofing band that protects cells inside the endodermis from flooding.

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 can divide, even after they mature. They can give rise to *lateral* (branch) *roots* or, in dicots, to part of the *vascular cambium.*

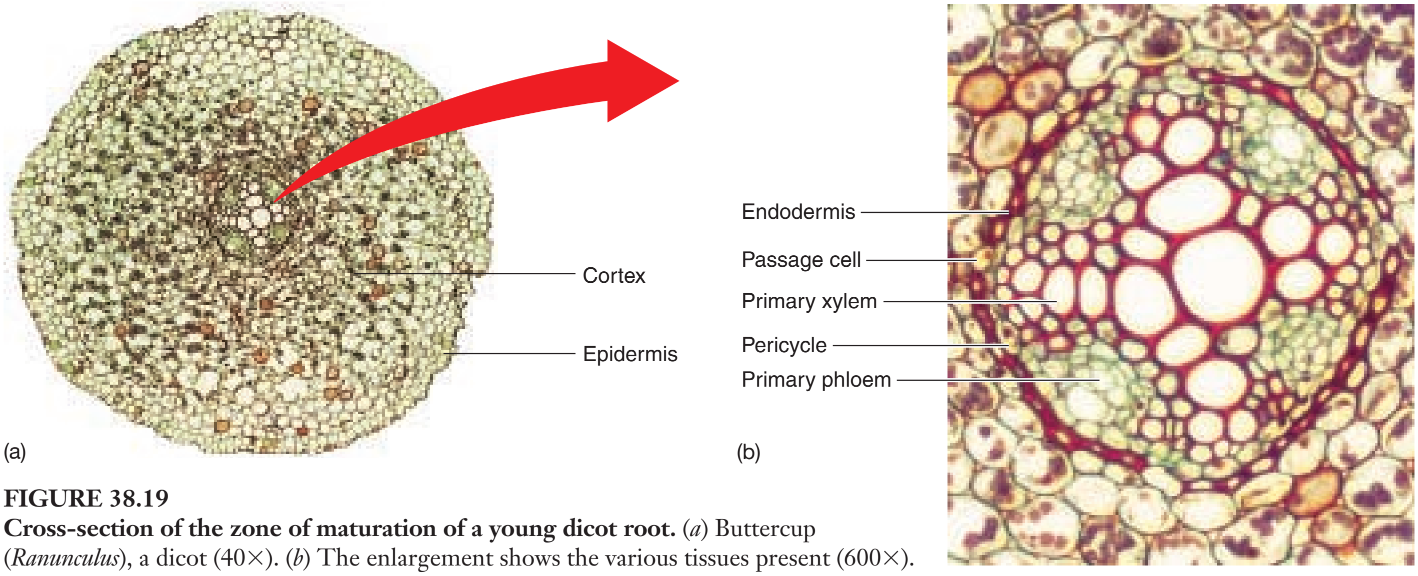


FIGURE 38.19
Cross-section of the zone of maturation of a young dicot root. (*a*) Buttercup (*Ranunculus*), a dicot (40×). (*b*) The enlargement shows the various tissues present (600×).

The water-conducting cells of the *primary xylem* are differentiated as a solid core in the center of young dicot roots. In a cross-section of a dicot root, the central core of primary xylem often is somewhat star-shaped, with one or two to several radiating arms that point toward the pericycle (figure 38.19). In monocot (and a few dicot) roots, the primary xylem is in discrete **vascular bundles** arranged in a ring, which surrounds parenchyma cells, called **pith,** at the very center of the root. **Primary phloem,** composed of cells involved in food conduction, is differentiated in discrete groups of cells between the arms of the xylem in both dicot and monocot roots.

In dicots and other plants with **secondary growth,** part of the pericycle and the parenchyma cells between the phloem patches and the xylem arms become the root vascular cambium, which starts producing **secondary xylem** to the inside and **secondary phloem** to the outside (figure 38.20). 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 produces bark which will be discussed in the section on stems (see figure 38.26). In the case of secondary growth in dicot roots, everything outside the stele is lost and replaced with bark.

Root apical meristems produce a root cap at the tip and root tissue on the opposite side. Cells mature as the root cap and meristem grows away from them. Transport systems, external barriers, and a branching root system develop from the primary root as it matures.

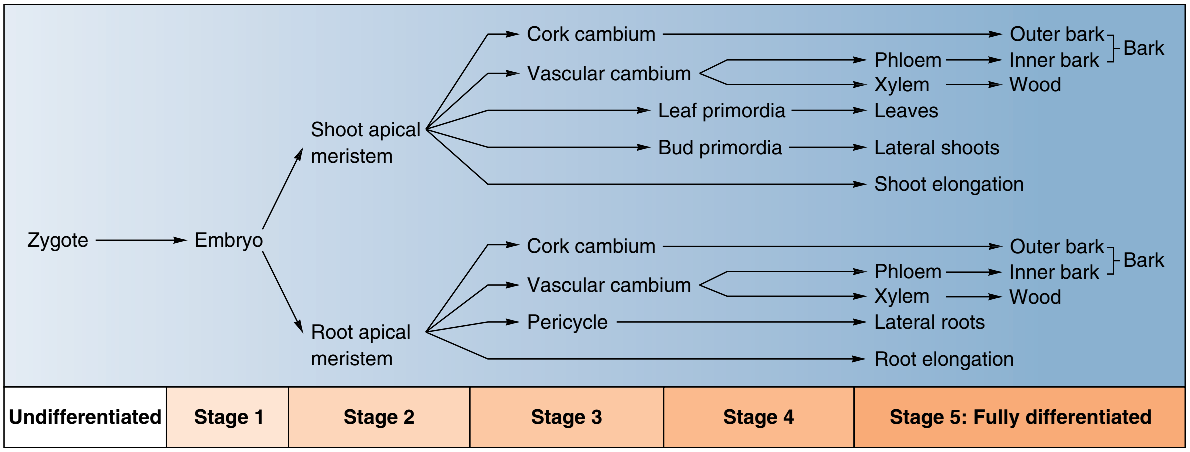


FIGURE 38.20
Stages in the differentiation of plant tissues.

Modified Roots

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

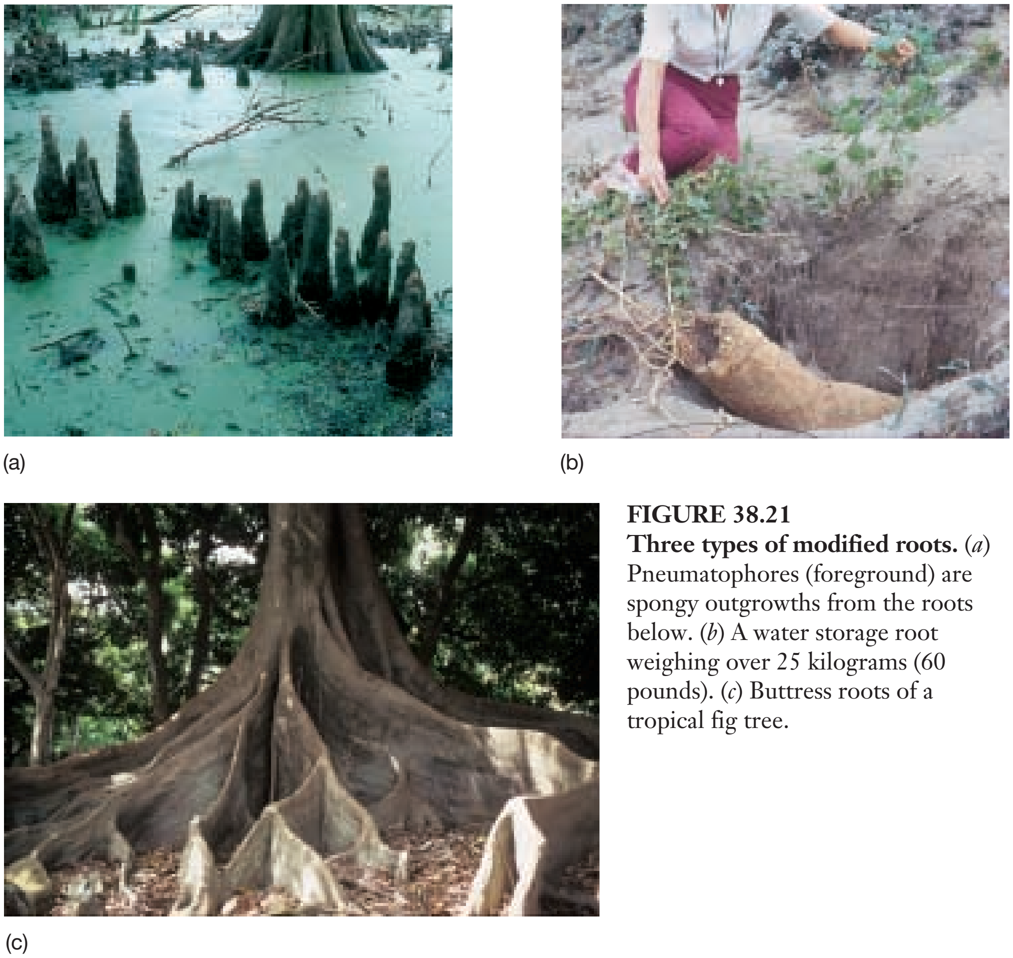

(a) (b) (c)

FIGURE 38.21
Three types of modified roots. (*a*) Pneumatophores (foreground) are spongy outgrowths from the roots below. (*b*) A water storage root weighing over 25 kilograms (60 pounds). (*c*) Buttress roots of a tropical fig tree.

Aerial roots. Some plants, such as epiphytic orchids (orchids that are attached to tree branches and grow unconnected to the ground without being parasitic in any way) have roots that extend out into the air. Some aerial roots have an epidermis that is several cells thick, an adaptation to reduce water loss. These aerial roots may also be green and photosynthetic, as in the vanilla orchid. Some monocots, such as corn, produce thick roots from the lower parts of the stem; these *prop roots* grow down to the ground and brace the plants against wind. Climbing plants such as ivy also produce roots from their stems; these anchor the stems to tree trunks or a brick wall. Any root that arises along a stem or in some place other than the root of the plant is called an *adventitious root.* Adventitious root formation in ivy depends on the developmental stage of the shoot. When the shoot transitions to the adult phase of development, it is no longer capable of initiating these roots.

Pneumatophores. Some plants that grow in swamps and other wet places may produce spongy outgrowths called *pneumatophores* from their underwater roots (figure 38.21*a*). The pneumatophores commonly extend several centimeters above water, facilitating the oxygen supply to the roots beneath.

Contractile roots. The roots from the bulbs of lilies and of 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 temperatures. The roots may contract to a third of 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*), 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.

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.

Water storage roots. Some members of the pumpkin family (Cucurbitaceae), especially those that grow in arid regions, may produce water-storage roots weighing 50 or more kilograms (figure 38.21*b*).

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 38.21*c*).

Some plants have modified roots that carry out photosynthesis, gather oxygen, parasitize other plants, store food or water, or support the stem.

38.4 Stems are the backbone of the shoot, transporting nutrients and supporting the aerial plant organs.

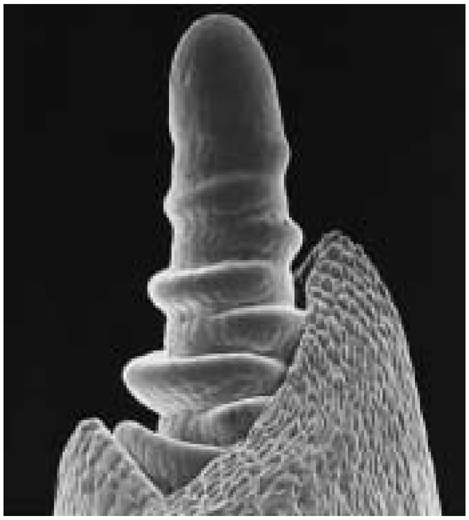


FIGURE 38.22
A shoot apex (200×). Scanning electron micrograph of the apical meristem of wheat (*Triticum*).

Stem Structure

External Form

The shoot apical meristem initiates stem tissue and intermittently produces bulges (**primordia**) that will develop into leaves, other shoots, or even flowers (figure 38.22). The stem is an axis from which organs grow. Leaves may be arranged in a spiral around the stem, or they may be in pairs opposite one another; they also may occur in *whorls* (circles) of three or more. Spirals are 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, that is found in nature (the angle of coiling in some shells, for example), classical architecture (the Parthenon wall dimensions), and even modern art (Mondrian). The pattern of leaf arrangement is called **phyllotaxy** and may optimize exposure of leaves to the sun.

The *region* or *area* (no structure is involved) of leaf attachment 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). When the petiole is missing, the leaf is then said to be **sessile.** Note that the word *sessile* as applied to plants has a different meaning than it does when applied to animals (probably obvious, as plants don't get up and move around!); in plants, it means *immobile* or *attached*. The space between a 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, which, with its associated leaf primordia, is called a **terminal bud.** Axillary buds frequently develop into branches or may form meristems that will develop into flowers. (Refer back to figure 38.6 to review these terms.)

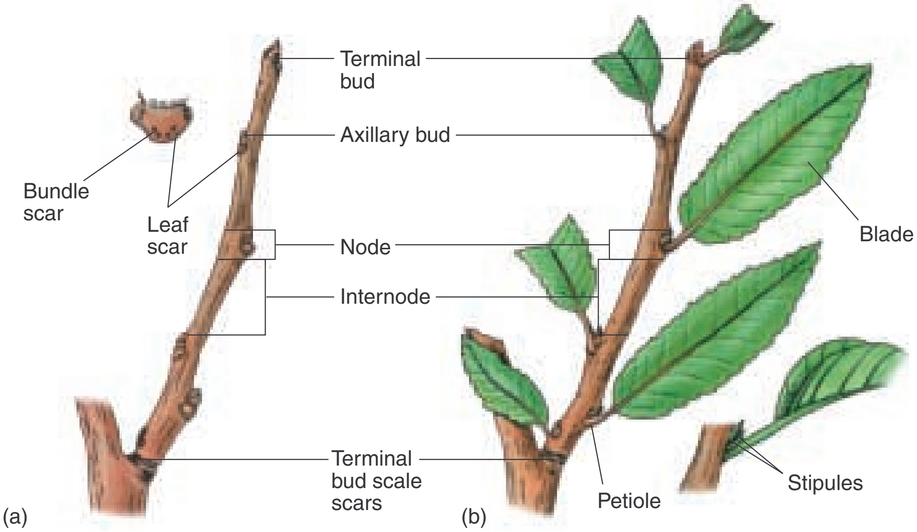


FIGURE 38.23
A woody twig. (*a*) In winter. (*b*) In summer.

Herbaceous stems do not produce a cork cambium. The stems 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. Terminal buds usually extend the length of the shoot 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 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 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 the plants in winter (figure 38.23).

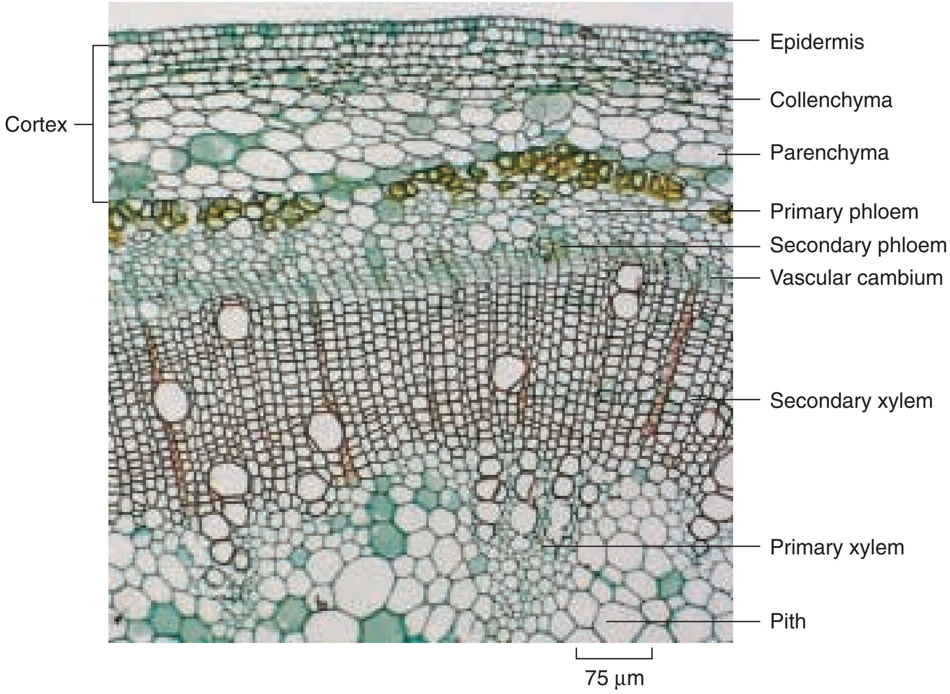


FIGURE 38.24
Early stage in differentiation of vascular cambium in the castor bean, *Ricirus* (25x). The outer part of the cortex consists of collenchyma, and the inner part of parenchyma.

Internal Form

As in roots, there is an *apical meristem* at the tip of each stem, which produces *primary tissues* that contribute to the stem's increases in length. Three primary meristems develop from the apical meristem. The *protoderm* gives rise to the *epidermis.* The *ground meristem* produces parenchyma cells. Parenchyma cells in the center of the stem constitute the *pith;* parenchyma cells away from the center constitute the *cortex.* The *procambium* produces cylinders of *primary xylem* and *primary phloem*, which are surrounded by ground tissue.

A strand of xylem and phloem, called a *trace*, branches off from the main cylinder of xylem and phloem and enters the developing leaf, flower, or shoot. These spaces in the main cylinder of conducting tissues are called **gaps.** In dicots, a **vascular cambium** develops between the primary xylem and primary phloem (figure 38.24). In many ways, this is a connect-the-dots game where the vascular cambium connects the ring of primary vascular bundles. In monocots, these bundles are scattered throughout the ground tissue (figure 38.25) and there is no logical way to connect them that would allow a uniform increase in girth. This is why monocots do not have secondary growth.

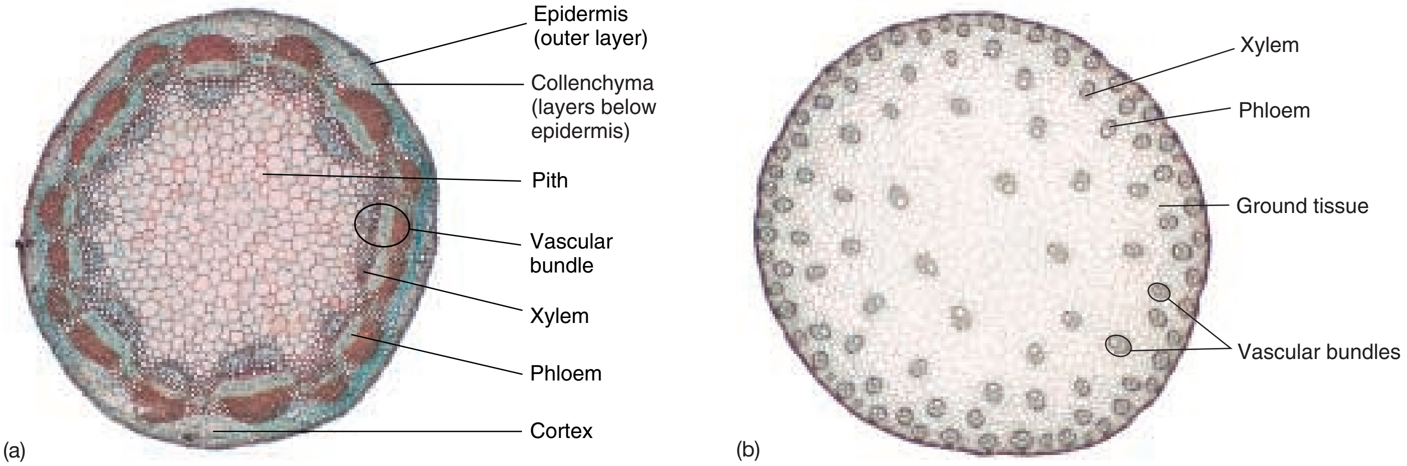


FIGURE 38.25
Stems. Transverse sections of a young stem in (*a*) a dicot, the common sunflower, *Helianthus annuus*, in which the vascular bundles are arranged around the outside of the stem (10×); and (*b*) a monocot, corn, *Zea mays*, with the scattered vascular bundles characteristic of the class (5×).

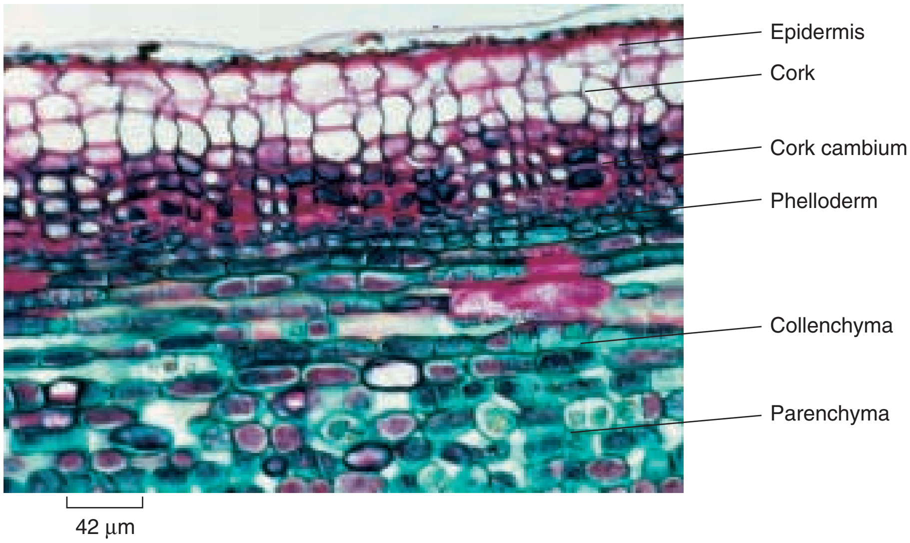


FIGURE 38.26
Section of periderm (50×). An early stage in the development of periderm in cottonwood (*Populus* sp.).

The cells of the vascular cambium divide indefinitely, producing **secondary tissues** (mainly *secondary xylem* and *secondary phloem*). The production of xylem is extensive in trees and is called wood. Rings in the stump of a tree reveal annual patterns of growth; cell size varies depending on growth conditions. In woody dicots, a second cambium, the *cork cambium*, arises in the outer cortex (occasionally in the epidermis or phloem) and produces boxlike *cork cells* to the outside and also may produce parenchyma-like *phelloderm* cells to the inside; the cork cambium, cork, and phelloderm are collectively referred to as the *periderm* (figure 38.26). Cork tissues, whose cells become impregnated with *suberin* shortly after they are formed and then die, constitute the **outer bark.** The cork tissue, whose suberin is impervious to moisture, 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 38.27).

The stem results from the dynamic growth of the shoot apical meristem which initiates stem tissue and organs including leaves. Shoot apical meristems initiate new apical meristems at the junction of leaf and stem. These meristems can form buds which reiterate the growth pattern of the terminal bud or they can make flowers directly.


(a)

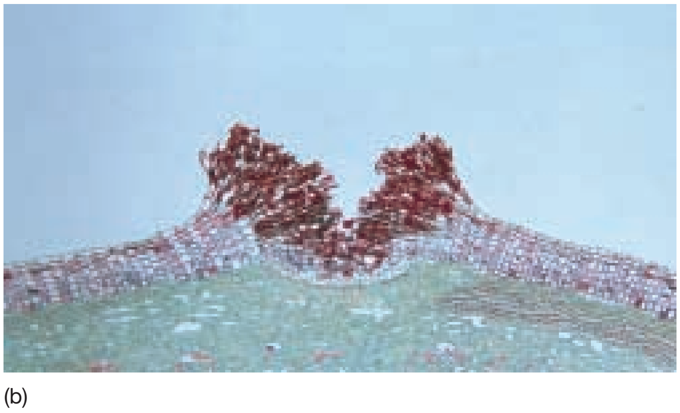

(b)

FIGURE 38.27
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. Highly variable in form in different species, lenticels are an aid to the identification of deciduous trees and shrubs in winter. (*b*) Transverse section through a lenticel (extruding area) in a stem of elderberry, *Sambucus canadensis* (30×).

Modified Stems

Although most stems grow erect, there are some modifications that serve special purposes, including that of natural *vegetative propagation*. In fact, the widespread artificial vegetative propagation of plants, both commercial and private, frequently involves the cutting of modified stems into segments, which are then planted and produce 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, while 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 38.28*a*). Most of a *bulb* consists of fleshy leaves attached to a small, knoblike stem. In onions, the fleshy leaves are surrounded by papery, scalelike leaf bases of the long, green aboveground leaves.

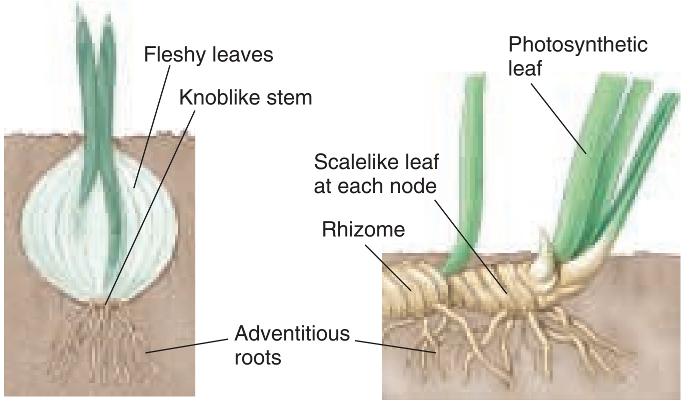
Corms. Crocuses, gladioluses, and other popular garden plants produce *corms* that superficially resemble bulbs. Cutting a corm in half, however, reveals no fleshy leaves. Instead, almost all of a corm consists of stem, with a few papery, brown nonfunctional leaves on the outside, and adventitious roots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

Rhizomes. Perennial grasses, ferns, irises, and many other plants produce *rhizomes*, which typically are horizontal stems that grow underground, often close to the surface (figure 38.28*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, which, unlike rhizomes, usually grow along the surface of the ground. Several *runners* may radiate out from a single plant (figure 38.28*c*). Some botanists use the term *stolon* synonymously with runner; others reserve the term stolon for a stem with long internodes that grows underground, as seen in Irish (white) potato plants. An Irish potato itself, however, is another type of modified stem—a *tuber*.

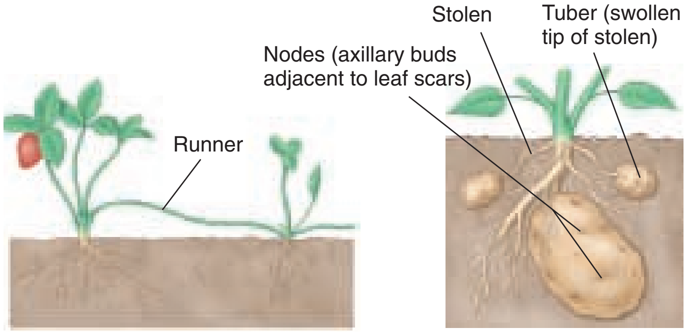
Tubers. In Irish potato plants, carbohydrates may accumulate at the tips of stolons, which swell, becoming *tubers;* the stolons die after the tubers mature (figure 38.28*d*). The "eyes" of a potato are axillary buds formed in the axils of scalelike leaves. The scalelike leaves, which are present when the potato is starting to form, soon drop off; the tiny ridge adjacent to each "eye" of a mature potato is a leaf scar.

Tendrils. Many climbing plants, such as grapes and Boston ivy, produce modified stems knows as *tendrils*, which twine around supports and aid in climbing (figure 38.28*e*). Some tendrils, such as those of peas and pumpkins, are actually modified leaves or leaflets.



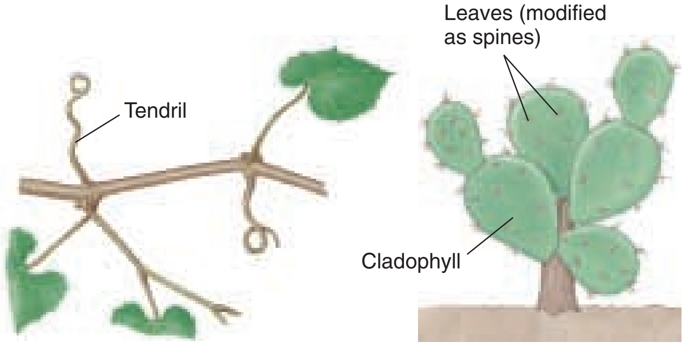
(a) Bulbs (onion)

(b) Rhizomes (iris)



(c) Runners (strawberry)

(d) Tubers (potato)



(e) Tendrils (grape)

(f) Cladophylls (prickly pear)

FIGURE 38.28
Types of modified stems.

Cladophylls. Cacti and several other plants produce flattened, photosynthetic stems called *cladophylls* that resemble leaves (figure 38.28*f*). In cacti, the real leaves are modified as spines.

Some plants possess modified stems that serve special purposes including food storage, support, or vegetative propagation.

38.5 Leaves are adapted to support basic plant functions.

Leaf External Structure

Leaves, which are initiated as *primordia* by the apical meristems (see figure 38.2), are vital to life as we know it. They are the principal sites of photosynthesis on land. Leaves expand primarily by cell enlargement and some cell division. Like our arms and legs, they are determinate structures which means 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.

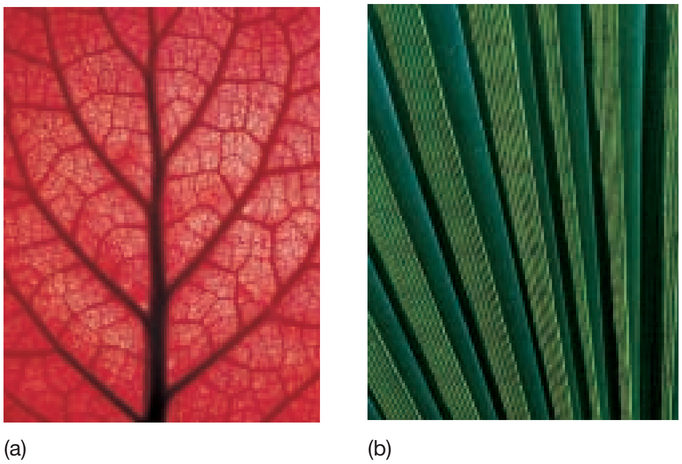
Leaves are really an extension of the shoot apical meristem and stem development. Leaves first emerge as primordia as discussed in the section on stems. At that point, they are not committed to be leaves. Experiments where very young leaf primordia in fern and in coleus are isolated and grown in culture demonstrate this. If the primordia are young enough, they will form an entire shoot rather than a leaf. So, positioning the primordia and beginning the initial cell divisions occurs before those cells are committed to the leaf developmental pathway.

Leaves fall into two different morphological groups which may reflect differences in evolutionary origin. A *microphyll* is a leaf with one vein that does not leave a gap when it branches from the vascular cylinder of the stem; microphylls are mostly small and are associated primarily with the phylum Lycophyta (see chapter 37). Most plants have leaves called *megaphylls*, which have several to many veins; a megaphyll's conducting tissue leaves a gap in the stem's vascular cylinder as it branches from it.

Most dicot 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. We're just beginning to understand how this shift occurs by analyzing mutants like *phantastica* which prevents this transition (figure 38.29). In addition, a pair of *stipules* may be present 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 cherry trees—*Prunus cerasifera*), vary considerably in size from microscopic to almost half the size of the leaf blade. Development of stipules appears to be independent of development of the rest of the leaf.

Grasses and other monocot leaves usually lack a petiole and tend to sheathe the stem toward the base. **Veins** (a term used for the vascular bundles in leaves), consisting of both xylem and phloem, are distributed throughout the leaf blades. The main veins are parallel in most monocot leaves; the veins of dicots, on the other hand, form an often intricate network (figure 38.30).

FIGURE 38.29
The *phantastica* mutant in snapdragon. Snapdragon leaves are usually flattened with a top and bottom side (plant on *left*). In the *phantastica* mutant (plant on *right*), the leaf never flattens but persists as a radially symmetrical bulge.



(a) (b)

FIGURE 38.30
Dicot and monocot leaves. The leaves of dicots, such as this (*a*) African violet relative from Sri Lanka, have netted, or reticulate, veins; (*b*) those of monocots, like this cabbage palmetto, have parallel veins. The dicot leaf has been cleared with chemicals and stained with a red dye to make the veins show up more clearly.

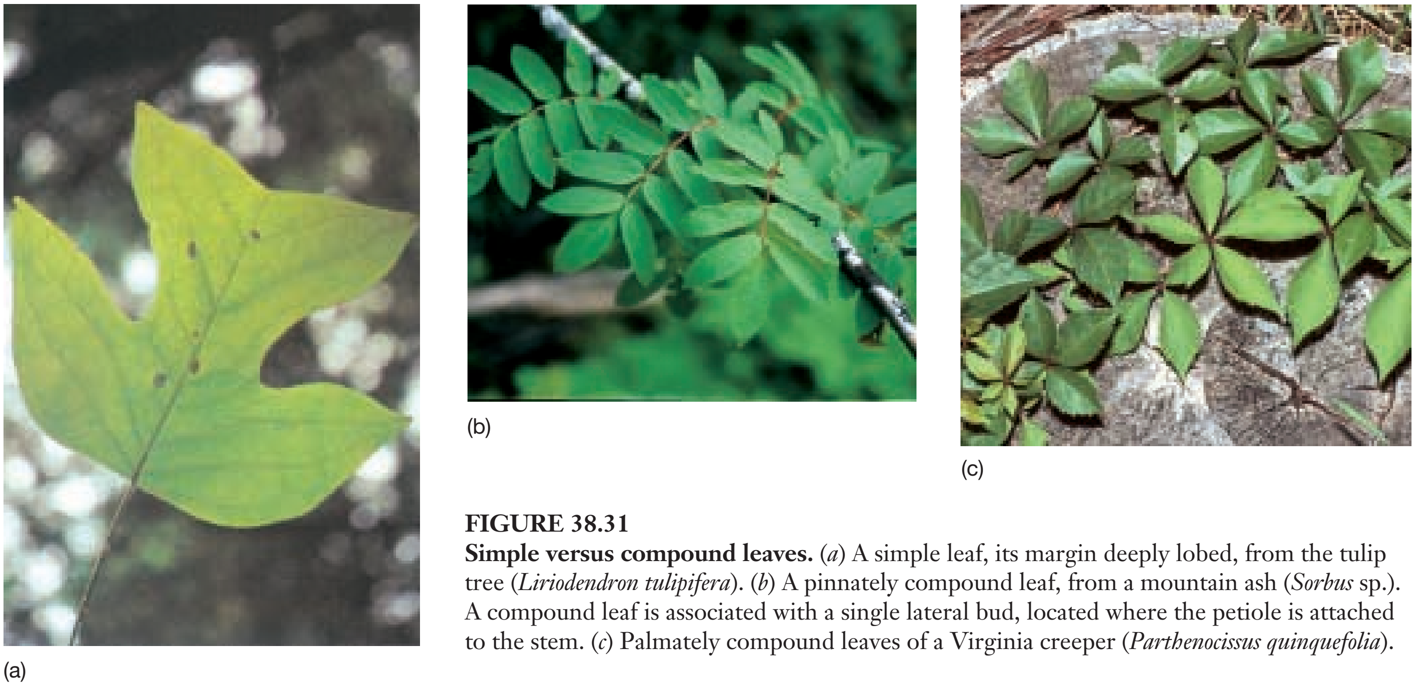


FIGURE 38.31
Simple versus compound leaves. (*a*) A simple leaf, its margin deeply lobed, from the tulip tree (*Liriodendron tulipifera*). (*b*) A pinnately compound leaf, from a mountain ash (*Sorbus* sp.). A compound leaf is associated with a single lateral bud, located where the petiole is attached to the stem. (*c*) Palmately compound leaves of a Virginia creeper (*Parthenocissus quinquefolia*).

Leaf blades come in a variety of forms from oval to deeply lobed to having separate leaflets. In **simple leaves** (figure 38.31*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**, 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. There are single mutations that convert compound leaves to simple leaves which are being used to address this debate. If the leaflets are arranged in pairs along a common axis (the axis is called a *rachis*—the equivalent of the main central vein, or *midrib*, in simple leaves), the leaf is **pinnately compound** (figure 38.31*b*)**.** If, however, the leaflets radiate out from a common point at the blade end of the petiole, the leaf is **palmately compound** (figure 38.31*c*)**.** Palmately compound leaves occur in buckeyes (*Aesculus* spp.) and Virginia creeper (*Parthenocissus quinquefolia*). The leaf blades themselves may have similar arrangements of their veins, and are said to be **pinnately** or **palmately** veined.

Leaves, regardless of whether they are simple or compound, may be **alternately** arranged (alternate leaves usually spiral around a shoot) or they may be in **opposite** pairs. Less often, three or more leaves may be in a **whorl,** a circle of leaves at the same level at a node (figure 38.32).

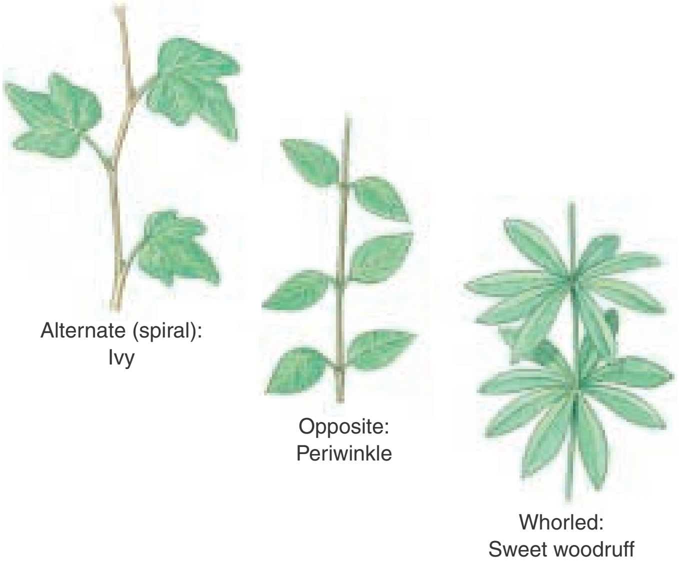


FIGURE 38.32
Types of leaf arrangements. The three common types of leaf arrangements are alternate, opposite, and whorled.

Leaves are the principal sites of photosynthesis. Their blades may be arranged in a variety of ways. In simple leaves the blades are undivided, while in compound leaves the leaf is composed of two or more leaflets.

Leaf Internal Structure

The entire surface of a leaf is covered by a transparent epidermis, most of whose cells have no chloroplasts. The epidermis itself has a waxy *cuticle* of variable thickness, and may have different types of glands and trichomes (hairs) present. The lower epidermis (and occasionally the upper epidermis) of most leaves contains numerous slit-like or mouth-shaped *stomata* (figure 38.33). Stomata, as discussed earlier, are flanked by *guard cells* and function in gas exchange and regulation of water movement through the plant.

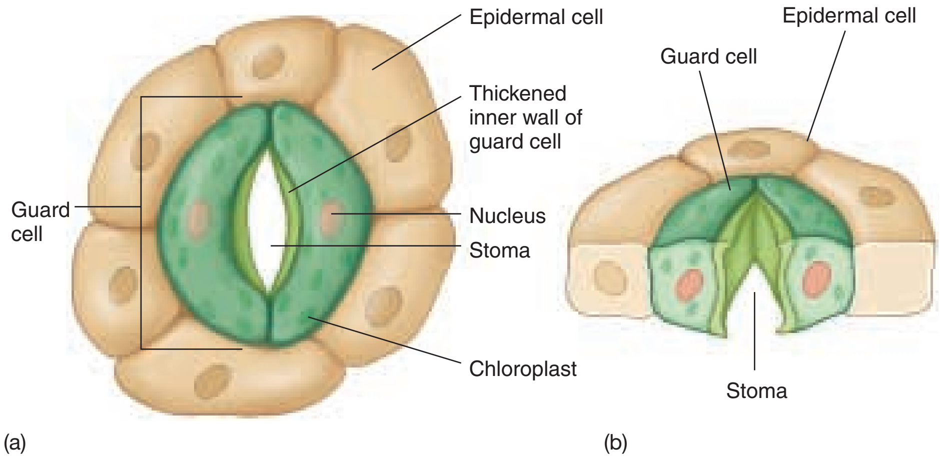


FIGURE 38.33
A stoma. (*a*) Surface view. (*b*) View in cross-section.

The tissue between the upper and lower epidermis is called **mesophyll.** Mesophyll is interspersed with veins (vascular bundles) of various sizes. In most dicot leaves, there are 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 38.34). Some plants, including species of *Eucalyptus*, have leaves that hang down, rather than extending horizontally. They have palisade parenchyma on both sides of the leaf, and there is, in effect, no upper side. In nearly all leaves there are 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 is not differentiated into palisade and spongy layers and there is often little distinction between the upper and lower epidermis. This anatomical difference often correlates with a modified photosynthetic pathway that maximizes the amount of CO_2 relative to O_2 to reduce energy loss through photorespiration (refer to chapter 10). Leaf anatomy directly relates to its juggling act to balance water loss, gas exchange, and transport of photosynthetic products to the rest of the plant.

Leaves are basically flattened bags of epidermis containing vascular tissue and tightly packed palisade mesophyll rich in chloroplasts and loosely packed spongy mesophyll with many interconnected air spaces that function in gas and water vapor exchange.

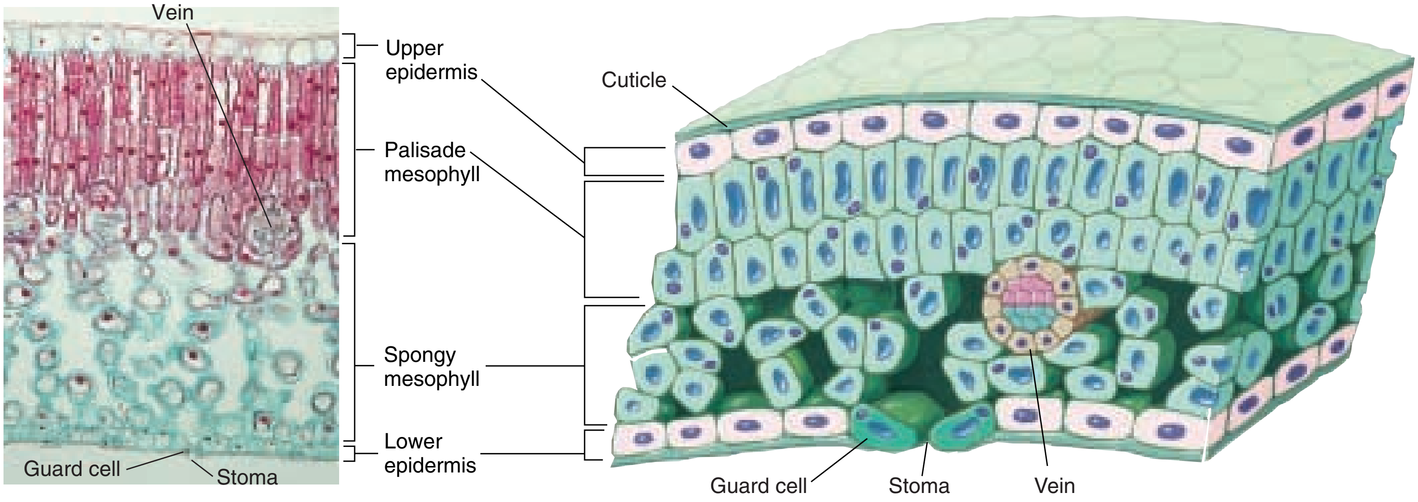


FIGURE 38.34
A leaf in cross-section. Transection of a leaf showing the arrangement of palisade and spongy mesophyll, a vascular bundle or vein, and the epidermis with paired guard cells flanking the stoma.

Modified Leaves

As plants colonized a wide variety of environments, from deserts to lakes to tropical rain forests, modifications of plant organs that would adapt the plants to their specific habitats arose. 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 (figure 38.35). It should be noted, however, that bracts can also be quite small and not as conspicuous as those of the examples mentioned.

Spines. The leaves of many cacti, barberries, and other plants are modified as **spines** (see figure 38.28*f*). In the case of cacti, the reduction of leaf surface reduces water loss and also may deter predators. Spines should not be confused with *thorns*, such as those on honey locust (*Gleditsia triacanthos*), which are modified stems, or with the *prickles* on raspberries and rose bushes, 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. While leaf tissue isolated from many species will regenerate a whole plant, this in vivo regeneration is unique 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 in sand blown by the wind, but the transparent tips, which have a thick epidermis and cuticle, admit light to the hollow interiors. This allows photosynthesis to take place beneath the surface of the ground.

Shade leaves. Leaves produced where they receive significant amounts of shade 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, as both types of leaves on the plant have exactly the same genes. 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, with some digesting their soft parts. Plants with insectivorous leaves often grow in acid swamps deficient in needed elements, or containing elements in forms not readily available to the plants; this inhibits the plants' capacities to maintain metabolic processes sufficient to meet their growth requirements. Their needs are, however, met by the supplementary absorption of nutrients from the animal kingdom.

Pitcher plants (for example, *Sarracenia*, *Darlingtonia*, *Nepenthes*) have cone-shaped leaves in which rainwater can accumulate. The insides of the leaves are very smooth, but there are stiff, downward-pointing hairs at the rim. An insect falling into such a leaf finds it very difficult to escape and eventually drowns. The nutrients released when bacteria, and in most species digestive enzymes, decompose the insect bodies are absorbed into the leaf. Other plants, such as sundews (*Drosera*), have glands that secrete sticky mucilage that trap 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 will not survive in a nitrogen-rich environment, perhaps a trade-off made in the intricate evolutionary process that resulted in its ability to capture and digest insects.

FIGURE 38.35
Modified leaves. In this dogwood "flower," the white-colored bracts (modified leaves) surround the several true flowers without petals in the center.

The leaves of plants exhibit a variety of adaptations, including spines, vegetative reproduction, and even leaves that are carnivorous.

Chapter 38

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Summary | *Questions* | *Media Resources*

38.1 Meristems elaborate the plant body plan after germination.

- A plant body is basically an axis that includes two parts: root and shoot—with associated leaves. There are four basic types of tissues in plants: meristems, ground tissue, epidermis, and vascular tissue.

1. What are the three major tissue systems in plants? What are their functions?

- Art Activity: Plant Body Organization
- Art Activity: Stem Tip Structure
- Art Activity: Primary Meristem Structure
- Characteristics of Plants
- Meristems
- Cambia

38.2 Plants have three basic tissues, each composed of several cell types.

- Ground tissue supports the plant and stores food and water.
- Epidermis forms an outer protective covering for the plant.
- Vascular tissue conducts water, carbohydrates, and dissolved minerals to different parts of the plant. Xylem conducts water and minerals from the roots to shoots and leaves, and phloem conducts food molecules from sources to all parts of the plant.

2. What is the function of xylem? How do primary and secondary xylem differ in origin? What are the two types of conducting cells within xylem?

3. What is the function of phloem? How do the two types of conducting cells in phloem differ?

- Effect of Water on Leaves
- Girth Increase in Woody Dicots
- Vascular System of Plants
- Activity: Vascular Tissue
- Ground Tissue
- Dermal Tissue
- Vascular Tissue
- Student Research: Leaf Structure Wetness

38.3 Root cells differentiate as they become distanced from the dividing root apical meristem.

- Roots have four growth zones: the root cap, zone of cell division, zone of elongation, and zone of maturation.
- Some plants have modified roots, adapted for photosynthesis, food or water storage, structural support, or parasitism.

4. Compare monocot and dicot roots. How does the arrangement of the tissues differ?

5. How are lateral branches of roots formed?

- Art Activity: Dicot Root Structure
- Roots

38.4 Stems are the backbone of the shoot, transporting nutrients and supporting the aerial plant organs.

- Plants branch by means of buds derived from the primary apical meristem. They are found in the junction between the leaf and the stem.
- The vascular cambium is a cylinder of dividing cells found in both roots and shoots. As a result of their activity, the girth of a plant increases.

6. What types of cells are produced when the vascular cambium divides outwardly, inwardly, or laterally?

7. Why don't monocots have secondary growth?

- Art Activity: Dicot Stem Structure
- Art Activity: Secondary Growth
- Art Activity: Herbaceous Dicot Stem Anatomy
- Activity: Cambium
- Stems

38.5 Leaves are adapted to support basic plant functions.

- Leaves emerge as bulges on the meristem in a variety of patterns, but most form a spiral around the stem. The bulge lengthens and loses its radial symmetry as it flattens.
- Photosynthesis occurs in the ground tissue system which is called mesophyll in the leaf. Vascular tissue forms the venation patterns in the leaves, serving as the endpoint for water conduction and often the starting point for the transport of photosynthetically produced sugars.

8. How do simple and compound leaves differ from each other? Name and describe the three common types of leaf growth patterns.

- Art Activity: Plant Anatomy
- Art Activity: Leaf Structure
- Leaves