

Figure 40.1 Shoots in reserve. Axillary shoots give plants a second chance when the terminal shoot breaks off, as is the case with this storm-felled tree.

their DNA-replicating mechanisms to self-replicate. Some invaders kill the plant cells immediately, leading to necrosis (brown, dead tissue). Certain insects may tap into the phloem of a plant seeking carbohydrates, but leave behind a hitchhiking virus or bacterium.

The threat of these attackers is reduced when they have natural predators themselves. One of the greatest problems with nonnative invasive species, such as the alfalfa plant bug (figure 40.2), is the lack of natural predators in the new environment.

Dermal tissue provides first-line defense

The first defense all plants have is the dermal tissue system (see chapter 36). Epidermal cells throughout the plant secrete wax, which is a mixture of hydrophobic lipids. Layers of lipid material protect exposed plant surfaces from water loss and attack. Above-ground plant parts are also covered with cutin, a macromolecule consisting of long-chain fatty acids linked together. **Suberin**, another version of linked fatty acid chains, is found in cell walls of subterranean plant organs; suberin forms the water-impermeable Casparyan strips of roots. Silica inclusions, trichomes, bark, and even thorns can also protect the nutrient-rich plant interior.



Figure 40.2 Alfalfa plant bug. This invasive species is an agricultural problem because it arrived in the United States without any natural predators and feeds on alfalfa.

Invaders can penetrate dermal defenses

Unfortunately, these exterior defenses can be penetrated in many ways. Mechanical wounds leave an open passageway through which microbial organisms can enter. Parasitic nematodes use their sharp mouthparts to get through the plant cell walls. Their actions either trigger the plant cells to divide, forming a tumorous growth, or, in species that attach to a single plant cell, cause the cell to enlarge and transfer carbohydrates from the plant to the hungry nematode (figure 40.3). In some cases, the wounding makes it

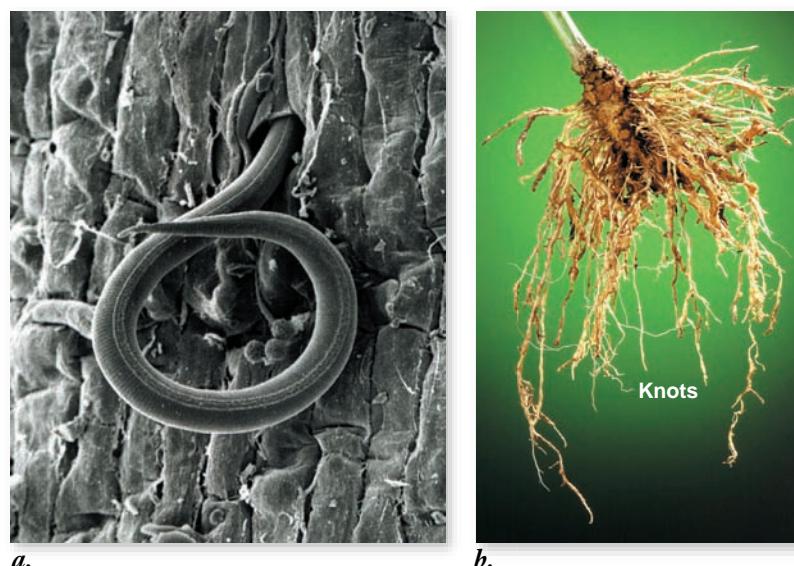


Figure 40.3 Nematodes attack the roots of crop plants.

a. A nematode breaks through the epidermis of the root. b. Root-knot nematodes form tumors on roots.

SCIENTIFIC THINKING

Hypothesis: Nematodes increase the severity of a potato wilt fungal disease by wounding roots and allowing the fungus to penetrate root tissue.

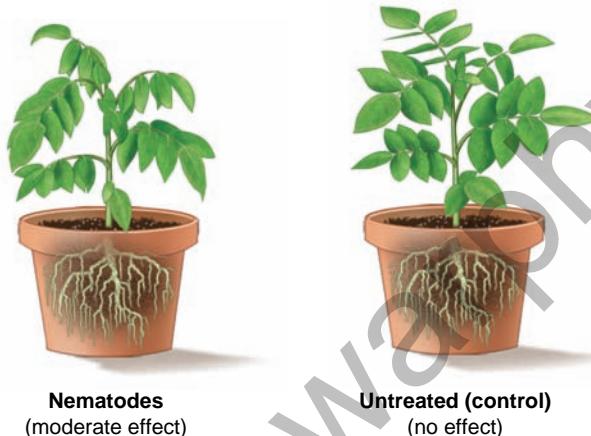
Prediction: Leaf wilt will be more severe when the root system is exposed to both the nematode and the fungus than when the root system is exposed to neither or either separately.

Test: Establish four treatments with four plants in each treatment group. Add the nematodes and the fungal pathogen to the soil of plants in group 1. Group 2 will only have fungus. Group 3 will have only nematodes, and group 4 will be untreated. Allow plants to grow for 42 days and record the extent of leaf wilt on each plant.



Nematodes and fungus
(severe effect)

Fungus
(moderate effect)



Nematodes
(moderate effect)

Untreated (control)
(no effect)

Result: Plants that are cointfected with the nematodes and fungus have more severe wilting than plants treated with nematodes or fungus alone. Control plants do not wilt.

Conclusion: Nematodes increase the severity of the wilting infection.

Further Experiments: Design an experiment to test the hypothesis that increased fungal wilt symptoms are the result of damage to the roots by the nematode, making it easier for the fungus to enter the plant. Could you mechanically wound the roots instead of exposing them to nematodes?

Figure 40.4 Nematodes increase susceptibility of plant to fungal infection.

easier for other pathogens, including fungi, to infect the plant (figure 40.4). In some cases simply having bacteria on the leaf surface can increase the risk of frost damage. The bacteria function as sites for ice nucleation; the resulting ice crystals severely damage the leaves.

Fungi strategically seek out the weak spot in the dermal system, the stomatal openings, to enter the plant. Some fungi have coevolved with a monocot that has evenly spaced stomata. These fungi appear to be able to measure distance to locate these evenly spaced stomatal openings and invade the plant. Figure 40.5 shows the phases of fungal invasion, which can include the following:

1. Windblown spores land on leaves. A germ tube emerges from the spore. Host recognition is necessary for spore germination.
2. The spore germinates and forms an adhesion pad, allowing it to stick to the leaf.
3. Hyphae grow through cell walls and press against the cell membrane.
4. Hyphae differentiate into specialized structures called haustoria. They expand, surrounded by cell membrane, and nutrient transfer begins.

Bacteria and fungi can also be beneficial to plants

Mutualistic and parasitic relationships are often just opposite sides of the evolutionary coin. A parasitic relationship can evolve to become mutualistic, and a mutualistic relationship

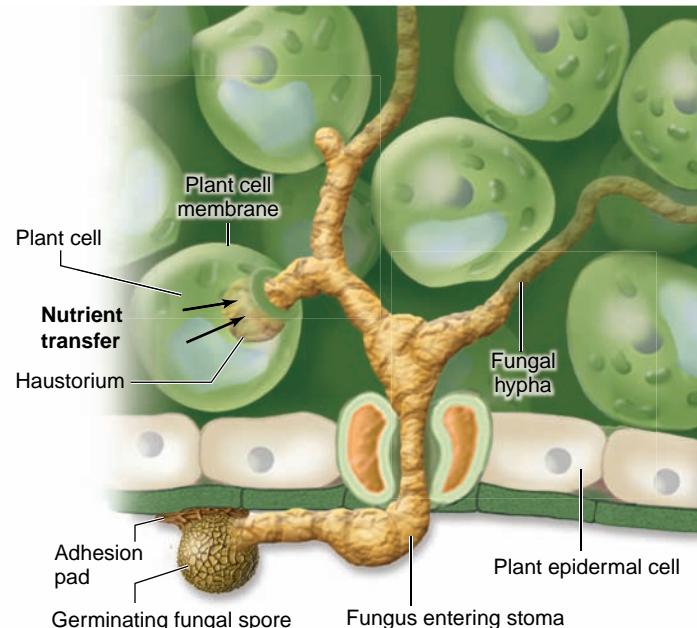


Figure 40.5 Fungi sneak in through stomata. Fungal hyphae penetrate cell walls, but not plasma membranes. The close contact between the fungal hyphae and the plant plasma membrane allows for ready transfer of plant nutrients to the fungus.

can transform into a parasitic one. In chapters 31 and 39, you saw how mycorrhizal fungi use a mechanism similar to the one just described to the mutual benefit of both the plant and the fungus. In the case of the relationship between legumes and nitrogen-fixing bacteria, the *Rhizobium* bacteria seeks out a root hair, infects it along with other tissues, and forms a root nodule. Other soil bacteria can also enhance plant growth, and are called plant growth-promoting rhizobacteria (PGPR). The term *rhizobacteria* refers to bacteria that live around the root system and often benefit from root exudates. In return they provide substances that support plant growth. *Azospirillum* spp., for example, provide gibberellins, which are growth hormones, for rice plants when the bacteria are living in close proximity to the root system. PGPR can also limit the growth of pathogenic soil bacteria.

Learning Outcomes Review 40.1

Epidermal cells secrete protective compounds, including wax and suberin. Fungal spores may germinate and stick to plant leaves; hyphae enter the leaf through stomata, and produce haustoria to take up plant nutrients. Mutualistic partners with plants include mycorrhizal fungi that assist with nutrient absorption and nitrogen-fixing bacteria that provide nutrients.

- Why would protective substances on leaves include lipid-based compounds?

reveals the ancient origins of innate immunity. Between 15 and 50 defensin genes have been identified in plant genomes, and over 317 defensin-like genes exist in the *Arabidopsis* genome. The exact mechanisms are being worked out, but in some cases plant defensins inhibit protein synthesis. When expression of defensin genes is suppressed in plants, they are more susceptible to bacterial and fungal infections. In addition to toxins that kill, plants can produce chemical compounds that make potential herbivores ill or that repel them with strong flavors or odors.

Plants maintain chemical arsenals

How did the biosynthetic pathways that produce these toxins evolve? Growing evidence indicates that the metabolic pathways needed to sustain life in plants have taken some evolutionary side trips, leading to the production of a stockpile of chemicals known as **secondary metabolites**. Many of these secondary metabolites affect herbivores as well as humans (table 40.1).

Alkaloids, including caffeine, nicotine, cocaine, and morphine, can affect multiple cellular processes; if a plant cannot kill its attackers, it can overstimulate them with caffeine or sedate them with morphine. For example, the tobacco hornworm (*Manduca sexta*) can level a field of tobacco (figure 40.6); however, wild species of tobacco appear to have elevated levels of nicotine that are lethal to tobacco hornworms.

Tannins bind to proteins and inactivate them. For example, some act by blocking enzymes that digest proteins, which reduces the nutritional value of the plant tissue. An insect that gets sick from a strong dose of tannins is likely to associate the flavor with illness and to avoid having that type of plant for lunch another time. Small doses of tannins and most other secondary metabolites are unlikely to cause any major digestive difficulties in larger animals, including humans. Animals, including humans, can avoid many of the cumulative toxic effects of secondary metabolites by eating a varied diet.

40.2 Chemical Defenses

Learning Outcomes

1. Describe the role of secondary metabolites in plant defense.
2. Define allelopathy.
3. List three examples of the medicinal value of secondary metabolites.

Many plants are filled with toxins that kill herbivores or, at the very least, make them quite ill. One example is the production of cyanide, (HCN). Over 3000 species of plants produce cyanide-containing compounds called *cyanogenic glycosides* that break down into cyanide when cells are damaged. Cyanide stops electron transport, blocking cellular respiration.

Cassava (genus *Manihot*), a major food staple for many Africans, is filled with cyanogenic glycosides (specifically, manihotoxins) in the outer layers of the edible root. Unless these outer layers are scrubbed off, the cumulative effect of eating primarily cassava can be deadly.

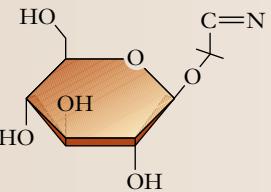
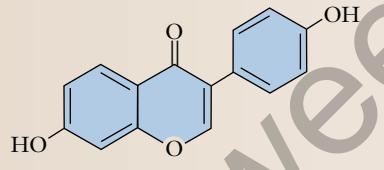
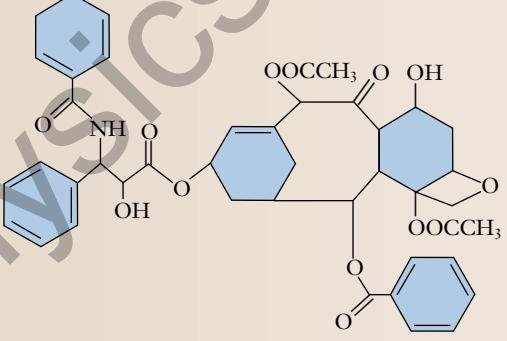
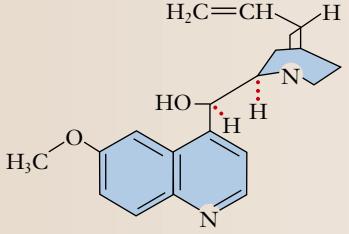
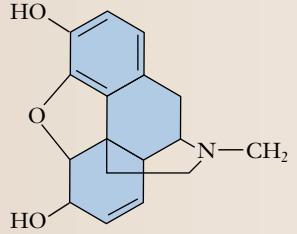
Some toxins are unique to plants, but others are found in plants, vertebrates, and invertebrates and are called **defensins**. Defensins are small, cysteine-rich peptides with antimicrobial activity. The conservation of defensins in animals and plants



Figure 40.6 Herbivores can kill plants. Tobacco hornworms, *Manduca sexta*, consume huge amounts of tobacco leaf tissue, as well as tomato leaves.

TABLE 40.1

Secondary Metabolites

Compound	Source	Structure	Effect on Humans
Manihotoxin (cyanogenic glycoside)	Cassava, <i>Manihot esculenta</i> 		Metabolized to release lethal cyanide
Genistein (phytoestrogen)	Soybean, <i>Glycine max</i> 		Estrogen mimic
Taxol (terpenoid)	Pacific yew, <i>Taxus brevifolia</i> 		Anticancer drug
Quinine (alkaloid)	Quinine bark, <i>Cinchona officinalis</i> 		Antimalarial drug
Morphine (alkaloid)	Opium poppy, <i>Papaver somniferum</i> 		Narcotic pain killer

Plant oils, particularly those found in plants of the mint family, which includes peppermint, sage, pennyroyal, and many others, repel insects with their strong odors. At high concentrations, some of these oils can also be toxic if ingested.

Why don't the toxins kill the plant? One strategy is for a plant to sequester a toxin in a membrane-bound structure, so that it does not come into contact with the cell's metabolic processes. The second solution is for the plant to produce a compound that is not toxic unless it is metabolized, often by microorganisms, in the intestine of an animal. Cyanogenic glycosides are a good example of the latter solution. The plant produces a sugar-bound cyanide compound that does not affect electron transport chains. Once an animal ingests cyanogenic glycoside, the compound is enzymatically broken down, releasing the toxic hydrogen cyanide.

Coevolution has led to defenses against some plant toxins. A tropical butterfly, *Heliconius sara*, can sequester the cyanogenic glycosides it ingests from its sole food source, the passion vine. Even more intriguing is a biochemical pathway that allows the butterfly to safely break down cyanogenic glycosides and use the released nitrogen in its own protein metabolism.

Plants can poison other plants

Some chemical toxins protect plants from other plants. **Allelopathy** occurs when a chemical compound secreted by the roots of one plant blocks the germination of nearby seeds or inhibits the growth of a neighboring plant. This strategy minimizes shading and competition for nutrients, while it maximizes the ability of a plant to use radiant sunlight for photosynthesis. Allelopathy works with both a plant's own species and different species. Black walnut trees (*Juglans nigra*) are a good example. Very little vegetation will grow under a black walnut tree because of allelopathy (figure 40.7).



Figure 40.7

Black walnuts are allelopathic.

Seedlings die when their roots come in contact with the root secretions of a black walnut tree.

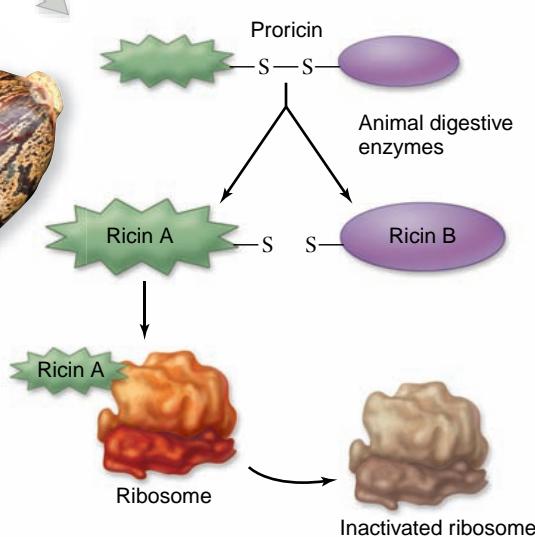


Figure 40.8 Ricin from castor beans blocks translation.

When the ricin A subunit is released from prorcin, it binds to rRNA in ribosomes and prevents mRNA from being translated into protein.

Ricin is found in the endosperm of the seed as a heterodimer composed of ricin A and ricin B, joined by a single disulfide bond. This heterodimer (proricin) is nontoxic, but when the disulfide bond is broken in humans or other animals, ricin A targets the GAGA sequence of the 28s rRNA of the ribosome. A single ricin molecule can inactivate 1500 ribosomes per minute, blocking translation of proteins.

In 1978, Bulgarian expatriate and dissident Georgi Markov was about to board a bus in London on his way to work at the BBC when he felt a sharp stabbing pain in his thigh. A man near him picked up an umbrella from the ground and hurriedly left. Markov had been injected via a mechanism in the umbrella tip with a pinhead-sized metal sphere containing 0.2 mg of ricin. He died four days later. After the collapse of the Soviet Union, former KGB officers revealed that the KGB had set up the assassination at the behest of the Bulgarian Communist Party leadership.

Inquiry question



Explain how ricin led to Markov's death.

Secondary metabolites may have medicinal value

Major research efforts on plant secondary metabolites are in progress because of their potential benefits, as well as dangers, to human health (see table 40.1).

Soy and phytoestrogens

One example of the benefits and dangers is the presence of **phytoestrogens**, compounds very similar to the human hormone estrogen, in soybean products. In soybean plants, genistein is one of the major phytoestrogens.

Comparative studies between Asian populations that consume large amounts of soy foods and populations with lower dietary intake of soy products are raising intriguing questions and some conflicting results. For example, the lower rate of prostate cancer in Asian males might be accounted for by the down-regulation of androgen and estrogen receptors by a phytoestrogen. Soy is being marketed as a means for minimizing menopausal symptoms caused by declining estrogen levels in older women.

In humans, dietary phytoestrogens cross the placenta and can be found in the amniotic fluid during the second trimester of pregnancy. Questions have been raised about the effect of phytoestrogens on developing fetuses and even on babies who consume soy-based formula because of allergies to cow's milk formula. Because hormonal signaling is so complex, much more research is needed to fully understand how or even if phytoestrogens affect human physiology and development.

Taxol and breast cancer

Taxol, a secondary metabolite found in the Pacific yew (*Taxus brevifolia*), is effective in fighting cancer, especially breast cancer. The discovery of taxol's pharmaceutical value raised an environmental challenge. The very existence of the Pacific yew was being threatened as the shrubs were destroyed so that taxol could be extracted. Fortunately, it became possible to synthesize taxol in the laboratory.

Taxol is not an isolated case of drug discovery in plants. The hidden pharmaceutical value of many plants may lead to increased conservation efforts to protect plants that have the potential to make contributions toward human health. Although the plant pharmaceutical industry is growing, it is certainly not a new field. Until recent times, almost all medicines used by humans came from plants.

Quinine and malaria

In the 1600s, the Incas of Peru were treating malaria with a drink made from the bark of *Cinchona* trees. Malaria is caused by four types of human malaria parasites in the genus *Plasmodium*, which are carried by female *Anopheles* mosquitoes. *Plasmodium falciparum* is the most lethal of the four types. Symptoms include severe fevers and vomiting. The parasite feeds on red blood cells, and death can result from anemia or blocking of blood flow to the brain.

By 1820, the active ingredient in the bark of *Cinchona* trees, **quinine**, had been identified (see table 40.1). In the 19th century, British soldiers in India used quinine-containing "tonic water" to fight malaria. They masked the bitter taste of quinine with gin, creating the first gin and tonic drinks. In 1944, Robert Woodward and William Doering synthesized quinine. Now several other synthetic drugs are available to treat malaria.

Exactly how quinine and synthetic versions of this drug family work has puzzled researchers for a long time. Quinine can affect DNA replication, and also, when *P. falciparum* breaks down hemoglobin from red blood cells in its digestive vacuole, an intermediary toxic form of heme is released. Quinine may interfere with the subsequent polymerization of these hemes, leading to a build up of toxic hemes that poison the parasite.

Unfortunately, even today malaria is a major threat to human health, causing over a million deaths per year. Ninety percent of these deaths occur in sub-Saharan Africa. An estimated 300,000,000 individuals are infected. *P. falciparum* strains have acquired resistance to synthetic drugs, and quinine is once again the drug of choice in some cases.

Herbal remedies have been used for centuries in most cultures. A resurgence of interest in plant-based remedies is resulting in a growing and unregulated industry. Although herbal remedies have great promise, we need to be aware that each plant contains many secondary metabolites, many of which have evolved to cause harm to herbivores including humans.

Learning Outcomes Review 40.2

Plants accumulate secondary metabolites that can poison or otherwise harm herbivores. Plants also secrete chemicals that inhibit the growth of neighboring plants, a process termed allelopathy. Secondary metabolites may also have beneficial uses, such as phytoestrogens from soy, which may reduce menopausal symptoms in women; taxol from the Pacific yew, which acts as an anticancer agent; and quinine from *Cinchona* trees, which helps treat malaria.

- *In what ways would a drug prepared from a whole plant differ from a drug prepared from an isolated chemical compound?*

40.3 Animals That Protect Plants

Learning Outcomes

1. *Describe the benefit Acacia trees receive from ants that live in them.*
2. *Explain how some plants use parasitoid wasps to destroy caterpillars.*

Not only do individual species and their traits evolve over time, but so do relationships between species. For example, evolution of chemicals to deter herbivores may often be accompanied over time by adaptation on the part of herbivores to withstand these chemicals. This evolutionary pattern is called coevolution. Here we consider two cases of mutualism that coevolved between animal and plant species.

Acacia trees and ants. Several species of ants provide small armies to protect some species of *Acacia* trees from other herbivores. These stinging ants may inhabit an enlarged thorn of the tree; they attack other insects (figure 40.9) and sometimes small mammals and epiphytic plants. Some of the *Acacia* species provide their ants with sugar in nectaries located away from the flowers, and even with lipid food bodies at the tips of leaves.

The only problem with ants chasing away other insects is that acacia trees depend on bees to pollinate their flowers. What keeps the ants from swarming and stinging a bee that stops by to pollinate? Evidence indicates that when a flower opens on an acacia tree, it produces some type of chemical ant deterrent that does not deter the bees. This chemical has not yet been identified.

Parasitoid wasps, caterpillars, and leaves. Caterpillars fill up on leaf tissue before they metamorphose into a moth or a butterfly. In some cases, proteinase inhibitors in leaves are sufficient to deter very hungry caterpillars. But some plants have developed another strategy: As the caterpillar



Figure 40.9 Ants attacking a katydid to protect “their” *Acacia*. Through coevolution, ants are sheltered by acacia trees and attack otherwise harmful herbivores.

chews away, a wound response in the plant leads to the release of a volatile compound. This compound wafts through the air, and if a female parasitoid wasp happens to be in the neighborhood, it is immediately attracted to the source. Parasitoid wasps are so named because they are parasitic on caterpillars. The wasp lays her fertilized eggs in the body of the caterpillar that is feeding on the leaf of the plant. These eggs hatch, and the emerging larvae kill and eat the caterpillar (figure 40.10).

Learning Outcomes Review 40.3

Mutualism is an interaction between species that is beneficial to both. Ants protect *Acacia* by attacking feeding herbivores. Parasitoid wasps are attracted by compounds released from plant tissues damaged by feeding caterpillars; they lay eggs in the caterpillars, which later are killed by the emerging larvae.

- *Would you expect that wasps kill all the caterpillars? Explain.*

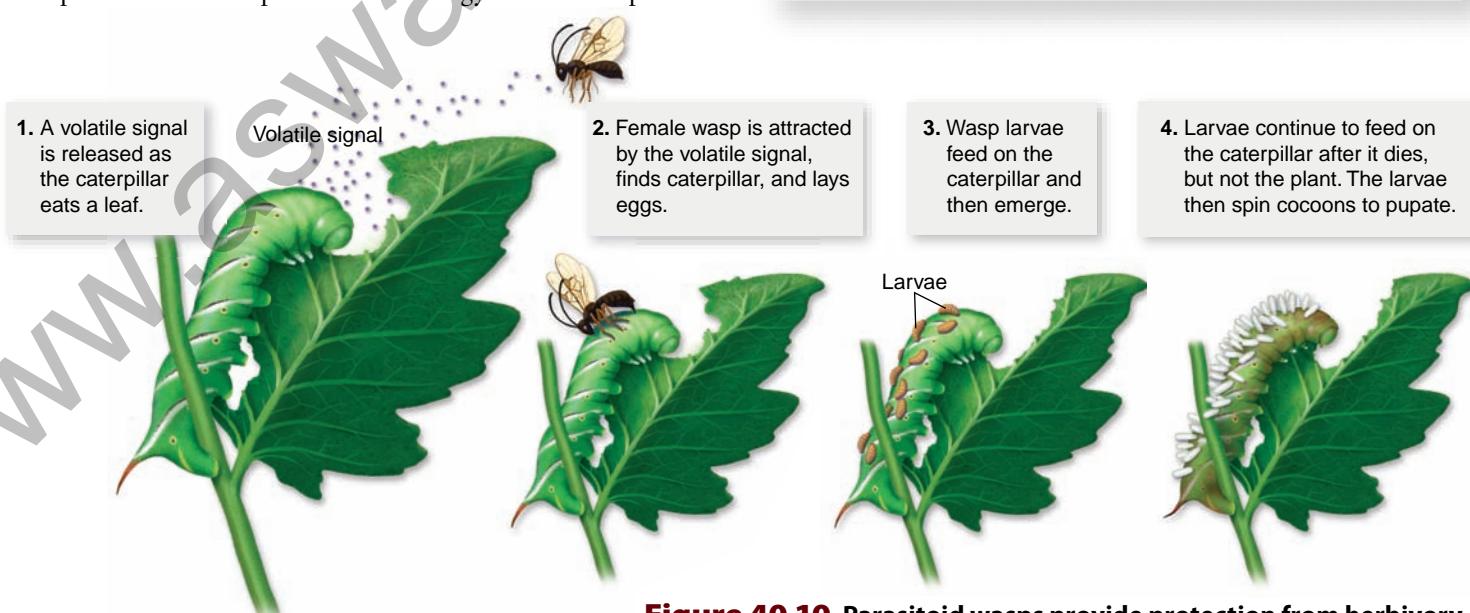


Figure 40.10 Parasitoid wasps provide protection from herbivory.

40.4 Systemic Responses to Invaders

Learning Outcomes

1. Outline the sequence of events that leads to the production of a wound response.
2. Describe the gene-for-gene hypothesis.
3. Define systemic acquired resistance.

So far, we have focused mainly on static plant responses to threats. Most of the deterrent chemicals such as toxins are maintained at steady-state levels. In addition, the morphological structures such as thorns or trichomes that help defend plants are part of the normal developmental program. Because these defenses are maintained whether an herbivore or other invader is present or not, they have an energetic downside. By contrast, resources could be conserved if the response to being under siege was inducible—that is, if the defense response could be launched only when a threat had been recognized. In this section, we explore these inducible defense mechanisms.

Wound responses protect plants from herbivores

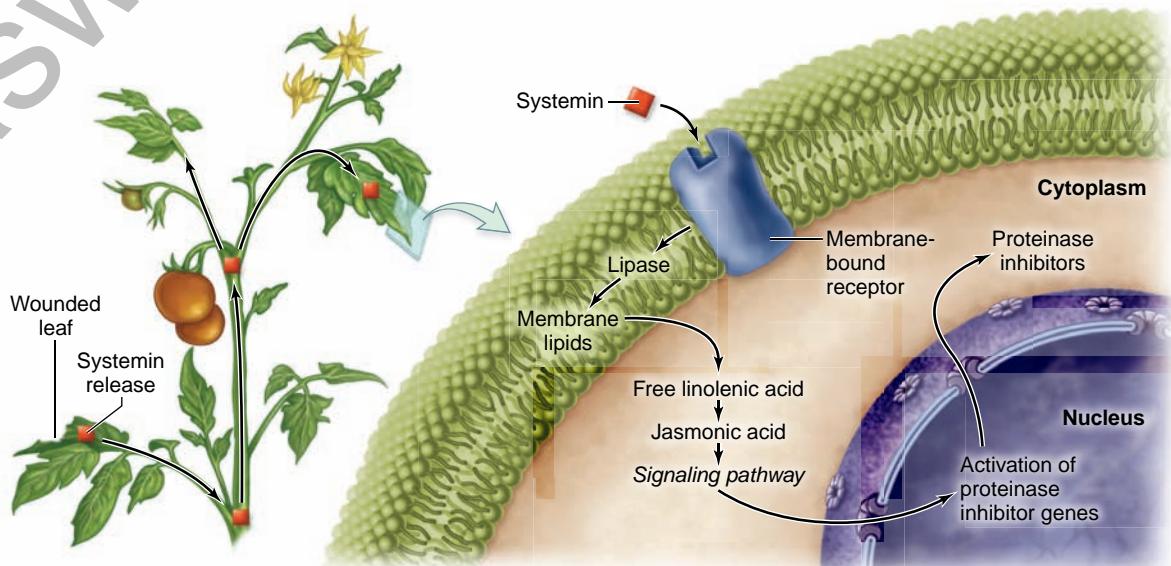
As you just learned from the example of the parasitoid wasp, a **wound response** may occur when a leaf is chewed or injured. One induced outcome is the rapid production of proteinase inhibitors. These chemical toxins do not exist in the stockpile of defenses, but instead are produced in response to wounding.

Proteinase inhibitors bind to digestive enzymes in the gut of the herbivore. The proteinase inhibitors are produced throughout the plant, and not just at the wound site. How are cells in distant parts of the plant signaled to produce proteinase inhibitors? In tomato plants, the following sequence of events is responsible for this systemic response (figure 40.11):

1. Wounded leaves produce an 18-amino-acid peptide called **systemin** from a larger precursor protein.

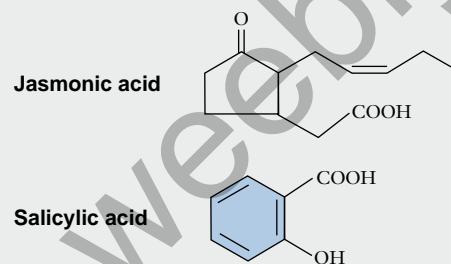
Figure 40.11 Wound response in tomato.

Wounding a tomato leaf leads to the production of jasmonic acid in other parts of the plant. Jasmonic acid initiates a signaling pathway that turns on genes needed to synthesize a proteinase inhibitor.



2. Systemin moves through the apoplast (the space between cell walls) of the wounded tissue and into the nearby phloem. This small peptide-signaling molecule then moves throughout the plant in the phloem.
3. Cells with a systemin receptor bind the systemin, which leads to the production of **jasmonic acid**.
4. Jasmonic acid activates the transcription of defense genes, including the production of a proteinase inhibitor.

Although we know the most about the signaling pathway involving jasmonic acid, other molecules are involved in wound response as well. **Salicylic acid**, which is found in the bark of plants such as the white willow (*Salix alba*) is one example. Cell fragments also appear to be important signals for triggering an induced response, as is discussed shortly.



Mechanical damage separate from herbivore attack also elicits wound responses, which presents a challenge in designing plant experiments that involve cutting or otherwise mechanically damaging the tissue. Experimental controls, which should be cut or manipulated in the same way but without the test treatment, are especially important to ensure that any changes observed are not due only to the wound response.

Defense responses can be pathogen-specific

Wound responses are independent of the type of herbivore or other agent causing the damage, but other responses are triggered by a specific pathogen that carries a specific allele in its genome.

Pathogen recognition

Half a century ago, the geneticist H. H. Flor proposed the existence of a plant resistance gene (*R*), the product of which interacts with the product of an avirulence gene (*avr*) carried by a pathogen. *Avirulent* means not virulent (disease-causing). An **avirulent pathogen** is one that can utilize host resources for its own use and reproduction without causing severe damage or death. The product of this pathogen's *avr* protein interacts with the plant's *R* protein to signal the pathogen's presence. In this way, the plant under attack can mount defenses, thus ensuring that the pathogen remains avirulent. If the pathogen's *avr* protein is not recognized by the plant, disease symptoms appear.

Flor's proposal is called the **gene-for-gene hypothesis** (figure 40.12), and several pairs of *avr* and *R* genes have been cloned in different species pathogenized by microbes, fungi, and even insects in one case. This research has been motivated partially by the agronomic benefit of identifying genes that can be added via gene technology to crop plants to protect them from invaders.

The *avr/R* gene interaction is an example of ongoing co-evolution. An avirulent invader can be detected and recognized. Mutations arising in the avirulent pathogen can result in a virulent pathogen that overcomes a plant's defenses and kills it—often leading to the pathogen's demise as well.

Specific defenses and the hypersensitive response

Much is now known about the signal transduction pathways that follow the recognition of the pathogen by the *R* gene product. These pathways lead to the triggering of the **hypersensitive response (HR)**, which leads to rapid cell death around the source of the invasion and also to a longer term, whole-plant resistance (figures 40.12 and 40.13). A gene-for-gene response does not always occur, but plants still have defense responses to pathogens in general as well as to mechanical wounding. Some of the response pathways may be similar. Also, fragments of cell wall carbohydrates may serve as recognition and signaling molecules.

When a plant is attacked and a gene-for-gene recognition occurs, the HR leads to very rapid cell death around the site of attack. This seals off the wounded tissue to prevent the pathogen or pest from moving into the rest of the plant. Hydrogen peroxide and nitric oxide are produced and may signal a cascade of bio-

chemical events resulting in the localized death of host cells. These chemicals may also have negative effects on the pathogen, although protective mechanisms have coevolved in some pathogens.

Other antimicrobial agents produced include the **phytoalexins**, which are antimicrobial chemical defense agents. A variety of pathogenesis-related genes (*PR* genes) are also expressed, and their proteins can function as either antimicrobial agents or signals for other events that protect the plant.

In the case of virulent invaders for which there is no *R* recognition, changes in local cell walls at least partially block the pathogen or pest from moving further into the plant. In this case, an HR does not occur, and the local plant cells do not die.

Long-term protection

In addition to the HR or other local responses, plants are capable of a systemic response to a pathogen or pest attack, called a **systemic acquired resistance (SAR)** (see figure 40.12). Several pathways lead to broad-ranging resistance that lasts for a period of days.

The long-distance signal that induces SAR is likely salicylic acid, rather than systemin, which is the long-distance signal in wound responses. At the cellular level, jasmonic acid (which was mentioned earlier in the context of the wound response pathways) is involved in SAR signaling. SAR allows the plant to respond more quickly if it is attacked again. This response, however, is not the same as the human or mammalian immune response, in which antibodies (proteins) that recognize specific antigens (foreign proteins) persist in the body. SAR is neither as specific nor as long-lasting.

Learning Outcomes Review 40.4

A wounded leaf initiates a signaling chain that stimulates production of proteinase inhibitors. When a plant has a resistance gene with a product that recognizes the product of an avirulence gene in the pathogen, the plant carries out a defense response; this recognition is called the gene-for-gene hypothesis. Systemic acquired resistance is a temporary broad form of resistance that may be induced by exposure to a pathogen.

- How does local cell death help preserve a plant under attack by a pathogen?

Figure 40.12 Gene-for-gene hypothesis.

Flor proposed that pathogens have an avirulence (*avr*) gene that recognizes the product of a plant resistance gene (*R*). If the virus, bacterium, fungus, or insect has an *avr* gene product that matches the *R* gene product, a defense response will occur.

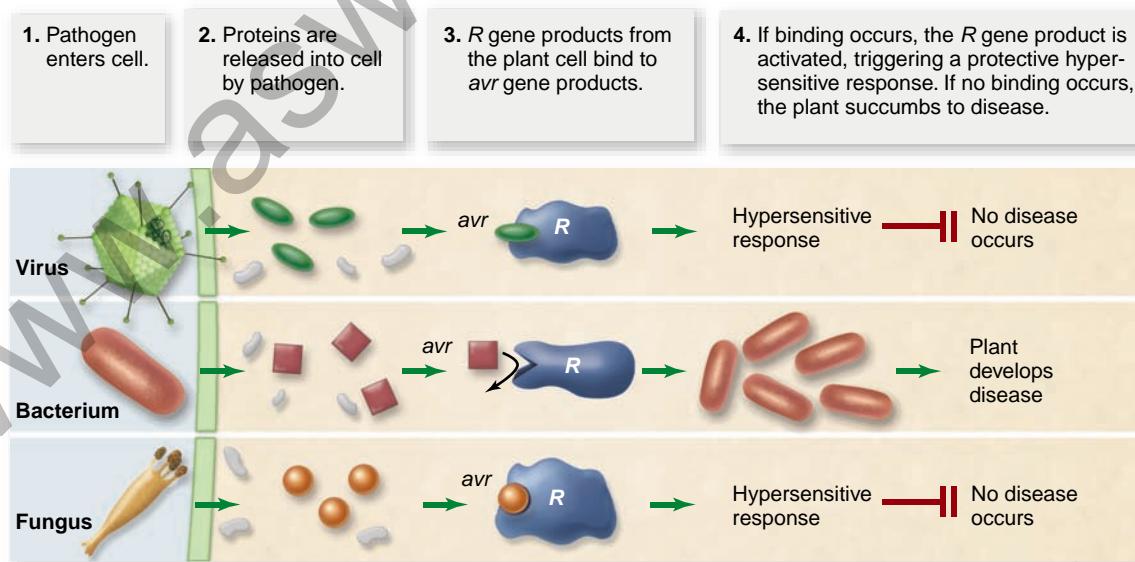
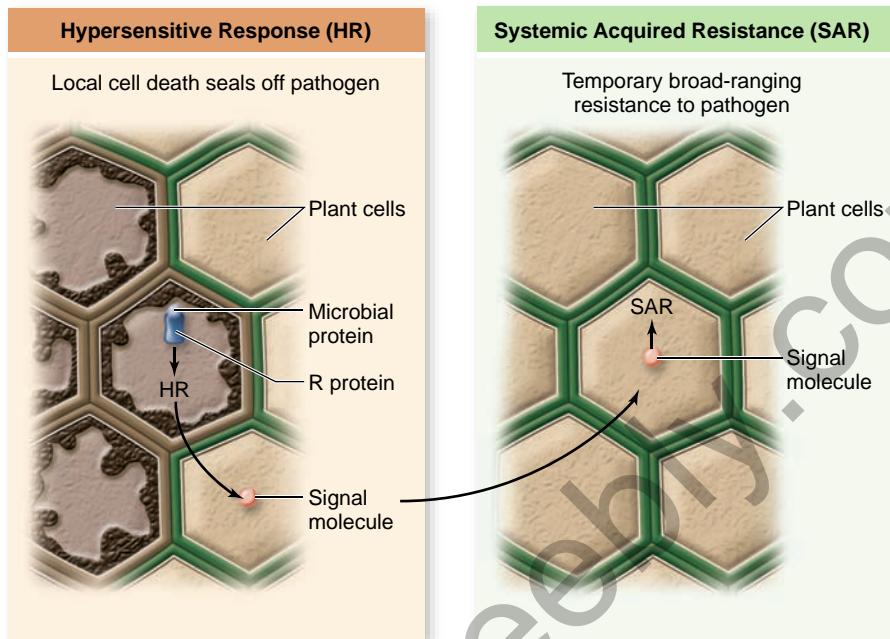




Figure 40.13 Plant defense responses.

In the gene-for-gene response, a cascade of events is triggered, leading to local cell death (HR) and to the production of a mobile signal that provides longer term resistance in the rest of the plant (SAR).



Chapter Review

40.1 Physical Defenses

Pathogens can harm plants in many ways, including exploiting nutrient resources and taking over DNA replication machinery.

Dermal tissue provides first-line defense.

Dermal tissues are covered with lipids such as cutin and suberin, which reduce water loss and prevent attack. Morphological features such as trichomes, bark, and thorns protect some plants.

Invaders can penetrate dermal defenses.

In spite of defense mechanisms, invaders can cause damage by piercing plants, eating plant parts, or entering the plant through the stomata.

Bacteria and fungi can also be beneficial to plants.

Mycorrhizal fungi form beneficial relationships with plants by enhancing uptake of water and minerals. Nitrogen-fixing bacteria provide nitrogen to plants in a usable form.

40.2 Chemical Defenses

Plants maintain chemical arsenals.

Plants may produce and stockpile secondary metabolites such as alkaloids, tannins, and oils that provide protection from predators (see table 40.1). Plants protect themselves from their own toxins either by sequestering them in vesicles or producing compounds that are not toxic until they are ingested by a predator.

Plants can poison other plants.

Allelopathic plants secrete chemicals to block seed germination or inhibit growth of nearby plants. This strategy minimizes competition for resources such as light and nutrients.

Humans are susceptible to plant toxins.

Ricin is an example of a powerful plant toxin. It is found in the endosperm of castor beans (see figure 40.8). Ricin is six times more lethal than cyanide.

Secondary metabolites may have medicinal value.

Plant secondary metabolites such as phytoestrogens, taxol, and quinine have pharmaceutical value for humans. Many other plant-based remedies have been used for centuries in human cultures.

40.3 Animals That Protect Plants

Mutualistic associations are beneficial to both the plant and animal partners. One example is the relationship between acacia trees and ants, in which ants protect the trees from herbivores.

Another example is the association between certain plants, caterpillars, and parasitoid wasps. When chewed or damaged, the leaves release compounds that attract the wasps, which lay their eggs in the caterpillars. The wasps' larvae feed on the caterpillar, killing it (see figure 40.10).

40.4 Systemic Responses to Invaders

Plants avoid an unnecessary expenditure of energy if they produce defense mechanisms only when needed.

Wound responses protect plants from herbivores.

Wound responses are generalized reactions that occur regardless of the cause of the injury.

During a wound response, a signal spreads throughout the phloem, inducing the production of proteinase inhibitors that bind to digestive enzymes in the gut of the animal eating the plant (see figure 40.11).

Defense responses can be pathogen-specific.

In many plants, the plant *R* gene product may interact with an avirulence gene product of a pathogen in a gene-for-gene reaction that induces a defense response.

Plants can also produce antimicrobial agents such as phytoalexins as defense compounds.

After exposure to a pathogen, a plant may be protected against pathogen attack in the short-term future through a mechanism called systemic acquired resistance.



Review Questions

UNDERSTAND

- Nonnative invasive species are often a threat to native species because they
 - typically grow larger than other plants.
 - are not susceptible to any diseases.
 - are parasitic.
 - do not have natural enemies in their new location.
- Fungal pathogens transfer nutrients across a plant cell membrane using
 - an adhesion pad.
 - a haustorium.
 - guard cells.
 - tumors.
- Casparian strips in roots contain _____, which helps to defend against invaders.
 - wax
 - suberin
 - cutin
 - cuticle
- Which of the following is not a secondary metabolite?
 - Caffeine
 - Morphine
 - Taxol
 - Glucose
- Parasitoid wasps protect plants from caterpillars by
 - stinging them.
 - repelling them.
 - eating them.
 - enclosing them in a capsule.
- In response to wounding, a tomato plant first produces a peptide called
 - systemin.
 - jasmonic acid.
 - ricin.
 - salicylic acid.
- When a cell undergoes a hypersensitive response, it
 - builds cell walls quickly.
 - releases defense response molecules from its vacuole.
 - dies rapidly.
 - destroys avirulence gene products.
- The wound response products that bind to digestive enzymes in herbivores are
 - proteinase inhibitors.
 - proteinase promoters.
 - lipase inhibitors.
 - lipase promoters.
- If a plant has been attacked by a pathogen, then it is likely to be able to respond more quickly to a subsequent attack due to a mechanism called
 - basal defense.
 - induced hypersensitive response.
 - antimicrobial pathogen resistance.
 - systemic acquired resistance.

APPLY

- Some plants have developed a mutualistic relationship with parasitoid wasps. This mutualistic relationship would not occur if
 - the plant quit producing nectar for the wasp.
 - the wasp ceased to live on the plant.
 - the plant quit producing volatile compounds that attract the wasp.
 - the plant attracted too many caterpillars.
- Both plant and animal immune systems can
 - develop memory of past pathogens to more effectively deal with subsequent infections.
 - initiate expression of proteins to help fight the infection.

- kill their own cells to prevent spread of the infection.
- all of the above

- Your friend informs you that it is highly likely all of the plants in your yard are “infected” with some kind of fungi or bacteria. The plants look perfectly healthy to you at this time. The most prudent thing for you to do would be:
 - Remove all your plants because they are likely to die.
 - Spray your plants with chemicals to remove all bacteria and fungi.
 - Remove all your plants and replace the soil.
 - Do nothing because many of these bacteria and fungi may be beneficial.
- Some plants are recognized by fungal pathogens on the basis of their stomatal pores. Which of the following would provide these plants immunity from fungal infection?
 - Removing all of the stomata from the plant
 - Changing the spacing of stomatal pores in these plants
 - Reinforcing the cell wall in the guard cells of stomatal pores
 - Increasing the number of trichomes on the surfaces
- You decide to plant a garden with a beautiful black walnut at one end and a majestic white oak at the other end. You are quite disappointed, however, when none of the seeds you plant around the walnut tree grow. What might explain this observation?
 - The walnut tree filters out too much light, so the seeds fail to germinate.
 - The roots of the walnut tree deplete all of the nutrients from the soil, so the new seedlings starve.
 - The walnut tree produces chemical toxins that prevent seed germination.
- If a pathogen contains an *avr* gene not recognized by a plant, the plant will most likely
 - develop a disease.
 - eliminate the pathogen because it is unrecognized.
 - develop proteinase inhibitors.
 - develop a different *R* gene.

SYNTHESIZE

- During the domestication of crops, humans have intentionally or inadvertently selected for lower levels of toxic compounds. Explain why each of these two types of selection would have occurred.
- Parasitoid wasps seem like an effective method to control caterpillars. Discuss some limitations of this strategy. That is, outline some scenarios in which a plant might not be effectively protected by the wasps.
- Systemin is transported through the phloem of a tomato plant to induce a wound response to herbivores. However, the direction of phloem movement is always from source to sink. Explain how the sites that receive the wound signal may vary with stages of the plant’s life cycle.

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41

Chapter

Sensory Systems in Plants

Chapter Outline

- 41.1 Responses to Light
- 41.2 Responses to Gravity
- 41.3 Responses to Mechanical Stimuli
- 41.4 Responses to Water and Temperature
- 41.5 Hormones and Sensory Systems

Introduction

All organisms sense and interact with their environments. This is particularly true of plants. Plant survival and growth are critically influenced by abiotic factors, including water, wind, and light. The effect of the local environment on plant growth also accounts for much of the variation in adult form within a species. In this chapter, we explore how a plant senses such factors and transduces these signals to elicit an optimal physiological, growth, or developmental response. Although responses can be observed on a macroscopic scale, the mechanism of response occurs at the level of the cell. Signals are perceived when they interact with a receptor molecule, causing a shape change and altering the receptor's ability to interact with signaling molecules. Hormones play an important role in the internal signaling that brings about environmental responses and are keyed in many ways to the environment.

41.1 Responses to Light

Learning Outcomes

1. Compare the pigments phytochrome and chlorophyll.
2. List growth responses influenced by phytochrome.
3. Define phototropism.

In chapter 8 we covered the details of photosynthesis, the process by which plants convert light energy into chemical bond energy. We described pigments, molecules that are capable of absorbing light energy; you learned that chlorophylls are the primary pigment molecules of photosynthesis. Plants contain other pigments as well, and one of the functions of these other pigments is to detect light and to mediate plants' response to light by passing on information.

Several environmental factors, including light, can initiate seed germination, flowering, and other critical developmental events in the life of a plant. **Photomorphogenesis** is the term used for nondirectional, light-triggered development. It can result in complex changes in form, including flowering.

Unlike photomorphogenesis, phototropisms are directional growth responses to light. Both photomorphogenesis and phototropisms compensate for the plant's inability to walk away from unfavorable environmental conditions.

P_{fr} facilitates expression of light-response genes

Phytochrome is present in all groups of plants and in a few genera of green algae, but not in other protists, bacteria, or fungi. Phytochrome systems probably evolved among the green algae and were present in the common ancestor of the plants.

The phytochrome molecule exists in two interconvertible forms: The first form, **P_r**, absorbs red light at 660 nm wavelength; the second, **P_{fr}**, absorbs far-red light at 730 nm. Sunlight has more red than far-red light. P_r is biologically inactive; it is converted into P_{fr}, the active form, when red photons are present. P_{fr} is converted back into P_r when far-red photons are available. In other words, biological reactions that are affected by phytochrome occur when P_{fr} is present. When most of the P_{fr} has been replaced by P_r, the reaction will not occur (figure 41.1).

The pigment-containing protein **phytochrome (P)** consists of two parts: a smaller part that is sensitive to light, called the *chromophore*, and a larger portion called the *apoprotein* (figure 41.2). The apoprotein facilitates expression of light-response genes. Over 2500 genes, 10% of the *Arabidopsis* genome, are involved in biological responses that begin with a conformational change in one of the phytochromes in response to red light. Phytochromes are involved in numerous signaling pathways that lead to gene expression. Some pathways also involve protein kinases or G proteins (described in chapter 9).

Phytochrome is found in the cytoplasm, but enters the nucleus to facilitate transcription of light response genes. When P_r is converted to P_{fr}, it can move into the nucleus. Once in the nucleus, P_{fr} binds with other proteins that form a transcription complex, leading to the expression of light-

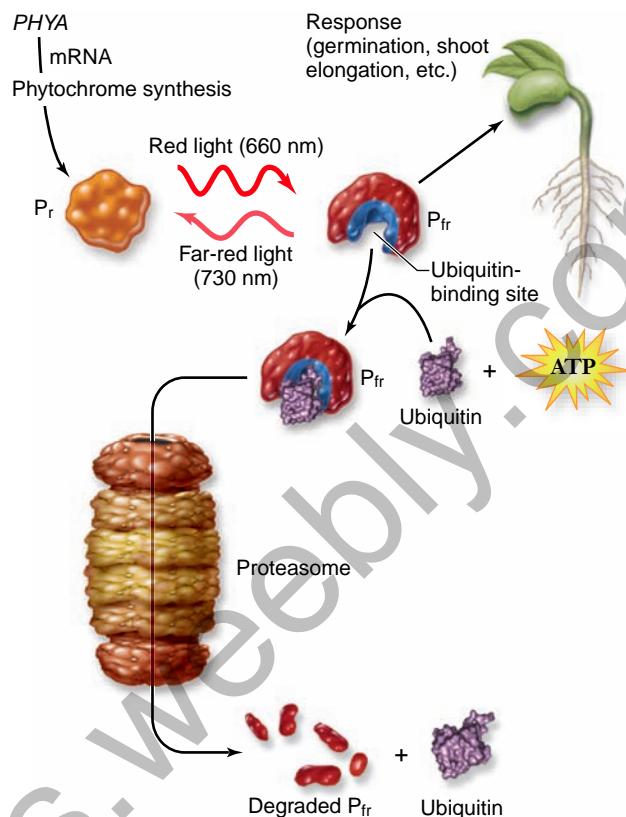


Figure 41.1 How phytochrome works. *PHYA* is one of the five *Arabidopsis* phytochrome genes. When exposed to red light, P_r changes to P_{fr}, the active form that elicits a response in plants. P_{fr} is converted to P_r when exposed to far-red light. The amount of P_{fr} is regulated by protein degradation. The protein ubiquitin tags P_{fr} for degradation in the proteasome.

regulated genes (figure 41.3). Phytochrome's protein-binding site (see figure 41.2) is essential for interactions with transcription factors.

Phytochrome also works through protein kinase-signaling pathways. When phytochrome converts to the P_{fr} form, the protein kinase domain of the apoprotein may phosphorylate a serine and the amino (N) terminus of the phytochrome itself

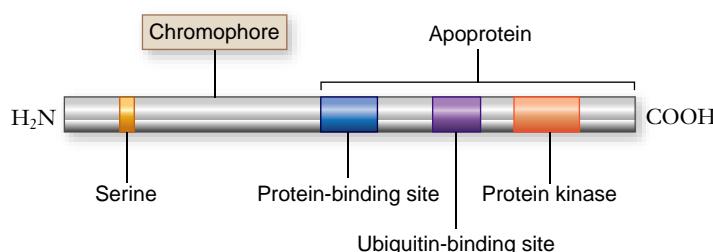
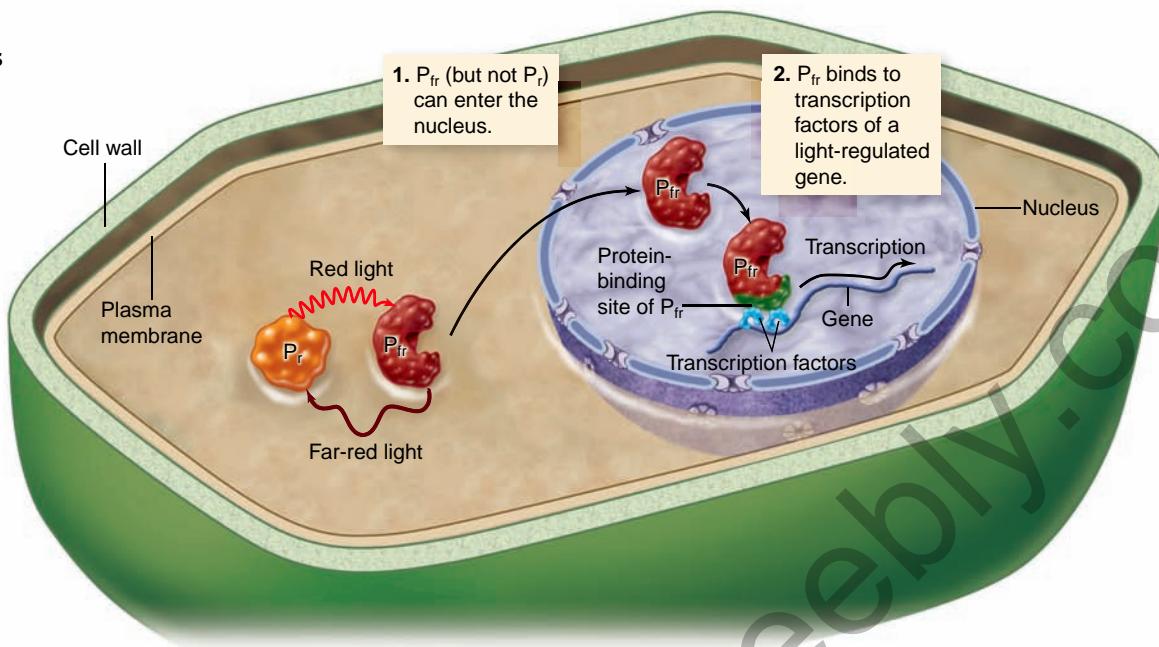


Figure 41.2 Phytochrome. Different parts of the phytochrome molecule have distinct roles in light regulation of growth and development. Phytochrome changes conformation when the chromophore responds to relative amounts of red and far-red light. The shape change affects the ability of phytochrome to bind to other proteins that participate in the signaling process. The ubiquitin-binding sites allow for degradation, and the protein kinase domain allows for further signaling via phosphorylation.

Figure 41.3 P_{fr} enters the nucleus and regulates gene expression.



(autophosphorylation), or it may phosphorylate the serine of another protein involved in light signaling (figure 41.4). Phosphorylation initiates a signaling cascade that can activate transcription factors and lead to the transcription of light-regulated genes.

Although phytochrome is involved in multiple signaling pathways, it does not directly initiate the expression of that 10% of the *Arabidopsis* plant genome. Rather, phytochrome initiates expression of master regulatory genes that manage the complex interactions leading to photomorphogenesis and phototropisms. Gene expression is just the first step, with hormones playing important roles as well.

Inquiry question

? You are given seed of a plant with a mutation in the protein kinase domain of phytochrome. Would you expect to see any red-light-mediated responses when you germinate the seed? Explain your answer.

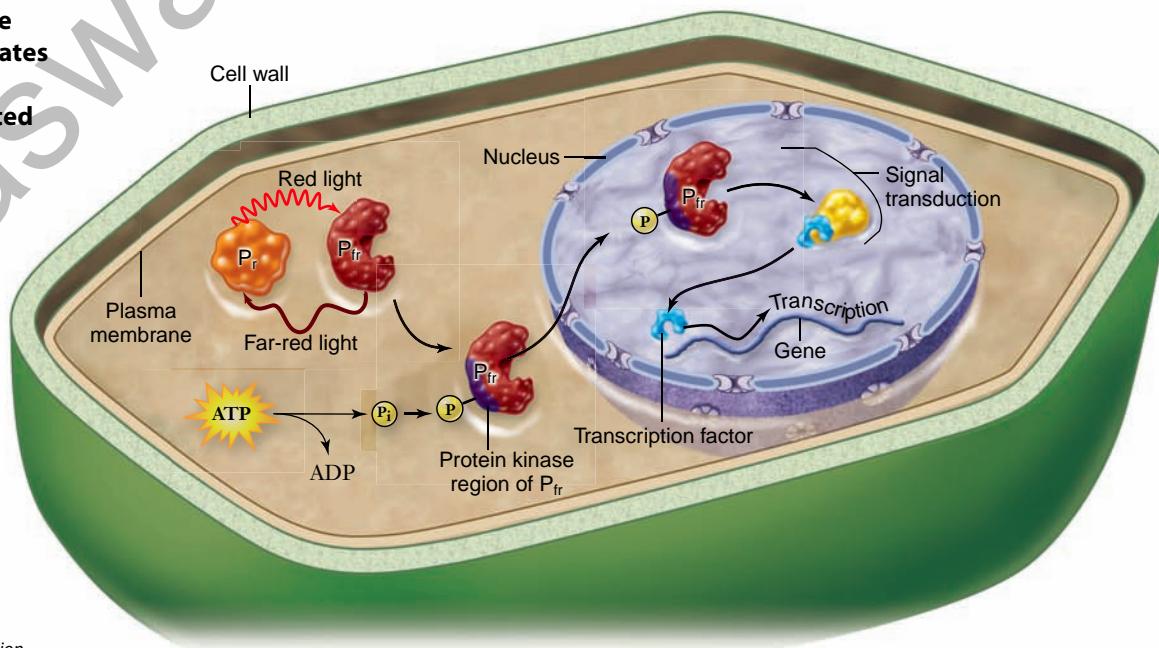
Figure 41.4 The kinase domain of P_{fr} phosphorylates P_{fr} , leading directly or indirectly to light-regulated gene expression.

In this example, signaling leads to the release of a transcription factor from a protein complex.

Chlorophyll also absorbs red light, but it is not a receptor like phytochrome. Unlike receptors that transduce information, chlorophyll transduces energy.

The amount of P_{fr} is also regulated by degradation. Ubiquitin is a protein that tags P_{fr} for transport to the **proteasome**, a protein shredder composed of 28 proteins. The proteasome has a channel in the center, and as proteins pass through, they are clipped into amino acids that can be used to build other proteins as described in chapter 16. The process of tagging and recycling P_{fr} is precisely regulated to maintain needed amounts of phytochrome in the cell.

Although we often refer to phytochrome as a single molecule here, several different phytochromes have been identified that appear to have specific functions. In *Arabidopsis* five forms of phytochrome, PHYA to PHYE, have been characterized, each playing overlapping but distinct roles in the light regulation of growth and development.



Many growth responses are linked

to phytochrome action

Phytochrome is involved in a number of plant growth responses, including seed germination, shoot elongation, and detection of plant spacing.

Seed germination

Seed germination is inhibited by far-red light and stimulated by red light in many plants. Because chlorophyll absorbs red light strongly but does not absorb far-red light, light filtered through the green leaves of canopy trees above a seed contains a reduced amount of red light. The far-red light inhibits seed germination by converting P_{fr} into the biologically inactive P_r form.

Consequently, seeds on the ground under deciduous plants, which lose their leaves in winter, are more apt to germinate in the spring after the leaves have decomposed and the seeds are exposed to direct sunlight and a greater amount of red light. This adaptation greatly improves the chances that seedlings will become established before leaves on taller plants shade the seedlings and reduce sunlight available for photosynthesis.

Shoot elongation

Elongation of the shoot in an etiolated seedling (one that is pale and slender from having been kept in the dark) is caused by a lack of red light. The morphology of such plants becomes normal when they are exposed to red light, increasing the amount of P_{fr}.

Etiolation is an energy conservation strategy to help plants growing in the dark reach the light before they die. They don't green up until light becomes available, and they divert energy to internode elongation. This strategy is useful for seedlings when they have sprouted underground or under leaf cover.

The de-etiolated (*det2*) *Arabidopsis* mutant has a poor etiolation response; seedlings fail to elongate in the dark (figure 41.5). The *det2* mutants are defective in an enzyme necessary for biosynthesis of a brassinosteroid hormone, leading researchers to propose that brassinosteroids play a role in plant responses to light through phytochrome. (Brassinosteroids and other hormones are discussed later in this chapter.)

Detection of plant spacing

Red and far-red light also signal plant spacing. Again, leaf shading increases the amount of far-red light relative to red light. Plants somehow measure the amount of far-red light bounced back to them from neighboring plants. The closer together plants are, the more far-red relative to red light they perceive and the more likely they are to grow tall, a strategy for outcompeting others for sunshine. If their perception is distorted by putting a light-blocking collar around the stem, the elongation response no longer occurs.

Light affects directional growth

Phototropisms, directional growth responses, contribute to the variety of overall plant shape we see within a species as shoots grow toward light. Tropisms are particularly intriguing because they challenge us to connect environmental signals with cellular perception of the signal, transduction into biochemical pathways, and ultimately an altered growth response.

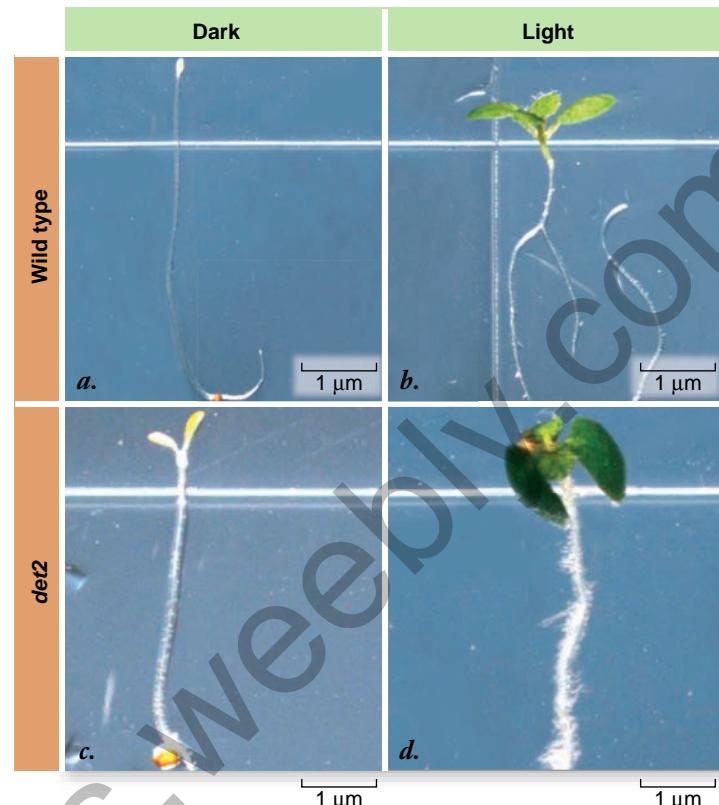


Figure 41.5 Etiolation is regulated by light and the *det2* gene in *Arabidopsis*. *det2* is needed for etiolation in dark grown plants.

Positive phototropism in stems

Phototropic responses include the bending of growing stems and other plant parts toward sources of light with blue wavelengths (460-nm range) (figure 41.6). In general, stems are positively phototropic, growing toward a light source, but most roots do not respond to light, or in exceptional cases, exhibit only a weak negative phototropic response.

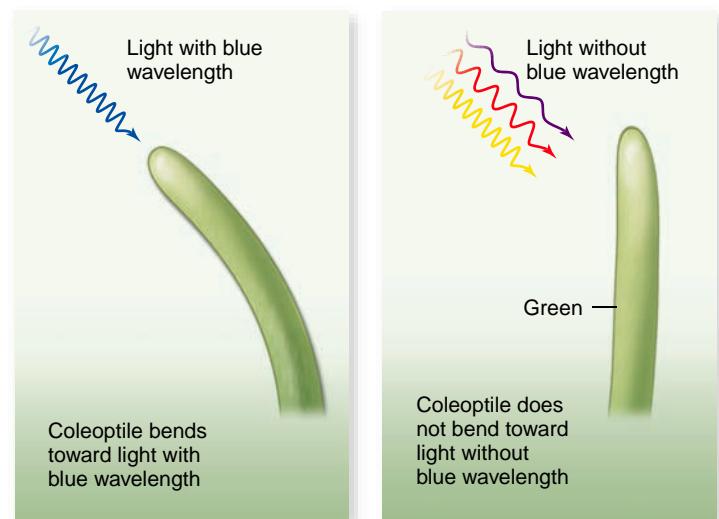


Figure 41.6 Phototropism. Oat coleoptiles growing toward light with blue wavelengths. Colors indicate the color of light shining on coleoptiles. Arrows indicate the direction of light.

The phototropic reactions of stems are clearly of adaptive value, giving plants greater exposure to available light. They are also important in determining the development of plant organs and, therefore, the appearance of the plant. Individual leaves may also display phototropic responses; the position of leaves is important to the photosynthetic efficiency of the plant. A plant hormone called *auxin*, discussed in a later section, is probably involved in most, if not all, of the phototropic growth responses of plants.

Blue-light receptors

The recent identification of blue-light receptors in plants is leading to exciting discoveries of how the light signal can ultimately be connected with a phototropic response. A blue-light receptor **phototropin 1 (PHOT1)** was identified through the characterization of a nonphototropic mutant.

The phot1 protein has two light-sensing regions, and they change conformation in response to blue light. This change activates another region of the protein that is a kinase. Both PHOT1 and a similar receptor, PHOT2, are receptor kinases unique to plants. A portion of PHOT1 is a kinase that autophosphorylates (figure 41.7). Currently, only the early steps in this signal transduction are understood. It will be intriguing to watch the story of the phot1 signal transduction pathway unfold, leading to an explanation of how plants grow toward the light.

Circadian clocks are independent of light but are entrained by light

Although shorter and much longer naturally occurring rhythms also exist, **circadian rhythms** (“around the day”) are particularly common and widespread among eukaryotic organisms. They relate the day–night cycle on Earth, although they are not exactly 24 hr in duration.

Jean de Mairan, a French astronomer, first identified circadian rhythms in 1729. He studied the sensitive plant (*Mimosa pudica*), which closes its leaflets and leaves at night. When

de Mairan put the plants in total darkness, they continued “sleeping” and “waking” just as they had when exposed to night and day. This is one of four characteristics of a circadian rhythm—it must continue to run in the absence of external inputs. Plants with a circadian rhythm do not actually have to be experiencing a pattern of day/light and darkness for their cycle to occur.

In addition, a circadian rhythm must be about 24 hr in duration, and the cycle can be reset or entrained. Although plants kept in darkness will continue the circadian cycle, the cycle’s period may gradually move away from the actual day–night cycle, becoming desynchronized. In the natural environment, the cycle is entrained to a daily cycle through the action of phytochrome and blue-light photoreceptors.

Other eukaryotes, including humans, have circadian rhythms, and perhaps you have experienced jet lag when you traveled by airplane across a few time zones. Recovery from jet lag involves entrainment to the new time zone.

Another characteristic of a circadian cycle is that the clock can compensate for differences in temperature, so that the duration remains unchanged. This characteristic is unique, considering what we know about biochemical reactions, because most rates of reactions vary significantly based on temperature. Circadian clocks exist in many organisms, and they appear to have evolved independently multiple times.

The reversible circadian rhythm changes in leaf movements are typically brought about by alteration of cells’ turgor pressure; we describe these changes in a later section.

Learning Outcomes Review 41.1

Plants grow and develop in response to environmental signals. Phytochrome, a red-light receptor, transduces information, while chlorophyll transduces energy. Phytochrome influences seed germination, shoot elongation, and other growth. Phototropism is directional growth in response to light and is controlled by a blue-light receptor. Circadian rhythms are 24-hr cycles entrained to the day–night cycle.

- Why would it be an advantage to have both phytochromes and chlorophylls as pigments?

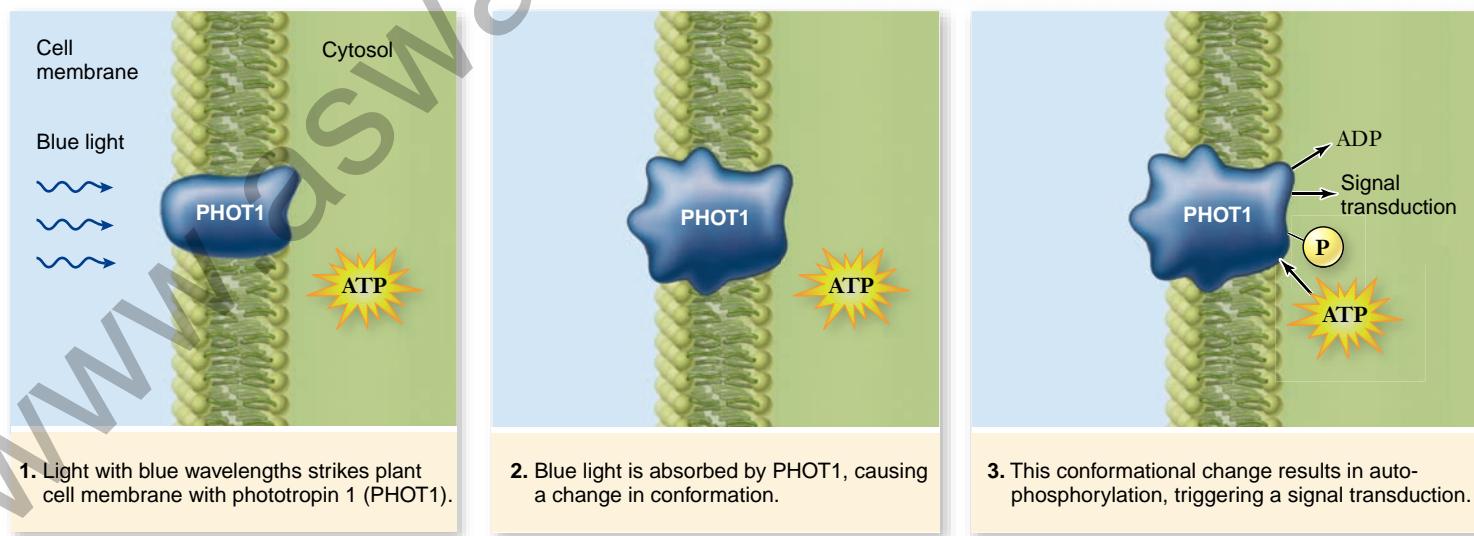


Figure 41.7 **Blue-light receptor.** Blue light activates the light-sensing region of PHOT1, which in turn stimulates the kinase region of PHOT1 to autophosphorylate. This is just the first step in a signal transduction pathway that leads to phototropic growth.

41.2 Responses to Gravity

Learning Outcomes

1. Identify the structures in cells that perceive gravity.
2. Explain how stems and roots bend in response to gravity.

When a potted plant is tipped over and left in place, the shoot bends and grows upward. The same thing happens when a storm pushes plants over in a field. These are examples of **gravitropism**, the response of a plant to the gravitational field of the Earth (figure 41.8; see also chapter opener). Because plants also grow in response to light, separating out phototropic effects is important in the study of gravitropism.

Plants align with the gravitational field: An overview

Gravitropic responses are present at germination, when the root grows down and the shoot grows up. Why does a shoot have a negative gravitropic response (growth away from gravity), while a root has a positive one? Auxins play a primary role in gravitropic responses, but they may not be the only way gravitational information is sent through the plant.

The opportunity to experiment on the Space Shuttle in a gravity-free environment has accelerated research in this area. Analysis of gravitropic mutants is also adding to our understanding of gravitropism. Investigators propose that four general steps lead to a gravitropic response:

1. Gravity is perceived by the cell.
2. A mechanical signal is transduced into a physiological signal in the cell that perceives gravity.
3. The physiological signal is transduced inside the cell and externally to other cells.
4. Differential cell elongation occurs, affecting cells in the “up” and “down” sides of the root or shoot.



Figure 41.8 Plant response to gravity. This plant was placed horizontally and allowed to grow for seven days. Note the negative gravitational response of the shoot.

Inquiry question

- ? Where would you expect to find the highest concentration of auxin?

Currently researchers are debating the steps involved in perception of gravity. In shoots, gravity is sensed along the length of the stem in the endodermal cells that surround the vascular tissue (figure 41.9a), and signaling occurs toward the outer epidermal cells. In roots, the cap is the site of gravity perception, and a signal must trigger differential cell elongation and division in the elongation zone (figure 41.9b).

In both shoots and roots, amyloplasts, plastids that contain starch, sink toward the center of the gravitational field and thus may be involved in sensing gravity. Amyloplasts interact with the cytoskeleton. Auxin evidently plays a role in transmitting a signal from the gravity-sensing cells that contain amyloplasts and the site where growth occurs. The link between amyloplasts and auxin is not fully understood.

Stems bend away from a center of gravity

Increased auxin concentration on the lower side in stems causes the cells in that area to grow more than the cells on the upper side. The result is a bending upward of the stem against the

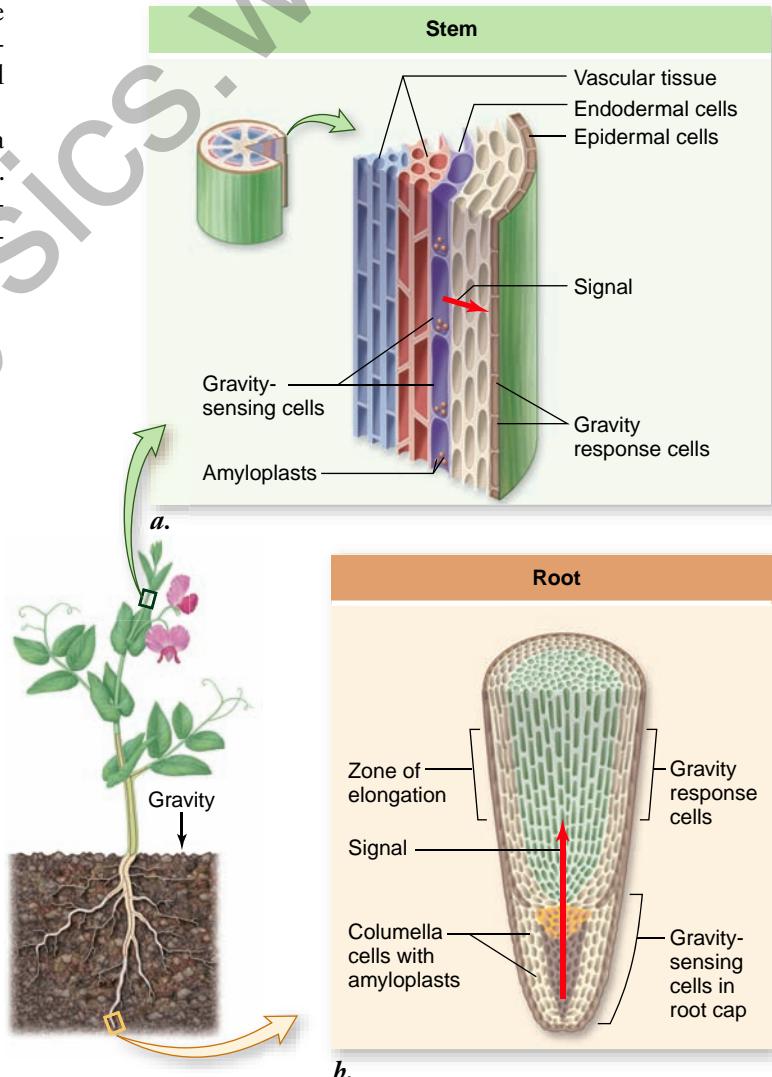


Figure 41.9 Sites of gravity sensing and response in roots and shoots.

force of gravity—in other words, a *negative gravitropic response*. Such differences in hormone concentration have not been as well documented in roots. Nevertheless, the upper sides of roots oriented horizontally grow more rapidly than the lower sides, causing the root ultimately to grow downward; this phenomenon is known as *positive gravitropic response*.

Two *Arabidopsis* mutants, *scarecrow* (*scr*) and *short root* (*shr*), were initially identified by aberrant root phenotypes, but they also affect shoot gravitropism (figure 41.10). Both genes are needed for normal endodermal development (see figure 36.16). Without a fully functional endodermis, stems lack a normal gravitropic response. These endodermal cells carry amyloplasts in the stems, and in the mutants, stem endodermis fails to differentiate and produce gravity-sensing amyloplasts.

Roots bend toward a center of gravity

In roots, the gravity-sensing cells are located in the root cap, and the cells that actually undergo asymmetrical growth are in the distal elongation zone, which is closest to the root cap. How the information is transferred over this distance is an intriguing question. Auxin may be involved, but when auxin transport is suppressed, a gravitropic response still occurs in the distal elongation zone. Some type of electrical signaling involving membrane polarization has been hypothesized, and this idea was tested aboard the Space Shuttle. So far, the jury is still out on the exact mechanism.

The growing number of auxin mutants in roots do confirm that auxin has an essential role in root gravitropism, even if it may not be the long-distance signal between the root cap and the elongation zone. Mutations that affect both auxin influx and efflux can eliminate the gravitropic response by altering the directional transport of this hormone.

It may surprise you to learn that in tropical rain forests, the roots of some plants may grow up the stems of neighboring plants, instead of exhibiting the normal positive gravitropic responses typical of other roots. It appears that rainwater dissolves nutrients, both while passing through the lush upper canopy of the forest, and subsequently while trickling down the tree trunks. This water is a more reliable source of nutrients for the roots than the nutrient-poor rain forest soils in which the plants are anchored. Explaining this observation in terms of current hypotheses is a challenge. It has been proposed that roots are more sensitive to auxin than are shoots, and that auxin may actually inhibit growth on the lower side of a root, resulting in a positive gravitropic response. Perhaps in these tropical plants, the sensitivity to auxin in roots is reduced.

Learning Outcomes Review 41.2

Gravitropism is the response of a plant to gravity. In endodermis cells of shoots and root cap cells of roots, amyloplasts settle to the bottom, allowing the plant to sense the direction of gravitational pull. In response, cells on the lower side of stems and the upper side of roots grow faster than other cells, causing stems to grow upward and roots to grow downward.

- What would happen to a plant growing under weightless conditions, such as in an orbiting spacecraft?

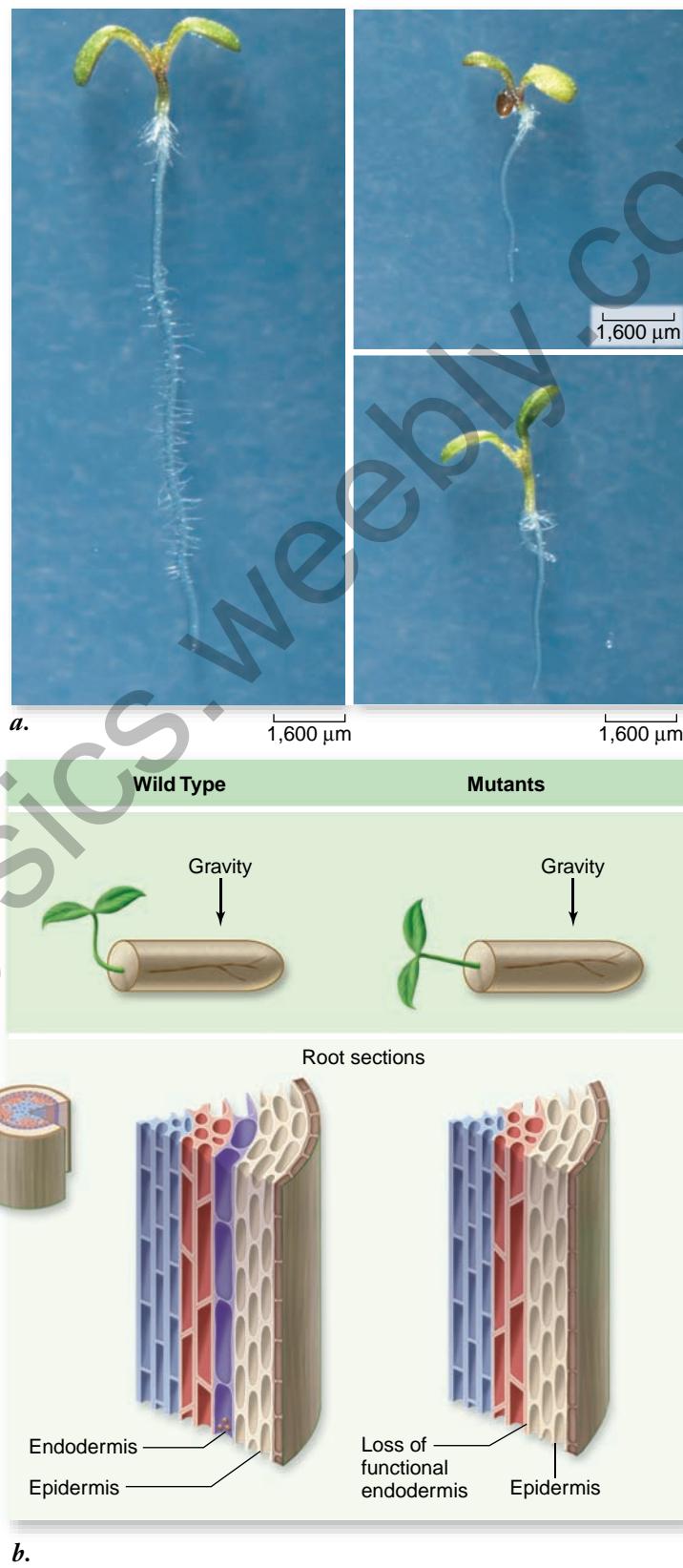


Figure 41.10 Amyloplasts in stem endodermis is needed for gravitropism. **a.** The *scr* and *shr* mutants of *Arabidopsis* have abnormal root development because they lack a fully differentiated endodermal layer. **b.** The endodermal defect extends into the stem, eliminating the positive gravitropic response of wild-type stems.

41.3 Responses to Mechanical Stimuli

Learning Outcomes

1. Define thigmomorphogenesis.
2. Contrast thigmotropism with thigmonastic responses.
3. Explain why the movement of leaves of a sensitive plant is not an example of a tropism.

Plants respond to touch and other mechanical stimuli in different ways, depending on the species and the type of stimulus. In some cases, plants permanently change form in response to mechanical stresses, a process termed **thigmomorphogenesis**. This change can be seen in trees growing where an almost constant wind blows from one direction. Other responses are reversible and occur in the short term, as when mimosa leaves droop in response to touch. These responses are not tropisms, but rather turgor movements that come about due to changes in the internal water pressure of cells.

Touch can trigger irreversible growth responses

A **thigmotropism** is directional growth of a plant or plant part in response to contact with an object, animal, other plant, or even the wind. Thigmonastic responses are very similar to thigmotropisms, except that the direction of the growth response is the same regardless of the direction of the stimulus.

Tall, slender plants are more likely to snap during a wind or rain storm than are plants with short, wide internodes. Environmental signals such as regularly occurring winds or the rubbing of one plant against another are sufficient to induce morphogenetic change leading to thicker, shorter internodes. In some cases, even repeated touching of a plant with a finger is enough to cause a change in plant growth.

Tendrils are modified stems that some species use to anchor themselves in the environment (figure 41.11). When a tendril makes contact with an object, specialized epidermal cells perceive the contact and promote uneven growth, causing the tendril to curl around the object, sometimes within only 3 to 10 min. Two hormones, auxin and ethylene, appear to be involved in tendril movements, and they can induce coiling even in the absence of any contact stimulus. Curiously, the tendrils of some species coil toward the site of the stimulus (thigmotropic growth), while those of other species may always coil clockwise, regardless of the side of the tendril that makes contact with an object. In some other plants, such as clematis, bindweed, and dodder, leaf petioles or unmodified stems twine around other stems or solid objects.

Perhaps the most dramatic touch response is the snapping of a Venus flytrap. As discussed in chapter 39, the modified leaves of the flytrap close in response to a touch stimulus, trapping insects or other potential sources of protein. A flytrap can shut in a mere 0.5 sec. The enlarged epidermal or mesophyll cells of the flytrap cause the trap to close. The speed



Figure 41.11 Thigmotropism. The thigmotropic response of these twining stems causes them to coil around the object with which they have come in contact.

of trap closure is enhanced by the shape of the leaf, which flips between a concave and convex form.

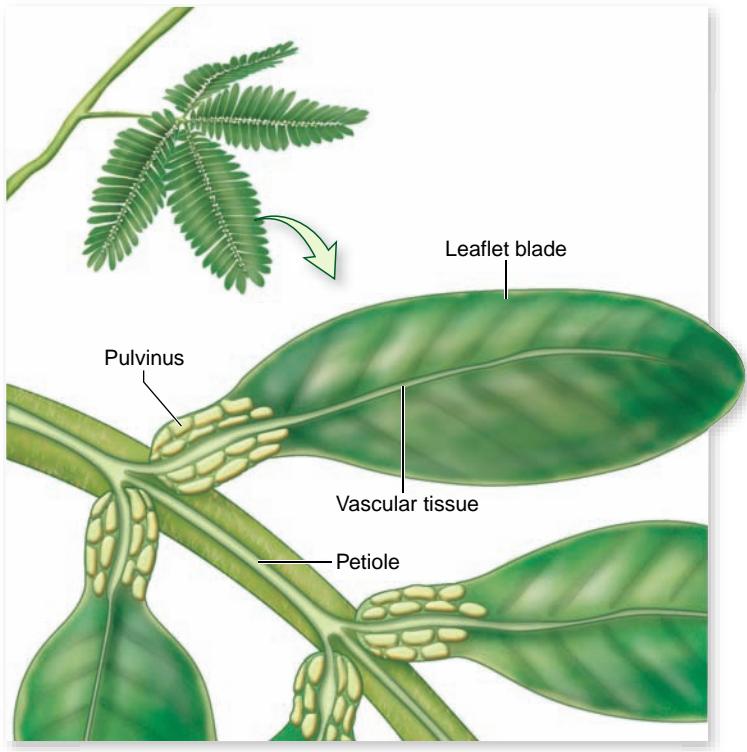
What is particularly amazing about this response is that the outer cells actually grow. The cell walls may soften in response to an electrical signal that moves through the leaf when the trigger hairs are touched, and the high pressure (turgor) of the water inside the cells pushes against the softened walls to enlarge the cell. This growth mechanism is distinct from other turgor movements (to be discussed shortly) because the water is already within the cell, not transferred into it in response to the electrical signal.

If digestible prey is caught, the trap will open about 24 hr later through the growth of inner cells of the flytrap. This growth response can only be triggered about four times before the leaf dies, presumably because so much energy is required for the individual flytrap to do this trick.

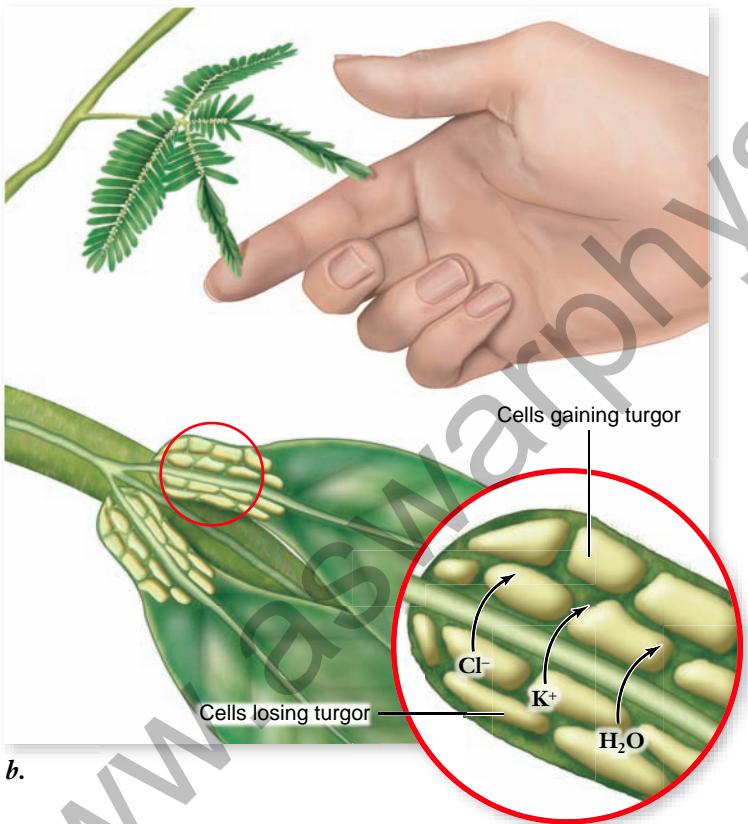
Arabidopsis is proving valuable as a model system to explore plant responses to touch. A gene has been identified that is expressed in 100-fold higher levels 10 to 30 min after touch. The gene codes for a calmodulin-like protein that binds Ca^{2+} , which is involved in a number of plant physiological processes. Given the value of a molecular genetics approach in dissecting the pathways leading from an environmental signal to a growth response, the touch gene provides a promising first step in understanding how plants respond to touch.

Reversible responses to touch and other stimuli involve turgor pressure

Unlike tropisms, some touch-induced plant movements are not based on growth responses, but instead result from reversible changes in the turgor pressure of specific cells. Turgor, as described in chapter 38, is pressure within a living cell resulting from diffusion of water into it. If water leaves turgid cells, the cells may collapse, causing plant movement; conversely, water



a.



b.

Figure 41.12 Sensitive plant (*Mimosa pudica*).

- a. The blades of *Mimosa* leaves are divided into numerous leaflets; at the base of each leaflet is a swollen structure called a pulvinus.
- b. Changes in turgor cause leaflets to fold in response to a stimulus. When leaves are touched (center two leaves), ions move to the outer side of the pulvinus, water follows by osmosis, and the decreased interior turgor pressure leads to folding.



Figure 41.13 Heliotropism. These sunflowers track the movement of the Sun every day.

entering a limp cell may also cause movement as the cell once more becomes turgid.

Many plants, including those of the legume family (Fabaceae), exhibit leaf movements in response to touch or other stimuli. After exposure to a stimulus, the changes in leaf orientation are mostly associated with rapid turgor pressure changes in pulvini (singular, *pulvinus*), two-sided multicellular swellings located at the base of each leaf or leaflet. When leaves with pulvini, such as those of the sensitive plant (*Mimosa pudica*), are stimulated by wind, heat, touch, or in some instances, intense light, an electrical signal is generated. The electrical signal is translated into a chemical signal, with potassium ions being pumped from the cells in one-half of a pulvinus to the intercellular spaces in the other half, leading to the rapid osmosis of water to one side of the pulvinus.

The loss of turgor in half of the pulvinus causes the leaf to “fold.” The movements of the leaves and leaflets of a sensitive plant are especially rapid; the folding occurs within a second or two after the leaves are touched (figure 41.12). Over a span of about 15 to 30 min after the leaves and leaflets have folded, water usually diffuses back into the same cells from which it left, and the leaf returns to its original position.

Some turgor movements are triggered by light. For example, the leaves of some plants may track the Sun, with their blades oriented at right angles to it; how their orientation is directed, however, is poorly understood. Such leaves can move quite rapidly (as much as 15 degrees an hour). This movement maximizes photosynthesis and is analogous to solar panels designed to track the Sun (figure 41.13).

Some of the most familiar reversible changes due to turgor pressure are the circadian rhythms seen in leaves and flowers that open during the day and close at night, or vice versa. For example, the flowers of four o’clocks open in the afternoon, and evening primrose petals open at night. As described earlier, sensitive plant leaves also close at night. Bean leaves are horizontal during the day when their pulvini are turgid, but become more or less vertical at night as the pulvini lose turgor (figure 41.14). These sleep movements reduce water loss from transpiration during the night, but maximize photosynthetic surface area during the day.

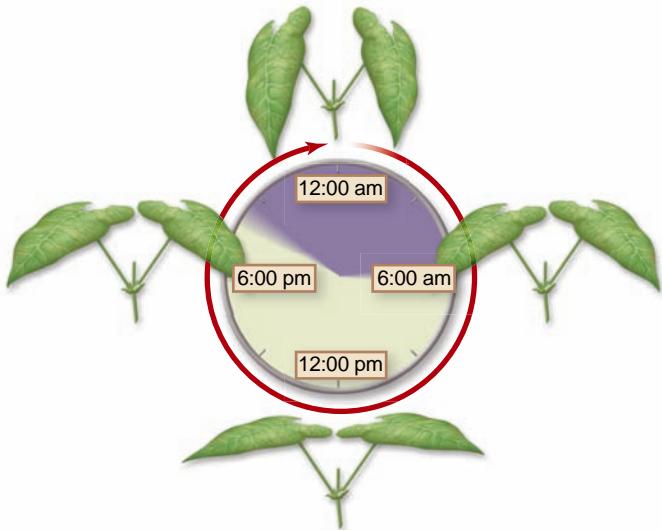


Figure 41.14 Sleep movements in bean leaves. In the bean plant, leaf blades are oriented horizontally during the day and vertically at night.

Learning Outcomes Review 41.3

Thigmomorphogenesis is a change in growth form in response to a mechanical stress (physical contact or wind). Thigmotropism is directional growth, whereas a thigmonastic response has no directionality. A tropism is an irreversible growth response; a touch-induced plant movement, such as exhibited by *Mimosa pudica*, is reversible and is based on changes in turgor pressure.

- What would be some advantages of having leaves that fold when stimulated?

41.4 Responses to Water and Temperature

Learning Outcomes

1. List the environmental factors that can lead to dormancy.
2. Explain why seed dormancy is an important evolutionary innovation.
3. Identify the types of biological molecules that are most directly affected by low and high temperatures.

Sometimes, modifying the direction of growth is not enough to protect a plant from harsh conditions. The ability to cease growth and go into a dormant stage when conditions become unfavorable, such as during seasonal changes in temperate climates, provides a survival advantage. The extreme example is seed dormancy, but there are intermediate approaches to waiting out the bad times as well.

Plants also have developed adaptations to more short-term fluctuations in temperature, such as might occur during a heat wave or cold snap. These strategies include changes in membrane composition and the production of heat shock proteins.

Dormancy is a response to water, temperature, and light

In temperate regions, we generally associate dormancy with winter, when freezing temperatures and the accompanying unavailability of water make it impossible for most plants to grow. During this season, buds of deciduous trees and shrubs remain dormant, and apical meristems remain well protected inside enfolding scales. Perennial herbs spend the winter underground, existing as stout stems or roots packed with stored food. Many other kinds of plants, including most annuals, pass the winter as seeds. Often dormancy begins with the dropping of leaves, which you have probably seen occur in deciduous trees in the autumn.

Organ abscission

Deciduous leaves are often shed as the plant enters dormancy. The process by which leaves or petals are shed is called **abscission**.

Abscission can be useful even before dormancy is established. For example, shaded leaves that are no longer photosynthetically productive can be shed. Petals, which are modified leaves, may senesce once pollination occurs. Orchid flowers remain fresh for long periods of time, even in a florist shop; however, once pollination occurs, a hormonal change is triggered that leads to petal senescence. This strategy makes sense in terms of allocation of energy resources because the petals are no longer necessary to attract a pollinator. One advantage of organ abscission, therefore, is that nutrient sinks can be discarded, conserving resources.

On a larger scale, deciduous plants in temperate areas produce new leaves in the spring and then lose them in the fall. In the tropics, however, the production and subsequent loss of leaves in some species is correlated with wet and dry seasons. Evergreen plants, such as most conifers, usually have a complete change of leaves every two to seven years, periodically losing some but not all of their leaves.

Abscission involves changes that take place in an *abscission zone* at the base of the petiole (figure 41.15). Young leaves produce

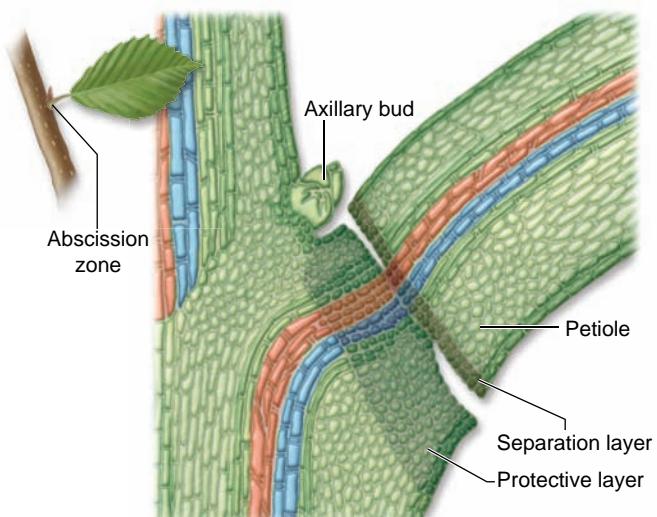


Figure 41.15 Leaf abscission. Hormonal changes in the leaf's abscission zone cause abscission. Two layers of cells in the abscission zone differentiate into a protective layer and a separation layer. As pectins in the separation layer break down, wind and rain can easily separate the leaf from the stem.

hormones (especially cytokinins) that inhibit the development of specialized layers of cells in this zone. Hormonal changes take place as the leaf ages, however, and two layers of cells become differentiated. A *protective layer*, which may be several cells wide, develops on the stem side of the petiole base. These cells become impregnated with suberin, which you may recall is a fatty substance impervious to moisture. A *separation layer* develops on the leaf-blade side; the cells of the separation layer sometimes divide, swell, and become gelatinous.

When temperatures drop, when the duration and intensity of light diminishes, or when other environmental changes occur, enzymes break down the pectins in the middle lamellae of the separation cells. Wind and rain can then easily separate the leaf from the stem. Left behind is a sealed leaf scar that is protected from invasion by bacteria and other disease organisms.

As the abscission zone develops, the green chlorophyll pigments present in the leaf break down, revealing the yellows and oranges of other pigments, such as carotenoids, that previously had been masked by the intense green colors. At the same time, water-soluble red or blue pigments called *anthocyanins* and *betacyanins* may also accumulate in the vacuoles of the leaf cells—all contributing to an array of fall colors in leaves (figure 41.16).

Seed dormancy

The extraordinary evolutionary innovation of the seed plants is the dormant seed that allows plant offspring to wait until conditions for germination are optimal. Sometimes the seeds can endure a wait of hundreds of years (figure 41.17). In seasonally dry climates, seed dormancy occurs primarily during the dry season, often the summer. Rainfalls trigger germination when conditions for survival are more favorable.

Annual plants occur frequently in areas of seasonal drought. Seeds are ideal for allowing annual plants to bypass the dry season, when there is insufficient water for growth.



Figure 41.16 Leaf color changes during abscission.

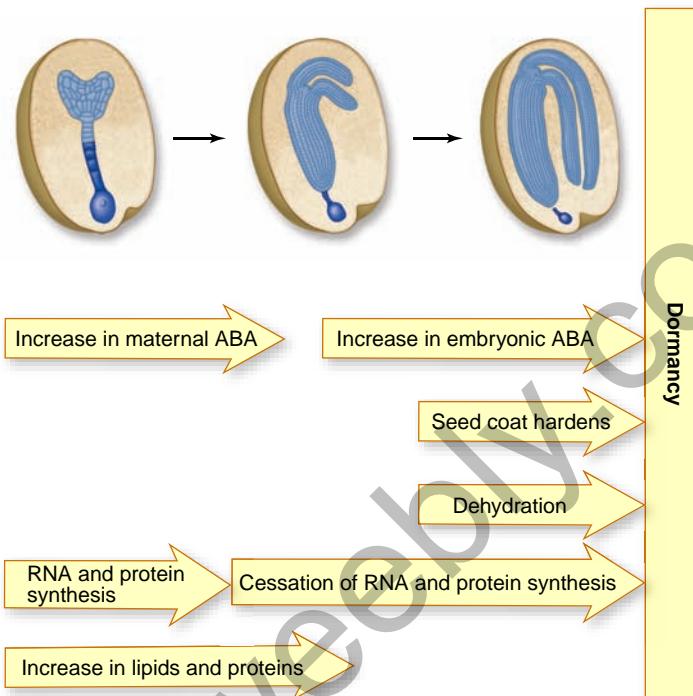


Figure 41.17 Seed dormancy. Accumulating food reserves, forming a protective seed coat, and dehydration are essential steps leading to dormancy. Abscisic acid (ABA) from both maternal and embryonic tissue is necessary for dormancy.

When it rains, these seeds can germinate, and the plants can grow rapidly, having adapted to the relatively short periods when water is available.

Chapter 37 covered some of the mechanisms involved in breaking seed dormancy and allowing germination under favorable circumstances. These include water leaching away the chemicals that inhibit germination or mechanically cracking the seed coats due to osmotic swelling, a procedure particularly suitable for promoting growth in seasonally dry areas.

Seeds may remain dormant for a surprisingly long time. Many legumes have tough seeds that are virtually impermeable to water and oxygen. These seeds often last decades and even longer without special care; they will eventually germinate when their seed coats have been cracked and water is available. Seeds that are thousands of years old have been successfully germinated!

Favorable temperatures, day length, and amounts of water can release buds, underground stems and roots, and seeds from a dormant state. Requirements vary among species. For example, some weed seeds germinate in cooler parts of the year and are inhibited from germinating by warmer temperatures. Day length differences can have dramatic effects on dormancy. For example, tree dormancy is common in temperate climates when the days are short, but is unusual in tropical trees growing near the equator, where day length remains about the same regardless of season.

Plants can survive temperature extremes

Sometimes temperatures change rapidly, and dormancy is not possible. How do plants survive temperature extremes? A number of adaptations, including some rapid response strategies, help plants overcome sudden chilling or extreme heat.

Chilling

Knowing the lipid composition of a plant's membranes can help predict whether the plant will be sensitive or resistant to chilling. Saturated lipids solidify at a higher temperature because they pack together more closely (see chapter 5), so the more unsaturated the membrane lipids are, the more resistant the plant is to chilling. *Arabidopsis* plants genetically modified to contain a higher percentage of saturated fatty acids have proved to be more sensitive to chilling.

When chilling occurs, the enzyme desaturase converts the single bonds in the saturated lipids to double bonds. This process lowers the temperature at which the membrane becomes rigid and cannot function properly.

Even highly unsaturated membranes are not enough to protect plants from freezing temperatures. At freezing, ice crystals form and the cells die from dehydration—not enough liquid water is available for metabolism. Some plants, however, have the ability to undergo deep supercooling and survive temperatures as low as -40°C . Supercooling occurs when ice crystal formation is limited, and the crystals occur in extracellular spaces where they cannot damage cell organelles. Furthermore, the cells of these plants must be able to withstand gradual dehydration.

Acquiring tolerance to chilling or freezing as the temperature drops can be explained by increased solute concentration. In addition, antifreeze proteins prevent ice crystals from forming. Ice crystals can also form (nucleate) around bacteria naturally found on the leaf surface. Some bacteria have been genetically engineered so that they do not nucleate ice crystals. Spraying leaves with these modified bacteria can provide frost tolerance in some crops.

High temperatures

High temperatures can be harmful because proteins denature and lose their function when heated. If temperatures suddenly rise 5° to 10°C , heat shock proteins (HSPs) are produced. These proteins can stabilize other proteins so that they don't unfold or misfold at higher temperatures. In some cases, HSPs induced by temperature increases can also protect plants from other stresses, including chilling.

Plants can survive otherwise lethal temperatures if they are gradually exposed to increasing temperature. These plants have *acquired thermotolerance*. More is being learned about temperature acclimation by isolating mutants that fail to acquire thermotolerance, including the aptly named *hot* mutants in *Arabidopsis*. One of the *HOT* genes codes for an HSP. Characterization of other *HOT* genes indicates that thermotolerance requires more than the synthesis of HSPs; some *HOT* genes stabilize membranes and are necessary for protein activity.

Learning Outcomes Review 41.4

Seasonal changes, such as reduction in temperature, light, and water availability, may lead to plant dormancy; in deciduous trees, leaf abscission is part of entering dormancy. Seed dormancy prevents germination until growth conditions are optimal. At low temperatures, lipids in membranes begin to solidify and ice crystals may form in tissues; at high temperatures, proteins denature.

- Why is it advantageous for broadleaf trees to drop leaves in autumn, when they must grow them again in spring?

41.5 Hormones and Sensory Systems

Learning Outcomes

1. Discuss properties of hormones.
2. Compare auxins with cytokinins.
3. Describe the major roles of abscisic acid.

Sensory responses that alter morphology rely on complex physiological networks. Many internal signaling pathways involve plant hormones, which are the focus of this section. Hormones are involved in responses to the environment, as well as in internally regulated development (see chapter 37).

The hormones that guide growth are keyed to the environment

Hormones are chemical substances produced in small, often minute quantities in one part of an organism and then transported to another part where they bring about physiological or developmental responses. How hormones act in a particular instance is influenced both by the hormone and the tissue that receives the message.

In animals, hormones are usually produced at definite sites, most commonly in organs such as glands. In plants, hormones are not produced in specialized tissues but, instead, in tissues that also carry out other, usually more obvious functions. Seven major kinds of plant hormones have been identified: auxin, cytokinins, gibberellins, brassinosteroids, oligosaccharins, ethylene, and abscisic acid (table 41.1). Current research is focused on the biosynthesis of hormones and on characterizing the hormone receptors involved in signal transduction pathways. Much of the molecular basis of hormone function remains enigmatic.

Because hormones are involved in so many aspects of plant function and development, we have chosen to integrate examples of hormone activity with specific aspects of plant biology throughout the text. In this section, our goal is to give a brief overview of these hormones.

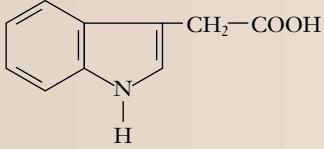
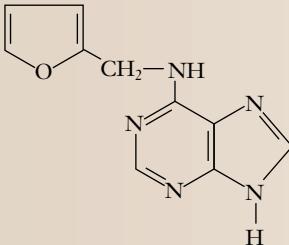
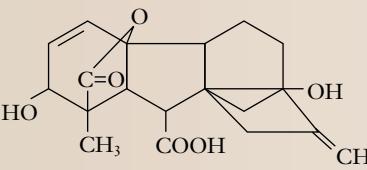
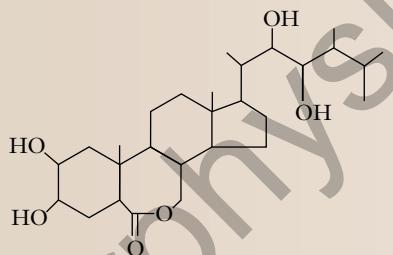
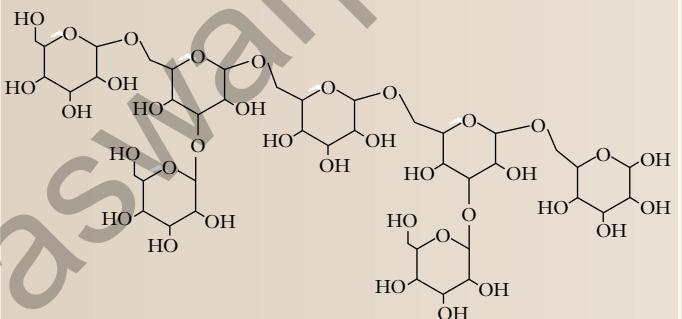
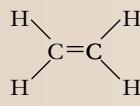
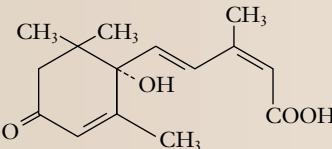
Auxin allows elongation and organizes the body plan

More than a century ago, an organic substance known as **auxin** was the first plant hormone to be discovered. Auxin increases the plasticity of plant cell walls and is involved in elongation of stems. Cells can enlarge in response to changes in turgor pressure, but cell walls must be fairly plastic for this expansion to occur. Auxin plays a role in softening cell walls. The discovery of auxin and its role in plant growth is an elegant example of thoughtful experimental design and is recounted here for that reason.

Discovery of auxin

Later in life, the great evolutionist Charles Darwin became increasingly devoted to the study of plants. In 1881, he and his

TABLE 41.1 Functions of the Major Plant Hormones

Hormone		Major Functions	Where Produced or Found in Plant
Auxins		Promotion of stem elongation and growth; formation of adventitious roots; inhibition of leaf abscission; promotion of cell division (with cytokinins); induction of ethylene production; promotion of lateral bud dormancy	Apical meristems; other immature parts of plants
Cytokinins		Stimulation of cell division, but only in the presence of auxin; promotion of chloroplast development; delay of leaf aging; promotion of bud formation	Root apical meristems; immature fruits
Gibberellins		Promotion of stem elongation; stimulation of enzyme production in germinating seeds	Roots and shoot tips; young leaves; seeds
Brassinosteroids		Overlapping functions with auxins and gibberellins	Pollen, immature seeds, shoots, leaves
Oligosaccharins		Pathogen defense, possibly reproductive development	Cell walls
Ethylene		Control of leaf, flower, and fruit abscission; promotion of fruit ripening	Roots, shoot apical meristems; leaf nodes; aging flowers; ripening fruits
Abscisic acid		Inhibition of bud growth; control of stomatal closure; some control of seed dormancy; inhibition of effects of other hormones	Leaves, fruits, root caps, seeds

son Francis published a book called *The Power of Movement of Plants*. In this book, the Darwins reported their systematic experiments on the response of growing plants to light—the responses that came to be known as phototropisms. They used germinating oat and canary grass seedlings in their experiments and made many observations in this field.

Charles and Francis Darwin knew that if light came primarily from one direction, seedlings would bend strongly toward it. If they covered the tip of a shoot with a thin glass tube, the shoot would bend as if it were not covered. However, if they used a metal foil cap to exclude light from the plant tip, the shoot would not bend (figure 41.18). They also found that using an opaque collar to exclude light from the stem below the tip did not keep the area above the collar from bending.

In explaining these unexpected findings, the Darwins hypothesized that when the shoots were illuminated from one side, they bent toward the light in response to an “influence” that was transmitted downward from its source at the tip of the shoot.

For some 30 years, the Darwins’ perceptive experiments remained the sole source of information about this interesting phenomenon. Then the Danish plant physiologist Peter Boysen-Jensen and the Hungarian plant physiologist Arpad Paal independently demonstrated that the substance causing the shoots to bend was a chemical. They showed that if the tip of a germinating grass seedling was cut off and then replaced, with a small block of agar separating it from the rest of the seedling, the seedling would still grow as if there had been no change. Something evidently was passing from the tip of the seedling through the agar into the region where the bending occurred.

On the basis of these observations under conditions of either uniform illumination or darkness, Paal suggested that an unknown substance continually moves down from the tips of grass seedlings and promotes growth on all sides. Such a light pattern would not, of course, cause the shoot to bend.



Inquiry question

Propose a mechanism to explain how seedlings could bend in the light using what Paal discovered.

Then, in 1926, the Dutch plant physiologist Frits Went carried Paal’s experiments a step further. Went cut off the tips of oat seedlings that had been illuminated normally and set these tips on agar. He then took oat seedlings that had been grown in the dark and cut off their tips in a similar way. Finally, Went cut tiny blocks from the agar on which the tips of the light-grown seedlings had been placed and placed them off-center on the tops of the decapitated dark-grown seedlings (figure 41.19). Even though these seedlings had not been exposed to the light themselves, they bent away from the side on which the agar blocks were placed.

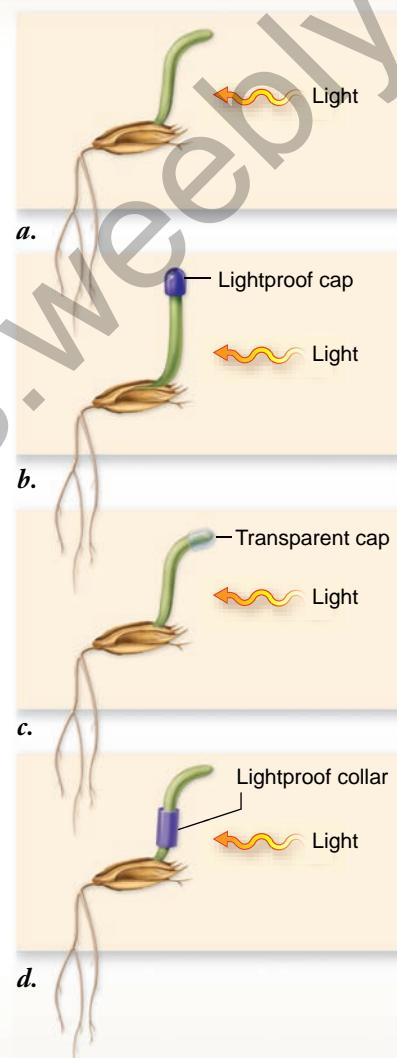
As an experimental control, Went put blocks of pure agar on the decapitated stem tips and noted either no effect or a slight bending toward the side where the agar blocks were placed. Finally, Went cut sections out of the lower portions of the light-grown seedlings. He placed these sections on the tips of decapitated, dark-green oat seedlings and again observed no effect.

SCIENTIFIC THINKING

Hypothesis: The shoot tip of a plant detects the direction of light.

Prediction: The shoot tip of a grass seedling will grow toward a unidirectional light source if it is not covered.

Test: Make four treatment groups, including (1) untreated seedling, (2) tip covered with lightproof cap, (3) tip covered with transparent cap, and (4) lightproof collar placed below tip.



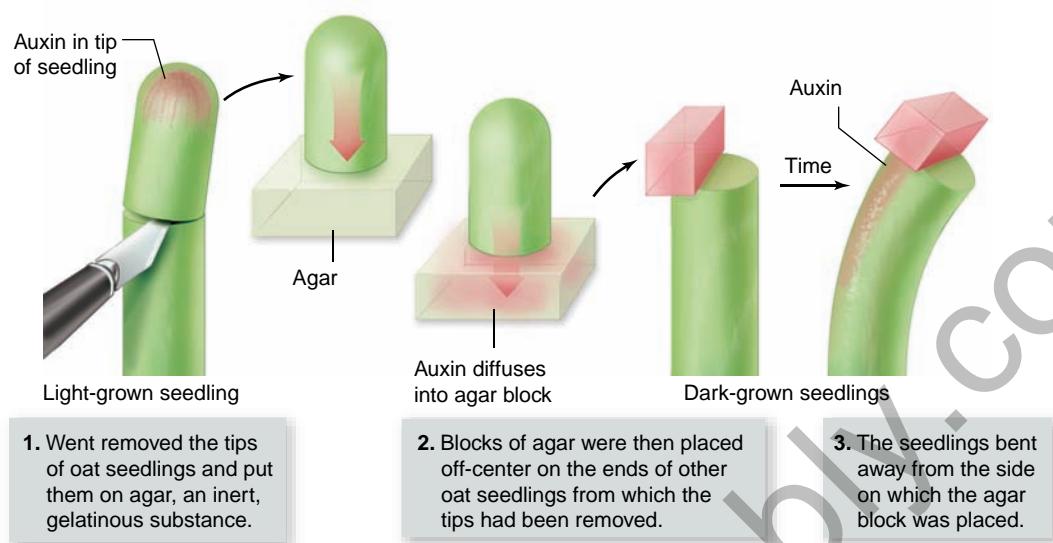
Result: a. Young grass seedlings normally bend toward the light. b. The bending did not occur when the tip of a seedling was covered with a lightproof cap. c. Bending did occur when it was covered with a transparent one. d. When a collar was placed below the tip, the characteristic light response took place.

Conclusion: In response to light, an “influence” that caused bending was transmitted from the tip of the seedling to the area below, where bending normally occurs.

Further Experiments: How could you determine if the light response in a shoot tip requires the movement of a signal from one side of the shoot to the other? (Hint: See Went’s experiment in figure 41.19).

Figure 41.18 Shoot tips perceive unidirectional light.

Figure 41.19 Frits Went's experiment. Went concluded that a substance he named *auxin* promoted the elongation of the cells and that it accumulated on the side of an oat seedling away from the light.



As a result of his experiments, Went was able to show that the substance that had diffused into the agar from the tips of light-grown oat seedlings could make seedlings bend when they otherwise would have remained straight. He also showed that this chemical messenger caused the cells on the side of the seedling into which it flowed to grow more than those on the opposite side (figure 41.20). In other words, the chemical enhanced rather than retarded cell elongation. He named the substance that he had discovered *auxin*.

Went's experiments provided a basis for understanding the responses that the Darwins had obtained some 45 years earlier. The oat seedlings bent toward the light because of differences in the auxin concentrations on the two sides of the shoot.

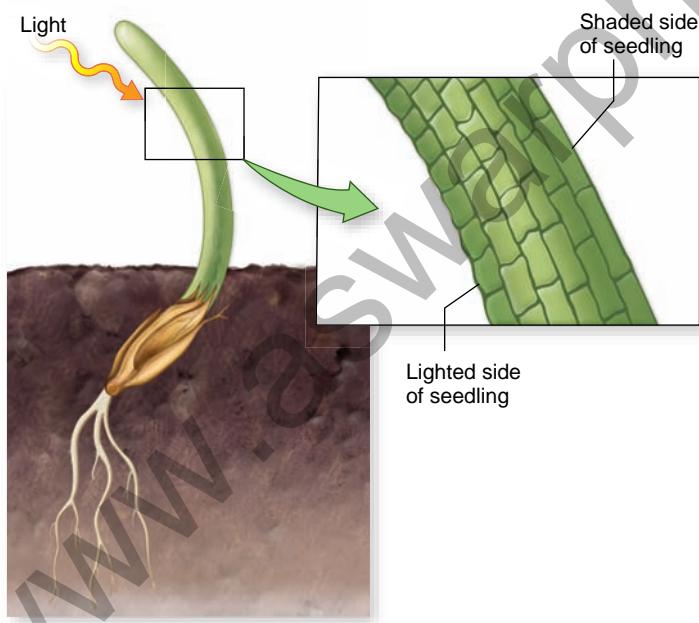


Figure 41.20 Auxin causes cells on the dark side to elongate.

Plant cells that are in the shade have more auxin and grow faster than cells on the lighted side, causing the plant to bend toward light. Further experiments showed exactly why there is more auxin on the shaded side of a plant.

The side of the shoot that was in the shade had more auxin, and its cells therefore elongated more than those on the lighted side, bending the plant toward the light.

The effects of auxin

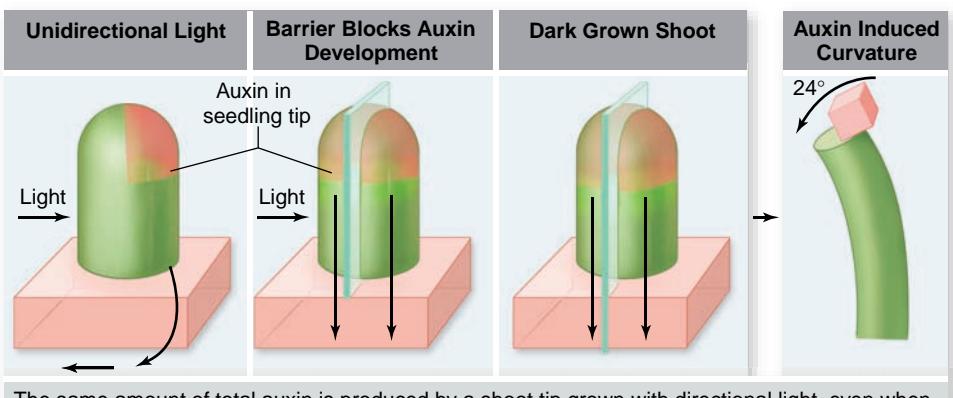
Auxin acts to adapt the plant to its environment in a highly advantageous way by promoting growth and elongation. Environmental signals directly influence the distribution of auxin in the plant. How does the environment—specifically, light—exert this influence? Theoretically, light might destroy the auxin, might decrease the cells' sensitivity to auxin, or might cause the auxin molecules to migrate away from the light into the shaded portion of the shoot. This last possibility has proved to be the case.

In a simple but effective experiment, Winslow Briggs inserted a thin sheet of transparent mica vertically between the half of the shoot oriented toward the light and the half of the shoot oriented away from it (figure 41.21). He found that light from one side does not cause a shoot with such a barrier to bend. When Briggs examined the illuminated plant, he found equal auxin levels on both the light and dark sides of the barrier. He concluded that a normal plant's response to light from one direction involves auxin migrating from the light side to the dark side, and that the mica barrier prevented a response by blocking the migration of auxin.

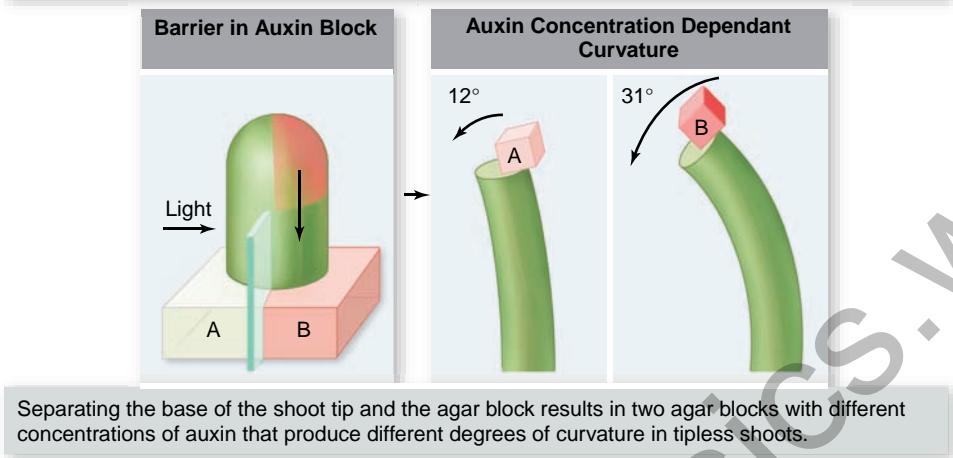
The effects of auxin are numerous and varied. Auxin promotes the activity of the vascular cambium and the vascular tissues. Also, auxin is present in pollen in large quantities and plays a key role in the development of fruits. Synthetic auxins are used commercially for the same purpose. Fruits will normally not develop if fertilization has not occurred and seeds are not present, but frequently they will develop if auxin is applied. Pollination may trigger auxin release in some species, leading to fruit development even before fertilization has taken place.

How auxin works

In spite of this long history of research, auxin's molecular basis of action has been an enigma. The chemical structure of the most common auxin, **indoleacetic acid (IAA)**, resembles that of the amino acid tryptophan, from which it is probably



The same amount of total auxin is produced by a shoot tip grown with directional light, even when a barrier divides the shoot tip, and a shoot tip grown in the dark. All three blocks of agar cause the same amount of curvature in a tipless shoot.



Separating the base of the shoot tip and the agar block results in two agar blocks with different concentrations of auxin that produce different degrees of curvature in tipless shoots.

Figure 41.21 Phototropism and auxin: The Winslow Briggs experiments.

Directional light causes the accumulation of auxin in the dark side of the shoot tip, which can move down the stem. Barriers inserted in the tip revealed that light affects auxin displacement rather than rate of auxin production.

synthesized by plants (figure 41.22). Although other forms of auxin exist, IAA is the most common natural auxin.

An auxin-binding protein (ABP1) was identified two decades ago. ABP1 is found in the cytoplasm and its role in auxin response is still unclear. Mutants that lack ABP1 do not make it past embryogenesis because cell elongation is inhibited and the basic body plan described in chapter 36 is not organized. But, the *abp1* mutant cells divide, which indicates that part of the auxin pathway is still functioning.

More recently, two families of proteins that mediate rapid, auxin-induced changes in gene expression have been identified: the auxin response factors (ARFs) and the Aux/IAA proteins. Transcription can be either enhanced or suppressed by ARFs, which are known to bind DNA. The Aux/IAA pro-

teins function a bit earlier in the auxin response pathway and have been shown to bind to and repress proteins that activate the expression of *ARF* genes.

ARF genes are activated when Aux/IAA proteins are degraded by ubiquitin tagging and protein degradation in the proteasome. Auxin binding to ARF protein is not sufficient to initiate gene expression in response to auxin signaling because of Aux/IAA repression of ARF activity. How then does a plant sense auxin and degrade Aux/IAA proteins?

The identification of the elusive auxin receptor in 2005 hints at how plants sense and respond to auxin. Auxin binds directly to a protein called the transport inhibitor response protein 1 (TIR1). TIR1 is the enigmatic auxin receptor. It is part of a protein complex known as SCF which is found

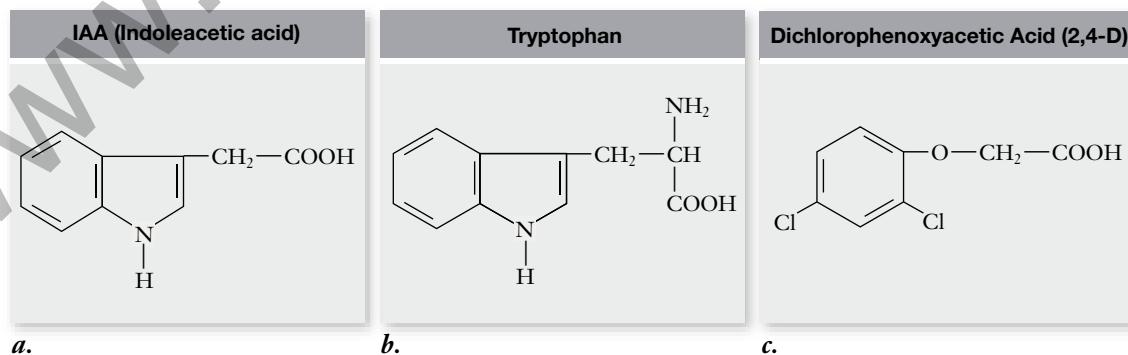


Figure 41.22 Auxins.

- a.** Indoleacetic acid (IAA), the principal naturally occurring auxin.
- b.** Tryptophan, the amino acid from which plants probably synthesize IAA.
- c.** Dichlorophenoxyacetic acid (2,4-D), a synthetic auxin, is a widely used herbicide.

throughout eukaryotes. SCF is shorthand for the three polypeptide subunits found in the complex: *Skp*, *Cullin*, and *F-box*. Auxin binds to TIR1 in the SCF complex if Aux/IAA proteins are present. Once auxin binds, the SCF complex degrades the Aux/IAA proteins through the ubiquitin pathway.

Five steps lead from auxin perception to auxin-induced gene expression (figure 41.23):

1. Auxin binds TIR1 in the SCF complex.
2. The activated SCF complex tags Aux/IAA proteins with ubiquitin.
3. Aux/IAA proteins are degraded in the proteasome.
4. Aux/IAA proteins are no longer available to bind and repress ARF (auxin response factor) transcriptional activators.
5. ARF transcription factors facilitate transcription of auxin-response genes.

Unlike with animal hormones, a specific signal is not sent to specific cells, eliciting a predictable response. Most likely, multiple auxin perception sites are present. Auxin is also unique among the plant hormones in that it is transported toward the base of the plant. Two families of genes have been identified in *Arabidopsis* that are involved in auxin transport. For example, one family of proteins (the PINs) are involved in the top-to-bottom transport of auxin, while two other proteins function in the root tip to regulate the growth response to gravity, described earlier.

One of the direct effects of auxin is an increase in the plasticity of the plant cell wall, but this effect works only on young cell walls lacking extensive secondary cell wall formation and may or may not involve rapid changes in gene expression. The acid

growth hypothesis provides a model linking auxin to cell wall expansion (figure 41.24). According to this hypothesis, auxin causes responsive cells to actively transport hydrogen ions from the cytoplasm into the cell wall space. This decreases the pH, which activates enzymes that can break the bonds between cell wall fibers.

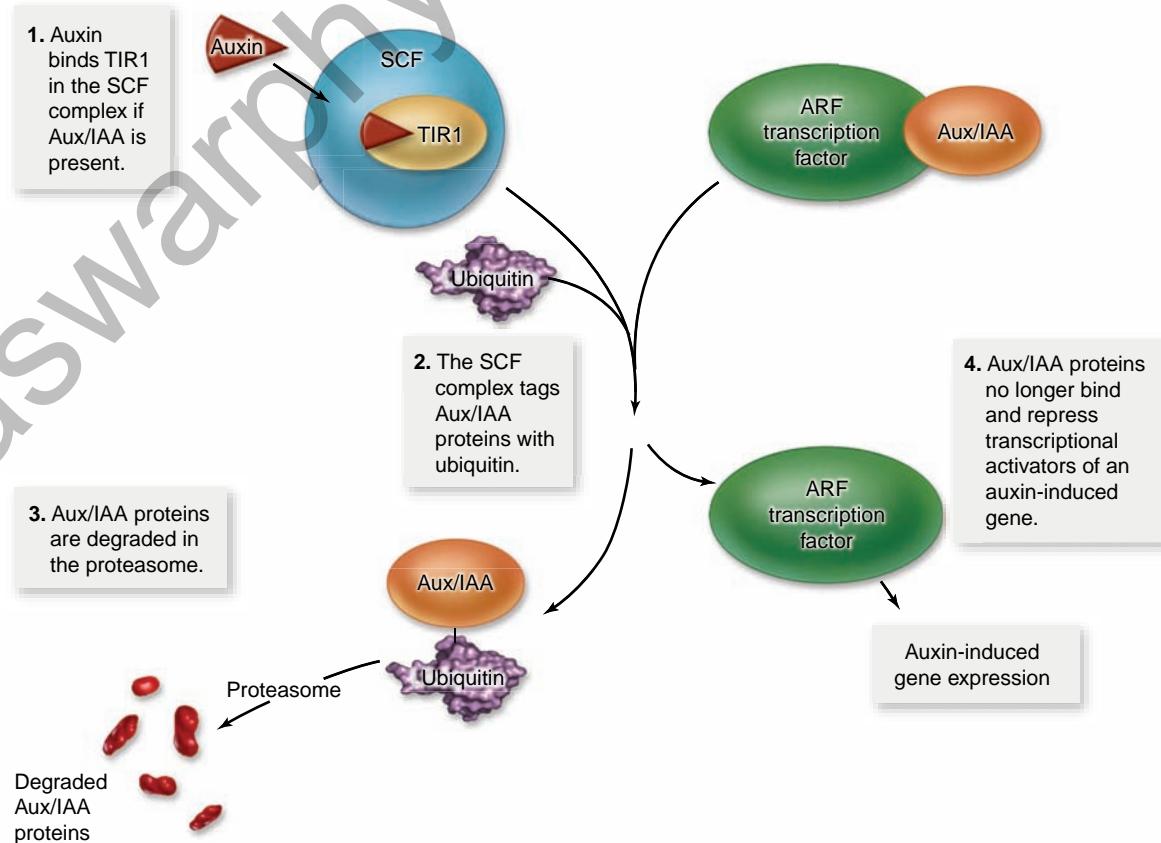
This hypothesis has been experimentally supported in several ways. Buffers that prevent cell wall acidification block cell expansion. And, other compounds that release hydrogen ions from the cell can also cause cell expansion. Finally, the movement of hydrogen ions has been observed in response to auxin treatment. The snapping of the Venus flytrap is postulated to involve an acid growth response that allows cells to grow in just 0.5 sec and close the trap.

Synthetic auxins

Synthetic auxins, such as *naphthalene acetic acid (NAA)* and *indolebutyric acid (IBA)*, have many uses in agriculture and horticulture. One of their most important uses is based on their prevention of abscission. Synthetic auxins are used to prevent fruit drop in apples before they are ripe and to hold berries on holly that is being prepared for shipping during the winter season. Synthetic auxins are also used to promote flowering and fruiting in pineapples and to induce the formation of roots in cuttings.

Synthetic auxins are routinely used to control weeds. When used as herbicides, they are applied in higher concentrations than IAA would normally occur in plants. One of the most important synthetic auxin herbicides is *2,4-dichlorophenoxyacetic acid*, usually known as **2,4-D** (see figure 41.22c). It kills weeds in grass lawns by selectively eliminating broad-leaved dicots. The stems of the dicot weeds cease all axial growth.

Figure 41.23 Auxin regulation of gene expression. Auxin activates a ubiquitination pathway that releases ARF transcription factors from repression by Aux/IAA proteins. The result is auxin-induced gene expression.



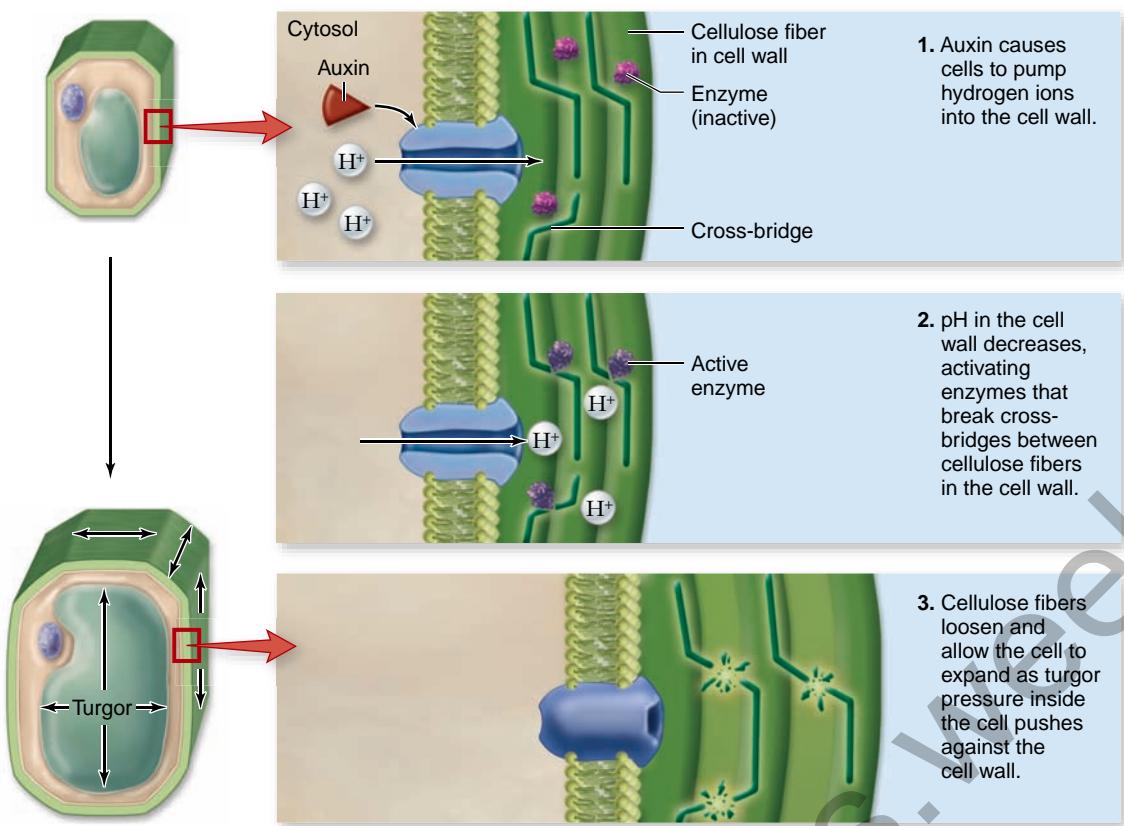


Figure 41.24 Acid growth hypothesis.

Auxin stimulates the release of hydrogen ions from the target cells, which alters the pH of the cell wall. This optimizes the activity of enzymes that break bonds in the cell wall, allowing the wall to expand.

The herbicide 2,4,5-trichlorophenoxyacetic acid, better known as 2,4,5-T, is closely related to 2,4-D. 2,4,5-T was widely used as a broad-spectrum herbicide to kill weeds and the seedlings of woody plants. It became notorious during the Vietnam War as a component of a jungle defoliant known as Agent Orange. When 2,4,5-T is manufactured, it is unavoidably contaminated with minute amounts of dioxin. Dioxin, in doses as low as a few parts per billion, has produced liver and lung diseases, leukemia, miscarriages, birth defects, and even death in laboratory animals. This chemical was banned in 1979 for most uses in the United States.

Cytokinins stimulate cell division and differentiation

Cytokinins comprise another group of naturally occurring growth hormones in plants. Studies by Gottlieb Haberlandt of Austria around 1913 demonstrated the existence of an unknown chemical in various tissues of vascular plants that, when applied

to cut potato tubers, would cause parenchyma cells to become meristematic, and would induce the differentiation of a cork cambium. In other research, coconut milk, subsequently found to contain cytokinins was used to promote the differentiation of organs in masses of plant tissue growing in culture. Subsequent studies have focused on the role cytokinins play in the differentiation of tissues from callus.

A *cytokinin* is a plant hormone that, in combination with auxin, stimulates cell division and differentiation. Most cytokinins are produced in the root apical meristems and transported throughout the plant. Developing fruits are also important sites of cytokinin synthesis. In mosses, cytokinins cause the formation of vegetative buds on the gametophyte. In all plants, cytokinins, working with other hormones, seem to regulate growth patterns.

Cytokinins are purines that appear to be derivatives of adenine (figure 41.25). Other chemically diverse molecules, not known to occur naturally, have effects similar to those of cytokinins. Cytokinins promote the growth of lateral buds into

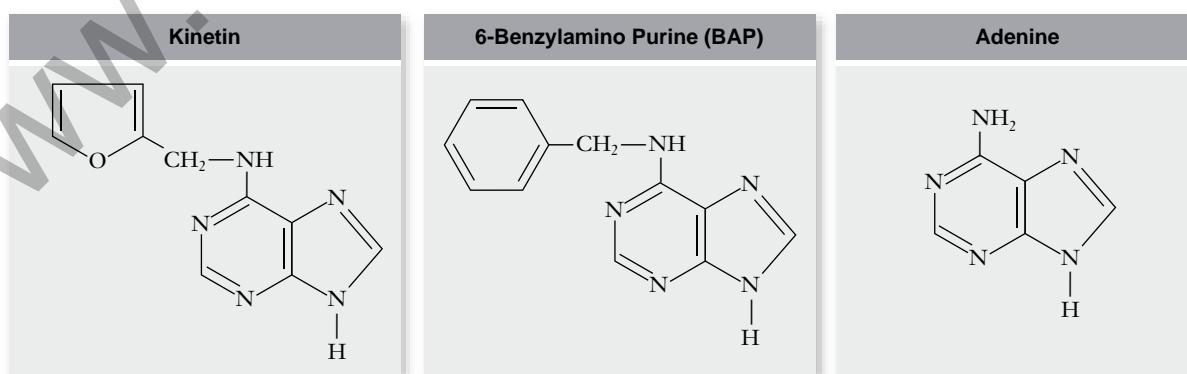
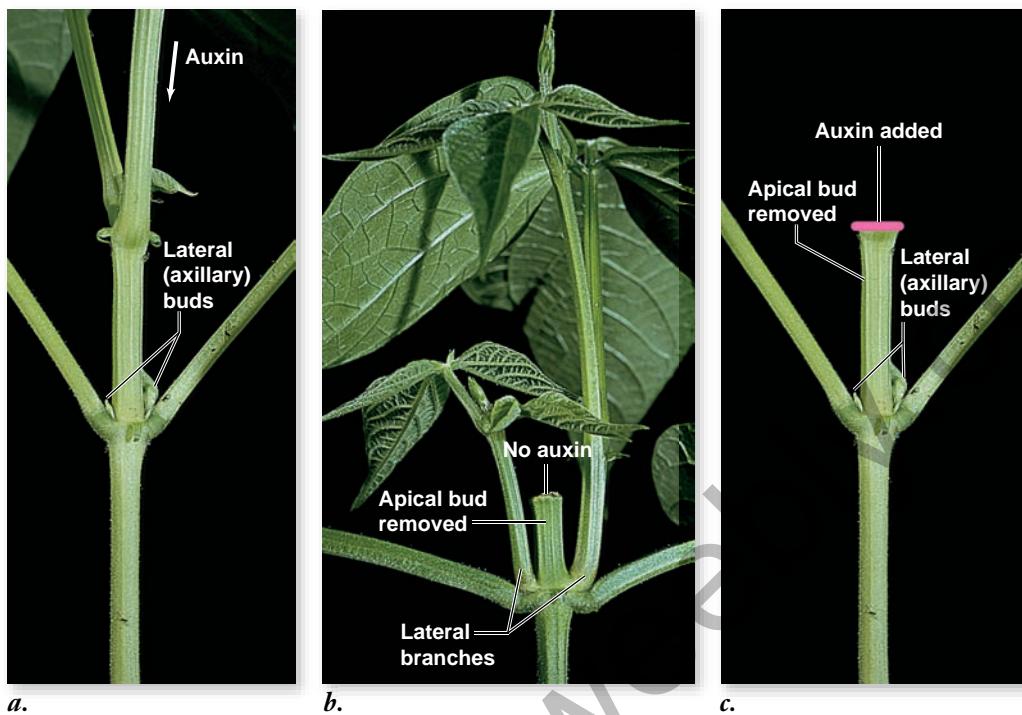


Figure 41.25 Some cytokinins.

Two commonly used synthetic cytokinins: kinetin and 6-benzylamino purine. Note their resemblance to the purine base adenine.

Figure 41.26 Cytokinins stimulate lateral bud growth.

- a. When the apical meristem of a plant is intact, auxin from the apical bud will inhibit the growth of lateral buds.
- b. When the apical bud is removed, cytokinins are able to induce the growth of lateral buds into branches.
- c. When the apical bud is removed and auxin is added to the cut surface, lateral bud outgrowth is suppressed.



branches (figure 41.26). Conversely, cytokinins inhibit the formation of lateral roots, while auxins promote their formation.

As a consequence of these relationships, the balance between cytokinins and auxin, along with many other factors, determines the form of a plant. In addition, the application of cytokinins to leaves detached from a plant retards their yellowing. Therefore, they function as antiaging hormones.

The action of cytokinins, like that of other hormones, has been studied in terms of its effects on the growth and differentiation of masses of tissue growing in defined media. Plant tissue can form shoots, roots, or an undifferentiated mass, depending on the relative amounts of auxin and cytokinin (figure 41.27).

In the early cell-growth experiments in culture, coconut milk was an essential factor. Eventually, researchers discovered that coconut milk is not only rich in amino acids and other reduced nitrogen compounds required for growth, but it also contains cytokinins. Cytokinins apparently promote the synthesis or activation of proteins specifically required for cytokinesis.

Cytokinins have also been used against plants by pathogens. The bacterium *Agrobacterium*, for example, introduces genes into the plant genome that increase the rate of cytokinin, as well as auxin, production. This causes massive cell division and the formation of a tumor called *crown gall* (figure 41.28). How these hormone-biosynthesis genes ended up in a bacterium is an intriguing evolutionary question. Coevolution does not always work to a plant's advantage.

Gibberellins enhance plant growth and nutrient utilization

Gibberellins are named after the fungus *Gibberella fujikuroi*, which causes rice plants, on which it is parasitic, to grow abnormally tall. The Japanese plant pathologist Eiichi Kurosawa investigated bakanae ("foolish seedling") disease in the 1920s.

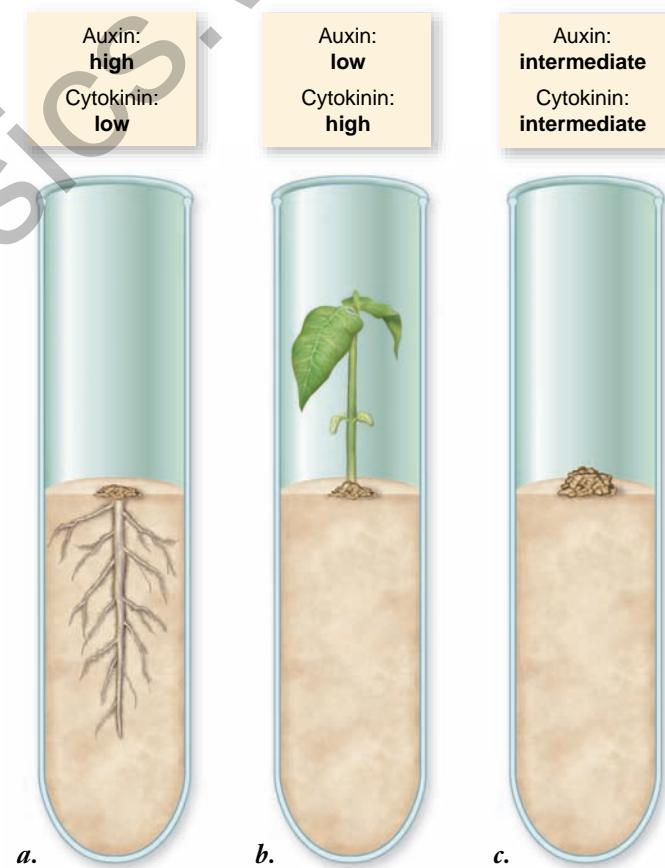


Figure 41.27 Relative amounts of cytokinins and auxin affect organ regeneration in culture. In tobacco, **a.** high auxin-to-cytokinin ratios favor root development; **b.** high cytokinin-to-auxin ratios favor shoot development; and **c.** intermediate concentrations result in the formation of undifferentiated cells. These developmental responses to cytokinin-auxin ratios in culture are species-specific.



Figure 41.28 Crown gall tumor. Sometimes cytokinins can be used against the plant by a pathogen. In this case, *Agrobacterium tumefaciens* (a bacterium) has incorporated a piece of its DNA into the plant genome. This DNA contains genes coding for enzymes necessary for cytokinin and auxin biosynthesis. The increased levels of these hormones in the plant cause massive cell division and the formation of a tumor.

He grew *Gibberella* in culture and obtained a substance that, when applied to rice plants, produced bakanae. This substance was isolated and its structural formula identified by Japanese chemists in 1939. British chemists reconfirmed the formula in 1954.

Although such chemicals were first thought to be only a curiosity, they have since turned out to belong to a large class of more than 100 naturally occurring plant hormones. All are acidic and are usually abbreviated GA (for gibberellic acid), with a different subscript (GA₁, GA₂, and so forth) to distinguish each one.

Gibberellins, which are synthesized in the apical portions of stems and roots, have important effects on stem elongation. The elongation effect is enhanced if auxin is also present. The application of gibberellins to certain dwarf mutants is known to restore normal growth and development in many plants (figure 41.29). Some dwarf mutants produce insufficient amounts of gibberellin and respond to GA applications; others lack the ability to respond to gibberellin.

The large number of gibberellins are all part of a complex biosynthetic pathway that has been unraveled using gibberellin-deficient mutants in maize (corn). Although many of these gibberellins are intermediate forms in the production of GA₁, recent work shows that some forms may have specific biological roles.

In chapter 37, we noted the role of gibberellins in stimulating the production of α -amylase and other hydrolytic enzymes needed for utilization of food resources during germination and establishment of cereal seedlings. How is transcription of the genes encoding these enzymes regulated?



Figure 41.29 Effects of gibberellins. This rapid-cycling member of the mustard family (*Brassica rapa*) will “bolt” and flower because of increased gibberellin levels. Mutants such as the rosette mutant (left) are defective in producing gibberellins. They can be rescued by applying gibberellins to the shoot tip (right). Other mutants have been identified that are defective in perceiving gibberellins, and they will not respond to gibberellin applications.

GA is used as a signal from the embryo that turns on transcription of one or more genes encoding hydrolytic enzymes in the aleurone layer. The GA receptor has been identified. When GA binds to its receptor, it frees GA-dependent transcription factors from a repressor. These transcription factors can now directly affect gene expression (figure 41.30). Synthesis of DNA does not seem to occur during the early stages of seed germination, but it becomes important when the radicle has grown through the seed coats.

Gibberellins also affect a number of other aspects of plant growth and development. In some cases, GAs hasten seed

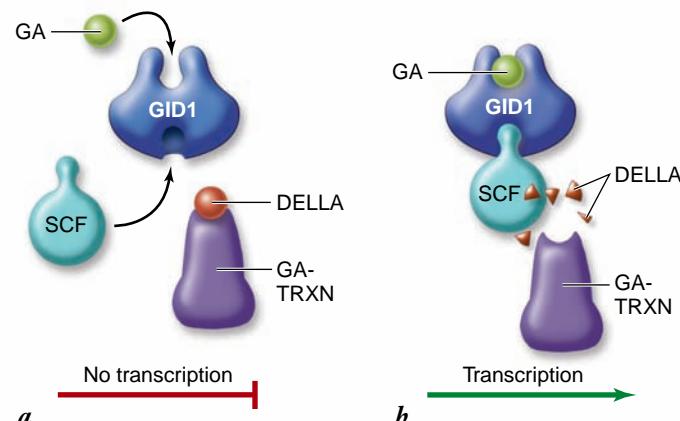


Figure 41.30 Gibberellins activate gibberellin-dependent transcription factors (GA-TRXN). *a.* GA-TRXN cannot bind to a promoter when they are bound to DELLA proteins. *b.* GA activates a protein complex that degrades DELLA proteins, freeing GA-TRXN to bind to a promoter, inducing gene transcription.



Figure 41.31 Applications of gibberellins increase the space between grapes. Larger grapes (right) develop because there is more room between individual grapes.

germination, apparently by substituting for the effects of cold or light requirements. Gibberellins are used commercially to increase space between grape flowers by extending internode length, so that the fruits have more room to grow. The result is a larger bunch of grapes containing larger individual fruits (figure 41.31).

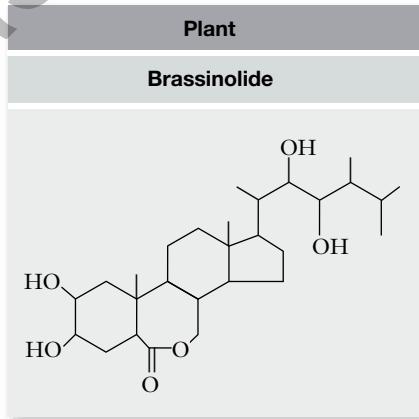
Although gibberellins function endogenously as hormones, they also function as pheromones in ferns. In ferns, gibberellin-like compounds released from one gametophyte can trigger the development of male reproductive structures on a neighboring gametophyte.

Brassinosteroids are structurally similar to animal hormones

Although plant biologists have known about *brassinosteroids* for 30 years, it is only recently that they have claimed their place as a class of plant hormones. They were first discovered

Figure 41.32 Brassinosteroids.

Brassinolide and other brassinosteroids have structural similarities to animal steroid hormones. Cortisol, testosterone, and estradiol (not shown) are animal steroid hormones.



in *Brassica* spp. pollen, hence the name. Their historical absence in discussions of hormones may be partially due to their functional overlap with other plant hormones, especially auxins and gibberellins. Additive effects among these three classes have been reported.

The application of molecular genetics to the study of brassinosteroids has advanced our understanding of how they are made and, to some extent, how they function in signal transduction pathways. What is particularly intriguing about brassinosteroids is their similarity to animal steroid hormones (figure 41.32). One of the genes coding for an enzyme in the brassinosteroid biosynthetic pathway has significant similarity to an enzyme used in the synthesis of testosterone and related steroids. Brassinosteroids have also been identified in algae, and they appear to be ubiquitous among the plants. It is plausible that their evolutionary origin predated the plant-animal split.

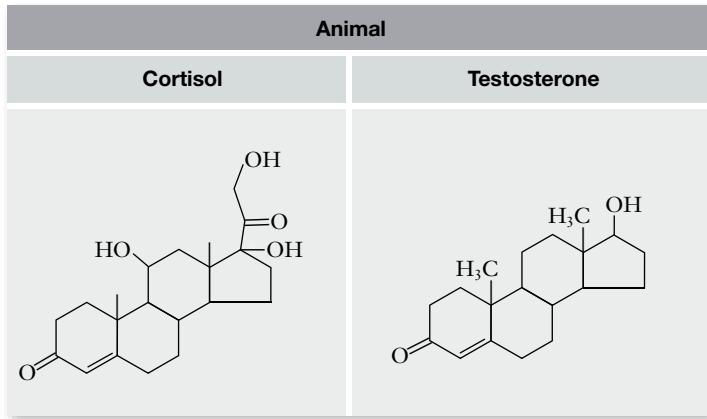
Brassinosteroids have a broad spectrum of physiological effects—elongation, cell division, bending of stems, vascular tissue development, delayed senescence, membrane polarization, and reproductive development. Environmental signals can trigger brassinosteroid actions. Mutants have been identified that alter the response to a brassinosteroid, but signal transduction pathways remain to be uncovered. From an evolutionary perspective, it will be quite interesting to see how these pathways compare with animal steroid signal transduction pathways.

Oligosaccharins act as defense-signaling molecules

Plant cell walls are composed not only of cellulose but also of numerous complex carbohydrates called *oligosaccharides*. Some evidence indicates that these cell wall components (when degraded by pathogens) function as signaling molecules as well as structural wall components. Oligosaccharides that are proposed to have a hormone-like function are called *oligosaccharins*.

Oligosaccharins can be released from the cell wall by enzymes secreted by pathogens. These carbohydrates are believed to signal defense responses, such as the hypersensitive response (HR) discussed in chapter 40.

Another oligosaccharin has been shown to inhibit auxin-stimulated elongation of pea stems. These molecules are active at concentrations one to two orders of magnitude less than those of the traditional plant hormones; you have seen how



auxin and cytokinin ratios can affect organogenesis in culture (see figure 41.27).

Oligosaccharins also affect the phenotype of regenerated tobacco tissue, inhibiting root formation and stimulating flower production in tissues that are competent to regenerate flowers. How the culture results translate to *in vivo* systems remains an open question.

Ethylene induces fruit ripening and aids plant defenses

Long before its role as a plant hormone was appreciated, the simple, gaseous hydrocarbon *ethylene* ($\text{H}_2\text{C}-\text{CH}_2$) was known to defoliate plants when it leaked from gaslights in old-fashioned streetlamps. Ethylene is, however, a natural product of plant metabolism that, in minute amounts, interacts with other plant hormones.

When auxin is transported down from the apical meristem of the stem, it stimulates the production of ethylene in the tissues around the lateral buds and thus retards their growth. Ethylene also suppresses stem and root elongation, probably in a similar way. An ethylene receptor has been identified and characterized, and it appears to have evolved early in

the evolution of photosynthetic organisms, sharing features with environmental-sensing proteins identified in bacteria.

Ethylene plays a major role in fruit development. At first, auxin, which is produced in significant amounts in pollinated flowers and developing fruits, stimulates ethylene production; this, in turn, hastens fruit ripening. Complex carbohydrates are broken down into simple sugars, chlorophylls are broken down, cell walls become soft, and the volatile compounds associated with flavor and scent in ripe fruits are produced.

One of the first observations that led to the recognition of ethylene as a plant hormone was the premature ripening in bananas produced by gases coming from oranges. Such relationships have led to major commercial uses of ethylene. For example, tomatoes are often picked green and artificially ripened later by the application of ethylene. Ethylene is widely used to speed the ripening of lemons and oranges as well. Carbon dioxide has the opposite effect of arresting ripening; fruits are often shipped in an atmosphere of carbon dioxide.

Also, a biotechnology solution has been developed in which one of the genes necessary for ethylene biosynthesis has been cloned, and its antisense copy inserted into the tomato genome (figure 41.33). The antisense copy of the gene is a nucleotide sequence that is complementary to the sense copy of the gene. In this transgenic plant, both the sense and antisense

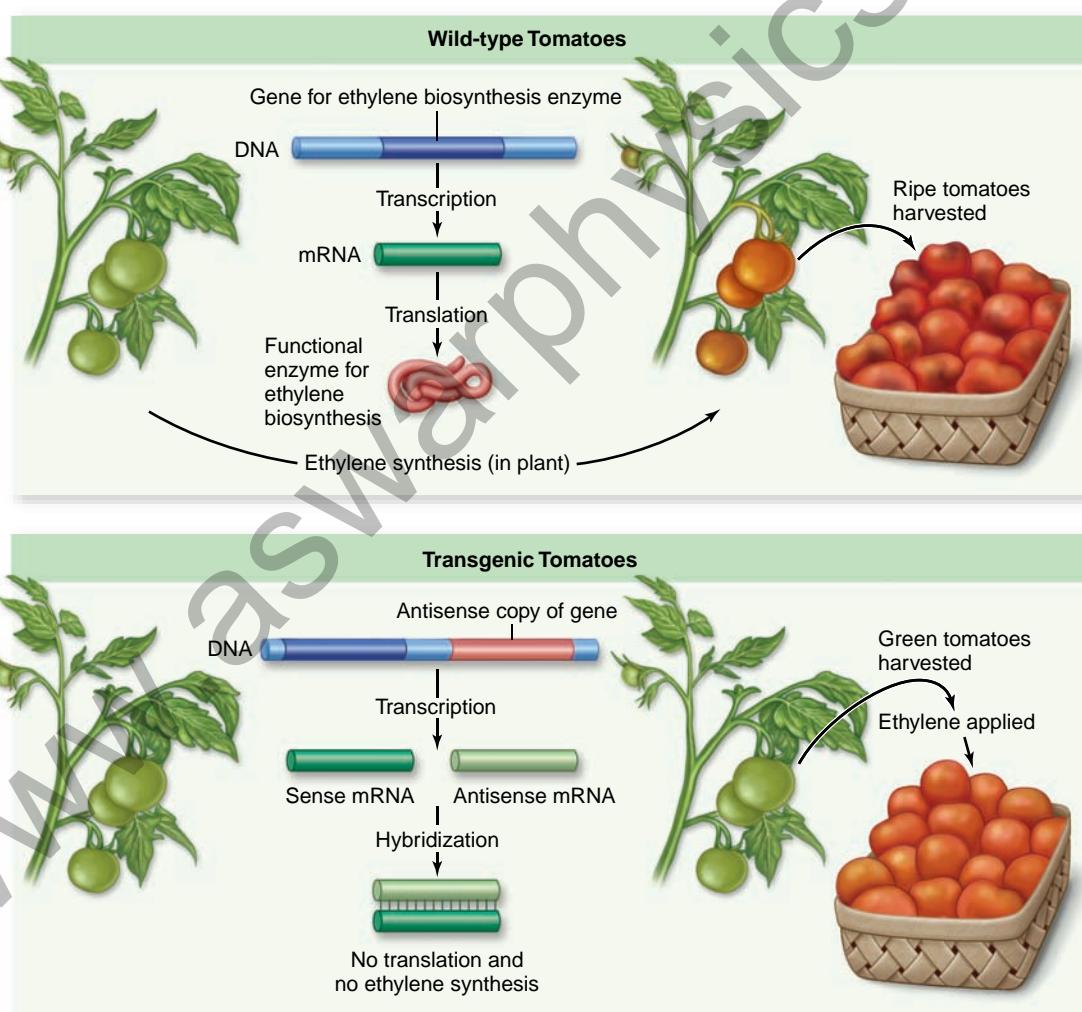


Figure 41.33 Genetic regulation of fruit ripening.

An antisense copy of the gene for ethylene biosynthesis prevents the formation of ethylene and subsequent ripening of transgenic fruit. The antisense strand is complementary to the sequence for the ethylene biosynthesis gene. After transcription, the antisense mRNA pairs with the sense mRNA, and the double-stranded mRNA cannot be translated into a functional protein. Ethylene is not produced, and the fruit does not ripen. The fruit is sturdier for shipping in its unripened form and can be ripened later with exposure to ethylene. Thus, while wild-type tomatoes may already be rotten and damaged by the time they reach stores, transgenic tomatoes stay fresh longer.

sequences for the ethylene biosynthesis gene are transcribed. The sense and antisense mRNA sequences then pair with each other. This pairing blocks translation, which requires single-stranded RNA; as a result, ethylene is not synthesized, and the transgenic tomatoes do not ripen. In this way, the sturdy green tomatoes can be shipped without ripening and rotting. Exposing these tomatoes to ethylene later induces them to ripen.

Studies have shown that ethylene plays an important ecological role. Ethylene production increases rapidly when a plant is exposed to ozone and other toxic chemicals, temperature extremes, drought, attack by pathogens or herbivores, and other stresses. The increased production of ethylene that occurs can accelerate the loss of leaves or fruits that have been damaged by these stresses. Some of the damage associated with exposure to ozone is due to the ethylene produced by the plants.

The production of ethylene by plants attacked by herbivores or infected with pathogens may be a signal to activate the defense mechanisms of the plants and may include the production of molecules toxic to the pests.

Abscisic acid suppresses growth and induces dormancy

Abscisic acid appears to be synthesized mainly in mature green leaves, fruits, and root caps. The hormone earned its name because applications of it appear to stimulate fruit abscission in cotton, but there is little evidence that it plays an important role in this process. Ethylene is actually the chemical that promotes senescence and abscission.

Abscisic acid probably induces the formation of winter buds—dormant buds that remain through the winter. The conversion of leaf primordia into bud scales follows (figure 41.34a). Like ethylene, abscisic acid may also suppress growth of dormant lateral buds. It appears that abscisic acid, by suppressing growth and elongation of buds, can counteract some of the effects of gibberellins; it also promotes senescence by counteracting auxin.

Abscisic acid plays a role in seed dormancy and is antagonistic to gibberellins during germination. Abscisic acid levels in seeds rise during embryogenesis (see figure 41.17). As maize embryos develop in the kernels on the cob, abscisic acid is necessary to

induce dormancy and prevent precocious germination, called vivipary (figure 41.34b). It is also important in controlling the opening and closing of stomata (figure 41.34c).

Found to occur in all groups of plants, abscisic acid apparently has been functioning as a growth-regulating substance since early in the evolution of the plant kingdom. Relatively little is known about the exact nature of its physiological and biochemical effects, but these effects are very rapid—often taking place within a minute or two—and therefore they must be at least partly independent of gene expression.

All of the genes have been sequenced in *Arabidopsis*, making it easier to identify which genes are transcribed in response to abscisic acid. Abscisic acid levels become greatly elevated when the plant is subject to stress, especially drought. Like other plant hormones, abscisic acid will probably prove to have valuable commercial applications when its mode of action is better understood.

Learning Outcomes Review 41.5

Hormones are chemicals produced in small quantities in one region of the plant and then transported to another region, where they cause a physiological or developmental response. Both auxins and cytokinins are produced in meristems and promote growth; however, auxins stimulate growth by cell elongation, while cytokinins stimulate cell division. In contrast, abscisic acid inhibits growth and promotes dormancy.

- What methods could you use to test whether abscisic acid produced in root caps can affect bud growth in stems?

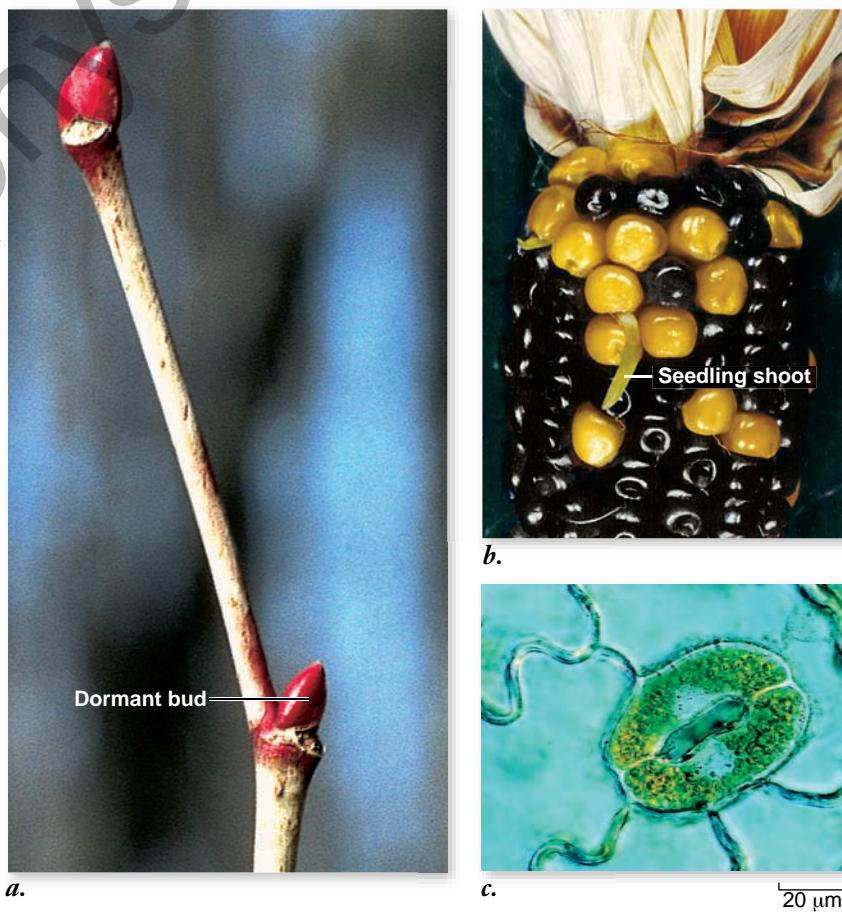


Figure 41.34 Effects of abscisic acid.

- a. Abscisic acid plays a role in the formation of these winter buds of an American basswood. These buds will remain dormant for the winter, and bud scales—modified leaves—will protect the buds from desiccation.
- b. In addition to bud dormancy, abscisic acid is necessary for dormancy in seeds. This viviparous mutant in maize is deficient in abscisic acid, and the embryos begin germinating on the developing cob. c. Abscisic acid also affects the closing of stomata by influencing the movement of potassium ions out of guard cells.



Chapter Review

41.1 Responses to Light

P_{fr} facilitates expression of light response genes (figure 41.1)

Phytochrome exists as two interconvertible forms. The inactive form, P_r , absorbs red light and is converted to the active form, P_{fr} . P_{fr} absorbs far-red light and is converted to the inactive form, P_r . P_{fr} enters the nucleus and binds with other proteins to form a transcription complex, leading to expression of light-regulated genes. It can also activate a cascade of transcription factors.

Many growth responses are linked to phytochrome action.

P_{fr} is involved in seed germination, shoot elongation, and detection of plant spacing. Far-red light inhibits germination by inactivating P_{fr} , and red light stimulates it by activating P_r .

Crowded plants receive a greater proportion of far-red light, which is reflected from neighboring plants. The plants respond by growing taller to compete more effectively for sunlight.

Light affects directional growth.

Phototropisms are directional growth responses of stems toward blue light. Blue-light receptors such as phototropin 1 are a recent discovery.

Circadian clocks are independent of light but are entrained by light.

Circadian rhythms entrain to the daily cycle through the action of phytochrome and blue-light photoreceptors. In the absence of light, the cycle's period may become desynchronized, but it resets when light is available.

41.2 Responses to Gravity

Plants align with the gravitational field: An overview.

Gravitropism is the growth response to a gravitational field.

Certain cells in plants perceive gravity when amyloplasts are pulled downward. Following the detection of gravity, a physiological signal causes cell elongation in other cells. The hormone auxin is believed to transmit the signal.

Stems bend away from a center of gravity.

Shoots bend away from gravity, so they exhibit negative gravitropism. When auxin accumulates on the lower side of the stem, those cells elongate, causing the stem to bend upward.

Roots bend toward a center of gravity.

Roots bend toward gravity, so they exhibit positive gravitropism. If the root cap is horizontally oriented, the cells on the upper side of the root become elongated, causing the root to grow downward.

41.3 Responses to Mechanical Stimuli

Touch can trigger irreversible growth responses.

Thigmotropism is a permanent directional growth of a plant toward or away from a physical stimulus. It results in thigmomorphogenesis, a change in growth form.

Thigmonastic responses are independent of the direction of the stimulus and are usually produced by changes in turgor pressure.

Reversible responses to touch and other stimuli involve turgor pressure.

Touch-induced responses result from changes in turgor pressure. A stimulus causes an electrical signal, which results in a loss of potassium ions and water from cells of the pulvini. The loss of turgor causes the leaves to move.

Light can induce changes in turgor pressure, resulting in leaf tracking of sunlight, flower opening, and leaf sleep movements.

41.4 Responses to Water and Temperature

Dormancy is a response to water, temperature, and light.

Dormancy is the cessation of growth that occurs when a plant is exposed to environmental stress. Seasonal leaf abscission occurs in deciduous trees in the fall. Seed dormancy suspends germination until environmental conditions are optimal.

Plants can survive temperature extremes.

Plants respond to cold temperatures by increasing unsaturated lipids in membranes, limiting ice crystal formation to extracellular spaces, and producing antifreeze proteins.

When exposed to rapid increases in temperature, plants produce heat shock proteins, which help to stabilize other proteins.

41.5 Hormones and Sensory Systems

The hormones that guide growth are keyed to the environment.

Hormones are produced in small quantities in one part of a plant and then transported to another, where they bring about physiological or developmental responses.

Auxin allows elongation and organizes the body plan.

Auxins are produced in apical meristems and immature parts of a plant. They affect DNA transcription by binding to proteins. Auxins promote stem elongation, adventitious root formation, cell division, and lateral bud dormancy. They also inhibit leaf abscission and induce ethylene production.

Cytokinins stimulate cell division and differentiation.

Cytokinins are purines produced in root apical meristems and immature fruits. They promote mitosis, chloroplast development, and bud formation. Cytokinins also delay leaf aging.

Gibberellins enhance plant growth and nutrient utilization.

Gibberellins are produced by root and shoot tips, young leaves, and seeds. They promote the elongation of stems and the production of enzymes in germinating seeds. In ferns, gibberellins function as pheromones.

Brassinosteroids are structurally similar to animal hormones.

Brassinosteroids are steroids produced in pollen, immature seeds, shoots, and leaves. They produce a broad spectrum of effects related to growth, senescence, and reproductive development.

Oligosaccharins act as defense-signaling molecules.

Pathogens secrete enzymes that release oligosaccharins from cell walls; these molecules induce pathogen defense responses. Oligosaccharins can also inhibit auxin-stimulated elongation, inhibit root formation, and stimulate flower production.

Ethylene induces fruit ripening and aids plant defenses.

Roots, shoot apical meristems, aging flowers, and ripening fruits produce ethylene, a gas that controls leaf, flower, and fruit abscission, promotes fruit ripening, and suppresses stem and root elongation. Ethylene may activate a defense response to attacks by pathogens and herbivores.

Abscisic acid suppresses growth and induces dormancy.

Mature green leaves, fruits, root caps, and seeds produce abscisic acid. Abscisic acid inhibits bud growth and the effects of other hormones, induces seed dormancy, and controls stomatal closure.



Review Questions

UNDERSTAND

1. Which of the following is stimulated by blue light?
 - a. Seed germination
 - b. Detection of plant spacing
 - c. Phototropism
 - d. Shoot elongation
2. Stems and roots, respectively, exhibit
 - a. a positive phototropic response and no phototropic response.
 - b. a negative phototropic response and no phototropic response.
 - c. no phototropic response and a positive phototropic response.
 - d. no phototropic response and a negative phototropic response.
3. In stems, gravity is detected by cells of the
 - a. epidermis.
 - b. cortex.
 - c. periderm.
 - d. endodermis.
4. Chilling most directly affects
 - a. nuclear proteins.
 - b. vacuolar inclusions.
 - c. the cytoskeleton.
 - d. membrane lipids.
5. Which of the following does not happen as a seed approaches a state of dormancy?
 - a. The seed loses water.
 - b. Abscisic acid levels in the embryo decrease.
 - c. The seed coat hardens.
 - d. Protein synthesis stops.
6. Dwarf mutants can sometimes be induced to grow normally by applying
 - a. auxin.
 - b. abscisic acid.
 - c. ethylene.
 - d. gibberellin.

APPLY

1. If you exposed seeds to a series of red-light versus far-red-light treatments, which of the following exposure treatments would result in seed germination?
 - a. Red; far-red
 - b. Far-red; red
 - c. Red; far-red; red; far-red; red; far-red
 - d. None of the above
2. If you were to plant a de-etiolated (*det2*) mutant *Arabidopsis* seed and keep it in a dark box, what would you expect to happen?
 - a. The seed would germinate normally, but the plant would not become tall and spindly while it sought a light source.
 - b. The seed would fail to germinate because it would not have light.
 - c. The seed would germinate, and the plant would become tall and spindly while it sought a light source.
 - d. The seed would germinate, and the plant would immediately die because it could not make sugar in the dark.
3. When Charles and Francis Darwin investigated phototropisms in plants, they discovered that
 - a. auxin was responsible for light-dependent growth.
 - b. light was detected at the shoot tip of a plant.

- c. light was detected below the shoot tip of a plant.
- d. only red light stimulated phototropism.
4. Auxin promotes a plant to grow toward a light source by
 - a. increasing the rate of cell division on the shaded side of the stem.
 - b. shortening the cells on the light side of the stem.
 - c. causing cells on the shaded side of the stem to elongate.
 - d. decreasing the rate of cell division on the light side of the stem.
5. You have come up with a brilliant idea to stretch your grocery budget by buying green fruit in bulk and then storing it in a bag that you have blown up like a balloon. As you need fruit, you would take it out of the bag, and it would miraculously ripen. How would this work?
 - a. The bag would block light from reaching the fruit, so it would not ripen.
 - b. The bag would keep the fruit cool, so it would not ripen.
 - c. The high CO₂ levels in the bag would prevent ripening.
 - d. The high O₂ levels in the bag would prevent ripening.
6. Gibberellins are used to increase productivity in grapes because they
 - a. cause fruits to be larger by promoting cell division within the fruit.
 - b. increase the internode length so the fruits have more room to grow.
 - c. increase the number of flowers produced, thus increasing the number of fruits.
 - d. do all of the above.
7. Which of the following might not be observed in a plant that is grown on the Space Shuttle in space?
 - a. Phototropism
 - b. Photomorphogenesis
 - c. Circadian rhythms
 - d. Gravitropism

SYNTHESIZE

1. If you buy a bag of potatoes and leave them in a dark cupboard for too long, they will begin to form long white sprouts with tiny leaves. Name this process and explain why the potatoes are behaving as they are.
2. Find the discussion of taxis in this book. Compare and contrast tropism with taxis.
3. The current model for gravitropism suggests that the accumulation of amyloplasts on the bottom of a cell allows the cell to sense gravity. Suggest a plausible mechanism for the sensing of gravity that does not involve the settling out of particles.
4. Farmers who grow crops that are planted as seedlings may prepare them for their transition from the greenhouse to the field by brushing them gently every day for a few weeks. Why is this beneficial?

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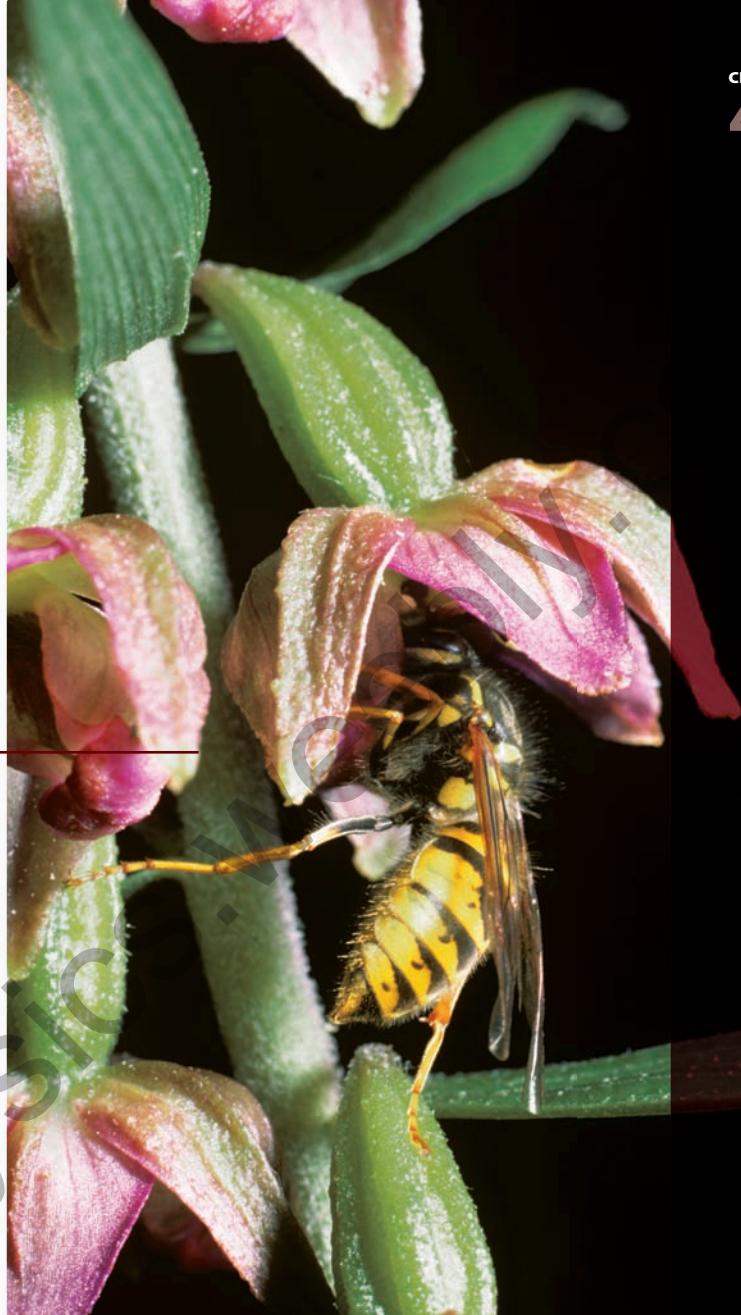
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Chapter **42**

Plant Reproduction

Chapter Outline

- 42.1** Reproductive Development
- 42.2** Flower Production
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Introduction

The remarkable evolutionary success of flowering plants can be linked to their novel reproductive strategies. In this chapter, we explore the reproductive strategies of the angiosperms and how their unique features—flowers and fruits—have contributed to their success. This is, in part, a story of coevolution between plants and animals that ensures greater genetic diversity by dispersing plant gametes widely. In a stable environment, however, there are advantages to maintaining the status quo genetically; asexual reproduction, for example, is a strategy that produces cloned individuals. An unusual twist to sexual reproduction in some flowering plants is that senescence and death of the parent plant immediately follow.

42.1 Reproductive Development

Learning Outcomes

1. Describe the general life cycle of a flowering plant.
2. Define phase change.
3. Identify two *Arabidopsis* mutants that have been used to study phase change.

In chapter 30, we noted that angiosperms represent an evolutionary innovation with their production of flowers and fruits. In chapter 37, we outlined the development of form, or morphogenesis, which a germinating seed undergoes to become a vegetative plant. In this section, we describe the additional changes that occur in a vegetative plant to produce the elaborate structures associated with flowering (figure 42.1).

Plants go through developmental changes leading to reproductive maturity just as many animals do. This shift from juvenile to adult development is seen in the metamorphosis of a tadpole to an adult frog or a caterpillar to a butterfly that can then reproduce. Plants undergo a similar metamorphosis that leads to the production of a flower. Unlike the juvenile frog, which loses its tail, plants just keep adding structures to existing structures with their meristems.

Carefully regulated processes determine when and where flowers will form. Moreover, plants must often gain competence to respond to internal or external signals regulating flowering.

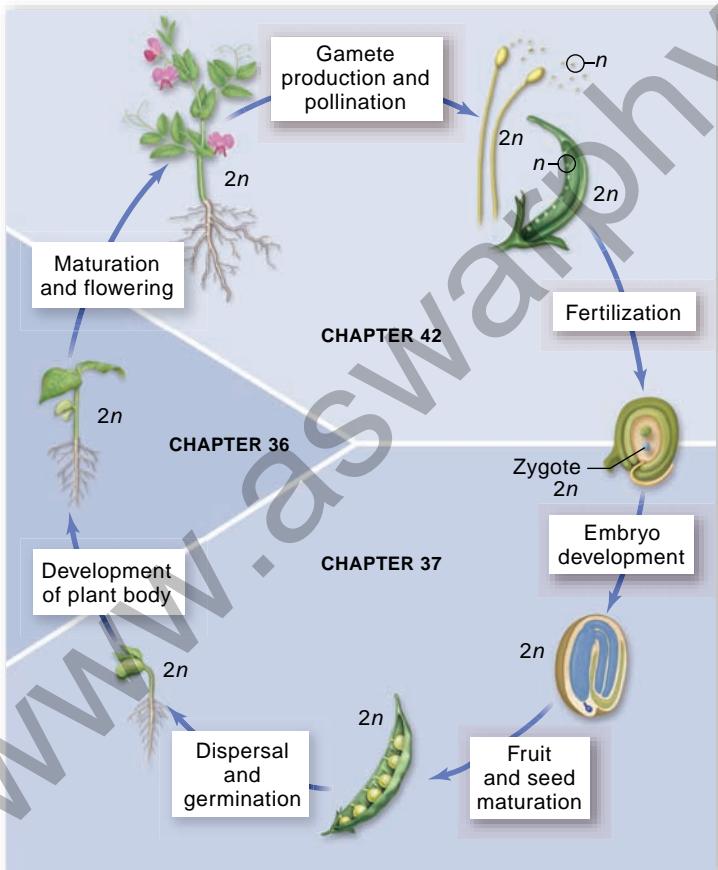


Figure 42.1 Life cycle of a flowering plant (*Angiosperm*).

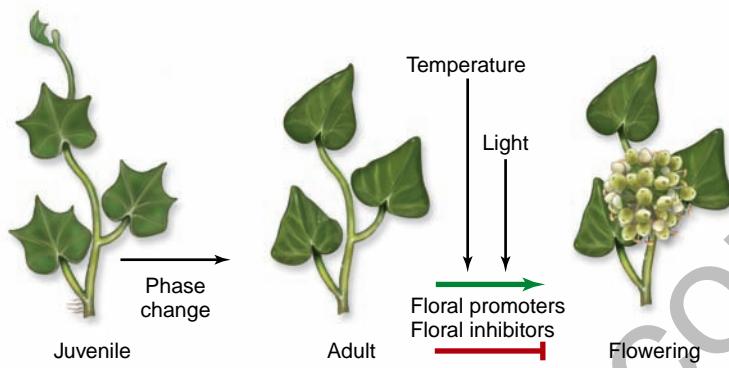


Figure 42.2 Factors involved in initiating flowering.

This model depicts the environmentally cued and internally processed events that result in a shoot meristem initiating flowers. During phase change, the plant acquires competence to respond to flowering signals.

tence to respond to internal or external signals regulating flowering. Once plants are competent to reproduce, a combination of factors—including light, temperature, and both promotive and inhibitory internal signals—determines when a flower is produced (figure 42.2). These signals turn on genes that specify formation of the floral organs—sepals, petals, stamens, and carpels. Once cells have instructions to become a specific floral organ, yet another developmental cascade leads to the three-dimensional construction of flower parts. We describe details of this process in the following sections.

The transition to flowering competence is termed phase change

At germination, most plants are incapable of producing a flower, even if all the environmental cues are optimal. Internal developmental changes allow plants to obtain competence to respond to external or internal signals (or both) that trigger flower formation. This transition is referred to as **phase change**.

Phase change can be morphologically obvious or very subtle. Take a look at an oak tree in the winter: Leaves will still be clinging to the lower branches until spring when the new buds push them off, but leaves on the upper branches will have fallen earlier (figure 42.3a). Those lower branches were initiated by a juvenile meristem. The fact that they did not respond to environmental cues and drop their leaves indicates that they are juvenile branches and have not made a phase change. Although the lower branches are older, their juvenile state was established when they were initiated and will not change.

Ivy also has distinct juvenile and adult phases of growth (figure 42.3b). Stem tissue produced by a juvenile meristem initiates adventitious roots that can cling to walls. If you look at very old brick buildings covered with ivy, you will notice that the uppermost branches are falling off because they have transitioned to the adult phase of growth and have lost the ability to produce adventitious roots.

It is important to note that even though a plant has reached the adult stage of development, it may or may not produce reproductive structures. Other factors may be necessary to trigger flowering.



a.



b.

Mutations have clarified how phase change is controlled

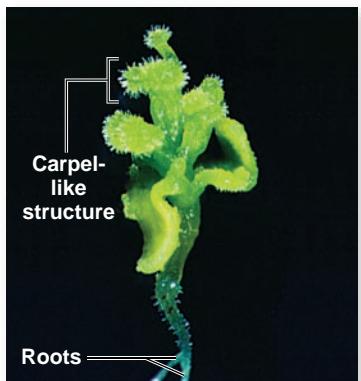
Generally it is easier to get a plant to revert from an adult to juvenile state than to induce phase change experimentally. Applications of the plant hormone gibberellin and severe pruning can cause reversion. In the latter case, new vegetative growth occurs, as when certain shrubs are cut back and put out lush new growth in response.

The *embryonic flower* (*emf*) mutant of *Arabidopsis* flowers almost immediately (figure 42.4), which is consistent with the hypothesis that the wild-type allele suppresses flowering. As the wild-type plant matures, *EMF* expression decreases. This finding suggests that flowering is the default state, and that mechanisms have evolved to delay flowering. This delay presumably allows the plant to store more energy to be allocated for reproduction.

An example of inducing the juvenile-to-adult transition comes from overexpressing a gene necessary for flowering that is found in many species. This gene, *LEAFY* (*LFY*), was cloned in *Arabidopsis*, and its promoter was replaced with a viral promoter that results in constant, high levels of *LFY* transcription. *LFY* with its viral promoter was then introduced into cultured aspen cells that were used to regenerate plants. When *LFY* is overexpressed in aspen, flowering occurs in weeks instead of years (figure 42.5).

Phase change requires both a sufficiently strong promotive signal and the ability to perceive the signal. Phase change can result in the production of receptors in the shoot to perceive a signal of a certain intensity. Alternatively an increase of promotive signal(s) or a decrease of inhibitory signal(s) can trigger phase change.

Figure 42.4 Embryonic flower (*EMF*) prevents early flowering. Mutant plants that lack *EMF* protein flower as soon as they germinate. The flowers have malformed carpels and other defective floral structures close to the roots.



Phase change, as we said earlier, results in an adult plant, but not necessarily a flowering plant. The ability to reproduce is distinct from actual reproductive development. Flower production depends on a number of factors, which we explore next.

Learning Outcomes Review 42.1

In a flowering plant life cycle, fertilization produces an embryo in a seed. The embryo develops into a plant that eventually flowers, and the flowers once again produce gametes. Phase change is the transition from vegetative to reproductive growth. In *Arabidopsis*, expression of the embryonic flower mutant (*emf*) or overexpression of the *LEAFY* gene (*LFY*) result in early flowering.

- In evolutionary terms, why is flower production the default state in plants?



a.



b.

Figure 42.5 Overexpression of a flowering gene can accelerate phase change. a. Normally, an aspen tree grows for several years before producing flowers (see inset). b. Overexpression of the *Arabidopsis* flowering gene, *LFY*, causes rapid flowering in a transgenic aspen (see inset).

Figure 42.3 Phase change.

a. The lower branches of this oak tree represent the juvenile phase of development; they cling to their leaves in the winter. The lower leaves are not able to form an abscission layer and break off the tree in the fall. Such visible changes are marks of phase change, but the real test is whether the plant is able to flower. b. Juvenile ivy (right) makes adventitious roots and has an alternating leaf phyllotaxy. Mature ivy (left) lacks adventitious roots, has spiral phyllotaxy, and can make flowers.

42.2 Flower Production

Learning Outcomes

1. Name the four genetically regulated flowering pathways.
2. Define floral determination.
3. Explain the relationship between floral meristem identity genes and floral organ identity genes.

Four genetically regulated pathways to flowering have been identified: (1) the light-dependent pathway, (2) the temperature-dependent pathway, (3) the gibberellin-dependent pathway, and (4) the autonomous pathway.

Plants can rely primarily on one pathway, but all four pathways can be present.

The environment can promote or repress flowering, and in some cases, it can be relatively neutral. For example, increasing light duration can be a signal that long summer days have arrived in a temperate climate and that conditions are favorable for reproduction. In other cases, plants depend on light to accumulate sufficient amounts of sucrose to fuel reproduction, but flower independently of day length.

Temperature can also be used as a signal. **Vernalization**, the requirement for a period of chilling of seeds or shoots for flowering, affects the temperature-dependent pathway. Assuming that regulation of reproduction first arose in more constant tropical environments, many of the day-length and temperature controls would have evolved as plants colonized more temperate climates. Plants with a vernalization requirement flower after, not during, a cold winter, enhancing reproductive success. The existence of redundant pathways to flowering helps ensure new generations.

The light-dependent pathway is geared to the photoperiod

Flowering requires much energy accumulated via photosynthesis. Thus, all plants require light for flowering, but this is distinct from the **photoperiodic**, or light-dependent, flowering pathway. Aspects of growth and development in most plants are keyed to changes in the proportion of light to dark in the daily 24-hr cycle (day length).

Sensitivity to the photoperiod provides a mechanism for organisms to respond to seasonal changes in the relative length of day and night. Day length changes with the seasons; the farther a region is from the equator, the greater the variation in day length.

Short-day and long-day plants

The flowering responses of plants to day length fall into several basic categories. In short-day plants, flowering is initiated when daylight becomes shorter than a critical length (figure 42.6). In **long-day plants**, flowering begins when daylight becomes longer. Other plants, such as snapdragons, roses, and many native to the tropics, flower when mature

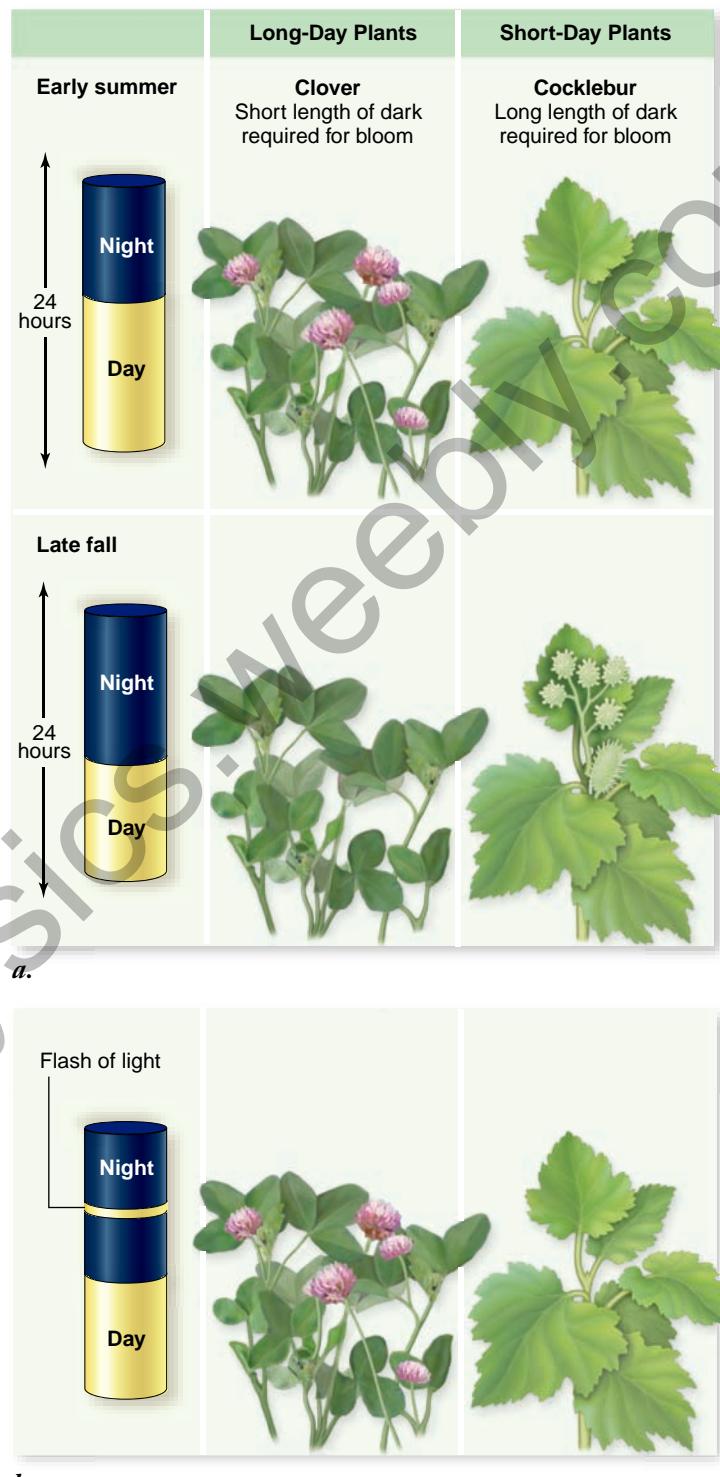


Figure 42.6 How flowering responds to day length.

a. Clover (center panels) is a long-day plant that is stimulated by short nights to flower in the spring. Cocklebur (right-hand panels) is a short-day plant that, throughout its natural distribution in the northern hemisphere, is stimulated by long nights to flower in the fall. **b.** If the long night of late fall is artificially interrupted by a flash of light, the cocklebur will not flower, and the clover will. Although the terms *long-day* and *short-day* refer to the length of day, in each case, it is the duration of uninterrupted darkness that determines when flowering will occur.

regardless of day length, as long as they have received enough light for normal growth. These are referred to as day-neutral plants. Still other plants, including ivy, have two critical photoperiods; they will not flower if the days are too long, and they also will not flower if the days are too short.

Although plants are referred to as long-day or short-day plants, it is actually the amount of darkness that determines whether a plant flowers. In obligate long- or short-day species, there is a sharp distinction between short and long nights, respectively. Flowering occurs in obligate long-day plants when the night length is less than the maximal amount of required darkness (critical night length) for that species. For obligate short-day plants, the amount of darkness must exceed the critical night length for the species.

In other long- or short-day plants, flowering occurs more rapidly or slowly depending on the length of day. These plants, which rely on other flowering pathways as well, are called **facultative long- or short-day** plants because the photoperiodic requirement is not absolute. The garden pea is an example of a facultative long-day plant.

Advantages of photoperiodic control of flowering

Using light as a cue permits plants to flower when abiotic environmental conditions are optimal, pollinators are available, and competition for resources with other plants may be less. For example, the spring herbaceous plants termed *ephemerals* flower in the woods before the tree canopy leafs out and blocks the sunlight necessary for photosynthesis. An example is the trailing arbutus (*Epigaea repens*) of the Northeast woods, which is also known as mayflower because of the time of year in which it blooms.

At middle latitudes, most long-day plants flower in the spring and early summer; examples of such plants include clover, irises, lettuce, spinach, and hollyhocks. Short-day plants usually flower in late summer and fall; these include chrysanthemums, goldenrods, poinsettias, soybeans, and many weeds, such as ragweed. Commercial plant growers use these responses to day length to bring plants into flower at specific times. For example, photoperiod is manipulated in greenhouses so that poinsettias flower just in time for the winter holidays (figure 42.7). The geographic distribution of certain plants may be determined by their flowering responses to day length.

The mechanics of light signaling

Photoperiod is perceived by several different forms of phytochrome and also by a blue-light-sensitive molecule (cryptochrome). Another type of blue-light-sensitive molecule (phototropin) was discussed in chapter 41. Phototropin affects photomorphogenesis, and cryptochrome affects photoperiodic responses.

The conformational change in a phytochrome or cryptochrome light-receptor molecule triggers a cascade of events that leads to the production of a flower. There is a link between light and the circadian rhythm regulated by an internal clock that facilitates or inhibits flowering. At a molecular level, the gaps in information about how light signaling and flower production are related are rapidly being filled in, and the control mechanisms have been found to be quite complex.



Figure 42.7 Flowering time can be altered.

Manipulation of photoperiod in greenhouses ensures that short-day poinsettias flower in time for the winter holidays. Even after flowering is induced, many developmental events must occur in order to produce species-specific flowers.

Photoperiodic Regulation of Transcription of the CO Gene.

Arabidopsis, which as you know is commonly used in plant studies, is a facultative long-day plant that flowers in response to both far-red and blue light. Phytochrome and cryptochrome, the red- and blue-light receptors, respectively, regulate flowering via the gene *CONSTANS* (*CO*). Precise levels of *CO* protein are maintained in accordance with the circadian clock, and phytochrome regulates the transcription of *CO*. Levels of *CO* mRNA are low at night and increase at daybreak. In addition, *CO* protein levels are modulated through the action of cryptochrome. *CO* is an important protein because it links the perception of day length with the production of a signal that moves from the leaves to the shoot where a change in gene transcription leads to the production of flowers.

Inquiry question



If levels of *CO* mRNA follow a circadian pattern, how could you determine whether protein levels are modulated by a mechanism other than transcription? Why would an additional level of control even be necessary?

The importance of posttranslational regulation of *CO* activity became apparent through studies of transgenic *Arabidopsis* plants. These plants contain a *CO* gene fused to a viral promoter that is always on and produces high levels of *CO* mRNA regardless of whether it is day or night. The regulation of *CO* gene expression by phytochrome A is therefore eliminated when this viral promoter is fused to the gene. Curiously, *CO* protein levels still follow a circadian pattern.

Although CO protein is produced day and night, levels of CO are lower at night because of targeted protein degradation. Ubiquitin tags the CO protein, and it is degraded by the proteasome as was described in chapter 41 for phytochrome degradation. Blue light acting via cryptochrome stabilizes CO during the day and protects it from ubiquitination and subsequent degradation.

CO and *LFY* Expression. CO is a transcription factor that turns on other genes, which results in the expression of *LFY*. As discussed in connection with phase change earlier in this section, *LFY* is one of the key genes that “tells” a meristem to switch over to flowering. We will see that other pathways also converge on this important gene. Genes that are regulated by *LFY* are discussed later in this chapter.

Florigen—The elusive flowering hormone

Long before any genes regulating flowering were cloned, a flowering hormone called florigen was postulated to trigger flower production. A considerable amount of evidence demonstrates the existence of substances that promote flowering and substances that inhibit it. Grafting experiments have shown that these substances can move from leaves to shoots. The complexity of their interactions, as well as the fact that multiple chemical messengers are evidently involved, has made this scientifically and commercially interesting search very difficult. The existence of a flowering hormone remains strictly hypothetical even after a scientific quest of 50 years.

One intriguing possibility is that CO protein is a graft-transmissible flowering signal or that it affects such a signal. CO has been found in the phloem that moves throughout the plant body. When *co* mutant shoots are grafted to stocks that produce CO, flowering occurs. Because CO is found in the

phloem, it is possible that this is the protein that moves in the grafted plant to cause flowering. Equally likely, however, is the possibility that CO directly or indirectly affects a separate graft-transmissible factor that is essential for flowering.

The temperature-dependent pathway is linked to cold

Cold temperatures can accelerate or permit flowering in many species. As with light, this environmental connection ensures that plants flower at more optimal times.

Some plants require a period of chilling before flowering, called *vernization*. This phenomenon was discovered in the 1930s by the Ukrainian scientist T. D. Lysenko while trying to solve the problem of winter wheat rotting in the fields. Because winter wheat would not flower without a period of chilling, Lysenko chilled the seeds and then planted them in the spring. The seeds successfully sprouted, grew, and produced grain.

Although this discovery was scientifically significant, Lysenko erroneously concluded that he had converted one species, winter wheat, to another, spring wheat, by simply altering the environment. Lysenko's point of view was supported by the communist philosophy of the time, which held that people could easily manipulate nature to increase production. Unfortunately, this philosophy led to a great many problems, including mistreatment of legitimate geneticists in the former Soviet Union. In addition, genetics and Darwinian evolution were suspect in the Soviet Union until the mid-1960s.

Vernalization is necessary for some seeds or plants in later stages of development. Analysis of mutants in *Arabidopsis* and pea plants indicate that vernalization is a separate flowering pathway.

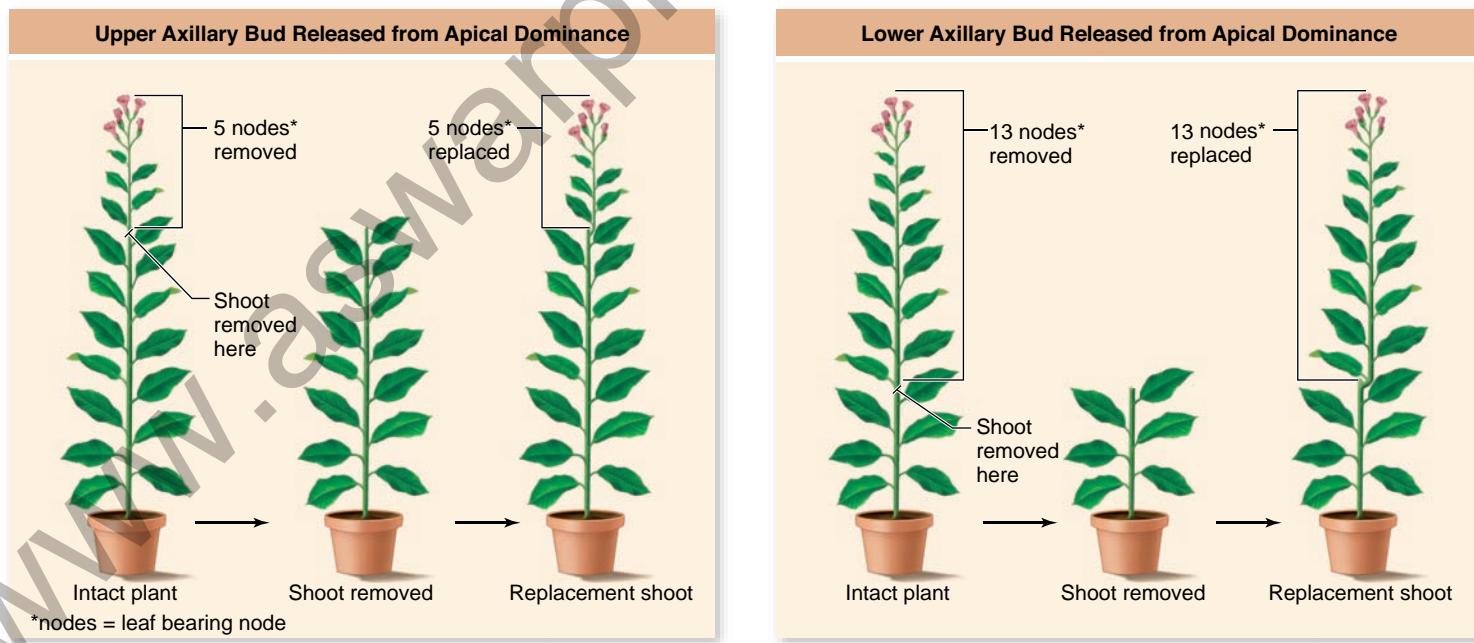


Figure 42.8 Plants can “count.” When axillary buds of flowering, day-neutral tobacco plants are released from apical dominance by removing the main shoot, they replace the number of nodes that were initiated by the main shoot.

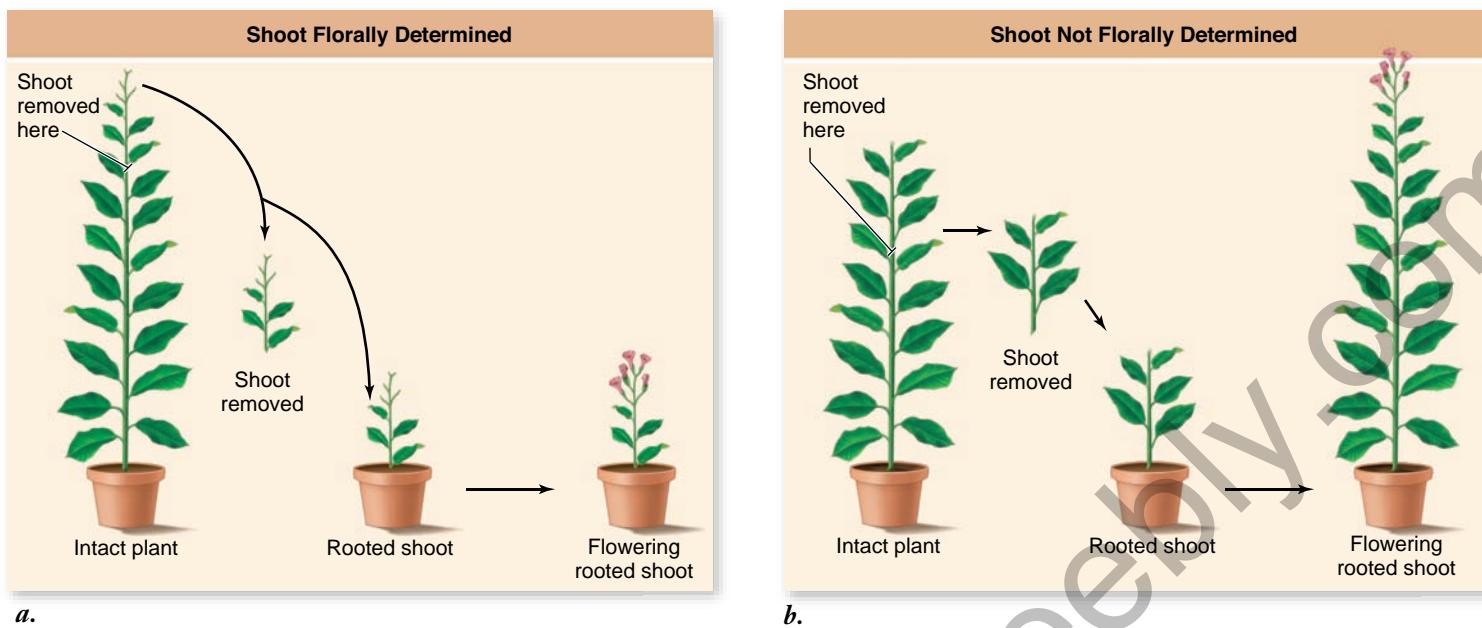


Figure 42.9 Plants can “remember.” At a certain point in the flowering process, shoots become committed to making a flower. This is called floral determination. **a.** Florally determined shoots “remember” their position when rooted in a pot. That is, they produce the same number of nodes that they would have if they had grown out on the plant, and then they flower. **b.** Shoots that are not yet florally determined cannot remember how many nodes they have left, so they start counting again. That is, they develop like a seedling and then flower.

The gibberellin-dependent pathway requires an increased hormone level

In *Arabidopsis* and some other species, decreased levels of gibberellins delay flowering. Thus the gibberellin pathway is proposed to promote flowering. It is known that gibberellins enhance the expression of *LFY*. Gibberellin actually binds the promoter of the *LFY* gene, so its effect on flowering is direct.

The autonomous pathway is independent of environmental cues

The autonomous pathway to flowering does not depend on external cues except for basic nutrition. Presumably, this was the first pathway to evolve. Day-neutral plants often depend primarily on the autonomous pathway, which allows plants to “count” and “remember.”

As an example, a field of day-neutral tobacco plants will produce a uniform number of nodes before flowering. If the shoots of these plants are removed at different positions, axillary buds will grow out and produce the same number of nodes as the removed portion of the shoot (figure 42.8). The upper axillary buds of flowering tobacco will remember their position when rooted or grafted. The terminal shoot tip becomes committed, or determined, to flower about four nodes before it actually initiates a flower (figure 42.9). In some other species, this commitment is less stable or it occurs later.

How do shoots “know” where they are and at some point “remember” that information? It has become clear that inhibitory signals are sent from the roots. When bottomless pots are

continuously placed over a growing tobacco plant and filled with soil, flowering is delayed by the formation of adventitious roots (figure 42.10). Control experiments with leaf removal show that the addition of roots, and not the loss of leaves, delays flowering. A balance between floral promoting and inhibiting signals may regulate when flowering occurs in the autonomous pathway and the other pathways as well.

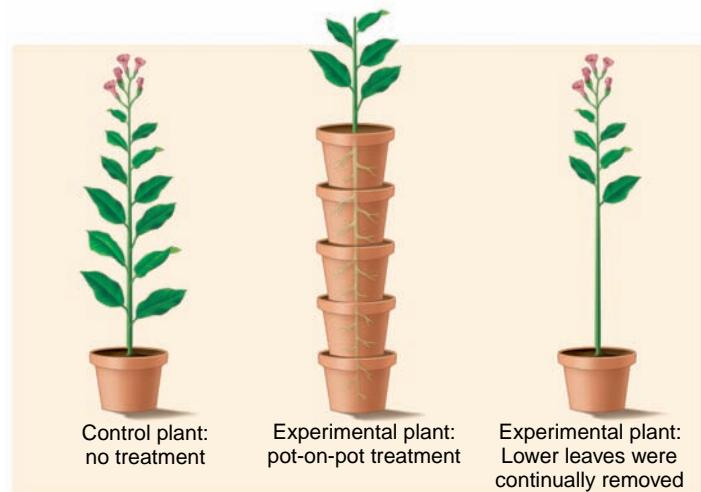


Figure 42.10 Roots can inhibit flowering. Adventitious roots formed as bottomless pots were continuously placed over growing tobacco plants, delaying flowering. The delay in flowering is caused by the roots, not by the loss of the leaves. This was shown by removing leaves on plants at the same time and in the same position as leaves on experimental plants that became buried as pots were added.

Determination for flowering is tested at the organ or whole-plant level by changing the environment and ascertaining whether the developmental fate has changed. In *Arabidopsis*, floral determination correlates with the increase of *LFY* gene expression, and it has already occurred by the time a second flowering gene, *APETALA1* (*AP1*), is expressed. Because all four flowering pathways appear to converge with increased levels of *LFY*, this determination event should occur in species with a variety of balances among the pathways (figure 42.11).

Inquiry question

Why would it be advantageous for a plant to have four distinct pathways that all affect the expression of *LFY*?

Floral meristem identity genes activate floral organ identity genes

Arabidopsis and snapdragons are valuable model systems for identifying flowering genes and understanding their interactions. The four flowering pathways discussed earlier in this section lead to an adult meristem becoming a floral meristem by either activating or repressing the inhibition of floral meristem identity genes (see figure 42.11). Two of the key floral meristem identity genes are *LFY* and *AP1*. These genes establish the meristem as a flower meristem. They then turn on floral organ identity genes. The floral organ identity genes define four concentric whorls, moving inward in the floral meristem, as sepal, petal, stamen, and carpel.

The ABC model

To explain how three classes of floral organ identity genes could specify four distinct organ types, the ABC model was developed

(figure 42.12). The ABC model proposes that three classes of organ identity genes (*A*, *B*, and *C*) specify the floral organs in the four floral whorls. By studying mutants, the researchers have determined the following:

1. Class *A* genes alone specify the sepals.
2. Class *A* and class *B* genes together specify the petals.
3. Class *B* and class *C* genes together specify the stamens.
4. Class *C* genes alone specify the carpels.

The beauty of the ABC model is that it is entirely testable by making different combinations of floral organ identity mutants. Each class of genes is expressed in two whorls, yielding four different combinations of the gene products. When any one class is missing, aberrant floral organs occur in predictable positions.

Modifications to the ABC model

As compelling as the ABC model is, it cannot fully explain specification of floral meristem identity. Class *D* genes that are essential for carpel formation have been identified, but even this discovery did not explain why a plant lacking *A*, *B*, and *C* gene function produced four whorls of sepals rather than four whorls of leaves. Floral parts are thought to have evolved from leaves; therefore, if the floral organ identity genes are removed, whorls of leaves, rather than sepals, would be predicted.

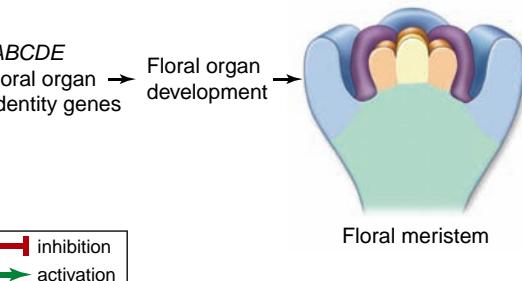
The answer to this puzzle is found in the more recently discovered class *E* genes, *SEPALATA1* (*SEP1*) through *SEPALATA4* (*SEP4*). The triple mutant *sep1 sep2 sep3* and the *sep4* mutant both produce four whorls of leaves. The proteins encoded by the *SEP* genes can interact with class *A*, *B*, and *C* proteins and possibly affect transcription of genes needed for the development of floral organs. Identification of the *SEP*

Figure 42.11 Model for flowering.

The temperature-dependent, gibberellin-dependent, and light-dependent flowering pathways promote the formation of floral meristems from adult meristems by repressing floral inhibitors and activating floral meristem identity genes.

Inquiry question

Would you expect plants to flower at a different time if there were no flower-repressing genes and the vernalization and autonomous pathway genes induced expression of flower-promoting genes?



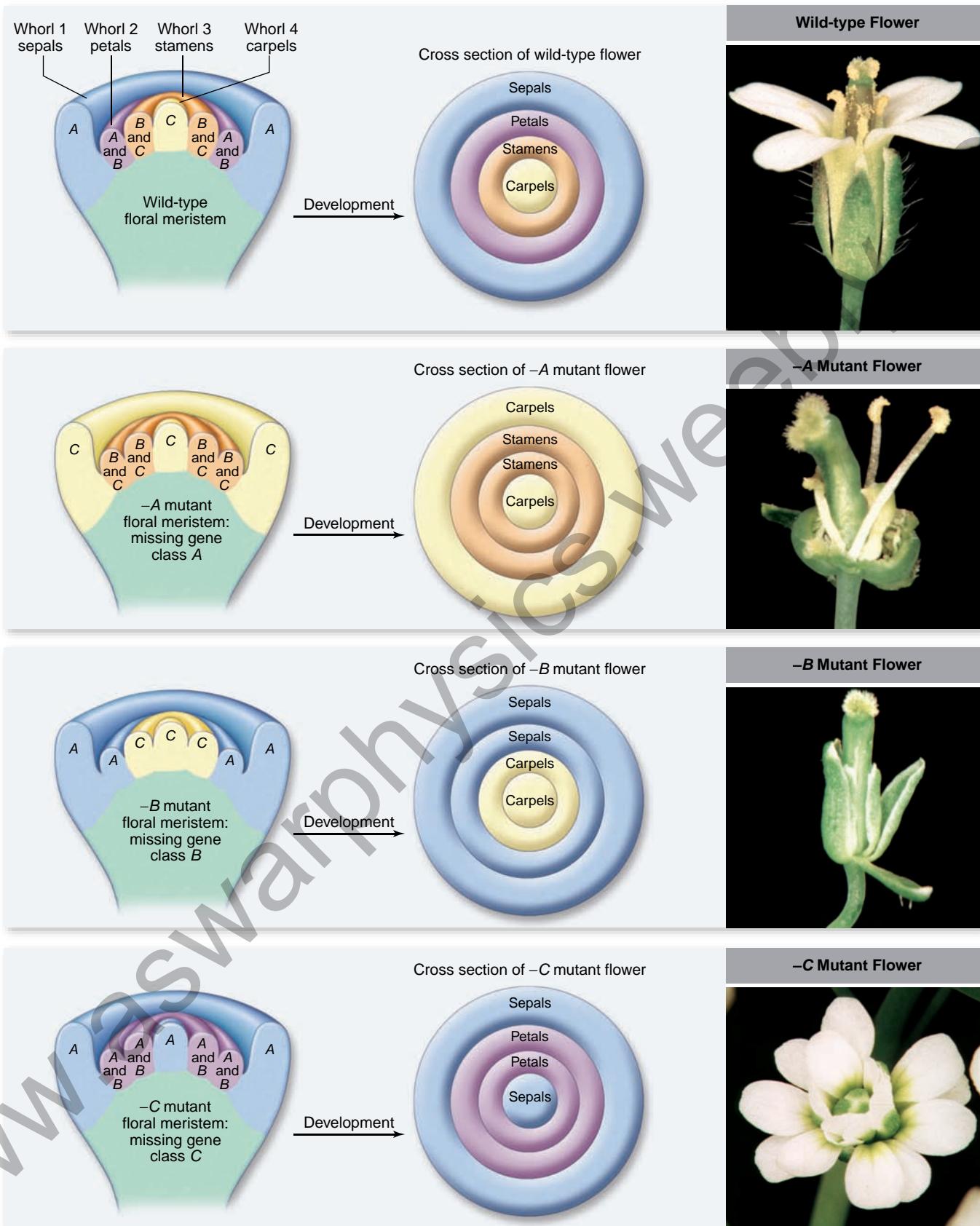


Figure 42.12 ABC model for floral organ specification. Letters labeling whorls indicate which gene classes are active. When *A* function is lost ($-A$), *C* expands to the first and second whorls. When *B* function is lost ($-B$), the outer two whorls have just *A* function, and both inner two whorls have just *C* function; none of the whorls have dual gene function. When *C* function is lost ($-C$), *A* expands into the inner two whorls. These new combinations of gene expression patterns alter which floral structures form in each whorl.

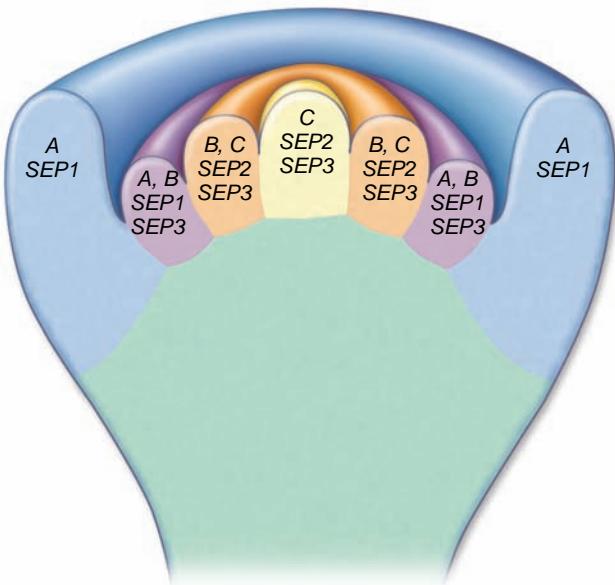


Figure 42.13 Class E genes are needed to specify floral organ identity. When all three *SEP* genes are mutated, four whorls of leaves are produced.

genes lead to a new floral organ identity model that includes these class *E* genes (figure 42.13).

It is important to recognize that the *ABCDE* genes are actually only the beginning of the making of a flower. These organ identity genes are transcription factors that turn on many more genes that actually give rise to the three-dimensional flower. Other genes “paint” the petals—that is, complex biochemical pathways lead to the accumulation of anthocyanin pigments in petal cell vacuoles. These pigments can be orange, red, or purple, and the actual color is influenced by pH as well.

Learning Outcomes Review 42.2

Four pathways have been identified that lead to flowering: light-dependent, temperature-dependent, gibberellin-dependent, and autonomous. Floral determination marks the point at which shoots become committed to making flowers. Floral meristem identity genes turn on floral organ identity genes, which control the development of flower parts.

- How would you test whether day length or night length determines flowering in plants with light-dependent flowering pathways?

42.3 Structure and Evolution of Flowers

Learning Outcomes

1. List the parts of a typical angiosperm flower.
2. Distinguish between bilateral symmetry and radial symmetry.
3. Differentiate between microgametophytes and megagametophytes.

The complex and elegant process that gives rise to the reproductive structure called the flower is often compared with metamorphosis in animals. It is indeed a metamorphosis, but the subtle shift from mitosis to meiosis in the megasporangium mother cell that leads to the development of a haploid, gamete-producing gametophyte is perhaps even more critical. The same can be said for pollen formation in the anther of the stamen.

The flower not only houses the haploid generations that will produce gametes, but it also functions to increase the probability that male and female gametes from different (or sometimes the same) plants will unite.

Flowers evolved in the angiosperms

The evolution of the angiosperms is a focus of chapter 30. The diversity of angiosperms is partly due to the evolution of a great variety of floral phenotypes that may enhance the effectiveness of pollination. As mentioned previously, floral organs are thought to have evolved from leaves. In some early angiosperms, these organs maintain the spiral developmental pattern often found in leaves. The trend has been toward four distinct whorls of parts. A complete flower has four whorls (calyx, corolla, androecium, and gynoecium) (figure 42.14). An incomplete flower lacks one or more of the whorls.

Flower morphology

In both complete and incomplete flowers, the **calyx** usually constitutes the outermost whorl; it consists of flattened appendages, called sepals, which protect the flower in the bud. The petals collectively make up the **corolla** and may be fused. Many petals function to attract pollinators. Although these two outer whorls of floral organs are not involved directly in gamete production or fertilization, they can enhance reproductive success.

Male structures. Androecium is a collective term for all the **stamens** (male structures) of a flower. Stamens are specialized

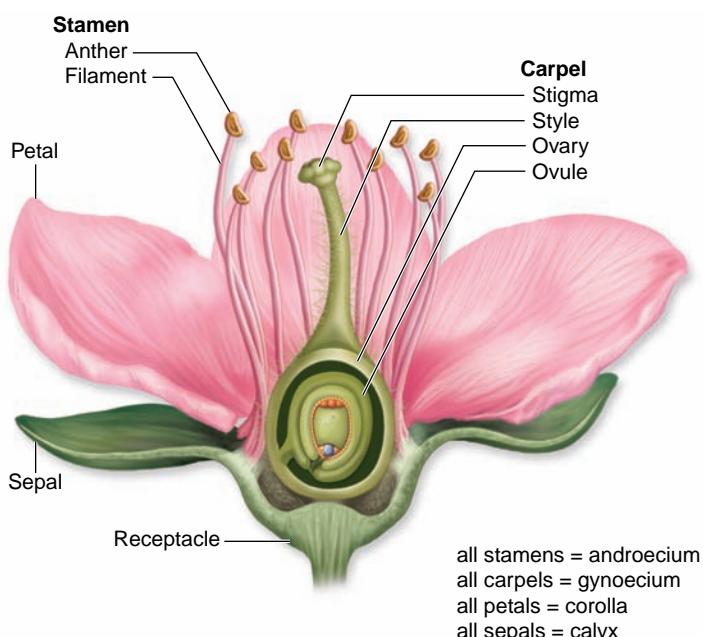


Figure 42.14 A complete angiosperm flower.

structures that bear the angiosperm microsporangia. Similar structures bear the microsporangia in the pollen cones of gymnosperms. Most living angiosperms have stamens with filaments ("stalks") that are slender and often threadlike; four microsporangia are evident at the apex in a swollen portion, the **anther**. Some of the more primitive angiosperms have stamens that are flattened and leaflike, with the sporangia produced from the upper or lower surface.

Female structures. The gynoecium is a collective term for all the female parts of a flower. In most flowers, the gynoecium, which is unique to angiosperms, consists of a single carpel or two or more fused carpels. Single or fused carpels are often referred to as simple or compound pistils, respectively. Most flowers with which we are familiar—for example, those of tomatoes and oranges—have a compound pistil. Other, less specialized flowers—for example, buttercups and stonecups—may have several to many separate, simple pistils, each formed from a single carpel.

Ovules (which develop into seeds) are produced in the pistil's swollen lower portion, the **ovary**, which usually narrows at the top into a slender, necklike style with a pollen-receptive stigma at its apex. Sometimes the stigma is divided, with the number of stigma branches indicating how many carpels compose the particular pistil.

Carpels are essentially rolled floral leaves with ovules along the margins. It is possible that the first carpels were leaf blades that folded longitudinally; the leaf margins, which had hairs, did not actually fuse until the fruit developed, but the hairs interlocked and were receptive to pollen. In the course of evolution, evidence indicates that the hairs became localized into a stigma; a style was formed; and the fusing of the carpel margins ultimately resulted in a pistil. In many modern flowering plants, the carpels have become highly modified and are not visually distinguishable from one another unless the pistil is cut open.

Trends of floral specialization

Two major evolutionary trends led to the wide diversity of modern flowering plants: (1) Separate floral parts have grouped together, or fused, and (2) floral parts have been lost or reduced (figure 42.15).

In the more advanced angiosperms, the number of parts in each whorl has often been reduced from many to few. The spiral patterns of attachment of all floral parts in primitive an-

Figure 42.15
Trends in floral specialization. Wild geranium, *Geranium maculatum*, a typical eudicot. The petals are reduced to five each, the stamens to ten, compared with early angiosperms.



Figure 42.16
Bilateral symmetry in an orchid.

Although more basal flowers are usually radially symmetrical, flowers of many derived groups, such as the orchid family (Orchidaceae), are bilaterally symmetrical.

giosperms have, in the course of evolution, given way to a single whorl at each level. The central axis of many flowers has shortened, and the whorls are close to one another. In some evolutionary lines, the members of one or more whorls have fused with one another, sometimes joining into a tube. In other kinds of flowering plants, different whorls may be fused together.

Whole whorls may even be lost from the flower, which may lack sepals, petals, stamens, carpels, or various combinations of these structures. Modifications often relate to pollination mechanisms, and in plants such as the grasses, wind has replaced animals for pollen dispersal.

Trends in floral symmetry

Other trends in floral evolution have affected the symmetry of the flower. Primitive flowers such as those of buttercups are radially symmetrical; that is, one could draw a line anywhere through the center and have two roughly equal halves. Flowers of many advanced groups are bilaterally symmetrical; they are divisible into two equal parts along only a single plane. Examples of such flowers are snapdragons, mints, and orchids (figure 42.16). Bilaterally symmetrical flowers are also common among violets and peas. In these groups, they are often associated with advanced and highly precise pollination systems.

Bilateral symmetry has arisen independently many times. In snapdragons, the *CYCLOIDIA* gene regulates floral symmetry, and in its absence flowers are more radial (figure 42.17).



a.



b.

Figure 42.17 **Genetic regulation of asymmetry in flowers.** a. Snapdragon flowers normally have bilateral symmetry. b. The *CYCLOIDIA* gene regulates floral symmetry, and *cycloidea* mutant snapdragons have radially symmetrical flowers.

Here the experimental alteration of a single gene is sufficient to cause a dramatic change in morphology. Whether the same gene or functionally similar genes arose naturally in parallel in other species is an open question.

The human influence on flower morphology

Although much floral diversity is the result of natural selection related to pollination, it is important to recognize the effect breeding (artificial selection) has on flower morphology. Humans have selected for practical or aesthetic traits that may have little adaptive value to species in the wild. For example, maize (corn) has been bred to satisfy the human palate. Human intervention ensures the reproductive success of each generation; however, in a natural setting, modern corn would not have the same protection from herbivores as its ancestors, and the fruit dispersal mechanism would be quite different.

Gametes are produced

in the gametophytes of flowers

Reproductive success depends on uniting the gametes (egg and sperm) found in the embryo sacs and pollen grains of flowers. As you learned in chapter 30, plant sexual life cycles are characterized by an *alternation of generations*, in which a diploid sporophyte generation gives rise to a haploid gametophyte generation. In angiosperms, the gametophyte generation is

very small and is completely enclosed within the tissues of the parent sporophyte. The male gametophytes, or microgametophytes, are **pollen grains**. The female gametophyte, or megagametophyte, is the **embryo sac**. Pollen grains and the embryo sac both are produced in separate, specialized structures of the angiosperm flower.

Like animals, angiosperms have separate structures for producing male and female gametes (figure 42.18), but the reproductive organs of angiosperms are different from those of animals in two ways. First, both male and female structures usually occur together in the same individual flower. Second, angiosperm reproductive structures are not permanent parts of the adult individual. Angiosperm flowers and reproductive organs develop seasonally, at times of the year most favorable for pollination. In some cases, reproductive structures are produced only once, and the parent plant dies. And, as you learned earlier in this chapter, the germ line in angiosperms is not set aside early on, but forms quite late during phase change.

Pollen formation

Anthers contain four microsporangia, which produce microspore mother cells ($2n$). Microspore mother cells produce microspores (n) through meiotic cell division. The microspores, through mitosis and wall differentiation, become pollen. Inside each pollen grain is a generative cell; this cell later divides to produce two sperm cells.

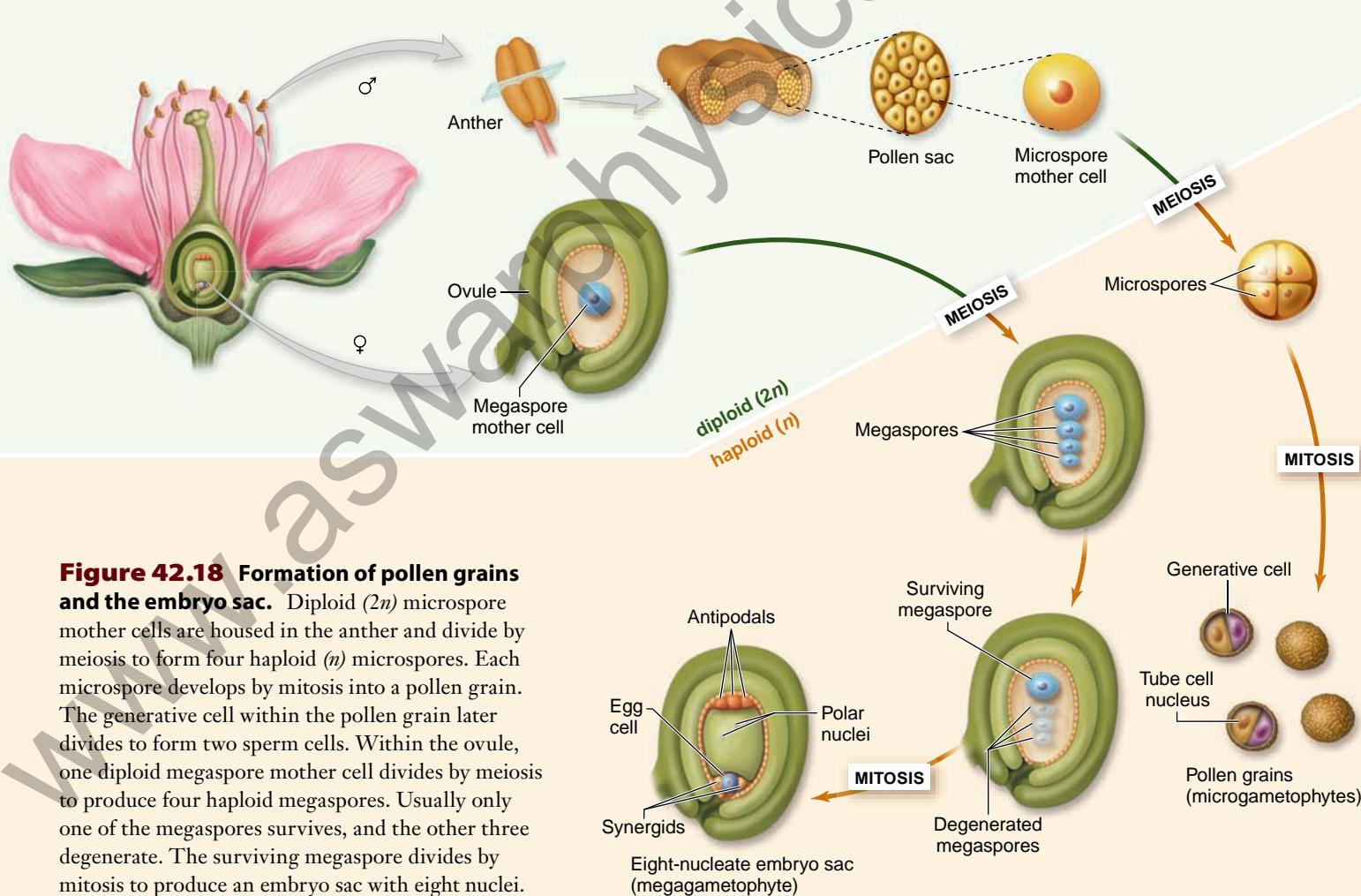
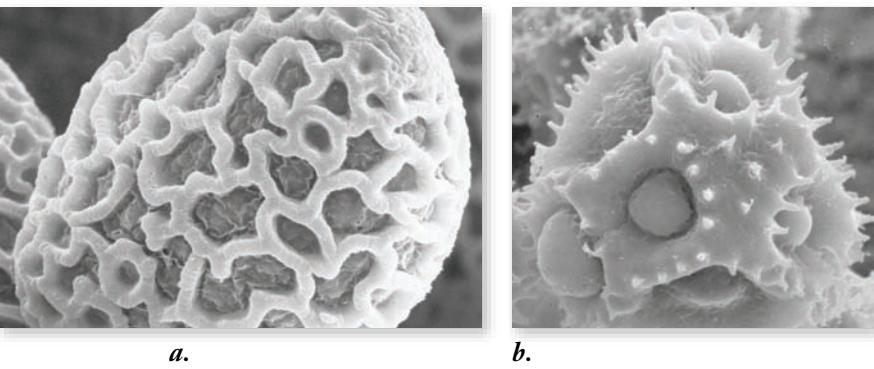


Figure 42.18 Formation of pollen grains

and the embryo sac. Diploid ($2n$) microspore mother cells are housed in the anther and divide by meiosis to form four haploid (n) microspores. Each microspore develops by mitosis into a pollen grain. The generative cell within the pollen grain later divides to form two sperm cells. Within the ovule, one diploid megasporangium divides by meiosis to produce four haploid megasporocytes. Usually only one of the megasporocytes survives, and the other three degenerate. The surviving megasporocyte divides by mitosis to produce an embryo sac with eight nuclei.



a.

b.

Figure 42.19 Pollen grains. *a.* In the Easter lily, *Lilium candidum*, the pollen tube emerges from the pollen grain through the groove or furrow that occurs on one side of the grain. *b.* In a plant of the sunflower family, *Hyoseris longiloba*, three pores are hidden among the ornamentation of the pollen grain. The pollen tube may grow out through any one of them.

Pollen grain shapes are specialized for specific flower species. As discussed in more detail later in this section, fertilization requires that the pollen grain grow a tube that penetrates the style until it encounters the ovary. Most pollen grains have a furrow or pore from which this pollen tube emerges; some grains have three furrows (figure 42.19).

Embryo sac formation

Eggs develop in the ovules of the angiosperm flower. Within each ovule is a megasporangium containing a megasporangium mother cell. Just as in pollen production, the megasporangium mother cell undergoes meiosis to produce four haploid megasporangia. In most plants, however, only one of these megasporangia survives; the rest are absorbed by the ovule. The lone remaining megasporangium enlarges and undergoes repeated mitotic divisions to produce eight haploid nuclei that are enclosed within a seven-celled embryo sac.

Within the embryo sac, the eight nuclei are arranged in precise positions. One nucleus is located near the opening of the embryo sac in the egg cell. Two others are located together in a single cell in the middle of the embryo sac; these are called *polar nuclei*. Two more nuclei are contained in individual cells called synergids that flank the egg cell; the other three nuclei reside in cells called the antipodal cells, located at the end of the sac, opposite the egg cell (figure 42.20).

The first step in uniting the two sperm cells in the pollen grain with the egg and polar nuclei is the germination of pollen on the stigma of the carpel and its growth toward the embryo sac.

Learning Outcomes Review 42.3

An angiosperm flower consists of four concentric whorls: calyx, corolla, androecium, and gynoecium. Bilaterally symmetrical flowers are divisible into two equal parts along only a single plane; radially symmetrical flowers can be divided equally on any plane. The microspore mother cells in flowers undergo meiosis to produce microspores, which undergo mitosis to produce microgametophytes (pollen grains). Megasporangium mother cells undergo a similar process to produce megasporangia, which result in megagametophytes (embryo sacs).

- What is the main evolutionary advantage of the flower?

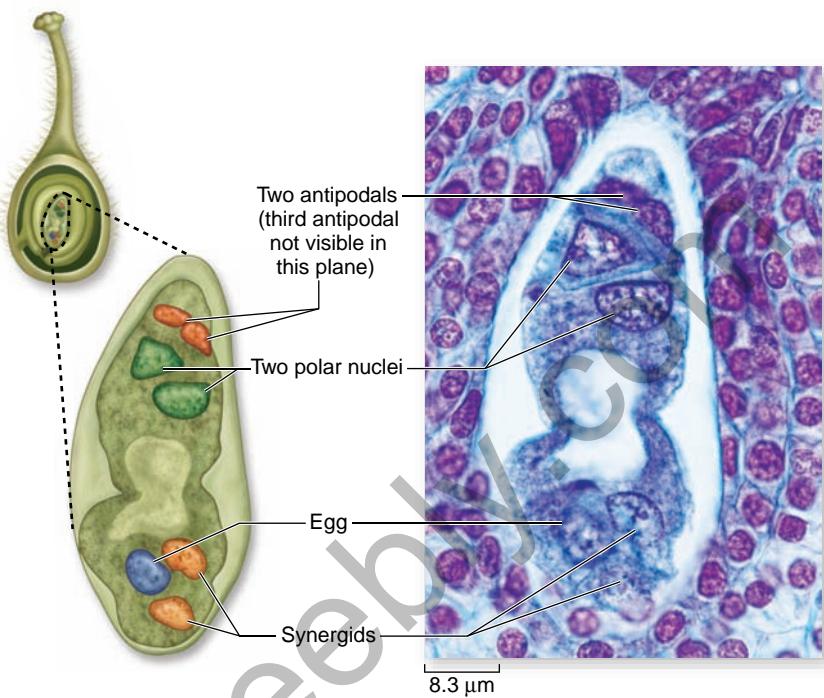


Figure 42.20 A mature embryo sac of a lily. Eight nuclei are produced by mitotic divisions of the haploid megasporangium. One is in the egg, two are polar nuclei, two occur in synergid cells, and three are in antipodal cells. The micrograph is falsely colored.

42.4 Pollination and Fertilization

Learning Outcomes

- Discuss conditions under which self-pollination may be favored.
- Describe three evolutionary strategies that promote outcrossing.
- List the products of double fertilization.

Pollination is the process by which pollen is placed on the stigma. Pollen may be carried to the flower by wind or by animals, or it may originate within the individual flower itself. When pollen from a flower's anther pollinates the same flower's stigma, the process is called *self-pollination*. When pollen from the anther of one flower pollinates the stigma of a different flower, the process is termed *cross-pollination*, or *outcrossing*.

As you just learned, pollination in angiosperms does not involve direct contact between the pollen grain and the ovule. When pollen reaches the stigma, it germinates, and a pollen tube grows down, carrying the sperm nuclei to the embryo sac. After double fertilization takes place, development of the embryo and endosperm begins. The seed matures within the ripening fruit; eventually, the germination of the seed initiates another life cycle.

Successful pollination in many angiosperms depends on the regular attraction of **pollinators**, such as insects, birds, and other animals, which transfer pollen between plants of the same

species. When animals disperse pollen, they perform the same function for flowering plants that they do for themselves when they actively search out mates.

The relationship between plant and pollinator can be quite intricate. Mutations in either partner can block reproduction. If a plant flowers at the “wrong” time, the pollinator may not be available. If the morphology of the flower or pollinator is altered, the result may be physical barriers to pollination. Clearly, floral morphology has coevolved with pollinators, and the result is a much more complex and diverse morphology, going beyond the simple initiation and development of four distinct whorls of organs.

Early seed plants were wind-pollinated

Early seed plants were pollinated passively, by the action of the wind. As in present-day conifers, great quantities of pollen were shed and blown about, occasionally reaching the vicinity of the ovules of the same species.

Individual plants of any wind-pollinated species must grow relatively close to one another for such a system to operate efficiently. Otherwise, the chance that any pollen will arrive at an appropriate destination is very small. The vast majority of windblown pollen travels less than 100 m. This short distance is significant compared with the long distances pollen is routinely carried by certain insects, birds, and other animals.

Flowers and animal pollinators have coevolved

The spreading of pollen from plant to plant by pollinators visiting flowers of an angiosperm species has played an important role in the evolutionary success of the group. It now seems clear that the earliest angiosperms, and perhaps their ancestors also, were insect-pollinated, and the coevolution of insects and plants has been important for both groups for over 100 million years. Such interactions have also been important in bringing about increased floral specialization. As flowers become increasingly specialized, so do their relationships with particular groups of insects and other animals.

Bees

Among insect-pollinated angiosperms, the most numerous groups are those pollinated by bees (figure 42.21). Like most insects, bees initially locate sources of food by odor and then orient themselves on the flower or group of flowers by its shape, color, and texture.

Flowers that bees characteristically visit are often blue or yellow. Many have stripes or lines of dots that indicate the location of the nectaries, which often occur within the throats of specialized flowers. Some bees collect nectar, which is used as a source of food for adult bees and occasionally for larvae. Most of the approximately 20,000 species of bees visit flowers to obtain pollen, which is used to provide food in cells where bee larvae complete their development.

Except for a few hundred species of social and semisocial bees and about 1000 species that are parasitic in the nests of other bees, the great majority of bees—at least 18,000 species—are solitary. Solitary bees in temperate regions characteristically



Figure 42.21 Pollination by a bumblebee. As this bumblebee, *Bombus* sp., collects nectar, pollen sticks to its body. The pollen will be distributed to the next plant the bee visits.

produce only a single generation in the course of a year. Often, they are active as adults for as little as a few weeks a year.

Solitary bees often use the flowers of a particular group of plants almost exclusively as sources of their larval food. The highly constant relationships of such bees with those flowers may lead to modifications, over time, in both the flowers and the bees. For example, the time of day when the flowers open may correlate with the time when the bees appear; the mouth-parts of the bees may become elongated in relation to tubular flowers; or the bees' pollen-collecting apparatuses may be adapted to the anthers of the plants that they normally visit. When such relationships are established, they provide both an efficient mechanism of pollination for the flowers and a constant source of food for the bees that “specialize” on them.

Insects other than bees

Among flower-visiting insects other than bees, a few groups are especially prominent. Flowers such as phlox, which are visited regularly by butterflies, often have flat “landing platforms” on which butterflies perch. They also tend to have long, slender floral tubes filled with nectar that is accessible to the long, coiled proboscis characteristic of Lepidoptera, the order of insects that includes butterflies and moths.

Flowers such as jimsonweed (*Datura stramonium*), evening primrose (*Oenothera biennis*), and others visited regularly by moths are often white, yellow, or some other pale color; they also tend to be heavily scented, making the flowers easy to locate at night (figure 42.22).

Birds

Several interesting groups of plants are regularly visited and pollinated by birds, especially the hummingbirds of North and South America and the sunbirds of Africa (figure 42.23). Such plants must produce large amounts of nectar because birds will not continue to visit flowers if they do not find enough food to

SCIENTIFIC THINKING

Hypothesis: Moths are more effective than bumblebees at moving pollen long distances.

Prediction: The pollen donors of seeds of wild plants are more widely distributed if moths carried the pollen than if bees carried it.

Test: Locate a large natural patch of the wild plant. Make sure that both moths and bees are abundant and that the plants are variable for a genetically controlled trait. In this case, assume the population contains some purple-flowered plants (a dominant trait) and some with white flowers (a recessive trait). Remove all the flowers from the purple-flowered plants except those at the edge of the population. Find a white-flowered plant at the center of the population to use as the test plant. Cover some flowers during the day and uncover them in the evening so moths, but not bees, can pollinate them. With other flowers, cover in the evening but not during the day, so bees, but not moths, can pollinate them. Collect seeds from each set of flowers and grow the plants. For each treatment, count the number of plants that produce purple flowers. These will have pollen donors that were a long distance from the test plant.



Cover some flowers during the day and others in the evening. Count the number of purple flowered plants obtained from each treatment.

Result: Seeds produced by bee pollination produced the same number of plants with purple flowers as those produced by moth pollination.

Conclusion: The hypothesis is not supported. Bees carry pollen as far as moths do.

Further Experiments: Growing plants from seed to check for flower color is very time-consuming. Propose another way to determine the source of the pollen in this experiment.

Figure 42.22 Bees and moths as pollinators.

maintain themselves. But flowers producing large amounts of nectar have no advantage in being visited by insects, because an insect could obtain its energy requirements at a single flower and would not cross-pollinate the flower. How are these different selective forces balanced in flowers that are “specialized” for hummingbirds and sunbirds?

The answer involves the evolution of flower color. Ultraviolet light is highly visible to insects. Carotenoids, the yellow



Figure 42.23 Hummingbirds and flowers. A long-tailed hermit hummingbird (*Phaethornis superciliosus*) extracts nectar from the flowers of *Heliconia imbricata* in the forests of Costa Rica. Note the pollen on the bird's beak. Hummingbirds of this group obtain nectar primarily from long, curved flowers that more or less match the length and shape of their beaks.

or orange pigments we described in chapter 8 in the context of photosynthesis, are responsible for the colors of many flowers, including sunflowers and mustard. Carotenoids reflect both in the yellow range and in the ultraviolet range, the mixture resulting in a distinctive color called “bee’s purple.” Such yellow flowers may also be marked in distinctive ways normally invisible to us, but highly visible to bees and other insects (figure 42.24). These markings can be in the form of a bull’s-eye or a landing strip.



a.



b.

Figure 42.24 How a bee sees a flower. *a.* The yellow flower of *Ludwigia peruviana* (Peruvian primrose) photographed in normal light and *(b)* with a filter that selectively transmits ultraviolet light. The outer sections of the petals reflect both yellow and ultraviolet, a mixture of colors called “bee’s purple”; the inner portions of the petals reflect yellow only and therefore appear dark in the photograph that emphasizes ultraviolet reflection. To a bee, this flower appears as if it has a conspicuous central bull’s-eye.

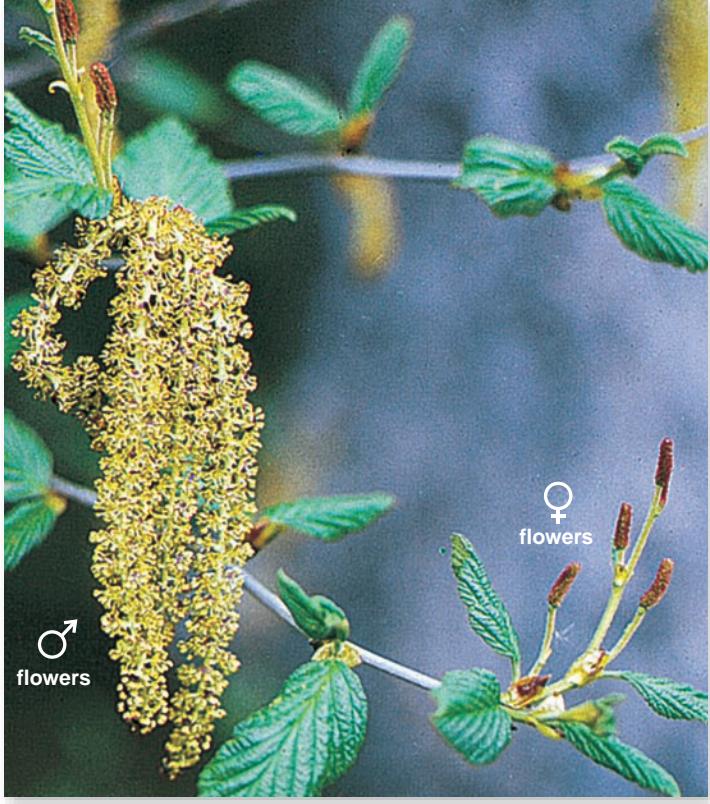


Figure 42.25 Stamine and pistillate flowers of a birch, *Betula* sp. Birches are monoecious; their stamine flowers hang down in long, yellowish tassels, and their pistillate flowers mature into clusters of small, brownish, conelike structures.

In contrast, red does not stand out as a distinct color to most insects, but it is a very conspicuous color to birds. To most insects, the red upper leaves of poinsettias look just like the other leaves of the plant. Consequently, even though the flowers produce abundant supplies of nectar and attract hummingbirds, insects tend to bypass them. Thus, the red color both signals to birds the presence of abundant nectar and makes that nectar as inconspicuous as possible to insects. Red is also seen again in fruits that are dispersed by birds (see chapter 37).

Other animal pollinators

Other animals, including bats and small rodents, may aid in pollination. The signals here are also species-specific. As an example, the saguaro cactus (*Carnegiea gigantea*) of the Sonoran desert is pollinated by bats that feed on nectar at night, as well as by birds and insects.

These animals may also assist in dispersing the seeds and fruits that result from pollination. Monkeys are attracted to orange and yellow, and thus can be effective in dispersing fruits of this color in their habitats.

Some flowering plants continue to use wind pollination

A number of groups of angiosperms are wind-pollinated—a characteristic of early seed plants. Among these groups are oaks, birches, cottonwoods, grasses, sedges, and nettles. The flowers of these plants are small, greenish, and odorless; their corollas are reduced or absent (figures 42.25 and 42.26). Such flowers often are grouped together in fairly large numbers

and may hang down in tassels that wave about in the wind and shed pollen freely.

Many wind-pollinated plants have stamen- and carpel-containing flowers separated between individuals or physically separated on a single individual. Maize is a good example, with pollen-producing tassels at the top of the plant and axillary shoots with female flowers lower down. Separation of pollen-producing and ovule-bearing flowers is a strategy that greatly promotes outcrossing, since pollen from one flower must land on a different flower for fertilization to have any chance of occurring. Some wind-pollinated plants, especially trees and shrubs, flower in the spring, before the development of their leaves can interfere with the wind-borne pollen. Wind-pollinated species do not depend on the presence of a pollinator for species survival, which may be another survival advantage.

Self-pollination is favored in stable environments

Thus far we have considered examples of pollination that tend to lead to outcrossing, which is as highly advantageous for plants and for eukaryotic organisms generally. Nevertheless, self-pollination also occurs among angiosperms, particularly in temperate regions. Most self-pollinating plants have small, relatively inconspicuous flowers that shed pollen directly onto the stigma, sometimes even before the bud opens.

You might logically ask why many self-pollinated plant species have survived if outcrossing is as important genetically



Figure 42.26 Wind-pollinated flowers. The large yellow anthers, dangling on very slender filaments, are hanging out, about to shed their pollen to the wind. Later, these flowers will become pistillate, with long, feathery stigmas—well suited for trapping windblown pollen—sticking far out of them. Many grasses, like this one, are therefore dichogamous.

for plants as it is for animals. Biologists propose two basic reasons for the frequent occurrence of self-pollinated angiosperms:

1. Self-pollination is ecologically advantageous under certain circumstances because self-pollinators do not need to be visited by animals to produce seed. As a result, self-pollinated plants expend less energy in producing pollinator attractants and can grow in areas where the kinds of insects or other animals that might visit them are absent or very scarce—as in the Arctic or at high elevations.
2. In genetic terms, self-pollination produces progenies that are more uniform than those that result from outcrossing. Remember that because meiosis is involved, recombination still takes place, as described in chapter 11—and therefore the offspring will not be identical to the parent. However, such progenies may contain high proportions of individuals well-adapted to particular habitats.

Self-pollination in normally outcrossing species tends to produce large numbers of ill-adapted individuals because it brings together deleterious recessive alleles—but some of these combinations may be highly advantageous in particular habitats. In these habitats, it may be advantageous for the plant to continue self-pollinating indefinitely.

Several evolutionary strategies promote outcrossing

Outcrossing, as we have stressed, is critically important for the adaptation and evolution of all eukaryotic organisms, with a few exceptions. Often, flowers contain both stamens and pistils,

which increases the likelihood of self-pollination. One general strategy to promote outcrossing, therefore, is to separate stamens and pistils. Another strategy involves self-incompatibility that prevents self-fertilization.

Separation of male and female structures in space or in time

In a number of species—for example, willows and some mulberries—staminate and pistillate flowers may occur on separate plants. Such plants, which produce only ovules or only pollen, are called **dioecious**, meaning “two houses.” These plants clearly cannot self-pollinate and must rely exclusively on outcrossing. In other kinds of plants, such as oaks, birches, corn (maize), and pumpkins, separate male and female flowers may both be produced on the same plant. Such plants are called **monoecious**, meaning “one house” (see figure 42.25). In monoecious plants, the separation of pistillate and staminate flowers, which may mature at different times, greatly enhances the probability of outcrossing.

Even if, as usually is the case, functional stamens and pistils are both present in each flower of a particular plant species, these organs may reach maturity at different times. Plants in which this occurs are called **dichogamous**. If the stamens mature first, shedding their pollen before the stigmas are receptive, the flower is effectively staminate at that time. Once the stamens have finished shedding pollen, the stigma or stigmas may become receptive, and the flower may become essentially pistillate (see figures 42.26 and 42.27). This separation in time has the same effect as if individuals were dioecious; the outcrossing rate is thereby significantly increased.

Many flowers are constructed such that the stamens and stigmas do not come in contact with each other. With this

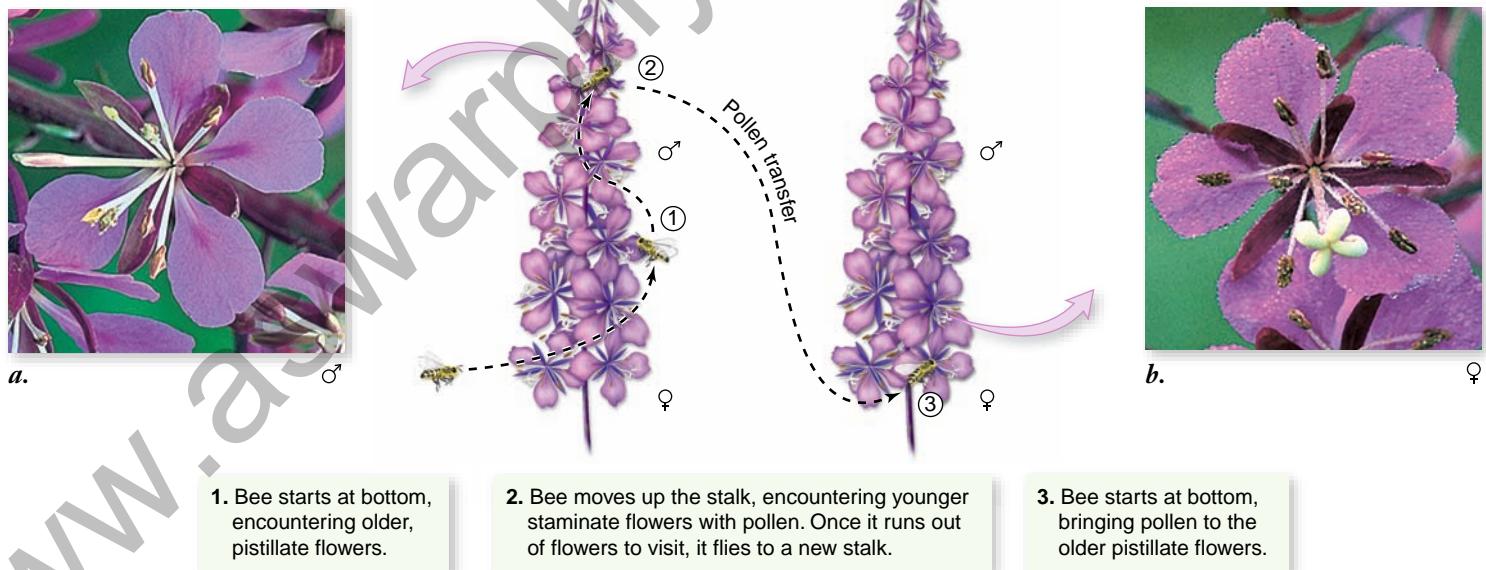


Figure 42.27 **Dichogamy, as illustrated by the flowers of fireweed, *Epilobium angustifolium*.** More than 200 years ago (in the 1790s) fireweed, which is outcrossing, was one of the first plant species to have its process of pollination described. First, the anthers shed pollen, and then the style elongates above the stamens while the four lobes of the stigma curl back and become receptive. Consequently, the flowers are functionally staminate at first, becoming pistillate about two days later. The flowers open progressively up the stem, so that the lowest are visited first, promoting outcrossing. Working up the stem, the bees encounter pollen-shedding, staminate-phase flowers and become covered with pollen, which they then carry to the lower, functionally pistillate flowers of another plant. Shown here are flowers in (a) the staminate phase and (b) the pistillate phase.

arrangement, the natural tendency is for the pollen to be transferred to the stigma of another flower, rather than to the stigma of its own flower, thereby promoting outcrossing.

Self-incompatibility

Even when a flower's stamens and stigma mature at the same time, genetic self-incompatibility, which is widespread in flowering plants, increases outcrossing. Self-incompatibility results when the pollen and stigma recognize each other as being genetically related, and pollen tube growth is blocked (figure 42.28).

Self-incompatibility is controlled by the *S* (self-incompatibility) locus. Many alleles at the *S* locus regulate recognition responses between pollen and stigma. Researchers have identified two types of self-incompatibility. *Gametophytic self-incompatibility* depends on the haploid *S* locus of the pollen and the diploid *S* locus of the stigma. If either of the *S* alleles in the stigma matches the pollen's *S* allele, pollen tube growth stops before it reaches the embryo sac. Petunias exhibit gametophytic self-incompatibility.

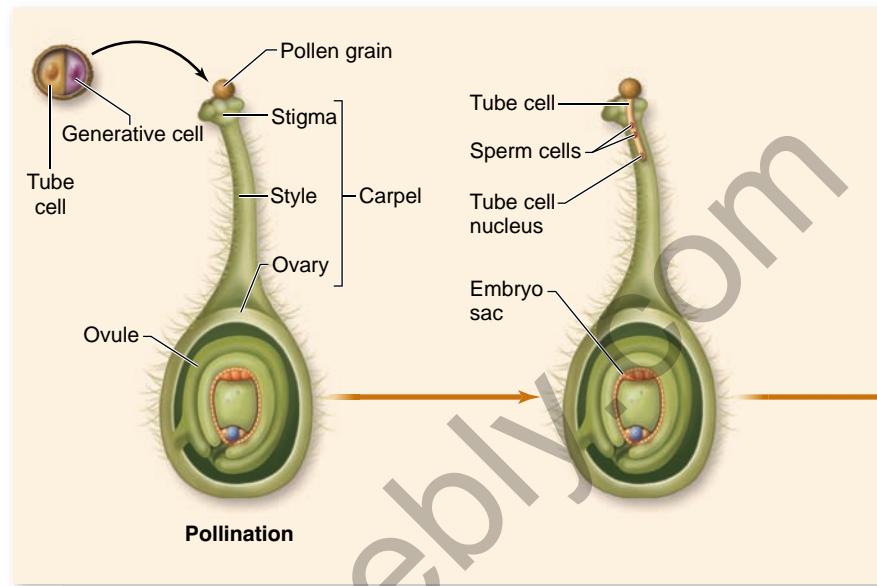
In *sporophytic self-incompatibility*, as occurs in broccoli, both *S* alleles of the pollen parent, not just the *S* allele of the pollen itself, are important. If the alleles in the stigma match either of the pollen parent's *S* alleles, the haploid pollen will not germinate.

Pollen-recognition mechanisms may have originated in a common ancestor of the gymnosperms. Fossils with pollen tubes from the Carboniferous period are consistent with the hypothesis that they had highly evolved pollen-recognition systems.

Angiosperms undergo double fertilization

Fertilization in angiosperms is a complex, somewhat unusual process in which two sperm cells are utilized in a unique process called double fertilization. Double fertilization results in two key developments: (1) the fertilization of the egg, and (2) the formation of a nutrient substance called endosperm that nourishes the embryo.

Once a pollen grain has been spread by wind, by animals, or through self-pollination, it adheres to the sticky, sugary sub-



stance that covers the stigma and begins to grow a pollen tube that pierces the style (figure 42.29). The pollen tube, nourished by the sugary substance, grows until it reaches the ovule in the ovary. Meanwhile, the generative cell within the pollen grain tube cell divides to form two sperm cells.

The pollen tube eventually reaches the embryo sac in the ovule. At the entry to the embryo sac, one of the nuclei flanking the egg cell degenerates, and the pollen tube enters that cell. The tip of the pollen tube bursts and releases the two sperm cells. One of the sperm cells fertilizes the egg cell, forming a zygote. The other sperm cell fuses with the two polar nuclei located at the center of the embryo sac, forming the triploid ($3n$) primary endosperm nucleus. The primary endosperm nucleus eventually develops into the endosperm (food supply).

Once fertilization is complete, the embryo develops as its cells divide numerous times. Meanwhile, protective tissues

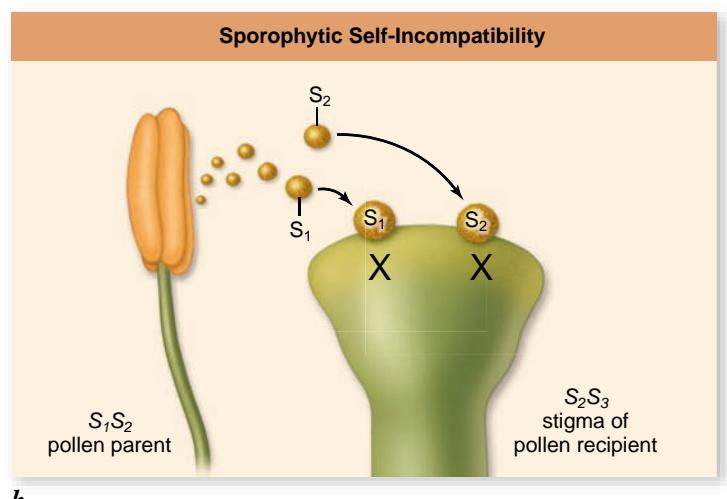
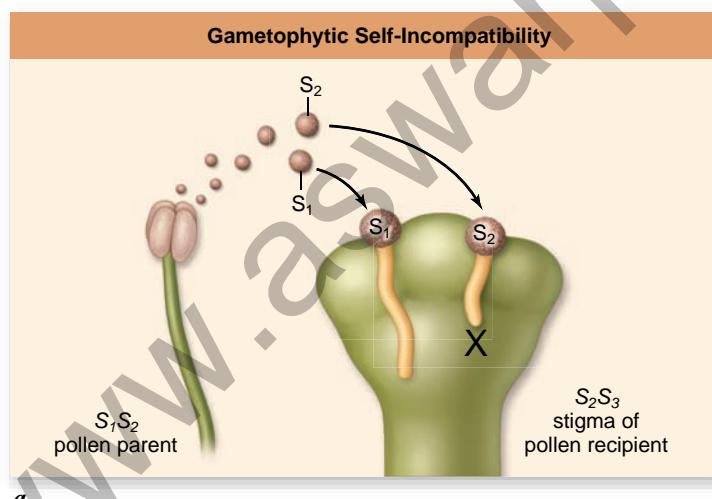


Figure 42.28 Genetic control can block self-pollination. *a.* Gametophytic self-incompatibility is determined by the haploid pollen genotype. *b.* Sporophytic self-incompatibility recognizes the genotype of the diploid pollen parent, not just the haploid pollen genotype. The pollen contains proteins produced by the S_1S_2 parent. In both cases, the recognition is based on the *S* locus, which has many different alleles. The subscript numbers indicate the *S* allele genotype. In gametophytic self-incompatibility, the block comes after pollen tube germination. In sporophytic self-incompatibility, the pollen tube fails to germinate.

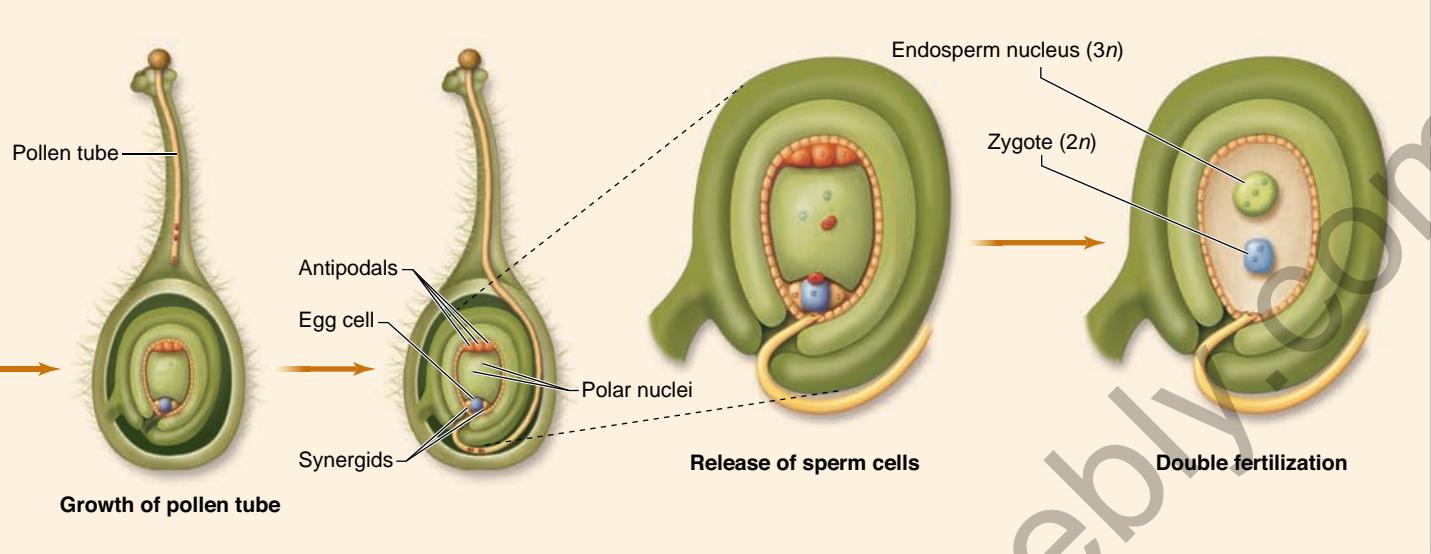


Figure 42.29 The formation of the pollen tube and double fertilization. When pollen lands on the stigma of a flower, the pollen tube cell grows toward the embryo sac, forming a pollen tube. While the pollen tube is growing, the generative cell divides to form two sperm cells. When the pollen tube reaches the embryo sac, it enters one of the synergids and releases the sperm cells. In a process called double fertilization, one sperm cell nucleus fuses with the egg cell to form the diploid ($2n$) zygote, and the other sperm cell nucleus fuses with the two polar nuclei to form the triploid ($3n$) endosperm nucleus.

enclose the embryo, resulting in the formation of the seed. The seed, in turn, is enclosed in another structure, called the fruit. These typical angiosperm structures evolved in response to the need for seeds to be dispersed over long distances to ensure genetic variability.

Learning Outcomes Review 42.4

Self-pollination may be favored when pollinators are absent or when plants are adapted to a stable environment, and therefore uniform offspring are advantageous. Mechanisms to promote outcrossing include the production of separate male and female flowers, maturation of male flowers at a different time than female flowers, and genetically controlled self-incompatibility. Double fertilization produces a diploid embryo and triploid endosperm that provides nutrition.

- Are all offspring of a self-pollinating plant identical?

Self-pollination reduces genetic variability, but asexual reproduction results in genetically identical individuals because only mitotic cell divisions occur. In the absence of meiosis, individuals that are highly adapted to a relatively unchanging environment persist for the same reasons that self-pollination is favored. Should conditions change dramatically, there will be less variation in the population for natural selection to act on, and the species may be less likely to survive.

Asexual reproduction is also used in agriculture and horticulture to propagate a particularly desirable plant with traits that would be altered by sexual reproduction or even by self-pollination. Most roses and potatoes, for example, are vegetatively (asexually) propagated.

Apomixis involves development of diploid embryos

In certain plants, including some citrus, certain grasses (such as Kentucky bluegrass), and dandelions, the embryos in the seeds may be produced asexually from the parent plant. This kind of asexual reproduction is known as apomixis. Seeds produced in this way give rise to individuals that are genetically identical to their parents.

Although these plants reproduce by cloning diploid cells in the ovule, they also gain the advantage of seed dispersal, an adaptation usually associated with sexual reproduction. Asexual reproduction in plants is far more common in harsh or marginal environments, where there is little leeway for variation. For example, a greater proportion of asexual plants occur in the Arctic than in temperate regions.

42.5 Asexual Reproduction

Learning Outcomes

1. Define apomixis.
2. List examples of plant parts involved in vegetative reproduction.
3. Outline the steps involved in protoplast regeneration.



Figure 42.30 Vegetative reproduction. Small plants arise from notches along the leaves of the house plant *Kalanchoe daigremontiana*. The plantlets can fall off and grow into new plants, an unusual form of vegetative reproduction.

In vegetative reproduction, new plants arise from nonreproductive tissues

In a very common form of asexual reproduction called vegetative reproduction, new plant individuals are simply cloned from parts of adults (figure 42.30). The forms of vegetative reproduction in plants are many and varied.

Runners or stolons. Some plants reproduce by means of *runners* (also called *stolons*)—long, slender stems that grow along the surface of the soil. In the cultivated strawberry, for example, leaves, flowers, and roots are produced at every other node on the runner. Just beyond

each second node, the tip of the runner turns up and becomes thickened. This thickened portion first produces adventitious roots and then a new shoot that continues the runner.

Rhizomes. Underground horizontal stems, or *rhizomes*, are also important reproductive structures, particularly in grasses and sedges. Rhizomes invade areas near the parent plant, and each node can give rise to a new flowering shoot. The noxious character of many weeds results from this type of growth pattern, and many garden plants, such as irises, are propagated almost entirely from rhizomes. Corms and bulbs are vertical underground stems. Tubers are also stems specialized for storage and reproduction. Tubers are the terminal storage portion of a rhizome. Potatoes (*Solanum spp.*) are propagated artificially from tuber segments, each with one or more “eyes.” The eyes, or “seed pieces,” of a potato give rise to the new plant.

Suckers. The roots of some plants—for example, cherry, apple, raspberry, and blackberry—produce *suckers*, or sprouts, which give rise to new plants. Commercial varieties of banana do not produce seeds and are propagated by suckers that develop from buds on underground stems. When the root of a dandelion is broken, as it may be if one attempts to pull it from the ground, each root fragment may give rise to a new plant.

Adventitious plantlets. In a few plant species, even the leaves are reproductive. One example is the houseplant *Kalanchoe daigremontiana* (see figure 42.30), familiar to many people as the “maternity plant,” or “mother of thousands.” The common names of this plant are based on the fact that numerous plantlets arise from meristematic tissue located in notches along the leaves. The maternity plant is ordinarily propagated by means of these small plants, which, when they mature, drop to the soil and take root.

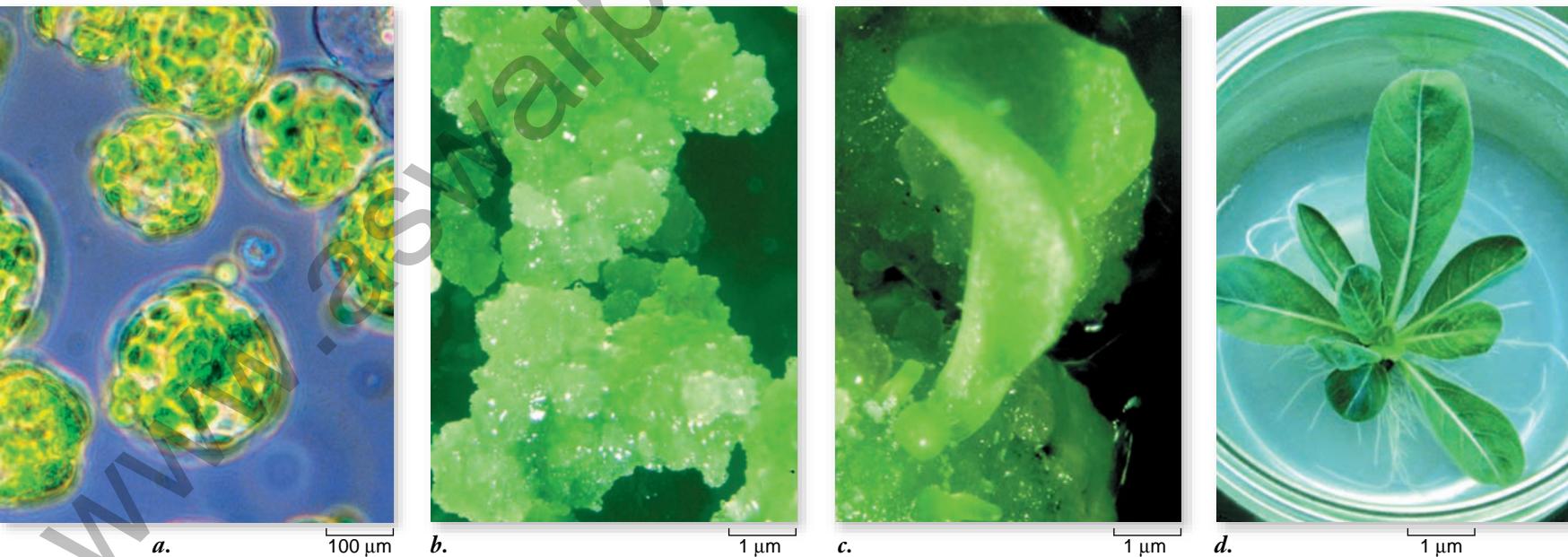


Figure 42.31 Protoplast regeneration. Different stages in the recovery of intact plants from single plant protoplasts of evening primrose. **a.** Individual plant protoplasts. **b.** Regeneration of the cell wall and the beginning of cell division. **c.** Production of somatic cell embryos from the callus. **d.** Recovery of a plantlet from the somatic cell embryo in culture. The plant can later be rooted in soil.

Plants can be cloned from isolated cells in the laboratory

Whole plants can be cloned by regenerating plant cells or tissues on nutrient medium with growth hormones. This is another form of asexual reproduction. Cultured leaf, stem, and root tissues can undergo organogenesis in culture and form roots and shoots. In some cases, individual cells can also give rise to whole plants in culture.

Individual cells can be isolated from tissues with enzymes that break down cell walls, leaving behind the *protoplast*, a plant cell enclosed only by a plasma membrane. Plant cells have greater developmental plasticity than most vertebrate animal cells, and many, but not all, cell types in plants maintain the ability to generate organs or an entire organism in culture. Consider the limited number of adult stem cells in vertebrates and the challenges associated with cloning discussed in chapter 19.

When single plant cells are cultured, wall regeneration takes place. Cell division follows to form a *callus*, an undifferentiated mass of cells (figure 42.31). Once a callus is formed, whole plants can be produced in culture. Whole-plant development can go through an embryonic stage or can start with the formation of a shoot or root.

Tissue culture has many agricultural and horticultural applications. Virus-free raspberries and sugarcane can be propagated by culturing meristems, which are generally free of viruses, even in an infected plant. As with other forms of asexual reproduction, genetically identical individuals can be propagated.

Learning Outcomes Review 42.5

In apomixis, embryos are produced by mitosis rather than fertilization; in contrast, asexual vegetative reproduction occurs from vegetative plant parts. Examples include runners, stolons, rhizomes, suckers, and adventitious plant parts. In the laboratory, protoplasts are produced by isolating cells and removing the cell walls. Inducing mitosis results in a cluster of undifferentiated cells called a callus, which can then be stimulated to differentiate into a plant.

- Under what conditions would vegetative reproduction benefit survival?

42.6 Plant Life Spans

Learning Outcomes

1. Distinguish between herbaceous and woody perennials.
2. Define perennial and annual plants.
3. Describe the life cycle of a biennial plant.

Once established, plants live for highly variable periods of time, depending on the species. Life span may or may not correlate with reproductive strategy. Woody plants, which have extensive secondary growth, nearly always live longer than herbaceous plants, which have limited or no secondary growth. Bristlecone pine, for example, can live upward of 4000 years.



a.



b.

Figure 42.32 Annual and perennial plants. Plants live for very different lengths of time. *a.* Desert annuals complete their entire life span in a few weeks, flowering just once. *b.* Some trees, such as the giant redwood (*Sequoia sempervirens*), which occurs in scattered groves along the western slopes of the Sierra Nevada in California, live 2000 years or more, and flower year after year.

Some herbaceous plants send new stems above the ground every year, producing them from woody underground structures. Others germinate and grow, flowering just once before they die. Shorter-lived plants rarely become very woody because there is not enough time for secondary tissues to accumulate. Depending on the length of their life cycles, herbaceous plants may be annual, biennial, or perennial, whereas woody plants are generally perennial (figure 42.32).

Determining life span is even more complicated for clonally reproducing organisms. Aspen trees (*Populus tremuloides*) form huge clones from asexual reproduction of their roots. Collectively, an aspen clone may form the largest “organism” on Earth. Other asexually reproducing plants may cover less territory but live for thousands of years. Creosote bushes (*Larrea tridentata*) in the Mojave Desert have been identified that are up to 12,000 years old!

Perennial plants live for many years

Perennial plants continue to grow year after year and may be herbaceous (as are many woodland, wetland, and prairie wildflowers), or woody (as are trees and shrubs). The majority of vascular plant species are perennials. Perennial plants in general are able to flower and produce seeds and fruit for an indefinite number of growing seasons.

Herbaceous perennials rarely experience any secondary growth in their stems; the stems die each year after a period of relatively rapid growth and food accumulation. Food is often stored in the plants’ roots or underground stems, which can

become quite large in comparison with their less substantial aboveground counterparts.

Trees and shrubs generally flower repeatedly, but there are exceptions. Bamboo lives for many seasons as a nonreproducing plant, but senesces and dies after flowering. The same is true for at least one tropical tree (*Tachigali versicolor*), which achieves great heights before flowering and senescing. Considering the tremendous amount of energy that goes into the growth of a tree, this particular reproductive strategy is quite curious.

Trees and shrubs are either *deciduous*, with all the leaves falling at one particular time of year and the plants remaining bare for a period, or *evergreen*, with the leaves dropping throughout the year and the plants never appearing completely bare. In northern temperate regions, conifers are the most familiar evergreens, but in tropical and subtropical regions, most angiosperms are evergreen, except where there is severe seasonal drought. In these areas, many angiosperms are deciduous, losing their leaves during the drought and thus conserving water.

Annual plants grow, reproduce, and die in a single year

Annual plants grow, flower, and form fruits and seeds within one growing season and die when the process is complete. Many crop plants are annuals, including corn, wheat, and soybeans. Annuals generally grow rapidly under favorable conditions and in proportion to the availability of water or nutrients. The lateral meristems of some annuals, such as sunflowers or giant ragweed, do produce some secondary tissues for support, but most annuals are entirely herbaceous.

Annuals typically die after flowering once; the developing flowers or embryos use hormonal signaling to reallocate nutrients, so the parent plant literally starves to death. This can be demonstrated by comparing a population of bean plants in

which the beans are continually picked with a population in which the beans are left on the plant. The frequently picked population will continue to grow and yield beans much longer than the untouched population. The process that leads to the death of a plant is called **senescence**.

Biennial plants follow a two-year life cycle

Biennial plants, which are much less common than annuals, have life cycles that take two years to complete. During the first year, biennials store the products of photosynthesis in underground storage organs. During the second year of growth, flowering stems are produced using energy stored in the underground parts of the plant. Certain crop plants, including carrots, cabbage, and beets, are biennials, but these plants generally are harvested for food during their first season, before they flower. They are grown for their leaves or roots, not for their fruits or seeds.

Wild biennials include evening primroses, Queen Anne's lace (*Daucus carota*), and mullein (*Verbascum thapsis*). Many plants that are considered biennials actually do not flower until they are three or more years of age, but all biennial plants flower only once before they die.

Learning Outcomes Review 42.6

Woody perennials produce secondary growth, but herbaceous perennials typically do not. Perennial plants continue to grow year after year, whereas annual plants die after one growing season. During the first year of a biennial plant life cycle, food is produced and stored in underground storage organs. During the second year of growth, the stored energy is used to produce flowering stems.

- **What are the advantages and disadvantages of a biennial life cycle compared to an annual cycle?**



Chapter Review

42.1 Reproductive Development

Plant life cycles are characterized by an alternation of generations.

The transition to flowering competence is termed phase change.

Phase change prepares a plant to respond to external and internal signals to begin flowering. External factors include light and temperature, and internal factors include hormone production.

Mutations have clarified how phase change is controlled.

In experiments with *Arabidopsis*, plants that flower earlier than normal result from mutations in phase change genes. The implication is that mechanisms have evolved to delay flowering.

42.2 Flower Production

Four genetically regulated pathways to flowering have been identified. The balance between floral-promoting and floral-inhibiting signals regulates flowering.

The light-dependent pathway is geared to the photoperiod.

The light-dependent pathway induces flowering based on the length of the dark period a plant experiences during 24 hr. Plants may be short-day, long-day, or day-neutral, depending on their flowering response.

The temperature-dependent pathway is linked to cold.

Some plants require vernalization, or exposure of seeds or plants to chilling in order to induce flowering.

The gibberellin-dependent pathway requires an increased hormone level.

Decreased levels of gibberellins delay flowering in plants with this pathway. Gibberellins likely affect phase-change gene expression.

The autonomous pathway is independent of environmental cues.

The autonomous pathway is typical of day-neutral plants. A balance between floral-promoting and floral-inhibiting signals controls flower development.

Floral meristem identity genes activate floral organ identity genes.

Once floral organ identity genes are turned on, the four floral organs develop according to the ABC model. Class *A* genes alone specify sepals, classes *A* and *B* together specify petals, classes *B* and *C* specify stamens, and class *C* genes alone specify carpels.

42.3 Structure and Evolution of Flowers

Flowers evolved in the angiosperms.

Floral organs are believed to have evolved from leaves.

Complete flowers have four whorls corresponding to the four floral organs: the calyx, corolla, androecium, and gynoecium. Incomplete flowers lack one or more of the whorls.

Angiosperms may have radially or bilaterally symmetrical flowers.

Gametes are produced in the gametophytes of flowers.

Meiosis in the anthers produces microspores, which undergo mitosis to produce pollen grains, which are the male gametophytes or microgametophytes.

Each pollen grain contains the generative cell that later divides to produce two sperm cells and a tube cell.

Meiosis in the ovules produces megasporangia, which undergo mitosis to produce embryo sacs, which are the female gametophytes or megagametophytes.

The embryo sac contains seven cells, one of which is the egg cell and one of which contains two polar nuclei. The latter cell develops into triploid endosperm after fertilization.

42.4 Pollination and Fertilization

Early seed plants were wind-pollinated.

Wind-pollination is a passive process and does not carry pollen over long distances. Consequently, plants must be relatively close together to ensure that pollination occurs.

Flowers and animal pollinators have coevolved.

Animal pollinators provide an efficient transfer of pollen that may cover long distances. Animal-pollinated flowers produce odors and visual cues to guide pollinators.

Some flowering plants continue to use wind pollination.

Many wind-pollinated plant species have male and female flowers on separate individuals or on separate parts of each individual. The flowers are grouped in large numbers and exposed to the wind.

Self-pollination is favored in stable environments.

Plants adapted to a stable environment benefit from having uniform progeny that are likely to be more successful than those arising from

cross-pollination. Offspring from self-pollination are not genetically identical, however.

Self pollination is also favored where animal pollinators are scarce.

Several evolutionary strategies promote outcrossing.

Outcrossing is promoted in plants in which male and female flowers are physically separated on the same plant or on different plants, or in which the two flowers mature on a different schedule.

Self-incompatibility prevents self-fertilization by preventing pollen tube growth.

Angiosperms undergo double fertilization.

Double fertilization produces a diploid zygote and triploid endosperm that provides nourishment to the zygote.

42.5 Asexual Reproduction

Asexual reproduction results in genetically identical individuals because progeny are produced by mitosis.

Apomixis involves development of diploid embryos.

Apomixis is the production of embryos by mitosis rather than fertilization. These embryos develop in seeds.

In vegetative reproduction, new plants arise from nonreproductive tissues.

Vegetative parts such as runners, rhizomes, suckers, and adventitious plantlets may give rise to new individual clones.

Plants can be cloned from isolated cells in the laboratory.

Stripping away the cell wall produces a protoplast, which can then be induced to undergo mitosis to produce a callus. With the proper treatments, the callus can differentiate into a complete plant.

42.6 Plant Life Spans

Perennial plants live for many years.

Perennials live for years, although they may undergo dormancy.

Annual plants grow, reproduce, and die in a single year.

Many crop plants are annuals and require replanting every year, such as corn, wheat, and soy beans.

Biennial plants follow a two-year life cycle.

During the first year, biennials grow and store nutrients. In the second year, they produce flowers and seeds. Biennial crop plants are often harvested during the first year, such as carrots.



Review Questions

UNDERSTAND

1. Morphogenesis is the development of
 - a. growth form.
 - b. reproductive structures.
 - c. a phase change.
 - d. meristems.
2. Vernalization induces flowering following exposure to
 - a. water.
 - b. drought.
 - c. cold.
 - d. heat.
3. Photoperiod is perceived by
 - a. phytochrome and cryptochromes.
 - b. phytochrome and chlorophyll.
 - c. cryptochromes and chlorophyll.
 - d. phytochrome, cryptochromes, and chlorophyll.
4. Which of the following is not a component of a flower?
 - a. Sepal
 - b. Stamen
 - c. Carpels
 - d. Bract

5. Megaspores are produced in
 - a. anthers by mitosis.
 - c. ovules by mitosis.
 - b. anthers by meiosis.
 - d. ovules by meiosis.
6. A stamen contains a
 - a. style.
 - c. filament.
 - b. stigma.
 - d. carpel.
7. Unlike bee-pollinated flowers, bird-pollinated flowers
 - a. produce a strong fragrance.
 - b. contain a landing pad.
 - c. produce a bull's-eye pattern.
 - d. are red.
8. Asexual reproduction is likely to be most common in which ecosystem?
 - a. Tropical rainforest
 - c. Arctic tundra
 - b. Temperate grassland
 - d. Deciduous forest
9. Protoplasts are plant cells that lack
 - a. nuclei.
 - c. plasma membranes.
 - b. cell walls.
 - d. protoplasm.
10. Perennial plants are
 - a. always herbaceous.
 - b. always woody.
 - c. either herbaceous or woody.
 - d. neither herbaceous nor woody.
11. Senescence refers to
 - a. plant death.
 - d. the accumulation of storage reserves.
 - b. reproductive growth.
 - c. pollination.

APPLY

1. Under which of the following conditions would pollen from an S_2S_5 plant successfully pollinate an S_1S_5 flower?
 - a. Using pollen from a carpelate flower to fertilize a staminate flower would be successful.
 - b. If the plants used gametophytic self-incompatibility, half of the pollen would be successful.
 - c. If the plants used sporophytic self-incompatibility, half of the pollen would be successful.
 - d. Pollen from an S_2S_5 plant can never pollinate an S_1S_5 flower.
2. Your roommate is taking biology with you this semester and thinks he understands short- and long-day plants. He purchases one plant of each type and decides to see the difference himself by first trying to cause the short-day plant to flower. He places both plants under the same conditions and exposes each to a regimen of 10-hr days, expecting that the short-day plant will flower, and the long-day plant will not. You play a trick on your roommate and reverse the outcome. Specifically, what did you have to do?
 - a. Lengthen the time each is exposed to light
 - b. Shorten the time each is exposed to light
 - c. Quickly expose the plants to light during the middle of the night
 - d. None of the above
3. In Iowa, a company called Team Corn works to ensure that fields of seed corn outcross so that hybrid vigor can be maintained. They do this by removing the staminate (that is, pollen-producing) flowers from the corn plants. In an attempt to put Team Corn out of business, you would like to develop genetically engineered corn plants that
 - a. contain Z genes to prevent germination of pollen on the stigmatic surface.

- b. contain S genes to stop pollen tube growth during self-fertilization.
- c. express B -type homeotic genes throughout developing flowers.
- d. express A -type homeotic genes throughout developing flowers.
4. Monoecious plants such as corn have either staminate or carpelate flowers. Knowing what you do about the molecular mechanisms of floral development, which of the following might explain the development of single-sex flowers?
 - a. Expression of B -type genes in the presumptive carpel whorl will generate staminate flowers.
 - b. Loss of A -type genes in the presumptive petal whorl will allow C -type and B -type genes to produce stamens instead of petals in that whorl.
 - c. Restricting B -type gene expression to the presumptive petal whorl will generate carpelate flowers.
 - d. All of these are correct.
5. One of the most notable differences between gamete formation in most animals and gamete formation in plants is that
 - a. plants produce gametes in somatic tissue, whereas animals produce gametes in germ tissue.
 - b. plants produce gametes by mitosis, whereas animals produce gametes by meiosis.
 - c. plants produce only one of each gamete, but animals produce many gametes.
 - d. plants produce gametes that are diploid, but animals produce gametes that are haploid.

SYNTHESIZE

- ◆ 1. A commercial greenhouse in a remote location produces poinsettias. However, after a highway is built near the greenhouse, the poinsettias fail to flower. Explain what has happened.
- 2. If you live in a north temperate region, explain why it is advantageous to grow spinach for your salad in early spring rather than during the summer.
- 3. In wild columbine, flower morphology encourages cross-pollination. However, during the middle of the receptive period of the stigma, self-pollination can occur if the flower was not previously pollinated. If cross-pollination occurs after self-pollination, then that pollen reaches the base of the style before the self-pollen. Discuss the adaptive significance of this reproduction strategy.
- 4. In most parts of the world, commercial potato crops are produced asexually by planting tubers. However, in some regions of the world, such as Southeast Asia and the Andes, some potatoes are grown from true seeds. Discuss the advantages and disadvantages of growing potatoes from true seed.

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Chapter **43**

The Animal Body and Principles of Regulation

Chapter Outline

- 43.1** Organization of the Vertebrate Body
- 43.2** Epithelial Tissue
- 43.3** Connective Tissue
- 43.4** Muscle Tissue
- 43.5** Nerve Tissue
- 43.6** Overview of Vertebrate Organ Systems
- 43.7** Homeostasis
- 43.8** Regulating Body Temperature



Introduction

When people think of animals, they may think of pet dogs and cats, the animals in a zoo, on a farm, in an aquarium, or wild animals living outdoors. When thinking about the diversity of animals, people may picture the differences between the predatory lions and tigers and the herbivorous deer and antelope, or between a dangerous shark and a playful dolphin. Despite the differences among these animals, they are all vertebrates. All vertebrates share the same basic body plan, with similar tissues and organs that operate in much the same way. The micrograph shows a portion of the duodenum, part of the digestive system, which is made up of multiple types of tissues. In this chapter, we begin a detailed consideration of the biology of the vertebrates and the fascinating structure and function of their bodies. We conclude this chapter by exploring the principles involved in regulation and control of complex functional systems.

43.1 Organization of the Vertebrate Body

Learning Outcomes

1. List the levels of organization in the vertebrate body.
2. Identify the tissue types found in vertebrates.
3. Describe how body cavities are organized.

The vertebrate body has four levels of organization: (1) cells, (2) tissues, (3) organs, and (4) organ systems. Like those of all animals, the bodies of vertebrates are composed of different cell types. Depending on the group, between 50 and several hundred different kinds of cells contribute to the adult vertebrate body. Humans have 210 different types of cells.

Tissues are groups of cells of a single type and function

Groups of cells that are similar in structure and function are organized into *tissues*. Early in development, the cells of the growing embryo differentiate into the three fundamental embryonic tissues, called **germ layers**. From the innermost to the outermost layers, these are the *endoderm*, *mesoderm*, and *ectoderm*. Each germ layer, in turn, differentiates into the scores of different cell types and tissues that are characteristic of the vertebrate body.

In adult vertebrates, there are four principal kinds of tissues, or **primary tissues**: (1) **epithelial**, (2) **connective**, (3) **muscle**, and (4) **nerve tissue**. Each type is discussed in separate sections of this chapter.

Organs and organ systems provide specialized functions

Organs are body structures composed of several different types of tissues that form a structural and functional unit (figure 43.1). One example is the heart, which contains cardiac muscle, connective tissue, and epithelial tissue. Nerve tissue connects the brain and spinal cord to the heart and helps regulate the heartbeat.

An **organ system** is a group of organs that cooperate to perform the major activities of the body. For example, the circulatory system is composed of the heart and blood vessels (arteries, capillaries, and veins) (see chapter 50). These organs cooperate in the transport of blood and help distribute substances about the body. The vertebrate body contains 11 principal organ systems.

The general body plan of vertebrates is a tube within a tube, with internal support

The bodies of all vertebrates have the same general architecture. The body plan is essentially a tube suspended within a tube. The inner tube is the digestive tract, a long tube that travels from the mouth to the anus. An internal skeleton made of jointed bones or cartilage that grows as the body grows supports the outer tube, which forms the main vertebrate body. The outermost layer of the vertebrate body is the integument, or skin, and its many accessory organs and parts—hair, feathers, scales, and sweat glands.

Vertebrates have both dorsal and ventral body cavities

Inside the main vertebrate body are two identifiable cavities. The *dorsal body cavity* forms within a bony skull and a column of bones, the vertebrae. The skull surrounds the brain, and within the stacked vertebrae is a channel that contains the spinal cord.

The *ventral body cavity* is much larger and extends anteriorly from the area bounded by the rib cage and vertebral column posteriorly to the area contained within the ventral body muscles (the abdominals) and the pelvic girdle. In mammals, a sheet of muscle, the diaphragm, breaks the ventral body cavity anteriorly into the *thoracic cavity*, which contains the heart and lungs, and posteriorly into the *abdominopelvic cavity*, which contains many organs, including the stomach, intestines, liver, kidneys, and urinary bladder (figure 43.2a).

Recall from the discussion of the animal body plan in chapter 32 that a coelom is a fluid-filled body cavity completely formed within the embryonic mesoderm layer of some animals

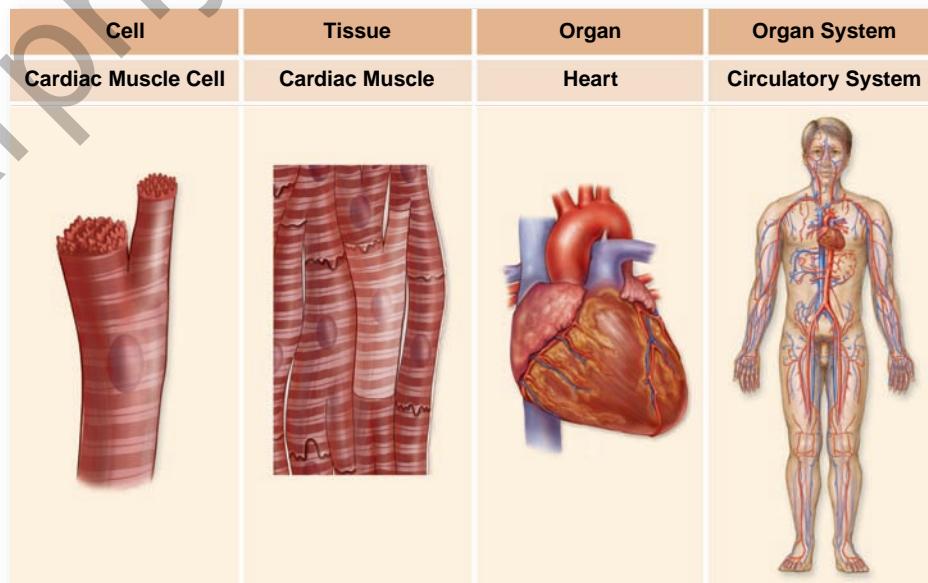


Figure 43.1 Levels of organization within the body. Similar cell types operate together and form tissues. Tissues functioning together form organs such as the heart, which is composed primarily of cardiac muscle with a lining of epithelial tissue. An organ system consists of several organs working together to carry out a function for the body. An example of an organ system is the circulatory system, which consists of the heart, blood vessels, and blood.

(vertebrates included). The coelom is present in vertebrates, but compared to invertebrates it is constricted, folded, and subdivided. The mesodermal layer that lines the coelom extends from the body wall to envelop and suspend several organs within the ventral body cavity (figure 43.2b). In the abdominopelvic cavity, the coelomic space is the **peritoneal cavity**.

In the thoracic cavity, the heart and lungs invade and greatly constrict the coelomic space. The thin space within mesodermal layers around the heart is the **pericardial cavity**, and the two thin spaces around the lungs are the **pleural cavities** (figure 43.2b).

Learning Outcomes Review 43.1

The body's cells are organized into tissues, which in turn are organized into organs and organ systems. The main types of tissues in vertebrates are epithelial, connective, muscle, and nerve tissue. The bodies of humans and other mammals contain dorsal and ventral cavities. The ventral cavity is divided by the diaphragm into thoracic and abdominopelvic cavities. The adult coelom subdivides into the peritoneal, pericardial, and pleural cavities.

- Can an organ be made of more than one tissue?

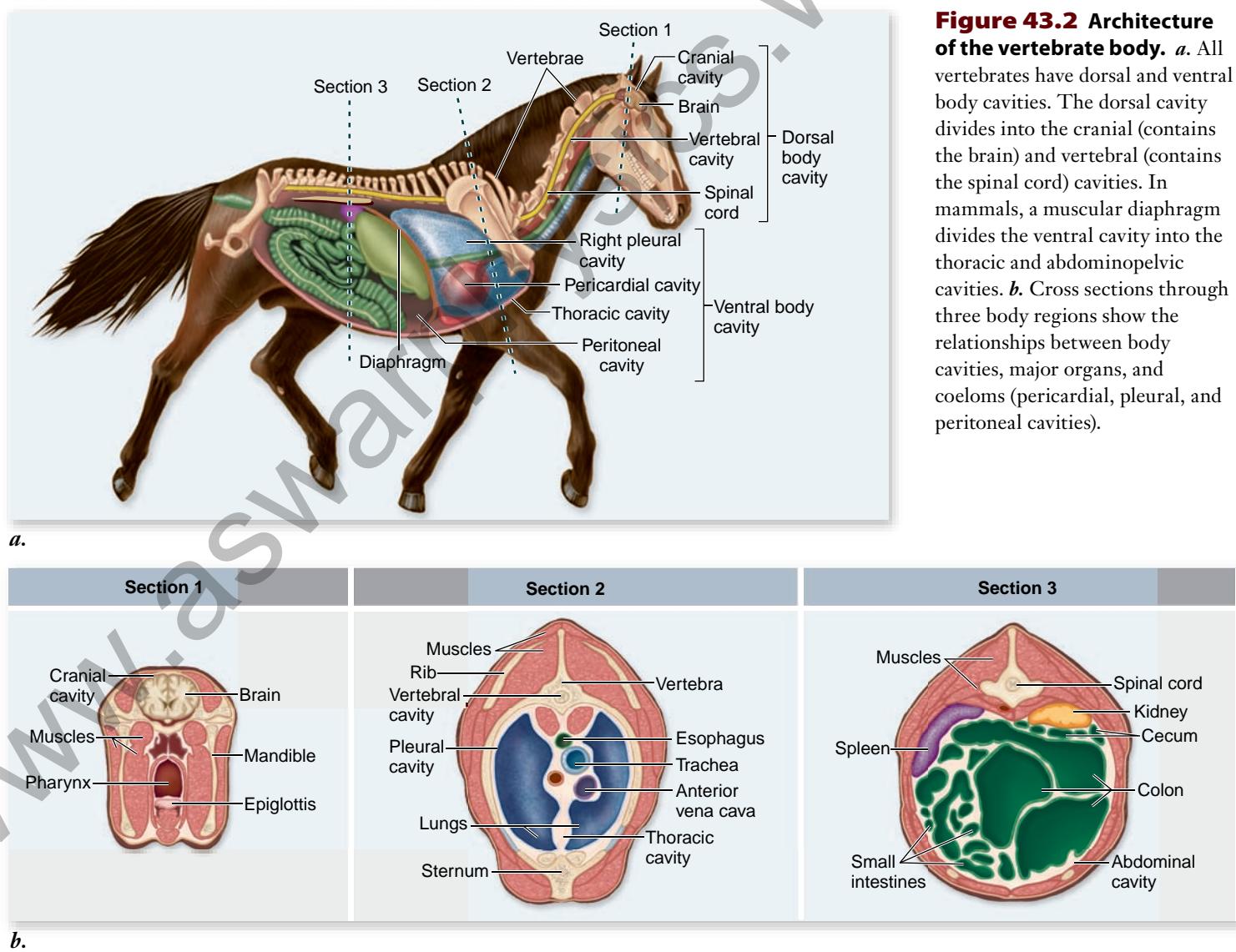
43.2 Epithelial Tissue

Learning Outcomes

1. Describe the structure and function of an epithelium.
2. Identify the cell types found in an epithelial membrane.
3. Explain the structure and function of different epithelia.

An epithelial membrane, or **epithelium** (plural, *epithelia*), covers every surface of the vertebrate body. Epithelial membranes can come from any of the three germ layers. For example, the epidermis, derived from ectoderm, constitutes the outer portion of the skin. An epithelium derived from endoderm lines the inner surface of the digestive tract, and the inner surfaces of blood vessels derive from mesoderm. Some epithelia change in the course of embryonic development into glands, which are specialized for secretion.

Figure 43.2 Architecture of the vertebrate body. *a.* All vertebrates have dorsal and ventral body cavities. The dorsal cavity divides into the cranial (contains the brain) and vertebral (contains the spinal cord) cavities. In mammals, a muscular diaphragm divides the ventral cavity into the thoracic and abdominopelvic cavities. *b.* Cross sections through three body regions show the relationships between body cavities, major organs, and coeloms (pericardial, pleural, and peritoneal cavities).



b.

Epithelium forms a barrier

Because epithelial membranes cover all body surfaces, a substance must pass through an epithelium in order to enter or leave the body. Epithelial membranes thus provide a barrier that can impede the passage of some substances while facilitating the passage of others. For land-dwelling vertebrates, the relative impermeability of the surface epithelium (the epidermis) to water offers essential protection from dehydration and from airborne pathogens. The epithelial lining of the digestive tract, in contrast, must allow selective entry of the products of digestion while providing a barrier to toxic substances. The epithelium of the lungs must allow for the rapid diffusion of gases into and out of the blood.

A characteristic of all epithelia is that the cells are tightly bound together, with very little space between them. Nutrients and oxygen must diffuse to the epithelial cells from blood vessels supplying underlying connective tissues. This places a limit on the thickness of epithelial membranes; most are only one or a few cell layers thick.

Epithelial regeneration

Epithelium possesses remarkable regenerative powers, constantly replacing its cells throughout the life of the animal. For example, the liver, a gland formed from epithelial tissue, can readily regenerate, even after surgical removal of substantial portions. The epidermis renews every two weeks, and the epithelium inside the stomach is completely replaced every two to three days. This ability to regenerate is useful in a surface tissue because it constantly renews the surface and also allows quick replacement of the protective layer should damage or injury occur.

Structure of epithelial tissues

Epithelial tissues attach to underlying connective tissues by a fibrous membrane. The secured side of the epithelium is called the *basal surface*, and the free side is the *apical surface*. This difference gives epithelial tissues an inherent polarity, which is often important in the function of the tissue. For example, proteins stud the basal surfaces of some epithelial tissues in the kidney tubules; these proteins actively transport Na^+ into the intercellular spaces, creating an osmotic gradient that helps return water to the blood (see chapter 51).

Epithelial types reflect their function

The two general classes of epithelial membranes are termed *simple* (single layer of cells) and *stratified* (multiple layers of cells). These classes are further subdivided into squamous, cuboidal, and columnar, based on the shape of the cells (table 43.1). *Squamous cells* are flat, *cuboidal cells* are about as wide as they are tall, and *columnar cells* are taller than they are wide.

Simple epithelium

As mentioned, *simple epithelial membranes* are one cell thick. A simple squamous epithelium is composed of squamous epithelial cells that have a flattened shape when viewed in cross section. Examples of such membranes are those that line the lungs and blood capillaries, where the thin, delicate nature of these membranes permits the rapid movement of molecules (such as the diffusion of gases).

A simple cuboidal epithelium lines kidney tubules and several glands. In the case of glands, these cells are specialized for secretion.

A simple columnar epithelium lines the airways of the respiratory tract and the inside of most of the gastrointestinal tract, among other locations. Interspersed among the columnar epithelial cells of mucous membranes are numerous *goblet cells*, which are specialized to secrete mucus. The columnar epithelial cells of the respiratory airways contain cilia on their apical surface (the surface facing the lumen, or cavity), which move mucus and dust particles toward the throat. In the small intestine, the apical surface of the columnar epithelial cells forms fingerlike projections called *microvilli*, which increase the surface area for the absorption of food.

The expanded size of both cuboidal and columnar cells accommodates the added intracellular machinery needed for production of glandular secretions, active absorption of materials, or both. The glands of vertebrates form from invaginated epithelia. In **exocrine glands**, the connection between the gland and the epithelial membrane remains as a duct. The duct channels the product of the gland to the surface of the epithelial membrane, and thus to the external environment (or to an interior compartment that opens to the exterior, such as the digestive tract). A few examples of exocrine glands include sweat and sebaceous (oil) glands as well as the salivary glands. **Endocrine glands** are ductless glands; their connections with the epithelium from which they are derived has been lost during development. Therefore, their secretions (hormones) do not channel onto an epithelial membrane. Instead, hormones enter blood capillaries and circulate through the body. Endocrine glands are covered in more detail in chapter 46.

Stratified epithelium

Stratified epithelial membranes are two to several cell layers thick and are named according to the features of their apical cell layers. For example, the epidermis is a *stratified squamous epithelium*; its properties are discussed in chapter 52. In terrestrial vertebrates, the epidermis is further characterized as a *keratinized epithelium* because its upper layer consists of dead squamous cells and is filled with a water-resistant protein called *keratin*.

The deposition of keratin in the skin increases in response to repeated abrasion, producing calluses. The water-resistant property of keratin is evident when comparing the skin of the face to the red portion of the lips, which can easily become dried and chapped. Lips are covered by a nonkeratinized, stratified squamous epithelium.

Learning Outcomes Review 43.2

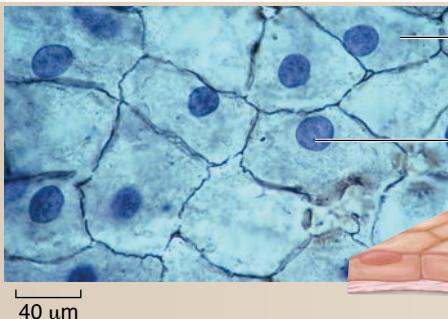
Epithelial tissues generally form barriers and include membranes that cover all body surfaces and glands. An epidermis has a basal surface that attaches to an underlying connective tissue and an apical surface that is free. Some epithelia are specialized for protection, whereas those that cover the surfaces of hollow organs may be specialized for transport and secretion. Simple epithelium has a single cell layer and may be classified as squamous, cuboidal, columnar, or pseudostratified; stratified epithelium is primarily squamous.

- How does the epithelium in a gland function differently from that in the lining of your gut?

TABLE 43.1

Epithelial Tissue

SIMPLE EPITHELIUM



Simple squamous epithelial cell

Nucleus

**Squamous***Typical Location*

Lining of lungs, capillary walls, and blood vessels

Function

Cells form thin layer across which diffusion can readily occur

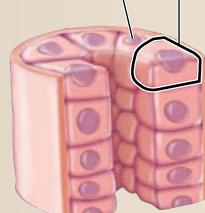
Characteristic Cell Types

Epithelial cells



Cuboidal epithelial cell

Nucleus

**Cuboidal***Typical Location*

Lining of some glands and kidney tubules; covering of ovaries

Function

Cells rich in specific transport channels; functions in secretion and absorption

Characteristic Cell Types

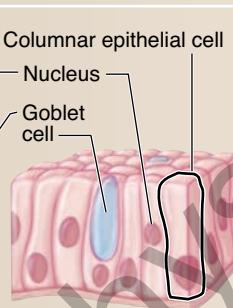
Gland cells



Columnar epithelial cell

Nucleus

Goblet cell

**Columnar***Typical Location*

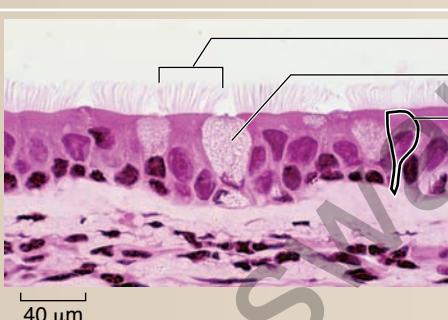
Surface lining of stomach, intestines, and parts of respiratory tract

Function

Thicker cell layer; provides protection and functions in secretion and absorption

Characteristic Cell Types

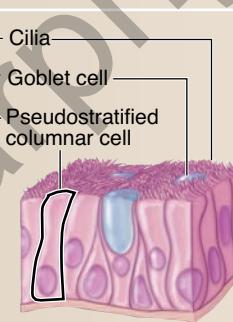
Epithelial cells



Cilia

Goblet cell

Pseudostratified columnar cell

**Pseudostratified Columnar***Typical Location*

Lining of parts of the respiratory tract

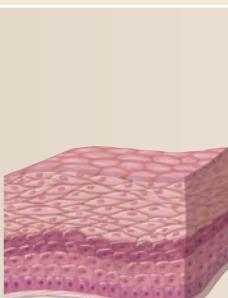
Function

Secretes mucus; dense with cilia that aid in movement of mucus; provides protection

Characteristic Cell Types

Gland cells; ciliated epithelial cells

STRATIFIED EPITHELIUM

**Squamous***Typical Location*

Outer layer of skin; lining of mouth

Function

Tough layer of cells; provides protection

Characteristic Cell Types

Epithelial cells