

39

Plant Responses to Internal and External Signals



▲ **Figure 39.1** Can flowers tell you the time of day?

KEY CONCEPTS

- 39.1** Signal transduction pathways link signal reception to response
- 39.2** Plant hormones help coordinate growth, development, and responses to stimuli
- 39.3** Responses to light are critical for plant success
- 39.4** Plants respond to a wide variety of stimuli other than light
- 39.5** Plants respond to attacks by herbivores and pathogens

OVERVIEW

Stimuli and a Stationary Life

Carolus Linnaeus, the father of taxonomy, was a keen naturalist. He noted that each plant species opened and closed its flowers at a characteristic time of the day. Therefore, one could estimate the time of day by observing which species

had open or closed flowers. If the times of opening and closing were arranged in sequence, they could serve as a kind of floral clock, or *horologium florum*, as Linnaeus called it. **Figure 39.1** shows a modern representation as a 12-hour clock face. Why does the timing vary? The time at which flowers open presumably reflects the time when their insect pollinators are most active, just one example of the numerous environmental factors that a plant must sense to compete successfully.

This chapter focuses on the mechanisms by which flowering plants sense and respond to external and internal cues. At the organismal level, plants and animals respond to environmental stimuli by different means. Animals, being mobile, respond mainly by moving toward positive stimuli and away from negative stimuli. In contrast, plants are stationary and generally respond to environmental cues by adjusting their individual patterns of growth and development. For this reason, plants of the same species vary in body form much more than do animals of the same species. But just because plants do not move in the same manner as animals does not mean that plants lack sensitivity. Before a plant can initiate alterations to growth patterns in response to environmental signals, it must first detect the change in its environment. As we will see, the molecular processes underlying plant responses are as complex as those used by animal cells and are often homologous to them.

CONCEPT 39.1

Signal transduction pathways link signal reception to response

Plants receive specific signals and respond to them in ways that enhance survival and reproductive success. Consider, for example, a forgotten potato in the back corner of a kitchen cupboard. This modified underground stem, or tuber, has sprouted shoots from its “eyes” (axillary buds). These shoots, however, scarcely resemble those of a typical plant. Instead of sturdy stems and broad green leaves, this plant has ghostly pale stems and unexpanded leaves, as well as short, stubby roots (**Figure 39.2a**). These morphological adaptations for growing in darkness, collectively referred to as **etiolation**, make sense if we consider that a young potato plant in nature usually encounters continuous darkness when sprouting underground. Under these circumstances, expanded leaves would be a hindrance to soil penetration and would be damaged as the shoots pushed through the soil. Because the leaves are unexpanded and underground, there is little evaporative loss of water and little requirement for an extensive root system to replace the water lost by transpiration. Moreover, the energy expended in producing



(a) Before exposure to light. A dark-grown potato has tall, spindly stems and nonexpanded leaves—morphological adaptations that enable the shoots to penetrate the soil. The roots are short, but there is little need for water absorption because little water is lost by the shoots.



(b) After a week's exposure to natural daylight. The potato plant begins to resemble a typical plant with broad green leaves, short sturdy stems, and long roots. This transformation begins with the reception of light by a specific pigment, phytochrome.

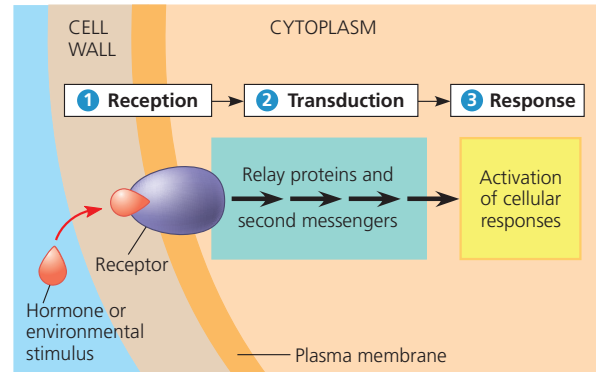
▲ **Figure 39.2 Light-induced de-etiolation (greening) of dark-grown potatoes.**

green chlorophyll would be wasted because there is no light for photosynthesis. Instead, a potato plant growing in the dark allocates as much energy as possible to elongating its stems. This adaptation enables the shoots to break ground before the nutrient reserves in the tuber are exhausted. The etiolation response is one example of how a plant's morphology and physiology are tuned to its surroundings by complex interactions between environmental and internal signals.

When a shoot reaches light, the plant undergoes profound changes, collectively called **de-etiolation** (informally known as greening). Stem elongation slows; leaves expand; roots elongate; and the shoot produces chlorophyll. In short, it begins to resemble a typical plant (**Figure 39.2b**). In this section, we will use this de-etiolation response as an example of how a plant cell's reception of a signal—in this case, light—is transduced into a response (greening). Along the way, we will explore how studies of mutants provide insights into the molecular details of the stages of cell signal processing: reception, transduction, and response (**Figure 39.3**).

Reception

Signals are first detected by receptors, proteins that undergo changes in shape in response to a specific stimulus. The receptor involved in de-etiolation is a type of *phytochrome*, a member of a class of photoreceptors that we'll discuss more fully later in the chapter. Unlike most receptors, which are built into the plasma membrane, the type of phytochrome that functions in de-etiolation is located in the cytoplasm. Researchers demonstrated the requirement for phytochrome in



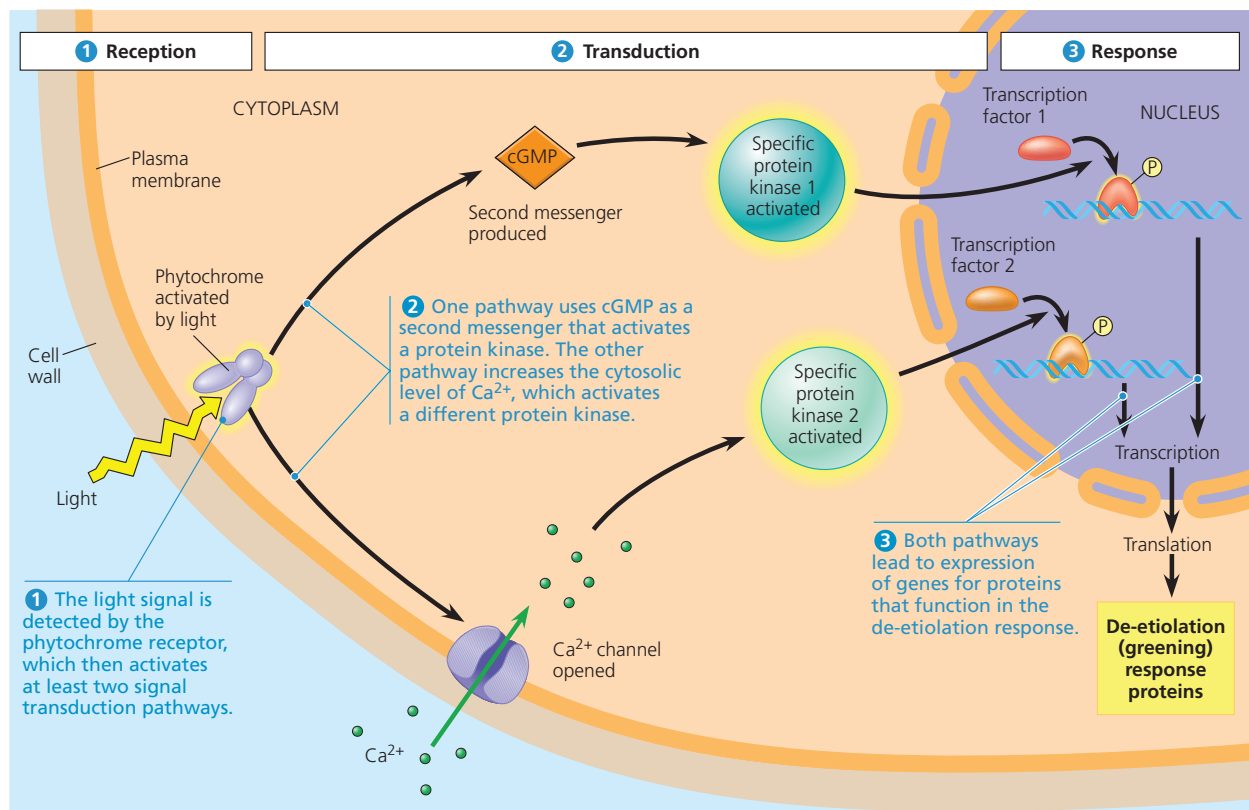
▲ **Figure 39.3 Review of a general model for signal transduction pathways.** As discussed in Chapter 11, a hormone or other kind of stimulus interacting with a specific receptor protein can trigger the sequential activation of relay proteins and also the production of second messengers that participate in the pathway. The signal is passed along, ultimately bringing about cellular responses. In this diagram, the receptor is on the surface of the target cell; in other cases, the stimulus interacts with receptors inside the cell.

de-etiolation through studies of the tomato, a close relative of the potato. The *aurea* mutant of tomato, which has reduced levels of phytochrome, greens less than wild-type tomatoes when exposed to light. (*Aurea* is Latin for “gold.” In the absence of chlorophyll, the yellow and orange accessory pigments called carotenoids are more obvious.) Researchers produced a normal de-etiolation response in individual *aurea* leaf cells by injecting phytochrome from other plants and then exposing the cells to light. Such experiments indicated that phytochrome functions in light detection during de-etiolation.

Transduction

Receptors can be sensitive to very weak environmental or chemical signals. Some de-etiolation responses are triggered by extremely low levels of light, in certain cases as little as the equivalent of a few seconds of moonlight. The transduction of these extremely weak signals involves **second messengers**—small molecules and ions in the cell that amplify the signal and transfer it from the receptor to other proteins that carry out the response (**Figure 39.4**). In Chapter 11, we discussed several kinds of second messengers (see Figures 11.12 and 11.14). Here, we examine the particular roles of two types of second messengers in de-etiolation: calcium ions (Ca^{2+}) and cyclic GMP (cGMP).

Changes in cytosolic Ca^{2+} levels play an important role in phytochrome signal transduction. The concentration of cytosolic Ca^{2+} is generally very low (about 10^{-7} M), but phytochrome activation leads to the opening of Ca^{2+} channels and a transient 100-fold increase in cytosolic



▲ **Figure 39.4** An example of signal transduction in plants: the role of phytochrome in the de-etiolation (greening) response.

MAKE CONNECTIONS Which panel in Figure 11.18 (p. 222) best exemplifies the phytochrome-dependent signal transduction pathway during de-etiolation? Explain.

Ca^{2+} levels. In response to light, phytochrome undergoes a change in shape that leads to the activation of guanylyl cyclase, an enzyme that produces the second messenger cyclic GMP. Both Ca^{2+} and cGMP must be produced for a complete de-etiolation response. The injection of cGMP into *aurea* tomato leaf cells, for example, induces only a partial de-etiolation response.

Response

Ultimately, second messengers regulate one or more cellular activities. In most cases, these responses involve the increased activity of particular enzymes. There are two main mechanisms by which a signaling pathway can enhance an enzymatic step in a biochemical pathway: post-translational modification and transcriptional regulation. Post-translational modification activates preexisting enzymes. Transcriptional regulation increases or decreases the synthesis of mRNA encoding a specific enzyme.

Post-Translational Modification of Preexisting Proteins

In most signal transduction pathways, preexisting proteins are modified by the phosphorylation of specific amino acids, which alters the protein's hydrophobicity and activity. Many second messengers, including cGMP and Ca^{2+} , activate protein kinases directly. Often, one protein kinase will phosphorylate another protein kinase, which then phosphorylates another, and so on (see Figure 11.10). Such kinase cascades may link initial stimuli to responses at the level of gene expression, usually via the phosphorylation of transcription factors. As we'll discuss on the next page, many signal transduction pathways ultimately regulate the synthesis of new proteins by turning specific genes on or off.

Signal transduction pathways must also have a means for turning off when the initial signal is no longer present, such as when a sprouting potato is put back into the cupboard. Protein phosphatases, which are enzymes that dephosphorylate specific proteins, are important in these "switch-off"

processes. At any particular moment, a cell's functioning depends on the balance of activity of many types of protein kinases and protein phosphatases.

Transcriptional Regulation

As discussed in Chapter 18, the proteins we call *specific transcription factors* bind to specific regions of DNA and control the transcription of specific genes (see Figure 18.9). In the case of phytochrome-induced de-etiolation, several such transcription factors are activated by phosphorylation in response to the appropriate light conditions. The activation of some of these transcription factors depends on their phosphorylation by protein kinases activated by cGMP or Ca^{2+} .

The mechanism by which a signal promotes developmental changes may depend on transcription factors that are activators (which *increase* transcription of specific genes) or repressors (which *decrease* transcription) or both. For example, some *Arabidopsis* mutants, except for their pale color, have a light-grown morphology when grown in the dark; they have expanded leaves and short, sturdy stems but are not green because the final step in chlorophyll production requires light directly. These mutants have defects in a repressor that normally inhibits the expression of other genes that are activated by light. When the repressor is eliminated by mutation, the pathway that is normally blocked proceeds. Thus, these mutants appear to have been grown in the light, except for their pale color.

De-Etiolation ("Greening") Proteins

What types of proteins are either activated by phosphorylation or newly transcribed during the de-etiolation process? Many are enzymes that function in photosynthesis directly; others are enzymes involved in supplying the chemical precursors necessary for chlorophyll production; still others affect the levels of plant hormones that regulate growth. For example, the levels of auxin and brassinosteroids, hormones that enhance stem elongation, decrease following the activation of phytochrome. That decrease explains the slowing of stem elongation that accompanies de-etiolation.

We have discussed the signal transduction involved in the de-etiolation response of a potato plant in some detail to give you a sense of the complexity of biochemical changes that underlie this one process. Every plant hormone and every environmental stimulus triggers one or more signal transduction pathways of comparable complexity. As in the studies on the *aurea* mutant tomato, the isolation of mutants (a genetic approach) and techniques of molecular biology are helping researchers identify these various pathways. But this recent research builds on a long history of careful physiological and biochemical investigations

into how plants work. As you will read in the next section, classic experiments provided the first clues that transported signaling molecules called hormones are internal regulators of plant growth.

CONCEPT CHECK 39.1

1. What are the morphological differences between dark- and light-grown plants? Explain how etiolation helps a seedling compete successfully.
2. Cycloheximide is a drug that inhibits protein synthesis. Predict what effect cycloheximide would have on de-etiolation.
3. **WHAT IF?** The sexual dysfunction drug Viagra inhibits an enzyme that breaks down cyclic GMP. If tomato leaf cells have a similar enzyme, would applying Viagra to these cells cause a normal de-etiolation of *aurea* mutant tomato leaves?

For suggested answers, see Appendix A.

CONCEPT 39.2

Plant hormones help coordinate growth, development, and responses to stimuli

A **hormone**, in the original meaning of the term, is a signaling molecule that is produced in tiny amounts by one part of an organism's body and transported to other parts, where it binds to a specific receptor and triggers responses in target cells and tissues. In animals, hormones are usually transported through the circulatory system, a criterion often included in definitions of the term.

The hormone concept originated from studies of animals and was adopted by plant physiologists in the early 1900s. Many modern plant biologists, however, argue that it is too limiting to describe plant physiological processes using the narrow definitions established by animal physiologists. For example, plants don't have circulating blood to transport hormone-like signaling molecules. Moreover, some signaling molecules that are considered plant hormones act only locally. Finally, there are some signaling molecules in plants, such as sucrose, that typically occur in plants at concentrations that are hundreds of thousands times greater than a typical hormone. Nevertheless, they are transported through plants and activate signal transduction pathways that greatly alter the functioning of plants in a manner similar to a hormone. Thus, many plant biologists prefer the broader term *plant growth regulator* to describe organic compounds, either natural or synthetic, that modify or control one or more specific physiological processes within a plant.

At this point in time, the terms *plant hormone* and *plant growth regulator* are used about equally, but for historical continuity we will use the term *plant hormone* and adhere to the criterion that plant hormones are active at very low concentrations.

Virtually every aspect of plant growth and development is under hormonal control to some degree. A single hormone can regulate an amazingly diverse array of cellular and developmental processes. Conversely, multiple hormones can influence a single process.

The Discovery of Plant Hormones

The idea that chemical messengers exist in plants emerged from a series of classic experiments on how stems respond to light. As you know, the shoot of a houseplant on a windowsill grows toward light. Any growth response that results in plant organs curving toward or away from stimuli is called a **tropism** (from the Greek *tropos*, turn). The growth of a shoot toward light or away from it is called **phototropism**; the former is positive phototropism, and the latter is negative phototropism.

In natural ecosystems where plants may be crowded, phototropism directs shoot growth toward the sunlight that powers photosynthesis. This response results from a differential growth of cells on opposite sides of the shoot; the cells on the darker side elongate faster than the cells on the brighter side.

Charles Darwin and his son Francis conducted some of the earliest experiments on phototropism in the late 1800s (Figure 39.5). They observed that a grass seedling ensheathed in its coleoptile (see Figure 38.9b) could bend toward light only if the tip of the coleoptile was present. If the tip was removed, the coleoptile did not curve. The seedling also failed to grow toward light if the tip was covered with an opaque cap; but neither a transparent cap over the tip nor an opaque shield placed below the coleoptile tip prevented the phototropic response. It was the tip of the coleoptile, the Darwins concluded, that was responsible for sensing light. However, they noted that the differential growth response that led to curvature of the coleoptile occurred some distance below the tip. The Darwins postulated that some signal was transmitted downward from the tip to the elongating region of the coleoptile. A few decades later, the Danish scientist Peter Boysen-Jensen demonstrated that the signal was a mobile chemical substance. He separated the tip from the remainder of the coleoptile by a cube of gelatin, which prevented cellular contact but allowed chemicals to pass through. These seedlings responded normally, bending toward light. However, if the tip was experimentally separated from the lower coleoptile by an impermeable barrier, such as the mineral mica, no phototropic response occurred.

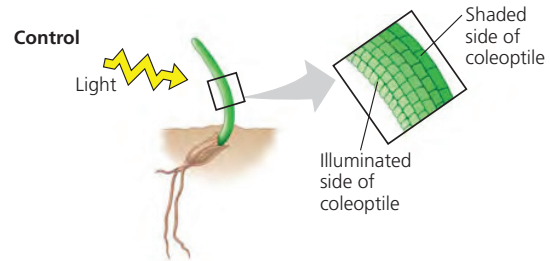
▼ Figure 39.5

INQUIRY

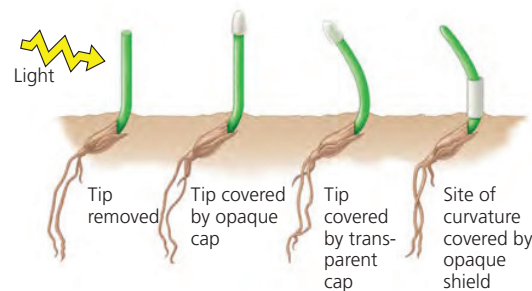
What part of a grass coleoptile senses light, and how is the signal transmitted?

EXPERIMENT In 1880, Charles and Francis Darwin removed and covered parts of grass coleoptiles to determine what part senses light. In 1913, Peter Boysen-Jensen separated coleoptiles with different materials to determine how the signal for phototropism is transmitted.

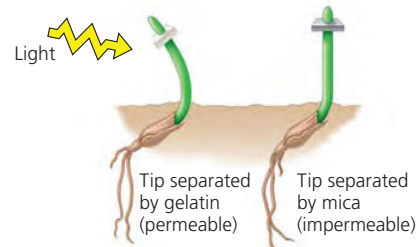
RESULTS



Darwin and Darwin: Phototropism occurs only when the tip is illuminated.



Boysen-Jensen: Phototropism occurs when the tip is separated by a permeable barrier but not an impermeable barrier.



CONCLUSION The Darwins' experiment suggested that only the tip of the coleoptile senses light. The phototropic bending, however, occurred at a distance from the site of light perception (the tip). Boysen-Jensen's results suggested that the signal for the bending is a light-activated mobile chemical.

SOURCE C. R. Darwin, *The power of movement in plants*, John Murray, London (1880). P. Boysen-Jensen, *Concerning the performance of phototropic stimuli on the Avena coleoptile*, *Berichte der Deutschen Botanischen Gesellschaft (Reports of the German Botanical Society)* 31:559–566 (1913).

WHAT IF? How could you experimentally determine which colors of light cause the most phototropic bending?

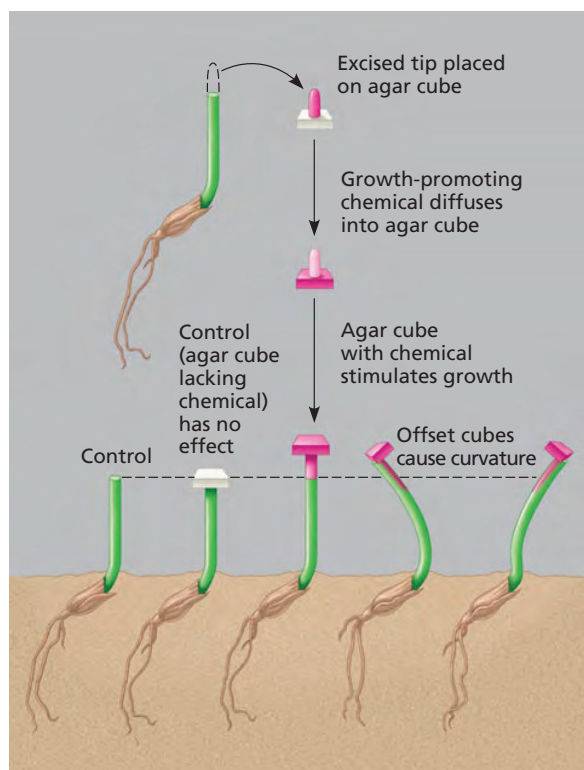
▼ Figure 39.6

INQUIRY

Does asymmetrical distribution of a growth-promoting chemical cause a coleoptile to grow toward the light?

EXPERIMENT In 1926, Frits Went's experiment identified how a growth-promoting chemical causes a coleoptile to grow toward light. He placed coleoptiles in the dark and removed their tips, putting some tips on agar cubes that he predicted would absorb the growth-promoting chemical. On a control coleoptile, he placed a cube that lacked the chemical. On others, he placed cubes containing the chemical, either centered on top of the coleoptile to distribute the chemical evenly or offset to increase the concentration on one side.

RESULTS The coleoptile grew straight if the growth-promoting chemical was distributed evenly. If the chemical was distributed unevenly, the coleoptile curved away from the side with the cube, as if growing toward light, even though it was grown in the dark.



CONCLUSION Went concluded that a coleoptile curves toward light because its dark side has a higher concentration of the growth-promoting chemical, which he named auxin.

SOURCE F. Went, A growth substance and growth, *Recueils des Travaux Botaniques Néerlandais* (Collections of Dutch Botanical Works) 25:1–116 (1928).

See the related Experimental Inquiry Tutorial in MasteringBiology.

WHAT IF? Triiodobenzoic acid (TIBA) inhibits auxin transport. If a tiny agar bead containing TIBA were placed off center on the tip of an intact coleoptile, which way would the coleoptile bend: toward the side with the bead or away from it? Explain.

In 1926, Frits Went, a Dutch graduate student, extracted the chemical messenger for phototropism by modifying the experiments of Boysen-Jensen (Figure 39.6). Went removed the coleoptile tip and placed it on a cube of agar, a gelatinous material. The chemical messenger from the tip, Went reasoned, should diffuse into the agar, and the agar block should then be able to substitute for the coleoptile tip. Went placed the agar blocks on decapitated coleoptiles that were kept in the dark. A block that was centered on top of the coleoptile caused the stem to grow straight upward. However, when the block was placed off center, the coleoptile began to bend away from the side with the agar block, as though growing toward light. Went concluded that the agar block contained a chemical produced in the coleoptile tip, that this chemical stimulated growth as it passed down the coleoptile, and that a coleoptile curved toward light because of a higher concentration of the growth-promoting chemical on the darker side of the coleoptile. For this chemical messenger, or hormone, Went chose the name auxin (from the Greek *auxein*, to increase). The major type of auxin was later purified, and its chemical structure was determined to be indoleacetic acid (IAA).

The classic hypothesis for what causes grass coleoptiles to grow toward light, based on the work of the Darwins, Boysen-Jensen, and Went, is that an asymmetrical distribution of auxin moving down from the coleoptile tip causes cells on the darker side to elongate faster than cells on the brighter side. But studies of phototropism in organs other than grass coleoptiles provide less support for this idea. There is no evidence that illumination from one side causes asymmetrical distribution of auxin in stems of sunflowers or other eudicots. There is, however, asymmetrical distribution of certain substances that may act as growth inhibitors, and these substances are more concentrated on the lighted side of a stem.

A Survey of Plant Hormones

The discovery of auxin stimulated the search for other plant hormones. Table 39.1 previews some major classes of plant hormones: auxin, cytokinins, gibberellins, brassinosteroids, abscisic acid, strigolactones, and ethylene. Many molecules in plants that function in defense against pathogens are probably plant hormones as well. (We'll discuss these molecules later in the chapter.)

Plant hormones are produced in very low concentrations, but a tiny amount of hormone can have a profound effect on the growth and development of a plant organ. Signal transduction pathways amplify the hormonal signal and connect it to a cell's specific responses. In general, hormones control plant growth and development by affecting the division, elongation, and differentiation of cells. Some hormones also mediate shorter-term physiological responses of plants to environmental stimuli. Each hormone has multiple effects,

Table 39.1 Overview of Plant Hormones

Hormone	Where Produced or Found in Plant	Major Functions
Auxin (IAA)	Shoot apical meristems and young leaves are the primary sites of auxin synthesis. Root apical meristems also produce auxin, although the root depends on the shoot for much of its auxin. Developing seeds and fruits contain high levels of auxin, but it is unclear whether it is newly synthesized or transported from maternal tissues.	Stimulates stem elongation (low concentration only); promotes the formation of lateral and adventitious roots; regulates development of fruit; enhances apical dominance; functions in phototropism and gravitropism; promotes vascular differentiation; retards leaf abscission.
Cytokinins	These are synthesized primarily in roots and transported to other organs, although there are many minor sites of production as well.	Regulate cell division in shoots and roots; modify apical dominance and promote lateral bud growth; promote movement of nutrients into sink tissues; stimulate seed germination; delay leaf senescence.
Gibberellins	Meristems of apical buds and roots, young leaves, and developing seeds are the primary sites of production.	Stimulate stem elongation, pollen development, pollen tube growth, fruit growth, and seed development and germination; regulate sex determination and the transition from juvenile to adult phases.
Brassinosteroids	These compounds are present in all plant tissues, although different intermediates predominate in different organs. Internally produced brassinosteroids act near the site of synthesis.	Promote cell expansion and cell division in shoots; promote root growth at low concentrations; inhibit root growth at high concentrations; promote xylem differentiation and inhibit phloem differentiation; promote seed germination and pollen tube elongation.
Absciscic acid (ABA)	Almost all plant cells have the ability to synthesize abscisic acid, and its presence has been detected in every major organ and living tissue; may be transported in the phloem or xylem.	Inhibits growth; promotes stomatal closure during drought stress; promotes seed dormancy and inhibits early germination; promotes leaf senescence; promotes desiccation tolerance.
Strigolactones	These carotenoid-derived hormones and extracellular signals are produced in roots in response to low phosphate conditions or high auxin flow from the shoot.	Promote seed germination, control of apical dominance, and the attraction of mycorrhizal fungi to the root.
Ethylene	This gaseous hormone can be produced by most parts of the plant. It is produced in high concentrations during senescence, leaf abscission, and the ripening of some types of fruits. Synthesis is also stimulated by wounding and stress.	Promotes ripening of many types of fruit, leaf abscission, and the triple response in seedlings (inhibition of stem elongation, promotion of lateral expansion, and horizontal growth); enhances the rate of senescence; promotes root and root hair formation; promotes flowering in the pineapple family.

depending on its site of action, its concentration, and the developmental stage of the plant.

Response to a hormone usually depends not so much on the amount of that hormone as on its relative concentration compared with other hormones. It is often the interactions between different hormones, rather than hormones acting in isolation, that control growth and development. These interactions will become apparent in the following survey of hormone function.

Auxin

The term **auxin** is used for any chemical substance that promotes elongation of coleoptiles, although auxins have multiple functions in flowering plants. The major natural auxin in plants is indoleacetic acid (IAA), although several other compounds, including some synthetic ones, have auxin activity.

(Unless mentioned otherwise, we will use the term *auxin* synonymously with IAA.) Although IAA was the first plant hormone to be discovered, much remains to be learned about auxin signal transduction and the regulation of auxin biosynthesis.

Auxin is produced predominantly in shoot tips and is transported from cell to cell down the stem at a rate of about 1 cm/hr. It moves only from tip to base, not in the reverse direction. This unidirectional transport of auxin is called *polar transport*.

Polar transport has nothing to do with gravity; experiments have shown that auxin travels upward when a stem or coleoptile segment is placed upside down. Rather, the polarity of auxin movement is attributable to the polar distribution of auxin transport protein in the cells. Concentrated at the basal end of a cell, the auxin transporters move the

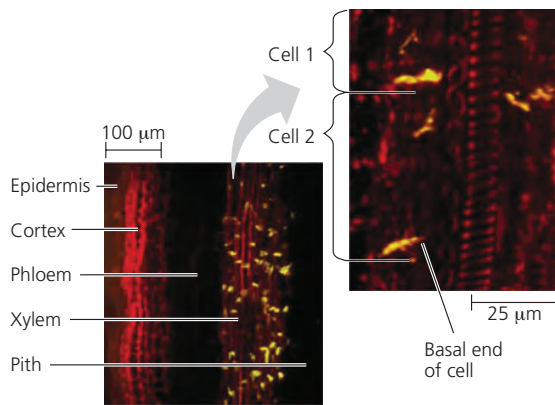
▼ Figure 39.7

INQUIRY

What causes polar movement of auxin from shoot tip to base?

EXPERIMENT To investigate how auxin is transported unidirectionally, Leo Gälweiler and colleagues designed an experiment to identify the location of the auxin transport protein. They used a greenish yellow fluorescent molecule to label antibodies that bind to the auxin transport protein. Then they applied the antibodies to longitudinally sectioned *Arabidopsis* stems.

RESULTS The light micrograph on the left shows that auxin transport proteins are not found in all stem tissues, but only in the xylem parenchyma. In the light micrograph on the right, a higher magnification reveals that these proteins are primarily localized at the basal ends of the cells.



CONCLUSION The results support the hypothesis that concentration of the auxin transport protein at the basal ends of cells mediates the polar transport of auxin.

SOURCE L. Gälweiler et al., Regulation of polar auxin transport by AtPIN1 in *Arabidopsis* vascular tissue, *Science* 282:2226–2230 (1998).

WHAT IF? If auxin transport proteins were equally distributed at both ends of the cells, would polar auxin transport still be possible? Explain.

hormone out of the cell. The auxin can then enter the apical end of the neighboring cell (Figure 39.7). Auxin has a variety of effects, including stimulating cell elongation and regulating plant architecture.

The Role of Auxin in Cell Elongation One of auxin's chief functions is to stimulate elongation of cells within young developing shoots. As auxin from the shoot apex moves down to the region of cell elongation (see Figure 35.16), the hormone stimulates cell growth, probably by binding to a receptor in the plasma membrane. Auxin stimulates growth only over a certain concentration range, from about 10^{-8} to 10^{-4} M. At higher concentrations, auxin may inhibit cell elongation, probably by inducing production of ethylene, a hormone that

generally hinders growth. We will return to this hormonal interaction when we discuss ethylene.

According to a model called the *acid growth hypothesis*, proton pumps play a major role in the growth response of cells to auxin. In a shoot's region of elongation, auxin stimulates the plasma membrane's proton (H^+) pumps. This pumping of H^+ increases the voltage across the membrane (membrane potential) and lowers the pH in the cell wall within minutes (Figure 39.8). Acidification of the wall activates enzymes called **expansins** that break the cross-links (hydrogen bonds) between cellulose microfibrils and other cell wall constituents, loosening the wall's fabric. (Expansins can even weaken the integrity of filter paper made of pure cellulose.) Increasing the membrane potential enhances ion uptake into the cell, which causes osmotic uptake of water and increased turgor. Increased turgor and increased cell wall plasticity enable the cell to elongate.

Auxin also rapidly alters gene expression, causing cells in the region of elongation to produce new proteins within minutes. Some of these proteins are short-lived transcription factors that repress or activate the expression of other genes. For sustained growth after this initial spurt, cells must make more cytoplasm and wall material. Auxin also stimulates this sustained growth response.

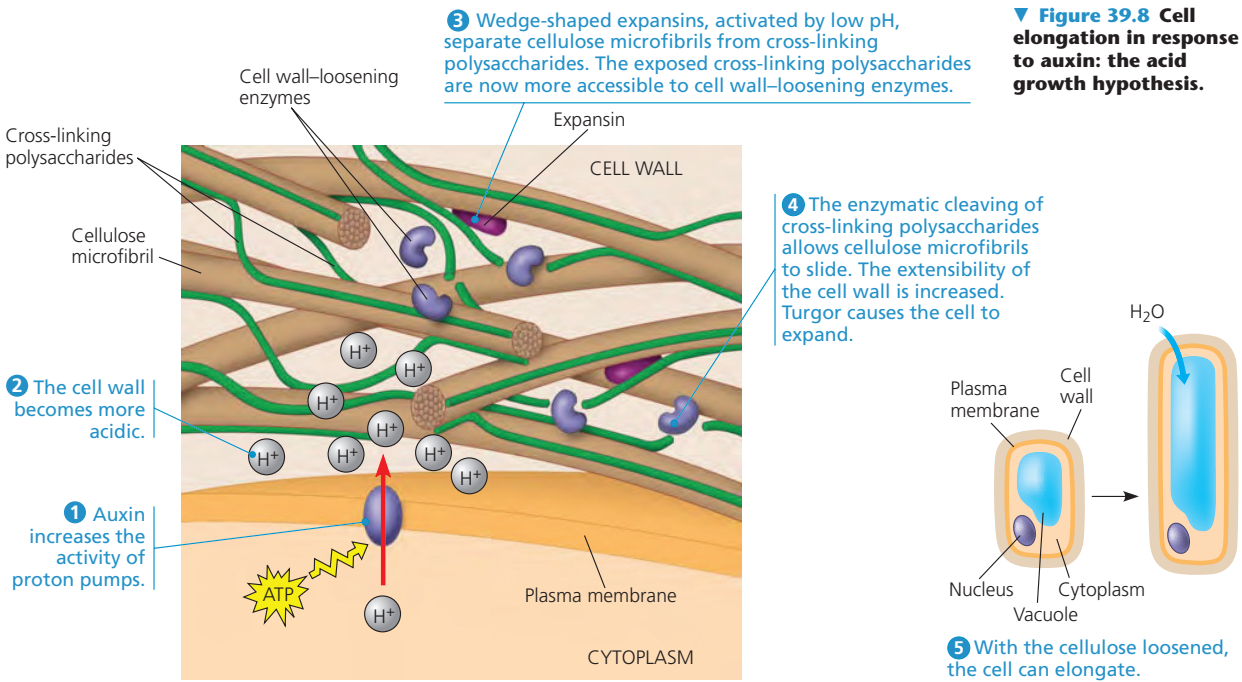
Auxin's Role in Plant Development The polar transport of auxin is a central element controlling the spatial organization, or *pattern formation*, of the developing plant. As we will see, auxin plays a role in almost all aspects of plant pattern formation.

Auxin is synthesized in shoot tips, and it carries integrated information about the development, size, and environment of individual branches. This flow of information controls branching patterns. A reduced flow of auxin from a branch, for example, indicates that the branch is not being sufficiently productive: New branches are needed elsewhere. Thus, lateral buds below the branch are released from dormancy and begin to grow.

Auxin transport also plays a key role in establishing *phyllotaxy* (see Figure 36.3), the arrangement of leaves on the stem. A leading model proposes that polar auxin transport in the shoot apex generates local peaks in auxin concentration that determine the site of leaf primordium formation and thereby the different phyllotaxies found in nature.

The polar transport of auxin from the leaf margin also directs the patterns of leaf veins. Inhibitors of polar auxin transport result in leaves that lack vascular continuity through the petiole and have broad, loosely organized main veins, an increased number of secondary veins, and a dense band of irregularly shaped vascular cells adjacent to the leaf margin.

The activity of the vascular cambium, the meristem that produces woody tissues, is also under the control of auxin transport. When a plant becomes dormant at the end of a



growing season, there is a reduction in auxin transport capacity and the expression of genes encoding auxin transporters.

Auxin's effects on plant development are not limited to the familiar sporophyte plant that we see. Recent evidence suggests that the organization of the microscopic angiosperm female gametophytes is regulated by an auxin gradient.

Practical Uses for Auxins Auxins, both natural and synthetic, have many commercial applications. For example, the natural auxin indolebutyric acid (IBA) is used in the vegetative propagation of plants by cuttings. (The formation of lateral roots in intact plants is one case where IBA seems to be a more important auxin than IAA.) Treating a detached leaf or stem with powder containing IBA often causes adventitious roots to form near the cut surface.

Certain synthetic auxins, including 2,4-dichlorophenoxyacetic acid (2,4-D), are widely used as herbicides. Monocots, such as maize and turfgrass, can rapidly inactivate such synthetic auxins. However, eudicots cannot and therefore die from hormonal overdose. Spraying cereal fields or turf with 2,4-D eliminates eudicot (broadleaf) weeds.

Developing seeds produce auxin, which promotes fruit growth. In tomato plants grown in greenhouses, often fewer seeds are produced, resulting in poorly developed tomato fruits. However, spraying synthetic auxins on greenhouse-grown tomato vines induces normal fruit development, making the greenhouse-cultivated tomatoes commercially viable.

Cytokinins

Trial-and-error attempts to find chemical additives that would enhance the growth and development of plant cells in tissue culture led to the discovery of **cytokinins**. In the 1940s, researchers stimulated the growth of plant embryos in culture by adding coconut milk, the liquid endosperm of a coconut's giant seed. Subsequent researchers found that they could induce cultured tobacco cells to divide by adding degraded DNA samples. The active ingredients of both experimental additives turned out to be modified forms of adenine, a component of nucleic acids. These growth regulators were named cytokinins because they stimulate cytokinesis, or cell division. The most common natural cytokinin is zeatin, so named because it was discovered first in maize (*Zea mays*). Although much remains to be learned about cytokinin synthesis and signal transduction, the effects of cytokinins on cell division and differentiation, apical dominance, and aging are well documented.

Control of Cell Division and Differentiation Cytokinins are produced in actively growing tissues, particularly in roots, embryos, and fruits. Cytokinins produced in roots reach their target tissues by moving up the plant in the xylem sap. Acting in concert with auxin, cytokinins stimulate cell division and influence the pathway of differentiation. The effects of cytokinins on cells growing in tissue culture provide clues about how this class of hormones may function in an intact plant. When a piece of parenchyma tissue from a stem is cultured in the absence of cytokinins, the cells grow very large but do not

divide. But if cytokinins are added along with auxin, the cells divide. Cytokinins alone have no effect. The ratio of cytokinins to auxin controls cell differentiation. When the concentrations of these two hormones are at certain levels, the mass of cells continues to grow, but it remains a cluster of undifferentiated cells called a callus (see Figure 38.14). If cytokinin levels increase, shoot buds develop from the callus. If auxin levels increase, roots form.

Control of Apical Dominance Cytokinins, auxin, and newly discovered plant hormones called strigolactones interact in the control of apical dominance, the ability of the apical bud to suppress the development of axillary buds (Figure 39.9a). Until recently, the leading hypothesis to explain the hormonal regulation of apical dominance—the direct inhibition hypothesis—proposed that auxin and cytokinins act antagonistically in regulating axillary bud growth. According to this view, auxin transported down the shoot from the apical bud directly inhibits axillary buds from growing, causing a shoot to lengthen at the expense of lateral branching. Meanwhile, cytokinins entering the shoot system from roots counter the action of auxin by signaling axillary buds to begin growing. Thus, the ratio of auxin and cytokinins was viewed as the critical factor in controlling axillary bud inhibition.

Many observations are consistent with the direct inhibition hypothesis. If the apical bud, the primary source of auxin, is removed, the inhibition of axillary buds is removed and the plant becomes bushier (Figure 39.9b). Applying

auxin to the cut surface of the decapitated shoot resuppresses the growth of the lateral buds (Figure 39.9c). Mutants that overproduce cytokinins or plants treated with cytokinins also tend to be bushier than normal. It now appears, however, that auxin's effects are partially indirect. The polar flow of auxin down the shoot triggers the synthesis of strigolactones, which repress bud growth. Moreover, another signal, perhaps an electrical one, appears to cause buds to begin growing much earlier than can be explained by disrupted auxin flow. Thus, the control of apical dominance is much more complicated than previously thought.

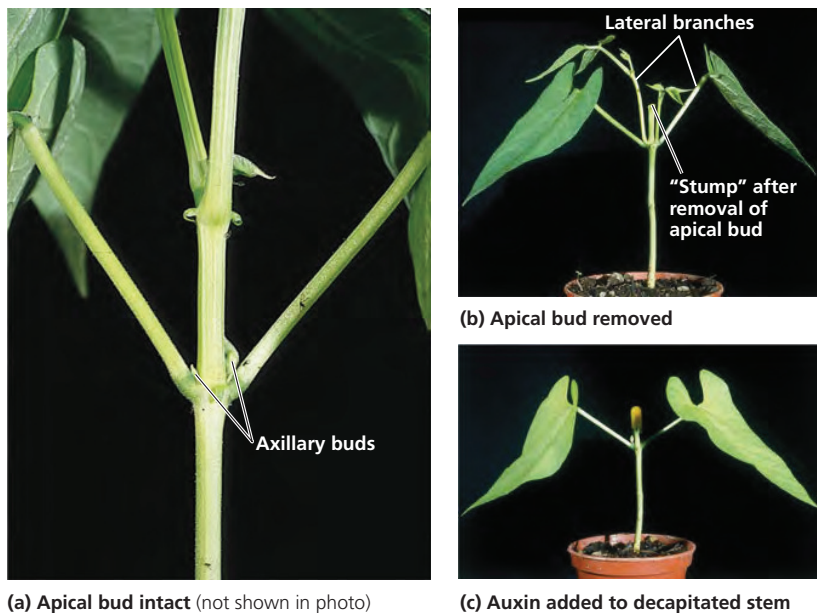
Anti-Aging Effects Cytokinins slow the aging of certain plant organs by inhibiting protein breakdown, stimulating RNA and protein synthesis, and mobilizing nutrients from surrounding tissues. If leaves removed from a plant are dipped in a cytokinin solution, they stay green much longer than otherwise. Cytokinins also slow the progress of **apoptosis**, a type of programmed cell death.

Gibberellins

In the early 1900s, farmers in Asia noticed that some rice seedlings in their paddies grew so tall and spindly that they toppled over before they could mature. In 1926, it was discovered that a fungus of the genus *Gibberella* causes this “foolish seedling disease.” By the 1930s, it was determined that the fungus causes hyperelongation of rice stems by secreting a chemical, which was given the name **gibberellin**. In the 1950s, researchers discovered that plants also produce gibberellins (GAs). Since that time, scientists have identified more than 100 different gibberellins that occur naturally in plants, although a much smaller number occur in each plant species. “Foolish rice” seedlings, it seems, suffer from too much gibberellin. Gibberellins have a variety of effects, such as stem elongation, fruit growth, and seed germination.

Stem Elongation The major sites of gibberellin production are young roots and leaves. Gibberellins are best known for stimulating stem and leaf growth by enhancing cell elongation and cell division. One hypothesis proposes that they activate enzymes that loosen cell walls, facilitating entry of expansin proteins. Thus, gibberellins act in concert with auxin to promote stem elongation.

The effects of gibberellins in enhancing stem elongation are evident when certain dwarf (mutant) varieties of plants



▲ Figure 39.9 Apical dominance. (a) The inhibition of growth of axillary buds, possibly influenced by auxin from the apical bud, favors elongation of the shoot's main axis. (b) Removal of the apical bud from the same plant enables lateral branches to grow. (c) Applying a gelatin capsule containing auxin to the stump prevents the lateral branches from growing.



(a) Some plants develop in a rosette form, low to the ground with very short internodes, as in the *Arabidopsis* plant shown at the left. As the plant switches to reproductive growth, a surge of gibberellins induces bolting: Internodes elongate rapidly, elevating floral buds that develop at stem tips (right).



(b) The Thompson seedless grape bunch on the left is from an untreated control vine. The bunch on the right is growing from a vine that was sprayed with gibberellin during fruit development.

◀ **Figure 39.10 Effects of gibberellins on stem elongation and fruit growth.**

are treated with gibberellins. For instance, some dwarf pea plants (including the variety Mendel studied; see Chapter 14) grow tall if treated with gibberellins. But there is often no response if the gibberellins are applied to wild-type plants. Apparently, these plants already produce an optimal dose of the hormone. The most dramatic example of gibberellin-induced stem elongation is *bolting*, rapid growth of the floral stalk (Figure 39.10a).

Fruit Growth In many plants, both auxin and gibberellins must be present for fruit to develop. The most important commercial application of gibberellins is in the spraying of Thompson seedless grapes (Figure 39.10b). The hormone makes the individual grapes grow larger, a trait valued by the consumer. The gibberellin sprays also make the internodes of the grape bunch elongate, allowing more space for the individual grapes. By enhancing air circulation between the grapes, this increase in space also makes it harder for yeasts and other microorganisms to infect the fruit.

Germination The embryo of a seed is a rich source of gibberellins. After water is imbibed, the release of gibberellins from the embryo signals the seed to break dormancy and germinate. Some seeds that normally require particular environmental conditions to germinate, such as exposure to light or low temperatures,

break dormancy if they are treated with gibberellins. Gibberellins support the growth of cereal seedlings by stimulating the synthesis of digestive enzymes such as α -amylase that mobilize stored nutrients (Figure 39.11).

Brassinosteroids

Brassinosteroids are steroids similar to cholesterol and the sex hormones of animals. They induce cell elongation and division in stem segments and seedlings at concentrations as low as 10^{-12} M. They also slow leaf abscission (leaf drop) and promote xylem differentiation. These effects are so qualitatively similar to those of auxin that it took years for plant physiologists to determine that brassinosteroids were not types of auxins.

The identification of brassinosteroids as plant hormones arose from studies of an *Arabidopsis* mutant that exhibited morphological features similar to those of light-grown plants even when grown in the dark. The researchers discovered that the mutation affects a gene that normally codes for an enzyme similar to one involved in steroid synthesis in mammals. They also found that this brassinosteroid-deficient mutant could be restored to the wild-type phenotype by applying brassinosteroids.

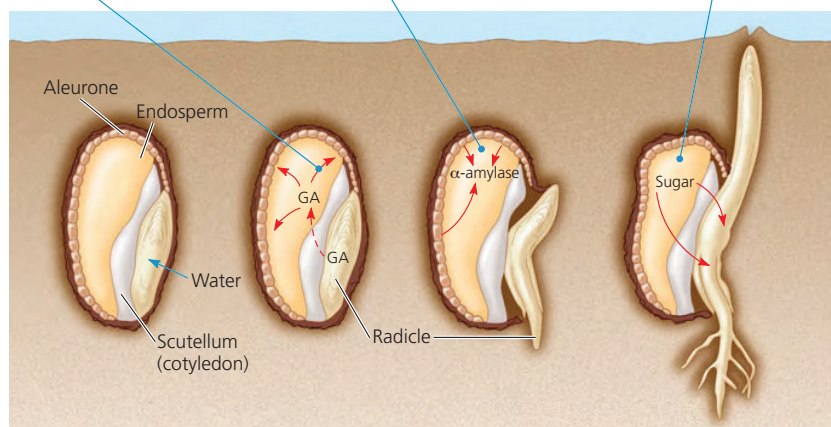
Abscisic Acid

In the 1960s, one research group studying the chemical changes that precede bud dormancy and leaf abscission in deciduous trees and another team investigating chemical changes preceding abscission of cotton fruits isolated the same compound, **abscisic acid (ABA)**. Ironically, ABA is no longer thought to play a primary role in bud dormancy or leaf abscission, but it is very

1 After a seed imbibes water, the embryo releases gibberellin (GA), which sends a signal to the aleurone, the thin outer layer of the endosperm.

2 The aleurone responds to GA by synthesizing and secreting digestive enzymes that hydrolyze nutrients stored in the endosperm. One example is α -amylase, which hydrolyzes starch.

3 Sugars and other nutrients absorbed from the endosperm by the scutellum (cotyledon) are consumed during growth of the embryo into a seedling.



▲ **Figure 39.11 Mobilization of nutrients by gibberellins during the germination of grain seeds such as barley.**

important in other functions. Unlike the growth-stimulating hormones we have discussed so far—auxin, cytokinins, gibberellins, and brassinosteroids—ABA *slows* growth. ABA often antagonizes the actions of growth hormones, and the ratio of ABA to one or more growth hormones determines the final physiological outcome. We will consider here two of ABA's many effects: seed dormancy and drought tolerance.

Seed Dormancy Seed dormancy increases the likelihood that seeds will germinate only when there are sufficient amounts of light, temperature, and moisture for the seedlings to survive (see Chapter 38). What prevents seeds dispersed in autumn from germinating immediately, only to die in the winter? What mechanisms ensure that such seeds do not germinate until spring? For that matter, what prevents seeds from germinating in the dark, moist interior of the fruit? The answer to these questions is ABA. The levels of ABA may increase 100-fold during seed maturation. The high levels of ABA in maturing seeds inhibit germination and induce the production of proteins that help the seeds withstand the extreme dehydration that accompanies maturation.

Many types of dormant seeds germinate when ABA is removed or inactivated. The seeds of some desert plants break dormancy only when heavy rains wash ABA out of them. Other seeds require light or prolonged exposure to cold to inactivate ABA. Often, the ratio of ABA to gibberellins determines whether seeds remain dormant or germinate, and adding ABA to seeds that are primed to germinate makes them dormant again. Inactivated ABA or low levels of ABA can lead to precocious (early) germination (**Figure 39.12**). For example, a maize mutant with grains that germinate while still on the cob lacks a functional transcription factor required for ABA to induce expression of certain genes. Precocious germination of red mangrove seeds, due to low ABA levels, is actually an adaptation that helps the young seedlings to plant themselves like darts in the soft mud below the parent tree.

Drought Tolerance ABA plays a major role in drought signaling. When a plant begins to wilt, ABA accumulates in the leaves and causes stomata to close rapidly, reducing transpiration and preventing further water loss. By affecting second messengers such as calcium, ABA causes potassium channels in the plasma membrane of guard cells to open, leading to a massive loss of potassium ions from the cells. The accompanying osmotic loss of water reduces guard cell turgor and leads to closing of the stomatal pores (see Figure 36.15). In some cases, water shortage stresses the root system before the shoot system, and ABA transported from roots to leaves may function as an “early warning system.” Many mutants that are especially prone to wilting are deficient in ABA production.

Strigolactones

The hormones called **strigolactones** are upwardly mobile signals that stimulate seed germination, help establish



◀ Red mangrove (*Rhizophora mangle*) seeds produce only low levels of ABA, and their seeds germinate while still on the tree. In this case, early germination is a useful adaptation. When released, the radicle of the dart-like seedling deeply penetrates the soft mudflats in which the mangroves grow.



▲ Precocious germination in this maize mutant is caused by lack of a functional transcription factor required for ABA action.

▲ **Figure 39.12 Precocious germination of wild-type mangrove and mutant maize seeds.**

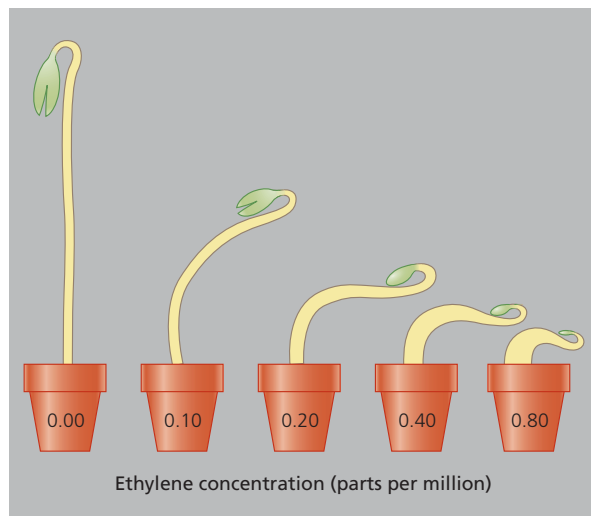
mycorrhizal associations, and (as noted earlier) help control apical dominance. Their recent discovery relates back to studies of their namesake, *Striga*, a colorfully named genus of rootless parasitic plants that penetrate the roots of other plants, diverting essential nutrients from them and stunting their growth. (In Romanian legend, *Striga* is a vampire-like creature that lives for thousands of years, only needing to feed every 25 years or so.) Also known as witchweed, *Striga* may be the greatest obstacle to food production in Africa, infesting about two-thirds of the area devoted to cereal crops. Each *Striga* plant produces tens of thousands of tiny seeds that can remain dormant in the soil for many years until a suitable host begins to grow. Thus, *Striga* cannot be eradicated by growing non-grain crops for several years. Strigolactones, exuded by the host roots, were first identified as the chemical signals that stimulate the germination of *Striga* seeds.

Ethylene

During the 1800s, when coal gas was used as fuel for streetlights, leakage from gas pipes caused nearby trees to drop leaves prematurely. In 1901, the gas **ethylene** was demonstrated to be the active factor in coal gas. But the idea that it is a plant hormone was not widely accepted until the advent of a technique called gas chromatography simplified its identification.

Plants produce ethylene in response to stresses such as drought, flooding, mechanical pressure, injury, and infection. Ethylene is also produced during fruit ripening and programmed cell death and in response to high concentrations of externally applied auxin. Indeed, many effects previously ascribed to auxin, such as inhibition of root elongation, may be due to auxin-induced ethylene production. We will focus here on four of ethylene's many effects: response to mechanical stress, senescence, leaf abscission, and fruit ripening.

The Triple Response to Mechanical Stress Imagine a pea seedling pushing upward through the soil, only to come up against a stone. As it pushes against the obstacle, the stress in its delicate tip induces the seedling to produce ethylene. The hormone then instigates a growth maneuver known as the **triple response** that enables the shoot to avoid the obstacle. The three parts of this response are a slowing of stem elongation, a thickening of the stem (which makes it stronger), and a curvature that causes the stem to start growing horizontally. As the effects of the initial ethylene pulse lessen, the stem resumes vertical growth. If it again contacts a barrier, another burst of ethylene is released, and horizontal growth resumes. However, if the upward touch detects no solid object, then ethylene production decreases, and the stem, now clear of the obstacle, resumes its normal upward growth. It is ethylene that induces the stem to grow horizontally rather than the physical obstruction itself; when ethylene is applied to normal seedlings growing free of physical impediments, they still undergo the triple response (Figure 39.13).

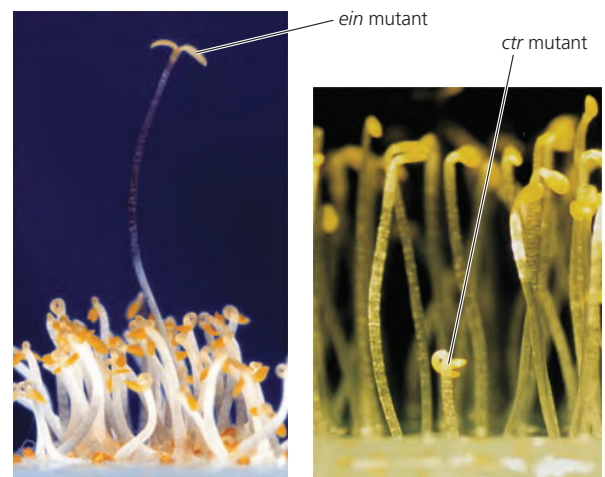


▲ **Figure 39.13 The ethylene-induced triple response.** In response to ethylene, a gaseous plant hormone, germinating pea seedlings grown in the dark undergo the triple response—slowing of stem elongation, stem thickening, and horizontal stem growth. The response is greater with increased ethylene concentration.

Studies of *Arabidopsis* mutants with abnormal triple responses are an example of how biologists identify a signal transduction pathway. Scientists isolated ethylene-insensitive (*ein*) mutants, which fail to undergo the triple response after exposure to ethylene (Figure 39.14a). Some types of *ein* mutants are insensitive to ethylene because they lack a functional ethylene receptor. Mutants of a different sort undergo the triple response even out of soil, in the air, where there are no physical obstacles. Some of these mutants have a regulatory defect that causes them to produce ethylene at rates 20 times normal. The phenotype of such ethylene-overproducing (*eto*) mutants can be restored to wild-type by treating the seedlings with inhibitors of ethylene synthesis. Other mutants, called constitutive triple-response (*ctr*) mutants, undergo the triple response in air but do not respond to inhibitors of ethylene synthesis (Figure 39.14b). (Constitutive genes are genes that are continually expressed in all cells of an organism.) In *ctr* mutants, ethylene signal transduction is permanently turned on, even though ethylene is not present.

The affected gene in *ctr* mutants codes for a protein kinase. The fact that this mutation *activates* the ethylene response suggests that the normal kinase product of the wild-type allele is a *negative* regulator of ethylene signal transduction. Thus, binding of the hormone ethylene to the ethylene receptor normally leads to inactivation of the kinase; and the inactivation of this negative regulator allows synthesis of the proteins required for the triple response.

Senescence Consider the shedding of a leaf in autumn or the death of an annual after flowering. Or think about the final



(a) ***ein* mutant.** An ethylene-insensitive (*ein*) mutant fails to undergo the triple response in the presence of ethylene.

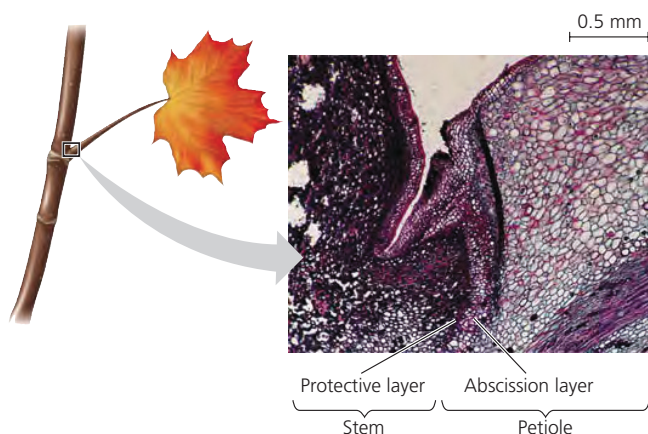
(b) ***ctr* mutant.** A constitutive triple-response (*ctr*) mutant undergoes the triple response even in the absence of ethylene.

▲ **Figure 39.14 Ethylene triple-response *Arabidopsis* mutants.**

step in differentiation of a vessel element, when its living contents are destroyed, leaving a hollow tube behind. Such events involve **senescence**—the programmed death of certain cells or organs or the entire plant. Cells, organs, and plants genetically programmed to die on a schedule do not simply shut down cellular machinery and await death. Instead, at the molecular level, the onset of the programmed cell death called apoptosis is a very busy time in a cell's life, requiring new gene expression (see pp. 223–225). During apoptosis, newly formed enzymes break down many chemical components, including chlorophyll, DNA, RNA, proteins, and membrane lipids. The plant salvages many of the breakdown products. A burst of ethylene is almost always associated with the apoptosis of cells during senescence.

Leaf Abscission The loss of leaves from deciduous trees helps prevent desiccation during seasonal periods of climatic stress that severely limit the availability of water to the roots. Before dying leaves abscise, many essential elements are salvaged from them and stored in stem parenchyma cells. These nutrients are recycled back to developing leaves the following spring. Autumn leaf color is due to newly made red pigments as well as yellow and orange carotenoids (see Chapter 10) that were already present in the leaf and are rendered visible by the breakdown of the dark green chlorophyll in autumn.

When an autumn leaf falls, the breaking point is an abscission layer that develops near the base of the petiole (**Figure 39.15**). The small parenchyma cells of this layer have very thin walls, and there are no fiber cells around the vascular tissue. The abscission layer is further weakened when enzymes hydrolyze polysaccharides in the cell walls. Finally, the weight of the leaf, with the help of the wind, causes a separation within the abscission layer. Even before the leaf falls, a



▲ **Figure 39.15 Abscission of a maple leaf.** Abscission is controlled by a change in the ratio of ethylene to auxin. The abscission layer is seen in this longitudinal section as a vertical band at the base of the petiole. After the leaf falls, a protective layer of cork becomes the leaf scar that helps prevent pathogens from invading the plant (LM).

layer of cork forms a protective scar on the twig side of the abscission layer, preventing pathogens from invading the plant.

A change in the ratio of ethylene to auxin controls abscission. An aging leaf produces less and less auxin, rendering the cells of the abscission layer more sensitive to ethylene. As the influence of ethylene on the abscission layer prevails, the cells produce enzymes that digest the cellulose and other components of cell walls.

Fruit Ripening Immature fleshy fruits are generally tart, hard, and green—features that help protect the developing seeds from herbivores. After ripening, the mature fruits help *attract* animals that disperse the seeds (see Figures 30.8 and 30.9). In many cases, a burst of ethylene production in the fruit triggers the ripening process. The enzymatic breakdown of cell wall components softens the fruit, and the conversion of starches and acids to sugars makes the fruit sweet. The production of new scents and colors helps advertise ripeness to animals, which eat the fruits and disperse the seeds.

A chain reaction occurs during ripening: Ethylene triggers ripening, and ripening triggers more ethylene production. The result is a huge burst in ethylene production. Because ethylene is a gas, the signal to ripen spreads from fruit to fruit. If you pick or buy green fruit, you may be able to speed ripening by storing the fruit in a paper bag, allowing ethylene to accumulate. On a commercial scale, many kinds of fruits are ripened in huge storage containers in which ethylene levels are enhanced. In other cases, fruit producers take measures to slow ripening caused by natural ethylene. Apples, for instance, are stored in bins flushed with carbon dioxide. Circulating the air prevents ethylene from accumulating, and carbon dioxide inhibits synthesis of new ethylene. Stored in this way, apples picked in autumn can still be shipped to grocery stores the following summer.

Given the importance of ethylene in the postharvest physiology of fruits, the genetic engineering of ethylene signal transduction pathways has potential commercial applications. For example, by engineering a way to block the transcription of one of the genes required for ethylene synthesis, molecular biologists have created tomato fruits that ripen on demand. These fruits are picked while green and will not ripen unless ethylene gas is added. As such methods are refined, they will reduce spoilage of fruits and vegetables, a problem that ruins almost half the produce harvested in the United States.

Systems Biology and Hormone Interactions

As we have discussed, plant responses often involve the interactions of many hormones and their signal transduction pathways. The study of hormone interactions can be a complex problem. For example, as you saw in the description of apical dominance, the growth of lateral buds is controlled by cross-talk between the signal transduction pathways triggered by cytokinins, auxin, and strigolactones. Imagine yourself as a

molecular biologist assigned the task of genetically engineering a bushier plant phenotype. Would the best molecular target for genetic manipulation be an enzyme that inactivates IAA? An enzyme that produces more cytokinin? A strigolactone receptor? It is difficult to predict. And this is by no means an unusual problem. Virtually every plant response discussed in this chapter is of comparable complexity. Because of the pervasive nature of complex interactions in plant physiology, many plant biologists are promoting a new, systems-based approach to plant biology.

In Chapter 1, we provided a general description of systems biology, which attempts to discover and understand biological properties that emerge from the interactions of many system elements (for example, mRNAs, proteins, hormones, and metabolites). Using genomic techniques, biologists can now identify all the genes in a plant. The genomes of many plant species have now been sequenced, including *Arabidopsis*, rice, grape, maize, and poplar trees. Moreover, using microarray and proteomic techniques (see Chapters 20 and 21), scientists can determine which genes are activated or inactivated during development or in response to an environmental change. However, simply identifying all the genes and proteins (system elements) in an organism is comparable to listing all the parts of an airplane. Although such a list provides a catalog of components, it is not sufficient for understanding the complexity underlying the integrated system. What plant biologists really need to know is how all these system elements interact.

A systems-based approach may greatly alter how plants are studied. One vision is laboratories equipped with high-throughput robotic scanners that record which genes in a plant's genome are activated in which cells and under what conditions. New hypotheses and avenues of research will emerge from analysis of these comprehensive data sets. Ultimately, one goal of systems biology is to model an entire living plant. Armed with such detailed knowledge, a biologist attempting to genetically engineer a bushier plant could proceed much more efficiently. The ability to model a living plant could make it possible to predict the result of a genetic manipulation before setting foot in the laboratory.

CONCEPT CHECK 39.2

1. Suggest a reason why cut flowers such as carnations are often treated with cytokinins prior to shipping.
2. Fusicoccin is a fungal toxin that stimulates the plasma membrane H^+ pumps of plant cells. How may it affect the growth of isolated stem sections?
3. **WHAT IF?** If a plant has the double mutation *ctr* and *ein*, what is its triple-response phenotype? Explain your answer.
4. **MAKE CONNECTIONS** What type of feedback process is exemplified by the production of ethylene during fruit ripening? Explain. (See Figure 1.13, on p. 11.)

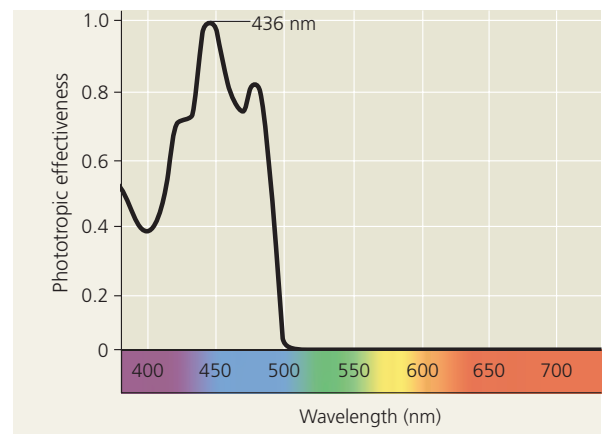
For suggested answers, see Appendix A.

CONCEPT 39.3

Responses to light are critical for plant success

Light is an especially important environmental factor in the lives of plants. In addition to being required for photosynthesis, light triggers many key events in plant growth and development. The effects of light on plant morphology are called **photomorphogenesis**. Light reception also allows plants to measure the passage of days and seasons.

Plants detect not only the presence of light but also its direction, intensity, and wavelength (color). As you saw in Figure 10.10b for photosynthesis, a graph called an **action spectrum** depicts the relative effectiveness of different wavelengths of radiation in driving a particular process. Action spectra are useful in studying *any* process that depends on light, including phototropism (Figure 39.16). By comparing action spectra of various plant responses, researchers determine which responses are mediated by the same photoreceptor (pigment).



(a) This action spectrum illustrates that only light wavelengths below 500 nm (blue and violet light) induce curvature.



(b) These photographs of coleoptiles were taken before and after 90-minute exposures to light sources of the colors indicated.

▲ **Figure 39.16 Action spectrum for blue-light-stimulated phototropism in maize coleoptiles.** Phototropic bending toward light is controlled by phototropin, a photoreceptor sensitive to blue and violet light, particularly blue light.

They also compare action spectra with absorption spectra of pigments; a close correspondence for a given pigment suggests that the pigment is the photoreceptor mediating the response. Action spectra reveal that red and blue light are the most important colors in regulating a plant's photomorphogenesis. These observations led researchers to two major classes of light receptors: **blue-light photoreceptors** and **phytochromes**, photoreceptors that absorb mostly red light.

Blue-Light Photoreceptors

Blue light initiates a variety of responses in plants, including phototropism, the light-induced opening of stomata (see Figure 36.14), and the light-induced slowing of hypocotyl elongation that occurs when a seedling breaks ground. The biochemical identity of the blue-light photoreceptor was so elusive that in the 1970s, plant physiologists began to call this receptor "cryptochrome" (from the Greek *kryptos*, hidden, and *chrom*, pigment). In the 1990s, molecular biologists analyzing *Arabidopsis* mutants found that plants use as many as three different types of pigments to detect blue light. *Cryptochromes*, molecular relatives of DNA repair enzymes, are involved in the blue-light-induced inhibition of stem elongation that occurs, for example, when a seedling first emerges from the soil. *Phototropin* is a protein kinase involved in mediating phototropic curvatures, such as those studied in grass seedlings by the Darwins, and in chloroplast movements in response to light. There is currently much debate about whether phototropin or a carotenoid-based photoreceptor called *zeaxanthin* is the major blue-light photoreceptor involved in blue-light-mediated stomatal opening.

Phytochromes as Photoreceptors

When introducing signal transduction in plants earlier in the chapter, we discussed the role of the plant pigments called phytochromes in the de-etiolation process. Phytochromes regulate many plant responses to light. Let's look at two more examples: seed germination and shade avoidance.

Phytochromes and Seed Germination

Studies of seed germination led to the discovery of phytochromes. Because of limited nutrient reserves, many types of seeds, especially small ones, germinate only when the light environment and other conditions are near optimal. Such seeds often remain dormant for years until light conditions change. For example, the death of a shading tree or the plowing of a field may create a favorable light environment.

In the 1930s, scientists at the U.S. Department of Agriculture determined the action spectrum for light-induced germination of lettuce seeds. They exposed water-swollen seeds to a few minutes of monochromatic (single-colored) light of various wavelengths and then stored the seeds in the dark. After two days, the researchers counted the

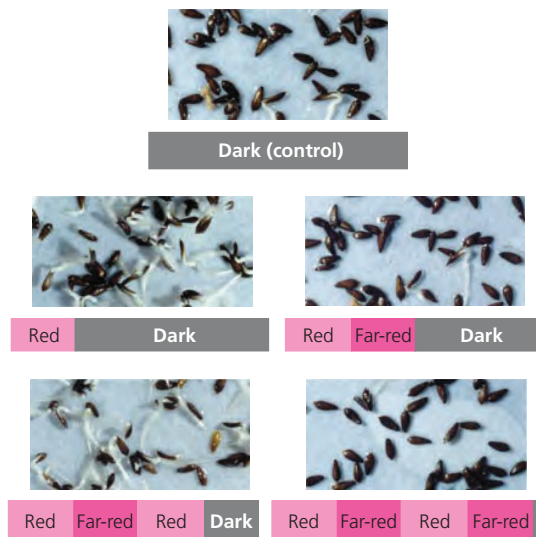
▼ Figure 39.17

INQUIRY

How does the order of red and far-red illumination affect seed germination?

EXPERIMENT Scientists at the U.S. Department of Agriculture briefly exposed batches of lettuce seeds to red light or far-red light to test the effects on germination. After the light exposure, the seeds were placed in the dark, and the results were compared with control seeds that were not exposed to light.

RESULTS The bar below each photo indicates the sequence of red light exposure, far-red light exposure, and darkness. The germination rate increased greatly in groups of seeds that were last exposed to red light (left). Germination was inhibited in groups of seeds that were last exposed to far-red light (right).

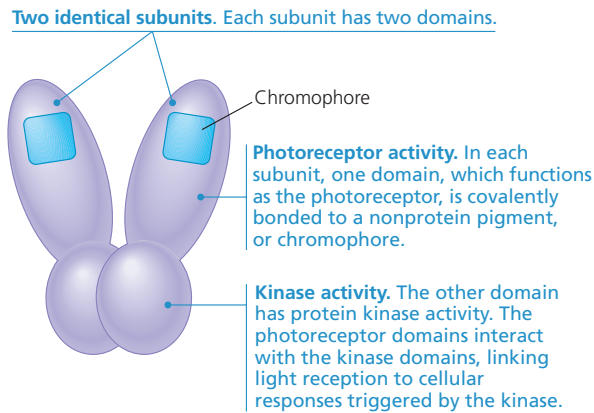


CONCLUSION Red light stimulates germination, and far-red light inhibits germination. The final light exposure is the determining factor. The effects of red and far-red light are reversible.

SOURCE H. Borthwick et al., A reversible photoreaction controlling seed germination, *Proceedings of the National Academy of Sciences, USA* 38:662–666 (1952).

WHAT IF? Phytochrome responds faster to red light than to far-red. If the seeds had been placed in white light instead of the dark after their red and far-red light treatments, would the results have been different?

number of seeds that had germinated under each light regimen. They found that red light of wavelength 660 nm increased the germination percentage of lettuce seeds maximally, whereas far-red light—that is, light of wavelengths near the upper edge of human visibility (730 nm)—inhibited germination compared with dark controls (Figure 39.17). What happens when the lettuce seeds are subjected to a flash of red light followed by a flash of far-red light or, conversely, to far-red light followed by red

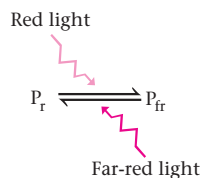


▲ **Figure 39.18** Structure of a phytochrome.

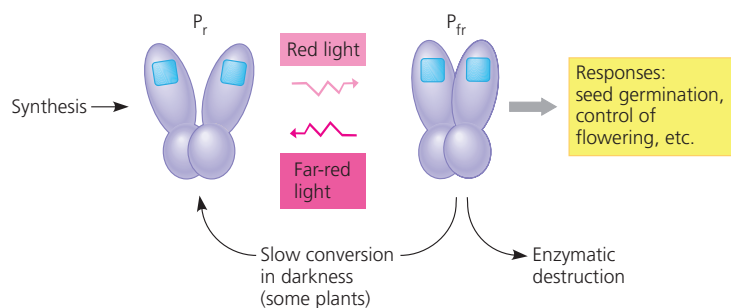
light? The *last* flash of light determines the seeds' response: The effects of red and far-red light are reversible.

The photoreceptors responsible for the opposing effects of red and far-red light are phytochromes. A phytochrome has two identical subunits, each consisting of a polypeptide component covalently bonded to a nonpolypeptide *chromophore*, the light-absorbing part of the subunit (**Figure 39.18**). So far, researchers have identified five phytochromes in *Arabidopsis*, each with a slightly different polypeptide component.

The chromophore of a phytochrome is photoreversible, reverting back and forth between two isomeric forms, depending on the color of light provided (see Figure 4.7 to review isomers). In its P_r isomer form, a phytochrome absorbs red (r) light maximally, whereas in its P_{fr} isomer form, it absorbs far-red (fr) light:



► **Figure 39.19** **Phytochrome: a molecular switching mechanism.** Absorption of red light causes the P_r to change to the P_{fr} . Far-red light reverses this conversion. In most cases, it is the P_{fr} form of the pigment that switches on physiological and developmental responses in the plant.



This $P_r \longleftrightarrow P_{fr}$ interconversion is a switching mechanism that controls various light-induced events in the life of the plant (**Figure 39.19**). P_{fr} is the form of phytochrome that triggers many of a plant's developmental responses to light. For example, P_r in lettuce seeds exposed to red light is converted to P_{fr} , stimulating the cellular responses that lead to germination. When red-illuminated seeds are then exposed to far-red light, the P_{fr} is converted back to P_r , inhibiting the germination response.

How does phytochrome switching explain light-induced germination in nature? Plants synthesize phytochrome as P_r , and if seeds are kept in the dark, the pigment remains almost entirely in the P_r form (see Figure 39.19). Sunlight contains both red light and far-red light, but the conversion to P_{fr} is faster than the conversion to P_r . Therefore, the ratio of P_{fr} to P_r increases in the sunlight. When seeds are exposed to adequate sunlight, the production and accumulation of P_{fr} will trigger their germination.

Phytochromes and Shade Avoidance

The phytochrome system also provides the plant with information about the *quality* of light. Because sunlight includes both red and far-red radiation, during the day the $P_r \longleftrightarrow P_{fr}$ interconversion reaches a dynamic equilibrium, with the ratio of the two phytochrome forms indicating the relative amounts of red and far-red light. This sensing mechanism enables plants to adapt to changes in light conditions. Consider, for example, the "shade avoidance" response of a tree that requires relatively high light intensity. If other trees in a forest shade this tree, the phytochrome ratio shifts in favor of P_r because the forest canopy screens out more red light than far-red light. This is because the chlorophyll pigments in the leaves of the canopy absorb red light and allow far-red light to pass. The shift in the ratio of red to far-red light induces the tree to allocate more of its resources to growing taller. In contrast, direct sunlight increases the proportion of P_{fr} , which stimulates branching and inhibits vertical growth.

In addition to helping plants detect light, phytochrome helps a plant keep track of the passage of days and seasons. To understand phytochrome's role in these timekeeping processes, we must first examine the nature of the plant's internal clock.

Biological Clocks and Circadian Rhythms

Many plant processes, such as transpiration and the synthesis of certain enzymes, undergo a daily oscillation. Some of these cyclic variations are responses to the changes in light levels, temperature, and relative humidity that accompany the 24-hour cycle of day and night. We can control these external factors by growing plants in growth chambers under rigidly maintained conditions of light, temperature, and humidity. But even under artificially constant conditions, many physiological processes in plants, such as the opening and closing of stomata and the production of photosynthetic enzymes, continue to oscillate with a frequency of about 24 hours. For example, many legumes lower their leaves in the evening and raise them in the morning (Figure 39.20). A bean plant continues these “sleep movements” even if kept in constant light or constant darkness; the leaves are not simply responding to sunrise and sunset. Such cycles, with a frequency of about 24 hours and not directly controlled by any known environmental variable, are called **circadian rhythms** (from the Latin *circa*, approximately, and *dies*, day).

Recent research supports the idea that the molecular “gears” of the circadian clock really are internal and not a daily response to some subtle but pervasive environmental cycle, such as geomagnetism or cosmic radiation. Organisms, including plants and humans, continue their rhythms even when placed in deep mine shafts or when orbited in satellites, conditions that alter these subtle geophysical periodicities. However, daily signals from the environment can entrain (set) the circadian clock to a period of precisely 24 hours.

If an organism is kept in a constant environment, its circadian rhythms deviate from a 24-hour period (a period is the duration of one cycle). These free-running periods, as they are called, vary from about 21 to 27 hours, depending on the particular rhythmic response. The sleep movements of bean plants, for instance, have a period of 26 hours when the plants are kept in the free-running condition of constant darkness. Deviation of the free-running period from exactly

24 hours does not mean that biological clocks drift erratically. Free-running clocks are still keeping perfect time, but they are not synchronized with the outside world. To understand the mechanisms underlying circadian rhythms, we must distinguish between the clock and the rhythmic processes it controls. For example, the leaves of the bean plant in Figure 39.20 are the clock’s “hands” but are not the essence of the clock itself. If bean leaves are restrained for several hours and then released, they will reestablish the position appropriate for the time of day. We can interfere with a biological rhythm, but the underlying clockwork continues to tick.

At the heart of the molecular mechanisms underlying circadian rhythms are oscillations in the transcription of certain genes. The monitoring of *Arabidopsis* over a 24-hour cycle revealed that approximately 5% of its mRNAs undergo a circadian rhythm in synthesis. Some of these mRNAs are more abundant at dawn, others at dusk, and some in the middle of the day. Mathematical models propose that the 24-hour period arises from negative-feedback loops involving the transcription of a few central “clock genes.” Some clock genes may encode transcription factors that inhibit, after a time delay, the transcription of the gene that encodes the transcription factor itself. Such negative-feedback loops, together with a time delay, are enough to produce oscillations.

Researchers have recently used a novel technique to identify clock mutants of *Arabidopsis*. One prominent circadian rhythm in plants is the daily production of certain photosynthesis-related proteins. Molecular biologists traced the source of this rhythm to the promoter that initiates the transcription of the genes for these photosynthesis proteins. To identify clock mutants, scientists spliced the gene for an enzyme responsible for the bioluminescence of fireflies, called luciferase, to the promoter. When the biological clock turned on the promoter in the *Arabidopsis* genome, it also turned on the production of luciferase. The plants began to glow with a circadian periodicity. Clock mutants were then isolated by selecting specimens that glowed for a longer or shorter time than normal. The genes altered in some of these mutants affect proteins that normally bind photoreceptors. Perhaps these particular mutations disrupt a light-dependent mechanism that sets the biological clock.

The Effect of Light on the Biological Clock

As we have discussed, the free-running period of the circadian rhythm of bean leaf movements is 26 hours. Consider a bean plant placed at dawn in a dark cabinet for 72 hours: Its leaves would not rise again until 2 hours after natural dawn on the second day, 4 hours after natural dawn on the third day, and so on. Shut off from environmental cues, the plant becomes desynchronized. Desynchronization happens to humans when we fly across several time zones; when we reach our destination, the clocks on the wall are not synchronized with our internal clocks. Most organisms are probably prone to jet lag.



▲ **Figure 39.20 Sleep movements of a bean plant (*Phaseolus vulgaris*).** The movements are caused by reversible changes in the turgor pressure of cells on opposing sides of the pulvini, motor organs of the leaf.

The factor that entrains the biological clock to precisely 24 hours every day is light. Both phytochromes and blue-light photoreceptors can entrain circadian rhythms in plants, but our understanding of how phytochromes do this is more complete. The mechanism involves turning cellular responses on and off by means of the $P_r \longleftrightarrow P_{fr}$ switch.

Consider again the photoreversible system in Figure 39.19. In darkness, the phytochrome ratio shifts gradually in favor of the P_r form, partly as a result of turnover in the overall phytochrome pool. The pigment is synthesized in the P_r form, and enzymes destroy more P_{fr} than P_r . In some plant species, P_{fr} present at sundown slowly converts to P_r . In darkness, there is no means for the P_r to be reconverted to P_{fr} , but upon illumination, the P_{fr} level suddenly increases again as P_r is rapidly converted. This increase in P_{fr} each day at dawn resets the biological clock: Bean leaves reach their most extreme night position 16 hours after dawn.

In nature, interactions between phytochrome and the biological clock enable plants to measure the passage of night and day. The relative lengths of night and day, however, change over the course of the year (except at the equator). Plants use this change to adjust activities in synchrony with the seasons.

Photoperiodism and Responses to Seasons

Imagine the consequences if a plant produced flowers when pollinators were not present or if a deciduous tree produced leaves in the middle of winter. Seasonal events are of critical importance in the life cycles of most plants. Seed germination, flowering, and the onset and breaking of bud dormancy are all stages that usually occur at specific times of the year. The environmental stimulus that plants use most often to detect the time of year is the photoperiod, the relative lengths of night and day. A physiological response to photoperiod, such as flowering, is called **photoperiodism**.

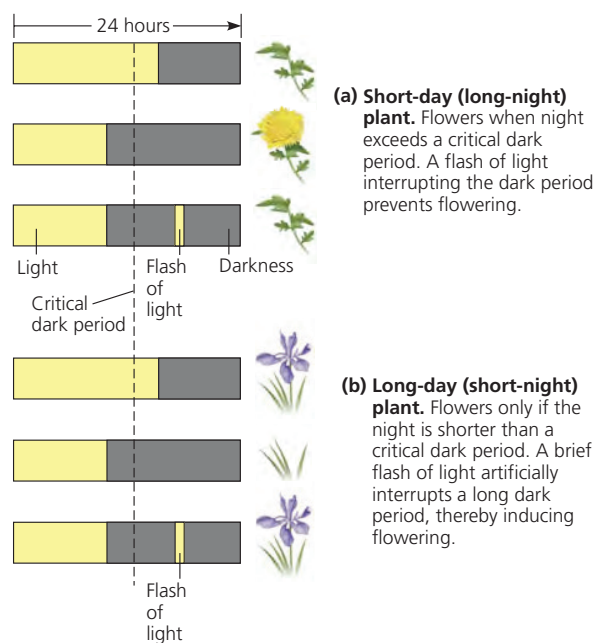
Photoperiodism and Control of Flowering

An early clue to how plants detect seasons came from a mutant variety of tobacco, Maryland Mammoth, which grew tall but failed to flower during summer. It finally bloomed in a greenhouse in December. After trying to induce earlier flowering by varying temperature, moisture, and mineral nutrition, researchers learned that the shortening days of winter stimulated this variety to flower. If the plants were kept in light-tight boxes so that lamps could manipulate “day” and “night,” flowering occurred only if the day length was 14 hours or shorter. It did not flower during summer because at Maryland’s latitude, the summer days were too long.

The researchers called Maryland Mammoth a **short-day plant** because it apparently required a light period *shorter* than a critical length to flower. Chrysanthemums, poinsettias, and some soybean varieties are also short-day plants, which generally flower in late summer, fall, or winter. Another group of plants flower only when the light period is *longer* than a certain

number of hours. These **long-day plants** generally flower in late spring or early summer. Spinach, for example, flowers when days are 14 hours or longer. Radishes, lettuce, irises, and many cereal varieties are also long-day plants. **Day-neutral plants**, such as tomatoes, rice, and dandelions, are unaffected by photoperiod and flower when they reach a certain stage of maturity, regardless of day length.

Critical Night Length In the 1940s, researchers learned that flowering and other responses to photoperiod are actually controlled by night length, not day length. Many of these scientists worked with cocklebur (*Xanthium strumarium*), a short-day plant that flowers only when days are 16 hours or shorter (and nights are at least 8 hours long). These researchers found that if the light portion of the photoperiod is broken by a brief exposure to darkness, flowering proceeds. However, if the dark part of the photoperiod is interrupted by even a few minutes of dim light, cocklebur will not flower, and this turned out to be true for other short-day plants as well (Figure 39.21a). Cocklebur is unresponsive to day length, but it requires at least 8 hours of continuous darkness to flower. Short-day plants are really long-night plants, but the older term is embedded firmly in the lexicon of plant physiology. Similarly, long-day plants are actually short-night plants. A long-day plant grown on photoperiods of long nights that would not normally induce flowering will flower if the period of continuous darkness is interrupted by a few minutes of light (Figure 39.21b). Notice that we distinguish long-day from short-day plants *not* by an absolute night length but by whether the critical night length sets a maximum



▲ **Figure 39.21** Photoperiodic control of flowering.

(long-day plants) or minimum (short-day plants) number of hours of darkness required for flowering. In both cases, the actual number of hours in the critical night length is specific to each species of plant.

Red light is the most effective color in interrupting the nighttime portion of the photoperiod. Action spectra and photoreversibility experiments show that phytochrome is the pigment that detects the red light (Figure 39.22). For example, if a flash of red (R) light during the dark period is followed by a flash of far-red (FR) light, then the plant detects no interruption of night length. As in the case of phytochrome-mediated seed germination, red/far-red photoreversibility occurs.

Plants detect night length very precisely; some short-day plants will not flower if night is even 1 minute shorter than the critical length. Some plant species always flower on the same day each year. It appears that plants use their biological clock, entrained by night length with the help of phytochrome, to tell the season of the year. The floriculture (flower-growing) industry applies this knowledge to produce flowers out of season. Chrysanthemums, for instance, are short-day plants that normally bloom in fall, but their blooming can be stalled until Mother's Day in May by punctuating each long night with a flash of light, thus turning one long night into two short nights.

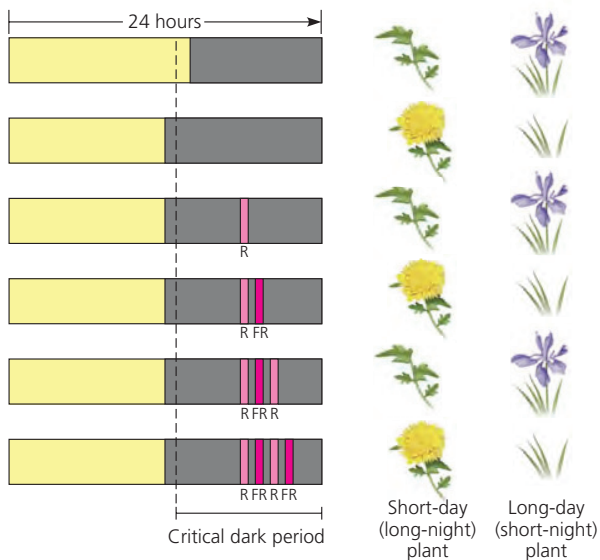
Some plants bloom after a single exposure to the photoperiod required for flowering. Other species need several successive days of the appropriate photoperiod. Still others respond to a photoperiod only if they have been previously exposed

to some other environmental stimulus, such as a period of cold. Winter wheat, for example, will not flower unless it has been exposed to several weeks of temperatures below 10°C. The use of pretreatment with cold to induce flowering is called **vernalization** (from the Latin for “spring”). Several weeks after winter wheat is vernalized, a photoperiod with long days (short nights) induces flowering.

A Flowering Hormone?

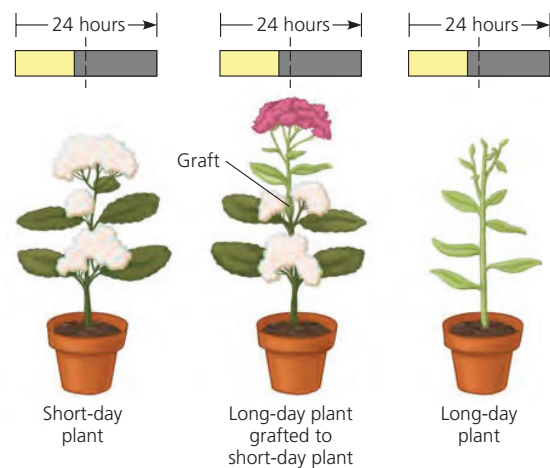
Although flowers form from apical or axillary bud meristems, it is leaves that detect changes in photoperiod and produce signaling molecules that cue buds to develop as flowers. In many short-day and long-day plants, exposing just one leaf to the appropriate photoperiod is enough to induce flowering. Indeed, as long as one leaf is left on the plant, photoperiod is detected and floral buds are induced. If all leaves are removed, the plant is insensitive to photoperiod.

Classic experiments revealed that the floral stimulus could move across a graft from an induced plant to a noninduced plant and trigger flowering in the latter. Moreover, the flowering stimulus appears to be the same for short-day and long-day plants, despite the different photoperiodic conditions required for leaves to send this signal (Figure 39.23). The hypothetical signaling molecule for flowering, called **florigen**, remained unidentified for over 70 years as scientists focused on small hormone-like molecules. However, as discussed in Chapter 36, large macromolecules, such as mRNA and proteins, can move



▲ **Figure 39.22 Reversible effects of red and far-red light on photoperiodic response.** A flash of red (R) light shortens the dark period. A subsequent flash of far-red (FR) light cancels the red flash's effect.

? How would a single flash of full-spectrum light affect each plant?



▲ **Figure 39.23 Experimental evidence for a flowering hormone.** If grown individually under short-day conditions, a short-day plant will flower and a long-day plant will not. However, both will flower if grafted together and exposed to short days. This result indicates that a flower-inducing substance (florigen) is transmitted across grafts and induces flowering in both short-day and long-day plants.

WHAT IF? If flowering were inhibited in both parts of the grafted plants, what would you conclude?

by the symplastic route via plasmodesmata (see Figure 36.6) and regulate plant development. It now appears that florigen is a macromolecule. A gene called *FLOWERING LOCUS T* (*FT*) is activated in leaf cells during conditions favoring flowering, and the FT protein travels through the symplasm to the shoot apical meristem and initiates flowering.

Whatever combination of environmental cues (such as photoperiod or vernalization) and internal signaling molecules (such as the FT protein) is necessary for flowering, the outcome is the transition of a bud's meristem from a vegetative to a flowering state. This transition requires changes in the expression of genes that regulate pattern formation. Meristem identity genes that induce the bud to form a flower instead of a vegetative shoot must be switched on. Then the organ identity genes that specify the spatial organization of the floral organs—sepals, petals, stamens, and carpels—are activated in the correct regions of the meristem (see Figure 35.34).

CONCEPT CHECK 39.3

1. If an enzyme in field-grown soybean leaves is most active at noon and least active at midnight, is its activity under circadian regulation?
2. A guard absentmindedly turns on the lights in a greenhouse one night, but the plants still flower on schedule. Suggest two reasons why they were not affected by the interruption of darkness.
3. Some vine seedlings grow toward darkness until reaching an upright structure. This adaptation helps them “find” a shaded object to climb. How might you test whether this negative phototropism is mediated by blue-light photoreceptors or by phytochrome?
4. **WHAT IF?** If a plant flowers in a controlled chamber with a daily cycle of 10 hours of light and 14 hours of darkness, is it a short-day plant? Explain.
5. **MAKE CONNECTIONS** Plants detect the quality of their light environment by using blue-light photoreceptors and red-light-absorbing phytochromes. After reviewing Figure 10.10 (p. 191), suggest a reason why plants are so sensitive to these colors of light.

For suggested answers, see Appendix A.

CONCEPT 39.4

Plants respond to a wide variety of stimuli other than light

EVOLUTION Plants can neither migrate to a watering hole when water is scarce nor seek shelter from wind. A seed landing upside down in the soil cannot maneuver itself into an upright position. Plants are immobile, but mechanisms have evolved by natural selection that enable them to adjust to a

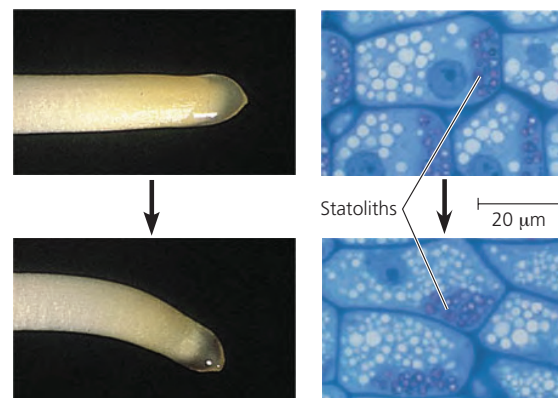
wide range of environmental circumstances by developmental or physiological means. Light is so important in the life of a plant that we devoted the entire previous section to a plant's reception of and response to this one environmental factor. In this section, we examine responses to some of the other environmental stimuli that a plant commonly encounters.

Gravity

Because plants are solar-powered organisms, it is not surprising that mechanisms for growing toward sunlight have evolved. But what environmental cue does the shoot of a young seedling use to grow upward when it is completely underground and there is no light for it to detect? Similarly, what environmental factor prompts the young root to grow downward? The answer to both questions is gravity.

Place a plant on its side, and it adjusts its growth so that the shoot bends upward and the root curves downward. In their responses to gravity, or **gravitropism**, roots display positive gravitropism (Figure 39.24a) and shoots exhibit negative gravitropism. Gravitropism occurs as soon as a seed germinates, ensuring that the root grows into the soil and the shoot grows toward sunlight, regardless of how the seed is oriented when it lands.

Plants may detect gravity by the settling of **statoliths**, dense cytoplasmic components that settle under the influence of gravity to the lower portions of the cell. The statoliths of vascular plants are specialized plastids containing dense starch grains (Figure 39.24b). In roots, statoliths are located in certain cells of the root cap. According to one



(a) Over the course of hours, a horizontally oriented primary root of maize bends gravitropically until its growing tip becomes vertically oriented (LMs).

(b) Within minutes after the root is placed horizontally, plastids called statoliths begin settling to the lowest sides of root cap cells. This settling may be the gravity-sensing mechanism that leads to redistribution of auxin and differing rates of elongation by cells on opposite sides of the root (LMs).

▲ Figure 39.24 Positive gravitropism in roots: the statolith hypothesis.

hypothesis, the aggregation of statoliths at the low points of these cells triggers a redistribution of calcium, which causes lateral transport of auxin within the root. The calcium and auxin accumulate on the lower side of the root's zone of elongation. At high concentration, auxin inhibits cell elongation, an effect that slows growth on the root's lower side. The more rapid elongation of cells on the upper side causes the root to curve as it grows. This tropism continues until the root grows straight down.

Based on new experiments, plant physiologists are refining the "falling statolith" hypothesis of root gravitropism. For example, they have found mutants of *Arabidopsis* and tobacco that lack statoliths but are still capable of gravitropism, though the response is slower than in wild-type plants. It could be that the entire cell helps the root sense gravity by mechanically pulling on proteins that tether the protoplast to the cell wall, stretching the proteins on the "up" side and compressing the proteins on the "down" side of the root cells. Dense organelles, in addition to starch granules, may also contribute by distorting the cytoskeleton as they are pulled by gravity. Statoliths, because of their density, may enhance gravitational sensing by a mechanism that simply works more slowly in their absence.

Mechanical Stimuli

A tree growing on a windy mountain ridge usually has a shorter, stockier trunk than a tree of the same species growing in a more sheltered location. The advantage of this stunted morphology is that it enables the plant to hold its ground against strong gusts of wind. The term **thigmomorphogenesis** (from the Greek *thigma*, touch) refers to the changes in form that result from mechanical perturbation. Plants are very sensitive to mechanical stress: Even the act of measuring the length of a leaf with a ruler alters its subsequent growth. Rubbing the stems of a young plant a couple of times daily results in plants that are shorter than controls (**Figure 39.25**).

Some plant species have become, over the course of their evolution, "touch specialists." Acute responsiveness to mechanical stimuli is an integral part of these plants' "life strategies." Most vines and other climbing plants have tendrils that coil rapidly around supports (see Figure 35.7). These grasping organs usually grow straight until they touch something; the contact stimulates a coiling response caused by differential growth of cells on opposite sides of the tendril. This directional growth in response to touch is called **thigmotropism**, and it allows the vine to take advantage of whatever mechanical supports it comes across as it climbs upward toward a forest canopy.

Other examples of touch specialists are plants that undergo rapid leaf movements in response to mechanical stimulation. For example, when the compound leaf of the sensitive plant *Mimosa pudica* is touched, it collapses and its leaflets fold



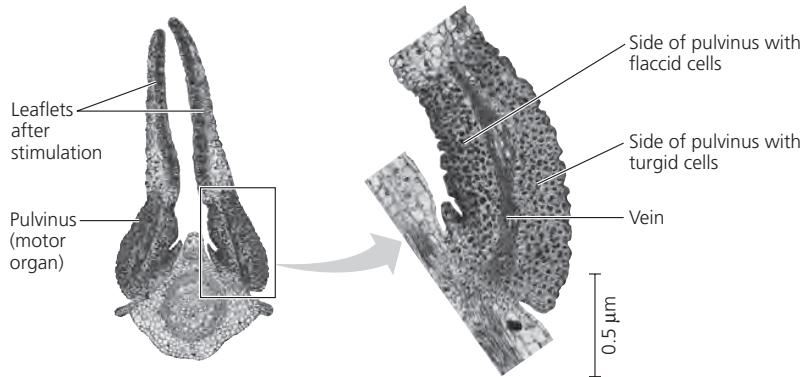
▲ **Figure 39.25 Altering gene expression by touch in *Arabidopsis*.** The shorter plant on the left was rubbed twice a day. The untouched plant (right) grew much taller.

together (**Figure 39.26**). This response, which takes only a second or two, results from a rapid loss of turgor in cells within pulvini, specialized motor organs located at the joints of the leaf. The motor cells suddenly become flaccid after stimulation because they lose potassium ions, causing water to leave the cells by osmosis. It takes about 10 minutes for the cells to regain their turgor and restore the "unstimulated" form of the leaf. The function of the sensitive plant's behavior invites speculation. Perhaps by folding its leaves and reducing its surface area when jostled by strong winds, the plant conserves water. Or perhaps because the collapse of the leaves exposes thorns on the stem, the rapid response of the sensitive plant discourages herbivores.

A remarkable feature of rapid leaf movements is the mode of transmission of the stimulus through the plant. If one leaflet on a sensitive plant is touched, first that leaflet responds, then the adjacent leaflet responds, and so on, until all the leaflet pairs have folded together. From the point of stimulation, the signal that produces this response travels at a speed of about 1 cm/sec. An electrical impulse traveling at the same rate can be detected when electrodes are attached to the leaf. These impulses, called **action potentials**, resemble nerve impulses in animals, though the action potentials of plants are thousands of times slower. Action potentials have been discovered in many species of algae and plants and may be used as a form of internal communication. For example, in the Venus flytrap (*Dionaea muscipula*), action potentials are transmitted from sensory hairs in the trap to the cells that respond by closing the trap (see Figure 37.15). In the case of *Mimosa pudica*, more violent stimuli, such as touching a leaf



(a) Unstimulated state (leaflets spread apart) (b) Stimulated state (leaflets folded)



(c) Cross section of a leaflet pair in the stimulated state (LM). The pulvinus (motor organ) becomes curved when motor cells on one side of the pulvinus lose water and become flaccid while cells on the opposite side retain their turgor.

▲ **Figure 39.26** Rapid turgor movements by the sensitive plant (*Mimosa pudica*).

with a hot needle, causes *all* the leaves and leaflets on a plant to droop, but this whole-plant response involves the spread of signaling molecules released from the injured area to other parts of the shoot.

Environmental Stresses

Certain factors in the environment may change severely enough to have a potentially adverse effect on a plant's survival, growth, and reproduction. Environmental stresses, such as flooding, drought, or extreme temperatures, can have a devastating impact on crop yields in agriculture. In natural ecosystems, plants that cannot tolerate an environmental stress will either succumb or be outcompeted by other plants, and they will become locally extinct. Thus, environmental stresses are an important factor in determining the geographic ranges of plants. Here we will consider some of the more common **abiotic** (nonliving) stresses that plants encounter. In the last section of this chapter, we will examine the defensive responses of plants to common **biotic** (living) stresses, such as herbivores and pathogens.

Drought

On a sunny, dry day, a plant may wilt because its water loss by transpiration exceeds the ability of the root system to absorb water from the soil. Prolonged drought can stress crops and the plants of natural ecosystems for weeks or months. Severe water deficit, of course, will kill a plant, as you may know from experience with neglected houseplants. But plants have control systems that enable them to cope with less extreme water deficits.

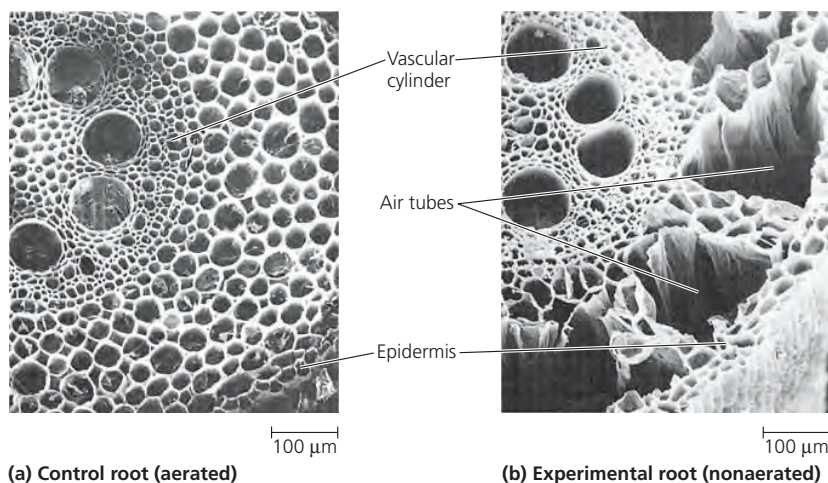
Many of a plant's responses to water deficit help the plant conserve water by reducing the rate of transpiration. Water deficit in a leaf causes guard cells to lose turgor, a simple control mechanism that slows transpiration by closing stomata (see Figure 36.15). Water deficit also stimulates increased synthesis and release of abscisic acid in the leaf; this hormone helps keep stomata closed by acting on guard cell membranes. Leaves respond to water deficit in several other ways. For example, when the leaves of grasses wilt, they roll into a tubelike shape that reduces transpiration by exposing less leaf surface to dry air and wind. Other plants, such as ocotillo (see Figure 36.16), shed their leaves in response to seasonal drought. Although these leaf responses

conserve water, they also reduce photosynthesis, which is one reason why a drought diminishes crop yield.

Root growth also responds to water deficit. During a drought, the soil usually dries from the surface down. This inhibits the growth of shallow roots, partly because cells cannot maintain the turgor required for elongation. Deeper roots surrounded by soil that is still moist continue to grow. Thus, the root system proliferates in a way that maximizes exposure to soil water.

Flooding

Too much water is also a problem for a plant. An overwatered houseplant may suffocate because the soil lacks the air spaces that provide oxygen for cellular respiration in the roots. Some plants are structurally adapted to very wet habitats. For example, the submerged roots of mangroves, which inhabit coastal marshes, are continuous with aerial roots exposed to oxygen (see Figure 35.4). But how do less specialized plants cope with oxygen deprivation in waterlogged soils? Oxygen deprivation stimulates the production of ethylene, which causes some



▲ Figure 39.27 A developmental response of maize roots to flooding and oxygen deprivation. (a) A cross section of a control root grown in an aerated hydroponic medium. (b) A root grown in a nonaerated hydroponic medium. Ethylene-stimulated apoptosis (programmed cell death) creates the air tubes (SEMs).

cells in the root cortex to undergo apoptosis. The destruction of these cells creates air tubes that function as “snorkels,” providing oxygen to the submerged roots (**Figure 39.27**).

Salt Stress

An excess of sodium chloride or other salts in the soil threatens plants for two reasons. First, by lowering the water potential of the soil solution, salt can cause a water deficit in plants even though the soil has plenty of water. As the water potential of the soil solution becomes more negative, the water potential gradient from soil to roots is lowered, thereby reducing water uptake (see Chapter 36). Another problem with saline soil is that sodium and certain other ions are toxic to plants when their concentrations are so high that they overwhelm the selective permeability capabilities of the root cell membranes. Many plants can respond to moderate soil salinity by producing solutes that are well tolerated at high concentrations: These mostly organic compounds keep the water potential of cells more negative than that of the soil solution without admitting toxic quantities of salt. However, most plants cannot survive salt stress for long. The exceptions are halophytes, salt-tolerant plants with adaptations such as salt glands that pump salts out across the leaf epidermis.

Heat Stress

As is true for other organisms, excessive heat harms and even kills a plant by denaturing its enzymes and disrupting its metabolism. One result of transpiration is evaporative cooling. On a warm day, for example, the temperature of a leaf may be 3–10°C below the ambient air temperature. Hot, dry weather also tends to dehydrate many plants; the closing of stomata in

response to this stress conserves water but then sacrifices evaporative cooling. This dilemma is one reason why very hot, dry days take a toll on most plants.

Most plants have a backup response that enables them to survive heat stress. Above a certain temperature—about 40°C for most plants in temperate regions—plant cells begin synthesizing **heat-shock proteins**, which help protect other proteins from heat stress. This response also occurs in heat-stressed animals and microorganisms. Some heat-shock proteins are chaperone proteins (chaperonins), which function in unstressed cells as temporary scaffolds that help other proteins fold into their functional shapes (see Chapter 5). In their roles as heat-shock proteins, perhaps these molecules bind to other proteins and help prevent their denaturation.

Cold Stress

One problem plants face when the temperature of the environment falls is a change in the fluidity of cell membranes. Recall from Chapter 7 that a biological membrane is a fluid mosaic, with proteins and lipids moving laterally in the plane of the membrane. When a membrane cools below a critical point, it loses its fluidity as the lipids become locked into crystalline structures. This alters solute transport across the membrane and also adversely affects the functions of membrane proteins. Plants respond to cold stress by altering the lipid composition of their membranes. For example, membrane lipids increase in their proportion of unsaturated fatty acids, which have shapes that help keep membranes fluid at lower temperatures by impeding crystal formation (see Figure 7.8a). Such membrane modification requires from several hours to days, which is one reason why unseasonably cold temperatures are generally more stressful to plants than the more gradual seasonal drop in air temperature.

Freezing is another type of cold stress. At subfreezing temperatures, ice forms in the cell walls and intercellular spaces of most plants. The cytosol generally does not freeze at the cooling rates encountered in nature because it contains more solutes than the very dilute solution found in the cell wall, and solutes lower the freezing point of a solution. The reduction in liquid water in the cell wall caused by ice formation lowers the extracellular water potential, causing water to leave the cytoplasm. The resulting increase in the concentration of ions in the cytoplasm is harmful and can lead to cell death. Whether the cell survives depends largely on how well it resists dehydration. In regions with cold winters, native plants are adapted to cope with freezing stress. For example, before

the onset of winter, the cells of many frost-tolerant species increase cytoplasmic levels of specific solutes, such as sugars, that are well tolerated at high concentrations and that help reduce the loss of water from the cell during extracellular freezing. The unsaturation of membrane lipids also increases, thereby maintaining proper levels of membrane fluidity.

Many organisms, including certain vertebrates, fungi, bacteria, and many species of plants, have special proteins that hinder ice crystals from growing, helping the organism escape freezing damage. First described in Arctic fish in the 1950s, these *antifreeze proteins* permit survival at temperatures below 0°C. Antifreeze proteins bind to small ice crystals and inhibit their growth or, in the case of plants, prevent the crystallization of ice. The five major classes of antifreeze proteins differ markedly in their amino acid sequences but have a similar three-dimensional structure, suggesting convergent evolution. Surprisingly, antifreeze proteins from winter rye are homologous to antifungal proteins called PR proteins that you'll learn about later in the chapter, but they are produced in response to cold temperatures and shorter days, not fungal pathogens. Progress is being made in increasing the freezing tolerance of crop plants by genetically engineering antifreeze protein genes into their genomes.

CONCEPT CHECK 39.4

1. Thermal images are photographs of the heat emitted by an object. Researchers have used thermal imaging of plants to isolate mutants that overproduce abscisic acid. Suggest a reason why these mutants are warmer than wild-type plants under conditions that are normally nonstressful.
2. A greenhouse worker finds that potted chrysanthemums nearest to the aisles are often shorter than those in the middle of the bench. Explain this “edge effect,” a common problem in horticulture.
3. **WHAT IF?** If you removed the root cap from a root, would the root still respond to gravity? Explain.

For suggested answers, see Appendix A.

CONCEPT 39.5

Plants respond to attacks by herbivores and pathogens

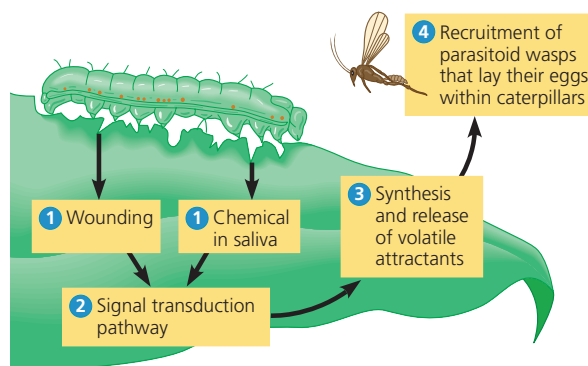
EVOLUTION Through natural selection, plants have evolved many types of interactions with other species in their communities. Some interspecific interactions are mutually beneficial, such as the associations of plants with mycorrhizal fungi (see Figure 37.13) or with pollinators (see Figure 38.4). Most of a plant's interactions with other organisms, however, do not benefit the plant. As primary producers, plants are at the

base of most food webs and are subject to attack by a wide range of plant-eating (herbivorous) animals. A plant is also subject to infection by diverse viruses, bacteria, and fungi that can damage tissues or even kill the plant. Plants counter these threats with defense systems that deter herbivory and prevent infection or combat pathogens that infect the plant.

Defenses Against Herbivores

Herbivory—animals eating plants—is a stress that plants face in any ecosystem. Plants prevent excessive herbivory by using both physical defenses, such as thorns and trichomes, and chemical defenses, such as the production of distasteful or toxic compounds. For example, some plants produce an unusual amino acid called *canavanine*, named for one of its sources, the jackbean (*Canavalia ensiformis*). Canavanine resembles arginine, one of the 20 amino acids that organisms incorporate into their proteins. If an insect eats a plant containing canavanine, the molecule is incorporated into the insect's proteins in place of arginine. Because canavanine is different enough from arginine to adversely affect the shape and hence the function of the proteins, the insect dies.

Some plants even “recruit” predatory animals that help defend the plant against specific herbivores. Consider the insects called parasitoid wasps, which inject their eggs into caterpillars feeding on plants. The eggs hatch within the caterpillars, and the larvae eat through their organic containers from the inside out. The plant, which benefits from the destruction of the herbivorous caterpillars, has an active role in this drama. A leaf damaged by caterpillars releases volatile compounds that attract parasitoid wasps. The stimulus for this response is a combination of physical damage to the leaf caused by the munching caterpillar and a specific compound in the caterpillar's saliva (Figure 39.28).



▲ **Figure 39.28** A maize leaf “recruiting” a parasitoid wasp as a defensive response to an armyworm caterpillar, an herbivore.

The volatile molecules a plant releases in response to herbivore damage can also function as an early warning system for nearby plants of the same species. For example, lima bean plants infested with spider mites release a cocktail of volatile chemicals, including methyljasmonic acid, that signal “news” of the attack to neighboring, noninfested lima bean plants. In response to these volatile compounds, the neighbors instigate biochemical changes that make themselves less susceptible, including the release of volatile chemicals that attract another predatory mite species that feeds on spider mites. Researchers have even transgenically engineered *Arabidopsis* plants to produce two volatile chemicals that normally are not made by *Arabidopsis* but which have been found to attract carnivorous predatory mites in other plants. The predatory mites become attracted to the genetically modified *Arabidopsis*, a finding that could have implications for the genetic engineering of insect resistance in crop plants.

Defenses Against Pathogens

A plant’s first line of defense against infection is the physical barrier presented by the epidermis and periderm of the plant body (see Figure 35.19). This first defense system, however, is not impenetrable. The mechanical wounding of leaves by herbivores, for example, opens up portals for invasion by pathogens. Even when plant tissues are intact, viruses, bacteria, and the spores and hyphae of fungi can still enter the plant through natural openings in the epidermis, such as stomata.

When a pathogen invades a plant, the plant mounts a second line of defense, a chemical attack that destroys the pathogen and prevents its spread from the site of infection. This second defense system is enhanced by the plant’s ability to recognize certain pathogens. Successful pathogens cause disease because they evade recognition or suppress the host’s defense mechanisms.

Host-Pathogen Coevolution

Pathogens against which a plant has little specific defense are **virulent** pathogens. Strains of pathogens that mildly harm but do not kill the host plant are said to be **avirulent** pathogens. Virulent pathogens are the exceptions. If they were not, hosts and pathogens would soon perish together. Complete resistance to a pathogen often comes at an energetic cost to the plant, however, and in the absence of the pathogen, resistant plants are outcompeted by those with less resistance. Of course, plants with no resistance will succumb to a pathogen outbreak. Thus, a “compromise” has evolved between plants and most of their pathogens: The pathogen gains enough access to its host to enable it to perpetuate itself without severely damaging or killing the plant.

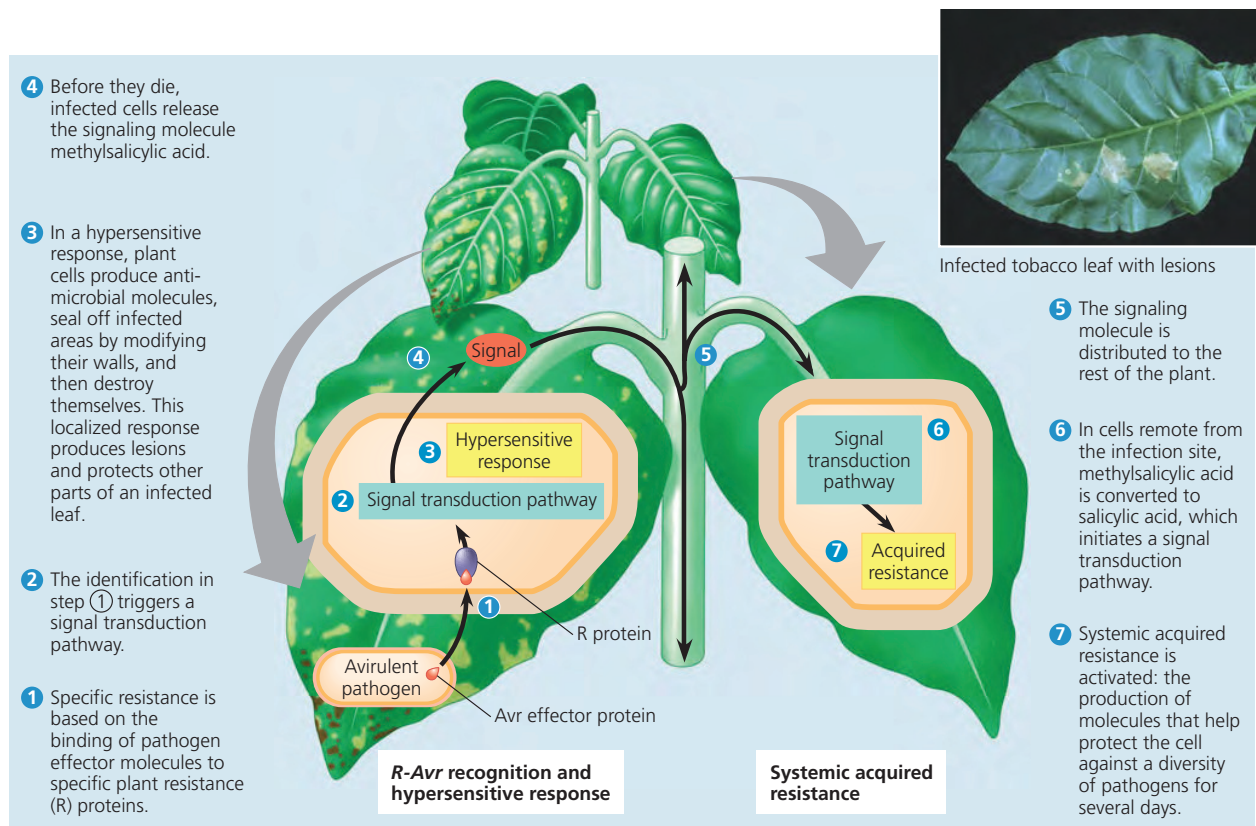
Gene-for-gene recognition is a form of plant disease resistance in which pathogen-derived molecules called *effectors* are recognized by one of the hundreds of resistance (*R*) genes in a plant’s genome. Protein effectors, encoded by the pathogen’s avirulence (*Avr*) genes, can facilitate infection in plants that lack the appropriate *R* protein by redirecting the host’s metabolism to the pathogen’s advantage. In those plants that do have the appropriate *R* protein, however, such effector proteins can directly trigger a suite of strong defense responses. The recognition of effectors by *R* proteins triggers signal transduction pathways leading to the activation of an arsenal of defense responses, including a local defense called the hypersensitive response and a general defense called systemic acquired resistance. **Local and systemic responses to pathogens require extensive genetic reprogramming and commitment of cellular resources. Therefore, a plant activates these defenses only after detecting an invading pathogen.**

The Hypersensitive Response

The **hypersensitive response** is a defense response that causes cell and tissue death near the infection site, thereby restricting the spread of a pathogen. **After the cells at the infection site mount a chemical defense and seal off the area, they destroy themselves.** As indicated in **Figure 39.29**, the hypersensitive response is initiated when pathogen effectors bind to *R* proteins and stimulate the production of phytoalexins, which are compounds having fungicidal and bactericidal properties. The hypersensitive response also induces production of *PR proteins* (pathogenesis-related proteins), many of which are enzymes that hydrolyze components in the cell walls of pathogens. Infection also stimulates the formation of lignin and the cross-linking of molecules within the plant cell wall, responses that hinder the spread of the pathogen to other parts of the plant. We can see the result of a hypersensitive response as lesions on a leaf, as shown at the upper right in the figure. As “sick” as such a leaf appears, it will still survive, and its defensive response will help protect the rest of the plant.

Systemic Acquired Resistance

The hypersensitive response is localized and specific. However, as noted previously, pathogen invasions can also produce signaling molecules that **“sound the alarm” of infection to the whole plant. The resulting systemic acquired resistance arises from** the plant-wide expression of defense genes. It is nonspecific, providing protection against a diversity of pathogens that lasts for days. The search for a signaling molecule that moves from the infection site to elicit systemic acquired resistance led to the identification of *methylsalicylic acid* as the most likely candidate. Methylsalicylic acid is produced around the infection site and carried by the phloem throughout the plant, where it is converted to



▲ **Figure 39.29 Defense responses against an avirulent pathogen.** Plants can often prevent the systemic spread of infection by instigating a hypersensitive response. This response helps isolate the pathogen by producing lesions that form “rings of death” around the sites of infection.

salicylic acid in areas remote from the sites of infection. Salicylic acid activates a signal transduction pathway that induces the production of PR proteins and resistance to pathogen attack (see Figure 39.29).

Plant disease epidemics, such as the potato blight (see pp. 588–589) that caused the Irish potato famine of the 1840s, can lead to incalculable human misery. Other diseases, such as chestnut blight (see p. 650) and sudden oak death (see p. 1214), can dramatically alter community structures. Plant epidemics are often the result of infected plants or timber being inadvertently transported around the world. As global commerce increases, such epidemics will become increasingly more common. To prepare for such outbreaks, plant biologists are stockpiling the seeds of wild relatives of crop plants in special storage facilities. Scientists hope that undomesticated relatives may have genes that will be able to curb the next plant epidemic. These scientists, along with thousands of other plant biologists, are extending an age-old tradition of curiosity about the green organisms that feed our species and the biosphere.

CONCEPT CHECK 39.5

1. What are some drawbacks of spraying fields with general-purpose insecticides?
2. Chewing insects mechanically damage plants and lessen the surface area of leaves for photosynthesis. In addition, these insects make plants more vulnerable to pathogen attack. Suggest a reason why.
3. Many fungal pathogens get their food by causing plant cells to become leaky, thereby releasing nutrients into the intercellular spaces. Would it benefit the fungus to kill the host plant in a way that results in all the nutrients leaking out?
4. **WHAT IF?** Suppose a scientist finds that a population of plants growing in a breezy location is more prone to herbivory by insects than a population of the same species growing in a sheltered area. Suggest a hypothesis to account for this observation.

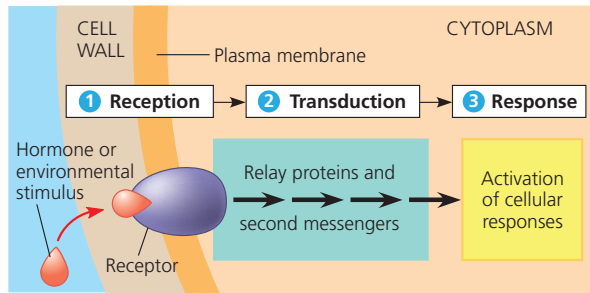
For suggested answers, see Appendix A.

39 CHAPTER REVIEW

SUMMARY OF KEY CONCEPTS

CONCEPT 39.1

Signal transduction pathways link signal reception to response (pp. 821–824)



? What are two common ways by which signal transduction pathways enhance the activity of specific enzymes?

CONCEPT 39.2

Plant hormones help coordinate growth, development, and responses to stimuli (pp. 824–835)

- Hormones control plant growth and development by affecting the division, elongation, and differentiation of cells. Some hormones also mediate the responses of plants to environmental stimuli.

Plant Hormone	Major Responses
Auxin	Stimulates cell elongation; regulates branching and organ bending.
Cytokinins	Stimulate plant cell division; promote later bud growth; slow organ death.
Gibberellins	Promote stem elongation; help seeds break dormancy and use stored reserves.
Brassinosteroids	Chemically similar to the sex hormones of animals; induce cell elongation and division.
Absciscic acid	Promotes stomatal closure in response to drought; promotes seed dormancy.
Strigolactones	Regulate apical dominance, seed germination, and mycorrhizal associations.
Ethylene	Mediates fruit ripening.

? Is there any truth to the old adage, “One bad apple spoils the whole bunch?” Explain.

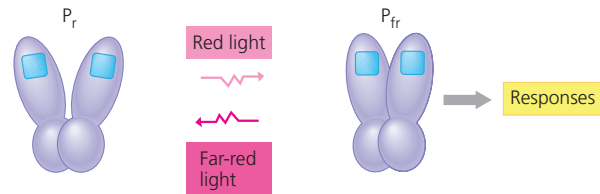
CONCEPT 39.3

Responses to light are critical for plant success (pp. 835–841)

- Blue-light photoreceptors** control hypocotyl elongation, stomatal opening, and phototropism.

- Phytochromes** act like molecular “on-off” switches. Red light turns phytochrome “on,” and far-red light turns it “off.” Phytochrome regulates shade avoidance and the germination of many seed types.

Photoreversible states of phytochrome:



- Phytochrome conversion also provides information about the relative lengths of day and night (photoperiod) and hence the time of year. Photoperiodism regulates the time of flowering in many species. **Short-day plants** require a night longer than a critical length to flower. **Long-day plants** need a night length shorter than a critical period to flower.
- Many daily rhythms in plant behavior are controlled by an internal circadian clock. Free-running circadian cycles are approximately 24 hours long but are entrained to exactly 24 hours by dawn and dusk effects on phytochrome form.

? Why did plant physiologists propose the existence of a mobile molecule (florigen) that triggers flowering?

CONCEPT 39.4

Plants respond to a wide variety of stimuli other than light (pp. 841–845)

- Gravitropism** is the bending of an organ in response to gravity. Roots show positive gravitropism, and stems show negative gravitropism. **Statoliths**, starch-filled plastids, enable plant roots to detect gravity.
- Plants are highly sensitive to touch. **Thigmotropism** is a growth response to touch. Rapid leaf movements involve transmission of electrical impulses called action potentials.
- Plants are sensitive to environmental stresses, including drought, flooding, high salinity, and extremes of temperature.

Environmental Stress	Major Response
Drought	ABA production, reducing water loss by closing stomata
Flooding	Formation of air tubes that help roots survive oxygen deprivation
Salt	Avoiding osmotic water loss by producing solutes tolerated at high concentrations
Heat	Synthesis of heat-shock proteins, which reduce protein denaturation at high temperatures
Cold	Adjusting membrane fluidity; avoiding osmotic water loss; producing antifreeze proteins

? Plants that have acclimated to drought stress are often more resistant to freezing stress as well. Suggest a reason why.

CONCEPT 39.5

Plants respond to attacks by herbivores and pathogens (pp. 845–847)

- In addition to physical defenses such as thorns and trichomes, plants produce distasteful or toxic chemicals, as well as attractants that recruit animals that destroy herbivores.
- The **hypersensitive response** seals off an infection and destroys both pathogen and host cells in the region. **Systemic acquired resistance** is a generalized defense response in organs distant from the infection site.

? How do chewing insects make plants more susceptible to pathogens?

TEST YOUR UNDERSTANDING

LEVEL 1: KNOWLEDGE/COMPREHENSION

- The hormone that helps plants respond to drought is
 - auxin.
 - gibberellin.
 - cytokinin.
 - ethylene.
 - abscisic acid.
- Auxin enhances cell elongation in all of these ways *except*
 - increased uptake of solutes.
 - gene activation.
 - acid-induced denaturation of cell wall proteins.
 - increased activity of plasma membrane proton pumps.
 - cell wall loosening.
- Charles and Francis Darwin discovered that
 - auxin is responsible for phototropic curvature.
 - auxin can pass through agar.
 - light destroys auxin.
 - light is perceived by the tips of coleoptiles.
 - red light is most effective in shoot phototropism.
- How may a plant respond to *severe* heat stress?
 - by reorienting leaves to increase evaporative cooling
 - by creating air tubes for ventilation
 - by initiating a systemic acquired resistance response
 - by increasing the proportion of unsaturated fatty acids in cell membranes, reducing their fluidity
 - by producing heat-shock proteins, which may protect the plant's proteins from denaturing

LEVEL 2: APPLICATION/ANALYSIS

- The signaling molecule for flowering might be released earlier than usual in a long-day plant exposed to flashes of
 - far-red light during the night.
 - red light during the night.
 - red light followed by far-red light during the night.
 - far-red light during the day.
 - red light during the day.
- If a long-day plant has a critical night length of 9 hours, which 24-hour cycle would prevent flowering?
 - 16 hours light/8 hours dark
 - 14 hours light/10 hours dark
 - 15.5 hours light/8.5 hours dark
 - 4 hours light/8 hours dark/4 hours light/8 hours dark
 - 8 hours light/8 hours dark/light flash/8 hours dark
- A plant mutant that shows normal gravitropic bending but does not store starch in its plastids would require a reevaluation of the role of _____ in gravitropism.
 - auxin
 - calcium
 - statoliths
 - light
 - differential growth

- Which type of mutant would be most likely to produce a bushier phenotype?
 - auxin overproducer
 - strigolactone overproducer
 - cytokinin underproducer
 - gibberellin overproducer
 - strigolactone underproducer
- DRAW IT** Indicate the response to each condition by drawing a straight seedling or one with the triple response.

	Control	Ethylene added	Ethylene synthesis inhibitor
Wild-type			
Ethylene insensitive (<i>ein</i>)			
Ethylene overproducing (<i>eto</i>)			
Constitutive triple response (<i>ctr</i>)			

LEVEL 3: SYNTHESIS/EVALUATION

10. EVOLUTION CONNECTION

As a general rule, light-sensitive germination is more pronounced in small seeds compared with large seeds. Suggest a reason why.

11. SCIENTIFIC INQUIRY

A plant biologist observed a peculiar pattern when a tropical shrub was attacked by caterpillars. After a caterpillar ate a leaf, it would skip over nearby leaves and attack a leaf some distance away. Simply removing a leaf did not deter caterpillars from eating nearby leaves. The biologist suspected that an insect-damaged leaf sent out a chemical that signaled nearby leaves. How could the researcher test this hypothesis?

12. SCIENCE, TECHNOLOGY, AND SOCIETY

Describe how our knowledge about the control systems of plants is being applied to agriculture or horticulture.

13. WRITE ABOUT A THEME

Environmental Interactions In a short essay (100–150 words), summarize phytochrome's role in altering shoot growth for the enhancement of light capture.

For selected answers, see Appendix A.

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1. MasteringBiology® Assignments

Experimental Inquiry Tutorial What Effect Does Auxin Have on Coleoptile Growth?

Tutorial Plant Responses to Light

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Questions Student Misconceptions • Reading Quiz • Multiple Choice • End-of-Chapter

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