Sunflower plants *(Helianthus)* with flower heads oriented toward the sun's rays—an example of a plant response to the environment.

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35 Control of Plant Growth and Development

STUDY PLAN

WHY IT MATTERS

In the early 1920s, a researcher in Japan, Eiichi Kurosawa, was studying a rice plant disease that the Japanese called *bakanae*—the "foolish seedling" disease. Stems of rice seedlings that had become infected with the fungus *Gibberella fujikuroi* elongated twice as much as uninfected plants. The lanky stems were weak and eventually toppled over before the plants could produce seeds. Kurosawa discovered that extracts of the fungus also could trigger the disease. Eventually, other investigators purified the fungus's disease-causing substance, naming it gibberellin (GA).

Botanists today recognize more than 100 chemically different gibberellins, the largest class of plant hormones. Gibberellins have been isolated from fungi and from flowering plants, and may exist in other plant groups as well. Like other hormones, gibberellins are intercellular signaling molecules. In flowering plants, gibberellins have major, predictable effects **(Figure 35.1),** beginning with seed germination.

Basic aspects of plant growth and development are adaptations that promote the survival of organisms that cannot move through their environment. These adaptations range from the triggers for seed germination to the development of a particular body form, the shift


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Figure 35.1
Effects of the hormone gibberellin on stem growth of rice plants (Oryza).

from a vegetative phase to a reproductive one, and the timed death of flowers, leaves, and other parts. Although many of the details remain elusive or disputed, ample evidence exists that an elaborate system of molecular signals regulates many of these phenomena. We know, for example, that plant hormones alter patterns of growth, cell metabolism, and morphogenesis in response to changing environmental rhythms, including seasonal changes in day length and temperature and the daily rhythms of light and dark. They also adjust those patterns in response to environmental conditions, such as the amount of sunlight or shade, moisture, soil nutrients, and other factors. Some hormones govern growth responses to directional stimuli, such as light, gravity, or the presence of nearby structures. Often, hormonal effects involve changes in gene expression, although sometimes other mechanisms are at work.

We begin by surveying the different groups of plant hormones and other signaling molecules, and then turn our attention to the remarkable diversity of responses to both internal and environmental signals.

35.1 Plant Hormones

In plants, a **hormone** (*horman* = to stimulate) is a signaling molecule that regulates or helps coordinate some aspect of the plant's growth, metabolism, or development. Plant hormones act in response to two general types of cues: Internal chemical conditions related to growth and development, and circumstances in the external environment that affect plant growth, such as light and the availability of water. Some plant hormones are transported from the tissue that produces them to another plant part, while others exert their effects in the tissue where they are synthesized.

All plant hormones share certain characteristics. They are rather small organic molecules, and all are active in extremely low concentrations. Another shared feature is specificity: each one affects a given tissue in a particular way. Hormones that have effects outside the tissue where they are produced typically are transported to their target sites in vascular tissues, or they diffuse from one plant part to another. Within these general parameters, however, plant hormones vary greatly in their effects. Some stimulate one or more aspects of the plant's growth or development, whereas others have an inhibiting influence. Adding to the potential for confusion, a given hormone can have different effects in different tissues, and the effects also can differ depending on a target tissue's stage of development. And as researchers have increasingly discovered, many physiological responses result from the interaction of two or more hormones.

Biologists recognize at least seven major classes of plant hormones **(Table 35.1):** auxins, gibberellins, cytokinins, ethylene, brassinosteroids, abscisic acid (ABA), and jasmonates. Recent discoveries have added other hormonelike signaling agents to this list of established plant hormones. We now consider each major class of plant hormones and discuss some of the newly discovered signaling molecules as well.

Auxins Promote Growth

Auxins are synthesized primarily in the shoot apical meristem and young stems and leaves. Their main effects are to stimulate plant growth by promoting cell elongation in stems and coleoptiles, and by governing growth responses to light and gravity. Our focus here is indoleacetic acid (IAA), the most important natural auxin. Botanists often use the general term "auxin" to refer to IAA, a practice we follow here.

Experiments Leading to the Discovery of Auxins. Auxins were the first plant hormones identified. The path to their discovery began in the late nineteenth century in the library of Charles Darwin's home in the English countryside (see *Focus on Research* in Chapter 19). Among his many interests, Darwin was fascinated by plant **tropisms**—movements such as the bending of a houseplant toward light. This growth response, triggered by exposure to a directional light source, is an example of a **phototropism.**

Working with his son Francis, Darwin explored phototropisms by germinating seeds of two species of grasses, oat *(Avena sativa)* and canary grass *(Phalaris canariensis),* in pots on the sill of a sunny window. Re-

Table 35.1 Major Plant Hormones and Signaling Molecules

Hormone/Signaling Compound	Where Synthesized	Tissues Affected	Effects
Auxins	Apical meristems, developing leaves and embryos	Growing tissues, buds, roots, leaves, fruits, vascular tissues	Promote growth and elongation of stems; promote formation of lateral roots and dormancy in lateral buds; promote fruit development; inhibit leaf abscission; orient plants with respect to light, gravity
Gibberellins	Root and shoot tips, young leaves, developing embryos	Stems, developing seeds	Promote cell divisions and growth and elongation of stems; promote seed germination and bolting
Cytokinins	Mainly in root tips	Shoot apical meristems, leaves, buds	Promote cell division; inhibit senescence of leaves; coordinate growth of roots and shoots (with auxin)
Ethylene	Shoot tips, roots, leaf nodes, flowers, fruits	Seeds, buds, seedlings, mature leaves, flowers, fruits	Regulates elongation and division of cells in seedling stems, roots; in mature plants regulates senescence and abscission of leaves, flowers, and fruits
Brassinosteroids	Young seeds; shoots and leaves	Mainly shoot tips, developing embryos	Stimulate cell division and elongation, differentiation of vascular tissue
Abscisic acid	Leaves	Buds, seeds, stomata	Promotes responses to environmental stress, including inhibiting growth/promoting dormancy; stimulates stomata to close in water-stressed plants
Jasmonates	Roots, seeds, probably other tissues	Various tissues, including damaged ones	In defense responses, promote transcription of genes encoding protease inhibitors; possible role in plant responses to nutrient deficiencies
Oligosaccharins	Cell walls	Damaged tissues; possibly active in most plant cells	Promote synthesis of phytoalexins in injured plants; may also have a role in regulating growth
Systemin	Damaged tissues	Damaged tissues	To date known only in tomato; roles in defense, including triggering jasmonate-induced chemical defenses
Salicylic acid	Damaged tissues	Many plant parts	Triggers synthesis of pathogenesis-related (PR) proteins, other general defenses

call from Chapter 34 that the shoot apical meristem and plumule of grass seedlings are sheathed by a protective coleoptile—a structure that is extremely sensitive to light. Darwin did not know this detail, but he observed that as the emerging shoots grew, within a few days they bent toward the light. He hypothesized that the tip of the shoot somehow detected light and communicated that information to the coleoptile. Darwin tested this idea in several ways **(Figure 35.2)** and concluded that when seedlings are illuminated from the side, "some influence is transmitted from the upper to the lower part, causing them to bend."

The Darwins' observations spawned decades of studies—a body of work that illustrates how scientific understanding typically advances step-by-step, as one set of experimental findings stimulates new research. First, scientists in Denmark and Poland showed that the bending of a shoot toward a light source was caused by something that could move through agar (a jellylike culture material derived from certain red algae) but not through a sheet of the mineral mica. This finding prompted experiments establishing that indeed the stimulus was a chemical produced in the shoot tip. Soon afterward, in 1926, experiments by the Dutch plant physiologist Frits Went confirmed that the growth-promoting chemical diffuses downward from the shoot tip to the stem below **(Figure 35.3).** Using oat seeds, Went first sliced the tips from young shoots that had been grown under normal light conditions. He then placed the tips on agar blocks and left them there long enough for diffusible substances to move into the agar. Meanwhile, the decapitated stems stopped growing, but growth quickly resumed in seedlings that Went "capped" with the agar blocks (see Figure 35.3a). Clearly, a growth-promoting substance in the excised shoot tips had diffused into the agar, and from there into the seedling stems. Went also attached an agar block to one side of a decapitated shoot tip; when the shoot began growing again it bent away from the agar (see Figure 35.3b). Importantly, Went performed his experiments in total darkness, to avoid any "contamination" of his results by the possible effects of light.

Went did not determine the mechanism—differential elongation of cells on the shaded side of a shoot—by which the growth promoter controlled phototropism. However, he did develop a test that correlated specific amounts of the substance, later named auxin (*auxein* = to increase), with particular growth effects. This careful groundwork culminated several years later when other researchers identified auxin as indoleacetic acid (IAA).

Effects of Auxins. As already noted, auxin stimulates aspects of plant growth and development. In fact, recent studies of plant development have revealed that auxin is one of the first chemical signals to help shape the plant body. When the zygote first divides, forming an embryo that consists of a basal cell and an apical cell (see Section 34.3), auxin exported by the basal cell to the apical cell helps guide the development of the various features of the embryonic shoot. As the embryo develops further, IAA is produced mainly by the leaf primordium of the young shoot (see Figure 34.22). While the developing shoot is underground, IAA is actively transported downward, stimulating the primary growth of the stem and root **(Figure 35.4).** Once an elongating shoot breaks through the soil surface, its tip is exposed to sunlight, and the first leaves unfurl and begin photosynthesis. Shortly thereafter the leaf tip stops producing IAA and that task is assumed first by cells at the leaf edges, then by cells at base of the young leaf. Even so, as Section 35.3 discusses more fully, IAA continues to influence a plant's responses to light and plays a role in plant growth responses to gravity as well. IAA also stimulates cell division in the vascular cambium and promotes the formation of secondary xylem, as well as the formation of new root apical meristems, including lateral meristems. Not all of auxin's effects promote growth, however. IAA also maintains apical dominance, which inhibits growth of lateral meristems on shoots and restricts the formation of branches (see Section 31.3). Hence, auxin is a signal that the shoot apical meristem is present and active.

Commercial orchardists spray synthetic IAA on fruit trees because it promotes uniform flowering and helps set the fruit; it also helps prevent premature fruit drop. These effects mean that all the fruit may be picked at the same time, with considerable savings in labor costs.

Some synthetic auxins are used as herbicides, essentially stimulating a target plant to "grow itself to death." An **herbicide** is any compound that, at proper concentration, kills plants. Some herbicides are selective, killing one class of plants and not others. The most widely used herbicide in the world is the synthetic auxin 2,4-D (2,4-dichlorophenoxyacetic acid). This chemical is used extensively to prevent broadleaf weeds (which are eudicots) from growing in fields of cereal crops such as corn (which are monocots). By an unknown mechanism, 2,4-D causes an abnormal burst of growth in which eudicot stems elongate more than 10 times faster than normal—much faster than the plant can support metabolically.

Auxin Transport. To exert their far-reaching effects on plant tissues, auxins must travel away from their main synthesis sites in shoot meristems and young leaves.

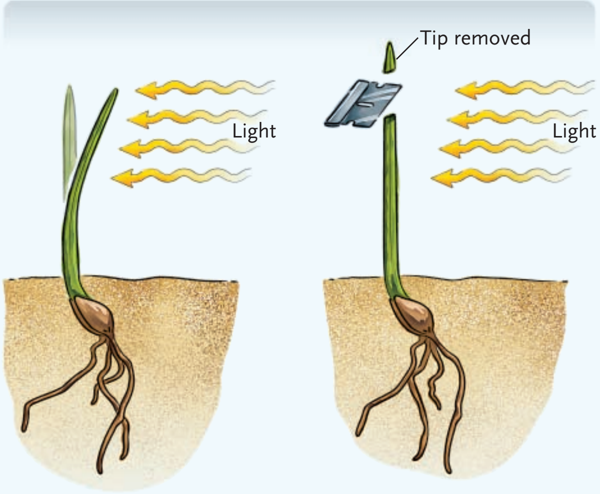
Figure 35.2 Experimental Research

The Darwins' Experiments on Phototropism

QUESTION: Why does a plant stem bend toward the light?

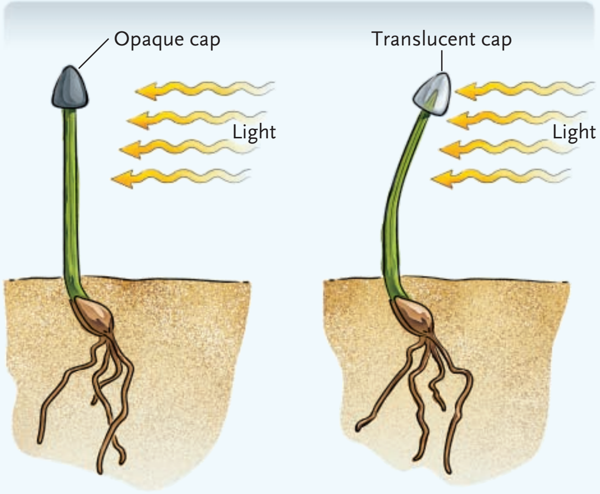
EXPERIMENT 1: The Darwins observed that the first shoot of an emerging grass seedling, which is sheathed by a coleoptile, bends toward sunlight shining through a window. They removed the shoot tip from a seedling and illuminated one side of the seedling.

Original observation



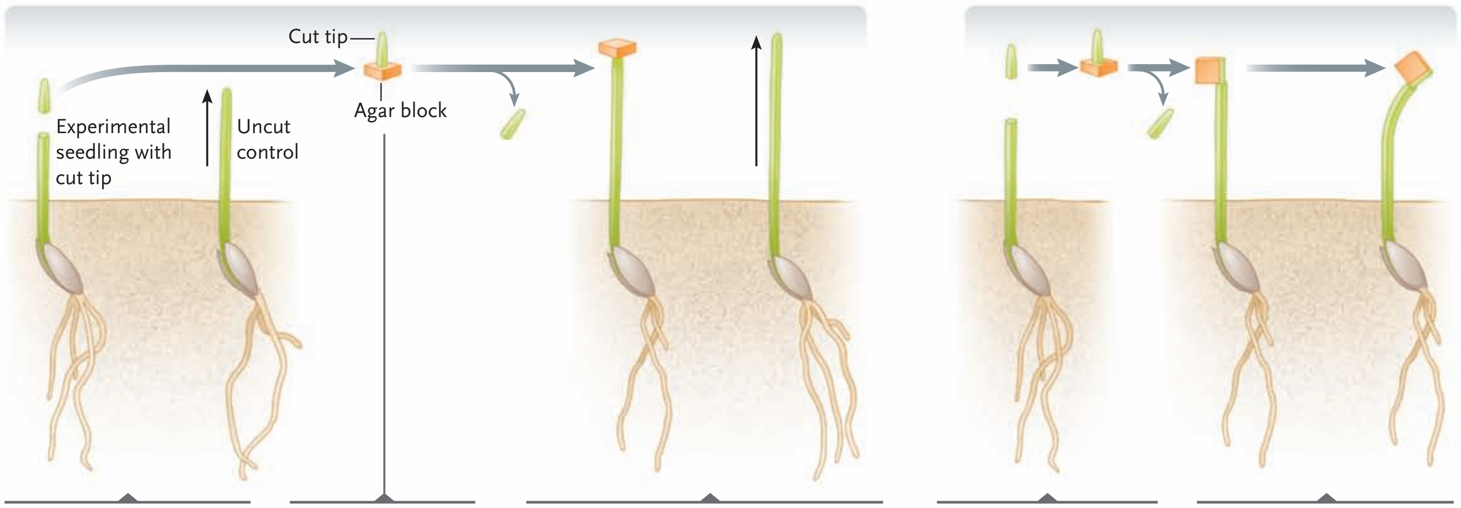
RESULT: The seedling neither grew nor bent.

EXPERIMENT 2: The Darwins divided seedlings into two groups. They covered the shoot tips of one group with an opaque cap and the shoot tips of the other group with a translucent cap. All the seedlings were illuminated from the same side.



RESULT: The seedlings with opaque caps grew but did not bend. Those with translucent caps both grew *and* bent toward the light.

CONCLUSION: When seedlings are illuminated from one side, an unknown factor transmitted from a seedling's tip to the tissue below causes it to bend toward the light.



a. The procedure showing that IAA promotes elongation of cells below the shoot tip

b. The procedure showing that cells in contact with IAA grow faster than those farther away

a.

1. After Went cut off the tip of an oat seedling, the shoot stopped elongating, while a control seedling with an intact tip continued to grow.
2. He placed the excised tip on an agar block for 1–4 hours. During that time, IAA diffused into the agar block from the cut tip.
3. Went then placed the agar block containing auxin on another detipped oat shoot, and the shoot resumed elongation, growing about as rapidly as in a control seedling with an intact shoot tip.

b.

1. Went removed the tip of a seedling and placed it on an agar block.
2. He placed the agar block containing auxin on one side of the shoot tip. Auxin moved into the shoot tip on that side, causing it to bend away from the hormone.

Figure 35.3
Two experiments by Frits Went demonstrating the effect of IAA on an oat coleoptile. Went carried out the experiments in darkness to prevent effects of light from skewing the results.

Yet xylem and phloem sap usually do not contain auxins. Moreover, experiments have shown that while IAA moves through plant tissues slowly—roughly 1 cm/hr—this rate is 10 times faster than could be explained by simple diffusion. How, then, is auxin transported?

Plant physiologists adapted the agar block method pioneered by Went to trace the direction and rate of auxin movements in different kinds of tissues. A research team led by Winslow Briggs at Stanford University determined that the shaded side of a shoot tip contains more IAA than the illuminated side. Hypothesizing that light causes IAA to move laterally from the illuminated to the shaded side of a shoot tip, the team then inserted a vertical barrier (a thin slice of mica) between the shaded and illuminated sides of a shoot tip. IAA could not cross the barrier, and when the shoot tip was illuminated it did not bend. In addition, the concentrations of IAA in the two sides of the shoot tip remained about the same. When the barrier was shortened so that the separated sides of the tip again touched, the IAA concentration in the shaded area increased significantly, and the tip *did* bend. The study confirmed that IAA initially moves laterally in the shoot tip, from the illuminated side to the shaded side, where it triggers the elongation of cells and curving of the tip toward light. Subsequent research showed that IAA then moves downward in a shoot by way of a top-to-bottom mechanism called **polar transport.** That is, IAA in a coleoptile or shoot tip travels from the apex of the tissue to its base, such as from the tip of a developing leaf to the stem. **Figure 35.5** outlines the experimental method that demonstrated polar transport. When IAA reaches roots, it moves toward the root tip.

Inside a stem, IAA appears to be transported via parenchyma cells adjacent to vascular bundles. IAA again moves by polar transport as it travels through and between cells: It enters at one end by diffusing passively through cell walls and exits at the opposite end by active transport across the plasma membrane. The mostly widely accepted explanation for polar IAA transport from cell to cell proposes different mechanisms for moving IAA into and out of plant cells. In this model, IAA enters cells as the result of a high outside/low inside hydrogen ion (H^+) concentration gradient produced by the H^+ pumps in the plasma membrane of all plant cells **(Figure 35.6)**. The movement of H^+ ions out of the cytoplasm into the cell wall also produces an electrochemical gradient. In a neutral pH environment, IAA bears a negative charge (IAA^-), but in acidic surroundings, such as in a cell wall into which H^+ has been pumped, IAA^- reacts with H^+ to form an uncharged molecule, IAAH. The uncharged molecules may then dif-

Kingsley R. Stern

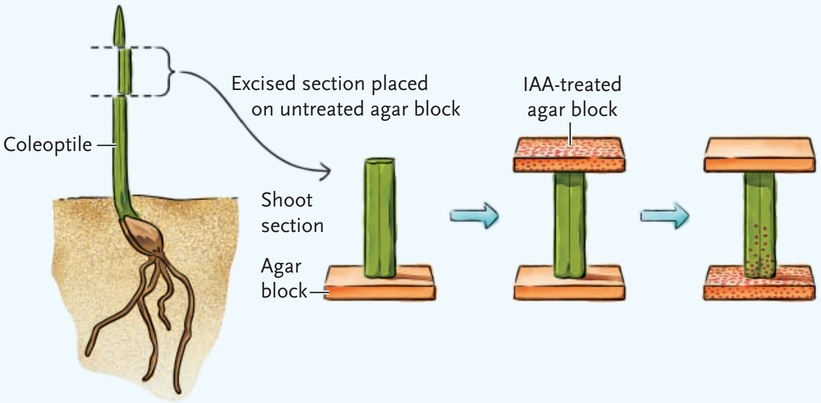
Figure 35.4
The effect of auxin treatment on a gardenia *(Gardenia)* cutting. Four weeks after an auxin was applied to the base of the cutting on the left, its stem and roots have elongated, but the number of leaves is unchanged. The plant cutting on the right was not treated.

Figure 35.5 Experimental Research

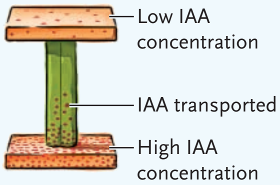
Evidence for the Polar Transport of Auxin in Plant Tissues

QUESTION: Can IAA move both upward and downward in a plant shoot?

EXPERIMENT 1: As a preliminary step, the researchers excised sections of shoot tips from grass seedlings and placed them between blocks of agar containing different concentrations of IAA labeled with radioactive carbon-14. Labeling the IAA allowed them to easily track its movements. The researchers positioned an upright shoot tip section on an untreated agar block, and then placed a second, "donor" agar block containing labeled IAA atop the section.

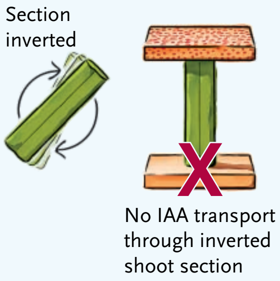


RESULT: IAA traveled from the upper block to the lower one, indicating that the hormone moved downward through the vertical shoot tip.



EXPERIMENT 2: The researchers positioned an upright shoot tip section on an agar block containing a high concentration of labeled IAA and placed a donor agar block containing a lower concentration of IAA on top.

RESULT: Even against its concentration gradient, IAA was transported from the upper block to the lower one.



EXPERIMENT 3: The shoot tip from step 2 was inverted (reversing its normal orientation), and the same procedure was performed.

RESULT: No IAA was transported downward.

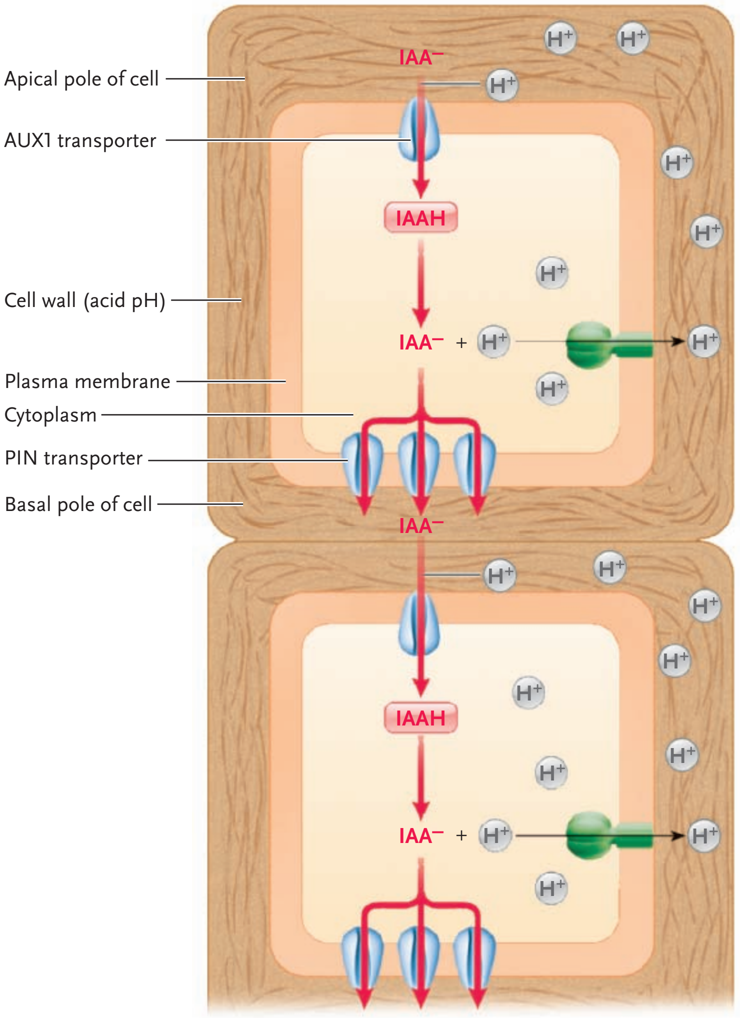
CONCLUSION: In plant shoot tips, IAA is transported in only one direction, from the shoot tip downward to plant parts below.

fuse across the plasma membrane through membrane transporters called AUX1 proteins (after the gene that encodes them in *Arabidopsis thaliana* plants), or they may enter via cotransport with H^+—or perhaps they move by both means.

A different mechanism moves IAA out of the cell at the opposite pole. Once IAAH reaches the electrically neutral cytoplasm at the apical end of the cell, it dissociates into H^+ and IAA^-. Then, the hormone crosses the cell and diffuses out of it by way of transporters called PIN proteins, which tend to be clustered at the cell's basal end. When the IAA^- diffuses through the transport proteins into the acidic cell wall, it reacts again with H^+, and the process continues with the next cell in line.

There is increasing evidence that auxin also may travel rapidly through plants in the phloem. As this work continues, researchers will undoubtedly gain a clearer understanding of how plants distribute this crucial hormone to their growing parts.

Possible Mechanisms of IAA Action. Ever since auxin was discovered, researchers have actively sought to understand how IAA stimulates cell elongation. You learned in Section 34.5 that as a plant cell elongates, the cellulose meshwork of the cell wall is first loosened



1 As auxin (IAA$^-$) diffuses through the cell wall, the acid pH makes H$^+$ bind to it. The resulting nonionized form is IAAH.

2 AUX1 transports IAAH into the cell cytoplasm.

3 In the less acidic cytoplasm, auxin gives up H$^+$ and reverts to its ionized form.

4 As H$^+$ is pumped out of the cell, the acidity of the wall increases.

5 Auxin moves out passively through PIN transporters.

6 These steps are repeated in each adjoining parenchyma cell. Thus the auxin transport shows polarity, from auxin's source in a shoot tip and leaves, downward toward the base of the stem.

Figure 35.6
A model for polar auxin transport. A plasma membrane H$^+$ pump maintains gradients of pH and electrical charge across the membrane, moving H$^+$ out of the cell using energy from ATP hydrolysis. These gradients are key to transporting IAA from the apical region to the basal region of a cell in a column. Following the gradients, at the basal end of a cell IAA diffuses through transport proteins into the cell wall, then (as IAAH) into the next cell in line.

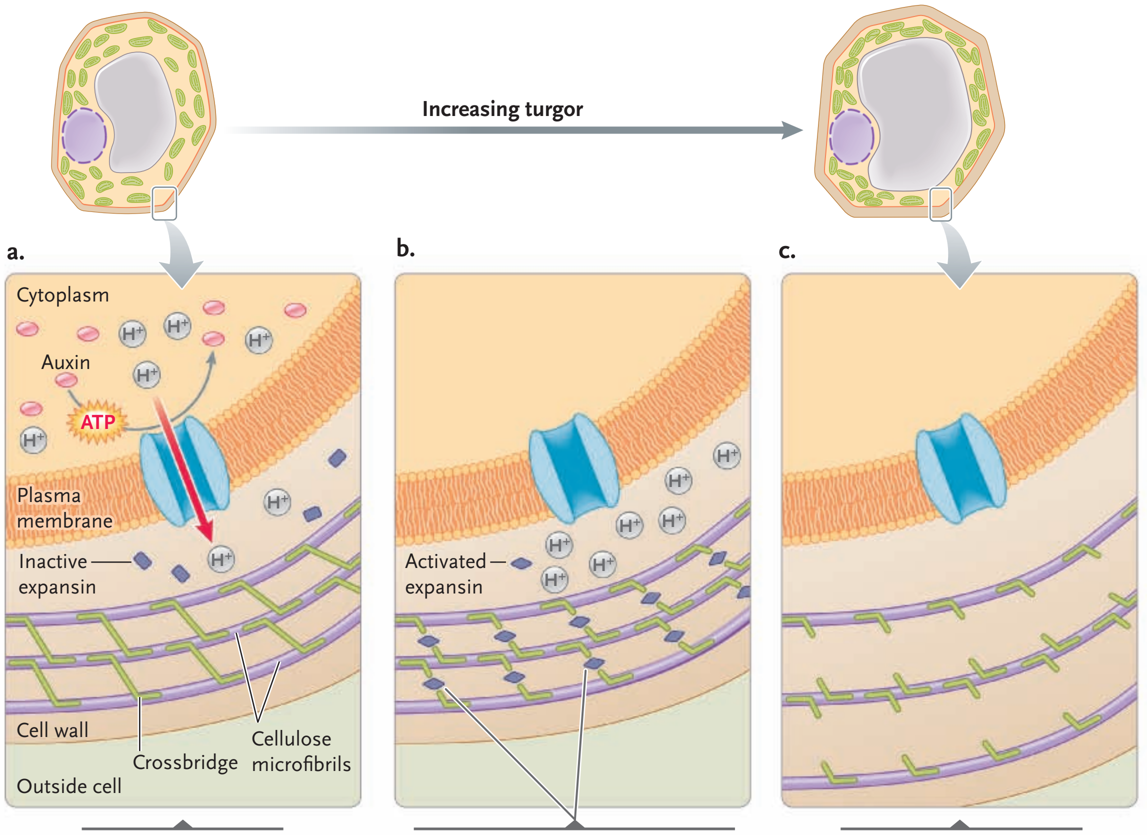
and then stretched by turgor pressure. Several hormones, and auxin especially, apparently increase the plasticity (irreversible stretching) of the cell wall. Two major hypotheses seek to explain this effect, and both may be correct.

Plant cell walls grow much faster in an acidic environment—that is, when the pH is less than 7. The **acid-growth hypothesis** suggests that auxin causes cells to secrete acid (H$^+$) into the cell wall by stimulating the plasma membrane H$^+$ pumps to move hydrogen ions from the cell interior into the cell wall; the increased acidity activates proteins called *expansins,* which penetrate the cell wall and disrupt bonds between cellulose microfibrils in the wall **(Figure 35.7).** In the laboratory, it is easy to measure an increase in the rate at which coleoptiles or stem tissues release acid when they are treated with IAA. Activation of the plasma membrane H$^+$ pump also produces a membrane potential that pulls K$^+$ and other cations into the cell; the resulting osmotic gradient draws water into the cell, increasing turgor pressure and helping to stretch the "loosened" cell walls.

A second hypothesis, which also is supported by experimental evidence, suggests that auxin triggers the expression of genes encoding enzymes that play roles in the synthesis of new wall components. Plant cells exposed to IAA don't show increased growth if they are treated with a chemical that inhibits protein synthesis. However, researchers have identified mRNAs that rapidly increase in concentration within 10 to 20 minutes after stem sections have been treated with auxin, although they still do not know exactly which proteins these mRNAs encode.

Gibberellins Also Stimulate Growth, Including the Elongation of Stems

Gibberellins stimulate several aspects of plant growth. Perhaps most apparent to humans is their ability to promote the lengthening of plant stems by stimulating both cell division and cell elongation. Synthesized in shoot and root tips and young leaves, gibberellins, like auxin, modify the properties of plant cell walls in ways that promote expansion (although the gibberellin mechanism does not involve acidification of the cell wall). It may be that the two hormones both affect expansins, or are functionally linked in some other way yet to be discovered. Gibberellins have other known effects as well, such as helping to break the dormancy of seeds and buds.



Auxin triggers pumping of H^+ into the cell wall.

Activated expansin breaks cross-bridges between cellulose microfibrils.

Cellulose microfibrils loosen.

Figure 35.7

How auxin may regulate expansion of plant cells. According to the acid-growth hypothesis, plant cells secrete acid (H^+) when auxin stimulates the plasma membrane H^+ pumps to move hydrogen ions into the cell wall; the increased acidity activates enzymes called *expansins,* which disrupt bonds between cellulose microfibrils in the wall. As a result, the wall becomes extensible and the cell can expand.

Of the 100-plus compounds of the gibberellin family, relatively few are biologically active as hormones. The others are inactive forms or serve as precursors to active forms.

Gibberellins are active in eudicots as well as in a few monocots. In most plant species that have been analyzed, the main controller of stem elongation is the gibberellin called GA_1. Normally, GA_1 is synthesized in small amounts in young leaves and transported throughout the plant in the phloem. When GA_1 synthesis goes awry, the outcome is a dramatic change in the plant's stature. For example, experiments with a dwarf variety of peas *(Pisum sativum)* and some other species show that these plants and their taller relatives differ at a single gene locus. Normal plants make an enzyme required for gibberellin synthesis; dwarf plants of the same species lack the enzyme, and their internodes elongate very little.

Another stark demonstration of the effect gibberellins can have on internode growth is **bolting**, growth of a floral stalk in plants that form vegetative rosettes, such as cabbages *(Brassica oleracea)* and iceberg lettuce *(Lactuca sativa)*. In a rosette plant, stem internodes are so short that the leaves appear to arise from a single node. When these plants flower, however, the stem elongates rapidly and flowers develop on the new stem parts. An experimenter can trigger exaggerated bolting by spraying a plant with gibberellin **(Figure 35.8).** In nature, external cues such as increasing day length or warming after a cold snap stimulate gibberellin synthesis, and bolting occurs soon afterward. This observation supports the hypothesis that in rosette plants and possibly some others, gibberellins switch on internode lengthening when environmental conditions favor a shift from vegetative growth to reproductive growth.

Other experiments using gibberellins have turned up a striking number of additional roles for this hormone family. For example, a gibberellin helps stimulate buds and seeds to break dormancy and resume growth in the spring. Research on barley embryos showed that gibberellin provides signals during germination that lead to the enzymatic breakdown of endosperm, releasing nutrients that nourish the developing seedling (see Section 34.3). In monoecious species, which have flowers of both sexual types on the same plant, applications of gibberellin seem to encourage proportionately more "male" flowers to develop. As a result, there may be more pollen available to pollinate "female" flowers and, eventually, more fruit produced. A gibberellin used by commercial grape growers promotes fruit set and lengthens the stems on which fruits develop, allowing space for individual grapes to grow larger. One result is fruit with greater consumer appeal **(Figure 35.9).**

Cytokinins Enhance Growth and Retard Aging

Cytokinins play a major role in stimulating cell division (hence the name, which refers to cytokinesis). These hormones were first discovered during experiments designed to define the nutrient media required for plant tissue culture. Researchers found that in addition to a carbon source such as sucrose or glucose, minerals, and certain vitamins, cells in culture also required two other substances. One was auxin, which promoted the elongation of plant cells but did not stimulate the cells to divide. The other substance could be coconut milk, which is actually liquid endosperm, or it could be DNA that had been degraded into smaller molecules by boiling. When either was added to a culture medium along with an auxin, the cultured cells would begin dividing and grow normally.

We now know that the active ingredients in both boiled DNA and endosperm are cytokinins, which have a chemical structure similar to that of the nucleic acid base adenine. The most abundant natural cytokinin is zeatin, so-called because it was first isolated from the endosperm of young corn seeds *(Zea mays)*. In endosperm, zeatin probably promotes the burst of cell division that takes place as a fruit matures. As you might expect, cytokinins also are abundant in the rapidly dividing meristem tissues of root and shoot tips. Cytokinins occur not only in flowering plants but also in many conifers, mosses, and ferns. They are also synthesized by many soil-dwelling bacteria and fungi and may be crucial to the growth of mycorrhizae, which help nourish thousands of plant species (see Section 33.3). Conversely, *Agrobacterium* and other microbes that cause plant tumors carry genes that regulate the production of cytokinins.

Cytokinins are synthesized largely (although not only) in root tips and apparently are transported through the plant in xylem sap. Besides promoting cell division, they have a range of effects on plant metabolism and development, probably by regulating protein synthesis. For example, cytokinins promote expansion of young leaves (as leaf cells expand), cause chloroplasts to mature, and retard leaf aging. Another cytokinin effect—coordinating the growth of roots and shoots, in concert with auxin—underscores the point that plant hormones often work together to evoke a particular response. Investigators culturing tobacco tissues found that the relative amounts of auxin and a cytokinin strongly influenced not only growth, but also development **(Figure 35.10).** When the auxin-to-cytokinin ratio is about 10:1, the growing tissue did not differentiate but instead remained as a loose mass of cells, or *callus*. When the relative auxin concentration was increased slightly, the callus produced roots. When the relative concentration of the cytokinin was increased, chloroplasts in the callus cells matured, the callus became green and more compact, and it produced shoots. In nature, the interaction of a cytokinin and auxin may produce the typical balanced growth of roots and shoots, with each region providing the other with key nutrients.

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Figure 35.8
A dramatic example of bolting in cabbage *(Brassica oleracea)*, a plant commonly grown as a winter vegetable. The rosette form (left) reflects the plant's growth habit when days are short (and nights are long). Gibberellin was applied to the plants at the right, triggering the rapid stem elongation and subsequent flowering, characteristic of bolting.

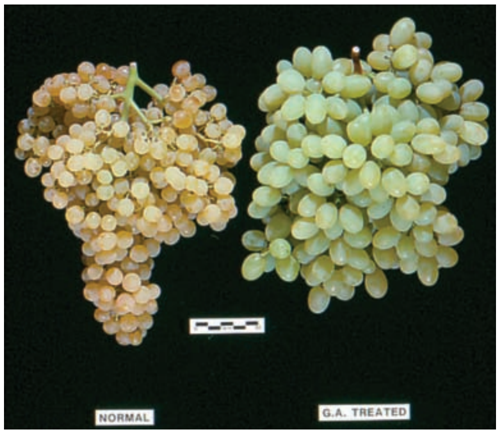
Natural cytokinins can prolong the life of stored vegetables. Similar synthetic compounds are already widely used to prolong the shelf life of lettuces and mushrooms and to keep cut flowers fresh.

Ethylene Regulates a Range of Responses, Including Senescence

Most parts of a plant can produce **ethylene,** which is present in fruits, flowers, seeds, leaves, and roots. In different species it helps regulate a wide variety of plant physiological responses, including dormancy of seeds and buds, seedling growth, stem elongation, the ripening of fruit, and the eventual separation of fruits, leaves, and flowers from the plant body. Ethylene is an unusual hormone, in part because it is structurally simple (see Table 35.1) and in part because it is a gas at normal temperature and pressure.

Before a bean or pea seedling emerges from the soil, ethylene simultaneously slows elongation of the stem and stimulates cell divisions that increase stem girth.

Figure 35.9
Effect of gibberellin on seedless grapes *(Vitis vinifera)*. The grapes on the right developed on vines that were treated with a gibberellin.



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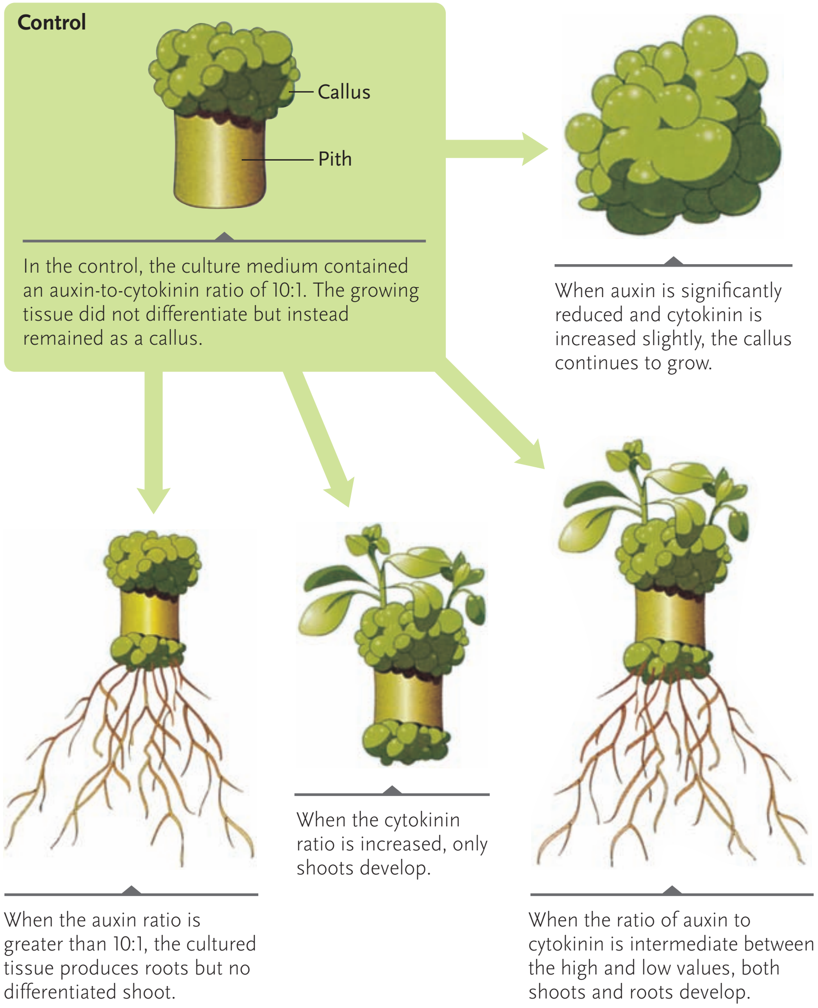


In the control, the culture medium contained an auxin-to-cytokinin ratio of 10:1. The growing tissue did not differentiate but instead remained as a callus.

When auxin is significantly reduced and cytokinin is increased slightly, the callus continues to grow.

When the auxin ratio is greater than 10:1, the cultured tissue produces roots but no differentiated shoot.

When the cytokinin ratio is increased, only shoots develop.

When the ratio of auxin to cytokinin is intermediate between the high and low values, both shoots and roots develop.

Figure 35.10
Effects of varying ratios of auxin and cytokinin on tobacco tissues *(Nicotiana tabacum)* grown in culture. The method starts with a block of stem pith, essentially a core of ground tissue removed from the center of a stem. The callus growing on the pith is a disorganized mass of undifferentiated cells.

These alterations push the curved hypocotyl through the soil and into the air (see Figure 34.12). Such ethylene-induced horizontal growth also can help a growing seedling "find its way" into the air if the seed happens to germinate under a pebble or some other barrier.

Ethylene also governs the biologically complex process of aging, or **senescence,** in plants. Senescence is a closely controlled process of deterioration that leads to the death of plant cells. In autumn the leaves of deciduous trees senesce, often turning yellow or red as chlorophyll and proteins break down, allowing other pigments to become more noticeable. Ethylene triggers the expression of genes leading to the synthesis of chlorophyllases and proteases, enzymes that launch the breakdown process. In many plants, senescence is associated with **abscission,** the dropping of flowers, fruits, and leaves in response to environmental signals. In this process, ethylene apparently stimulates the activity of enzymes that digest cell walls in an abscission zone—a localized region at the base of the petiole. The petiole detaches from the stem at that point **(Figure 35.11).**

For some species, the funneling of nutrients into reproductive parts may be a cue for senescence of leaves, stems, and roots. When the drain of nutrients is halted by removing each newly emerging flower or seed pod, a plant's leaves and stems stay green and vigorous much longer **(Figure 35.12).** Gardeners routinely remove flower buds from many plants to maintain vegetative growth. Senescence requires other cues, however. For instance, when a cocklebur is induced to flower under winterlike conditions, its leaves turn yellow regardless of whether the nutrient-demanding young flowers are left on or pinched off. It is as if a "death signal" forms that leads to flowering and senescence when there are fewer hours of daylight (typical of winter days). This observation underscores the general theme that many plant responses to the environment involve the interaction of multiple molecular signals.

Fruit ripening is a special case of senescence. Although the precise mechanisms are not well understood, ripening begins when a fruit starts to synthesize ethylene. The ripening process may involve the conversion of starch or organic acids to sugars, the softening of cell walls, or the rupturing of the cell membrane and loss of cell fluid. The same kinds of events occur in wounded plant tissues, which also synthesize ethylene.

Ethylene from an outside source can stimulate senescence responses, including ripening, when it binds to specific protein receptors on plant cells. The ancient Chinese observed that they could induce picked fruit to ripen faster by burning incense; later, it was found that the incense smoke contains ethylene. Today ethylene gas is widely used to ripen tomatoes, pineapples, bananas, honeydew melons, mangoes, papayas, and other fruit that has been picked and shipped while still green. Ripening fruit itself gives off ethylene, which is why placing a ripe banana in a closed sack of unripe peaches (or some other green fruit) often can cause the fruit to ripen. Oranges and other citrus fruits may be exposed to ethylene to brighten the color of their rind. Conversely, limiting fruit exposure to ethylene can delay ripening. Apples will keep for months without rotting if they are exposed to a chemical that inhibits ethylene production or if they are stored in an environment that inhibits the hormone's effects—including low atmospheric pressure and a high concentration of CO_2, which may bind ethylene receptors.

Brassinosteroids Regulate Plant Growth Responses

The dozens of steroid hormones classed as **brassinosteroids** all appear to be vital for normal growth in plants, for they stimulate cell division and elongation in a wide range of plant cell types. Confirmed as plant hormones in the 1980s, brassinosteroids now are the subject of intense research on their sources and effects. While brassinosteroids have been detected in a wide variety of plant tissues and organs, the highest concentrations are found in shoot tips and in developing seeds and embryos—all examples of young, actively developing parts. In laboratory studies, the hormones have different effects depending on the tissue where they are active. They have promoted cell elongation, differentiation of vascular tissue, and elongation of a pollen tube after a flower is pollinated. By contrast, they inhibit the elongation of roots. First isolated from pollen of a plant in the mustard family, *Brassica napus* (a type of canola), in nature brassinosteroids seem to regulate the expression of genes associated with a plant's growth responses to light. This role was underscored by the outcomes of experiments using mutant *Arabidopsis* plants that were homozygous for a defective genes called *bri1* (for brassinosteroid-insensitive receptor) **(Figure 35.13);** the results provided convincing evidence that brassinosteroids mediate growth responses to light.

N.R. Lersten

Figure 35.11 Abscission zone in a maple *(Acer)*. This longitudinal section at the left is through the base of the petiole of a leaf.

Abscisic Acid Suppresses Growth and Influences Responses to Environmental Stress

Plant scientists ascribe a variety of effects to the hormone **abscisic acid** (ABA), many of which represent evolutionary adaptations to environmental challenges. Plants apparently synthesize ABA from carotenoid pigments inside plastids in leaves and possibly other plant parts. Several ABA receptors have been identified, and in general, we can group its effects into changes in gene expression that result in long-term inhibition of growth, and rapid, short-term physiological changes that are responses to immediate stresses, such as a lack of water, in a plant's surroundings. As its name suggests, at one time ABA was thought to play a major role in abscission. As already described, however, abscission is largely the domain of ethylene.

Suppressing Growth in Buds and Seeds. Operating as a counterpoint to growth-stimulating hormones like gibberellins, ABA inhibits growth in response to environmental cues, such as seasonal changes in temperature and light. This growth suppression can last for many months or even years. For example, one of ABA's major growth-inhibiting effects is apparent in perennial plants, in which the hormone promotes dormancy in leaf buds—an important adaptive advantage in places where winter cold can damage young leaves. If ABA is applied to a growing leaf bud, the bud's normal development stops, and instead protective *bud scales*—modified, nonphotosynthetic leaves that are small, dry, and tough—form around the apical meristem and insulate it from the elements **(Figure 35.14).** After the scales develop, most cell metabolic activity shuts down and the leaf bud becomes dormant.

In some plants that produce fleshy fruits, such as apples and cherries, abscisic acid is associated with the dormancy of seeds as well. As the seed develops, ABA accumulates in the seed coat, and the embryo does not germinate even if it becomes hydrated. Before such a seed can germinate, it usually will require a long period of cool, wet conditions, which stimulate the breakdown of ABA. The buildup of ABA in developing seeds does more than simply inhibit development, however. As early development draws to a close, ABA stimulates the transcription of certain genes, and large amounts of their protein products are synthesized. These proteins are thought to store nitrogen and other nutrients that the embryo will use when it eventually does germinate. ABA and related growth inhibitors are often applied to plants slated to be shipped to plant nurseries. Dormant plants suffer less shipping damage, and the effects of the inhibitors can be reversed by applying a gibberellin.

Responses to Environmental Stress. ABA also triggers plant responses to various environmental stresses, including cold snaps, high soil salinity, and drought. A

Larry D. Nooden

Figure 35.12 Experimental results showing that the removal of seed pods from a soybean plant *(Glycine max)* delays its senescence.

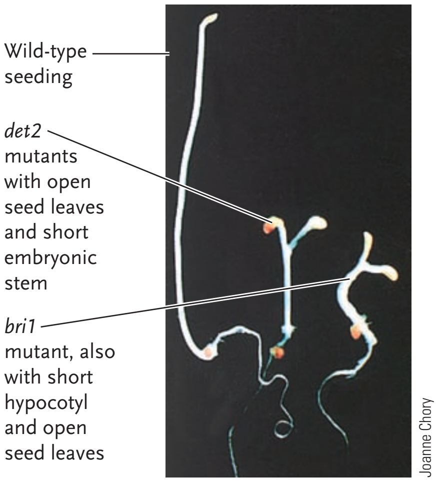


Figure 35.13
Experimental evidence that brassinosteroids can mediate a plant's responses to light by regulating gene expression. In *Arabidopsis,* wild-type seedlings synthesize a protein (encoded by the *DET2* gene) that prevents leaves from developing *(seedling at left)* until photosynthesis is possible, after the seedling breaks out of the dark environment of soil. When the gene is defective, a mutant *det2* plant *(center)* will develop a short hypocotyl (embryonic stem) and open seed leaves (cotyledons) even when there is no light for photosynthesis. Experiments with *bri1* mutants, which lack functioning receptors for a brassinosteroid, resulted in a similar phenotype *(right)*. These findings supported the hypothesis that a brassinosteroid is necessary for normal expression of the *DET2* gene.

great deal of research has focused on how ABA influences plant responses to a lack of water. When a plant is water-stressed, ABA helps prevent excessive water loss by stimulating stomata to close. As described in Section 32.3, flowering plants depend heavily on the proper functioning of stomata. When a lack of water leads to wilting, mesophyll cells in wilted leaves rapidly synthesize and secrete ABA. The hormone diffuses to guard cells, where an ABA receptor binds it. Binding stimulates the release of K^+ and water from the guard cells, and within minutes the stomata close.

Once bound to its receptor, ABA may exert its effects through a cascade of signals that includes phosphorylated proteins. Experiments have shown that an *Arabidopsis* mutant unable to respond to ABA lacks an enzyme that removes phosphate groups from certain proteins. This condition suggests that cleaving phosphates is one step in the ABA response. *Insights from the Molecular Revolution* highlights recent research filling in other steps in the ABA-induced response pathway.

Figure 35.14 Bud scales, here on the bud of a perennial cornflower *(Centaurea montana)*.

Jasmonates and Oligosaccharins Regulate Growth and Have Roles in Defense

In recent years, studies of plant growth and development have helped define the roles—or revealed the existence—of several other hormonelike compounds in plants. Like the well-established plant hormones just described, these substances are organic molecules and only tiny amounts are required to alter some aspect of a plant's functioning. Some have long been known to exist in plants, but the extent of their signaling roles has only recently become better understood. This group includes **jasmonates** (JA), a family of about 20 compounds derived from fatty acids. Experiments with *Arabidopsis* and other plants have revealed numerous genes that respond to JA, including genes that help regulate root growth and seed germination. JA also appears to help plants "manage" stresses due to deficiencies of certain nutrients (such as K^+). The JA family is best known, however, as part of the plant arsenal to limit damage by pathogens and predators, the topic of the following section.

Some other substances also are drawing keen interest from plant scientists, but because their signaling roles are still poorly understood they are not widely accepted as confirmed plant hormones. A case in point involves the complex carbohydrates that are structural elements in the cell walls of plants and some fungi. Several years ago, researchers observed that in some plants, some of these oligosaccharides could serve as signaling molecules. Such compounds were named **oligosaccharins,** and one of their known roles is to defend the plant against pathogens. In addition, oligosaccharins have been proposed as growth regulators that adjust the growth and differentiation of plant cells, possibly by modulating the influences of growth-promoting hormones such as auxin. At this writing, researchers in many laboratories are pursuing a deeper understanding of this curious subset of plant signaling molecules.

Study Break

1. Which plant hormones promote growth and which inhibit it?
2. Give examples of how some hormones have both promoting and inhibiting effects in different parts of the plant at different times of the life cycle.

35.2 Plant Chemical Defenses

Plants don't have immune systems like those that have evolved in animals (the subject of Chapter 43). Even so, over the millennia, in higher plants virtually constant exposure to predation by herbivores and the onslaught

INSIGHTS FROM THE MOLECULAR REVOLUTION

Stressing Out in Plants and People

Unlike people, plants cannot move to more favorable locations when an environmental stress threatens. Instead, to survive stresses plants adjust their responses to environmental factors such as temperature and the availability of water. Recent molecular work shows that responses to stress imposed by drought and cold involve some of the same chemical steps in plants and humans, indicating an ancient link to a common evolutionary ancestor. The research may also point the way to genetic engineering strategies to modify major crop plants for earlier and better responses to stress.

Many plant stress responses are triggered by the hormone abscisic acid (ABA). Although individual steps in the response pathway are unclear, it is known that calcium ions increase in concentration in the cytoplasm when plant cells are exposed to ABA. Soon after the rise in Ca^{2+}, genes are activated that compensate for the stressful situation.

Nam-Hai Chua and his colleagues at the Rockefeller University and the University of Minnesota were interested in piecing together the molecular steps in the plant pathway. One substance they thought might be involved is *cyclic ADP-ribose (cADPR),* a signaling molecule that was first implicated in calcium release pathways in animal cells.

The Chua team began by injecting two plant genes, *rd29A* and *kin2,* into tomato cells. The two genes are activated by ABA as part of the stress response. Each of the injected genes was linked to an unrelated marker gene that would also be turned on if the gene became active. When ABA was injected into stressed tomato plants grown from the injected cells, the markers were activated, indicating that *rd29A* and *kin2* were turned on by ABA.

The next step was to inject Ca^{2+} and to note whether the injected genes were activated. The injection activated the *rd29A* and *kin2* genes, confirming the role of calcium ions in the pathway. A chemical called EGTA that removes Ca^{2+} from the cytoplasm cancelled the gene activation, as expected if calcium is part of the response pathway.

Then, the investigators injected cADPR to see if it activated *rd29A* and *kin2.* This result was also positive; cADPR had the same effect as either ABA or Ca^{2+}. EGTA blocked the positive response to cADPR, indicating that cADPR lies between ABA and calcium release in the signal pathway.

Another experiment determined whether protein phosphorylation might be part of the pathway. To accomplish this, the investigators injected an inhibitor of protein kinases, the enzymes that phosphorylate proteins as a part of many cellular response pathways (see Section 7.2). After the inhibitor was added, injecting ABA, cADPR, or Ca^{2+} failed to activate *rd29A* and *kin2,* indicating that protein phosphorylation occupies a critical step following these elements in the pathway.

From these results the Chua team was able to reconstruct a major part of the pathway:

ABA → ? → cADPR →
Ca^{2+} → protein kinases →
? → stress gene activation

The question marks indicate one or more unknown steps. Most significant is the specific ABA receptor that carries out the first step in the response pathway. A recently identified ABA receptor that is involved in the events that cause stomata to close (among other effects) may be this "missing link."

In addition to possible benefits for agriculture, the Chua team's research may also shed light on signal pathways in animals in which cADPR plays a part, including one that adjusts the heartbeat and another that regulates insulin release in response to elevated blood glucose. Thus Chua's work may help fill in steps in both plant and animal responses, in pathways inherited from a common ancestor predating both plants and people.

of pathogens have resulted in a striking array of chemical defenses that ward off or reduce damage to plant tissues from infectious bacteria, fungi, worms, or plant-eating insects **(Table 35.2).** You will discover in this section that as with the defensive strategies of animals, plant defenses include both general responses to any type of attack and specific responses to particular threats. Some get underway almost as soon as an attack begins, while others help promote the plant's long-term survival. And more often than not, multiple chemicals interact as the response unfolds.

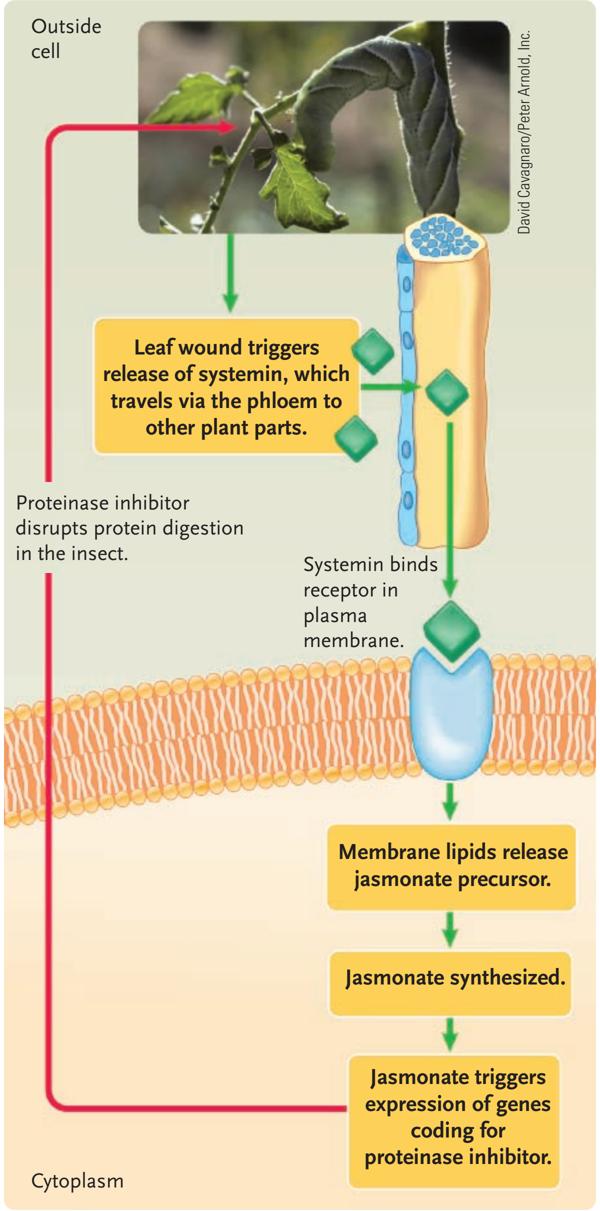
Jasmonates and Other Compounds Interact in a General Response to Wounds

When an insect begins feeding on a leaf or some other plant part, the plant may respond to the resulting wound by launching what in effect is a cascade of chemical responses. These complex signaling pathways often rely on interactions among jasmonates, ethylene, or some other plant hormone. As the pathway unfolds it triggers expression of genes leading to chemical and physical defenses at the wound site. For example, in some plants jasmonate induces a response leading to the synthesis of protease inhibitors, which disrupt an insect's capacity to digest proteins in the plant tissue. The protein deficiency in turn hampers the insect's growth and functioning.

A plant's capacity to recognize and respond to the physical damage of a wound apparently has been a strong selection pressure during plant evolution. When a plant is wounded experimentally, numerous defensive chemicals can be detected in its tissues in relatively short order. One of these, **salicylic acid,** or **SA** (a compound similar to aspirin, which is acetylsalicylic acid), seems to have multiple roles in plant defenses,

Table 35.2 Summary of Plant Chemical Defenses

Type of Defense	Effects
General Defenses	
Jasmonate (JA) responses to wounds/injury by pathogens; pathways often include other hormones such as ethylene	Synthesis of defensive chemicals such as protease inhibitors
Hypersensitive response to infectious pathogens (e.g., fungi, bacteria)	Physically isolates infection site by surrounding it with dead cells
PR (pathogenesis-related) proteins	Enzymes, other proteins that degrade cell walls of pathogens
Salicylic acid (SA)	Mobilized during other responses and independently; induces the synthesis of PR proteins, operates in systemic acquired resistance
Systemin (in tomato)	Triggers JA response
Secondary metabolites	
Phytoalexins	Antibiotic
Oligosaccharins	Trigger synthesis of phytoalexins
Systemic acquired resistance (SAR)	Long-lasting protection against some pathogens; components include SA and PR proteins that accumulate in healthy tissues
Specific Defenses	
Gene-for-gene recognition of chemical features of specific pathogens (by binding with receptors coded by R genes)	Triggers defensive response (e.g., hypersensitive response, PR proteins) against pathogens
Other	
Heat-shock responses (encoded by heat-shock genes)	Synthesis of chaperone proteins that reversibly bind other plant proteins and prevent denaturing due to heat stress
"Antifreeze" proteins	In some species, stabilize cell proteins under freezing conditions



David Cavagnaro/Peter Arnold, Inc.

Figure 35.15
The systemin response to wounding. When a plant is wounded, it responds by releasing the protein hormone systemin. Transported through the phloem to other plant parts, in receptive cells systemin sets in motion a sequence of reactions that lead to the expression of genes encoding protease inhibitors—substances that can seriously disrupt an insect predator's capacity to digest protein.

including interacting with jasmonates in signaling cascades.

Researchers are regularly discovering new variations of hormone-induced wound responses in plants. For example, experiments have elucidated some of the steps in an unusual pathway that thus far is known only in tomato *(Lycopersicum esculentum)* and a few other plant species. As diagrammed in **Figure 35.15,** the wounded plant rapidly synthesizes **systemin**, the first peptide hormone to be discovered in plants. (Various animal hormones are peptides, a topic covered in Chapter 40.) Systemin enters the phloem and is transported throughout the plant. Although various details of the signaling pathway have yet to be worked out, when receptive cells bind systemin, their plasma membranes release a lipid that is the chemical precursor of jasmonate. Next jasmonate is synthesized, and it in turn sets in motion the expression of genes that encode protease inhibitors, which protect the plant against attack, even in parts remote from the original wound.

The Hypersensitive Response and PR Proteins Are Other General Defenses

Often, a plant that becomes infected by pathogenic bacteria or fungi counters the attack by way of a **hypersensitive response**—a defense that physically cordons off an infection site by surrounding it with dead cells. Initially, cells near the site respond by producing a burst of highly reactive oxygen-containing compounds (such as hydrogen peroxide, H_2O_2) that can break down nucleic acids, inactivate enzymes, or have other toxic effects on cells. The burst is catalyzed by enzymes in the plant cell's plasma membrane. It may begin the process of killing cells close to the attack site and, as the response advances, programmed cell death may also come into play. In short order, the "sacrificed" dead cells wall off the infected area from the rest of the plant. Thus denied an ongoing supply of nutrients, the invading pathogen dies. A common sign of a successful hypersensitive response is a dead spot surrounded by healthy tissue **(Figure 35.16).**

While the hypersensitive response is underway, salicylic acid triggers other defensive responses by an infected plant. One of its effects is to induce the synthesis of **pathogenesis-related proteins**, or **PR proteins.** Some PR proteins are hydrolytic enzymes that break down components of a pathogen's cell wall. Examples are chitinases that dismantle the chitin in the cell walls of fungi and so kill the cells. In some cases, plant cell receptors also detect the presence of fragments of the disintegrating wall and set in motion additional defense responses.

Secondary Metabolites Defend against Pathogens and Herbivores

Many plants counter bacteria and fungi by making **phytoalexins,** biochemicals of various types that function as antibiotics. When an infectious agent breaches a plant part, genes encoding phytoalexins begin to be transcribed in the affected tissue. For instance, when a fungus begins to invade plant tissues, the enzymes it secretes may trigger the release of oligosaccharins. In addition to their roles as growth regulators (described in Section 35.1), these substances also can promote the production of phytoalexins, which have toxic effects on a variety of fungi. Plant tissues may also synthesize phytoalexins in response to attacks by viruses.

Phytoalexins are among many *secondary metabolites* produced by plants. Such substances are termed "secondary" because they are not routinely synthesized in all plant cells as part of basic metabolism. A wide range of plant species deploy secondary metabolites as defenses against feeding herbivores. Examples are alkaloids such as caffeine, cocaine, and the poison strychnine (in seeds of the *nux vomica* tree, *Strychnos nux-vomica*), tannins such as those in oak acorns, and various terpenes. The terpene family includes insect-repelling substances in conifer resins and cotton, and essential oils produced by sage and basil plants. Because these terpenes are volatile—they easily diffuse out of the plant into the surrounding air—they also can provide indirect defense to a plant. Released from the wounds created by a munching insect, they attract other insects that prey on the herbivore. Chapter 50 looks in detail at the interactions between plants and herbivores.

Nigel Cattlin/Photo Researchers, Inc.

Figure 35.16 **Evidence of the hypersensitive response.** The dead spots on these leaves of a strawberry plant *(Fragaria)* are sites where a pathogen invaded, triggering the defensive destruction of the surrounding cells.

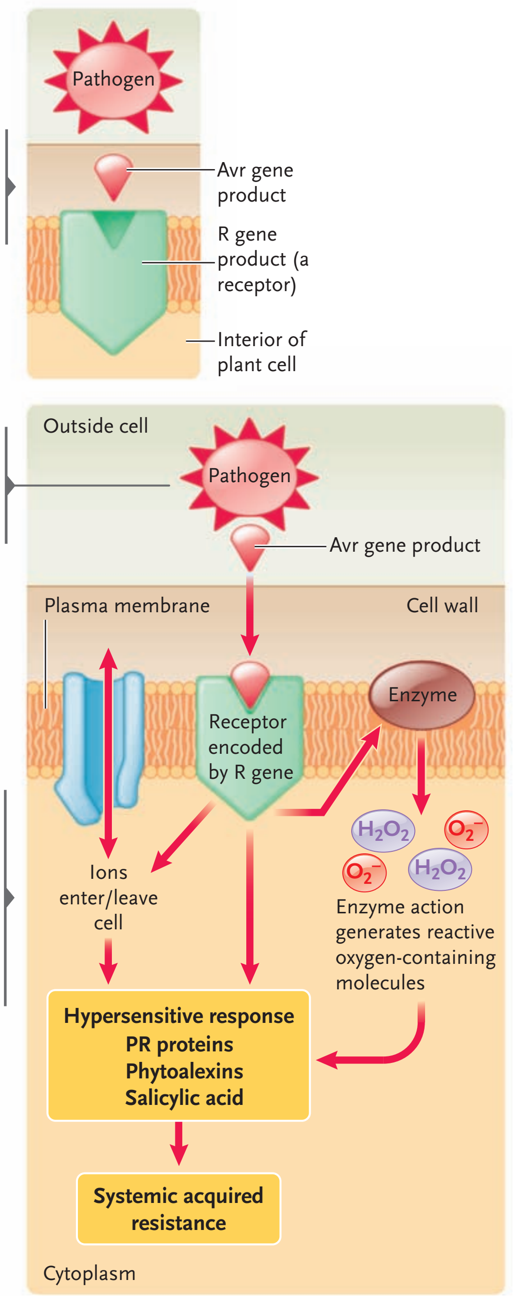
Gene-for-Gene Recognition Allows Rapid Responses to Specific Threats

One of the most interesting questions with respect to plant defenses is how plants first sense that an attack is underway. In some instances plants apparently can detect an attack by a specific predator through a mechanism called **gene-for-gene recognition.** This term refers to a matchup between the products of dominant alleles of two types of genes: a so-called **R gene** (for "resistance") in a plant, and an **Avr gene** (for "avirulence") in a particular pathogen. Thousands of R genes have been identified in a wide range of plant species. Dominant R alleles confer enhanced resistance to plant pathogens including bacteria, fungi, and nematode worms that attack roots.

The basic mechanism of gene-for-gene recognition is simple: The dominant R allele encodes a receptor in plasma membranes of a plant's cells, and the dominant pathogen Avr allele encodes a molecule that can bind the receptor. "Avirulence" implies "not virulent," and binding of the Avr gene product triggers an immediate defense response in the plant. Trigger molecules run the gamut from proteins to lipids to carbohydrates that have been secreted by the pathogen or released from its surface **(Figure 35.17).** Experiments have demonstrated a rapid-fire sequence of early biochemical changes that follow binding of the Avr-encoded molecule; these include changes in ion concentrations inside and outside plant cells and the production of biologically active oxygen compounds that heralds the hypersensitive response. In fact, of the instances of gene-for-gene recognition plant scientists have observed thus far, most trigger the hypersensitive response and the ensuing synthesis of PR proteins, with their antibiotic effects.

Systemic Acquired Resistance Can Provide Long-Term Protection

The defensive response to a microbial invasion may spread throughout a plant, so that the plant's healthy tissues become less vulnerable to infection. This phenomenon is called **systemic acquired resistance,** and experiments using *Arabidopsis* plants have shed light on how it comes about **(Figure 35.18).** In a key early step, salicylic acid builds up in the affected tissues. By some route, probably through the phloem, the SA passes



Required precondition
A plant has a dominant R gene encoding a receptor that can bind the product of a specfic pathogen dominant Avr gene.

1 When the R-encoded receptor binds its matching Avr product, the binding triggers signaling pathways, leading to various defense responses in the plant.

2 Fluxes of ions and enzyme activity at the plasma membrane contribute to the hypersensitive response. Soon PR proteins, phytoalexins, and salicylic acid (SA) are synthesized. The PR proteins and phytoalexins combat pathogens directly. SA promotes systemic acquired resistance.

Figure 35.17
Model of how gene-for-gene resistance may operate. For resistance to develop, the plant must have a dominant R gene and the pathogen must have a corresponding dominant Avr gene. Products of such "matching" genes can interact physically, rather like the lock-and-key mechanism of an enzyme and its substrate. Most R genes encode receptors at the plasma membranes of plant cells. As diagrammed in step 1, when one of these receptors binds an Avr gene's product, the initial result may be changes in the movements of specific ions into or out of the cell and the activation of membrane enzymes that catalyze the formation of highly reactive oxygen-containing molecules. Such events help launch other signaling pathways that lead to a variety of defensive responses, including the hypersensitive response (step 2).

from the infected organ to newly forming organs such as leaves, which begin to synthesize PR proteins—again, providing the plant with a "home-grown" antimicrobial arsenal. How does the SA exert this effect? It seems that when enough SA accumulates in a plant cell's cytoplasm, a regulatory protein called NPR-1 (for *n*onexpressor of *p*athogenesis-*r*elated genes) moves from the cytoplasm into the cell nucleus. There it interacts with factors that promote the transcription of genes encoding PR proteins.

In addition to synthesizing SA that will be transported to other tissues by a plant's vascular system, the damaged leaf also synthesizes a chemically similar compound, methyl salicylate. This substance is volatile, and researchers speculate that it may serve as an airborne "harm" signal, promoting defense responses in the plant that synthesized it and possibly in nearby plants as well.

Extremes of Heat and Cold Also Elicit Protective Chemical Responses

Plant cells also contain **heat-shock proteins (HSPs)**, a type of chaperone protein (see Section 3.5) found in cells of many species. HSPs bind and stabilize other proteins, including enzymes, that might otherwise stop functioning if they were to become denatured by rising temperature. Plant cells may rapidly synthesize HSPs in response to a sudden temperature rise. For example, experiments with cells and seedlings of soybean *(Glycine max)* showed that when the temperature rose 10°–15°C, in less than five minutes mRNA transcripts coding for as many as 50 different HSPs were present in cells. When the temperature returns to a normal range, HSPs release bound proteins, which can then resume their usual functions. Further studies have revealed that heat-shock proteins help protect plant cells subjected to other environmental stresses as well, including drought, salinity, and cold.

Like extreme heat, freezing can also be lethal to plants. If ice crystals form in cells they can literally tear the cell apart. In many cold-resistant species, dormancy (discussed in Section 35.4) is the long-term strategy for dealing with cold, but in the short term, such as an unseasonable cold snap, some species also undergo a rapid shift in gene expression that equips cold-stressed cells with so-called antifreeze proteins. Like heat-shock proteins, these molecules are thought to help maintain the structural integrity of other cell proteins.

STUDY BREAK

1. Which plant chemical defenses are general responses to attack, and which are specific to a particular pathogen?
2. Why is salicylic acid considered to be a general systemic response to damage?
3. How is the hypersensitive response integrated with other chemical defenses?

35.3 Plant Responses to the Environment: Movements

Although a plant cannot move from place to place as external conditions change, plants do alter the orientation of their body parts in response to environmental stimuli. As noted earlier in the chapter, growth toward or away from a unidirectional stimulus, such as light or gravity, is called a tropism. Tropic movement involves permanent changes in the plant body because cells in particular areas or organs grow differentially in response to the stimulus. Plant physiologists do not fully understand how tropisms occur, but they are fascinating examples of the complex abilities of plants to adjust to their environment. This section will also touch upon two other kinds of movements—developmental responses to physical contact, and changes in the position of plant parts that are not related to the location of the stimulus.

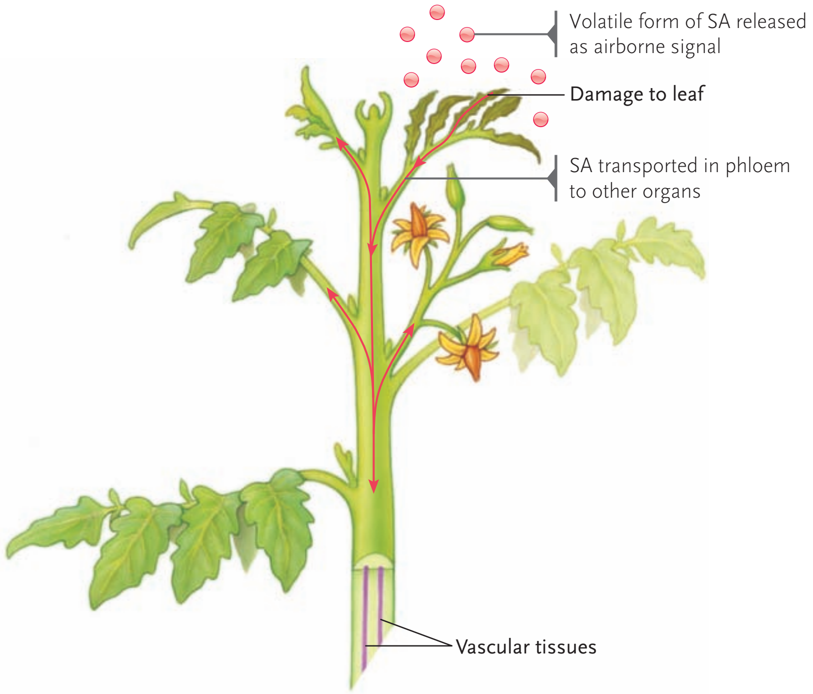


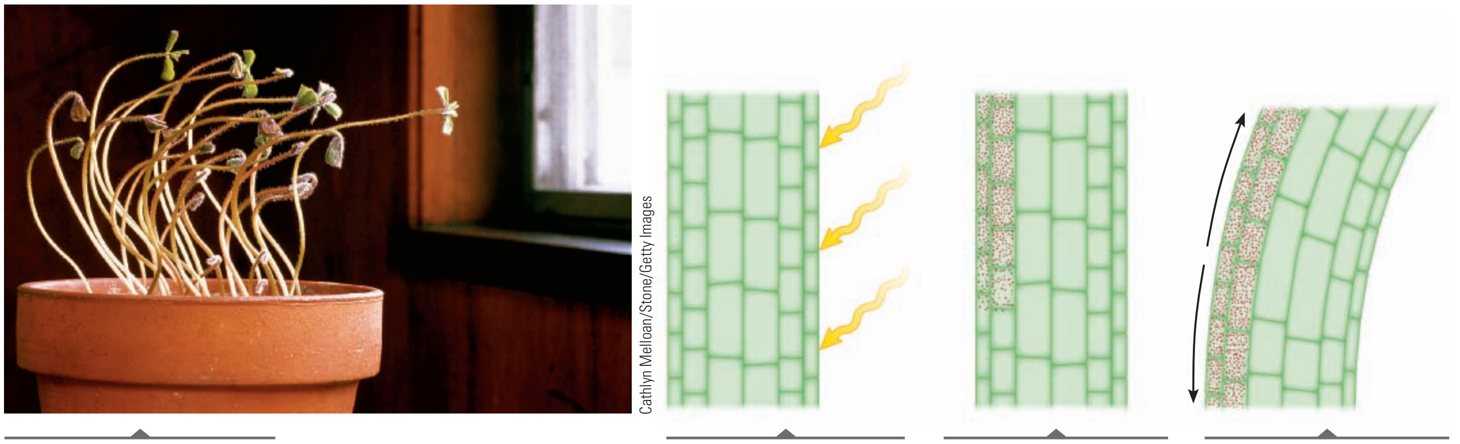
Figure 35.18
A proposed mechanism for systemic acquired resistance. When a plant successfully fends off a pathogen, the defensive chemical salicylic acid (SA) is transported in the phloem to other plant parts, where it may help protect against another attack by stimulating the synthesis of PR proteins. In addition, the plant synthesizes and releases a slightly different, more volatile form of SA. This chemical may serve as an airborne signal to other parts of the plant as well as to neighboring plants.

Phototropisms Are Responses to Light

Light is a key environmental stimulus for many kinds of organisms. Phototropisms, which we have already discussed in the section on auxins, are growth responses to a directional light source. As the Darwins discovered, if light is more intense on one side of a stem, the stem may curve toward the light **(Figure 35.19a).** Phototropic movements are extremely adaptive for photosynthesizing organisms because they help maximize the exposure of photosynthetic tissues to sunlight.

How do auxins influence phototropic movements? In a coleoptile that is illuminated from one side, IAA moves by polar transport into the cells on the shaded side **(Figure 35.19b–d).** Phototropic bending occurs because cells on the shaded side elongate more rapidly than do cells on the illuminated side.

The main stimulus for phototropism is light of blue wavelengths. Experiments on corn coleoptiles have shown that a large, yellow pigment molecule


Cathlyn Melloan/Stone/Getty Images

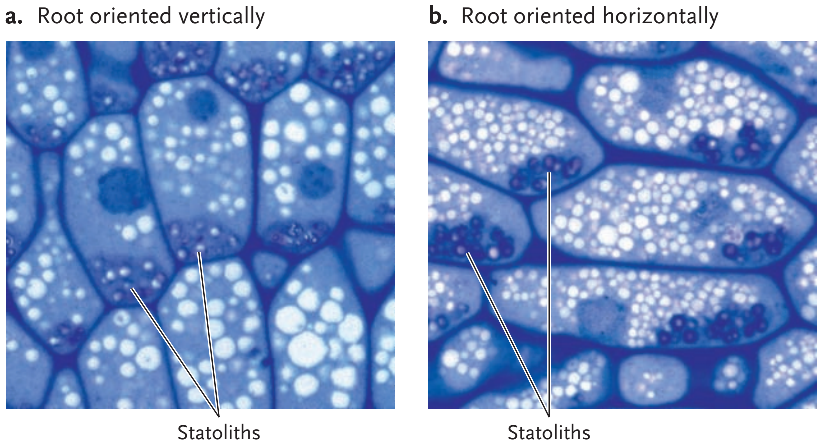
a. Seedlings bend toward light.

b. Rays from the sun strike one side of a shoot tip.

c. Auxin (red) diffuses down from the shoot tip to cells on its shaded side.

d. The auxin-stimulated cells elongate more quickly, causing the seedling to bend.

Figure 35.19
Phototropism in seedlings. (a) Tomato seedlings grown in darkness; their right side was illuminated for a few hours before they were photographed. **(b–d)** Hormone-mediated differences in the rates of cell elongation bring about the bending toward light. (Auxin is shown in red.)


a. Root oriented vertically

b. Root oriented horizontally

Figure 35.20
Evidence that supports the statolith hypothesis. When a corn root was laid on its side, amyloplasts—statoliths—in cells from the root cap settled to the bottom of the cells within 5 to 10 minutes. Statoliths may be part of a gravity-sensing mechanism that redistributes auxin through a root tip.

(Micrographs courtesy of Randy Moore, from "How Roots Respond to Gravity," M. L. Evans, R. Moore, and K. Hasenstein, *Scientific American,* December 1986.)

called phototropin can absorb blue wavelengths, and it may play a role in stimulating the initial lateral transport of IAA to the dark side of a shoot tip. Studies with *Arabidopsis* suggest there is more than one blue light receptor, however. One is a light-absorbing protein called **cryptochrome,** which is sensitive to blue light and may also be an important early step in the various light-based growth responses. As you will read later, cryptochrome appears to have a role in other plant responses to light as well.

Gravitropism Orients Plant Parts to the Pull of Gravity

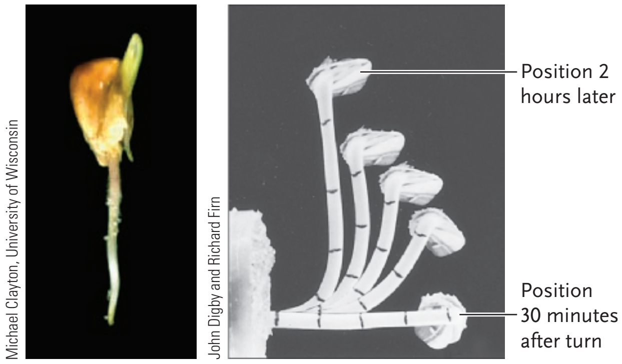
Plants show growth responses to Earth's gravitational pull, a phenomenon called **gravitropism.** After a seed germinates, the primary root curves down, toward the "pull" (positive gravitropism), and the shoot curves up (negative gravitropism).

Several hypotheses seek to explain how plants respond to gravity. The most widely accepted hypothesis proposes that plants detect gravity much as animals do—that is, particles called **statoliths** in certain cells move in the direction gravity pulls them. In the semicircular canals of human ears, tiny calcium carbonate crystals serve as statoliths; in most plants the statoliths are amyloplasts, modified plastids that contain starch grains (see Chapter 5). In eudicot angiosperm stems, amyloplasts often are present in one or two layers of cells just outside the vascular bundles. In monocots such as cereal grasses, amyloplasts are located in a region of tissue near the base of the leaf sheath. In roots, amyloplasts occur in the root cap. If the spatial orientation of a plant cell is shifted experimentally, its amyloplasts sink through the cytoplasm until they come to rest at the bottom of the cell **(Figure 35.20).**

How do amyloplast movements translate into an altered growth response? The full explanation appears to be fairly complex, and there is evidence that somewhat different mechanisms operate in stems and in roots. In stems, the sinking of amyloplasts may provide a mechanical stimulus that triggers a gene-guided redistribution of IAA. **Figure 35.21** shows what happens when a potted sunflower seedling is turned on its side in a dark room. Within 15–20 minutes, cell elongation decreases markedly on the upper side of the growing horizontal stem, but increases on the lower side. With the adjusted growth pattern, the stem curves upward, even in the absence of light. Using different types of tests, researchers have been able to document the shifting of IAA from the top to the bottom side of the stem. The changing auxin gradient correlates with the altered pattern of cell elongation.

In roots, a high concentration of auxin has the opposite effect—it inhibits cell elongation. If a root is placed on its side, amyloplasts in the root cap accumulate near the side wall that now is the bottom side of the cap. In some way this stimulates cell elongation in the opposite wall, and within a few hours the root once again curves downward. In root tips of many plants, however, especially eudicots, researchers have not been able to detect a shift in IAA concentration that correlates with the changing position of amyloplasts. One hypothesis is that IAA is redistributed over extremely short distances in root cells, and therefore is difficult to measure. Root cells are much more sensitive to IAA than are cells in stem tissue, and even a tiny shift in IAA distribution could significantly affect their growth.

Along with IAA, calcium ions (Ca^{2+}) appear to play a major role in gravitropism. For example, if Ca^{2+} is added to an otherwise untreated agar block that is then placed on one side of a root cap, the root will bend toward the block. In this way, experimenters have been able to manipulate the direction of growth so that the elongating root forms a loop. Similarly, if an actively bending root is deprived of Ca^{2+}, the gravitropic response abruptly stops. By contrast, the negative gravitropic response of a shoot tip is inhibited when the tissue is exposed to excess calcium.



Michael Clayton, University of Wisconsin

John Digby and Richard Firn

Figure 35.21
Gravitropism in a young shoot. A newly emerged sunflower seedling was grown in the dark for 5 days. Then it was turned on its side and marked at 0.5 cm intervals. Negative gravitropism turned the stem upright in 2 hours.

Just how Ca^{2+} interacts with IAA in gravitropic responses is unknown. One hypothesis posits that calcium functions as an activator. Calcium binds to a small protein called *calmodulin,* activating it in the process. Activated calmodulin in turn can activate a variety of key cell enzymes in many organisms, both plants and animals. One possibility is that calcium-activated calmodulin stimulates cell membrane pumps that enhance the flow of both IAA and calcium through a gravity-stimulated plant tissue.

Some of the most active research in plant biology focuses on the intricate mechanisms of gravitropism. For example, there is increasing evidence that in many plants, cells in different regions of stem tissue are more or less sensitive to IAA, and that gravitropism is linked in some fundamental way to these differences in auxin sensitivity. In a few plants, including some cultivated varieties of corn and radish, the direction of the gravitropic response by a seedling's primary root is influenced by light. Clearly there is much more to be learned.

Thigmotropism and Thigmomorphogenesis Are Responses to Physical Contact

Varieties of peas, grapes, and some other plants demonstrate **thigmotropism** (*thigma* = touch), which is growth in response to contact with a solid object. Thigmotropic plants typically have long, slender stems and cannot grow upright without physical support. They often have *tendrils,* modified stems or leaves that can rapidly curl around a fencepost or the sturdier stem of a neighboring plant. If one side of a grape vine stem grows against a trellis, for example, specialized epidermal cells on that side of the stem tendril shorten while cells on the other side of the tendril rapidly elongate. Within minutes the tendril starts to curl around the trellis, forming tight coils that provide strong support for the vine stem. **Figure 35.22** shows thigmotropic twisting in the passionflower *(Passiflora)*. Auxin and ethylene may be involved in thigmotropism, but most details of the mechanism remain elusive.

The rubbing and bending of plant stems caused by frequent strong winds, rainstorms, grazing animals, and even farm machinery can inhibit the overall growth of plants and can alter their growth patterns. In this phenomenon, called **thigmomorphogenesis**, a stem stops elongating and instead adds girth when it is regularly subjected to mechanical stress. Merely shaking some plants daily for a brief period will inhibit their upward growth **(Figure 35.23).** But although such plants may be shorter, their thickened stems will be stronger. Thigmomorphogenesis helps explain why plants growing outdoors are often shorter, have somewhat thicker stems, and are not as easily blown over as plants of the same species grown indoors. Trees growing near the snowline of windswept mountains show an altered growth pattern that reflects this response to wind stress.

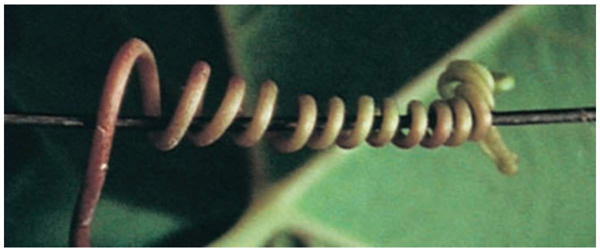
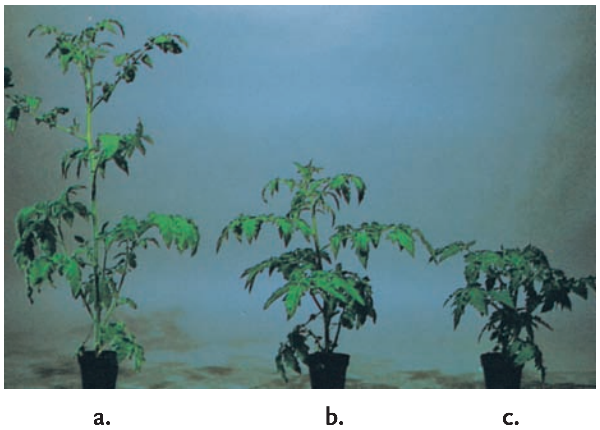


Figure 35.22
Thigmotropism in a passionflower *(Passiflora)* tendril, which is twisted around a support.

Research on the cellular mechanisms of thigmomorphogenesis has begun to yield tantalizing clues. In one study, investigators repeatedly sprayed *Arabidopsis* plants with water and imposed other mechanical stresses, then sampled tissues from the stressed plants. The samples contained as much as double the usual amount of mRNA for at least four genes, which had been activated by the stress. The mRNAs encoded calmodulin and several other proteins that may have roles in altering *Arabidopsis* growth responses. The test plants were also short, generally reaching only half the height of unstressed controls.

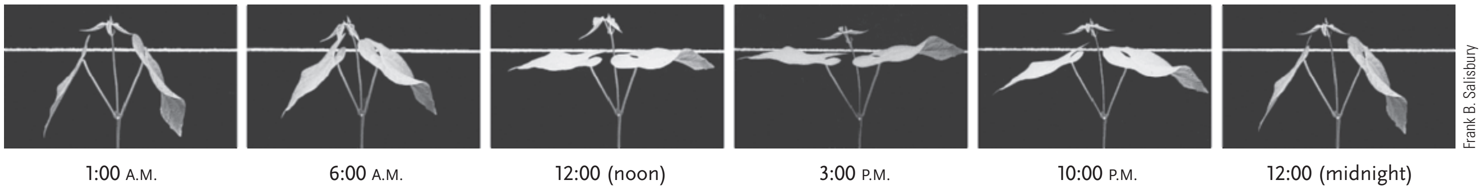
Nastic Movements Are Nondirectional

Tropisms are responses to directional stimuli, such as light striking one side of a shoot tip, but many plants also exhibit **nastic movements** (*nastos* = pressed close together)—reversible responses to nondirectional stimuli, such as mechanical pressure or humidity. We see nastic movements in leaves, leaflets, and even flowers. For instance, certain plants exhibit nastic sleep movements, holding their leaves (or flower petals) in roughly horizontal positions during the day but folding



Cary Mitchell

Figure 35.23
Effect of mechanical stress on tomato plants *(Lycopersicon esculentum)*. **(a)** This plant was the control; it was grown in a greenhouse, protected from wind and rain. **(b)** Each day for 28 days this plant was mechanically shaken for 30 seconds at 280 rpm. **(c)** This plant received the same shaking treatment, but twice a day for 28 days.



Frank B. Salisbury

Figure 35.24
Nastic sleep movements in leaves of a bean plant. Although this plant was kept in constant darkness for 23 hours, its sleep movements continued independently of sunrise (6 A.M.) and sunset (6 P.M.). Folding the leaves closer to the stem may prevent phytochrome from being activated by bright moonlight, which could interrupt the dark period necessary to trigger flowering. Or perhaps it helps slow heat loss from leaves otherwise exposed to the cold night air.

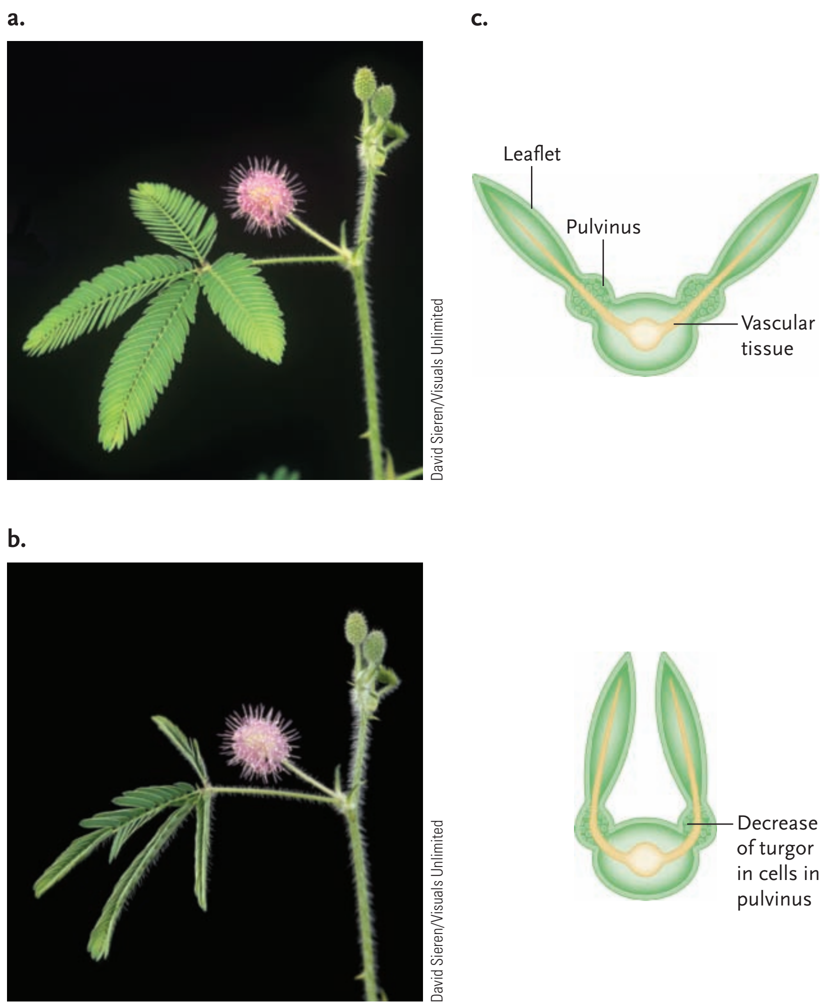
them closer to the stem at night **(Figure 35.24).** Tulip flowers "go to sleep" in this way.

Many nastic movements are temporary and result from changes in cell turgor. For example, the daily opening and closing of stomata in response to changing light levels are nastic movements, as is the traplike closing of the lobed leaves of the Venus flytrap when an insect brushes against hairlike sensory structures on the leaves. The leaves of *Mimosa pudica,* the sensitive plant, also close in a nastic response to mechanical pressure. Each *Mimosa* leaf is divided into pairs of leaflets **(Figure 35.25a).** Touching even one leaflet at the leaf tip triggers a chain reaction in which each pair of leaflets closes up within seconds **(Figure 35.25b).**

In many turgor-driven nastic movements, water moves into and out of the cells in **pulvini** (*pulvinus* = cushion), thickened pads of tissue at the base of a leaf or petiole. Stomatal movements depend on changing concentrations of ions within guard cells, and pulvinar cells drive nastic leaf movements in *Mimosa* and numerous other plants by the same mechanism **(Figure 35.25c).**

How is the original stimulus transferred from cells in one part of a leaf to cells elsewhere? The answer lies in the polarity of charge across cell plasma membranes (see Chapter 6). Touching a *Mimosa* leaflet triggers an **action potential**—a brief reversal in the polarity of the membrane charge. When an action potential occurs at the plasma membrane of a pulvinar cell, the change in polarity causes potassium ion (K^+) channels to open, and ions flow out of the cell, setting up an osmotic gradient that draws water out as well. As water leaves by osmosis, turgor pressure falls, pulvinar cells become flaccid, and the leaflets move together. Later, when the process is reversed, the pulvinar cells regain turgor and the leaflets spread apart. Action potentials travel between parenchyma cells in the pulvini via plasmodesmata at the rate of about 2 cm/sec. Animal nerves conduct similar changes in membrane polarity along their plasma membranes (see Chapter 37). These changes in polarity, which are also called action potentials, occur much more rapidly—at velocities between 1 and 100 m/sec.

Stimuli other than touch also can trigger action potentials leading to nastic movements. Cotton, soybean, sunflower, and some other plants display *solar tracking,* nastic movements in which leaf blades are oriented toward the east in the morning, then steadily change their position during the day, following the sun across the sky.



David Sieren/Visuals Unlimited

David Sieren/Visuals Unlimited

Figure 35.25
Nastic movements in leaflets of *Mimosa pudica*, the sensitive plant. (a) In an undisturbed plant the leaflets are open. If a leaflet near the leaf tip is touched, changes in turgor pressure in pulvini at the base cause the leaf to fold closed. **(b, c).** The diagram sketches this folding movement in cross section. Other leaflets close in sequence as action potentials transmit the stimulus along the leaf.

Such movements maximize the amount of time that leaf blades are perpendicular to the sun, which is the angle at which photosynthesis is most efficient.

Study Break

1. What is the direct stimulus for phototropisms? For gravitropism?
2. Explain how nastic movements differ from tropic movements.

35.4 Plant Responses to the Environment: Biological Clocks

Like all eukaryotic organisms, plants have internal time-measuring mechanisms called **biological clocks** that adapt the organism to recurring environmental changes. In plants biological clocks help adjust both daily and seasonal activities.

Circadian Rhythms Are Based on 24-Hour Cycles

Some plant activities occur regularly in cycles of about 24 hours, even when environmental conditions remain constant. These are **circadian rhythms** (*circa* = around, *dies* = day). In Chapter 32, we noted that stomata open and close on a daily cycle, even where plants are kept in total darkness. Nastic sleep movements, described earlier, are another example of a circadian rhythm. Even when such a plant is kept in constant light or darkness for a few days, it folds its leaves into the "sleep" position at roughly 24-hour intervals. In some way, the plant measures time without sunrise (light) and sunset (darkness). Such experiments demonstrate that internal controls, rather than external cues, largely govern circadian rhythms.

Circadian rhythms and other activities regulated by a biological clock help ensure that plants of a single species do the same thing, such as flowering, at the same time. For instance, flowers of the aptly named four-o'clock plant *(Mirabilis jalapa)* open predictably every 24 hours—in nature, in the late afternoon. Such coordination can be crucial for successful pollination. Although some circadian rhythms can proceed without direct stimulus from light, many biological clock mechanisms are influenced by the relative lengths of day and night.

Photoperiodism Involves Seasonal Changes in the Relative Length of Night and Day

Obviously, environmental conditions in a 24-hour period are not the same in summer as they are in winter. In North America, for instance, winter temperatures are cooler and winter day length is shorter. Experimenting with tobacco and soybean plants in the early 1900s, two American botanists, Wightman Garner and Henry Allard, elucidated a phenomenon they called **photoperiodism**, in which plants respond to changes in the relative lengths of light and dark periods in their environment during each 24-hour period. Through photoperiodism, the biological clocks of plants (and animals) make seasonal adjustments in their patterns of growth, development, and reproduction.

In plants, we now know that a blue-green pigment called **phytochrome** often serves as a switching mechanism in the photoperiodic response, signaling the plant to make seasonal changes. Plants synthesize phytochrome in an inactive form, P_r, which absorbs light of red wavelengths. Sunlight contains relatively more red light than far-red light. During daylight hours when red wavelengths dominate, P_r absorbs red light. Absorption of red light triggers the conversion of phytochrome to an active form designated P_{fr}, which absorbs light of far-red wavelengths. At sunset, at night, or even in shade, where far-red wavelengths predominate, P_{fr} reverts to P_r **(Figure 35.26).**

In nature a high concentration of P_{fr} "tells" a plant that it is exposed to sunlight, an adaptation that is vital given that over time sunlight provides favorable conditions for leaf growth, photosynthesis, and flowering. The exact mechanism of this crucial transfer of environmental information still is not fully understood. Phytochrome activation may stimulate plant cells to take up Ca^{2+} ions, or it may induce certain plant organelles to release them. Either way, when free calcium ions combine with calcium-binding proteins (such as calmodulin), they may initiate at least some responses to light. Botanists suspect that P_{fr} controls the types of

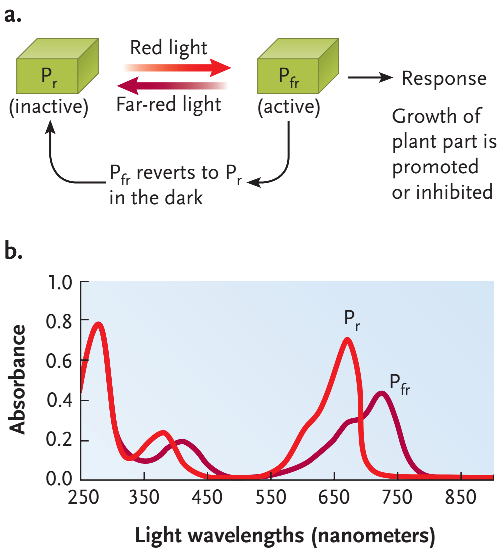


Figure 35.26
The phytochrome switching mechanism, which can promote or inhibit growth of different plant parts. **(a)** Interconversion of phytochrome from the active form (P_{fr}) to the inactive form (P_r). **(b)** The absorption spectra associated with the interconversion of P_r and P_{fr}.


Dwight Kuhn

Figure 35.27
Effects of the absence of light on young bean plants *(Phaseolus)*. The two plants at the right, the control group, were grown in a greenhouse. The other two were grown in darkness for 8 days. Note that the dark-grown plants are yellow; they could form carotenoid pigments but not chlorophyll in darkness. They have longer stems, smaller leaves, and smaller root systems than the controls.

enzymes being produced in particular cells—and different enzymes are required for seed germination, stem elongation and branching, leaf expansion, and the formation of flowers, fruits, and seeds. When plants adapted to full sunlight are grown in darkness, they put more resources into stem elongation and less into leaf expansion or stem branching **(Figure 35.27).**

Cryptochrome—which, recall, is sensitive to blue light and appears to influence light-related growth responses—also interacts with phytochromes in producing circadian responses. Researchers have recently discovered that cryptochrome occurs not only in plants but also in animals such as fruit flies and mice. Does it act as a circadian photoreceptor in both kingdoms? Only further study will provide the answer.

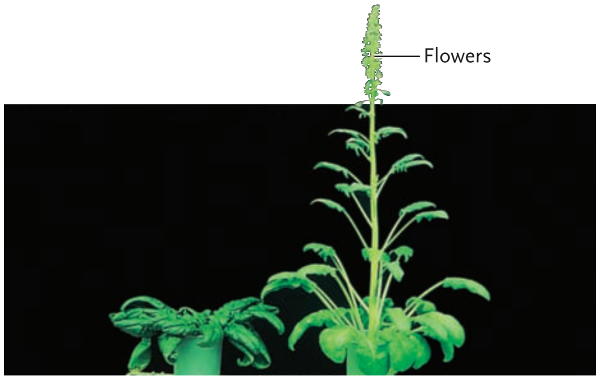
Cycles of Light and Dark Often Influence Flowering

Photoperiodism is especially apparent in the flowering process. Like other plant responses, flowering is often keyed to changes in day length through the year and to the resulting changes in environmental conditions. Corn, soybeans, peas, and other annual plants begin flowering after only a few months of growth. Roses and other perennials typically flower every year or after several years of vegetative growth. Carrots, cabbages, and other biennials typically produce roots, stems, and leaves the first growing season, die back to soil level in autumn, then grow a new flower-forming stem the second season.

In the late 1930s Karl Hamner and James Bonner grew cocklebur plants *(Xanthium strumarium)* in chambers in which the researchers could carefully control environmental conditions, including photoperiod. And they made an unexpected discovery: Flowering occurred only when the test plants were exposed to at least a single night of 8.5 hours of uninterrupted darkness. The length of the "day" in the growth chamber did not matter, but if light interrupted the dark period for even a minute or two, the plant would not flower at all. Subsequent research confirmed that for most angiosperms, it is the length of darkness, not light, that controls flowering.

Kinds of Flowering Responses. The photoperiodic responses of flowering plants are so predictable that botanists have long used them to categorize plants **(Figure 35.28).** The categories, which refer to day length, reflect the fact that scientists recognized the phenomenon of photoperiodic flowering responses long before they understood that darkness, not light, was the cue. **Long-day plants**, such as irises, daffodils, and corn, usually flower in spring when dark periods become shorter and day length becomes longer than some critical value—usually 9–16 hours. **Short-day plants**, including cockleburs, chrysanthemums, and potatoes, flower in late summer or early autumn when dark periods become longer and day length becomes shorter than some critical value. **Intermediate-day plants**, such as sugarcane, flower only when day length falls in between the values for long-day and short-day plants. **Day-neutral plants**, such as dandelions and roses, flower whenever they become mature enough to do so, without regard to photoperiod.

Experiments demonstrate what happens when plants are grown under the "wrong" photoperiod regimes. For instance, spinach, a long-day plant, flowers and produces seeds only if it is exposed to no more than 10 hours of darkness each day for two weeks (see Figure 35.28). **Figure 35.29** illustrates the results of an experiment to test the responses of short-day and long-day plants to night length. In this experiment, bearded iris plants (*Iris* species), which are long-day plants, and chrysanthemums, which are short-day plants, were exposed to a range of light conditions. In each case, when the researchers interrupted a critical dark period



Jan Zeevart

Figure 35.28
Effect of day length on spinach *(Spinacia oleracea)*, a long-day plant.

with a pulse of red light, the light reset the plants' clocks. The experiment provided clear evidence that short-day plants flower only when nights are longer than a critical value—and long-day plants flower only when nights are shorter than a critical value.

Chemical Signals for Flowering. When photoperiod conditions are right, what sort of chemical message stimulates a plant to develop flowers? In the 1930s botanists began postulating the existence of "florigen," a hypothetical hormone that served as the flowering signal. In a somewhat frustrating scientific quest, researchers spent the rest of the twentieth century seeking this substance in vain. Recently, however, molecular studies using *Arabidopsis* plants have defined a sequence of steps that may collectively provide the internal stimulus for flowering. Here again, we see one of the recurring themes in plant development—major developmental changes guided by several interacting genes.

Figure 35.30 traces the steps of the proposed flowering signal. To begin with, a gene called *CONSTANS* is expressed in a plant's leaves in tune with the daily light/dark cycle, with expression peaking at dusk (step 1). The gene encodes a regulatory protein called CO (not to be confused with carbon monoxide). As days lengthen in spring, the concentration of CO rises in leaves, and as a result a second gene is activated (step 2). The product of this gene, a regulatory protein called FT, travels in

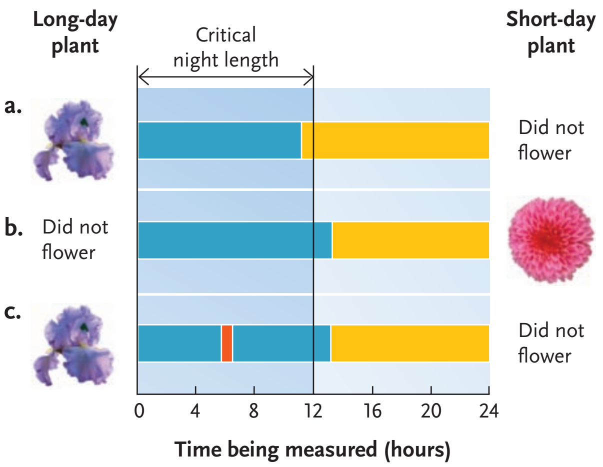
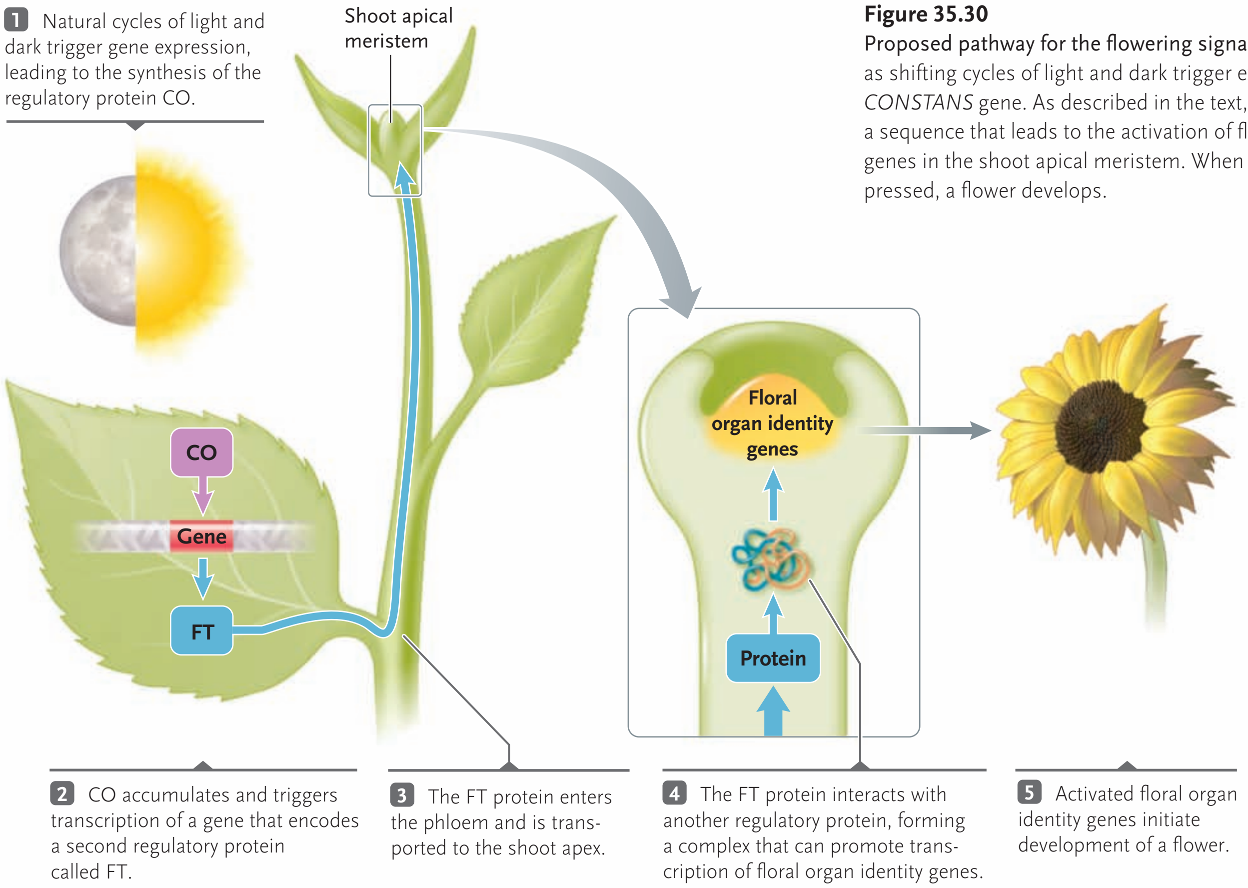


Figure 35.29
Experiments showing that short-day and long-day plants flower by measuring night length. Each horizontal bar signifies 24 hours. Blue bars represent night, and yellow bars day. **(a)** Long-day plants such as bearded irises flower when the night is shorter than a critical length, while **(b)** short-day plants such as chrysanthemums flower when the night is longer than a critical value. **(c)** When an intense red flash interrupts a long night, both kinds of plants respond as if it were a short night; the irises flowered but the chrysanthemums did not.

(Long-day plant photos: Clay Perry/Corbis; short-day plant photo: Eric Chrichton/Corbis.)

Figure 35.30
Proposed pathway for the flowering signal. The pathway starts as shifting cycles of light and dark trigger expression of the *CONSTANS* gene. As described in the text, this step is the first in a sequence that leads to the activation of floral organ identity genes in the shoot apical meristem. When these genes are expressed, a flower develops.



1 Natural cycles of light and dark trigger gene expression, leading to the synthesis of the regulatory protein CO.

2 CO accumulates and triggers transcription of a gene that encodes a second regulatory protein called FT.

3 The FT protein enters the phloem and is transported to the shoot apex.

4 The FT protein interacts with another regulatory protein, forming a complex that can promote transcription of floral organ identity genes.

5 Activated floral organ identity genes initiate development of a flower.

the phloem to shoot tips (step 3). Once there, the mRNA is translated into a second regulatory protein (step 4) that in some way interacts with yet a third regulatory protein that is synthesized only in shoot apical meristems (step 5). The encounter apparently sparks the development of a flower (step 6) by promoting the expression of floral organ identity genes in the meristem tissue (see Section 34.5). Key experiments that uncovered this pathway all relied on analysis of DNA microarrays, a technique introduced in Chapter 18 and featured in this chapter's *Focus on Research*.

Vernalization and Flowering. Flowering is more than a response to changing night length. Temperatures also change with the seasons in most parts of the world, and they too influence flowering. For instance, unless buds of some biennials and perennials are exposed to low winter temperatures, flowers do not form on stems in spring. Low-temperature stimulation of flowering is called **vernalization** ("making springlike").

In 1915 the plant physiologist Gustav Gassner demonstrated that it was possible to influence the flowering of cereal plants by controlling the temperature of seeds while they were germinating. In one case, he maintained germinating seeds of winter rye *(Secale cereale)* at just above freezing (1°C) before planting them. In nature, winter rye seeds in soil germinate during the winter, giving rise to a plant that flowers months later, in summer. Plants grown from Gassner's test seeds, however, flowered the same summer even when the seeds were planted in the late spring. Home gardeners can induce flowering of daffodils and tulips by putting the bulbs (technically, *corms*) in a freezer for several weeks before early spring planting. Commercial growers use vernalization to induce millions of plants, such as Easter lilies, to flower just in time for seasonal sales.


R. J. Downs

Figure 35.31
Effect of the relative length of day and night on the growth of Douglas firs *(Pseudotsuga menziesii)*. The young tree at the left was exposed to alternating periods of 12 hours of light followed by 12 hours of darkness for a year; its buds became dormant because day length was too short. The tree at the right was exposed to a cycle of 20 hours of light and 4 hours of darkness; its buds remained active and growth continued. The middle plant was exposed each day to 12 hours of light and 11 hours of darkness, with a 1-hour light in the middle of the dark period. This light interruption of an otherwise long dark period also prevented buds from going dormant.

Dormancy Is an Adaptation to Seasonal Changes or Stress

As autumn approaches and days grow shorter, growth slows or stops in many plants even if temperatures are still moderate, the sky is bright, and water is plentiful. When a perennial or biennial plant stops growing under conditions that seem (to us) quite suitable for growth, it has entered a state of **dormancy.** Ordinarily, its buds will not resume growth until early spring.

Short days and long nights—conditions typical of winter—are strong cues for dormancy. In one experiment, in which a short period of red light interrupted the long dark period for Douglas firs, the plants responded as if nights were shorter and days were longer; they continued to grow taller **(Figure 35.31).** Conversion of P_r to P_{fr} by red light during the dark period prevented dormancy. In nature, buds may enter dormancy because less P_{fr} can form when day length shortens in late summer. Other environmental cues are at work also. Cold nights, dry soil, and a deficiency of nitrogen apparently also promote dormancy.

The requirement for multiple dormancy cues has adaptive value. For example, if temperature were the only cue, plants might flower and seeds might germinate in warm autumn weather—only to be killed by winter frost.

A dormancy-breaking process is at work between fall and spring. Depending on the species, breaking


Eric Welzel/Fox Hill Nursery, Freeport, Maine

Potted plant grown inside a greenhouse did not flower.

Branch exposed to cold outside air flowered.

Figure 35.32
Effect of cold temperature on dormant buds of a lilac *(Syringa vulgaris)*. In this experiment, a plant was grown in winter inside a warm greenhouse with one branch growing out of a hole. Only the buds on the branch exposed to low outside temperatures resumed growth in spring. This experiment suggests that low-temperature effects are localized.

FOCUS ON RESEARCH

Research Methods: Using DNA Microarray Analysis to Track Down "Florigen"

The more plant scientists learn about plant genomes, the more they are relying on DNA microarray assays to elucidate the activity of plant genes.

Recall from Section 18.3 that a DNA microarray, also called a DNA chip, allows an investigator to explore questions such as how the expression of a particular gene differs in different types of cells. To quantify the expression of specific genes in particular types of cells, mRNA transcripts are isolated from the cells; then a cDNA library is created from each mRNA sample, using nucleotides labeled with fluorescent dyes. Probes (nucleotide sequences) representing every gene in the organism's genome are fixed onto a slide; when the labeled cDNAs are added to the slide, each will hybridize to the gene that expressed the mRNA from which it was made. Next, the DNA microarray is scanned with a laser that can detect fluorescence. When a gene is expressed in a cell, the dye fluoresces and gives a color that accords with the degree of its expression. The procedure can be manipulated to reveal the relative amounts of expression of more than one of a cell's genes.

Philip A. Wigge and his colleagues used this method to learn more about the signaling pathway that causes a plant's apical meristem to give rise to flowers. Previous research had established that in leaves, lengthening spring days coincided with rising concentrations of CO, a regulatory protein encoded by the *CONSTANS* gene. But what did CO regulate? Working with *Arabidopsis thaliana,* Wigge's group was able to narrow down the field to four genes, and using microarray analysis of DNA from leaf cells they pinpointed one called FT (for flowering locus T). The researchers found that in leaves, CO causes strong expression of FT: When enough CO is present, FT mRNA is rapidly transcribed, then enters the phloem. (The transport of mRNA in phloem is not unusual.) By contrast, when they tested CO's effects in shoot apex cells, they found that it triggers far less gene expression there. Clearly, CO was not directly triggering the development of flowers. However, FT mRNA moves in the phloem to the shoot apex, where it is translated into protein. Was that protein the direct flowering signal? Other studies had implicated a regulatory protein called FD, which microarray analysis had shown was expressed *only*—but very strongly—in the shoot apex.

To sort out this final piece of the puzzle, the Wigge team examined flowering responses in normal *A. thaliana* plants as well as in mutants having a normal FT protein but a defective *fd,* and vice versa. Flowering was abnormal in both types of mutants, possibly because the mutated "partner" suppressed some aspect of the functioning of the normal protein. On the other hand, in wild-type plants, which had a functioning FD protein, expression of FT triggered a marked increased in the expression of the floral organ gene *APETALA1* **(Figure a).** These results have two major implications. First, they support the hypothesis that FT and FD interact in a normal flowering response. Second, the study suggests that FT, the CO-induced signal from leaves, conveys the environmental signal that it is time for a plant to flower. In that sense, FT may be the long sought "florigen." However, only by interacting with FD does FT "know" where to deliver its flowering signal—in the apical meristems of shoots.

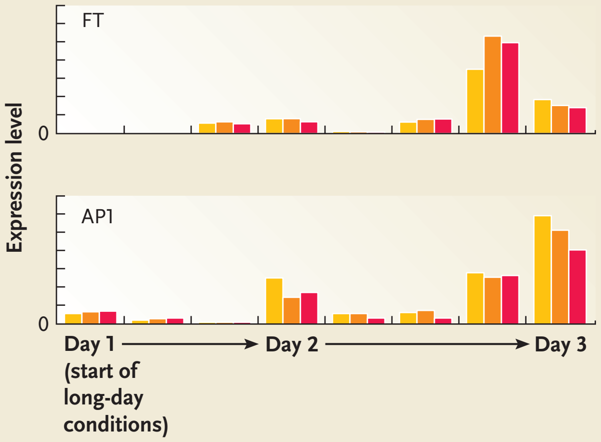


Figure a
Effect of the FT protein on expression of the *APETALA1 (AP1)* floral organ identity gene. In nature, *Arabidopsis thaliana* is a long-day plant, and the experiment was carried out under long-day (that is, short-night) conditions. Three groups of replicates shown here in yellow, orange, and red respectively, were monitored for both AP1 and FT. After a brief delay, the expression of AP1 closely tracked the appearance of the FT regulatory protein, which had been activated by its interaction with the FD protein.

dormancy probably involves gibberellins and abscisic acid, and it requires exposure to low winter temperatures for specific periods **(Figure 35.32).** The temperature needed to break dormancy varies greatly among species. For example, the Delicious variety of apples grown in Utah requires 1230 hours near 43°F (6°C); apricots grown there require only 720 hours at that temperature. Generally, trees growing in the southern United States or in Italy require less cold exposure than those growing in Canada or in Sweden.

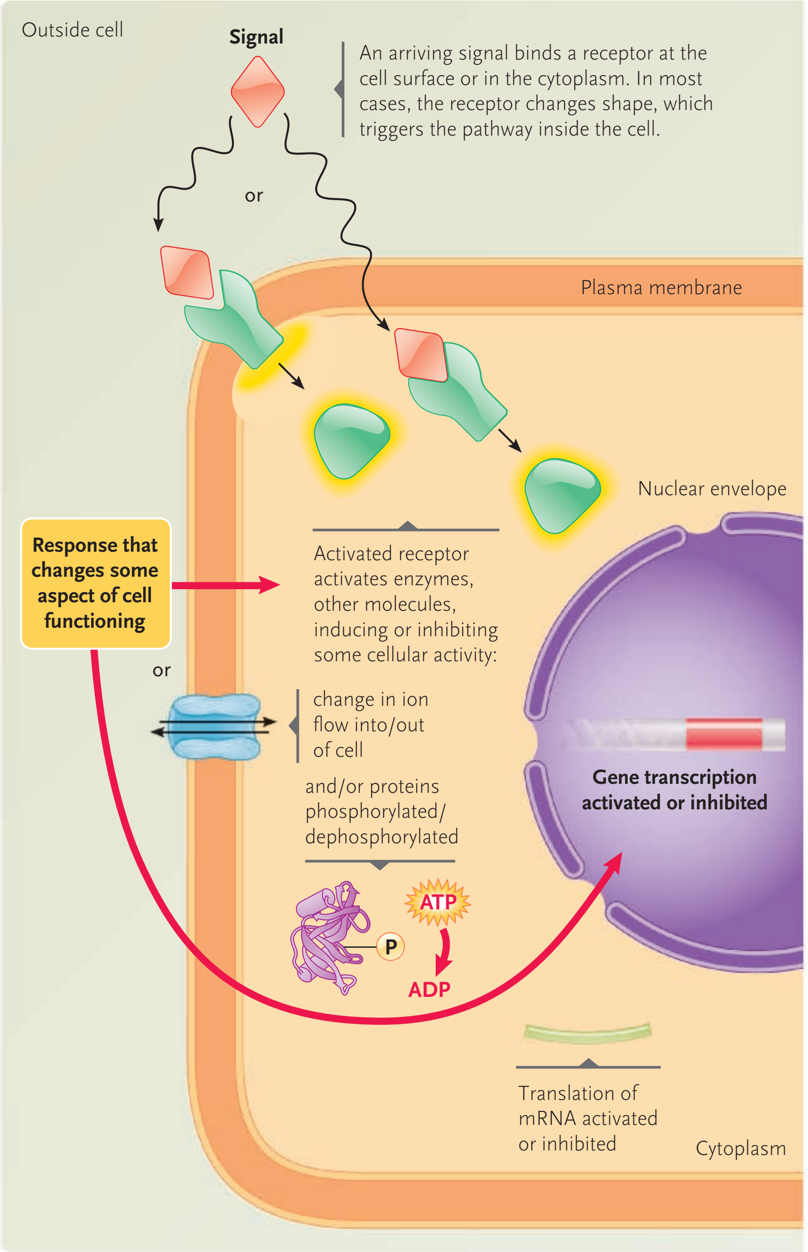
STUDY BREAK

1. Summarize the switching mechanism that operates in plant responses to changes in photoperiod.
2. Give some examples of how relative lengths of dark and light can influence flowering.
3. Explain why dormancy is an adaptive response to a plant's environment.

35.5 Signal Responses at the Cellular Level

Environmental stimuli such as changing light, temperature, or chemicals on the surface of an attacking pathogen are cues that signal a plant to alter its growth or physiology. For decades plant physiologists have looked avidly for clues about how those signals are converted into a chemical message that produces a change in cell metabolism or growth. As Chapter 7 describes, research on the ways animal cells respond to external signals has revealed some basic mechanisms, and at least some of these mechanisms also apply to plant cells.

Figure 35.33 Signal response pathways in plant cells.



An arriving signal binds a receptor at the cell surface or in the cytoplasm. In most cases, the receptor changes shape, which triggers the pathway inside the cell.

Activated receptor activates enzymes, other molecules, inducing or inhibiting some cellular activity:

change in ion flow into/out of cell

and/or proteins phosphorylated/ dephosphorylated

Translation of mRNA activated or inhibited

Several Signal Response Pathways Operate in Plants

Hormones and environmental stimuli alter the behavior of target cells, which have receptors to which specific signal molecules can bind and elicit a cellular response. By means of a response pathway, a signal can induce changes in the cell's shape and internal structure or influence the transport of ions and other substances into and out of cells. Some signals cause cells to alter gene activation and the rate of protein synthesis; others set in motion events that modify existing cell proteins. Section 7.1 presents some general features of the signaling process. Here, we'll briefly consider how signal molecules may operate in plants.

Certain hormones and growth factors bind to receptors at the target cell's plasma membrane, on its endoplasmic reticulum (ER), or in the cytoplasm. For example, ethylene receptors are on the ER, and the auxin receptor is a protein in the cytoplasm called TIR1. Research in several laboratories recently confirmed that auxin binds directly to TIR1, setting in motion events that break down protein factors that inhibit transcription. As a result, previously repressed genes are turned on. In many cases (although not with TIR1), binding causes the receptor to change shape. Regardless, binding of a hormone or growth factor triggers a complex pathway that leads to the cell response—the opening of ion channels, activation of transport proteins, or some other event.

Only some cells can respond to a particular signaling molecule, because not all cells have the same types of receptors. For example, particular cells in ripening fruits and developing seeds have ethylene receptors, but few if any cells in stems do. Different signals also may have different effects on a single cell, and may exert those effects by way of different response pathways. One type of signal might stimulate transcription, and another might inhibit it. In addition, as we've seen, some genes controlled by particular receptors encode proteins that regulate still *other* genes.

In plants we know the most about pathways involving auxin, ethylene, salicylic acid, and blue light. **Figure 35.33** diagrams a general model for these response pathways in plant cells. As the figure shows, the response may lead to a change in the cell's structure, its metabolic activity, or both, either directly or by altering the expression of one or more genes.

Second Messenger Systems Enhance the Plant Cell's Response to a Hormone's Signal

We can think of plant hormones and other signaling molecules as external first messengers that deliver the initial physiological signal to a target cell. Often, as with salicylic acid, binding of the signal molecule triggers the synthesis of internal second messengers (introduced in Section 7.4). These intermediary molecules diffuse rapidly through the cytoplasm and provide the main chemical signal that alters cell functioning.

Second messengers usually are synthesized in a sequence of chemical reactions that converts an external signal into internal cell activity. For many years the details of plant second-messenger systems were sketchy and hotly debated. More recently, however, reaction sequences that occur in the cells of animals and some fungi have also been found in plants. The following example describes reactions that close plant stomata in response to a signal from abscisic acid.

As discussed in Section 35.1, abscisic acid helps regulate several responses in plants, including the maturation of seeds and the closing of stomata (see Section 32.3). ABA's role in stomatal closure—triggered by water stress or some other environmental cue—begins when the hormone activates a receptor in the plant cell plasma membrane. Experiments have shown that this binding activates G proteins that in turn activate phospholipase C (see Figure 7.12). This enzyme stimulates the synthesis of second messengers, such as inositol triphosphate (IP_3).

The second messenger diffuses through the cytoplasm and binds with calcium channels in cell structures such as the endoplasmic reticulum, vacuole, and plasma membrane. The bound channels then open, releasing calcium ions that activate protein kinases in the cytoplasm. In turn, the activated enzymes activate their target proteins (by phosphorylating them). Each protein kinase can convert a large number of substrate molecules into activated enzymes, transport proteins, open ion channels, and so forth. Soon the number of molecules representing the final cellular response to the initial signal is enormous.

Recent experimental evidence indicates that, in similar fashion, auxin's hormonal signal is conveyed by cAMP (cyclic adenosine monophosphate), another major second messenger in cells of animals and other organisms.

In addition to the basic pathways described here, other routes may exist that are unique to plant cells.

UNANSWERED QUESTIONS

Do plants have a "backup" copy of their genome?

As described at the beginning of this chapter, land plants manifest adaptations that allow them to survive and reproduce in unfavorable or hostile conditions. Adaptations include changes in growth and development reflecting responses to environmental fluctuations that occur naturally during the normal life cycle of plants. Being physically anchored in one place has driven plant adaptation so that changes in the plant body can facilitate survival. It is also possible, however, that the sessile existence of land plants may have selected for unusual adaptive strategies. Might plants have devised a strategy to utilize previously unknown genetic resources and thereby expand their potential repertoire of adaptive responses? Recent findings demonstrating the existence of a previously unknown mechanism of genetic instability suggest that such a strategy may indeed have been in place during the evolution of land plants. These findings suggest that, at least in *Arabidopsis thaliana,* a "backup" copy of the genome exists that can be accessed under unfavorable conditions.

Why have a backup copy of the genome? Simply put, if the system crashes, it can be restored. By analogy, the genome could be considered the "operating system" stored on the "hard drive" of the organism. If that operating system becomes corrupted, for example by a devastating power surge or a computer virus, a global systems failure might occur. However, if a backup copy were maintained at least in a subset of the population, then, under conditions that might lead to extinction, the backup copy could be used to "restore" the system and increase the chances of survival for that organism or population. In other words, the genome could adapt using the stored information.

An intriguing possibility is that such a backup genome might exist in the form of RNA. The fact that backup copies have not been found using conventional DNA-based detection methods or classical genetic approaches leaves open the exciting possibility that RNA might serve as the storage medium for this information. In a sense, having the information stored in an alternative chemical form (analogous to a different computer language or code) might also make it less susceptible to corruption. Furthermore, it may be that this backup genome is a remnant of an ancestral condition where the genome was RNA-based.

How would you go about testing these different possibilities? First, the findings would have to be independently verified and the existence of a "restoration" mechanism would have to be confirmed by other research groups working on *Arabidopsis* or other plant species. Second, the source and chemical nature of the backup information would need to be identified. Where is it, and is it RNA, DNA, protein, or a combination of these? The question of mechanism would also need to be addressed. How is the system restored, and when does it happen? The question of how widespread this phenomenon is would also need to be considered. Do all plant species maintain a backup copy and do organisms outside of the plant kingdom have a backup genome?

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Light is the driving force for photosynthesis, and it may not be farfetched to suppose that plants have evolved other unique light-related biochemical pathways as well. For instance, exciting experiments are extending our knowledge of how plant cells respond to blue light, which, as we have discussed, triggers some photoperiod responses such as the opening and closing of stomata. In all likelihood, much remains to be discovered about this and many other aspects of plant functioning.

STUDY BREAK

1. Summarize the various ways that chemical signals reaching plant cells are converted to changes in cell functioning.
2. What basic task does a second messenger accomplish?
3. Thinking back to Chapter 7, can you describe parallels between signal transduction mechanisms in the cells of plants and animals?

Review

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35.1 Plant Hormones

- At least seven classes of hormones govern flowering plant development, including germination, growth, flowering, fruit set, and senescence (Table 35.1).
- Auxins, mainly IAA, promote elongation of cells in the coleoptile and stem (Figures 35.2–35.7).
- Gibberellins promote stem elongation and help seeds and buds break dormancy (Figures 35.1, 35.8, and 35.9).
- Cytokinins stimulate cell division, promote leaf expansion, and retard leaf aging (Figure 35.10).
- Ethylene promotes fruit ripening and abscission (Figures 35.11 and 35.12).
- Brassinosteroids stimulate cell division and elongation (Figure 35.13).
- Abscisic acid (ABA) promotes stomatal closure and may trigger seed and bud dormancy (Figure 35.14).
- Jasmonates regulate growth and have roles in defense.

Animation: Plant development

Animation: Auxin's effects

35.2 Plant Chemical Defenses

- Plants have diverse chemical defenses that limit damage from bacteria, fungi, worms, or plant-eating insects (Figure 35.15).
- The hypersensitive response isolates an infection site by surrounding it with dead cells (Figure 35.16). During the response salicylic acid (SA) induces the synthesis of PR (pathogenesis-related) proteins.
- Oligosaccharins can trigger the synthesis of phytoalexins, secondary metabolites that function as antibiotics.
- Gene-for-gene recognition enables a plant to chemically recognize a specific pathogen and mount a defense (Figure 35.17).
- Systemic acquired resistance provides long-term protection against some pathogens. Salicylic acid passes from the infected organ to newly forming organs such as leaves, which then synthesize PR proteins (Figure 35.18).
- Heat-shock proteins can reversibly bind enzymes and other proteins in plant cells and prevent them from denaturing when the plant is under heat stress.
- Some plants can synthesize "antifreeze" proteins that stabilize cell proteins when cells are threatened with freezing.

35.3 Plant Responses to the Environment: Movements

- Plants adjust their growth patterns in response to environmental rhythms and unique environmental circumstances. These responses include tropisms.
- Phototropisms are growth responses to a directional light source. Blue light is the main stimulus for phototropism (Figures 35.3 and 35.19).
- Gravitropism is a growth response to Earth's gravitational pull. Stems exhibit negative gravitropism, growing upward, while roots show positive gravitropism (Figures 35.20 and 35.21).
- Some plants or plant parts demonstrate thigmotropism, growth in response to contact with a solid object (Figure 35.22).
- Mechanical stress can cause thigmomorphogenesis, which causes the stem to add girth (Figure 35.31).
- In nastic leaf movements, water enters or exits cells of a pulvinus, a pad of tissue at the base of a leaf or petiole, in response to action potentials (Figures 35.24 and 35.25).

Animation: Gravitropism

Animation: Gravity and statolith distribution

Animation: Phototropism

35.4 Plant Responses to the Environment: Biological Clocks

- Plants have biological clocks, internal time-measuring mechanisms with a biochemical basis. Environmental cues can "reset" the clocks, enabling plants to make seasonal adjustments in growth, development, and reproduction.
- In photoperiodism, plants respond to a change in the relative length of daylight and darkness in a 24-hour period. A switching mechanism involving the pigment phytochrome promotes or inhibits germination, growth, and flowering and fruiting.
- Phytochrome is converted to an active form (P_{fr}) during daylight, when red wavelengths dominate. It reverts to an inactive form (P_r) at sunset, at night, or in shade, when far-red wavelengths predominate. P_{fr} may control the types of metabolic pathways that operate under specific light conditions (Figure 35.26).
- Long-day plants flower in spring or summer, when day length is long relative to night. Short-day plants flower when day length is relatively short, and intermediate-day plants flower when day length falls in between the values for long-day and short-day

plants. Flowering of day-neutral plants is not regulated by light. In vernalization, a period of low temperature stimulates flowering (Figures 35.27–35.29).

- The direct trigger for flowering may begin in leaves, when the regulatory protein CO triggers the expression of the FT gene. The resulting mRNA transcripts move in phloem to apical meristems where translation of the mRNAs yields a second regulatory protein, which in turn interacts with a third. This final interaction activates genes that encode the development of flower parts (Figure 35.30).
- Senescence is the sum of processes leading to the death of a plant or plant structure.
- Dormancy is a state in which a perennial or biennial stops growing even though conditions appear to be suitable for continued growth (Figures 35.31 and 35.32).

Animation: Phytochrome conversions

Animation: Vernalization

Animation: Day length and dormancy

Animation: Flowering response experiments

35.5 Signal Responses at the Cellular Level

- Hormones and environmental stimuli alter the behavior of target cells, which have receptors to which signal molecules can bind. By means of a response pathway that ultimately alters gene expression, a signal can induce changes in the cell's shape or internal structure or influence its metabolism or the transport of substances across the plasma membrane (Figure 35.33).
- Some plant hormones and growth factors may bind to receptors at the target cell's plasma membrane, changing the receptor's shape. This binding often triggers the release of internal second messengers that diffuse through the cytoplasm and provide the main chemical signal that alters gene expression.
- Second messengers usually act by way of a reaction sequence that amplifies the cell's response to a signal. An activated receptor activates a series of proteins, including G proteins and enzymes that stimulate the synthesis of second messengers (such as IP_3) that bind ion channels on endoplasmic reticulum.
- Binding releases calcium ions, which enter the cytoplasm and activate protein kinases, enzymes that activate specific proteins that produce the cell response.

Questions

Self-Test Questions

1. Which of the following plant hormones does *not* stimulate cell division?
   a. auxins
   b. cytokinins
   c. ethylene
   d. gibberellins
   e. abscisic acid
2. Which is the correct pairing of a plant hormone and its function?
   a. salicylic acid: triggers synthesis of general defense proteins
   b. brassinosteroids: promote responses to environmental stress
   c. cytokinins: stimulate stomata to close in water-stressed plants
   d. gibberellins: slow seed germination
   e. ethylene: promotes formation of lateral roots
3. A characteristic of auxin (IAA) transport is:
   a. IAA moves by polar transport from the base of a tissue to its apex.
   b. IAA moves laterally from a shaded to an illuminated side of a plant.
   c. IAA enters a plant cell in the form of IAAH, an uncharged molecule that can diffuse across cell membranes.
   d. IAA exits one cell and enters the next by means of transporter proteins clustered at both the apical and basal ends of the cells.
   e. All of the above are characteristics of auxin transport in different types of cells.
4. Hanging wire fruit baskets have many holes or open spaces. The major advantage of these spaces is that they:
   a. prevent gibberellins from causing bolting or the formation of rosettes on the fruit.
   b. allow the evaporation of ethylene and thus slow ripening of the fruit.
   c. allow oxygen in the air to stimulate the production of ethylene, which hastens the abscission of fruits.
   d. allow oxygen to stimulate brassinosteroids, which hasten the maturation of seeds in/on the fruits.
   e. allow carbon dioxide in the air to stimulate the production of cytokinins, which promotes mitosis in the fruit tissue and hastens ripening.
5. Which of the following is *not* an example of a plant chemical defense?
   a. ABA inhibits leaves from budding if conditions favor attacks by sap-sucking insects.
   b. Jasmonate activates plant genes encoding protease inhibitors that prevent insects from digesting plant proteins.
   c. Acting against fungal infections, the hypersensitive response allows plants to produce highly reactive oxygen compounds that kill selected tissue, thus forming a dead tissue barrier that walls off the infected area from healthy tissues.
   d. Chitinase, a PR hydrolytic protein produced by plants, breaks down chitin in the cell walls of fungi and thus halts the fungal infection.
   e. Attack by fungi or viruses triggers the release of oligosaccharins, which in turn stimulate the production of phytoalexins having antibiotic properties.
6. Which of the following statements about plant responses to the environment is true?
   a. The heat-shock response induces a sudden halt to cellular metabolism when an insect begins feeding on plant tissue.
   b. In gravitropism, amyloplasts sink to the bottom of cells in a plant stem, causing the redistribution of IAA.
   c. The curling of tendrils around a twig is an example of thigmotropism.
   d. Phototropism results when IAA moves first laterally, then downward in a shoot tip when one side of the tip is exposed to light.
   e. Nastic movements, such as the sudden closing of the leaves of a Venus flytrap, are examples of a plant's ability to respond to specific directional stimuli.
7. In nature the poinsettia, a plant native to Mexico, blooms only in or around December. This pattern suggests:
   a. the long daily period of darkness (short day) in December stimulates the flowering.
   b. vernalization stimulates the flowering.
   c. the plant is dormant for the rest of the year.
   d. phytochrome is not affecting the poinsettia flowering cycle.
   e. a circadian rhythm is in effect.

8. Which of the following steps is *not* part of the sequence that is thought to trigger flowering?
    a. Cycles of light and dark stimulate the expression of the *CONSTANS* gene in a plant's leaves.
    b. CO proteins accumulate in the leaves and trigger expression of a second regulatory gene.
    c. mRNA transcribed during expression of a second regulatory gene moves via the phloem to the shoot apical meristem.
    d. Interactions among regulatory proteins promote the expression of floral organ identity genes in meristem tissue.
    e. CO proteins in the floral meristem interact with florigen, a so-called flowering hormone, which provides the final stimulus for expression of floral organ identity genes.
9. Damage from an infectious bacterium, fungus, or worm may trigger a plant defensive response when the pathogen or a substance it produces binds to:
    a. a receptor encoded by the plant's *avirulence (Avr)* gene.
    b. an *R* gene in the plant cell nucleus.
    c. a receptor encoded by a dominant R gene.
    d. PR proteins embedded in the plant cell plasma membrane.
    e. salicylic acid molecules released from the besieged plant cell.
10. In the sequence that unfolds after molecules of a hormone such as ABA bind to receptors at the surface of a target plant cell:
    a. first messenger molecules in the cytoplasm are mobilized, then G proteins carry the signal to second messengers such as protein kinases, which alter the activity of cell proteins such as IP_3.
    b. binding activates G proteins, which in turn activate second messengers such as IP_3; subsequent steps are thought to involve activation of genes that encode protein kinases.
    c. binding activates phospholipase C, which in turn activates G proteins, which then activate molecules of IP_3, a step that leads to the synthesis of protein kinases.
    d. binding stimulates G proteins to activate protein kinases, which then bind calcium channels in ER; the flux of calcium ions activates second messenger molecules that alter the activity of cell proteins or enter the cell nucleus and alter the expression of target genes.
    e. binding activates G proteins, which in turn activate phospholipase C; this substance then stimulates the synthesis of second messenger molecules, the second messengers bind calcium channels in the cell's ER, and finally protein kinases alter the activity of proteins by phosphorylating them.

Questions for Discussion

1. You work for a plant nursery and are asked to design a special horticultural regimen for a particular flowering plant. The plant is native to northern Spain, and in the wild it grows a few long, slender stems that produce flowers each July. Your boss wants the nursery plants to be shorter, with thicker stems and more branches, and she wants them to bloom in early December in time for holiday sales. Outline your detailed plan for altering the plant's growth and reproductive characteristics to meet these specifications.
2. Synthetic auxins such as 2,4-D can be weed killers because they cause an abnormal growth burst that kills the plant within a few days. Suggest reasons why such rapid growth might be lethal to a plant.
3. In some plant species, an endodermis is present in both stems and roots. In experiments, the shoots of mutant plants lacking differentiated endodermis in their root and shoot tissue don't respond normally to gravity, but roots of such plants do respond normally. Explain this finding, based on your reading in this chapter.
4. In *A. thaliana* plants carrying a mutation called *pickle (pkl)*, the primary root meristem retains characteristics of embryonic tissue—it spontaneously regenerates new embryos that can grow into mature plants. However, when the mutant root tissue is exposed to a gibberellin (GA), this abnormal developmental condition is suppressed. Explain why this finding suggests that additional research is needed on the fundamental biological role of GA.

Experimental Analysis

Tiny, thornlike trichomes on leaves are a common plant adaptation to ward off insects. Those trichomes develop very early on, as outgrowths of a seedling's epidermal cells. Biologists have observed, however, that many mature plants develop more leaf trichomes after the fact, as a *response* to insect damage. Researchers at the University of Chicago decided to study this phenomenon, and specifically wanted to determine the effects, if any, of jasmonate, salicylic acid, and gibberellin in stimulating trichome development. Keeping in mind that plant hormones often interact, how many separate experiments, at a minimum, would the research team have had to carry out in order to obtain useful initial data? Do you suppose they used mutant plants for some or all of the tests? Why or why not?

Evolution Link

Cryptochrome occurs in plants and animals. If it was inherited from their shared ancestor, what other major groups of organisms might also have it?

How Would You Vote?

1-Methylcyclopropene, or MCP, is a gas that keeps ethylene from binding to cells in plant tissues. It is used to prolong the shelf life of cut flowers and the storage time for fruits. Should produce that is treated this way be labeled to alert consumers? Go to www.thomsonedu.com/login to investigate both sides of the issue and then vote.