32 PLANT GROWTH AND DEVELOPMENT

Foolish Seedlings, Gorgeous Grapes

A few years before the runaway growth and catastrophic collapse of the American stock market in 1929, a researcher in Japan came across a substance that caused runaway growth and subsequent collapse of young rice plants. Ewiti Kurosawa had been studying what Japanese call *bakane*, the "foolish seedling" effect on rice plants. The stems of rice seedlings that had become infected with the fungus *Gibberella fujikuroi* grew twice the length of seedlings that were infection-free. The abnormally elongated stems were weak and spindly. They soon toppled, and infected plants died. Kurosawa discovered that he could cause the infection by applying extracts of the fungus to seedlings. Many years later, other researchers purified the substance from fungal extracts that brought about the lengthening. They named it gibberellin.

Gibberellins, as we now know, are a major class of plant hormones. All **hormones** are signaling molecules secreted by some cells that travel to target cells, where they may stimulate or inhibit gene activity (Section 15.1). Any cell that bears molecular receptors for a given hormone is its target. A hormone's targets may be in the same tissue or some distance away from the cell that secretes it.

Researchers have isolated more than eighty different forms of gibberellin from seeds of flowering plants as well as from fungi. These signaling molecules cause young cells to elongate, and the collective elongation lengthens plant parts (Figure 32.1). In nature, gibberellins also help seeds and buds break dormancy and resume growth in spring.

Applications of synthetic gibberellins make celery stalks longer and crispier. They prevent the rind of navel oranges in orchard groves from ripening before pickers can get to them. Walk past plump seedless grapes in produce bins of grocery stores and marvel at how fleshy fruits of the grape plant (*Vitis*) grow in dense clusters along stems. Gibberellin applications made young grape cells elongate and stems lengthen between their nodes. The lengthening opened up more space between individual grapes, which had more room to get bigger. Air circulated better between grapes, which made it harder for pathogenic, grape-loving fungi to take hold and do damage.

Gibberellin and other plant hormones interact as part of controls over plant growth and development. Cells secrete them in response to environmental cues, as when warm spring rains arrive after winter and the hours of daylight increase. Grapes, cabbage leaves, and celery stalks that we eat are the culmination of exquisitely controlled programs of growth and development.

Here we continue with this unit on plant structure and function. So far, you have surveyed flowering plant anatomy—the tissue organization of primary and secondary growth. You considered the tissue systems by which plants acquire and distribute water and solutes

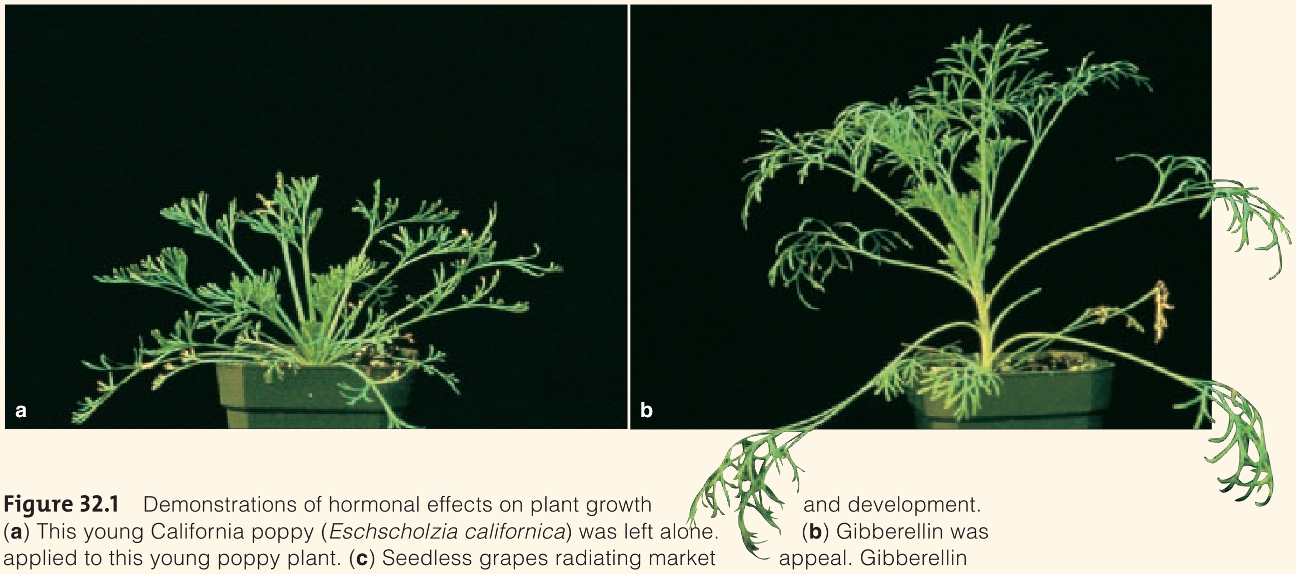
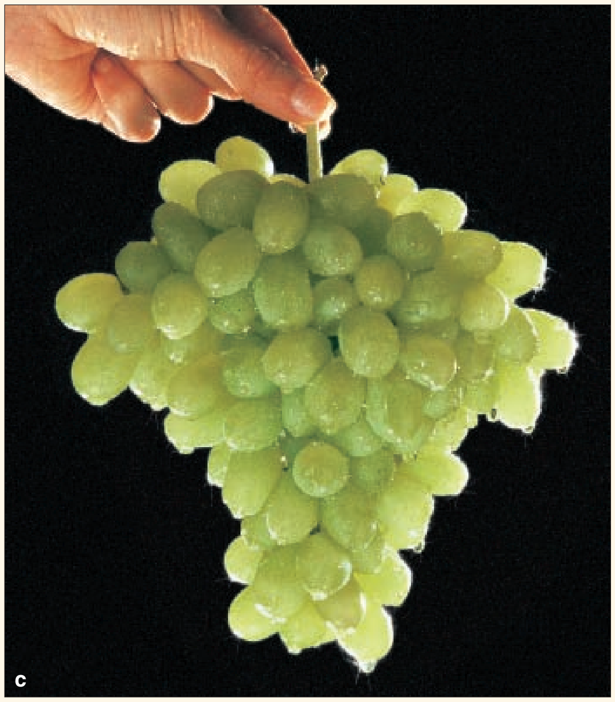


Figure 32.1 Demonstrations of hormonal effects on plant growth and development. (**a**) This young California poppy (*Eschscholzia californica*) was left alone. (**b**) Gibberellin was applied to this young poppy plant. (**c**) Seedless grapes radiating market appeal. Gibberellin causes grape stems to lengthen, which improves air circulation around grapes and gives them more room to grow. Grapes get larger and weigh more, making growers happy (grapes are sold by weight).

IMPACTS, ISSUES



that sustain their growth. You considered how these plants reproduce, from gamete formation and pollination on through the formation of a mature embryo sporophyte inside a protective seed coat.

At some point after its dispersal from a parent plant, remember, a seed germinates and growth resumes. In time, the mature sporophyte typically forms flowers, then seeds of its own. Depending on the species, it may drop old leaves throughout the year or all at once, in autumn.

Continue now with the heritable, internal mechanisms that govern plant development, and the environmental cues that turn mechanisms on or off at different times, in different seasons.

☑ How Would You Vote?

1-Methlycyclopropene, 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? See BiologyNow for details, then vote online.

Key Concepts

CONTROLS OVER GROWTH AND DEVELOPMENT

From the time a seed germinates, hormones influence plant growth and development. Different plant cells signal one another with hormones. Five major classes of plant hormones are gibberellins, auxins, cytokinins, ethylene, and abscisic acid. Since their discovery, other growth regulators have been identified. Sections 32.1, 32.2

MECHANISMS OF HORMONE ACTION

Plant hormones are part of signal transduction pathways. Their action stimulates growth and development by triggering gene transcription and other cell activities.

Plant hormones also help adjust growth patterns, as when they induce a lengthening shoot to bend toward a source of light. Section 32.3

RESPONSES TO ENVIRONMENTAL CUES

Plant hormones are synthesized when receptors of specific cells detect environmental stimuli. Gravity, sunlight, and seasonal shifts in night length and temperature are among the environmental cues that affect hormone production.

Hormone synthesis starts when a seed germinates and continues to guide all events of the life cycle, such as root and shoot development, flowering, fruit formation, and dormancy. Sections 32.4–32.8

PERSPECTIVE AT UNIT'S END

Knowledge of plant structure, function, and diversity has practical applications for human populations. Section 32.9

Links to Earlier Concepts

This chapter builds on an earlier introduction to controls over growth and development, including genetic control of flower formation (Sections 15.1–15.3). You will come across more cases of cell communication (28.5). You may wish to review where meristems are located (29.1) and how primary roots and shoots are organized (29.3, 29.5). You will build on your understanding of wavelengths of light (7.1), pH (2.6), primary cell walls (4.9), active transport (5.4), turgor pressure (5.5), stomata (30.4), and transport through phloem (30.5).

CONTROLS OVER GROWTH AND DEVELOPMENT

32.1 Overview of Plant Development

LINKS TO SECTIONS 5.5, 15.1,31.1

In the preceding chapter, we left the embryo sporophyte after its dispersal from the parent plant. Its growth idles inside the seed coat until conditions favor germination. Then, in response to genetically prescribed programs and environmental cues, growth and development resume. The sporophyte matures, then enters a phase of sexual reproduction, and the life cycle turns again.

SEED GERMINATION

Section 31.1 explains how plant tissues and structures start forming while an embryo sporophyte is still in its seed coat. Focus now on a corn grain, a type of dry fruit (Figure 32.2). This grain germinates in response to seasonal factors, such as soil's temperature and its levels of oxygen and moisture. In plants, **germination** is a process by which the embryo sporophyte resumes growth after a time of arrested development.

Mature seeds do not hold enough water to support cell expansion or metabolism. Where water is scarce for much of the year, seed germination coincides with seasonal rains. Water molecules infiltrate seeds, being attracted by hydrophilic groups of storage proteins in endosperm. Each seed swells with water, and its coat ruptures. As the seed coat splits, more oxygen reaches the embryo, and aerobic respiration provides the ATP required for growth. The embryo's meristematic cells now divide rapidly. Germination is completed when a primary root breaks out of the seed coat.

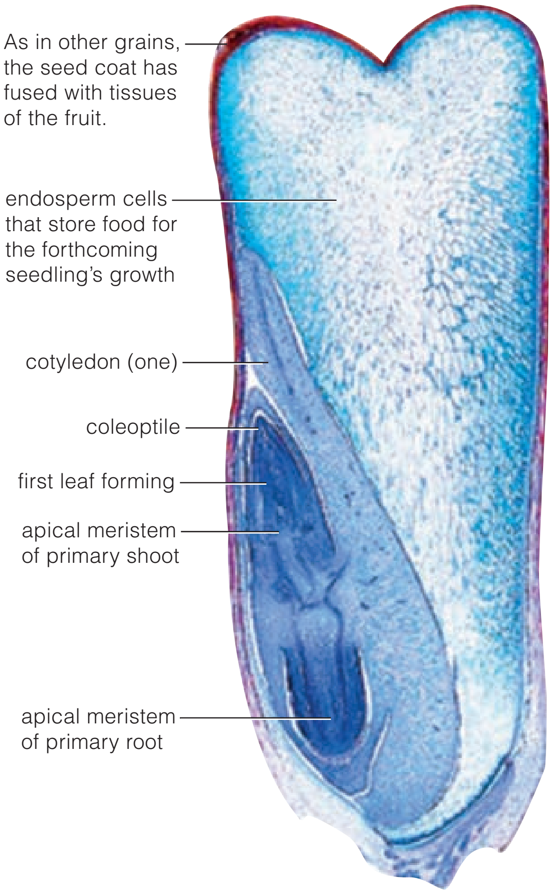


Figure 32.2 Embryo sporophyte and food reserves inside a grain of corn (*Zea mays*).

PATTERNS OF EARLY GROWTH

Figures 32.3 and 32.4 give two patterns of germination, growth, and development. The patterns have a genetic basis. All cells in a plant are descended from the same cell—a zygote—so they generally have inherited the same genes. Yet cells in different tissues of a growing plant body use subsets of genes in selective ways and differentiate into specialized types (Section 15.1).

Growth, again, refers to an increase in the number, size, and volume of cells. For plants, the mitotic cell divisions that increase the number of cells take place only at meristems (Section 29.1). Some meristematic cells never differentiate; they keep dividing and make more new cells. Others are the basis for **development**. They divide, lengthen or widen in certain directions, and become different in composition and function as a result of selective gene expression. They form roots, stems, leaves, and other parts of the multicelled body that differ in size, shape, location, and function.

Young cells enlarge as a plant takes up water. Fluid pressure, or *turgor* pressure, builds up against their still-soft, primary wall (Section 5.5). The wall and the cell expand under the pressure, something like a soft balloon being inflated.

In short, plant growth and development start with the selective transcription and translation of genes. As you will see, at certain times and in certain tissues, genes for hormones and other signaling molecules become transcribed. Signaling molecules interact and control what happens in different tissues. Environmental cues —especially water availability, the hours of darkness versus daylight, gravity, and temperature—also guide plant growth and development.

The body plan of flowering plants starts taking form while the embryo sporophyte is still part of a seed. Starting with its germination, signaling molecules and environmental cues stimulate or inhibit the formation of roots, stems, leaves, fruits, and other plant parts at specific times.

Hormones and other molecules control plant growth and development. Their formation and their action depends on selective gene transcription and translation.

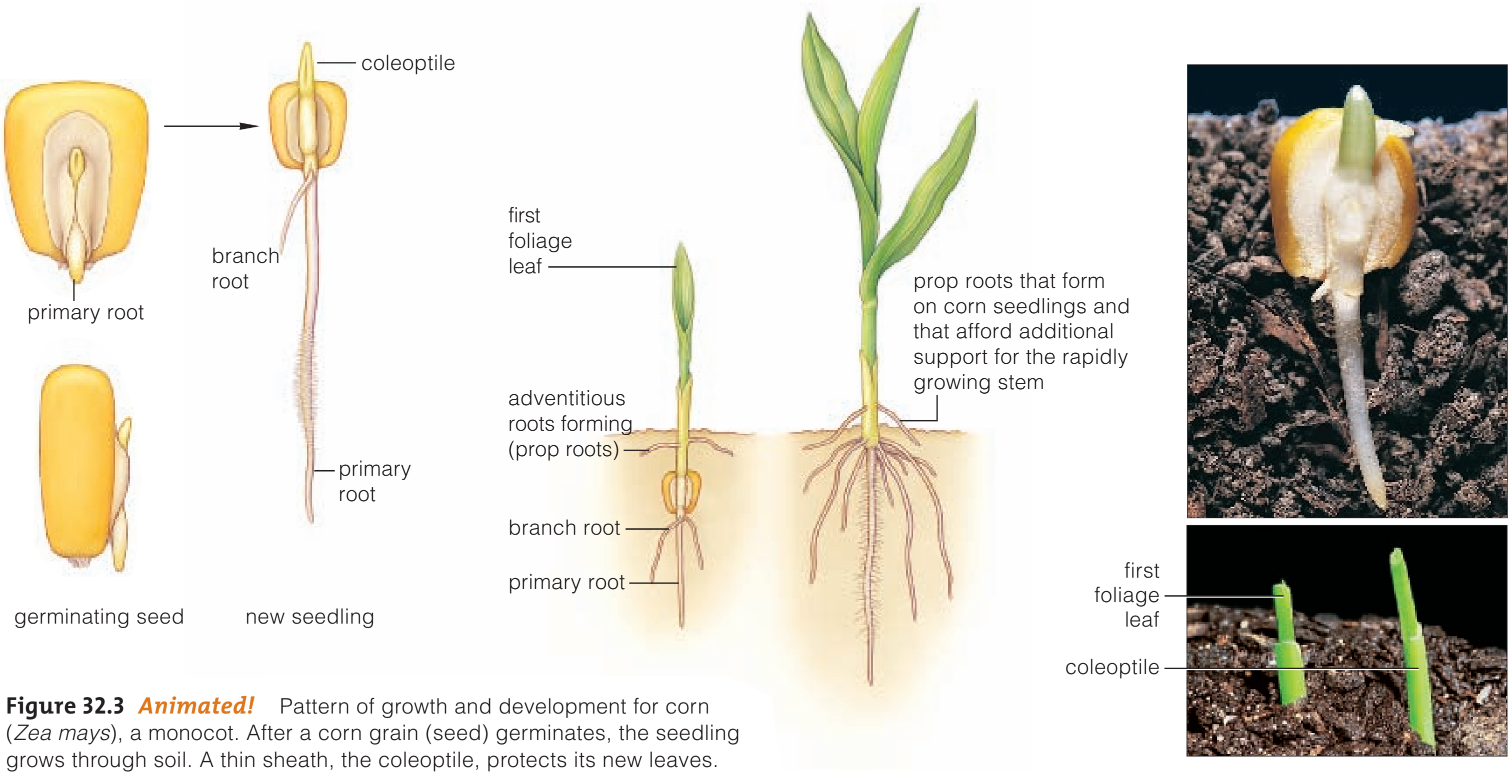


Figure 32.3 ***Animated!*** Pattern of growth and development for corn (*Zea mays*), a monocot. After a corn grain (seed) germinates, the seedling grows through soil. A thin sheath, the coleoptile, protects its new leaves. In this plant, adventitious roots develop at the base of the coleoptile.

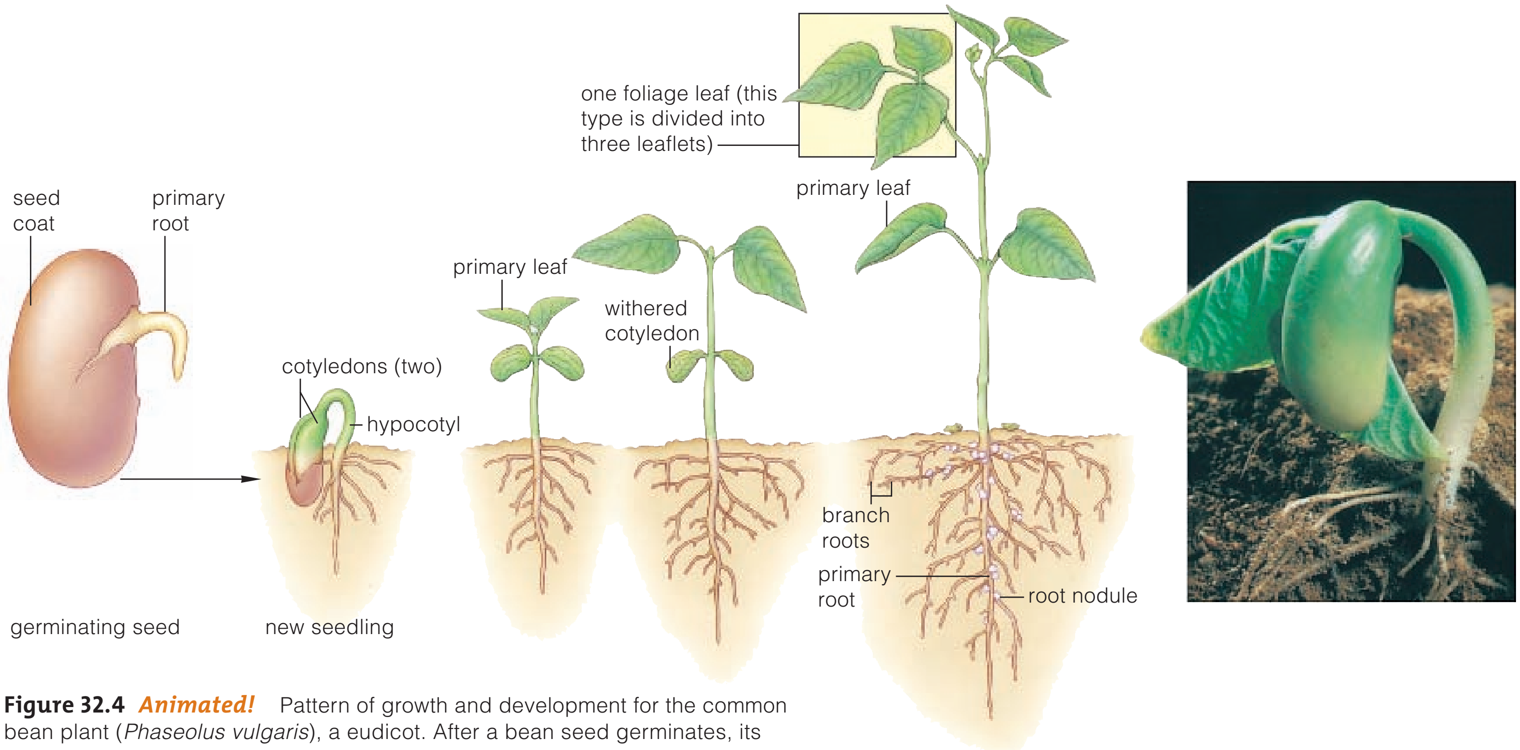


Figure 32.4 ***Animated!*** Pattern of growth and development for the common bean plant (*Phaseolus vulgaris*), a eudicot. After a bean seed germinates, its primary shoot bends in the shape of a hook just below the cotyledons. Sunlight makes this "hypocotyl" straighten, which forces a channel through soil for the cotyledons. Photosynthetic cells in the cotyledons make food for several days, then foliage leaves take over the task. The cotyledons wither and fall off.

32.2 Plant Hormones and Other Signaling Molecules

LINKS TO SECTIONS 15.1, 15.2, 28.5

As a plant grows and develops, its diverse cells increase in number, size, and volume—and specialized tissues form. These events require chemical communication among different cell types that secrete and respond to hormones and growth regulators.

MAJOR TYPES OF PLANT HORMONES

Table 32.1 lists five major classes of plant hormones—gibberellins, auxins, cytokinins, ethylene, and abscisic acid. These hormones interact in ways that stimulate or inhibit growth and development.

Gibberellins Let us first look at those **gibberellins** you read about in the chapter introduction. They are acidic compounds synthesized in seeds and young shoot tissues. As seeds germinate, gibberellins induce primary roots and shoots to grow. Their action causes the release of stored nutrients, which fuel cell divisions and elongation—especially between stem nodes, as in Figure 32.5. They also induce biennials and long-day plants to flower (Section 32.5). They are present in all flowering plants, mosses, gymnosperms, ferns, and some fungi.

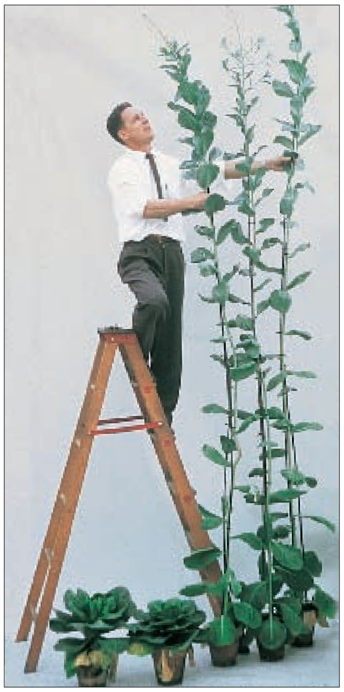


Figure 32.5 Foolish cabbages! At left, in front of the ladder, are two untreated cabbages that were the controls. At right, three cabbage plants treated with gibberellins.

Remember Mendel's dwarf pea plants (Section 11.3)? As in other dwarf varieties of plants, the short stems result from a mutation that affects gibberellin's action.

Auxins Cells at apical meristems of roots and shoots produce **auxins**. So do developing leaves and seeds. In monocots, an auxin is synthesized in the coleoptile, a protective sheath that surrounds the early seedling. As Section 32.3 explains, auxins induce cell walls to soften, so young cells can expand. Gradients of auxin affect which genes are transcribed in different tissues. They cause leaves to grow in certain patterns, stems to bend toward a light source, and roots to grow down through soil. Auxins induce vascular tissue formation and the division of vascular cambium cells. Maturing seeds produce auxins that encourage fruit formation.

Auxins also have inhibitory effects. Auxin diffusing down from a lengthening shoot tip stops lateral buds from growing. This inhibitory control is called *apical dominance*. When gardeners pinch off shoot tips, lateral buds along stems can grow and plants can get bushier.

Auxins help to prevent **abscission**—the dropping of leaves, flowers, or fruits. IAA (indoleacetic acid) is the most pervasive auxin in nature. Synthetic auxins have important commercial applications (Table 32.2).

Cytokinins Unlike other plant hormones, **cytokinins** are also synthesized by animal cells. They signal cells to start dividing rapidly. Root cells produce most of a plant's cytokinins, and xylem moves them into shoots. Cytokinins induce divisions in apical meristems and in maturing fruits. They also can release lateral buds

Table 32.1 Major Classes of Plant Hormones and Their Main Effects

Hormone	Source and Mode of Transport	Stimulatory or Inhibitory Effects
Gibberellins	Young tissues of shoots, seeds, possibly roots. May travel in xylem and phloem	Make stems lengthen greatly (stimulates cell division, elongation). Help seeds germinate; help induce flowering in some plants
Auxins	Apical meristems of shoots, coleoptiles, seeds. Polar transport through parenchyma cells of shoots toward base of root	Lengthen shoots, coleoptiles. Promote vascular cambium activity, vascular tissue differentiation. Inhibit abscission. Fruit formation. Block lateral bud formation (apical dominance)
Cytokinins	Mainly the root tip. Travels from roots to shoots inside xylem	Stimulate cell division in roots and shoots, leaf expansion. Inhibit leaf aging. Applications release buds from apical dominance
Ethylene (a gas)	Most tissues undergoing ripening, aging, or stress. Diffusion in all directions	Affects orientation of tissues by promoting or inhibiting cell growth; fruit ripening; promotes abscission; aging and death (senescence)
Abscisic acid (ABA)	Root cells in response to water stress. Travels from roots to leaves inside xylem	Stimulates stomatal closure. Induces transport of photosynthetic products from leaves to seeds. Stimulates embryo formation in seeds. May induce and maintain dormancy in some species

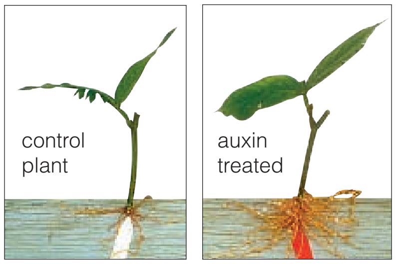


Figure 32.6 Plant cutting dipped into a rooting powder with 0.8 percent synthetic auxin. It developed more roots than the untreated control.

Table 32.2 Some Applications of Plant Hormones

Gibberellins	Increase fruit size; delay citrus fruit ripening; synthetic forms can make some dwarf mutants grow tall.
Synthetic Auxins	Promote root formation in cuttings; induce seedless fruit production before pollination; keep mature fruit on trees until harvest time; widely used as herbicides against broad-leaf weeds in agricultural lands.
Cytokinins	Tissue culture propagation; biotechnology; prolong shelf life of cut flowers, other horticultural prizes.
Ethylene	Permits shipment of green, still-hard fruit (e.g., tomatoes, grapes, and walnuts) to market to minimize bruising and to slow deterioration. Carbon dioxide application inhibits ripening during transit, then ethylene is applied to ripen the distributed fruit quickly.
ABA	Induces nursery stock to enter dormancy before shipment to minimize damage during handling.

from apical dominance, and they can stop leaves from aging prematurely.

Ethylene The only gaseous hormone, **ethylene**, can promote or inhibit cell growth so that tissues expand in the most suitable directions. Ethylene also induces fruit ripening. Its concentration is highest in apples, bananas, avocados, and other fruits that dramatically step up aerobic respiration as they mature. Ethylene concentrations also are high when a plant is stressed, as happens in autumn or near the end of the life cycle. At such times, ethylene induces abscission of leaves and fruits, and often the death of the whole plant.

Abscisic Acid Growth and reproduction depend on water and dissolved minerals. When a plant is water stressed, root cells produce more **abscisic acid** (ABA), which xylem moves swiftly to leaves. ABA is part of a stress response that causes stomata to close so that the plant minimizes water loss (Section 30.4). Also, when the growing season ends, ABA's influence overrides growth-promoting effects of gibberellins, auxins, and cytokinins. ABA causes photosynthetic products to be diverted from leaves to seeds, where it promotes the synthesis of storage forms of proteins and also helps the embryo mature. It may affect dormancy in some plants. This growth-inhibiting hormone actually was misnamed; it has little to do with abscission.

OTHER SIGNALING MOLECULES

As we now know, other signaling molecules have roles in plant growth and development. *Brassinosteroids* are like animal steroid hormones in their structure. They help promote cell division and elongation; stems stay short in their absence. *Jasmonates*, derived from fatty acids, help other hormones control seed germination, root growth, and tissue defense. *FT protein* is part of a signaling pathway that induces flower formation.

Signaling molecules also function in plant defenses. *Salicylic acid* is a phenol structurally similar to aspirin. Together with *nitric oxide*, it induces synthesis of gene products that help plants survive pathogenic attacks. *Systemin* forms when insects feed on plant tissues. This peptide activates transcription of genes for substances that cripple an insect's capacity to digest proteins.

COMMERCIAL USES

Table 32.2 lists natural and synthetic plant hormones of commercial interest. An auxin in a rooting powder makes cuttings of a desired plant develop roots faster (Figure 32.6). Applications of ethylene make orchard fruits ripen all together, and quickly. Many fruits are harvested "green" to minimize bruising when shipped, and they are doused with ethylene after they arrive at distribution centers. Gibberellin applications promote increases in fruit sizes. Growers spray synthetic auxins on unpollinated flowers to get seedless fruits. Another synthetic auxin, dichlorophenoxyacetate (2,4–D), finds wide use as an herbicide. It so accelerates the growth of eudicot weeds that cells cannot take up or distribute enough water, nutrients, and photosynthetic products to keep up. The weeds grow themselves to death.

Interactions among hormones and other kinds of signaling molecules govern the normal growth, development, daily functioning, and reproduction of plants.

Plant hormones are signaling molecules secreted by specific cells that alter activities in target cells. At specific times, they promote or arrest growth by stimulating or inhibiting cell division, elongation, differentiation, and other events.

The five main classes are gibberellins, auxins, cytokinins, abscisic acid, and ethylene. Brassinosteroids and other growth regulators have been discovered.

32.3 Mechanisms of Plant Hormone Action

LINKS TO SECTIONS 2.6, 3.2, 3.3, 5.3, 28.5

How do plant hormones exert their effects? Here are two examples, one from a germinating seed, and the other from a lengthening seedling.

SIGNAL TRANSDUCTION

Plants, too, have pathways of cell communication, as introduced in Chapters 15 and 28. First, one cell type secretes a hormone or another signaling molecule that binds with a receptor on a target cell. Then the signal is transduced to a form that may influence a metabolic pathway, gene expression, or membrane properties. Often the receptor's shape changes, which activates enzymes or other cytoplasmic components. Reactions begin, and they bring about a cellular response to the initial signal. Figure 32.7 is one way to think about this pathway of cell-to-cell communication.

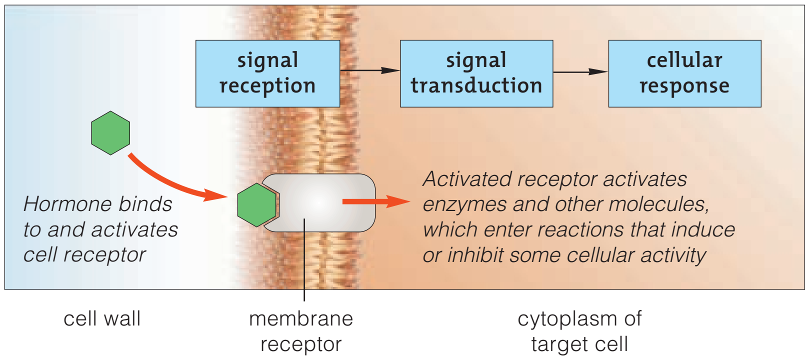


Figure 32.7 Pathway of cell communication in plants.

HORMONE ACTION IN GERMINATION

Figure 32.8 shows a barley seed. During germination, the imbibed water moves through cells of the embryo, which release gibberellin. Molecules of this hormone act in the endosperm's aleurone, a layer of cells that stores protein. (The brown part of brown rice is an example of the aleurone.) The hormonal signal induces transcription of the gene for amylase, an enzyme that can hydrolyze starch molecules (Sections 3.2 and 3.3).

Meanwhile, incoming water is activating protein-digesting enzymes in the aleurone. They break down proteins to free amino acids, some of which are taken up as building blocks in the synthesis of amylase.

The amylase is released into the starch-rich part of endosperm, where its action makes sugar monomers available. The transportable sugars, as well as amino acids, fuel the young plant's rapid growth.

a Imbibed water stimulates cells of embryo to release gibberellin, which water moves to cells of aleurone. Water also activates protein-digesting enzymes.

b In cells of the aleurone layer, this hormone triggers transcription and translation of a gene for amylase, an enzyme that digests starch into a transportable sugar.

c Amylase moves into endosperm's starch-rich cells. Sugar monomers released from starch fuel aerobic respiration.

d The ATP from aerobic respiration provides the energy for growth of the primary root and shoot.

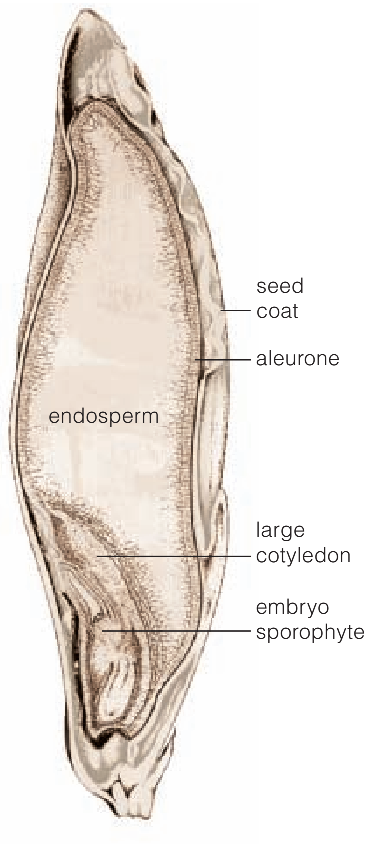


Figure 32.8 Action of gibberellin in barley seed germination.

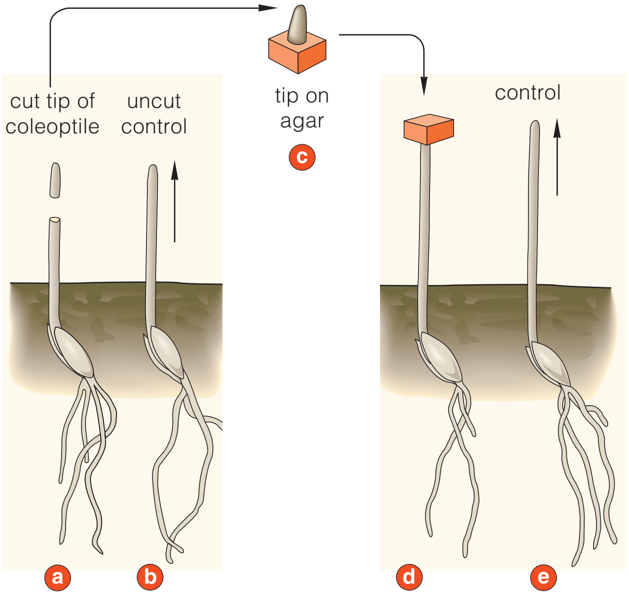


Figure 32.9 *Animated!* Experiment to test whether auxin from a coleoptile tip induces seedling elongation. (**a**) A seedling with its tip cut off will not lengthen as much as an uncut control seedling (**b**). (**c**) Put a tiny block of agar under a cut tip for several hours so auxin can move into it. (**d**) Place the agar on top of a different de-tipped coleoptile. Cells below it will lengthen about as fast as the control (**e**).

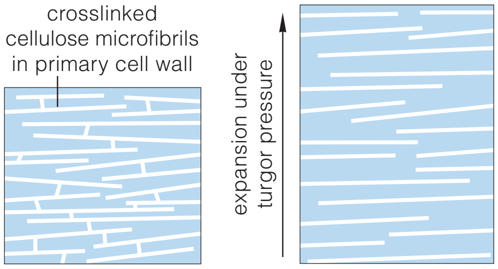


Figure 32.10 Auxin-induced enzyme action that loosens crosslinks between cellulose microfibrils in primary walls.

POLAR TRANSPORT OF AUXIN

Auxin concentration gradients start forming during early cell divisions of the embryo sporophyte. Cells exposed to higher concentrations transcribe different genes than those exposed to lower concentrations. The regionally different gene products help form plant parts, such as leaves, in expected patterns. Auxin also helps young cells elongate. It causes crosslinks among cellulose microfibrils in cell walls to loosen, so shoots and roots can lengthen (Figures 32.9 through 32.11).

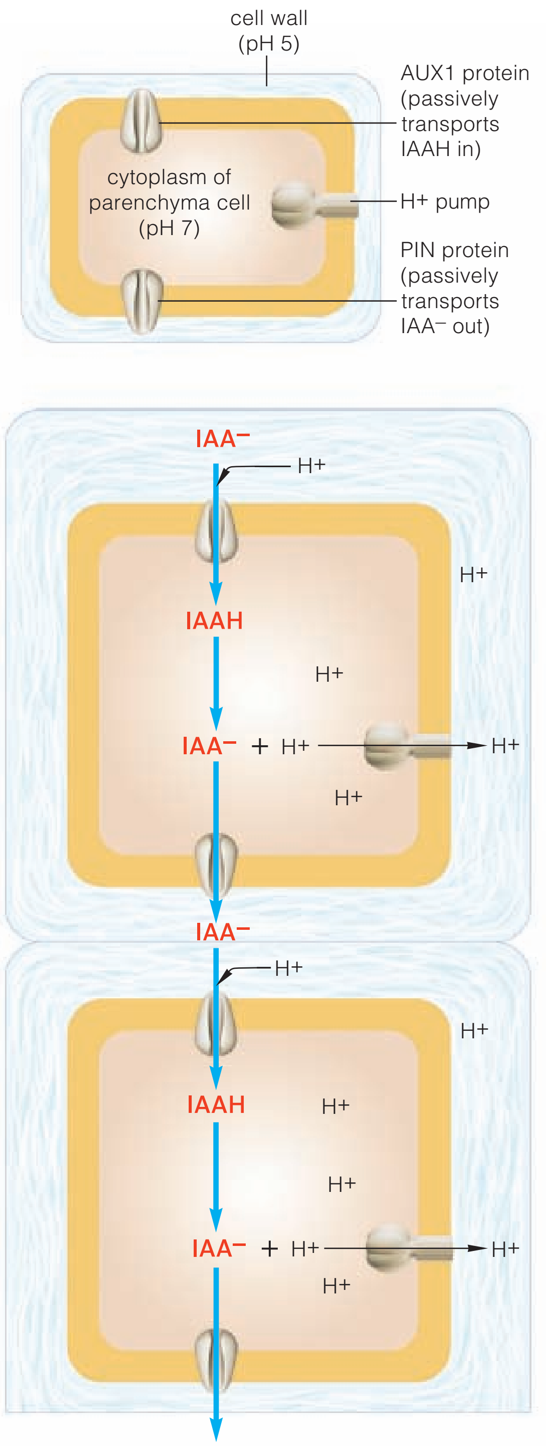
The auxin concentration is highest at its source, the apical meristem in a shoot (or coleoptile). From there, auxin is transported down, toward the shoot's base. This polar transport takes place in parenchyma cells, at membrane transporters that actively move ionized auxin into and out of their cytoplasm (Figure 32.11). Auxin gives up hydrogen in each cell, which alters the cytoplasmic pH. Membrane pumps actively transport the H^+ outside, which lowers the pH of the moist cell wall. Enzymes in the wall become active at a low pH. They cleave crosslinks between the microfibrils, which support the wall. Meanwhile, water is diffusing into the cell, so turgor pressure builds up against the wall. Because the microfibrils are now free to move apart, the wall is free to expand, and so the cell lengthens.

The pH changes also activate transcription factors. Within twenty minutes after auxin exposure, proteins that help a cell assume its new shape are synthesized.

Plant hormones exert their effects by pathways of signal reception, signal transduction, and a cellular response.

The nutrients in endosperm become available for growth when the embryo sporophyte releases gibberellin.

Auxin is actively transported down from shoot tips. By inducing pH changes, it causes cellulose microfibrils to loosen in cell walls, so the walls (and cells) can expand during growth. It also triggers regional gene transcription.



a As auxin diffuses through cell wall, the low pH makes H^+ bind to it. The resulting non-ionized form is IAAH.

b AUX1 transports IAAH into cytoplasm.

c The higher cytoplasmic pH makes auxin give up H and revert to ionized form.

d H^+ pumped out of cell, pH in wall decreases and prods enzymes to cleave cellulose crosslinks.

e PIN protein passively transports auxin out.

f Steps **a** through **e** are repeated in each adjoining parenchyma cell. The auxin transport shows polarity, from its source in a shoot tip and leaves, downward toward the base of the stem.

Auxin moves down to roots through parenchyma cells of the vascular cylinder. A different transport process takes over in the root tip. Transport proteins in the parenchyma cells of the root epidermis and cortex move auxin up toward the root–shoot junction.

Figure 32.11 Polar transport of auxin (IAA) in primary shoots and roots. The uppermost sketch simply identifies the components involved. Parenchyma cells transport auxin from apical meristem downward, to the shoot–root junction. The resulting changes in hydrogen ion concentration gradients across the plasma membrane cause an enzyme-induced loosening of cellulose crosslinks in the cell wall. The wall, and the cell, can expand during growth, as turgor pressure builds up in the cytoplasm.

A different mechanism moves auxin molecules upward from the root tip to the shoot–root junction.

32.4 Adjusting the Direction and Rates of Growth

LINKS TO SECTIONS 7.1, 29.5

Young plant roots and shoots adjust their direction of growth by turning toward or away from an environmental stimulus. Such responses are tropisms (after the Greek trope, for turning). Roots and shoots also alter their growth patterns in response to mechanical stress.

RESPONSES TO GRAVITY

Figure 32.12*a* shows the normal direction of growth of a corn seedling. Its primary root—the first to break through the seed coat—curves down, and the coleoptile and primary shoot curve up. Turn the seedling upside down, and its primary root curves down and the shoot curves up, as in Figure 32.12*b*. Any growth response to Earth's gravitational force is a form of **gravitropism**.

Turn the seedling on its side in a dark room and it still makes a gravitropic response. Its shoot curves up even in the absence of light. What makes the plant do this? In that horizontally oriented stem, cells do not elongate much on the side facing up, but those on the lower side elongate rapidly. The different elongation rates result in an upward-bended shoot.

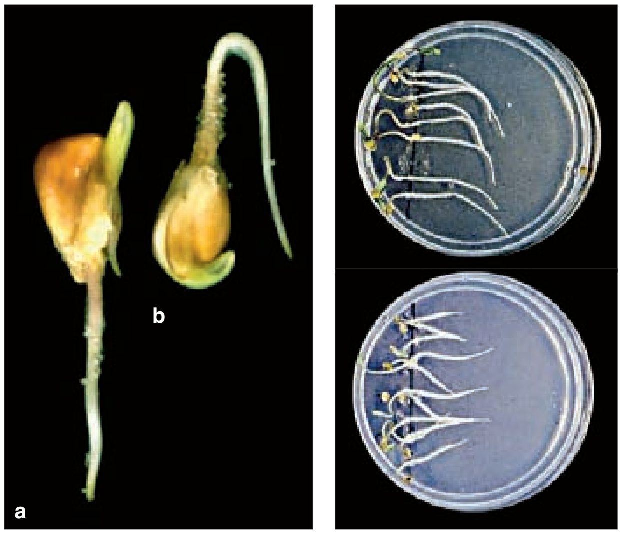
Auxin, and auxin transporters in cell membranes, function in gravitropism. How do we know? Position seedlings perpendicular to Earth's surface and expose them to a substance that inhibits auxin transporters. Unlike untreated control seedlings, the seedlings will not bend (Figure 32.12*c*, *d*).

Gravity-sensing mechanisms of many organisms are based on **statoliths**. Plant statoliths are modified plastids made denser by clusters of starch grains. In response to gravity, statoliths in specialized root cap cells settle until they rest in the lowest cytoplasmic region (Figure 32.13). When a root is reoriented with respect to gravity, the shifting statoliths (and possibly other organelles) may redistribute auxin in root cells. Such a change initiates the gravitropic response.

RESPONSES TO LIGHT

When light streams in from one direction only, a stem or leaf adjusts its rate and direction of growth so that it grows toward the light source. This response is a form of **phototropism**. In plants, it orients photosynthetic cells in ways that maximize light interception.

Charles Darwin was the first to make note of the directional bending of a coleoptile in response to light. Later, Fritz Went proposed that a growth-promoting substance, which he called auxin, moves down from the coleoptile tip and causes the bending. Because the auxin moves down faster through cells on the side less exposed to light, it makes them elongate faster than



c Control group (in a petri dish, all seedlings are oriented perpendicular to gravitational force of Earth)

d Experimental group (seedlings oriented the same way as in (**c**) but exposed to an inhibitor of auxin transport protein)

Figure 32.12 Gravitropic responses of a corn primary root and shoot growing in a normal orientation (**a**), and turned upside down (**b**).

(**c**) Experimental test of whether gravitropism requires auxin transport proteins in root cell membranes. In primary roots turned on their side, auxin is laterally transported to the down-facing side, where it stops cells from lengthening. Cells of the upward-facing side continue to lengthen, so the roots bend downward. (**d**) In an experimental group exposed to auxin transport inhibitors, downward bending stopped. Mutations in genes that encode auxin transport proteins also stop the bending.

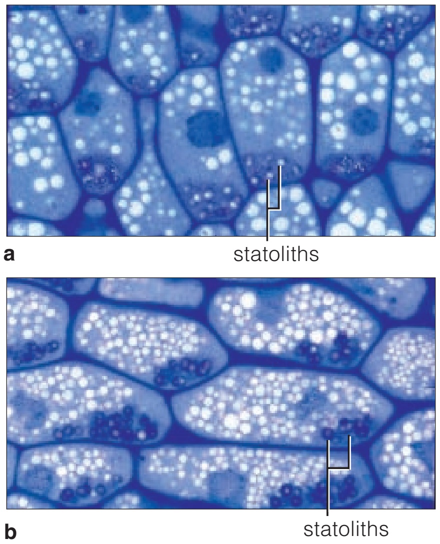


Figure 32.13 *Animated!* Gravity and statolith distribution. (**a**) Normal orientation of gravity-sensing cells in a corn root cap. Statoliths in the cells settle downward. (**b**) Turn the root sideways. Ten minutes later, the statoliths have settled to the new "bottom" of the cells. A gravity-sensing mechanism using statoliths may induce auxin redistribution in root tips. A difference in auxin concentrations makes cells on the top side of a horizontal root lengthen faster than cells on the bottom. Differences in elongation rates make the root tip curve downward.

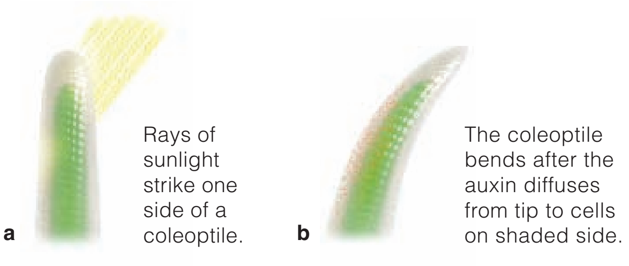


Figure 32.14 ***Animated!*** Phototropism. (**a**,**b**) Hormone-mediated differences in cell elongation rates along its length will induce a coleoptile to bend toward light. (**c**) Flowering shamrock (*Oxalis*) seedlings responding to light.

cells on the illuminated side. The difference in growth rates bends the coleoptile, as Figure 32.14*a*,*b* indicates. Position seedlings of a sun-loving plant in a dark room next to a window through which sunlight is streaming. They, too, bend toward the light (Figure 32.14*c*).

In plants, wavelengths of blue light stimulate the strongest phototropic responses. *Flavoproteins* absorb them. These nonphotosynthetic, yellow pigments are light-sensitive membrane receptors. They transduce energy of sunlight into signals that can stimulate the redistribution of auxin to the shaded side of a shoot or coleoptile. Auxin is moved by the polar transport mechanism explained earlier, in Figure 32.11.

RESPONSES TO CONTACT

In **thigmotropism**, auxin and ethylene induce plants to adjust the direction of growth if they contact objects. Soft, flimsy vines and tendrils (new, modified leaves or stems) cannot grow upright unless they make such a response. When cells at the shoot tip touch a stable object, cells on the contact side stop elongating and the cells on the other side keep growing. Their unequal rates of growth make the vine or tendril curl around the object, often more than once (Figure 32.15). Then cells on both sides resume growth at the same rate.

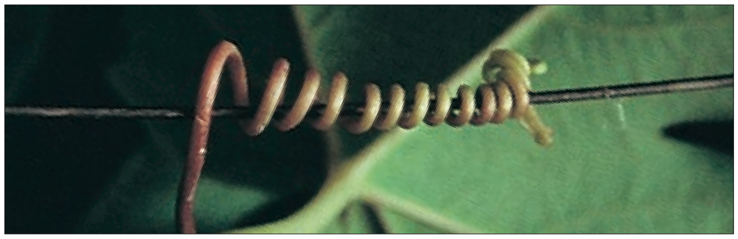


Figure 32.15 Passion flower (*Passiflora*) tendril twisting thigmotropically.

RESPONSES TO MECHANICAL STRESS

Mechanical stress, as inflicted by prevailing winds and grazing animals, inhibits stem lengthening. Trees high up in windswept mountains are stubbier than sheltered trees of the same species at lower elevations (Section 23.7). Similarly, plants grown outdoors commonly have shorter stems than the same kinds of plants grown in a greenhouse. Briefly shake a plant every day and you will inhibit its overall growth (Figure 32.16).

Figure 32.16 Effect of mechanical stress on tomato plants. (**a**) This plant, the control, grew in a greenhouse. (**b**) Each day for twenty-eight days, this plant was mechanically shaken for thirty seconds. (**c**) This one had two shakings each day.

Plants adjust the direction and rate of growth in response to environmental stimuli, as when hormones induce a shoot to bend by making some cells lengthen faster than others. Plants also adjust growth patterns by changing gene expression in response to mechanical stimulation.

32.5 Seasonal Shifts in Growth

LINKS TO
SECTIONS
7.1, 15.2, 28.3

Plant growth responses correlate with environmental cues, such as seasonal shifts in night length and temperature.

A *circadian* cycle is one that is completed in a period of about twenty-four hours. **Photoperiodism** refers to a biological response to alternations in the length of darkness relative to daylight during a circadian cycle. For example, the number of hours a plant spends in darkness and in daylight shifts with the seasons. The shift is more pronounced the farther away you move from Earth's equator, as Section 48.1 explains. The life cycles of different plant species show adaptations to shifts in the hours of daylight (Figure 32.17).

Like other organisms, plants have **biological clocks**: internal mechanisms that preset the time for recurring shifts in daily tasks or seasonal patterns of growth, development, and reproduction. Some clocks in plants use **phytochrome**. This blue-green pigment functions as a receptor for red and far-red light. The red light at sunrise causes phytochrome to shift from its inactive form (Pr) to its active form (Pfr). The far red light at sunset, and darkness, shift phytochrome to inactive form (Figure 32.18). The longer the nights, the longer the interval when phytochrome is inactivated.

Phytochrome's active form—Pfr—can induce gene transcription. The gene products are diverse signaling molecules that bring about seed germination, shoot elongation and branching, leaf expansion, and flower, fruit, and seed formation, then dormancy.

Photoperiodic responses involve phytochrome. The activated form of this photoreceptor triggers secretion of one or more hormones that can induce and inhibit plant growth.

32.6 When To Flower?

Hormones activate the genes for flower formation. But what activates the hormone-secreting cells?

RESPONSES TO HOURS OF DARKNESS

Different species are known as short-day, long-day, and day-neutral plants. The names are misleading. The cue is length of *darkness*. "Short-day" plants flower in early spring or fall, when nights are longer than some critical value; "long-day" plants flower in summer, when nights are shorter than a critical value (Figure 32.19*a*,*b*). Day-neutral plants flower whenever they are mature enough to do so.

Phytochrome is the trigger for flowering. In certain experiments, a pulse of red light interrupted the dark phase of the circadian cycle for a long-day plant and a short-day plant (Figure 32.20*a*,*b*). The light activated phytochrome, which made the plants act as if nights were short. In other experiments with the same kinds of plant, a pulse of far-red light after a pulse of red light inactivated phytochrome molecules. Both plants acted as if nights were long, and again they responded in predictable ways (Figure 32.20*c*).

Detection of a photoperiod occurs in leaves, where hormones inhibit or induce a shift from leaf growth to flower formation. Signals from leaves may travel in phloem to floral buds. In one experiment, a short-day plant called cocklebur was stripped of all but one leaf, which was kept in darkness for 8–1/2 hours a day to simulate long nights. The plant flowered. Later on, the leaf was grafted onto a cocklebur that had *not* been exposed to long dark periods. The plant flowered.

Apparently, flower-inducing and flower-inhibiting substances participate in flowering. Intriguingly, the gibberellins can induce flowering in some species.

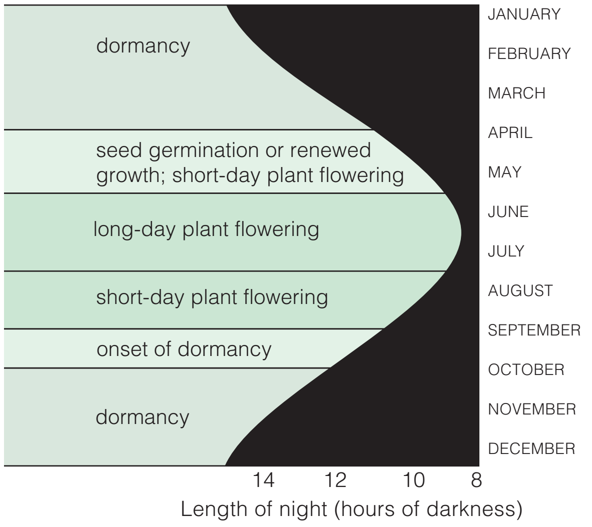


Figure 32.17 Plant growth and development correlated with seasonal changes in hours of darkness. The data reflect photoperiodic responses of diverse plants in northern temperate zones, where the temperature and rainfall shift over the year.

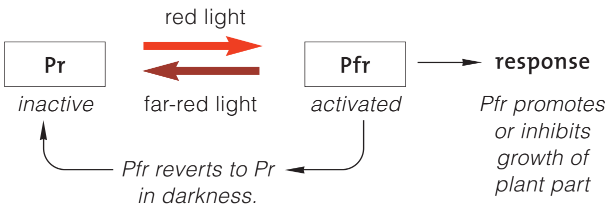


Figure 32.18 *Animated!* Conversion of phytochrome, a light-sensitive receptor, from inactive to active form: Pr to Pfr. When activated, this light-sensitive receptor induces gene transcription. The signal induces cells to take up free calcium ions (Ca^{++}) or it induces organelles to release them. The response starts as the ions combine with calcium-binding proteins. At sunset, at night, or in the shade, far-red light predominates, and so the signal transduction pathway is reversed. At such times, Pfr reverts to Pr.

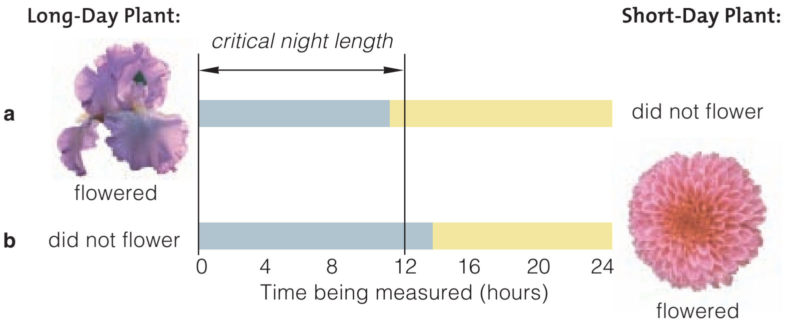


Figure 32.19 ***Animated!*** Experiments showing that plants flower in response to night length. Each horizontal bar represents 24 hours. *Yellow* signifies daylight; *blue-gray* signifies night. (**a**) This long-day plant, an iris, flowered only when hours of darkness were *less* than the value that is critical for flowering of its species. (**b**) This short-day plant, a chrysanthemum, flowered only when hours of darkness were *more* than a critical value for its species.

REVISITING THE MASTER GENES

In Sections 15.2 and 17.8, you read about the genetic basis for flowering. Briefly, three groups of master genes, designated *A*, *B*, and *C*, control the formation of floral structures from the whorls of a floral shoot.

For some time, no one knew what switches on the master genes. Indirect evidence pointed to some kind of signal, which was tentatively named "florigen." We now know that, in response to photoperiods or other environmental cues, leaf cells transcribe a flowering gene. The mRNA transcripts travel in phloem to as-yet undifferentiated floral buds, where they are translated into *FT* protein. This signaling molecule, along with a transcription factor, turns on master genes that cause cellular descendants of an as-yet uncommitted bud of meristematic tissue to develop into a flower.

VERNALIZATION

Unless certain biennials and perennials are exposed to low winter temperatures, flowers will not form on their stems in spring (Figure 32.21). Low-temperature stimulation of flowering is known as **vernalization** (from *vernalis*, meaning "to make springlike"). In one experiment, stored seeds of winter rye (*Secale cereale*) were exposed to near-freezing temperatures in late spring (not winter) and then planted. Plants grown from the seeds still flowered in summer.

The main environmental cue for flowering is night length, which varies seasonally. Genes influence the time of flowering in different species.

Photoperiodic responses to red and far-red light involve phytochrome. The activated form of this photoreceptor, Pfr, may trigger secretion of one or more hormones that induce and inhibit flowering at different times of year.

Low winter temperatures stimulate the flowering of many plant species in spring.

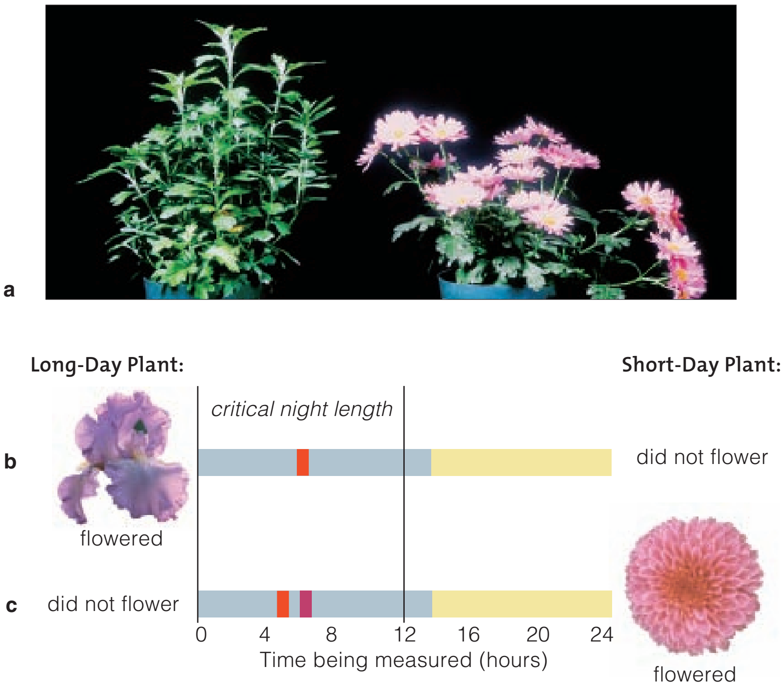


Figure 32.20 (**a**) Flowering responses of chrysanthemum, a short-day plant, to (*left*) long-day exposure and (*right*) short-day exposure. Two experiments that pointed to phytochrome as a trigger for flowering in long-day and short-day plants. (**b**) When an intense red flash interrupts a long night, both plants respond as if it were a short night (long day). The long-day plant flowers; the short-day plant does not. (**c**) A short pulse of far-red light after the red flash cancels the disruptive effect of the red flash by inactivating phytochrome. The long-day plant does not flower, but the short-day plant does.

Figure 32.21 Local effect of cold temperature on dormant buds of a lilac (*Syringa*) plant. For this experiment, a single branch was positioned to protrude from a greenhouse through a cold winter. The rest of the plant was kept inside and exposed only to warm temperatures. Only buds exposed to the low outside temperatures resumed growth and flowered in springtime.

32.7 Entering and Breaking Dormancy

LINKS TO SECTIONS 4.9, 29.2, 30.4

In midsummer, days almost imperceptibly begin to grow shorter, and many herbaceous and woody perennials of temperate zones start to shut down growth. They do so even when temperatures are mild, the sky is bright, and water is plentiful. They prepare for ***dormancy****, a period of arrested growth that will not end until the arrival of special environmental cues.*

ABSCISSION AND SENESCENCE

As leaves and fruits grow in early summer, their cells make auxin, which moves into stems. Together with cytokinins and gibberellins, the auxin helps maintain growth. By midsummer, the hours of daylight start to decrease. Plants start to divert nutrients from leaves, stems, and roots to flowers, fruits, and seeds. As the growing season comes to an end, deciduous species move nutrients to storage sites in twigs, stems, and roots before the leaves die and drop. The dropping of flowers, leaves, fruits, and other plant parts is called **abscission**. Parenchyma cells form an abscission layer as well as a protective, suberized layer at the base of a petiole or some other structure about to drop from the plant. Figure 32.22 shows a suberized layer.

Abscission occurs in response to decreasing hours of daylight, even to drought, injuries, and nutrient deficiencies. Auxin production declines in leaves and fruits. A different signal stimulates cells of abscission zones to make ethylene. Cells enlarge, deposit suberin in their walls, and make enzymes that digest cellulose and pectin in the middle lamella, the cementing layer between plant cell walls (Section 4.9). Cells separate from their neighbors as they enlarge and as enzymes digest the walls. Eventually leaves or other structures above the abscission zones drop away.

What happens when you interrupt the diversion of nutrients into flowers, seeds, and fruits? Remove all flowers or seed pods from a plant, and its leaves and stems stay green much longer (Figure 32.23).

Senescence refers to the phase from full maturity until the eventual death of plant parts or the whole plant. Aging and death are part of plant life cycles.

BUD DORMANCY

By midsummer, buds of many trees do not lengthen even when the meristems are active. Their embryonic shoots, complete with nodes and internodes as well as rudimentary leaves, are housed in bud scales that will insulate them and keep them from drying out.

Short days, long, cold nights, and dry soil that is deficient in nitrogen are strong cues for dormancy. Researchers tested this by interrupting the long dark period of some Douglas firs with a short period of red light. The plants responded as if nights were shorter and days longer. They continued to grow taller (Figure

Figure 32.22 In autumn, the changing colors of leaves of a horse chestnut tree (*Aesculus hippocastanum*). The leaf scar at *right* is all that remains of an abscission zone. Before the leaf detached from the tree, a tissue formed in a horseshoe-shaped zone (hence the tree's name). The tissue helps prevent water loss and infection after plant parts drop away.

control (pods not removed)

experimental plant (pods removed)

Figure 32.23 The observable results from an experiment in which seed pods were removed from a soybean plant. Removal delayed its senescence.

Figure 32.24 Experimental test of the effect of night length on Douglas firs. The fir at left was exposed to 12-hour light/12-hour dark cycles for one year. Its buds stayed dormant; "daylength" was too short. The fir at right was exposed to 20-hour light/4-hour dark cycles. It continued growing. The middle fir was exposed to 12-hour light/11-hour dark cycles. But 1 hour of light interrupted the middle of the dark period and prevented bud dormancy. The interruption caused Pfr to form at a sensitive time in the normal day–night cycle.

32.24). In this experiment, conversion of Pr to Pfr by red light during the dark period prevented dormancy. In nature, buds might enter dormancy because less Pfr can form when daylength shortens in late summer.

The requirement for multiple cues for dormancy has adaptive value. If temperature were the only cue, warm autumn weather might make plants flower and seeds germinate—and winter frost would kill them.

Dormancy-breaking mechanisms operate between late fall and spring. Temperatures often grow milder, and rains and nutrients become available. Breaking dormancy requires gibberellins and abscisic acid, and often prior exposure to low temperatures at specific times of year. Generally, trees in the southern United States require less cold exposure than trees growing in the northern states and Canada.

With environmental cues and hormone interactions, many plants seasonally enter and break dormancy.

32.8 Plants Move

FOCUS ON THE ENVIRONMENT

In this chapter, we have focused primarily on plant growth responses to seasonal changes in environmental cues. Bear in mind, plants also respond to daily changes in ways that indirectly affect growth. Some of these responses may be considered homeostatic, because they help maintain internal operating conditions for cells. Remember those folding leaves in Section 28.4? Here is one more example for you to consider.

LINKS TO SECTIONS 28.4, 30.4

Many plants track the course of the sun as it appears to arc overhead during the day. On hot, dry days, the plants move their soft petioles so that the flat surfaces of leaves (and flowers) are less perpendicular to the sun. A petiole, remember, is the stalk that attaches a leaf to a stem. In this orientation, heat absorption is minimized. At other times, the plants continually reposition the flat surfaces of leaves and flowers to intercept the sun's rays. Those sunflowers shown in Figure 32.25 make this response. So do lupine, cotton, and soybean plants.

Any photoperiodic response to the changing angle of the sun through the day is called **solar tracking**. Unlike the photo*tropic* responses explained in Section 32.4, such a response does not involve asymmetric growth (whereby cells on the shaded side of a shoot elongate faster than those in the light). Rather, petiole cells undergo reversible changes. The mechanisms involved are similar to those associated with the opening and closing of stomata; they cause reversible changes in turgor pressure in the cells. Collectively, the changes bend and straighten the petiole.

Figure 32.25 From the American Midwest, a field of sunflowers (*Helianthus*) that are busily demonstrating solar tracking.

32.9 Regarding the World's Most Nutritious Plant

In this unit, you explored the nature of plant structure, function, and behavior. Consider, finally, an example of how individuals put knowledge of plants to use in ways that have tremendous impact on human lives.

Alejandro Bonifacio was raised in poverty in rural Bolivia. As a child he spoke Aymaran, a language that predates the Incas. He learned Quechua, the language of the Incas, then learned Spanish before college. He earned a bachelor's degree in agriculture and became a plant breeder for Bolivia's equivalent of the United States Department of Agriculture.

His research interest is *Chenopodium quinoa*, a plant that originated in the Andes. Quinoa is a leafy eudicot, a distant relative of spinach and beets. Its seeds are not a cereal grain, but they are nutritional treasures, and for many thousands of years the seeds have been a staple of Latin American diets.

Quinoa seeds are 16 percent protein, on average. By comparison, wheat seeds are about 12 percent protein and rice seeds, about 8 percent. However, the proteins in both wheat and rice are deficient in the amino acid lysine. The array of amino acids in quinoa is as good as that in milk. The seeds also contain more iron than most cereal grains and are a notable source of calcium, phosphorus, and many B vitamins. In addition, quinoa plants are highly resistant to drought, frost, and saline soils. It is the only food crop that can grow in the arid salt deserts that prevail in much of Bolivia.

Far to the north, even before Alejandro received his college scholarship, Daniel Fairbanks had accepted a position as a botanist at Brigham Young University (BYU). He, too, became interested in quinoa because of its potential to feed millions in Bolivia and Peru, the most impoverished countries of Latin America. There, the majority of families eke out a living as subsistence farmers, and *kwashiorkor* is common.

Kwashiorkor is a form of malnutrition that results from protein-deficient diets. Fatigue, drowsiness, and irritability are its early symptoms. Continued protein deficiency adversely affects body growth. Edema sets in, and muscle mass decreases. The immune system starts to weaken. The abdomen of a malnourished person often protrudes. Epidermal conditions, such as vitiligo and thinning hair, are common. Severe cases result in mental and physical problems that can lead to coma and death. Kwashiorkor is most common in impoverished countries, but as many as 50 percent of the elderly in nursing homes also may be affected.

In 1991, Alejandro and Daniel met at a conference on Andean crops and became friends. Later, the World Bank awarded Alejandro a fellowship to study in the United States, and Dan became his advisor at BYU. Alejandro earned his PhD and also learned a fourth language—English.

The two are now codirectors of an international program of quinoa research, funded by the McKnight Foundation. They have taken a holistic approach to improving quinoa production for farmers who are now locked in poverty. As they look for new ways to conserve, improve, and use genetic diversity, they also research the economic impact of new quinoa strains, agricultural technologies, nutrition, hygiene, health, and community programs. Today, more than twenty scientists in four countries are a part of the program.

Thousands of Bolivian families are now producing more food, thanks to the new quinoa strains. Children who would otherwise have died from kwashiorkor are now attending school.

In a recent letter, Dan told us that he learned more from Alejandro than Alejandro learned from him. He appended a photograph of his colleague in a research field, standing next to one of his new quinoa varieties, so that we can put a face with the name.

Plants enrich our world in uncountable ways. Researchers around the world are taking part in wide-ranging efforts to develop new varieties that can improve human life.

Figure 32.26 Alejandro Bonifacio in a field of hybrid quinoa plants.

Summary

Section 32.1 The seeds dispersed from a flowering plant enter a period of dormancy. The body plan of the embryo sporophyte is already mapped out.

A seed germinates by way of imbibition. It absorbs water, resumes growth, and breaks through its seed coat. The seedling increases in volume and mass. Its tissues and organs grow and develop.

From the time of germination until the end of its life cycle, a plant's growth and development require gene products—enzymes, and other proteins with diverse roles in cell structure and function. Hormones and other signaling molecules affect how and when genes are transcribed and when gene products function.

Plant hormones, which have many and sometimes overlapping roles, bring about predictable patterns of growth and development by stimulating or inhibiting gene expression. They are synthesized in response to environmental cues, such as seasonal changes in night length, temperature, and oxygen and water in soil.

BiologyNow

Compare the growth and development of a monocot and a eudicot with the animation on BiologyNow.

Section 32.2 Like other signaling molecules, plant hormones are secreted by one cell type and dock at receptors on target cells. At specific times in the life cycle, they promote or arrest growth by stimulating or inhibiting cell division, elongation, differentiation, and other events. Five main classes are gibberellins, auxins, cytokinins, abscisic acid, and ethylene. Other growth regulators include brassinosteroids, which promote cell divisions and cell elongations, and stimulators and inhibitors of flowering, as yet unidentified.

Gibberellins promote stem elongation, help seeds and buds break dormancy in spring, and stimulate the flowering process in some species.

Auxins promote the elongation of shoots and coleoptiles. They also function in phototropism and gravitropism, which are both adjustments in the direction of elongation during primary growth.

Cytokinins stimulate cell division, promote leaf expansion, and retard leaf aging.

Ethylene promotes fruit ripening and abscission (the dropping of leaves, fruits, and other plant parts).

Abscisic acid promotes bud and seed dormancy, and it limits water loss by promoting stomatal closure.

Section 32.3 Plant hormones act in pathways of signal reception, signal transduction, and response.

One pathway starts in the seed. Gibberellin released from cells of the embryo sporophytes cause target cells to release endosperm's nutrients, which thus become available as fuel for rapid growth of the seedling.

Another pathway involves the polar transport of auxin from the tip to the base of shoots. Concentration gradients of auxin form and trigger transcription of different genes in different tissue regions. They also promote cell elongation. The polar transport brings about shifts in pH between the cytoplasm and wall of target cells. When pH decreases in the wall, crosslinks between cellulose microfibrils in the wall break apart. Because the young cell is expanding fast under turgor pressure, the softened wall is free to expand also.

BiologyNow

Observe the effect of auxin on plant growth with the animation on BiologyNow.

Section 32.4 Hormones control patterns of growth and development, but they also trigger adjustments in the direction and rate of growth in response to environmental stimuli.

In gravitropism, roots grow downward and stems grow upright in response to Earth's gravity. The polar transport of auxin causes this pattern. When a primary root is turned on its side, unequal rates of transport cause cells to elongate faster on the top side, so the root bends down. Statoliths (clusters of particles in cells) are gravity-sensing mechanisms in some plants.

In phototropism, stems and leaves adjust rates and directions of growth toward or away from light. A flavoprotein is the receptor for blue wavelengths that trigger the strongest response.

With thigmotropism, plants adjust their direction of growth in response to contact with solid objects.

Plants respond to mechanical stress, as when strong winds inhibit stem elongation and plant growth.

BiologyNow

Investigate plant tropisms with the animation on BiologyNow.

Section 32.5 A circadian cycle is some event that is completed in about a twenty-four-hour period. Plants have biological clocks that measure the cycle. That is, internal mechanisms set the time for a shift in specific cell activities that underlie daily tasks as well as seasonal patterns of growth, development, and reproduction.

In plants, photoperiodism is a biological response to the length of darkness relative to daylength in the circadian cycle. Phytochrome, a blue-green pigment, functions as a receptor for red and far-red light. It is like an alarm button for an internal timing mechanism, or biological clock. It promotes or inhibits germination, stem elongation, leaf expansion, stem branching, and flower, fruit, and seed formation.

Section 32.6 Short-day plants flower mainly in spring or fall, when there are more hours of darkness relative to daylight in the circadian cycle. Long-day plants flower in summer, when there are fewer hours of darkness relative to daylight hours. Day-neutral plants flower whenever they are mature enough to do so.

BiologyNow

Learn how plants respond to daylength (night length) with the animation on BiologyNow.

Section 32.7 Dormancy is a period of arrested growth that does not end until the arrival of specific dormancy-breaking environmental cues. Declining Pfr levels may trigger dormancy. Typically it involves the dropping of flowers, leaves, fruits, and other plant parts, a process known as abscission.

Breaking dormancy might involve exposure to certain temperatures and hormonal action, including gibberellins and abscisic acid.

Section 32.8 In response to environmental cues, many plants make daily movements that affect growth only indirectly. Solar tracking, a reversible repositioning of leaves and flowers relative to the angle of the sun overhead during the day, is an example.

Section 32.9 Knowledge of plant structure and function can improve the human condition.

Self-Quiz

Answers in Appendix II

1. Seed germination is over when the ________ .
   a. embryo sporophyte absorbs water
   b. embryo sporophyte resumes growth
   c. primary root pokes out of the seed coat
   d. cotyledons unfurl

2. Which of the following statements is false?
   a. Auxins and gibberellins promote stem elongation.
   b. Cytokinins promote cell division but retard leaf aging.
   c. Abscisic acid promotes water loss and dormancy.
   d. Ethylene promotes fruit ripening and abscission.

3. Plant hormones ________ .
   a. interact with one another
   b. are influenced by environmental cues
   c. are active in plant embryos within seeds
   d. are active in adult plants
   e. all of the above

4. Plant growth depends on ________ .
   a. cell division
   b. cell enlargement
   c. hormones
   d. all of the above

5. ________ are the strongest stimulus for phototropism.
   a. Red wavelengths
   b. Far-red wavelengths
   c. Green wavelengths
   d. Blue wavelengths

6. Light of ________ wavelengths makes phytochrome switch from inactive to active form; light of ________ wavelengths has the opposite effect.
   a. red; far-red
   b. red; blue
   c. far-red; red
   d. far-red; blue

7. The flowering process is a ________ response.
   a. phototropic
   b. gravitropic
   c. photoperiodic
   d. thigmotropic

8. Leaves and fruits drop from a plant when there is a decrease in ________ in their tissues and an increase in ________ at abscission zones.
   a. auxin; ethylene
   b. ethylene; auxin
   c. phytochrome; gibberellin
   d. gibberellin; abscisic acid

9. Match the plant reproduction and development terms.
   ____ vernalization
   ____ polar transport
   ____ imbibition
   ____ thigmotropism
   ____ apical dominance
   a. water moves into seeds
   b. unequal growth following contact with solid objects
   c. lateral bud formation inhibited
   d. low-temperature stimulation of the flowering process
   e. auxin from shoot tip toward base of shoot

Additional questions are available on **Biology Now™**

Critical Thinking

1. Given what you know about the growth of plants (Chapter 29), would you expect hormones to influence primary growth only? What about secondary growth in, say, a coast redwood or a hundred-year-old oak tree?

2. Plant growth depends on photosynthesis, which depends on inputs of light energy from the sun. How, then, can seedlings that were germinated in a dark room grow taller than different seedlings that germinated in the sun?

3. Belgian scientists isolated a mutated gene in common wall cress (*Arabidopsis thaliana*) that produces excess amounts of auxin molecules. Predict what some of the resulting phenotypic traits might be.

4. Cattle typically are given somatotropin, an animal hormone that makes them grow bigger (the added weight means greater profits). There is a major concern that such hormones may have unforeseen side effects on beef-eating humans. Would you think plant hormones applied to crop plants can affect humans also? Why or why not?

5. Like tulips and many other plants, a spinach plant flowers in spring under the mediation of gibberellins. It grows best when night length is about ten hours. Figure 32.27 shows the results from an experiment involving its flowering response. Which plant was grown under short-day conditions? Which was grown under long-day conditions?

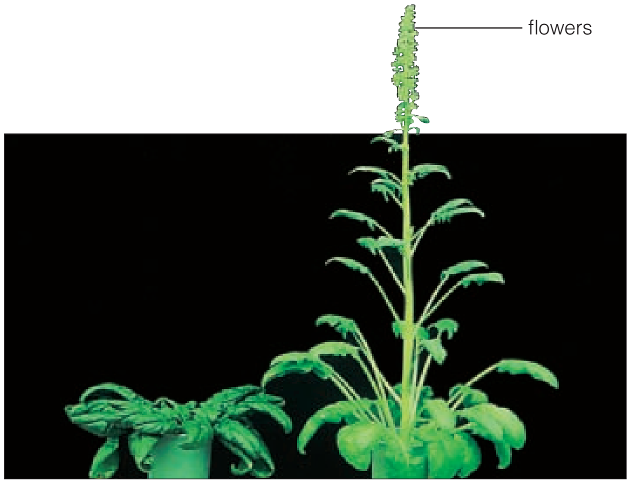


Figure 32.27 Experiment involving flowering responses of spinach (*Spinacia oleracea*), a long-day plant.

VI How Animals Work

How many and what kinds of body parts does it take to function as a lizard in a tropical forest? Make a list of what comes to mind as you start reading Unit VI, then see how resplendent the list can become at the unit's end.