Chapter 39

Plant Responses to Internal and External Signals

Key Concepts

39.1 Signal transduction pathways link signal reception to response

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

39.3 Responses to light are critical for plant success

39.4 Plants respond to a wide variety of stimuli other than light

39.5 Plants defend themselves against herbivores and pathogens

Framework

Environmental stimuli and internal signals are linked by signal-transduction pathways to cellular responses such as changes in gene expression and activation of enzymes. Plant hormones—auxin, cytokinins, gibberellins, brassinosteroids, abscisic acid, and ethylene—control growth, development, flowering, and senescence, as plants respond and adapt to their environments. Plant movements in response to environmental stimuli include phototropism, gravitropism, and thigmotropism. The biological clock of plants controls circadian rhythms, such as stomatal opening and sleep movements. Phytochromes function as photoreceptors and are involved in the photoperiodic control of flowering. Plants have various physiological responses to environmental stresses and pathogens.

Chapter Review

Plants are able to sense and adaptively respond to their environments, generally by altering their patterns of growth and development.

39.1 Signal transduction pathways link signal reception to response

Plants have cellular receptors that initiate signal transduction pathways, which couple reception of a stimulus to a response. The growth pattern of a sprouting potato shoot growing in darkness, called **etiolation,** facilitates the shoot breaking ground. When the shoot reaches sunlight, stem elongation slows, leaves expand, the root system elongates, and chlorophyll production begins—all part of a process known as **de-etiolation** or greening.

Reception Signals are detected by receptors, proteins that change shape in response to a specific stimulus. A *phytochrome* is the photoreceptor involved in de-etiolation, and, unlike receptors built into the plasma membrane, it is located in the cytosol. Researchers have studied the role of phytochrome in de-etiolation using the tomato mutant *aurea,* which has lower than normal levels of phytochrome.

Transduction **Second messengers** are small molecules that amplify the signal from the receptor and transfer it to proteins that produce the specific response. Each light-activated phytochrome may lead to the production of hundreds of second messenger molecules, each of which may activate hundreds of specific enzymes. The second messenger cyclic GMP affects membrane ion channels or activates protein kinases. Phytochrome signal transduction also opens calcium channels. Increases in cytoplasmic Ca^{2+} also activate certain protein kinases.

Response The response to a signal-transduction pathway usually involves the activation of specific enzymes, either by stimulating gene expression for those enzymes or by activating existing enzymes.

Several transcription factors are activated during phytochrome-induced de-etiolation, some by cGMP and others by Ca^{2+}. Changes in gene expression may involve the activation of positive transcriptional factors or negative transcriptional factors.

Post-translational modification of existing proteins usually involves phosphorylations, catalyzed by protein kinases. Cascades of protein kinase activations may lead to the phosphorylation of transcription factors, and thus, ultimately, to changes in gene expression. Protein phosphatases are enzymes that dephosphorylate specific proteins, allowing signal pathways to be turned off when a signal is no longer present.

INTERACTIVE QUESTION 39.1

In the process known as de-etiolation,

a. what is the signal and the receptor?

b. Briefly describe some of the steps in the transduction of this signal.

c. What is the plant's response?

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

Hormones, chemical signals that coordinate the parts of an organism, are transported through the plant body, where minute concentrations are able to trigger responses in target cells and tissues.

The Discovery of Plant Hormones A **tropism** is a growth response of plant organs toward or away from stimuli. The growth of a shoot toward light is called positive **phototropism.** A coleoptile, enclosing the shoot of a grass seedling, bends toward the light when illuminated from one side because of the elongation of cells on the darker side.

Darwin and his son observed that a grass seedling would not bend toward light if its tip were removed or covered by an opaque cap. They postulated that a signal must be transmitted from the tip to the elongating region of the coleoptile. P. Boysen-Jensen demonstrated that the signal was a mobile substance, capable of being transmitted through a block of gelatin separating the tip from the rest of the coleoptile.

In 1926 F. Went placed coleoptile tips on blocks of agar to extract the chemical messenger. From his studies he concluded that the chemical produced in the tip, which he called auxin, promoted growth and that it was in higher concentration on the side away from the light.

Researchers have not found a light-induced asymmetrical distribution of auxin in eudicots, but certain substances that may act as growth inhibitors have been shown to be more concentrated on the lighted sides of such stems.

A Survey of Plant Hormones Several major classes of plant hormones have been identified. These small molecules, which may move from cell to cell across cell walls, usually affect cell division, elongation, and differentiation. Depending on the site of action, the developmental stage of the plant, and relative hormone concentrations, the effect of a hormone will vary. Very low concentrations of hormones, acting through signal-transduction pathways, may affect the expression of genes, the activity of enzymes, or the properties of membranes.

Auxins include any substance that stimulates elongation of coleoptiles. The natural auxin extracted from plants is indoleacetic acid (IAA).

Auxin is transported through parenchyma tissue from the shoot tip down the shoot. This polar transport involves auxin transporters located only at the basal ends of cells.

Auxin is synthesized in the apical meristems of a shoot. According to the acid growth hypothesis, auxin initiates cell growth in the region of elongation by binding to a plasma membrane receptor and stimulating proton pumps. The proton pumps lower pH in the cell wall, activating enzymes called **expansins** that break cross-links between cellulose microfibrils. The proton pumps also increase the membrane potential, enhancing ion uptake and the resulting osmotic uptake of water. For continued growth after this relatively fast elongation, the cell must produce more cytoplasm and wall material, processes that rely on changes in gene expression that are also stimulated by auxin.

Auxin is involved in root branching and is used commercially to enhance formation of adventitious roots at the cut base of stems. Synthetic auxins, such as 2,4-D, are used as herbicides, killing eudicot (broadleaf) weeds with a hormonal overdose. Auxin stimulates cell division in the vascular cambium and differentiation of secondary xylem. Auxin produced by developing seeds promotes fruit growth; synthetic auxins can induce seedless fruit development.

In tissue culture, coconut milk and degraded DNA were found to induce plant cell growth; later, cytokinins were identified as the active ingredients. **Cytokinins** are modified forms of adenine, named because they stimulate cytokinesis. Zeatin is the most common naturally occurring cytokinin.

Cytokinins are produced in actively growing roots, embryos, and fruits. Acting with auxin, they stimulate cell division and affect differentiation.

According to the direct inhibition hypothesis, the control of apical dominance involves the interaction between auxin, transported down from the terminal bud, which restrains axillary bud development, and cytokinins, transported up from the roots, which stimulate bud growth. Several lines of evidence support this hypothesis. Biochemical analyses, however, have shown that removal of the apical bud leads to an increase in auxin levels in the axillary buds, exactly opposite the prediction of the direct inhibition hypothesis.

Cytokinins can retard aging of some plant organs, because they stimulate RNA and protein synthesis, mobilize nutrients, and inhibit protein breakdown.

In the 1930s Japanese scientists determined that the fungus *Gibberella* secreted a chemical that caused the hyperelongation of rice stems or "foolish seedling disease." More than 100 different naturally occurring gibberellins have now been identified.

Gibberellins, which are produced by roots and young leaves, stimulate growth in both leaves and stem, affecting cell division and elongation in stems. Gibberellins may promote cell elongation by stimulating cell wall-loosening enzymes, thus facilitating the penetration of expansins into the cell wall.

Gibberellin applied to dwarf plants may cause them to grow to normal height. Bolting, the growth of an elongated floral stalk, is caused by a surge of gibberellins. In many plants, both auxin and gibberellins contribute to fruit set. Gibberellins are sprayed in the production of Thompson seedless grapes. The release of gibberellins from the embryo signals seeds of many plants to break dormancy.

Similar to cholesterol and animal sex hormones, **brassinosteroids** have effects very similar to those of auxin: They promote cell elongation and division, retard leaf abscission, and promote xylem differentiation. Identification of a brassinosteroid-deficient mutant of *Arabidopsis* helped to establish these compounds as nonauxin plant hormones.

The hormone **abscisic acid** (ABA) generally slows growth. The high concentration of ABA in maturing seeds inhibits germination and stimulates production of proteins that protect the seeds during dehydration. For dormancy to be broken in some seeds, ABA must be removed or inactivated, or the ratio of gibberellins to ABA must increase.

ABA also reduces drought stress. In a wilting plant, ABA causes stomata in the leaves to close. ABA may be produced in the roots in response to water shortage and transported to the leaves.

Plants produce the gas **ethylene** in response to stress and during fruit ripening and programmed cell death. Ethylene production may be induced by a high concentration of auxin.

The mechanical stress of a seedling pushing against an obstacle as it grows upward through the soil induces the production of ethylene. Ethylene then initiates a growth pattern called the **triple response,** consisting of a slowing of stem elongation, a thickening of the stem, and initiation of horizontal growth. When the growing tip no longer detects a solid object above it, ethylene production decreases and normal upward growth resumes. Researchers have identified *Arabidopsis* mutants that are ethylene insensitive *(ein)*, ethylene overproducing *(eto)*, and that undergo the triple response in the absence of ethylene. In these latter constitutive triple response *(ctr)* mutants, the ethylene signal-transduction pathway is permanently turned on. Their mutant gene codes for a protein kinase, suggesting that the normal kinase product is a negative regulator of ethylene signal transduction. Binding of ethylene to the ethylene receptor may normally lead to the inactivation of the negative kinase, which allows the synthesis of the proteins involved in the triple response.

Apoptosis, or programmed cell death, requires the synthesis of new enzymes that break down many cellular components, which the plant may salvage. Ethylene is almost always associated with this programmed death of cells or organs, or of the entire plant.

Deciduous leaf loss protects against winter desiccation. Before leaves abscise in the autumn, many of their compounds are stored in the stem awaiting recycling to new leaves. A change in the balance of auxin and ethylene initiates changes in the abscission layer located near the base of the petiole, including the production of enzymes that hydrolyze polysaccharides in cell walls. A layer of cork forms a protective covering on the twig side of the abscission layer.

Ethylene initiates the breakdown of cell walls and conversion of starches to sugars associated with fruit ripening. In a rare example of positive feedback, ethylene triggers ripening, and ripening triggers even more ethylene production. Many commercial fruits are ripened in huge containers perfused with ethylene gas.

■ INTERACTIVE QUESTION 39.2

Fill in the name of the hormone that is responsible for each of the following functions:

a. ____________ promotes fruit ripening; initiates triple response; involved in apoptosis

b. ____________ stimulate cell division, growth, and germination; anti-aging

c. ____________ inhibits growth; maintains dormancy; closes stomata during water stress

d. ____________ stimulates stem elongation, root branching, fruit development; apical dominance

e. ____________ promote cell elongation and division, xylem differentiation; retard leaf abscission

f. ____________ promote stem elongation, seed germination; contributes to fruit set

Systems Biology and Hormone Interactions Systems biology studies properties that emerge from interactions of many system elements. Biologists can identify all the genes in a plant, and microarray and proteomic techniques can indicate which genes are activated or inactivated in response to environmental stimuli or during development. A systems-based approach may allow biologists to determine how these gene products interact in producing plant responses and to predict the results of genetic manipulation.

39.3 Responses to light are critical for plant success

The effect of light on plant growth and development is called **photomorphogenesis.** An **action spectrum** graphs a physiological response across different wavelengths of light. An absorption spectrum shows the wavelengths of light a pigment absorbs. Close correlation between an action spectrum for a plant response and the absorption spectrum of a pigment may indicate that the pigment is the photoreceptor involved in the response. Red and blue light have the most influence on a plant's photomorphogenesis. **Blue-light photoreceptors** and **phytochromes** that absorb mostly red light are the two major classes of light receptors.

Blue-Light Photoreceptors Molecular biologists have determined that plants use at least three different types of pigments to detect blue light: *cryptochrome* (for inhibition of hypocotyl elongation when a seedling breaks ground), *phototropin* (for phototropism), and *zeaxanthin* (for stomatal opening).

Phytochromes as Photoreceptors Studies of lettuce seed germination in the 1930s determined that red light (660 nm wavelength) increased germination the most and far-red light (730 nm) inhibited germination. The effects of red and far-red light are reversible, with the seed's response determined by the last flash of light it receives.

Five different phytochromes have been identified in *Arabidopsi.* A phytochrome is a photoreceptor that consists of a protein component bonded to a nonprotein light-absorbing chromophore. The chromophore alternates between two isomers, one of which absorbs red light and the other, far-red light. These two variations of phytochrome are photoreversible; the P_r to P_{fr} interconversion acts as a switch, controlling various events in the life of the plant.

Phytochrome tells the plant that light is present by the conversion of P_r, which is the form the plant synthesizes, to P_{fr} in the presence of sunlight. P_{fr} triggers many plant responses to light, such as breaking seed dormancy.

■ INTERACTIVE QUESTION 39.3

Explain how phytochrome can also indicate the quality of light available to a plant. What effect might this have on a shaded tree?

Biological Clocks and Circadian Rhythms A **circadian rhythm** is a physiological cycle with about a 24-hour frequency. These rhythms persist, even when the organism is sheltered from environmental cues. Research indicates that the circadian clock is endogenous, although it is set (entrained) to a 24-hour period by daily environmental signals.

■ INTERACTIVE QUESTION 39.4

What are free-running periods?

The molecular mechanism of the biological clock, which may be common to all eukaryotes, may be the cyclical changes in the concentration of a protein that is a transcription factor that inhibits the expression of its own gene.

Researchers have identified clock mutants of *Arabidopsis* by splicing the gene for luciferase to the promoter for genes for photosynthesis-related proteins that follow a circadian rhythm in their production. When the biological clock turned on the promoter for these genes, the plants glowed, and plants that glowed for a nonnormal amount of time were isolated as clock mutants. Some of these mutants had defects in proteins that normally bind photoreceptors, pointing to a light-dependent mechanism that sets the biological clock.

The Effect of Light on the Biological Clock Both blue-light photoreceptors and phytochrome can entrain the biological clock in plants. In darkness, the phytochrome ratio shifts toward P_r, in part because P_{fr} converts slowly to P_r in some plants, and also because P_{fr} is degraded and new pigment is synthesized as P_r. When the sun rises, P_r is rapidly converted to P_{fr}, resetting the biological clock each day at dawn.

Photoperiodism and Responses to Seasons Seasonal events in the life cycle of plants usually are cued by photoperiod, the relative length of night and day. A physiological response to photoperiod is called **photoperiodism.**

Researchers discovered that a variety of tobacco plant flowered only when the day length was 14 hours or shorter. They termed it a **short-day plant. Long-day plants** flower when days are longer than a certain number of hours. The flowering of **day-neutral plants** is unaffected by photoperiod.

Researchers have found that it is night length, not day length, that controls flowering and other photoperiod responses. If the dark period is interrupted by even a few minutes of light, a short-day (long-night) plant such as the cocklebur will not flower. Photoperiodic responses thus depend on a critical night length.

Red light was found to be the most effective in interrupting a plant's perception of night length. A brief exposure to red light breaks a dark period of sufficient length and prevents short-day plants from flowering, whereas a flash of red light during a dark period longer than the critical length will induce flowering in a long-day plant. Due to the photoreversibility of phytochrome, a subsequent flash of far-red light negates the effect of the red light.

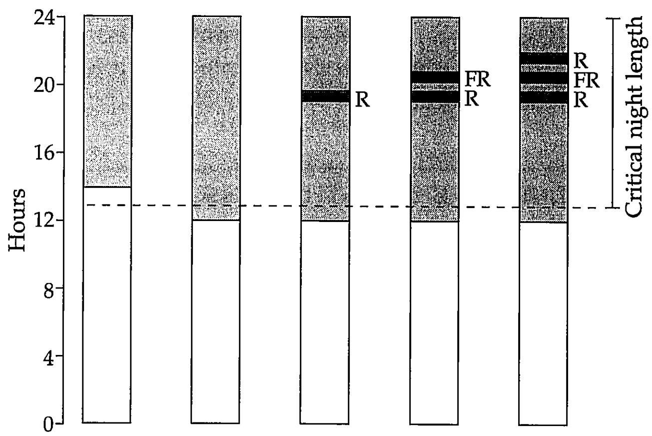
Some plants bloom after a single exposure to the required photoperiod. Others respond to photoperiod only after exposure to another environmental stimulus. The need for pretreatment with cold before flowering is called **vernalization.**

Leaves detect the photoperiod. The signal for flowering, called **florigen,** travels from leaves to buds. The signal is believed to be a hormone or change in the concentration of two or more hormones, but it has yet to be identified.

In order for flowering to occur, the bud meristem must transition from a vegetative to a flowering state, a change that requires the activation of meristem-identity genes, followed by organ-identity genes. Researchers are looking for the signal-transduction pathways that link photoperiod and hormonal cues to such changes in gene expression.

■ INTERACTIVE QUESTION 39.5

Indicate whether a short-day plant (a–e) and a long-day plant (f–j) would flower or not flower under the indicated light conditions.



a. _____ b. _____ c. _____ d. _____ e. _____

Short-day (long-night) plant

f. _____ g. _____ h. _____ i. _____ j. _____

Long-day (short-night) plant

How do these results demonstrate the red/far-red photoreversibility of phytochrome?

39.4 Plants respond to a wide variety of stimuli other than light

Gravity Roots exhibit positive **gravitropism,** whereas shoots show negative gravitropism. According to one hypothesis, the settling of **statoliths,** plastids containing dense starch grains, in cells of the root cap triggers movement of calcium, which causes the lateral transport of auxin. Both of these accumulate on the lower side of the growing root, where the high concentration of auxin inhibits cell elongation, causing the root to curve downward. The settling of the protoplast and large organelles may distort the cytoskeleton and also signal gravitational direction.

Mechanical Stimuli The stunting of growth in height and increase in girth of plants that are exposed to wind is an example of **thigmomorphogenesis,** changes in plant form in response to mechanical stimulation. Mechanical stimuli initiate a signal-transduction pathway that results in specific gene activations that alter growth patterns and cell wall properties.

Most climbing plants have tendrils that coil rapidly around supports, exhibiting **thigmotropism** or directional growth in response to touch.

The sensitive plant *Mimosa* folds its leaves after being touched due to the rapid loss of turgor by cells in specialized motor organs called pulvini, located at the joints of the leaf. The message travels through the plant from the point of stimulation, perhaps as the result of electrical impulses, called **action potentials.** These electrical messages may be used in plants as a form of internal communication.

■ INTERACTIVE QUESTION 39.6

a. Name the types of tropisms that a stem exhibits.

b. Name and describe the growth mechanism that produces the coiling of a tendril.

Environmental Stress An **abiotic** environmental stress may be severe enough to threaten a plant's growth, reproduction, and survival. Plants also have defensive responses to **biotic** stresses such as pathogens and herbivores.

Mechanisms that reduce transpiration help a plant respond to water deficit. Guard cells lose turgor and stomata close. Abscisic acid, produced by leaves in response to water deficit, acts on guard cell membranes to keep stomata closed. Growth of young leaves is inhibited by the lack of cell-expanding water, and wilted leaves may roll up, further reducing transpiration. All of these responses, however, reduce photosynthesis. During a drought, root growth in shallow, dry soil decreases while deeper roots in moist soil continue to grow.

Plants adapted to wet habitats may have aerial roots that provide oxygen to their submerged roots. When roots of other plants are in waterlogged soils, oxygen deprivation may stimulate ethylene production, causing some root cortical cells to undergo apoptosis, opening up air tubes within the roots.

Excess salts in the soil may lower the water potential of the soil solution below that of roots, causing roots to lose water. The plasma membranes of root cells can reduce the uptake of sodium and some other ions that are toxic to plants in high concentrations. Plants may respond to moderate soil salinity by producing organic solutes that lower the water potential of root cells. Special adaptations for dealing with high soil salinity have evolved in halophytes.

Transpiration creates evaporative cooling for a plant, but this effect may be lost on hot, dry days when stomata close to reduce water loss. Above critical temperatures, plant cells produce **heat-shock proteins** that may provide temporary support to reduce protein denaturation.

Plants respond to cold stress by increasing the proportion of unsaturated fatty acids in membrane lipids in order to maintain the fluidity of cell membranes. Subfreezing temperatures cause ice to form in cell walls, lowering the extracellular water potential and causing cells to dehydrate. Plants adapted to cold winters have adaptations to deal with freezing stress, such as changing the solute composition of the cytosol.

■ INTERACTIVE QUESTION 39.7

a. A plant is exposed to a spell of very hot and dry weather. How might it survive this stress?

b. How might a plant adapt to an unusually cold and very wet fall?

39.5 Plants defend themselves against herbivores and pathogens

Defenses Against Herbivores Physical defenses, such as thorns, and chemical defenses, such as distasteful or toxic compounds, help plants cope with herbivory. Some plants produce *canavanine,* which resembles arginine and may be incorporated into an insect's proteins, altering protein conformation and causing death.

Some plants recruit predators of their herbivores. A combination of a compound in a caterpillar's saliva and the damage caused by its eating stimulates leaves to release volatile compounds that attract parasitoid wasps. The wasps lay their eggs inside the caterpillar, and the wasp larvae eat their host. These volatile compounds may also signal neighboring plants to activate defense genes. These gene activations are similar in pattern to those produced by exposure to the important plant defense molecule **jasmonic acid.**

Defenses Against Pathogens The physical barrier of the plant's epidermis and/or periderm is the first line of defense against pathogenic viruses, bacteria, and fungi. Should pathogens enter the plant due to injuries or through openings such as stomata, the plant mounts a chemical defense.

Virulent pathogens are those to which the plant has no specific defense. Plants are generally resistant to most pathogens. These **avirulent** pathogens do not extensively harm or kill the plant.

Specific resistance is based on **gene-for-gene recognition** between the protein products of a plant's disease resistance (*R*) genes and a pathogen molecule coded for by an *Avr* gene. According to the receptor-ligand model, binding of an AVR protein to an R protein receptor triggers a signal-transduction pathway that produces a plant defense response. Plants have many different *R* genes, corresponding to the many different potential pathogens.

In response to chemical signals released from plant cells damaged by a pathogen, the plant mounts a localized attack. **Elicitors,** often cellulose fragments called **oligosaccharins,** stimulate the production of antimicrobial **phytoalexins.** Infection also activates genes for **PR proteins** (some of which are antimicrobial, while others serve as alarm signals to neighboring cells) and stimulates strengthening of the cell walls to slow the spread of the pathogen. A **hypersensitive response (HR)** is triggered when the pathogen is avirulent and there is an *R-Avr* match. This more vigorous defense includes increased production of phytoalexins and PR proteins and a more effective sealing of the area.

A hypersensitive response also triggers release of alarm hormones, which stimulate phytoalexin and PR protein production throughout the plant, creating a **systemic acquired resistance (SAR).** This generalized defense response helps protect uninfected tissue. One of the hormones involved in activating SAR is probably **salicylic acid,** which humans have modified as the active ingredient in aspirin.

Word Roots

aux- = grow, enlarge (*auxins:* a class of plant hormones, including indoleacetic acid, having a variety of effects, such as phototropic response through the stimulation of cell elongation, stimulation of secondary growth, and the development of leaf traces and fruit)

circ- = a circle (*circadian rhythm:* a physiological cycle of about 24 hours, present in all eukaryotic organisms, that persists even in the absence of external cues)

crypto- = hidden; **-chromo** = color (*cryptochrome:* the name given to the unidentified blue-light photoreceptor)

cyto- = cell; **-kine** = moving (*cytokinins:* a class of related plant hormones that retard aging and act in concert with auxins to stimulate cell division, influence the pathway of differentiation, and control apical dominance)

gibb- = humped (*gibberellins:* a class of related plant hormones that stimulate growth in the stem and leaves, trigger the germination of seeds and breaking of bud dormancy, and stimulate fruit development with auxin)

hyper- = excessive (*hypersensitive response:* a vigorous, localized defense response to a pathogen that is avirulent based on an *R-Avr* match)

photo- = light; **-trop** = turn, change (*phototropism:* growth of a plant shoot toward or away from light)

phyto- = a plant; **-alexi** to ward off (*phytoalexin:* an antibiotic, produced by plants, that destroys microorganisms or inhibits their growth)

stato- = standing, placed; **-lith** = a stone (*statolith:* specialized plastids that help a plant tell up from down)

thigmo- = a touch; **morpho-** = form; **-genesis** = origin (*thigmomorphogenesis:* a response in plants to chronic mechanical stimulation, resulting from increased ethylene production; an example is thickening stems in response to strong winds)

zea- = a grain; **-xantho** = yellow (*zeaxanthin:* a blue-light photoreceptor involved in stomatal opening)

Structure Your Knowledge

1. List some agricultural uses of plant hormones.
2. Develop a concept map to illustrate your understanding of photoperiodism and the control of flowering. Do not forget to include the role of the biological clock.
3. Briefly describe the steps in the hypersensitive response and systemic acquired resistance that result from a plant's encounter with an avirulent pathogen.

Test Your Knowledge

TRUE OR FALSE: *Indicate T or F and then correct the false statements.*

_________ 1. Abscisic acid is necessary for a seed to break dormancy.

_________ 2. Roots exhibit negative phototropism and positive gravitropism.

_________ 3. Gibberellins, synthesized in the root, counteract apical dominance.

_________ 4. Thigmomorphogenesis is a growth response of a seedling that encounters an obstacle while pushing upward through the soil.

_________ 5. The application of gibberellins or auxin may induce the development of seedless fruit.

_________ 6. Action potentials are electrical impulses that may be used as internal communication in plants.

_________ 7. A physiological response to day or night length is called a circadian rhythm.

_________ 8. Vernalization is the need for pretreatment with cold before seed germination.

_________ 9. A virulent pathogen is one to which a plant has a specific resistance based on gene-for-gene recognition.

_________ 10. A cryptochrome is the light-absorbing portion of a phytochrome that reverts between two isomeric forms.

MULTIPLE CHOICE: *Choose the one best answer.*

1. The body form within a species of plants may vary more than that within a species of animals because
   a. growth in animals is indeterminate.
   b. plants respond adaptively to their environments by altering their patterns of growth and development.
   c. plant growth and development are governed by many hormones.
   d. plants can respond to environmental stress.
   e. all of the above are true.

2. Polar transport of auxin involves
   a. the accumulation of higher concentrations on the side of a shoot away from light.
   b. the movement of auxin from roots to shoots.
   c. movement of auxin ions through carrier proteins located at the basal end of cells.
   d. the unidirectional active transport of auxin into and out of parenchyma cells.
   e. the settling of statoliths.

3. According to the acid growth hypothesis,
   a. auxin stimulates membrane proton pumps.
   b. a lowered pH outside the cell activates expansins that break cross-links between cellulose microfibrils.
   c. the membrane potential created by the proton pumps enhances ion uptake, increasing the osmotic movement of water into cells.
   d. cells elongate when they take up water by osmosis.
   e. all of the above are involved in cell elongation.

4. Which of the following situations would most likely stimulate the development of axillary buds?
   a. a large quantity of auxin traveling down from the shoot and a small amount of cytokinin produced by the roots
   b. a small amount of auxin traveling down from the shoot and a large amount of cytokinin traveling up from the roots
   c. an equal ratio of gibberellins to auxin
   d. the absence of cytokinins caused by the removal of the terminal bud
   e. an increase in the concentration of brassinosteroids produced by leaves

5. The growth inhibitor in seeds is usually
   a. abscisic acid.
   b. ethylene.
   c. gibberellin.
   d. a small amount of ABA combined with a larger concentration of gibberellins.
   e. a high cytokinin-to-auxin ratio.

6. A circadian rhythm
   a. is controlled by an external oscillator.
   b. is a physiological cycle of approximately a 24-hour frequency.
   c. involves an internal biological clock that is not set by daily environmental signals.
   d. provides the signal for seasonal flowering.
   e. involves all of the above.

7. Which of the following is *not* a component of the signal-transduction pathway involved in the deetiolation process when a shoot breaks ground?
   a. reception of light by a phytochrome located in the cytosol
   b. inhibition of the triple response and initiation of phototropism as the shoot bends toward light
   c. production of second messengers such as cGMP and Ca^{2+}
   d. cascades of protein kinase activations that phosphorylate transcription factors
   e. activation of genes that code for photosynthesis-related enzymes

8. Injecting phytochrome into cells of the tomato mutant *aurea*
   a. causes the plant to undergo the triple response above ground when exposed to ethylene.
   b. causes the plant to undergo the triple response above ground without exposure to ethylene.
   c. helps researchers identify clock mutants.
   d. initiates flowering even when nights are longer than a critical period.
   e. causes the plant to develop a normal de-etiolation response to light.

9. A flash of far-red light during a critical-length dark period
   a. will induce flowering in a long-day plant.
   b. will induce flowering in a short-day plant.
   c. will not influence flowering.
   d. will increase the P_{fr} level suddenly.
   e. will be negated by a second flash of far-red light.

10. The conversion of P_r to P_{fr}
    a. occurs slowly at night.
    b. may be the way in which plants sense daybreak and serves to entrain the biological clock.
    c. is the molecular mechanism responsible for the biological clock.
    d. occurs when P_r absorbs far-red light.
    e. occurs in flower buds and induces flowering.

11. A plant may withstand salt stress by
    a. releasing abscisic acid that closes stomata to salt accumulation.
    b. the production of organic solutes that lower the water potential of root cells.
    c. wilting, which reduces water and salt uptake by reducing transpiration.
    d. producing canavanine that reduces the toxic effect of sodium ions.
    e. releasing ethylene that leads to apoptosis of damaged cells.

12. Which of the following hormones would be sprayed on barley seeds to speed germination in the production of malt for making beer?
    a. abscisic acid
    b. auxin
    c. cytokinin
    d. ethylene
    e. gibberellin

13. Many plants will flower in response to a specific
    a. flowering hormone that is produced in the apical bud.
    b. elicitor, which is a cellulose fragment.
    c. minimal temperature that appears to signal a seasonal change.
    d. photoperiod, which seems to be measured by the length of darkness to which the leaves of the plant are exposed.
    e. combination of a high level of auxin and a low level of cytokinin.

14. Which of the following is *not* a plant defense against herbivory?
    a. production of distasteful compounds.
    b. production of toxic compounds such as canavanine.
    c. physical defenses such as thorns.
    d. initiation of a hypersensitive response with production of phytoalexins and PR proteins.
    e. release of volatile compounds that recruit parasitoid wasps.

15. Which of the following is *not* true of the hypersensitive response?
    a. It relies on an *R-Avr* recognition between a specific plant cell receptor protein and a pathogen molecule.
    b. It increases the production of PR proteins that may have antimicrobial or signaling functions.
    c. It enhances the production of ethylene that serves as a signal molecule transported throughout the plant to activate SAR (systemic acquired resistance).
    d. It contains an infection by stimulating cross-linking of cell wall molecules and production of lignin.
    e. The plant cells involved in the defense destroy themselves, leaving lesions that indicate the site of the contained infection.