BLY 122 A. Hunter

Chapter 39 Plant Sensory Systems, Signals, and Responses

I. Information Processing: Plants have sophisticated systems for collecting information about their environment and for responding in ways that maximize their chances of surviving, thriving, and producing offspring. The process can be analyzed in three steps **(Fig 39.1)**

A. Receptor cell receives an external signal and transduces it to an intracellular signal

B. Receptor cell sends a signal to cells in another part of the body that can respond to the information

C.) Responder cells receive this long-distance signal, transduce it to an intracellular signal and change activity.

Signal Transduction (information change from an external signal to an intracellular signal

2 Types (phosphorylation cascade) and second messengers **(Fig 39.2)**

Cells that receive information from signal transduction are not the cells that respond to the information.

Signal transduction in a receptor cell often results in the release of a hormone that carries information to responder cells.

Because plants perceive a wide variety of stimuli, they have a wide array of hormones.

Target cells routinely receive information from several different hormones at the same time, so it is common for different types of hormones to interact with each other and modulate the cell's response.

Plant hormones have several important properties in common: (1) they can elicit a response only if a cell has an appropriate receptor, and (2) they are active at extremely small concentrations.

How Do Cells Respond to Cell–Cell Signals?

- If a receptor on or in a cell binds to a hormone and changes shape in response, the signal at the cell's periphery is rapidly transduced to increased activity inside the cell, via s signal transduction pathway.
- The phosphorylated proteins or second messengers that result from the signal transduction cascade result in changes in cell activity.
- Activation of a signal transduction cascade results in the production of many phosphorylated proteins or release of many secondary messengers to amplify the original signal many times.
- When cells respond to a hormone, the change in their activity helps the individual cope with the environmental change sensed by the receptor cell.

Most of our general principles of plant communication emerged from studies of how plants respond to light.

Light Sensing

A. Plants sense different wavelengths of light and respond with particular behaviors.

B. What Do Plants See?

1. What is the effect of unidirectional light on the growth of grass seedling coleoptiles?—Charles and Francis Darwin
   a. Experiment: Expose dark-grown coleoptiles to candlelight from one direction.
   b. Plants bend toward the light source. (**Fig. 39.7**)
   c. Conclusion: Coleoptiles are positively phototropic and grow toward light.
2. What type of light do plants bend toward?—Charles and Francis Darwin

a. Experiment: Solution that filters out blue light was placed between the seedlings and the candle.
b. Plants do not bend toward the light. (**Fig. 39.4**)
c. Conclusion: Phototropism is a response to blue light.

Blue-light receptor

a. The Darwins' experiment indicated that a blue-light receptor responsible for phototropism is located in the shoot tip.
   (1) Blue light is absorbed by photosynthetic pigments.
   (2) Therefore, plants benefit by growing toward light that contains the wavelengths necessary for photosynthesis.
b. What is the receptor of blue light in plants, and where is it located? Biologists hypothesized that the receptor might be a membrane protein because the light receptor in animals is a membrane protein.
   (1) Membrane protein phosphorylated in presence of blue light isolated.
   (2) Because phosphorylation converts an inactive protein to an active protein, researchers suggested that the phosphorylated membrane protein is involved in the blue-light response.
   (3) In many sensory systems the removal of a phosphate from ATP and the subsequent phosphorylation of a receptor molecule are catalyzed by a protein kinase.
   (4) The sequence of events initiated by the protein kinase leads to a response by the cell to the sensory stimulus.
c. Blue-light receptor gene isolated in *A. thaliana*
   (1) Experiments with non-phototrophic hypocotyl mutants of *A. thaliana* led researchers to the gene.
   (2) The gene is called *phot1*.
   (3) Injecting the *phot1* gene into cultured insect cells showed that the PHOT1 protein could autophosphorylate and become activated in response to blue-light exposure.
   (4) More recent studies have found more blue-light receptors that are related to *phot1*, collectively called phototropins.

The Role of Auxin in Phototropism

A. Phototropic signal is a diffusible, water-soluble chemical—Boysen-Jensen tested the Darwins' hormone hypothesis in 1913.
   1. Tips of oat shoots were cut off, and porous gelatin or nonporous mica placed between tip and shoot.
   2. Only shoots treated with porous gelatin showed normal phototropism.
   3. They concluded that the phototropic signal was a diffusible water-soluble chemical.

B. Hormone can cause bending in darkness—Went.
   1. Hormone from oat shoots collected in agar blocks.
   2. Agar blocks with hormone placed asymmetrically on decapitated shoots in darkness.
   3. Shoots bent away from the side where the agar block, the source of hormone, was placed. (**Fig. 39.8**)
   4. Follow-up research illustrated that phototropism is caused by hormone-induced cell elongation in shoot cells on the side opposite a light source.
   5. This phototropic hormone was named "auxin" by Went.

C. Phototropism is due to the asymmetric distribution of auxin in response to light.
   1. Redistribution hypothesis—Cholodny-Went hypothesis

a. Auxin produced in shoot tips moves from the sunny side to the shady side of the shoot in response to light.
b. Auxin is transported down the shoot.
c. Auxin concentration is higher in cells on the shady side than those on the sunny side.
d. Cells with higher auxin concentration elongate more than those with lower concentration and bending toward light occurs.

2. Auxin-destruction hypothesis
   a. Light leads to the destruction of auxin on the sunny side.
   b. This leaves a higher auxin concentration on the shady side.
3. Testing the redistribution and destruction hypotheses—Briggs et al.
   a. Experiment 1—refutation of auxin destruction hypothesis (**Fig. 39.9)**
      (1) Tips of dark-grown corn seedlings cut off and placed on agar blocks.
      (2) Shoot tips on agar blocks kept in dark or exposed to unidirectional light.
      (3) Agar blocks placed on one side of decapitated shoots and amount of bending measured.
      (4) Bending was the same in each treatment.
      (5) Results contradictory to auxin destruction hypothesis; shoots with blocks exposed to light would be expected to bend less than those kept in darkness.
   b. Experiment 2—confirmation of Cholodny-Went redistribution hypothesis (**Fig. 39.10**)
      (1) Shoot tips divided completely or partially with nonporous mica placed on agar blocks and exposed to light from one direction.
      (2) Agar blocks placed on one side of decapitated shoots and amount of bending measured.
      (3) In completely divided tips, no difference in bending response by the sunny or shady side was observed.
      (4) In partially divided tips, the shaded side exhibited greater bending than the sunny side did.
      (5) Results support the hypothesis that light leads to redistribution of auxin and increased bending on the shady side of the shoot.

D. How does auxin produce the phototropic response?

1. Auxin binds to a receptor in target cells and initiates a series of events resulting in cell elongation and phototropism.
   a. Most of the time, the sensory cell produces the hormone.
   b. It travels through the plant via diffusion and when it arrives at the target cell, it binds to a receptor.
   c. Hormone action is specific because only target cells have those receptors.
2. The search for the auxin receptor involved researchers putting a radioactive label on auxin.
   a. The radioactive auxin was applied to plant cells in culture.
   b. The protein that it bound to was isolated.
   c. Auxin-binding protein 1 (ABP1) in corn plants was purified in 1985.
   d. Since then, ABP1 has been confirmed to be the auxin receptor in stem cells, and its gene has been sequenced.
   e. ABP1 induces cell elongation in cells when it binds auxin.
3. How does auxin induce cell elongation?
   a. Auxin-receptor binding leads to water influx and cell-wall expansion that results in elongation.
   b. Acid-growth hypothesis proposes that auxin triggers production or activation of proton pumps—H^+-ATPases.
      (1) Protons pumped out of cell and positively charged ions, such as K^+, enter cell.
      (2) Ion concentration inside cell increases; water enters by osmosis.

(3) As water enters cell, turgor pressure increases and cell-wall expansion occurs via proteins called expansins.

c. Acid growth hypothesis tested:

(1) Studies using fluorescent antibodies to proton pumps have shown that the number of proton pumps increased by 80% in presence of auxin.

(2) Other studies have shown that auxin lowers pH of cell wall from pH 5.5 to pH 4.5.

39.3. Red and far-red light: Germination, Flowering and Stem Elongation

Research indicates that in addition to blue wavelengths, plants are sensitive to wavelengths in the red and far-red portions of the visible spectrum. Interesting Point: Red wavelengths drive photosynthesis (just as blue light does) However, far-red wavelengths are not absorbed strongly by photosynthetic pigments. Therefore, they pass through leaves instead of being absorbed. Far-red wavelengths are prominent in light that is filtered through tree leaves before it reaches the forest floor. **Far-red light indicates shade.**

Question: How do red and far-red light affect the germination of lettuce seeds? (Table 39.1) Germination rates peaked when exposed to red light. However, germination was inhibited by far-red light.

Red and far-red light act as a type of on-off switch for lettuce seed germination. How?

Hypothesis: The same pigment absorbs both types of wavelength.

Hypothesis: The pigment exists in two shapes or conformations---one shape absorbs red light, the other shape absorbs far-red light. Light absorption makes the pigment change shapes. This switching behavior is known as **photoreversibility. (Fig. 39.12)** The proposed pigment was termed **phytochrome**.

Stem Elongation—another response to far-red light

Example: Bean seeds grown indoors.

(Box 39.2) Flowering is response to changes in length of day **(photoperiodism)** also showed photoreversibility.

4. Photoperiodism: Plants can sense the relative length of day and night.

a. Plants sense photoperiod in order to flower when pollinators are available.

(1) Long-day plants bloom in midsummer when days are longer than night.

(2) Short-day plants bloom in spring, late summer, or fall when days are shorter than a species-specific critical length.

(3) Day-neutral plants flower without regard to photoperiod.

b. Plants sense photoperiod by sensing the length of night.

(1) Researchers found in photoperiod experiments that interrupting light periods with dark had no effect.

(2) However, interrupting dark periods with light disrupted the plant's ability to accurately sense photoperiod.

c. The red/far-red switch

(1) In photoperiod/flowering experiments, night interruptions with red light disrupted the photoperiod; however, subsequent interruptions with far-red light erased the effect.

How were phytochromes isolated?

1. Phytochrome, light-receptor molecule, hypothesized by researchers to be pigment responsible for on-off nature of the red/far-red switch.
    a. Phytochrome is a protein that exists in two forms:
        (1) Red-light absorbing form, P_r
        (2) Far-red-light absorbing form, P_{fr}
    b. Photoreversibility between the two forms occurs. (**Fig. 39.15**)
        (1) P_r absorbs red light and is converted to P_{fr}.
        (2) $P_{fr\ r}$ absorbs far-red light and is converted to P_r.
    c. P_r is the biologically inactive form; P_{fr} is the form that stimulates plant responses.
2. Isolation and identification of a photoreversible red and far-red absorbing pigment
    a. Protein purified from corn shoots switches color from blue to blue-green when exposed to alternating red and far-red light.
    b. Protein isolated is the previously hypothesized phytochrome protein.
    c. Five loci that encode phytochrome proteins have been isolated and sequenced in *Arabidopsis thaliana*.
        (1) All phytochromes absorb red and far-red light; are photoreversible, but may trigger different responses.
        (2) Example: Mutant form of one phytochrome, PHYB, has abnormal stem elongation response.
    d. Unanswered questions
        (1) Are different phytochromes responsible for different effects?
        (2) How is the information in phytochromes converted into the responses of elongation, germination, and others?

39.4 Gravity Perception

A. Plants respond to gravity and grow downward—**gravitropism**. (**Fig. 39.16**)

B. The root cap is the gravity sensor. (**Fig. 39.17**)
1. Historical background: Charles and Francis Darwin in 1881
    a. Removed the root caps and found roots no longer responded to gravity
    b. Concluded that gravity sensor is in the cap
2. Recent studies have identified specific root-cap cells that sense gravity.
    a. These studies used the laser to identify specific root-cap cells that sense gravity in *Arabidopsis*.
    b. The data indicate that cells directly under epidermal cells of tip are responsible for gravitropism.

C. How Do Plants Sense Gravity?
1. Statolith hypothesis
    a. Many plant cells contain amyloplasts—starch-containing plastids.
    b. Researchers hypothesize that gravity pulls the amyloplasts to the bottom of cells.
        (1) The force of amyloplasts on cell membranes, or the distention of amyloplast membrane, activates receptors that initiate gravity response. (**Fig. 39.18**)
        (2) This mechanism is similar to the sand-grain statoliths in animals.
3. Recent experimental evidence supports the statolith hypothesis
    a. Some scientists believe that the weight of the amyloplast on receptors in the cell membrane elicits the gravitropic response.
    b. Other scientists believe that the amyloplasts pull on cytoskeletal elements, which activate receptors in the plasma membrane.

Is Auxin the Graviotropic Signal? (Fig 39.19)

III. How Do Plants Respond to Wind and Touch?

A. Plants respond to repeated motion (wind) or touch by increasing stem thickness. (**Box. 39.3**)

B. Touch is converted to an electrical signal.
   1. Proton pumps create a charge difference between the interior and exterior of plant cells.
      a. Interior has a negative charge compared to the exterior.
      b. Charge difference across the cell membrane is membrane polarization.
   2. Charge difference across the membrane creates membrane voltage, a form of potential energy.
      a. Potential energy of voltage across a membrane is membrane potential.
      b. Size of the potential is a function of the amount of charge separation between the interior and exterior of the cell.
         (1) Membrane potentials are measured with electrodes and expressed in millivolts (mV).
         (2) Membrane potential compares the interior of the cell relative to the exterior.
         (3) Resting potential is the normal membrane potential and is negative.

C. The Venus Flytrap and Electrical Signaling
   1. Electrode inserted into flytrap cells recorded voltage change when sensory cells were stimulated.
   2. Venus flytrap voltage change has characteristic action potential pattern.
      a. Action potential is very rapid change in membrane potential—from negative to positive to negative.
      b. Depolarization refers to the situation when charges on interior and exterior of the membrane become alike.
      c. The pattern of the action potential can be explained by the flow of ions into and out of the cell, leading to voltage differences across the membrane.
      d. After the action potential fires, positively charged ions flow out of the cell, returning it to its resting membrane potential via a process called repolarization.
   3. Electrical signaling is similar to nerve impulses in animals; it is how some plants transduce a signal into a very rapid response.
   4. Flytrap closure involves conversion of mechanical signal to electrical signal, leading to turgor change and trap closure.
      a. When touched, membranes of receptor hairs on trap surface depolarize.
      b. Depolarization of receptor cell triggers action potentials in other cells across leaf.
      c. When action potentials reach effector cells on outer trap surface, cells swell and trap shuts.
      d. Mechanism for increase in cell size is under study.
         (1) It may be due to uptake of water.
         (2) It may be the result of change in length of cell wall.
      e. It is known that ATP levels and pH drop in the effector cells—Williams and Bennett.

39.5 Youth, Maturity, and Aging: The Growth Responses

Auxin and Apical Dominance

A. Apical dominance refers to stem elongation at the apical meristem of the main shoot, while meristems in lateral buds below are inhibited. (**Fig. 39.5**)

1. When the apical meristem of the main shoot is removed, branches grow out from the axillary buds.
2. If auxin is added to the end of a decapitated shoot, lateral branch growth is inhibited.
3. Auxin is a chemical signal from shoot tips that determines the direction of growth.
4. Disruption of the chemical signal when the tip is removed indicates an interruption of growth, and lateral branches take over for the main shoot.

B. Auxin is transported in one direction from the shoot tip downward to the root tip.
  1. The unidirectional movement of auxin is known as **polar transport**.
     a. Polar transport sets up a strong concentration gradient for auxin in the plant body.
     b. Auxin is much more concentrated in shoots than in roots.
  2. In the root tip, auxin moves toward the epidermal cells and up in a "fountain" pattern. (**Fig. 39.6a**)
  3. Gravitotropism occurs due of asymmetrical auxin distribution leading to unequal cell elongation (**Fig. 39.6b**), as predicted in the Cholodny-Went model.

C. An Overview of Auxin Action
  1. Auxin plays an important role in phototropism, gravitotropism, and apical dominance.
  2. Auxin is also involved in:
     a. Fruit development: Seeds produce auxin to stimulate fruit development.
     b. Abscission: Falling concentration of auxin is involved in the falling of leaves (abscission) associated with aging (senescence).
     c. Differentiation of xylem and phloem in vascular tissue
     d. Stimulating the development of adventitious roots in cuttings
  3. Auxin concentration identifies cell location in relation to long axis of plant.
     a. Change in conditions affecting long axis of plant body lead to changes in auxin concentrations.
     b. Altered auxin concentrations signal how tissues should respond.
  4. Auxin does not act alone.
     a. Plant growth is mediated by an antagonistic relationship between auxin and cytokinins.
     b. Auxin and ethylene work in concert to mediate senescence.

Cytokinins and Cell Division

A. Cytokinins promote cell division.
  1. Originally discovered because coconut milk was shown to promote the growth of cells and plant embryos in culture.
  2. Later experiments with corn and apples showed that a molecule derived from the amino acid adenine could stimulate growth.

B. Cytokinins are synthesized in root tips, young fruits, seeds, growing buds, and other developing structures.

C. The cytokinin in most plant species is called zeatin.
  1. Zeatin exists as two structural isomers that are enzymatically interconverted and are active in different tissues and different species.
  2. Most zeatin is made in apical meristem of roots and transported to shoots via the xylem.
  3. Cytokinins bind to receptors on target cells and trigger the activation of certain genes.

D. How do cytokinins function on a molecular level?
  1. Because cytokinins stimulate mitosis, scientists hypothesized that they may be activating cyclins and cyclin-dependent kinases that initiate mitosis.
  2. *Arabidopsis* cells were cultured so their growing environment could be controlled.

        a. The cells were starved of cytokinins for a day and were then treated with hormone.
        b. The presence of the hormone induced an increase in the *CycD3* gene that encodes for a cyclin.
        c. In the absence of cytokinins, plant cells arrest at the G_1 checkpoint.
        d. This is all strong evidence that cytokinins exert their effect by activating genes that move the cell cycle beyond G_1.

V. Regulation of Dormancy and Growth by Abscisic Acid and Gibberellic Acid

A. Many plants initiate growth in spring, grow during the summer and fall, and lie dormant during the winter.

B. The Role of GA in Shoot Elongation
    1. Gibberellin in stems produces elongation.
        a. Rice seedlings infected with the fungus, *Gibberella fujikuroi*, elongate abnormally.
        b. Fungal extract, named gibberellin, induced elongation.
        c. Plants naturally produce gibberellin, though they will elongate excessively when additional gibberellin is applied.
    2. Identification of the *Le* gene—locus responsible for stem-length variation.
        a. Forward genetics was used to identify gene locus responsible for the mutant dwarf phenotype.
        b. Mendel's studies of dwarf and tall pea plants indicated that a single locus was involved.
        c. Mutants at *Le* locus grow to normal size when treated with gibberellin GA1.
            (1) Suggested that while dwarf plants respond to GA1, they are unable to make their own.
            (2) Dwarf plants treated with radioactive precursor to GA1 do not synthesize GA1.
            (3) *Le* locus appears to be involved in GA synthesis.
        d. *Le* gene specifies enzyme, 3β-hydroxylase, which converts GA20 to active GA1 in pea plants.
            (1) Enzyme of normal-height plants has alanine at active site.
            (2) Enzyme of dwarfed plants has threonine at active site.
            (3) Mutant enzyme unable to carry out conversion of GA20 to GA1 is genetic basis for dwarf phenotype in pea plants.
        e. Recent studies indicate that auxin activates the *Le* gene leading to GA production.

C. Gibberellins and abscisic acid differentially affect a-amylase in seed germination.
    1. The enzyme, α-amylase, is released from the aleurone layer of germinating oat and barley seeds.
    2. α-amylase diffuses to the endosperm tissue, where it breaks bonds in the starch molecules and releases sugars.
    3. Gibberellin, GA, added to the aleurone layer increases α-amylase production, thus promoting seed germination.
    4. Abscisic acid (ABA) decreases α-amylase levels when added to aleurone layer, thus inhibiting seed germination.

D. Activation of α-amylase production by GA.
    1. The promoter sequence of α-amylase gene and the sequence for DNA transcription factors (Myb proteins) are similar.
    2. Researchers proposed that a transcription factor activates α-amylase production in response to GA.
        a. Hypothesis: GA receptor on cell membrane of aleurone-layer cell receives signal.
        b. Receptor activates production of transcription factor, Myb.
        c. Myb travels to nucleus, binds to α-amylase promoter, and initiates transcription.

d. Experiment 1: Search for an Myb in activated aleurone layer.
   (1) All mRNAs in aleurone layer of germinating barley seeds isolated.
   (2) cDNA made with reverse transcriptase.
   (3) cDNA reacted with *Myb* DNA sequence.
   (4) One DNA copy complementary to *Myb* DNA identified.
   (5) Myb protein present in activated aleurone tissue.
e. Experiment 2: Identify Myb produced in response to GA.
   (1) mRNAs from aleurone layers exposed or not exposed to GA.
   (2) Performed a Northern blot with *Myb* gene DNA from aleurone tissue.
   (3) mRNA for Myb protein found only in tissue exposed to GA.
   (4) Myb protein, GAMyb, binds to -amylase promoter and activates transcription of gene for enzyme synthesis.

E. Interaction of GA and ABA
   1. GA activates Myb proteins that activate enzyme production.
   2. Preliminary studies indicate ABA activates Myb proteins that repress enzyme synthesis.
   3. Activators and repressors compete for same site on DNA.
   4. If ABA concentration is high, gene repression and dormancy occur.
   5. When GA concentration is high, gene activation and germination take place.
   6. Some important generalizations to draw from the a-amylase experiments:
      a. A target cell's response to a hormone is likely mediated by activation or inactivation of certain genes.
      b. Hormones rarely act on DNA directly.
      c. Different hormones interact at the molecular level because they induce different transcriptional activators and repressors.

F. Effect of ABA on Guard-Cell Closure
   1. Guard cells close when plant roots are unable to replace water lost from leaves.
   2. Studies with ABA indicate that guard cells close when ABA is applied to their exterior.
   3. Researchers designed an experiment to determine whether ABA in roots acts as a signal to leaves that water shortage is occurring.
      a. Experimental plants grown in pot with roots divided into two parts—half the roots received water, and the other half were allowed to dry.
      b. Water potential in leaves of control and experimental plants was the same.
      c. Stoma of experimental plants close, even though leaves are not experiencing water shortage.
      d. Roots from dry side of pot signaled decrease in available water.
      e. ABA levels in roots on dry side of pot were high, as was ABA concen-tration in leaves of experimental plants compared to control plant leaves.
      f. Conclusion: ABA is the signal carried from roots to leaves where response to water shortage results in guard cell closure.
   4. How do stomata open and close?
      a. Stomata consist of a pore surrounded by two guard cells that can change shape to open or close the pore.
      b. When guard-cell vacuoles are full of water, they are turgid and take on a curved shape that opens the pore, allowing for gas exchange and transpiration.
      c. When the vacuoles of guard cells lose water and are flaccid, they close the pore.
      d. Activation of zeaxanthin causes water entry into guard cells.
         (1) Activation of zeaxanthin by blue light leads to an increase in activity of an H+-ATPase that pumps protons out of each guard cell.
         (2) This creates a strong electrochemical gradient that triggers the entry of potassium and chloride into the cell.

(3) This, in turn, lowers the water potential in the guard cell, and water enters via osmosis.

e. Activation of ABA receptors on guard cells leads to water exit.

(1) In response to ABA, calcium ions are released from intracellular storage.

(2) This inhibits the H+-ATPases and potassium channels.

(3) It also creates an electrochemical gradient that sends chloride and other anions outside the cell.

(4) When the anions leave, the membrane potential changes, potassium channels open, and potassium exits the cell.

(5) This lowers the water potential outside the guard cell and water leaves, making them flaccid.

VI. Ethylene and Senescence

A. Senescence is the process of aging, decline and eventual death of any part of a plant.

B. Senescence is triggered by interactions between several different hormones in response to changes in light, temperature, and so forth.

1. Ethylene is the hormone most closely associated with senescence.
   a. It is a gas that is active at small concentrations.
   b. It is synthesized from the amino acid methionine.
2. Ethylene is involved in . . .
   a. fruit ripening, which at its extreme leads to fruit rotting and death.
   b. fading of flowers.
   c. the abscission or detachment of leaves.
   d. a plant's stress reaction in response to drought.
3. Ethylene was discovered when . . .
   a. Chinese fruit growers noticed that burning incense increased pear ripening.
   b. people noticed that plants growing near gas street lamps lost their leaves faster.
   c. biologists found sharp increases in ethylene during fruit ripening of many different plants.
4. Ethylene triggers fruit ripening by inducing the production of enzymes that . . .
   a. convert stored starch to sugar.
   b. remove protective toxins.
   c. break down and degrade cellulose to soften cell walls.
   d. break down chlorophyll.
   e. produce pigments and aromas that signal ripeness.
5. Fruit growers manipulate ethylene to lengthen the life of fruit.
   a. Green bananas are picked and transported, then ripened quickly by exposure to ethylene.
   b. Apples are picked ripe and stored in warehouses that keep low oxygen levels to prevent the production of ethylene, extending their shelf life.
6. Leaf senescence and abscission involve interactions between auxin and ethylene.
   a. Healthy leaves produce auxin until temperature, day length, or plant age inhibits its production.
   b. When auxin concentrations drop, the cells in the abscission zone of the leaf petiole become more sensitive to ethylene.
   c. Ethylene activates enzymes in these cells that weaken the cell walls at the base of the petiole to the point where it eventually falls from the plant.
   d. Chlorophyll in the leaf begins to degrade, and starch is transported out of the leaf.
   e. Application of cytokinins can extend the life of leaves.

Review Summary Table 39.2 Plant Growth Regulators

39.6 Pathogens and Herbivores: The Defense Responses

A. Like animals, plants can be infected or attacked by pathogens.
   1. Plants must be able to sense attacks by pathogens and stop those attacks.
   2. Plants use the **hypersensitive response (HR)** to kill infected cells.

B. How do plants know that they have been infected by a disease-causing pathogen?
   1. The gene-for-gene hypothesis (Fig 39.34)
      a. Plants have resistance (*R*) genes for resisting pathogens.
      b. Infecting microorganisms have genes (*avr*) that determine if they are virulent (cause disease) or avirulent (do not cause disease).
      c. If the *R* genes in the plant match the *avr* genes in the pathogen, then the plant initiates a hypersensitive response.
         (1) *R* genes likely act as receptors for the *avr* gene product.
         (2) Many *R* and *avr* genes exist.
   2. Why do so many resistance genes exist?
      a. Likely arose through gene duplication
      b. Different *R* alleles allow plants to recognize different *avr* alleles in pathogens.

The hypersensitive response (HR) that protects the plant against bacterial and fungal infections is supplemented by systemic acquired resistance (SAR).
   1. These events prepare the root and shoot cells for assault by the pathogen, even if they are not yet infected.
   2. The interaction between the HR and SAR involves *R* and *avr* gene products.
      a. The *R* gene product triggers production of a signal that initiates the SAR.
      b. This signaling molecule was identified to be salicyclic acid.

B. Plants protect themselves by producing insecticides.
   1. Many different types of plants make proteinase inhibitors that block protein-digesting enzymes in animal mouths, and ultimately make the animal sick.
   2. Insect attack in one part of a plant induces the formation of proteinase inhibitors in other parts of the plant.
      a. The inducing hormone was identified and named systemin.
      b. Systemin binds to a receptor on the membrane of an uninjured cell, inducing the production of proteinase inhibitors.

C. Pheromones released from plant wounds recruit parasitic wasps that destroy herbivores.
   1. Caterpillars can be infected with parasitoids (wasp larvae) that infect the caterpillar, hatch, and eat the caterpillar from the inside out.
   2. Parasitoid infections are common in herbivore outbreaks in croplands.
   3. Researchers predicted that plants release a substance that recruits parasitoids when an herbivore is present.
      a. They found that insect damaged leaves produced 11 volatile chemicals that undamaged leaves did not produce.
      b. Other experiments indicated that wasps tended to fly toward insect-damaged leaves.