BLY 122
Chapter 39 Communication: chemical signals

I. Plant Hormones—An Overview

  A. The plant cells that sense light and other stimuli are not necessarily the cells that respond to those conditions.
    1. Example: The Darwins' studies of phototropism
      a. Coleoptiles are phototropic, and grow toward light, specifically blue light.
      b. To find which part of the coleoptile sensed the light, they cut off the tip. (**Fig. 39.1**)
        (1) Decapitated coleoptiles did not grow toward the light.
        (2) They capped different parts of the coleoptile, and found that capping the tip prevented phototropism.
      c. They concluded that some "matter" was made in the tip in response to the light affecting the rest of the coleoptile, making it grow toward the light.
    2. This "matter" is now known to be a plant hormone.
      a. A hormone is an organic compound produced in small amounts in one part of the plant and transported to target cells in another part of the plant.
      b. When the hormone binds to the target cell, the appropriate physiological response is triggered.

  B. Studying plant hormones is not easy because:
    1. A single plant hormone can affect many different target tissues and trigger many different responses.
    2. No plant hormone works alone; most responses involve the concerted action of several hormones in varying concentrations. (**Table 39.1**)
    3. Hormones are active in tissues at very small concentrations, and they may exist in multiple chemical forms.
    4. Despite these challenges, technological advances are allowing scientists to learn more about how plant hormones exert their actions on target cells.

II. The Role of Auxin in Phototropism

  A. Phototropic signal is a diffusible, water-soluble chemical—Boysen-Jensen.
    1. Tips of oat shoots were cut off, and porous gelatin or nonporous mica placed between tip and shoot. (**Fig. 39.2a**)
    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. 39.2b**)
    4. Follow-up research illustrated that phototropism is caused by hormone-induced cell elongation in shoot cells on the side opposite a light source. (**Fig. 39.2c**)
    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. 39.3**)
      (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. 39.4**)
      (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. Isolation and Characterization of Auxin
   1. Auxin is indolic acid, IAA.
   2. Small, simple molecule found in very low concentrations.

E. 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.

III. 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.

IV. 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. (**Box 39.1; Fig. 39.7**)
   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. (**Fig. 39.8**)
   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 □-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. (**Fig. 39.9a**)
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. (**Fig. 39.9b**)
   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. (**Fig. 39.10**)
      (4) Myb protein, GAMyb, binds to α-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. (**Fig. 39.11**)
    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. (**Fig. 39.12a**)
      (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. (**Fig. 39.12b**)
      (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. (**Fig. 39.13**)
        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.

VII. Salicylic Acid, Systemin, and Pheromones: Defense Signals

A. 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. (**Fig. 39.14**)
        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. (**Fig. 39.15**)

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. (**Fig. 39.16**)
    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.

Chapter Vocabulary

coleoptile
phototropic
phototropins
auxin
hormone
target tissue
acid-growth hypothesis
expansins
apical dominance
axillary buds

receptor
polar transport
chemiosmotic model
influx carrier
efflux carrier
gravitotropism
abscission
senescence

cytokinins
tissue culture
callus

gibberellin
dormancy
germination
a-amylase
aleurone layer
Myb proteins
Northern blotting
endosperm tissue
transcription activator
cyclins

abscisic acid
stomata
guard cells
pore

ethylene
abscission zone
herbicides
broad spectrum
synthetic auxins
Agent Orange
forward genetics