

I. 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. 38.1a**)
 - 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. 38.1b**)
 - c. Conclusion: Phototropism is a response to blue light.
3. Plants can “see” red and far-red light as well as blue light.
 - a. Question: Why do plants from sunny habitats grow tall and spindly when they are grown in shady environments?
 - b. Experiment: Grew plants from sunny and forest-floor habitats in chambers with constant amounts of the red and blue light necessary for photosynthesis, but with varying amounts of the far-red light that dominates in shaded environments. (**Fig. 38.2**)
 - c. Observations: Stems of sunny-habitat species elongate more in the presence of far-red light than do species from shaded environments.
 - d. Conclusion: Plants adapted to sunny habitats sense far-red light and respond by elongating their stems so that they are more accessible to sunlight.
4. Photoperiodism: Plants can sense the relative length of day and night.
 - a. Plants sense photoperiod in order to flower when pollinators are available. (**Fig. 38.3a**)
 - (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. (**Fig. 38.3b**)
 - (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. (**Fig. 38.4**)
 - (2) Similar effect seen in lettuce-seed germination; red light will stimulate germination, but far-red light inhibits germination. (**Table 38.1**)
 - (3) This mechanism prevents germination in the shade and promotes it in the full sun.

C. How Do Plants See?

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. 38.5**)
 - (1) P_r absorbs red light and is converted to P_{fr} .
 - (2) P_{fr} 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?
3. 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-phototropic 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. (**Fig. 38.6**)
 - (4) More recent studies have found more blue-light receptors that are related to *phot1*, collectively called phototropins.
 - d. Other blue-light receptors mediate other responses to sunlight.
 - (1) Zeaxanthin, a carotenoid, initiates the opening of stomata in the presence of light.
 - (2) Cryptochromes are involved in stem elongation in shady conditions and flower induction.

4. How do plants translate what they sense into an appropriate response?
 - a. Signal transduction—the process whereby an outside signal is converted into a response.
 - (1) Usually involves energy conversion
 - (2) Phototropism—light energy converted into the chemical energy in phosphorylated PHOT1 protein.
 - (3) Often involves a phosphorylation event and change in activity of a response protein that initiates various responses: (**Fig. 38.7**)
 - (a) Changes ion flow through a channel or pump.
 - (b) Activates or represses gene transcription.
 - (c) Activates or represses mRNA translation.

II. Gravity Perception

- A. Plants respond to gravity and grow downward—gravitropism. (**Fig. 38.8**)
- B. The root cap is the gravity sensor. (**Fig. 38.9a**)
 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. (**Fig. 38.9b**)
- C. How Do Plants Sense Gravity?
 1. Two hypotheses—statolith hypothesis and gravitational pressure hypothesis
 - a. Both agree that unidentified pressure or stretch receptors are somewhere in the root cells.
 - b. Differ about the part of the cell that activates gravitropism.
 2. 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. 38.10**)
 - (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.
 4. Observations that do not support statolith hypothesis:
 - a. *Arabidopsis* mutants that cannot synthesize starch have small and light amyloplasts.
 - b. But they still exhibit a gravitropic response, though less than normal.
 5. Gravitational pressure hypothesis
 - a. Proposal: The pressure exerted by all cell contents, including amyloplasts, on bottom of cell activates a gravity receptor between the cell membrane and extracellular matrix.
 - b. Experiment with rice roots in pond water and high-buoyancy solution—Staves et al.
 - (1) Rice roots placed horizontally in pond water exhibit downward curvature.
 - (2) Similarly arranged roots in high-buoyancy solution have reduced gravitational response, even though amyloplasts settled to the bottom of the cells.

- (3) Results consistent with hypothesis, because high-buoyancy solution lessens the effect of gravity, decreases pressure on extracellular matrix, and reduces amount of gravitropic response.
6. Is the gravity sensor a transmembrane protein?
 - a. Integrins are membrane proteins in animal systems that form a link between the extracellular environment and the interior of the cell.
 - (1) Many biologists have proposed that integrins exist in plants as well.
 - (2) Hypothesis: Integrins may act as gravity sensors in plants by reacting to the pressure differential between the top and bottom of cells.
 - b. Integrin proteins have been found in *A. thaliana* and the green alga *Chara*.
 - (1) Fluorescent-tagged antibodies to animal integrin were used to localize integrin in these species.
 - (2) Integrins were found in root-cap cells of *A. thaliana*.
 - (3) More evidence is needed to confirm integrins act as gravity receptors in plants.

III. How Do Plants Respond to Wind and Touch?

- A. Plants respond to repeated motion (wind) or touch by increasing stem thickness. (**Fig. 38.11**)
- B. Touch is converted to an electrical signal.
 1. Proton pumps create a charge difference between the interior and exterior of plant cells. (**Fig. 38.12a**)
 - 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. (**Fig. 38.12b**)
 - (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. (**Fig. 38.13a**)
 - 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. (**Fig. 38.13b**)
 - 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. (Fig. 38.14)
- 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.

IV. How Do Plants Sense Attacks by Parasites?

- A. Like animals, plants can be infected or attacked by parasites.
 - 1. Plants must be able to sense attacks by pathogens and stop those attacks.
 - 2. Plants use the hypersensitive response 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. 38.15)
 - 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.

Chapter Vocabulary

coleoptile

phototropism

photoperiodism

long-day plants

short-day plants

day-neutral plants

red/far-red

phytochrome

photoreversibility

P_r

P_{fr}

PHYA/PHYB genes

photoreceptor

phototropins

phosphorylation

dephosphorylation

protein kinase

hypocotyl

autophosphorylation

signal transduction

cryptochrome

zeaxanthin

cryptochromes

gravitropism

root cap

statolith hypothesis

amyloplast

statolith

gravitational pressure hypothesis

integrins

auxin

electrical signaling

membrane voltage

membrane potential

millivolts

resting potential

action potential

depolarization

repolarization

plasmodesmata

circadian rhythm

biological clock

oscillators