Plant Growth and Development

KEY CONCEPTS

Growth and development are influenced by a plant's internal conditions and signals from its external environment.

A plant may respond to an external stimulus, such as light, gravity, or touch, by a directional growth response, or tropism. Study of tropisms has helped biologists elucidate links between the external environment and internal signals such as hormones.

Hormones are chemical signals responsible for coordinating and regulating many aspects of plant development. Although there are many plant hormones, five have been well-characterized: auxins, gibberellins, cytokinins, ethylene, and abscisic acid.

Plants have different receptors that detect various colors of light. Phytochrome detects red and far-red light, which affect several aspects of development, including the timing of flowering.

The ultimate control of plant growth and development, which includes all the changes that take place during the entire life of an individual, is genetic. If the genes required for development of a particular trait, such as the shape of a leaf, the color of a flower, or the type of root system, are not present, that characteristic does not develop. When a particular gene is present, its expression—that is, how it exhibits itself as an observable feature of an organism—is determined by several factors, including signals from other genes and from the environment. The location of a cell in the young plant body also has a profound effect on gene expression during development. Chemical signals from adjacent cells help a cell "perceive" its location within the plant body. Each cell's spatial environment helps determine what that cell ultimately becomes.

Growth and development, including a plant's responses to various changes in its environment, are controlled by plant hormones, organic compounds that are present in very low concentrations in plant tissues and that act as chemical signals between cells. Environmental cues, such as changing day length and variations in precipitation and temperature, exert an important influence on gene expression and hormone production, as they do on all aspects of plant growth and development.

For example, the initiation of sexual reproduction is often under environmental control, particularly in temperate latitudes, and plants switch to reproductive growth after receiving appropriate signals from the environment. Many flowering plants are sensitive to changes in the relative amounts of daylight and darkness that accompany the changing seasons, and these plants flower in re-
Plants exhibit movements in response to environmental stimuli such as light, gravity, and touch. A plant may respond to such an external stimulus by directional growth—that is, the direction of growth depends on the direction of the stimulus. Such a directional growth response, called a tropism, results in a change in the position of a plant part. Tropisms are irreversible and may be positive or negative, depending on whether the plant grows toward the stimulus (a positive tropism) or away from it (a negative tropism). Tropisms are under hormonal control, which is discussed later in the chapter.

Phototropism is the directional growth of a plant caused by light (Fig. 37-1). Most growing shoot tips exhibit positive phototropism by bending (growing) toward light, something you may have observed if you place houseplants near a sunny window. This growth response increases the likelihood that stems and leaves receive adequate light for photosynthesis. The bending response of phototropism is triggered by blue light with wavelengths less than 500 nm. (You may recall from Chapter 33 that blue light also induces stomata to open.)

For a plant or any organism to have a biological response to light, it must contain a light-sensitive substance, called a photoreceptor, to absorb the light. The photoreceptor that absorbs blue light and triggers the phototropic response and other blue-light responses (such as stomatal opening) is a family of yellow pigments called phototropins. Phototropins are light-activated kinases, enzymes that transfer phosphate groups. There is evidence that phototropins become phosphorylated—that is, a phosphate group is added—in response to blue light. Thus, phosphorylation is an early step in the blue light–signaling pathway.

Growth in response to the direction of gravity is called gravitropism. Most stem tips exhibit negative gravitropism by growing away from Earth’s center, whereas most root tips exhibit positive gravitropism (Fig. 37-2). The root cap is the site of gravity perception in roots, when the root cap is removed, the root con-
continues to grow, but it loses any ability to perceive gravity. Special cells in the root cap possess starch-containing amyloplasts that collect toward the bottom of the cells in response to gravity, and these amyloplasts may initiate at least some of the gravitropic response. If the root is put in a different position, as when a potted plant is laid on its side, the amyloplasts tumble to a new position, always settling in the direction of gravity. The gravitropic response (bending) occurs shortly thereafter and involves the hormone auxin (discussed later in the chapter). Despite the movement of amyloplasts in response to gravity, researchers question their role in gravitropism. A mutant Arabidopsis plant that lacks amyloplasts in its root cap still responds gravitropically when placed on its side, indicating that roots do not necessarily need amyloplasts to respond to gravity. Ongoing research may clarify how roots perceive gravity.

Thigmotropism is growth in response to a mechanical stimulus, such as contact with a solid object. The twining or curling growth of tendrils or stems, which helps attach a climbing plant such as a vine to some type of support, is an example of thigmotropism (see Fig. 33-13b).

Learning Objectives
1. Describe a general mechanism of action for plant hormones, using auxin as your example.
2. Describe early auxin experiments involving phototropism.
3. List several ways that each of these hormones affects plant growth and development: auxins, gibberellins, cytokinins, ethylene, and abscisic acid.
4. Summarize the activities of these plant hormones and hormone-like signaling molecules: brassinosteroids, jasmonates, salicylic acid, systemin, and oligosaccharins.

A plant hormone is an organic compound that acts as a chemical signal eliciting a variety of responses that regulate growth and development. The study of plant hormones is challenging because hormones are effective in extremely small concentrations (less than 10⁻¹⁰ mol/L). In addition, the effects of different plant hormones overlap, and it is difficult to determine which hormone, if any, is the primary cause of a particular response. Plant hormones may also stimulate a response at one concentration and inhibit that same response at a different concentration.

Plant hormones are different from animal hormones in several ways. For example, most plant hormones are not produced in one part of the plant and transported over long distances to another part, where they cause a particular response; instead, the effects of plant hormones often occur close to where hormones are produced. Also, plant hormones are generally small molecules, not large, complex molecules like many animal hormones.

For many years, biologists studied five major classes of plant hormones: auxins, gibberellins, cytokinins, ethylene, and abscisic acid. More recently, researchers have uncovered compelling evidence for a variety of signaling molecules, such as brassinosteroids, jasmonates, salicylic acid, systemin, and oligosaccharins. (Table 37-1 summarizes plant hormones and hormone-like signaling molecules discussed in this chapter.)

Plant hormones act by signal transduction

Researchers have used molecular genetic techniques to better understand the biology of plant hormones. Arabidopsis mutants are particularly useful. For example, different mutants have defects...
in hormone synthesis, hormone transport, signal reception, or signal transduction. In signal transduction, a receptor converts an extracellular signal into an intracellular signal that causes some change in the cell. Such mutants enable plant biologists to identify and clone genes involved in these aspects of hormone biology. Studying the mutant phenotypes helps plant biologists establish connections between the mutant genes and specific physiological activities involved in growth and development.

Using this research, biologists are elucidating the general mechanism of plant hormone action. It appears that many plant hormones bind to enzyme-linked receptors located in the plasma membrane; the hormone binds to the receptor, where it triggers an enzymatic reaction of some sort. Let us consider a specific example that involves the plant hormone auxin, which is known to cause rapid changes in gene expression (Fig. 37-3). As shown in step 1, the receptor for auxin is located in the plasma membrane and has a three-dimensional shape that binds to the auxin molecule. The binding of auxin to its receptor catalyzes the attachment of the molecule ubiquitin to repressor proteins that inhibit certain genes (step 2). Whenever ubiquitin is attached to protein molecules, the cell targets those molecules for destruction (step 3). As a result, the genes that were repressed by those repressor proteins are now activated, resulting in changes in cell growth and development (step 4).

The identification of the receptor for auxin was reported in 2005 by two groups working independently. This receptor, called transport inhibitor response 1 (TIR1), is an F-box protein. The F-box is a short sequence of amino acids found in molecules that catalyze the addition of ubiquitin tags to proteins targeted for destruction. Interestingly, all animals, plants, and fungi examined to date use ubiquitin to target proteins for destruction, but bacteria do not. This suggests that the use of ubiquitin tags evolved early in eukaryote evolution and was conserved as the various groups of eukaryotes diversified. Plants have about 700 F-box proteins, but not much is known about most of them. Future research may identify other plant hormones and signaling molecules that use F-box proteins as receptors.

**Auxins promote cell elongation**

Charles Darwin, the British naturalist best known for developing the theory of natural selection to explain evolution, also provided the first evidence for the existence of auxins. The experiments that Darwin and his son Francis performed in the 1870s involved positive phototropism, the directional growth of plants toward light. The plants they used were newly germinated canary grass seedlings. As in all grasses, the first part of a canary grass seedling to emerge from the soil is the coleoptile, a protective sheath that encircles the stem. When coleoptiles are exposed to light from only one direction, they bend toward the light. The bending occurs below the tip of the coleoptile.

The Darwins tried to influence this bending in several ways (Fig. 37-4). For example, they covered the tip of the coleoptile as soon as it emerged from the soil. When they covered that part of the coleoptile above where the bend would be expected...
Circadian rhythms in plants affect such biological events as gene expression, the timing of photoperiodism (that is, of seasonal reproduction), the rate of photosynthesis, and the opening and closing of stomata. Sleep movements observed in the common bean and other plants are another example of a circadian rhythm (Fig. 37-19). During the day, bean leaves are horizontal, possibly for optimal light absorption, but at night the leaves fold down or up, a movement that orients them perpendicular to their daytime position. The biological significance of sleep movements is unknown at this time.

When constant environmental conditions are maintained, circadian rhythms such as sleep movements repeat every 20 to 30 hours, at least for several days. In nature, the rising and setting of the sun reset the biological clock so that the cycle repeats every 24 hours. What happens if a plant’s circadian clock is mutated so that it is not resynchronized by the day–night cycle? In 2005, biologists at the University of Cambridge in England reported the identification of mutants of the model plant Arabidopsis in which the circadian clock is not synchronized to match the external day–night cycle. The mutant plants were found to contain less chlorophyll, fix less carbon by photosynthesis, grow more slowly, and have less of a competitive advantage than Arabidopsis plants with a normal circadian clock.

For many plants, two photoreceptors—the red light–absorbing phytochrome and the blue/ultraviolet-A light–absorbing cryptochrome—are implicated in resetting the biological clock. Certain amino acid sequences of the protein portion of phytochrome are homologous with amino acid sequences of clock proteins in fruit flies, fungi, mammals, and bacteria; this molecular evidence strongly supports the circadian-clock role of phytochrome.

The evidence for cryptochrome as a clock protein is also convincing. First discovered in plants, cryptochrome counterparts are found in the fruit fly and mouse biological-clock proteins. Possibly both photoreceptors are involved in resetting the biological clock in plants; researchers have evidence that phytochrome and cryptochrome sometimes interact to regulate similar responses.

**Review**

- What is phytochrome? What are two roles of phytochrome?
- What are the steps in phytochrome signal transduction?
- In what process is cryptochrome involved?
coleoptile tip, the plant did not bend. When they removed the coleoptile tip, bending did not occur. When the bottom of the coleoptile was shielded from the light, the coleoptile bent. The Danesins concluded that some substance is transmitted from the upper to the lower part that causes the plant to bend.

In the 1920s, Frits Went isolated the phototropic hormone from oat coleoptiles by removing the coleoptile tips and placing them on agar blocks. Normal growth resumed when he put one of these agar blocks squarely on the decapitated coleoptile, the substance had diffused from the coleoptile tip into the agar and, later, from the agar into the decapitated coleoptile. Went named this substance auxin.

**ThomsonNOW**  See the auxin experiments in action by clicking on the figure in ThomsonNOW.

4. List several ways that each of these hormones affects plant growth and development. Auxins, gibberellins, cytokinins, ethylene, and abscisic acid (page 791).

- **Auxin** is involved in cell elongation; tropisms; **apical dominance**, the inhibition of axillary buds by the apical meristem; and fruit development. Auxin also stimulates root development on stem cuttings.
- **Gibberellins** are involved in stem elongation, flowering, and germination.
- **Cytokinins** promote cell division and differentiation; delay senescence, the natural aging process; and interact with auxin and ethylene in apical dominance. Cytokinins induce cell division in tissue culture, a technique in which cells are isolated from plants and grown in a nutrient medium.
- **Ethylene** plays a role in opening fruits; apical dominance; leaf abscission; wound response; **thigmomorphogenesis**, a developmental response to mechanical stress such as wind; and senescence.
- **Abscisic acid** is an environmental stress hormone involved in stomatal closure caused by water stress and in seed dormancy, a temporary state of reduced physiological activity.

5. Summarize the activities of these plant hormones and hormone-like signaling molecules: brassinosteroids, jasmonates, salicylic acid, systemin, and oligosaccharins (page 791).

- **Brassinosteroids** are involved in several aspects of plant growth and development, such as cell division, cell elongation, light-induced differentiation, seed germination, and vascular development.
- **Jasmonates** affect several plant processes, such as pollen development, root growth, fruit ripening, and senescence. They are also produced in response to the presence of insect pests and disease-causing organisms.

- **Salicylic acid** triggers systemic acquired resistance that helps defend plants against pathogens and insect pests.
- **Systemin**, a polypeptide with hormonal properties, stimulates a natural defense mechanism in which the plant produces molecules that disrupt insect digestion.
- **Oligosaccharins**, short branched chains of sugar molecules, inhibit flowering and stimulate vegetative growth.

6. Explain how varying amounts of light and darkness induce flowering (page 800).

- **Photoperiodism** is any response of plants to the duration and timing of light and dark. Flowering is a photeperiodic response in many plants. **Short-day plants** detect the lengthening nights of late summer or fall and flower at that time. **Long-day plants** detect the shortening nights of spring and early summer and flower at that time. **Intermediate-day plants** flower when exposed to days and nights of intermediate length.

**ThomsonNOW**  Learn more about photoperiodism by clicking on the figure in ThomsonNOW.

7. Describe the role of phytochrome in flowering, including a brief discussion of phytochrome signal transduction (page 800).

- The photoreceptor in photoperiodism is **phytochrome**, a family of about five blue-green pigments. Each type of phytochrome has two forms, Pr and Pfr, named by the wavelength of light they absorb. Pr is the active form, triggering or inhibiting physiological responses such as flowering, shade avoidance, and a light requirement for germination.
- The pathway in phytochrome **signal transduction** begins when inactive phytochrome in the cytoplasm absorbs red light and is converted into the active form, Pfr, which moves into the nucleus. There, phytochrome binds to the transcription factor FIF3 (phytochrome-interacting factor) and activates or represses the transcription of light-responsive genes.

**ThomsonNOW**  Learn more about phytochrome by clicking on the figure in ThomsonNOW.

8. Define circadian rhythm, and give an example (page 800).

- A **circadian rhythm** is a regular period in an organism’s growth or activities that approximates the 24-hour day and is reset by the rising and setting of the sun. Two examples of circadian rhythms are the opening and closing of stomata and sleep movements.

9. Distinguish between phytochrome and **cryptochrome** (page 800).

- Both phytochrome and **cryptochrome** are photoreceptors that sometimes interact to regulate similar responses, such as resetting the biological clock. Phytochrome strongly absorbs red light, whereas cryptochrome absorbs blue and ultraviolet-A light.

**TEST YOUR UNDERSTANDING**

1. In the signal transduction process for the hormone auxin, the molecule ubiquitin (a) absorbs blue light (b) becomes phosphorylated (c) tags certain proteins for destruction (d) interacts antagonistically with gibberellins (e) binds to a receptor in the plant cell’s plasma membrane.

2. When you prune shrubs to make them “bushier”—that is, to prevent apical dominance—you are affecting the distribution and action of which plant hormone? (a) auxin (b) jasmonic acid (c) systemin (d) ethylene (e) abscisic acid.
3. A synthetic known as 2,4-D is used as a selective herbicide. (a) auxin (b) gibberellin (c) cytokinin (d) ethylene (e) abscisic acid

4. Research on a fungal disease of rice provided the first clues about the plant hormone (a) auxin (b) gibberellin (c) cytokinin (d) ethylene (e) abscisic acid

5. This plant hormone interacts with auxin during the formation of plant organs in tissue culture. (a) florigen (b) gibberellin (c) cytokinin (d) ethylene (e) abscisic acid

6. The plant hormone delays senescence, whereas the plant hormone promotes senescence. (a) cytokinin; auxin (b) gibberellin (c) cytokinin; ethylene (d) abscisic acid; ethylene (e) gibberellin; auxin

7. The stress hormone that helps plants respond to drought is (a) auxin (b) gibberellin (c) cytokinin (d) ethylene (e) abscisic acid

8. This hormone promotes seed dormancy. (a) auxin (b) gibberellin (c) cytokinin (d) ethylene (e) abscisic acid

9. Which signaling molecule triggers the release of volatile substances that attract parasitic wasps to plant-eating caterpillars? (a) brassinosteroid (b) jasmonic acid (c) systemin (d) salicylic acid (e) oligosaccharin

10. The three classes of photoreceptors that enable plants to sense the presence and duration of light are (a) phytochrome, cryptochrome, and circadian rhythms (b) chlorophyll, photosynthesis, and photoperiodism (c) phytochrome, photoperiodism, and chlorophyll (d) phytochrome, cryptochrome, and phototropism (e) phototropin, photosynthesis, and photoperiodism

11. A plant's response to the relative amounts of daylight and darkness is (a) apical dominance (b) bolting (c) gravitropism (d) photoperiodism (e) phototropism

CRITICAL THINKING

1. Predict whether flowering in a short-day plant with a minimum critical night length of 14 hours would be expected to occur in the following situations. Explain each answer.
   (a) The plant is exposed to 15 hours of daylight and 9 hours of uninterrupted darkness. (b) The plant is exposed to 9 hours of daylight and 15 hours of darkness. (c) The plant is exposed to 9 hours of daylight and 15 hours of darkness, with a 10-minute exposure to red light in the middle of the night.

2. If you transplanted a short-day plant discussed in question 1 to the tropics, would it flower? Explain your answer.

3. Evolution Link. What adaptive advantages are conferred on a plant whose stems are positively phototropic and whose roots are positively gravitropic?

4. Evolution Link. Explain why a plant with a mutation in one of its phytochrome genes that affects flowering time would be at an evolutionary disadvantage.

5. Analyzing Data. Examine Figure 37-14a. When the day length is 10 hours and the night length is 14 hours, what percent of the plants flower? When the day length is 16 hours and the night length is 8 hours, what percent of the plants flower? What is the critical night length for this plant?