

# Control Systems in Plants

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## Objectives

**Introduction** Describe the benefits and risks of soybeans in the human diet.

### Plant Hormones

- 33.1 Describe the experiments and conclusions of the phototropism research performed by the Darwins, Boysen-Jensen, and Went. Explain why the role of auxin in grasses does not seem to be the same for sunflowers, radishes, and other dicots.
- 33.2–33.7 Describe the roles of the five major types of plant hormones.
- 33.8 Describe the uses of plant hormones in modern agriculture and note the ethical issues associated with their use.

### Growth Responses and Biological Rhythms in Plants

- 33.9 Define phototropism, gravitropism, and thigmotropism and explain their significance in plants.
- 33.10 Explain how biological clocks work and how they influence the lives of plants.
- 33.11 Distinguish between short-day plants and long-day plants. Explain why these terms are misleading.
- 33.12 Describe the roles of phytochromes in plants.
- 33.13 Describe some of the advances in botany that have resulted from the study of *Arabidopsis*.

### Plant Defenses

- 33.14 Explain how plants defend themselves against herbivores. Describe the systemic acquired resistance defense response in plants.
- 33.15 Define zoopharmacognosy and explain its significance to human health.

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## Key Terms

phototropism	tropism	short-day plant
auxin	gravitropism	long-day plant
cytokinin	thigmotropism	phytochrome
gibberellin	circadian rhythm	herbivore
abscisic acid (ABA)	biological clock	systemic acquired resistance
ethylene	photoperiod	

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## 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)

**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)

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

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## Lecture Outline

### Introduction *The Benefits of Soy*

- A. The dietary benefits of soy protein have started to catch on among Americans, as indicated by sales quadrupling in the last decade.
- B. Soy protein contains all seven essential amino acids, and is low in fat and high in fiber. Soy protein is a heart-healthy food and a good meat substitute. But soy has its downside, too.
- C. All plants have phytochemicals, plant hormones that regulate the growth and development of plants. Soybeans contain a plant hormone (phytoestrogen) that is structurally similar to estrogen. One type of phytoestrogen called isoflavin has been shown to have small hormonal effects on women. Moderate amounts of estrogen can assuage menopausal symptoms while too much increases the risk of breast cancer. Since soy products are considered a dietary supplement they are not under strict FDA regulation (like drugs); therefore, the level of isoflavins varies widely between products.
- D. The risks and benefits of soy protein are still being researched, but there is an increasing body of evidence in favor of soy protein consumption by humans. This chapter investigates the role of plant hormones like isoflavins, with particular emphasis on plant growth and development.

### I. Plant Hormones

#### Module 33.1 Experiments on how plants turn toward light led to the discovery of a plant hormone.

- A. **Phototropism** is an adaptive response of plant shoots and seedlings to grow toward a source of light (Figure 33.1A). Examination of the cellular events during a phototropic response by a shoot tip shows that the cells on the darker side of the shoot have elongated faster (Figure 33.1B).
- B. A series of classic experiments showed how a particular hormone controls the phototropic response. The series begins with experiments by Charles Darwin and his son, Francis, in the 1800s. They showed that grass seedlings bend toward light only if

their tips are present and uncovered, suggesting that the tip was responsible for the sensing of light (Figure 33.1C).

**NOTE:** Because these plant parts are mentioned in Chapter 31, indicate that these classical experiments were performed in young seedlings that still had the sheath that covers the young shoots of monocots.

- C. In 1913, Boysen-Jensen showed that a gelatin block placed between the plant tip and the lower plant would not inhibit the response, whereas a mica block would. This suggested that a chemical that could diffuse through the gelatin but not through the mica mediated the response.
- D. In 1926, Went extended Boysen-Jensen's experiments to actually discover the hormone. He collected the hormone from severed shoot tips into agar blocks, and then applied the agar blocks in various positions to decapitated seedlings growing in the dark. Agar blocks placed off-center caused the seedlings to bend, away from the side the block was on. Went called the diffusible substance auxin (Figure 33.1D).
- E. Follow-up experiments showed that shoot tips secrete auxin in equal amounts in light or dark, but that auxin diffuses from lighted sides of shoot tips to shaded sides. In the 1930s, biochemists identified the chemical structure of auxin: a small organic molecule made from the amino acid tryptophan.
- F. Although auxins have still not been shown conclusively to be the sole regulator of plant growth in light, the discovery of auxin was the impetus for research on plant hormones.

### **Module 33.2** Five major types of hormones regulate plant growth and development.

- A. General overview (Table 33.2).
- B. Three of the hormone types (auxins, cytokinins, and gibberellins) are actually classes, including several chemicals with similar molecular structure and function. The other two types of plant hormones are abscisic acid (ABA) and ethylene.
- C. Plant hormones produce their effects in very small amounts and may do so by triggering signal-transduction pathways (Module 11.13) that activate or inhibit enzymes or result in changes in membranes.
- D. All five types influence growth, and four (all except abscisic acid) affect development. Hormones regulate plant growth and development by controlling cell differentiation, division, and elongation.
- E. The effects of a hormone depend on plant species, the site of action, the developmental stage of the plant, the concentration of the hormone at the target site, and the balance of concentrations of different hormones.
- F. The study of plant hormones has moved toward the field of molecular biology in an effort to find clarity of hormone structure, function, and relatedness.

### **Module 33.3** Auxin stimulates the elongation of cells in young shoots.

- A. **Auxins** are a class of chemicals that promote the elongation of developing seedlings. *Review:* The elongation of shoots is discussed in Module 31.7.
- B. Indoleacetic acid (IAA) is the auxin that has been extracted from plants. The major site of auxin synthesis is the apical meristem of the shoot tips. When auxins are discussed in this chapter, assume it is in reference to IAA (Figure 33.3A).
- C. Relatively high concentrations of IAA stimulate shoot cell elongation and inhibit root cell elongation. However, higher levels of IAA stimulate the synthesis of ethylene.

Ethylene counters the effects of IAA and is the likely cause of the inhibition of shoot growth at higher IAA levels (Figure 33.3B).

- D. Relatively low concentrations of IAA have no effect on shoot cell elongation, but stimulate root cell elongation (Figure 33.3B).
- E. One hypothesis about how auxin elicits its effect on cells is that auxins may stimulate certain  $H^+$  pumps in plasma membranes. The increase in  $H^+$  outside the membrane but within the cell wall would stimulate enzymes that break bonds between cellulose molecules, thereby causing the walls to be more elastic and allowing cells to elongate in response to turgor pressure (Figure 33.3C).
- F. Auxins can also trigger the development of vascular tissue and induce vascular cambium cell division and thus growth in stem diameter (Module 31.8). Auxins produced in seeds promote the growth of fruit tissues.
- G. An agricultural use of auxin sprays is to promote fruit formation from seedless, unfertilized flowers (e.g., in tomatoes, cucumbers, and eggplants). Synthetic auxins are also used as herbicides.

#### Module 33.4 Cytokinins stimulate cell division.

- A. **Cytokinins** promote cell division, are produced in actively growing tissues in roots, embryos, and fruits, and reach target tissues by flowing in xylem sap.
- B. The effects of cytokinins are often influenced by the concentrations of auxins; it is the ratio of the concentrations of these two types of hormones that has the effect.
- C. In unpinched plants, the balance of auxin (diffusing down from the shoot tip) to cytokinin (flowing in xylem up from roots) affects where axillary buds will begin to extend laterally and may also help coordinate the growth of root and shoot systems.
- D. When a terminal bud is removed, the elongating effects and inhibitory effects on lateral bud growth of auxin are removed, and the axillary bud-stimulating effects of cytokinins (still at the same concentration as when auxins dominate) activate lateral buds (Figure 33.4).
- E. An agricultural use of cytokinins is their use in influencing the branching pattern of Christmas trees.

#### Module 33.5 Gibberellins affect stem elongation and have numerous other effects.

- A. **Gibberellins** were first isolated from species of fungus of the genus *Gibberella* in Japan, where the fungus causes “foolish seedling disease” on rice plants. This disease is characterized by aberrant growth of rice shoots that causes weakening of the shoots (Figure 33.5A).
- B. Lower concentrations of gibberellins occur naturally in plants where the hormone functions as a growth regulator. Over 100 different gibberellins are known.
- C. Gibberellins are made in tips of shoots and roots; their main effect is to enhance the action of auxin on cell elongation and fruit development; and they have a role in seed development. In seeds, they seem to be the link between environmental cues and the metabolic processes required for the renewal of embryo growth during seed germination.
- D. Gibberellins, in combination with auxins, are used to make apples, currants, and eggplants develop without fertilization. Gibberellins also influence grape size and cluster pattern (Figure 33.5B).

- E. In some plants, gibberellins are antagonistic to abscisic acid.

**Module 33.6** Abscisic acid inhibits many plant processes.

- A. **Abscisic acid (ABA)** is produced in buds and produces effects that are adaptive for inducing or maintaining seed dormancy during unfavorable times.
- B. ABA does not have a primary effect on bud dormancy or leaf abscission as indicated by its name.
- C. ABA seems to act as a growth inhibitor in seeds, particularly of annual plants, until a certain volume of rainwater washes the ABA out of the seeds. It may actually be the ratio of ABA to gibberellins that promotes germination. Seeds often require prolonged cold periods to allow sufficient ABA breakdown and removal of the inhibitory effect.
- D. ABA also acts as a stress hormone, accumulating in leaves during times of drought, and causing stomata to close, thus reducing transpiration.

**Module 33.7** Ethylene triggers fruit ripening and other aging processes.

- A. The role of this gas in fruit ripening was discovered when sheds warmed by kerosene stoves were used to ripen grapefruit. The gas was a by-product of the kerosene, which was absent from cleaner heaters.
- B. **Ethylene** is produced in tissues of ripening fruits. It has a positive-feedback effect on ripening by inducing programmed cell death (apoptosis) and color changes, and additional production of ethylene (Figure 33.7A). This process is adaptive and is used to attract animals to eat the fruit, thus promoting seed dispersal.
- C. To retard ripening and fruit spoilage, growers flush out stored fruit with CO<sub>2</sub> to remove the accumulating ethylene.
- D. Ethylene probably also plays a role in the color changes in and falling of leaves during autumn. Pigment complexes are induced to change, and a breakable layer (abscission layer) of cells at the bases of leaves is induced to form when the shorter days and cooler temperatures of fall occur. Abscission is promoted by a change in the balance of ethylene to auxin (Figure 33.7B).

**Module 33.8** Connection: Plant hormones have many agricultural uses.

- A. *Review:* The roles of hormones mentioned in the last five modules. The additional uses below are also important.
- B. Auxins are used to control when plants will drop their fruit (Figure 33.8).
- C. Ethylene is used to thin peaches and to loosen berries so that machines can more easily pick them.
- D. With auxins, gibberellins are used for producing seedless fruit (Module 33.5). In contrast, large doses of gibberellins promote early (first-year rather than second-year) flowering and seed production in biennial plants such as carrots, beets, and cabbage.
- E. 2,4-D is a synthetic auxin applied to eliminate dicot weeds in monocot grain crop plantings. Dicots are more sensitive to the toxic effects of this compound than are monocots. One drawback to the use of 2,4-D is that a by-product of its production is dioxin, a compound known to be toxic to humans.

*Review:* The economics and ethics of the use of such hormones (Module 32.10).

*Preview:* Biological magnification and the pesticide DDT (Module 38.3).

## II. Growth Responses and Biological Rhythms in Plants

**Module 33.9** Tropisms orient plant growth toward or away from environmental stimuli.

- Plants are immobile and must have some mechanism of responding to the environmental clues that benefit their survival. Most plants respond to environmental cues by slow growth responses known as **tropisms**. Phototropism, gravitropism, and thigmotropism are irreversible growth responses to light, gravity, and touch, respectively.

*NOTE:* Differentiate the term *tropism*, growth, from *taxis*, movement. Taxis is a common form of response seen in animals and motile protists.

- Review:* The mechanism for phototropism is the differential rate of cell elongation, largely under the control of auxin produced by shoot tips and differentially distributed in shoots by the effect of light and shade (Modules 33.1 and 33.3).
- Plants show positive **gravitropism** in roots and negative gravitropism in shoots. The cellular mechanism is unknown but may involve the effect of gravity on starch grain-containing organelles in cells and their response to auxins (Figure 33.9A).
- Tendrils (modified leaves) and stems of climbing plants exhibit **thigmotropism**. Contact on one side of these structures elicits cell growth on the opposite side. This causes the structure to coil and grasp the object that contacts the plant (Figure 33.9B).

**Module 33.10** Plants have internal clocks.

- Review:* The opening and closing of stomata discussed in Module 32.4 is an example of an internal clock.
- Like animals, plants display rhythmic activities, particularly those that exhibit **circadian rhythms**, cycles of about 24 hours. Plants will continue these activities if placed in completely dark environments or in orbiting satellites. The molecular bases of biological clocks are not known (Figure 33.10).

*Preview:* The biological clocks of animals are discussed in Module 37.9.

- Interestingly, most **biological clocks** are not precisely timed with the external environmental factors to which they keep the organism (plant or animal) tuned. For example, the sleep movements of plants kept in the dark exhibit 26-hour cycles. These imprecise timekeepers seem to be naturally reset each day by environmental cues.
- The biological clock of mammals is located in the hypothalamus (Module 28.15). For most organisms, the location and types of cells involved in biological clocks are not known. However, the biological clocks of all organisms may involve the same molecular mechanism. There are genes found in many different organisms that encode a transcription factor that turns off the gene that codes for it when it is present at higher concentrations and, when the concentration of the transcription factor falls, that gene is turned on.
- Another interesting aspect of biological clocks is that their timing is not temperature-sensitive (this is an advantage), so, since most chemical reactions are temperature dependent, the chemical bases of the timing must adjust for changes in temperature.

**Module 33.11** Plants mark the seasons by measuring photoperiod.

- Biological clocks may also function in seasonal events such as flowering, seed germination, and the onset and ending of plant dormancy during seasonal periods of environmental stress.
- The relative lengths of day and night (**photoperiod**, and, specifically, the length of the night) are the principal environmental cues for plants (Figure 33.11).

- C. **Short-day** (actually, long-night) **plants** (e.g., chrysanthemums and poinsettias) flower in late summer or winter when light periods shorten. These plants respond to nighttime darkness of a critically long duration. A brief flash of light in the middle of this period will stop blossoming.
- D. **Long-day** (actually, short-night) **plants** (e.g., spinach, lettuce, iris, and many cereal grains and other domesticated food plants) flower in late spring or early summer when light periods lengthen. These plants respond to nighttime darkness of a critically short duration. A brief flash of light in the middle of a longer period of darkness will induce blossoming.

**Module 33.12** Phytochrome is a light detector that may help set the biological clock.

- A. *Review:* The electromagnetic spectrum (Module 7.6).
- B. **Phytochrome** is a blue or bluish green protein that absorbs light. This protein has been found in all species of plants and algae examined to date, and seems to help these photosynthetic organisms stay synchronized with seasonal changes in light conditions. It may also help trigger certain seasonal responses such as seed germination and flowering.
- C. Phytochrome alternates between two forms that differ slightly in structure and wavelength of absorption, depending on which part of the spectrum has been most recently absorbed. Phytochrome is synthesized as  $P_r$ , and any  $P_{fr}$  that forms is converted to  $P_r$  in the dark.  $P_r$  is converted to  $P_{fr}$  at sunrise. A plant can measure photoperiod by keeping track of the sudden increase in  $P_{fr}$  (Figure 33.12B). By keeping track of the photoperiod, a plant can respond to the changes in the length of daylight as needed and thus flower, produce seed, and go dormant at the right time.
- D. This can be tested experimentally by exposing plants to brief flashes of red light (660 nm) or far-red light (730 nm). The wavelength of the last flash of light affects a plant's measurement of night length. In long-day plants (lower part of Figure 33.12), if the last flash is red light (signifying sunrise, and the shortened night), flowering is induced. In short-day plants (upper part of Figure 33.12), if the last flash is far-red light (signifying sunset, and the continued lengthening night), flowering is induced (Figure 33.12A).
- E. A phytochrome that absorbs blue light has been shown to regulate stomatal opening at daybreak and phototropism.

**Module 33.13** Talking About Science: Joanne Chory studies the effect of light and hormones in the model plant *Arabidopsis*.

- A. Dr. Chory is a professor of biology and a Howard Hughes Medical Institute Investigator at the Salk Institute for Biological Studies.
- B. She has used the small, fast-growing plant, *Arabidopsis*, to investigate the role of signal-transduction pathways and how light regulates plant development. Dr. Chory has discovered the role of steroid hormones (brassinosteroids) and identified the receptor to these hormones.
- C. The announcement in 2000 that the genome of *Arabidopsis* had been completely sequenced opened a new opportunity to investigate gene function. The information obtained from such research has led to improvements in agricultural practice.

### III. Plant Defenses

**Module 33.14** Defenses against herbivores and infectious microbes have evolved in plants.

- A. Plants have evolved several mechanisms to thwart **herbivores**, including physical defenses such as thorns and chemical defenses such as canavanine. Canavanine is

similar enough to arginine to be incorporated into herbivore proteins in place of arginine; it is different enough from arginine that the function of such a protein will be abnormal and will lead to the death of an insect herbivore. Some plants recruit predatory animals for protection from certain herbivores.

- B. The first line of defense against pathogens is the physical barrier provided by the epidermis (Module 31.6). Once infected, a plant will release microbe-killing chemicals and will make changes in their cell walls that will slow the spread of the pathogen.
- C. Plants and their pathogens also illustrate the results of coevolution. Plants have many *R* (resistance) genes and pathogens have *Avr* (*avirulence*) genes. It is thought that the products of these plant and pathogen genes are complementary, the result being that the area of the plant that is infected will be sealed off from the rest of the plant.
- D. Another component of the response at the site of infection is **systemic acquired resistance**. In this instance alarm hormones, one of which may be salicylic acid, are released at the site of infection. These hormones trigger signal-transduction pathways throughout the plant that result in the production of defensive chemicals.

**Module 33.15 Talking About Science:** Plant biochemist Eloy Rodriguez studies how animals use defensive chemicals made by plants.

- A. Dr. Rodriguez, a professor of plant biochemistry at Cornell University, is one of the world's leading authorities on defensive chemicals produced by plants. He is involved in a relatively new field of study called zoopharmacognosy, the study of how animals may medicate themselves with plants. Currently, Rodriguez's work focuses on the medicinal potential of rain forest plants.

*Preview:* The consequence of ecosystem destruction is the topic of Chapter 38.

- B. There are numerous examples of defensive chemicals produced by plants that are now commonly used by humans. For example, aspirin was originally derived from willow trees and helps plants fight off infections; and chilies contain a naturally occurring antibiotic.

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## Class Activities

1. Ask your students to try to find analogies between plant and animal hormones (Chapter 26) and plant and animal taxes (Chapter 37).
2. Plants have evolved various defenses against herbivores and pathogens, many of which have been coopted by humans (Module 33.15). Ask your students for examples of this as well as for speculation on the potential for future exploitation of plant defenses. Also, ask your students to consider plant defenses and animal/pathogen counters to these defenses in a coevolutionary sense.

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## Transparency Acetates

Chapter 33 Introduction Figure A: Chemical structures of human estrogen and a phytoestrogen

Figure 33.1B Phototropism in a grass seedling

Figure 33.1C Early experiments on phototropism: Detection of light by shoot tips and evidence for a chemical signal

Figure 33.1D Went's experiments: Isolation of the chemical signal (Layer 1)  
 Figure 33.1D Went's experiments: Isolation of the chemical signal (Layer 2)  
 Figure 33.1D Went's experiments: Isolation of the chemical signal (Layer 3)  
 Figure 33.1D Went's experiments: Isolation of the chemical signal (Layer 4)  
 Table 33.2 Hormones and functions  
 Figure 33.3B The effect of auxin concentration on cell elongation  
 Figure 33.3C A hypothesis to explain how auxins stimulate cell elongation  
 Figure 33.7B Abscission layer at the base of a leaf  
 Figure 33.11 Photoperiodic control of flowering  
 Figure 33.12A The reversible effects of red and far-red light  
 Figure 33.12B Interconversion of the two forms of phytochrome  
 Figure 33.14A Recruitment of a wasp in response to an herbivore  
 Figure 33.14B Defense responses against an avirulent pathogen  
 Thinking as a Scientist Question 3: Isoprene emissions and plants

## Media

See the beginning of this book for a complete description of all media available for instructors and students. Animations and videos are available in the Campbell Image Presentation Library. Media Activities and Thinking as a Scientist investigations are available on the student CD-ROM and web site.

### Animations and Videos

	File Name
Phototropism Video	33-01-PhototropismVideo-B.mov
Phototropism Video	33-01-PhototropismVideo-S.mov
Gravitropism Video	33-09A-GravitropismVideo-B.mov
Gravitropism Video	33-09A-GravitropismVideo-S.mov
<i>Mimosa</i> Leaf Video	33-09B-MimosaLeafVideo-B.mov
<i>Mimosa</i> Leaf Video	33-09B-MimosaLeafVideo-S.mov

### Activities and Thinking as a Scientist

	Module Number
Web/CD Thinking as a Scientist: <i>What Plant Hormones Affect Organ Formation?</i>	33.2
Web/CD Activity 33A: <i>Leaf Abscission</i>	33.7
Web/CD Activity 33B: <i>Flowering Lab</i>	33.12