

CHAPTER 41: HOW PLANTS GROW IN RESPONSE TO THEIR ENVIRONMENT

CHAPTER SYNOPSIS

Plants exhibit three primary kinds of tropism: phototropism, gravitropism, and thigmotropism. Phototropism is the bending of plants toward a unidirectional light source. Photomorphogenesis is light-triggered development, as occurs in seed germination. Plants perceive red light as a result of two forms of phytochrome, Pr and Pfr. Pr absorbs red light and is converted to active Pfr. Pfr responds to far red light and is converted to inactive Pr. Phytochrome is involved in such plant growth responses as seed germination and elongation of etiolated shoots. Gravitropism is a plant's response to gravity that causes stems to grow upward and roots to grow downward. The perception of gravity may be associated with the position and movement of amyloplasts in individual cells and is mediated primarily by auxins. Thigmotropism is the response of a plant to touch and is associated with the curling of tendrils and vines.

Many plants become dormant during adverse conditions. In temperate climates dormancy is associated with winter when water is frozen and unavailable to plants. Many trees drop their leaves, new buds remain dormant, perennials subsist as underground parts and annuals exist only as seeds. A great number of plants in seasonally dry areas are annuals, their seeds capable of surviving several dry seasons. These seeds germinate in response to sufficient water, the plants grow rapidly, flower, and produce new seeds before the drought conditions return.

Plant hormones are chemicals produced in minute quantities and transported to other locations where they elicit specific responses. Charles and Francis Darwin first observed the actions of auxins in the phototropic response of seedlings to light. Later experiments identified a chemical substance concentrated on the nonilluminated side of the seedling tip. This compound migrated from the light side to the dark side and had an elongating effect on the cells causing the tip to bend toward the light. The only naturally occurring auxin is indoleacetic acid (IAA), a compound synthesized from tryptophan. It is

produced in the shoot apex and diffuses downward to the base of the plant. It acts primarily by increasing the plasticity of young cell walls. Synthetic auxins are used as weed killers, to promote flowering and fruiting, and to prevent fruit drop.

Cytokinins promote cell division and differentiation of callus tissue in plant cell culture. They are chemically derived from adenine, produced in the roots, and transported throughout a plant. Antagonistic to auxins, they promote growth of lateral branches and inhibit formation of lateral roots. Gibberellins were first observed in abnormally tall plants infected with a fungus. They are produced in the apical regions of stems and roots. They promote internodal elongation and speed seed germination. Brassinosteroids have only recently been classified as plant hormones. They have a wide range of physiological effects, that include elongation, cell division, membrane polarization, stem bending, vascular and reproductive tissue development, and delayed senescence. Oligosaccharins have a variety of effects in plant tissues. One kind signals defense responses like the hypersensitive response (HR), another type inhibits auxin-stimulated elongation of pea stems.

Ethylene gas suppresses root and stem elongation and hastens fruit ripening. A variety of tomato has been developed that has an antisense strand of the gene needed for ethylene biosynthesis inserted into its genome. Translation is blocked which prevents the production of ethylene. These fruit are picked and shipped green and are later ripened through exposure to ethylene gas. Natural ethylene production is often increased after exposure to adverse conditions like toxic chemicals and ozone. Absciscic acid induces formation of winter buds, plays a role in seed dormancy, is antagonistic to gibberellins in germination, and controls the opening and closing of stomata. Its levels are greatly elevated with plant stress, particularly drought. Plant flowering is still not a simple response and

involves as phase change as plants develop reproductive maturity. Plants can be forced to revert to an earlier stage or juveniles can be experimentally induced to become adults. Flowering is either promoted or repressed by environmental signals, the most common of which is light. When days get shorter, in the late summer and early autumn, short-day plants produce flowers. Long-day plants flower when days get longer, during the spring and early summer. Day neutral plants flower regardless of day length and depend upon other environmental stimuli. The photoperiodic response is chemically moderated by several phytochromes and cryptochrome. Flowering also involves a temperature dependent pathway associated with vernalization. There is also an autonomous pathway that is probably independent of external cues other than basic nutrition. Much of

the recent research in flowering, including examination of the floral organ identity genes, utilizes *Arabidopsis* and snapdragons.

Plants must respond quickly to environmental changes like touch or the position of the sun. Many of these responses are associated with changes in turgor pressure at the leaf pulvinus. Plants also exhibit circadian cycles associated with the 24 hour day-night cycles on earth. They must respond to various kinds of invaders, from bacteria and fungi to parasitic plants to animal herbivores. Various pathways can trigger a hypersensitive response (HR) leading to cell death around the source of invasion and long-term resistance against the individual pathogen. They also exhibit a systemic acquired resistance (SAR) that allows them to respond more quickly to a subsequent attack.

CHAPTER OBJECTIVES

- ä Understand the chemical basis of the phototropic and photomorphogenic responses and how they are altered by light of various wavelengths.
- ä Describe the physical versus physiological basis of gravitropism.
- ä Understand the numerous kinds of movement exhibited by otherwise immobile plants.
- ä List the seven major types of plant hormones, their basic effects on plant tissues, and several of their commercial applications.
- ä Describe the chemical nature of the only naturally occurring plant auxin.
- ä Explain the physiological effects of auxin and 2,4-D 2 on monocot and dicot plants.
- ä Indicate which plant hormones affect fruit and flowers and the nature of these effects.
- ä Differentiate among short-day, long-day, and day neutral plants.
- ä Describe the three pathways leading to flower production.
- ä Describe the HR and SAR responses of plants to invaders and pathogens.

KEY TERMS

abscisic acid
acid growth hypothesis
auxin
competence
cytokinin
day neutral plant
determined
ethylene

etiolated
gibberellic acid (GA)
gibberellin
gravitropism
long-day plants
phase change
photoperiodic

phototropism
phytochrome
pulvinus
short-day plant
tropism
turgor movement
vernalization

CHAPTER OUTLINE

41.0 Introduction

I. PLANTS SENSE AND INTERACT WITH THEIR ENVIRONMENT

A. Plant Survival and Growth Influenced by Abiotic Factors

1. Includes water, wind, and light
2. Signals transduced to elicit physiological, growth, or developmental response
3. Hormones involved in internal signalling

B. Local Environment Accounts for Variation within a Species

fig 41.1

1. Regulated responses allow for plant survival
2. Determine when plant will flower

41.1 Plant growth is often guided by environmental cues

I. GROWTH RESPONSES

A. Plant Responses to Environmental Signals

1. Some growth patterns that are not very reversible
2. Tropisms are positive or negative patterns that usually come from only one direction
3. Nastic movements
 - a. Occur independently of direction of stimuli
 - b. Example: Coiling of pea plant tendril is always in one direction
4. Tropisms are directional
 - a. Compensate for plant's inability to walk away from unfavorable conditions
 - b. Contribute branching patterns found within a species
5. Three major classes
 - a. Phototropism
 - b. Gravitropism
 - c. Thigmotropism
6. Connect signals with perception, transduction, and altered growth response
7. Photomorphogenesis is a nondirectional response resulting in complex form changes

B. Phototropism and Photomorphogenesis

1. Phototropism is the bending of plants toward sources of light fig 41.2
 - a. Stems grow toward light and are positively phototropic
 - b. Roots are not responsive or slightly negatively phototropic
 - c. Stem response is adaptive so leaves capture greater amounts of light
 - d. Important in determining development of plant organs, appearance of plant
 - e. Most phototropic responses mediated by auxins
2. Photomorphogenesis is light triggered development, includes seed germination
3. Phototropic and photomorphogenic response mechanism
 - a. First step is perceiving the light
 - 1) Photoreceptors respond to different wavelengths
 - 2) Blue and red most common
 - b. Just beginning to understand how plants "see blue"
 - 1) Blue light receptors now being characterized
 - 2) Blue light signals many phototropic responses
 - 3) Red light generally signals photomorphogenesis
 - c. How plants "see red" is better understood
 - 1) Presence of two forms of pigment-containing protein called phytochrome
 - a) P_r absorbs red light and is converted to P_{fr}

- b) P_{fr} absorbs far-red light and is converted to P_r
 - c) P_{fr} is biologically active, P_r is biologically inactive
 - d) When P_{fr} is present, reaction affected by phytochrome will occur
 - e) If P_{fr} replaced by P_r reaction will not occur fig 41.3
 - 2) Structure of phytochrome
 - a) Composed of small light sensitive part and larger protein part
 - b) Protein initiates signal transduction that leads to particular tropism
 - c) Found in all plants, some green algae
 - d) Not found in bacteria, fungi, or protists
 - e) May have evolved in green algae, present in common ancestor of plants
 - 4. Phytochrome involved in many plant growth responses
 - a. Seed germination inhibited by far-red light, stimulated by red light
 - 1) Chlorophyll absorbs red, but not far-red light
 - 2) Light passing through leaves inhibits seed germination
 - 3) Seeds under deciduous plants more likely to germinate in spring
 - 4) When leaves decompose, plants exposed to direct sunlight
 - b. Elongation of shoots in etiolated seedlings
 - 1) Seedlings are pale and slender from being kept in the dark
 - a) Plants become normal when exposed to light, especially red light
 - b) Linked with brassinosteroid hormones
 - 2) Etiolation is an energy conservation strategy
 - a) Shoot grows, but doesn't become green unless light is present
 - b) All energy put into elongating to reach sun
 - 3) De-etiolated *Arabidopsis* mutant *det2* has poor etiolation response
 - a) Lacks elongated internodes, greens in dark
 - b) Are defective in enzyme needed for brassinosteroid biosynthesis
 - c) Brassinosteroids play role in phytochrome response
 - c. Red and far-red light involved in plant spacing signals
 - 1) Plants grown close will grow tall to outcompete others for sunlight
 - 2) Plants measure far-red light bounced back from neighbors
- C. Gravitropism
- 1. Shoot of a tipped plant will grow upward
 - 2. Response is to gravitational field of earth fig 41.1,4
 - 3. Must separate phototropic and gravitropic effects
 - 4. At germination causes roots to grow downward and shoots upward
 - a. Shoot has negative response, root has positive response
 - b. Studied responses in gravity-free environment of space shuttle
 - c. Auxins play primary, but not sole role
 - 5. Four steps lead to gravitropic response
 - a. Gravity perceived by cell
 - b. Signals for in that cell
 - c. Signal transduced intra- and intercellularly
 - d. Differential cell elongation occurs
 - 6. Perception of gravity may be associated with amyloplasts
 - a. Amyloplasts sink in direction of gravity and may interact with cytoskeleton
 - b. Net effect to have greater concentration of auxin on lower side of stem
 - c. More auxin on lower side causes these cells to elongate, stem bends upwards
 - d. A negative gravitropic response results
 - 7. Hormone concentration gradient not well documented in roots
 - a. Upper sides of horizontal roots grow more rapidly than lower sides
 - b. Root ultimately grows downward, a positive gravitropism
 - 8. Location of gravity sensing cells
 - a. In shoots, cells are in endoderm

- 1) Discovered by studying *Arabidopsis* scarecrow and short root mutants
- 2) Endodermal cells are sites of amyloplasts
- b. In roots, cells are located in root cap
 - 1) Cells that grow asymmetrically are in distal elongation zone close to root cap
 - 2) Auxin may be involved in transfer of signal
 - 3) Response still occurs when auxin transport is suppressed
 - 4) Electrical signalling involving membrane polarization may occur
9. Roots of plants in tropical rain forests often grow upward on other plants
 - a. Soil is very nutrient poor
 - b. Precipitation is more reliable source of nutrients
 - c. Sensitivity of roots to auxin may be reduced in tropical plants

D. Thigmotropism

1. Response of plants to touch
 - a. Specialized cells of tendril perceive contact
 - b. Promote uneven growth
 - c. Causes curling around object, often within 3 to 10 minutes
2. Coiling of tendrils is associated with auxin and ethylene
3. *Arabidopsis* is a valuable model system
 - a. Certain gene is expressed in 100 fold higher levels after touch
 - b. Promising aid to research in touch responses

fig 41.5

E. Other Tropisms

1. Electrotropism is a response to electricity
2. Chemotropism is a response to chemicals
3. Traumatropism a response to wounding
4. Thermotropism is a response to temperature
5. Aerotropism is a response to oxygen
6. Skototropism is a response to dark
7. Geomagnetotropism is a response to magnetic fields
8. Hydrotropism is not a true response, although roots do grow toward water

II. DORMANCY

A. Provides Survival Advantage in Harsh Climates

1. Includes seed dormancy
2. Termination signals include temperature, water, and light

B. Temperate Climates

1. Associate dormancy with winter
2. Low temperatures and unavailability of water prevent growth
 - a. Tree buds of deciduous trees and shrubs are dormant
 - b. Perennials reduced to underground parts
 - c. Other plants like most annuals exist as only seeds

C. Seasonally Dry Climates

1. Dormancy occurs during dry season, often during summer
2. Rainfall triggers germination
3. Plants in regions of severe drought are often annuals
 - a. Seeds easily survive dry season
 - b. Germinate with rain, grow rapidly
4. Seeds are capable of surviving indeterminate dry seasons
 - a. Seeds may contain chemicals that must leach out with sufficient water
 - b. Rapidly germinate, grow, and flower when water becomes available

fig 41.6

D. Dormancy Can Last Very Long

1. Seeds remain viable for long periods of time, especially legumes
2. Bud, underground stem and root, and seed dormancy released by environmental changes
 - a. Varies by species
 - b. Some weed seeds germinate in cooler temperature, inhibited by warmth
3. Day-length differences near equator and in temperate regions effect dormancy
 - a. Tree dormancy common in temperate climates when days are short
 - b. Unusual in tropical trees near the equator

41.2 The hormones that guide growth are keyed to the environment

I. PLANT HORMONES

A. Internal Signalling Pathways Utilize Plant Hormones

1. Involved in responses to the environment
2. Associated with internally regulated development

B. Chemical Nature of Hormones

1. Chemical substances produced in small quantities in one location
2. Transported to another location to effect physiological or developmental response
3. Response can be stimulatory or inhibitory fig 41.7
4. Animal hormones produced at definite sites, organs of hormone production
5. Plant hormones not produced in such specialized tissues
6. Seven major kinds of plant hormones tbl 41.1
 - a. Auxin
 - b. Cytokinins
 - c. Gibberellins
 - d. Brassinosteroids
 - e. Oligosaccharins
 - f. Ethylene
 - g. Absciscic acid

II. AUXIN

A. Basic Effects of Auxins

1. First plant hormone discovered
2. Increases plasticity of plant cell walls and involved in stem elongation
3. Cells enlarge in response to changes in turgor pressure

B. Discovery of Auxin

1. Experiments by Charles and Francis Darwin
 - a. Observed phototropism: Bending of seedlings toward light
 - b. Response occurred if tip of seedling covered with glass tube
 - c. Response prevented in seedling tips covered with foil fig 41.8
 - d. Response occurred if stem below tip covered with opaque collar
 - e. Conclusion
 - 1) Substance produced in response to light was transmitted downward
 - 2) Caused shoot to bend toward the light
2. Experiments by Boysen-Jensen and Paal
 - a. Identified substance as a chemical
 - b. Normal response if tip separated from shoot by agar block
 - c. In darkness or normal illumination
 - 1) Chemical passed down shoot evenly on all sides
 - 2) Thus no bending occurred

3. Experiments by Went fig 41.9
 - a. Cut tips from illuminated seedlings, placed them on agar
 - b. Cut tips from seedlings grown in the dark
 - c. Placed tiny agar blocks off-center on tipless seedlings grown in dark
 - d. Seedlings bent away from side on which block was placed
 - e. Conclusion: Substance diffused from agar, enhanced cell elongation
 - f. Named substance auxin from Greek "to increase"
 4. Dark side of seedling has more auxin, its cells elongate more, which bends the seedling
- C. The Effects of Auxin
1. Auxin acts to adapt plant to its environment in advantageous way
 - a. Promotes growth and elongation, facilitates plant's response to environment
 - b. Environmental signals directly influence distribution of auxin in plant
 - c. May exert this influence in several ways
 - 1) Light might destroy auxin
 - 2) Light may decrease cells' sensitivity to auxin
 - 3) Light might cause auxin to migrate away from light into shaded part of shoot
 - d. Last possibility is the actual mode of influence
 2. Experiments by Briggs fig 41.11
 - a. Vertical sheet of transparent mica separated light and dark sides of the tip
 - b. No bending, same amount of auxin on both sides of barrier
 - c. Conclusion: Auxin migrates laterally from light side to dark side
 3. Auxins promote a variety of responses
 - a. Promotes activity of vascular cambium and vascular tissues
 - b. Are present in large quantity in pollen
 - c. Play key role in development of fruit, use synthetic auxins for same purpose
 - 1) Fruits do not develop properly without fertilization and presence of seeds
 - 2) Will form if auxins are applied
 - 3) Pollination may trigger auxin release in some species
 - 4) Leads to fruit development beginning before fertilization
- D. How Auxins Work
1. Chemical nature of auxin
 - a. Only naturally occurring compound is indoleacetic acid (IAA) fig 41.12
 - b. Resembles and is probably synthesized from tryptophan
 2. Multiple auxin perception sites may exist
 - a. Unlike animal hormones
 - b. Specific signal not sent to specific cells
 3. Of plant hormones, auxin alone is transported towards base of plant
 - a. Two gene families in *Arabidopsis* involved in auxin transport
 - 1) One protein involved in top to bottom transport
 - 2) Two proteins in root tip regulate growth response to gravity
 4. Downstream effect of auxin : Increases plasticity of cell wall
 - a. Works only in young cells lacking extensive secondary wall formation
 - b. More plastic wall stretches more as protoplast swells with cell growth
 - c. Called acid growth hypothesis, occurs with presence of auxin fig 41.13
 - 1) Responsive cells actively transport cytoplasmic H^+ into cell wall space
 - 2) Decreases pH, enzymes that break bonds between cell wall fibers activated
 - 3) Buffers that prevent acidification block cell wall expansion
 - 4) Other H^+ releasing compounds cause similar cell expansion
 - 5) Movement of H^+ seen in response to auxin treatment
 - 6) Results in rapid growth response to an environmental signal

5. Synthetic auxins
 - a. Examples: Naphthalene acetic acid (NAA) and indolebutyric acid (IBA)
 - b. Primarily used to prevent abscission, separation of organ from plant
 - c. Commercial applications
 - 1) Prevent fruit drop
 - 2) Promote flowering and fruiting in pineapples
 - 3) Induce formation of roots on cuttings
 - 4) Herbicides to control weeds: 2,4-D fig 41.12c
 - a) Selectively eliminates broad-leaved dicots
 - b) Stems of dicot weeds halt axial growth
 - 5) Herbicide 2,4,5-T used as broad spectrum herbicide
 - a) Defoliant Agent Orange during Vietnam War
 - b) Contaminated with dioxin, a toxic by-product
 - c) Dioxin produces serious diseases, birth defects, death

III. CYTOKININS

A. Actions of Cytokinins

1. Promote differentiation of organs in masses of cultured plant tissue
 - a. Induces parenchyma cells to become meristematic
 - b. Induce differentiation of cork cambium
 - c. Cytokinins in coconut milk promotes organ differentiation
 - d. Causes differentiation of callus tissue in plant tissue culture
2. Mechanism of action
 - a. When combined with auxin, cell division stimulated and differentiation induced
 - b. Mostly produced in roots and transported throughout plant, also by fruit
 - 1) Cause formation of vegetative buds on moss gametophyte
 - 2) Regulate growth patterns in concert with other hormones

B. Formation of Cytokinins

1. Purines that are chemically derived from or related to adenine fig 41.14
2. Other similarly acting chemicals exist, but are not produced naturally
3. Act opposite of auxin
 - a. Promote growth of lateral buds into branches fig 41.15
 - b. Inhibit formation of lateral roots
 - c. In balance with auxin, determines form of plant
 - d. Prevents yellowing of leaves detached from plant, anti-aging hormones
4. Action studied in terms of effects on masses of tissues grown in culture
 - a. Tissue formed dependent on relative amounts of auxin and cytokinin fig 41.16
 - b. Coconut needed for early experiments contains cytokinins
 - c. Appear to be necessary for mitosis and cell division
 - d. Promote synthesis or activation of proteins needed for mitosis
5. Pathogens use cytokinins against plants
 - a. *Agrobacterium* introduces genes to increase rate of cytokinin production
 - b. Causes cell division and formation of crown gall tumor fig 41.17

IV. GIBBERELLINS

A. Discovery of Gibberellin

1. Named for fungus that causes "foolish seedling" disease in rice
 - a. Isolated from fungal filtrate
 - b. Causes infected plant to grow abnormally tall
2. Large class of chemicals additionally found in normal plants
 - a. Acidic compounds abbreviated GA, for gibberellic acid

- b. Subscripts added to distinguish individual compounds
 - 3. Also functions as pheromone in ferns
 - a. Gibberellin-like compounds released from one gametophyte
 - b. Triggers development of male reproductive structures on neighbor
- B. Mode of Action
 - 1. Synthesized in apical portions of stems and roots
 - 2. Promotes internodal elongation
 - a. Enhanced by auxin
 - b. Restored normal growth to certain dwarf plant mutants fig 41.18
 - c. Two kinds of dwarf mutants
 - 1) Some produce insufficient amounts of hormone, respond to GA application
 - 2) Others lack ability to perceive hormone
 - 3. Biosynthetic pathway studied in gibberellin-deficient corn mutants
 - a. Many gibberellins are intermediates in formation of GA₁
 - b. Different forms may have specific biological roles
 - 4. Gibberellins stimulate hydrolytic enzyme production in germinating grain seed
 - a. Transcription of the genes encoding enzymes must be regulated somehow
 - b. GA enhances DNA binding proteins, allows DNA transcription of a gene
 - c. Occurs when radicle has grown through seed coats
 - 5. Affects other aspects of plant growth and development
 - a. May hasten seed germination, substitutes for requirements of cold or light
 - b. Used to space grape flowers to give fruit more growing room fig 41.19

V. BRASSINOSTEROIDS AND OLIGOSACCHARINS

- A. Brassinosteroids
 - 1. Known of chemical for 30 years, only recently classified as plant hormone
 - a. First discovered in *Brassica* pollen
 - b. Functional overlap with other plant hormones
 - c. Additive effects among it and auxins and gibberellins
 - 2. Knowledge base broadened with application of molecular genetics fig 41.20
 - a. Share similarities with animal steroid hormones
 - b. Found in algae, common in many plants
 - c. May have evolved before plant-animal split
 - 3. Have wide range of physiological effects
 - a. Include elongation, cell division, bending of stems, development of vascular tissue
 - b. Also delayed senescence, membrane polarization, reproductive development
 - 4. Actions can be triggered by environmental signals
 - 5. Have found mutants that alter response to brassinosteroids
- B. Oligosaccharins
 - 1. Plant cell walls composed of cellulose and complex oligosaccharides
 - a. Oligosaccharins function as signalling molecules, not just structural components
 - b. Released from cell wall by enzymes secreted by pathogens
 - 2. Functions of oligosaccharins
 - a. Some signal defense responses like HR (hypersensitive response)
 - b. Another inhibits auxin-stimulated elongation of pea stems
 - c. Molecular activity 1 to 2 times greater than other hormones
 - d. Affect phenotype of regenerated tobacco tissue
 - 1) Inhibit root formation
 - 2) Stimulate flower production in appropriate tissues

VI. ETHYLENE

A. Action of Ethylene

1. Initial observation of ethylene gas from street lamps inducing defoliation
2. Natural plant byproduct that interacts with other plant hormones
 - a. Suppresses lateral bud formation when combined with auxin
 - b. Suppresses stem and root elongation
3. Ethylene receptor has been identified and characterized
 - a. Evolved early in evolution of photosynthetic organisms
 - b. Shares features with bacterial environmental-sensing proteins
4. Plays major role in development of fruit
 - a. Auxins from pollen and developing fruit stimulate ethylene production
 - b. Further hastens fruit ripening
 - c. Complex carbohydrates broken down into simple sugars
 - d. Chlorophylls broken down, cell walls become soft
 - e. Volatile chemicals produced, associated with flavor and scent of ripe fruit
5. Recognition of ethylene as plant hormone associated with premature ripening
 - a. Bananas ripened early in presence of oranges
 - b. Lead to commercial uses of ethylene
 - 1) Tomatoes picked green, artificially ripened with ethylene
 - 2) Speed ripening of oranges, limes
 - 3) Carbon dioxide has opposite effect, fruit shipped in CO₂ atmosphere
 - c. Development of biotechnology solution fig 41.21
 - 1) Cloned one gene needed for ethylene biosynthesis
 - 2) Antisense copy placed in tomato genome
 - 3) Both sense and antisense sequences transcribed in transgenic tomato
 - 4) Strands of mRNA pair with each other, blocking translation
 - 5) Prevents synthesis of ethylene, halts tomato ripening
 - 6) Green tomatoes readily shipped, later exposed to ethylene to ripen

B. Ecological Role

1. Ethylene production increased after exposure to adverse conditions
 - a. Includes exposure to ozone and toxic chemicals
 - b. Includes temperature extremes, drought, attack by pathogens and herbivores
2. Can accelerate loss of leaves or fruit damaged by stresses
3. Damage from exposure to ozone due to ethylene production
4. Produced by plants attacked by herbivores
 - a. May signal activation of plants' defense mechanisms
 - b. May include production of molecules toxic to pests

VII. ABSCISIC ACID

A. Discovery of Absciscic Acid

1. Synthesized primarily in mature green leaves, fruit, and root caps
 - a. Application seemed to stimulate fruit abscission in cotton
 - b. Little evidence it plays an important role in this process
2. Aging effects due to ethylene

B. Actions of Absciscic Acid

1. Application on leaves causes yellow spots (opposite effect as cytokinins)
2. May induce formation of dormant winter buds
3. Followed by conversion of leaf primordia into bud scales fig 41.22a
4. Suppresses growth of dormant lateral buds, along with ethylene
 - a. Counters effects of gibberellins

- b. Promotes senescence by countering auxin
- 5. Plays role in dormancy of seeds, antagonistic to gibberellins during germination
- 6. Helps control opening and closing of stomata fig 41.22b
- 7. Occurs in all groups of plants, evolved early in history of plants
- 8. Physiological effects are extremely rapid
 - a. Partly independent of gene expression
 - b. Long term effects involve regulation of gene expression
- 9. Levels become greatly elevated with plant stress, particularly drought

41.3 The environment influences flowering

I. PLANTS UNDERGO METAMORPHOSIS

A. Overview of Initiating Flowering

- 1. Flower production is a carefully regulated process
 - a. Plants must gain competence to respond to internal or external signals
 - b. Competent flowers respond to a combination of factors fig 41.23
 - 1) Include light and temperature
 - 2) Signals are both promotive and inhibitory
 - c. Signals turn on genes to specify location of floral parts
- 2. Second developmental cascade leads to 3-D construction of flower parts

B. Phase Change

- 1. Plants must develop reproductive maturity, just like animals
 - a. Animals undergo metamorphosis from juvenile to adult
 - b. Plants undergo similar metamorphosis, adding on structures at meristems
 - c. Most plants incapable of flowering at germination
- 2. Transition to competence called phase change
 - a. Can be obvious or subtle
 - b. Example: Observe an oak tree in winter fig 41.21a
 - 1) Leaves cling to lower branches, upper branches bare
 - 2) Lower branches initiated by juvenile meristem
 - a) Do not respond to environmental cues to drop leaves
 - b) Branches are young and have not made phase change
 - c. Example: Ivy fig 41.21b
 - 1) Juvenile meristem stem tissue can produce adventitious roots
 - 2) Upper branches transition to adult phase, no adventitious roots
- 3. Even though phase change has occurred, other factors needed to initiate flowering
- 4. Plants can be forced to revert to earlier stage
 - a. Apply gibberellin or prune severely
 - b. Repression of flowering may be controlled genetically fig 41.25
 - 1) *Arabidopsis* mutant *embryonic flower* flowers almost immediately
 - 2) Suggests that wild-type allele suppresses flowering
 - 3) Flowering may be default state, mechanisms evolved to delay it
 - 4) Delay allows plant to store more energy for reproduction
- 5. Juvenile to adult transition can be induced experimentally
 - a. *LEAFY* gene cloned in *Arabidopsis*
 - b. Promotor replaced with viral promotor
 - c. Causes high levels of *LEAFY* transcription
 - d. Gene then introduced into cultured aspen cells, used to regenerate plants
 - e. Overexpression of *LEAFY* caused aspen to flower in weeks, not years fig 41.26
- 6. Phase change requires both signal and ability to perceive signal
 - a. Some plants acquire competence to perceive signal
 - b. Other plants do so to produce promotive signals or decrease inhibitory signals

II. PATHWAYS LEADING TO FLOWER PRODUCTION

A. Flowering Promoted or Repressed by Environmental Signals

1. Have identified three genetically regulated pathways to flowering
 - a. Light dependent pathway
 - b. Temperature dependent pathway
 - c. Autonomous pathway
2. Light can promote, repress, or have a neutral effect on flowering
3. Light as a signal
 - a. May indicate favorable conditions of long, summer days in temperate climates
 - b. May be needed to accumulate sufficient amounts of sucrose, flowering is independent
4. Temperature may be a signal
 - a. Importance of gibberellins in vernalization pathway
 - b. Reproductive success unlikely in middle of blizzard
5. Regulation probably arose first in constant tropical environments
 - a. Daylength and temperature controls evolved as temperate zones were colonized
 - b. May rely on one pathway, but all three may be present
 - c. Redundancy of pathways ensures formation of a new generation

B. Light Dependent Pathway

1. Flowering requires substantial energy derived from photosynthesis
2. Photoperiodic pathway depends on light to support flowering
 - a. Most plants keyed to changes in proportion of light to dark in 24-hour cycle
 - b. Mechanism to respond to seasonal changes in relative length of day and night
 - 1) Day length changes with seasons
 - 2) Variation greater farther from the equator
3. Three categories of response associated with day length
 - a. Short-day plants flower when days get shorter than critical length fig 41.27
 - b. Long-day plants flower when days get longer than critical length
 - c. Day-neutral plants
 - 1) Produce flowers regardless of day length, as long as enough light received
 - a) Some grasses have two critical photoperiods
 - b) Respond to various segments of day length
 - c) Will not flower if day too long or too short
 - 2) Speed of flowering may be associated with length of day
 - d. Facultative long- or short-day plants rely on other pathways as well
 - 1) Example: Garden pea is facultative long-day plant
 - 2) Significant stimulus is length of darkness not length of day
 - a) Light cue is associated with abiotic environmental conditions
 - b) Also associated with presence of pollinators, competition from other plants
 - 3) Long-day plants
 - a) Bloom in spring and early summer
 - b) Include clover, iris, lettuce, spinach, hollyhocks
 - 4) Short day plants
 - a) Bloom in late summer and autumn
 - b) Include chrysanthemums, goldenrods, poinsettias, soybeans, many weeds
 - e. Light artificially controlled to force plants to flower out of season fig 41.28
 - f. Helps control distribution of plants
4. The chemical basis of the photoperiodic response
 - a. Photoperiod perceived by several phytochromes and cryptochrome
 - b. Conformational change occurs in a light receptor molecule
 - 1) Triggers cascade of events that ends in flower production
 - 2) Link between light and circadian rhythm of plant's internal clock
 - 3) Control mechanisms are complex

- c. Example: *Arabidopsis*, a facultative long day plant
 - 1) Flowers in response to far-red and blue light
 - 2) Red light inhibits flowering
 - 3) *CONSTANS* (*CO*) gene expressed under long days, not short days
 - a) Loss of *CO* product has no effect when plant flowers under short days
 - b) Delays flowering under long days
 - 4) Gene is positively regulated by cryptochrome
 - a) Perceives blue light under long days
 - b) Inhibits inhibition of flowering by phytochrome B exposed to red light
 - 5) Flowering is promoted by repressing a gene that represses flowering
 - a) *CO* turns on other genes that result in expression of *LEAFY*
 - b) *LEAFY* tells meristem to switch to flowering
 - 5. The flowering hormone: Does it exist?
 - a. Considerable amount of evidence gathered over 50 years
 - 1) Some substances promote flowering
 - 2) Other substances inhibit flowering
 - b. Substances move from leaves to shoots in grafting experiments
 - c. Search made difficult, existence strictly hypothetical
 - 1) *LEAFY* is expressed in vegetative and reproductive parts
 - 2) Day length data gathered by leaves is transmitted to shoot apices
 - 3) Several signals may facilitate communication between leaves and shoots
 - 4) Roots can also inhibit flowering
- C. Temperature Dependent Pathway
- 1. The problem of winter wheat seed rotting in ground over winter in Russia
 - a. Chill seeds (vernalization) and plant in spring
 - b. Winter wheat requires vernalization for flowering to occur
 - c. Lysenko wrongly concluded that such treatment converted one species to another
 - 1) Changed winter wheat to spring wheat by altering environment
 - 2) Damaged genetic studies in Russia for 50 years
 - d. Link to temperature ensures plant will flower at optimal time
 - 2. Vernalization may also be necessary at later developmental stages
 - a. Is a separate flowering pathway linked to gibberellin
 - b. Repression of repression may also lead to flowering
 - 1) High levels of a gene product may block promotion of flowering by gibberellins
 - 2) Less product made when plants are chilled, may increase gibberellin activity
 - 3) Gibberellins enhance expression of *LEAFY*
 - 4) Gibberellin binds promoter of *LEAFY*, effect on flowering is direct
- D. Autonomous Pathway
- 1. Independent of external cues other than basic nutrition
 - 2. Probably the first pathway to evolve
 - 3. Day-neutral plant depend on this pathway
 - a. Plants “count” and “remember” fig 41.29
 - 1) Tobacco produce a uniform number of nodes before flowering
 - 2) Remove shoots at different positions
 - 3) Axillary buds grow, produce same number of nodes as removed portion
 - b. Shoots become committed or determined to flower fig 41.30
 - 1) Upper axillary buds of tobacco remember position when rooted or grafted
 - 2) Terminal shoot tip florally determined 4 nodes before initiating a flower
 - 4. Remembering position may be associated with signals from roots fig 41.31
 - a. Flowering delayed if plants grown in bottomless pots
 - b. Plant forms adventitious roots

5. Floral determination and molecular changes in *Arabidopsis*
 - a. Floral determination correlates with increase of *LEAFY* gene expression
 - b. Occurs by the time *APETALA1* is expressed
6. All three pathways converge with increased levels of *LEAFY*

III. IDENTITY GENES AND THE FORMATION OF FLORAL MERISTEMS AND FLORAL ORGANS

- A. Study Model Systems to Identify Flowering Genes and Their Interactions
 1. Use *Arabidopsis* and snapdragon
 2. Three pathways lead to adult meristem becoming a floral meristem
 - a. Either activate or repress inhibition of floral meristem identity genes fig 41.32
 - b. Key genes are *LEAFY* and *APETALA1*
 - 1) Establish meristem as flower meristem
 - 2) Then turn on floral organ identity genes
 3. Floral organ identity genes define 4 concentric whorls
 - a. Moving inwardly, are sepal, petal, stamen, and carpel
 - b. ABC model explains how 3 classes of genes can specify 4 organ types fig 41.33
 - 1) Class A genes alone specify sepals
 - 2) Class A + B genes specify petals
 - 3) Class B + C genes specify stamens
 - 4) Class C genes alone specify carpels
 - c. Model is entirely testable via floral organ identity mutants
 - 1) Each class expressed in 2 whorls, yields 4 combinations of gene products
 - 2) If class is missing aberrant organs are produced in predictable positions
 4. This only explains the beginning to making a flower
 - a. More genes turned on to give rise to 3-D flower
 - b. Certain genes “paint” petals
 - 1) Biochemical pathways lead to accumulation of anthocyanin pigments
 - 2) Pigments may be orange, red, or purple; color influenced by pH
- B. The Formation of Gametes
 1. Ovule in the carpel has evolutionary history older than angiosperms
 - a. Floral parts are modified leaves
 - b. Female gametophyte is within ovule
 - c. Next generation develops from placental tissue in ovary
 - d. Megaspore mother cell develops, gives rise to embryo sac via meiosis
 - e. Two layers of integument form around embryo sac and become seed coat
 - 1) Genes identified for initiation of integuments
 - 2) Also know genes responsible for formation of integuments
 - 3) Some also affect leaf structure
 2. Shift from mitosis to meiosis in megaspore mother cell is critical
 - a. Leads to development of haploid, gamete-producing gametophyte
 - b. Similar event associated with pollen formation in anther
 3. Flower houses haploid generations that produce gametes
 4. Also increases probability that gametes will unite

41.4 Many short-term responses to the environment do not require growth

I. PLANTS EXPOSED TO STRESS MUST RESPOND QUICKLY

- A. Evoke a Variety of Responses
 1. Growth is too slow to elicit a proper reaction
 2. Environmental cues trigger rapid and reversible plant responses
 - a. Rapid leaf folding to startle predator

- b. Leaf folding to reduce water loss by transpiration
 - 3. Some movements result from unpredictable signals
 - 4. Other movements are tied to daily internal rhythms
- B. Signaling May be Electrical in Nature
- 1. Plants lack conventional nervous system
 - 2. Electrical charge may cause wave of membrane ion exchange
 - 3. Translated into movement by changes in cell turgor pressure

II. TURGOR MOVEMENTS

- A. Movement Via Reversible Turgor Pressure Changes in Specific Cells
- 1. Water leaving cells may cause them to collapse
 - 2. Water entering limp cells may cause them to become turgid
- B. Types of Movements
- 1. Movement in response to touch
 - a. Associated with rapid turgor pressure changes in pulvinus
 - 1) Multicellular swellings at base of leaf or leaflet
 - 2) Causes immediate change in leaf position
 - b. Example: Touch sensitive plants like *Mimosa* fig 41.22
 - c. Stimulus generates electrical signal
 - d. Electric signal changed to chemical signal
 - e. Potassium ions and water migrate from one half of pulvinus to other
 - f. Loss of turgor causes leaf to fold within a second or two
 - g. In 15 to 30 minutes, water flows back and leaf returns to original position
 - 2. Leaves of some plants track the sun
 - a. Blades held at right angles to sun
 - b. Cause for orientation largely unknown, movement maximizes photosynthesis
 - 3. Daily changes in position of flowers and leaves
 - a. Seen in flowers that “open” during the day and “close” at night
 - b. Orientation of leaves and petals change due to turgor movements
 - c. Bean plant leaves are horizontal in day, vertical at night fig 41.21
 - 1) Reduces water loss from transpiration at night
 - 2) Maximizes photosynthetic surface area during day
 - d. Movement tied to internal rhythm
- C. Circadian Clocks
- 1. Plants have endogenous clocks with a period of nearly 24 hours
 - 2. Cycles are common due to day-night cycles on earth
 - 3. First studied in sensitive plant by de Mairan in 1729
 - a. Closes leaves and leaflets at night
 - b. Plants retained cycle even in continued darkness
 - 4. Cycle continues to run in absence of external inputs
 - a. Can be reset or entrained
 - b. Can compensate for differences in temperature
 - 5. Circadian clocks have evolved independently in many organisms

III. PLANT DEFENSE RESPONSES

- A. Interactions Exist between Plants and Other Organisms
- 1. May be symbiotic or pathogenic
 - 2. Result from coevolution of species that signal and respond to each other
 - 3. Occur at level of surface barriers, respond at cellular level

B. Recognizing the Invader

1. Gene-for-gene model
 - a. Proposition of plant resistance gene (*R*) in 1950s
 - b. Product interacts with pathogen avirulence gene (*avr*)
 - c. Several pairs of *avr* and *R* genes cloned in different species
2. Agronomic application to insert genes in plants to protect them from invaders
3. Elucidation of signal transduction pathways associated with *R* gene fig 41.36
 - a. Pathways lead to triggering of hypersensitive response (HR)
 - b. Leads to rapid cell death around source of invasion
 - c. Also leads to longer term resistance
4. Response is not always gene-for-gene
 - a. Plants still have defensive responses to pathogens and mechanical wounding
 - b. Some response pathways are similar
 - c. May be associated with oligosaccharins
5. Parasitic plants also attack other plants
 - a. Specific molecules are released from root hairs of the host
 - b. Parasite recognizes these and responds with an invasive action
 - c. Less is known about the host response
 - d. Different defense genes are activated, appear to be ineffective

C. Responding to the Invader

1. In some cases there is a direct gene-for-gene recognition
 - a. HR response leads to rapid cell death around site of attack
 - b. Seals off wounded tissue to prevent spread of pathogen or pest
 - c. Cells produce hydrogen peroxide and nitric oxide
 - 1) May signal cascade resulting in localized death of host cells
 - 2) May have negative effects on pathogen
 - 3) Pathogen may have coevolved antioxidant abilities
 - d. Produce other antimicrobial agents
 - e. Express a variety of pathogenesis-related (*PR*) genes
 - 1) Proteins can function as antimicrobial agents
 - 2) May signal for other events to protect the plant
2. Virulent invaders produce no *R* gene recognition
 - a. Local cell walls affect changes to partly block movement of invader into plant
 - b. No HR response occurs, cells are not suicidal
3. Defense responses to herbivores
 - a. Example: Insect taking a bite out of a leaf
 - b. Mechanical damage causes similar, but slower responses
 - c. Called wound response
 - 1) Common response to cutting plant tissue
 - 2) Must carefully design controlled experiments to negate response to wounding

D. Preparing for Future Attacks

1. Plants also elicit a systemic response to a pathogen or pest attack
 - a. Called a systemic acquired resistance (SAR)
 - b. Several pathways lead to broad-ranging resistance lasting days
 - c. SAR induced by salicylic acid (aspirin) and jasmonic acid
 - d. Allows plant to respond more quickly with next attack
2. Reaction is not the same as human immune response
 - a. In humans, antibodies (proteins) recognize specific antigens (foreign proteins)
 - b. SAR is not so specific nor long lasting

INSTRUCTIONAL STRATEGY

PRESENTATION ASSISTANCE:

Growth is the only means plants have to move (other than human interference and seed production). A plant can't uproot itself to go to water or to light, but it can send out branches or roots. Speculate on other sessile forms of life that respond in a similar manner.

Researchers at U of C San Diego have identified a set of genes (*SEP*) that appear to regulate the transformation of leaves into petals. Genes *ABC* plus *SEP* contain everything needed to induce blooming in a reengineered *Arabidopsis* plant. (*Discover*, May 2001, page 12)

Many of the herbicides that have been outlawed in the U.S. are still being produced here and sold to third world countries. Discuss the ethical and environmental implications of this issue.

In case your students don't realize it, the subscript in P_r should be associated with the red light that it absorbs. Similarly, the fr of P_{fr} should be associated with far-red.

Explain why day length rather than temperature or moisture is a better indicator of the seasons (for animals too!). Discuss the methods used to initiate flowering at certain seasons. Easter lilies do not bloom in early March without being forced by altering light and temperature. Certain succulents are similarly forced and produce blooms at Easter, Thanksgiving, or Christmas. Many temperate plants will not bloom when grown in southern climates, including lilacs, forsythia, and gladiolus. These all require exposure to cold for a certain period. (But farther north than the Appalachians gladiolus will freeze if left in the ground over winter.) In addition, most varieties of apples do not flower or fruit when grown beyond certain latitudes.

Relate seed dormancy to the various animals that produce hard-walled eggs resistant to adverse conditions, like drought and cold. Compare plant dormancy to animal estivation and hibernation.

VISUAL RESOURCES:

Bring in examples of cloned plants at different stages. If these are not normally available, plants or cloning kits can be ordered from several biological supply companies at a relatively low cost. Also bring in examples of cuttings with developing roots, sprouting rhizomes or stems of various dracaenas and kalanchoe leaves with

tiny plantlets at the edges. With large classes it may suffice to have photographs of these materials or have the real thing available in the laboratory session.

Bring in examples or photographs of plants treated with various hormones and weed killers.