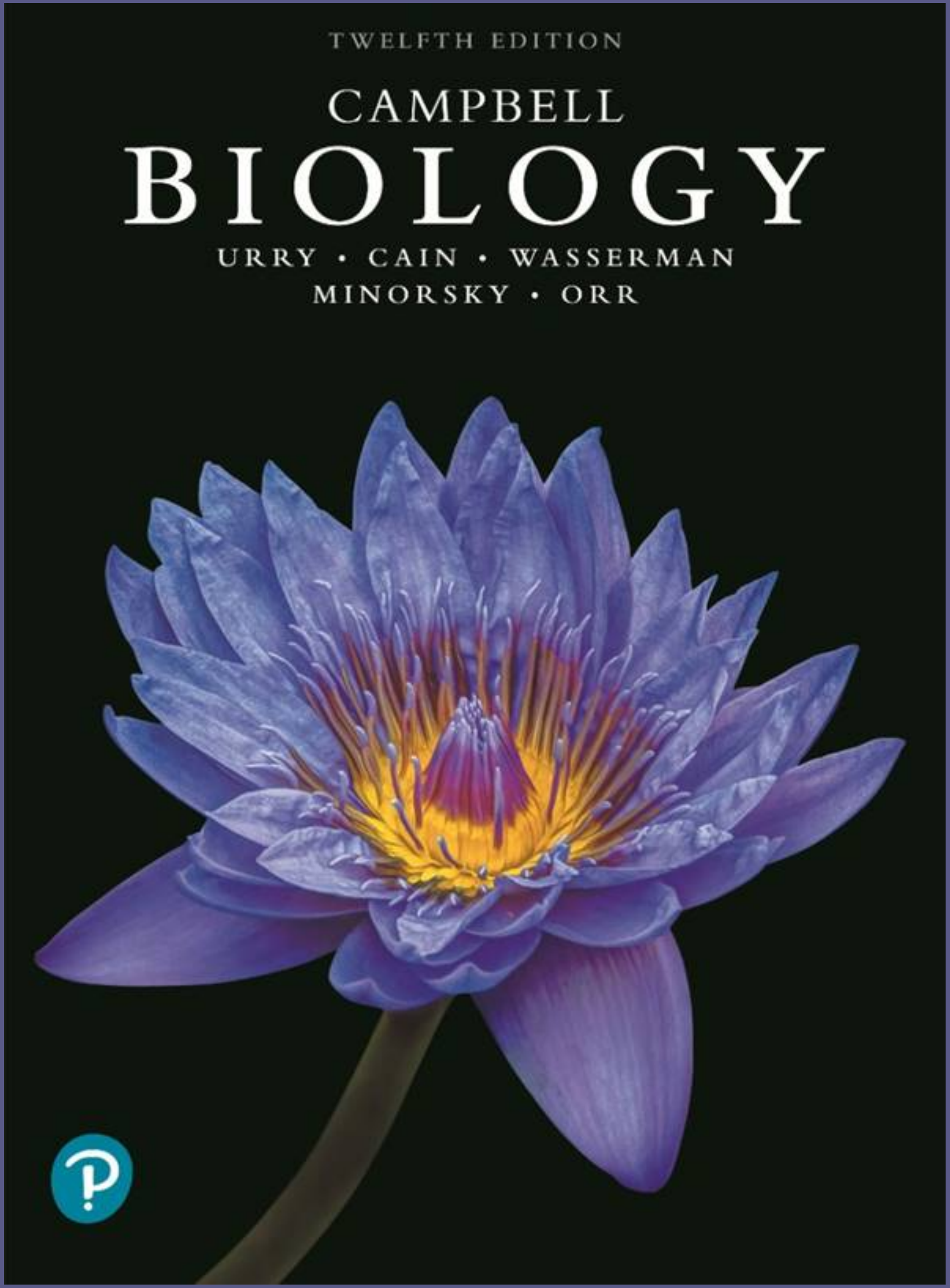


Chapter 39

Plant Responses to Internal and External Signals

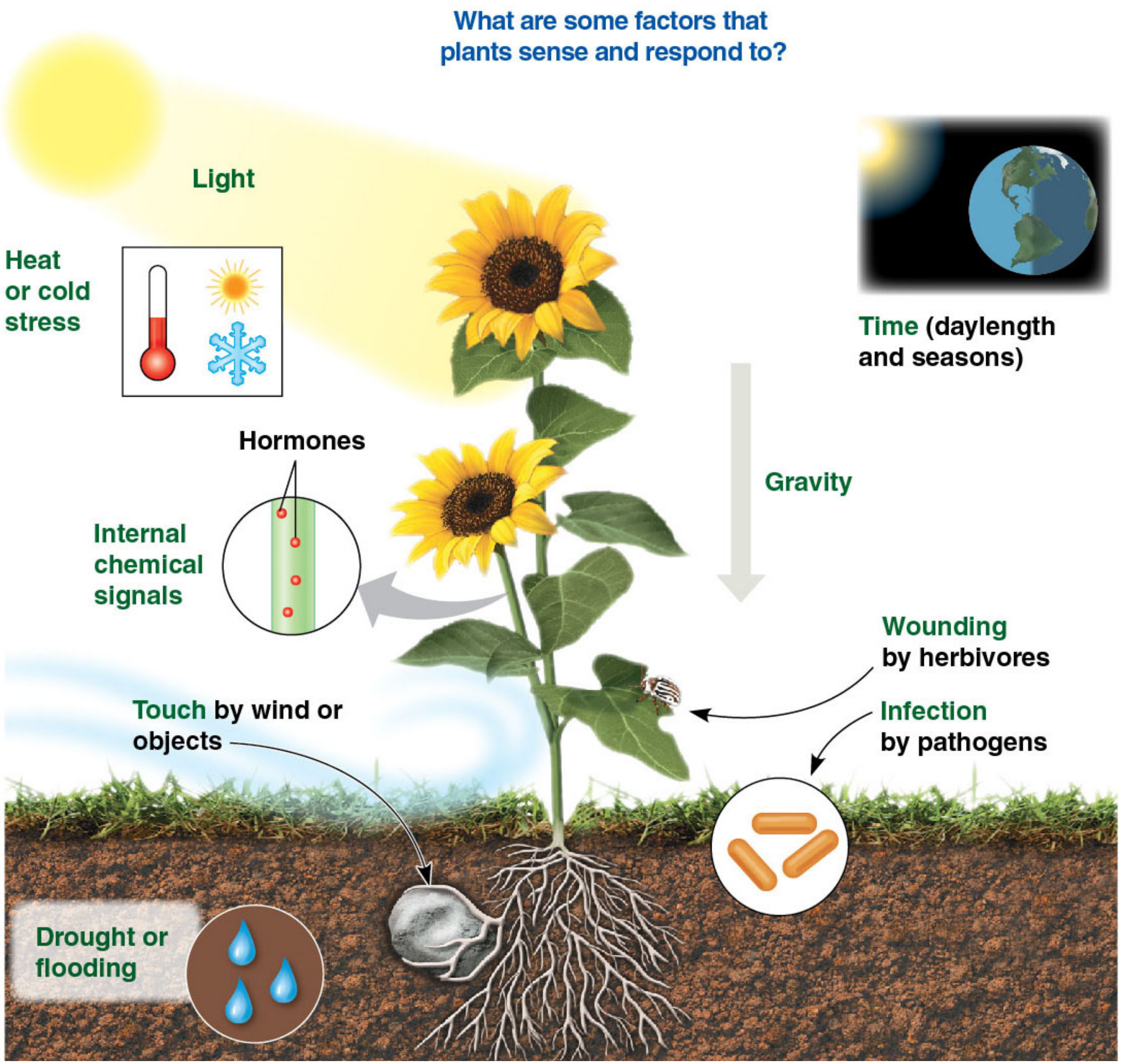
Lecture Presentations by
Nicole Tunbridge and
Kathleen Fitzpatrick

What are some factors that plants sense and respond to?

- Plants receive and respond to many signals from the environment
  - For example, sunflowers track the sun from east to west each day
  - Exposure to sunlight warms the flower heads, releasing chemicals to attract pollinators

Figure 39.1

Figure 39.1b

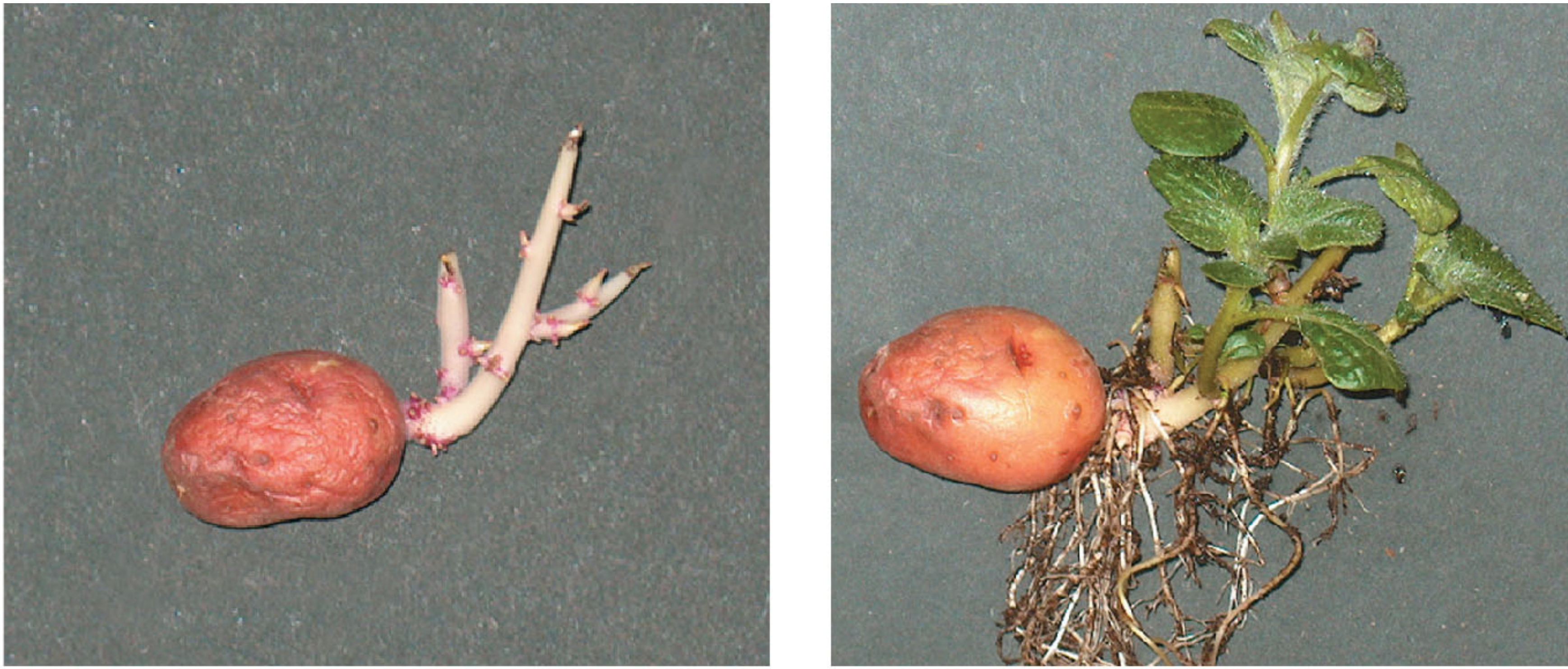

What are some factors that
plants sense and respond to?
Light
Heat
or cold
stress
Time (daylength
and seasons)
Hormones
Gravity
Internal
chemical
signals
Wounding
by herbivores
Touch by wind or
objects
Infection
by pathogens
Drought or
flooding

CONCEPT 39.1: Signal transduction pathways link signal reception to response

- Plants are not inert or passive; they sense and integrate information from their environment
- Plant development is simple, but their cells and molecular biology are as complex as that of animal cells
- Whereas, animals respond to the environment by movement, plants respond to the environment by altering growth and development

- A potato left growing in darkness produces pale stems, unexpanded leaves, and short roots
- These are physical adaptations for growing in darkness, collectively called **etiolation**
- After exposure to light, a potato undergoes **de-etiolation** (greening), in which shoots and roots grow normally

Figure 39.2

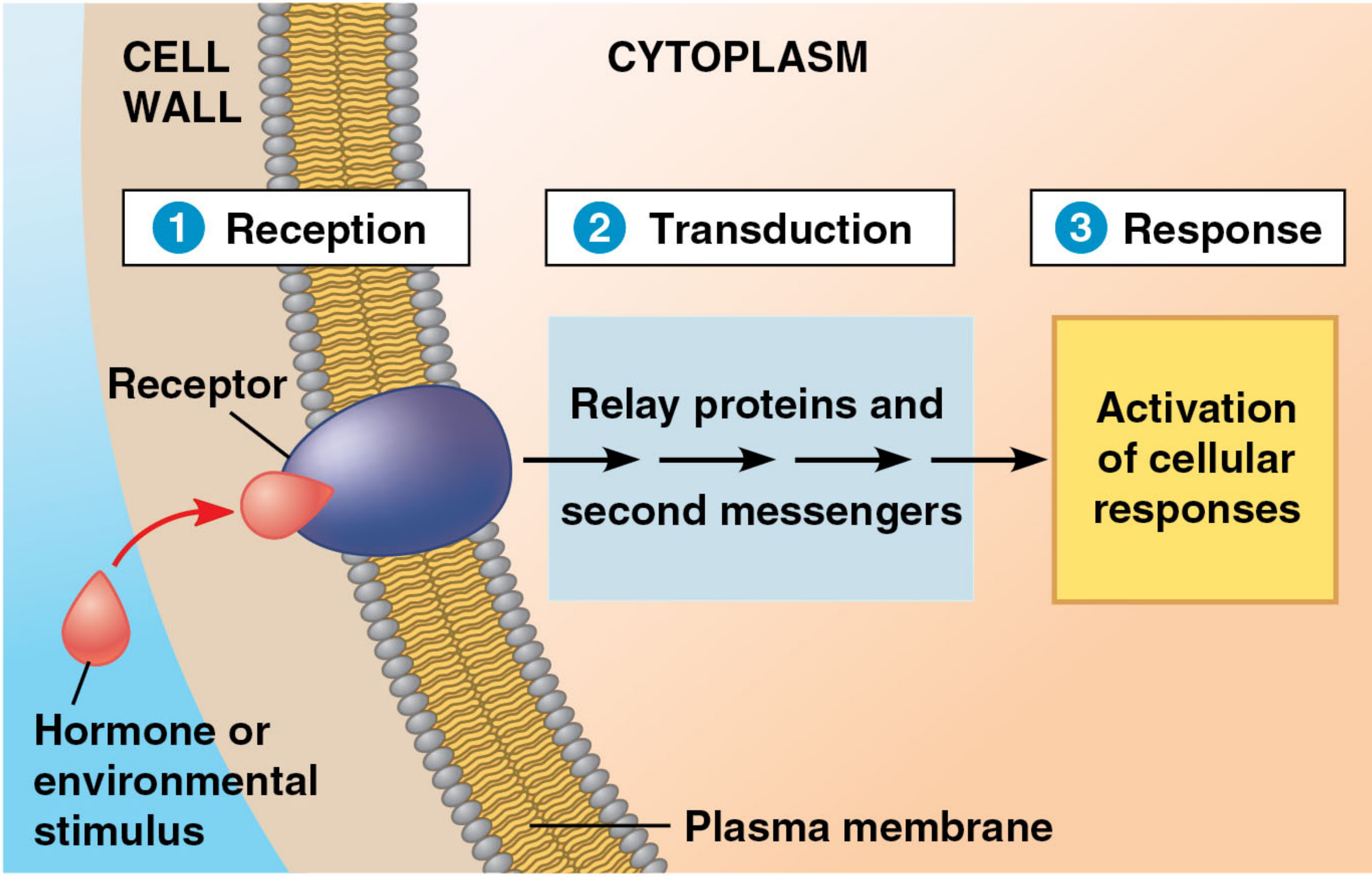


(a) Before exposure to light

(b) After a week's exposure to natural daylight

- De-etiolation is an example of how a cell’s reception of a signal (light) is transduced into a response (greening)
- The stages of cell signal processing include the following: reception, transduction, and response

Figure 39.3


CELL WALL
CYTOPLASM
1 Reception
2 Transduction
3 Response
Receptor
Relay proteins and second messengers
Activation of cellular responses
Hormone or environmental stimulus
Plasma membrane

Reception

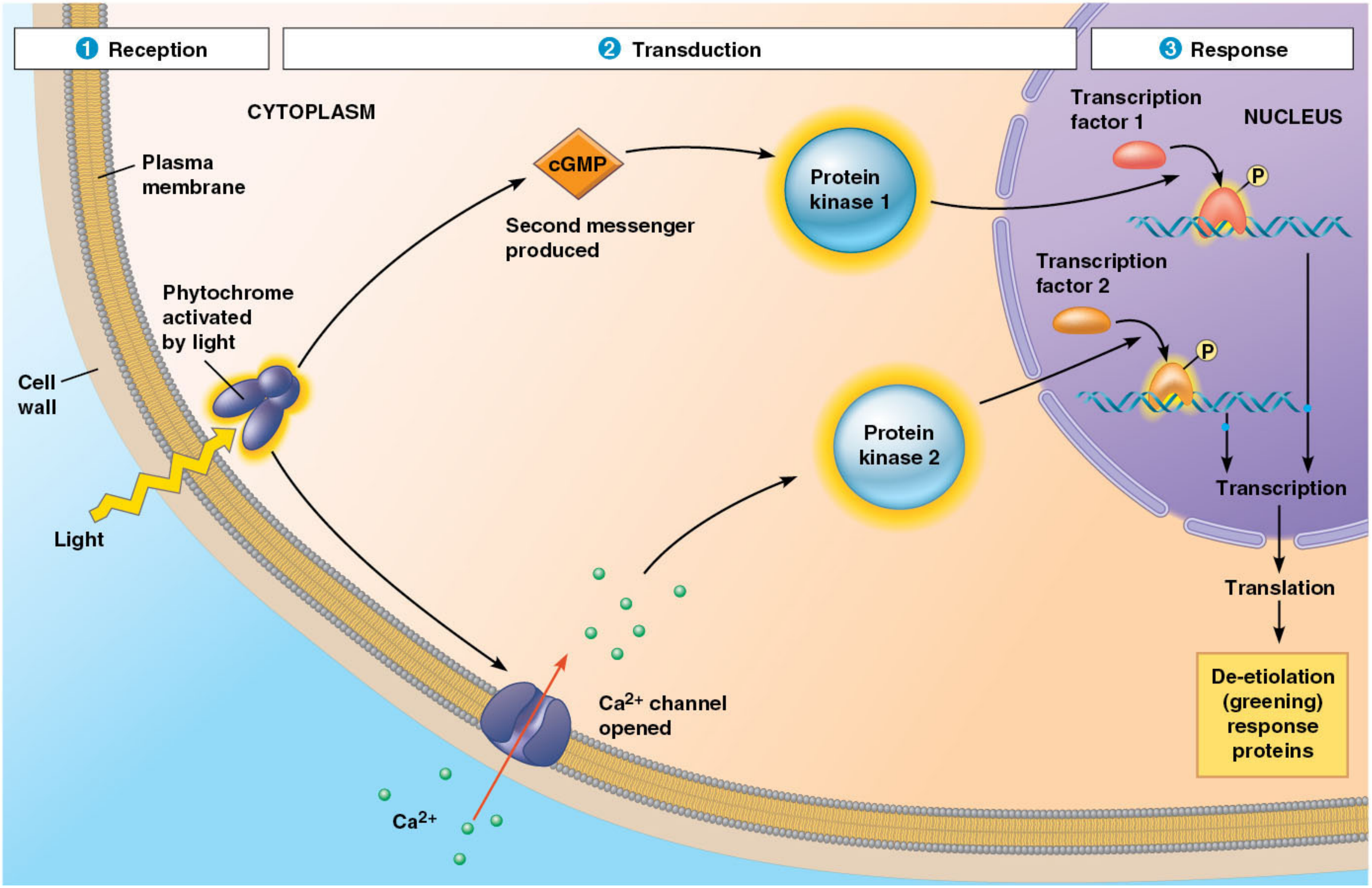
- Signals are detected by receptors, proteins that change in shape in response to specific stimuli
- Phytochrome is the light-detecting receptor involved in de-etiolation

Transduction

- **Second messengers** transfer and amplify signals from receptors to proteins that cause responses
- Two types of second messengers are required for the de-etiolation response: calcium ions (Ca^{2+}) and cyclic GMP (cGMP)

- Phytochrome signal transduction is carried out in response to light by
  - Opening Ca^{2+} channels, which increases Ca^{2+} levels in the cytosol
  - Activating an enzyme that produces cGMP

Figure 39.4



1 Reception
2 Transduction
3 Response
CYTOPLASM
Plasma membrane
Cell wall
Phytochrome activated by light
Light
cGMP
Second messenger produced
Protein kinase 1
Protein kinase 2
Ca^{2+} channel opened
Ca^{2+}
NUCLEUS
Transcription factor 1
Transcription factor 2
P
P
Transcription
Translation
De-etiolation (greening) response proteins

Response

- A signal transduction pathway leads to regulation of one or more cellular activities
- In most cases, these responses involve increased enzyme activity
- This can occur by transcriptional regulation or post-translational modification

Post-translational Modification of Preexisting Proteins

- Post-translational modification activates preexisting proteins
- Modification typically involves the phosphorylation of specific amino acids, which alters the hydrophobicity and activity of the enzyme
- The second messengers cGMP and Ca^{2+} activate protein kinases directly

- Protein kinases often work in a cascade linking initial stimuli to gene expression through phosphorylation of transcription factors
- Protein phosphatases “switch off” the signal transduction pathways by dephosphorylating proteins

Transcriptional Regulation

- Specific transcription factors bind directly to regions of DNA and control transcription of specific genes
- Some transcription factors are activators that increase the transcription of specific genes
- Other transcription factors are repressors that decrease the transcription of specific genes

De-etiolation ("Greening") Proteins

- De-etiolation activates enzymes that
  - function in photosynthesis directly
  - supply the chemical precursors for chlorophyll production
  - affect the levels of plant hormones that regulate growth

CONCEPT 39.2: Plants use chemicals to communicate

- Plants use chemicals to communicate both with the external environment and between different parts of the plant
- Unlike animals, plants can transport macromolecules such as proteins cell to cell through plasmodesmata

General Characteristics of Plant Hormones

- A **hormone** is a signaling molecule that is produced in low concentrations in one part of the body and transported to other parts
- Hormones bind to specific receptors and trigger responses in target cells and tissues

- In plants, some signaling molecules only act locally and others occur in concentrations much greater than typical hormones
- Plant hormones, also called plant growth regulators, are molecules that control one or more specific physiological processes within a plant

- Plant hormones are produced in very low concentrations, but can have profound effects on growth and development
- Each hormone has multiple effects, but multiple hormones can also influence a single process
- Plant responses depend on amount, concentration, and combination of specific hormones present

A Survey of Plant Hormones

- The major plant hormones include
  - Auxin (IAA)
  - Cytokinins
  - Gibberellins (GA)
  - Abscisic acid (ABA)
  - Ethylene
  - Brassinosteroids
  - Jasmonates
  - Strigolactones

Table 39.1

Table 39.1 Overview of Plant Hormones

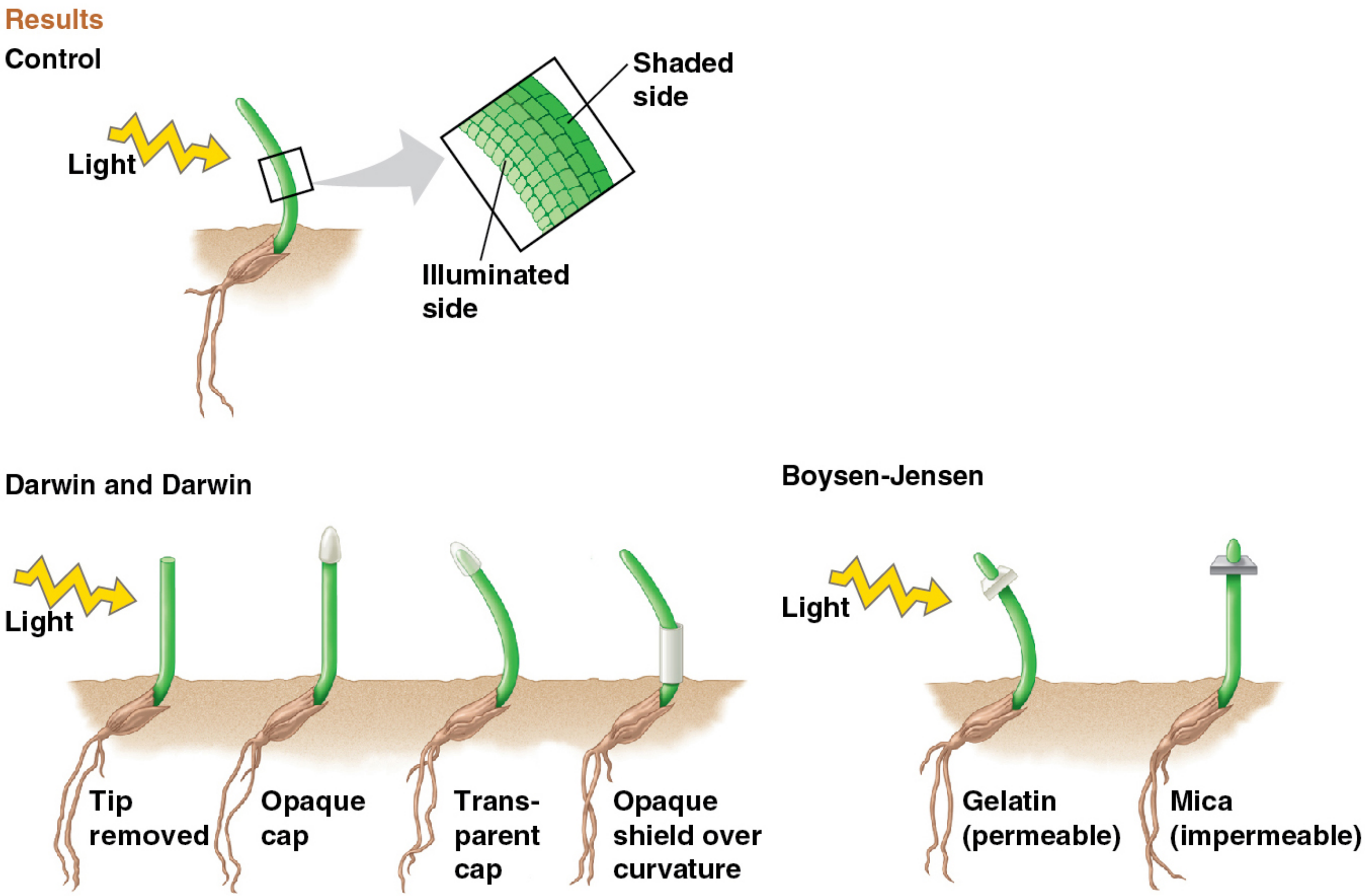
Hormone	Where Produced or Found in Plant	Major Functions
Auxin (IAA)	Shoot apical meristems and young leaves are the primary sites of auxin synthesis. Root apical meristems also produce auxin, although the root depends on the shoot for much of its auxin. Developing seeds and fruits contain high levels of auxin, but it is unclear whether it is newly synthesized or transported from maternal tissues.	Stimulates stem elongation (low concentration only); promotes the formation of lateral and adventitious roots; regulates development of fruit; enhances apical dominance; functions in phototropism and gravitropism; promotes vascular differentiation; retards leaf abscission
Cytokinins	These are synthesized primarily in roots and transported to other organs, although there are many minor sites of production as well.	Regulate cell division in shoots and roots; modify apical dominance and promote lateral bud growth; promote movement of nutrients into sink tissues; stimulate seed germination; delay leaf senescence
Gibberellins (GA)	Meristems of apical buds and roots, young leaves, and developing seeds are the primary sites of production.	Stimulate stem elongation, pollen development, pollen tube growth, fruit growth, and seed development and germination; regulate sex determination and the transition from juvenile to adult phases
Abscisic acid (ABA)	Almost all plant cells have the ability to synthesize abscisic acid, and its presence has been detected in every major organ and living tissue; it may be transported in the phloem or xylem.	Inhibits growth; promotes stomatal closure during drought stress; promotes seed dormancy and inhibits early germination; promotes leaf senescence; promotes desiccation tolerance
Ethylene	This gaseous hormone can be produced by most parts of the plant. It is produced in high concentrations during senescence, leaf abscission, and the ripening of some types of fruits. Synthesis is also stimulated by wounding and stress.	Promotes ripening of many types of fruit, leaf abscission, and the triple response in seedlings (inhibition of stem elongation, promotion of lateral expansion, and horizontal growth); enhances the rate of senescence; promotes root and root hair formation; promotes flowering in the pineapple family
Brassinosteroids	These compounds are present in all plant tissues, although different intermediates predominate in different organs. Internally produced brassinosteroids act near the site of synthesis.	Promote cell expansion and cell division in shoots; promote root growth at low concentrations; inhibit root growth at high concentrations; promote xylem differentiation and inhibit phloem differentiation; promote seed germination and pollen tube elongation
Jasmonates	These are a small group of related molecules derived from the fatty acid linolenic acid. They are produced in several parts of the plant and travel in the phloem to other parts of the plant.	Regulate a wide variety of functions, including fruit ripening, floral development, pollen production, tendril coiling, root growth, seed germination, and nectar secretion; also produced in response to herbivory and pathogen invasion
Strigolactones	These carotenoid-derived hormones and extracellular signals are produced in roots in response to low phosphate conditions or high auxin flow from the shoot.	Promote seed germination, control of apical dominance, and the attraction of mycorrhizal fungi to the root

Auxin

- Any response resulting in curvature of organs toward or away from a stimulus is called a **tropism**
- The growth of a shoot toward or away from light is called **phototropism**
  - Growth toward light is positive phototropism
  - Growth away from light is negative phototropism

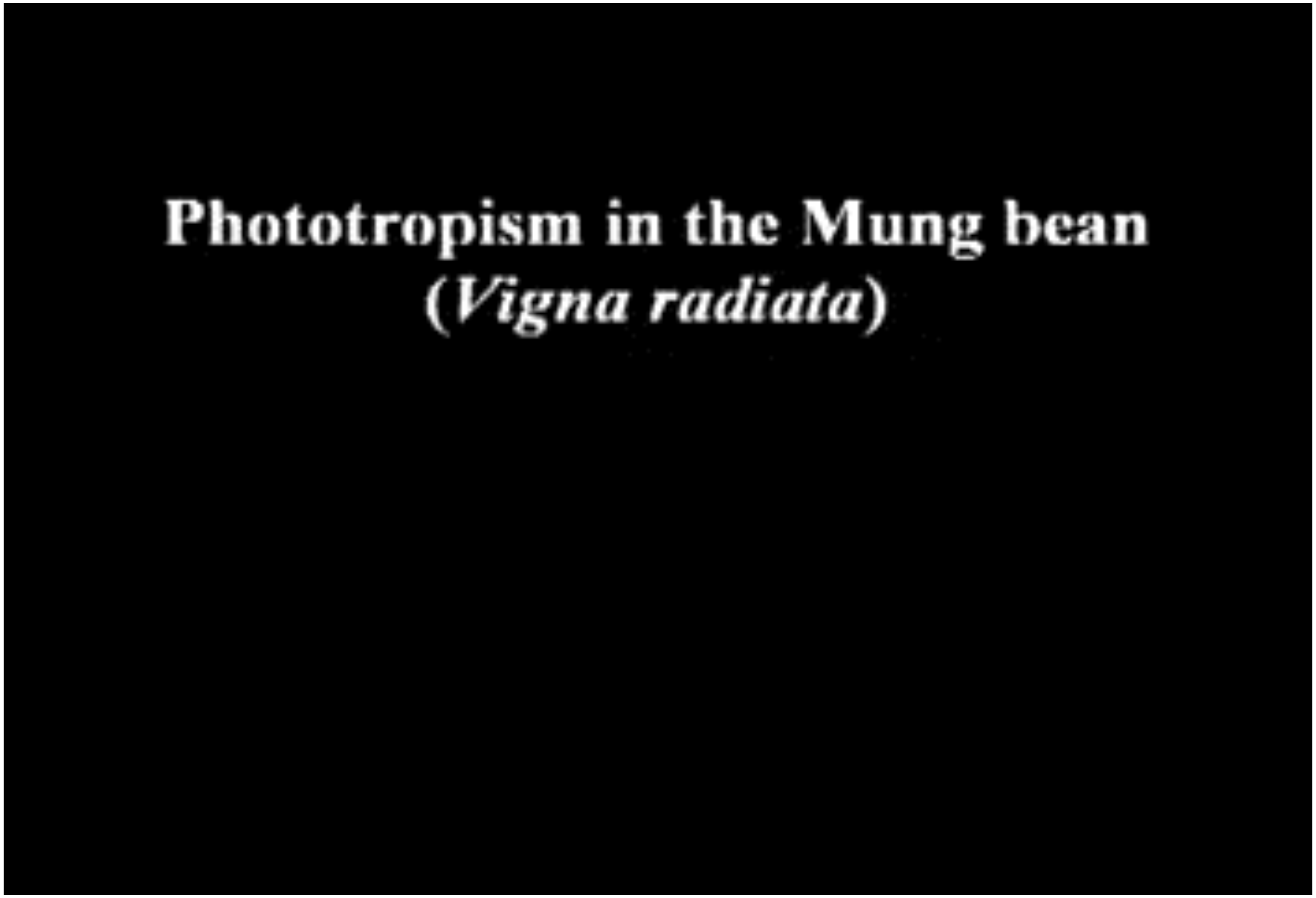
- Charles Darwin conducted experiments on phototropism with his son Francis
- They observed positive phototropism in grass seedlings only if the tip of the coleoptile was present and exposed to light
- They postulated that a signal was transmitted from the tip to the elongating region
- The mobile chemical substance responsible was later identified by Peter Boysen-Jensen

Figure 39.5



Data from C. R. Darwin, *The Power of Movement in Plants*, John Murray (1880). P. Boysen-Jensen, Concerning the performance of phototropic stimuli on the Avenacoleoptile, *Berichte der Deutschen Botanischen Gesellschaft* (*Reports of the German Botanical Society*) 31:559–566 (1913).

Video: Phototropism

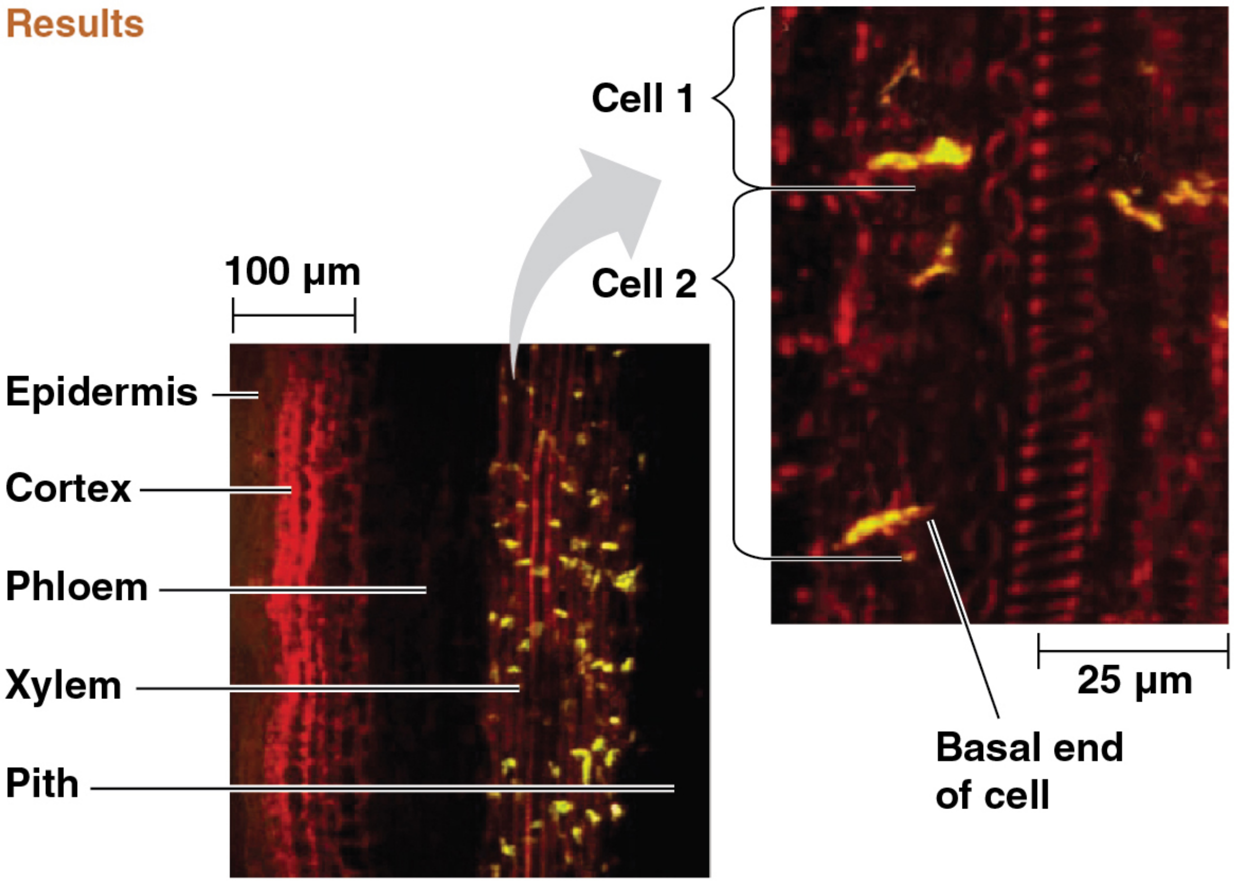


- The term **auxin** refers to any chemical that promotes elongation of coleoptiles
- Indoleacetic acid (IAA) is a common auxin in plants; in this lecture the term *auxin* refers specifically to IAA

- Transport of auxin is polar; it is produced in shoot tips and is transported cell to cell down the stem
- Auxin transporter proteins move the hormone from the basal end of one cell into the apical end of the neighboring cell
- The direction of auxin does not change in response to gravity

Figure 39.6

Results



Data from L. Gälweiler et al., Regulation of polar auxin transport by AtPIN1 in *Arabidopsis* vascular tissue, *Science* 282:2226–2230 (1998).

The Role of Auxin in Cell Elongation

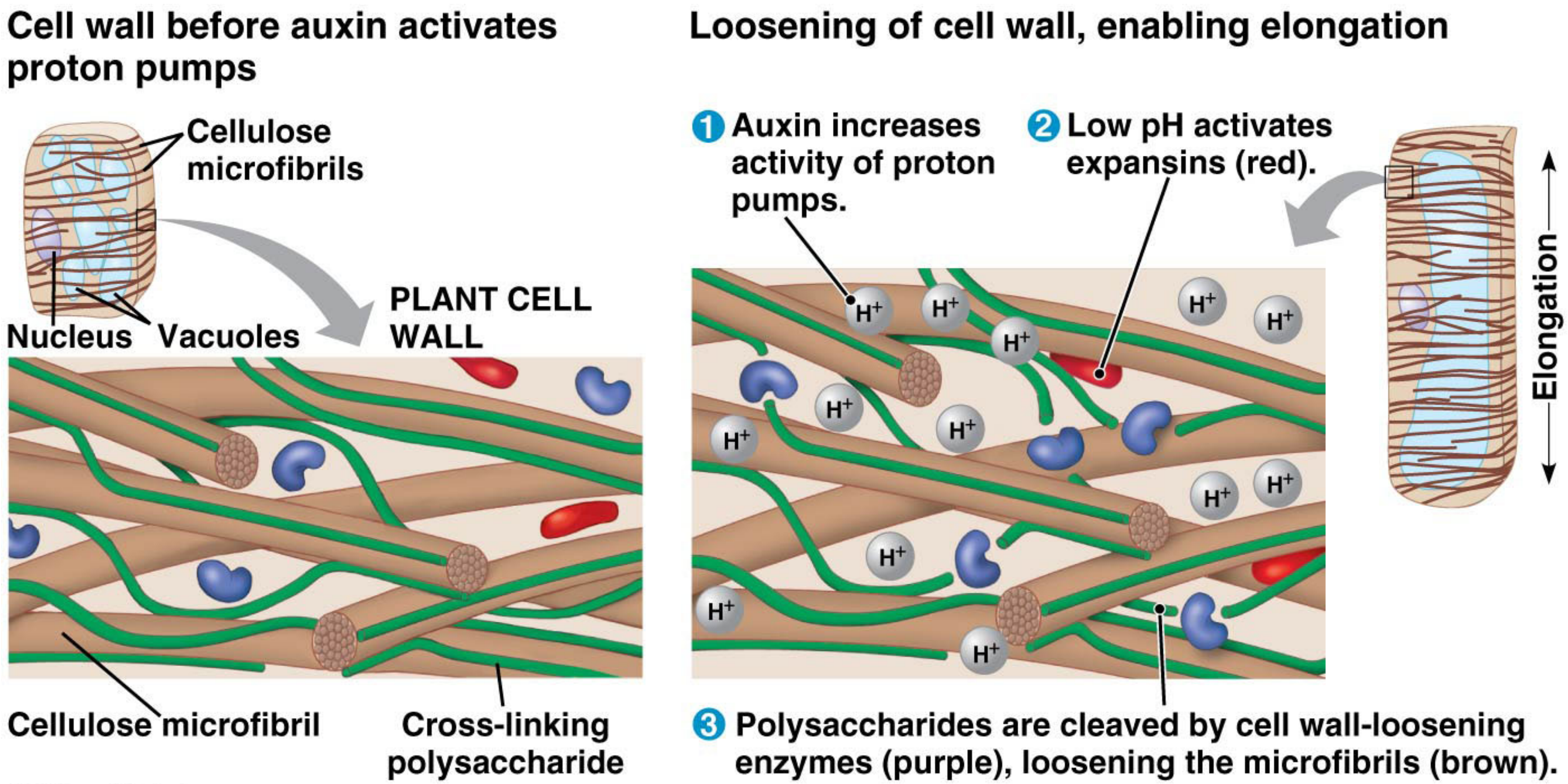
The Role of Auxin in Cell Elongation

- One of auxin's chief functions is to stimulate elongation of cells in young developing shoots
- Auxin stimulates cell growth by binding to a receptor in the nucleus
- Auxin concentration within the range of about 10^{-8} to 10^{-4} *M* is required to stimulate growth; at higher concentrations, it inhibits cell elongation

- According to the *acid growth hypothesis*, auxin stimulates proton pumps in the plasma membrane
- Proton pumps move H^+ into the cell, lowering the pH in the cell wall and increasing the membrane potential

- Reduced pH activates **expansins**, enzymes that loosen the fabric of the cell wall
- Osmotic uptake of water into the cell increases turgor pressure
- Increased cell wall plasticity combined with increased turgor pressure enable the cell to elongate

Figure 39.7



Cell wall before auxin activates proton pumps
Cellulose microfibrils
Nucleus
Vacuoles
PLANT CELL WALL
Cellulose microfibril
Cross-linking polysaccharide
Loosening of cell wall, enabling elongation
1 Auxin increases activity of proton pumps.
2 Low pH activates expansins (red).
H+
Elongation
3 Polysaccharides are cleaved by cell wall-loosening enzymes (purple), loosening the microfibrils (brown).

- Auxin also rapidly alters gene expression and stimulates a sustained growth response

Auxin’s Role in Plant Development

- Polar transport of auxin plays a role in *pattern formation* of the developing plant
- Reduced auxin flow from the shoot of a branch stimulates growth in lower branches
- Auxin transport also plays a role in phyllotaxy, the arrangement of leaves on the stem
- Polar transport of auxin from leaf margins directs leaf venation pattern

- The activity of the vascular cambium is under control of auxin transport
- Reduction in auxin transport capacity and expression of genes encoding auxin transporters occurs at the end of the growing season
- Organization of female angiosperm gametophytes is regulated by an auxin gradient

Practical Uses for Auxins

- The natural auxin indolebutyric acid (IBA) is used in vegetative propagation of cuttings because it stimulates growth of adventitious roots
- Synthetic auxins used in herbicides such as 2,4-D, kill eudicots by causing a hormonal overdose; monocots are able to inactivate these hormones

- Developing seeds produce auxin, which promotes fruit development
- Greenhouse tomatoes produce few seeds
- Spraying synthetic auxins on greenhouse tomatoes improves fruit development

Cytokinins

- **Cytokinins** are so named because they stimulate cytokinesis (cell division)
- The most common natural cytokinin is zeatin because it was first discovered in maize (*Zea mays*)
- Cytokinins influence cell division, cell differentiation, and apical dominance

Control of Cell Division and Differentiation

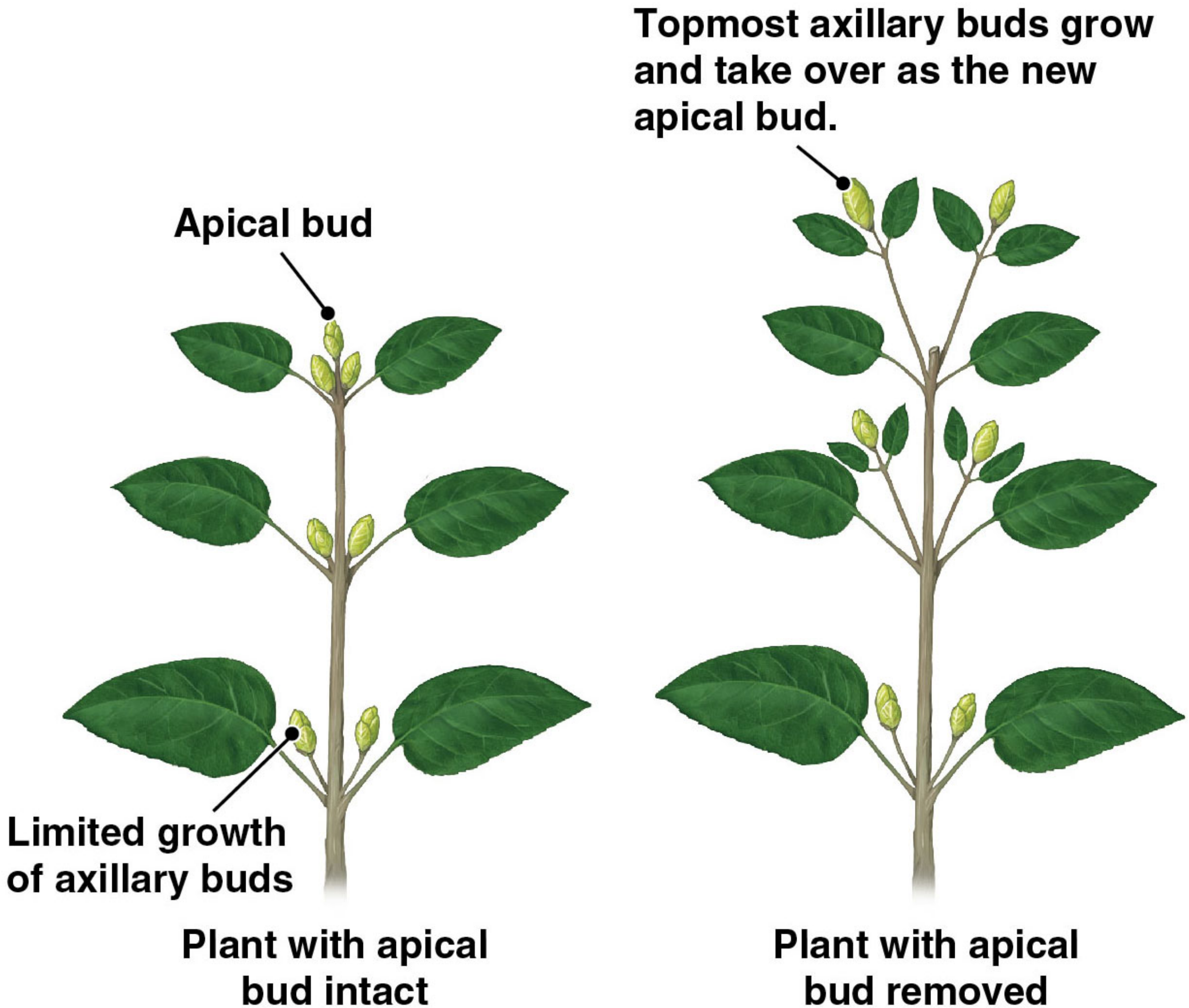
- Cytokinins are produced in actively growing tissues such as roots, embryos, and fruits
- Cytokinins work together with auxin to control cell division and differentiation

- When plant stem tissue is cultured in the absence of cytokinins, the cells grow large but do not undergo mitosis
- If cytokinins are added along with auxin, the cells divide; the ratio controls cell differentiation
  - If auxin and cytokinins are in equal concentration, a mass of undifferentiated cells grows
  - If cytokinin levels increase, shoot buds develop; if auxin levels increase, roots form

Control of Apical Dominance

- Apical dominance is a terminal bud's ability to suppress development of axillary buds
- It is under the control of sugar, cytokinins, auxin, and strigolactones
- Removal of the apical bud increases sugar availability and decreases auxin and strigolactone levels in the stem, initiating axillary bud growth
- Applying auxin to the shoot tip re-suppresses the growth of lateral buds

Figure 39.8


Topmost axillary buds grow and take over as the new apical bud.
Apical bud
Limited growth of axillary buds
Plant with apical bud intact
Plant with apical bud removed

Anti-aging Effects

- Cytokinins inhibit protein breakdown, stimulate RNA and protein synthesis, and mobilize nutrients from surrounding tissues to slow the aging in plant organs

Gibberellins

- **Gibberellins** have a variety of effects, such as stem elongation, fruit growth, and seed germination
  - For example, in "foolish seedling disease," gibberellins produced by a pathogenic fungus causes rice seedlings to grow so tall and spindly that they fall over

Stem Elongation

- Gibberellins are produced in young roots and leaves
- They stimulate growth of leaves and stems by enhancing cell elongation and cell division
- They are hypothesized to activate the enzymes that loosen cell walls and facilitate entry of expansin proteins
- Bolting, rapid growth of the floral stalk, is induced by gibberellins

Figure 39.9

(a) Rosette form (left) and gibberellin-induced bolting (right)

Fruit Growth

- In many plants, both auxin and gibberellins must be present for fruit to develop
- Gibberellin spray is used on Thompson seedless grapes to make them grow much larger than normal
- Gibberellin spray also makes the internodes elongate, creating more space between individual grapes

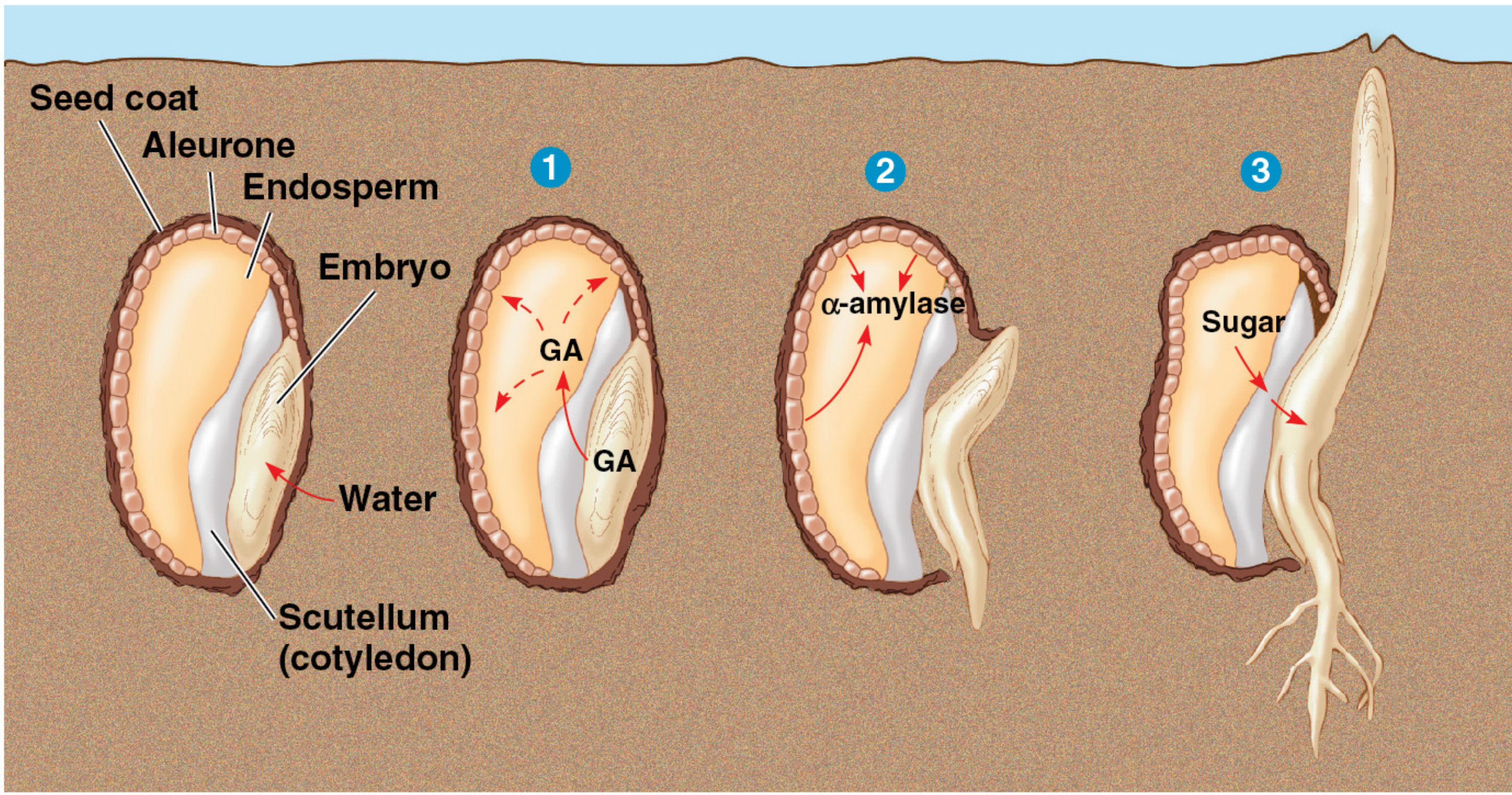
Figure 39.9

(b) Grapes from control vine (left) and gibberellin-treated vine (right)

Germination

- After water is imbibed, release of gibberellins from the embryo signals seeds to break dormancy
- Treatment with gibberellins can induce germination in seeds that normally require specific environmental conditions to break dormancy

Figure 39.10



Seed coat
Aleurone
Endosperm
Embryo
Water
Scutellum (cotyledon)
1
GA
GA
2
α-amylase
3
Sugar

Abscisic Acid

- **Abscisic acid (ABA)** slows growth, often by antagonizing the actions of growth hormones
- ABA has many other effects on plants including seed dormancy and drought tolerance

Seed Dormancy

- Seed dormancy increases the likelihood that the seed will germinate only in optimal conditions
- Many dormant seeds germinate when ABA is removed or inactivated
- The ratio of ABA to gibberellins often affects whether seeds will break dormancy
- Precocious (early) germination can be caused by inactive or low levels of ABA

Figure 39.11

◀ **Red mangrove (*Rhizophora mangle*) seeds**

▲ **Maize mutant**

Drought Tolerance

- ABA is the primary internal signal that enables plants to withstand drought
- ABA accumulation in wilting leaves causes stomata to close rapidly
- Transport of ABA from water-stressed root systems to leaves can act as an “early warning system”

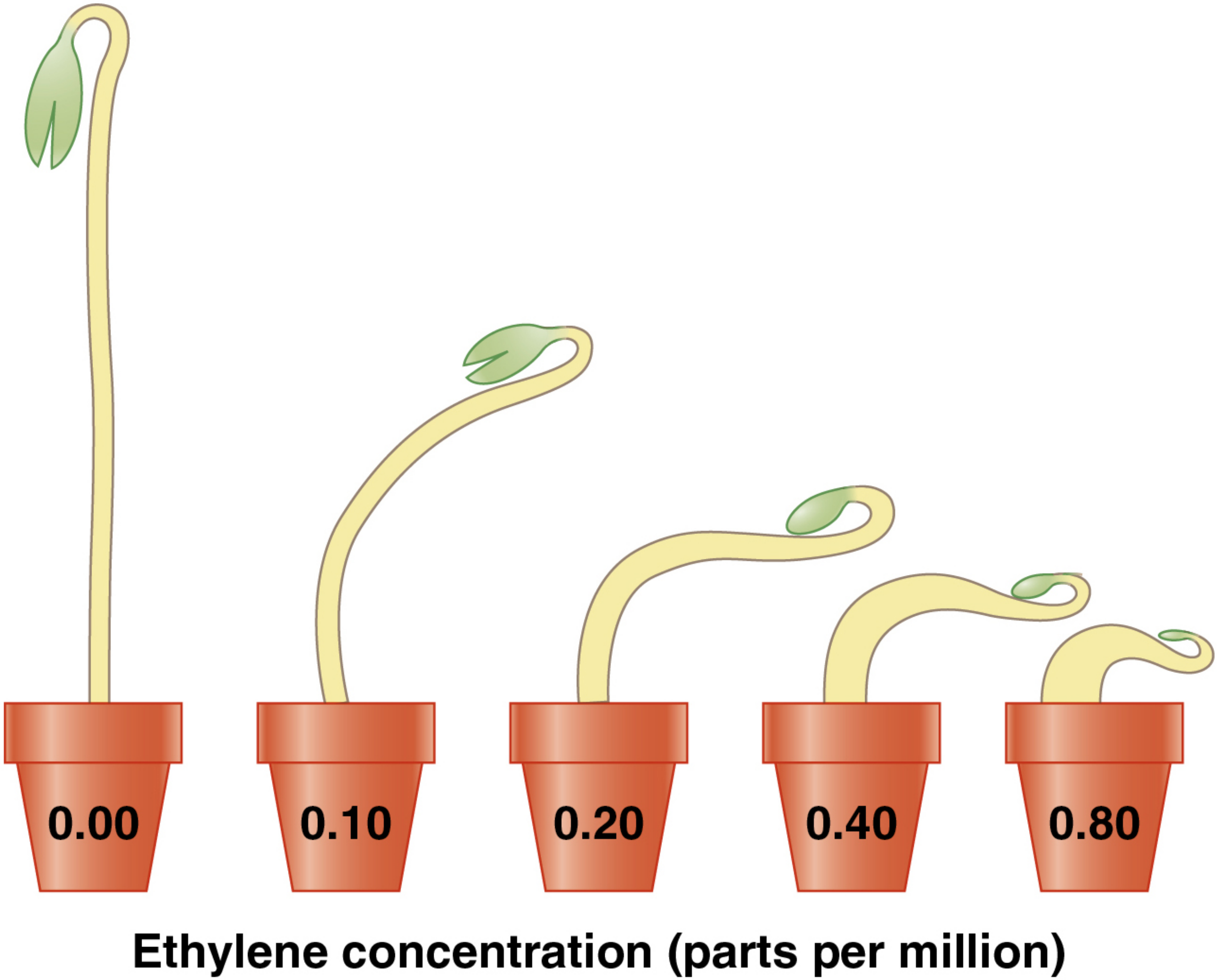
Ethylene

- Plants produce **ethylene** in response to stresses such as drought, flooding, mechanical pressure, injury, and infection
- It is also produced during fruit ripening and programmed cell death and in response to application of high concentration auxin
- Ethylene's effects include response to mechanical stress, senescence, leaf abscission, and fruit ripening

The Triple Response to Mechanical Stress

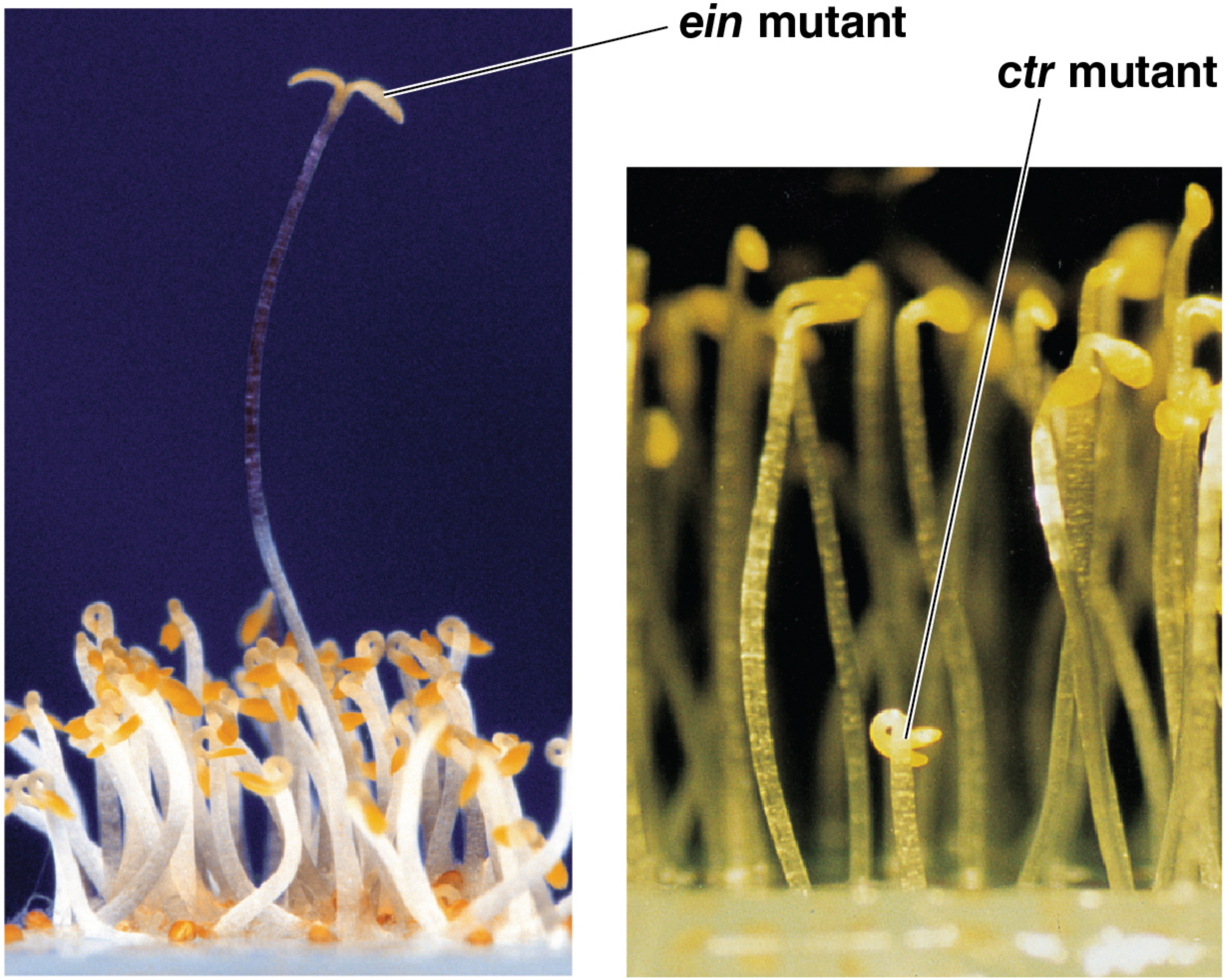
- Ethylene is produced when a seedling tip pushes against an obstacle
- The production of ethylene induces a **triple response** that slows stem elongation, thickens the stem, and causes it to grow horizontally
- Vertical growth resumes when the effects of the ethylene wear off

Figure 39.12


0.00
0.10
0.20
0.40
0.80
Ethylene concentration (parts per million)

- Some *Arabidopsis* mutants have abnormal triple responses
  - Ethylene-insensitive (*ein*) mutants fail to undergo the triple response after exposure to ethylene
  - Ethylene-overproducing (*eto*) mutants undergo the triple response even in the absence of obstacles
  - Constitutive triple-response (*ctr*) mutants undergo a triple response even if ethylene is not present

Figure 39.13



(a) *ein* mutant **(b) *ctr* mutant**

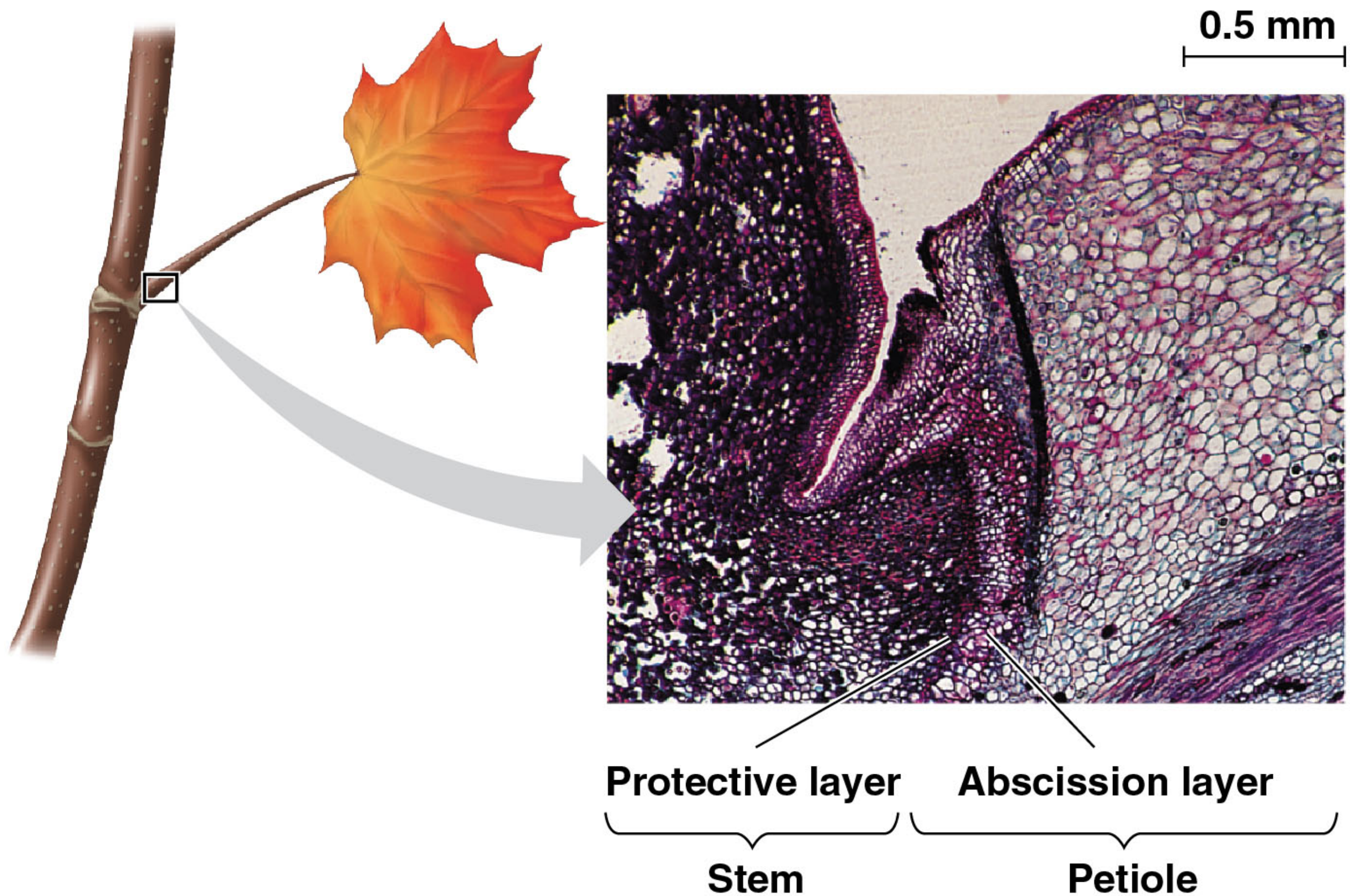
Senescence

- **Senescence** is the programmed death of certain cells, organs, or entire plants
- A burst of ethylene is associated with the onset of apoptosis, programmed cell death

Leaf Abscission

- When a leaf falls in autumn, it breaks off at an abscission layer near the base of the petiole
- The balance of ethylene to auxin controls leaf abscission
- Leaf abscission occurs when ethylene prevails over auxin

Figure 39.14



Animation: Leaf Abscission

Fruit Ripening

- In many cases, a burst of ethylene production in a fruit triggers the ripening process
- Ethylene triggers ripening, and ripening triggers release of more ethylene
- Fruit producers can control ripening by picking green fruit and controlling ethylene levels

More Recently Discovered Plant Hormones

- **Brassinosteroids** are chemically similar to cholesterol and the sex hormones of animals
- They induce cell elongation and division in stem segments and seedlings at low concentration
- They slow leaf abscission and promote xylem differentiation

- **Jasmonates**, including jasmonate (JA) and methyl jasmonate (MeJA) play important roles in plant defense and development
- They are produced in response to wounding and are involved in controlling plant defenses

- Jasmonates also regulate many other physiological processes, including
  - Nectar secretion
  - Fruit ripening
  - Pollen production
  - Flowering time
  - Seed germination
  - Root growth
  - Tuber formation
  - Mycorrhizal symbioses
  - Tendril coiling

- **Strigolactones** are xylem-mobile chemicals that
  - Stimulate seed germination
  - Suppress adventitious root formation
  - Help establish mycorrhizal associations
  - Help control apical dominance
- Strigolactones are named for parasitic *Striga* plants
- *Striga* seeds germinate when host plants exude strigolactones through their roots

CONCEPT 39.3: Responses to light are critical for plant success

- Light cues many key events in plant growth and development
- Effects of light on plant morphology are called **photomorphogenesis**

- Plants detect not only the presence of light but also its direction, intensity, and wavelength (color)
- A graph called an **action spectrum** depicts the relative response of a process to different wavelengths of light
- Action spectra are useful in studying any process that depends on light

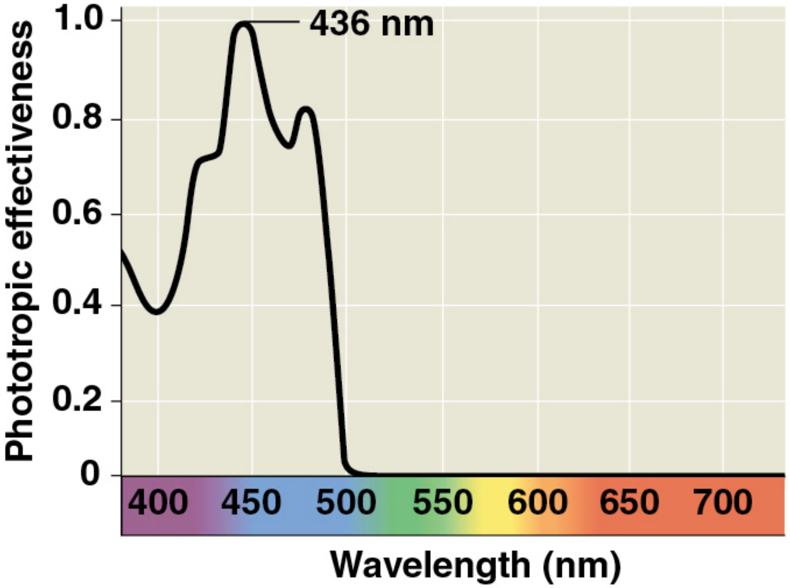
- Action spectra can be used to determine which responses are mediated by a specific photoreceptor
- There are two major classes of light receptors: blue-light photoreceptors and phytochromes

Blue-Light Photoreceptors

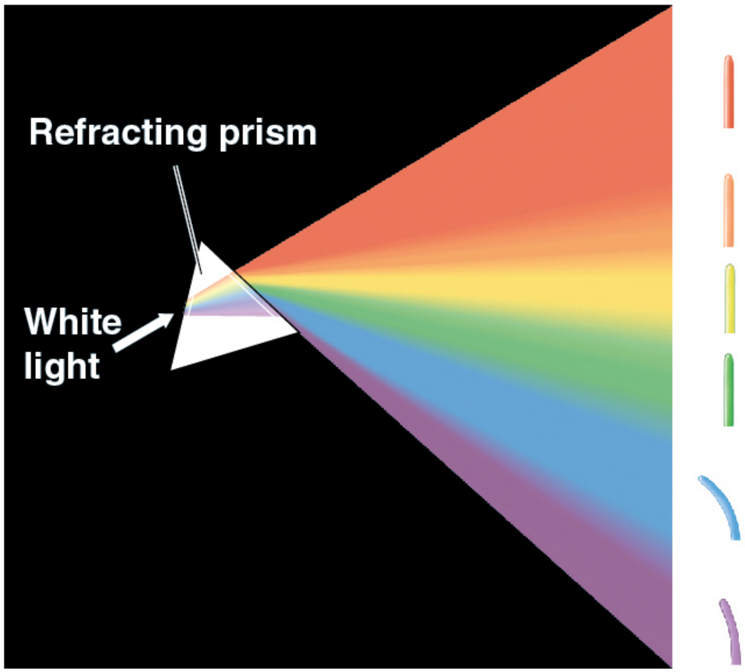
- Pigments that absorb blue light are called **blue-light photoreceptors**
- Blue light initiates a variety of plant responses such as hypocotyl elongation, stomatal opening, and phototropism

- Cryptochromes are blue-light receptors involved in the inhibition of stem elongation
- Phototropin is a protein kinase involved in mediating blue-light-mediated stomatal opening, chloroplast movements, and phototropic curvatures

Figure 39.15



(a) Light wavelengths below 500nm induce curvature.



(b) Blue light induces the most curvature of coleoptiles.

Phytochrome Photoreceptors

- **Phytochromes** are pigments that absorb mostly red and far-red light
- They regulate many of a plant's responses to light including de-etiolation, seed germination, and shade avoidance

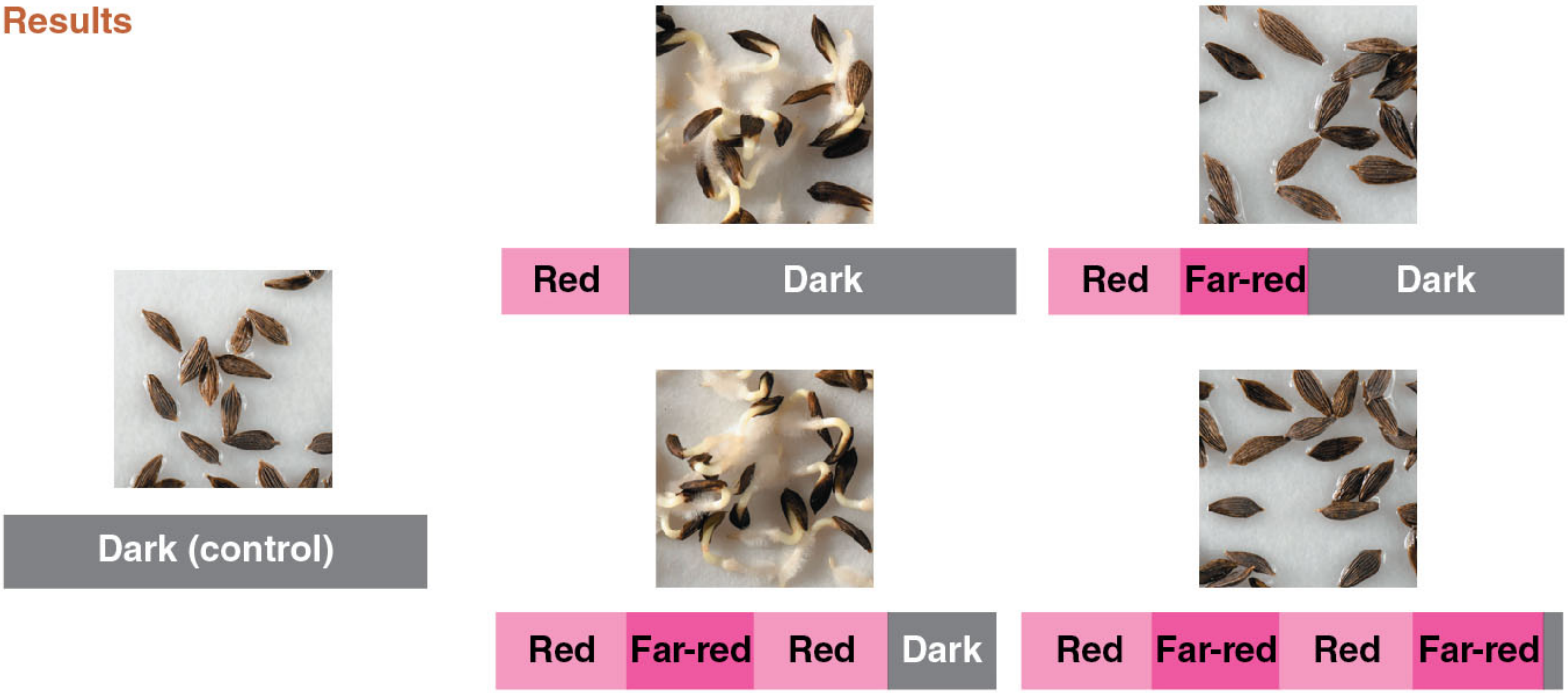
Phytochromes and Seed Germination

- Many seeds remain dormant until light and other conditions are near optimal
- Seeds can remain dormant for years until light conditions change

- Scientists determined the action spectrum for light-induced germination of lettuce seeds in the 1930s
- Red light increased germination, while far-red light inhibited germination
- The effects of red and far-red light are reversible; the final light exposure determines the response
- The photoreceptors responsible for the opposing effects of red and far-red light are phytochromes

Figure 39.16

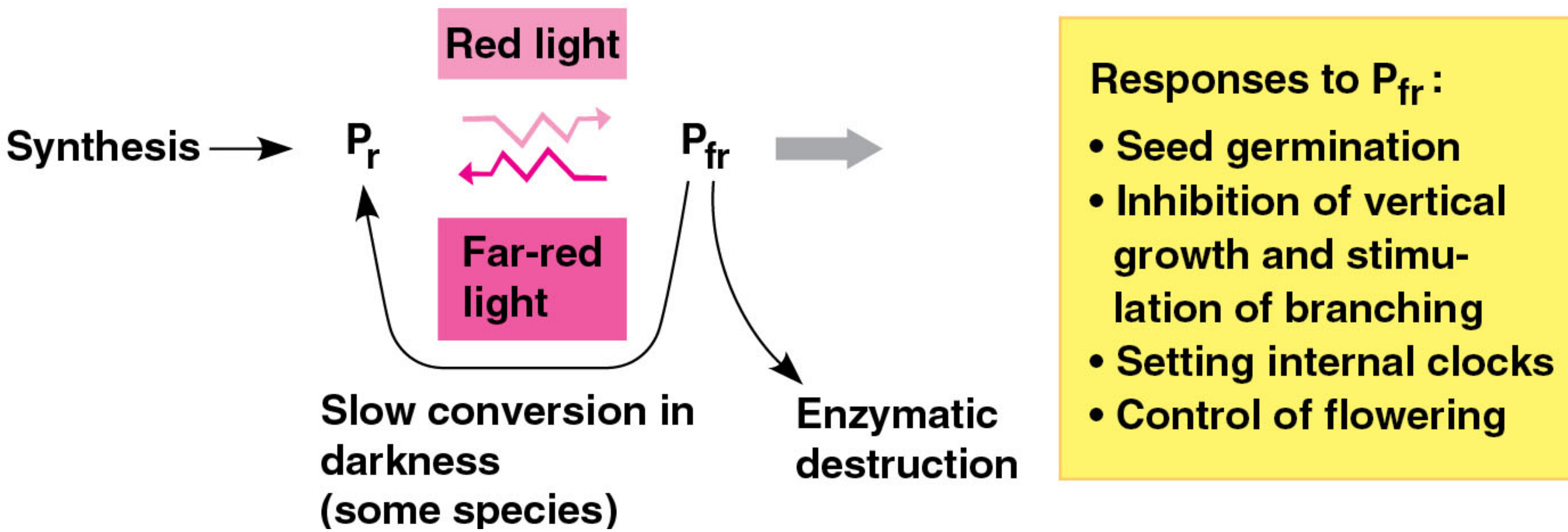
Results



Data from H. Borthwick et al., A reversible photoreaction controlling seed germination, *Proceedings of the National Academy of Sciences USA* 38:662–666 (1952).

- Phytochromes exist in two photoreversible states, with conversion of P_r to P_{fr} triggering many developmental responses
- Red light triggers the conversion of P_r to P_{fr}
- Far-red light triggers the conversion of P_{fr} to P_r
- Conversion of P_r to P_{fr} is faster than P_{fr} to P_r
- Sunlight contains both red and far-red light; it increases the ratio of P_{fr} to P_r triggering germination

Figure 39.17


Synthesis
P_r
Red light
Far-red light
P_{fr}
Slow conversion in darkness (some species)
Enzymatic destruction
Responses to P_{fr}:
• Seed germination
• Inhibition of vertical growth and stimulation of branching
• Setting internal clocks
• Control of flowering

Phytochromes and Shade Avoidance

- The phytochrome system also provides the plant with information about the quality of light
- Leaves in the canopy absorb red light and allow far-red light to pass through to the shaded plants below
- When a tree is shaded, the phytochrome ratio shifts in favor of P_r, inducing vertical growth
- This is called the “shade avoidance” response

Biological Clocks and Circadian Rhythms

- Many plant processes oscillate during the day in response to light and temperature changes
- Many other processes oscillate with a frequency of 24 hours, even under constant environmental conditions
  - For example, many legumes lower their leaves in the evening and raise them in the morning, even when kept in constant light or darkness

Figure 39.18

Noon 10:00 PM

- **Circadian rhythms** are cycles that are about 24 hours long and are governed by an internal “clock”
- These cycles can be free-running, varying from 21 to 27 hours, when organisms are kept in a constant environment
- The 24-hour period arises from the transcription of “clock genes” regulated through negative-feedback loops

The Effect of Light on the Biological Clock

- Light is the factor that entrains the biological clock to precisely 24 hours every day
- Both phytochromes and blue-light photoreceptors can entrain circadian rhythms in plants
- Phytochrome conversion marks sunrise and sunset, providing the biological clock with environmental cues

Photoperiodism and Responses to Seasons

- Many critical events in plant life cycles, such as seed germination and flowering, occur seasonally
- Plants detect the time of year based on changes in *photoperiod*, the relative lengths of night and day
- **Photoperiodism** is a physiological response to photoperiod

Photoperiodism and Control of Flowering

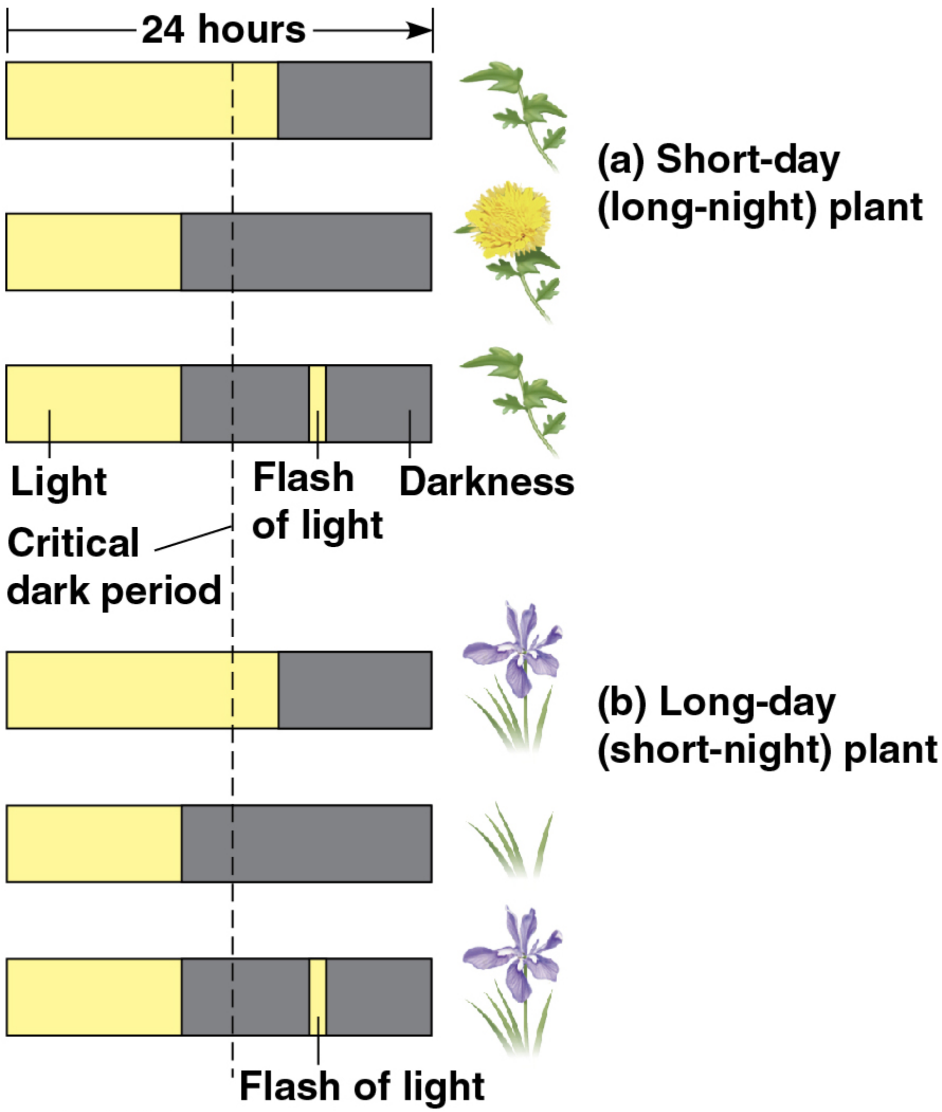
- In many species, flowering only occurs during a specific photoperiod
- Plants that flower when a light period is shorter than a critical length are called **short-day plants**
- Plants that flower when a light period is longer than a certain number of hours are called **long-day plants**
- Flowering in **day-neutral plants** is controlled by plant maturity, not photoperiod

Critical Night Length

- In the 1940s, researchers discovered that flowering and other responses to photoperiod are actually controlled by night length, not day length

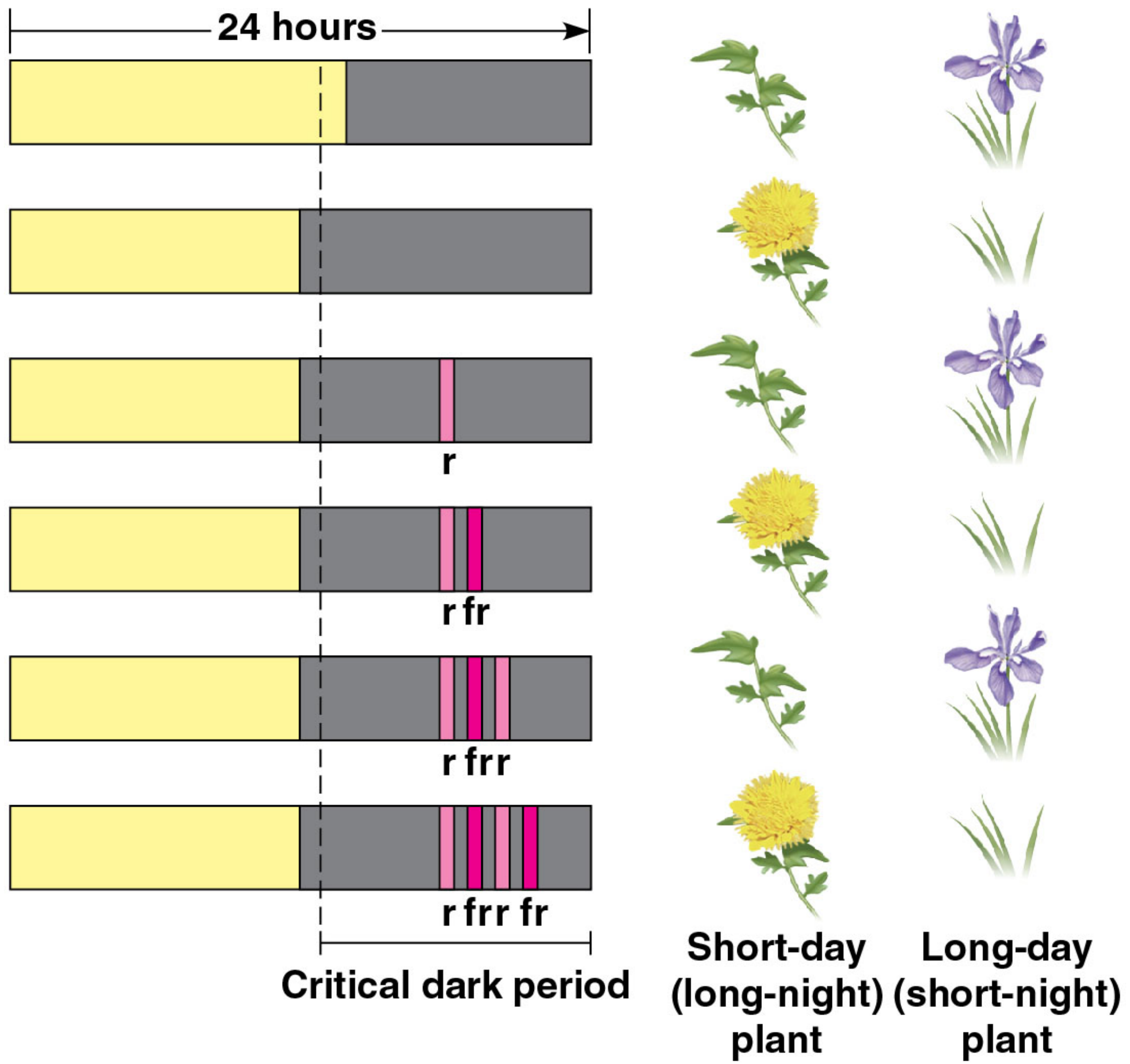
- Short-day plants are governed by whether the critical night length sets a minimum number of hours of darkness
- Long-day plants are governed by whether the critical night length sets a maximum number of hours of darkness

Figure 39.19


24 hours
(a) Short-day (long-night) plant
Light
Flash of light
Darkness
Critical dark period
(b) Long-day (short-night) plant
Flash of light

- Red light is the most effective color in interrupting the night length
- Phytochrome is the pigment that detects the red light
- A flash of red light followed by a flash of far-red light does not disrupt night length

Figure 39.20

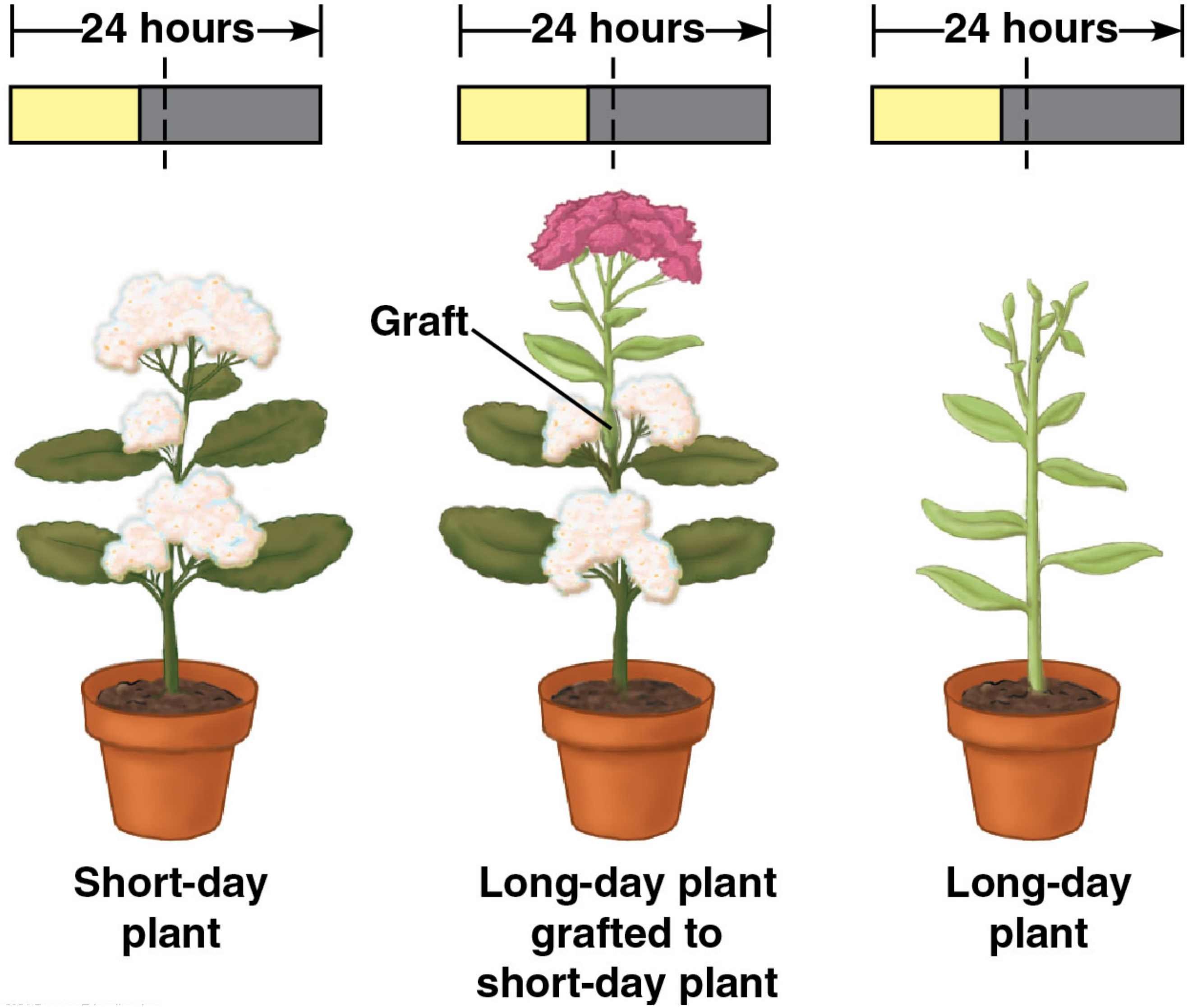

24 hours
r
r fr
r fr r
r fr r fr
Critical dark period
Short-day
(long-night)
plant
Long-day
(short-night)
plant

- Some plants flower after only a single exposure to the required photoperiod
- Other plants need several successive days of the required photoperiod
- Still others need an environmental stimulus in addition to the required photoperiod
  - For example, **vernalization** is a pretreatment with cold to induce flowering

A Flowering Hormone?

- Photoperiod is detected by leaves, which cue buds to develop as flowers
- The flowering signal molecule is called **florigen**
- Florigen is a protein governed by the *FLOWERING LOCUS T* (*FT*) gene

Figure 39.21


24 hours
24 hours
24 hours
Graft
Short-day plant
Long-day plant grafted to short-day plant
Long-day plant

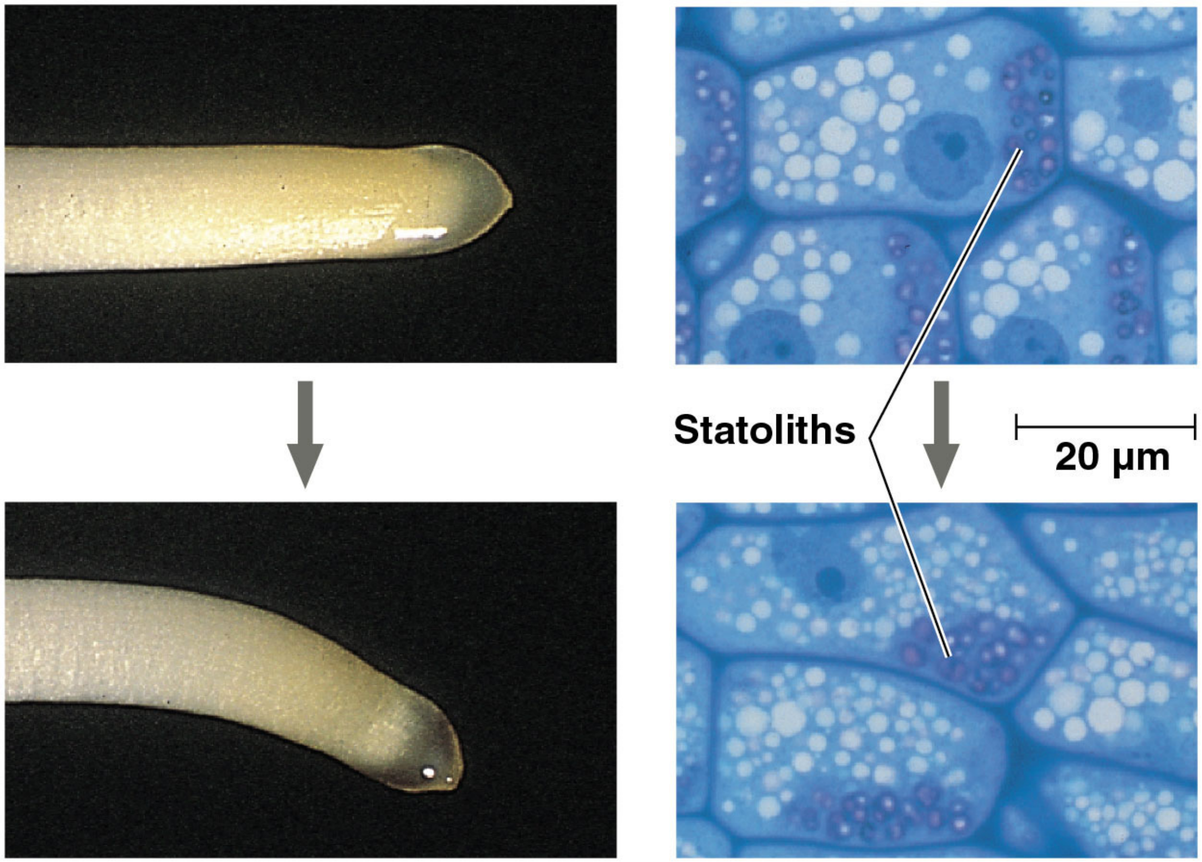
CONCEPT 39.4: Plants respond to a wide variety of stimuli other than light

- Because they are immobile, plants must adjust to a range of environmental circumstances through developmental and physiological mechanisms

Gravity

- Response to gravity is known as **gravitropism**
- Roots show positive gravitropism and grow downward; shoots show negative gravitropism and grow upward
- Plants may detect gravity by the settling of **statoliths**, dense cytoplasmic components

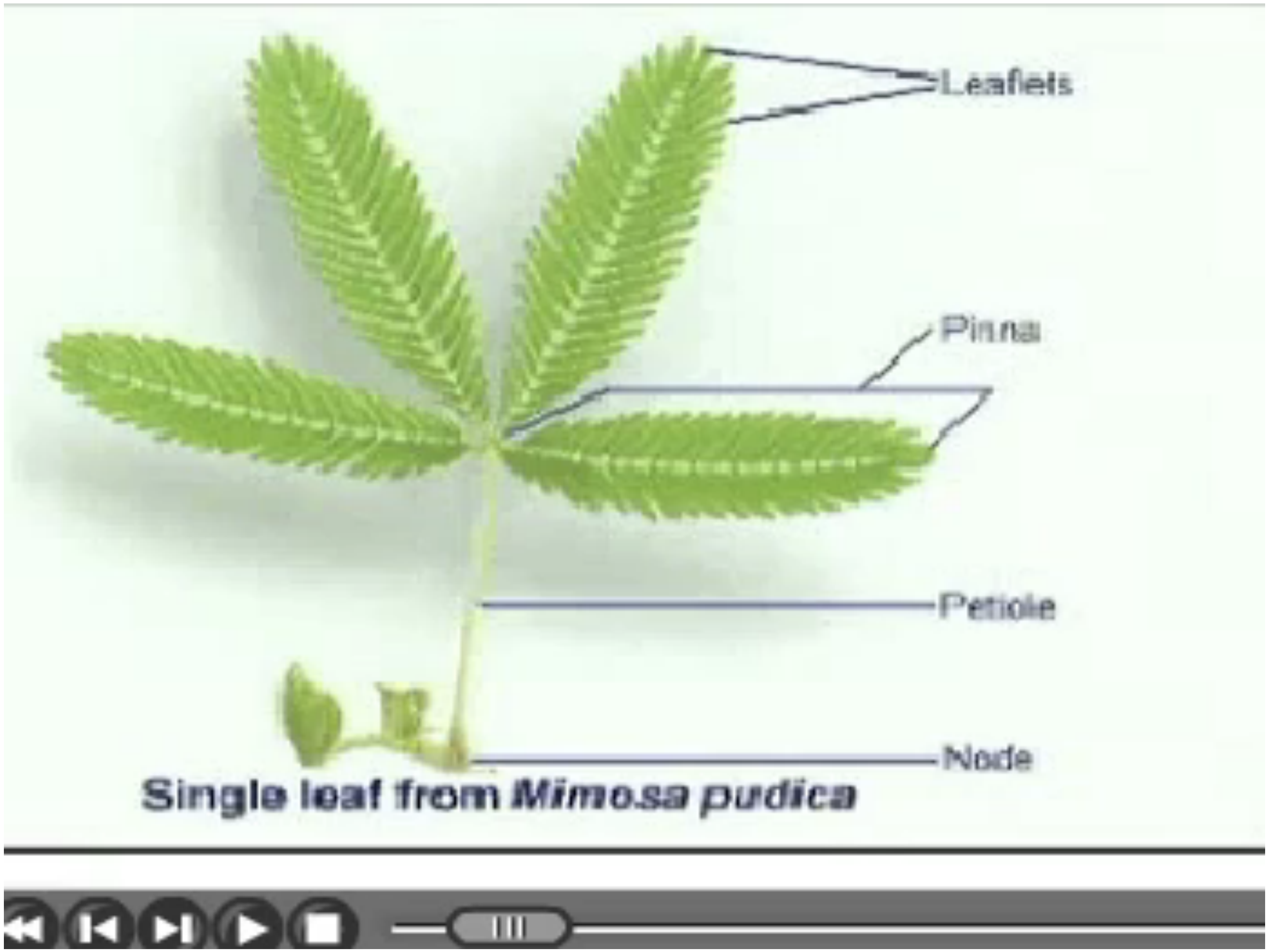
Figure 39.22



(a) Primary root of maize bending gravitropically (LMs)

(b) Statoliths settling to the lowest sides of root cap cells (LMs)

Video: Gravitropism



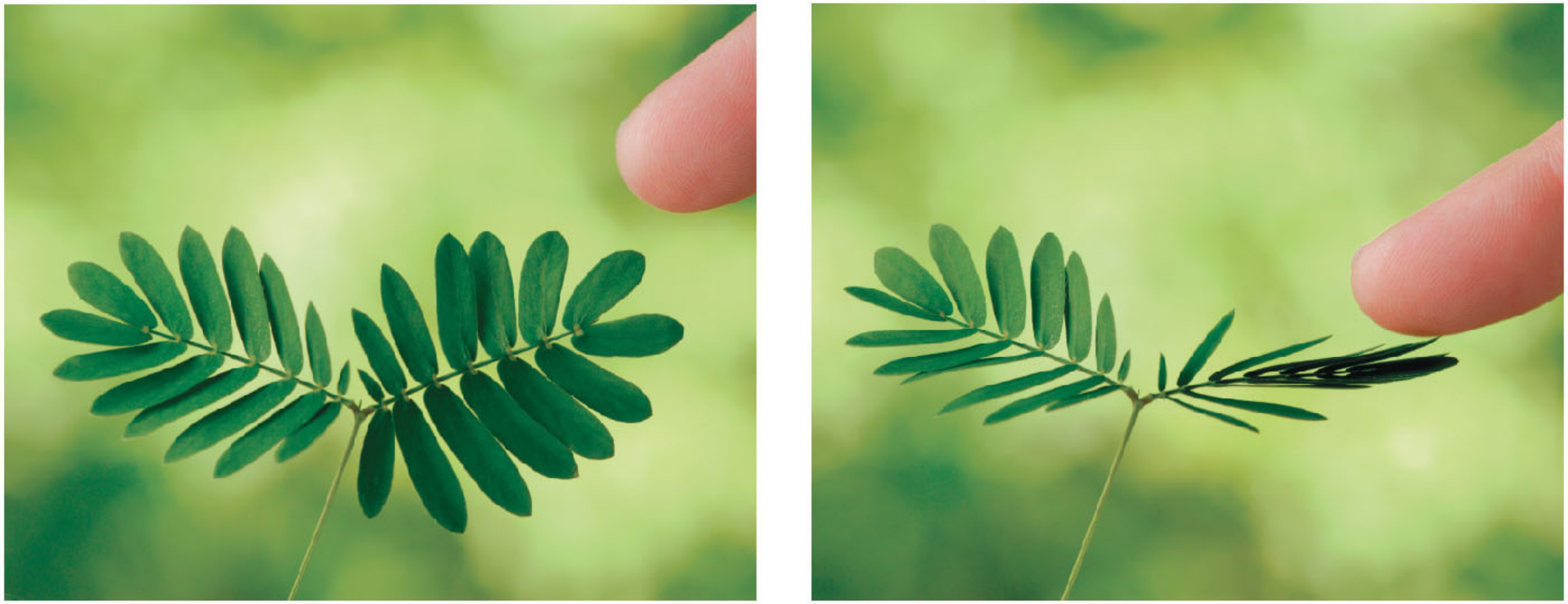
- Some *Arabidopsis* mutants that lack statoliths are still capable of gravitropism
- Dense organelles, in addition to starch granules, may contribute to gravity detection

Mechanical Stimuli

- The term **thigmomorphogenesis** refers to changes in form that result from mechanical disturbance
  - For example, rubbing stems of young plants a couple of times daily results in plants that are shorter than controls

Figure 39.23

- **Thigmotropism** is growth in response to touch
- It occurs in vines and other climbing plants
- Some plants undergo rapid leaf movements in response to mechanical stimulation
  - For example, *Mimosa pudica* folds its leaflets and collapses in response to touch
- The touch response results from the transmission of electrical impulses called **action potentials**



(a) Unstimulated state (leaflets spread apart)

(b) Stimulated state (leaflets folded)

Video: Mimosa Leaves

Environmental Stresses

- Environmental stresses, such as flooding, drought, or extreme temperatures, can have adverse effects on survival, growth, and reproduction
- Stresses can be **biotic** (living) or **abiotic** (nonliving)
  - Biotic stresses include herbivores and pathogens
  - Abiotic stresses include drought, flooding, salt stress, heat stress, and cold stress

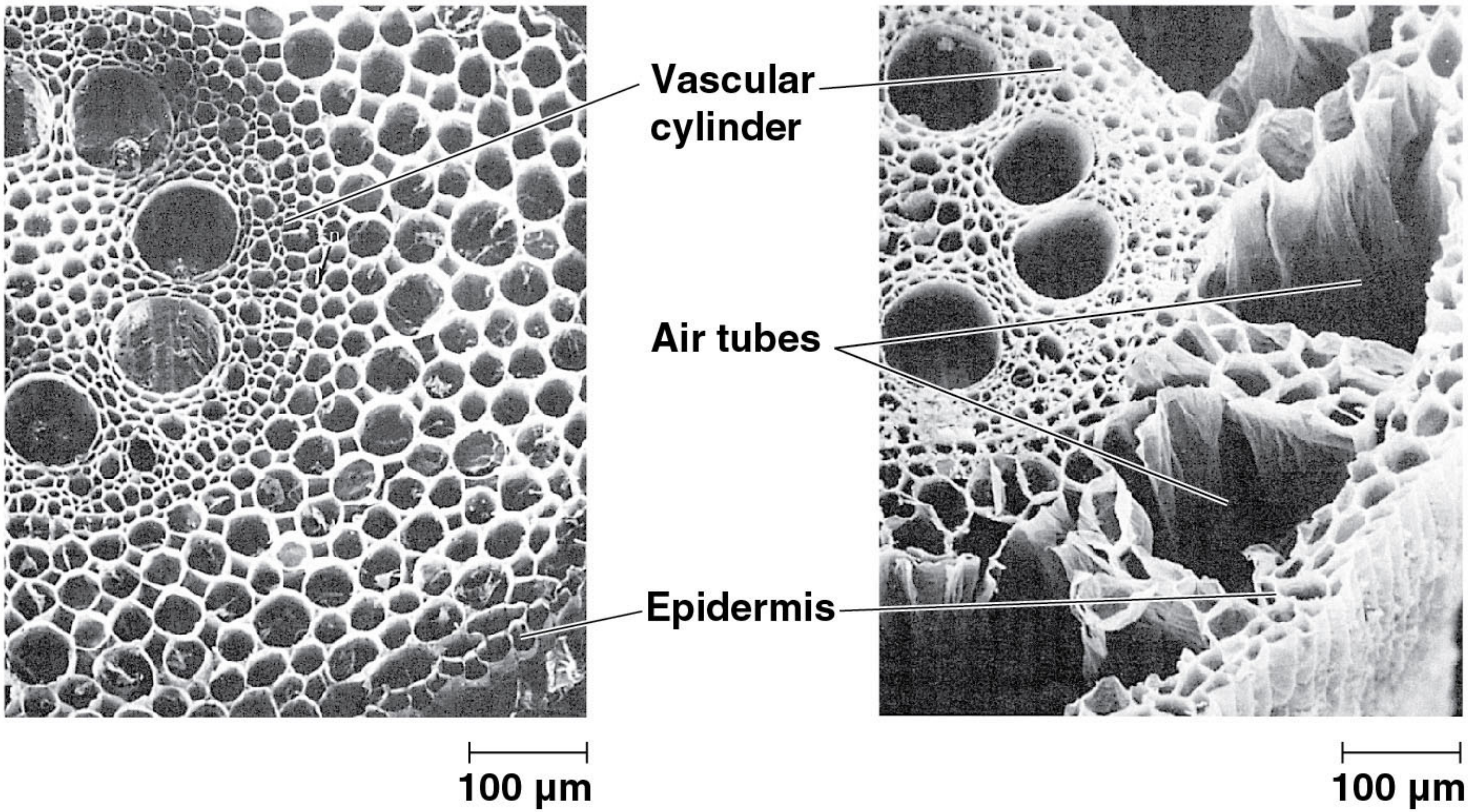
Drought

- Plants may wilt or die when water loss by transpiration exceeds water absorption
- During drought, plants reduce transpiration by closing stomata, reducing exposed surface area, and in some species, shedding leaves
- Plants respond to chemical signals from wilting neighbors, priming themselves to respond to drought stress

Flooding

- Waterlogged soils lack the air spaces needed to provide oxygen for cellular respiration in roots
- Enzymatic destruction of root cortex cells creates air tubes that function as “snorkels” helping plants survive oxygen deprivation during flooding
- Some plants, such as mangroves, also produce aerial roots

Figure 39.25



(a) Control root (aerated)

(b) Experimental root (nonaerated)

Salt Stress

- Sodium and some other ions are toxic to plants in high concentrations
- Salt can also lower the water potential of the soil solution and reduce water uptake
- Plants respond to salt stress by producing solutes well tolerated at high concentrations
- This process keeps the water potential of cells more negative than that of the soil solution

Heat Stress

- Excessive heat can denature a plant's enzymes
- Closing stomata can reduce water loss, but at the cost of the evaporative cooling provided by transpiration
- **Heat-shock proteins** are produced at temperatures above 40ºC to help protect other proteins from heat stress

Cold Stress

- Cold temperatures decrease membrane fluidity
- Membrane fluidity is maintained in the cold by increasing the proportion of unsaturated fatty acids

- Ice formation during freezing reduces water potential outside the cell
- Frost-tolerant species reduce water loss by increasing solute concentration of the cytoplasm
- Plants, and many other organisms, have *antifreeze proteins* that hinder the formation of ice crystals
- Frost tolerance is increased in some crop plants by engineering antifreeze genes into their genomes

CONCEPT 39.5: Plants respond to attacks by pathogens and herbivores

- Plants have formed mutually beneficial interspecific interactions with many species including mycorrhizal fungi and animal pollinators
- Plants are also subject to attack by herbivorous animals and pathogenic viruses, bacteria, and fungi
- Defense systems have evolved to deter herbivory, prevent infection, and combat pathogens

Defenses Against Pathogens

- A plant’s first line of defense against infection is the barrier presented by the epidermis and periderm
- Pathogens can enter through wounds or natural openings, such as stomata
- Two types of immune response defend the plant after pathogens enter: PAMP-triggered immunity and effector-triggered immunity

PAMP-Triggered Immunity

- The first line of immune defense depends on the plant's ability to recognize **pathogen-associated molecular patterns (PAMPs)**
- These molecular sequences are specific to certain pathogens
- PAMP recognition starts a chain of signaling events leading to the production of antimicrobial chemicals and toughening of the cell wall

Effector-Triggered Immunity

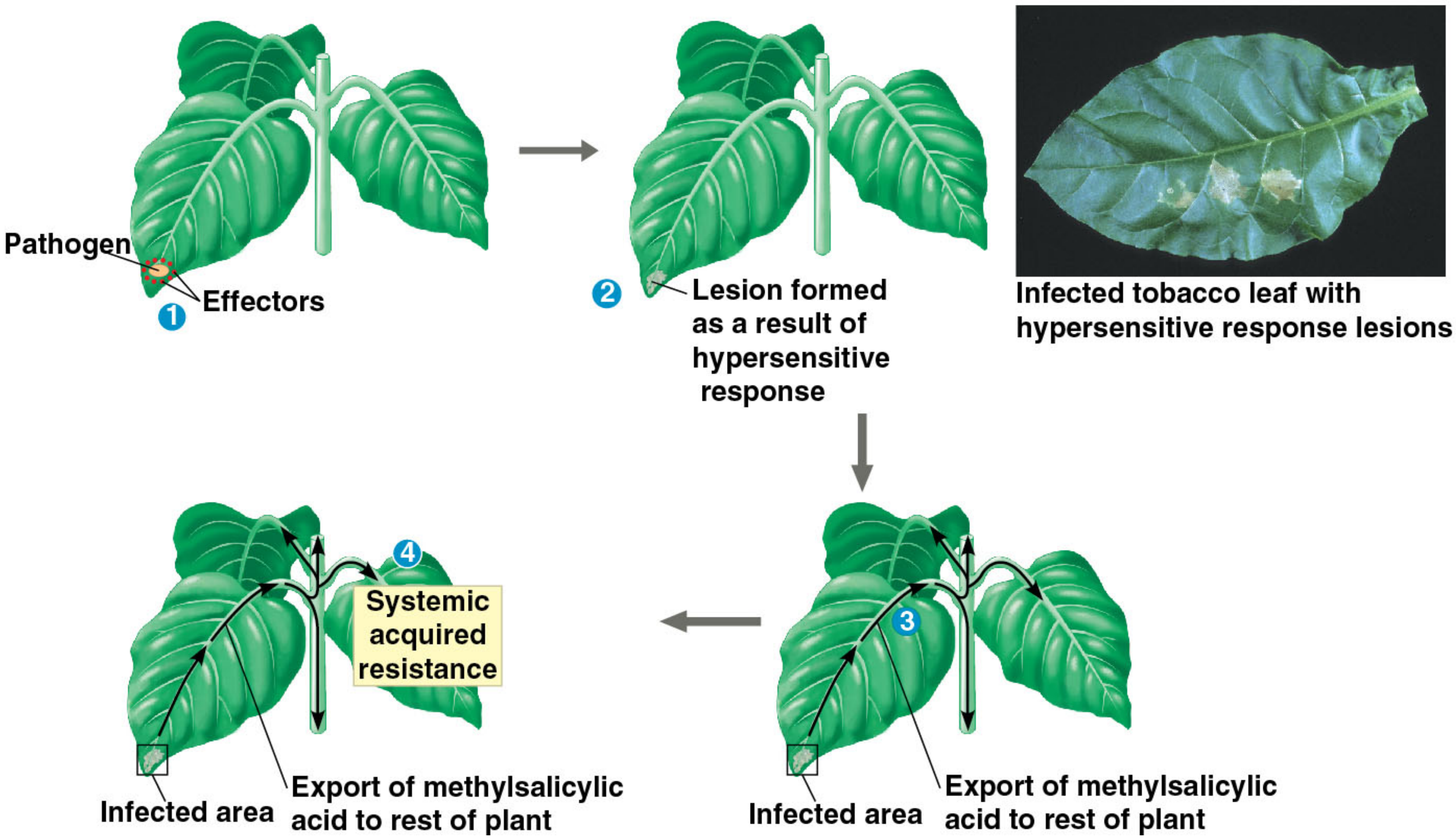
- Plants and pathogens have engaged in an evolutionary arms race
- Some pathogens have evolved the ability to deliver **effectors**, proteins that suppress PAMP-triggered immunity, to shut down plant immune systems
- Effector-triggered immunity evolved in response to these pathogens

- Effector-triggered immunity results from the action of hundreds of disease resistance (*R*) genes
- Each R protein is activated by a specific effector
- R proteins trigger signal transduction pathways that activate defenses in response to pathogen detection
- Defenses include the *hypersensitive response* and *systemic acquired resistance*

The Hypersensitive Response

- Local cell and tissue death at and near the infection site is the **hypersensitive response**
- This response induces production of enzymes and chemicals that attack the pathogen
- It also stimulates changes in cell walls, such as lignin formation, that confine the pathogen

Figure 39.26



Pathogen
Effectors
1
2
Lesion formed as a result of hypersensitive response
Infected tobacco leaf with hypersensitive response lesions
3
Infected area
Export of methylsalicylic acid to rest of plant
4
Systemic acquired resistance
Infected area
Export of methylsalicylic acid to rest of plant

Systemic Acquired Resistance

- **Systemic acquired resistance** arises from the plant-wide expression of defense genes
- It "sounds the alarm" of infection to the whole plant and provides protection from a diversity of pathogens for several days

- Methylsalicylic acid is a signaling molecule produced around the infection site
- It is carried to other remote sites in the phloem and converted to **salicylic acid**
- Salicylic acid triggers the defense system to respond rapidly to another infection

- Plant disease epidemics can alter plant community structure when they occur in natural populations
- In crop plants, they have the potential to cause starvation and suffering in human populations
- Plant biologists are stockpiling the seeds of wild relatives of crop plants to preserve the genetic diversity required to curb future plant epidemics

Defenses Against Herbivores

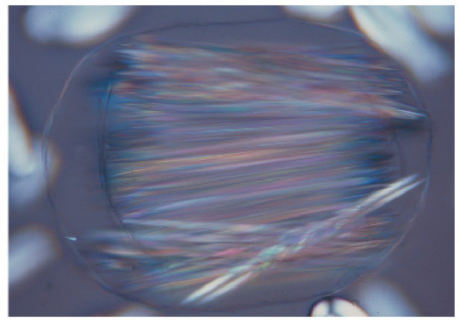
- **Herbivory**, animals eating plants, can restrict plant growth because energy is diverted into defense
- Plants counter excessive herbivory with defenses that can be observed at multiple levels of biological organization

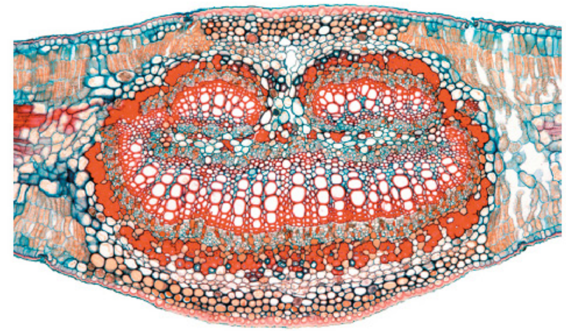
MAKE CONNECTIONS:
Levels of Plant Defenses Against Herbivores

Molecular Level

Cellular Level

Tissue Level





Organ Level

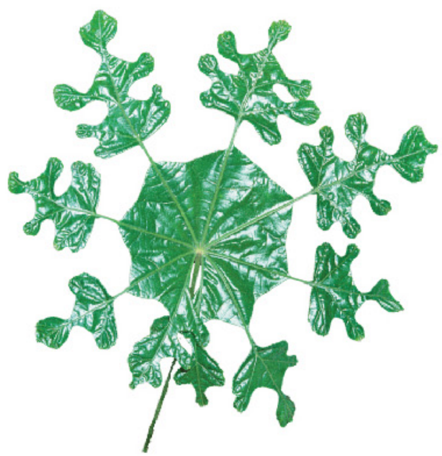


Figure 39.27 Make connections: levels of plant defenses against herbivores

Molecular-Level Defenses

- Chemical compounds such as terpenoids, phenolics, and alkaloids are produced to deter attackers
- These chemicals can disrupt herbivore development or digestion, or make plants taste unpleasant

Figure 39.27

Molecular-Level Defenses

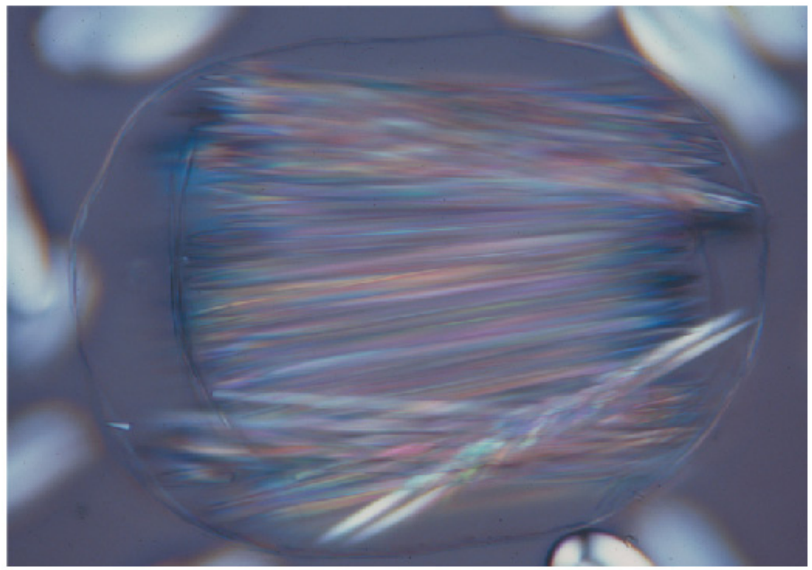
Opium poppy fruit

Cellular-Level Defenses

- Cells may be specialized to form trichomes, store chemical deterrents, or produce irritants

Figure 39.27

Cellular-Level Defenses

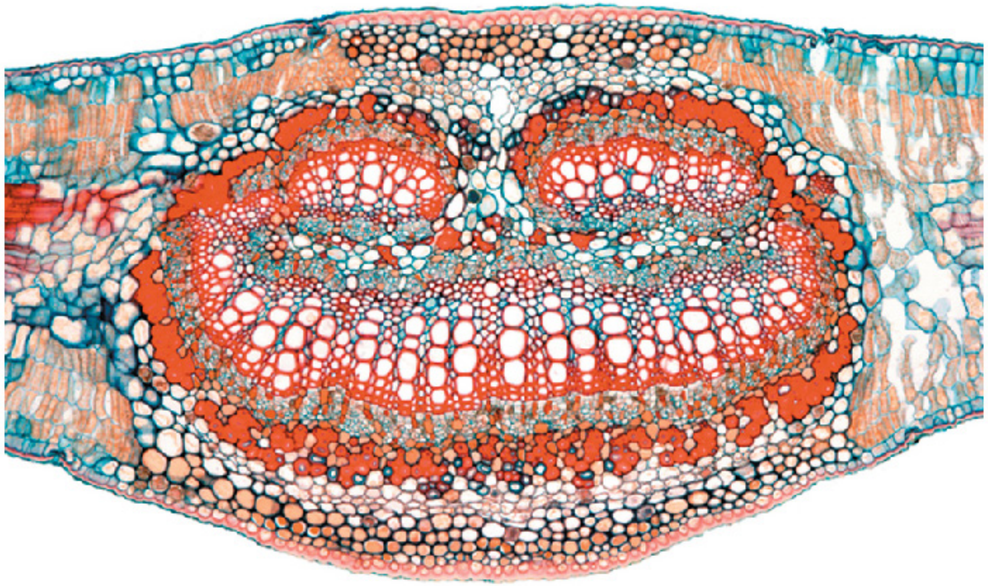


Raphide crystals from taro plant

Tissue-Level Defenses

- Some leaves are toughened with sclerenchyma tissue, making them difficult for herbivores to chew

Tissue-Level Defenses



Cross section through the major vein of an olive leaf

Organ-Level Defenses

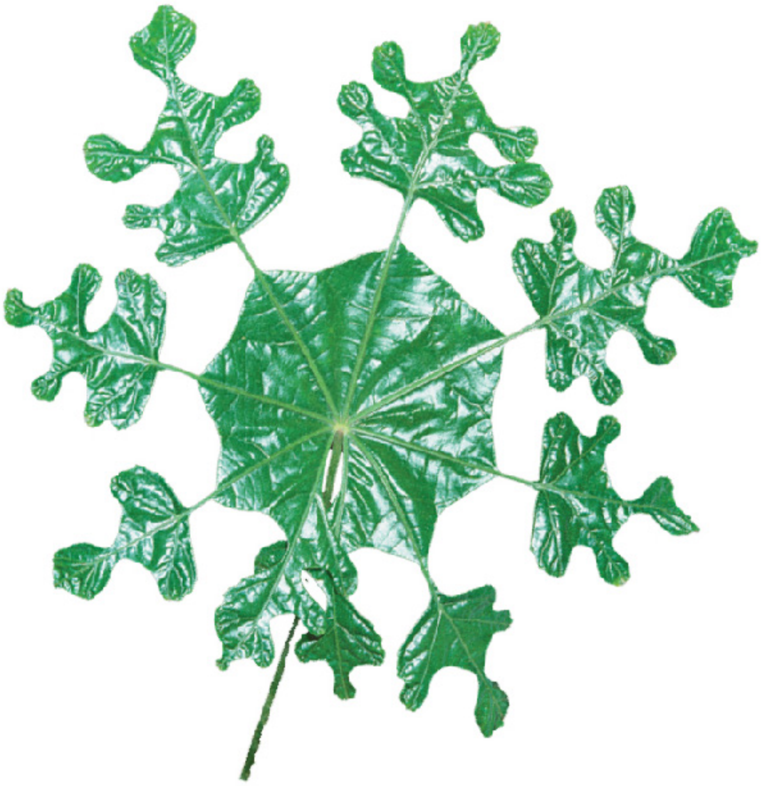
- Leaves can be modified into spines and bristles to provide mechanical defense
- Some species have adaptations that make the leaves appear less attractive to herbivores
  - For example, leaves may appear partially eaten, as in the snowflake plant
  - Other species have structures that mimic insect eggs to deter female insects from laying eggs

Figure 39.27

Organ-Level Defenses

Bristies on cactus spines

Organ-Level Defenses



Leaf of snowflake plant

Organ-Level Defenses

Egg mimicry on leaf of passion flower plant

Organismal-Level Defenses

- Plants may alter their physiology in response to attack by herbivores
  - For example, tobacco plants alter their flowering time from night to morning in response to feeding by hawk-moth larvae

Organismal-Level Defenses

Hummingbird pollinating wild tobacco plant

Population-Level Defenses

- Some plants release chemicals in response to herbivore attack that trigger defense responses in other nearby plants
- Other plant populations use masting, synchronous mass seed production following long intervals, to ensure at least some seeds survive herbivory

Figure 39.27

Population-Level Defenses

Flowering bamboo plants

Community-Level Defenses

- Some plants “recruit” predatory animals that help defend against specific herbivores
  - For example, in response to herbivore attack, some plants release chemicals that attract parasitoid wasps
  - The wasps lay eggs inside caterpillars feeding on the plant; the developing larvae feed on the caterpillar

Community-Level Defenses

Parasitoid wasp cocoons on caterpillar host

Community-Level Defenses

Adult wasp emerging from a cocoon

Figure 39.UN01

How the Experiment Was Done

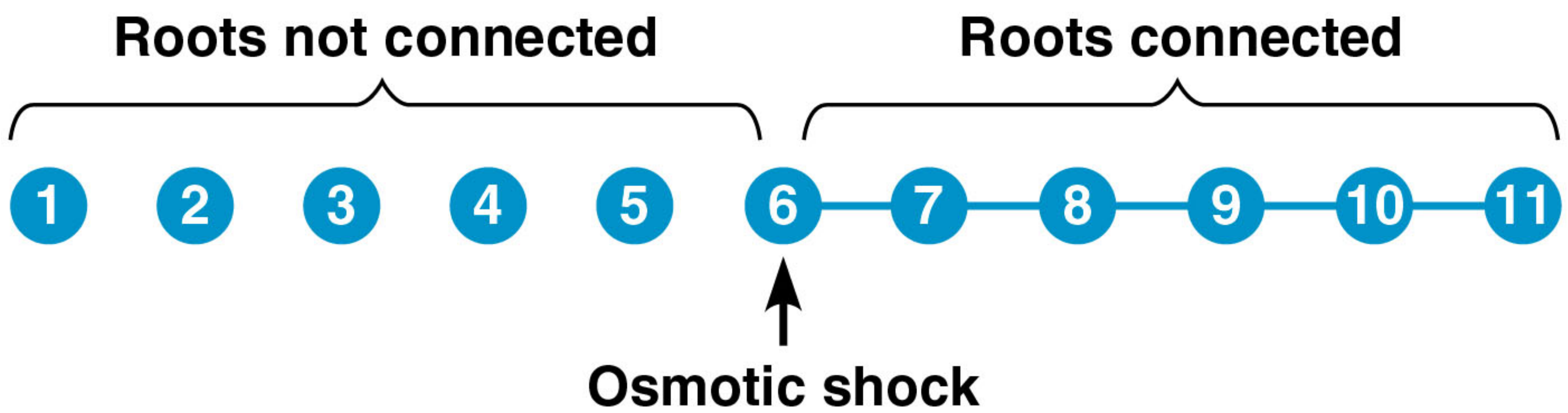
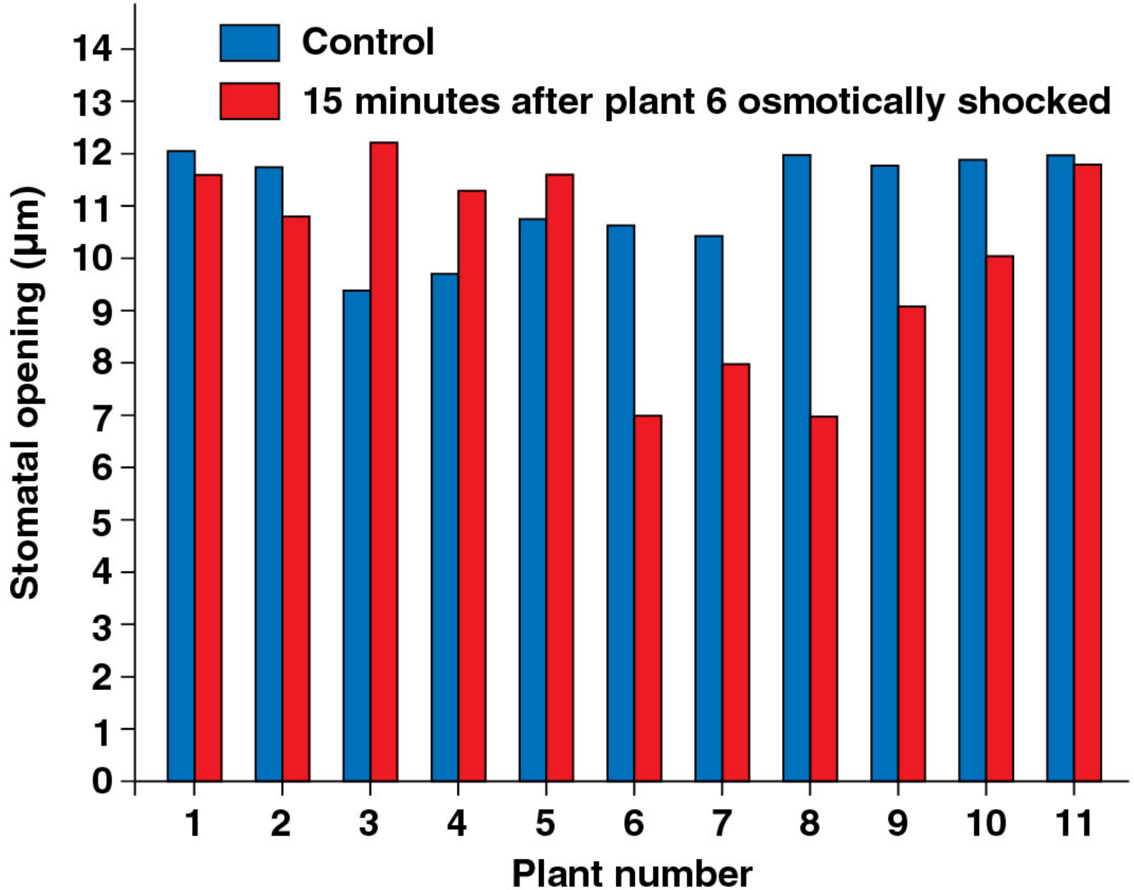


Figure 39.UN02

Data from the Experiment



Data from O. Falik et al., Rumor has it. . . : Relay communication of stress cues in plants, *PLoS ONE* 6(11):e23625 (2011).

Figure 39.UN03

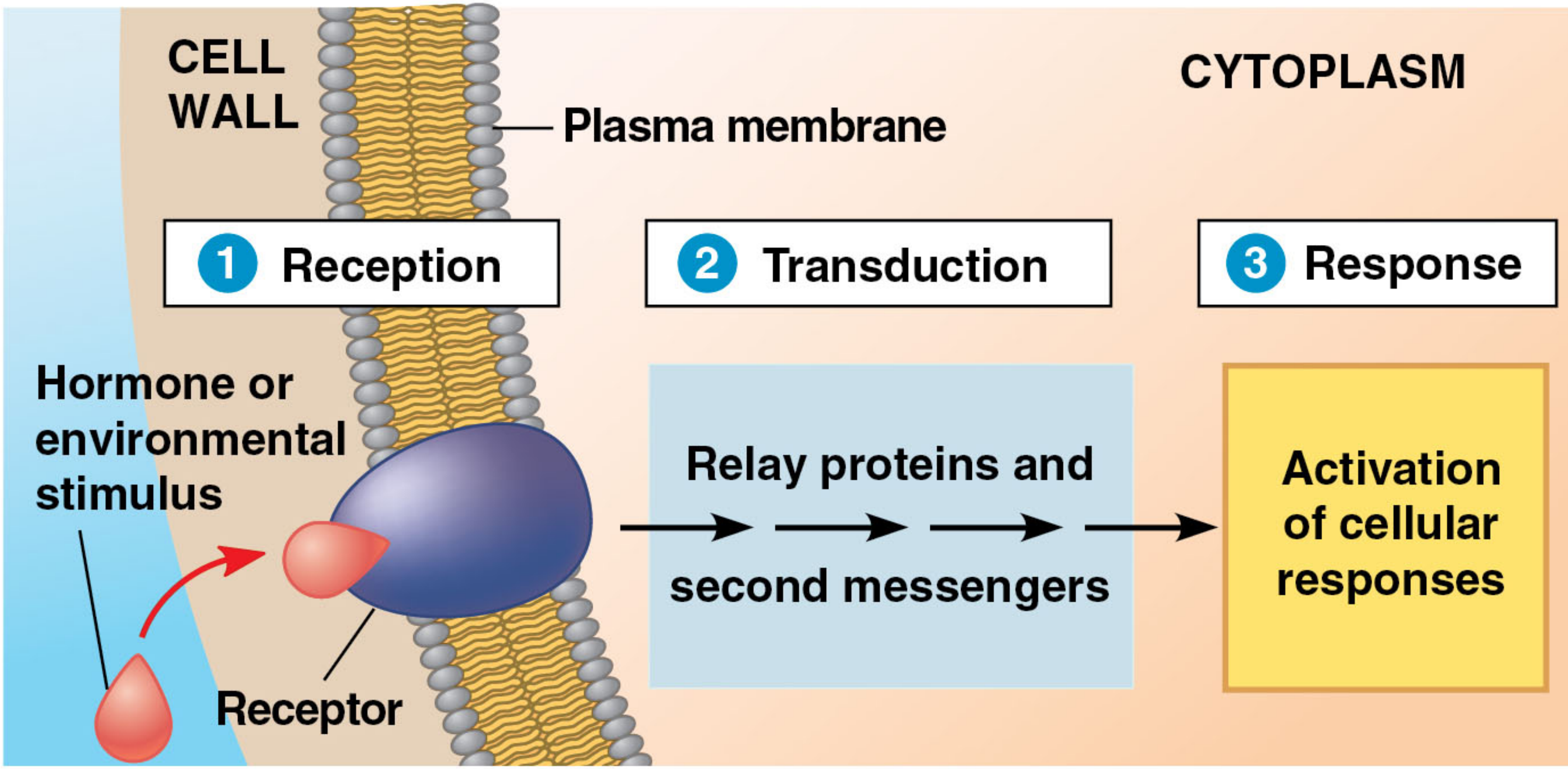


Figure 39.UN04

Plant Hormone	Major Responses
Auxin (IAA)	Stimulates cell elongation; regulates branching and organ bending (phototropism and gravitropism)
Cytokinins	Stimulate plant cell division and differentiation; promote axillary bud growth
Gibberellins	Promote stem elongation; help seeds break dormancy and use stored reserves
Abscisic acid (ABA)	Promotes stomatal closure in response to drought; promotes seed dormancy
Ethylene	Mediates senescence, leaf abscission, fruit ripening, and obstacle avoidance by shoots (the triple response)
Brassinosteroids	Chemically similar to the sex hormones of animals; induce cell elongation and division
Jasmonates	Mediate plant defenses against insect herbivores; regulate a wide range of physiological processes
Strigolactones	Regulate apical dominance, seed germination, and mycorrhizal associations

Figure 39.UN05

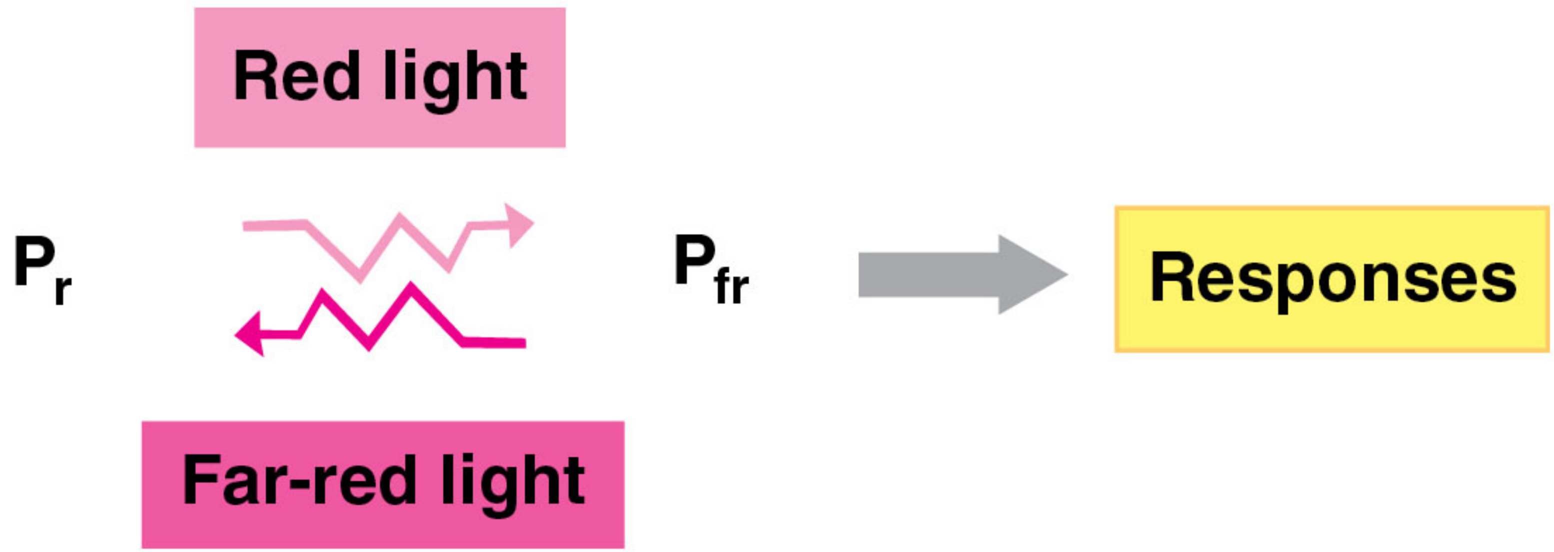


Figure 39.UN06

Environmental Stress	Major Response
Drought	ABA production, reducing water loss by closing stomata
Flooding	Formation of air tubes that help roots survive oxygen deprivation
Salt	Avoiding osmotic water loss by producing solutes tolerated at high concentrations
Heat	Synthesis of heat-shock proteins, which reduce protein denaturation at high temperatures
Cold	Adjusting membrane fluidity; avoiding osmotic water loss; producing antifreeze proteins

Figure 39.UN07

	Control	Ethylene added	Ethylene synthesis inhibitor
Wild-type			
Ethylene insensitive (*ein*)			
Ethylene overproducing (*eto*)			
Constitutive triple response (*ctr*)			

Figure 39.UN07