CAMPBELL BIOLOGY IN FOCUS

Urry • Cain • Wasserman • Minorsky • Jackson • Reece

31

Plant Responses to Internal and External Signals

Lecture Presentations by
Kathleen Fitzpatrick and Nicole Tunbridge

Overview: The Race to Live

- Young seedlings must outcompete their neighbors in the race for resources in order to survive
- Unlike animals, which respond through movement, plants must respond to environmental challenges by altering their growth and development

Figure 31.1

Concept 31.1: Plant hormones help coordinate growth, development, and responses to stimuli

- Plant **hormones** are chemical signals that modify or control one or more specific physiological processes within a plant

- Plant hormones are produced in very low concentration, but a minute amount can greatly affect growth and development of a plant organ
- Most aspects of plant growth and development are under hormonal control

The Discovery of Plant Hormones

- Any response resulting in curvature of organs toward or away from a stimulus is called a **tropism**
- In the late 1800s, Charles Darwin and his son Francis conducted experiments on **phototropism**, a plant's response to light
- They observed that a grass seedling could bend toward light only if the tip of the coleoptile was present

- They postulated that a signal was transmitted from the tip to the elongating region

Figure 31.2

Results

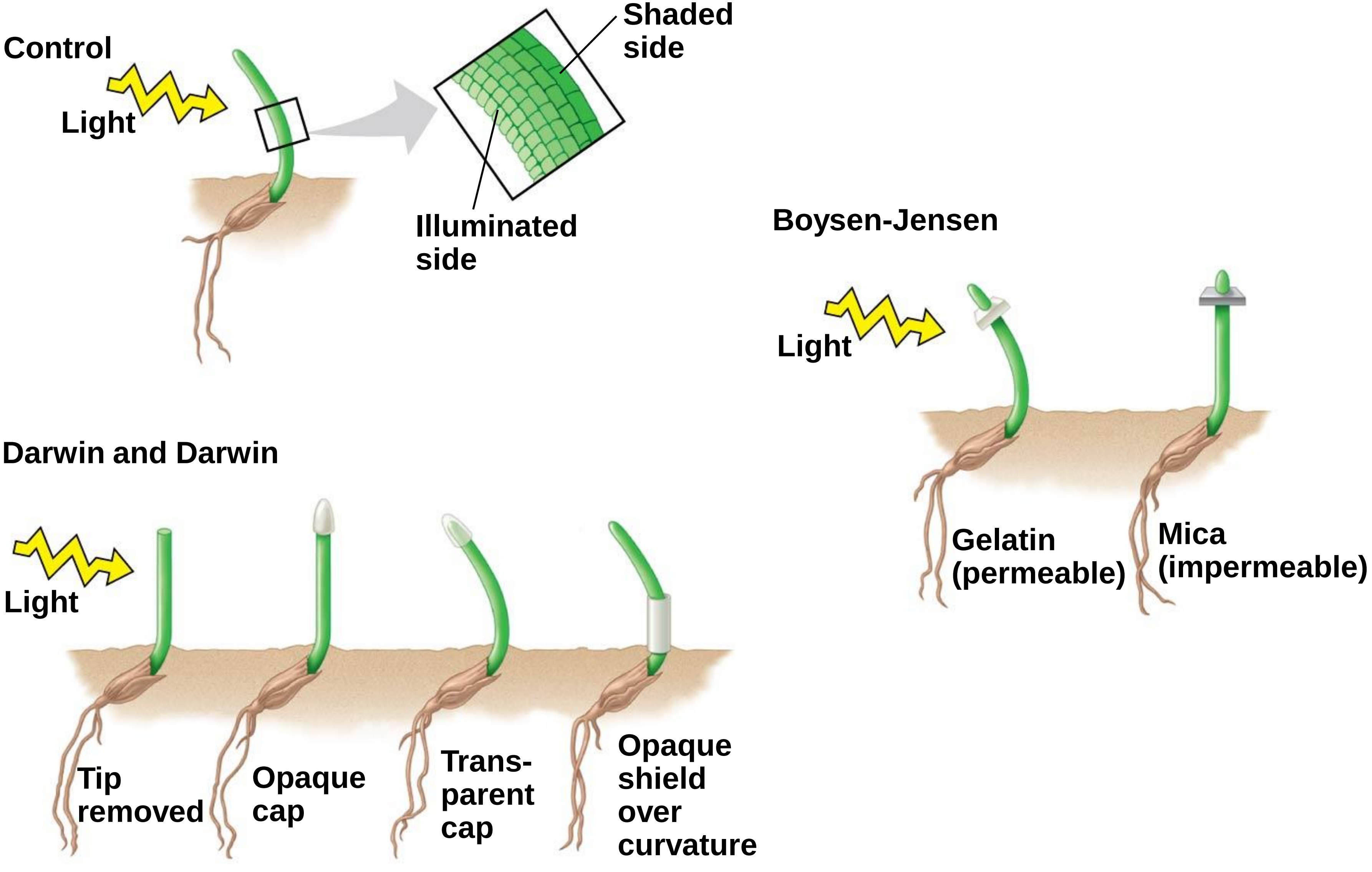
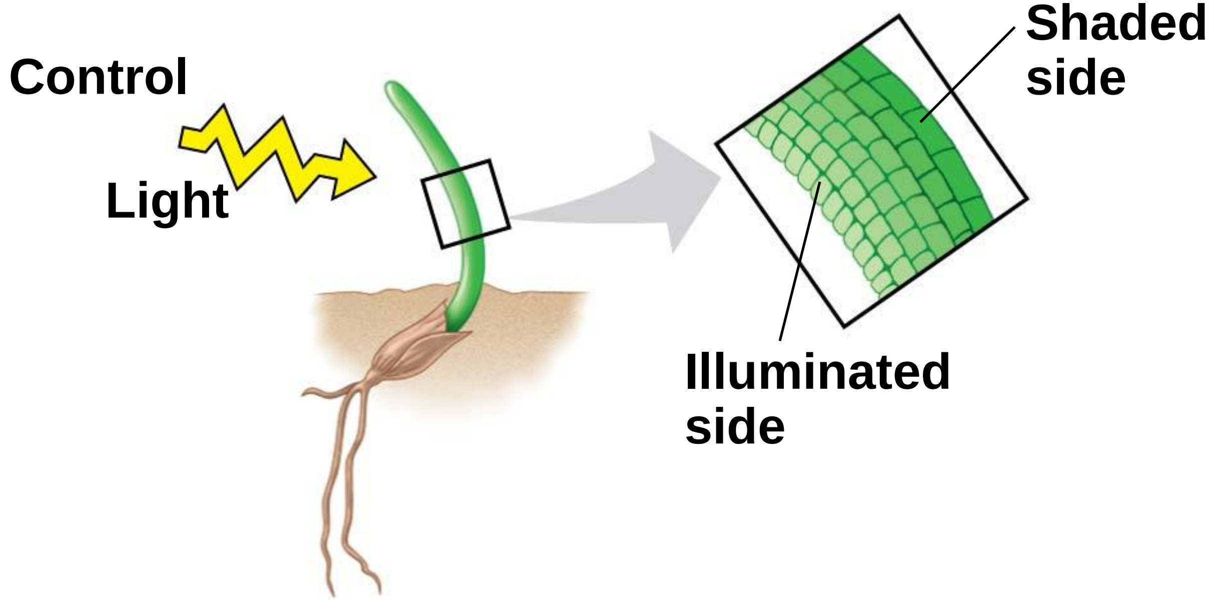
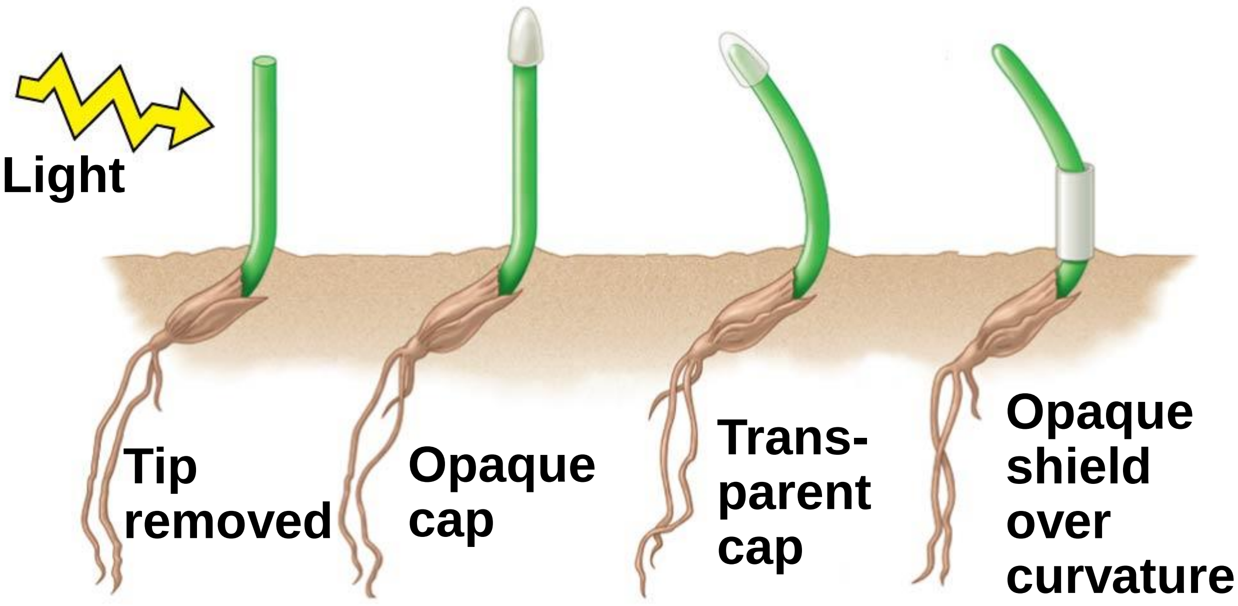


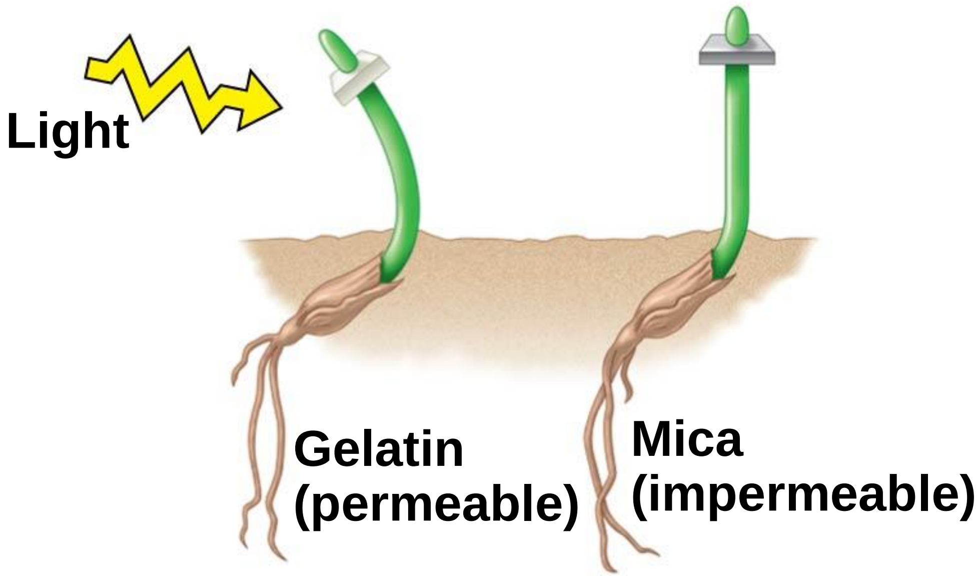
Figure 31.2a



Darwin and Darwin: Phototropism occurs only when the tip is illuminated.



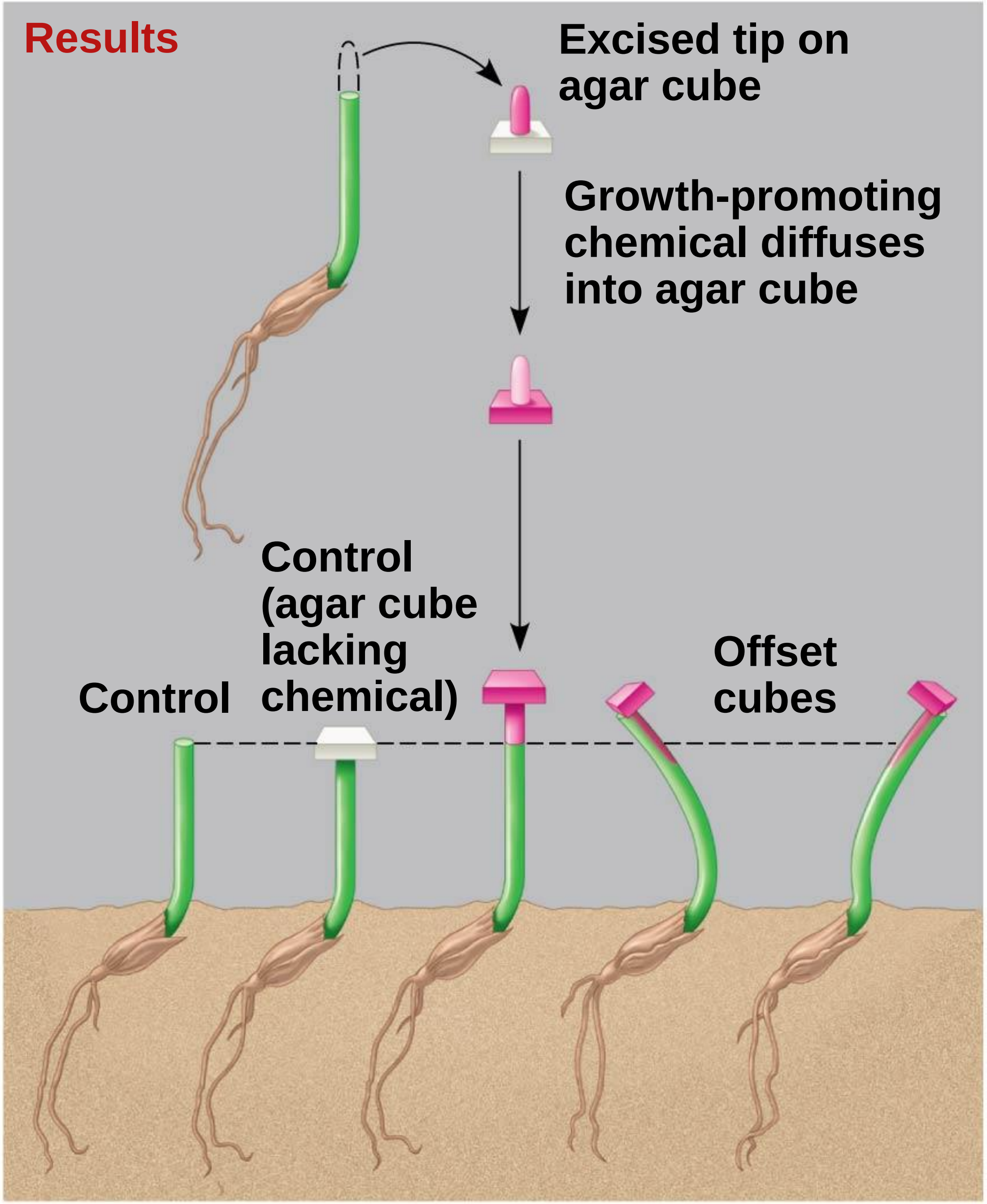
Boysen-Jensen: Phototropism occurs when the tip is separated by a permeable barrier but not an impermeable barrier.



- In 1913, Peter Boysen-Jensen demonstrated that the signal was a mobile chemical substance

- In 1926, Frits Went extracted the chemical messenger for phototropism, auxin, by modifying earlier experiments

Figure 31.3



Results
Excised tip on agar cube
Growth-promoting chemical diffuses into agar cube
Control
Control (agar cube lacking chemical)
Offset cubes

A Survey of Plant Hormones

- The major classes of plant hormones include
  - Auxin
  - Cytokinins
  - Gibberellins
  - Brassinosteroids
  - Abscisic acid
  - Ethylene

Table 31.1 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	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.
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.
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; 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 fruit. 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.

Auxin

- 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
- Auxin is produced in shoot tips and is transported down the stem
- Auxin transporter proteins move the hormone from the basal end of one cell into the apical end of the neighboring cell

Figure 31.4

Results

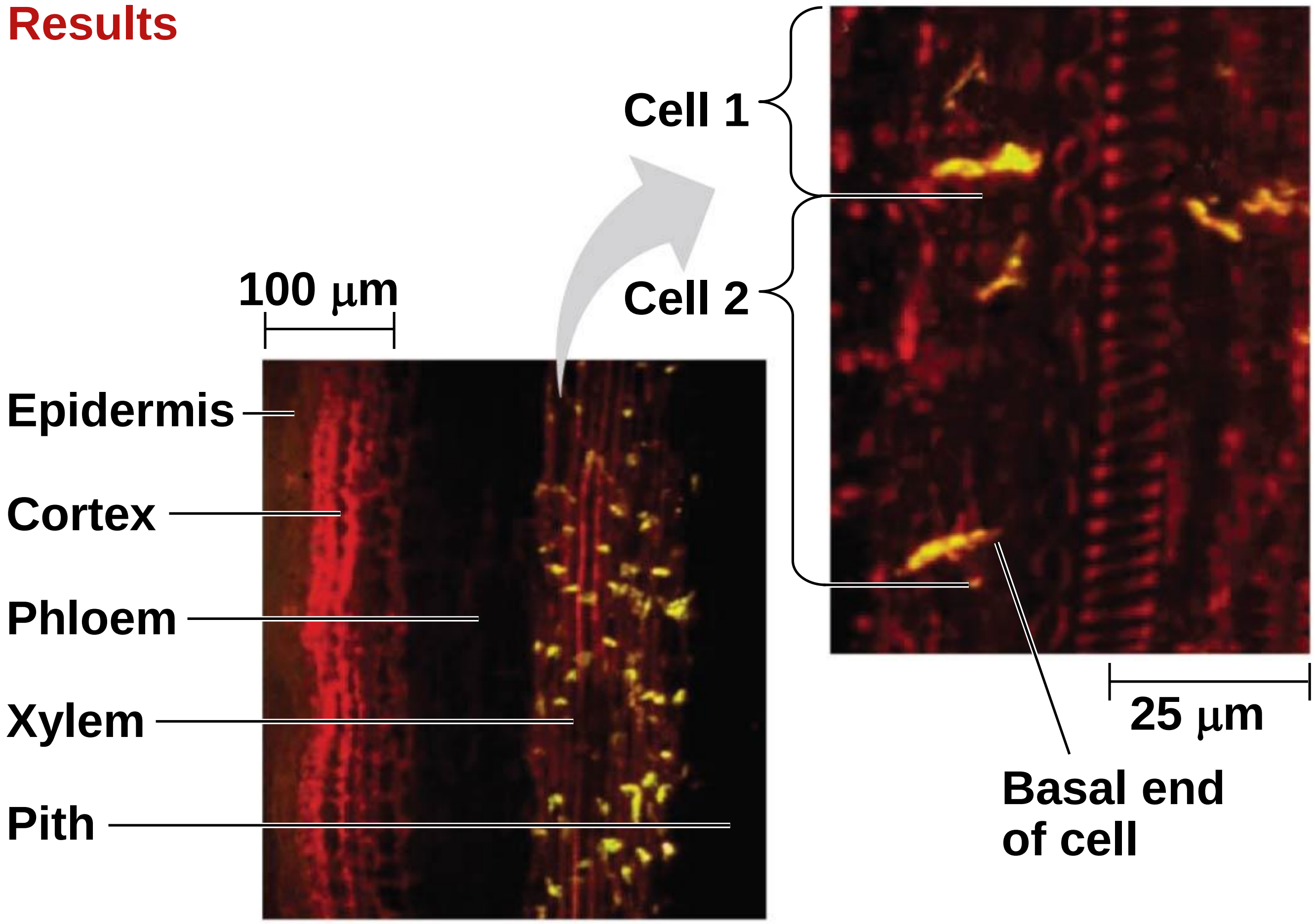


Figure 31.4a

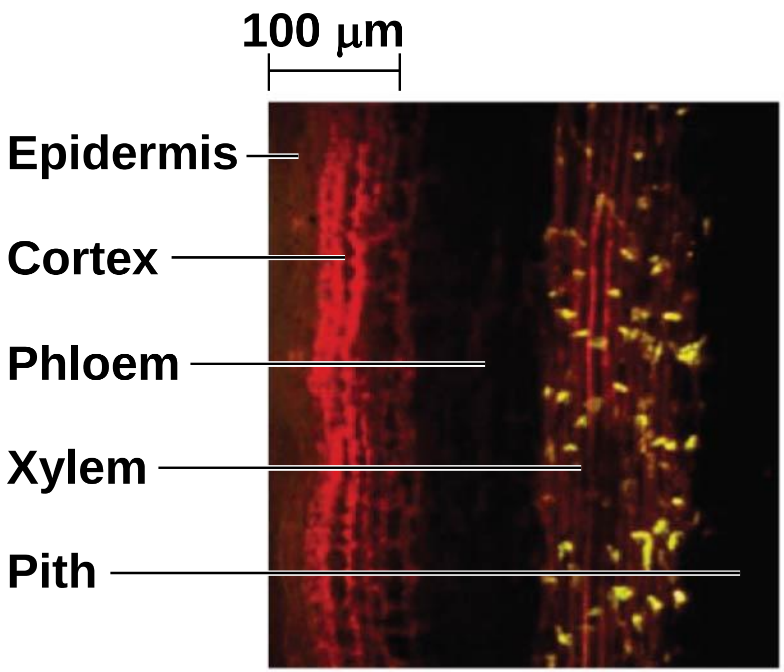
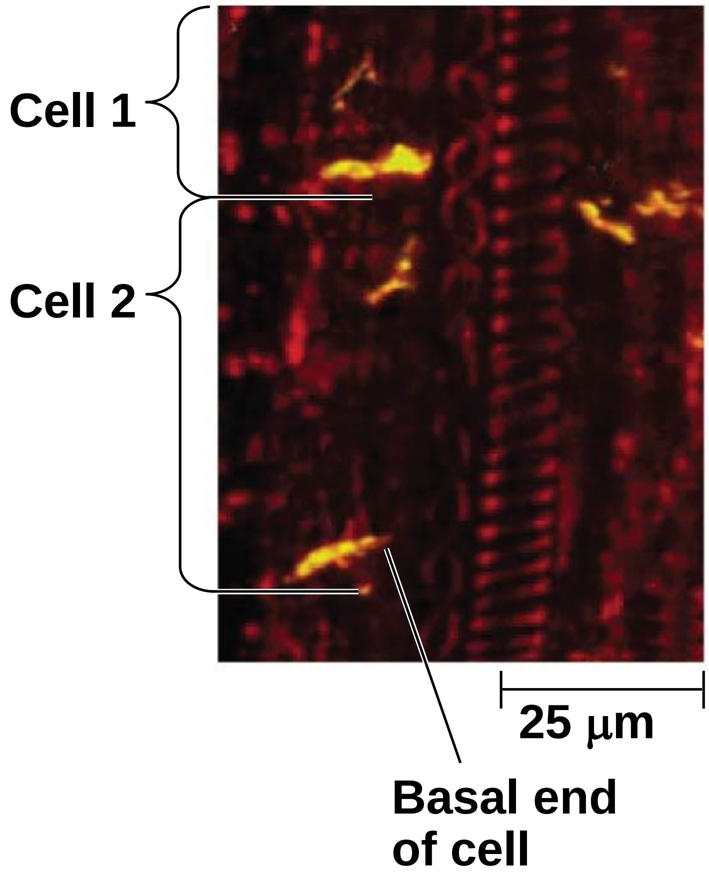
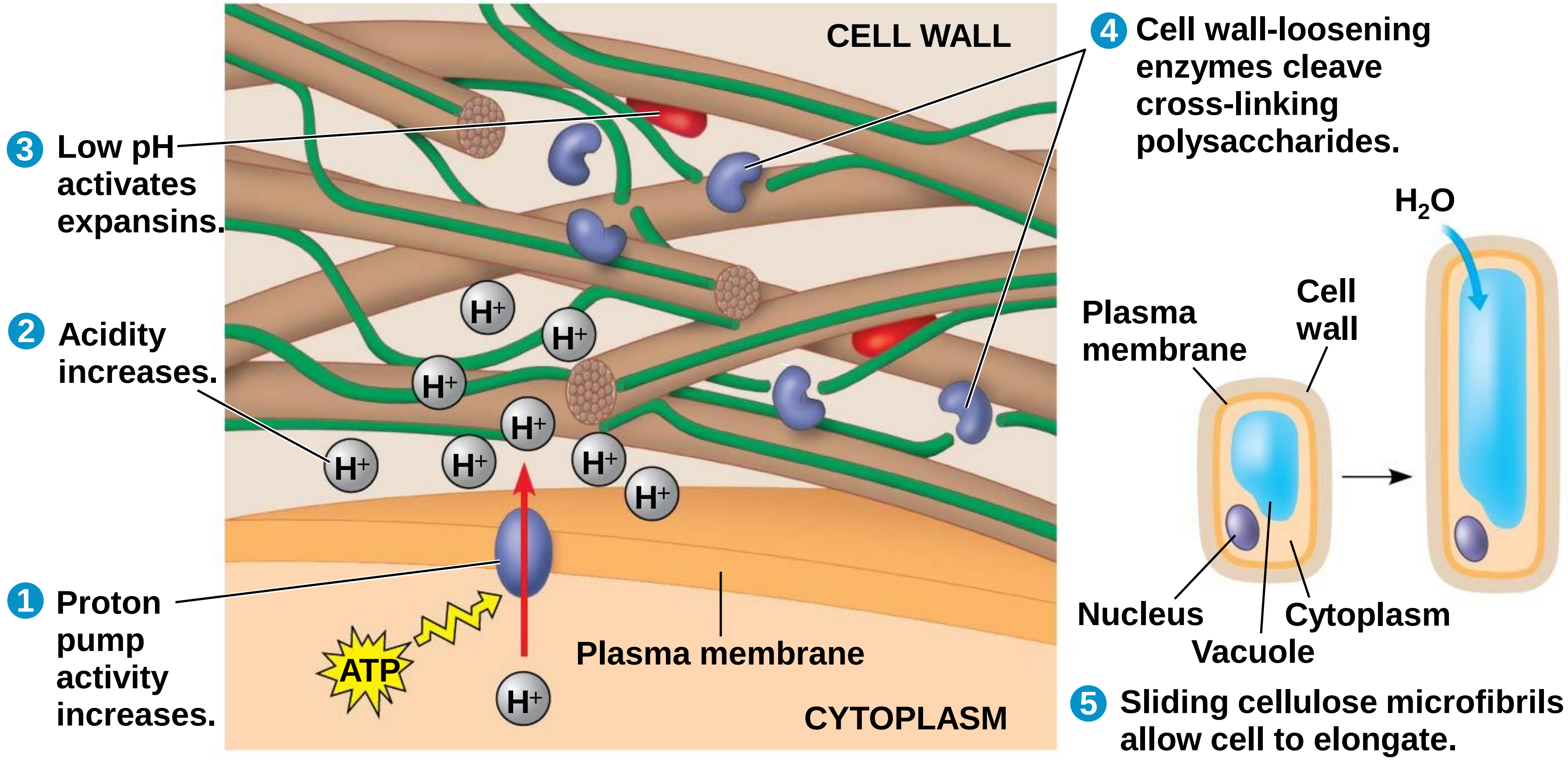


Figure 31.4b



- **The role of auxin in cell elongation:** Polar transport of auxin stimulates proton pumps in the plasma membrane
- According to the acid growth hypothesis, the proton pumps lower the pH in the cell wall, activating **expansins**, enzymes that loosen the wall’s fabric
- With the cellulose loosened, the cell can elongate

Figure 31.5



CELL WALL
4 Cell wall-loosening enzymes cleave cross-linking polysaccharides.
3 Low pH activates expansins.
2 Acidity increases.
1 Proton pump activity increases.
H+
ATP
Plasma membrane
CYTOPLASM
H_2O
Plasma membrane
Cell wall
Nucleus
Vacuole
Cytoplasm
5 Sliding cellulose microfibrils allow cell to elongate.

Figure 31.5a

4 **Cell wall-loosening enzymes cleave cross-linking polysaccharides.**

3 **Low pH activates expansins.**

2 **Acidity increases.**

1 **Proton pump activity increases.**

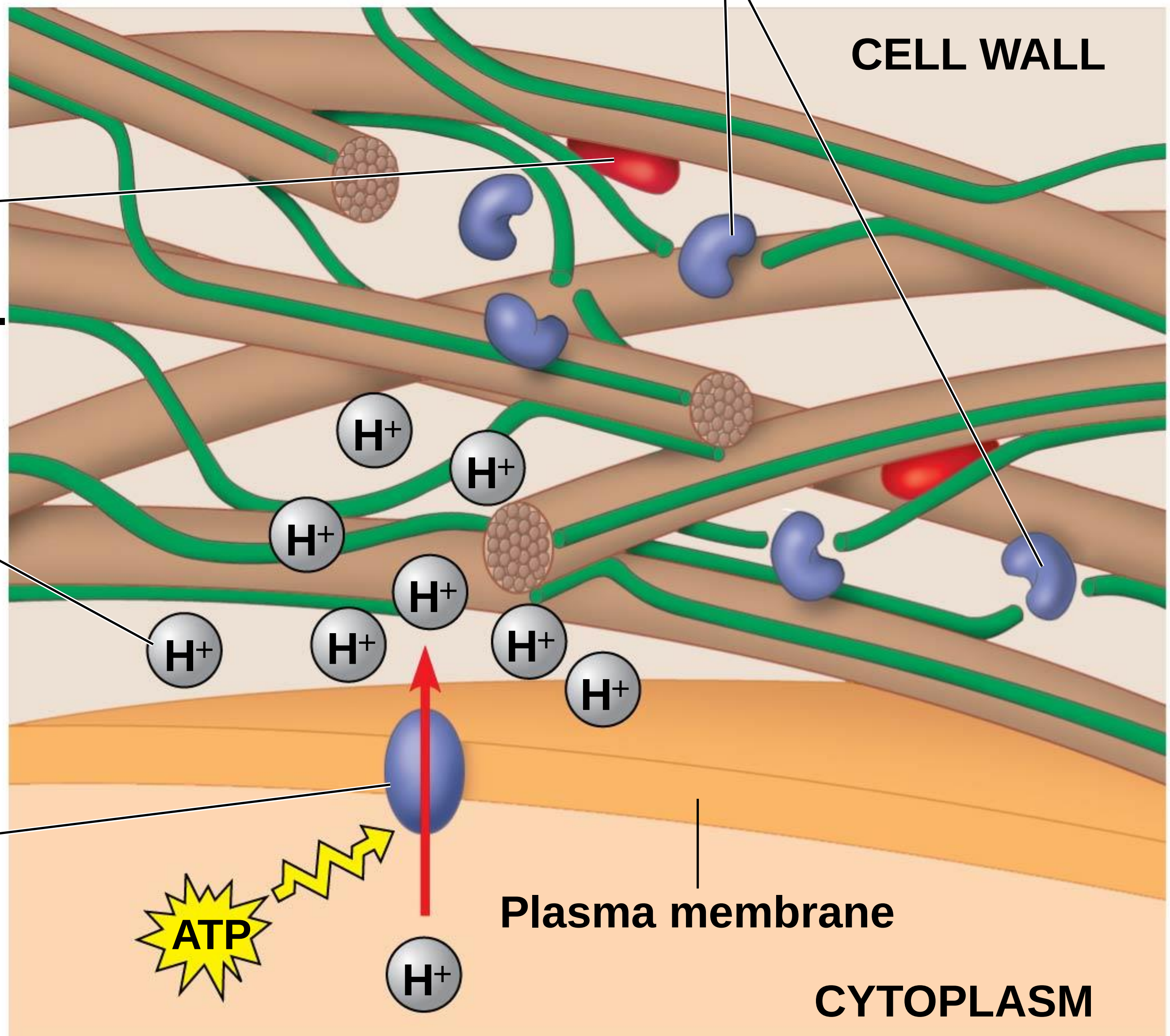
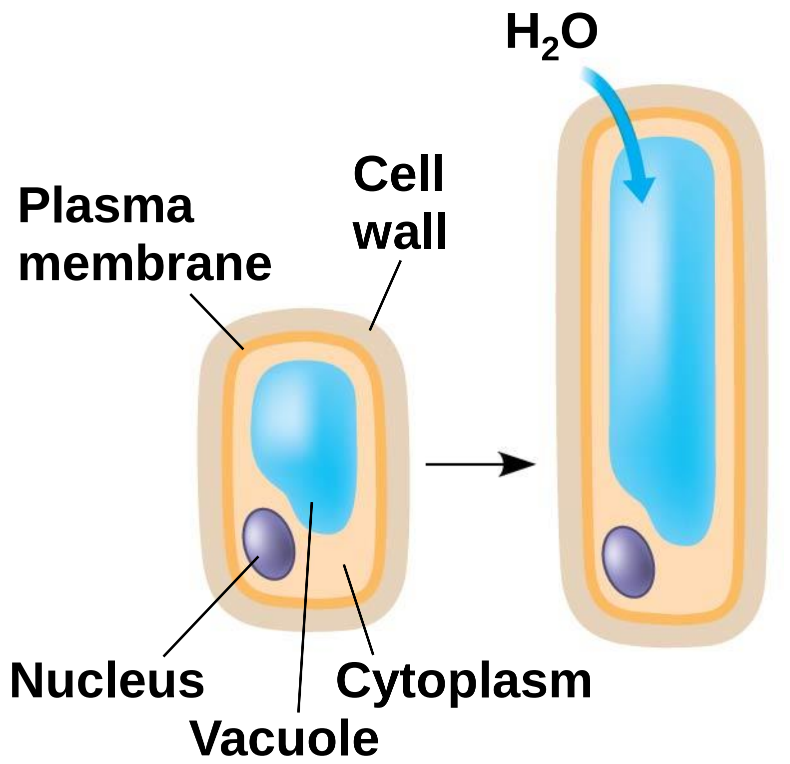


Figure 31.5b



5 **Sliding cellulose microfibrils allow cell to elongate.**

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

- **Auxin's role in plant development:** Polar transport of auxin controls the spatial organization of the developing plant
- Reduced auxin flow from the shoot of a branch stimulates growth in lower branches
- Auxin transport plays a role in phyllotaxy, the arrangement of leaves on the stem

- **Practical uses for auxins**
  - The auxin indolbutyric acid (IBA) stimulates adventitious roots and is used in vegetative propagation of plants by cuttings
  - An overdose of synthetic auxins can kill plants
    - For example 2,4-D is used as an herbicide on eudicots
  - Tomato growers spray their plants with synthetic auxins to stimulate fruit growth

Cytokinins

- **Cytokinins** are so named because they stimulate cytokinesis (cell division)

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

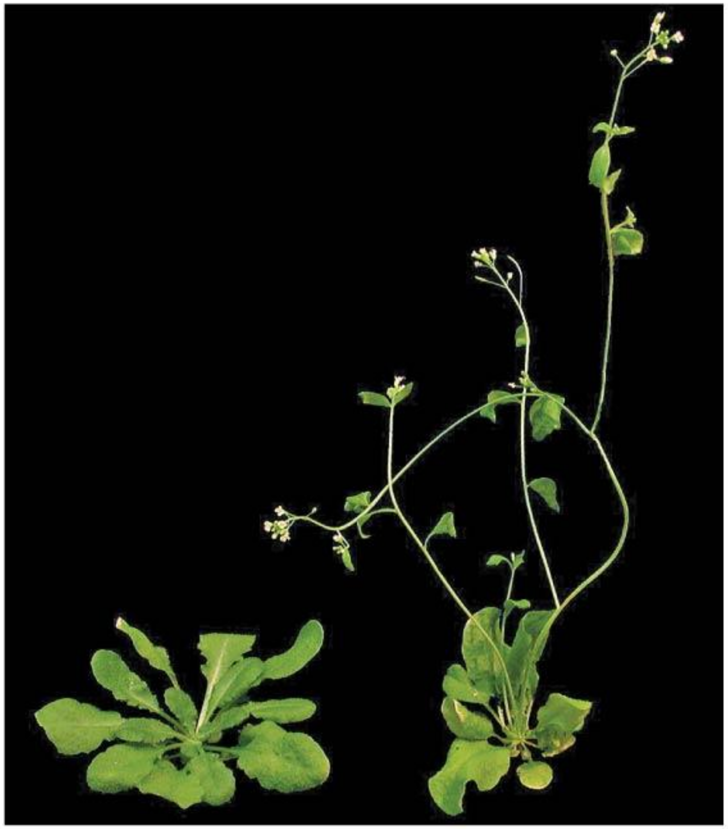
- **Anti-aging effects:** Cytokinins slow the aging of some plant organs by inhibiting protein breakdown, stimulating RNA and protein synthesis, and mobilizing nutrients from surrounding tissues

Gibberellins

- **Gibberellins** (GAs) have a variety of effects, such as stem elongation, fruit growth, and seed germination

- **Stem elongation:** Gibberellins stimulate stem and leaf growth by enhancing cell elongation and cell division
- Gibberellins are produced in young roots and leaves
- They can induce bolting, rabid growth of the floral stalk

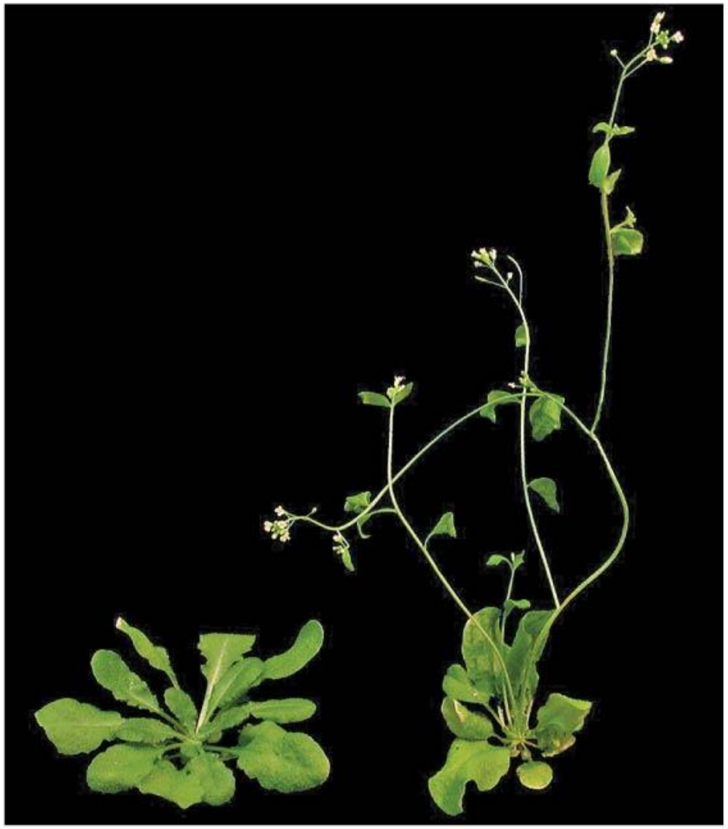
Figure 31.6



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

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

Figure 31.6a



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

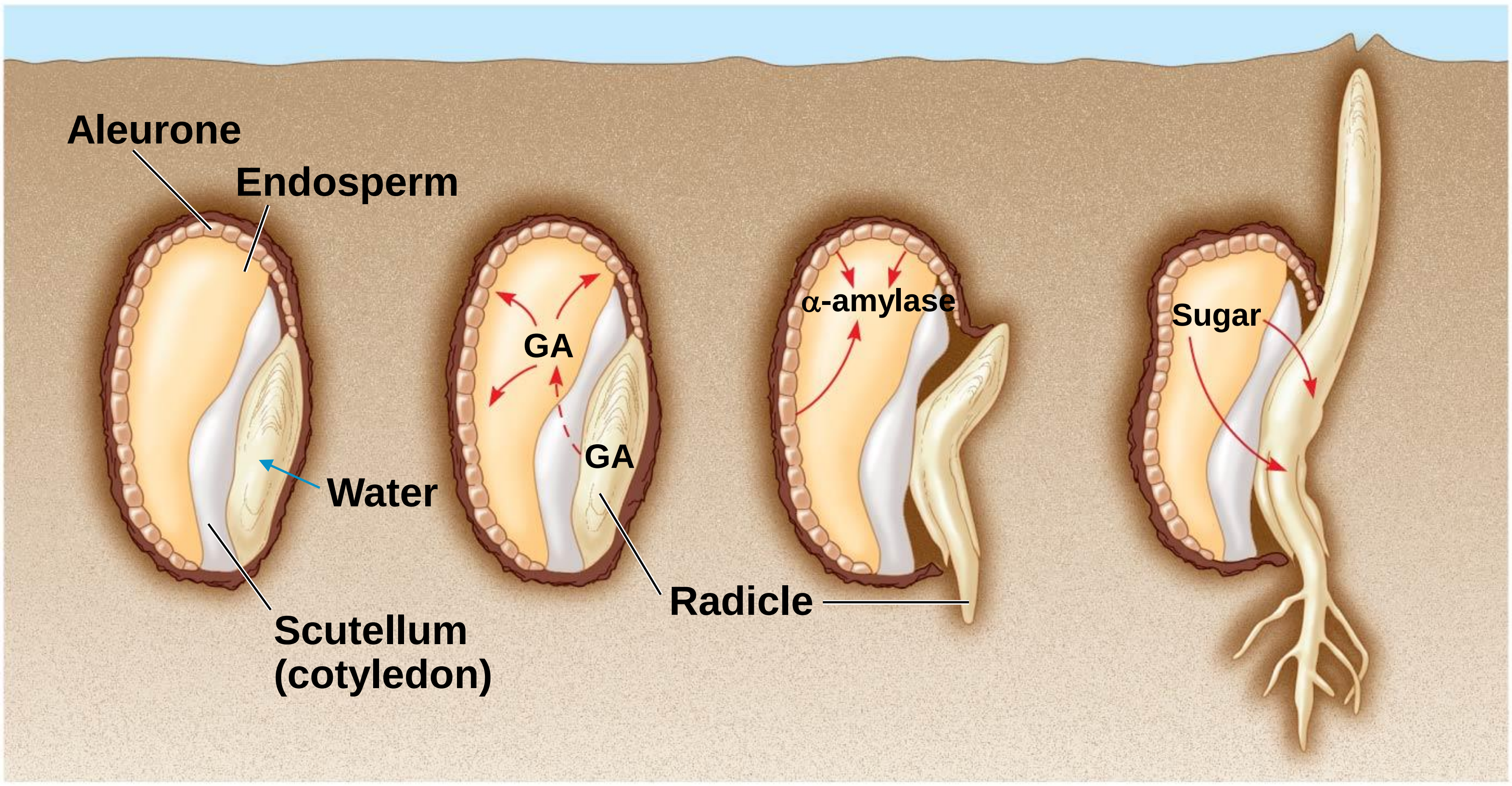
Figure 31.6b

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

- **Fruit growth:** In many plants, both auxin and gibberellins must be present for fruit to develop
- Gibberellins are used in spraying of Thompson seedless grapes

- **Germination:** After water is imbibed, release of gibberellins from the embryo signals seeds to germinate

Figure 31.7



Aleurone
Endosperm
Water
Scutellum (cotyledon)
GA
GA
Radicle
α-amylase
Sugar

Brassinosteroids

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

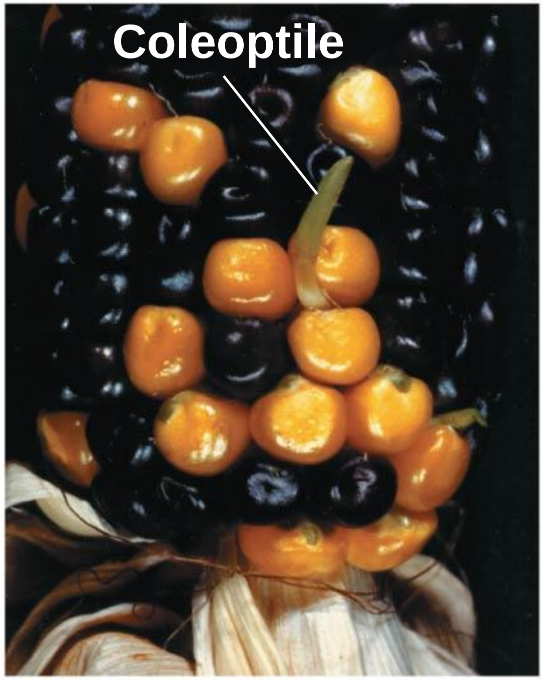
Abscisic Acid

- **Abscisic acid (ABA)** slows growth
- Two of the many effects of ABA include
  - Seed dormancy
  - Drought tolerance

- **Seed dormancy** ensures that the seed will germinate only in optimal conditions
- In some seeds, dormancy is broken when ABA is removed by heavy rain, light, or prolonged cold
- Precocious (early) germination can be caused by inactive or low levels of ABA

Figure 31.8

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

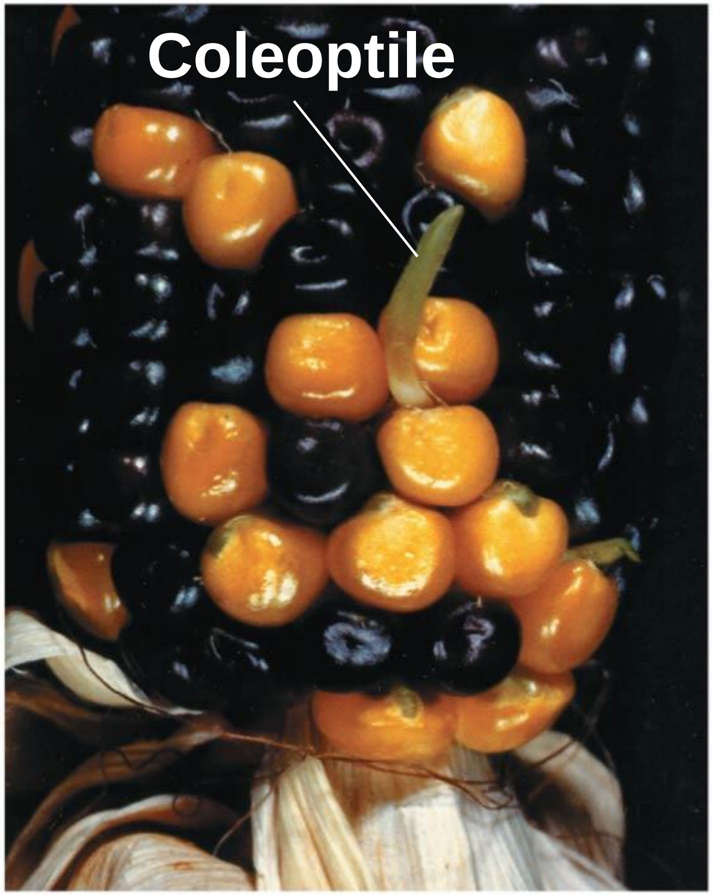


▲ **Maize mutant**

Figure 31.8a

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

Figure 31.8b



▲ **Maize mutant**

- **Drought tolerance:** ABA is the primary internal signal that enables plants to withstand drought
- ABA accumulation causes stomata to close rapidly

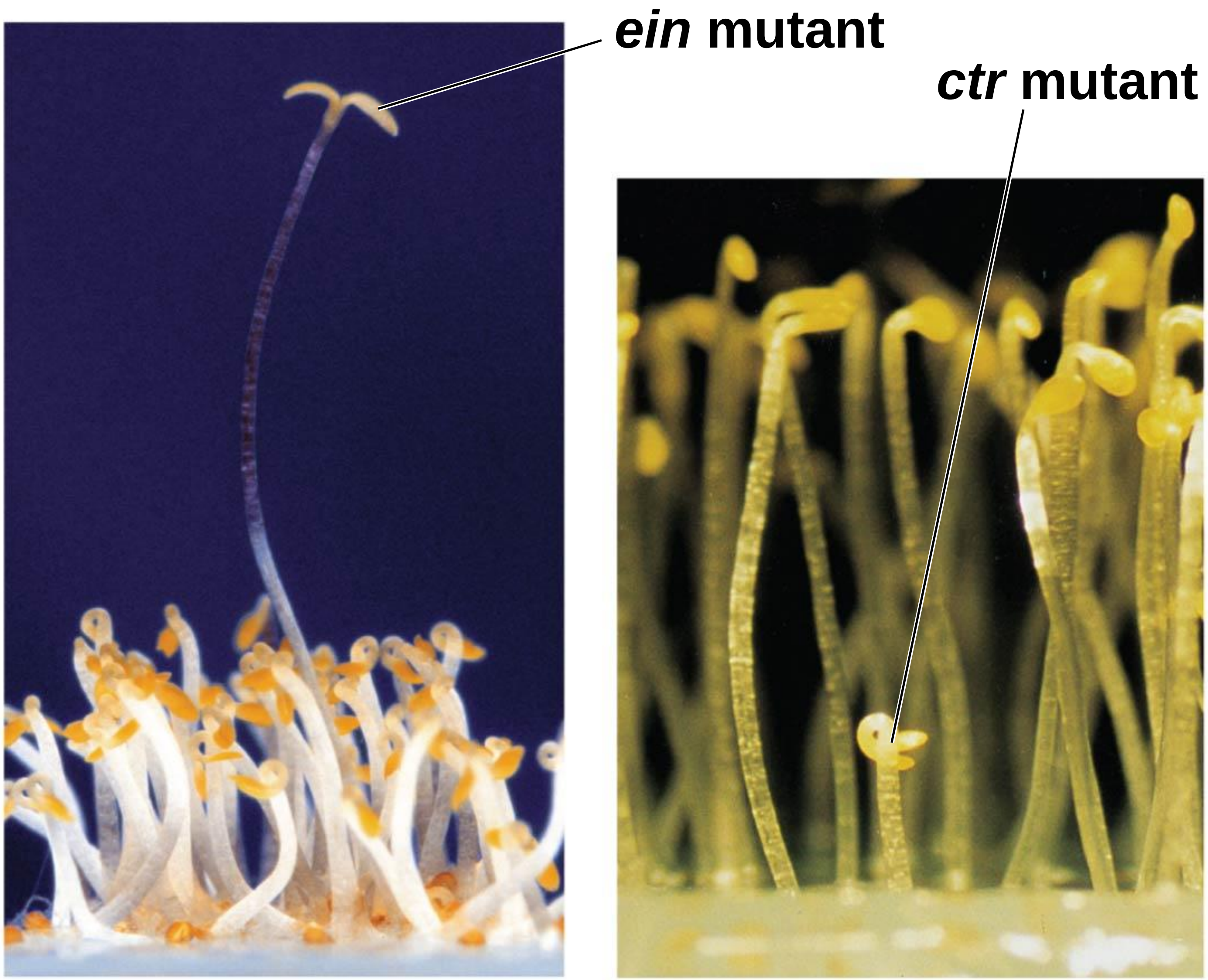
Ethylene

- Plants produce **ethylene** in response to stresses such as drought, flooding, mechanical pressure, injury, and infection
- The effects of ethylene include response to mechanical stress, senescence, leaf abscission, and fruit ripening

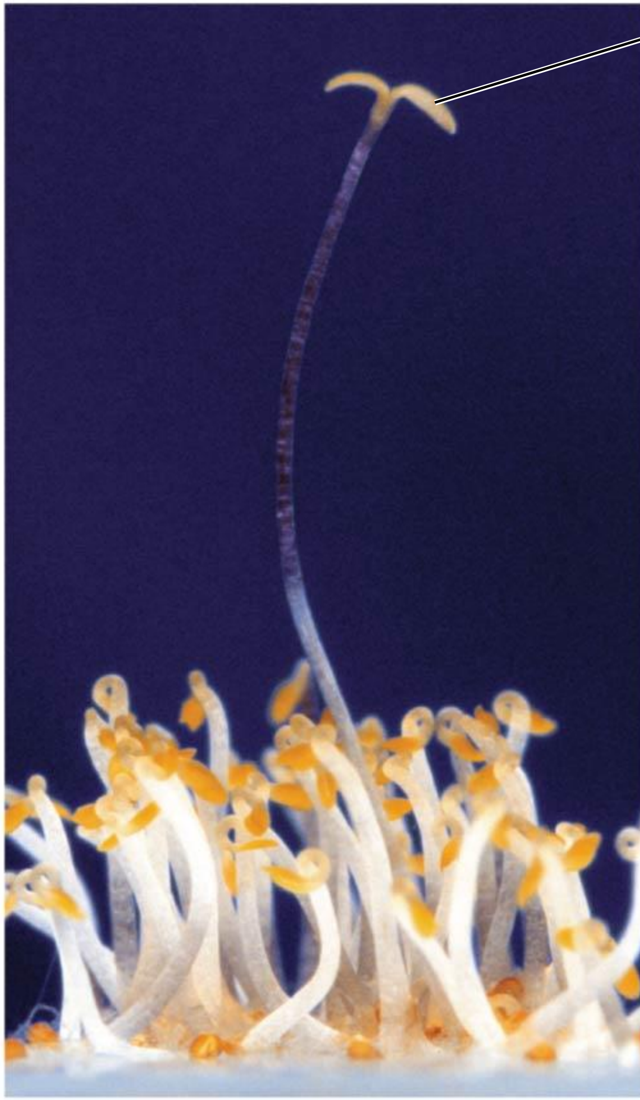
- **The triple response to mechanical stress:** Ethylene induces the **triple response**, which allows a growing shoot to avoid obstacles
- The triple response consists of a slowing of stem elongation, a thickening of the stem, and horizontal growth

- Ethylene-insensitive mutants fail to undergo the triple response after exposure to ethylene
- Some ethylene-overproducing mutants undergo the triple response even in air but are returned to normal growth when treated with ethylene synthesis inhibitors
- Other mutants are not responsive to inhibitors of ethylene synthesis

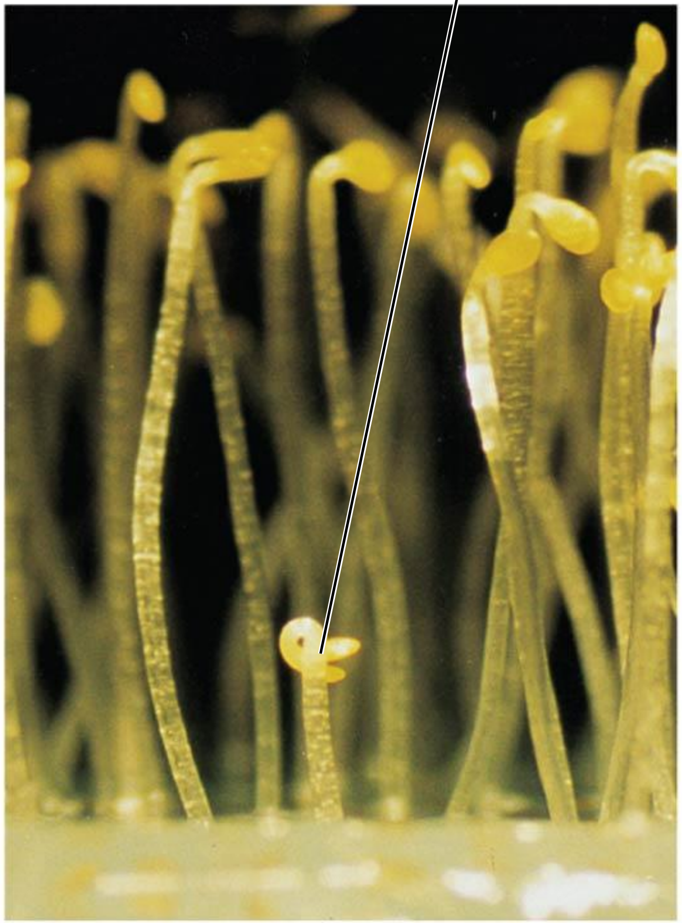
Figure 31.9



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



(a) *ein* mutant



(b) *ctr* mutant

- **Senescence:** Senescence is the programmed death of cells or organs
- A burst of ethylene is associated with apoptosis, the programmed destruction of cells, organs, or whole plants

- **Leaf abscission:** A change in the balance of auxin and ethylene controls leaf abscission, the process that occurs in autumn when a leaf falls

Figure 31.10

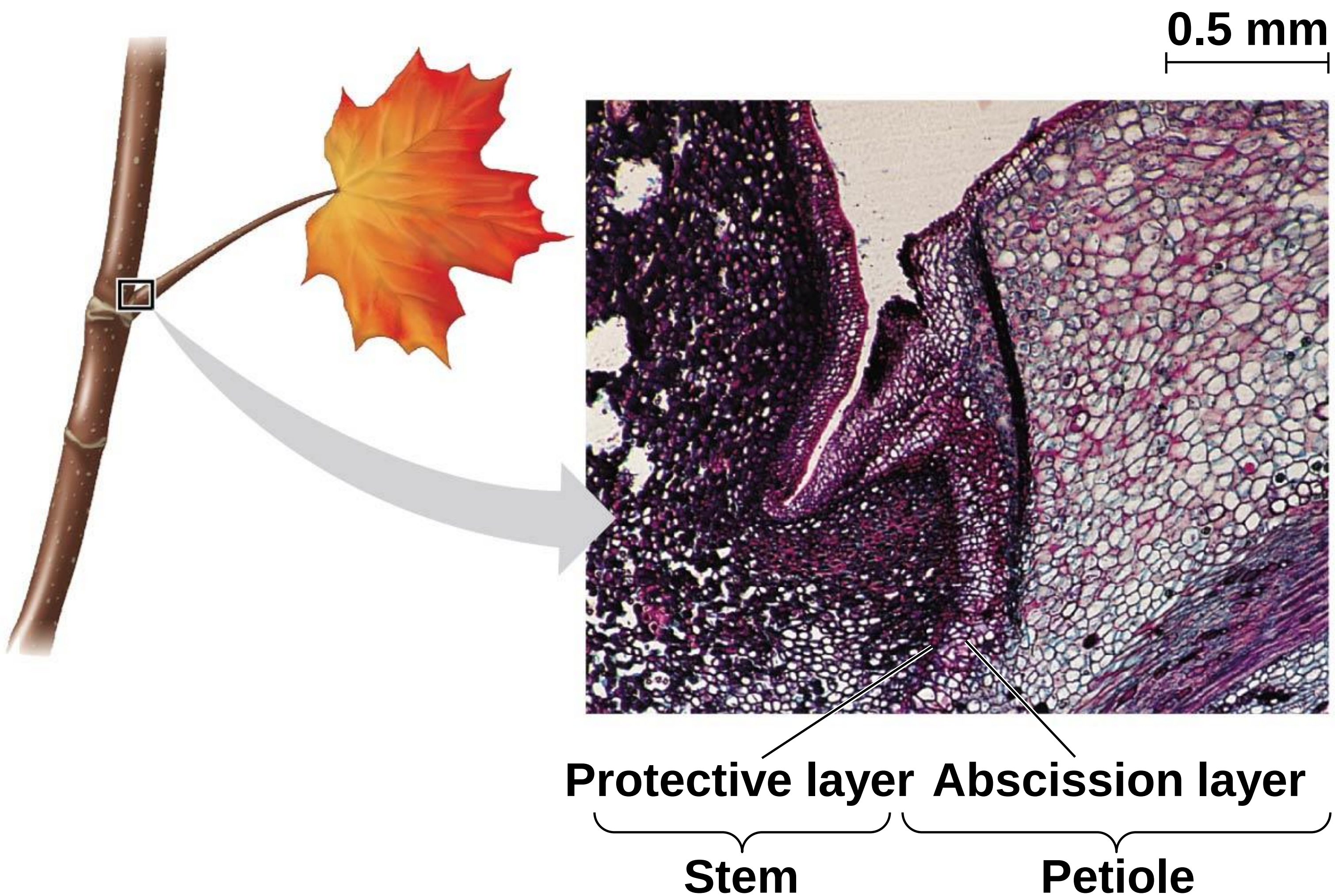
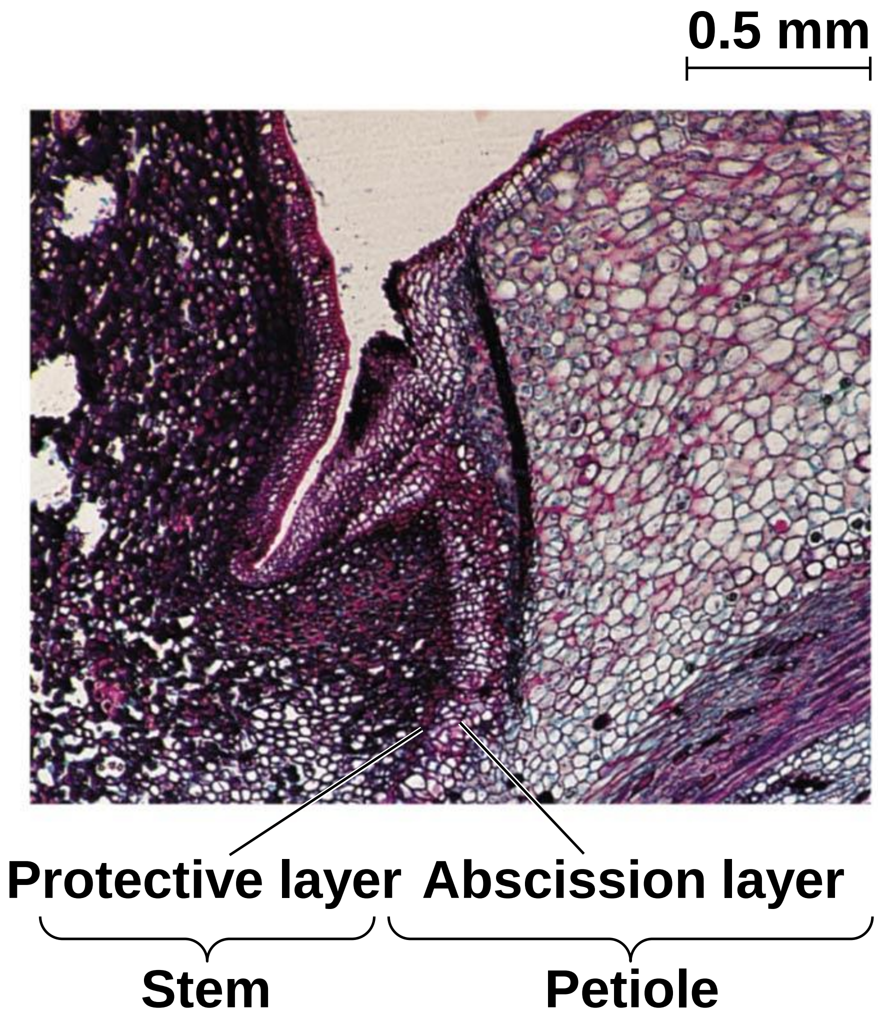


Figure 31.10a



- **Fruit ripening:** 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

Concept 31.2: Responses to light are critical for plant success

- Light triggers many key events in plant growth and development, collectively known as **photomorphogenesis**

Photomorphogenesis

- A potato left growing in darkness produces shoots that look unhealthy, and it lacks elongated roots
- These are morphological adaptations for growing in darkness, collectively called **etiolation**
- After exposure to light, a potato undergoes changes called **de-etiolation**, in which shoots and roots grow normally

Figure 31.11

(a) Before exposure to light

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

Figure 31.11a

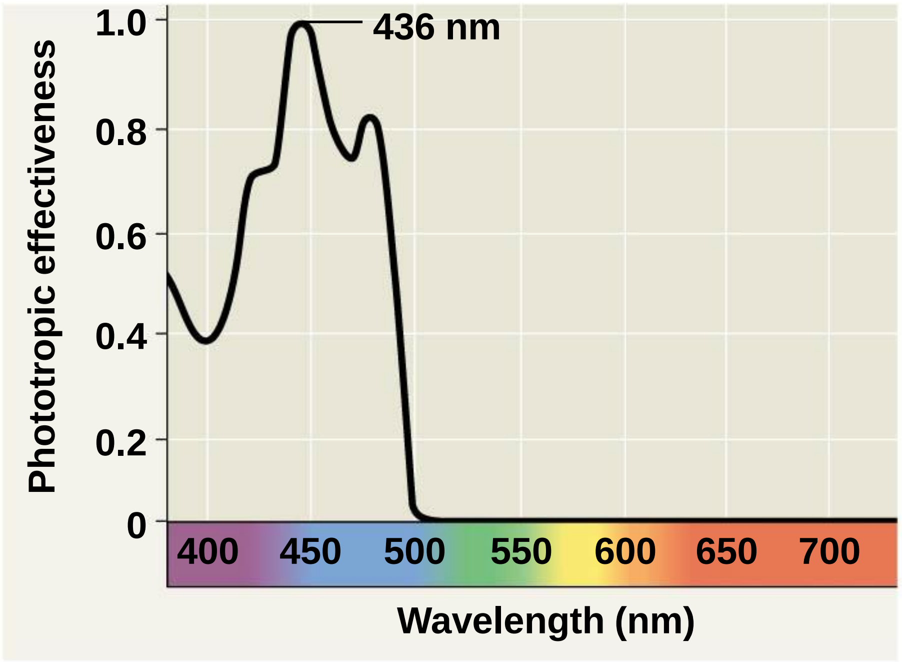
(a) Before exposure to light

Figure 31.11b

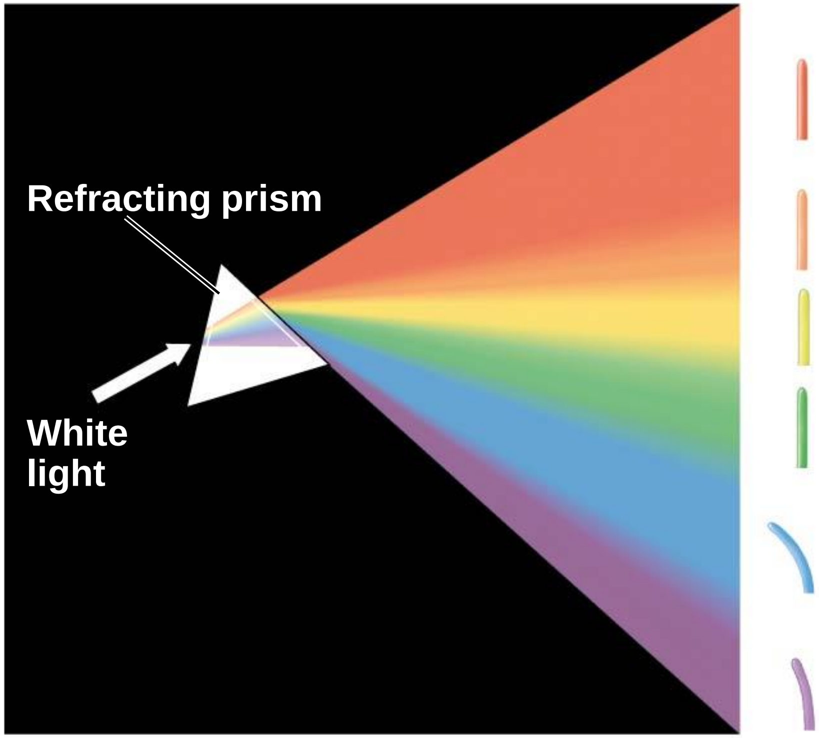
(b) After a week's exposure to natural daylight

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

Figure 31.12

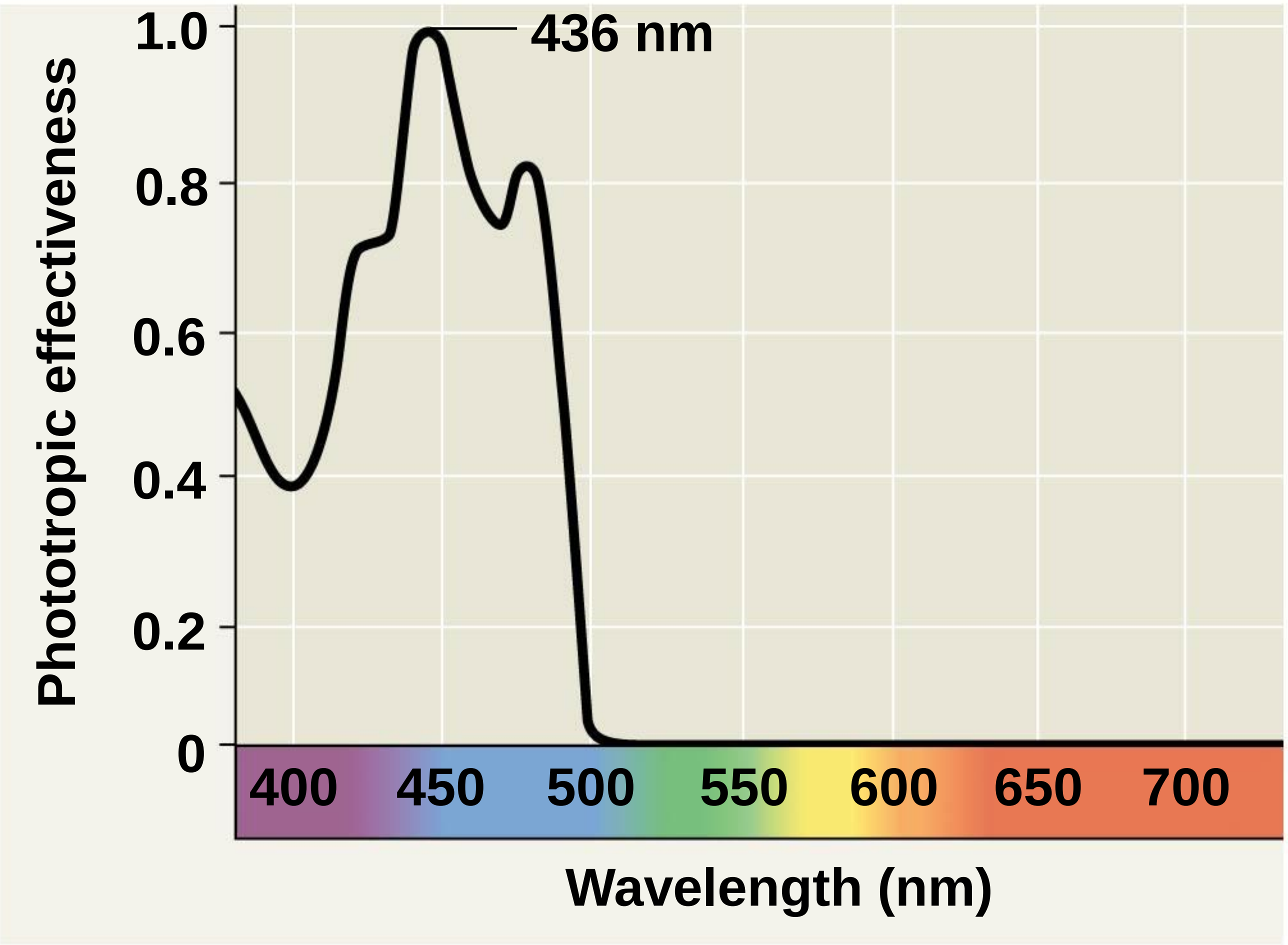


(a) Light wavelengths below 500nm induce curvature.



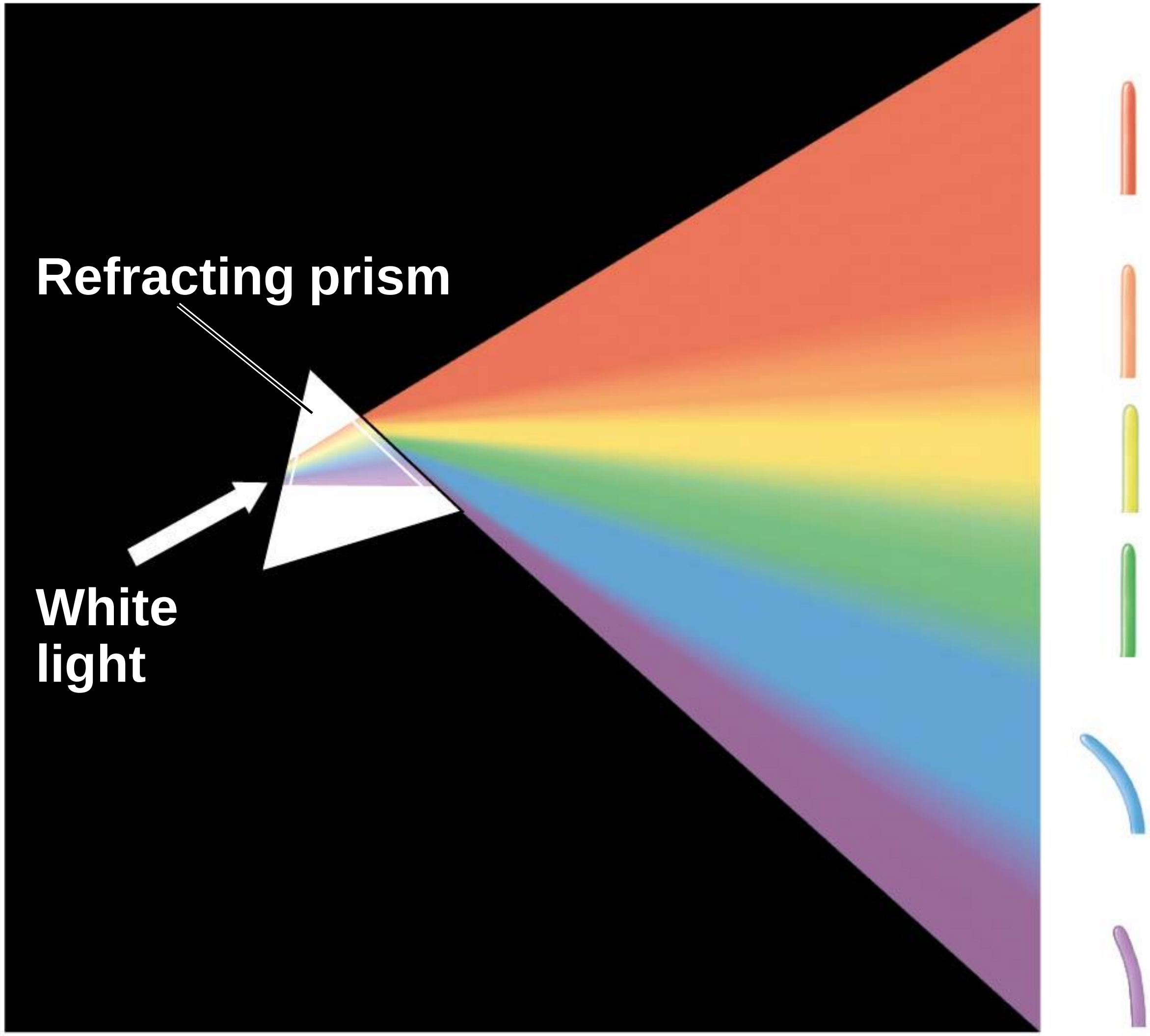
(b) Blue light induces the most curvature of coleoptiles.

Figure 31.12a



(a) Light wavelengths below 500nm induce curvature.

Figure 31.12b



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

- Different plant responses can be mediated by the same or different photoreceptors
- There are two major classes of light receptors: **blue-light photoreceptors** and **phytochromes**, photoreceptors that absorb mostly red light

Blue-Light Photoreceptors

- Various blue-light photoreceptors control phototropism (movement in response to light), stomatal opening, and hypocotyl elongation

Phytochrome Photoreceptors

- Phytochromes are pigments that regulate many of a plant's responses to light throughout its life
- These responses include seed germination and shade avoidance

- **Phytochromes and seed germination:** Many seeds remain dormant until light conditions are optimal
- In the 1930s, scientists at the U.S. Department of Agriculture determined the action spectrum for light-induced germination of lettuce seeds

- Red light increased germination, while far-red light inhibited germination
- The photoreceptor responsible for the opposing effects of red and far-red light is a phytochrome

Figure 31.13

Results

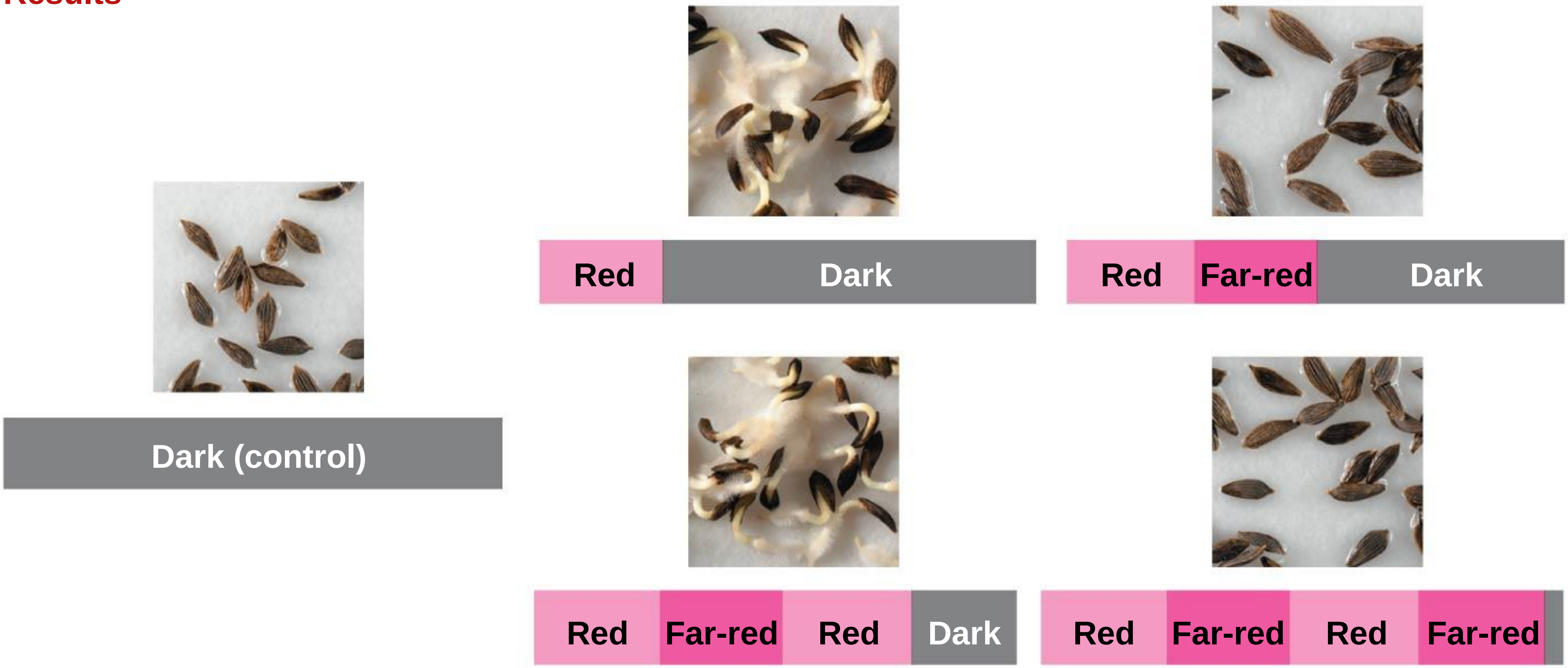


Figure 31.13a

Dark (control)

Figure 31.13b

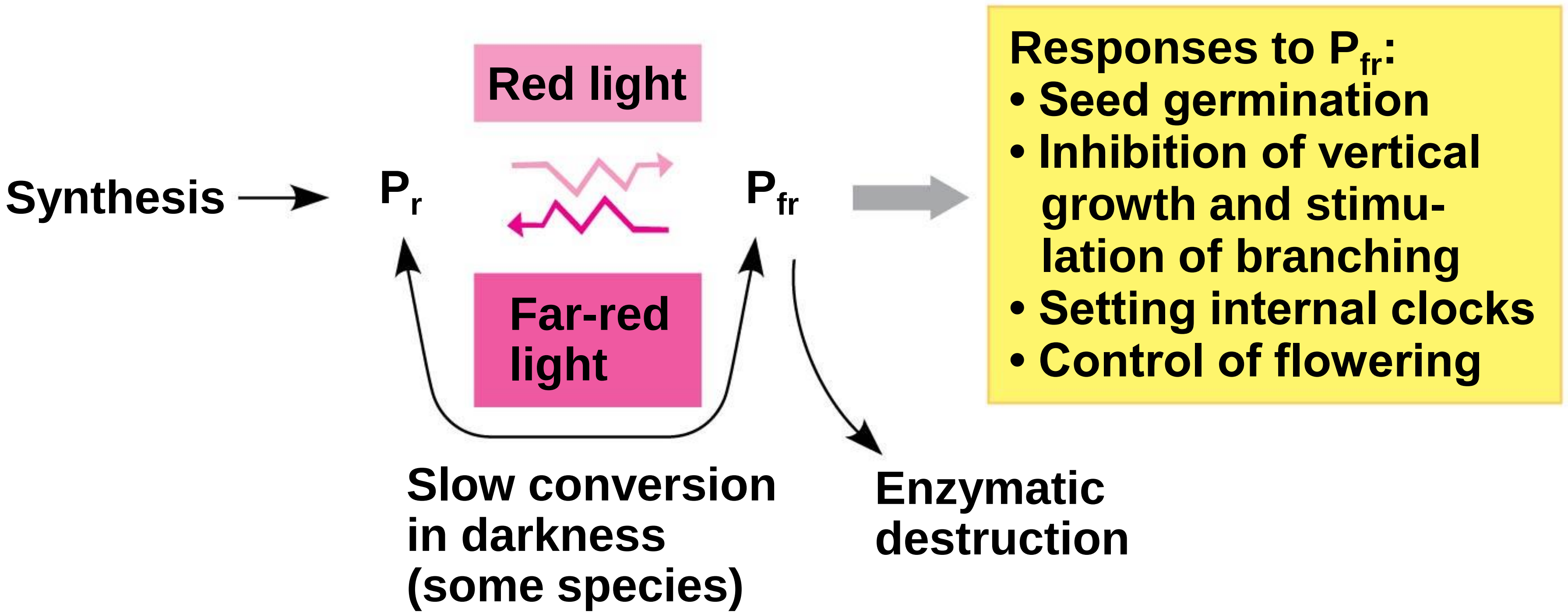
Figure 31.13c

Figure 31.13d

Figure 31.13e

- 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
- The conversion to P_{fr} is faster than the conversion to P_r
- Sunlight increases the ratio of P_{fr} to P_r and triggers germination

Figure 31.14



Red light
Synthesis
P_r
P_{fr}
Far-red light
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
- Shaded plants receive more far-red than red light
- In the "shade avoidance" response, the phytochrome ratio shifts in favor of P_r when a tree is shaded
- This shift induces the vertical growth of the plant

Biological Clocks and Circadian Rhythms

- Many plant processes oscillate during the day
- Many legumes lower their leaves in the evening and raise them in the morning, even when kept under constant light or dark conditions

Figure 31.15

Noon

10:00 PM

Figure 31.15a

Noon

Figure 31.15b

10:00 PM

- **Circadian rhythms** are cycles that are about 24 hours long and are governed by an internal "clock"
- Circadian rhythms can be entrained to exactly 24 hours by the day/night cycle
- The clock may depend on synthesis of a protein regulated through feedback control

The Effect of Light on the Biological Clock

- Phytochrome conversion marks sunrise and sunset, providing the biological clock with environmental cues

Photoperiodism and Responses to Seasons

- Photoperiod, the relative lengths of night and day, is the environmental stimulus plants use most often to detect the time of year
- **Photoperiodism** is a physiological response to photoperiod

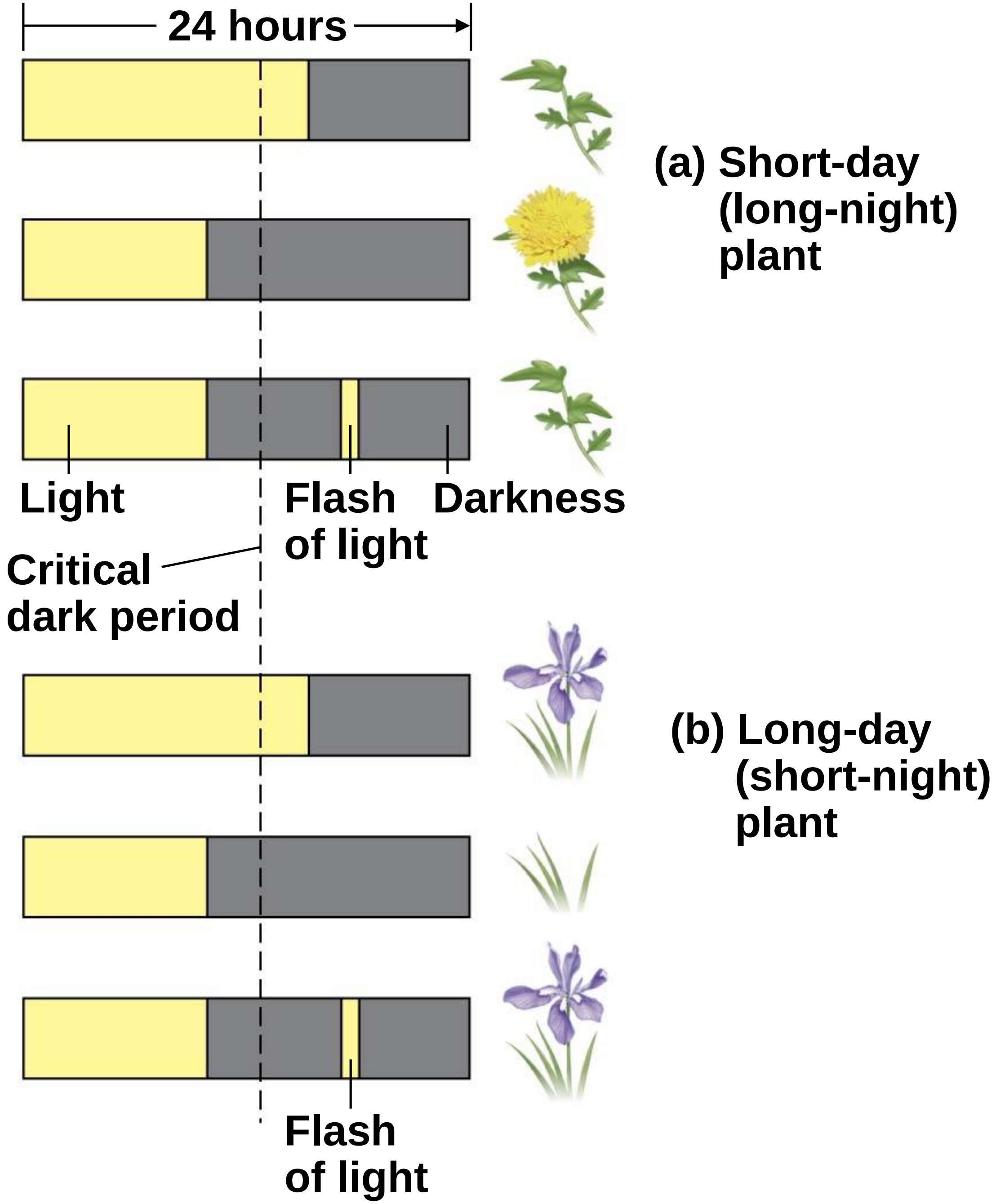
Photoperiodism and Control of Flowering

- Some processes, including flowering in many species, require a certain 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

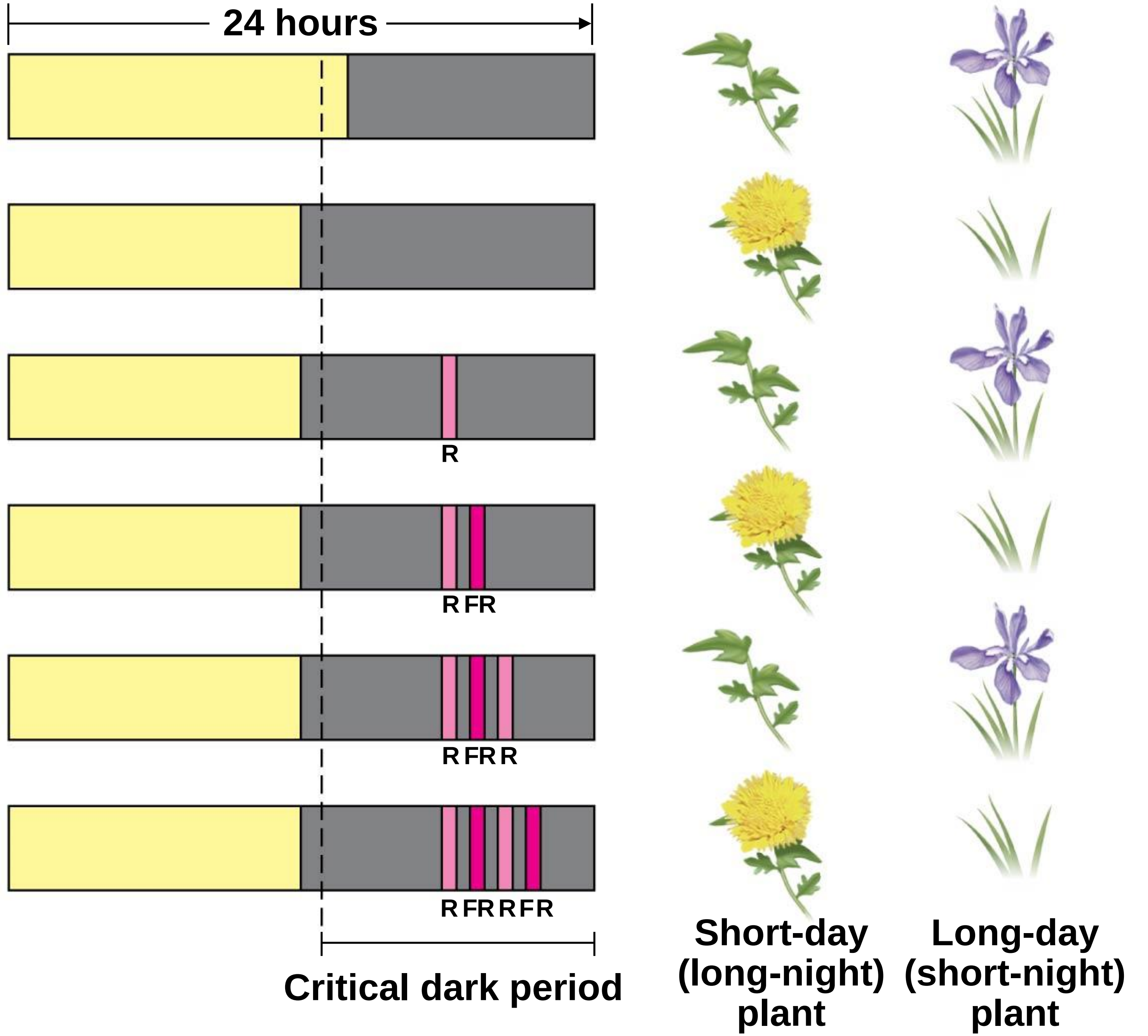
Figure 31.16



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

- Red light can interrupt the nighttime portion of the photoperiod
- A flash of red light followed by a flash of far-red light does not disrupt night length
- Action spectra and photoreversibility experiments show that phytochrome is the pigment that receives red light

Figure 31.17

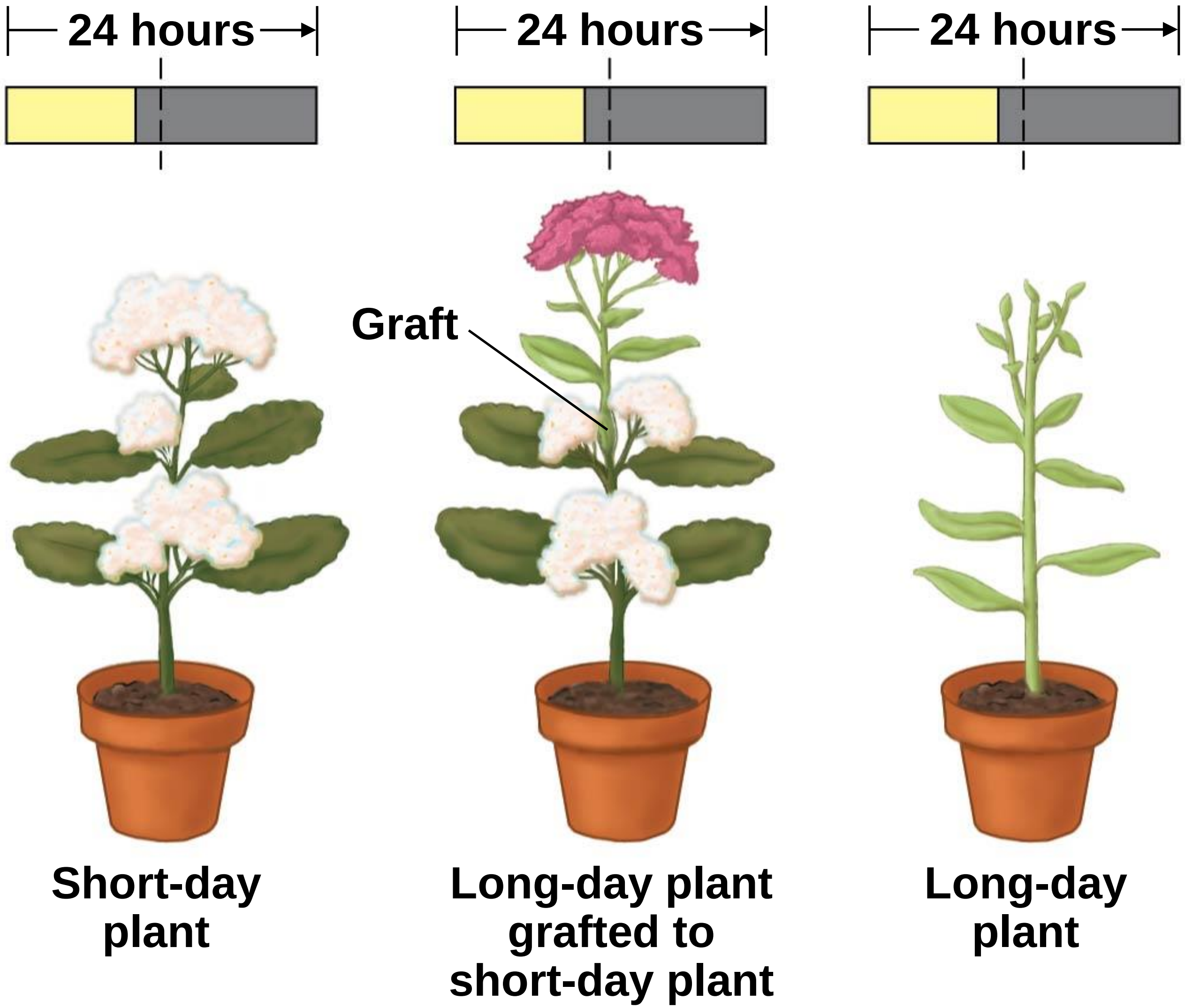

24 hours
R
R FR
R FR R
R FR R FR
Critical dark period
Short-day (long-night) plant
Long-day (short-night) plant

- 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 is called **florigen**
- Florigen may be a protein governed by the *FLOWERING LOCUS T* (*FT*) gene

Figure 31.18


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

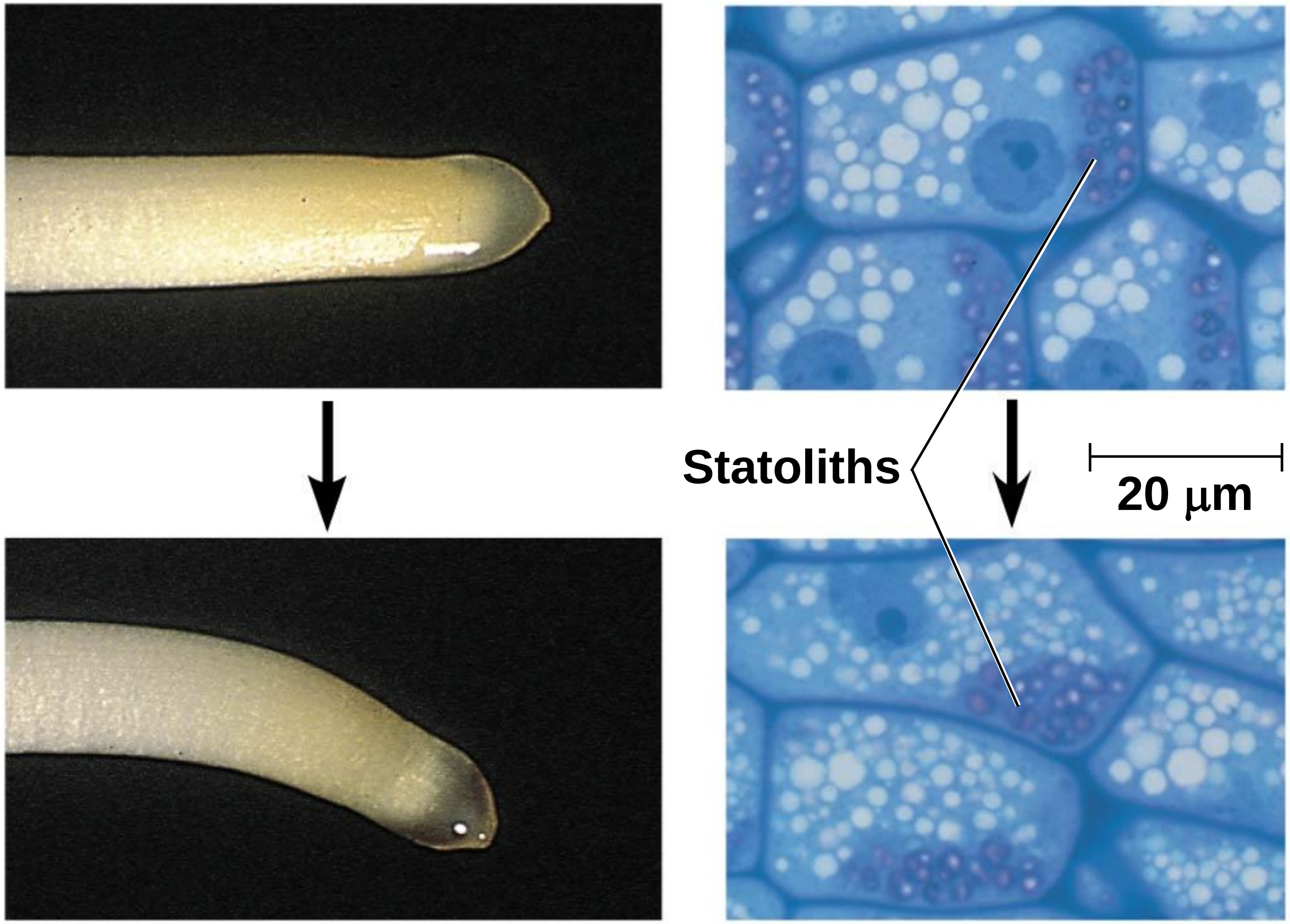
Concept 31.3: Plants respond to a wide variety of stimuli other than light

- Because of immobility, 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 by growing downward; shoots show negative gravitropism by growing upward
- Plants may detect gravity by the settling of **statoliths**, dense cytoplasmic components

Figure 31.19



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

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

Figure 31.19a

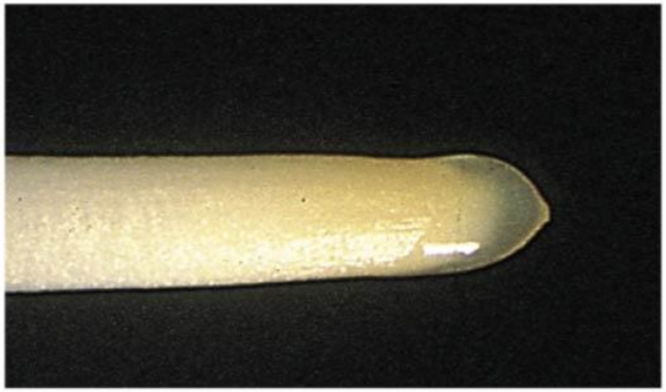


Figure 31.19b

Figure 31.19c

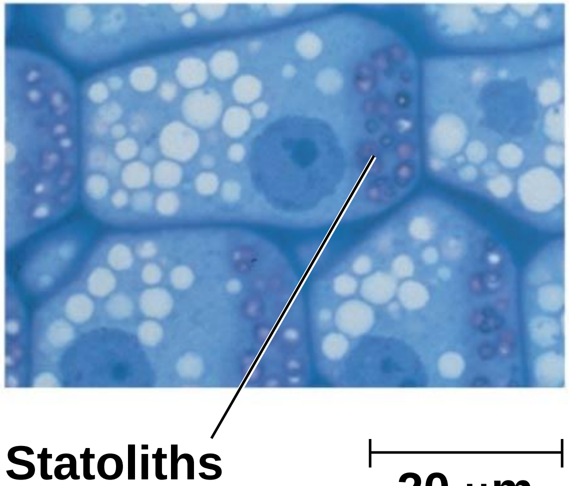
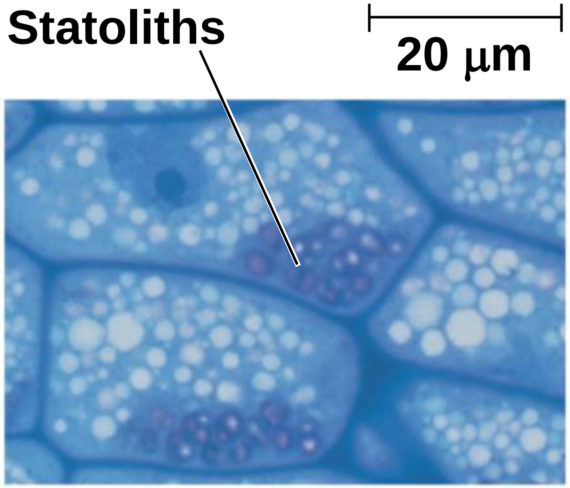


Figure 31.19d



- Some mutants that lack statoliths are still capable of gravitropism
- Mechanical pulling on proteins that connect the protoplast to the cell wall may aid in gravity detection
- Dense organelles and starch granules may also contribute to gravity detection

Mechanical Stimuli

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

Figure 31.20

- **Thigmotropism** is growth in response to touch
- It occurs in vines and other climbing plants
- Another example of a touch specialist is the sensitive plant, *Mimosa pudica*, which folds its leaflets and collapses in response to touch
- Rapid leaf movements in response to mechanical stimulation are examples of transmission of electrical impulses called **action potentials**

(a) Unstimulated state (leaflets spread apart)

(b) Stimulated state (leaflets folded)

Figure 31.21a

(a) Unstimulated state (leaflets spread apart)

Figure 31.21b

(b) Stimulated state (leaflets folded)

Environmental Stresses

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

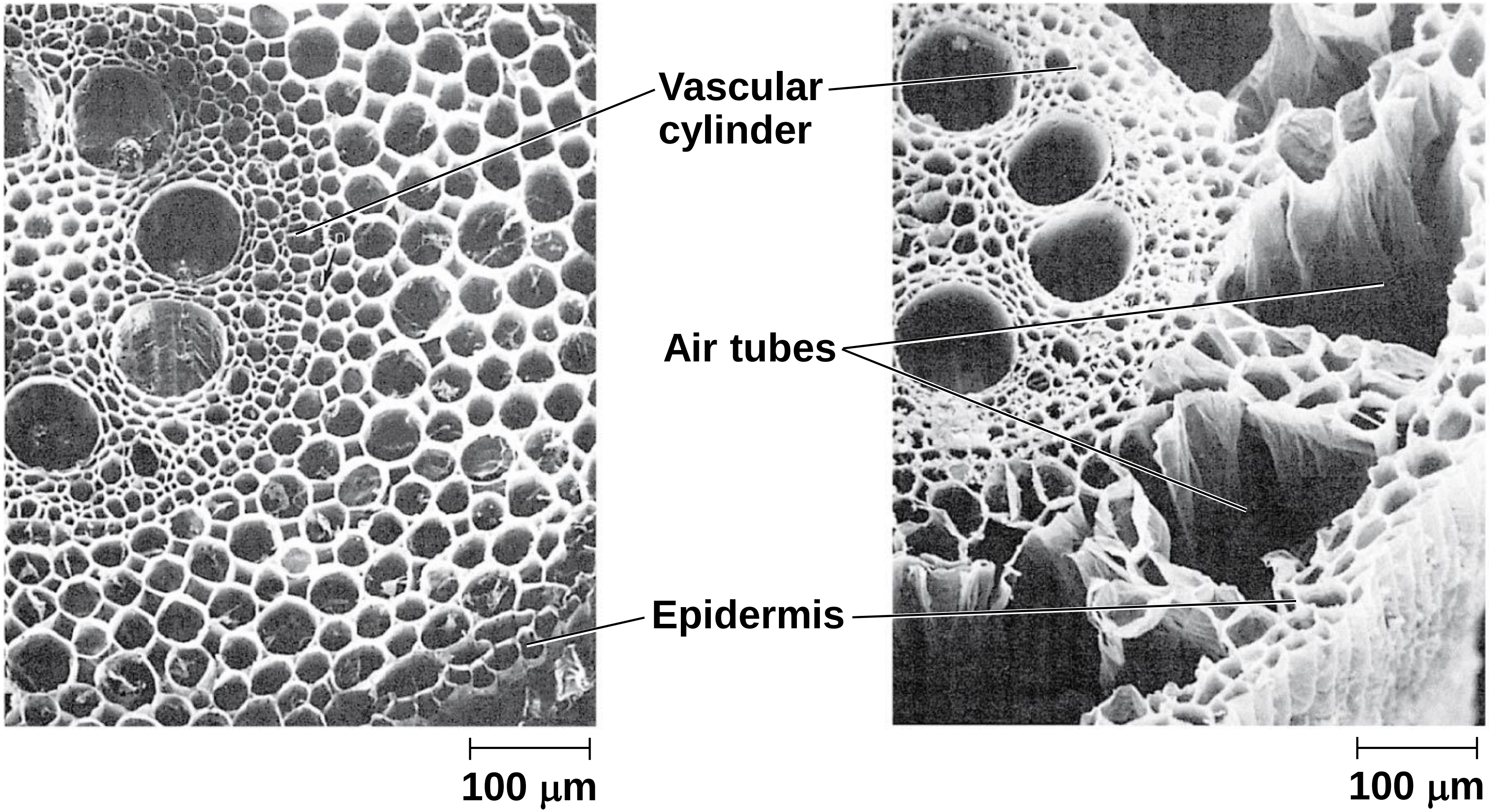
Drought

- During drought, plants reduce transpiration by closing stomata, reducing exposed surface area, or even shedding their leaves

Flooding

- Enzymatic destruction of root cortex cells creates air tubes that help plants survive oxygen deprivation during flooding

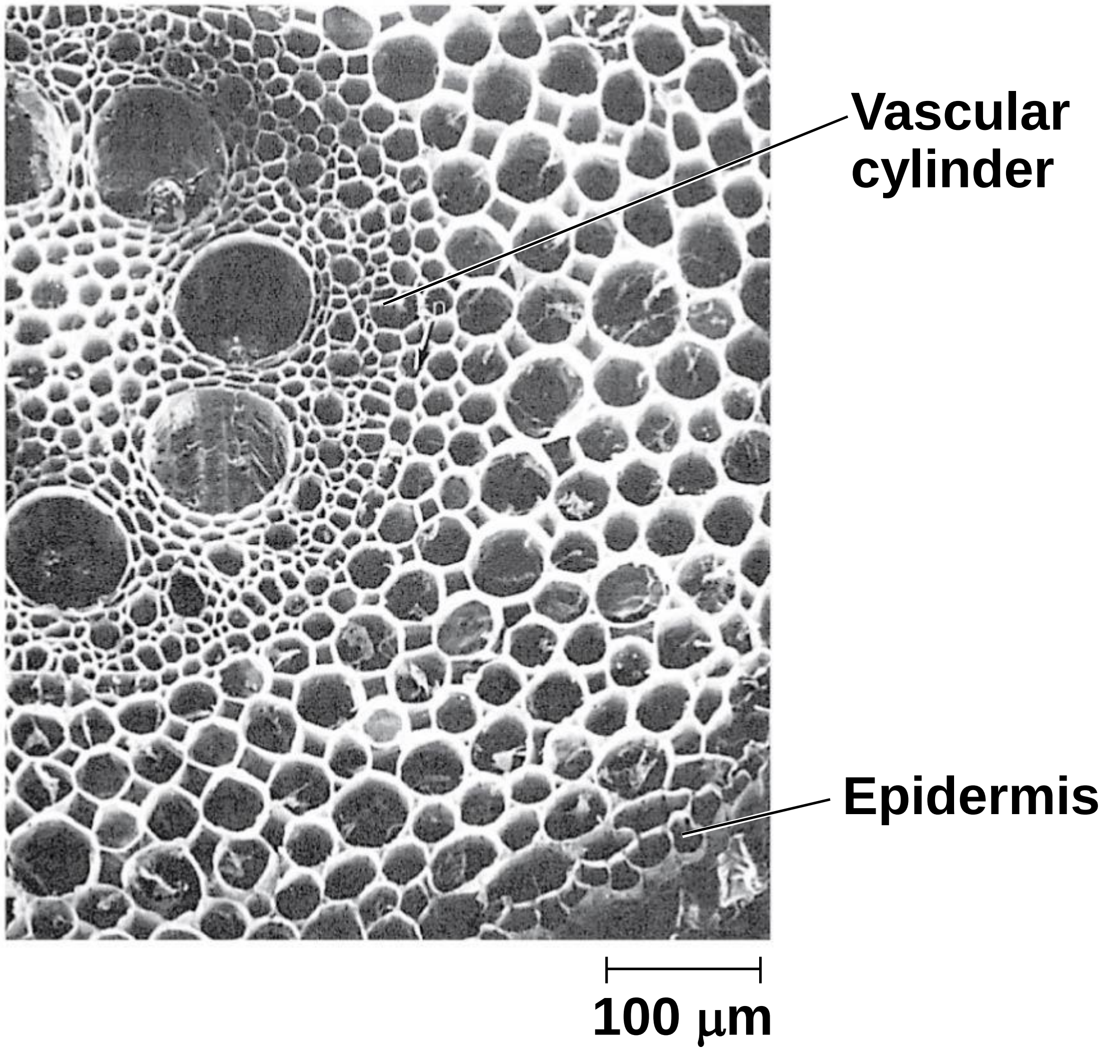
Figure 31.22



(a) Control root (aerated)

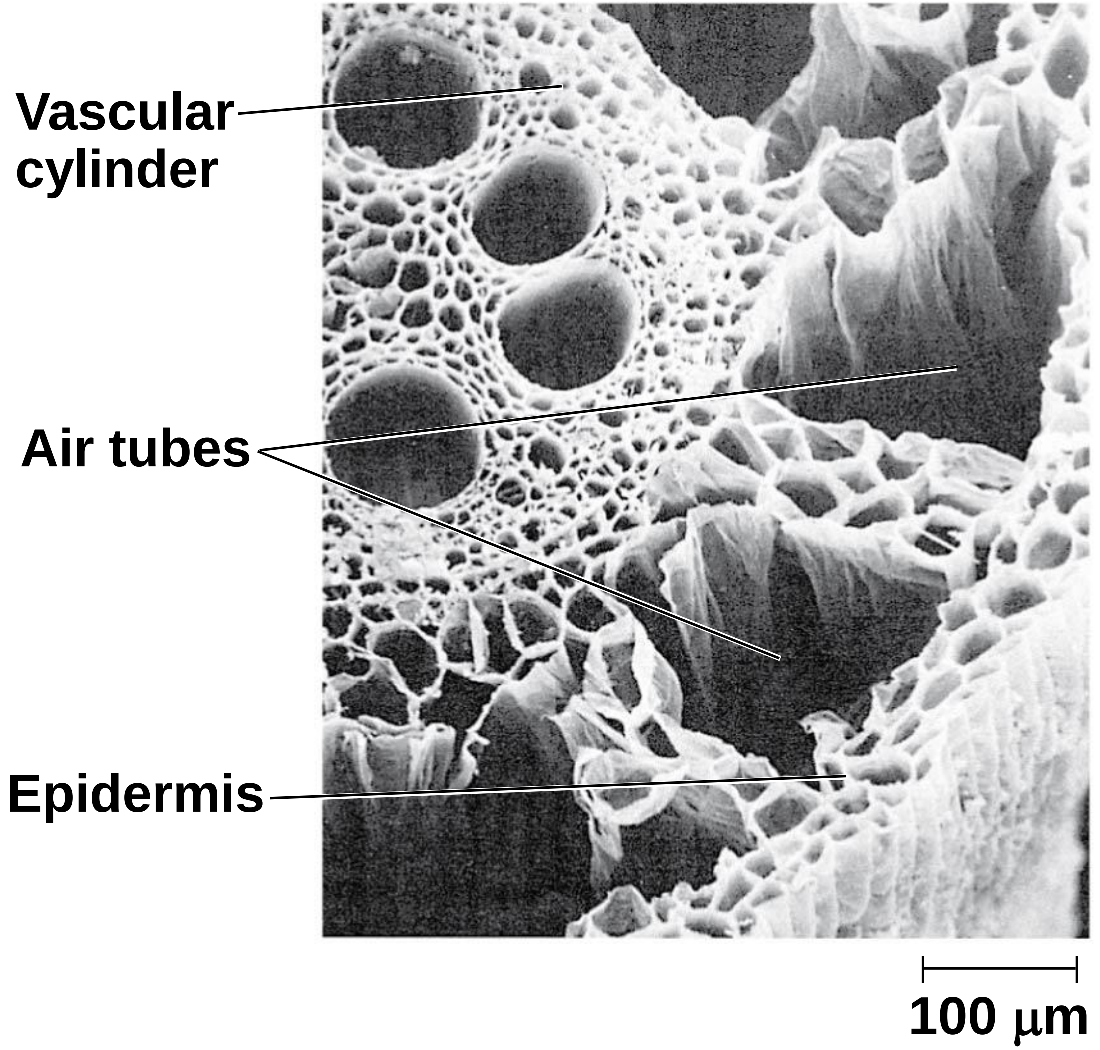
(b) Experimental root (nonaerated)

Figure 31.22a



(a) Control root (aerated)

Figure 31.22b



(b) Experimental root (nonaerated)

Salt Stress

- Salt can lower the water potential of the soil solution and reduce water uptake
- Plants respond to salt stress by producing solutes 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
- **Heat-shock proteins**, which help protect other proteins from heat stress, are produced at high temperatures

Cold Stress

- Cold temperatures decrease membrane fluidity
- Altering lipid composition of membranes is a response to cold stress
- Freezing causes ice to form in a plant’s cell walls and intercellular spaces
- Water leaves the cell in response to freezing, leading to toxic solute concentrations in the cytoplasm

- Many plants, as well as other organisms, have antifreeze proteins that prevent ice crystals from growing and damaging cells
- The five classes of antifreeze proteins have markedly different amino acid sequences but similar structure, indicating they arose through convergent evolution

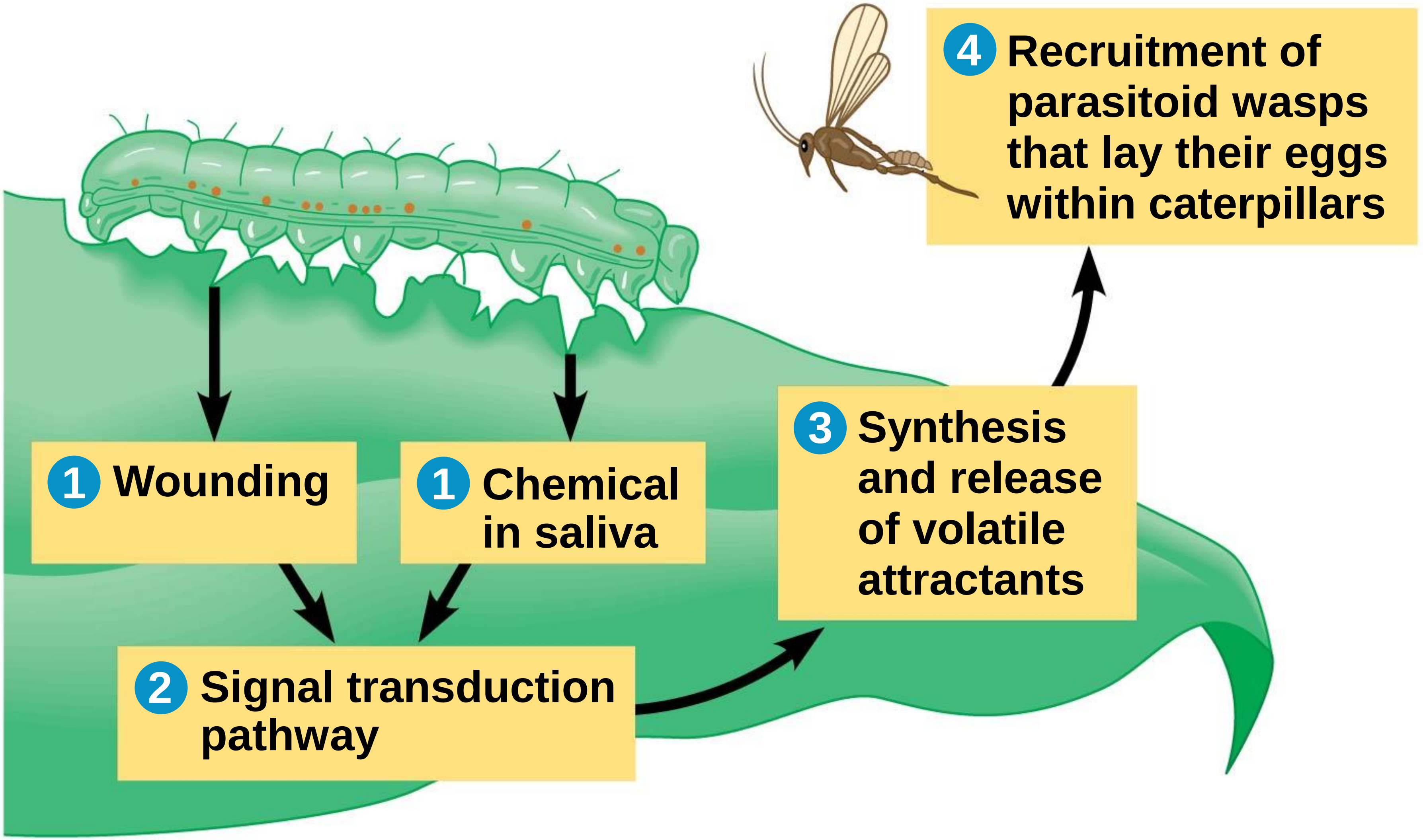
Concept 31.4: Plants respond to attacks by herbivores and pathogens

- Through natural selection, plants have evolved defense systems to deter herbivory, prevent infection, and combat pathogens

Defenses Against Herbivores

- Herbivory, animals eating plants, is a stress that plants face in any ecosystem
- Plants counter excessive herbivory with physical defenses, such as thorns and trichomes, and chemical defenses, such as distasteful or toxic compounds
- Some plants even "recruit" predatory animals that help defend against specific herbivores

Figure 31.23



1 Wounding
1 Chemical in saliva
2 Signal transduction pathway
3 Synthesis and release of volatile attractants
4 Recruitment of parasitoid wasps that lay their eggs within caterpillars

- Plants damaged by insects can release volatile chemicals to warn other plants of the same species
- *Arabidopsis* can be genetically engineered to produce volatile components that attract predatory mites

Defenses Against Pathogens

- A plant's first line of defense against infection is the barrier presented by the epidermis and periderm
- If a pathogen penetrates the dermal tissue, the second line of defense is a chemical attack that kills the pathogen and prevents its spread
- This second defense system is enhanced by the plant's ability to recognize certain pathogens

Host-Pathogen Coevolution

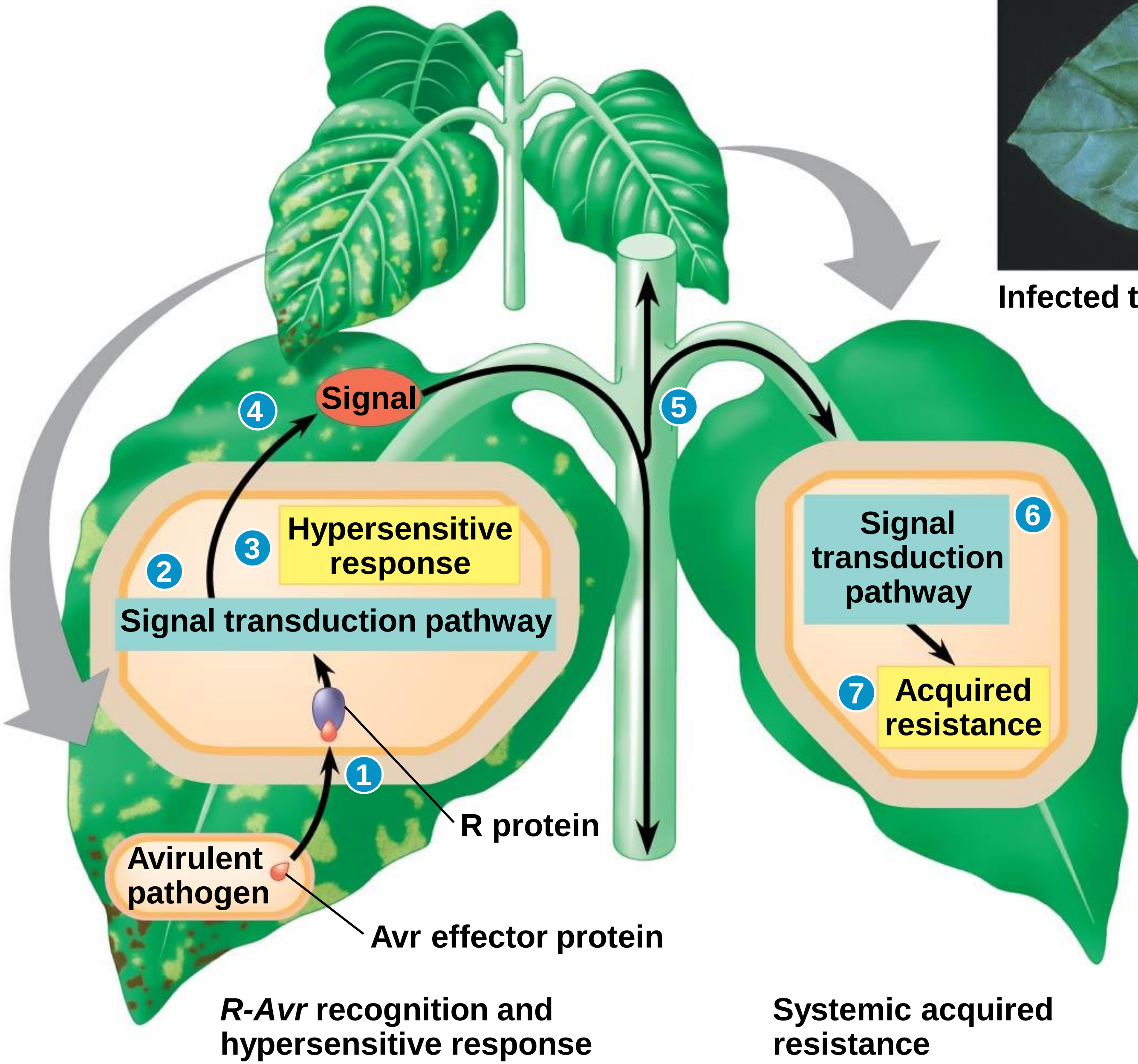
- A **virulent** pathogen is one that a plant has little specific defense against
- An **avirulent** pathogen is one that may harm but does not kill the host plant

- **Gene-for-gene recognition** involves recognition of effector molecules by the protein products of specific plant disease resistance (*R*) genes
- An R protein recognizes a corresponding molecule made by the pathogen's *Avr* gene
- R proteins activate plant defenses by triggering signal transduction pathways
- These defenses include the hypersensitive response and systemic acquired resistance

The Hypersensitive Response

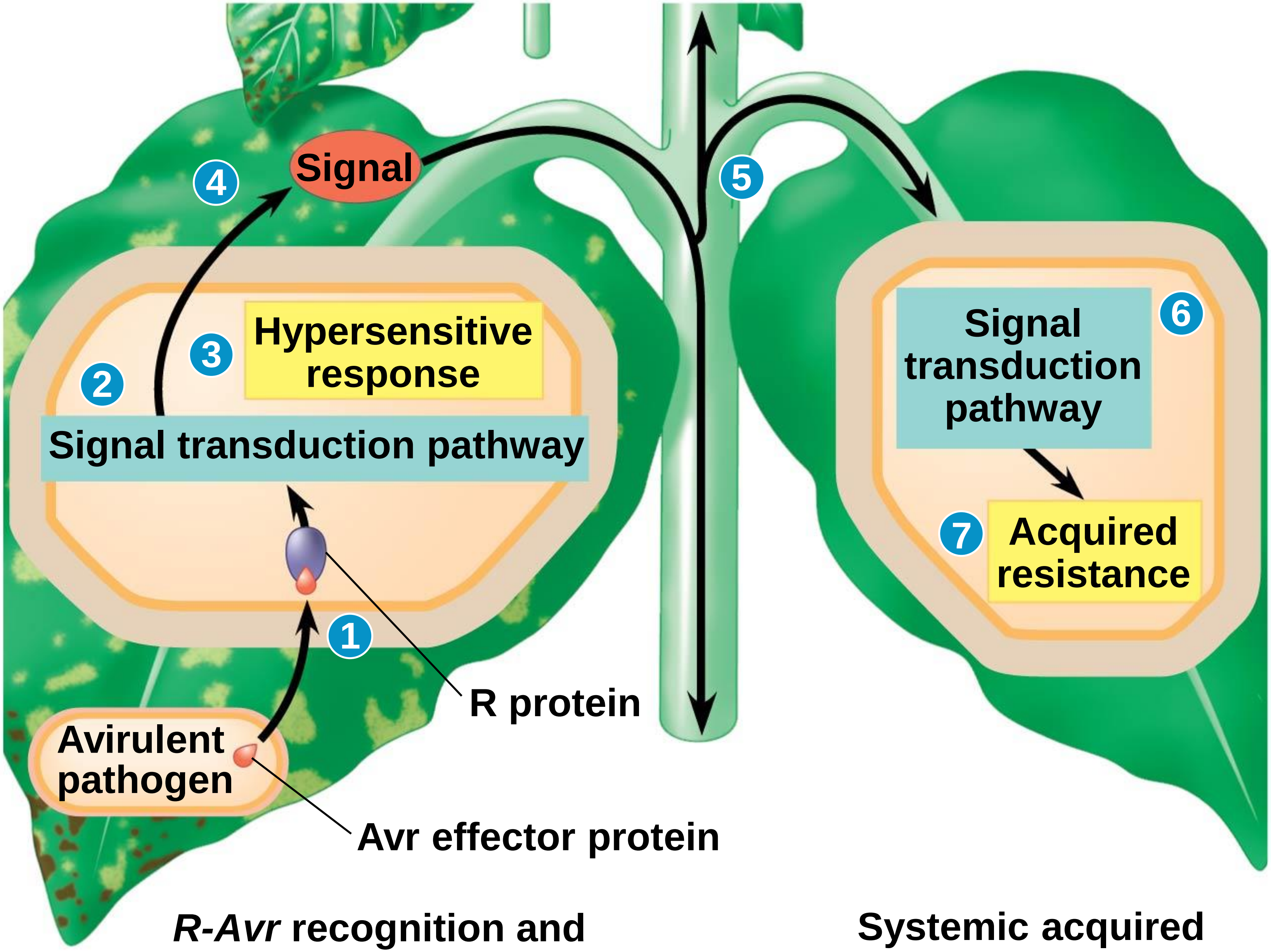
- The **hypersensitive response**
  - Causes localized cell and tissue death near the infection site
  - Induces production of phytoalexins and PR proteins, which attack the specific pathogen
  - Stimulates changes in the cell wall that confine the pathogen

Figure 31.24



Infected tobacco leaf with lesions

Figure 31.24a



R-Avr recognition and hypersensitive response

Systemic acquired resistance

Figure 31.24b

Infected tobacco leaf with lesions

Systemic Acquired Resistance

- **Systemic acquired resistance**
  - Causes plant-wide expression of defense genes
  - Protects against a diversity of pathogens
  - Provides a long-lasting response
- Methylsalicylic acid travels from an infection site to remote areas of the plant where it is converted to **salicylic acid**, which initiates pathogen resistance

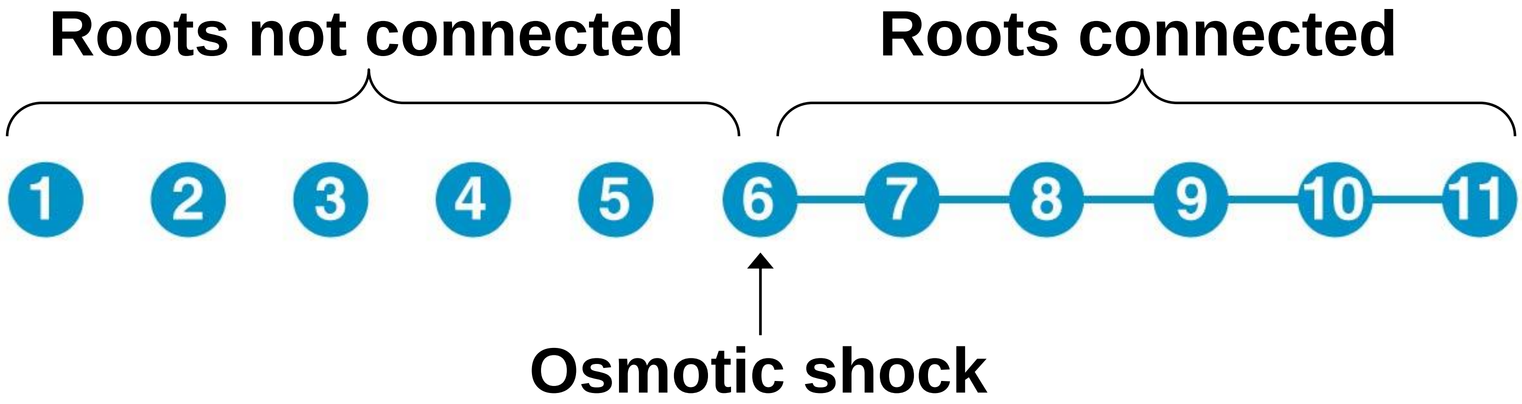

Roots not connected
Roots connected
1
2
3
4
5
6
7
8
9
10
11
Osmotic shock

Figure 31.UN01b

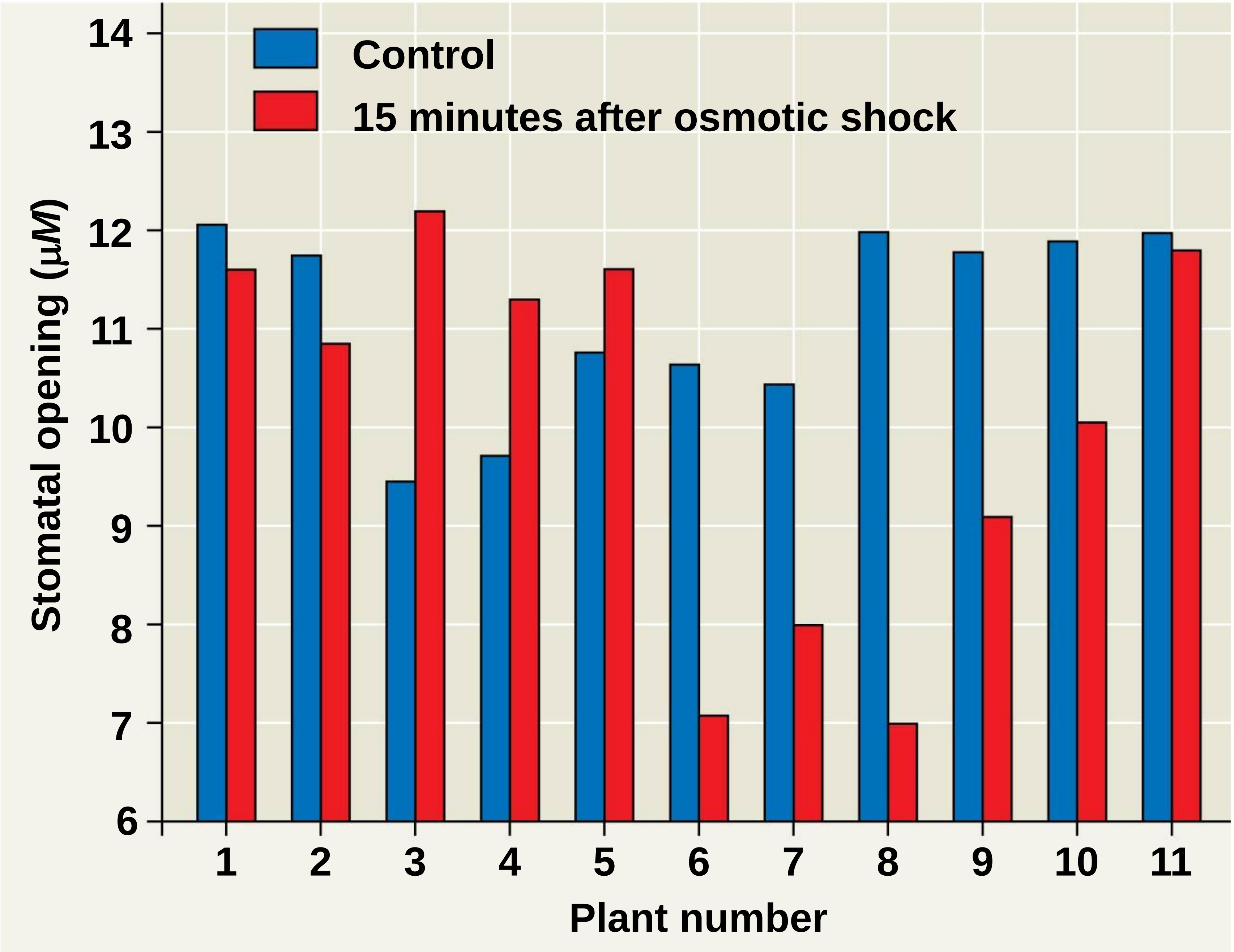


Figure 31.UN02

Plant Hormone	Major Responses
Auxin	Stimulates cell elongation; regulates branching and organ bending
Cytokinins	Stimulate plant cell division; promote later bud growth; slow organ death
Gibberellins	Promote stem elongation; help seeds break dormancy and use stored reserves
Brassinosteroids	Chemically similar to the sex hormones of animals; induce cell elongation and division
Abscisic acid	Promotes stomatal closure in response to drought; promotes seed dormancy
Ethylene	Mediates fruit ripening

Figure 31.UN04

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 31.UN01c

Pea plant *(Pisum sativum)*

Figure 31.UN03

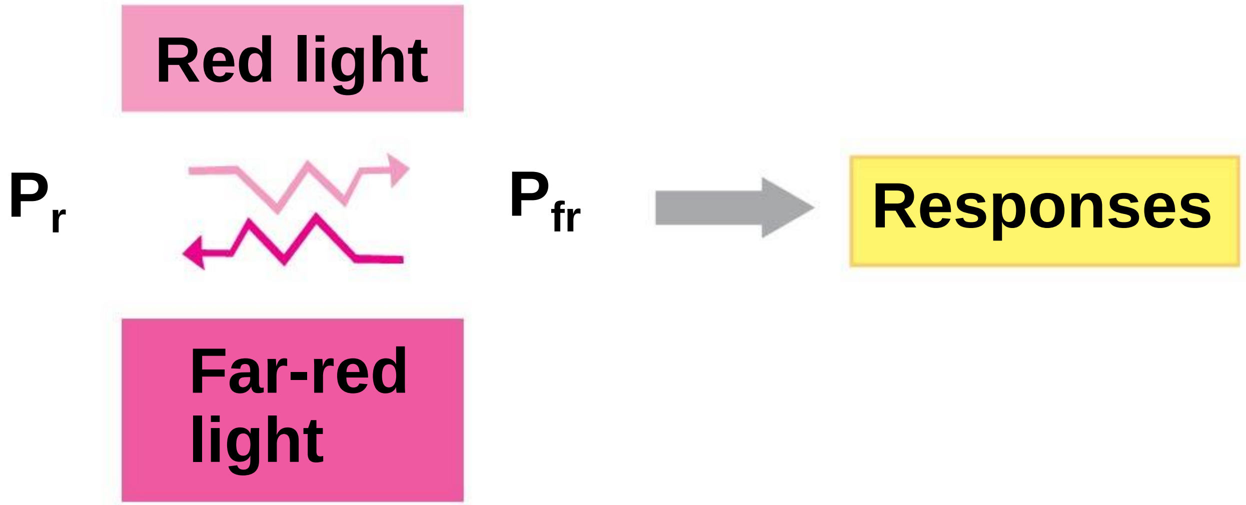


Figure 31.UN05

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