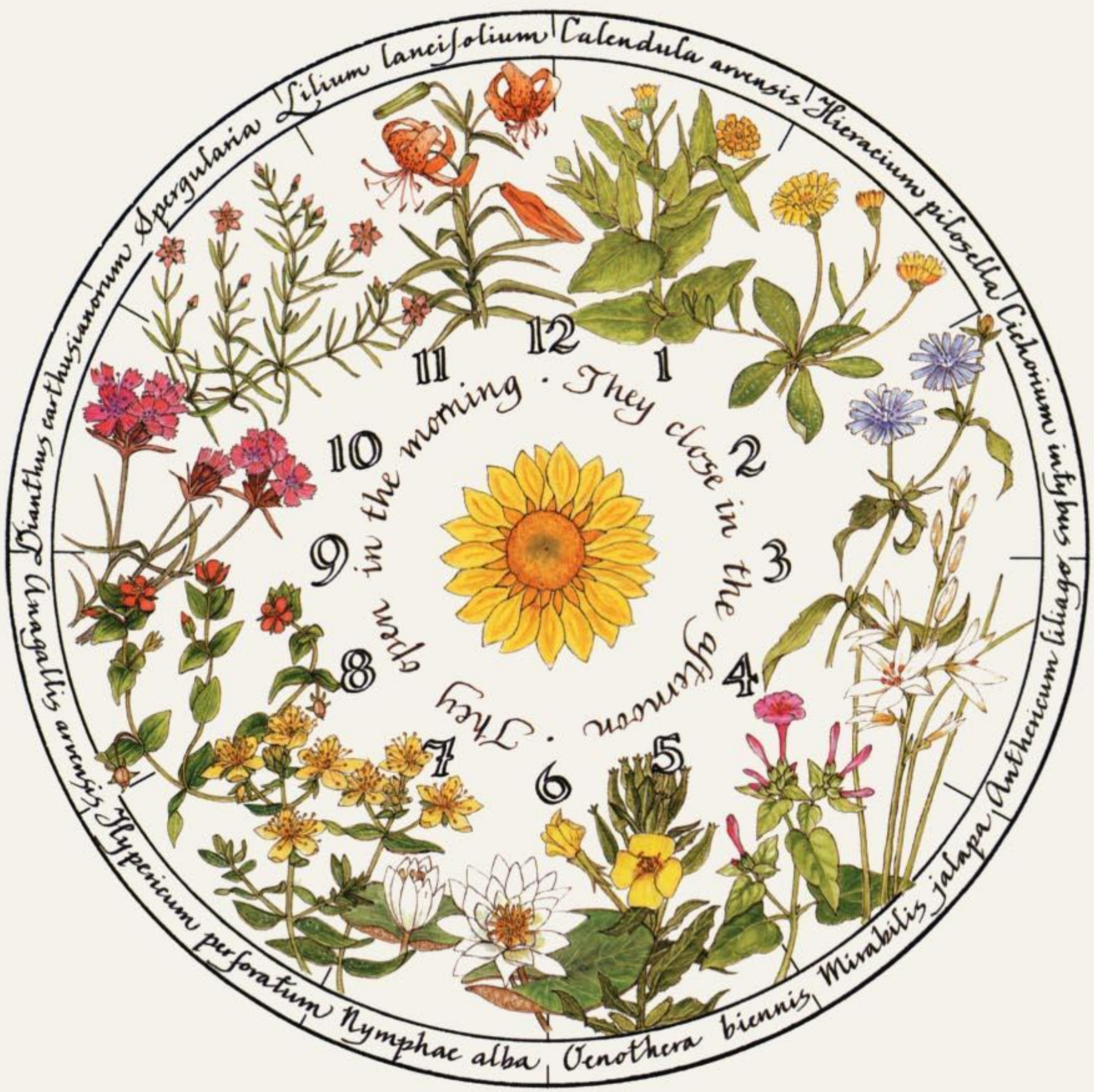
Plant Responses to Internal and External Signals

Overview: Stimuli and a Stationary Life

- Linnaeus noted that flowers of different species opened at different times of day and could be used as a *horologium florae*, or floral clock
- Plants, being rooted to the ground, must respond to environmental changes that come their way
- For example, the bending of a seedling toward light begins with sensing the direction, quantity, and color of the light

Fig. 39-1


Lilium lancifolium
Calendula arvensis
Hieracium pilosella
Cichorium intybus
Anthericum liliago
Mirabilis jalapa
Oenothera biennis
Nymphae alba
Hypericum perforatum
Anagallis arvensis
Dianthus carthusianorum
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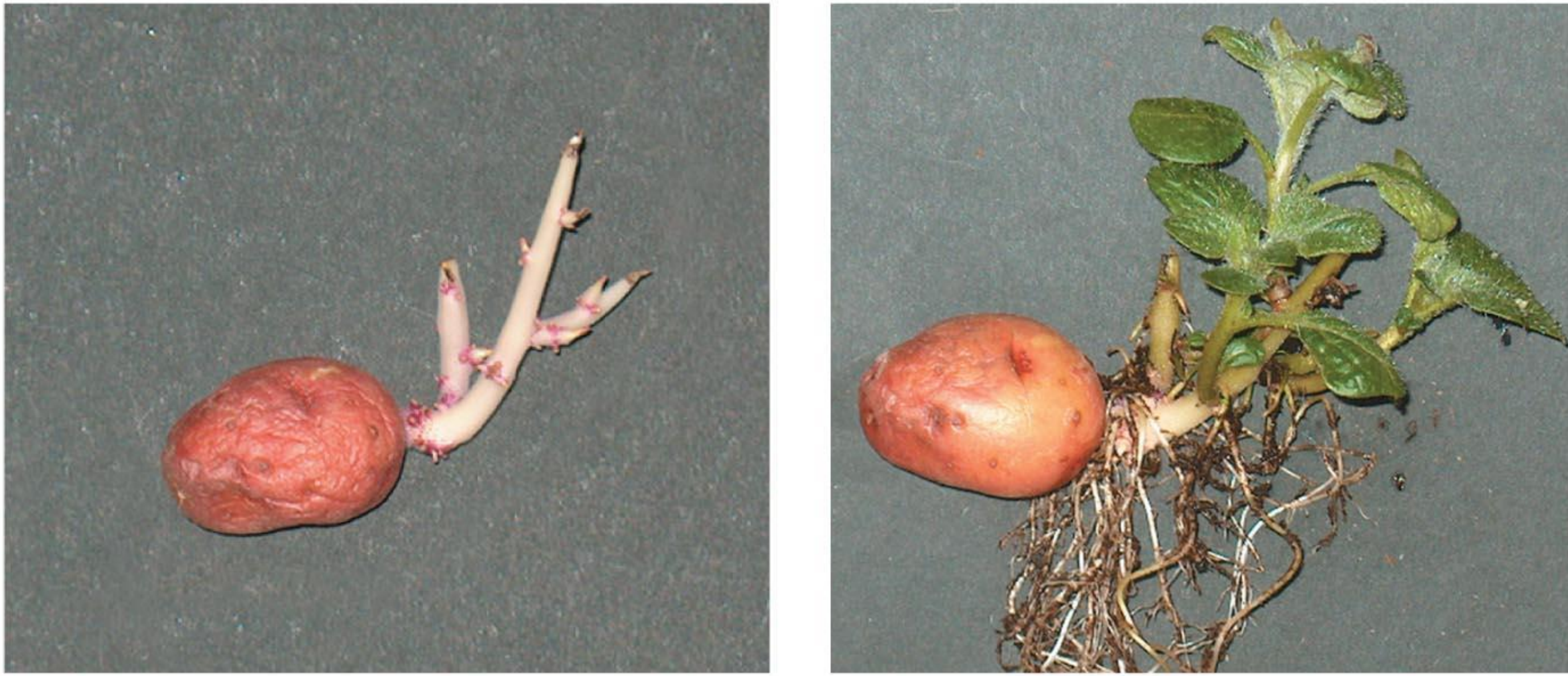
They open in the morning · They close in the afternoon ·

Concept 39.1: Signal transduction pathways link signal reception to response

- Plants have cellular receptors that detect changes in their environment
- For a stimulus to elicit a response, certain cells must have an appropriate receptor
- Stimulation of the receptor initiates a specific signal transduction pathway

- A potato left growing in darkness produces shoots that look unhealthy and 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

Fig. 39-2

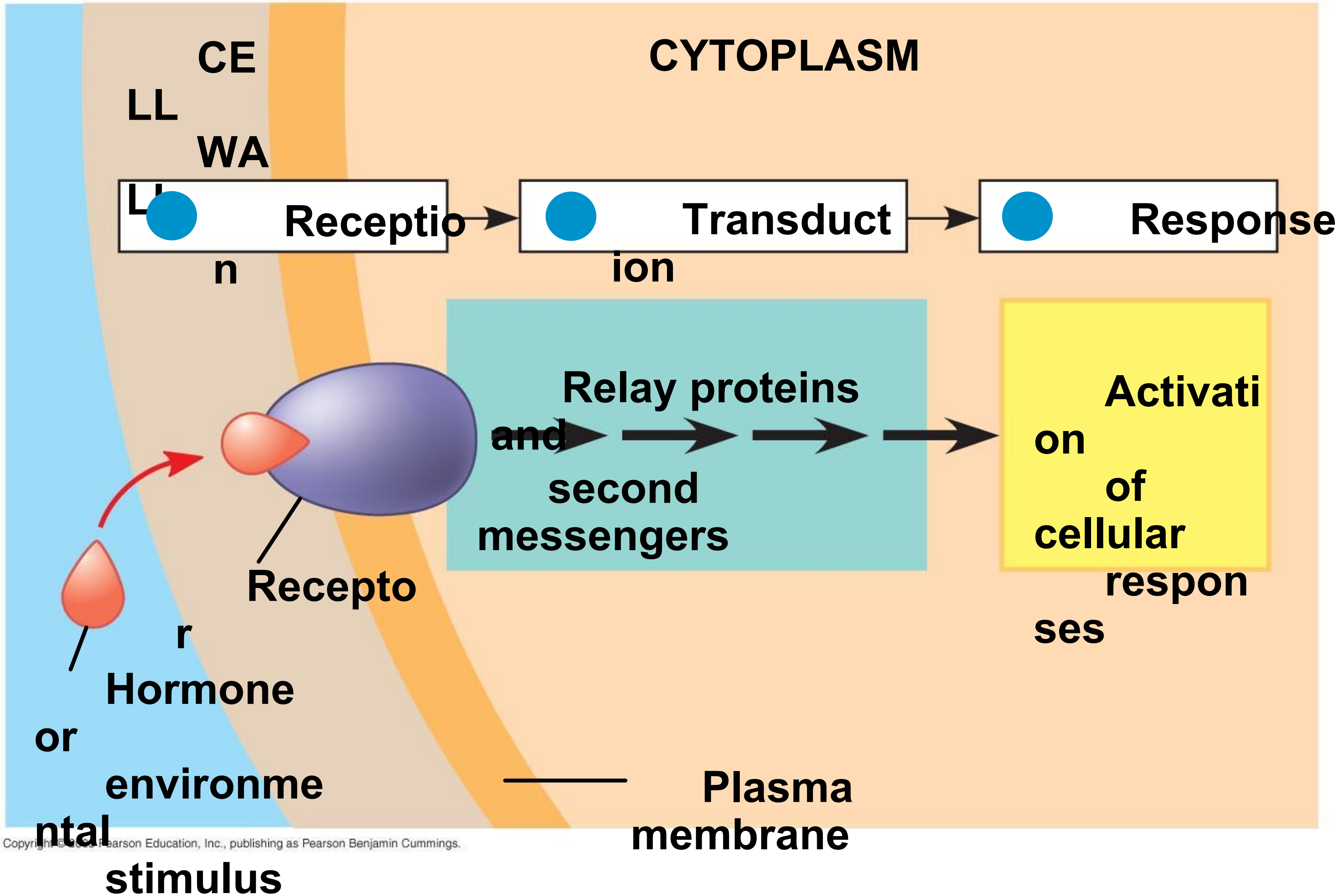


(a) Before exposure to light

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

- A potato's response to light is an example of cell-signal processing
- The stages are reception, transduction, and response

Fig. 39-3



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Reception

- Internal and external signals are detected by receptors, proteins that change in response to specific stimuli

Transduction

- **Second messengers** transfer and amplify signals from receptors to proteins that cause responses

Fig. 39-4-1

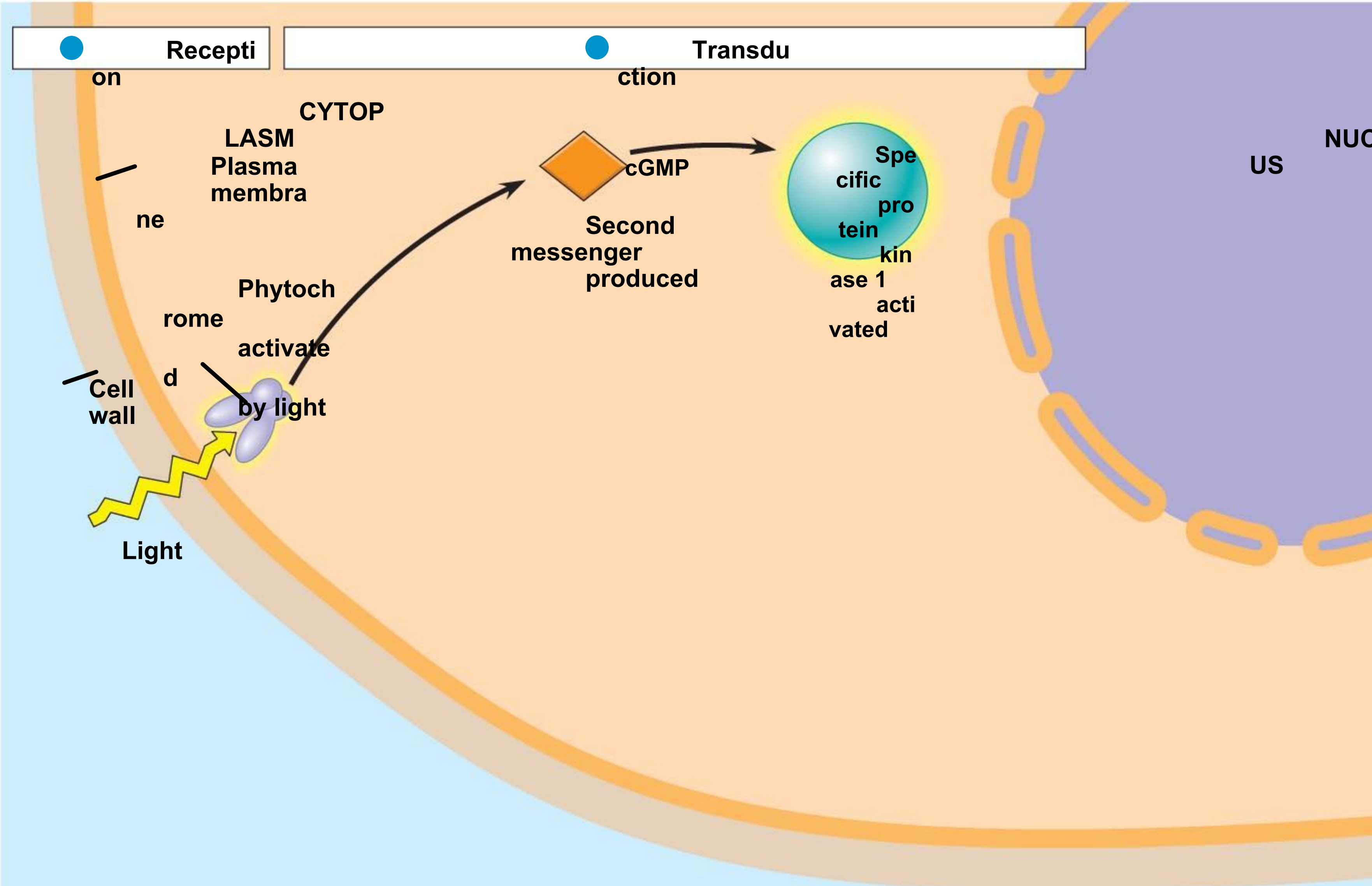

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Fig. 39-4-2

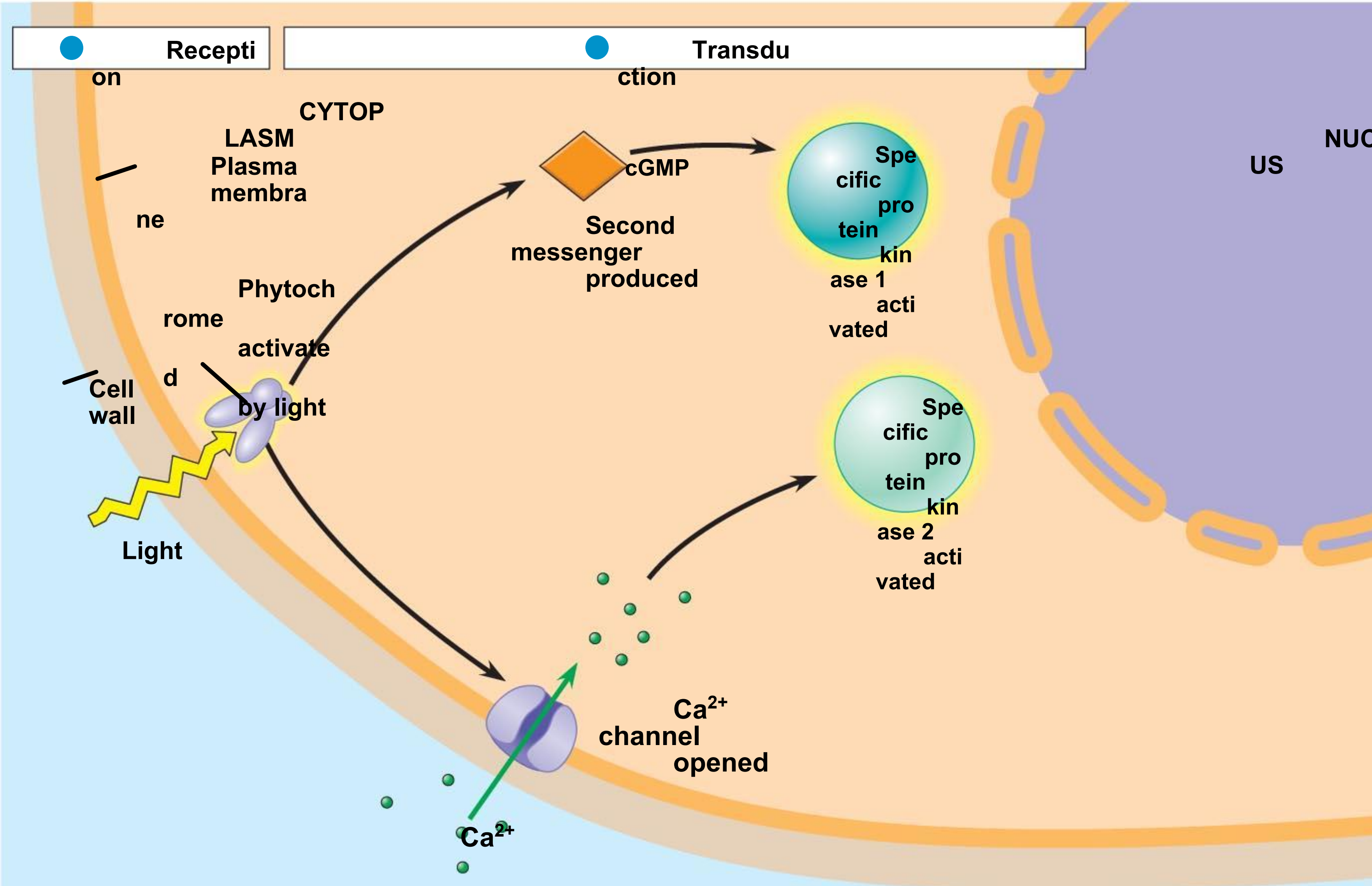

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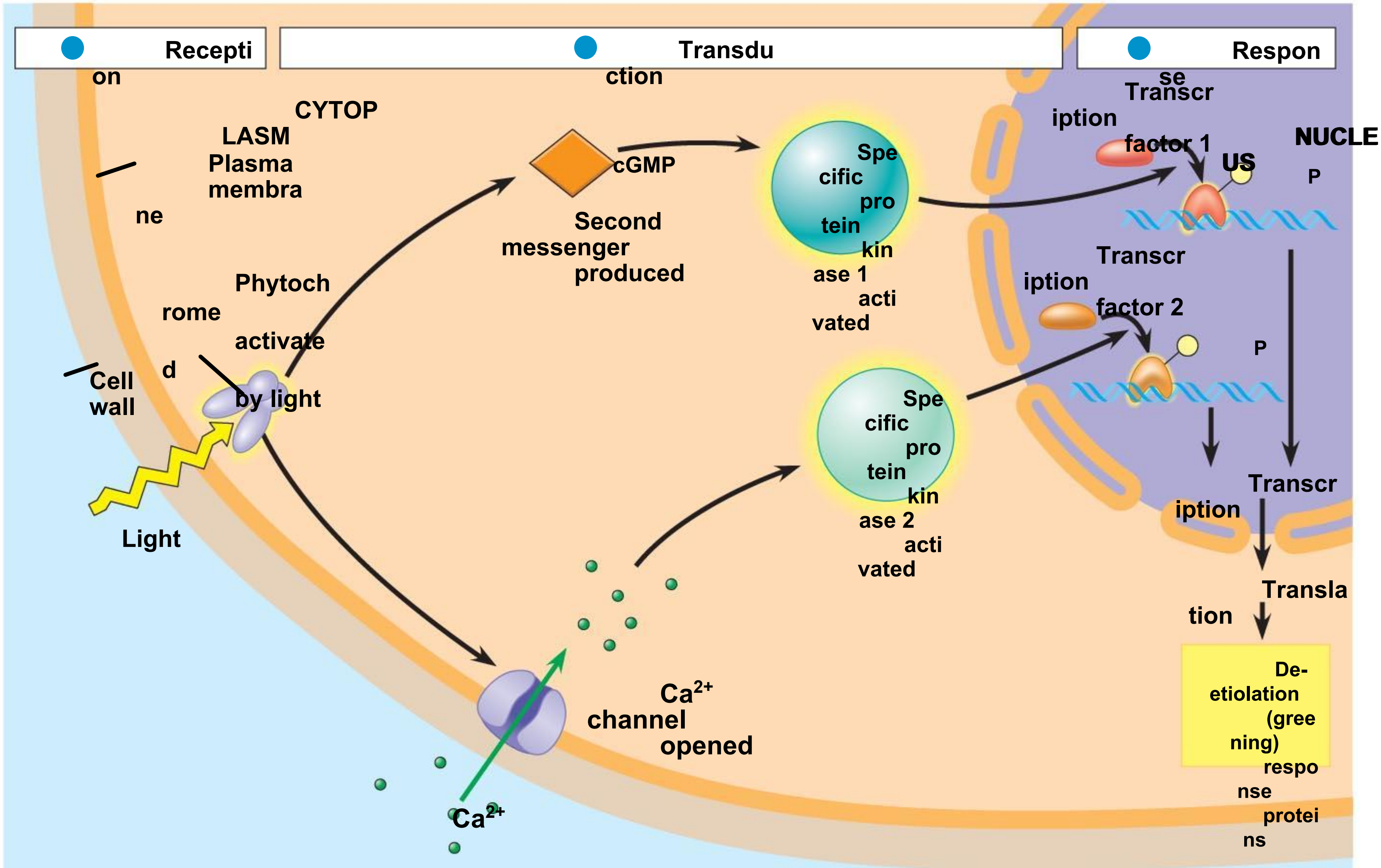
Fig. 39-4-3



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Response

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

Transcriptional Regulation

- *Specific transcription factors* bind directly to specific regions of DNA and control transcription of genes
- Positive transcription factors are proteins that *increase* the transcription of specific genes, while negative transcription factors are proteins that *decrease* the transcription of specific genes

Post-Translational Modification of Proteins

- Post-translational modification involves modification of existing proteins in the signal response
- Modification often involves the phosphorylation of specific amino acids

De-Etiolation ("Greening") Proteins

- Many enzymes that function in certain signal responses are directly involved in photosynthesis
- Other enzymes are involved in supplying chemical precursors for chlorophyll production

Concept 39.2: Plant hormones help coordinate growth, development, and responses to stimuli

- **Hormones** are chemical signals that coordinate different parts of an organism

The Discovery of Plant Hormones

- Any response resulting in curvature of organs toward or away from a stimulus is called a **tropism**
- Tropisms are often caused by hormones

- 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

PLAY

Video: Phototropism

Fig. 39-5

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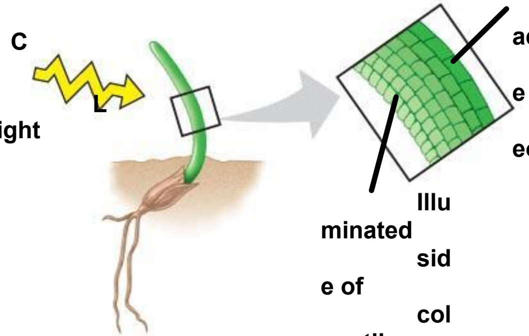
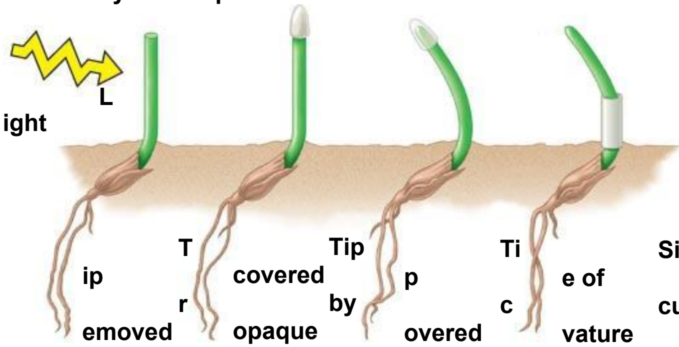


Darwin and Darwin: phototropic
response
only when tip is illuminated



Boysen-Jensen: phototropic response when tip
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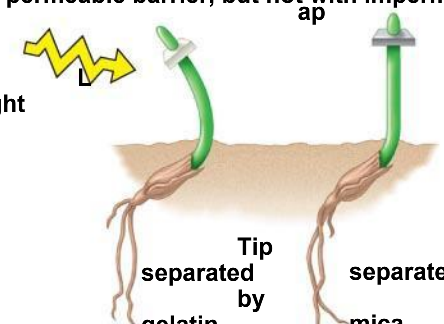

Fig. 39-5a

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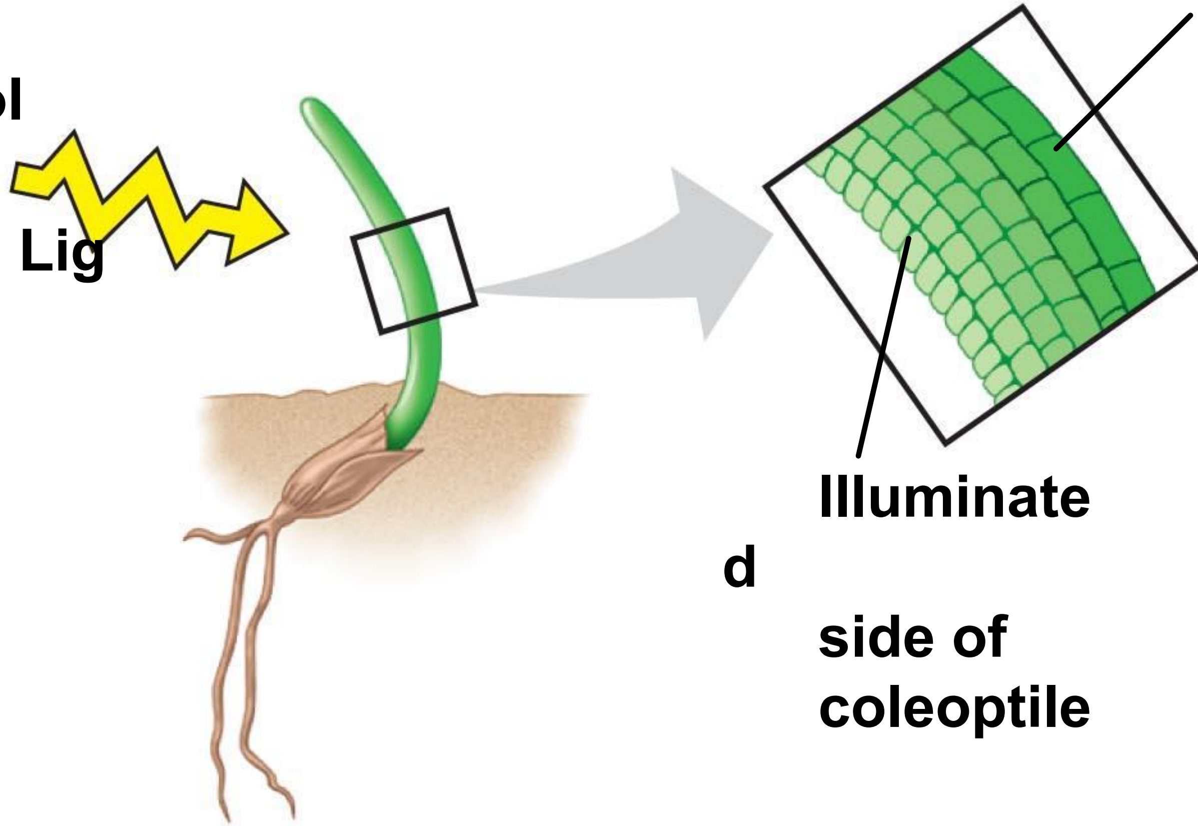
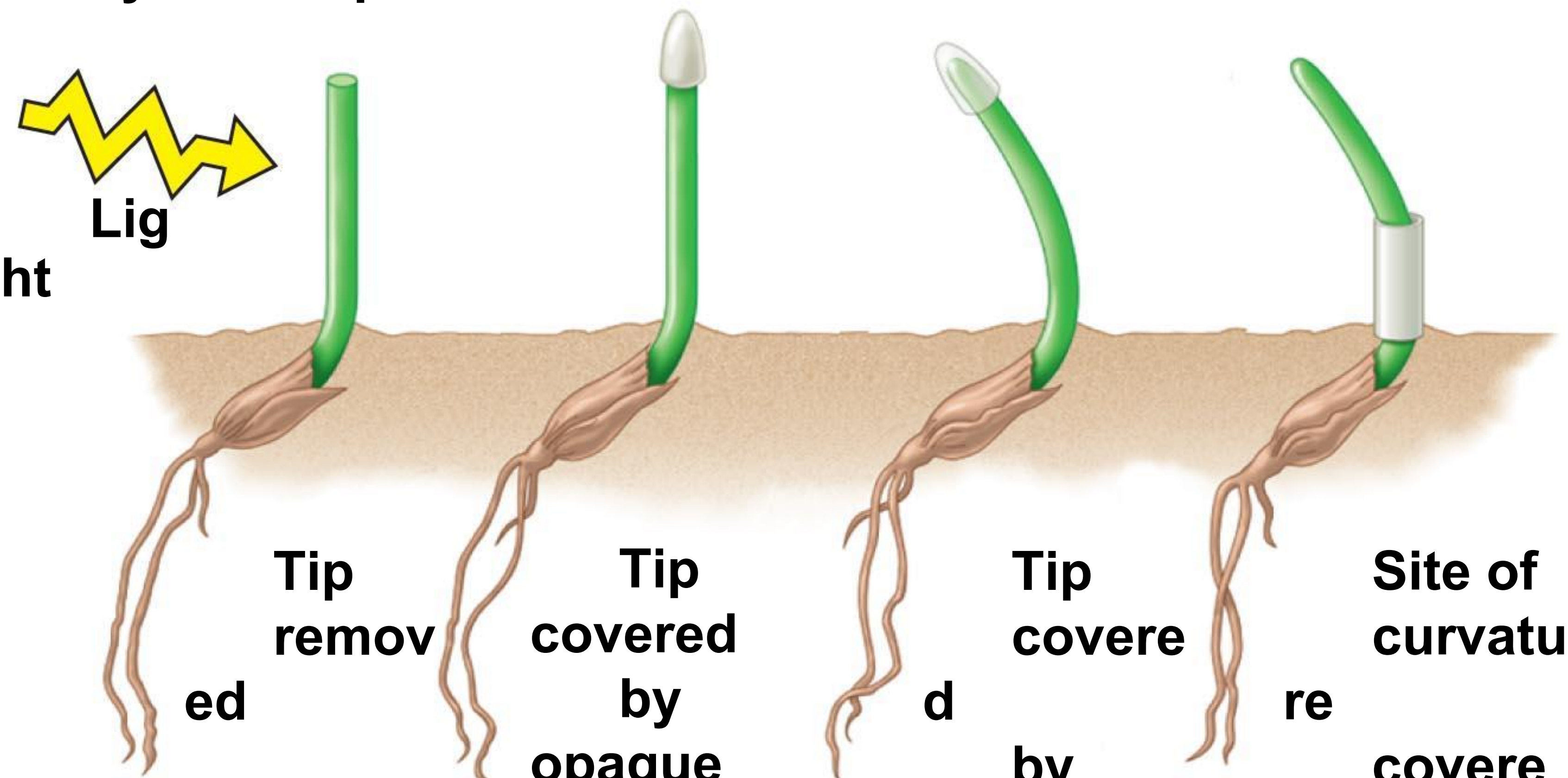


Fig. 39-5b

RESULTS

Darwin and Darwin: phototropic response only when tip is illuminated

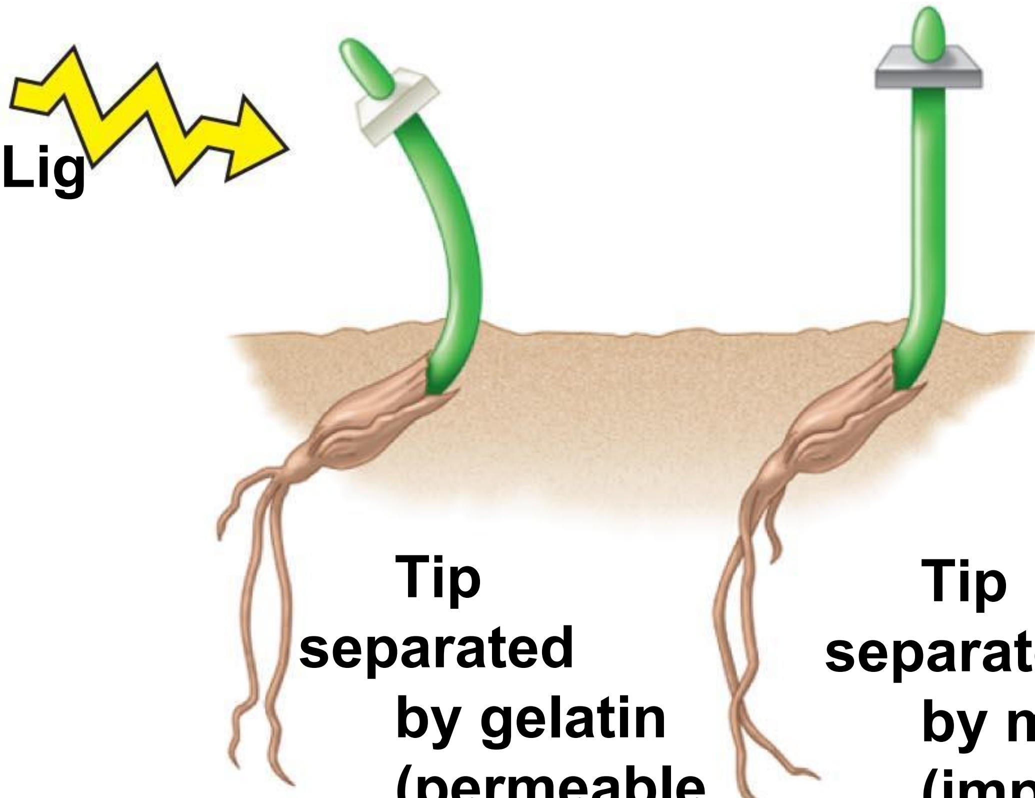


- In 1913, Peter Boysen-Jensen demonstrated that the signal was a mobile chemical substance

Fig. 39-5c

RESULTS

Boysen-Jensen: phototropic response when tip is separated by permeable barrier, but not with impermeable barrier



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

Fig. 39-6

RESU
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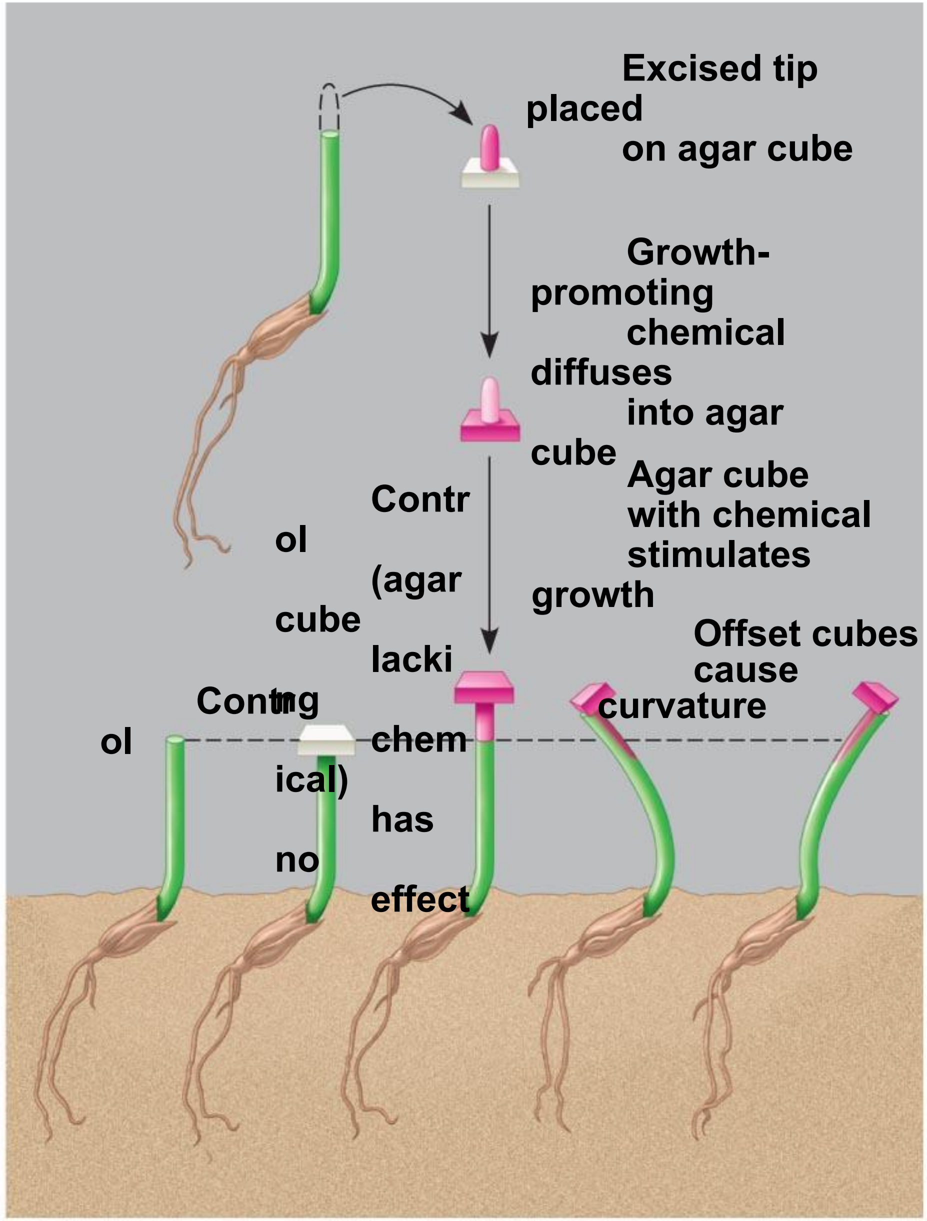


A Survey of Plant Hormones

- In general, hormones control plant growth and development by affecting the division, elongation, and differentiation of cells
- Plant hormones are produced in very low concentration, but a minute amount can greatly affect growth and development of a plant organ

Table 39-1

Table 39.1 Overview of Plant Hormones

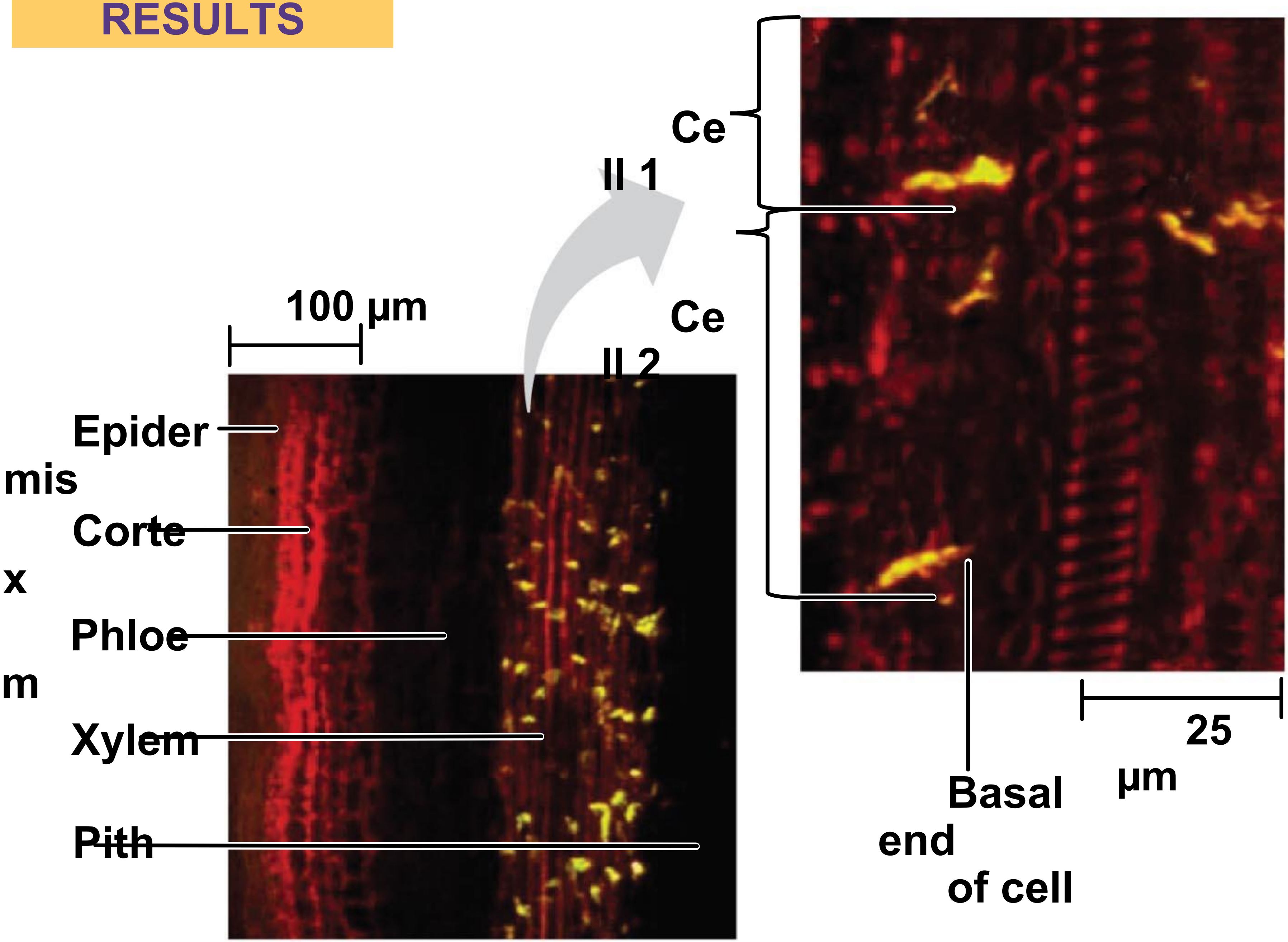
Hormone	Where Produced or Found in Plant	Major Functions
Auxin (IAA)	Shoot apical meristems and young leaves are the primary sites of auxin synthesis. Root apical meristems also produce auxin, although the root depends on the shoot for much of its auxin. Developing seeds and fruits contain high levels 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	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 almost all 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.

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 transporter proteins move the hormone from the basal end of one cell into the apical end of the neighboring cell

Fig. 39-7

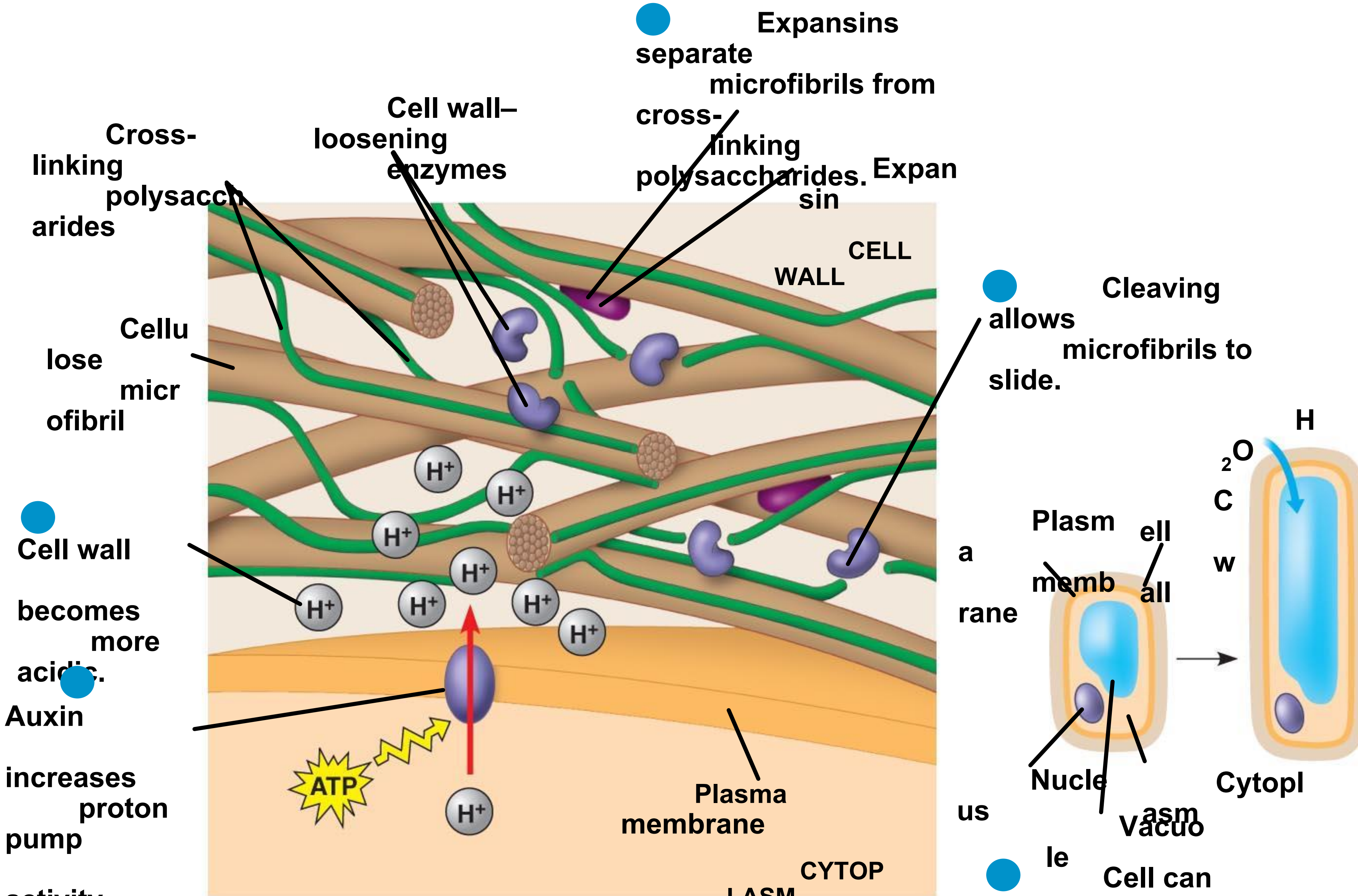
RESULTS



The Role of Auxin in Cell Elongation

- According to the *acid growth hypothesis*, auxin stimulates proton pumps in the plasma membrane
- 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

Fig. 39-8



Expansins
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Lateral and Adventitious Root Formation

- Auxin is involved in root formation and branching

Auxins as Herbicides

- An overdose of synthetic auxins can kill eudicots

Other Effects of Auxin

- Auxin affects secondary growth by inducing cell division in the vascular cambium and influencing differentiation of secondary xylem

Cytokinins

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

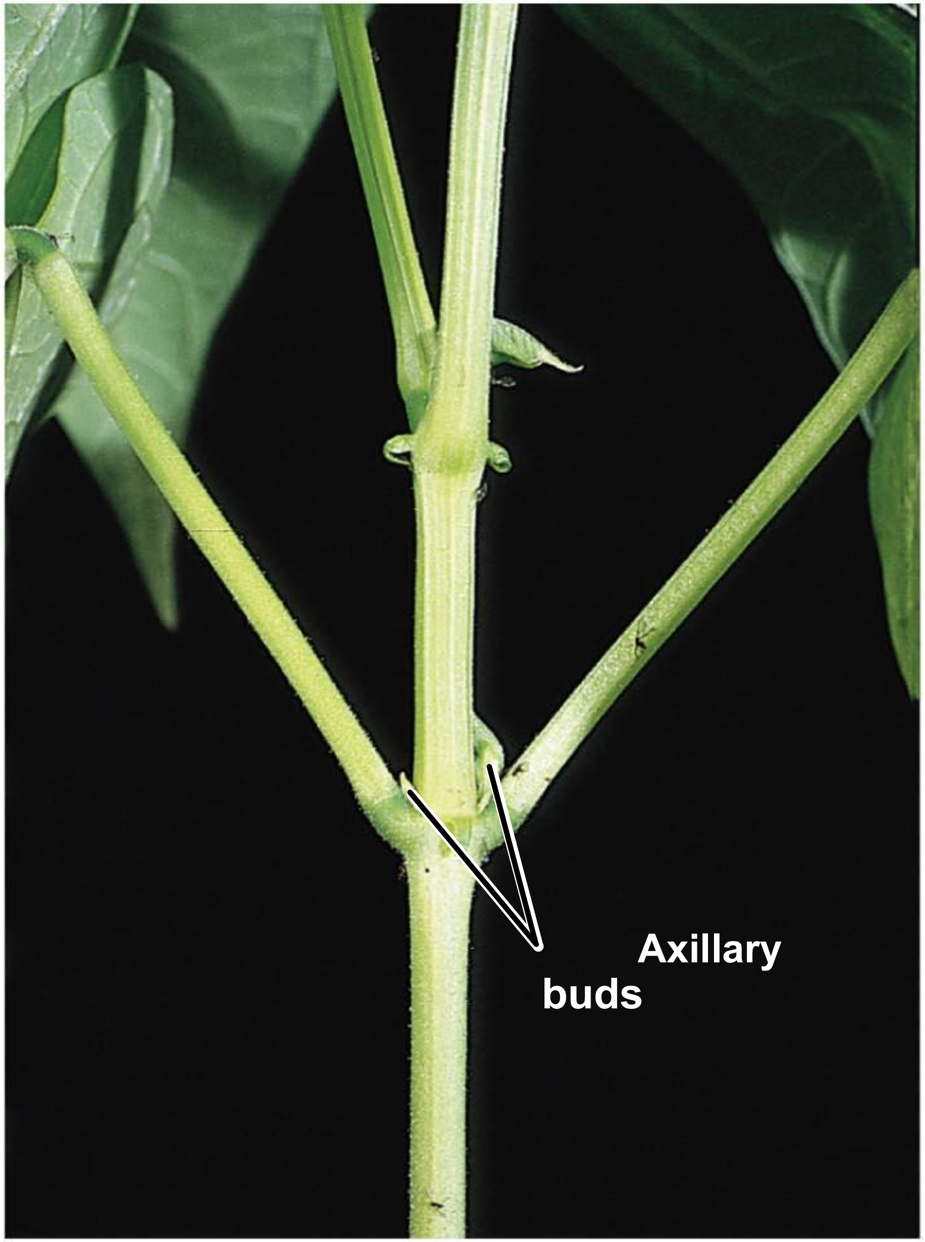
Control of Cell Division and Differentiation

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

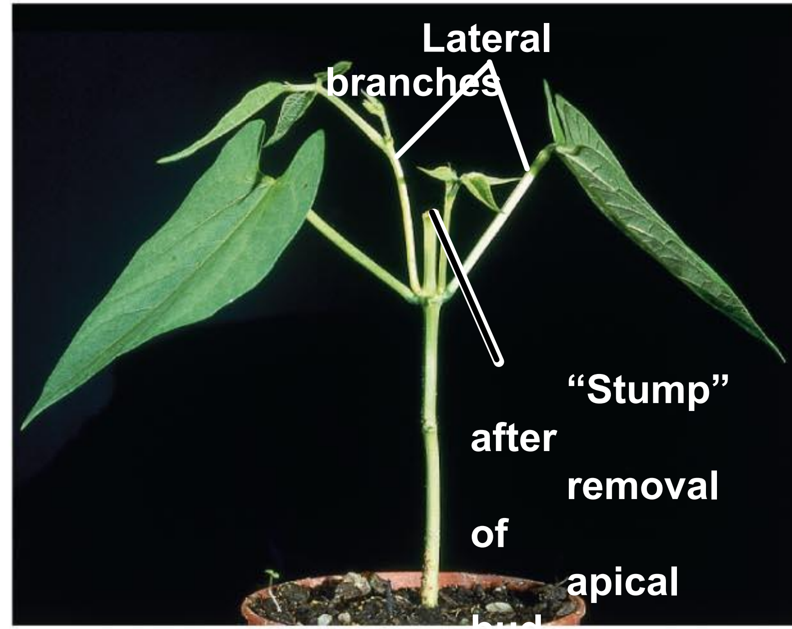
Control of Apical Dominance

- Cytokinins, auxin, and other factors interact in the control of apical dominance, a terminal bud’s ability to suppress development of axillary buds
- If the terminal bud is removed, plants become bushier

Fig. 39-9



(a) Apical bud intact (not shown in photo)



(b) Apical bud removed

(c) Auxin added to decapitated stem

Anti-Aging Effects

- Cytokinins retard the aging of some plant organs by inhibiting protein breakdown, stimulating RNA and protein synthesis, and mobilizing nutrients from surrounding tissues

Gibberellins

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

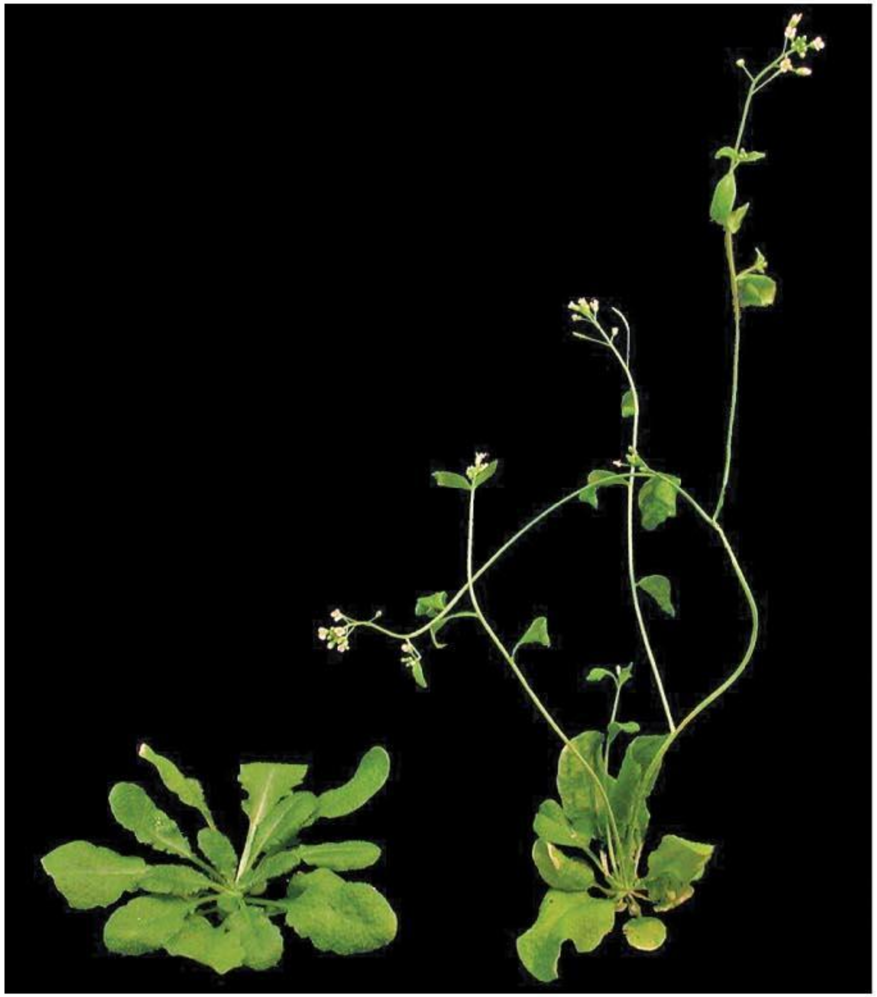
Stem Elongation

- Gibberellins stimulate growth of leaves and stems
- In stems, they stimulate cell elongation and cell division

Fruit Growth

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

Fig. 39-10



a. **Gibberellin-induced stem growth**

(b) Gibberellin-induced fruit growth

Germination

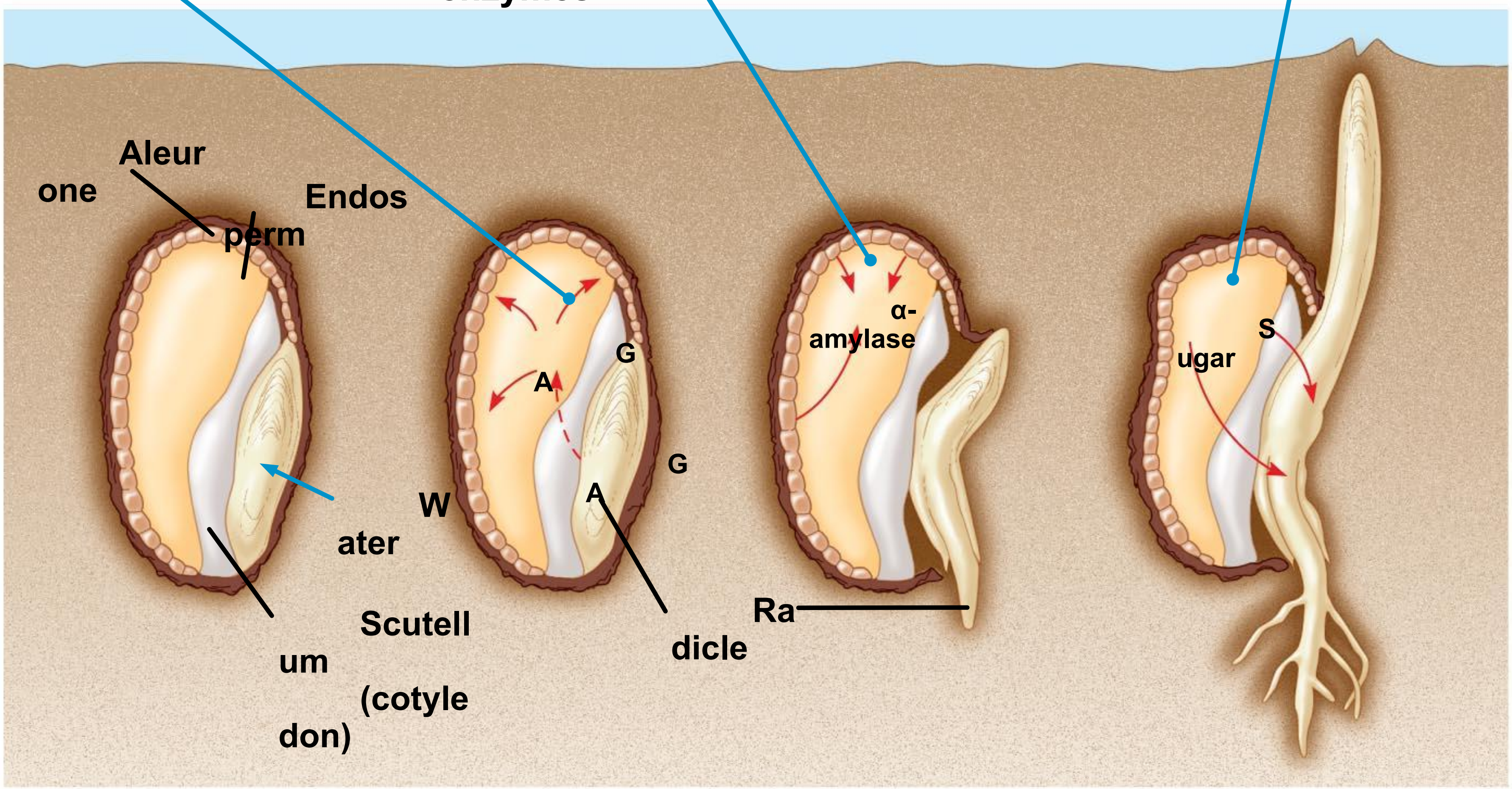
- After water is imbibed, release of gibberellins from the embryo signals seeds to germinate

Fig. 39-11

Gibberellins (GA) send signal to aleurone.

Aleurone secretes α-amylase and other enzymes.

Sugars and other nutrients are consumed.



Brassinosteroids

- **Brassinosteroids** are chemically similar to the sex hormones of animals
- They induce cell elongation and division in stem segments

Abscisic Acid

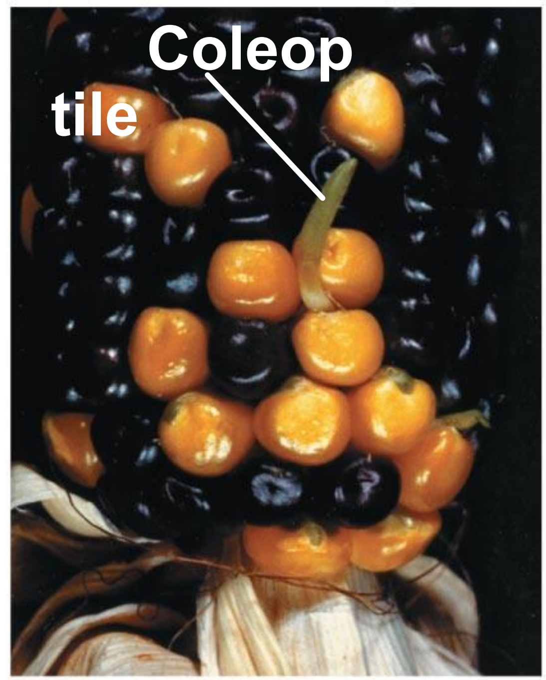
- **Abscisic acid (ABA)** slows growth
- Two of the many effects of ABA:
  - Seed dormancy
  - Drought tolerance

Seed Dormancy

- 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 germination is observed in maize mutants that lack a transcription factor required for ABA to induce expression of certain genes

Fig. 39-12

Early germination in red mangrove



Early germination in maize mutant

Drought Tolerance

- ABA is the primary internal signal that enables plants to withstand drought

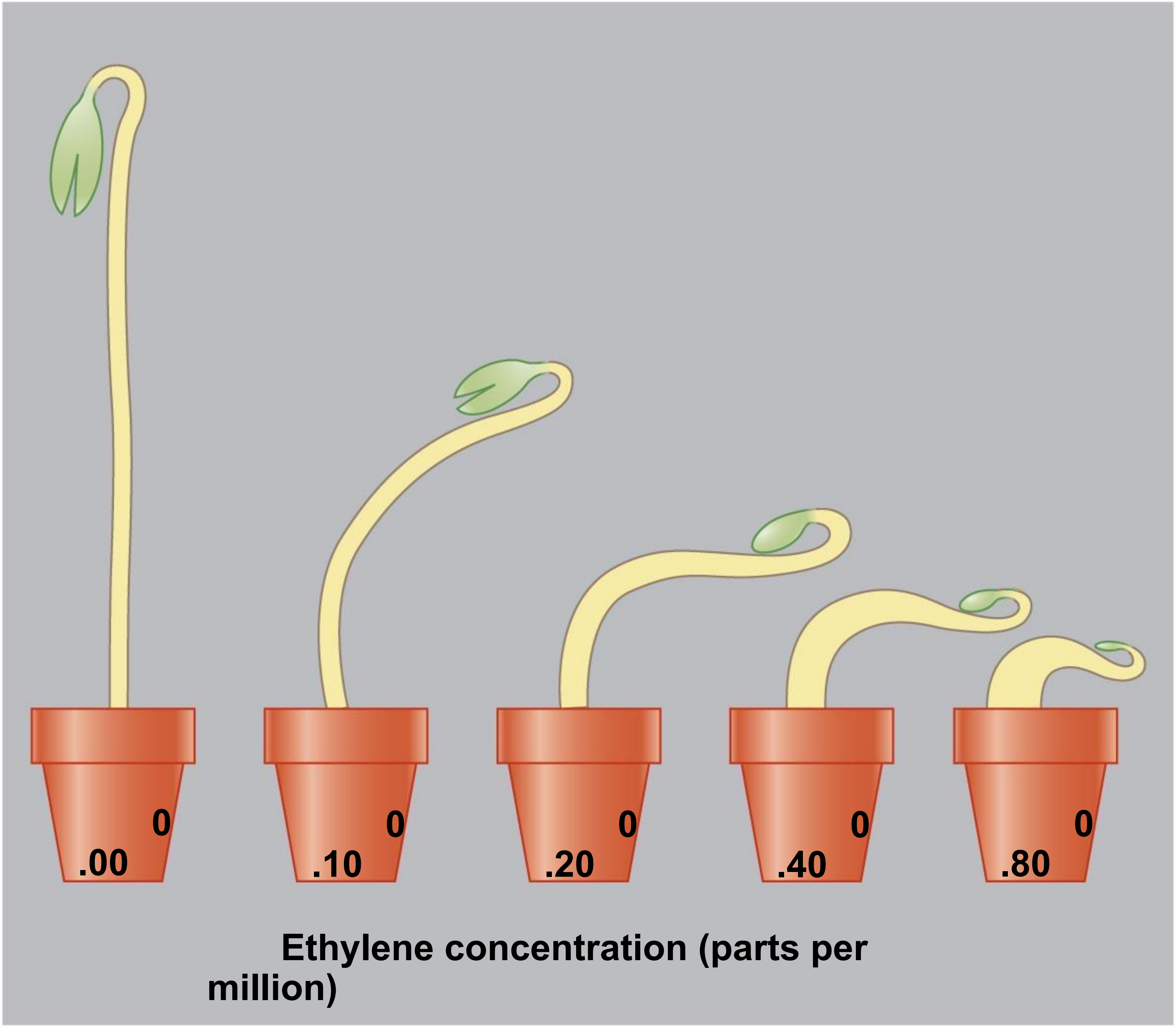
Ethylene

- 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

Fig. 39-13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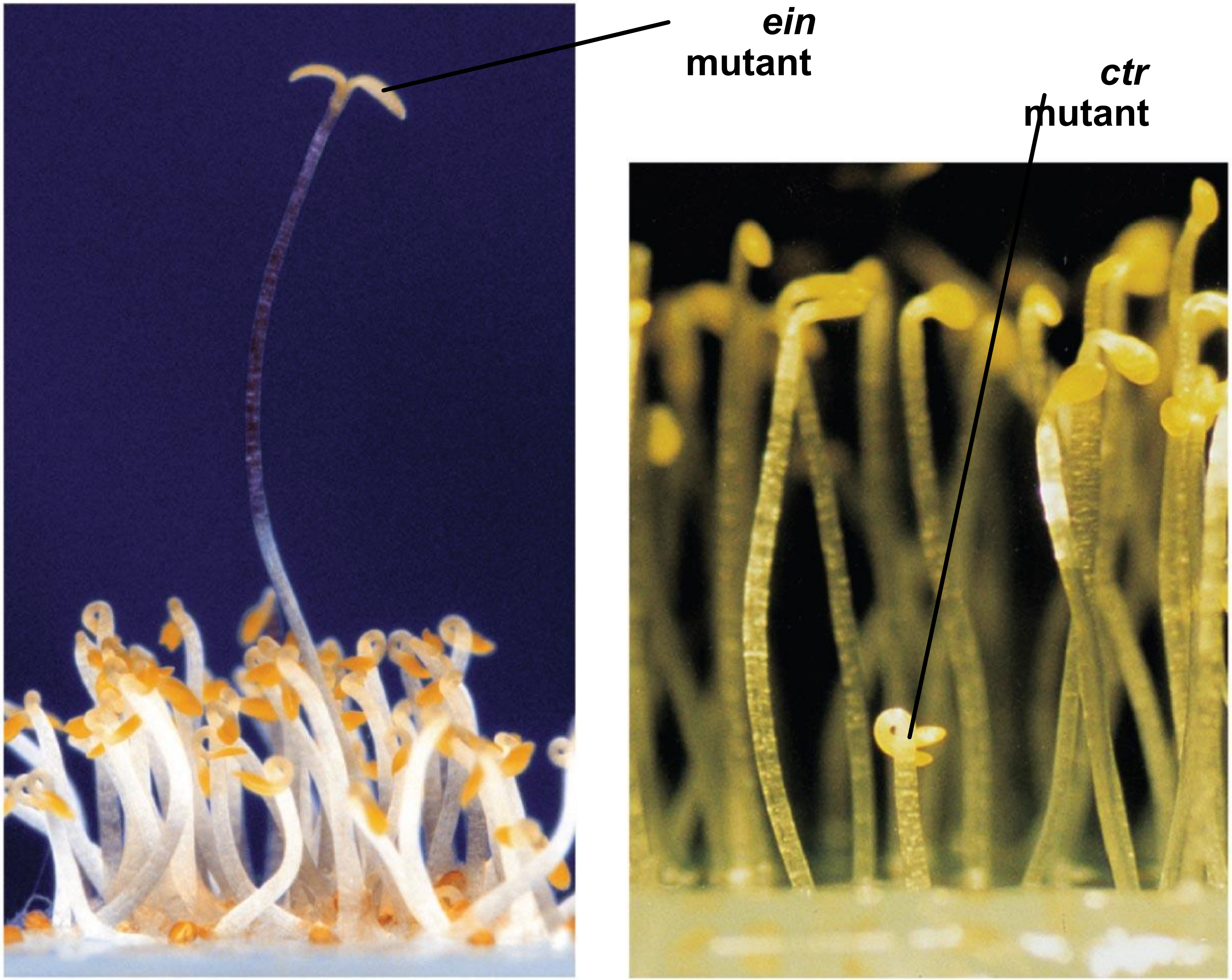
Ethylene concentration (parts per million)

- Ethylene-insensitive mutants fail to undergo the triple response after exposure to ethylene
- Other mutants undergo the triple response in air but do not respond to inhibitors of ethylene synthesis

Fig. 39-14



(a) *ein* mutant

(b) *ctr* mutant

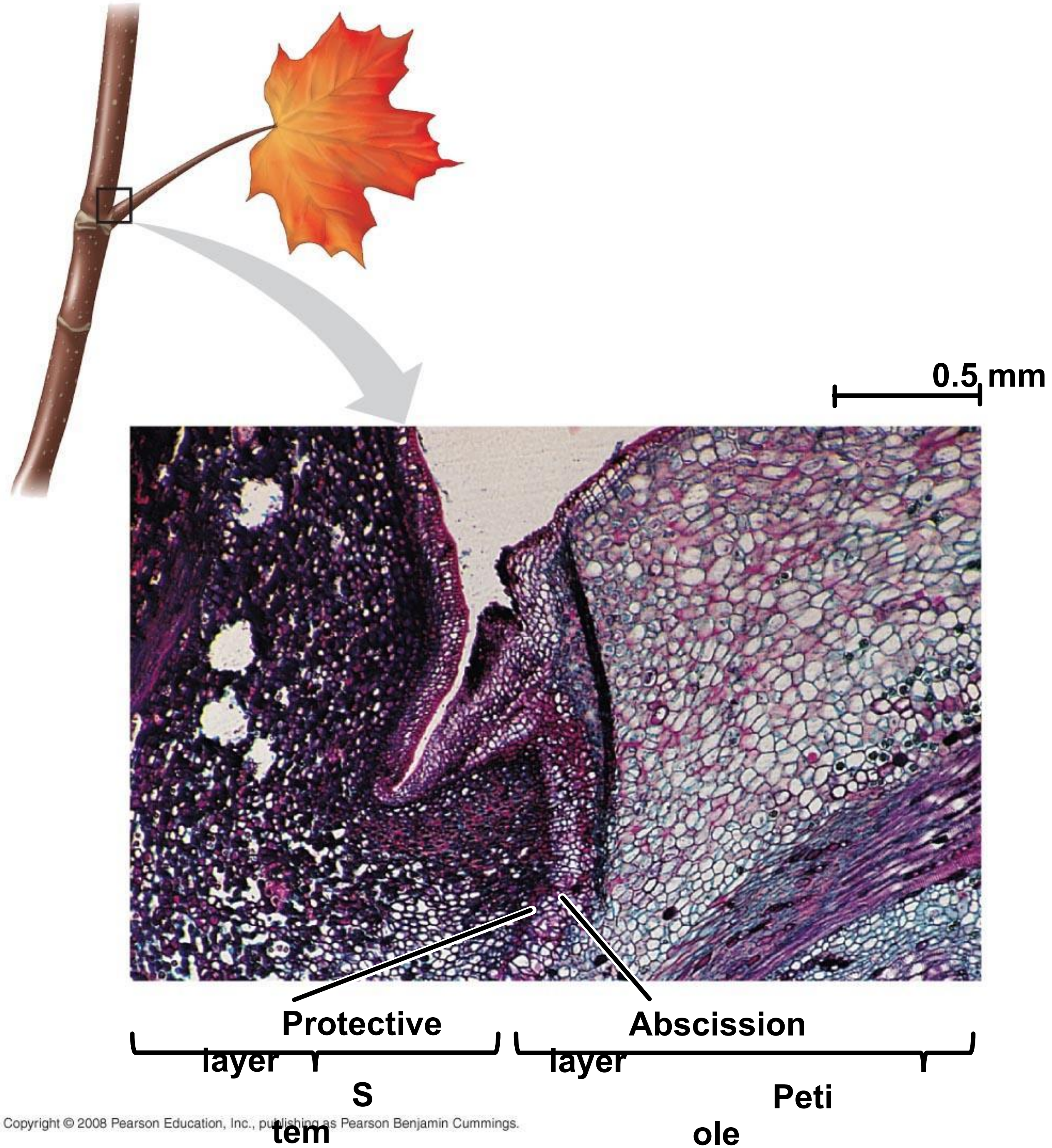
Senescence

- **Senescence** is the programmed death of plant 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

Fig. 39-15



Fruit Ripening

- A burst of ethylene production in a fruit triggers the ripening process

Systems Biology and Hormone Interactions

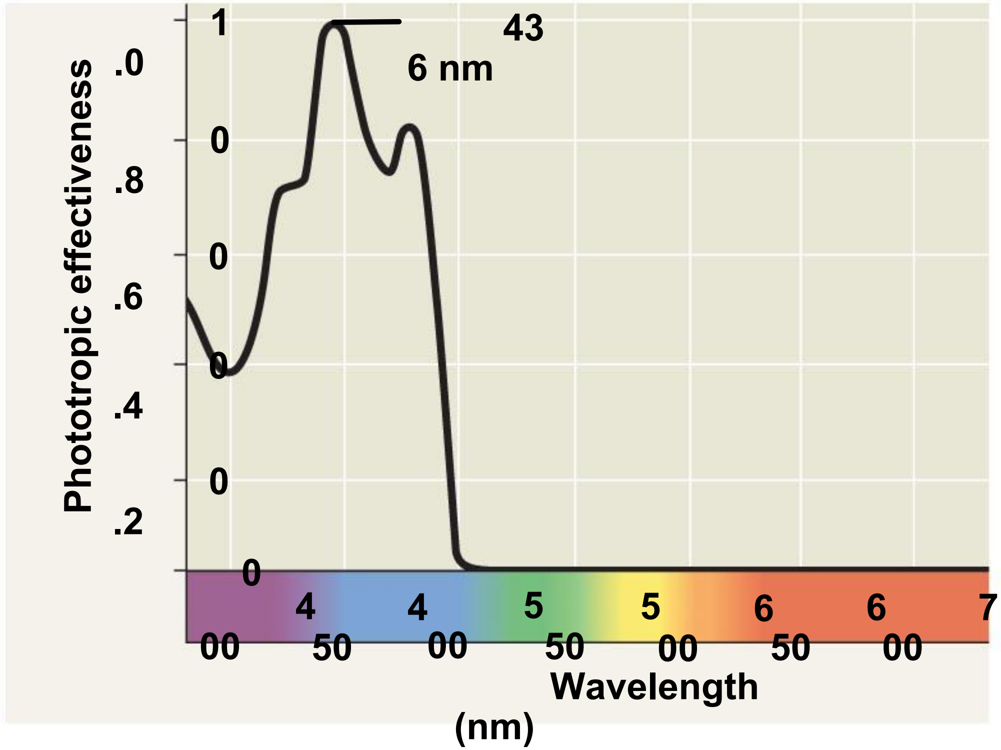
- Interactions between hormones and signal transduction pathways make it hard to predict how genetic manipulation will affect a plant
- Systems biology seeks a comprehensive understanding that permits modeling of plant functions

Concept 39.3: Responses to light are critical for plant success

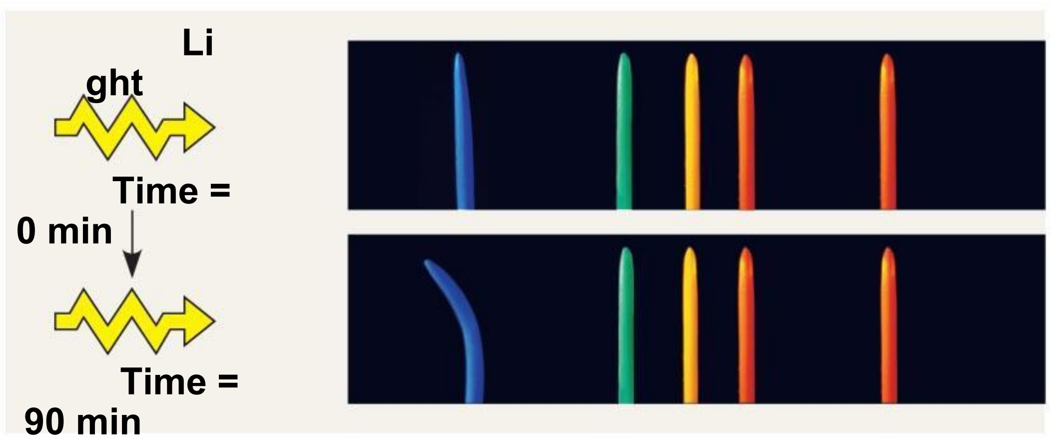
- Light cues many key events in plant growth and development
- Effects of light on plant morphology are called **photomorphogenesis**

- Plants detect not only 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

Fig. 39-16

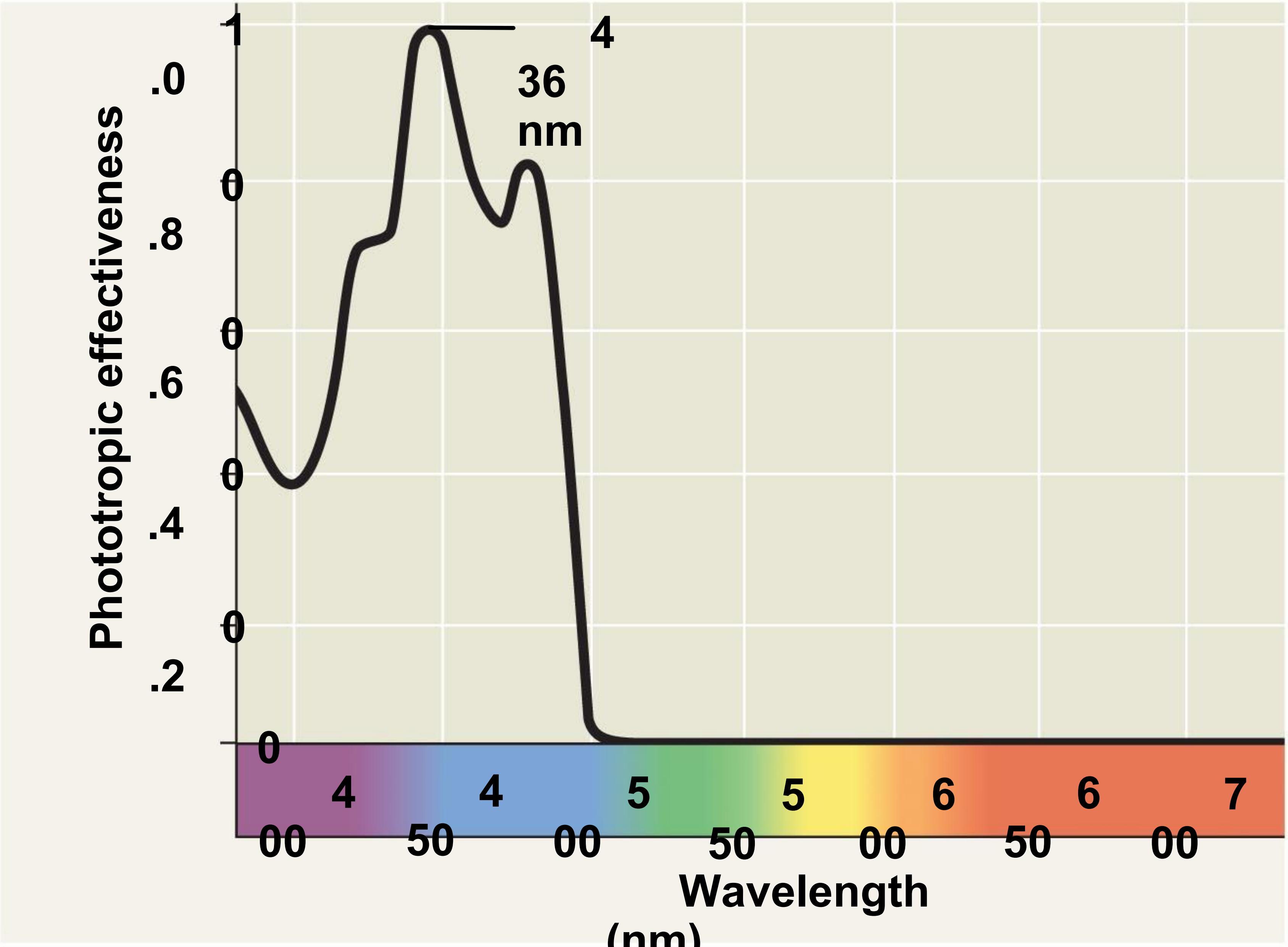


(a) Action spectrum for blue-light phototropism



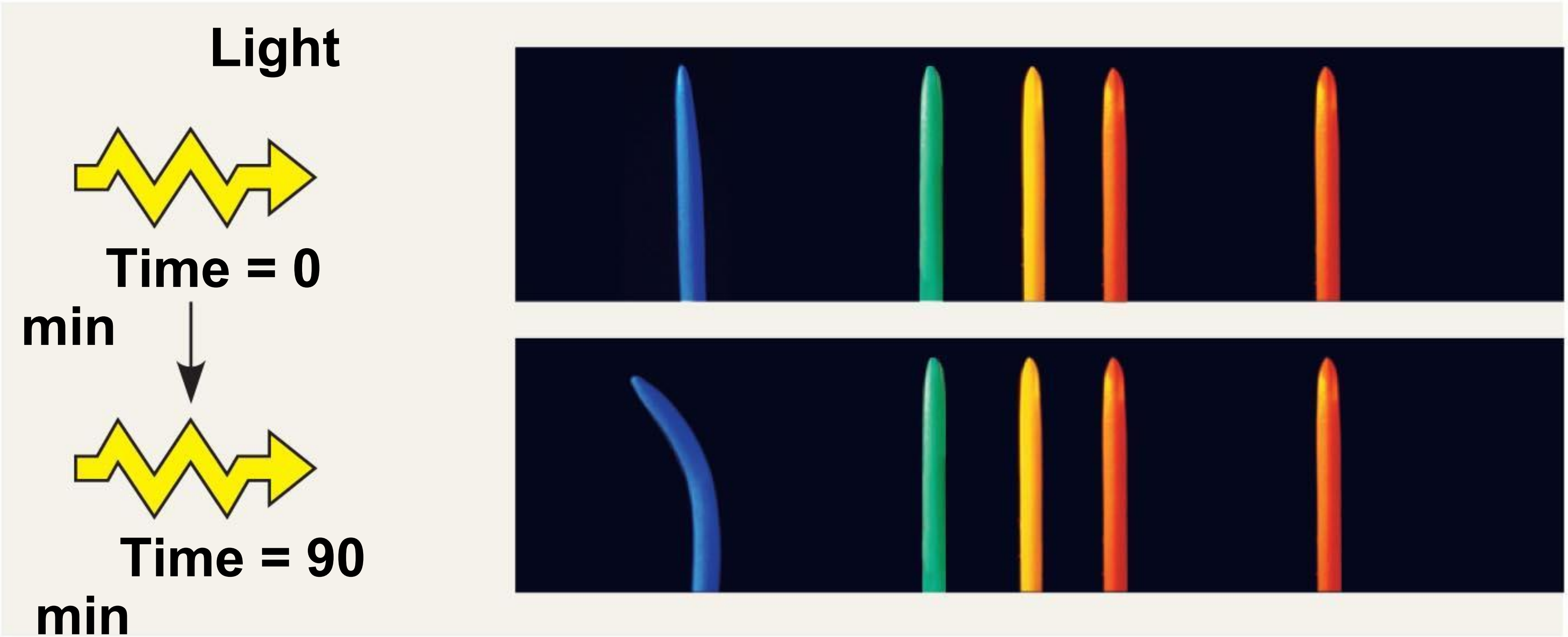
(b) Coleoptile response to light colors

Fig. 39-16a



(a) Action spectrum for blue-light phototropism

Fig. 39-16b



(b) Coleoptile response to light colors

- There are two major classes of light receptors: **blue-light photoreceptors** and **phytochromes**

Blue-Light Photoreceptors

- Various blue-light photoreceptors control hypocotyl elongation, stomatal opening, and phototropism

Phytochromes as 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 change
- In the 1930s, scientists at the U.S. Department of Agriculture determined the action spectrum for light-induced germination of lettuce seeds

Fig. 39-17

RESULT
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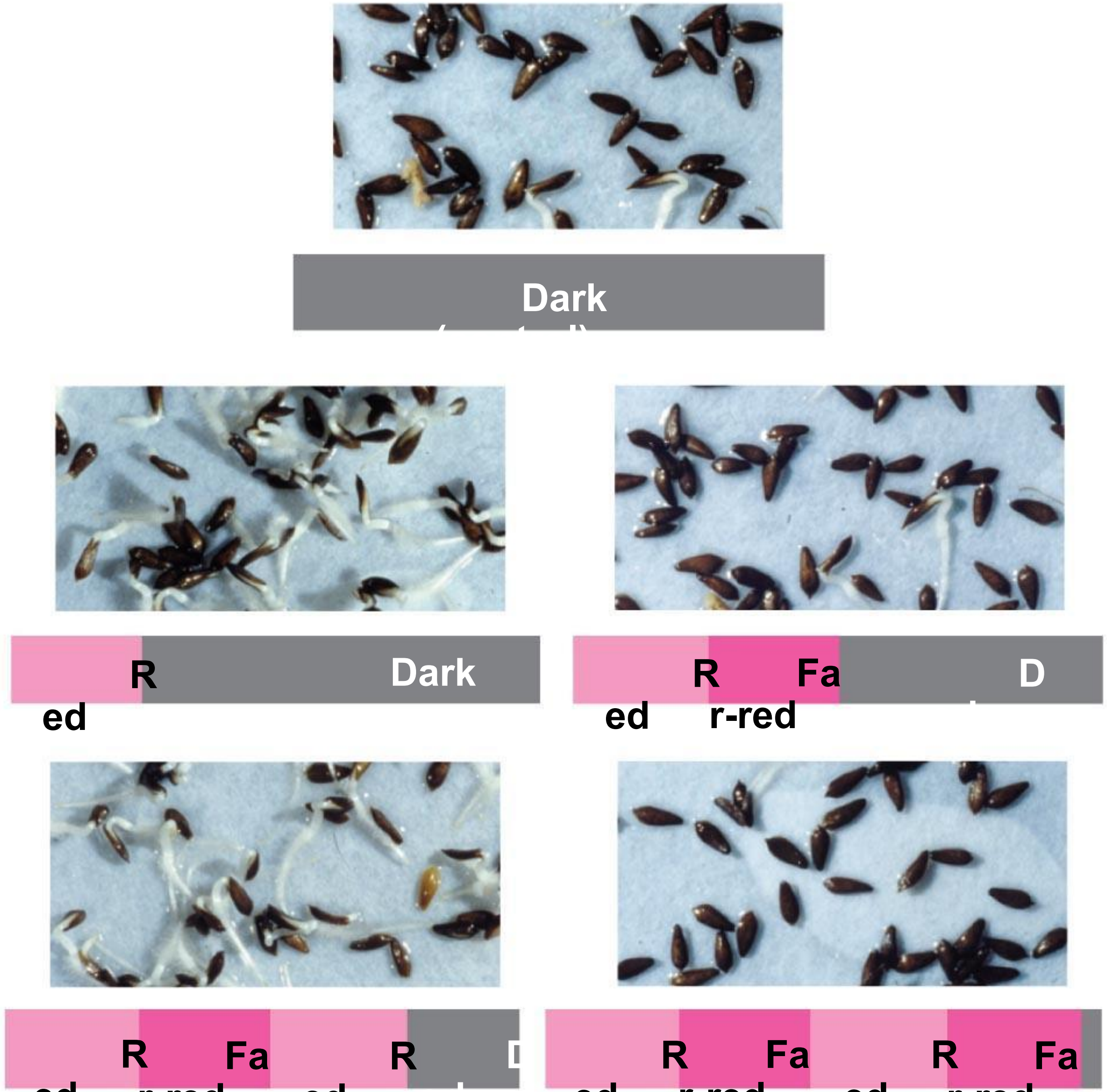


- Red light increased germination, while far-red light inhibited germination
- The photoreceptor responsible for the opposing effects of red and far-red light is a phytochrome

Fig. 39-18

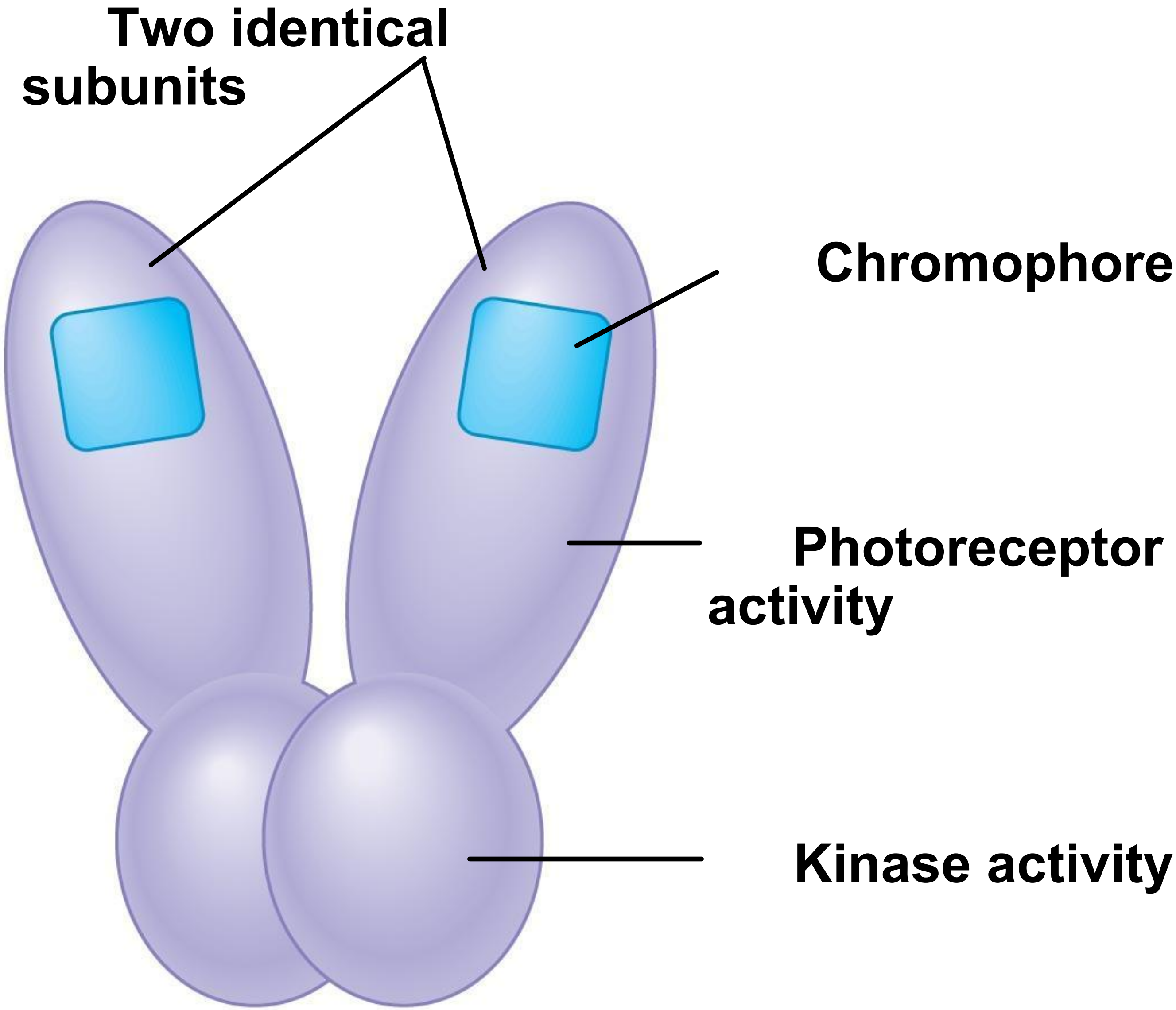
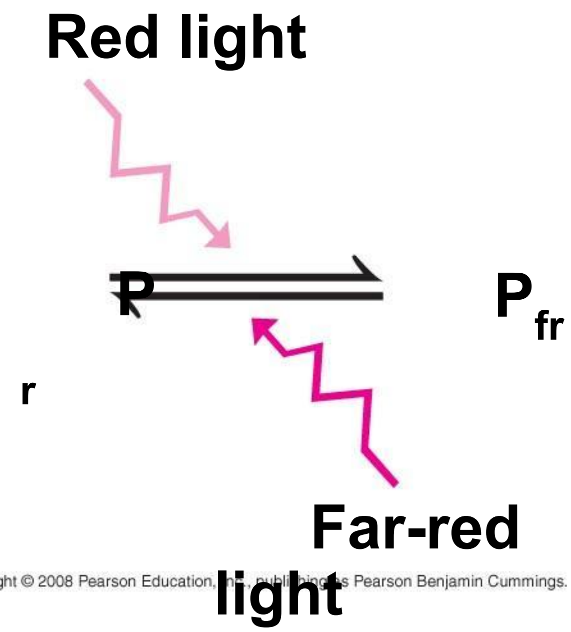
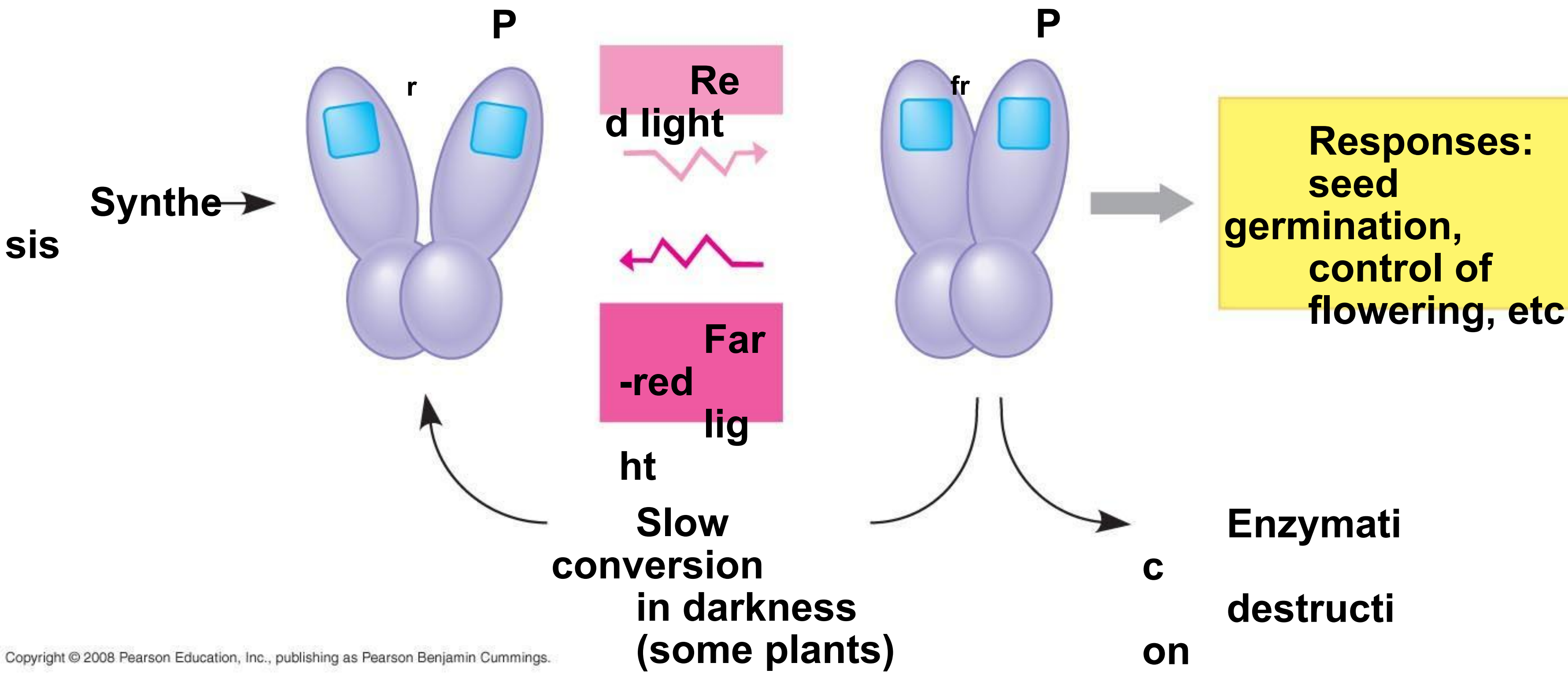

Two identical subunits
Chromophore
Photoreceptor activity
Kinase activity

Fig. 39-UN1



- Phytochromes exist in two photoreversible states, with conversion of P_r to P_{fr} triggering many developmental responses

Fig. 39-19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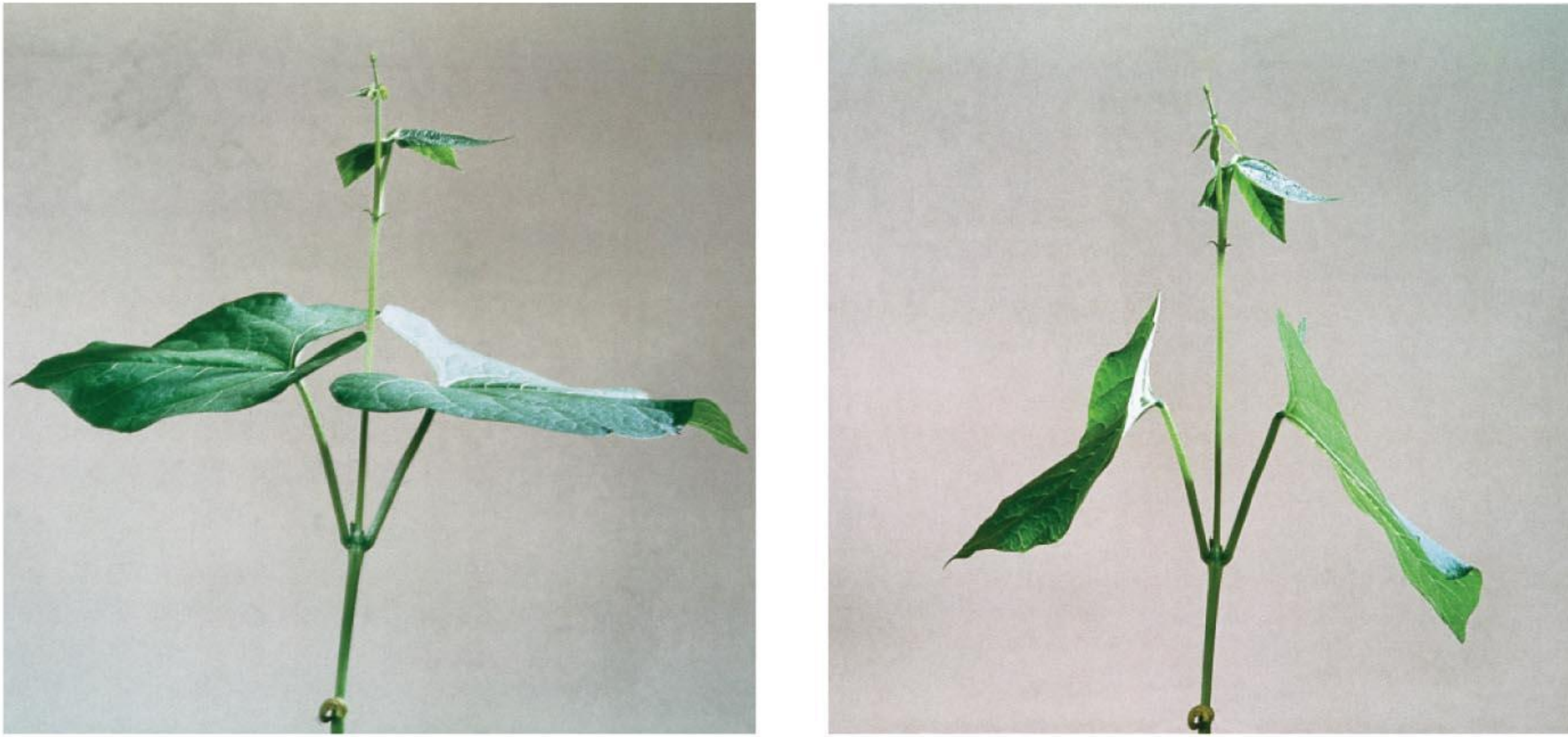
Phytochromes and Shade Avoidance

- The phytochrome system also provides the plant with information about the *quality* of 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

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

Fig. 39-20



Noon

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- **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 and may be common to all eukaryotes

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

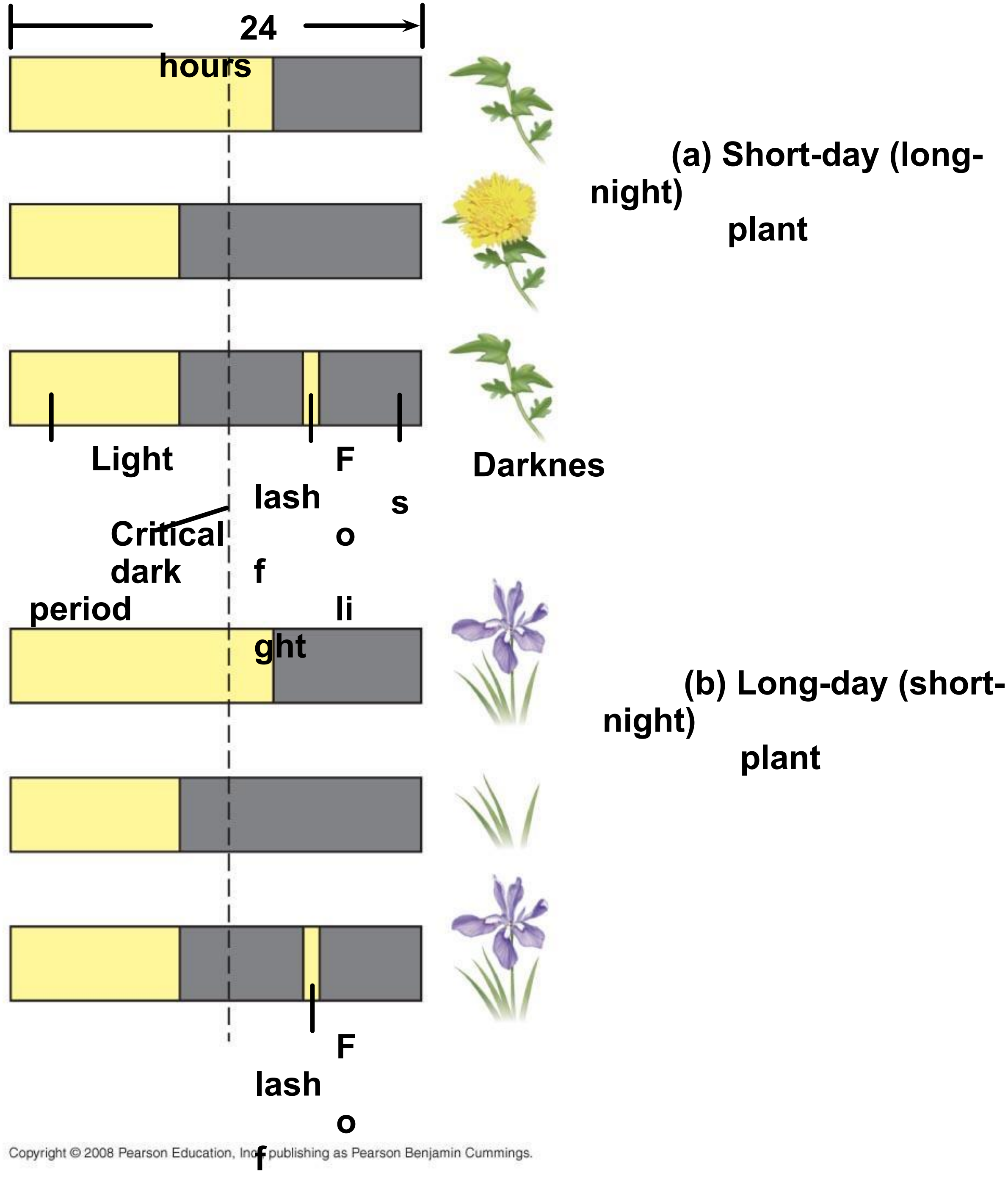
- Some processes, including flowering in many species, require a certain photoperiod
- Plants that flower when a light period is shorter than a critical length are called **short-day plants**
- Plants that flower when a light period is longer than a certain number of hours are called **long-day plants**
- 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

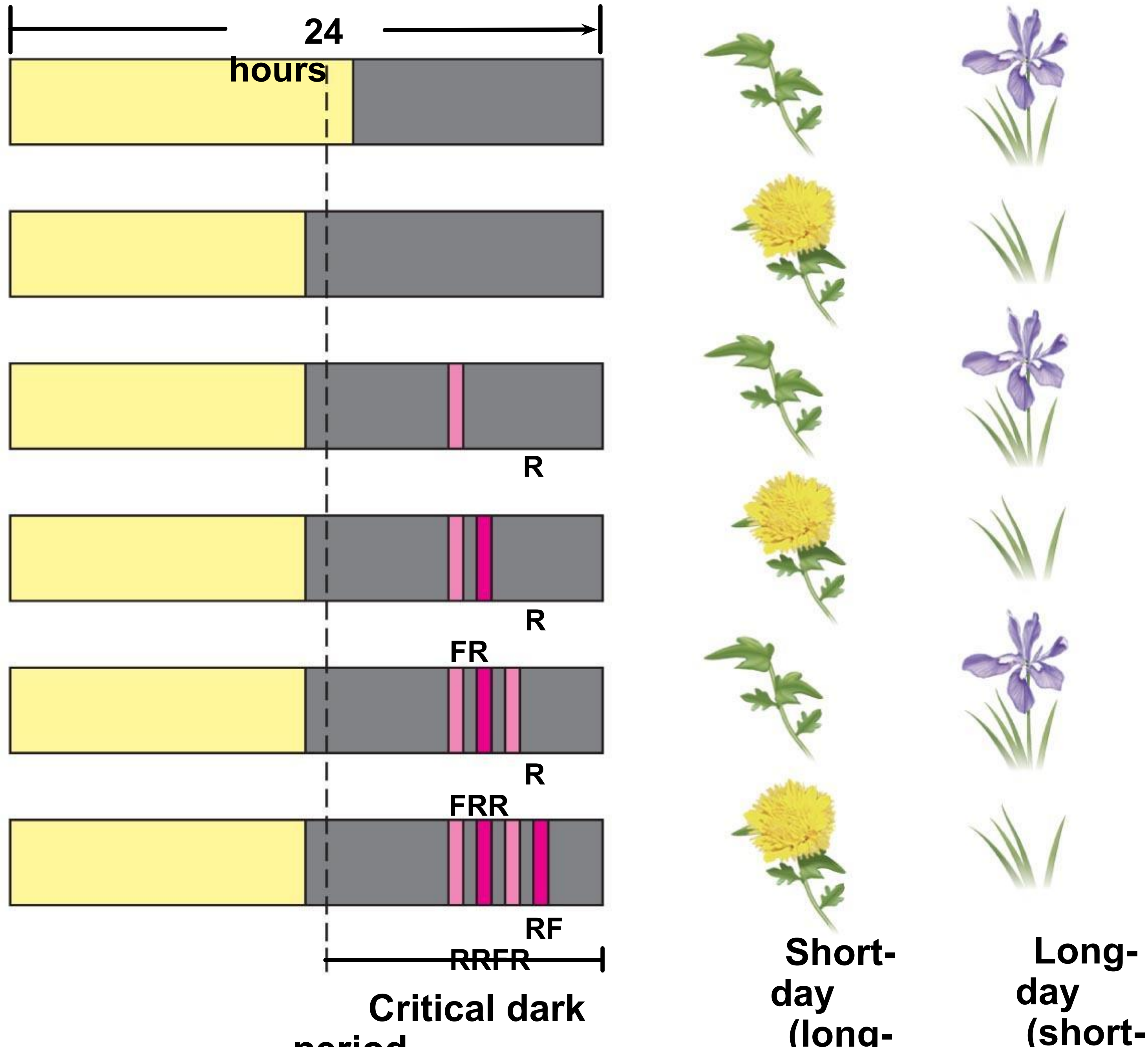
- Short-day plants are governed by whether the critical night length sets a minimum number of hours of darkness
- Long-day plants are governed by whether the critical night length sets a maximum number of hours of darkness

Fig. 39-21


24
hours
(a) Short-day (long-
night)
plant
Light
F
lash
o
f
li
ght
Darknes
s
Critical
dark
period
(b) Long-day (short-
night)
plant
F
lash
o
f

- Red light can interrupt the nighttime portion of the photoperiod
- Action spectra and photoreversibility experiments show that phytochrome is the pigment that receives red light

Fig. 39-22



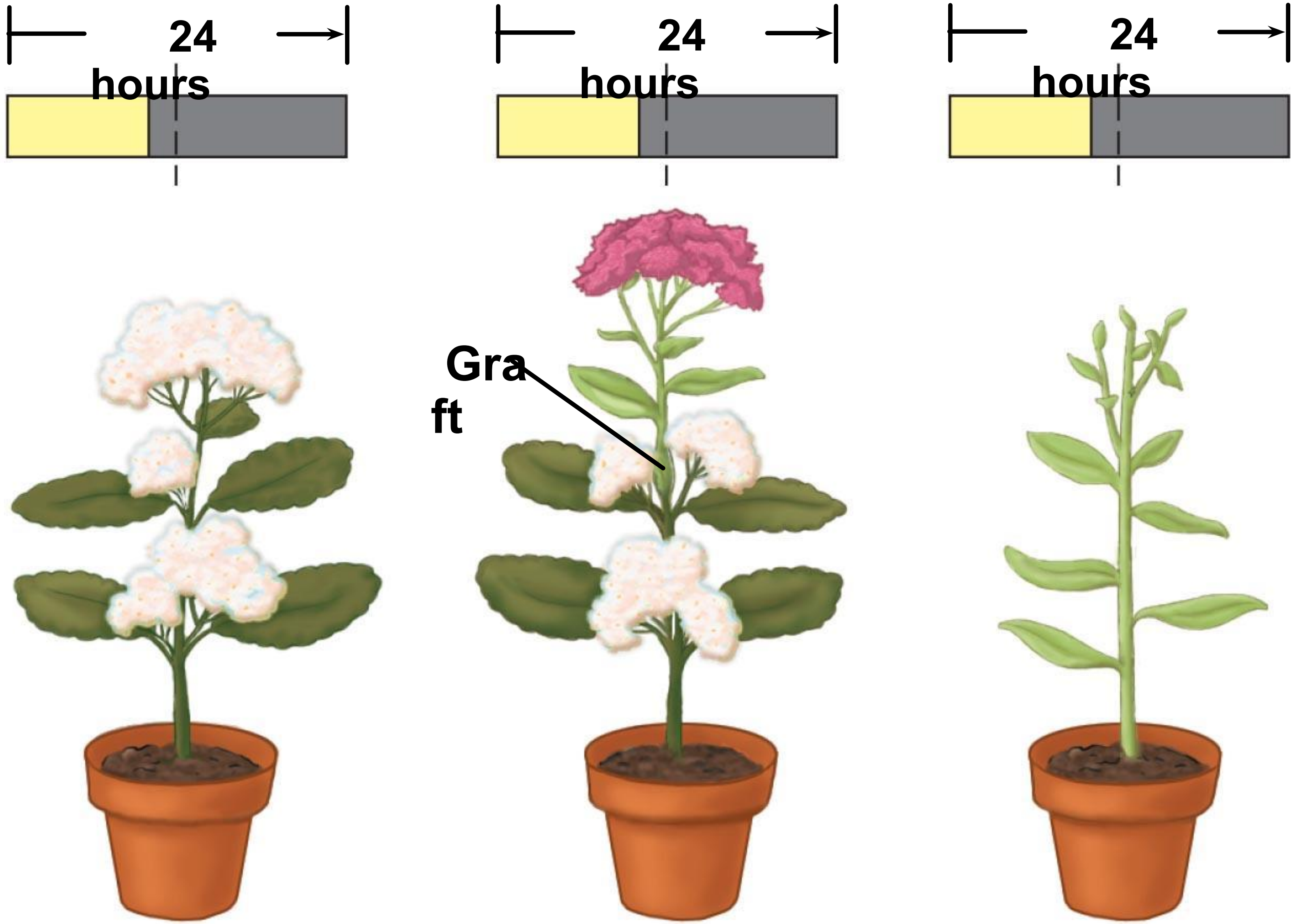
24 hours
R
R
FR
R
FRR
RF
RRFR
Critical dark period
Short-day (long-night)
Long-day (short-night)

- 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?

- The flowering signal, not yet chemically identified, is called **florigen**
- Florigen may be a macromolecule governed by the *CONSTANS* gene

Fig. 39-23



Short-day plant

Long-day plant grafted to short-day

Long-day plant

Meristem Transition and Flowering

- For a bud to form a flower instead of a vegetative shoot, meristem identity genes must first be switched on
- Researchers seek to identify the signal transduction pathways that link cues such as photoperiod and hormonal changes to the gene expression required for flowering

Concept 39.4: 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

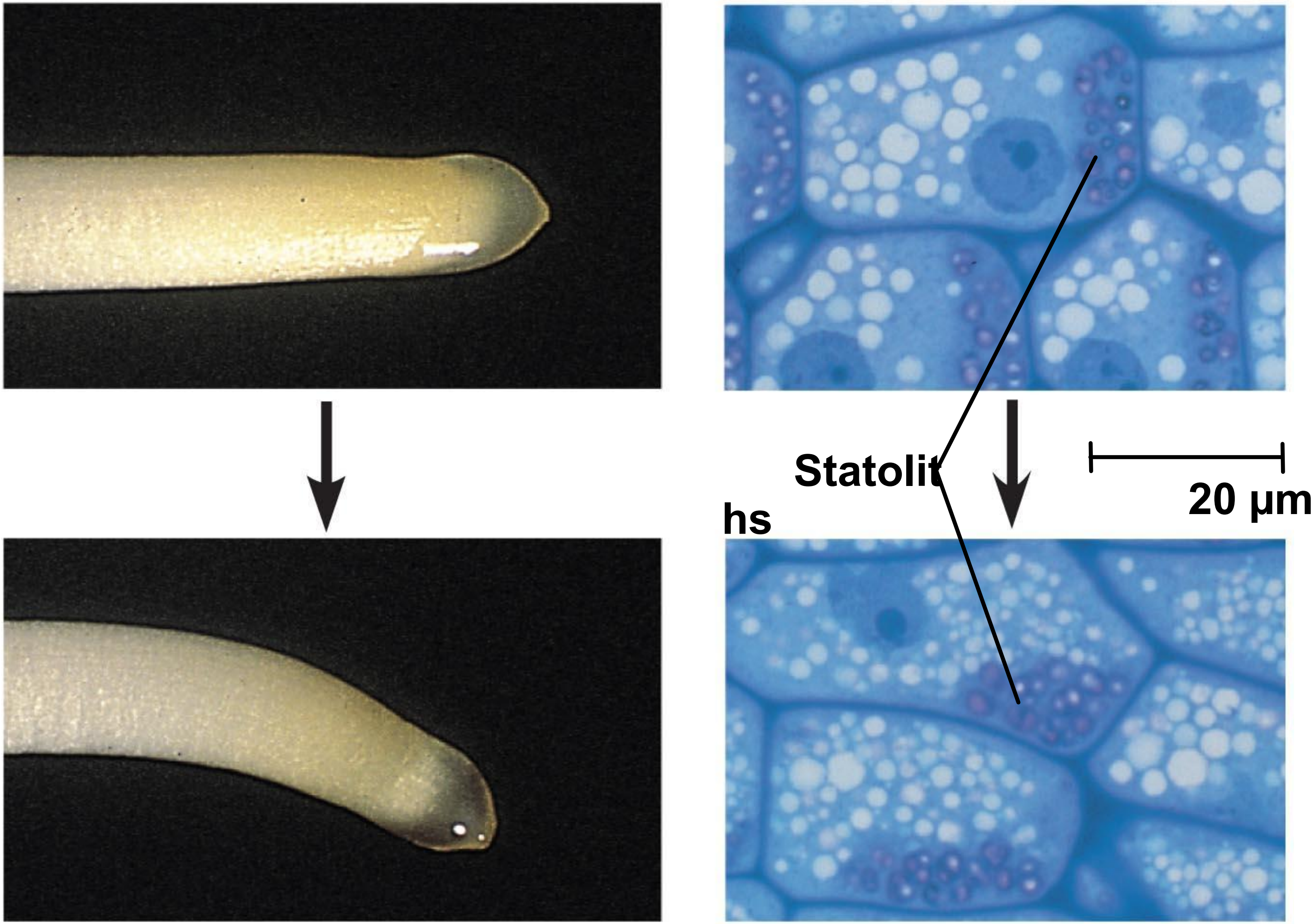
Gravity

- Response to gravity is known as **gravitropism**
- Roots show positive gravitropism; shoots show negative gravitropism

- Plants may detect gravity by the settling of **statoliths**, specialized plastids containing dense starch grains

PLAY Video: Gravitropism

Fig. 39-24



(a) Root gravitropic bending

(b) Statoliths settling

- Some 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
- Rubbing stems of young plants a couple of times daily results in plants that are shorter than controls

Fig. 39-25

- **Thigmotropism** is growth in response to touch
- It occurs in vines and other climbing plants
- Rapid leaf movements in response to mechanical stimulation are examples of transmission of electrical impulses called **action potentials**

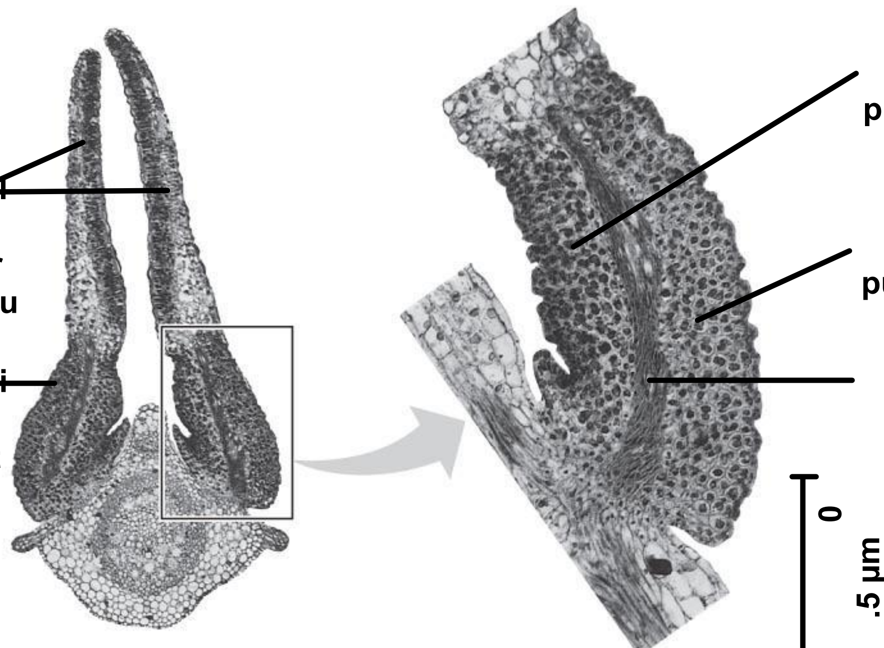
PLAY

Video: Mimosa Leaf

Fig. 39-26

(a) Unstimulated state

(b) Stimulated state



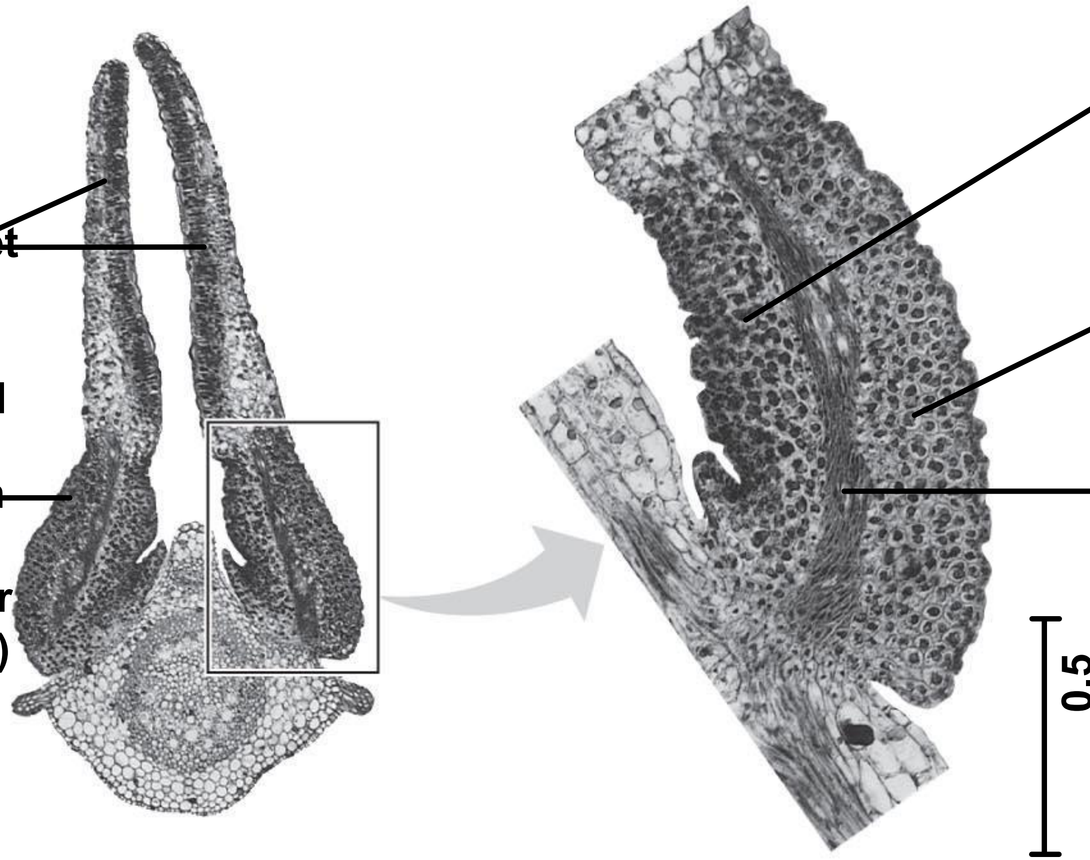
(c) Cross section of a leaflet pair in the stimulated state (LM)

Fig. 39-26ab

(a) Unstimulated state

(b) Stimulated state

Fig. 39-26c



(c) Cross section of a leaflet pair in the stimulated state (LM)

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

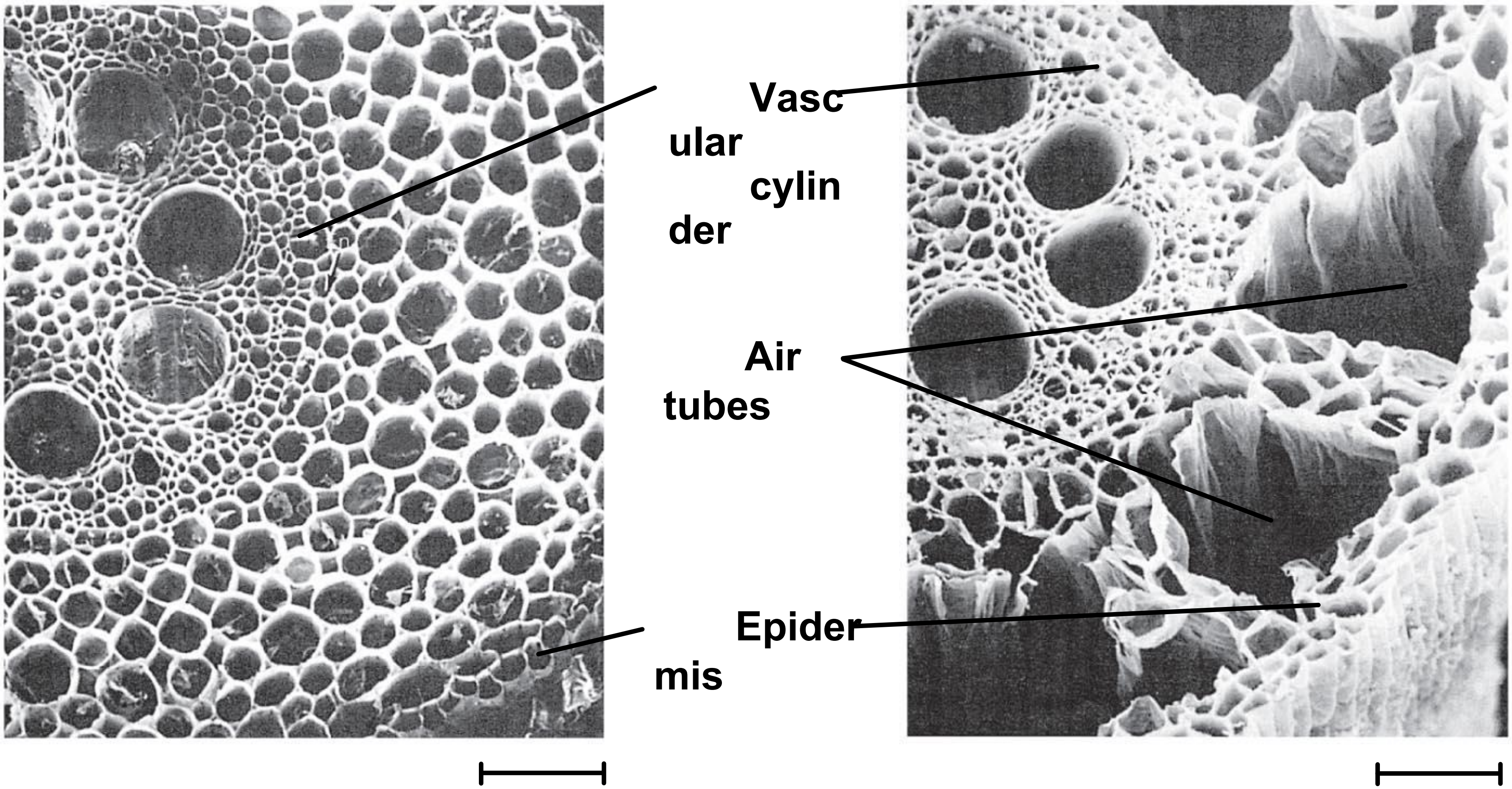
Drought

- During drought, plants reduce transpiration by closing stomata, slowing leaf growth, and reducing exposed surface area
- Growth of shallow roots is inhibited, while deeper roots continue to grow

Flooding

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

Fig. 39-27



(a) Control root
(aerated)

(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** help protect other proteins from heat stress

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

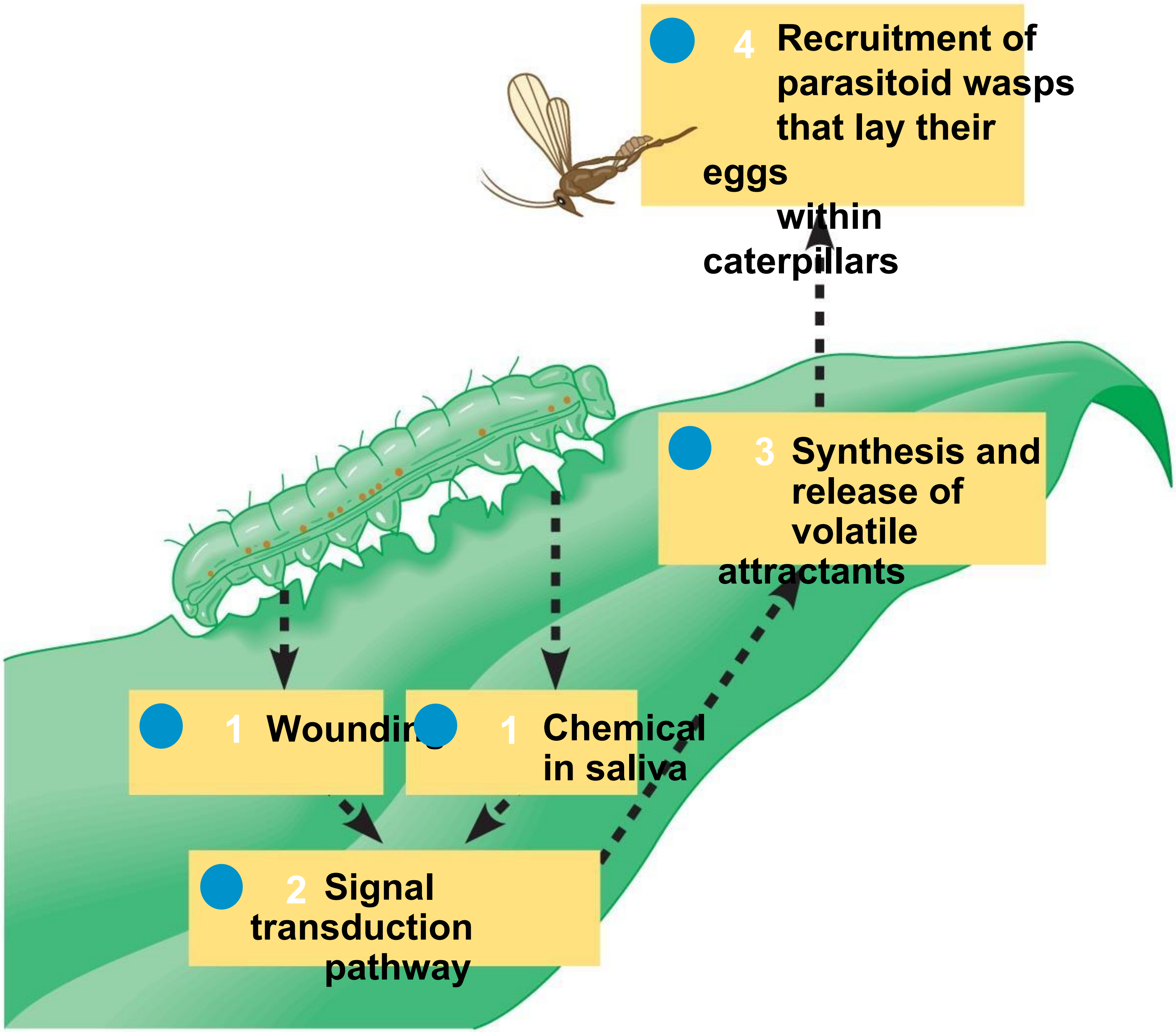
Concept 39.5: Plants respond to attacks by herbivores and pathogens

- Plants use 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 chemical defenses such as distasteful or toxic compounds
- Some plants even “recruit” predatory animals that help defend against specific herbivores

Fig. 39-28


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

- Plants damaged by insects can release volatile chemicals to warn other plants of the same species
- **Methyljasmonic acid** can activate the expression of genes involved in plant defenses

Defenses Against Pathogens

- A plant's first line of defense against infection is 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 inherited ability to recognize certain pathogens

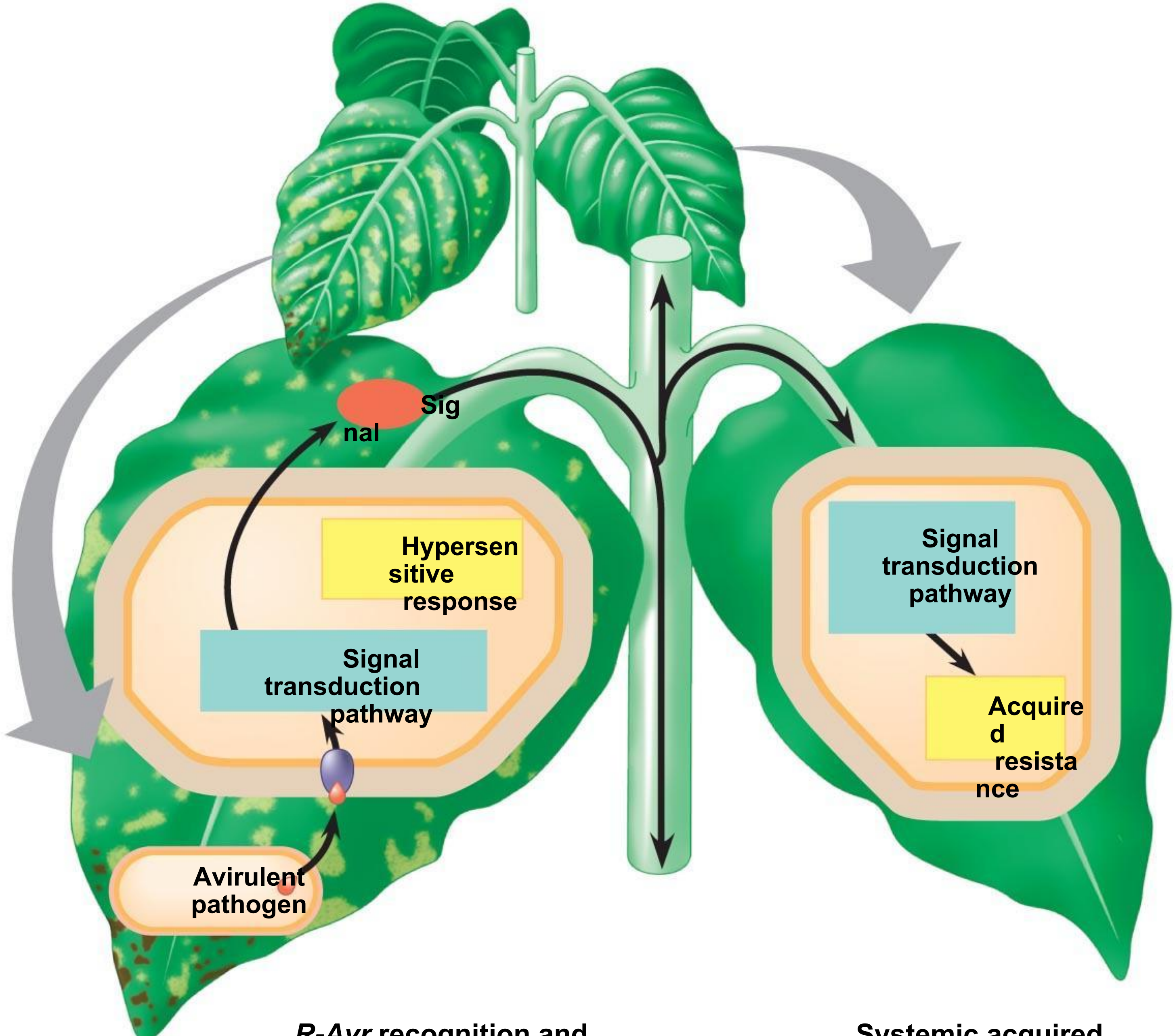
- A **virulent** pathogen is one that a plant has little specific defense against
- An **avirulent** pathogen is one that may harm but does not kill the host plant

- **Gene-for-gene recognition** involves recognition of pathogen-derived molecules by 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 cell and tissue death near the infection site
  - Induces production of phytoalexins and PR proteins, which attack the pathogen
  - Stimulates changes in the cell wall that confine the pathogen

Fig. 39-29



R-Avr recognition and hypersensitive response

Systemic acquired resistance

Systemic Acquired Resistance

- **Systemic acquired resistance** causes systemic expression of defense genes and is a long-lasting response
- **Salicylic acid** is synthesized around the infection site and is likely the signal that triggers systemic acquired resistance

Fig. 39-UN2

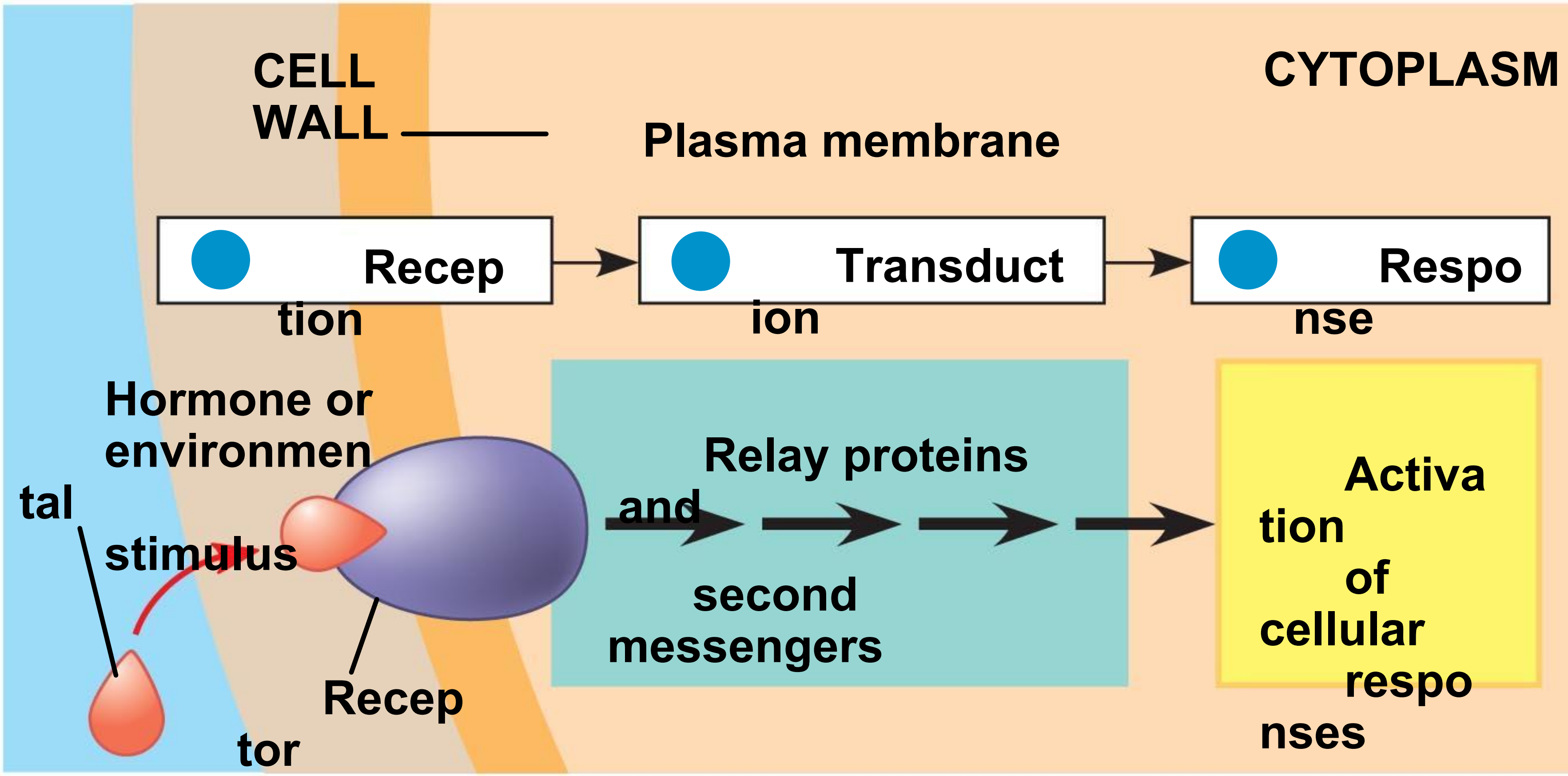

CELL
WALL
CYTOPLASM
Plasma membrane
Recep
tion
Transduct
ion
Respo
nse
Hormone or
environmen
tal
stimulus
Recep
tor
Relay proteins
and
second
messengers
Activa
tion
of
cellular
respo
nses

Fig. 39-UN3

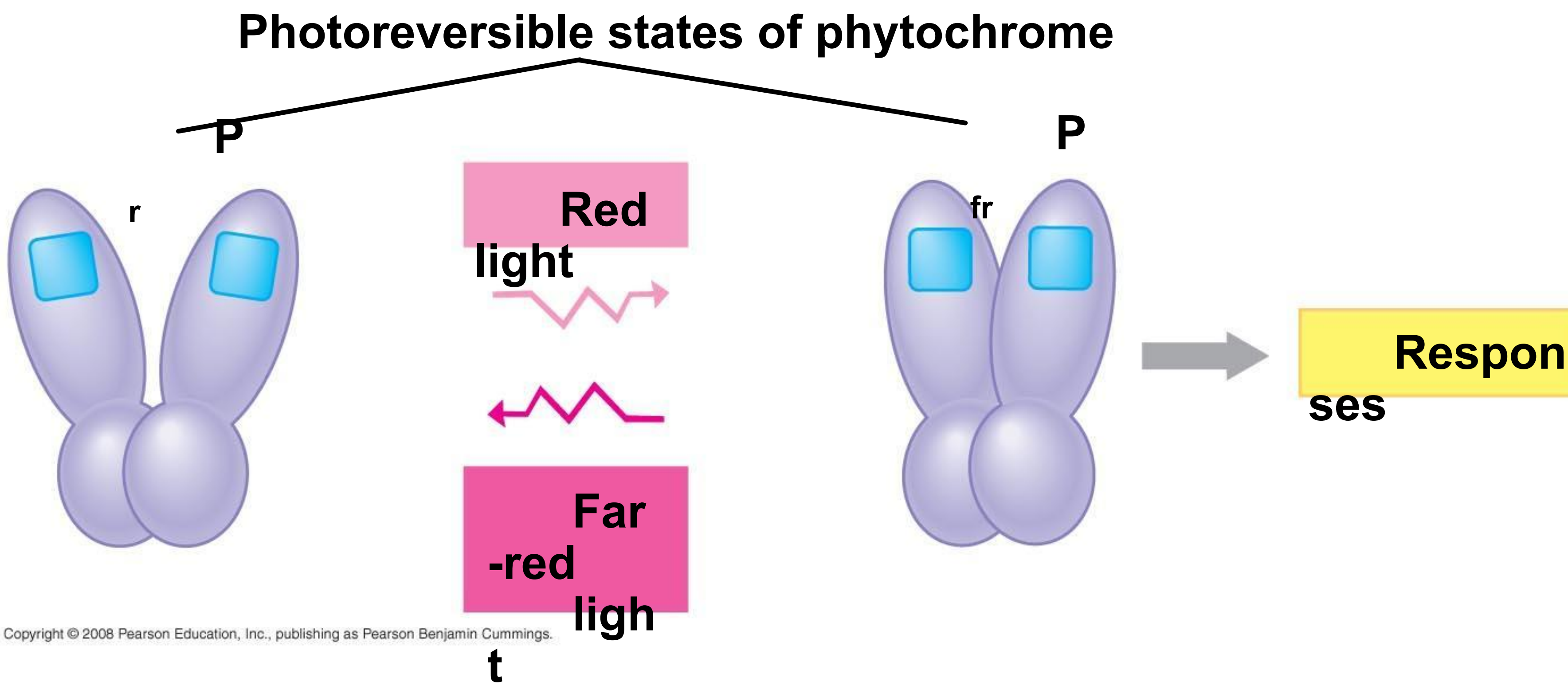
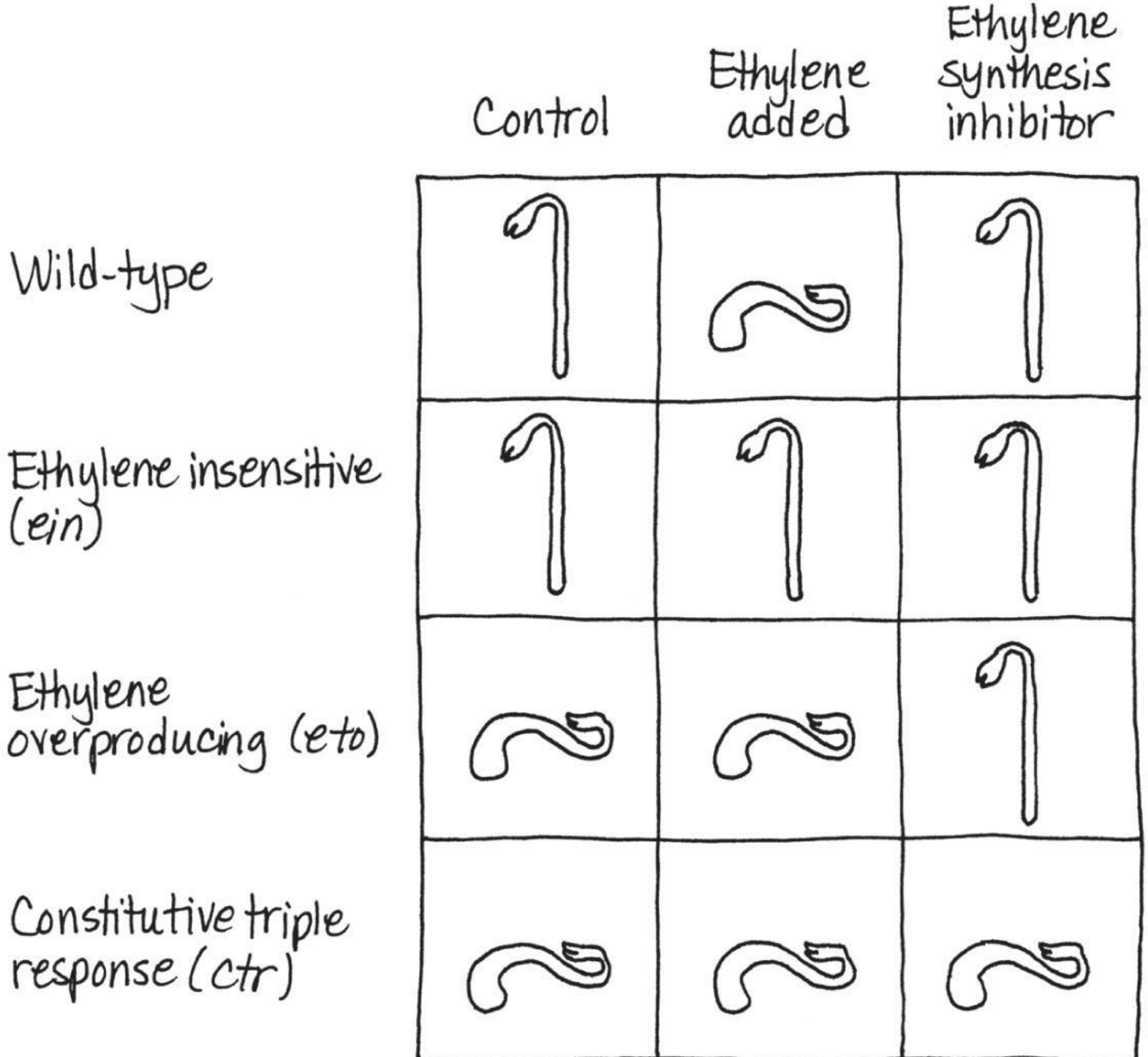

Photoreversible states of phytochrome
P
r
Red
light
Far
-red
ligh
t
P
fr
Respon
ses

Fig. 39-UN4

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

Fig. 39-UN5


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

You should now be able to:

1. Compare the growth of a plant in darkness (etiolation) to the characteristics of greening (de-etiolation) ***5-7***

****8-17 cell communication "AP Bio core concept"***

2. List six classes of plant hormones and describe their major functions ***27***

3. Describe the phenomenon of phytochrome photoreversibility and explain its role in light-induced germination of lettuce seeds ***67-72***

4. Explain how light entrains biological clocks ***79-81***

5. Distinguish between short-day, long-day, and day-neutral plants; explain why the names are misleading ***82-86***

6. Describe how plants tell up from down ***92-98***

7. Distinguish between thigmotropism and thigmomorphogenesis ***97-101***

8. Describe the challenges posed by, and the responses of plants to, drought, flooding, salt stress, heat stress, and cold stress ***107-111***

9. Describe how the hypersensitive response helps a plant limit damage from a pathogen attack ***117-122***