# 植物生理
## 植物荷爾蒙

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# A Survey of Plant Hormones

- The major plant hormones include
  - Auxin
  - Cytokinins
  - Gibberellins
  - Abscisic acid
  - Ethylene
  - Brassinosteroids
  - Jasmonates
  - Strigolactones

Table 39.1

**Table 39.1 Overview of Plant Hormones**

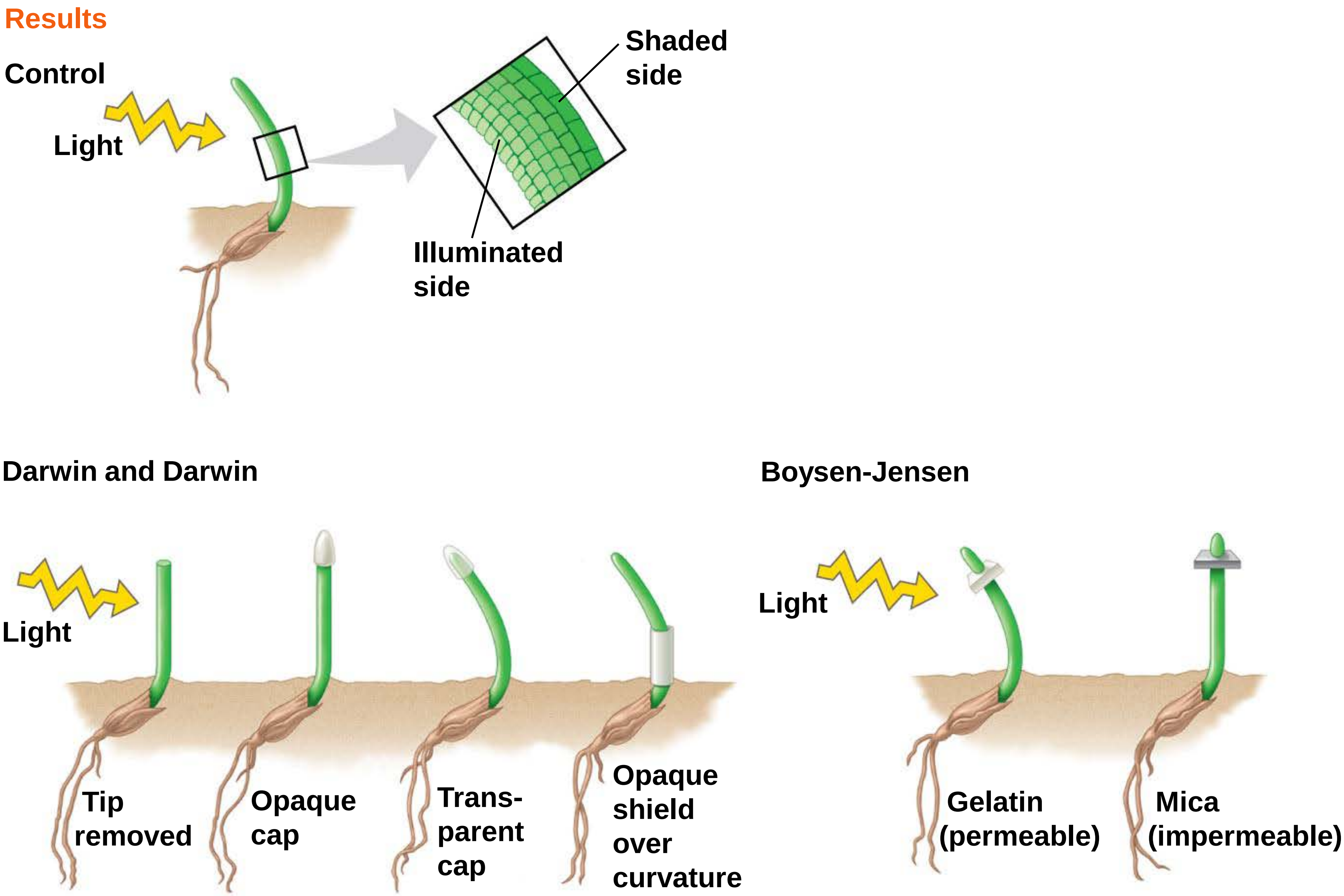
| Hormone | Where Produced or Found in Plant | Major Functions |
|---|---|---|
| Auxin (IAA) | Shoot apical meristems and young leaves are the primary sites of auxin synthesis. Root apical meristems also produce auxin, although the root depends on the shoot for much of its auxin. Developing seeds and 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**
- 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
- In 1913, Peter Boysen-Jensen demonstrated that the signal was a mobile chemical substance

Figure 39.5



Results
Control
Light
Shaded side
Illuminated side
Darwin and Darwin
Light
Tip removed
Opaque cap
Trans-parent cap
Opaque shield over curvature
Boysen-Jensen
Light
Gelatin (permeable)
Mica (impermeable)

Figure 39.5a

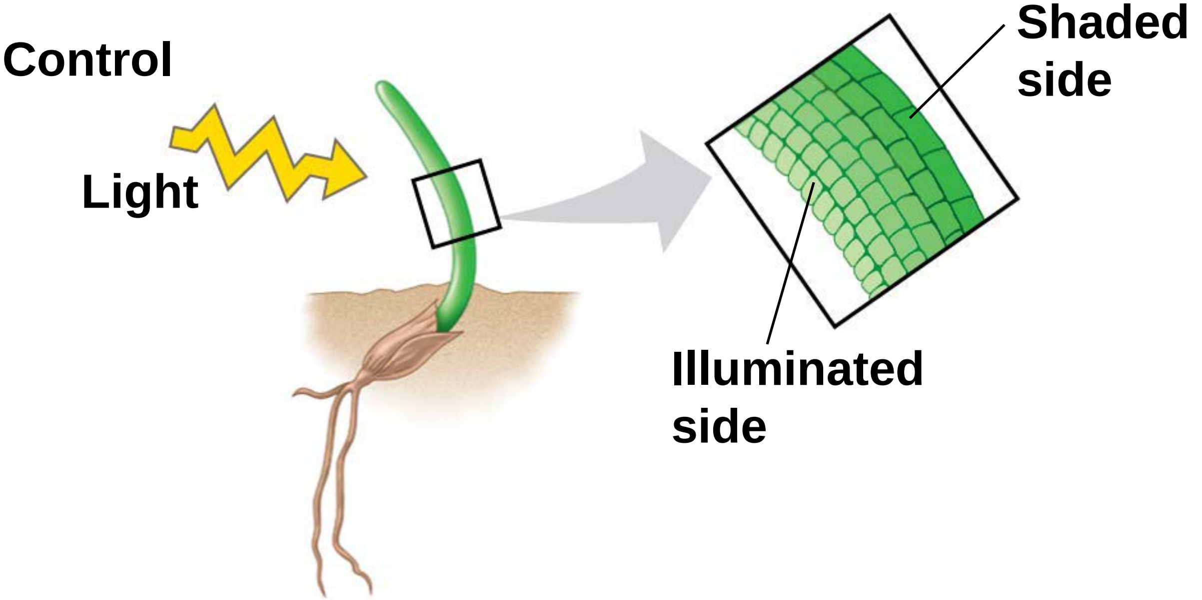
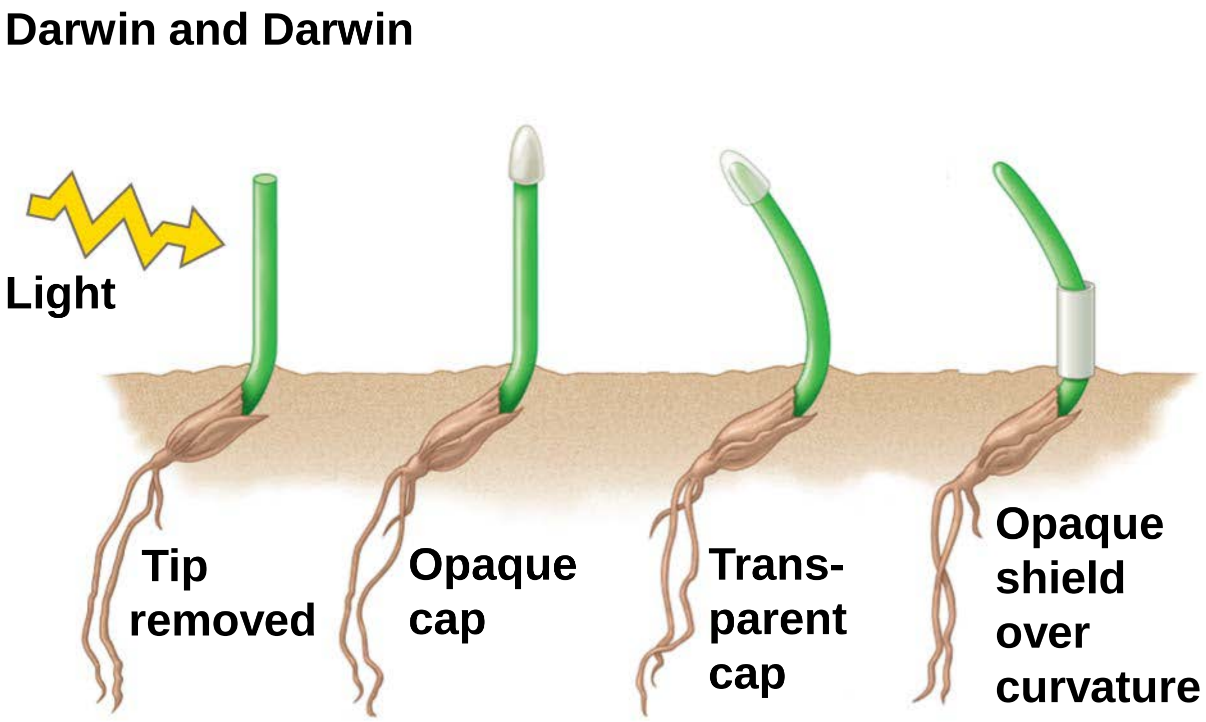
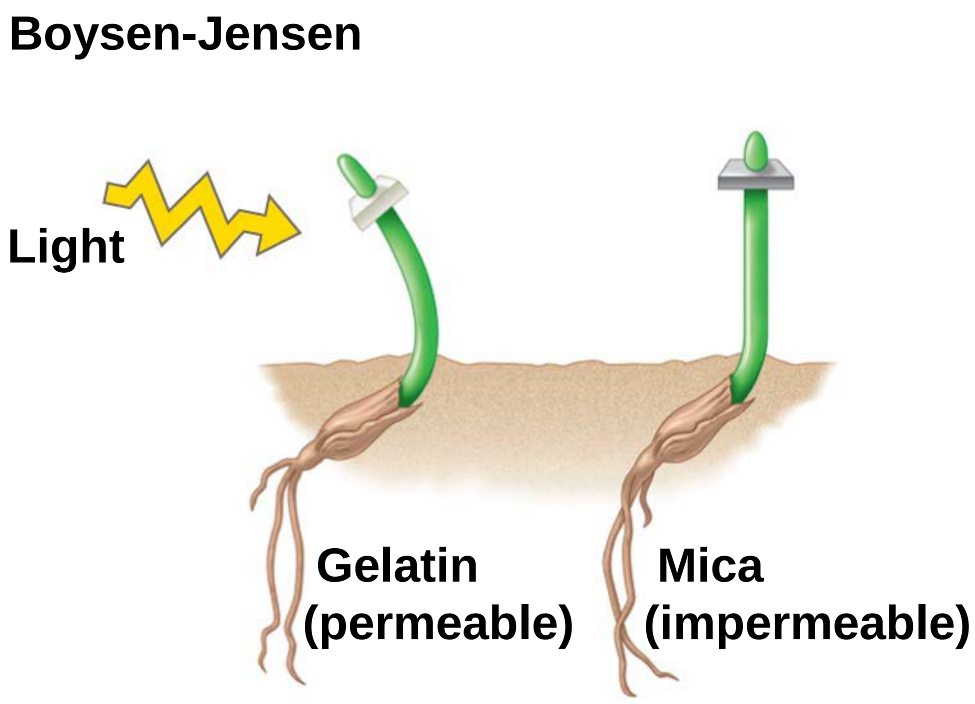


Figure 39.5b

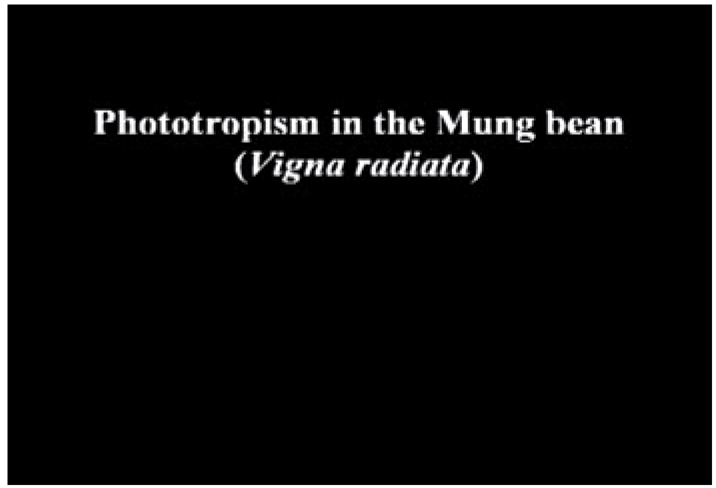


Darwin and Darwin
Light
Tip removed
Opaque cap
Trans-parent cap
Opaque shield over curvature

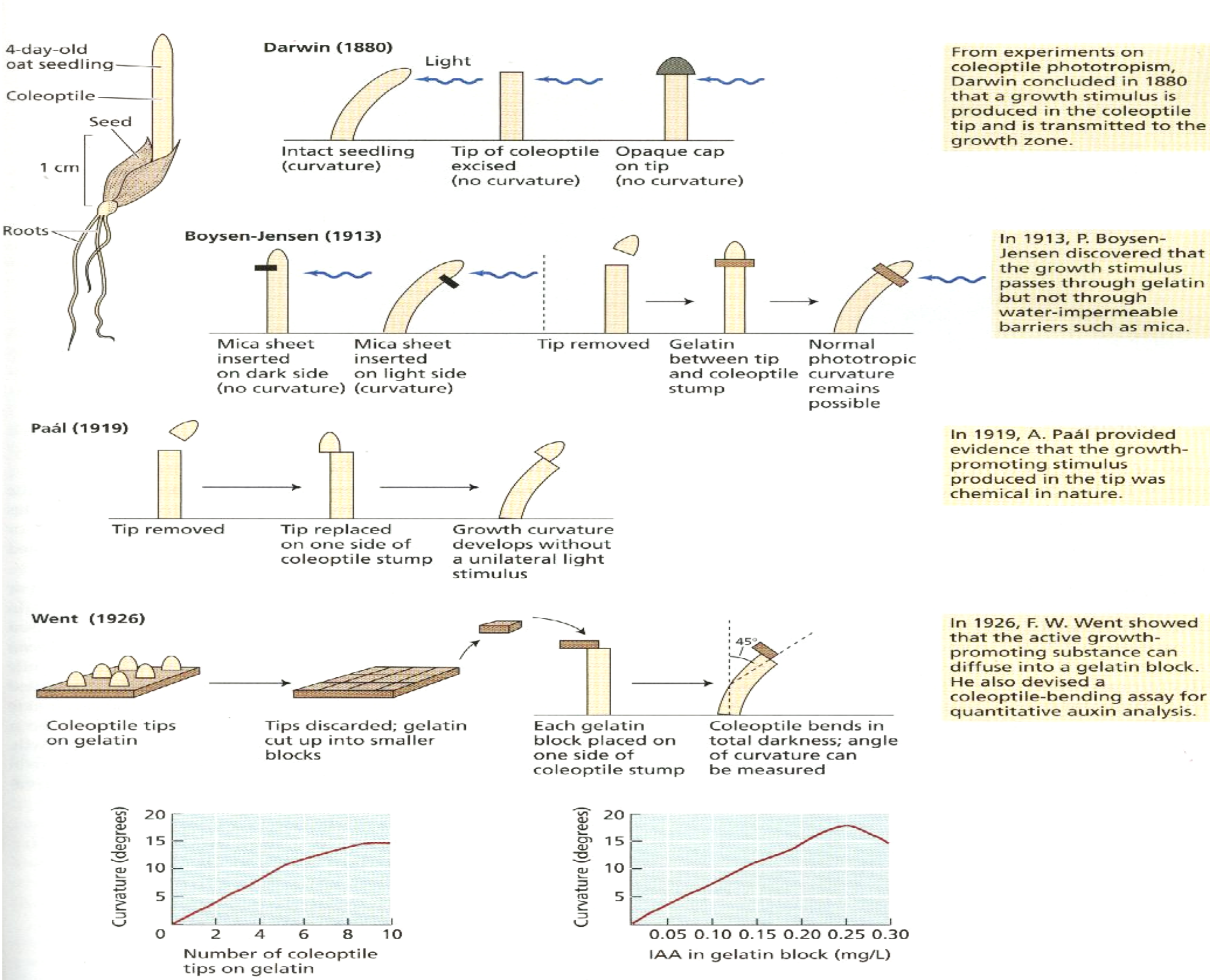
Figure 39.5c



# Video: Phototropism



# Auxin


4-day-old oat seedling
Coleoptile
Seed
1 cm
Roots
Darwin (1880)
Light
Intact seedling (curvature)
Tip of coleoptile excised (no curvature)
Opaque cap on tip (no curvature)
From experiments on coleoptile phototropism, Darwin concluded in 1880 that a growth stimulus is produced in the coleoptile tip and is transmitted to the growth zone.
Boysen-Jensen (1913)
Mica sheet inserted on dark side (no curvature)
Mica sheet inserted on light side (curvature)
Tip removed
Gelatin between tip and coleoptile stump
Normal phototropic curvature remains possible
In 1913, P. Boysen-Jensen discovered that the growth stimulus passes through gelatin but not through water-impermeable barriers such as mica.
Paál (1919)
Tip removed
Tip replaced on one side of coleoptile stump
Growth curvature develops without a unilateral light stimulus
In 1919, A. Paál provided evidence that the growth-promoting stimulus produced in the tip was chemical in nature.
Went (1926)
Coleoptile tips on gelatin
Tips discarded; gelatin cut up into smaller blocks
Each gelatin block placed on one side of coleoptile stump
45°
Coleoptile bends in total darkness; angle of curvature can be measured
In 1926, F. W. Went showed that the active growth-promoting substance can diffuse into a gelatin block. He also devised a coleoptile-bending assay for quantitative auxin analysis.
Curvature (degrees)
20
15
10
5
0
2
4
6
8
10
Number of coleoptile tips on gelatin
Curvature (degrees)
20
15
10
5
0.05 0.10 0.15 0.20 0.25 0.30
IAA in gelatin block (mg/L)

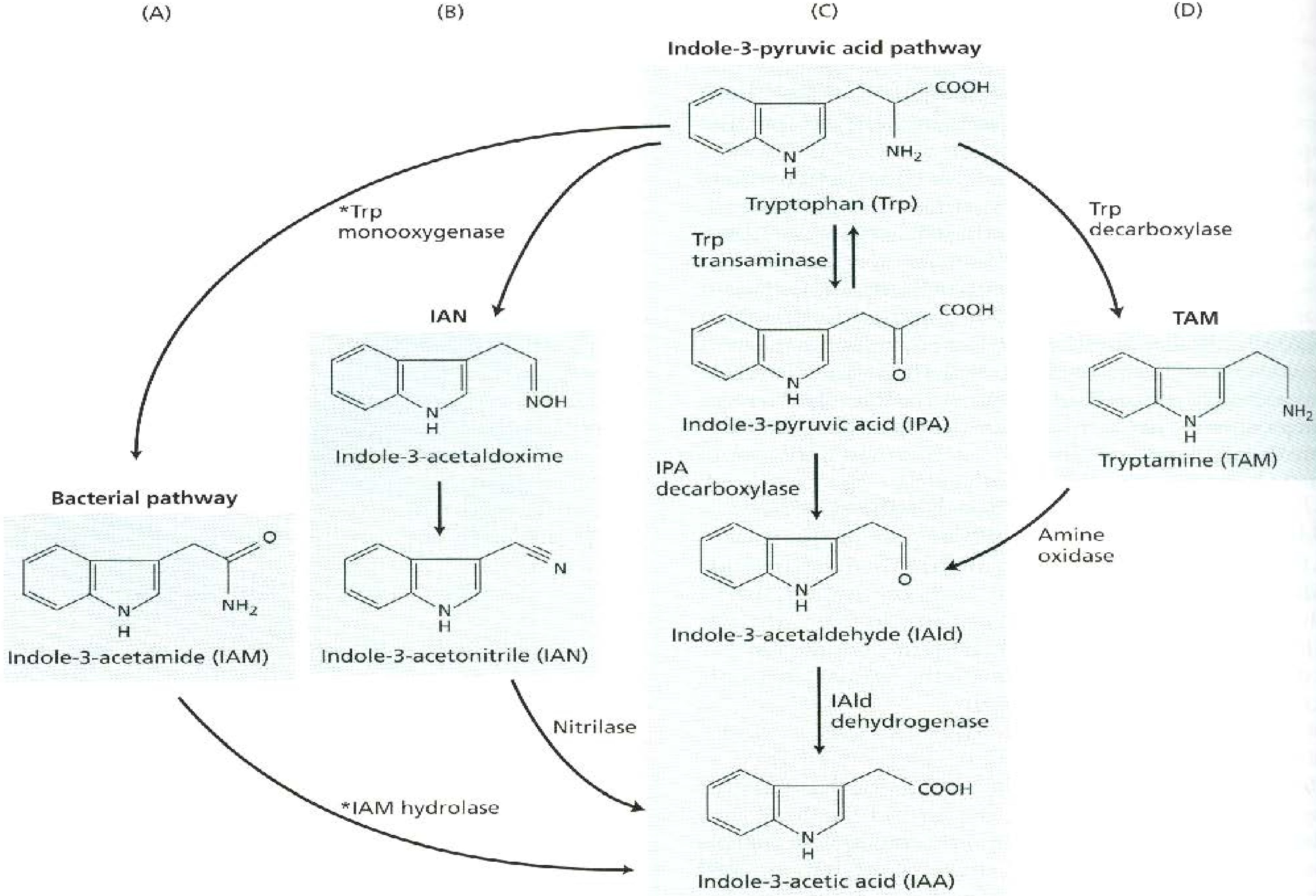



**FIGURE 19.6** Tryptophan-dependent pathways of IAA biosynthesis in plants and bacteria. The enzymes that are present only in bacteria are marked with an asterisk. (After Bartel 1997.)

# Polar transport

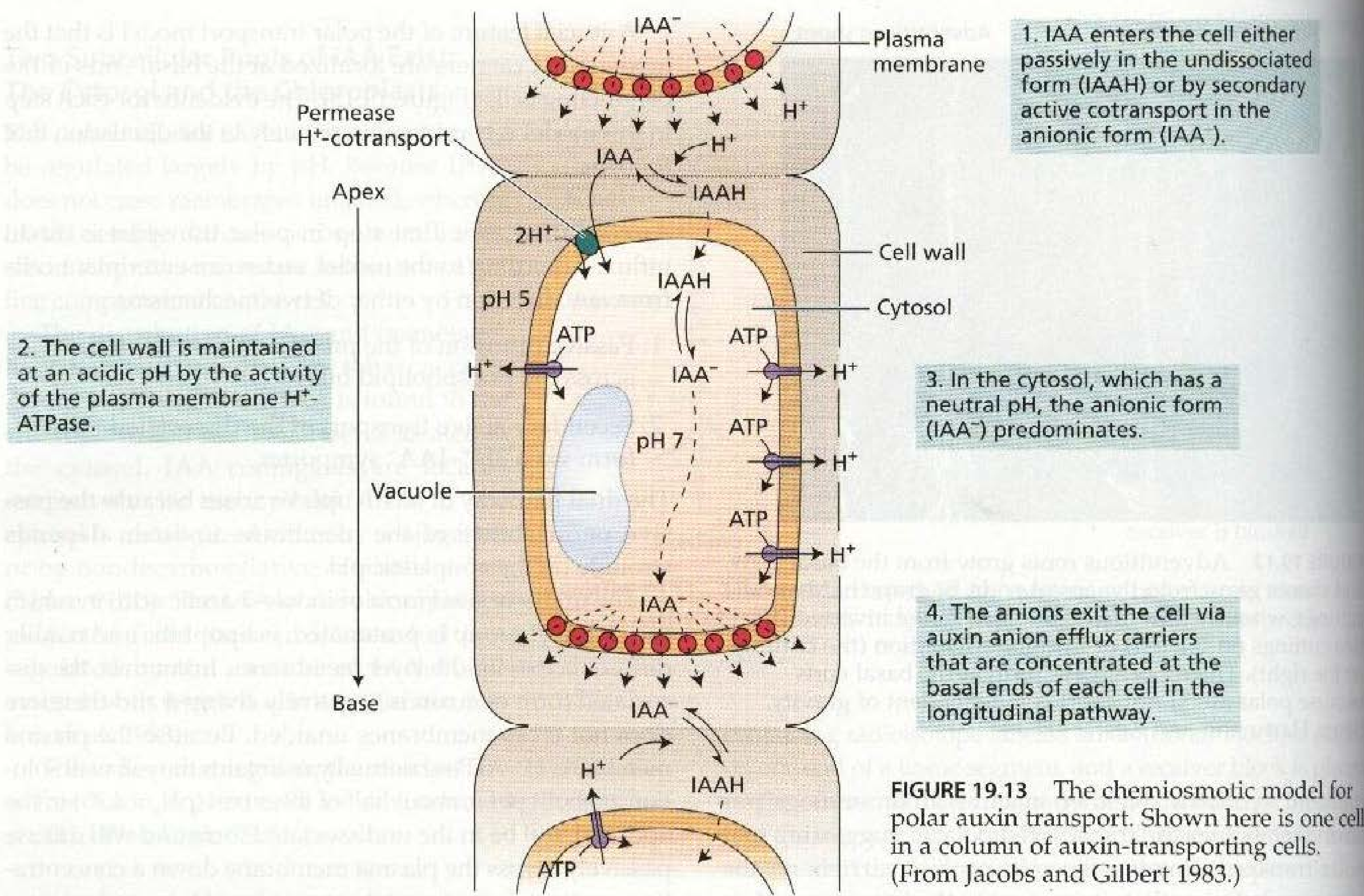



FIGURE 19.13 The chemiosmotic model for polar auxin transport. Shown here is one cell in a column of auxin-transporting cells. (From Jacobs and Gilbert 1983.)

- 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 39.6

## Results

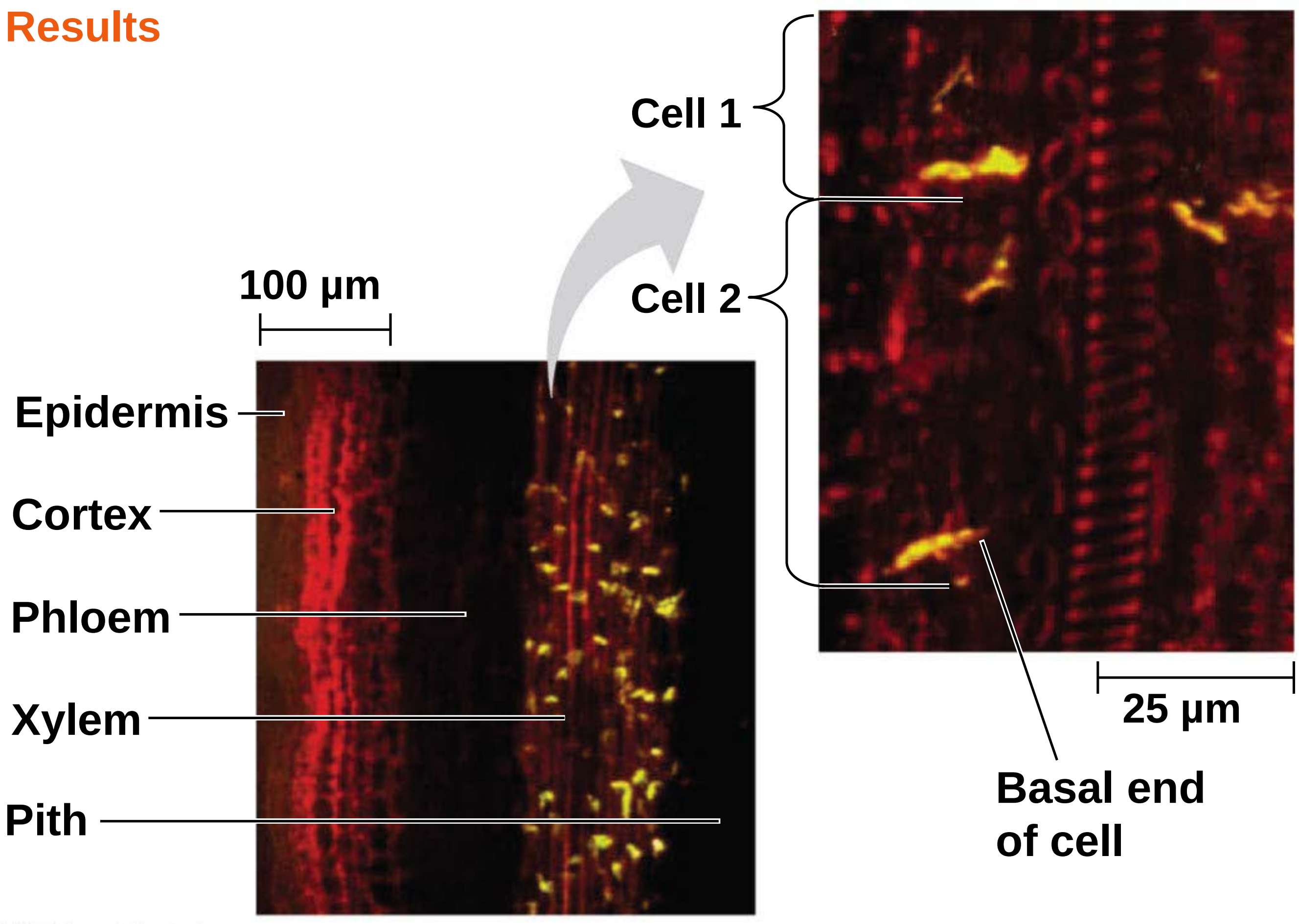


Figure 39.6a

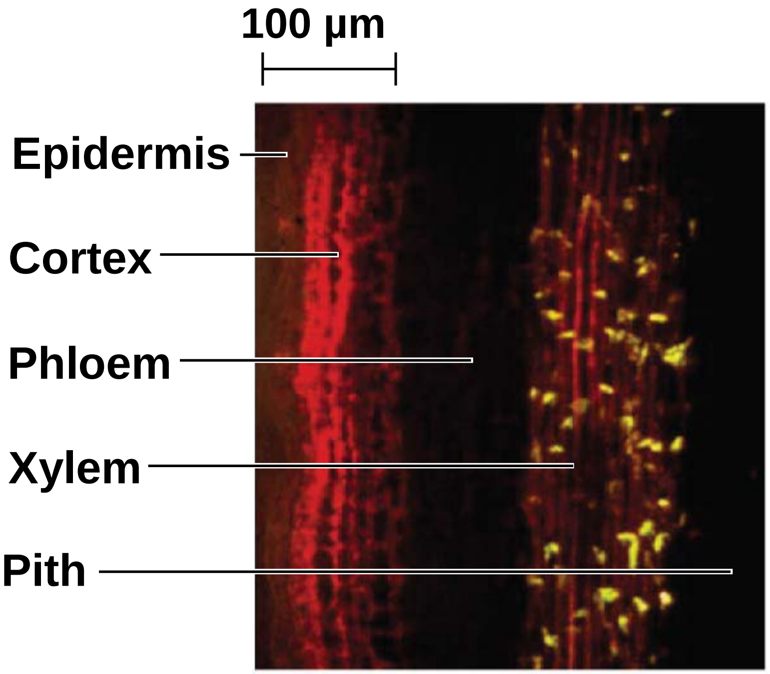
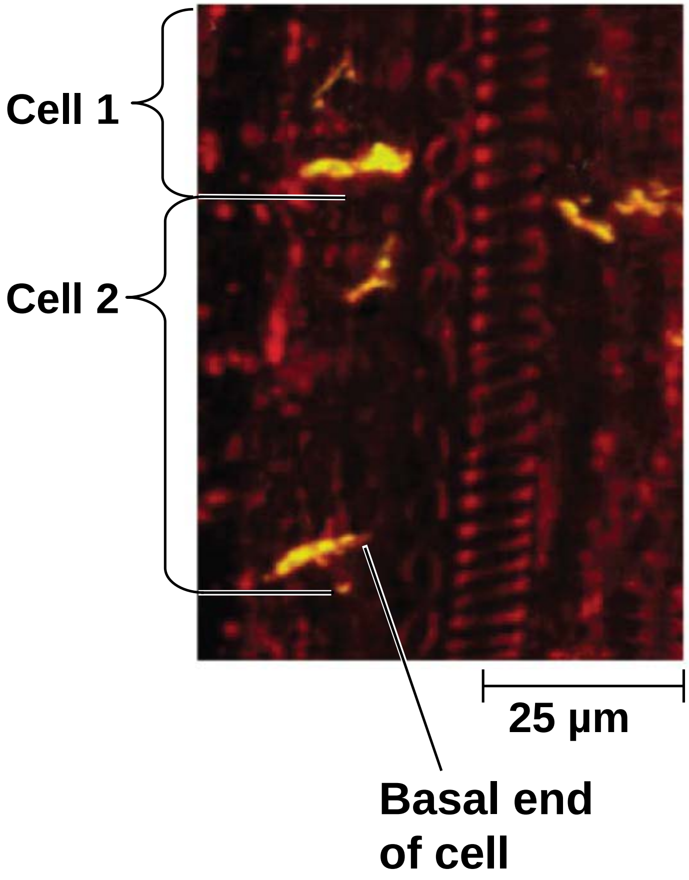


Figure 39.6b



# acid growth theory

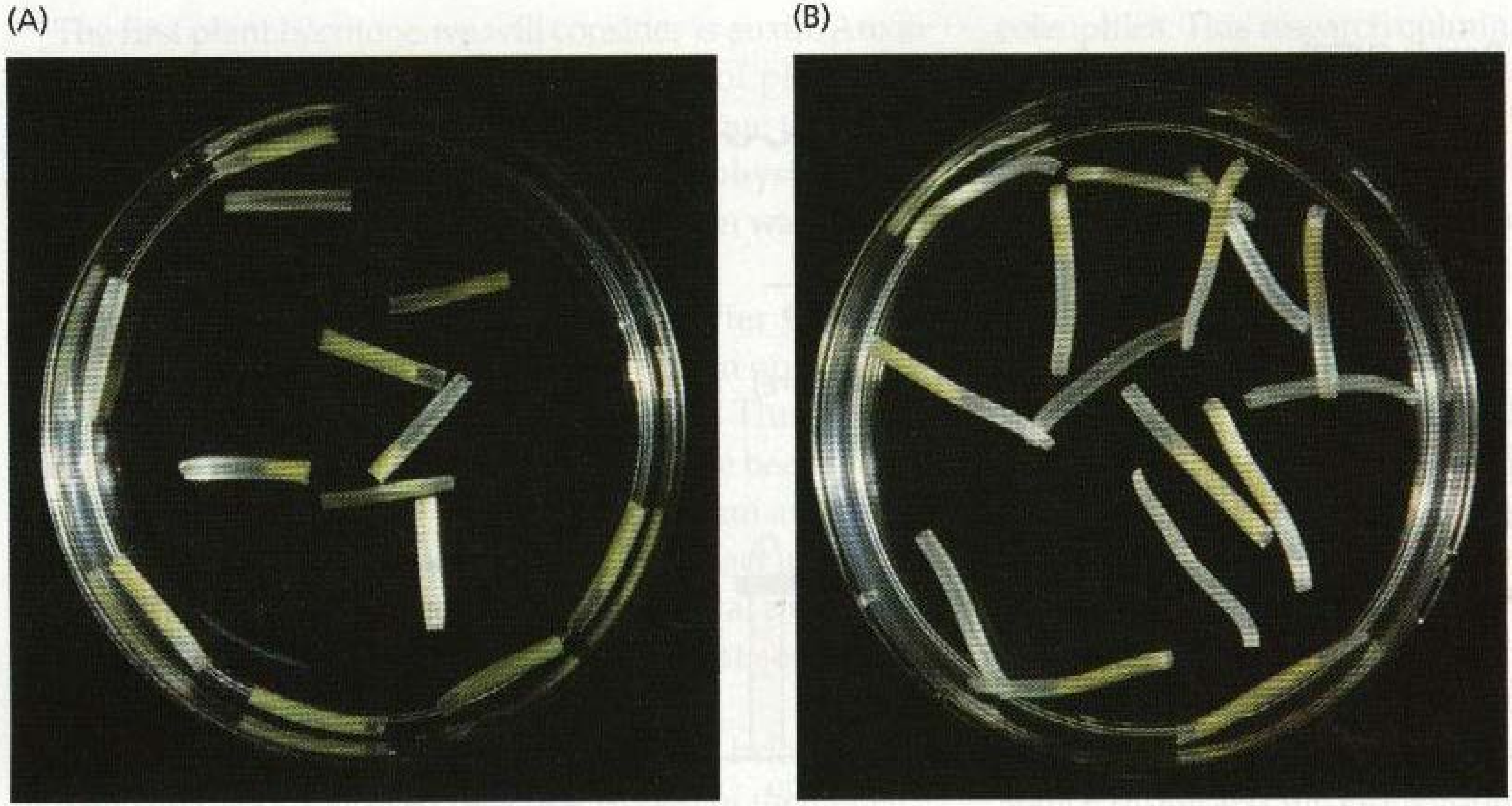
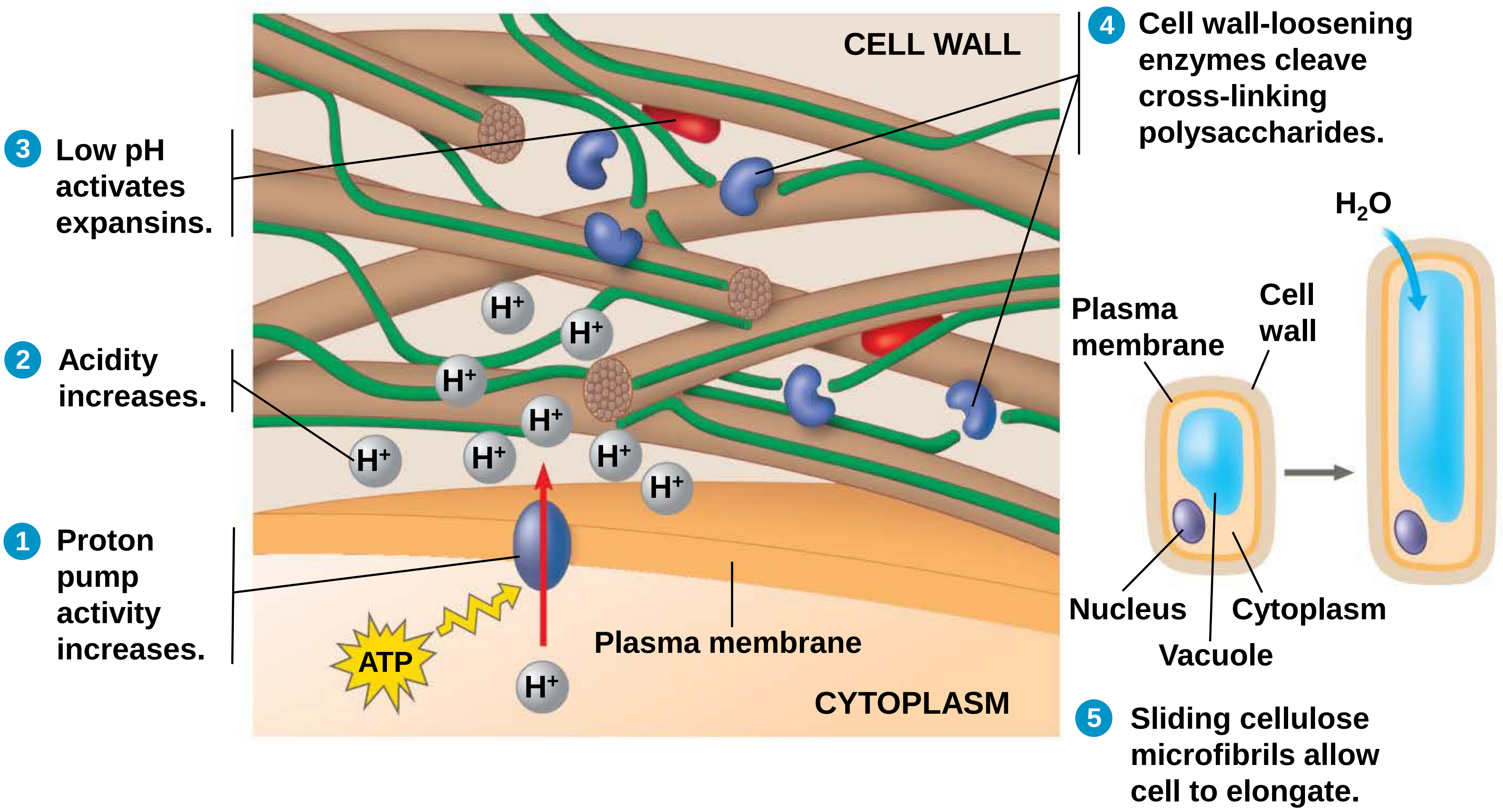



**FIGURE 19.2** Auxin stimulates the elongation of oat coleoptile sections. These coleoptile sections were incubated for 18 hours in either water (A) or auxin (B). The yellow tissue inside the translucent coleoptile is the primary leaves. (Photos © M. B. Wilkins.)

## The Role of Auxin in Cell Elongation

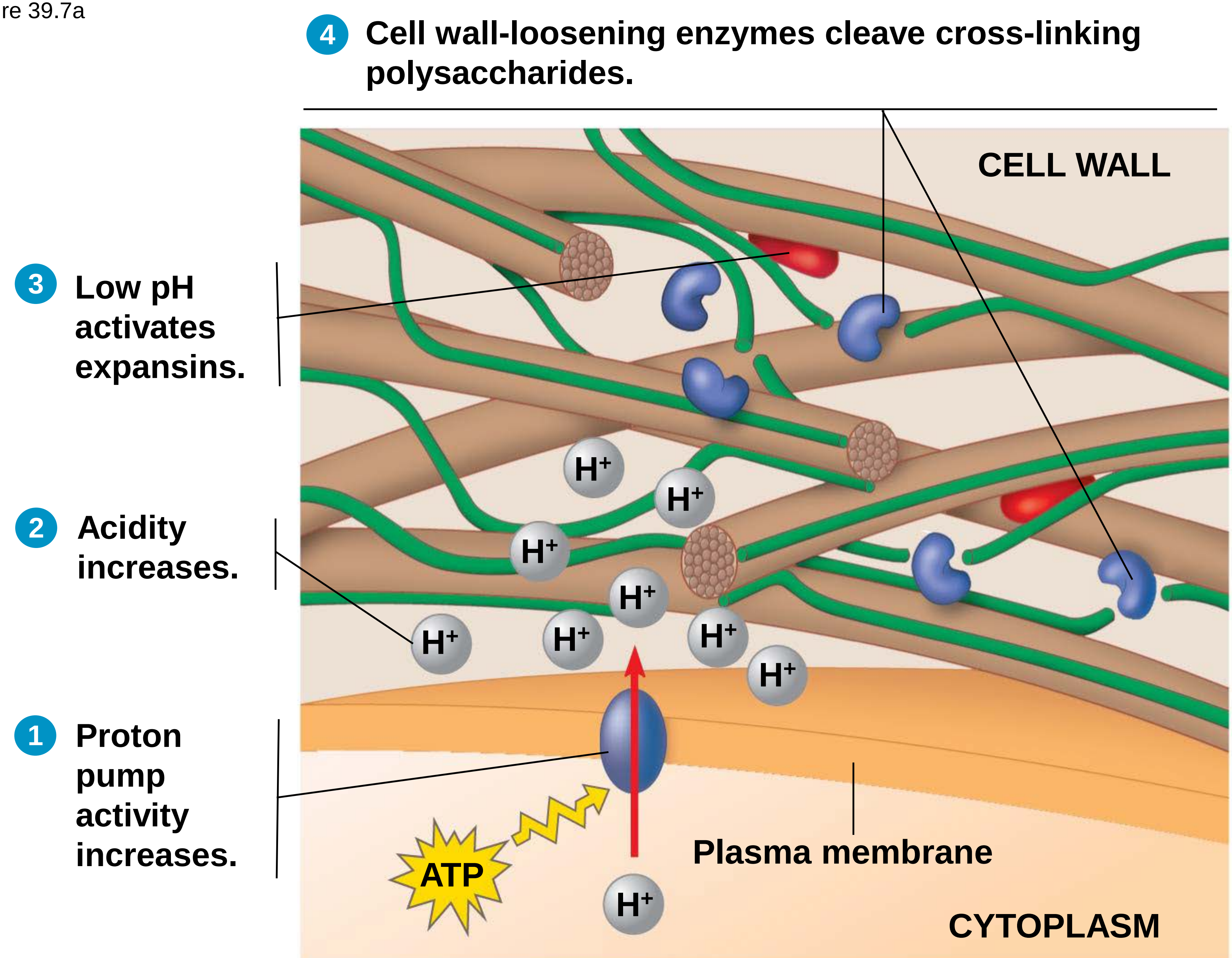
- According to the acid growth hypothesis, auxin stimulates proton pumps in the plasma membrane
- The proton pumps lower the pH in the cell wall, activating **expansins**, enzymes that loosen the wall’s fabric
- With the cellulose loosened, the cell can elongate

Figure 39.7



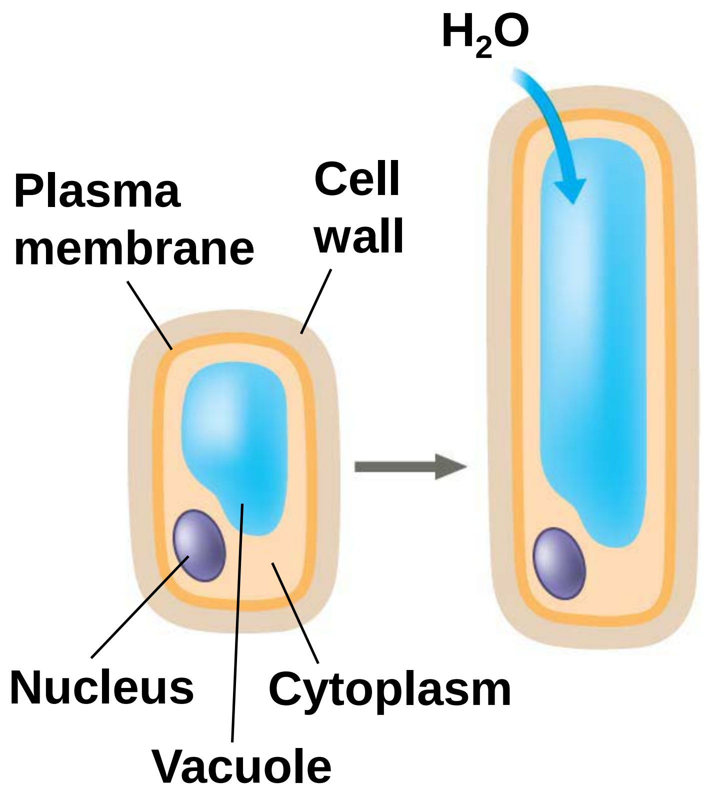
CELL WALL
3 Low pH activates expansins.
2 Acidity increases.
1 Proton pump activity increases.
H+
ATP
Plasma membrane
CYTOPLASM
4 Cell wall-loosening enzymes cleave cross-linking polysaccharides.
H2O
Plasma membrane
Cell wall
Nucleus
Cytoplasm
Vacuole
5 Sliding cellulose microfibrils allow cell to elongate.

Figure 39.7a



4 Cell wall-loosening enzymes cleave cross-linking polysaccharides.
CELL WALL
3 Low pH activates expansins.
2 Acidity increases.
1 Proton pump activity increases.
H+
ATP
Plasma membrane
CYTOPLASM

Figure 39.7b




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 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 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

# 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

# *Cytokinins*

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

# Cytokinin

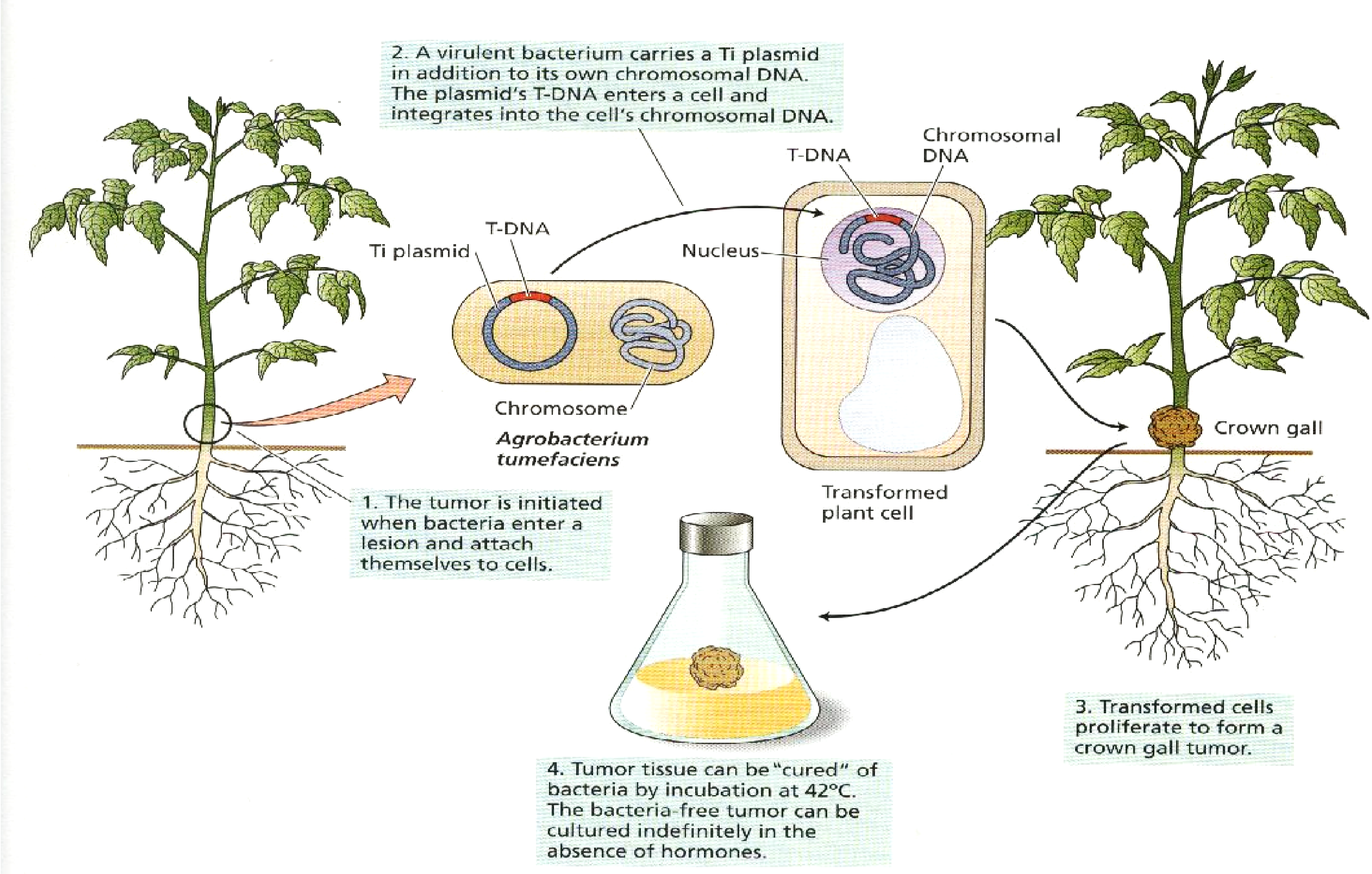



**FIGURE 21.4** Tumor induction by *Agrobacterium tumefaciens*. (After Chilton 1983.)

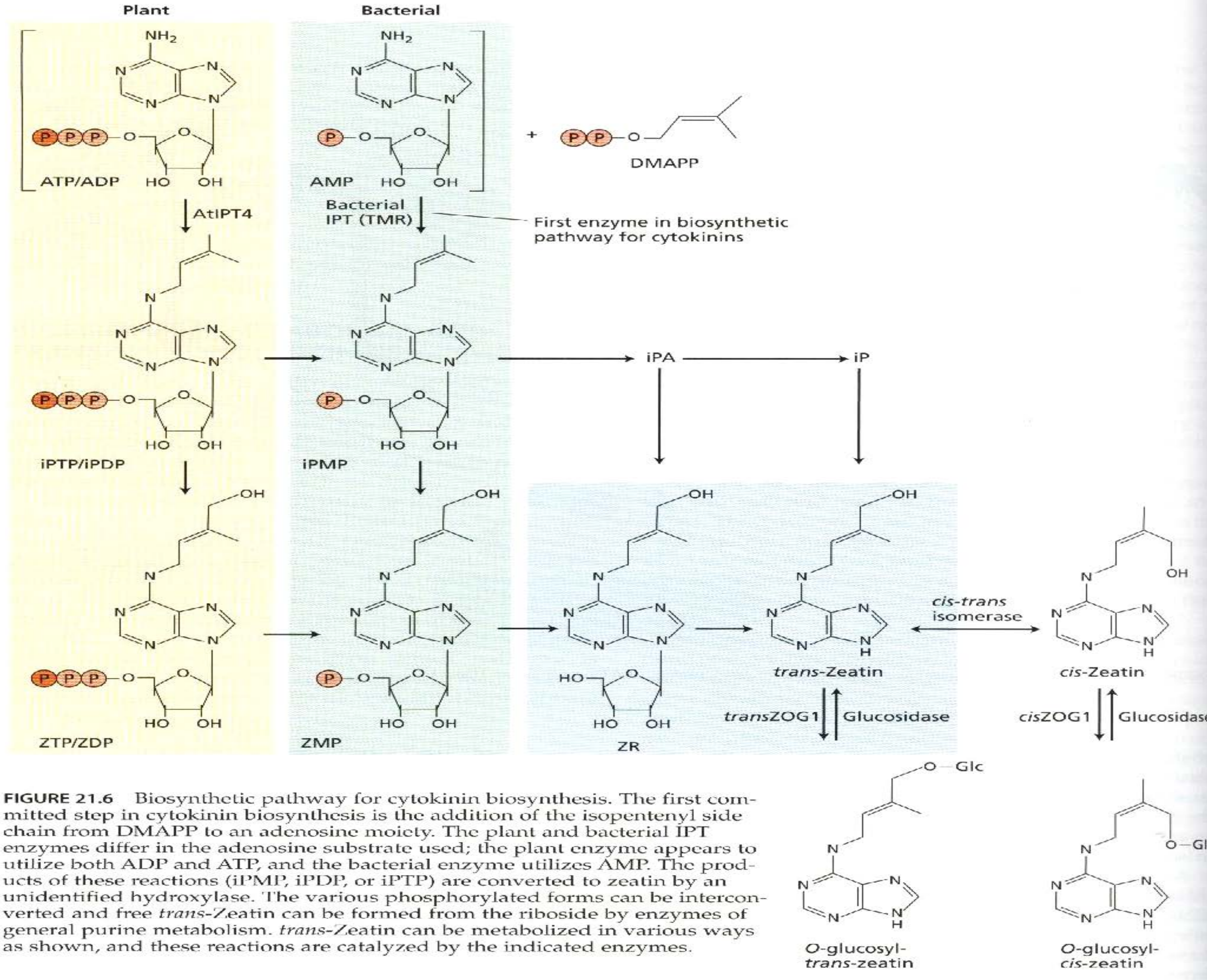



**FIGURE 21.6** Biosynthetic pathway for cytokinin biosynthesis. The first committed step in cytokinin biosynthesis is the addition of the isopentenyl side chain from DMAPP to an adenosine moiety. The plant and bacterial IPT enzymes differ in the adenosine substrate used; the plant enzyme appears to utilize both ADP and ATP, and the bacterial enzyme utilizes AMP. The products of these reactions (iPMP, iPDP, or iPTP) are converted to zeatin by an unidentified hydroxylase. The various phosphorylated forms can be interconverted and free *trans*-Zeatin can be formed from the riboside by enzymes of general purine metabolism. *trans*-Zeatin can be metabolized in various ways as shown, and these reactions are catalyzed by the indicated enzymes.

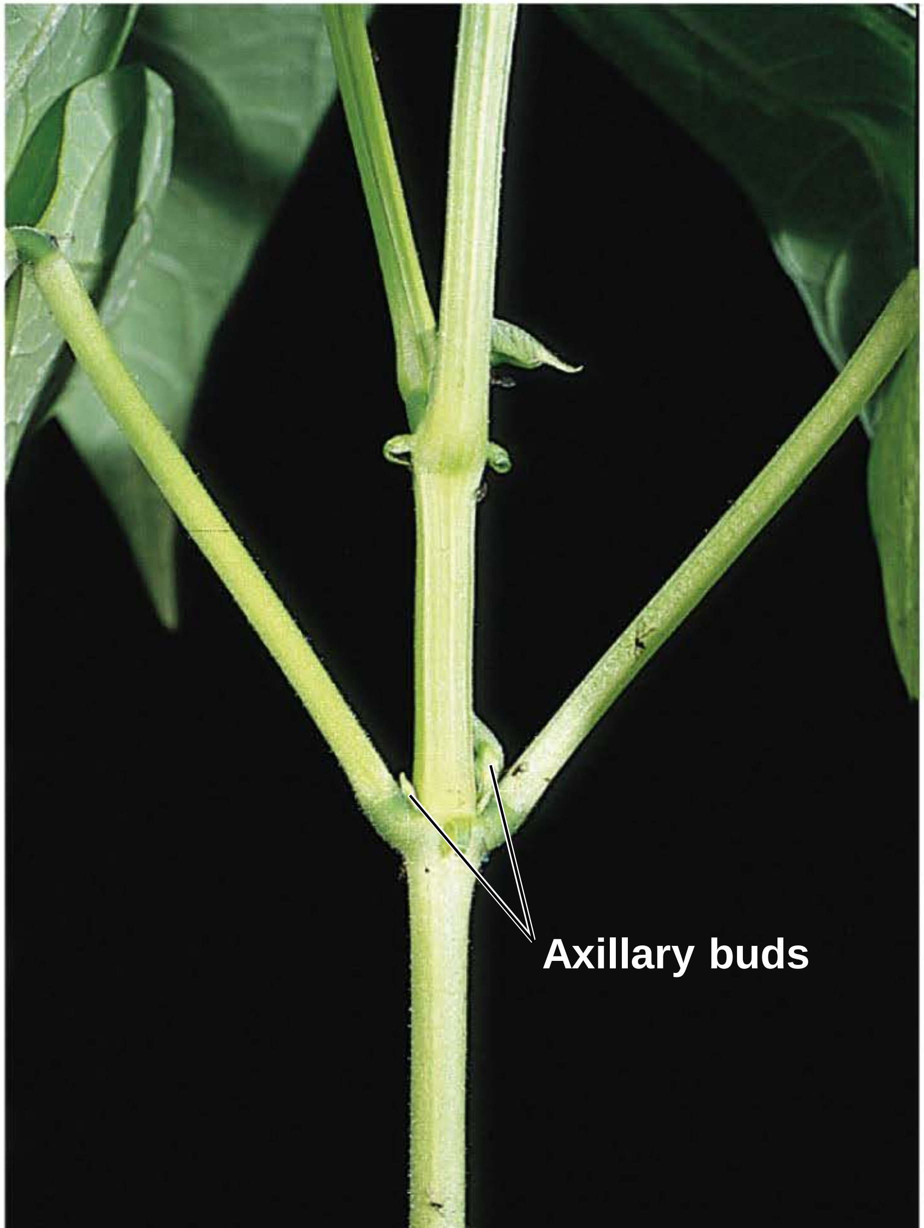
## Control of Cell Division and Differentiation

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

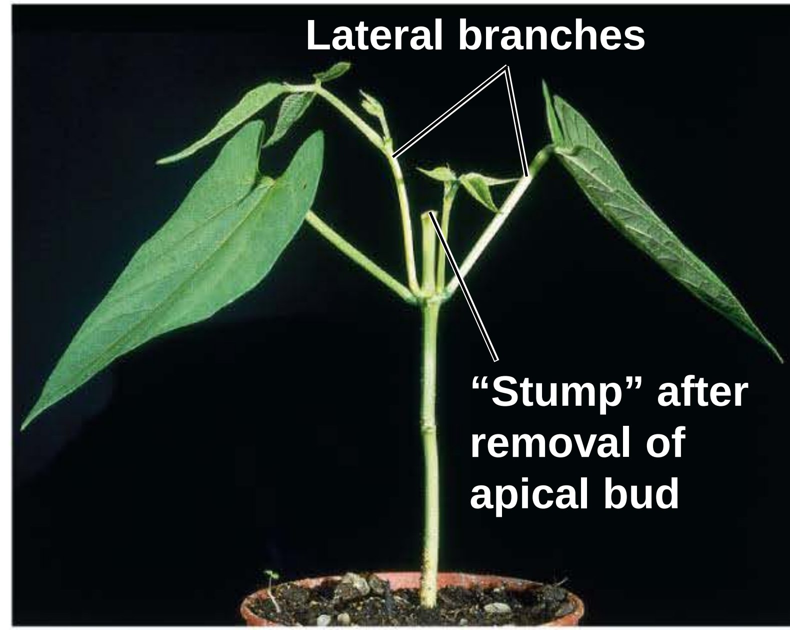
## Control of Apical Dominance

- Cytokinins, auxin, and strigolactone 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

Figure 39.8



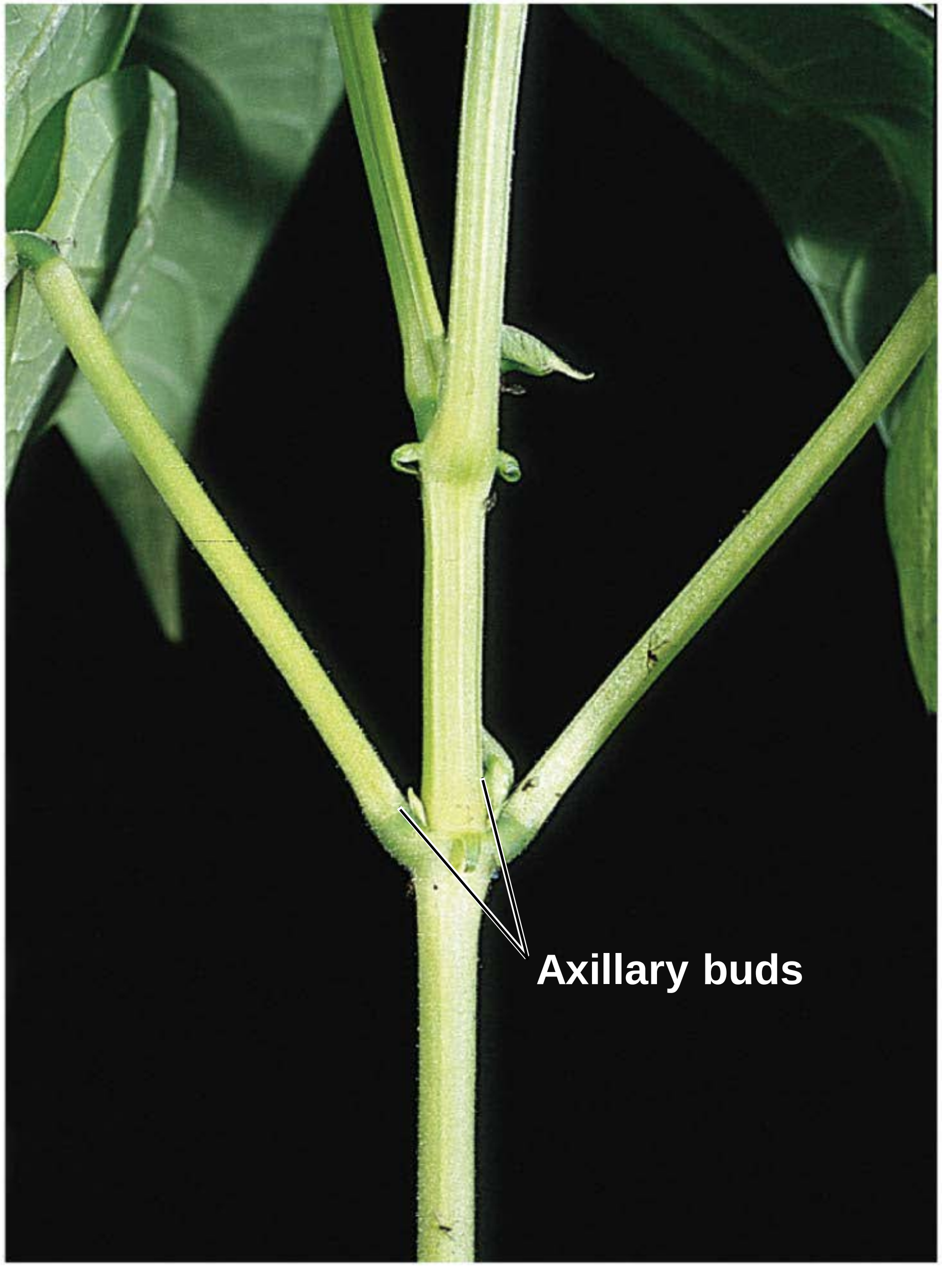

**(a) Apical bud intact (not shown in photo)**




**(b) Apical bud removed**

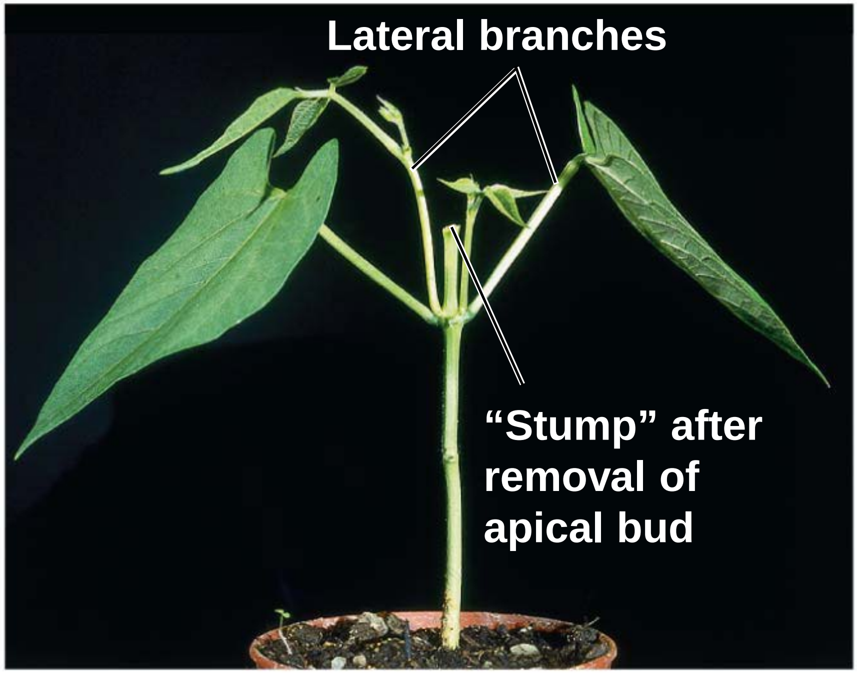
**(c) Auxin added to decapitated stem**

Figure 39.8a




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

Figure 39.8b




(b) Apical bud removed

Figure 39.8c

**(c) Auxin added to decapitated stem**

# Gibberellin

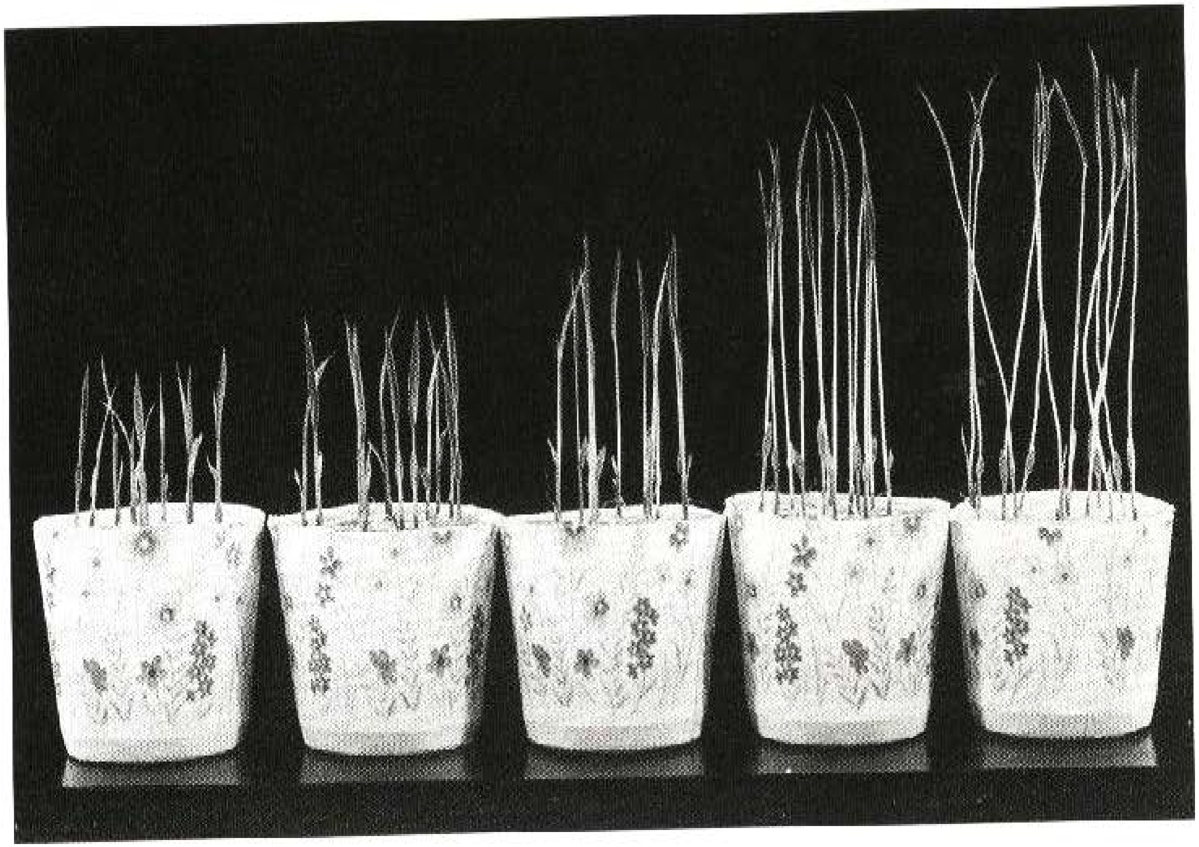


FIGURE 20.5 Gibberellin causes elongation of the leaf sheath of rice seedlings, and this response is used in the dwarf rice leaf sheath bioassay. Here 4-day-old seedlings were treated with different amounts of GA and allowed to grow for another 5 days. (Courtesy of P. Davies.)

ent-kaurine

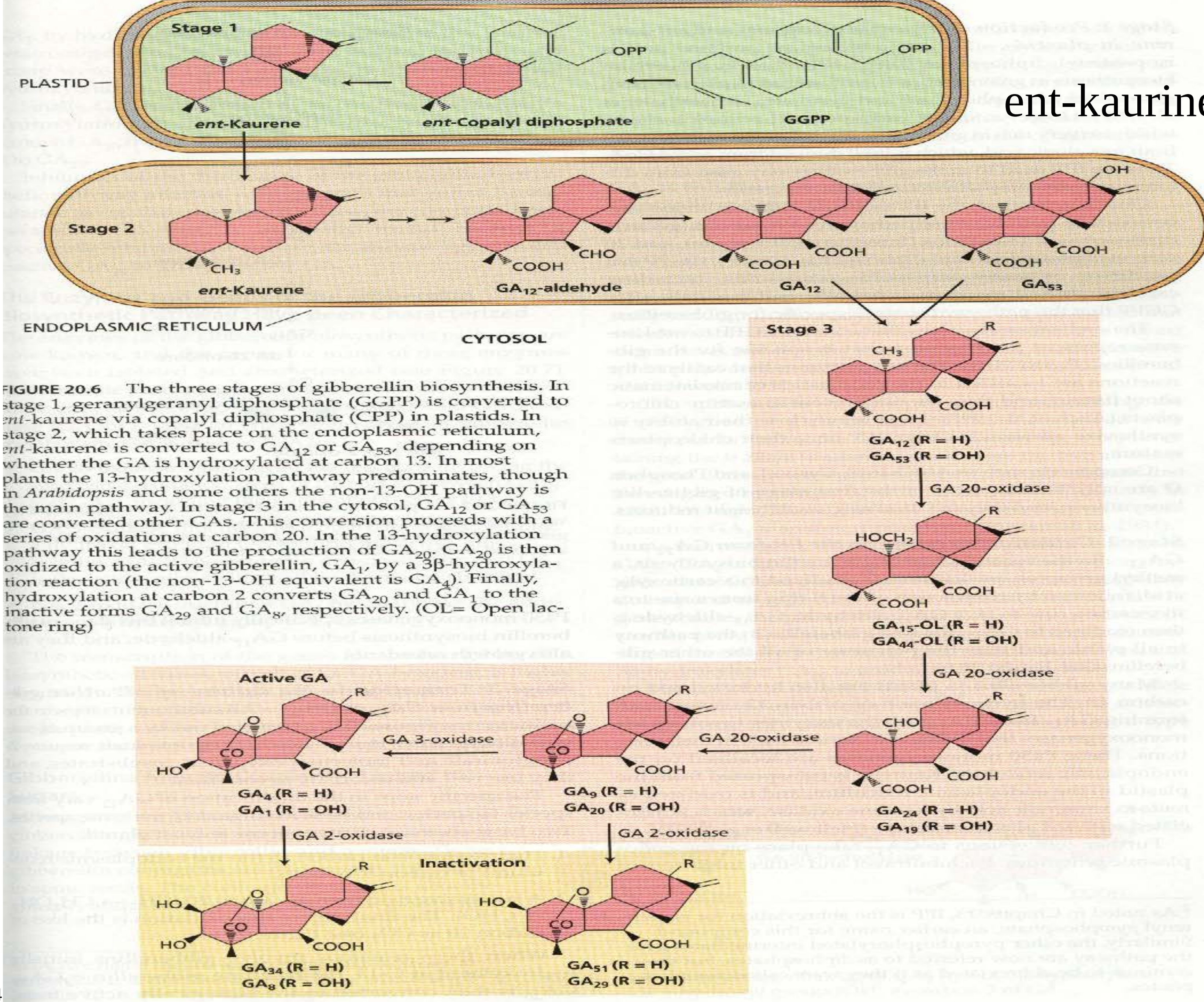



**FIGURE 20.6** The three stages of gibberellin biosynthesis. In stage 1, geranylgeranyl diphosphate (GGPP) is converted to *ent*-kaurene via copalyl diphosphate (CPP) in plastids. In stage 2, which takes place on the endoplasmic reticulum, *ent*-kaurene is converted to $GA_{12}$ or $GA_{53}$, depending on whether the GA is hydroxylated at carbon 13. In most plants the 13-hydroxylation pathway predominates, though in *Arabidopsis* and some others the non-13-OH pathway is the main pathway. In stage 3 in the cytosol, $GA_{12}$ or $GA_{53}$ are converted other GAs. This conversion proceeds with a series of oxidations at carbon 20. In the 13-hydroxylation pathway this leads to the production of $GA_{20}$. $GA_{20}$ is then oxidized to the active gibberellin, $GA_1$, by a 3β-hydroxylation reaction (the non-13-OH equivalent is $GA_4$). Finally, hydroxylation at carbon 2 converts $GA_{20}$ and $GA_1$ to the inactive forms $GA_{29}$ and $GA_8$, respectively. (OL= Open lactone ring)

## Anti-Aging Effects

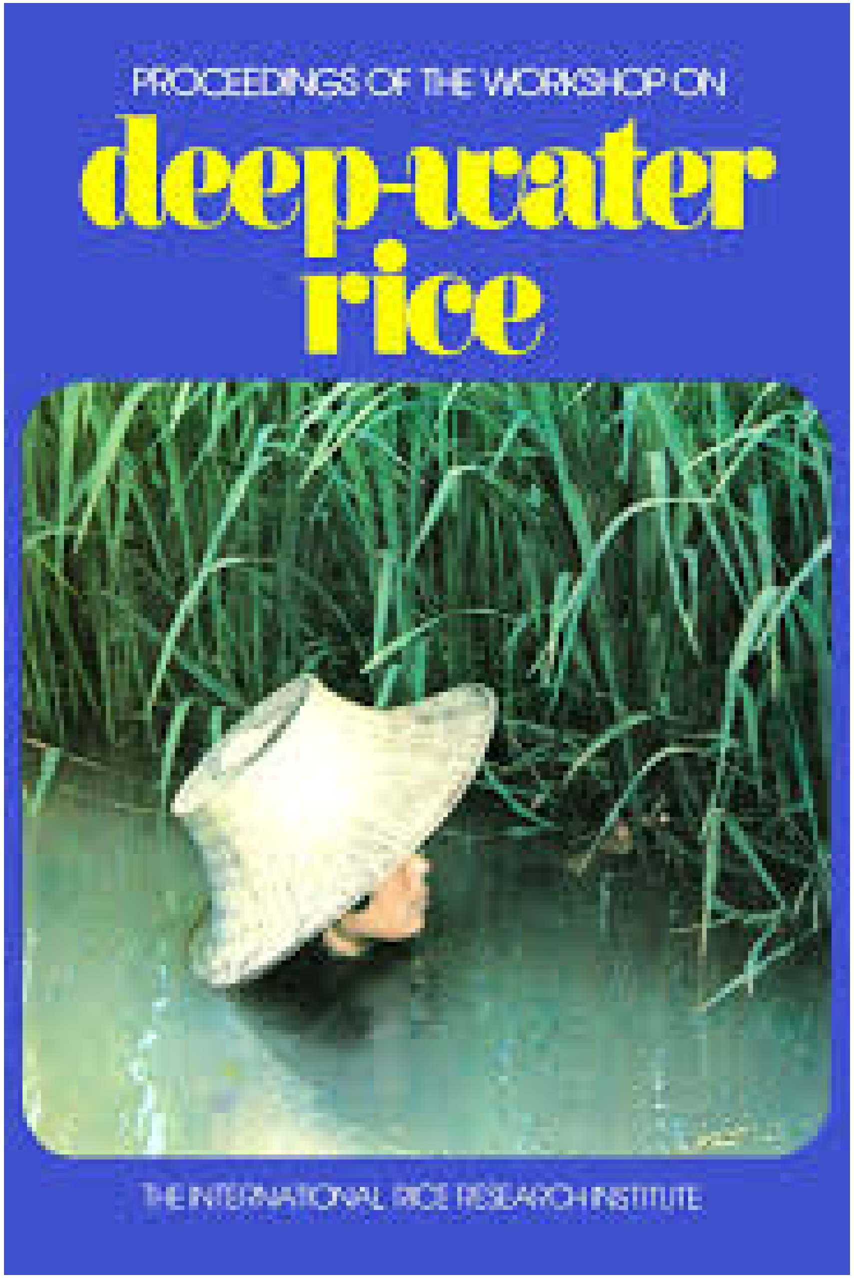
- Cytokinins slow the aging of some plant organs by inhibiting protein breakdown, stimulating RNA and protein synthesis, and mobilizing nutrients from surrounding tissues

# *Gibberellins*

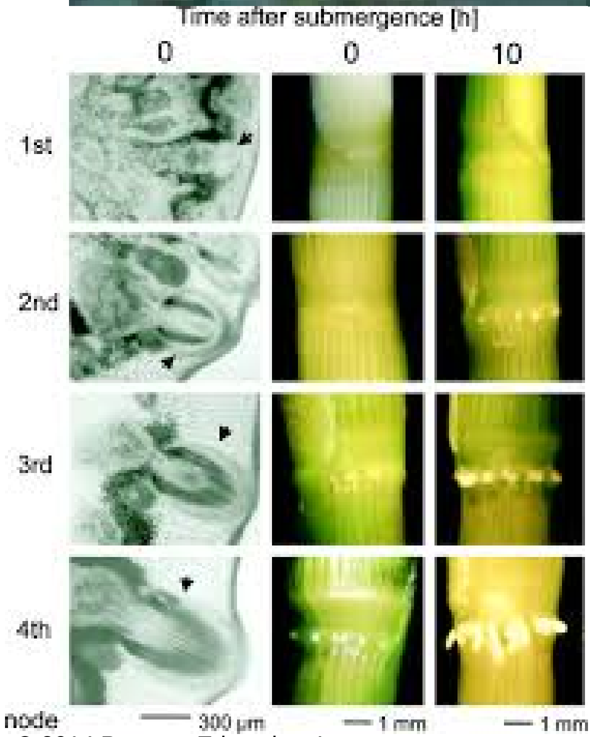
- **Gibberellins** have a variety of effects, such as stem elongation, fruit growth, and seed germination

## Stem Elongation

- Gibberellins are produced in young roots and leaves
- Gibberellins stimulate growth of leaves and stems
- In stems, they stimulate cell elongation and cell division


PROCEEDINGS OF THE WORKSHOP ON
deep-water rice
THE INTERNATIONAL RICE RESEARCH INSTITUTE

# Deepwater rice-vietnam



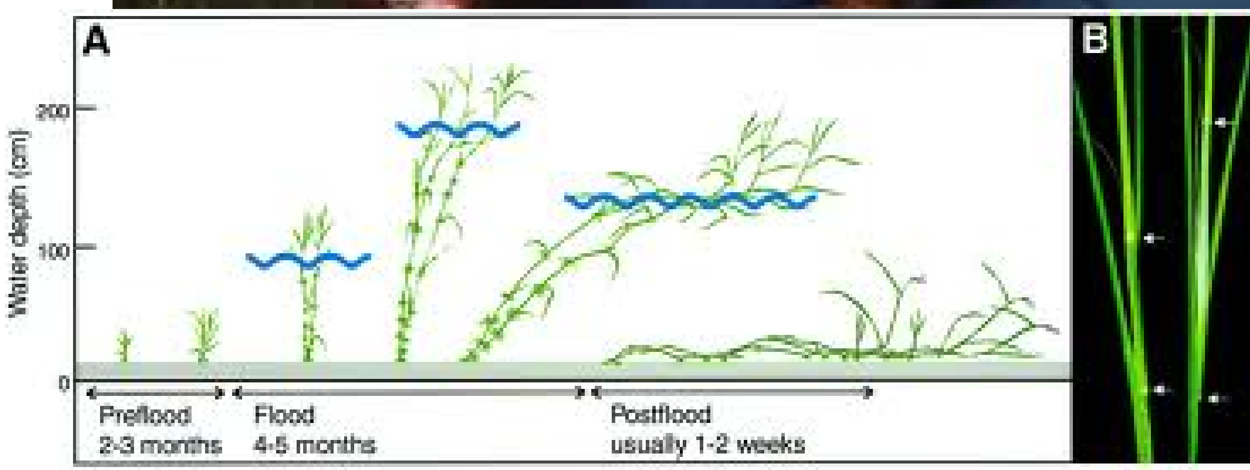
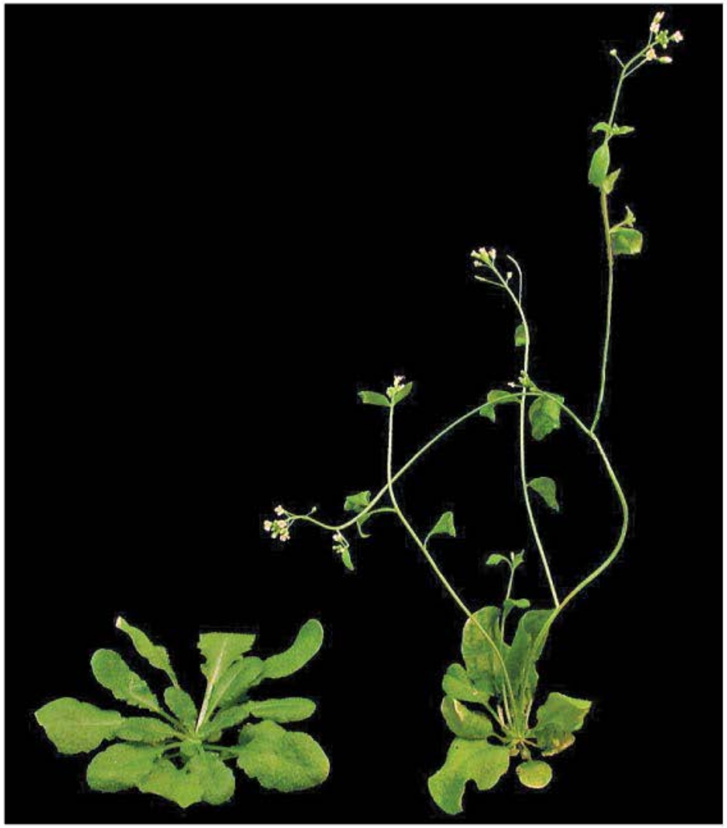
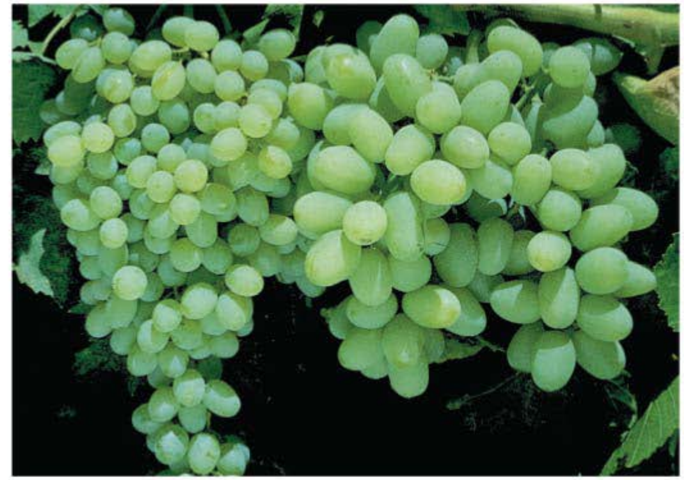



Figure 39.9

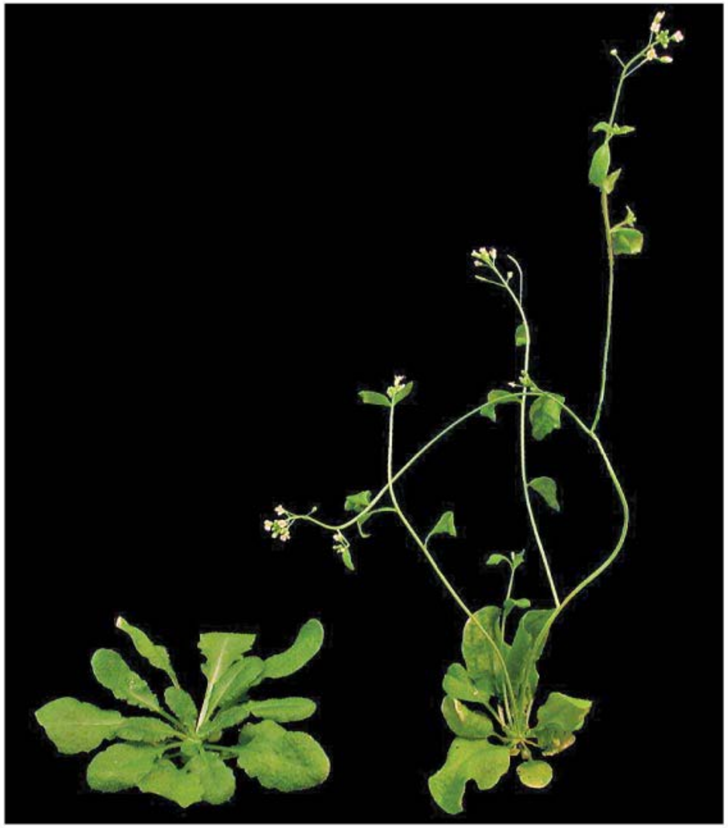


(a) Rosette form (left) and gibberellin-induced bolting 螺栓 (right)



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

Figure 39.9a



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

Figure 39.9b

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

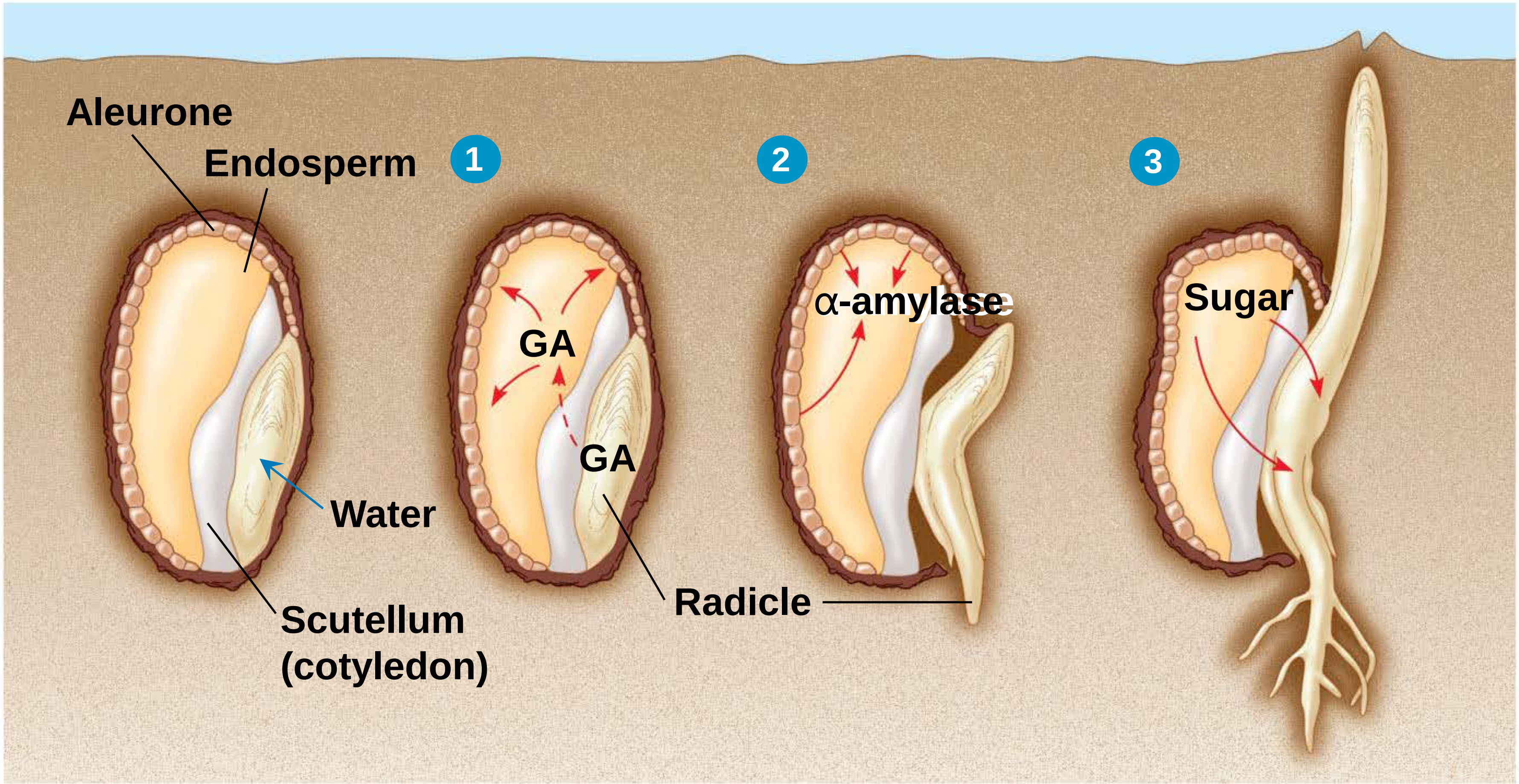
## Fruit Growth

- 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 39.10


Aleurone
Endosperm
1
2
3
GA
GA
α-amylase
Sugar
Water
Radicle
Scutellum
(cotyledon)

# Germination **aleurone layer endosperm**

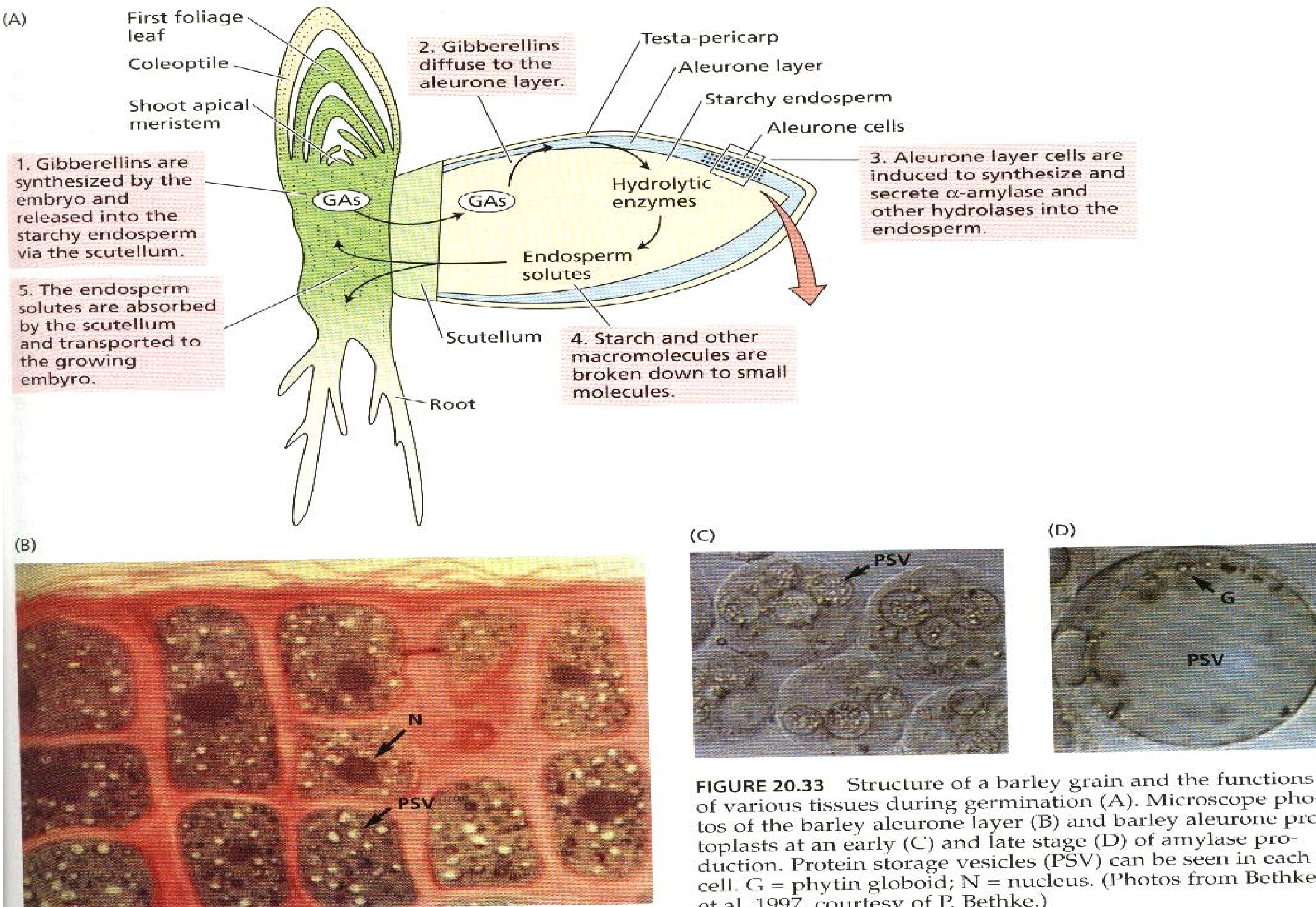



**FIGURE 20.33** Structure of a barley grain and the functions of various tissues during germination (A). Microscope photos of the barley aleurone layer (B) and barley aleurone protoplasts at an early (C) and late stage (D) of amylase production. Protein storage vesicles (PSV) can be seen in each cell. G = phytin globoid; N = nucleus. (Photos from Bethke et al. 1997, courtesy of P. Bethke.)

1. $GA_1$ from the embryo first binds to a cell surface receptor.

2. The cell surface GA receptor complex interacts with a heterotrimeric G-protein, initiating two separate signal transduction chains.

3. A calcium-independent pathway, involving cGMP, results in the activation of a signaling intermediate.

4. The activated signaling intermediate binds to DELLA repressor proteins in the nucleus.

5. The DELLA repressors are degraded when bound to the GA signal.

6. The inactivation of the DELLA repressors allows the expression of the *MYB* gene, as well as other genes, to proceed through transcription, processing, and translation.

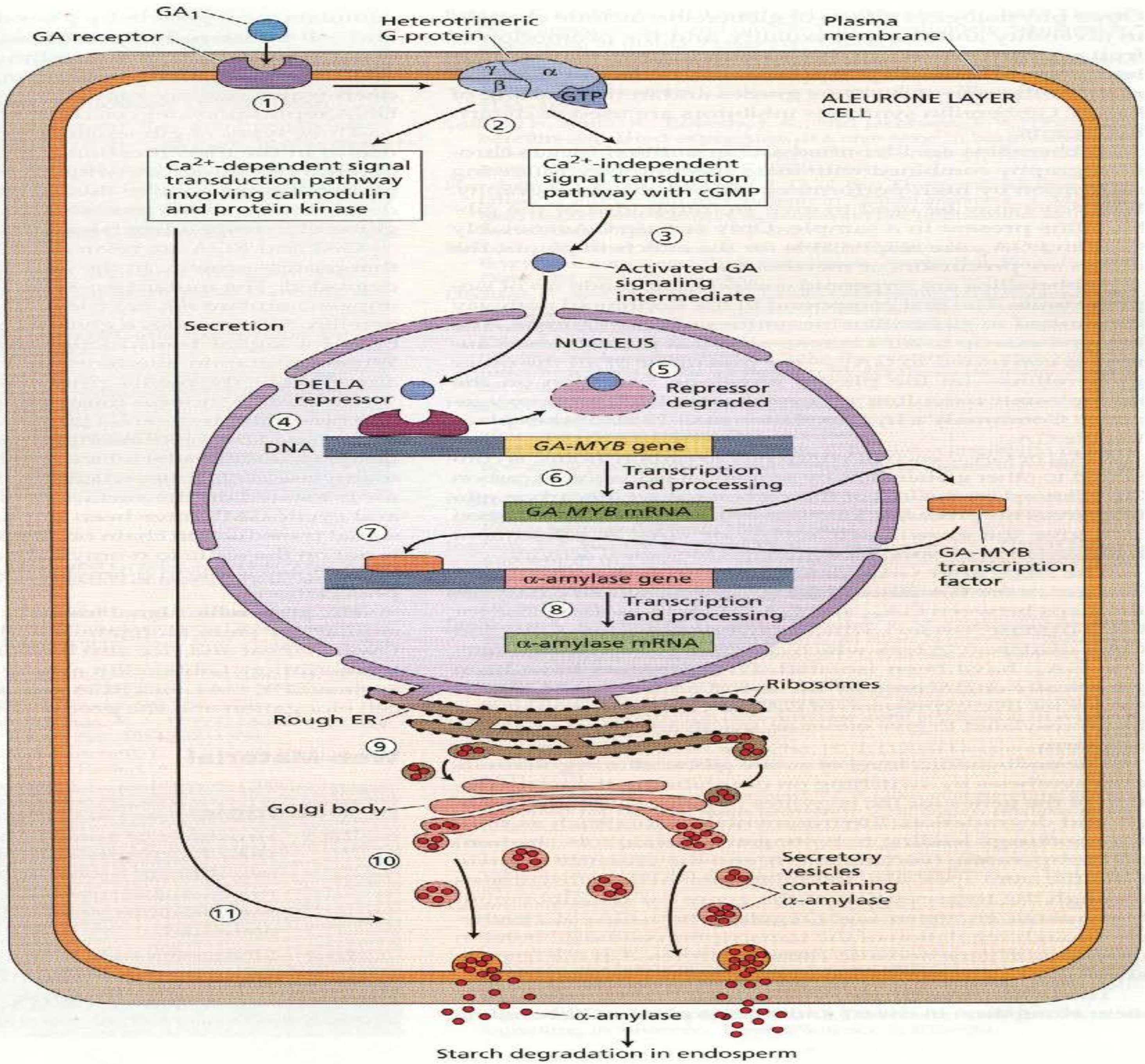
7. The newly synthesized MYB protein then enters the nucleus and binds to the promoter genes for α-amylase and other hydrolytic enzymes.

8. Transcription of α-amylase and other hydrolytic genes is activated.

9. α-Amylase and other hydrolases are synthesized on the rough ER.

10. Proteins are secreted via the Golgi.

11. The secretory pathway requires GA stimulation via a calcium–calmodulin-dependent signal transduction pathway.



## *Abscisic Acid*

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

IPP

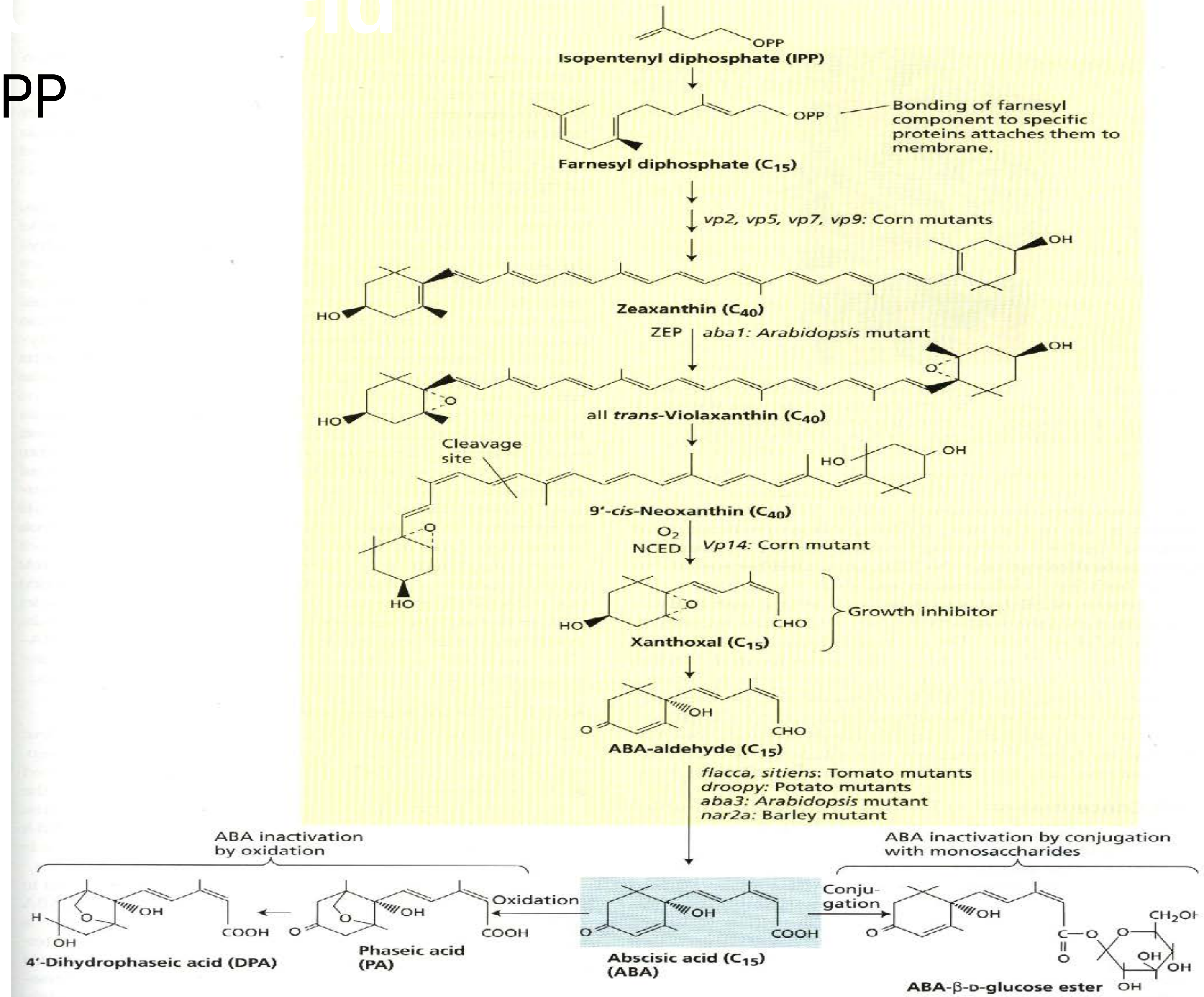



**FIGURE 23.2** ABA biosynthesis and metabolism. In higher plants, ABA is synthesized via the terpenoid pathway (see Chapter 13). Some ABA-deficient mutants that have been helpful in elucidating the pathway are shown at the steps at which they are blocked. The pathways for ABA catabolism include conjugation to form ABA-β-D-glucosyl ester or oxidation to form phaseic acid and then dihydrophaseic acid. ZEP = zeaxanthin epoxidase; NCED = 9-cis-epoxy-carotenoids dioxygenase.

**FIGURE 23.3** Precocious germination in the ABA-deficient *vp14* mutant of maize. The VP14 protein catalyzes the cleavage of 9-*cis*-epoxycarotenoids to form xanthoxal, a precursor of ABA. (Courtesy of Bao Cai Tan and Don McCarty.)

# Stomotal opening

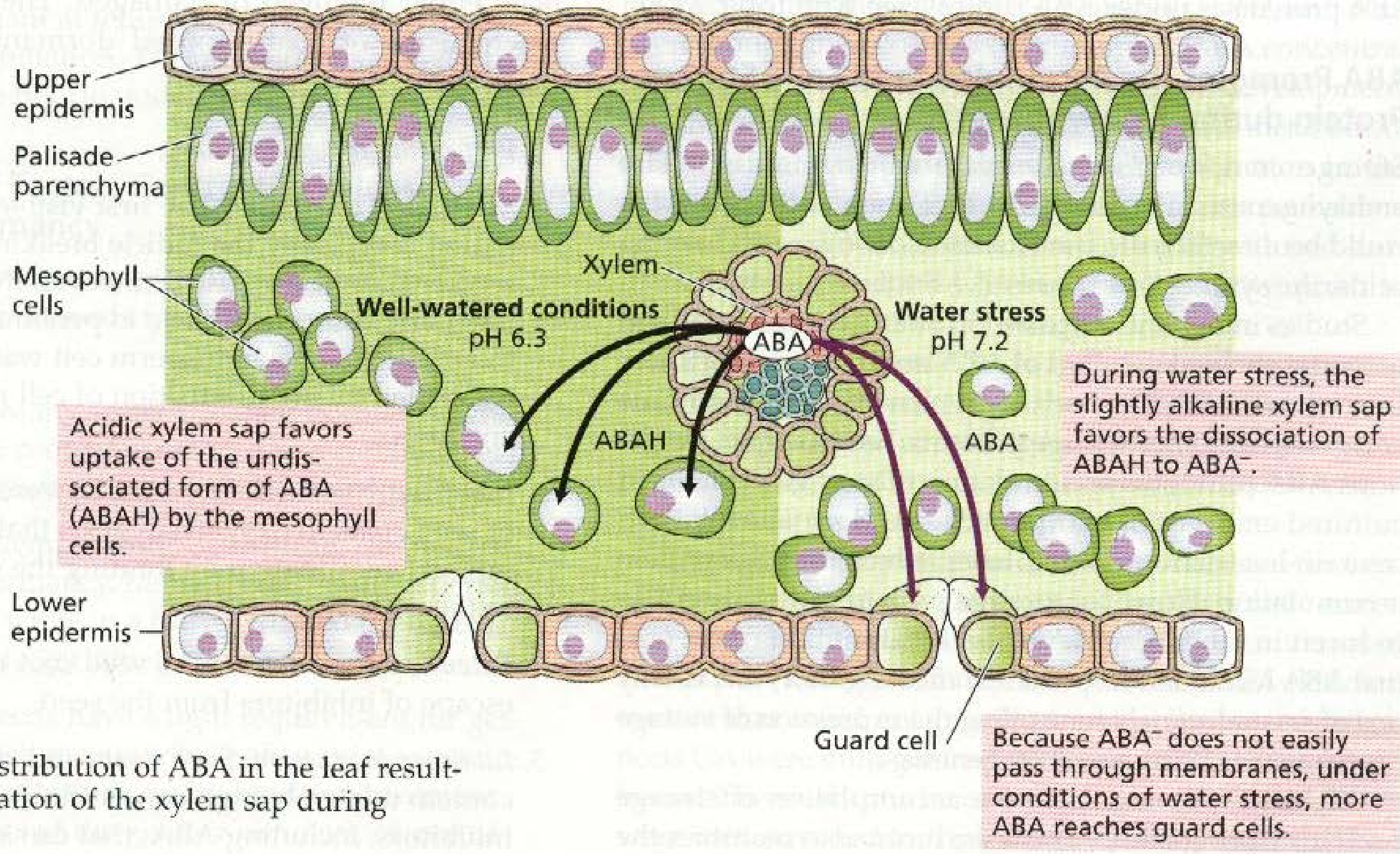



**FIGURE 23.4** Redistribution of ABA in the leaf resulting from alkalinization of the xylem sap during water stress.

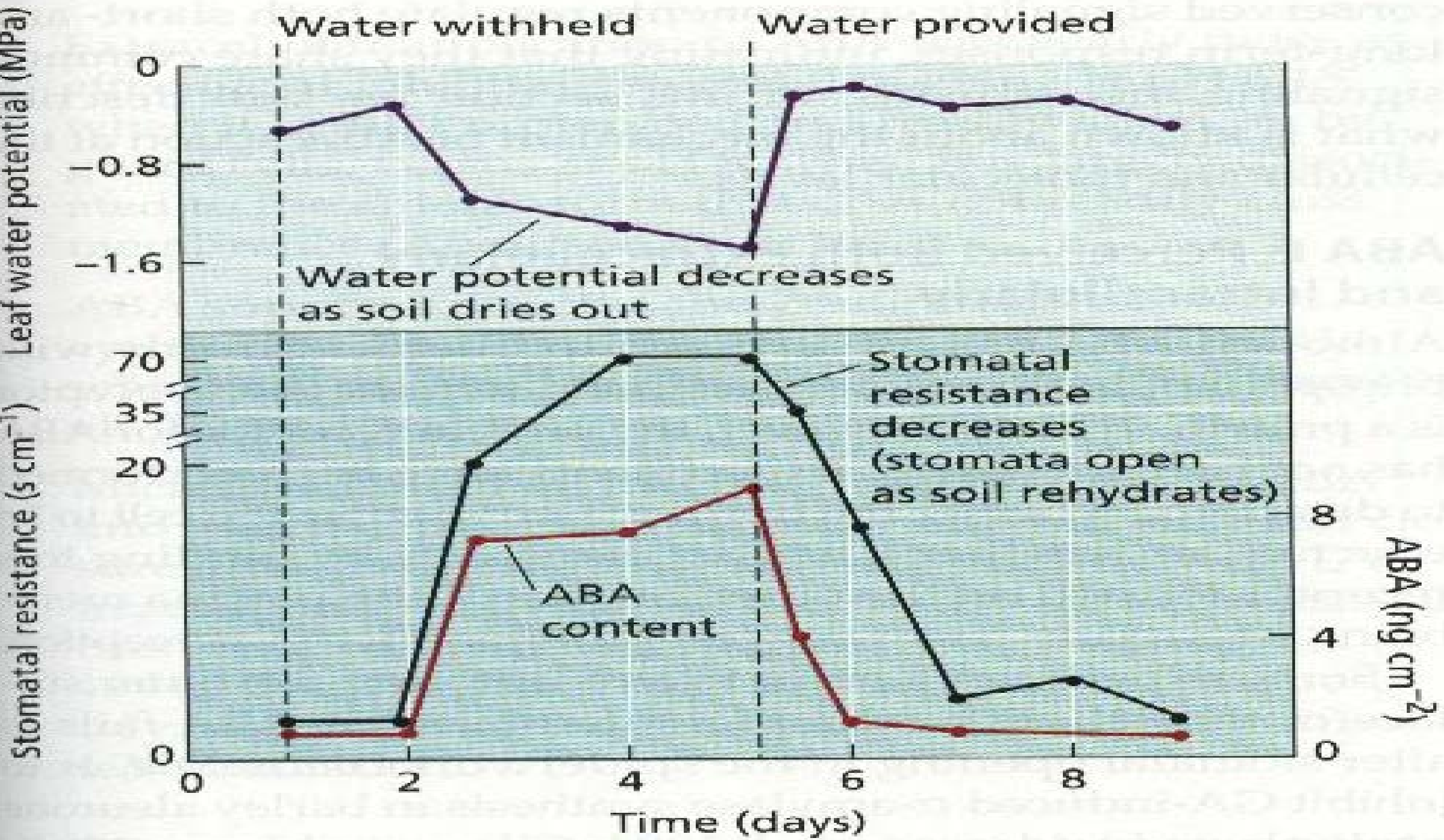


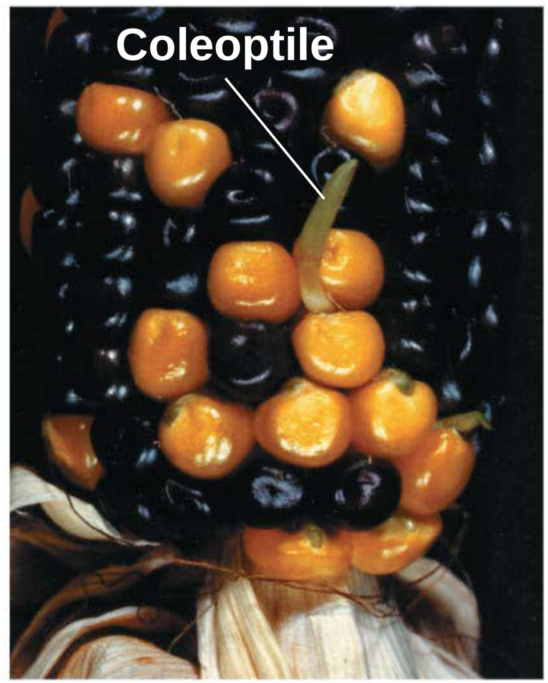

**FIGURE 23.5** Changes in water potential, stomatal resistance (the inverse of stomatal conductance), and ABA content in maize in response to water stress. As the soil dried out, the water potential of the leaf decreased, and the ABA content and stomatal resistance increased. The process was reversed by rewatering. (After Beardsell and Cohen 1975.)

## 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 (early) germination can be caused by inactive or low levels of ABA

Figure 39.11

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

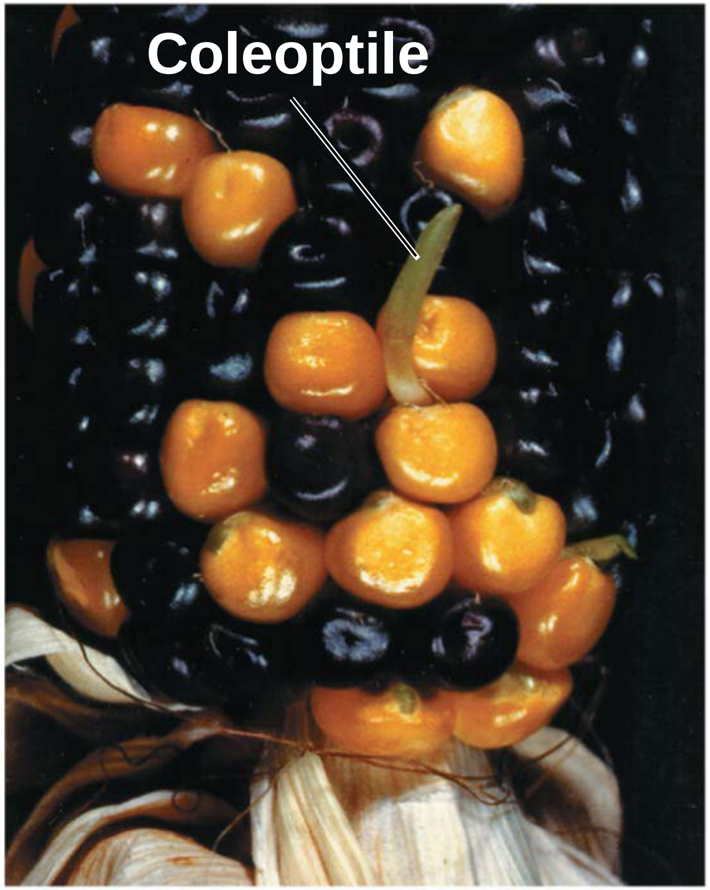



▲ **Maize mutant**

Figure 39.11a

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

Figure 39.11b



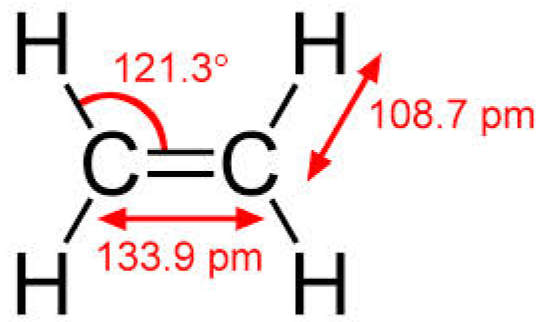

**Maize mutant**

## Drought Tolerance

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

# *Ethylene*

$C_2H_4$




- 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 Role of Ethylene in Post Harvest Biology

Name : T.W.G.F.A Nijamdeen

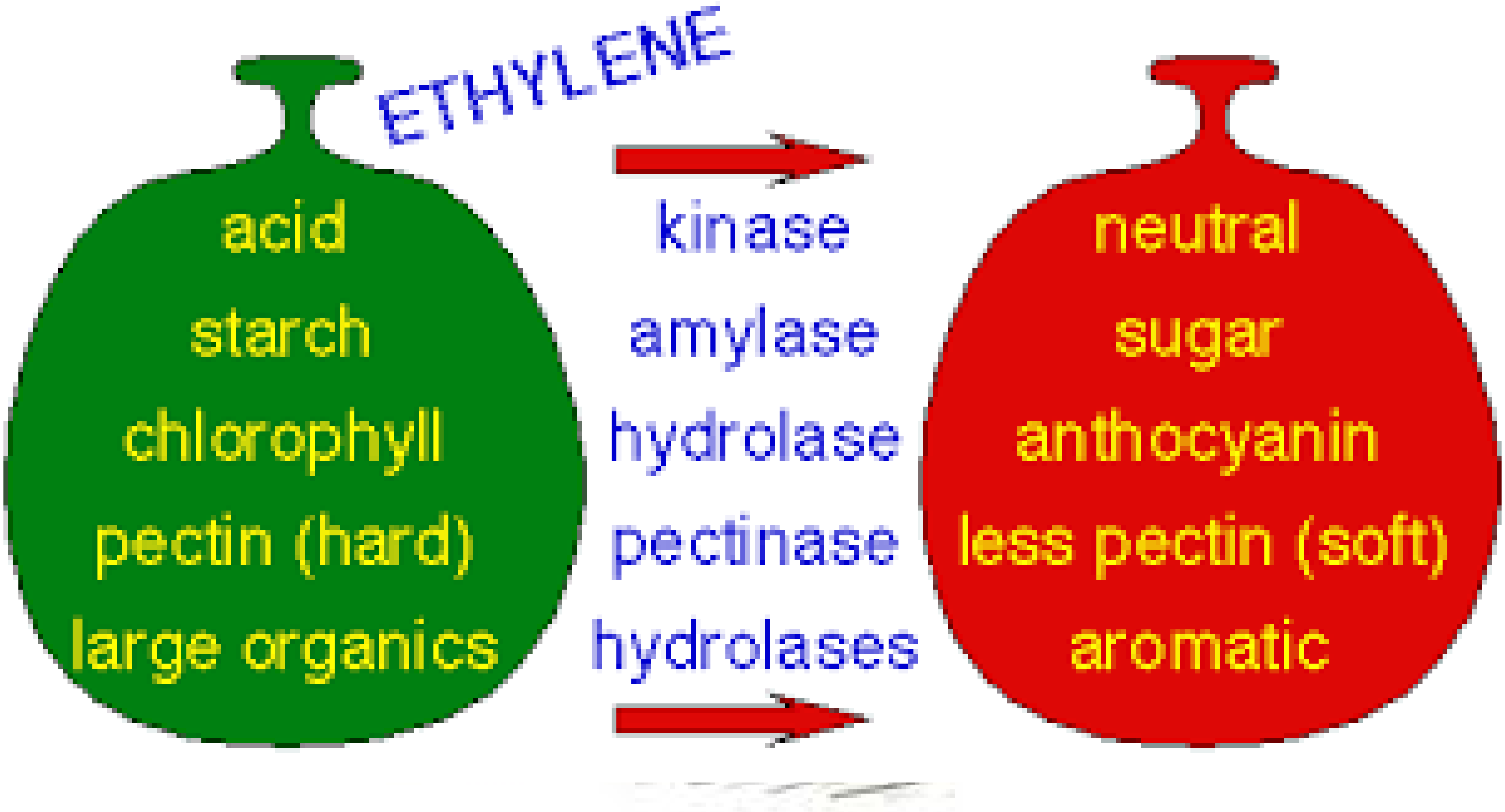
Reg.No: 612260302

## Climacteric fruits

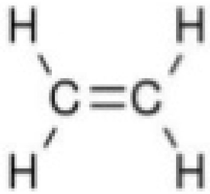
- Eg: Banana,Apple,Avocado, Tomato,Mango, Apricot,pears

## Non-Climacteric fruits

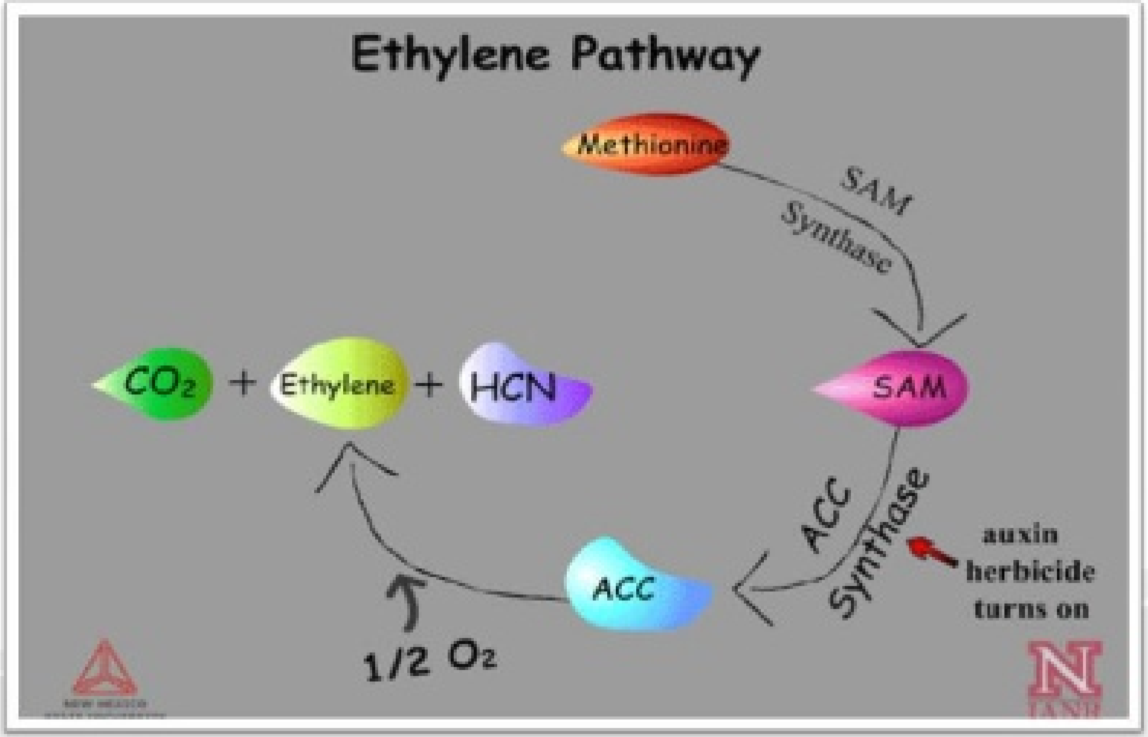
- Eg: Strawberry,Cucumber,Eggplant,Grape,Orange.


ETHYLENE
acid
starch
chlorophyll
pectin (hard)
large organics
kinase
amylase
hydrolase
pectinase
hydrolases
neutral
sugar
anthocyanin
less pectin (soft)
aromatic

# Ethylene-Structure and Biosynthesis

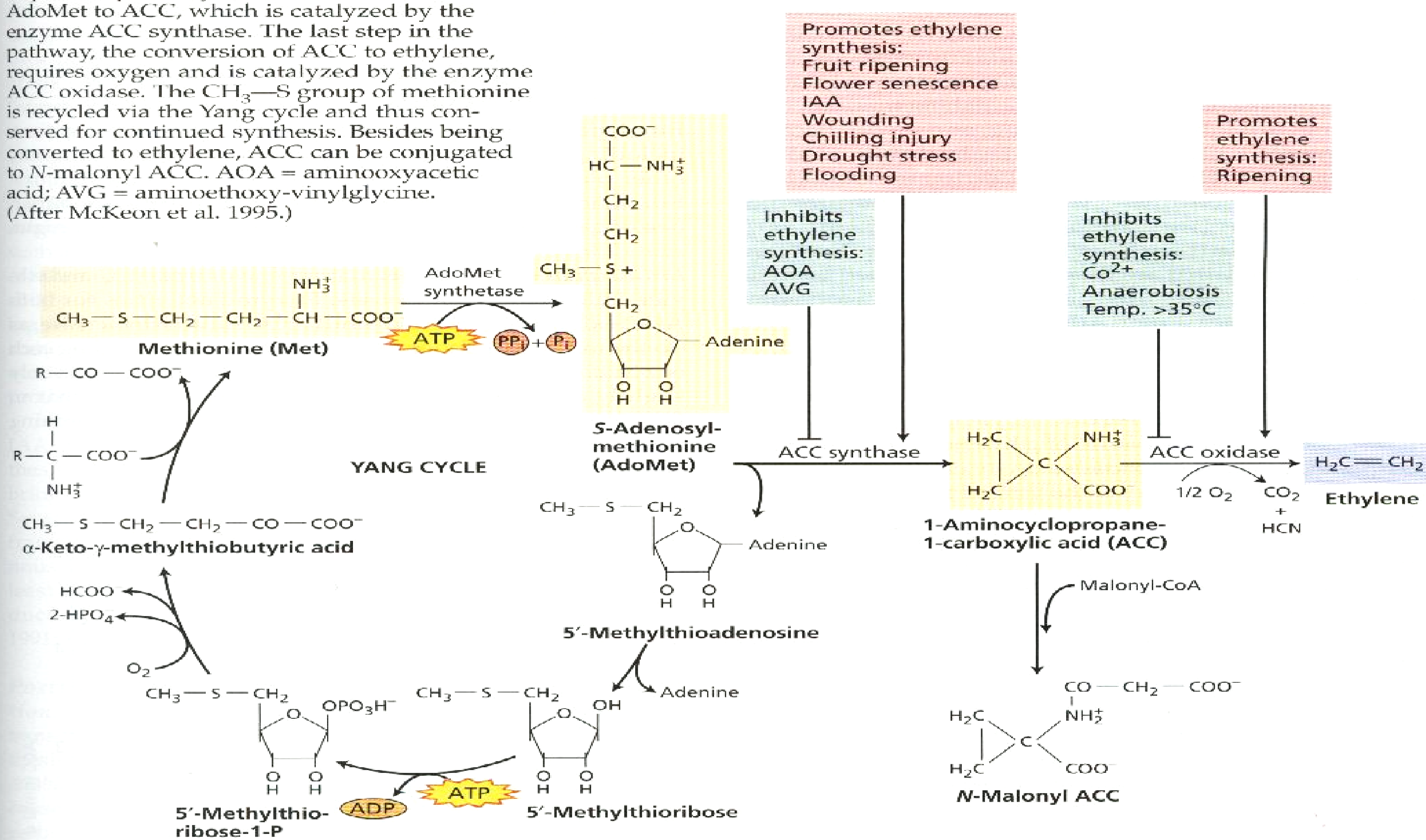


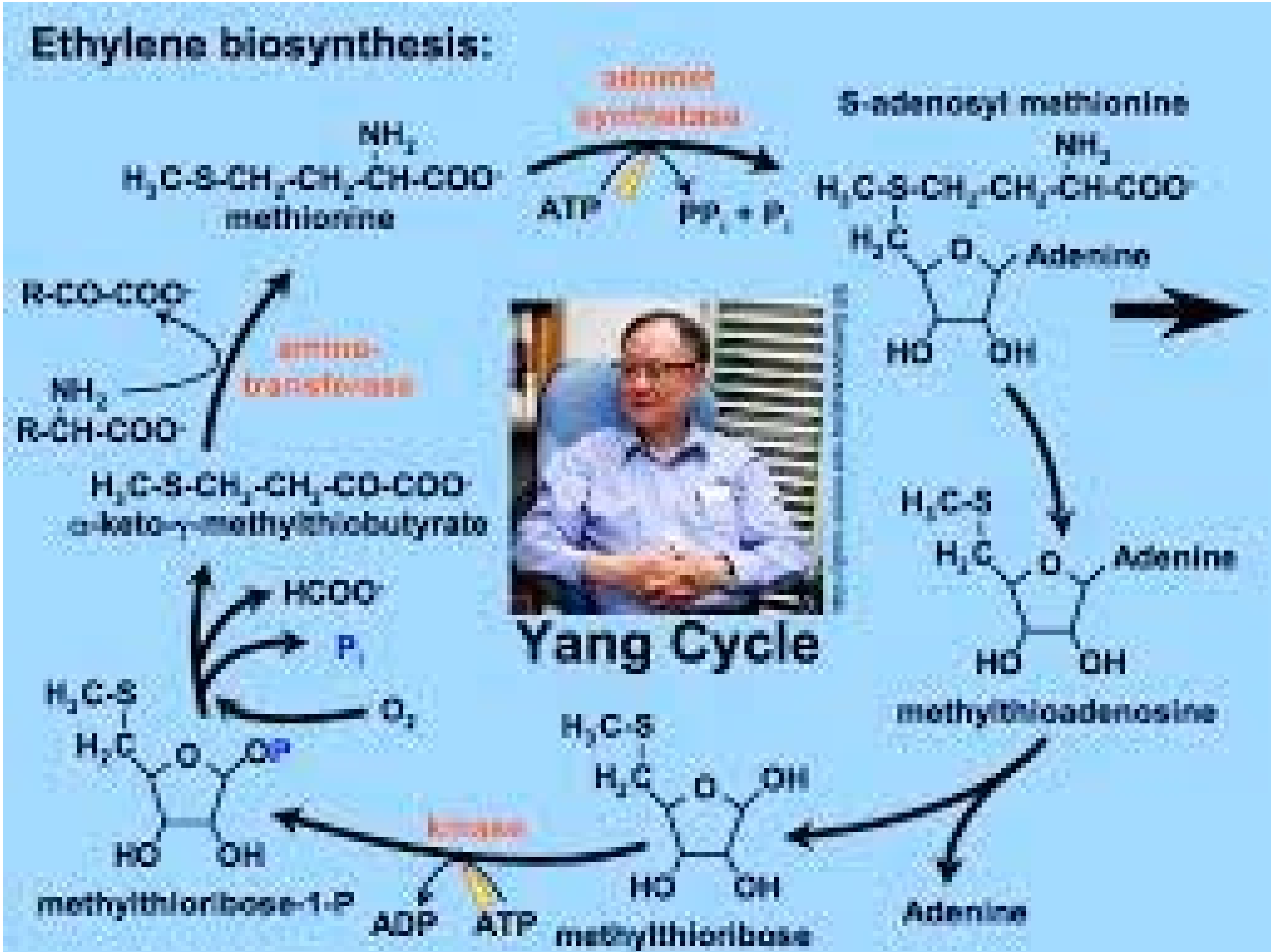

Structure of the ethylene molecule



# Ethylene $C_2H_4$

**FIGURE 22.1** Ethylene biosynthetic pathway and the Yang cycle. The amino acid methionine is the precursor of ethylene. The rate-limiting step in the pathway is the conversion of AdoMet to ACC, which is catalyzed by the enzyme ACC synthase. The last step in the pathway, the conversion of ACC to ethylene, requires oxygen and is catalyzed by the enzyme ACC oxidase. The $CH_3$—S group of methionine is recycled via the Yang cycle and thus conserved for continued synthesis. Besides being converted to ethylene, ACC can be conjugated to *N*-malonyl ACC. AOA = aminooxyacetic acid; AVG = aminoethoxy-vinylglycine. (After McKeon et al. 1995.)

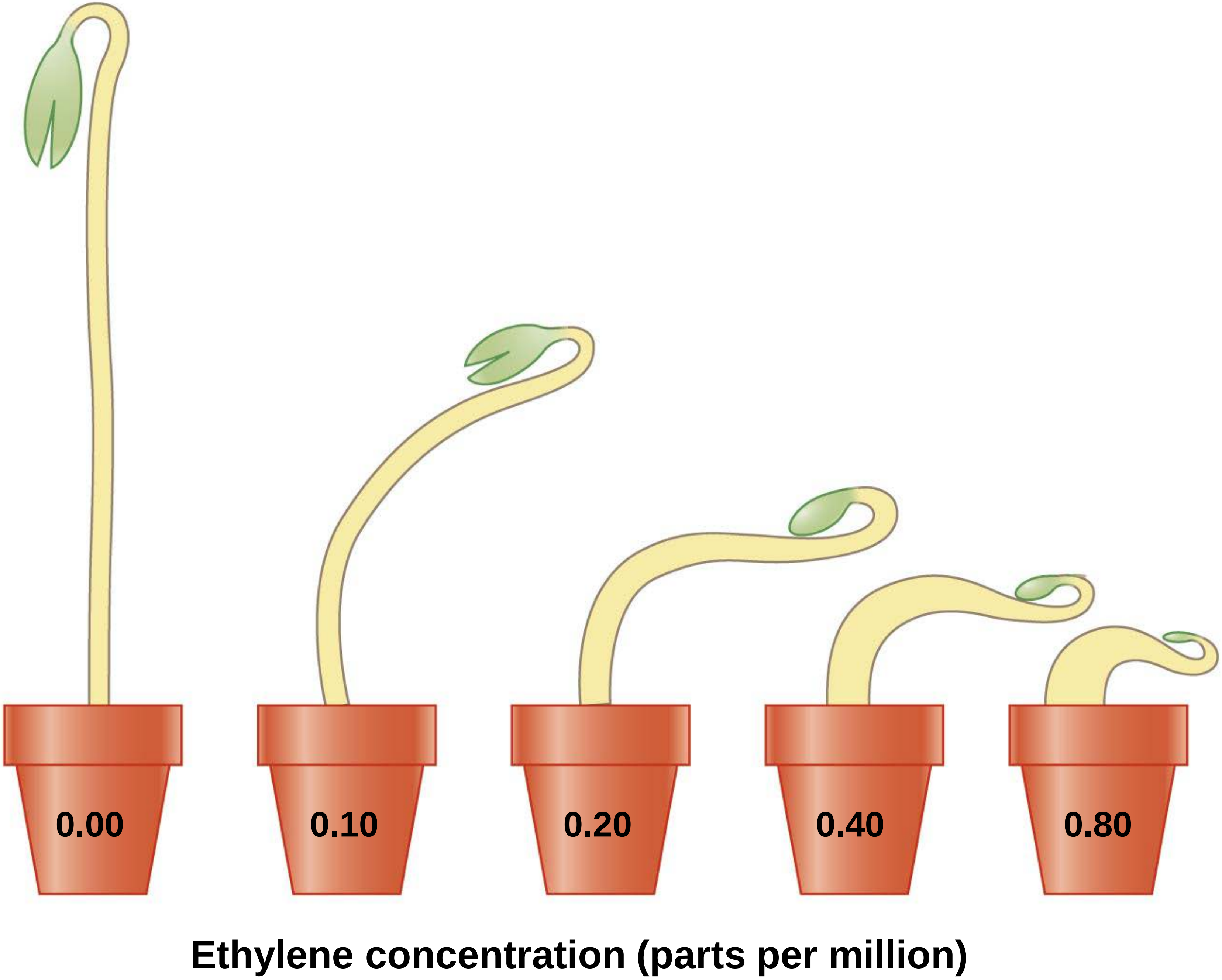



Ethylene biosynthesis:
S-adenosyl methionine
NH2
H3C-S-CH2-CH2-CH-COO-
methionine
ATP
PPi + Pi
H3C-S-CH2-CH2-CH-COO-
H2C
O
Adenine
HO
OH
R-CO-COO-
NH2
R-CH-COO-
H3C-S-CH2-CH2-CO-COO-
α-keto-γ-methylthiobutyrate
HCOO-
Pi
O2
Yang Cycle
H3C-S
H2C
O
Adenine
HO
OH
methylthioadenosine
H3C-S
H2C
O
OP
HO
OH
methylthioribose-1-P
ADP
ATP
H3C-S
H2C
O
OH
HO
OH
methylthioribose
Adenine

## The Triple Response to Mechanical Stress

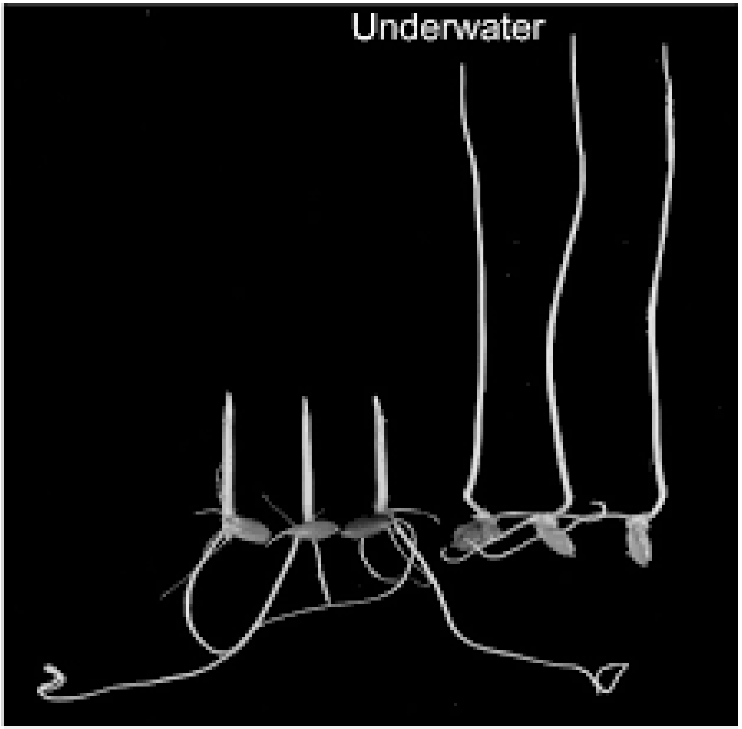
- Ethylene induces the triple response, which allows a growing shoot to avoid obstacles
- The **triple response** consists of a slowing of stem elongation, a thickening of the stem, and horizontal growth

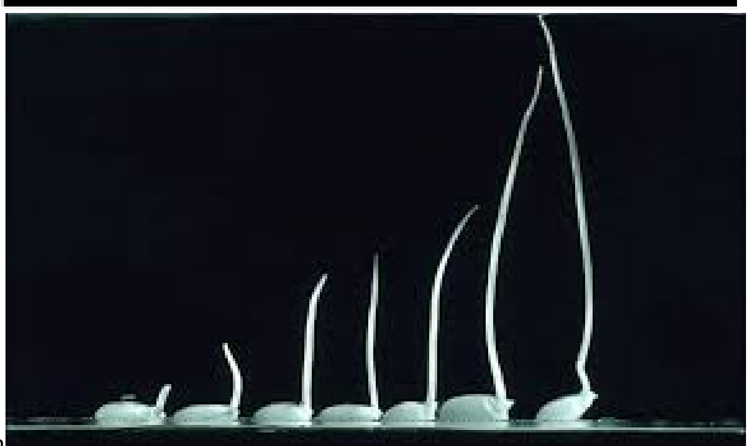
Figure 39.12

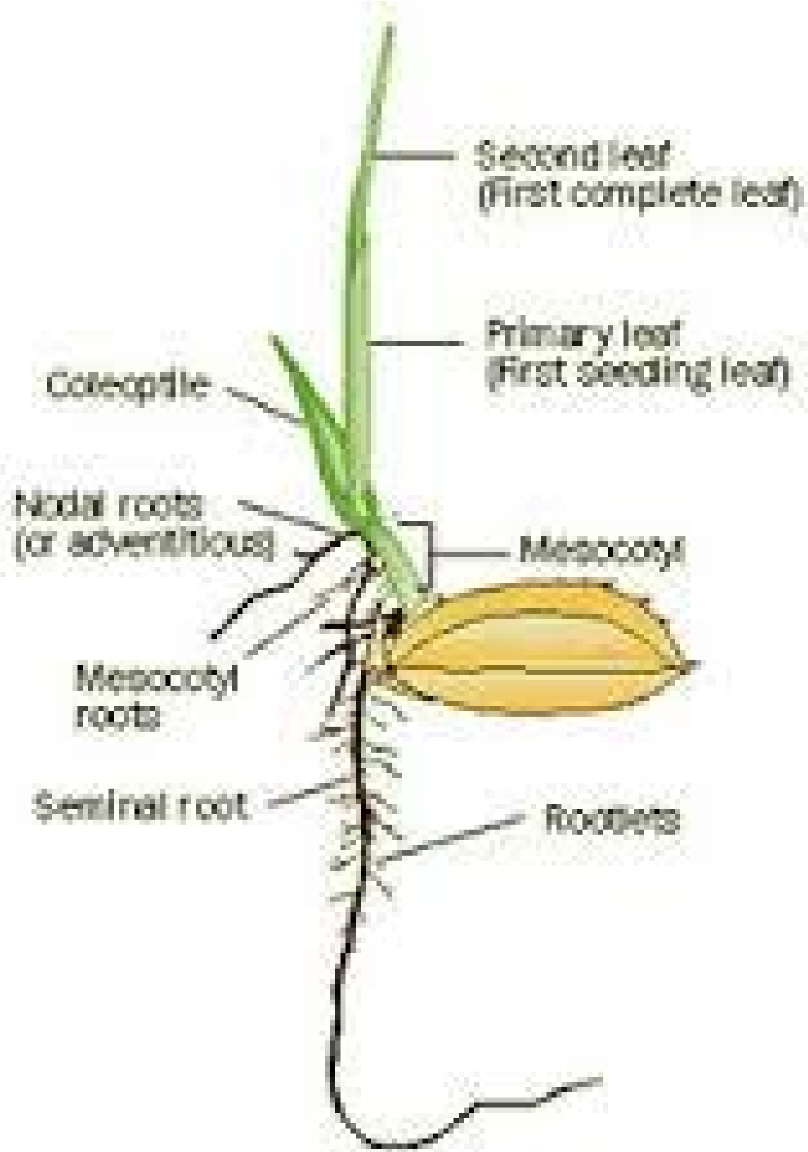

0.00
0.10
0.20
0.40
0.80
Ethylene concentration (parts per million)

- 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

# Rice coleoptile elongation – anoxia and ethylene





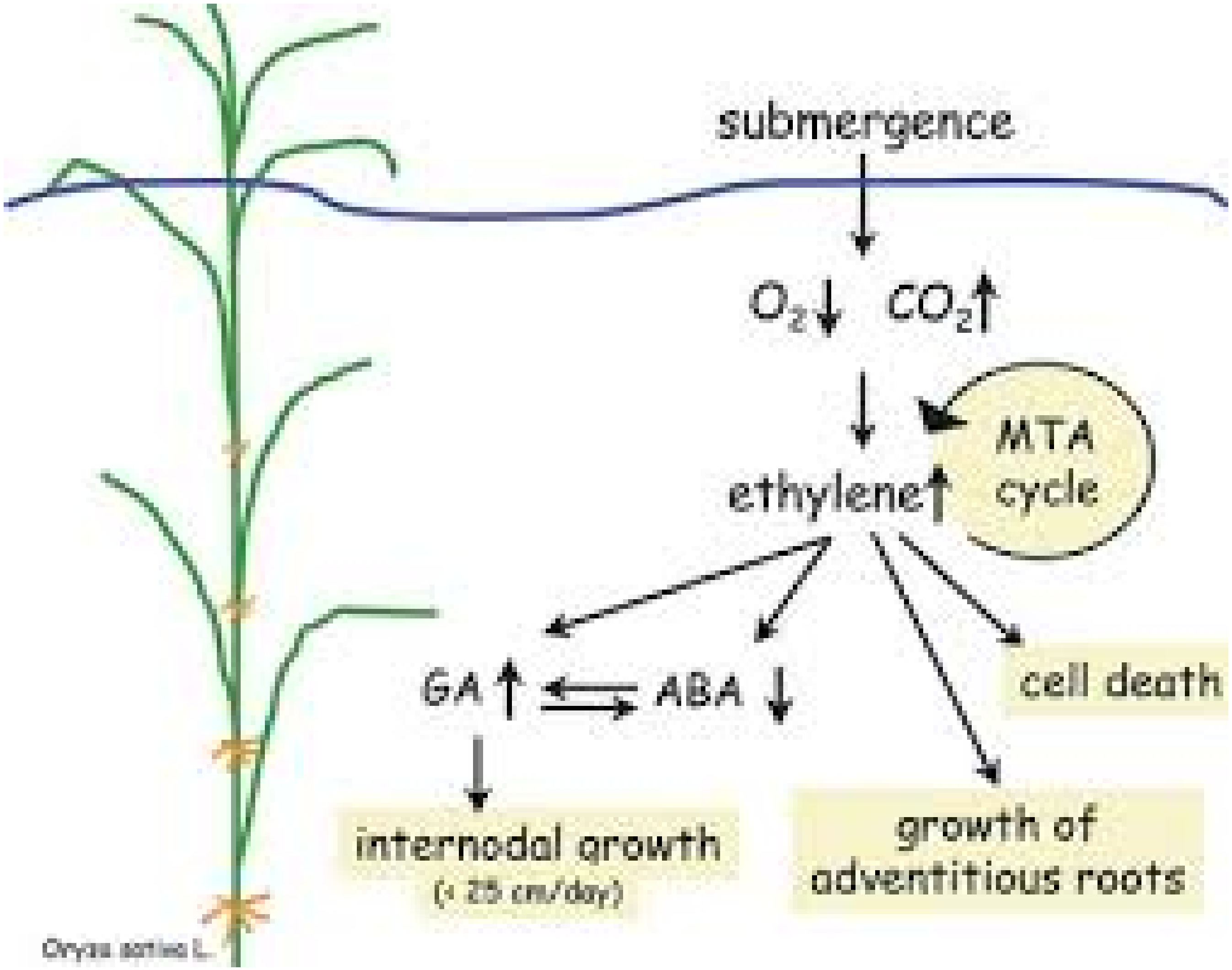
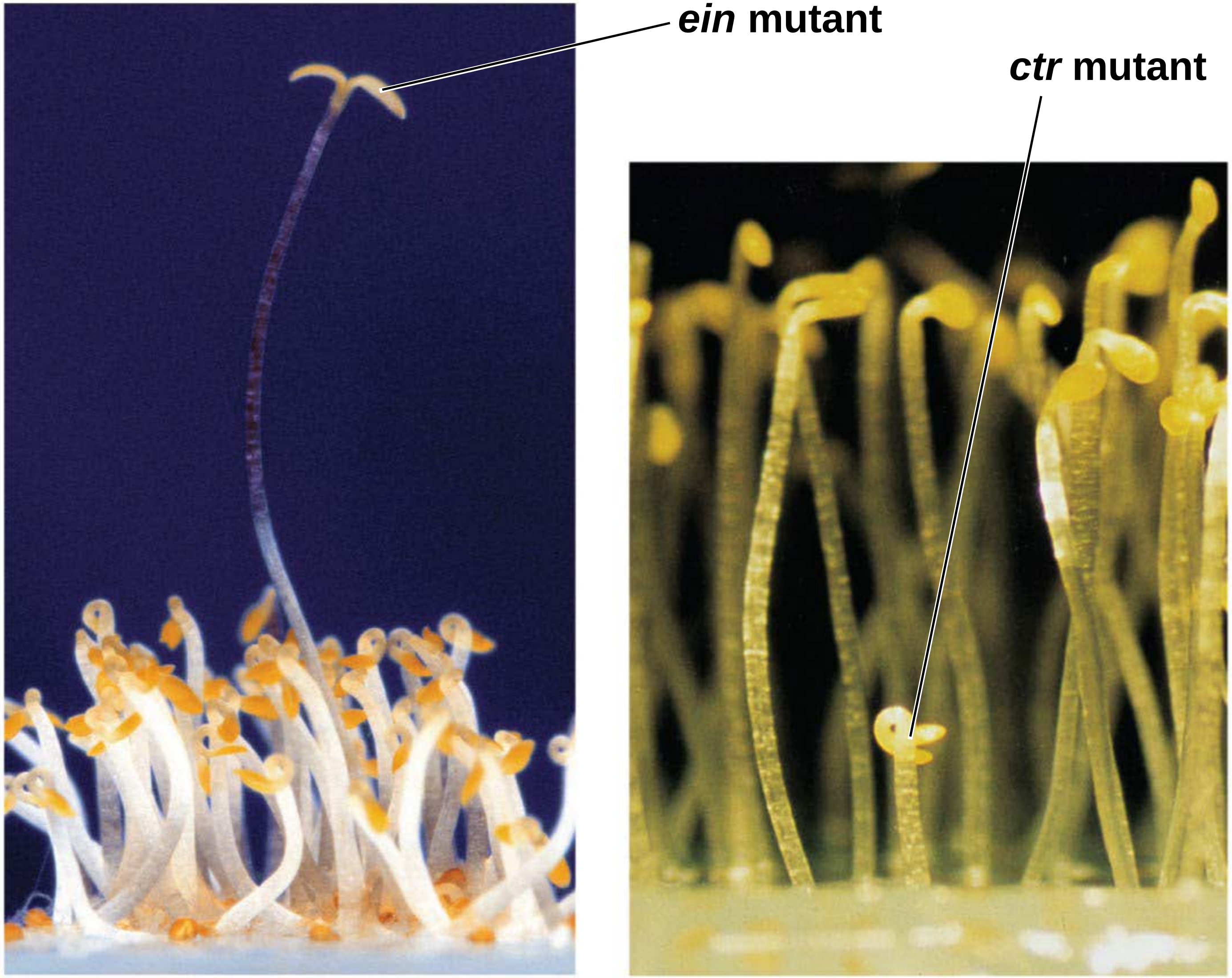
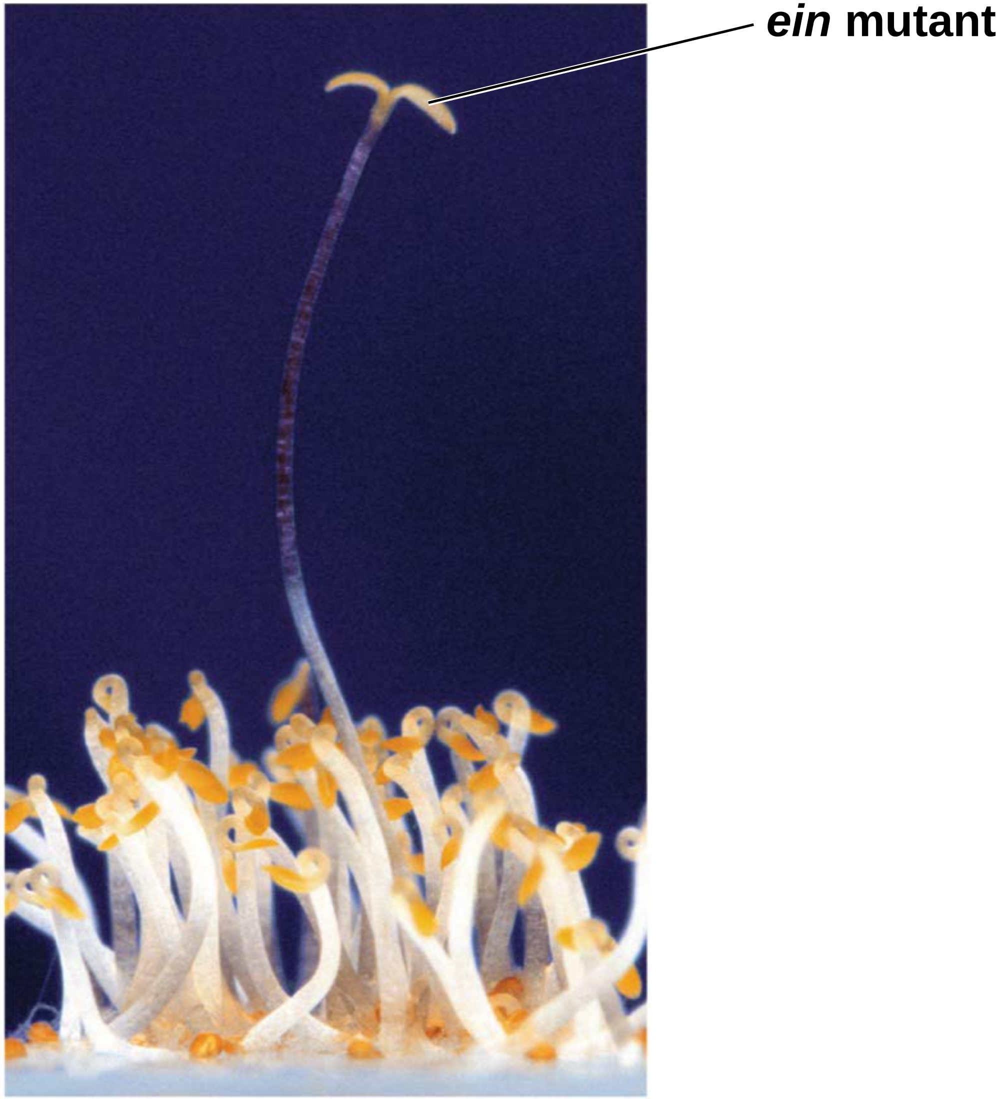

submergence
$O_2$↓ $CO_2$↑
MTA cycle
ethylene↑
GA ↑
ABA ↓
cell death
internodal growth
growth of adventitious roots
Oryza sativa L.

Figure 39.13



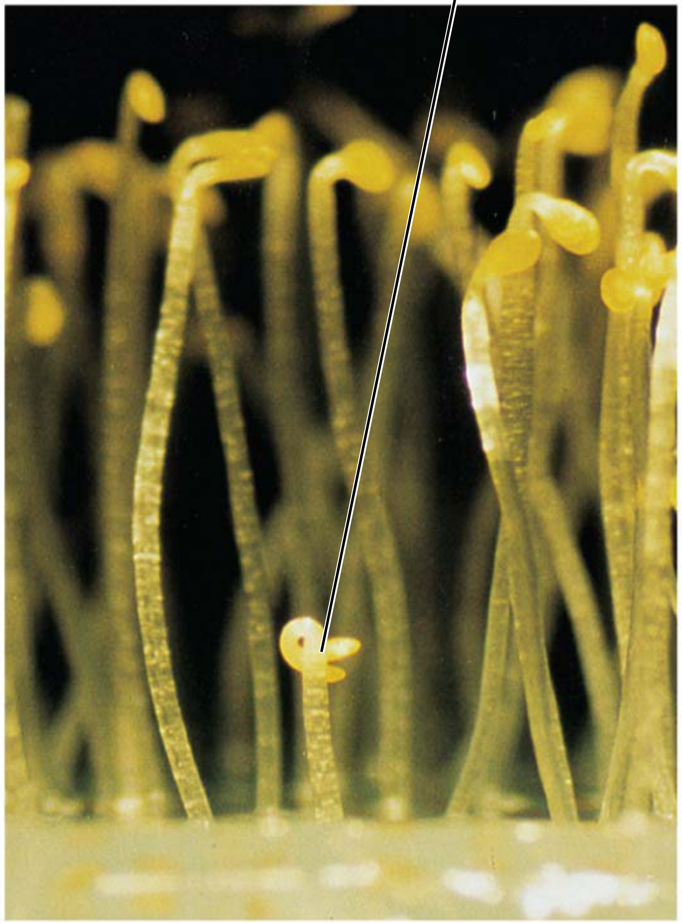

**(a) *ein* mutant** **(b) *ctr* mutant**

Figure 39.13a




(a) *ein* mutant

Figure 39.13b




**(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 39.14

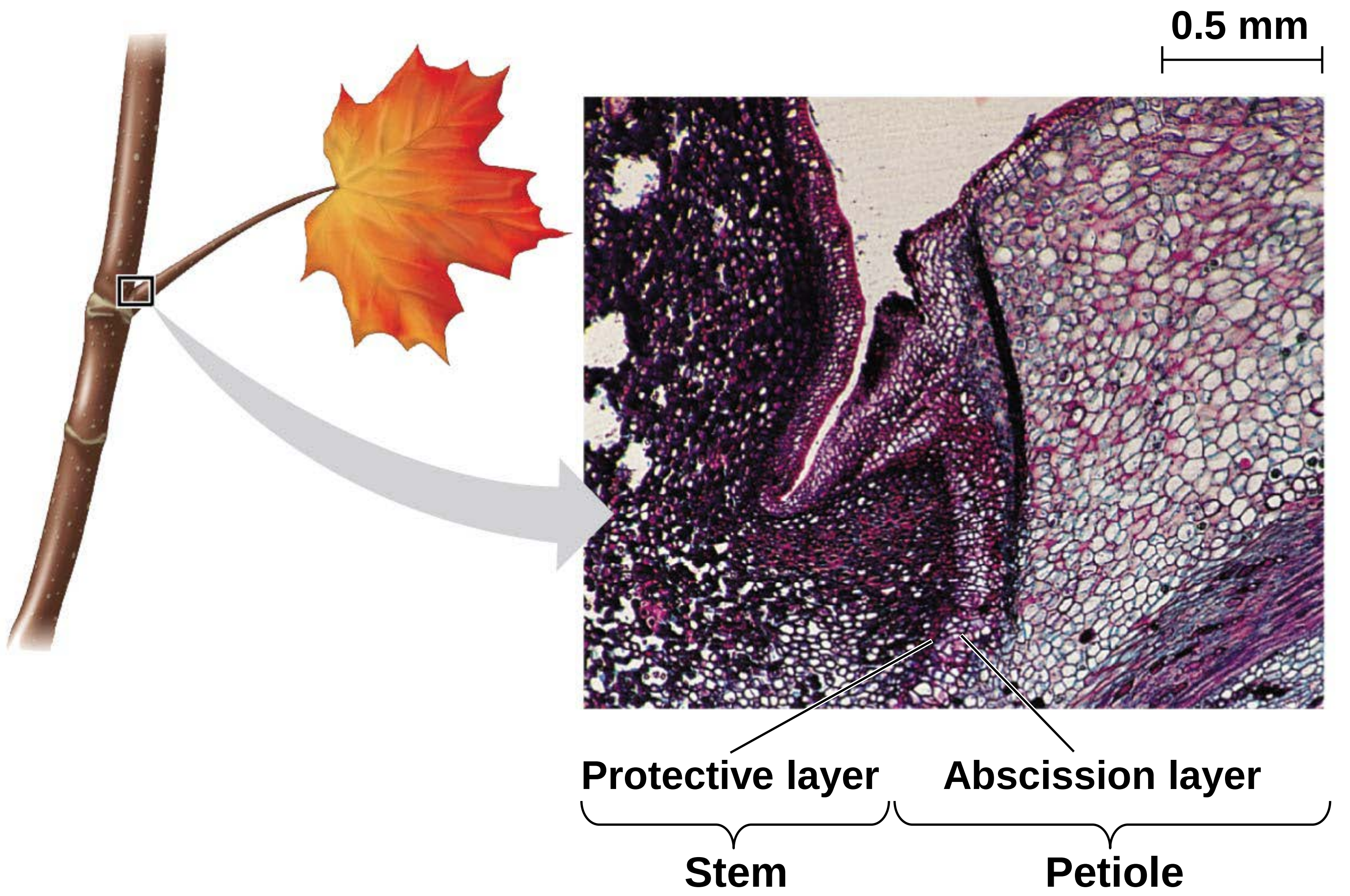
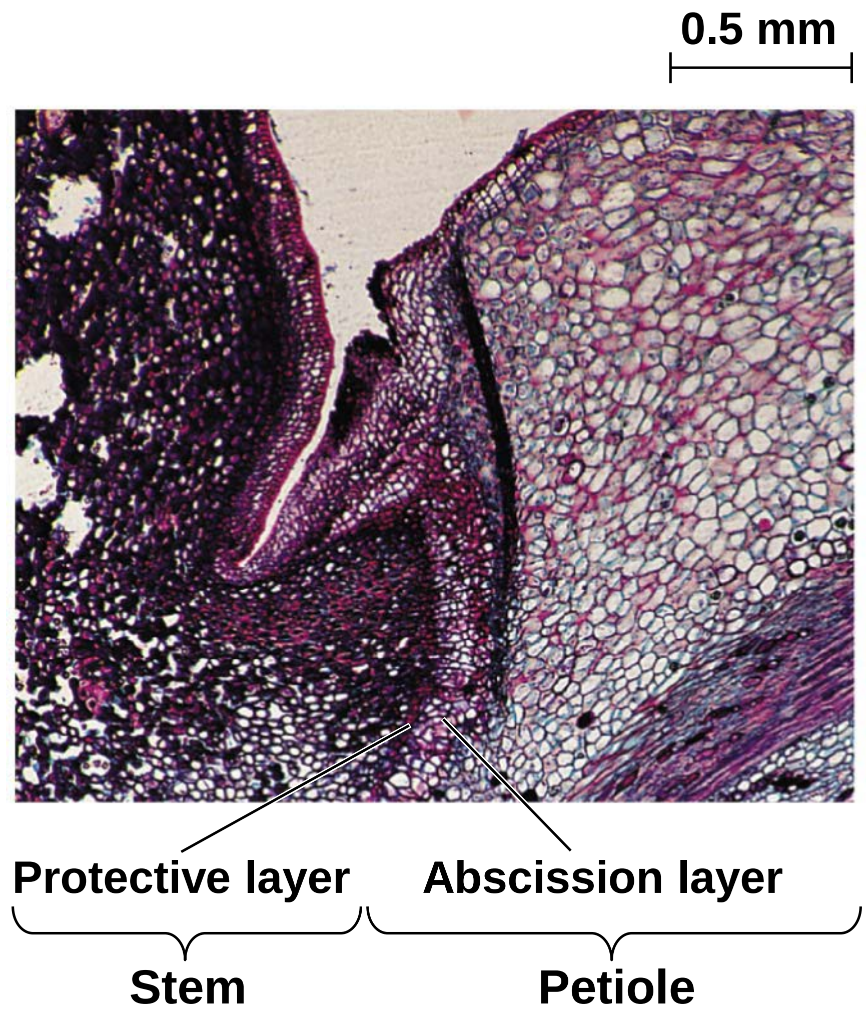


Figure 39.14a



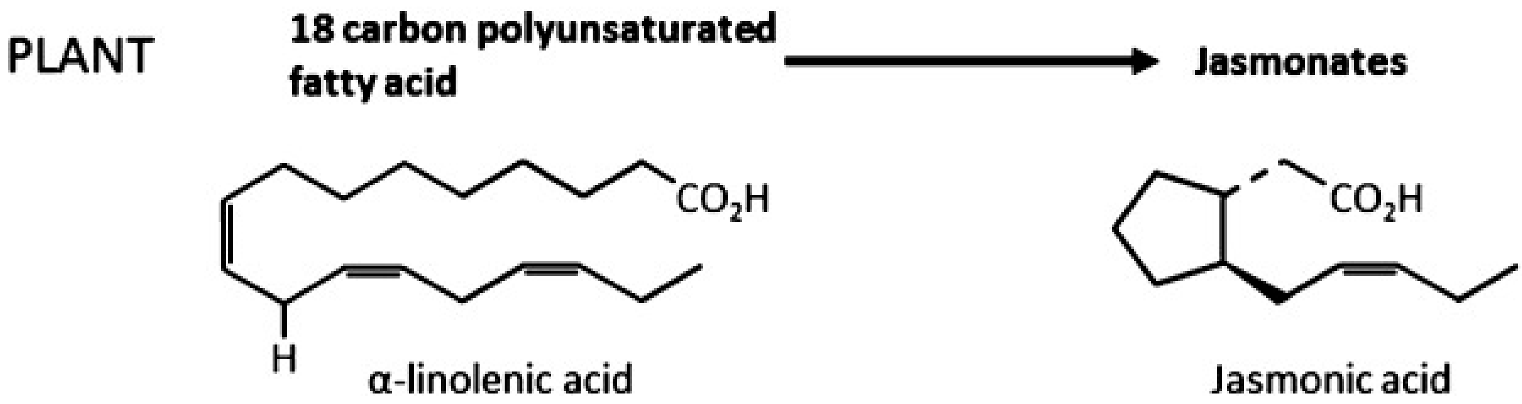
## Fruit Ripening

- 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

# *More Recently Discovered Plant Hormones*

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