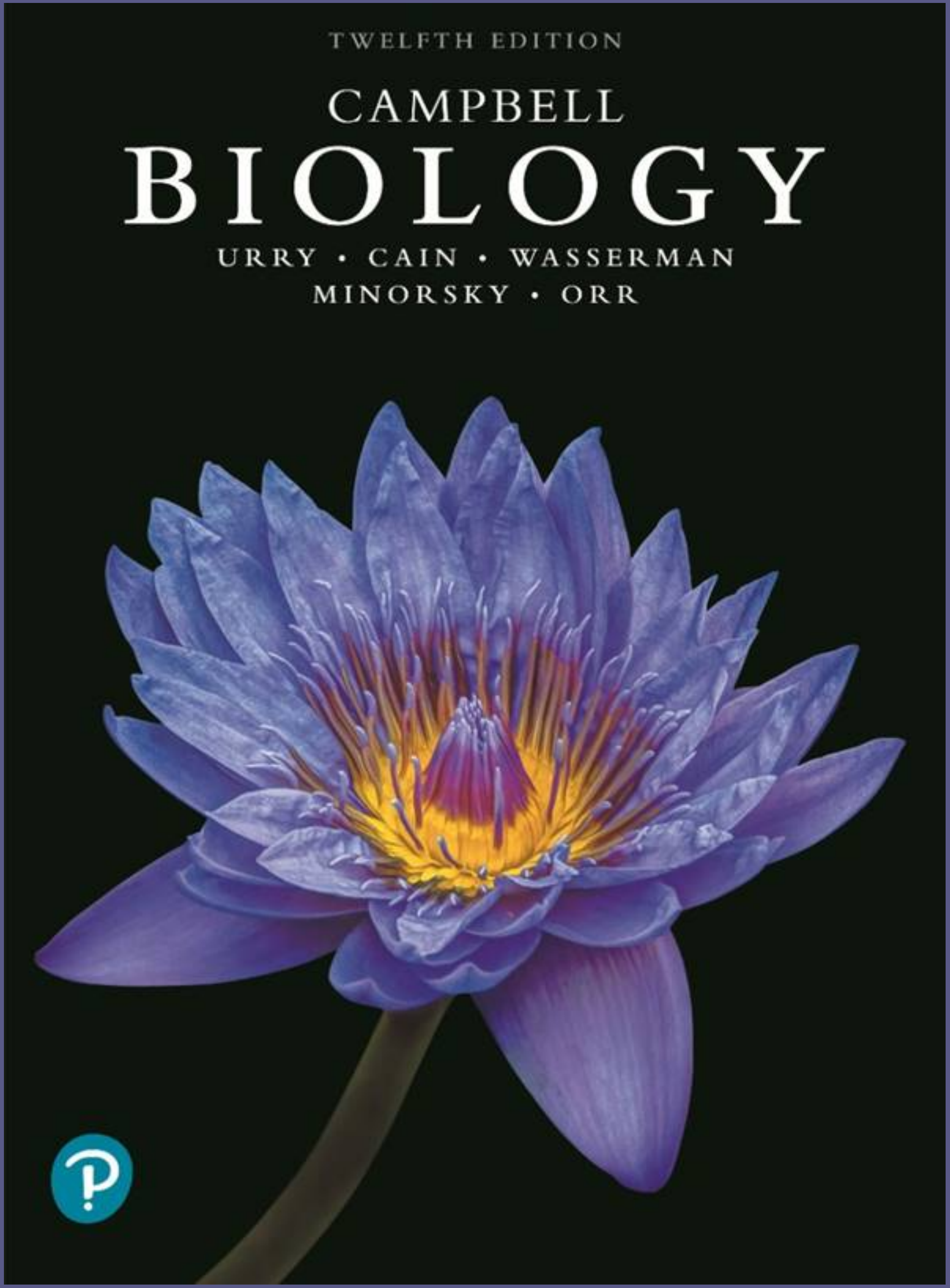


Chapter 36

Resource Acquisition and Transport in Vascular Plants

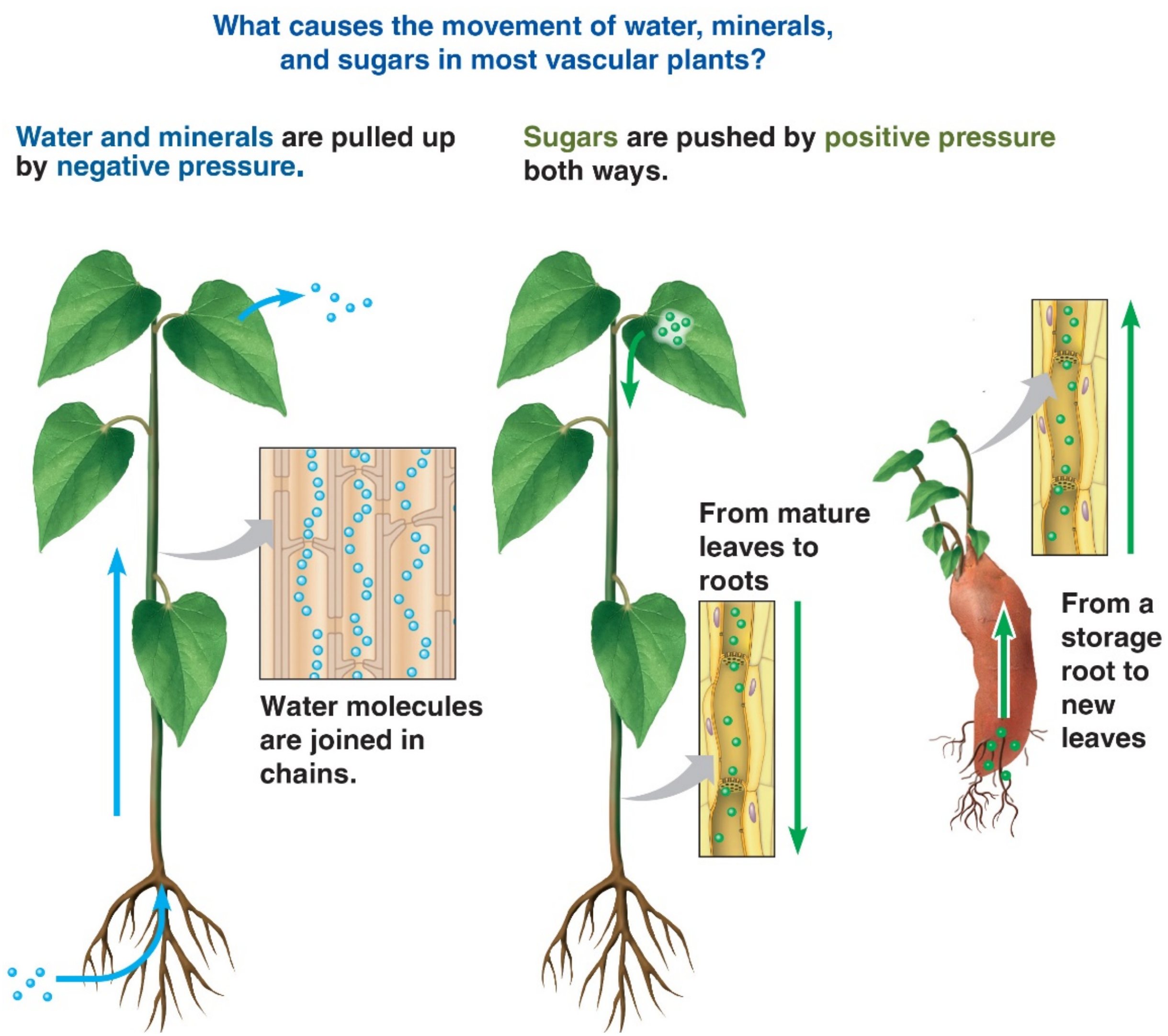
Lecture Presentations by
Nicole Tunbridge and
Kathleen Fitzpatrick

What causes the movement of water, minerals, and sugars in most vascular plants?

- Water and minerals are pulled up from the roots by negative pressure generated by evaporation from leaves
- Sugars are pushed by positive pressure from where they are produced or stored to where they are needed

Figure 36.1a

Figure 36.1b

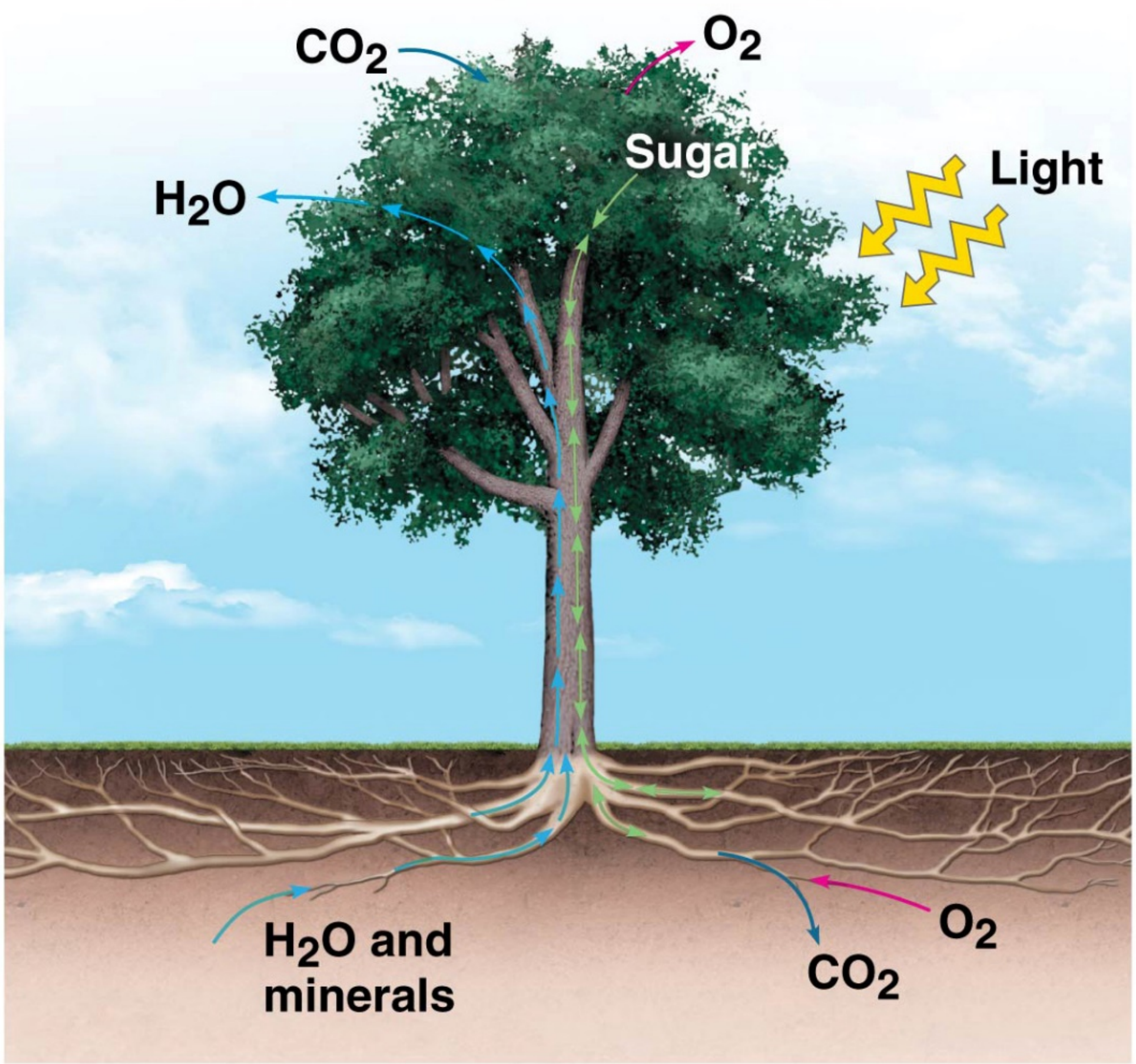

What causes the movement of water, minerals, and sugars in most vascular plants?
Water and minerals are pulled up by negative pressure.
Sugars are pushed by positive pressure both ways.
Water molecules are joined in chains.
From mature leaves to roots
From a storage root to new leaves

CONCEPT 36.1: Adaptations for acquiring resources were key steps in the evolution of vascular plants

- Algal ancestors of plants absorbed water, minerals, and CO_2 directly from the surrounding water
- Early nonvascular land plants lived in shallow water and had aerial shoots
- Natural selection favored taller plants with flat appendages, multicellular branching roots, and efficient transport

- Long distance transport of water, minerals and sugar was possible after the evolution of xylem and phloem
  - **Xylem** transports water and minerals from roots to shoots
  - **Phloem** transports photosynthetic products from where they are made to where they are needed

Figure 36.2



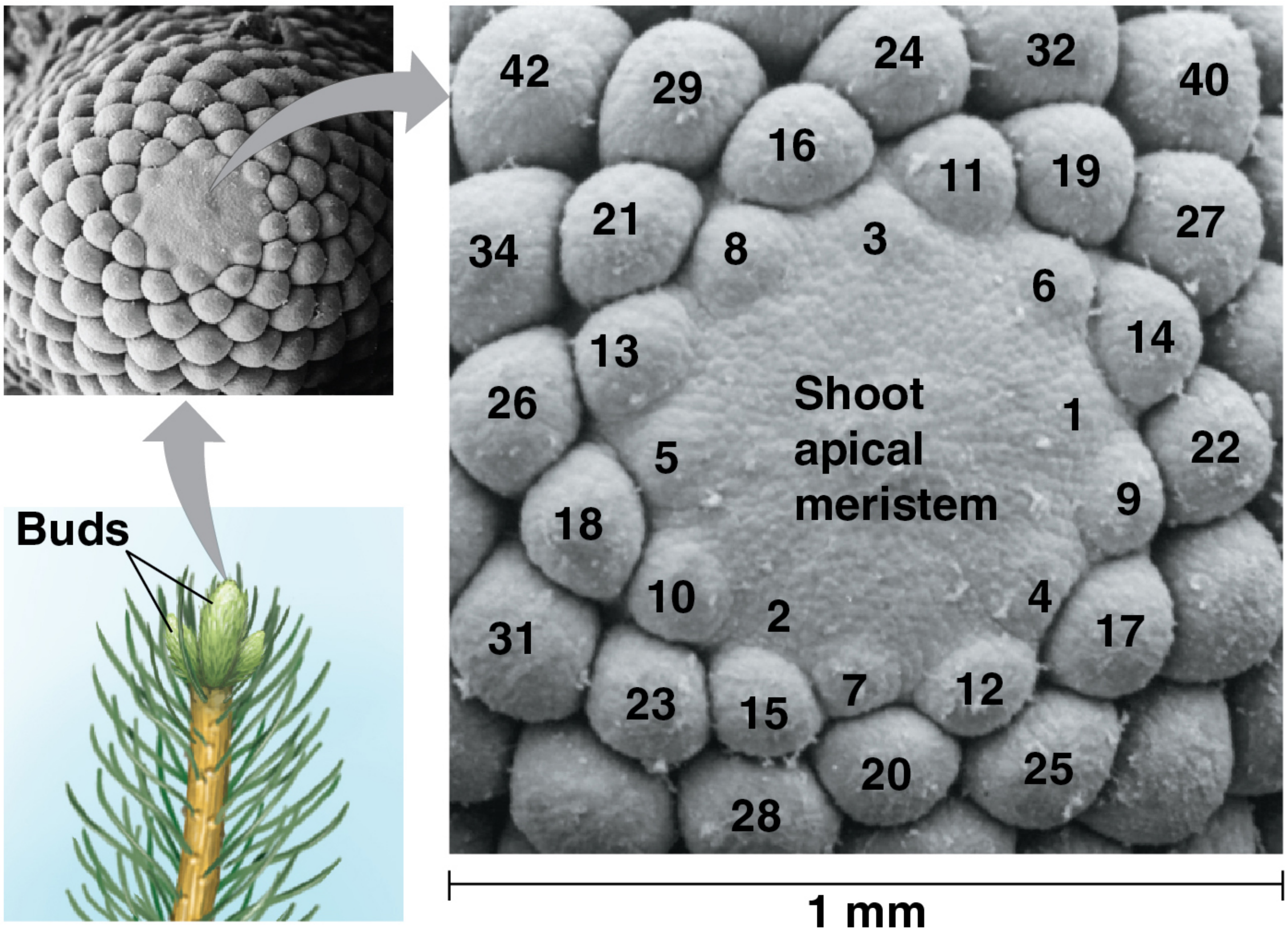
Shoot Architecture and Light Capture

- Stems transport water and nutrients and provide structural support for leaves
- Shoot length and branching pattern affect light capture; taller plants with more branches are better able access sunlight for photosynthesis
- There is a trade-off between height and branching; the more energy invested into branching, the less energy available for growth in height

- There is generally a positive correlation between water availability and leaf size
- The largest leaves are found in tropical rain forests, whereas the smallest are usually found in dry or very cold environments such as deserts

- **Phyllotaxy**, the arrangement of leaves on a stem, is a species-specific trait, important for light capture
  - Alternate, or spiral, phyllotaxy is when a species has one leaf per node
  - Opposite is when there are two leaves per node
  - Whorled is when there are more than two leaves per node
- Most angiosperms have alternate phyllotaxy with leaves arranged in a spiral at 137.5º angles

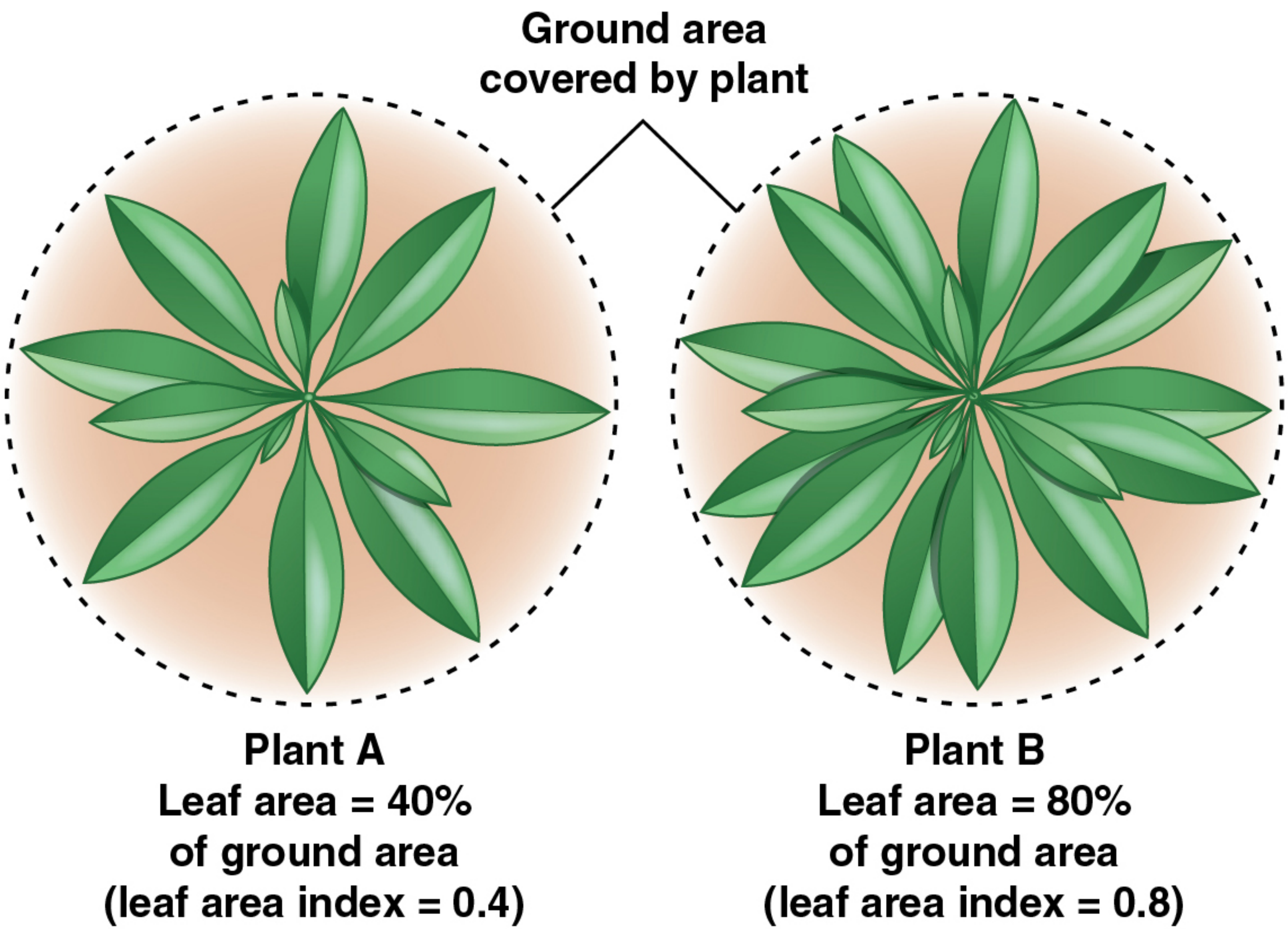
Figure 36.3


Buds
42
29
24
32
40
16
11
19
34
21
8
3
27
6
13
14
Shoot
apical
meristem
26
1
22
5
9
18
10
2
4
17
31
7
12
23
15
20
25
28
1 mm

- The total area of the leafy portions of all the plants in a community affects the productivity of each plant
- The rate of photosynthesis can drop below that of respiration in the lower, shaded leaves
- These nonproductive leaves undergo programmed cell death and drop, a process called *self-pruning*

- Plants that reduce self-shading capture more light
- *Leaf area index*, the ratio of total upper leaf surface of a plant or crop divided by the surface area of land on which it grows
- Leaf area indexes higher than 7 result in shading to the point that self-pruning occurs

Figure 36.4



Ground area
covered by plant
Plant A
Leaf area = 40%
of ground area
(leaf area index = 0.4)
Plant B
Leaf area = 80%
of ground area
(leaf area index = 0.8)

- Leaf orientation affects light absorption
- In low-light conditions, horizontal leaves capture more sunlight
- In sunny conditions, vertical leaves are less damaged by sun and allow light to reach lower leaves

The Photosynthesis–Water Loss Compromise

- Stomatal pores are necessary to allow diffusion of CO_2 into the photosynthetic tissues of leaves
- Over 90% of the water lost by plants is by evaporation from stomatal pores
- Shoot adaptations represent compromises between enhancing photosynthesis and minimizing water loss

Root Architecture and Acquisition of Water and Minerals

- Roots can respond to local changes in soil conditions to maximize nutrient uptake
  - In pockets of soil with high nitrate availability, roots branch extensively and increase production of proteins involved in nitrate transport and assimilation
  - Roots extend straight through low nitrate pockets instead of branching within them

- Roots from the same plant are less competitive with each other than with roots from different plants of the same species
  - For example, buffalo grass cuttings develop fewer, shorter roots in the presence of cuttings from the same plant than those from another buffalo grass plant

- Roots and the hyphae of soil fungi form mutualistic associations called **mycorrhizae**
- Mycorrhizal fungi increase the surface area for absorbing water and minerals, especially phosphate
- Mutualisms with fungi helped plants colonize land

CONCEPT 36.2: Different mechanisms transport substances over short or long distances

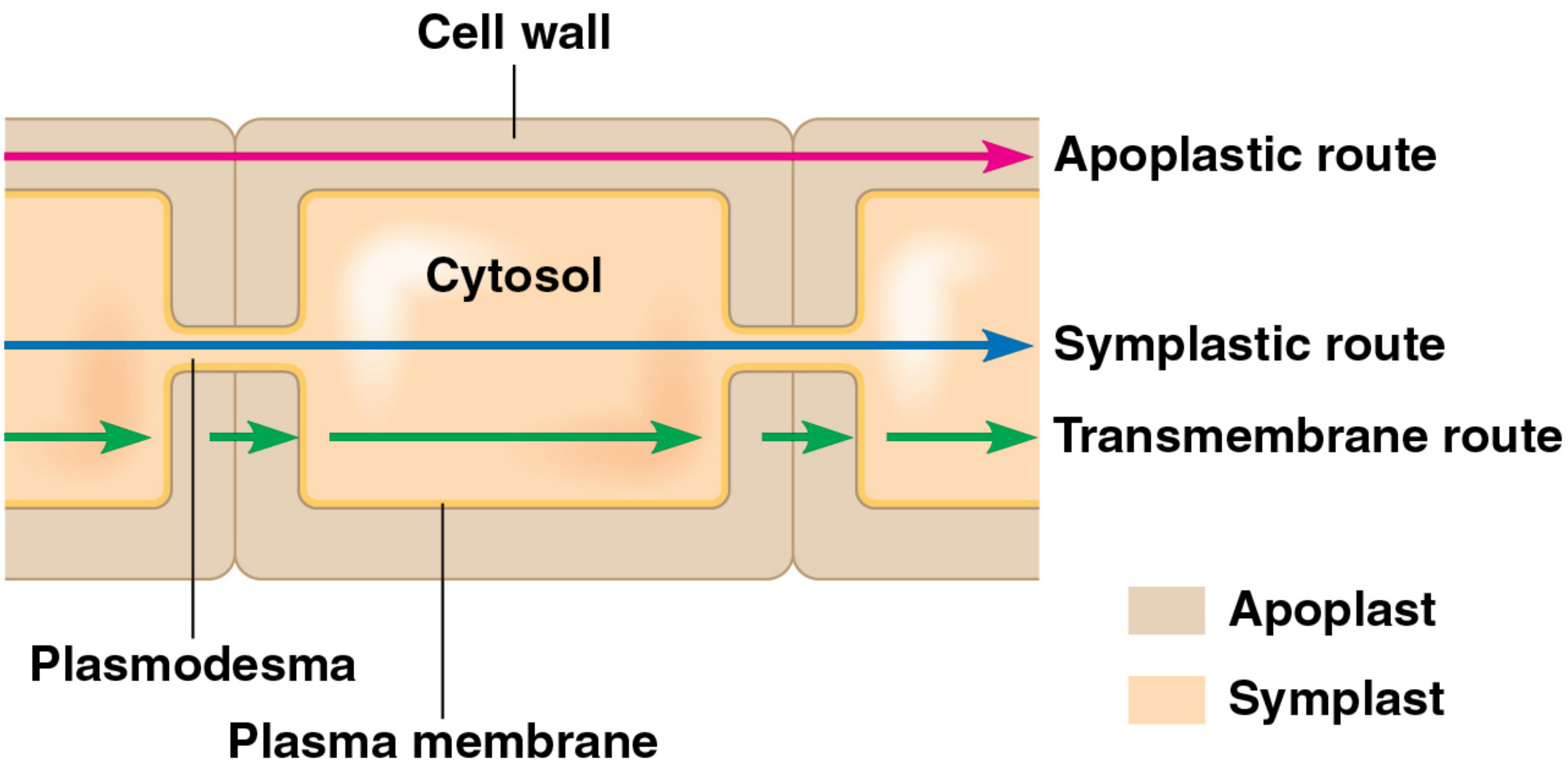
- Plants have two major transport pathways: the apoplast and the symplast

The Apoplast and Symplast: Transport Continuums

- The **apoplast** consists of everything external to the plasma membranes of living cells
  - It includes the cell walls, extracellular spaces, and the interior of dead cells such as vessel elements and tracheids
- The **symplast** consists of the cytosol of all the living cells in a plant, as well as the plasmodesmata

- Three transport routes for water and solutes include
  - The apoplastic route, outside cells through cell walls and extracellular spaces
  - The symplastic route, through the cytosol after crossing one plasma membrane to enter a cell
  - The transmembrane route, where water and solutes repeatedly cross plasma membranes as they pass from cell to cell

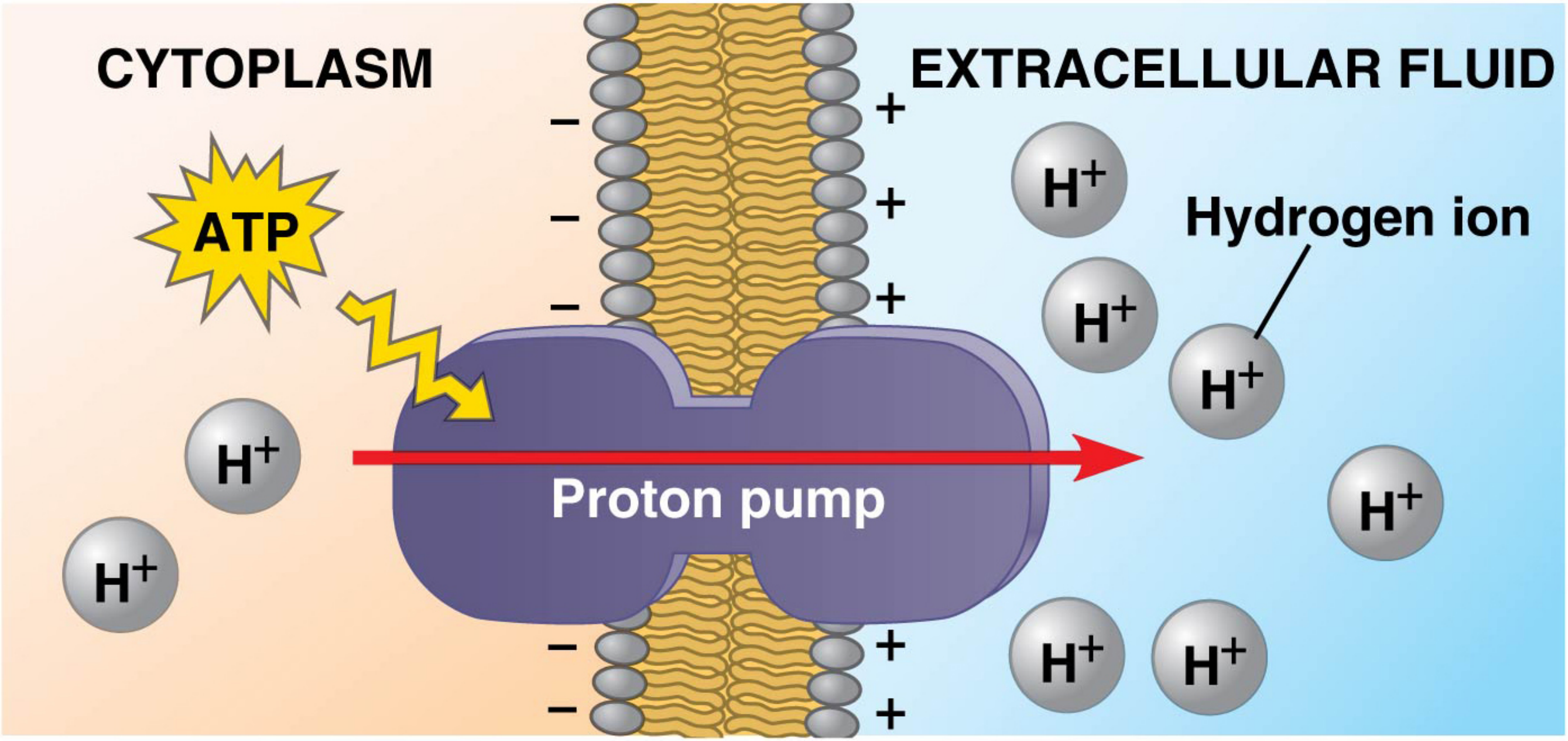
Figure 36.5


Cell wall
Apoplastic route
Cytosol
Symplastic route
Transmembrane route
Apoplast
Symplast
Plasmodesma
Plasma membrane

Short-Distance Transport of Solutes Across Plasma Membranes

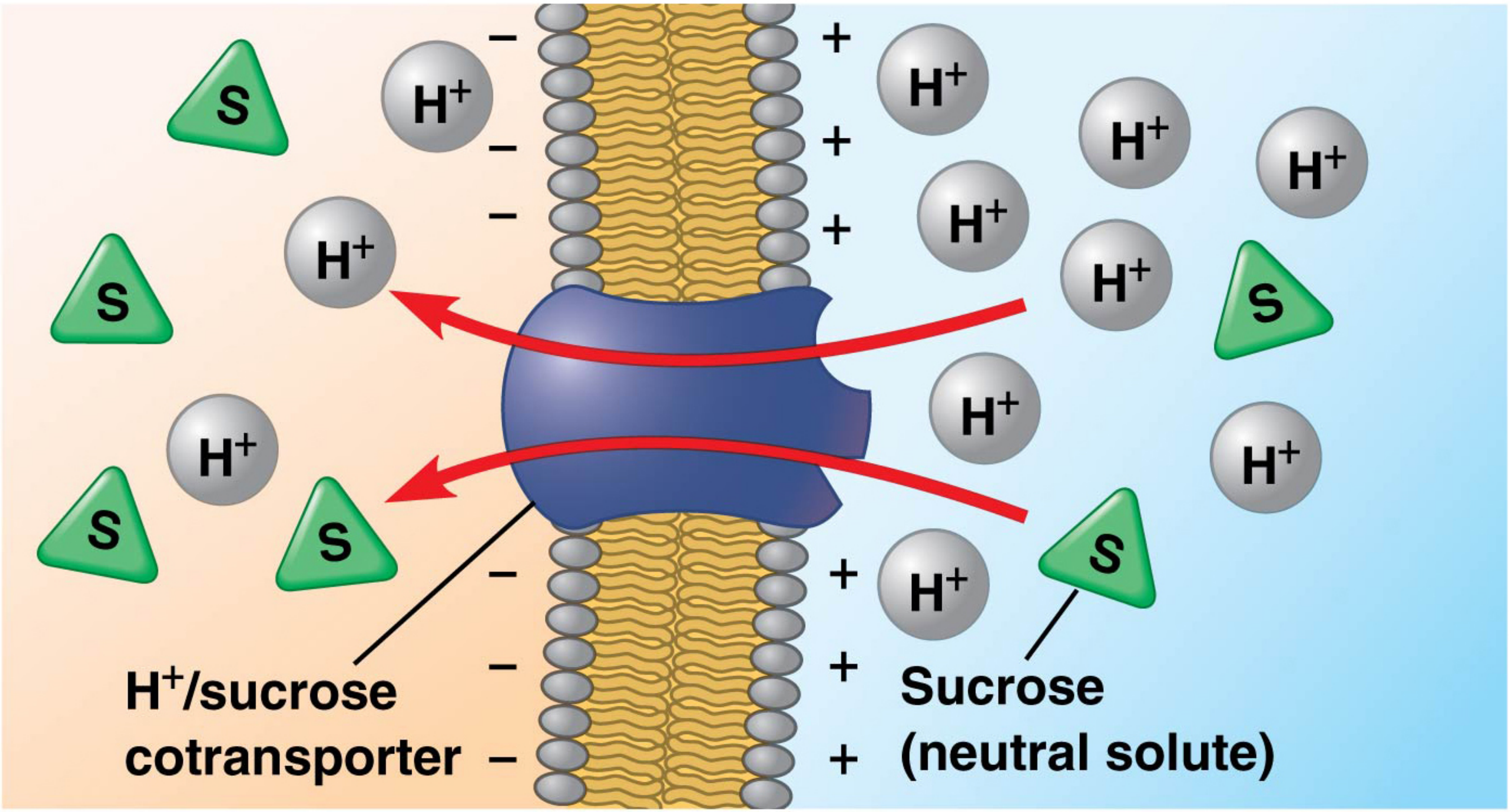
- Plasma membrane permeability controls short-distance movement of substances
- Plants have the same types of pumps and transport proteins as animals, with some specific differences
  - In plants, membrane potential is established through pumping H^+ by proton pumps
  - In animals, membrane potential is established through pumping Na^+ by sodium-potassium pumps

Figure 36.6

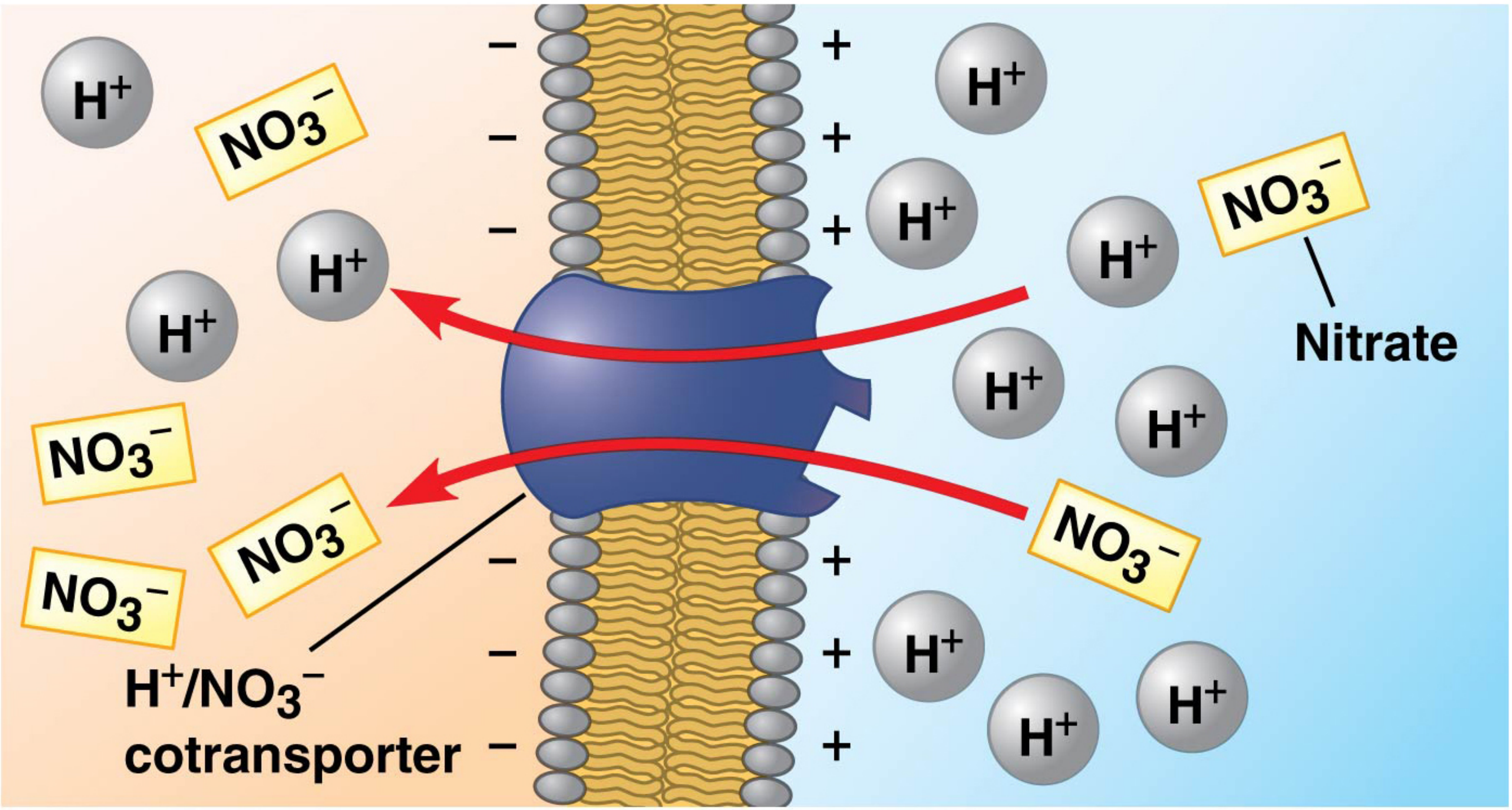


(a) H^+ and membrane potential

- Cells use the energy of electrochemical gradients and membrane potential to drive the active transport of other solutes
  - In plant cells, H^+ gradients are used to cotransport sucrose and nitrate (NO_3^-)
  - In animal cells, Na^+ is typically cotransported rather than H^+

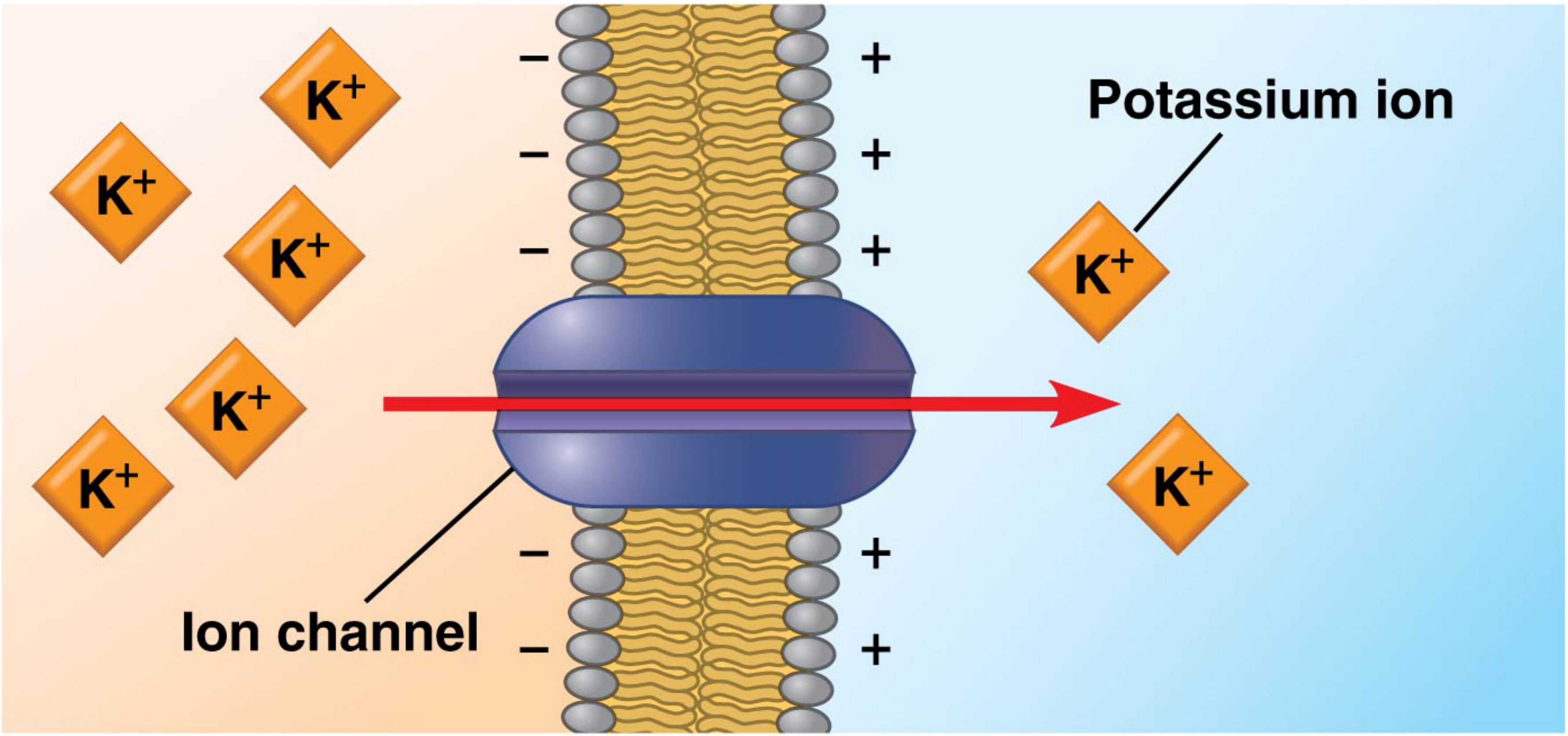


(b) H^+ and cotransport of neutral solutes



(c) H^+ and cotransport of ions

- Plant cell membranes have ion channels that allow only certain ions to pass
  - For example, potassium ion channels in guard cells facilitate opening and closing of stomata



(d) Ion channels

Short-Distance Transport of Water Across Plasma Membranes

- **Osmosis** is the diffusion of free water—water not bound by solutes or surfaces—across a cell membrane
- **Water potential** is the physical property that predicts the direction of water flow across a membrane
- The effects of solute concentration and physical pressure are included in water potential

- Free water flows from regions of higher water potential to regions of lower water potential
- *Potential* refers to water's capacity to perform work
  - For example, water moving into a cell from a solution of higher water potential causes the cell to expand and exert force on its surroundings

- Water potential is denoted by Ψ and measured in a unit of pressure called the **megapascal** (MPa)
- $\Psi = 0$ MPa for pure water at sea level and room temperature
- The internal pressure of a living plant cell is about 0.5 MPa, or about twice the air pressure in a car tire

How Solutes and Pressure Affect Water Potential

- Solute concentration and physical pressure are the major determinants of water potential in plants
- This is expressed by the water potential equation: $\Psi = \Psi_S + \Psi_P$, where
  - Ψ = water potential
  - Ψ_S = solute potential
  - Ψ_P = pressure potential

- The **solute potential** (Ψ_S), or osmotic potential, of a solution is directly proportional to its molarity
- The Ψ_S of pure water is 0
- As solute concentration increases, Ψ_S becomes more negative and Ψ is reduced

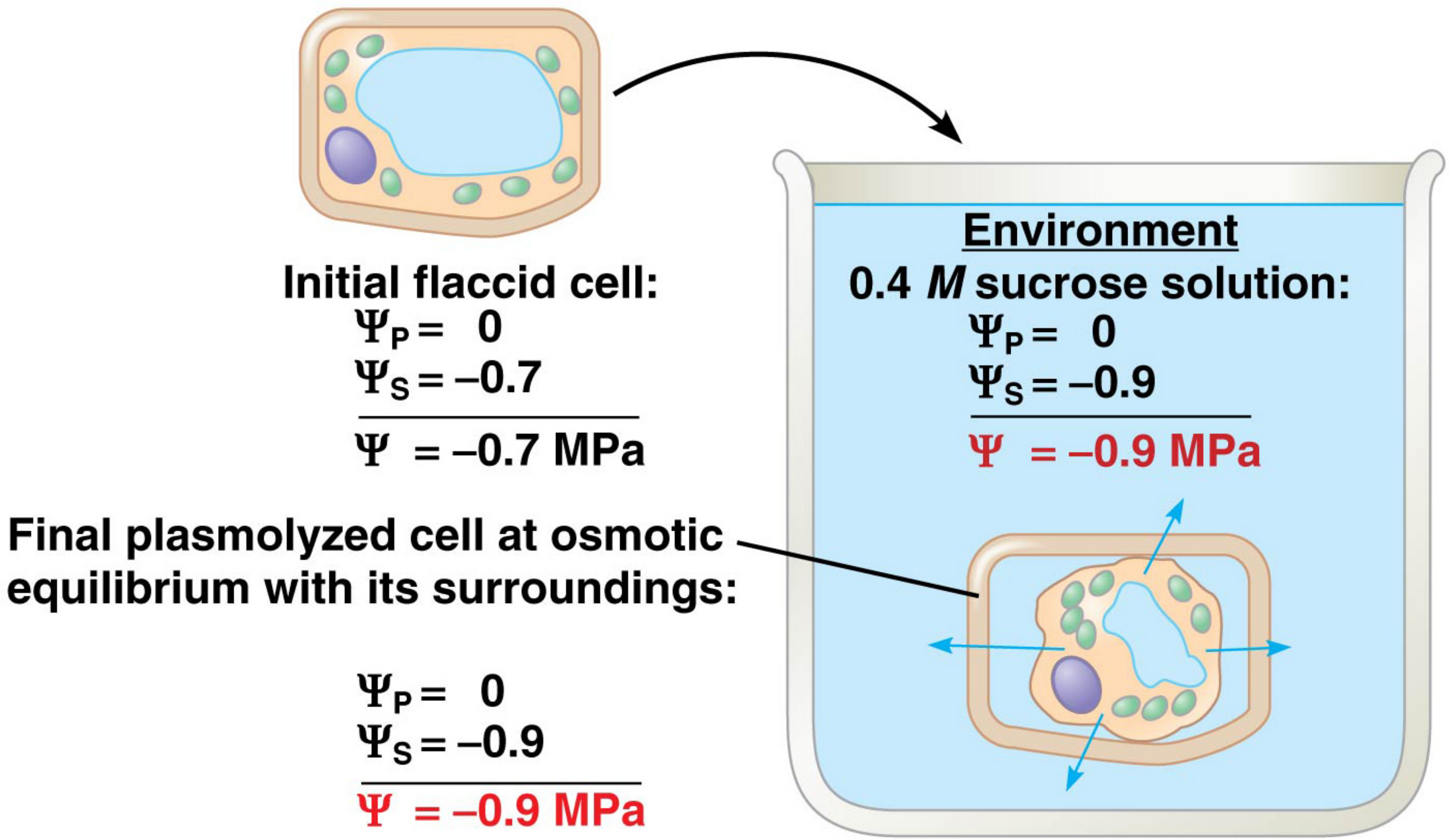
- **Pressure potential** (Ψ_P) is the physical pressure on a solution
- Pressure potential can be positive or negative
  - For example, solution withdrawn by a syringe is under negative pressure; it is under positive pressure when it is being expelled by the syringe
- The water in living cells is usually under positive pressure

- The **protoplast** is the living part of the cell, which also includes the plasma membrane
- **Turgor pressure** is the positive pressure exerted by the protoplast against the cell wall

Water Movement Across Plant Cell Membranes

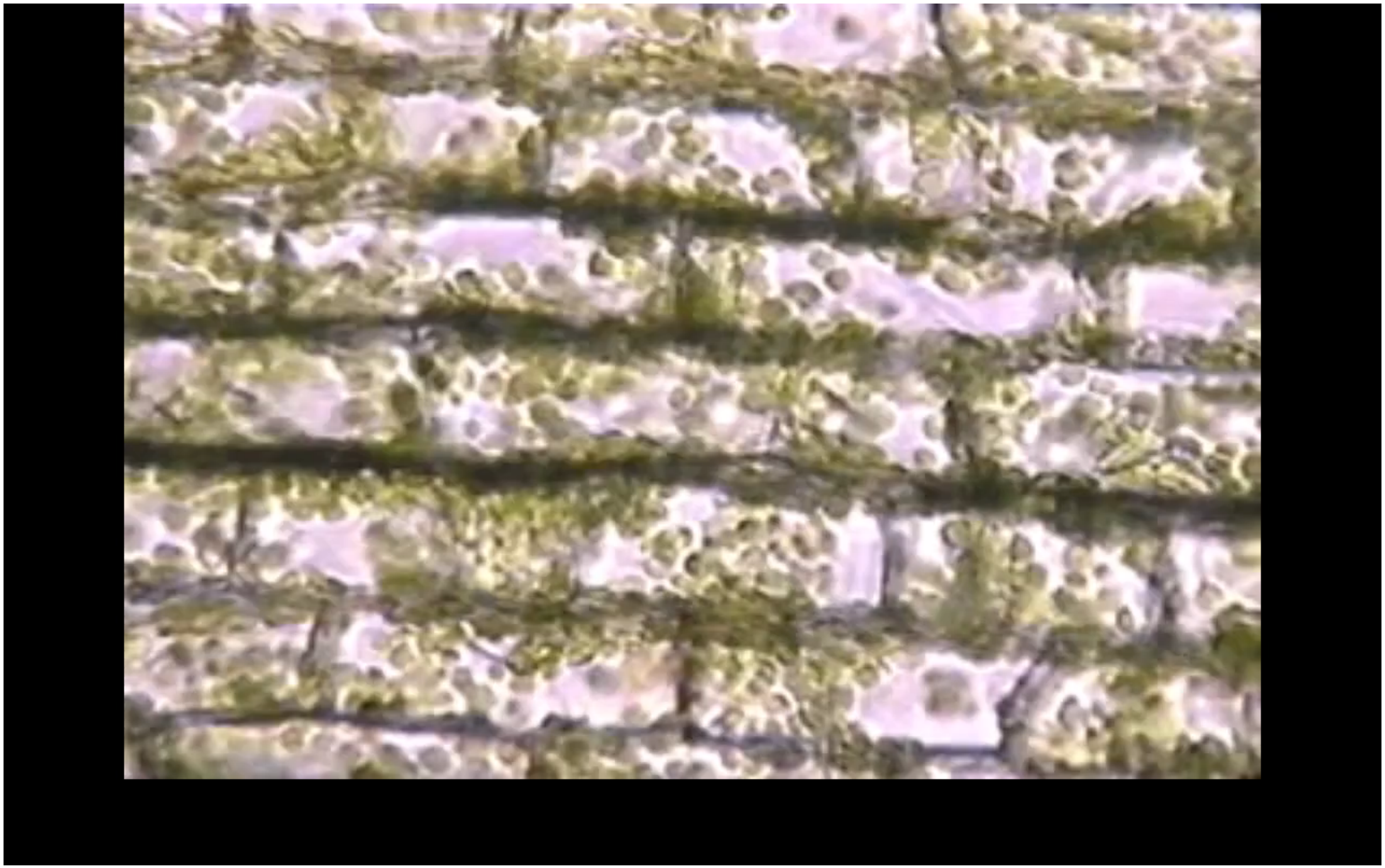
- Water potential affects uptake and loss of water by plant cells
- If a **flaccid** (limp) cell is placed in an environment with a higher solute concentration, the cell will lose water and undergo plasmolysis
- **Plasmolysis** occurs when the protoplast shrinks and pulls away from the cell wall

Figure 36.7



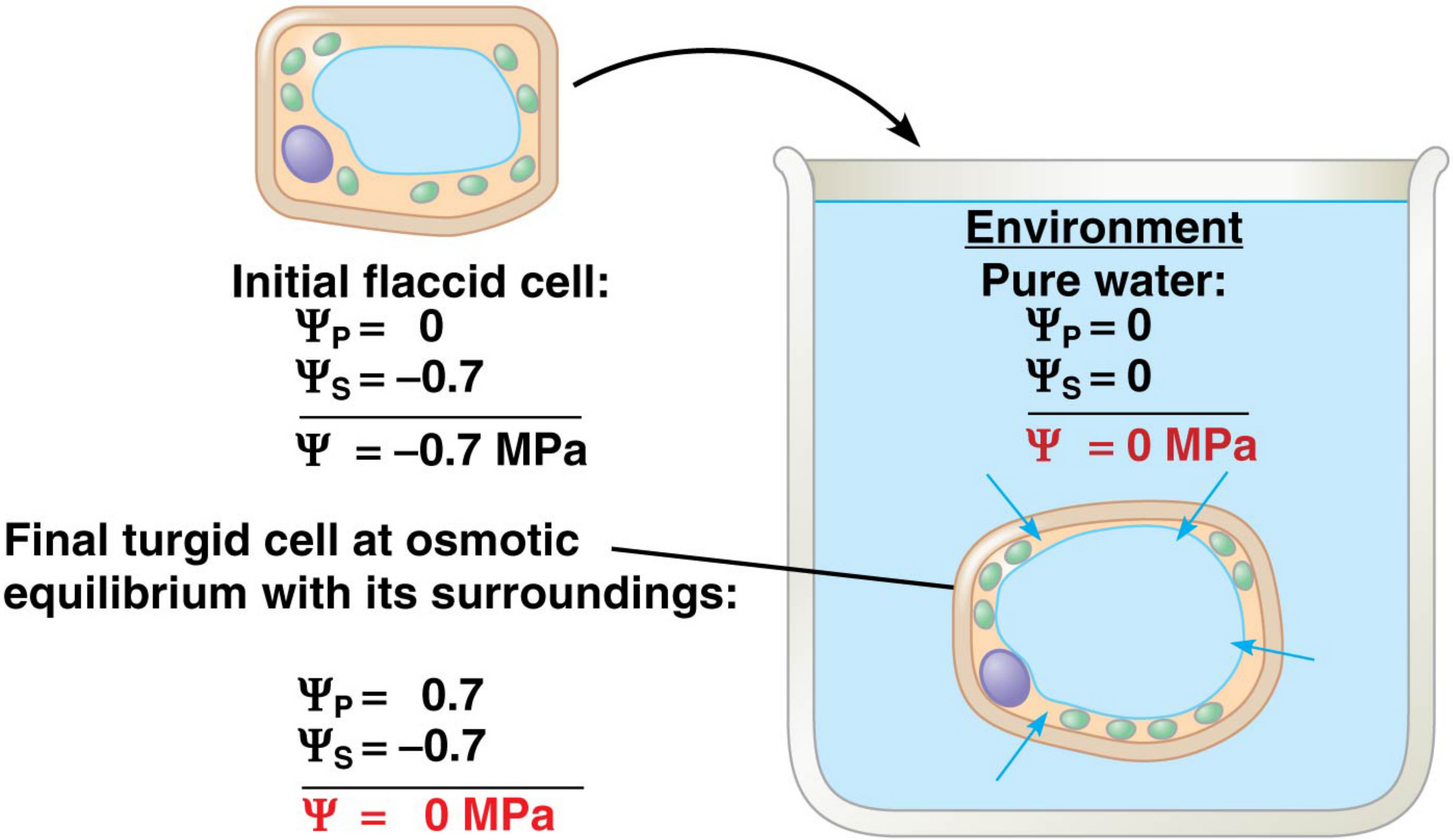
(a) Initial conditions: cellular Ψ > environmental Ψ

Video: Plasmolysis



- If a flaccid cell is placed in a solution with a lower solute concentration, the cell will gain water and become **turgid**

Figure 36.7



(b) Initial conditions: cellular Ψ < environmental Ψ

Video: Turgid *Elodea*

- Turgor loss in plants causes **wilting**, which can be reversed when the plant is watered

Figure 36.UN01

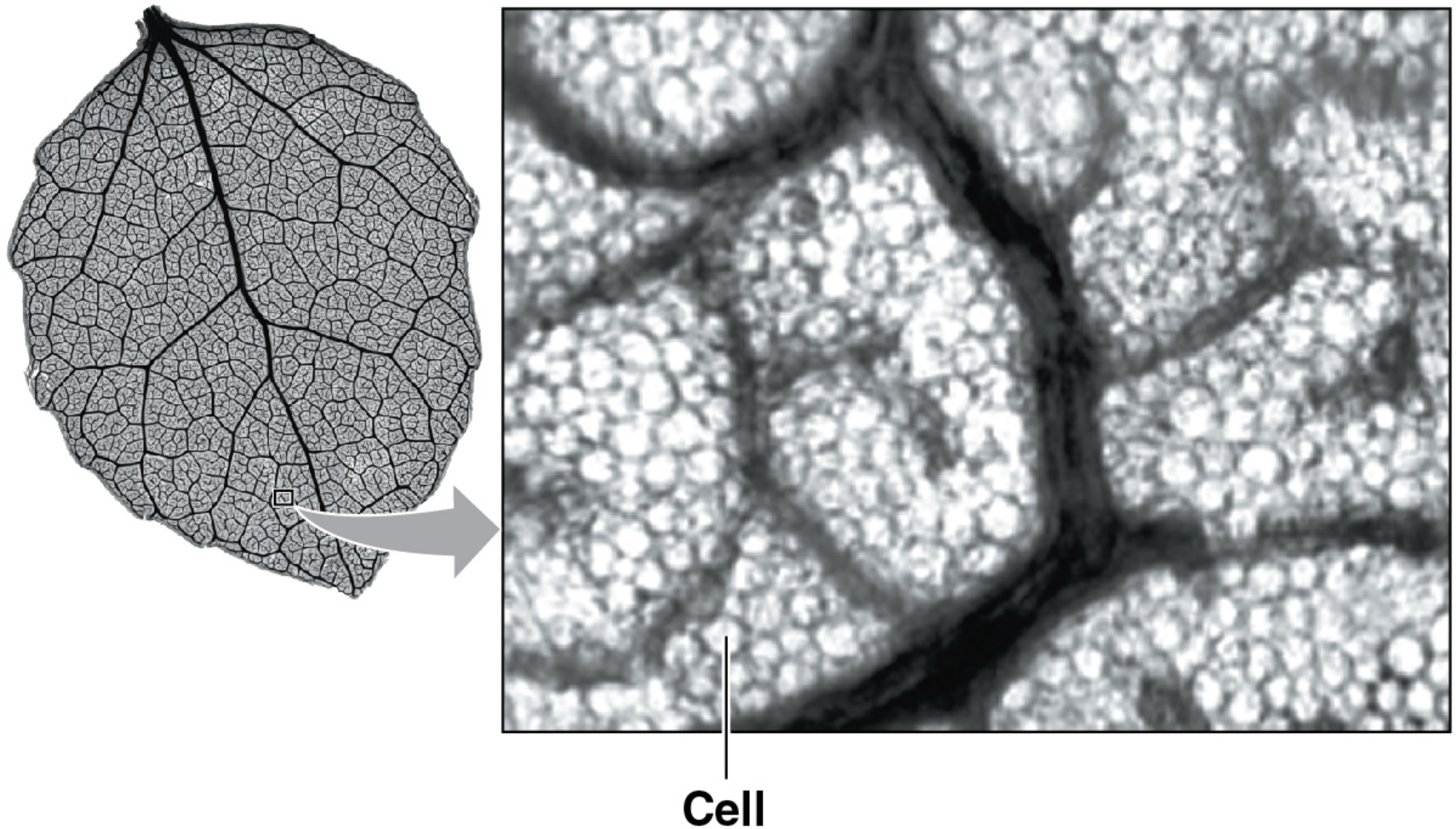
Aquaporins: Facilitating Diffusion of Water

- Water molecules are small enough to diffuse directly across the plasma membrane, but the rate of diffusion is too fast to be completely unaided
- **Aquaporins** are transport proteins in the cell membrane that facilitate the passage of water
- Opening and closing of aquaporins affect the rate of osmotic water movement across the membrane

Long-Distance Transport: The Role of Bulk Flow

- Efficient long-distance transport of fluid requires **bulk flow**, the movement of a fluid driven by a pressure gradient
- Water and solutes move together through the tracheids and vessel elements of the xylem and the sieve-tube elements of the phloem
- The branching veins in leaves ensure that all cells are within a few cells of the vascular tissue

Figure 36.8



- Bulk flow is enhanced by the structural adaptations of xylem and phloem cells
  - Mature tracheids and vessel elements have no cytoplasm, whereas sieve-tube elements have cytoplasm, but contain few organelles
  - Perforation plates connect vessel elements, and porous sieve plates connect sieve-tube elements

- Bulk flow is enhanced by the structural adaptations of xylem and phloem cells
  - Mature tracheids and vessel elements have no cytoplasm, whereas sieve-tube elements have cytoplasm, but contain few organelles
  - Perforation plates connect vessel elements, and porous sieve plates connect sieve-tube elements

- Diffusion, active transport, and bulk flow act together to transport resources throughout the plant

CONCEPT 36.3: Transpiration drives the transport of water and minerals from roots to shoots via the xylem

- Plants move large volumes of water from their roots to shoots every day

Absorption of Water and Minerals by Root Cells

- Most water and mineral absorption occurs near root tips, where root hairs are located and the epidermis is permeable to water
- Root hairs account for much of the surface area of roots
- After soil solution enters the roots, the extensive surface area of cortical cell membranes enhances uptake of water and selected minerals

- Active transport enables essential minerals to accumulate at much higher concentrations in roots compared to the surrounding soil

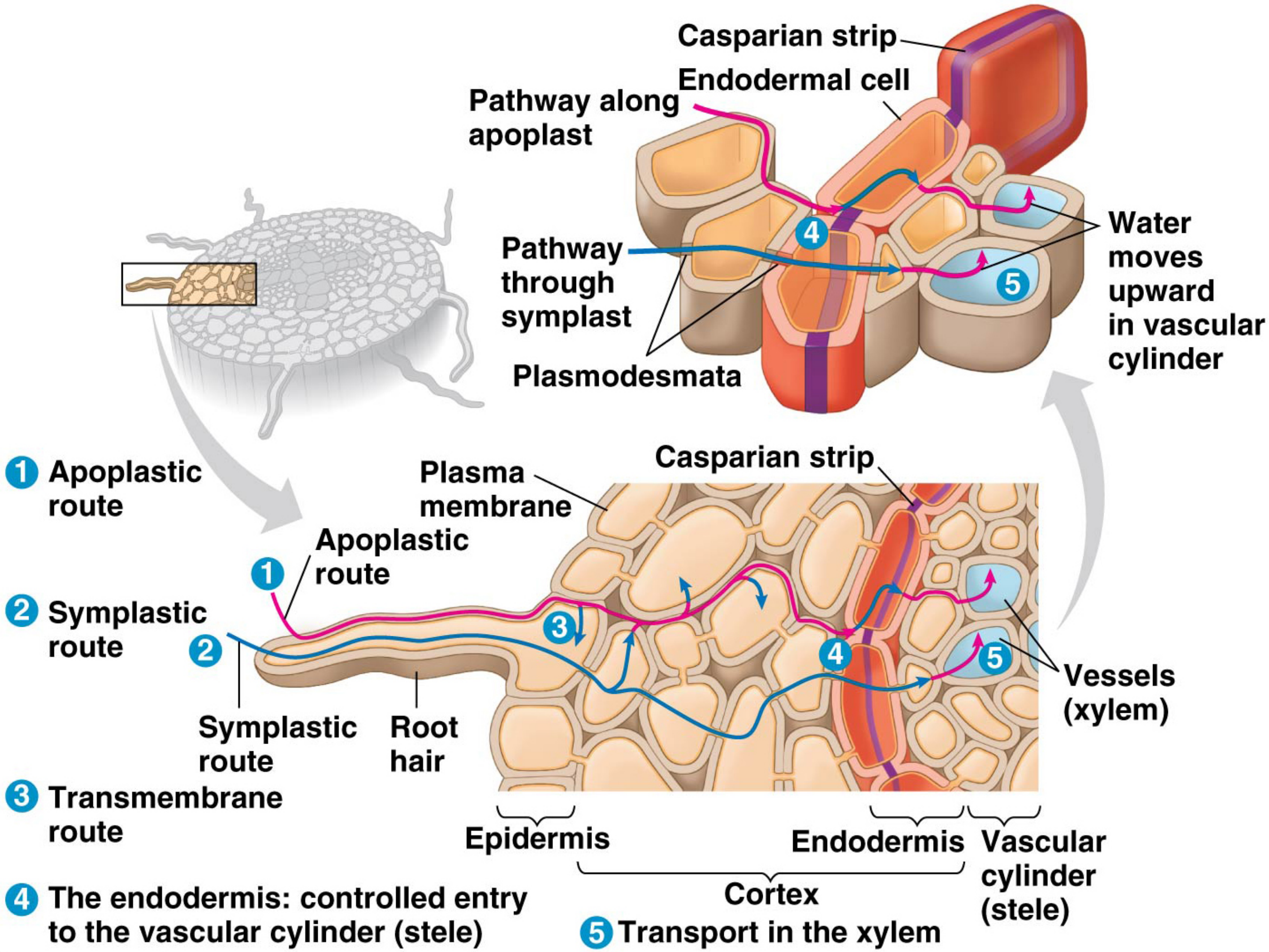
Transport of Water and Minerals into the Xylem

- The **endodermis** is the innermost layer of cells in the root cortex
- It surrounds the vascular cylinder and is the last checkpoint for selective passage of minerals from the cortex into the vascular tissue

- The waxy **Casparian strip** of the endodermal wall blocks apoplastic transfer of minerals from the cortex to the vascular cylinder
- Water and minerals in the apoplast must cross the plasma membrane of an endodermal cell to enter the vascular cylinder
- The selectively permeable membrane prevents the uptake of toxins or unneeded materials

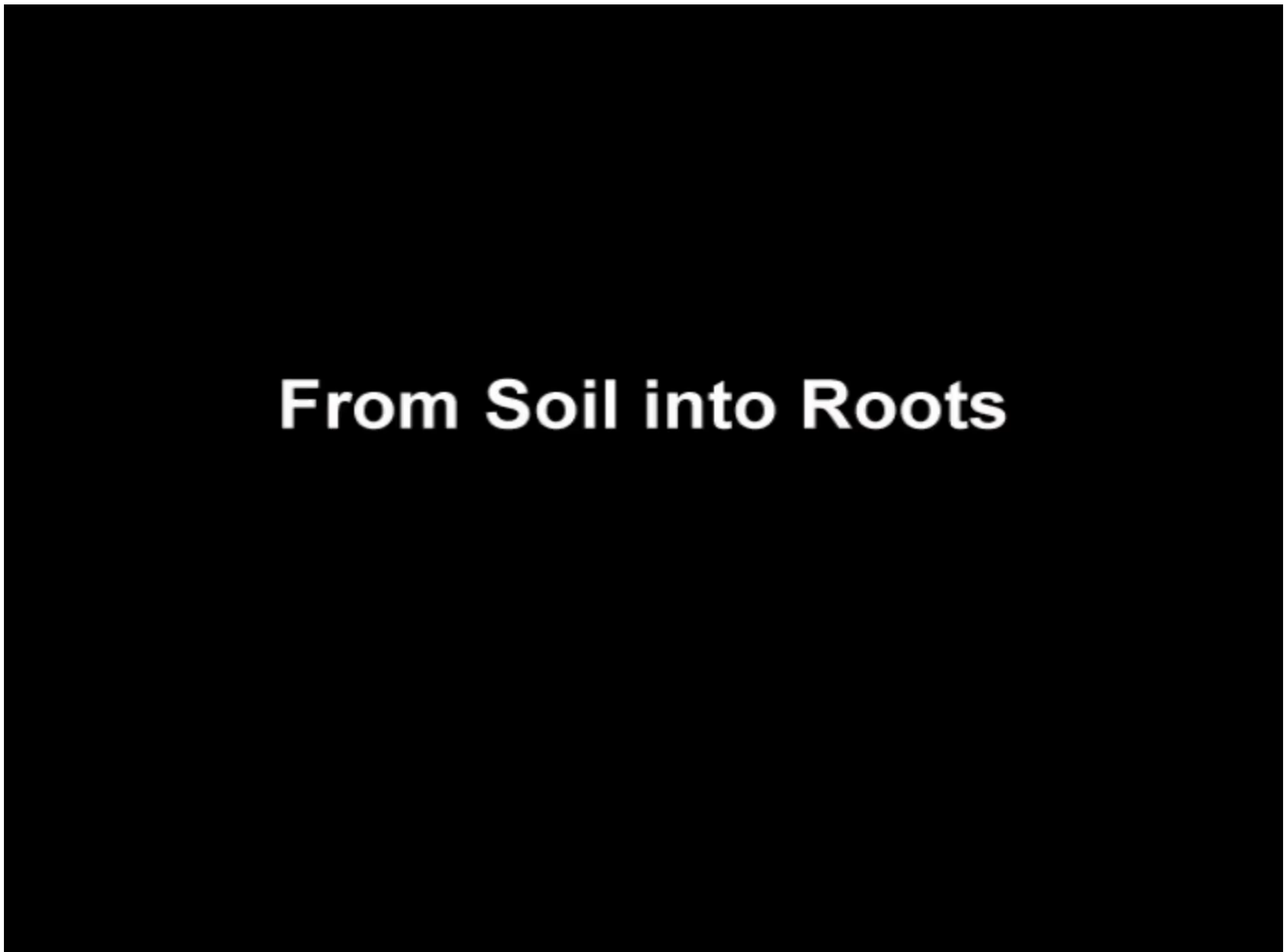
- The endodermis regulates and transports needed minerals from the soil into the xylem
- Endodermal cells discharge water and minerals from their protoplasts into their own cell walls
- Diffusion and active transport are involved in this movement from symplast to apoplast
- Once in the apoplast, water and minerals can enter the tracheids and vessel elements

Figure 36.9



Casparian strip
Endodermal cell
Pathway along apoplast
Pathway through symplast
Plasmodesmata
4
5
Water moves upward in vascular cylinder
1 Apoplastic route
2 Symplastic route
3 Transmembrane route
4 The endodermis: controlled entry to the vascular cylinder (stele)
5 Transport in the xylem
Plasma membrane
Casparian strip
Apoplastic route
Symplastic route
Root hair
Vessels (xylem)
Epidermis
Endodermis
Vascular cylinder (stele)
Cortex

Figure Walkthrough BioFlix® Animation: Water Transport from Soil into Roots



Bulk Flow Transport via the Xylem

- **Xylem sap** containing water and dissolved minerals is transported from roots to leaves by bulk flow
- Peak velocities in transport of xylem sap can range from 15 to 45 m/hr for some trees
- The transport of xylem sap involves **transpiration**, the evaporation of water from a plant's surface
- Transpired water is replaced as water travels up from the roots

Pushing Xylem Sap: Root Pressure

- At night, root cells lower water potential by actively pumping mineral ions into the xylem
- Water flows in from the root cortex, generating **root pressure**, a push of xylem sap
- Root pressure sometimes results in **guttation**, the exudation of water droplets on tips or edges of leaves

Figure 36.10

- Positive root pressure is too weak to overcome the gravitational force of the water column in the xylem
- In most plants, root pressure is only a minor mechanism driving the ascent of xylem sap
- Xylem sap is mainly pulled up, rather than pushed from below by root pressure

Pulling Xylem Sap: The Cohesion-Tension Hypothesis

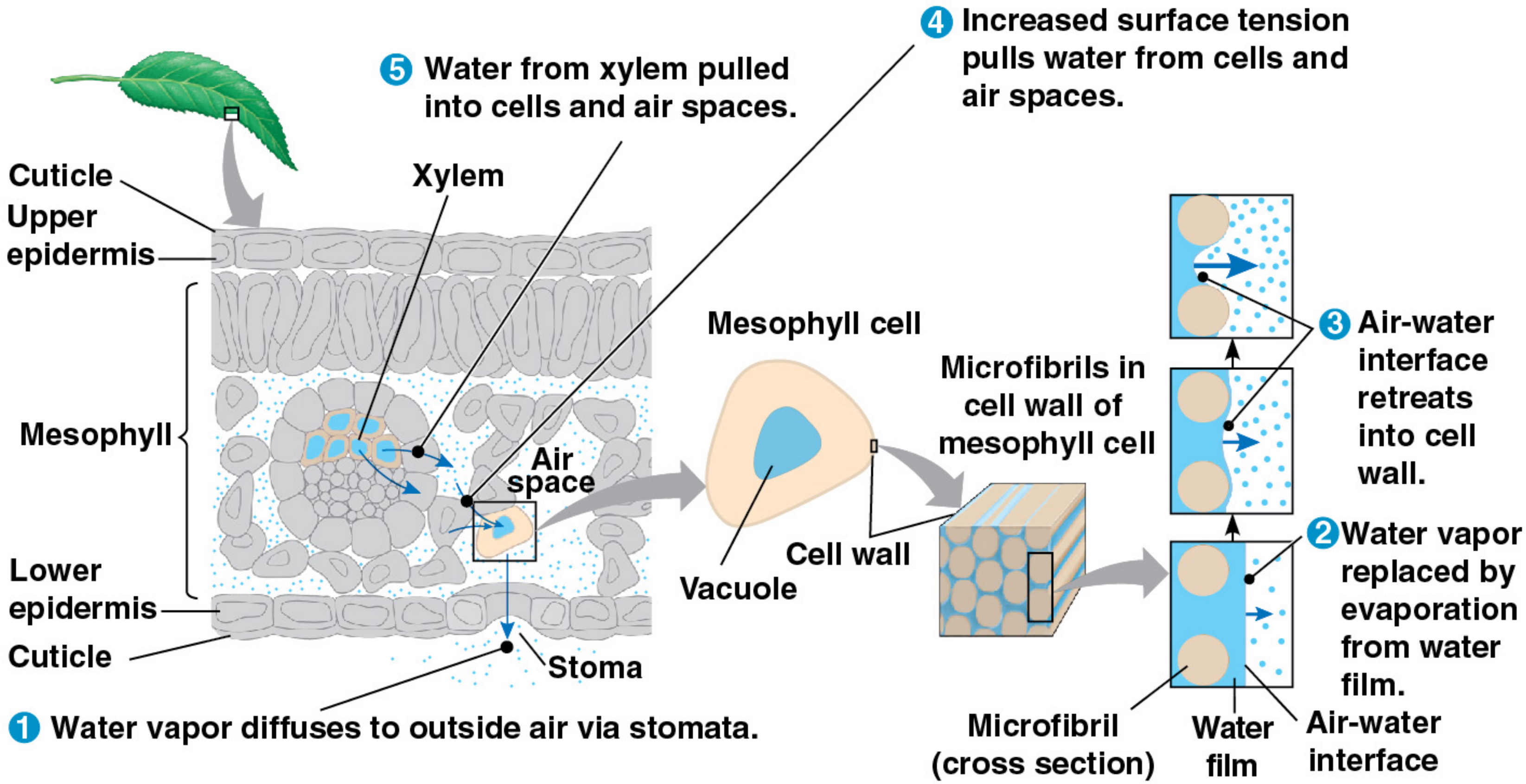
- According to the **cohesion-tension hypothesis**, transpiration provides the pull for the ascent of xylem sap and water cohesion transmits this pull along the entire length of the xylem from shoots to roots
- Xylem sap is normally under negative pressure, or tension

Transpirational Pull

- Water vapor in the air spaces of a leaf diffuses down its water potential gradient and exits the leaf via stomata
- As water evaporates, the air-water interface retreats into the mesophyll cell walls
- The surface tension of water at the air-water interface creates a negative pressure potential

- Negative pressure potential lowers water potential
- Water molecules are pulled from more hydrated areas of the leaf by the negative pressure potential created at the air-water interface
- The cohesion of water molecules transfers the pulling forces to the water in the xylem
- The transpirational pull on xylem sap is transmitted all the way from the leaves to the roots

Figure 36.11



4 Increased surface tension pulls water from cells and air spaces.
5 Water from xylem pulled into cells and air spaces.
Cuticle
Upper epidermis
Xylem
Mesophyll
Air space
Lower epidermis
Cuticle
Stoma
1 Water vapor diffuses to outside air via stomata.
Mesophyll cell
Vacuole
Cell wall
Microfibrils in cell wall of mesophyll cell
3 Air-water interface retreats into cell wall.
2 Water vapor replaced by evaporation from water film.
Microfibril (cross section)
Water film
Air-water interface

BioFlix® Animation: Transpiration

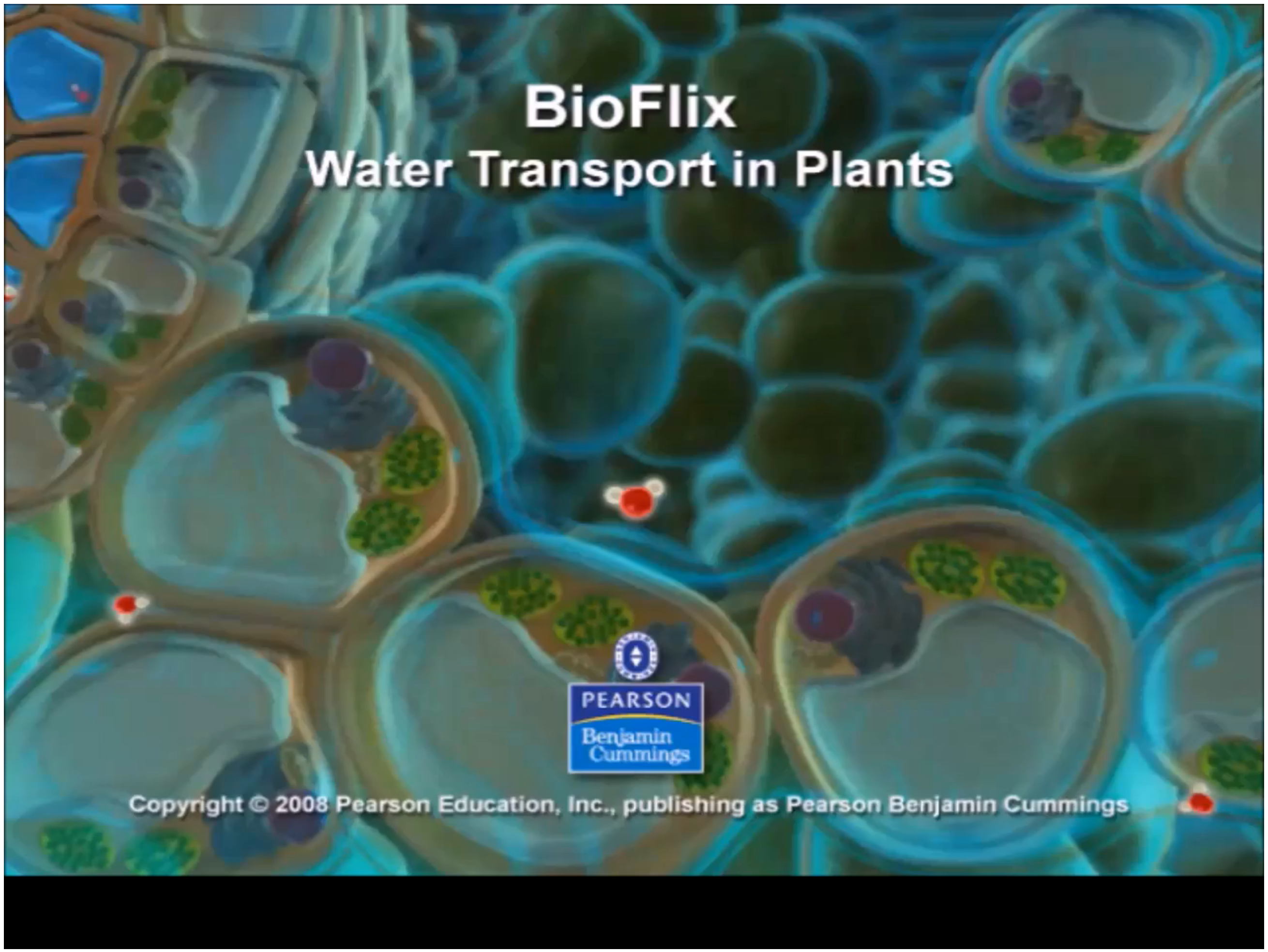
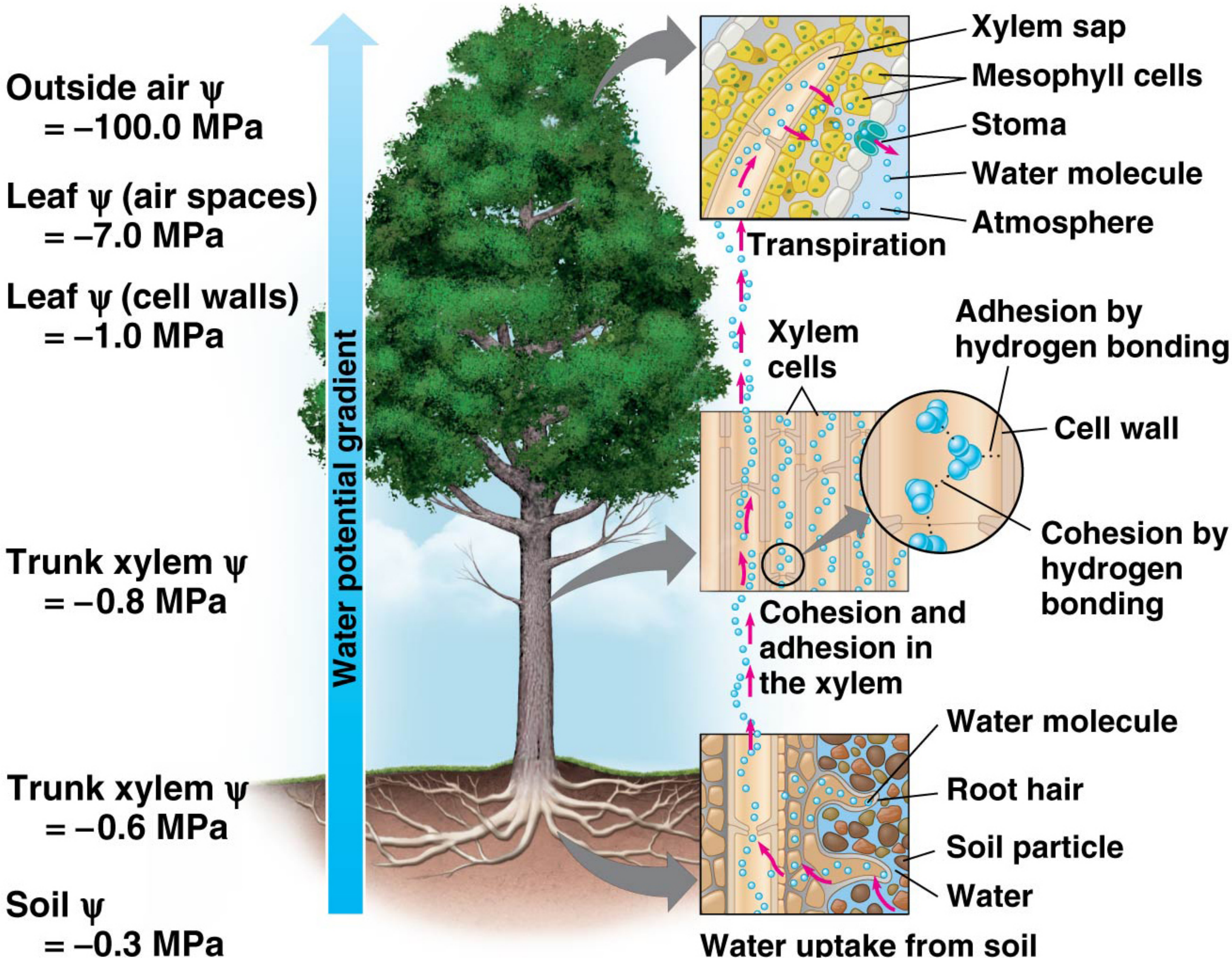
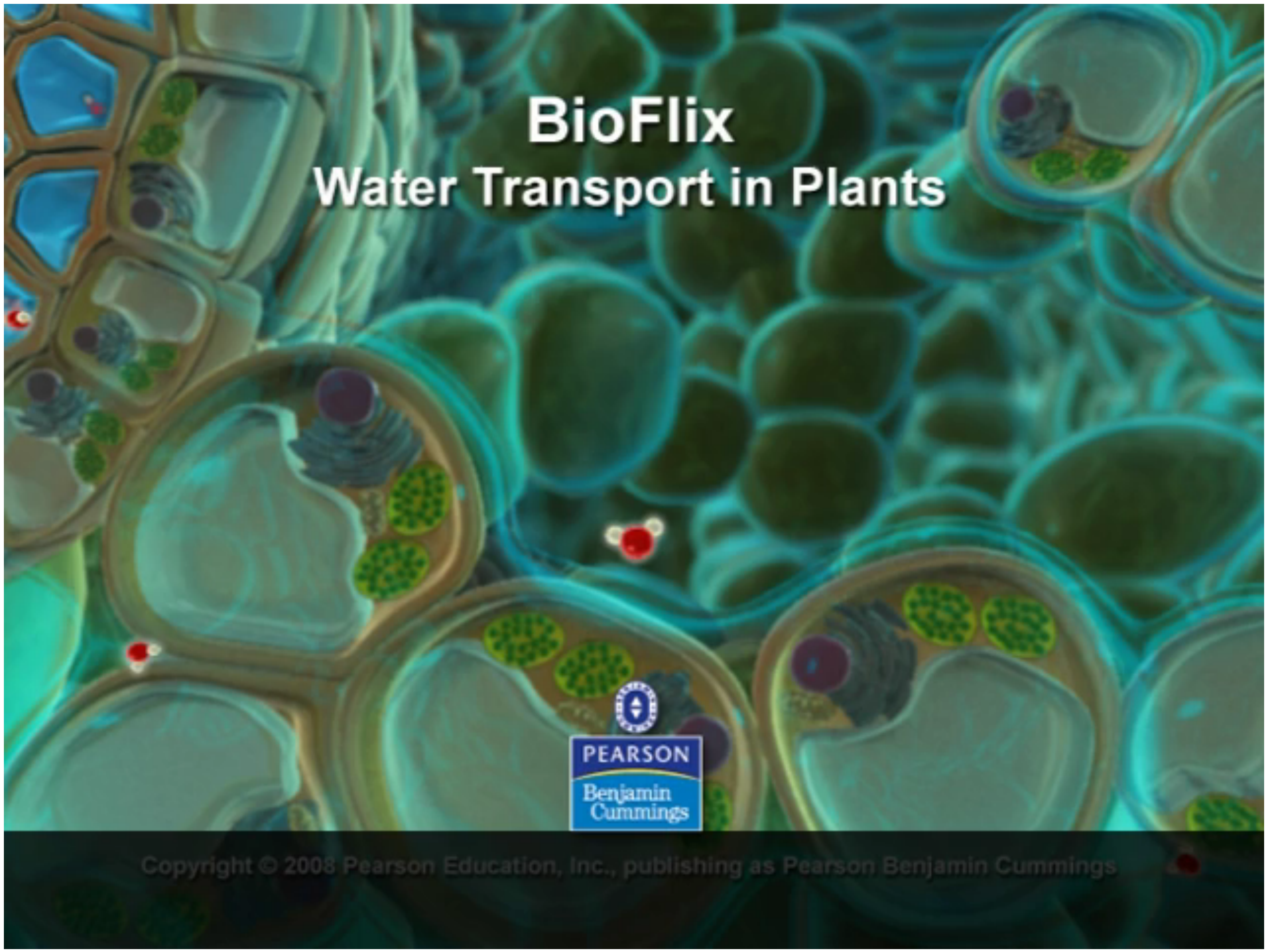


Figure 36.12



Outside air ψ = –100.0 MPa
Leaf ψ (air spaces) = –7.0 MPa
Leaf ψ (cell walls) = –1.0 MPa
Trunk xylem ψ = –0.8 MPa
Trunk xylem ψ = –0.6 MPa
Soil ψ = –0.3 MPa
Water potential gradient
Xylem sap
Mesophyll cells
Stoma
Water molecule
Atmosphere
Transpiration
Xylem cells
Adhesion by hydrogen bonding
Cell wall
Cohesion by hydrogen bonding
Cohesion and adhesion in the xylem
Water molecule
Root hair
Soil particle
Water
Water uptake from soil

BioFlix® Animation: Water Transport in Plants



Cohesion and Adhesion in the Ascent of Xylem Sap

- Water molecules are attracted to each other through cohesion
- Water molecules exiting the xylem tug on adjacent water molecules down the column
- Adhesion of water molecules to xylem cell walls helps offset the force of gravity

- Thick secondary walls prevent vessel elements and tracheids from collapsing under negative pressure
- Drought stress or freezing can cause a break in the chain of water molecules through cavitation, the formation of a water vapor pocket

- Xylem sap transport can often continue after cavitation by
  - moving between adjacent xylem cells through pits
  - moving from xylem to phloem tissue and back again
  - repairing the cavitation
  - adding new xylem during secondary growth

Xylem Sap Ascent by Bulk Flow: *A Review*

- The movement of xylem sap against gravity is maintained by the cohesion-tension mechanism
- Bulk flow is driven by a water potential difference at opposite ends of xylem tissue
- Bulk flow is driven by transpiration and does not require energy from the plant; like photosynthesis, it is solar powered

- Bulk flow differs from diffusion:
  - It is driven by differences in pressure potential, not solute potential
  - It occurs in hollow dead cells, not across the membranes of living cells
  - It moves the entire solution, not just water or solutes
  - It is much faster

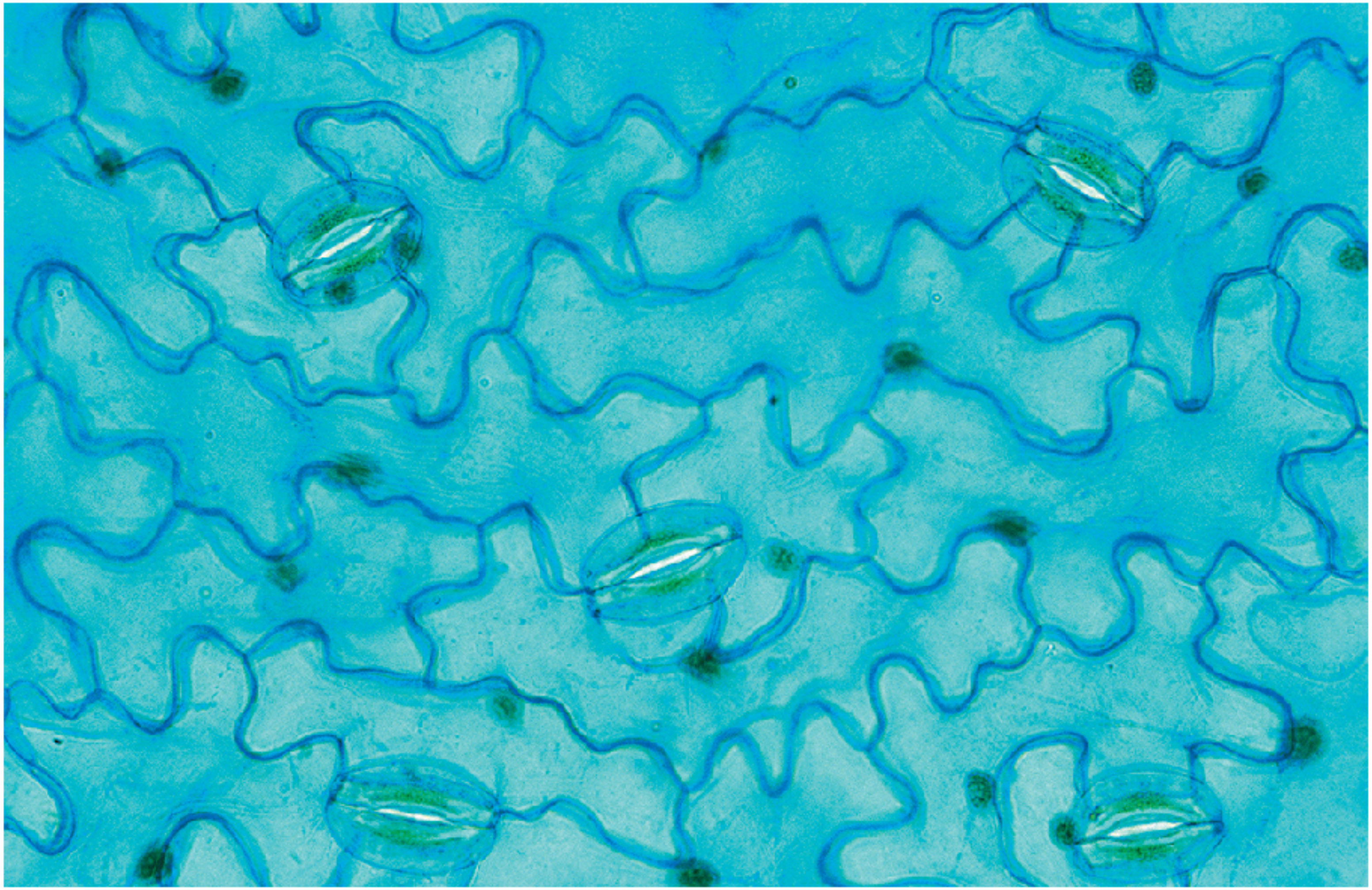
CONCEPT 36.4: The rate of transpiration is regulated by stomata

- Leaves generally have large surface areas and high surface-to-volume ratios
- These characteristics increase rates of both photosynthesis and water loss
- Guard cells balance water conservation with the need for gas exchange by opening and closing stomata

Stomata: Major Pathways for Water Loss

- About 95% of the water a plant loses escapes through stomata; water loss is limited elsewhere on leaves by the waxy cuticle
- Each stoma is flanked by a pair of guard cells, which control the diameter of the stoma by changing shape
- The amount of water lost per leaf depends largely on stomatal density and average stoma size

Figure 36.13



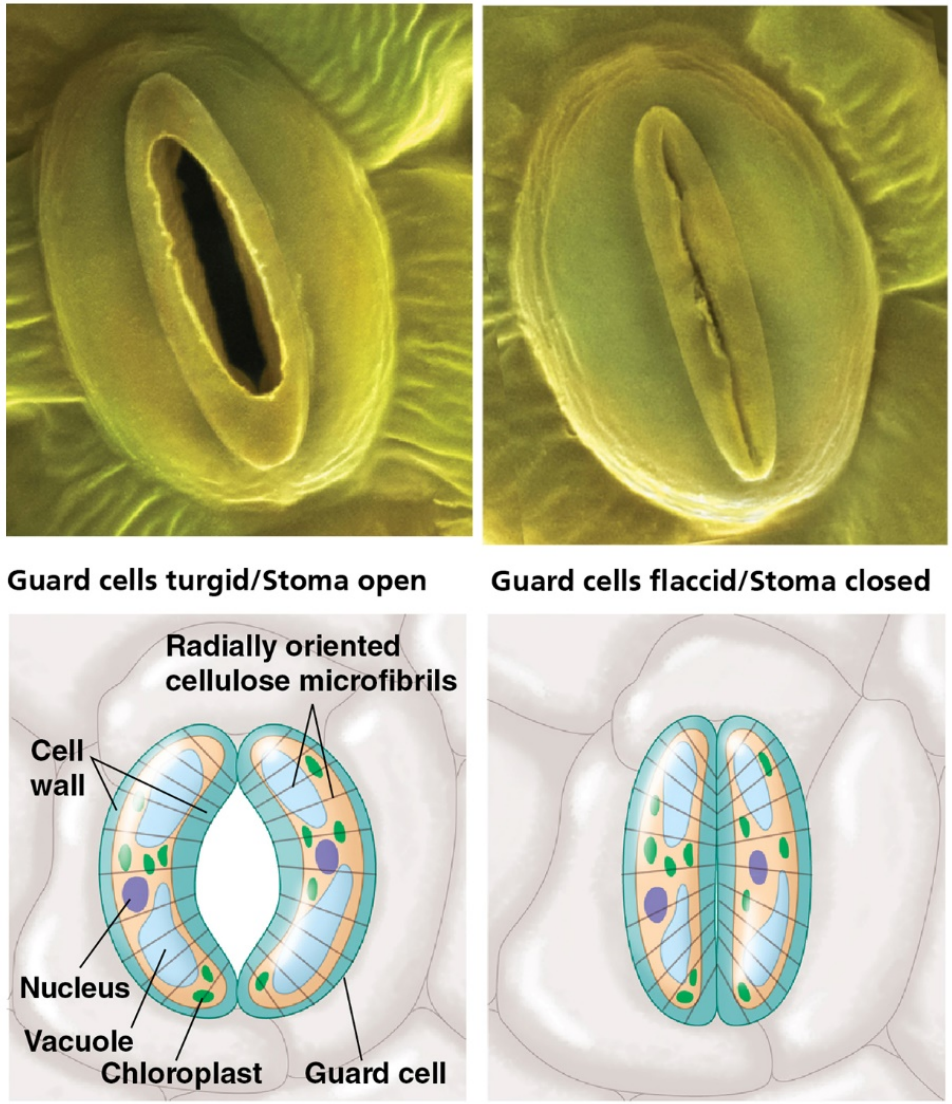
- Stomatal density is under both genetic and environmental control
- Shade-tolerant species have evolved lower stomatal densities by natural selection because CO_2 uptake doesn't limit photosynthesis in shady conditions
- Low CO_2 levels during leaf development can result in increased stomatal densities in many species

- Measuring stomatal density in leaf fossils provides insight into atmospheric CO_2 levels in past climates
- Decreases in stomatal density in British woodland plants since 1927 are consistent with increases in atmospheric CO_2 levels during the late 1900s

Mechanisms of Stomatal Opening and Closing

- Changes in turgor pressure open and close stomata
  - When turgid, guard cells bow outward and the pore between them opens
  - When flaccid, guard cells become less bowed and the pore closes

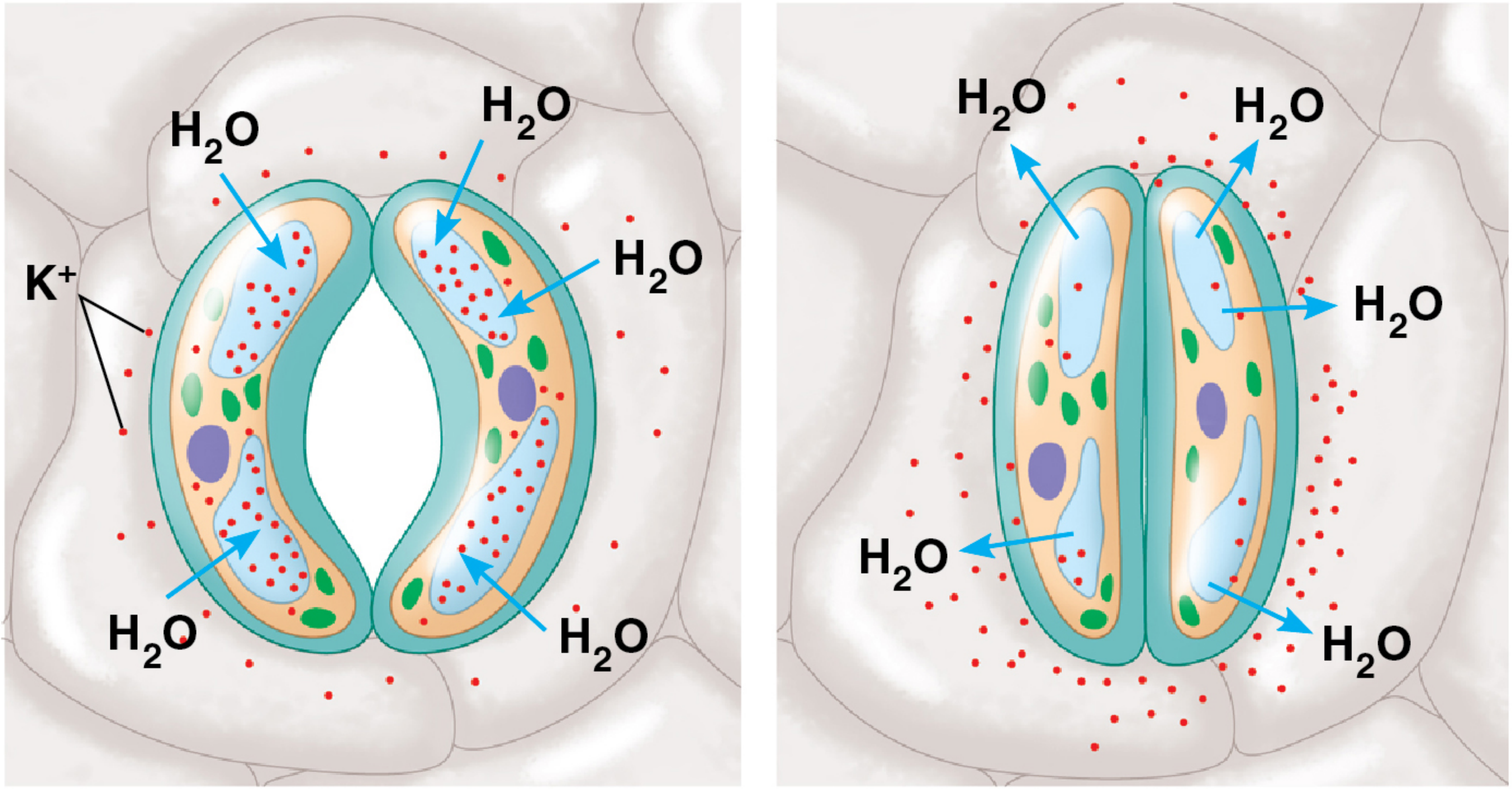
Figure 36.14



(a) Changes in guard cell shape and stomatal opening and closing (surface view)

- Changes in turgor pressure result from absorption and loss of potassium ions (K^+) by the guard cells
- Proton pumps generate the membrane potential required to move K^+ across the plasma membrane
  - Guard cells become turgid on absorption of K^+ and water enters by osmosis, causing the stomata to open
  - Guard cells become flaccid when K^+ leaves the guard cells, which leads to an osmotic loss of water and stomata close

Figure 36.14



(b) Role of potassium ions (K^+) in stomatal opening and closing

Stimuli for Stomatal Opening and Closing

- Generally, stomata open during the day and close at night to minimize water loss
- Stomatal opening at dawn is triggered by
  - Light
  - CO_2 depletion
  - An internal "clock" in guard cells
- Plants, like all eukaryotic organisms, have internal clocks; **circadian rhythms** are 24-hour cycles

- Drought stress can cause stomata to close during the daytime
- The hormone **abscisic acid (ABA)** is produced in response to water deficiency; it signals guard cells to close the stomata

Effects of Transpiration on Wilting and Leaf Temperature

- Sunny, warm, dry, and windy conditions cause transpiration rates to increase
- If uptake and transport are not sufficient to replace the lost water, the plant will wilt
- Transpiration also protects leaves from overheating by lowering the internal temperature through evaporative cooling

Adaptations That Reduce Evaporative Water Loss

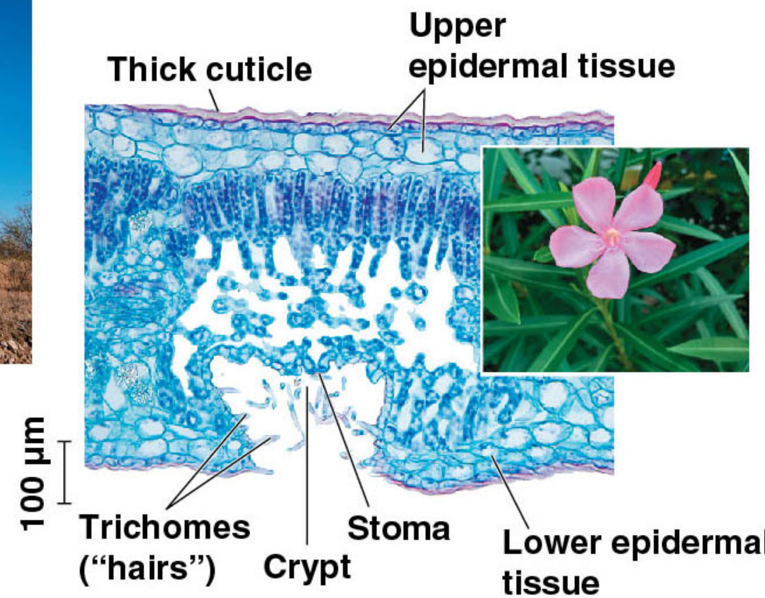
- Water availability is a major determinant of plant productivity
- Freely available water is required to keep stomata open for uptake of CO_2
- **Xerophytes** are plants adapted to arid climates
- Some xerophytes avoid drying out by completing their entire life cycle during the rainy season

- Other xerophytes have morphological or physiological adaptations to reduce water loss
  - Fleshy stems for water storage
  - Highly reduced leaves and photosynthetic stems
  - Crassulacean acid metabolism (CAM) in which stomata close during the day and open at night for gas exchange

Figure 36.15

▶ **Ocotillo (*Fouquieria splendens*)**

▼ **Oleander (*Nerium oleander*)**



▶ **Old man cactus (*Cephalocereus senilis*)**

CONCEPT 36.5: Sugars are transported from sources to sinks via the phloem’

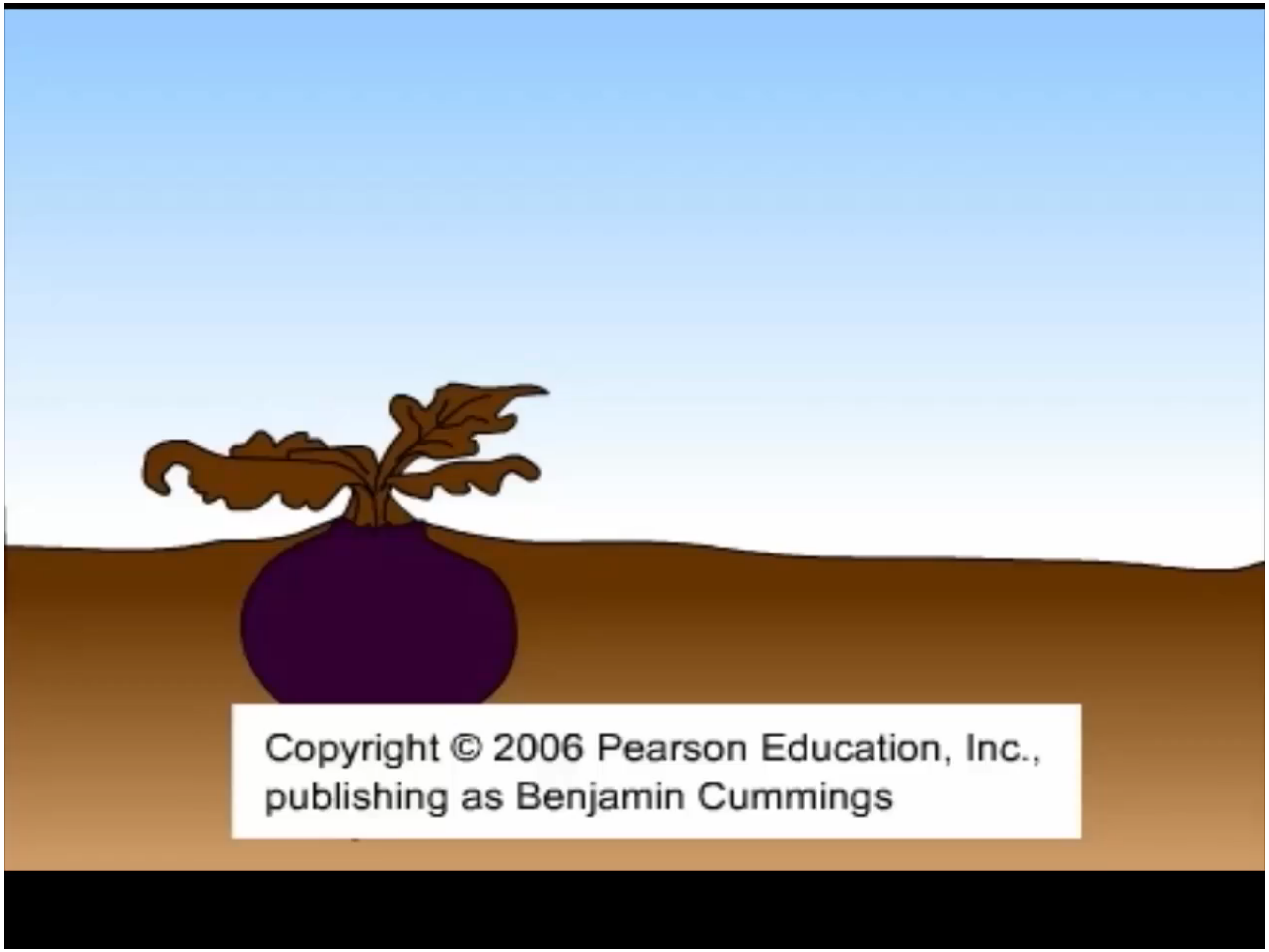
- Sugars are often transported from mature leaves, where they are produced to lower parts of the plant, where they are needed for energy or growth
- The products of photosynthesis are transported through phloem by the process of **translocation**

Movement from Sugar Sources to Sugar Sinks

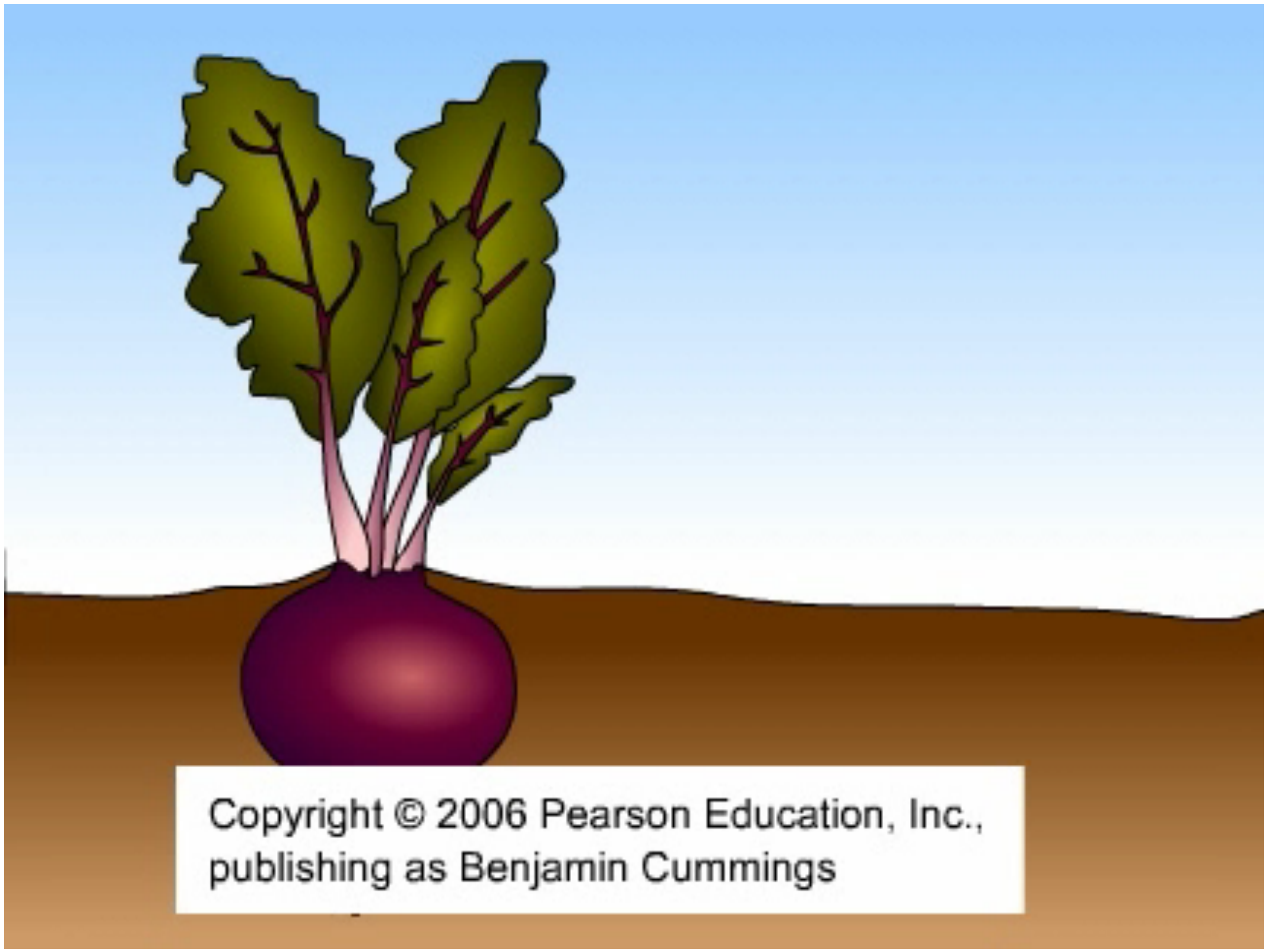
- In angiosperms, **phloem sap**, an aqueous solution high in sucrose, travels from a sugar source to a sugar sink through sieve-tube elements
  - A **sugar source** is an organ that is a net producer of sugar, such as mature leaves
  - A **sugar sink** is an organ that is a net consumer or depository of sugar, such as roots, buds, and fruits

- A storage organ may be a sugar source or a sink, depending on the season
  - When stockpiling carbohydrates in summer, it is a sugar sink
  - In spring, it becomes a sugar source, supplying sugar to growing shoot tips

Animation: Translocation of Phloem Sap in Spring

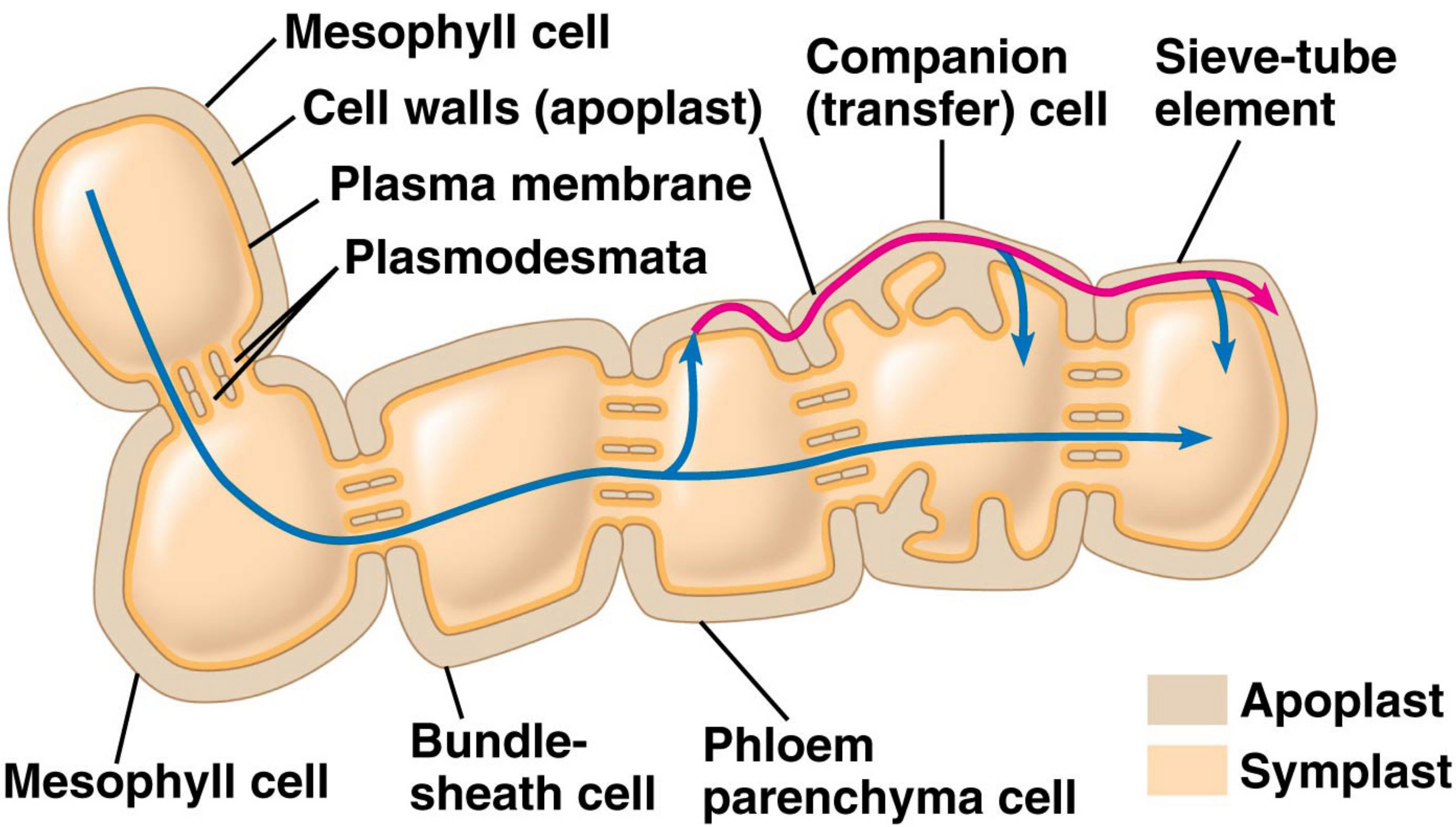


Animation: Translocation of Phloem Sap in Summer



- Sinks usually receive sugar from the nearest sources
- Sugar is loaded into companion cells and sieve-tube elements before being exported to sinks
- Whether sugar moves only by symplastic or by both symplastic and apoplastic pathways is species dependent

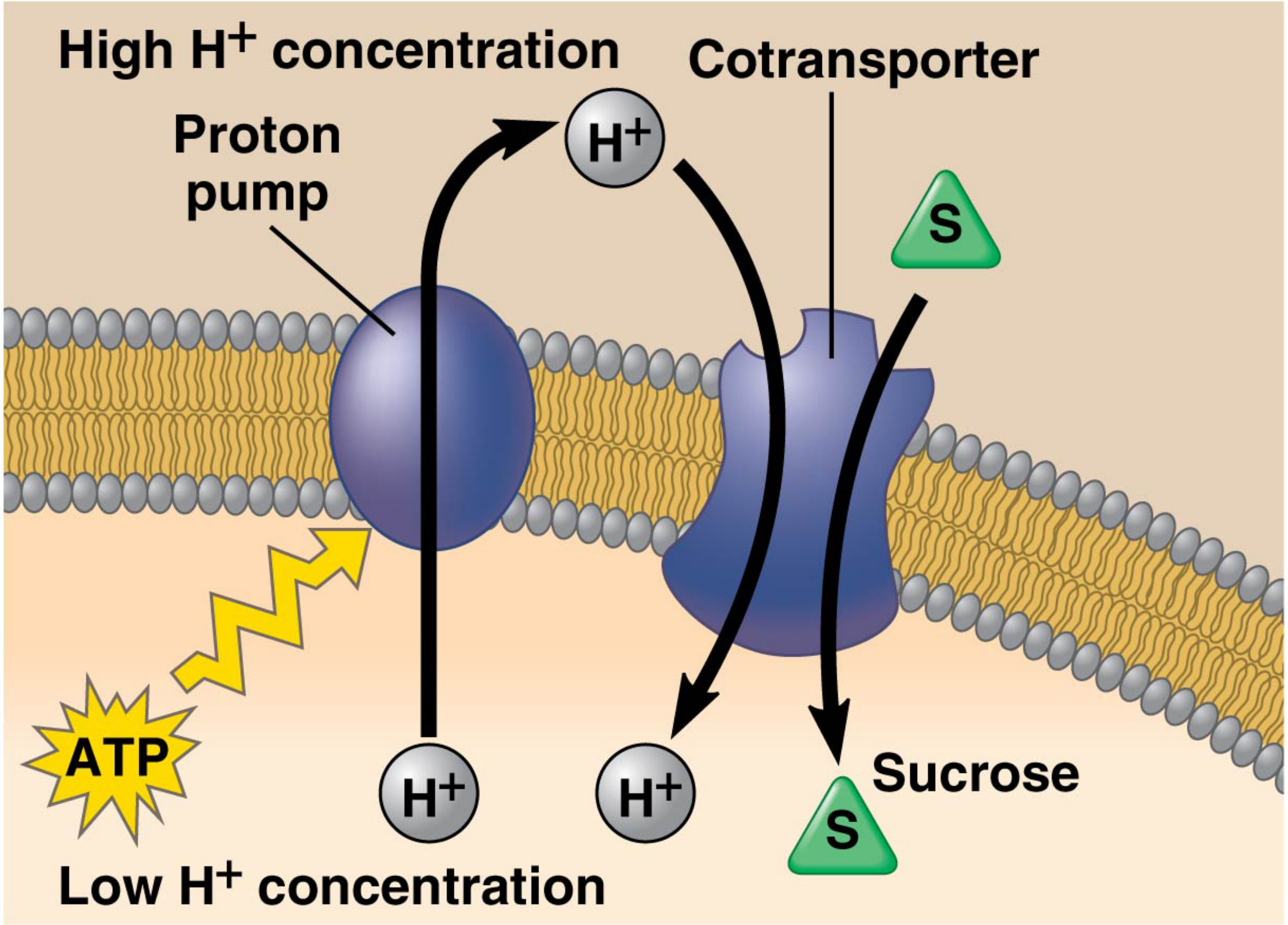
Figure 36.16



(a) Sucrose manufactured in mesophyll cells can travel via the symplast (blue arrows) to sieve-tube elements.

- Phloem loading often requires active transport because sugar is more concentrated in sieve-tube elements and companions cells than source cells
- Proton pumping and cotransport of sucrose and H^+ enable sucrose to accumulate in the phloem

Figure 36.16



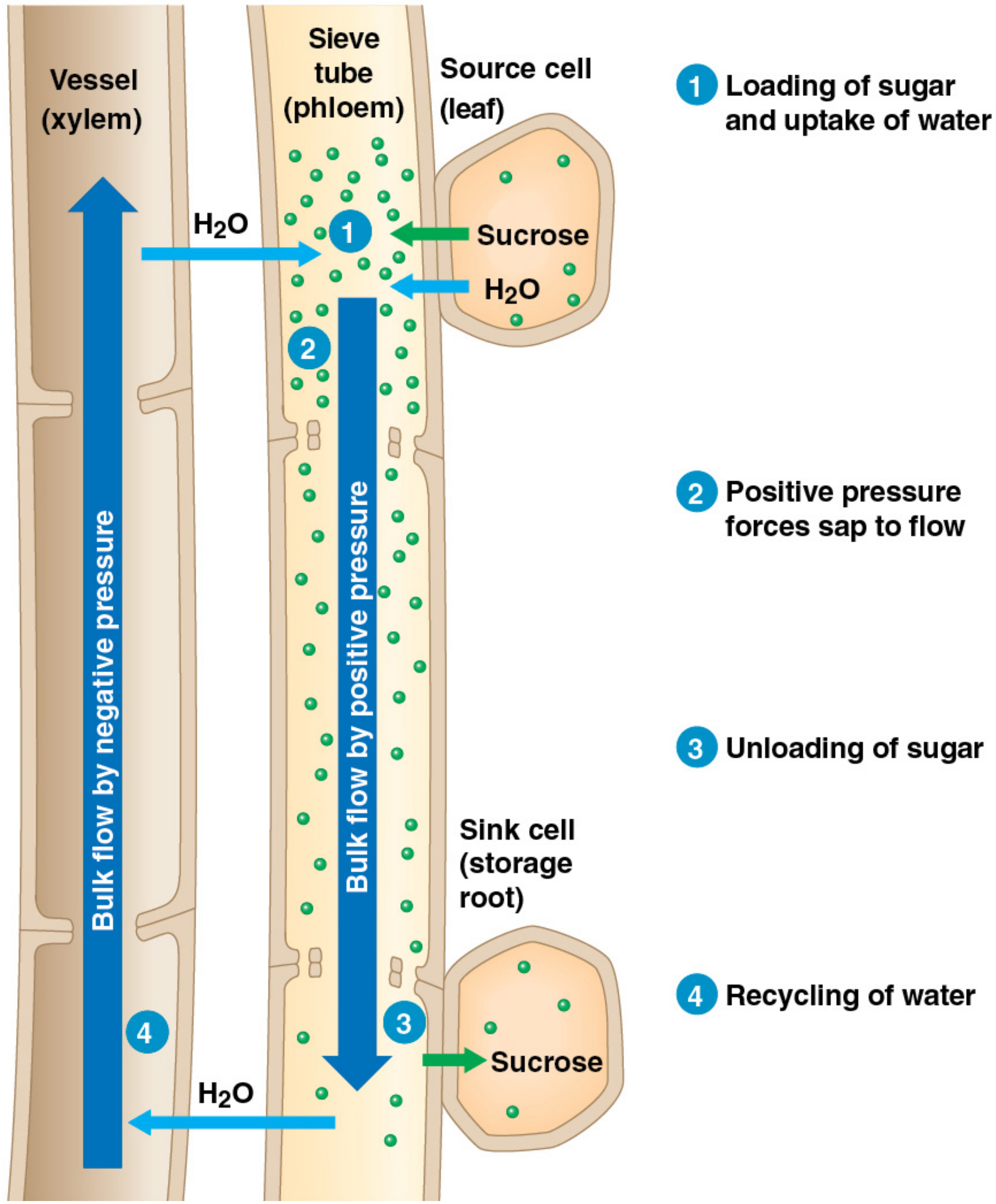
(b) A chemiosmotic mechanism is responsible for the active transport of sucrose.

- At the sink, sugar molecules diffuse from the phloem to sink tissues and water follows by osmosis
- Sugar concentration is lower in the sink than in the sieve tube because unloaded sugar is either consumed or converted to polymers such as starch

Bulk Flow by Positive Pressure: The Mechanism of Translocation in Angiosperms

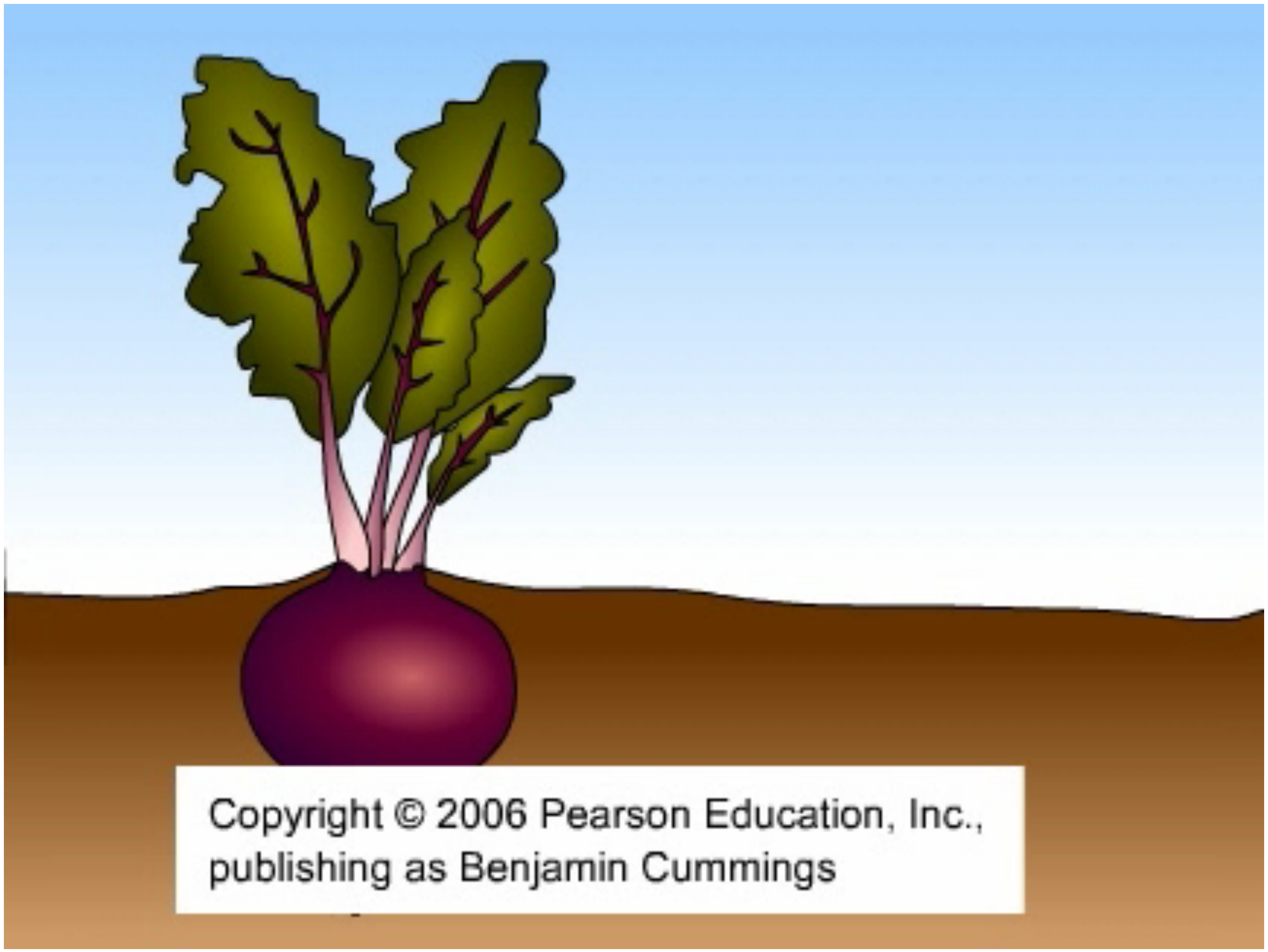
- Phloem sap moves through the sieve tubes of angiosperms by bulk flow driven by positive pressure, called *pressure flow*
- Phloem sap flows from sources, where pressure is high, to sinks, where pressure is low

Figure 36.17



Vessel (xylem)
Sieve tube (phloem)
Source cell (leaf)
H2O
1
Sucrose
H2O
2
Bulk flow by negative pressure
Bulk flow by positive pressure
Sink cell (storage root)
3
4
Sucrose
H2O
1 Loading of sugar and uptake of water
2 Positive pressure forces sap to flow
3 Unloading of sugar
4 Recycling of water

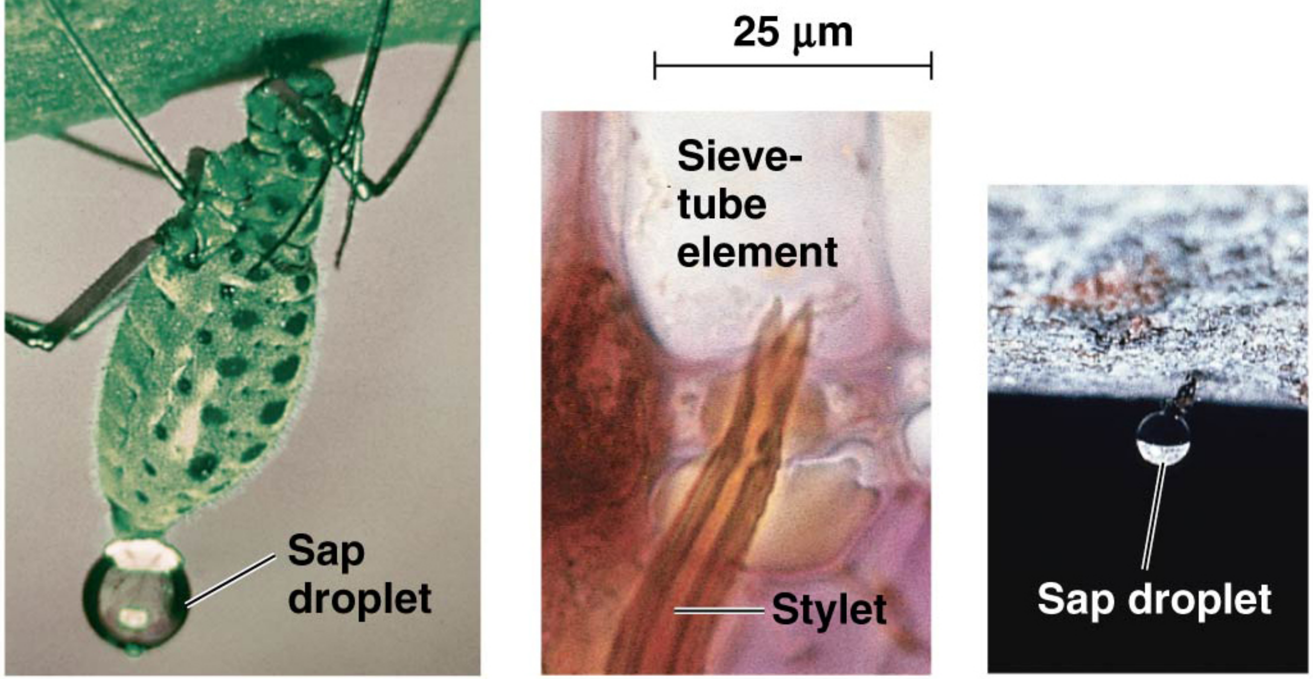
Animation: Phloem Transport



- The pressure flow hypothesis predicts that phloem sap near sugar sources should have higher sugar content than phloem sap near sinks

Figure 36.18

Experiment



Aphid feeding | **Stylet in sieve-tube element** | **Separated stylet exuding sap**

Results **The closer the stylet was to a sugar source, the higher its sugar concentration was.**

Data from S. Rogers and A. J. Peel, Some evidence for the existence of turgor pressure in the sieve tubes of willow (*Salix*), *Planta* 126:259–267 (1975).

- Self-thinning, the dropping of sugar sinks such as flowers, seeds, or fruits, occurs when there are more sugar sinks than the sources can support

CONCEPT 36.6: The symplast is highly dynamic

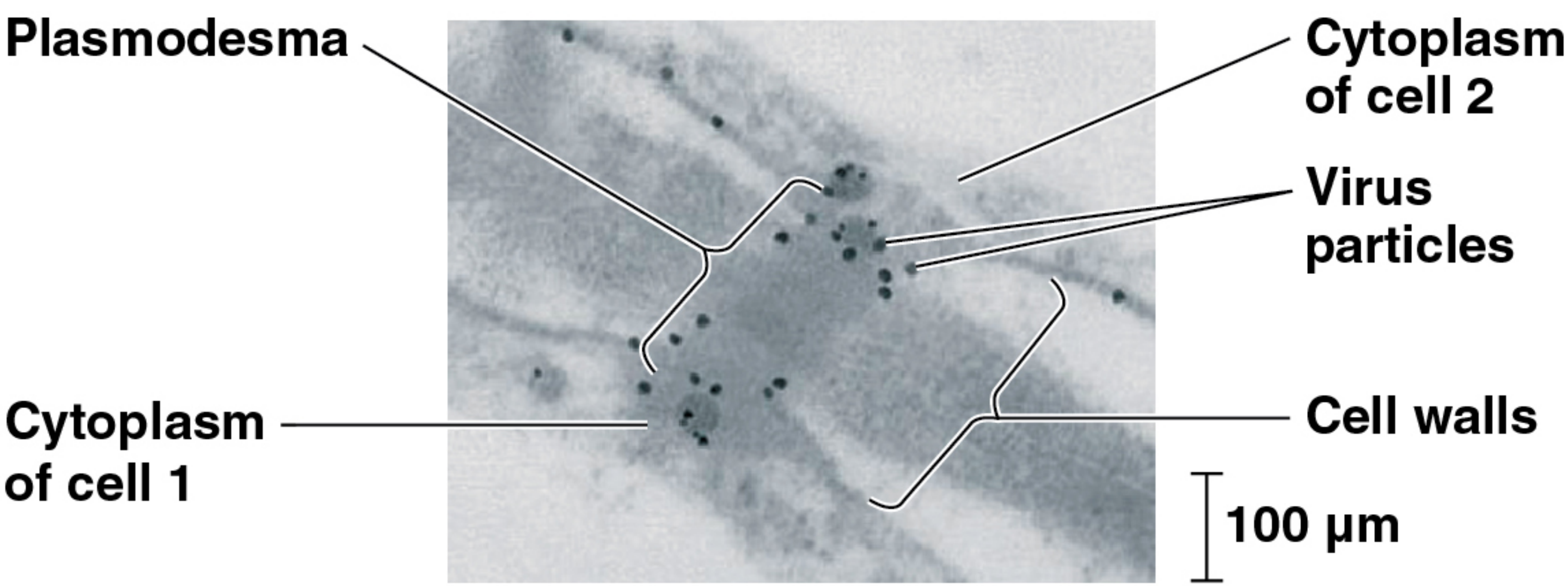
- As a living tissue, the symplast is largely responsible for dynamic changes in plant transport processes
- Plant transport changes during development
  - For example, a leaf will transition from a sugar sink to spend most of its life as a sugar source
  - Water stress can activate signal transduction pathways that alter membrane transport

Changes in Plasmodesmatal Number and Pore Size

- Plasmodesmata are highly dynamic
  - They can open or close in response to turgor pressure, cytosolic Ca^{2+} levels, or cytosolic pH
  - They can close or be eliminated with leaf transition from sink to source

- Pore sizes of plasmodesmata are approximately 2.5 nm
- Plant cells can regulate pore size as part of a communication network
- Plant viruses can cause plasmodesmata to dilate as much as 10 nm, allowing large viral RNA to pass between cells

Figure 36.19


Plasmodesma
Cytoplasm of cell 2
Virus particles
Cytoplasm of cell 1
Cell walls
100 µm

Phloem: An Information Superhighway

- Phloem is a "superhighway" for systemic transport of macromolecules and viruses
- Systemic communication through the phloem helps integrate functions of the whole plant
  - For example, in a defense response to local infection, chemical signals travel through the phloem and activate defense genes in noninfected tissues

Electrical Signaling in the Phloem

- The phloem allows for rapid electrical communication between widely separated organs
  - For example, it transports electrical signals in rapid leaf movements in the sensitive plant (*Mimosa pudica*)

Figure 36.UN02

Data from the Experiment

Temperature	% Increase in Mass Due to Water Uptake After 30 Minutes
5°C	18.5
15°C	26.0
25°C	31.0
35°C	36.2

Data from J. D. Murphy and D. L. Noland, Temperature effects on seed imbibition and leakage mediated by viscosity and membranes, *Plant Physiology* 69:428–431 (1982).

Figure 36.UN03

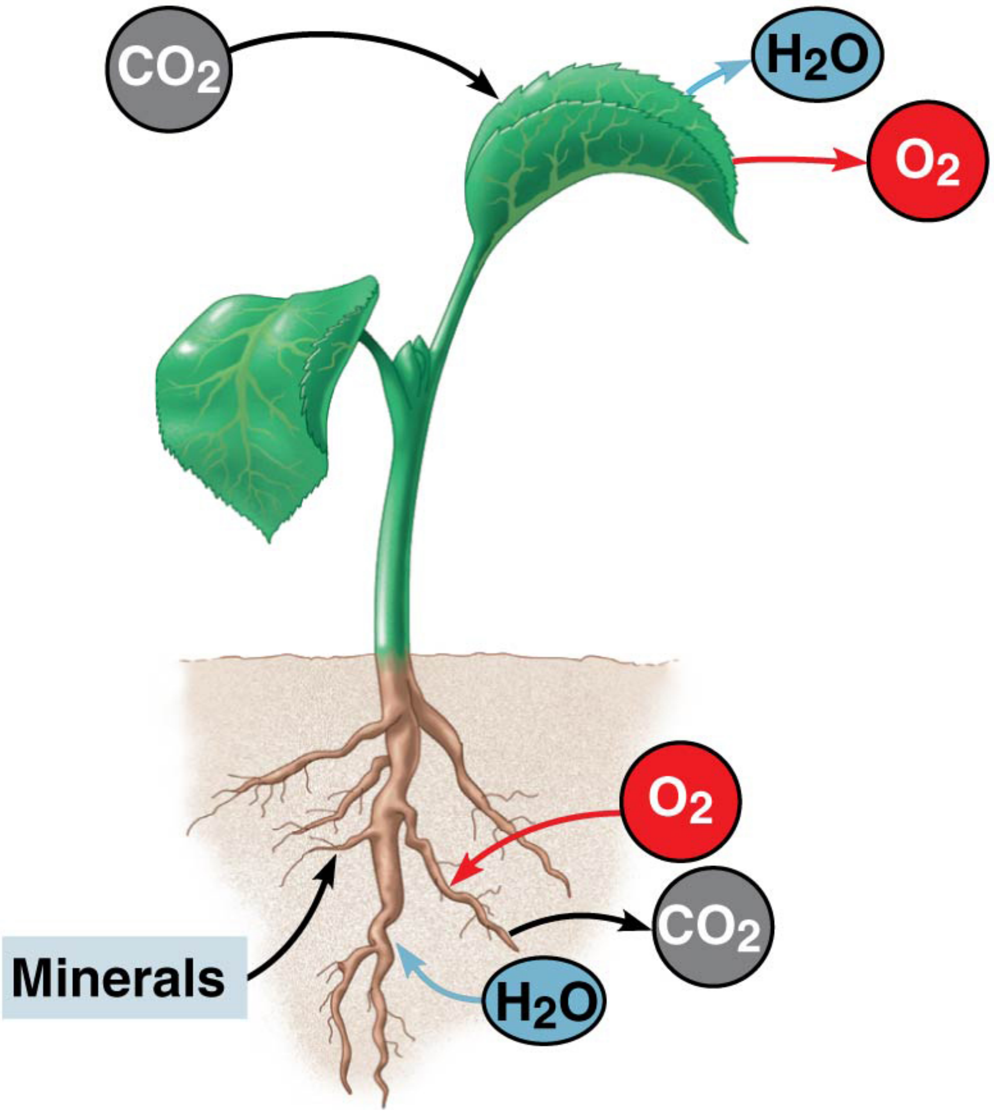


Figure 36.UN03