

35

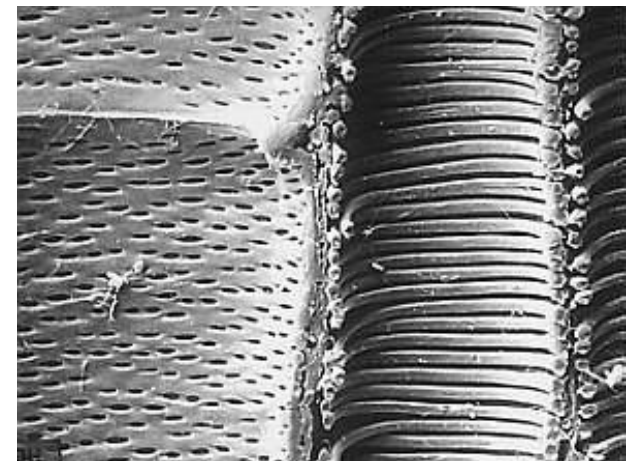
Transport in Plants



35 Transport in Plants

- 35.1 How Do Plants Take Up Water and Solutes?
- 35.2 How Are Water and Minerals Transported in the Xylem?
- 35.3 How Do Stomata Control the Loss of Water and the Uptake of CO₂?
- 35.4 How Are Substances Translocated in the Phloem?

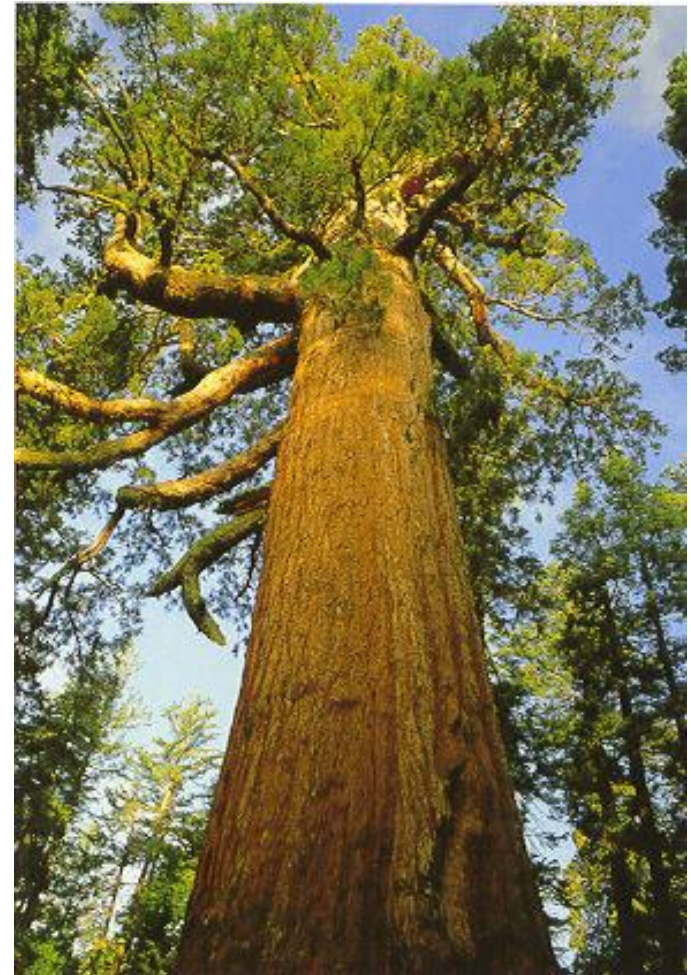
**Scanning EM of
pumpkin xylem**



35.1 How Do Plant Cells Take Up Water and Solutes?

Terrestrial plants obtain water and mineral nutrients from soil

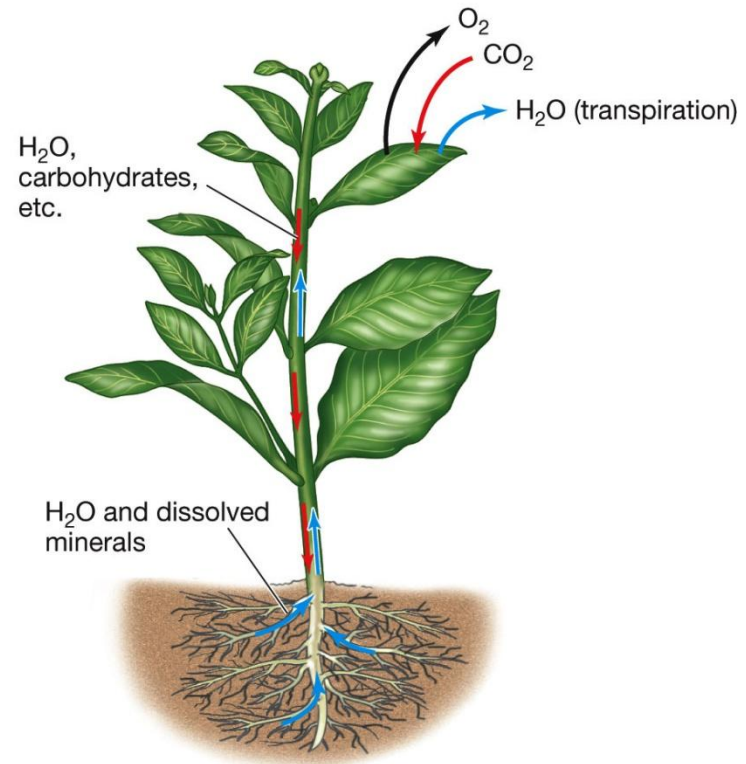
- Water needed for...
 - photosynthesis
 - essential for transporting solutes up and down
 - cooling plant
 - internal pressure to support plant
- Plants lose large quantities of water to evaporation, which must be replaced



35.1 How Do Plant Cells Take Up Water and Solutes?

Plants usually obtain water & minerals from soil via roots

- Water uptake requires water to enter through cell membranes via osmosis
- Mineral uptake requires transport proteins
- Roots obtain carbohydrates from leaves.



Review from Bio I

Osmosis

- movement of water through a membrane in accordance with laws of diffusion
- Osmosis is *passive*: no input of energy is required

35.1 How Do Plant Cells Take Up Water and Solutes?

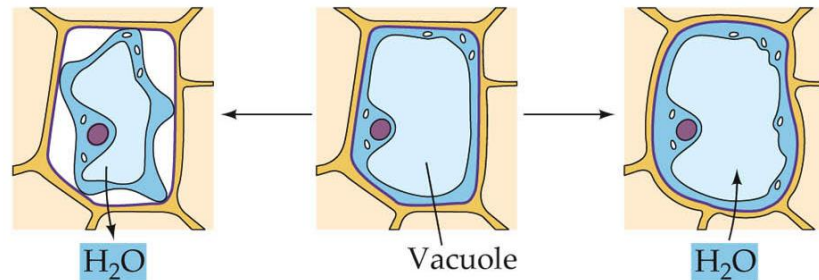
Review from Bio I

Solute potential (aka. **osmotic potential**)

- Determines direction of water movement across membrane
- The greater the solute concentration of a solution, the *more negative the solute potential*, and...
- the greater the tendency for water to move into it from another solution of lower solute concentration

• *i.e. water moves from low solute concentration to higher solute conc.*

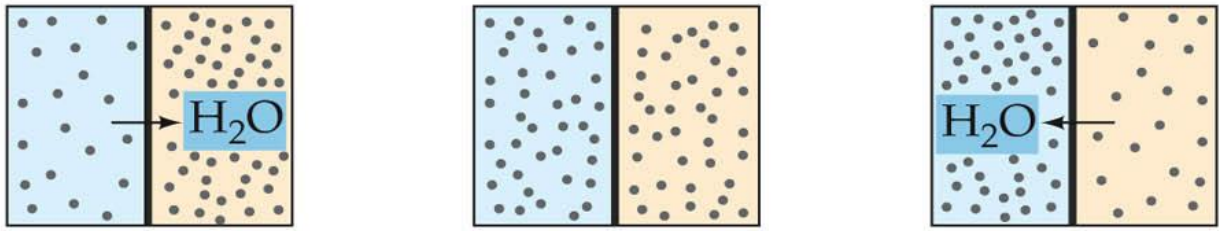
Plant cell



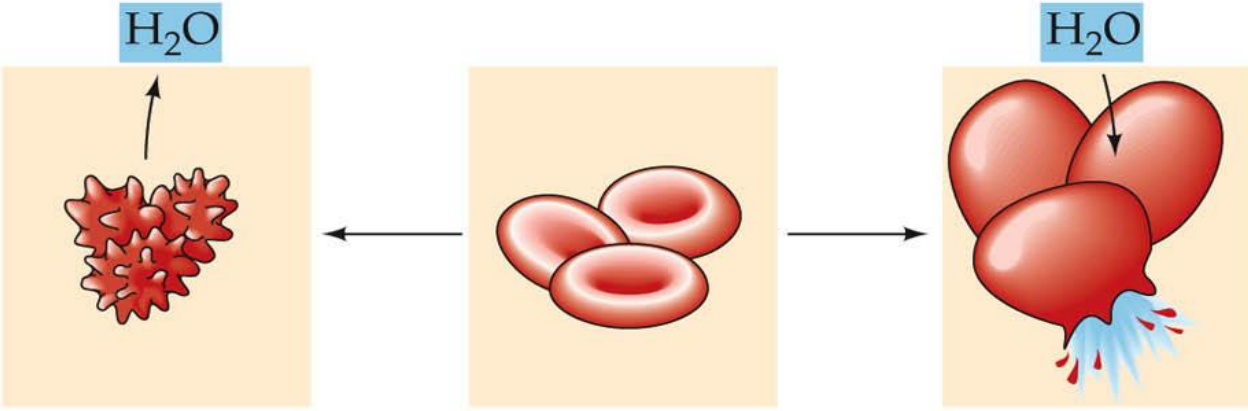
Review from Bio I

Hypertonic **Isotonic** **Hypotonic**

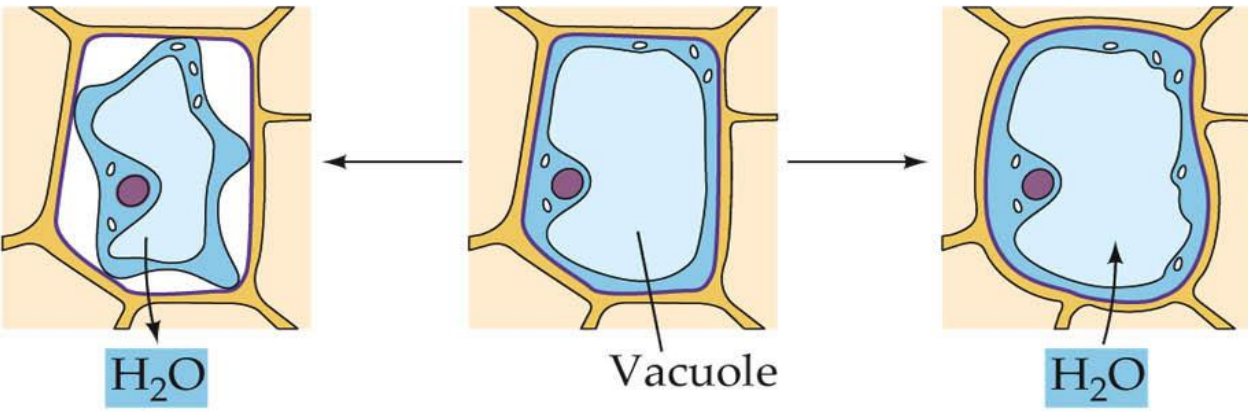
Inside of cell Outside of cell



Animal cell



Plant cell



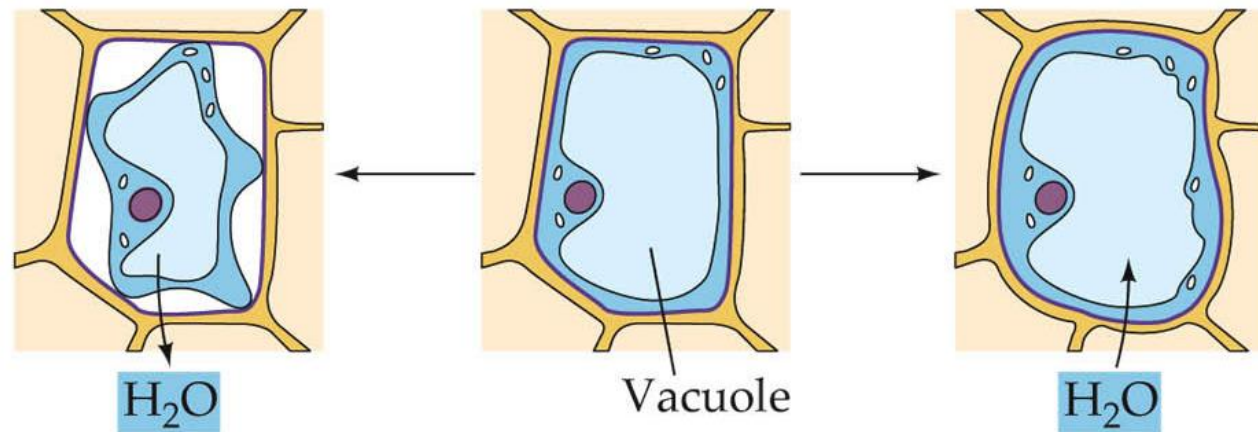
35.1 How Do Plant Cells Take Up Water and Solutes?

Review from Bio I

For osmosis to occur, two solutions must be separated by ***selectively permeable membrane***

- permeable to water, but not to solute

Plant cell

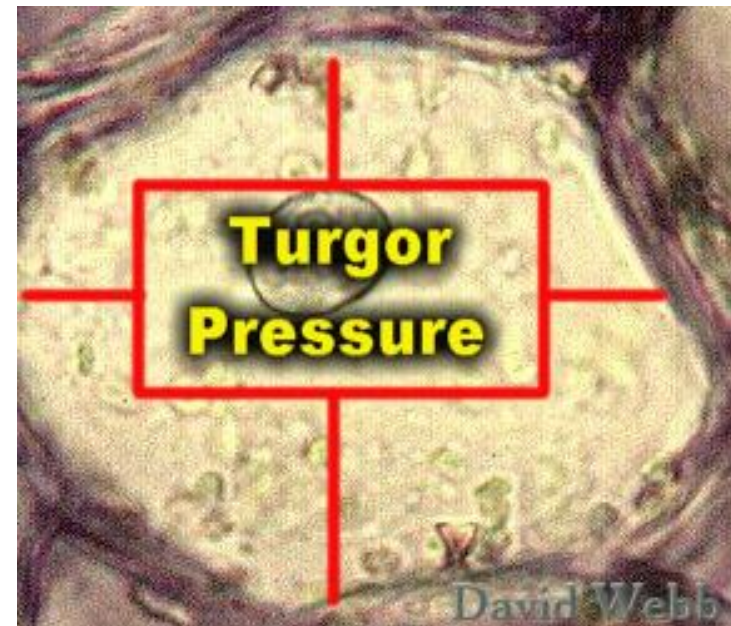


35.1 How Do Plant Cells Take Up Water and Solutes?

Review from Bio I

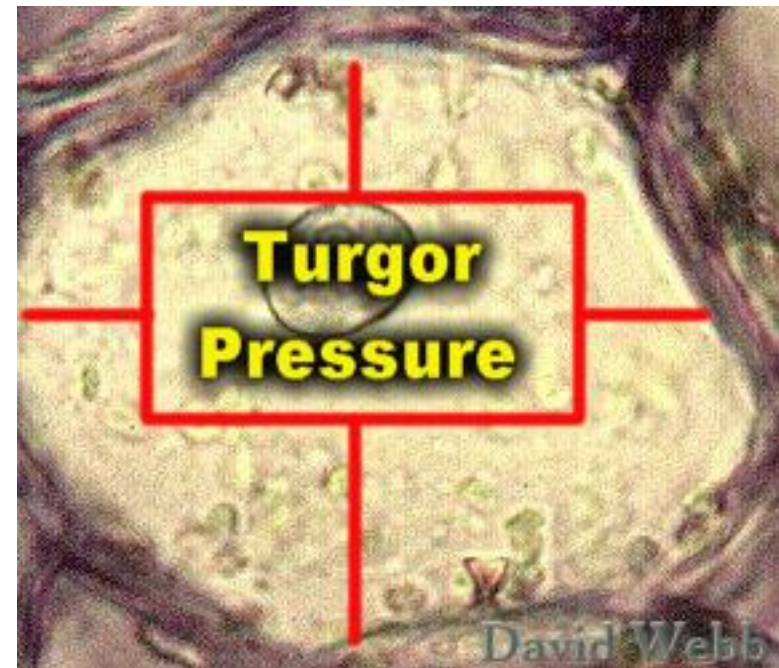
Plants have rigid cell walls

- As water enters cell due to its negative solute potential,...
- entry of more water is resisted by an opposing **pressure potential (turgor pressure)**.



35.1 How Do Plant Cells Take Up Water and Solutes?

- Water enters plant cells until pressure potential *exactly balances* solute potential
- At this point the cell is **turgid** – It has significant positive pressure potential (but balanced by turgor pressure)



35.1 How Do Plant Cells Take Up Water and Solutes?

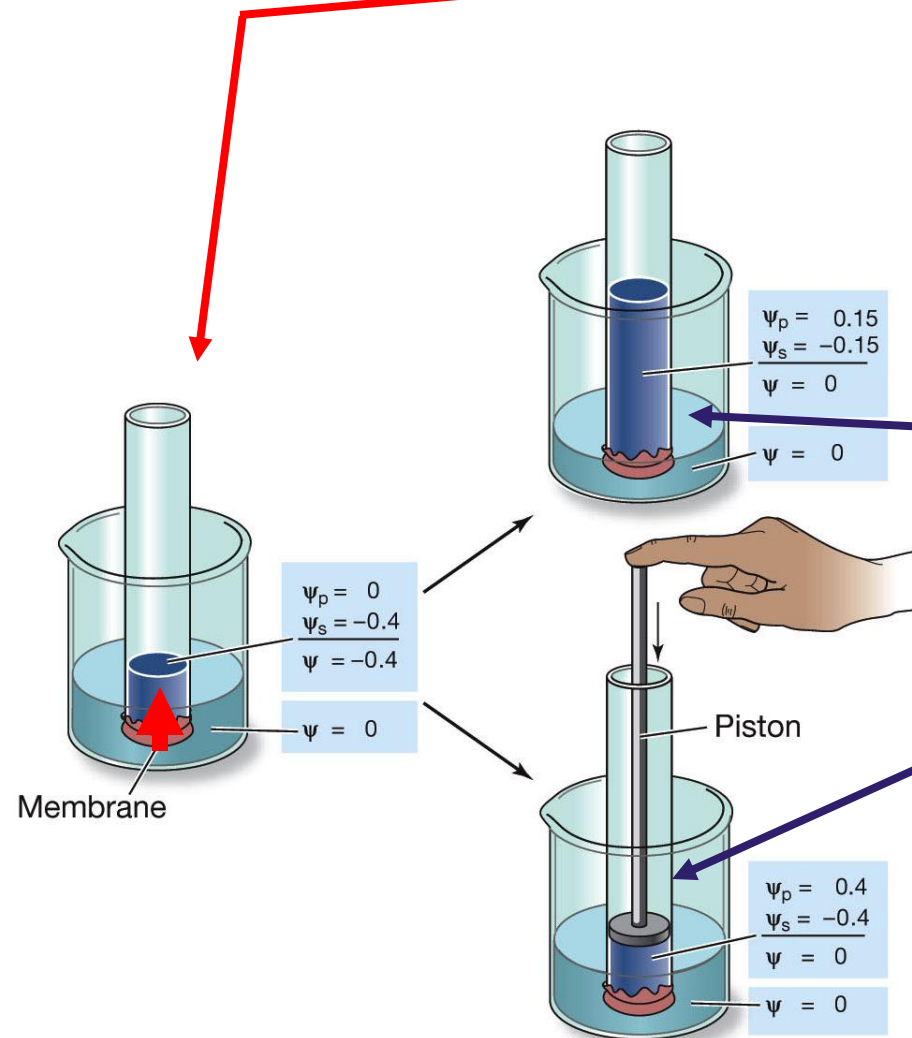
Water potential (ψ)

- overall tendency of solution to take up water from pure water across a membrane
- Water potential = sum of its negative solute potential (ψ_s) + positive pressure potential (ψ_p)

$$\psi = \psi_s + \psi_p$$

Re: $\psi = \psi_s + \psi_p$ (see Fig. 36.2)

- Salt solution inside tube has negative $\psi \rightarrow$ thus its *not at equilibrium* with pure water outside membrane
- Water moves into tube until pressure from weight of water (ψ_p) balances solute potential (ψ_s) which decreases as it becomes diluted.
- Piston pushes (ψ_p) water out of tube (measuring potential), restoring solute concentration and solute potential (ψ_s), until ψ balances with water outside.

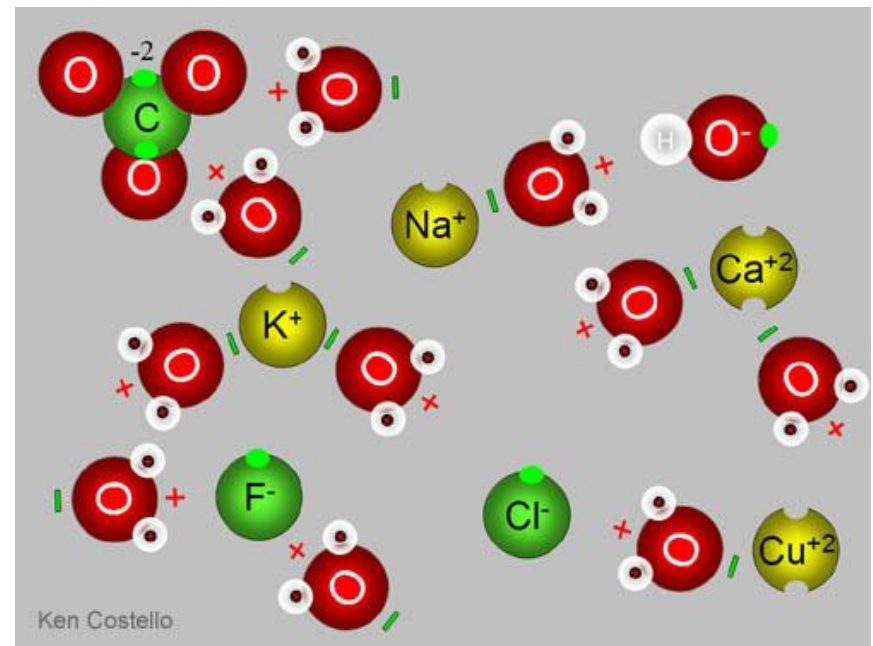


35.1 How Do Plants Take Up Water and Solutes?

Solute potential

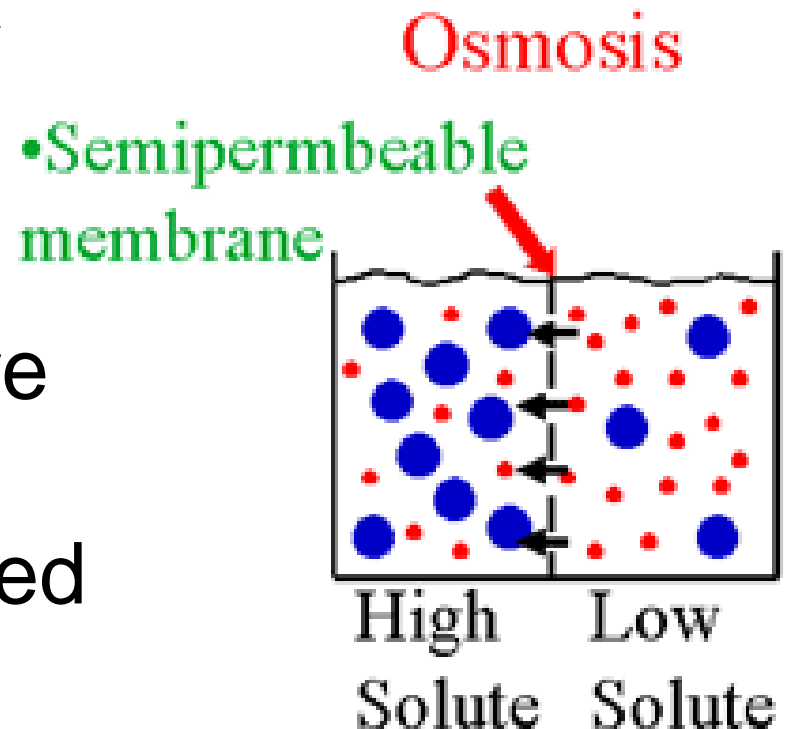
(*osmotic potential*, ψ_s):

- Solutes bind water molecules and thus remove free water from the solution.
- This lowers the water potential and water moves through the membrane to the region of lower ψ .



35.1 How Do Plant Cells Take Up Water and Solutes?

- Water *always* moves across selectively permeable membrane toward a region of lower (more negative) water potential
- Solute potential, pressure potential, and water potential can be measured in *megapascals* (MPa)



35.1 How Do Plant Cells Take Up Water and Solutes?

Osmosis is extremely important to transport in plants


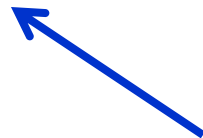
- Physical structure maintained by positive pressure potential
 - **Wilting** is caused by loss of pressure potential
- Over long distances in xylem and phloem, flow of water and dissolved solutes is ***driven by a gradient of pressure potential***



Figure 35.4 A Wilted Plant



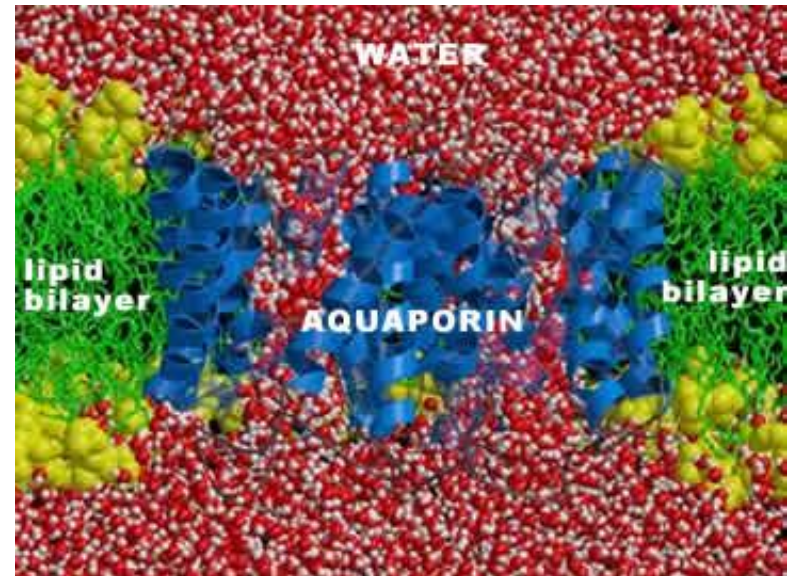
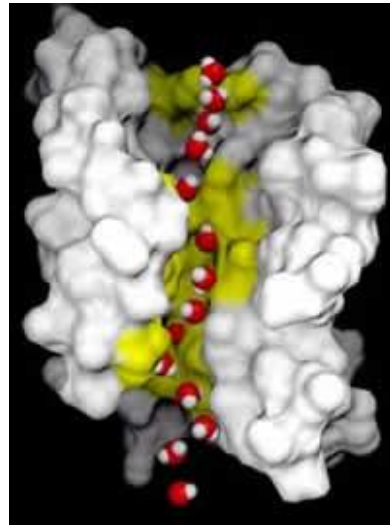
Bulk flow

- movement of solution due to difference in pressure potential over long distances
- in xylem movement is between regions of different ***negative*** pressure potential (tension) – “sucking” 
- in phloem movement is between regions of different ***positive*** pressure potential (turgidity) – “pushing” 

35.1 How Do Plant Cells Take Up Water and Solutes?

Aquaporins

- membrane channel proteins through which water moves rapidly and passively
- Abundance in plasma membrane and tonoplast (vacuole membrane) depends on cell's need to obtain or retain water
- Rate of H₂O movement is regulated *but not direction*



35.1 How Do Plant Cells Take Up Water and Solutes?

Mineral ions

- Require transport proteins to cross membrane
- Molecules and ions (see next slide) move down their charge and concentration gradients as permitted by membrane characteristics
- Soil concentration of most ions is lower than in plant, so uptake must be by active transport, requiring energy

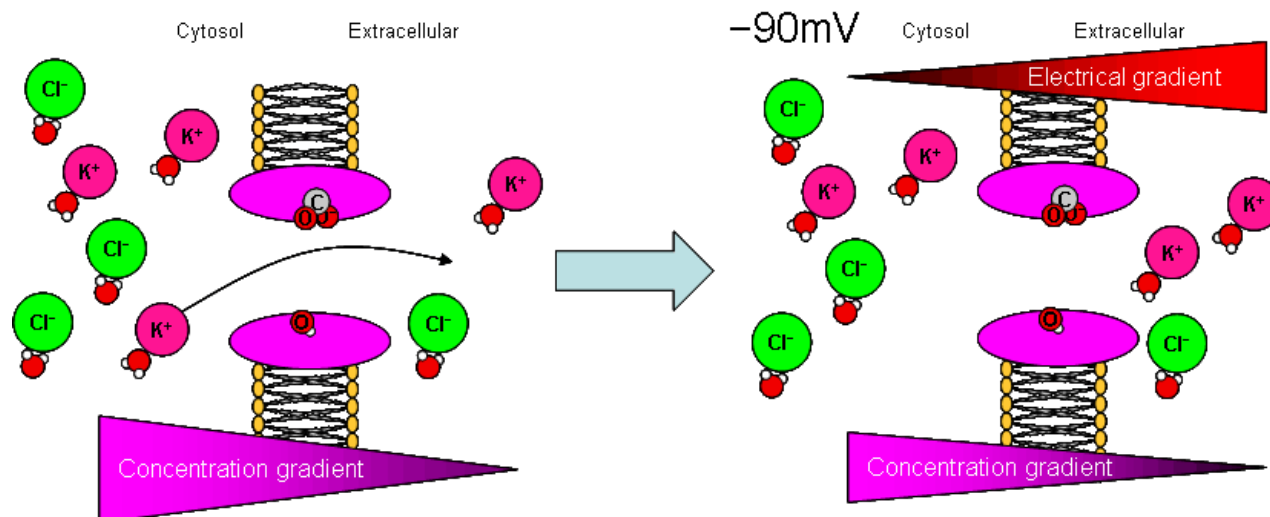
Wild type *Arabidopsis* (right) and a mutant with a defective potassium transporter



35.1 How Do Plant Cells Take Up Water and Solutes?

Electrical gradients also affect cell's ability to take up ions

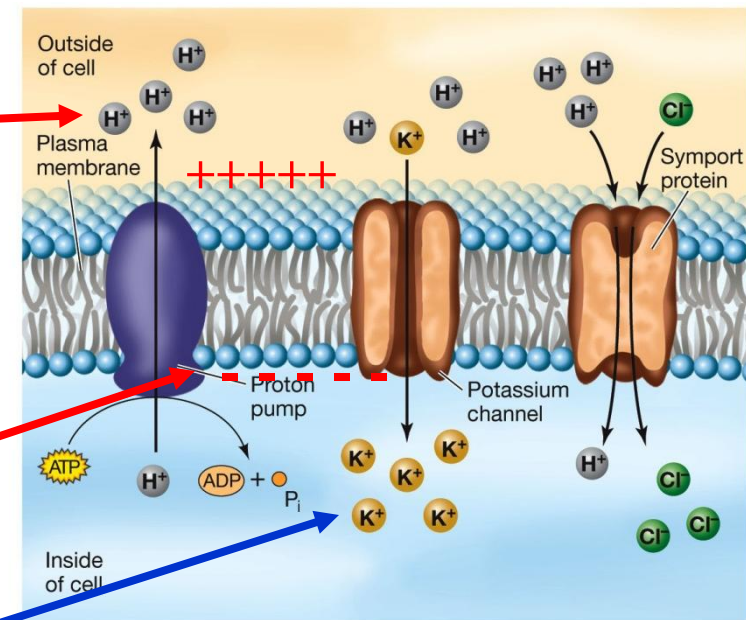
- *Ions move in response to **electrochemical gradient***
 - Combination of concentration + electrical gradients
 - Uptake against an electrochemical gradient is active transport requires ATP energy



35.1 How Do Plant Cells Take Up Water and Solutes?

Plants use **proton pumps** (requires ATP) to move protons (H^+) out of cells against gradient

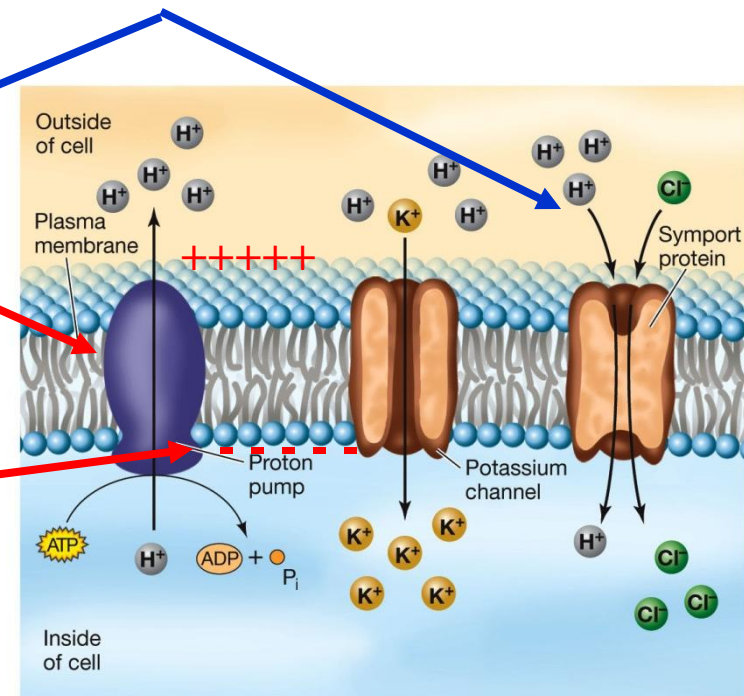
- Accumulation of H^+ outside cell results in electrical gradient *and* concentration gradient of protons
- Inside of cell is now more negative than outside
- Cations (e.g. K^+) can move in by facilitated diffusion



LIFE 8e, Figure 35.3

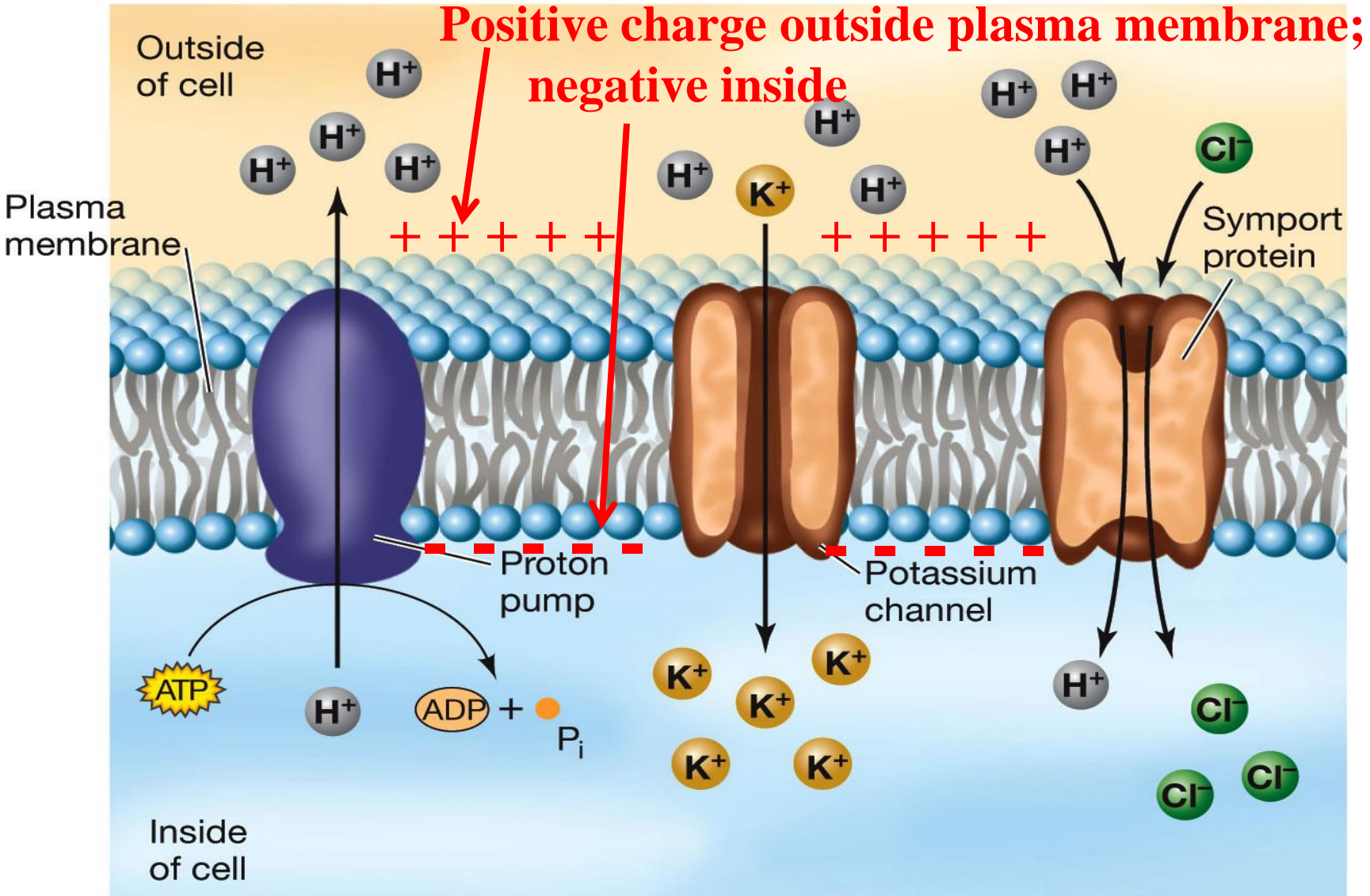
35.1 How Do Plant Cells Take Up Water and Solutes?

- Proton gradient harnessed to drive active transport of anions into cell against its gradient
 - **Symport** couples movement of H^+ and Cl^-
 - **Secondary active transport**
- Proton pump and other transport activities results in cell interior being very negative \rightarrow build up membrane potential of about -120 mV



LIFE 8e, Figure 35.3

Figure 35.5 The Proton Pump in Transport of K^+ and Cl^-

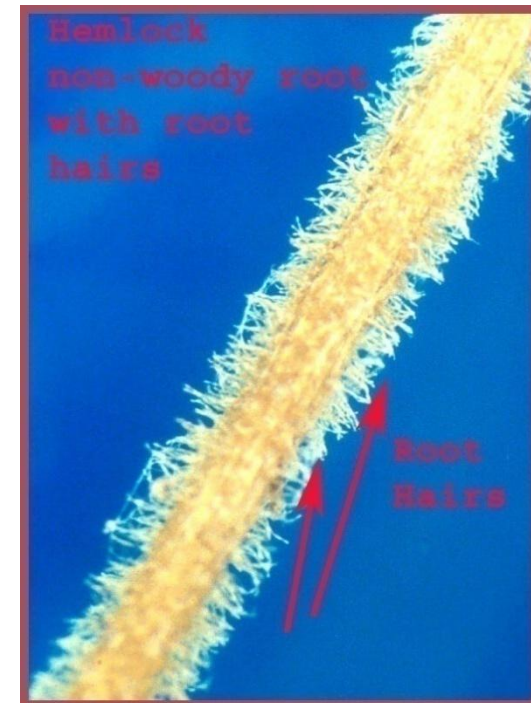
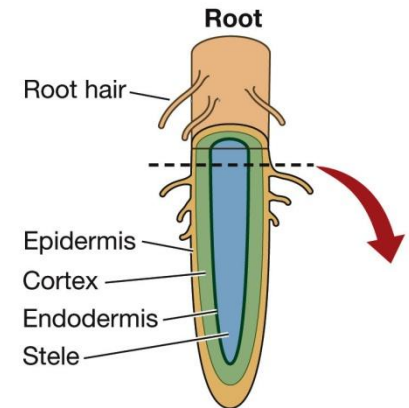


LIFE 9e, Figure 35.5

35.1 How Do Plant Cells Take Up Water and Solutes?

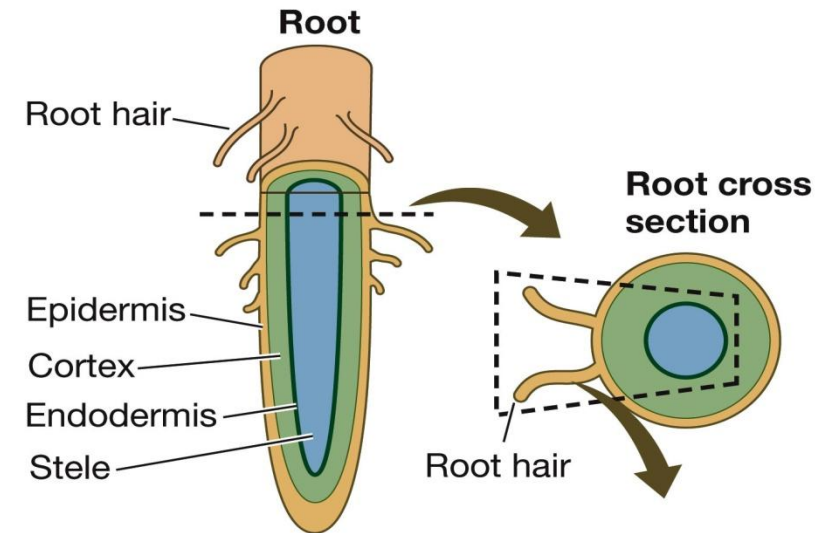
Water and mineral ion movement is linked

- Where water moves by bulk flow, dissolved minerals are carried along
- Water & minerals also move by diffusion
- Minerals may move by active transport (e.g., at root hairs).
 - Ions must cross other membranes (opportunity for regulation) to reach vessels and tracheids



35.1 How Do Plant Cells Take Up Water and Solutes?

- Ion movement across membranes can result in water movement
 - Water moves into root because root has more negative water potential than soil (i.e. higher solute concentration than soil)
 - Water moves from cortex into stele because stele has more negative water potential than cortex

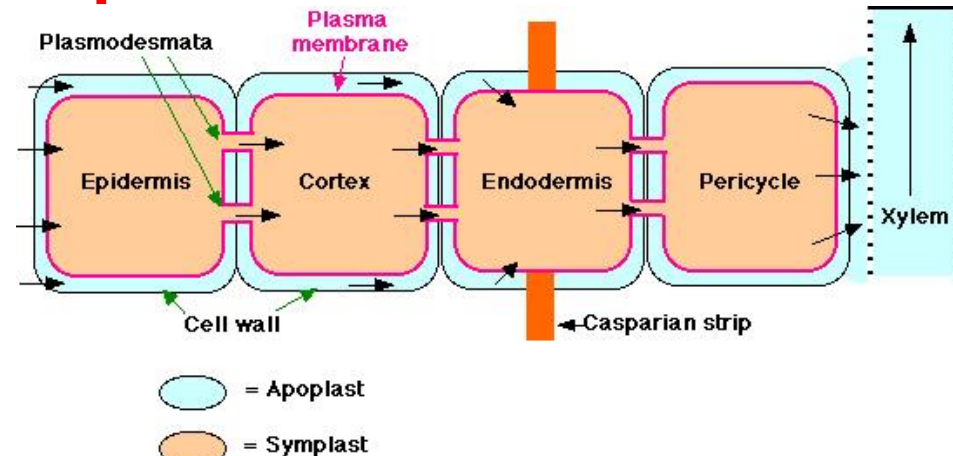


LIFE 9e, Figure 35.6 (Part 1)

35.1 How Do Plant Cells Take Up Water and Solutes?

Water and minerals can move into stele by two paths: **apoplast** and **symplast**

- **Apoplast** (“fast lane”)
 - Cell walls and intercellular spaces form continuous meshwork that water can move through, *without crossing membranes*
 - Water movement is fast and unregulated until it reaches **Casparian strips** of endodermis



35.1 How Do Plant Cells Take Up Water and Solutes?

▪ **Symplast** (“slow lane”)

- H₂O passes thru cells via plasmodesmata
- Selectively permeable membranes of *root hair cells* control access to the symplast → *allows regulation of uptake*

Anytime minerals cross a membrane, allows for regulation

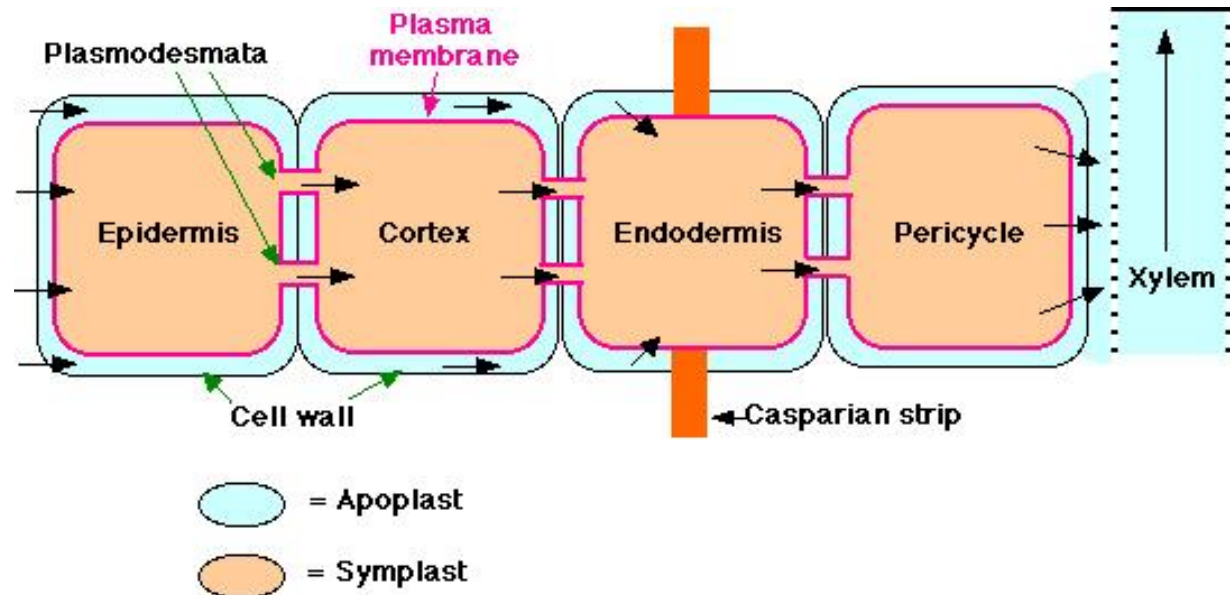


Figure 35.6 Apoplast and Symplast (Part 1)

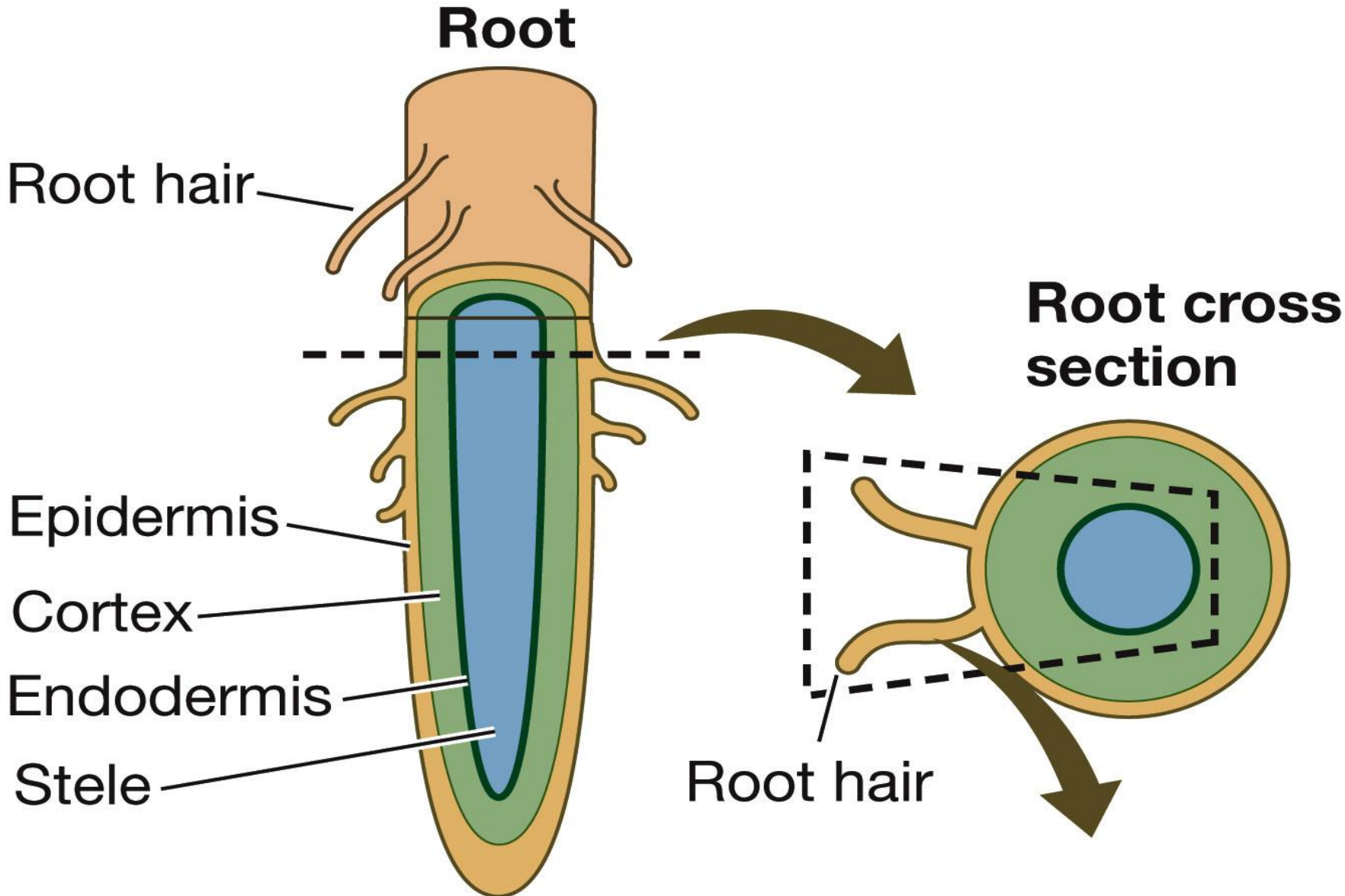
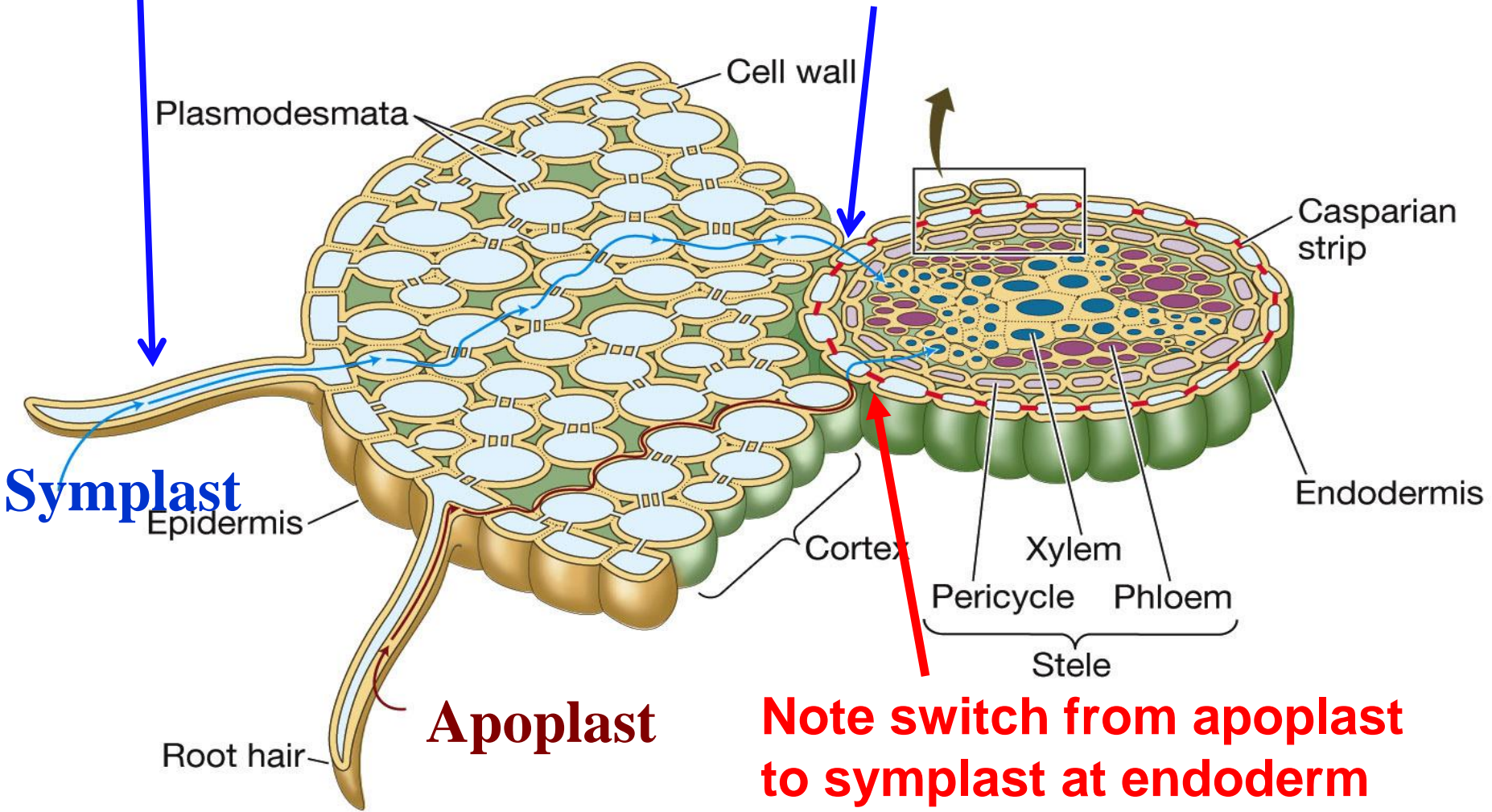


Figure 35.6 Apoplast and Symplast (Part 2)

Once in symplast, stays in symplast all the way to stele



Symplast

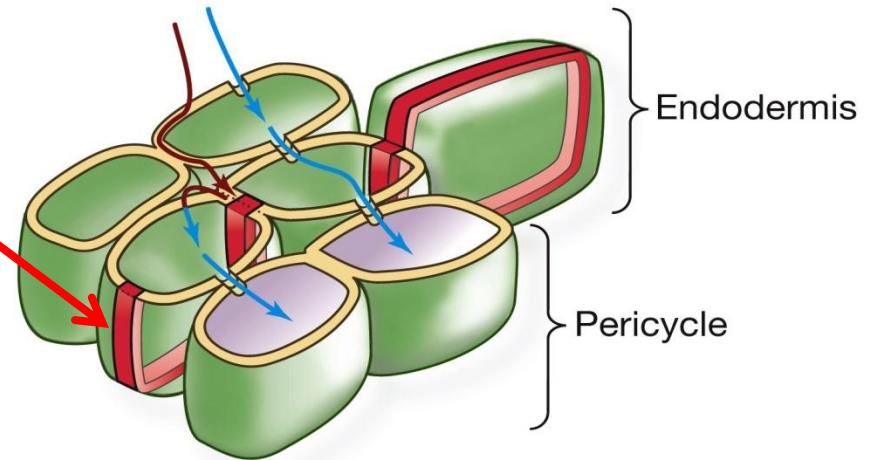
Apoplast

Note switch from apoplast to symplast at endoderm due to Casparian strip

35.1 How Do Plant Cells Take Up Water and Solutes?

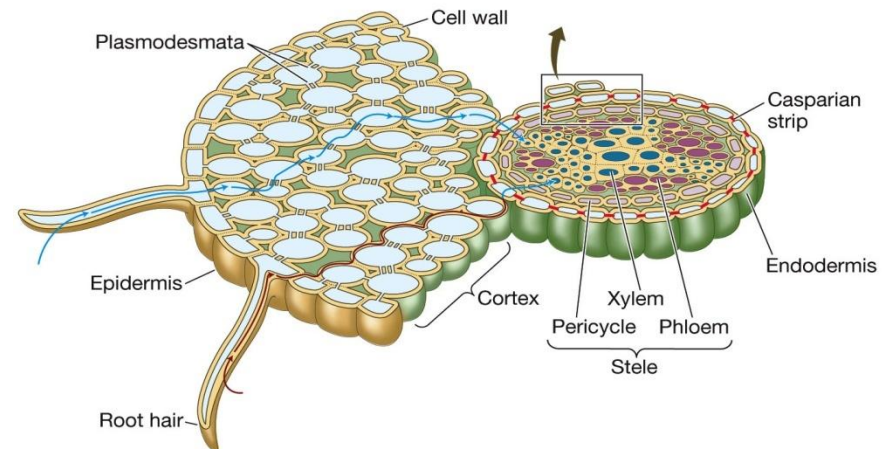
Casparian strips

- Regions of suberin-impregnated endodermal cell walls
- Form water-repelling belt around each endodermal cell
- Separates apoplast of cortex from apoplast of stele
- Water and ions can enter stele only through endodermal cells → *allows regulation of uptake*



LIFE 9e, Figure 35.6 (Part 3)

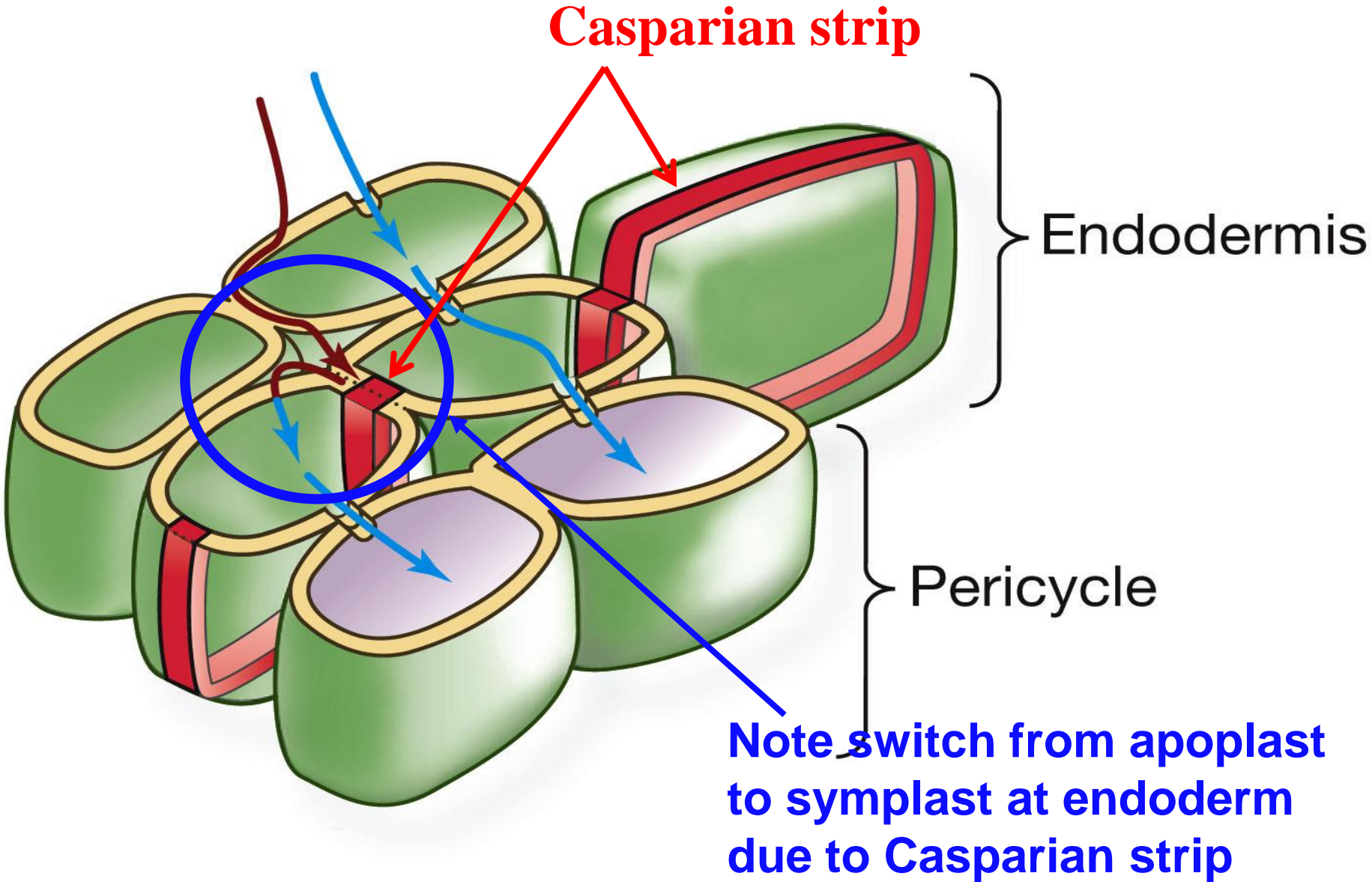
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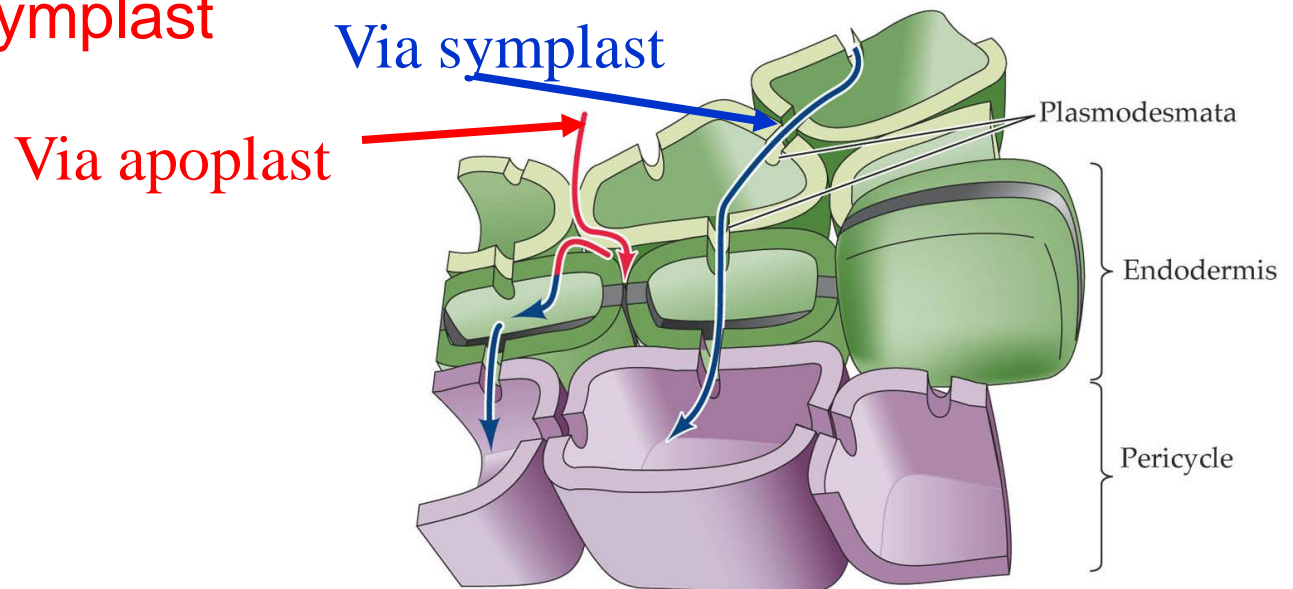
LIFE 9e, Figure 35.6 (Part 2)

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Figure 35.6 Apoplast and Symplast (Part 3)



- Water & ions enter stele *only thru symplast* → by entering and passing thru endodermal cytoplasm
 - Symplast transport (initially selected at root hair cells) passes directly to stele, bypassing strip, OR...
 - Initially via apoplast transport, water and ions must go around Casparian strip *at endoderm* through cell membrane where selectivity occurs before moving into stele via symplast

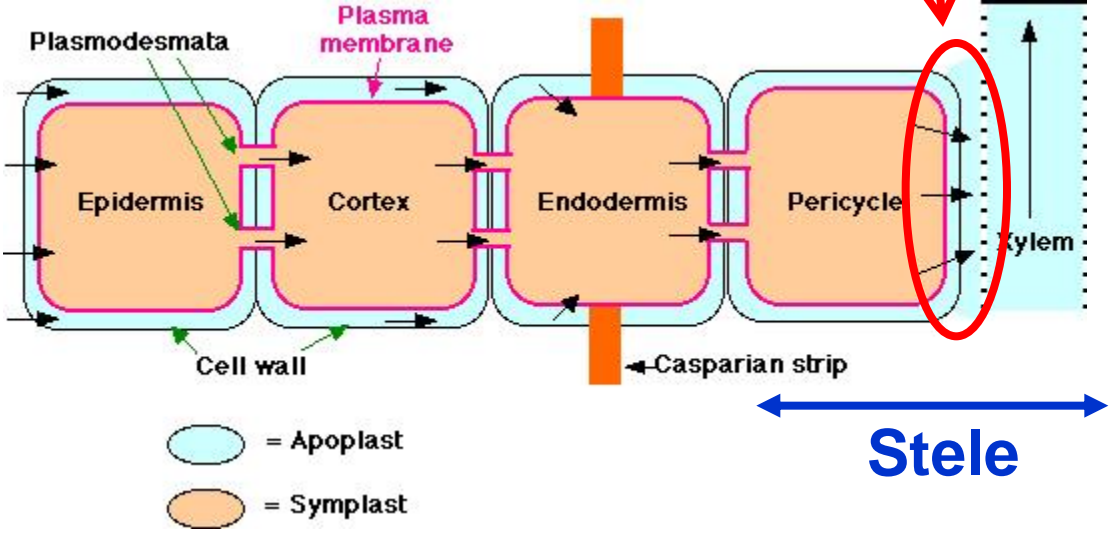
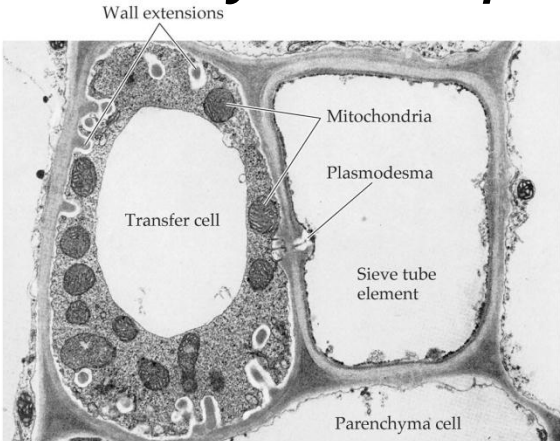


35.1 How Do Plant Cells Take Up Water and Solutes?

http://www.progressivegardens.com/knowledge_tree/waterpath.jpg

Once within **stele**...

- Minerals enter apoplast via **active transport** by **transfer cells** →
- Water potential in cell walls becomes more negative, and **water moves into apoplast by osmosis**
- Water and minerals end up in xylem, forming **xylem sap**



35.2 How Are Water and Minerals Transported in the Xylem?

Xylem transport

- Xylem vessels are dead and have no cell contents
→ fused end to end forming long tubular “straw” of lignified cell walls
- Tallest trees exceed 110 meters – xylem must transport lots of water to great height
- Several models for xylem transport have been proposed

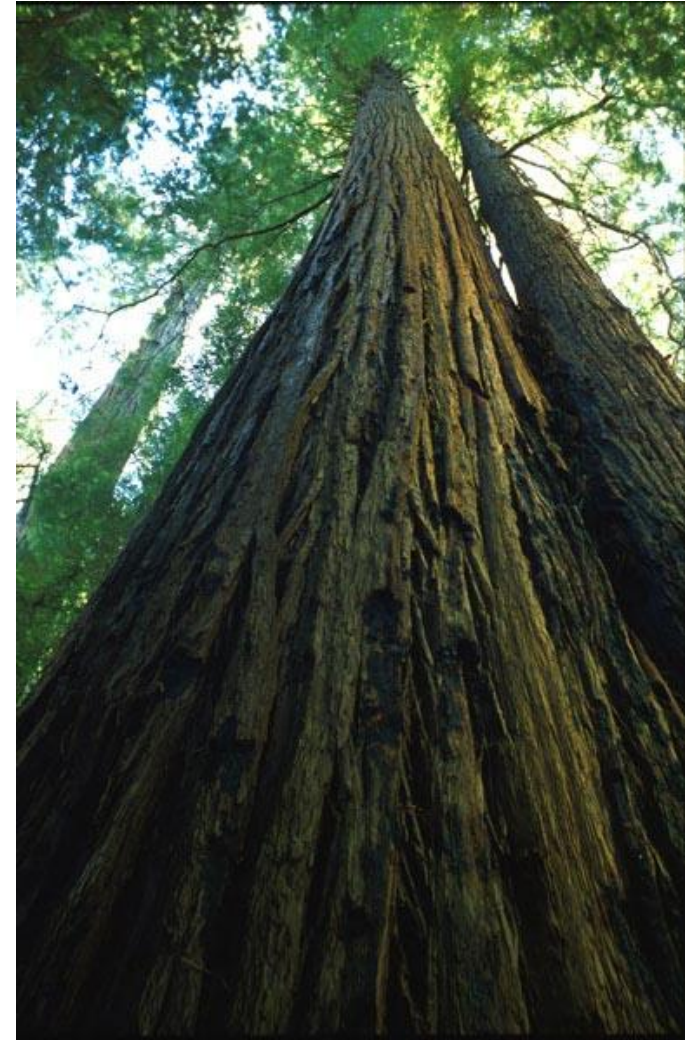
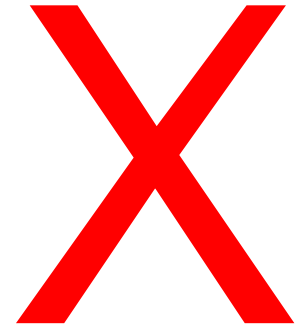


Photo 35.3 Trunk of coastal redwood (*Sequoia sempervirens*).

35.2 How Are Water and Minerals Transported in the Xylem?

1. First proposal was pumping action by living cells.

- Ruled out in 1893 by classic experiment
- Cut trees were placed in poison solution
- Solution rose through trunk to leaves (which died), then stopped rising



35.2 How Are Water and Minerals Transported in the Xylem?

- This experiment established three points:
 - Live, “pumping” cells were not involved
 - Leaves were crucial – solution continued to rise until leaves were dead
 - Movement was not caused by roots

35.2 How Are Water and Minerals Transported in the Xylem?

2. Some hypothesized that xylem transport is based on **root pressure**
 - Higher solute concentration and more negative water potential in roots than in soil solution
 - Perhaps water enters stele and from there water has no where to go but up

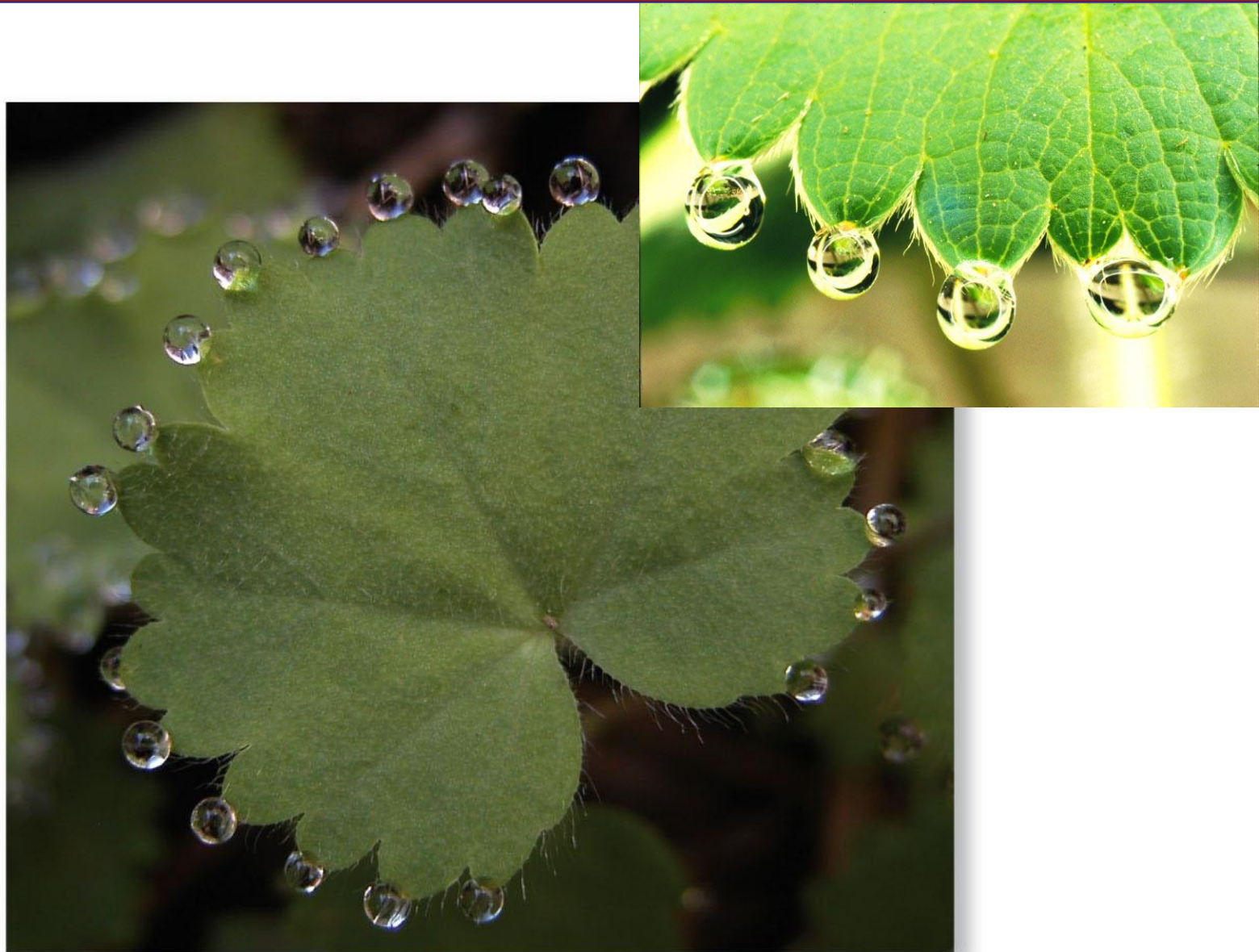
Online-analysis of xylem sap in *Ricinus communis* L., cultivated in aeroponic spray system and monitored in shoot cuvette. Note separate chambers for controlling pressure of roots and stem.



35.2 How Are Water and Minerals Transported in the Xylem?

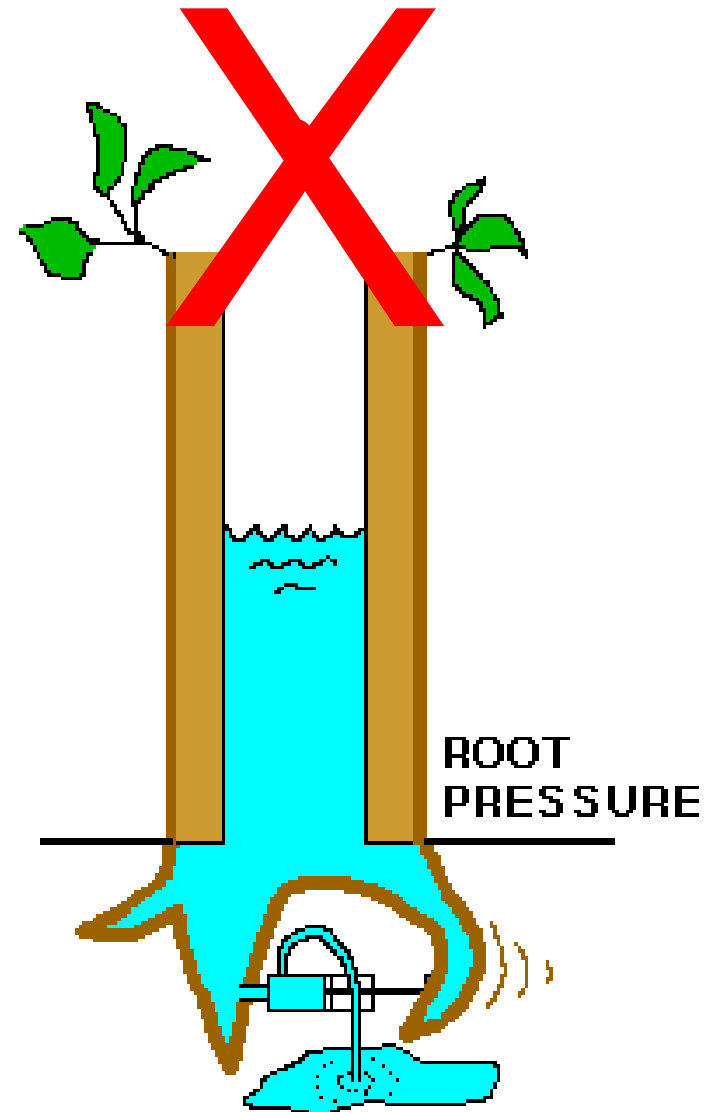
- **Guttation** is evidence of root pressure → water is forced out through openings in leaves
 - Root pressure also causes sap to ooze from cut stumps





35.2 How Are Water and Minerals Transported in the Xylem?

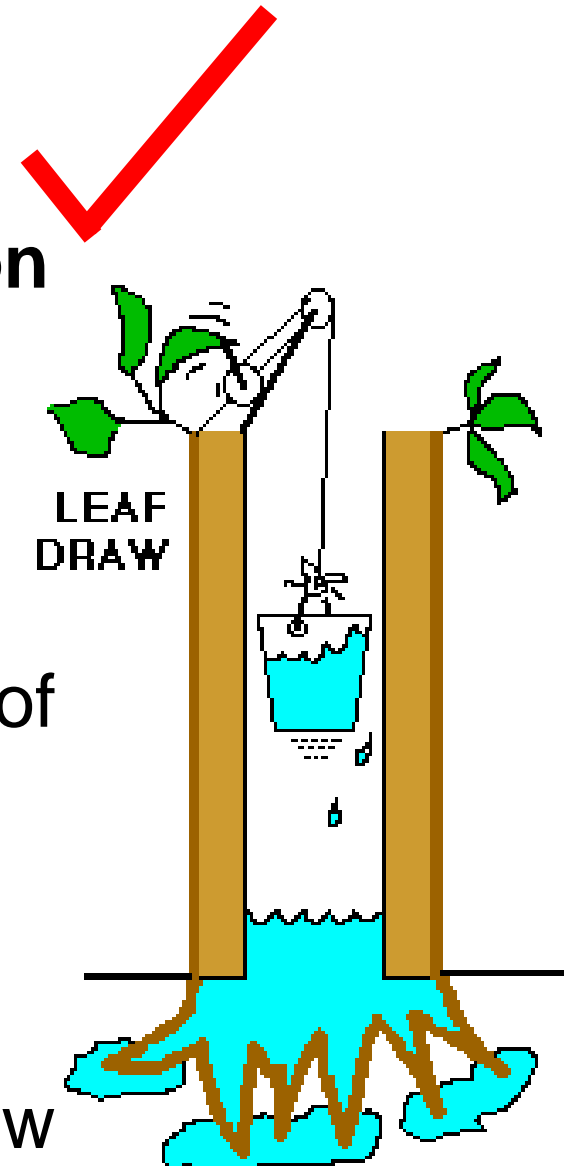
- But root pressure can not account for ascent of sap in trees
 - If root pressure was pushing sap up the xylem, there would be a positive pressure potential in xylem at all times
 - But xylem sap in most trees is under tension, i.e. negative pressure potential



35.2 How Are Water and Minerals Transported in the Xylem?

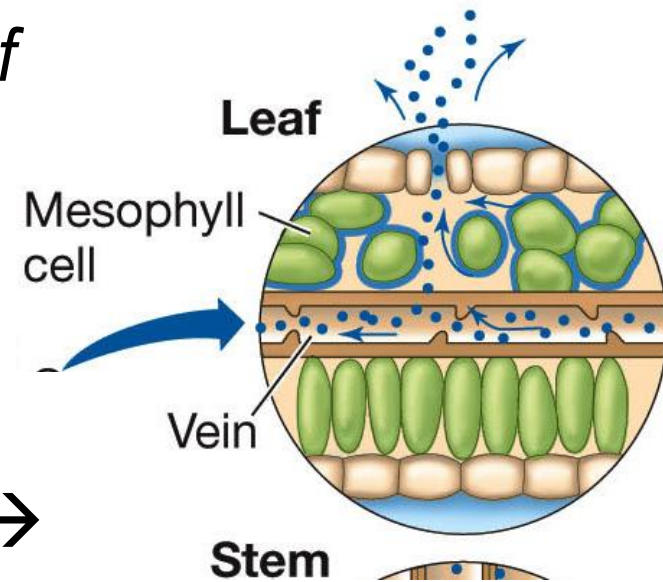
3. Current model: Alternative to pushing is pulling

- **Transpiration–cohesion–tension mechanism**
- Leaves pull xylem sap upwards
 - Evaporative water loss from leaves creates pulling force (tension) on water in apoplast of leaves
 - Hydrogen bonding between water molecules makes sap cohesive enough to withstand the tension and rise by bulk flow



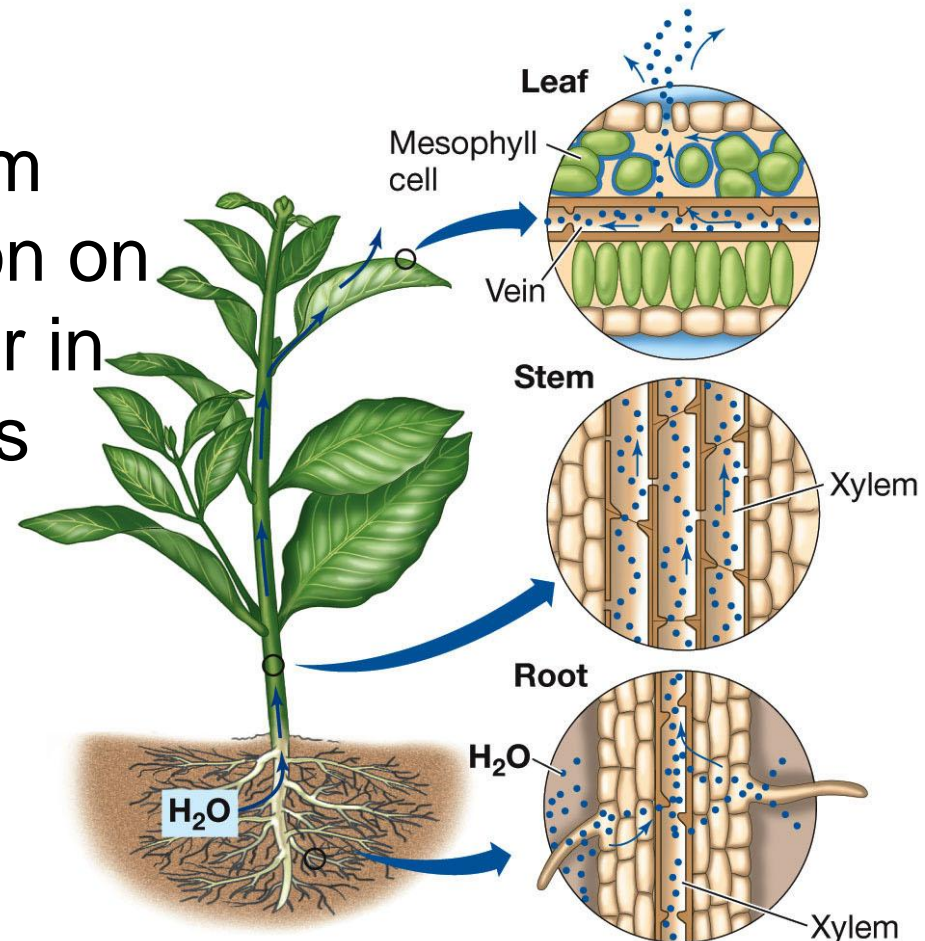
35.2 How Are Water and Minerals Transported in the Xylem?

- Concentration of water vapor in atmosphere is lower than in leaf
 - Water vapor *diffuses from leaf through the stomata:*
transpiration
 - Within leaf, water evaporates from walls of mesophyll cells, film of water on cells shrinks → creating more surface tension (negative pressure potential).
 - Draws more water into cell walls to replace what was lost



35.2 How Are Water and Minerals Transported in the Xylem?

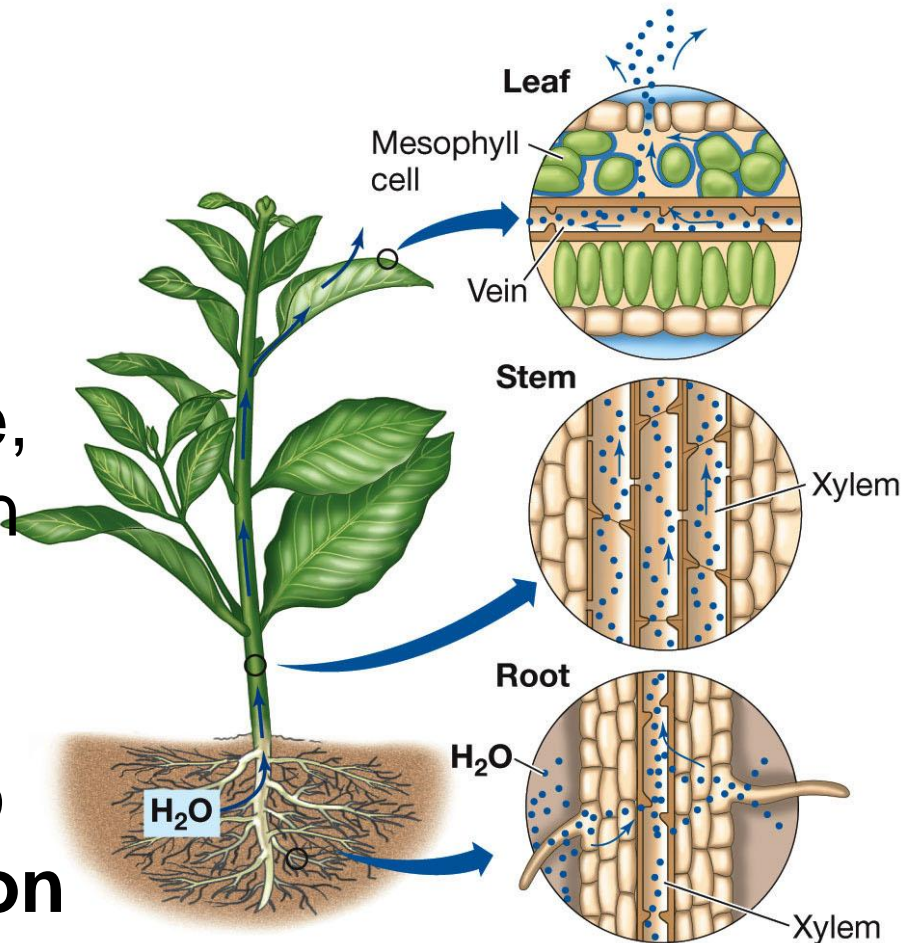
- Resulting tension in mesophyll cells draws water from nearest vein
- Removal of water from veins results in tension on entire column of water in xylem, so that water is drawn up



LIFE 8e, Figure 35.6

35.2 How Are Water and Minerals Transported in the Xylem?

- Ability of water to be drawn up through tiny tubes is due to **cohesion**
 - water molecules stick together because of hydrogen-bonding
 - The narrower the tube, the greater the tension the water column can withstand
 - Water also *adheres* to xylem walls – **adhesion**

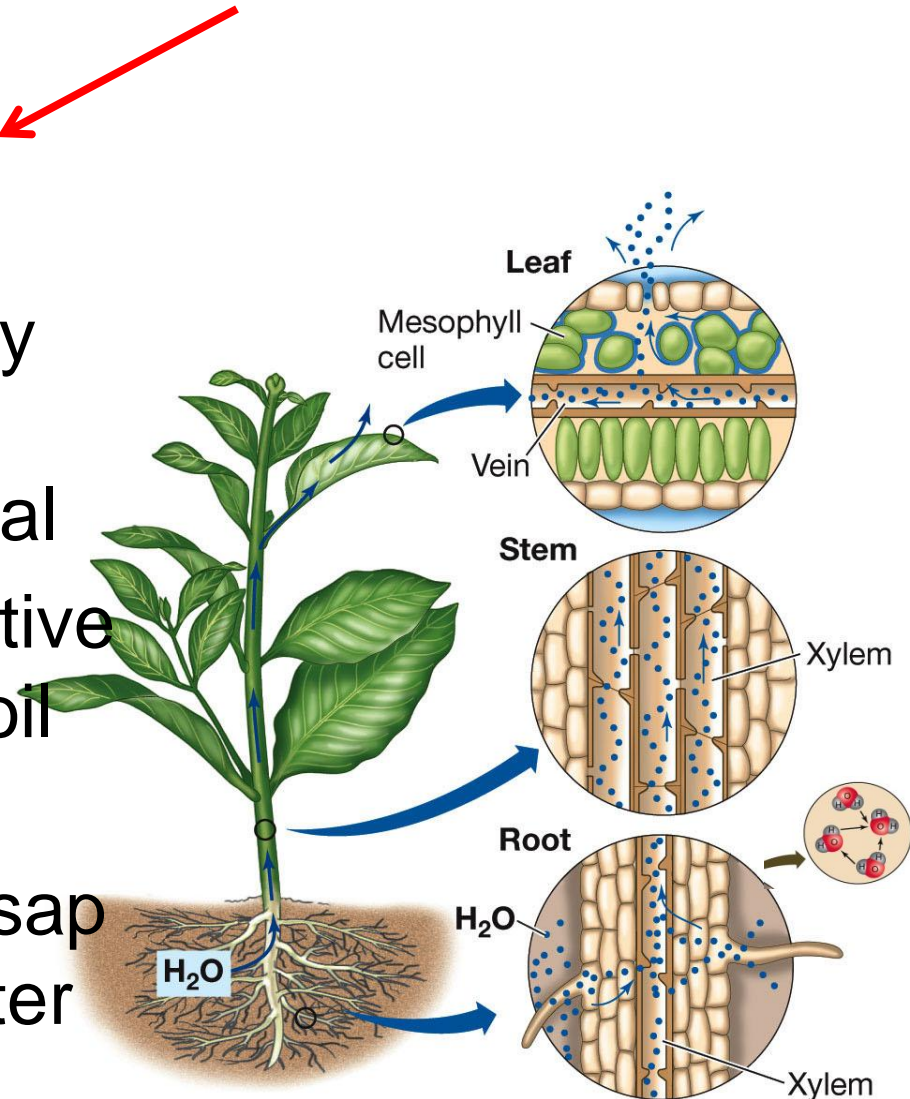


LIFE 8e, Figure 35.6

35.2 How Are Water and Minerals Transported in the Xylem?

- **Transpiration–cohesion–tension mechanism**
requires no energy from plant

- Water moves passively toward region of more negative water potential
- Dry air has most negative water potential, and soil solution has least
- Mineral ions in xylem sap rise passively with water



LIFE 8e, Figure 35.6

Figure 35.7 The Transpiration–Cohesion–Tension Mechanism (Part 1)

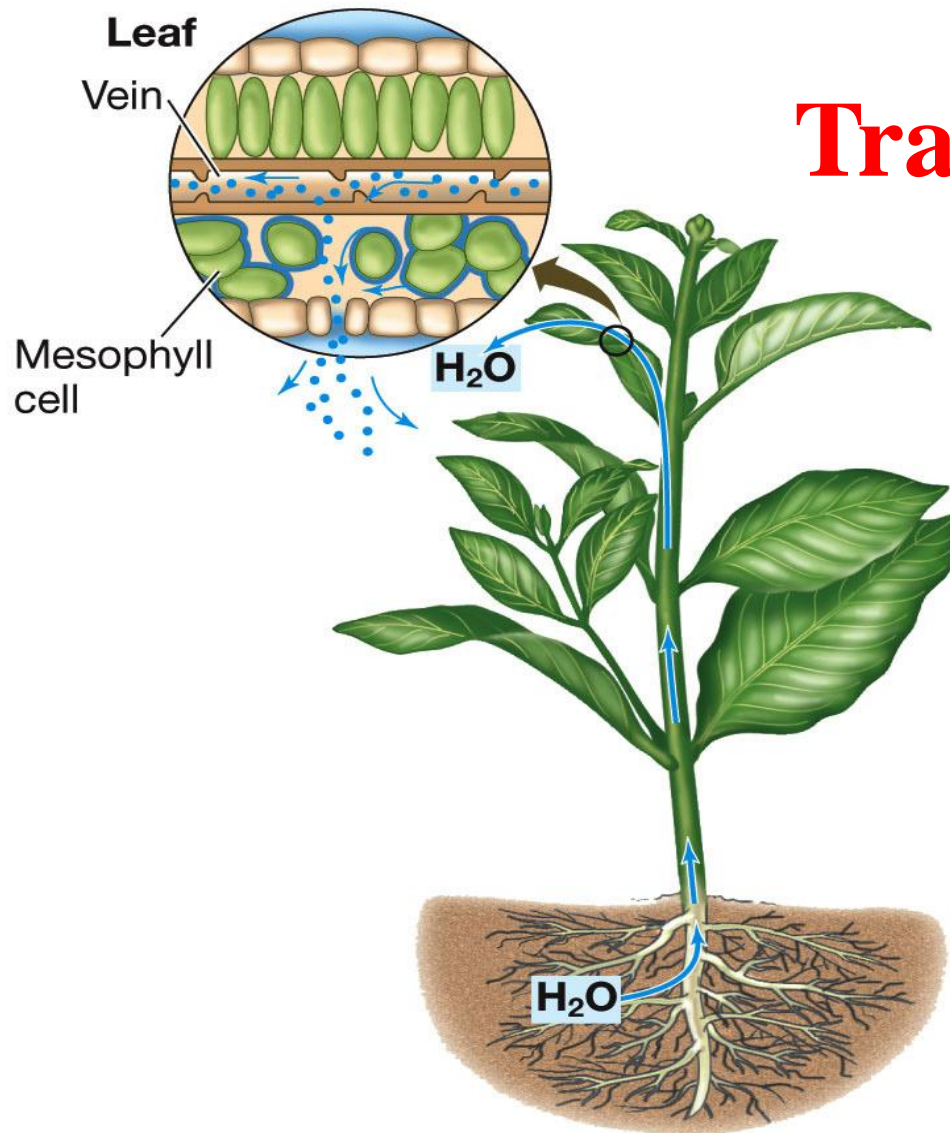


Figure 35.7 The Transpiration–Cohesion–Tension Mechanism (Part 2)

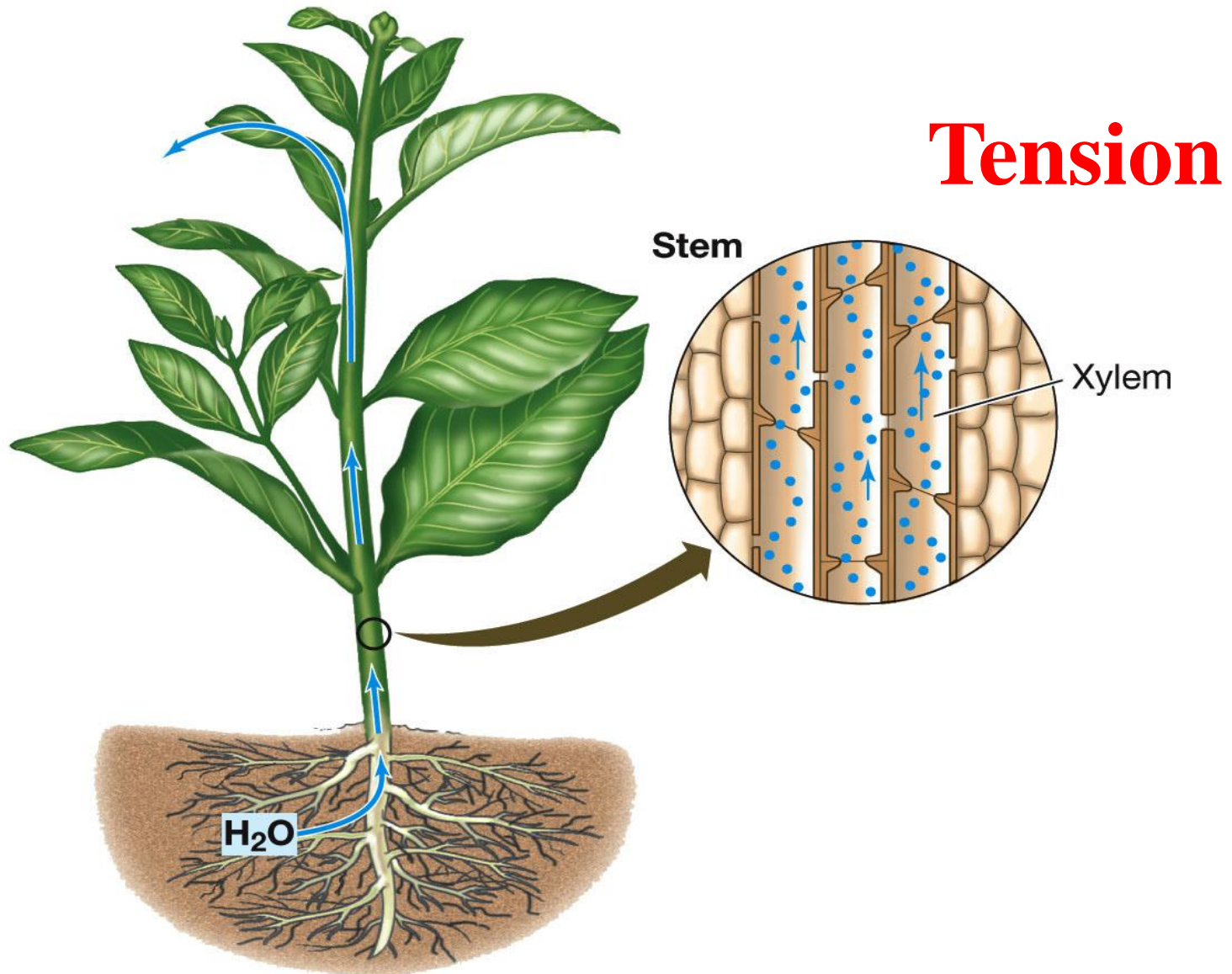
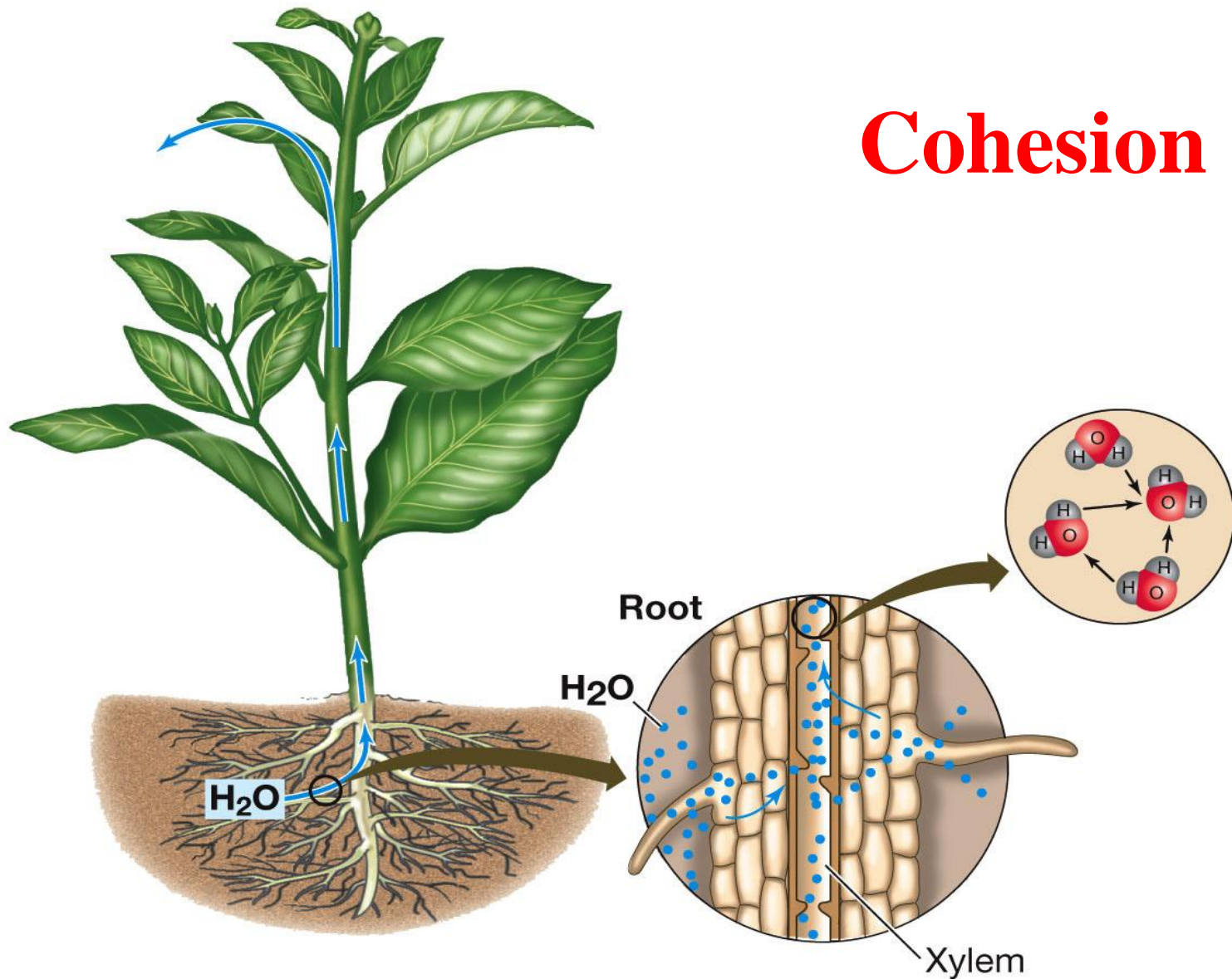
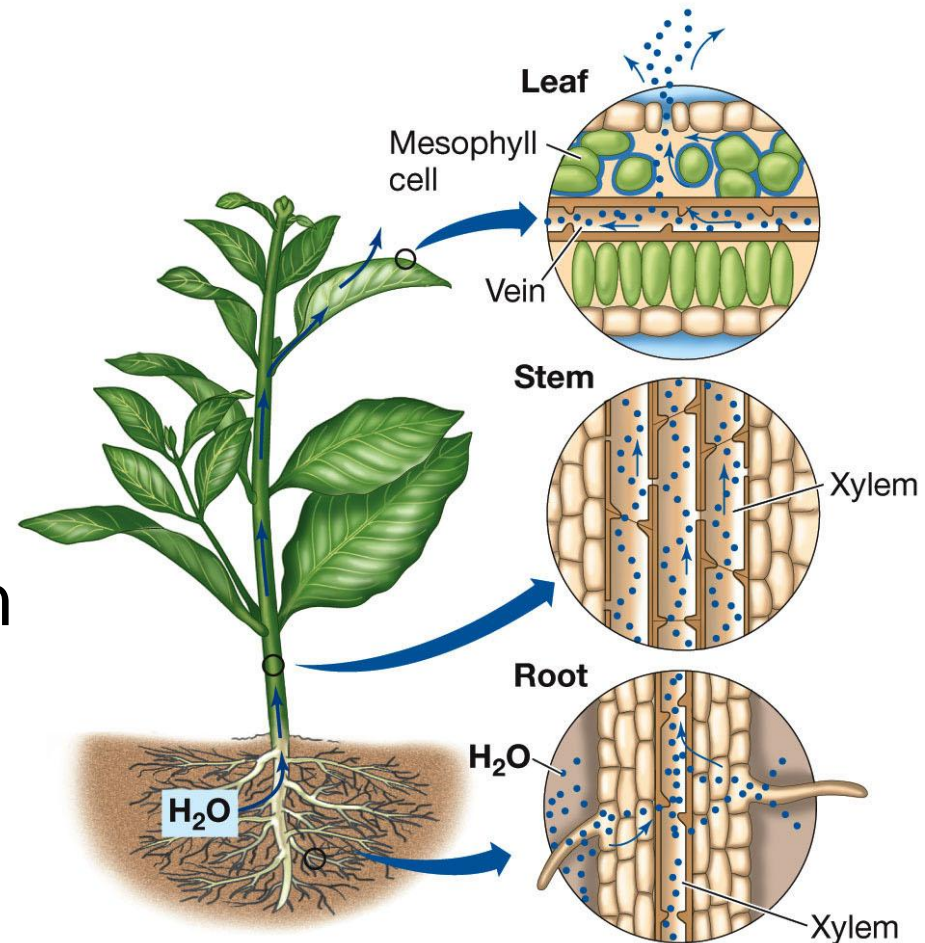


Figure 35.7 The Transpiration–Cohesion–Tension Mechanism (Part 3)



35.2 How Are Water and Minerals Transported in the Xylem?

- Transpiration also helps cool plants via **evaporative cooling**
 - As water evaporates from mesophyll cells, heat is taken up from cells, and leaf temperature drops
 - Important for plants in hot environments



LIFE 8e, Figure 35.6

Animated Tutorial 35.1 Xylem Transport

35.2 How Are Water and Minerals Transported in the Xylem?

Demonstration of negative pressure potential, or tension, in xylem sap was done by measuring tension with **pressure chamber**

- Also determined that tension disappeared at night in some plants, when transpiration stopped

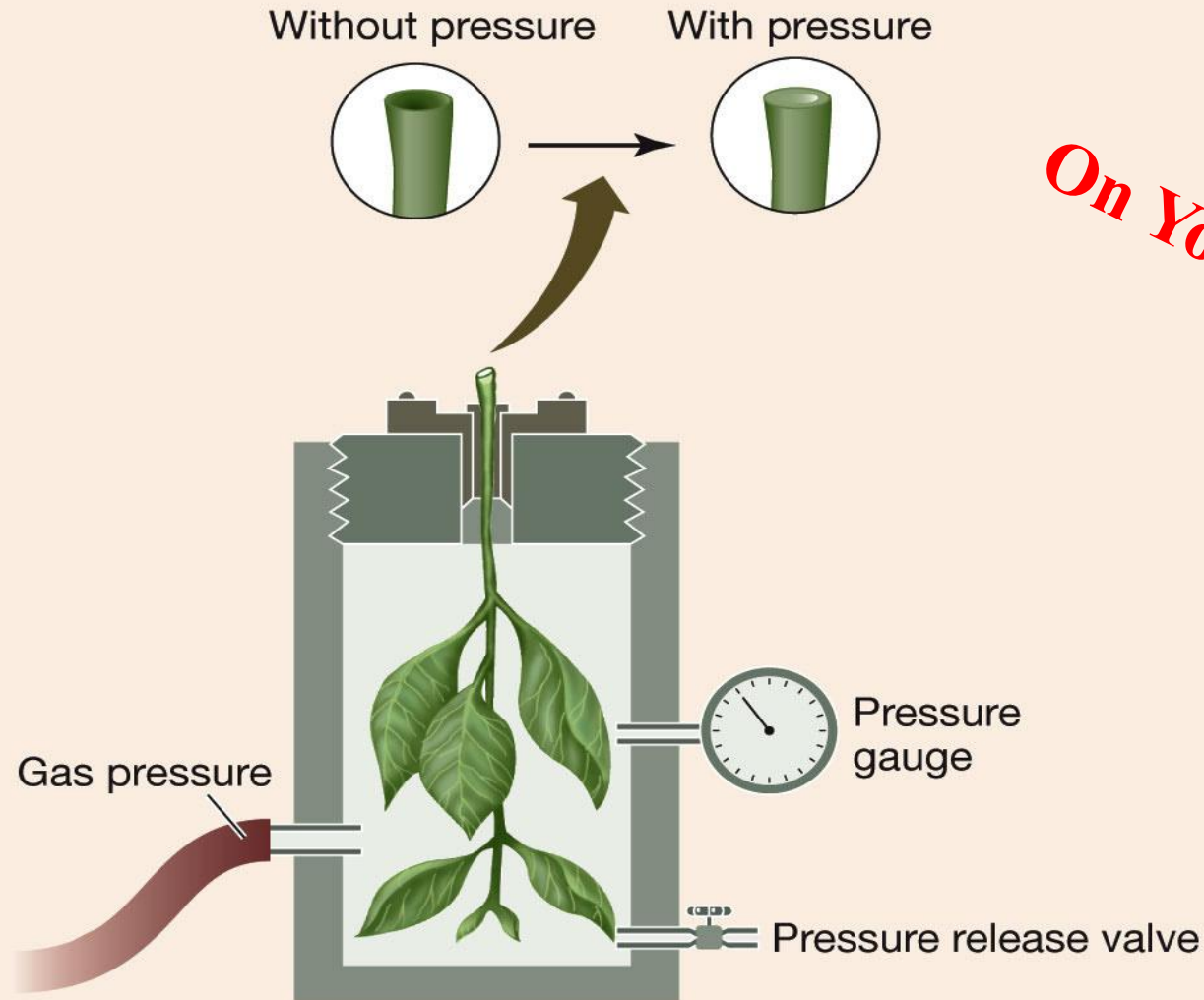
On Your Own

Online-analysis of xylem sap in *Ricinus communis* L., cultivated in aeroponic spray system and monitored in shoot cuvette. Note separate chambers for controlling pressure of roots and stem.



Figure 35.8 Measuring the Pressure of Xylem Sap with a Pressure Chamber

TOOLS FOR INVESTIGATING LIFE



On Your Own

35.3 How Do Stomata Control the Loss of Water and the Uptake of CO₂?

Leaf and stem epidermis has a waxy cuticle to minimize water loss, but it also prevents gas exchange

Stomata

- pores in leaf epidermis
- allow CO₂ to enter by diffusion.
- **Guard cells** control opening and closing

(A)

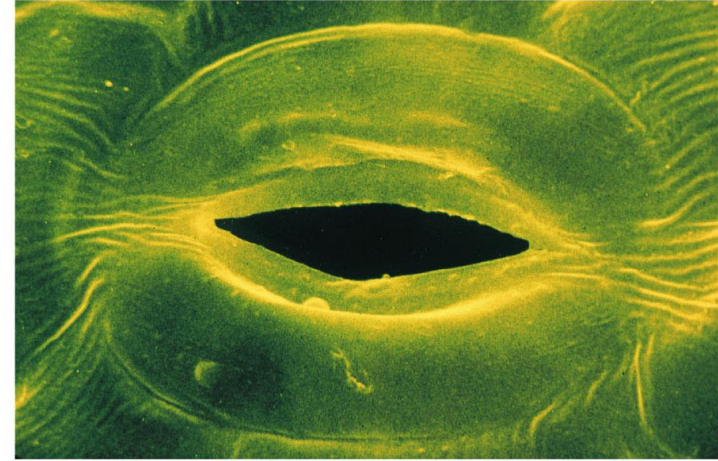


Photo 35.5 Corn leaf epidermis; two guard cells at the edge of a pore. TEM.

35.3 How Do Stomata Control the Loss of Water and the Uptake of CO₂?

Most plants open stomata when light intensity is enough for moderate rate of photosynthesis

- At night, stomata remain closed
 - CO₂ not needed, and no water is lost
- During day, stomata close if water is being lost too rapidly

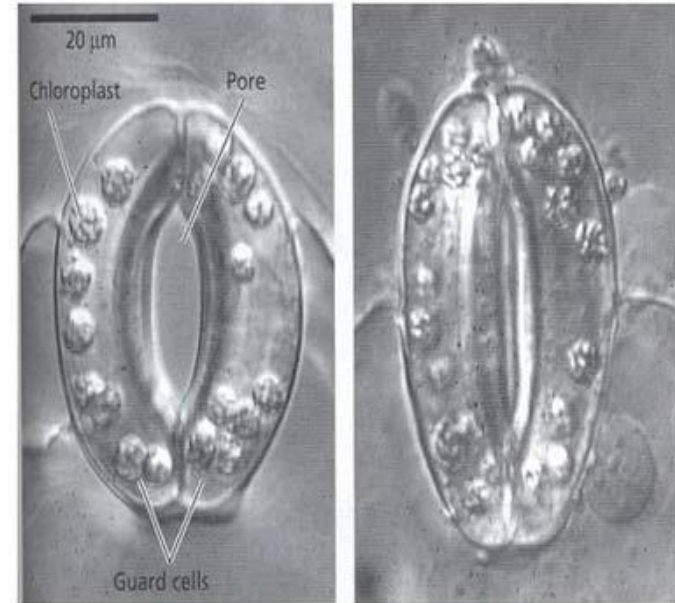


Image reproduced from Plant Physiology, Eds: L. Taiz and E. Zeiger, 2nd edition, Sinauer Associates, Inc. Publisher, Sunderland MA, USA. p. 523

35.3 How Do Stomata Control the Loss of Water and the Uptake of CO₂?

Cues for stomatal opening include light, and concentration of CO₂ in intercellular spaces in the leaf

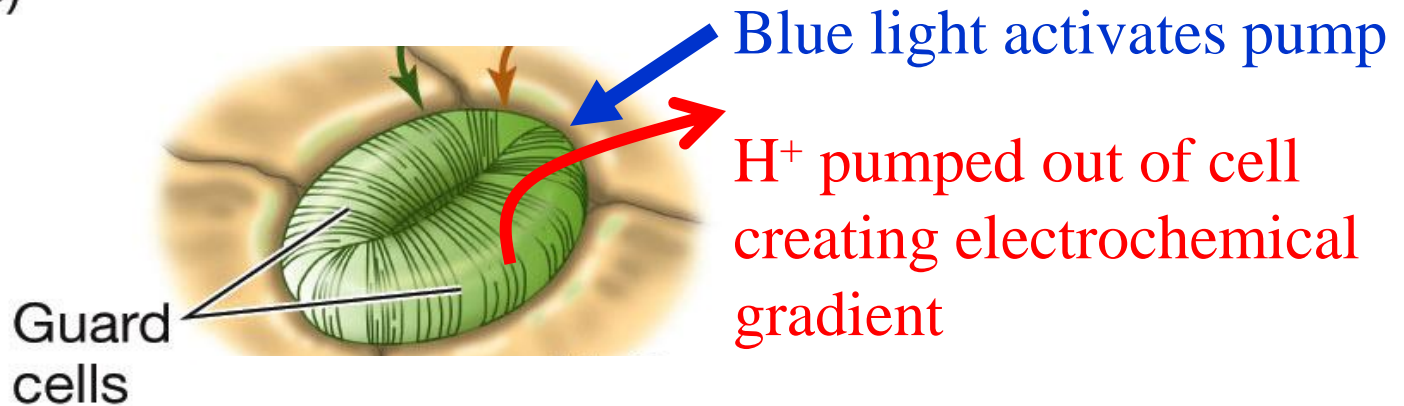
- Low CO₂ levels favor opening of stomata



Photo 35.2 Wilting tomato shoot under water stress

35.3 How Do Stomata Control the Loss of Water and the Uptake of CO₂?

(B)



Opening and closing of stomata is controlled by turgor pressure changes in guard cells driven by blue light, and H⁺ and K⁺

- **Blue light** is absorbed by pigments in guard cells and activates **proton pump**

35.3 How Do Stomata Control the Loss of Water and the Uptake of CO₂?

- Resulting gradient drives **K⁺ and Cl⁻** into guard cell, making its water potential more negative
- **Water enters cell** by osmosis → cells swell
- Increased pressure potential **causes guard cells to change shape**, and a gap appears between them → opening stomata

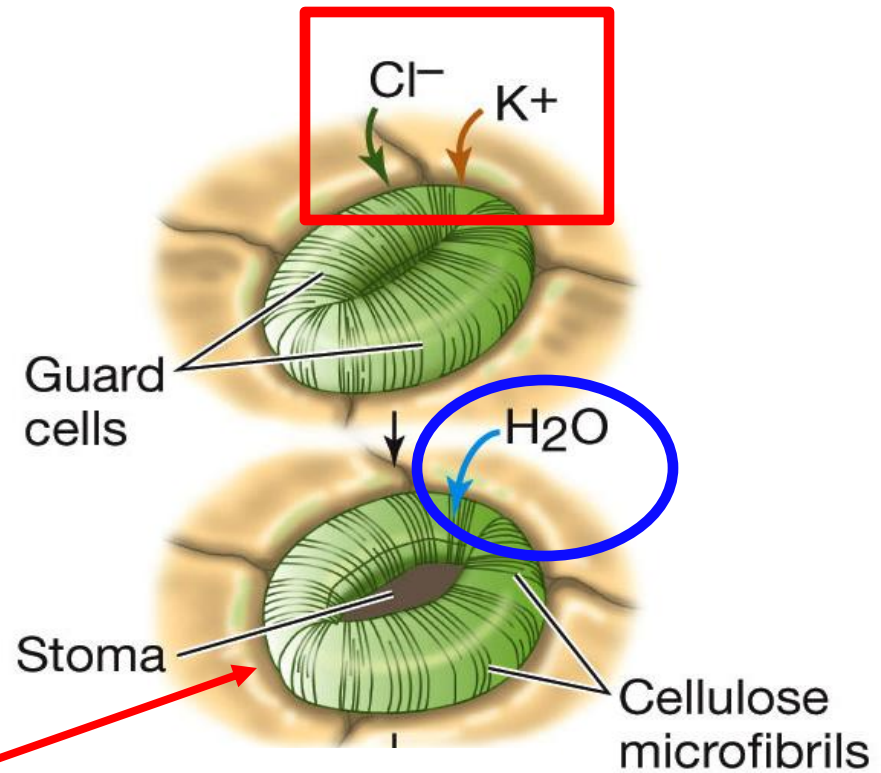
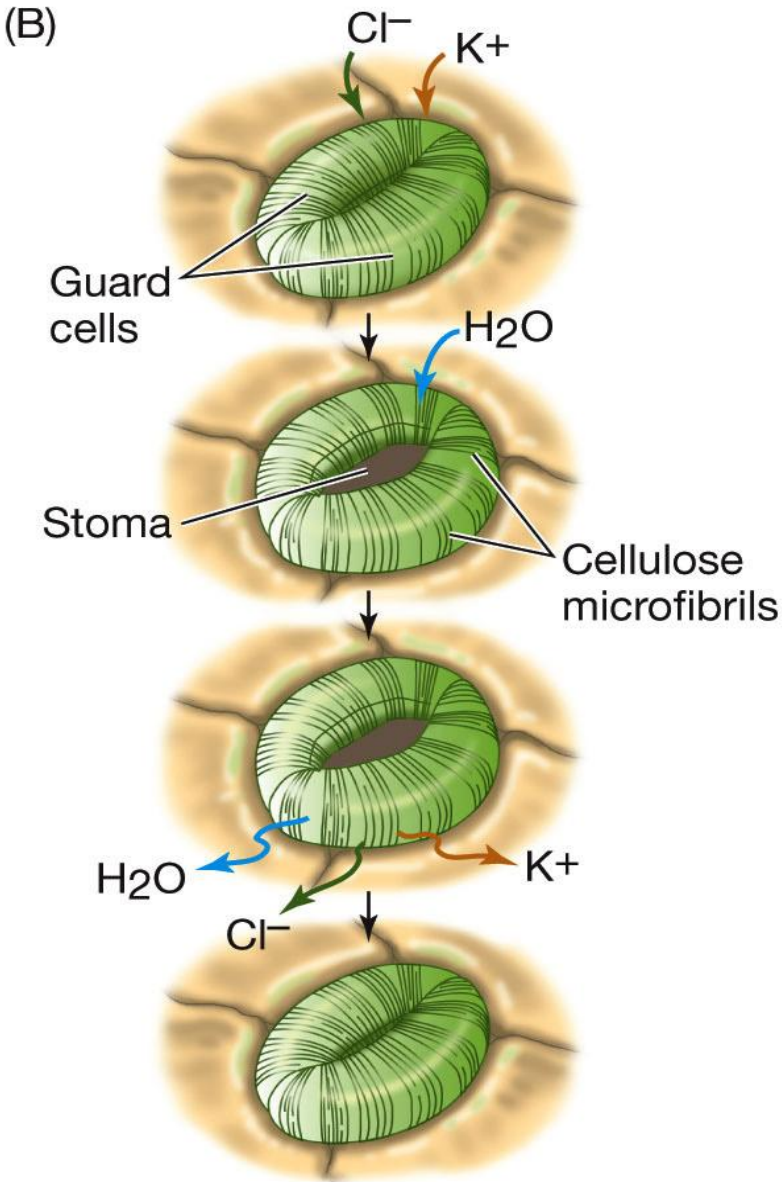
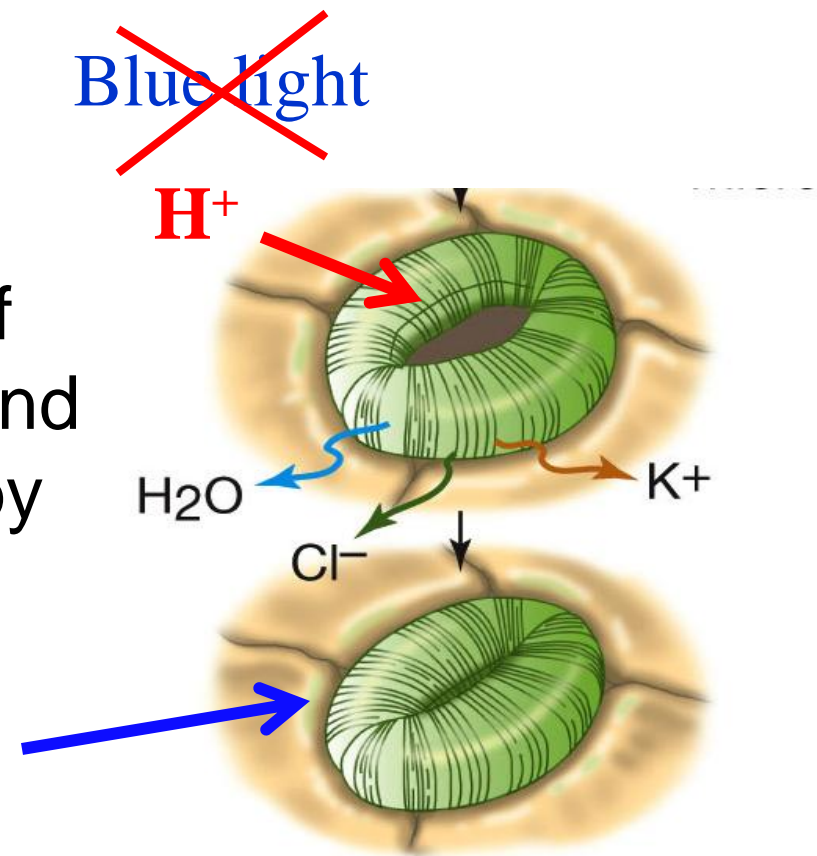


Figure 35.9 Stomata (Part 2)



35.3 How Do Stomata Control the Loss of Water and the Uptake of CO₂?

- Stomata close in absence of light → process is reversed when active transport of protons slows
 - H⁺ move inwards
 - K⁺ and Cl⁻ diffuse out of guard cells passively, and water follows outward by osmosis
- Pressure potential decreases, and **cells sag, closing gap between them**

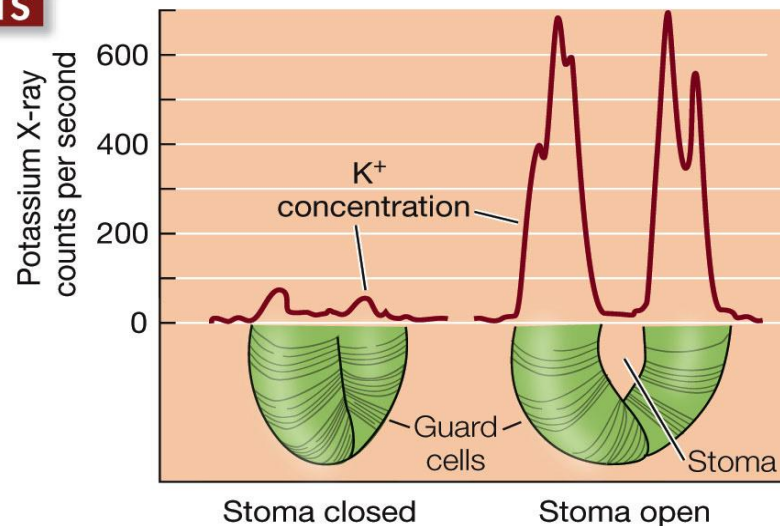


35.3 How Do Stomata Control the Loss of Water and the Uptake of CO₂?

Demonstration of how much K⁺ moves in and out of guard cells was done by using an *electron probe microanalyzer*

On your own

RESULTS



CONCLUSION

K⁺ concentration within the guard cells surrounding an open stoma was much greater than that in the guard cells surrounding a closed stoma.

INVESTIGATING LIFE

HYPOTHESIS

Guard cells of open stomata contain more potassium ions than do those of closed stomata.

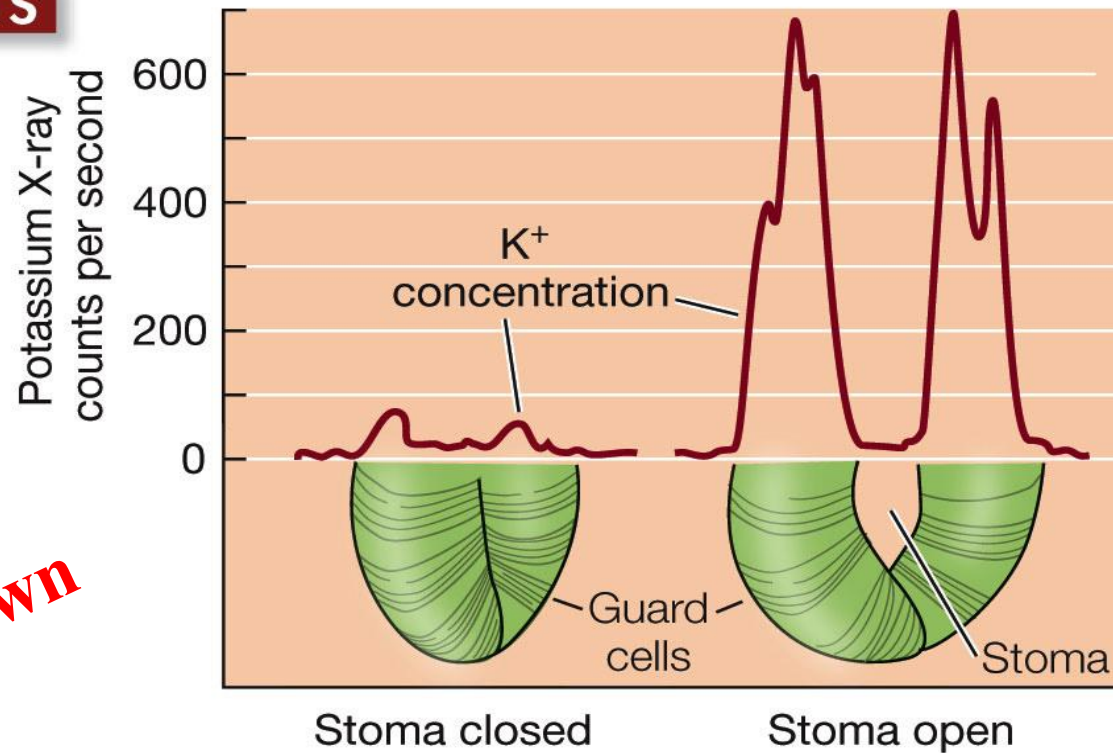
METHOD

1. Peel strips of epidermis from leaves of broad beans in the dark (closed stomata) and in the light (open stomata).
2. Examine the strips to locate stomata.
3. Scan across guard cells with the electron probe microanalyzer set to measure K^+ concentration.

On your own

Figure 35.10 Measuring Potassium Ion Concentration in Guard Cells (Part 2)

RESULTS



On your own

CONCLUSION

K⁺ concentration within the guard cells surrounding an open stoma was much greater than that in the guard cells surrounding a closed stoma.

35.3 How Do Stomata Control the Loss of Water and the Uptake of CO₂?

Plants limit water loss by controlling stomata in two ways:

- By regulating stomatal opening and closing
- By controlling the total number of stomata

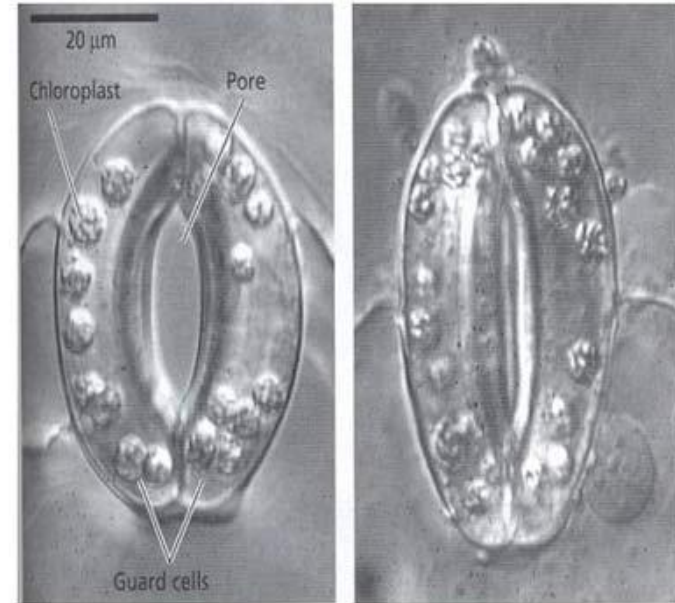
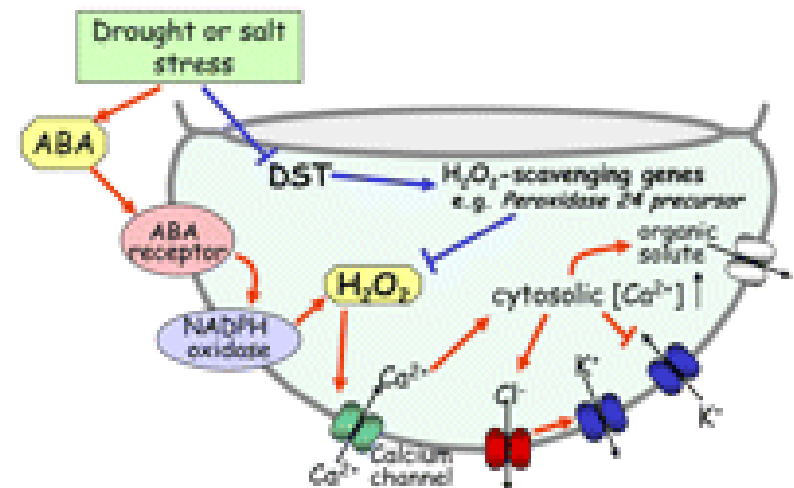


Image reproduced from Plant Physiology, Eds: L. Taiz and E. Zeiger, 2nd edition, Sinauer Associates, Inc. Publisher, Sunderland MA, USA. p. 523

35.3 How Do Stomata Control the Loss of Water and the Uptake of CO₂?

Plants regulate stomatal opening/closing when under water stress or the water potential of mesophyll cells is too negative

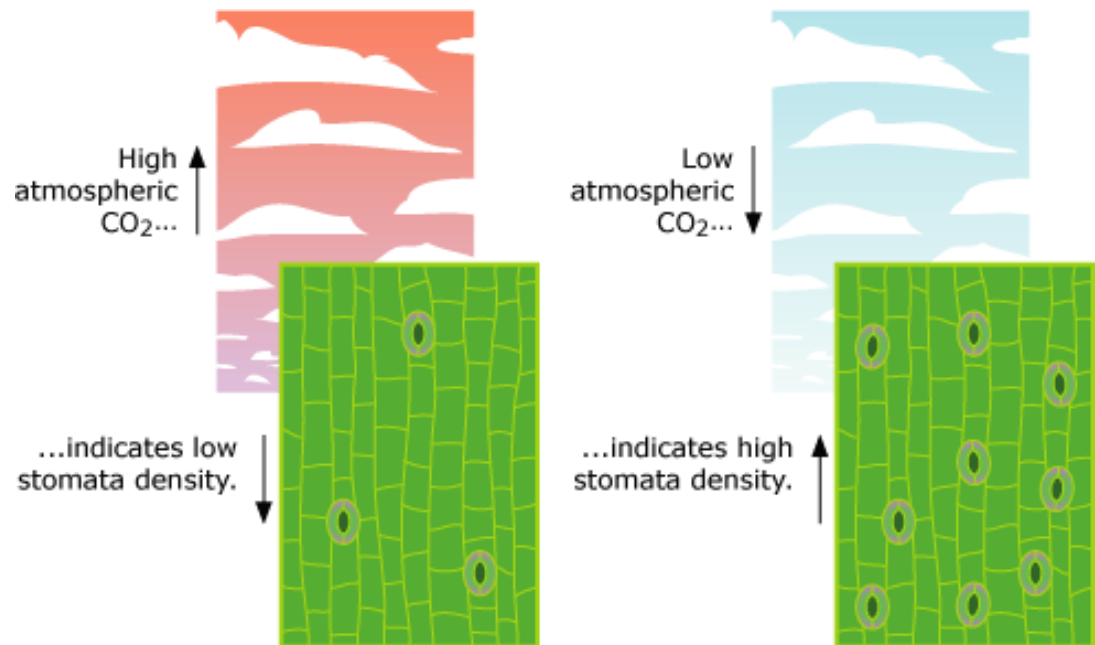
- They release the hormone **abscisic acid** —acts on guard cells and causes them to close
- This reduces photosynthesis, but protects the plant from desiccation
- Stomata also close when CO₂ levels in mesophyll spaces are high



35.3 How Do Stomata Control the Loss of Water and the Uptake of CO₂?

Plants can reduce the number of stomata when water is in short supply

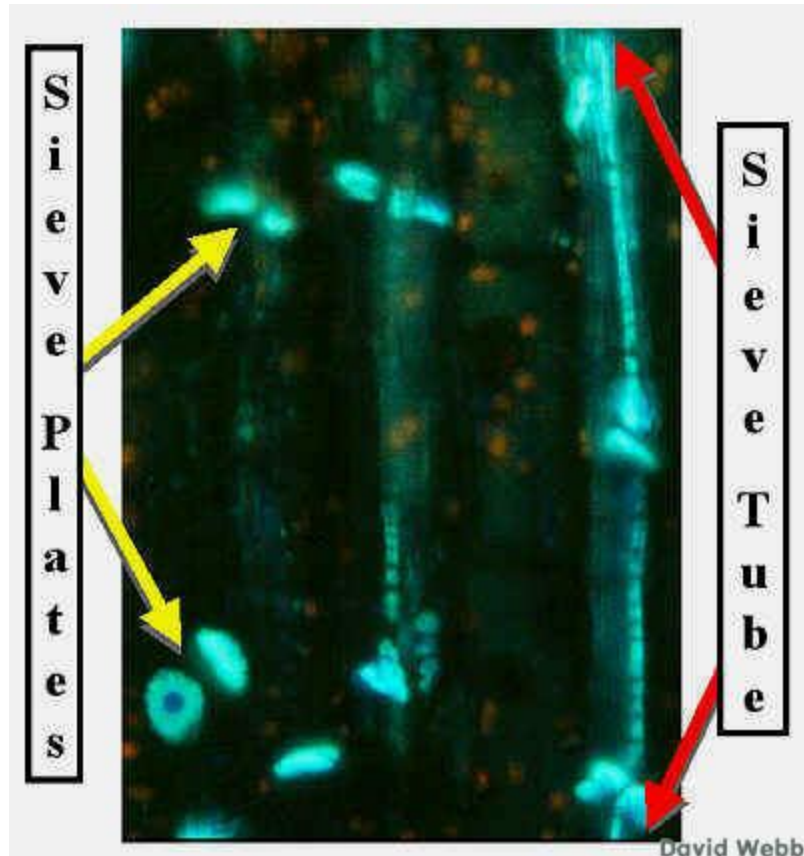
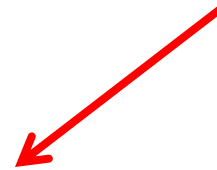
- Trees can do this by losing some leaves.
- Other plants reduce the number of stomata on new leaves
 - If *Arabidopsis* is exposed to high CO₂ levels, new leaves have fewer stomata than under normal conditions.



35.4 How Are Substances Translocated in the Phloem?

Movement of carbohydrates and other solutes through phloem is **translocation** → move from sources to sinks

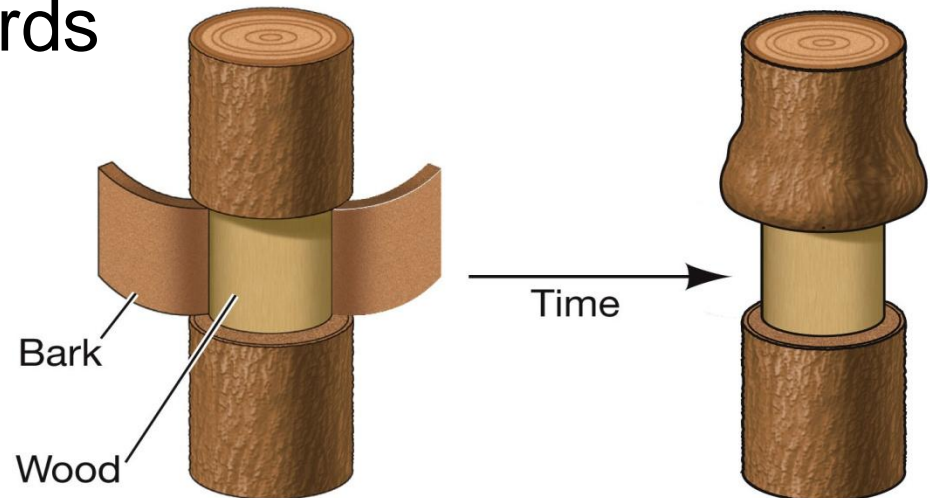
- **Sources** (e.g., leaves) produce more sugars than they require
- **Sinks** consume sugars for growth or storage (root, flower, developing fruit)



35.4 How Are Substances Translocated in the Phloem?

In a classic experiment, a tree was *girdled*

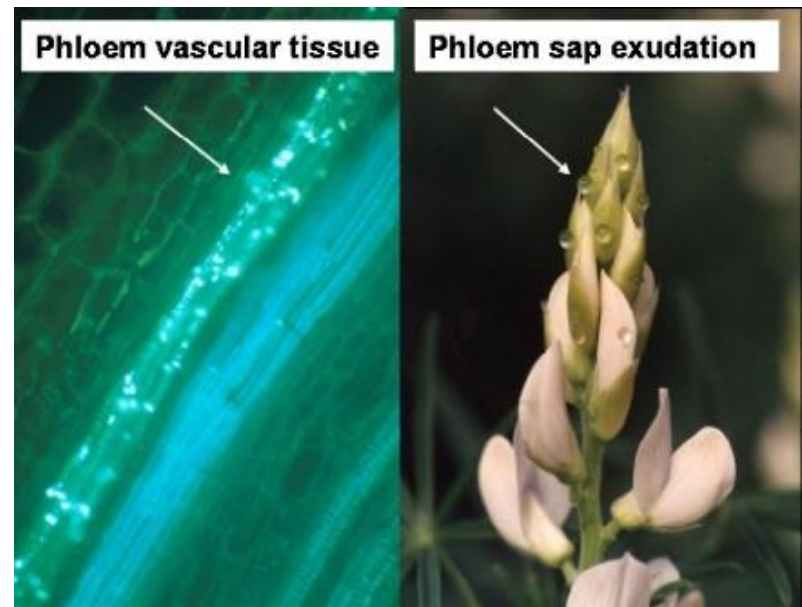
- Ring of bark containing phloem was removed
- Organic solutes collect in phloem above girdle, causing it to swell
- Eventually bark, then roots below, and whole tree die because sugars are not being translocated downwards



35.4 How Are Substances Translocated in the Phloem?

Characteristics of **translocation**:

- Movement of organic solutes
- Stops if phloem is killed
- Proceeds in both directions simultaneously
- Inhibited by compounds that inhibit respiration and limit ATP supply



35.4 How Are Substances Translocated in the Phloem?

Structure of phloem:

- **Sieve tube elements** meet end-to-end; plasmodesmata in end walls enlarge to form **sieve plates**, and most of the cell contents are lost.
- **Companion cells** are produced as daughter cells along with the sieve tube element when a parent cell divides.

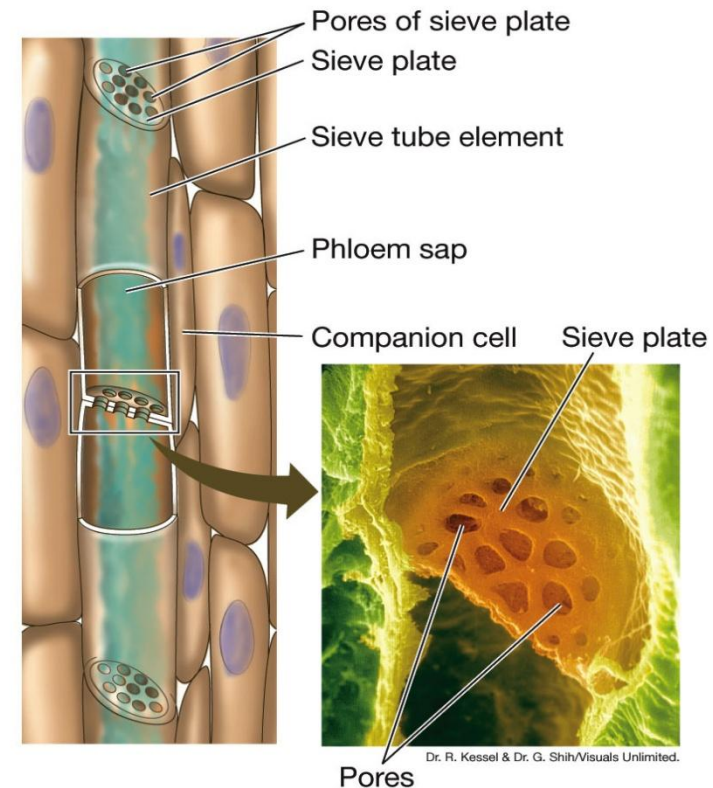
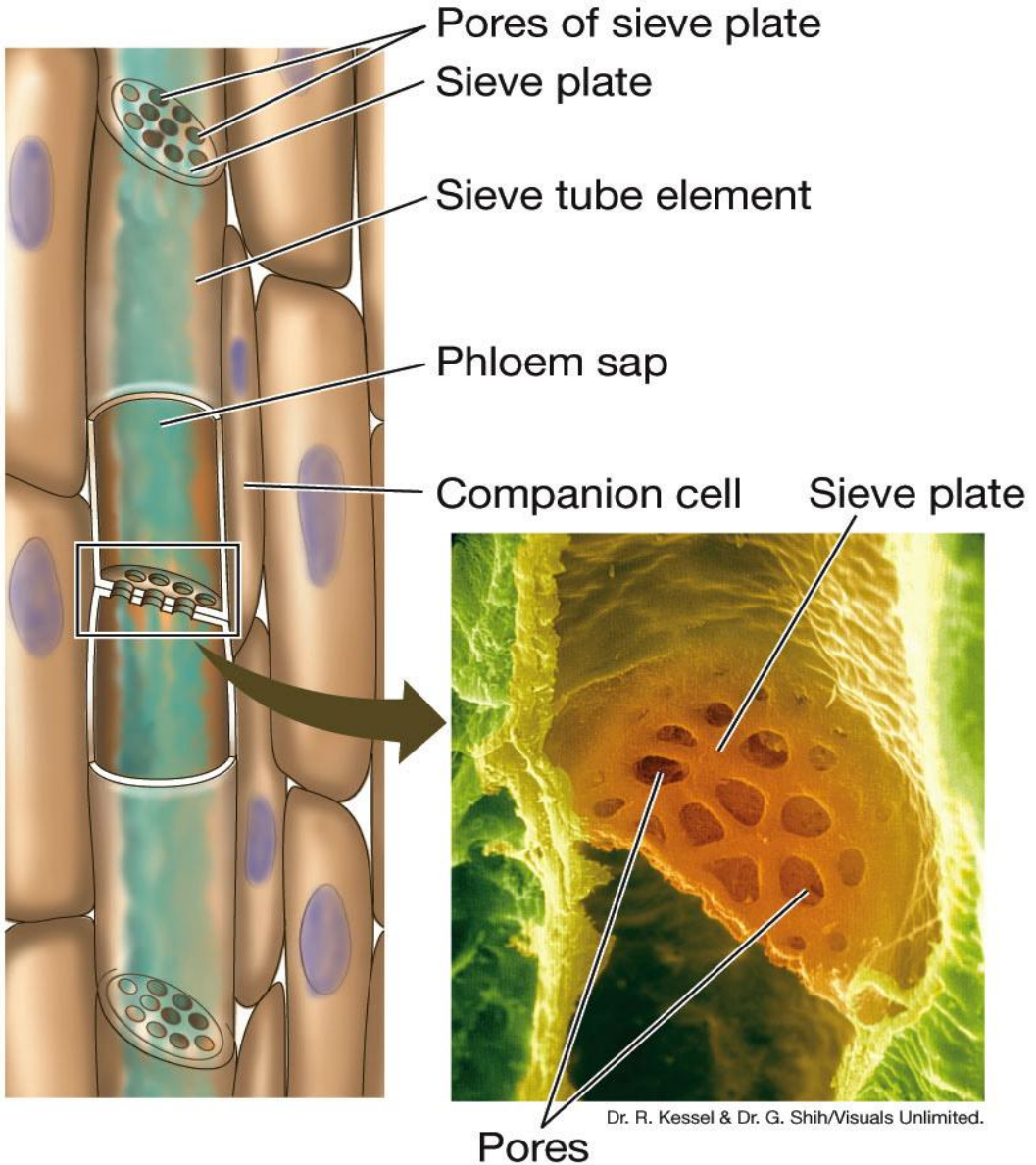


Figure 35.12 Sieve Tubes

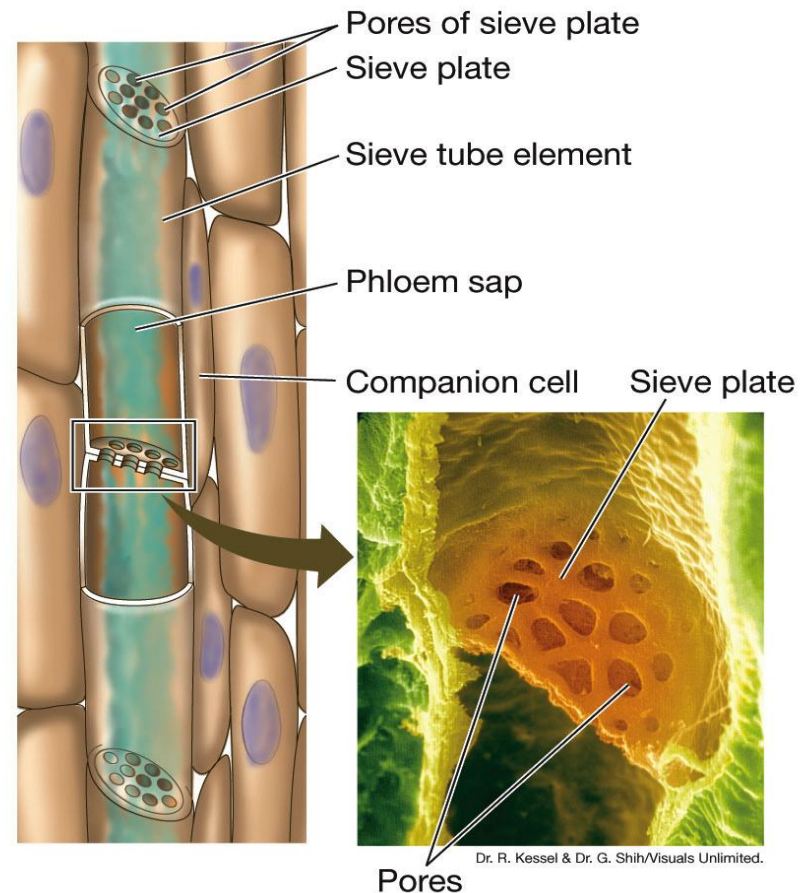


LIFE 9e, Figure 35.12

35.4 How Are Substances Translocated in the Phloem?

Plasmodesmata link companion cells with sieve tube elements

- Companion cells retain all their organelles and provide all functions needed to maintain sieve tube elements
- Phloem sap is able to move rapidly by bulk flow



35.4 How Are Substances Translocated in the Phloem?

Plant physiologists needed to sample pure phloem sap from individual sieve tube elements

- Aphids feed on plants by drilling into sieve tubes and inserting their *stylet*
- Pressure in sieve tube forces sap through stylet and into aphid's digestive tract.

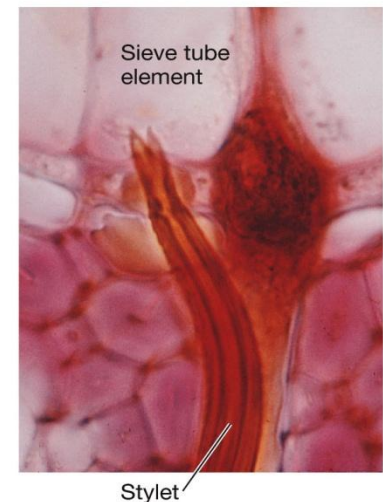
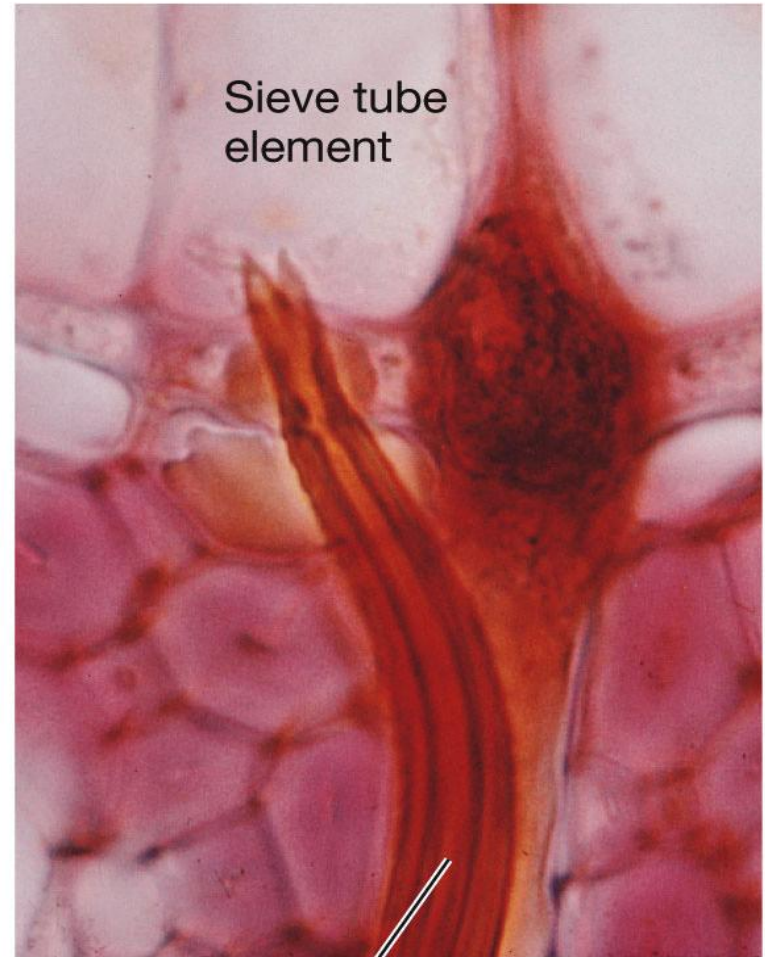


Figure 35.13 Aphids Collect Sap



Sap droplet

Longistigma caryae



Sieve tube element

Stylet

35.4 How Are Substances Translocated in the Phloem?

Plant physiologists use aphids by cutting the body away from the stylet

- Phloem sap continues to flow for hours and can be collected and analyzed
- Using radioactive tracers, they can infer how long it takes for translocation to occur
- These and other experiments led to development of **pressure flow model**



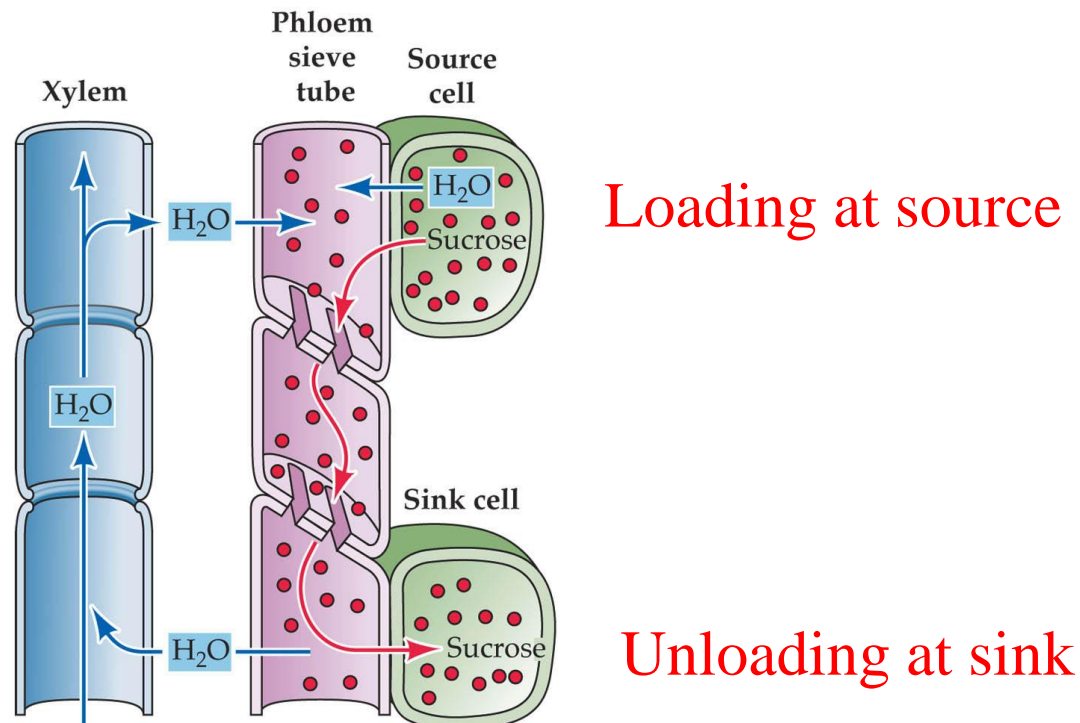
Sap droplet

Longistigma caryae

35.4 How Are Substances Translocated in the Phloem?

Two steps in translocation require energy:

- **Loading** – transport of solutes from sources into sieve tubes
- **Unloading** – removal of solutes at sinks



35.4 How Are Substances Translocated in the Phloem?

Pressure flow model

- **Sucrose actively transported** into sieve tube cells at source
- → sieve tube cells at source have greater sucrose conc. than surrounding cells
- → **water enters by osmosis**
- → causes greater pressure potential at the source
- → sap moves by bulk flow towards sink
- **At the sink**, sucrose is unloaded by active transport, maintaining the solute and water potential gradients.

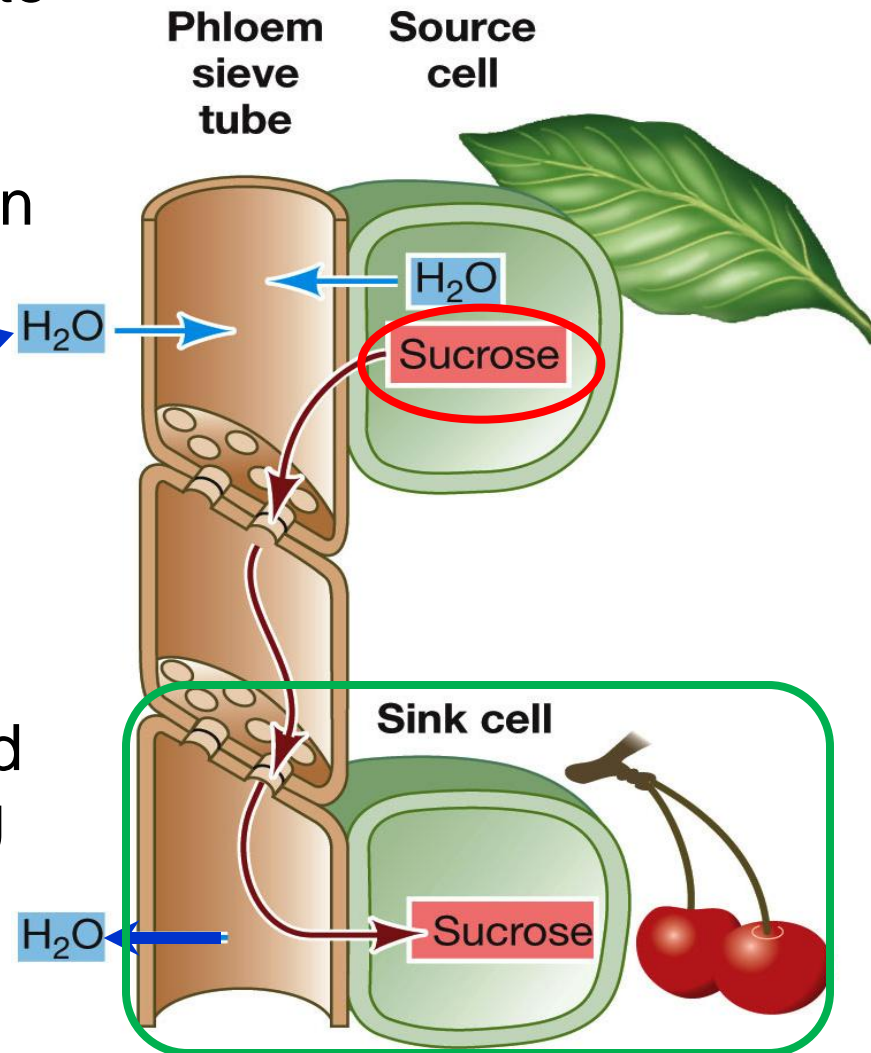
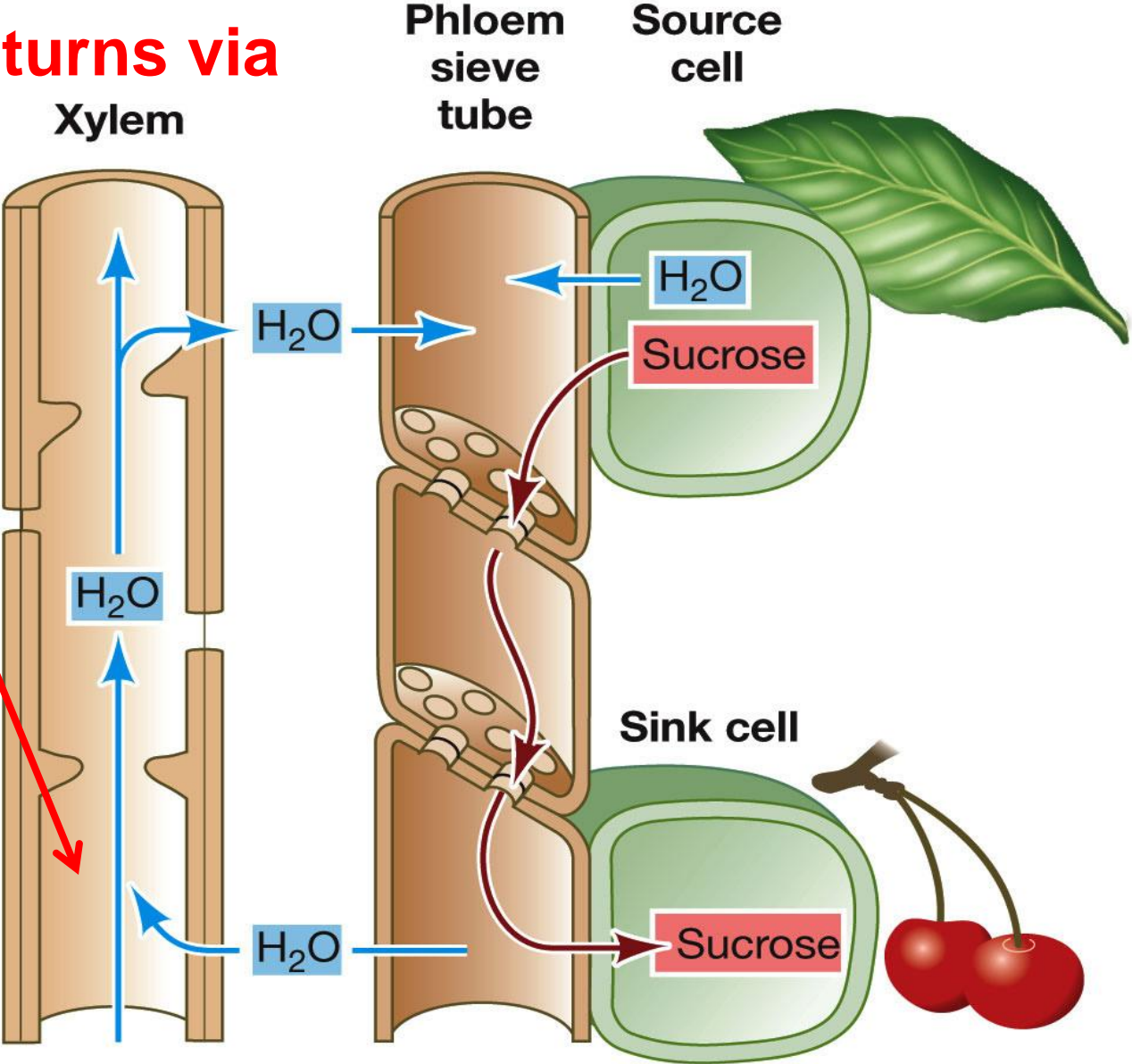


Figure 35.14 The Pressure Flow Model

- Water returns via xylem



LIFE 9e, Figure 35.14

The Pressure Flow Model

TABLE 35.1

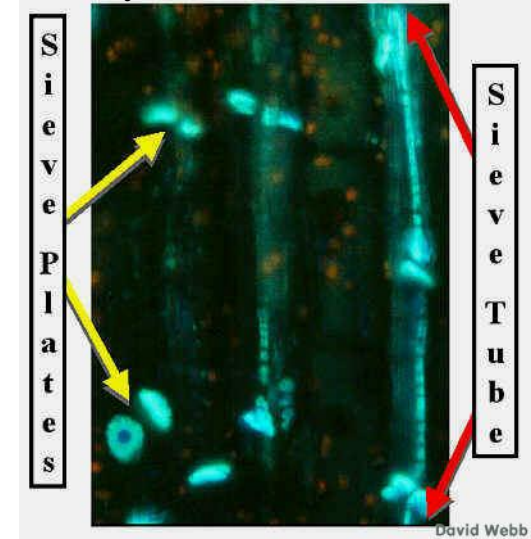
Mechanisms of Sap Flow in Plant Vascular Tissues

	XYLEM	PHLOEM
Driving force for bulk flow	Transpiration from leaves	Active transport of sucrose at source
Site of bulk flow	Nonliving vessel elements and tracheids	Living sieve tube elements
Pressure potential in sap	Negative (pull from top; tension)	Positive (push from source; pressure)

35.4 How Are Substances Translocated in the Phloem?

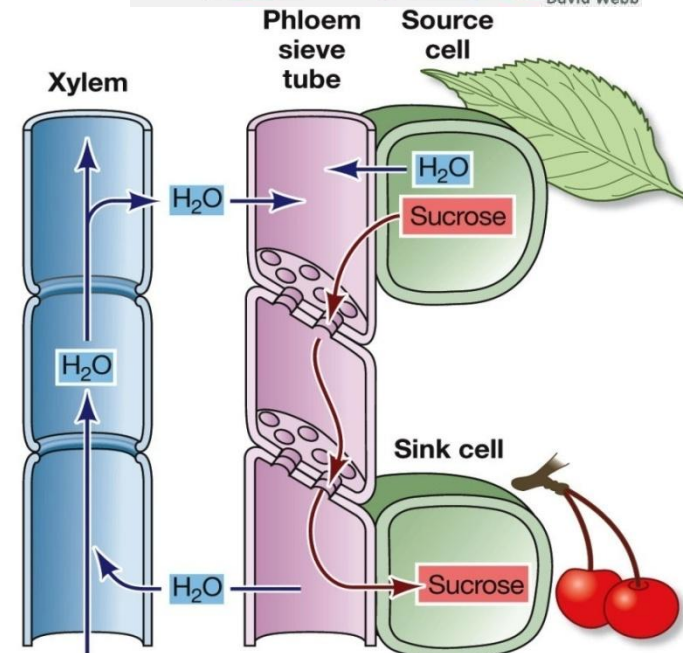
www.botany.hawaii.edu/faculty/webb/BOT410/Phloem

Sieve tubes and plates fluoresce from Aniline Blue when illuminated with UV light (blue). The red fluorescence is due to autofluorescence by chloroplasts.



For the pressure flow model to be valid, two requirements must be met:

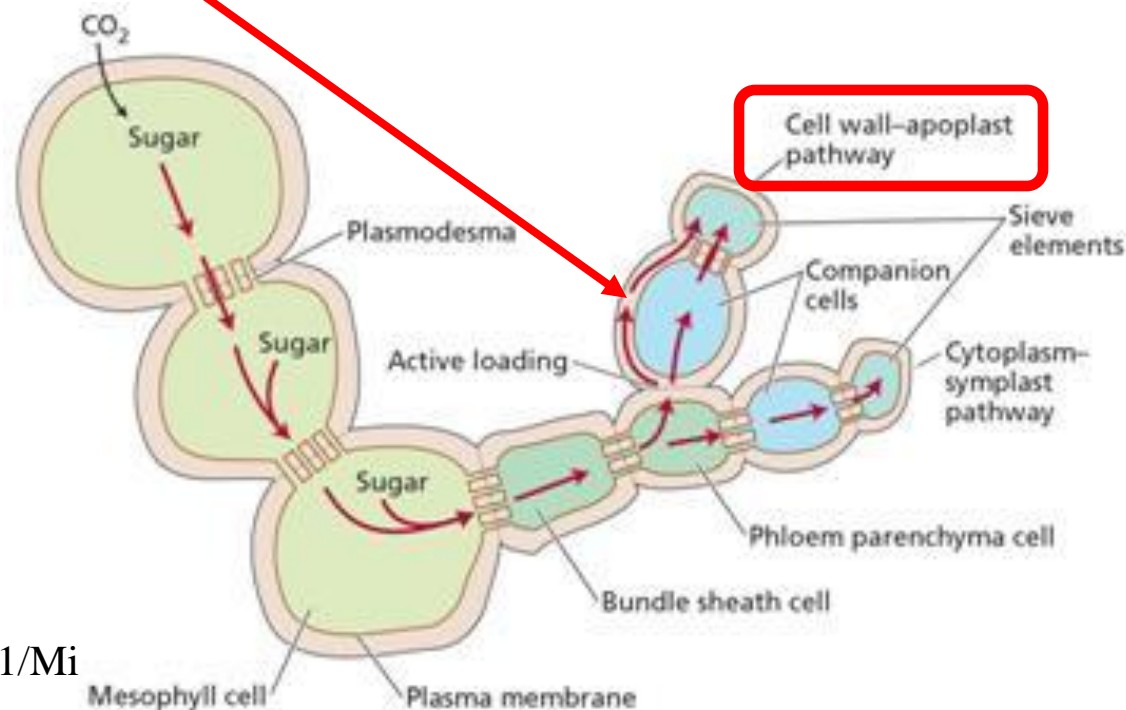
- Sieve plates must be unobstructed so that bulk flow is possible
- There must be effective methods for loading and unloading solutes



35.4 How Are Substances Translocated in the Phloem?

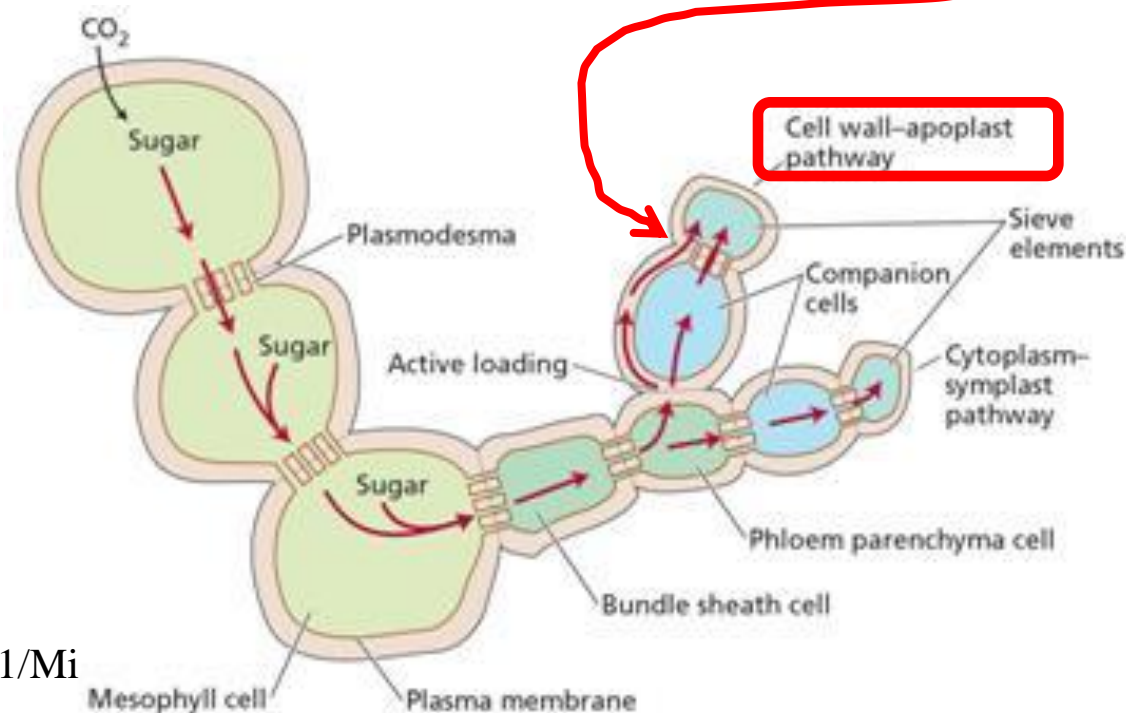
Solutes can move from mesophyll cells to the phloem by **apoplastic** or **symplastic** pathways

- Sugars and other solutes produced in mesophyll (chlorenchyma cells) can move to phloem by **apoplastic pathway**



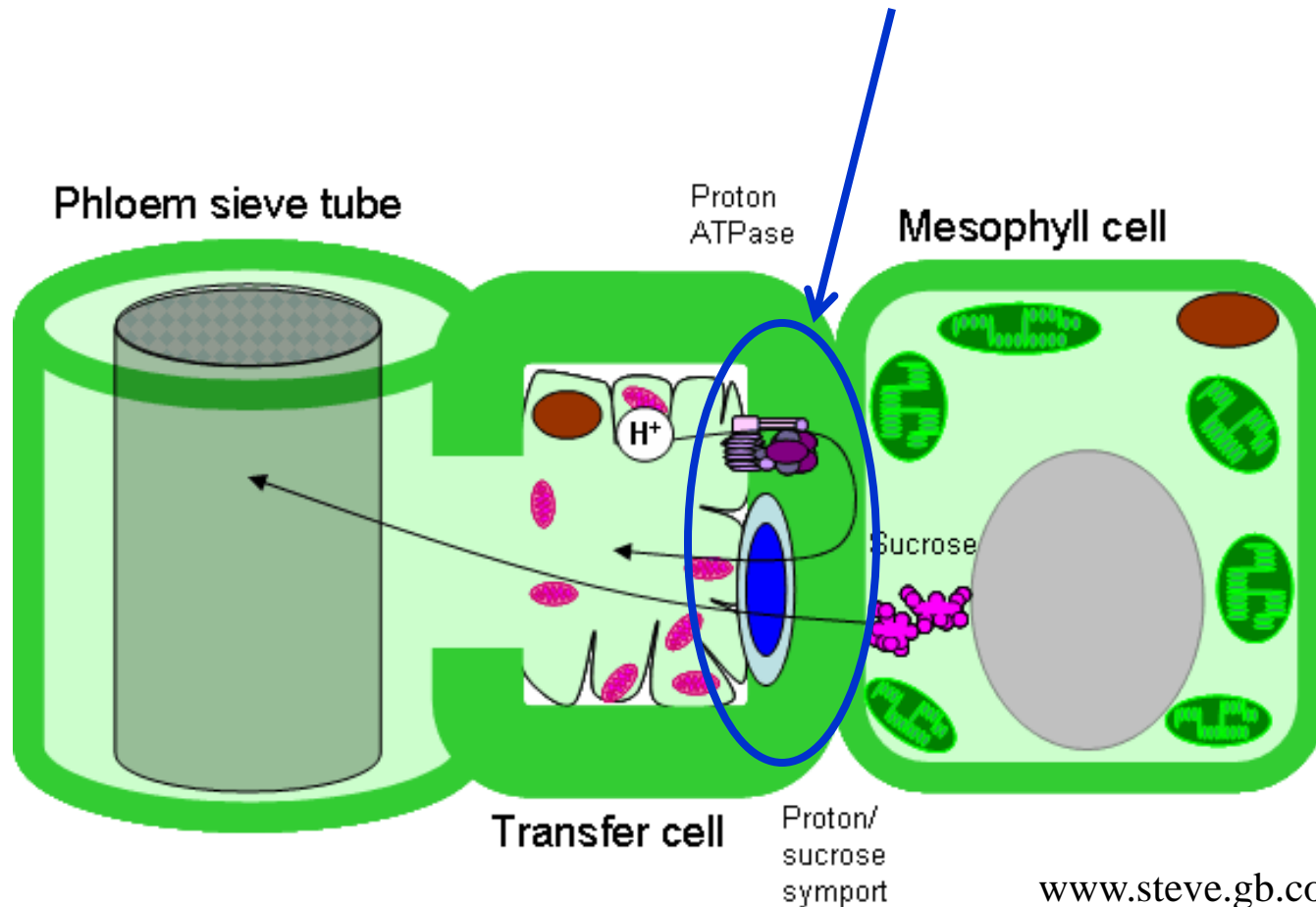
35.4 How Are Substances Translocated in the Phloem?

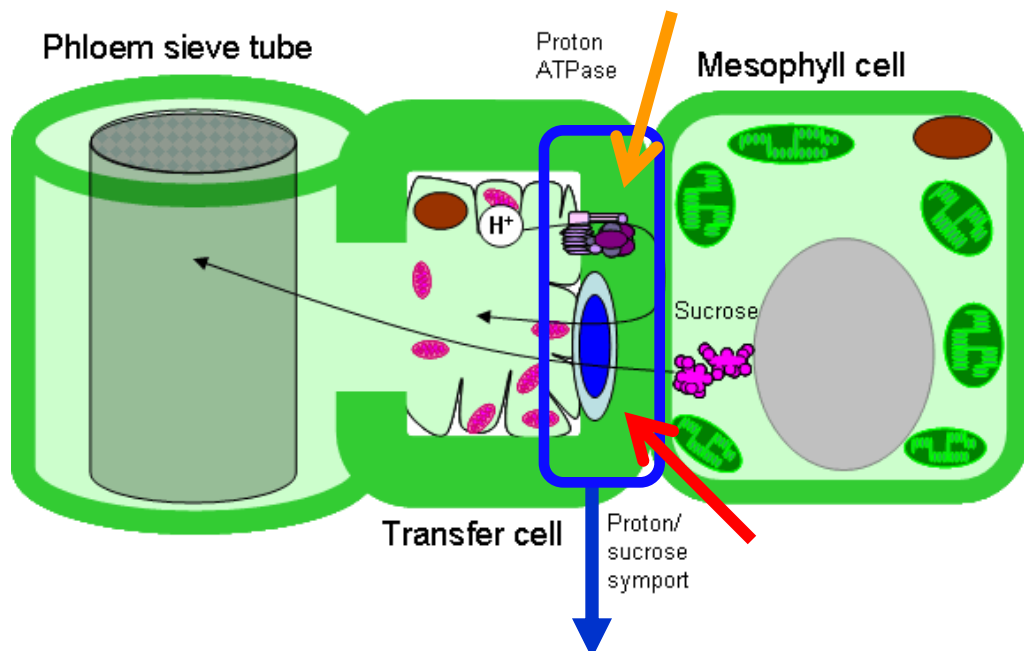
- Solutes are (secondarily) **actively transported to companion cells and sieve tubes**,
- → **reenter symplast**
- *Selectivity of solutes to be transported* allowed by passage of solutes to apoplast and back to symplast



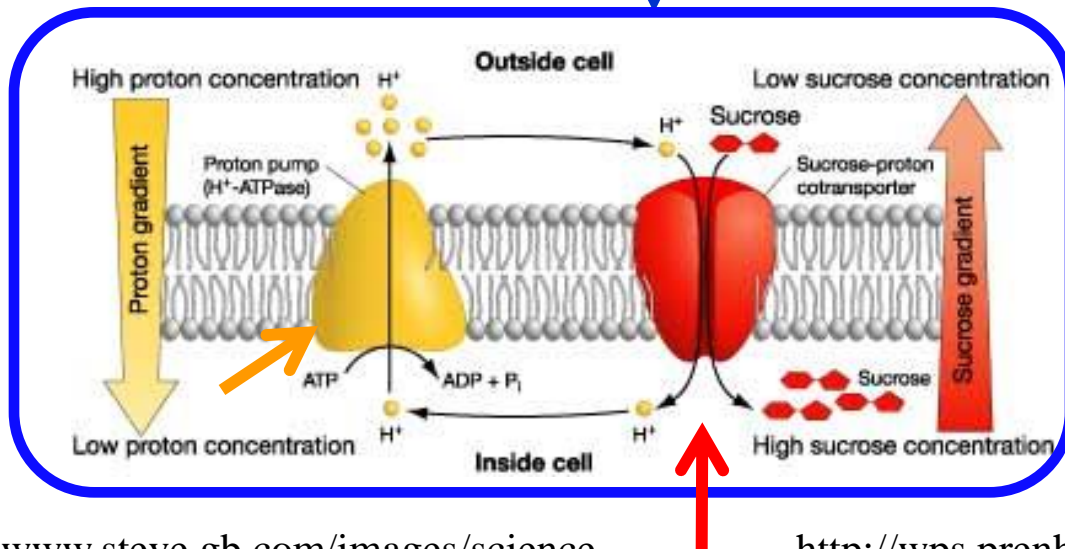
35.4 How Are Substances Translocated in the Phloem?

- **Secondary active transport** loads sucrose into modified companion cells (transfer cells), then sieve tubes by **sucrose–proton symport**



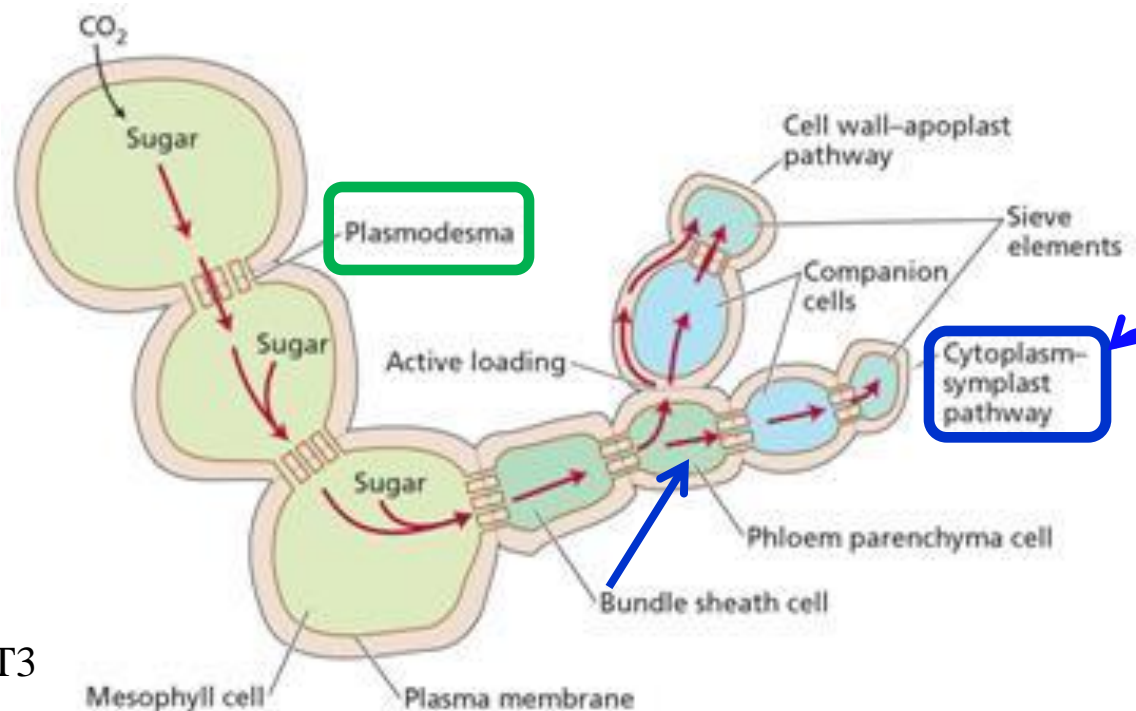


- **Apoplast** must have high concentration of H^+ to run **symport** secondary active transport
- H^+ are supplied by **H^+ -ATPase pump** (primary active transport)



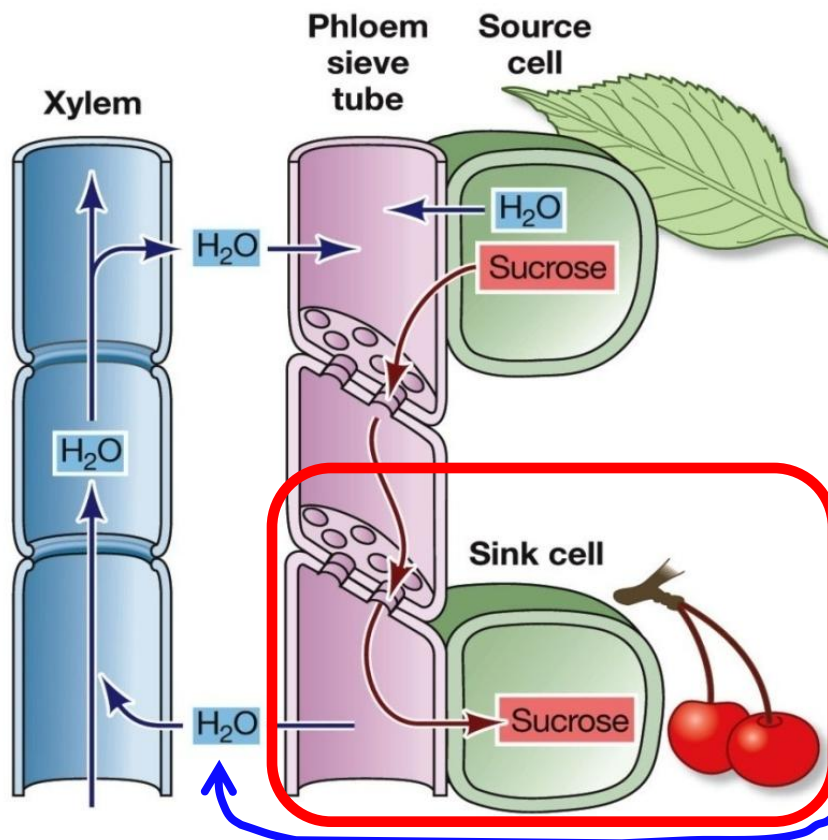
35.4 How Are Substances Translocated in the Phloem?

- In a ***symplastic pathway*** solutes remain in the symplast at all times
 - Solutes pass from cell to cell via **plasmadesmata**
 - Because no membranes are crossed, the loading mechanism does not involve membrane transport.



35.4 How Are Substances Translocated in the Phloem?

At sinks, sucrose unloading is actively transported out of sieve tubes and into surrounding tissues



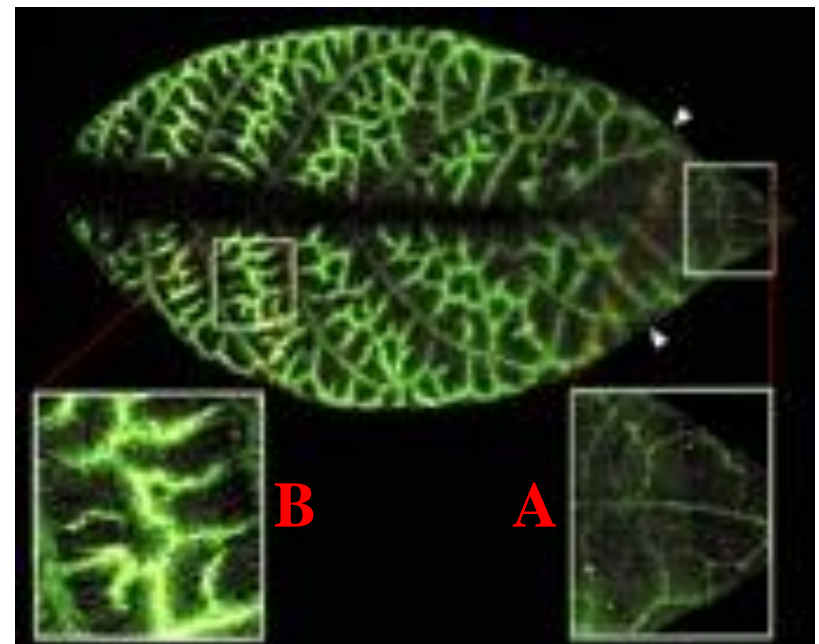
- This maintains pressure gradient for bulk flow toward sink, and
- Promotes buildup of sugars and starches in storage areas, e.g. developing fruits, seeds
- H_2O also flows out, returning via xylem

35.4 How Are Substances Translocated in the Phloem?

Many substances move thru symplast via plasmodesmata, including at loading & unloading sites

- In sink tissues, plasmodesmata are abundant and allow passage of large molecules.

Transgenic tobacco leaf showing GFP (green fluorescent protein) expressed from *Arabidopsis* SUC2, sucrose transporter promoter. The sink-source transition (darts) during leaf development has commenced in the tip of the leaf. Apical (A), source tissue shows companion cell-specific, punctate GFP fluorescence in veins that are phloem loading. Basal (B), sink tissue shows a diffuse pattern of GFP unloading from major veins.



Animated Tutorial 35.2 The Pressure Flow Model