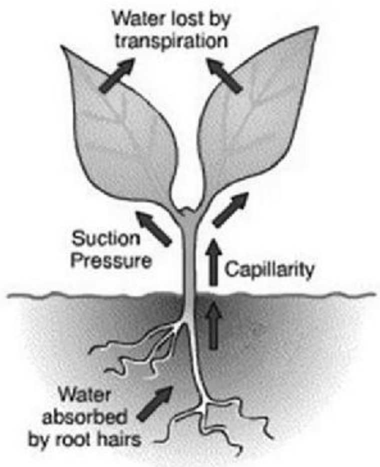
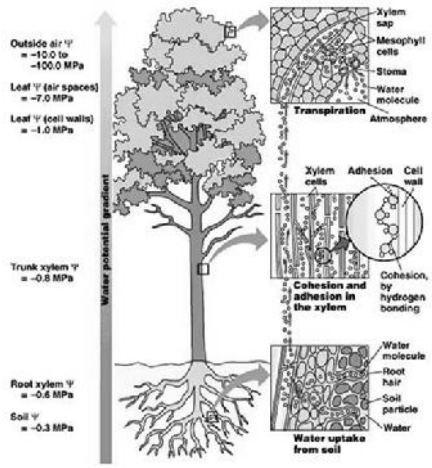
LECTURE 5. NUTRIENT TRANSPORT: LONG-DISTANCE TRANSPORT





VOCABULARY

1. Adherent
2. Sever
3. Immerse
4. Impregnate
5. Twig
6. result from
7. Pits
8. Taper
9. Allow
10. Stick together
11. driving force

LECTURE OUTCOMES

After completing this lecture and mastering the lecture materials, students are expected to be able

- to explain the transport pathway of nutrients for long-distance transport
- to explain the driving force of water transport and nutrient transport
- to explain water potential that is the potential energy of water per unit volume relative to pure water in reference conditions

What would you like to know

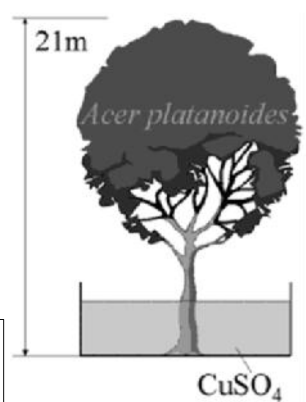
1. What is the pathway used to transport nutrients in plant? →*xylem*
2. What is the driving force of water transport? →*water potential difference (·)*
3. What is water potential? → the potential energy of water per unit volume relative to pure water in reference conditions
4. Root Pressure?
5. Transpiration Mechanism?
6. Xylem Loading and Unloading?
7. Mobilization of Nutrients?
8. Nutrient Partitioning?

LECTURE FLOW

1. Transport Pathway
2. Driving force
3. Water Potential
4. Root Pressure
5. Transpiration Mechanism
6. Xylem Loading and Unloading
7. Mobilization of Nutrients

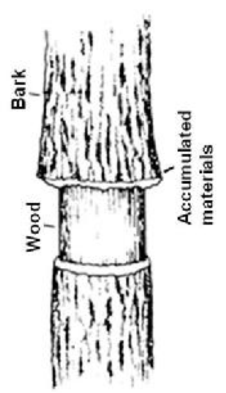
1. Transport Pathway

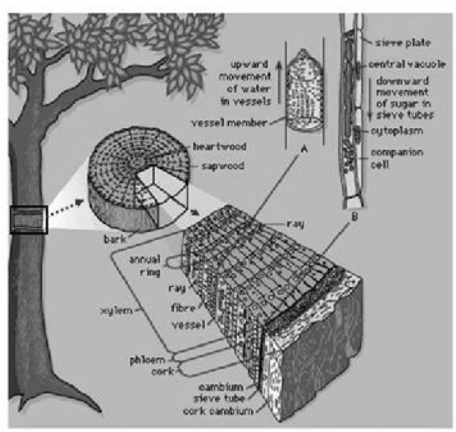
- Eduard Strasburger, an adherent of the school of physics, demonstrated **dead cells** of trees as the transport pathway of water in plants.
- Woody stems with their lower, severed end immersed in concentrated solutions of copper sulfate ($CuSO_4$) or picric acid ($C_6H_3N_3O_7$) sucked the solution up.

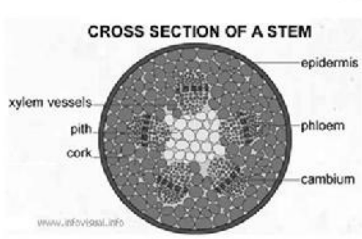


Strasburger's great work (ca. 1890)
–30 liters/14 days
–wood impregnated up to 20 m

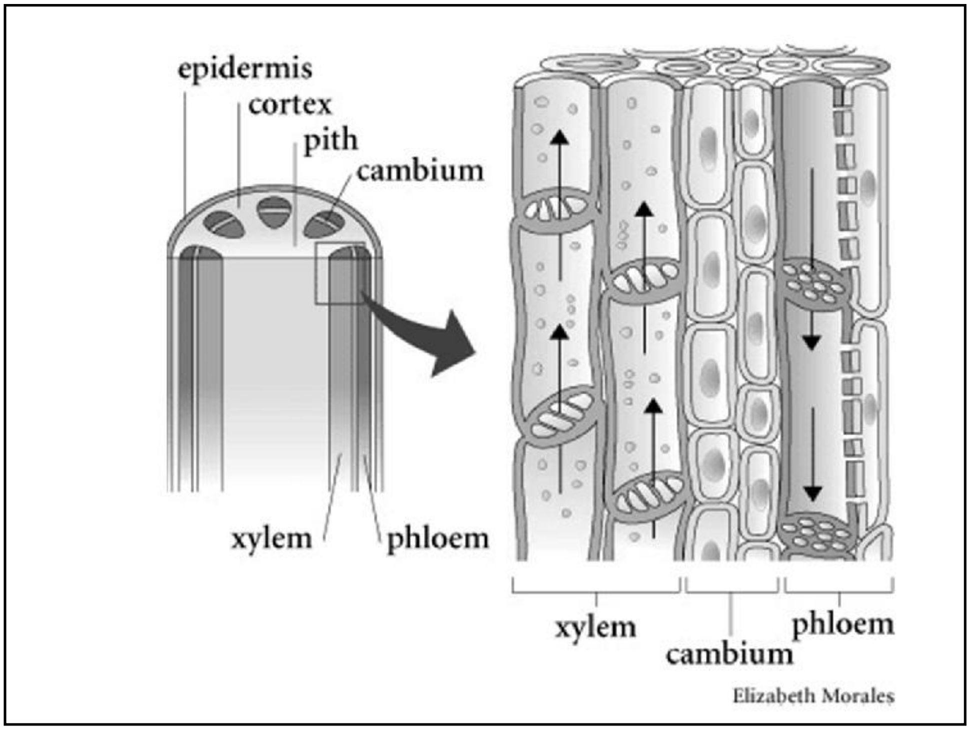
- Immediately upon contact, the poisonous fluid kills all living cells in its way, but the copper or the acid arrive in the transpiring leaves and kill them as well.
- The uptake of the solution and the loss of water from the dead leaves may continue for several weeks, and new solutions of a different color may be lifted in a dead stem.
- Joseph Boehm provided an equally impressive demonstration in 1892. He showed that water could be lifted to considerable heights even by dead twigs (killed in boiling water).

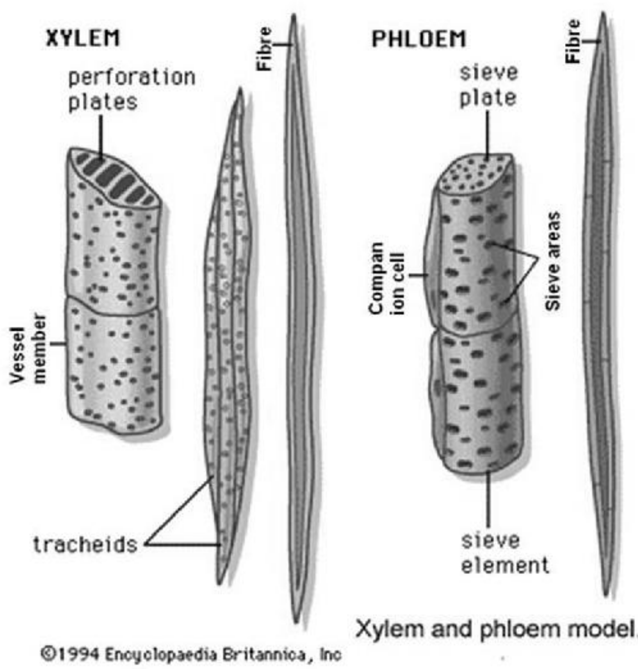






- **Xylem.** The transport of solutes (elements and low-molecular weight organic compounds) occurs predominantly in the nonliving **xylem vessels**





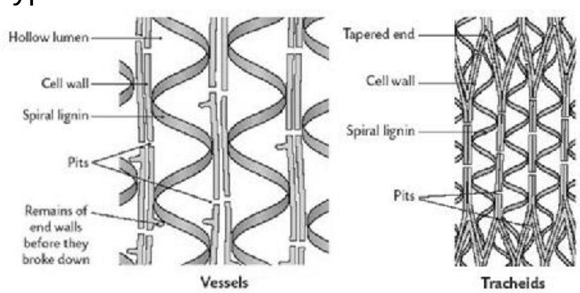
Xylem and phloem model.

Xylem Transport

1. **Mechanism**
   - Mass flow is the main mechanism of solute transport in the xylem sap in the nonliving xylem vessels (i.e. in the apoplast)
   - Interactions occur between solutes and both the cell walls of the vessels and the surrounding xylem parenchyma cells
   - The major interactions are exchange adsorption of polyvalent cations and reabsorption of mineral elements and the release (excretion) of organic compounds by surrounding living cells (xylem parenchyma and phloem)

Xylem consists of 2 types of cells: **Vessels** and **Tracheids.**

- Both tracheids and vessels are tubes that allow water and dissolved minerals to pass throughout the plant



- They also give support for the plant resulting from lignin in their cell walls. The water and minerals go in and out of the tubes through the pits on the sides of the tubes
- The vessels form continuous tubes while the tracheids are tapered at one end to allow one cell to overlap around another at their ends

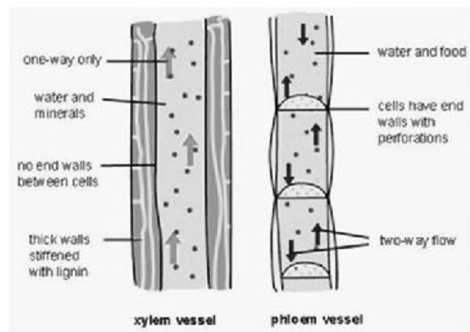
2. **Characteristics**
   - **Non-living xylem vessel members ("apoplast"),** predominantly
   - **Uni-directional**
   - **Primarily nutrient ions** & small amount of amino acids and other low MW organics.
3. **Xylem Sap Composition**
   - ~acidic (5.5 – 6.0 pH)
   - Very dilute (rel. low levels of dry matter, mostly in inorganic form)
   - Nutrients
     - Cations: K, Ca, Mg, Na in dec. concentration
     - Anions: P, Cl, S, and NO3-* in some species

- Amino acids & amides
- Organic Acids
- Much smaller amounts of hormones and enzymes (e.g. peroxidases for lignin formation)

4. **Form of N in xylem**
   - Primary form depends on where NO_3 reduction occurs:
   - ***Nitrate*** for species that reduce nitrate in the shoot.
   - **Reduced N** (glutamine, glutamate, Asp, Arg*) transported in species in which NO_3 reduction occurs in the root

2. Driving force

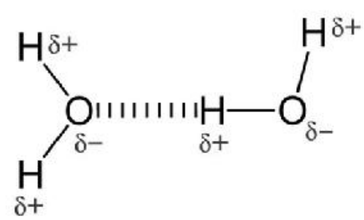
- The xylem transport is driven by the gradient in hydrostatic pressure (root pressure) and the gradient in the **water potential**
- Them flow of water and nutrients in the xylem resulting from the **water potential difference** is related to the properties of water (cohesion and adhesion) and transpiration



Xylem & Phloem Transport

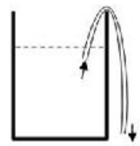
A. Cohesion and Adhesion

- **Water is a polar molecule**, and forms hydrogen bonds between the positively charged hydrogen atoms and the negatively charged oxygen atoms.
- Hydrogen bonds make water molecules stick together, a process known as **cohesion**.



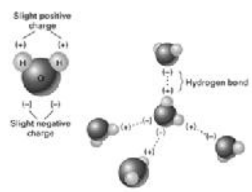
- When water molecules form hydrogen bonds with other molecules, such as carbohydrates, it is called **adhesion**.

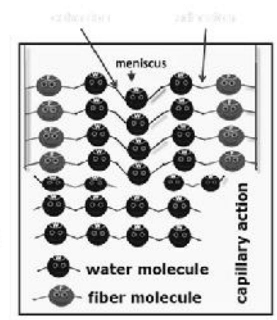
- The hydrogen bonds have tension between them, so water molecules stick together and move together.



- When water is pulled out through a leaf at the top of a plant via transpiration, the rest of the water molecules in the xylem are under tension and are pulled up the plant stem
- Capillary rise is

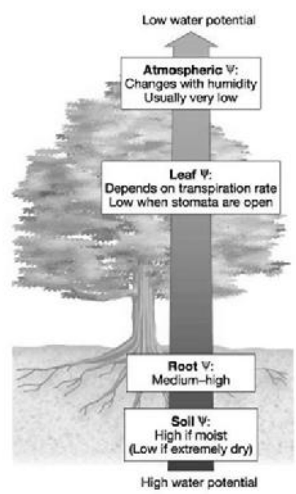
$$\mathbf{h}\ (\mathbf{m}) = \frac{14.9\mathbf{x}10^{-6}\mathbf{m}^2}{\mathbf{radius}\ (\mathbf{r}, \mathbf{m})}$$





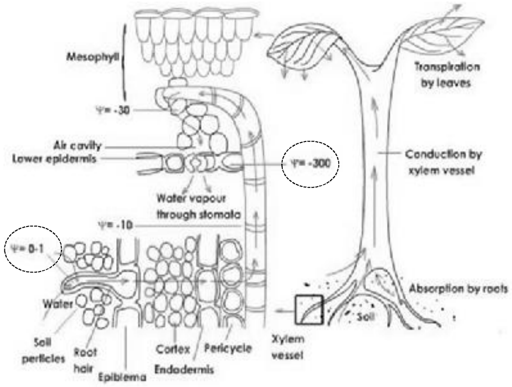
B Transpiration

1. In xylem, it is actually tension (negative pressure) that drives long-distance transport.
   - Transpiration, the evaporation of water from a leaf, reduces pressure in the leaf xylem.
   - This creates a tension that pulls xylem sap upward from the roots.
   - Transport greatest during day because gradient steepest & transpirational pull is greatest.
   - Root pressure allows limited xylem flow at night or times of day when transpiration limited.



Driving force = transpiration

2. An increase in the transpiration rate enhances both the uptake and the translocation of mineral elements in the xylem
3. On a smaller scale, gradients of water potential drive the osmotic movement of water from cell to cell within root and leaf tissue.



- Differences in both solute concentration and pressure contribute to this microscopic transport.

Driving force = transpiration

4. In contrast, bulk or mass flow, the mechanism for long-distance transport up xylem vessels, depends only on pressure.
   - Bulk flow moves the whole solution, water plus minerals and any other solutes dissolved in the water.
5. The plant expends none its own metabolic energy to lift xylem sap up to the leaves by bulk flow.

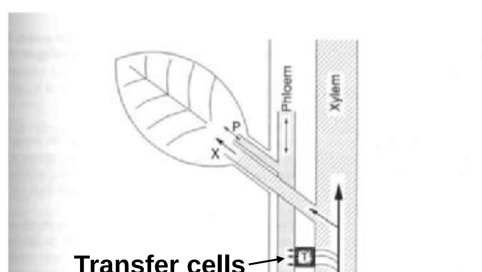


Fig. 3.11 Long-distance transport in xylem (X) and phloem (P) in a stem with a connected leaf, and xylem-to-phloem transfer mediated by a transfer cell (T).

6. The absorption of sunlight drives transpiration by causing water to evaporate from the moist walls of mesophyll cells and by maintaining a high humidity in the air spaces within a leaf.
7. Thus, the ascent of xylem sap is ultimately solar powered.
8. Diffusion in a solution is fairly efficient for transport over distances of cellular dimensions (<100 microns or 0.1 mm).
9. However, diffusion is much too slow for long-distance transport within a plant - for example, the movement of water and minerals from roots to leaves.

10. **Flow rates** depend on a pipe's internal diameter.
    - To maximize bulk flow, the sieve-tube members are almost entirely devoid of internal organelles.
    - Vessel elements and tracheids are dead at maturity.
    - The porous plates that connect contiguous sieve-tube members and the perforated end walls of xylem vessel elements also enhance bulk flow.

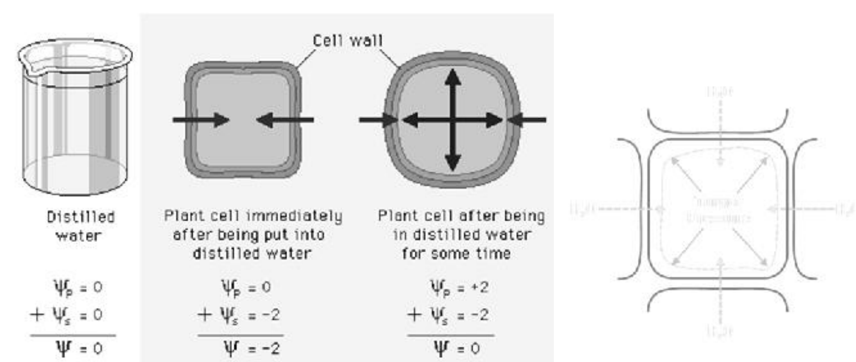
3. Water Potential

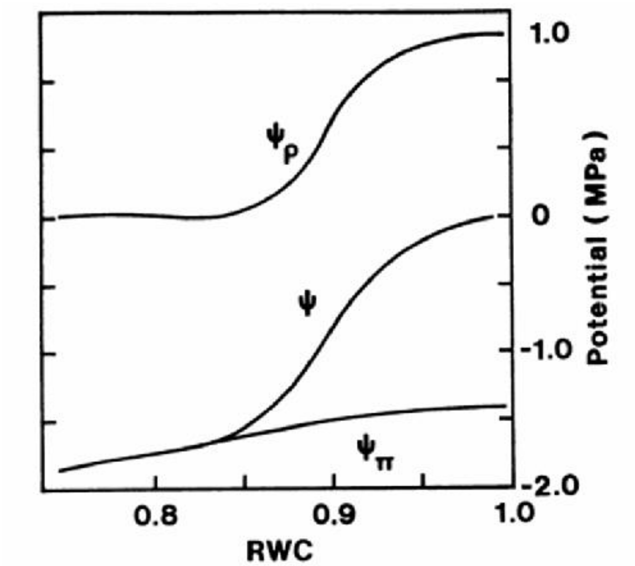
1. The survival of plant cells depends on their ability to balance water uptake and loss.
2. The transport of water in plants cells, and hence nutrients (mass flow), is driven by differences in **water potential**
3. The net uptake or loss of water by a cell occurs by **osmosis**, the passive transport of water across a membrane.
   - In the case of a plant cell, the direction of water movement depends on solute concentration and physical pressure, together called **water potential**, abbreviated by the Greek letter "psi (v)."

$$v = v_{®} + v_{\mathbf{p}}$$

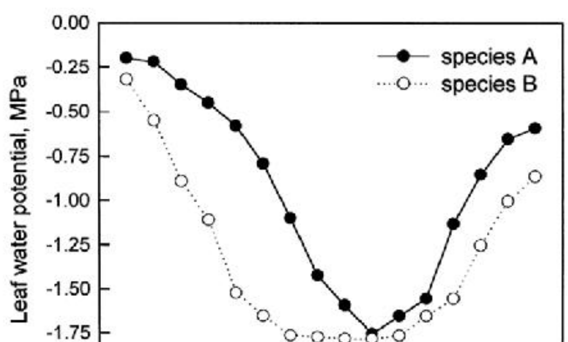
Ψ_π = Osmotic potential or Solute potential (Ψ_s)

Ψ_p = Pressure potential (turgor pressure)





RWC = relative water content = (FW-DW)/FW
FW = Fresh weight & DW = Dry weight



Notes: Note that both pre-dawn and minimum leaf water potential are virtually the same in the two species, although the two curves have apparently different shapes. Note also the longer duration of minimum diurnal leaf water potential in species B

http://www.emeraldinsight.com/journals.htm?articleid=871413&show=html

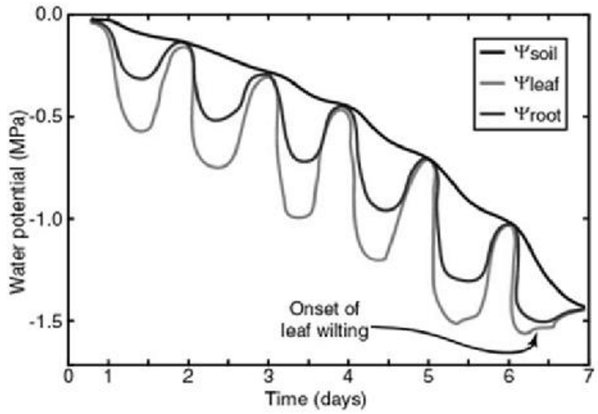


Figure 10.2. Schematic representation of daily changes in the water potential in the soil, root and leaf of a plant in an initially wet soil that dries out over a one week period. Shown are curves for the soil water potential, root xylem water potential and leaf (mesophyll) water potential, as adapted by Noble (1983; his figure 9.13) freely adapted from an article by Slatyer (1967, p 276).

Water Potential

4. Water will move across a membrane from the solution with the higher water potential to the solution with the lower water potential.
   - For example, if a plant cell is immersed in a solution with a higher water potential than the cell, osmotic uptake of water will cause the cell to swell.
   - By moving, water can perform work.
   - Therefore the *potential* in water potential refers to the potential energy that can be released to do work when water moves from a region with higher psi to lower psi.

Water Potential

5. Plant biologists measure ψ (psi, **MPa; 1 Mpa = about 10 atm** = 10 bars)
   - An atmosphere is the pressure exerted at sea level by an imaginary column of air - about 1 kg of pressure per square centimeter.
   - A car tire is usually inflated to a pressure of about 0.2 MPa and water pressure in home plumbing is about 0.25 MPa.
6. For purposes of comparison, the water potential of pure water in an container open to the atmosphere is zero.

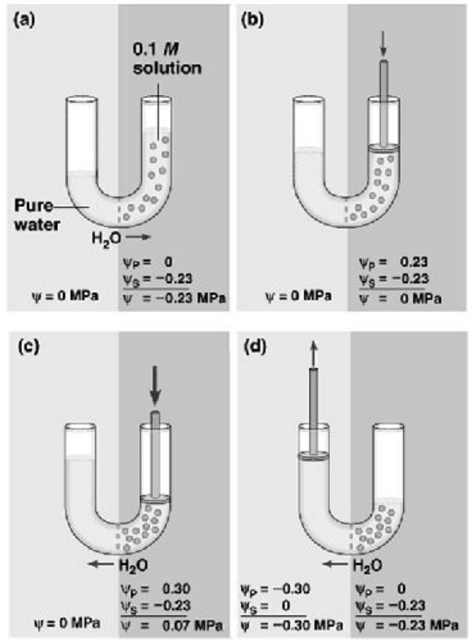
Water Potential

- The addition of solutes lowers the water potential because the water molecules that form shells around the solute have less freedom to move than they do in pure water.
- Any solution at atmospheric pressure has a negative water potential.
  - For instance, a 0.1 molar (*M*) solution of any solute has a water potential of -0.23 MPa.

7. If a 0.1 M solution is separated from pure water by a selectively permeable membrane, water will move by osmosis into the solution.
   - Water will move from the region of higher ψ (0 MPa) to the region of lower ψ (-0.23 MPa).

Water Potential

8. Application of physical pressure can balance or even reverse the water potential.
   - A negative potential can decrease water potential.



Water Potential

9. The combined affects of pressure and solute concentrations on water potential are incorporated into the following equation:

$$\cdot = \cdot_p + \cdot_s$$

- Where $\cdot_p$ is the pressure potential and $\cdot_s$ is the solute potential (or osmotic potential).

10. Water potential impacts the uptake and loss of water in plant cells.
    - In a **flaccid** cell, $\cdot_P$ = 0 and the cell is not firm.
    - If this cell is placed in a solution with a higher solute concentration (and therefore a lower $\cdot$), water will leave the cell by osmosis.

Water Potential

- Eventually, the cell will **plasmolyze**, shrinking and pulling away from its wall.

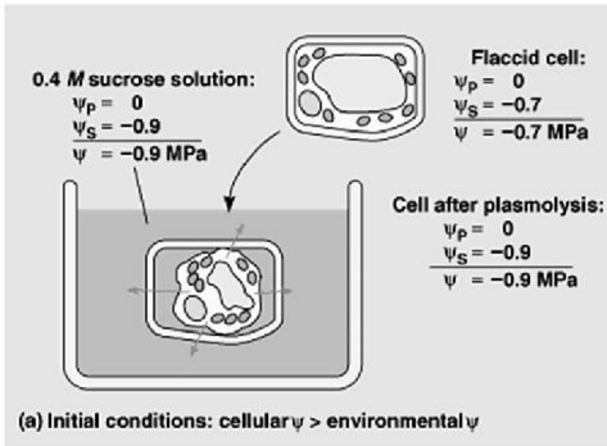


Fig. 36.4a

Water Potential

11. If a flaccid cell is placed pure water (· = 0), the cell will have lower water potential due to the presence of solutes than that in the surrounding solution, and water will enter the cell by osmosis.
12. As the cell begins to swell, it will push against the wall, producing a **turgor pressure**.
13. The partially elastic wall will push back until this pressure is great enough to offset the tendency for water to enter the cell because of solutes.

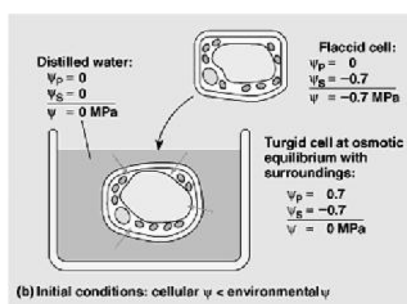


Fig. 36.4b

Water Potential

14. When $\cdot_p$ and $\cdot_s$ are equal in magnitude (but opposite in sign), $\cdot$ = 0, and the cell reaches a dynamic equilibrium with the environment, with no further net movement of water in or out.
15. A walled cell with a greater solute concentration than its surroundings will be **turgid** or firm.
    - Healthy plants are turgid most of the time as turgor contributes to support in nonwoody parts of the plant.

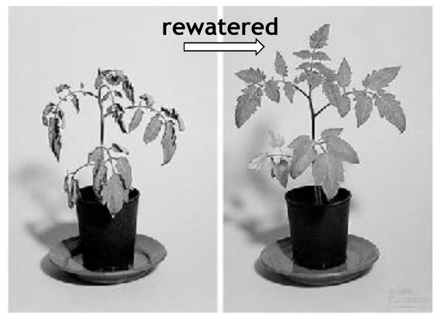


Fig. 36.5

4. Root Pressure

1. Root Pressure causes guttation, the exudation of water droplets that can be seen in the morning on the tips of grass blades or the leaf margins of some small, herbaceous dicots.
    - During the night, when transpiration is low, the roots of some plants continue to accumulate ions, and root pressure pushes xylem sap into the shoot system.
    - More water enters leaves than is transpired, and the excess is forced out as guttation fluid.

Root Pressure

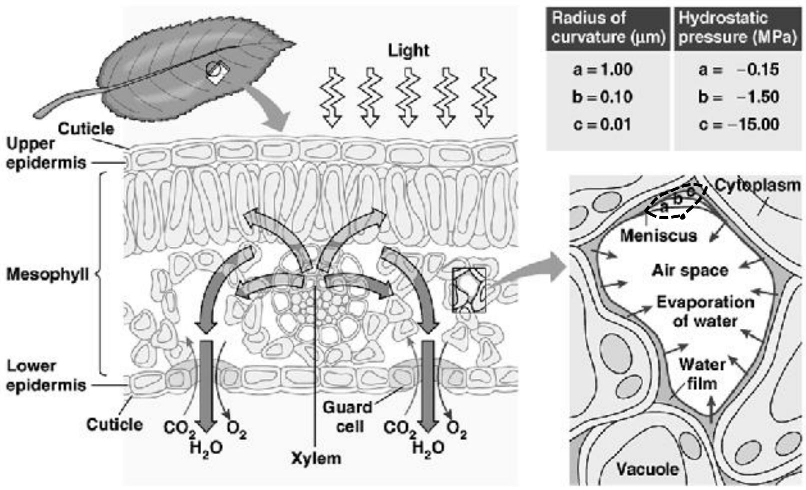
2. In most plants, root pressure is not the major mechanism driving the ascent of xylem sap.
   - At most, root pressure can force water upward only a few meters, and many plants generate no root pressure at all.
3. For the most part, xylem sap is not pushed from below by root pressure but pulled upward by the leaves themselves.
   - Transpiration provides the pull, and the cohesion of water due to hydrogen bonding transmits the upward pull along the entire length of the xylem to the roots.

5. Transpiration Mechanism

1. The mechanism of transpiration depends on the generation of negative pressure (tension) in the leaf due to unique physical properties of water.
   - As water transpires from the leaf, water coating the mesophyll cells replaces water lost from the air spaces.
   - The remaining film of liquid water retreats into the pores of the cell walls, attracted by adhesion to the hydrophilic walls.
   - Cohesive forces in the water resist an increase in the surface area of the film.
   - Adhesion to the wall and surface tension causes the surface of the water film to form a meniscus, “pulling on” the water by adhesive and cohesive forces.

Transcription Mechanism

2. The water film at the surface of leaf cells has a negative pressure, a pressure less than atmospheric pressure.



Transpiration Mechanism

- The more concave the meniscus, the more negative the pressure of the water film.
- This tension is the pulling force that draws water out of the leaf xylem, through the mesophyll, and toward the cells and surface film bordering the air spaces.

3. The tension generated by adhesion and surface tension *lowers* the water potential, drawing water from where its potential is higher to where it is lower.
   - Mesophyll cells will loose water to the surface film lining the air spaces, which in turn looses water by transpiration.
   - The water lost via the stomata is replaced by water pulled out of the leaf xylem.

Transcription Mechanism

4. The transpirational pull on xylem sap is transmitted all the way from the leaves to the root tips and even into the soil solution.
   - Cohesion of water due to hydrogen bonding makes it possible to pull a column of sap from above without the water separating.
   - Helping to fight gravity is the strong adhesion of water molecules to the hydrophilic walls of the xylem cells.
   - The very small diameter of the tracheids and vessel elements exposes a large proportion of the water to the hydrophilic walls.
5. The upward pull on the cohesive sap creates tension within the xylem

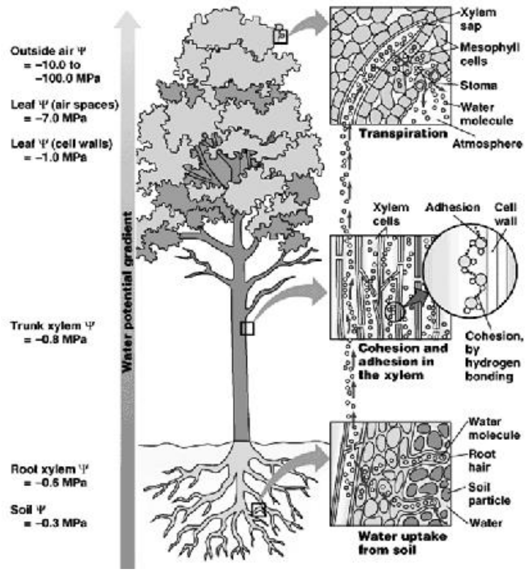
Transpiration Mechanism

- This tension can actually cause a decrease in the diameter of a tree on a warm day.
- Transpiration puts the xylem under tension all the way down to the root tips, lowering the water potential in the root xylem and pulling water from the soil.

6. Transpirational pull extends down to the roots only through an unbroken chain of water molecules
   - Cavitation, the formation of water vapor pockets in the xylem vessel, breaks the chain.
     - This occurs when xylem sap freezes in water.
   - Small plants use root pressure to refill xylem vessels in spring, but trees cannot push water to the top and a vessel with a water vapor pocket can never function as a water pipe again.

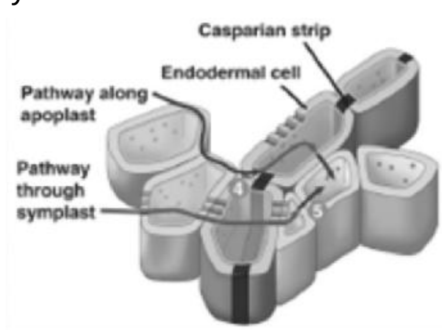
Transpiration Mechanism

- The transpirational stream can detour around the water vapor pocket, and secondary growth adds a new layer of xylem vessels each year. The older xylem supports the tree.



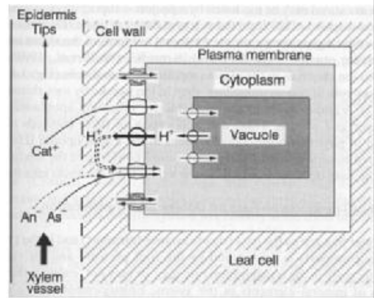
6. Xylem Loading and Unloading

1. **Xylem loading in root**
   - After radial transport (passive & active) to the stele of the root, most of the ions & organic solutes (amino acids, organic acids) are released ("loaded") into the xylem
   - Represents a transfer back into the apoplasm.



Xylem Loading and Unloading

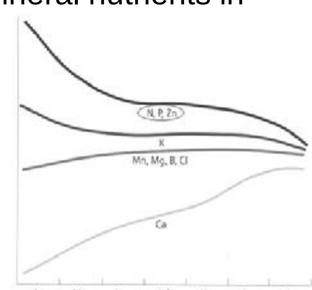
2. **Xylem unloading: upper portions of root or stem**
- Ions *unloaded* ("re-absorbed") from xylem vessels prior to reaching leaves.
  - For K+ unloading, a proton pump in PM of xylem parenchyma cells secretes H+ into the xylem.
  - K+ and H+ then flow down an electrochemical gradient into the xylem parenchyma cells and then into cortex of root or stem
    - Purpose: nutritional needs of these tissues or sequestering of toxic ions (Al, Na, Cl)

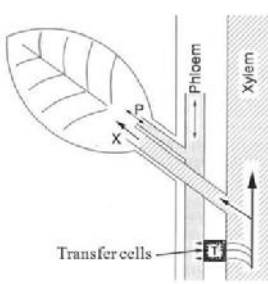


Model of scavenging solutes from the xylem sap ('xylew unloading') in leaf cells. As^- = amino acids

7. Nutrient Mobilization

Mobilization of Nutrients (leaves to sinks via phloem)
Generalized concentration curves of mineral nutrients in leaves during the growing season.
The curves show trends, not actual level : (a) N, P, Zn are translocated in largest amounts, (b) Boron: mobile in some species and not in others





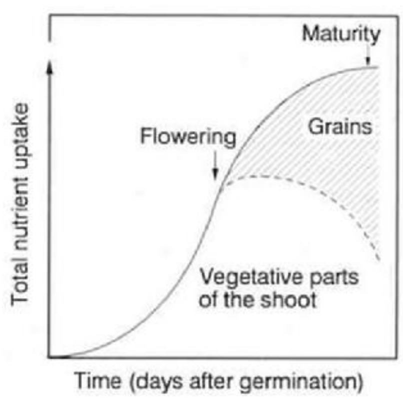
Phloem loading & translocation
Long-distance transport in xylem and phloem in a stem with a connected leaf and xylem-to phloem transfer mediated by a transfer cell (T)

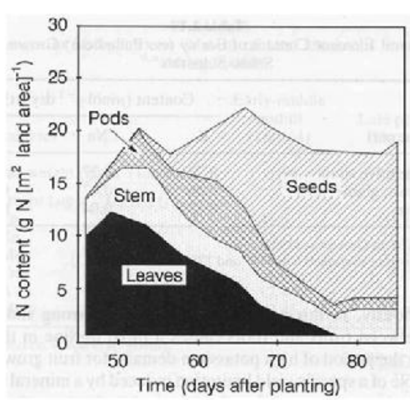
8. Nutrient Partitioning

- Xylem & phloem transport coordinated & interactive
  - storage of K^+ in leaves important for translocation of sugars as fruits sizing
  - Large amount of Ca^{++} must be translocated to developing fruits, to strengthen cell walls, e.g. for post-harvest integrity
  - P is stored in grains (generally. as phytate)
  - N is stored in beans and nuts
- Due to low transpiration of fruits & storage organs, **phloem transport from leaves** more important than xylem transport from roots

Nutrient Partitioning

Nutrient Partitioning– what is the final destination?
Schematic representation of the mineral nutrient distribution in cereal plant during ontogeny





Nitrogen partitioning in field-grown bean (*Phaseolus vulgaris* L., genotype G 5059) during reproductive growth (Lynch and White, 1992)

Marschner, MNH, 1995

So what determines where a nutrient goes?

1. Local demand vs. sink demand
2. Overall nutrient supply
   # and type of ion transporters on membranes frequently changing
3. Function of the nutrient and if toxic or not
4. Charge balancing
5. Time of the year
6. Ambient conditions (infl. amt. of transpiration)

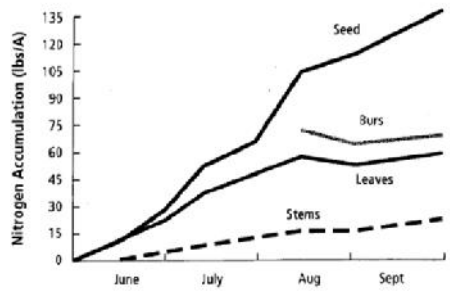
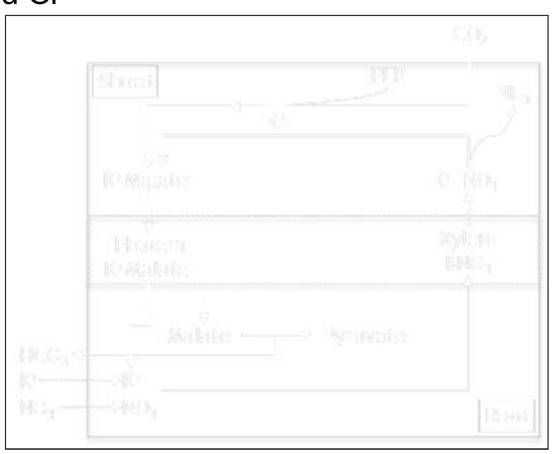


Figure 17.2 Nitrogen uptake and accumulation in cotton plant parts (from Bassett, Anderson, and Werkhoven 1970).

Why re-circulate?

- Changes in demand
- Counter-ion for transport & charge balancing (next example)
- Common for K^+ and Cl^-

Model for the circulation of potassium between root and shoot in relation to nitrate and malate transport (PEP = phosphoenol pyrupate). Based on Ben-Zioni et al., 1971 and Kirby and Knight, 1977



- After nitrate reduction in the shoot, charge balance has to be maintained by corresponding net increase in organic acid anions.

- As an alternative to storage in the leaf cell vacuoles, the organic acid anions (mainly malate) and potassium as accompanying cation can be retranslocated in the phloem to the roots. After decarboxylation of the organic acids, potassium may act again as counterion for nitrate transport in the xylem to the shoot.