Differences in water potential drive water transport in plant cells

- The survival of plant cells depends on their ability to balance water uptake and loss.
- 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."
- 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 placed 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 impacts the uptake and loss of water in plant cells.
  - In a **flaccid** cell, $psi_p = 0$ and the cell is not firm.
  - If this cell is placed in a solution with a higher solute concentration (and therefore a lower psi), water will leave the cell by osmosis.
  - Eventually, the cell will **plasmolyze**, shrinking and pulling away from its wall.
- If a flaccid cell is placed pure water (psi = 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.
- As the cell begins to swell, it will push against the wall, producing a **turgor pressure**.
- 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.
- When psi_p and psi_s are equal in magnitude (but opposite in sign), psi = 0, and the cell reaches a dynamic equilibrium with the environment, with no further net movement of water in or out.
- 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 non woody parts of the plant.

Vacuolated plant cells have three major compartments

- While the thick cell wall helps maintain cell shape, it is the cell membrane, and not the cell wall, that regulates the traffic of material into and out of the protoplast.
  - This membrane is a barrier between two major compartments: the wall and the cytosol.
  - Most mature plants have a third major compartment, the vacuole.
- The membrane that bounds the vacuole, the **tonoplast**, regulates molecular traffic between the cytosol and the contents of the vacuole, called the cell sap.
- In most plant tissues, two of the three cellular compartments are continuous from cell to cell.
  - Plasmodesmata connect the cytosolic compartments of neighboring cells.
  - This cytoplasmic continuum, the **symplast**, forms a continuous pathway for transport.
  - The walls of adjacent plant cells are also in contact, forming a second continuous compartment, the **apoplast**.

Both the symplast and the apoplast function in transport within tissues and organs

- Three routes are available for lateral transport, the movement of water and solutes from one location to another within plant tissues and organs.
  - This often occurs along the radial axis of plant organs.
- In one route, substances move out of one cell, across the cell wall, and into the neighboring cell, which may then pass the substances along to the next cell by same mechanism.
  - This transmembrane route requires repeated crossings of plasma membranes.
- The second route, via the symplast, requires only one crossing of a plasma membrane.
  - After entering one cell, solutes and water move from cell to cell via plasmodesmata.
- The third route is along the apoplast, the extracellular pathway consisting of cell wall and extracellular spaces.
  - Water and solutes can move from one location to another within a root or other organ through the continuum of cell walls before ever entering a cell.

Absorption of water and minerals by roots: Short distance transport between cells in the soil-to-xylem pathway

- Much of the absorption of water and minerals occurs near root tips, where the epidermis is permeable to water and where root hairs are located.
  - Root hairs, extensions of epidermal cells, account for much of the ***surface area*** of roots.
  - The soil solution flows into the hydrophilic walls of epidermal cells and passes freely along the apoplast into the root cortex, exposing all the parenchyma cells to soil solution and increasing membrane surface area.
- As the soil solution moves along the apoplast into the roots, cells of the epidermis and cortex take up water and certain solutes into the symplast.
- Most plants from partnerships with symbiotic fungi for absorbing water and minerals from soil.
- “Infected” roots form **mycorrhizae**, symbiotic structures consisting of the plant’s roots united with the fungal hyphae.
- Hyphae absorb water and selected minerals, transferring much of these to the host plants.
- The mycorrhizae create an enormous surface area for absorption and can even enable older regions of the roots to supply water and minerals to the plant.

The Endodermis: A Selective Sentry

- Water and minerals in the root cortex cannot be transported to the rest of the plant until they enter the xylem of the stele (vascular cylinder).
  - The **endodermis**, the innermost layers of the root cortex, surrounds the stele and functions as a last checkpoint for the selective passage of minerals from the cortex into the vascular tissue.
  - Minerals already in the symplast continue through the plasmodesmata of the endodermal cells and pass into the stele.
- Those minerals that reach the endodermis via the apoplast are blocked by the **Casparian strip** in the walls of each of the endodermal cells.
  - This strip is a belt of suberin, a waxy material that is impervious to water and dissolved minerals.
- These materials must cross the plasma membrane of the endodermal cell and enter the stele via the symplast.
  - The endodermis, with its Casparian strip, ensures that no minerals reach the vascular tissue of the root without crossing a selectively permeable plasma membrane.
  - The endodermis acts as a sentry on the cortex-vascular cylinder border.
- The last segment in the soil-to-xylem pathway is the passage of water and minerals into the tracheids and vessel elements of the xylem.
  - Because these cells lack protoplast, the lumen and the cells walls are part of the apoplast.
  - Endodermal cells and parenchyma cells within the stele discharge minerals into their walls.
  - Both diffusion and active transport are probably involved in the transfer of solutes from the symplast to apoplast, entering the tracheids and xylem vessels.
  - The water and minerals we have tracked from the soil to the root xylem can now be transported upward as xylem sap to the shoot system.

Transport of Xylem Sap Upward

- Xylem sap flows upward to veins that branch throughout each leaf, providing each leaf with water.
- Plants lose a huge amount of water by **transpiration**, the loss of water vapor from leaves and other aerial parts of the plant.
    - An average-sized maple tree losses more than 200 L of water per hour during the summer.
- The flow of water transported up from the xylem replaces the water lost in transpiration and also carries minerals to the shoot system.
- Before we go any further, you need to remember what two terms mean…***adhesion*** of water and ***cohesion*** of water…

The upward movement of xylem sap depends mainly on transpiration and the physical properties of water

- Xylem sap rises *against gravity*, without the help of any mechanical pump, to reach heights of more than 100 m in the tallest trees.
- At night, when transpiration is very low or zero, the root cells are still expending energy to pump mineral ions into the xylem.
    - The accumulation of minerals in the stele (vascular cylinder) ***lowers*** water potential there, generating a positive pressure, called **root pressure**, that forces fluid up the xylem.
- Root pressure causes **guttation**, the discharge 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 the leaves than is transpired, and the excess is forced out as guttation fluid.
- In most plants, root pressure is ***not*** the major mechanism driving the ascent of xylem sap.
- 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.
- Stomata lead to a maze of internal air spaces that expose the mesophyll cells to the CO_2 they need for photosynthesis.
    - The air in these spaces is saturated with water vapor because it is in contact with the moist walls of the cells (think sauna☺).
    - On most days, the air outside the leaf is drier (lower water concentration) and gaseous water diffuses out of the leaf via the stomata.
    - ***It is this loss of water vapor from the leaf that we call transpiration.***
- The mechanism of transpiration depends on the generation of negative pressure (tension) in the leaf due to the 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.
- The water film at the surface of leaf cells has a negative pressure, a pressure less than atmospheric pressure.
    - 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.
- 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 lose water to the surface film lining the air spaces, which in turn loses water by transpiration.
    - The water lost via the stomata is replaced by water pulled out of the leaf xylem.
- 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.
- The upward pull on the cohesive sap creates tension within the xylem
    - 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.
- 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.

Xylem sap ascends by solar-powered bulk flow: *a review*

- Long-distance transport of water from roots to leaves occurs by bulk flow, the movement of fluid driven by a pressure difference at opposite ends of a conduit, the xylem vessels or chains of tracheids.
    - The pressure difference is generated at the leaf end by transpirational pull, which lowers pressure (increases tension) at this “upstream” end of the xylem.
- 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.
- In contrast, bulk 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.
- The plant expends none its own metabolic energy to lift xylem sap up to the leaves by bulk flow.
- 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.
- Thus, the ascent of xylem sap is ultimately solar powered.