During the past few weeks, we examined the structure of the "higher" plant body, with occasional references to the functions of plant systems. In the next few days we shall look at how plants:

- Maintain water balance and transport water throughout the plant
- Transport nutrients and solutes to cells and tissues
- Obtain nutrients for growth and survival from their substrate and from the atmosphere
- Regulate growth and developmental activities

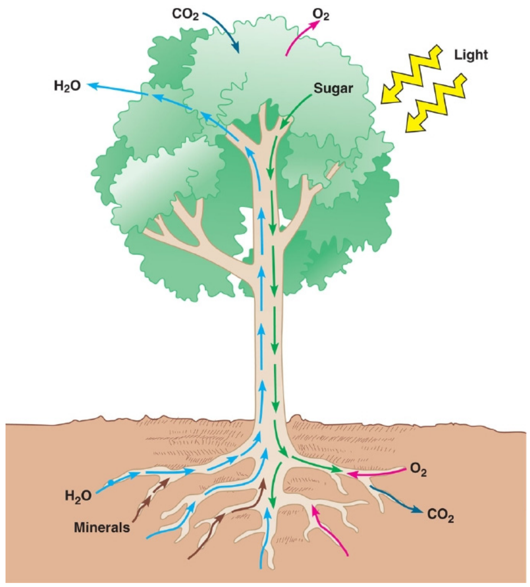
As we look at these subjects, keep in mind how other organisms with which you are more familiar accomplish these same functions.

Our plant ancestors were aquatic filamentous or laminar (sheet like) organisms whose cells came into contact with their environmental medium, which also supported the plant body. Water and needed nutrients were readily available to individual cells, and little if any differentiation of plant tissues occurred.

Migration to land and differentiation of the plant body into tissues and organs required systems to transport needed materials to cells in different parts of the plant from the region where they were obtained. In addition, land plants needed structural support. Both support and conduction are accomplished with secondary vascular tissue in woody plants. As studied previously, herbaceous plants use water pressure to maintain turgor.

Plant transport involves three activities:

- Movement of water, gases and solutes into and out of individual cells throughout the plant, from the environment into the plant (generally from soil into roots), and from the plant out into the environment
- Localized transport of materials from cell to cell in tissue regions, such as loading solutes into phloem sieve tubes
- Distance transport of water and solutes through the vascular tissues of the plant. The tallest trees (coast Redwood and Australian Eucalyptus) need to be able to transport water and solutes to heights of over 300 feet.

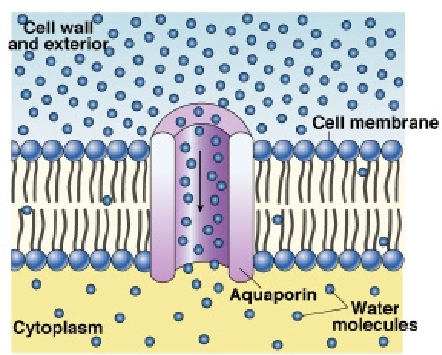


Vascular Plant Transport

Review of Membrane Transport Mechanisms

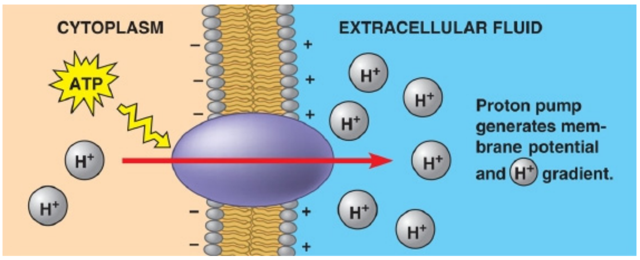
Prior to discussing localized and distance transport of water and nutrients in the plant, let's review a few things about membranes and membrane transport. The plasma membrane is selectively permeable. Materials that enter and leave a cell must pass through the membrane. The direction of water movement is dependent on the gradient between a cell's internal and external environment.

Although membranes are permeable to water, small membrane transport proteins, called **aquaporins**, also facilitate the diffusion of water, particularly across the central plant vacuole tonoplast.

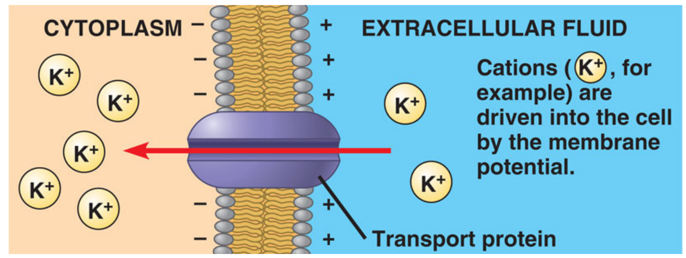


Most solutes, even if permeable, do not diffuse readily, and rely on transport proteins or membrane protein transport channels for facilitated diffusion. Recall that transport proteins have a selective binding site for the solute to attach on one side of the membrane and then carry the solute through the membrane releasing it on the other side. Channels allow free passage of specific substances, and some channels are gated to control solute passage. K^+ channels are common in the membranes of plant cells, and K^+ plays a vital role in opening and closing of stomata *(see later)*.

Plant cells also rely on active transport. The H^+ proton pump is a common use of active transport. The cell creates a **proton gradient** by pumping H^+ out of the cell, which is a source of **potential energy** (for the passive diffusion of the H+ back into the cell through the membrane), and creates the **membrane potential** (the differential charge between the interior, more negative charge, and external more positive charge), a second source of potential energy.



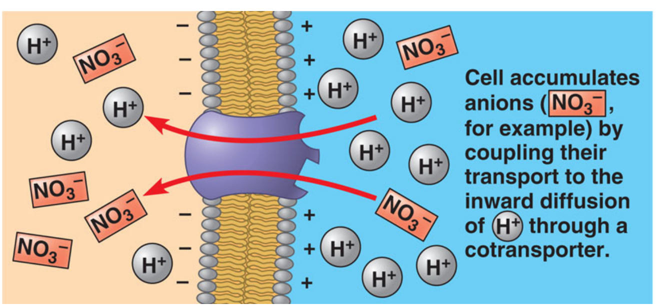
Proton Gradient and Membrane Potential



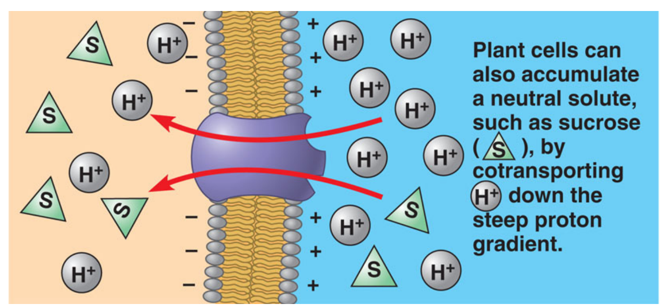
Membrane Potential favors diffusion of $^+$ ions

The membrane potential facilitates the movement of **positively charged ions** into cells. The ion movement is "passive" but is a consequence of the active movement of H^+ through the proton pump that maintains the membrane potential. The proton pump moves many minerals into cells in quantities greater than what is found in the environment.

Negative ion movement can be coupled to H^+ flow along the H^+ gradient. The negative charges are attracted to the H^+ and can be moved against their gradient, in a process called **cotransport.**



Cotransport of negative ions



Cotransport of neutral solutes

Cotransport is also used to move neutral solutes such as sucrose against a gradient. As H^+ moves down its gradient it is coupled to a substance being moved against its gradient. Sugar is loaded and unloaded from phloem sieve tubes by cotransport. Use of proton pumps for solute movement is a variant of the general process of chemiosmosis, which generates ATP in photosynthesis and cell respiration.

To add to the information about membranes and membrane transport, we also need a brief diversion on water potential before discussing the transport of water in cells and throughout the plant body.

Water in? Water out? – The Water Potential (Ψ) Discussion

Ultimately, whether water is gained or lost by cells is a consequence of osmosis (although aquaporins also play a role in water uptake). With the exception of cells that have thickened secondary walls, plant cells need to have adequate water in their cells to keep a physical pressure on the cell wall to maintain turgor.

There are two factors involving water and osmosis in plant cells:

- **solute concentration**
- **turgor pressure.**

These two factors combined comprise the **water potential**, which is known as Ψ (psi). In plants water always moves from greater water potential to a lesser water potential. Water potential (Ψ) in plants is measured in some arcane thing called **megapascals** (Mpa) which is equal to about 10 atmospheres of pressure (that famous 15 lb/in^2 or 1 kg/cm^2)

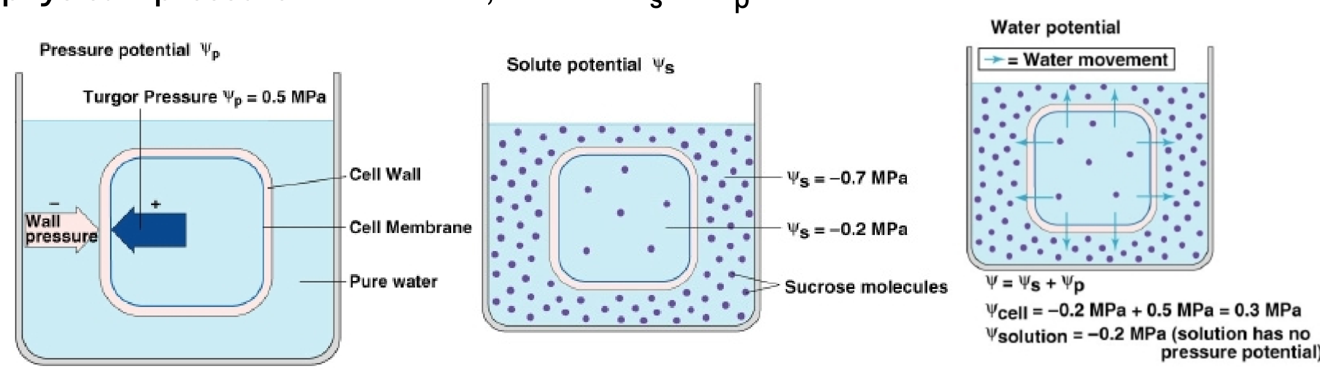
How can we use this information to discuss how water moves in plants?

- Pure water has a water potential of 0 Mpa (Ψ = 0 Mpa).
- Any solution will have a negative water potential relative to pure water.

With osmosis, pure water will pass through a membrane into a solution whose water potential is negative.

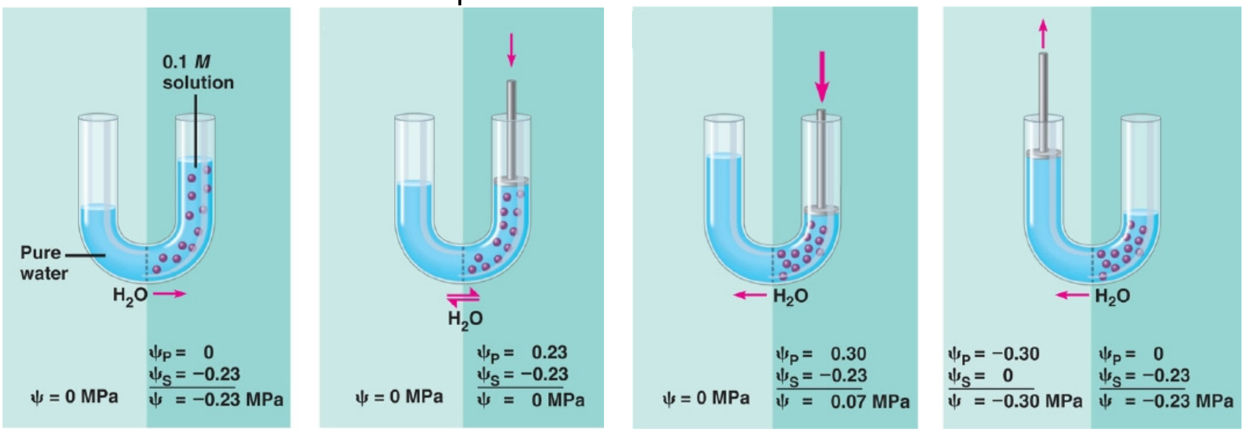
But for a plant it's not this simple. Plants have that **physical pressure** against the cell wall (called the pressure potential) that affects water potential. So the movement of water into and out of a plant cell needs to have that information, too.

True water potential equals the sum of the **solute (osmotic) potential** plus the **physical pressure** of the wall, or $\Psi = \Psi_s + \Psi_p$



What might seem really tricky here for plants is that one can also have a negative pressure or tension (a suction pressure such as we use when we suck beverages through a straw). This means that although Ψ_s is always negative, Ψ_p can be positive or negative, although in plants it is "always" positive, and that affects whether the water potential will be positive or negative.

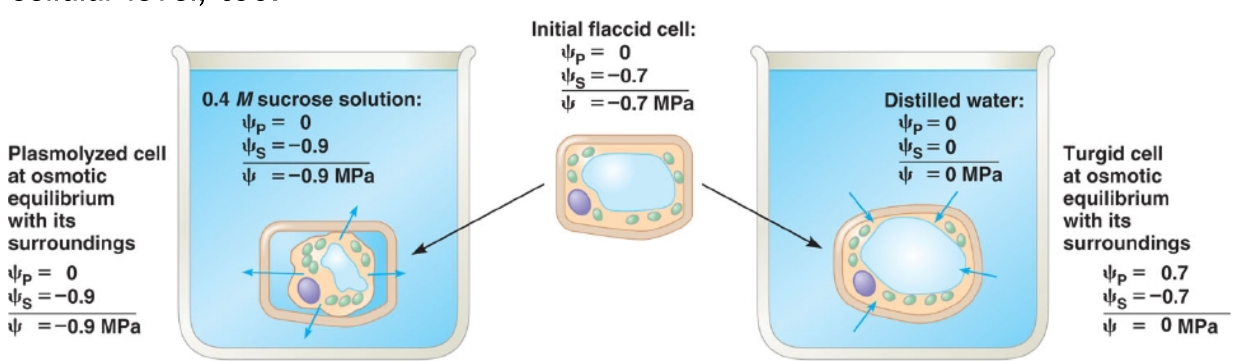
Solute and wall pressure effects on water movement



Adding solutes reduces water potential | Adding pressure increases water potential | Negative pressure decreases water potential

Having said a lot, all that we really need to remember here is that water moves from a greater to a lesser water potential and that's important for plants. And when we measure water potential in plants, as we move from soil, to roots to stem to leaves we get a more negative water potential.

To Summarize:
When the water potential inside the cell is higher than the environment, water will leave cells and **plasmolysis** results. This phenomenon is frequently observed in plants left in hot sunny windows and not watered adequately. It can be observed on the cellular level, too.



Plasmolysis and Water Potential | Turgor and Water Potential

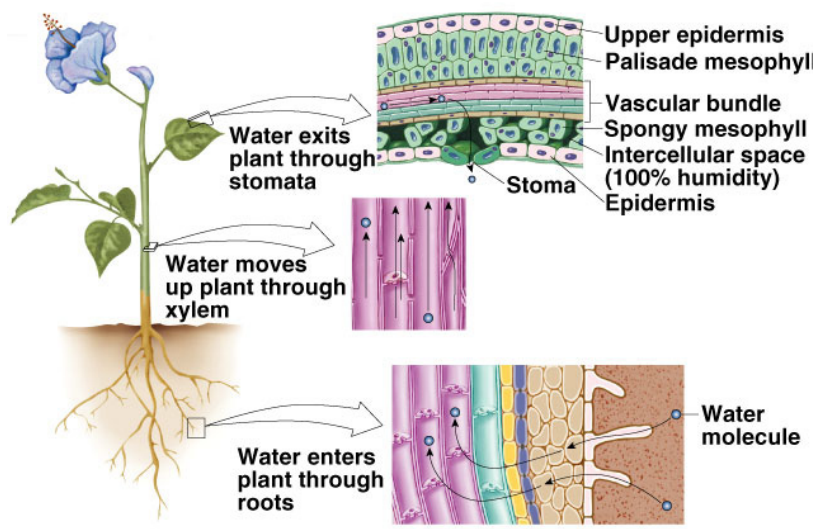
When the cell's water potential is less than the environment, water will move into the cell until the water potential is equalized. The water pressure inside the cell results in **turgor**, which we have previously discussed, and is important to plant structure and strength for primary growth tissues. Most plant cells achieve turgor for their normal functioning state. The plant **central vacuole** helps maintain turgor. The vacuole holds water and other substances that help maintain proton gradients within the cytosol. Maintaining water balance is critical to plants, just as it is to animals.

Water Balance, Water Movement and Transpiration

Plants are 80-90% water (wet weight). Soil and atmosphere usually contain a much lower proportion of water (winters in Puget Sound excepted). Most plants present large surface areas to their surroundings; both the root and leaf surface areas are large: roots to absorb water and nutrients, leaves for exposure to sun for photosynthesis. Plants consume and lose much more water than we do, about 17 times as much.

Plants are especially vulnerable to water loss simply because they need open surfaces for gas exchange. Most water lost from plants is by the process of **transpiration**, the evaporation of water from the plant through open stomata and other plant surfaces. Transpiration also plays a role in the movement of water throughout the plant as we shall discuss.

Transpiration loss is significant – a mature maple tree can evaporate more than 50 gallons of water a day. In cornfields, as much as 90% or more of the water absorbed by the roots is lost by transpiration.



Naturally, plants have a number of ways to conserve water and minimize transpiration losses:

- Epidermal cells on above-ground structures have a cuticle layer (cutin) to prevent water loss; the walls of cork cells contain impermeable suberin.
- Plant cells have vacuoles to accumulate water, and cell walls to help maintain turgor. (However, this works better at preventing excess water than it does at preventing dehydration.)
- Many cells and tissues need not be maintained because they're dead (saves energy as well as water needed for metabolic functions)
- Xeromorphic plants frequently have anatomical adaptations to minimize transpiration loss as well as physiological adaptations such as the CAM metabolism discussed with photosynthesis

- Most transpiration loss is through stomata. Guard cells open and close so that water loss by transpiration is minimized when plants can't use CO_2 for photosynthesis. *(The mechanism for stomatal operation will be discussed in a bit.)*

Even so, taking in sufficient water for metabolic needs and to counter transpiration loss is a challenge that plants must meet and physicists can explain.

Moving Water – the Mechanisms

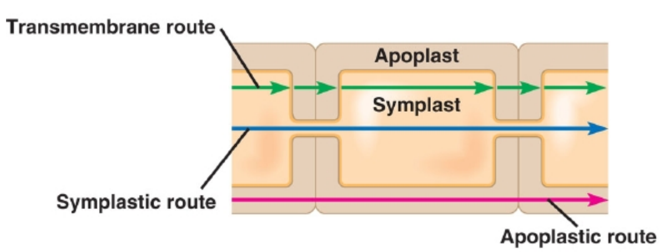
We need to answer the following in our discussion of water movement mechanisms:

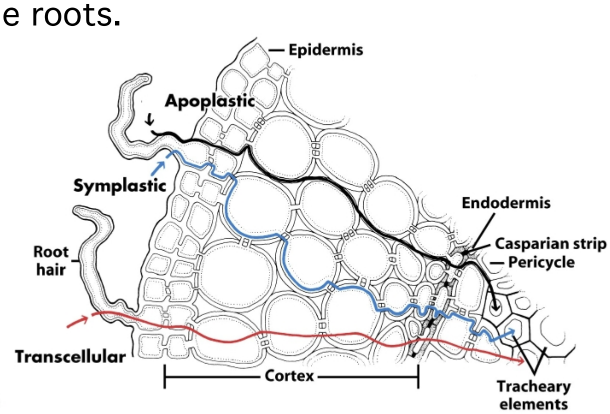
- How does water enter and move through the plant when plants have no pumps?
- How does a plant move water upward as much as 300 feet above the ground against the forces of gravity?

Water and other substances move into and within the plant root in a variety of ways:

- **Apoplastic** movement is movement of water through intercellular spaces and cell walls
- **Transmembrane** movement moves water from cell to cell via membrane transport
- **Symplastic** movement is movement of water through plasmodesmata from cell to cell, once water has entered a cell (Transmembrane and symplastic movement are sometimes considered to be the same.)

Root hairs increase the surface area for absorption, and soil particles with their surrounding water films adhere to root hairs to promote a diffusion gradient. Root hairs may also use active transport for uptake. Mycorrhizae associates absorb both water and minerals and transfer them into the roots.

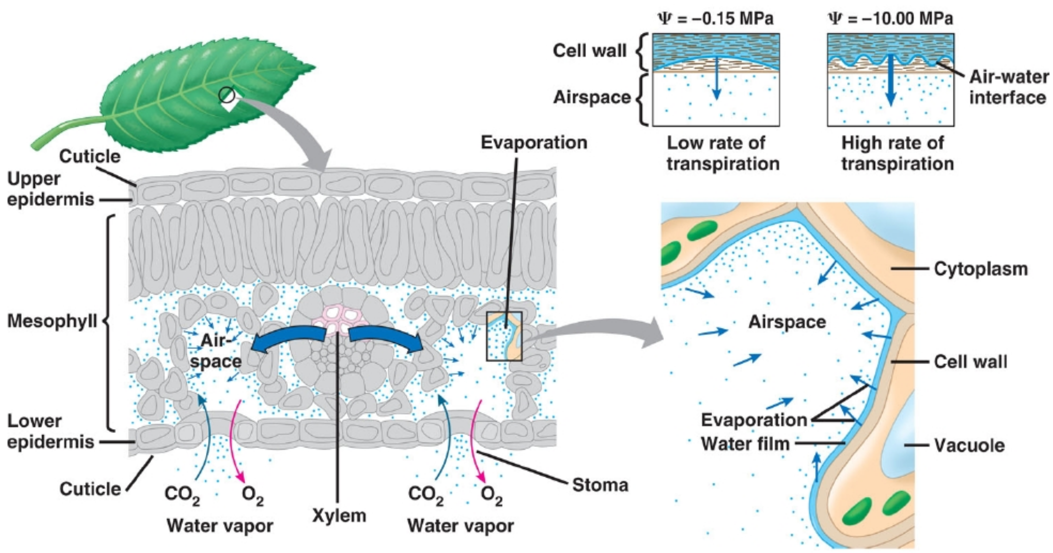




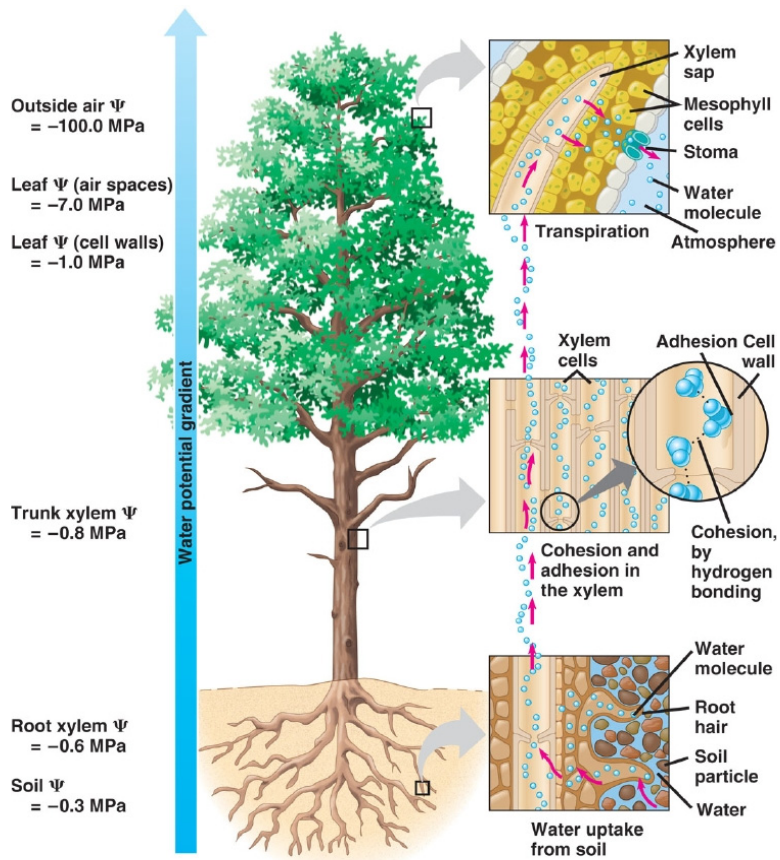
Once through the root cortex, substances pass into the cells of the endodermis (protected by the casparian strip) and from root stele parenchyma cells into xylem tissue for upward movement throughout the plant. Dilute minerals also move with water. In spring, even very dilute solutes can move with water through the xylem. The substances that move through xylem are called sap.

Moving through Xylem — The Cohesion–Tension Theory

- Water lost by transpiration creates a **negative water potential** in cells that exerts a “pull” on the H_2O in cell walls that is connected (by cohesion) to H_2O in xylem resulting in a strong tension in the xylem.
- As water evaporates out of the stomata, the film of water that coats mesophyll cells diminishes. Pimary cell walls have **adhesive** properties; the remaining water is attracted to the walls (cellulose is very hydrophilic – think of the paper towel commercials), resulting in even less water and the water potential of the mesophyll cells decreases.



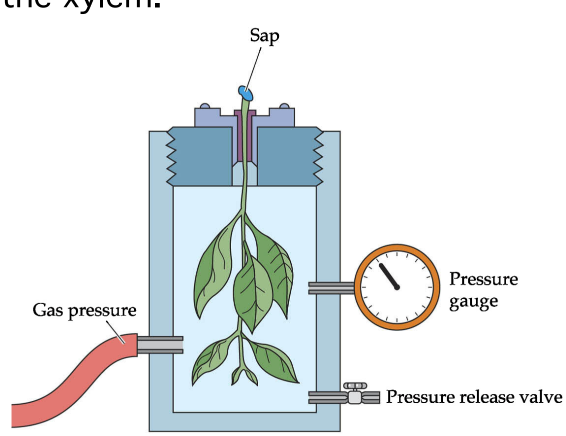
- Water molecules also tend to **cohere** (stick to each other -the surface tension property of water). This second force tends to make water molecules take on a concave shape that resists the increasing surface area. The two forces together (adhesion and cohesion) generate a negative water pressure that literally pulls water in the leaf out of the xylem.
- This transpiration pull can be exerted throughout the xylem down to the roots making the root water potential negative, too.
  - When transpiration rate is high, the osmotic gradient across the endodermis decreases as dissolved ions are drawn upward in the xylem. The depletion of water in the root hair zone can draw water from surrounding soil areas.
- This combination of forces (transpiration and cohesion) is sufficient to move water upward against the forces of gravity.
- In addition, the diameter of vessels and tracheids promotes cohesion.
- It also means that a plant disadvantage, water lost by transpiration, can be turned around to do something beneficial for the plant.



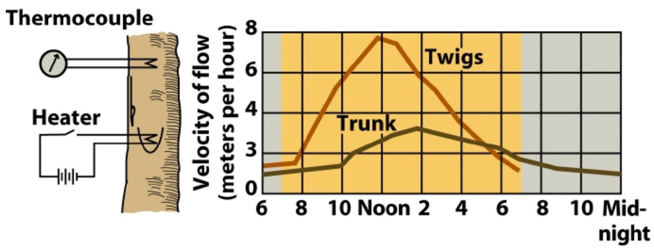
For all of this to work, one must have an unbroken column of water. Air bubbles in the column dramatically affect water movement. A rupture of the water column is called **cavitation** and vessels affected will no longer function. The air or water vapor blockage that forms after the cavitation is called an **embolism.**

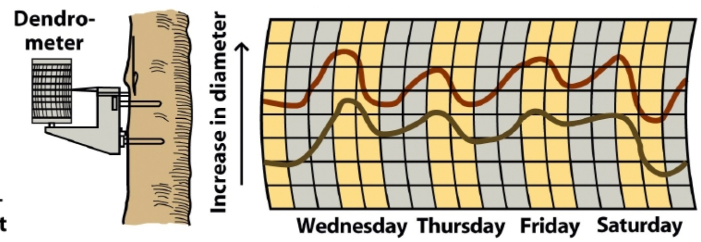
In case you were curious about if this idea of sucking water up the tree "holds water", there are ways of measuring all of this.

- **Pressure bombs** measure the hydrostatic pressure within the xylem. When a twig is cut, water recedes into the interior. The twig is put into a pressure chamber and gas pressure is applied until water appears at the cut end of the twig. That pressure can be measured. It is a positive pressure that equates to the tension within the xylem.

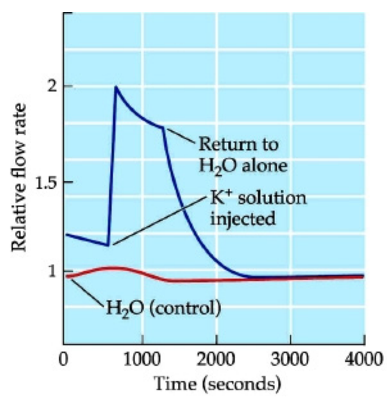


- Thermocouples have been used to measure the velocity of movement of small amounts of “heated” xylem. Xylem movement is always detected earlier in twigs than in the trunk of trees.
- The negative pressures (tensions) caused by transpiration are reflected by a narrowing of the diameter of the tree as xylem cells narrow in diameter from the tension generated.





In addition, the rate of xylem movement varies. Virtually no movement occurs at night, when there is no transpiration. In the daytime, the rate of xylem movement depends on environmental conditions such as temperature, wind velocity, and light intensity, as well as solutes in the sap. Studies have shown that the rate of xylem movement increases with K^+ concentration in the sap, and slows when K^+ diminishes.



Transpiration may also be responsible for some water and dissolved ion movement from soil into the roots. When transpiration rate is high, the osmotic gradient across the endodermis decreases as dissolved ions are drawn upward in the xylem. The depletion of water in the root hair zone can draw water from surrounding soil areas.

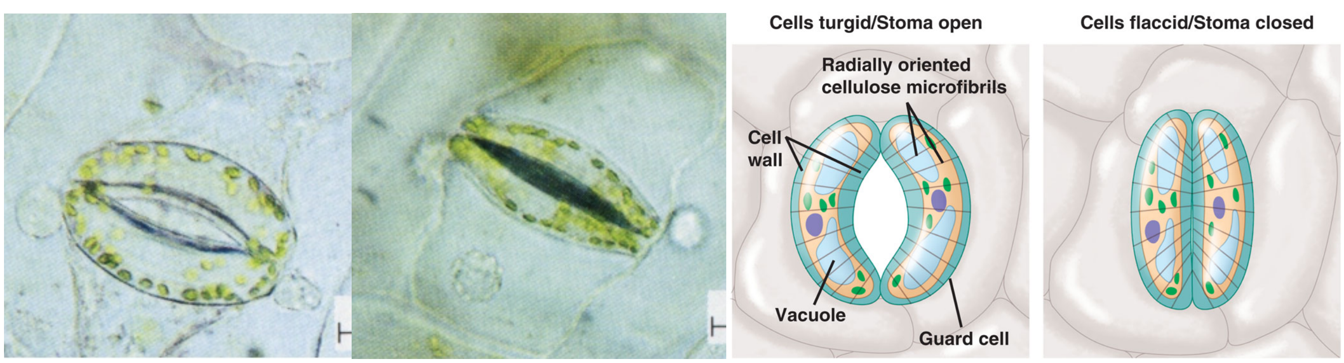
Although the transpiration-cohesion explanation for water movement through xylem is "widely" accepted, many questions remain and water movement through xylem is an active area of research in plant physiology. For example, many vessel walls are lipid lined, so no water adhesion occurs in such vessels. Others question the accuracy of pressure bombs and other mechanisms for measuring water potential. In addition, the rate of water movement in xylem is not uniform within "equivalent" regions of plants. Transpiration-cohesion is surely a force in water movement through xylem. As techniques improve, as with all science, better explanations may result.

Controlling Transpiration — The Stomatal Mechanism

Transpiration is, in large part, a consequence of the process of photosynthesis. Plants must have access to CO_2 from the atmosphere. CO_2 diffuses into plants through open stomata. There may be as many as 12,000 – 20,000 stomata per cm^2 in the leaf epidermis. (*As an aside, stomatal density is affected by CO_2 concentration in some plants. Stomatal density has decreased in one woodland area of England that has been studied since 1927 corresponding to an increase in ambient CO_2 levels.*) At the same time water is lost through the stomata by transpiration. Since it is important to conserve as much water as possible, plants have mechanisms to open and close their stomata to minimize water loss during non-photosynthetic times and/or when transpiration exceeds the ability of the plant to metabolically function. (This latter affects photosynthesis.)

How stomata work

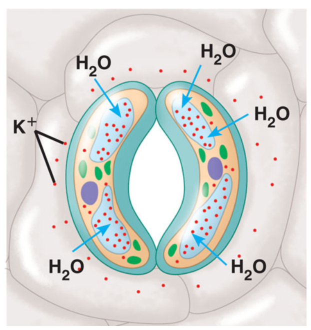
The mechanical operation of stomata is a phenomenon of turgor, osmotic balance and active transport, helped by the structure of the guard cells. Guard cells are bean shaped with radially oriented cellulose microfibrils in their walls that limit stretching to one direction when water is absorbed by the cell. The pair of guard cells are attached at their ends, so when they stretch, they become distorted. This distortion of the pair of guard cells results in a shape that causes a gap between the guard cell pair's inner walls. This gap is the stoma. When guard cells lose turgor, they "shrink", and the collapsed cells force the inner walls of the guard cell pair together, closing the stoma.



To produce these changes in turgor, a ratio of potassium K^+ and H_2O is maintained within guard cells that is different in daytime than nighttime. In addition, in contrast to other epidermal cells, guard cells contain chloroplasts, and the process of photosynthesis is used to maintain turgor when stomata are open.

Daytime

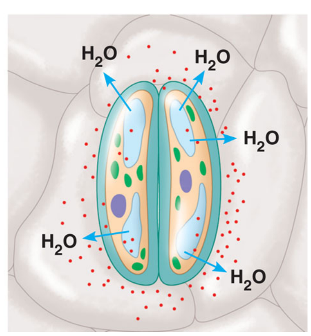
1. K^+ moves into guard cells in response to presence of light through membrane channels using the proton gradient generated by hydrogen proton pumps. H^+ is actively pumped out of guard cells at the time stomata are opening. The pumps, which are activated by blue-light receptors in the guard cell membrane, create a negative water potential in the cell. (More solutes = more negative water potential).
2. The increasing "+" charge (K^+ may be 4 – 8 time higher within the cell) is countered in some plants by the active transport of Cl^- into the cell. The Cl^- uptake is coupled to a proton pump generated by the release of H^+ from a number of organic acids within the guard cells. The acids also help increase the "-" balance.
3. H_2O moves by osmosis into cell in response to K^+ solute concentration, increasing the cell volume (a turgor phenomenon) swelling guard cells which "open" forming stomata. The water is stored in the vacuole.
4. Photosynthesis product solutes, along with the H^+/ K^+ pump maintain the osmotic gradient needed for turgor, keeping the stomata open during photosynthetic hours.



K^+ and water movement into guard cell

Nighttime, water deficit or some other harmful conditions*

1. K^+ leaches out of guard cells passively.
2. H_2O follows.
3. Guard cells lose turgor and "close".



K^+ and water movement out of guard cell

Things that affect stomatal opening and closing

Stomatal Opening

- As stated, blue light receptors in the guard cells activate the H+/K+ pumps.
- Photosynthesis maintains a high solute concentration for turgor and also provides a source of ATP for the proton pumps to function. Guard cell chloroplasts respond to red light.
- Low CO_2 in the mesophyll, which occurs when photosynthesis starts, can trigger stomatal opening. Artifically low CO_2 levels even in the absence of light can trigger stomatal opening.
- Stomata opening may also be under the influence of circadian rhythms.

Stomatal Closing

- Abscisic acid produced in roots and translocated through xylem monitors water concentration in the plant (root and leaf mesophyll cells) and when there is a water deficit, serves as a signal for a transduction pathway (that has a Ca^{++} secondary messenger) which results in ion (K^+ especially, but possibly Cl^- and malate) movement from the guard cells, closing stomata within minutes.
- High CO_2 levels detected in guard cells will promote stomatal closure
- High temperatures also trigger stomatal closure (but may be related to the CO_2 concentrations at higher temperature).
- Some chemicals, such as ozone, also promote stomatal closure.

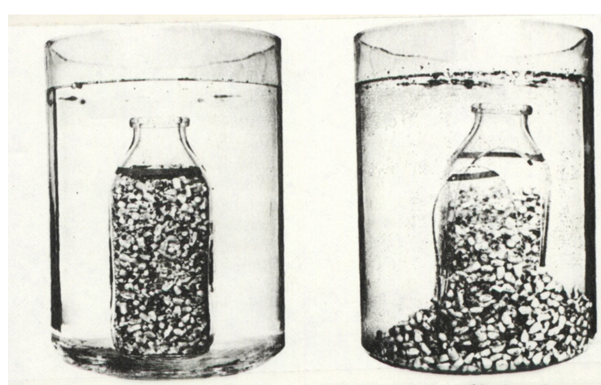
Other Water Movements

Before we leave our discussion of movement of water in plants, let's look at a few other water phenomena.

Imbibition

Water can be absorbed rapidly into cells by means other than osmosis. Certain molecules, especially starch and cellulose, "attract" water molecules when they are wet because of surface charges (+ and -). Since water is polar, it is attracted to the surfaces of these molecules, and large amounts of water can be taken into cells in this manner. Imbibition is very important for the process of germination, causing the seeds to swell rapidly with the uptake of water.

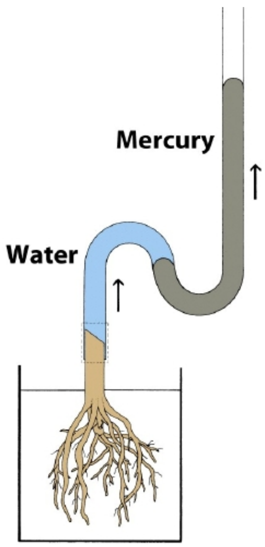
Imbibition



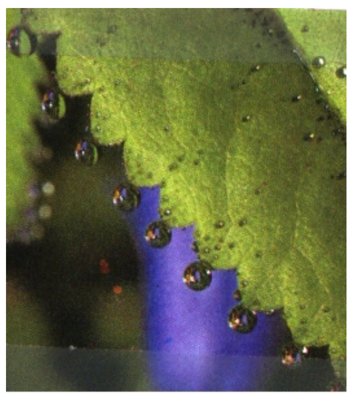
Force of Imbibition

Positive Root Pressure and Guttation

Roots actively move nutrient ions from the soil all of the time, and when transpiration is low, the increasing concentration of ions within the cortex cells creates a water potential gradient for moving water into the roots. This results in a positive pressure. Simple diffusion pressure in roots moves H_2O upward — often forcing the H_2O to be exuded from vein tips in leaves, a phenomenon called **guttation.** The special leaf tip cells are called **hydathodes.** Guttation is limited. Positive root pressure is soon matched by the atmospheric pressure, and in daylight, transpiration rates rapidly exceed any positive pressure generated.



Root Pressure



Guttation

Guttation occurs when there is high soil moisture and low evaporation stress (minimal transpiration). You can typically see guttation in Puget Sound during the spring and early summer, in the early mornings before the sunlight evaporates the water. Grasses and many herbaceous plants, such as strawberries, guttate nicely. Guttation cannot be observed during rain, since the rain drops coat the plant surfaces, and guttation should not be confused with dew, which can condense from the atmosphere onto plant surfaces.

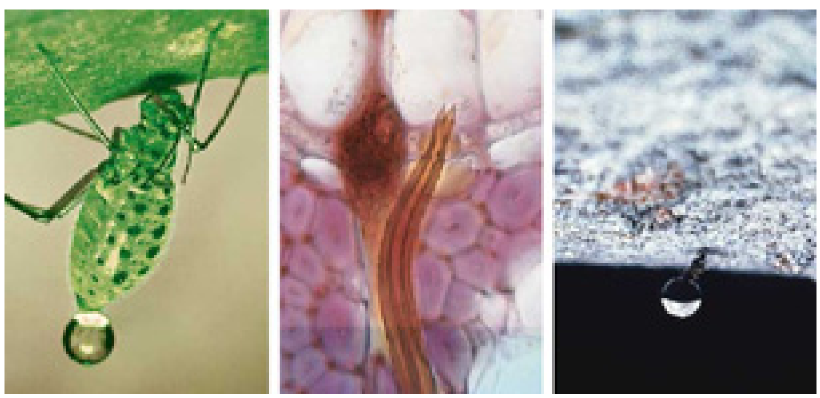
Movement of Solutes in plant

While some solutes are moved through xylem, most organic solutes, especially sucrose, are transported, or translocated, in phloem. Phloem is also responsible for the translocation of many signal molecules, including hormones and various RNA molecules that activate systemic changes such as defense responses and induction of flowering shoots. Electrical signals also move through phloem

Phloem Movement

The discovery of phloem movement is credited to Malpighi who recorded that when one rings a tree, the tree dies by lack of "nourishment" below the ring. Although this was noted a long time ago, learning how phloem transports solutes was inhibited because access to the phloem tissue was difficult. (The cells collapsed and quit functioning when manipulated.)

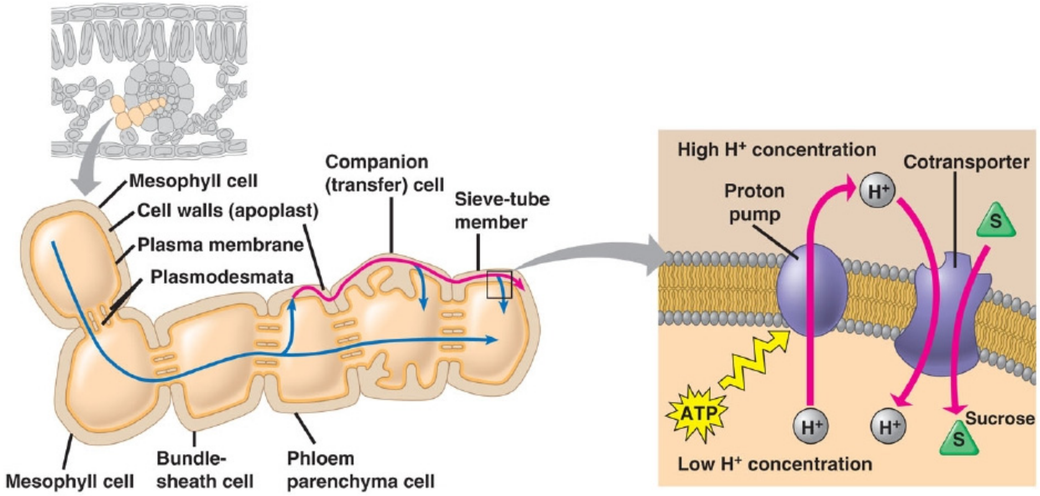
Ultimately, the common aphid was used as a research tool. Aphids normally penetrate into phloem to feed, and their actions do not stop the phloem activity in the plant. Aphids merely divert the flow into (and sometimes through) the aphid body.



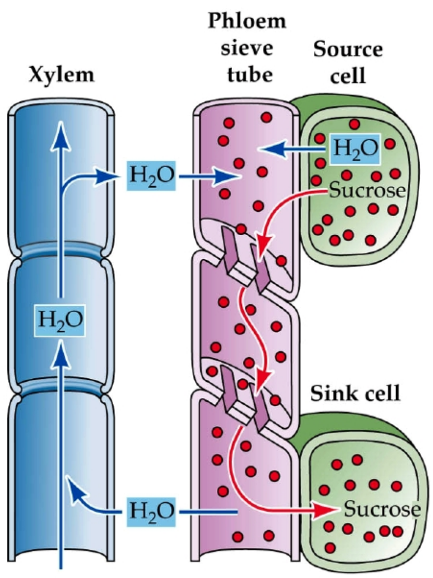
Sucrose has a high osmotic potential (hydrostatic pressure). While sucrose, like any substance, can move by diffusion, the normal rate of phloem movement is much faster than simple diffusion.

Movement in phloem is always in a direction of more concentrated solute to less concentrated, or from where you have solutes (mostly sugars from photosynthesis) to where you need the solutes. Phloem can also be used to move solutes from storage areas to where solutes are needed. This **pressure-flow** gradient between the "source" of solutes and the "sink", the location to which the solutes are being moved, explains how solutes are moved through phloem.

Solutes move through leaf mesophyll or storage parenchyma cells both symplastically and apoplastically to the vascular tissue. Solutes are then actively secreted, or **loaded**, from the source into a sieve tube. **Transfer companion cells** do this. Proton pumps use cotransport to transfer the sugars, which may accumulate concentrations two to three times the surrounding areas.



- Once the sugars are in the sieve tubes, movement is facilitated by osmotic potential (turgor increases the hydrostatic pressure in the cells). The presence of sugar in a sieve tube attracts water.
- Water moves into the sieve tube from a\adjacent xylem cells increasing the pressure in the sieve tube
- Increased pressure forces the solutes into the next cell of the sieve tube. This mechanism is called **pressure flow**, a type of bulk flow.



Active transport (cotransport with proton pumps) is again used at the sink, to move the solutes into the cells where they will be needed or stored.

Revisiting the Symplast and Plasmodesmata

When cell wall structure is discussed in biology, plasmodesmata, membrane channels between adjacent plant cells are described. Earlier in this section, the role of plasmodesmata in symplast movement of water in roots was also mentioned.

In recent years, research on plasmodesmata had resulted in more information on these intercellular connections and their structure and function. The plasmodesmata are critical to the overall communication that maintains localized symplast domains within the plant.

Environmental changes are rapidly transmitted through the dynamic symplast, particularly in relation to plant transport, and plasmodesmata appear to change in response to a number of signals.

Plasmodesmata may open and close rapidly in response to turgor changes, pH and/or Ca^{++} concentrations affecting symplast movement. The number of plasmodesmata can change during development and functioning of the cell. Leaf cells have many plasmodesmata during development because they need solutes for cell maturation. Once mature, photosynthesis supplies the solutes and the number of plasmodesmata decreases.

Recent studies on plant viral infections have shown the viral proteins can dilate plasmodesmata facilitating viral movement from cell to cell. However, the viral proteins are mimicking plant proteins that normally regulate plasmodesmata diameter.

Investigating plasmodesmata and the symplast is just one area of active research on how plants communicate and the relationship of structure to function.