Translocation – refers to the movement of water and dissolved solutes through the plant, especially

The Transpiration Stream – water flow in the xylem
The Assimilate Stream – water flow in the phloem

It helps to first review some relevant basic physical principles including some of the special properties of water.
Water ($H_2O$)

A polar molecule – overall no charge, but regions of charge. Hydrogen side positive, Oxygen side negative

Polarity allow attraction between charged parts of molecules

1. Cohesion – attraction between water molecules (hydrogen bonds). Results in “tensile strength” resists being pulled apart. Cause of “surface tension”.
2. Adhesion – attraction to other polar molecules (e.g. cellulose).
Water Movement – how does a plant move water?
three main types -bulk flow, diffusion, osmosis

In all water movement, the direction of flow is determined by potential energy.
Water potential – the potential energy of water at any point in the plant. ($\Psi = \text{psi}$)

$$\Psi_t = \Psi_g + \Psi_p + \Psi_s$$

Water *always* moves from high to low potential
gravity potential – up to down ($\Psi_g$)
pressure potential – high pressure to low ($\Psi_p$)
osmotic potential – high water concentration to low ($\Psi_s$)

Water potential is measured in units of pressure – required to stop water movement -units of megaPascals (Mpa)
1. **Bulk Flow** – movement of mass of water molecules together (river, pipe)

   Pressure and gravity – 2 drivers
   - both important to plants
2. **Diffusion** – net effect of individual movement of molecules

Molecules in a liquid or gas collide and move in random directions – no net movement.

If there are differences in concentration (e.g., drop of ink) there is a net movement from high to low concentration, until concentrations are equalized.
3. **Osmosis** – diffusion of water across a semi-permeable membrane (permeable to water, but not solutes)

Biological membranes have this characteristic, with special water transport proteins - Aquaporins

Osmosis – water will move from region of high water concentration (= low solute concentration) to low
Osmotic Pressure – pressure required to stop water movement by osmosis

Note also the possibility of putting water under negative pressure (tension) in (d)

36.8/36.5
Diffusion and osmosis are slow (compared to bulk flow), most efficient when
1. Distance is short
2. Concentration difference is large (steep gradient)

Many important living functions involve controlling levels of dissolved substances on one or both sides of a membrane
**Turgor Pressure** – plants cells often kept under positive pressure by osmotic potential – solutes cause water to move into cell (low water concentration), push against the cell wall. This can be important for plant structure. Loss of turgor can result in

1. Wilting
2. Plasmolysis – death of cell from pulling of membrane away from wall
How does a plant control concentration gradients (differences) across cell membranes?

Basic cell membrane structure
– lipid bilayer with embedded proteins
Proteins regulate molecule movement across membranes

1. **Diffusion** – small non-polar lipid soluble molecules may pass directly through the lipid bilayer (follows concentration gradient – called “passive transport”). CO$_2$, O$_2$ e.g. No energy expended.

2. **Facilitated diffusion** – transport proteins assist in passage of selected molecules, sometimes by binding. Aquaporins, e.g., special water transporting proteins. Can follow concentration and charge – “electrochemical gradient”

3. **Active transport** – proteins coupled to ATP drive transport – this can move molecules against (and even create) the electrochemical gradient
Translocation in the xylem – the transpiration stream

Water is lost when stomates are opened for CO$_2$ uptake – called transpiration.

Most of the water taken up (>90%) is lost through stomata, and must be replaced by root uptake.

“Transpiration stream” refers to this flow of water from the soil, into the roots, up the stem to the leaves and out through stomates.
Transpiration

Problem: a typical tree contains a large column of water, how can it be raised up against the pull of gravity?

Solution: a chain of water potential initiated in the leaf, called the “adhesion-cohesion-tension mechanism”
To enter the plant from the soil, water must be moving from higher to lower water potential. In transpiration this is created by tension in the xylem – a pressure potential.
The loss of water from the leaf from the stomates creates *tension* (stretching – negative pressure) in the leaf water xylem. This lowers the water potential, causing water further down (at higher potential) to move up, creating lower potential there, still lower water moves up, and so on down to the roots and even out into the soil. The text describes this as “pulling up”.

*Cuticle Xylem Upper epidermis Mesophyll Lower epidermis Cuticle Air space Microfibrils in cell wall of mesophyll cell Air-water interface Microfibril (cross section) Water film*
What holds the water in the tree?
Adhesion of water to xylem walls,
Cohesion of water with itself (tensile strength)

Adhesion and cohesion can hold water in a thin column, and even cause it to rise up ("capillary action") like a bridge – strength of adhesion and cohesion determine how long the bridge can be and still resist gravity.

From Dr. Dirt
The height water will rise in a small cylinder, or capillary tube, is dependent on the diameter of the tube, and is affected by the density of the water and the gas (which are functions of temperature), the acceleration of gravity, the contact angle (water with the glass), and the surface tension of the liquid. But with water in air, the formula simplifies to $h = 0.3 / d$, where $h$ is the height of rise, and $d$ is the diameter of the capillary tube, when both are measured in centimeters.

In the larger image, it can be seen that the height of water in the dish is 5 mm. The height of rise in the capillary tubes above the water level in the dish ranges from 1 mm in the straw on the left to 42 mm in the small capillary on the right. So the smallest capillary diameter is 0.07 cm, or 0.7 mm. The height of rise in the straws is less than would be expected in a glass capillary because of lower adhesion between water and plastic.

$$\text{xylem } 50 \mu \text{m} = 0.005 \text{ cm}$$

$$h = 0.3 / 0.005 = 60 \text{ cm}$$

From Dr. Dirt

http://www.wtamu.edu/~crobinson/SoilWater/capillar.html
Actually, these same forces cause *resistance* to flow in such thin tubes – adhesion causes molecules at edge of tube to flow little – maximum flow rate is in the center, and a function of tube diameter

**Max. velocity (h/t)** = \( \frac{\text{pressure gradient (dp/l)} \times \text{radius}^2}{4 \times \text{Viscosity (4v)}} \)

Rate of flow depends on

1. Pressure gradient – rate of evaporation
2. Viscosity (coke vs. milkshake)
3. Vessel thickness (radius)
   - wide vessels – 30m/hr
   - narrow vessels – 3m/hr

Calculations show this mechanism more than adequate to support columns of water in the tallest trees.
\( \delta \) = Boundary layer thickness

\( R \) = Radius of pipe

\( L \) = Transition length

\( v \) = Velocity

Development of boundary-layer flow in pipe

http://www.msubbu.com/ln/fm/Unit-II/boundary-layer-pipe.gif
So, water is hauled up the stem (bulk flow) via a cascade of water potential initiated in the leaves.

Note the role of solar energy (leaf temperature) driving this flow.
Note all those negative pressures in the xylem during active transpiration – but still high to low.

Think again about xylem structure – thick walls to resist this tension – a force of collapse.
Stomatal control of transpiration

Plants regulate transpirational water loss by regulating stomatal opening. 98% or more of the water is lost through the stomates.

Stomatal opening is regulated by adjustment of the turgor pressure of the guard cells. Perhaps counter-intuitively,

High turgor – stomates open
Low turgor – stomates close
Increased turgor opens stomates due to the structure of the guard cells – attached at ends, with radially oriented microfibrils.

Guard cell turgor is increased by active transport of potassium ($K^+$) ion into the guard cells, using metabolic energy.
Transpiration rate is affected by the environment

1. Temperature. The rate of evaporation doubles for each 10° C. Light increases leaf temperature.
2. Humidity. Higher humidity, lower rate of water loss (smaller difference in water concentration)
3. Wind. Moving air reduces boundary layer and increases water loss
Stomatal opening responds to the environment.
1. Leaf water – low leaf turgor closes stomates
2. Root water – produce hormonal signal (Abscisic acid – ABA) when water stressed that closes stomates
3. CO\textsubscript{2} – increases in mesophyll CO\textsubscript{2} cause stomates to close.
4. Light – stomates open in light, close in dark – partly a CO\textsubscript{2} effect. Also, special blue light receptor pigments in guard cells cause opening. Also, intrinsic cycle (circadian rhythm).
5. Temperature – high temperatures cause closing – probably a CO\textsubscript{2} effect (increased respiration)
Translocation in Phloem – the Assimilate stream

Problem: sugars produced in leaves must be exported out to other parts of the plant where needed.

Solution: phloem loading and unloading generate a circulation of water that moves sugars to areas of active use.

More generally, in phloem, sugars move from a source to a sink:
- sources: leaves, storage tissue
- sinks: any plant part requiring assimilates for growth or maintenance

So sugars are loaded at sources, and unloaded at sinks.
Phloem – contains 10-25% sucrose, also amino acids
much more viscous than xylem
Flow rates – 1m/hr, slower than xylem (1-50m/hr)
Phloem is under *positive* pressure

Studies of phloem have used aphids – specialized phloem
feeding insects – sever stylet and sample phloem

36.21/36.19
Mechanism – the Pressure-flow hypothesis

Since photosynthesis builds up sugars in the leaf, diffusion alone could result in the spread of sugars throughout the plant. BUT, measured velocities in the phloem are too fast – it is bulk flow. HOW?

1. At source, loading of sugars into the phloem causes water to move in (from the xylem) creating an osmotic potential that pressurizes the phloem.
2. At sink, unloading of sugars reduces the osmotic potential, so the positive pressure forces water out (to the xylem).
3. Thus the osmotic gradient is converted into bulk flow. In fact, this creates a circulation between the phloem and xylem including flow in the xylem that is independent of transpiration.
Note that both loading and unloading are both active membrane driven processes using metabolic energy (active transport).

Also – note that this mechanism causes sugars to move preferentially to areas of greatest demand (unloading).
In addition, recent work suggests that phloem may be a key regulatory system in plants

1. Other ions (K\(^+\)) may be translocated – to adjust flow independently of sugar concentrations

2. Information molecules (hormones) may also be spread via the phloem

3. Phloem may also conduct electrical signals – function not well understood
Summary of Translocation

Plant vascular design takes advantage of properties of water, especially polarity, to create a circulation of water and materials that allows the integration of uptake and utilization of resources to create more plant.

This circulation is driven primarily by “passive” forces (evaporation, diffusion, osmosis, bulk flow, adhesion, cohesion) that are manipulated at critical points by active membrane driven processes that serve to regulate the flows, particularly

1. Nutrient uptake
2. Stomatal opening
3. Phloem loading and unloading