Chapter 36 Transport in Vascular Plants
Lecture Outline

Overview: Pathways for Survival

- The algal ancestors of plants obtained water, minerals and CO2 from the water in which they were completely immersed.
- For vascular plants, the evolutionary journey onto land involved the differentiation of the plant body into roots, which absorb water and minerals from the soil, and shoots, which absorb light and atmospheric CO2 for photosynthesis.
- This morphological solution created a new problem: the need to transport materials between roots and shoots.
- Xylem transports water and minerals from the roots to the shoots.
- Phloem transports sugars from the site of production to the regions that need them for growth and metabolism.

Concept 36.1 Physical forces drive the transport of materials in plants over a range of distances

- Transport in plants occurs on three levels:

1. The uptake and loss of water and solutes by individual cells, such as root hairs.
2. Short-distance transport of substances from cell to cell at the level of tissues or organs, such as the loading of sugar from photosynthetic leaf cells into the sieve tubes of phloem.
3. Long-distance transport of sap within xylem and phloem at the level of the whole plant.

Transport at the cellular level depends on the selective permeability of membranes.

- The selective permeability of a plant cell's plasma membrane controls the movement of solutes between the cell and the extracellular solution.
- Molecules tend to move down their concentration gradient. Diffusion across a membrane is called passive transport and occurs without the direct expenditure of metabolic energy by the cell.
- Active transport is the pumping of solutes across membranes against their electrochemical gradients, and requires expenditure of energy by the cell.
- The cell must expend metabolic energy, usually in the form of ATP, to transport solutes "uphill."
- Transport proteins embedded in the membrane can speed movement across the membrane.
- Some transport proteins bind selectively to a solute on one side of the membrane and release it on the opposite side.
- Others act as selective channels, providing a selective passageway across the membrane.
- For example, the membranes of most plant cells have potassium channels that allow potassium ions (K+) to pass, but not similar ions, such as sodium (Na+).

- Some channels are gated, opening or closing in response to certain environmental or biochemical stimuli.

Proton pumps play a central role in transport across plant membranes.

- The most important active transport protein in the plasma membrane of plant cells is the proton pump.
- It hydrolyzes ATP and uses the released energy to pump hydrogen ions (H^+) out of the cell.
- This creates a proton gradient because the H^+ concentration is higher outside the cell than inside.
- It also creates a membrane potential or voltage, a separation of opposite charges across a membrane.
- Both the concentration gradient and the membrane potential are forms of potential (stored) energy that can be harnessed to perform cellular work.
- This potential energy is used to drive the transport of many different solutes.
- For example, the membrane potential generated by proton pumps contributes to the uptake of potassium ions (K^+) by root cells.
- The proton gradient also functions in cotransport, in which the downhill passage of one solute (H^+) is coupled with the uphill passage of another, such as NO3? or sucrose.
- The role of proton pumps in transport is a specific application of the general mechanism called chemiosmosis, a unifying process in cellular energetics.
- In chemiosmosis, a transmembrane proton gradient links energy-releasing processes to energy-consuming processes.
- The ATP synthases that couple H^+ diffusion to ATP synthesis during cellular respiration and photosynthesis function somewhat like proton pumps.
- However, proton pumps normally run in reverse, using ATP energy to pump H^+ against its gradient.

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.
- The combined effects of solute concentration and pressure are called water potential, represented 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 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, such as expanding the cell.

- 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.
- Plant biologists measure psi in units called megapascals (MPa), where one MPa is equal to about 10 atmospheres of pressure.
- 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; water pressure in home plumbing is about 0.25 MPa.
- In contrast, plant cells exist at approximately 1 MPa.
- Both pressure and solute concentration affect water potential.
- The combined effects of pressure and solute concentrations on water potential are incorporated into the following equation, where psip is the pressure potential and psis is the solute potential (or osmotic potential).

  psi = psip + psis

- Pressure potential is the physical pressure on a solution and can be positive or negative.
- The water in the dead vessel element cells of xylem may be under negative pressure of less than ?2 MPa.
- Water in living cells is usually under positive pressure. The cell contents press the plasma membrane against the cell wall, producing turgor pressure.
- The solute potential (or osmotic potential) of a solution is proportional to the number of dissolved solute molecules.
- By definition, the solute potential of pure water is 0.
- The addition of solutes lowers the water potential because the solutes bind water molecules, which 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.
- 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 psi (0 MPa) to the region of lower psi (?0.23 MPa).
- Water potential affects the uptake and loss of water in plant cells.
- In a flaccid cell, psip = 0 and the cell is limp.
- 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 by shrinking and pulling away from its wall.
- If a flaccid cell is placed in pure water (psi = 0), the cell will have lower water potential than pure water due to the presence of solutes, and water will enter the cell by osmosis.
- As the cell begins to swell, it will push against the cell wall, producing 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 psip and psis are equal in magnitude (but opposite in sign), psi = 0, and the cell has reached 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, and their turgor contributes to support in nonwoody parts of the plant.
- You can see the effects of turgor loss in wilting, the drooping of leaves and stems as plant cells become flaccid.

Aquaporins affect the rate of water transport across membranes.

- Both plant and animal membranes have specific transport proteins, aquaporins, which facilitate the passive movement of water across a membrane.
- Aquaporins do not affect the water potential gradient or the direction of water flow, but rather increase the rate at which water diffuses down its water potential gradient.
- Evidence is accumulating that the rate of water movement through aquaporins is regulated by changes in second messengers such as calcium ions (Ca2+).
- This raises the possibility that the cell can regulate its rate of water uptake or loss when its water potential is different from that of its environment.

Vacuolated plant cells have three major compartments.

- While the thick cell wall helps maintain cell shape, it is the cell membrane, not the cell wall, which regulates the traffic of material into and out of the protoplast.
- This membrane is a barrier between two major compartments: the cell wall and the cytosol.
- Most mature plants have a third major compartment, the vacuole, a large organelle that can occupy as much as 90% of the protoplast's volume.
- The membrane that bounds the vacuole, the tonoplast, regulates molecular traffic between the cytosol and the contents of the vacuole, called the cell sap.
- Proton pumps in the tonoplast expel H+ from the cytosol into the vacuole.
- The resulting pH gradient is used to move other ions across the tonoplast by chemiosmosis.
- 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 of certain molecules between cells.
- The walls of adjacent plant cells are also in contact, forming a second continuous compartment, the apoplast.
- The vacuole is not shared with neighboring cells.

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

- Short-distance transport in plants, the movement of water and solutes from one location to another within plant tissues and organs, is called lateral transport because its usual direction is along the radial axis of plant organs, rather than up or down the length of the plant.
- Three routes are available for lateral transport.
- 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 the 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 without ever entering a cell.

Bulk flow functions in long-distance transport.

- Diffusion in a solution is fairly efficient for transport over distances of cellular dimensions (less than 100 microns).
- However, diffusion is much too slow for long-distance transport within a plant, such as the movement of water and minerals from roots to leaves.
- Water and solutes move through xylem vessels and sieve tubes by bulk flow, the movement of a fluid driven by pressure.
- In phloem, hydrostatic pressure generated at one end of a sieve tube forces sap to the opposite end of the tube.
- 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.
- Rate of flow through a pipe depends 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.

Concept 36.2 Roots absorb water and minerals from the soil

- Water and mineral salts from soil enter the plant through the epidermis of roots, cross the root cortex, pass into the vascular cylinder, and then flow up xylem vessels to the shoot system.

1. The uptake of soil solution by the hydrophilic epidermal walls of root hairs provides access to the apoplast, and water and minerals can soak into the cortex along this route.
2. Minerals and water that cross the plasma membranes of root hairs enter the symplast.

3. Some water and minerals are transported into cells of the epidermis and cortex and then move inward via the symplast.
4. Materials flowing along the apoplastic route are blocked by the waxy Casparian strip at the endodermis. Some minerals detour around the Casparian strip by crossing the plasma membrane of an endodermal cell to pass into the vascular cylinder.
5. Endodermal and parenchyma cells within the vascular cylinder discharge water and minerals into their walls (apoplast). The water and minerals enter the dead cells of xylem vessels and are transported upward into the shoots.

Root hairs, mycorrhizae, and a large surface area of cortical cells enhance water and mineral absorption.

- 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.
- Selective transport proteins of the plasma membrane and tonoplast enable root cells to extract essential minerals from the dilute soil solution and concentrate them hundreds of times higher than in the soil solution.
- This selective process enables the cell to extract K^+, an essential mineral nutrient, and exclude most Na^+.
- Most plants form partnerships with symbiotic fungi to absorb 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 enable older regions of the roots to supply water and minerals to the plant.

The endodermis functions as a selective sentry between the root cortex and vascular tissue.

- Water and minerals in the root cortex cannot be transported to the rest of the plant until they enter the xylem of the vascular cylinder.
- The endodermis, the innermost layer of cells in the root cortex, surrounds the vascular cylinder and functions as a final 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 vascular cylinder.

- These minerals were already screened by the selective membrane they crossed to enter the symplast.
- Those minerals that reach the endodermis via the apoplast are blocked by the Casparian strip in the walls of each endodermal cell.
- This strip is a belt of suberin, a waxy material that is impervious to water and dissolved minerals.
- To enter the vascular cylinder, minerals must cross the plasma membrane of the endodermal cell and enter the vascular cylinder 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 cell walls are part of the apoplast.
- Endodermal cells and parenchyma cells within the vascular cylinder discharge minerals into their walls.
- Both diffusion and active transport are involved in the transfer of solutes from the symplast to apoplast, finally entering the tracheids and xylem vessels.

Concept 36.3 Water and minerals ascend from roots to shoots through the xylem

- Xylem sap flows upward to veins that branch throughout each leaf, providing each with water.
- Plants lose an astonishing amount of water by transpiration, the loss of water vapor from leaves and other aerial parts of the plant.
- A single corn plant transpires 125 L of water during its growing season.
- The flow of water transported up from the xylem replaces the water lost in transpiration and also carries minerals to the shoot system.

The ascent of xylem sap depends mainly on transpiration and the physical properties of water.

- Xylem sap rises against gravity to reach heights of more than 100 m in the tallest trees.
- At night, when transpiration is very low or zero, the root cells continue to expend energy while pumping mineral ions into the xylem.
- The accumulation of minerals in the vascular cylinder lowers water potential there, generating a positive pressure, called root pressure, which forces fluid up the xylem.
- 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.
- 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.
- For the most part, xylem sap is not pushed from below by root pressure but is pulled upward by the leaves themselves.

- Transpiration provides the pull, and the cohesion and adhesion of water due to hydrogen bonding transmits the upward pull along the entire length of the xylem to the roots.
- 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.
- As water evaporates, the remaining film of liquid water retreats into the pores of the cell walls, attracted by adhesion to the hydrophilic walls.
- Cohesive forces in water resist an increase in the surface area of the film.
- Adhesion to the wall and surface tension cause 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 an area of high water potential to an area of lower water potential.
- Mesophyll cells 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 molecules 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 measurable 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.
- Small plants use root pressure to refill xylem vessels in spring.
- Root pressure cannot push water to the top of a tree. In trees, a xylem vessel with a water vapor pocket can never function as a water pipe again.
- The transpirational stream can detour around the water vapor pocket, and secondary growth adds a new layer of xylem vessels each year.

- Only the youngest, outermost secondary xylem vessels in trees transport water. The older xylem vessels no longer function in water transport but do provide support for the tree.

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 is driven by a water potential difference at opposite ends of a conduit, the xylem vessels or chains of tracheids.
- The water potential difference is generated at the leaf end by transpirational pull, which lowers water potential (increases tension) at the "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 turgor pressure contribute to this microscopic transport.
- In contrast, bulk flow, the mechanism for long-distance transport up xylem vessels, depends only on pressure.
- In contrast to osmosis, bulk flow moves the whole solution, water plus minerals and any other solutes dissolved in the water.
- The plant expends none of 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 lowering the water potential in the air spaces within a leaf.
- Thus, the ascent of xylem sap is ultimately solar powered.

Concept 36.4 Stomata help regulate the rate of transpiration

Most leaves have broad surface areas and high ratios of surface area to volume.

- These features are morphological adaptations to enhance the absorption of light for photosynthesis.
- They also increase water loss through stomata.
- To make food, a plant must spread its leaves to the sun and obtain CO_2 from air.
- Carbon dioxide diffuses into and oxygen diffuses out of the leaf via the stomata.
- Within the leaf, CO_2 enters a honeycomb of air spaces formed by the irregularly shaped parenchyma cells.
- This internal surface may be 10 to 30 times greater than the external leaf surface.
- This structural feature increases exposure to CO_2 but also increases the surface area for evaporation.
- A leaf may transpire more than its weight in water each day.
- Water flows in xylem vessels may reach 75 cm/min.
- Transpiration also results in evaporative cooling, which can lower the temperature of a leaf by as much as 10–15°C relative to the surrounding air.

- About 90% of the water that a plant loses escapes through stomata, though these pores account for only 1–2% of the external leaf surface.
- The amount of water lost by a leaf depends on the number of stomata and the average size of their apertures.
- The stomatal density of a leaf is under both genetic and environmental control.
- Desert plants have lower stomatal densities than do marsh plants.
- High light intensities and low carbon dioxide levels during plant development tend to increase stomatal density in many plant species.
- A recent British survey found that stomatal density of many woodland species has decreased since 1927. This is consistent with the dramatic increases in CO2 levels due to burning of fossil fuels.
- This prevents the leaf from reaching temperatures that could denature enzymes.

Guard cells mediate the photosynthesis-transpiration compromise.

- Each stoma is flanked by a pair of guard cells that are suspended by other epidermal cells over an air chamber, leading to the internal air space.
- Guard cells control the diameter of the stoma by changing shape, thereby widening or narrowing the gap between the two cells.
- When guard cells take in water by osmosis, they become more turgid, and because of the orientation of cellulose microfibrils, the guard cells buckle outward.
- This increases the gap between cells.
- When guard cells lose water and become flaccid, they become less bowed, and the space between them closes.
- Changes in turgor pressure that open and close stomata result primarily from the reversible uptake and loss of potassium ions (K+) by guard cells.
- Stomata open when guard cells actively accumulate K+ into the vacuole.
- This decreases water potential in guard cells, leading to an inflow of water by osmosis and increasing cell turgor.
- Stomatal closing results from an exodus of K+ from guard cells, leading to osmotic loss of water.
- Regulation of aquaporins may also be involved in the swelling and shrinking of guard cells by varying the permeability of the membranes to water.
- The K+ fluxes across the guard cell membranes are coupled to the generation of membrane potentials by proton pumps.
- Stomatal opening correlates with active transport of H+ out of guard cells.
- The resulting voltage (membrane potential) drives K+ into the cell through specific membrane channels.
- In general, stomata are open during the day and closed at night to minimize water loss when it is too dark for photosynthesis.
- At least three cues contribute to stomatal opening at dawn.
- First, blue-light receptors in the guard cells stimulate the activity of ATP-powered proton pumps in the plasma membrane, promoting the uptake of K+.

- A second stimulus is depletion of CO_2 within air spaces of the leaf as photosynthesis begins.
- A third cue in stomatal opening is an internal "clock" located in the guard cells.
- Even in the dark, stomata will continue their daily rhythm of opening and closing due to the presence of internal clocks that regulate cyclic processes.
- The opening and closing cycle of the stomata is an example of a circadian rhythm, cycles that have intervals of approximately 24 hours.
- Various environmental stresses can cause stomata to close during the day.
- When the plant is suffering a water deficiency, guard cells may lose turgor and close stomata.
- Abscisic acid, a hormone produced by the mesophyll cells in response to water deficiency, signals guard cells to close stomata.
- While reducing further wilting, this also slows photosynthesis.

Xerophytes have evolutionary adaptations that reduce transpiration.

- Plants adapted to arid climates, called xerophytes, have various leaf modifications that reduce the rate of transpiration.
- Many xerophytes have small, thick leaves, reducing leaf surface area relative to leaf volume.
- A thick cuticle gives some of these leaves a leathery consistency.
- During the driest months, some desert plants shed their leaves, while others (such as cacti) subsist on water stored in fleshy stems during the rainy season.
- In most plants, the stomata are concentrated on the lower (shady) leaf surface.
- In xerophytes, they are often located in depressions ("crypts") that shelter the pores from the dry wind.
- Trichomes ("hairs") also help minimize transpiration by breaking up the flow of air, keeping humidity higher in the crypt than in the surrounding atmosphere.
- An elegant adaptation to arid habitats is found in ice plants, in succulent species of the family Crassulaceae, and in representatives of many other families.
- These assimilate CO_2 by an alternative photosynthetic pathway, crassulacean acid metabolism (CAM).
- Mesophyll cells in CAM plants store CO_2 in organic acids during the night and release the CO_2 from these organic acids during the day.
- This CO_2 is used to synthesize sugars by the conventional (C_3) photosynthetic pathway, allowing the stomata to remain closed during the day when transpiration is greatest.

Concept 36.5 Organic nutrients are translocated through the phloem

- The phloem transports the organic products of photosynthesis throughout the plant via a process called translocation.
- In angiosperms, the specialized cells of the phloem that function in translocation are the sieve-tube members.
- These are arranged end to end to form long sieve tubes with porous cross-walls between cells along the tube.

- Phloem sap is an aqueous solution in which sugar, primarily the disaccharide sucrose, is the most common solute.
- Sucrose concentration in sap can be as high as 30% by weight.
- Sap may also contain minerals, amino acids, and hormones.

Phloem translocates its sap from sugar sources to sugar sinks.

- In contrast to the unidirectional flow of xylem sap from roots to leaves, the direction that phloem sap travels can vary.
- Sieve tubes always carry food from a sugar source to a sugar sink.
- A sugar source is a plant organ (especially mature leaves) in which sugar is being produced by either photosynthesis or the breakdown of starch.
- A sugar sink is an organ (such as growing roots, shoots, or fruit) that is a net consumer or store of sugar.
- Mature leaves are the primary sugar sources.
- Growing roots, buds, stems, and fruits are sugar sinks.
- A storage organ, such as a tuber or a bulb, may be either a source or a sink, depending on the season.
- When the storage organ is stockpiling carbohydrates during the summer, it is a sugar sink.
- After breaking dormancy in the early spring, the storage organ becomes a source as its starch is broken down to sugar, which is carried away in the phloem to the growing buds of the shoot system.
- Other solutes, such as minerals, are also transported to sinks along with sugar.
- A sugar sink usually receives its sugar from the sources nearest to it.
- The upper leaves on a branch may send sugar to the growing shoot tip, whereas the lower leaves of the same branch export sugar to roots.
- One sieve tube in a vascular bundle may carry phloem sap in one direction while sap in a different tube in the same bundle may flow in the opposite direction.
- The direction of transport in each sieve tube depends only on the locations of the source and sink connected by that tube.
- Sugar from mesophyll cells or other sources must be loaded into sieve-tube members before it can be exported to sugar sinks.
- In some species, sugar moves from mesophyll cells to sieve-tube members via the symplast.
- In other species, sucrose reaches sieve-tube members by a combination of symplastic and apoplastic pathways.
- For example, in corn leaves, sucrose diffuses through the symplast from mesophyll cells into small veins.
- Much of this sugar moves out of the cells into the apoplast in the vicinity of sieve-tube members and companion cells.
- Companion cells pass the sugar they accumulate into the sieve-tube members via plasmodesmata.

- In some plants, companion cells (transfer cells) have numerous ingrowths in their walls to increase the cell's surface area and enhance the transfer of solutes between apoplast and symplast.
- In corn and many other plants, sieve-tube members accumulate sucrose at concentrations two to three times higher than those in mesophyll cells.
- This requires active transport to load the phloem.
- Proton pumps generate an H+ gradient, which drives sucrose across the membrane via a cotransport protein that couples sucrose transport to the diffusion of H+ back into the cell.
- Downstream, at the sink end of the sieve tube, phloem unloads its sucrose.
- The mechanism of phloem unloading is highly variable and depends on plant species and type of organ.
- Regardless of mechanism, because the concentration of free sugar in the sink is lower than in the phloem, sugar molecules diffuse from the phloem into the sink tissues.
- Water follows by osmosis.

Pressure flow is the mechanism of translocation in angiosperms.

- Phloem sap flows from source to sink at rates as great as 1 m/hr, faster than can be accounted for by either diffusion or cytoplasmic streaming.
- Phloem sap moves by bulk flow driven by positive pressure.
- Higher levels of sugar at the source lowers the water potential and causes water to flow into the tube.
- Removal of sugar at the sink increases the water potential and causes water to flow out of the tube.
- The difference in hydrostatic pressure drives phloem sap from the source to the sink.
- Pressure flow in a sieve tube drives the bulk flow of phloem sap.

1. Loading of sugar into the sieve tube at the source reduces the water potential inside the sieve-tube members and causes the uptake of water.
2. This absorption of water generates hydrostatic pressure that forces the sap to flow along the tube.
3. The pressure is relieved by unloading of sugar and loss of water from the tube at the sink.
4. For leaf-to-root translocation, xylem recycles water from sink to source

- The pressure flow model explains why phloem sap always flows from source to sink.
- Researchers have devised several experiments to test this model, including an innovative experiment that exploits natural phloem probes: aphids that feed on phloem sap.
- The closer the aphid's stylet is to a sugar source, the faster the sap will flow and the greater its sugar concentration.
- In our study of how sugar moves in plants, we have seen examples of plant transport on three levels.

0. At the cellular level across membranes, sucrose accumulates in phloem cells by active transport.
1. At the short-distance level within organs, sucrose migrates from mesophyll to phloem via the symplast and apoplast.

2. At the long-distance level between organs, bulk flow within sieve tubes transports phloem sap from sugar sources to sugar sinks.

- Interestingly, the transport of sugar from the leaf, not photosynthesis, limits plant yields.
- Genetic engineering of higher-yielding crop plants may depend on a better understanding of factors that limit bulk flow of sugars.