Chapter 36

Resource Acquisition and Transport in Vascular Plants

Lecture Outline

Overview: Underground Plants

- The perennial stone plant *(Lithops)* lives underground in the Kalahari Desert of southern Africa.
  - o Only the tips of two succulent leaves are exposed at the surface.
  - o Each leaf tip has a region of clear, lens-like cells that allow light to penetrate to the underground photosynthetic tissues.
  - o Stone plants conserve moisture, while avoiding the high temperatures and light intensity of the desert.
- The success of plants depends largely on their ability to gather and conserve limiting resources from their environment.
  - o There may be trade-offs in specialized ways of life.
  - o For example, the mostly subterranean lifestyle of stone plants reduces water loss from evaporation but inhibits photosynthesis. As a result, stone plants grow very slowly.

Concept 36.1 Adaptations for aquiring resources were key steps in the evolution of vascular plants.

- Land plants live in two worlds: above ground, where shoot systems acquire light and CO_2 for photosynthesis, and below ground, where root systems acquire water and minerals from the soil.
- The algal ancestors of plants obtained water, minerals, and CO_2 from the water in which they were completely immersed.
  - o Each cell was close to the source of these materials.
- The earliest land plants were nonvascular, leafless shoots with waxy cuticles and few stomata, anchored by the base of the stem or by threadlike rhizoids.
- As land plants evolved, competition for light, water, and nutrients intensified.
- Taller plants with broad, flat leaves had an advantage in absorbing light.
  - o The increased surface area of tall plants resulted in greater evaporation and a greater need for water.
- Larger shoots required more anchorage, which favored the production of branching roots.
- This morphological solution created a new problem: the need for efficient, long-distance transport of water, minerals, and photosynthetic products between roots and shoots.
- The evolution of vascular tissue consisting of xylem and phloem made possible the development of extensive root and shoot systems capable of long-distance transport.

- 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.

- Plants have evolved many structural adaptations for acquiring light from the sun, CO_2 from the air, and water from the ground more efficiently.
- Land plants must also minimize the evaporative loss of water, especially in environments where water is scarce.
  - The adaptations of each species represent compromises between enhancing photosynthesis and minimizing water loss in the species' particular habitat.

Shoot architecture is designed to capture light.

- Stems support leaves and serve as conduits for the transport of water and nutrients.
- Shoot systems vary in the arrangement and form of leaves, the outgrowth of axillary buds, and the relative growth in stem length and thickness.
  - Leaves range in length from the tiny 1.3-mm leaves of the pygmy weed *(Crassula* e*recta)*, a native weed of dry, sandy regions in the western United States, to the 20-m leaves of the palm *Raphia regalis*, a native of African rain forests.
  - The largest leaves are generally found in tropical rain forests, and the smallest are usually found in dry or very cold environments where liquid water is scarce and evaporative loss from leaves must be reduced.
- **Phyllotaxy**, the way in which leaves are arranged on a stem, is determined by the shoot apical meristem and is specific to each species.
  - A species may have one leaf per node (alternate, or spiral, phyllotaxy), two leaves per node (opposite phyllotaxy), or more (whorled phyllotaxy).
  - Most angiosperms have alternate phyllotaxy, with leaves arranged in an ascending spiral around the stem.
  - Each successive leaf emerges about 137.5° from the site of the previous one, minimizing shading of lower leaves by those above.
- The *leaf area index* is the ratio of the leaf surface of a plant or crop to the surface area of the land on which the plant or crop grows.
  - Leaf area index values as high as 7 are common for many mature crops.
- The addition of leaves results in increased shading of lower leaves, to the point that they respire more than photosynthesize.
  - When this happens, the nonproductive leaves or branches undergo programmed cell death and are shed, a process called *self-pruning*.
- Leaf orientation affects light absorption.
  - Some plants have horizontally oriented leaves, whereas grasses have leaves that are vertically oriented.
- In low-light conditions, horizontal leaves capture sunlight more effectively than vertical leaves.
- In grasslands, horizontal orientation may expose upper leaves to levels of light that are too high, resulting in leaf injury and reduced photosynthesis.
  - If a plant's leaves are nearly vertical, light rays are parallel to the leaf surfaces, no leaf receives too much light, and light penetrates more deeply to the lower leaves.
- Plants that grow tall avoid shading from neighboring plants.

- Most tall plants require thick stems, which provide greater vascular flow to, and mechanical support for, the leaves.
  - Vines, though tall, have narrow stems and rely on other plants to raise their leaves higher.
- Branching generally enables plants to harvest sunlight for photosynthesis more effectively.
  - However, some species, such as the coconut palm, do not branch at all.
- Variation in branching patterns results from tradeoffs between branching patterns and shoot height.
  - Plants have only a finite amount of energy to devote to shoot growth.
  - If most of that energy goes into branching, there is less energy to devote toward growing tall, and as a result there is increased risk of being shaded by taller plants. If most of the energy goes into growing tall, the plants are not optimally exploiting the resources above ground.
- Natural selection has produced varieties of shoot architectures among species, optimizing light absorption in the ecological niche each species occupies.

Root architecture is designed to acquire water and minerals.

- As plants became less dependent on very moist environments, the evolution of root branching allowed them to acquire more water and nutrients and provided strong anchorage.
- The tallest plant species are usually gymnosperms or eudicots, anchored by strong taproot systems with many lateral roots.
  - The fibrous root systems of monocots do not anchor a tall plant as strongly as a taproot system.
- The architecture and physiology of roots can be adjusted rapidly to exploit patches of available nutrients in the soil.
  - The roots of many plants respond to pockets of low nitrate availability in soils by extending straight through the pockets without branching.
  - When a root encounters a pocket rich in nitrate, it will often branch extensively.
- Root cells also respond to high soil nitrate levels by synthesizing more proteins involved in nitrate transport and assimilation.
- Physiological mechanisms prevent competition within the root system of a plant.
- For example, cuttings from the stolons of buffalo grass *(Buchloe dactyloides)* developed fewer and shorter roots in the presence of cuttings from the same plant than they did in the presence of cuttings from another buffalo grass plant.
- The mechanism underlying this ability to distinguish self from nonself is unknown, but it reduces competition between roots of the same plant for the same limited pool of resources.
  - The evolution of mutualistic associations between roots and fungi was important in the successful colonization of land by plants, especially in poorly developed early soils.
- About 80% of extant land plant species form **mycorrhizal** associations with soil fungi.
- Mycorrhizal hyphae endow the fungus and plant roots with an enormous surface area for absorption of water and minerals, particularly phosphate.

Concept 36.2 Different mechanisms transport substances over short or long distances.

- Plant tissues have two major compartments—the apoplast and the symplast.

- The **apoplast** consists of everything external to the plasma membrane and includes cell walls, extracellular spaces, and the interior of dead cells such as vessel elements and tracheids.
- The **symplast** consists of the entire mass of cytosol of all the living cells in a plant, as well as the plasmodesmata, the cytoplasmic channels that interconnect them.

The compartmental structure of plant cells provides three routes for transport.

- The compartmental structure of plant cells provides three routes for transport within a plant tissue or organ: apoplastic, symplastic, and transmembrane routes.
- In the *apoplastic route*, water and solutes move along continuum of cell walls and extracellular spaces without entering any cells.
- In the *symplastic route,* water and solutes move along the continuum of cytosol within a plant tissue.
    - This route requires only one crossing of a plasma membrane.
    - After entering one cell, solutes and water move from cell to cell via plasmodesmata.
- In the *transmembrane route*, water and solutes 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 selective permeability of the plasma membrane controls the short-distance movement of solutes into and out of cells.
- Both active and passive transport mechanisms occur in plants, and plant cell membranes are equipped with the same general types of pumps and transport proteins (channel proteins, carrier proteins, and cotransporters) that function in other cells.

Plants differ in some ways from animals in solute transport across plasma membranes.

- Hydrogen ions (H^+), rather than sodium ions (Na^+), play the primary role in basic transport processes in plant cells.
    - In plant cells, the membrane potential is established mainly through the pumping of H^+ by proton pumps, rather than the pumping of Na^+ by sodium-potassium pumps.
- H^+ is most often cotransported in plants, whereas Na^+ is typically cotransported in animals.
- During cotransport, plant cells use the energy in the H^+ gradient and membrane potential to drive the active transport of many different solutes.
    - For instance, cotransport with H^+ is responsible for absorption of neutral solutes, such as sucrose, by phloem cells and other plant cells.
    - An H^+/sucrose cotransporter couples movement of sucrose against its concentration gradient with movement of H^+ down its electrochemical gradient.
- Cotransport with H^+ also facilitates movement of ions, as in the uptake of nitrate (NO_3^-) by root cells.
- The membranes of plant cells also have ion channels that allow only certain ions to pass.
    - As in animal cells, most channels are gated, opening or closing in response to stimuli such as chemicals, pressure, or voltage.
- Ion channels are also involved in producing electrical signals analogous to the action potentials of animals.
    - However, these signals are 1,000 times slower and employ Ca^{2+}-activated anion channels rather than the Na^+ ion channels used by animal cells.

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 absorption or loss of water by a cell occurs by **osmosis**, the diffusion of water across a membrane.
- The physical property that predicts the direction in which water will flow is called **water potential**, a quantity that includes the effects of solute concentration and physical pressure.
  - Free water moves from regions of higher water potential to regions of lower water potential if there is no barrier to its flow.
  - For example, if a plant cell is immersed in a solution with higher water potential than the cell, osmotic uptake of water causes the cell to swell.
- As it moves, water can perform work, such as cell expansion.
  - The word *potential* in the term *water potential* refers to water's potential energy—water's capacity to perform work when it moves from a region of higher water potential to a region of lower water potential.
- Water potential is represented by the Greek letter ψ.
- Plant biologists measure ψ in units called **megapascals** (**MPa**), where 1 MPa is equal to about 10 atmospheres of pressure.
  - An atmosphere is the pressure exerted at sea level by a volume of air extending though the height of the atmosphere—about 1 kg of pressure per square centimeter.
  - The internal pressure of a plant cell is approximately 0.5 MPa, twice the air pressure inside a tire.

Both pressure and solute concentration affect water potential.

- Both solute concentration and physical pressure can effect water potential, as expressed in the *water potential equation*, where ψ_P is the pressure potential and ψ_S is the solute potential (or osmotic potential):

$$\psi = \psi_S + \psi_P$$

- The **solute potential** (ψ_S) of a solution is directly proportional to its molarity.
  - Solute potential is also called *osmotic potential* because solutes affect the direction of osmosis.
- By definition, the ψ_S of pure water is 0.
- Solutes bind water molecules, reducing the number of free water molecules and lowering the capacity of water to move and do work.
- Adding solutes always lowers water potential; the ψ_S of a solution is always negative.
- **Pressure potential** (ψ_P) is the physical pressure on a solution and can be positive or negative relative to atmospheric pressure.
  - The water in the hollow, nonliving xylem cells (vessel elements and tracheids) 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, and the cell wall then presses against the **protoplast**, producing **turgor pressure**.
  - This internal pressure is critical for plant function because it helps maintain the stiffness of plant tissues and serves as the driving force for cell elongation.

Water potential affects the uptake and loss of water in plant cells.

- Remember: *Water moves from regions of higher water potential to regions of lower water potential*.
- In a **flaccid** cell, ψ_P = 0 MPa and the cell is limp.
- If this cell is placed in a solution with a higher solute concentration (and, therefore, a lower ψ), water will leave the cell by osmosis.
    - The cell's protoplast undergoes **plasmolysis** by shrinking and pulling away from its wall.
- If a flaccid cell is placed in pure water (ψ= 0 MPa), 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, which exerts turgor pressure.
- The partially elastic wall will push back and confine the pressurized protoplast until this pressure is great enough to offset the tendency for water to enter the cell because of solutes.
- When ψ_P and ψ_S are equal in magnitude but opposite in sign, ψ = 0, and the cell has reached a dynamic equilibrium with the environment, with no further net movement of water.
- A walled cell with a greater solute concentration than its surroundings is **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 lose water.

Aquaporins affect the rate of water transport across membranes.

- A difference in water potential determines the *direction* of water movement across membranes, but how do water molecules actually cross the membrane?
- 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 moves osmotically across the membrane.
- Aquaporin channels are highly dynamic: their permeability is decreased by increases in cytoplasmic calcium ions or increases in cytoplasmic pH.

Bulk flow functions in long-distance transport.

- Diffusion is efficient for transport within a cell or between cells.
    - 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 a pressure gradient.
    - The bulk flow of material always occurs from higher to lower pressure, independent of solute concentration.
- Within the tracheids and vessel elements of the xylem and within the sieve-tube elements of the phloem, water and dissolved solutes move together in the same direction by bulk flow.
- The structures of the conducting cells of the xylem and phloem help to make bulk flow possible.
    - Tracheids and vessel elements are dead at maturity and lack cytoplasm. The cytoplasm of sieve-tube elements has few internal organelles.
    - Loss of cytoplasm in a plant's "plumbing" allows for efficient bulk flow through the xylem and phloem.

- The perforation plates at the ends of vessel elements and the porous sieve plates connecting sieve-tube elements also enhance bulk flow.
- Diffusion, active transport, and bulk flow act in concert to transport resources throughout the whole plant.
    - For example, bulk flow due to a pressure difference is the mechanism of the long-distance transport of sugars in the phloem, but active transport of sugar at the cellular level maintains this pressure difference.

Concept 36.3 Transpiration drives the transport of water and minerals from roots to shoots via the xylem.

- Most water and mineral absorption occurs in the cells at the tips of roots.
- Epidermal cells at the root tip are permeable to water, and many are differentiated into root hairs, modified cells specialized for water absorption.
- The root hairs absorb the soil solution, which consists of water molecules and dissolved mineral ions that are not bound tightly to soil particles.
- The soil solution is drawn through the hydrophilic walls of epidermal cells and travels along the cell walls and the intercellular spaces into the root cortex.
- Although the soil solution usually has a low mineral concentration, active transport enables roots to accumulate essential minerals, such as K^+, to concentrations hundreds of times greater than in the soil.

Water and minerals cross the endodermis to reach the vascular cylinder.

- Water and minerals that pass from the soil into the root cortex cannot be transported to the rest of the plant until they enter the xylem of the vascular cylinder, or stele.
- The **endodermis**, the innermost layer of cells in the root cortex, surrounds the stele and regulates the selective passage of minerals from the cortex into the stele.
- Minerals already in the symplast when they reach the endodermis continue through the plasmodesmata of endodermal cells and pass into the stele.
    - These minerals already crossed a plasma membrane to enter the symplast in the epidermis or cortex.
- The endodermis, with its Casparian strip, ensures that no minerals can reach the vascular tissue of the root without crossing a selectively permeable plasma membrane.
    - The **Casparian strip**, located in the transverse and radial walls of each endodermal cell, is a belt made of suberin, a waxy material impervious to water and dissolved minerals.
    - The Casparian strip prevents water and minerals from crossing the endodermis and entering the vascular tissue via the apoplast.
    - Water and minerals that are passively moving through the apoplast must cross the plasma membrane of an endodermal cell and enter the stele via the symplast.
- The endodermis also prevents solutes that have accumulated in the xylem from leaking back into the soil solution.
- Tracheids and vessel elements of the xylem lack protoplasts when mature and are parts of the apoplast.
    - Endodermal cells and living cells within the vascular cylinder discharge minerals from their protoplasts into their own cell walls.

- Both diffusion and active transport are involved in the transfer of solutes from symplast to apoplast.
- Water and minerals enter the tracheids and vessel elements, where they are transported to the shoot system by bulk flow.

Water and minerals ascend from roots to shoots through the xylem.

- **Xylem sap**, the water and dissolved minerals in the xylem, is transported long distances by bulk flow from the stele of roots to veins that branch throughout each leaf.
  - Bulk flow is much faster than diffusion or active transport.
  - Peak velocities in the transport of xylem sap can range from 15 to 45 m/hr for trees with wide vessel elements.
- 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 maize plant transpires 60 L of water during its growing season.
  - A maize crop grow of 60,000 plants per hectare transpires almost 4 million L of water per hectare every growing season.
  - Unless transpired water is replaced by water transported up from the roots, the leaves will wilt, and the plants will eventually die.
- Xylem sap rises against gravity to reach heights of more than 120 m in the tallest trees.
- At night, when transpiration is very low or zero, the root cells continue pumping mineral ions into the xylem.
- The accumulation of minerals in the vascular cylinder lowers the water potential there, generating a positive pressure called **root pressure** that pushes xylem sap.
- 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 plants.
- In most plants, root pressure is not a minor 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.

The transpiration-cohesion-tension mechanism transports xylem sap against gravity.

- Transpiration provides the pull for the ascent of xylem sap, and the cohesion of water molecules transmits the upward pull along the entire length of the xylem from shoots to roots.
- Stomata on a leaf's surface lead to internal air spaces that become saturated with water vapor.
- Most of the time, the air outside the leaf is drier and has lower water potential than the air inside the leaf.
  - Water vapor diffuses down its water potential gradient and exits the leaf via the stomata.
- The loss of water vapor by diffusion and evaporation translates into a pulling force for the upward movement of water through a plant.
- The cell wall lining the mesophyll cells acts like a very thin capillary network.
  - Water adheres to the cellulose microfibrils of the cell wall.
  - As water evaporates from the water film that covers the cell walls of mesophyll cells, the air-water interface withdraws into the cell wall.

- Because of the high surface tension of water, the curvature of the interface induces a tension, or negative pressure potential, in the water.
    - As more water evaporates from the cell wall, the curvature of the air-water interface increases and the pressure of the water becomes more negative.
    - Water molecules from the more hydrated parts of the leaf are then pulled toward this area to reduce the tension.
- These pulling forces are transferred to the xylem because each water molecule is cohesively bound to the next by hydrogen bonds.
- Transpirational pull depends on three properties of water: adhesion, cohesion, and surface tension.
- The role of negative pressure potential in transpiration is consistent with the water potential equation because negative pressure potential (tension) *lowers* water potential.
    - The negative water potential of leaves provides the "pull" in transpirational pull.

Cohesion and adhesion facilitate the ascent of xylem sap.

- 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 and adhesion facilitate this long-distance transport by bulk flow.
- Adhesion is the attractive force between water molecules and other polar substances.
    - Because both water and cellulose are polar molecules, there is a strong attraction between water molecules and the cellulose molecules in the xylem cell walls.
- Cohesion is the attractive force between molecules of the same substance.
    - Water has an unusually high cohesive force due to the hydrogen bonds each water molecule can potentially make with other water molecules.
    - Water's cohesive force within the xylem gives it a tensile strength equivalent to that of a steel wire of similar diameter.
- The cohesion of water due to hydrogen bonding makes it possible to pull a column of xylem 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 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.
- The upward pull on the sap creates tension within the vessel elements and tracheids, which are like elastic pipes.
- Positive pressure causes an elastic pipe to swell, whereas tension pulls the walls of the pipe inward.
    - On a warm day, a decrease in the diameter of a tree trunk can even be measured.
- As transpirational pull puts the vessel elements and tracheids under tension, their thick secondary walls prevent them from collapsing, much as wire rings maintain the shape of a vacuum-cleaner hose.

- The tension produced by transpirational pull lowers water potential in the root xylem to such an extent that water flows passively from the soil, across the root cortex, and into the vascular cylinder.

- 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.
  - Cavitation is more common in wide vessel elements than in tracheids and can occur under drought stress or when xylem sap freezes in water.
  - The air bubbles resulting from cavitation expand and block the water channels of the xylem.
- Root pressure is used by small plants to refill blocked vessels in spring.
- Cavitation may even be repaired when the xylem sap is under negative pressure, although the mechanism is not well understood.
- 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.

- The transpiration-cohesion-tension mechanism transports xylem sap against gravity.
- Long-distance transport of water from roots to leaves occurs by bulk flow, with the movement of fluid driven by a water potential difference at opposite ends of xylem tissue.
  - The water potential difference is created at the leaf end of the xylem by evaporation of water from leaf cells.
- Evaporation lowers the water potential at the air-water interface, generating the negative pressure (tension) that pulls water through the xylem.
- Bulk flow, the mechanism for long-distance transport up xylem vessels, differs from diffusion in some key ways.
  - Bulk flow is driven by differences in ψ_P, so ψ_S is not a factor.
  - The water potential gradient within the xylem is essentially a pressure gradient.
  - The flow occurs within hollow, dead cells.
- Unlike osmosis, bulk flow moves the entire solution—not just water or solutes—at much greater speed.
- The plant expends no 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 The rate of transpiration is regulated by stomata.

- Most leaves have large surface areas and high surface-to-volume ratios.
  - The large surface area enhances the absorption of light for photosynthesis.

- The high surface-to-volume ratio aids in CO_2 absorption and O_2 release during photosynthesis.

- Within the leaf, CO_2 enters a honeycomb of air spaces formed by the irregularly shaped spongy mesophyll cells.
    - This internal surface may be 10–30 times larger than the external leaf surface.
- The large surface area and high surface-to-volume ratio of leaves increase the rate of photosynthesis but also increase water loss through stomata.
- A plant's need for water is largely a negative consequence of the shoot system's need for gas exchange for photosynthesis.
- By regulating the opening and closing of the stomata, guard cells help to conserve water.

Stomata are major pathways for water loss.

- About 95% of the water that a plant loses escapes through stomata, although these pores account for only 1–2% of the external leaf surface.
    - The waxy cuticle reduces water loss through the remaining leaf surface.
- Each stoma is flanked by a pair of guard cells.
    - Guard cells control the diameter of the stoma by changing shape, thereby widening or narrowing the gap between the two cells.
- The amount of water lost by a leaf depends on the number of stomata and the average size of their pores.
- The stomatal density of a leaf, which may be as high as 20,000 per cm^2, is under both genetic and environmental control.
    - Desert plants have lower stomatal densities than do marsh plants.
- High light intensities and low CO_2 levels during leaf development tend to increase stomatal density in many species.
    - A recent British survey found that the stomatal density of many woodland species has decreased since 1927. This is consistent with the dramatic increases in CO_2 levels during the 1900s.

Guard cells mediate the photosynthesis-transpiration compromise.

- When guard cells take in water by osmosis, they become more turgid.
- In most angiosperms, the thickness of cell walls is uneven.
- Because of the orientation of cellulose microfibrils in the cell wall, the guard cells buckle outward when turgid.
    - The buckling increases the size of the pore between the guard cells.
- When guard cells lose water and become flaccid, they become less bowed, and the pore 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^+ from neighboring epidermal cells.
- 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.

- The absorption of K^+ decreases water potential in guard cells, leading to an inflow of water by osmosis and increasing cell turgor.
  - Most of the K^+ and water are stored in the vacuole, and the vacuolar membrane also plays an important regulatory role.
- Stomatal closing results from an exodus of K^+ from guard cells, leading to osmotic loss of water.
- Aquaporins may also be involved in the swelling and shrinking of guard cells by varying the permeability of the membranes to water.

Internal and environmental cues contribute to the opening and closing of stomata.

- In general, stomata are open during the day and closed at night to minimize water loss when it is too dark for photosynthesis to occur.
- At least three cues contribute to stomatal opening at dawn: light, CO_2 depletion, and an internal "clock" in guard cells.
  - Illumination of blue-light receptors in the guard cells stimulates the activity of ATP-powered proton pumps in the plasma membrane, promoting the uptake of K^+.
  - The amount of CO_2 within the air spaces of the leaf is depleted as photosynthesis begins.
  - Even in the dark, stomata continue their daily rhythm of opening and closing due to the presence of internal clocks in the guard cells 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, such as drought, high temperature, and wind can cause stomata to close during the daytime.
- When the plant is suffering a water deficiency, guard cells may lose turgor and close stomata.
  - **Abscisic acid**, a hormone produced by the roots and leaves in response to water deficiency, signals guard cells to close stomata.
  - While reducing further wilting, closing the stomata also restricts CO_2 absorption and slows photosynthesis.
  - Since turgor is necessary for cell elongation, growth of the plant ceases.
- Guard cells control stomatal opening on a moment-to-moment basis, reacting to a cloud or transient shaft of sunlight.
- In general, transpiration is greatest on sunny, warm, dry, and windy days because these environmental factors increase evaporation.
- If transpiration cannot pull sufficient water to the leaves, the shoot becomes slightly wilted, as cells lose turgor pressure.
  - Under prolonged drought conditions, leaves can become severely wilted and irreversibly injured.
- Transpiration also results in evaporative cooling, which can lower the temperature of a leaf by as much as 10°C relative to the surrounding air.
  - This cooling prevents the leaf from reaching temperatures that could denature enzymes involved in photosynthesis and other metabolic processes.

Xerophytes have evolutionary adaptations that reduce evaporative water loss.

- Plants adapted to arid environment are called **xerophytes**.

- Dry soils are relatively unproductive because photosynthesis depends strongly on the quantity of liquid water available to a plant.
    - The reason that water availability is so tied to plant productivity is not related to photosynthesis's direct need for water as a substrate but rather because freely available water allows plants to keep stomata open and take up more CO_2.
- Many species of desert plants avoid drying out by completing their short life cycles during the brief rainy seasons.
- Longer-lived species have unusual physiological or morphological adaptations.
    - Many xerophytes, such as cacti, have very small leaves that reduce excessive water loss; photosynthesis is carried out mainly in their stems.
    - Many xerophytes store water in fleshy stems for use during prolonged drought.
    - Some desert plants, such as mesquite, have roots more than 20 meters long, allowing them to acquire moisture at or near the water table.
- Another adaptation to arid habitats is crassulacean acid metabolism (CAM), a specialized form of photosynthesis found in succulent species of the family Crassulaceae and several other families.
    - The leaves of CAM plants take in CO_2 at night, allowing the stomata to remain closed during the day when transpiration is greatest.

Concept 36.5 Sugars are transported from sources to sinks via the phloem.

- The phloem transports the organic products of photosynthesis by a process called **translocation**.
- In angiosperms, the specialized cells of the phloem that function in translocation are the sieve-tube elements.
    - These elements are arranged end to end to form long sieve tubes with porous sieve plates between cells along the tube.
- **Phloem sap** is an aqueous solution that flows through sieve tubes.
    - Sugar, primarily the disaccharide sucrose, is the most common solute in phloem sap.
    - 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 in which sugar is produced by either photosynthesis or the breakdown of starch.
    - A **sugar sink** is an organ that is a net consumer or depository of sugar.
- Growing roots, buds, stems, and fruits are sugar sinks.
- Expanding leaves are sugar sinks, but mature leaves are sugar sources.
- A storage organ, such as a tuber or a bulb, may be 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.

- 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, while the lower leaves of the same branch export sugar to roots.
  - A growing fruit may monopolize the sugar sources that surround it.
- 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 elements before it can be exported to sugar sinks.
- In some species, sugar moves from mesophyll cells to sieve-tube elements via the symplast, passing through plasmodesmata.
- In other species, sucrose reaches sieve-tube elements by a combination of symplastic and apoplastic pathways.
  - In maize leaves, sucrose diffuses through the symplast from mesophyll cells into small veins.
  - Much of this sugar moves out of the cells into the apoplast and is accumulated by nearby sieve-tube elements, either directly or through companion cells.
- In some plants, companion cells have numerous ingrowths in their walls, enhancing the transfer of solutes between apoplast and symplast.
- In many plants, sieve-tube elements and companion cells accumulate sucrose at higher concentrations than those in mesophyll cells. This requires active transport.
  - Proton pumping and cotransport of sucrose and H^+ promote the movement of sucrose from mesophyll cells to sieve-tube elements or companion cells.
- Downstream, at the sink end of the sieve tube, phloem unloads its sucrose.
- The mechanism of phloem unloading is highly variable and depends on the plant species and type of organ.
- Regardless of the mechanism, because the concentration of free sugar in the sink is lower than the concentration 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 fast as 1 m/hr, faster than diffusion or cytoplasmic streaming.
- Phloem sap moves by bulk flow driven by positive pressure, known as *pressure flow*.
- The buildup of pressure at the source end and the reduction of pressure at the sink end cause water to flow from source to sink, carrying sugar along.
- The pressure flow hypothesis explains why phloem sap always flows from source to sink.

- Studies using electron microscopes suggest that in nonflowering vascular plants, the pores between phloem may be too small or obstructed to permit pressure flow.

- Sinks vary in energy demands and capacity to unload sugars.
- Plants may have more sinks than can be supported by sources.
  - In that case, a plant may abort some flowers, seeds, or fruits in a process of *self-thinning*.

Concept 36.6 The symplast is highly dynamic.

- Plant transport is a dynamic process because the transport needs of a plant cell change during its development.
  - For example, a leaf may begin as a sugar sink but spend most of its life as a sugar source.
- Environmental changes may alter plant transport processes.
  - Water stress may activate signal transduction pathways that greatly alter the membrane transport proteins governing the overall transport of water and minerals.
- Since the symplast is living tissue, it is largely responsible for the dynamic changes in plant transport processes.

Plasmodesmata are highly dynamic structures that can change in permeability and number.

- Plasmodesmata can open or close rapidly in response to changes in turgor pressure, cytoplasmic calcium levels, or cytoplasmic pH.
- Plasmodesmata may form during cytokinesis but may also form much later. Loss of function is common during differentiation.
  - For example, as a leaf matures from being a sink to a source, phloem unloading ceases as the plasmodesmata either close or are eliminated.
- Early studies by plant physiologists and pathologists came to differing conclusions regarding the pore sizes of plasmodesmata.
- Physiologists injected fluorescent probes of different molecular sizes into cells and recorded whether the molecules passed into adjacent cells.
  - Based on these observations, they concluded that the pore sizes were approximately 2.5 nm—too small for macromolecules such as proteins.
- In contrast, pathologists provided electron micrographs showing evidence of the passage of viral particles with diameters of 10 nm or larger.
  - These discordant findings are explained by the hypothesis that viruses can greatly dilate plasmodesmata.
  - Plant viruses produce *viral movement proteins* that cause plasmodesmata to dilate, enabling viral RNA to pass between cells.
- More recent evidence shows that plant cells themselves can dilate plasmodesmata as part of a dynamic communication network.
  - Viruses subvert this network by mimicking the cell's regulators of plasmodesmata.
- A high degree of cytoplasmic interconnectedness exists within groups of cells and tissues known as *symplastic domains*.
- Proteins and RNAs coordinate development between cells within a symplastic domain.
  - If symplastic communication is disrupted, development can be grossly effected.

The phloem acts as an information superhighway in the plant.

- In addition to transporting sugars, the phloem is a "superhighway" for the systemic transport of macromolecules and viruses.
  - Macromolecules translocated through the phloem include proteins and RNA that enter the sieve tubes through plasmodesmata.
  - Unlike gap junctions between animal cells, plasmodesmata can traffic proteins and RNA.
- Systemic communication through the phloem helps integrate the functions of the whole plant.
  - One classic example is the delivery of a flower-inducing signal from leaves to vegetative meristems.
  - Another is a defensive response to localized infection, in which signals traveling through the phloem activate defense genes in noninfected tissues.
- Electrical signaling through phloem has been studied in plants with rapid leaf movements, such as the sensitive plant *(Mimosa pudica)* and Venus' flytrap *(Dionaea muscipula)*.
  - The role of electrical signaling in other species is less clear.
- Studies have revealed that a stimulus in one part of a plant can trigger an electrical signal in the phloem that affects another part of the plant, eliciting changes in gene transcription, respiration, photosynthesis, phloem unloading, or hormonal levels.
  - Thus, the phloem serves a nerve-like function, allowing for swift electrical communication between widely separated organs.
- The coordinated transport of materials and information is central to plant survival, making optimal use of limited resources.
- Ultimately, the successful acquisition and optimal distribution of resources are the most critical determinants of whether the plant will compete successfully.