Guard cell control the photosynthesis-transpiration compromise

- A leaf may transpire more than its weight in water each day.
- Guard cells, by controlling the size of stomata, help balance the plant's need to conserve water with its requirements for photosynthesis.

- To make food, a plant must spread its leaves to the sun and obtain CO_2 from air.
  - Carbon dioxide diffuses in and oxygen diffuses out of the leaf via the stomata.
  - This structural feature increases exposure to CO_2, but it also increases the surface area for evaporation.
  - 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 transpiration stream also assists in the delivery of minerals and other substances from roots to the shoots and leaves.
- Transpiration also results in evaporative cooling, which can lower the temperature of a leaf by as much as 10-15 ^{o}C compared with the surrounding air.
  - This prevents the leaf from reaching temperatures that could denature enzymes involved in photosynthesis and other metabolic processes.
  - Cacti and other desert succulents, which have low rates of transpiration, can tolerate high leaf ***temperatures…so what does that tell us about the optimal temperature of their metabolic enzymes??????***
- When transpiration exceeds the delivery of water by xylem, as when the soil begins to dry out, the leaves begin to wilt as the cells lose turgor pressure.
  - The potential rate of transpiration will be greatest on sunny, warm, dry, windy days that increase the evaporation of water.
  - Regulation of the size of the stomatal opening can adjust the photosynthesis-transpiration compromise.
- Each stoma is flanked by a pair of guard cells which 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 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^+ from neighboring epidermal cells into the vacuole.
  - This decreasing water potential in guard cells leads to a flow of water by osmosis and increasing turgor.
  - Stomatal closing results from an exodus of K^+ from guard cells, leading to osmotic loss of water.
- 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.
  - Abscisic acid, a hormone produced by the mesophyll cells in response to water deficiency, signals guard cells to close stomata.
    - While reducing further wilting, it also slows photosynthesis.
  - High temperatures, by stimulating CO_2 production by respiration, and excessive transpiration may combine to cause stomata to close briefly during mid-day.

Translocation of Phloem Sap

- 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 in most plants, is the most prevalent solute.
  - It 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 is variable.
- In general, sieve tubes 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 storer of sugar.
- 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 ***sugar 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 wall to increase the cell’s surface area and these 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***.
- 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 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