1. Guard cells mediate the photosynthesis-transpiration compromise
2. Xerophytes have evolutionary adaptations that reduce transpiration
1. Guard cell mediate the photosynthesis-transpiration compromise

- A leaf may transpire more than its weight in water each day.
  - To keep the leaf from wilting, flows in xylem vessels may reach 75 cm/min.
- 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\textsubscript{2} from air.

• Carbon dioxide diffuses in and oxygen diffuses out of the leaf via the stomata.

• Within the leaf, CO\textsubscript{2} enters a honeycomb of air spaces formed by the irregularly shape parenchyma cells.
  
  • This internal surface may be 10 to 30 times greater than the external leaf surface.

• This structural feature increases exposure to CO\textsubscript{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.
One gauge of how efficiently a plant uses water is the transpiration-to-photosynthesis ratio, the amount of water lost per gram of CO₂ assimilated into organic molecules by photosynthesis.

For many plant species, this ration is about 600:1.

However, corn and other plants that assimilate atmospheric CO₂ by the C₄ pathway have transpiration-to-photosynthesis ratios of 300:1 or less.

C₄ plants are more efficient in assimilating CO₂ for each gram of water sacrificed than C₃ plants when stomata are partially closed.
• 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 °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.
• 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.
(a) Changes in guard cell shape and stomatal opening and closing (surface view)

Fig. 36.13a
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.
(b) Role of potassium in stomatal opening and closing

Fig. 36.13b
• The $K^+$ fluxes across the guard cell membranes are probably passive, being 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.
Plant physiologists use a technique called patch clamping to study the regulation of guard cell’s proton pumps and K⁺ channels.

- In patch clamping a very tiny “patch” of membrane is isolated on a micropipette.
- The micropipette functions as an electrode to record ion fluxes across the tiny patch of membrane, focusing on a single kind of ion through selective channels or pumps.
• 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⁺.

  • Also, photosynthesis in guard cells (the only epidermal cells with chloroplasts) may provide ATP for the active transport of hydrogen ions.
• A second stimulus is depletion of CO₂ 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 CO₂ production by respiration, and excessive transpiration may combine to cause stomata to close briefly during mid-day.
2. 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 some xerophytes, the stomata are concentrated on the lower (shady) leaf surface.

• 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 and other succulent species of the family Crassulaceae and in representatives of many other families.

These assimilate CO\textsubscript{2} by an alternative photosynthetic pathway, crassulacean acid metabolism (CAM).

Mesophyll cells in CAM plants store CO\textsubscript{2} in organic acids during the night and release the CO\textsubscript{2} from these organic acid during the day.

This CO\textsubscript{2} is used to synthesize sugars by the conventional (C\textsubscript{3}) photosynthetic pathway, but the stomata can remain closed during the day when transpiration is most severe.