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Chapter 37 Water and Sugar Transport in Plants

I. Water Potential and Cell-to-Cell Movement of Water

A. Plants lose water to the environment via transpiration.

1. Transpiration occurs when two conditions are met:
   - a. Stomata are open; happens during the day when photosynthesis occurs
   - b. When the environmental air is drier than the air inside the leaves
2. Plants replace water lost by transpiration with water absorbed from the roots.
   - a. This process is passive; it does not require ATP.
   - b. Movement of water up a plant occurs due to differences in the potential energy of water.
     - (1) Water potential is the potential energy of water in a certain situation, versus pure water at atmospheric pressure at the same temperature.
     - (2) Water always flows from areas of high water potential to areas of low water potential.
   - c. There is a water potential gradient between the roots and leaves.

B. Cell-to-cell movement is dependent on solute potential and pressure potential.

1. Solute potential (φ_s) = difference in solute concentration between two solutions.
   - a. In a cell with solute concentration equal to solute concentration of surrounding solution, the solute potentials are the same (isotonic) and no net movement of water occurs.
   - b. For a cell in a solution with a solute concentration less than that of the cell, solute potentials are different and water moves into the cell. (**Fig. 37.1a**)
     - (1) Addition of solutes lowers the solute potential.
     - (2) This cell is hypertonic relative to the solution in the beaker.
     - (3) Water moves from high solute potential to low solute potential.
   - c. Osmosis is the process by which water moves across the semipermeable cell membrane.
   - d. Solute potential is also known as osmotic potential.
2. Pressure potential (φ_p) describes any kind of physical pressure on water; in a cell, pressure potential consists of turgor pressure and wall pressure.
   - a. Turgor pressure is the pressure of the cell membrane on the cell wall as water moves into the cell. (**Fig. 37.1b**)
   - b. Wall pressure is the equal and opposite force exerted by the cell wall against the cell membrane.
     - (1) Cells that experience wall pressure are turgid.
     - (2) High wall pressure counteracts osmotic uptake of water into the cell.

C. Water potential (φ) is the sum of solute potential (φ_s) and pressure potential (φ_p).

1. Water potential is the tendency of water to move from one location to another depending on the solute and pressure potentials at the other location.
2. Water potential is measured in the unit known as megapascal (MPa).
3. Water potentials of cells are usually negative because solute potentials of cells are negative.
   - a. Solute potential of pure water is 0 because it contains no dissolved solutes.
   - b. Cell solute potential is measured relative to solute potential of pure water, thus it is negative.
   - c. Dissolved solutes in cells lower water potential and reduce the probability that water will move out of the cell by osmosis.
4. Pressure potential from turgor pressure is positive, thus increasing water potential and increasing the probability that water will move out of cell.
5. Water moves from regions of high water potential to regions of low water potential. (**Fig. 37.3**)
   - a. In most situations, water potential of plant cells is lower than surrounding solution; water moves into cells, and cells become turgid.
   - b. Cells exposed to solutions with extremely low water potential lose water and undergo plasmolysis.

D. Water Potentials in Soils, Plants and the Atmosphere

1. Plant tissues, root and shoot systems, and entire plants have measurable water potentials.
2. Soil and air have water potentials.
   - a. Soil often has high water potential relative to plants.
   - b. Air often has very low water potential relative to plants.
3. Water potential differences between soil, plants, and air create a water potential gradient that dictates the direction of water flow in a system. (**Fig. 37.4**)

        a. Plants gain water from soil and lose it to atmosphere.
        b. Loss of water from plant cells results in cell shrinkage, plasmolysis, dehydration, and potential cell death.
        c. Loss of water from plant tissues leads to wilting and possible plant death if not corrected. (**Fig. 37.5**)

II. Root Pressure and Short-Distance Transport
    A. Root Anatomy (**Fig. 37.7**)
        1. The epidermis is the outermost layer of cells; protects the root and produces root hairs that increase the absorptive area of the root.
        2. Cortex consists of ground tissue (parenchyma cells) that stores carbohydrates.
        3. Endodermis is a ring of cells that separates the cortex from the vascular tissue.
        4. Pericycle is a population of potentially meristematic cells that can produce lateral roots.
        5. Vascular tissues are in the center of the root.

    B. Water moves along a water potential gradient from the soil through the root to the vascular tissues.
        1. Water enters via the root hairs and moves through the cortex following one of two paths. (**Fig. 37.8a**)
            a. Water moving through apoplast moves between cells via porous cell walls.
            b. Water moving through symplast moves from one cell to another through the plasmodesmat
        2. Once water reaches the endodermis, it can no longer travel via the apoplast.
            a. Endodermal cells are surrounded by the waxy Casparian strip composed of a water-repelling substance called suberin.
            b. The Casparian strip acts like a gasket around endodermal cells, preventing water movement through the apoplast. (**Fig. 37.8b**)
            c. This forces the water to pass through the cytoplasm of endodermal cells (which act as filters) before it reaches the vascular tissue.
                (1) These cells allow needed ions such as potassium, but filter out dangerous ions such as sodium.
                (2) These cells prevent movement of water out of the vascular tissue of the root, back into the soil during dry conditions.
            d. The endodermis is also responsible for root pressure.
                (1) At night, the root accumulates ions taken up by the epidermal cells.
                (2) The ions are transported to the xylem, decreasing its water potential.
                (3) Water flows into the xylem, creating positive pressure and pushing the water up the xylem toward the leaves.
                (4) Since transpiration is low at night, water being pushed into leaves escapes via small pressure valves, resulting in guttation. (**Fig. 37.9**)

III. Transpiration and Long-Distance Water Transport

    A. Movement of water in some plants is based on the phenomenon of capillarity.
        1. When a thin glass tube is placed in a pan of water, the water creeps up the tube. (**Fig. 37.10a**)
        2. This happens because of surface tension, adhesion, and cohesion.
            a. Surface tension is a pull that exists on water molecules at an air-water interface, forming a meniscus. (**Fig. 37.10b**)
                (1) Polar nature of water molecules leads to hydrogen bond formation between water molecules.
                (2) Water molecules at air-water interface form hydrogen bonds in only one direction, pulling the surface of the water downward.
            b. Cohesion is the attraction among like molecules; water molecules bind each other via hydrogen bonds.
            c. Adhesion is the attraction of unlike molecules; water forms hydrogen bonds with other polar molecules.
        3. Only very small plants can depend on water transport via capillarity alone.
        4. Larger plants depend on capillarity combined with the “pulling” force of transpiration to move water over long distances.

    B. Transpiration is the loss of water from aerial plant parts.
        1. Leaf area below stomatal pore is filled with moist air. (**Fig 37.11**)
        2. When stomatal pore opens, humid air inside leaf is exposed to dry air in atmosphere.
        3. Steep water potential gradient between the dry air and moist leaf space results in exit of water through pore.
        4. Humidity in space decreases as water leaves and evaporates from cell walls.
        5. Menisci form at water-air interfaces of cell walls.

6. In 1894 Henry Dixon and John Joly hypothesized that menisci produce a force sufficient to pull water up from the roots.

C. Surface tension at air-water interface pulls water up from soil.
  1. As water evaporates from the leaf via transpiration, a steep water potential gradient leads to deepening of menisci, and inward pull (surface tension) on remaining water molecules becomes stronger.
  2. This generates a pulling force on water molecules that form a continuum of cohesively bonded molecules throughout the entire plant (through the xylem, roots, and ultimately the soil).

D. Evidence that Xylem Sap Is under Tension
  1. The dendrograph (**Fig 37.13**)
    a. This instrument measures the changes in tree trunk diameter over time.
    b. When transpiration increases and the tension on the xylem increase, the tree trunk should decrease in diameter.
    c. Dendrograph data show that the tree trunk decreased in diameter on hot days, and increased in diameter at night.
  2. Visual observation
    a. When an actively transpiring leaf is cut, the xylem sap will withdraw up into the petiole.
    b. This occurs because of the transpirational pull at the air-water interface within the spaces between spongy mesophyll cells.
  3. Pressure bomb measures water potential in plant tissues—Scholander, Hammel et al.
    a. Tension in xylem sap should correlate with water potential of surrounding tissues.
    b. Cut branch or leaf placed in bomb and increasing pressure applied to push the xylem sap to the cut surface. (**Fig. 37.12**)
    c. The pressure applied is equal to tension on xylem sap and correlates with the water potential.
  4. Pressure bomb can be used to study water transport.
    a. Water potential in Sitka spruce leaves measured at various times over several days.
    b. Results demonstrated that water potential dropped during the day when transpiration occurred and rose at night when stomata were closed. (**Fig. 37.13**)
  5. Direct Tests of Cohesion-Tension Theory
    a. Theory has been challenged because the predicted rapid change in xylem sap pressure in response to changing environmental conditions has not been documented in some studies.
    b. Experiment designed to measure pressure changes in xylem vessels instantly and directly (**Fig. 37.14**)—Wei, Tyree, and Steudle.
      (1) Studied the effect of two variables on xylem pressure.
        (*a*) Increased root pressure applied with a root bomb.
        (*b*) Altered light levels at three intensities.
      (2) Probe inserted directly into xylem vessel measured pressure changes.
      (3) Based on the cohesion-tension theory, increased root pressure should decrease xylem sap tension, and light would be expected to increase xylem sap tension resulting from increased transpiration.
      (4) Results confirmed predictions of theory.
        (*a*) As pressure is added to the root system, xylem sap tension decreases.
        (*b*) As light levels and transpiration increase, tension on xylem sap increases.

E. Important Components of the Cohesion-Tension Theory
  1. Expenditure of energy by plants is not required.
    a. Sun provides the energy required to break hydrogen bonds of water, causing transpiration.
    b. Transpiration creates menisci at air-water interface in leaves.
    c. Hydrogen bonding of water molecules at menisci creates tension that pulls water from roots to shoots.
  2. Water moves along a water potential gradient by bulk flow.
  3. In dry conditions stomata close to conserve water, but carbon dioxide available for photosynthesis decreases—the photosynthesis-transpiration compromise.

F. Adaptations to Limit Water Loss
  1. Plants in dry environments need to cope with soils that have very low water potentials and must conserve as much water as possible. (**Fig. 37.16**)
  2. Morphological traits reduce water loss in plants native to dry habitats. (**Fig. 37.16**)
    a. Sunken stomata with hairs

        - b. Stomata on lower epidermis
        - c. Thick cuticle on leaf surfaces
    - 3. Obtaining carbon dioxide under water stress
        - a. CAM plants have stomata open at night to collect carbon dioxide, store it for use in the day. This allows them to keep stomata closed during the day.
        - b. C_4 plants efficiently fix CO_2 under hot, dry conditions, limiting the amount of time their stomata need to be open.

IV. Translocation—the Movement of Sugars in Plants

- A. Sugars move from sources to sinks. (**Fig 37.17**)
    - 1. Source is tissue where sugar enters the phloem.
    - 2. Sink is tissue where sugar exits the phloem.
    - 3. Sinks and sources vary depending on time of year.
        - a. In growing season, leaves and stems are sources; apical and lateral meristems, seeds, fruits, and storage cells in roots are sinks.
        - b. Early in growing season, root storage cells are sources, and developing leaves are sinks.
    - 4. Location of sources and sinks was demonstrated by tracking radioactively labeled sugars in sugar beets.
        - a. Results: Sugars moved from a mature leaf, a source, to growing leaves, the sink.
        - b. Sugars moved from leaves (the source) to roots (the sink).
    - 5. Sources and sinks are physically related.
        - a. Sugars from a source move to a sink on the same side of the plant. (**Fig. 37.17a**)
        - b. Sources on the upper part of the stem send sugar to sinks at apical meristems; sources on lower part send sugar to sinks in roots. (**Fig. 37.17b**)
        - c. Phloem in leaves on one side of plant connects with phloem in stem and roots on same side.
    - 6. Sugars are transported rapidly.

- B. Sugars Move through Cells in Phloem Tissue
    - 1. Two cell types comprise phloem tissue.
        - a. Sieve-tube elements
            - (1) Alive at maturity, but usually lack nuclei and many organelles
            - (2) Connect to each other end to end by sieve-like open pores (**Fig. 37.19**)
            - (3) Conduct phloem sap
        - b. Companion cells
            - (1) Alive at maturity with nuclei and numerous organelles
            - (2) Function in support
    - 2. Early demonstration that phloem transports sugars—Mason and Maskell
        - a. Bark removed from tree; water transport continues, sugar transport stops.
        - b. Phloem tissue contains high concentration of sucrose.

- C. The Pressure-Flow Hypothesis for Sugar Transport
    - 1. Hypothesis for sugar movement was proposed by Ernst Münch in 1930.
        - a. Sugars are transported from source to sink along a turgor pressure gradient in the phloem. (**Fig. 37.20**)
        - b. Force responsible for movement is generated by turgor pressure differences at source and sink tissues.
    - 2. Events at the source
        - a. Sucrose moves from source cells to companion cells, then to sieve-tube elements.
        - b. Phloem sap at source has high sucrose concentration, low water potential.
        - c. Adjacent xylem cells have high water potential and water moves from xylem into sieve-tube elements along a water potential gradient.
        - d. Turgor pressure at source increases.
        - e. Sugars move by bulk flow along the pressure gradient.
    - 3. Events at the sink
        - a. Cells in the sink remove sucrose from phloem sap.
        - b. Water potential in sieve-tube elements increases as sucrose is removed until it is higher than water potential in adjacent xylem cells.
        - c. Water flows from sieve-tube elements into xylem along water potential gradient.
        - d. Turgor pressure of phloem at sink drops.

   e. Outcome is a continuous loop of water flow driven by water potential gradients between xylem and phloem and unidirectional movement of sucrose molecules driven by pressure potential gradient in phloem.
4. Confocal microscopy studies—researchers followed the movement of a dye injected into phloem of a leaf—confirmed bulk flow hypothesis.
5. Phloem loading at source requires ATP
   a. Sucrose is transported into phloem cells against concentration gradient (**Fig. 37.22** for a review of membrane transport mechanisms).
   b. Observation of pH differences between interior and exterior of phloem cells supported the existence of the proton pump (H$^+$-ATPase) and cotransporter.
      (1) Proton pump (H$^+$-ATPase) that transports H$^+$ to cell exterior creates electrochemical gradient between inside and outside of cell. (**Fig. 37.22**)
      (2) Cotransporter protein uses proton motive force as protons flow back into cell to transport sucrose.
   c. H$^+$-ATPase purified from phloem-cell membranes proved proton pumps involved in transport.
   d. Localization of proton pumps with *Arabidopsis thaliana*—DeWitt and Sussman
      (1) *Arabidopsis* genome encodes 10 pump proteins; one protein, AHA3, is expressed in vascular tissues.
      (2) Hypothesis: *AHA3* gene encodes proton pump for phloem loading.
         (*a*) Researchers made antibodies to AHA3 protein.
         (*b*) They attached gold particles to antibodies to permit visualization with electron microscope.
         (*c*) They treated *Arabidopsis* leaves with antibodies and observed with electron microscope.
      (3) Results: Antibodies localized in companion cell membranes, indicating proton pump located there. (**Fig. 37.23**)
      (4) Phloem loading model holds that sucrose moves from source cells into companion cells and travels from them into sieve-tube elements.
6. Phloem unloading at sink
   a. Energy is required at some point in the process.
   b. Mechanism varies with different sinks in the same plant, as well as between different plant species.
   c. Sugar beets employ two different mechanisms for unloading at different sinks.
      (1) Growing leaves—sugar moves passively into sink, where energy-requiring synthesis of organic molecules occurs. (**Fig. 37.25a**)
      (2) Roots—sucrose is actively transported across vacuolar membrane of root cells, where sucrose is stored in vacuoles against its concentration gradient. (**Fig. 37.25b**)

Chapter Vocabulary

solute potential/osmotic potential
turgor pressure
wall pressure
turgid

pressure potential
water potential
paschal/megapaschal
plasmolysis
wilt
water potential gradient

solution
solute

isotonic
hypotonic

epidermis
root hairs
cortex
endodermis
pericycle
vascular tissues
apoplast
symplast
Casparian strip
suberin
root pressure
guttation

transpiration
capillarity
surface tension

meniscus

halophytes

cohesion
adhesion
cohesion-tension theory
xylem sap

dendrograph
pressure bomb
negative result
root bomb
xylem pressure probe
bulk flow

photosynthesis-transpiration compromise
C_4 photosynthesis
CAM photosynthesis
rubisco
bundle-sheath cells

translocation
source
sink
pressure-flow hypothesis

sieve-tube elements
sieve plates
companion cells
phloem loading
passive transport
active transport
facilitated diffusion
proton pump
cotransporter
symporter

phloem unloading
tonoplast