CHAPTER 26 NUTRITION AND TRANSPORT IN PLANTS

Chapter Outline

26.1 Plant Nutrition and Soil

A. Early Views
   1. Ancient Greeks considered plants "soil-eaters" that converted soil into plant tissue.
   2. The 17^{th} Century Dutchman Jean-Baptiste Van Helmont conducted an experiment.
      a. He planted a five pound young willow tree in a pot with 200 pounds of soil.
      b. After five years of watering, the tree weighed 170 pounds but only a few ounces of soil was missing.
      c. He concluded the increase in tree weight came from water; he was unaware of substances in air.

B. Essential Inorganic Nutrients
   1. **Essential inorganic nutrients** (e.g., carbon, hydrogen, oxygen) comprise 96% of plant dry weight.
      a. Carbon dioxide is the source of carbon for a plant.
      b. Water is the source of hydrogen.
      c. Oxygen can come from either atmospheric oxygen, carbon dioxide, or water.
   2. **Essential nutrient**s must fulfill the following criteria.
      a. They have an identifiable nutritional role.
      b. No other element can substitute and fulfill the same role.
      c. A deficiency of the element causes the plant to die.
   3. These elements are divided into **macronutrients** and **micronutrients** by concentration in plant tissue.
   4. **Beneficial nutrients** are elements required for or improving growth of a particular plant.
      a. Horsetails require silicon as a mineral nutrient.
      b. Sugar beets show better growth in the presence of sodium.
      c. Soybeans use nickel when root nodules are present.

C. Determination of Essential Nutrients
   1. When a plant is burned, most mineral elements (except for nitrogen) remain in the ash.
   2. **Hydroponics** is the preferred method for determining plant mineral requirements.
      a. Hydroponics is cultivation of plants in water.
      b. Nutrient requirements of plants are determined by omitting a mineral and observing the effects.
      c. If plant growth suffers, it can be concluded that the omitted mineral is a required nutrient.
      d. This works for macronutrients but impurities make micronutrient measurement difficult.

D. Soil Formation
   1. Soil formation begins with weathering of rock by freezing, glacier flow, stream flow, and chemicals.
   2. Lichens and mosses grow on barren rock and trap particles and leave decaying tissues.
   3. Decayed organic matter (humus) takes time to accumulate; its acidity leaches minerals from rocks.
   4. Depending on parent material and weathering, a centimeter of soil may develop within 15 years.

E. The Nutritional Function of Soil
   1. Soil consists of soil particles, decaying organic matter, living organisms, air and water.
   2. The best soil includes particles of different sizes; this provides critical air spaces.
   3. Soil Particles
      a. Particles vary by size.
         1) Sand particles are larger: 0.05–2.0 mm in diameter.
         2) Sand particles are medium sized: 0.002–0.05 mm in diameter.
         3) Clay particles are smallest: below 0.002 mm in diameter.
      b. Sandy soils lose water too readily; clay packs tight to hold water and clumps in your hand.
      c. Clay particles are negatively charged and attract positively charged ions (e.g., calcium [Ca^{2+}] and potassium [K^{+}]).

   d. In acidic soils, hydrogen ions replace positively charged nutrients and the nutrient ions float free and are leached; this is why acid rain kills trees.
   e. Clay cannot retain negatively charged NO_3^-, and the nitrogen content of clay soil is low.
   f. Loam (a mixture of the three soil particles) retains water and nutrients; roots take up oxygen in the air spaces.
4. Humus
   a. A mixture of 10–20% humus mixed with a top layer of soil particles is best for plants.
   b. Humus keeps soil loose and crumbly, decreases runoff and aerates soil.
   c. Humus is acidic and retains positively charged minerals for plants to use later.
   d. Bacteria and fungi break down organic matter in humus and return inorganic nutrients to plants.
5. Living Organisms
   a. Small plants play a major role in formation of soil from rock and in succession.
   b. Roots of larger plants penetrate the soil and weather rocks.
   c. Larger moles and badgers and smaller earthworms help turn over the soil.
   d. Soil animals, from mites to millipedes help break down leaves and other plant remains.
   e. Fungi, protozoa, algae and bacteria complete decomposition.
   f. Soil bacteria make nitrate available to plants.
   g. Some soil organisms (roundworms and insects) are crop pests that feed on roots.
6. Soil Profiles
   a. The A horizon is the uppermost topsoil layer that contains litter and humus.
   b. The B horizon lacks organic matter but contains inorganic nutrients leached from the A horizon.
   c. The C horizon is weathered and shattered bedrock.
   d. Soil profiles vary by parent material, climate and ecosystem.
   e. Grassland soils have deep A horizons from turnover of decaying grasses and lack of leaching.
   f. Forest soils have thinner A horizons but enough inorganic nutrients for tree root growth.
   g. Tropical rain forest A horizons are shallow due to rapid decomposition; the B horizon is deeper due to extensive leaching.
7. Soil Erosion
   a. Erosion is caused by water or wind carrying away soil.
   b. Erosion removes 25 billion tons of topsoil worldwide annually.
   c. Deforestation and desertification contribute to erosion.
   d. U.S. farmlands lose soil faster than it is formed on one-third of cropland.

26.2 Uptake of Water and Minerals

A. Pathways
1. Minerals follow the path of water uptake.
   a. Some mineral ions diffuse in between the cells.
   b. Because of the impermeable **Casparian strip**, water must eventually enter the cytoplasm of endodermal cells.
   c. Water can move directly into the cytoplasm of **root hair** epidermal cells and is transported across the cortex and endodermis of a root.
   d. In contrast to water, minerals are actively taken up by plant cells.
   e. Mineral nutrient concentration in roots may be 10,000 times more than in surrounding soil.
   f. During transport throughout a plant, minerals can exit xylem and enter cells that require them.
2. Mineral ions cross plasma membranes by a chemiosmotic mechanism.
   a. Plants absorb minerals in ionic form: nitrate (NO_3^-), phosphate ($HPO_4^=$), and potassium ions (K^+); all have difficulty crossing a charged plasma membrane.
   b. It has long been known plants expend energy to actively take up and concentrate mineral ions.
   c. A plasma membrane pump called a proton pump hydrolyzes ATP to transport H^+ ions out of cell; this sets up an electrochemical gradient that causes positive ions to flow into cells.
   d. Negative ions are carried across the plasma membrane in conjunction with H^+ ions as H^+ ions diffuse down their concentration gradient.

B. Adaptations of Roots for Mineral Uptake
   1. Two symbiotic relationships are known to assist roots in acquiring nutrients.
   2. Legumes have **nodules** infected with the bacterium *Rhizobium.*
      a. Plants cannot use atmospheric nitrogen because they lack enzymes to break the $N \equiv N$ bond.
      b. *Rhizobium* makes nitrogen compounds available to plants in exchange for carbohydrates.
      c. Bacteria live in **root nodules—**structures on plant roots that contain nitrogen-fixing bacteria.
      d. Rhizobial bacteria reduce atmospheric nitrogen (N_2) to ammonium (NH_4^+) (**nitrogen-fixation**).
      e. Other plants have a relationship with free-living, nitrogen-fixing microorganisms in soil.
   3. Most plants have **mycorrhizas**; those lacking mycorrhizas are limited in where they can grow.
      a. Mycorrhizae are a mutualistic symbiotic relationship between soil fungi and plant roots.
      b. The fungal hyphae may enter the cortex of roots but do not enter plant cells.
      c. Ectomycorrhizae form a mantle exterior to the root, and they grow between cell walls.
      d. Fungus increases the surface area for mineral and water uptake and breaks down organic matter.
      e. In return the root furnishes the fungus with sugars and amino acids.
      f. Orchid seeds are small with limited nutrients; they germinate only when invaded by mycorrhizae.
      g. Nonphotosynthetic plants (e.g., Indian pipe) use mycorrhizae to extract nutrients from nearby trees.
   4. Some plants have poorly developed roots or no roots; other mechanisms supply minerals and water.
      a. **Epiphytes** take nourishment from air; their attachment to other plants gives them support.
      b. Parasitic plants (e.g., dodders, broomrapes, pinedrops) send out **haustoria** (rootlike projections) that grow into host and tap into xylem and phloem of host.
      c. Venus's-flytrap and sundew obtains nitrogen and minerals as leaves capture and digest insects.

26.3 Transport Mechanisms in Plants

A. Transport Tissues
   1. Vascular plants have transport tissues as an adaptation to living on land.
   2. **Xylem** vascular tissue passively conducts water and mineral solutes from roots to leaves; it contains two types of conducting cells: tracheids and vessel elements.
      a. **Tracheids:**
         1) are hollow, nonliving cells with tapered overlapping ends;
         2) are thinner and longer than vessel elements; and
         3) water crosses the end and sidewalls because of pits in secondary cell wall.
      b. **Vessel elements:**
         1) are hollow, nonliving cells that lack tapered ends;
         2) are wider and shorter than tracheids;
         3) lack transverse end walls; and
         4) form a continuous pipeline for water and mineral transport.
   3. **Phloem** is vascular tissue that conducts organic solutes in plants mainly from leaves to roots; contains **sieve-tube cells** and **companion cells.**
      a. **Sieve-tube cells** lack a nucleus, are arranged end to end and have channels in end walls (thus, the name "sieve-tube") through which plasmodesmata extend from one cell to another.
      b. **Companion cells** connect to sieve-tube cells by numerous plasmodesmata, are smaller and more generalized than sieve-tube cells; they have a nucleus.
   4. These transport systems rely on the mechanical properties of water.
      a. **Diffusion** moves molecules from higher to lower concentrations.
      b. **Water potential** considers both water pressure and osmotic pressure.
   5. They also rely on the chemical properties of water: polarity of water and hydrogen bonding.

B. The Concept of Water Potential
   1. Water flows from a region of higher **water potential** (the potential energy of water) to a region of lower **water potential**.
   2. **Water potential** is a measure of the capacity to release or take up water; in cells, water potential includes the following:
      a. **Pressure potential**, the effect that pressure has on water potential; water will move from a region of higher pressure to a region of lower pressure; and
      b. **Osmotic potential**, the effect that solutes have on water potential; water tends to move by osmosis from an area of lower solute concentration to area of higher solute concentration.

    3. Water flows by osmosis into a plant cell with greater solute concentration than a surrounding solution.
        a. As water enters, pressure increases inside the cell; the strong plant cell wall allows water pressure to build up.
        b. Pressure potential inside the cell increases and balances the osmotic potential outside cell; water stops entering.
        c. **Turgor pressure** is the pressure potential that increases due to process of osmosis; it is critical to plants, since plants depend on it to maintain the turgidity of their bodies.
        d. Wilted plant cells have insufficient turgor pressure and the plant droops.

C. Water Transport
    1. Movement of water and minerals in a plant involves entry into roots, xylem, and leaves.
    2. Water and minerals enter root cells before they reach xylem by the two routes already described.
    3. Water entering root cells creates a positive pressure called root pressure.
        a. **Root pressure** (primarily at night) tends to push xylem sap upward in a plant.
        b. **Guttation** is the appearance of drops of water along the edge of leaves, as a result of water being forced out of leaf vein endings; it is the result of root pressure.
        c. Root pressure is not a sufficient mechanism for water to rise to the tops of trees.

D. Cohesion-Tension Model of Xylem Transport
    1. Water and dissolved minerals must be transported upward from roots to xylem, perhaps as high as 90 meters.
    2. The **cohesion-tension model** states that transpiration creates a tension (i.e., a negative pressure) that pulls water upward in xylem.
    3. Water molecules are *cohesive* with one another, *adhesive* with xylem walls.
    4. **Transpiration** is a plant's loss of water to atmosphere through evaporation at leaf stomata.
    5. **Cohesion** is the tendency of water molecules to cling together due to their forming hydrogen bonds.
    6. **Adhesion** is the ability of water (a polar molecule) to interact with molecules comprising the walls of xylem vessels; adhesion gives a water column extra strength and prevents it from slipping back down.
    7. In daytime, the negative water potential created by transpiration extends from leaves to roots; the water column must be continuous.
    8. If a water column within xylem is broken by cutting a stem, the water column will drop back down the xylem vessel away from the site of breakage, making it more difficult for conduction to occur.
    9. At least 90% of the water taken up by roots is lost through stomata by transpiration.
    10. With plenty of water, stomata will remain open, allowing CO_2 to enter the leaf and photosynthesis to occur.
    11. Transpiration exerts a driving force or **tension** that draws the water column up in vessels.
    12. Under water stress, more water is lost through a leaf than can be brought up and the stomata close.
    13. Photosynthesis requires CO_2 to enter the leaf; there must be sufficient water so stomata can remain open and allow CO_2 to enter.

E. Opening and Closing of Stomata
    1. Each **stoma** has two **guard cells** with a pore between them.
    2. Stomata open from turgor pressure when guard cells take up water; when they lose water, turgor pressure decreases and stomata close.
    3. Guard cells are attached to each other at their ends; the inner walls are thicker than outer walls.
    4. Radial expansion is prevented by cellulose microfibrils in the walls but outer walls can expand lengthwise.
    5. As they take up water, they buckle out, thereby creating an opening between cells.
    6. Since 1968, it has been known that when stomata open, there is accumulation of K^+ ions in guard cells.
    7. A proton pump run by breakdown of ATP to ADP and P transports H^+ outside the cell; this establishes an electrochemical gradient allowing K^+ to enter by way of a channel protein.
    8. The blue-light component of sunlight is a signal that can cause stomata to open.
        a. There is evidence that flavin pigments absorb blue light.
        b. This pigment sets in motion a cytoplasmic response activating the proton pump that causes K^+ ions to accumulate in guard cells.
    9. Evidence suggests a receptor in the plasma membrane of guard cells brings about inactivation of the proton pump when CO_2 concentration rises, as happens when photosynthesis ceases.

10. Abscisic acid (ABA) produced by cells in wilting leaves, also causes stomata to close; photosynthesis cannot occur but water is conserved.
11. In plants kept in dark, stomata open and close on a 24-hour basis as if responding to sunlight in daytime and the absence of sunlight at night; some sort of internal **biological clock** must keep time.

F. Organic Nutrient Transport
1. Marcello Malpighi (1679) suggested bark transferred sugars from leaves to roots.
    a. He observed the results of removing a strip of bark from a tree (**girdling**).
    b. Bark swells just above the cut and sugar accumulates in the swollen tissue.
    c. Today, we know phloem was removed but xylem remained; therefore, phloem does transport sugars.
2. Radioactive tracer studies using ^{14}C confirmed phloem transports organic nutrients.
    a. When ^{14}C-labeled carbon is supplied to mature leaves, radioactively labeled sugar moves to roots.
    b. Similar studies confirm phloem transports amino acids, hormones, and mineral ions.
3. Aphids Used in Study
    a. It is difficult to take samples of sap from just the phloem cells without injuring the phloem.
    b. Aphids (small insects) drive their mouth stylets into a sieve-tube cell; then samples are easily taken.
    c. The aphid body is cut off; the stylet becomes a small needle from which phloem is collected.
    d. Such research indicates sap can move through phloem from 60–100 cm per hour or more.

G. Pressure-Flow Model of Phloem Transport
1. The **pressure-flow model** explains the transport of sap through sieve tubes by a positive pressure potential.
2. The buildup of water creates a positive **pressure potential** within the sieve tubes that moves water and sucrose to a sink (e.g., at the roots).
3. Pressure exists from the leaves to the roots; at the roots, sucrose is transported out and water also flows through due to the pressure.
4. Consequently, this pressure gradient causes a flow of water from leaves to roots.
5. The conducting cells of phloem are sieve tubes lined end to end.
6. Cytoplasm extends through the sieve plates of adjoining cells to form a continuous tube system.
7. During the growing season, leaves produce sugar.
8. Sucrose is actively transported into phloem by an electrochemical gradient established by a H^+ pump.
9. Water flows passively into sieve tubes by osmosis.
10. A sink can be at the roots or any other part of the plant that requires nutrients.
11. Because phloem sap flows from source to sink, sap can move any direction along phloem.