CHAPTER 32

Plant Nutrition and Transport

Objectives

Introduction Describe the process, advantages, and disadvantages, and give examples, of phytoremediation.

The Uptake and Transport of Plant Nutrients

32.1 Describe the experiments and conclusions of the work by van Helmont and Stephen Hales. Explain what happens to the materials that plants take up from the air and soil.
32.2 Compare the intracellular and extracellular routes of material movements into the xylem. Describe the function of the Casparian strip.
32.3 Explain the transpiration-cohesion-tension mechanism responsible for the ascent of sap in xylem.
32.4 Explain how guard cells control transpiration.
32.5 Explain how, when, and where phloem conducts sap.

Plant Nutrients and the Soil

32.6 Distinguish between micronutrients and macronutrients and note examples of each. Explain how hydroponics help to determine which nutrients are essential.
32.7 Describe the signs of nitrogen, phosphorus, and potassium deficiency in plants.
32.8 Describe the properties of different layers of soil. Explain how these properties relate to the health of a plant.
32.9 Explain how irrigation and the use of fertilizers impacts agriculture. Describe techniques that minimize soil erosion and the buildup of salts in soils.
32.10 Compare the processes and products of organic and conventional agriculture.
32.11 Explain how fungi help most plants absorb nutrients from the soil.
32.12 Describe examples of parasitic and carnivorous plants. Explain why carnivorous plants are typically found in bogs.
32.13 Explain how and why most plants depend upon bacteria to supply nitrogen.
32.14 Describe the special relationship between legumes and nitrogen-fixing bacteria.

Plant Nutrients and Agriculture

32.15 Describe the new strategies to improve the protein content of crops.
32.16 Explain how gene guns and bacterial plasmids are being used to increase crop yields.

Key Terms

Casparian strip	cohesion	phloem sap
xylem sap	adhesion	sugar source
root pressure	transpiration-cohesion-tension mechanism	sugar sink
transpiration		pressure-flow mechanism

macronutrient	topsoil	mycorrhiza
micronutrient	humus	nitrogen fixation
soil horizon	cation exchange	root nodule

Word Roots

macro- = large (*macronutrient:* elements required by plants and animals in relatively large amounts)

micro- = small (*micronutrient:* elements required by plants and animals in very small amounts)

myco- = a fungus; **-rhizo** = a root (*mycorrhizae:* mutualistic associations of plant roots and fungi)

Lecture Outline

Introduction *Plants that Clean Up Poisons*

A. Plants have an innate ability to accumulate metals at very high concentrations. Environmentalists use this unique characteristic when cleaning polluted soil and water (phytoremediation).

B. Brake ferns *(Pteris vittata)* have been shown to preferentially absorb the toxin arsenic. This is very useful, particularly around wood treatment facilities that use arsenic. Other plants such as the sunflower have been used to clean up other environmentally hazardous sites. At the nuclear power plant in Chernobyl and at a car factory in Detroit, sunflowers were used to remove radioactive elements from water and lead from the soil, respectively.

C. Phytoremediation has several problems.
   1. The process is slow and may take several growing seasons.
   2. The plants still need to be properly disposed of.
   3. There may be some evaporation of toxins through the leaves into the air.

I. The Uptake and Transport of Plant Nutrients

Module 32.1 Plants acquire their nutrients from soil and air.

A. *Review:* Mature plants are mostly composed of elements that were not obtained from soil, but rather CO_2 from the air and water from the soil. Also review the equation for photosynthesis (see Chapter 7, particularly the Opening Essay).

B. A terrestrial plant has an efficient evolutionary design to obtain resources from terrestrial sources. A plant gets CO_2 from air through its leaves, and water, minerals, and some O_2 from the soil through its roots. All other materials are produced from mixtures of these raw materials and particularly from the sugars produced by photosynthesis (Figure 32.1A).

C. Plants, like all aerobic organisms, obtain energy from the respiration of sugars. Leaves are net producers of O_2 and do not need to absorb more. Roots take up atmospheric O_2 through the soil for their respiratory needs.

D. Mineral forms of nitrogen, magnesium, and phosphorus (among others) are needed to make proteins, nucleic acids, phospholipids, ATP, chlorophyll, enzyme cofactors, and hormones.

E. That some plants support bodies over 100 m in height is astounding but explainable (Figure 32.1B).

Module 32.2 The plasma membranes of root cells control solute uptake.

A. Because of its large root surface area (particularly root hairs), a plant can absorb enough water and inorganic ions to survive and grow (Figure 32.2A).
Review: Passive transport (Modules 5.14 and 5.15) and the tissues of roots (Module 31.6).

B. *Preview:* Virtually all plants in the wild obtain nutrients and water through mycorrhizal fungal interconnections that may bypass root hairs. Root hairs are more important in laboratory seed cultures and fertilized agricultural plants (Module 32.11).

C. Substances enter roots in solution and make their way toward vascular tissue by two routes, intracellularly and extracellularly, and combinations of these two. In the end, nutrients must pass through at least one membrane before arriving at the vascular tissue. This allows plants to control the entry of substances into their roots (Figure 32.2B).

D. The intracellular pathway goes through the cell membrane of a root hair and then, by means of cytoplasmic continuity through plasmodesmata, throughout the cytoplasmic content of cortex cells and endodermal cells, and finally into the xylem vessels.

E. The extracellular pathway goes through the porous cell walls of all epidermal and cortex cells, but it is forced, by the impervious **Casparian strip** in the walls of endodermal cells, through cell membranes and then into the xylem.

Module 32.3 Transpiration pulls water up xylem vessels.

A. *Review:* The properties of water, diffusion, and osmosis (Modules 2.9–2.11, 2.14, 5.14, and 5.15).

B. Getting water from the soil, against the force of gravity, up to the leaves where it is needed, is a major adaptation of land plants. Water and dissolved nutrients, **xylem sap,** travel in the xylem. Several mechanisms combine to produce forces that move the water.
Review: Xylem is composed of dead cells (Modules 17.1 and 31.5).

C. In some plants, **root pressure** pushes the column of water up the xylem. Root cell membranes actively pump inorganic ions into the xylem, and osmosis causes water molecules to follow.
Review: Active transport (Module 5.18).

D. The main motive force through xylem is by the **transpiration-cohesion-tension mechanism. Transpiration** is the evaporation of water from internal leaf cell surfaces and diffusion out stomata. Water molecules in xylem stick together by **cohesion** through hydrogen bonds, and the column of water in xylem is pulled up. The **adhesion** of water molecules to the cellulose molecules of the cell walls helps counteract the downward pull of gravity on the water column (Figure 32.3).

Module 32.4 Guard cells control transpiration.

A. Transpiration works for and against plants. More than 200 L of water can be lost through transpiration in one day.

B. Stomata are changeable openings in the leaf surface. Their size is regulated by two surrounding guard cells that change shape in response to changing environmental conditions (Figure 32.4).

C. Guard cells buckle outward, opening the stomata; they actively pump in K^+, and water follows by osmosis, increasing the turgor. Guard cells close the stomata when they lose K^+.
Review: Osmosis and water balance (Modules 5.15 and 5.16).

D. Increased sunlight and decreased internal CO_2 cause guard cells to take up K^+, and if the plant loses water too fast, the guard cells close. In addition, an internal daily timing mechanism triggers K^+ uptake in the morning, stomatal opening, and K^+ release, stomatal closing, in the evening.
Preview: This internal timing mechanism is a type of biological clock. The biological clocks of plants are discussed in greater detail in Module 33.10.

Module 32.5 Phloem transports sugars.

A. Phloem is composed of sieve-tube members arranged end to end, each bounded at the end with a pitted plate. Each sieve-tube member's plasma membrane is continuous with the next, so the **phloem sap** can flow easily from one to another (Figure 32.5A).
Review: The structure of phloem is also discussed in Modules 17.1 and 31.5.

B. Phloem sap contains a watery solution of inorganic ions, amino acids, hormones, and, principally, sucrose.

C. Phloem sap flows from **sugar sources** (areas where sugar is made by photosynthesis or released from stored starch) to **sugar sinks** (areas where sugar molecules are used directly, flower nectar, or stored for future use, taproots).

D. The **pressure-flow mechanism** is the most widely accepted model for the movement of phloem sap. At the sugar source, sugar is loaded into the phloem by active transport. Water follows by osmosis, raising the water pressure. At the sugar sink, sugar leaves the phloem, and water follows by osmosis, lowering the water pressure. Phloem sap flows from source to sink down a gradient of hydrostatic pressure. Excess water returns to the sugar source through the xylem (Figure 32.5B).

E. This model is supported by tests using natural phloem tappers, aphids. Their mouthpieces (stylets) are severed while they feed on sap. The closer the aphid stylet is to a sugar source, the faster the sap flows out (Figure 32.5C).

II. Plant Nutrients and the Soil

Module 32.6 Plant health depends on a complete diet of essential inorganic nutrients.

NOTE: A comparison can be made here with the nutritional needs of humans (Modules 21.13–18).

A. Plants do not need (and cannot use) a supply of organic nutrients because they make their own. All they need, in addition to raw materials for photosynthesis, are inorganic nutrients.

B. Inorganic nutrients are essential if a plant must obtain them to complete its life cycle. The most common symptoms of nutrient deficiency are stunted growth and leaf discoloration. Hydroponic culture can be used to determine which elements are essential (Figure 32.6A).

C. Seventeen elements are essential in all plants. A few others are essential in only certain plant groups.

D. Nine of the essential nutrients are required in relatively large amounts and are known as **macronutrients.** Six are major atomic components of organic compounds: carbon, oxygen, hydrogen, nitrogen, sulfur, and phosphorus. Calcium, potassium, and magnesium are important in inorganic compounds.

E. Calcium is important in the formation of cells walls, in the functioning of certain proteins that help glue plant cells together in tissues, for the maintenance of cell membrane structure, and in regulating the selective permeability of cell membranes.

F. Potassium is an important part of several enzymes and plays a role in maintaining osmotic balance and in elongation during primary growth.

G. Magnesium is an important component of chlorophyll and is a cofactor for several enzymes.
Review: Figure 2.1 illustrates the position of magnesium in chlorophyll.

H. Eight essential nutrients are required in very small amounts and are known as **micronutrients.** Iron, chlorine, copper, manganese, zinc, molybdenum, boron, and nickel mainly function as components or cofactors of enzymes and are used over and over.
Review: Cofactors are discussed in Module 5.7.

I. Growing plants in soil deficient in essential nutrients can produce plants of lower quality (in terms of nutritional value for humans, appearance, etc.) (Figure 32.6B).

Module 32.7 Connection: You can diagnose some nutrient deficiencies in your own plants.

A. The most common nutrient deficiencies seen in plants are those of nitrogen, phosphorus, and potassium.

B. Symptoms of many forms of nutrient deficiency are often distinct enough to allow visual determination of the deficiency. Compare the following affected tomato plants with healthy plants (Figure 32.7A).

C. Nitrogen deficiency (in the form plants can use, NO_3^- or NH_4^+) exhibits stunted growth and yellow-green leaves (Figure 32.7B).

D. Phosphorus deficiency (in the form plants can use, $H_2PO_4^-$ or HPO_4^{2-}) exhibits green leaves but growth rate is greatly reduced and the new growth may be spindly and brittle (Figure 32.7C).

E. Potassium deficiency (in K^+ ions) exhibits yellow or dead brown spots or edges in localized areas on leaves. Stems and roots exhibit stunted growth (Figure 32.7D).
NOTE Commercial fertilizers give the values of these three nutrients, in percent weight in the fertilizer, of nitrogen, phosphoric acid (H_3PO_4), and potash (K_2O). A fertilizer labeled 4-8-4 is 4% N, 8% H_3PO_4, and 4% K_2O.

Module 32.8 Soil contains rock particles, humus, organisms, water, and crucial solutes.

A. The structure and nutrient content of soil are important characteristics in plant root absorption. Soil structure is categorized according to horizons. The microscopic details of structure affect the availability of nutrients. There are three **soil horizons,** labeled A, B, and C.

B. The A horizon is the **topsoil.** It is subject to weathering, and contains rock particles (such as sand and clay) and high levels of decomposing organic matter called **humus.** This horizon is usually intensely active with the decomposing activity of bacteria, fungi, protozoans, and small animals. Most plant roots branch out in the A horizon.
NOTE: Much nutrient uptake takes place in the A horizon. It is also the region of most active mycorrhiza formation (Module 32.11).

C. The B horizon contains fewer organisms and less organic matter, and is less subject to weathering.
NOTE: The lower levels of the B horizon represent the deepest regions at which water is obtained by plant roots and mycorrhizae.

D. The C horizon is broken-down rock that has only been slightly weathered.

E. Water, dissolved oxygen, and nutrients are removed by root hairs in direct contact with water films on soil particles (Figure 32.8B).

F. **Cation exchange** is the release of H^+ ions by root hairs to displace positive nutrient ions (such as Ca^{2+}, Mg^{2+}, and K^+) that naturally adhere to negatively charged clay particles and thus free these nutrients for absorption by the root hairs (Figure 32.8B).

G. Anions (such as NO_3^-) are not bound to soil particles. This makes anions more readily available to plants. However, it also makes it more likely for anions to be leached out of the soil.

Module 32.9 Connection: Soil conservation is essential to human life.

A. Irrigation makes possible the agricultural use of otherwise dry areas, but it has the disadvantages of overusing water and making the soil salty (Figure 32.9A). Modern drip irrigation methods are the most efficient at avoiding these problems.

B. Wind and water erosion can be prevented by minimal-tillage farming, planting trees as windbreaks, and contour tillage (Figure 32.9B). However, minimal-tillage farming often relies on herbicides to destroy weeds that plowing would otherwise remove, and herbicides may contribute to chemical pollution of the soil.

C. Most farmers use fertilizers containing nutrients that are either mined or produced by industrial processes. These fertilizers contain a mixture of N, P, and K that is rapidly released in soil and that may rapidly leach out to pollute groundwater. Organic fertilizers are of biological origin and release nutrients gradually.
NOTE: Organic fertilizers also tend to help maintain beneficial soil structure, including humus.
Review: The environmental impact of agriculture (Module 19.9).

Module 32.10 Connection: Organic farmers avoid the use of commercial chemicals.

A. Peaches at the farmers market and at the "Super" grocery store are both labeled "organic" (Figure 32.10). But how does one define and then guarantee that a product is in fact grown organically?

B. Organic farming uses the principles of ecology and is farming without pesticides or inorganic fertilizers. Natural fertilizers like manure are used and predatory insects are added to fields to eat the unwanted insects.

C. Approximately 12,000 farmers in the United States use organic methods of farming and each is monitored to ensure that organic farming guidelines are followed.

D. Although the operating expenses of organic farming are higher, some people are willing to pay more for safer, more nutritious food. In conventional farming, there are hidden costs, such as the loss of soil fertility and increased problems with pests from unbalanced soil conditions.

E. Organic farming methods are still being improved with two goals in mind:
   1. Feed the people of the world.
   2. Preserve and improve the quality of the air, water, and soil.

Module 32.11 Fungi help most plants absorb nutrients from the soil.

A. *Review:* The characteristics of fungi, particularly hyphae (Modules 17.15–17.20).

B. **Mycorrhizae** are structures formed by the roots of plants and fungi that invade these roots. Virtually all plants in naturally competitive situations have mycorrhizae. In the form of mycorrhiza shown in Figure 32.11, the fungal hyphae envelop the root with a covering, and some tips enter between the cortex cells of the root. In other mycorrhizae, fungal hyphae enter through root hairs or the root's epidermal surface into cells of the epidermis and the cortex.

C. The plant supplies the fungus with required carbohydrates, while the fungus supplies the plant with increased efficiency of nutrient (particularly phosphorus, but not nitrogen) and water uptake, and in some forms of mycorrhizae, protection against pathogenic organisms found in the soil.
Preview: Symbiotic relationships, such as mutualism, are discussed in Module 36.5).

Module 32.12 The plant kingdom includes parasites and carnivores.

A. Dodder is a nonphotosynthetic plant that parasitizes other plant species using modified roots to tap the host plant's vascular tissue (Figure 32.12A).

B. Mistletoes are photosynthetic parasites of trees that supplement their diets by tapping into the host's vascular tissue (Figure 32.12B).

C. The sundew and Venus flytrap use ingenious insect traps formed from highly adapted leaves to trap, kill, and digest insects, and enhance their supplies of nitrogen (Figure 32.12C, D). These carnivorous plants are found in bogs where nitrogen is limited because the acid conditions impede the decomposition of dead vegetation.

Module 32.13 Most plants depend on bacteria to supply nitrogen.

Preview: The nitrogen cycle (Module 36.16).

A. All plants and, indirectly, all animals depend on nitrogen supplies in soils in which plants grow. Nitrogen is available to plants only as NH_4^+ (ammonium ions) and NO_3^- (nitrate ions).

B. Although nitrogen is 80% of our atmosphere, this gas is not usable by plants but must be converted to organic form by bacteria. **Nitrogen fixation** is the conversion process used by bacteria (Module 16.17) to convert gaseous nitrogen to ammonium (Figure 32.13).

C. Ammonifying bacteria convert organic forms of nitrogen to NH_4^+. Little NH_4^+ is absorbed by plants because, being positive, it usually remains firmly bound to negative clay particles.

D. Nitrifying bacteria convert NH_4^+ to NO_3^-. NO_3^- is the form of nitrogen most often used by plants because it is negative and readily released from soils.

Module 32.14 Legumes and certain other kinds of plants house nitrogen-fixing bacteria.

A. Legume roots house nitrogen-fixing bacteria of the genus *Rhizobium* in **root nodules.** (Figure 32.14A, B).

B. Nonlegume plants, such as alders, have root nodules containing the nitrogen-fixing bacteria actinomycetes.

C. The plant provides the bacteria with carbohydrates and other organic compounds, while the bacteria provide ammonium.

D. Legume crops can be rotated with other crops or plowed into the soil prior to planting a second crop, both providing increased nitrogen to the soil.

III. Plant Nutrients and Agriculture

Module 32.15 Connection: A major goal of agricultural research is to improve the protein content of crops.

A. The majority of people in the world have vegetarian diets, but the plants they eat are low in protein. Therefore, increasing the protein content of such grains as rice would be most beneficial to a large portion of the world's population (Figure 32.15A). Many high-yielding modern crop plants require very high levels of nitrogen fertilization, which is difficult to obtain in developing countries.

B. One promising approach is improving the output of the *Rhizobium* bacteria found in the root nodules of legumes. There are mutant strains of *Rhizobium* that continue to fix nitrogen even after nitrogen compounds have accumulated. The goal is to incorporate such strains into host plants in the future (Figure 32.15B).

Module 32.16 Connection: Genetic engineering is increasing crop yields.

A. *Review:* Recombinant DNA technology used in agriculture (Module 12.20).

B. A novel approach in genetically engineering plants is to use a .22-caliber gun to fire DNA-coated pellets into the cells. The pellets pass through the walls, into the cytoplasm where the DNA becomes integrated with that of the cell (Figure 32.16).

C. Using genes introduced by this approach and by plasmids, several transgenic plants have been produced, including potato plants that synthesize their own insecticide and tomato plants with fruit that is slow to spoil.

D. Not-yet-attained goals are to transfer nitrogen-fixing genes into nonlegume crop plants, and to develop plants that can synthesize pharmaceuticals and industrial oils.

E. In this work, as in the work with transgenic animals, questions continue to arise about potential problems and risks.

Class Activities

1. I cannot keep alive plants that are kept in soil; I always either overwater or forget to water them and they end up dying; have your class consider the physiological basis of the death of these plants. I do like plants that do not require soil and can survive in water; have your class consider why these plants do not suffer from overwatering and how they obtain sufficient minerals to survive and thrive.
2. Foreshadowing the chapters concerned with the environment, have your students consider how transpiration might influence weather/climatic patterns.

Transparency Acetates

Figure 32.1A	The uptake of nutrients by a plant
Figure 32.2B	Routes of water and solutes from soil to root xylem
Figure 32.3	The flow of water up a tree (Layer 1)
Figure 32.3	The flow of water up a tree (Layer 2)
Figure 32.3	The flow of water up a tree (Layer 3)
Figure 32.4	How guard cells control stomata

Figure 32.5B	Pressure flow in plant phloem from a sugar source to a sugar sink (and the return of water to the source via xylem)
Figure 32.6A	A hydroponic culture experiment
Figure 32.8B	A close-up view of root hairs in soil
Figure 32.8C	Cation exchange
Figure 32.13	The roles of bacteria in supplying nitrogen to plants
Figure 32.15B	Regulation of nitrogen fixation in *Rhizobium* bacteria
Figure 32.16	Using a gene gun

Media

See the beginning of this book for a complete description of all media available for instructors and students. Animations and videos are available in the Campbell Image Presentation Library. Media Activities and Thinking as a Scientist investigations are available on the student CD-ROM and web site.

Animations and Videos	File Name
Sun Dew Trapping Prey Video	32-12C-SunDewTrapVideo-B.mov
Sun Dew Trapping Prey Video	32-12C-SunDewTrapVideo-S.mov
Water Flow Up a Tree Animation	32-03-WaterFlowUpTreeAnim.mov

Activities and Thinking as a Scientist	Module Number
Web/CD Thinking as a Scientist: *How Is the Rate of Transpiration Calculated?*	32.3
Web/CD Thinking as a Scientist: *How Are Water and Solute Potentials Calculated?*	32.3
Web/CD Activity 32A: *Transpiration*	32.4
Web/CD Activity 32B: *Transport in Phloem*	32.5
Web/CD Activity 32C: *Absorption of Nutrients from Soil*	32.8
Web/CD Thinking as a Scientist: *Connection: How Does Acid Precipitation Affect Mineral Deficiency?*	32.8
Web/CD Activity 32D: *Connection: Genetic Engineering of Golden Rice*	32.16