Chapter 37

Plant Nutrition

Key Concepts

37.1 Plants require certain chemical elements to complete their life cycle

37.2 Soil quality is a major determinant of plant distribution and growth

37.3 Nitrogen is often the mineral that has the greatest effect on plant growth

37.4 Plant nutritional adaptations often involve relationships with other organisms

Framework

The nutritional requirements of plants include essential macronutrients and micronutrients. Carbon dioxide enters the plant through the leaves, but water and minerals must be absorbed through the roots. Soil fertility is influenced by its texture and composition. Nitrogen assimilation by plants is made possible by the decomposition of humus by microbes and nitrogen fixation by bacteria. Mycorrhizae are important associations between fungi and plant roots that increase mineral and water absorption.

Chapter Review

Plants, as photoautotrophs, make their own organic compounds. Their roots, shoots, and leaves are structurally adapted to obtain water, minerals, and carbon dioxide from the soil and air.

37.1 Plants require certain chemical elements to complete their life cycle

Early scientists speculated on whether soil, water, or air provides the substance for plant growth. **Mineral nutrients,** essential inorganic ions absorbed from the soil, make only a small contribution to the mass of a plant. Water makes up more than three-fourths of the weight of a plant; supplies most of the hydrogen incorporated into organic compounds; and is used as a solvent, for growth by cell elongation, or for support through turgor pressure. By weight, CO_2 from the air is the source of most of the organic material of a plant. Carbon, oxygen, and hydrogen, as the main components of organic compounds such as cellulose, are the most abundant elements making up the dry weight of a plant. Nitrogen, sulfur, and phosphorus—ingredients of some organic compounds—are relatively abundant.

Macronutrients and micronutrients

Essential elements are those required for a plant to complete its life cycle from a seed to an adult that produces more seeds. **Hydroponic culture** has been used to determine which of the mineral elements found in plants are essential nutrients. Seventeen elements have been identified as essential in all plants.

Nine **macronutrients** are required by plants in relatively large amounts and include the six major elements of organic compounds as well as calcium, potassium, and magnesium.

Eight **micronutrients** have been identified as needed by plants in very small amounts, functioning mainly as cofactors of enzymatic reactions.

■ INTERACTIVE QUESTION 37.1

a. What is a function of the macronutrient magnesium in plants?

b. What is a function of the macronutrient phosphorus?

c. What is a function of the micronutrient iron?

Symptoms of Mineral Deficiency A mobile nutrient will move to young, growing tissues, so that a deficiency will show up first in older parts of the plant. Symptoms of a mineral deficiency may be distinctive enough for the cause to be diagnosed by a plant physiologist or farmer. Soil and plant analysis can confirm a specific deficiency. Nitrogen, potassium, and phosphorus deficiencies are most common.

■ INTERACTIVE QUESTION 37.2

Where would you expect a deficiency of a relatively immobile element to be seen first?

37.2 Soil quality is a major determinant of plant distribution and growth

Texture and Composition of Soils The formation of soil begins with the weathering of rock and accelerates with the secretion of acids by lichens, fungi, bacteria, and plant roots. **Topsoil** is a mixture of broken-down rock, living organisms, and **humus** (decomposing organic matter). Several other distinct soil layers, or **horizons,** are found under the topsoil layer.

The texture of topsoil depends on particle size, which varies from coarse sand to fine clay. **Loams,** made up of a mixture of sand, silt, and clay, are often the most fertile soils, having enough fine particles to provide a large surface area for retaining water and minerals but enough coarse particles to provide air spaces with oxygen for respiring roots.

The activities of the numerous soil inhabitants, such as bacteria, fungi, algae, other protists, insects, worms, nematodes, and plant roots, affect the physical and chemical properties of soil.

Humus builds a crumbly soil that retains water, provides good aeration of roots, and supplies mineral nutrients.

Water containing dissolved minerals binds to hydrophilic soil particles and is held there in small spaces, available for uptake by plant roots. Positively charged minerals, such as K^+, Ca^{2+}, and Mg^{2+}, adhere to the negatively charged surfaces of finely divided clay particles. Negatively charged minerals, such as nitrate (NO_3^-), phosphate ($H_2PO_4^-$), and sulfate (SO_4^{2-}), tend to leach away more quickly. The release of H^+ by roots facilitates **cation exchange,** in which hydrogen ions displace positively charged mineral ions from the clay particles, making the ions available for absorption.

■ INTERACTIVE QUESTION 37.3

Describe the characteristics of a fertile soil.

Soil Conservation and Sustainable Agriculture Without good soil conservation, agriculture can quickly destroy the fertility of a soil that has built up over centuries. Agriculture diverts essential elements from the chemical cycles when crops are harvested, and many crops use more water than the natural vegetation.

Historically, farmers used manure to fertilize their crops. Today in developed nations, commercially produced fertilizers, usually containing nitrogen, phosphorus, and potassium, are used. Manure, fishmeal, and compost are called organic fertilizers because they contain organic material that is in the process of decomposing. These fertilizers decompose into inorganic nutrients, which are taken up by the plant in the same form supplied by commercial fertilizers. Commercial fertilizers may be rapidly leached from the soil, polluting streams and lakes.

The acidity of the soil affects cation exchange and can alter the chemical form of minerals and thus their ability to be absorbed by the plant. Managing the pH of soil is an important aspect of maintaining fertility.

Irrigation can make farming possible in arid regions, but it places a huge drain on water resources and raises soil salinity. New methods of irrigation and new varieties of plants that can tolerate less water may reduce some of these problems.

In the United States, topsoil from thousands of acres of farmland is lost to water and wind erosion each year. Agricultural use of cover crops, windbreaks, and terracing can minimize erosion.

■ INTERACTIVE QUESTION 37.4

a. How could a genetically engineered "smart plant" help reduce fertilizer use?

b. What is **sustainable agriculture?**

The use of plants to extract heavy metals and other pollutants from contaminated soils is an emerging technology known as **phytoremediation.**

37.3 Nitrogen is often the mineral that has the greatest effect on plant growth

Soil Bacteria and Nitrogen Availability To be absorbed by plants, nitrogen must be converted to nitrate (NO_3^-) or ammonium (NH_4^+) by the action of microbes, such as ammonifying bacteria, that decompose humus. Some nitrate is lost to the atmosphere by the action of denitrifying bacteria. **Nitrogen-fixing bacteria** convert atmospheric nitrogen into ammonia through the process of **nitrogen fixation.**

Bacteria capable of nitrogen fixation contain **nitrogenase,** an enzyme complex that reduces N_2 by adding H^+ and electrons to form ammonia (NH_3). This process is energetically expensive, and nitrogen-fixing bacteria rely on organic material in soils or symbiotic relationships with plant roots to supply fuel for their cellular respiration. In the soil solution, ammonia forms ammonium, which plants can absorb. Nitrifying bacteria oxidize ammonium, producing nitrate, the form of nitrogen most readily absorbed by roots. Most plants incorporate nitrogen into amino acids or other organic compounds in the roots and then transport it through the xylem to shoots (see Interactive Question 37.5).

Improving the Protein Yield of Crops Protein deficiency is the most common form of human malnutrition. Agricultural research attempts to improve the quality and quantity of proteins in crops. Varieties of corn, wheat, and rice have been developed that are enriched in protein, but they require the addition of large quantities of expensive nitrogen fertilizer.

37.4 Plant nutritional adaptations often involve relationships with other organisms

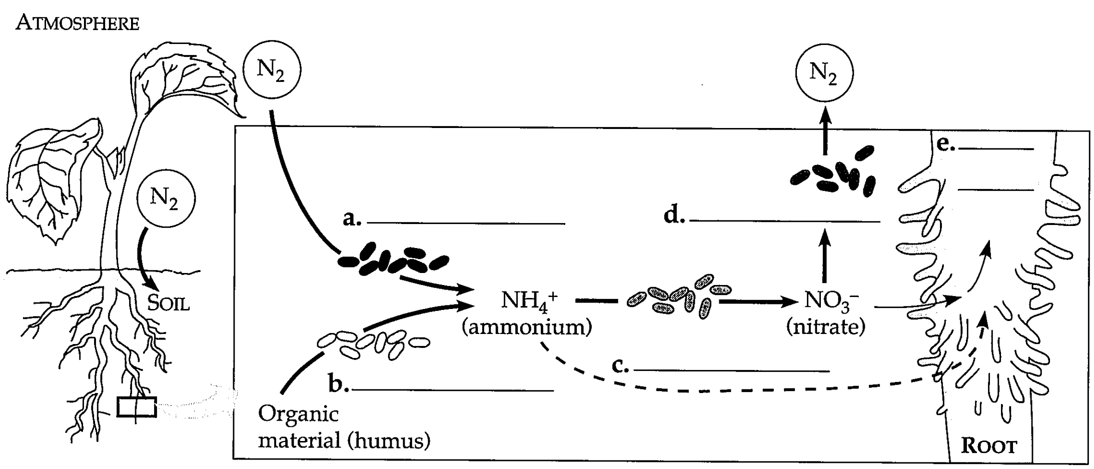
The Role of Bacteria in Symbiotic Nitrogen Fixation Plants of the legume family have root swellings, called **nodules,** composed of plant cells with nitrogen-fixing *Rhizobium* bacteria in a form called **bacteroids** contained in vesicles. Nitrogen fixation requires an anaerobic environment. Lignified external layers of nodule cells may limit gas exchange. In some nodules, the presence of oxygen-binding leghemoglobin keeps the concentration of free O_2 low and regulates the oxygen supply for the bacterial respiration required to provide ATP for nitrogen fixation.

Mutual signaling between roots and bacteria lead to root hair elongation and formation of an infection thread within a root hair. Bacteria form bacteroids as they bud into dividing cortical cells from the infection thread. Dividing cells of the cortex and pericycle fuse to form the nodule, which develops vascular tissue into the vascular cylinder. The plant provides the bacteria with carbohydrates and other organic molecules. Nodule cells use most of the fixed nitrogen to make amino acids, which are then transported throughout the plant.

The plant initiates the chemical dialogue with *Rhizobium* by secreting flavonoids that are detected and absorbed only by its particular *Rhizobium* species. The plant signal activates a gene-regulating protein that turns on the bacterial genes called *nod* (for "nodulation") genes. The enzymes produced from these genes catalyze the production of Nod factors that are secreted by the bacterial cells. Nod factors signal the

■ INTERACTIVE QUESTION 37.5

Fill in the types of bacteria (a–d) that participate in the nitrogen nutrition of plants. Indicate the form (e) in which nitrogen is transported in xylem to the shoot system.



activation of a plant's early nodulin genes, which initiate formation of an infection thread.

Symbiotic nitrogen fixation benefits agriculture. Legume seeds are coated with their specific *Rhizobium* before planting. Rice farmers culture a water fern that has symbiotic cyanobacteria that fix nitrogen, improving the fertility of rice paddies.

■ INTERACTIVE QUESTION 37.6

a. What is **crop rotation?**

b. What is "green manure"?

Mycorrhizae and Plant Nutrition Most plants have symbiotic associations of roots and fungi called mycorrhizae. The fungus receives food from the plant, while providing a large surface area for the absorption of water and minerals, which it provides to the plant. The fungus secretes growth hormones that stimulate root growth and branching and may help protect the plant from some soil pathogens.

Especially common in woody plants, **ectomycorrhizae** form a dense sheath or mantle of mycelium over the root surface. Hyphae extending from the mantle provide a huge surface area for the absorption of water and minerals, especially phosphate. Hyphae also grow into extracellular spaces in the root cortex and facilitate exchange between plant and fungus.

Endomycorrhizae do not form a sheath but extend fine fungal hyphae into the soil. Hyphae also penetrate into root cell walls and form tubes that invaginate the root cell's membrane. Some of these tubes form dense branched structures called arbuscles that facilitate nutrient exchange. Eighty-five percent of plant species have endomycorrhizae.

Most plants form mycorrhizae when they grow in their natural habitat. When seeds are planted in foreign soil where their particular species of fungus may not be found, or when soil fungi are poisoned, plants show signs of malnutrition. Foresters now inoculate seeds with spores of their mycorrhizal fungi to improve the growth of seedlings.

■ INTERACTIVE QUESTION 37.7

Why is it thought that mycorrhizae were important to the colonization of land by the first plants?

Epiphytes, Parasitic Plants, and Carnivorous Plants **Epiphytes** are plants that grow on the surface of another plant but do not take nourishment from it. Parasitic plants, such as the mistletoe or dodder, produce **haustoria** that may invade a host plant and siphon xylem or phloem sap from its vascular tissue.

Living in acid bogs or other nutrient-poor soils, carnivorous plants obtain nitrogen and minerals by killing and digesting insects that are caught in traps formed from modified leaves.

Word Roots

ecto- = outside; **-myco-** = a fungus; **-rhizo** = a root (*ectomycorrhizae:* a type of mycorrhizae in which the mycelium forms a dense sheath, or mantle, over the surface of the root; hyphae extend from the mantle into the soil, greatly increasing the surface area for water and mineral absorption)

endo- = inside (*endomycorrhizae:* a type of mycorrhizae that unlike ectomycorrhizae, do not have a dense mantle ensheathing the root; instead, microscopic fungal hyphae extend from the root into the soil)

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)

-phyto = a plant (*phytoremediation:* an emerging, nondestructive technology that seeks to cheaply reclaim contaminated areas by taking advantage of the remarkable ability of some plant species to extract heavy metals and other pollutants from the soil and to concentrate them in easily harvested portions of the plant)

Structure Your Knowledge

1. Develop a concept map that organizes your understanding of the basic nutritional requirements of plants.
2. What are the differences between root nodules and mycorrhizae? How are each beneficial to plants?
3. What is a similarity between root nodules and mycorrhizae?

Test Your Knowledge

MULTIPLE CHOICE: *Choose the one best answer.*

1. The inorganic compound that contributes most of the mass to a plant's organic matter is
   - **a.** H_2O.
   - **b.** CO_2.
   - **c.** NO_3^-.
   - **d.** O_2.
   - **e.** $C_6H_{12}O_6$.

2. The effects of mineral deficiencies involving fairly mobile nutrients will first be observed in
   - **a.** older portions of the plant.
   - **b.** new leaves and shoots.
   - **c.** the root system.
   - **d.** the color of the leaves.
   - **e.** the flowers.

3. Micronutrients may be
   - **a.** cofactors in enzymes.
   - **b.** required in very minute quantities.
   - **c.** components of cytochromes.
   - **d.** identified by hydroponic culture.
   - **e.** all of the above.

4. The most fertile type of soil is usually
   - **a.** sand because its large particles allow room for air spaces.
   - **b.** loam, which has a mixture of fine and coarse particles.
   - **c.** clay, because the fine particles provide much surface area to which minerals and water adhere.
   - **d.** humus, which is decomposing organic material.
   - **e.** wet and alkaline.

5. Chlorosis is
   - **a.** a symptom of a mineral deficiency indicated by yellowing leaves due to decreased chlorophyll production.
   - **b.** the uptake of the micronutrient chlorine by a plant, which is facilitated by symbiotic bacteria.
   - **c.** the production of chlorophyll within the thylakoid membranes of a plant.
   - **d.** a contamination of glassware in hydroponic culture.
   - **e.** a mold of roots caused by wet soil conditions.

6. Negatively charged minerals
   - **a.** are released from clay particles by cation exchange.
   - **b.** are reduced by cation exchange before they can be absorbed.
   - **c.** are converted into amino acids before they are transported through the plant.
   - **d.** are bound when roots release acids into the soil.
   - **e.** are leached away by the action of rainwater more easily than positively charged minerals.

7. Nitrogenase
   - **a.** is an enzyme complex that reduces atmospheric nitrogen to ammonia.
   - **b.** is found in *Rhizobium* and other nitrogen-fixing bacteria.
   - **c.** catalyzes the energy-expensive fixation of nitrogen.
   - **d.** provides a model for chemical engineers to design catalysts to make nitrogen fertilizers.
   - **e.** is or does all of the above.

8. Epiphytes
   - **a.** have haustoria for anchoring to their host plants and obtaining xylem or phloem sap.
   - **b.** are symbiotic relationships between leaves and fungi.
   - **c.** live in poor soil and digest insects to obtain nitrogen.
   - **d.** grow on other plants but do not obtain nutrients from their hosts.
   - **e.** are able to fix their own nitrogen.

9. The nitrogen content of some agricultural soils may be improved by
   - **a.** the synthesis of leghemoglobin by ammonifying bacteria.
   - **b.** mycorrhizae on legumes.
   - **c.** water ferns with symbiotic cyanobacteria, or other plants with nitrogen-fixing bacteria.
   - **d.** cation exchange.
   - **e.** the action of denitrifying bacteria.

10. An advantage of organic fertilizers over chemical fertilizers is that they
    - **a.** are more natural.
    - **b.** release their nutrients over a longer period of time and are less likely to be lost to runoff.
    - **c.** provide nutrients in the forms most readily absorbed by plants.
    - **d.** are easier to mass produce and transport.
    - **e.** are all of the above.

11. The early nodulin genes

a. code for cytokinin plant hormones.

b. produce Nod factors that are signals released from bacteria to roots.

c. are turned on by Nod factor signals from *Rhizobium* and initiate nodule development in roots.

d. code for receptors for signals released by *Rhizobium*.

e. are fungal genes that control the development of arbuscles within root cells.

12. Which of the following takes the form of a mycelial sheath over plant roots with hyphae extending out that increase the surface area for absorption?

a. root nodules

b. haustoria

c. endomycorrhizae

d. ectomycorrhizae

e. infection threads

13. Which of the following is an example of phytoremediation?

a. dusting legume seeds with spores of *Rhizobium* to increase nodule formation

b. inoculating seeds with fungal spores to ensure mycorrhizal formation

c. using plants to remove toxic heavy metals from contaminated soils

d. genetic engineering of plants to increase protein content

e. seeding the ocean with iron to create algal blooms that reduce atmospheric CO_2 levels

14. What created the Dust Bowl in the Great Plains in the 1930s?

a. several years of drought

b. building dams that removed the normal supply of water to the region

c. removal of prairie grasses for wheat and cattle farming

d. lack of crop rotation so that soil fertility was destroyed

e. Both a and c were important factors.

15. Place these steps in the sequence of root nodule formation in proper order:

1. production of infection thread through which bacteria enter root

2. secretion of flavonoids by root

3. continuation of nodule growth and connection to vascular stele of root

4. activation of gene regulating protein, which turns on bacterial *nod* genes

5. activation of plant early nodulin genes by bacterial Nod factors

6. bacteria wrapped in vesicles in cortical cells, becoming bacteroids

a. 3, 5, 6, 1, 4, 2

b. 2, 4, 5, 1, 6, 3

c. 2, 1, 4, 5, 6, 3

d. 5, 4, 2, 1, 3, 6

e. 1, 2, 4, 5, 6, 3