PLANT NUTRITION

Section A: Nutritional Requirements of Plants

1. The chemical composition of plants provides clues to their nutritional requirements
2. Plants require nine macronutrients and at least eight micronutrients

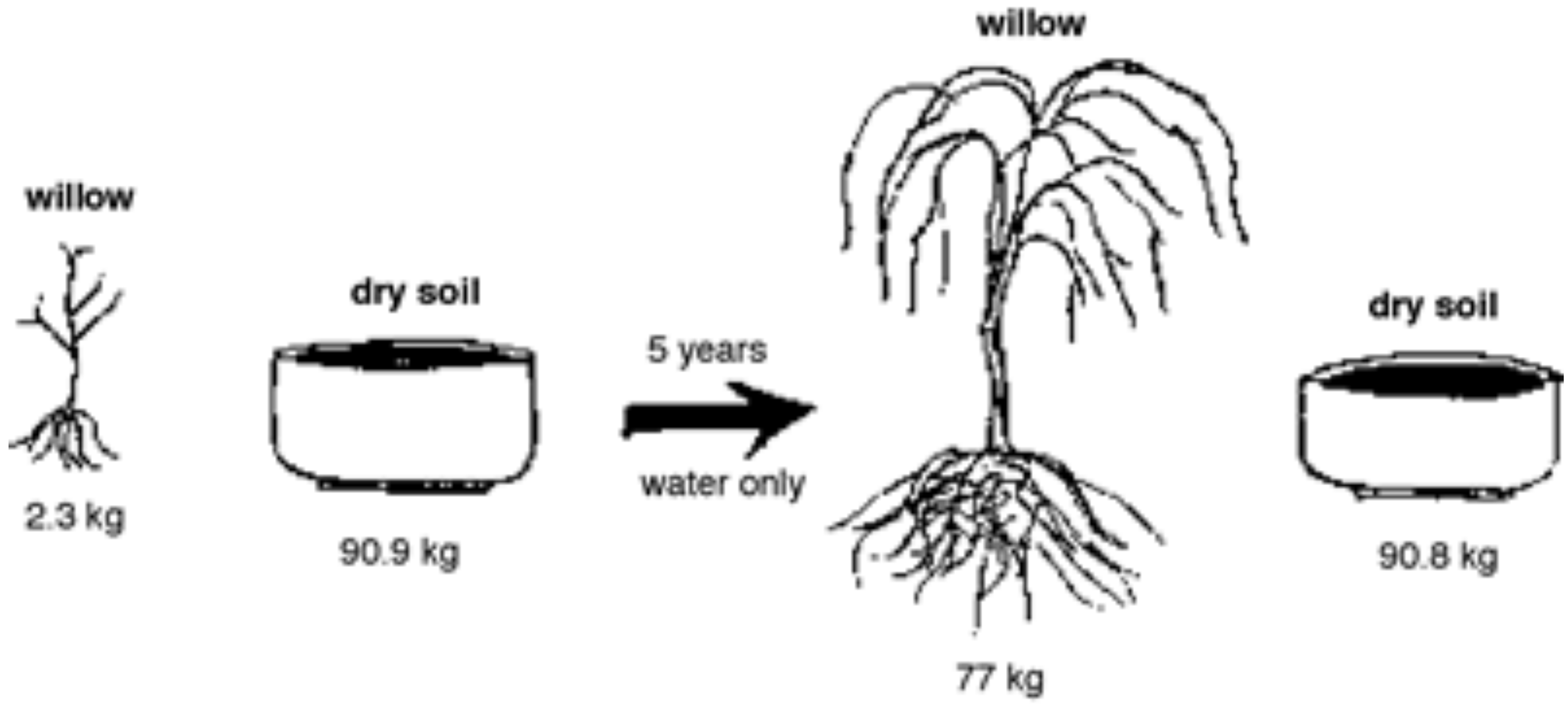
Introduction

- Every organism is an open system connected to its environment by a continuous exchange of energy and materials.
    - In the energy flow and chemical cycling that keep an ecosystem alive, plants and other photosynthetic autotrophs perform the key step of transforming inorganic compounds into organic ones.
    - At the same time, a plant needs sunlight as its energy source for photosynthesis and raw materials, such as CO_2 and inorganic ions, to synthesize organic molecules.
    - The root and shoot systems extensively network a plant with its environment.

1. The chemical composition of plants provides clues to their nutritional requirements

- Early ideas about plant nutrition were not entirely correct and included:
  - Aristotle's hypothesis that soil provided the substance for plant growth.
  - Van Helmont's conclusion from his experiments that plants grow mainly from water.
  - Hale's postulate that plants are nourished mostly by air.
- Plants *do* extract minerals from the soil.

Van Helmont Experiment



- **Mineral nutrients** are essential chemical elements absorbed from soil in the form of inorganic ions.
  - For example, plants acquire nitrogen mainly in the form of nitrate ions (NO_3^-).
- However, as indicated by van Helmont's data, mineral nutrients from the soil make only a small contribution to the overall mass of a plant.
  - About 80 - 85% of a herbaceous plant is water.
  - Because water contributes most of the hydrogen ions and some of the oxygen atoms that are incorporated into organic atoms, one can consider water a nutrient too.

- However, only a small fraction of the water entering a plant contributes to organic molecules.
  - Over 90% is lost by transpiration.
  - Most of the water retained by a plant functions as a solvent, provides most of the mass for cell elongation, and helps maintain the form of soft tissues by keeping cells turgid.
- By weight, the bulk of the organic material of a plant is derived not from water or soil minerals, but from the CO_2 assimilated from the atmosphere.

- The uptake of nutrients occurs at both the roots and the leaves.
  - Roots, through mycorrhizae and root hairs, absorb water and minerals from the soil.
  - Carbon dioxide diffuses into leaves from the surrounding air through stomata.

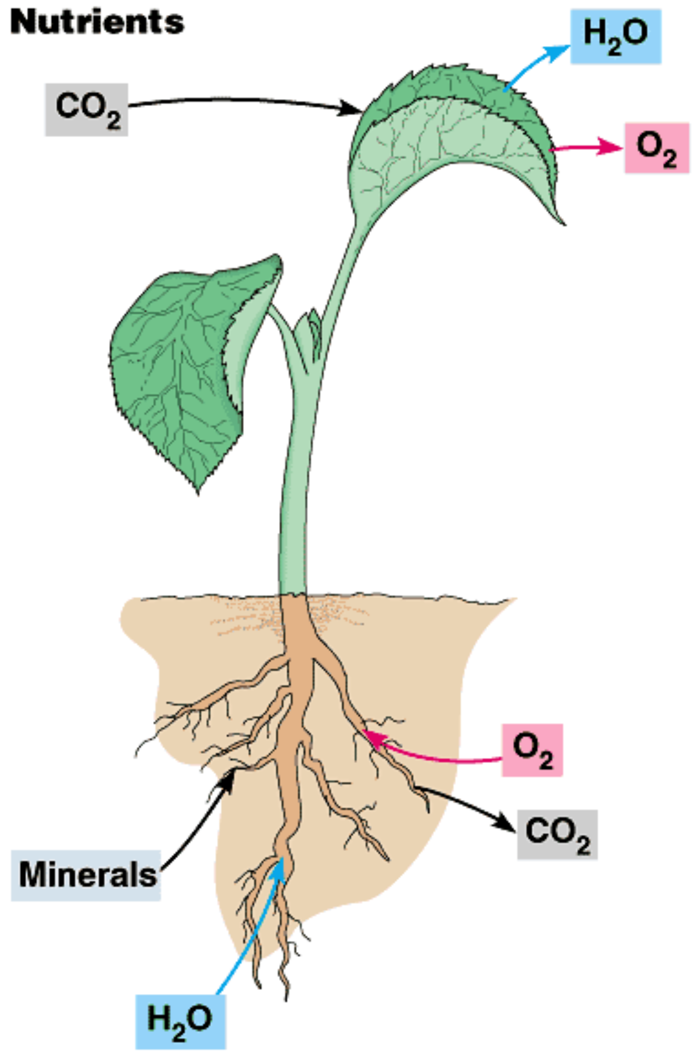
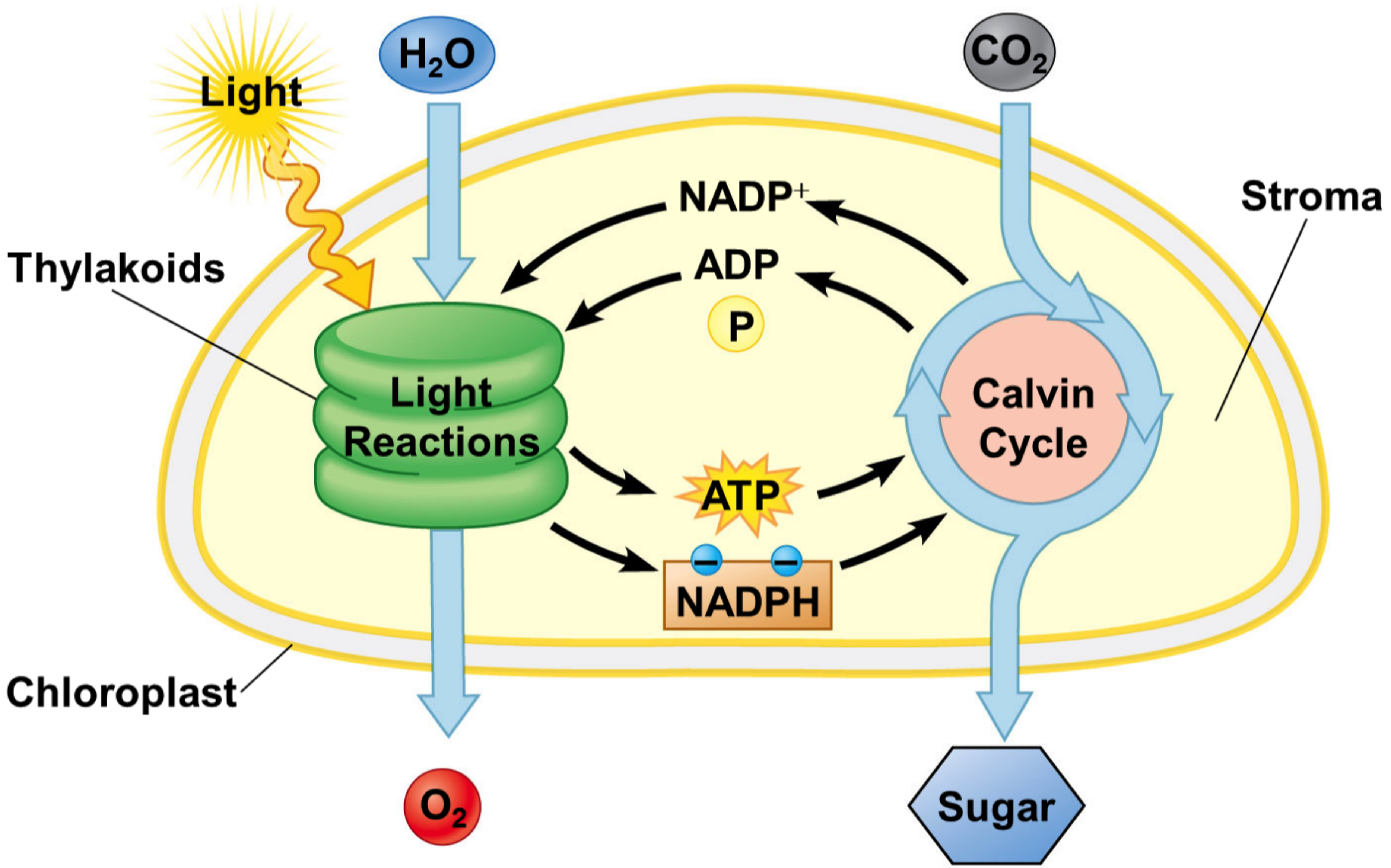
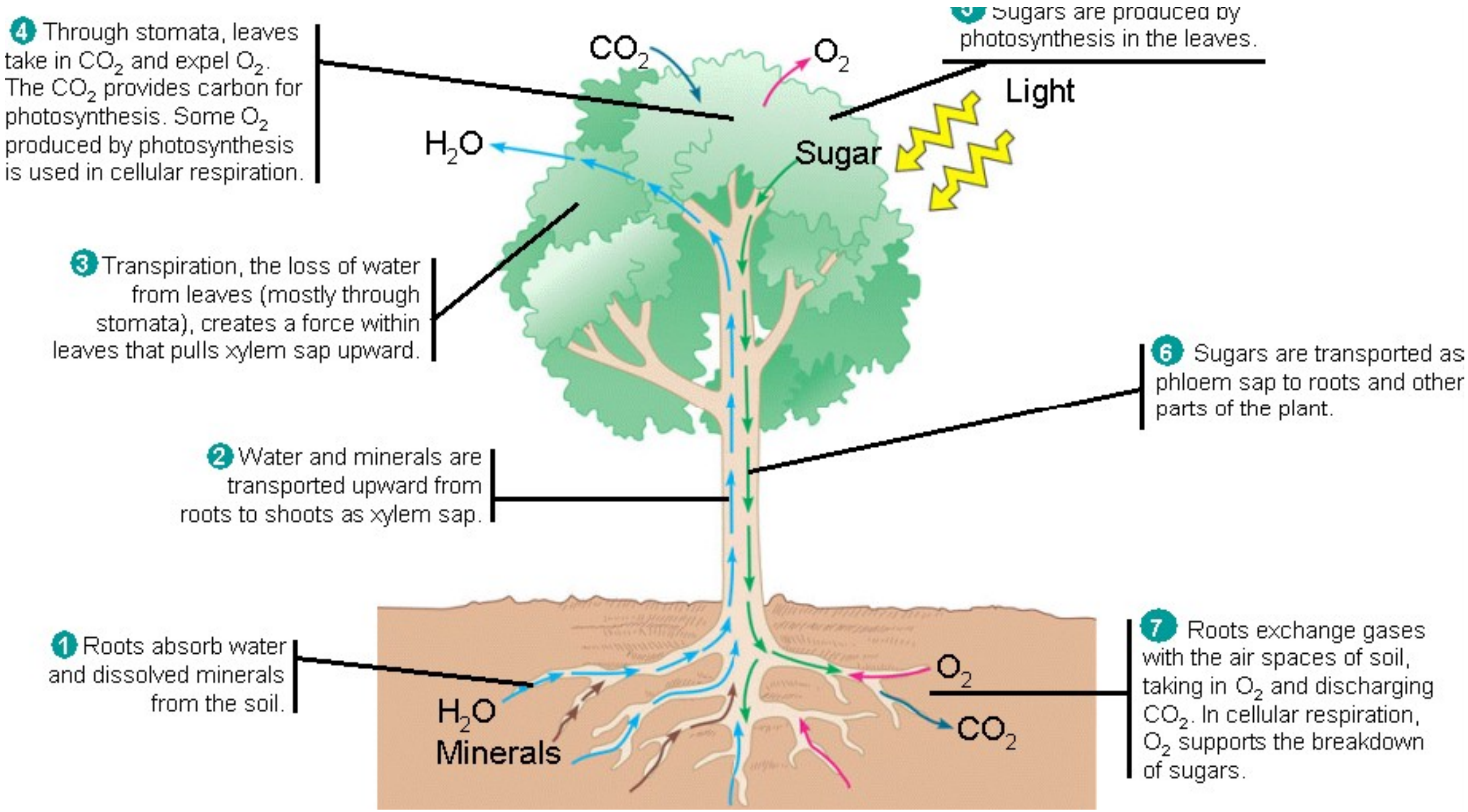


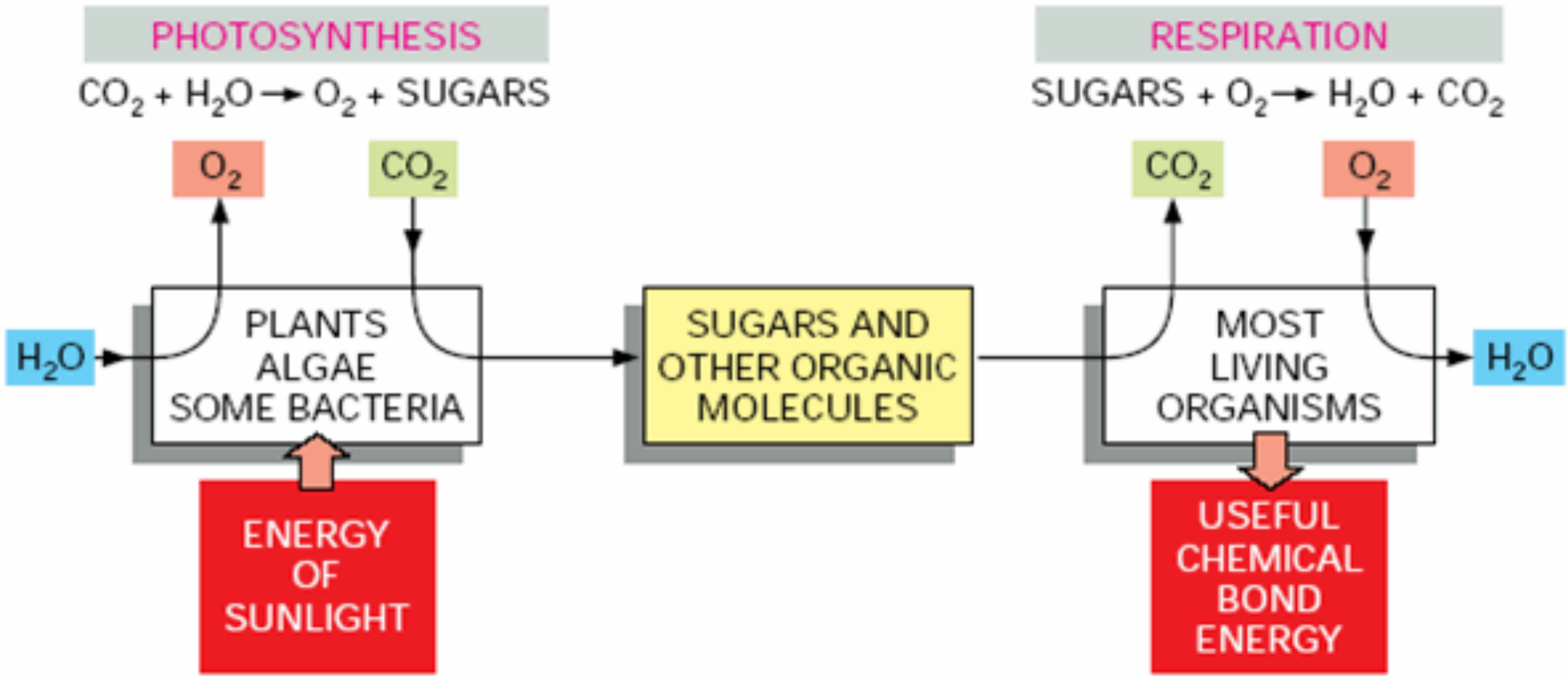
Fig. 37.1


Light
H₂O
CO₂
NADP+
ADP
P
Thylakoids
Stroma
Light Reactions
Calvin Cycle
ATP
NADPH
Chloroplast
O₂
Sugar



4 Through stomata, leaves take in CO_2 and expel O_2. The CO_2 provides carbon for photosynthesis. Some O_2 produced by photosynthesis is used in cellular respiration.
CO_2
O_2
Sugars are produced by photosynthesis in the leaves.
Light
H_2O
Sugar
3 Transpiration, the loss of water from leaves (mostly through stomata), creates a force within leaves that pulls xylem sap upward.
6 Sugars are transported as phloem sap to roots and other parts of the plant.
2 Water and minerals are transported upward from roots to shoots as xylem sap.
1 Roots absorb water and dissolved minerals from the soil.
H_2O
Minerals
O_2
CO_2
7 Roots exchange gases with the air spaces of soil, taking in O_2 and discharging CO_2. In cellular respiration, O_2 supports the breakdown of sugars.

Photosynthesis and Respiration



= ATP !!!

- Of the 15-20% of a herbaceous plant that is not water, about 95% of the dry weight is organic substance and the remaining 5% is inorganic substance.
  - Most of the organic material is carbohydrate, including cellulose in cell walls.
    - Thus, carbon, hydrogen, and oxygen are the most abundant elements in the dry weight of a plant.
    - Because some organic molecules contain nitrogen, sulfur, and phosphorus, these elements are also relatively abundant in plants.

Reminder : carbohydrates = energy ! (biofuels …)

- More than 50 chemical elements have been identified among the inorganic substances present in plants.
  - However, it is unlikely that all are essential.
- Roots are able to absorb minerals somewhat selectively, enabling the plant to accumulate essential elements that may be present in low concentrations in the soil.
  - However, the minerals in a plant reflect the composition of the soil in which the plant is growing.
  - Therefore, some of the elements in a plant are merely present, while others are essential.

2. Plants require nine macronutrients and at least eight micronutrients

- A particular chemical element is considered an **essential nutrient** if it is required for a plant to grow from a seed and complete the life cycle.
  - Cultures have identified 17 elements that are essential nutrients in all plants and a few other elements that are essential to certain groups of plants.

- Elements required by plants in relatively large quantities are **macronutrients**.
  - There are nine macronutrients in all, including the six major ingredients in organic compounds: carbon, oxygen, hydrogen, nitrogen, sulfur, and phosphorus.
  - The other three are potassium, calcium, and magnesium.

- Elements that plants need in very small amounts are **micronutrients**.
  - The eight micronutrients are iron, chlorine, copper, zinc, magnanese, molybdenum, boron, and nickel.
  - Most of these function as cofactors of enzymatic reactions.
  - For example, iron is a metallic component in cytochromes, proteins that function in the electron transfer chains of chloroplasts and mitochondria.
  - While the requirement for these micronutrients is so modest (only one atom of molybdenum for every 16 million hydrogen atoms in dry materials), a deficiency of a micronutrient can weaken or kill a plant.

Table 37.1 Essential Nutrients in Plants

Element	Form Available to Plants	Major Functions
Macronutrients		
Carbon	CO_2	Major component of plant's organic compounds
Oxygen	CO_2	Major component of plant's organic compounds
Hydrogen	H_2O	Major component of plant's organic compounds
Nitrogen	NO_3^-, NH_4^+	Component of nucleic acids, proteins, hormones, and coenzymes
Sulfur	SO_4^{2-}	Component of proteins, coenzymes
Phosphorus	$H_2PO_4^-$, HPO_4^{2-}	Component of nucleic acids, phospholipids, ATP, several coenzymes
Potassium	K^+	Cofactor that functions in protein synthesis; major solute functioning in water balance; operation of stomata
Calcium	Ca^{2+}	Important in formation and stability of cell walls and in maintenance of membrane structure and permeability; activates some enzymes; regulates many responses of cells to stimuli
Magnesium	Mg^{2+}	Component of chlorophyll; activates many enzymes
Micronutrients		
Chlorine	Cl^-	Required for water-splitting step of photosynthesis; functions in water balance
Iron	Fe^{3+}, Fe^{2+}	Component of cytochromes; activates some enzymes
Boron	$H_2BO_3^-$	Cofactor in chlorophyll synthesis; may be involved in carbohydrate transport and nucleic acid synthesis
Manganese	Mn^{2+}	Active in formation of amino acids; activates some enzymes; required for water-splitting step of photosynthesis
Zinc	Zn^{2+}	Active in formation of chlorophyll; activates some enzymes
Copper	Cu^+, Cu^{2+}	Component of many redox and lignin-biosynthetic enzymes
Molybdenum	MoO_4^{2-}	Essential for nitrogen fixation; cofactor that functions in nitrate reduction
Nickel	Ni^{2+}	Cofactor for an enzyme functioning in nitrogen metabolism

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Section B: The Role of Soil in Plant Nutrition

1. Soil characteristics are key environmental factors in terrestrial ecosystems
2. Soil conservation is one step toward sustainable agriculture

1. Soil characteristics are key environmental factors in terrestrial ecosystems

- The texture and chemical composition of soil are major factors determining what kinds of plants can grow well in a particular location.
  - Plants that grow naturally in a certain type of soil are adapted to its mineral content and texture and are able to absorb water and extract essential nutrients from that soil.
  - Plants, in turn, affect the soil.
  - The soil-plant interface is a critical component of the chemical cycles that sustain terrestrial ecosystems.

- Soil has its origin in the weathering of solid rock.
  - Water that seeps into crevices and freezes in winter fractures the rock, and acids dissolved in the water also help break down the rock.
  - Organisms, including lichens, fungi, bacteria, mosses, and the roots of vascular plants, accelerate the breakdown by the secretion of acids and as the expansion of their roots in fissures cracks rocks and pebbles.

- This activity eventually results in **topsoil**, a mixture of rock, living organisms, and **humus**, a residue of partially decayed organic material.
- Topsoil and other distinct soil layers, called **horizons**, are often visible in vertical profile.

Fig. 37.5

- Topsoil is home to an astonishing number and variety of organisms.
  - A teaspoon of soil has about 5 billion bacteria that cohabit with various fungi, algae and other protists, insects, earthworms, nematodes, and the roots of plants.
- The activities of these organisms affect the physical and chemical properties of the soil.
  - For example, earthworms aerate soil by their burrowing and add mucus that holds fine particles together.
  - Bacterial metabolism alters mineral composition of soil.
  - Plant roots extract water and minerals but also affect soil pH and reinforce the soil against erosion.

- Humus is the decomposing organic material formed by the action of bacteria and fungi on dead organisms, feces, fallen leaves, and other organic refuse.
  - Humus prevents clay from packing together and builds a crumbly soil that retains water but is still porous enough for the adequate aeration of roots.
  - Humus is also a reservoir of mineral nutrients that are returned to the soil by decomposition.

- After a heavy rainfall, water drains away from the larger spaces of the soil, but smaller spaces retain water because of its attraction for the soil particles, which have electrically charged surfaces.
  - Some water adheres so tightly to hydrophilic particles that it cannot be extracted by plants, but some water bound less tightly to the particles can be absorbed by roots.

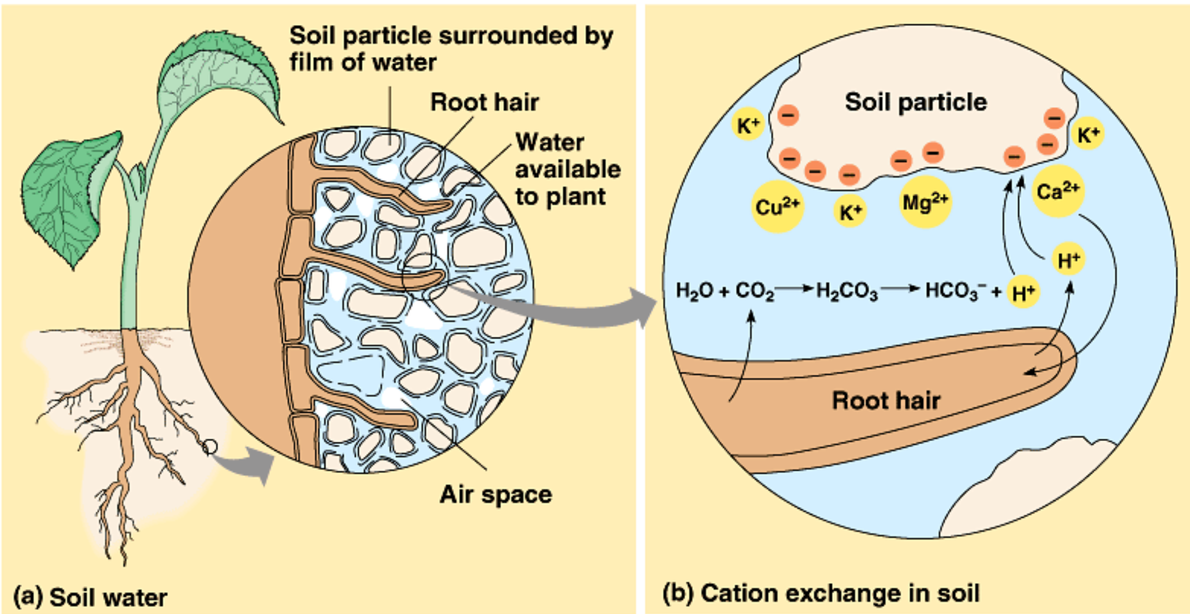

Fig. 37.6

- Many minerals, especially those with a positive charge, such as potassium (K^+), calcium (Ca^{2+}), and magnesium (Mg^{2+}), adhere by electrical attraction to the negatively charged surfaces of clay particles.
  - Clay in soil prevents the leaching of mineral nutrients during heavy rain or irrigation because of the large surface area for binding minerals.
  - Minerals that are negatively charges, such as nitrate (NO_3^-), phosphate ($H_2PO_4^-$), and sulfate (SO_4^{2-}), are usually not bound tightly to soil particles and thus tend to leach away more quickly.

- Some areas have become unfit for agriculture or wildlife as the result of human activities that contaminate the soil or groundwater with toxic heavy metals or organic pollutants.
  - In place of costly and disruptive remediation technologies, such as removal and storage of contaminated soils, **phytoremediation** takes advantage of the remarkable abilities of some plant species to extract heavy metals and other pollutants from the soil.
  - These are concentrated in the plant tissue where they can be harvested.
  - For example, alpine pennycress (*Thlaspi caerulescens*) can accumulate zinc in its shoots at concentrations that are 300 times the level that most plants tolerate.

Section C: The Special Case of Nitrogen as a Plant Nutrient

1. The metabolism of soil bacteria makes nitrogen available to plants
2. Improving the protein yield of crops is a major goal of agricultural research

1. The metabolism of soil bacteria makes nitrogen available to plants

- It is ironic that plants sometimes suffer nitrogen deficiencies, for the atmospheres is nearly 80% nitrogen.
  - Plants cannot use nitrogen in the form of N_2.
  - It must first be converted to ammonium (NH_4^+) or nitrate (NO_3^-).
  - In the short term, the main source of nitrogen is the decomposition of humus by microbes, including ammonifying bacteria.

- Nitrogen is lost from this local cycle when soil microbes called denitrifying bacteria converts NO_3^- to N_2 which diffuses to the atmosphere.
- Other bacteria, **nitrogen-fixing bacteria**, restock nitrogenous minerals in the soil by converting N_2 to NH_3 (ammonia), via **nitrogen fixation**.

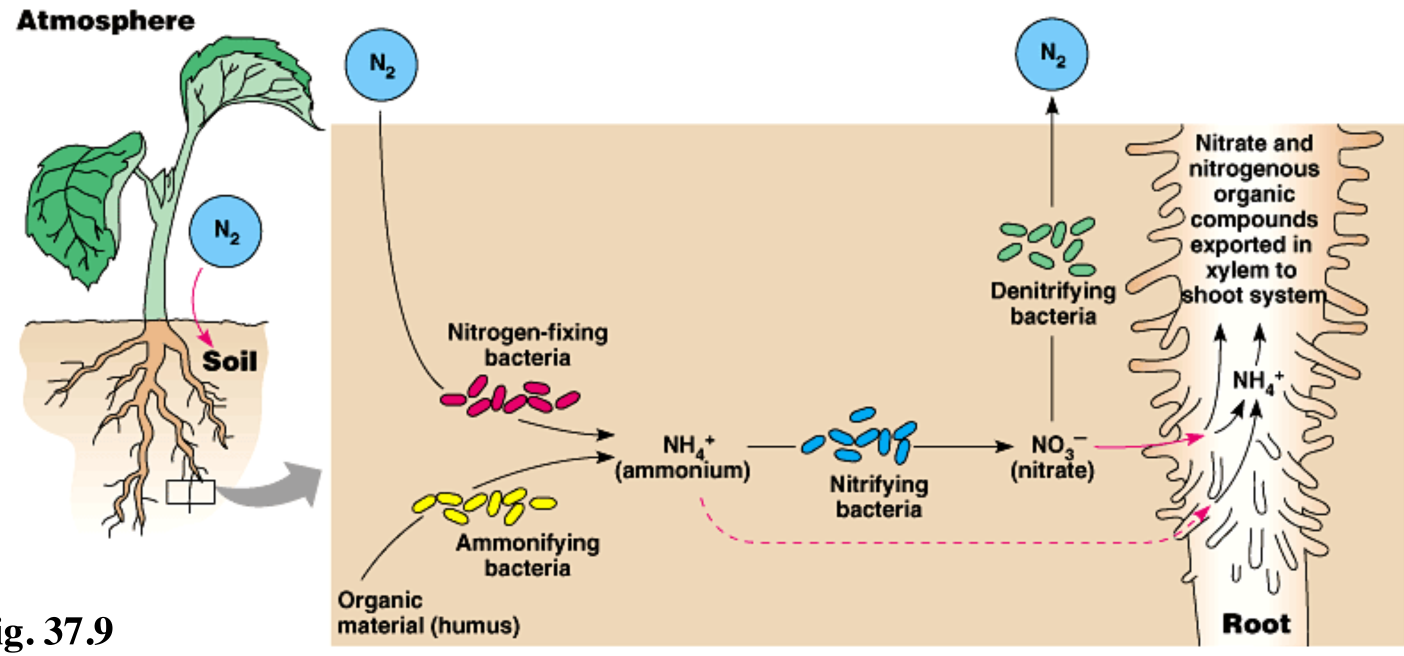

Fig. 37.9

- All life on Earth depends on nitrogen fixation, a process performed only by certain prokaryotes.
  - In the soil, these include several species of free-living bacteria and several others that live in symbiotic relationships with plants.
  - The reduction of N_2 to NH_3 is a complicated, multi-step process, catalyzed by one enzyme complex, **nitrogenase**:
  - $N_2 + 8e^- + 8H^+ + 16ATP \rightarrow 2NH_3 + H_2 + 16ADP + 16P_i$
  - Nitrogen-fixing bacteria are most abundant in soils rich in organic materials, which provide fuels for cellular respiration that supports this expensive metabolic process.

- In the soil solution, ammonia picks up another hydrogen ion to form ammonium (NH_4^+), which plants can absorb.
- However, nitrifying bacteria in the soil quickly oxidize ammonium to nitrate (NO_3^-) which plants can also absorb.
  - After nitrate is absorbed by roots, plant enzymes reduce nitrate back to ammonium, which other enzymes then incorporate into amino acids and other organic compounds.
  - Most plant species export nitrogen from roots to shoots, via the xylem, in the form of nitrate or organic compounds that have been synthesized in the roots.

2. Improving the protein yield of crops is a major goal of agricultural research

- The ability of plants to incorporate fixed nitrogen into proteins and other organic substances has a major impact on human welfare.
  - Protein deficiency is the most common form of malnutrition.
  - Either by choice or economic necessity, the majority of the world's people have a predominately vegetarian diet.
  - Unfortunately, plants are a poor source of protein and may be deficient in one or more of the amino acids that humans need from their diet.

- Plant breeding has resulted in new varieties of corn, wheat, and rice that are enriched in protein.
    - However, many of these “super” varieties have an extraordinary demand for nitrogen which is usually supplied by commercial fertilizer produced by energy-intensive industrial production.
        - Generally, the countries that most need high-protein crops are the ones least able to afford to pay for the fossil fuels that power the factories.

- Agricultural scientists are pursuing a variety of strategies to overcome this protein deficiency.
  - For example, the use of new catalysts based on those used by nitrogenase to fix nitrogen may make commercial production of nitrogen fertilizers cheaper.
  - Alternatively, improvements of the productivity of symbiotic nitrogen fixation may potentially increase protein yields of crops.

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Section D: Nutritional Adaptations: Symbiosis of Plants and Soil Microbes

1. Symbiotic nitrogen fixation results from intricate interactions between roots and bacteria
2. Mycorrhizae are symbiotic associations of roots and fungi that enhance plant nutrition
3. Mycorrhizae and root nodules may have an evolutionary relationship

Introduction

- The roots of plants belong to subterranean communities that include a diversity of other organisms.
  - Among these are certain species of bacteria and fungi that have coevolved with specific plants, forming symbiotic relationships with roots that enhance the nutrition of both partners.
  - The two most important examples are symbiotic nitrogen fixation (roots and bacteria) and the formation of mycorrhizae (roots and fungi).

1. Symbiotic nitrogen fixation results from intricate interactions between roots and bacteria

- Many plant families include species that form symbiotic relationships with nitrogen-fixing bacteria.
  - This provides their roots with a built-in source of fixed nitrogen for assimilation into organic compounds.
  - Much of the research on this symbiosis has focused the agriculturally important members of the legume family, including peas, beans, soybeans, peanuts, alfalfa, and clover.

- A legume's roots have swellings called **nodules**, composed of plant cells that contain nitrogen-fixing bacteria of the genus *Rhizobium*.
  - Inside the nodule, *Rhizobium* bacteria assume a form called **bacteriods**, which are contained within vesicles formed by the root cell.

Fig. 37.10

- The development of root nodules begins after bacteria enter the root through an infection thread.

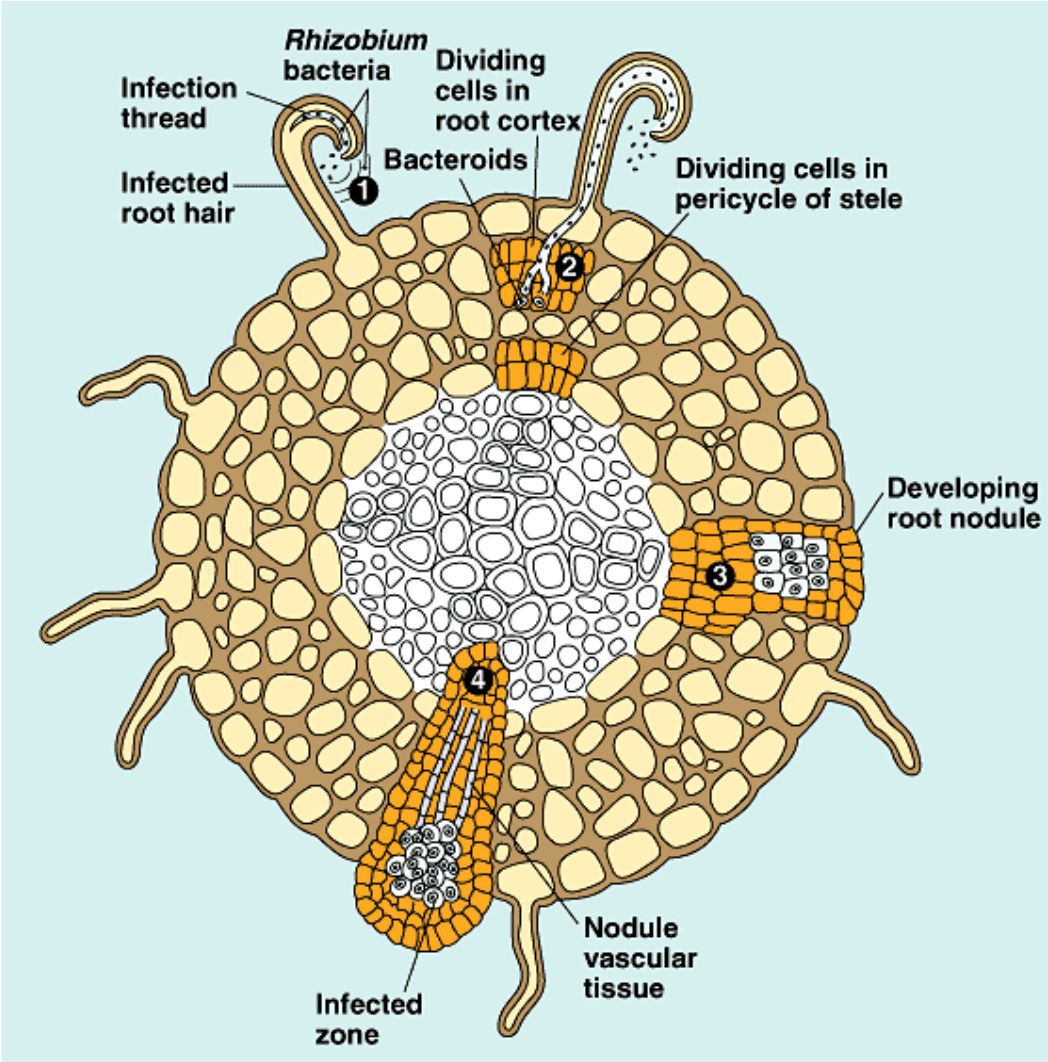

Fig. 37.11

(1) Chemical signals from the root attract the *Rhizobium* bacteria and chemical signals from the bacteria lead to the production of an infection thread.

(2) The bacteria penetrate the root cortex within the infection thread.

(3) Growth in cortex and pericycle cells which are “infected” with bacteria in vesicles continues until the two masses of dividing cells fuse, forming the nodule.

(4) As the nodule continues to grow, vascular tissue connects the nodule to the xylem and phloem of the stele, providing nutrients to the nodule and carrying away nitrogenous compounds for the rest of the plant.

- The symbiotic relationship between a legume and nitrogen-fixing bacteria is mutualistic, with both partners benefiting.
  - The bacteria supply the legume with fixed nitrogen.
    - Most of the ammonium produced by symbiotic nitrogen fixation is used by the nodules to make amino acids, which are then transported to the shoot, and leaves via the xylem.
  - The plant provides the bacteria with carbohydrates and other organic compounds.

- The common agricultural practice of crop rotation exploits symbiotic nitrogen fixation.
  - One year a nonlegume crop such as corn is planted, and the following year alfalfa or another legume is planted to restore the concentration of fixed soil nitrogen.
  - Often, the legume crop is not harvested but is plowed under to decompose as “green manure.”
  - To ensure the formation of nodules, the legume seeds may be soaked in a culture of the correct *Rhizobium* bacteria or dusted with bacterial spores before sowing.

Fig. 37.12

2. Mycorrhizae are symbiotic associations of roots and fungi that enhance plant nutrition

- **Mycorrhizae** ("fungus roots") are modified roots, consisting of symbiotic associations of fungi and roots.
- The symbiosis is mutualistic.
  - The fungus benefits from a hospitable environment and a steady supply of sugar donated by the host plant.

- The fungi provide several potential benefits to the host plants.
  - First, the fungus increases the surface area for water uptake and selectively absorbs phosphate and other minerals in the soil and supplies them to the plant.
  - The fungi also secrete growth factors that stimulate roots to grow and branch.
  - The fungi produce antibiotics that may help protect the plant from pathogenic bacteria and pathogenic fungi in the soil.

- Almost all plant species produce mycorrhizae.
  - This plant-fungus symbiosis may have been one of the evolutionary adaptations that made it possible for plants to colonize land in the first place.
    - Fossilized roots from some of the earliest land plants include mycorrhizae.
  - Mycorrhizal fungi are more efficient at absorbing minerals than roots, which may have helped nourish pioneering plants, especially in the nutrient poor soils present when terrestrial ecosystems were young.
  - Today, the first plants to become established on nutrient-poor soils are usually well endowed with mycorrhizae

PLANT NUTRITION

Section E: Nutritional Adaptations: Parasitism and Predation by Plants

1. Parasitic plants extract nutrients from other plants
2. Carnivorous plants supplement their mineral nutrition by digesting animals

1. Parasitic plants extract nutrients from other plants

- A variety of plants parasitize other plants to extract nutrients that supplement or even replace the production of organic molecules by photosynthesis by the parasitic plant.
  - An example of the former is mistletoe which supplements its nutrition by using projections called haustoria to siphon xylem sap from the vascular tissue of the host tree.

- Both dodder and Indian pipe are parasitic plants that do not perform photosynthesis at all.
  - The haustoria (modified roots) of dodder tap into the host's vascular tissue for water and nutrients.
  - Indian pipe obtains its nutrition indirectly via its association with fungal hyphae of the host tree's mycorrhizae.

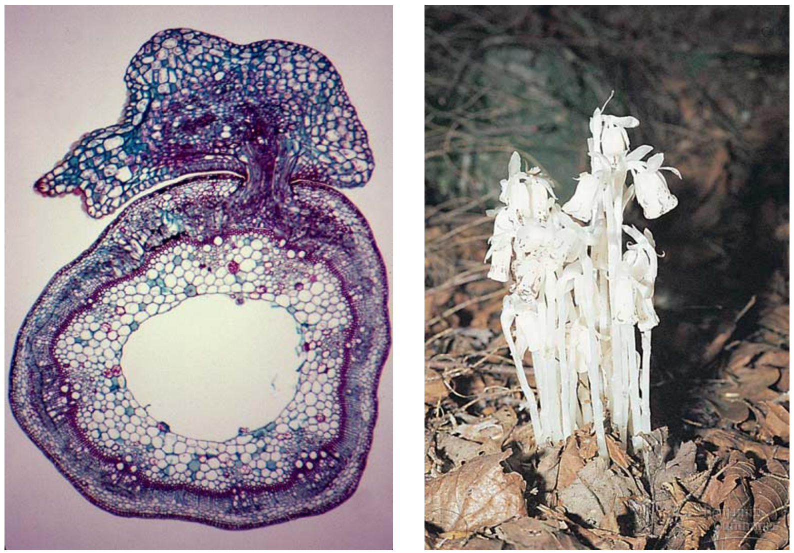

Fig. 37.15

- Plants called epiphytes are sometimes mistaken for parasites.
  - An epiphyte is an autotrophic plant that nourishes itself but grows on the surface of another plant, usually on the branches or trunks of trees.
  - While an epiphyte is anchored to its living substratum, it absorbs water and minerals mostly from rain that falls on its leaves.
  - Examples of epiphytes are staghorn ferns, some mosses, Spanish moss, and many species of bromeliads and orchids.

2. Carnivorous plants supplement their mineral nutrition by digesting animals

- Living in acid bogs and other habitats where soil conditions are poor are plants that fortify themselves by occasionally feeding on animals.
  - These carnivorous plants make their own carbohydrates by photosynthesis, but they obtain some of their nitrogen and minerals by killing and digesting insects and other small animals.

- Various types of insect traps have evolved by the modification of leaves.
    - The traps are usually equipped with glands that secrete digestive juices.

Fig. 37.16