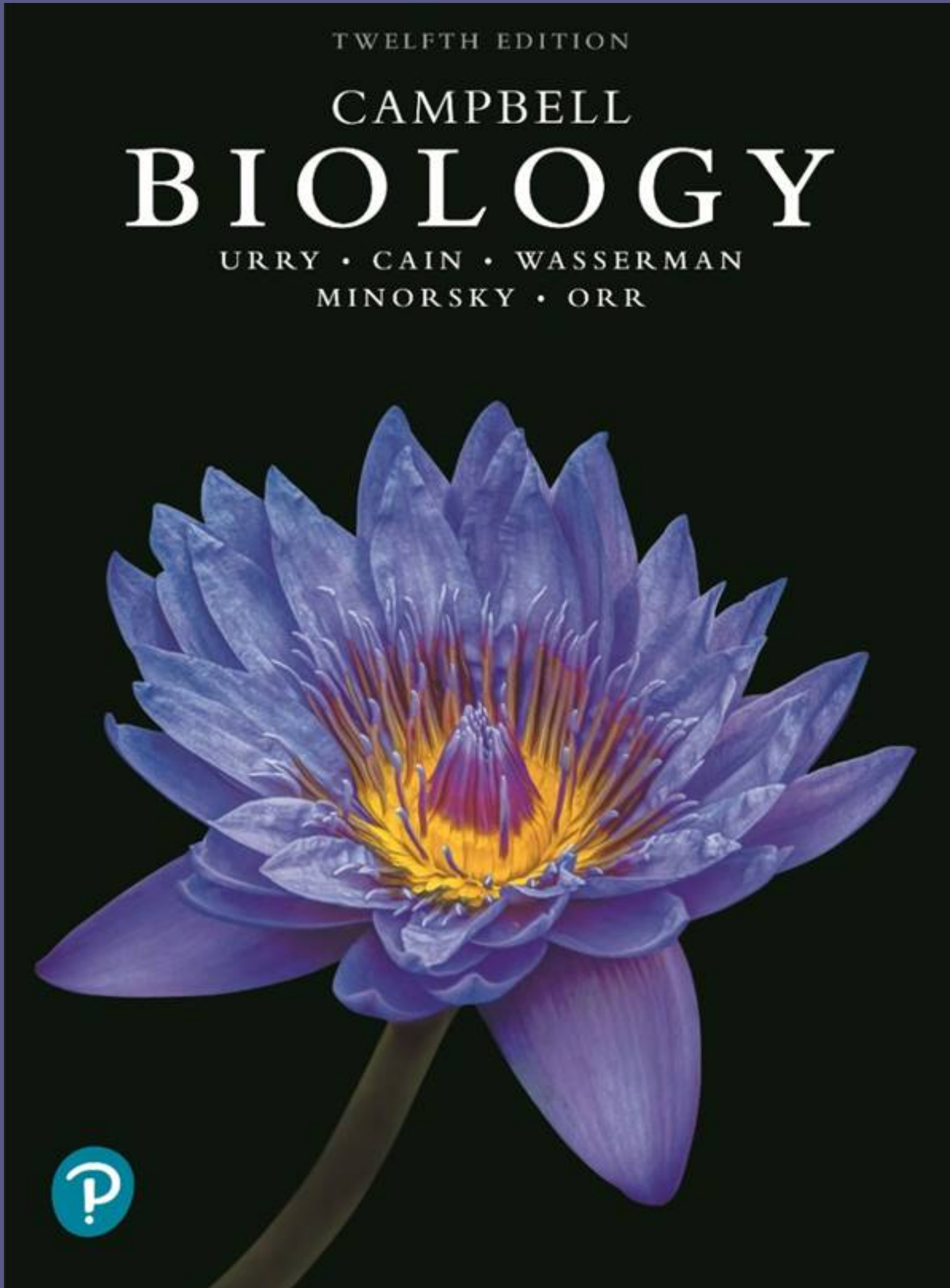


Chapter 37

Soil and Plant Nutrition

Lecture Presentations by
Nicole Tunbridge and
Kathleen Fitzpatrick

Why do plants need minerals from the soil?

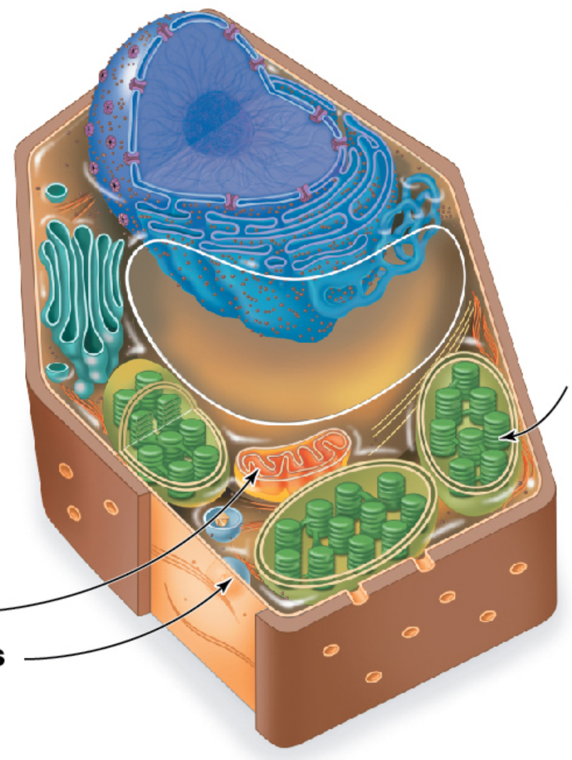
- Nitrogen, phosphorus, potassium, and other minerals are essential for plant growth
- They play important roles in both cell structure and cell function

Figure 37.1a

Figure 37.1b

Why do plants need minerals from the soil?

Nitrogen, phosphorus, potassium, and other minerals are essential for plant growth because of their roles in the structure and function of plant cells.



Nitrogen is a component of
- **DNA and RNA (throughout the cell)**
- **proteins (throughout the cell)**
- **chlorophyll**

Phosphorus is a component of
- **DNA and RNA (throughout the cell)**
- **ATP produced by mitochondria**
- **phospholipids in cell membranes**

Potassium is a cofactor for enzymes used throughout the cell; plays a major role in maintaining turgor

CONCEPT 37.1: Soil contains a living, complex ecosystem

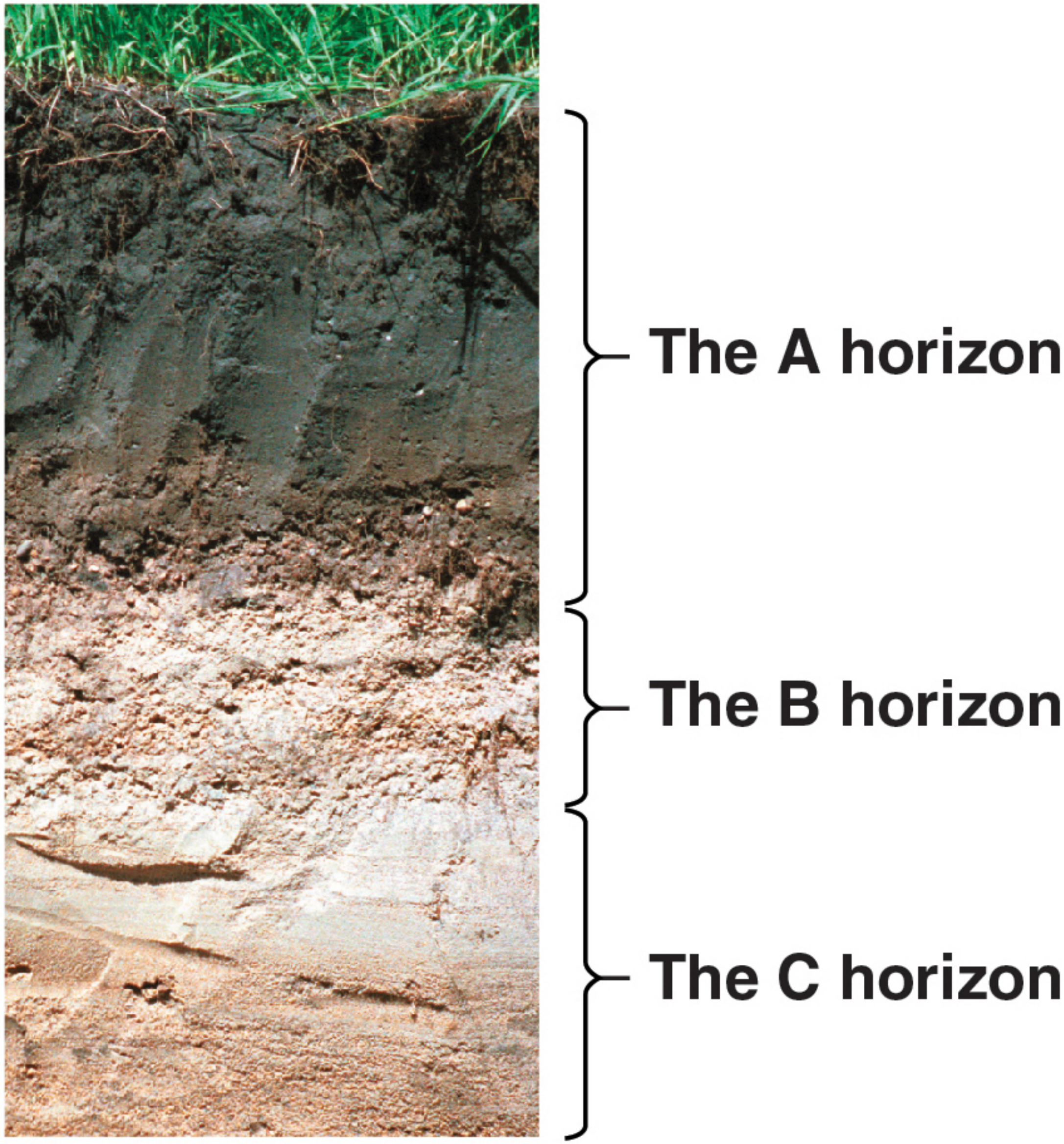
- Plants obtain most of their water and minerals from the upper layers of soil
- Living organisms play an important role in these soil layers
- The basic physical properties of soil are texture and composition

Soil Texture

- Rock is fractured into soil particles by freezing water, chemical breakdown, and penetration by plant roots
- Soil particles vary in size from the largest, sand (0.02–2 mm diameter), to silt (0.002–0.02 mm), and finally clay (<0.002 mm)

- Soil is stratified into layers called **soil horizons**
- The A horizon, or **topsoil**, consists of mineral particles, living organisms, and **humus**, which is decaying organic material
- The B horizon has less organic matter and is less weathered than the A horizon
- The C horizon is mainly partially broken down rock

Figure 37.2



- Topsoil is the most important layer for plant growth
- **Loams** are the most fertile topsoils and contain equal amounts of sand, silt, and clay
- Soil solution, water and dissolved minerals, is retained in the pores between small soil particles
- Water drains freely from the large spaces between sand particles

- Sandy soils don’t retain enough water to support plant growth; clay soils retain too much and lack sufficient oxygen to support plant roots
- The most fertile topsoils typically have pores containing about half water and half air
- The physical properties of soil can be amended by adding peat moss, compost, manure, or sand

Topsoil Composition

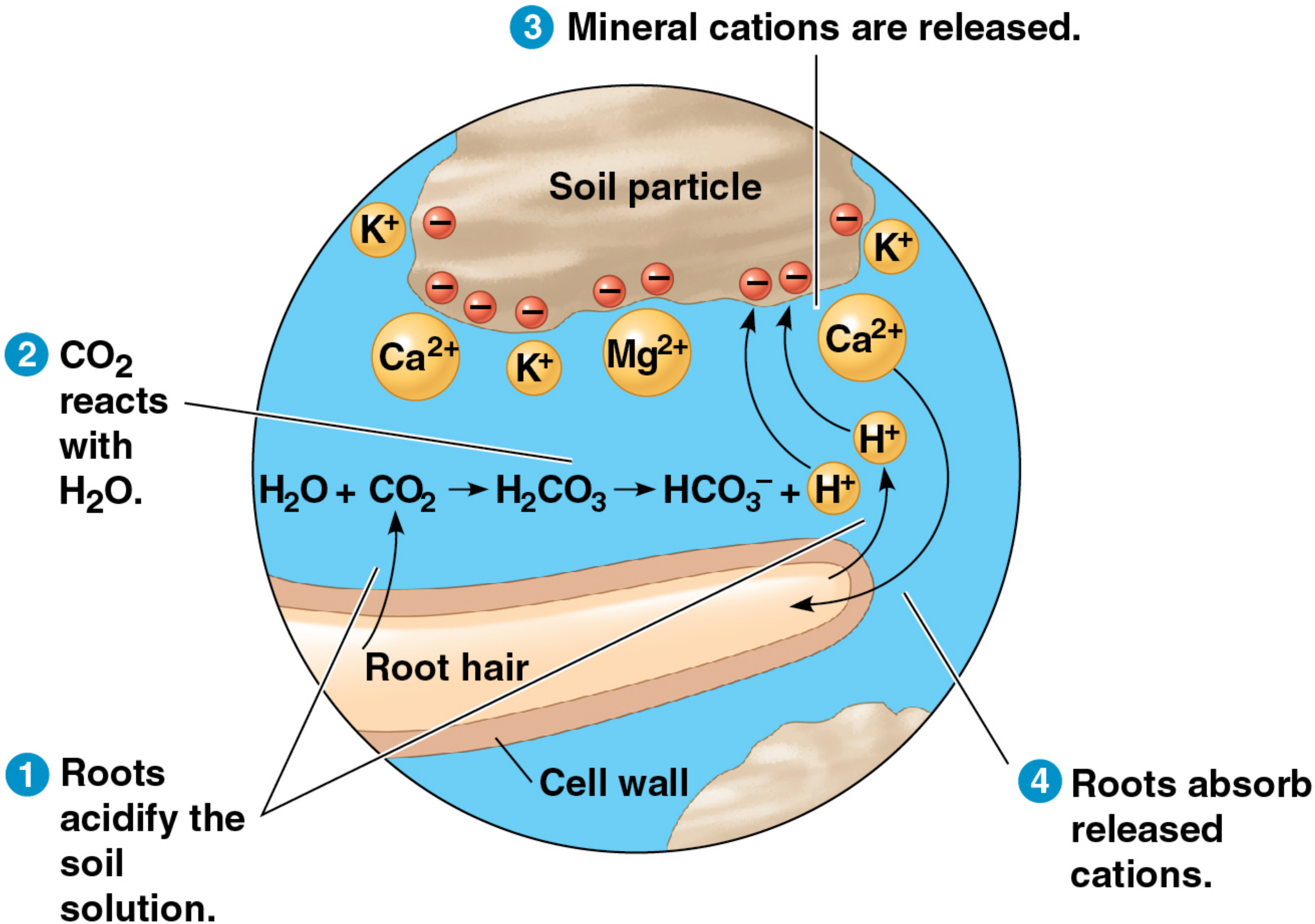
- In addition to water and air, topsoil is composed of inorganic (mineral) and organic chemical components

Inorganic Components

- Most particles in productive soils are negatively charged ions (anions)
- Many plant nutrients are also anions (for example NO_3^-, $H_2PO_4^-$, SO_4^{2-}), and cannot bind to soil particles
- Cations (for example K^+, Ca^{2+}, and Mg^{2+}) adhere to negatively charged soil particles

- During **cation exchange**, cations are displaced from soil particles by other cations, particularly H^+
- Displaced cations enter the soil solution and can be taken up by plant roots
- Negatively charged ions do not bind with soil particles and can be lost from the soil by leaching
- The more clay and organic matter in the soil, the greater the cation exchange capacity

Figure 37.3



3 Mineral cations are released.
Soil particle
K+
Ca2+
K+
Mg2+
K+
Ca2+
H+
2 CO2 reacts with H2O.
H2O + CO2 → H2CO3 → HCO3− + H+
Root hair
Cell wall
1 Roots acidify the soil solution.
4 Roots absorb released cations.

Animation: How Plants Obtain Minerals from Soil

Organic Components

- Humus prevents packing of clay particles, and forms a crumbly soil that retains water but allows adequate root aeration
- It also increases cation exchange capacity of soil
- Organic components provide a reservoir of nutrients that are gradually released through decomposition

- Topsoil contains a diversity of organisms including bacteria, fungi, algae and other protists, insects, earthworms, nematodes, and plant roots
- The activities of these organisms affect the physical and chemical properties of soil
  - For example, earthworms mix and clump soil particles, improving gas diffusion and water retention

Soil Conservation and Sustainable Agriculture

- Cultivating crops in the same location over many seasons depletes nutrients and reduces crop yields
- **Fertilization**, the addition of mineral nutrients to the soil, combats this problem
- Soil management, by fertilization and other practices, allowed for sedentary agriculture and the formation of permanent villages

- In contrast with natural ecosystems, agriculture depletes the mineral content of soil, taxes water reserves, and encourages erosion
- Mismanagement of soils during the American Dust Bowl (1930s) resulted in widespread soil erosion
- Exposed fertile soil was blown away in “black blizzards,” rendering farmland useless

Figure 37.4

- At present, 30% of the world's farmland has reduced productivity due to soil mismanagement
- The goal of **sustainable agriculture** is to use farming methods that are conservation-minded, environmentally safe, and profitable

Irrigation

- Irrigation is a huge drain on water resources when used for farming in arid regions
  - For example, 75% of global freshwater use is devoted to agriculture
- The primary source of irrigation water is underground water reserves called *aquifers*
- Aquifer depletion can result in *land subsidence*, gradual settling or sudden sinking of land

Figure 37.5

- Irrigation can lead to *salinization*, the concentration of salts in soil as water evaporates
- Salinization reduces the water potential of the soil solution and diminishes water uptake by plants
- *Drip irrigation* reduces water use and salinization by slowly releasing water directly at the root zone

Fertilization

- Repeated harvesting of crop plants can lead to nutrient depletion in agricultural soils
- Fertilization replaces mineral nutrients that have been lost from the soil
- Commercial fertilizers are enriched in nitrogen (N), phosphorus (P), and potassium (K)

- Organic fertilizers, composed of manure, fishmeal, or compost, gradually release N, P, and K as they decompose
- Minerals in commercial fertilizers are immediately available, but may not be retained by soil for long
- Minerals not absorbed by roots are leached from soil and carried to aquatic ecosystems in runoff
- Resulting algal blooms deplete oxygen and kill fish

Adjusting Soil pH

- Soil pH affects mineral availability through cation exchange and the chemical form of minerals
- Cations are more available in slightly acidic soil, as H^+ ions displace mineral cations from clay particles
- The availability of different minerals varies with pH
  - For example, at pH 8, plants can absorb calcium but not iron

- At soil pH 5 or lower, toxic aluminum ions (Al^{3+}) become more soluble
- Uptake of Al^{3+} stunts root growth and prevents calcium uptake
- Some plants can cope with Al^{3+} by secreting organic anions that bind with it, rendering it harmless

Controlling Erosion

- Water and wind erosion are major causes of topsoil removal and loss of soil nutrients
- Erosion can be reduced by planting trees as windbreaks, terracing hillside crops, and cultivating in a contour pattern
- **No-till agriculture** also reduces erosion by creating furrows for seeds and fertilizer with minimal soil disturbance

Figure 37.6

Phytoremediation

- Some areas are unfit for agriculture due to contamination of soil or groundwater with pollutants
- **Phytoremediation** involves the uptake and concentration of soil pollutants in plant tissues that are then removed for safe disposal
- This nondestructive biotechnology can help reclaim contaminated areas

CONCEPT 37.2: Plant roots absorb many types of essential elements from the soil

- Water, air, and soil minerals all contribute to plant growth
  - 80–90% of a plant's fresh mass is water
  - 96% of a plant's dry mass is from CO_2 assimilated into carbohydrates during photosynthesis
  - 4% of a plant's dry mass is inorganic substances from soil

Essential Elements

- Not all of the more than 50 chemical elements identified in plants are essential
- There are 17 **essential elements**, chemical elements required for a plant to complete its life cycle and reproduce
- Researchers use **hydroponic culture** to determine which chemical elements are essential

Figure 37.7

Control: Solution containing all minerals

Experimental: Solution without iron

- Nine of the essential elements are called **macronutrients** because plants require them in relatively large amounts
- The macronutrients are carbon, oxygen, hydrogen, nitrogen, phosphorus, sulfur, potassium, calcium, and magnesium
- Nitrogen contributes the most to plant growth and crop yields

- The remaining essential elements, **micronutrients**, are required only in very small amounts
- The micronutrients include chlorine, iron, boron, manganese, zinc, copper, nickel, and molybdenum
- Plants with C_4 and CAM photosynthetic pathways also require sodium
- Micronutrients function as cofactors, nonprotein helpers in enzymatic reactions

- Many animals, including humans, get their essential mineral nutrients from plants
- People who receive enough calories, but lack other dietary factors, such as essential minerals, are malnourished

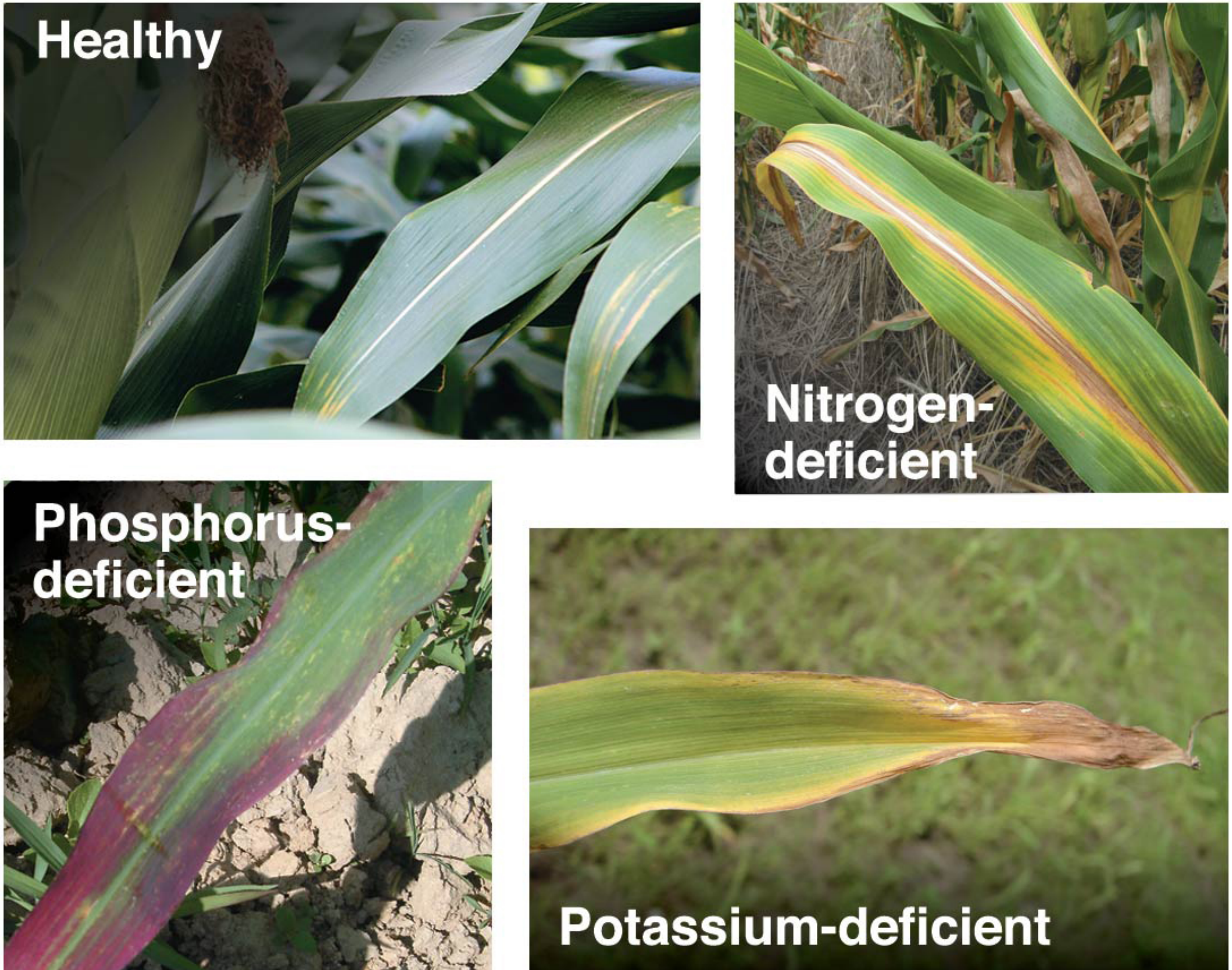
Table 37.1

Element (Form Primarily Absorbed by Plants)	% Mass in Dry Tissue	Major Function(s)	Early Visual Symptom(s) of Nutrient Deficiencies
Macronutrients			
Carbon (CO_2)	45%	Major component of organic compounds	Poor growth
Oxygen(CO_2)	45%	Major component of organic compounds	Poor growth
Hydrogen (H_2O)	6%	Major component of organic compounds	Wilting, poor growth
Nitrogen (NO_3^-, NH_4^+)	1.5%	Component of nucleic acids, proteins, and chlorophyll	Chlorosis at tips of older leaves (common in heavily cultivated soils or soils low in organic material)
Potassium (K^+)	1.0%	Enzyme cofactor; major solute functioning in water balance; operation of stomata	Mottling of older leaves, drying of leaf edges; weak stems; roots poorly developed (common in acidic or sandy soils)
Calcium (Ca^{2+})	0.5%	Important component of middle lamella and cell walls; maintains membrane function; signal transduction	Crinkling of young leaves; death of terminal buds (common in acidic or sandy soils)
Magnesium (Mg^{2+})	0.2%	Component of chlorophyll; cofactor of many enzymes	Chlorosis between veins, found in older leaves (common in acidic or sandy soils)
Phosphorus ($H_2PO_4^-$, HPO_4^{2-})	0.2%	Component of nucleic acids, phospholipids, ATP	Healthy appearance but very slow development; thin stems; purpling of veins; poor flowering and fruiting (common in acidic, wet, or cold soils)
Sulfur (SO_4^{2-})	0.1%	Component of proteins	General chlorosis in young leaves (common in sandy or very wet soils)
Micronutrients			
Chlorine (Cl^-)	0.01%	Photosynthesis (water-splitting); functions in water balance	Wilting; stubby roots; leaf mottling (uncommon)
Iron (Fe^{3+}, Fe^{2+})	0.01%	Respiration; photosynthesis: chlorophyll synthesis; N_2 fixation	Chlorosis between veins, found in young leaves (common in basic soils)
Manganese (Mn^{2+})	0.005%	Active in formation of amino acids; activates some enzymes; required for water-splitting step of photosynthesis	Chlorosis between veins, found in young leaves (common in basic soils rich in humus)
Boron ($H_2BO_3^-$)	0.002%	Cofactor in chlorophyll synthesis; role in cell wall function; pollen tube growth	Death of meristems; thick, leathery, and discolored leaves (occurs in any soil; most common micronutrient deficiency)
Zinc (Zn^{2+})	0.002%	Active in formation of chlorophyll; cofactor of some enzymes; needed for DNA transcription	Reduced internode length; crinkled leaves (common in some geographic regions)
Copper (Cu^+, Cu^{2+})	0.001%	Component of many redox and lignin-biosynthetic enzymes	Light green color throughout young leaves, with drying of leaf tips; roots stunted and excessively branched (common in some geographic regions)
Nickel (Ni^{2+})	0.001%	Nitrogen metabolism	General chlorosis in all leaves; death of leaf tips (common in acidic or sandy soils)
Molybdenum (MoO_4^{2-})	0.0001%	Nitrogen metabolism	Death of root and shoot tips; chlorosis in older leaves (common in acidic soils in some geographic areas)

Symptoms of Mineral Deficiency

- Symptoms of mineral deficiency depend on the nutrient’s function and mobility within the plant
- Deficiency of a mobile nutrient usually affects older organs more than young ones
- Deficiency of a less mobile nutrient usually affects younger organs more than older ones
- The most common deficiencies are those of nitrogen, potassium, and phosphorus

Figure 37.8


Healthy
Nitrogen-deficient
Phosphorus-deficient
Potassium-deficient

Global Climate Change and Food Quality

- Global food production is predicted to increase in response to rising CO_2 and temperatures, but only in certain parts of the world
- The nutritional quality of wild and crop plants has declined, possibly due to insufficient uptake of nutrients to keep pace with increased carbon fixation
- Pollinators declines may be linked to declining quality of their food source

CONCEPT 37.3: Plant nutrition often involves relationships with other organisms

- Plants have a mutualistic relationships with soil bacteria and fungi
  - Dead plants provide energy needed by soil-dwelling microorganisms
  - Secretions from living roots support a wide variety of microbes in the near-root environment

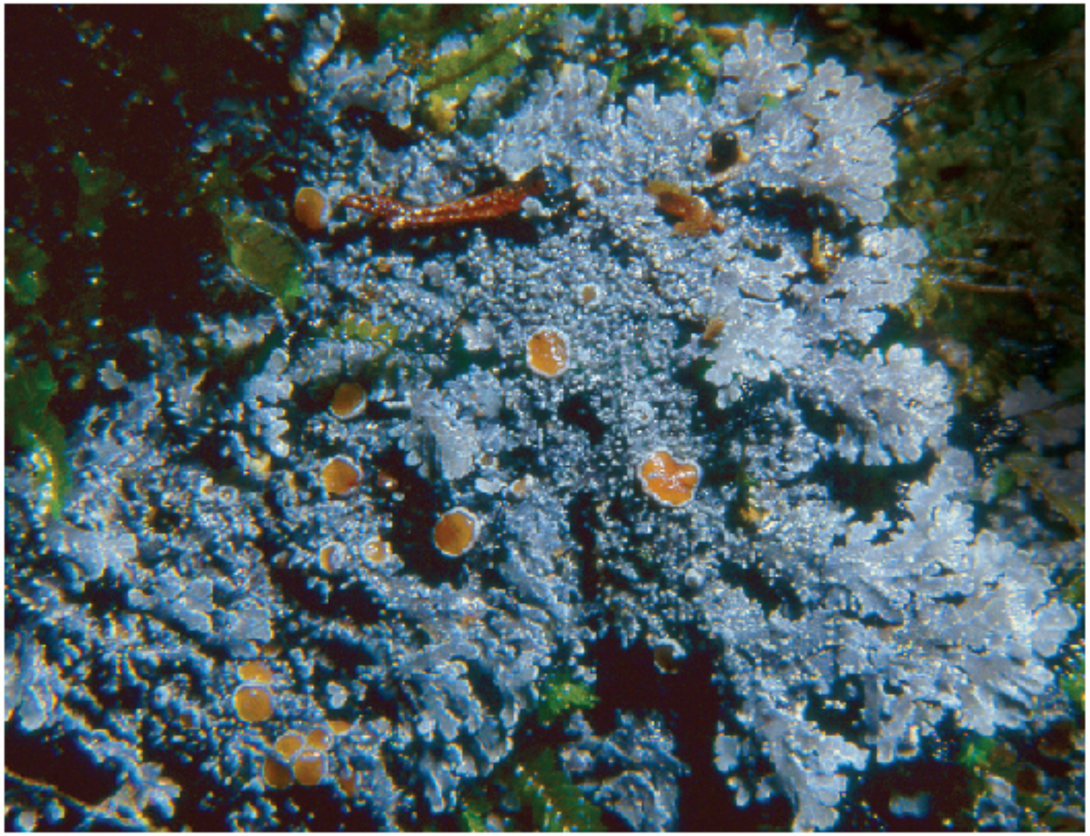
- Many mutually beneficial relationships occur between species from different kingdoms or domains

Figure 37.9 Make Connections: Mutualism Across Kingdoms and Domains

Fungus–Bacterium

- A lichen is a mutualistic association between a fungus and a photosynthetic partner
- The cyanobacterium provide carbohydrates, while the fungus provides anchorage, protection, minerals, and water in return

Fungus–Bacterium



The lichen *Peltigera*

Animal–Bacterium

- Most puffer fish form a mutualistic association with a bacterium that produces a nerve toxin called tetrodotoxin
- The fish gains a chemical defense, while the bacteria live in a high nutrient, low competition environment

Figure 37.9b

Animal–Bacterium

Plant–Bacterium

- The floating fern *Azolla* forms mutualistic associations with nitrogen-fixing cyanobacteria
- The cyanobacterium provides the fern with nitrogen, while the fern provides it with carbohydrates

Plant–Bacterium

The floating fern *Azolla*

Animal–Fungus

- Leaf-cutter ants harvest leaves to provide nutrition to fungal gardens in their nests
- In return for the nutrients provided to the fungus in the leaves, the ants are able to eat part of the fungus

Animal–Fungus

Ants tending a fungal garden in a nest

Plant–Fungus

- Most plant species are associated with mycorrhizal fungi
- The fungus absorbs carbohydrates in return for expanding the absorptive surface of the plant roots for uptake of water and minerals

Plant–Fungus

A fungus growing on the root of a sorghum plant (SEM)

Plant–Animal

- Some species of *Acacia* plants provide carbohydrate–rich nectar to ants that protect them from predators and competitors

Plant–Animal

Protective ant harvesting nectar

Bacteria and Plant Nutrition

- A variety of soil bacteria play roles in plant nutrition
- Some are mutualists; others increase nutrient availability by enhancing decomposition

Rhizobacteria

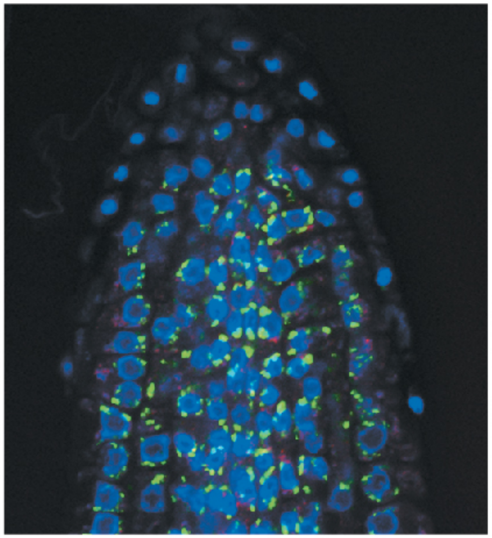
- The layer of soil closely surrounding the plant's roots is the **rhizosphere**
- **Rhizobacteria** are bacteria that live in close association with plant roots or in the rhizosphere
- Some rhizobacteria are free-living; others are **endophytes**, nonpathogenic bacteria that live between the cells of host plant tissues

- Endophytes and rhizobacteria depend on nutrients secreted by plant cells and, in return, help to enhance plant growth by
  - producing antibiotics that protect roots from disease
  - absorbing toxic metals or increasing nutrient availability
  - converting nitrogen gas into forms usable by the plant
  - producing chemicals that stimulate plant growth

- The species composition of bacterial communities living endophytically and in the rhizosphere vary markedly

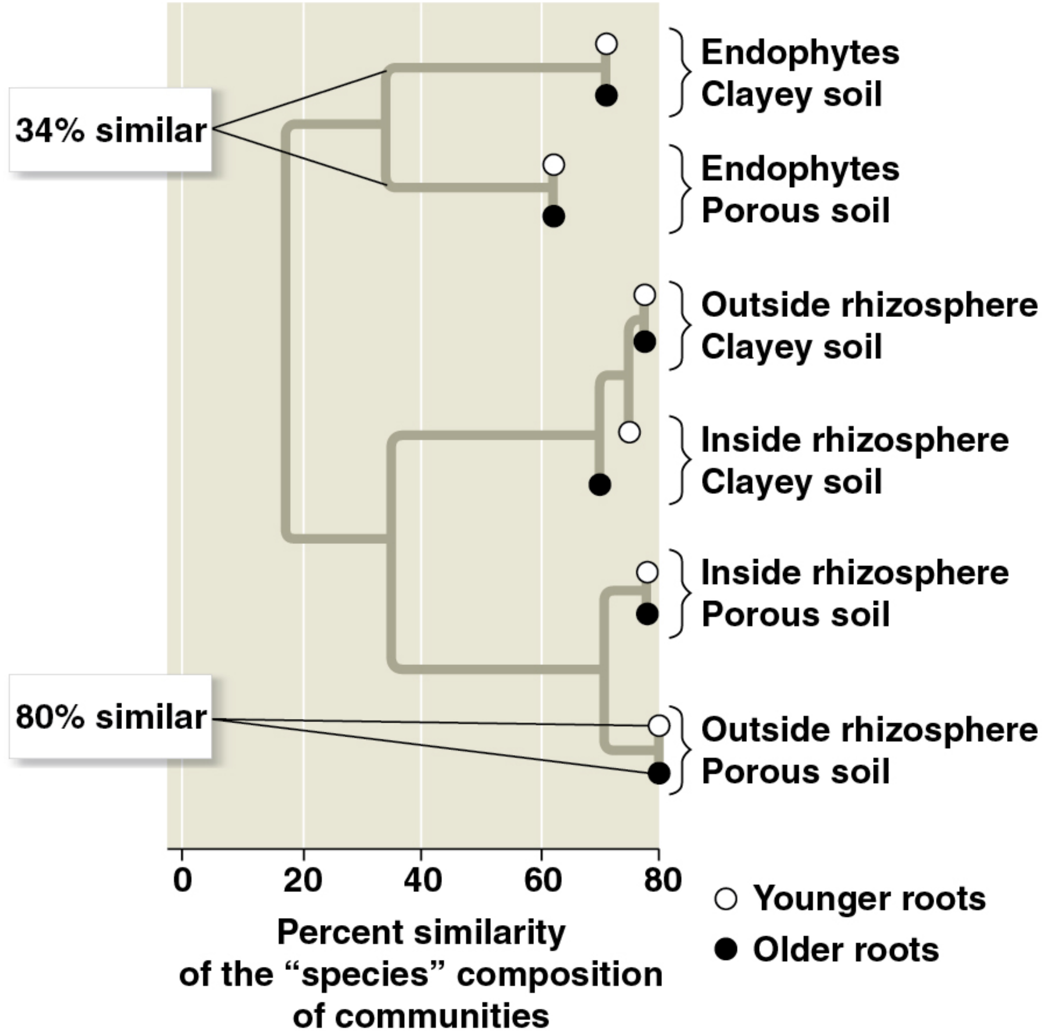
Figure 37.10

Experiment



Bacteria (green) on surface of root (fluorescent LM)

Results



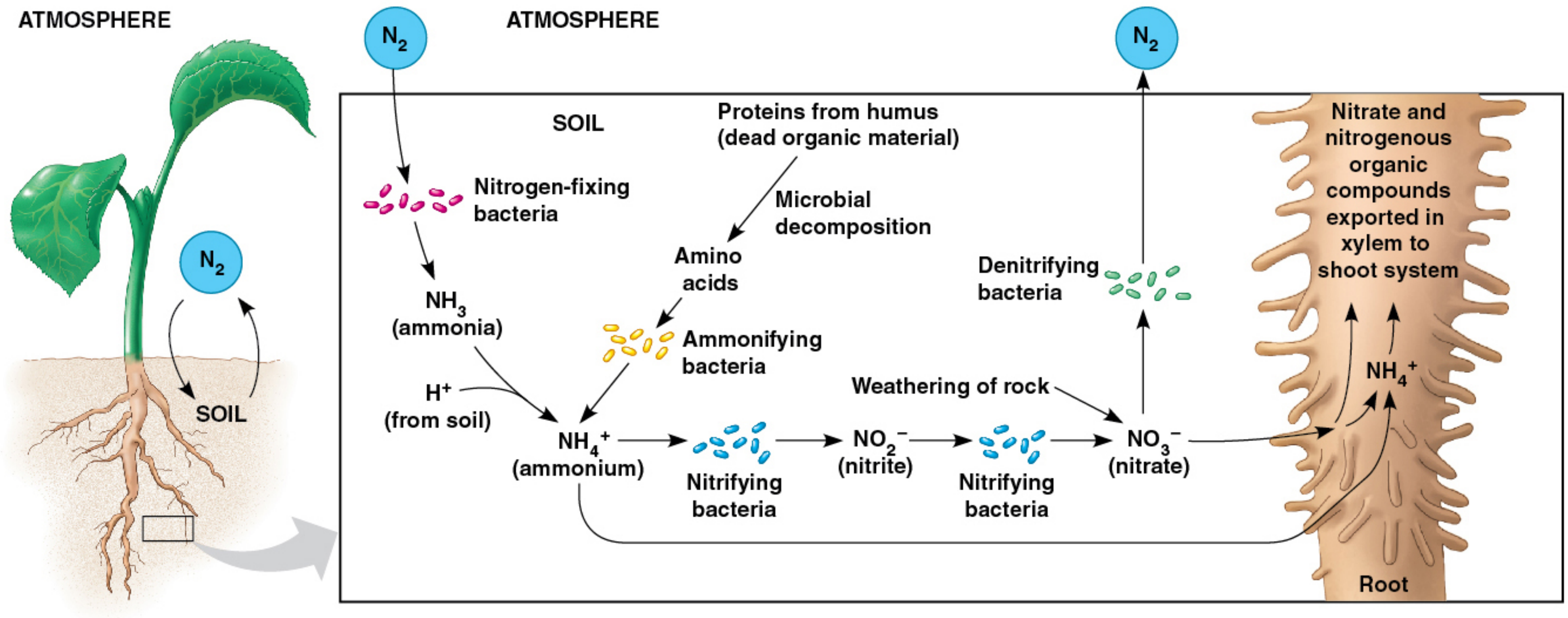
Data from D. S. Lundberg et al., Defining the core Arabidopsis thaliana root microbiome, *Nature* 488:86–94 (2012).

Bacteria in the Nitrogen Cycle

- Because it is required in large amounts to produce proteins and nucleic acids, nitrogen deficiency can be the most limiting to plant growth
- Plants can absorb nitrogen as NO_3^- or NH_4^+
- Some soil nitrogen derives from inorganic sources, but most comes from the activity of soil bacteria

- The **nitrogen cycle** is a series of natural processes that transform nitrogen and nitrogen-containing compounds

Figure 37.11



ATMOSPHERE
N_2
SOIL
ATMOSPHERE
N_2
N_2
SOIL
Proteins from humus
(dead organic material)
Nitrogen-fixing
bacteria
Microbial
decomposition
Amino
acids
NH_3
(ammonia)
Ammonifying
bacteria
Denitrifying
bacteria
Nitrate and
nitrogenous
organic
compounds
exported in
xylem to
shoot system
H^+
(from soil)
Weathering of rock
NH_4^+
NH_4^+
(ammonium)
NO_2^-
(nitrite)
NO_3^-
(nitrate)
Nitrifying
bacteria
Nitrifying
bacteria
Root

- Plants commonly acquire nitrogen as nitrate (NO_3^-)
- Soil NO_3^- is formed in a two-step process called nitrification
  - Nitrifying bacteria oxidize ammonia (NH_3) to nitrite (NO_2^-)
  - Different nitrifying bacteria oxidize NO_2^- to NO_3^-
- Plant enzymes convert NO_3^- to ammonium (NH_4^+), which is incorporated into organic compounds

- Some soil nitrogen is lost to the atmosphere when denitrifying bacteria convert NO_3^- to gaseous nitrogen (N_2)

- Plants can also use NH_4^+, which is acquired through two separate processes
  - Nitrogen-fixing bacteria convert N_2 into NH_3; NH_3 picks up an H^+ in the soil solution and forms NH_4^+
  - Ammonifying bacteria break down dead organic compounds and release NH_4^+

Bacteria and Nitrogen Fixation

- Nitrogen is abundant in the atmosphere but unavailable to plants because of the triple bond between atoms in N_2
- **Nitrogen fixation** is the conversion of nitrogen from N_2 to NH_3

$$N_2 + 8e^- + 8\,H^+ + 16\,ATP \longrightarrow 2\,NH_3 + H_2 + 16\,ADP + 16\,P_i$$

- Some nitrogen-fixing bacteria are free-living in the soil; others are rhizospheric

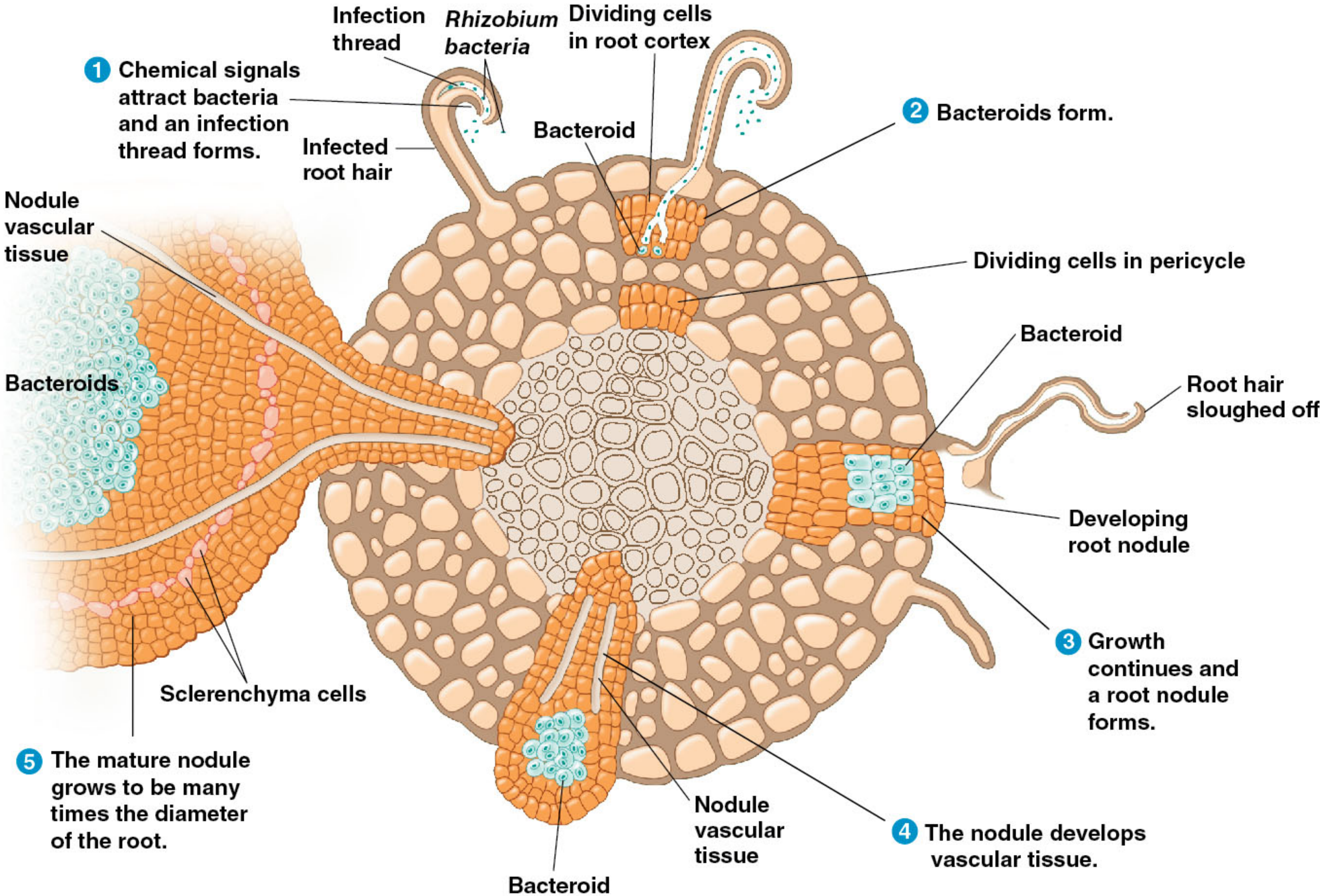
- Symbiotic relationships with nitrogen-fixing *Rhizobium* (“root-living”) bacteria provide some plant species (e.g., legumes) with fixed nitrogen
- Along a legume’s roots are swellings called **nodules** composed of plant cells “infected” by *Rhizobium* bacteria

Figure 37.12

- Inside the root nodule, *Rhizobium* bacteria assume a form called **bacteroids**, which are contained within vesicles formed by the root cell
- The plant obtains fixed nitrogen from *Rhizobium*, and *Rhizobium* obtains sugar and an anaerobic environment

- Each legume species is associated with a particular strain of *Rhizobium* bacteria
- The development of a nitrogen-fixing root nodule depends on chemical dialogue between *Rhizobium* bacteria and root cells of their specific plant hosts

Figure 37.13



Infection thread
Rhizobium bacteria
Dividing cells in root cortex
1 Chemical signals attract bacteria and an infection thread forms.
Infected root hair
Bacteroid
2 Bacteroids form.
Nodule vascular tissue
Dividing cells in pericycle
Bacteroid
Bacteroids
Root hair sloughed off
Developing root nodule
3 Growth continues and a root nodule forms.
Sclerenchyma cells
5 The mature nodule grows to be many times the diameter of the root.
Nodule vascular tissue
4 The nodule develops vascular tissue.
Bacteroid

Nitrogen Fixation and Agriculture

- **Crop rotation** takes advantage of the agricultural benefits of symbiotic nitrogen fixation
- A nonlegume such as maize is planted one year, and the next year a legume is planted to restore the concentration of fixed nitrogen in the soil
- Instead of being harvested, the legume crop is often plowed under to decompose as “green manure”

- Nonlegumes such as alder trees and certain tropical grasses are associated with nitrogen-fixing bacteria
- Rice farmers culture an aquatic fern, *Azolla*, which has mutualistic, nitrogen-fixing cyanobacteria
- The rice shades and eventually kills the fern; decomposition releases the nitrogen into the rice paddy

Fungi and Plant Nutrition

- **Mycorrhizae** are mutualistic associations of fungi and roots
- The host plant provides the fungus with a steady supply of sugar
- The fungus increases the surface area for water uptake by the host plant and supplies the plant with mineral nutrients from the soil

- Mycorrhizal fungi secrete growth factors that stimulate root growth and branching
- They also secrete antibiotics to help protect the plant from soil pathogens

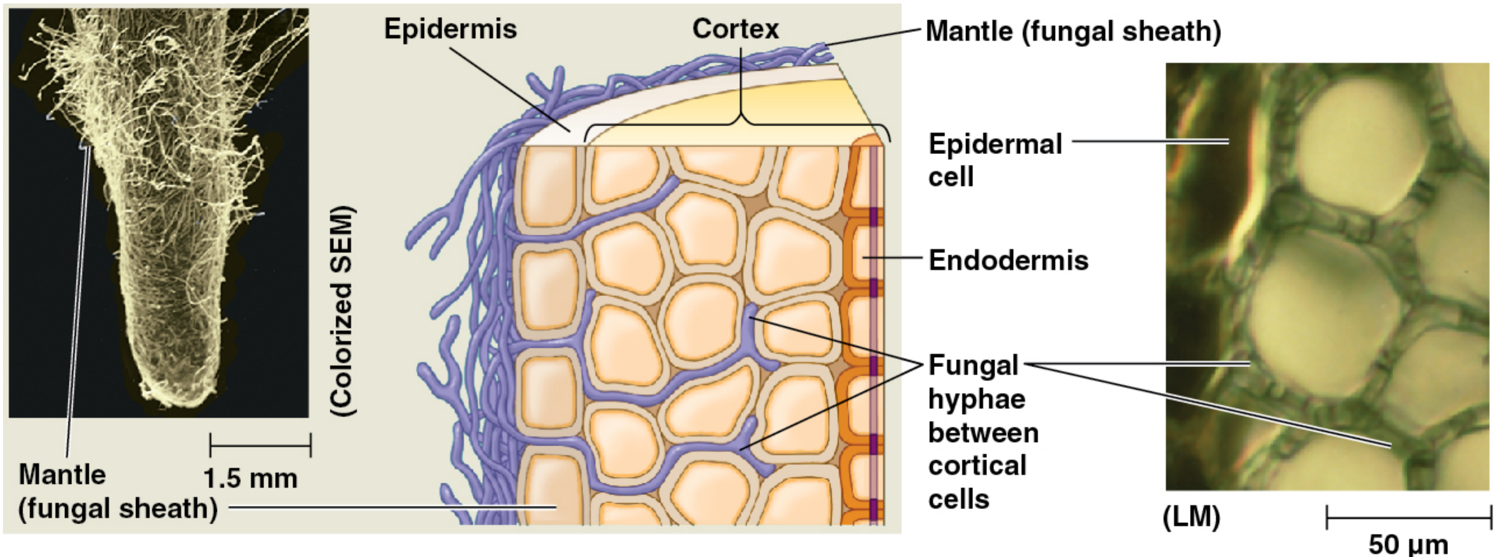
Mycorrhizae and Plant Evolution

- Early land plants would have encountered harsh conditions 400 to 500 million years ago
- These plants lacked the ability to extract essential nutrients from the soil, while fungi were unable to produce carbohydrates
- The mycorrhizal association between early land plants and fungi allowed both to exploit the terrestrial environment

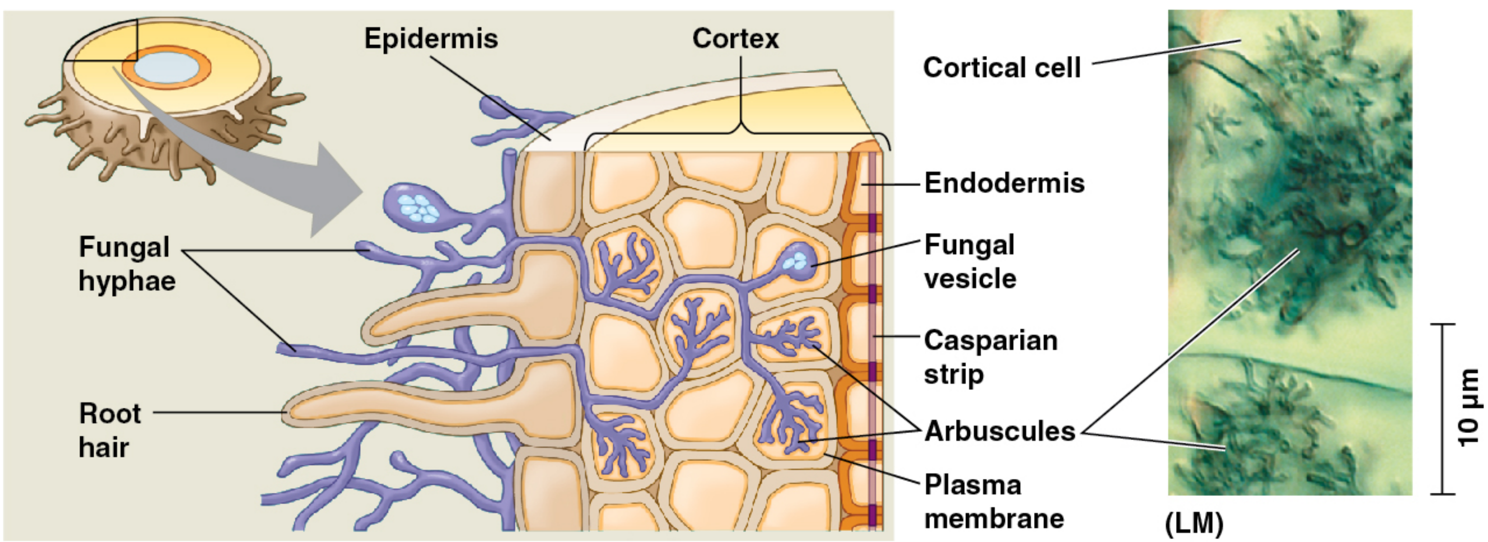
Types of Mycorrhizae

- Mycorrhizal associations consist of two major types:
  - Ectomycorrhizae
  - Arbuscular mycorrhizae

Figure 37.14



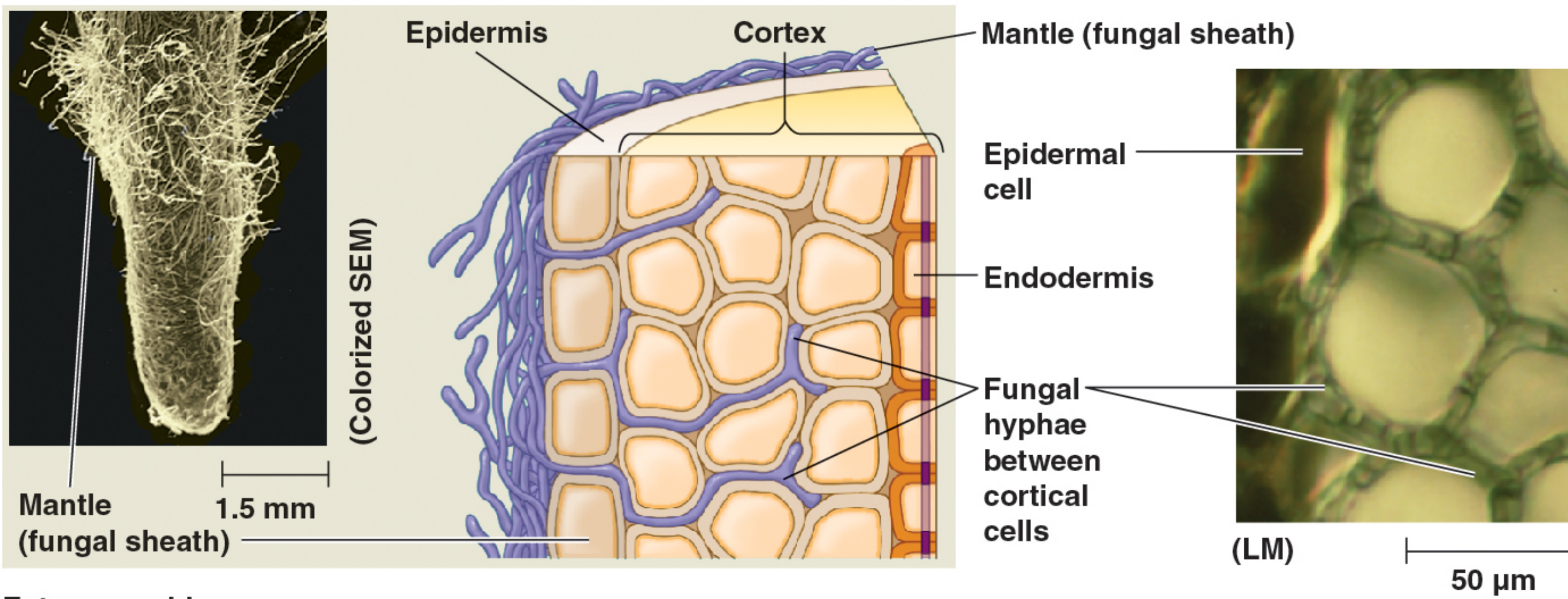
Ectomycorrhizae



Arbuscular mycorrhizae (endomycorrhizae)

- In **ectomycorrhizae**, the mycelium of the fungus forms a dense sheath, or mantle, over the surface of the root
- These hyphae form a network in the apoplast, but do not penetrate the root cells
- Ectomycorrhizae occur in about 10% of plant families, most of which are woody

Figure 37.14a

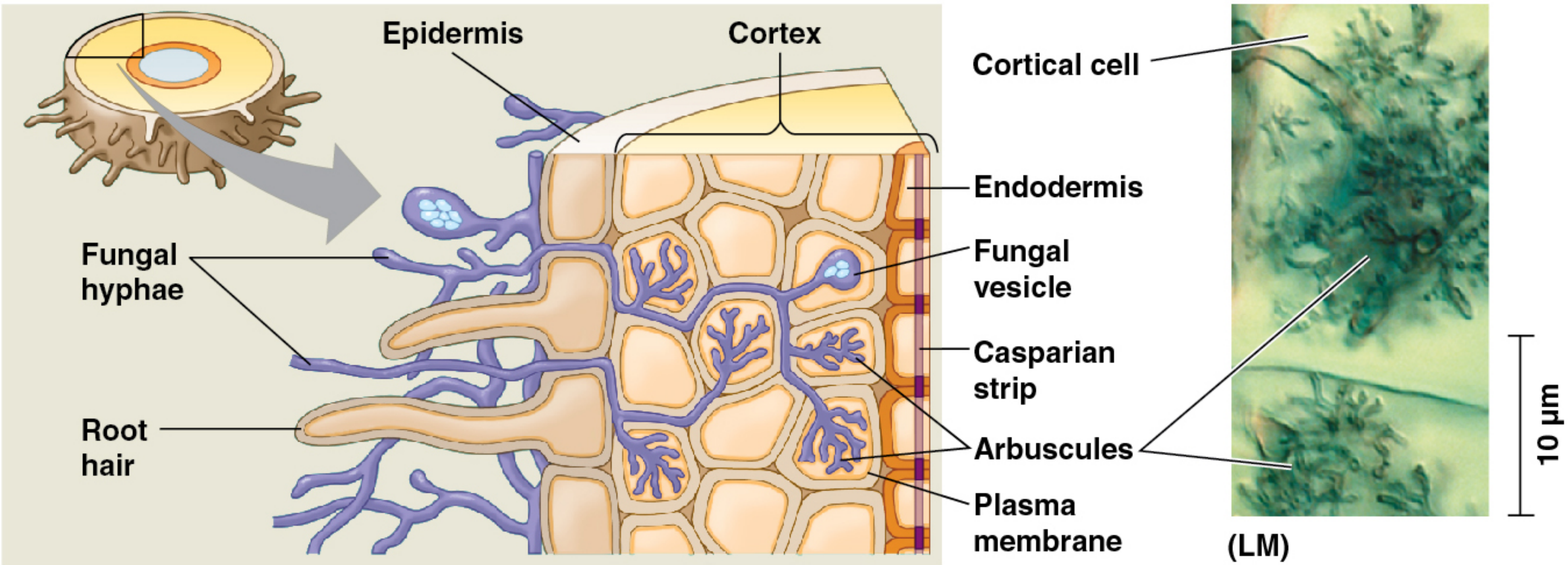


Ectomycorrhizae

- In **arbuscular mycorrhizae**, microscopic fungal hyphae extend into the root cortex
- These mycorrhizae penetrate the cell wall but not the plasma membrane
- Hyphae form branched arbuscules within invaginations of the cell membranes; these are important sites of nutrient transfer

- Arbuscular mycorrhizae occur in about 85% of plant species, including most crops
- About 5% of plant species do not form mycorrhizal associations

Figure 37.14b



Arbuscular mycorrhizae (endomycorrhizae)

Agricultural and Ecological Importance of Mycorrhizae

- Farmers and foresters often inoculate seeds with fungal spores to promote formation of mycorrhizae
- Some invasive exotic plants disrupt interactions between native plants and their mycorrhizal fungi
  - For example, garlic mustard slows growth of other plants by preventing the growth of mycorrhizal fungi

Epiphytes, Parasitic Plants, and Carnivorous Plants

- Some plants have nutritional adaptations that use other organisms in nonmutualistic ways
- Epiphytes, parasitic, and carnivorous plants all have unusual adaptations that facilitate exploiting other organisms

Figure 37.15 Exploring Unusual Nutritional Adaptations in Plants

Epiphytes

- An **epiphyte** grows on another plant and obtains water and minerals from rain
- Epiphytes do not tap into hosts for sustenance
- Examples include staghorn ferns, bromeliads, and many orchids

Figure 37.15a

Staghorn fern, an epiphyte

Parasitic Plants

- Parasitic plants absorb water, minerals, and sugars from their living host plant
- Some species also photosynthesize, but others rely entirely on the host plant for sustenance
- Some species parasitize the mycorrhizal hyphae of other plants

Figure 37.15b

Parasitic Plants

Mistletoe, a photosynthetic parasite

Dodder, a nonphotosynthetic parasite (orange)

Indian pipe, a nonphotosynthetic parasite of mycorrhizae

Carnivorous Plants

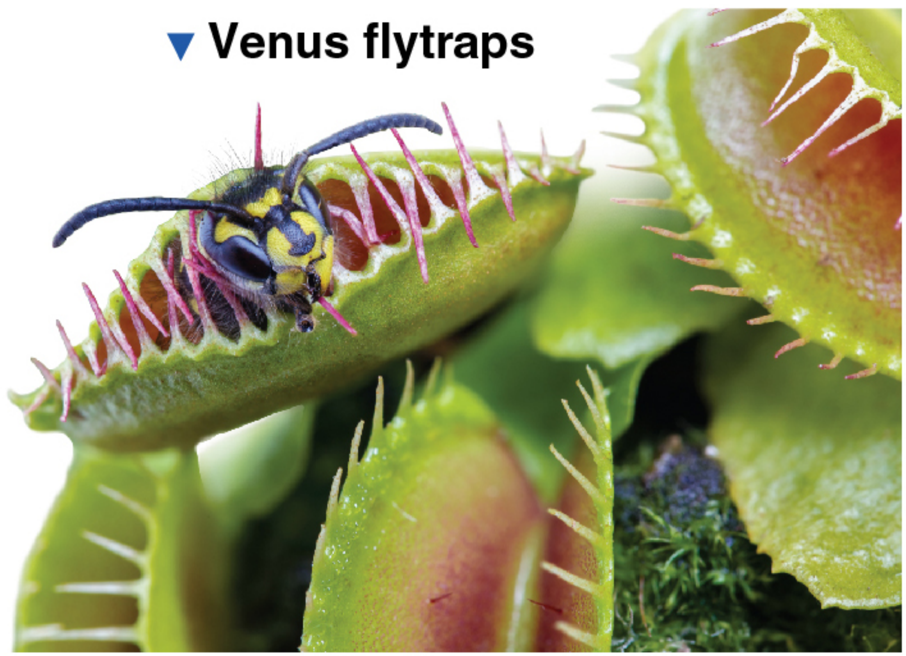
- Carnivorous plants have adaptations for trapping insects and other small animals
- They are photosynthetic, but obtain nitrogen by killing and digesting mostly insects

Carnivorous Plants

◀ Pitcher plants

▲ Sundew

▼ Venus flytraps



Video: Sundew Trapping Prey

Figure 37.UN01

Figure 37.UN02

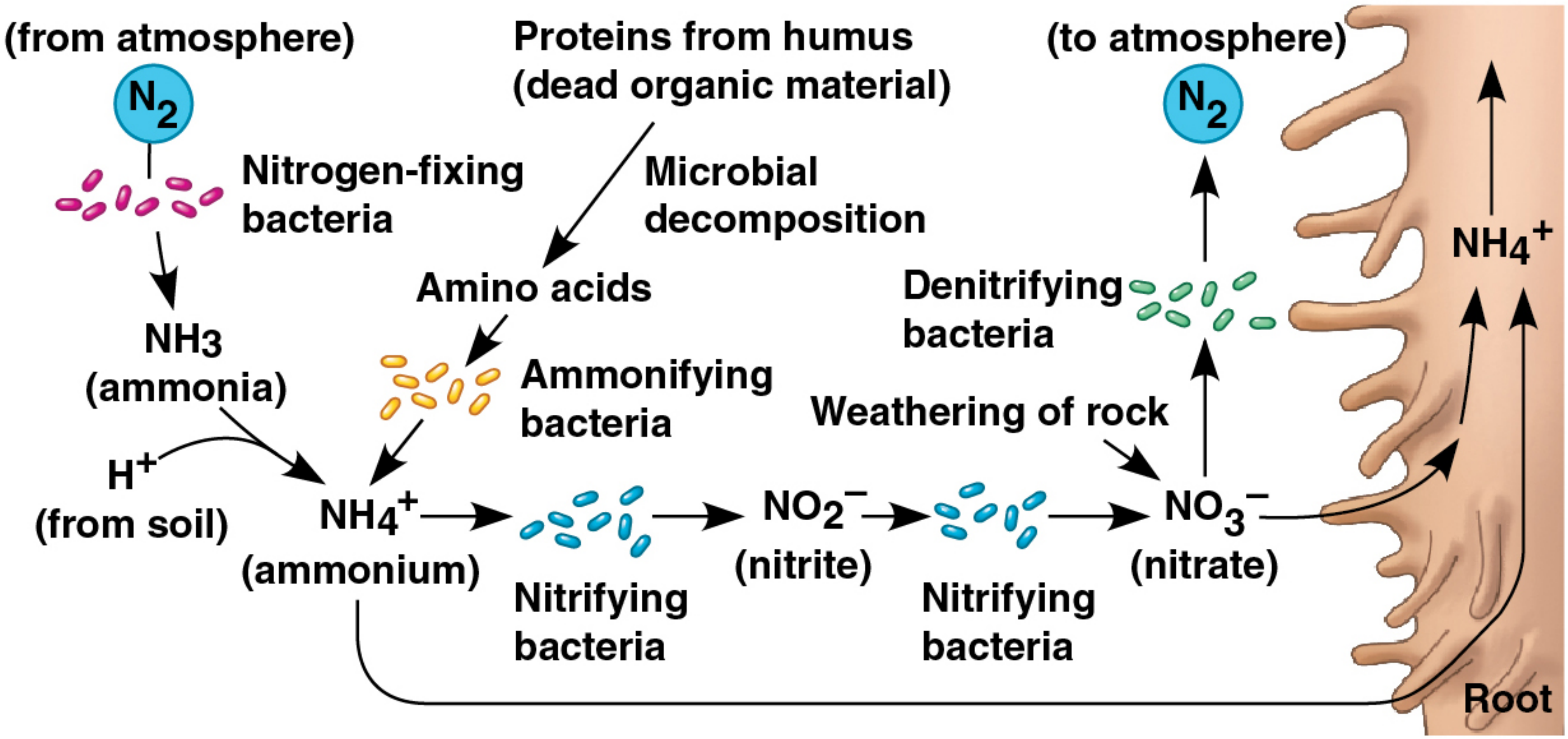


Figure 37.UN03