

Chapter

5

Mineral Nutrition

MINERAL NUTRIENTS ARE ELEMENTS acquired primarily in the form of inorganic ions from the soil. Although mineral nutrients continually cycle through all organisms, they enter the biosphere predominantly through the root systems of plants, so in a sense plants act as the “miners” of Earth’s crust (Epstein 1999). The large surface area of roots and their ability to absorb inorganic ions at low concentrations from the soil solution make mineral absorption by plants a very effective process. After being absorbed by the roots, the mineral elements are translocated to the various parts of the plant, where they are utilized in numerous biological functions. Other organisms, such as mycorrhizal fungi and nitrogen-fixing bacteria, often participate with roots in the acquisition of nutrients.

The study of how plants obtain and use mineral nutrients is called **mineral nutrition**. This area of research is central to modern agriculture and environmental protection. High agricultural yields depend strongly on fertilization with mineral nutrients. In fact, yields of most crop plants increase linearly with the amount of fertilizer that they absorb (Loomis and Conner 1992). To meet increased demand for food, world consumption of the primary fertilizer mineral elements—nitrogen, phosphorus, and potassium—rose steadily from 112 million metric tons in 1980 to 143 million metric tons in 1990 and has remained constant through the last decade.

Crop plants, however, typically use less than half of the fertilizer applied (Loomis and Conner 1992). The remaining minerals may leach into surface waters or groundwater, become attached to soil particles, or contribute to air pollution. As a consequence of fertilizer leaching, many water wells in the United States no longer meet federal standards for nitrate concentrations in drinking water (Nolan and Stoner 2000). On a brighter note, plants are the traditional means for recycling animal wastes and are proving useful for removing deleterious minerals from toxic-waste dumps (Macek et al. 2000). Because of the complex nature of plant–soil–atmosphere relationships, studies in the area of mineral nutrition involve atmospheric chemists, soil scientists, hydrologists, microbiologists, and ecologists, as well as plant physiologists.

In this chapter we will discuss first the nutritional needs of plants, the symptoms of specific nutritional deficiencies, and the use of fertilizers to ensure proper plant nutrition. Then we will examine how soil and root structure influence the transfer of inorganic nutrients from the environment into a plant. Finally, we will introduce the topic of mycorrhizal associations. Chapters 6 and 12 address additional aspects of solute transport and nutrient assimilation, respectively.

ESSENTIAL NUTRIENTS, DEFICIENCIES, AND PLANT DISORDERS

Only certain elements have been determined to be essential for plant growth. An **essential element** is defined as one whose absence prevents a plant from completing its life cycle (Arnon and Stout 1939) or one that has a clear physiological role (Epstein 1999). If plants are given these essential elements, as well as energy from sunlight, they can synthesize all the compounds they need for normal growth. Table 5.1 lists the elements that are considered to be essential for most, if not all, higher plants. The first three elements—hydrogen, carbon, and oxygen—are not considered mineral nutrients because they are obtained primarily from water or carbon dioxide.

Essential mineral elements are usually classified as macronutrients or micronutrients, according to their relative concentration in plant tissue. In some cases, the differences in tissue content of macronutrients and micronutrients are not as great as those indicated in Table 5.1. For example, some plant tissues, such as the leaf mesophyll, have almost as much iron or manganese as they do sulfur or magnesium. Many elements often are present in concentrations greater than the plant's minimum requirements.

Some researchers have argued that a classification into macronutrients and micronutrients is difficult to justify physiologically. Mengel and Kirkby (1987) have proposed that the essential elements be classified instead according to their biochemical role and physiological function. Table 5.2 shows such a classification, in which plant nutrients have been divided into four basic groups:

1. The first group of essential elements forms the organic (car-

bon) compounds of the plant. Plants assimilate these nutrients via biochemical reactions involving oxidation and reduction.

2. The second group is important in energy storage reactions or in maintaining structural integrity. Elements in this group are often present in plant tissues as phosphate, borate, and silicate esters in which the elemental group is bound to the hydroxyl group of an organic molecule (i.e., sugar-phosphate).
3. The third group is present in plant tissue as either free ions or ions bound to substances such as the pectic acids present in the plant cell wall. Of particular importance are their roles as enzyme cofactors and in the regulation of osmotic potentials.
4. The fourth group has important roles in reactions involving electron transfer.

Naturally occurring elements, other than those listed in Table 5.1, can also accumulate in plant tissues. For example, aluminum is not considered to be an essential element, but plants commonly contain from 0.1 to 500 ppm aluminum, and addition of low levels of aluminum to a nutrient solution may stimulate plant growth (Marschner 1995).

TABLE 5.1
Adequate tissue levels of elements that may be required by plants

Element	Chemical symbol	Concentration in dry matter (% or ppm) ^a	Relative number of atoms with respect to molybdenum
Obtained from water or carbon dioxide			
Hydrogen	H	6	60,000,000
Carbon	C	45	40,000,000
Oxygen	O	45	30,000,000
Obtained from the soil			
Macronutrients			
Nitrogen	N	1.5	1,000,000
Potassium	K	1.0	250,000
Calcium	Ca	0.5	125,000
Magnesium	Mg	0.2	80,000
Phosphorus	P	0.2	60,000
Sulfur	S	0.1	30,000
Silicon	Si	0.1	30,000
Micronutrients			
Chlorine	Cl	100	3,000
Iron	Fe	100	2,000
Boron	B	20	2,000
Manganese	Mn	50	1,000
Sodium	Na	10	400
Zinc	Zn	20	300
Copper	Cu	6	100
Nickel	Ni	0.1	2
Molybdenum	Mo	0.1	1

Source: Epstein 1972, 1999.

^aThe values for the nonmineral elements (H, C, O) and the macronutrients are percentages. The values for micronutrients are expressed in parts per million.

TABLE 5.2
Classification of plant mineral nutrients according to biochemical function

Mineral nutrient	Functions
Group 1	Nutrients that are part of carbon compounds
N	Constituent of amino acids, amides, proteins, nucleic acids, nucleotides, coenzymes, hexoamines, etc.
S	Component of cysteine, cystine, methionine, and proteins. Constituent of lipoic acid, coenzyme A, thiamine pyrophosphate, glutathione, biotin, adenosine-5'-phosphosulfate, and 3-phosphoadenosine.
Group 2	Nutrients that are important in energy storage or structural integrity
P	Component of sugar phosphates, nucleic acids, nucleotides, coenzymes, phospholipids, phytic acid, etc. Has a key role in reactions that involve ATP.
Si	Deposited as amorphous silica in cell walls. Contributes to cell wall mechanical properties, including rigidity and elasticity.
B	Complexes with mannitol, mannan, polymannuronic acid, and other constituents of cell walls. Involved in cell elongation and nucleic acid metabolism.
Group 3	Nutrients that remain in ionic form
K	Required as a cofactor for more than 40 enzymes. Principal cation in establishing cell turgor and maintaining cell electroneutrality.
Ca	Constituent of the middle lamella of cell walls. Required as a cofactor by some enzymes involved in the hydrolysis of ATP and phospholipids. Acts as a second messenger in metabolic regulation.
Mg	Required by many enzymes involved in phosphate transfer. Constituent of the chlorophyll molecule.
Cl	Required for the photosynthetic reactions involved in O ₂ evolution.
Mn	Required for activity of some dehydrogenases, decarboxylases, kinases, oxidases, and peroxidases. Involved with other cation-activated enzymes and photosynthetic O ₂ evolution.
Na	Involved with the regeneration of phosphoenolpyruvate in C ₄ and CAM plants. Substitutes for potassium in some functions.
Group 4	Nutrients that are involved in redox reactions
Fe	Constituent of cytochromes and nonheme iron proteins involved in photosynthesis, N ₂ fixation, and respiration.
Zn	Constituent of alcohol dehydrogenase, glutamic dehydrogenase, carbonic anhydrase, etc.
Cu	Component of ascorbic acid oxidase, tyrosinase, monoamine oxidase, uricase, cytochrome oxidase, phenolase, laccase, and plastocyanin.
Ni	Constituent of urease. In N ₂ -fixing bacteria, constituent of hydrogenases.
Mo	Constituent of nitrogenase, nitrate reductase, and xanthine dehydrogenase.

Source: After Evans and Sorger 1966 and Mengel and Kirkby 1987.

Many species in the genera *Astragalus*, *Xylorhiza*, and *Stanleya* accumulate selenium, although plants have not been shown to have a specific requirement for this element.

Cobalt is part of cobalamin (vitamin B₁₂ and its derivatives), a component of several enzymes in nitrogen-fixing microorganisms. Thus cobalt deficiency blocks the development and function of nitrogen-fixing nodules. Nonetheless, plants that do not fix nitrogen, as well as nitrogen-fixing plants that are supplied with ammonium or nitrate, do not require cobalt. Crop plants normally contain only relatively small amounts of nonessential elements.

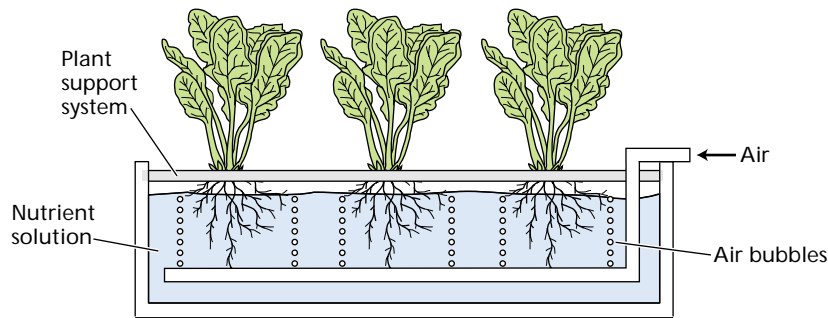
Special Techniques Are Used in Nutritional Studies

To demonstrate that an element is essential requires that plants be grown under experimental conditions in which only the element under investigation is absent. Such conditions are extremely difficult to achieve with plants grown in

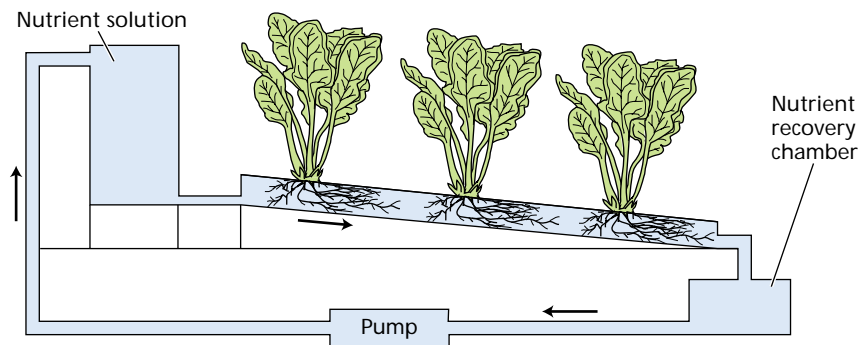
a complex medium such as soil. In the nineteenth century, several researchers, including Nicolas-Théodore de Saussure, Julius von Sachs, Jean-Baptiste-Joseph-Dieudonné Boussingault, and Wilhelm Knop, approached this problem by growing plants with their roots immersed in a **nutrient solution** containing only inorganic salts. Their demonstration that plants could grow normally with no soil or organic matter proved unequivocally that plants can fulfill all their needs from only inorganic elements and sunlight.

The technique of growing plants with their roots immersed in nutrient solution without soil is called solution culture or **hydroponics** (Gericke 1937). Successful hydroponic culture (Figure 5.1A) requires a large volume of nutrient solution or frequent adjustment of the nutrient solution to prevent nutrient uptake by roots from producing radical changes in nutrient concentrations and pH of the medium. A sufficient supply of oxygen to the root sys-

(A) Hydroponic growth system



(B) Nutrient film growth system



(C) Aeroponic growth system

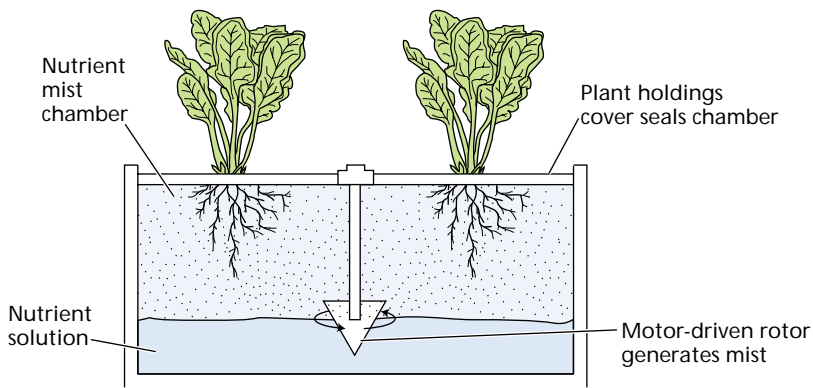


FIGURE 5.1 Hydroponic and aeroponic systems for growing plants in nutrient solutions in which composition and pH can be automatically controlled. (A) In a hydroponic system, the roots are immersed in the nutrient solution, and air is bubbled through the solution. (B) An alternative hydroponic system, often used in commercial production, is the nutrient film growth system, in which the nutrient solution is pumped as a thin film down a shallow trough surrounding the plant roots. In this system the composition and pH of the nutrient solution can be controlled automatically. (C) In the aeroponic system, the roots are suspended over the nutrient solution, which is whipped into a mist by a motor-driven rotor. (C after Weathers and Zobel 1992.)

tem—also critical—may be achieved by vigorous bubbling of air through the medium.

Hydroponics is used in the commercial production of many greenhouse crops. In one form of commercial hydro-

ponic culture, plants are grown in a supporting material such as sand, gravel, vermiculite, or expanded clay (i.e., kitty litter). Nutrient solutions are then flushed through the supporting material, and old solutions are removed by leaching. In another form of hydroponic culture, plant roots lie on the surface of a trough, and nutrient solutions flow in a thin layer along the trough over the roots (Cooper 1979, Asher and Edwards 1983). This **nutrient film growth system** ensures that the roots receive an ample supply of oxygen (Figure 5.1B).

Another alternative, which has sometimes been heralded as the medium of the future, is to grow the plants **aeroponically** (Weathers and Zobel 1992). In this technique, plants are grown with their roots suspended in air while being sprayed continuously with a nutrient solution (Figure 5.1C). This approach provides easy manipulation of the gaseous environment around the root, but it requires higher levels of nutrients than hydroponic culture does to sustain rapid plant growth. For this reason and other technical difficulties, the use of aeroponics is not widespread.

Nutrient Solutions Can Sustain Rapid Plant Growth

Over the years, many formulations have been used for nutrient solutions. Early formulations developed by Knop in Germany included only KNO_3 , $\text{Ca}(\text{NO}_3)_2$, KH_2PO_4 , MgSO_4 , and an iron salt. At the time this nutrient solution was believed to contain all the minerals required by the plant, but these experiments were carried out with chemicals that were contaminated with other elements that are now known to be essential (such as boron or molybdenum). Table 5.3 shows a more modern formulation for a nutrient solution. This formulation is called a modified **Hoagland solution**, named after Dennis R. Hoagland, a researcher who was prominent in the development of modern mineral nutrition research in the United States.

TABLE 5.3
Composition of a modified Hoagland nutrient solution for growing plants

Compound	Molecular weight	Concentration of stock solution	Concentration of stock solution	Volume of stock solution per liter of final solution	Element	Final concentration of element	
	g mol ⁻¹	mM	g L ⁻¹	mL		μM	ppm
Macronutrients							
KNO ₃	101.10	1,000	101.10	6.0	N	16,000	224
Ca(NO ₃) ₂ ·4H ₂ O	236.16	1,000	236.16	4.0	K	6,000	235
NH ₄ H ₂ PO ₄	115.08	1,000	115.08	2.0	Ca	4,000	160
MgSO ₄ ·7H ₂ O	246.48	1,000	246.49	1.0	P	2,000	62
					S	1,000	32
					Mg	1,000	24
Micronutrients							
KCl	74.55	25	1.864	2.0	Cl	50	1.77
H ₃ BO ₃	61.83	12.5	0.773		B	25	0.27
MnSO ₄ ·H ₂ O	169.01	1.0	0.169		Mn	2.0	0.11
ZnSO ₄ ·7H ₂ O	287.54	1.0	0.288		Zn	2.0	0.13
CuSO ₄ ·5H ₂ O	249.68	0.25	0.062		Cu	0.5	0.03
H ₂ MoO ₄ (85% MoO ₃)	161.97	0.25	0.040		Mo	0.5	0.05
NaFeDTPA (10% Fe)	468.20	64	30.0	0.3–1.0	Fe	16.1–53.7	1.00–3.00
Optional^a							
NiSO ₄ ·6H ₂ O	262.86	0.25	0.066	2.0	Ni	0.5	0.03
Na ₂ SiO ₃ ·9H ₂ O	284.20	1,000	284.20	1.0	Si	1,000	28

Source: After Epstein 1972.

Note: The macronutrients are added separately from stock solutions to prevent precipitation during preparation of the nutrient solution. A combined stock solution is made up containing all micronutrients except iron. Iron is added as sodium ferric diethylenetriaminepentaacetate (NaFeDTPA, trade name Ciba-Geigy Sequestrene 330 Fe; see Figure 5.2); some plants, such as maize, require the higher level of iron shown in the table.

^aNickel is usually present as a contaminant of the other chemicals, so it may not need to be added explicitly. Silicon, if included, should be added first and the pH adjusted with HCl to prevent precipitation of the other nutrients.

A modified Hoagland solution contains all of the known mineral elements needed for rapid plant growth. The concentrations of these elements are set at the highest possible levels without producing toxicity symptoms or salinity stress and thus may be several orders of magnitude higher than those found in the soil around plant roots. For example, whereas phosphorus is present in the soil solution at concentrations normally less than 0.06 ppm, here it is offered at 62 ppm (Epstein 1972). Such high initial levels permit plants to be grown in a medium for extended periods without replenishment of the nutrients. Many researchers, however, dilute their nutrient solutions severalfold and replenish them frequently to minimize fluctuations of nutrient concentration in the medium and in plant tissue.

Another important property of the modified Hoagland formulation is that nitrogen is supplied as both ammonium (NH₄⁺) and nitrate (NO₃⁻). Supplying nitrogen in a balanced mixture of cations and anions tends to reduce the rapid rise

in the pH of the medium that is commonly observed when the nitrogen is supplied solely as nitrate anion (Asher and Edwards 1983). Even when the pH of the medium is kept neutral, most plants grow better if they have access to both NH₄⁺ and NO₃⁻ because absorption and assimilation of the two nitrogen forms promotes cation–anion balance within the plant (Raven and Smith 1976; Bloom 1994).

A significant problem with nutrient solutions is maintaining the availability of iron. When supplied as an inorganic salt such as FeSO₄ or Fe(NO₃)₂, iron can precipitate out of solution as iron hydroxide. If phosphate salts are present, insoluble iron phosphate will also form. Precipitation of the iron out of solution makes it physically unavailable to the plant, unless iron salts are added at frequent intervals. Earlier researchers approached this problem by adding iron together with citric acid or tartaric acid. Compounds such as these are called **chelators** because they form soluble complexes with cations such as iron and cal-

cium in which the cation is held by ionic forces, rather than by covalent bonds. Chelated cations thus are physically more available to a plant.

More modern nutrient solutions use the chemicals ethylenediaminetetraacetic acid (EDTA) or diethylenetriaminepentaacetic acid (DTPA, or pentetic acid) as chelating agents (Sievers and Bailar 1962). Figure 5.2 shows the structure of DTPA. The fate of the chelation complex during iron uptake by the root cells is not clear; iron may be released from the chelator when it is reduced from Fe^{3+} to Fe^{2+} at the root surface. The chelator may then diffuse back into the nutrient (or soil) solution and react with another Fe^{3+} ion or other metal ions. After uptake, iron is kept soluble by chelation with organic compounds present in plant cells. Citric acid may play a major role in iron chelation and its long-distance transport in the xylem.

Mineral Deficiencies Disrupt Plant Metabolism and Function

Inadequate supply of an essential element results in a nutritional disorder manifested by characteristic deficiency symptoms. In hydroponic culture, withholding of an essential element can be readily correlated with a given set of symptoms for acute deficiencies. Diagnosis of soil-grown plants can be more complex, for the following reasons:

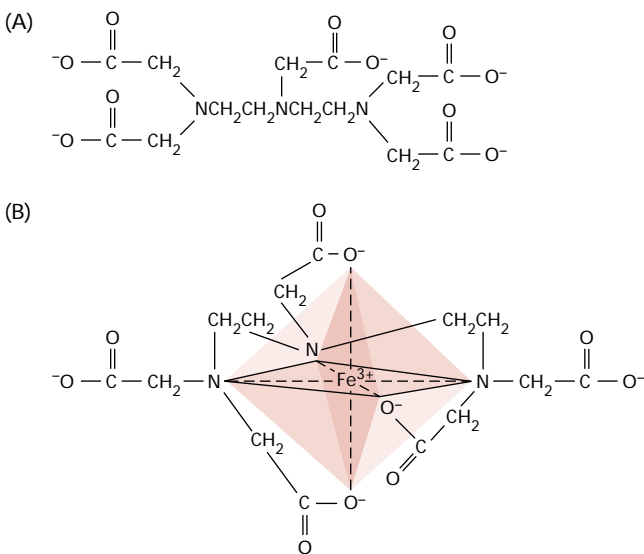


FIGURE 5.2 Chemical structure of the chelator DTPA by itself (A) and chelated to an Fe^{3+} ion (B). Iron binds to DTPA through interaction with three nitrogen atoms and the three ionized oxygen atoms of the carboxylate groups (Sievers and Bailar 1962). The resulting ring structure clamps the metallic ion and effectively neutralizes its reactivity in solution. During the uptake of iron at the root surface, Fe^{3+} appears to be reduced to Fe^{2+} , which is released from the DTPA-iron complex. The chelator can then bind to other available Fe^{3+} ions.

- Both chronic and acute deficiencies of several elements may occur simultaneously.
- Deficiencies or excessive amounts of one element may induce deficiencies or excessive accumulations of another.
- Some virus-induced plant diseases may produce symptoms similar to those of nutrient deficiencies.

Nutrient deficiency symptoms in a plant are the expression of metabolic disorders resulting from the insufficient supply of an essential element. These disorders are related to the roles played by essential elements in normal plant metabolism and function. Table 5.2 lists some of the roles of essential elements.

Even though each essential element participates in many different metabolic reactions, some general statements about the functions of essential elements in plant metabolism are possible. In general, the essential elements function in plant structure, metabolic function, and osmoregulation of plant cells. More specific roles may be related to the ability of divalent cations such as calcium or magnesium to modify the permeability of plant membranes. In addition, research continues to reveal specific roles of these elements in plant metabolism; for example, calcium acts as a signal to regulate key enzymes in the cytosol (Hepler and Wayne 1985; Sanders et al. 1999). Thus, most essential elements have multiple roles in plant metabolism.

When relating acute deficiency symptoms to a particular essential element, an important clue is the extent to which an element can be recycled from older to younger leaves. Some elements, such as nitrogen, phosphorus, and potassium, can readily move from leaf to leaf; others, such as boron, iron, and calcium, are relatively immobile in most plant species (Table 5.4). If an essential element is mobile, deficiency symptoms tend to appear first in older leaves. Deficiency of an immobile essential element will become evident first in younger leaves. Although the precise mechanisms of nutrient mobilization are not well understood,

TABLE 5.4
Mineral elements classified on the basis of their mobility within a plant and their tendency to retranslocate during deficiencies

Mobile	Immobile
Nitrogen	Calcium
Potassium	Sulfur
Magnesium	Iron
Phosphorus	Boron
Chlorine	Copper
Sodium	
Zinc	
Molybdenum	

Note: Elements are listed in the order of their abundance in the plant.

plant hormones such as cytokinins appear to be involved (see Chapter 21). In the discussion that follows, we will describe the specific deficiency symptoms and functional roles for the mineral essential elements as they are grouped in Table 5.2.

Group 1: Deficiencies in mineral nutrients that are part of carbon compounds. This first group consists of nitrogen and sulfur. Nitrogen availability in soils limits plant productivity in most natural and agricultural ecosystems. By contrast, soils generally contain sulfur in excess. Nonetheless, nitrogen and sulfur share the property that their oxidation–reduction states range widely (see Chapter 12). Some of the most energy-intensive reactions in life convert the highly oxidized, inorganic forms absorbed from the soil into the highly reduced forms found in organic compounds such as amino acids.

NITROGEN. Nitrogen is the mineral element that plants require in greatest amounts. It serves as a constituent of many plant cell components, including amino acids and nucleic acids. Therefore, nitrogen deficiency rapidly inhibits plant growth. If such a deficiency persists, most species show **chlorosis** (yellowing of the leaves), especially in the older leaves near the base of the plant (for pictures of nitrogen deficiency and the other mineral deficiencies described in this chapter, see [Web Topic 5.1](#)). Under severe nitrogen deficiency, these leaves become completely yellow (or tan) and fall off the plant. Younger leaves may not show these symptoms initially because nitrogen can be mobilized from older leaves. Thus a nitrogen-deficient plant may have light green upper leaves and yellow or tan lower leaves.

When nitrogen deficiency develops slowly, plants may have markedly slender and often woody stems. This woodiness may be due to a buildup of excess carbohydrates that cannot be used in the synthesis of amino acids or other nitrogen compounds. Carbohydrates not used in nitrogen metabolism may also be used in anthocyanin synthesis, leading to accumulation of that pigment. This condition is revealed as a purple coloration in leaves, petioles, and stems of some nitrogen-deficient plants, such as tomato and certain varieties of corn.

SULFUR. Sulfur is found in two amino acids and is a constituent of several coenzymes and vitamins essential for metabolism. Many of the symptoms of sulfur deficiency are similar to those of nitrogen deficiency, including chlorosis, stunting of growth, and anthocyanin accumulation. This similarity is not surprising, since sulfur and nitrogen are both constituents of proteins. However, the chlorosis caused by sulfur deficiency generally arises initially in mature and young leaves, rather than in the old leaves as in nitrogen deficiency, because unlike nitrogen, sulfur is not easily remobilized to the younger leaves in most species. Nonetheless, in many plant species sulfur chlorosis may

occur simultaneously in all leaves or even initially in the older leaves.

Group 2: Deficiencies in mineral nutrients that are important in energy storage or structural integrity. This group consists of phosphorus, silicon, and boron. Phosphorus and silicon are found at concentrations within plant tissue that warrant their classification as macronutrients, whereas boron is much less abundant and considered a micronutrient. These elements are usually present in plants as ester linkages to a carbon molecule.

PHOSPHORUS. Phosphorus (as phosphate, PO_4^{3-}) is an integral component of important compounds of plant cells, including the sugar–phosphate intermediates of respiration and photosynthesis, and the phospholipids that make up plant membranes. It is also a component of nucleotides used in plant energy metabolism (such as ATP) and in DNA and RNA. Characteristic symptoms of phosphorus deficiency include stunted growth in young plants and a dark green coloration of the leaves, which may be malformed and contain small spots of dead tissue called **necrotic spots** (for a picture, see [Web Topic 5.1](#)).

As in nitrogen deficiency, some species may produce excess anthocyanins, giving the leaves a slight purple coloration. In contrast to nitrogen deficiency, the purple coloration of phosphorus deficiency is not associated with chlorosis. In fact, the leaves may be a dark greenish purple. Additional symptoms of phosphorus deficiency include the production of slender (but not woody) stems and the death of older leaves. Maturation of the plant may also be delayed.

SILICON. Only members of the family Equisetaceae—called *scouring rushes* because at one time their ash, rich in gritty silica, was used to scour pots—require silicon to complete their life cycle. Nonetheless, many other species accumulate substantial amounts of silicon within their tissues and show enhanced growth and fertility when supplied with adequate amounts of silicon (Epstein 1999).

Plants deficient in silicon are more susceptible to lodging (falling over) and fungal infection. Silicon is deposited primarily in the endoplasmic reticulum, cell walls, and intercellular spaces as hydrated, amorphous silica ($\text{SiO}_2 \cdot n\text{H}_2\text{O}$). It also forms complexes with polyphenols and thus serves as an alternative to lignin in the reinforcement of cell walls. In addition, silicon can ameliorate the toxicity of many heavy metals.

BORON. Although the precise function of boron in plant metabolism is unclear, evidence suggests that it plays roles in cell elongation, nucleic acid synthesis, hormone responses, and membrane function (Shelp 1993). Boron-deficient plants may exhibit a wide variety of symptoms, depending on the species and the age of the plant.

A characteristic symptom is black necrosis of the young leaves and terminal buds. The necrosis of the young leaves occurs primarily at the base of the leaf blade. Stems may be unusually stiff and brittle. Apical dominance may also be lost, causing the plant to become highly branched; however, the terminal apices of the branches soon become necrotic because of inhibition of cell division. Structures such as the fruit, fleshy roots, and tubers may exhibit necrosis or abnormalities related to the breakdown of internal tissues.

Group 3: Deficiencies in mineral nutrients that remain in ionic form. This group includes some of the most familiar mineral elements: The macronutrients potassium, calcium, and magnesium, and the micronutrients chlorine, manganese, and sodium. They may be found in solution in the cytosol or vacuoles, or they may be bound electrostatically or as ligands to larger carbon-containing compounds.

POTASSIUM. Potassium, present within plants as the cation K^+ , plays an important role in regulation of the osmotic potential of plant cells (see Chapters 3 and 6). It also activates many enzymes involved in respiration and photosynthesis. The first observable symptom of potassium deficiency is mottled or marginal chlorosis, which then develops into necrosis primarily at the leaf tips, at the margins, and between veins. In many monocots, these necrotic lesions may initially form at the leaf tips and margins and then extend toward the leaf base.

Because potassium can be mobilized to the younger leaves, these symptoms appear initially on the more mature leaves toward the base of the plant. The leaves may also curl and crinkle. The stems of potassium-deficient plants may be slender and weak, with abnormally short internodal regions. In potassium-deficient corn, the roots may have an increased susceptibility to root-rotting fungi present in the soil, and this susceptibility, together with effects on the stem, results in an increased tendency for the plant to be easily bent to the ground (lodging).

CALCIUM. Calcium ions (Ca^{2+}) are used in the synthesis of new cell walls, particularly the middle lamellae that separate newly divided cells. Calcium is also used in the mitotic spindle during cell division. It is required for the normal functioning of plant membranes and has been implicated as a second messenger for various plant responses to both environmental and hormonal signals (Sanders et al. 1999). In its function as a second messenger, calcium may bind to **calmodulin**, a protein found in the cytosol of plant cells. The calmodulin–calcium complex regulates many metabolic processes.

Characteristic symptoms of calcium deficiency include necrosis of young meristematic regions, such as the tips of roots or young leaves, where cell division and wall formation are most rapid. Necrosis in slowly growing plants may

be preceded by a general chlorosis and downward hooking of the young leaves. Young leaves may also appear deformed. The root system of a calcium-deficient plant may appear brownish, short, and highly branched. Severe stunting may result if the meristematic regions of the plant die prematurely.

MAGNESIUM. In plant cells, magnesium ions (Mg^{2+}) have a specific role in the activation of enzymes involved in respiration, photosynthesis, and the synthesis of DNA and RNA. Magnesium is also a part of the ring structure of the chlorophyll molecule (see Figure 7.6A). A characteristic symptom of magnesium deficiency is chlorosis between the leaf veins, occurring first in the older leaves because of the mobility of this element. This pattern of chlorosis results because the chlorophyll in the vascular bundles remains unaffected for longer periods than the chlorophyll in the cells between the bundles does. If the deficiency is extensive, the leaves may become yellow or white. An additional symptom of magnesium deficiency may be premature leaf abscission.

CHLORINE. The element chlorine is found in plants as the chloride ion (Cl^-). It is required for the water-splitting reaction of photosynthesis through which oxygen is produced (see Chapter 7) (Clarke and Eaton-Rye 2000). In addition, chlorine may be required for cell division in both leaves and roots (Harling et al. 1997). Plants deficient in chlorine develop wilting of the leaf tips followed by general leaf chlorosis and necrosis. The leaves may also exhibit reduced growth. Eventually, the leaves may take on a bronzelike color (“bronzing”). Roots of chlorine-deficient plants may appear stunted and thickened near the root tips.

Chloride ions are very soluble and generally available in soils because seawater is swept into the air by wind and is delivered to soil when it rains. Therefore, chlorine deficiency is unknown in plants grown in native or agricultural habitats. Most plants generally absorb chlorine at levels much higher than those required for normal functioning.

MANGANESE. Manganese ions (Mn^{2+}) activate several enzymes in plant cells. In particular, decarboxylases and dehydrogenases involved in the tricarboxylic acid (Krebs) cycle are specifically activated by manganese. The best-defined function of manganese is in the photosynthetic reaction through which oxygen is produced from water (Marschner 1995). The major symptom of manganese deficiency is intervenous chlorosis associated with the development of small necrotic spots. This chlorosis may occur on younger or older leaves, depending on plant species and growth rate.

SODIUM. Most species utilizing the C_4 and CAM pathways of carbon fixation (see Chapter 8) require sodium ions (Na^+). In these plants, sodium appears vital for regenerating phosphoenolpyruvate, the substrate for the first car-

boxylation in the C_4 and CAM pathways (Johnstone et al. 1988). Under sodium deficiency, these plants exhibit chlorosis and necrosis, or even fail to form flowers. Many C_3 species also benefit from exposure to low levels of sodium ions. Sodium stimulates growth through enhanced cell expansion, and it can partly substitute for potassium as an osmotically active solute.

Group 4: Deficiencies in mineral nutrients that are involved in redox reactions. This group of five micronutrients includes the metals iron, zinc, copper, nickel, and molybdenum. All of these can undergo reversible oxidations and reductions (e.g., $Fe^{2+} \rightleftharpoons Fe^{3+}$) and have important roles in electron transfer and energy transformation. They are usually found in association with larger molecules such as cytochromes, chlorophyll, and proteins (usually enzymes).

IRON. Iron has an important role as a component of enzymes involved in the transfer of electrons (redox reactions), such as cytochromes. In this role, it is reversibly oxidized from Fe^{2+} to Fe^{3+} during electron transfer. As in magnesium deficiency, a characteristic symptom of iron deficiency is interveinous chlorosis. In contrast to magnesium deficiency symptoms, these symptoms appear initially on the younger leaves because iron cannot be readily mobilized from older leaves. Under conditions of extreme or prolonged deficiency, the veins may also become chlorotic, causing the whole leaf to turn white.

The leaves become chlorotic because iron is required for the synthesis of some of the chlorophyll–protein complexes in the chloroplast. The low mobility of iron is probably due to its precipitation in the older leaves as insoluble oxides or phosphates or to the formation of complexes with phytoferritin, an iron-binding protein found in the leaf and other plant parts (Oh et al. 1996). The precipitation of iron diminishes subsequent mobilization of the metal into the phloem for long-distance translocation.

ZINC. Many enzymes require zinc ions (Zn^{2+}) for their activity, and zinc may be required for chlorophyll biosynthesis in some plants. Zinc deficiency is characterized by a reduction in internodal growth, and as a result plants display a rosette habit of growth in which the leaves form a circular cluster radiating at or close to the ground. The leaves may also be small and distorted, with leaf margins having a puckered appearance. These symptoms may result from loss of the capacity to produce sufficient amounts of the auxin indoleacetic acid. In some species (corn, sorghum, beans), the older leaves may become interveinously chlorotic and then develop white necrotic spots. This chlorosis may be an expression of a zinc requirement for chlorophyll biosynthesis.

COPPER. Like iron, copper is associated with enzymes involved in redox reactions being reversibly oxidized from

Cu^+ to Cu^{2+} . An example of such an enzyme is plastocyanin, which is involved in electron transfer during the light reactions of photosynthesis (Haehnel 1984). The initial symptom of copper deficiency is the production of dark green leaves, which may contain necrotic spots. The necrotic spots appear first at the tips of the young leaves and then extend toward the leaf base along the margins. The leaves may also be twisted or malformed. Under extreme copper deficiency, leaves may abscise prematurely.

NICKEL. Urease is the only known nickel-containing enzyme in higher plants, although nitrogen-fixing microorganisms require nickel for the enzyme that reprocesses some of the hydrogen gas generated during fixation (hydrogen uptake hydrogenase) (see Chapter 12). Nickel-deficient plants accumulate urea in their leaves and, consequently, show leaf tip necrosis. Plants grown in soil seldom, if ever, show signs of nickel deficiency because the amounts of nickel required are minuscule.

MOLYBDENUM. Molybdenum ions (Mo^{4+} through Mo^{6+}) are components of several enzymes, including nitrate reductase and nitrogenase. Nitrate reductase catalyzes the reduction of nitrate to nitrite during its assimilation by the plant cell; nitrogenase converts nitrogen gas to ammonia in nitrogen-fixing microorganisms (see Chapter 12). The first indication of a molybdenum deficiency is general chlorosis between veins and necrosis of the older leaves. In some plants, such as cauliflower or broccoli, the leaves may not become necrotic but instead may appear twisted and subsequently die (whiptail disease). Flower formation may be prevented, or the flowers may abscise prematurely.

Because molybdenum is involved with both nitrate assimilation and nitrogen fixation, a molybdenum deficiency may bring about a nitrogen deficiency if the nitrogen source is primarily nitrate or if the plant depends on symbiotic nitrogen fixation. Although plants require only small amounts of molybdenum, some soils supply inadequate levels. Small additions of molybdenum to such soils can greatly enhance crop or forage growth at negligible cost.

Analysis of Plant Tissues Reveals Mineral Deficiencies

Requirements for mineral elements change during the growth and development of a plant. In crop plants, nutrient levels at certain stages of growth influence the yield of the economically important tissues (tuber, grain, and so on). To optimize yields, farmers use analyses of nutrient levels in soil and in plant tissue to determine fertilizer schedules.

Soil analysis is the chemical determination of the nutrient content in a soil sample from the root zone. As discussed later in the chapter, both the chemistry and the biology of soils are complex, and the results of soil analyses vary with sampling methods, storage conditions for the

samples, and nutrient extraction techniques. Perhaps more important is that a particular soil analysis reflects the levels of nutrients *potentially* available to the plant roots from the soil, but soil analysis does not tell us how much of a particular mineral nutrient the plant actually needs or is able to absorb. This additional information is best determined by plant tissue analysis.

Proper use of **plant tissue analysis** requires an understanding of the relationship between plant growth (or yield) and the mineral concentration of plant tissue samples (Bouma 1983). As the data plot in Figure 5.3 shows, when the nutrient concentration in a tissue sample is low, growth is reduced. In this **deficiency zone** of the curve, an increase in nutrient availability is directly related to an increase in growth or yield. As the nutrient availability continues to increase, a point is reached at which further addition of nutrients is no longer related to increases in growth or yield but is reflected in increased tissue concentrations. This region of the curve is often called the **adequate zone**.

The transition between the deficiency and adequate zones of the curve reveals the **critical concentration** of the nutrient (see Figure 5.3), which may be defined as the minimum tissue content of the nutrient that is correlated with maximal growth or yield. As the nutrient concentration of the tissue increases beyond the adequate zone, growth or yield declines because of toxicity (this is the **toxic zone**).

To evaluate the relationship between growth and tissue nutrient concentration, researchers grow plants in soil or nutrient solution in which all the nutrients are present in

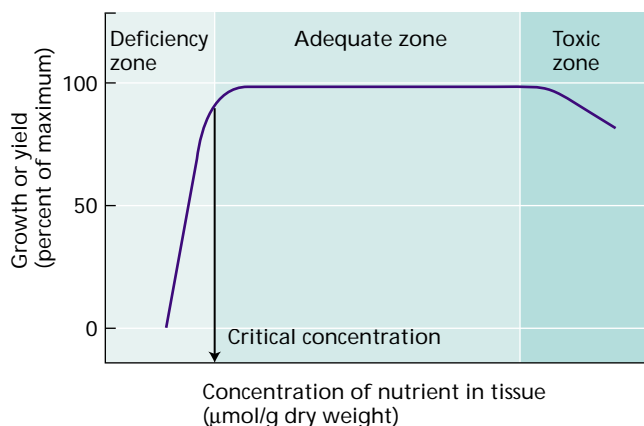


FIGURE 5.3 Relationship between yield (or growth) and the nutrient content of the plant tissue. The yield parameter may be expressed in terms of shoot dry weight or height. Three zones—deficiency, adequate, and toxic—are indicated on the graph. To yield data of this type, plants are grown under conditions in which the concentration of one essential nutrient is varied while all others are in adequate supply. The effect of varying the concentration of this nutrient during plant growth is reflected in the growth or yield. The critical concentration for that nutrient is the concentration below which yield or growth is reduced.

adequate amounts except the nutrient under consideration. At the start of the experiment, the limiting nutrient is added in increasing concentrations to different sets of plants, and the concentrations of the nutrient in specific tissues are correlated with a particular measure of growth or yield. Several curves are established for each element, one for each tissue and tissue age.

Because agricultural soils are often limited in the elements nitrogen, phosphorus, and potassium, many farmers routinely use, at a minimum, curves for these elements. If a nutrient deficiency is suspected, steps are taken to correct the deficiency before it reduces growth or yield. Plant analysis has proven useful in establishing fertilizer schedules that sustain yields and ensure the food quality of many crops.

TREATING NUTRITIONAL DEFICIENCIES

Many traditional and subsistence farming practices promote the recycling of mineral elements. Crop plants absorb the nutrients from the soil, humans and animals consume locally grown crops, and crop residues and manure from humans and animals return the nutrients to the soil. The main losses of nutrients from such agricultural systems ensue from leaching that carries dissolved ions away with drainage water. In acid soils, leaching may be decreased by the addition of lime—a mix of CaO , CaCO_3 , and Ca(OH)_2 —to make the soil more alkaline because many mineral elements form less soluble compounds when the pH is higher than 6 (Figure 5.4).

In the high-production agricultural systems of industrial countries, the unidirectional removal of nutrients from the soil to the crop can become significant because a large portion of crop biomass leaves the area of cultivation. Plants synthesize all their components from basic inorganic substances and sunlight, so it is important to restore these lost nutrients to the soil through the addition of fertilizers.

Crop Yields Can Be Improved by Addition of Fertilizers

Most chemical fertilizers contain inorganic salts of the macronutrients nitrogen, phosphorus, and potassium (see Table 5.1). Fertilizers that contain only one of these three nutrients are termed **straight fertilizers**. Some examples of straight fertilizers are superphosphate, ammonium nitrate, and muriate of potash (a source of potassium). Fertilizers that contain two or more mineral nutrients are called **compound fertilizers** or **mixed fertilizers**, and the numbers on the package label, such as 10-14-10, refer to the effective percentages of N, P_2O_5 , and K_2O , respectively, in the fertilizer.

With long-term agricultural production, consumption of micronutrients can reach a point at which they, too, must be added to the soil as fertilizers. Adding micronutrients to the soil may also be necessary to correct a preexisting deficiency. For example, some soils in the United States are

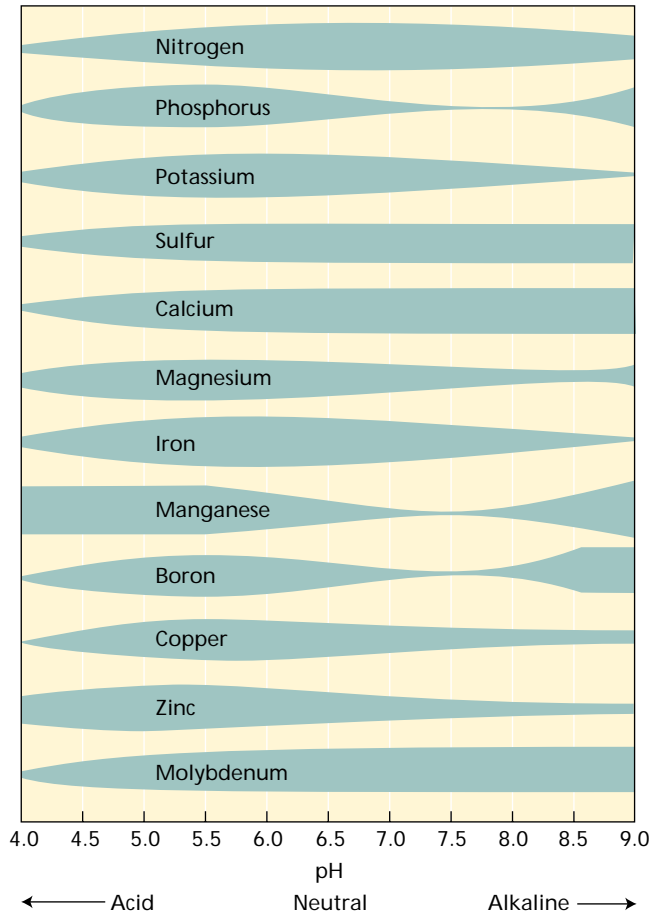


FIGURE 5.4 Influence of soil pH on the availability of nutrient elements in organic soils. The width of the shaded areas indicates the degree of nutrient availability to the plant root. All of these nutrients are available in the pH range of 5.5 to 6.5. (From Lucas and Davis 1961.)

deficient in boron, copper, zinc, manganese, molybdenum, or iron (Mengel and Kirkby 1987) and can benefit from nutrient supplementation.

Chemicals may also be applied to the soil to modify soil pH. As Figure 5.4 shows, soil pH affects the availability of all mineral nutrients. Addition of lime, as mentioned previously, can raise the pH of acidic soils; addition of elemental sulfur can lower the pH of alkaline soils. In the latter case, microorganisms absorb the sulfur and subsequently release sulfate and hydrogen ions that acidify the soil.

Organic fertilizers, in contrast to chemical fertilizers, originate from the residues of plant or animal life or from natural rock deposits. Plant and animal residues contain many of the nutrient elements in the form of organic compounds. Before crop plants can acquire the nutrient elements from these residues, the organic compounds must be broken down, usually by the action of soil microorganisms through a process called **mineralization**. Mineralization depends on many factors, including temperature,

water and oxygen availability, and the type and number of microorganisms present in the soil.

As a consequence, the rate of mineralization is highly variable, and nutrients from organic residues become available to plants over periods that range from days to months to years. The slow rate of mineralization hinders efficient fertilizer use, so farms that rely solely on organic fertilizers may require the addition of substantially more nitrogen or phosphorus and suffer even higher nutrient losses than farms that use chemical fertilizers. Residues from organic fertilizers do improve the physical structure of most soils, enhancing water retention during drought and increasing drainage in wet weather.

Some Mineral Nutrients Can Be Absorbed by Leaves

In addition to nutrients being added to the soil as fertilizers, some mineral nutrients can be applied to the leaves as sprays, in a process known as **foliar application**, and the leaves can absorb the applied nutrients. In some cases, this method can have agronomic advantages over the application of nutrients to the soil. Foliar application can reduce the lag time between application and uptake by the plant, which could be important during a phase of rapid growth. It can also circumvent the problem of restricted uptake of a nutrient from the soil. For example, foliar application of mineral nutrients such as iron, manganese, and copper may be more efficient than application through the soil, where they are adsorbed on soil particles and hence are less available to the root system.

Nutrient uptake by plant leaves is most effective when the nutrient solution remains on the leaf as a thin film (Mengel and Kirkby 1987). Production of a thin film often requires that the nutrient solutions be supplemented with surfactant chemicals, such as the detergent Tween 80, that reduce surface tension. Nutrient movement into the plant seems to involve diffusion through the cuticle and uptake by leaf cells. Although uptake through the stomatal pore could provide a pathway into the leaf, the architecture of the pore (see Figures 4.13 and 4.14) largely prevents liquid penetration (Ziegler 1987).

For foliar nutrient application to be successful, damage to the leaves must be minimized. If foliar sprays are applied on a hot day, when evaporation is high, salts may accumulate on the leaf surface and cause burning or scorching. Spraying on cool days or in the evening helps to alleviate this problem. Addition of lime to the spray diminishes the solubility of many nutrients and limits toxicity. Foliar application has proved economically successful mainly with tree crops and vines such as grapes, but it is also used with cereals. Nutrients applied to the leaves could save an orchard or vineyard when soil-applied nutrients would be too slow to correct a deficiency. In wheat, nitrogen applied to the leaves during the later stages of growth enhances the protein content of seeds.

SOIL, ROOTS, AND MICROBES

The soil is a complex physical, chemical, and biological substrate. It is a heterogeneous material containing solid, liquid, and gaseous phases (see Chapter 4). All of these phases interact with mineral elements. The inorganic particles of the solid phase provide a reservoir of potassium, calcium, magnesium, and iron. Also associated with this solid phase are organic compounds containing nitrogen, phosphorus, and sulfur, among other elements. The liquid phase of the soil constitutes the soil solution, which contains dissolved mineral ions and serves as the medium for ion movement to the root surface. Gases such as oxygen, carbon dioxide, and nitrogen are dissolved in the soil solution, but in roots gases are exchanged predominantly through the air gaps between soil particles.

From a biological perspective, soil constitutes a diverse ecosystem in which plant roots and microorganisms compete strongly for mineral nutrients. In spite of this competition, roots and microorganisms can form alliances for their mutual benefit (**symbioses**, singular *symbiosis*). In this section we will discuss the importance of soil properties, root structure, and mycorrhizal symbiotic relationships to plant mineral nutrition. Chapter 12 addresses symbiotic relationships with nitrogen-fixing bacteria.

Negatively Charged Soil Particles Affect the Adsorption of Mineral Nutrients

Soil particles, both inorganic and organic, have predominantly negative charges on their surfaces. Many inorganic soil particles are crystal lattices that are tetrahedral arrangements of the cationic forms of aluminum and silicon (Al^{3+} and Si^{4+}) bound to oxygen atoms, thus forming aluminates and silicates. When cations of lesser charge replace Al^{3+} and Si^{4+} , inorganic soil particles become negatively charged.

Organic soil particles originate from the products of the microbial decomposition of dead plants, animals, and microorganisms. The negative surface charges of organic particles result from the dissociation of hydrogen ions from the carboxylic acid and phenolic groups present in this component of the soil. Most of the world's soil particles, however, are inorganic.

Inorganic soils are categorized by particle size:

- Gravel has particles larger than 2 mm.
- Coarse sand has particles between 0.2 and 2 mm.
- Fine sand has particles between 0.02 and 0.2 mm.

- Silt has particles between 0.002 and 0.02 mm.
- Clay has particles smaller than 0.002 mm (see Table 4.1).

The silicate-containing clay materials are further divided into three major groups—kaolinite, illite, and montmorillonite—based on differences in their structure and physical properties (Table 5.5). The kaolinite group is generally found in well-weathered soils; the montmorillonite and illite groups are found in less weathered soils.

Mineral cations such as ammonium (NH_4^+) and potassium (K^+) adsorb to the negative surface charges of inorganic and organic soil particles. This cation adsorption is an important factor in soil fertility. Mineral cations adsorbed on the surface of soil particles are not easily lost when the soil is leached by water, and they provide a nutrient reserve available to plant roots. Mineral nutrients adsorbed in this way can be replaced by other cations in a process known as **cation exchange** (Figure 5.5). The degree to which a soil can adsorb and exchange ions is termed its *cation exchange capacity (CEC)* and is highly dependent on the soil type. A soil with higher cation exchange capacity generally has a larger reserve of mineral nutrients.

Mineral anions such as nitrate (NO_3^-) and chloride (Cl^-) tend to be repelled by the negative charge on the surface of soil particles and remain dissolved in the soil solution. Thus the anion exchange capacity of most agricultural soils is small compared to the cation exchange capacity. Among anions, nitrate remains mobile in the soil solution, where it is susceptible to leaching by water moving through the soil.

Phosphate ions (H_2PO_4^-) may bind to soil particles containing aluminum or iron because the positively charged iron and aluminum ions (Fe^{2+} , Fe^{3+} , and Al^{3+}) have hydroxyl (OH^-) groups that exchange with phosphate. As a result, phosphate can be tightly bound, and its mobility and availability in soil can limit plant growth.

Sulfate (SO_4^{2-}) in the presence of calcium (Ca^{2+}) forms gypsum (CaSO_4). Gypsum is only slightly soluble, but it releases sufficient sulfate to support plant growth. Most

TABLE 5.5
Comparison of properties of three major types of silicate clays found in the soil

Property	Type of clay		
	Montmorillonite	Illite	Kaolinite
Size (μm)	0.01–1.0	0.1–2.0	0.1–5.0
Shape	Irregular flakes	Irregular flakes	Hexagonal crystals
Cohesion	High	Medium	Low
Water-swelling capacity	High	Medium	Low
Cation exchange capacity (milliequivalents 100 g^{-1})	80–100	15–40	3–15

Source: After Brady 1974.

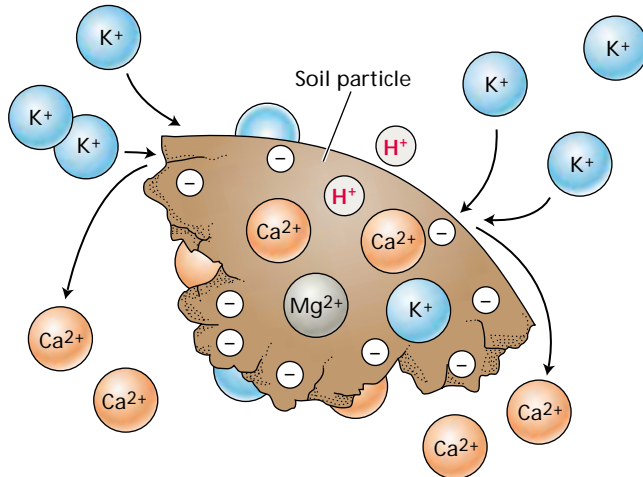


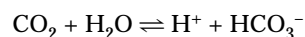
FIGURE 5.5 The principle of cation exchange on the surface of a soil particle. Cations are bound to the surface of soil particles because the surface is negatively charged. Addition of a cation such as potassium (K^+) can displace another cation such as calcium (Ca^{2+}) from its binding on the surface of the soil particle and make it available for uptake by the root.

nonacid soils contain substantial amounts of calcium; consequently, sulfate mobility in these soils is low, so sulfate is not highly susceptible to leaching.

Soil pH Affects Nutrient Availability, Soil Microbes, and Root Growth

Hydrogen ion concentration (pH) is an important property of soils because it affects the growth of plant roots and soil microorganisms. Root growth is generally favored in slightly acidic soils, at pH values between 5.5 and 6.5. Fungi generally predominate in acidic soils; bacteria become more prevalent in alkaline soils. Soil pH determines the availability of soil nutrients (see Figure 5.4). Acidity promotes the weathering of rocks that releases K^+ , Mg^{2+} , Ca^{2+} , and Mn^{2+} and increases the solubility of carbonates, sulfates, and phosphates. Increasing the solubility of nutrients facilitates their availability to roots.

Major factors that lower the soil pH are the decomposition of organic matter and the amount of rainfall. Carbon dioxide is produced as a result of the decomposition of organic material and equilibrates with soil water in the following reaction:



This reaction releases hydrogen ions (H^+), lowering the pH of the soil. Microbial decomposition of organic material also produces ammonia and hydrogen sulfide that can be oxidized in the soil to form the strong acids nitric acid (HNO_3) and sulfuric acid (H_2SO_4), respectively. Hydrogen ions also displace K^+ , Mg^{2+} , Ca^{2+} , and Mn^{2+} from the cation

exchange complex in a soil. Leaching then may remove these ions from the upper soil layers, leaving a more acid soil. By contrast, the weathering of rock in arid regions releases K^+ , Mg^{2+} , Ca^{2+} , and Mn^{2+} to the soil, but because of the low rainfall, these ions do not leach from the upper soil layers, and the soil remains alkaline.

Excess Minerals in the Soil Limit Plant Growth

When excess minerals are present in the soil, the soil is said to be saline, and plant growth may be restricted if these mineral ions reach levels that limit water availability or exceed the adequate zone for a particular nutrient (see Chapter 25). Sodium chloride and sodium sulfate are the most common salts in saline soils. Excess minerals in soils can be a major problem in arid and semiarid regions because rainfall is insufficient to leach the mineral ions from the soil layers near the surface. Irrigated agriculture fosters soil salinization if insufficient water is applied to leach the salt below the rooting zone. Irrigation water can contain 100 to 1000 g of minerals per cubic meter. An average crop requires about 4000 m^3 of water per acre. Consequently, 400 to 4000 kg of minerals may be added to the soil per crop (Marschner 1995).

In saline soil, plants encounter **salt stress**. Whereas many plants are affected adversely by the presence of relatively low levels of salt, other plants can survive high levels (**salt-tolerant plants**) or even thrive (**halophytes**) under such conditions. The mechanisms by which plants tolerate salinity are complex (see Chapter 25), involving molecular synthesis, enzyme induction, and membrane transport. In some species, excess minerals are not taken up; in others, minerals are taken up but excreted from the plant by salt glands associated with the leaves. To prevent toxic buildup of mineral ions in the cytosol, many plants may sequester them in the vacuole (Stewart and Ahmad 1983). Efforts are under way to bestow salt tolerance on salt-sensitive crop species using both classic plant breeding and molecular biology (Hasegawa et al. 2000).

Another important problem with excess minerals is the accumulation of heavy metals in the soil, which can cause severe toxicity in plants as well as humans (see [Web Essay 5.1](#)). Heavy metals include zinc, copper, cobalt, nickel, mercury, lead, cadmium, silver, and chromium (Berry and Wallace 1981).

Plants Develop Extensive Root Systems

The ability of plants to obtain both water and mineral nutrients from the soil is related to their capacity to develop an extensive root system. In the late 1930s, H. J. Dittmer examined the root system of a single winter rye plant after 16 weeks of growth and estimated that the plant had 13×10^6 primary and lateral root axes, extending more than 500 km in length and providing 200 m^2 of surface area (Dittmer 1937). This plant also had more than 10^{10} root hairs, providing another 300 m^2 of surface area.

In the desert, the roots of mesquite (genus *Prosopis*) may extend down more than 50 m to reach groundwater. Annual crop plants have roots that usually grow between 0.1 and 2.0 m in depth and extend laterally to distances of 0.3 to 1.0 m. In orchards, the major root systems of trees planted 1 m apart reach a total length of 12 to 18 km per tree. The annual production of roots in natural ecosystems may easily surpass that of shoots, so in many respects, the aboveground portions of a plant represent only “the tip of an iceberg.”

Plant roots may grow continuously throughout the year. Their proliferation, however, depends on the availability of water and minerals in the immediate microenvironment surrounding the root, the so-called **rhizosphere**. If the rhizosphere is poor in nutrients or too dry, root growth is slow. As rhizosphere conditions improve, root growth increases. If fertilization and irrigation provide abundant nutrients and water, root growth may not keep pace with shoot growth. Plant growth under such conditions becomes carbohydrate limited, and a relatively small root system meets the nutrient needs of the whole plant (Bloom et al. 1993). Roots growing below the soil surface are studied by special techniques (see [Web Topic 5.2](#)).

Root Systems Differ in Form but Are Based on Common Structures

The *form* of the root system differs greatly among plant species. In monocots, root development starts with the emergence of three to six **primary** (or seminal) root axes from the germinating seed. With further growth, the plant extends new adventitious roots, called **nodal roots** or *brace roots*. Over time, the primary and nodal root axes grow and branch extensively to form a complex fibrous root system (Figure 5.6). In fibrous root systems, all the roots generally have the same diameter (except where environmental conditions or pathogenic interactions modify the root structure), so it is difficult to distinguish a main root axis.

In contrast to monocots, dicots develop root systems with a main single root axis, called a **taproot**, which may thicken as a result of secondary cambial activity. From this main root axis, lateral roots develop to form an extensively branched root system (Figure 5.7).

The development of the root system in both monocots and dicots depends on the activity of the root apical meristem and the production of lateral root meristems. Figure 5.8 shows a generalized diagram of the apical region of a plant root and identifies the three zones of activity: meristematic, elongation, and maturation.

In the **meristematic zone**, cells divide both in the direction of the root base to form cells that will differentiate into the tissues of the functional root and in the direction of the root apex to form the **root cap**. The root cap protects the delicate meristematic cells as the root moves through the soil. It also secretes a gelatinous material called *mucigel*, which commonly surrounds the root tip. The precise function of the mucigel is uncertain, but it has been suggested

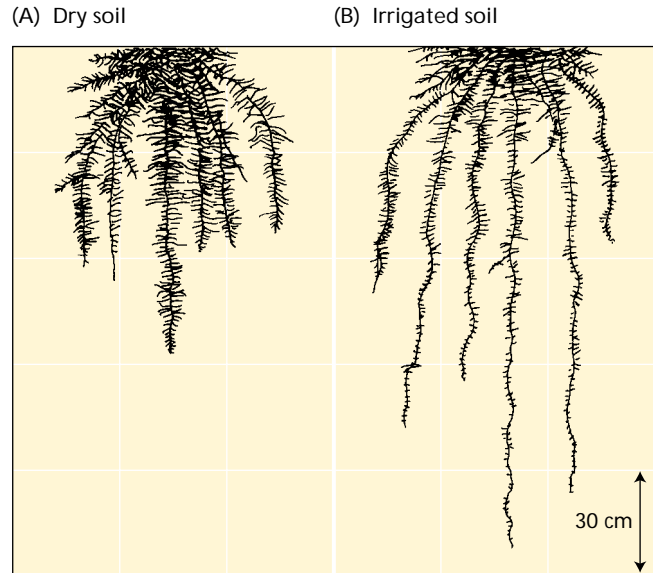


FIGURE 5.6 Fibrous root systems of wheat (a monocot). (A) The root system of a mature (3-month-old) wheat plant growing in dry soil. (B) The root system of a wheat plant growing in irrigated soil. It is apparent that the morphology of the root system is affected by the amount of water present in the soil. In a fibrous root system, the primary root axes are no longer distinguishable. (After Weaver 1926.)

that it lubricates the penetration of the root through the soil, protects the root apex from desiccation, promotes the transfer of nutrients to the root, or affects the interaction between roots and soil microorganisms (Russell 1977). The root cap is central to the perception of gravity, the signal that directs the growth of roots downward. This process is termed the **gravitropic response** (see Chapter 19).

Cell division at the root apex proper is relatively slow; thus this region is called the **quiescent center**. After a few generations of slow cell divisions, root cells displaced from the apex by about 0.1 mm begin to divide more rapidly. Cell division again tapers off at about 0.4 mm from the apex, and the cells expand equally in all directions.

The **elongation zone** begins 0.7 to 1.5 mm from the apex (see Figure 5.8). In this zone, cells elongate rapidly and undergo a final round of divisions to produce a central ring of cells called the **endodermis**. The walls of this endodermal cell layer become thickened, and suberin (see Chapter 13) deposited on the radial walls forms the **Casparian strip**, a hydrophobic structure that prevents the apoplastic movement of water or solutes across the root (see Figure 4.3). The endodermis divides the root into two regions: the **cortex** toward the outside and the **stele** toward the inside. The stele contains the vascular elements of the root: the **phloem**, which transports metabolites from the shoot to the root, and the **xylem**, which transports water and solutes to the shoot.

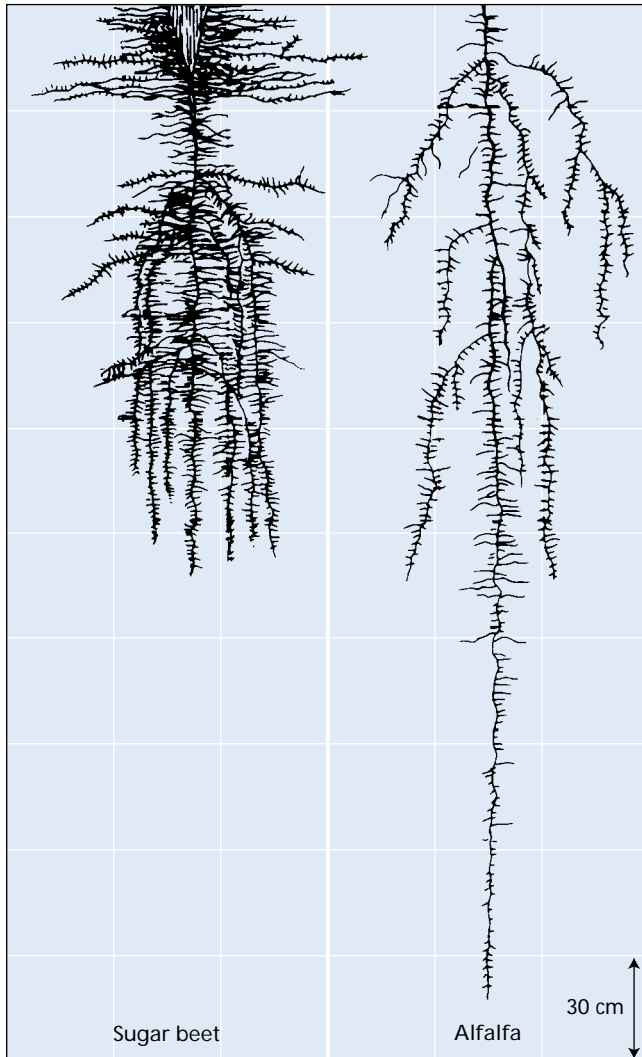


FIGURE 5.7 Taproot system of two adequately watered dicots: sugar beet and alfalfa. The sugar beet root system is typical of 5 months of growth; the alfalfa root system is typical of 2 years of growth. In both dicots, the root system shows a major vertical root axis. In the case of sugar beet, the upper portion of the taproot system is thickened because of its function as storage tissue. (After Weaver 1926.)

Phloem develops more rapidly than xylem, attesting to the fact that phloem function is critical near the root apex. Large quantities of carbohydrates must flow through the phloem to the growing apical zones in order to support cell division and elongation. Carbohydrates provide rapidly growing cells with an energy source and with the carbon skeletons required to synthesize organic compounds. Six-carbon sugars (hexoses) also function as osmotically active solutes in the root tissue. At the root apex, where the phloem is not yet developed, carbohydrate movement depends on symplastic diffusion and is relatively slow

(Bret-Harte and Silk 1994). The low rates of cell division in the quiescent center may result from the fact that insufficient carbohydrates reach this centrally located region or that this area is kept in an oxidized state (see [Web Essay 5.2](#)).

Root hairs, with their large surface area for absorption of water and solutes, first appear in the **maturation zone** (see Figure 5.8), and it is here that the xylem develops the capacity to translocate substantial quantities of water and solutes to the shoot.

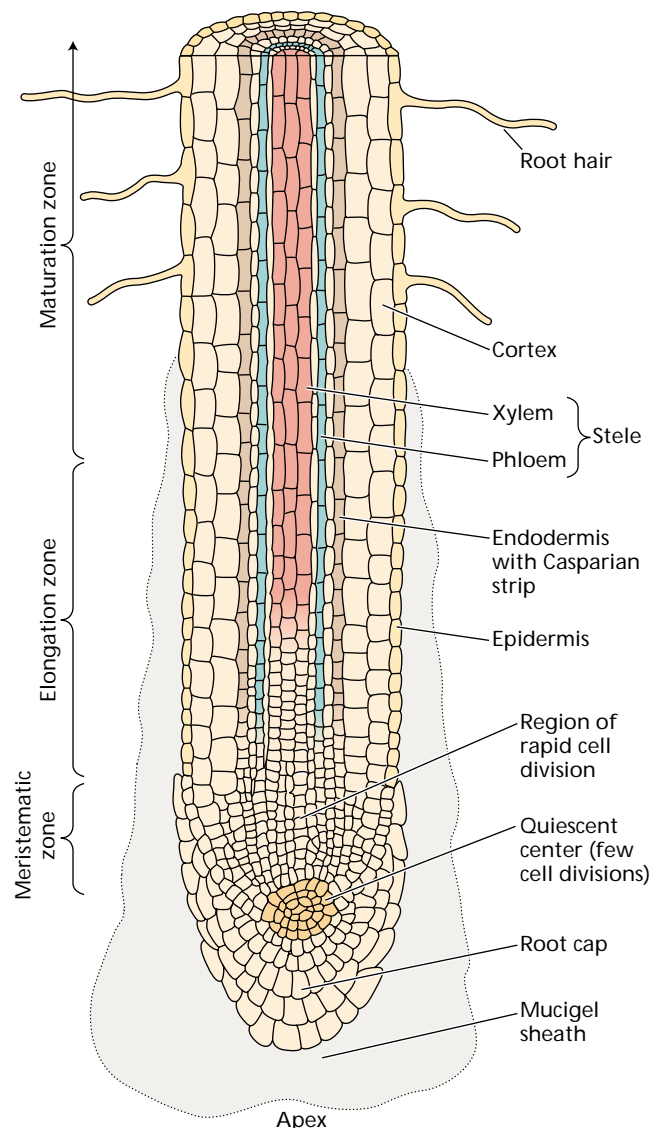


FIGURE 5.8 Diagrammatic longitudinal section of the apical region of the root. The meristematic cells are located near the tip of the root. These cells generate the root cap and the upper tissues of the root. In the elongation zone, cells differentiate to produce xylem, phloem, and cortex. Root hairs, formed in epidermal cells, first appear in the maturation zone.

Different Areas of the Root Absorb Different Mineral Ions

The precise point of entry of minerals into the root system has been a topic of considerable interest. Some researchers have claimed that nutrients are absorbed only at the apical regions of the root axes or branches (Bar-Yosef et al. 1972); others claim that nutrients are absorbed over the entire root surface (Nye and Tinker 1977). Experimental evidence supports both possibilities, depending on the plant species and the nutrient being investigated:

- Root absorption of calcium in barley appears to be restricted to the apical region.
- Iron may be taken up either at the apical region, as in barley (Clarkson 1985), or over the entire root surface, as in corn (Kashirad et al. 1973).
- Potassium, nitrate, ammonium, and phosphate can be absorbed freely at all locations of the root surface (Clarkson 1985), but in corn the elongation zone has the maximum rates of potassium accumulation (Sharp et al. 1990) and nitrate absorption (Taylor and Bloom 1998).
- In corn and rice, the root apex absorbs ammonium more rapidly than the elongation zone does (Colmer and Bloom 1998).
- In several species, root hairs are the most active in phosphate absorption (Fohse et al. 1991).

The high rates of nutrient absorption in the apical root zones result from the strong demand for nutrients in these tissues and the relatively high nutrient availability in the soil surrounding them. For example, cell elongation depends on the accumulation of solutes such as potassium, chloride, and nitrate to increase the osmotic pressure within the cell (see Chapter 15). Ammonium is the preferred nitrogen source to support cell division in the meristem because meristematic tissues are often carbohydrate limited, and the assimilation of ammonium consumes less energy than that of nitrate (see Chapter 12). The root apex and root hairs grow into fresh soil, where nutrients have not yet been depleted.

Within the soil, nutrients can move to the root surface both by bulk flow and by diffusion (see Chapter 3). In bulk flow, nutrients are carried by water moving through the soil toward the root. The amount of nutrient provided to the root by bulk flow depends on the rate of water flow through the soil toward the plant, which depends on transpiration rates and on nutrient levels in the soil solution. When both the rate of water flow and the concentrations of nutrients in the soil solution are high, bulk flow can play an important role in nutrient supply.

In diffusion, mineral nutrients move from a region of higher concentration to a region of lower concentration. Nutrient uptake by the roots lowers the concentration of nutrients at the root surface, generating concentration gradients in the soil solution surrounding the root. Diffusion

of nutrients down their concentration gradient and bulk flow resulting from transpiration can increase nutrient availability at the root surface.

When absorption of nutrients by the roots is high and the nutrient concentration in the soil is low, bulk flow can supply only a small fraction of the total nutrient requirement (Mengel and Kirkby 1987). Under these conditions, diffusion rates limit the movement of nutrients to the root surface. When diffusion is too slow to maintain high nutrient concentrations near the root, a **nutrient depletion zone** forms adjacent to the root surface (Figure 5.9). This zone extends from about 0.2 to 2.0 mm from the root surface, depending on the mobility of the nutrient in the soil.

The formation of a depletion zone tells us something important about mineral nutrition: Because roots deplete the mineral supply in the rhizosphere, their effectiveness in mining minerals from the soil is determined not only by the rate at which they can remove nutrients from the soil solution, but by their continuous growth. *Without growth, roots would rapidly deplete the soil adjacent to their surface. Optimal nutrient acquisition therefore depends both on the capacity for nutrient uptake and on the ability of the root system to grow into fresh soil.*

Mycorrhizal Fungi Facilitate Nutrient Uptake by Roots

Our discussion thus far has centered on the direct acquisition of mineral elements by the root, but this process may be modified by the association of mycorrhizal fungi with the root system. **Mycorrhizae** (singular *mycorrhiza*, from the Greek words for “fungus” and “root”) are not unusual; in fact, they are widespread under natural conditions. Much of the world’s vegetation appears to have roots associated

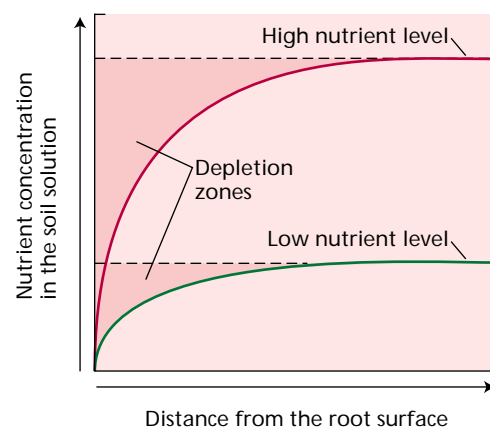


FIGURE 5.9 Formation of a nutrient depletion zone in the region of the soil adjacent to the plant root. A nutrient depletion zone forms when the rate of nutrient uptake by the cells of the root exceeds the rate of replacement of the nutrient by diffusion in the soil solution. This depletion causes a localized decrease in the nutrient concentration in the area adjacent to the root surface. (After Mengel and Kirkby 1987.)

with mycorrhizal fungi: 83% of dicots, 79% of monocots, and all gymnosperms regularly form mycorrhizal associations (Wilcox 1991).

On the other hand, plants from the families Cruciferae (cabbage), Chenopodiaceae (spinach), and Proteaceae (macadamia nuts), as well as aquatic plants, rarely if ever have mycorrhizae. Mycorrhizae are absent from roots in very dry, saline, or flooded soils, or where soil fertility is extreme, either high or low. In particular, plants grown under hydroponics and young, rapidly growing crop plants seldom have mycorrhizae.

Mycorrhizal fungi are composed of fine, tubular filaments called *hyphae* (singular *hypha*). The mass of hyphae that forms the body of the fungus is called the *mycelium* (plural *mycelia*). There are two major classes of mycorrhizal fungi: ectotrophic mycorrhizae and vesicular-arbuscular mycorrhizae (Smith et al. 1997). Minor classes of mycorrhizal fungi include the ericaceous and orchidaceous mycorrhizae, which may have limited importance in terms of mineral nutrient uptake.

Ectotrophic mycorrhizal fungi typically show a thick sheath, or “mantle,” of fungal mycelium around the roots, and some of the mycelium penetrates between the cortical cells (Figure 5.10). The cortical cells themselves are not penetrated by the fungal hyphae but instead are surrounded by a network of hyphae called the **Hartig net**. Often the amount of fungal mycelium is so extensive that its total

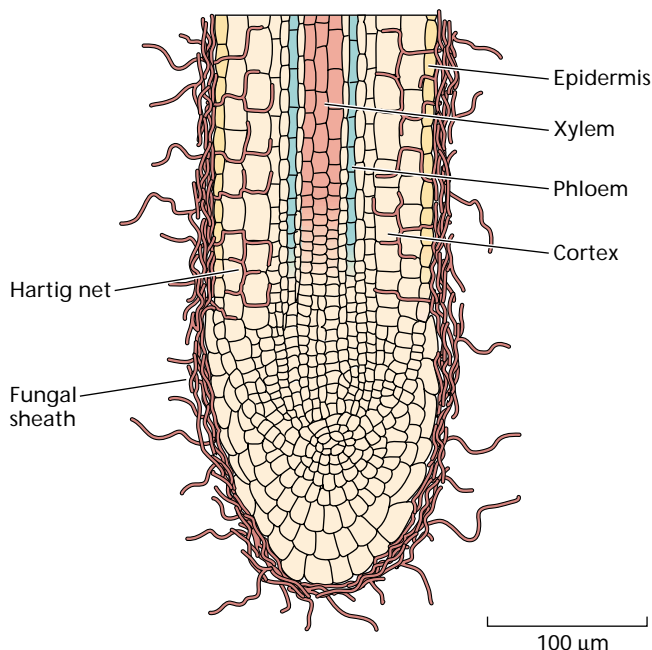


FIGURE 5.10 Root infected with ectotrophic mycorrhizal fungi. In the infected root, the fungal hyphae surround the root to produce a dense fungal sheath and penetrate the intercellular spaces of the cortex to form the Hartig net. The total mass of fungal hyphae may be comparable to the root mass itself. (From Rovira et al. 1983.)

mass is comparable to that of the roots themselves. The fungal mycelium also extends into the soil, away from this compact mantle, where it forms individual hyphae or strands containing fruiting bodies.

The capacity of the root system to absorb nutrients is improved by the presence of external fungal hyphae that are much finer than plant roots and can reach beyond the areas of nutrient-depleted soil near the roots (Clarkson 1985). Ectotrophic mycorrhizal fungi infect exclusively tree species, including gymnosperms and woody angiosperms.

Unlike the ectotrophic mycorrhizal fungi, **vesicular-arbuscular mycorrhizal fungi** do not produce a compact mantle of fungal mycelium around the root. Instead, the hyphae grow in a less dense arrangement, both within the root itself and extending outward from the root into the surrounding soil (Figure 5.11). After entering the root through either the epidermis or a root hair, the hyphae not only extend through the regions between cells but also penetrate individual cells of the cortex. Within the cells, the hyphae can form oval structures called **vesicles** and branched structures called **arbuscules**. The arbuscules appear to be sites of nutrient transfer between the fungus and the host plant.

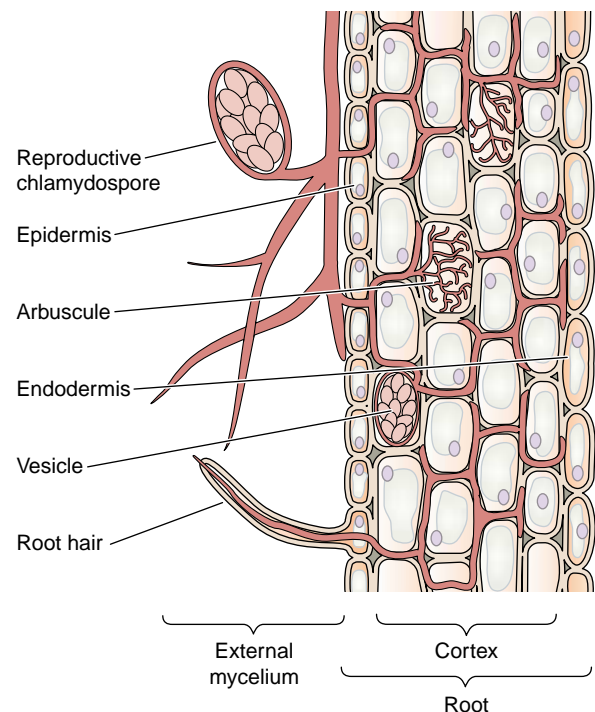


FIGURE 5.11 Association of vesicular-arbuscular mycorrhizal fungi with a section of a plant root. The fungal hyphae grow into the intercellular wall spaces of the cortex and penetrate individual cortical cells. As they extend into the cell, they do not break the plasma membrane or the tonoplast of the host cell. Instead, the hypha is surrounded by these membranes and forms structures known as arbuscules, which participate in nutrient ion exchange between the host plant and the fungus. (From Mauseth 1988.)

Outside the root, the external mycelium can extend several centimeters away from the root and may contain spore-bearing structures. Unlike the ectotrophic mycorrhizae, vesicular-arbuscular mycorrhizae make up only a small mass of fungal material, which is unlikely to exceed 10% of the root weight. Vesicular-arbuscular mycorrhizae are found in association with the roots of most species of herbaceous angiosperms (Smith et al. 1997).

The association of vesicular-arbuscular mycorrhizae with plant roots facilitates the uptake of phosphorus and trace metals such as zinc and copper. By extending beyond the depletion zone for phosphorus around the root, the external mycelium improves phosphorus absorption. Calculations show that a root associated with mycorrhizal fungi can transport phosphate at a rate more than four times higher than that of a root not associated with mycorrhizae (Nye and Tinker 1977). The external mycelium of the ectotrophic mycorrhizae can also absorb phosphate and make it available to the plant. In addition, it has been suggested that ectotrophic mycorrhizae proliferate in the organic litter of the soil and hydrolyze organic phosphorus for transfer to the root (Smith et al. 1997).

Nutrients Move from the Mycorrhizal Fungi to the Root Cells

Little is known about the mechanism by which the mineral nutrients absorbed by mycorrhizal fungi are transferred to the cells of plant roots. With ectotrophic mycorrhizae, inorganic phosphate may simply diffuse from the hyphae in the Hartig net and be absorbed by the root cortical cells. With vesicular-arbuscular mycorrhizae, the situation may be more complex. Nutrients may diffuse from intact arbuscules to root cortical cells. Alternatively, because some root arbuscules are continually degenerating while new ones are forming, degenerating arbuscules may release their internal contents to the host root cells.

A key factor in the extent of mycorrhizal association with the plant root is the nutritional status of the host plant. Moderate deficiency of a nutrient such as phosphorus tends to promote infection, whereas plants with abundant nutrients tend to suppress mycorrhizal infection.

Mycorrhizal association in well-fertilized soils may shift from a symbiotic relationship to a parasitic one in that the fungus still obtains carbohydrates from the host plant, but the host plant no longer benefits from improved nutrient uptake efficiency. Under such conditions, the host plant may treat mycorrhizal fungi as it does other pathogens (Brundrett 1991; Marschner 1995).

SUMMARY

Plants are autotrophic organisms capable of using the energy from sunlight to synthesize all their components

from carbon dioxide, water, and mineral elements. Studies of plant nutrition have shown that specific mineral elements are essential for plant life. These elements are classified as macronutrients or micronutrients, depending on the relative amounts found in plant tissue.

Certain visual symptoms are diagnostic for deficiencies in specific nutrients in higher plants. Nutritional disorders occur because nutrients have key roles in plant metabolism. They serve as components of organic compounds, in energy storage, in plant structures, as enzyme cofactors, and in electron transfer reactions. Mineral nutrition can be studied through the use of hydroponics or aeroponics, which allow the characterization of specific nutrient requirements. Soil and plant tissue analysis can provide information on the nutritional status of the plant-soil system and can suggest corrective actions to avoid deficiencies or toxicities.

When crop plants are grown under modern high-production conditions, substantial amounts of nutrients are removed from the soil. To prevent the development of deficiencies, nutrients can be added back to the soil in the form of fertilizers. Fertilizers that provide nutrients in inorganic forms are called chemical fertilizers; those that derive from plant or animal residues are considered organic fertilizers. In both cases, plants absorb the nutrients primarily as inorganic ions. Most fertilizers are applied to the soil, but some are sprayed on leaves.

The soil is a complex substrate—physically, chemically, and biologically. The size of soil particles and the cation exchange capacity of the soil determine the extent to which a soil provides a reservoir for water and nutrients. Soil pH also has a large influence on the availability of mineral elements to plants.

If mineral elements, especially sodium or heavy metals, are present in excess in the soil, plant growth may be adversely affected. Certain plants are able to tolerate excess mineral elements, and a few species—for example, halophytes in the case of sodium—grow under these extreme conditions.

To obtain nutrients from the soil, plants develop extensive root systems. Roots have a relatively simple structure with radial symmetry and few differentiated cell types. Roots continually deplete the nutrients from the immediate soil around them, and such a simple structure may permit rapid growth into fresh soil.

Plant roots often form associations with mycorrhizal fungi. The fine hyphae of mycorrhizae extend the reach of roots into the surrounding soil and facilitate the acquisition of mineral elements, particularly those like phosphorus that are relatively immobile in the soil. In return, plants provide carbohydrates to the mycorrhizae. Plants tend to suppress mycorrhizal associations under conditions of high nutrient availability.

Web Material

Web Topics

5.1 Symptoms of Deficiency in Essential Minerals

Deficiency symptoms are characteristic of each essential element and can be used as diagnostic for the deficiency. These color pictures illustrate deficiency symptoms for each essential element in a tomato.

5.2 Observing Roots below Ground

The study of roots growing under natural conditions requires means to observe roots below ground. State-of-the-art techniques are described in this essay.

Web Essays

5.1 From Meals to Metals and Back

Heavy metal accumulation by plants is toxic. Understanding of the involved molecular process is helping to develop better phytoremediation crops.

5.2 Redox Control of the Root Quiescent Center

The redox status of the quiescent center seems to control the cell cycle of these cells.

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