

*immobilization* occurs over a wide range of environmental conditions, but activity is maximized at about the same relative moisture and temperature conditions optimum for plant growth. Microbial transformations important to nutrient availability will be detailed in Chapter 4.

## MOVEMENT OF IONS FROM SOILS TO ROOTS

Ion absorption by plant roots requires contact between the ion and the root surface. There are generally three ways in which nutrients reach the root surface: (1) root interception, (2) mass flow, and (3) diffusion. The relative importance of these mechanisms in supplying nutrients to plant roots is shown in Table 2-6.

### Root Interception

Root interception represents exchange of ions through physical contact between the root and mineral surfaces (Fig. 2-18). Ion absorption by root interception is enhanced by increasing the quantity of absorbing roots in a given volume of soil. As roots develop and exploit more soil, soil solution and soil surfaces retaining adsorbed ions are exposed to the increasing root mass. Ions such as  $H^+$  adsorbed to the surface of root hairs may exchange with ions held on the surface of clays and OM because of the intimate contact between roots and soil particles. The ions held by electrostatic forces at these sites oscillate within a certain volume (Fig. 2-18). When the oscillation volumes of two ions ( $H^+$  and  $K^+$ ) overlap, ion exchange occurs. In this way,  $Ca^{+2}$  on a clay surface could then presumably be absorbed by the root and utilized by the plant.

The quantity of nutrients that can come in direct contact with plant roots is the amount in a volume of soil equal to the volume of roots. Roots usually occupy 1–3% of the soil volume.

Root interception of nutrients can be enhanced by *mycorrhiza*, a symbiotic association between fungi and plant roots. The beneficial effect of mycorrhiza is greatest when plants are growing in infertile soils. The extent of mycorrhizal colonization is also enhanced under conditions of slightly acidic soil pH, low P, adequate N, and

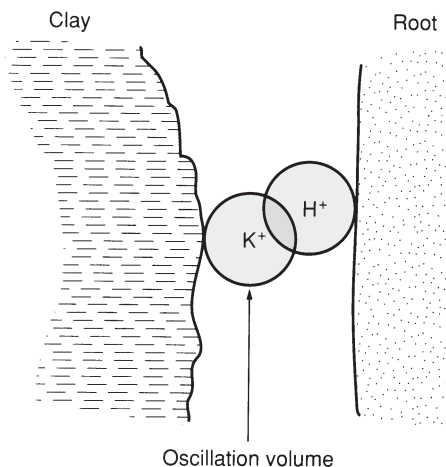
**TABLE 2-6**  
**SIGNIFICANCE OF ROOT INTERCEPTION, MASS FLOW, AND DIFFUSION IN ION TRANSPORT TO CORN ROOTS**

Nutrient	Nutrients Required for 200 bu/a of Corn	Percentage Supplied by		
		Root Interception	Mass Flow	Diffusion
N	225	1	99	0
P	45	2	4	94
K	200	2	20	78
Ca	50	120	440	0
Mg	55	27	280	0
S	25	4	94	2
Cu	0.12	8	400	0
Zn	0.40	25	30	45
B	0.25	8	350	0
Fe	2.5	8	40	52
Mn	10.40	25	130	0
Mo	0.012	8	200	0

Note: The contribution of diffusion was estimated by the difference between total nutrient needs and the amounts supplied by interception and mass flow. If root interception + mass flow  $\geq$  100%, then diffusion = 0.

**Figure 2-18**

Conceptual model for root interception or contact exchange of nutrients between ions on soil and root exchange sites. Overlapping oscillation volumes cause exchange of  $H^+$  on the root with  $K^+$  on the clay mineral surface.



low soil temperatures. The hyphal threads of mycorrhizal fungi act as extensions of plant root systems, resulting in greater soil contact. (See Fig. 5-6 for a diagrammatic representation of a mycorrhizal infected root.) The two major groups of mycorrhizas are ectomycorrhizas and endomycorrhizas. The ectomycorrhizas occur mainly in the tree species of the temperate zones but can also be found in semiarid zones. The endomycorrhizas are more widespread. The roots of most agronomic crops have vesicular arbuscular mycorrhiza. The fungus grows into the cortex. Inside the plant cells, small structures known as arbuscules, considered to be the site of transfer of nutrients from fungi to host plants, are formed. Increased nutrient absorption is due to the larger nutrient-absorbing surface provided by the fungi, which can be up to 10 times that of uninfected roots. Fungal hyphae can extend up to 8 cm into the soil surrounding the roots, thus increasing absorption of nutrients. Enhanced P uptake is the primary cause of improved plant growth from mycorrhiza, which results in improved uptake of other elements (Table 2-7).

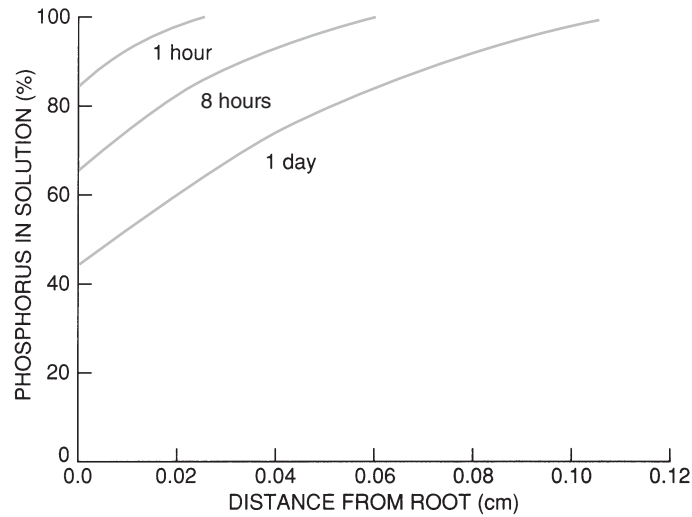
### Mass Flow

Mass flow occurs when ions in soil solution are transported to the root as a result of water uptake (transpiration) by the plant, water evaporation at the soil surface, and percolation of water in the soil profile. Transport of ions in the soil solution to

**TABLE 2-7**  
EFFECT OF INOCULATION OF ENDOMYCORRHIZA AND P ON NUTRIENT CONTENT IN CORN SHOOTS

Nutrient	Content in Shoots ( $\mu g$ )			
	No P		25 ppm P Added	
	No Mycorrhiza	Mycorrhiza	No Mycorrhiza	Mycorrhiza
P	750	1,340	2,970	5,910
K	6,000	9,700	17,500	19,900
Ca	1,200	1,600	2,700	3,500
Mg	430	630	990	1,750
Zn	28	95	48	169
Cu	7	14	12	30
Mn	72	101	159	238
Fe	80	147	161	277

Source: Adapted from Lambert et al., 1979, SSSAJ, 43:976.

**Figure 2-19**

The influence of P uptake on the distribution of P in the soil solution as a function of distance from the root surface.

root surfaces by mass flow is an important factor in supplying nutrients to plants (Table 2-6).

The quantity of nutrients reaching roots by mass flow is determined by the rate of water flow or the water consumption of plants and the average nutrient concentrations in the soil water. Mass flow can supply an excess of  $\text{Ca}^{+2}$ ,  $\text{Mg}^{+2}$ , several micronutrients, and most of the soluble nutrients, such as  $\text{NO}_3^-$ ,  $\text{Cl}^-$ , and  $\text{SO}_4^{-2}$  (Table 2-6). As soil moisture is reduced (increased soil moisture tension), water transport to the root surface decreases. Mass flow is also reduced at low temperatures because transpiration demand by plants and water evaporation at the soil surface decreases at low soil temperature.

## Diffusion

Diffusion occurs when an ion moves from an area of high concentration to one of low concentration. As roots absorb nutrients from the surrounding soil solution, the nutrient concentration at the root surface decreases compared with the “bulk” soil solution concentration (Fig. 2-19).

Therefore, a nutrient concentration gradient is established that causes ions to diffuse toward the root. A high plant requirement for a nutrient results in a large concentration gradient, favoring a high rate of ion diffusion from the soil solution to the root surface. Most of the P and K move to the root by diffusion (Table 2-6). Ion diffusion in soils can be quantified by the following equation (Fick’s law) that helps us understand the factors that influence diffusion in soil:

$$\frac{dC}{dt} = De \cdot A \cdot \frac{dC}{dX}$$

where  $dC/dt$  = rate of diffusion (change in concentration C with time)

$dC/dX$  = concentration gradient (change in concentration with distance)

$De$  = effective diffusion coefficient

$A$  = cross-sectional area through which the ions diffuse

The diffusion equation shows that the rate of nutrient diffusion ( $dC/dt$ ) is directly proportional to the concentration gradient ( $dC/dX$ ). As the difference in nutrient concentration between the root surface and the bulk solution increases, the rate of nutrient diffusion increases. Also, increasing the cross-sectional area for diffusion increases  $dC/dt$ , which means diffusion should be greater in a clay compared to a sand because of greater water-filled pore space. The diffusion rate is also proportional to the diffusion coefficient,  $De$ , which partially controls nutrient diffusion to the root. For

a given spacing between roots,  $D_e$  determines the fraction of nutrients in the soil that can reach the roots during a specific period of plant growth.  $D_e$  is described as follows:

$$D_e = D_w \cdot \theta \cdot \frac{1}{T} \cdot \frac{1}{b}$$

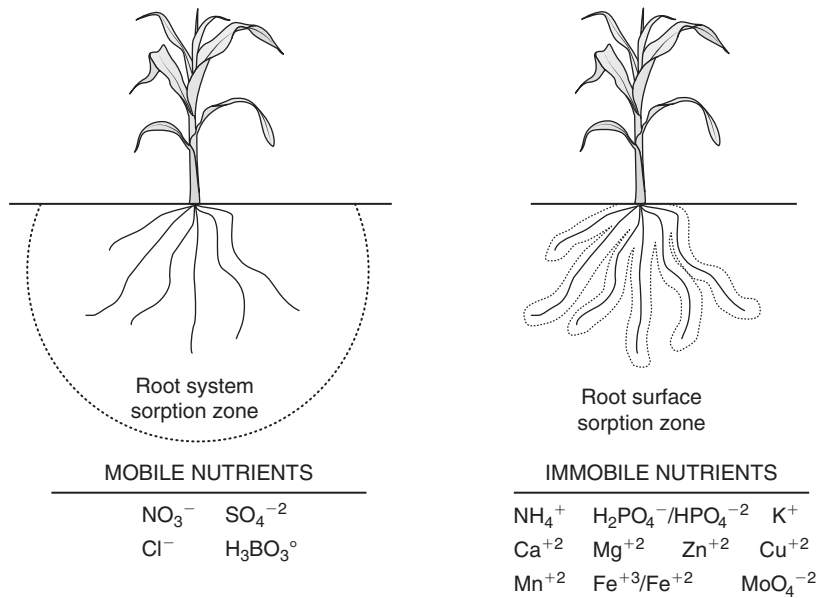
where  $D_w$  = diffusion coefficient in water  
 $\theta$  = volumetric soil water content  
 $T$  = tortuosity factor  
 $b$  = soil BC

This relationship shows the diffusion coefficient in soil ( $D_e$ ) is directly related to the diffusion coefficient for the same nutrient in water ( $D_w$ ). Inherent in the  $D_w$  term is a temperature factor such that increasing temperature increases  $D_w$ , which increases  $D_e$ , and then  $dC/dt$ . Also, as soil moisture content ( $\theta$ ) increases,  $D_e$  increases, which results in an increase in diffusion rate,  $dC/dt$ . As moisture content decreases, moisture films around soil particles become thinner and ion diffusion through these films becomes more *tortuous*. Transport of nutrients to the root surface is most effective at field capacity soil moisture content. Therefore, raising  $\theta$  reduces tortuosity, or the diffusion path length, which in turn increases  $dC/dt$ . Tortuosity ( $T$ ) is also related to soil texture. Nutrients diffusing in coarse-textured soils experience a more tortuous path to the root surface (less water-filled pore space). As  $T$  increases with increasing sand content,  $1/T$  decreases, which reduces the  $D_e$  and thus  $dC/dt$ . While tortuosity is less in clay soils (increasing diffusion rate  $dC/dt$ ), clay soils also have a greater buffer capacity ( $b$ ) than sandy soils, which would decrease  $dC/dt$ . Thus,  $D_e$  is inversely related to  $b$ . Increasing BC of the soil decreases  $D_e$ , which decreases  $dC/dt$ . Compared to a soil with a high BC, a low BC soil would likely have higher nutrient concentration in solution resulting in a higher  $D_e$ , and higher potential  $dC/dt$ . Increasing the solution ion concentration also increases the diffusion gradient,  $dC/dX$ , which contributes to increased  $dC/dt$ .

Ion uptake by roots, which is responsible for creating and maintaining the diffusion gradient, is strongly influenced by temperature. Within the range of about 10–30°C, an increase of 10°C usually causes the rate of ion absorption to go up by a factor of two or more. Nutrient diffusion is slow under most soil conditions and occurs over very short distances in the vicinity of the root surface. Typical diffusion distances are 1 cm for N, 0.2 cm for K, and 0.02 cm for P. The mean distance between corn roots in the top 15 cm of soil is about 0.7 cm, indicating that some nutrients would need to diffuse half of this distance, or 0.35 cm, before they would be in a position to be absorbed by the plant root.

Roots do not absorb all nutrients at the same rate, causing certain ions to accumulate at the root surface, especially during periods of rapid absorption of water. This situation results in back diffusion, where the concentration gradient is away from the root surface and back toward the “bulk” soil solution. Nutrient diffusion away from the root is much less common than diffusion toward the root; however, higher concentrations of some nutrients in the rhizosphere can affect the uptake of other nutrients.

The importance of diffusion and mass flow in supplying ions to the root surface depends on the ability of the solid phase of the soil to replenish or buffer the soil solution (Fig. 2-2). Ion concentrations are influenced by the types of clay minerals in the soil and the distribution of cation and anions on the CEC or AEC. For example, the ease of replacement of  $\text{Ca}^{+2}$  from colloids varies in this order: peat > kaolinite > illite > montmorillonite. An 80% Ca-saturated 2:1 clay provides the same percentage of  $\text{Ca}^{+2}$  release as a 35% Ca-saturated kaolinite or a 25% Ca-saturated peat.

**Figure 2-20**

Relationship between nutrient mobility and nutrient extraction zones. Plants obtain mobile nutrients from the whole soil volume occupied by plant roots. In contrast, plants obtain immobile nutrients from the small soil volume immediately surrounding the plant root.

(Courtesy B. Raun and G. Johnson, Oklahoma State University)

Mass flow and diffusion processes are also important in nutrient management. Soils that exhibit low diffusion rates because of high BC, low soil moisture, or high clay content may require application of immobile nutrients near the roots to maximize nutrient availability and plant uptake.

### Nutrient Mobility in Soil

Inherent in any discussion of ion transport to plant roots is the principle of nutrient mobility in soil. Nutrient mobility varies between ions, where  $\text{NO}_3^-$ ,  $\text{SO}_4^{-2}$ ,  $\text{Cl}^-$  and  $\text{H}_3\text{BO}_3^\circ$  are not strongly attracted to exchange sites and are soluble in soils so they can readily move through the root zone with water. As a result, mobile nutrients within the whole soil volume occupied by the plant root system are available for transport to the root in percolating and transpirational water (Fig. 2-20). The relative mobility of each nutrient will depend on soil pH, temperature, moisture, soil texture, type of clay, and OM content.

Immobile nutrients interact with mineral and OM surfaces, are less soluble, and do not readily move throughout the root zone (Fig. 2-20). While classified as immobile nutrients in soil, some are more mobile than others. Generally,  $\text{NH}_4^+$ ,  $\text{K}^+$ ,  $\text{Ca}^{+2}$ , and  $\text{Mg}^{+2}$  are more soluble and mobile than the micronutrient cations, and much more mobile than  $\text{H}_2\text{PO}_4^-/\text{HPO}_4^{-2}$  and  $\text{MoO}_4^{-2}$ . Since these nutrients are relatively immobile in soil, plant roots access these nutrients from a small volume of soil surrounding individual roots. Plants create a small zone around the root that has very low concentration of these immobile nutrients due to plant uptake. The concentration gradient allows diffusion to transport nutrients that are further away from the root surface toward the root. If the soil has a high BC for an immobile nutrient, then the solution can be replenished and diffusion continues. With a low BC, solution concentration (and diffusion) ultimately decreases, causing a nutrient deficiency.

Understanding nutrient mobility in soils is essential to managing nutrient applications to maximize plant growth and recovery of applied nutrients by the plant (Chapter 10). For example, N can be broadcast or band applied with fairly similar results because of its mobility in soil. However, P is generally placed in concentrated bands because it is generally immobile in soil.

## ION ABSORPTION BY PLANTS

Once nutrients are at the root surface, they enter the outermost root cells where they are transported through the plant. Ion transport out of the root also occurs and can influence rhizosphere pH. Thus, it is important to understand how ions and water move into plant roots. While only a basic description is presented in this text, selected references provide a thorough treatment of ion absorption processes.

Plant uptake of ions from the soil solution can be described by *passive* and *active* processes, where ions passively move to a “boundary” through which ions are actively transported to organs in plant cells that metabolize the nutrient ions. Solution composition or ion concentrations outside and inside of the boundary are controlled by different processes, each essential to plant nutrition and growth.

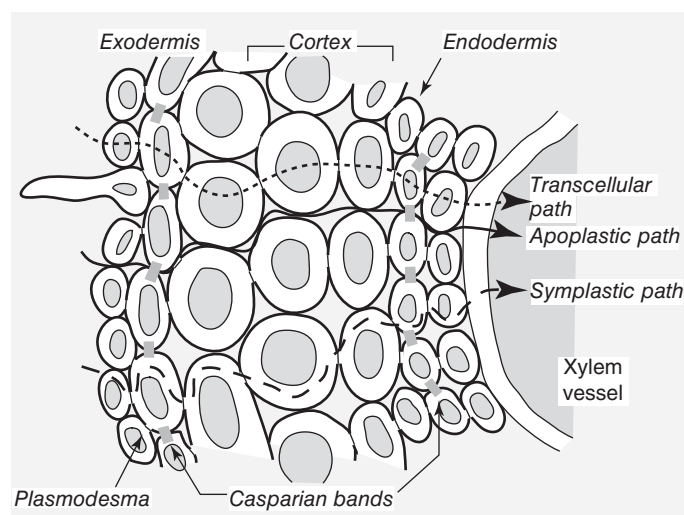
### Water and Ion Uptake by Roots

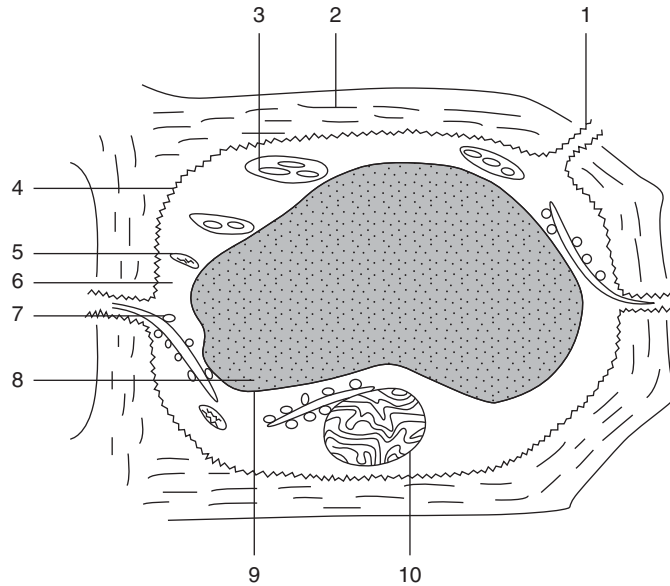
A considerable fraction of the total volume of the root is accessible for the passive absorption of ions. Water and ion uptake occurs at the root hairs and the rest of the root epidermis (Fig. 2-21). The apparent free space or *apoplast* is the intercellular spaces of the epidermal and cortical cells. The apoplast allows transport of water and ions in root tissue regions that do not require transport across an impermeable membrane. Water uptake from the soil into the apoplast occurs through *capillary action* and *osmosis*. Capillary action results when the intercellular space is smaller than the water-filled space in the soil, thus the matrix potential in the cortex is more negative than in the surrounding soil, and water will move to areas of lower water potential. Osmosis is the transport of water from an area of low to high solute concentration.

The *casparian bands* in the endodermis function as an impermeable barrier, which allows the endodermis to select and regulate ion absorption. Water transport through the apoplastic pathway into the xylem vessels occurs primarily in young tissues where casparian bands are not fully developed (Fig. 2-21). In older tissues, the casparian band prevents water and ion transport directly into the xylem. Thus, water and ions entering the cell or cytoplasm must be transported across the plasma membrane (Fig. 2-22). Once inside the cell, water and ion transport can occur through the symplastic pathway through cellular connections or plasmodesma (Fig. 2-22).

The concentration of ions in the apparent free space is normally less than the bulk solution concentration; therefore, diffusion occurs in response to the resulting high to low concentration gradient. Interior surfaces of cells in the cortex are negatively charged, attracting cations. Cation exchange readily occurs along the extracellular surfaces and

**Figure 2-21**  
Cross-section of a plant root. Site of passive uptake is the apparent free space, which is outside of the casparian strip in the cortex.





- |                  |   |
|------------------|---|
| 1. Plasmodesma   | 6. Cytoplasm                            |
| 2. Cell wall     | 7. Endoplasmic reticulum with ribosomes |
| 3. Chloroplast   | 8. Vacuole                              |
| 4. Plasmalemma   | 9. Nucleus                              |
| 5. Mitochondrion | 10. Tonoplast                           |

**Figure 2-22**

Diagram of a plant cell.  
Active ion uptake occurs  
at the plasmalemma.

(Mengel and Kirkby, 1987, Principles  
of Plant Nutrition, IPI.)

explains why cation uptake usually exceeds anion uptake. To maintain electrical neutrality, the root cells release  $H^+$ , decreasing soil solution pH near the root surface. Diffusion and ion exchange are passive processes because uptake into the apoplast is controlled by ion concentration (diffusion) and electrical (ion exchange) gradients.

These processes are nonselective and do not require energy produced from metabolic reactions within the cell.

### Passive and Active Ion Uptake by Cells

In a plant cell, the plasma membrane (plasmalemma) and tonoplast are selectively permeable barriers consisting primarily of phospholipids and proteins that regulate transport of water, ions, and metabolites into the cell and vacuole, respectively (Fig. 2-22). Plasma membranes are permeable to  $O_2$ ,  $CO_2$ , and some neutral compounds; are slightly permeable to water; and are nearly impermeable to inorganic ions and small-molecular-weight organic compounds (i.e., sucrose, amino acids). Proteins are required to transport  $H^+$ , inorganic ions, and organic solutes across the plasma membrane and the tonoplast at rates sufficient to meet the needs of the cell. To maintain a relatively constant internal environment, membrane permeability properties ensure that ions and molecules such as glucose, amino acids, and lipids readily enter the cell, metabolic intermediates remain in the cell, and unneeded compounds leave the cell.

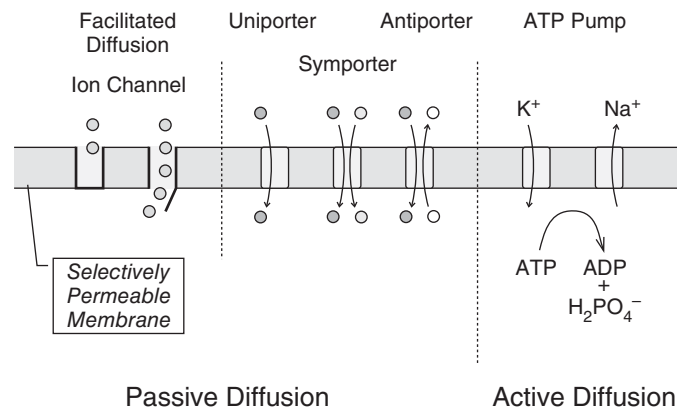
Whether a molecule or ion is transported actively or passively across a membrane (casparian band, plasma membrane, or tonoplast) depends on the concentration and charge of the ion or molecule, which in combination represent the electrochemical driving force. Ions and molecules diffuse from areas of high to low concentrations. Thus, diffusion does not require the plant to expend energy. In contrast, for ions diffusing against the concentration gradient, energy is required. Thus, passive transport across the plasma membrane occurs with the electrochemical potential and active transport occurs against the electrochemical potential, a process that requires the cell to expend energy.

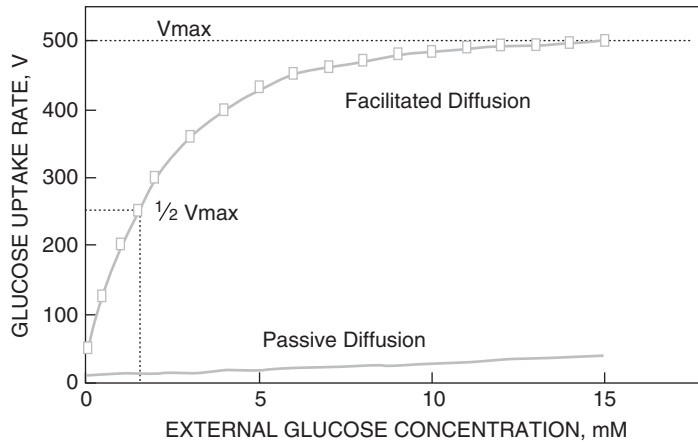
As a result, ion concentration on either side of the plasma membrane and tonoplast is different. The  $H^+$  concentration can be a 1,000-fold higher (lower pH) in the apoplast and vacuole than in the cytoplasm ( $\sim$  pH 7), but  $Ca^{+2}$  concentration gradients can vary over an even wider range ( $Ca^{+2}$  concentration is  $\sim$  100 nM in the cytoplasm). At  $\sim$  pH 7 proteins in the cytoplasm are negatively charged. These and other charge imbalances result in the establishment of an electrical potential gradient at the plasma membrane. This potential creates a strong electric field that provides the energy for ion transport against concentration gradients, and the opening and closing of channels through the selectively permeable membranes (voltage-gated channels).

**Passive transport** *Simple diffusion* through membranes occurs with small, nonpolar molecules (i.e.,  $O_2$ ,  $CO_2$ ). For small, polar species (i.e.,  $H_2O$ , ions, amino acids), specific proteins in the membrane facilitate the diffusion down the electrochemical gradient. This mechanism is referred to as *facilitated diffusion*. These proteins form channels, which can open and close, and through which ions or  $H_2O$  molecules pass in single file at very rapid rates (Fig. 2-23). For example, water movement across the tonoplast and plasma membrane is determined by osmotic pressure gradients and by passive transport through channel proteins called *aquaporins* that act as “water channels” to facilitate water transport across membranes. Aquaporins account for 5–10% of the total protein in a membrane. A  $K^+$  and  $NH_4^+$  transport channel has been suggested that is lined with (–) charges, where  $K^+$  moves across the membrane because of the net negative charge inside the cell. In addition,  $Na^+$  can also enter the cell by facilitated diffusion since the concentration inside is less than that outside the cell; however,  $Na^+$  transport outside the cell requires an active transport mechanism, since it is against the electrochemical gradient.

Another mechanism involves *transporters* or *cotransporters* responsible for the transport of ions and molecules across membranes (Fig. 2-23). Transporter proteins, in contrast to channel proteins, bind only one or a few substrate molecules at a time. After binding a molecule or ion, the transporter undergoes a structural change specific to a specific ion or molecule. As a result, the transport rate across a membrane is slower than that associated with channel proteins. Three types of transporters have been identified. *Uniporters* transport one molecule (i.e., glucose, amino acids) at a time down a concentration gradient. In contrast, *antiporters* and *symporters* catalyze movement of one type of ion or molecule against its concentration gradient coupled to movement of a different ion or molecule down its concentration gradient (Fig. 2-23). Therefore, the energy for *antiporter* and *symporter* transport originates from the electric potential and/or chemical gradient of a secondary ion or molecule, which is often  $H^+$ . The high  $H^+$  concentration in the apoplast provides the energy for symporter

**Figure 2-23**  
Generalized diagram of passive and active transport processes that include protein channels and other facilitated diffusion transport mechanisms, as well as ATP pump mechanism to transport ions and molecules against a concentration gradient.



**Figure 2-24**

Comparison between simple diffusion and facilitated transport on the rate of glucose transport across a membrane.

transport of  $\text{NO}_3^-$  and other anions. Examples of antiporter transport are  $\text{H}^+\text{-Na}^+$  and  $\text{H}^+\text{-Ca}^{+2}$  transport into the vacuole. Evidence of facilitated transport is shown in Fig. 2-24, where the rate of glucose uptake is substantially greater than that observed with simple diffusion along a concentration gradient.

**Active transport** Larger, more-charged molecules have greater difficulty in moving across a membrane, requiring active transport mechanisms (i.e., sugars, amino acids, DNA, ATP, ions, phosphate, proteins). Active transport across a selectively permeable membrane occurs through ATP-powered pumps that transport ions against their concentration gradients (Fig. 2-23). This mechanism utilizes energy released by hydrolysis of ATP. In plant cells,  $\text{H}^+$ -ATP pumps transfer  $\text{H}^+$  across the plasma membrane or tonoplast to acidify the cytoplasm or vacuole, respectively. The  $\text{Na}^+\text{-K}^+$  ATP pump transports  $\text{K}^+$  into the cell and  $\text{Na}^+$  out of the cell, which maintains a high cytoplasm  $\text{K}^+$  concentration essential for maintaining the electrical potential gradient across the plasma membrane. The  $\text{Ca}^{+2}$  ATP pump transports  $\text{Ca}^{+2}$  out of the cytoplasm, which maintains  $\text{Ca}^{+2}$  concentration lower than in extracellular areas, which is essential for establishing a high concentration gradient that provides the energy for facilitated  $\text{Ca}^{+2}$  diffusion into the cell.

## STUDY QUESTIONS

1. Define *cation exchange capacity* (CEC). What units are commonly used to express CEC?
2. A soil test shows  $\text{CEC} = 14.3 \text{ meq}/100 \text{ g soil}$ . Calculate the CEC in  $\text{cmol}/\text{kg soil}$ .
3. Identify the origin of CEC in mineral soil colloids and factors that influence CEC.
4. Explain the influence of the following on CEC in soils:
  - a. increasing pH from 6.0 to 7.5
  - b. increasing weathering intensity (over the long term)
  - c. adding bases such as  $\text{Ca}^{+2}$  or  $\text{Mg}^{+2}$
5. Which clay minerals would likely be present in a weathered acid soil?
6. Why are 2:1 clay minerals more common in soils of the Midwest or Great Plains regions of North America?
7. As soils age from thousands of years of weathering, some soil properties change. List two of these properties and how these changes might affect soil productivity.
8. What are the two sources of negative charge in clay minerals?
9. Explain how isomorphic substitution in the tetrahedral or the octahedral layer influences shrink-swell potential in soils.
10. What is meant by *buffer capacity* (BC)? What soil properties influence the soil BC?