Plants develop extensive root system

- 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. 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 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. Indeed, crops under fertilization and irrigation allocate more resources to the shoot and reproductive structures than to roots, and this shift in allocation patterns often results in higher yields.
- The extent to which roots proliferate within a soil patch varies with nutrient levels. Root growth is minimal in poor soils because the roots become nutrient-limited. As soil nutrient availability increases, roots proliferate.

- Within the soil, nutrients can move to the root surface both by **bulk flow** and by **diffusion**. In bulk flow, nutrients are carried by water moving through the soil toward the root. The amounts of nutrients provided to the root by bulk flow depend 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 roots lowers the concentrations of nutrients at the root surface, generating concentration gradients in the soil solution surrounding the root.

3. How plants take up mineral elements from soil

A. Bulk flow: Uptake in the transpiration stream

Nutrients diffuse to regions of low concentration and roots grow into and proliferate in soil zones with high nutrient concentrations (horse manure in sand).

Dominant in mineral soils:

B. Mycorrhizae: symbiotic relationship with fungi

Roots are slow growing but mycorrhizal fungi proliferate and ramify through the soil. Symbiotic relationship: carbon-nitrogen exchange.

Dominant in organic soils:

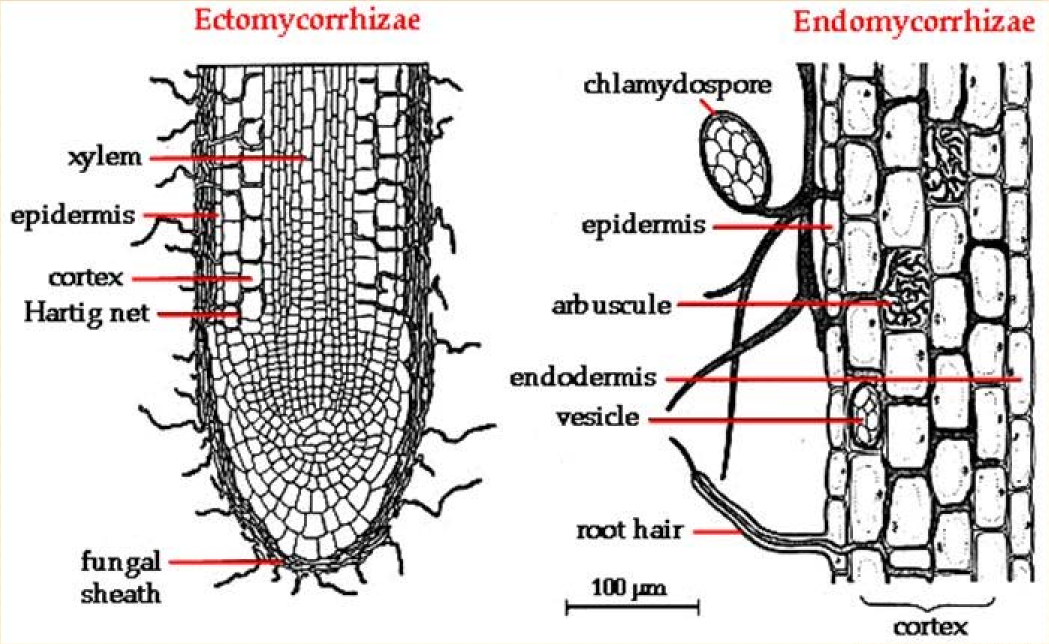
Mycorrhizal fungi facilitate nutrient uptake by roots

- ***Mycorrhizae*** are not unusual; in fact, they are widespread under natural conditions. Much of the world's vegetation appears to have roots associated with mycorrhizal fungi: 83% of dicots, 79% of monocots, and all gymnosperms regularly form mycorrhizal associations. Mycorrhizae are absent from roots in very dry, saline, or flooded soils, or where soil fertility is extreme, either high or low. The host plant provides its associated mycorrhizae with carbohydrates. 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 that are important in terms of mineral nutrient uptake by plants: **ectotrophic mycorrhizae** and **arbuscular mycorrhizae**.

- *Ectotrophic mycorrhizal fungi* typically form a thick sheath, or mantle, of mycelium around roots, and some of the mycelium penetrates between the cortical cells (**Figure**). 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 mass is comparable to that of the roots themselves. The fungal mycelium also extends into the soil. The capacity of the root system to absorb nutrients is improved by the presence of external fungal hyphae because they are much finer than plant roots and can reach beyond the nutrient depletion zone near the roots.

- Unlike the ectotrophic mycorrhizal fungi, *arbuscular mycorrhizal fungi* (previously called vesicular-arbuscular mycorrhizae) 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. After entering the root through either the epidermis or a root hair via a mechanism that has commonalities with the entry of the bacteria responsible for the nitrogen-fixing symbiosis, the hyphae not only extend through the regions between cells, but also penetrate individual cells of the cortex. Within these 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.

- The association of arbuscular mycorrhizae with plant roots facilitates the uptake of phosphorus, trace metals such as zinc and copper, and water. By extending beyond the depletion zone for phosphorus around the root, the external mycelium improves phosphorus absorption.



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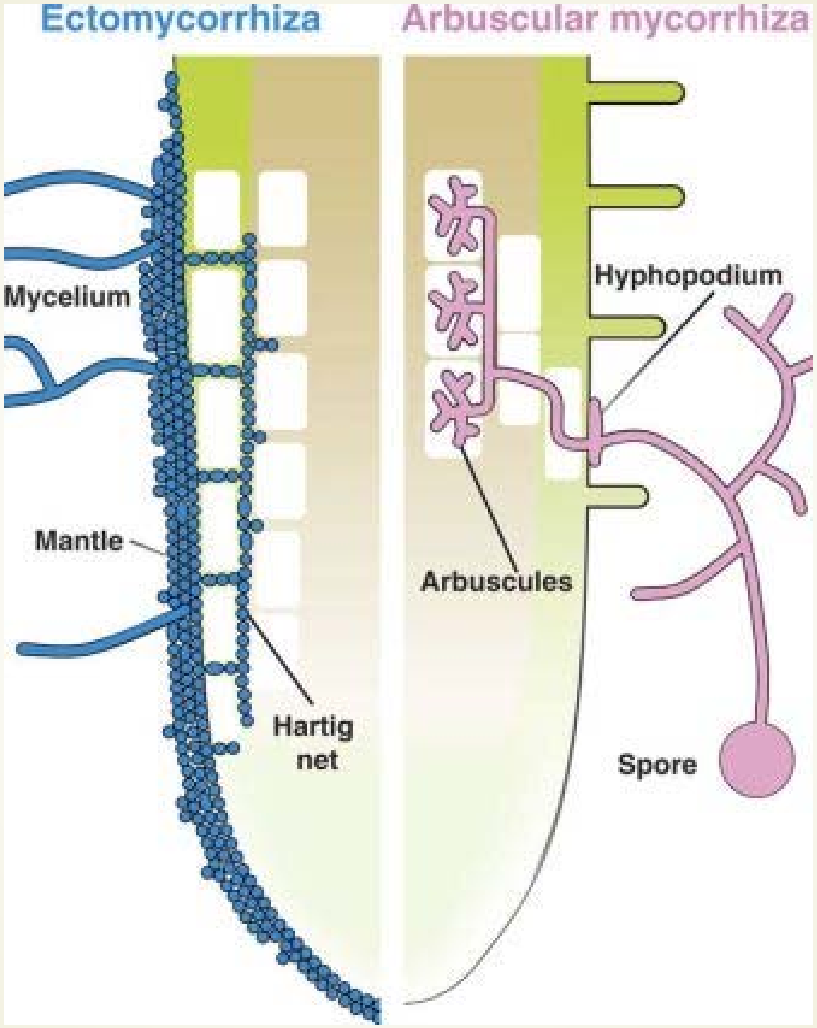
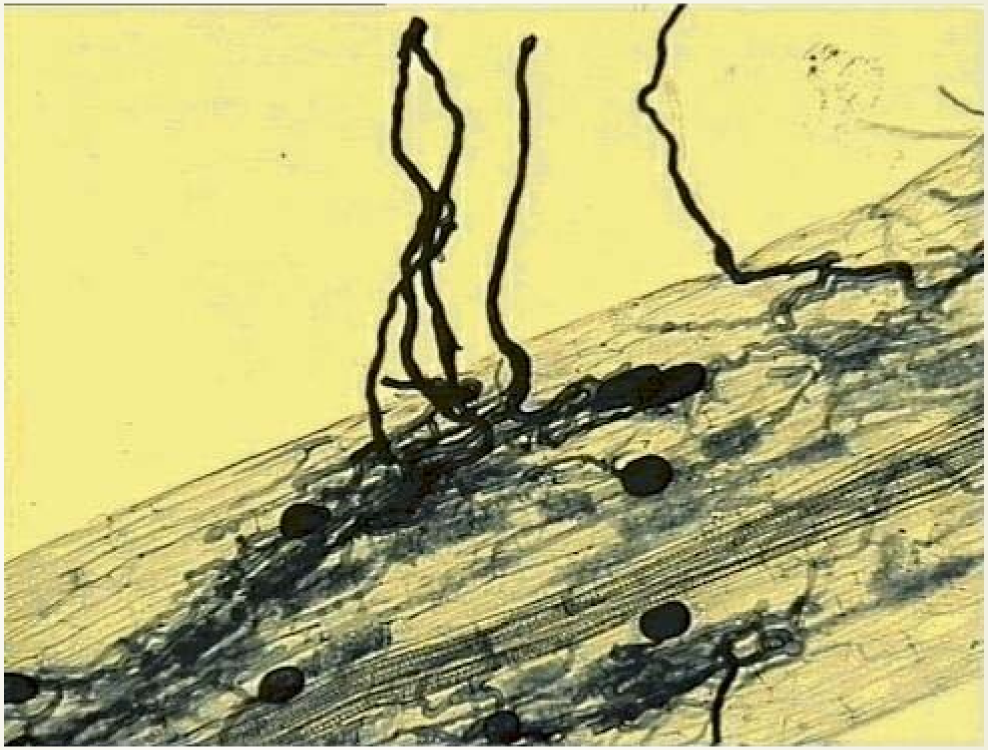
Ectomycorrhiaze and Endomycorrhizae

1.Ectotrophic mycorrhizal symbiosis:
Fungal mycorrhizal mycelium densely grows around the absorbing roots.
2. Endotrophic mycorrhizal symbiosis:
Mycorrhizal hyphae are able to colonise the cortical cells.


Ectomycorrhiza
Arbuscular mycorrhiza
Mycelium
Mantle
Hartig net
Hyphopodium
Arbuscules
Spore



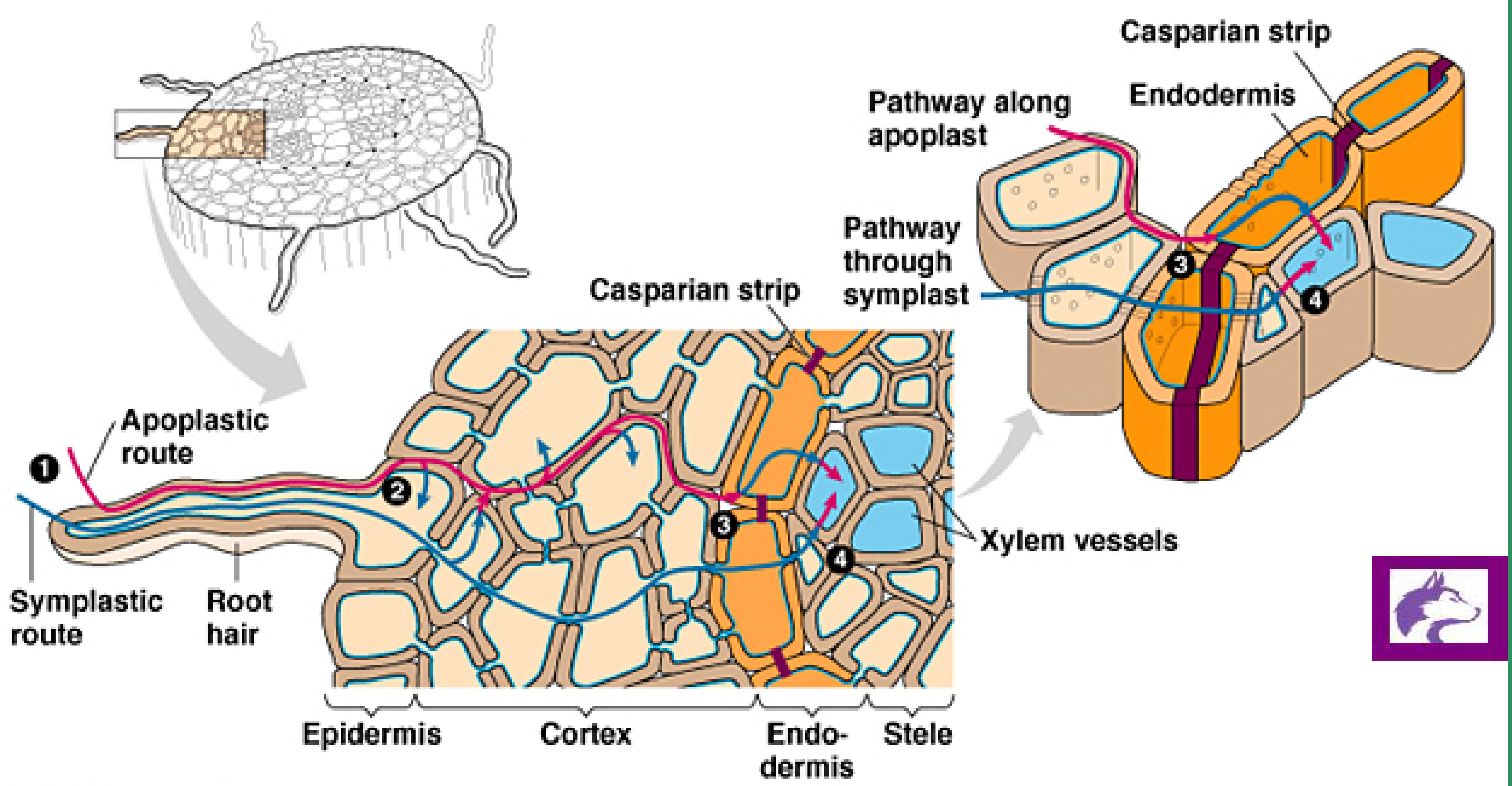
Root infected with ectotrophic mycorrhizal fungi

Ion transport in roots

- Mineral nutrients absorbed by the root are carried to the shoot by the transpiration stream moving through the xylem. Both the initial uptake of nutrients and water and the subsequent movement of these substances from the root surface across the cortex and into the xylem are highly specific, well-regulated processes. Ion transport across the root obeys the same biophysical laws that govern cellular transport.

Solutes move through both apoplast and symplast

Uptake of water and nutrients by roots



See Equivalent Fig. 32.2B

In terms of the transport of small molecules, the cell wall is an open lattice of polysaccharides through which mineral nutrients diffuse readily. Because all plant cells are separated by cell walls, ions can diffuse across a tissue (or be carried passively by water flow) entirely through the cell wall space without ever entering a living cell. This continuum of cell walls is called the extracellular space, or **apoplast**. Typically, 5 to 20% of the plant tissue volume is occupied by cell walls. Just as the cell walls form a continuous phase, so do the cytoplasms of neighboring cells, collectively referred to as the **symplast**. Plant cells are interconnected by cytoplasmic bridges called *plasmodesmata*, cylindrical pores 20 to 60 nm in diameter (**Figure**). Each plasmodesma is lined with plasma membrane and contains a narrow tubule, the *desmotubule*, that is a continuation of the endoplasmic reticulum.

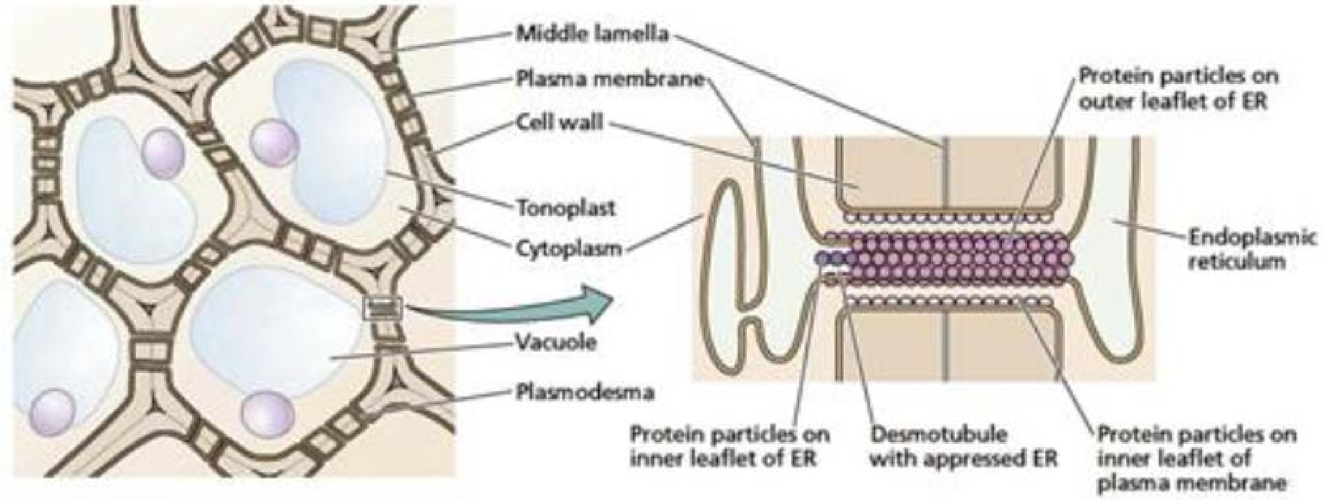


Figure 1.16 Plasmodesmata connect the cytoplasms of neighbouring cells facilitating cell-to-cell communication and solute transport (*source: Taiz L., Zeiger E., 2010*)

- Ion absorption by the root is more pronounced in the root hair zone than in the meristem and elongation zones.

- An ion that enters a root may immediately enter the symplast by crossing the plasma membrane of an epidermal cell, or it may enter the apoplast and diffuse between the epidermal cells through the cell walls.

- The apoplast forms a continuous phase from the root surface through the cortex. However, in all cases, ions must enter the symplast before they can enter the stele, because of the presence of the Casparian strip.

- Once an ion has entered the stele through the symplastic connections across the endodermis, it continues to diffuse from cell to cell into the xylem. The presence of the Casparian strip allows the plant to maintain a higher ion concentration in the xylem than exists in the soil water surrounding the roots.

Passive and active transport

Molecular and ionic movement from one location to another is known as **transport**.

Local transport of solutes into or within cells is regulated mainly by **membranes**.

Larger-scale transport between plant organs, or between plant and environment, is also controlled by membrane transport at the cellular level. (For example, the transport of sucrose from leaf to root through the phloem, referred to as **translocation**, is driven and regulated by membrane transport into the phloem cells of the leaf and from the phloem to the storage cells of the root).

- According to Fick's first law, the movement of molecules by diffusion always proceeds spontaneously, down a gradient of free energy or chemical potential, until equilibrium is reached.
- The spontaneous "downhill" movement of molecules is termed **passive transport**.
- At equilibrium, no further net movements of solutes can occur without the application of a driving force.
- The movement of substances against a gradient of chemical potential, or "uphill", is termed **active transport**.
- It is not spontaneous, and it requires that work be done on the system by the application of cellular energy. One common way (but not the only way) of accomplishing this task is to couple transport to the hydrolysis of ATP.

- The **chemical potential** for any solute is defined as the sum of the concentration, electric, and hydrostatic potentials (and the chemical potential under standard conditions). The importance of the concept of chemical potential is that it sums all the forces that may act on a molecule to drive net transport. In general, diffusion (passive transport) always moves molecules energetically downhill from areas of higher chemical potential to areas of lower chemical potential. Movement against a chemical-potential gradient is indicative of active transport.

Membrane transport processes

- biological membranes contain *transport proteins* that facilitate the passage of selected ions and other molecules. The general term transport proteins encompasses three main categories of proteins: **channels, carriers, and pumps** (**Figure)**

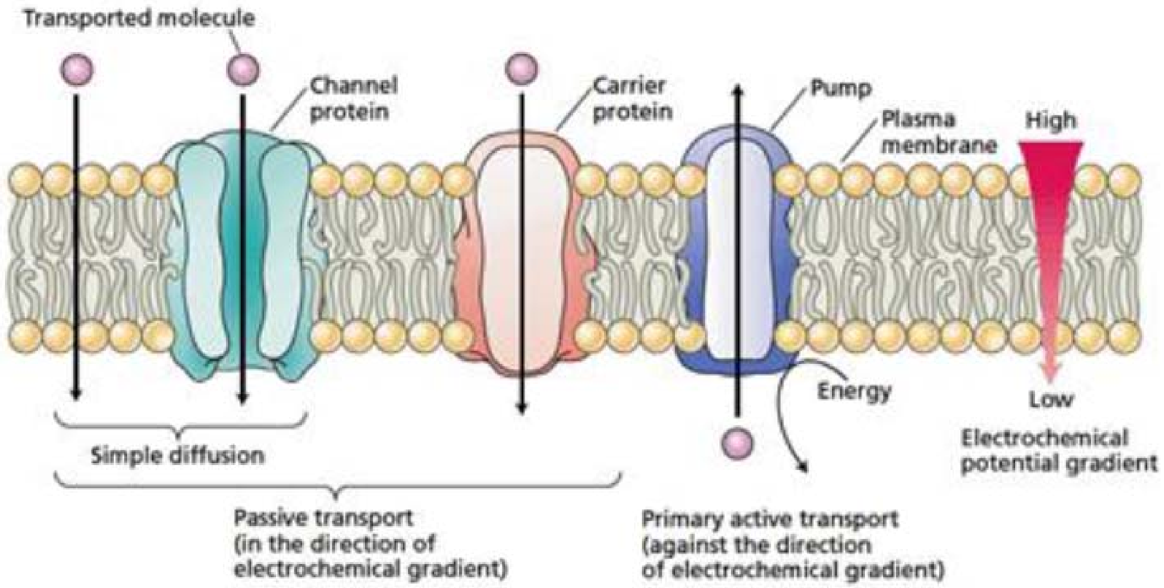


Figure 1.19 Three classes of membrane transport proteins: channels, carriers, and pumps (*source: Taiz L., Zeiger E., 2010*)

Channels are transmembrane proteins that function as selective pores through which molecules or ions can diffuse across the membrane.

Unlike channels, **carrier proteins** do not have pores that extend completely across the membrane. In transport mediated by a carrier, the substance being transported is initially bound to a specific site on the carrier protein. This requirement for binding allows carriers to be highly selective for a particular substrate to be transported. Carriers therefore specialize in the transport of specific ions or organic metabolites.

To carry out **active** transport, a **carrier** must couple the energetically uphill transport of a solute with another, energy-releasing event so that the overall free-energy change is negative. *Primary active transport* is coupled directly to a source of energy, such as ATP hydrolysis, an oxidation-reduction reaction (as in the electron transport chain of mitochondria and chloroplasts), or the absorption of light by the carrier protein (such as bacteriorhodopsin in halobacteria). Membrane proteins that carry out primary active transport are called **pumps**. Most pumps transport ions, such as H+ or Ca2+.