

Absorption and Transport Systems



TRANSPORT AND LIFE

TRANSPIRATION AND WATER FLOW

*Many Factors Affect the Flow of Water in Air, Cells, and Soil
Water Potential Defines the Direction of Water Flow
Transpiration Pulls Water through the Plant*

MINERAL UPTAKE AND TRANSPORT

*Mineral Nutrients Are Solutes in the Soil Solution
Minerals Are Actively Accumulated by Root Cells
Root Pressure Is the Result of an Osmotic Pump*

PHLOEM TRANSPORT

*Osmosis Can Pump Solutes
Plants Use Osmotic Pumps to Transport Sucrose through Sieve Tubes*

SUMMARY

ECONOMIC BOTANY: *Fertilizer*
ECONOMIC BOTANY: *Soils*

KEY CONCEPTS

1. Water flows into, through, and out of a plant in response to a gradient of forces. The various forces that move water into, through, and out of the plant are combined in the concept of *water potential*. As water flows through the plant, it is moving "downhill" from regions of higher to lower water potential.
2. Water is lost from leaves by transpiration. Plants control the rate of water loss by opening and closing their stomata. To replace the water that is lost, water is pulled through the xylem.
3. Mineral elements in solution in the soil are taken up by root cells through an active, energy-requiring process. A fraction of the minerals are secreted into the xylem and rise to the shoot in the transpirational stream.
4. The products of photosynthesis are transported in the phloem from the leaves (where they are produced) to other parts of the plant (where they are used or stored). An osmotic pump provides the pressure that pushes sap through the phloem sieve tubes.

11.1 TRANSPORT AND LIFE

Is there just a heartbeat between life and death? Often we characterize life in animals by movement, and in higher animals, it is specifically the movement of a beating heart that circulates oxygen, nutrients, and hormones around the body in the blood. Plants clearly lack a heart and blood, yet they have the same general need as animals for transporting substances from one organ to another. Although the mechanisms by which plant transport systems work differ from those of animals, the processes are just as effective and impressive.

The need for transport in plants derives from their complex anatomy and their photosynthetic lifestyle. Plants obtain their energy and carbon from photosynthesis. Photosynthesis requires a constant source of carbon dioxide (CO₂), which comes from the air into the leaf through open stomata and then spreads into the air spaces between the mesophyll cells. However, the existence of such open pathways between the cells inside the leaves and the outside air means that water vapor can move out of the leaf, into the drier air, at the same time that CO₂ is moving in. That water must be replaced. Plant cells need a supply of water for maintaining structures, photosynthesis, and growth, and they die if they become dehydrated. The replacement water comes from the soil through the roots. Thus, there must be an effective transport system to get the water from the soil into the roots and on up to the leaves.

Growth of the plant requires mineral nutrients, such as nitrogen, phosphorus, potassium, and iron, as well as carbon. Because emerging leaves and growing stems may be a considerable distance from the source of minerals, the soil, plant must also have a system for transporting minerals to meristematic regions.

Photosynthesis produces carbohydrates that provide energy and carbon skeletons (covalently linked carbons) for the synthesis of other organic molecules. Energy and carbon are needed in all parts of the plant, especially in meristematic regions of stem and roots, and also in flowers, seeds, and fruits. Consequently, there must be a means of transporting carbohydrates from photosynthetic organs to living cells throughout the plant.

The four sections of this chapter describe the mechanisms by which water, mineral nutrients, and carbohydrates are transported from one part of a plant to another (Fig. 11.1).

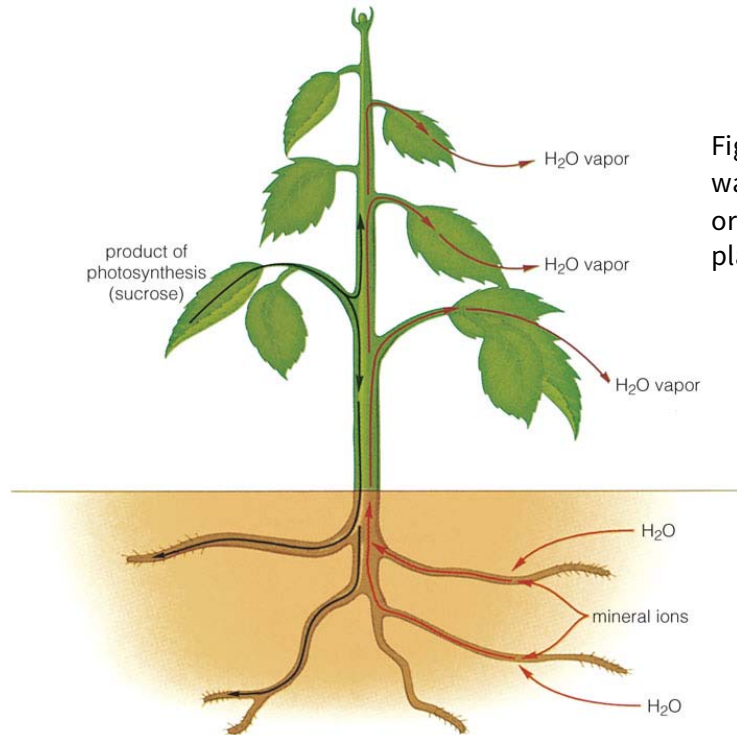


Figure 11.1. The conduction of water, mineral elements, and organic nutrients through a plant.

11.2 TRANSPIRATION AND WATER FLOW

Water is the most abundant compound in a living cell. Without water solutes cannot move from place to place, and enzymes cannot acquire the three-dimensional shape that they need for catalytic activity. Water is a substrate or reactant for many biochemical reactions, and it provides strength and structure to herbaceous plant organs through the turgor pressure it exerts (see Chapter 3). As much as 85% to 95% of the weight of a growing herbaceous plant is water. Because water molecules are connected to each other by hydrogen bonds (see Chapter 2), the water in a plant forms a continuous network of molecules. This network extends into every apical bud, leaf, and root cells; it permeates, with few exceptions, every cell wall and much of the intercellular space. Because the network is continuous, a loss of water from one area affects the entire system.

Although the cuticle that covers the stems and leaves of terrestrial plants is relatively hydrophobic and thus mostly impermeable to the diffusion of water, stomata, lenticels, and cracks in the cuticle allow a loss of water vapor from the interior of the plant. This loss is called **transpiration**. The amount of water

transpired by plants is considerable. In one study, a single corn (*Zea mays*) plant in Kansas transpired 196 liters of water between May 5 and September 8. One hectare (2.5 acres) of such plants (at least 14,800 plants, a low density) would transpire more than 3 million liters (800,000 gallons) of water during the season, an amount equivalent to a sheet of water 28 cm in depth over the entire hectare.

Many Factors Affect the Flow of Water in Air, Cells, and Soil

To understand how water moves within a plant and why it is transpired, we must first find out why water moves at all. There are five major forces that move water from place to place: diffusion, osmosis, hydrostatic pressure, capillary forces, and gravity.

The description of these forces begins with molecules, which, far from being static, are in constant motion. In a gas, the individual molecules move independently in random directions. Overall, however, the net flow is from regions of higher concentration to regions of lower concentration. This principle applies to every element and compound in air; and in particular it applies to water vapor, which flows from areas of higher humidity to areas of lower humidity. The net flow of molecules from regions of higher to lower concentration is called diffusion. Diffusion is a major force directing the flow of water in the gas phase (Fig. 11.2a).

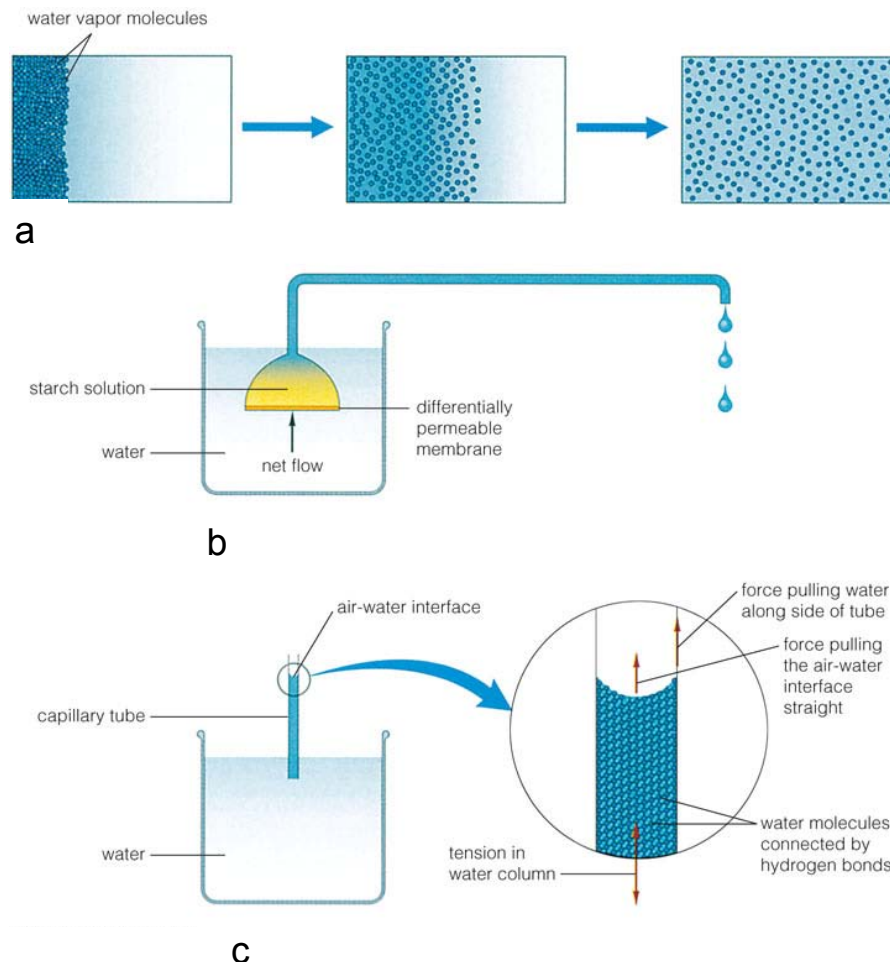


Figure 11.2. Some of the major forces that move water. (a) Diffusion of water vapor molecules gives a net movement from high to low concentration until the concentration at all points is equal. (b) An osmotic pump pulls water from a dilute solution to a more concentrated solution. (c) Capillary forces pull water into a narrow tube or any other narrow space.

Liquids are quite different from gases, but liquid water and solute molecules are also in constant motion and also diffuse from regions of higher to lower concentrations. To witness diffusion, place a drop of dye in a glass of water. You will see the dye disperse throughout the water. What you may not see is that the water also diffuses into the region of dye. This process becomes very important when the dye (or any other solute) is confined by a **differentially permeable** membrane, such as the plasma membrane, that allows water but not solutes to flow across it. Solute molecules displace water; therefore liquid with a higher concentration of solute has a lower concentration of water. The diffusion of water across a selectively permeable membrane from a dilute solution (less solute, more water) to a more concentrated solution (more solute, less water) is called **osmosis**.

A device that uses osmosis to power a flow of water out of a chamber is called an **osmotic pump** (Fig. 11.2b). An osmotic pump is one that works by pressure generated through osmosis. It is easy to set up an example in the laboratory. One ties a bag formed from a dialysis membrane around a tube. A dialysis membrane is a thin sheet made of modified cellulose fibers. It has pores large enough to pass water molecules but small enough to retain large solute molecules, such as starch or proteins. Inside the bag is a solution of large solute molecules; outside the bag is pure water. Osmosis forces water into the bag. As the volume of water in the bag increases, pressure builds up. Because there is an outlet through the capillary tubing, the pressure forces solution through this outlet. Later, this chapter examines how osmotic pumps function in a plant (see Section 11.4)

Osmosis represents a potent force moving water into cells. As explained in Chapter 3, so long as the apoplast solution--the solution outside of the plasma membrane--is more dilute than cytoplasm, water will tend to flow into cells from the apoplast. As the cell wall expands, it exerts a hydrostatic pressure that opposes the flow (see Fig. 3.7). Hydrostatic pressure in cells is called **turgor pressure**; it is important because it stiffens the cells and the tissue they constitute.

Outside the cells, water is pulled into the small spaces between the hydrophilic cellulose microfibrils of the wall and is held there tightly. Water molecules are **cohesive**: they stick together. They are also **adhesive**: they stick to hydrophilic molecules such as carbohydrates in the cell wall. The hydrogen bonds between water molecules and the cellulose molecules tend to drag the water along so that it covers as much surface as possible. At the same time, the hydrogen bonds between the water molecules at the interface between water and air tend to minimize the area of the interface by pulling it flat. The liquid is then pulled along behind the interface by the hydrogen bonds that connect the individual molecules. Together these forces can generate a great tension--a negative hydrostatic pressure--that pulls water into the smallest spaces.

We can visualize the forces by putting a glass tube with a narrow bore into water. The water is pulled up the tube until enough water has risen that its weight balances the pull (Fig. 11.2c). Because such a tube is called a *capillary tube*, the forces pulling water into it are called **capillary forces**. Capillary forces produce a tension in the water like that in a stretched rubber band. The strength of the bonds holding water molecules together is surprising. In one type of experiment, investigators were able to exert a tension of 1,000 atmospheres, equivalent to about 15,000 lbs per square inch, on a narrow column of water before it broke. The maximum tension

that can develop in a capillary tube depends on the cross-sectional area of the bore, with the narrowest bores supporting the greatest tensions. Once the capillary bore is filled, there is no more tension, but if water is removed, for instance, by evaporation, tension will be re-established.

Soil particles also are hydrophilic, and they have small spaces that function like capillary tube bores. For this reason, water is pulled into the soil and held there by capillary forces, just as it is pulled into the cell walls. The strength of these forces depends on how much water is present. If the soil is very wet, the spaces will be filled and the tension holding the water will be weak. If the soil is dry, the tension will be stronger. For a plant to pull water from the soil, the root cells must generate an attractive force greater than the tension holding the water in the soil.

Water also moves in response to gravity. It takes force to move water upward. With small herbs, plant physiologists need not be concerned with this effect because from the bottom of the root to the top of the shoot there is little change in height. However, gravity can be a significant factor in tall trees. To move water to the top of a 33-m elm tree takes a tension of 0.67 megapascals (MPa, 6.7 atmospheres); for a 100-m redwood tree, it takes a tension of about 2 MPa (20 atmospheres).

Water Potential Defines the Direction of Water Flow

To describe how a combination of forces determines the direction water flow, plant physiologists use the concept of **water potential**. Water potential takes into account the many forces that move water and combines them to determine when and where water will move through a plant. If we know the relative water potentials in two regions, we know the direction that water will flow. Water always tends to flow from a region of high water potential to a region of low water potential. This is true even if we are thinking of quite different phases, such as liquid water in a solution and water vapor in air. For instance, if the water potential of a solution is greater than the water potential of the water vapor immediately above it, the solution will evaporate. If the water potential of the soil around a root is less than the water potential of the root cells, water will flow out of the root into the soil. It is possible to calculate the water potential of a particular plant tissue (or air or soil) from physical measurements. This is particularly useful to agriculturalists, who must estimate the water needs of their plants and the availability of water in the soil.

Transpiration Pulls Water through the Plant

Under most conditions, the flow of water through a plant is powered by the loss of water from the leaves. Water is *pulled* up the plant by transpiration, not pushed by pumping from the roots. In transpiration, the primary event is the diffusion of water vapor from the humid air inside the leaf to the drier air outside the leaf. The loss of water from the leaf generates a strong attractive force that pulls water into the leaf from the vascular system, up the vascular system from the roots to the shoot, and eventually into the roots from the soil. There are many steps in the pathway by which the water moves and many factors that influence and control the rate of movement, as discussed in the following sections.

DIFFUSION OF WATER VAPOR THROUGH THE STOMATA The intercellular air spaces in the leaves are close to being in equilibrium with the solution in the cellulose fibrils of the cell walls. This means that they are nearly saturated with water vapor, whereas the bulk air outside the leaves is generally quite dry. The difference means that there is strong tendency for diffusion of water vapor out of the leaf. This diffusion can occur if there is a pathway with reasonably low resistance. Most of the leaf is covered with the epidermal cuticle, which has a high resistance to water diffusion. However, stomata have a low resistance when they are open, and water vapor diffuses out through them. This is the route by which most water is lost from a plant.

Water molecules that leave the leaf first pass through the boundary layer, an unstirred layer of air close to the leaf, and then enter the bulk air. The rate of diffusion out of the stomata depends in part of the steepness of the gradient of water vapor concentration (Fig. 11.3). All else being equal, a thick boundary layer has a more gentle gradient and slower diffusion; a thin boundary layer has a steeper gradient and faster diffusion. Wind stirs up the air close to the leaf and makes the boundary layer thinner. This is why plants transpire much faster on a windy day than on a still one. Anatomical features of a leaf may slow the rate of diffusion by stabilizing a relatively thick boundary layer. For instance, a dense layer of trichomes on the surface of a leaf tends to preserve a boundary layer of relatively motionless air. **Stomatal crypts** (Fig. 11.4), also called sunken stomata, depressions of the leaf surface into which the stomata open, form an effective boundary layer because the air in the crypts is quite still.

Temperature has a major effect on the saturation of air. Warm air holds much more water than cool air. Thus, the concentration of water vapor inside a warm leaf is much greater than inside a cool leaf, and the gradient between the leaf air and the bulk outside air is steeper when the temperature is high (unless the bulk air is saturated). For this reason, plants tend to lose water faster when the temperature is high.

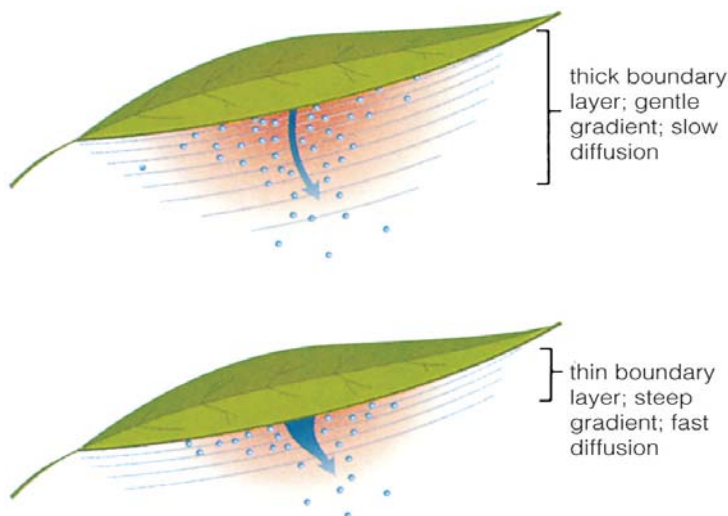


Figure 11.3. The diffusion of water out of stomata through a boundary layer. The thinner the boundary layer, the steeper the gradient.

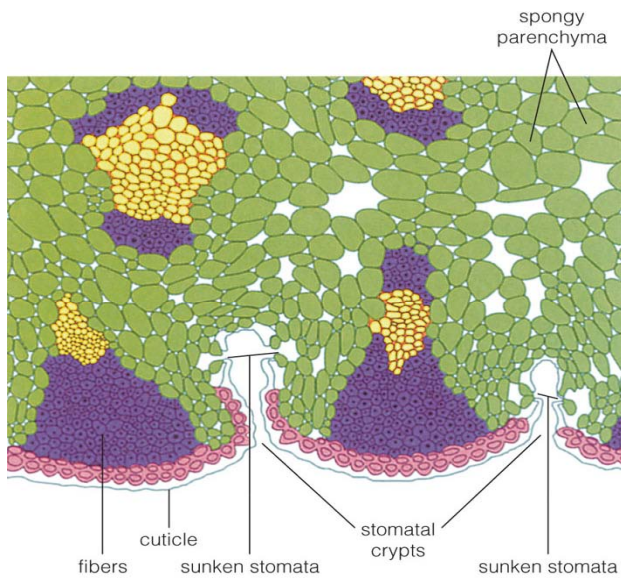


Figure 11.4. Cross section of a yucca leaf. Note the stomatal crypts that provide a layer of unstirred air over the "sunken" stomata; the thick epidermal cuticle, which limits evaporation from the leaf surface; and the large bundles of fibers, which keep the leaf from drooping if the parenchymal cells wilt.

FLOW OF WATER WITHIN LEAVES The loss of water vapor from the intercellular spaces of a leaf decreases the relative humidity of those spaces. This allows water to evaporate from the surrounding cell walls. (Note that the evaporation occurs inside the leaf, not outside.) The removal of water from the cell walls partially dries them, producing capillary forces that attract water from adjacent areas in the leaf (Fig. 11.5).

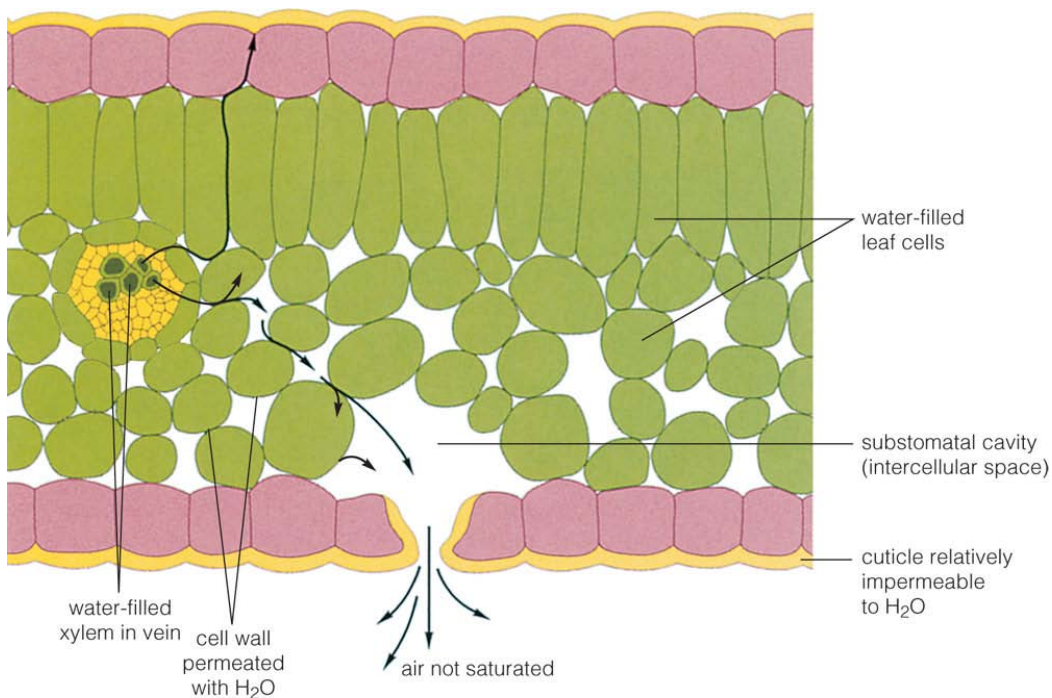


Figure 11.5. Diagram of the flow of water from minor veins along cell walls to the leaf cells, evaporation into the leaf intercellular spaces, and diffusion of water vapor out of a stoma into the surrounding air.

Some of the replacement water will come from the inside of the leaf cells across the plasma membrane. As water leaves the cells, they become smaller. This will decrease turgor pressure as the cell wall springs back from a more extended to a less extended state and concentrate the solutes, increasing the net osmotic effect. If much water is removed, the cell may plasmolyze (see Fig 3.7), and the turgor pressure will decrease to zero. The cells become flaccid and lose their ability to support the leaf. We recognize this when the plant wilts.

If the plant is well watered, the water lost from cell walls and from inside the cells will be replaced by water from the xylem. This water flows out of tracheids through the pits in the lignified secondary cell walls and into the fibrous primary cell walls of the mesophyll cells. The spaces between the fibrils of the primary cell walls are vary small, but the distance are short--most cells in a leaf are within two to six cell lengths of a small vein--so the resistance to flow is fairly low. This means that the replacement of the cell wall water is rapid, so long as water can be pulled out of the xylem.

FLOW OF WATER THROUGH THE XYLEM The flow of water out of xylem tracheids has an interesting effect: it pulls on the rest of the water in the tracheid, and it pulls on the walls of the tracheid (Fig. 11.6). Pull one water molecule out of the central space of the tracheid, and the force is transferred by hydrogen bonds to a network of molecules. The water that is removed from the tracheid cannot be replaced by air because the tiny pores and pits leading into the central space are too small for air bubbles to pass through. The removal of water cannot collapse the walls, because they are strong and rigid. Thus, the loss of water results in a hydrostatic tension on the rest of the water in the tracheid. The tension pulls water from adjacent tracheids and vessels, which in turn induces a tension in them. If water continues to flow from the leaf tracheid into the leaf cell walls, there will be a constant stream of water flowing up the xylem, powered by a gradient of tension.

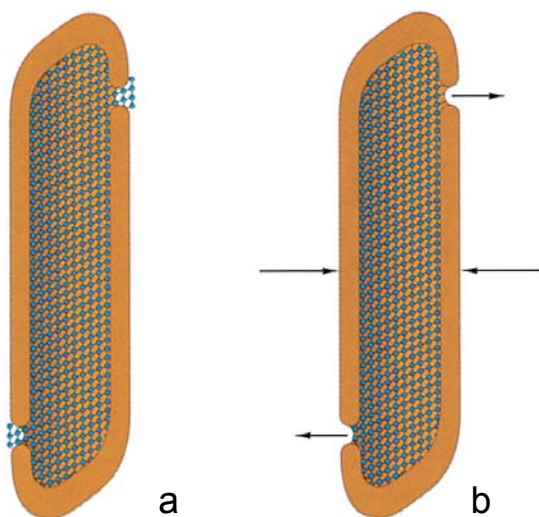


Figure 11.6. How capillary forces can convert the loss of water into a tension within a tracheid. Diagram shows pits (exaggerated size) in the wall of a tracheid; dots are water molecules. Note that the water molecules are connected to each other and the wall by hydrogen bonds. (a) Before evaporation, there is little tension. (b) After evaporation, there is high tension. Arrows: capillary forces pull water into the pits; tension in water pulls the tracheid wall inward.

The smaller tracheids, which are separated by pits, provide fairly high resistance to the water flow, and thus they require a relatively steep gradient of tension to maintain an adequate flow rate. Vessels, with their larger diameters and longer lengths uninterrupted by pits, pose a much lower resistance to water flow. On the other hand, vessels are more easily blocked by air bubbles. Air bubbles may form in xylem when gases dissolved in the xylem fluid come out of solution under the influence of high tension or freezing temperatures. A bubble in xylem under tension acts like a cut in a stretched rubber band: it breaks the tension. That is because once formed, the bubble expands almost instantly to fill the tracheid or vessel. However, it stops at the end of the tracheid or vessel because it cannot pass through the pores in the pits.

Because there are many small tracheids, a bubble in one tracheid may make that tracheid useless but will have no effect on the overall flow. Because there are fewer vessels, a bubble in a vessel may block a substantial fraction of the water flow. Conifers have only tracheids, no vessels. This is thought to provide an advantage in dry, cold climates, where these trees often are the dominant vegetation, because these are the conditions most likely to produce bubbles in the xylem.

SYMPASTIC AND APOPLASTIC FLOW THROUGH ROOTS Eventually, the loss of water throughout the xylem decreases the water potential in the xylem of a growing primary root. The xylem is directly connected to the **apoplast** of the stele (central region inside the endodermis; see Chapter 7) of that root. Thus low water potential in the xylem pulls in water from the apoplast. In turn, water in the apoplast is replaced by water flowing into the stele from the root cortex and into the cortex from the soil.

The path of water through the cortex of the root and into the stele involves both the apoplast and the **symplast**, the interconnected cytoplasm of adjacent cells (Fig. 11.7). Because there is no cuticle over the epidermis of a primary root, water can flow in between the cells of the epidermis directly into the apoplast of the cortex and all the way to the endodermis. However, it cannot cross the endodermis in the apoplast because of the **Casparian strip**, the suberized cell walls that separate the apoplast of the cortex from the apoplast of the stele. To move farther into the root, the water must enter the symplast by crossing the plasma membrane of an endodermal cell. Water may also cross the plasma membrane of cells at the root hairs or in the cortex. Once it does this, it can flow from cell to cell through the symplast via the plasmodesmata. It can cross the endodermis in the symplast, then enter the apoplast, and flow into the xylem.

Note that water must pass through at least two plasma membranes to reach the root xylem from the soil. There is a significant resistance to the flow of water through these membranes, although it is not easy to measure. One indication of this resistance is that transpiration--and therefore water flow--increases if a plant's roots are placed in boiling water long enough to kill the root cells and destroy the cell membranes.

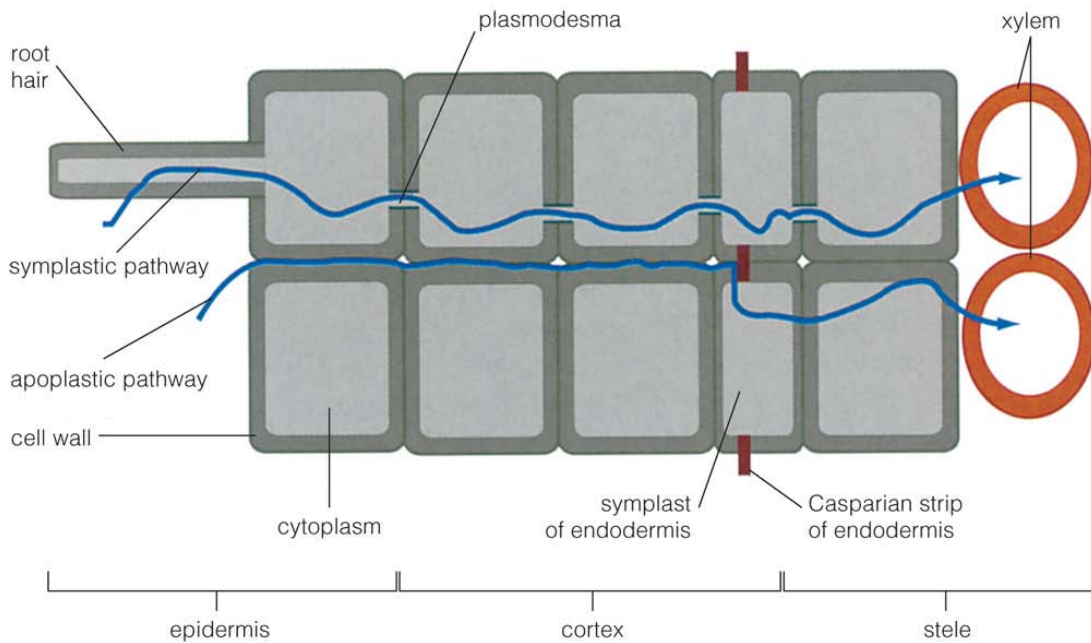


Figure 11.7. Apoplastic and symplastic pathways of water transport through the epidermis and cortex of the root. Water must flow through the symplast of the endodermis to enter the stele.

FLOW THROUGH SOIL The flow of water from the soil into the roots reduces the amount of water in the region of soil around the roots. Most of the water in soil is in small capillary spaces between the soil particles and is bound to the hydrophilic particles by hydrogen bonds. The removal of water near the roots increases the capillary forces that hold water in the soil particles. This results in a gradient of capillary forces between the soil particles near the roots and those farther away. Water flows along the surfaces of the particles and through the capillary spaces in response to this gradient, finally reaching the roots.

Because the capillary spaces are small and the distances may be long, there can be considerable resistance to the flow of water through the soil. This resistance, together with the resistance to flow across the root membranes and through the xylem, is important because it limits the rate at which water can reach the leaves. Even a plant in well-watered soil will wilt in a sudden hot, dry breeze because water cannot move in the roots and up the xylem quickly enough to replace the water lost from the leaves. This is called *temporary wilt*, because such a plant will recover in a few minutes if the loss of water can be stopped. *Permanent wilt* occurs if the osmotic forces pulling water into cells are not as great as the attractive forces holding water to the soil particles.

CONTROL OF WATER FLOW The daily cycle of transpiration is very striking. For most plants, transpiration is very slow at night; it increases starting some minutes after the sun comes up; it peaks in the middle of the day; and it decreases to its night level over the afternoon. By testing plants in experimental growth chambers, researchers have shown that the rate of transpiration is directly related to the

intensity of light impinging on the leaves. Other important environmental factors are temperature, relative humidity of the bulk air, and wind speed.

Microscopic examination of the leaf surfaces shows that light affects the opening of the stomata. In dim or no light, the stomata of most plants are closed; as the light intensity increases, the stomata open up to some maximum value. The mechanism by which light controls stomatal aperture has been the subject of investigation for many years, and the following paragraphs provide a detailed, although not complete, description of many steps.

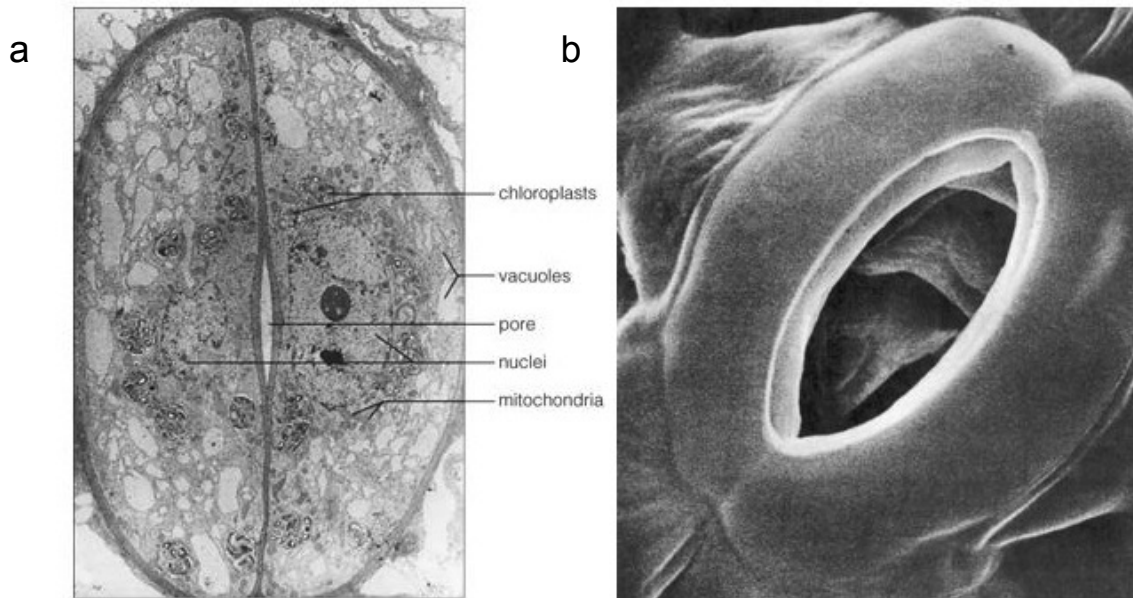


Figure 11.8. Guard cells. (a) Transmission electron micrograph of closed bean (*Phaseolus*) guard cells. (b) Scanning electron micrograph of guard cells and an open stoma.

The primary sensing organs of the stomata are the guard cells (Fig. 11.8). . . Under illumination, the concentration of solutes in the vacuoles of the guard cells increases. How does the solute concentration increase? First starch, a storage carbohydrate in the chloroplasts of the guard cells, is converted into malic acid (Fig. 11.9). Second, the proton pump in the guard cell plasma membrane is activated. The proton pump moves H^+ , some of which comes from malic acid, across the plasma membrane. (After malic acid loses an H^+ , it is called malate ion.) This increases the electrical gradient and the pH gradient across the plasma membrane. Potassium ions (K^+) flow into the cell through a channel in response to the charge difference, and chloride ions (Cl^-), in association with H^+ ions, flow into the cell through another channel in response to the H^+ concentration difference.

The accumulation of malate, K^+ , and Cl^- increases the osmotic effect drawing water into the guard cells. The signals that turn on the enzymes that form malate and activate the proton pump in the plasma membrane include both red and blue light, but these seem to act in different ways.

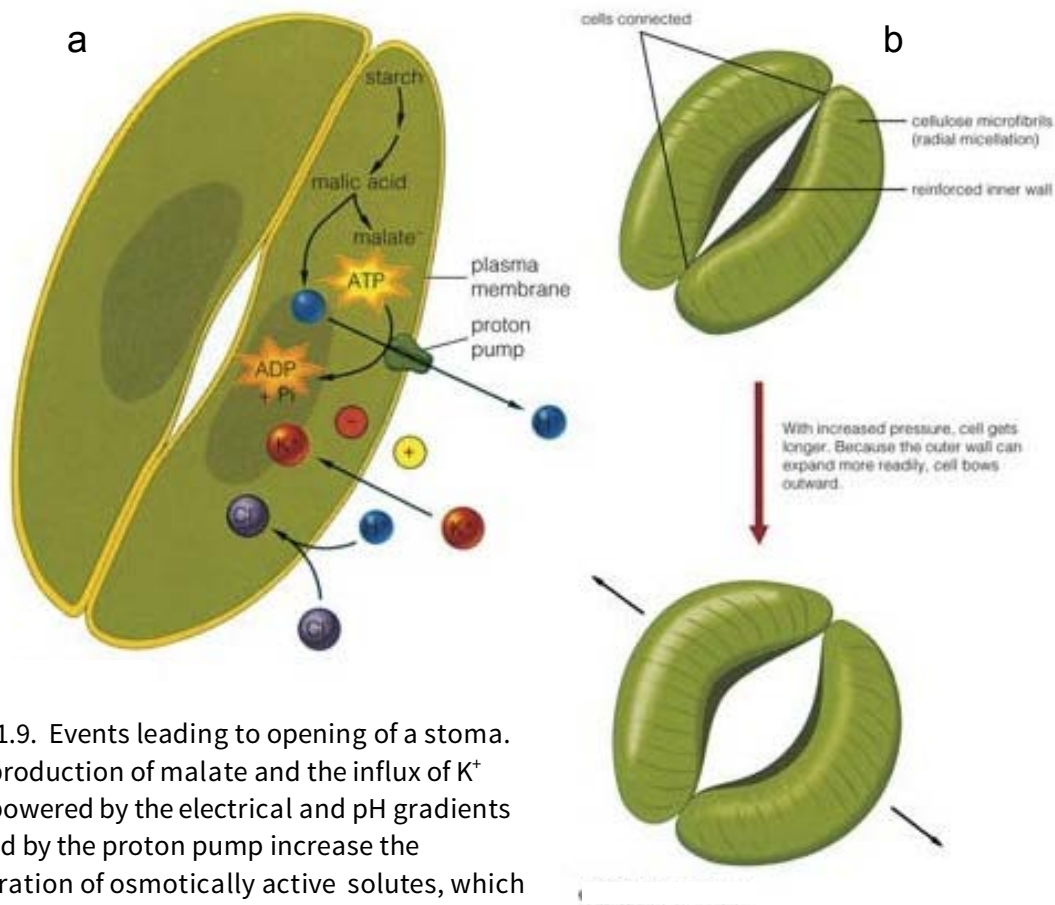


Figure 11.9. Events leading to opening of a stoma. (a) The production of malate and the influx of K^+ and Cl^- powered by the electrical and pH gradients produced by the proton pump increase the concentration of osmotically active solutes, which pulls water into the cells by osmosis. (b) Radial micellation and reinforcement of guard cell walls force the expanding cells to bow outward.

As just stated, the increased solute concentration increases the force drawing water into the guard cells. The additional water increases the turgor pressure and expands the cell walls. Most cells expand in one, two, or sometimes three dimensions as the internal pressure increases. In contrast, guard cells bend away from each other, thus opening the stoma between them (Fig. 11.9). This is because they have specialized cell walls: first, an arrangement of cellulose microfibrils wrapped around the long axis of the cells (radial micellation); second, a heavier and less extensible wall adjacent to the stoma. The radial micellation is like a girdle, limiting the direction of cell expansion. The cells get longer, not thicker, when they expand. The less extensible central wall means that the cells bow outward as they get longer.

Darkness reverses the process. As light decreases, there is a reduction in the charge difference and the pH difference across the plasma membrane. Also, channels open that can conduct K^+ and Cl^- out of the cells. Other stimuli that have the same effect as darkness are an increase in the CO_2 concentration inside the leaf and a loss of water to the point where the leaf wilts. The wilting stimulates mesophyll cells to produce a plant hormone, abscisic acid (see Chapter 15), which

diffuses to the guard cells and specifically stimulates these cells to release K^+ and Cl^- . As these ions leave the guard cells, the osmotic forces cease to balance turgor pressure, and water leaves the cells. The guard cells contract, and the elastic properties of the cell walls pull the cells together, effectively closing the stoma.

Although the opening and closing of stomata is the primary mechanism by which plants regulate the loss of water from their leaves, there are other ways that they can moderate water loss when the stomata are open. The unstirred boundary layer of air close to the leaf is the key to such control. The larger the unstirred layer, the slower the loss of water. As already mentioned, anatomical adaptations can make the boundary layer thicker and more stable. A large concentration of leaf hairs (trichomes) tends to stabilize the boundary layer. Stomatal crypts, indentations of the leaf surface into which the stomata open, are especially effective. These adaptations are most often found in plants that live in deserts and other dry or windy areas, where the loss of water could be extreme. Some leaves tend to curl up as they dry out, effectively forming a crypt containing unstirred air.

11.3 MINERAL UPTAKE AND TRANSPORT

One of the roles of water in plants is to dissolve and transport mineral elements. These elements occur in natural and synthetic fertilizers (see "ECONOMIC BOTANY: Fertilizers" sidebar). Although the need of plants for fertilizer has been known since the development of agriculture, it has been only in the last century that the important components in fertilizer have been identified. Although organic fertilizers (for instance, fish extracts) often are effective, plants do not need to take up organic compounds, such as proteins, vitamins, or carbohydrates. They synthesize all these compounds themselves. What they need are elements that are substrates or catalysts for the synthetic reactions (Table 11.1). The specific elements that are required have been determined by growing the plants *hydroponically*, with their roots in aerated solutions containing different combinations of elements (Fig. 11.10).

Certain elements are required in fairly high amounts: potassium (K), calcium (Ca), nitrogen (N), phosphorus (P), magnesium (Mg), iron (Fe), and sulfur (S). Also needed are carbon (C), hydrogen (H), and oxygen (O), but carbon and oxygen come from the air; oxygen also comes from water, as does hydrogen, and we have already considered the transport of water. (The classical mnemonic for remembering these elements is: C. HOPKiNS CaFe--Mighty good.) These elements form the common compounds synthesized by plant cells.

For instance, carbon, hydrogen, and oxygen are essential parts of all protein, carbohydrate, and nucleic acid molecules. Nitrogen is found in both proteins and nucleic acids, sulfur is found in proteins, and phosphorus is found in nucleic acids. Calcium is a component of the cell wall, helping to hold other parts of the wall together. Magnesium is a component of chlorophyll, and iron is part of some photosynthetic and respiratory enzymes; both atoms help to activate certain other enzymes.

Other elements are required in smaller amounts: manganese (Mn), boron (B), molybdenum (Mo), copper (Cu), zinc (Zn), and chlorine (Cl). These compounds are needed as coenzymes for certain enzyme with important synthetic functions.

Table 11.1 Roles of Mineral Elements in Plants

Element	Primary Roles
Potassium (K)	Osmotic solute, activation of some enzymes
Nitrogen (N)	Structure of amino acids and nucleic acid bases
Phosphorus (P)	Structure of phospholipids, nucleic acids, adenosine triphosphate
Sulfur (S)	Structure of some amino acids
Calcium (Ca)	Structure of cell walls, transmission of developmental signals
Magnesium (Mg)	Structure of chlorophyll, activation of some enzymes
Iron (Fe)	Structure of heme in respiratory, photosynthetic enzymes
Manganese (Mn)	Activation of photosynthetic enzyme
Chloride (Cl)	Activation of photosynthetic enzyme, osmotic solute
Boron (B), cobalt (Co), copper (Cu), zinc (Zn)	Activation of some enzymes

Mineral Nutrients Are Solutes in the Soil Solution

SOIL TYPES Most of the elements that plants need exist in the soil. **Soil** is the part of the earth's crust that has been changed by contact with the biotic and abiotic environment. Soil is a weathered, superficial layer typically only 1 to 3 m (3 to 10 feet) in thickness, made up of physically and chemically modified mineral material associated with organic matter in various stages of decomposition (see "ECONOMIC BOTANY: Soils" sidebar).

Each environment creates its own unique soil. Soils differ in depth, texture, chemistry, and sequence of layers. Soils are formally named, described, and classified on the basis of these differences. The basic soil classification unit is the soil type. Soil types are grouped into soil series, families, and orders. In the entire world there are only 11 soil orders. Representatives of the orders, including more than 14,000 soil series and probably more than 50,000 soil types, occur within the United States. The distribution of particular types of plants often is correlated with the present of particular soil types. Rhododendrons, for instance, grow only in acid (low pH) soils.

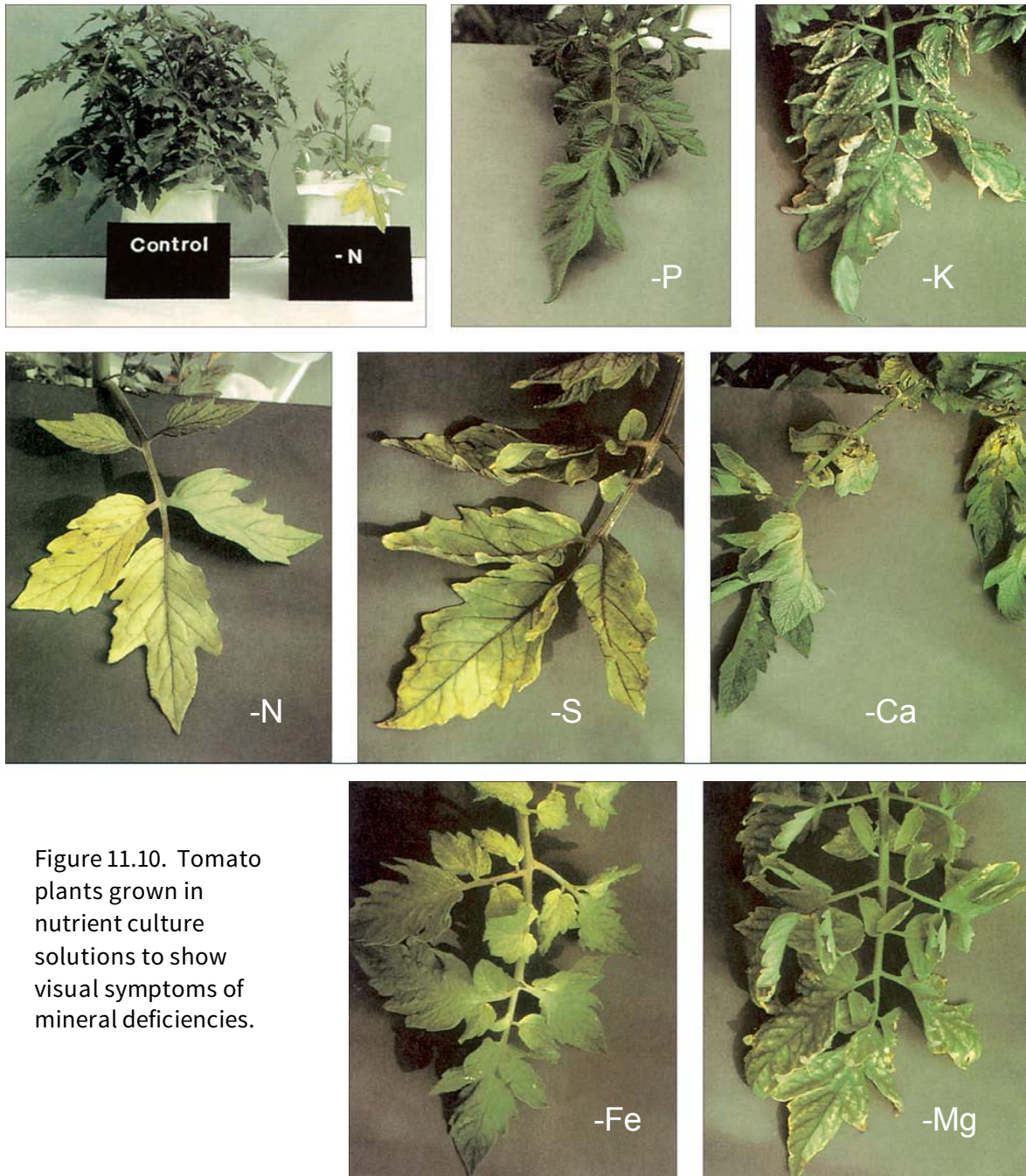


Figure 11.10. Tomato plants grown in nutrient culture solutions to show visual symptoms of mineral deficiencies.

Plant cells, like cells of other organisms, take up mineral elements only when the elements are in solution. In general, that means that the elements are taken up as simple or complex ions--for instance, potassium as K^+ , calcium as Ca^{2+} , phosphorus as $H_2PO_4^-$ and nitrogen as NH_4^+ or NO_3^- . These ions are found in the soil solution. They enter the solution from the dissolution of crystals in rock and soil particles or from the decomposition of organic matter in the soil.

SOIL FORMATION The process of dissolving elements from rock starts with acidic rain (Fig. 11.11). Rain becomes acidic by dissolving CO_2 and, to a lesser extent, sulfur and nitrogen oxide gases such as SO_2 and N_2O_5 . In solution, these combine with water to form acids: H_2CO_3 , H_2SO_3 , and HNO_3 . These acids dissociate (lose H^+), increasing the concentration of H^+ and making the raindrop slightly acidic. When this rain falls on rock, it can rapidly or gradually dissolve many of the rock's crystals. Limestone (CaCO_3) dissolves relatively rapidly through the reaction, $\text{CaCO}_3 + \text{H}^+ \rightarrow \text{Ca}^{2+} + \text{HCO}_3^-$. Other minerals, such as hematite (Fe_2O_3) and feldspar ($\text{K(AlSi}_3\text{O}_8)$), sulfides such as chalcopyrite (CuFeS_2), and magnesium and calcium phosphate rocks--dissolve more slowly.

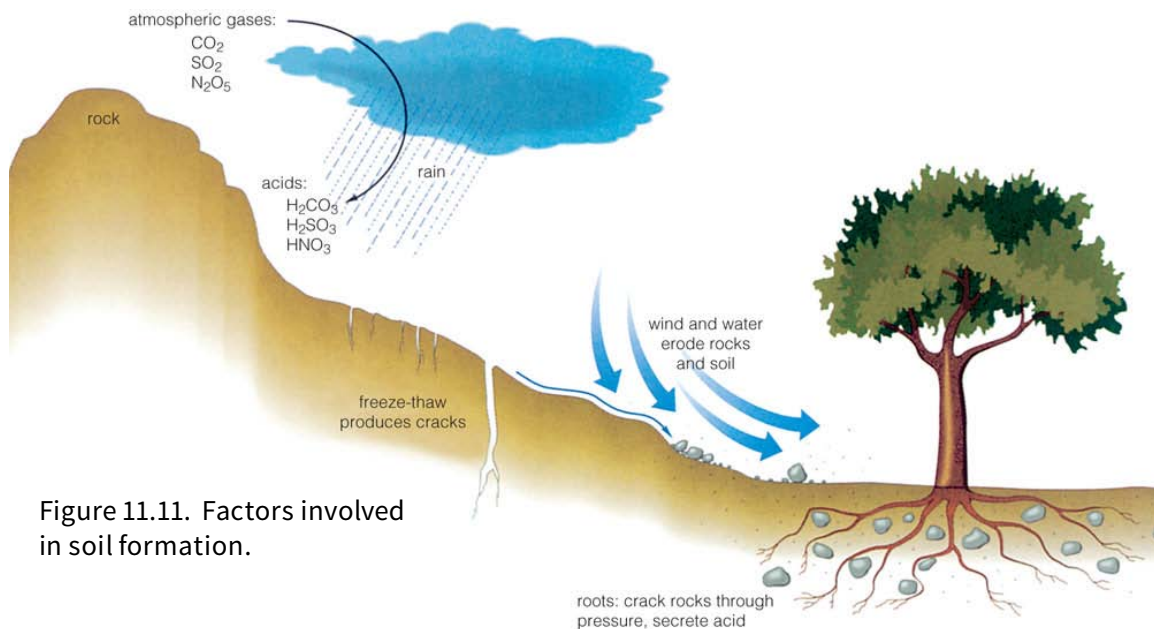


Figure 11.11. Factors involved in soil formation.

The rate at which crystals dissolve depends on the amount of crystal surface area in contact with water. Many processes increase the surface area. The dissolving of crystals itself forms cracks. Other crystals on the sides of these cracks come into contact with water. Freezing and thawing of water in a crack breaks off pieces of rock and forms new fissures. This starts the process of soil formation. Water and wind erosion pulverize rock particles; and the smaller the particles, the greater the total surface area. Once there is a small amount of soil solution, lichens and small plants can start to grow. These also accelerate the processes of soil formation and dissolution of minerals. Their rhizoids and roots enlarge the cracks through turgor pressure and emit respiratory CO_2 , which forms H_2CO_3 and thus more acid.

Young soils, such as those formed as described above, can be a good source of minerals, depending on the composition of the parent rock and the size of the soil particles, with smaller particles providing a richer source of minerals. However, the best soils are not those with the greatest concentration of minerals in their soil solutions. A high concentration of ions increases the osmotic effect of the soil, thus

limiting the movement of water into plants. More importantly, high concentrations of certain ions, such as aluminum (Al^{3+}) and sodium (Na^+), are toxic to plants. Even the essential ion Mg^{2+} is toxic at high concentrations, and the nutrient H_2BO_4^- is toxic at a concentration no more than twice the optimal concentration. It is better to have a lower concentration of the nutrients, with a source that releases ions into the solution as they are taken up by plants. Mature soils contain clay particles and decomposed organic matter that have fixed negative charges. These negative charges bind electrostatically to cations, decreasing their concentrations in the solution but releasing them as they are needed. These soils are said to have a high cation exchange capacity. As roots grow, they respire CO_2 , which acidifies the soil, releasing H^+ . The H^+ binds to the fixed negative charges of the soil in exchange for mineral cations.

NITROGEN FIXATION Nitrogen is a special case. This element is needed in relatively large amounts by plants, but few soils contain much of it. From a global viewpoint, the major storehouse of nitrogen is nitrogen gas (N_2) in the atmosphere, but plants cannot use that form of nitrogen. N_2 must first be converted to NH_4^+ or NO_3^- by a reaction known as nitrogen fixation. Lightning and meteors can oxidize N_2 to NO_3^- , but most nitrogen fixation by far is catalyzed by enzymes in certain bacteria, which reduce N_2 to NH_4^+ . Some of these are free-living bacteria in the soil. Some have developed mutualistic associations with specific plants, so that they donate a part of the nitrogen they fix to the plant and receive carbohydrates and other favorable living conditions in return. The best-known example is the bacterium *Rhizobium*, which lives in root cells of legumes (beans, clover, and so forth). However, more examples have been discovered. Alder trees (*Alnus* sp.), for instance, form association with bacteria of the actinomycete type.

Although nitrogen can be taken up from soil in either of two forms, NH_4^+ or NO_3^- , it is unusual to find soils that have large quantities of either ion. NH_4^+ (in equilibrium with NH_3) is volatile. NH_4^+ is converted to NO_3^- by some soil bacteria during a process known as nitrification, but NO_3^- is very soluble and is easily leached from the soil. This is why the application of nitrogenous fertilizers is so effective in increasing crop yield. The nitrification of NH_4^+ and fixation of N_2 are just two examples of the chemical reactions that interconvert nitrogen-containing molecules. NO_3^- , once it is taken up by plants, can be converted to NH_4^+ , a process known as nitrate reduction. NO_3^- in the soil also can be converted to N_2 by certain bacteria; this is denitrification. Collectively, these reactions are known as the nitrogen cycle, in recognition that nitrogen moves back and forth between the abiotic and biotic components of the environment (see Fig. 27.4).

Minerals Are Actively Accumulated by Root Cells

All plant cells, particularly those in meristematic regions, require a source of minerals. Young root cells can absorb minerals directly from the soil solution, but minerals must be transported through the plant to shoot cells, often over long distances. Because the minerals are in water solution, they are in part transported passively in the stream of water that is pulled through the plant by transpiration.

However, there are some active processes that contribute to the uptake and transport of mineral ions. Active processes are ones coupled to strongly downhill reactions, such as the hydrolysis of adenosine triphosphate (ATP) or the oxidation of nicotinamide adenine dinucleotide phosphate (NADPH)

MAINTAINING A SUPPLY OF MINERALS If a plant is actively taking up minerals, it will deplete the supply in the area immediately around the roots. There are three processes that replenish the supply of minerals.

The first process is the bulk flow of water in response to transpiration. Water in the soil is pulled toward the roots by the gradient of attractive forces created by the removal of water around the roots. Ions in solution are swept along with the water, although local concentrations of charged organic molecules might withdraw ions from the stream (or release ions into it).

The second process is diffusion, the tendency of materials in solution to move down their concentration gradients. Even if the bulk flow of water were to stop, there would be a net movement of ions toward the roots to replace those taken up by the roots.

The third process depends on the plant, not the solution. This process is growth. Roots continue to grow, more or less rapidly, throughout their lifetime. The rate of growth can be surprisingly rapid. The uptake of ions occurs just behind the root tip, so that as a root grows it moves to new regions of soil, where it comes in contact with a new supply of mineral ions.

UPTAKE OF MINERALS INTO ROOT CELLS The next step in the travels of a mineral ion into a plant is its transport across the plasma membrane into a root cell. As mentioned earlier, this occurs just behind the growing root tip, in the region where primary tissues--for instance, epidermis, endodermis, and xylem--have differentiated, but where secondary growth has not begun. On entering the epidermis, the ions can move along the symplast--that is, through the plasmodesmata toward parenchymal cells in the center (stele) of the root. Ions may travel as far as the endodermis through the apoplastic pathway. Just as water molecules must cross a plasma membrane to cross the endodermis, so must mineral ions. In fact, this is probably the primary importance of the endodermis. Forcing ions to cross a plasma membrane before they enter the vascular system allows a plant to exclude toxic ions and to concentrate nutrient ions that are present at low concentrations in the soil solution.

In general, the uptake of mineral ions across the plasma membrane involves pumps and channels. Root cells have the ability to accumulate ions against their concentration gradients--that is, to pull them into the cell, even though their concentration in the soil solution is less than their concentration in the cytoplasm. This requires energy (ATP) and thus active metabolism. It is one of the most important reasons why the growth of plants requires live, healthy roots.

ATP-generated energy is used to accumulate ions indirectly (Fig. 11.12). The process starts with the plasma membrane proton pump, which uses ATP and pumps H^+ (protons) from the cytoplasm to the apoplast. The pumping of the protons generates a membrane potential difference, with the inside of the membrane

negative by more than 100 millivolts (mV) relative to the outside of the membrane. Such a potential difference tends to pull cations, such as K^+ , into the cell. A potential difference of approximately 60 mV will support a concentration difference of 10-fold—that is K^+ will tend to be pulled into the cell until its concentration in the cytoplasm is 10 times greater than that immediately outside the plasma membrane. The relation between membrane potential and concentration difference is logarithmic; therefore, a potential difference of approximately 120 mV will support a concentration difference of 100-fold. The potential difference does not ensure that the cations will in fact enter the cell, however. To enter, the cations must pass through specific channels in the plasma membrane, and those channels must be open. The need for specific channels is the molecular mechanism by which the root excludes toxic ions such as Al^{3+}

The plasma membrane proton pump also generates a proton gradient across the plasma membrane, with a greater concentration of H^+ at the outside. At certain channels, protons form complexes with such anions (negatively charged ions) as NO_3^- and HSO_4^- (Fig. 11.12). The protons neutralize the negative charges of the anions, which would tend to keep the anions out of the cell. If multiple H^+ ions form a complex with the anion, the net charge will pull the complex into the cell through an appropriate channel.

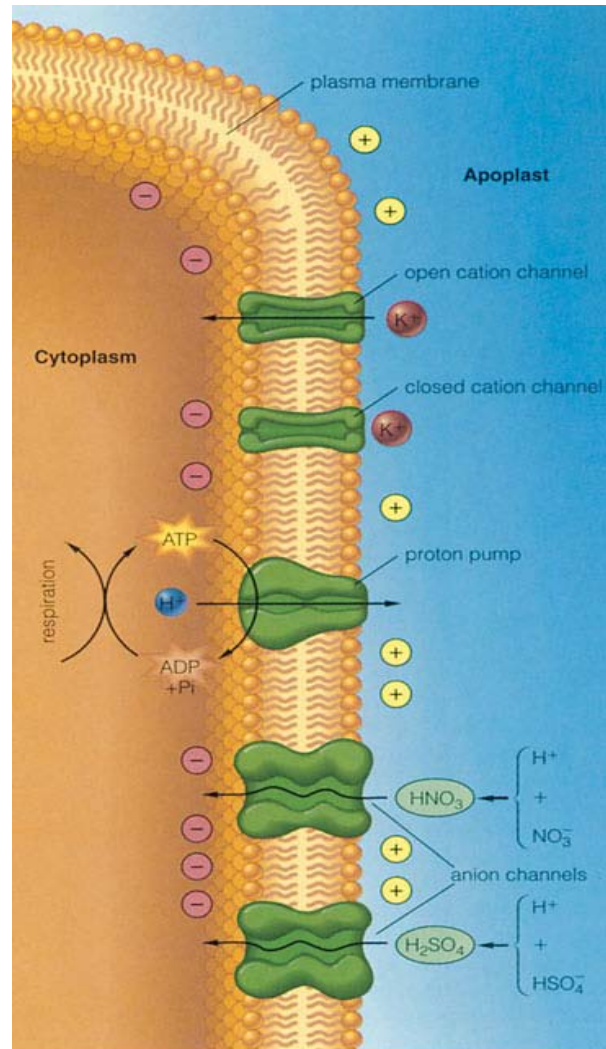


Figure 11.12. Pumps and channels in the plasma membrane. The ATP-utilizing proton pump, which forces H^+ out of the cell, provides the energy charge across the plasma membrane. Channels allow ions to flow into the cytoplasm in response to electrical charge and pH gradients.

MYCORRHIZAE It is a remarkable fact that some roots in soil do not live alone but are closely associated with filaments of fungi as mycorrhizae (see Fig. 7.21). There

are different types of mycorrhizae, depending on the plant and fungus. In some case, the fungi form a sheath around the root and grow into the spaces between the cortical cells; in other, the fungi penetrate the cortical cell walls. One might be tempted to think of the fungus as a parasite on the plant, obtaining food without providing anything to the plant in exchange. However, plants with mycorrhizae often grow better than plants without mycorrhizae. Pine trees (*Pinus* sp.) in many infertile soils grow only in the presence of mycorrhizal fungi. It turns out that mycorrhizal fungi have high-affinity systems for taking up phosphate, systems lacking in the root cells. The fungi provide phosphate to the root, and the root provides carbon- and energy-rich nutrients to the fungi. This is a classic example of a mutualistic association, one that operates to the mutual advantage of both participants.

Ions Are Transported from the Root to the Shoot

Once mineral ions have entered the root cells, they can function in metabolic reactions in those cells. However, if they are to promote growth in the shoot, they must first be transported there. This requires, first, that the ions move from the stelar cells into the apoplast of the stele. Little is known about the mechanisms involved in this process. One hypothesis suggests that there are special mechanisms by which ions are transported across the plasma membrane of living stelar cells out into the apoplast. If this is true, these mechanisms are regulated in a quite different way from those in cortical cells, which take ions into the cells. The mechanisms are probably selective, requiring special channels, and possibly active. If they are active, they require ATP, and they can pump ions into the apoplast even if those ions are more concentrated in the apoplast than in the cytoplasm. An alternate hypothesis suggests that ions are accumulated in the vacuoles of developing tracheary elements, probably to a high concentration. Then the ions are released into the apoplast and xylem stream when the xylem elements become mature and their cytoplasm breaks down (see Chapter 4). Currently, there is not enough evidence to reject either of these hypotheses, and both may be operating.

Ions secreted into the apoplast can be swept into and through the xylem in the transpiration stream. This process takes the ions to whatever region of the plant has stomata open and transpiration occurring.

Ions that have been transported to the shoot may be taken up into the shoot cells. The uptake requires processes similar to those in root cells, except that the concentrations of ions are probably greater, because they accumulate as the solvent water evaporates.

If the salt concentrations in the xylem stream are high, the rate of evaporation is high, and the production of new leaves is low, then salts may be secreted from the leaves and appear on the surface as crystals. This secretion may occur from specialized trichomes with salt gland cells that actively accumulate and secrete the salts. Even if the salt concentrations in the soil solution are low, salts will tend to build up in the leaves. Eventually, they may reach toxic concentrations. The dead tips of the older leaves of slow-growing houseplants are a sign that salt has accumulated to a toxic level in those leaves. To slow this process, one should water these plants infrequently, but thoroughly. Allow excess water to drain through the

pot, carrying away ions that have been accumulated in the soil. Fertilize the plants infrequently and only as long as they show signs of growth.

Root Pressure Is the Result of an Osmotic Pump

As described earlier, Mineral ions are taken up into root cells, passed through the symplast into cells of the stele, and then secreted into the apoplast of the stele. The concentration of ions in the stelar apoplast and in the flowing xylem sap depends in part on the rate of water uptake. If transpiration is occurring, the concentration of ions in the xylem sap may be quite low. But if no transpiration is occurring, ions can accumulate in the apoplast of the stele.

The accumulation of ions in the stele has an osmotic effect. If the soil is saturated with water, the water concentration of the soil solution will be greater than that in the xylem. In this case, water tends to enter the root and stele, building up pressure (**root pressure**) in the xylem and forcing the xylem sap up into the shoot (Fig. 11.13a). The flow of xylem sap, when caused by the accumulation of osmotically active salts in the stele, is an example of an osmotic pump. In some grasses and small herbs, water is forced out special openings in the leaves called **hydathodes**. You may see droplets of **guttation** water on the tips of grass leaves on a cool, moist, still morning (Fig. 11.13b). This is water forced out of hydathodes by root pressure and should not be confused with dew (water vapor condensed on a cold surface).

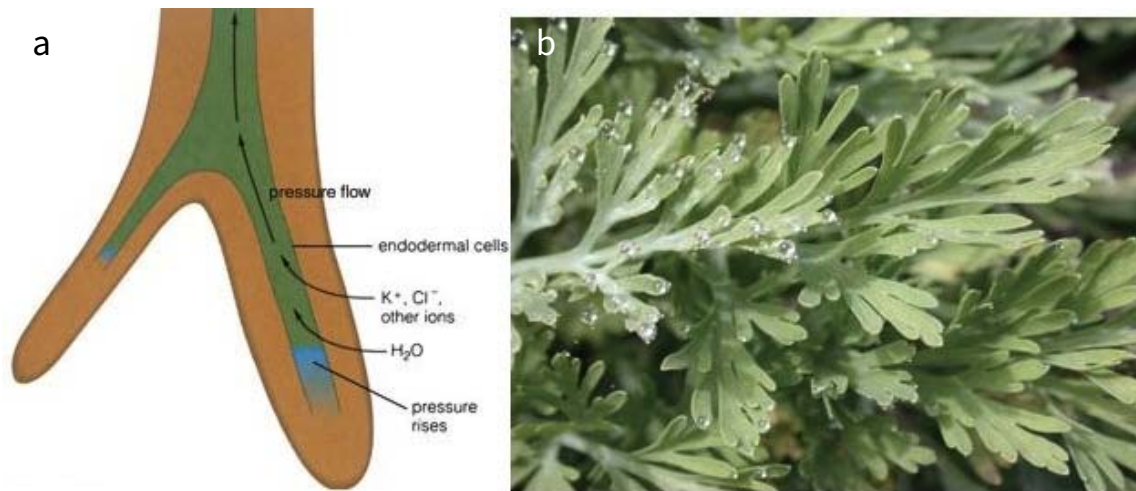


Figure 11.13. Root pressure. (a) Root pressure is generated by an osmotic pump. Solutes accumulate in the root stele. Water is pulled in and forced up the xylem. Note that the endodermal cells provide the differentially permeable membrane need for osmosis. (b) Guttation on a California poppy (*Eschscholzia californica*) leaf.

11.4 PHLOEM TRANSPORT

Osmosis Can Pump Solutions

Of all the nutrients that must be transported through the plant, the most important is carbohydrate, the product of photosynthesis. Carbohydrate is a source of carbon for the synthesis of all other organic molecules. It is also a source of energy, which

is converted into a more useful form, ATP, when the carbohydrate is metabolized in respiration. Transport of carbohydrate is sometimes called **translocation**.

Carbohydrate is synthesized by photosynthesis in the chloroplasts of mature leaf cells. It may be stored temporarily as starch in the chloroplasts. Later, it may be exported from the leaf in the form of sucrose (common table sugar) or, less commonly, other sugars.

The carbohydrate is transported through the phloem. This can be demonstrated by labeling the carbohydrate with radioactive $^{14}\text{CO}_2$. When the petioles are sampled shortly after the labeling, sectioned, and tested, the radioactivity is found in the sieve tubes. Using this same labeling technique, it is possible to measure the rate of carbohydrate transport. This rate, 1 to 2 cm or 0.4 to 0.8 inches per minute, is faster than diffusion or transport from individual cell to cell but not as fast as the rate at which water is pulled through xylem by transpiration. This suggests that the mechanism of translocation is different from diffusion, cell-to-cell transport, or transpiration.

One of the most interesting observations about phloem transport is its ability to change direction. Generally, sucrose is transported from leaves, which are net producers of carbohydrate, to roots, which use carbohydrate for growth or storage. Sometimes, for instance when roots are sprouting new shoots, sucrose is transported up from the roots to the shoots.

The mechanism by which sucrose moves through the phloem was the subject of much research and many arguments by scientists in the 1960s and 1970s. The accumulated evidence, however, currently supports the idea that the sucrose flows through sieve tubes as one component in a bulk flow of solution. The flow is directed by a gradient of hydrostatic pressure and is powered by an osmotic pump.

Plants Use Osmotic Pumps to Transport Sucrose through Sieve Tubes

The phloem can be seen as a dynamic osmotic pump, with a source of solute at one end and a sink at the other. This chapter has already discussed one example of an osmotic pump in the section "Root Pressure Is the Result of an Osmotic Pump." The difference between the greater concentration of ions in the apoplast of the stele and the lower concentration in the soil solution forces water into the stele. The resulting buildup of hydrostatic pressure pushed the xylem sap, with its ions, up the xylem and into the shoot.

In the phloem, sucrose is the main osmotically active solute. It is pumped from photosynthetically active leaf parenchymal cells, or from cells releasing stored carbohydrate, into sieve tubes of the minor veins (Fig. 11.14). The mechanism of pumping probably involves a carrier that transports sucrose together with one or more protons across a plasma membrane. The pH and electric charge differences across the membrane provide the pumping energy. The exact pathway from parenchymal cells to sieve tube is still uncertain.

The accumulation of sucrose in a sieve tube pulls water into the sieve tube from the apoplast by osmosis. This increases hydrostatic pressure inside the sieve tube at the source. The pressure, which can reach more than 20 times atmospheric pressure, starts a flow of solution that will travel to any attached sieve tube in which the pressure is less.

The pressure gradient along the sieve tube depends on the gradient established by differences in sucrose concentration. Because the flow of solution along the sieve tube carries sucrose along with it, you would expect the concentration of sucrose at the source sieve-tube member to decrease and the concentration at the sink sieve tube element to increase. This would eliminate the concentration gradient, and the flow would stop. The loss of the concentration gradient is prevented by two mechanisms: The continual pumping in of sucrose at the source and the removal of sucrose at the sink.

These two processes explain how the direction of phloem transport can change. If an organ is a source, it pumps sucrose into the phloem, the hydrostatic pressure increases, and phloem sap flows out of it. If an organ is a sink, it removes sucrose from the phloem and decreases the hydrostatic pressure, so that more phloem sap containing sucrose flows toward it. Growing tissues, such as shoot and root meristems and expanding fruits, are always sinks. The parenchyma cells of stems and roots may, however, be sinks or sources at different times. A storage root, such as a carrot root, is a sink during the first growing season. It removes sucrose from the phloem and stores starch and sugar in its parenchyma cells. After a winter and once the shoot starts to bolt and flower, the carbohydrate in the root is converted to sucrose and pumped into the sieve tubes. At that point the root becomes a source.

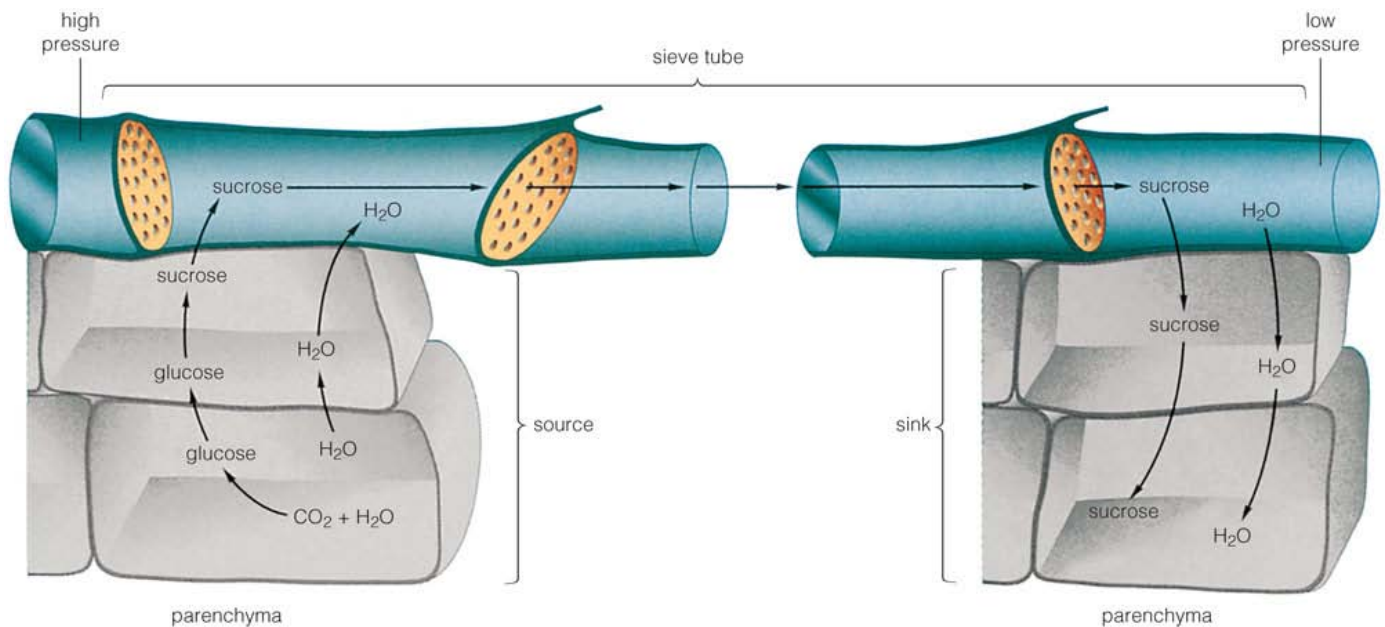


Figure 11.14. The mass-flow mechanism of phloem transport. Sucrose is actively transported into the sieve tubes at the food source region of the plant (leaves or storage organs) and removed at the sink regions (regions of growth or new storage). Water follows by osmosis, increasing the pressure in the sieve tubes at the source region and decreasing the pressure at the sink region. The sieve-tube contents flow *en masse* from high- to low-pressure areas.

The osmotic pump is actively regulated. The mesophyll cells of a young dicot leaf start to photosynthesize early, producing carbohydrate, but the leaf also is

growing and using carbohydrate. On balance, a growing leaf is a net user of carbohydrate; therefore, it imports sucrose from the phloem system. Once mature, though, the leaf exports sucrose to the phloem system. One might imagine that the transition is gradual as the leaf's rate of growth tapers off. Instead, measurements show that it is abrupt. This suggests that an off/on switch regulates the direction of sucrose transport at the sieve-tube plasma membrane, but the nature of that switch remains a mystery.

KEY TERMS

adhesion	osmotic pump
apoplast	root pressure
capillary forces	soil
Casparian strip	stomatal crypts
cohesion	symplast
differentially permeable	translocation
guttation	transpiration
hydathodes	turgor pressure
osmosis	water potential

SUMMARY

1. Plants lose water to the atmosphere by transpiration, which involves the diffusion of water vapor from air spaces inside the plant through stomata, lenticels, or cracks in the cuticle to the outside air. Plants transpire a large amount of water.
2. The movement of water depends on diffusion, osmosis, capillary forces, hydrostatic pressure, and gravity. The concept of water potential allows one to predict how water will flow in response to a combination of these forces.
3. Under most conditions, water is pulled through a plant. As a first step, water vapor diffuses outward through a relative unstirred boundary layer of air into the bulk atmosphere. Water evaporates from the cell walls, replacing what was lost. Water is pulled by tension up the xylem and into the cell walls. Finally, water moves from the soil to the xylem of young, growing roots through symplastic and apoplastic pathways.
4. Transpiration is controlled by the size of the stomatal opening, which depends on the guard cells. Under certain conditions (in the light, with low CO₂ concentration), guard cells accumulate solutes. A resulting influx of water increases their turgor pressure and stretches them in a way that opens the stoma. In the dark, in high CO₂, or under drought conditions, the process is reversed.
5. The essential minerals for plants are C, H, O, K, N, P, S, Ca, Mg, and Fe, and, in smaller amounts, Mn, B, Co, Cu, Zn, and Cl.

6. Mineral elements are taken up by roots from the soil solution. The minerals reach the soil solution by dissolving from rock crystals into acidified rainwater or through the decomposition of organic matter.

7. Minerals are taken up into root cells actively and specifically. This means that the processes transporting minerals use ATP and channels in the membrane that pass only the desired mineral ions. The hydrolysis of ATP is used to pump protons out of the cell. Part of the energy released is saved in the proton and electrical gradients across the membrane. The proton and electrical gradients are used to force ions into the cell, where they can be concentrated 100 times or more relative to the outside solution.

8. In the absence of transpiration, the accumulation of ions in the root stele pulls water into the stele by osmosis and increases the hydrostatic pressure. This so-called root pressure forces water up to and out of leaves, where it appears as guttation.

9. Sucrose, a carbohydrate formed from the products of photosynthesis, is transported from sources (photosynthetic or storage tissue) to sinks (growing or expanding tissue) in the sieve tubes of the phloem.

10. The pressure that forces sucrose and other compounds through the sieve tubes comes from a gradient of hydrostatic (turgor) pressure, which is high near sources and low near sinks. The gradient is produced and maintained by the pumping of sucrose into the sieve tube at the source and its removal at the sink.

Questions

1. Match the forces in the left column with their effects in the right column:

Osmosis	Creates a tension in the water within tracheids
Gravity	Tends to push water out of a cell
Capillary forces	Moves water vapor molecules out of a leaf
Turgor	Opposes the transpirational flow of water up a tree
Diffusion	Tends to pull water into a cell

2. Predict how each of the following changes will affect the tendency of water to move into or out of a leaf cell.
 - a. placing the leaf in a closed, humid chamber
 - b. doubling the concentration of solutes inside the cell
 - c. soaking a piece of leaf containing the cell in a concentrated solution of sucrose

3. Explain why the rate of transpiration increases when:
 - a. dawn breaks and the sun comes up.
 - b. the weather becomes very windy.
 - c. after a period of neglect, you water your house plant.

4. Is the circumference of a tree's trunk greater, less, or the same during the day, when the tree is transpiring rapidly, compared with the night, when there is little transpiration? Hint: consider what happens to a single xylem vessel during transpiration.

5. List the seven mineral elements needed in the greatest amounts for optimal growth of a plant. How does each contribute to the structure or function of the plant?

6. What role does acidic rain (in moderate amounts) play in making minerals available to a plant?

7. Can a K^+ ion travel all the way from the soil to the xylem of a root by either the symplastic or the apoplastic pathway? Explain your answer.

8. Why is respiration an important process in roots? Explain how biochemical energy is used to power the uptake of mineral ions into the cytoplasm of a plant cell.

9. Explain the difference between a root in association with *Rhizobium* and in association with a mycorrhiza.

10. What causes the guttation water seen on the tips of grass leaves early in the morning? Why is guttation water not seen in the afternoon?

11. Why does sucrose exported from photosynthesizing leaves in the phloem always travel down the stem to the roots? Explain your answer.

12. Which is greater: the hydrostatic pressure in a sieve tube of a photosynthesizing leaf, or the hydrostatic pressure in a sieve tube of a developing flower?

ECONOMIC BOTANY: Fertilizer



Good soils provide most of the inorganic nutrients needed by a plant for its growth, but these nutrients eventually can be depleted--absorbed by plants and removed in the harvest, or leached (washed) away by water percolating through the soil. Adding fertilizers replenishes the soil. *Complete fertilizers* contain the three elements whose lack is most likely to limit plant growth: nitrogen (N), phosphorus (P), and potassium (K). Containers of commercial fertilizers have a three-number code that tells how much of each nutrient is found in the preparation. One "all-purpose plant food," for instance, is labeled 12-10-12, which means that it contains 12% nitrogen, 10% phosphorus (measured as P_2O_5), and 12% potassium (measured as soluble potash, K_2O). The label generally also tells the form(s) of nitrogen in the preparation. These may include nitrate (NO_3^-), which is soluble and absorbed quickly by plant roots; ammonium ion (NH_4^+ , often called *ammonical nitrogen*), which may bind to the soil particles and be released slowly to the plant as nitrate through bacterial action; and organic nitrogen (urea or methylenediurea), which is available to the plant even more slowly as it is broken down by bacteria. Various fertilizers have different proportions of these nutrients, which are sometimes recommended (by the manufacturers) for specific kinds of plants.

Some fertilizers also contain trace elements such as boron, copper, manganese, molybdenum, zinc, and especially iron. These additions may be important for houseplants growing in containers with a limited amount of soil and for plants growing in nutrient-poor soils, such as sandy soils and overly leached acidic soils in high rainfall areas. Some fertilizers are formulated to acidify soils, which releases bound trace elements such as zinc and cobalt. Plants such as camellias (*Camellia japonica*), sweet gums (*Liquidambar styraciflua*), and cranberries (*Vaccinium macrocarpon*) need acid soils in order to take up iron and other trace elements.

Organic fertilizers provide nitrogen, phosphorus, and potassium from digested animal or plant matter--one liquid fish emulsion is labeled 5-1-1. These are generally good fertilizers, with slow-release forms of nitrogen and possibly with trace elements (generally unspecified on the label); but they do not provide anything beyond what inorganic fertilizers do. For legumes, such as peas (*Pisum sativum*) and beans (*Phaseolus vulgaris*), you can purchase an inoculum of *Rhizobium*, which will promote the formation of nitrogen-fixing nodules.

Incomplete fertilizers often are cheap and effective. Potassium nitrate (KNO_3), for example, gives a quick shot of two of the major nutrients, as does

ammonium phosphate ($(\text{NH}_4)_3\text{PO}_4$). Gypsum (calcium sulfate, CaSO_4) is a good soil acidifier; so is sulfur, which soil bacteria oxidize to acidic sulfur oxides, including sulfuric acid (sulfate). Ferric sulfate ($\text{Fe}_2(\text{SO}_4)_3$) provides iron in an acidic environment. If you use these or any fertilizers, be careful to read the labels or consult a gardening handbook, because it is possible to overdose plants.

What should you feed your plants? There are a few common signs of nutrient stress that can help you decide (see Fig. 11.10). Yellowing of the lower leaves suggests that the plant is deficient in nitrogen or possibly sulfur; a high-nitrogen complete fertilizer or some ammonium sulfate ($(\text{NH}_4)_2\text{SO}_4$) would help. A dark purplish color suggests a lack of phosphorus; the plants could use a high-phosphorus complete fertilizer or bone meal (calcium phosphate, Ca_3PO_4). Light yellow or white leaves at the shoot tip indicate a lack of iron; iron sulfide (FeS) or an acidic iron chelate (for example, Fe-EDTA) is indicated. If the tips of the leaves are dying, it may be a sign that the plants are taking up and accumulating too many salts. This may come from overfertilizing or from minerals in the water. Give potted plants distilled water or enough tap water to leach high concentrations of mineral out through the bottom of the pot.

ECONOMIC BOTANY: Soils

Soils vary greatly in their physical properties and chemical compositions, as well as in the organisms that live in them. The constituents of soils depend on their parent material and the processes by which they were formed. Different soil constituents include: (1) sand and silt (granular particles of quartz, feldspar, or basalt, with sand particles being much larger than silt); (2) clay (microscopic particles of complex minerals such as mica); and (3) humus (decayed organic matter). Soils occur in layers or horizons. The topsoil ("A" horizon) generally has the smallest particles and the most organic material. Subsoil constitutes the "B" horizon; and parent material ("C" horizon) consists of underlying rock fragments that extend to bedrock (Figure).

In judging the capacity of a soil to support plant growth, several properties are important, including water-holding capacity, aeration, cation-exchange capacity, salinity and toxicity, and biota.

Water-holding capacity is the amount of water that stays after the soil is allowed to drain by gravity, less the amount that is held to soil particles by forces stronger than those the plant can exert. This is the maximum amount of water available to plants. Well-balanced soils with considerable humus have the best water-holding capacity. Sandy soils tend to allow water to drain away. High-clay soils may become compacted, with little space for water beyond that held tightly to the clay particles.

Aeration is the amount of air in the spaces between soil particles. Root growth and function require respiration, and thus oxygen. The best soils have about equal amounts of air and water in their interparticulate spaces. Sand, which promotes drainage, also promotes aeration. Swampy soils often become anaerobic.

Cation-exchange capacity describes the quantity of cations (for instance, K^+ , Ca^{2+} , Mg^{2+}) that can bind to the soil material but be released in the presence of acid generated by the respiration of roots and microorganisms. Clays and humus are the soil constituents that contribute cation-exchange capacity.

The pH of a soil indicates where the soil solution stands on the acid-base scale. The amount of acidic and basic parent material also is important. Neutral

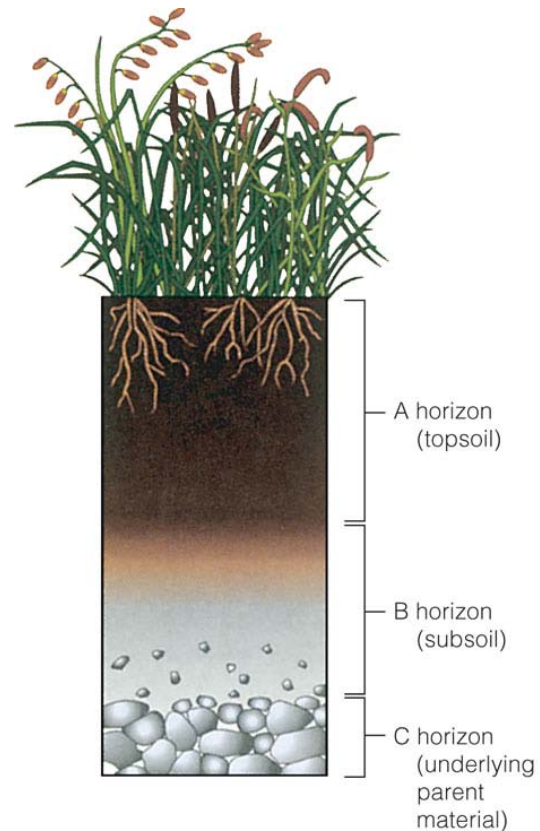


Figure: The soil of grassland.

soils are good at supporting root function. In basic soils, iron and other elements may be bound into compounds that make them unavailable to plants; in acidic soils, these elements are free, but they may leach from the soil and thus be depleted. In high-rainfall areas such as tropical rain forests, the soils are acidic and generally nutrient-poor because of leaching. The growth of plants depends on the nutrients that are held in decaying organic material and those that are delivered by wind and water from other regions.

Salinity and toxicity measure the presence of high concentrations of elements that interfere with root growth or function. High concentrations of sodium (Na^+) and other elements in saline soils are generally caused by poor drainage--for example, in a "dry lake" with no outflowing river--or by the presence of seawater. Toxic concentrations of some ions may reflect the composition of the parent rock. For example, serpentine soils have toxic concentrations of Mg^{2+} and nickel and low concentrations of Ca^{2+} because they are formed from a magnesium silicate rock containing crystals of heavy metals.

Biota, the organisms living in the soil, may be extremely important in determining the nutrient value of the soil. Nitrogen-fixing bacteria and other bacteria contribute to the nitrogen cycle. Mycorrhizal fungi promote the uptake of phosphate and perhaps other nutrients. Worms, insects, and small mammals break apart compacted soil and improve its texture. All these organisms contribute humus to the soil composition. On the negative side, herbivores and pathogens may kill roots, thus limiting nutrient uptake into the plant.

Although different plants may prefer different types of soils, a good start for a garden can generally be made with a loam, which contains a mixture of clay, silt, and sand particles with a considerable amount of organic matter. The soil should drain well, yet not dry too readily. It should have good air spaces for root respiration. The solution that drains from the soil should be chemically neutral (pH 7). If the soil in your garden is not loam, you often can improve it by tilling in organic soil amendments, for instance, ground bark, peat moss, or compost. This is a good idea each year in any case, because organic components break down through bacterial and fungal metabolism. If your soil is too acid (pH less than 7), you can correct the pH by adding lime (calcium oxide). If your soil is too alkaline (pH greater than 7), you can acidify it with gypsum (calcium sulfate). Both lime and gypsum provide calcium, which improves roots' ability to accumulate nutrients and exclude toxic ions. But before using either lime or gypsum, consult a gardening expert or a handbook for guidelines.

Figure Credits

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11.10(a-h) E. Epstein, University of California, Davis

11.13(b) H.M. Metcalf, University of California, Davis

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