CHAPTER 9

Water in Plants

OVERVIEW

This chapter begins by introducing molecular movement through a comparison between balls in motion in a room and molecular activity. This is followed by a discussion of diffusion, osmosis, turgor, plasmolysis, imbibition, and active transport.

The entry of water into the plant is then explored; this is followed by a discussion of the movement of water through the plant, the evaporation of water into leaf air spaces, and transpiration. A discussion of mineral requirements for growth concludes the chapter.

Some Learning Goals

1. In simple terms, explain diffusion, osmosis, turgor, imbibition, and active transport.
2. Discuss the pressure-flow hypothesis and the cohesion--tension theory.
3. Know the pathway, movement, and utilization of water in plants.
4. Explain how a stomatal apparatus opens and closes the pore.
5. Know and understand mineral requirements for growth.

early everyone has had the experience of driving along a highway or city street when someone in the car says, “What’s that smell?” Soon a bakery, or a paper mill, or perhaps a dead skunk comes into view, and the smell gets stronger. Then it fades away as the source is left behind (Fig. 9.1). We take for granted the fact that there is a correlation between our proximity to an odor source and the intensity of the odor, but how and why does the odor reach us?

By way of an answer, imagine two adjacent rooms identical in height, width, and length, with no windows, doors, fixtures, or furniture. Now suppose we lift a small flap in the ceiling of one of them and drop in 100 tennis balls. These are ordinary tennis balls except for one extraordinary feature: they have perpetual-motion motors in them that cause them to travel in any direction at 30 MPH. The tennis balls quickly make the room seem like a battlefield as they whiz around, bounce off the walls, floor, and ceiling, and also collide with one another, each time being deflected at a different angle. Shortly after they are introduced, the tennis balls will become randomly distributed throughout the room.

Now what would you expect to happen if we opened up a small hole in the wall between the two rooms? Eventually, a tennis ball should travel at just the right angle to go through the hole into the other room. Theoretically, it could then bounce straight back into the first room, but it seems unlikely that it would. Reason tells us that long before it might happen to strike the exact angle it needed to return, several more balls will come in from the first room. Given enough time, some balls might indeed bounce back into the first room, but in the long run, each of the two rooms would end up with roughly 50 tennis balls, with an occasional ball going between the rooms in either direction.

The situation just described is analogous to what takes place in nature on a molecular level.

MOLECULAR MOVEMENT

Molecules and ions (discussed in Chapter 2) are constantly in random motion. Visual evidence of this can be seen with an ordinary light microscope. If a drop of India ink is diluted with water and observed through a microscope under high power, the tiny carbon particles of the ink appear to be in constant motion. This motion, known as *Brownian movement*, is the result of the bombardment of the visible particles by invisible water molecules, which are in constant motion themselves.

Diffusion

The differing intensity of smells discussed earlier involves molecules behaving somewhat like the tennis balls. Through their random motion, molecules tend to become distributed throughout the space available to them. Accordingly, if perfume molecules are kept in a bottle, they will become distributed throughout the bottle, but if the stopper is removed, they will eventually become dispersed throughout the room, even if there is no fan or other device to move the air.

This movement of molecules or ions from a region of higher concentration to a region of lower concentration is called **diffusion** (Fig. 9.2). Molecules that are moving from a region of higher concentration to a region of lower concentration are said to be moving *along a diffusion gradient,* while molecules going in the opposite direction are said to be moving *against a diffusion gradient.* When the molecules, through their random movement, have become distributed throughout the space available, they are considered to be in a state of *equilibrium.* The rate of diffusion depends on several factors, including temperature and the density of the medium through which it is taking place.

Except within the area immediately surrounding the source, unaided diffusion requires a great deal of time because molecules and ions are infinitesimally small. Something that is less than a millionth of a millimeter in diameter is going to take a long time to move just 1 millimeter, even though the amount of movement may be great in proportion to the size of the particle concerned. In gases, there is a great deal of space between the molecules and correspondingly less chance of the molecules bumping into each other and thus being slowed down. Accordingly, gas molecules occupy a space that becomes available to them relatively rapidly, while liquids do so more slowly, and solids are slower yet.

Large molecules move much more slowly than small molecules. If you added a tiny drop of a dye (which has relatively large molecules) to one end of a bathtub of water without disturbing the water in any way, it would take years for the dye molecules to diffuse throughout the tub and reach a state of equilibrium. In nature, however, wind and water currents distribute molecules much faster than they ever could be distributed by diffusion alone.

Osmosis

Solvents are liquids in which substances dissolve. Despite the fact that the cytoplasm of living cells is bounded by membranes, it is now well known that water (a solvent) moves freely from cell to cell. This has led scientists to believe that plasma, vacuolar, and other membranes have tiny holes or spaces in them, even though such holes or spaces are invisible to the instruments presently available. It also has led to the construction of models of such membranes (see Fig. 3.11). Membranes through which different substances diffuse at different rates are described as **semipermeable.** All plant cell membranes appear to be semipermeable.

In plant cells, **osmosis** is essentially the *diffusion of water through a semipermeable membrane from a region where the water is more concentrated to a region where it is less concentrated.* Osmosis ceases if the concentration of water on both sides of the membrane becomes equal.

A demonstration of osmosis can be made by tying a membrane over the mouth of a thistle tube that has been filled with a solution of 10% sugar in water (i.e., the solution consists of 10% sugar and 90% water). Fluid rises in the narrow part of the tube as osmosis occurs when the thistle tube is immersed in water (Fig. 9.3).

Although the previous simple definition of osmosis serves our purposes, plant physiologists prefer to define and discuss osmosis more precisely in terms of *potentials.* It is possible to prevent osmosis by applying pressure. Just enough pressure to prevent fluid from moving as a result of osmosis is referred to as the *osmotic potential* of the solution. In other words, osmotic potential is the pressure required to prevent osmosis.

Water enters a cell by osmosis until the osmotic potential is balanced by the resistance to expansion of the cell wall. Water gained by osmosis may keep a cell firm, or **turgid,** and the **turgor pressure** that develops against the walls as a result of water entering the vacuole of the cell is called **pressure potential.**

The release of turgor pressure can be heard each time you bite into a crisp celery stick or the leaf of a young head of lettuce. When we soak carrot sticks, celery, or lettuce in pure water to make them crisp, we are merely assisting the plant in bringing about an increase in the turgor of the cells (Fig. 9.4).

The *water potential* of a plant cell is essentially its osmotic potential and pressure potential combined. If we have two adjacent cells of different water potentials, water will move from the cell having the higher water potential to the cell having the lower water potential.

Osmosis is the primary means by which water enters plants from their surrounding environment. In land plants, water from the soil enters the cell walls and intercellular spaces of the epidermis and the root hairs and travels along the walls until it reaches the endodermis. Here it crosses the differentially permeable membranes and cytoplasm of the endodermal cells on its way to the xylem. Water flows from the xylem to the leaves, evaporates within the leaf air spaces, and diffuses out (*transpires*) through the stomata into the atmosphere. The movement of water takes place because there is a water potential gradient from relatively high soil water potential to successively lower water potentials in roots, stems, leaves, and the atmosphere.

Plasmolysis

If you place turgid carrot and celery sticks in a 10% solution of salt in water, they soon lose their rigidity and become limp enough to curl around your finger. The water potential inside the carrot cells is greater than the water potential outside, and so diffusion of water out of the cells into the salt solution takes place. If you were to examine such cells with a microscope, you would see that the vacuoles, which are largely water, had disappeared and that the cytoplasm was clumped in the middle of the cell, having shrunken away from the walls. Such cells are said to be *plasmolyzed.* This loss of water through osmosis, which is accompanied by the shrinkage of protoplasm away from the cell wall, is called **plasmolysis** (Fig. 9.5). If plasmolyzed cells are placed in fresh water before permanent damage is done, water reenters the cell by osmosis, and the cells become turgid once more.

Imbibition

Osmosis is not the only force involved in the absorption of water by plants. *Colloidal* materials (i.e., materials that contain a permanent suspension of fine particles) and large molecules, such as cellulose and starch, usually develop electrical charges when they are wet. The charged colloids and molecules attract water molecules, which adhere to the internal surfaces of the materials. Because water molecules are polar, they can become both highly adhesive to large organic molecules such as cellulose and cohesive with one another. As discussed in Chapter 2, polar molecules have slightly different electrical charges at each end due to their asymmetry. This process, known as **imbibition,** results in the swelling of tissues, whether they are alive or dead, often to several times their original volume. Imbibition is the initial step in the germination of seeds (Fig. 9.6).

The physical forces developed during germination can be tremendous, even to the point of causing a seed to split a rock weighing several tons (Fig. 9.7). It has been found, for example, that a pressure of 42.2 kilograms per square centimeter (600 pounds per square inch) is needed to break the seed coat of a fresh walnut from within and that water being imbibed by a cocklebur seed develops a force of up to 1,000 times that of normal atmospheric pressure. Yet, when water and oxygen reach walnut and cocklebur seeds, they germinate readily, as do seeds that fall into the crevices of rocks or have boulders roll over on them.

The huge stone blocks used in the construction of the pyramids of Egypt are believed to have been quarried by hammering rounded wooden stakes into holes made in the face of the stone and then soaking the stakes with water. As the stakes swelled, the force created by imbibition split the rocks.

Active Transport

Return for a moment to our two rooms with the tennis balls. Suppose that, besides the 100 tennis balls, we drop in 50 slightly underinflated basketballs; these basketballs are also extraordinary in having perpetual-motion motors that propel them in any direction at 12 MPH. They should also become randomly distributed throughout the room shortly after they are introduced. Assume, however, that the hole in the wall (which is large enough for the passage of a tennis ball) is not quite large enough to allow a basketball to pass through freely. The basketballs will then remain in the first room. However, if we were to install a mechanical arm next to the hole in the second room, and if this arm could grab basketballs that come near the hole and squeeze them through in one direction, basketballs would be transported into the second room *through the expenditure of energy***.** The basketballs obviously would gradually accumulate in the second room in greater numbers.

Plants expend energy to move substances, too. Plant cells generally have a larger number of mineral molecules and ions than exist in the soil immediately next to the root hairs. If it were not for the barriers imposed by the semipermeable membranes, these molecules and ions would move from a region of higher concentration in the cells to a region of lower concentration in the soil.

Most molecules needed by cells are polar, and those of solutes may set up an electrical gradient across a semi-permeable membrane of a living cell. To pass through the membrane, molecules require special embedded transport proteins (see Fig. 3.7). The transport proteins are believed to occur in two forms: one facilitating the transport of specific ions to the outside of the cell and the other facilitating the transport of specific ions into the cell.

The plants absorb and retain these solutes against a diffusion (or electrical) gradient through the expenditure of energy. This process is called **active transport.** The precise mechanism of active transport is not fully understood, but recent evidence suggests that this process involves an enzyme complex and what has been referred to as a *proton pump.* The pump involves the plasma membrane of plant and fungal cells and sodium and potassium ions in animal cells. Both pumps are energized by special energy-storing ATP molecules (discussed in Chapter 10).

Mangroves, saltbush, and certain algae thrive in areas where the water or soil contains enough salt to kill most vegetation. Such plants accumulate large amounts of organic solutes, including the carbohydrate *mannitol* and the amino acid *proline.* The organic solutes facilitate osmosis, despite the otherwise adverse environment (Fig. 9.8). The leaves of some mangroves also have salt glands through which they excrete excess salt.

WATER AND ITS MOVEMENT THROUGH THE PLANT

If you were to cover the soil at the base of a plant with foil, place the pot where it receives light, and then put the potted plant under a glass bell jar, you would notice moisture accumulating on the inside of the jar within an hour or two. Because of the foil barrier, the water could not have come directly from the soil; it had to have come through the plant. More than 90% of the water entering a plant passes through and evaporates—primarily into leaf air spaces and then through the stomata into the atmosphere (see Fig. 9.10)—with usually less than 5% of the water escaping through the cuticle. This process of water vapor loss from the internal leaf atmosphere is called *transpiration* (Fig. 9.9).

The amount of water transpired by plants is greater than one might suspect. For example, mature corn plants each transpire about 15 liters (4 gallons) of water per week, while four-tenths of a hectare (1 acre) of corn may transpire more than 1,325,000 liters (350,000 gallons) in a 100-day growing season. A hardwood tree uses about 450 liters (120 gallons) of water while producing 0.45 kilogram (1 pound) of wood (or 1,800 liters while producing 0.45 kilogram of dry weight substance), and the 200,000 leaves of an average-sized birch tree will transpire from 750 to more than 3,785 liters (200 to 1,000 gallons) per day during the growing season. Humans recycle much of their water via the circulatory system, but if they were to have requirements similar to those of plants, each adult would have to drink well over 38 liters (10 gallons) of water per day.

Why do living plants require so much water? Water constitutes about 90% of the weight of young cells. The thousands of enzyme actions and other chemical activities of cells take place in water, and additional, although relatively negligible, amounts are used in the process of photosynthesis. The exposed surfaces of the mesophyll cells within the leaf have to be moist at all times, for it is through this film of water that the carbon dioxide molecules needed for the process of photosynthesis enter the cell from the air. Water is also needed for cell turgor, which gives rigidity to herbaceous plants.

Consider also what it must be like in the mesophyll of a flattened leaf that is fully exposed to the midsummer sun in areas where the air temperature soars to well over 38°C (100°F) in the shade. If it were not for the evaporation of water molecules from the moist surfaces, which brings about cooling, and reradiation of energy by the leaf, the intense heat could damage the plant. Sometimes, the transpiration is so rapid that more water is lost than is taken in. The stomata may then close, preventing wilting. The relation and role of abscisic acid in excessive water loss is discussed in Chapter 11.

How does water travel through the roots from 3 to 6 meters (10 to 20 feet) or more beneath the surface and then up the trunk to the topmost leaves of a tree that is more than 90 meters (300 feet) tall? We know that interconnected tubes of xylem extend throughout the plant, from the young roots up through the stem and branches to the tiny veinlets of the leaves. We also know that the water, following a water potential gradient, gets to the start of this "plumbing system" by osmosis. Water is then raised through the columns apparently by a combination of factors, and the process has been the subject of much debate for the past 200 years (Fig. 9.10).

One of the earliest explanations for the rise of water in a living plant was given in 1682 by the English scientist Nehemiah Grew. He suggested that cells surrounding the xylem vessels and tracheids performed a pumping action that propelled the water along. This was questioned, however, when it was found that water will also rise in lengths of dead stems. Then, after Marcello Malpighi suggested it, the belief that capillary action moved the water became popular.

It is well known that the height water will rise in a narrow tube is inversely proportional to the diameter of the tube. It is also known that this rise occurs through the forces involved in the forming of a concave *meniscus* (curved surface) at the top of the water column (Fig. 9.11). Even though water can, indeed, rise 1 meter (3 feet) or more in a very narrow tube, air must be present above the column for the forces to work, which is not the case in a plant. In fact, any air introduced into a water column in xylem interferes with the rise of water. Also, while capillarity might produce enough force to raise water a meter or two, the diameter of the tubes is not small enough to raise it more than that.

The pioneer plant physiologist Stephen Hales discovered and measured *root pressure* as one means by which water moves through plants. When some plants are pruned after growth has begun in the spring, water will exude from the cut ends. This is the result of root pressure. Some plants do not "bleed" when they are pruned, and the force exerted by root pressure has been shown generally to be less than 30 grams per square centimeter (a few pounds per square inch). This is considerably less than what is needed to raise water to the tops of tall trees. Furthermore, root pressure seems to drop to negligible amounts in the summer, when the greatest amounts of water are moving through the plant.

The Cohesion-Tension Theory

Stephen Hales also identified a pulling force due to evaporation of water from leaves and stems. This has led to the cohesion-tension theory, the most satisfactory explanation for the rise of water in plants thus far suggested. Water molecules are electrically neutral, but they are asymmetrical in shape (see Fig. 2.4). This results in the molecules having very slight positive charges at one end and very slight negative charges at the other end. Such molecules are said to be *polar.* When the negatively charged end of one water molecule comes close to the positively charged end of another water molecule, weak hydrogen bonds hold the molecules together.

We know that water molecules adhere to capillary walls (e.g., those of xylem tracheids and vessels) and cohere to each other, creating a certain amount of tension. It is possible, for example, to fill a small glass with water, place a thin, smooth sheet of cardboard over the mouth, and invert the glass without the water spilling. This is because the adhesion of the water molecules to the cardboard and the cohesiveness of the water molecules to one another hold the cardboard against the rim of the glass.

When water evaporates from the mesophyll cells in a leaf and diffuses out of the stomata (*transpires*), the cells involved develop a lower water potential than the adjacent cells. Because the adjacent cells then have a correspondingly higher water potential, replacement water moves into the first cells by osmosis. This continues across rows of mesophyll cells until a small vein is reached. Each small vein is connected to a larger vein, and the larger veins are connected to the main xylem in the stem, and that, in turn, is connected to the xylem in the roots that receive water, via osmosis, from the soil. As transpiration takes place, it creates a "pull," or tension, on water columns, drawing water from one molecule to another all the way through an entire span of xylem cells. The cohesion required to move water to the top of a tall tree is considerable, but the cohesive strength of the water columns is usually more than adequate. Any breaking of the tension through the introduction of a gas bubble results in a temporary or permanent blocking of water transport. This seldom is a problem, however, because small bubbles may be redissolved and larger gas bubbles rarely block more than a few of the numerous capillary tubes of xylem at any time the tissue is functioning.

Water molecules move partly through cell cytoplasm and partly through spaces between cells; they also move between cellulose fibers in the walls and through spaces in the centers of dead cells. Most water and solutes can travel across the epidermis and cortex via the cell walls until they reach the endodermis. There, the water and solutes are forced by *Casparian strips* to cross the cytoplasm of the endodermal cells on their way to the vessels or tracheids of the xylem (Fig. 9.12; see also Chapter 5).

If significant transpiration is occurring, the roots are likely to grow rapidly toward available water. In corn plants, for example, the main roots may grow at a rate of more than 6 centimeters (2.3 inches) a day. Solutes, as well as water, may move so rapidly during periods of rapid transpiration that there is little osmosis taking place across the endodermis. Scientists believe that at such times water may be pulled through the roots by bulk flow, which is the passive movement of a liquid from higher to lower water potential.

In summary: "columns" of water molecules are pulled through the plant from roots to leaves, and the abundant water of a normally moist soil supplies these "columns" as the water continues to enter the root by osmosis (see Fig. 9.10); simply put, the difference between the water potentials (water "concentrations") of two areas (e.g., soil and the air around stomata) generates the force to transport water in a plant.

REGULATION OF TRANSPIRATION

Two guard cells and an opening called the *stoma* (plural: *stomata*) comprise the stomatal apparatus. These stomatal apparatuses, which often occupy 1% or more of the surface area of a leaf, *regulate transpiration and gas exchange*. Control of transpiration is, however, strongly influenced by the water-vapor concentration of the atmo-sphere. The guard cells bordering each stoma have relatively elastic walls with radially oriented microfibrils, making them analogous to pairs of sausage-shaped balloons joined at each end, each with a row of rubber bands around it. The part of the wall adjacent to the hole itself is considerably thicker than the remainder of the wall (Fig. 9.13). This thickness allows each stoma to be opened and closed by means of changes in the turgor of the guard cells. The stoma is closed when turgor pressure is low and open when turgor pressure is high. Changes in turgor pressures in the guard cells, which contain chloroplasts, take place when they are exposed to changes in light intensity, carbon dioxide concentration, or water concentration.

Changes in turgor pressure take place when osmosis and active transport between the guard cells and other epidermal cells bring about shifts in solute concentrations. While photosynthesis is occurring in the guard cells, they expend energy to acquire potassium ions from adjacent epidermal cells, leading to the opening of the stomata. When photosynthesis is not occurring in the guard cells, the potassium ions leave, and the stomata close. With an increase in potassium ions, the water potential in the guard cells is lowered, and the osmosis that takes place as a result brings in water that makes the cells turgid. The departure of potassium ions also results in water leaving, making the cells less turgid and causing the stomata to close (see Fig. 9.13).

Stomata will close passively whenever water stress occurs, but there is evidence that the hormone abscisic acid is produced in leaves subject to water stress and that this hormone causes membrane leakages, which induce a loss of potassium ions from the guard cells and cause them to deflate.

The stomata of most plants are open during the day and closed at night. However, the stomata of a number of desert plants are open only at night when there is less water stress on the plants. This conserves water but makes carbon dioxide needed for photosynthesis inaccessible during the day. Such plants convert the carbon dioxide available at night to organic acids, which are stored in cell vacuoles. The organic acids are then converted back to carbon dioxide during the day when photosynthesis occurs (Fig. 9.14). A specialized form of photosynthesis called *CAM photosynthesis* uses the carbon dioxide released from the organic acids. CAM photosynthesis is discussed in Chapter 10.

Other desert plants have their stomata recessed below the surface of the leaf or stem in small chambers. These chambers, called stomatal crypts, often are partially filled with epidermal hairs, which further reduce water loss by slowing down air movement. Similar recessed stomata are found in the leaves of pine trees, which have little water available to them in winter when the soil is frozen (see Fig. 7.12). A few tropical plants that occur in damp, humid areas (e.g., ruellias; see also Fig. 4.13B) have stomata that are raised above the surface of the leaf, while plants of wet habitats generally lack stomata on submerged surfaces.

Although light and carbon dioxide concentration affect transpiration rates, several other factors play at least an indirect role. For example, air currents speed up transpiration as they sweep away water molecules emerging from stomata.

Humidity plays an inverse but direct role in transpiration rates: high humidity reduces transpiration, and low humidity accelerates it. Temperature also plays a role in the movement of water molecules out of a leaf. The transpiration rate of a leaf at 30°C (86°F), for example, is about twice as great as it is for the same leaf at 20°C (68°F). The various adaptive modifications of leaves and their surfaces and the availability of water to the roots also may play important roles in influencing the amount of water transpired. Leaf modifications are discussed in Chapter 7.

If a cool night follows a warm, humid day, water droplets may be produced through structures called **hydathodes** at the tips of veins of the leaves of some herbaceous plants. This loss of water in liquid form is called **guttation** (Fig. 9.15). Minerals absorbed at night are pumped into the intercellular spaces surrounding the vessels and tracheids of the xylem. As a result, the water potential of the xylem elements is lowered, and water moves into them from the surrounding cells. In the absence of transpiration at night, the pressure in the xylem elements builds to the point of forcing liquid water out of the hydathodes in the leaves. Although the droplets resemble dew, the two should not be confused. Dew is water that is condensed from the air, while guttation water is literally forced out of the plant by root pressure. As the sun strikes the droplets in the morning, they dry up, leaving a residue of salts and organic substances, one of which is used in the manufacture of commercial flavor enhancers (e.g., the monosodium glutamate in products such as Accent®). In the tropics, the amount of water produced by guttation can be considerable. In taro plants, used by the Polynesians to make poi, a single leaf may overnight produce as much as a cupful (about 240 milliliters) of water through guttation.

TRANSPORT OF FOOD SUBSTANCES (ORGANIC SOLUTES) IN SOLUTION

One of the most important functions of water in the plant involves the *translocation* (transportation) of food substances in solution by the phloem, a process that has only recently come to be better understood. Many of the studies that led to our present knowledge of the subject used aphids (small, sucking insects) and organic compounds designed as radioactive tracers.

Most aphids feed on phloem by inserting their tiny, tubelike mouthparts (*stylets*) through the leaf or stem tissues until a sieve tube is reached and punctured. The turgor pressure of the sieve tube then forces the fluid present in the tube through the aphid's digestive tract, and it emerges at the rear as a droplet of "honeydew." In some studies, research workers anesthetized feeding aphids and cut their stylets so that much of the tiny tube remained where it had been inserted. Fluid exuded (sometimes for many hours) from the cut stylets and was then collected and analyzed (Fig. 9.16).

Carbon dioxide, a basic raw material of photosynthesis, can be synthesized with radioactive carbon. By exposing a photosynthesizing leaf to radioactive carbon dioxide, the pathway of manufactured food substances can be traced. The radioactive substances produce on photographic film an image corresponding to the food pathway. Data obtained from such studies reveal that food substances in solution are confined entirely to the sieve tubes while they are being transported. At one time, it was believed that ordinary diffusion and cyclosis (discussed in Chapter 3) were responsible for the movement of the substances from one sieve tube member to the next, but it is now known that the substances move through the phloem at approximately 100 centimeters (almost 40 inches) per hour—far too rapid a movement to be accounted for by diffusion and cyclosis alone.

The Pressure-Flow Hypothesis

At present, the most widely accepted theory for movement of substances in the phloem is called the **pressure-flow** (or **mass-flow**) **hypothesis.** According to this theory, food substances in solution (organic solutes) flow from a *source,* where water enters by osmosis (e.g., a food-storage tissue, such as the cortex of a root or rhizome, or a food-producing tissue, such as the mesophyll tissue of a leaf). The water exits at a *sink,* which is a place where food is utilized, such as the growing tip of a stem or root. Food substances in solution (organic solutes) are moved along concentration gradients between sources and sinks (Fig. 9.17).

First, in a process called *phloem-loading*, sugar, by means of active transport, enters the sieve tubes of the smallest veinlets. This decreases the water potential in the sieve tubes, and water then enters these phloem cells by osmosis. Turgor pressure, which develops as this osmosis occurs, is responsible for driving the fluid through the sieve-tube network toward the sinks.

As the food substances (largely sucrose) in solution are actively removed at the sink, water also exits the sink ends of sieve tubes, and the pressure in these sieve tubes is lowered, causing a mass flow from the higher pressure at the source to the lower pressure at the sink. Most of the water diffuses back to the xylem, where it then returns to the source and is transpired or recirculated. The pressure-flow hypothesis explains how nontoxic dyes applied to leaves or substances entering the sieve tubes, such as viruses introduced by aphids, are carried through the phloem.

MINERAL REQUIREMENTS FOR GROWTH

Growth phenomena are not entirely controlled by internal means. Light, temperature, soil structure, minerals, and other external factors all play a role. In fact, growth depends on a complex, interrelated combination of chemical and physical forces, both internal and external, which are in delicate balance with one another.

Plants may take up many elements from the soil, but besides the carbon and oxygen obtained from carbon dioxide and the hydrogen obtained from water, only 15 elements are essential to most plants as building blocks for the many compounds they synthesize. Sodium, a comparatively abundant element, is apparently required by few plants. The **essential elements** can be remembered by a sentence (Fig. 9.18) that includes the symbols of the elements involved.

Macronutrients and Micronutrients

The mineral elements are usually put into two categories: (1) *macronutrients*, which are used by plants in greater amounts and constitute from 0.5% to 3.0% of the dry weight of the plant; and (2) *micronutrients,* which are needed by the plant in very small amounts, often constituting only a few parts per million of the dry weight.

The macronutrients are nitrogen, potassium, calcium, phosphorus, magnesium, and sulfur, with the first four usually making up about 99% of the nutrient total. Those -elements remaining, the micronutrients, are present in amounts ranging from bare traces—as in the case of sodium and cobalt, neither of which may actually be essential for some plants—to 1,500 parts per million of iron and manganese and up to 10,000 parts per million of chlorine.

In addition to these widely required elements, specific organisms may require others. For example, certain algae apparently require the elements vanadium, silicon, or iodine, while some ferns utilize aluminum. Several loco weeds absorb and accumulate selenium in amounts constituting up to 5 micrograms per gram of dry weight. Selenium, which is often fatally poisonous to livestock, appears to enhance the growth of these plants by reducing toxic effects of phosphates, but there is no direct evidence it is essential to them.

When any of these elements is deficient in the soil, the plants exhibit characteristic symptoms of the deficiency, which disappear after the problem has been corrected (Fig. 9.19). Table 9.1 shows some of the uses of essential elements in plants and describes the symptoms of deficiency for each element.

See the discussion of fertilizers and fertilizing in Appendix 4 for further information on ratios of nitrogen, phosphorus, and potassium (NPK) needed for plants and organic versus inorganic fertilizers. (See also pages 297–298 in Chapter 17 for a discussion of compost and composting.)

Summary

1. Molecules and ions are in constant random motion and tend to distribute themselves evenly in the space available to them. They move from a region of higher concentration to a region of lower concentration by simple diffusion along a diffusion gradient; they may also move against a diffusion gradient. Evenly distributed molecules are in a state of equilibrium. Diffusion rates are affected by temperature, molecule size and density, and other factors.
2. Osmosis is the diffusion of water through a semipermeable membrane. It takes place in response to concentration differences of dissolved substances.
3. Osmotic pressure or potential is the pressure required to prevent osmosis from taking place. The pressure that develops in a cell as a result of water entering it is called turgor. Water moves from a region of higher water potential (osmotic potential and pressure potential combined) to a region of lower water potential when osmosis is occurring. Osmosis is the primary means by which plants obtain water from their environment.
4. Plasmolysis is the shrinkage of the cytoplasm away from the cell wall as a result of osmosis taking place when the water potential inside the cell is greater than outside.
5. Imbibition is the attraction and adhesion of water molecules to the internal surfaces of materials; it results in swelling and is the initial step in the germination of seeds.
6. Active transport is the expenditure of energy by a cell that results in molecules or ions entering or leaving the cell against a diffusion gradient.
7. Water that enters a plant passes through it and mostly transpires into the atmosphere via stomata. Water retained by the plant is used in photosynthesis and other metabolic activities.
8. The cohesion-tension theory postulates that water rises through plants because of the adhesion of water molecules to the walls of the capillary-conducting elements of the xylem, cohesion of the water molecules, and tension on the water columns created by the pull developed by transpiration.
9. The translocation of food substances takes place in a water solution, and according to the pressure-flow hypothesis, such substances flow along concentration gradients between their sources and sinks.

10. Transpiration is regulated by humidity and the stomata, which open and close through changes in turgor pressure of the guard cells. These changes, which involve potassium ions, result from osmosis and active transport between the guard cells and the adjacent epidermal cells.
11. Aquatic, desert, tropical, and some cold-zone plants have modifications of stomatal apparatuses or specialized forms of photosynthesis that adapt them to their particular environments.
12. Guttation is the loss of water at night in liquid form through hydathodes at the tips of leaf veins.
13. Growth phenomena are controlled by both internal and external means and by chemical and physical forces in balance with one another. Besides carbon, hydrogen, and oxygen, 15 other elements are essential to most plants. When any of the essential elements are deficient in the plant, characteristic deficiency symptoms appear.

Review Questions

1. Distinguish among diffusion, osmosis, active transport, plasmolysis, and imbibition.
2. Why do living plants need a great deal of water for their activities?
3. Explain how a tall tree gets water to its tips without the aid of mechanical pumps.
4. What is the difference between transpiration and -guttation?
5. Explain the pressure-flow hypothesis.
6. What are macronutrients? List them.
7. When nutrients are deficient in the soil, how are the deficiencies manifested in plants?

Discussion Questions

1. Why is salted meat less likely to spoil than unsalted meat?
2. Why would dye molecules in a bathtub of water take a long time to diffuse completely throughout the tub, but perfume molecules released in a closed room take considerably less time to do the same thing?
3. Why does osmosis not cause submerged water plants to swell up and burst?
4. Some bodies of water, such as the Dead Sea, have considerably higher salt concentrations than those of the human body. If you were swimming in such water, would you expect your cells to become plasmolyzed? Why?

Additional Reading

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Floating leaves of a giant water lily (*Victoria amazonica*), which sometimes attain a diameter of 2 meters (6.5 feet). The larger leaves are capable of supporting, without sinking, the weight of a child.
Figure 9.1

Figure 9.2 Simple diffusion. *A.* A barrier separates two kinds of molecules. *B.* When the barrier is removed, random movement of individual molecules results in both kinds moving from a region of higher concentration to a region of lower concentration. *C.* Eventually, equilibrium (even distribution) is reached. The rate of diffusion gradually slows down as equilibrium is approached.

Figure 9.4 *A.* A turgid cell. Water has entered the cell by osmosis, and turgor pressure is pushing the cell contents against the cell walls. *B.* Water has left the cell, and turgor pressure has dropped, leaving the cell flaccid. The vacuole has disappeared. ×200.

Figure 9.3 A simple osmometer, made by tying a differentially permeable membrane over the mouth of a thistle tube.

Figure 9.5 A portion of a leaf of the water weed *Elodea. A.* Normal cells. *B.* Plasmolyzed cells. ×100.
A.

B.

Figure 9.6 Black-eyed pea seeds before (top) and after (bottom) imbibition of water.

Figure 9.7 A live oak that grew from an acorn lodged in a small crack in the rock. When it rained, the acorn imbibed water, and the force of the swelling split the rock. A root is now slowly widening the split.

Figure 9.8 A mangrove tree. Mangroves flourish in tropical tidal zones where the salt content of the water is high enough to plasmolyze the cells of most other plants. The mangroves still obtain water via osmosis, which takes place because the mangrove cells accumulate an unusually high concentration of organic solutes; some are also able to excrete excess salt.

Figure 9.9 A potted plant sealed under a bell jar. The surface of the soil has been covered with foil so that no water could evaporate from it. Note the accumulation of moisture on the inside of the glass. The moisture came through the plant by transpiration.

Figure 9.10 Pathway of water through a plant.

Figure 9.11 Capillarity in narrow tubes. The smaller the diameter of the tube, the greater the rise of the fluid.

Figure 9.12 Part of the center of a buttercup root, showing endodermal cells with Casparian strips. ×600.

Figure 9.13 *A.* A small portion of the leaf epidermis of Wandering Jew (*Zebrina* sp.) with several stomata interspersed among ordinary epidermal cells. Each stoma is bordered by a pair of guard cells, and each guard cell is flanked to the outside by a small epidermal cell called a *subsidiary cell.* ×100. *B. Left.* An open stoma. The guard cells swell when turgor pressure in them increases and the stoma opens as the thinner outer walls stretch more than the thicker inner walls. *Right.* The stoma closes when the turgor pressure in the guard cells decreases. The reasons for the changes in turgor pressure are discussed in the text. ×400 (A. © BioPhot; B. © Jeremy Burgess/SPL/Photo Researchers, Inc. From Sylvia S. Mader, *Inquiry into Life*, 9th edition. © 2000 The McGraw-Hill Companies. All rights reserved.)

A.

B.

Figure 9.14 A barrel cactus (*Ferrocactus*). The stems store, in the form of organic acids, carbon dioxide taken in at night; the carbon dioxide is then released inside the plant during the day for use in photosynthesis.
Figure 9.15 Droplets of guttation water at the tips of leaves of young barley plants.

Figure 9.16 An aphid feeding on a young stem of basswood (*Tilia*). A droplet of "honeydew" is emerging from the rear of the aphid. ×10. (*From Martin H. Zimmerman, "Movements of Organic Substances in Trees"* Science *133:73–79, 1961, American Association for the Advancement of Science.*)

Figure 9.17 The pressure-flow hypothesis.
Figure 9.18 Elements essential as building blocks for compounds synthesized by plants.

TABLE 9.1

Uses of Essential Elements in Plants

ELEMENT	SOME FUNCTIONS	DEFICIENCY SYMPTOMS
Nitrogen	Part of proteins, nucleic acids, chlorophyll	Relatively uniform loss of color in leaves, occurring first on the oldest ones

Potassium	Activates enzymes; concentrates in meristems	Yellowing of leaves, beginning at the margins and continuing toward center; lower leaves mottled and often brown at the tip
Calcium	Essential part of middle lamella; involved in movement of substances through cell	Terminal bud often dead; young leaves often appearing hooked at tip; tips and margins of leaves withered; roots dead or dying
Phosphorus	Necessary for respiration and cell division; high-energy cell compounds such as ATP	Plants stunted; leaves darker green than normal; lower leaves often purplish between veins
Magnesium	Part of the chlorophyll molecule; activates enzymes	Veins of leaves green but yellow between them, with dead spots appearing suddenly;
Sulfur	Part of some amino acids	Leaves pale green with dead spots; veins lighter in color than the rest of the leaf
Iron	Needed to make chlorophyll and in respiration	Larger veins remaining green while rest of leaf yellows; mainly in young leaves*
Manganese	Activates some enzymes	Dead spots scattered over leaf surface; all veins and veinlets remain green; effects
Boron	Influences utilization of calcium ions, but functions	Petioles and stems brittle; bases of young leaves break down

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*NOTE: The symptoms of iron deficiency may be caused by several factors, such as overwatering, cold temperatures, and nematodes (small roundworms) in the roots. The iron may be relatively abundant in the soil, but its uptake may be prevented or sharply reduced by these environmental conditions. Iron becomes more soluble under acid conditions—so much so that it can produce toxic conditions for most plants. Acid soil plants, on the other hand, have a much higher iron requirement than plants that require more non-acid conditions; accordingly, azaleas and other plants having high iron requirements can achieve normal growth in a non-acid soil.

All the micronutrients are harmful to plants when present in excessive quantities. Copper will kill algae in concentrations of one part per million, and boron has been used in weed killers. Even macronutrients are harmful if present in heavy amounts, although non-essential elements sometimes can counteract their toxicity.

Figure 9.19 Leaves of bean plants grown in media deficient in various elements to show deficiency symptoms. *A.* A normal plant that has been furnished with all the essential elements. The other plants were grown in media deficient in specific elements, as follows: *B.* Potassium. *C.* Phosphorus. *D.* Calcium. *E.* Nitrogen. *F.* Sulfur. *G.* Micronutrients. *H.* Magnesium. *I.* Iron. *(© The McGraw-Hill Companies, Inc./Doug Sherman, photographer)*