4

Basic Metabolism, Translocation of Water, and Mineral Nutrition

The bodies and metabolism of all plants—indeed of all organisms—are based on the fundamental principles of chemistry and physics. Although organisms can be alive, can reproduce, and can evolve, they have no special substances or powers not present in rocks or air or any other ordinary substance. Biology is easier to study because the same rules and equations you learned in chemistry class can be used to understand organisms.

Because biology is based on chemistry and physics there are two consequences we should take time to think about in a Plants and People book. First, living creatures are natural aspects of the world of rocks, minerals, mountains, air, and so on; we are not set apart from it, not detached from it. And second, we humans have the capacity and intellect to be aware of our world and to study it, to understand it, to appreciate and love it. We have the capacity to realize that our actions can either harm the world or sustain it. During the last several hundred years, especially since the Industrial Revolution, we have emphasized our ability to domesticate plants and animals and to use the world and its living beings as sources of raw materials that can be manufactured into things without worrying greatly about the pollution we have caused. But now we do see the harm we are doing and realize we must alter some of our actions.

Death is a natural part of life for both plants and people. By shedding these leaves in autumn, the parent tree was able to minimize the amount of tissue it would need to protect in winter. Furthermore, as these leaves are decomposed by fungi, bacteria, and tiny animals, their minerals will be released and may be taken up by the roots of some plant, perhaps even the plant that shed the leaves. (Courtesy of Byran Hoyt.)

We share Earth with all living creatures, and we must consider the consequences of our actions. We must also value our humanity, our human spirit, and our human responsibilities, and just as we take pride in our technological accomplishments, we can also take pride in our recent and ongoing efforts to minimize the pollution we cause and the steps we are taking to restore damaged parts of the environment. The principles introduced in this chapter help us understand the chemical and physical methods we can use to live more harmoniously in our world.

To whom much is given, much is expected (Luke 12:48).

Part 1: Atoms and Molecules

All substances are made up of **atoms**. Each atom is composed of a central nucleus containing positively charged protons and neutral neutrons, surrounded by clouds of negatively charged electrons (**FIGURE 4.1**). The various types of atoms differ in the number of protons present in each nucleus: hydrogen has one, helium has two, and so on (**TABLE 4.1**). The number of neutrons in each nucleus varies, but is similar to that of the protons. If the number of electrons in each atom is exactly equal to the number of protons, then the negative charges of the electrons balance those of the protons and the atom is neutral. If there are extra electrons, the atom is said to be a **negative ion** (an anion); if there are too few electrons, the atom is a **positive ion** (a cation; pronounced cat eye on). If all atoms of a substance are the same, the substance is an element; for example, hydrogen is an element, and all atoms of hydrogen have just one proton in each nucleus. Other elements important to biology are carbon (6 protons), nitrogen (7 protons), and oxygen (8 protons).

Atoms combine with each other to make **molecules**. For example, each molecule of water is made up of two atoms of hydrogen and one of oxygen (abbreviated H_2O), each molecule of carbon dioxide has one atom of carbon and two of oxygen (CO_2), and the sugar glucose has six carbon atoms, twelve hydrogens, and six oxygens ($C_6H_{12}O_6$) (**FIGURE 4.2**). Because each molecule of water, carbon dioxide, and glucose contains more than one kind of atom, they are compounds, not elements. Some molecules are composed of several identical atoms: the air we breathe is composed mostly of molecules of nitrogen (N_2) and oxygen (O_2). The atoms in a molecule are held together by interactions of the electrons of each; if the electrons hold the atoms together tightly, we say that they are strongly bonded, but if some part of the molecule can separate from another part easily, we say it has a weak bond. Molecules may be neutral or either positively or negatively charged.

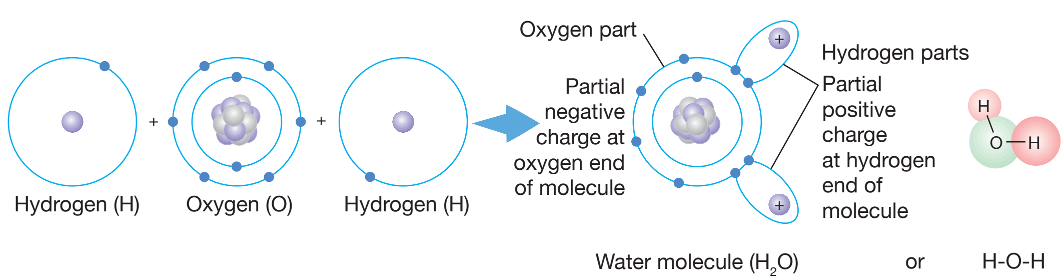


FIGURE 4.1. An atom of hydrogen has one proton and one electron, whereas an atom of oxygen has eight of each (plus eight neutrons in its nucleus). If two atoms of hydrogen combine with one of oxygen, they give off energy and become a molecule of water.

TABLE 4.1. The Number of Protons in Several Elements Important for Life

Element	Symbol	Number of protons (atomic number)*
Hydrogen	H	1
Carbon	C	6
Nitrogen	N	7
Oxygen	O	8
Magnesium	Mg	12
Phosphorus	P	15
Sulfur	S	16
Potassium	K	19
Calcium	Ca	20
Iron	Fe	26

* The number of protons in the nucleus of each element is known as the element's atomic number.

Water

Water has many characteristics important for life, and many of them are due to water molecules being small and "sticky." The two hydrogen atoms lie more or less on the same side of the oxygen atom, so each molecule is slightly positive on one side but slightly negative on the other; water molecules are **polar**, with a positive pole and a negative one. Opposite charges attract, so each water molecule attracts nearby water molecules, as well as any other charged molecule. Water's attraction to itself is called cohesion. Cohesion makes it difficult to boil water or to melt ice, and difficult for water to evaporate, so lakes and rivers tend to be very stable and safe for living organisms, remaining liquid unless temperatures are extremely cold, and not evaporating away unless droughts are prolonged (**FIGURE 4.3**).

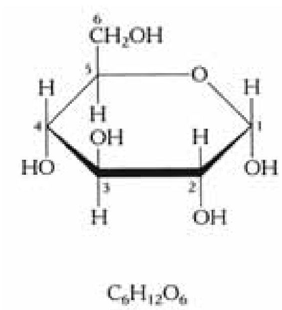


FIGURE 4.2. A molecule of the simple sugar glucose has six atoms of carbon, twelve of hydrogen, and six of oxygen. It is possible for this number of carbons, hydrogens, and oxygens to combine in many different ways and to also have the formula of $C_6H_{12}O_6$; when they are arranged as in this diagram, they are glucose.

FIGURE 4.3. Snowshoeing in Zion National Park. Because water molecules are cohesive (they stick to each other), water is extremely stable and does not melt, freeze, evaporate, or condense easily. Water is present here in its solid form (snow and ice), its liquid form (inside the bodies of the living organisms), and as a gas (water vapor in the air, which is invisible to us). A great deal of solar energy is needed to melt the snow to liquid and then cause it to evaporate; and similarly, temperatures must be very cold for water vapor to condense to rain or snow.

Water's attraction to substances other than itself is called adhesion. Because each water molecule is very small, water easily interacts with many other molecules that have positive or negative regions. The positive sides of many water molecules surround negative portions of substances and cause them to dissolve, and the same is true for the negative sides causing positive regions to dissolve. For example, sugar molecules also have both positive and negative regions, and consequently sugar quickly dissolves in water. Substances that interact with water this way are said to be **hydrophilic** (water loving). In contrast, substances in which all parts are neutral, such as oils and waxes, are **hydrophobic** (water fearing): they do not interact with water and do not dissolve in it.

Acids and Bases

As a first step to understanding acids and bases, we can say that **acids** are compounds that break down and release a **proton** (an H^+) into a solution, whereas a **base** is any compound that releases a **hydroxyl ion** (an OH^-) when it breaks down. This is important because other compounds in the same solution may then pick up a proton and become positively charged (or neutral if they were already negative); others may pick up a hydroxyl and become negatively charged. Adding an acid or base to a solution can potentially change many other molecules in the same solution. Protoplasm is an extremely complex solution of thousands of types of molecules, most of which will be affected by the presence of acids or bases.

In a weak acid, the proton is held tightly so only a few of the acid molecules in a solution release a proton. The solution does not become very acidic and has only a low concentration of protons able to affect other molecules; examples are vinegar (acetic acid) and lemon juice (citric acid). Strong acids break down extensively and many protons are released, strongly affecting the solution; examples are sulfuric acid and hydrochloric acid. There are also weak bases (bleach, sodium hypochlorite), and strong ones (lye, sodium hydroxide), depending on how many hydroxyls are released. **pH** is a measure of acidity: solutions with a pH near 7 are neutral; those between 0 to 6.9 are acidic; and those with pH of 7.1 to 14 are basic. Limestone is basic and causes ground water, streams, and lakes in an area to be basic (**alkaline**), whereas soils rich in leaf litter and humus are acidic as are waters that flow from them. Pure water, unaffected by soil, plants, or animals, is neutral.

Acids and bases are important in biology for several reasons. First, many common organic compounds are acids and bases. Examples of common acids are amino acids in proteins, fatty acids in oily and greasy foods, and nucleic acids in cell nuclei. In most of these, the neutral molecule is relatively inactive, but when the proton or hydroxyl comes off in solution, the remainder of the molecule has a charge and can react with another molecule that has an opposite charge. Also, many mineral elements that roots must obtain from soil are soluble in acidic solutions but not alkaline ones. If the soil is too alkaline, the minerals do not dissolve and cannot be absorbed by roots.

Water is unusual in being both an acid and a base: in a body of water (in a drinking glass, in a lake, snow, ocean) almost all water molecules are complete, that is, they are H_2O, but a tiny fraction spontaneously break down into H^+ and OH^-. Because one acidic H^+ is produced every time one basic OH^- is, the solution remains neutral (pH 7), but still there are protons and hydroxyls available to affect other molecules in the solution.

Organic Molecules

Millions of organic compounds—those that contain at least one carbon atom—are possible, but fortunately they can be classified into just a few families of compounds,

TABLE 4.2. Main Groups of Macromolecules in Cells

Carbohydrates composed of sugars	Lipids composed of fatty acids
Proteins composed of amino acids	Nucleic acids composed of nucleotides

such as carbohydrates, proteins, lipids, and so on (**TABLE 4.2**). This is because most carbon atoms in an organic compound carry a chemical group, known as a **functional group**, and these give the compound its particular properties. A carbon compound that has an acid functional group is an acid; those with an –OH functional group are alcohols, and so on. Because most organic compounds have several or many carbons, each compound can have several functional groups and simultaneously be an acid and an alcohol or other things.

Another thing that simplifies biological chemistry is that many important compounds are **polymers**. Each is made up of smaller units (**monomers**) that tend to be similar to each other. For example, simple sugars can be joined together to make complex sugars; the cellulose molecules in cell walls are giant molecules with thousands of carbon atoms and thousands of functional groups, but each is really a very simple polymer of the simple sugar glucose. Similarly, proteins are polymers of amino acids.

Carbohydrates

Carbohydrates are familiar organic compounds such as sugars, starches, and cellulose. The basic unit of carbohydrates are **simple sugars** (**monosaccharides**), sugars that cannot be broken down into smaller sugars. Monosaccharides can be polymerized into **disaccharides** (two sugars) and **polysaccharides**. There are hundreds of monosaccharides, most which are made only by plants and algae, not by animals. The great diversity of monosaccharides makes it possible to have thousands of types of disaccharides and polysaccharides, but only a few need to be mentioned here.

Monosaccharides are classified by the number of carbon atoms they contain. Simple sugars called tetroses have four carbon atoms, pentoses five, hexoses six, and so on. One important pentose is deoxyribose, the D in DNA (deoxyribonucleic acid). Familiar hexoses are glucose (refer back to Figure 4.2), fructose (often called corn syrup on food labels), and galactose. All hexoses have more or less the same formula ($C_6H_{12}O_6$), but they differ in the arrangement of their atoms such that each hexose differs from all others in its shape and the position of side groups. This allows enzymes to easily distinguish one hexose from another. The enzyme that polymerizes glucose into starch (amylose synthase) only interacts with glucose and never accidentally puts fructose or galactose into the growing starch molecule.

It is difficult to overstate the importance of glucose. Too much sugar is bad for our health, but glucose is what photosynthesis produces, and using only glucose and some inorganic ions like ammonium, sulfate, and a few others, plants build their entire bodies, everything. Glucose can be converted not only into all the other hexoses, but into all the other sugars. From these, plants make many types of acids, including amino acids, fatty acids, and nucleic acids. Every organic molecule in a plant began as glucose in a chloroplast. And because all of our own food is also ultimately derived from plants (meat comes from animals that eat grass, oats, and corn), all our organic molecules began as glucose as well. Plants also polymerize glucose into various long-chain polysaccharides. Bonded end to end in a particular way (with a beta-1,4 bond), glucoses become cellulose, a structural material used to build cell walls. Bonded in a different way (with an alpha-1,4 bond), glucoses become starch (amylose), a means of safely storing glucose for many days, months, or years.

Beyond converting glucose to other materials, almost all organisms have enzymes that break down starch, releasing the glucose molecules when they are needed. The glucose is then converted into other molecules or respired for energy. Much of our own energy comes from digesting and respiring starch in our food. Surprisingly, very few organisms can break cellulose down to get its glucose molecules; instead cellulose passes right through us as “dietary fiber.” Glucose itself cannot be stored in large quantities because it interacts with water and would cause a cell to swell. This interaction does not occur with starch; starch grains can be stored in cells with no adverse effects.

When a plant needs to transfer energy from one area to another, such as from leaves to growing tissues or developing fruits, it uses energy-rich molecules, typically the disaccharide sucrose. A cell converts part of its glucose to fructose, then bonds one glucose to one fructose in such a way that the resulting sucrose molecule is very stable and has little tendency to react with other molecules. Sucrose can be safely transported from one end of a plant to the other in phloem. Phloem sap of white lupine has as much as 154 grams (about 5.4 ounces) of sucrose per liter. Other small polysaccharides are also transported: raffinose (a trisaccharide of galactose, glucose, and fructose) and stachyose (a tetrasaccharide similar to raffinose but with two galactose molecules instead of just one).

Amino Acids and Proteins

Amino acids are small organic molecules that are both an acid and a base. One end of each is a carboxyl group (acidic), the other end is an amino group (basic), in between is the rest of the molecule with a side group that is a functional group with some special property. Some side groups are hydrophilic, others hydrophobic, some are long, others short, and so on. Only 20 different amino acids are used to construct all proteins. The carboxyl group of one amino acid forms a chemical bond (called a peptide bond) with the amino group of a second amino acid (**FIGURE 4.4**). Even after an amino acid has reacted this way, it still has a reactive end, so more amino acids can be added, creating a long, unbranched molecule called a **protein** (very short proteins are sometimes called peptides). Any particular organism has thousands of types of proteins; we know that humans have at least 30,000 types, and when all organisms on earth are considered, there must be millions of types of protein. Each differs from all others in the number of amino acids it contains and in their sequence.

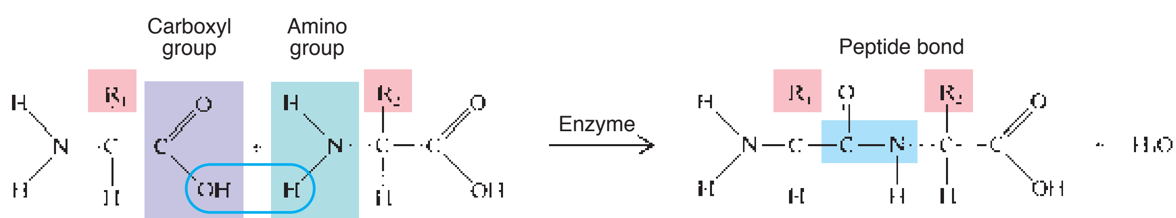


FIGURE 4.4. Proteins are composed of amino acids that bond to each other by having a carboxyl group on one react with an amino group on another. After the reaction, another amino acid can be added, then another, and so on until the protein is complete. The bonding of amino acids like this occurs only in ribosomes and only when guided by messenger RNA. The boxes marked R_1 and R_2 are side groups, and each of the twenty amino acids has a unique side group and thus unique chemical characteristics.

The amino acids in any particular type of protein occur in extremely precise sequences, and this gives the protein distinctive properties. Each protein molecule spontaneously folds into a distinctive shape because of its sequence of amino acids. Positively charged amino acids repel each other but are attracted to negatively charged ones, and this may cause one part of a long protein to fold back, bringing oppositely charged regions together. Similarly, various hydrophilic regions attract each other or interact with the water of the protoplasm whereas hydrophobic regions cause the protein to fold such that as many hydrophobic regions as possible are brought together to form a pocket. If part of a protein has amino acids that make it hydrophobic, such regions will tend to dissolve into the lipids of membranes. By organizing the 20 amino acids in various sequences, and by making proteins of various lengths, a huge number of proteins, each with distinctive properties, is possible.

The sequence of amino acids is said to be the **primary structure** of the protein. The particular shape caused by the attraction and repulsion between amino acids is called its **tertiary structure** (in between, short regions form an alpha helix, others form a beta pleated sheet; these are its **secondary structure**) (**FIGURE 4.5**). In many cases, once a protein has folded into its tertiary structure, its surface has the correct shape and characteristics to adhere to other proteins; the entire grouping is **quaternary structure**. This ability to automatically organize a shape simply due to characteristics of the molecule itself is called **self-assembly**.

Proteins have many roles in biology. Some are simply storage forms of amino acids. As a flower produces seeds, it fills them with nutrients that will allow the embryo to grow rapidly when the seed germinates. Amino acids are polymerized into seed storage proteins that fold into such a compact mass (their tertiary structure) that almost all water is excluded from it; the protein is dry, stable, and lightweight (**FIGURE 4.6**). We eat storage proteins in beans, peas, whole wheat, and other protein-rich plant-based foods. Other proteins play a structural role; they interact with each other (forming a quaternary structure) to form long strong microtubules or microfilaments that act as

FIGURE 4.5. This is a model of a protein that has folded into its tertiary structure due to the interactions of the side groups on each of its amino acids. When folded like this, the protein has the correct structure to carry out a particular function. (Structure from Protein Data Bank 2AAS. J. Santoro, et al., *J. Mol. Biol.* 229 [1993]: 722–734. Prepared by B. E. Tropp.)

FIGURE 4.6. As these corn kernels mature, their cells synthesize and store large amounts of a protein called zein. Protein makes corn nutritious for us: after we eat corn, our stomach and small intestine digest the zein down to its amino acids, which we then absorb and use to synthesize the proteins our bodies need.

a skeleton inside each cell. Microtubules are composed of two proteins that associate into pairs, then the pairs aggregate into microtubules.

Some proteins act as **hydrophilic channels** in membranes. Their primary structure has alternating regions of hydrophilic and hydrophobic amino acids; the protein folds in such a way that the hydrophilic amino acids form a channel in the center whereas hydrophobic ones face outward. Such a protein does not remain in water for long but instead sinks into a hydrophobic membrane. Once there, the central channel acts as a passageway allowing hydrophilic molecules to pass through the membrane.

Many proteins act as biological catalysts called **enzymes**. Catalysts enter a chemical reaction and cause it to proceed faster or more easily or at a lower temperature than the reaction would without the catalyst. The catalyst itself emerges unaffected by the reaction, so it can then catalyze another and another, often participating in several hundred per second. To be an effective catalyst, an enzyme must have an **active site**, a set of amino acid side groups that are brought together by the protein's folding. The combined properties of each of the active site's side groups create a chemical environment that speeds up a reaction. The active site must have exactly the right size, shape, and set of side groups, which means that the protein must be folded into the correct tertiary shape. If the cell's pH is too acidic or alkaline it might cause the protein to fold improperly and no active site will form. Too much heat or cold, or too many ions like calcium (Ca^{++}) and magnesium (Mg^{++}) can also affect the active site for better or worse. A protein that is inactivated is denatured.

Each enzyme catalyzes only one type of reaction because each active site must be precise. The enzyme that polymerizes glucose into cellulose is called cellulose synthase, and its active site accepts only glucose, no other monosaccharide. Proteases depolymerize proteins back into amino acids, and lipases digest lipids. The fact that each enzyme catalyzes only one type of reaction is **substrate specificity**, and it allows a cell to control its metabolism by controlling the types of enzymes it produces: if it makes all the enzymes necessary for photosynthesis, it will develop into a chlorenchyma cell; if it makes the ones for secondary walls and lignin, it becomes a sclerenchyma cell and so on.

Lipids

Lipids are familiar to us as oils, grease, lard, and butter: things that do not dissolve in water unless soap is added. Unlike water, lipids have no positive and negative regions; they are neutral, described as being **nonpolar**. The basic units of many lipids are **fatty acids**, long chains containing up to 26 carbons and having an acid group (a carboxyl, just as in amino acids) at one end (**FIGURE 4.7**). If every carbon is bonded to two hydrogens, the fatty acid is **saturated** and tends to be a straight molecule that lies closely to neighboring fatty acids. In a group, saturated fatty acids fit together so well they tend to crystallize and be firm or hard at room temperature (butter, grease). If some hydrogen is missing, the fatty acid is **unsaturated** and has a kink in it, and it cannot lie tightly against its neighbors. It has less tendency to crystallize, so unsaturated fatty acids are soft or even liquid at room temperature (olive oil, corn oil) (**BOX 4.1**).

Fatty acids tend to polymerize. We have seen two examples in earlier chapters. Epidermis cells secrete fatty acids on to their outer wall where they polymerize into cutin if they are moderately long, or into wax if they are very long fatty acids. Almost all other fatty acids react with glycerol, which can hold three fatty acids, forming a **triglyceride** (**FIGURE 4.8**). This is the main storage form found in lipid droplets in cells of oily seeds and fruits, such as avocado, peanuts, and sunflower seeds. Being nonpolar and hydrophobic, triglycerides have even less tendency to attract water than does starch, and because most enzymes are water-soluble not lipid-soluble, a lipid droplet in a cell is almost inert.

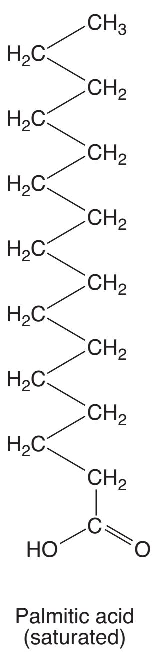


FIGURE 4.7. All fatty acids have a carboxyl group at one end; the rest of the molecule is just carbon and hydrogen. If no double bond is present, the molecule is a saturated fatty acid and it can be straight. This allows them to align side by side; these are often solid at room temperature (a fat).

BOX 4.1. Lipids: Oils, Fats, and *Trans*-fats

The term "lipid" covers both fats and oils and several other compounds (see previous page and page 85). **Fats**, by definition, are solid at room temperature whereas **oils** have a lower melting point and thus are liquid at room temperature. If oils are cooled sufficiently, they solidify, and if fats are heated, as when we use them for frying, they liquefy. Fatty acids are long, unbranched backbones of carbon atoms with hydrogen attached and with an acid group at one end. In a saturated fatty acid, each carbon is attached to two others by what is called a carbon-carbon single bond, and each carbon also has two hydrogens attached to it (**FIGURE B4.1**). In an **unsaturated fatty acid**, at some point in the backbone, two adjacent carbon atoms are attached to each other by a carbon-carbon double bond, and each of these two carbons has only a single hydrogen attached to it. The fatty acid is not saturated with hydrogens. If an unsaturated fatty acid has one double bond, it is **monounsaturated**; if two or more double bonds, it is **polyunsaturated**.

Saturated fatty acids tend to align easily with each other and have an orderly, stable packing. They have to be heated to disrupt their orderliness and make them move around as a liquid, so saturated fatty acids make up the solid lipids, the fats. The double bond of an unsaturated fatty acid causes a kink in the backbone, so neighboring fatty acids cannot align well; instead they make a jumble and move around even when cool; unsaturated fatty acids are the oils.

Within the bodies of plants and animals, the relative proportions of saturated and unsaturated fatty acids determine whether a membrane or a lipid droplet is solid, soft, or liquid. The proportions can be changed by the cells as the surrounding temperatures change. In plants and cold-blooded animals, body temperature is similar to environmental temperature and changes with the seasons. Membranes must remain fluid at all times, so these organisms often add oily unsaturated fatty acid in winter, and then replace them with saturated fatty acids in summer because the saturated fatty acids will not become too fluid (too "runny") in the heat.

Two types of double bond are possible in unsaturated fatty acids. If the two parts of the backbone lie on the same side of the double bond, this is a ***cis*-unsaturated fatty acid**, but if the two parts lie on opposite sides, it is a ***trans*-unsaturated fatty acid**, usually just called a ***trans*-fat**. A polyunsaturated fatty acid can have both types of double bond. Neither plants nor animals ever make *trans*-fats naturally in their bodies. Whereas natural dietary fats are generally beneficial, *trans*-fats are not essential and are never healthful in our diets. They increase the risk of heart disease; they raise the level of "bad" LDL cholesterol and reduce our "good" HDL cholesterol.

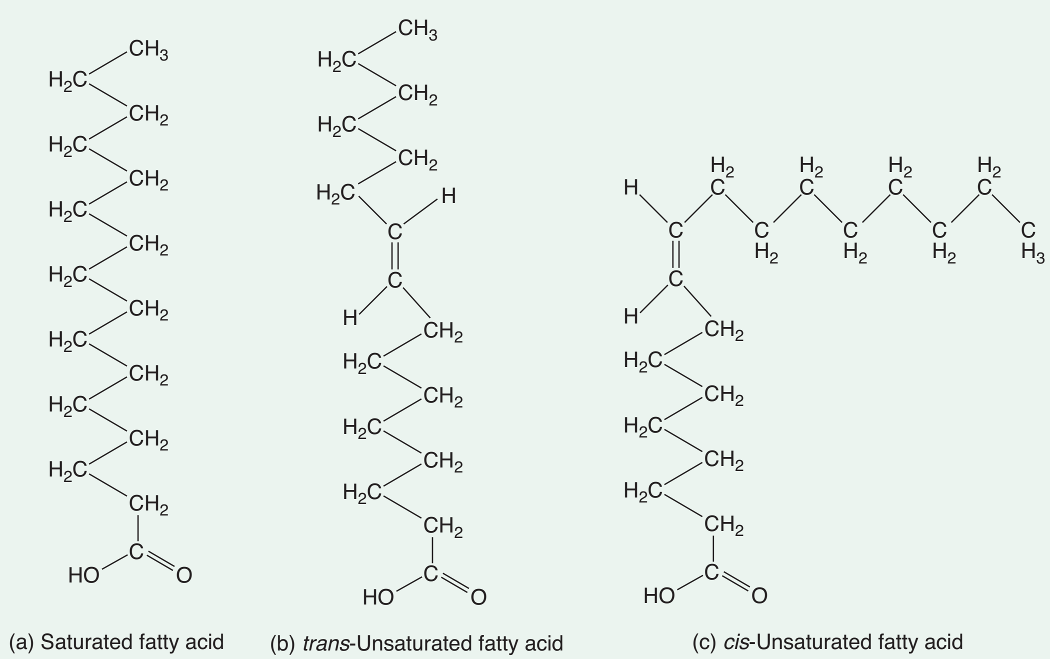
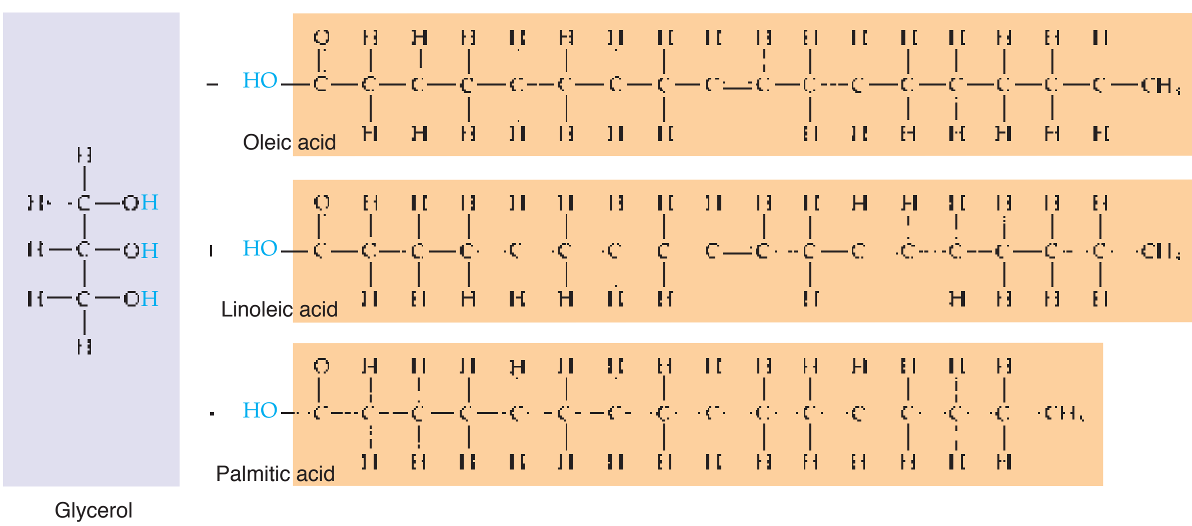


FIGURE B4.1. The various types of fatty acids. **(a)** Saturated, **(b)** *cis*-unsaturated, and **(c)** *trans*-unsaturated.

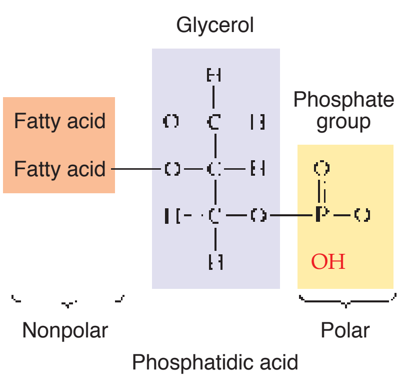
(continued)

The only source of *trans*-fats in our diets is through food processing: we synthesize them artificially in factories. Unsaturated fatty acids, being oils, often cannot be heated enough to use for frying because they tend to smoke, scorch, and develop a "burnt" flavor. Also, in baked goods like cakes, cookies, health food bars, and so on, the food tastes better if it is not "oily" at room temperature. In contrast, many fats can be heated to high temperatures; they melt into a liquid at about the temperature needed for cooking. And in baked goods, they give the food a good texture. Furthermore, unsaturated fatty acids (oils) and foods made with them do not have a shelf-life as long as that of saturated fatty acids (fats) because oxygen reacts with double-bonded carbons, and we perceive this as the fat becoming rancid and inedible. If unsaturated oils are used in foods that need to be stored (such as most commercially prepared, packaged foods), then artificial antioxidants such as BHA and BHT must be added (you will see them in many labels, near the end of the ingredients).

Although it would be possible to find adequate supplies of natural fats needed for baking (such as lard), it is easier and cheaper to start with plant oils and **hydrogenate** them (chemically force hydrogen onto their double bonds). If the oils were hydrogenated to saturation, they would become extremely hard, too hard. Instead, the oils are **partially hydrogenated**, which merely saturates some double bonds and leaves others. This results in fats that have a longer shelf-life than the original oil, and they have a better texture for baking and frying. The problem is that partial hydrogenation converts some of the natural *cis*-fatty acids into unnatural *trans*-fatty acids. The danger of *trans*-fats has only recently become known, and most food processors have redesigned their products so that they no longer use *trans*-fats, but this is not true of all processors or of all processed foods. It is always best for you to check the label and avoid anything with ingredients listed as "*trans*-fats" or "partially hydrogenated."



(a)



(b)

FIGURE 4.8. **(a)** If three fatty acids combine with a molecule of glycerol, the result is a triglyceride; no part of such a molecule can dissolve easily in water, so triglycerides form droplets in cells. **(b)** In a phospholipid, the phosphate group is hydrophilic whereas the fatty acids are hydrophobic: the phosphate associates with water and the fatty acids associate with other lipids. Cell membranes are composed of phospholipids.

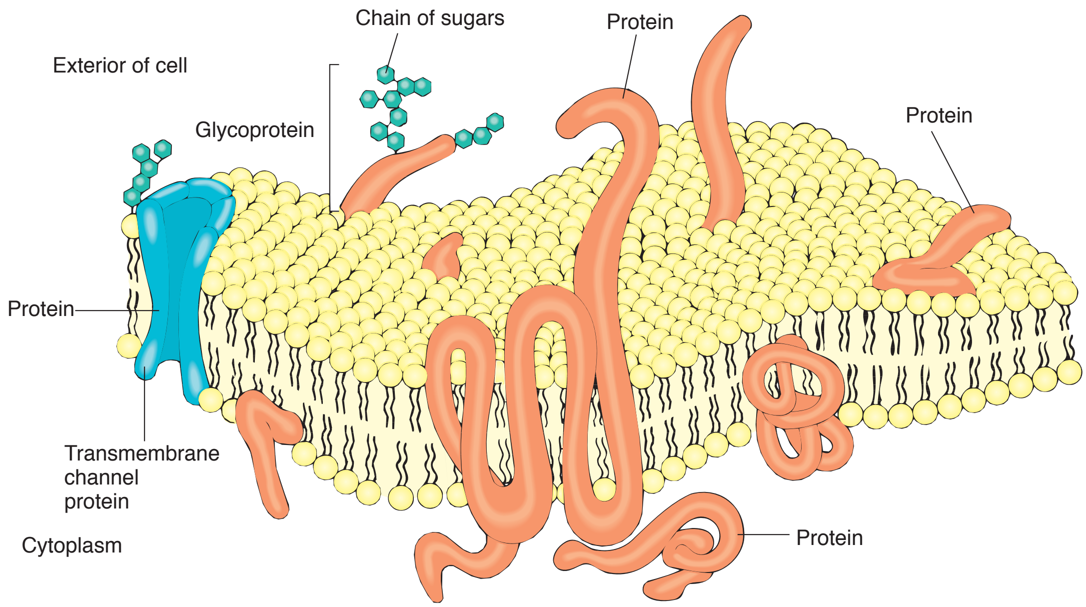


FIGURE 4.9. Cell membranes are composed of two layers of phospholipids with the fatty acids of one layer facing those of the other. Cell membranes also contain many proteins. The parts of the proteins that are inside the membrane must contain amino acids that have lipid soluble (hydrophobic) side groups.

Phospholipids are formed when glycerol combines with two fatty acids and a phosphate group. Phosphate routinely gives off a proton (an H^+) in water, so the rest of the phosphate group has a negative charge. Like other lipids, phospholipids are neutral and hydrophobic over most of their surface but are charged and hydrophilic at the end with the phosphate group; the phosphate causes the molecule to be polar. If a small amount of phospholipid is poured onto water, it will spread into a film one molecule thick, with the phosphate end of each lipid facing the water and the rest of the lipid protruding upward, as far away from the water as possible. In cells, which have water everywhere, phospholipids form themselves into membranes two molecules thick (a bilayer): the phosphate groups in each layer face outward and interact with water, the hydrophobic fatty acids face inward and interact with each other (**FIGURE 4.9**). This is the basic arrangement of all membranes in cells. Each membrane is completed by having proteins associate with them: proteins that have hydrophobic surface regions sink into the membranes, those with hydrophilic regions lie on its surface. Membranes must be flexible because they produce and receive vesicles, and different organelles fuse with each other. In cold climates, where lipids tend to solidify, plants add more unsaturated fatty acid to their membrane phospholipids; in hot climates they use more saturated fatty acids.

Nucleic Acids

Nucleic acids are organic polymers involved in storing and transmitting information. How does a molecule store information? The monomers of nucleic acids are **nucleotides**, and we can think of each of them as being similar to a letter in an alphabet: with the 26 letters in our alphabet, we can write sentences, articles, and books (information storage) and then make copies of those to send that information to various places where it is needed. Someone reads that information and uses it to guide his or her actions or thoughts. **Deoxyribonucleic acid** (**DNA**) is the nucleic

TABLE 4.3. Nucleic Acids

Nucleic Acid	Function
DNA	Located in the nucleus, plastids, and mitochondria; stores information and guides protein synthesis.
RNA	
messenger RNA	Carries information necessary for protein synthesis from DNA to ribosomes.
ribosomal RNA	Is part of the quaternary structure of ribosomes.
transfer RNA	Carries amino acids to ribosomes so that they can be used for protein synthesis.

acid most often used for information storage, and it has only four "letters" (the deoxyribonucleotides A, T, G, C; see **TABLE 4.3**) (**FIGURE 4.10**).

The information in DNA guides the synthesis of proteins, but DNA never participates directly. Instead, the sequence of nucleotides in a certain section of DNA, called a **gene**, guides the formation of a complementary sequence in **messenger RNA** (**mRNA**), which leaves the nucleus, moves to the cytoplasm, and, working with ribosomes, provides the information needed to assemble amino acids into the proper sequence (primary structure). A ribosome has two subunits, each consisting of several molecules of nucleic acid (**ribosomal RNA**, **rRNA**) and enzymes. When the proper proteins and rRNAs encounter each other, they automatically self-assemble into a large complex with elaborate quaternary structure. The presence of mRNA then causes the two ribosome subunits to come together around it (**FIGURE 4.11**). Amino acids are brought to the ribosome by **transfer RNA** (**tRNA**) molecules; one part of each tRNA can "read" three "letters" of the mRNA. Whichever tRNA has the amino acid that corresponds to those three letters is allowed to enter the ribosome, bind just long enough for the amino acid

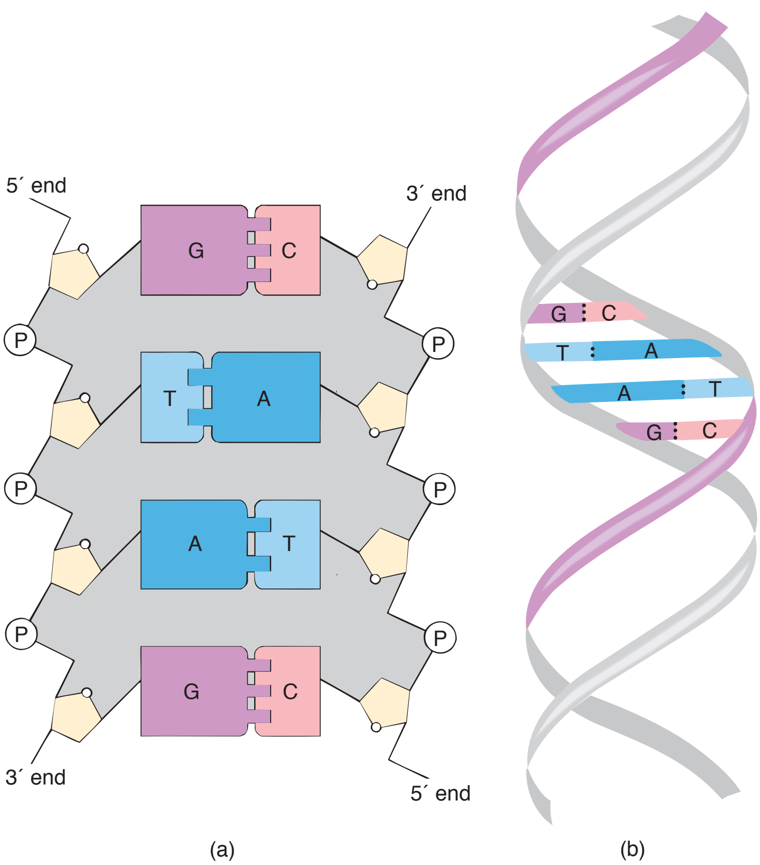


FIGURE 4.10. A molecule of DNA consists of a linear sequence of nucleic acids abbreviated as A, T, G, and C. Each molecule of DNA is paired with another such that each A is paired with a T and each G is paired with a C. The pairing is done by the enzyme that synthesizes DNA.

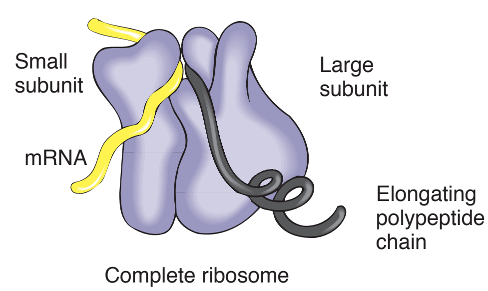


FIGURE 4.11. Ribosomes consist of two parts that have several grooves in them: messenger RNA fits into one, transfer RNA brings amino acids into another, and the protein that is being synthesized emerges from a third groove.

to be attached to the growing protein, then the empty tRNA is ejected. The ribosome pulls the next three mRNA "letters" into the active site and waits for the proper tRNA to bring the proper amino acid. As the growing protein emerges from the ribosome, it folds into its tertiary structure, forming active sites, or clustering with other proteins.

DNA also guides the formation of small pieces of RNA that do not do any of the above. These have regulatory roles: some complex with mRNA and inactivate it, others might bind to parts of DNA and either active or repress it. These small regulatory RNAs have many names, but in general are referred to as **microRNAs**.

Plastids and mitochondria also have DNA and ribosome and all the other components necessary for protein synthesis.

Secondary Metabolites

Many other types of compounds are synthesized by plants and play distinctive roles in their metabolism. These are often given the general label of **secondary metabolites**, and they include diverse compounds such as pigments, fragrances, poisons, and chemicals that give many of our foods their flavors. The taste of vanilla, chocolate, mint, and cinnamon are due to secondary compounds, as are the burning chemicals in poison ivy and hot peppers. An extremely common type of secondary metabolite is a class of chemicals called tannins; they are bitter and astringent, they cause our mouths to pucker when we eat unripe fruit. More importantly, tannins denature proteins, so when animals eat tannin-rich plants, their mouths and stomachs are damaged, and the animal either dies or learns to avoid that plant. We use tannins in several ways; in high concentrations, we use them to tan hides, that is, to denature the proteins in animal skins so that our leather shoes and belts do not rot. In lower concentrations, tannins give tea and red wine their mild astringency.

Several groups of secondary metabolites are familiar and easy to see: pigments. There are several distinct types of pigments, each type being made by its own particular metabolic pathway. Carotenoids are a group of lipid-soluble pigments similar to each other in their structure and in the enzymes that make them. Carotenoids are mostly yellow and orange and occur in chromoplasts and chloroplasts. Animals need carotenoids but do not synthesize them, and must get them in their diet, from the plants they eat. The yellow of egg yolks is entirely plant-derived carotenoids, and chickens are often fed yellow plant material so that their egg yolk will be more appealing to us. People need carotenoids as a necessary material for our vision and the synthesis of vitamin A. Anthocyanins are water-soluble pigments, predominantly blues and reds. For some reason, an entirely new type of water-soluble flower pigments, betalains, evolved in cacti, four-o'clocks, amaranths, and their relatives. Plants that have betalains do not have anthocyanins. Chlorophylls are a very small family of pigments: true plants have only two, chlorophyll *a* and chlorophyll *b* (both are green and both capture the light used in photosynthesis), but algae have a few other types of chlorophyll as well.

Part 2: The Movement of Water Throughout a Plant

Water molecules, just like all other molecules, are in constant motion. In liquids and gasses, molecules move a short distance until they strike another molecule; then, unless they combine chemically, the two bounce off each other and move in new directions. The hotter the material, the more rapidly molecules move, but even when frozen into ice, water molecules vibrate in place and occasionally break away from their neighbors and move away.

Water Movement Across Membranes

If two substances are mixed together, their constant motion causes each to gradually mix with the other. This is **diffusion**, technically defined as the movement of molecules from areas where they are more concentrated to areas where they are less concentrated; this is an important principle to remember. If water is added to a material that is also hydrophilic and interacts with it, water diffuses into that substance and tends to stay there. For example, a central vacuole might contain a mix of water and glucose. If water is more concentrated in the cytoplasm, then water will move from the cytoplasm, across the vacuole membrane and into the central vacuole (**FIGURE 4.12**). Movement across a membrane like this is **osmosis**. Water will continue to move into the central vacuole until either of two things happens: so much water enters the vacuole that the concentration of water is equal in both the cytoplasm and the vacuole, or until the vacuole swells so much that its pressure against the wall is so great that no more water molecules can force their way in. It is important that the membrane be selectively permeable; that is, some materials can diffuse through it whereas others cannot. In this case, the vacuole membrane is permeable to water but not to glucose. If it were permeable to glucose, glucose would diffuse out and there would be no build up of pressure.

The tendency of glucose or any other hydrophobic molecule to attract and hold water is its **osmotic effect**. A dilute solution of glucose will have only a weak osmotic effect, a weak ability to attract more water to itself. A concentrated, syrupy solution has a stronger osmotic effect and a stronger ability to attract more water. Dry saltine crackers and table salt have such strong osmotic effects that they can pull water out of humid air.

Plants control osmotic effects very precisely. If a cell needs to be turgid or to swell and grow, it can pump solutes (especially sugars and potassium) into the vacuole and cause water to diffuse in and build up pressure. If the cell needs to shrink, it can pump the solutes out and water will follow, causing turgor pressure to drop.

Using osmotic effects, central vacuoles and walls function together to provide strength to cells, leaves, flowers, and other soft organs. As the vacuole membrane pumps material into the vacuole, the vacuole becomes "osmotically drier"; that is, its tendency to absorb water increases. As water enters, the vacuole swells and presses the rest of the protoplasm outward against the wall, but the wall resists, becomes stretched and taut. We say the cell becomes **turgid**; examples are fresh lettuce and crisp apples

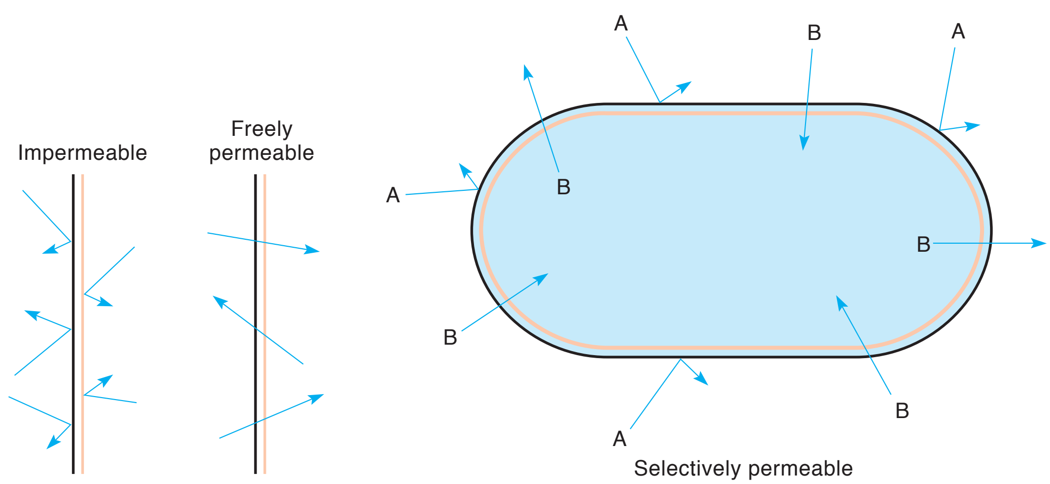


FIGURE 4.12. If a vacuole membrane pumps material into a central vacuole, the vacuole becomes "drier," causing water to move into the vacuole, which creates turgor pressure. Diffusion of material through a membrane is osmosis.

FIGURE 4.13. These leaves are being supported by turgor pressure in all their cells. They are able to support themselves only if they have enough solutes and water in their central vacuoles.

FIGURE 4.14. These leaves are wilted because the leaves are losing water to dry air faster than the roots are able to bring water in from the dry soil: there is not enough water in the plant to fill all the central vacuoles full enough to generate turgor pressure.

(**FIGURES 4.13** and **4.14**). If there is not enough water, the vacuole does not put pressure on the wall and the plant is **wilted**. This is similar to putting air in a tire: when air is pumped into the tire, the tire becomes strong enough to support a bicycle or car. Turgor pressure in plant cells is not strong enough to hold up entire trees (wood is necessary for that), but it does maintain the shape of leaves, flowers, and many stems: if something can wilt, it is being supported by turgor pressure. We animals use this type of hydrostatic pressure to maintain the size and shape of our eyeballs, and males use it when sexually aroused.

When a cell needs to grow, it softens the cell wall just enough that vacuole pressure causes the wall to stretch. Once the cell has reached its proper size, it reinforces the wall enough to stop further growth. Familiar examples of this are flowers: just before a flower opens, its petals are fully formed but all their cells are extremely tiny with miniscule central vacuoles. The vacuole membranes pump enough material into the vacuoles so quickly that they absorb water, swell and stretch the cell walls causing the petal to grow to its full size in just a few hours. Once the petal is fully expanded, the central vacuoles make up almost the entire cell volume, and the walls are stretched so thin that the petals are delicate, easily damaged, and usually die within a few days. In contrast, leaves, stems, and roots must be permanent and must not be so delicate; as they grow, the cell adds new cellulose, hemicellulose, and other wall components at a rate just fast enough to strengthen the walls but not stop growth.

Osmotic effects are also the basis for opening and closing stomatal pores. At sunrise, guard cells pump potassium into their central vacuole, causing water to follow it. The guard cells swell into a kidney bean shape, push away from each other, and the stomatal pore opens, allowing carbon dioxide to enter the leaf (**FIGURE 4.15**). At sunset, the cells reverse

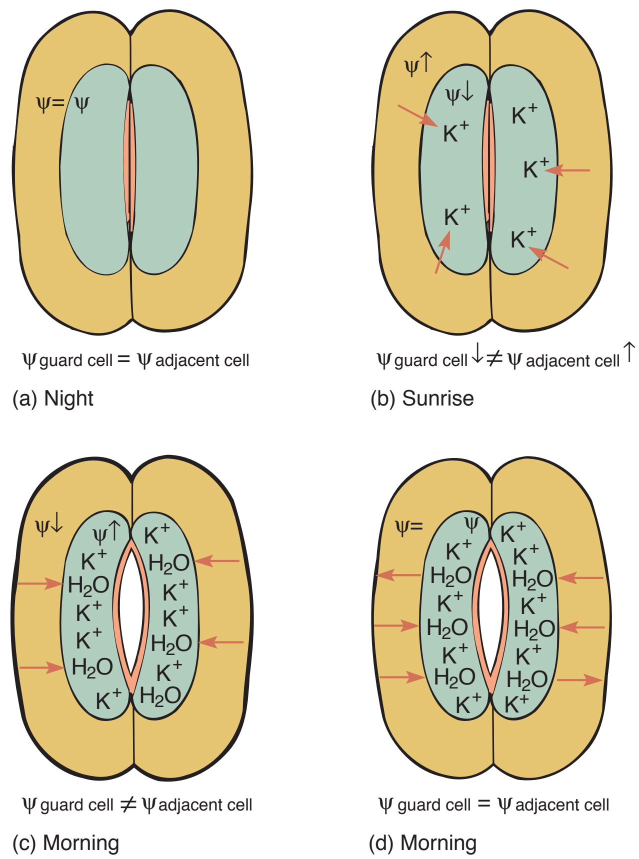


FIGURE 4.15. At night, guard cells and adjacent cells are in hydraulic equilibrium **(a)**, but at sunrise, potassium is pumped into guard cells **(b)** and water follows **(c)**, generating turgor pressure. This causes the guard cells to swell, bend, and open the stomatal pore **(d)**. At sunset, when the pores must be closed, the process is reversed. The symbol Ψ (pronounced "sigh") is a measure of a solution's tendency to absorb more water or to lose water.

this: they pump potassium out of the vacuole, and again water follows it, turgor pressure drops, the cells relax, and the stomatal pore is closed.

Some leaves have motor cells in their petioles. When the leaf blade needs to be held out into the sun, the motor cells pump potassium into their central vacuoles, swell, and become turgid. But at night or if the sunlight becomes too intense, the motor cells wilt and the leaf blade folds downward.

Remember that all of this depends on selectively permeable membranes. If glucose or potassium or other solutes could leak out of the central vacuole, no pressure would build up and these processes would not be possible.

Sugar and Water Are Pushed Through Phloem

Plants, just like animals, must move water and nutrients from certain parts of their body to other parts. Conduction through sieve tubes is easy to understand. In organs that produce sugars (called **sources**, such as leaves), sugars are forced into the sieve tube members by molecular pumps in the plasma membrane. As sugar increases in the cells, they become osmotically drier and water follows automatically. If these were ordinary parenchyma cells, they would become turgid or would grow, but these cells have holes (the sieve pores) interconnecting them. The sugar water (the phloem sap) is just squeezed into the next cell in the sieve tube and a flow begins (**FIGURE 4.16**). In areas that need sugars (called **sinks**), membrane pumps extract sugar from the sieve tubes, and water follows again. Compare this with the water supply of a city: many large tanks put water into the city's network of pipes, and many faucets let water out. The volume of flow depends on which tanks and faucets are open at any moment.

Any plumbing system will have leaks and must have a repair mechanism. Phloem is always in danger of leaking if an animal bites into it, if a stem breaks and tears the phloem open, or even whenever leaves, flowers, or fruits fall off a plant. Sieve tubes contain two chemicals, **callose** and **p-protein**, that lie quietly in the sieve tubes if they are functioning normally. But if the phloem is broken open, the high turgor pressure inside it causes a sudden rush of phloem sap toward the leak. This sweeps the callose and p-protein toward the damaged area, where both form sticky masses (a **callose plug** and

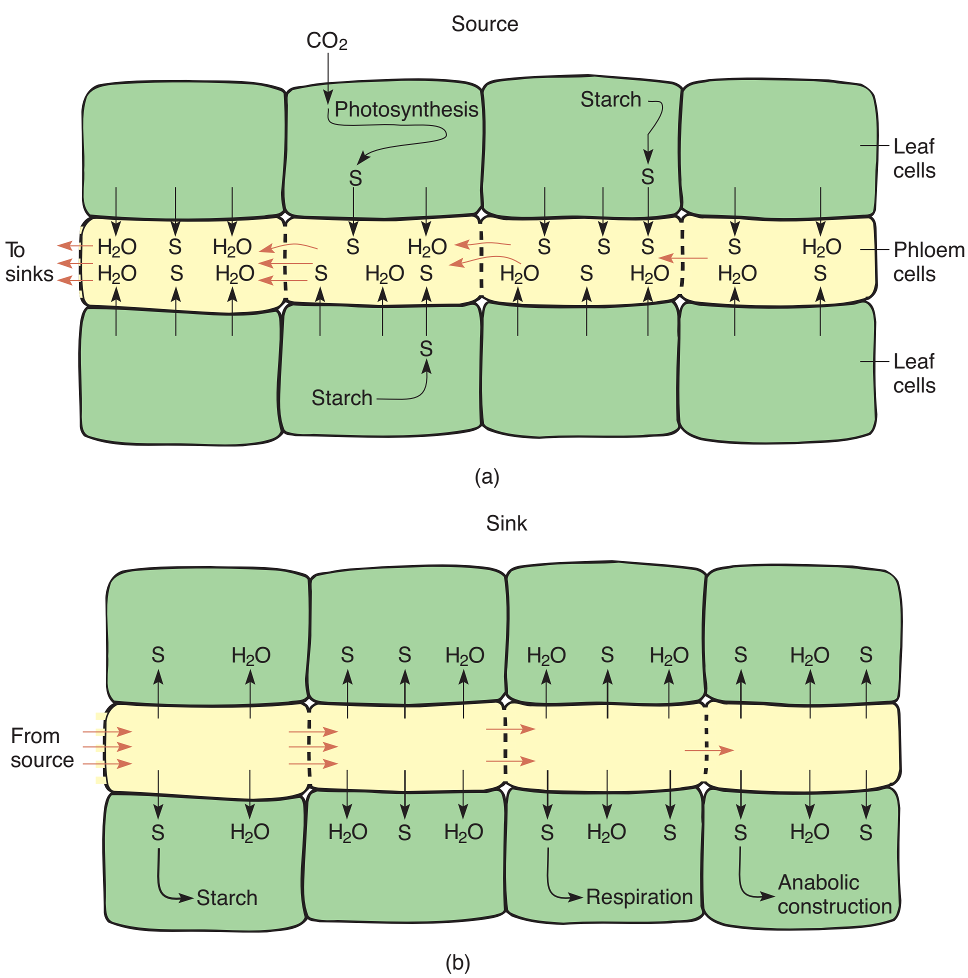


FIGURE 4.16. This diagram illustrates sugar transport through phloem; the details are given in the text.

a **p-protein plug**) that instantly seal the tube and prevent any further leakage (**FIGURE 4.17**). These act instantly, much more rapidly than the way our blood vessels seal themselves.

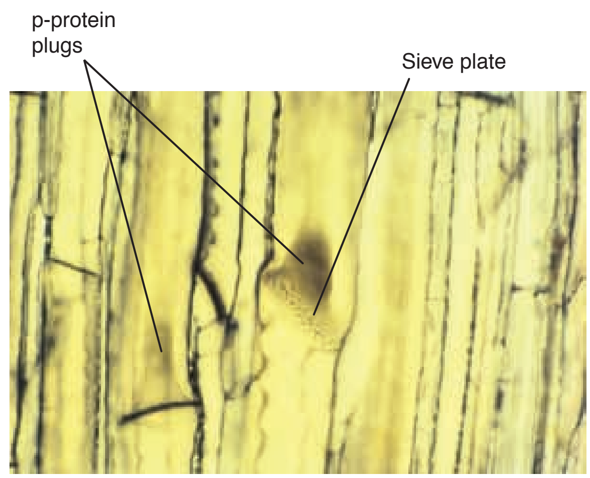


FIGURE 4.17. When this material of squash was being prepared for microscopy, it was cut open, causing the phloem sap to surge toward the cut, sweeping p-protein along and forming p-protein plugs, visible as dark brown masses. Sieve pores in the sieve plates are also visible (×500).

Water and Minerals Are Pulled Through Xylem

The movement of water and minerals upward through xylem is completely different from the transport of phloem sap or blood. Whereas water is under pressure and being pushed through phloem (and our blood vessels), water is *pulled* through xylem. Water molecules cohere (stick to each other); this is easy to see when water freezes into ice. Imagine grasping just the top of a long icicle and lifting: you will lift all the water molecules, not just the ones you are touching. A similar thing happens in plants: as water molecules escape from leaves, the leaf cells become osmotically drier, so they pull water into themselves from the xylem. Each water molecule pulls on the ones below themselves, and these pull on the next and so on down to the roots. This pull causes water to flow through the mass of tracheids or vessels, passing from one to the next as the water molecules move upward. Notice that this is completely different from blood flow in our body: our blood flows in the space between the living cells of our blood vessel walls; xylem sap is pulled through a mass of dead cells.

Safety and Flow Volume Are Important in Water Transport

Recall that xylem has two kinds of conducting cells, tracheids and vessel elements. Vessel elements tend to be very wide and are interconnected by perforations, which are complete holes: vessels allow relatively large volumes of water to be conducted with very little friction. Tracheids tend to be narrow and they do not have perforations, so each water molecule must move across pit membranes every time it goes from one tracheid to another. Tracheids provide a conducting system that does not allow high volume flow, and it has considerable friction, but they provide greater safety. Imagine the icicle again: if you pull on it and its lower end is frozen to something or if it is so long that it is very heavy, it will break and the top and bottom portions separate. The same can happen to water in xylem: if both air and soil are dry, both pull on the water and the water column (the water column is the mass of water itself, not the cells) may break (**cavitate**): the pull on the water has overcome its cohesion (**FIGURE 4.18**). Water in the upper part will continue to be pulled upward, but now there is nothing pulling on the lower water, so it sinks back down due to its weight, and an air bubble (an embolism) forms between the two. If this happens in a tracheid, the air bubble will expand only until it fills the tracheid: it cannot cross the pit membrane so it cannot damage any other tracheid. But if the cavitation occurs in a vessel member, the embolism expands right through the perforations because they have nothing similar to pit membranes to stop the expansion. The embolism can fill all the hundreds or thousands of vessel members in a vessel. Thus, a cavitation in a tracheid causes the plant to lose

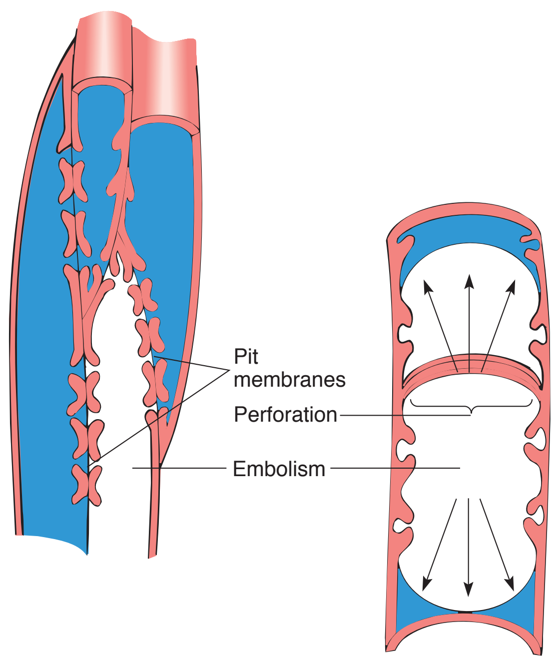


FIGURE 4.18. Severe tension can overcome the cohesion of water molecules and cause an air bubble to form and expand. The air bubble can pass through holes such as perforations but is stopped by pit membranes. If an air bubble forms in a tracheid, it cannot spread beyond the tracheid, but if a vessel element cavitates, the air bubble spreads throughout the entire vessel.

the use of just that one tracheid, whereas a cavitation in a vessel causes the plant to lose the use of thousands of vessel members. In dry habitats where cavitations occur frequently, tracheids offer a safer means of conduction, but in moist or even moderate habitats, cavitations are so rare that the benefits of low friction in vessels outweigh the risk of spreading embolisms.

It is important to compare our water conduction with that of plants. We have a hollow heart that uses a great deal of energy pumping our blood out through our wide aorta, which then branches out to smaller arteries, arterioles, then capillaries. Capillaries return blood to venules, to veins, and then back to the heart in a closed loop: each water molecule in the blood, and each red blood cell follows this circuit over and over thousands of times a day. We have an extremely low safety system with almost no redundancy: failure of our single heart or our single aorta, or one of our few major arteries is usually fatal. In contrast, plants pull water through many, many tracheids or vessels; even small plants have thousands, and large trees have billions. Plants do not have anything like an aorta or artery; there never is just one or a few very wide tracheids or vessels that all or most water must pass through. Xylem, and phloem as well, are extremely redundant and have a high margin of safety.

Consequences of Water Movement

Plants and animals handle water very differently, and the consequences are important. We animals take in water as a liquid, either by drinking it or eating foods that contain moisture. We also lose most of our water as a liquid, such as urine or sweat, and some of it as a gas from our lungs when we exhale. Liquid water can contain dissolved minerals, so a danger we face is that of losing minerals by too much sweating, urination, or diarrhea. But plants don't urinate or sweat; they almost never lose water in the liquid form, it is mostly just as water vapor escaping through the epidermis, and water vapor cannot carry mineral or other solutes. What is a consequence? Plants trap minerals: they bring them in from the soil as they absorb liquid water, move them upward through the xylem, but then cannot lose them as the water goes out through the epidermis. Day after day, minerals accumulate in the plant body. What happens to them? Plants need many of them for their own metabolism, as described below. And when animals eat plants, the minerals end up inside the animal and are essential for the animal's metabolism. Think of the iron in our blood, the calcium and phosphate in our bones, and so on . . . it all comes in as part of our food and it all came in to the biological world by means of plants. We never have to eat dirt to get minerals.

BOX 4.2. Plants, People, and Irrigation of Farms

Plants and people interact in many ways because of water. The earliest civilizations quickly learned to master two types of large construction projects: walls around their cities and canals to irrigate their fields. Even today, irrigation projects are massive and redirect the flows of large rivers. At Grand Coulee Dam, much of the Columbia River is diverted into canals that distribute irrigation water across hundreds of square miles of eastern Washington. Huge canals also irrigate the massive Central Valley in California as well extensive areas in Arizona. Lesser projects have been built almost everywhere in the western United States. In many areas, for example in west Texas, farms are irrigated by water pumped from aquifers beneath the farms.

The redirecting of water has many consequences for both plants and people. Rivers have less water after irrigation water has been removed, so there is slower flow, waterfalls are less vigorous, river bottoms are not as agitated. All of these areas are natural habitats for many plants and animals, and removing water for irrigation disturbs the creatures in these habitats. So much water is removed from the Rio Grande River in Texas and from the Colorado River in California and Arizona that neither is actually a river at its mouth, where it meets the ocean. Instead, both are just slow moving brackish marshes.

Irrigation water must go somewhere. Only a small fraction is actually absorbed by roots and then transpired out through leaves. The rest just moves past the plant, through the soil. Much of it sinks downward, especially in sandy soils, which do not hold water tightly. The water enters aquifers and then flows horizontally underground until it emerges as a spring or empties into a river. For many of us, a new spring or increased flow from an existing one would be a pleasant sight; there would be a small creek or pond, some aquatic plants and animals, some waterfowl. But however pleasant, these all are habitats that have been altered from their natural state due to extra water, we have interrupted a natural ecology.

If the irrigation system is in a deep valley that has no river draining it, the excess irrigation water has no means of draining away. It flows to the lowest part of the valley, accumulates there as a lake or marsh, and evaporates. Examples are California's Imperial Valley, the Great Salt Lake area in Utah, and the "basin and range" area of Nevada. Because water enters these valleys as a liquid and leaves as water vapor, minerals are trapped and accumulate. Also the irrigation water has picked up fertilizers from fields, so it is very rich in minerals. As the water evaporates, the minerals become more concentrated, the lake becomes saltier, osmotically drier, and at some point plants can no longer grow in it: its minerals attract water molecules more strongly than roots can. The lake becomes a salt marsh or salt lake, or if all water evaporates, it becomes a salt desert in which few things can live. Making otherwise fertile soil salty is called **salinization** (**FIGURE B4.2**), and it is an important problem in many irrigation projects.

In areas where fields are irrigated with ground water that has been pumped up, aquifers become depleted. Because the aquifer has lost some of its water, the natural springs and seeps that it feeds may have reduced flow or may dry up completely, and again natural habitats are damaged.

FIGURE B4.2. Rain water accumulates in this low-lying area and forms a temporary pond. But it evaporates before the pond becomes deep enough to drain away by a stream. Consequently, all the salts that were in the water remain here after the water evaporates, and the soil becomes too salty for any plants to grow here. This pasture is being damaged by salinization.

Part 3: Mineral Nutrition

All organisms need a small number of chemical elements for their metabolism and structure. Our own bodies need iron for our blood; calcium and phosphorus are necessary for our bones and teeth. All in all, our bodies need about 17 different chemical elements, and if our diets lack even one of them, we become ill. In the same way, plants too have a small number of chemical elements that are essential for their life, and these are therefore called the **essential elements** (**TABLE 4.4**). For the most part, the elements that are essential for plants are also essential for us animals; a noteworthy exception is that plants do not need sodium (Na^+) at all whereas we can't live without it.

Carbon, hydrogen, and oxygen come from air and water, but other chemicals come from the minerals present in soil. The ways that plants obtain and process these minerals is called **mineral nutrition**. As rocks weather and break down, they release minerals, which roots absorb. Nitrogen is an important exception; it is never part of a rock matrix. It has to be captured from air and will be discussed separately below.

TABLE 4.4. Essential Elements in Plants

Macro Essential Elements	
Carbon	Almost all organic compounds
Hydrogen	Almost all organic compounds
Oxygen	Many organic compounds
Nitrogen	All amino acids; all nucleic acids; chlorophyll
Potassium	Osmotic balance; enzyme activator; movement of guard cells and motor cells
Calcium	Controls the activity of many enzymes; component of the middle lamella; affects membrane properties
Phosphorus	Phospholipids; nucleic acids; many sugars have phosphate attached to them during certain reactions
Magnesium	Chlorophyll; activates many enzymes
Sulfur	Some amino acids
Micro Essential Elements	
Iron	Chlorophyll synthesis; enzymes involved in respiration
Chlorine	Unknown; possibly involved in photosynthetic reactions that produce oxygen
Copper	Plastocyanin, a compound involved in transporting electrons
Manganese	Chlorophyll synthesis; necessary for the activity of many enzymes
Zinc	Activates many enzymes
Molybdenum	Involved in nitrogen reduction
Boron	Unknown

All of these except for boron are also essential elements for us humans; we cannot live without these. Unlike plants, however, we also need fluorine, iodine, cobalt, selenium, chromium, and sodium. We obtain fluorine by adding it to our drinking water (fluoridation) and iodine is obtained by adding it to salt or by eating seafood. Notice that sodium is not an essential element for plants; even though our lives depend on it, and we can become sick just by losing too much sodium by sweating, plants do not need it at all.

Essential Elements

An element is an essential element if a plant cannot live normally without it. There are three criteria that determine if an element is essential:

1. The element must be necessary for complete, normal plant development through a full life cycle. This includes surviving stresses such as droughts, freezes, insect attacks, and so on, not just an easy life in a greenhouse.
2. There must be no substitute for the element.
3. The element must be acting within the plant, not outside it. This third criterion sometimes causes confusion. For example, iron is an essential element, but in alkaline soils, iron is mostly present as an insoluble compound that roots cannot absorb. If we add other elements to the soil, they might acidify the soil and thus release the iron, making the plant flourish. It would be easy to conclude that the elements we added were essential, even though all they are doing is making iron more readily available.

Certain elements do not need to be tested because they are so obvious. No organism at all can live without carbohydrates, lipids, or proteins, so carbon, hydrogen, oxygen, and nitrogen are automatically known to be essential. Also, magnesium is part of the chlorophyll molecule so it will be essential to any green, photosynthetic plant, and because phospholipids make up cell membranes, the phosphorus of phosphate groups must be essential.

We use **hydroponic experiments** to actually test if an element is essential. Seedlings or cuttings of a plant are grown in solutions with numerous chemicals that are thought to be necessary (and without any that are believed to be poisonous). If the plants die, we obviously made a bad guess, and either some element must be added or something must be removed. Once we have a solution that supports growth, we can prepare a second solution that is identical except that one single element is left out. If the new plants grow in that new solution, then the eliminated chemical was not essential. But if the plants die or show disease symptoms, then the element needs to be examined more closely.

At present, we believe there are 16 elements that are essential to all plants (Table 4.4). However, when we prepare the hydroponic solutions, we know that the chemicals we are using, as well as the water and the glass containers, are contaminated with miniscule amounts of various elements, and it may be that some of those are essential in extremely low amounts.

Some essential elements are needed in rather large amounts, for example the nitrogen needed to build the amino acids of proteins, the nucleic acids, and many other compounds, or the phosphorus used in the phosphate groups of many organic compounds. These are called the **macro essential elements**. But certain essential elements, called **minor essential elements** or **trace essential elements**, are needed in tiny amounts.

Soils Provide Essential Elements for Most Plants

Soils are derived from the breakdown of rocks. Volcanoes deposit basalt; upwelling magma cools into granite; old sea floors may become exposed as limestone, marble, or sandstone. These rocks have a hard, crystalline structure that roots cannot penetrate, but as these rocks are broken down (**weathered**) by rain, wind, freezing, or acids from lichens and mosses, the crystal matrix releases various elements (**FIGURE 4.19**). Some were part of the matrix itself, some were merely trapped there as the rock formed.

FIGURE 4.19. These rocks will last for thousands of years but not forever; they are gradually being broken down by rain, snow, and especially by the action of acids formed by the lichens growing on their surface. As bits and pieces break off, they form a thin layer of soil that allows mosses and small flowering plants to grow, which accelerates the weathering of the rocks.

Initially, rock may be broken down into boulders and other large pieces, but gradually it is weathered into finer and finer pieces. An important classification of soil is based on the size of soil particles: coarse sand has particles that range from 2.0 mm down to 0.2 mm; fine sand is 0.2 to 0.02 mm; silt is 0.02 to 0.002 mm in diameter. Soils in which most particles are finer than 0.002 mm are clay soils.

Soil particle size is important because it affects water-holding capacity and mineral availability. In coarse and fine sand, much of a soil's volume is occupied by spaces between soil particles. Such soils have plenty of room for air (necessary for keeping roots alive) and water. However, sandy soils do not hold water for long, because it moves through the large soil pores easily and either evaporates into the air or drains away into an aquifer. Even though water is adhesive, there is just not much soil particle surface area for water molecules to adhere to in sandy soils. Once a rain stops and water has drained away, the water that does remain, held by adhesion to soil particles, is called the soil's field capacity (**FIGURE 4.20**). In silty soils, the tiny soil particles occupy more of the soil volume yet still there is plenty of room for air and water. Silt particles have more surface area, so they hold water better than sandy soils, and have a higher field capacity. Silty soils tend to be very good for most plants. In clay soils, particles are so small that there is an overabundance of surface: clay particles hold water so tightly it cannot drain away, but roots are not very successful at pulling the water away from the clay particles' surface. With so much water, there is little room for air, and roots may suffer from lack of oxygen.

FIGURE 4.20. The very slight depression in the center of this slope is an area where fine soil particles accumulate, giving the soil more water-holding capacity (a greater field capacity). This area stays moist longer after a rain, and the plants that grow in the depression do not have to be as drought-tolerant as the sagebrush on the hilltops.

As a rock's matrix breaks down and mineral nutrients are released, most come off as positively charged cations (K^+, Cu^{++}, Mg^{++}, Ca^{++}) and they remain close to the rock's surface, which has a negative charge. This is beneficial because otherwise rains would wash the minerals away as quickly as they are released by weathering. However, roots face the problem of pulling the nutrients away from the rock. This is done by cation exchange. As roots respire, they release carbon dioxide, which is converted to carbonic acid. Being an acid, carbonic acid gives off one or two protons, and if this occurs next to a soil particle, the proton's positive charge might loosen a nutrient from the soil's surface. With luck, the nutrient will diffuse in the direction of the root and be absorbed. One cation (a proton) has been exchanged for another (a mineral nutrient).

Once water and minerals reach a root hair, they may cross the cell wall and enter the protoplasm, or they may just penetrate deep into the root by diffusing through the water and pectin in the cell walls of the epidermis and cortex. As mentioned in Chapter 3, they can only do this until they reach the Casparian strip; at that point, the wall is incrusted with hydrophobic material and further diffusion through the wall is impossible. The minerals must be accepted by an endodermis cell plasma membrane if they are to reach the xylem and phloem. Casparian strips prevent unwanted, harmful minerals from reaching the rest of the plant.

Nitrogen Is Essential and Unique

Nitrogen is an essential element that differs from the mineral elements: it is found in air but not as part of a rock matrix. Also, it is in a form, N_2, that plants cannot use. Surprisingly, even though all plants, animals, fungi, and all other organisms must have nitrogen for many critically important molecules, only a tiny number of bacteria have an enzyme, nitrogenase, that can bind N_2 and use it. These are called nitrogen-fixing bacteria. The processing of nitrogen is called nitrogen metabolism, and it involves three steps: fixation, reduction, and assimilation. In nitrogen **fixation** and **reduction**, nitrogenase binds N_2 and forces electrons onto it (adding electrons to a chemical is a reduction). This converts the nitrogen into an ammonium ion, a state similar to that of nitrogen in amino acids. During nitrogen **assimilation**, the bacterium attaches ammonium ions to various acids, converting them to amino acids; at this point the nitrogen is part of the bacterium's body, it has been assimilated. Some of the amino acids are then used to build proteins; others are converted into nucleic acids and other compounds. The bacterium might be eaten by tiny soil animals or digested by soil fungi, or if it dies and decays, the nitrogenous compounds that are released might be absorbed by roots. Whatever happens, the nitrogen that was assimilated by this bacterium is now part of another organism. Some soil microbes convert the nitrogenous compounds back to ammonium, and others respire it, much like we respire carbohydrates. This converts the nitrogen to nitrate (NO_3^-) or nitrite (NO_2^-). Roots can absorb all three forms, ammonium, nitrate, and nitrite. If roots have ammonium available, they can immediately use it to make amino acids just as the bacterium did. If the roots absorb nitrate or nitrite, they must force electrons onto it, reducing it, but roots have no problem with this, it is just N_2 that they cannot process. Once the nitrogen is assimilated, some is used by the roots themselves for their own metabolism, but a large part is loaded into phloem and conducted up to the shoots.

Most microbes that fix nitrogen are **free-living**; that is, they live on their own and are not intimately associated with other organisms. One of the most common free-living microbes is *Nostoc*, a cyanobacterium that forms colonies large enough to see easily: they look like dark pieces of cellophane when dry, or like rubbery sheets

FIGURE 4.21. Nitrogen-fixing bacteria live in the nodules on the roots of this cowpea (a legume). The bacteria obtain sugar and other nutrients from the cowpea, and use part of their energy to convert atmospheric nitrogen to organic nitrogen. Root cells absorb part of the nitrogen from the bacteria. (© Nigel Cattlin/Alamy.)

when wet. They are common on desert soils. Other nitrogen-fixing microbes are **symbiotic**, they live in a close association with plants. Roots of legumes like alfalfa, peanuts, and soybeans form nodules that contain millions of cells of the nitrogen-fixing bacterium *Rhizobium* (**FIGURE 4.21**). The roots actually provide the bacteria with sugars and other nutrients, and they also protect the bacteria from oxygen (nitrogenase is poisoned by oxygen). The bacteria secrete nitrogenous compounds to the roots. Symbiotic nitrogen-fixing cyanobacteria also associate with alders, the water fern *Azolla*, and with many liverworts and hornworts. Because the plants live symbiotically with nitrogen-fixing bacteria, they can grow on very poor soils deficient in nitrogen. These plants are often the first to colonize bare, rocky areas.

Mycorrhizae and Phosphorus Absorption

Although roots can absorb phosphate from soil on their own, they cannot do it as well as many fungi can. Roots of most plants form a symbiotic relationship with certain soil fungi, a relationship in which fungi absorb phosphate and pass much of it on to roots while roots provide the fungi with sugars. This symbiotic relationship is called a **mycorrhiza** ("fungus root"), and there are several types. In ectomycorrhizae, the fungi form a dense sheath of fungal cells around the surface of the root. In endomycorrhizae, the most common type, the fungi actually penetrate into the root, all the way to the endodermis, and even penetrate root cells. Within the root

BOX 4.3. Fertilizers, Pollution, and Limiting Factors

Plants in nature usually do not grow as vigorously as they potentially could. For example, desert plants typically grow more rapidly if given extra water, plants in shady areas grow better if given a bit more light, whereas some extra nitrogen fertilizer usually helps prairie grasses, which already have enough water and light. Any plant grows at a particular speed and vigor because it is limited by some factor, such as too little water or light or nitrogen fertilizer. An important concept is that there is only one single **limiting factor** at a time for any plant. If we give desert plants more light or fertilizer, they will not grow faster, it is water that is limiting them. But if we do give them extra water, their growth rate will increase until some other factor becomes limiting, perhaps lack of nitrogen. While growing slowly, the plants could get nitrogen quickly enough, but now that they are growing faster, their ability to obtain nitrogen from the soil may be limiting. If we give the plants both water and nitrogen fertilizer, they may grow even more rapidly, but finally, some other factor will become limiting. On many farms, plants are irrigated and fertilized, and they are planted far enough apart that they do not shade each other and their roots do not interfere with each other. Such plants grow much more rapidly than they would in nature, but they are still limited, in this case, by their own genetics, their own innate metabolic capacity. There is always a limiting factor.

The concept of a limiting factor is important in understanding techniques for reducing the damage caused by pollution. Under natural conditions, the water in rivers and lakes has so few nutrients that algae grow slowly, and they are so sparse that the water is blue. In the middle of the twentieth century, pollution from farms and cities fertilized rivers and lakes and allowed algae to grow more vigorously. As rain drained from fields, lawns, gardens, and golf courses, it carried much of the fertilizers that had been applied to stimulate the growth of crops, flowers, and grass. Also, most household waste that is flushed down toilets is an excellent organic fertilizer. With all these extra inputs of nutrients, populations of algae became so dense that "pond scum" floated near the surface of rivers and lakes, and the water was green because of the abundance of microscopic algae (**FIGURE B4.3**).

FIGURE B4.3. When livestock such as cattle, pigs, or poultry are kept in outdoor pens, rain washes manure into streams, fertilizing them and causing algae to grow profusely.

It would have been difficult to stop all pollution, but people realized that it was only necessary to control one single pollutant so as to create a limiting factor. Phosphate was chosen as the target. Phosphorus is an essential element, and it is naturally low in pure water. A large amount of the phosphate pollution in the rivers was coming from laundry detergent and dishwashing soap. With a little effort, phosphate-free detergents were invented, and now they are used almost universally, so there is much less phosphate pollution. The concentration of phosphate in rivers dropped so low that algae could no longer thrive, and their populations fell to more normal levels. Even though the water is still heavily polluted with nitrates, sulfates, and other nutrients, the algae cannot use them as long as phosphate is kept low enough to limit their growth. If we could reduce the phosphate runoff from farms and lawns, the levels of algae would drop even more and rivers and lakes would be even cleaner.

It would be better to control and reduce all types of pollutants, but by keeping one at limiting levels, we can at least minimize some of the damage caused by pollution.

cell, fungus cells branch into tiny tree-like structures called arbuscules. The fungi fill these with phosphorus, which is then transferred to the plant. The fungi benefit from this by receiving sugars and other nutrients from the roots.

Diseases Caused by Lack of Essential Elements

If a plant grows in a soil that has too little of one of the essential elements, the plant will suffer from a **deficiency disease**. Such diseases are most likely to be encountered in cultivated plants if they are grown in unsuitable soils. One of the most frequent situations that cause deficiency disease is cultivating plants that need acid soils in areas with alkaline soils; such plants have difficulty absorbing enough iron.

Deficiency of certain minerals causes specific symptoms. Lack of iron causes chlorosis, a yellowing of leaves due to inability to synthesize chlorophyll (**FIGURE 4.22**). Necrosis is the death of patches of tissue; if the leaf tips and margins die, it is probably caused by a lack of potassium. Deficiency of manganese causes necrosis of tissues between leaf veins even though the veins themselves remain alive and green.

FIGURE 4.22. This azalea leaf is from a plant growing in alkaline soil. Azaleas require acidic soil and suffer iron deficiency in alkaline soils.

Important Terms

acid
active site of enzyme
alkaline
amino acid
atom
base
callose
callose plug
cavitate
deficiency disease
deoxyribonucleic acid
diffusion
disaccharide
DNA
enzyme
essential element
fatty acid
free-living organism
functional group
gene
hydrophilic
hydrophilic channel
hydrophobic
hydroponic experiment
hydroxyl ion
limiting factor
macro essential element
messenger RNA (mRNA)
microRNA
mineral nutrition
minor essential element
molecule
monomer
monosaccharide
mycorrhiza
negative ion
nitrogen assimilation
nitrogen fixation
nitrogen reduction
nonpolar molecule
nucleic acid
nucleotide
osmosis
osmotic effect
p-protein
p-protein plug
pH
phospholipid
pit membrane
polar molecule
polymer
polysaccharide
positive ion
primary structure of protein
protein
proton
quaternary structure of protein
ribosomal RNA (rRNA)
salinization
saturated fatty acid
secondary metabolite
secondary structure of protein
self-assembly
simple sugar
sink
source
substrate specificity
symbiotic organisms
tertiary structure of protein
trace essential element
transfer RNA (tRNA)
triglyceride
turgid
unsaturated fatty acid
weathered
wilted

Concepts

- The bodies and metabolisms of all organisms are based on the fundamental principles of chemistry and physics.
- Millions of organic compounds are possible, but most can be classified into just a few families of compounds.
- Many important biological compounds are polymers composed of monomers.
- Using only glucose, water, and a few inorganic minerals, plants build all the molecules of their bodies.
- Self-assembly is the tendency to automatically organize shape due to characteristics of a molecule itself.
- Wherever water is mixed with a hydrophilic substance, water tends to move from where it is more concentrated to where it is less concentrated.
- Because all plants absorb water as a liquid and lose it as a gas, they accumulate minerals.
- The growth rate of all organisms is determined by a limiting factor.