BOTANY

A BRIEF INTRODUCTION TO PLANT BIOLOGY

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preface

Our objective was to provide an abridged and shortened version of *Botany: An Introduction to Plant Biology,* Fifth Edition, by Weier, Stocking, and Barbour. However, this text is significantly different from that text and is more than a simple abridgement.

Like the parent text, this is intended for introductory courses at the university, college, or community college level. Prior courses in biology, mathematics, or physics are not required, but some acquaintance with elementary inorganic chemistry is helpful for understanding Chapters 2, 5, and 6. Appendix A introduces the basic ideas of chemistry that are needed, and should be valuable for students who have no background in chemistry. Much of the parent text has been rewritten and many new illustrations have been added. Topics in the fifth edition of *Botany* by Weier et al. that have been extensively revised include: metabolism, absorption and transport, photosynthesis, growth, algae, fungi, and angiosperms. Many detailed new drawings by Alice B. Addicott and Jacqueline L. Lockwood accompany these and other chapters. All the drawings convey important information in a dramatic manner, but we think that some are original enough in themselves to be contributions to botany. The chapters on bacteria and viruses in the larger text have been deleted in this adaptation, and much of the material on genetics has been condensed and placed in Chapters 3, 7, 10, and Appendix B.

We believe that this text has several features not shared by any other botany books of comparable size: (1) A complete, unbiased coverage of botanical topics with equally detailed sections on anatomy, cytology, economic botany, ecology, evolution, morphology, physiology, taxonomy, and a survey of the plant kingdom. (2) Many original drawings and photographs that are large, detailed, and numerous enough to be true learning aids. (3) A traditional pedagogic organization written in a clear and direct style. (4) An extensive glossary that defines frequently used terms in the text and that shows their etymological derivation.

We take pleasure in acknowledging the following individuals for their help in the development of the manuscript in whole or in part or for providing the materials that are in this book: Alice B. Addicott, Dorothy Brandon, Dr. Edward Butler, Robin Camp, Dr. Norma Lang, Jacqueline Lockwood, Walter Russell, Lorna R. Thornton, and Dr. John Tucker. We also wish to thank the following individuals who reviewed the manuscript: Charles H. Field, Cochise College; Jerry Davis, University of Wisconsin, La Crosse; David Dallas, Northeastern Oklahoma A & M College; and Mary McLanathan, Foothill College. We are especially grateful to Ted Barkley of Kansas State University for his meticulous and detailed suggestions on the entire manuscript. Others who provided illustrations are cited at the end of the book. The many students who have provided suggestions for the improvement of the general botany course taught at the University of California, Davis, cannot be acknowledged individually, yet they should be aware of our appreciation for them collectively. We apologize for the unintentional omission here of others who have contributed to the text.

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contents

1 CHAPTER

introduction

The Scope of Botany

Botany began with tribal lore about edible, medicinal, and poisonous plants. From this narrow focus on familiar leafy plants and mushrooms, curiosity spread to diverse forms until today more than 550,000 kinds, or **species**, of organisms are identified as part of the plant kingdom. New species are found continuously because there are still regions of the world that have not been thoroughly explored: the tropics, with their lush rain forests; the arctic; and the microscopic worlds of soils, oceans, and sediments.

Perhaps in the earliest days of botany the field could easily be defined as the study of life forms that are rooted and essentially immobile. But the identification of additional species and more detailed study have erased any clear boundaries. Thus for example the mosses, or Bryophytes (Fig. 1.1), have always been considered "plants" and appropriate subjects for botanists to study. But in its early development the moss plant consists of green, threadlike filaments that resemble certain species of aquatic organisms, the **algae** (Fig. 1.2). Furthermore, both the moss and the filamentous alga have a phase of the life cycle in which they produce free-living reproductive cells (Fig. 1.3). These cells swim by means of flagella resembling those of animal sperm cells. Still other algae spend their whole lives as actively swimming, flagellated single cells. These discoveries confirm the fact that true natural boundaries between groups of organisms are hard to find.

Is there any constant feature that is characteristic of all the organisms that botanists study and not of other forms of life? The answer is, "not quite." But two features—the presence of cell walls and the ability to perform photosynthesis—almost serve that purpose and are worth special comment.

Whenever large, complex forms of life are closely inspected, they are found to be composed of numerous microscopic units of living material called **cells.** In all but one kind of organism that botanists study, each cell is surrounded by a tough, fibrous **cell wall.** The walls of adjacent cells are cemented together, giving the plant as a whole a rigid shape and preventing individual cells from moving. The one exception is a small group of organisms known as **slime molds** (Fig. 1.4), which do not have walls during most of their life cycle. In this feature the slime molds are like animals. Animal cells do not have walls, and, thus, possess the flexibility needed for cooperative movements such as muscle contraction.

Even though most plant cells have walls, there are major differences in wall structure and composition among the organisms of the plant kingdom. In green plants the strength of the walls results from a network of **cellulose** fibers. In the fungi **chitin** is usually found instead of cellulose, while the bacteria and blue-green algae have walls with a fishnet structure built from polymers of another, more complex set of subunits. These major differences in wall structure create a suspicion that the fungi, the bacteria, and the rooted green plants may be only remotely related.

The ability to perform photosynthesis is an extremely important property of plants (Fig. 1.5). This process enables the organism to trap radiant energy from sunlight in order to construct organic materials. The foods produced by photosynthetic organisms are essential not only for the organisms themselves but also for life forms such as animals (including human beings) that cannot trap sunlight. However, some of the "plants" discussed in this book do not perform photosynthesis. An example is "Indian pipe," a parasitic plant that has roots, stems, and flowers (Fig. 1.6). Most bacteria do not photosynthesize; nor do any of the 200,000 species of fungi (Fig. 1.7). We have no reason to suspect that the fungi ever had any photosynthetic ancestors. It is clear that botanists study these life forms because they have cell walls and some of the life cycle characteristics of the green, photosynthetic plants.

Ancestry and Classification of Plants

Because of the difficulties just described, not all botanists agree on the proper way to sort and group the organisms included in the Plant Kingdom. Nevertheless, classification is both a practical necessity and an important intellectual goal of botanists. In this regard the highest goal is to organize a true or *natural* classification of the organisms.

The idea of a natural system depends on the belief that present-day organisms are related by common ancestry and that the differences we observe between organisms

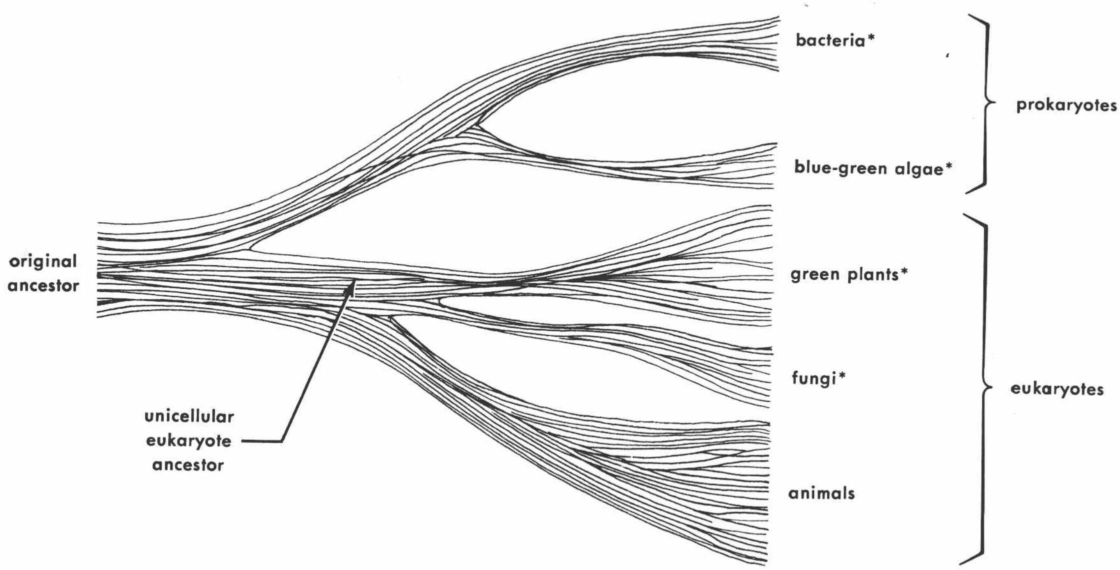


Figure 1.8 Ancestral relationships between modern organisms as deduced from protein structure and the structure and function of cells. The starred groups are all studied in botany.

are a result of extensive changes in heredity (the process of **organic evolution**) over the three billion years that plants have been on Earth. In a perfect natural classification organisms would be grouped according to the closeness of their ancestry. Of course the construction of such a classification must depend on indirect evidence, since human observers did not trace events earlier than a few thousand years ago. This evidence includes fossils of ancient plants as well as observations of similarities and differences between present-day plants (Chapter 10).

The most fundamental dividing line among life forms separates the **prokaryotes** from the **eukaryotes** (Fig. 1.8). The differences can be seen in the structure of the cells. One of several fundamental differences is that prokaryotes have their hereditary material (DNA) floating free in the same fluid mass as the rest of the cellular material, whereas the eukaryotes have their DNA separated from the rest of the cell contents by a surrounding membranous envelope. All the common plants are eukaryotes whereas the bacteria and the blue-green algae represent the world's only known prokaryotes. The entire animal kingdom consists of eukaryotes.

One of the most recent and promising tools for judging the hereditary relations between species depends on examining and comparing protein molecules. The hereditary information that is passed from generation to generation consists largely of instructions for building protein molecules. Since the number of possible different proteins is astronomical, a high degree of similarity between the proteins in two organisms indicates a common heredity. Two organisms are not likely to have arrived at similarly constructed proteins by chance. The proteins built by eukaryotes and prokaryotes are similar enough to indicate that they arose from a common ancestor, but different enough to suggest that the eukaryotes and prokaryotes diverged long before there were any organisms higher than unicells and before there were any distinctions between plants and animals.

Probably the most significant way to divide up the large group of eukaryotes is according to whether or not they have chloroplasts. These are bodies in the cell that perform photosynthesis. Animal and fungal cells lack them. They are present in all the trees and shrubs and nearly all the herbs that make up our familiar landscape. They are also present in a multitude of less familiar forms, including many microscopic unicells.

There is evidence to suggest that chloroplasts may be the descendants of free-living bacteria that entered the cells of early eukaryotes, forming a symbiosis that became permanent. Comparable symbioses can be seen today between bacteria and plants in the root nodules of legumes (Chapter 5), but in these, the partners are still separable. If chloroplasts did arise from symbiosis, there may have been many points in evolution where various species acquired chloroplasts. Alternatively, chloroplasts may have originated within a single line of ancient cells, without symbiosis. These questions remain to be resolved, and they leave us uncertain about how far back we must reach to find ancestral connections between the bacteria, the fungi, and the green plants.

2 CHAPTER

metabolism

The life of the plant cannot be understood without discussing its chemistry.[1] Since muscular movements and nervous responses are lacking, the visible signs of life in most plants are limited to slow changes such as the growth of organs. But if we consider the units of matter called molecules, of which plants are composed, the plant body proves to be a place of incessant, complex activity. This chemical activity is known collectively as **metabolism**. It occurs throughout the plant body, at all stages of life except the state known as dormancy. (We shall meet the subject of dormancy later in discussing seeds and buds.) With its thousands of different chemical reactions, metabolism makes the plant body millions of times more active chemically than the surrounding nonliving environment.

Principal Materials

Raw Materials

The plant extracts raw materials from the environment and converts them into a great variety of more complex products.

Water is the substance that plants take up in the greatest quantity. The plant acts as a wick between the moist soil and dry air; about 90% of the water that enters the plant is later evaporated away. The remaining 10% remains in the plant, where it provides bulk, serves as a medium for storing and transporting dissolved materials, and contributes atoms to the metabolic system. Water is directly consumed or produced in many reactions. Having the formula H_2O, water is a major source of the elements hydrogen (H) and oxygen (O).

Carbon dioxide (CO_2) is taken up by the land plant from the air. This compound is the plant's chief source of carbon (C) and oxygen.

Mineral elements are also taken up by the plant from the environment. These are discussed extensively in Chapter 5. They include nitrogen (N), phosphorus (P), sulfur (S), and several other elements. They are usually taken up from the soil, where they occur as ions in solution with water. Some of them (e.g., magnesium and potassium) are present as single charged atoms, whereas others occur as ionic compounds with oxygen and hydrogen (e.g., NO_3^-, NH_4^+, SO_4^{-2}, and HPO_4^{-2}).

[1] Readers who have not previously studied chemistry may find it useful to read the Appendix before pursuing this chapter.

Common Metabolic Products

There is a noticeable difference between the simple raw materials that the plant takes in, such as CO_2, H_2O, and mineral elements, and the complex final products of metabolism. For example, the compound NAD^+, which we will meet again later, has the formula $C_{21}H_{28}O_{14}N_7P_2^+$ and is formed from raw materials by a complex series of reactions.

Nearly all the molecules formed in metabolism contain carbon and hydrogen; other elements may or may not be present. Such molecules are called **organic compounds** because they are rarely found in nature except as the products of metabolic activity by living organisms. By contrast, the simple molecules that plants take in as raw materials are termed **inorganic compounds.**

Organic compounds are produced in such great variety that only a few types can be discussed here. But there are several classes of organic compounds that have universal importance and can be used as the basis of an introduction to metabolism.

Carbohydrates are composed of the elements C, H, and O; they have the general formula $(CH_2O)_n$, where n may be any number. The simplest carbohydrates are the **sugars**, which are important both as sources of energy and as building units in the construction of many other kinds of compounds.

Let us consider briefly the structure of a sugar molecule. In one group of simple sugars, the **hexoses**, each molecule contains six carbon atoms and has the general formula $C_6H_{12}O_6$. For example, **glucose** has the straight-chain structure shown in Fig. 2.1*A*. The —CHO end is an **aldehyde** group. The sugar molecule may occur in two forms. When not in solution the carbon atoms form a straight chain. When the sugar is in solution, four or five of the carbon atoms (depending on the kind of sugar) and an oxygen atom form a closed ring (Fig. 2.1*C*). In the straight-chain form, note the difference in the end carbon atom of glucose and fructose. As noted, the —CHO of glucose is an aldehyde. The C═O of fructose (Fig. 2.1*B*) characterizes a **ketone.**

The —OH and —H groups of the sugar molecule may be arranged in different positions in the ring without changing the relative numbers of carbon, hydrogen, and oxygen in the formula. In fact, a shifting of these atoms, as in the examples of glucose and fructose, results in sugars with different chemical properties. Sixteen different hexoses are possible, but only a few occur naturally in plants. Molecules such as these sugars with the same

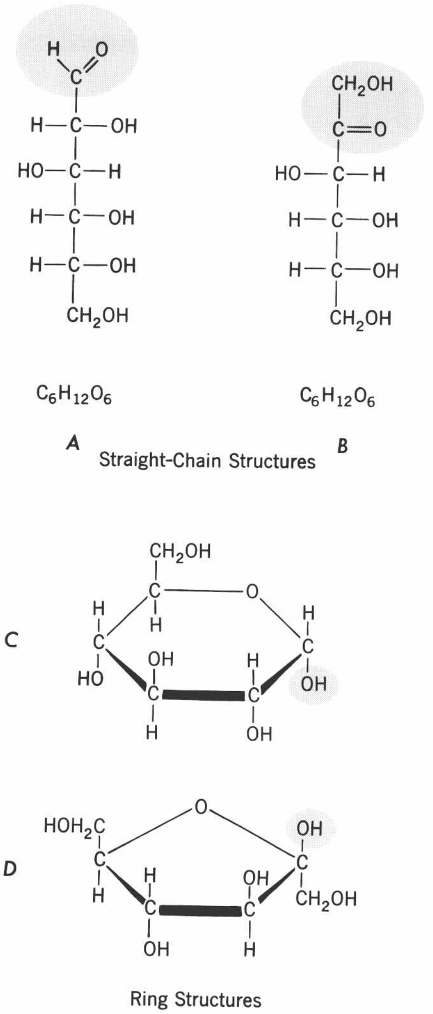


Figure 2.1 Glucose and fructose, two hexose sugars, have the same formula but different structures. Both can exist as a straight chain or ring. *A* and *C,* glucose; *B* and *D,* fructose.

chemical composition but a different internal arrangement are called **isomers.**

The most common hexoses in plants are glucose and fructose. Sugars with three carbon atoms are called **trioses;** with five and seven carbon atoms, **pentoses** and **heptoses.** The pentose sugar **ribose** is a constituent of the giant molecules that carry hereditary information (the nucleic acids). Ribose is also part of several energy-carrying molecules such as ATP (Fig. 2.8).

Simple sugars are called **monosaccharides.** The union of two of these molecules produces a **disaccharide** and a

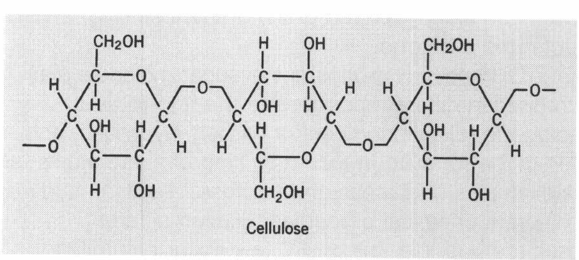
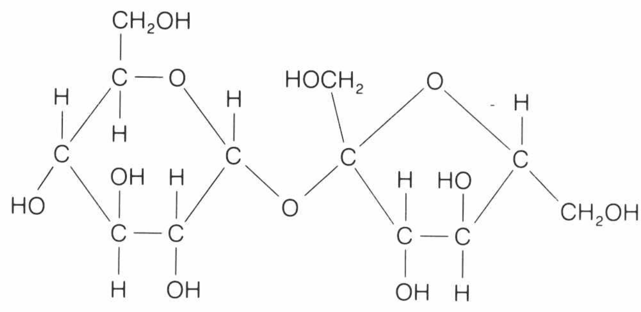


Figure 2.2 Structural formula of glucose units in cellulose.

water molecule. For example, the disaccharide produced from glucose and fructose is the commonest of all sugars, **sucrose:**



Sucrose can easily be split into fructose and glucose. One water molecule is consumed in the process. Reactions such as this, where water splits another compound, are called **hydrolysis** reactions. They are important steps in breaking down stored food molecules. Sucrose, our common table sugar, is very important as a mobile food storage compound in most plants.

Three or more monosaccharide molecules may join to form tri-, tetra-, or **polysaccharides.** The latter are composed of the union of many simple sugar molecules. As with the formation of a disaccharide a water molecule is given off for each pair of simple sugar molecules united. Polysaccharides are not generally soluble in water, nor are they sweet. **Starch** and **cellulose** are the two most abundant polysaccharides in plants. Each is composed of a long chain of glucose molecules. In starch, the chain may be coiled because of the way the glucose units are linked together and some chains are branched, while in cellulose the chains are unbranched and more or less straight. Cellulose (Fig. 2.2) is a major structural material in the plant, while starch is a reserve, water-insoluble food.

The union of relatively simple molecules, like sugar, into long-chain gigantic molecules composed of the repetition of simple units is a common chemical process known as **polymerization.** We shall meet it again in our discussion of proteins and nucleic acids.

Lipids form a very diverse collection of compounds; the chief similarity among all of them is a tendency to be insoluble in water (that is, molecules of lipids do not readily mingle with water molecules).

Cutin and **suberin** are two waxy lipids that often coat the surfaces of plant organs and serve to limit water loss. Some plant waxes (e.g., carnauba) are widely used in furniture and automobile waxing compounds.

Fats are simple and abundant lipids that are composed of **fatty acids** united with the three-carbon alcohol, **glycerol.** A fatty acid is a molecule that has an acidic group at one end; the rest of the molecule is a long carbon chain to which little other than hydrogen is attached. In **lauric acid** (Fig. 2.3) the chain is composed of 12 carbon atoms.

Figure 2.3 shows the structure of glycerol and fatty acids, and the way in which they react to produce a fat. Three molecules of water are produced in the process. The fat molecule itself is nonpolar and does not mingle readily with water. This means that fat molecules tend to

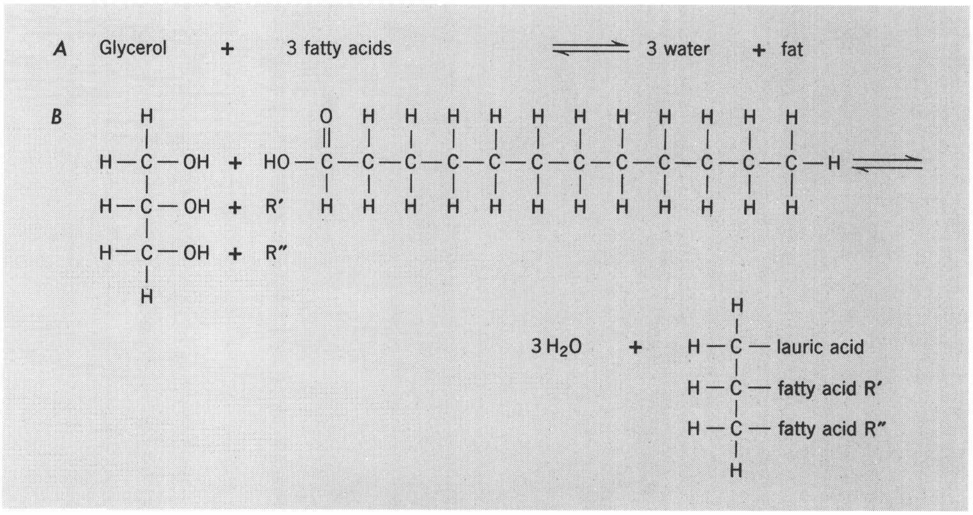
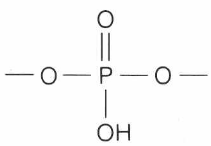


Figure 2.3 Formation of a fat by condensing fatty acids with glycerol. *A*, in words; *B*, structural formulas. The fatty acid shown in detail is lauric acid.

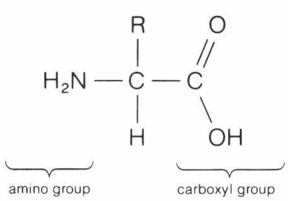
accumulate in droplets. They are rich in energy and their insolubility makes them good food storage compounds.

Phospholipids are similar to fats, but here one of the fatty acids is replaced by a **phosphoryl group**:



One end of the phosphoryl group binds to the glycerol unit, while the other end of the phosphoryl may be attached to any of several different organic groups. The phospholipids are unusual in that they are water-soluble at one end (the phosphoryl part, which is polar) while insoluble at the other end (the nonpolar fatty acid tails). These molecules tend to line up at the boundary of any water mass in which they happen to be immersed; the insoluble parts jut out of the water. Phospholipids are essential to the structure of **membranes** in the plant cell (Chapter 3), and their importance is a result of their semisoluble property.

Amino acids are important as the molecular units from which **proteins** are built. Some of the amino acids also serve as carriers for temporarily storing nitrogenous groups. There are 20 common kinds of amino acids. With one exception they are alike in their basic structure:



The **carboxyl group** readily donates its hydrogen nucleus to water; hence it acts as an acid. Thus the amino and carboxyl groups give the compound its name, amino acid. The symbol R signifies a special group of atoms called a **side chain**. The side chain is not shown in detail here because it differs from one amino acid to another. The 20 kinds of amino acids differ from one another according to the side chains they possess. The exception to the picture shown above is the amino acid **proline**, in which the R group bends over and attaches to the N of the amino group. Several amino acids are shown in Fig. 2.4.

Proteins are polymers built by attaching amino acids together, end to end (Fig. 2.5). The bond is made between the amino group of one molecule and the carboxyl group of another. A molecule of water is released in making this bond.

The bond between the amino acids is termed a **peptide bond** and therefore proteins are sometimes called **polypeptides**. Some proteins have as few as 16 amino acids while others may contain hundreds. An average protein might contain 150 to 200 amino acids. Proteins also differ in the kinds of amino acids they contain and in their sequence along the chain. With these differences an immense variety of proteins is possible. No single organism can manufacture more than a small number of the possibilities.

It is impossible to exaggerate the importance of proteins. They serve structural roles, storage roles, and regulatory roles; in addition they are the agents **(enzymes)** that govern chemical reactions in metabolism. Their ability to perform such a variety of functions is a result of their structural variety. Each kind of protein, with its unique amino acid sequence, performs just one function. Proteins can perform hundreds of different functions because there are hundreds of different proteins in the organism.

The precise shape of the protein determines its function. The shape is determined by the sequence of amino acids. But that sequence alone is not the only factor responsible for the definite shape of the protein. Since rotation is possible around some of the bonds in the protein polymer, the protein has a potential for assuming many different patterns of coiling or folding. Of these possibilities, there is usually only one pattern of folding that is associated with a biological function (Fig. 2.6). An improperly folded protein has no function except as a store of amino acids.

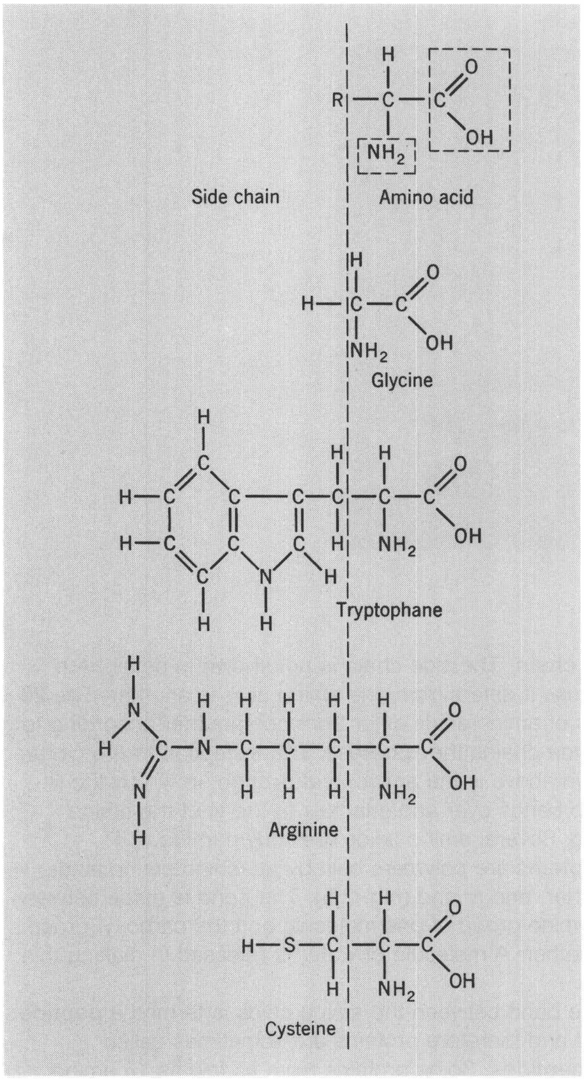


Figure 2.4 Some amino acids.

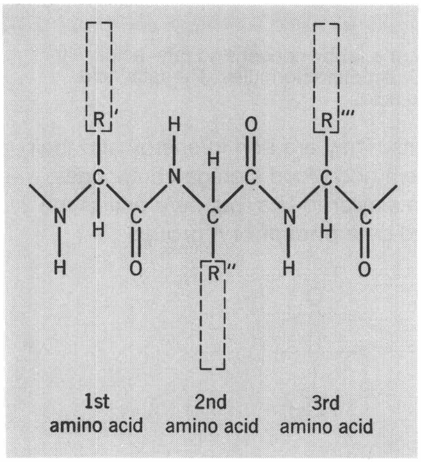


Figure 2.5 A polypeptide chain is a part of a protein molecule. The backbone of the protein molecule is formed by many amino acids joined by the union of the amino group (NH_2) of one amino acid to the acid group (COOH) of another amino acid by the removal of a water molecule. The R groups represent side chains of the different amino acids.

In the living organism each protein ordinarily maintains the pattern of folding that has functional value. Several forces contribute to the stability of the folding. Most important, the surrounding water forms a cage, with polar water molecules attracted to one another by hydrogen bonds. Some of the side chains of the protein molecule are also polar and can interact with the surrounding water, ionizing or forming hydrogen bonds. But other side chains are nonpolar. These cannot break through the web of forces that unites the surrounding water mass. Therefore the protein folds in a shape that places the nonpolar side chains out of contact with water. Most proteins assume a globular or rounded shape with the interior occupied by nonpolar parts and the surface, in contact with water, carrying the parts that are attracted to water.

Dehydration (removal of water) allows the protein to unfold. This is one reason why an abundance of water is vital to the normal operation of the organism.

The folding of the protein molecule may also be influenced by interactions between the side chains. For instance, the groups

$$\overset{O}{\underset{}{\overset{\|}{—C—}}} \quad \text{and} \quad \overset{H}{\overset{|}{—N—}}$$

occur regularly along the polymer; if the folding brings them close together, they can form a hydrogen bond (dotted line):

$$>C{=}O{-}{-}{-}{-}{-}H{—}N<$$

Many such hydrogen bonds form within the folds of a typical protein, often giving rise to coiled or helical foldings in part of the protein chain. In addition, attractions and repulsions can occur between ionized side chains. Strong electron-sharing bonds known as **disulfide bridges** can also occur to firmly cross-link two folds of the protein when the two side chains of the amino acid **cysteine** (Fig. 2.4) come together.

Most of the forces that maintain the folding of proteins are relatively weak. For this reason the folding, hence the function, can be disrupted by such factors as elevated temperatures (which leave the amino acid sequence intact but tangle or **denature** the protein); changes in acidity; and the addition of specific small molecules that may bind to the protein and modify the balance of internal forces. The environmental sensitivity of proteins goes far toward explaining the physical limits of life.

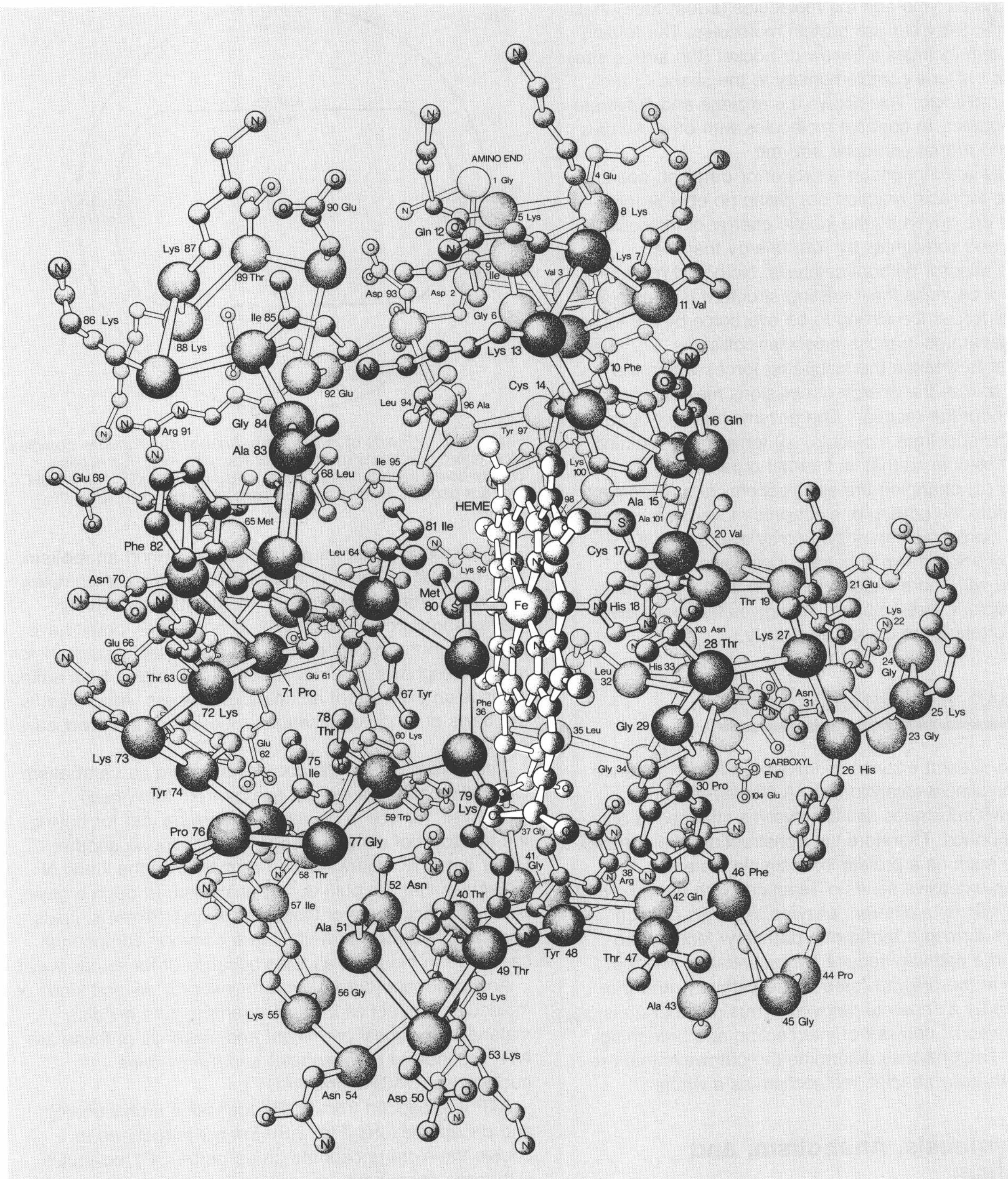


Figure 2.6 Proposed folded configuration of a molecule of cytochrome c, a plant protein.

Enzymes and Catalysis

Enzymes are vital in two ways. First, in their absence the molecules in the body react so slowly that life would be nonexistent at the pace at which we know it, even at the slow pace of plant life. *Enzymes speed reactions.* Second, the molecules of life are capable of an almost infinite variety of reactions, involving different combinations of raw materials and products. The development of an organized plant body with a shape determined by heredity implies a careful selection of the chemical reactions that occur and when they occur. *Enzymes are selective* in speeding reactions. Each kind of enzyme affects only a narrow range of reactions.

The property of selectivity or **specificity** mentioned above is widely attributed to a "lock and key" relationship between the enzyme and the molecules **(substrates)** that react with it. Enzymes are protein molecules. The folding of the protein includes a furrow or pocket (the **active site**) which has a shape complementary to the shape of the substrate molecule. This allows the enzyme and substrate to bind together; in contrast molecules with other shapes cannot bind to that particular enzyme.

The enzyme functions as a broker or **catalyst**, opening an avenue for rapid reaction but giving no energy for it. Reactions are driven by the kinetic energy of molecular collisions and sometimes by light energy that the molecules absorb. Without catalysts, biological molecules rarely react because their existing structure is maintained by internal forces too strong to be overcome by the forces that are generated in most molecular collisions. Enzymes often serve to weaken the stabilizing forces within the molecule so that the energy of collisions may be enough to bring about the reaction. The enzyme may act by (a) warping the substrate molecule; (b) temporarily reacting with the molecule so that its internal organization is altered; or (c) changing the electrochemical environment, which affects the pattern of electronic movements in the molecule. Sometimes an enzyme may also speed a reaction by holding two substrate molecules together longer and with more exact orientation than would have been possible in free solution. This gives the molecules more opportunities to collide effectively.

Phases of Metabolism

The action of each enzyme is limited to the performance of only one simple catalytic task. A single reaction between two substrates usually involves changes in only about two bonds. Therefore the construction of a complex substance such as a protein from simple materials requires an extensive series of reactions with almost every step catalyzed by a different enzyme. A series of such reactions is termed a **metabolic pathway.** Most of the reactions in a pathway require two substrates, one that was made in the previous step of the pathway, and the other made by a separate pathway. Thus metabolism is actually a web or network of intersecting and branching pathways. The enzymes determine the pathways that are available, thereby shaping metabolism as a whole.

Photosynthesis, Anabolism, and Catabolism

The whole of metabolism is far too complex to discuss here. However, we can distinguish three general phases of metabolism (Fig. 2.7). One phase is **photosynthesis.** This is a complex system of pathways by which green plants use light energy to build sugar molecules. It is the primary way in which energy is brought into the living system to power chemical constructions, growth, and repair. Its occurrence in plants is especially important to man because we cannot use light energy ourselves but must derive food (i.e., energy-rich molecules such as sugars) from other organisms and ultimately from plants.

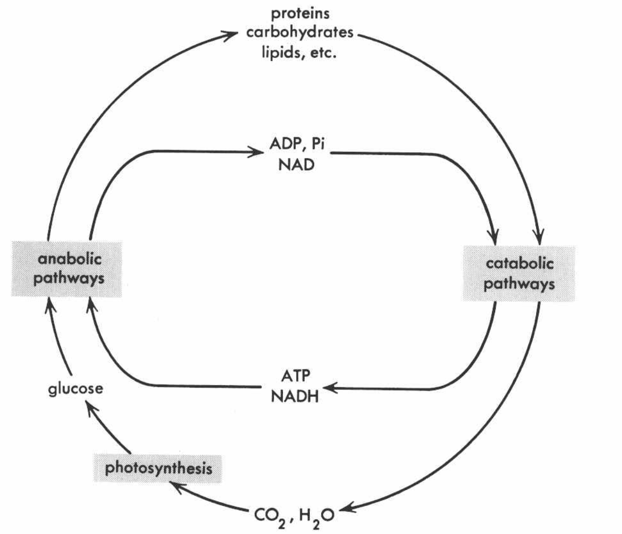


Figure 2.7 Phases of metabolism. Anabolism produces complex, high-energy products from simpler raw materials. Catabolism breaks down fuels to form compounds such as ATP and NADH that are needed for anabolism. Photosynthesis completes the cycle.

The second phase of metabolism is termed **anabolism.** This heading refers to pathways that build more complex molecules from simpler ones. Photosynthesis, which makes sugar from carbon dioxide and water, could have been put in this category but was discussed separately for special emphasis. The construction of proteins from amino acids is an example of an anabolic process. Anabolism is the basis of all developmental processes and reproductive events.

The third phase of metabolism is known as **catabolism.** Catabolic pathways extract energy from fuel (food) molecules, for use in powering anabolism and for driving the transport of materials from one location to another. Other catabolic pathways can dismantle all the kinds of molecules that are built during anabolism (though a given plant may lack some of these pathways). Proteins, lipids, and carbohydrates as well as less common compounds can serve in the plant as fuels because of these pathways.

Anabolism and catabolism are linked by several kinds of molecules that act as carriers of energy and building materials. The most prominent and universal of these are **ATP** (adenosine triphosphate) and the pyridine nucleotides ($NADP^+$ and NAD^+).

ATP is produced from ADP (adenosine diphosphate) and phosphate ions (Fig. 2.8). Energy is required to couple the extra phosphate group onto ADP; molecules with three phosphate groups joined in series are unstable,

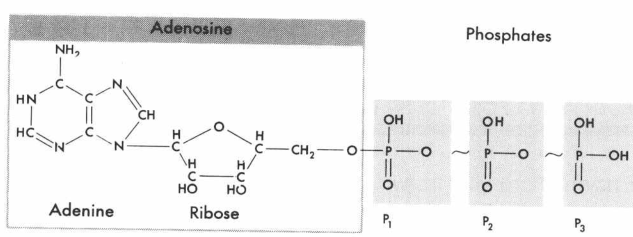


Figure 2.8 The structure of ATP (adenosine triphosphate). ADP has only two phosphate groups and AMP has only one. AMP is an example of a *nucleotide*.

ATP + H-OH ⟶ ADP-H + P-OH

ATP + H-OR ⟶ ADP-H + P-OR

Figure 2.9 Two reactions of ATP. The first is hydrolysis; the energy stored in ATP is released as heat. In the second, an organic compound replaces water and accepts phosphate from ATP, storing part of the energy and becoming more reactive as a result. R can be any of a wide array of organic groups.

reactive, and rich in energy. If molecules of ATP and water are put in contact and supplied with a suitable catalyst, hydrolysis will spontaneously occur and heat will be released, resulting in a final equilibrium that very strongly favors ADP and inorganic phosphate (Fig. 2.9). The role of catabolism is to drive this hydrolysis reaction in reverse, using energy from fuel molecules. By means of suitable enzymes, the anabolic system allows ATP to react with organic molecules but not with water (Fig. 2.9). With a portion of the ATP molecule attached, the organic product inherits some of the reactivity (energy) of the ATP and can participate more readily in reactions that yield complex products. Note that the organic reactant in Fig. 2.9 is exchanging an H atom for a phosphate-containing group. Evidently, attachment to phosphorus-containing groups tends to make organic compounds more reactive and energy-rich. In most reaction pathways the phosphate-containing group is eventually released, to be recycled back to catabolism and built into new ATP molecules (Fig. 2.7). Thus we can characterize ADP as a phosphate carrier as well as an energy carrier, which travels back and forth between catabolism and anabolism. These relationships help to explain why phosphorus is an essential element in the life of the plant.

Just as ADP picks up phosphate and (in the form of ATP) carries it to anabolic pathways, so also NAD^+ picks up electrons and hydrogen ions at several points in catabolism. Carbon dioxide, the starting material from which plants build organic materials, contains no hydrogen, but all the complex functional molecules of metabolism are rich in hydrogen. Carriers such as NAD^+ get hydrogen from the fuel molecules (e.g., sugars) that are being broken down in catabolism. The hydrogen is then supplied to anabolic pathways.

Respiration

The principal events in catabolism form a series of reactions known as **respiration**. Dozens of reactions are involved in this process, using many enzymes. All of these reactions cannot be presented in detail here, but we can outline some of their most important aspects in general terms. Three distinct phases in the respiration system can be distinguished.

The first phase is known as **glycolysis** (Fig. 2.10). This is a series of some 11 reactions in which molecules of the sugar glucose are trimmed and modified for entry into the

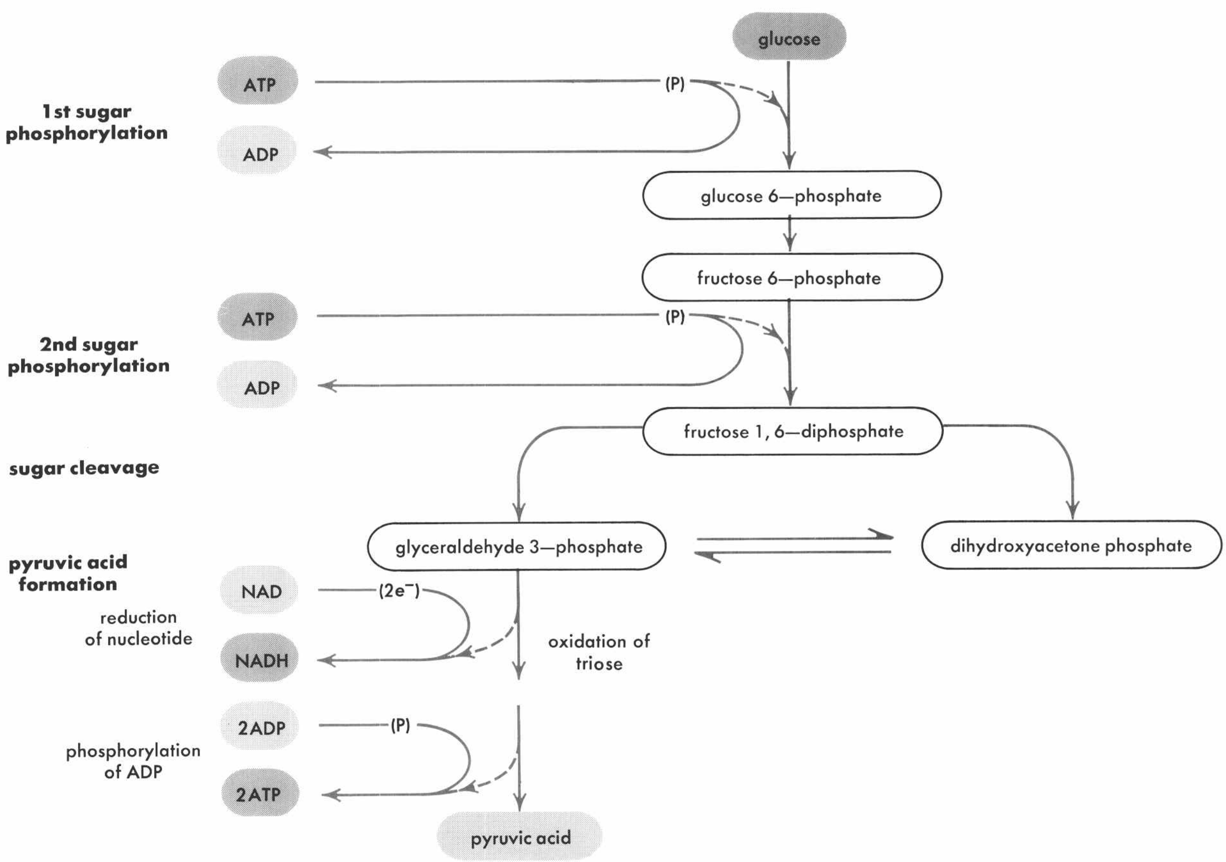


Figure 2.10 Steps in the process of glycolysis.