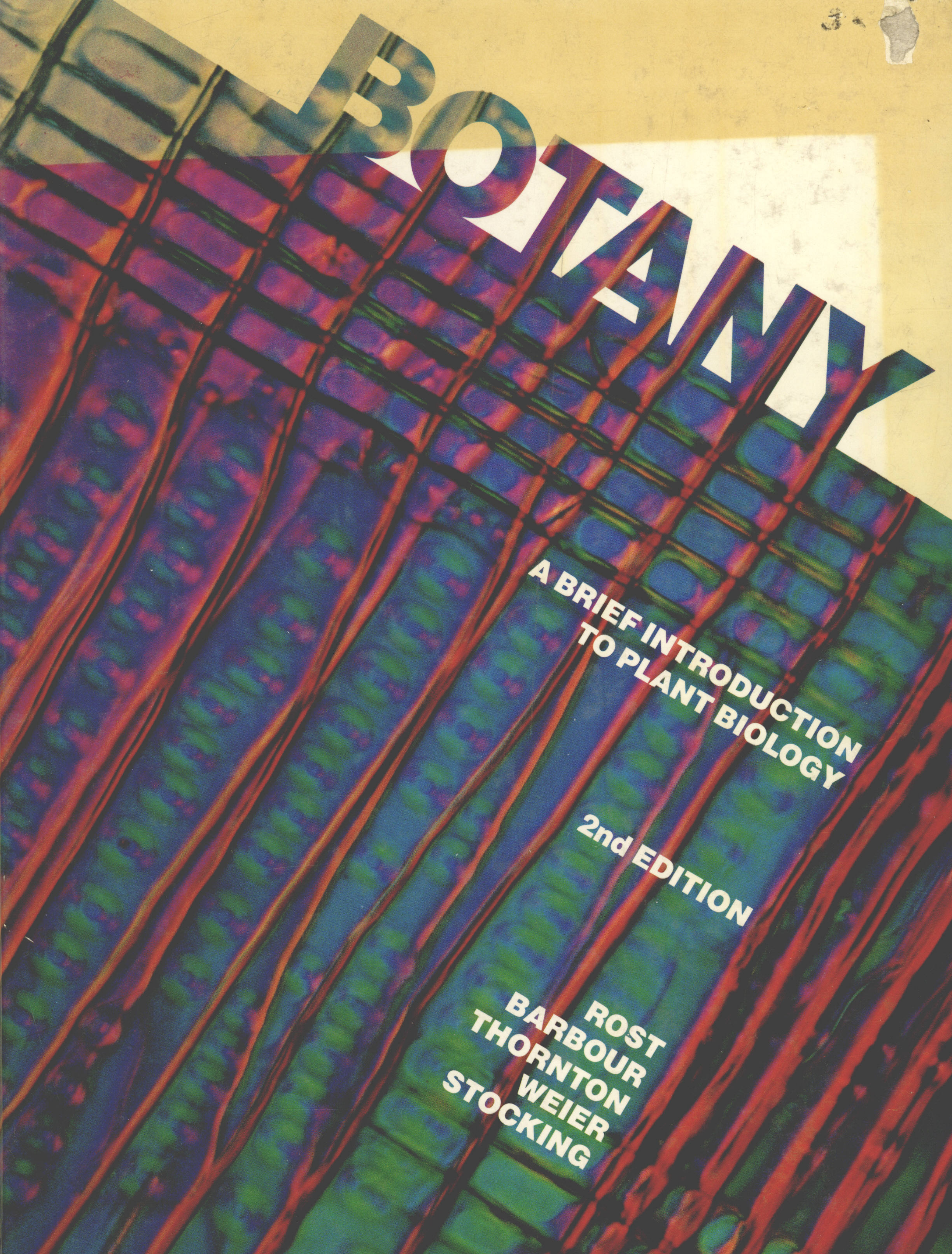

BOTANY

A BRIEF INTRODUCTION TO PLANT BIOLOGY

2nd EDITION

ROST
BARBOUR
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WEIER
STOCKING

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A BRIEF INTRODUCTION TO PLANT BIOLOGY

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PREFACE

As science advances, it becomes increasingly more difficult to select topics for the introductory textbook. Texts tend to grow bulky and encyclopedic, far exceeding the material that can be covered in an academic quarter or semester. Some texts have been kept to a reasonable length through their authors emphasizing certain topics, such as human uses of plants, at the expense of other topics. Other texts have simply grown very large.

This text stands apart, offering a balanced yet compact introduction to all aspects of botany. Brevity was achieved by concentrating on the central facts and principles that are needed to understand the form, function, and evolution of plants and fungi. Illustrations, including both figures and examples, were carefully chosen for their educational value. The text covers all primary aspects of botany and the first edition served very well at many colleges and universities. We believe this revision preserves the virtues of the first edition, while offering significant improvements in several areas.

A major change is in the treatment of genetics and plant breeding. At users' request, the original genetics appendix has been expanded to a full chapter. Here are discussed reproduction and life cycles, principles of genetics with a slant toward plant improvement, and genetic engineering. Even for a course that omits genetics, the part of this chapter dealing with life cycles provides valuable background for the study of flowers and the survey of plant groups. The introduction to genetic engineering will also be of interest to many students.

Another change is in the use of color. We have included the most useful color plates from the sixth edition of *Botany* by T. E. Weier, C. R. Stocking, M. G. Barbour, and T. L. Rost (Wiley, New York, 1982). Most of the color photos deal with plant anatomy, a topic in which color is especially useful to the students.

There is more emphasis on evolution in this text than in the first edition. The adaptation to life on land is a unifying theme in the survey of plant groups (Chapters 16–20). As each division of land plants is introduced, the text singles out advanced traits and explains how they contribute to success in the terrestrial habitat. We think this unifying thread will make the survey chapters more interesting and easier to learn.

Much is happening in the fields of taxonomy and evolution; new methods and ideas have led to perspectives that were not available a few decades ago. Evolutionists argue whether evolution is gradual or whether it goes by jumps ("punctuated equilibria"); taxonomists armed with computers debate with more traditional workers as to how well we can define groups based on evolutionary connections. Chapter 14, "Classification and Evolution," has been almost totally rewritten to express these issues. It dwells on the mechanism of evolution and on the principles used to define plant groups. The survey of ancient plants, a mainstay of the original chapter, has been divided among the later survey chapters.

This text departs from the first edition in adopting a five-kingdom classification system. Such a move is consonant with current trends in taxonomy. Unfortunately, taxonomists differ in their criteria for defining the five kingdoms. The alternatives are discussed in Chapter 14. We chose the scheme described by L. Margulis and K. Schwartz in the book *Five Kingdoms* (Freeman, San Francisco, 1982) over the older Whittaker scheme, because the former reflects more clearly the evolutionary connections between groups. The change has an impact on lower levels of classification. Some groups previously ranked as classes are now divisions, and the fungi are now divided between two kingdoms. A table of kingdoms and divisions can be found inside the back cover of this book.

Lesser changes were made in the chapters on metabolism and photosynthesis. Chapter 2, "Metabolism," now has more illustrations, a slower pace, and less material. Chapter 8, "Photosynthesis," has also been lightened, but we responded to user requests by adding material on the C_4 pathway and photorespiration.

Those familiar with the first edition will find that the number of chapters has risen from 16 to 20. The two old chapters on vegetative and reproductive anatomy have been split into separate chapters on the stem, root, leaf, flower, and seed/fruit. The change is primarily one of packaging. Except for genetics, the new chapters retain the original depth of coverage. The text as a whole is slightly longer than before, but that is largely due to added illustrations.

The authors gratefully acknowledge the efforts of all those who have helped in developing the first edition and this revision. We are particularly grateful to Dr. James A. Doyle, University of California, Davis, for his meticulous review of Chapter 14 and for his advice in the areas of evolution and systematics. We are equally grateful to Professor Peter

Wejksnora, University of Wisconsin for his careful review of Chapter 11; to Dr. Norma J. Lang, University of California, Davis, for her advice on Chapter 16; and to Dr. Gerald C. Farr, Southwest Texas State University; Dr. William G. Lipke, Northern Arizona University; Professor Clifford M. Wetmore, University of Minnesota; Professor Jerry M. Baskin, University of Kentucky; Professor Harold Hopkins, St. Cloud State University; Professor William J. Pietraface, State University of New York at Oneonta; Dr. David Biesbore, University of Minnesota for their valuable review comments on the whole manuscript. Alice B. Addicott deserves our special thanks for providing many new drawings, in addition to those of the first edition. We also wish to thank Robyn Bem for her fine editorial work. Finally, we thank all the students in the botany courses at Davis, who made it clear where we could best improve the text.

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1 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 included in the realm of botany. 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.

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 studies have shown this to be an oversimplification. For example, the mosses **(Fig. 1.1, Color Plate 1)** have always been considered to be plants and appropriate subjects for botanists to study. But in early development the moss plant consists of green, threadlike filaments that resemble certain species of aquatic organisms, the **algae (Fig. 1.2, Color Plate 1).** 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, Color Plate 1).** These cells swim by means of flagella that resemble 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 difficult 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 photosynthesize—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 most kinds of organisms 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. But some of the unicellular algae do not have true walls. The slime molds **(Fig. 1.4, Color Plate 1)** also lack walls during most of their life cycle. This allows the slime mold to move about and pursue a predatory way of life reminiscent of animals (animal cells also have no walls).

Although cell walls are a characteristic of botanical life, there are major differences in wall structure and composition among organisms. 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.

Another property found only in botanical life is the ability to photosynthesize **(Fig. 1.5, Color Plate 1).** Photosynthesis uses the energy of sunlight to produce foods and other 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 photosynthesize. An example is "Indian pipe," a parasitic plant that has roots, stems, and flowers **(Fig. 1.6, Color Plate 1).** Most bacteria do not photosynthesize; nor do any of the 200,000 species of fungi **(Fig. 1.7, Color Plate 1).** 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 scientists agree on the proper way to sort and classify the organisms included in botany. Nevertheless, classification is both a practical necessity and an important intellectual goal of botanists.

The highest goal in classification is to define natural groups of organisms that are related by common ancestry. To approach this goal we must reason from indirect evidence, since human observers did not trace events earlier than a few thousand years ago. The evidence includes fossils of ancient plants as well as similarities and differences between present-day plants (Chapter 14).

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

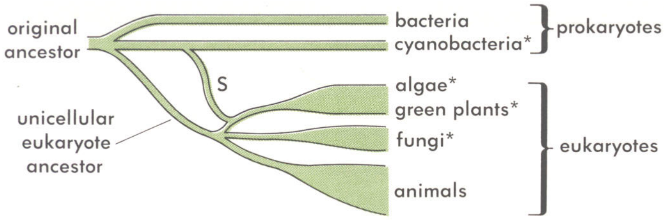


Figure 1.8. Ancestral relationships between modern organisms as deduced from protein structure and the structure and function of cells. **S** marks the symbiotic association between a cyanobacterium and a primitive eukaryote, by which chloroplasts are believed to have arisen. The starred groups are all studied in botany.

the common plants and fungi 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. The proteins built by eukaryotes and prokaryotes are similar enough to indicate that they arose from a common ancestor, but they are 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.

Biologists divide the eukaryotes into kingdoms, but the number of kingdoms is subject to debate. One common approach is to define kingdoms on the basis of nutrition. The resulting groups are shown in Fig. 1.8. *Animals* typically ingest solid foods, a trait that is possible because their cells lack walls. *Fungi* are like animals in that they take in organic foods from the environment, but they have walls and can only absorb food molecules in dissolved form. *Plants,* in this classification, are eukaryotes that perform photosynthesis. Other points of view are presented in Chapter 14.

An interesting complication arises when we consider the origin of structures that occur within eukaryotic cells. For example, units called **chloroplasts** carry out photosynthesis in the cells of plants. Chloroplasts resemble certain bacteria in many ways, and it has been suggested that chloroplasts are descended from bacteria that entered early eukaryotic cells. In such a symbiotic association the bacterium might have been protected from harm and the eukaryote would have shared in the products of photosynthesis. With time, the association became permanent, so that modern chloroplasts cannot survive outside the eukaryotic cell. Comparable symbioses can be seen today between bacteria and the roots of legumes (Chapter 6), but in these, the partners are still separable. Certain other cell parts are also suspected of having arisen through symbioses between bacteria and eukaryotes. If these symbiotic origins really took place, the distinction between eukaryotes and prokaryotes may be less clear than once was thought. Such ideas leave us uncertain about how far back we must reach to find ancestral connections between the many forms of life that make up the subject matter of botany.

2 METABOLISM

The visible signs of life in most plants are limited to slow changes such as the growth of organs. But if we look at the units of matter called molecules, of which plants are composed, the plant body proves to be a place of incessant, rapid activity. This chemical activity is called **metabolism.** The metabolic system within the plant generates thousands of chemical products, many of which are formed nowhere else in nature.

This chapter will show the principal molecules of life, how they are formed, and how they contribute to the life of the plant.[1]

RAW MATERIALS

Plants absorb raw materials from the environment and convert them into many complex products. Though the uptake of raw materials is discussed in detail in Chapter 7, it will be useful to introduce the raw materials now as a background for discussing the molecules manufactured by plants.

Water (H_2O) is the substance that plants take up in the greatest quantity. About 90% of the water that enters the plant is later evaporated away. Most of the retained water simply provides bulk and serves as a medium for transporting materials. However, water also provides atoms for building biological molecules. It is the chief source of the element hydrogen (H).

Carbon dioxide (CO_2) is taken up from the air (or from water, if the plant is aquatic). This compound is the plant's chief source of carbon (C) and is also a major source of oxygen.

Oxygen molecules (O_2) are also taken up. Molecular oxygen is needed to extract energy from the compounds that serve as fuels. During the day, the green parts of the plant make their own oxygen molecules from water. However, nongreen stems and roots must get oxygen from the air or water, and at night even leaves absorb oxygen from the air.

Mineral elements are absorbed from soil or water. They include nitrogen (N), phosphorus (P), sulfur (S), and many other elements. They occur as ions dissolved in water. Some ions, such as magnesium (Mg^{+2}) and potassium (K^+) are single charged atoms, but most are bound to hydrogen (as in ammonium, NH_4^+) or to oxygen (nitrate, NO_3^+, and sulfate, SO_4^{-2}) or both (phosphate, HPO_4^{-2}).

[1]Readers who have not previously studied chemistry may find it useful to read Appendix A along with this chapter.

MAJOR BIOLOGICAL MOLECULES

From the raw materials, plants make a great variety of compounds: at least 100,000 kinds have been described, and many more remain to be discovered. Fortunately, most biological compounds fall into just four categories: *carbohydrates, lipids, proteins,* and *nucleic acids*. The first three will be discussed immediately below, while nucleic acids are reserved for the discussion of hereditary information on page 11.

CARBOHYDRATES

The **carbohydrates** include sugars and compounds that are made by joining sugars into chains. They serve mainly as fuels and building materials.

Sugars have the general formula $(CH_2O)_n$, where n is an integer between 3 and about 10. Two of the most abundant sugars are **glucose** and **fructose,** shown in Fig. 2.1. They illustrate the common features of sugars as well as some ways in which sugars can differ from one another. First note that each sugar molecule can assume two forms: it can switch between being an open chain and a ring. This is possible because every open-chain sugar has a C=O group at the first or second carbon atom. The oxygen of C=O is reactive, and the rest of the molecule can twist around until this atom meets and joins another carbon atom to make the ring. (This cannot happen if the sugar has only three carbon atoms.)

Sugars are classified by the number of carbon atoms in their skeletons. Those with six carbons are called **hexoses;** *hex* means "six," and the ending *-ose* denotes a sugar. *Glucose* and *fructose* are hexoses. Sugars that contain five carbon atoms are called **pentoses.** An important example is **ribose,** which occurs in the molecules that carry hereditary information (see page 11). Ribose is also part of ATP, a compound that carries energy.

Most sugars have an OH group on every carbon except the one with the single oxygen (C=O). Many different sugars can be made by changing the orientation of the OH groups. As you see in Fig. 2.1*a*, glucose has one OH directed toward the left and the others directed toward the right. The sugar **galactose** (not shown) is exactly like glucose except that all the OH groups point to the right. These molecules are examples of **isomers,** or molecules with the same general structure but minor differences in organization.

Sugars can join into chains, which are classified by their length. The shortest chains have just two sugars and are

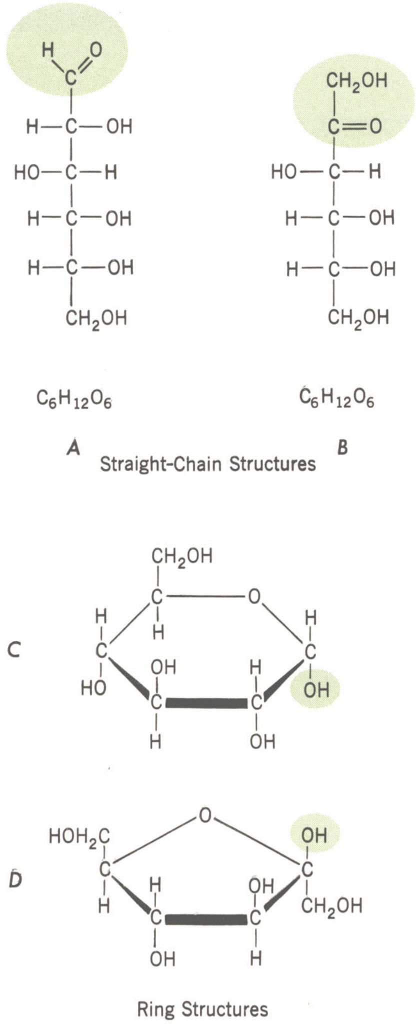


Figure 2.1. Glucose and fructose, two hexose sugars, have the same formula but different structures. Both can exist as a straight chain or ring. A and C, glucose; B and D, fructose.

called **disaccharides;** the longest have thousands of sugar units and are called **polysaccharides.** In these names the *-saccharide* portion means "sugar unit," while the prefix indicates the number. Thus *di-* means "two," and *poly-* means "many." A simple sugar such as glucose is a **monosaccharide;** *mono-* means "one."

The disaccharide **sucrose** (Fig. 2.2) is especially important to plant and human life. Sucrose is composed of a glucose molecule linked to a fructose molecule. It is the main circulating energy storage compound in most plants; it is produced in leaves and transported to other parts of the plant. Sugar beets and sugarcane (the sources of table sugar) store large quantities of sucrose.

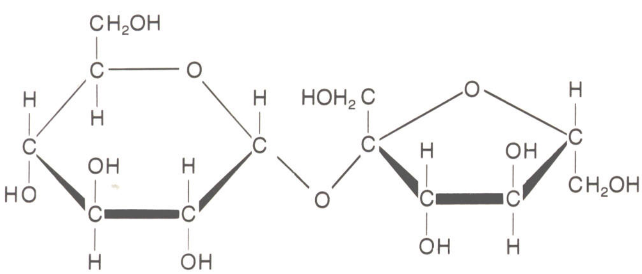


Figure 2.2. Sucrose, the disaccharide that we use as table sugar, is made of glucose and fructose.

The polysaccharides illustrate the concept of **polymers:** that is, complex molecules constructed by linking many smaller repeating molecules into chains. Some polysaccharides contain just one kind of sugar, while others contain two or more kinds. *Starch* is composed entirely of glucose molecules. The starch molecule coils and may also branch because of the way the glucose units are linked together. Starch molecules clump together into grains that form a compact food reserve. *Cellulose* (Fig. 2.3) is also made entirely of glucose, but the sugars are linked in a way that leads to a straight, unbranched polymer. Cellulose molecules line up side-by-side to form tough, straight fibers. Cellulose contains as much energy as starch but is more resistant to attack. Appropriately, plants employ cellulose as a structural material rather than a food reserve. It makes up a large part of wood.

LIPIDS

Lipids are varied compounds with just one feature in common: they do not readily mix with water. Some lipids serve as energy reserves, some protect against water loss, and some serve structural roles in the plant.

Waxes such as **cutin** and **suberin** are solid lipids that coat the surfaces of plants and limit the loss of water. Some plant waxes (e.g., carnauba) are used in furniture and automobile polishing compounds.

Fats are excellent storage compounds because they have a high energy content and a tendency to accumulate in droplets. A fat molecule is composed of three **fatty acids** that are joined to a molecule of **glycerol** (Fig. 2.4). A fatty acid molecule has an acidic group at one end; the rest of the molecule is a long chain of carbon and hydrogen atoms. These **hydrocarbon chains** are insoluble in water.

Phospholipids are important structural compounds. To describe their function, it will be necessary to anticipate Chapter 3 and say a little about the organization of material in the plant. As shown in Fig. 2.5, the plant body consists of numerous units called *cells,* each of which contains functional units called *organelles*. Every cell is surrounded by a

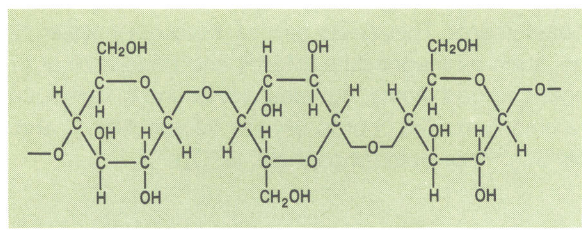


Figure 2.3. Cellulose is an unbranched polymer composed of many thousands of glucose units. The diagram shows three of the units.

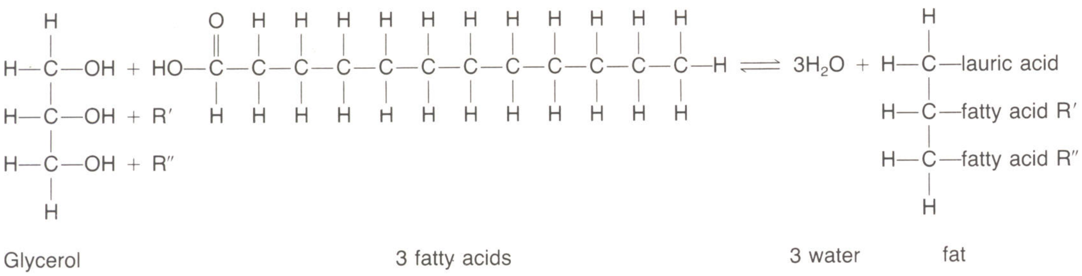


Figure 2.4. A fat is formed by joining three fatty acid molecules to a molecule of glycerol. One fatty acid (lauric acid, $C_{12}H_{25}O_2$) is shown in full; the others are symbolized as R′ and R″.

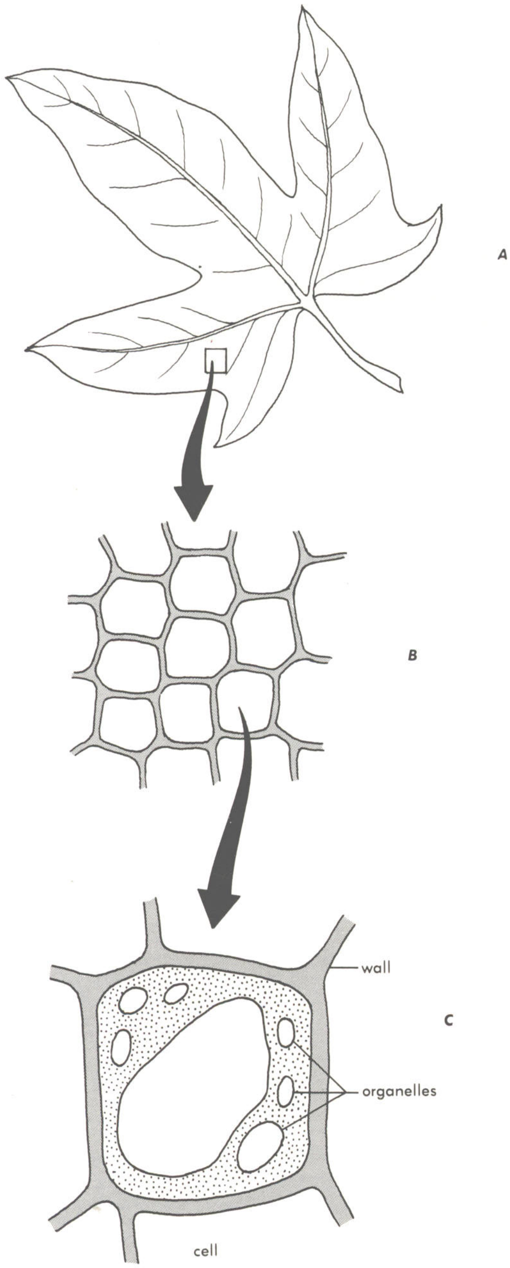
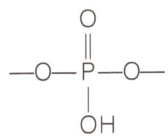


Figure 2.5. Levels of organization in the plant body. *A,* an organ, the leaf, *B,* on magnification, organs are found to contain cells within walls. *C,* further magnification shows that cells contain functional units, the organelles.

thin sheet of material called a **membrane,** and additional membranes surround most organelles. Phospholipids make up from one-fourth to two-thirds of the weight of each membrane. They combine into sheets because one end of the molecule is compatible with water and the other end is not. Therefore, when phospholipids are surrounded by water (as in the plant body), they line up in a double layer that keeps one end of each molecule away from the water. The arrangement is shown in Fig. 3.4, p. 22.

Phospholipids resemble fats, except that one of the fatty acids is replaced by a **phosphoryl group:**

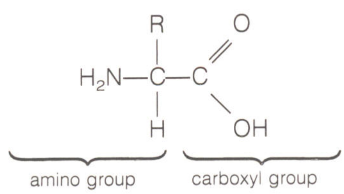


One end of the phosphoryl group binds to the glycerol unit, while any of several organic groups may bind to the other end of the phosphoryl group.

PROTEINS

Proteins perform many functions in the plant. Some proteins regulate and control the chemical processes of life; some act as structural materials in membranes and elsewhere; and some are involved in generating motion.

Proteins are polymers made from subunits called **amino acids.** There are 20 common amino acids, 19 of which have the following structure[2]:



The symbol **R** signifies a group of atoms called a **side-chain.** The 20 amino acids have different side-chains; four of them are shown in Fig. 2.6.

[2]The 20th amino acid, **proline,** differs from the rest in that its R group bends over and binds to the N of the amino group.

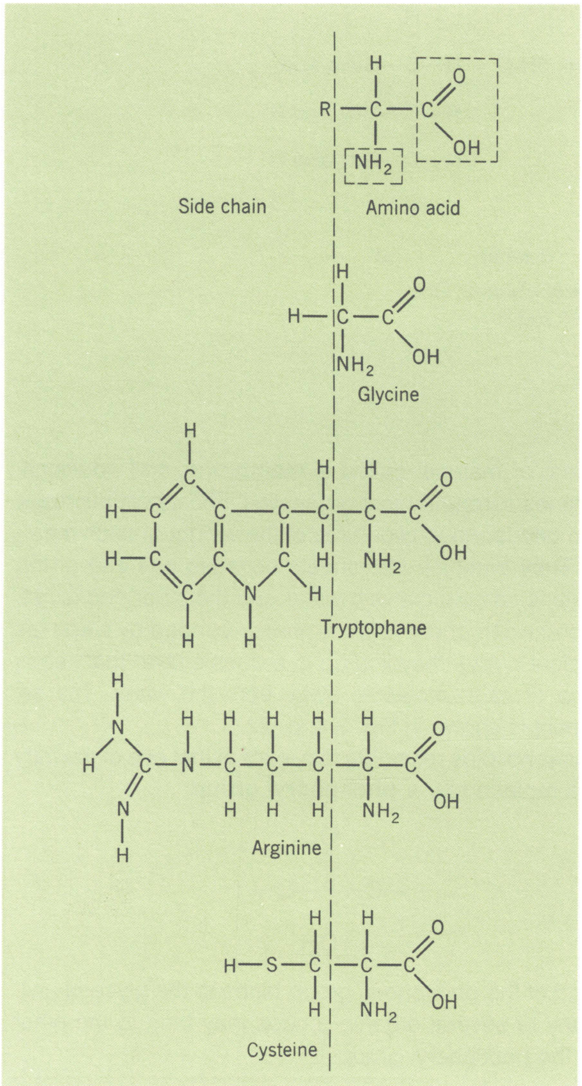


Figure 2.6. Some amino acids.

To form a protein, the amino acids are linked together as in Fig. 2.7. The link between two amino acids is a **peptide bond,** and for this reason proteins are often called **polypeptides.**

Proteins can perform many functions because they vary widely in structure. They range in size from below 100 to over 1000 amino acids. They combine the amino acids in different sequences, so countless different proteins are possible.

Proteins are flexible in shape, and each one can fold in many ways. This is important because each protein must fold into a specific shape to have a biological function. Figure 2.8 shows a folded protein. Unfortunately, the forces that stabilize the folding are quite weak. Proteins can be unfolded by mild heat and by many chemical agents. Unfolded proteins often become irreversibly tangled and cannot return to their original shapes. This process is called **denaturation.**

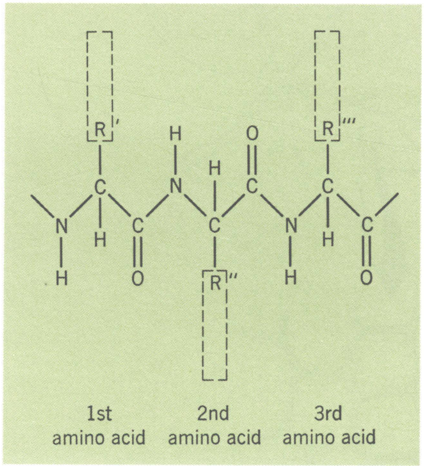


Figure 2.7. A polypeptide chain is a part of a protein molecule. The backbone of the protein molecule is formed by many amino acids joined by the union of the amino group (NH_2) of one amino acid to the acid group (COOH) of another amino acid by the removal of a water molecule. The R groups represent side-chains of the different amino acids.

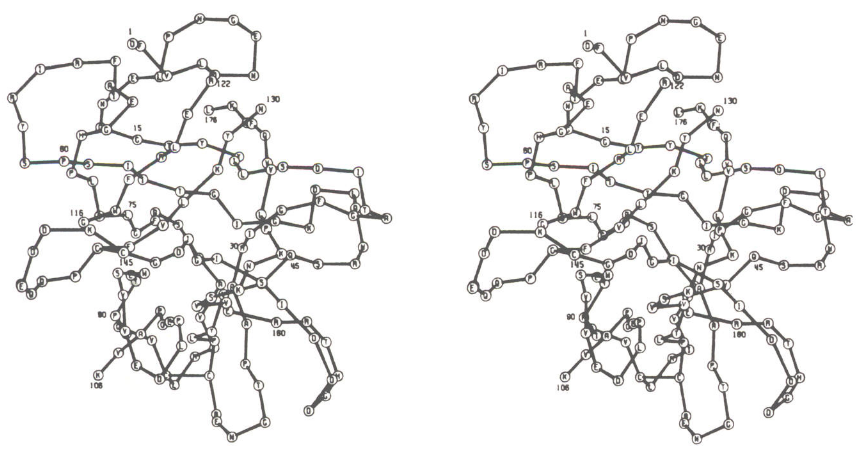


Figure 2.8. A protein that is found in soybeans. You can fuse the two drawings into a single image that looks three-dimensional if you stare at a point between the two pictures and let the images drift together. The drawing only shows the course of the protein's "backbone." In reality, side-chains fill the spaces between loops of the protein.

Several factors determine how a protein will fold. Most important is the influence of water, which completely surrounds most proteins in the living plant. Water molecules form hydrogen bonds with one another and resist being separated. Some of the side-chains of proteins are nonpolar and cannot break through the web of hydrogen bonds. Therefore, the surrounding water forces most proteins into a compact shape, with the nonpolar parts in the interior and the polar parts at the water surface. This is one reason why dehydration (excessive water loss) is fatal: it allows proteins to denature.

ENZYMES AND CATALYSIS

Life is based on chemical activity. However, most compounds are stable and will not react at useful rates without help from **catalysts.** A catalyst is an agent that speeds reactions without being consumed in the process. Catalysts in living plant cells are special proteins called **enzymes.** They have two important properties: they are selective in their action, and they work very rapidly.

Enzymes are selective in two ways. First, an enzyme reacts with only a few kinds of other molecules (the enzyme's **substrates**); secondly, each enzyme catalyzes only one kind of reaction.

Enzymes achieve their specificity by matching the shape of the substrate molecule. The enzyme has a pit or groove called the **active site** where the substrate must bind before the enzyme can react (Fig. 2.9).

With the substrate in place, an enzyme generates products as much as a billion times faster than an uncatalyzed reaction. Enzymes achieve their speed by varied mechanisms, and we know the full details in just a few cases. Here, we can only mention the most well-known aspect.

Uncatalyzed reactions tend to be slow because there are stabilizing forces within each molecule that resist change. To overcome these forces, a molecule must acquire an amount of energy called the **activation energy.** A collision between molecules can supply the energy; however, very few collisions provide enough energy to meet the activation requirement. In most collisions the molecules rebound without being changed.

How do enzymes speed reactions? The obvious answer, that they provide energy to the reactions, is wrong. Enzymes work primarily by *reducing the activation energy*. This is done by providing a new pathway of change that involves weaker stabilizing forces and, therefore, smaller activation energies. To open up a new pathway, the enzyme itself reacts with the substrate. Rapid stepwise changes occur, and each step presents only a small energy barrier. These small energy demands can easily be met when molecules collide with the enzyme.

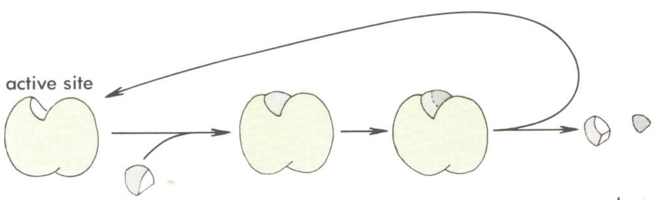


Figure 2.9. Outline of enzyme catalysis, illustrating the match between the substrate and the active site. The process can be reversed.

PHASES OF METABOLISM

Complex products are made by **metabolic pathways**—sequences of reactions in which one enzyme after another works on the product. Metabolism includes hundreds of pathways, some of which are shown in the following pages. As a framework for studying the pathways, let us point out that metabolism has a higher level of organization: the pathways can be grouped into several phases of chemical activity, and each phase plays a different part in the life of the plant. The phases of metabolism are *photosynthesis, anabolism,* and *catabolism.* Figure 2.10 shows their relationship.

In **photosynthesis,** the plant uses light energy to make organic acids from carbon dioxide and water. The organic acids are later converted to sugars or amino acids. Photosynthesis is the primary source of energy for the construction of plants. It is also the primary way in which carbon is brought into the living world. Photosynthesis in plants is especially important to humans because our own tissues cannot use light energy. Therefore, we must use other organisms, including plants, for food. Chapter 8 describes photosynthesis in detail.

Anabolic pathways build complex molecules from sim-

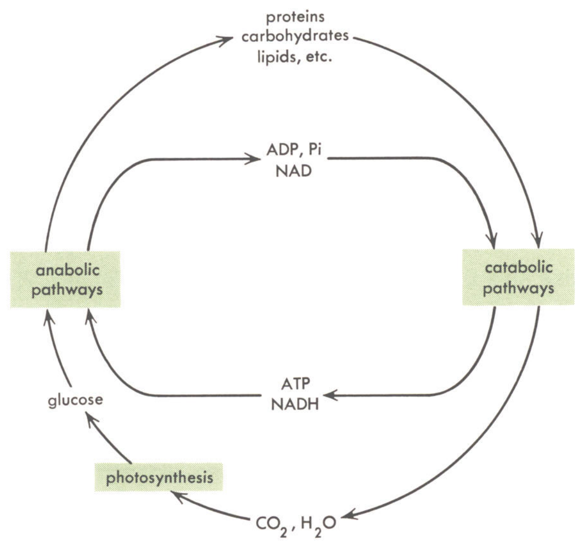


Figure 2.10. Phases of metabolism. Anabolism produces complex, high-energy products from simpler raw materials. Catabolism breaks down fuels to form compounds such as ATP and NADH that are needed for anabolism. Photosynthesis retrieves carbon from CO_2 and captures light energy.