PLANT PHYSIOLOGY

THIRD EDITION

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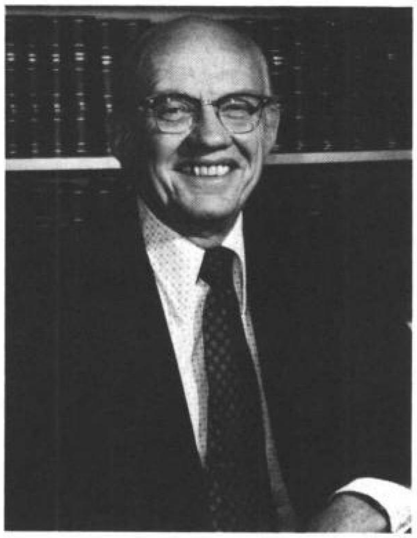
To
Herman Henry Wiebe
1921–1984



This edition of *Plant Physiology* is dedicated to the memory of Herman H. Wiebe, who died on March 14, 1984. Professor Wiebe made major contributions to this book and to the two previous editions. He reviewed every chapter and was especially helpful with the chapters in his own speciality, which included most of the section on plant–water relations. Professor Wiebe was a doctoral student of Paul Kramer at Duke University and taught at Utah State University since 1954. He had a deep concern for students, and this concern is reflected in many ways in this book and in other books that he reviewed for Wadsworth Publishing Company. As it happens, Cleon Ross was a doctoral student of Herman Wiebe, and Frank Salisbury and Herman Wiebe were close friends and colleagues for the eighteen years since Salisbury came to Utah State University. We will miss our dear friend and advisor.

Preface

Much new information has been gained in the field of plant physiology since 1978 when the second edition of our textbook appeared. It would have been relatively easy to double the size of our third edition just by adding new information to our second. Yet as teachers of plant physiology, we realize that time always limits what can be presented in a plant physiology course. Hence, it has been our assignment to choose and summarize those new findings that are most representative of the status of the science in the mid-1980s. We hope that you as students and teachers will agree with many of our choices. We also realize that our book contains more information than can be presented in the typical one-quarter or one-semester course in plant physiology. Thus teachers will also have to choose topics most relevant for their classes, but we hope that all students will gain some impression of the breadth of our science by surveying those topics in our text that are not assigned in class.

The organization of this text is basically the same as in previous editions. We realize that beginning plant physiology students have studied the plant cell in previous courses, but we have greatly expanded the discussion of the cell in our prologue. Knowledge of the cell is so fundamental that a complete review seems justified—and was requested by many reviewers. The rest of our text is divided into four sections: The first seven chapters (Section 1) deal with physical processes, the middle seven chapters (Section 2) with metabolism and biochemistry, and the eight chapters of Section 3 with growth and development. The last two chapters (Section 4) are built upon the other twenty-two to relate plant function to the environment that so strongly influences it. We assume that students have some knowledge of organic chemistry as background for our biochemistry section. We also assume that students have studied DNA replication and protein synthesis (molecular biology), topics usually covered in basic biology courses. Nevertheless, in Appendix C we present several topics about molecular biology for quick review. Of course, students will also have covered many other topics that we describe; we hope our presentation will be appropriate review and reinforcement.

In preparing this edition and in teaching plant physiology, it is apparent that biochemical information is becoming increasingly important in understanding the so-called physical processes of plant function (mostly plant–water relations), although physics is still of central importance to water relations. We have retained the previous order (physical processes before biochemical), because a survey of teachers by our publisher revealed that a significant majority of users still prefer this organization. Nevertheless, we suggest that some teachers might like to discuss Section 2 before Section 1, since little background in physical processes is required to understand the biochemistry chapters. We might reverse the order of these two sections in our fourth edition, and we would greatly appreciate comments from teachers about such an approach.

We have retained most of the features (teaching and learning aids) of our second edition, since they were well received by many users. In addition, we have made a few changes, partially as a result of our own teaching experiences and partially in response to reviewers suggestions.

The Format Our publisher designed a new format for this edition, one that is a bit more conventional and should be easier for readers to handle. This format provides fewer words on a page than in our previous editions, so the number of pages has increased significantly. Part of the page increase is because of new material added in this edition, although we compensated by condensing our writing and by eliminating some older material. We also added many new illustrations, deleted a few of the older ones, and had some of our earlier illustrations redrawn. Many of the new illustrations were prepared by Darwen and Vally Hennings, a pair of talented botanical illustrators.

Guest Essays and Boxed Essays For the 1978 edition, we requested that several plant physiologists write guest essays that often related some of their own personal experiences and impressions of our science and that sometimes presented facts and applications of topics in the text. In this third edition we kept many of these guest essays and added some new ones. We find them enjoyable and informative, and we hope that you will too. We retained and added a number of small boxed essays as well. (In Chapter 7 on phloem transport, it was necessary to add a rather large boxed essay on the chemistry of carbohydrates, because numerous carbohydrates and related compounds occur in the phloem translocation stream.)

Appendices In our second edition we presented a number of special topics at the end of the book. Most reviewers suggested that these either be deleted or incorporated into appropriate chapters. We have followed this suggestion, but three important topics are not amenable to incorporation in other chapters. These are now Appendices. The first presents tables and some discussion describing the Système Internationale (SI units). The use of SI units has expanded considerably in all sciences during recent years. Our goal in this edition has been to use SI units whenever they are being used by current journals that publish major advances in plant physiology. We were thus able to use SI units almost exclusively, although a few of the older units are still in wide use and will probably continue to be used (liter for volume; molality and molarity for solution concentrations; and minute, hour, and day for time). The second appendix is an updated version of our previous Special Topic on radiant energy. It seems logical to consider this topic as a unit in an appendix rather than discussing several aspects of it in various chapters in the text or to give it undue emphasis by including it with other material in a single chapter. As noted, our third appendix concerns molecular biology.

References to the Literature of Plant Physiology Users of our previous editions have commented favorably on the references in our text. Thus, on the one hand we were tempted to document most of our important conclusions. We did this by referring to authors by last name and year of publication. On the other hand, we realized that frequent references distract some students. In the prologue and the first few chapters, not many references to the literature are given in the text, although the bibliography at the end of the book contains many reviews and other references for these chapters. The interested user can scan the titles in these lists to find specific sources of information. After the first few chapters, we provided many more references. Students should realize that they must become accustomed to such references, because they are an essential part of the scientific literature.

The increased use of references in this edition has led to some other problems. In the first (1969) edition of our book, we provided first names of authors if we knew them and otherwise provided initials when scientists were first mentioned in the text. Frequently, we also mentioned where their work was performed. We felt that this was one way to make it apparent to students that plant physiology is the product of many individuals working in diverse places all over the world. That is, we hoped that we could personalize our science somewhat. We realize, however, that some students may become frustrated by feeling that they should remember all about who did what and when. In this edition, we have often retained the use of first names (and some locations), but we have not made an effort to use first names and intials of everyone whose name is mentioned. Be admonished that full names are there mainly to personalize our science, but references are given for scientific documentation of important discoveries and recent facts and to point out recent reviews.

Some Specific Chapter Changes All chapters were thoroughly revised for this edition, although the first three chapters (water potential, osmosis, and transpiration) have less new material than the others. The first three were revised to make them easier for students to follow. The order of Chapters 5 and 6 was reversed, so that students would learn about the elemental composition of plants before they investigated how such elements are absorbed. Chapter 7 (phloem transport) was substantially reorganized and expanded in response to suggestions from teachers and students. We reorganized Chapters 8 to 11 less than Chapter 7, although we placed photorespiration in Chapter 10 instead of Chapter 11. We also deleted a section on cell-wall chemistry from Chapter 10 to save space; some of that material (as related to growth) is now in Chapter 15. Chapter 14 was expanded almost as much as Chapter 7. This chapter describes numerous chemical reactions and products common to most organisms plus reactions that occur only in plants; it also describes ecological functions of lipids and several other natural products. This chapter and others in Section 2 (except for Chapter 12 on respiration) emphasize the unique biochemistry of green plants. The chapters in Section 3 on growth and development have all been thoroughly revised (Chapter 20 on the biological clock perhaps the least). Stress physiology has been advancing rapidly in recent years, so Chapter 24 was extensively revised and expanded.

The Reviewers As in our previous editions, we are indebted to the reviewers retained by our publisher or requested by us to examine individual chapters or the entire manuscript. These reviewers, along with many others who volunteered comments, provided many valuable suggestions that we followed. We are grateful to them, but of course we accept complete responsibility for the text in its present form.

Final Observations Preparation of any text involves frustrations in checking details and reconciling points of view, yet we have learned much about our science in writing for you. Although we each write somewhat differently, we hope that our writing displays organization and readability as well as facts and major principles. Frequently, we emphasize or imply that many problems remain unsolved. If that were not true, our science could not advance. Current and future researchers (many of whom are now students) must solve many present and future problems, so that years from now plant physiology texts will be somewhat less speculative and contain even more principles.

We hope that our enthusiasm and love for the science of plant physiology is apparent to you and that you will come to share these feelings with us. These are the feelings that motivate the rapid advances now being made in virtually all scientific disciplines.

Frank B. Salisbury, Logan, Utah
Cleon W. Ross, Fort Collins, Colorado
December 1984

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Plant Physiology and Plant Cells

Plant physiology is the science that studies plant function: what is going on in plants that accounts for their being alive. The promise of plant physiology is to give you some insight into these functions.

Of course you know that plants are not really as inanimate as they appear. (It is often difficult to tell a plastic plant from its real counterpart.) But studying plant physiology should greatly broaden your appreciation for the many things that are happening inside plants. Water and dissolved materials are moving through special transport pathways: water from soil through roots, stems, and leaves to the atmosphere; and inorganic salts and organic molecules in many directions within the plant. Thousands of kinds of chemical reactions are underway in every living cell, transforming water, mineral salts, and gases from the environment into organized plant tissues and organs. And from the moment of conception, when a new plant begins as a zygote, until the plant's death, which could be thousands of years later, organized processes of development are enlarging the plant, increasing its complexity, and initiating such qualitative changes in its growth as the formation of flowers in season and the loss of leaves in autumn.

Plant physiology studies all these things.

P.1 Some Basic Postulates

Plant physiology is one of many branches of biological science. Like the other branches, it studies life processes, which are often similar or identical in many organisms, including plants. In this prologue, we shall state eleven postulates, or generalizations, about science in general and plant physiology in particular. These postulates are presented with a minimum of discussion, but information on cells is so fundamental to plant physiology that after the list we provide a review of plant cells as the main body of this prologue. Here are the postulates:

1. *Plant function can ultimately be understood on the basis of the principles of physics and chemistry.* Plant physiologists accept the philosophical statement called the Law of the Uniformity of Nature, which states that the same circumstances or causes will produce the same effects or responses. This concept of cause and effect must be accepted as a working hypothesis (i.e., on faith). Although there is no way to prove that the principle always applies everywhere in the universe, there is also no reason to doubt that it does. It is possible that life depends on a spirit or entelchy not subject to scientific investigation; but if that is presumed, then by definition science cannot be applied to anything. The assumption that plants are mechanistic leads to fruitful research; the contrary assumption, called **vitalism,** has been completely unproductive in science. For example, convictions (yours or ours) about the existence of a Creator may help or hinder your appreciation of plant physiology, but they cannot play a direct role in the science itself.

2. *Modern plant physiology in particular and biology in general depend upon the physical sciences: upon physics and chemistry, with their reliance on mathematics.* Plant physiology is essentially an application of modern physics and chemistry to the understanding of plants. Indeed, progress in plant physiology has been almost completely dependent upon progress in the physical sciences. Today, the technology of applied physical science provides the instrumentation upon which research in plant physiology depends.

3. *Botanists and plant physiologists study members of four of the five kingdoms of organisms presently recognized by many biologists (Table P-1); but much discussion in this book is concerned with the true plants and, indeed, with a relatively few species of gymnosperms and angiosperms.*

Table P-1 A Simplified Outline of the Classification of Organisms.

VIRUSES: Exhibit properties of life only when present in cells of other organisms; considered by most biologists not to be alive when isolated.

1. MONERA:* prokaryotic organisms (no organized nucleus or cellular organelles); include bacteria, blue-green algae (sometimes called cyanobacteria), and mycoplasms.
2. PROTISTA: Eukaryotic (true organelles and nucleus), mostly single-celled organisms; include protozoa (single-celled "animals"), some algae,* and slime molds.* (Some authors include all the eukaryotic algae, even multicellular forms.)
3. FUNGI:* The true fungi
4. PLANTAE:* Most algae and all green plants; include the following plus some minor groups not mentioned:
   - Brown algae
   - Red algae
   - Green algae**
   - Mosses and liverworts*
   - Vascular plants (higher plants)
     - Ferns and relatives*
     - Cycads and rare gymnosperms*
     - Conifers (common gymnosperms)**
     - Flowering plants (angiosperms)**
       - Monocotyledons (monocots)
       - Dicotyledons (dicots)
5. ANIMALIA: Multicellular animals

*Studied by plant physiologists
**Emphasized by plant physiologists

Modern biologists feel that a five-kingdom approach to a classification of living organisms is far superior to the previous attempts to classify all organisms as either plants or animals. Nevertheless, there is still much controversy about the placement of certain groups such as the slime molds and some of the algae. Suffice it to say that plant physiologists study the blue-green algae (or cyanobacteria) and other prokaryotes studied by bacteriologists, various groups of algae, slime molds, true fungi, and representatives of all major groups in the plant kingdom. Nevertheless, our discussions here will strongly emphasize gymnosperms and the flowering plants, only occasionally referring to the other groups.

4. *The cell is the fundamental unit of life; all living organisms consist of cells, which contain either membrane-bound nuclei or comparable structures without membranes. Life does not exist in units smaller than cells. Cells arise only from the division of pre-existing cells.* Collectively, these statements are known as the **cell theory.** Coenocytic organisms (certain algae, fungi, and slime molds) do not have their organelles (mitochondria, nuclei, etc.) partitioned into cells by cell membranes and walls, but other typical structures of cells are present.

5. *Eukaryotic cells contain such membrane-bound organelles as chloroplasts, mitochondria, nuclei, and vacuoles, whereas prokaryotic cells (by definition) contain no membrane-bound organelles.*

6. *Cells are characterized by special macromolecules, such as starch and cellulose, which consist of hundreds to thousands of identical sugar or other molecules, or repeating groups of molecules.*

7. *Cells are also characterized by such macromolecules as proteins and nucleic acids (RNA and DNA), which consist of chains of hundreds to thousands of simpler molecules of various kinds (20 or more amino acids in protein and 4 or 5 nucleotides in nucleic acids). These chains include long segments of nonrepeating sequences that are preserved and duplicated when the molecules are reproduced.* These molecules, so typical of life, contain *information,* much as the sequence of letters in this sentence accounts for the information in the sentence. Information is transferred from cell generation to generation through DNA and from DNA to protein via RNA. The information in a protein bestows upon the molecule certain physical characteristics and the ability to catalyze (speed up) chemical reactions in cells; proteins that catalyze reactions are called **enzymes** and are fundamental to life function.

8. *In multicellular organisms, cells are organized into tissues and organs; different cells in a multicellular organism often have different structures and functions.* The tissue–organ concept is more difficult to apply to plants than to animals; but typical plant-stem tissues include, for example, epidermis, cortex, vascular tissues, and pith. The principal organs of plants include roots, stems, leaves, flowers, and fruits.

9. *Living organisms are self-generating structures.* Through the process called **development,** which includes cell divisions, cell enlargement (especially elongation in stems and roots), and cell specialization, a multicellular organism begins as a single cell (fertilized egg, the **zygote**) and eventually becomes a mature organism. Though much descriptive information is available, development is probably the least understood phenomenon of contemporary biology (about as mysterious as the functioning of the human brain).

10. *Organisms grow and develop within environments and interact with these environments and with each other in many ways.* For example, plant development is influenced by temperature, light, gravity, wind, and humidity.

11. *In living organisms, as in other machines, structure and function are intimately wedded.* Clearly, there could be no life functions without the structures of genes, enzymes, organelles, cells, and often tissues and or-

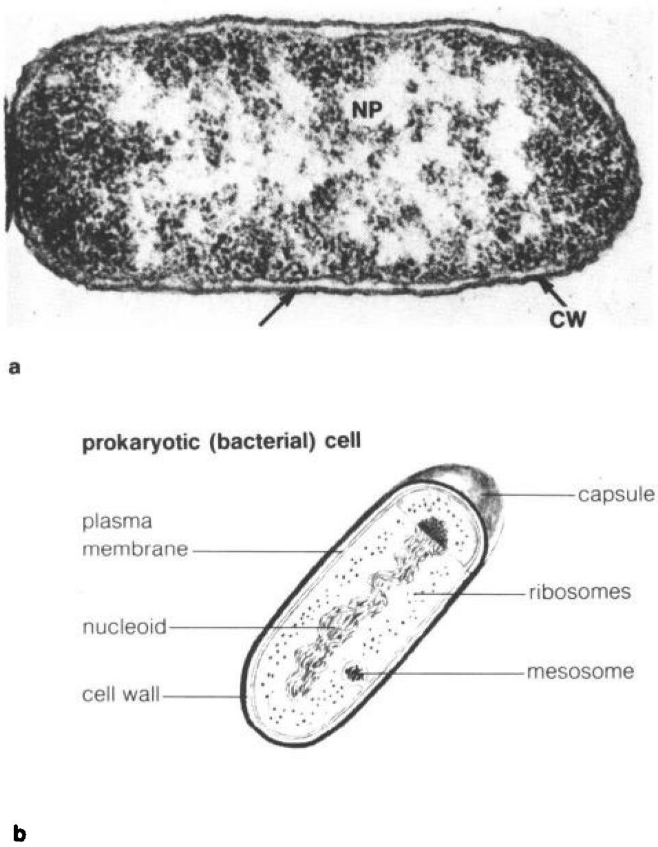

Figure P-1 (**a**) A prokaryotic cell, the bacterium *Escherichia coli*, magnified 21,500 times. The nucleoid (NP), the prokaryote equivalent of a nucleus, occupies the center of the cell. The cytoplasm surrounding the nucleus is packed with ribosomes. The cell is surrounded by the cell wall (CW): the plasma membrane (arrow) lies just beneath the cell wall. (Micrograph courtesy of William A. Jensen.) (**b**) An interpretation of a generalized prokaryotic cell. (W. A. Jensen and F. B. Salisbury, 1984, *Botany*, p. 47.)

gans. Yet the functions of growth and development create the structures. Studies in plant physiology depend strongly upon plant anatomy and **cytology** (study of cells) and also upon structural and functional chemistry. At the same time, such structural sciences as anatomy become more meaningful because of plant physiology.

P.2 Prokaryotic Cells: Bacteria and Blue-green Algae*

Membranes are the extremely thin layers of material, consisting mostly of lipids and protein, that separate cells, and most cell parts, from their surroundings. We discuss their nature in later chapters, especially Chapter 6. **Prokaryotic cells,** those of bacteria, blue-green algae (cyanobacteria), and mycoplasms, have only the surface membrane that surrounds each cell. Any membranous material found inside such cells is likely to be an inward extension of the cell membrane. **Eukaryotic cells,** on the other hand, contain several kinds of **organelles** ("little organs"), each surrounded by a single or a double membrane system.

The **nucleus** of the eukaryotic cell is surrounded by a double membrane; but the prokaryotic cell has only a central body called a **nucleoid,** which is surrounded by **cytoplasm** (all the substance enclosed by the plasma membrane and outside the nucleoid) but not by a membrane. In bacteria, the nucleoid consists of a single piece of DNA about 1 millimeter (mm) long, closed into a circle. This is the essential genetic material.

The term *prokaryotic* means "*before* a nucleus" (from the Greek) and not *without* a nucleus. Indeed, fossil prokaryotes as old as 3.3 billion years are known, whereas the oldest eukaryotic fossils are less than 1 billion years old. (*Eukaryote,* also from the Greek, means *true nucleus.*)

Prokaryotic cells are comparatively small, seldom more than a few micrometers (μm) long and only about 1 μm thick (Fig. P-1). (Metric and SI units are summarized in Appendix A.) Blue-green algae cells are usually much larger than bacterial cells. Also, all blue-green algae carry out photosynthesis with chlorophyll *a*, not found in bacteria, and by metabolic pathways common to plants and algae but not bacteria. Thus, the term *cyanobacteria,* which implies that blue-green algae are just another form of bacteria, is unfortunate.

Prokaryotic cells are surrounded by **cell walls,** usually lacking cellulose and, hence, chemically different from the typical walls of higher plants. The wall may be anywhere from 10 to 20 nanometers (nm) thick and sometimes is coated with a relatively thick, jellylike **capsule** or slime of proteinaceous material. Inside the wall, and tightly pressed against it, is the outer membrane of the prokaryotic cell, the **plasma membrane** or **plasmalemma,** which may be smooth or have infoldings that extend into the cell, forming structures called **mesosomes.** Besides controlling what enters and leaves the cells, membranes have other important functions. Many enzymatic reactions including photosynthesis and respiration take place on the proteins contained in membranes, and the plasma membranes of prokaryotes are thought to play a role in cell replication.

Small spherical bodies about 15 nm in diameter, the **ribosomes,** crowd the cytoplasm and are the sites of protein synthesis. The cytoplasm of the more complex prokaryotes may also contain **vacuoles** (sac-like structures), **vesicles** (small vacuoles), and reserve

*The rest of this prologue has been condensed and updated from W. A. Jensen and F. B. Salisbury, 1984, *Botany*, Second Edition. Wadsworth Publishing Company, Belmont, California. Chapter 3 (originally prepared by Salisbury).

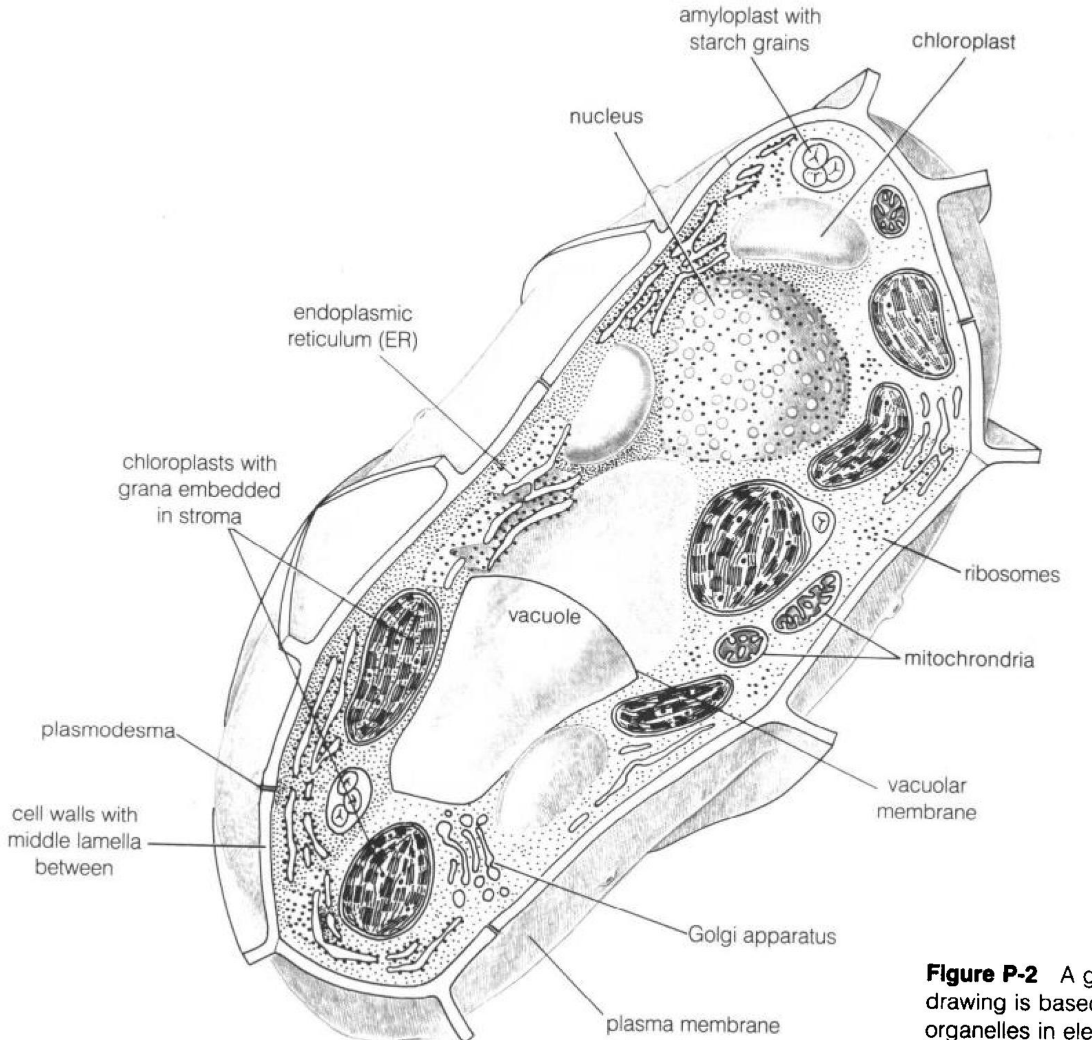

Figure P-2 A generalized plant cell. The drawing is based on the appearances of cellular organelles in electron micrographs. (W. A. Jensen and F. B. Salisbury, 1984, *Botany*, p. 46.)

Table P-2 The Components of a Prokaryotic Cell.

I. CELL WALL (with or without a capsule)
II. PLASMA MEMBRANE or PLASMALEMMA (sometimes with infoldings called mesosomes)
III. NUCLEOID (single circular strand of DNA—the genetic material)
IV. CYTOPLASM (all the substance enclosed by the plasma membrane except the nucleoid)
   1. RIBOSOMES (sites of protein synthesis)
   2. VACUOLES (saclike structures)
   3. VESICLES (small vacuoles)
   4. RESERVE DEPOSITS (complex sugars and other materials)
V. FLAGELLA (threadlike structures protruding from cell surfaces; capable of beating to cause cell movement; consist of single protein fibers)

Source: W. A. Jensen and F. B. Salisbury, 1984, *Botany*, p. 46.

deposits of complex sugars or inorganic materials. In some rare blue-green algae, the vacuoles are filled with nitrogen gas.

Many bacteria are capable of relatively rapid movement, generated by the action of threadlike structures, the **flagella**, that protrude from the cell surface. Table P-2 summarizes the structures of prokaryotic cells.

P.3 Eukaryotic Cells: Protist, Fungal, and Plant

The principal structures of prokaryotic cells are also present in eukaryotic cells, but the latter have several additional structures as well, most of them bound by membranes. A useful fiction in studying eukaryotic cells is the "typical" plant cell, illustrated in Fig. P-2 and summarized in Table P-3. There is, of course, no such thing as the typical cell or the "average teenager." Both are statistical creations, composites of features characteristic of a class but seldom found together in one individual. Nevertheless, the **parenchyma cells** (thin-walled, often isodiametric living cells) found in pith, cortex, root and shoot tips, and so forth, have most of the features of the typical plant cell. Let's begin from the outside of our typical cell and work toward the cellular inclusions. The exercise will provide a basic idea of how plants, protistans, and fungi differ at the cellular level from each other and from animals.

The Cell Wall Many protistans and virtually all fungal and plant cells are surrounded by a cell wall. Indeed no other feature is more characteristic of fungal and plant cells than the wall. All cells have membranes that enclose their contents, but animal and some protist cells have no walls—*only* membranes. Wall structures and other cell features are illustrated in Fig. P-3. Young growing cells, storage cells, the photosynthesizing cells of leaves, and some other cell types have only a **primary wall,** a wall characterized by being thin and formed while the cell is undergoing rapid growth and elongation. The cell wall surrounds the **protoplast,** which includes the plasma membrane and all that it encloses. This membrane is usually pressed tightly against the wall because of the pressure of the fluids inside. Many mature plant cells, especially those that have finished growing, have laid down a **secondary wall** between the primary wall and the cell membrane. Between the primary walls of adjacent cells is the **middle lamella** that cements the two cell walls together.

The primary cell wall Compared with an entire cell, or even with the secondary wall, the primary wall is thin, on the order of 1 to 3 μm thick. It consists of about 9 to 25 percent **cellulose.** About 30 to 40 pairs

Table P-3 The Components of a Eukaryotic Plant Cell.

I. CELL WALL*
  A. Primary wall (about ¼ cellulose); about 1 to 3 μm thick
  B. Secondary wall (½ cellulose + ¼ lignin); may be 4 μm thick or more
  C. Middle lamella (pectin-cementing layer between cells)
  D. Plasmodesmata (strands of cytoplasm penetrating wall); 40 to 100 nm thick
  E. Simple and bordered pits

II. PROTOPLAST (contents of the cell exclusive of the cell wall); 10 to 100 μm diameter
  A. Cytoplasm (cytoplasm + nucleus = protoplasm)
    1. Plasma membrane (plasmalemma); 0.0075 μm (7.5 nm) thick
    2. Vacuolar membrane (tonoplast); 7.5 nm thick
    3. Microtubules; 18 to 27 nm thick
    4. Microfilaments; 5 to 7 nm thick
    5. Endoplasmic reticulum (ER); 7.5 nm thick (each membrane)
    6. Ribosomes; about 15 to 25 nm diameter
    7. Golgi bodies (dictyosomes); 0.5 to 2.0 μm diameter
    8. Mitochondria; 0.5 to 1.0 by 1 to 4 μm
    9. Plastids†
      a. Proplastids (immature plastids)
      b. Leucoplasts (colorless plastids)
      c. Amyloplasts (contain starch grains) and other food-storage plastids
      d. Chloroplasts; 2 to 4 μm thick by 5 to 10 μm diameter (may also contain starch grains)
      e. Chromoplasts (colored plastids other than chloroplasts; often red, orange, yellow, etc.)
    10. Microbodies; 0.3 to 1.5 μm diameter
    11. Spherosomes; 0.5 to 2.0 μm diameter
    12. Cytosol
  B. Nucleus (cytoplasm + nucleus = protoplasm)
    1. Nuclear envelope (double membrane); 20 to 50 nm thick
    2. Nucleoplasm (granular and fibrillar substance of nucleus)
    3. Chromatin (chromosomes become apparent during cell division)
    4. Nucleolus; 3 to 5 μm
  C. Vacuoles (up to 95% of cell volume or more)
  D. Ergastic substances (inclusions of relatively pure materials, often in plastids)*
    1. Crystals (such as calcium oxalate)
    2. Tannins †
    3. Fats and oils
    4. Starch grains (in amyloplasts and chloroplasts, see above)†
    5. Protein bodies
  E. Flagella and cilia; 0.2 μm thick, 2 to 150 μm long

*Occur in fungal, plant, and some protistan cells but seldom in animals.
†Occur only in plant cells and some protistans.

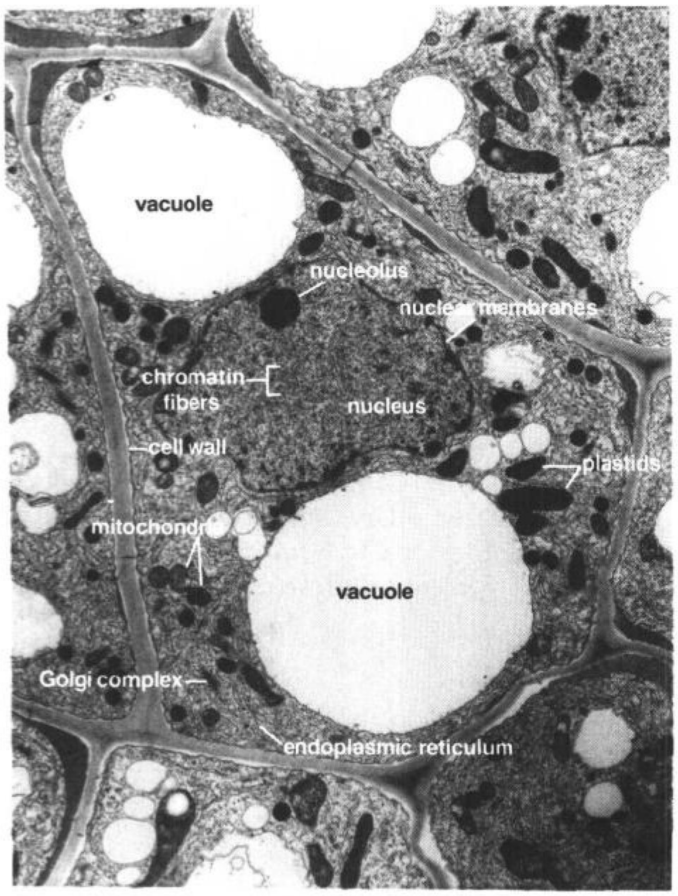

Figure P-3 An electron micrograph of a cell from the developing fruit of cotton, showing cell walls and other cell parts. The cell wall is conspicuous in this photograph, and the middle lamella can be seen joining the walls of adjacent cells (especially at the corners). The nucleus shows some DNA-protein (genetic material or chromatin) just inside the nuclear membranes, and a prominent nucleolus. Two large vacuoles take up much of the cell volume, but not as much as in more mature plant cells, especially those in stems and roots. Also visible in the cell are plastids, mitochondria, parts of the endoplasmic reticulum, and at least one faint Golgi body. (Micrograph by William A. Jensen and Paula Stetler.)

of long, unbranched cellulose molecules form a long cylindrical fiber called a **microfibril.** Recent data suggest that microfibrils are about 3.5 nm thick (Fig. P-4). Because of the parallel arrangement of the cellulose molecules, microfibrils behave like crystals and have as much tensile strength, for their weight, as steel wires in a cable.

The microfibrils are laid down roughly at right angles to the long axis of the cell. They are like hoops around the *inside* of a barrel. As the cell elongates, the microfibrils slip past each other and are pulled into the long axis of the cell (discussed in Chapter 15). Since the most recent microfibrils to be deposited are still laid down predominantly parallel to the circumference, the microfibrils cross each other almost as threads in cloth (but do not go over and under each other as do woven threads).

The cellulose microfibrils are embedded in a **matrix** of other materials, which are chemically much more complex. Principal among these are the **hemicelluloses,** which form a branching, molecular network filled with water. A typical primary wall may contain 25 to 50 percent hemicelluloses. Closely related are the **pectic substances,** which make up 10 to 35 percent of a primary wall. Primary walls also usually have about 10 percent protein. The matrix materials of the primary wall are not crystalline like cellulose, so the matrix cannot be seen in Fig. P-5; it was dissolved away to make the microfibrils more visible (also see Fig. 6-11). The primary wall is admirably adapted to growth. In response to growth-regulating chemicals, it softens in some way so the microfibrils can slide past each other in the water-filled matrix (Chapter 16). This sliding occurs as the protoplast absorbs water, expanding like a balloon and creating pressure against the wall. Thus the wall stretches **plastically** (irreversibly, like bubble gum) rather than **elastically** (like a rubber balloon) as the cell grows. Some primary walls increase their area as much as 20 times during growth.

When the cell is not growing, even the primary wall resists stretching, thanks to the high tensile strength of its cellulose microfibrils, which can't slip past each other. Yet the wall is porous enough to allow the free passage of water and materials dissolved in the water. The pore diameters are about 3.5 to 5.2 nm (Carpita et al., 1979; Carpita, 1982) compared with about 0.3 nm diameter for a water molecule and about 1 nm for a sugar molecule.

Imagine a cotton (mostly cellulose) cloth bag with a water-filled balloon inside. The cloth is porous, freely allowing the passage of water and materials dissolved in the water. It also has tensile strength, resisting stretching as one tries to force more water into the balloon. Yet it collapses when the water is released from the balloon. Likewise, if the cell loses water and hence its hydraulic pressure, the primary cell wall collapses (although not as much as a cotton bag). Leaves and young stems are made of cells that have mostly primary walls. They are rigid while the fluid in their cells pushes against their walls, but they wilt when enough water is lost to decrease the internal pressure (Fig. P-6).

The secondary cell wall In many plant cells, especially those that will provide support for the plant or will be involved in the conduction of fluids under tension (negative pressure), the protoplast begins to secrete a