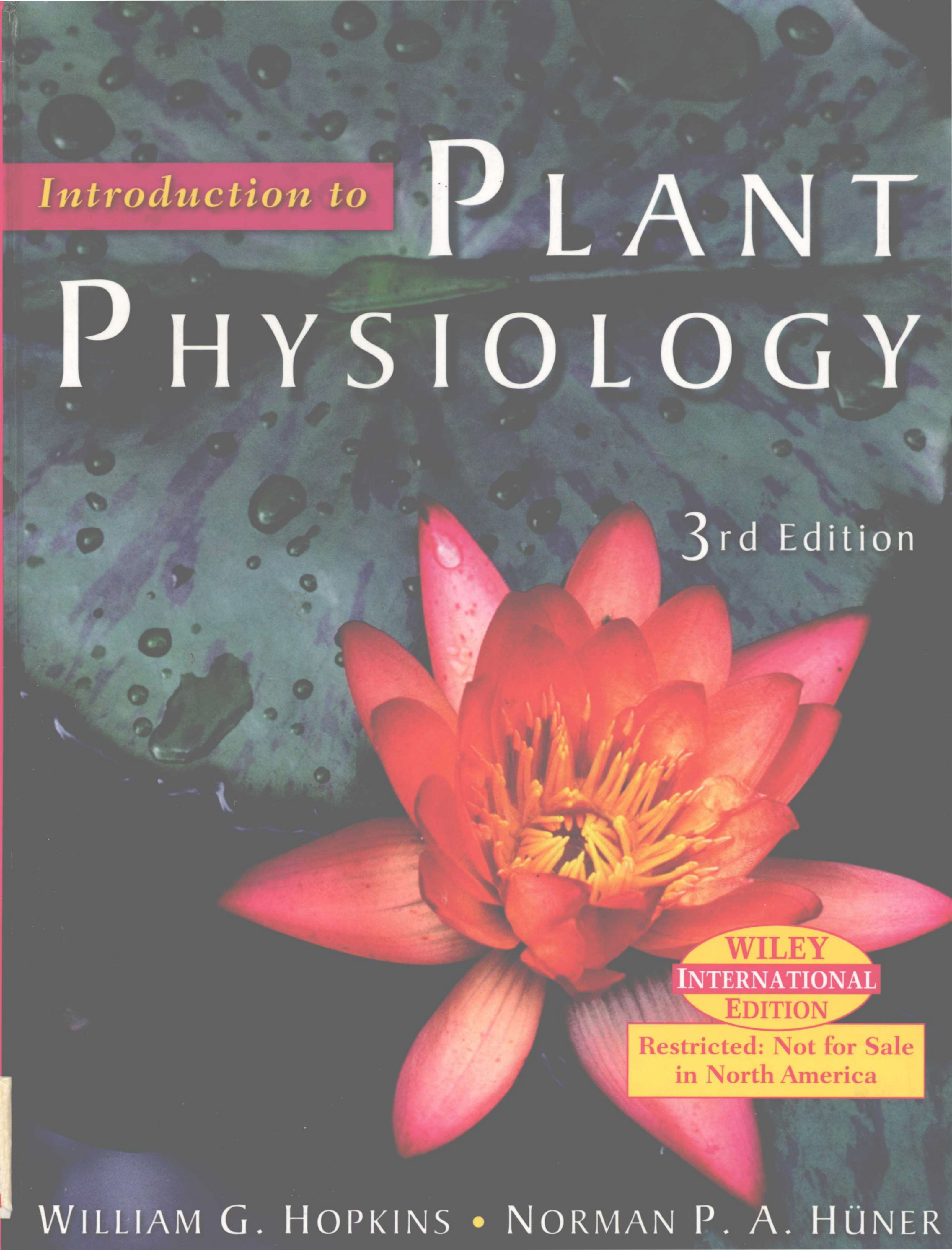

Introduction to

PLANT PHYSIOLOGY

3rd Edition

WILEY INTERNATIONAL EDITION
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WILLIAM G. HOPKINS • NORMAN P. A. HÜNER

Introduction to Plant Physiology

Third Edition

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and
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The University of Western Ontario

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Preface

This third edition of *INTRODUCTION TO PLANT PHYSIOLOGY* is, like its predecessors, intended as a textbook for undergraduate students encountering plant physiology for the first time. Its purpose is to help students gain a solid foundation in fundamental concepts of plant physiology and to illustrate how those concepts are supported by evidence from physiological, biochemical, biophysical, molecular, and genomic experiments.

The text assumes that the student has completed a first course in botany (or biology with a strong botanical component) and chemistry. It is appropriate for a one-semester course in plant physiology for general students, and as an introduction for those who will go on to advanced studies in agonomy, plant physiology, environmental plant physiology, or physiological plant ecology.

Users of the two prior editions will find familiar ground as well as significant changes. In this edition, we have retained both the emphasis on "whole plant" physiology and the epistemological approach, or how we know what we think we know. Modern textbooks, in an effort to present all the latest information in the field, often fall short in the presentation of the scientific process. However, rather than simply cataloging the current state of our knowledge, we have focused on ideas and experimental approaches. We have attempted to illustrate how we arrived at our present level of understanding, where there is significant uncertainty, and where we might be headed in the future. Finally, by interpreting laboratory studies in the context of environmental physiology, we hope to show students how plants work in the real world.

The organization of the third edition differs significantly from the earlier two editions. Part 1 (Chaps. 2–9) begins with an introduction to the principles of bioenergetics and discusses energy metabolism and the assimilation of carbon and nitrogen. Cell and plant water relations and the uptake of mineral nutrients are covered in Part 2 (Chaps. 10–13). Plant growth and development and their control by hormones, light, and temperature are the subject of Part 3 (Chaps. 14–20). In Part 4 (Chaps. 21–22), we discuss the physiology and biochemistry of plant acclimation to environmental and biotic stress. In Part 5 we review the significant potential for plant physiology in modern biotechnology. We believe that this organization represents a logical flow of concepts and information essential to an understanding of plant form and function. We want to help the student understand the importance of sunlight as the ultimate source of energy for the biosphere and to underscore the critical dependence of water relations, growth and development, and metabolism on the fundamental principles of energy flow.

We begin with an introductory chapter that provides an overview of the plant cell. The emphasis is on the principal macromolecules that serve as building blocks for cells, followed by cell structure and the organization of cells into tissue and organ systems. This chapter is intended as an introduction and review, touching on the terminology of botany and cell biology that provides a foundation for the discussions that follow. Chapter 2 summarizes the general principles of bioenergetics, which are used throughout the book. Since light is the ultimate source of energy to sustain life on Earth, we discuss the physical nature of sunlight in Chapter 3 with an emphasis on the dual role of sunlight—as both a source of energy and information to the plant with respect to its environment. Chapters 4 to 7 deal with energy trapping, energy utilization in the biosynthesis of carbohydrates, and the subsequent allocation and partitioning of carbohydrate throughout the plant. An underlying theme of these chapters is the notion of the leaf as a photosynthetic "green machine." In addition, we have added discussions of recent advances in our understanding of metabolic feedback regulation, photoinhibition, and photoprotection. These chapters are followed by a discussion of carbon oxidation processes (Chapter 7) which release the stored energy for use in growth and development. We have chosen to integrate the chapter on nitrogen assimilation (Chapter 8) with the chapters on photosynthesis and carbon metabolism. Our rationale for this is based on the fact that N-assimilation is dependent on photosynthesis and respiration as the sources of both reducing potential for nitrogen fixation and carbon skeletons for the biosynthesis of amino acids. Part I ends with a discussion of the role that these metabolic processes play in regulating plant productivity (Chapter 9).

For this edition, many arguments have been rewritten in order to clarify their presentation. As well, many topics have been expanded and new concepts introduced. In Chapter 1, the biochemistry of lipids, proteins, and carbohydrates has been integrated into the text in order to better reflect the significance of these macromolecules as fundamental cellular building blocks. A description of ubitquitin, proteosomes, and the processing of proteins has been added to the chapter on patterns in plant development. The treatment of hormones has been revised. Their biochemistry and metabolism are treated in one chapter in order to better compare biochemical origins and metabolic relationships. The second chapter reviews hormonal control of development. This chapter emphasizes the interactive roles of hormones in the control of specific developmental processes, such as seed germination, stem elongation, and flowering. A Box describing the cell cycle and control of cell division has been added to Chapter 16, and the text has been revised to reflect what is known about the interactions of cytokinins with the cell cycle.

The chapter on stress physiology has been revised to reflect growing interest in ecophysiology and includes a discussion of recent advances in the molecular biology of plant stress tolerance, a very active area of research in plant biology with important implications with respect to agricultural productivity and a sustainable environment. We have added two new boxes to this chapter. One box describes the theory and use of chlorophyll fluorescence, an increasingly important tool for assessing plant stress and acclimation. The other box compares plant adaptation and acclimation to two distinct and important biomes, deserts and rainforests. Overall, this chapter integrates many of the basic concepts that are developed in early chapters in order to illustrate how plants adjust to an ever changing environment.

In order to enhance the flow of ideas and concepts, we have avoided the use of literature citations in the text. At the end of each chapter is a list of recommended readings, through which students may access the primary literature.

We are grateful to the many colleagues who have generously provided photographs or who have consented to have their work included in this book. Finally, we acknowledge our debt to the many students who, over the years, have contributed far more to this book than they might ever know. In the end, of course, responsibility for any omissions or errors is ours alone.

William G. Hopkins
Norman P. A. Hüner
London, Ontario
January, 2003

To the Student

This book is about how plants work. It is about the questions that plant physiologists ask and how they go about seeking answers to those questions. Most of all, it is about how plants do the things they do in their everyday life.

In spite of its presumed objectivity, science ultimately relies on the interpretation of experimental results by scientists—interpretations that are often found to be inadequate and filled with uncertainty. However, as results and observations accumulate, interpretations are refined and the degree of uncertainty diminishes. This is the nature of scientific discovery and source of the real excitement of doing science. In this book, we have attempted to convey some sense of this scientific process.

The book contains several pedagogic features that are intended to assist your learning. New terms and concepts are identified with boldfaced type. Some of these terms may be boldfaced when encountered a second time, for emphasis. You should attempt to understand each boldfaced term—what it means and its significance to the problem under discussion.

Each chapter concludes with a Summary, which attempts to highlight the principal topics discussed in that chapter. There is also a series of review questions called Chapter Review. For many of these questions, there is no single or simple answer. The questions are intended as a guide to your review of the chapter and, perhaps, as a stimulus to help you integrate diverse aspects or to extend what you have learned to new situations.

At the end of each chapter, however, we provide a selection of further readings. Some of these readings are reports of research results and some are review articles or opinion. If you find a particular topic interesting and wish to learn more about it, the listed publications are your gateway into the relevant primary research literature. Plant physiology is a very active field of study and new revelations about how plants work are reported in the literature almost daily. To learn what has happened since this book was written, seek out recent publications in the same journals cited in the reference lists. Many of the listed journals publish review articles that summarize the status of a topic up to that point.

We hope that, through this book, we are able to share with you some of our fascination with the excitement, mystery, and challenge of plant physiology.

William G. Hopkins
Norman P. A. Hüner

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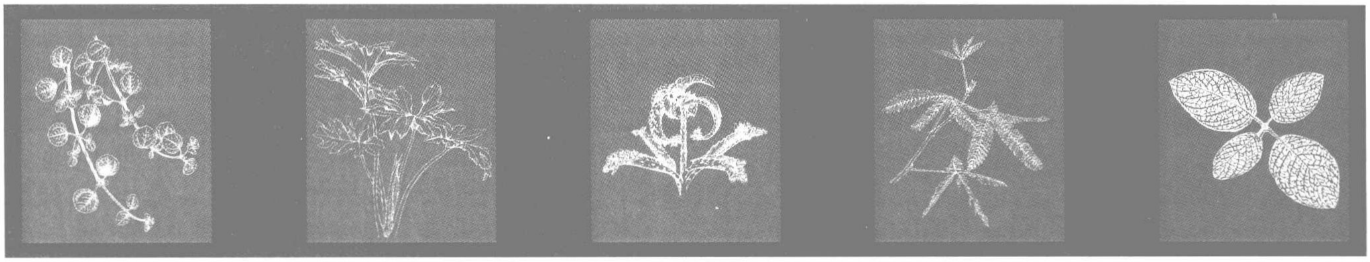

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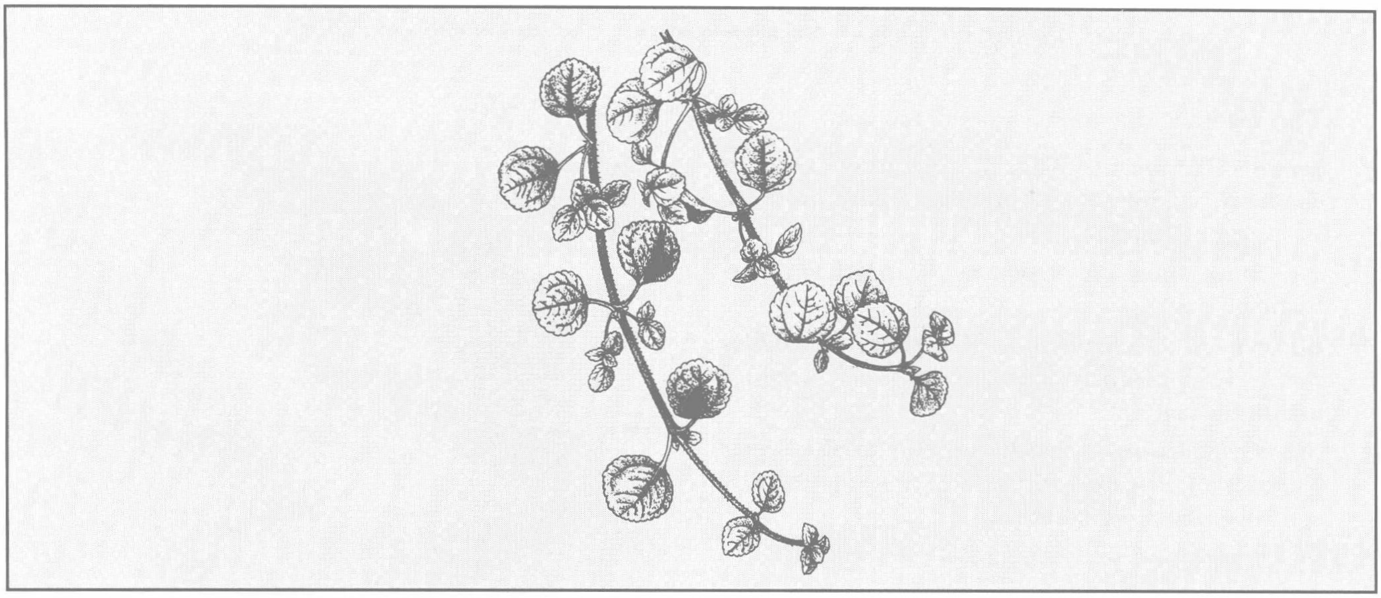

1

Cells, Tissues, and Organs: The Architecture of Plants

The term **physiology** is constructed from the Greek words *physis*, meaning nature, and *logos*, meaning discourse. Taken literally, then, plant physiology is a discourse about the nature of plants. This is a rather broad mandate, encompassing virtually everything within the realm of botany. For good reason, plant physiologists have traditionally taken a more limited, more mechanistic approach to the study of plants. From the physiological perspective, plants are viewed primarily as biochemical machines; machines that take in simple inorganic molecules and energy from their surrounding environment and use them to assemble complex chemical structures. The processes that enable plants to carry out these activities are themselves the sum of a multitude of coordinated chemical reactions. Ultimately, everything that plants are and everything that they do are based on chemical and physical processes.

Plant physiology is about how plants use the energy of the sun to assimilate carbon, and how they convert that carbon to the stuff of which they are made. It is about how plants obtain and distribute nutrients and water, how they grow and develop, how they respond to their environment, how they react to stress, and how they reproduce. In short, plant physiology is about how plants work. To this end, plant physiologists apply the tools of chemistry, biochemistry, physics, molecular biology, genetics, and a variety of other subdisciplines of science in order to explain plant functions in terms of known chemical, physical, and biological laws.

How plants work, however, cannot be separated from the way plants are built. In biology, form and function are inseparable. For example, the anatomy and morphology of stems and leaves closely reflect their respective functions of support and transport, on the one hand, or photosynthesis on the other hand. This means that in order to understand the physiology of plants, it is also necessary to have some understanding of plant structure and to be conversant with some of the terminology involved.

As with all living organisms, the smallest functional unit of a plant is the cell. Indeed, the study of plant physiology is very much a study of the physiology of plant cells and how their coordinated activities are reflected in the physiology of the whole organism. In a similar fashion, the morphology, or form, of a plant reflects the number, morphology, and arrangement of its individual cells. Cells, in turn, are an assembly of a vast number and array of biochemicals, many of which are indispensable building blocks used in the structure of cells.

The purpose of this chapter is to introduce the essential features of plant cell structure, beginning with the primary biochemical building blocks, and show how cells are organized into the principal tissue systems and organs of plants.

This introduction and review will include

- in general terms, the essential structures of the biochemical building blocks of cells—lipids, proteins, and carbohydrates;
- the composition and structure of biological membranes;
- the general characteristics of cellular organelles that serve to compartmentalize metabolic activities within the cell;
- the cytoskeleton—a fibrous protein network that provides a framework for cellular organization and controls cellular dynamics;
- the composition and structure of cell walls; and
- the major tissue and organ systems of flowering plants.

1.1 THE PLANT CELL

Although plants, like all multicellular organisms, exhibit a wide variation in cellular morphology and function, these disparate cells are, in fact, remarkably alike. All cells are built according to a common basic plan and at least start out with the same fundamental structures. In its simplest form, a cell is an aqueous solution of chemicals called **protoplasm** surrounded by a **plasma membrane**. The membrane and the protoplasm it contains are collectively referred to as a **protoplast**. Of course, all of the components that make up protoplasm have important roles to play in the life of a cell, but the plasma membrane is particularly significant because it represents the boundary between the living and nonliving worlds. The plasma membrane is also **selectively permeable**, which means that it allows some materials to pass through but not others. The plasma membrane thus not only physically defines the limits of a cell, it also controls the exchange of material and serves to maintain essential differences between the cell and its environment. The plant protoplast is, in turn, surrounded by a **cell wall**. The cell wall defines the shape of the cell and, through adhesion to the walls of adjacent cells, provides support for the plant as a whole.

In an electron micrograph (an image seen through the electron microscope), membranes are a singularly prominent feature (Figs. 1.1, 1.2). In addition to the plasma membrane, other membranes are found throughout the protoplast where they form a variety of subcellular structures called **organelles** ("little organs"). Organelles serve to compartmentalize major metabolic activities within the cell, much in the same way that an automobile factory is set up for metal fabrication, paint shop, assembly line, and so forth. One of these organelles, the **nucleus**, contains the genetic information and is the control center of the cell. The nucleus and its

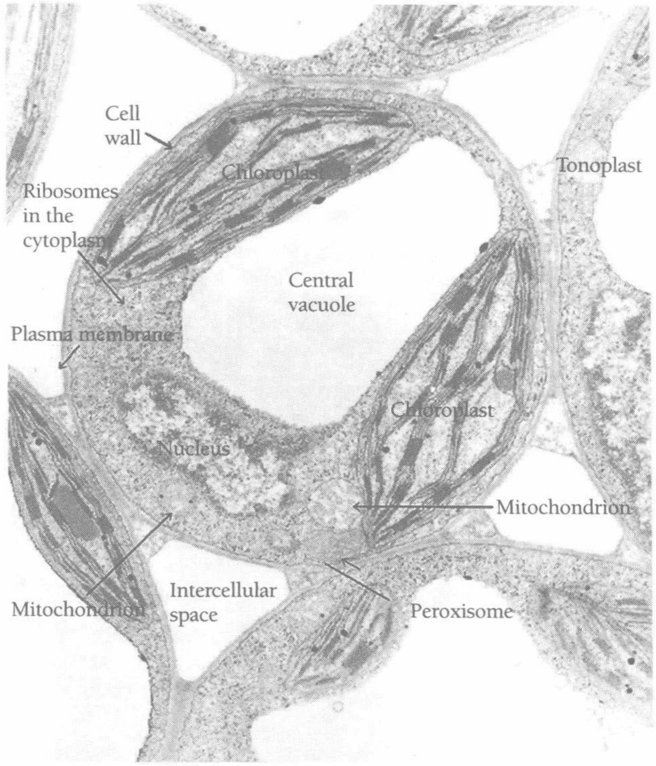

FIGURE 1.1 The plant cell. A mature mesophyll cell from a *Coleus* leaf, as seen in the electron microscope. Note the prominent large central vacuole and chloroplasts. (Electron micrograph by Wm. P. Wergin, courtesy of E. H. Newcomb, University of Wisconsin–Madison.)

contents are known as **nucleoplasm**. The balance of the protoplasm, excluding the nucleus but including other organelles, is called **cytoplasm**. Different organelles in the cytoplasm contain the enzymes and other machinery for cellular respiration, photosynthesis, protein synthesis, secretion, and so forth. The remaining portion of the cytoplasm, not including membrane-bound organelles, is referred to as the **cytosol**. The cytosol may comprise as much as half the cytoplasm in the cell and is the principal site of protein synthesis and much of the **intermediary metabolism**—the complex series of reactions by which small molecules are degraded and reassembled to provide precursors for the larger building blocks of the cell.

1.2 BUILDING BLOCKS: LIPIDS, PROTEINS, AND CARBOHYDRATES

Green plants, along with a few bacteria, stand alone in the world in their ability to use the energy of the sun to synthesize simple sugars from carbon dioxide and water. Through subsequent metabolic conversions, the glucose is converted to other small organic molecules, such