

Introduction to

PLANT PHYSIOLOGY

3rd Edition

WILEY
INTERNATIONAL
EDITION

**Restricted: Not for Sale
in North America**

WILLIAM G. HOPKINS • NORMAN P. A. HÜNER

Introduction to Plant Physiology

Third Edition

William G. Hopkins
and
Norman P. A. Hüner

The University of Western Ontario




WILEY

John Wiley & Sons, Inc.

ACQUISITIONS EDITOR *Keri Witman*
MARKETING MANAGER *Clay Stone*
SENIOR PRODUCTION EDITOR *Valerie A. Vargas*
SENIOR DESIGNER *Karin Gerdes Kincheloe*

Cover credit: © Stuart Westmorland/The Image Bank/Getty Images

This book was set in 10/12 Janson Text by UG / GGS Information Services, Inc. and printed and bound by Courier/Westford. The cover was printed by Phoenix Color.

This book is printed on acid free paper. 

Copyright © 2004 John Wiley & Sons, Inc. All rights reserved.

No part of this publication may be reproduced, stored in a retrieval system or transmitted in any form or by any means, electronic, mechanical, photocopying, recording, scanning or otherwise, except as permitted under Sections 107 or 108 of the 1976 United States Copyright Act, without either the prior written permission of the Publisher, or authorization through payment of the appropriate per-copy fee to the Copyright Clearance Center, Inc. 222 Rosewood Drive, Danvers, MA 01923, (508) 750-8400, fax (508) 750-4470. Requests to the Publisher for permission should be addressed to the Permissions Department, John Wiley & Sons, Inc., 111 River Street, Hoboken, NJ 07030, (201) 748-6011, fax (201) 748-6008, E-Mail: PERMREQ@WILEY.COM. To order books or for customer service please call 1-800-CALL WILEY (225-5945).

ISBN 0-471-38915-3

ISBN 0-471-37917-4 (WIE)

Printed in the United States of America

10 9 8 7 6 5 4 3 2 1

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 agronomy, 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 understand-

ing 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 ubiquitin, 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

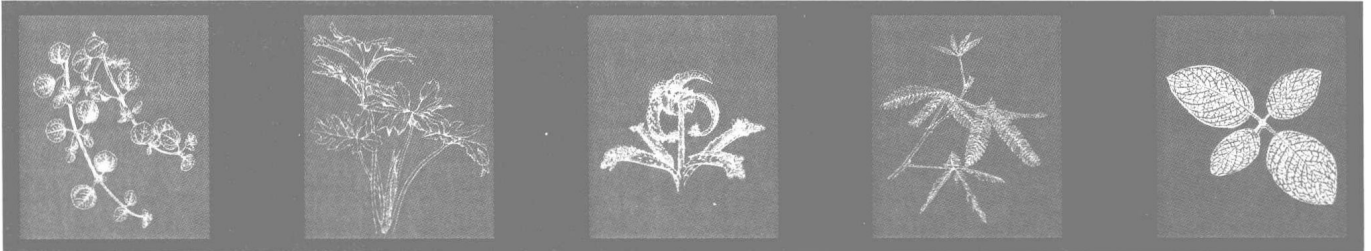
Chapter Review. For many of these questions, there is no single or simple answer. The questions are intended as a guide to your review of the chapter and, perhaps, as a stimulus to help you integrate diverse aspects or to extend what you have learned to new situations.

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

Contents



Chapter 1 • Cells, Tissues, and Organs: The Architecture of Plants 1

1.1 The Plant Cell 2

1.2 Building Blocks: Lipids, Proteins, and Carbohydrates 2

- 1.2.1 Lipids Are a Class of Molecules That Includes Fats, Oils, Sterols, and Pigments 4
- 1.2.2 Proteins Play a Central Role in the Biochemistry of Cells and Are Responsible for Virtually All the Properties of Life as We Know it 6
- 1.2.3 Carbohydrates Are the Most Abundant Class of Biological Molecules 8

1.3 Biological Membranes 11

- 1.3.1 The Membrane Lipid Forms a Bilayer, a Highly Fluid but Very Stable Structure 11
- 1.3.2 Membranes Contain Significant Amounts of Protein 12

1.4 Cellular Organelles 13

- 1.4.1 Most Mature Plant Cells Contain a Large, Central Vacuole 13
- 1.4.2 The Nucleus Is the Information Center of the Cell 13
- 1.4.3 The Endoplasmic Reticulum and Golgi Apparatus Are Centers of Membrane Biosynthesis and Secretory Activities 14
- 1.4.4 The Mitochondrion Is the Principal Site of Cellular Respiration 15
- 1.4.5 Plastids Are a Family of Organelles with a Variety of Functions 15
- 1.4.6 Microbodies Are Metabolically Very Active 16

1.5 Cytoskeleton 16

1.6 The Extracellular Matrix 17

- 1.6.1 The Primary Cell Wall Is a Flexible Network of Cellulose Microfibrils and Cross-Linking Glycans 17
- 1.6.2 The Cellulose–Glycan Lattice is Embedded in a Matrix of Pectin and Protein 19
- 1.6.3 Cellulose Microfibrils Are Assembled at the Plasma Membrane as They Are Extruded into the Cell Wall 20

- 1.6.4 The Secondary Cell Wall Is Deposited on the Inside of the Primary Wall in Maturing Cells 21
- 1.6.5 Plasmadesmata Are Cytoplasmic Channels Extend Through the Wall to Connect the Protoplasts of Adjacent Cells 21

1.7 Tissues and Organs 22

- 1.7.1 Tissues Are Groups of Cells That Form an Organized, Functional Unit 22
- 1.7.2 Meristems Are Regions of Perpetually Dividing Cells 22
- 1.7.3 Parenchyma Is the Most Abundant Living Tissue in Plants 24
- 1.7.4 Supporting Tissues Are Distributed Throughout the Primary and Secondary Plant Bodies 24
- 1.7.5 Vascular Tissues Are the Principal Conducting Tissues for Water and Nutrients 25
- 1.7.6 Epidermis Is a Superficial Tissue That Forms a Continuous Layer over the Surface of the Primary Plant Body 25

1.8 Plant Organs 26

- 1.8.1 Roots Anchor the Plant and Absorb Water and Minerals from the Soil 26
- 1.8.2 Stems Elevate the Photosynthetic Organs, the Leaves, Toward the Sun 26
- 1.8.3 Leaves Are the Principal Photosynthetic Organs 27

Summary 27

Chapter Review 28

Further Reading 28

Part 1 • Plants and Energy 29

Chapter 2 • Bioenergetics and ATP Synthesis 31

2.1 Bioenergetics and Energy Transformations in Living Organisms 31

- 2.1.1 The Sun Is a Primary Source of Energy 31
 - 2.1.2 What Is Bioenergetics? 32
-

- 2.1.3 The First Law of Thermodynamics Refers to Energy Conservation 32
- 2.1.4 The Second Law of Thermodynamics Refers to Entropy and Disorder 33
- 2.1.5 The Ability to Do Work is Dependent on the Availability of Free Energy 33
- 2.1.6 Free Energy Is Related to Chemical Equilibria 34
- 2.2 Energy Transformations and Coupled Reactions 35**
 - 2.2.1 Free Energy of ATP Is Associated with Coupled Phosphate Transfer Reactions 35
 - 2.2.2 Free Energy Changes Are Associated with Coupled Oxidation-Reduction Reactions 36
- 2.3 Energy Transduction and the Chemiosmotic Synthesis of ATP 39**
 - 2.3.1 Chloroplasts and Mitochondria Exhibit Specific Compartments 39
 - 2.3.2 Chloroplasts and Mitochondria Synthesize ATP by Chemiosmosis 41
 - Summary 43*
 - Chapter Review 43*
 - Further Reading 43*

Chapter 3 • The Dual Role of Sunlight: Energy and Information 45

- 3.1 The Physical Nature of Light 45**
 - 3.1.1 Light Is Electromagnetic Energy Which Exists in Two Forms 45
 - 3.1.2 Light Can Be Characterized as a Wave Phenomenon 46
 - 3.1.3 Light Can Be Characterized as a Stream of Discrete Particles 46
 - 3.1.4 Light Energy Can Interact with Matter 47
 - 3.1.5 How Does One Illustrate the Efficiency of Light Absorption and Its Physiological Effects 49
 - 3.1.6 Accurate Measurement of Light Is Important in Photobiology 50
- 3.2 The Natural Radiation Environment 51**
- 3.3 Photoreceptors Absorb Light for Use in a Physiological Process 52**
 - 3.3.1 Chlorophylls Are Primarily Responsible for Harvesting Light Energy for Photosynthesis 52
 - 3.3.2 Pycobilins Serve as Accessory Light-Harvesting Pigments in the Red Algae and Cyanobacteria or as a Critical Regulatory System in Green Plants 54
 - 3.3.3 Carotenoids Account for the Autumn Colors 55
 - 3.3.4 Cryptochrome Is a Photoreceptor Sensitive to Blue and UV-A Light 57
 - 3.3.5 UV-B Radiation May Act as a Developmental Signal 57
 - 3.3.6 Flavonoids Provide the Myriad of Flower Colors and Act as a Natural Sunscreen 58
 - 3.3.7 Betacyanins and Beets 60
 - Summary 60*
 - Chapter Review 61*
 - Further Reading 61*

Chapter 4 • Energy Conservation in Photosynthesis: Harvesting Sunlight 63

- 4.1 Leaves Are Photosynthetic Machines Which Maximize the Absorption of Light 64**

- 4.2 Photosynthesis Is an Oxidation-Reduction Process 66**
- 4.3 Photosynthetic Electron Transport 68**
 - 4.3.1 Photosystems Are Major Components of the Photosynthetic Electron Transport Chain 68
 - 4.3.2 Photosystem II Oxidizes Water to Produce Oxygen 71
 - 4.3.3 The Cytochrome Complex and Photosystem I Oxidize Plastoquinol 72
- 4.4 Photophosphorylation Is the Light-Dependent Synthesis of ATP 73**
- 4.5 Lateral Heterogeneity Is the Unequal Distribution of Thylakoid Complexes 75**
- 4.6 Light-Harvesting Complexes Are Superantenna Complexes that Regulate Energy Distribution 76**
- 4.7 Photoinhibition of Photosynthesis: Photoprotection versus Photodamage 78**
 - 4.7.1 Carotenoids Serve a Dual Function: Light Harvesting and Photoprotection 78
 - 4.7.2 Oxygen May Protect against Photoinhibition by Acting as an Alternative Electron Acceptor 80
 - 4.7.3 The D1 Repair Cycle Overcomes Photodamage to PSII 82
- 4.8 Inhibitors of Photosynthetic Electron Transport Are Effective Herbicides 83**
 - Summary 86*
 - Chapter Review 86*
 - Further Reading 87*

Box 4.1 • Historical Perspective—The Discovery of Photosynthesis 66

Box 4.2 • The Case for Two Photosystems 84

Chapter 5 • Energy Conservation in Photosynthesis: CO₂ Assimilation 89

- 5.1 Stomatal Complex Controls Leaf Gas Exchange and Water Loss 90**
- 5.2 CO₂ Enters the Leaf by Diffusion 92**
- 5.3 How Do Stomata Open and Close? 94**
- 5.4 Stomatal Movements Are Also Controlled By External Environmental Factors 96**
 - 5.4.1 Light and Carbon Dioxide Regulate Stomatal Opening 96
 - 5.4.2 Water Status and Temperature Influence Stomatal Opening 98
 - 5.4.3 Stomatal Movements Follow Endogenous Rhythms 98
- 5.5 The Photosynthetic Carbon Reduction (PCR) Cycle 98**
 - 5.5.1 The PCR Cycle Reduces CO₂ to Produce a 3-Carbon Sugar 98
 - 5.5.2 The Carboxylation Reaction Fixes the CO₂ 99
 - 5.5.3 ATP and NADPH Are Consumed in the PCR Cycle 102
 - 5.5.4 What Are the Energetics of the PCR Cycle? 102
- 5.6 The PCR Cycle Is Highly Regulated 102**
 - 5.6.1 The Regeneration of RuBP Is Autocatalytic 102
 - 5.6.2 Rubisco Activity Is Regulated Indirectly by Light 103
 - 5.6.3 Other PCR Enzymes Are also Regulated by Light 104

- 5.7 **Chloroplasts of C3 Plants also Exhibit Competing Carbon Oxidation Processes** 104
 - 5.7.1 Rubisco Catalyzes the Fixation of Both CO₂ and O₂ 105
 - 5.7.2 Why Photorespiration? 106
 - 5.7.3 In Addition to PCR, Chloroplasts Exhibit an Oxidative Pentose Phosphate Cycle (OPPC) 108
- 5.8 **The C4 Syndrome: Another Biochemical Mechanism to Assimilate CO₂** 108
- 5.9 **The C4 Syndrome Is Usually Associated with Kranz Leaf Anatomy** 112
- 5.10 **The C4 Syndrome Has Ecological Significance** 112
 - 5.10.1 The C4 Syndrome Is Differentially Sensitive to Temperature 113
 - 5.10.2 The C4 Syndrome Is Associated with Water Stress 113
- 5.11 **Crassulacean Acid Metabolism (CAM): An Adaptation to Life in the Desert** 115
 - 5.11.1 Is CAM a Variation of the C4 Syndrome? 115
 - 5.11.2 CAM Plants Are Particularly Suited to Dry Habitats 115
- 5.12 **C4 and CAM Photosynthesis Require Precise Regulation and Temporal Integration** 117
 - Summary* 121
 - Chapter Review* 122
 - Further Reading* 122

Box 5.1 • Enzymes 118

Chapter 6 • Allocation, Translocation, and Partitioning of Photoassimilates 123

- 6.1 **Starch and Sucrose Are Biosynthesized in Two Different Compartments** 124
 - 6.1.1 Starch Is Biosynthesized in the Stroma 124
 - 6.1.2 Sucrose Is Biosynthesized in the Cytosol 125
- 6.2 **Starch and Sucrose Biosynthesis Are Competitive Processes** 126
- 6.3 **Photoassimilates Are Translocated over Long Distances** 128
 - 6.3.1 What Is the Composition of the Photoassimilate Translocated by the Phloem? 129
- 6.4 **Sieve Elements Are the Principal Cellular Constituents of the Phloem** 131
 - 6.4.1 Phloem Exudate Contains a Significant Amount of Protein 132
- 6.5 **Direction of Translocation Is Determined by Source-Sink Relationships** 133
- 6.6 **Phloem Translocation Occurs by Mass Transfer** 133
- 6.7 **Phloem Loading and Unloading Regulate Translocation and Partitioning** 136
 - 6.7.1 Phloem Loading Can Occur Symplastically or Apoplastically 136
 - 6.7.2 Phloem Unloading May Occur Symplastically or Apoplastically 138
- 6.8 **Photoassimilate Is Distributed Between Different Metabolic Pathways and Plant Organs** 139
 - 6.8.1 Photoassimilates May Be Allocated to a Variety of Metabolic Functions in the Source or the Sink 140

- 6.8.2 Distribution of Photoassimilates Between Competing Sinks Is Determined By Sink Strength 141

6.9 **Xenobiotic Agrochemicals Are Translocated in the Phloem** 143

- Summary* 144
- Chapter Review* 144
- Further Reading* 144

Chapter 7 • Cellular Respiration: Unlocking the Energy Stored in Photoassimilates 145

- 7.1 **Cellular Respiration Consists of a Series of Pathways by Which Photoassimilates Are Oxidized** 146
- 7.2 **Sucrose and Starch Are Broken Down into Glucose** 147
 - 7.2.1 α -Amylase Produces Maltose and Limit Dextrins 148
 - 7.2.2 β -Amylase Produces Maltose 148
 - 7.2.3 Limit Dextrinase Is a Debranching Enzyme 148
 - 7.2.4 α -Glucosidase Hydrolyzes Maltose 148
 - 7.2.5 Starch Phosphorylase Catalyzes the Phosphorolytic Degradation of Starch 149
- 7.3 **Glycolysis Converts Sugars to Pyruvic Acid** 150
 - 7.3.1 Hexoses Must Be Phosphorylated to Enter Glycolysis 150
 - 7.3.2 Triose Phosphates Are Oxidized to Pyruvate 151
- 7.4 **The Oxidative Pentose Phosphate Pathway Is an Alternative Route for Glucose Metabolism** 151
- 7.5 **The Fate of Pyruvate Depends on the Availability of Molecular Oxygen** 152
- 7.6 **Oxidative Respiration Is Carried Out by the Mitochondrion** 153
 - 7.6.1 In the Presence of Molecular Oxygen, Pyruvate Is Completely Oxidized to CO₂ and Water by the Citric Acid Cycle 153
 - 7.6.2 Electrons Removed from Substrate in the Citric Acid Cycle Are Passed to Molecular Oxygen Through the Mitochondrial Electron Transport Chain 154
- 7.7 **Energy Is Conserved in the Form of ATP in Accordance with Chemiosmosis** 156
- 7.8 **Plants Contain Several Alternative Electron Pathways** 157
 - 7.8.1 Plant Mitochondria Contain External Dehydrogenases 157
 - 7.8.2 Plants Have a Rotenone-Insensitive NADH Dehydrogenase 158
 - 7.8.3 Plants Exhibit Cyanide-Resistant Respiration 158
- 7.9 **Many Seeds Store Carbon as Oils Which Are Converted to Sugar** 159
- 7.10 **Respiration Provides Carbon Skeletons for Biosynthesis** 161
- 7.11 **Respiration Rate Varies with Development and Metabolic State** 162
- 7.12 **Respiration Rate Responds to Environmental Conditions** 163
 - 7.12.1 Light 163
 - 7.12.2 Temperature 164
 - 7.12.3 Oxygen Availability 164
 - Summary* 165
 - Chapter Review* 165
 - Further Reading* 165

Chapter 8 • Nitrogen Assimilation 167

- 8.1 **The Nitrogen Cycle: A Complex Pattern of Exchange** 167
 - 8.1.1 Ammonification, Nitrification, and Denitrification Are Essential Processes in the Nitrogen Cycle 168
 - 8.1.2 Nitrogen Fixation Reduces N_2 to Ammonia 168
- 8.2 **Biological Nitrogen Fixation Is Exclusively Prokaryotic** 169
 - 8.2.1 Some Nitrogen-Fixing Bacteria Are Free-Living Organisms 169
 - 8.2.2 Symbiotic Nitrogen Fixation Involves Specific Associations Between Bacteria and Plants 169
- 8.3 **Legumes Exhibit Symbiotic Nitrogen Fixation** 170
 - 8.3.1 Rhizobia Infect the Host Roots Which Induces Nodule Development 170
- 8.4 **The Biochemistry of Nitrogen Fixation** 174
 - 8.4.1 Nitrogen Fixation Is Catalyzed by the Enzyme Dinitrogenase 174
 - 8.4.2 Nitrogen Fixation Is Energetically Costly 175
 - 8.4.3 Dinitrogenase Is Sensitive to Oxygen 175
 - 8.4.4 Dinitrogenase Results in the Production of Hydrogen Gas 176
- 8.5 **The Genetics of Nitrogen Fixation** 177
 - 8.5.1 *nif* Genes Code for Nitrogenase 177
 - 8.5.2 *nod* Genes and *nif* Genes Regulate Nodulation 177
 - 8.5.3 What Is the Source of Heme for Leghemoglobin? 177
- 8.6 **NH_3 Produced by Nitrogen Fixation is Converted to Organic Nitrogen** 178
 - 8.6.1 Ammonium Is Assimilated by GS/GOGAT 178
 - 8.6.2 Fixed Nitrogen Is Exported As Asparagine and Ureides 179
- 8.7 **Plants Generally Take up Nitrogen in the Form of Nitrate** 181
- 8.8 **Nitrogen Cycling: Simultaneous Import and Export** 182
- 8.9 **Agricultural and Ecosystem Productivity Is Dependent on Nitrogen Supply** 183
 - Summary* 184
 - Chapter Review* 185
 - Further Reading* 185
- BOX 8.1 • **Lectins—Proteins with a Sweet Tooth** 172

Chapter 9 • Carbon Assimilation and Productivity 187

- 9.1 **Productivity Refers to an Increase in Biomass** 187
- 9.2 **Carbon Economy Is Dependent on the Balance Between Photosynthesis and Respiration** 188
- 9.3 **Productivity Is Influenced by a Variety of Genetic and Environmental Factors** 189
 - 9.3.1 Fluence Rate 189
 - 9.3.2 Available CO_2 190
 - 9.3.3 Temperature 192
 - 9.3.4 Soil Water Potential 193
 - 9.3.5 Nutrient Supply, Pathology, and Pollutants 193
 - 9.3.6 Leaf Factors 194

9.4 Primary Productivity on a Global Scale 196

- Summary* 197
- Chapter Review* 197
- Further Reading* 198

Part 2 • Plants, Water, and Minerals 200

Chapter 10 • Plant Cells and Water 201

- 10.1 **Water Has Unique Physical and Chemical Properties** 202
- 10.2 **The Thermal Properties of Water Are Biologically Important** 203
 - 10.2.1 Water Exhibits a Unique Thermal Capacity 203
 - 10.2.2 Water Exhibits a High Heat of Fusion and Heat of Vaporization 203
- 10.3 **Water Is the Universal Solvent** 204
- 10.4 **Polarity of Water Molecules Results in Cohesion and Adhesion** 205
- 10.5 **Water Movement May Be Governed by Diffusion or by Bulk Flow** 205
 - 10.5.1 Bulk Flow Is Driven by Hydrostatic Pressure 205
 - 10.5.2 Fick's First Law Describes the Process of Diffusion 206
- 10.6 **Osmosis Is the Diffusion of Water Across a Selectively Permeable Membrane** 207
 - 10.6.1 Osmosis in Plant Cells Is Indirectly Energy Dependent 207
 - 10.6.2 The Chemical Potential of Water Has an Osmotic as Well as Pressure Component 209
- 10.7 **Hydrostatic Pressure and Osmotic Pressure Are Two Components of Water Potential** 210
- 10.8 **Water Potential Is the Sum of Its Component Potentials** 211
- 10.9 **Dynamic Flux of H_2O Is Associated with Changes in Water Potential** 212
- 10.10 **How Elastic Are Cell Walls?** 213
 - Summary* 217
 - Chapter Review* 217
 - Further Reading* 217

BOX 10.1 • Osmosensors 214

Chapter 11 • Whole Plant Water Relations 219

- 11.1 **Transpiration Is Driven by Differences in Vapor Pressure** 220
- 11.2 **Transpiration Can Be Measured by Weight Loss and Gas Exchange** 221
- 11.3 **The Driving Force of Transpiration Is Differences in Vapor Pressure** 221
- 11.4 **The Rate of Transpiration Is Influenced by Environmental Factors** 222
 - 11.4.1 What Are the Effects of Humidity? 223
 - 11.4.2 What Is the Effect of Temperature? 224
 - 11.4.3 What Is the Effect of Wind? 224
- 11.5 **Water Conduction Occurs via Tracheary Elements** 225

11.6	The Ascent of Xylem Sap Is Explained by Combining Transpiration with Cohesive Forces of Water	228
11.6.1	Root Pressure Is Related to Root Structure	229
11.6.2	Water Rise by Capillarity Is Due to Adhesion and Surface Tension	231
11.6.3	The Cohesion Theory Best Explains the Ascent of Xylem Sap	231
11.7	Water Loss Due to Transpiration Must Be Replenished	235
11.7.1	Soil Is a Complex Medium	235
11.8	Roots Absorb and Transport Water	237
11.9	The Permeability of Roots to Water Varies	237
11.10	Radial Movement of Water Through the Root Involves Two Possible Pathways	238
	Summary	240
	Chapter Review	240
	Further Reading	240
BOX 11.1	• Why Transpiration?	226
BOX 11.2	• Forces Involved in Capillary Rise	232
Chapter 12	• Plants and Inorganic Nutrients	241

12.1	Methods and Nutrient Solutions	242
12.1.1	Interest in Plant Nutrition Is Rooted in the Study of Agriculture and Crop Productivity	242
12.1.2	The Use of Hydroponic Culture Helped to Define the Mineral Requirements of Plants	242
12.1.3	Modern Techniques Overcome Inherent Disadvantages of Simple Solution Culture	243
12.2	The Essential Nutrient Elements	245
12.2.1	Seventeen Elements Are Deemed to Be Essential for Plant Growth and Development	245
12.2.2	The Essential Nutrients Are Generally Classed as either Macronutrients or Micron Nutrients	245
12.2.3	Determining Essentiality of Micronutrients Presents Special Problems	245
12.3	Beneficial Elements	246
12.3.1	Sodium Is an Essential Micronutrient for C4 Plants	247
12.3.2	Silicon May Be Beneficial for a Variety of Species	247
12.3.3	Cobalt Is Required by Nitrogen-Fixing Bacteria	247
12.3.4	Some Plants Tolerate High Concentrations of Selenium	247
12.4	Nutrient Functions and Deficiency Symptoms	247
12.4.1	A Plant's Requirement for a Particular Element Is Defined in Terms of Critical Concentration	248
12.4.2	Nitrogen Is a Constituent of Many Critical Macromolecules	249
12.4.3	Phosphorous Is Part of the Nucleic Acid Backbone and Has a Central Function in Intermediary Metabolism	249
12.4.4	Potassium Activates Enzymes and Functions in Osmoregulation	250
12.4.5	Sulfur Is an Important Constituent of Proteins, Coenzymes, and Vitamins	250

12.4.6	Calcium Is Important in Cell Division, Cell Adhesion, and as a Secondary Messenger	251
12.4.7	Magnesium Is a Constituent of the Chlorophyll Molecule and Is an Important Regulator of Enzyme Reaction	251
12.4.8	Iron Is Required for Chlorophyll Synthesis and Electron Transfer Reactions	251
12.4.9	Boron Appears to Have a Role in Cell Division and Elongation and Contributes to the Structural Integrity of the Cell Wall	253
12.4.10	Copper Is a Necessary Cofactor for Oxidative Enzymes	254
12.4.11	Zinc Is an Activator of Numerous Enzymes	254
12.4.12	Manganese Is an Enzyme Cofactor as Well as Part of the Oxygen-Evolving Complex in the Chloroplast	254
12.4.13	Molybdenum Is a Key Component of Nitrogen Metabolism	254
12.4.14	Chlorine Has a Role in Photosynthetic Oxygen Evolution and Balances Charge Across Cellular Membranes	255
12.4.15	The Role of Nickel Is Not Clear	255
12.5	Toxicity of Micronutrients	256
	Summary	256
	Chapter Review	256
	Further Reading	257

Chapter 13 • Roots, Soils, and Nutrient Uptake 259

13.1	The Soil as a Nutrient Reservoir	260
13.1.1	Colloids Are a Significant Component of Most Soils	260
13.1.2	Colloids Present a Large, Negatively Charged Surface Area	260
13.1.3	Soil Colloids Reversibly Adsorb Cations from the Soil Solution	261
13.1.4	The Anion Exchange Capacity of Soil Colloids Is Relatively Low	261
13.2	Nutrient Uptake	262
13.2.1	Nutrient Uptake by Plants Requires Transport of the Nutrient across Root Cell Membranes	262
13.2.2	Simple Diffusion Is a Purely Physical Process	262
13.2.3	The Movement of Most Solutes across Membranes Requires the Participation of Specific Transport Proteins	263
13.2.4	Active Transport Requires the Expenditure of Metabolic Energy	263
13.3	Selective Accumulation of Ions by Roots	266
13.4	Electrochemical Gradients and Ion Movement	266
13.4.1	Ions Move in Response to Electrochemical Gradients	266
13.4.2	The Nernst Equation Helps to Predict Whether an Ion Is Exchanged Actively or Passively	267
13.5	Active Transport and Electrogenic Pumps	269
13.5.1	Active Transport Is Driven by ATPase-Proton Pumps	269
13.5.2	The ATPase-Proton Pumps of Plasma Membranes and Vacuolar Membranes Are Different	270
13.5.3	K ⁺ Exchange Is Mediated by Two Classes of Transport Proteins	271

- 13.6 Ion Uptake by Roots 272**
 13.6.1 A First Step in Mineral Uptake by Roots Is Diffusion into the Apparent Free Space 272
 13.6.2 Apparent Free Space Is Equivalent to the Apoplast of the Root Epidermal and Cortical Cells 273
- 13.7 The Radial Path of Ion Movement Through Roots 274**
 13.7.1 Ions Entering the Stele Must First Be Transported from the Apparent Free Space into the Symplast 274
 13.7.2 Ions Are Actively Secreted into the Xylem Apoplast 274
 13.7.3 Emerging Secondary Roots May Contribute to the Uptake of Some Solutes 275
- 13.8 Root-Microbe Interactions 276**
 13.8.1 Bacteria Other Than Nitrogen Fixers Contribute to Nutrient Uptake by Roots 276
 13.8.2 Mycorrhizae Are Fungi that Increase the Volume of the Nutrient Depletion Zone Around Roots 276
Summary 279
Chapter Review 279
Further Reading 280
- Box 13.1 • Electrophysiology—Exploring Ion Channels 264**

Part 3 • Plant Development 281

Chapter 14 • Patterns in Plant Development 283

- 14.1 Growth, Differentiation, and Development 283**
 14.1.1 Development Is the Sum of Growth and Differentiation 283
 14.1.2 Growth Is an Irreversible Increase in Size 284
 14.1.3 Differentiation Refers to Qualitative Changes That Normally Accompany Growth 284
- 14.2 Control of Development 285**
 14.2.1 The Orderly Development of a Plant Requires a Programmed Sequence of Gene Expression 285
 14.2.2 Hormones Coordinate Cell-Cell Interactions 287
 14.2.3 A Continuous Stream of Environmental Signals Provide Information That Plants Use to Modify Their Development 287
- 14.3 Signal Perception and Transduction 287**
 14.3.1 Signals Are Perceived by Protein Receptors 288
 14.3.2 Signal Transduction Includes a Diverse Array of Second Messengers and Biochemical Mechanisms 288
 14.3.3 There Is Extensive Cross-Talk among Signal Pathways 291
- 14.4 Cell Walls and Cell Growth 291**
 14.4.1 Cell Growth Is Driven by Water Uptake and Limited by the Strength and Rigidity of the Cell Wall 291
 14.4.2 Extension of the Cell Wall Requires Wall-Loosening Events That Enable Load-Bearing Elements in the Wall to Yield to Turgor Pressure 292
 14.4.3 Wall Loosening and Cell Expansion Are Stimulated by Low pH and Expansins 293

- 14.5 A Survey of Plant Development 294**
 14.5.1 Seed Structure and Development 294
 14.5.2 Seed Germination 295
 14.5.3 Shoot Development 295
 14.5.4 Root Development 299
 14.5.5 Flower Evocation and Development 301
 14.5.6 Flower and Fruit Development 301
 14.5.7 Senescence and Programmed Cell Death Are the Final Stages of Development 302
- 14.6 Kinetic Analysis of Growth 303**
 14.6.1 Growth of Microorganisms in Culture Exhibit Exponential Growth 303
 14.6.2 Growth of Multicellular Organisms Is Determined by the Activity of the Meristem 306
Summary 306
Chapter Review 306
Further Reading 306

Box 14.1 • Development in a Mutant Weed 286

Box 14.2 • Ubiquitin and Proteasomes—Cleaning Up Unwanted Proteins 304

Chapter 15 • The Plant Hormones: Biochemistry and Metabolism 309

- 15.1 Do Plants Have Hormones? 309**
 15.1.1 There Are Subtle Differences Between Animal and Plant Hormones 310
 15.1.2 The List of Plant Hormones Is Growing 312
 15.1.3 The Amount of Hormone in a Tissue Is Governed by Several Factors 312
- 15.2 Auxin 313**
 15.2.1 The Principal Auxin in Plants Is Indole-3-Acetic Acid (IAA) 314
 15.2.2 IAA Is Synthesized from the Amino Acid L-Tryptophan 316
 15.2.3 Some Plants Do Not Require Tryptophan for IAA Biosynthesis 316
 15.2.4 IAA May Be Stored As Inactive Conjugates 318
 15.2.5 There Are Two Principal Mechanisms for Deactivation of IAA 318
- 15.3 Gibberellins 320**
 15.3.1 There Are Three Principal Sites for Gibberellin Biosynthesis 320
 15.3.2 Gibberellins Are Terpenes, Sharing a Core Pathway with Several Other Hormones and a Wide Range of Secondary Products 322
 15.3.3 Gibberellins Are Synthesized from Geranylgeranyl Pyrophosphate (GGPP) 323
 15.3.4 Growth Retardants Block the Synthesis of Gibberellins 324
 15.3.5 Gibberellins Are Deactivated by 2 β -Hydroxylation 324
 15.3.6 Gibberellin Transport Is Poorly Understood 325
- 15.4 Cytokinins 325**
 15.4.1 Cytokinins Are Synthesized Primarily in the Root 325
 15.4.2 Cytokinin Biosynthesis Begins with the Condensation of an Isopentenyl Group with the Amino Group of Adenosine Monophosphate 326
 15.4.3 Cytokinins May Be Reversibly or Irreversibly Deactivated by Conjugation and Irreversibly Deactivated by Oxidation 329

15.5. Absciscic Acid 329

- 15.5.1 Absciscic Acid Is Synthesized Primarily in Mature Leaves 330
- 15.5.2 Absciscic Acid Is Synthesized from the Cleavage Product of a 40-Carbon Carotenoid Precursor 330
- 15.5.3 Absciscic Acid Is Degraded by Oxidation to Phaseic Acid 332

15.6 Ethylene 332

- 15.6.1 Ethylene Is Synthesized from the Amino Acid Methionine 332
- 15.6.2 Ethylene and Polyamine Biosynthesis Share a Common Precursor 334
- 15.6.3 Excess Ethylene Is Subject to Oxidation 334

15.7 Brassinosteroids 334

- 15.7.1 Brassinosteroids Are Polyhydroxylated Sterols Derived from the Triterpene Squalene 335
- 15.7.2 Several Routes for Deactivation of Brassinosteroids Have Been Identified 335

15.8 Polyamines 335

- 15.8.1 The Pathway for Polyamine Biosynthesis Is the Same in Plants, Microorganisms, and Mammals 337
- Summary* 338
- Chapter Review* 338
- Further Reading* 339

Box 15.1 • Historical Perspectives—Discovering Plant Hormones 311**Chapter 16 • The Plant Hormones: Control of Development 341****16.1 Cell Division, Enlargement, and Differentiation 341**

- 16.1.1 Cytokinins Are a Significant Factor in Regulating Cell Division 341
- 16.1.2 Cytokinins Regulate Progression Through the Cell Cycle 342
- 16.1.3 Auxins Stimulate Cell Enlargement in Excised Tissues 344
- 16.1.4 The Acid-Growth Hypothesis Explains Auxin Control of Cell Enlargement 344
- 16.1.5 Maintenance of Auxin-Induced Growth Requires Gene Activation 347
- 16.1.6 Many Aspects of Plant Development Are Linked to the Polar Transport of Auxin 349
- 16.1.7 Auxins and Cytokinins Regulate Vascular Differentiation 351

16.2 Seed Development and Germination 352

- 16.2.1 The Level and Activities of Various Hormones Change Dramatically During Seed Development 352
- 16.2.2 Gibberellins Stimulate Mobilization of Nutrient Reserves During Germination of Cereal Grains 353

16.3 Shoot and Root Development 356

- 16.3.1 Gibberellins Stimulate Hyperelongation of Intact Stems, Especially in Dwarf and Rosette Plants 356
- 16.3.2 Inhibition of Gibberellin Biosynthesis Has Commercial Applications 357
- 16.3.3 Hormone Mutants Indicate a Role for Brassinosteroids and Ethylene in Stem Growth 358

- 16.3.4 The Ratio of Auxin to Cytokinin Controls the Growth of Axillary Buds 358

- 16.3.5 Root Elongation and Development Is Particularly Sensitive to Auxin and Ethylene 359

16.4 Senescence and Abscission 360

- 16.4.1 Cytokinins and Ethylene Are Antagonistic in the Regulation of Nutrient Mobilization and Senescence 360
- 16.4.2 Auxin Regulates Leaf Abscission 362

16.5 Flower and Fruit Development 362

- 16.5.1 Gibberellins Promote Precocious Flowering in Some Species 363
- 16.5.2 Auxin and Gibberellin Influence the Sex of Flowers 363
- 16.5.3 Hormones Influence Fruit Set and Development 364

16.6 Ethylene 364

- 16.6.1 The Study of Ethylene Presents a Unique Set of Problems 364
- 16.6.2 Ethylene Affects Many Aspects of Vegetative Development 364
- Summary* 365
- Chapter Review* 366
- Further Reading* 366

Box 16.1 • The Cell Cycle and Control of Cell Division 343**Box 16.2 • Commercial Applications of Hormones 348****Chapter 17 • Photomorphogenesis: Responding to Light 367****17.1 Photomorphogenesis 368****17.2 Phytochrome: Responses to Red and Far-Red Light 368**

- 17.2.1 Photoreversibility Is the Hallmark of Phytochrome Action 370
- 17.2.2 Phytochromes Are Phycobilin Pigments 371
- 17.2.3 Conversion of Pr to Pfr in Etiolated Seedlings Leads to a Loss of Both Pfr and Total Phytochrome 372

17.3 Phytochrome Responses Can Be Grouped According to Their Fluence Requirements 374

- 17.3.1 The Most Studied Low Fluence Responses (LFRs) Are De-etiolation and Seed Germination 374
- 17.3.2 Very Low Fluence Responses Are Not Photoreversible 376
- 17.3.3 High Irradiance Reactions Require Prolonged Exposure to Relatively High Fluence Rates 377

17.4 Phytochrome under Natural Conditions 377

- 17.4.1 PhA May Function to Detect the Presence of Light 378
- 17.4.2 Phytochrome Detects Canopy Shading and End-of-Day Signals 378

17.5 Responses to Blue and UV-A Light 381

- 17.5.1 Cryptochrome Is a Flavoprotein 381
- 17.5.2 Phototropin Is a Blue Light-Dependent Kinase 382
- 17.5.3 A Hybrid Blue-Light Photoreceptor Has Been Isolated from a Fern 382

- 17.6 De-etiolation in Arabidopsis. A Case Study in Photoreceptor Interactions 383**
- 17.7 Photoreceptor Signal Transduction 384**
- 17.7.1 Phytochromes Have Kinase Activity 384
- 17.7.2 Pfr Regulates Gene Expression 384
- 17.7.3 Phytochrome May Migrate from the Cytoplasm to the Nucleus 386
- 17.8 Some Plant Responses Are Regulated by UV-B Light 387**
- Summary 387*
- Chapter Review 388*
- Further Reading 388*

Box 17.1 • Historical Perspectives: The Discovery of Phytochrome 369

Chapter 18 • Plant Movements—Orientation in Space 391

- 18.1 Phototropism 392**
- 18.1.1 Phototropism Is a Response to a Light Gradient across an Organ 392
- 18.1.2 Phototropism in Coleoptiles Is Mediated by a Flavoprotein 393
- 18.1.3 Fluence Response Curves Illustrate the Complexity of Phototropic Responses 394
- 18.1.4 The Phototropic Response Is Attributed to a Lateral Redistribution of Diffusible Auxin 395
- 18.2 Gravitropism 398**
- 18.2.1 Gravitropism Is More Than Simply Up and Down 398
- 18.2.2 The Gravitational Stimulus Is the Product of Intensity and Time 399
- 18.2.3 In Roots, Gravity Is Perceived in the Root Cap 401
- 18.2.4 The Sedimentation of Starch-Filled Amyloplasts Is an Initial Gravity-Sensing Event 402
- 18.2.5 Gravitropism, Like Phototropism, Is an Auxin-Dependent Differential Growth Response 403
- 18.2.6 The Gravitropic Signal Transduction Chain May Involve Stretch-Activated Ion Channels, pH Changes in the Root Cap, and Redistribution of Calcium Ions 405
- 18.2.7 Gravitropism in Grass Stems Occurs in the False Pulvinus 407
- 18.2.8 Plants Follow Different Rules in the Microgravity Environment of Space 408
- 18.3 Nastic Movements 408**
- 18.3.1 Nyctinastic Movements Are Rhythmic Movements Involving Reversible Turgor Changes 408
- 18.3.2 Nyctinastic Movements Are Due to Ion Fluxes and Resulting Osmotic Responses in Specialized Motor Cells 409
- 18.3.3 Seismonasty Is a Response to Mechanical Stimulation 412
- Summary 413*
- Chapter Review 414*
- Further Reading 414*

Box 18.1 • Methods in the Study of Gravitropism 400

Chapter 19 • Measuring Time: The Control of Development by Photoperiod and Endogenous Clocks 415

- 19.1 Photoperiodism 416**
- 19.1.1 Photoperiodic Responses May Be Characterized By a Variety of Response Types 416
- 19.1.2 Critical Daylength Defines Short-Day and Long-Day Responses 417
- 19.1.3 Plants Actually Measure the Length of the Dark Period 419
- 19.1.4 The Photoperiodic Signal Is Perceived by the Leaves 420
- 19.1.5 Phytochrome Is the Principal Photoreceptor for Photoperiodism 421
- 19.1.6 Photoperiodism Normally Requires a Period of High Fluence Light Before or After the Dark Period 422
- 19.1.7 Three Different Hypotheses Have Been Proposed to Account for the Floral Stimulus 422
- 19.1.8 Photoperiodic Behavior Is Often Modified by Temperature 423
- 19.2 The Biological Clock 426**
- 19.2.1 Clock-Driven Rhythms Persist under Constant Conditions 426
- 19.2.2 The Circadian Clock Is Temperature-Compensated 428
- 19.2.3 Light Resets the Biological Clock on a Daily Basis 428
- 19.2.4 The Circadian Clock Is a Significant Component in Photoperiodic Time Measurement 429
- 19.2.5 Several Clock-Associated Genes Have Been Identified 431
- 19.2.6 The Circadian Clock in Insects, Animals, and Cyanobacteria Is a Negative Feedback Loop 432
- 19.3 Floral Induction 433**
- 19.3.1 Flower Initiation and Development Involves the Sequential Action of Three Sets of Genes 433
- 19.3.2 Flowering Time Genes Influence the Duration of Vegetative Growth 434
- 19.3.3 Floral Identity Genes and Organ Identity Genes Overlap in Time and Function 435
- 19.4 Photoperiodism in Nature 436**
- Summary 438*
- Chapter Review 438*
- Further Reading 439*

Box 19.1 • Historical Perspectives: The Discovery of Photoperiodism 416

Box 19.2 • Historical Perspectives: The Biological Clock 424

Chapter 20 • Temperature: Plant Development and Distribution 441

- 20.1 Temperature in the Plant Environment 441**
- 20.2 Temperature and Flowering Response 443**
- 20.2.1 Vernalization Occurs Most Commonly in Winter Annuals and Biennials 443
- 20.2.2 The Effective Temperature for Vernalization Is Variable 444

- 20.2.3 The Vernalization Treatment Is Perceived by the Shoot Apex 445
- 20.2.4 The Vernalized State Is Transmissible 445
- 20.2.5 Gibberellin and Vernalization Operate Through Independent Genetic Pathways 446
- 20.3 Bud Dormancy 446**
 - 20.3.1 Bud Dormancy Is Induced Primarily by Photoperiod 447
 - 20.3.2 Temperature Is a Significant Factor in Breaking Bud Dormancy 447
- 20.4 Seed Dormancy and Germination 448**
 - 20.4.1 Numerous Factors Influence Seed Dormancy and Germination 448
 - 20.4.2 Temperature Has a Significant Impact on Seed Dormancy 449
- 20.5 Responses to Change in Temperature 450**
- 20.6 Influence of Temperature on Growth and Plant Distribution 451**
 - 20.6.1 Coasts and Deserts: A Case Study 452
 - 20.6.2 Temperature Influences the Distribution of C3 and C4 Grasses on Mountain Slopes 454
 - Summary 454*
 - Chapter Review 455*
 - Further Reading 455*

Part 4 • Stress and Secondary Metabolism 457

Chapter 21 • Plant Environmental Stress Physiology 459

- 21.1 What Is Plant Stress? 459**
- 21.2 Plants Respond to Stress in Several Different Ways 460**
- 21.3 Abiotic Stress 461**
 - 21.3.1 Water Stress Is a Persistent Threat to Plant Survival 461
 - 21.3.2 Water Stress Leads to Membrane Damage 462
 - 21.3.3 Photosynthesis Is Particularly Sensitive to Water Stress 462
 - 21.3.4 Stomata Respond to Water Deficit 463
 - 21.3.5 Osmotic Adjustment Is a Response to Water Stress 465
 - 21.3.6 Water Deficit Affects Shoot and Root Growth 466
 - 21.3.7 Water Stress May Induce a Decrease in Leaf Area 467
- 21.4 Temperature Stress 467**
 - 21.4.1 Many Plants Are Chilling Sensitive 468
 - 21.4.2 North Temperate Overwintering Plants Survive Freezing Stress 468
 - 21.4.3 Cold Acclimation Increases Resistance to Freezing Stress 470
 - 21.4.4 Cold Acclimation and Freezing Tolerance in Herbaceous Species Is a Complex Interaction Between Light and Low Temperature 471
 - 21.4.5 High Temperature Stress Is a Major Factor in Plant Productivity 472
- 21.5 Salt Stress, Water Deficits and Ion Toxicity 474**
- 21.6 Pollution Represents a Relatively New Abiotic Stress 476**
 - 21.6.1 Heavy Metals 476
 - 21.6.2 Air Pollution 477

- 21.7 Insects and Disease Represent Potential Biotic Stresses 479**
 - 21.7.1 Hypersensitive Reaction Is a Sensing/Signalling Mechanism Initiated by a Biotic Stress 479
 - 21.7.2 How Do Plants Recognize Potential Pathogens and Initiate Defense Responses? 479
 - 21.7.3 Systemic Acquired Resistance Represents a Plant Immune Response 480
 - 21.7.4 Jasmonates Mediate Insect and Disease Resistance 481
 - Summary 490*
 - Chapter Review 491*
 - Further Reading 491*

Box 21.1 • Monitoring Plant Stress by Chlorophyll Fluorescence 482

Box 21.2 • Ecophysiology, Plant Biomes, and Weather 484

Chapter 22 • Secondary Plant Metabolites 493

- 22.1 Primary and Secondary Metabolites 493**
- 22.2 Terpenoids 494**
 - 22.2.1 The Terpenoids Are a Chemically and Functionally Diverse Group of Molecules That Share a Common Biosynthetic Pathway 494
 - 22.2.2 Many Terpenoids Are Active against Insect Herbivory 495
 - 22.2.3 Steroids and Sterols Are Tetracyclic Triterpenoids 497
 - 22.2.4 Polyterpenes Include the Carotenoid Pigments and Natural Rubber 497
- 22.3 Glycosides 499**
 - 22.3.1 Saponins Are Terpene Glycosides with Detergent Properties 499
 - 22.3.2 Cardian Glycosides Are Highly Toxic, Modified Steroid Glycosides 500
 - 22.3.3 Cyanogenic Glycosides Are a Natural Source of Hydrogen Cyanide 501
 - 22.3.4 Glucosinolates Are Sulfur-Containing Precursors to Mustard Oils 502
- 22.4 Phenylpropanoids 503**
 - 22.4.1 Shikimic Acid Is a Key Intermediate in the Synthesis of Aromatic Amino Acids and Phenylpropanoids 503
 - 22.4.2 The Simplest Phenolic Molecules Are Essentially Deaminated Versions of the Corresponding Amino Acids 503
 - 22.4.3 Coumarins and Coumarin Derivatives Function as Anticoagulants 506
 - 22.4.4 Lignin Is a Major Structural Component of Secondary Cell Walls 507
 - 22.4.5 Flavonoids and Stilbenes Have Parallel Biosynthetic Pathways 508
 - 22.4.6 Tannins Denature Proteins and Provide an Astringent Taste to Foods 508
- 22.5 Alkaloids 510**
 - 22.5.1 Alkaloids Are a Large Family of Chemically Unrelated Molecules 510
 - 22.5.2 Alkaloids Are Noted Primarily for Their Pharmacological Properties and Medical Applications 510

- 22.5.3 Like Many Other Secondary Metabolites, Alkaloids Serve as Preformed Chemical Defense Molecules 512

Summary 513

Chapter Review 513

Further Reading 513

Part 5 • Biotechnology 515

Chapter 23 • Biotechnology: Engineering Plants for the Future 517

23.1 Modern Biotechnology Is Synonymous with Recombinant DNA Technology 518

- 23.1.1 DNA Recombination Allows the Movement of Selected Genes Between Organisms 518
- 23.1.2 The Most Widely Used Vector for Introducing Foreign Genes into Plants is the Ti Plasmid of the Crown-Gall Bacterium *Agrobacterium Tumefaciens* 519
- 23.1.3 Electroporation and Biolistics Are Methods for Direct Delivery of DNA into Plant Cells 522
- 23.1.4 Genetic Engineering Is a New Chapter in the Long History of Plant Breeding 522

23.2 Tissue and Cell Culture and Protoplast Fusion 523

- 23.2.1 The Culture of Plant Cells and Tissues Has Been Exploited Since the 1930s 523
- 23.2.2 Protoplasts Are Naked Plant Cells That Can Be Fused to Make Somatic Hybrids 523
- 23.2.3 Tissue Culture Has Made Possible Large-Scale Cloning of Plants 524

23.3 Plant Protection 524

- 23.3.1 Herbicide-Resistant Crops Encourage More Efficient Use of Herbicides 525
- 23.3.2 Herbicide Resistance Can Be Achieved by Overexpression of Tolerant Enzymes 525

- 23.3.3 Herbicide Resistance in Weeds Is a Potentially Undesirable Side-Effect of Herbicide Use 526
- 23.3.4 Several Strategies Are Available for Protection against Insects and Disease 527

23.4 Metabolic Engineering: Improving Yield and Nutrition 528

- 23.4.1 One Target of Biotechnology Is Improved Carbon Gain and Nitrogen Metabolism 528
- 23.4.2 Boosting Vitamin Content Is One Way to Improve the Nutritional Quality of Foods 529
- 23.4.3 Oilseed Crops May Be Engineered to Produce Healthier Edible Oils 529

23.5 Molecular Farming Uses Plants as Living Factories 530

- 23.5.1 Transgenic Plants May Provide a Low-Cost Delivery System for Vaccines 531
- 23.5.2 Plants Can Be Engineered to Produce Biodegradable Plastics 531

23.6 Plants Have Potential as an Alternative Source of Renewable Fuels 532

23.7 Plants Remain Useful as a Source of Secondary Products 533

Summary 533

Chapter Review 534

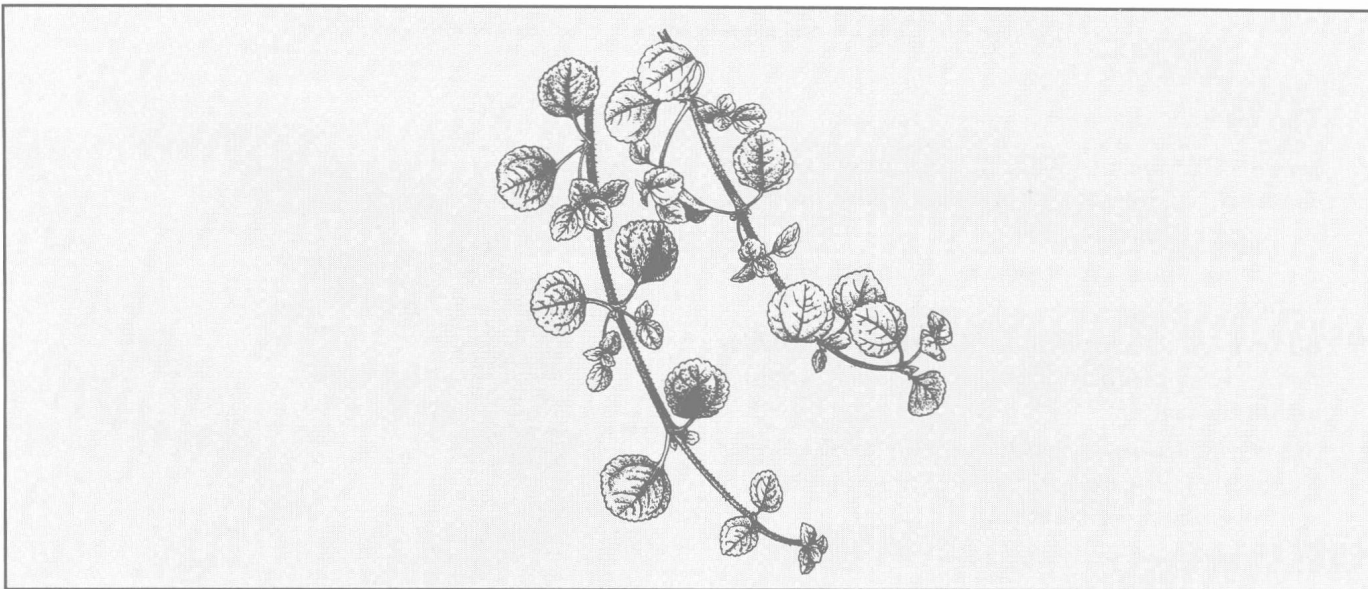
Further Reading 534

BOX 23.1 • Engineering Plants with Their Own Genes 519

Appendix I • Standard Amino Acids and Their Structures 535

Appendix II • Measuring Water Potential and Its Components 539

Index 545



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 **protoplast** surrounded by a **plasma membrane**. The membrane and the protoplast it contains are collectively referred to as a **protoplast**. Of course, all of the components that make up protoplast 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

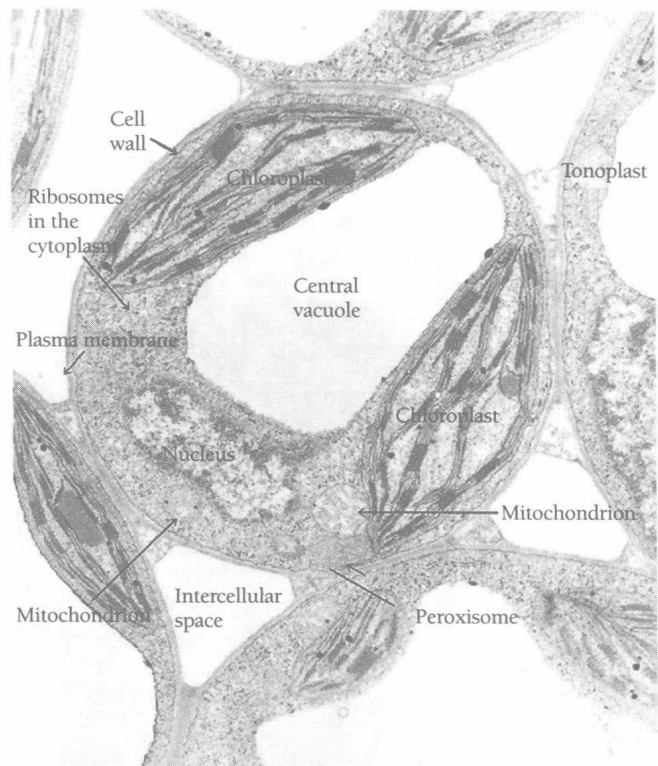


FIGURE 1.1 The plant cell. A mature mesophyll cell from a *Coleus* leaf, as seen in the electron microscope. Note the prominent large central vacuole and chloroplasts. (Electron micrograph by Wm. P. Wergin, courtesy of E. H. Newcomb, University of Wisconsin–Madison.)

contents are known as **nucleoplasm**. The balance of the protoplast, 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