



Plant Physiology and Development

SIXTH EDITION

Lincoln Taiz • Eduardo Zeiger
Ian Max Møller • Angus Murphy

Plant Physiology and Development

SIXTH EDITION

Plant Physiology and Development

SIXTH EDITION

Lincoln Taiz

Professor Emeritus, University of California, Santa Cruz

Eduardo Zeiger

Professor Emeritus, University of California, Los Angeles

Ian Max Møller

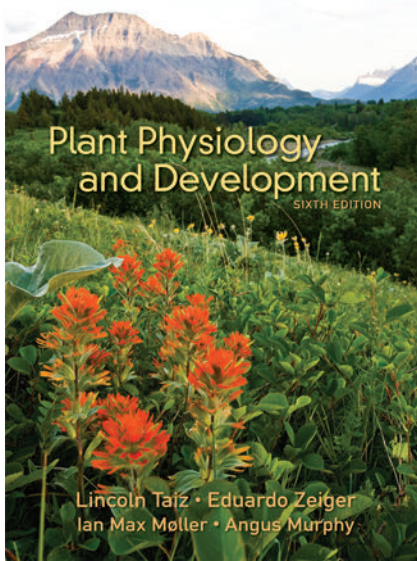
Associate Professor, Aarhus University, Denmark

Angus Murphy

Professor, University of Maryland



Sinauer Associates, Inc • Publishers
Sunderland, Massachusetts U.S.A.



Front Cover

Red Indian Paintbrush (*Castilleja miniata*) grows on hillside in Waterton Lakes National Park, Alberta, Canada. © All Canada Photos/Corbis.

About the Book

Editor: Andrew D. Sinauer

Project Editors: Laura Green and Stephanie Bonner

Production Manager: Christopher Small

Book and Cover Design: Jefferson Johnson

Photo Researcher: David McIntyre

Copyeditor: Liz Pierson

Indexer: Grant Hackett

Illustrator: Elizabeth Morales

Book and Cover Manufacturer: Courier Corporations, Inc.

Plant Physiology and Development, Sixth Edition

Copyright © 2015 by Sinauer Associates, Inc.

All rights reserved. This book may not be reproduced in whole or in part without permission from the publisher.

For information, address

Sinauer Associates, Inc., P.O. Box 407, Sunderland, MA 01375 U.S.A.

FAX: 413-549-1118

E-mail: publish@sinauer.com

Internet: www.sinauer.com

Library of Congress Cataloging-in-Publication Data

Plant physiology

Plant physiology and development / editors, Lincoln Taiz, University of California, Santa Cruz, Eduardo Zeiger, University of California, Los Angeles. -- Sixth edition.

pages cm

Revised edition of: Plant physiology. Fifth edition. c2010.

ISBN 978-1-60535-255-8 (casebound)

1. Plant physiology. 2. Plants--Development. I. Taiz, Lincoln. II. Zeiger, Eduardo. III. Title.

QK711.2.T35 2014

571.2--dc23 2014030480

Printed in U.S.A.

10 9 8 7 6 5 4 3 2 1

Brief Contents

CHAPTER 1 *Plant and Cell Architecture 1*

CHAPTER 2 *Genome Structure and Gene Expression 51*

UNIT I *Transport and Translocation of Water and Solutes 81*

CHAPTER 3 *Water and Plant Cells 83*

CHAPTER 4 *Water Balance of Plants 99*

CHAPTER 5 *Mineral Nutrition 119*

CHAPTER 6 *Solute Transport 143*

UNIT II *Biochemistry and Metabolism 169*

CHAPTER 7 *Photosynthesis: The Light Reactions 171*

CHAPTER 8 *Photosynthesis: The Carbon Reactions 203*

CHAPTER 9 *Photosynthesis: Physiological and Ecological Considerations 245*

CHAPTER 10 *Stomatal Biology 269*

CHAPTER 11 *Translocation in the Phloem 285*

CHAPTER 12 *Respiration and Lipid Metabolism 317*

CHAPTER 13 *Assimilation of Inorganic Nutrients 353*

UNIT III *Growth and Development 377*

CHAPTER 14 *Cell Walls: Structure, Formation, and Expansion 379*

CHAPTER 15 *Signals and Signal Transduction 407*

CHAPTER 16 *Signals from Sunlight 447*

CHAPTER 17 *Embryogenesis 477*

CHAPTER 18 *Seed Dormancy, Germination, and Seedling Establishment 513*

CHAPTER 19 *Vegetative Growth and Organogenesis 553*

CHAPTER 20 *The Control of Flowering and Floral Development 591*

CHAPTER 21 *Gametophytes, Pollination, Seeds, and Fruits 625*

CHAPTER 22 *Plant Senescence and Cell Death 665*

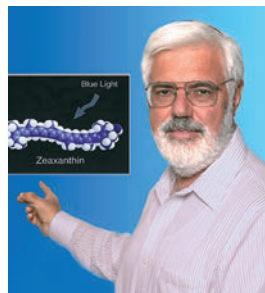
CHAPTER 23 *Biotic Interactions 693*

CHAPTER 24 *Abiotic Stress 731*

Editors



Lincoln Taiz is Professor Emeritus of Molecular, Cellular, and Developmental Biology at the University of California at Santa Cruz. He received his Ph.D. in Botany from the University of California at Berkeley. Dr. Taiz's main research focus has been on the structure, function, and evolution of vacuolar H⁺-ATPases. He has also worked on gibberellins, cell wall mechanical properties, metal transport, auxin transport, and stomatal opening. (Chapters 15, 16, 18, 19, 20, 21, 22, and 23)



Eduardo Zeiger is Professor Emeritus of Biology at the University of California at Los Angeles. He received a Ph.D. in Plant Genetics at the University of California at Davis. His research interests include stomatal function, the sensory transduction of blue-light responses, and the study of stomatal acclimations associated with increases in crop yields. (Chapter 10)

Sub-Editors



Ian Max Møller is Associate Professor at Department of Molecular Biology and Genetics at Aarhus University, Denmark. He received his Ph.D. in Plant Biochemistry from Imperial College, London, UK. He has worked at Lund University, Sweden and, more recently, at Risø National Laboratory and the Royal Veterinary and Agricultural University in Copenhagen, Denmark. Professor Møller has investigated plant respiration throughout his career. His current interests include turnover of reactive oxygen species and the role of protein oxidation in plant cells. (Chapter 12)



Angus Murphy is Professor and Chair of the Department of Plant Science and Landscape Architecture at the University of Maryland. He earned his Ph.D. in Biology from the University of California, Santa Cruz in 1996. Dr. Murphy studies ATP-binding cassette transporters, auxin transport proteins, and the role of auxin transport in programmed and plastic growth. (Chapters 15, 16, 17, 18, and 19)

Principle Contributors



Sarah M. Assmann is a Professor in the Biology Department at the Pennsylvania State University. She received a Ph.D. in the Biological Sciences at Stanford University. Dr. Assmann studies how plants respond to environmental stresses, with a focus on abiotic stress regulation of RNA structure, heterotrimeric G-protein signaling, and guard cell systems biology. (Chapter 6)



Arnold J. Bloom is a Professor in the Department of Sciences at the University of California at Davis. He received a Ph.D. in Biological Sciences at Stanford University in 1979. His research focuses on plant-nitrogen relationships, especially the differences in plant responses to ammonium and nitrate as nitrogen sources. He is the co-author with Emanuel Epstein of the textbook, *Mineral Nutrition of Plants* and author of the textbook, *Global Climate Change: Convergence of Disciplines*. (Chapters 5 and 13)



Christine Beveridge is a Professor in the School of Biological Sciences at the University of Queensland. She received a Ph.D. in Plant Sciences at the University of Tasmania in 1994. Her research focuses on shoot architecture and hormonal control of development, especially strigolactones, and involves genetic approaches, molecular physiology and plant modelling. (Chapter 19)



Eduardo Blumwald is a Professor of Cell Biology and the Will W. Lester Endowed Chair at the Department of Plant Sciences, University of California at Davis. He received his Ph.D. in Bioenergetics from the Hebrew University of Jerusalem in 1984. His research focuses on the adaptation of plants to environmental stress and the cellular and molecular bases of fruit quality. (Chapter 24)



Robert E. Blankenship is a Professor of Biology and Chemistry at Washington University in St. Louis. He received his Ph.D. in Chemistry from the University of California at Berkeley in 1975. His professional interests include mechanisms of energy and electron transfer in photosynthetic organisms, and the origin and early evolution of photosynthesis. (Chapter 7)



John Browse is a Professor in the Institute of Biological Chemistry at Washington State University. He received his Ph.D. from the University of Auckland, New Zealand, in 1977. Dr. Browse's research interests include the biochemistry of lipid metabolism and the responses of plants to low temperatures. (Chapter 12)



Bob B. Buchanan is a Professor of Plant and Microbial Biology at the University of California at Berkeley. He continues to work on thioredoxin-linked regulation in photosynthesis, seed germination, and related processes. His findings with cereals hold promise for societal application. (Chapter 8)



Victor Busov is a Professor at Michigan Technological University. His work is focused on understanding the molecular mechanisms that regulate growth and development of woody perennial species. He is interested in how these mechanisms are important for adaptation to environment, evolution of different life forms and applications to tree improvement and biotechnology. (Chapter 19)



John Christie holds an undergraduate degree in Biochemistry and Ph.D. from the University of Glasgow and is currently Professor of Photobiology at the University. During his postdoc with Winslow Briggs at Stanford, he contributed to uncovering the molecular identity of higher plant phototropins. He established his own research group at the University of Glasgow in 2002 and continues to investigate the molecular basis of plant UV/blue light receptor function and signaling. His research also extends to developing new technologies derived from photoreceptor characterization. (Chapter 16)



Daniel J. Cosgrove is a Professor of Biology at the Pennsylvania State University at University Park. His Ph.D. in Biological Sciences was earned at Stanford University. Dr. Cosgrove's research interest is focused on plant growth, specifically the biochemical and molecular mechanisms governing cell enlargement and cell wall expansion. His research team discovered the cell wall loosening proteins called expansins and is currently studying the structure, function, and evolution of this gene family. (Chapter 14)



Susan Dunford is an Associate Professor of Biological Sciences at the University of Cincinnati. She received her Ph.D. from the University of Dayton in 1973 with a specialization in plant and cell physiology. Dr. Dunford's research interests include long-distance transport systems in plants, especially translocation in the phloem, and plant water relations. (Chapter 11)



James Ehleringer is at the University of Utah where he is a Distinguished Professor of Biology and serves as Director of both the Global Change and Sustainability Center and of the Stable Isotope Ratio Facility for Environmental Research (SIRFER). His research focuses on understanding terrestrial ecosystem processes through stable isotope analyses, gas exchange and biosphere-atmosphere interactions, and water relations. (Chapter 9)



Jürgen Engelberth is an Associate Professor of Plant Biochemistry at the University of Texas at San Antonio. He received his Ph.D. in Plant Physiology at the Ruhr-University Bochum, Germany in 1995 and did postdoctoral work at the Max Planck Institute for Chemical Ecology, at USDA, ARS, CMAVE in Gainesville, and at Penn State University. His research focuses on signaling involved in plant-insect and plant-plant interaction. (Chapter 23)



Lawrence Griffing is an Associate Professor in the Biology Department at Texas A&M University. He received his Ph.D. in Biological Sciences at Stanford University. Dr. Griffing's research mainly focuses on plant cell biology, concentrating on the interaction between the endoplasmic reticulum and other membranes and the dynamics of endomembranes through their interactions with the cytoskeleton. His teaching focuses on incorporating authentic inquiry and scientific discovery into undergraduate courses. (Chapter 1)



N. Michele Holbrook is a Professor in the Department of Organismic and Evolutionary Biology at Harvard University. She received her Ph.D. from Stanford University in 1995. Dr. Holbrook's research group focuses on water relations and long-distance transport through xylem and phloem. (Chapters 3 and 4)



Andreas Madlung is a Professor in the Department of Biology at the University of Puget Sound. He received a Ph.D. in Molecular and Cellular Biology from Oregon State University in 2000. Research in his laboratory addresses fundamental questions concerning the influence of genome structure on plant physiology and evolution, especially with respect to polyploidy. (Chapter 2)



Ron Mittler is a Professor in the Department of Biological Sciences at the University of North Texas. He got his Ph.D. in biochemistry from Rutgers the State University of New Jersey. His current research is focused on plant responses to abiotic stress and reactive oxygen signaling and metabolism in plant and cancer cells. (Chapter 24)



Gabriele B. Monshausen is an Assistant Professor of Biology at the Pennsylvania State University. She received her PhD in plant biology at the University of Bonn, Germany. Dr. Monshausen's research focuses on mechanisms of cellular ion signaling in plant hormone responses and plant responses to mechanical forces. (Chapter 15)



Wendy Peer is an Assistant Professor in the Department of Environmental Science and Technology and an affiliate in the Department of Plant Science and Landscape Architecture at the University of Maryland, College Park. Wendy Peer's research focuses on seedling establishment and the integration of developmental and environmental signals that lead to successful seedling establishment. (Chapters 15, 18, and 19)



Allan G. Rasmusson is Professor in Plant Physiology at Lund University in Sweden. He received his Ph.D. in plant physiology at Lund University in 1994, and made a postdoc at IGF Berlin. Dr. Rasmusson's current research centers on redox control in respiratory metabolism and on peptide-membrane interactions. (Chapter 12)



Darren R. Sandquist is a Professor of Biological Science at California State University, Fullerton. He received his Ph.D. from the University of Utah. His research focuses on plant ecophysiological responses to disturbance, invasion, and climate change in arid and semi-arid ecosystems. (Chapter 9)



Graham B. Seymour is Professor of Plant Biotechnology and Head of the Plant and Crop Science Division at the University of Nottingham in the UK. His major research interests are the mechanistic basis of fruit quality traits and understanding the role of the epigenome in regulating the ripening process. (Chapter 21)



Sally Smith is an Emeritus and Adjunct Professor in the Soils Group, School of Agriculture, Food and Wine, the University of Adelaide, Australia. She is a fellow of the Australian Academy of Science and co-author of a major research text on mycorrhizas. Her research interests include interactions between arbuscular mycorrhizal fungi and plants, especially roles of the symbiosis in plant phosphate nutrition and growth. (Chapter 5)



Joe H. Sullivan is a Professor in the department of Plant Science and Landscape Architecture at the University of Maryland. He received his Ph.D. in Plant Physiology at Clemson University in 1985. His research interests include Plant Physiological Ecology in natural and urban ecosystems with particular interest in the response of plants to ultraviolet radiation and other parameters of global climate change. (Chapter 16)



Heven Sze is a Professor at the University of Maryland at College Park. She earned a Ph.D. in plant physiology at Purdue University, and was a postdoctoral fellow at Harvard Medical School. Her research has focused on the mechanism and regulation of ion transport and how ion and pH homeostasis are integrated with growth, development and reproduction. (Chapter 21)



Bruce Veit is a senior scientist at AgResearch in Palmerston North, New Zealand. He received his Ph.D. in Genetics from University of Washington, Seattle in 1986 before undertaking postdoctoral research at the Plant Gene Expression Center in Albany, California. Dr. Veit's current research interests focus on mechanisms that influence the determination of cell fate. (Chapter 17)



Philip A. Wigge is a Principal Investigator at the Sainsbury Laboratory, Cambridge University, UK. He received his Ph.D. in Cell Biology from the University of Cambridge, UK, in 2001. Dr. Wigge has studied how florigen controls plant development at the Salk Institute, CA, in the laboratory of Detlef Weigel. His research group is fascinated by how plants are able to sense and respond to climate change. (Chapter 20)



Ricardo A. Wolosiuk is Professor at the University of Buenos Aires and senior scientist at Instituto Leloir (Buenos Aires). He received his Ph.D. in Chemistry from the University of Buenos Aires in 1974. His current research centers on the modulation of photosynthetic CO₂ assimilation and the structure and function of plant proteins. (Chapter 8)

Reviewers

Javier Abadía
*Aula Dei Experimental Station, Spanish
Council for Scientific Research*

Elizabeth A. Ainsworth
USDA Agricultural Research Service

Richard Amasino
University of Wisconsin

Diane Bassham
Iowa State University

Tom Beeckman
VIB/Ghent University

J. Derek Bewley
Emeritus, University of Guelph

Winslow Briggs
Carnegie Institution for Science, Stanford

Alice Y. Cheung
University of Massachusetts, Amherst

Karl-Josef Dietz
Bielefeld University

Anna Dobritsa
The Ohio State University

Xinnian Dong
Duke University

Anna F. Edlund
Lafayette College

Christian Fankhauser
University of Lausanne

Ruth Finkelstein
University of California, Santa Barbara

James J. Giovannoni
Cornell University

Heiner E. Goldbach
University of Bonn

Sigal Sivaldi Goldstein
*The Technion – Israel Institute of
Technology*

Michael Gutensohn
Purdue University

Philip J. Harris
University of Auckland, New Zealand

George Haughn
University of British Columbia

J. S. (Pat) Heslop-Harrison
University of Leicester

Joseph Kieber
The University of North Carolina

Kenneth L. Korth
University of Arkansas

Clark Lagarias
University of California, Davis

Jane Langdale
University of Oxford

Andrew R. Leitch
Queen Mary University of London

Gerhard Leubner-Metzger
Royal Holloway, University of London

David Macherel
University of Angers

Massimo Maffei
University of Turin

Ján A. Miernykj
University of Missouri

June B. Nasrallah
Cornell University

Lars Østergaard
The John Innes Centre

Jarmila Pittermann
University of California, Santa Cruz

Jerry Roberts
University of Nottingham

John Roden
Southern Oregon University

Jocelyn K. C. Rose
Cornell University

Rowan F. Sage
University of Toronto

Pill-Soon Song
Jeju National University

Valerie Sponsel
The University of Texas at San Antonio

Venkatesan Sundaresan
University of California, Davis

Dan Szymanski
Purdue University

Lawrence D. Talbott
University of California, Los Angeles

Paolo Trost
University of Bologna

Miltos Tsiantis
University of Oxford

Robert Turgeon
Cornell University

David Twell
University of Leicester

Michael Udvardi
The Samuel Roberts Noble Foundation

Luis Vidali
Worcester Polytechnic Institute

Rick Vierstra
University of Wisconsin, Madison

John M. Ward
University of Minnesota

John C. Watson
*Indiana University–Purdue University
Indianapolis*

Dolf Weijers
Wageningen University

Ramin Yadegari
University of Arizona

Preface

Readers of previous editions of this text will notice a significant new feature of the Sixth Edition from the cover alone: the title has been changed from *Plant Physiology* to *Plant Physiology and Development*. The new title reflects a major reorganization of Unit III (*Growth and Development*) along developmental lines. Instead of separate chapters on the structure and function of individual photoreceptors and hormones, the interactions of photoreceptors and hormones are described in the context of the plant life cycle, from seed to seed. This change in approach has been facilitated by the virtual explosion of information on the interactions of signaling pathways and gene networks during the past four years. Among the many new topics that are being covered for the first time in the Sixth Edition are seed dormancy, germination, seedling establishment, root and shoot architecture, gametophyte development, pollination, seed development, fruit development, biotic interactions, and plant senescence. The resulting up-to-date, comprehensive, and meticulously illustrated presentation of plant development will provide students with an unprecedented appreciation of the integration of light, hormones, and other signaling agents that regulate the various stages of the plant life cycle.

The chapters in Units I and II covering traditional plant physiological topics such as water relations, mineral nutrition, transport, photosynthesis, and respiration, have also been extensively updated for the Sixth Edition. These processes function more or less continuously throughout the life of the plant and, in our view, attempting to insert them arbitrarily into a particular stage of the life cycle is not only misleading, it disrupts the flow of the developmental narrative. Therefore, for pedagogical reasons, we have

maintained the integrity of the physiological chapters at the front end of the book. After mastering the basic physiological processes discussed in Units I and II, students are fully prepared to focus their attention on the signaling pathways and gene networks that govern the temporal changes that occur during the plant life cycle, as described in Unit III.

Besides the title change, a second important novel feature of the Sixth Edition can be gleaned from the cover: the addition of two new editors, Ian Max Møller, Associate Professor at the Department of Molecular Biology and Genetics at Aarhus University, Denmark, and Angus Murphy, Professor and Chair, Department of Plant Science and Landscape Architecture at the University of Maryland in College Park. Max Møller served as a Developmental Editor for the text as a whole, assessing every chapter for level, consistency, and pedagogy. Angus Murphy spearheaded the reorganization of Unit III and was a contributing author on several of the chapters. Both new editors have been invaluable during the preparation of the Sixth Edition, and their presence ensures that continuity will be preserved for many more editions of the text. In addition, Wendy Peer, Assistant Professor in the Department of Environmental Science and Technology at the University of Maryland, also made important contributions to the redesign of Unit III as well as serving as a contributing author to several chapters.

Editors

L. T.
E. Z.

Sub-editors

I. M. M.
A. M.

Media and Supplements

to accompany *Plant Physiology and Development*, Sixth Edition

For the Student

Companion Website (www.plantphys.net)

Available free of charge, this website supplements the coverage provided in the textbook with additional and more advanced material on selected topics of interest and current research. In-text references to Web Topics and Essays are included throughout the textbook, and the end of each chapter includes a complete list of Topics and Essays for that chapter. The site includes the following:

- *Web Topics*: Additional coverage of selected topics
- *Web Essays*: Articles on cutting-edge research, written by the researchers themselves
- *Study Questions*: A set of short-answer questions for each chapter
- *References*: A set of chapter-specific references, categorized by section heading.
- *Appendices*: New for the Sixth Edition, four complete appendices are available online:
 - Appendix 1: Energy and Enzymes
 - Appendix 2: The Analysis of Plant Growth
 - Appendix 3: Hormone Biosynthetic Pathways
 - Appendix 4: Secondary Metabolites

For the Instructor

Instructor's Resource Library

(Available to qualified adopters)

The *Plant Physiology and Development*, Sixth Edition Instructor's Resource Library includes a collection of visual resources from the textbook for use in preparing lectures and other course materials. The textbook figures have all been sized and formatted for optimal legibility when projected. The IRL includes all textbook figures and tables in JPEG (both high- and low-resolution) and PowerPoint formats.

Value Options

eBook

Plant Physiology and Development is available as an eBook, in several different formats, including VitalSource CourseSmart, Yuzu, and BryteWave. The eBook can be purchased as either a 180-day rental or a permanent (non-expiring) subscription. All major mobile devices are supported. For details on the eBook platforms offered, please visit www.sinauer.com/ebooks.

Looseleaf Textbook (ISBN 978-1-60535-353-1)

Plant Physiology and Development is available in a three-hole punched, looseleaf format. Students can take just the sections they need to class and can easily integrate instructor material with the text.

Table of Contents

CHAPTER 1

Plant and Cell Architecture 1

Plant Life Processes: Unifying Principles 2

Plant Classification and Life Cycles 2

Plant life cycles alternate between diploid and haploid generations 3

Overview of Plant Structure 5

Plant cells are surrounded by rigid cell walls 5

Plasmodesmata allow the free movement of molecules between cells 8

New cells originate in dividing tissues called meristems 8

Plant Cell Organelles 10

Biological membranes are phospholipid bilayers that contain proteins 10

The Endomembrane System 13

The nucleus contains the majority of the genetic material 13

Gene expression involves both transcription and translation 17

The endoplasmic reticulum is a network of internal membranes 17

Secretion of proteins from cells begins with the rough ER 19

Glycoproteins and polysaccharides destined for secretion are processed in the Golgi apparatus 20

The plasma membrane has specialized regions involved in membrane recycling 22

Vacuoles have diverse functions in plant cells 23

Independently Dividing or Fusing Organelles Derived from the Endomembrane System 23

Oil bodies are lipid-storing organelles 23

Microbodies play specialized metabolic roles in leaves and seeds 24

Independently Dividing, Semiautonomous Organelles 25

Proplastids mature into specialized plastids in different plant tissues 27

Chloroplast and mitochondrial division are independent of nuclear division 29

The Plant Cytoskeleton 29

The plant cytoskeleton consists of microtubules and microfilaments 29

Actin, tubulin, and their polymers are in constant flux in the living cell 31

Cortical microtubules move around the cell by treadmilling 33

Cytoskeletal motor proteins mediate cytoplasmic streaming and directed organelle movement 33

Cell Cycle Regulation 35

Each phase of the cell cycle has a specific set of biochemical and cellular activities 35

The cell cycle is regulated by cyclins and cyclin-dependent kinases 36

Mitosis and cytokinesis involve both microtubules and the endomembrane system 37

Plant Cell Types 39

Dermal tissues cover the surfaces of plants 39

Ground tissues form the bodies of plants 40

Vascular tissues form transport networks between different parts of the plant 44

CHAPTER 2

Genome Structure and Gene Expression 51

Nuclear Genome Organization 51

The nuclear genome is packaged into chromatin 52

Centromeres, telomeres, and nucleolar organizer regions contain repetitive sequences 52

Transposons are mobile sequences within the genome 53

Chromosome organization is not random in the interphase nucleus 54

Meiosis halves the number of chromosomes and allows for the recombination of alleles 54

Polyploids contain multiple copies of the entire genome 56

Phenotypic and physiological responses to polyploidy are unpredictable 58

The role of polyploidy in evolution is still unclear 60

Plant Cytoplasmic Genomes: Mitochondria and Plastids 61

The endosymbiotic theory describes the origin of cytoplasmic genomes 61

Organelle genomes vary in size 61

Organelle genetics do not obey Mendelian principles 61

Transcriptional Regulation of Nuclear Gene Expression 62

RNA polymerase II binds to the promoter region of most protein-coding genes 62

Conserved nucleotide sequences signal transcriptional termination and polyadenylation 64

Epigenetic modifications help determine gene activity 65

Posttranscriptional Regulation of Nuclear Gene Expression 67

All RNA molecules are subject to decay 67

Noncoding RNAs regulate mRNA activity via the RNA interference (RNAi) pathway 67

Posttranslational regulation determines the life span of proteins 71

Tools for Studying Gene Function 72

Mutant analysis can help elucidate gene function 72

Molecular techniques can measure the activity of genes 73

Gene fusions can introduce reporter genes 74

Genetic Modification of Crop Plants 76

Transgenes can confer resistance to herbicides or plant pests 77

Genetically modified organisms are controversial 77

UNIT I Transport and Translocation of Water and Solutes 81

CHAPTER 3

Water and Plant Cells 83

Water in Plant Life 83

The Structure and Properties of Water 84

Water is a polar molecule that forms hydrogen bonds 84

Water is an excellent solvent 85

Water has distinctive thermal properties relative to its size 85

Water molecules are highly cohesive 85

Water has a high tensile strength 86

Diffusion and Osmosis 87

Diffusion is the net movement of molecules by random thermal agitation 87

Diffusion is most effective over short distances 88

Osmosis describes the net movement of water across a selectively permeable barrier 88

Water Potential 89

The chemical potential of water represents the free-energy status of water 89

Three major factors contribute to cell water potential 90

Water potentials can be measured 90

Water Potential of Plant Cells 91

Water enters the cell along a water potential gradient 91

Water can also leave the cell in response to a water potential gradient 92

Water potential and its components vary with growth conditions and location within the plant 93

Cell Wall and Membrane Properties 93

Small changes in plant cell volume cause large changes in turgor pressure 93

The rate at which cells gain or lose water is influenced by cell membrane hydraulic conductivity 94

Aquaporins facilitate the movement of water across cell membranes 95

Plant Water Status 96

Physiological processes are affected by plant water status 96

Solute accumulation helps cells maintain turgor and volume 96

CHAPTER 4

Water Balance of Plants 99

Water in the Soil 99

A negative hydrostatic pressure in soil water lowers soil water potential 100

Water moves through the soil by bulk flow 101

Water Absorption by Roots 101

Water moves in the root via the apoplast, symplast, and transmembrane pathways 102

Solute accumulation in the xylem can generate “root pressure” 103

Water Transport through the Xylem 104

The xylem consists of two types of transport cells 104

Water moves through the xylem by pressure-driven bulk flow 105

Water movement through the xylem requires a smaller pressure gradient than movement through living cells 106

What pressure difference is needed to lift water 100 meters to a treetop? 107

The cohesion–tension theory explains water transport in the xylem 107

Xylem transport of water in trees faces physical challenges 108

Plants minimize the consequences of xylem cavitation 110

Water Movement from the Leaf to the Atmosphere 110

Leaves have a large hydraulic resistance 111

The driving force for transpiration is the difference in water vapor concentration 111

Water loss is also regulated by the pathway resistances 112

Stomatal control couples leaf transpiration to leaf photosynthesis 112

The cell walls of guard cells have specialized features 113

An increase in guard cell turgor pressure opens the stomata 115

The transpiration ratio measures the relationship between water loss and carbon gain 116

Overview: The Soil–Plant–Atmosphere Continuum 116

CHAPTER 5

Mineral Nutrition 119

Essential Nutrients, Deficiencies, and Plant Disorders 120

Special techniques are used in nutritional studies 122

Nutrient solutions can sustain rapid plant growth 122

Mineral deficiencies disrupt plant metabolism and function 125

Analysis of plant tissues reveals mineral deficiencies 129

Treating Nutritional Deficiencies 129

Crop yields can be improved by the addition of fertilizers 130

Some mineral nutrients can be absorbed by leaves 131

Soil, Roots, and Microbes 131

Negatively charged soil particles affect the adsorption of mineral nutrients 131

Soil pH affects nutrient availability, soil microbes, and root growth 132

Excess mineral ions in the soil limit plant growth 133

Some plants develop extensive root systems 133

Root systems differ in form but are based on common structures 134

Different areas of the root absorb different mineral ions 135

Nutrient availability influences root growth 137

Mycorrhizal symbioses facilitate nutrient uptake by roots 137

Nutrients move between mycorrhizal fungi and root cells 140

CHAPTER 6

Solute Transport 143

Passive and Active Transport 144

Transport of Ions across Membrane Barriers 145

Different diffusion rates for cations and anions produce diffusion potentials 146

How does membrane potential relate to ion distribution? 146

The Nernst equation distinguishes between active and passive transport 147

Proton transport is a major determinant of the membrane potential 148

Membrane Transport Processes 149

Channels enhance diffusion across membranes 150

Carriers bind and transport specific substances 151

Primary active transport requires energy 151

Kinetic analyses can elucidate transport mechanisms 154

Membrane Transport Proteins 155

The genes for many transporters have been identified 157

Transporters exist for diverse nitrogen-containing compounds 157

Cation transporters are diverse 158

Anion transporters have been identified 160

Transporters for metal and metalloid ions transport essential micronutrients 160

Aquaporins have diverse functions 160

Plasma membrane H⁺-ATPases are highly regulated P-type ATPases 161

The tonoplast H^+ -ATPase drives solute accumulation in vacuoles 162
 H^+ -pyrophosphatases also pump protons at the tonoplast 163

Ion Transport in Roots 163

Solutes move through both apoplast and symplast 164
 Ions cross both symplast and apoplast 164
 Xylem parenchyma cells participate in xylem loading 164

UNIT II

Biochemistry and Metabolism 169

CHAPTER 7

Photosynthesis: The Light Reactions 171

Photosynthesis in Higher Plants 171

General Concepts 172

Light has characteristics of both a particle and a wave 172
 When molecules absorb or emit light, they change their electronic state 173
 Photosynthetic pigments absorb the light that powers photosynthesis 175

Key Experiments in Understanding Photosynthesis 175

Action spectra relate light absorption to photosynthetic activity 176
 Photosynthesis takes place in complexes containing light-harvesting antennas and photochemical reaction centers 176
 The chemical reaction of photosynthesis is driven by light 178
 Light drives the reduction of $NADP^+$ and the formation of ATP 178
 Oxygen-evolving organisms have two photosystems that operate in series 179

Organization of the Photosynthetic Apparatus 180

The chloroplast is the site of photosynthesis 180
 Thylakoids contain integral membrane proteins 181
 Photosystems I and II are spatially separated in the thylakoid membrane 181
 Anoxygenic photosynthetic bacteria have a single reaction center 182

Organization of Light-Absorbing Antenna Systems 183

Antenna systems contain chlorophyll and are membrane-associated 183
 The antenna funnels energy to the reaction center 183
 Many antenna pigment-protein complexes have a common structural motif 183

Mechanisms of Electron Transport 185

Electrons from chlorophyll travel through the carriers organized in the Z scheme 185
 Energy is captured when an excited chlorophyll reduces an electron acceptor molecule 186
 The reaction center chlorophylls of the two photosystems absorb at different wavelengths 187
 The PSII reaction center is a multi-subunit pigment-protein complex 188
 Water is oxidized to oxygen by PSII 188
 Pheophytin and two quinones accept electrons from PSII 189
 Electron flow through the cytochrome b_6f complex also transports protons 191
 Plastoquinone and plastocyanin carry electrons between photosystems II and I 192
 The PSI reaction center reduces $NADP^+$ 192
 Cyclic electron flow generates ATP but no NADPH 193
 Some herbicides block photosynthetic electron flow 193

Proton Transport and ATP Synthesis in the Chloroplast 193

Repair and Regulation of the Photosynthetic Machinery 195

Carotenoids serve as photoprotective agents 196
 Some xanthophylls also participate in energy dissipation 197
 The PSII reaction center is easily damaged 197
 PSI is protected from active oxygen species 198
 Thylakoid stacking permits energy partitioning between the photosystems 198

Genetics, Assembly, and Evolution of Photosynthetic Systems 198

Chloroplast genes exhibit non-Mendelian patterns of inheritance 198
 Most chloroplast proteins are imported from the cytoplasm 199
 The biosynthesis and breakdown of chlorophyll are complex pathways 199
 Complex photosynthetic organisms have evolved from simpler forms 199

CHAPTER 8**Photosynthesis:
The Carbon Reactions 203****The Calvin–Benson Cycle 204**

The Calvin–Benson cycle has three phases:
carboxylation, reduction, and regeneration 204

The fixation of CO₂ via carboxylation of ribulose
1,5-bisphosphate and the reduction of the product
3-phosphoglycerate yield triose phosphates 206

The regeneration of ribulose 1,5-bisphosphate ensures
the continuous assimilation of CO₂ 207

An induction period precedes the steady state of
photosynthetic CO₂ assimilation 208

Many mechanisms regulate the Calvin–Benson
cycle 209

Rubisco-activase regulates the catalytic activity of
rubisco 209

Light regulates the Calvin–Benson cycle via the
ferredoxin–thioredoxin system 210

Light-dependent ion movements modulate enzymes of
the Calvin–Benson cycle 211

Light controls the assembly of chloroplast enzymes into
supramolecular complexes 211

**The C₂ Oxidative Photosynthetic Carbon
Cycle 211**

The oxygenation of ribulose 1,5-bisphosphate sets
in motion the C₂ oxidative photosynthetic carbon
cycle 213

Photorespiration is linked to the photosynthetic electron
transport system 217

Enzymes of the plant C₂ oxidative photosynthetic carbon
cycle derive from different ancestors 217

Cyanobacteria use a proteobacterial pathway for
bringing carbon atoms of 2-phosphoglycolate back to
the Calvin–Benson cycle 217

The C₂ oxidative photosynthetic carbon cycle interacts
with many metabolic pathways 218

Production of biomass may be enhanced by engineering
photorespiration 219

**Inorganic Carbon–Concentrating
Mechanisms 220****Inorganic Carbon–Concentrating Mechanisms:
The C₄ Carbon Cycle 220**

Malate and aspartate are the primary carboxylation
products of the C₄ cycle 221

The C₄ cycle assimilates CO₂ by the concerted action of
two different types of cells 222

The C₄ cycle uses different mechanisms for
decarboxylation of four-carbon acids transported to
bundle sheath cells 224

Bundle sheath cells and mesophyll cells exhibit
anatomical and biochemical differences 224

The C₄ cycle also concentrates CO₂ in single cells 225

Light regulates the activity of key C₄ enzymes 225

Photosynthetic assimilation of CO₂ in C₄ plants
demands more transport processes than in C₃
plants 225

In hot, dry climates, the C₄ cycle reduces
photorespiration 228

**Inorganic Carbon–Concentrating Mechanisms:
Crassulacean Acid Metabolism (CAM) 228**

Different mechanisms regulate C₄ PEPCase and CAM
PEPCase 230

CAM is a versatile mechanism sensitive to
environmental stimuli 230

**Accumulation and Partitioning of
Photosynthates—Starch and Sucrose 230****Formation and Mobilization of Chloroplast
Starch 231**

Chloroplast stroma accumulates starch as insoluble
granules during the day 233

Starch degradation at night requires the phosphorylation
of amylopectin 236

The export of maltose prevails in the nocturnal
breakdown of transitory starch 237

The synthesis and degradation of the starch granule are
regulated by multiple mechanisms 237

Sucrose Biosynthesis and Signaling 238

Triose phosphates from the Calvin–Benson cycle build
up the cytosolic pool of three important hexose
phosphates in the light 238

Fructose 2,6-bisphosphate regulates the hexose
phosphate pool in the light 239

Sucrose is continuously synthesized in the cytosol 239

CHAPTER 9**Photosynthesis: Physiological and
Ecological Considerations 245****Photosynthesis Is Influenced by Leaf
Properties 246**

Leaf anatomy and canopy structure maximize light
absorption 247

Leaf angle and leaf movement can control light
absorption 249

Leaves acclimate to sun and shade environments 249

**Effects of Light on Photosynthesis in the Intact
Leaf 250**

Light-response curves reveal photosynthetic
properties 250

Leaves must dissipate excess light energy 252

Absorption of too much light can lead to photoinhibition 254

Effects of Temperature on Photosynthesis in the Intact Leaf 255

Leaves must dissipate vast quantities of heat 255

There is an optimal temperature for photosynthesis 256

Photosynthesis is sensitive to both high and low temperatures 256

Photosynthetic efficiency is temperature-sensitive 257

Effects of Carbon Dioxide on Photosynthesis in the Intact Leaf 258

Atmospheric CO₂ concentration keeps rising 258

CO₂ diffusion to the chloroplast is essential to photosynthesis 258

CO₂ imposes limitations on photosynthesis 260

How will photosynthesis and respiration change in the future under elevated CO₂ conditions? 262

Stable Isotopes Record Photosynthetic Properties 264

How do we measure the stable carbon isotopes of plants? 264

Why are there carbon isotope ratio variations in plants? 265

CHAPTER 10

Stomatal Biology 269

Light-dependent Stomatal Opening 270

Guard cells respond to blue light 270

Blue light activates a proton pump at the guard cell plasma membrane 271

Blue-light responses have characteristic kinetics and lag times 273

Blue light regulates the osmotic balance of guard cells 273

Sucrose is an osmotically active solute in guard cells 275

Mediation of Blue-light Photoreception in Guard Cells by Zeaxanthin 276

Reversal of Blue Light-Stimulated Opening by Green Light 278

A carotenoid-protein complex senses light intensity 280

The Resolving Power of Photophysiology 280

CHAPTER 11

Translocation in the Phloem 285

Pathways of Translocation 286

Sugar is translocated in phloem sieve elements 286

Mature sieve elements are living cells specialized for translocation 287

Large pores in cell walls are the prominent feature of sieve elements 288

Damaged sieve elements are sealed off 289

Companion cells aid the highly specialized sieve elements 290

Patterns of Translocation: Source to Sink 291

Materials Translocated in the Phloem 292

Phloem sap can be collected and analyzed 292

Sugars are translocated in a nonreducing form 293

Other solutes are translocated in the phloem 293

Rates of Movement 295

The Pressure-Flow Model, a Passive Mechanism for Phloem Transport 295

An osmotically generated pressure gradient drives translocation in the pressure-flow model 295

Some predictions of pressure flow have been confirmed, while others require further experimentation 296

There is no bidirectional transport in single sieve elements, and solutes and water move at the same velocity 297

The energy requirement for transport through the phloem pathway is small in herbaceous plants 297

Sieve plate pores appear to be open channels 298

Pressure gradients in the sieve elements may be modest; pressures in herbaceous plants and trees appear to be similar 298

Alternative models for translocation by mass flow have been suggested 299

Does translocation in gymnosperms involve a different mechanism? 299

Phloem Loading 300

Phloem loading can occur via the apoplast or symplast 300

Abundant data support the existence of apoplastic loading in some species 301

Sucrose uptake in the apoplastic pathway requires metabolic energy 301

Phloem loading in the apoplastic pathway involves a sucrose-H⁺ symporter 302

Phloem loading is symplastic in some species 302

The polymer-trapping model explains symplastic loading in plants with intermediary-type companion cells 303

Phloem loading is passive in several tree species 304
 The type of phloem loading is correlated with several significant characteristics 304

Phloem Unloading and Sink-to-Source Transition 305

Phloem unloading and short-distance transport can occur via symplastic or apoplastic pathways 305
 Transport into sink tissues requires metabolic energy 306
 The transition of a leaf from sink to source is gradual 307

Photosynthate Distribution: Allocation and Partitioning 309

Allocation includes storage, utilization, and transport 309
 Various sinks partition transport sugars 309
 Source leaves regulate allocation 310
 Sink tissues compete for available translocated photosynthate 310
 Sink strength depends on sink size and activity 311
 The source adjusts over the long term to changes in the source-to-sink ratio 311

Transport of Signaling Molecules 311

Turgor pressure and chemical signals coordinate source and sink activities 312
 Proteins and RNAs function as signal molecules in the phloem to regulate growth and development 312
 Plasmodesmata function in phloem signaling 313

CHAPTER 12

Respiration and Lipid Metabolism 317

Overview of Plant Respiration 317

Glycolysis 321

Glycolysis metabolizes carbohydrates from several sources 321
 The energy-conserving phase of glycolysis extracts usable energy 322
 Plants have alternative glycolytic reactions 322
 In the absence of oxygen, fermentation regenerates the NAD⁺ needed for glycolysis 323
 Plant glycolysis is controlled by its products 324

The Oxidative Pentose Phosphate Pathway 324

The oxidative pentose phosphate pathway produces NADPH and biosynthetic intermediates 326
 The oxidative pentose phosphate pathway is redox-regulated 326

The Citric Acid Cycle 326

Mitochondria are semiautonomous organelles 327

Pyruvate enters the mitochondrion and is oxidized via the citric acid cycle 328

The citric acid cycle of plants has unique features 329

Mitochondrial Electron Transport and ATP Synthesis 329

The electron transport chain catalyzes a flow of electrons from NADH to O₂ 330
 The electron transport chain has supplementary branches 332
 ATP synthesis in the mitochondrion is coupled to electron transport 333
 Transporters exchange substrates and products 334
 Aerobic respiration yields about 60 molecules of ATP per molecule of sucrose 334
 Several subunits of respiratory complexes are encoded by the mitochondrial genome 336
 Plants have several mechanisms that lower the ATP yield 336
 Short-term control of mitochondrial respiration occurs at different levels 338
 Respiration is tightly coupled to other pathways 339

Respiration in Intact Plants and Tissues 340

Plants respire roughly half of the daily photosynthetic yield 340
 Respiration operates during photosynthesis 341
 Different tissues and organs respire at different rates 341
 Environmental factors alter respiration rates 342

Lipid Metabolism 343

Fats and oils store large amounts of energy 343
 Triacylglycerols are stored in oil bodies 343
 Polar glycerolipids are the main structural lipids in membranes 344
 Fatty acid biosynthesis consists of cycles of two-carbon addition 344
 Glycerolipids are synthesized in the plastids and the ER 346
 Lipid composition influences membrane function 348
 Membrane lipids are precursors of important signaling compounds 348
 Storage lipids are converted into carbohydrates in germinating seeds 348

CHAPTER 13

Assimilation of Inorganic Nutrients 353

Nitrogen in the Environment 354

Nitrogen passes through several forms in a biogeochemical cycle 354
 Unassimilated ammonium or nitrate may be dangerous 355

Nitrate Assimilation 356

- Many factors regulate nitrate reductase 356
- Nitrite reductase converts nitrite to ammonium 357
- Both roots and shoots assimilate nitrate 357

Ammonium Assimilation 358

- Converting ammonium to amino acids requires two enzymes 358
- Ammonium can be assimilated via an alternative pathway 360
- Transamination reactions transfer nitrogen 360
- Asparagine and glutamine link carbon and nitrogen metabolism 360

Amino Acid Biosynthesis 360**Biological Nitrogen Fixation 360**

- Free-living and symbiotic bacteria fix nitrogen 361
- Nitrogen fixation requires microanaerobic or anaerobic conditions 362
- Symbiotic nitrogen fixation occurs in specialized structures 363
- Establishing symbiosis requires an exchange of signals 364

- Nod factors produced by bacteria act as signals for symbiosis 364
- Nodule formation involves phytohormones 365
- The nitrogenase enzyme complex fixes N_2 366
- Amides and ureides are the transported forms of nitrogen 367

Sulfur Assimilation 367

- Sulfate is the form of sulfur transported into plants 368
- Sulfate assimilation requires the reduction of sulfate to cysteine 368
- Sulfate assimilation occurs mostly in leaves 369
- Methionine is synthesized from cysteine 369

Phosphate Assimilation 369**Cation Assimilation 370**

- Cations form noncovalent bonds with carbon compounds 370
- Roots modify the rhizosphere to acquire iron 371
- Iron cations form complexes with carbon and phosphate 372

Oxygen Assimilation 372**The Energetics of Nutrient Assimilation 372****UNIT
III****Growth and Development 377****CHAPTER 14****Cell Walls: Structure, Formation, and Expansion 379****Overview of Plant Cell Wall Functions and Structures 380**

- Plants vary in structure and function 380
- Components differ for primary and secondary cell walls 382
- Cellulose microfibrils have an ordered structure and are synthesized at the plasma membrane 384
- Matrix polymers are synthesized in the Golgi apparatus and secreted via vesicles 387
- Pectins are hydrophilic gel-forming components of the primary cell wall 388
- Hemicelluloses are matrix polysaccharides that bind to cellulose 390

Primary Cell Wall Structure and Function 392

- The primary cell wall is composed of cellulose microfibrils embedded in a matrix of pectins and hemicelluloses 392

- New primary cell walls are assembled during cytokinesis and continue to be assembled during growth 392

Mechanisms of Cell Expansion 393

- Microfibril orientation influences growth directionality of cells with diffuse growth 394
- Cortical microtubules influence the orientation of newly deposited microfibrils 395

The Extent and Rate of Cell Growth 397

- Stress relaxation of the cell wall drives water uptake and cell expansion 397
- Acid-induced growth and wall stress relaxation are mediated by expansins 397
- Cell wall models are hypotheses about how molecular components fit together to make a functional wall 399
- Many structural changes accompany the cessation of wall expansion 400

Secondary Cell Wall Structure and Function 400

- Secondary cell walls are rich in cellulose and hemicellulose and often have a hierarchical organization 400
- Lignification transforms the SCW into a hydrophobic structure resistant to deconstruction 402

CHAPTER 15

Signals and Signal Transduction 407

Temporal and Spatial Aspects of Signaling 408

Signal Perception and Amplification 409

- Receptors are located throughout the cell and are conserved across kingdoms 409
- Signals must be amplified intracellularly to regulate their target molecules 411
- The MAP kinase signal amplification cascade is present in all eukaryotes 411
- Ca²⁺ is the most ubiquitous second messenger in plants and other eukaryotes 411
- Changes in the cytosolic or cell wall pH can serve as second messengers for hormonal and stress responses 412
- Reactive oxygen species act as second messengers mediating both environmental and developmental signals 413
- Lipid signaling molecules act as second messengers that regulate a variety of cellular processes 414

Hormones and Plant Development 414

- Auxin was discovered in early studies of coleoptile bending during phototropism 417
- Gibberellins promote stem growth and were discovered in relation to the “foolish seedling disease” of rice 417
- Cytokinins were discovered as cell division–promoting factors in tissue culture experiments 418
- Ethylene is a gaseous hormone that promotes fruit ripening and other developmental processes 419
- Abscisic acid regulates seed maturation and stomatal closure in response to water stress 419
- Brassinosteroids regulate photomorphogenesis, germination, and other developmental processes 420
- Strigolactones suppress branching and promote rhizosphere interactions 421

Phytohormone Metabolism and Homeostasis 421

- Indole-3-pyruvate is the primary intermediate in auxin biosynthesis 421
- Gibberellins are synthesized by oxidation of the diterpene *ent*-kaurene 422
- Cytokinins are adenine derivatives with isoprene side chains 423
- Ethylene is synthesized from methionine via the intermediate ACC 426
- Abscisic acid is synthesized from a carotenoid intermediate 426
- Brassinosteroids are derived from the sterol campesterol 428

Strigolactones are synthesized from β -carotene 429

Signal Transmission and Cell–Cell Communication 429

Hormonal Signaling Pathways 431

- The cytokinin and ethylene signal transduction pathways are derived from the bacterial two-component regulatory system 431
- Receptor-like kinases mediate brassinosteroid and certain auxin signaling pathways 433
- The core ABA signaling components include phosphatases and kinases 436
- Plant hormone signaling pathways generally employ negative regulation 436
- Several plant hormone receptors encode components of the ubiquitination machinery and mediate signaling via protein degradation 437
- Plants have evolved mechanisms for switching off or attenuating signaling responses 439
- The cellular response output to a signal is often tissue-specific 441
- Cross-regulation allows signal transduction pathways to be integrated 441

CHAPTER 16

Signals from Sunlight 447

Plant Photoreceptors 448

- Photoresponses are driven by light quality or spectral properties of the energy absorbed 449
- Plants responses to light can be distinguished by the amount of light required 450

Phytochromes 452

- Phytochrome is the primary photoreceptor for red and far-red light 452
- Phytochrome can interconvert between Pr and Pfr forms 452
- Pfr is the physiologically active form of phytochrome 453
- The phytochrome chromophore and protein both undergo conformational changes in response to red light 453
- Pfr is partitioned between the cytosol and the nucleus 454

Phytochrome Responses 457

- Phytochrome responses vary in lag time and escape time 457
- Phytochrome responses fall into three main categories based on the amount of light required 457
- Phytochrome A mediates responses to continuous far-red light 459
- Phytochrome B mediates responses to continuous red or white light 459

Roles for phytochromes C, D, and E are emerging 459

Phytochrome Signaling Pathways 459

Phytochrome regulates membrane potentials and ion fluxes 459

Phytochrome regulates gene expression 460

Phytochrome interacting factors (PIFs) act early in signaling 460

Phytochrome signaling involves protein phosphorylation and dephosphorylation 461

Phytochrome-induced photomorphogenesis involves protein degradation 461

Blue-Light Responses and Photoreceptors 462

Blue-light responses have characteristic kinetics and lag times 462

Cryptochromes 463

The activated FAD chromophore of cryptochrome causes a conformational change in the protein 463

cry1 and cry2 have different developmental effects 465

Nuclear cryptochromes inhibit COP1-induced protein degradation 465

Cryptochrome can also bind to transcriptional regulators directly 465

The Coaction of Cryptochrome, Phytochrome, and Phototropins 466

Stem elongation is inhibited by both red and blue photoreceptors 466

Phytochrome interacts with cryptochrome to regulate flowering 467

The circadian clock is regulated by multiple aspects of light 467

Phototropins 467

Blue light induces changes in FMN absorption maxima associated with conformation changes 468

The LOV2 domain is primarily responsible for kinase activation in response to blue light 469

Blue light induces a conformational change that “uncages” the kinase domain of phototropin and leads to autophosphorylation 469

Phototropism requires changes in auxin mobilization 469

Phototropins regulate chloroplast movements via F-actin filament assembly 470

Stomatal opening is regulated by blue light, which activates the plasma membrane H⁺-ATPase 471

The main signal transduction events of phototropin-mediated stomatal opening have been identified 472

Responses to Ultraviolet Radiation 473

CHAPTER 17

Embryogenesis 477

Overview of Plant Growth and Development 478

Sporophytic development can be divided into three major stages 479

Embryogenesis: The Origins of Polarity 480

Embryogenesis differs between eudicots and monocots, but also features common fundamental processes 480

Apical–basal polarity is established early in embryogenesis 481

Position-dependent mechanisms guide embryogenesis 483

Intercellular signaling processes play key roles in guiding position-dependent development 484

Embryo development features regulate communication between cells 484

The analysis of mutants identifies genes for signaling processes that are essential for embryo organization 485

Auxin functions as a mobile chemical signal during embryogenesis 487

Plant polarity is maintained by polar auxin streams 487

Auxin transport is regulated by multiple mechanisms 489

The GNOM protein establishes a polar distribution of PIN auxin efflux proteins 491

MONOPTEROS encodes a transcription factor that is activated by auxin 492

Radial patterning guides formation of tissue layers 492

The origin of epidermis: a boundary and interface at the edge of the radial axis 492

Procambial precursors for the vascular stele lie at the center of the radial axis 493

The differentiation of cortical and endodermal cells involves the intercellular movement of a transcription factor 494

Meristematic Tissues: Foundations for Indeterminate Growth 495

The root and shoot apical meristems use similar strategies to enable indeterminate growth 495

The Root Apical Meristem 496

The root tip has four developmental zones 497

The origin of different root tissues can be traced to specific initial cells 497

Cell ablation experiments implicate directional signaling processes in determination of cell identity 499

Auxin contributes to the formation and maintenance of the RAM 499

Responses to auxin are mediated by several distinct families of transcription factors 499

Cytokinin is required for normal root development 500

The Shoot Apical Meristem 500

The shoot apical meristem has distinct zones and layers 502

Shoot tissues are derived from several discrete sets of apical initials 502

Factors involved in auxin movement and responses influence SAM formation 503

Embryonic SAM formation requires the coordinated expression of transcription factors 503

A combination of positive and negative interactions determines apical meristem size 505

KNOX class homeodomain genes help maintain the proliferative ability of the SAM through regulation of cytokinin and GA levels 506

Localized zones of auxin accumulation promote leaf initiation 507

The Vascular Cambium 508

The maintenance of undetermined initials in various meristem types depends on similar mechanisms 508

CHAPTER 18

Seed Dormancy, Germination, and Seedling Establishment 513

Seed Structure 514

Seed anatomy varies widely among different plant groups 514

Seed Dormancy 515

Dormancy can be imposed on the embryo by the surrounding tissues 516

Embryo dormancy may be caused by physiological or morphological factors 516

Non-dormant seeds can exhibit vivipary and precocious germination 516

The ABA:GA ratio is the primary determinant of seed dormancy 517

Release from Dormancy 519

Light is an important signal that breaks dormancy in small seeds 519

Some seeds require either chilling or after-ripening to break dormancy 519

Seed dormancy can be broken by various chemical compounds 520

Seed Germination 520

Germination can be divided into three phases corresponding to the phases of water uptake 520

Mobilization of Stored Reserves 522

The cereal aleurone layer is a specialized digestive tissue surrounding the starchy endosperm 522

Gibberellins enhance the transcription of α -amylase mRNA 522

The gibberellin receptor, *GID1*, promotes the degradation of negative regulators of the gibberellin response 523

GA-MYB is a positive regulator of α -amylase transcription 524

DELLA repressor proteins are rapidly degraded 524

ABA inhibits gibberellin-induced enzyme production 524

Seedling Growth and Establishment 526

Auxin promotes growth in stems and coleoptiles, while inhibiting growth in roots 526

The outer tissues of eudicot stems are the targets of auxin action 526

The minimum lag time for auxin-induced elongation is 10 minutes 526

Auxin-induced proton extrusion induces cell wall creep and cell elongation 528

Tropisms: Growth in Response to Directional Stimuli 528

Gravitropism involves the lateral redistribution of auxin 528

Polar auxin transport requires energy and is gravity independent 529

According to the starch–statolith hypothesis, specialized amyloplasts serve as gravity sensors in root caps 530

Auxin movements in the root are regulated by specific transporters 532

The gravitropic stimulus perturbs the symmetric movement of auxin from the root tip 533

Gravity perception in eudicot stems and stemlike organs occurs in the starch sheath 533

Gravity sensing may involve pH and calcium ions (Ca^{2+}) as second messengers 533

Phototropism 535

Phototropism is mediated by the lateral redistribution of auxin 535

Phototropism occurs in a series of posttranslational events 536

Photomorphogenesis 537

Gibberellins and brassinosteroids both suppress photomorphogenesis in the dark 538

Hook opening is regulated by phytochrome and auxin 539

Ethylene induces lateral cell expansion 539

Shade Avoidance 540

Phytochrome enables plants to adapt to changes in light quality 540

Decreasing the R:FR ratio causes elongation in sun plants 540

Reducing shade avoidance responses can improve crop yields 542

Vascular Tissue Differentiation 542

Auxin and cytokinin are required for normal vascular development 543

Zinnia suspension-cultured cells can be induced to undergo xylogenesis 544

Xylogenesis involves chemical signaling between neighboring cells 544

Root Growth and Differentiation 545

Root epidermal development follows three basic patterns 546

Auxin and other hormones regulate root hair development 546

Lateral root formation and emergence depend on endogenous and exogenous signals 547

Regions of lateral root emergence correspond with regions of auxin maxima 548

Lateral roots and shoots have gravitropic setpoint angles 549

CHAPTER 19

Vegetative Growth and Organogenesis 553

Leaf Development 553

The Establishment of Leaf Polarity 554

Hormonal signals play key roles in regulating leaf primordia emergence 555

A signal from the SAM initiates adaxial–abaxial polarity 555

ARP genes promote adaxial identity and repress the *KNOX1* gene 556

Adaxial leaf development requires HD-ZIP III transcription factors 556

The expression of HD-ZIP III genes is antagonized by miR166 in abaxial regions of the leaf 558

Antagonism between *KANADI* and HD-ZIP III is a key determinant of adaxial–abaxial leaf polarity 558

Interactions between adaxial and abaxial tissues are required for blade outgrowth 558

Blade outgrowth is auxin dependent and regulated by the *YABBY* and *WOX* genes 558

Leaf proximal–distal polarity also depends on specific gene expression 559

In compound leaves, de-repression of the *KNOX1* gene promotes leaflet formation 559

Differentiation of Epidermal Cell Types 561

Guard cell fate is ultimately determined by a specialized epidermal lineage 562

Two groups of bHLH transcription factors govern stomatal cell fate transitions 563

Peptide signals regulate stomatal patterning by interacting with cell surface receptors 563

Genetic screens have led to the identification of positive and negative regulators of trichome initiation 563

GLABRA2 acts downstream of the GL1–GL3–TTG1 complex to promote trichome formation 565

Jasmonic acid regulates Arabidopsis leaf trichome development 565

Venation Patterns in Leaves 565

The primary leaf vein is initiated discontinuously from the preexisting vascular system 566

Auxin canalization initiates development of the leaf trace 566

Basipetal auxin transport from the L1 layer of the leaf primordium initiates development of the leaf trace procambium 568

The existing vasculature guides the growth of the leaf trace 568

Higher-order leaf veins differentiate in a predictable hierarchical order 569

Auxin canalization regulates higher-order vein formation 570

Localized auxin biosynthesis is critical for higher-order venation patterns 571

Shoot Branching and Architecture 572

Axillary meristem initiation involves many of the same genes as leaf initiation and lamina outgrowth 573

Auxin, cytokinins, and strigolactones regulate axillary bud outgrowth 573

Auxin from the shoot tip maintains apical dominance 574

Strigolactones act locally to repress axillary bud growth 574

Cytokinins antagonize the effects of strigolactones 576

The initial signal for axillary bud growth may be an increase in sucrose availability to the bud 577

Integration of environmental and hormonal branching signals is required for plant fitness 577

Axillary bud dormancy in woody plants is affected by season, position, and age factors 578

Root System Architecture 579

Plants can modify their root system architecture to optimize water and nutrient uptake 579

Monocots and eudicots differ in their root system architecture 580

Root system architecture changes in response to phosphorous deficiencies 580

Root system architecture responses to phosphorus deficiency involve both local and systemic regulatory networks 582

Mycorrhizal networks augment root system architecture in all major terrestrial ecosystems 583

Secondary Growth 583

- The vascular cambium and cork cambium are the secondary meristems where secondary growth originates 584
- Secondary growth evolved early in the evolution of land plants 585
- Secondary growth from the vascular cambium gives rise to secondary xylem and phloem 585
- Phytohormones have important roles in regulating vascular cambium activity and differentiation of secondary xylem and phloem 585
- Genes involved in stem cell maintenance, proliferation, and differentiation regulate secondary growth 586
- Environmental factors influence vascular cambium activity and wood properties 587

CHAPTER 20**The Control of Flowering and Floral Development 591****Floral Evocation: Integrating Environmental Cues 592****The Shoot Apex and Phase Changes 592**

- Plant development has three phases 592
- Juvenile tissues are produced first and are located at the base of the shoot 592
- Phase changes can be influenced by nutrients, gibberellins, and other signals 593

Circadian Rhythms: The Clock Within 594

- Circadian rhythms exhibit characteristic features 595
- Phase shifting adjusts circadian rhythms to different day–night cycles 596
- Phytochromes and cryptochromes entrain the clock 596

Photoperiodism: Monitoring Day Length 597

- Plants can be classified according to their photoperiodic responses 597
- The leaf is the site of perception of the photoperiodic signal 599
- Plants monitor day length by measuring the length of the night 599
- Night breaks can cancel the effect of the dark period 599
- Photoperiodic timekeeping during the night depends on a circadian clock 599
- The coincidence model is based on oscillating light sensitivity 600

- The coincidence of *CONSTANS* expression and light promotes flowering in LDPs 601
- SDPs use a coincidence mechanism to inhibit flowering in long days 603
- Phytochrome is the primary photoreceptor in photoperiodism 603
- A blue-light photoreceptor regulates flowering in some LDPs 604

Vernalization: Promoting Flowering with Cold 605

- Vernalization results in competence to flower at the shoot apical meristem 605
- Vernalization can involve epigenetic changes in gene expression 606
- A range of vernalization pathways may have evolved 607

Long-Distance Signaling Involved in Flowering 608

- Grafting studies provided the first evidence for a transmissible floral stimulus 608
- Florigen is translocated in the phloem 609

The Identification of Florigen 610

- The Arabidopsis protein FLOWERING LOCUS T (FT) is florigen 610
- Gibberellins and ethylene can induce flowering 610
- The transition to flowering involves multiple factors and pathways 612

Floral Meristems and Floral Organ Development 612

- The shoot apical meristem in Arabidopsis changes with development 613
- The four different types of floral organs are initiated as separate whorls 613
- Two major categories of genes regulate floral development 614
- Floral meristem identity genes regulate meristem function 614
- Homeotic mutations led to the identification of floral organ identity genes 616
- The ABC model partially explains the determination of floral organ identity 616
- Arabidopsis Class E genes are required for the activities of the A, B, and C genes 618
- According to the Quartet Model, floral organ identity is regulated by tetrameric complexes of the ABCE proteins 618
- Class D genes are required for ovule formation 619
- Floral asymmetry in flowers is regulated by gene expression 620

CHAPTER 21

**Gametophytes, Pollination,
Seeds, and Fruits 625****Development of the Male and Female
Gametophyte Generations 625****Formation of Male Gametophytes in the
Stamen 626**

Pollen grain formation occurs in two successive stages 627

The multilayered pollen cell wall is surprisingly complex 628

**Female Gametophyte Development in the
Ovule 630**

The *Arabidopsis* gynoecium is an important model system for studying ovule development 630

The vast majority of angiosperms exhibit *Polygonum*-type embryo sac development 630

Functional megaspores undergo a series of free nuclear mitotic divisions followed by cellularization 631

Embryo sac development involves hormonal signaling between sporophytic and gametophytic generations 632

**Pollination and Fertilization in Flowering
Plants 632**

Delivery of sperm cells to the female gametophyte by the pollen tube occurs in six phases 633

Adhesion and hydration of a pollen grain on a compatible flower depend on recognition between pollen and stigma surfaces 634

Ca²⁺-triggered polarization of the pollen grain precedes tube formation 635

Pollen tubes grow by tip growth 635

Receptor-like kinases are thought to regulate the ROP1 GTPase switch, a master regulator of tip growth 635

Pollen tube tip growth in the pistil is directed by both physical and chemical cues 637

Style tissue conditions the pollen tube to respond to attractants produced by the synergids of the embryo sac 637

Double fertilization occurs in three distinct stages 638

Selfing versus Outcrossing 639

Hermaphroditic and monoecious species have evolved floral features to ensure outcrossing 639

Cytoplasmic male sterility (CMS) occurs in the wild and is of great utility in agriculture 640

Self-incompatibility (SI) is the primary mechanism that enforces outcrossing in angiosperms 640

The Brassicaceae sporophytic SI system requires two *S*-locus genes 641

Gametophytic self-incompatibility (GSI) is mediated by cytotoxic S-RNases and F-box proteins 642

Apomixis: Asexual Reproduction by Seed 643**Endosperm Development 643**

Cellularization of coenocytic endosperm in *Arabidopsis* progresses from the micropylar to the chalazal region 645

Cellularization of the coenocytic endosperm of cereals progresses centripetally 646

Endosperm development and embryogenesis can occur autonomously 646

Many of the genes that control endosperm development are maternally expressed genes 647

The FIS proteins are members of a Polycomb repressive complex (PRC2) that represses endosperm development 647

Cells of the starchy endosperm and aleurone layer follow divergent developmental pathways 649

Two genes, *DEK1* and *CR4*, have been implicated in aleurone layer differentiation 649

Seed Coat Development 650

Seed coat development appears to be regulated by the endosperm 650

Seed Maturation and Desiccation Tolerance 652

Seed filling and desiccation tolerance phases overlap in most species 652

The acquisition of desiccation tolerance involves many metabolic pathways 653

During the acquisition of desiccation tolerance, the cells of the embryo acquire a glassy state 653

LEA proteins and nonreducing sugars have been implicated in seed desiccation tolerance 653

Specific LEA proteins have been implicated in desiccation tolerance in *Medicago truncatula* 653

Abscisic acid plays a key role in seed maturation 654

Coat-imposed dormancy is correlated with long-term seed-viability 654

Fruit Development and Ripening 655

Arabidopsis and tomato are model systems for the study of fruit development 655

Fleshy fruits undergo ripening 657

Ripening involves changes in the color of fruit 657

Fruit softening involves the coordinated action of many cell wall-degrading enzymes 658

Taste and flavor reflect changes in acids, sugars, and aroma compounds 658

The causal link between ethylene and ripening was demonstrated in transgenic and mutant tomatoes 658

Climacteric and non-climacteric fruit differ in their ethylene responses 658

The ripening process is transcriptionally regulated 660

Angiosperms share a range of common molecular mechanisms controlling fruit development and ripening 660
 Fruit ripening is under epigenetic control 660
 A mechanistic understanding of the ripening process has commercial applications 661

CHAPTER 22

Plant Senescence and Cell Death 665

Programmed Cell Death and Autolysis 666

PCD during normal development differs from that of the hypersensitive response 668
 The autophagy pathway captures and degrades cellular constituents within lytic compartments 669
 A subset of the autophagy-related genes controls the formation of the autophagosome 669
 The autophagy pathway plays a dual role in plant development 671

The Leaf Senescence Syndrome 671

The developmental age of a leaf may differ from its chronological age 672
 Leaf senescence may be sequential, seasonal, or stress-induced 672
 Developmental leaf senescence consists of three distinct phases 673
 The earliest cellular changes during leaf senescence occur in the chloroplast 675
 The autolysis of chloroplast proteins occurs in multiple compartments 675
 The STAY-GREEN (SGR) protein is required for both LHCP II protein recycling and chlorophyll catabolism 676
 Leaf senescence is preceded by a massive reprogramming of gene expression 677

Leaf Senescence: The Regulatory Network 678

The *NAC* and *WRKY* gene families are the most abundant transcription factors regulating leaf senescence 678
 ROS serve as internal signaling agents in leaf senescence 680
 Sugars accumulate during leaf senescence and may serve as a signal 681
 Plant hormones interact in the regulation of leaf senescence 681

Leaf Abscission 684

The timing of leaf abscission is regulated by the interaction of ethylene and auxin 685

Whole Plant Senescence 686

Angiosperm life cycles may be annual, biennial, or perennial 687

Whole plant senescence differs from aging in animals 688
 The determinacy of shoot apical meristems is developmentally regulated 688
 Nutrient or hormonal redistribution may trigger senescence in monocarpic plants 689
 The rate of carbon accumulation in trees increases continuously with tree size 689

CHAPTER 23

Biotic Interactions 693

Beneficial Interactions between Plants and Microorganisms 695

Nod factors are recognized by the Nod factor receptor (NFR) in legumes 695
 Arbuscular mycorrhizal associations and nitrogen-fixing symbioses involve related signaling pathways 695
 Rhizobacteria can increase nutrient availability, stimulate root branching, and protect against pathogens 697

Harmful Interactions between Plants, Pathogens, and Herbivores 697

Mechanical barriers provide a first line of defense against insect pests and pathogens 698
 Plant secondary metabolites can deter insect herbivores 700
 Plants store constitutive toxic compounds in specialized structures 701
 Plants often store defensive chemicals as nontoxic water-soluble sugar conjugates in the vacuole 703
 Constitutive levels of secondary compounds are higher in young developing leaves than in older tissues 705

Inducible Defense Responses to Insect Herbivores 705

Plants can recognize specific components of insect saliva 706
 Modified fatty acids secreted by grasshoppers act as elicitors of jasmonic acid accumulation and ethylene emission 706
 Phloem feeders activate defense signaling pathways similar to those activated by pathogen infections 707
 Calcium signaling and activation of the MAP kinase pathway are early events associated with insect herbivory 707
 Jasmonic acid activates defense responses against insect herbivores 708
 Jasmonic acid acts through a conserved ubiquitin ligase signaling mechanism 709
 Hormonal interactions contribute to plant–insect herbivore interactions 709

- JA initiates the production of defense proteins that inhibit herbivore digestion 710
- Herbivore damage induces systemic defenses 710
- Glutamate receptor-like (GLR) genes are required for long-distance electrical signaling during herbivory 712
- Herbivore-induced volatiles can repel herbivores and attract natural enemies 712
- Herbivore-induced volatiles can serve as long-distance signals between plants 713
- Herbivore-induced volatiles can also act as systemic signals within a plant 714
- Defense responses to herbivores and pathogens are regulated by circadian rhythms 714
- Insects have evolved mechanisms to defeat plant defenses 715

Plant Defenses against Pathogens 715

- Microbial pathogens have evolved various strategies to invade host plants 715
- Pathogens produce effector molecules that aid in the colonization of their plant host cells 716
- Pathogen infection can give rise to molecular “danger signals” that are perceived by cell surface pattern recognition receptors (PRRs) 717
- R* genes provide resistance to individual pathogens by recognizing strain-specific effectors 718
- Exposure to elicitors induces a signal transduction cascade 719
- Effectors released by phloem-feeding insects also activate NBS–LRR receptors 719
- The hypersensitive response is a common defense against pathogens 720
- Phytoalexins with antimicrobial activity accumulate after pathogen attack 721
- A single encounter with a pathogen may increase resistance to future attacks 721
- The main components of the salicylic acid signaling pathway for SAR have been identified 723
- Interactions of plants with nonpathogenic bacteria can trigger systemic resistance through a process called induced systemic resistance (ISR) 723

Plant Defenses against Other Organisms 724

- Some plant parasitic nematodes form specific associations through the formation of distinct feeding structures 724
- Plants compete with other plants by secreting allelopathic secondary metabolites into the soil 725
- Some plants are biotrophic pathogens of other plants 726

CHAPTER 24

Abiotic Stress 731

Defining Plant Stress 732

- Physiological adjustment to abiotic stress involves trade-offs between vegetative and reproductive development 732

Acclimation and Adaptation 733

- Adaptation to stress involves genetic modification over many generations 733
- Acclimation allows plants to respond to environmental fluctuations 733

Environmental Factors and Their Biological Impacts on Plants 734

- Water deficit decreases turgor pressure, increases ion toxicity, and inhibits photosynthesis 735
- Salinity stress has both osmotic and cytotoxic effects 736
- Light stress can occur when shade-adapted or shade-acclimated plants are subjected to full sunlight 736
- Temperature stress affects a broad spectrum of physiological processes 736
- Flooding results in anaerobic stress to the root 737
- During freezing stress, extracellular ice crystal formation causes cell dehydration 737
- Heavy metals can both mimic essential mineral nutrients and generate ROS 737
- Mineral nutrient deficiencies are a cause of stress 737
- Ozone and ultraviolet light generate ROS that cause lesions and induce PCD 737
- Combinations of abiotic stresses can induce unique signaling and metabolic pathways 738
- Sequential exposure to different abiotic stresses sometimes confers cross-protection 739

Stress-Sensing Mechanisms in Plants 739

- Early-acting stress sensors provide the initial signal for the stress response 740

Signaling Pathways Activated in Response to Abiotic Stress 740

- The signaling intermediates of many stress-response pathways can interact 740
- Acclimation to stress involves transcriptional regulatory networks called *regulons* 743
- Chloroplast genes respond to high-intensity light by sending stress signals to the nucleus 744
- A self-propagating wave of ROS mediates systemic acquired acclimation 745
- Epigenetic mechanisms and small RNAs provide additional protection against stress 745

Hormonal interactions regulate normal development and abiotic stress responses 745

Developmental and Physiological Mechanisms That Protect Plants against Abiotic Stress 747

Plants adjust osmotically to drying soil by accumulating solutes 748

Submerged organs develop aerenchyma tissue in response to hypoxia 749

Antioxidants and ROS-scavenging pathways protect cells from oxidative stress 750

Molecular chaperones and molecular shields protect proteins and membranes during abiotic stress 751

Plants can alter their membrane lipids in response to temperature and other abiotic stresses 752

Exclusion and internal tolerance mechanisms allow plants to cope with toxic ions 753

Phytochelatins and other chelators contribute to internal tolerance of toxic metal ions 754

Plants use cryoprotectant molecules and antifreeze proteins to prevent ice crystal formation 754

ABA signaling during water stress causes the massive efflux of K^+ and anions from guard cells 755

Plants can alter their morphology in response to abiotic stress 757

Metabolic shifts enable plants to cope with a variety of abiotic stresses 759

The process of recovery from stress can be dangerous to the plant and requires a coordinated adjustment of plant metabolism and physiology 759

Developing crops with enhanced tolerance to abiotic stress conditions is a major goal of agricultural research 759

Glossary G–1

Illustration Credits IC–1

Photo Credits PC–1

Subject Index SI–1

1

Plant and Cell Architecture

Plant physiology is the study of plant *processes*—how plants grow, develop, and function as they interact with their physical (abiotic) and living (biotic) environments. Although this book will emphasize the physiological, biochemical, and molecular functions of plants, it is important to recognize that, whether we are talking about gas exchange in the leaf, water conduction in the xylem, photosynthesis in the chloroplast, ion transport across membranes, signal transduction pathways involving light and hormones, or gene expression during development, all of these functions depend entirely on structures.

Function derives from structures interacting at every level of scale. It occurs when tiny molecules recognize and bind each other to produce a complex with new functions. It occurs as a new leaf unfolds, as cells and tissues interact during the process of plant development. It occurs when huge organisms shade, nourish, or mate with each other. At every level, from molecules to organisms, structure and function represent different frames of reference of a biological unity.

The fundamental organizational unit of plants, and of all living organisms, is the cell. The term *cell* is derived from the Latin *cella*, meaning “storeroom” or “chamber.” It was first used in biology in 1665 by the English scientist Robert Hooke to describe the individual units of the honeycomb-like structure he observed in cork under a compound microscope. The cork “cells” Hooke observed were actually the empty lumens of dead cells surrounded by cell walls, but the term is an apt one, because cells are the basic building blocks that define plant structure.

Moving outward from the cell, groups of specialized cells form specific tissues, and specific tissues arranged in particular patterns are the basis of three-dimensional organs. Just as plant anatomy, the study of the macroscopic arrangements of cells and tissues within organs, received its initial impetus from improvements to the light microscope in the seventeenth century, so plant cell biology, the study of the interior of cells, was stimulated by the first application of the electron microscope to biological material in the



mid-twentieth century. Subsequent improvements in both light and electron microscopy have revealed astonishing variety and dynamics in the components that make up cells—the cellular organelles, whose combined activities are required for the wide range of cellular and physiological functions that characterize biological organisms.

This chapter provides an overview of the basic anatomy and cell biology of plants, from the macroscopic structure of organs and tissues to the microscopic ultrastructure of cellular organelles. Subsequent chapters will treat these structures in greater detail from the perspective of their physiological and developmental functions at different stages of the plant life cycle.

Plant Life Processes: Unifying Principles

The spectacular diversity of plant size and form is familiar to everyone. Plants range in height from less than 1 cm to more than 100 m. Plant morphology, or form, is also surprisingly diverse. At first glance, the tiny plant duckweed (*Lemna*) seems to have little in common with a giant saguaro cactus or a redwood tree. No single plant shows the entire spectrum of adaptations to the range of environments that plants occupy on Earth, so plant physiologists often study **model organisms**, plants with short generation times and small **genomes** (the sum of their genetic information) (see **WEB TOPIC 1.1**). These models are useful because all plants, regardless of their specific adaptations, carry out fundamentally similar processes and are based on the same architectural plan.

We can summarize the major unifying principles of plants as follows:

- As Earth's primary producers, plants and green algae are the ultimate solar collectors. They harvest the energy of sunlight by converting light energy to chemical energy, which they store in bonds formed when they synthesize carbohydrates from carbon dioxide and water.
- Other than certain reproductive cells, plants do not move from place to place; they are sessile. As a substitute for motility, they have evolved the ability to grow toward essential resources, such as light, water, and mineral nutrients, throughout their life span.
- Plants are structurally reinforced to support their mass as they grow toward sunlight against the pull of gravity.
- Plants have mechanisms for moving water and minerals from the soil to the sites of photosynthesis and growth, as well as mechanisms for moving the products of photosynthesis to nonphotosynthetic organs and tissues.
- Plants lose water continuously by evaporation and have evolved mechanisms for avoiding desiccation.

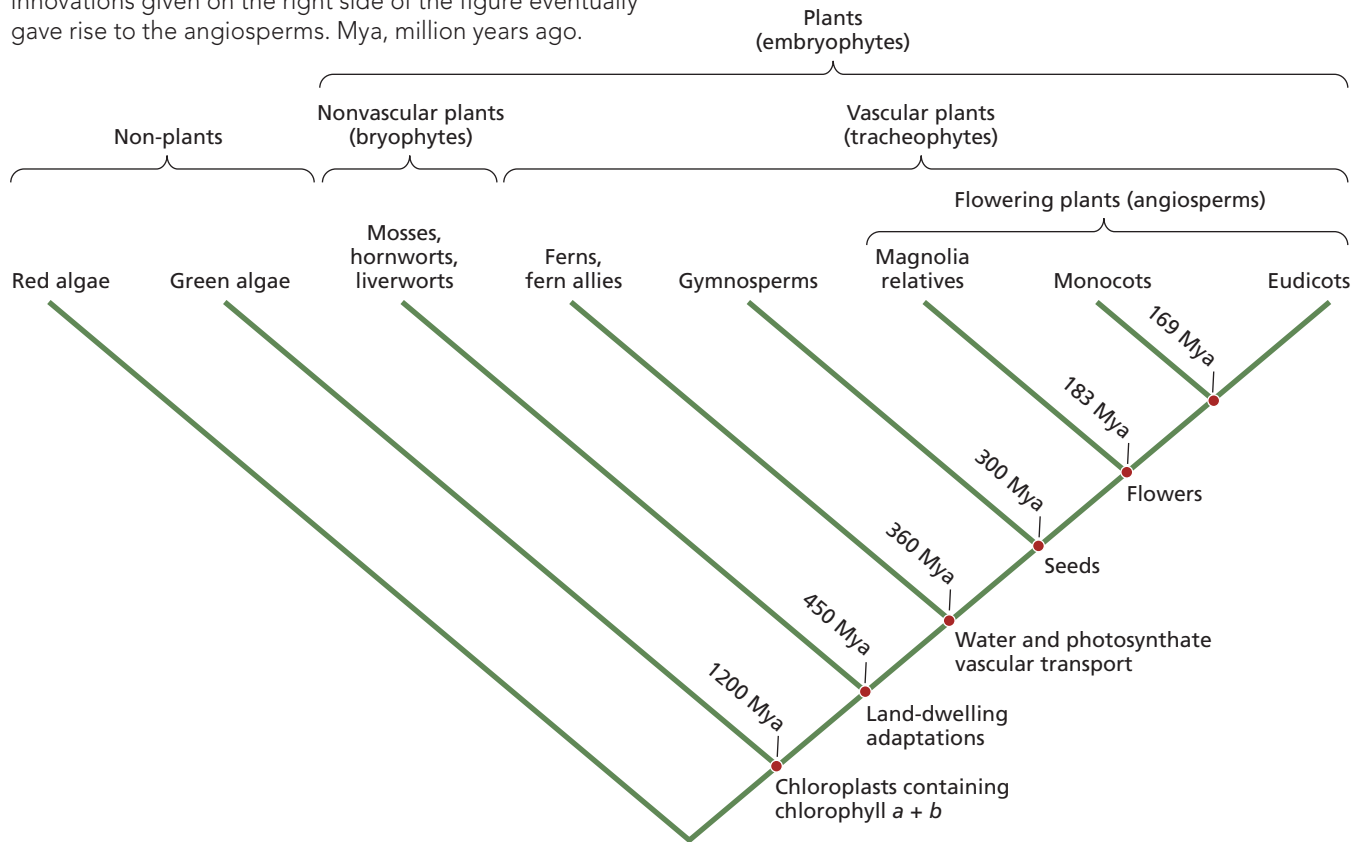
- Plants develop from embryos that derive nutrients from the mother plant, and these additional food stores facilitate the production of large self-supporting structures on land.

Plant Classification and Life Cycles

Based on the principles listed above, we can define plants generally as sessile, multicellular organisms derived from embryos, adapted to land, and able to convert carbon dioxide into complex organic compounds through the process of photosynthesis. This broad definition includes a wide spectrum of organisms, from the mosses to the flowering plants, as illustrated in the diagram, or cladogram, depicting evolutionary lineage as branches, or clades, on a tree (**Figure 1.1**). The relationships of current and past plant identification systems, classification systems (taxonomies), and evolutionary thought are discussed in **WEB TOPIC 1.2**. Plants share with (mostly aquatic) green algae the primitive trait that is so important for photosynthesis in both clades: their chloroplasts contain the pigments chlorophyll *a* and *b* and β -carotene. **Plants**, or **embryophytes**, share the evolutionarily derived traits for surviving on land that are absent in the algae. Plants include the **nonvascular plants**, or **bryophytes** (mosses, hornworts, and liverworts), and the **vascular plants**, or **tracheophytes**. The vascular plants, in turn, consist of the **non-seed plants** (ferns and their relatives) and the **seed plants** (gymnosperms and angiosperms). The characteristics of many of these plant clades are in the descriptions of their representative model species (see **WEB TOPIC 1.1**).

Because plants have many agricultural, industrial, timber, and medical uses, as well as an overwhelming dominance in terrestrial ecosystems, most research in plant biology has focused on the plants that have evolved in the last 300 million years, the seed plants (see Figure 1.1). The **gymnosperms** (from the Greek for “naked seed”) include the conifers, cycads, ginkgo, and gnetophytes (which include *Ephedra*, a popular medicinal plant). About 800 species of gymnosperms are known. The largest group of gymnosperms is the **conifers** (“cone-bearers”), which include such commercially important forest trees as pine, fir, spruce, and redwood. The **angiosperms** (from the Greek for “vessel seed”) evolved about 145 million years ago and include three major groups: the **monocots**, **eudicots**, and so-called basal angiosperms, which include the Magnolia family and its relatives. Except in the great coniferous forests of Canada, Alaska, and northern Eurasia, angiosperms dominate the landscape. About 120,000 species are known, with an additional 17,000 undescribed species predicted by taxonomists using computer models. Most of the predicted species are imperiled because they occur primarily in regions of rich biodiversity where habitat destruction is common. The major anatomical innovation of the angiosperms is the

Figure 1.1 Cladogram showing the evolutionary relationships among the various members of the plants and their close relatives, the algae. The sequence of evolutionary innovations given on the right side of the figure eventually gave rise to the angiosperms. Mya, million years ago.



flower; hence they are referred to as **flowering plants**. **WEB TOPIC 1.3** discusses the relationship between flower anatomy and the plant life cycle.

Plant life cycles alternate between diploid and haploid generations

Plants, unlike animals, alternate between two distinct multicellular generations to complete their life cycle. This is called **alternation of generations**. One generation has **diploid** cells, cells with two copies of each chromosome and abbreviated as having **2N** chromosomes, and the other generation has **haploid** cells, cells with only one copy of each chromosome, abbreviated as **1N**. Each of these multicellular generations may be more or less physically dependent on the other, depending on their evolutionary grouping.

When diploid ($2N$) animals, as represented by humans on the inner cycle in **Figure 1.2**, produce haploid **gametes**, egg ($1N$) and sperm ($1N$), they do so directly by the process of **meiosis**, cell division resulting in a reduction of the number of chromosomes from $2N$ to $1N$. In contrast, the products of meiosis in diploid plants are **spores**, and diploid plant forms are therefore called **sporophytes**. Each spore is capable of undergoing **mitosis**, cell division that

doesn't change the number of chromosomes in the daughter cells, to form a new haploid multicellular individual, the **gametophyte**, as shown by the outer cycles in **Figure 1.2**. The haploid gametophytes produce gametes, egg and sperm, by simple mitosis, whereas haploid gametes in animals are produced by meiosis. This is a fundamental difference between plants and animals and gives the lie to some stories about "the birds and the bees"—bees don't carry around sperm to fertilize female flowers, they carry around the male gametophyte, the **pollen**, which is a multicellular structure that produces sperm cells. When placed on receptive sporophytic tissue, the pollen grain germinates to form a pollen tube that must grow through sporophytic tissue until it reaches the female gametophyte. The male gametophyte penetrates the female gametophyte and releases sperm to fertilize the egg. This hidden nature of sex in plants, where it occurs deep inside sporophytic tissue, made its discovery difficult, and when discovered, was so "shocking" that it was frequently denied.

Once the haploid gametes fuse and **fertilization** takes place to create the $2N$ zygote, the life cycles of animals and plants are similar (see **Figure 1.2**). The $2N$ zygote undergoes a series of mitotic divisions to produce the embryo, which eventually grows into the mature diploid adult.

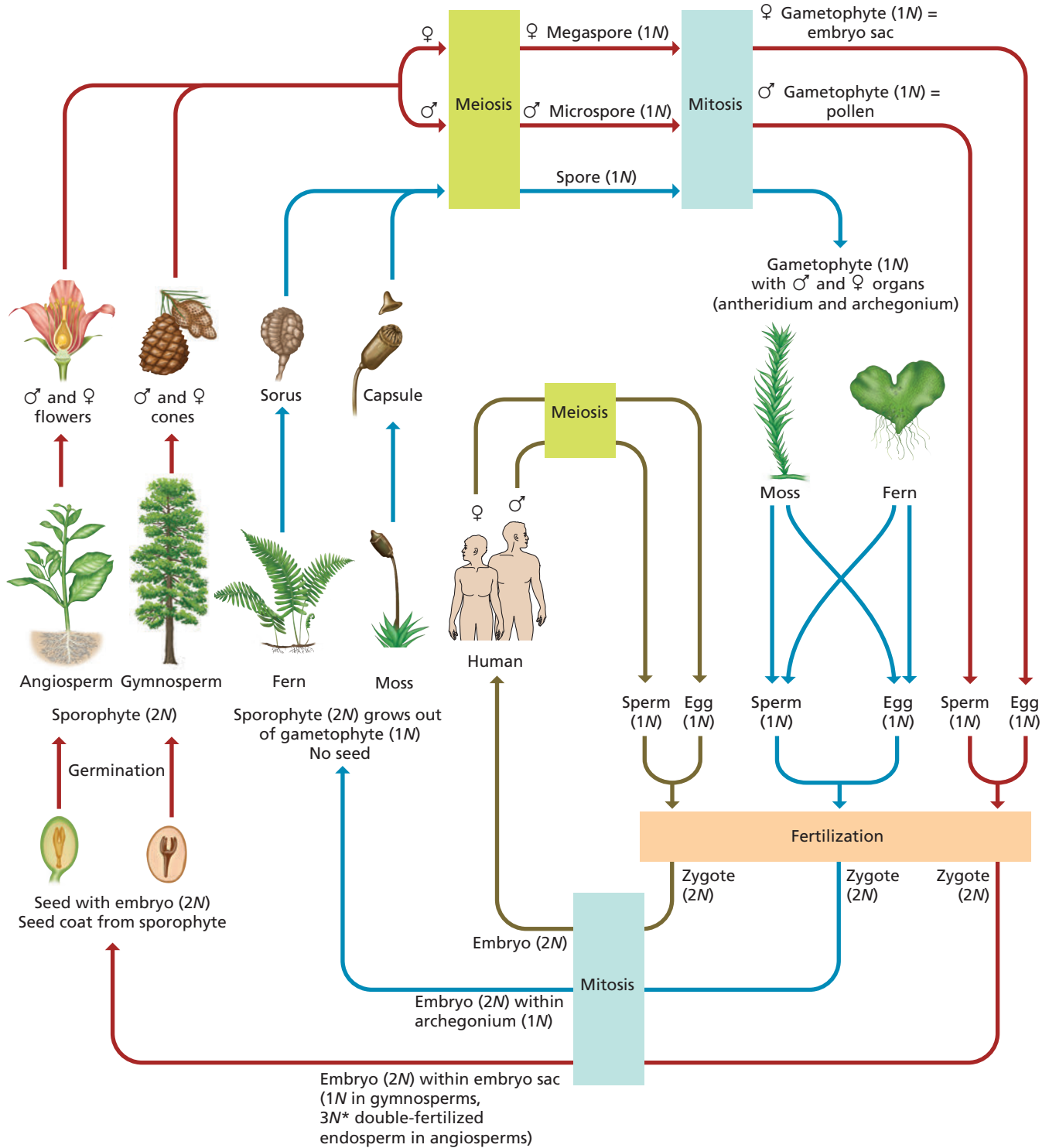


Figure 1.2 Diagram of the generalized life cycles of plants and animals. In contrast to animals, plants exhibit alternation of generations. Rather than producing gametes directly by meiosis as animals do, plants produce vegetative spores by meiosis. These 1N (haploid) spores divide to produce a second multicellular individual called the gametophyte. The gametophyte then produces gametes (sperm and egg) by mitosis. Following fertilization, the resulting 2N (diploid) zygote develops into the mature sporophyte generation, and the cycle begins again. In angiosperms, the process of double fertilization produces a 3N (triploid) or higher ploidy level (*; see Chapter 21) feeding tissue called the endosperm.

Thus, all plant life cycles encompass two separate generations: the diploid, spore-producing **sporophyte generation** and the haploid, gamete-producing **gametophyte generation**. A line drawn between fertilization and meiosis divides these two separate stages of the generalized plant life cycle (see Figure 1.2). Increasing the number of mitoses between fertilization and meiosis increases the size of the sporophyte generation and the number of spores that can be produced. Having more spores per fertilization event could compensate for low fertility when water becomes scarce on land. This could explain the marked tendency for the increase in size of the sporophyte generation, relative to the gametophyte generation, during the evolution of plants.

The sporophyte generation is dominant in the seed plants, the gymnosperms and angiosperms, and gives rise to different spores: the **megaspores**, which develop into the female gametophyte, and the **microspores**, which develop into the male gametophyte (see Figure 1.2). The way the resulting male and female gametophytes are separated is quite diverse. In angiosperms, a single individual in a **monoecious** (from the Greek for “one house”) species has flowers that produce both male and female gametophytes; both can occur in the single “perfect” flower as in tulips, or they can occur in separate male (staminate) and female (pistillate) flowers as in maize (corn; *Zea mays*). If male and female flowers occur on separate individuals, as in willow or poplar trees, then the species is **dioecious** (from the Greek for “two houses”). In gymnosperms, ginkos and cycads are dioecious, while conifers are monoecious. Conifers produce female cones, **megastrobili** (from the Greek for “large cones”; singular *megastrobilus*), usually higher up on the plant than the male cones, **microstrobili** (from the Greek for “small cones”; singular *microstrobilus*). Both megaspores and microspores produce gametophytes with only a few cells, compared with the sporophyte.

Sperm and egg production, as well as the dynamics of fertilization, differs among gametophytes of the seed plants (see **WEB TOPIC 1.3**). In angiosperms there is the amazing process of **double fertilization**, whereby two sperm are produced, only one of which fertilizes the egg. The other sperm fuses with two nuclei in the female gametophyte to produce the $3N$ (three sets of chromosomes) endosperm, the storage tissue for the angiosperm seed. (Some angiosperms produce endosperm of higher ploidy levels; see Chapter 21.) The storage tissue for the seed in gymnosperms is $1N$ gametophytic tissue because there is no double fertilization (see Figure 1.2). So the seed of seed plants is not at all a spore (defined as a cell that produces the gametophyte generation), but it does contain gametophytic ($1N$) storage tissue in gymnosperms and gametophyte-derived $3N$ storage tissue in angiosperms.

In the lower plants, the ferns and mosses, the sporophyte generation gives rise to spores that grow into adult

gametophytes that then have regions that differentiate into male and female structures, the male **antheridium** and the female **archegonium**. In ferns the gametophyte is a small monoecious **prothallus**, which has antheridia and archegonia that divide mitotically to produce motile sperm and egg cells, respectively. The dominant leafy gametophyte generation in mosses contains antheridia and archegonia on the same (monoecious) or different (dioecious) individuals. The motile sperm then enters the archegonium and fertilizes the egg, to form the $2N$ zygote, which develops into an embryo enclosed in the gametophytic tissue, but no seed is formed. The embryo directly develops into the adult $2N$ sporophyte.

Overview of Plant Structure

Despite their apparent diversity, all seed plants have the same basic body plan (**Figure 1.3**). The vegetative body is composed of three organs—the stem, the root, and the leaves—each with a different direction, or polarity, of growth. The **stem** grows upward and supports the above-ground part of the plant. The **root**, which anchors the plant and absorbs nutrients and water, grows down below the ground. The **leaves**, whose primary function is photosynthesis, grow out laterally from the stem at the **nodes**. Variations in leaf arrangement can give rise to many different forms of **shoots**, the term for the leaves and stem together. For example, leaf nodes can spiral around the stem, rotating by a fixed angle between each **internode** (the region between two nodes). Alternatively, leaves can arise oppositely or alternating on either side of the stem.

Organ shape is defined by directional patterns of growth. The polarity of growth of the **primary plant axis** (the main stem and taproot) is vertical, whereas the typical leaf grows laterally at the margins to produce the flattened **leaf blade**. The growth polarities of these organs are adapted to their functions: leaves function in light absorption, stems elongate to lift the leaves toward sunlight, and roots elongate in search of water and nutrients from the soil. The cellular component that directly determines growth polarity in plants is the cell wall.

Plant cells are surrounded by rigid cell walls

The outer fluid boundary of the living cytoplasm of plant cells is the **plasma membrane** (also called **plasmalemma**), similar to the situation in animals, fungi, and bacteria. The **cytoplasm** is defined as all of the organelles and cytoskeleton suspended within the **cytosol**, the water-soluble and colloidal phase, residing within the plasma membrane, but which excludes the nucleoplasm, the internal compartment of the membrane-bounded nucleus in eukaryotes. However, plant cells, unlike animal cells, are further enclosed by a rigid, cellulosic **cell wall** (**Figure 1.4**). Because of the absence of cell walls in animals, embryonic cells are able to migrate from one location to another; developing tissues

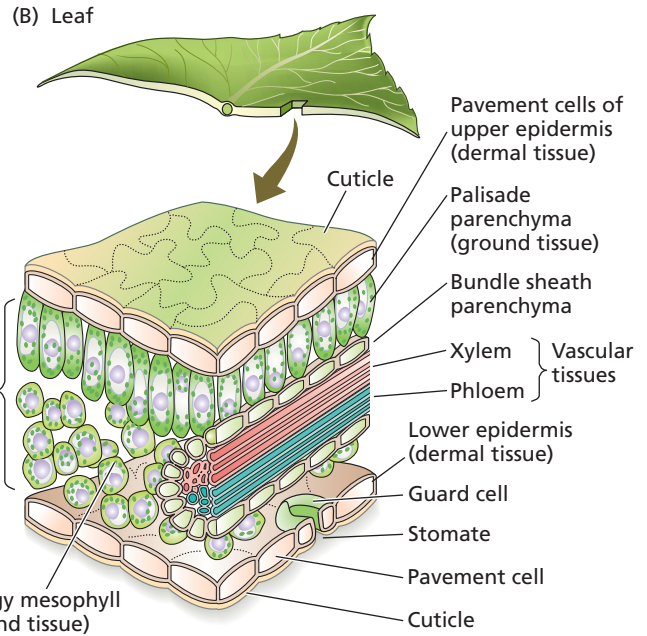
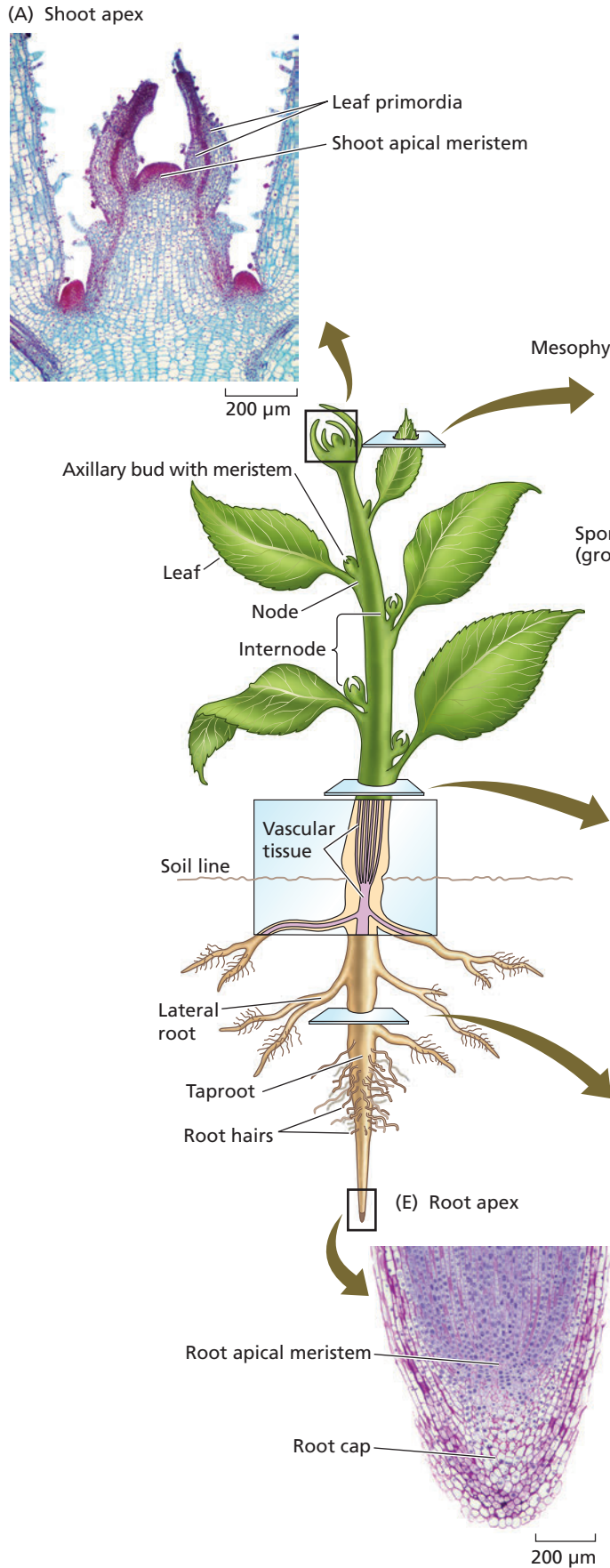
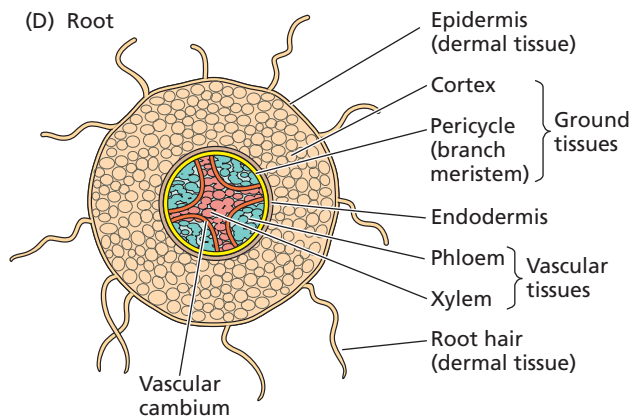
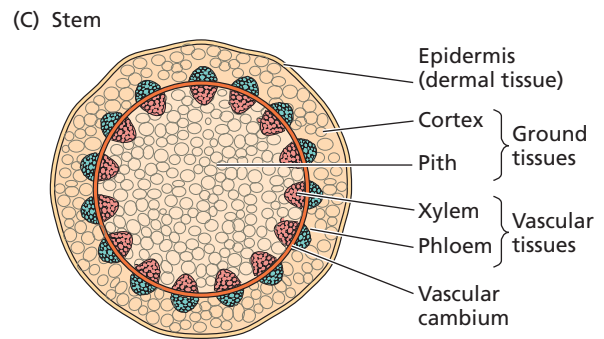


Figure 1.3 Schematic representation of the body of a typical eudicot. Cross sections of the (A) shoot apex, (B) leaf, (C) stem, (D) root, and (E) root apex are also shown. The longitudinal sections of the shoot apex and the root apex are from flax (*Linum usitatissimum*).



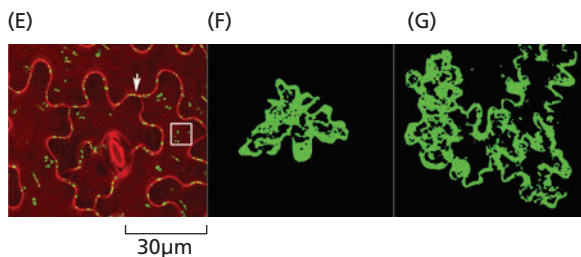
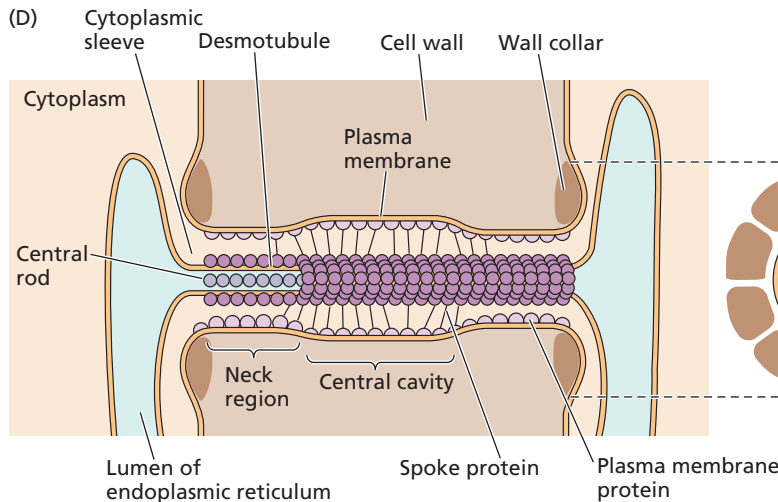
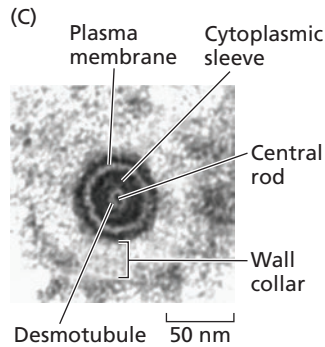
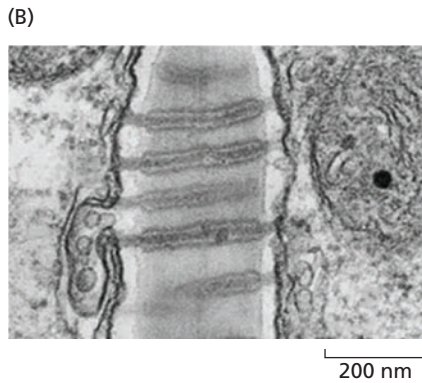
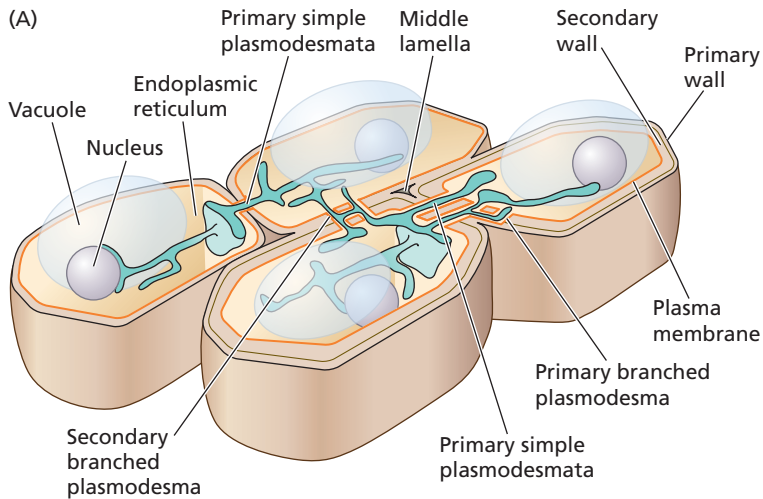


Figure 1.4 Plant cell walls and their associated plasmodesmata. (A) Diagrammatic representation of the cell walls surrounding four adjacent plant cells. Cells with only primary walls and with both primary and secondary walls are illustrated. The secondary walls form inside the primary walls. The cells are connected by both simple (unbranched) and branched plasmodesmata. Plasmodesmata formed during cell division are primary plasmodesmata. (B) Electron micrograph of a wall separating two adjacent cells, showing simple plasmodesmata in longitudinal view. (C) Tangential section through a cell wall showing a plasmodesma. (D) Schematic surface and cross-section views of a plasmodesma. The pore consists of a central cavity down which the desmotubule runs, connecting the endoplasmic reticulum of the adjoining cells. (E) Epidermal cells of an Arabidopsis leaf imaged with fluorescence microscopy showing the cell wall in red and complex plasmodesmata in green. The arrow points to the high number of plasmodesmata at cell three-way junctions, and the rectangle outlines plasmodesmata that connect the epidermal cells to cells beneath them, the mesophyll cells. (F) A single tobacco leaf epidermal cell expressing a green fluorescent viral movement protein imaged with fluorescence microscopy. (G) After a single tobacco leaf epidermal cell expresses the gene for a viral movement protein, several tobacco leaf epidermal cells express green fluorescent viral movement protein because it has moved to them through plasmodesmata. (B from Robinson-Beers and Evert 1991, courtesy of R. Evert; C from Bell and Oparka 2011; E from Fitzgibbon et al. 2013; F and G from Ueki and Citovsky 2011.)

and organs may thus contain cells that originated in different parts of the organism. In plants such cell migrations are prevented, because each walled cell is cemented to its neighbors by a **middle lamella**. As a consequence, plant development, unlike animal development, depends solely on patterns of cell division and cell enlargement.

Plant cells have two types of walls: primary and secondary (see Figure 1.4A). **Primary cell walls** are typically thin (less than 1 μm) and are characteristic of young, growing cells. **Secondary cell walls** are thicker and stronger than primary walls and are deposited on the inner surface of the primary wall after most cell enlargement has ended. Secondary cell walls owe their strength and toughness to **lignin**, a brittle, glue-like material (see Chapter 14). The evolution of lignified secondary cell walls provided plants with the structural reinforcement necessary to grow vertically above the soil and to colonize the land. Bryophytes, which lack lignified cell walls, are unable to grow more than a few centimeters above the ground.

Plasmodesmata allow the free movement of molecules between cells

The cytoplasm of neighboring cells is usually connected by means of **plasmodesmata** (singular *plasmodesma*), tubular channels 40 to 50 nm in diameter and formed by the connected plasma membranes of adjacent cells (see Figure 1.4A–D). They facilitate intercellular communication during plant development, enabling cytoplasmic exchange of vital developmental signals in the form of proteins, nucleic acids, and other macromolecules (see Chapters 18–20). Plant cells interconnected in this way form a cytoplasmic continuum referred to as the **symplast**. Intercellular transport of small molecules through plasmodesmata is called **symplastic transport** (see Chapters 4 and 6). Transport through the wall spaces, which constitute the apoplast, is called **apoplastic transport**. Both forms of transport are important in the vascular system of plants (see Chapter 6).

Primary plasmodesmata are created as the primary cell wall assembles during and following cell division (discussed later in the chapter). **Secondary plasmodesmata** form after cell division is completed, across primary or secondary cell walls (see Figure 1.4A), when small regions of the cell walls are digested by enzymes and plasma membranes of adjacent cells fuse to form the channel. The endoplasmic reticulum network (see the section *The Endomembrane System*, below) of adjacent cells is also connected, forming the **desmotubule** (see Figure 1.4C and D) that runs through the center of the channel. Proteins line the outer surface of the desmotubule and the inner surface of the plasma membrane (see Figure 1.4D); the two surfaces are thought to be connected by filamentous proteins (**spokes**), which divide the **cytoplasmic sleeve** into microchannels. Valvelike **wall collars**, composed of the polysaccharide callose, surround the necks of the channel at either end and serve to restrict the size of the pore.

The symplast can transport water, solutes, and macromolecules between cells without crossing the plasma membrane. However, there is a restriction on the size of molecules that can be transported via the symplast; this restriction is called the **size exclusion limit**, which varies with cell type, environment, and developmental stage. The transport can be followed by studying the movement of fluorescently labeled proteins or dyes between cells (see Figure 1.4E–G). The movement through plasmodesmata can be regulated, or gated, by altering the dimensions of the wall collars, the cytoplasmic sleeve, and the lumen inside the desmotubule. In addition, adjacent plasmodesmata can form interconnections that alter the size exclusion limit. Thus, single channels, referred to as **simple plasmodesmata**, can form **branched plasmodesmata** (see Figure 1.4A) when they connect with each other.

In a situation that occurs all too frequently, plant viruses can hijack the plasmodesmata and use them to spread from cell to cell. **Movement proteins**, encoded by the virus genome, facilitate viral movement by interacting with plasmodesmata through one of two mechanisms. Movement proteins from some viruses coat the surface of the viral genome (typically RNA), forming ribonucleoprotein complexes. The 30-kDa movement protein of tobacco mosaic virus acts in this way. It can move between cells in leaves that are susceptible to the virus, where it recruits other proteins in the cell that reduce the amount of callose in the wall collar, increasing the size of the plasmodesmatal pore. As a result, even virus-sized particles can readily move through the plasmodesmata to a neighboring cell (see Figure 1.4F and G). Other viruses, such as cowpea mosaic virus and tomato spotted wilt virus, encode movement proteins that form a transport tubule within the plasmodesmatal channel that enhances the passage of mature virus particles through plasmodesmata.

New cells originate in dividing tissues called meristems

Plant growth is concentrated in localized regions of cell division called **meristems**. Nearly all nuclear division (mitosis) and cell division (cytokinesis) occurs in these meristematic regions. In a young plant, the most active meristems are the **apical meristems**; they are located at the tips of the stem and the root (see Figure 1.3A and E). The phase of plant development that gives rise to new organs and to the basic plant form is called **primary growth**, which gives rise to the **primary plant body**. Primary growth results from the activity of apical meristems. Cell division in the meristem produces cuboidal cells about 10 μm on each side. Division is followed by progressive cell enlargement, typically elongation, whereby cells become much longer than they are wide (30–100 μm long, 10–25 μm wide—about half the width of a baby's fine hair and about 50 times the width of a typical bacterium). The increase in length produced by primary growth amplifies

the plant's axial (top-to-bottom) polarity, which is established in the embryo.

Cell differentiation into specialized tissues follows cell enlargement (Figure 1.5, see also Figure 1.3). There are three major tissue systems present in all plant organs: dermal tissue, ground tissue, and vascular tissue (see Figure 1.3B–D). **Dermal tissue** forms the outer protective layer of the plant and is called the **epidermis** in the pri-

mary plant body; **ground tissue** fills out the three-dimensional bulk of the plant and includes the **pith** and **cortex** of primary stems and roots, and the **mesophyll** in leaves. **Vascular tissue**, which moves, or **translocates**, water and solutes throughout the length of the plant, consists of two types of tissues: **xylem** and **phloem**, each of which consists of conducting cells, generalized parenchyma cells, and thick-walled fibers. Some of the different cell types that

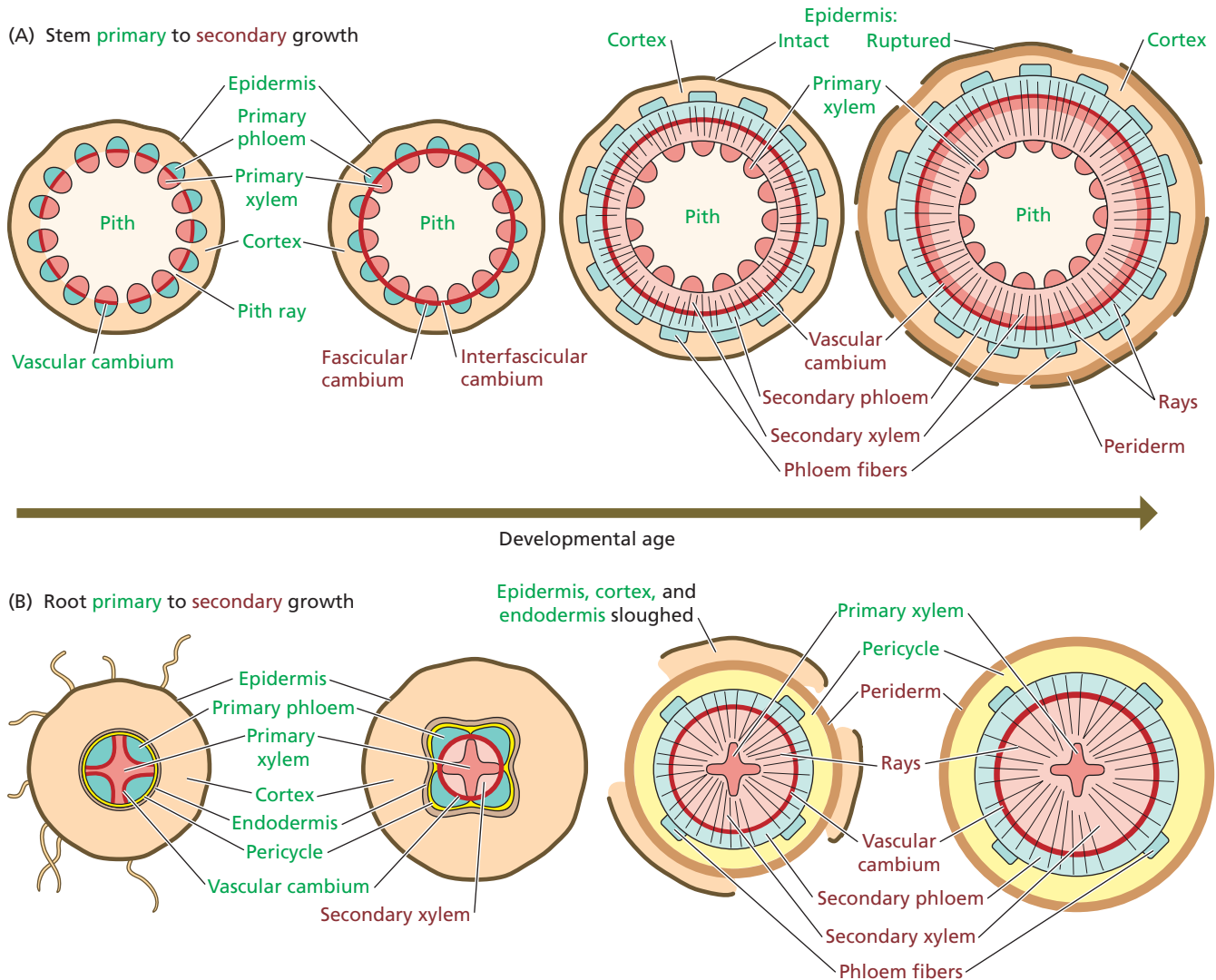


Figure 1.5 Secondary growth in stems and roots. (A) Stem primary to secondary growth. Primary growth is labeled in green, while secondary growth is labeled in red. The vascular cambium starts as separated growth regions in the vascular bundles, or fasciae, of primary xylem and phloem. As the plant grows, the bundled, fascicular cambium becomes connected by interfascicular cambium between the bundles. Once the vascular cambium forms a continuous ring, it divides inward to generate secondary xylem and it divides outward to generate the secondary phloem. Regions in the cortex develop into phloem fibers and the periderm, which contains the phellogen, or cork

cambium, and the outer phelloderm. With growth, the epidermis ruptures and rays connect the inner and outer vasculature. (B) Root primary to secondary growth. The central vascular cylinder contains the primary phloem and primary xylem. As in the stem, the vascular cambium becomes connected and grows outward, generating secondary phloem and rays. As roots increase in girth, the pericycle generates the root periderm, while the outer epidermis, cortex, and endodermis are sloughed off. The pericycle produces the phloem fibers and rays as well as lateral roots (not shown). The vascular cambium produces secondary phloem and rings of secondary xylem.