
Contents

Chapter 1 • Plant Cells and Water 1

- 1.1 Water has Unique Physical and Chemical Properties 2
- 1.2 The Thermal Properties of Water are Biologically Important 3
 - 1.2.1 Water Exhibits a Unique Thermal Capacity 3
 - 1.2.2 Water Exhibits a High Heat of Fusion and Heat of Vaporization 3
- 1.3 Water is the Universal Solvent 4
- 1.4 Polarity of Water Molecules Results in Cohesion and Adhesion 4
- 1.5 Water Movement may be Governed by Diffusion or by Bulk Flow 5
 - 1.5.1 Bulk Flow is Driven by Hydrostatic Pressure 5
 - 1.5.2 Fick's First Law Describes the Process of Diffusion 5
- 1.6 Osmosis is the Diffusion of Water Across a Selectively Permeable Membrane 6
 - 1.6.1 Plant Cells Contain an Array of Selectively Permeable Membranes 7
 - 1.6.2 Osmosis in Plant Cells is Indirectly Energy Dependent 8
 - 1.6.3 The Chemical Potential of Water has an Osmotic as Well as a Pressure Component 9
- 1.7 Hydrostatic Pressure and Osmotic Pressure are Two Components of Water Potential 11
- 1.8 Water Potential is the Sum of its Component Potentials 11
- 1.9 Dynamic Flux of H_2O is Associated with Changes in Water Potential 12

- 1.10 Aquaporins Facilitate the Cellular Movement of Water 13
- 1.11 Two-Component Sensing/Signalling Systems are Involved in Osmoregulation 15
 - Summary 17
 - Chapter Review 17
 - Further Reading 17

Chapter 2 • Whole Plant Water Relations 19

- 2.1 Transpiration is Driven by Differences in Vapor Pressure 20
- 2.2 The Driving Force of Transpiration is Differences in Vapor Pressure 21
- 2.3 The Rate of Transpiration is Influenced by Environmental Factors 22
 - 2.3.1 What are the Effects of Humidity? 23
 - 2.3.2 What are the Effects of Temperature? 23
 - 2.3.3 What is the Effect of Wind? 24
- 2.4 Water Conduction Occurs via Tracheary Elements 24
- 2.5 The Ascent of Xylem SAP is Explained by Combining Transpiration with the Cohesive Forces of Water 27
 - 2.5.1 Root Pressure is Related to Root Structure 28
 - 2.5.2 Water Rise by Capillarity is due to Adhesion and Surface Tension 29
 - 2.5.3 The Cohesion Theory Best Explains the Ascent of Xylem Sap 30

- 2.6 Water Loss due to Transpiration must be Replenished 33**
 - 2.6.1 Soil is a Complex Medium 33
- 2.7 Roots Absorb and Transport Water 34**
- 2.8 The Permeability of Roots to Water Varies 35**
- 2.9 Radial Movement of Water Through the Root Involves Two Possible Pathways 36**
 - Summary 37*
 - Chapter Review 37*
 - Further Reading 37*

Box 2.1 • Why Transpiration? 25

Chapter 3 • Roots, Soils, and Nutrient Uptake 39

- 3.1 The Soil as a Nutrient Reservoir 40**
 - 3.1.1 Colloids are a Significant Component of Most Soils 40
 - 3.1.2 Colloids Present a Large, Negatively Charged Surface Area 40
 - 3.1.3 Soil Colloids Reversibly Adsorb Cations from the Soil Solution 41
 - 3.1.4 The Anion Exchange Capacity of Soil Colloids is Relatively Low 41
- 3.2 Nutrient Uptake 42**
 - 3.2.1 Nutrient Uptake by Plants Requires Transport of the Nutrient Across Root Cell Membranes 42
 - 3.2.2 Simple Diffusion is a Purely Physical Process 42
 - 3.2.3 The Movement of Most Solutes Across Membranes Requires the Participation of Specific Transport Proteins 43
 - 3.2.4 Active Transport Requires the Expenditure of Metabolic Energy 43
- 3.3 Selective Accumulation of Ions by Roots 46**
- 3.4 Electrochemical Gradients and Ion Movement 46**
 - 3.4.1 Ions Move in Response to Electrochemical Gradients 46
 - 3.4.2 The Nernst Equation Helps to Predict Whether an Ion is Exchanged Actively or Passively 47
- 3.5 Electrogenic Pumps are Critical for Cellular Active Transport 49**
 - 3.5.1 Active Transport is Driven by ATPase-Proton Pumps 49
 - 3.5.2 The ATPase-Proton Pumps of Plasma Membranes and Vacuolar Membranes are Different 50
 - 3.5.3 K^+ Exchange is Mediated by Two Classes of Transport Proteins 51

- 3.6 Cellular Ion Uptake Processes are Interactive 52**
- 3.7 Root Architecture is Important to Maximize Ion Uptake 52**
 - 3.7.1 A First Step in Mineral Uptake by Roots is Diffusion into the Apparent Free Space 53
 - 3.7.2 Apparent Free Space is Equivalent to the Apoplast of the Root Epidermal and Cortical Cells 54
- 3.8 The Radial Path of Ion Movement Through Roots 54**
 - 3.8.1 Ions Entering the Stele Must First be Transported from the Apparent Free Space into the Symplast 54
 - 3.8.2 Ions are Actively Secreted into the Xylem Apoplast 55
 - 3.8.3 Emerging Secondary Roots may Contribute to the Uptake of Some Solutes 55
- 3.9 Root-Microbe Interactions 56**
 - 3.9.1 Bacteria Other than Nitrogen Fixers Contribute to Nutrient Uptake by Roots 56
 - 3.9.2 Mycorrhizae are Fungi that Increase the Volume of the Nutrient Depletion Zone Around Roots 57
 - Summary 58*
 - Chapter Review 58*
 - Further Reading 59*

Box 3.1 • Electrophysiology—Exploring Ion Channels 44

Chapter 4 • Plants and Inorganic Nutrients 61

- 4.1 Methods and Nutrient Solutions 62**
 - 4.1.1 Interest in Plant Nutrition is Rooted in the Study of Agriculture and Crop Productivity 62
 - 4.1.2 The Use of Hydroponic Culture Helped to Define the Mineral Requirements of Plants 62
 - 4.1.3 Modern Techniques Overcome Inherent Disadvantages of Simple Solution Culture 63
- 4.2 The Essential Nutrient Elements 65**
 - 4.2.1 Seventeen Elements are Deemed to be Essential for Plant Growth and Development 65
 - 4.2.2 The Essential Nutrients are Generally Classed as Either Macronutrients or Micronutrients 65
 - 4.2.3 Determining Essentiality of Micronutrients Presents Special Problems 65

4.3 Beneficial Elements 66

- 4.3.1 Sodium is an Essential Micronutrient for C4 Plants 66
- 4.3.2 Silicon May be Beneficial for a Variety of Species 67
- 4.3.3 Cobalt is Required by Nitrogen-Fixing Bacteria 67
- 4.3.4 Some Plants Tolerate High Concentrations of Selenium 67

4.4 Nutrient Functions and Deficiency Symptoms 67

- 4.4.1 A Plant's Requirement for a Particular Element is Defined in Terms of Critical Concentration 67
- 4.4.2 Nitrogen is a Constituent of Many Critical Macromolecules 68
- 4.4.3 Phosphorous is Part of the Nucleic Acid Backbone and has a Central Function in Intermediary Metabolism 69
- 4.4.4 Potassium Activates Enzymes and Functions in Osmoregulation 69
- 4.4.5 Sulfur is an Important Constituent of Proteins, Coenzymes, and Vitamins 70
- 4.4.6 Calcium is Important in Cell Division, Cell Adhesion, and as a Second Messenger 70
- 4.4.7 Magnesium is a Constituent of the Chlorophyll Molecule and an Important Regulator of Enzyme Reaction 70
- 4.4.8 Iron is Required for Chlorophyll Synthesis and Electron Transfer Reactions 71
- 4.4.9 Boron Appears to have a Role in Cell Division and Elongation and Contributes to the Structural Integrity of the Cell Wall 73
- 4.4.10 Copper is a Necessary Cofactor for Oxidative Enzymes 73
- 4.4.11 Zinc is an Activator of Numerous Enzymes 73
- 4.4.12 Manganese is an Enzyme Cofactor as Well as Part of the Oxygen-Evolving Complex in the Chloroplast 74
- 4.4.13 Molybdenum is a Key Component of Nitrogen Metabolism 74
- 4.4.14 Chlorine has a Role in Photosynthetic Oxygen Evolution and Charge Balance Across Cellular Membranes 74
- 4.4.15 The Role of Nickel is not Clear 74

4.5 Toxicity of Micronutrients 75

Summary 75
Chapter Review 76
Further Reading 76

Chapter 5 • Bioenergetics and ATP Synthesis 77**5.1 Bioenergetics and Energy Transformations in Living Organisms 78**

- 5.1.1 The Sun is a Primary Source of Energy 78
- 5.1.2 What is Bioenergetics? 78
- 5.1.3 The First Law of Thermodynamics Refers to Energy Conservation 79
- 5.1.4 The Second Law of Thermodynamics Refers to Entropy and Disorder 79
- 5.1.5 The Ability to do Work is Dependent on the Availability of Free Energy 80
- 5.1.6 Free Energy is Related to Chemical Equilibria 80

5.2 Energy Transformations and Coupled Reactions 81

- 5.2.1 Free Energy of ATP is Associated with Coupled Phosphate Transfer Reactions 81
- 5.2.2 Free Energy Changes are Associated with Coupled Oxidation–Reduction Reactions 83

5.3 Energy Transduction and the Chemiosmotic Synthesis of ATP 85

- 5.3.1 Chloroplasts and Mitochondria Exhibit Specific Compartments 85
- 5.3.2 Chloroplasts and Mitochondria Synthesize ATP by Chemiosmosis 90

Summary 91*Chapter Review* 91*Further Reading* 91**Box 5.1 • Plastid Biogenesis 86****Chapter 6 • The Dual Role of Sunlight: Energy and Information 93****6.1 The Physical Nature of Light 93**

- 6.1.1 Light is Electromagnetic Energy, Which Exists in Two Forms 93
- 6.1.2 Light can be Characterized as a Wave Phenomenon 94
- 6.1.3 Light Can be Characterized as a Stream of Discrete Particles 94
- 6.1.4 Light Energy can Interact with Matter 95
- 6.1.5 How Does One Illustrate the Efficiency of Light Absorption and its Physiological Effects? 97
- 6.1.6 Accurate Measurement of Light is Important in Photobiology 98

6.2 The Natural Radiation Environment 99**6.3 Photoreceptors Absorb Light for use in a Physiological Process 100**

- 6.3.1 Chlorophylls are Primarily Responsible for Harvesting Light Energy for Photosynthesis 100
- 6.3.2 Phycobilins Serve as Accessory Light-Harvesting Pigments in Red Algae and Cyanobacteria 102
- 6.3.3 Carotenoids Account for the Autumn Colors 103
- 6.3.4 Cryptochrome and Phototropin are Photoreceptors Sensitive to Blue Light and UV-A radiation 103
- 6.3.5 UV-B Radiation May Act as a Developmental Signal 105
- 6.3.6 Flavonoids Provide the Myriad Flower Colors and Act as a Natural Sunscreen 105
- 6.3.7 Betacyanins and Beets 106
- Summary* 107
- Chapter Review* 107
- Further Reading* 107

Chapter 7 • Energy Conservation in Photosynthesis: Harvesting Sunlight 109

- 7.1 Leaves are Photosynthetic Machines that Maximize the Absorption of Light 110
- 7.2 Photosynthesis is an Oxidation–Reduction Process 112
- 7.3 Photosynthetic Electron Transport 114
 - 7.3.1 Photosystems are Major Components of the Photosynthetic Electron Transport Chain 114
 - 7.3.2 Photosystem II Oxidizes Water to Produce Oxygen 117
 - 7.3.3 The Cytochrome Complex and Photosystem I Oxidize Plastoquinol 119
- 7.4 Photophosphorylation is the Light-Dependent Synthesis of ATP 120
- 7.5 Lateral Heterogeneity is the Unequal Distribution of Thylakoid Complexes 122
- 7.6 Cyanobacteria are Oxygenic 123
- 7.7 Inhibitors of Photosynthetic Electron Transport are Effective Herbicides 124
 - Summary* 127
 - Chapter Review* 127
 - Further Reading* 128

Box 7.1 • Historical Perspective—The Discovery of Photosynthesis 113

Box 7.2 • The Case for Two Photosystems 125

Chapter 8 • Energy Conservation in Photosynthesis: CO₂ Assimilation 129

- 8.1 Stomatal Complex Controls Leaf Gas Exchange and Water Loss 130
- 8.2 CO₂ Enters the Leaf by Diffusion 132
- 8.3 How Do Stomata Open and Close? 133
- 8.4 Stomatal Movements are Also Controlled by External Environmental Factors 135
 - 8.4.1 Light and Carbon Dioxide Regulate Stomatal Opening 135
 - 8.4.2 Stomatal Movements Follow Endogenous Rhythms 136
- 8.5 The Photosynthetic Carbon Reduction (PCR) Cycle 136
 - 8.5.1 The PCR Cycle Reduces CO₂ to Produce a Three-Carbon Sugar 137
 - 8.5.2 The Carboxylation Reaction Fixes the CO₂ 137
 - 8.5.3 ATP and NADPH are Consumed in the PCR Cycle 138
 - 8.5.4 What are the Energetics of the PCR Cycle? 139
- 8.6 The PCR Cycle is Highly Regulated 139
 - 8.6.1 The Regeneration of RuBP is Autocatalytic 140
 - 8.6.2 Rubisco Activity is Regulated Indirectly by Light 140
 - 8.6.3 Other PCR Enzymes are also Regulated by Light 141
- 8.7 Chloroplasts of C₃ Plants also Exhibit Competing Carbon Oxidation Processes 142
 - 8.7.1 Rubisco Catalyzes the Fixation of Both CO₂ and O₂ 142
 - 8.7.2 Why Photorespiration? 143
 - 8.7.3 In Addition to PCR, Chloroplasts Exhibit an Oxidative Pentose Phosphate Cycle 145
 - Summary* 149
 - Chapter Review* 149
 - Further Reading* 150

Box 8.1 • Enzymes 146

Chapter 9 • Allocation, Translocation, and Partitioning of Photoassimilates 151

- 9.1 Starch and Sucrose are Biosynthesized in Two Different Compartments 152
 - 9.1.1 Starch is Biosynthesized in the Stroma 152
 - 9.1.2 Sucrose is Biosynthesized in the Cytosol 153

- 9.2 **Starch and Sucrose Biosynthesis are Competitive Processes** 154
 - 9.3 **Fructan Biosynthesis is An Alternative Pathway For Carbon Allocation** 156
 - 9.4 **Photoassimilates are Translocated Over Long Distances** 156
 - 9.4.1 What is the Composition of the Photoassimilate Translocated by the Phloem? 158
 - 9.5 **Sieve Elements are the Principal Cellular Constituents of the Phloem** 159
 - 9.5.1 Phloem Exudate Contains a Significant Amount of Protein 160
 - 9.6 **Direction of Translocation is Determined by Source-Sink Relationships** 161
 - 9.7 **Phloem Translocation Occurs by Mass Transfer** 161
 - 9.8 **Phloem Loading and Unloading Regulate Translocation and Partitioning** 163
 - 9.8.1 Phloem Loading can Occur Symplastically or Apoplastically 164
 - 9.8.2 Phloem Unloading May Occur Symplastically or Apoplastically 166
 - 9.9 **Photoassimilate is Distributed Between Different Metabolic Pathways and Plant Organs** 166
 - 9.9.1 Photoassimilates May be Allocated to a Variety of Metabolic Functions in the Source or The Sink 167
 - 9.9.2 Distribution of Photoassimilates Between Competing Sinks is Determined by Sink Strength 168
 - 9.10 **Xenobiotic Agrochemicals are Translocated in the Phloem** 170
 - Summary* 170
 - Chapter Review* 171
 - Further Reading* 171
- Chapter 10 • Cellular Respiration: Unlocking the Energy Stored in Photoassimilates** 173
- 10.1 **Cellular Respiration Consists of a Series of Pathways by Which Photoassimilates are Oxidized** 174
 - 10.2 **Starch Mobilization** 175
 - 10.2.1 The Hydrolytic Degradation of Starch Produces Glucose 175
 - 10.2.2 α -Amylase Produces Maltose and Limit Dextrins 176
 - 10.2.3 β -Amylase Produces Maltose 176
 - 10.2.4 Limit Dextrinase is a Debranching Enzyme 176
 - 10.2.5 α -Glucosidase Hydrolyzes Maltose 177
 - 10.2.6 Starch Phosphorylase Catalyzes the Phosphorolytic Degradation of Starch 177
 - 10.3 **Fructan Mobilization is Constitutive** 178
 - 10.4 **Glycolysis Converts Sugars to Pyruvic Acid** 178
 - 10.4.1 Hexoses Must be Phosphorylated to Enter Glycolysis 178
 - 10.4.2 Triose Phosphates are Oxidized to Pyruvate 180
 - 10.5 **The Oxidative Pentose Phosphate Pathway is an Alternative Route for Glucose Metabolism** 180
 - 10.6 **The Fate of Pyruvate Depends on the Availability of Molecular Oxygen** 181
 - 10.7 **Oxidative Respiration is Carried out by the Mitochondrion** 182
 - 10.7.1 In The Presence of Molecular Oxygen, Pyruvate is Completely Oxidized to CO_2 and Water by the Citric Acid Cycle 182
 - 10.7.2 Electrons Removed from Substrate in the Citric Acid Cycle are Passed to Molecular Oxygen Through the Mitochondrial Electron Transport Chain 183
 - 10.8 **Energy is Conserved in the Form of ATP in Accordance with Chemiosmosis** 185
 - 10.9 **Plants Contain Several Alternative Electron Transport Pathways** 186
 - 10.9.1 Plant Mitochondria Contain External Dehydrogenases 186
 - 10.9.2 Plants have a Rotenone-Insensitive NADH Dehydrogenase 186
 - 10.9.3 Plants Exhibit Cyanide-Resistant Respiration 187
 - 10.10 **Many Seeds Store Carbon as Oils that are Converted to Sugar** 188
 - 10.11 **Respiration Provides Carbon Skeletons for Biosynthesis** 189
 - 10.12 **Respiratory Rate Varies with Development and Metabolic State** 191
 - 10.13 **Respiration Rates Respond to Environmental Conditions** 192
 - 10.13.1 Light 192
 - 10.13.2 Temperature 192
 - 10.13.3 Oxygen Availability 193
- Summary* 193
Chapter Review 194
Further Reading 194

Chapter 11 • Nitrogen Assimilation 195

- 11.1 **The Nitrogen Cycle: A Complex Pattern of Exchange 195**
 - 11.1.1 Ammonification, Nitrification, and Denitrification are Essential Processes in the Nitrogen Cycle 196
- 11.2 **Biological Nitrogen Fixation is Exclusively Prokaryotic 196**
 - 11.2.1 Some Nitrogen-Fixing Bacteria are Free-Living Organisms 196
 - 11.2.2 Symbiotic Nitrogen Fixation Involves Specific Associations Between Bacteria and Plants 197
- 11.3 **Legumes Exhibit Symbiotic Nitrogen Fixation 197**
 - 11.3.1 Rhizobia Infect the Host Roots, Which Induces Nodule Development 198
- 11.4 **The Biochemistry of Nitrogen Fixation 200**
 - 11.4.1 Nitrogen Fixation is Catalyzed by the Enzyme Dinitrogenase 200
 - 11.4.2 Nitrogen Fixation is Energetically Costly 201
 - 11.4.3 Dinitrogenase is Sensitive to Oxygen 202
 - 11.4.4 Dinitrogenase Results in the Production of Hydrogen Gas 202
- 11.5 **The Genetics of Nitrogen Fixation 203**
 - 11.5.1 *NIF* Genes Code for Dinitrogenase 203
 - 11.5.2 *NOD* Genes and *NIF* Genes Regulate Nodulation 203
 - 11.5.3 What is the Source of Heme For Leghemoglobin? 204
- 11.6 **NH₃ Produced by Nitrogen Fixation is Converted to Organic Nitrogen 204**
 - 11.6.1 Ammonium is Assimilated by GS/GOGAT 204
 - 11.6.2 PII Proteins Regulate GS/GOGAT 205
 - 11.6.3 Fixed Nitrogen is Exported as Asparagine and Ureides 206
- 11.7 **Plants Generally Take up Nitrogen in the Form of Nitrate 207**
- 11.8 **Nitrogen Cycling: Simultaneous Import and Export 208**
- 11.9 **Agricultural and Ecosystem Productivity is Dependent on Nitrogen Supply 209**
 - Summary 211
 - Chapter Review 211
 - Further Reading 211

Chapter 12 • Carbon and Nitrogen Assimilation and Plant Productivity 213

- 12.1 **Productivity Refers to an Increase in Biomass 213**

- 12.2 **Carbon Economy is Dependent on the Balance Between Photosynthesis and Respiration 214**
- 12.3 **Productivity is Influenced by a Variety of Environmental Factors 215**
 - 12.3.1 Fluence Rate 215
 - 12.3.2 Available CO₂ 216
 - 12.3.3 Temperature 218
 - 12.3.4 Soil Water Potential 219
 - 12.3.5 Nitrogen Supply Limits Productivity 219
 - 12.3.6 Leaf Factors 220
 - Summary 221
 - Chapter Review 222
 - Further Reading 222

Chapter 13 • Responses of Plants to Environmental Stress 223

- 13.1 **What is Plant Stress? 223**
- 13.2 **Plants Respond to Stress in Several Different Ways 224**
- 13.3 **Too Much Light Inhibits Photosynthesis 225**
 - 13.3.1 The D1 Repair Cycle Overcomes Photodamage to PSII 227
- 13.4 **Water Stress is a Persistent Threat to Plant Survival 229**
 - 13.4.1 Water Stress Leads to Membrane Damage 230
 - 13.4.2 Photosynthesis is Particularly Sensitive to Water Stress 230
 - 13.4.3 Stomata Respond to Water Deficit 230
- 13.5 **Plants are Sensitive to Fluctuations in Temperature 233**
 - 13.5.1 Many Plants are Chilling Sensitive 233
 - 13.5.2 High-Temperature Stress Causes Protein Denaturation 234
- 13.6 **Insect Pests and Disease Represent Potential Biotic Stresses 235**
 - 13.6.1 Systemic Acquired Resistance Represents a Plant Immune Response 236
 - 13.6.2 Jasmonates Mediate Insect and Disease Resistance 237
- 13.7 **There are Features Common to all Stresses 237**
 - Summary 238
 - Chapter Review 238
 - Further Reading 238

Box 13.1 • Monitoring Plant Stress by Chlorophyll Fluorescence 228

Chapter 14 • Acclimation to Environmental Stress 241

- 14.1 **Plant Acclimation is a Time-Dependent Phenomenon 242**
- 14.2 **Acclimation is Initiated by Rapid, Short-Term Responses 242**
 - 14.2.1 State Transitions Regulate Energy Distribution in Response to Changes in Spectral Distribution 242
 - 14.2.2 Carotenoids Serve a Dual Function: Light Harvesting and Photoprotection 244
 - 14.2.3 Osmotic Adjustment is a Response to Water Stress 247
 - 14.2.4 Low Temperatures Induce Lipid Unsaturation and Cold Regulated Genes in Cold Tolerant Plants 248
 - 14.2.5 Q_{10} for Plant Respiration Varies as a Function of Temperature 248
- 14.3 **Long-Term Acclimation Alters Phenotype 249**
 - 14.3.1 Light Regulates Nuclear Gene Expression and Photoacclimation 249
 - 14.3.2 Does the Photosynthetic Apparatus Respond to Changes in Light Quality? 252
 - 14.3.3 Acclimation to Drought Affects Shoot–Root Ratio and Leaf Area 253
 - 14.3.4 Cold Acclimation Mimics Photoacclimation 254
- 14.4 **Freezing Tolerance in Herbaceous Species is a Complex Interaction Between Light and Low Temperature 255**
 - 14.4.1 Cold Acclimated Plants Secrete Antifreeze Proteins 256
 - 14.4.2 North Temperate Woody Plants Survive Freezing Stress 256
- 14.5 **Plants Adjust Photosynthetic Capacity in Response to High Temperature 257**
- 14.6 **Oxygen may Protect During Accimation to Various Stresses 258**
 - Summary* 259
 - Chapter Review* 259
 - Further Reading* 260

Chapter 15 • Adaptations to the Environment 261

- 15.1 **Sun and Shade Adapted Plants Respond Differentially to Irradiance 262**
- 15.2 **C4 Plants are Adapted to High Temperature and Drought 263**
 - 15.2.1 The C4 Syndrome is Another Biochemical Mechanism to Assimilate CO_2 263

- 15.2.2 The C4 Syndrome is Usually Associated with Kranz Leaf Anatomy 265
- 15.2.3 The C4 Syndrome has Ecological Significance 265
- 15.2.4 The C4 Syndrome is Differentially Sensitive to Temperature 265
- 15.2.5 The C4 Syndrome is Associated with Water Stress 266

15.3 **Crassulacean Acid Metabolism is an Adaptation to Desert Life 267**

- 15.3.1 Is CAM a Variation of the C4 Syndrome? 268
- 15.3.2 CAM Plants are Particularly Suited to Dry Habitats 269

15.4 **C4 and CAM Photosynthesis Require Precise Regulation and Temporal Integration 269**

15.5 **Plant Biomes Reflect Myriad Physiological Adaptations 270**

- 15.5.1 Tropical Rain Forest Biomes Exhibit the Greatest Plant Biodiversity 270
- 15.5.2 Evapotranspiration is a Major Contributor to Weather 271
- 15.5.3 Desert Perennials are Adapted to Reduce Transpiration and Heat Load 272
- 15.5.4 Desert Annuals are Ephemeral 273

Summary 273

Chapter Review 274

Further Reading 274

Chapter 16 • Development: An Overview 275

16.1 **Growth, Differentiation, and Development 275**

- 16.1.1 Development is the Sum of Growth and Differentiation 275
- 16.1.2 Growth is an Irreversible Increase in Size 276
- 16.1.3 Differentiation Refers To Qualitative Changes That Normally Accompany Growth 276

16.2 **Meristems are Centers of Plant Growth 277**

16.3 **Seed Development and Germination 279**

- 16.3.1 Seeds are Formed in the Flower 279
- 16.3.2 Seed Development and Maturation 280
- 16.3.3 Seed Germination 281
- 16.3.4 The Level and Activities of Various Hormones Change Dramatically During Seed Development 283
- 16.3.5 Many Seeds Have Additional Requirements for Germination 284

16.4 **From Embryo to Adult 285**

16.5 Senescence and Programmed Cell Death are the Final Stages of Development 286

Summary 287

Chapter Review 287

Further Reading 288

Box 16.1 • Development in a Mutant Weed 282

Chapter 17 • Growth and Development of Cells 289

17.1 Growth of Plant Cells is Complicated by the Presence of a Cell Wall 289

17.1.1 The Primary Cell Wall is a Network of Cellulose Microfibrils and Cross-Linking Glycans 289

17.1.2 The Cellulose–Glycan Lattice is Embedded in a Matrix of Pectin and Protein 290

17.1.3 Cellulose Microfibrils are Assembled at the Plasma Membrane as they are Extruded into the Cell Wall 292

17.2 Cell Division 292

17.2.1 The Cell Cycle 292

17.2.2 Cytokinesis 293

17.2.3 Plasmodesmata are Cytoplasmic Channels that Extend Through the Wall to Connect the Protoplasts of Adjacent Cells 294

17.3 Cell Walls and Cell Growth 294

17.3.1 Cell Growth is Driven by Water Uptake and Limited by the Strength and Rigidity of the Cell Wall 296

17.3.2 Extension of the Cell Wall Requires Wall-Loosening Events that Enable Load-Bearing Elements in the Wall to Yield to Turgor Pressure 296

17.3.3 Wall Loosening and Cell Expansion is Stimulated by Low Ph and Expansins 297

17.3.4 In Maturing Cells, a Secondary Cell Wall is Deposited on the Inside of the Primary Wall 298

17.4 A Continuous Stream of Signals Provides Information that Plant Cells Use to Modify Development 298

17.4.1 Signal Perception and Transduction 299

17.4.2 The G-Protein System is a Ubiquitous Receptor System 299

17.5 Signal Transduction Includes a Diverse Array of Second Messengers 300

17.5.1 Protein Kinase-Based Signaling 300

17.5.2 Phospholipid-Based Signaling 300

17.5.3 Calcium-Based Signaling 301

17.5.4 Transcriptional-Based Signaling 303

17.6 There is Extensive Crosstalk Among Signal Pathways 303

Summary 304

Chapter Review 304

Further Reading 304

Box 17.1 • Cytoskeleton 295

Box 17.2 • Ubiquitin and Proteasomes—Cleaning up Unwanted Proteins 302

Chapter 18 • Hormones I: Auxins 305

18.1 The Hormone Concept in Plants 305

18.2 Auxin is Distributed Throughout the Plant 306

18.3 The Principal Auxin in Plants is Indole-3-Acetic Acid (IAA) 307

18.4 IAA is Synthesized from the Amino Acid l-Tryptophan 309

18.5 Some Plants do not Require Tryptophan for IAA Biosynthesis 310

18.6 IAA may be Stored as Inactive Conjugates 310

18.7 IAA is Deactivated by Oxidation and Conjugation with Amino Acids 311

18.8 Auxin is Involved in Virtually Every Stage of Plant Development 311

18.8.1 The Principal Test for Auxins is the Stimulation of Cell Enlargement in Excised Tissues 311

18.8.2 Auxin Regulates Vascular Differentiation 311

18.8.3 Auxin Controls the Growth of Axillary Buds 313

18.9 The Acid-Growth Hypothesis Explains Auxin Control of Cell Enlargement 314

18.10 Maintenance of Auxin-Induced Growth and Other Auxin Effects Requires Gene Activation 316

18.11 Many Aspects of Plant Development are Linked to the Polar Transport of Auxin 317

Summary 320

Chapter Review 321

Further Reading 321

Box 18.1 • Discovering Auxin 307

Box 18.2 • Commercial Applications of Auxins 314

Chapter 19 • Hormones II: Gibberellins 323

- 19.1 There are a Large Number of Gibberellins 323
- 19.2 There are Three Principal Sites for Gibberellin Biosynthesis 324
- 19.3 Gibberellins are Terpenes, Sharing a Core Pathway with Several Other Hormones and a Wide Range of Secondary Products 325
- 19.4 Gibberellins are Synthesized from Geranylgeranyl Pyrophosphate (GGPP) 327
- 19.5 Gibberellins are Deactivated by 2β -Hydroxylation 329
- 19.6 Growth Retardants Block the Synthesis of Gibberellins 329
- 19.7 Gibberellin Transport is Poorly Understood 330
- 19.8 Gibberellins Affect Many Aspects of Plant Growth and Development 330
 - 19.8.1 Gibberellins Stimulate Hyper-elongation of Intact Stems, Especially in Dwarf and Rosette Plants 330
 - 19.8.2 Gibberellins Stimulate Mobilization of Nutrient Reserves During Germination of Cereal Grains 332
- 19.9 Gibberellins Act by Regulating Gene Expression 333
 - Summary 336
 - Chapter Review 336
 - Further Reading 337

BOX 19.1 • Discovery of Gibberellins 325

BOX 19.2 • Commercial Applications of Gibberellins 330

BOX 19.3 • DELLA Proteins and the Green Revolution 335

Chapter 20 • Hormones III: Cytokinins 339

- 20.1 Cytokinins are Adenine Derivatives 339
 - 20.1.1 Cytokinin Biosynthesis Begins with the Condensation of an Isopentenyl Group with the Amino Group of Adenosine Monophosphate 339
 - 20.1.2 Cytokinins may be Deactivated by Conjugation or Oxidation 340

20.2 Cytokinins are Synthesized Primarily in the Root and Translocated in the Xylem 341

20.3 Cytokinins are Required for Cell Proliferation 343

- 20.3.1 Cytokinins Regulate Progression through the Cell Cycle 343
- 20.3.2 The Ratio of Cytokinin to Auxin Controls Root and Shoot Initiation in Callus Tissues and the Growth of Axillary Buds 344
- 20.3.3 Crown Gall Tumors are Genetically Engineered to Overproduce Cytokinin and Auxin 345
- 20.3.4 Cytokinins Delay Senescence 346
- 20.3.5 Cytokinins Have an Important Role in Maintaining the Shoot Meristem 347
- 20.3.6 Cytokinin Levels in the Shoot Apical Meristem Are Regulated by Master Control Genes 348

20.4 Cytokinin Receptor and Signaling 350

- 20.4.1 The Cytokinin Receptor is a Membrane-Based Histidine Kinase 350
- 20.4.2 The Cytokinin Signaling Chain Involves a Multistep Transfer of Phosphoryl Groups to Response Regulators 351

Summary 353

Chapter Review 353

Further Reading 354

BOX 20.1 • The Discovery of Cytokinins 341

BOX 20.2 • Tissue Culture has Made Possible Large-Scale Cloning of Plants by Micropropagation 345

Chapter 21 • Hormones IV: Absciscic Acid, Ethylene, and Brassinosteroids 355

21.1 Absciscic Acid 355

- 21.1.1 Absciscic Acid is Synthesized from a Carotenoid Precursor 355
- 21.1.2 Absciscic Acid is Degraded to Phaseic Acid by Oxidation 357
- 21.1.3 Absciscic Acid is Synthesized in Mesophyll Cells, Guard Cells, and Vascular Tissue 357
- 21.1.4 Absciscic Acid Regulates Embryo Maturation and Seed Germination 358
- 21.1.5 Absciscic Acid Mediates Response to Water Stress 358
- 21.1.6 Other Absciscic Acid Responses 359
- 21.1.7 ABA Perception and Signal Transduction 359

21.2 Ethylene 362

- 21.2.1 Ethylene is Synthesized from the Amino Acid Methionine 362
- 21.2.2 Excess Ethylene is Subject to Oxidation 364
- 21.2.3 The Study of Ethylene Presents a Unique Set of Problems 364
- 21.2.4 Ethylene Affects Many Aspects of Vegetative Development 364
- 21.2.5 Ethylene Receptors and Signaling 365

21.3 Brassinosteroids 367

- 21.3.1 Brassinosteroids are Polyhydroxylated Sterols Derived from the Triterpene Squalene 367
- 21.3.2 Several Routes for Deactivation of Brassinosteroids have been Identified 369
- 21.3.3 Brassinolide receptors and Signaling 369
- Summary* 369
- Chapter Review* 370
- Further Reading* 370

BOX 21.1 • The Discovery of Absciscic Acid 356**BOX 21.2 • The Discovery of Ethylene 363****BOX 21.3 • Mitogenactivated Protein Kinase: A Widespread Mechanism for Signal Transduction 366****Chapter 22 • Photomorphogenesis: Responding to Light 373****22.1 Photomorphogenesis is Initiated by Photoreceptors 373****22.2 Phytochromes: Responding to Red and Far-Red Light 374**

- 22.2.1 Photoreversibility is the Hallmark of Phytochrome Action 376
- 22.2.2 Conversion of Pr to Pfr in Etiolated Seedlings Leads to a Loss of Both Pfr and Total Phytochrome 377
- 22.2.3 Light Establishes a State of Dynamic Photoequilibrium Between Pr and Pfr 378
- 22.2.4 Phytochrome Responses can be Grouped According to their Fluence Requirements 378

22.3 Cryptochrome: Responding to Blue and UV-A Light 379**22.4 Phytochrome and Cryptochrome Mediate Numerous Developmental Responses 379**

- 22.4.1 Seed Germination 379
- 22.4.2 De-Etiolation 380
- 22.4.3 Shade Avoidance 381
- 22.4.4 Detecting End-of-day Signals 381
- 22.4.5 Control of Anthocyanin Biosynthesis 382
- 22.4.6 Rapid Phytochrome Responses 382
- 22.4.7 PhyA may Function to Detect the Presence of Light 383

22.5 Chemistry and Mode of Action of Phytochrome and Cryptochrome 383

- 22.5.1 Phytochrome is a Phycobiliprotein 383
- 22.5.2 Phytochrome Signal Transduction 384
- 22.5.3 Cryptochrome Structure is Similar to DNA Repair Enzymes 386
- 22.5.4 Cryptochrome Signal Transduction 386

22.6 Some Plant Responses are Regulated by UV-B Light 387**22.7 De-Etiolation in Arabidopsis: A Case Study in Photoreceptor Interactions 387***Summary* 388*Chapter Review* 389*Further Reading* 389**BOX 22.1 • Historical Perspectives—The Discovery of Phytochrome 375****Chapter 23 • Tropisms and Nastic Movements: Orienting Plants in Space 391****23.1 Phototropism: Reaching for the Sun 392**

- 23.1.1 Phototropism is a Response to a Light Gradient 392
- 23.1.2 Phototropism is a Blue-Light Response 393
- 23.1.3 Phototropism Orients a Plant for Optimal Photosynthesis 393
- 23.1.4 Fluence Response Curves Illustrate the Complexity of Phototropic Responses 394
- 23.1.5 The Phototropic Response is Attributed to a Lateral Redistribution of Diffusible Auxin 395
- 23.1.6 Phototropism and Related Responses are Regulated by a Family of Blue-Sensitive Flavoproteins 396
- 23.1.7 A Hybrid Red/Blue Light Photoreceptor has been Isolated from a Fern 397

- 23.1.8 Phototropin Activity and Signal Chain 397
- 23.1.9 Phototropism in Green Plants is Not Well Understood 398
- 23.2 Gravitropism 398**
 - 23.2.1 Gravitropism is More than Simply Up and Down 399
 - 23.2.2 The Gravitational Stimulus is the Product of Intensity and Time 399
 - 23.2.3 Root Gravitropism Occurs in Four Phases 401
- 23.3 Nastic Movements 405**
 - 23.3.1 Nyctinastic Movements are Rhythmic Movements Involving Reversible Turgor Changes 406
 - 23.3.2 Nyctinastic Movements are due to Ion Fluxes and Resulting Osmotic Responses in Specialized Motor Cells 407
 - 23.3.3 Seismonasty is a Response to Mechanical Stimulation 409
- Summary 410*
- Chapter Review 411*
- Further Reading 411*

Box 23.1 • Methods in the Study of Gravitropism 400

Chapter 24 • Measuring Time: Controlling Development by Photoperiod and Endogenous Clocks 413

- 24.1 Photoperiodism 414**
 - 24.1.1 Photoperiodic Responses may be Characterized by a Variety of Response Types 415
 - 24.1.2 Critical Daylength Defines Short-Day and Long-Day Responses 415
 - 24.1.3 Plants Actually Measure the Length of the Dark Period 417
 - 24.1.4 Phytochrome and Cryptochrome are the Photoreceptors for Photoperiodism 418
 - 24.1.5 The Photoperiodic Signal is Perceived by the Leaves 419
 - 24.1.6 Control of Flowering by Photoperiod Requires a Transmissible Signal 420
 - 24.1.7 Photoperiodism Normally Requires a Period of High Fluence Light Before or After the Dark Period 421
- 24.2 The Biological Clock 423**
 - 24.2.1 Clock-Driven Rhythms Persist Under Constant Conditions 423

- 24.2.2 Light Resets the Biological Clock on a Daily Basis 425
- 24.2.3 The Circadian Clock is Temperature-Compensated 426
- 24.2.4 The Circadian Clock is a Significant Component in Photoperiodic Time Measurement 427
- 24.2.5 Daylength Measurement Involves an Interaction Between an External Light Signal and a Circadian Rhythm 428
- 24.2.6 The Circadian Clock is a Negative Feedback Loop 429
- 24.3 Photoperiodism in Nature 430**
 - Summary 431*
 - Chapter Review 432*
 - Further Reading 432*

Box 24.1 • Historical Perspectives: The Discovery of Photoperiodism 414

Box 24.2 • Historical Perspectives: The Biological Clock 422

Chapter 25 • Flowering and Fruit Development 433

- 25.1 Flower Initiation and Development Involves the Sequential Action of Three Sets of Genes 433**
 - 25.1.1 Flowering-Time Genes Influence the Duration of Vegetative Growth 434
 - 25.1.2 Floral-Identity Genes and Organ-Identity Genes Overlap in Time and Function 436
- 25.2 Temperature can Alter the Flowering Response to Photoperiod 437**
 - 25.2.1 Vernalization Occurs most Commonly in Winter Annuals and Biennials 438
 - 25.2.2 The Effective Temperature for Vernalization is Variable 439
 - 25.2.3 The Vernalization Treatment is Perceived by the Shoot Apex 440
 - 25.2.4 The Vernalized State is Transmissible 440
 - 25.2.5 Gibberellin and Vernalization Operate through Independent Genetic Pathways 440
 - 25.2.6 Three Genes Determine the Vernalization Requirement in Cereals 441
- 25.3 Fruit Set and Development is Regulated by Hormones 442**
 - 25.3.1 The Development of Fleshy Fruits can be Divided into Five Phases 442

- 25.3.2 Fruit Set is Triggered by Auxin 442
- 25.3.3 Ripening is Triggered by Ethylene in Climacteric Fruits 444

Summary 445

Chapter Review 446

Further Reading 446

Box 25.1 • Ethylene: It's a Gas! 445

Chapter 26 • Temperature: Plant Development and Distribution 447

26.1 Temperature in the Plant Environment 447

26.2 Bud Dormancy 449

- 26.2.1 Bud Dormancy is Induced by Photoperiod 450

- 26.2.2 A Period of Low Temperature is Required to Break Bud Dormancy 451

26.3 Seed Dormancy 451

- 26.3.1 Numerous Factors Influence Seed Dormancy 451

- 26.3.2 Temperature has a Significant Impact on Seed Dormancy 453

26.4 Thermoperiodism is a Response to Alternating Temperature 454

26.5 Temperature Influences Plant Distribution 454

Summary 457

Chapter Review 457

Further Reading 457

Box 26.1 • Bulbs and Corms 450

Chapter 27 • Secondary Metabolites 459

27.1 Secondary Metabolites: A.K.A Natural Products 459

27.2 Terpenes 460

- 27.2.1 The Terpenes are a Chemically and Functionally Diverse Group of Molecules 460
- 27.2.2 Terpenes are Constituents of Essential Oils 460
- 27.2.3 Steroids and Sterols are Tetracyclic Triterpenoids 462
- 27.2.4 Polyterpenes Include the Carotenoid Pigments and Natural Rubber 462

27.3 Glycosides 463

- 27.3.1 Saponins are Terpene Glycosides with Detergent Properties 464
- 27.3.2 Cardiac Glycosides are Highly Toxic Steroid Glycosides 465

- 27.3.3 Cyanogenic Glycosides are A Natural Source of Hydrogen Cyanide 466

- 27.3.4 Glucosinolates are Sulfur-Containing Precursors to Mustard Oils 466

27.4 Phenylpropanoids 467

- 27.4.1 Shikimic Acid is a Key Intermediate in the Synthesis of Both Aromatic Amino Acids and Phenylpropanoids 468

- 27.4.2 The Simplest Phenolic Molecules are Essentially Deaminated Versions of the Corresponding Amino Acids 468

- 27.4.3 Coumarins and Coumarin Derivatives Function as Anticoagulants 468

- 27.4.4 Lignin is a Major Structural Component of Secondary Cell Walls 470

- 27.4.5 Flavonoids and Stilbenes have Parallel Biosynthetic Pathways 471

- 27.4.6 Tannins Denature Proteins and Add an Astringent Taste to Foods 472

27.5 Secondary Metabolites are Active Against Insects and Disease 474

- 27.5.1 Some Terpenes and Isoflavones have Insecticidal and Anti-Microbial Activity 474

- 27.5.2 Recognizing Potential Pathogens 475

- 27.5.3 Salicylic Acid, a Shikimic Acid Derivative, Triggers Systemic Acquired Resistance 475

27.6 Jasmonates are Linked to Ubiquitin-Related Protein Degradation 476

27.7 Alkaloids 476

- 27.7.1 Alkaloids are a Large Family of Chemically Unrelated Molecules 476

- 27.7.2 Alkaloids are Noted Primarily for their Pharmacological Properties and Medical Applications 476

- 27.7.3 Like Many Other Secondary Metabolites, Alkaloids Serve as Preformed Chemical Defense Molecules 479

Summary 479

Chapter Review 480

Further Reading 480

Appendix • Building Blocks: Lipids, Proteins, and Carbohydrates 481

I.1 Lipids 481

I.2 Proteins 483

I.3 Carbohydrates 485

- I.3.1 Monosaccharides 485

- I.3.2 Polysaccharides 486

Index/Glossary 489