

# Table of Contents

**Preface** v

**Authors and Contributors** vii

## 1 **Plant Cells** 1

**Plant Life: Unifying Principles** 1

**Overview of Plant Structure** 2

Plant Cells Are Surrounded by Rigid Cell Walls 2

New Cells Are Produced by Dividing Tissues Called Meristems 2

Three Major Tissue Systems Make Up the Plant Body 2

**The Plant Cell** 5

Biological Membranes Are Phospholipid Bilayers That Contain Proteins 6

The Nucleus Contains Most of the Genetic Material of the Cell 6

Protein Synthesis Involves Transcription and Translation 9

The Endoplasmic Reticulum Is a Network of Internal Membranes 10

Secretion of Proteins from Cells Begins with the Rough ER 10

Proteins and Polysaccharides for Secretion Are Processed in the Golgi Apparatus 13

The Central Vacuole Contains Water and Solutes 13

Mitochondria and Chloroplasts Are Sites of Energy Conversion 14

Mitochondria and Chloroplasts Are Semiautonomous Organelles 15

Different Plastid Types Are Interconvertible 17

Microbodies Play Specialized Metabolic Roles in Leaves and Seeds 18

Oleosomes Are Lipid-Storing Organelles 19

**The Cytoskeleton** 19

Plant Cells Contain Microtubules, Microfilaments, and Intermediate Filaments 19

Microtubules and Microfilaments Can Assemble and Disassemble 20

Microtubules Function in Mitosis and Cytokinesis 21

Microfilaments Are Involved in Cytoplasmic Streaming and in Tip Growth 22

Intermediate Filaments Occur in the Cytosol and Nucleus of Plant Cells 23

**Cell Cycle Regulation** 23

Each Phase of the Cell Cycle Has a Specific Set of Biochemical and Cellular Activities 23

The Cell Cycle Is Regulated by Protein Kinases 23

**Plasmodesmata** 24

There Are Two Types of Plasmodesmata: Primary and Secondary 25

Plasmodesmata Have a Complex Internal Structure 25

**Summary** 26

## 2 **[On the web site] Energy and Enzymes** 29



# UNIT I

## *Transport and Translocation of Water and Solutes 31*

### 3 *Water and Plant Cells 33*

#### **Water in Plant Life 33**

##### **The Structure and Properties of Water 34**

- The Polarity of Water Molecules Gives Rise to Hydrogen Bonds 34
- The Polarity of Water Makes It an Excellent Solvent 35
- The Thermal Properties of Water Result from Hydrogen Bonding 35
- The Cohesive and Adhesive Properties of Water Are Due to Hydrogen Bonding 36
- Water Has a High Tensile Strength 36

##### **Water Transport Processes 36**

- Diffusion Is the Movement of Molecules by Random Thermal Agitation 37
- Diffusion Is Rapid over Short Distances but Extremely Slow over Long Distances 37
- Pressure-Driven Bulk Flow Drives Long-Distance Water Transport 39

- Osmosis Is Driven by a Water Potential Gradient 39
- The Chemical Potential of Water Represents the Free-Energy Status of Water 39
- Three Major Factors Contribute to Cell Water Potential 39
- Water Enters the Cell along a Water Potential Gradient 40
- Water Can Also Leave the Cell in Response to a Water Potential Gradient 42
- Small Changes in Plant Cell Volume Cause Large Changes in Turgor Pressure 43
- Water Transport Rates Depend on Driving Force and Hydraulic Conductivity 43
- The Water Potential Concept Helps Us Evaluate the Water Status of a Plant 44
- The Components of Water Potential Vary with Growth Conditions and Location within the Plant 45

#### **Summary 45**

### 4 *Water Balance of Plants 47*

#### **Water in the Soil 47**

- A Negative Hydrostatic Pressure in Soil Water Lowers Soil Water Potential 48
- Water Moves through the Soil by Bulk Flow 49

#### **Water Absorption by Roots 49**

- Water Moves in the Root via the Apoplast, Transmembrane, and Symplast Pathways 50
- Solute Accumulation in the Xylem Can Generate "Root Pressure" 51

#### **Water Transport through the Xylem 52**

- The Xylem Consists of Two Types of Tracheary Elements 52
- Water Movement through the Xylem Requires Less Pressure Than Movement through Living Cells 53
- What Pressure Difference Is Needed to Lift Water 100 Meters to a Treetop? 53
- The Cohesion-Tension Theory Explains Water Transport in the Xylem 54
- Xylem Transport of Water in Trees Faces Physical Challenges 54
- Plants Minimize the Consequences of Xylem Cavitation 55

- Water Evaporation in the Leaf Generates a Negative Pressure in the Xylem 55

#### **Water Movement from the Leaf to the Atmosphere 57**

- Water Vapor Diffuses Quickly in Air 57
- The Driving Force for Water Loss Is the Difference in Water Vapor Concentration 58
- Water Loss Is Also Regulated by the Pathway Resistances 58
- Stomatal Control Couples Leaf Transpiration to Leaf Photosynthesis 59
- The Cell Walls of Guard Cells Have Specialized Features 60
- An Increase in Guard Cell Turgor Pressure Opens the Stomata 61
- The Transpiration Ratio Measures the Relationship between Water Loss and Carbon Gain 62

#### **Overview: The Soil-Plant-Atmosphere Continuum 62**

#### **Summary 63**

## 5 *Mineral Nutrition* 67

### **Essential Nutrients, Deficiencies, and Plant Disorders** 68

- Special Techniques Are Used in Nutritional Studies 69
- Nutrient Solutions Can Sustain Rapid Plant Growth 70
- Mineral Deficiencies Disrupt Plant Metabolism and Function 72
- Analysis of Plant Tissues Reveals Mineral Deficiencies 75

### **Treating Nutritional Deficiencies** 76

- Crop Yields Can Be Improved by Addition of Fertilizers 76
- Some Mineral Nutrients Can Be Absorbed by Leaves 77

### **Soil, Roots, and Microbes** 78

- Negatively Charged Soil Particles Affect the

- Adsorption of Mineral Nutrients 78
- Soil pH Affects Nutrient Availability, Soil Microbes, and Root Growth 79
- Excess Minerals in the Soil Limit Plant Growth 79
- Plants Develop Extensive Root Systems 79
- Root Systems Differ in Form but Are Based on Common Structures 80
- Different Areas of the Root Absorb Different Mineral Ions 82
- Mycorrhizal Fungi Facilitate Nutrient Uptake by Roots 82
- Nutrients Move from the Mycorrhizal Fungi to the Root Cells 84

### **Summary** 84

## 6 *Solute Transport* 87

### **Passive and Active Transport** 88

#### **Transport of Ions across a Membrane Barrier** 89

- Diffusion Potentials Develop When Oppositely Charged Ions Move across a Membrane at Different Rates 90
- The Nernst Equation Relates the Membrane Potential to the Distribution of an Ion at Equilibrium 90
- The Nernst Equation Can Be Used to Distinguish between Active and Passive Transport 91
- Proton Transport Is a Major Determinant of the Membrane Potential 92

#### **Membrane Transport Processes** 93

- Channel Transporters Enhance Ion and Water Diffusion across Membranes 94
- Carriers Bind and Transport Specific Substances 95
- Primary Active Transport Is Directly Coupled to Metabolic or Light Energy 96
- Secondary Active Transport Uses the Energy Stored in Electrochemical-Potential Gradients 96

#### **Membrane Transport Proteins** 99

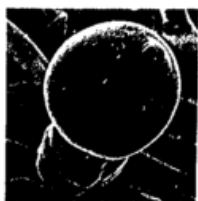
- Kinetic Analyses Can Elucidate Transport Mechanisms 99

- The Genes for Many Transporters Have Been Cloned 100
- Genes for Specific Water Channels Have Been Identified 101
- The Plasma Membrane  $H^+$ -ATPase Has Several Functional Domains 101
- The Vacuolar  $H^+$ -ATPase Drives Solute Accumulation into Vacuoles 102
- Plant Vacuoles Are Energized by a Second Proton Pump, the  $H^+$ -Pyrophosphatase 104
- Calcium Pumps, Antiports, and Channels Regulate Intracellular Calcium 104

#### **Ion Transport in Roots** 104

- Solutes Move through Both Apoplast and Symplast 104
- Ions Moving through the Root Cross Both Symplastic and Apoplastic Spaces 105
- Xylem Parenchyma Cells Participate in Xylem Loading 105

#### **Summary** 107



## UNIT II

### *Biochemistry and Metabolism 109*

## 7 **Photosynthesis: The Light Reactions 111**

### **Photosynthesis in Higher Plants 111**

#### **General Concepts 112**

- Light Has Characteristics of Both a Particle and a Wave 112
- When Molecules Absorb or Emit Light, They Change Their Electronic State 113
- Photosynthetic Pigments Absorb the Light That Powers Photosynthesis 115

#### **Key Experiments in Understanding Photosynthesis 115**

- Action Spectra Relate Light Absorption to Photosynthetic Activity 116
- Photosynthesis Takes Place in Complexes Containing Light-Harvesting Antennas and Photochemical Reaction Centers 117
- The Chemical Reaction of Photosynthesis Is Driven by Light 118
- Light Drives the Reduction of NADP and the Formation of ATP 118
- Oxygen-Evolving Organisms Have Two Photosystems That Operate in Series 119

#### **Organization of the Photosynthetic Apparatus 120**

- The Chloroplast Is the Site of Photosynthesis 120
- Thylakoids Contain Integral Membrane Proteins 121
- Photosystems I and II Are Spatially Separated in the Thylakoid Membrane 122
- Anoxygenic Photosynthetic Bacteria Have a Reaction Center Similar to That of Photosystem II 122

#### **Organization of Light-Absorbing Antenna Systems 123**

- The Antenna Funnels Energy to the Reaction Center 123
- Many Antenna Complexes Have a Common Structural Motif 123

#### **Mechanisms of Electron Transport 124**

- Electrons Ejected from Chlorophyll Travel Through a Series of Electron Carriers Organized in the "Z Scheme" 125
- Energy Is Captured When an Excited Chlorophyll Reduces an Electron Acceptor Molecule 126
- The Reaction Center Chlorophylls of the Two Photosystems Absorb at Different Wavelengths 127

The Photosystem II Reaction Center Is a Multisubunit Pigment-Protein Complex 127

Water Is Oxidized to Oxygen by Photosystem II 127

Pheophytin and Two Quinones Accept Electrons from Photosystem II 130

Electron Flow through the Cytochrome  $b_6f$  Complex Also Transports Protons 130

Plastoquinone and Plastocyanin Carry Electrons between Photosystems II and I 132

The Photosystem I Reaction Center Reduces NADP<sup>+</sup> 132

Cyclic Electron Flow Generates ATP but no NADPH 133

Some Herbicides Block Electron Flow 133

#### **Proton Transport and ATP Synthesis in the Chloroplast 133**

#### **Repair and Regulation of the Photosynthetic Machinery 135**

Carotenoids Serve as Photoprotective Agents 135

Some Xanthophylls Also Participate in Energy Dissipation 136

The Photosystem II Reaction Center Is Easily Damaged 138

Photosystem I Is Protected from Active Oxygen Species 138

Thylakoid Stacking Permits Energy Partitioning between the Photosystems 138

#### **Genetics, Assembly, and Evolution of Photosynthetic Systems 138**

Chloroplast, Cyanobacterial, and Nuclear Genomes Have Been Sequenced 138

Chloroplast Genes Exhibit Non-Mendelian Patterns of Inheritance 139

Many Chloroplast Proteins Are Imported from the Cytoplasm 139

The Biosynthesis and Breakdown of Chlorophyll Are Complex Pathways 139

Complex Photosynthetic Organisms Have Evolved from Simpler Forms 139

#### **Summary 141**

## 8 *Photosynthesis: Carbon Reactions* 145

### **The Calvin Cycle** 146

- The Calvin Cycle Has Three Stages: Carboxylation, Reduction, and Regeneration 146
- The Carboxylation of Ribulose Biphosphate Is Catalyzed by the Enzyme Rubisco 146
- Triose Phosphates Are Formed in the Reduction Step of the Calvin Cycle 148
- Operation of the Calvin Cycle Requires the Regeneration of Ribulose-1,5-Bisphosphate 149
- The Calvin Cycle Regenerates Its Own Biochemical Components 149
- Calvin Cycle Stoichiometry Shows That Only One-Sixth of the Triose Phosphate Is Used for Sucrose or Starch 150

### **Regulation of the Calvin Cycle** 150

- Light-Dependent Enzyme Activation Regulates the Calvin Cycle 151
- Rubisco Activity Increases in the Light 151
- Light-Dependent Ion Movements Regulate Calvin Cycle Enzymes 152
- Light-Dependent Membrane Transport Regulates the Calvin Cycle 152

### **The C<sub>2</sub> Oxidative Photosynthetic Carbon Cycle** 152

- Photosynthetic CO<sub>2</sub> Fixation and Photorespiratory Oxygenation Are Competing Reactions 152
- Competition between Carboxylation and Oxygenation Decreases the Efficiency of Photosynthesis 155
- Carboxylation and Oxygenation Are Closely Interlocked in the Intact Leaf 155

The Biological Function of Photorespiration Is Unknown 155

### **CO<sub>2</sub>-Concentrating Mechanisms I: Algal and Cyanobacterial Pumps** 156

### **CO<sub>2</sub>-Concentrating Mechanisms II: The C<sub>4</sub> Carbon Cycle** 156

- Malate and Aspartate Are Carboxylation Products of the C<sub>4</sub> Cycle 156
- The C<sub>4</sub> Cycle Concentrates CO<sub>2</sub> in Bundle Sheath Cells 158
- The Concentration of CO<sub>2</sub> in Bundle Sheath Cells Has an Energy Cost 159
- Light Regulates the Activity of Key C<sub>4</sub> Enzymes 160
- In Hot, Dry Climates, the C<sub>4</sub> Cycle Reduces Photorespiration and Water Loss 160

### **CO<sub>2</sub>-Concentrating Mechanisms III: Crassulacean Acid Metabolism** 160

- The Stomata of CAM Plants Open at Night and Close during the Day 161
- Phosphorylation Regulates the Activity of PEP Carboxylase in C<sub>4</sub> and CAM Plants 162
- Some Plants Adjust Their Pattern of CO<sub>2</sub> Uptake to Environmental Conditions 162

### **Synthesis of Starch and Sucrose** 162

- Starch Is Synthesized in the Chloroplast 162
- Sucrose Is Synthesized in the Cytosol 162
- The Syntheses of Sucrose and Starch Are Competing Reactions 164

### **Summary** 168

## 9 *Photosynthesis: Physiological and Ecological Considerations* 171

### **Light, Leaves, and Photosynthesis** 172

#### **Concepts and Units in the Measurement of Light** 172

- Leaf Anatomy Maximizes Light Absorption 173
- Chloroplast Movement and Leaf Movement Can Control Light Absorption 175
- Plants Adapt to Sun and Shade 176
- Plants Compete for Sunlight 177

#### **Photosynthetic Responses to Light by the Intact Leaf** 177

- Light-Response Curves Reveal Photosynthetic Properties 178
- Leaves Must Dissipate Excess Light Energy 179
- Leaves Must Dissipate Vast Quantities of Heat 181
- Isoprene Synthesis Helps Leaves Cope with Heat 181

Absorption of Too Much Light Can Lead to Photoinhibition 182

### **Photosynthetic Responses to Carbon Dioxide** 183

- Atmospheric CO<sub>2</sub> Concentration Keeps Rising 183
- Diffusion of CO<sub>2</sub> to the Chloroplast Is Essential to Photosynthesis 184
- Patterns of Light Absorption Generate Gradients of CO<sub>2</sub> Fixation within the Leaf 185
- CO<sub>2</sub> Imposes Limitations on Photosynthesis 186
- CO<sub>2</sub>-Concentrating Mechanisms Affect Photosynthetic Responses of Leaves 187
- Discrimination of Carbon Isotopes Reveals Different Photosynthetic Pathways 188

### **Photosynthetic Responses to Temperature** 188

### **Summary** 190

## 10 *Translocation in the Phloem* 193

### Pathways of Translocation 194

- Sugar Is Translocated in Phloem Sieve Elements 194
- Mature Sieve Elements Are Living Cells Highly Specialized for Translocation 194
- Sieve Areas Are the Prominent Feature of Sieve Elements 196
- Deposition of P-Protein and Callose Seals Off Damaged Sieve Elements 196
- Companion Cells Aid the Highly Specialized Sieve Elements 197

### Patterns of Translocation: Source to Sink 198

- Source-to-Sink Pathways Follow Anatomic and Developmental Patterns 199

### Materials Translocated in the Phloem: Sucrose, Amino Acids, Hormones, and Some Inorganic Ions 200

- Phloem Sap Can Be Collected and Analyzed 200
- Sugars Are Translocated in Nonreducing Form 200
- Phloem and Xylem Interact to Transport Nitrogenous Compounds 202

### Rates of Movement 202

- Velocities of Phloem Transport Far Exceed the Rate of Diffusion 202

### The Mechanism of Translocation in the Phloem: The Pressure-Flow Model 202

- A Pressure Gradient Drives Translocation 203
- The Predictions of the Pressure-Flow Model Have Been Confirmed 203
- Sieve Plate Pores Are Open Channels 203
- Bidirectional Transport Cannot Be Seen in Single Sieve Elements 204
- Translocation Rate Is Typically Insensitive to the Energy Supply of the Path Tissues 205
- Pressure Gradients Are Sufficient to Drive a Mass Flow of Solution 206
- The Mechanism of Phloem Transport in Gymnosperms May Be Different 206

### Phloem Loading: From Chloroplasts to Sieve Elements 206

- Photosynthate Can Move from Mesophyll Cells to the Sieve Elements via the Apoplast or the Symplast 207
- Sucrose Uptake in the Apoplastic Pathway Requires Metabolic Energy 207
- In the Apoplastic Pathway, Sieve Element Loading Involves a Sucrose- $H^+$  Symporter 207
- Phloem Loading Appears to Be Symplastic in Plants with Intermediary Cells 210
- The Polymer-Trapping Model Explains Symplastic Loading in Source Leaves 210
- The Type of Phloem Loading Is Correlated with Plant Family and with Climate 211

### Phloem Unloading and Sink-to-Source Transition 212

- Phloem Unloading Can Occur via Symplastic or Apoplastic Pathways 212
- Transport into Sink Tissues Requires Metabolic Energy 212
- The Transition of a Leaf from Sink to Source Is Gradual 213

### Photosynthate Allocation and Partitioning 214

- Allocation Includes the Storage, Utilization, and Transport of Fixed Carbon 215
- Transport Sugars Are Partitioned among the Various Sink Tissues 215
- Allocation in Source Leaves Is Regulated 215
- Sink Tissues Compete for Available Translocated Photosynthate 216
- Sink Strength Is a Function of Sink Size and Sink Activity 216
- Changes in the Source-to-Sink Ratio Cause Long-Term Alterations in the Source 217
- Long-Distance Signals May Coordinate the Activities of Sources and Sinks 217
- Long-Distance Signals May Also Regulate Plant Growth and Development 218

### Summary 219

## 11 *Respiration and Lipid Metabolism* 223

### Overview of Plant Respiration 223

### Glycolysis: A Cytosolic and Plastidic Process 226

- Glycolysis Converts Carbohydrates into Pyruvate, Producing NADH and ATP 226
- Plants Have Alternative Glycolytic Reactions 227
- In the Absence of  $O_2$ , Fermentation Regenerates the  $NAD^+$  Needed for Glycolysis 229
- Fermentation Does Not Liberate All the Energy Available in Each Sugar Molecule 229

- Plant Glycolysis Is Controlled by Its Products 230

- The Pentose Phosphate Pathway Produces NADPH and Biosynthetic Intermediates 230

### The Citric Acid Cycle: A Mitochondrial Matrix Process 232

- Mitochondria Are Semiautonomous Organelles 232
- Pyruvate Enters the Mitochondrion and Is Oxidized via the Citric Acid Cycle 233
- The Citric Acid Cycle of Plants Has Unique Features 235

**Electron Transport and ATP Synthesis at the Inner Mitochondrial Membrane 235**

- The Electron Transport Chain Catalyzes a Flow of Electrons from NADH to O<sub>2</sub> 236
- Some Electron Transport Enzymes Are Unique to Plant Mitochondria 236
- ATP Synthesis in the Mitochondrion Is Coupled to Electron Transport 237
- Transporters Exchange Substrates and Products 239
- Aerobic Respiration Yields about 60 Molecules of ATP per Molecule of Sucrose 239
- Several Subunits of Respiratory Complexes Are Encoded by the Mitochondrial Genome 241
- Plants Have Several Mechanisms That Lower the ATP Yield 242
- Mitochondrial Respiration Is Controlled by Key Metabolites 243
- Respiration Is Tightly Coupled to Other Pathways 244

**Respiration in Intact Plants and Tissues 245**

- Plants Respire Roughly Half of the Daily Photosynthetic Yield 245

- Respiration Operates during Photosynthesis 245
- Different Tissues and Organs Respire at Different Rates 245
- Mitochondrial Function Is Crucial during Pollen Development 246
- Environmental Factors Alter Respiration Rates 246

**Lipid Metabolism 247**

- Fats and Oils Store Large Amounts of Energy 247
- Triacylglycerols Are Stored in Oleosomes 248
- Polar Glycerolipids Are the Main Structural Lipids in Membranes 249
- Fatty Acid Biosynthesis Consists of Cycles of Two-Carbon Addition 249
- Glycerolipids Are Synthesized in the Plastids and the ER 252
- Lipid Composition Influences Membrane Function 253
- Membrane Lipids Are Precursors of Important Signaling Compounds 253
- Storage Lipids Are Converted into Carbohydrates in Germinating Seeds 253

**Summary 255**

# 12 *Assimilation of Mineral Nutrients* 259

**Nitrogen in the Environment 260**

- Nitrogen Passes through Several Forms in a Biogeochemical Cycle 260
- Stored Ammonium or Nitrate Can Be Toxic 261

**Nitrate Assimilation 262**

- Nitrate, Light, and Carbohydrates Regulate Nitrate Reductase 262
- Nitrite Reductase Converts Nitrite to Ammonium 263
- Plants Can Assimilate Nitrate in Both Roots and Shoots 263

**Ammonium Assimilation 264**

- Conversion of Ammonium to Amino Acids Requires Two Enzymes 264
- Ammonium Can Be Assimilated via an Alternative Pathway 264
- Transamination Reactions Transfer Nitrogen 266
- Asparagine and Glutamine Link Carbon and Nitrogen Metabolism 266

**Biological Nitrogen Fixation 266**

- Free-Living and Symbiotic Bacteria Fix Nitrogen 266
- Nitrogen Fixation Requires Anaerobic Conditions 266
- Symbiotic Nitrogen Fixation Occurs in Specialized Structures 268
- Establishing Symbiosis Requires an Exchange of Signals 269

- Nod Factors Produced by Bacteria Act as Signals for Symbiosis 269
- Nodule Formation Involves Several Phytohormones 270
- The Nitrogenase Enzyme Complex Fixes N<sub>2</sub> 270
- Amides and Ureides Are the Transported Forms of Nitrogen 272

**Sulfur Assimilation 272**

- Sulfate Is the Absorbed Form of Sulfur in Plants 273
- Sulfate Assimilation Requires the Reduction of Sulfate to Cysteine 273
- Sulfate Assimilation Occurs Mostly in Leaves 274
- Methionine Is Synthesized from Cysteine 275

**Phosphate Assimilation 275****Cation Assimilation 275**

- Cations Form Noncovalent Bonds with Carbon Compounds 275
- Roots Modify the Rhizosphere to Acquire Iron 275
- Iron Forms Complexes with Carbon and Phosphate 277

**Oxygen Assimilation 277****The Energetics of Nutrient Assimilation 278****Summary 279**

# 13 *Secondary Metabolites and Plant Defense* 283

## **Cutin, Waxes, and Suberin 283**

- Cutin, Waxes, and Suberin Are Made Up of Hydrophobic Compounds 284
- Cutin, Waxes, and Suberin Help Reduce Transpiration and Pathogen Invasion 285

## **Secondary Metabolites 285**

- Secondary Metabolites Defend Plants against Herbivores and Pathogens 285
- Plant Defenses Are a Product of Evolution 286
- Secondary Metabolites Are Divided into Three Major Groups 286

## **Terpenes 287**

- Terpenes Are Formed by the Fusion of Five-Carbon Isoprene Units 287
- There Are Two Pathways for Terpene Biosynthesis 287
- Isopentenyl Diphosphate and Its Isomer Combine to Form Larger Terpenes 287
- Some Terpenes Have Roles in Growth and Development 287
- Terpenes Defend against Herbivores in Many Plants 287

## **Phenolic Compounds 290**

- Phenylalanine Is an Intermediate in the Biosynthesis of Most Plant Phenolics 290
- Some Simple Phenolics Are Activated by Ultraviolet Light 291
- The Release of Phenolics into the Soil May Limit the Growth of Other Plants 292
- Lignin Is a Highly Complex Phenolic Macromolecule 293
- There Are Four Major Groups of Flavonoids 294

Anthocyanins Are Colored Flavonoids That Attract Animals 294

Flavonoids May Protect against Damage by Ultraviolet Light 295

Isoflavonoids Have Antimicrobial Activity 296

Tannins Deter Feeding by Herbivores 296

## **Nitrogen-Containing Compounds 297**

Alkaloids Have Dramatic Physiological Effects on Animals 297

Cyanogenic Glycosides Release the Poison Hydrogen Cyanide 300

Glucosinolates Release Volatile Toxins 301

Nonprotein Amino Acids Defend against Herbivores 301

Some Plant Proteins Inhibit Herbivore Digestion 302

Herbivore Damage Triggers a Complex Signaling Pathway 302

Jasmonic Acid Is a Plant Stress Hormone That Activates Many Defense Responses 303

## **Plant Defense against Pathogens 303**

Some Antimicrobial Compounds Are Synthesized before Pathogen Attack 303

Infection Induces Additional Antipathogen Defenses 303

Some Plants Recognize Specific Substances Released from Pathogens 305

Exposure to Elicitors Induces a Signal Transduction Cascade 305

A Single Encounter with a Pathogen May Increase Resistance to Future Attacks 306

## **Summary 306**



## UNIT III

### *Growth and Development 309*

## 14 [On the web site] *Gene Expression and Signal Transduction 311*

## 15 *Cell Walls: Structure, Biogenesis, and Expansion 313*

### **The Structure and Synthesis of Plant Cell Walls 314**

- Plant Cell Walls Have Varied Architecture 314
- The Primary Cell Wall Is Composed of Cellulose Microfibrils Embedded in a Polysaccharide Matrix 315
- Cellulose Microfibrils Are Synthesized at the Plasma Membrane 317
- Matrix Polymers Are Synthesized in the Golgi and Secreted in Vesicles 319
- Hemicelluloses Are Matrix Polysaccharides That Bind to Cellulose 321
- Pectins Are Gel-Forming Components of the Matrix 322
- Structural Proteins Become Cross-Linked in the Wall 325
- New Primary Walls Are Assembled during Cytokinesis 326
- Secondary Walls Form in Some Cells after Expansion Ceases 327

### **Patterns of Cell Expansion 328**

- Microfibril Orientation Determines Growth Directionality of Cells with Diffuse Growth 328

- Cortical Microtubules Determine the Orientation of Newly Deposited Microfibrils 329

### **The Rate of Cell Elongation 331**

- Stress Relaxation of the Cell Wall Drives Water Uptake and Cell Elongation 331
- The Rate of Cell Expansion Is Governed By Two Growth Equations 331
- Acid-Induced Growth Is Mediated by Expansins 333
- Glucanases and Other Hydrolytic Enzymes May Modify the Matrix 334
- Many Structural Changes Accompany the Cessation of Wall Expansion 335

### **Wall Degradation and Plant Defense 335**

- Enzymes Mediate Wall Hydrolysis and Degradation 335
- Oxidative Bursts Accompany Pathogen Attack 336
- Wall Fragments Can Act as Signaling Molecules 336

### **Summary 336**

## 16 *Growth and Development 339*

### **Embryogenesis 340**

- Embryogenesis Establishes the Essential Features of the Mature Plant 340
- Arabidopsis* Embryos Pass through Four Distinct Stages of Development 342
- The Axial Pattern of the Embryo Is Established during the First Cell Division of the Zygote 343
- The Radial Pattern of Tissue Differentiation Is First Visible at the Globular Stage 343
- Embryogenesis Requires Specific Gene Expression 345
- Embryo Maturation Requires Specific Gene Expression 348

### **The Role of Cytokinesis in Pattern Formation 348**

- The Stereotypic Cell Division Pattern Is Not Required for the Axial and Radial Patterns of Tissue Differentiation 348

- An *Arabidopsis* Mutant with Defective Cytokinesis Cannot Establish the Radial Tissue Pattern 349

### **Meristems in Plant Development 350**

- The Shoot Apical Meristem Is a Highly Dynamic Structure 350
- The Shoot Apical Meristem Contains Different Functional Zones and Layers 351
- Some Meristems Arise during Postembryonic Development 351
- Axillary, Floral, and Inflorescence Shoot Meristems Are Variants of the Vegetative Meristem 352

### **Leaf Development 352**

- The Arrangement of Leaf Primordia Is Genetically Programmed 353

### **Root Development 354**

- The Root Tip Has Four Developmental Zones 354

Root Stem Cells Generate Longitudinal Files of Cells 355  
 Root Apical Meristems Contain Several Types of Stem Cells 356

### **Cell Differentiation 357**

A Secondary Cell Wall Forms during Tracheary Element Differentiation 357

### **Initiation and Regulation of Developmental Pathways 359**

Transcription Factor Genes Control Development 359  
 Many Plant Signaling Pathways Utilize Protein Kinases 360  
 A Cell's Fate Is Determined by Its Position 360  
 Developmental Pathways Are Controlled by Networks of Interacting Genes 362  
 Development Is Regulated by Cell-to-Cell Signaling 363

### **The Analysis of Plant Growth 367**

Plant Growth Can Be Measured in Different Ways 367  
 The Production of Cells by the Meristem Is Comparable to a Fountain 368  
 Tissue Elements Are Displaced during Expansion 369  
 As Regions Move Away from the Apex, Their Growth Rate Increases 369  
 The Growth Velocity Profile Is a Spatial Description of Growth 369

### **Senescence and Programmed Cell Death 369**

Plants Exhibit Various Types of Senescence 370  
 Senescence Is an Ordered Series of Cytological and Biochemical Events 370  
 Programmed Cell Death Is a Specialized Type of Senescence 371

### **Summary 372**

## **17 Phytochrome and Light Control of Plant Development 375**

### **The Photochemical and Biochemical Properties of Phytochrome 376**

Phytochrome Can Interconvert between Pr and Pfr Forms 377  
 Pfr Is the Physiologically Active Form of Phytochrome 378  
 Phytochrome Is a Dimer Composed of Two Polypeptides 379  
 Phytochromobilin Is Synthesized in Plastids 379  
 Both Chromophore and Protein Undergo Conformational Changes 380  
 Two Types of Phytochromes Have Been Identified 380  
 Phytochrome Is Encoded by a Multigene Family 380  
*PHY* Genes Encode Two Types of Phytochrome 380

### **Localization of Phytochrome in Tissues and Cells 381**

Phytochrome Can Be Detected in Tissues Spectrophotometrically 381  
 Phytochrome Is Differentially Expressed In Different Tissues 381

### **Characteristics of Phytochrome-Induced Whole-Plant Responses 382**

Phytochrome Responses Vary in Lag Time and Escape Time 382  
 Phytochrome Responses Can Be Distinguished by the Amount of Light Required 383  
 Very-Low-Fluence Responses Are Nonphoto-reversible 383  
 Low-Fluence Responses Are Photoreversible 383  
 High-Irradiance Responses Are Proportional to the Irradiance and the Duration 383  
 The HIR Action Spectrum of Etiolated Seedlings Has Peaks in the Far-Red, Blue, and UV-A Regions 384  
 The HIR Action Spectrum of Green Plants Has a Major Red Peak 385

### **Ecological Functions: Shade Avoidance 385**

Phytochrome Enables Plants to Adapt to Changing Light Conditions 385

### **Ecological Functions: Circadian Rhythms 387**

Phytochrome Regulates the Sleep Movements of Leaves 387  
 Circadian Clock Genes of *Arabidopsis* Have Been Identified 389

### **Ecological Functions: Phytochrome Specialization 389**

Phytochrome B Mediates Responses to Continuous Red or White Light 389  
 Phytochrome A Is Required for the Response to Continuous Far-Red Light 389  
 Developmental Roles for Phytochromes C, D, and E Are Also Emerging 390  
 Phytochrome Interactions Are Important Early in Germination 390

### **Phytochrome Functional Domains 391**

### **Cellular and Molecular Mechanisms 392**

Phytochrome Regulates Membrane Potentials and Ion Fluxes 392  
 Phytochrome Regulates Gene Expression 393  
 Both Phytochrome and the Circadian Rhythm Regulate *LHCB* 393  
 The Circadian Oscillator Involves a Transcriptional Negative Feedback Loop 394  
 Regulatory Sequences Control Light-Regulated Transcription 394  
 Phytochrome Moves to the Nucleus 395  
 Phytochrome Acts through Multiple Signal Transduction Pathways 396  
 Phytochrome Action Can Be Modulated by the Action of Other Photoreceptors 398

### **Summary 398**

# 18 *Blue-Light Responses: Stomatal Movements and Morphogenesis* 403

## **The Photophysiology of Blue-Light Responses** 404

- Blue Light Stimulates Asymmetric Growth and Bending 404
- How Do Plants Sense the Direction of the Light Signal? 406
- Blue Light Rapidly Inhibits Stem Elongation 406
- Blue Light Regulates Gene Expression 406
- Blue Light Stimulates Stomatal Opening 407
- Blue Light Activates a Proton Pump at the Guard Cell Plasma Membrane 409
- Blue-Light Responses Have Characteristic Kinetics and Lag Times 410
- Blue Light Regulates Osmotic Relations of Guard Cells 411
- Sucrose Is an Osmotically Active Solute in Guard Cells 411

## **Blue-Light Photoreceptors** 413

- Cryptochromes Are Involved in the Inhibition of Stem Elongation 413
- Phototropins Are Involved in Phototropism and Chloroplast Movements 414
- The Carotenoid Zeaxanthin Mediates Blue-Light Photoreception in Guard Cells 415

## **Signal Transduction** 417

- Cryptochromes Accumulate in the Nucleus 417
- Phototropin Binds FMN 417
- Zeaxanthin Isomerization Might Start a Cascade Mediating Blue Light–Stimulated Stomatal Opening 418
- The Xanthophyll Cycle Confers Plasticity to the Stomatal Responses to Light 419

## **Summary** 420

# 19 *Auxin: The Growth Hormone* 423

## **The Emergence of the Auxin Concept** 424

### **Biosynthesis and Metabolism of Auxin** 424

- The Principal Auxin in Higher Plants Is Indole-3-Acetic Acid 424
- Auxins in Biological Samples Can Be Quantified 426
- IAA Is Synthesized in Meristems, Young Leaves, and Developing Fruits and Seeds 427
- Multiple Pathways Exist for the Biosynthesis of IAA 428
- IAA Is Also Synthesized from Indole or from Indole-3-Glycerol Phosphate 429
- Most IAA in the Plant Is in a Covalently Bound Form 429
- IAA Is Degraded by Multiple Pathways 430
- Two Subcellular Pools of IAA Exist: The Cytosol and the Chloroplasts 431

### **Auxin Transport** 432

- Polar Transport Requires Energy and Is Gravity Independent 432
- A Chemiosmotic Model Has Been Proposed to Explain Polar Transport 433
- Inhibitors of Auxin Transport Block Auxin Efflux 435
- PIN Proteins Are Rapidly Cycled to and from the Plasma Membrane 435
- Flavonoids Serve as Endogenous ATIs 436
- Auxin Is Also Transported Nonpolarly in the Phloem 437

### **Physiological Effects of Auxin: Cell Elongation** 438

- Auxins Promote Growth in Stems and Coleoptiles, While Inhibiting Growth in Roots 438
- The Outer Tissues of Dicot Stems Are the Targets of Auxin Action 439

- The Minimum Lag Time for Auxin-Induced Growth Is Ten Minutes 439

- Auxin Rapidly Increases the Extensibility of the Cell Wall 440

- Auxin-Induced Proton Extrusion Acidifies the Cell Wall and Increases Cell Extension 440

- Auxin-Induced Proton Extrusion May Involve Both Activation and Synthesis 441

### **Physiological Effects of Auxin: Phototropism and Gravitropism** 442

- Phototropism Is Mediated by the Lateral Redistribution of Auxin 442

- Gravitropism Also Involves Lateral Redistribution of Auxin 443

- Statoliths Serve as Gravity Sensors in Shoots and Roots 445

- Auxin Is Redistribution Laterally in the Root Cap 446

- PIN3 Is Relocated Laterally to the Lower Side of Root Columella Cells 448

- Gravity Sensing May Involve Calcium and pH as Second Messengers 448

### **Developmental Effects of Auxin** 449

- Auxin Regulates Apical Dominance 449

- Auxin Promotes the Formation of Lateral and Adventitious Roots 451

- Auxin Delays the Onset of Leaf Abscission 451

- Auxin Transport Regulates Floral Bud Development 452

- Auxin Promotes Fruit Development 452

- Auxin Induces Vascular Differentiation 452

- Synthetic Auxins Have a Variety of Commercial Uses 453

**Auxin Signal Transduction Pathways 454**

- ABP1 Functions as an Auxin Receptor 454
- Calcium and Intracellular pH Are Possible Signaling Intermediates 454
- Auxin-Induced Genes Fall into Two Classes: Early and Late 454

Auxin-Responsive Domains Are Composite Structures 455

Early Auxin Genes Are Regulated by Auxin Response Factors 455

**Summary 456**

## 20 *Gibberellins: Regulators of Plant Height* 461

**The Discovery of the Gibberellins 462****Effects of Gibberellin on Growth and Development 463**

- Gibberellins Stimulate Stem Growth in Dwarf and Rosette Plants 463
- Gibberellins Regulate the Transition from Juvenile to Adult Phases 464
- Gibberellins Influence Floral Initiation and Sex Determination 464
- Gibberellins Promote Fruit Set 464
- Gibberellins Promote Seed Germination 464
- Gibberellins Have Commercial Applications 465

**Biosynthesis and Metabolism of Gibberellin 466**

- Gibberellins Are Measured via Highly Sensitive Physical Techniques 466
- Gibberellins Are Synthesized via the Terpenoid Pathway in Three Stages 466
- The Enzymes and Genes of the Gibberellin Biosynthetic Pathway Have Been Characterized 469
- Gibberellins May Be Covalently Linked to Sugars 469
- GA<sub>1</sub> Is the Biologically Active Gibberellin Controlling Stem Growth 469
- Endogenous GA<sub>1</sub> Levels Are Correlated with Tallness 470
- Gibberellins Are Biosynthesized in Apical Tissues 471
- Gibberellin Regulates Its Own Metabolism 471
- Environmental Conditions Can Alter the Transcription of Gibberellin Biosynthesis Genes 471
- Auxin Promotes Gibberellin Biosynthesis 475
- Dwarfness Can Now Be Genetically Engineered 475

**Physiological Mechanisms of Gibberellin-Induced Growth 477**

Gibberellins Stimulate Cell Elongation and Cell Division 477

Gibberellins Enhance Cell Wall Extensibility without Acidification 477

Gibberellins Regulate the Transcription of Cell Cycle Kinases in Intercalary Meristems 478

Gibberellin Response Mutants Have Defects in Signal Transduction 478

Different Genetic Screens Have Identified the Related Repressors GAI and RGA 479

Gibberellins Cause the Degradation of RGA Transcriptional Repressors 480

DELLA Repressors Have Been Identified in Crop Plants 482

The Negative Regulator SPINDLY Is an Enzyme That Alters Protein Activity 482

SPY Acts Upstream of GAI and RGA in the Gibberellin Signal Transduction Chain 483

**Gibberellin Signal Transduction: Cereal Aleurone Layers 484**

Gibberellin from the Embryo Induces  $\alpha$ -Amylase Production by Aleurone Layers 484

Gibberellic Acid Enhances the Transcription of  $\alpha$ -Amylase mRNA 485

A GA-MYB Transcription Factor Regulates  $\alpha$ -Amylase Gene Expression 486

Gibberellin Receptors May Interact with G-Proteins on the Plasma Membrane 487

Cyclic GMP, Ca<sup>2+</sup>, and Protein Kinases Are Possible Signaling Intermediates 487

The Gibberellin Signal Transduction Pathway Is Similar for Stem Growth and  $\alpha$ -Amylase Production 488

**Summary 488**

## 21 *Cytokinins: Regulators of Cell Division* 493

**Cell Division and Plant Development 493**

- Differentiated Plant Cells Can Resume Division 494
- Diffusible Factors May Control Cell Division 494
- Plant Tissues and Organs Can Be Cultured 494

**The Discovery, Identification, and Properties of Cytokinins 495**

Kinetin Was Discovered as a Breakdown Product of DNA 495

Zeatin Is the Most Abundant Natural Cytokinin 495

Some Synthetic Compounds Can Mimic or Antagonize Cytokinin Action 496	Cytokinins Modify Apical Dominance and Promote Lateral Bud Growth 505
Cytokinins Occur in Both Free and Bound Forms 496	Cytokinins Induce Bud Formation in a Moss 506
The Hormonally Active Cytokinin Is the Free Base 497	Cytokinin Overproduction Has Been Implicated in Genetic Tumors 506
Some Plant Pathogenic Bacteria, Insects, and Nematodes Secrete Free Cytokinins 497	Cytokinins Delay Leaf Senescence 507
<b>Biosynthesis, Metabolism, and Transport of Cytokinins 498</b>	Cytokinins Promote Movement of Nutrients 508
Crown Gall Cells Have Acquired a Gene for Cytokinin Synthesis 498	Cytokinins Promote Chloroplast Development 508
IPT Catalyzes the First Step in Cytokinin Biosynthesis 498	Cytokinins Promote Cell Expansion in Leaves and Cotyledons 508
Cytokinins from the Root Are Transported to the Shoot via the Xylem 501	Cytokinins Regulate Growth of Stems and Roots 509
A Signal from the Shoot Regulates the Transport of Zeatin Ribosides from the Root 501	Cytokinin-Regulated Processes Are Revealed in Plants That Overproduce Cytokinin 509
Cytokinins Are Rapidly Metabolized by Plant Tissues 501	<b>Cellular and Molecular Modes of Cytokinin Action 510</b>
<b>The Biological Roles of Cytokinins 502</b>	A Cytokinin Receptor Related to Bacterial Two-Component Receptors Has Been Identified 510
Cytokinins Regulate Cell Division in Shoots and Roots 502	Cytokinins Cause a Rapid Increase in the Expression of Response Regulator Genes 511
Cytokinins Regulate Specific Components of the Cell Cycle 503	Histidine Phosphotransferases May Mediate the Cytokinin Signaling Cascade 512
The Auxin:Cytokinin Ratio Regulates Morphogenesis in Cultured Tissues 504	Cytokinin-Induced Phosphorylation Activates Transcription Factors 513
	<b>Summary 515</b>

## 22 *Ethylene: The Gaseous Hormone* 519

<b>Structure, Biosynthesis, and Measurement of Ethylene 520</b>	Ethylene Induces Flowering in the Pineapple Family 528
The Properties of Ethylene Are Deceptively Simple 520	Ethylene Enhances the Rate of Leaf Senescence 528
Bacteria, Fungi, and Plant Organs Produce Ethylene 520	The Role of Ethylene in Defense Responses Is Complex 529
Regulated Biosynthesis Determines the Physiological Activity of Ethylene 521	Ethylene Biosynthesis in the Abscission Zone Is Regulated by Auxin 529
Environmental Stresses and Auxins Promote Ethylene Biosynthesis 522	Ethylene Has Important Commercial Uses 531
Ethylene Production and Action Can Be Inhibited 523	<b>Cellular and Molecular Modes of Ethylene Action 532</b>
Ethylene Can Be Measured by Gas Chromatography 524	Ethylene Receptors Are Related to Bacterial Two-Component System Histidine Kinases 532
<b>Developmental and Physiological Effects of Ethylene 524</b>	High-Affinity Binding of Ethylene to Its Receptor Requires a Copper Cofactor 533
Ethylene Promotes the Ripening of Some Fruits 524	Unbound Ethylene Receptors Are Negative Regulators of the Response Pathway 534
Leaf Epinasty Results When ACC from the Root Is Transported to the Shoot 525	A Serine/Threonine Protein Kinase Is Also Involved in Ethylene Signaling 535
Ethylene Induces Lateral Cell Expansion 525	<i>EIN2</i> Encodes a Transmembrane Protein 535
The Hooks of Dark-Grown Seedlings Are Maintained by Ethylene Production 527	Ethylene Regulates Gene Expression 535
Ethylene Breaks Seed and Bud Dormancy in Some Species 528	Genetic Epistasis Reveals the Order of the Ethylene Signaling Components 535
Ethylene Promotes the Elongation Growth of Submerged Aquatic Species 528	<b>Summary 536</b>
Ethylene Induces the Formation of Roots and Root Hairs 528	

## 23 *Abscissic Acid: A Seed Maturation and Antistress Signal* 539

### **Occurrence, Chemical Structure, and Measurement of ABA** 539

The Chemical Structure of ABA Determines Its Physiological Activity 540

ABA Is Assayed by Biological, Physical, and Chemical Methods 540

### **Biosynthesis, Metabolism, and Transport of ABA** 540

ABA Is Synthesized from a Carotenoid Intermediate 540

ABA Concentrations in Tissues Are Highly Variable 542

ABA Can Be Inactivated by Oxidation or Conjugation 542

ABA Is Translocated in Vascular Tissue 542

### **Developmental and Physiological Effects of ABA** 543

ABA Levels in Seeds Peak during Embryogenesis 543

ABA Promotes Desiccation Tolerance in the Embryo 544

ABA Promotes the Accumulation of Seed Storage Protein during Embryogenesis 544

Seed Dormancy May Be Imposed by the Coat or the Embryo 544

Environmental Factors Control the Release from Seed Dormancy 545

Seed Dormancy Is Controlled by the Ratio of ABA to GA 545

ABA Inhibits Precocious Germination and Vivipary 546

ABA Accumulates in Dormant Buds 546

ABA Inhibits GA-Induced Enzyme Production 546

ABA Closes Stomata in Response to Water Stress 547

ABA Promotes Root Growth and Inhibits Shoot Growth at Low Water Potentials 547

ABA Promotes Leaf Senescence Independently of Ethylene 547

### **Cellular and Molecular Modes of ABA Action** 548

ABA Is Perceived Both Extracellularly and Intracellularly 548

ABA Increases Cytosolic  $\text{Ca}^{2+}$ , Raises Cytosolic pH, and Depolarizes the Membrane 549

ABA Activation of Slow Anion Channels Causes Long-Term Membrane Depolarization 551

ABA Stimulates Phospholipid Metabolism 552

Protein Kinases and Phosphatases Participate in ABA Action 552

ABI Protein Phosphatases Are Negative Regulators of the ABA Response 553

ABA Signaling Also Involves  $\text{Ca}^{2+}$ -Independent Pathways 553

ABA Regulation of Gene Expression Is Mediated by Transcription Factors 553

Other Negative Regulators of the ABA Response Have Been Identified 555

### **Summary** 555

## 24 *The Control of Flowering* 559

### **Floral Meristems and Floral Organ Development** 560

The Characteristics of Shoot Meristems in *Arabidopsis* Change with Development 560

The Four Different Types of Floral Organs Are Initiated as Separate Whorls 561

Three Types of Genes Regulate Floral Development 562  
Meristem Identity Genes Regulate Meristem Function 562

Homeotic Mutations Led to the Identification of Floral Organ Identity Genes 562

Three Types of Homeotic Genes Control Floral Organ Identity 563

The ABC Model Explains the Determination of Floral Organ Identity 564

### **Floral Evocation: Internal and External Cues** 565

#### **The Shoot Apex and Phase Changes** 566

Shoot Apical Meristems Have Three Developmental Phases 566

Juvenile Tissues Are Produced First and Are Located at the Base of the Shoot 567

Phase Changes Can Be Influenced by Nutrients, Gibberellins, and Other Chemical Signals 568

Competence and Determination Are Two Stages in Floral Evocation 568

### **Circadian Rhythms: The Clock Within** 570

Circadian Rhythms Exhibit Characteristic Features 570

Phase Shifting Adjusts Circadian Rhythms to Different Day–Night Cycles 572

Phytochromes and Cryptochromes Entrain the Clock 572

### **Photoperiodism: Monitoring Day Length** 572

Plants Can Be Classified by Their Photoperiodic Responses 573

Plants Monitor Day Length by Measuring the Length of the Night 575

Night Breaks Can Cancel the Effect of the Dark Period 576

The Circadian Clock Is Involved in Photoperiodic Timekeeping 576  
 The Coincidence Model Is Based on Oscillating Phases of Light Sensitivity 577  
 The Leaf Is the Site of Perception of the Photoperiodic Stimulus 577  
 The Floral Stimulus Is Transported via the Phloem 577  
 Phytochrome Is the Primary Photoreceptor in Photoperiodism 578  
 Far-Red Light Modifies Flowering in Some LDPs 579  
 A Blue-Light Photoreceptor Also Regulates Flowering 580

### **Vernalization: Promoting Flowering with Cold 580**

Vernalization Results in Competence to Flower at the Shoot Apical Meristem 581  
 Vernalization May Involve Epigenetic Changes in Gene Expression 581

## **25 Stress Physiology 591**

### **Water Deficit and Drought Resistance 592**

Drought Resistance Strategies Vary with Climatic or Soil Conditions 592  
 Decreased Leaf Area Is an Early Adaptive Response to Water Deficit 593  
 Water Deficit Stimulates Leaf Abscission 594  
 Water Deficit Enhances Root Extension into Deeper, Moist Soil 594  
 Stomata Close during Water Deficit in Response to Absciscic Acid 594  
 Water Deficit Limits Photosynthesis within the Chloroplast 595  
 Osmotic Adjustment of Cells Helps Maintain Plant Water Balance 596  
 Water Deficit Increases Resistance to Liquid-Phase Water Flow 597  
 Water Deficit Increases Wax Deposition on the Leaf Surface 598  
 Water Deficit Alters Energy Dissipation from Leaves 598  
 Osmotic Stress Induces Crassulacean Acid Metabolism in Some Plants 598  
 Osmotic Stress Changes Gene Expression 599  
 Stress-Responsive Genes Are Regulated by ABA-Dependent and ABA-Independent Processes 601

### **Heat Stress and Heat Shock 602**

High Leaf Temperature and Water Deficit Lead to Heat Stress 602  
 At High Temperatures, Photosynthesis Is Inhibited before Respiration 602  
 Plants Adapted to Cool Temperatures Acclimate Poorly to High Temperatures 603  
 High Temperature Reduces Membrane Stability 603

### **Biochemical Signaling Involved in Flowering 582**

Grafting Studies Have Provided Evidence for a Transmissible Floral Stimulus 582  
 Indirect Induction Implies That the Floral Stimulus Is Self-Propagating 584  
 Evidence for Antiflorigen Has Been Found in Some LDPs 585  
 Attempts to Isolate Transmissible Floral Regulators Have Been Unsuccessful 585  
 Gibberellins and Ethylene Can Induce Flowering in Some Plants 586  
 The Transition to Flowering Involves Multiple Factors and Pathways 586

### **Summary 588**

Several Adaptations Protect Leaves against Excessive Heating 603  
 At Higher Temperatures, Plants Produce Heat Shock Proteins 604  
 A Transcription Factor Mediates HSP Accumulation in Response to Heat Shock 605  
 HSPs Mediate Thermotolerance 605  
 Adaptation to Heat Stress Is Mediated by Cytosolic Calcium 606

### **Chilling and Freezing 607**

Membrane Properties Change in Response to Chilling Injury 607  
 Ice Crystal Formation and Protoplast Dehydration Kill Cells 608  
 Limitation of Ice Formation Contributes to Freezing Tolerance 608  
 Some Woody Plants Can Acclimate to Very Low Temperatures 609  
 Resistance to Freezing Temperatures Involves Supercooling and Slow Dehydration 609  
 Some Bacteria That Live on Leaf Surfaces Increase Frost Damage 610  
 ABA and Protein Synthesis Are Involved in Acclimation to Freezing 610  
 Numerous Genes Are Induced during Cold Acclimation 611  
 A Transcription Factor Regulates Cold-Induced Gene Expression 611

### **Salinity Stress 611**

Salt Accumulation in Soils Impairs Plant Function and Soil Structure 612  
 Salinity Depresses Growth and Photosynthesis in Sensitive Species 612

Salt Injury Involves Both Osmotic Effects and Specific Ion Effects 612	Roots Are Damaged in Anoxic Environments 616
Plants Use Different Strategies to Avoid Salt Injury 613	Damaged O <sub>2</sub> -Deficient Roots Injure Shoots 618
Ion Exclusion Is Critical for Acclimation and Adaptation to Salinity Stress 614	Submerged Organs Can Acquire O <sub>2</sub> through Specialized Structures 618
Sodium Is Transported across the Plasma Membrane and the Tonoplast 614	Most Plant Tissues Cannot Tolerate Anaerobic Conditions 619
<b>Oxygen Deficiency 616</b>	Acclimation to O <sub>2</sub> Deficit Involves Synthesis of Anaerobic Stress Proteins 620
Anaerobic Microorganisms Are Active in Water-Saturated Soils 616	<b>Summary 620</b>

***Glossary 625***

***Author Index 657***

***Subject Index 661***