

# 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 5

**The Plant Cell** 5

Biological membranes are phospholipid bilayers that contain proteins 6

The nucleus contains most of the genetic material of the cell 8

Protein synthesis involves transcription and translation 11

The endoplasmic reticulum is a network of internal membranes 11

Secretion of proteins from cells begins with the rough ER 11

Golgi stacks produce and distribute secretory products 14

Proteins and polysaccharides destined for secretion are processed in the Golgi apparatus 15

Two models for intra-Golgi transport have been proposed 15

Specific coat proteins facilitate vesicle budding 15

Vacuoles play multiple roles in plant cells 17

Mitochondria and chloroplasts are sites of energy conversion 17

Mitochondria and chloroplasts are semiautonomous organelles 20

Different plastid types are interconvertible 20

Microbodies play specialized metabolic roles in leaves and seeds 21

Oleosomes are lipid-storing organelles 21

**The Cytoskeleton** 23

Plant cells contain microtubules, microfilaments, and intermediate filaments 23

Microtubules and microfilaments can assemble and disassemble 24

Microtubules function in mitosis and cytokinesis 25

Motor proteins mediate cytoplasmic streaming and organelle movements 26

**Cell Cycle Regulation** 27

Each phase of the cell cycle has a specific set of biochemical and cellular activities 27

The cell cycle is regulated by cyclin-dependent kinases 27

**Plasmodesmata** 29

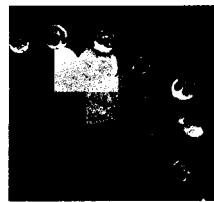
There are two types of plasmodesmata: primary and secondary 29

Plasmodesmata have a complex internal structure 29

Macromolecular traffic through plasmodesmata is important for developmental signaling 29

**Summary** 30

## 2 (Available at [www.plantphys.net](http://www.plantphys.net)) Energy and Enzymes 33



## UNIT I

### *Transport and Translocation of Water and Solutes* 35

## 3 Water and Plant Cells 37

### Water in Plant Life 37

#### The Structure and Properties of Water 38

The polarity of water molecules gives rise to hydrogen bonds 38

The polarity of water makes it an excellent solvent 39

The thermal properties of water result from hydrogen bonding 39

The cohesive and adhesive properties of water are due to hydrogen bonding 39

Water has a high tensile strength 40

#### Water Transport Processes 41

Diffusion is the movement of molecules by random thermal agitation 41

Diffusion is rapid over short distances but extremely slow over long distances 41

Pressure-driven bulk flow drives long-distance water transport 42

Osmosis is driven by a water potential gradient 42

## 4 Water Balance of Plants 53

### Water in the Soil 54

A negative hydrostatic pressure in soil water lowers soil water potential 54

Water moves through the soil by bulk flow 55

#### Water Absorption by Roots 56

Water moves in the root via the apoplast, symplast, and transmembrane pathways 56

Solute accumulation in the xylem can generate “root pressure” 58

#### Water Transport through the Xylem 59

The xylem consists of two types of tracheary elements 59

Water movement through the xylem requires less pressure than movement through living cells 59

What pressure difference is needed to lift water 100 meters to a treetop? 61

The cohesion-tension theory explains water transport in the xylem 61

Xylem transport of water in trees faces physical challenges 63

The chemical potential of water represents the free-energy status of water 43

Three major factors contribute to cell water potential 43

Water enters the cell along a water potential gradient 45

Water can also leave the cell in response to a water potential gradient 45

Small changes in plant cell volume cause large changes in turgor pressure 47

Water transport rates depend on driving force and hydraulic conductivity 48

Aquaporins facilitate the movement of water across cell membranes 49

The water potential concept helps us evaluate the water status of a plant 49

The components of water potential vary with growth conditions and location within the plant 50

#### Summary 51

Plants minimize the consequences of xylem cavitation 63

#### Water Movement from the Leaf to the Atmosphere 64

The driving force for water loss is the difference in water vapor concentration 65

Water loss is also regulated by the pathway resistances 65

Stomatal control couples leaf transpiration to leaf photosynthesis 66

The cell walls of guard cells have specialized features 67

An increase in guard cell turgor pressure opens the stomata 68

The transpiration ratio measures the relationship between water loss and carbon gain 69

#### Overview: The Soil-Plant-Atmosphere Continuum 69

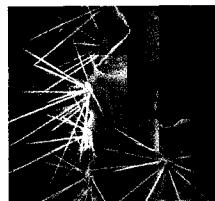
#### Summary 70

# 5 Mineral Nutrition 73

<b>Essential Nutrients, Deficiencies, and Plant Disorders</b>	<b>74</b>	of mineral nutrients 84
Special techniques are used in nutritional studies	76	Soil pH affects nutrient availability, soil microbes, and root growth 86
Nutrient solutions can sustain rapid plant growth	77	Excess minerals in the soil limit plant growth 86
Mineral deficiencies disrupt plant metabolism and function	77	Plants develop extensive root systems 86
Analysis of plant tissues reveals mineral deficiencies	82	Root systems differ in form but are based on common structures 87
<b>Treating Nutritional Deficiencies</b>	<b>83</b>	Different areas of the root absorb different mineral ions 88
Crop yields can be improved by addition of fertilizers	83	Mycorrhizal fungi facilitate nutrient uptake by roots 89
Some mineral nutrients can be absorbed by leaves	84	Nutrients move from the mycorrhizal fungi to the root cells 91
<b>Soil, Roots, and Microbes</b>	<b>84</b>	<b>Summary</b> 91
Negatively charged soil particles affect the adsorption		

# 6 Solute Transport 95

<b>Passive and Active Transport</b>	<b>96</b>	The genes for many transporters have been identified 108
<b>Transport of Ions across a Membrane Barrier</b>	<b>98</b>	Transporters exist for diverse nitrogen-containing compounds 110
Different diffusion rates for cations and anions produce diffusion potentials	98	Cation transporters are diverse 110
How does membrane potential relate to ion distribution?	98	Some anion transporters have been identified 112
The Nernst equation distinguishes between active and passive transport	100	Metals are transported by ZIP proteins 112
Proton transport is a major determinant of the membrane potential	101	Aquaporins may have novel functions 113
<b>Membrane Transport Processes</b>	<b>101</b>	The plasma membrane H <sup>+</sup> -ATPase has several functional domains 113
Channel transporters enhance diffusion across membranes	103	The tonoplast H <sup>+</sup> -ATPase drives solute accumulation into vacuoles 114
Carriers bind and transport specific substances	105	H <sup>+</sup> -pyrophosphatases also pump protons at the tonoplast 116
Primary active transport requires energy	105	<b>Ion Transport in Roots</b> 116
Secondary active transport uses stored energy	106	Solutes move through both apoplast and symplast 117
Kinetic analyses can elucidate transport mechanisms	106	Ions cross both symplast and apoplast 117
<b>Membrane Transport Proteins</b>	<b>108</b>	Xylem parenchyma cells participate in xylem loading 118
		<b>Summary</b> 119



## UNIT II

### *Biochemistry and Metabolism* 123

## 7 Photosynthesis: The Light Reactions 125

### Photosynthesis in Higher Plants 126

#### General Concepts 126

Light has characteristics of both a particle and a wave 126

When molecules absorb or emit light, they change their electronic state 127

Photosynthetic pigments absorb the light that powers photosynthesis 128

#### Key Experiments in Understanding Photosynthesis 130

Action spectra relate light absorption to photosynthetic activity 130

Photosynthesis takes place in complexes containing light-harvesting antennas and photochemical reaction centers 130

The chemical reaction of photosynthesis is driven by light 132

Light drives the reduction of NADP and the formation of ATP 132

Oxygen-evolving organisms have two photosystems that operate in series 133

#### Organization of the Photosynthetic Apparatus 134

The chloroplast is the site of photosynthesis 134

Thylakoids contain integral membrane proteins 135

Photosystems I and II are spatially separated in the thylakoid membrane 137

Anoxygenic photosynthetic bacteria have a single reaction center 137

#### Organization of Light-Absorbing Antenna Systems 137

The antenna funnels energy to the reaction center 138

Many antenna complexes have a common structural motif 138

#### Mechanisms of Electron Transport 139

Electrons from chlorophyll travel through the carriers organized in the "Z scheme" 139

Energy is captured when an excited chlorophyll reduces an electron acceptor molecule 140

The reaction center chlorophylls of the two photosystems absorb at different wavelengths 142

The photosystem II reaction center is a multisubunit pigment–protein complex 142

Water is oxidized to oxygen by photosystem II 142

Pheophytin and two quinones accept electrons from photosystem II 143

Electron flow through the cytochrome  $b_6f$  complex also transports protons 144

Plastoquinone and plastocyanin carry electrons between photosystems II and I 146

The photosystem I reaction center reduces NADP<sup>+</sup> 146

Cyclic electron flow generates ATP but no NADPH 147

Some herbicides block photosynthetic electron flow 147

#### Proton Transport and ATP Synthesis in the Chloroplast 148

#### Repair and Regulation of the Photosynthetic Machinery 151

Carotenoids serve as photoprotective agents 151

Some xanthophylls also participate in energy dissipation 152

The photosystem II reaction center is easily damaged 152

Photosystem I is protected from active oxygen species 153

Thylakoid stacking permits energy partitioning between the photosystems 153

#### Genetics, Assembly, and Evolution of Photosynthetic Systems 153

Chloroplast, cyanobacterial, and nuclear genomes have been sequenced 153

Chloroplast genes exhibit non-Mendelian patterns of inheritance 153

Many chloroplast proteins are imported from the cytoplasm 154

The biosynthesis and breakdown of chlorophyll are complex pathways 154

Complex photosynthetic organisms have evolved from simpler forms 154

#### Summary 156

# 8 Photosynthesis: Carbon Reactions 159

## The Calvin Cycle 160

The Calvin cycle has three stages: carboxylation, reduction, and regeneration 160

The carboxylation of ribulose-1,5-bisphosphate is catalyzed by the enzyme rubisco 161

Operation of the Calvin cycle requires the regeneration of ribulose-1,5-bisphosphate 163

The Calvin cycle regenerates its own biochemical components 164

The Calvin cycle uses energy very efficiently 164

## Regulation of the Calvin Cycle 165

Light regulates the Calvin cycle 165

The activity of rubisco increases in the light 166

The ferredoxin–thioredoxin system regulates the Calvin cycle 166

Light-dependent ion movements regulate Calvin cycle enzymes 168

## The C<sub>2</sub> Oxidative Photosynthetic Carbon Cycle 168

Photosynthetic CO<sub>2</sub> fixation and photorespiratory oxygenation are competing reactions 168

Photorespiration depends on the photosynthetic electron transport system 171

The biological function of photorespiration is under investigation 171

## CO<sub>2</sub>-Concentrating Mechanisms 172

### I. CO<sub>2</sub> and HCO<sub>3</sub><sup>-</sup> Pumps 173

### II. The C<sub>4</sub> Carbon Cycle 173

Malate and aspartate are carboxylation products of the C<sub>4</sub> cycle 173

Two different types of cells participate in the C<sub>4</sub> cycle 174

The C<sub>4</sub> cycle concentrates CO<sub>2</sub> in the chloroplasts of bundle sheath cells 176

The C<sub>4</sub> cycle also concentrates CO<sub>2</sub> in single cells 178

The C<sub>4</sub> cycle has higher energy demand than the Calvin cycle 179

Light regulates the activity of key C<sub>4</sub> enzymes 179

In hot, dry climates, the C<sub>4</sub> cycle reduces photorespiration and water loss 180

## III. Crassulacean Acid Metabolism (CAM) 180

The stomata of CAM plants open at night and close during the day 180

Some CAM plants change the pattern of CO<sub>2</sub> uptake in response to environmental conditions 180

## Starch and Sucrose 182

Chloroplast starch is synthesized during the day and degraded at night 183

Starch is synthesized in the chloroplast 183

Starch degradation requires phosphorylation of amylopectin 183

Triose phosphates synthesized in the chloroplast build up the pool of hexose phosphates in the cytosol 186

Fructose-6-phosphate can be converted to fructose-1,6-bisphosphate by two different enzymes 190

Fructose-2,6-bisphosphate is an important regulatory compound 190

The hexose phosphate pool is regulated by fructose-2,6-bisphosphate 190

Sucrose is continuously synthesized in the cytosol 191

## Summary 192

# 9 Photosynthesis: Physiological and Ecological Considerations 197

## Light, Leaves, and Photosynthesis 198

### Units in the Measurement of Light 199

Leaf anatomy maximizes light absorption 200

Plants compete for sunlight 201

Leaf angle and leaf movement can control light absorption 202

Plants acclimate and adapt to sun and shade 203

### Photosynthetic Responses to Light by the Intact Leaf 203

Light-response curves reveal photosynthetic properties 204

Leaves must dissipate excess light energy 206

Absorption of too much light can lead to photoinhibition 208

### Photosynthetic Responses to Temperature 209

Leaves must dissipate vast quantities of heat 209

Photosynthesis is temperature sensitive 210

## Photosynthetic Responses to Carbon Dioxide 211

Atmospheric CO<sub>2</sub> concentration keeps rising 211

CO<sub>2</sub> diffusion to the chloroplast is essential to photosynthesis 212

Patterns of light absorption generate gradients of CO<sub>2</sub> fixation 213

CO<sub>2</sub> imposes limitations on photosynthesis 214

## Crassulacean Acid Metabolism 216

Carbon isotope ratio variations reveal different photosynthetic pathways 216

How do we measure the carbon isotopes of plants? 216

Why are there carbon isotope ratio variations in plants? 217

## Summary 218

# 10 Translocation in the Phloem 221

## Pathways of Translocation 222

- Sugar is translocated in phloem sieve elements 222
- Mature sieve elements are living cells specialized for translocation 223
- Large pores in cell walls are the prominent feature of sieve elements 224
- Damaged sieve elements are sealed off 224
- Companion cells aid the highly specialized sieve elements 225

## Patterns of Translocation: Source to Sink 227

- Source-to-sink pathways follow anatomic and developmental patterns 227

## Materials Translocated in the Phloem 228

- Phloem sap can be collected and analyzed 229
- Sugars are translocated in nonreducing form 229

## Rates of Movement 231

### The Pressure-Flow Model for Phloem Transport 231

- A pressure gradient drives translocation in the pressure-flow model 231
- The predictions of mass flow have been confirmed 232
- Sieve plate pores are open channels 233
- There is no bidirectional transport in single sieve elements 233
- The energy requirement for transport through the phloem pathway is small 233
- Pressure gradients are sufficient to drive a mass flow of phloem sap 233
- Significant questions about the pressure-flow model still exist 235

## Phloem Loading 235

- Phloem loading can occur via the apoplast or symplast 236

Sucrose uptake in the apoplastic pathway requires metabolic energy 237

Phloem loading in the apoplastic pathway involves a sucrose-H<sup>+</sup> symporter 237

Phloem loading is symplastic in plants with intermediary cells 239

The polymer-trapping model explains symplastic loading 239

The type of phloem loading is correlated with plant family and with climate 239

## Phloem Unloading and Sink-to-Source Transition 241

Phloem unloading and short-distance transport can occur via symplastic or apoplastic pathways 241

Transport into sink tissues requires metabolic energy 242

The transition of a leaf from sink to source is gradual 242

## Photosynthate Distribution: Allocation and Partitioning 244

Allocation includes storage, utilization, and transport 244

Various sinks partition transport sugars 244

Source leaves regulate allocation 245

Sink tissues compete for available translocated photosynthate 246

Sink strength depends on sink size and activity 246

The source adjusts over the long term to changes in the source-to-sink ratio 246

## The Transport of Signaling Molecules 247

Turgor pressure and chemical signals coordinate source and sink activities 247

Signal molecules in the phloem regulate growth and development 247

## Summary 250

# 11 Respiration and Lipid Metabolism 253

## Overview of Plant Respiration 253

## Glycolysis: A Cytosolic and Plastidic Process 256

- Glycolysis converts carbohydrates into pyruvate, producing NADH and ATP 256

Plants have alternative glycolytic reactions 257

In the absence of O<sub>2</sub>, fermentation regenerates the NAD<sup>+</sup> needed for glycolysis 259

Fermentation does not liberate all the energy available in each sugar molecule 259

Plant glycolysis is controlled by its products 260

The pentose phosphate pathway produces NADPH and biosynthetic intermediates 260

## The Citric Acid Cycle: A Mitochondrial Matrix Process 262

Mitochondria are semiautonomous organelles 262

Pyruvate enters the mitochondrion and is oxidized via the citric acid cycle 263

The citric acid cycle of plants has unique features 265

## Mitochondrial Electron Transport and ATP Synthesis 265

The electron transport chain catalyzes a flow of electrons from NADH to O<sub>2</sub> 266

Some electron transport enzymes are unique to plant mitochondria 266

ATP synthesis in the mitochondrion is coupled to electron transport 268	Mitochondrial function is crucial during pollen development 276
Transporters exchange substrates and products 269	Environmental factors alter respiration rates 277
Aerobic respiration yields about 60 molecules of ATP per molecule of sucrose 271	
Several subunits of respiratory complexes are encoded by the mitochondrial genome 271	
Plants have several mechanisms that lower the ATP yield 272	
Mitochondrial respiration is controlled by key metabolites 273	
Respiration is tightly coupled to other pathways 274	
<b>Respiration in Intact Plants and Tissues 274</b>	<b>Lipid Metabolism 278</b>
Plants respire roughly half of the daily photosynthetic yield 274	Fats and oils store large amounts of energy 278
Respiration operates during photosynthesis 275	Triacylglycerols are stored in oil bodies 278
Different tissues and organs respire at different rates 276	Polar glycerolipids are the main structural lipids in membranes 279
	Fatty acid biosynthesis consists of cycles of two-carbon addition 279
	Glycerolipids are synthesized in the plastids and the ER 282
	Lipid composition influences membrane function 283
	Membrane lipids are precursors of important signaling compounds 283
	Storage lipids are converted into carbohydrates in germinating seeds 283
	<b>Summary 285</b>

## 12 Assimilation of Mineral Nutrients 289

<b>Nitrogen in the Environment 290</b>	Establishing symbiosis requires an exchange of signals 300
Nitrogen passes through several forms in a biogeochemical cycle 290	Nod factors produced by bacteria act as signals for symbiosis 300
Unassimilated ammonium or nitrate may be dangerous 291	Nodule formation involves phytohormones 301
<b>Nitrate Assimilation 292</b>	The nitrogenase enzyme complex fixes N <sub>2</sub> 301
Many factors regulate nitrate reductase 293	Amides and ureides are the transported forms of nitrogen 303
Nitrite reductase converts nitrite to ammonium 293	
Both roots and shoots assimilate nitrate 294	
<b>Ammonium Assimilation 294</b>	<b>Sulfur Assimilation 304</b>
Converting ammonium to amino acids requires two enzymes 294	Sulfate is the absorbed form of sulfur in plants 304
Ammonium can be assimilated via an alternative pathway 296	Sulfate assimilation requires the reduction of sulfate to cysteine 305
Transamination reactions transfer nitrogen 296	Sulfate assimilation occurs mostly in leaves 305
Asparagine and glutamine link carbon and nitrogen metabolism 296	Methionine is synthesized from cysteine 305
<b>Amino Acid Biosynthesis 296</b>	<b>Phosphate Assimilation 306</b>
<b>Biological Nitrogen Fixation 296</b>	<b>Cation Assimilation 306</b>
Free-living and symbiotic bacteria fix nitrogen 297	Cations form noncovalent bonds with carbon compounds 306
Nitrogen fixation requires anaerobic conditions 297	Roots modify the rhizosphere to acquire iron 306
Symbiotic nitrogen fixation occurs in specialized structures 299	Iron forms complexes with carbon and phosphate 308
	<b>Oxygen Assimilation 308</b>
	<b>The Energetics of Nutrient Assimilation 310</b>
	<b>Summary 311</b>

# 13 Secondary Metabolites and Plant Defense 315

## Cutin, Waxes, and Suberin 316

Cutin, waxes, and suberin are made up of hydrophobic compounds 316

Cutin, waxes, and suberin help reduce transpiration and pathogen invasion 317

## Secondary Metabolites 317

Secondary metabolites defend plants against herbivores and pathogens 318

Secondary metabolites are divided into three major groups 318

## Terpenes 318

Terpenes are formed by the fusion of five-carbon isoprene units 318

There are two pathways for terpene biosynthesis 318

Isopentenyl diphosphate and its isomer combine to form larger terpenes 319

Some terpenes have roles in growth and development 319

Terpenes defend against herbivores in many plants 321

## Phenolic Compounds 322

Phenylalanine is an intermediate in the biosynthesis of most plant phenolics 322

Some simple phenolics are activated by ultraviolet light 323

The release of phenolics into the soil may limit the growth of other plants 324

Lignin is a highly complex phenolic macromolecule 325

There are four major groups of flavonoids 326

Anthocyanins are colored flavonoids that attract animals 326

Flavonoids may protect against damage by ultraviolet light 327

Isoflavonoids have antimicrobial activity 328

Tannins deter feeding by herbivores 328

## Nitrogen-Containing Compounds 329

Alkaloids have dramatic physiological effects on animals 329

Cyanogenic glycosides release the poison hydrogen cyanide 332

Glucosinolates release volatile toxins 332

Nonprotein amino acids defend against herbivores 333

## Induced Plant Defenses against Insect Herbivores 334

Plants can recognize specific components of insect saliva 334

Jasmonic acid is a plant hormone that activates many defense responses 335

Some plant proteins inhibit herbivore digestion 336

Herbivore damage induces systemic defenses 336

Herbivore-induced volatiles have complex ecological functions 336

## Plant Defense against Pathogens 338

Some antimicrobial compounds are synthesized before pathogen attack 338

Infection induces additional antipathogen defenses 338

Some plants recognize specific substances released from pathogens 340

Exposure to elicitors induces a signal transduction cascade 340

A single encounter with a pathogen may increase resistance to future attacks 340

## Summary 341



## UNIT III

### *Growth and Development 345*

# 14 (Available at [www.plantphys.net](http://www.plantphys.net)) Gene Expression and Signal Transduction 347

# 15 Cell Walls: Structure, Biogenesis, and Expansion 349

## **The Structure and Synthesis of Plant Cell Walls 350**

Plant cell walls have varied architecture 350

The primary cell wall is composed of cellulose microfibrils embedded in a polysaccharide matrix 351

Cellulose microfibrils are synthesized at the plasma membrane 353

Matrix polymers are synthesized in the Golgi and secreted via vesicles 357

Hemicelluloses are matrix polysaccharides that bind to cellulose 357

Pectins are gel-forming components of the matrix 357

Structural proteins become cross-linked in the wall 361

New primary walls are assembled during cytokinesis 362

Secondary walls form in some cells after expansion ceases 363

## **Patterns of Cell Expansion 364**

Microfibril orientation influences growth directionality of cells with diffuse growth 364

Cortical microtubules influence the orientation of newly deposited microfibrils 366

## **The Rate of Cell Elongation 368**

Stress relaxation of the cell wall drives water uptake and cell elongation 368

The rate of cell expansion is governed by two growth equations 368

Acid-induced growth is mediated by expansins 370

Glucanases and other hydrolytic enzymes may modify the matrix 371

Structural changes accompany the cessation of wall expansion 372

## **Wall Degradation and Plant Defense 372**

Enzymes mediate wall hydrolysis and degradation 372

Oxidative bursts accompany pathogen attack 372

Wall fragments can act as signaling molecules 373

## **Summary 373**

# 16 Growth and Development 377

## **Overview of Plant Growth and Development 378**

Sporophytic development can be divided into three major stages 378

Development can be analyzed at the molecular level 381

## **Embryogenesis: The Origins of Polarity 382**

The pattern of embryogenesis differs in dicots and monocots 382

The axial polarity of the plant is established by the embryo 384

Position-dependent signaling guides embryogenesis 384

Auxin may function as a morphogen during embryogenesis 386

Genes control apical–basal patterning 387

Embryogenesis genes have diverse biochemical functions 388

*MONOPTEROS* activity is inhibited by a repressor protein 388

Gene expression patterns correlate with auxin 389

*GNOM* gene determines the distribution of efflux proteins 389

Radial patterning establishes fundamental tissue layers 389

Two genes regulate protoderm differentiation 392

Cytokinin stimulates cell divisions for vascular elements 392

Two genes control the differentiation of cortical and endodermal tissues through intercellular communication 393

Intercellular communication is central to plant development 394

## **Shoot Apical Meristem 396**

The shoot apical meristem forms at a position where auxin is low 396

Forming an embryonic SAM requires many genes 398

Shoot apical meristems vary in size and shape 398

The shoot apical meristem contains distinct zones and layers 398

Groups of relatively stable initial cells have been identified 398

SAM function may require intercellular protein movement 400

Protein turnover may spatially restrict gene activity 400

Stem cell population is maintained by a transcriptional feedback loop 400

## **Root Apical Meristem 402**

High auxin levels stimulate the formation of the root apical meristem 402

The root tip has four developmental zones 403

Specific root initials produce different root tissues 404

Root apical meristems contain several types of initials 404

## **Vegetative Organogenesis 405**

Periclinal cell divisions initiate leaf primordia	406	Branch roots and shoots have different origins	409
Local auxin concentrations in the SAM control leaf initiation	406	<b>Senescence and Programmed Cell Death</b>	410
Three developmental axes describe the leaf's planar form	407	Plants exhibit various types of senescence	410
Spatially regulated gene expression controls leaf pattern	407	Senescence involves ordered cellular and biochemical changes	411
MicroRNAs regulate the sidedness of the leaf	409	Programmed cell death is a specialized type of senescence	412
<b>Summary</b> 412			
<b>17 Phytochrome and Light Control of Plant Development</b> 417			
<b>The Photochemical and Biochemical Properties of Phytochrome</b>	418	<i>PHY</i> gene functions have diversified during evolution	428
Phytochrome can interconvert between Pr and Pfr forms	419	<b>Phytochrome Signaling Pathways</b>	430
Pfr is the physiologically active form of phytochrome	420	Phytochrome regulates membrane potentials and ion fluxes	430
<b>Characteristics of Phytochrome-Induced Responses</b>	420	Phytochrome regulates gene expression	430
Phytochrome responses vary in lag time and escape time	420	Phytochrome interacting factors (PIFs) act early in phy signaling	430
Phytochrome responses can be distinguished by the amount of light required	421	Phytochrome associates with protein kinases and phosphatases	431
Very low-fluence responses are nonphotoreversible	421	Phytochrome-induced gene expression involves protein degradation	432
Low-fluence responses are photoreversible	422	<b>Circadian Rhythms</b>	433
High-irradiance responses are proportional to the irradiance and the duration	422	The circadian oscillator involves a transcriptional negative feedback loop	433
<b>Structure and Function of Phytochrome Proteins</b>	423	<b>Ecological Functions</b>	435
Phytochrome has several important functional domains	424	Phytochrome regulates the sleep movements of leaves	435
Phytochrome is a light-regulated protein kinase	425	Phytochrome enables plant adaptation to light quality changes	437
Pfr is partitioned between the cytosol and nucleus	425	Decreasing the R:FR ratio causes elongation in sun plants	437
Phytochromes are encoded by a multigene family	425	Small seeds typically require a high R:FR ratio for germination	438
<b>Genetic Analysis of Phytochrome Function</b>	427	Phytochrome interactions are important early in germination	439
Phytochrome A mediates responses to continuous far-red light	427	Reducing shade avoidance responses can improve crop yields	439
Phytochrome B mediates responses to continuous red or white light	428	Phytochrome responses show ecotypic variation	440
Roles for phytochromes C, D, and E are emerging	428	Phytochrome action can be modulated	440
Phy gene family interactions are complex	428	<b>Summary</b>	440

## 18 Blue-Light Responses: Stomatal Movements and Morphogenesis 445

<b>The Photophysiology of Blue-Light Responses</b>	446
Blue light stimulates asymmetric growth and bending	446
How do plants sense the direction of the light signal?	448

Blue light rapidly inhibits stem elongation	448
Blue light regulates gene expression	448
Blue light stimulates stomatal opening	449
Blue light activates a proton pump at the guard cell plasma membrane	451

Blue-light responses have characteristic kinetics and lag times	452
Blue light regulates osmotic relations of guard cells	453
Sucrose is an osmotically active solute in guard cells	453
<b>Blue-Light Photoreceptors</b>	<b>455</b>
Cryptochromes are involved in the inhibition of stem elongation	455

Phototropins mediate blue light-dependent phototropism and chloroplast movements	456
The carotenoid zeaxanthin mediates blue-light photoreception in guard cells	457
Green light reverses blue light-stimulated opening	461
The xanthophyll cycle confers plasticity to the stomatal responses to light	462

**Summary** **462**

## 19 Auxin: The Growth Hormone

**467**

<b>The Emergence of the Auxin Concept</b>	<b>468</b>
<b>Identification, Biosynthesis, and Metabolism of Auxin</b>	<b>468</b>
The principal auxin in higher plants is indole-3-acetic acid	470
IAA is synthesized in meristems and young dividing tissues	471
Multiple pathways exist for the biosynthesis of IAA	471
IAA can also be synthesized from indole-3-glycerol phosphate	472
Seeds and storage organs contain large amounts of covalently bound auxin	474
IAA is degraded by multiple pathways	475
IAA partitions between the cytosol and the chloroplasts	475
<b>Auxin Transport</b>	<b>476</b>
Polar transport requires energy and is gravity independent	476
A chemiosmotic model has been proposed to explain polar transport	477
P-glycoproteins are also auxin transport proteins	480
Inhibitors of auxin transport block auxin influx and efflux	482
Auxin is also transported nonpolarly in the phloem	482
Auxin transport is regulated by multiple mechanisms	483
Polar auxin transport is required for development	484
<b>Actions of Auxin: Cell Elongation</b>	<b>484</b>
Auxins promote growth in stems and coleoptiles, while inhibiting growth in roots	484
The outer tissues of dicot stems are the targets of auxin action	485
The minimum lag time for auxin-induced growth is ten minutes	485
Auxin rapidly increases the extensibility of the cell wall	486

Auxin-induced proton extrusion increases cell extension	486
Auxin-induced proton extrusion may involve both activation and synthesis	487
<b>Actions of Auxin: Phototropism and Gravitropism</b>	<b>488</b>
Phototropism is mediated by the lateral redistribution of auxin	488
Gravitropism involves lateral redistribution of auxin	490
Dense plastids serve as gravity sensors	490
Gravity sensing may involve pH and calcium as second messengers	492
Auxin is redistributed laterally in the root cap	494
<b>Developmental Effects of Auxin</b>	<b>496</b>
Auxin regulates apical dominance	496
Auxin transport regulates floral bud development and phyllotaxy	498
Auxin promotes the formation of lateral and adventitious roots	498
Auxin induces vascular differentiation	499
Auxin delays the onset of leaf abscission	500
Auxin promotes fruit development	500
Synthetic auxins have a variety of commercial uses	500
<b>Auxin Signal Transduction Pathways</b>	<b>501</b>
A ubiquitin E <sub>3</sub> ligase subunit is an auxin receptor	501
Auxin-induced genes are negatively regulated by AUX/IAA proteins	502
Auxin binding to SCF <sup>TIR1</sup> stimulates AUX/IAA destruction	502
Auxin-induced genes fall into two classes: early and late	502
Rapid auxin responses may involve a different receptor protein	503

**Summary** **504**

# 20 Gibberellins: Regulators of Plant Height and Seed Germination 509

<b>Gibberellins: Their Discovery and Chemical Structure 510</b>	Mutations of negative regulators of GA may produce slender or dwarf phenotypes 522
Gibberellins were discovered by studying a disease of rice 510	Negative regulators with DELLA domains have agricultural importance 523
Gibberellin acid was first purified from <i>Gibberella</i> culture filtrates 510	Gibberellins signal the degradation of transcriptional repressors 524
All gibberellins are based on an <i>ent</i> -gibberellane skeleton 511	F-box proteins target DELLA domain proteins for degradation 524
<b>Effects of Gibberellins on Growth and Development 512</b>	A possible GA receptor has been identified in rice 526
Gibberellins can stimulate stem growth 512	<b>Gibberellin Responses: The Cereal Aleurone Layer 527</b>
Gibberellins regulate the transition from juvenile to adult phases 512	GA is synthesized in the embryo 528
Gibberellins influence floral initiation and sex determination 513	Aleurone cells may have two types of GA receptors 529
Gibberellins promote pollen development and tube growth 513	GA signaling requires several second messengers 529
Gibberellins promote fruit set and parthenocarpy 514	Gibberellins enhance the transcription of $\alpha$ -amylase mRNA 531
Gibberellins promote seed development and germination 514	GAMYB is a positive regulator of $\alpha$ -amylase transcription 532
Commercial uses of gibberellins and GA biosynthesis inhibitors 514	DELLA domain proteins are rapidly degraded 532
<b>Biosynthesis and Catabolism of Gibberellins 514</b>	<b>Gibberellin Responses: Flowering in Long-Day Plants 533</b>
Gibberellins are synthesized via the terpenoid pathway 515	There are multiple independent pathways to flowering 533
Some enzymes in the GA pathway are highly regulated 515	The long day and gibberellin pathways interact 533
Gibberellin regulates its own metabolism 518	GAMYB regulates flowering and male fertility 534
GA biosynthesis occurs at multiple cellular sites 518	MicroRNAs regulate MYBs after transcription 535
Environmental conditions can influence GA biosynthesis 519	<b>Gibberellin Responses: Stem Growth 535</b>
GA <sub>1</sub> and GA <sub>4</sub> have intrinsic bioactivity for stem growth 519	The shoot apical meristem interior lacks bioactive GA 535
Plant height can be genetically engineered 521	Gibberellins stimulate cell elongation and cell division 535
Dwarf mutants often have other defects in addition to dwarfism 521	GAs regulate the transcription of cell cycle kinases 537
<b>Gibberellin Signaling: Significance of Response Mutants 522</b>	Auxin promotes GA biosynthesis and signaling 537
	<b>Summary 538</b>

# 21 Cytokinins: Regulators of Cell Division 543

<b>Cell Division and Plant Development 544</b>	Zeatin was the first natural cytokinin discovered 545
Differentiated plant cells can resume division 544	Some synthetic compounds can mimic or antagonize cytokinin action 546
Diffusible factors may control cell division 544	Cytokinins occur in both free and bound forms 547
Plant tissues and organs can be cultured 544	The hormonally active cytokinin is the free base 547
<b>The Discovery, Identification, and Properties of Cytokinins 545</b>	Some plant pathogenic bacteria, fungi, insects, and nematodes secrete free cytokinins 547
Kinetin was discovered as a breakdown product of DNA 545	

**Biosynthesis, Metabolism, and Transport of Cytokinins 548**

- Crown gall cells have acquired a gene for cytokinin synthesis 548
- IPT catalyzes the first step in cytokinin biosynthesis 551
- Cytokinins from the root are transported to the shoot via the xylem 551
- A signal from the shoot regulates the transport of zeatin ribosides from the root 552
- Cytokinins are rapidly metabolized by plant tissues 552

**The Biological Roles of Cytokinins 552**

- Cytokinins regulate cell division in shoots and roots 553
- Cytokinins regulate specific components of the cell cycle 555
- The auxin:cytokinin ratio regulates morphogenesis in cultured tissues 556
- Cytokinins modify apical dominance and promote lateral bud growth 557

**22 Ethylene: The Gaseous Hormone 571****Structure, Biosynthesis, and Measurement of Ethylene 572**

- The properties of ethylene are deceptively simple 572
- Bacteria, fungi, and plant organs produce ethylene 572
- Regulated biosynthesis determines the physiological activity of ethylene 573
- Environmental stresses and auxins promote ethylene biosynthesis 574
- Ethylene biosynthesis can be stimulated by ACC synthase stabilization 575
- Ethylene biosynthesis and action can be blocked by inhibitors 575
- Ethylene can be measured by gas chromatography 576

**Developmental and Physiological Effects of Ethylene 576**

- Ethylene promotes the ripening of some fruits 576
- Leaf epinasty results when ACC from the root is transported to the shoot 577
- Ethylene induces lateral cell expansion 579
- The hooks of dark-grown seedlings are maintained by ethylene production 580
- Ethylene breaks seed and bud dormancy in some species 580
- Ethylene promotes the elongation growth of submerged aquatic species 580

Cytokinins induce bud formation in a moss 557

Cytokinin overproduction has been implicated in genetic tumors 558

Cytokinins delay leaf senescence 559

Cytokinins promote movement of nutrients 559

Cytokinins promote chloroplast development 560

Cytokinins promote cell expansion in leaves and cotyledons 561

Cytokinin-regulated processes are revealed in plants that overproduce cytokinins 561

**Cellular and Molecular Modes of Cytokinin Action 563**

- A cytokinin receptor related to bacterial two-component receptors has been identified 563
- Cytokinins increase expression of the type-A response regulator genes via activation of the type-B *ARR* genes 564
- Histidine phosphotransferases are also involved in cytokinin signaling 565

**Summary 567**

Ethylene induces the formation of roots and root hairs 581

Ethylene induces flowering in the pineapple family 581

Ethylene enhances the rate of leaf senescence 581

Some defense responses are mediated by ethylene 582

Ethylene regulates changes in the abscission layer that cause abscission 582

Ethylene has important commercial uses 584

**Ethylene Signal Transduction Pathways 584**

Ethylene receptors are related to bacterial two-component system histidine kinases 585

High-affinity binding of ethylene to its receptor requires a copper cofactor 586

Unbound ethylene receptors are negative regulators of the response pathway 586

A serine/threonine protein kinase is also involved in ethylene signaling 586

*EIN2* encodes a transmembrane protein 587

Ethylene regulates gene expression 588

Genetic epistasis reveals the order of the ethylene signaling components 588

**Summary 588**

## 23 Abscisic Acid: A Seed Maturation and Antistress Signal 593

### Occurrence, Chemical Structure, and Measurement of ABA 594

- The chemical structure of ABA determines its physiological activity 594
- ABA is assayed by biological, physical, and chemical methods 594

### Biosynthesis, Metabolism, and Transport of ABA 594

- ABA is synthesized from a carotenoid intermediate 594
- ABA concentrations in tissues are highly variable 596
- ABA can be inactivated by oxidation or conjugation 597
- ABA is translocated in vascular tissue 597

### Developmental and Physiological Effects of ABA 598

- ABA regulates seed maturation 598
- ABA inhibits precocious germination and vivipary 598
- ABA promotes seed storage reserve accumulation and desiccation tolerance 599
- The seed coat and the embryo can cause dormancy 599
- Environmental factors control the release from seed dormancy 600
- Seed dormancy is controlled by the ratio of ABA to GA 600

- ABA inhibits GA-induced enzyme production 601
- ABA closes stomata in response to water stress 601
- ABA promotes root growth and inhibits shoot growth at low water potentials 601
- ABA promotes leaf senescence independently of ethylene 602
- ABA accumulates in dormant buds 602

### ABA Signal Transduction Pathways 603

- ABA regulates ion channels and the PM-ATPase in guard cells 603
- ABA may be perceived by both cell surface and intracellular receptors 604
- ABA signaling involves both calcium-dependent and calcium-independent pathways 606
- ABA-induced lipid metabolism generates second messengers 608
- ABA signaling involves protein kinases and phosphatases 609
- ABA regulates gene expression 610
- Other negative regulators also influence the ABA response 611

### Summary 613

## 24 Brassinosteroids 617

### Brassinosteroid Structure, Occurrence, and Genetic Analysis 618

- BR-deficient mutants are impaired in photomorphogenesis 619

### Biosynthesis, Metabolism, and Transport of Brassinosteroids 621

- Brassinolide is synthesized from campesterol 621
- Catabolism and negative feedback contribute to BR homeostasis 623
- Brassinosteroids act locally near their sites of synthesis 624

### Brassinosteroids: Effects on Growth and Development 625

- BRs promote both cell expansion and cell division in shoots 626

- BRs both promote and inhibit root growth 627
- BRs promote xylem differentiation during vascular development 628
- BRs are required for the growth of pollen tubes 628
- BRs promote seed germination 629

### The Brassinosteroid Signaling Pathway 629

- BR-insensitive mutants identified the BR cell surface receptor 629
- Phosphorylation activates the BRI1 receptor 630
- BIN2 is a repressor of BR-induced gene expression 630
- BES1 and BZR1 regulate different subsets of genes 631

### Prospective Uses of Brassinosteroids in Agriculture 632

### Summary 632

# 25 The Control of Flowering 635

## **Floral Meristems and Floral Organ Development 636**

The shoot apical meristems in *Arabidopsis* change with development 636

The four different types of floral organs are initiated as separate whorls 637

Three types of genes regulate floral development 638

Meristem identity genes regulate meristem function 638

Homeotic mutations led to the identification of floral organ identity genes 638

Three types of homeotic genes control floral organ identity 639

The ABC model explains the determination of floral organ identity 640

## **Floral Evocation: Internal and External Cues 641**

### **The Shoot Apex and Phase Changes 641**

Shoot apical meristems have three developmental phases 642

Juvenile tissues are produced first and are located at the base of the shoot 643

Phase changes can be influenced by nutrients, gibberellins, and other chemical signals 644

Competence and determination are two stages in floral evocation 644

### **Circadian Rhythms: The Clock Within 646**

Circadian rhythms exhibit characteristic features 646

Phase shifting adjusts circadian rhythms to different day-night cycles 646

Phytochromes and cryptochromes entrain the clock 648

### **Photoperiodism: Monitoring Day Length 648**

Plants can be classified according to their photoperiodic responses 649

The leaf is the site of perception of the photoperiodic signal 650

The floral stimulus is transported in the phloem 650

Plants monitor day length by measuring the length of the night 651

Night breaks can cancel the effect of the dark period 652

The circadian clock and photoperiodic timekeeping 652

The coincidence model is based on oscillating light sensitivity 653

The coincidence of *CONSTANS* expression and light promotes flowering in LDPs 653

The coincidence of *Heading-date 1* expression and light inhibits flowering in SDPs 655

Phytochrome is the primary photoreceptor in photoperiodism 655

A blue-light photoreceptor regulates flowering in some LDPs 656

## **Vernalization: Promoting Flowering with Cold 657**

Vernalization results in competence to flower at the shoot apical meristem 658

Vernalization involves epigenetic changes in gene expression 658

A variety of vernalization mechanisms may have evolved 659

## **Biochemical Signaling Involved in Flowering 660**

Grafting studies have provided evidence for a transmissible floral stimulus 660

Indirect induction implies that the floral stimulus is self-propagating 661

Evidence for antiflorigen has been found in some LDPs 662

Florigen may be a macromolecule 663

*FLOWERING LOCUS T* is a candidate for the photoperiodic floral stimulus 663

Gibberellins and ethylene can induce flowering in some plants 664

The transition to flowering involves multiple factors and pathways 665

## **Summary 667**

# 26 Stress Physiology 671

## **Water Deficit and Drought Tolerance 672**

Drought resistance strategies can vary 672

Decreased leaf area is an early response to water deficit 673

Water deficit stimulates leaf abscission 674

Water deficit enhances root growth 674

Abscisic acid induces stomatal closure during water deficit 674

Water deficit limits photosynthesis 676

Osmotic adjustment of cells helps maintain water balance 676

Water deficit increases resistance to water flow 677

Water deficit increases leaf wax deposition 678

Water deficit alters energy dissipation from leaves 678

CAM plants are adapted to water stress 678

Osmotic stress changes gene expression 679

ABA-dependent and ABA-independent signaling pathways regulate stress tolerance 680

**Heat Stress and Heat Shock 682**

- High leaf temperature and minimal evaporative cooling lead to heat stress 682
- At high temperatures, photosynthesis is inhibited before respiration 683
- Plants adapted to cool temperatures acclimate poorly to high temperatures 683
- Temperature affects membrane stability 684
- Several adaptations protect leaves against excessive heating 684
- At higher temperatures, plants produce protective proteins 684
- A transcription factor mediates HSP accumulation 685
- HSPs mediate tolerance to high temperatures 685
- Several signaling pathways mediate thermotolerance responses 686

**Chilling and Freezing 687**

- Membrane properties change in response to chilling injury 687
- Ice crystal formation and protoplast dehydration kill cells 689
- Limitation of ice formation contributes to freezing tolerance 689
- Some woody plants can acclimate to very low temperatures 689
- Some bacteria living on leaf surfaces increase frost damage 690

Acclimation to freezing involves ABA and protein synthesis 690

Numerous genes are induced during cold acclimation 691

A transcription factor regulates cold-induced gene expression 692

**Salinity Stress 692**

Salt accumulation in irrigated soils impairs plant function 692

Plants show great diversity for salt tolerance 693

Salt stress causes multiple injury effects 693

Plants use multiple strategies to reduce salt stress 694

Ion exclusion and compartmentation reduce salinity stress 695

Plant adaptations to toxic trace elements 696

**Oxygen Deficiency 698**

Anaerobic microorganisms are active in water-saturated soils 698

Roots are damaged in anoxic environments 698

Damaged O<sub>2</sub>-deficient roots injure shoots 699

Submerged organs can acquire O<sub>2</sub> through specialized structures 700

Most plant tissues cannot tolerate anaerobic conditions 701

Synthesis of anaerobic stress proteins leads to acclimation to O<sub>2</sub> deficit 702

**Summary 702**

**Glossary 707**

**Author Index 739**

**Subject Index 745**