Brief Contents

CHAPTER 1 *Plant and Cell Architecture 1*
CHAPTER 2 *Genome Structure and Gene Expression 51*

UNIT I Transport and Translocation of Water and Solutes 81
CHAPTER 3 *Water and Plant Cells 83*
CHAPTER 4 *Water Balance of Plants 99*
CHAPTER 5 *Mineral Nutrition 119*
CHAPTER 6 *Solute Transport 143*

UNIT II Biochemistry and Metabolism 169
CHAPTER 7 *Photosynthesis: The Light Reactions 171*
CHAPTER 8 *Photosynthesis: The Carbon Reactions 203*
CHAPTER 9 *Photosynthesis: Physiological and Ecological Considerations 245*
CHAPTER 10 *Stomatal Biology 269*
CHAPTER 11 *Translocation in the Phloem 285*
CHAPTER 12 *Respiration and Lipid Metabolism 317*
CHAPTER 13 *Assimilation of Inorganic Nutrients 353*

UNIT III Growth and Development 377
CHAPTER 14 *Cell Walls: Structure, Formation, and Expansion 379*
CHAPTER 15 *Signals and Signal Transduction 407*
CHAPTER 16 *Signals from Sunlight 447*
CHAPTER 17 *Embryogenesis 477*
CHAPTER 18 *Seed Dormancy, Germination, and Seedling Establishment 513*
CHAPTER 19 *Vegetative Growth and Organogenesis 553*
CHAPTER 20 *The Control of Flowering and Floral Development 591*
CHAPTER 21 *Gametophytes, Pollination, Seeds, and Fruits 625*
CHAPTER 22 *Plant Senescence and Cell Death 665*
CHAPTER 23 *Biotic Interactions 693*
CHAPTER 24 *Abiotic Stress 731*

Plant physiology and development
2015

digitalisiert durch:
IDS Basel Bern

Table of Contents

CHAPTER 1
Plant and Cell Architecture 1

Plant Life Processes: Unifying Principles 2

Plant Classification and Life Cycles 2

Plant life cycles alternate between diploid and haploid generations 3

Overview of Plant Structure 5

Plant cells are surrounded by rigid cell walls 5

Plasmodesmata allow the free movement of molecules between cells 8

New cells originate in dividing tissues called meristems 8

Plant Cell Organelles 10

Biological membranes are phospholipid bilayers that contain proteins 10

The Endomembrane System 13

The nucleus contains the majority of the genetic material 13

Gene expression involves both transcription and translation 17

The endoplasmic reticulum is a network of internal membranes 17

Secretion of proteins from cells begins with the rough ER 19

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

The plasma membrane has specialized regions involved in membrane recycling 22

Vacuoles have diverse functions in plant cells 23

Independently Dividing or Fusing Organelles Derived from the Endomembrane System 23

Oil bodies are lipid-storing organelles 23

Microbodies play specialized metabolic roles in leaves and seeds 24

Independently Dividing, Semiautonomous Organelles 25

Proplastids mature into specialized plastids in different plant tissues 27

Chloroplast and mitochondrial division are independent of nuclear division 29

The Plant Cytoskeleton 29

The plant cytoskeleton consists of microtubules and microfilaments 29

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

Cortical microtubules move around the cell by treadmilling 33

Cytoskeletal motor proteins mediate cytoplasmic streaming and directed organelle movement 33

Cell Cycle Regulation 35

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

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

Mitosis and cytokinesis involve both microtubules and the endomembrane system 37

Plant Cell Types 39

Dermal tissues cover the surfaces of plants 39

Ground tissues form the bodies of plants 40

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

CHAPTER 2
Genome Structure and Gene Expression 51

Nuclear Genome Organization 51

The nuclear genome is packaged into chromatin 52

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

Transposons are mobile sequences within the genome 53

Chromosome organization is not random in the interphase nucleus 54

Meiosis halves the number of chromosomes and allows for the recombination of alleles 54
Polyploids contain multiple copies of the entire genome 56
Phenotypic and physiological responses to polyploidy are unpredictable 58
The role of polyploidy in evolution is still unclear 60

Plant Cytoplasmic Genomes: Mitochondria and Plastids 61

The endosymbiotic theory describes the origin of cytoplasmic genomes 61
Organellar genomes vary in size 61
Organellar genetics do not obey Mendelian principles 61

Transcriptional Regulation of Nuclear Gene Expression 62

RNA polymerase II binds to the promoter region of most protein-coding genes 62
Conserved nucleotide sequences signal transcriptional termination and polyadenylation 64
Epigenetic modifications help determine gene activity 65

Posttranscriptional Regulation of Nuclear Gene Expression 67

All RNA molecules are subject to decay 67
Noncoding RNAs regulate mRNA activity via the RNA interference (RNAi) pathway 67
Posttranslational regulation determines the life span of proteins 71

Tools for Studying Gene Function 72

Mutant analysis can help elucidate gene function 72
Molecular techniques can measure the activity of genes 73
Gene fusions can introduce reporter genes 74

Genetic Modification of Crop Plants 76

Transgenes can confer resistance to herbicides or plant pests 77
Genetically modified organisms are controversial 77

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

CHAPTER 3
Water and Plant Cells 83

Water in Plant Life 83

The Structure and Properties of Water 84

Water is a polar molecule that forms hydrogen bonds 84
Water is an excellent solvent 85
Water has distinctive thermal properties relative to its size 85
Water molecules are highly cohesive 85
Water has a high tensile strength 86

Diffusion and Osmosis 87

Diffusion is the net movement of molecules by random thermal agitation 87
Diffusion is most effective over short distances 88
Osmosis describes the net movement of water across a selectively permeable barrier 88

Water Potential 89

The chemical potential of water represents the free-energy status of water 89
Three major factors contribute to cell water potential 90
Water potentials can be measured 90

Water Potential of Plant Cells 91

Water enters the cell along a water potential gradient 91
Water can also leave the cell in response to a water potential gradient 92
Water potential and its components vary with growth conditions and location within the plant 93

Cell Wall and Membrane Properties 93

Small changes in plant cell volume cause large changes in turgor pressure 93
The rate at which cells gain or lose water is influenced by cell membrane hydraulic conductivity 94
Aquaporins facilitate the movement of water across cell membranes 95

Plant Water Status 96

Physiological processes are affected by plant water status 96
Solute accumulation helps cells maintain turgor and volume 96

CHAPTER 4
Water Balance of Plants 99

Water in the Soil 99

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

Water moves through the soil by bulk flow 101

Water Absorption by Roots 101

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

Solute accumulation in the xylem can generate "root pressure" 103

Water Transport through the Xylem 104

The xylem consists of two types of transport cells 104

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

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

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

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

Xylem transport of water in trees faces physical challenges 108

Plants minimize the consequences of xylem cavitation 110

Water Movement from the Leaf to the Atmosphere 110

Leaves have a large hydraulic resistance 111

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

Water loss is also regulated by the pathway resistances 112

Stomatal control couples leaf transpiration to leaf photosynthesis 112

The cell walls of guard cells have specialized features 113

An increase in guard cell turgor pressure opens the stomata 115

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

Overview: The Soil–Plant–Atmosphere Continuum 116

CHAPTER 5
Mineral Nutrition 119

Essential Nutrients, Deficiencies, and Plant Disorders 120

Special techniques are used in nutritional studies 122

Nutrient solutions can sustain rapid plant growth 122

Mineral deficiencies disrupt plant metabolism and function 125

Analysis of plant tissues reveals mineral deficiencies 129

Treating Nutritional Deficiencies 129

Crop yields can be improved by the addition of fertilizers 130

Some mineral nutrients can be absorbed by leaves 131

Soil, Roots, and Microbes 131

Negatively charged soil particles affect the adsorption of mineral nutrients 131

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

Excess mineral ions in the soil limit plant growth 133

Some plants develop extensive root systems 133

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

Different areas of the root absorb different mineral ions 135

Nutrient availability influences root growth 137

Mycorrhizal symbioses facilitate nutrient uptake by roots 137

Nutrients move between mycorrhizal fungi and root cells 140

CHAPTER 6
Solute Transport 143

Passive and Active Transport 144

Transport of Ions across Membrane Barriers 145

Different diffusion rates for cations and anions produce diffusion potentials 146

How does membrane potential relate to ion distribution? 146

The Nernst equation distinguishes between active and passive transport 147

Proton transport is a major determinant of the membrane potential 148

Membrane Transport Processes 149

Channels enhance diffusion across membranes 150

Carriers bind and transport specific substances 151

Primary active transport requires energy 151

Kinetic analyses can elucidate transport mechanisms 154

Membrane Transport Proteins 155

The genes for many transporters have been identified 157

Transporters exist for diverse nitrogen-containing compounds 157

Cation transporters are diverse 158

Anion transporters have been identified 160

Transporters for metal and metalloid ions transport essential micronutrients 160

Aquaporins have diverse functions 160

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

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

Ion Transport in Roots 163
Solutes move through both apoplast and symplast 164
Ions cross both symplast and apoplast 164
Xylem parenchyma cells participate in xylem loading 164

UNIT II **Biochemistry and Metabolism 169**

CHAPTER 7
Photosynthesis: The Light Reactions 171

Photosynthesis in Higher Plants 171

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

Key Experiments in Understanding Photosynthesis 175
Action spectra relate light absorption to photosynthetic activity 176
Photosynthesis takes place in complexes containing light-harvesting antennas and photochemical reaction centers 176
The chemical reaction of photosynthesis is driven by light 178
Light drives the reduction of $NADP^+$ and the formation of ATP 178
Oxygen-evolving organisms have two photosystems that operate in series 179

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

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

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

Proton Transport and ATP Synthesis in the Chloroplast 193

Repair and Regulation of the Photosynthetic Machinery 195
Carotenoids serve as photoprotective agents 196
Some xanthophylls also participate in energy dissipation 197
The PSII reaction center is easily damaged 197
PSI is protected from active oxygen species 198
Thylakoid stacking permits energy partitioning between the photosystems 198

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

CHAPTER 8
Photosynthesis: The Carbon Reactions 203

The Calvin–Benson Cycle 204

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

The fixation of CO_2 via carboxylation of ribulose 1,5-bisphosphate and the reduction of the product 3-phosphoglycerate yield triose phosphates 206

The regeneration of ribulose 1,5-bisphosphate ensures the continuous assimilation of CO_2 207

An induction period precedes the steady state of photosynthetic CO_2 assimilation 208

Many mechanisms regulate the Calvin–Benson cycle 209

Rubisco-activase regulates the catalytic activity of rubisco 209

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

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

Light controls the assembly of chloroplast enzymes into supramolecular complexes 211

The C_2 Oxidative Photosynthetic Carbon Cycle 211

The oxygenation of ribulose 1,5-bisphosphate sets in motion the C_2 oxidative photosynthetic carbon cycle 213

Photorespiration is linked to the photosynthetic electron transport system 217

Enzymes of the plant C_2 oxidative photosynthetic carbon cycle derive from different ancestors 217

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

The C_2 oxidative photosynthetic carbon cycle interacts with many metabolic pathways 218

Production of biomass may be enhanced by engineering photorespiration 219

Inorganic Carbon–Concentrating Mechanisms 220

Inorganic Carbon–Concentrating Mechanisms: The C_4 Carbon Cycle 220

Malate and aspartate are the primary carboxylation products of the C_4 cycle 221

The C_4 cycle assimilates CO_2 by the concerted action of two different types of cells 222

The C_4 cycle uses different mechanisms for decarboxylation of four-carbon acids transported to bundle sheath cells 224

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

The C_4 cycle also concentrates CO_2 in single cells 225

Light regulates the activity of key C_4 enzymes 225

Photosynthetic assimilation of CO_2 in C_4 plants demands more transport processes than in C_3 plants 225

In hot, dry climates, the C_4 cycle reduces photorespiration 228

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

Different mechanisms regulate C_4 PEPCase and CAM PEPCase 230

CAM is a versatile mechanism sensitive to environmental stimuli 230

Accumulation and Partitioning of Photosynthates—Starch and Sucrose 230

Formation and Mobilization of Chloroplast Starch 231

Chloroplast stroma accumulates starch as insoluble granules during the day 233

Starch degradation at night requires the phosphorylation of amylopectin 236

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

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

Sucrose Biosynthesis and Signaling 238

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

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

Sucrose is continuously synthesized in the cytosol 239

CHAPTER 9
Photosynthesis: Physiological and Ecological Considerations 245

Photosynthesis Is Influenced by Leaf Properties 246

Leaf anatomy and canopy structure maximize light absorption 247

Leaf angle and leaf movement can control light absorption 249

Leaves acclimate to sun and shade environments 249

Effects of Light on Photosynthesis in the Intact Leaf 250

Light-response curves reveal photosynthetic properties 250

Leaves must dissipate excess light energy 252
Absorption of too much light can lead to photoinhibition 254

Effects of Temperature on Photosynthesis in the Intact Leaf 255

Leaves must dissipate vast quantities of heat 255
There is an optimal temperature for photosynthesis 256
Photosynthesis is sensitive to both high and low temperatures 256
Photosynthetic efficiency is temperature-sensitive 257

Effects of Carbon Dioxide on Photosynthesis in the Intact Leaf 258

Atmospheric CO_2 concentration keeps rising 258
CO_2 diffusion to the chloroplast is essential to photosynthesis 258
CO_2 imposes limitations on photosynthesis 260
How will photosynthesis and respiration change in the future under elevated CO_2 conditions? 262

Stable Isotopes Record Photosynthetic Properties 264

How do we measure the stable carbon isotopes of plants? 264
Why are there carbon isotope ratio variations in plants? 265

CHAPTER 10
Stomatal Biology 269

Light-dependent Stomatal Opening 270

Guard cells respond to blue light 270
Blue light activates a proton pump at the guard cell plasma membrane 271
Blue-light responses have characteristic kinetics and lag times 273
Blue light regulates the osmotic balance of guard cells 273
Sucrose is an osmotically active solute in guard cells 275

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

Reversal of Blue Light–Stimulated Opening by Green Light 278

A carotenoid–protein complex senses light intensity 280

The Resolving Power of Photophysiology 280

CHAPTER 11
Translocation in the Phloem 285

Pathways of Translocation 286

Sugar is translocated in phloem sieve elements 286
Mature sieve elements are living cells specialized for translocation 287
Large pores in cell walls are the prominent feature of sieve elements 288
Damaged sieve elements are sealed off 289
Companion cells aid the highly specialized sieve elements 290

Patterns of Translocation: Source to Sink 291

Materials Translocated in the Phloem 292

Phloem sap can be collected and analyzed 292
Sugars are translocated in a nonreducing form 293
Other solutes are translocated in the phloem 293

Rates of Movement 295

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

An osmotically generated pressure gradient drives translocation in the pressure-flow model 295
Some predictions of pressure flow have been confirmed, while others require further experimentation 296
There is no bidirectional transport in single sieve elements, and solutes and water move at the same velocity 297
The energy requirement for transport through the phloem pathway is small in herbaceous plants 297
Sieve plate pores appear to be open channels 298
Pressure gradients in the sieve elements may be modest; pressures in herbaceous plants and trees appear to be similar 298
Alternative models for translocation by mass flow have been suggested 299
Does translocation in gymnosperms involve a different mechanism? 299

Phloem Loading 300

Phloem loading can occur via the apoplast or symplast 300
Abundant data support the existence of apoplastic loading in some species 301
Sucrose uptake in the apoplastic pathway requires metabolic energy 301
Phloem loading in the apoplastic pathway involves a sucrose–H^+ symporter 302
Phloem loading is symplastic in some species 302
The polymer-trapping model explains symplastic loading in plants with intermediary-type companion cells 303

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

Phloem Unloading and Sink-to-Source Transition 305

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

Photosynthate Distribution: Allocation and Partitioning 309

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

Transport of Signaling Molecules 311

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

CHAPTER 12
Respiration and Lipid Metabolism 317

Overview of Plant Respiration 317

Glycolysis 321

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

The Oxidative Pentose Phosphate Pathway 324

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

The Citric Acid Cycle 326

Mitochondria are semiautonomous organelles 327
Pyruvate enters the mitochondrion and is oxidized via the citric acid cycle 328
The citric acid cycle of plants has unique features 329

Mitochondrial Electron Transport and ATP Synthesis 329

The electron transport chain catalyzes a flow of electrons from NADH to O_2 330
The electron transport chain has supplementary branches 332
ATP synthesis in the mitochondrion is coupled to electron transport 333
Transporters exchange substrates and products 334
Aerobic respiration yields about 60 molecules of ATP per molecule of sucrose 334
Several subunits of respiratory complexes are encoded by the mitochondrial genome 336
Plants have several mechanisms that lower the ATP yield 336
Short-term control of mitochondrial respiration occurs at different levels 338
Respiration is tightly coupled to other pathways 339

Respiration in Intact Plants and Tissues 340

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

Lipid Metabolism 343

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

CHAPTER 13
Assimilation of Inorganic Nutrients 353

Nitrogen in the Environment 354

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

Nitrate Assimilation 356
Many factors regulate nitrate reductase 356
Nitrite reductase converts nitrite to ammonium 357
Both roots and shoots assimilate nitrate 357
Ammonium Assimilation 358
Converting ammonium to amino acids requires two enzymes 358
Ammonium can be assimilated via an alternative pathway 360
Transamination reactions transfer nitrogen 360
Asparagine and glutamine link carbon and nitrogen metabolism 360
Amino Acid Biosynthesis 360
Biological Nitrogen Fixation 360
Free-living and symbiotic bacteria fix nitrogen 361
Nitrogen fixation requires microanaerobic or anaerobic conditions 362
Symbiotic nitrogen fixation occurs in specialized structures 363
Establishing symbiosis requires an exchange of signals 364
Nod factors produced by bacteria act as signals for symbiosis 364
Nodule formation involves phytohormones 365
The nitrogenase enzyme complex fixes N_2 366
Amides and ureides are the transported forms of nitrogen 367
Sulfur Assimilation 367
Sulfate is the form of sulfur transported into plants 368
Sulfate assimilation requires the reduction of sulfate to cysteine 368
Sulfate assimilation occurs mostly in leaves 369
Methionine is synthesized from cysteine 369
Phosphate Assimilation 369
Cation Assimilation 370
Cations form noncovalent bonds with carbon compounds 370
Roots modify the rhizosphere to acquire iron 371
Iron cations form complexes with carbon and phosphate 372
Oxygen Assimilation 372
The Energetics of Nutrient Assimilation 372

UNIT III Growth and Development 377

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

Overview of Plant Cell Wall Functions and Structures 380
Plants vary in structure and function 380
Components differ for primary and secondary cell walls 382
Cellulose microfibrils have an ordered structure and are synthesized at the plasma membrane 384
Matrix polymers are synthesized in the Golgi apparatus and secreted via vesicles 387
Pectins are hydrophilic gel-forming components of the primary cell wall 388
Hemicelluloses are matrix polysaccharides that bind to cellulose 390
Primary Cell Wall Structure and Function 392
The primary cell wall is composed of cellulose microfibrils embedded in a matrix of pectins and hemicelluloses 392
New primary cell walls are assembled during cytokinesis and continue to be assembled during growth 392
Mechanisms of Cell Expansion 393
Microfibril orientation influences growth directionality of cells with diffuse growth 394
Cortical microtubules influence the orientation of newly deposited microfibrils 395
The Extent and Rate of Cell Growth 397
Stress relaxation of the cell wall drives water uptake and cell expansion 397
Acid-induced growth and wall stress relaxation are mediated by expansins 397
Cell wall models are hypotheses about how molecular components fit together to make a functional wall 399
Many structural changes accompany the cessation of wall expansion 400
Secondary Cell Wall Structure and Function 400
Secondary cell walls are rich in cellulose and hemi-cellulose and often have a hierarchical organization 400
Lignification transforms the SCW into a hydrophobic structure resistant to deconstruction 402

CHAPTER 15
Signals and Signal Transduction 407

Temporal and Spatial Aspects of Signaling 408
Signal Perception and Amplification 409
Receptors are located throughout the cell and are conserved across kingdoms 409
Signals must be amplified intracellularly to regulate their target molecules 411
The MAP kinase signal amplification cascade is present in all eukaryotes 411
Ca^{2+} is the most ubiquitous second messenger in plants and other eukaryotes 411
Changes in the cytosolic or cell wall pH can serve as second messengers for hormonal and stress responses 412
Reactive oxygen species act as second messengers mediating both environmental and developmental signals 413
Lipid signaling molecules act as second messengers that regulate a variety of cellular processes 414
Hormones and Plant Development 414
Auxin was discovered in early studies of coleoptile bending during phototropism 417
Gibberellins promote stem growth and were discovered in relation to the "foolish seedling disease" of rice 417
Cytokinins were discovered as cell division–promoting factors in tissue culture experiments 418
Ethylene is a gaseous hormone that promotes fruit ripening and other developmental processes 419
Abscisic acid regulates seed maturation and stomatal closure in response to water stress 419
Brassinosteroids regulate photomorphogenesis, germination, and other developmental processes 420
Strigolactones suppress branching and promote rhizosphere interactions 421
Phytohormone Metabolism and Homeostasis 421
Indole-3-pyruvate is the primary intermediate in auxin biosynthesis 421
Gibberellins are synthesized by oxidation of the diterpene *ent*-kaurene 422
Cytokinins are adenine derivatives with isoprene side chains 423
Ethylene is synthesized from methionine via the intermediate ACC 426
Abscisic acid is synthesized from a carotenoid intermediate 426
Brassinosteroids are derived from the sterol campesterol 428
Strigolactones are synthesized from β-carotene 429
Signal Transmission and Cell–Cell Communication 429
Hormonal Signaling Pathways 431
The cytokinin and ethylene signal transduction pathways are derived from the bacterial two-component regulatory system 431
Receptor-like kinases mediate brassinosteroid and certain auxin signaling pathways 433
The core ABA signaling components include phosphatases and kinases 436
Plant hormone signaling pathways generally employ negative regulation 436
Several plant hormone receptors encode components of the ubiquitination machinery and mediate signaling via protein degradation 437
Plants have evolved mechanisms for switching off or attenuating signaling responses 439
The cellular response output to a signal is often tissue-specific 441
Cross-regulation allows signal transduction pathways to be integrated 441

CHAPTER 16
Signals from Sunlight 447

Plant Photoreceptors 448
Photoresponses are driven by light quality or spectral properties of the energy absorbed 449
Plants responses to light can be distinguished by the amount of light required 450
Phytochromes 452
Phytochrome is the primary photoreceptor for red and far-red light 452
Phytochrome can interconvert between Pr and Pfr forms 452
Pfr is the physiologically active form of phytochrome 453
The phytochrome chromophore and protein both undergo conformational changes in response to red light 453
Pfr is partitioned between the cytosol and the nucleus 454
Phytochrome Responses 457
Phytochrome responses vary in lag time and escape time 457
Phytochrome responses fall into three main categories based on the amount of light required 457
Phytochrome A mediates responses to continuous far-red light 459
Phytochrome B mediates responses to continuous red or white light 459

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

Phytochrome Signaling Pathways 459

Phytochrome regulates membrane potentials and ion fluxes 459

Phytochrome regulates gene expression 460

Phytochrome interacting factors (PIFs) act early in signaling 460

Phytochrome signaling involves protein phosphorylation and dephosphorylation 461

Phytochrome-induced photomorphogenesis involves protein degradation 461

Blue-Light Responses and Photoreceptors 462

Blue-light responses have characteristic kinetics and lag times 462

Cryptochromes 463

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

cry1 and cry2 have different developmental effects 465

Nuclear cryptochromes inhibit COP1-induced protein degradation 465

Cryptochrome can also bind to transcriptional regulators directly 465

The Coaction of Cryptochrome, Phytochrome, and Phototropins 466

Stem elongation is inhibited by both red and blue photoreceptors 466

Phytochrome interacts with cryptochrome to regulate flowering 467

The circadian clock is regulated by multiple aspects of light 467

Phototropins 467

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

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

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

Phototropism requires changes in auxin mobilization 469

Phototropins regulate chloroplast movements via F-actin filament assembly 470

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

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

Responses to Ultraviolet Radiation 473

CHAPTER 17

Embryogenesis 477

Overview of Plant Growth and Development 478

Sporophytic development can be divided into three major stages 479

Embryogenesis: The Origins of Polarity 480

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

Apical–basal polarity is established early in embryogenesis 481

Position-dependent mechanisms guide embryogenesis 483

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

Embryo development features regulate communication between cells 484

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

Auxin functions as a mobile chemical signal during embryogenesis 487

Plant polarity is maintained by polar auxin streams 487

Auxin transport is regulated by multiple mechanisms 489

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

MONOPTEROS encodes a transcription factor that is activated by auxin 492

Radial patterning guides formation of tissue layers 492

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

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

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

Meristematic Tissues: Foundations for Indeterminate Growth 495

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

The Root Apical Meristem 496

The root tip has four developmental zones 497

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

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

Auxin contributes to the formation and maintenance of the RAM 499

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

Cytokinin is required for normal root development 500

The Shoot Apical Meristem 500

The shoot apical meristem has distinct zones and layers 502

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

Factors involved in auxin movement and responses influence SAM formation 503

Embryonic SAM formation requires the coordinated expression of transcription factors 503

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

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

Localized zones of auxin accumulation promote leaf initiation 507

The Vascular Cambium 508

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

CHAPTER 18

Seed Dormancy, Germination, and Seedling Establishment 513

Seed Structure 514

Seed anatomy varies widely among different plant groups 514

Seed Dormancy 515

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

Embryo dormancy may be caused by physiological or morphological factors 516

Non-dormant seeds can exhibit vivipary and precocious germination 516

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

Release from Dormancy 519

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

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

Seed dormancy can by broken by various chemical compounds 520

Seed Germination 520

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

***Mobilization of Stored Reserves* 522**

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

Gibberellins enhance the transcription of *α-amylase* mRNA 522

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

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

DELLA repressor proteins are rapidly degraded 524

ABA inhibits gibberellin-induced enzyme production 524

Seedling Growth and Establishment 526

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

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

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

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

Tropisms: Growth in Response to Directional Stimuli 528

Gravitropism involves the lateral redistribution of auxin 528

Polar auxin transport requires energy and is gravity independent 529

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

Auxin movements in the root are regulated by specific transporters 532

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

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

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

Phototropism 535

Phototropism is mediated by the lateral redistribution of auxin 535

Phototropism occurs in a series of posttranslational events 536

Photomorphogenesis 537

Gibberellins and brassinosteroids both suppress photomorphogenesis in the dark 538

Hook opening is regulated by phytochrome and auxin 539

Ethylene induces lateral cell expansion 539

Shade Avoidance 540

Phytochrome enables plants to adapt to changes in light quality 540

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

Reducing shade avoidance responses can improve crop yields 542

Vascular Tissue Differentiation 542

Auxin and cytokinin are required for normal vascular development 543

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

Xylogenesis involves chemical signaling between neighboring cells 544

Root Growth and Differentiation 545

Root epidermal development follows three basic patterns 546

Auxin and other hormones regulate root hair development 546

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

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

Lateral roots and shoots have gravitropic setpoint angles 549

CHAPTER 19

Vegetative Growth and Organogenesis 553

Leaf Development 553

The Establishment of Leaf Polarity 554

Hormonal signals play key roles in regulating leaf primordia emergence 555

A signal from the SAM initiates adaxial–abaxial polarity 555

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

Adaxial leaf development requires HD-ZIP III transcription factors 556

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

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

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

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

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

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

Differentiation of Epidermal Cell Types 561

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

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

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

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

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

Jasmonic acid regulates Arabidopsis leaf trichome development 565

Venation Patterns in Leaves 565

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

Auxin canalization initiates development of the leaf trace 566

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

The existing vasculature guides the growth of the leaf trace 568

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

Auxin canalization regulates higher-order vein formation 570

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

Shoot Branching and Architecture 572

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

Auxin, cytokinins, and strigolactones regulate axillary bud outgrowth 573

Auxin from the shoot tip maintains apical dominance 574

Strigolactones act locally to repress axillary bud growth 574

Cytokinins antagonize the effects of strigolactones 576

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

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

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

Root System Architecture 579

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

Monocots and eudicots differ in their root system architecture 580

Root system architecture changes in response to phosphorous deficiencies 580

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

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

Secondary Growth 583

The vascular cambium and cork cambium are the secondary meristems where secondary growth originates 584

Secondary growth evolved early in the evolution of land plants 585

Secondary growth from the vascular cambium gives rise to secondary xylem and phloem 585

Phytohormones have important roles in regulating vascular cambium activity and differentiation of secondary xylem and phloem 585

Genes involved in stem cell maintenance, proliferation, and differentiation regulate secondary growth 586

Environmental factors influence vascular cambium activity and wood properties 587

CHAPTER 20

The Control of Flowering and Floral Development 591

Floral Evocation: Integrating Environmental Cues 592

The Shoot Apex and Phase Changes 592

Plant development has three phases 592

Juvenile tissues are produced first and are located at the base of the shoot 592

Phase changes can be influenced by nutrients, gibberellins, and other signals 593

Circadian Rhythms: The Clock Within 594

Circadian rhythms exhibit characteristic features 595

Phase shifting adjusts circadian rhythms to different day–night cycles 596

Phytochromes and cryptochromes entrain the clock 596

Photoperiodism: Monitoring Day Length 597

Plants can be classified according to their photoperiodic responses 597

The leaf is the site of perception of the photoperiodic signal 599

Plants monitor day length by measuring the length of the night 599

Night breaks can cancel the effect of the dark period 599

Photoperiodic timekeeping during the night depends on a circadian clock 599

The coincidence model is based on oscillating light sensitivity 600

The coincidence of *CONSTANS* expression and light promotes flowering in LDPs 601

SDPs use a coincidence mechanism to inhibit flowering in long days 603

Phytochrome is the primary photoreceptor in photoperiodism 603

A blue-light photoreceptor regulates flowering in some LDPs 604

Vernalization: Promoting Flowering with Cold 605

Vernalization results in competence to flower at the shoot apical meristem 605

Vernalization can involve epigenetic changes in gene expression 606

A range of vernalization pathways may have evolved 607

Long-Distance Signaling Involved in Flowering 608

Grafting studies provided the first evidence for a transmissible floral stimulus 608

Florigen is translocated in the phloem 609

The Identification of Florigen 610

The Arabidopsis protein FLOWERING LOCUS T (FT) is florigen 610

Gibberellins and ethylene can induce flowering 610

The transition to flowering involves multiple factors and pathways 612

Floral Meristems and Floral Organ Development 612

The shoot apical meristem in Arabidopsis changes with development 613

The four different types of floral organs are initiated as separate whorls 613

Two major categories of genes regulate floral development 614

Floral meristem identity genes regulate meristem function 614

Homeotic mutations led to the identification of floral organ identity genes 616

The ABC model partially explains the determination of floral organ identity 616

Arabidopsis Class E genes are required for the activities of the A, B, and C genes 618

According to the Quartet Model, floral organ identity is regulated by tetrameric complexes of the ABCE proteins 618

Class D genes are required for ovule formation 619

Floral asymmetry in flowers is regulated by gene expression 620

CHAPTER 21
Gametophytes, Pollination, Seeds, and Fruits 625

Development of the Male and Female Gametophyte Generations 625

Formation of Male Gametophytes in the Stamen 626

Pollen grain formation occurs in two successive stages 627

The multilayered pollen cell wall is surprisingly complex 628

Female Gametophyte Development in the Ovule 630

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

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

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

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

Pollination and Fertilization in Flowering Plants 632

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

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

Ca^{2+}-triggered polarization of the pollen grain precedes tube formation 635

Pollen tubes grow by tip growth 635

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

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

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

Double fertilization occurs in three distinct stages 638

Selfing versus Outcrossing 639

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

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

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

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

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

Apomixis: Asexual Reproduction by Seed 643

Endosperm Development 643

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

Cellularization of the coenocytic endosperm of cereals progresses centripetally 646

Endosperm development and embryogenesis can occur autonomously 646

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

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

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

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

Seed Coat Development 650

Seed coat development appears to be regulated by the endosperm 650

Seed Maturation and Desiccation Tolerance 652

Seed filling and desiccation tolerance phases overlap in most species 652

The acquisition of desiccation tolerance involves many metabolic pathways 653

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

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

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

Abscisic acid plays a key role in seed maturation 654

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

Fruit Development and Ripening 655

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

Fleshy fruits undergo ripening 657

Ripening involves changes in the color of fruit 657

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

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

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

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

The ripening process is transcriptionally regulated 660

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

CHAPTER 22
Plant Senescence and Cell Death 665

Programmed Cell Death and Autolysis 666
PCD during normal development differs from that of the hypersensitive response 668
The autophagy pathway captures and degrades cellular constituents within lytic compartments 669
A subset of the autophagy-related genes controls the formation of the autophagosome 669
The autophagy pathway plays a dual role in plant development 671

The Leaf Senescence Syndrome 671
The developmental age of a leaf may differ from its chronological age 672
Leaf senescence may be sequential, seasonal, or stress-induced 672
Developmental leaf senescence consists of three distinct phases 673
The earliest cellular changes during leaf senescence occur in the chloroplast 675
The autolysis of chloroplast proteins occurs in multiple compartments 675
The STAY-GREEN (SGR) protein is required for both LHCP II protein recycling and chlorophyll catabolism 676
Leaf senescence is preceded by a massive reprogramming of gene expression 677

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

Leaf Abscission 684
The timing of leaf abscission is regulated by the interaction of ethylene and auxin 685

Whole Plant Senescence 686
Angiosperm life cycles may be annual, biennial, or perennial 687
Whole plant senescence differs from aging in animals 688
The determinacy of shoot apical meristems is developmentally regulated 688
Nutrient or hormonal redistribution may trigger senescence in monocarpic plants 689
The rate of carbon accumulation in trees increases continuously with tree size 689

CHAPTER 23
Biotic Interactions 693

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

Harmful Interactions between Plants, Pathogens, and Herbivores 697
Mechanical barriers provide a first line of defense against insect pests and pathogens 698
Plant secondary metabolites can deter insect herbivores 700
Plants store constitutive toxic compounds in specialized structures 701
Plants often store defensive chemicals as nontoxic water-soluble sugar conjugates in the vacuole 703
Constitutive levels of secondary compounds are higher in young developing leaves than in older tissues 705

Inducible Defense Responses to Insect Herbivores 705
Plants can recognize specific components of insect saliva 706
Modified fatty acids secreted by grasshoppers act as *elicitors of jasmonic acid accumulation and ethylene* emission 706
Phloem feeders activate defense signaling pathways similar to those activated by pathogen infections 707
Calcium signaling and activation of the MAP kinase pathway are early events associated with insect herbivory 707
Jasmonic acid activates defense responses against insect herbivores 708
Jasmonic acid acts through a conserved ubiquitin ligase signaling mechanism 709
Hormonal interactions contribute to plant–insect herbivore interactions 709

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

Plant Defenses against Pathogens 715

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

Plant Defenses against Other Organisms 724

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

CHAPTER 24
Abiotic Stress 731

Defining Plant Stress 732

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

Acclimation and Adaptation 733

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

Environmental Factors and Their Biological Impacts on Plants 734

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

Stress-Sensing Mechanisms in Plants 739

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

Signaling Pathways Activated in Response to Abiotic Stress 740

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

Hormonal interactions regulate normal development and abiotic stress responses 745

Developmental and Physiological Mechanisms That Protect Plants against Abiotic Stress 747

Plants adjust osmotically to drying soil by accumulating solutes 748

Submerged organs develop aerenchyma tissue in response to hypoxia 749

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

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

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

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

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

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

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

Plants can alter their morphology in response to abiotic stress 757

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

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

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

Glossary G–1

Illustration Credits IC–1

Photo Credits PC–1

Subject Index SI–1