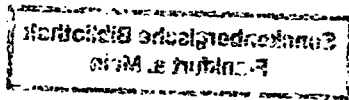

PLANT PHYSIOLOGY

FOURTH EDITION

Frank B. Salisbury
Utah State University

Cleon W. Ross
Colorado State University



Wadsworth Publishing Company
Belmont, California
A Division of Wadsworth, Inc.

SECTION ONE

Cells: Water, Solutions, and Surfaces 1

- 1 Plant Physiology and Plant Cells 3
- 2 Diffusion, Thermodynamics, and Water Potential 27
- 3 Osmosis 44
- 4 The Photosynthesis-Transpiration Compromise 66
- 5 The Ascent of Sap 93
- 6 Mineral Nutrition 116
- 7 Absorption of Mineral Salts 136
- 8 Transport in the Phloem 161

SECTION TWO

Plant Biochemistry 189

- 9 Enzymes, Proteins, and Amino Acids 191
- 10 Photosynthesis: Chloroplasts and Light 207
- 11 Carbon Dioxide Fixation and Carbohydrate Synthesis 225
- 12 Photosynthesis: Environmental and Agricultural Aspects 249
- 13 Respiration 266
- 14 Assimilation of Nitrogen and Sulfur 289
- 15 Lipids and Other Natural Products 308

SECTION THREE

Plant Development 327

- 16 Growth and Development 329
- 17 Hormones and Growth Regulators: Auxins and Gibberellins 357
- 18 Hormones and Growth Regulators: Cytokinins, Ethylene, Abscisic Acid, and Other Compounds 382
- 19 The Power of Movement in Plants 408
- 20 Photomorphogenesis 438
- 21 The Biological Clock: Rhythms of Life 464
- 22 Growth Responses to Temperature 485
- 23 Photoperiodism 504
- 24 Molecular Genetics and the Plant Physiologist 531

SECTION FOUR

Environmental Physiology 549

- 25 Topics in Environmental Physiology 551
- 26 Stress Physiology 575

APPENDICES

- A The Système Internationale: The Use of SI Units in Plant Physiology 601
- B Radiant Energy: Some Definitions 607
- C Gene Replication and Protein Synthesis: Terms and Concepts 616
References 620
Index of Species and Subjects 658
Author Index 674

Contents in Detail

SECTION ONE

Cells: Water, Solutions, and Surfaces 1

1 Plant Physiology and Plant Cells 3

- 1.1 Some Basic Postulates 3
- 1.2 Prokaryotic Cells: Bacteria and Blue-Green Algae 5
- 1.3 Eukaryotic Cells: Protist, Fungal, and Plant 6
- 1.4 The Cell Wall 8
- 1.5 Eukaryotic Protoplasts 12
- 1.6 The Components of Cytoplasm 13
- 1.7 The Nucleus 23
- 1.8 The Vacuole 24
- 1.9 Flagella and Cilia 25
- 1.10 The Plant Cell 26
- 1.11 A Definition of Life 26

2 Diffusion, Thermodynamics, and Water Potential 27

- 2.1 Plants and Water 27
- 2.2 Diffusion Versus Bulk Flow 31
- 2.3 Kinetic Theory 32
- 2.4 A Model of Diffusion 33
- 2.5 Thermodynamics 34
- 2.6 Chemical Potential and Water Potential 37
- 2.7 Chemical- and Water-Potential Gradients 38
- 2.8 Vapor Density, Vapor Pressure, and Water Potential 40
- 2.9 The Rate of Diffusion: Fick's First Law 42
- 2.10 Caveat 43

3 Osmosis 44

- 3.1 An Osmotic System 44
- 3.2 The Components of Water Potential 45
- 3.3 Units for Water Potential 47
 - Personal Essay: Pursuing the Questions of Soil-Plant-Atmosphere Water Relations, Ralph O. Slatyer 48*
- 3.4 Dilution 50
- 3.5 The Membrane 51
- 3.6 Measuring the Components of Water Potential 52
 - Boxed Essay: Colloids: Characteristic Components of Protoplasm 62*

4 The Photosynthesis-Transpiration Compromise 66

- 4.1 Measurement of Transpiration 66
- 4.2 The Paradox of Pores 70
- 4.3 Stomatal Anatomy 71
- 4.4 Environmental Effects on Stomates 74
 - Personal Essay: Must We Write? Page W. Morgan 76*
- 4.5 Stomatal Mechanics 76
- 4.6 Stomatal Control Mechanisms 78
- 4.7 The Role of Transpiration: "What Good Is Transpiration?" 81
- 4.8 The Role of Transpiration: Energy Exchange 82
- 4.9 Energy Exchanges of Plants in Ecosystems 87
- 4.10 The Heat-Balance Equations 88
 - Personal Essay: Ventilation in Waterlilies: A Biological Steam Engine, John Dacey 90*

5	The Ascent of Sap	93			
5.1	The Problem	93			
5.2	The Cohesion Mechanism of the Ascent of Sap	96			
5.3	The Anatomy of the Pathway	96			
5.4	The Driving Force: A Water-Potential Gradient	103			
5.5	Tension in the Xylem: Cohesion	108			
5.6	Xylem Anatomy: A Fail-Safe System	113			
	<i>Personal Essay: Studying Water, Minerals, and Roots, Paul J. Kramer</i>	114			
6	Mineral Nutrition	116			
6.1	The Elements in Plant Dry Matter	116			
6.2	Methods of Studying Plant Nutrition: Solution Cultures	117			
6.3	The Essential Elements	119			
	<i>Personal Essay: The Function of Sodium as a Plant Micronutrient, Peter F. Brownell</i>	122			
6.4	Quantitative Requirements and Tissue Analysis	125			
	<i>Boxed Essay: Selenium</i>	125			
	<i>Boxed Essay: Metal Toxicity and Resistance</i>	126			
6.5	Chelating Agents	127			
6.6	Functions of Essential Elements: Some Principles	129			
6.7	Nutrient Deficiency: Symptoms and Functions of Elements	129			
7	Absorption of Mineral Salts	136			
7.1	Roots as Absorbing Surfaces	136			
7.2	Mycorrhizae	138			
7.3	Ion Traffic into the Root	140			
7.4	The Nature of Membranes	142			
7.5	Early Observations about Solute Absorption	145			
7.6	Principles of Solute Absorption	147			
	<i>Personal Essay: Roots—Mining for Minerals, Emanuel Epstein</i>	150			
7.7	Passive and Active Transport: The Energetics	154			
7.8	How ATPase Pumps Transport Protons and Calcium	155			
7.9	How Carriers and Channels Speed Passive Transport	157			
7.10	How Membranes Take Advantage of Proton Pumps for Ion Transport	158			
7.11	Absorption of Very Large Molecules, Even Proteins, by Organelles	159			
7.12	Correlations Between Root and Shoot Functions in Mineral Absorption	160			
8	Transport in the Phloem	161			
8.1	Transport of Organic Solutes	161			
8.2	The Pressure-Flow Mechanism	164			
8.3	Testing the Hypothesis	166			
	<i>Boxed Essay: A Review of Carbohydrate Chemistry</i>	172			
8.4	Partitioning and Control Mechanisms	184			
	<i>Personal Essay: Discovery of the Empty-Ovule Technique, John H. Thorne</i>	188			
	SECTION TWO				
	Plant Biochemistry	189			
9	Enzymes, Proteins, and Amino Acids	191			
9.1	The Distribution of Enzymes in Cells	192			
9.2	Properties and Structure of Enzymes	192			
	<i>Boxed Essay: Plant Proteins and Human Nutrition</i>	199			
9.3	Mechanisms of Enzyme Action	200			
9.4	Denaturation	202			
9.5	Factors Influencing Rates of Enzymatic Reactions	202			
9.6	Allosteric Enzymes and Feedback Control	205			
10	Photosynthesis: Chloroplasts and Light	207			
10.1	Historical Summary of Early Photosynthesis Research	207			
10.2	Chloroplasts: Structures and Photosynthetic Pigments	209			
10.3	Some Principles of Light Absorption by Plants	211			
10.4	The Emerson Enhancement Effect: Cooperating Photosystems	213			
10.5	The Four Major Complexes of Thylakoids	214			
10.6	Oxidation of H ₂ O by Photosystem II: The Supply of Electrons from the Oxygen-Evolving Complex	216			
10.7	Electron Transport from H ₂ O to NADP ⁺ Across Thylakoids	217			
	<i>Boxed Essay: Herbicides and Photosynthetic Electron Transport</i>	219			

- 10.8 Photophosphorylation 220
Personal Essay: Role of Chlorophyll a in Photosynthesis, Govindjee 222
- 10.9 Distribution of Light Energy Between PS I and PS II 224
- 11 Carbon Dioxide Fixation and Carbohydrate Synthesis 225**
- 11.1 Products of Carbon Dioxide Fixation 225
- 11.2 The Calvin Cycle 227
Personal Essay: Exploring the Path of Carbon in Photosynthesis (I), James A. Bassham 228
Personal Essay: Exploring the Path of Carbon in Photosynthesis (II), Melvin Calvin 230
- 11.3 The C-4 Dicarboxylic Acid Pathway: Some Species Fix CO₂ Differently 233
- 11.4 Photorespiration 237
- 11.5 Light Control of Photosynthetic Enzymes in C-3 and C-4 Plants 240
- 11.6 CO₂ Fixation in Succulent Species (Crassulacean Acid Metabolism) 242
- 11.7 Formation of Sucrose, Starch, and Fructans 244
- 12 Photosynthesis: Environmental and Agricultural Aspects 249**
- 12.1 The Carbon Cycle 249
- 12.2 Photosynthetic Rates of Various Species 253
- 12.3 Factors Affecting Photosynthesis 254
- 12.4 Photosynthetic Rates, Efficiencies, and Crop Production 263
- 13 Respiration 266**
- 13.1 The Respiratory Quotient 266
- 13.2 Formation of Hexose Sugars from Reserve Carbohydrates 267
- 13.3 Glycolysis 270
- 13.4 Fermentation 272
- 13.5 Mitochondrial Structures and Respiration 272
- 13.6 The Krebs Cycle 274
- 13.7 The Electron-Transport System and Oxidative Phosphorylation 275
- 13.8 Energetics of Glycolysis, the Krebs Cycle, and the Electron-Transport System 278
- 13.9 Cyanide-Resistant Respiration 278
- 13.10 The Pentose Phosphate Pathway 279
- 13.11 Respiratory Production of Molecules Used for Synthetic Processes 280
- 13.12 Biochemical Control of Respiration 282
- 13.13 Factors Affecting Respiration 284
- 14 Assimilation of Nitrogen and Sulfur 289**
- 14.1 The Nitrogen Cycle 289
- 14.2 Nitrogen Fixation 290
- 14.3 Assimilation of Nitrate and Ammonium Ions 295
Boxed Essay: Many Grasses Also Support Nitrogen Fixation 296
- 14.4 The Photorespiratory Nitrogen Cycle 301
- 14.5 Nitrogen Transformations During Plant Development 302
- 14.6 Assimilation of Sulfate 305
- 15 Lipids and Other Natural Products 308**
- 15.1 Fats and Oils 308
- 15.2 Waxes, Cutin, and Suberin: Plant Protective Coats 314
- 15.3 The Isoprenoid Compounds 315
- 15.4 Phenolic Compounds and Their Relatives 318
- 15.5 Phytoalexins, Elicitors, and Plant Disease Protection 321
- 15.6 Lignin 322
- 15.7 Flavonoids 323
- 15.8 Betalains 325
- 15.9 Alkaloids 326
- SECTION THREE**
Plant Development 327
- 16 Growth and Development 329**
- 16.1 What Is Meant By Growth? 330
- 16.2 Patterns of Growth and Development 331
Personal Essay: A Special Importance of the Primary Cell Wall in Plant Development, Nicholas C. Carpita 334
- 16.3 Growth Kinetics: Growth Through Time 340
- 16.4 Plant Organs: How They Grow 346
- 16.5 Morphogenesis: Juvenility 353
- 16.6 Morphogenesis: Totipotency 353
- 16.7 Some Principles of Differentiation 355
- 17 Hormones and Growth Regulators: Auxins and Gibberellins 357**
- 17.1 Concepts of Hormones and Their Action 357
- 17.2 The Auxins 361

- 17.3 The Gibberellins 372
Personal Essay: Why a Biologist? Some Reflections, Frits W. Went 378
- 18 Hormones and Growth Regulators: Cytokinins, Ethylene, Absciscic Acid, and Other Compounds 382**
- 18.1 The Cytokinins 382
- 18.2 Ethylene, a Volatile Hormone 393
- 18.3 Triacntanol, Brassins, Salicylic Acid, and Turgorins 400
- 18.4 Polyamines 400
- 18.5 Absciscic Acid (ABA) 401
- 18.6 Other Inhibitory Growth Regulators 405
- 18.7 Hormones in Senescence and Abscission 406
- 19 The Power of Movement in Plants 408**
- 19.1 Some Basic Principles 408
- 19.2 Nastic Movements 409
- 19.3 Tropisms: Directional Differential Growth 416
- 19.4 Phototropism 416
- 19.5 Gravitropism 424
Personal Essay: Studying the Gravitropic Responses of Cereal Grasses, Peter B. Kaufman 434
- 19.6 Other Tropisms and Related Phenomena 435
- 20 Photomorphogenesis 438**
- 20.1 Discovery of Phytochrome 439
Personal Essay: The Discovery of Phytochrome, Sterling B. Hendricks 440
- 20.2 Physical and Chemical Properties of Phytochrome 441
- 20.3 Distribution of Phytochrome Among Species, Tissues, and Cells 443
Personal Essay: Antibodies and the Study of Phytochrome, Lee H. Pratt 444
- 20.4 Cryptochrome, the Blue/UV-A Photoreceptor 447
- 20.5 Dose-Response Relations in Photomorphogenesis 447
Personal Essay: Phytochrome Genes and Their Expression: Working in the Dark, James T. Colbert 448
- 20.6 The Role of Light in Seed Germination 451
- 20.7 The Role of Light in Seedling Establishment and Later Vegetative Growth 456
- 20.8 Photoperiodic Effects of Light 459
- 20.9 Light-Enhanced Synthesis of Anthocyanins and Other Flavonoids 460
- 20.10 Effects of Light on Chloroplast Arrangements 461
- 20.11 How Photoreceptors Cause Photomorphogenesis 462
- 21 The Biological Clock: Rhythms of Life 464**
- 21.1 Endogenous or Exogenous? 465
Personal Essay: Potato Cellars, Trains, and Dreams: Discovering the Biological Clock, Erwin Bünning 466
- 21.2 Circadian Rhythms 468
Personal Essay: Women in Science, Beatrice M. Sweeney 469
- 21.3 The Spectrum of Biological Rhythms 471
- 21.4 Basic Concepts and Terminology 474
- 21.5 Rhythm Responses to Environment 474
- 21.6 Clock Mechanisms 478
- 21.7 Photoperiodism 479
- 21.8 Photoperiod-Rhythm Interactions 480
- 21.9 How the Clocks Are Used 481
- 21.10 Some Important Implications of the Biological Clock 482
Boxed Essay: Biorhythms and Other Pseudosciences 483
- 22 Growth Responses to Temperature 485**
- 22.1 The Temperature-Enzyme Dilemma 485
- 22.2 Vernalization 488
- 22.3 Dormancy 492
- 22.4 Seed Longevity and Germination 493
- 22.5 Seed Dormancy 495
- 22.6 Bud Dormancy 497
- 22.7 Underground Storage Organs 499
- 22.8 Thermoperiodism 502
- 22.9 Mechanisms of the Low-Temperature Response 502
- 23 Photoperiodism 504**
- 23.1 Detecting Seasonal Time by Measuring Day Length 504
- 23.2 Some General Principles of Photoperiodism 507
- 23.3 Photoperiod During a Plant's Life Cycle 508
Boxed Essay: Some Early History 510
- 23.4 The Response Types 512
- 23.5 Ripeness to Respond (Competence) 514

- 23.6 Phytochrome and the Role of the Dark Period 515
- 23.7 Time Measurement in Photoperiodism 517
- 23.8 Detecting Dawn and Dusk 521
- 23.9 The Florigen Concept: Flowering Hormones and Inhibitors 523
- 23.10 Responses to Applied Plant Hormones and Growth Regulators 525
Personal Essay: Gibberellins, a Fascinating and Highly Diverse Class of Plant Hormones, Richard P. Pharis 526
- 23.11 The Induced State 529
- 23.12 Floral Development 529
- 23.13 Where Do We Go from Here? 529

24 Molecular Genetics and the Plant Physiologist, Ray A. Bressan and Avtar K. Handa 531

- 24.1 Gene Cloning 532
- 24.2 Analysis of Gene Expression in Plants 538
- 24.3 Genetic Modification of Plants Using Recombinant DNA Technology 541
- 24.4 Mechanisms Controlling Expression of Genes 543
- 24.5 Examples of Isolated Genes that Affect Physiological Processes 545

**SECTION FOUR
Environmental Physiology 549**

25 Topics in Environmental Physiology 551

Personal Essay: The Challenge of a New Field: Plant Physiological Ecology, Park S. Nobel 552

- 25.1 The Problems of Environmental Physiology 552
- 25.2 What Is the Environment? 555
- 25.3 Some Principles of Plant Response to Environment 556
Personal Essay: Limiting Factors and Maximum Yields: A Controlled Ecological Life-Support System (CELSS), Frank B. Salisbury 560
- 25.4 Ecotypes: The Role of Genetics 564
- 25.5 Plant Adaptations to the Radiation Environment 566

26 Stress Physiology 575

- 26.1 What Is Stress? 575
- 26.2 Stressful Environments 577
- 26.3 Water Stress: Drought, Cold, and Salt 581
- 26.4 Mechanisms of Plant Response to Water and Related Stresses 591
- 26.5 Chilling Injury 597
- 26.6 High-Temperature Stress 598
- 26.7 Acidic Soils 599
- 26.8 Other Stresses 600

APPENDICES

A The Système Internationale: The Use of SI Units in Plant Physiology 601

B Radiant Energy: Some Definitions 607

- B.1 Basic Concepts and Terms 607
- B.2 Wave Phenomena 608
- B.3 Particle Phenomena 608
- B.4 The Spectrum and Light Sources 609
- B.5 Radiation Quantities 612
- B.6 Mechanisms of Absorption and Emission 613
- B.7 Quantifying Absorption, Transmission, and Reflection 614
- B.8 Thermal Radiation 614

C Gene Replication and Protein Synthesis: Terms and Concepts 616

- C.1 The Central Dogma of Molecular Biology 616
- C.2 The Double Helix 616
- C.3 Transcription: Copying DNA to Make RNA 617
- C.4 Translation: Protein Synthesis in the Cytoplasm 617
- C.5 The Genetic Code 617
- C.6 The Steps of Protein Synthesis 618

References 620

Index of Species and Subjects 658

Author Index 674