Contents

1 Introduction: History, Assumptions, and Approaches 1
1.1 What Is Ecophysiology? 1
1.2 The Roots of Ecophysiology 1
1.3 Physiological Ecology and the Distribution of Organisms 2
1.4 Time Scale of Plant Response to Environment 5
1.5 Conceptual and Experimental Approaches 7
1.6 New Directions in Ecophysiology 8
1.7 The Structure of the Book 8
References 9

2 Photosynthesis, Respiration, and Long-Distance Transport: Photosynthesis 11
2.1 Introduction 11
2.2 General Characteristics of the Photosynthetic Apparatus . . . 11
2.2.1 The 'Light' and 'Dark' Reactions of Photosynthesis 11
2.2.2 Supply and Demand of CO_2 in the Photosynthetic Process 18
2.3 Response of Photosynthesis to Light 28
2.3.1 The Light Climate Under a Leaf Canopy 28
2.3.2 Physiological, Biochemical, and Anatomical Differences Between Sun and Shade Leaves 29
2.3.3 Effects of Excess Irradiance 39
2.3.4 Responses to Variable Irradiance 47
2.4 Partitioning of the Products of Photosynthesis and Regulation by Feedback 51
2.4.1 Partitioning Within the Cell 51
2.4.2 Short-Term Regulation of Photosynthetic Rate by Feedback 52
2.4.3 Sugar-induced Repression of Genes Encoding Calvin-Benson-Cycle Enzymes 56
2.4.4 Ecological Impacts Mediated by Source-Sink Interactions 56
2.4.5 Petiole and Stem Photosynthesis 59

2.5 Responses to Availability of Water 59
2.5.1 Regulation of Stomatal Opening 59
2.5.2 The A_n–C_c Curve as Affected by Water Stress . . . 61
2.5.3 Carbon-Isotope Fractionation in Relation to Water-Use Efficiency 61
2.5.4 Other Sources of Variation in Carbon-Isotope Ratios in C_3 Plants 64
2.6 Effects of Soil Nutrient Supply on Photosynthesis 65
2.6.1 The Photosynthesis-Nitrogen Relationship 65
2.6.2 Interactions of Nitrogen, Light, and Water 66
2.6.3 Photosynthesis, Nitrogen, and Leaf Life Span . . . 67
2.7 Photosynthesis and Leaf Temperature: Effects and Adaptations 67
2.7.1 Effects of High Temperatures on Photosynthesis . . . 67
2.7.2 Effects of Low Temperatures on Photosynthesis . . . 70
2.8 Effects of Air Pollutants on Photosynthesis 71
2.9 C_4 Plants 72
2.9.1 Introduction 72
2.9.2 Biochemical and Anatomical Aspects 73
2.9.3 Intercellular and Intracellular Transport of Metabolites of the C_4 Pathway 76
2.9.4 Photosynthetic Efficiency and Performance at High and Low Temperatures 76
2.9.5 C_3–C_4 Intermediates 80
2.9.6 Evolution and Distribution of C_4 Species 82
2.9.7 Carbon-Isotope Composition of C_4 Species 84
2.9.8 Growth Rates of C_4 Species 84
2.10 CAM Plants 85
2.10.1 Introduction 85
2.10.2 Physiological, Biochemical, and Anatomical Aspects 86
2.10.3 Water-Use Efficiency 91
2.10.4 Incomplete and Facultative CAM Plants 91
2.10.5 Distribution and Habitat of CAM Species 93
2.10.6 Carbon-Isotope Composition of CAM Species . . . 93
2.11 Specialized Mechanisms Associated with Photosynthetic Carbon Acquisition in Aquatic Plants 93
2.11.1 Introduction 93
2.11.2 The CO_2 Supply in Water 94
2.11.3 The Use of Bicarbonate by Aquatic Macrophytes 95
2.11.4 The Use of CO_2 from the Sediment 96
2.11.5 Crassulacean Acid Metabolism (CAM) in Aquatic Plants 97
2.11.6 Carbon-Isotope Composition of Aquatic Plants . . . 97
2.11.7 The Role of Aquatic Plants in Carbonate Sedimentation 99

2.12 Effects of the Rising CO_2 Concentration in the Atmosphere 100
2.12.1 Acclimation of Photosynthesis to Elevated CO_2 Concentrations 102
2.12.2 Effects of Elevated CO_2 on Transpiration - Differential Effects on C_3, C_4, and CAM Plants 103
2.13 Summary: What Can We Gain from Basic Principles and Rates of Single-Leaf Photosynthesis? 103
References 104

3 Photosynthesis, Respiration, and Long-Distance Transport: Respiration 115
3.1 Introduction 115
3.2 General Characteristics of the Respiratory System 115
3.2.1 The Respiratory Quotient 115
3.2.2 Glycolysis, the Pentose Phosphate Pathway, and the Tricarboxylic (TCA) Cycle 117
3.2.3 Mitochondrial Metabolism 118
3.2.4 A Summary of the Major Points of Control of Plant Respiration 121
3.2.5 ATP Production in Isolated Mitochondria and *in Vivo* 123
3.2.6 Regulation of Electron Transport *via* the Cytochrome and the Alternative Paths 125
3.3 The Ecophysiological Function of the Alternative Path . . . 128
3.3.1 Heat Production 128
3.3.2 Can We Really Measure the Activity of the Alternative Path? 130
3.3.3 The Alternative Path as an Energy Overflow 133
3.3.4 NADH Oxidation in the Presence of a High Energy Charge 133
3.3.5 NADH Oxidation to Oxidize Excess Redox Equivalents from the Chloroplast 135
3.3.6 Continuation of Respiration When the Activity of the Cytochrome Path Is Restricted 136
3.3.7 A Summary of the Various Ecophysiological Roles of the Alternative Oxidase 136
3.4 Environmental Effects on Respiratory Processes 137
3.4.1 Flooded, Hypoxic, and Anoxic Soils 137
3.4.2 Salinity and Water Stress 140
3.4.3 Nutrient Supply 141
3.4.4 Irradiance 142
3.4.5 Temperature 146
3.4.6 Low pH and High Aluminum Concentrations . . . 149
3.4.7 Partial Pressures of CO_2 150
3.4.8 Effects of Nematodes and Plant Pathogens 151

3.4.9 Leaf Dark Respiration as Affected by Photosynthesis 152
3.5 The Role of Respiration in Plant Carbon Balance 153
3.5.1 Carbon Balance 153
3.5.2 Respiration Associated with Growth, Maintenance, and Ion Uptake 155
3.6 Plant Respiration: Why Should It Concern Us from an Ecological Point of View? 164
References 165

4 Photosynthesis, Respiration, and Long-Distance Transport: Long Distance Transport of Assimilates 173
4.1 Introduction 173
4.2 Major Transport Compounds in the Phloem: Why Not Glucose? 173
4.3 Phloem Structure and Function 176
4.3.1 Symplastic and Apoplastic Transport 176
4.3.2 Minor Vein Anatomy 177
4.3.3 Phloem-Loading Mechanisms 178
4.4 Evolution and Ecology of Phloem Loading Mechanisms . . . 180
4.5 Phloem Unloading 181
4.6 The Transport Problems of Climbing Plants 184
4.7 Phloem Transport: Where to Move from Here? 185
References 185

5 Plant Water Relations 187
5.1 Introduction 187
5.1.1 The Role of Water in Plant Functioning 187
5.1.2 Transpiration as an Inevitable Consequence of Photosynthesis 189
5.2 Water Potential 189
5.3 Water Availability in Soil 193
5.3.1 The Field Capacity of Different Soils 194
5.3.2 Water Movement Toward the Roots 195
5.3.3 Rooting Profiles as Dependent on Soil Moisture Content 196
5.3.4 Roots Sense Moisture Gradients and Grow Toward Moist Patches 202
5.4 Water Relations of Cells 202
5.4.1 Osmotic Adjustment 203
5.4.2 Cell-Wall Elasticity 203
5.4.3 Osmotic and Elastic Adjustment as Alternative Strategies 206
5.4.4 Evolutionary Aspects 207
5.5 Water Movement Through Plants 207
5.5.1 The Soil-Plant-Atmosphere Continuum 207
5.5.2 Water in Roots 209
5.5.3 Water in Stems 215

5.5.4 Water in Leaves and Water Loss from Leaves . . . 230
5.5.5 Aquatic Angiosperms . . . 242
5.6 Water-Use Efficiency . . . 242
5.6.1 Water-Use Efficiency and Carbon-Isotope Discrimination . . . 242
5.6.2 Leaf Traits That Affect Leaf Temperature and Leaf Water Loss . . . 243
5.7 Water Availability and Growth . . . 244
5.8 Adaptations to Drought . . . 248
5.8.1 Desiccation-Avoidance: Annuals and Drought-Deciduous Species . . . 248
5.8.2 Dessication-Tolerance: Evergreen Shrubs . . . 249
5.8.3 'Resurrection Plants' . . . 249
5.9 Winter Water Relations and Freezing Tolerance . . . 252
5.10 Salt Tolerance . . . 252
5.11 Final Remarks: The Message That Transpires . . . 253
References . . . 254

6 Plant Energy Budgets: The Plant's Energy Balance . . . 265
6.1 Introduction . . . 265
6.2 Energy Inputs and Outputs . . . 265
6.2.1 A Short Overview of a Leaf's Energy Balance . . . 265
6.2.2 Shortwave Solar Radiation . . . 266
6.2.3 Longwave Terrestrial Radiation . . . 269
6.2.4 Convective Heat Transfer . . . 271
6.2.5 Evaporative Energy Exchange . . . 273
6.2.6 Metabolic Heat Generation . . . 276
6.3 Modeling the Effect of Components of the Energy Balance on Leaf Temperature . . . 276
6.4 A Global Perspective of Hot and Cool Topics . . . 277
References . . . 277

7 Plant Energy Budgets: Effects of Radiation and Temperature . . . 279
7.1 Introduction . . . 279
7.2 Radiation . . . 279
7.2.1 Effects of Excess Irradiance . . . 279
7.2.2 Effects of Ultraviolet Radiation . . . 279
7.3 Effects of Extreme Temperatures . . . 283
7.3.1 How Do Plants Avoid Damage by Free Radicals at Low Temperature? . . . 283
7.3.2 Heat-Shock Proteins . . . 284
7.3.3 Are Isoprene and Monoterpene Emissions an Adaptation to High Temperatures? . . . 284
7.3.4 Chilling Injury and Chilling Tolerance . . . 285
7.3.5 Carbohydrates and Proteins Conferring Frost Tolerance . . . 285

7.4 Global Change and Future Crops 288
References 288

8 Scaling-Up Gas Exchange and Energy Balance from the Leaf to the Canopy Level 291
8.1 Introduction 291
8.2 Canopy Water Loss 294
8.3 Canopy CO_2 Fluxes 296
8.4 Canopy Water-Use Efficiency 297
8.5 Canopy Effects on Microclimate: A Case Study 298
8.6 Aiming for a Higher Level 298
References 299

9 Mineral Nutrition 301
9.1 Introduction 301
9.2 Acquisition of Nutrients 302
9.2.1 Nutrients in the Soil 302
9.2.2 Root Traits That Determine Nutrient Acquisition 309
9.2.3 Sensitivity Analysis of Parameters Involved in Pi Acquisition 331
9.3 Nutrient Acquisition from 'Toxic' or 'Extreme' Soils 331
9.3.1 Acid Soils 333
9.3.2 Calcium-Rich Soils 338
9.3.3 Soils with High Levels of Metals 341
9.3.4 Saline Soils: An Ever-Increasing Problem in Agriculture 349
9.3.5 Flooded Soils 354
9.4 Plant Nutrient-Use Efficiency 355
9.4.1 Variation in Nutrient Concentration 355
9.4.2 Nutrient Productivity and Mean Residence Time 361
9.4.3 Nutrient Loss from Plants 363
9.4.4 Ecosystem Nutrient-Use Efficiency 367
9.5 Mineral Nutrition: A Vast Array of Adaptations and Acclimations 369
References 370

10 Growth and Allocation 385
10.1 Introduction: What Is Growth? 385
10.2 Growth of Whole Plants and Individual Organs 385
10.2.1 Growth of Whole Plants 386
10.2.2 Growth of Cells 387
10.3 The Physiological Basis of Variation in *RGR*—Plants Grown with Free Access to Nutrients 394
10.3.1 SLA Is a Major Factor Associated with Variation in *RGR* 394
10.3.2 Leaf Thickness and Leaf Mass Density 396
10.3.3 Anatomical and Chemical Differences Associated with Leaf Mass Density 396

10.3.4 Net Assimilation Rate, Photosynthesis, and Respiration 398
10.3.5 *RGR* and the Rate of Leaf Elongation and Leaf Appearance 398
10.3.6 *RGR* and Activities per Unit Mass 399
10.3.7 *RGR* and Suites of Plant Traits 399
10.4 Allocation to Storage 401
10.4.1 The Concept of Storage 401
10.4.2 Chemical Forms of Stores 402
10.4.3 Storage and Remobilization in Annuals 403
10.4.4 The Storage Strategy of Biennials 403
10.4.5 Storage in Perennials 404
10.4.6 Costs of Growth and Storage: Optimization 405
10.5 Environmental Influences 406
10.5.1 Growth as Affected by Irradiance 407
10.5.2 Growth as Affected by Temperature 413
10.5.3 Growth as Affected by Soil Water Potential and Salinity 417
10.5.4 Growth at a Limiting Nutrient Supply 419
10.5.5 Plant Growth as Affected by Soil Compaction . . . 424
10.5.6 Growth as Affected by Soil Flooding 428
10.5.7 Growth as Affected by Submergence 430
10.5.8 Growth as Affected by Touch and Wind 432
10.5.9 Growth as Affected by Elevated Atmospheric CO_2 Concentrations 434
10.6 Adaptations Associated with Inherent Variation in Growth Rate 435
10.6.1 Fast-Growing and Slow-Growing Species 435
10.6.2 Growth of Inherently Fast- and Slow-Growing Species under Resource-Limited Conditions 436
10.6.3 Are There Ecological Advantages Associated with a High or Low *RGR*? 437
10.7 Growth and Allocation: The Messages About Plant Messages 440
References 441

11 Life Cycles: Environmental Influences and Adaptations 451
11.1 Introduction 451
11.2 Seed Dormancy, Quiescence, and Germination 451
11.2.1 Hard Seed Coats 453
11.2.2 Germination Inhibitors in the Seed 454
11.2.3 Effects of Nitrate 455
11.2.4 Other External Chemical Signals 456
11.2.5 Effects of Light 457
11.2.6 Effects of Temperature 459
11.2.7 Physiological Aspects of Dormancy 462
11.2.8 Summary of Ecological Aspects of Seed Germination and Dormancy 462

11.3 Developmental Phases 463
11.3.1 Seedling Phase 463
11.3.2 Juvenile Phase 465
11.3.3 Reproductive Phase 469
11.3.4 Fruiting 477
11.3.5 Senescence 478
11.4 Seed Dispersal 479
11.4.1 Dispersal Mechanisms 479
11.4.2 Life-History Correlates 480
11.5 The Message to Disperse: Perception, Transduction, and Response 481
References 481

12 Biotic Influences: Symbiotic Associations 487
12.1 Introduction 487
12.2 Mycorrhizas 487
12.2.1 Mycorrhizal Structures: Are They Beneficial for Plant Growth? 488
12.2.2 Nonmycorrhizal Species and Their Interactions with Mycorrhizal Species 497
12.2.3 Phosphate Relations 497
12.2.4 Effects on Nitrogen Nutrition and Water Acquisition 503
12.2.5 Role of Mycorrhizas in Defense 506
12.2.6 Carbon Costs of the Mycorrhizal Symbiosis 506
12.2.7 Agricultural and Ecological Perspectives 507
12.3 Associations with Nitrogen-Fixing Organisms 510
12.3.1 Symbiotic N_2 Fixation Is Restricted to a Fairly Limited Number of Plant Species 511
12.3.2 Host–Guest Specificity in the Legume–Rhizobium Symbiosis 513
12.3.3 The Infection Process in the Legume–Rhizobium Association 513
12.3.4 Nitrogenase Activity and Synthesis of Organic Nitrogen 519
12.3.5 Carbon and Energy Metabolism of the Nodules 520
12.3.6 Quantification of N_2 Fixation *In Situ* 521
12.3.7 Ecological Aspects of the Symbiotic Association with N_2-Fixing Microorganisms That Do Not Involve Specialized Structures 525
12.3.8 Carbon Costs of the Legume-Rhizobium Symbiosis 526
12.3.9 Suppression of the Legume-Rhizobium Symbiosis at Low pH and in the Presence of a Large Supply of Combined Nitrogen 526
12.4 Endosymbionts 528
12.5 Plant Life Among Microsymbionts 530
References 530

13 Biotic Influences: Ecological Biochemistry: Allelopathy and Defense Against Herbivores 541
13.1 Introduction 541
13.2 Allelopathy (Interference Competition) 541
13.3 Chemical Defense Mechanisms 545
13.3.1 Defense Against Herbivores 546
13.3.2 Qualitative and Quantitative Defense Compounds 549
13.3.3 The Arms Race of Plants and Herbivores 551
13.3.4 How Do Plants Avoid Being Killed by Their Own Poisons? 553
13.3.5 Secondary Metabolites for Medicines and Crop Protection 556
13.4 Environmental Effects on the Production of Secondary Plant Metabolites 560
13.4.1 Abiotic and Biotic Factors 560
13.4.2 Induced Defense and Communication Between Neighboring Plants 561
13.4.3 Communication Between Plants and Their Bodyguards 568
13.5 The Costs of Chemical Defense 570
13.5.1 Diversion of Resources from Primary Growth . . . 570
13.5.2 Strategies of Predators 570
13.6 Detoxification of Xenobiotics by Plants: Phytoremediation 573
13.7 Secondary Chemicals and Messages That Emerge from This Chapter 575
References 575

14 Biotic Influences: Effects of Microbial Pathogens 583
14.1 Introduction 583
14.2 Constitutive Antimicrobial Defense Compounds 583
14.3 The Plant's Response to Attack by Microorganisms 587
14.4 Cross-Talk Between Induced Systemic Resistance and Defense Against Herbivores 591
14.5 Messages from One Organism to Another 593
References 593

15 Biotic Influences: Parasitic Associations 597
15.1 Introduction 597
15.2 Growth and Development 599
15.2.1 Seed Germination 599
15.2.2 Haustoria Formation 602
15.2.3 Effects of the Parasite on Host Development 605
15.3 Water Relations and Mineral Nutrition 606
15.4 Carbon Relations 608

15.5 What Can We Extract from This Chapter? 610
References 610

16 Biotic Influences: Interactions Among Plants 615
16.1 Introduction 615
16.2 Theories of Competitive Mechanisms 620
16.3 How Do Plants Perceive the Presence of Neighbors? 621
16.4 Relationship of Plant Traits to Competitive Ability 624
16.4.1 Growth Rate and Tissue Turnover 624
16.4.2 Allocation Pattern, Growth Form, and Tissue Mass Density 627
16.4.3 Plasticity 628
16.5 Traits Associated with Competition for Specific Resources 631
16.5.1 Nutrients 631
16.5.2 Water 632
16.5.3 Light 634
16.5.4 Carbon Dioxide 634
16.6 Positive Interactions among Plants 635
16.6.1 Physical Benefits 636
16.6.2 Nutritional Benefits 636
16.6.3 Allelochemical Benefits 637
16.7 Plant–Microbial Symbioses 637
16.8 Succession and Long-Term Ecosystem Development 640
16.9 What Do We Gain from This Chapter? 642
References 643

17 Biotic Influences: Carnivory 649
17.1 Introduction 649
17.2 Structures Associated with the Catching of the Prey and Subsequent Withdrawal of Nutrients from the Prey . . . 649
17.3 Some Case Studies 654
17.3.1 *Dionaea muscipula* 654
17.3.2 The Suction Traps of *Utricularia* 654
17.3.3 The Tentacles of *Drosera* 657
17.3.4 Pitchers of *Nepenthes* 658
17.3.5 Passive Traps of *Philcoxia* 660
17.4 The Message to Catch 660
References 662

18 Role in Ecosystem and Global Processes: Decomposition 665
18.1 Introduction 665
18.2 Litter Quality and Decomposition Rate 666
18.2.1 Species Effects on Litter Quality: Links with Ecological Strategy 666
18.2.2 Environmental Effects on Decomposition 669

18.3 The Link Between Decomposition Rate and Nutrient Supply 669
18.3.1 The Process of Nutrient Release 669
18.3.2 Effects of Litter Quality on Mineralization 670
18.3.3 Root Exudation and Rhizosphere Effects 672
18.4 The End-Product of Decomposition 673
References 674

19 Role in Ecosystem and Global Processes: Ecophysiological Controls 677
19.1 Introduction 677
19.2 Ecosystem Biomass and Production 677
19.2.1 Scaling from Plants to Ecosystems 677
19.2.2 Physiological Basis of Productivity 678
19.2.3 Disturbance and Succession 680
19.2.4 Photosynthesis and Absorbed Radiation 681
19.2.5 Net Carbon Balance of Ecosystems 683
19.2.6 The Global Carbon Cycle 685
19.3 Nutrient Cycling 687
19.3.1 Vegetation Controls Over Nutrient Uptake and Loss 687
19.3.2 Vegetation Controls Over Mineralization 688
19.4 Ecosystem Energy Exchange and the Hydrological Cycle 688
19.4.1 Vegetation Effects on Energy Exchange 688
19.4.2 Vegetation Effects on the Hydrological Cycle . . . 691
19.5 Moving to a Higher Level: Scaling from Physiology to the Globe 694
References 695

Glossary 699

Index 721