

Brief Contents

CHAPTER 1 The Science of Plant Ecology 1

PART I THE INDIVIDUAL AND ITS ENVIRONMENT 15

CHAPTER 2 Photosynthesis and the Light Environment 17

CHAPTER 3 Water Relations and Energy Balance 43

CHAPTER 4 Soils, Mineral Nutrition, and Belowground Interactions 71

PART II POPULATIONS AND EVOLUTION 99

CHAPTER 5 Population Structure, Growth, and Decline 101

CHAPTER 6 Evolutionary Processes and Outcomes 129

CHAPTER 7 Growth and Reproduction of Individuals 155

CHAPTER 8 Plant Life Histories 185

PART III COMMUNITIES AND THEIR CAUSES 203

CHAPTER 9 Community Properties 205

CHAPTER 10 Competition and Other Interactions Among Plants 225

CHAPTER 11 Herbivory and Plant-Pathogen Interactions 257

CHAPTER 12 Disturbance and Succession 283

CHAPTER 13 Local Abundance, Diversity, and Rarity 307

PART IV ECOSYSTEMS AND LANDSCAPES 325

CHAPTER 14 Ecosystem Processes 327

CHAPTER 15 Communities in Landscapes 353

CHAPTER 16 Landscape Ecology 369

PART V GLOBAL PATTERNS AND PROCESSES 389

CHAPTER 17 Climate and Physiognomy 391

CHAPTER 18 Biomes 417

CHAPTER 19 Regional and Global Diversity 445

CHAPTER 20 Paleoecology 469

CHAPTER 21 Global Change: Humans and Plants 485

Contents

1 *The Science of Plant Ecology* 1

Ecology as a Science 1

- The Genesis of Scientific Knowledge 2
- Objectivity, Subjectivity, Choice, and Chance in Scientific Research 4
- Experiments: The Heart of Research 4

Testing Theories 8

Specific Results versus General Understanding 9

Science and Other Ways of Knowing, Revisited 9

Scale and Heterogeneity 9

The Structure and History of Plant Ecology 11

Questions for Further Study 13

Additional Readings 13

PART I THE INDIVIDUAL AND ITS ENVIRONMENT

2 *Photosynthesis and the Light Environment* 17

The Process of Photosynthesis 18

Photosynthetic Rates 20

- Limitations Caused by Light Levels 20
- Limitations on Carbon Uptake 23
- Variation in Photosynthetic Rates Within and Between Habitats 24

The Three Photosynthetic Pathways 25

- C₃ Photosynthesis 25
- C₄ Photosynthesis 25

BOX 2A Photorespiration 26

BOX 2B Stable Isotopes and Photosynthesis 27

- Crassulacean Acid Metabolism (CAM Photosynthesis) 29

Evolution of the Three Photosynthetic Pathways 30

Phylogeny of the Photosynthetic Pathways 30

Photosynthesis through Evolutionary Time 31

Growth Form, Phenology, and Distribution of C₃, C₄, and CAM Plants 32

Growth Forms and Habitats 32

Phenology 34

Geographic Distributions 34

Adaptations to the Light Environment 36

Sun and Shade Leaves 36

Species' Adaptations to High-Light and Low-Light Habitats 37

BOX 2C Leaf Iridescence and Structural Coloration 38

Do Sun and Shade Adaptations Exist Within Species? 39

Day Length: Responses and Adaptations 40

- Summary 41
- Questions for Further Study 41
- Additional Readings 41

3 Water Relations and Energy Balance 43

- Adapting to Life on Land 44
- Water Potential 44
- The Soil-Plant-Atmosphere Continuum 45
- BOX 3A** Measuring Photosynthesis, Transpiration, and Water Potential 46
- Transpiration and the Control of Water Loss 48
 - Strategies for Coping with Different Water Availability Conditions 49
 - Water Use Efficiency 50
 - Whole-Plant Adaptations to Low Water Availability 50
 - Physiological Adaptations 52
 - Anatomical and Morphological Adaptations 54
- The Energy Balance of Leaves 61
 - Radiant Energy 62
- BOX 3B** Why the Sky Is Blue and the Setting Sun Is Red 63
 - Conduction and Convection 64
 - Latent Heat Exchange 65
 - Putting It All Together: Leaf and Whole-Plant Temperature 65
 - Adaptations to Extreme Temperature Regimes 67
- Summary 68
- Questions for Further Study 69
- Additional Readings 69

PART II POPULATIONS AND EVOLUTION

5 Population Structure, Growth, and Decline 101

- Some Issues in the Study of Plant Population Growth 102
- Population Structure 103
 - Some Population Structure Issues Specific to Plants 105
 - Sources of Population Structure 106

4 Soils, Mineral Nutrition, and Belowground Interactions 71

- Soil Composition and Structure 71
 - Soil Texture 72
 - Soil pH 74
 - Horizons and Profiles 75
 - Origins and Classification 77
 - Organic Matter and the Role of Organisms 80
- Water Movement within Soils 80
- Plant Mineral Nutrition 82
 - The Stoichiometry of Nutrients 82
 - Nitrogen in Plants and Soils 83
 - Biological Nitrogen Fixation 84
- BOX 4A** Symbioses and Mutualisms 86
 - Phosphorus in Soils 88
 - Nutrient Use Efficiency 88
 - Leaf Life Span and Evergreen versus Deciduous Leaves 90
- Mycorrhizae 92
 - Major Groups of Mycorrhizae 92
 - The Role of Mycorrhizae in Plant Phosphorus Nutrition 93
 - Other Functions of Mycorrhizae 94
 - Orchids and Their Mycorrhizal Associations 95
 - Mutualism or Parasitism? 95
 - Effects of Mycorrhizae on Plant Interactions 95
- Summary 96
- Questions for Further Study 97
- Additional Readings 97

- Studying Population Growth and Decline 106
 - Life Cycle Graphs 107
- BOX 5A** Life Table Calculations 108
- BOX 5B** Borrowing the Mark-Recapture Method from Animal Ecology 109
- BOX 5C** Constructing Matrix Models 110
 - Matrix Models 110
- BOX 5D** Demography of an Endangered Cactus 111

- BOX 5E** Multiplying a Population Vector by a Matrix 111
 Analyzing Matrix Models 112
 But Real Plants Live in Variable Environments 113
 Lifetime Reproduction: The Net Reproductive Rate 113
 Reproductive Value: The Contribution of Each Stage to Population Growth 113
- BOX 5F** Reproductive Value 114
- BOX 5G** How Do Changes in the Transition Probabilities Affect the Population Growth Rate? 115
 Sensitivity and Elasticity 115
 Life Table Response Experiments 116
 Age and Stage, Revisited 117
 Other Approaches to Modeling Plant Demography 118
- Demographic Studies of Long-Lived Plants 119**
- Random Variation in Population Growth and Decline 122**
 Causes of Random Variation 122
 Long-Term Growth Rates 123
 Studying Variable Population Growth 125
- Summary 126**
- Questions for Further Study 127**
- Additional Readings 127**

6 *Evolutionary Processes and Outcomes* 129

- Natural Selection 130**
 Variation and Natural Selection 130
 The Factors Necessary for Natural Selection 131
- Heritability 133**
 Resemblance among Relatives 133
 Partitioning Phenotypic Variation 134
- BOX 6A** A Simple Genetic System and the Resemblance of Relatives 135
 Genotype-Environment Interactions 136
 Gene-Environment Covariation 136
- Patterns of Adaptation 137**
 Heavy-Metal Tolerance 137
 Adaptive Plasticity 140
- Levels of Selection 142**
- Other Evolutionary Processes 143**
 Processes that Increase Variation 143
 Processes that Decrease Variation 143
- Variation among Populations 145**
 Ecotypes 145

- Speciation 149**
- Adaptation and Speciation through Hybridization 151**
- Summary 152**
- Questions for Further Study 153**
- Additional Readings 153**

7 *Growth and Reproduction of Individuals* 155

- Plant Growth 155**
- Ecology of Growth 157**
 Plant Architecture and Light Interception 157
 Growth of Clonal Plants 158
- Plant Reproduction 160**
 Vegetative Reproduction 160
 Seeds Produced Asexually 161
 Sexual Life Cycles of Plants 161
- Pollination Ecology 163**
 Wind Pollination 163
 Attracting Animal Visitors: Visual Displays 165
 Attracting Animal Visitors: Floral Odors and Acoustic Guides 166
 Limiting Unwanted Visits 168
 Pollination Syndromes 168
- BOX 7A** Specialized Plants and Pollinators 169
 Aquatic Plants and Pollination 170
- BOX 7B** Some Complex Plant-Pollinator Interactions 171
- Who Mates with Whom? 172**
 Plant Gender 172
- BOX 7C** Pollination Experiments 173
 Competition for Pollinators and among Pollen Grains 173
 Pollen Dispersal and Its Consequences 174
 Assortative Mating 176
 Frequency-Dependent Selection 176
 Factors that Shape Plant Mating Systems 177
 Applications of Pollination and Mating System Ecology 178
- The Ecology of Fruits and Seeds 179**
 Seed Dispersal Patterns 180
 Seed Banks 183
- Summary 183**
- Questions for Further Study 184**
- Additional Readings 184**

8 *Plant Life Histories* 185

Size and Number of Seeds 185

Life History Strategies 188

Life Span 189

r- and *K*-selection 190

Grime's Triangular Model 191

Demographic Life History Theory 193

Reproductive Allocation 193

Difficulties in Measuring Trade-Offs 194

Variation among years 195

Consequences of Variable Environments 195

Seed Germination 195

Masting 196

Phenology: Within-Year Schedules of Growth and Reproduction 198

Vegetative Phenology 198

Reproductive Phenology: Abiotic Factors 199

Reproductive Phenology: Biotic Factors 201

Summary 201

Questions for Further Study 202

Additional Readings 202

PART III COMMUNITIES AND THEIR CAUSES

9 *Community Properties* 205

What Is a Community? 205

The History of a Controversy 206

BOX 9A Communities, Taxa, Guilds, and Functional Groups 207

A Modern Perspective on the Issues in Contention 210

Are Communities Real? 211

BOX 9B A Deeper Look at Some Definitions: Abiotic Factors and Emergent Properties 212

Describing Communities 212

Species Richness 213

Diversity, Evenness, and Dominance 215

Sampling Methods and Parameters for Describing Community Composition 217

Physiognomy 219

Long-Term Studies 221

Summary 221

BOX 9C The Long-Term Ecological Research Network 222

Questions for Further Study 222

Additional Readings 223

10 *Competition and Other Interactions Among Plants* 225

Competition at the Level of Individuals 226

Seedlings: Density, Size, Inequality, and Timing of Emergence 226

Seedlings: Density and Mortality 229

Mechanisms of Competition for Resources 230

Size and Resource Competition 232

Experimental Methods for Studying Competition 233

Greenhouse and Garden Experiments 233

BOX 10A How Competition Is Measured, and Why That Matters 234

Field Experiments 236

From Interspecific Competition to Allelopathy to Facilitation 237

Trade-offs and Strategies 237

Competitive Hierarchies 239

Allelopathy 240

Facilitation 242

Modeling Competition and Coexistence 244

Equilibrium Models 245

Nonequilibrium Approaches to Modeling Competition 246

Effects of Competition on Species Coexistence and Community Composition 248

Competition along Environmental Gradients 249

- Conceptual Models of Competition in Habitats with Differing Productivities 249
- Experimental Evidence 251
- Evidence from Research Syntheses 253
- Resolution of Differing Results 255

Summary 255

Questions for Further Study 256

Additional Readings 256

11 Herbivory and Plant-Pathogen Interactions 257

Herbivory at the Level of Individuals 258

Herbivory and Plant Populations 259

- Herbivory and Spatial Distribution of Plants 260
- Granivory 261
- Biological Control 261

Effects of Herbivory at the Community Level 263

- Consequences of Herbivore Behavior 263
- Apparent Competition 263
- Introduced and Domesticated Herbivores 264
- Effects of Native Herbivores 265
- Generality 267

Plant Defenses against Herbivory 267

- Physical Defenses 267
- Plant Secondary Chemistry 269
- Constitutive versus Induced Defenses 271
- Evolutionary Consequences of Plant-Herbivore Interactions 272

Parasitic Plants 274

Pathogens 275

- Effects of Disease on Individual Plants 275

BOX 11A Effects of Plant Disease on Humans:

Potato Blight and the Irish Potato Famine 276

- Physiological and Evolutionary Responses to Pathogens 277

- Effects of Pathogens at the Population and Community Level 278

- More Complex Interactions 279

Summary 280

Questions for Further Study 280

Additional Readings 280

12 Disturbance and Succession 283

Theories of the Mechanisms of Succession 284

Disturbance 285

- Gaps 286
- Fire 287
- Wind 291
- Water 292
- Animals 292
- Earthquakes and Volcanoes 293
- Disease 293
- Humans 293

Colonization 293

Determining the Nature of Succession 294

- Interaction between Methodology and Understanding 294
- Mechanisms Responsible for Successional Change 297
- The Predictability of Succession 300
- Community Restoration 301

Primary Succession 302

Climax Revisited 303

Summary 304

Questions for Further Study 305

Additional Readings 305

13 Local Abundance, Diversity, and Rarity 307

Dominance 307

- Are Dominant Species Competitively Superior? 308
- Abundance Curves 308

Rarity and Commonness 309

- The Nature of Rarity 309
- Patterns of Rarity and Commonness 310
- Causes of Rarity and Commonness 311

Invasive Species and Community Susceptibility to Invasion 313

- Why Do Some Species Become Invasive? 314
- What Makes a Community Susceptible to Invasion? 315

Abundance and Community Structure 317

- Productivity and Diversity 318
- Niche Differentiation, Environmental Heterogeneity, and Diversity 320

- Gaps, Disturbance, and Diversity 321
- Effects of Increasing Diversity 321**
 - Testing the Effects of Diversity on Ecosystems 322
 - Diversity and Stability 323

- Regional Processes 323
- Summary 324**
- Questions for Further Study 324**
- Additional Readings 324**

PART IV ECOSYSTEMS AND LANDSCAPES

14 *Ecosystem Processes* 327

Biogeochemical Cycles: Quantifying Pools and Fluxes 328

The Global Water Cycle 330

Carbon in Ecosystems 332

- Productivity 332
- Methods for Estimating Productivity 335
- Decomposition and Soil Food Webs 337
- Carbon Storage 340
- Models of Ecosystem Carbon Cycles 341

Nitrogen and the Nitrogen Cycle at Ecosystem and Global Levels 342

- Nitrogen Fixation 342
- Other Sources of Nitrogen Input to Living Organisms 343
- Nitrogen Mineralization 344
- Denitrification and Leaching of Nitrogen 345
- Decomposition Rates and Nitrogen Immobilization 345
- Plant Uptake of Nitrogen 346

Phosphorus in Terrestrial Ecosystems 347

Ecosystem Nutrient Cycling and Plant Diversity 348

Ecosystem Processes for Some Other Elements 348

- Sulfur 348
- Calcium 349

BOX 14A Serpentine Soils 349

Summary 350

Questions for Further Study 351

Additional Readings 351

15 *Communities in Landscapes* 353

Comparing Communities 353

- Non-numerical Techniques 354
- Univariate Techniques 354
- Multivariate Techniques 354

Landscape Patterns 357

- Ordination: Describing Patterns 357
- Determining Causes of Patterns 358
- Types of Data 360
- Classification 360

BOX 15A Differentiating Vegetation Based on Spectral Quality 363

- Views on Continuous versus Discrete Landscapes 364

Landscape Diversity 364

- Differentiation Diversity 364
- Pattern Diversity 365

Summary 366

Questions for Further Study 366

Additional Readings 367

16 *Landscape Ecology* 369

Spatial Patterns 370

- Six Types of Species-Area Curves 371
- Defining Patches 373
- Quantifying Patch Characteristics and Interrelationships 373
- The Effects of Spatial Patterns on Ecological Processes 374

Scale 375

- Definitions and Concepts 375

- Process and Scale 377
- Spatial and Ecological Scale 377
- Quantifying Aspects of Spatial Pattern and Scale 378

Toward a Theoretical Basis for Landscape Patterns: Island Biogeography Theory 379

- Metapopulation Theory 380

BOX 16A Metapopulation Models 381

- Metapopulation Patterns 381

- Species-Time-Area Relationships 383

Landscape Ecology and Conservation 384

- Reserve Design 384
- Fragmentation 385
- Edges, Connectivity, and Nestedness 386

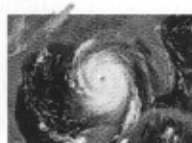
Summary 387

Questions for Further Study 388

Additional Readings 388

PART

V



GLOBAL PATTERNS AND PROCESSES

17 Climate and Physiognomy 391

Climate and Weather 391

Temperature 392

- Short-Term Variation in Radiation and Temperature 393
- Long-Term Cycles 397

Precipitation 398

- Global Patterns 399

BOX 17A The Coriolis Effect 400

- Continental-Scale Patterns 403
- Seasonal Variation in Precipitation 406
- The El Niño Southern Oscillation 407
- Predictability and Long-Term Change 410

Plant Physiognomy across the Globe 411

- Forests 411
- Tree Line 412
- Grasslands and Woodlands 413
- Shrublands and Deserts 414

Summary 415

Questions for Further Study 416

Additional Readings 416

18 Biomes 417

Categorizing Vegetation 417

Converging Biomes and Convergent Evolution 420

Moist Tropical Forests 423

- Tropical Rainforest 423
- Tropical Montane Forest 425

Seasonal Tropical Forests and Woodlands 425

- Tropical Deciduous Forest 426
- Thorn Forest 427
- Tropical Woodland 427

Temperate Deciduous Forest 428

Other Temperate Forests and Woodlands 429

- Temperate Rainforest 429
- Temperate Evergreen Forest 431
- Temperate Woodland 432

Taiga 432

Temperate Shrubland 433

Grasslands 435

- Temperate Grassland 435
- Tropical Savanna 436

Deserts 438

- Hot Desert 438
- Cold Desert 439

Alpine and Arctic Vegetation 439

- Alpine Grassland and Shrubland 439
- Tundra 441

Summary 442

Questions for Study and Thought 443

Additional Readings 443

19 Regional and Global Diversity 445

Large-Scale Patterns of Species Richness 446

General Factors Affecting Diversity 447

Levels of Explanation 447

Null Models 448

The Importance of Available Energy 449

Contributions of α , β , and γ Diversity 452

Diversity along Ecological Gradients 452

Productivity and Scale 453

Diversity along Latitudinal Gradients 455

An Array of Explanations 455

The Role of β Diversity 457

Continental Differences 457

Other Geographic Patterns 459

Species Diversity and Patterns of Overlap 459

Endemism, Centers of Diversification, and Isolation 460

Relationships between Regional and Local Diversity 461

BOX 19A The Fynbos and the Cape Region of Africa 462

Noisy Data and Limits to Methodology 464

Summary 466

Questions for Further Study 466

Additional Readings 467

20 Paleoecology 469

The Paleozoic Era 470

The Mesozoic Era 473

The Dominance of Gymnosperms 473

The Breakup of Pangaea and the Rise of the Angiosperms 474

The Cretaceous-Tertiary (K-T) Boundary 475

The Cenozoic Era 475

Paleoecology Methods 476

The Recent Past 477

At the Glacial Maximum 478

Glacial Retreat 480

Climatic Fluctuations in the Recent Past 482

Summary 484

Questions for Further Study 484

Additional Readings 484

21 Global Change: Humans and Plants 485

Carbon and Plant-Atmosphere Interactions 486

The Global Carbon Cycle 486

Direct Effects of Increasing CO₂ on Plants 487

Anthropogenic Global Climate Change 488

The Greenhouse Effect 488

Global Climate Change: Evidence 490

Global Climate Change: Predictions 493

BOX 21A Modeling Climate 492

Biotic Consequences of Climate Change 495

Anthropogenic Effects on the Global Carbon Cycle 498

Deforestation 498

Fossil Fuel Combustion 499

BOX 21B Daily Human Activities and CO₂ Generation 501

Acid Precipitation and Nitrogen Deposition 502

Declining Global Biodiversity and Its Causes 504

Habitat Fragmentation and Loss 504

Other Threats to Rare and Common Species in a Range of Communities 508

Invasive Species as Threats to Biodiversity 509

Human Populations and Land Use Patterns 509

A Ray of Hope? 512

Summary 512

Questions for Further Study 513

Additional Readings 513

Appendix: A Statistics Primer 515

Glossary 519

Photo Credits 530

Literature Cited 531

Index 554