

Contents

List of Boxes	page xvii
Preface	xix

Chapter 1 Plants Create the Biosphere 1

1.1	Introduction: The Importance of Plants	2
1.1.1	Plants Are Abundant and They Support Other Life Forms	2
1.1.2	Fundamentals and Overview	4
1.1.3	The Number of Species and Their Classification	4
1.1.4	Vegetation Types and Climate	5
1.2	The First Land Plants	6
1.3	Energy Flow Organizes Molecules	9
1.4	Membranes Are Necessary for Life	13
1.5	Eukaryotic Cells Originated as Symbioses	14
1.6	The Origin of Photosynthesis	16
1.7	The Oxygen Revolution Was a Consequence of Photosynthesis	18
1.7.1	Ocean Chemistry Changes With Oxygen	19
1.7.2	Atmospheric Composition Changes With Oxygen	19
1.7.3	The Ozone Layer Forms From Oxygen	20
1.8	The Cambrian Explosion of Multicellular Life	20
1.9	Plants Affect Climate	21
1.10	Sediment and Ice Cores Provide a Record of Past Environments	25
1.11	The Biosphere	27
	Conclusion	30
	Review Questions	30
	Further Reading	31

Chapter 2 The Search for Global Patterns 35

2.1	Introduction: There Are Two Ways to Classify Plants and Vegetation	36
2.2	Functional Classifications Are Based on Ecological Traits	36
2.2.1	Functional Classifications by von Humboldt, Raunkiaer and K�uchler	37
2.2.2	Climate Has a Major Impact on Plant Traits	43
2.2.3	Climate and Life Form Are Summarized as Biomes	46
2.2.4	Functional Classification Systems Have Limitations	47

2.3	Phylogenetic Classifications Are Based on Evolutionary History	48
2.3.1	Early Plant Classification by Linnaeus, Bentham and Hooker	48
2.3.2	Plant Evolution: Wallace, Darwin and Bessey	49
2.3.3	Molecular Techniques Provide New Insights	50
2.3.4	The Two Largest Families of Plants: Asteraceae and Orchidaceae	52
2.3.5	Grasses and Their Significance	55
2.3.6	World Floristic Regions Are Based on Phylogeny and Geography	57
2.3.7	Some Limitations of Phylogenetic Classifications for Ecological Research	58
	Conclusion	60
	Review Questions	62
	Further Reading	62

Chapter 3 Resources 65

3.1	Introduction: Plants Must Find Resources to Grow	66
3.1.1	The CHNOPS Perspective	66
3.1.2	The Costs of Acquisition	69
3.2	Carbon Dioxide: Foraging in an Atmospheric Reservoir	69
3.3	Light and Photosynthesis: Harvesting Photons	71
3.3.1	Three Measures of Photon Harvest	71
3.3.2	There are Different Photosynthetic Types	71
3.3.3	An Exception to the Rule: Root Uptake of CO ₂	72
3.3.4	Another View of Photosynthetic Types	73
3.3.5	Architecture Affects Photon Harvesting	74
3.3.6	The Overriding Importance of Height	76
3.4	Below-Ground Resources	77
3.4.1	Water	77
3.4.2	Nitrogen	78
3.4.3	Phosphorus	79
3.4.4	Experimental Tests for Nitrogen and Phosphorus Limitation	81
3.4.5	Other Sources of Evidence for Nutrient Limitation	85
3.4.6	Mineral Nutrients: A Single Cell Perspective	85
3.5	Resources Affect Entire Ecosystems	87
3.5.1	Primary Production is Controlled by Resources	87
3.5.2	Soils Are Produced by Two Causal Factors	89
3.5.3	Life After Death: Soils, Detritivores and Decomposers	92
3.5.4	Soil Resources Have Altered Human History	96
3.5.5	Two Historical Digressions: Jan Baptiste von Helmont and Titus Smith	97
3.6	Resources Vary in Space and Time	98
3.6.1	There is Small-Scale Heterogeneity	98
3.6.2	Resources Often Change Along Gradients	99
3.6.3	Resources Often Occur in Transitory Patches	103

3.6.4	Resource Fluctuations Complicate Short-Term Ecological Studies	104
3.6.5	Resources Provide a Habitat Template	107
3.7	Scarce Resources Have Many Consequences	109
3.7.1	Evergreen Plants Conserve Scarce Resources	109
3.7.2	Global Patterns in Leaf Architecture: The Leaf Economic Spectrum	111
3.7.3	Bizarre Botany: Some Strange Evolution for Resource Acquisition	112
	Conclusion	119
	Review Questions	120
	Further Reading	120

Chapter 4 Competition 123

4.1	Introduction: Plants Struggle Against One Another for Resources	124
4.2	There Are Many Kinds of Competition	126
4.2.1	Intraspecific Competition	126
4.2.2	Distinguishing Between Intraspecific and Interspecific Competition	126
4.2.3	Competition Intensity	129
4.2.4	Competitive Effect and Competitive Response	130
4.2.5	Competitive Dominance	130
4.3	Competition Has Many Consequences	132
4.3.1	Self-Thinning in Monocultures	132
4.3.2	Dominance Patterns in Monocultures	134
4.3.3	Density Dependence in Annual Plants	136
4.3.4	The Relationship Between Intensity and Asymmetry of Competition	139
4.4	Competitive Hierarchies Are Widespread	139
4.4.1	Methods for Establishing Hierarchies	139
4.4.2	The Consistency of Hierarchies Among Habitats	141
4.4.3	Light and Shoot Size as Key Factors Producing Hierarchies	143
4.5	Competition Gradients Are Widespread	146
4.5.1	Measuring Competition Intensity Along Gradients	146
4.5.2	Competition Intensity Gradients in an Old Field	147
4.5.3	Competition and Cacti	149
4.5.4	Competition Intensity Along a Soil Depth Gradient	149
4.5.5	Competition Intensity Gradients in Wetlands	150
4.5.6	Competition Along an Altitudinal Gradient	150
4.6	Foraging Ability Might Be a Competitive Trait	152
4.7	Mycorrhizae Can Affect Competition	153
4.8	Two Competition Models	154
4.8.1	The Problem of Coexistence	154
4.8.2	Patch Dynamics: A Model	155
4.8.3	Gradients and Zonation: A Model	157
4.9	The Role of Models in Ecology	159

Conclusion	160
Review Questions	160
Further Reading	161

Chapter 5 Disturbance 163

5.1	Introduction: Disturbance Removes Biomass	164
5.2	Disturbance Has Four Properties	165
5.2.1	Duration	165
5.2.2	Intensity	165
5.2.3	Frequency	165
5.2.4	Area	165
5.3	Examples of Disturbance	166
5.3.1	Fire Disturbs Many Kinds of Vegetation	166
5.3.2	Erosion Creates Bare Ground	173
5.3.3	Animals Create Gaps in Vegetation	175
5.3.4	Sediment From Flooding Can Bury Wetlands	178
5.3.5	Ice Reworks Shorelines	182
5.3.6	Waves	183
5.3.7	Storms	183
5.4	Catastrophes Have Low Frequency and High Intensity	185
5.4.1	Landslides	185
5.4.2	Volcanic Eruptions	187
5.4.3	Meteor Impacts	189
5.5	Measuring the Impacts of Disturbance With Experiments: Two Examples	196
5.5.1	Forested Watersheds at Hubbard Brook	196
5.5.2	Marshes Along the Ottawa River	198
5.6	Disturbance Creates Gap Dynamics	200
5.6.1	Many Kinds of Trees Regenerate in Gaps	200
5.6.2	Buried Seeds (“Seed Banks”) Allow Regeneration After Disturbance	202
5.6.3	Rivers Create Gaps by Depositing Sediment	204
5.7	Logging is a Disturbance Caused by Humans	205
5.8	Multiple Factors in Plant Communities: Fire, Flooding and Drought in the Everglades	206
	Conclusion	208
	Review Questions	209
	Further Reading	209

Chapter 6 Herbivory 211

6.1	Introduction: Herbivores Have Large Impacts Upon Plants	212
6.1.1	Two Cautions Are Necessary	213
6.2	Observations on Wildlife Diets: Four Examples	214

6.2.1	Herbivores in African Grasslands	214
6.2.2	Herbivorous Insects in Tropical Forest Canopies	215
6.2.3	Giant Tortoises on Islands	215
6.2.4	Herbivory in Anthropogenic Landscapes	217
6.3	Plants Have Defences Against Herbivores	217
6.3.1	Evolutionary Context	217
6.3.2	Structures That Protect Seeds: The Strobilus	218
6.3.3	Secondary Metabolites Also Defend Against Herbivores	222
6.3.4	Some Cautions When Interpreting Anti-Herbivore Defences	227
6.3.5	Food Quality Is Predicted by Nitrogen Content	229
6.4	Field Experiments Expand Understanding of Herbivory	230
6.4.1	Caterpillars Consume Deciduous Forest Canopies	231
6.4.2	Land Crabs Can Change the Composition of Tropical Forest	233
6.4.3	A Large Experiment on Grasslands in Tanzania	234
6.4.4	Some Lessons for Exclosure Experiments	235
6.5	Empirical Relationships Uncover General Patterns in Herbivory	237
6.6	Some Theoretical Explorations	241
6.6.1	Bottom-Up or Top-Down?	241
6.6.2	Trophic Cascades	242
6.6.3	Effects of Selective Herbivory on Plant Diversity	244
6.6.4	A Simple Model of Herbivory	245
6.6.5	When Herbivory Becomes Catastrophe	248
6.7	Two Final Examples of Large-Scale Changes from Herbivores	252
6.7.1	Mountain Pine Beetles Change Conifer Forests	252
6.7.2	White-Tailed Deer Change Deciduous Forests	254
	Conclusion	255
	Review Questions	256
	Further Reading	256

Chapter 7 Positive Interactions 259

7.1	Introduction: Plants Can Cooperate With Other Plants, Fungi and Animals	260
7.1.1	Definitions	260
7.1.2	A Brief History of Positive Interactions	261
7.2	Positive Interactions Occur Between Plants and Plants	262
7.2.1	Nurse Plants	262
7.2.2	Gradients Illustrate How Stress Affects Positive Interactions	265
7.2.3	Examples of Positive Interactions in Wetlands	265
7.2.4	Commensalism May Be Common in Plant Communities	267
7.3	There Are Many Positive Interactions Between Plants and Fungi	267
7.3.1	There Are Four Kinds of Mycorrhizae	267
7.3.2	Ectomycorrhizae Are Vital to Forests	270
7.3.3	Mycorrhizae May Be Less Important in Wet Habitats	272

7.3.4	Measuring Costs and Benefits	273
7.3.5	Lichens Are Somewhat Different, and Somewhat Similar	274
7.3.6	Fungi Can Also Occur in Shoots and Leaves	276
7.4	Positive Interactions Between Plants and Animals:	
	Part 1 Pollination	276
7.4.1	Animals Pollinate Flowers	276
7.4.2	What Are the Mutual Benefits?	278
7.4.3	Sexual Reproduction Has Costs	279
7.4.4	Pollination Ecology Was Founded by Sprengel and Darwin	281
7.4.5	Another Example: Some Flowers Are Pollinated by Flies	282
7.5	Positive Interactions Between Plants and Animals:	
	Part 2 Seed Dispersal	283
7.5.1	Animals Eat Fruits and Spread Seeds	283
7.5.2	Rodents, Nuts and Mast Years	284
7.5.3	Ants Disperse Seeds	286
7.5.4	Can Seed Dispersal Become an Obligate Mutualism?	287
7.6	Animals Can Defend Plants From Herbivores and Competitors	289
7.7	Mathematical Models of Mutualism	290
7.7.1	A Population Dynamics Model	290
7.7.2	A Cost–Benefit Model	292
7.8	Mutualism Generates Complex Networks	293
	Conclusion	294
	Review Questions	296
	Further Reading	297

Chapter 8 Time 299

8.1	Introduction: There Are Many Time Scales in Ecology	300
8.1.1	Each Ecological Process Has a Time Scale	300
8.1.2	Some Sources of Evidence: Tree Rings, Sediment Cores and Fossils	300
8.2	Millions of Years: Flowering Plants and Continental Drift	302
8.2.1	Flowering Plants Appear in the Cretaceous Era	302
8.2.2	Continents Derived from Gondawa Have Remarkable Plant Diversity	309
8.3	Thousands of Years: The Pleistocene Glaciations	312
8.3.1	Erosion and Deposition Were Caused by Glacial Ice	313
8.3.2	Loess Was Deposited by Wind	313
8.3.3	Pluvial Lakes Expanded	313
8.3.4	Drought Affected Tropical Forests	313
8.3.5	Sea Levels Fell as Ice Sheets Expanded	317
8.3.6	Plant Distributions Changed	318
8.3.7	Humans Appeared and Spread to New Continents	320
8.3.8	Sea Levels Rose as Ice Sheets Melted	320

8.4	Hundreds of Years: Succession	322
8.4.1	Succession Is Directional Change in Vegetation	322
8.4.2	Four Examples of Succession	323
8.4.3	Predictive Models for Plant Succession	330
8.4.4	More on Mechanisms of Succession	331
8.4.5	There Are Disagreements About Succession	332
	Conclusion	335
	Review Questions	336
	Further Reading	336

Chapter 9 Populations 339

9.1	Introduction: Working With Single Species	340
9.2	Population Models and Exponential Growth	341
9.3	How Many Seeds Will a Plant Produce?	343
9.4	The Fate of Seeds	344
9.4.1	A Typical Type III Survival Curve	344
9.4.2	Quantitative Studies of the Fates of Seeds	346
9.4.3	Dragon's Blood Trees in Deserts and Seedlings in Forests	348
9.4.4	More on Saguaro Seedlings	349
9.5	What Determines the Size of Seeds?	350
9.6	Clones and Genets	351
9.6.1	The Strawberry–Coral Model	353
9.6.2	The Elm–Oyster Model	353
9.6.3	The Aphid–Rotifer Model	354
9.7	A Population Study on the Effects of Herbivores	354
9.8	A Population Study on the Effects of Seed Transport Along a Gradient	355
9.9	Plant Life Spans	358
9.10	Population Ecology of the Brazil Nut Tree: A Size-structured Model	361
9.10.1	Economic Importance	361
9.10.2	Ecology	361
9.10.3	A Size-structured Model Using the Lefkovitch Matrix	361
	Conclusion	364
	Review Questions	364
	Further Reading	365

Chapter 10 Stress 367

10.1	Introduction: Stress Constrains Growth	368
10.2	Habitats That Lack Resources: Drought as a Widespread Example	369
10.2.1	Deserts	369
10.2.2	Grasslands	373
10.2.3	Mediterranean Shrublands	375
10.2.4	Rock Barrens	379

10.3	Habitats Where Resources Are Present, Yet Unavailable: Peatlands	382
10.4	Habitats Constrained by a Regulator: Cold	386
10.4.1	Arctic and Alpine Plants	386
10.4.2	Deciduous Forests	390
10.5	Habitats Constrained by a Regulator: Salinity	392
10.5.1	Salinity, Plant Zonation and Physiological Drought	392
10.5.2	Stress, Zonation and Competition	392
10.5.3	Salinity and Pulses of Regeneration	393
10.6	Two Extreme Cases of Stress Tolerance	394
10.6.1	Endolithic Plants	394
10.6.2	Flooded Plants	394
10.7	Pollution Is a Source of Stress for Plants	397
10.7.1	Acid Rain: Lessons From the Smoking Hills	398
10.7.2	Radiation: Lessons From the Brookhaven National Laboratory	398
10.8	Some Theory	399
10.8.1	Concepts of Stress and Strain	399
10.8.2	Competition Is a Source of Stress	400
10.8.3	Stress Creates Metabolic Costs	400
10.8.4	Evolution and Risk Aversion	401
10.8.5	Plants in Stressed Habitats Have Low Growth Rates	402
10.8.6	The CSR Synthesis	402
10.9	Stress Acts at Many Scales	406
	Conclusion	408
	Review Questions	409
	Further Reading	409

Chapter 11 Gradients and Plant Communities 411

11.1	Introduction: Gradients Create Pattern in Plant Communities	412
11.2	Describing Pattern Along Obvious Natural Gradients	412
11.3	Multivariate Methods for Pattern Detection	418
11.3.1	The Data Matrix	418
11.3.2	Measuring Similarity	419
11.3.3	Ordination Techniques	420
11.3.4	Ordinations Based Upon Species Data	421
11.3.5	Ordinations Can Combine Species and Environmental Data	422
11.3.6	Functional Simplification in Ordination	425
11.4	Vegetation Classification	426
11.4.1	Phytosociology	427
11.4.2	Classification for Land Management	431
11.5	Gradients and Communities	435
11.5.1	Clements and Gleason	435
11.5.2	The Temporary Victory of the Gleasonian View	436
11.5.3	Null Models and Patterns Along Gradients	440

11.6 Empirical Studies of Patterns Along Gradients	441
Conclusion	448
Review Questions	449
Further Reading	449

Chapter 12 Diversity 451

12.1 Introduction: Why Are There So Many Kinds of Plants?	452
12.2 Large Areas Have More Plant Species	453
12.3 Areas With More Kinds of Habitat Have More Plant Species	455
12.4 Equatorial Areas Have More Plant Species	457
12.5 More Examples of Plant Species Diversity	462
12.5.1 Mediterranean Climate Regions	462
12.5.2 Carnivorous Plants	463
12.5.3 Deciduous Forests	463
12.5.4 Diversity, Biogeography and the Concept of Endemism	464
12.6 Models to Describe Species Diversity at Smaller Scales	467
12.6.1 Intermediate Biomass	467
12.6.2 Intermediate Disturbance	468
12.6.3 Centrifugal Organization	472
12.7 Relative Abundance: Dominance, Diversity and Evenness	474
12.8 Microcosm Experiments on Richness and Diversity	479
12.9 Field Experiments on Richness and Diversity	482
12.10 Implications for Conservation	484
Conclusion	486
Review Questions	487
Further Reading	487

Chapter 13 Conservation and Management 491

13.1 Introduction: It Is Time to Apply What We Know	492
13.2 Some Historic Examples of Vegetation Degradation	492
13.2.1 Ancient Assyria	492
13.2.2 Ancient Rome	493
13.2.3 Louisiana Wetlands	493
13.2.4 Easter Island	498
13.2.5 The Galapagos: Pinta Island	500
13.3 The World Needs Large Protected Areas	502
13.3.1 Designing a Protected Area System	502
13.3.2 There Are Different Levels of Protection	504
13.3.3 Biological Hotspots Are a Priority	507
13.3.4 Large Forests Are a Priority	510
13.3.5 Large Wetlands Are a Priority	512
13.3.6 A Global Assessment of Endemic Plant Conservation	512

13.4	Five Advanced Topics in Conservation Management	514
13.4.1	Communities and Ecosystems Provide Services	514
13.4.2	A Full Protected Area System Has Buffers and Corridors	516
13.4.3	There Are Thresholds in the Process of Degradation	517
13.4.4	Restoration of Degraded Vegetation Types	518
13.4.5	Indicators Allow for Efficient Monitoring	520
	Conclusion	521
	Review Questions	523
	Further Reading	524
	References	525
	Figure and Table Credits	577
	Glossary	580
	Index	586