
Contents

Part I Introduction

Chapter 1 Introduction to Wetland Plants

I. Wetlands and Wetland Plants	4
II. What Is a Wetland Plant?	5
III. Types of Wetland Plants	7
A. Emergent Plants	7
B. Submerged Plants	12
C. Floating-Leaved Plants.....	13
D. Floating Plants.....	14
IV. Wetland Plant Distribution	16
V. The Evolution of Wetland Plants	17
A. Changes in Angiosperm Classification and Phylogeny	17
B. Evolutionary Processes in Wetland Plants.....	20
VI. Threats to Wetland Plant Species	20
A. Hydrologic Alterations.....	21
B. Exotic Species.....	21
C. Impacts of Global Change	22
D. Threatened and Endangered Species	23
Summary.....	27

Chapter 2 Wetland Plant Communities

I. Wetland Plant Habitats	29
II. Wetland Definitions and Functions	29
A. Ecological Definition	30
B. Legal Definitions	30
1. U.S. Army Corps of Engineers' Definition	30
2. U.S. Fish and Wildlife Classification of Wetlands	31
3. International Definition	31
C. Functions of Wetlands	32
1. Hydrology	32
a. Groundwater Supply	33
b. Flood Control.....	33
c. Erosion and Shoreline Damage Reduction	33
2. Biogeochemistry	33
3. Habitat	34
a. Wildlife and Fish Habitat.....	34

b. Plant Habitat	34
III. Broad Types of Wetland Plant Communities	34
A. Marshes	36
1. Coastal Marshes	36
a. Salt Marshes	36
b. Tidal Freshwater Marshes	39
2. Inland Marshes	39
a. Lacustrine Marshes	41
b. Riverine Marshes	42
c. Depressional Marshes	42
B. Forested Wetlands	44
1. Coastal Forested Wetlands: Mangrove Swamps	44
2. Inland Forested Wetlands	48
a. Southern Bottomland Hardwood	48
b. Northeastern Floodplain	49
c. Western Riparian Zones	50
d. Cypress Swamps	51
C. Peatlands	52
Summary	59

Chapter 3 The Physical Environment of Wetland Plants

I. An Introduction to the Wetland Environment	61
II. The Hydrology of Wetlands	61
A. Hydroperiod and the Hydrologic Budget	62
1. Transpiration and Evaporation	64
2. Measuring Transpiration and Evaporation	65
B. The Effects of Hydrology on Wetland Plant Communities	67
1. Hydrology and Primary Productivity	67
2. Hydrologic Controls on Wetland Plant Distribution	69
3. The Effects of Water Level Fluctuation on Wetland Plant Diversity	70
4. Riparian Wetland Vegetation and Stream Flow	72
C. Hydrological and Mineral Interactions and Their Effect on Species Distribution	72
III. Growth Conditions in Wetlands	74
A. Anaerobic Sediments	74
1. Reduced Forms of Elements	75
a. Nitrogen	75
b. Manganese	76
c. Iron	77
d. Sulfur	77
e. Carbon	78
2. Nutrient Availability under Reduced Conditions	78
3. The Presence of Toxins under Reduced Conditions	79
B. Substrate Conditions in Saltwater Wetlands	79
C. Substrate Conditions in Nutrient-Poor Peatlands	80
D. Growth Conditions for Submerged Plants	81
1. Light Availability	81

2. Carbon Dioxide Availability	83
Summary.....	83

Part II Wetland Plants: Adaptations and Reproduction

Chapter 4 Adaptations to Growth Conditions in Wetlands	
I. Introduction	87
A. Aerobic Respiration and Anaerobic Metabolism	87
B. Upland Plant Responses to Flooding	88
II. Adaptations to Hypoxia and Anoxia	88
A. Structural Adaptations.....	88
1. Aerenchyma	88
a. Aerenchyma Formation	89
b. Aerenchyma Function	91
2. Root Adaptations	91
a. Adventitious Roots.....	91
b. Shallow Rooting	93
c. Pneumatophores	93
d. Prop Roots and Drop Roots.....	95
3. Stem Adaptations	95
a. Rapid Underwater Shoot Extension.....	95
b. Hypertrophy	96
c. Stem Buoyancy	96
4. Gas Transport Mechanisms in Wetland Plants	97
a. Passive Molecular Diffusion	97
b. Pressurized Ventilation	97
c. Underwater Gas Exchange	101
d. Venturi-Induced Convection.....	101
5. Radial Oxygen Loss	102
6. Avoidance of Anoxia in Time and Space	104
7. Development of Carbohydrate Storage Structures	104
B. Metabolic Processes.....	104
1. Anaerobic Metabolism and the Pasteur Effect	106
2. Hypotheses Concerning Metabolic Responses to Anaerobiosis	106
a. McManmon and Crawford's Hypotheses.....	106
b. Davies' Hypothesis.....	108
3. Other Metabolic Responses to Anoxia	109
III. Adaptations in Saltwater Wetlands	110
A. Adaptations to High Salt Concentrations.....	110
1. Water Acquisition	110
2. Salt Avoidance	111
a. Exclusion.....	111
b. Secretion	111
c. Shedding.....	113

d. Succulence	113
B. Adaptations to High Sulfide Levels	113
IV. Adaptations to Limited Nutrients	114
A. Mycorrhizal Associations	114
B. Nitrogen Fixation	116
C. Carnivory	117
1. Habitat and Range of Carnivorous Plants	117
2. Types of Traps	118
a. Pitfall Trap	118
b. Lobster Pot Trap	119
c. Passive Adhesive Trap	120
d. Active Adhesive Trap	122
e. Bladder Trap	123
f. Snap-Trap	124
3. Benefits and Costs of Carnivory	126
D. Nutrient Translocation	126
E. Evergreen Leaves	127
V. Adaptations to Submergence	127
A. Submerged Plant Adaptations to Limited Light	127
B. Submerged Plant Adaptations to Limited Carbon Dioxide	129
1. Use of Bicarbonate	129
2. Aquatic Acid Metabolism	130
3. Lacunal Transport	131
4. Sediment-Derived CO ₂	131
C. Adaptations to Fluctuating Water Levels	131
VI. Adaptations to Herbivory	134
A. Chemical Defenses	135
B. Structural Defenses	135
VII. Adaptations to Water Shortages	136
Summary	138
Case Studies	139
4.A. Factors Controlling the Growth Form of <i>Spartina alterniflora</i>	139
4.B. Carnivory in <i>Sarracenia purpurea</i> (Northern Pitcher Plant)	142

Chapter 5 Reproduction of Wetland Angiosperms

I. Introduction	147
A. A Brief Review of Floral Structures Involved in Reproduction	147
B. Challenges to Sexual Reproduction in Wetland Habitats	148
II. Sexual Reproduction of Wetland Angiosperms	150
A. Pollination Mechanisms	150
1. Insect Pollination	150
2. Wind Pollination	152
3. Water Pollination	154
a. Planes of Water Pollination	155
b. Hydrophilous Pollen Adaptations	162
c. Hydrophilous Stigma Adaptations	163
d. The Evolution of Hydrophily	164
4. Self-Pollination	166
B. Fruits and Seeds	167

1. Types of Fruits Produced by Wetland Plants	167
2. Seed and Fruit Dispersal	171
3. Seed Dormancy and Germination	173
C. Seedling Adaptations	175
1. Seedling Dispersal and Establishment	175
2. Vivipary	176
III. Asexual Reproduction in Wetland Angiosperms	177
A. Structures and Mechanisms of Cloning.....	178
1. Shoot Fragments	178
2. Modified Buds	180
a. Turions	180
b. Pseudoviviparous Buds	182
c. Gemmiparous Buds	183
3. Modified Stems	183
a. Layers	183
b. Runners	184
c. Stolons	184
d. Rhizomes	184
e. Stem Tubers	184
4. Modified Shoot Bases	185
a. Bulbs	185
b. Corms	185
5. Modified Roots	185
a. Creeping Roots	185
b. Tap Roots	185
c. Root Tubers.....	185
B. Occurrence and Success of Cloning among Wetland Plants.....	186
Summary.....	188

Part III Wetland Plant Communities: Function, Dynamics, Disturbance

Chapter 6 The Primary Productivity of Wetland Plants

I. Introduction	191
A. Definition of Terms.....	191
1. Standing Crop	191
2. Biomass	192
3. Peak Biomass	193
4. Primary Production	193
5. Respiration	194
6. Primary Productivity	195
a. Gross Primary Productivity	195
b. Net Primary Productivity	195
7. Turnover	195
8. P/B Ratio	196
B. Reasons for Measuring Wetland Primary Productivity.....	196

1. To Quantify an Ecosystem Function	196
2. To Make Comparisons within a Wetland	196
3. To Make Comparisons among Wetlands	197
4. To Determine Forcing Functions and Limiting Factors of Primary Productivity	197
II. Methods for the Measurement of Primary Productivity in Wetlands	197
A. Phytoplankton	199
1. Dissolved Oxygen Concentration	199
a. Diurnal Dissolved Oxygen Method	199
b. Light Bottle/Dark Bottle Dissolved Oxygen Method	200
2. Carbon Assimilation: The ^{14}C Method	201
B. Periphyton	202
C. Submerged Macrophytes	204
1. Biomass	204
2. Oxygen Production	204
3. Carbon Assimilation	205
D. Emergent Macrophytes	205
1. Aboveground Biomass of Emergent Plants	205
a. The Peak Biomass Method	210
b. The Milner and Hughes Method	211
c. The Valiela et al. Method	212
d. The Smalley Method	213
e. The Wiegert and Evans Method	213
f. The Lomnicki et al. Method	215
g. The Allen Curve Method	216
h. The Summed Shoot Maximum Method	219
2. Belowground Biomass of Emergent Wetland Plants	219
a. Harvest Method	220
b. Decomposition Method	220
E. Floating and Floating-Leaved Plants	220
F. Trees	221
1. Measures of Dimension Analysis	221
a. Diameter at Breast Height	221
b. Height	222
2. Parameters Based on Dimension Analysis	222
a. Basal Area	222
b. Basal Area Increment	223
3. Calculations of NPP of Trees	223
a. Stem Production	223
b. Leaf Production	224
c. Branch Production	224
d. Root Production	224
4. Community Primary Productivity of Forested Wetlands	225
G. Shrubs	225
H. Moss	226
Summary	227
Case Studies	228
6.A. Salt Marsh Productivity: The Effect of Hydrological Alterations in Three Sites in San Diego County, California	228

6.B. Mangrove Productivity: Laguna de Terminos, Mexico.	230
6.C. Peatland Productivity: Forested Bogs of Northern Minnesota	232

Chapter 7 Community Dynamics in Wetlands

I. An Introduction to Community Dynamics	237
II. Ecological Succession	237
A. Holistic and Individualistic Approaches to Ecological Succession	238
B. The Replacement of Species	239
C. Developing and Mature Ecosystems	240
III. Ecological Succession in Wetlands	241
A. Models of Succession in Wetlands	241
1. Hydrarch Succession	241
2. Succession in Coastal Wetlands	246
3. The Environmental Sieve Model	248
B. The Role of Seed Banks in Wetland Succession.	250
1. The Relationship of the Seed Bank to the Existing Plant Community	250
2. Factors Affecting Recruitment from the Seed Bank	253
IV. Competition and Community Dynamics	253
A. Intraspecific Competition	254
B. Interspecific Competition	255
1. Competition and Physiological Adaptations	256
2. Competition and Life History Characteristics	257
3. Resource Availability and Competitive Outcome	261
4. Light in Submerged Communities	262
5. Light in Emergent Communities.	263
6. Competition and Salt Marsh Communities	263
C. Allelopathy	265
V. The Role of Disturbance in Community Dynamics	266
A. Hydrologic Disturbances	266
B. Severe Weather	269
1. Floods	269
2. Hurricanes	270
C. Fire	270
D. Biotic Disturbance	271
E. Human-Induced Disturbance	272
Summary	273
Case Studies	275
7.A. Successional Processes in Deltaic Lobes of the Mississippi River	275
7.B. Eutrophication of the Florida Everglades: Changing the Balance of Competition	276

Chapter 8 Invasive Plants in Wetlands

I. Characterization of Invasive Plants	279
II. The Extent of Exotic Invasions in Wetland Communities	282
III. Implications of Invasive Plant Infestations in Wetlands	284
A. Changes in Community Structure	284
B. Changes in Ecosystem Functions	286
C. Effects on Human Endeavors	287
IV. The Control of Invasive Plants in Wetlands	288

A. Habitat Alterations	288
1. Shading the Water's Surface	288
2. Shading the Sediment Surface	289
3. Dredging Sediments	289
4. Altering Hydrology	289
B. Mechanical Controls	290
C. Chemical Controls	294
D. Biological Controls	296
1. Insects	297
2. Fish	298
3. Pathogens	298
4. Fungi	299
5. Other Organisms	299
V. Case Studies of Invasive Plants in Wetland Communities	299
A. <i>Myriophyllum spicatum</i> (Eurasian Watermilfoil)	299
1. Biology	299
2. Origin and Extent	300
3. Effects in New Range	301
4. Control	301
5. The Natural Decline of Some <i>Myriophyllum spicatum</i> Populations	302
B. <i>Hydrilla verticillata</i> (Hydrilla)	303
1. Biology	303
2. Origin and Extent	304
3. Effects in New Range	305
4. Control	305
C. <i>Eichhornia crassipes</i> (Water Hyacinth)	306
1. Biology	306
2. Origin and Extent	307
3. Effects in New Range	308
4. Control	309
D. <i>Lythrum salicaria</i> (Purple Loosestrife)	310
1. Biology	310
2. Origin and Extent	310
3. Effects in New Range	312
4. Control	313
E. <i>Phragmites australis</i> (Common Reed)	313
1. <i>Phragmites australis</i> as an Invasive Species in North America	313
a. Biology	315
b. Origin and Extent	315
c. Effects on the Habitat	316
d. Control	317
2. <i>Phragmites australis</i> as a Declining Species in Europe	317
a. Extent of the Problem	317
b. Causes of the Decline	319
c. Solutions to the <i>Phragmites australis</i> Decline	319
Summary	321

Part IV Applications of Wetland Plant Studies

Chapter 9 Wetland Plants in Restored and Constructed Wetlands

I. Wetland Restoration and Creation	326
A. The Development of Plant Communities in Restored and Created Wetlands	327
1. Environmental Conditions	327
2. Self-Design and Designer Approaches	329
3. Seed Banks in Restored Wetlands	331
B. Planting Recommendations for Restoration and Creation Projects	332
II. Treatment Wetlands	333
A. Removal of Wastewater Contaminants	336
1. Nitrogen Removal	336
2. Phosphorus Retention	337
a. Biotic Uptake of Phosphorus	337
b. Sorption onto Soil Particles	337
c. Accretion of Wetland Soils	338
3. Pathogen Removal	338
4. Metal Removal	339
a. Plant Uptake of Metals	340
b. Phytoremediation	340
B. The Role of Vascular Plants in High-Nutrient Load Treatment Wetlands	341
1. Vegetation as a Growth Surface and Carbon Source for Microbes	341
2. Physical Effects of Vegetation	343
3. Nutrient Uptake	343
a. Tissue Nutrient Content of Wetland Plants	346
b. Factors Affecting Nutrient Uptake	347
c. The Accretion of Organic Sediments	347
4. Vegetation as a Source of Rhizospheric Oxygen	348
5. Wildlife Habitat and Public Recreation	349
C. Species Commonly Used in Treatment Wetlands	350
D. The Establishment and Management of Plants in Wastewater Treatment Wetlands	354
Summary	355
Case Studies	356
9.A. Integrating Wetland Restoration with Human Uses of Wetland Resources	356
9.B. Restoring the Habitat of an Endangered Bird in Southern California	359
9.C. Vegetation Patterns in Restored Prairie Potholes	360

Chapter 10 Wetland Plants as Biological Indicators

I. Introduction	363
II. Wetland Plants as Indicators of Wetland Boundaries	363
A. Hydrophytic Vegetation as a Basis for Delineation	368
B. Wetland Boundaries and Wetland Functions	369
C. The Use of Remotely Sensed Data in Wetland Identification and Classification	370
III. Wetland Plants as Indicators of Ecological Integrity	371

A. An Operational Definition of Ecological Integrity	372
B. Wetland Plant Community Composition as a Basis for Indicator Development	374
C. General Framework for Wetland Biological Indicator Development	375
D. Vegetation-Based Indicators	377
E. The Floristic Quality Assessment Index for Wetland Assessment	378
F. Using Biological Indicators to Assess Risk	382
Summary	383
Case Study	384
10.A. The Development of a Vegetation IBI	384
 References	 389
 Index	 439