

Contents

1	Introduction	1
	References	5
Part I Molecular Stress Physiology		
2	General Themes of Molecular Stress Physiology	9
2.1	Definitions and Concepts	10
2.1.1	Stress	10
2.1.2	Quantification of Stress	14
2.1.3	Escape–Resistance–Avoidance–Tolerance	19
2.1.4	Stress Responses–Acclimation–Adaptation	20
2.1.5	Filters Determining Species Distribution	22
2.2	Activation of Stress Tolerance and Avoidance Mechanisms	22
2.2.1	Stress Sensing and Signal Transduction	25
2.2.2	Transcriptional Control	27
2.2.3	Oxidative Stress	28
2.2.4	Long-Distance Stress Signalling	31
2.2.5	The Model System <i>Arabidopsis thaliana</i>	33
2.3	Stress and Growth Regulation	35
2.4	Molecular Basis of Escape and Anticipation of Stress	37
2.4.1	Circadian Rhythms	38
2.4.2	Anticipation of Seasonal Changes in Environmental Conditions	40
2.4.3	Developmental Switches Triggered by Favourable Conditions	47
2.4.4	Trans-Generational Stress Memory	49
	Summary	50
	References	53
3	Light	57
3.1	The Dual Significance of Light	58
3.2	Visible Light	59
3.2.1	Avoidance of Light Stress and Permanent or Dynamic Acclimation	59
3.2.2	Overexcitation and Damage to Photosynthetic Membranes	65

3.2.3	Flexible Acclimation to Changes in Light Intensity ..	66
3.2.4	Continuous Light	74
3.2.5	Light Triggers Plant Adaptation and Acclimation to the Environment.....	74
3.3	UV-B Radiation	78
3.3.1	Ranges of Ultraviolet Radiation and Biological Activity	78
3.3.2	Ultraviolet-B Damage and Repair Mechanisms	80
3.3.3	Avoidance of Ultraviolet-B-Induced Stress	81
3.3.4	Ultraviolet-B Perception and Signalling	83
3.3.5	Crosstalk Between Ultraviolet-B and Visible Light Responses.....	85
	Summary.....	86
	References.....	88
4	Temperature	91
4.1	The Temperature Challenge.....	92
4.1.1	Temperature Dependence of Life.....	92
4.1.2	Plants as Poikilothermic Organisms	92
4.1.3	Variations in Temperature Range.....	97
4.1.4	Strategies to Cope with Temperature Fluctuations and Temperature Extremes.....	105
4.2	Cold Acclimation and Freezing Tolerance.....	105
4.2.1	Adjustment of Membrane Fluidity.....	106
4.2.2	Prevention of Photoinhibition	109
4.2.3	Cryoprotective Proteins	109
4.2.4	Control of Ice Formation	110
4.2.5	Signalling Networks Involved in Cold Acclimation	117
4.2.6	Freezing Avoidance and Freezing Tolerance in Tropical High Mountain Plants	120
4.3	Heat Stress	122
4.3.1	Heat Stress Avoidance	124
4.3.2	Acquired Thermotolerance	124
4.3.3	The Heat Shock Response	126
4.4	Temperature Sensing	131
4.4.1	Sensing of Extreme Temperatures	133
4.4.2	Sensing of Ambient Temperature Changes	134
	Summary.....	135
	References.....	139
5	Oxygen Deficiency.....	143
5.1	Conditions of Flooded Soil	144
5.2	Hypoxia-Induced Damage: Energy Metabolism of Plants Under Oxygen Deficiency.....	146
5.3	Natural Variation in the Ability to Endure Inundation by Water.....	147
5.4	Adaptations to Flooding-Prone Habitats	149
5.4.1	Anatomical–Morphological Adaptations and Modifications.....	149

5.4.2	Biochemical Modifications	152
5.5	Sensing of Flooding and Ensuing Signal Transduction	155
5.5.1	Ethylene Signal Transduction	155
5.5.2	Oxygen Sensing	157
5.6	Regulation of Avoidance and Tolerance Strategies	157
	Summary	162
	References	163
6	Water Deficiency (Drought)	165
6.1	The Properties of Water	166
6.2	Water Acquisition and Movement: Cellular Aspects	168
6.2.1	The Water Potential	169
6.2.2	Facilitation of Intercellular and Intracellular Water Flow: Aquaporins	170
6.3	Drought Stress Responses: Avoidance and Tolerance	172
6.3.1	Control of the Osmotic Potential	175
6.3.2	Protective Proteins	177
6.3.3	Regulation of the Stomatal Aperture	180
6.4	Acclimation of Growth	183
6.4.1	Inhibition of Shoot Growth	184
6.4.2	Stimulation of Root Growth	186
6.5	Sensing of Water Status and Signal Transduction	186
6.5.1	Sensing of Water Status	187
6.5.2	ABA Signal Transduction	188
6.5.3	ABA-Independent Signalling	190
6.6	Photosynthesis Variants with Improved Water Use Efficiency	190
6.6.1	C ₄ Photosynthesis	190
6.6.2	Evolution of C ₄ Photosynthesis	192
6.6.3	Crassulacean Acid Metabolism	194
6.6.4	Evolution of Crassulacean Acid Metabolism Photosynthesis	198
	Summary	198
	References	201
7	Adverse Soil Mineral Availability	203
7.1	Mineral Nutrients	204
7.2	The Mineral Nutrition Challenge	206
7.2.1	Elements in the Soil	207
7.2.2	Element Toxicity	208
7.3	Nutrient Acquisition and Responses to Nutrient Scarcity	209
7.3.1	Modulation of Nutrient Availability	209
7.3.2	Cellular Ion Transport Mechanisms	212
7.3.3	Modulation of Nutrient Uptake in Response to Deficiency	218
7.3.4	Intracellular Transport and Cellular Aspects of Long-Distance Transport	220
7.3.5	Plasticity of Root Architecture and Responses to Nutrient Deficiency	222
7.3.6	Sensing of Nutrient Availability and Nutrient Status	224

7.4	Nutrient Acquisition Symbioses	224
7.4.1	Mycorrhizae.....	225
7.4.2	Nitrogen Fixation.....	227
7.4.3	The Common Sym Pathway	229
7.5	Responses to Element Toxicity and Tolerance Mechanisms	230
7.5.1	Essential Metal Toxicity and Tolerance.....	231
7.5.2	Metal Hyperaccumulators as Models for Adaptation to Extreme Environments.....	233
7.5.3	Sodium Toxicity.....	237
7.5.4	Aluminium Toxicity and Tolerance	246
7.5.5	Non-Essential Toxic Metals.....	249
	Summary.....	250
	References.....	254
8	Biotic Stress	257
8.1	Plant Disease Caused by Pathogens.....	258
8.1.1	Types of Pathogens: Viruses, Bacteria, Fungi, Oomycetes and Nematodes	259
8.1.2	Pathogenicity Mechanisms	260
8.2	Plant Defences Against Microbial Pathogens and Viruses.....	263
8.2.1	Preformed Defences Against Bacteria, Fungi and Oomycetes	264
8.2.2	Inducible Local Defences	266
8.2.3	Inducible Systemic Resistance.....	272
8.2.4	Defence Against Viruses via Gene Silencing.....	274
8.3	Herbivory	276
8.3.1	Constitutive Defences	277
8.3.2	Inducible Defences Against Herbivores.....	282
8.3.3	How Plant–Herbivore Interactions Drive Genetic Diversity.....	287
8.4	Parasitic Plants.....	290
8.5	Allelopathy.....	293
	Summary.....	294
	References.....	297

Part II Physiological and Biophysical Plant Ecology

9	Thermal Balance of Plants and Plant Communities	303
9.1	Energy Balance of the Atmospheric Boundary Layer	304
9.2	Microclimate Near the Ground Surface.....	312
9.2.1	Daily Changes in Temperature Near the Ground.....	312
9.2.2	Modification of Environmental Radiation and Temperature by Abiotic Factors.....	313

9.2.3	Modification of the Radiation Budget and Temperature by Biotic Factors	314
9.3	Energy Balance of Leaves	319
9.4	Acclimation and Adaptation to Temperature Extremes.....	321
9.4.1	Acclimation and Adaptation to High Temperatures	322
9.4.2	Acclimation and Adaptation to Low Temperatures ..	325
	Summary.....	326
	References.....	327
10	Water Relations.....	329
10.1	Water as an Environmental Factor.....	330
10.1.1	Water Use by Plants and Animals	330
10.1.2	Availability of Water on Earth	332
10.1.3	Drivers of Water Flow Between the Soil and the Atmosphere	335
10.2	Water Transport from the Soil to the Plant	339
10.2.1	Water Uptake	339
10.2.2	Xylem Water Transport	347
10.2.3	Phloem Water Transport.....	353
10.3	Transpiration	356
10.3.1	Stomatal Responses to Plant-Internal Factors	359
10.3.2	Stomatal Responses to Environmental Factors ..	360
	Summary.....	362
	References.....	363
11	Nutrient Relations.....	367
11.1	Availability of Soil Nutrients and Ion Use.....	368
11.1.1	Plant Nutrients	368
11.1.2	Availability of Nutrients in Soil.....	368
11.1.3	General Aspects of Plant Nutrition	371
11.1.4	Nutrient Deficiency and Excess.....	377
11.2	Nitrogen Nutrition	379
11.2.1	Nitrogen in Plant Metabolism	379
11.2.2	Nitrogen Uptake and Nutrition	379
11.2.3	Nitrogen Requirements for Growth.....	383
11.2.4	Nitrogen Storage	385
11.2.5	Insectivorous Plants	386
11.2.6	Nitrogen Deficiency and Excess	387
11.3	Sulphur Nutrition	387
11.3.1	Sulphur in Plant Metabolism	387
11.3.2	Sulphur Uptake and Plant Requirements.....	389
11.3.3	Indicators of Sulphur Deficiency and Excess ..	389
11.4	Phosphate Nutrition	390
11.4.1	Phosphorus in Plant Metabolism	390
11.4.2	Phosphate Uptake and Plant Requirements	390
11.4.3	Indicators of Phosphorus Deficiency and Excess ..	391

11.5	Alkaline Cation Nutrition	391
11.5.1	Magnesium.....	391
11.5.2	Calcium	393
11.5.3	Potassium.....	394
	Summary.....	396
	References.....	397
12	Carbon Relations	401
12.1	Photosynthetic CO ₂ Uptake: Physiological and Physical Basis.....	402
12.1.1	Photosynthesis as a Diffusion Process.....	402
12.1.2	Evolution of C ₃ , C ₄ and Crassulacean Acid Metabolism Plant Species	405
12.2	Photosynthesis Models and Calculation of ¹³ C/ ¹² C Fluxes (Contribution by A. Arneth).....	409
12.2.1	RubisCO-Limited or RuBP-Saturated Rate (A _v) ...	409
12.2.2	RuBP Regeneration-Dependent and Electron Transport-Limiting Rate (A _j).....	410
12.2.3	Supply of CO ₂ Through Stomata.....	410
12.2.4	¹³ C/ ¹² C Discrimination	411
12.3	Specific Leaf Area, Nitrogen Concentrations and Photosynthetic Capacity	412
12.3.1	Specific Leaf Area	412
12.3.2	Maximum Rates of CO ₂ Assimilation	414
12.4	Response of Photosynthesis to Environmental Variables ...	414
12.4.1	Light Response of CO ₂ Assimilation.....	414
12.4.2	Temperature Response of CO ₂ Assimilation	416
12.4.3	Relative Air Humidity Response of CO ₂ Assimilation.....	419
12.4.4	Nutrient Response of CO ₂ Assimilation.....	419
12.4.5	Water Stress Response of CO ₂ Assimilation	419
12.4.6	CO ₂ Response of CO ₂ Assimilation.....	420
12.4.7	Developmental Responses of CO ₂ Assimilation ...	421
12.4.8	Daily Courses of CO ₂ Assimilation and Water Use .	421
12.4.9	Distribution of C ₃ , C ₄ and Crassulacean Acid Metabolism Species in the Course of Earth History	426
12.5	Growth and Storage	428
12.5.1	Whole-Plant Carbon Balance and Biomass Production	428
12.5.2	Respiration.....	429
12.5.3	Growth	430
12.5.4	Storage and Feedback	432
12.6	Carbon and Nitrogen Balance in Different Plant Types....	434
12.6.1	Annual Species.....	435
12.6.2	Biennial Species.....	438
12.6.3	Perennial Herbaceous Plants	440
12.6.4	Woody Plants	442
	Summary.....	448
	References.....	449

Part III Ecosystem Ecology

13 Ecosystem Characteristics	459
13.1 Boundaries and Size of Ecosystems	461
13.2 Components of an Ecosystem	462
13.3 Ecosystem Complexity and Interactions of Processes and Drivers.....	463
13.3.1 Unpredicted Existence of Neighbours.....	463
13.3.2 Scaling up of Processes	464
13.3.3 Response Functions to Interacting Drivers	464
13.3.4 Self-Thinning.....	465
13.4 Concepts of Equilibrium, Resistance and Resilience, Susceptibility and Vulnerability.....	467
13.5 Impacts of Slow Continuous Forcing and Sudden Disturbances.....	468
13.5.1 Slow Continuous Forcing.....	469
13.5.2 Sudden Disturbances and Reallocation of Pools	469
13.5.3 Sudden Disturbances and Loss of Pools	471
13.5.4 Impacts on Species Composition.....	472
13.6 Ecosystem Budget Approach.....	475
13.6.1 Stand Growth	476
13.6.2 Mean Residence Times	476
13.6.3 Loss of Resources	477
Summary.....	479
References.....	479
14 Approaches to Study Terrestrial Ecosystems	481
14.1 Observations.....	483
14.1.1 Whole-Ecosystem Observations	484
14.1.2 Transects and Chronosequences	488
14.1.3 Grid-Based Inventories	490
14.1.4 Remote Sensing	491
14.1.5 “Natural Experiments”.....	493
14.2 Experiments	494
14.2.1 Manipulations of Pools and Processes.....	494
14.2.2 Manipulations of Environmental Conditions.....	496
14.2.3 Manipulations of Biodiversity	500
14.2.4 Manipulations of Management and Changes in Land Cover.....	502
14.2.5 Artificial Ecosystems	505
Summary.....	507
References.....	508
15 Approaches to Model Processes at the Ecosystem Level (Contribution by C. Sierra)	513
15.1 Classification of Ecosystem Models	514
15.1.1 Model Dichotomies	514
15.1.2 Model Classes	515
15.2 Basic Approach to Model Development	515
15.3 General Ecosystem Carbon Model	517

15.3.1	Carbon Uptake: $U(t)$	517
15.3.2	Carbon Allocation: b	518
15.3.3	Cycling Rates in Ecosystem Pools: C	518
15.3.4	Transfers and Transformations of Organic Material: A	518
15.3.5	Environmental Effects on Cycling Rates: $\xi(t)$	519
15.4	Examples of Ecosystem Carbon Models	519
15.4.1	Simple Vegetation–Soil Model	519
15.4.2	Eight-Pool Model of Luo and Weng (2011)	520
15.5	Properties of Ecosystem Carbon Models.....	523
15.5.1	Role of Inputs and Cycling Rates on Ecosystem Carbon Storage.....	523
15.5.2	Residence and Response Times	523
15.5.3	Disturbance Effects	524
	Summary	525
	References.....	526
16	Biogeochemical Fluxes in Terrestrial Ecosystems	529
16.1	Water Fluxes in Terrestrial Ecosystems	530
16.1.1	Water Budget at Ecosystem Scale	530
16.1.2	Water Uptake of Trees	533
16.1.3	Evapotranspiration at Canopy and Ecosystem Scales	535
16.1.4	Imposed and Equilibrium Evapotranspiration of Leaves and Canopies	540
16.1.5	Responses of Terrestrial Ecosystems to Drought... .	544
16.2	Carbon Fluxes in Terrestrial Ecosystems.....	545
16.2.1	Carbon Pools and Fluxes in Terrestrial Ecosystems.....	545
16.2.2	Decomposition and Stabilisation of Organic Matter in Terrestrial Ecosystems	550
16.2.3	Net Ecosystem Production and Net Biome Production	555
16.2.4	Fluxes of CH_4 and Other Biogenic Volatile Organic Compounds	560
16.3	Nitrogen Fluxes in Terrestrial Ecosystems	562
16.4	Cation Fluxes in Terrestrial Ecosystems	567
	Summary	571
	References.....	573

Part IV Community Ecology and Biological Diversity

17	Development of Plant Communities in Time	583
17.1	Introduction	584
17.2	Development of Plants during Life History on Earth	584
17.2.1	History of Vegetation to the End of the Tertiary ...	585
17.2.2	Change of Climate and Vegetation in Pleistocene ..	588
17.2.3	Late and Postglacial Climate and Vegetation History	589

17.2.4	Changes in Vegetation Owing to Human Influence .	596
17.2.5	Classification of Anthropogenic Influences and Their Consequences for Vegetation.....	612
17.2.6	Anthropogenic Influences on Vegetation in Mediterranean, Saharan and Tropical Environments	614
17.3	General Vegetation Dynamics	621
17.3.1	Short-Term and Seasonal Vegetation Dynamics ..	622
17.3.2	Long-Term Vegetation Dynamics	627
17.3.3	Vegetation Dynamics and Strategy Models.....	641
17.3.4	Vegetation Dynamics and Influence of Animals ..	647
17.3.5	Further Aspects for Understanding Vegetation Dynamics	648
17.4	Ecological Stability of Plant Communities and Disturbances.....	649
	Summary.....	650
	References.....	652
18	Spatial Distribution of Plants and Plant Communities	657
18.1	Introduction	658
18.2	Plant Dispersal	658
18.2.1	Traits and Vectors.....	659
18.2.2	Effectiveness of Dispersal Mechanisms.....	662
18.2.3	Propagule Bank and Seedling Establishment	664
18.2.4	Distribution Patterns	666
18.3	Vegetation Geography	667
18.3.1	Characterisation and Interpretation of Areas	667
18.3.2	Area Types-Floristic Elements-Plant Kingdoms ..	672
18.4	Species-Area Relationships.....	674
18.4.1	Equilibrium Theory of Island Biogeography.....	676
18.4.2	“Oceanic” and “Mainland” Islands	680
18.4.3	More Models of Island Biogeography Related to the Number of Species and Area	682
18.5	Problems of Pattern and Scale	684
	Summary.....	686
	References.....	686
19	Interactions Between Plants, Plant Communities and the Abiotic and Biotic Environment	689
19.1	Introduction	690
19.2	Influences of Vegetation on Site Conditions	690
19.2.1	Influences of Vegetation on Climatic Conditions..	691
19.2.2	Influences of Vegetation on Weathering and Topography	694
19.2.3	Influences of Vegetation on Soils.....	695
19.3	Interactions Among Plants (Contribution by C. F. Dormann).....	696
19.3.1	Positive and Neutral Plant-Plant Interactions	696
19.3.2	Competition and Coexistence	700
19.3.3	Competition and Its Consequences for Plant Community Structure and Diversity	709

19.3.4	Relevance of Plant–Plant Interactions for Practical Applications	711
19.4	Interactions Between Plants and Animals (Contribution by H. M. Schaefer)	714
19.4.1	Classification of Plant–Animal Interactions	717
19.4.2	Evolutionary History of Biological Interactions	718
19.4.3	Herbivory	722
19.4.4	Carnivory	727
19.4.5	Pollination	728
19.4.6	Seed Dispersal By Animals	733
19.4.7	Mycorrhizal Symbiosis	735
19.4.8	Influences of Abiotic Environment on Plant–Animal Interactions	736
	Summary	737
	References	738
20	Biodiversity	743
20.1	Introduction	744
20.2	Various Facets of Biodiversity	745
20.2.1	Compositional Diversity	746
20.2.2	Structural Diversity	754
20.2.3	Functional Diversity	756
20.2.4	Phylogenetic Diversity	763
20.3	Environmental Controls of Biodiversity	765
20.3.1	Latitudinal Gradients	767
20.3.2	Environmental Heterogeneity	769
20.3.3	Productivity—Species Richness Relationships	772
20.3.4	Biodiversity, Assembly Rules and Environmental Filters	776
20.4	Biodiversity and Ecosystem Functioning	779
20.4.1	Species Identity and Dominance Effects on Ecosystem Processes	781
20.4.2	Biodiversity Effects on Biomass Production	783
20.4.3	Biodiversity Effects on Other Ecosystem Functions	792
20.4.4	Biodiversity Effects on Other Trophic Levels	794
20.4.5	Biodiversity and Multifunctionality	795
20.4.6	Different Metrics of Biodiversity Affecting Ecosystem Functioning	797
20.4.7	Context Dependency of Biodiversity Effects on Ecosystems	798
20.4.8	Plant Biodiversity and the Stability of Ecosystem Functioning	801
20.4.9	Mechanisms Underlying Biodiversity–Ecosystem Functioning Relationships	802
20.4.10	Value of Biodiversity–Ecosystem Functioning Research	811
	Summary	814
	References	815

Part V Global Ecology

21 Global Biogeochemical Cycles	827
21.1 Distribution of Global Terrestrial Ecosystems	828
21.2 Global Biogeochemical Cycles	828
21.2.1 Global Carbon Cycle	831
21.2.2 Global Water Cycle	833
21.2.3 Global Nitrogen Cycle	836
21.2.4 Global Sulphur Cycle	837
21.3 Ecosystem Services	838
Summary	840
References	840
22 Dynamic Global Vegetation Models (Contribution by S. Zaehle)	843
22.1 Anatomy of a DGVM	844
22.2 Biogeochemical Cycling	846
22.2.1 Plant Carbon Assimilation	846
22.2.2 Plant Growth	847
22.2.3 Decay of Litter and Soil Organic Matter	848
22.2.4 Hydrological Cycle	848
22.2.5 Nutrient Cycles	848
22.3 Biogeography	849
22.3.1 Concept of Plant Functional Types in Models	849
22.3.2 Scaling from Plant to Community	850
22.3.3 Disturbances	851
22.3.4 Anthropogenic Land Use and Disturbance	852
22.4 Evaluating DGVMs	852
22.4.1 Ecosystem Gas Exchange Measurements	852
22.4.2 NPP and Inventories	854
22.4.3 Remotely Sensed Vegetation Greenness	854
22.4.4 Atmospheric CO ₂ Monitoring	854
22.4.5 Ecosystem Manipulation Experiments	855
22.5 Applications of DGVMs	856
22.6 Conclusions and Outlook	857
Summary	858
References	858
23 Global Change and Terrestrial Ecosystems	865
23.1 Global Change	866
23.2 Land Use and Land-Use Change	868
23.2.1 Agriculture and Forestry	869
23.2.2 Consequences of Land Use on Biogeochemical Pools and Fluxes	870
23.3 Climate Change	876
23.3.1 Changes in Atmospheric Conditions	876
23.3.2 Responses of Terrestrial Ecosystems to Climate Change	882
23.3.3 Feedbacks of Terrestrial Ecosystems to Climate	885

23.4 Changes in Biodiversity	887
23.5 Global Agreements to Address Global Ecological Challenges	891
23.5.1 Biological Diversity	891
23.5.2 Climate Change	893
Summary	894
References	895
Species Index.....	901
Subject Index.....	909