

Contents

1	Constraints on the Form and Function of Root Systems . .	1
	D. ROBINSON, A. HODGE and A. FITTER	
1.1	Introduction	1
1.2	Problems Associated with Life in Soil	2
1.2.1	Physical Problems	2
1.2.2	Chemical Reactivity	3
1.2.3	Biological Activity	3
1.2.4	Heterogeneity	4
1.3	Evolutionary Solutions	4
1.3.1	Penetration of Soil Pores	5
1.3.2	Heterotrophy	5
1.3.3	Hierarchical Branching	5
1.3.4	Long-Distance Transport	8
1.3.5	Maintenance Costs	8
1.3.6	Dehydration Risk	9
1.3.7	Compensation for Unpredictable Water and Nutrient Supplies	10
1.3.8	Conflicting Design Requirements	10
1.4	Emergent Properties	11
1.4.1	Topology	11
1.4.2	Size	15
1.4.3	Depth	19
1.4.4	Anchorage	20
1.4.5	Rhizosphere	21
1.4.6	Mycorrhizas	23
1.4.7	Specialised Morphologies	24
1.4.8	Global-Scale Processes	25
1.5	Concluding Remarks	26
	References	27

2	Distribution of Roots in Soil, and Root Foraging Activity	33
	M.J. HUTCHINGS and E.A. JOHN	
2.1	Introduction	33
2.2	Plant Rooting Patterns in the Vertical and Horizontal Dimensions	35
2.3	Segregation of Root Systems	40
2.3.1	Segregation of Root Systems in the Vertical Dimension	40
2.3.2	Segregation of Root Systems in the Horizontal Dimension	42
2.4	Foraging by Roots	44
2.4.1	Root Foraging Responses to Spatial Heterogeneity in Availability of Soil-Based Resources	45
2.4.2	Morphological vs. Physiological Plasticity: Responses to Total Resource Supply and to the Spatial and Temporal Patterns of Resource Provision	49
2.4.3	Patterns of Root Placement in Heterogeneous Environments and Their Consequences	50
2.5	Summary and Prospects	55
	References	56
 3	 Turnover of Root Systems	 61
	W.K. LAUENROTH and R. GILL	
3.1	Introduction	61
3.2	Overview of the Structure of Root Systems	62
3.2.1	Conifers and Woody Dicots	63
3.2.2	Herbaceous Dicots	63
3.2.3	Monocots	64
3.3	Methods of Assessing Root Turnover	64
3.3.1	Direct Estimates of Root System Turnover Coefficients Based on ^{14}C Turnover	65
3.3.2	Indirect Estimates of Root System Turnover Coefficients	66
3.3.2.1	Biomass	66
3.3.2.2	Ingrowth Cores	66
3.3.2.3	Nitrogen Balance	66
3.3.2.4	Minirhizotrons	67
3.4	The Growth, Life Span, and Death of Roots	68
3.4.1	Effects at the Individual Root Level	68
3.4.1.1	Water and Nutrients	68
3.4.1.2	Soil Temperature	69
3.4.1.3	Root Diameter	69
3.4.1.4	Root Symbionts	70

Contents	XI
3.4.1.5 Herbivory	70
3.4.2 Effects at the Whole-Plant Level	70
3.4.2.1 Elevated CO ₂	71
3.4.2.2 Pathogens and Herbivores	72
3.5 Field Estimates of Root Turnover and Net Primary Production	72
3.5.1 Forests	73
3.5.1.1 Temperate	73
3.5.1.2 Boreal	74
3.5.1.3 Tropical	75
3.5.2 Grasslands	75
3.5.2.1 Temperate	75
3.5.2.2 High Latitude	76
3.5.2.3 Tropical	76
3.5.3 Shrublands	77
3.5.3.1 Temperate	77
3.5.3.2 High Latitude	77
3.5.3.3 Tropical	78
3.6 Relationship of Root Turnover to Environmental Factors . .	78
3.7 Summary and Prospects	82
References	83

4 The Control of Carbon Acquisition by and Growth of Roots	91
J.F. FARRAR and D.L. JONES	
4.1 Introduction	91
4.2 Production of Carbohydrate in Source Leaves	92
4.3 Import of Carbohydrates by Roots: the Phloem Path	93
4.4 Import of Carbohydrates by Roots: Phloem Unloading and Short-Distance Transport	94
4.4.1 Fibrous Roots	95
4.4.2 Storage Roots	96
4.4.3 Is There Feedback Control of Import?	96
4.4.4 Are There Plant Growth Substances That Control Import? .	97
4.4.5 Are There Genes That Control Import?	98
4.5 Carbon Fluxes Within Roots and Their Role in Growth and Import	98
4.5.1 Fluxes That Increase C Content	99
4.5.2 Fluxes That Cause Loss of C	99
4.5.3 Turnover and Metabolism Within Roots	100
4.5.3.1 Localisation and Compartmentation	100
4.5.3.2 Size of Pools Relative to Fluxes	101

4.5.3.3	Flux to Structure (Including Maintenance)	101
4.5.3.4	Localisation of Metabolism to Different Cell Types	102
4.6	Exudation	103
4.6.1	How Large Is the Root Exudation C Flux?	103
4.6.2	What Are the Dominant Exudate Components?	104
4.6.3	Localisation of Root Exudation	106
4.6.4	Mechanistic Basis of Root Exudation	106
4.6.4.1	Root Exudation Regulated by C Influx	107
4.6.4.2	Root Exudation Regulated by C Efflux	108
4.6.5	Exudation: Conclusion	109
4.7	Integration of Fluxes	110
4.7.1	Shared Control of Carbon Flux	110
4.7.2	Additional Evidence for Shared Control of Import into Roots	111
4.7.3	Mechanisms Underlying Shared Control of Carbon Flux . .	112
4.7.4	What is Root 'Demand'?	113
4.7.5	The Remarkable Consequences of Darkening	114
4.8	Allocation of C and Dry Weights to Roots Relative to Shoots	115
4.8.1	The Conservation of Shoot/Root Ratio	115
4.8.2	The Case of Phosphate	116
4.8.3	Functional Equilibrium	117
4.9	Summary and Prospects	118
	References	119

5	Hydraulic Properties of Roots	125
	M.T. TYREE	
5.1	Introduction	126
5.2	Root Structure and Possible Pathways of Water Movement .	127
5.3	Driving Forces and the 'Composite Membrane'	130
5.4	Methods of Measuring Hydraulic Conductances	131
5.4.1	Root Chamber Methods	132
5.4.2	Nobel Method	132
5.4.3	Root Pressure Probe Method	134
5.4.4	The High Pressure Flowmeter Method	136
5.5	Distribution of Hydraulic Resistances in Roots	137
5.5.1	Axial Water Flow – Poiseuille's Law	137
5.5.2	Radial Water Flow and Role of Endodermis and Exodermis	138
5.5.3	Experiments to Locate Major Barriers to Water and Solute Flow	138
5.6	Models of Solute and Water Flux in Roots (Possible Reinterpretation of Ideas)	141

5.7	The Problem of Scaling for Root or Plant Size	146
5.8	Summary and Prospects	148
References		149

6	Root Growth and Function in Relation to Soil Structure, Composition, and Strength	151
	A.G. BENGOUGH	

6.1	Introduction	151
6.2	An Introduction to Soil Structure and Some Ways to Quantify It	152
6.3	Root Growth in Bulk Soil	155
6.3.1	Physical Limitations to Root Growth	155
6.3.2	Effects of Soil Strength on Root Growth and Physiology	158
6.3.2.1	Growth of Root Tips in Hard Soil	158
6.3.2.2	Root Branching in Hard Soil	160
6.3.3	Localised Compression of Soil Around Roots	160
6.3.4	Water and Nutrient Uptake	162
6.4	Root Growth in Macropores	163
6.4.1	Root Elongation and Distribution in Macropores	164
6.4.2	Effect of Root Clumping on Water and Nutrient Uptake	165
6.5	Ecological Consequences of Soil Structure and Strength	166
6.6	Summary and Prospects	167
References		168

7	Adaptation of Roots to Drought	173
	W.J. DAVIES and M.A. BACON	

7.1	Introduction	173
7.1.1	Soil Drying – a Composite Stress	173
7.1.1.1	Changes in Soil Water Status	173
7.1.1.2	The Pathway of Water Movement	174
7.1.1.3	Other Variables	175
7.2	Growth of Roots in Drying Soil	175
7.2.1	Morphological Adaptations to Drying Soil	175
7.2.2	Physiological Adaptation of Roots to Soil Drying	177
7.2.3	The Biochemical Adaptation of Roots to Drought	178
7.2.4	Regulation of the Morphological, Physiological and Biochemical Responses of Roots to Soil Drying	180
7.2.4.1	A Role for Abscisis Acid?	180
7.2.4.2	A Role for Ethylene?	182

XIV		Contents
7.3	Perception and Signalling of Soil Drying by Roots	182
7.3.1	Roots as Sensors of Soil Water Status	182
7.3.1.1	Abscisic Acid as a Root Signal	183
7.3.1.2	Ethylene as a Root Signal of the Effects of Soil Drying and Soil Compaction	186
7.3.1.3	Adaptive Significance of Chemically Based Signalling of Soil Drying	186
7.3.2	Signals from the Soil	188
7.4	Summary and Prospects	189
	References	190
 8	 Physiology, Biochemistry and Molecular Biology of Plant Root Systems Subjected to Flooding of the Soil . .	 193
	M.B. JACKSON and B. RICARD	
8.1	Introduction	193
8.2	Inhibition of Root Growth by Partial Oxygen Shortage . . .	193
8.3	Possible Causes of Severe Growth Inhibition and Cell Death in the Absence of Oxygen	194
8.3.1	ATP Supply and Demand	194
8.3.2	Self-Injury from Products of Anaerobic Metabolism	197
8.4	Hypoxic Acclimation to Anoxia	198
8.4.1	Oxygen Sensing and Signal Transduction	198
8.4.2	Regulation of Gene Expression	198
8.4.3	Selective Gene Expression and Enzyme Synthesis	199
8.4.4	Metabolic Basis of Improved Tolerance to Anoxia	200
8.4.4.1	Sugar Transport and Degradation	201
8.4.4.2	Glycolytic and Fermentative Enzymes	201
8.4.5	Cytoplasmic Acidosis	202
8.4.6	Other Routes to Tolerance	202
8.5	Aerenchyma and Avoidance of Anoxia	203
8.6	Stem Hypertrophy, Adventitious Rooting and Related Phenomena	204
8.7	Signalling by Oxygen-Deficient Roots	204
8.8	Summary and Prospects	206
	References	207

9	Root Competition: Towards a Mechanistic Understanding	215
	H. DE KROON, L. MOMMER and A. NISHIWAKI	
9.1	Introduction	215
9.2	What Traits Confer Belowground Competitive Ability?	216
9.3	Mechanisms of Root–Root Interactions	217
9.3.1	Indirect Effects Through Resource Depletion	217
9.3.2	Direct Chemical Interactions	219
9.4	Root Distributions as a Consequence of Root–Root Interactions	222
9.5	Belowground Competition as a Consequence of Root Distribution Patterns	225
9.5.1	Symmetric Competition for Space	225
9.5.2	Symmetric or Asymmetric Competition for Nutrients	226
9.5.3	The Dynamics of Competition	227
9.6	Summary and Prospects	231
	References	231
 10	 Root Exudates: an Overview	 235
	S.INDERJIT and L.A. WESTON	
10.1	Introduction	235
10.2	Examples of Root Exudation	237
10.3	Methods of Measuring Root Exudation	238
10.4	Fate and Movement of Exudates in Soil	241
10.5	Case Study: Root Exudation by Sorghum	243
10.6	Influence on Inorganic Nutrient Availability	246
10.7	Influence on Soil Organisms	248
10.8	Other Roles of Root Exudates	248
10.9	Summary and Prospects	250
	References	251
 11	 Mycorrhizas	 257
	F.A. SMITH, S.E. SMITH and S. TIMONEN	
11.1	Introduction	257
11.2	Classification and Root Structures	259
11.2.1	Arbuscular Mycorrhizas	259
11.2.2	Ectomycorrhizas and Ectendomycorrhizas	262
11.2.3	Mycorrhizas of the Ericales	264
11.2.4	Orchid Mycorrhizas	265

11.2.5	Surprises in Store?	265
11.2.6	Fungus–Plant Interfaces and Interactions	267
11.3	Mycorrhizal Plant Communities and Their Distribution . .	267
11.4	The Mycorrhizosphere	270
11.4.1	External Hyphae	270
11.4.2	The Soil Environment	272
11.4.3	Bacteria Associated with Mycorrhizal Fungi	272
11.5	Functional Bases of Mycorrhizal Symbioses	274
11.5.1	Transfer of Nutrients and Carbon	274
11.5.1.1	Individual Plants	274
11.5.1.2	Linked Plants	275
11.5.2	Non-nutritional Factors	276
11.6	Diversity in Plant Growth Responses	277
11.6.1	Carbon Costs of Mycorrhizal Symbioses	278
11.6.2	Growth Rates, Nutrient Demand and Mycorrhizal Responsiveness	279
11.7	Plant–Fungal Interactions at the Community Level	282
11.7.1	Plant Density, Competition and Succession	282
11.7.2	The Mycorrhizal Fungal Community	285
11.8	Summary and Prospects	285
	References	287

12 **Signalling in Rhizobacteria–Plant Interactions** 297

L.C. VAN LOON and P.A.H.M. BAKKER

12.1	Introduction	297
12.2	Plant Growth Promotion by Rhizobacteria	298
12.3	Rhizobium–Plant Interactions	303
12.4	Disease Suppression by Rhizobacteria	308
12.4.1	Competition for Substrate	309
12.4.2	Competition for Iron by Siderophores	309
12.4.3	Antibiosis	311
12.4.4	Lytic Activity	314
12.5	Rhizobacteria-Mediated Induced Systemic Resistance	314
12.6	Summary and Prospects	320
	References	321

13	Interactions Between Oxygen-Releasing Roots and Microbial Processes in Flooded Soils and Sediments . . .	331
	P.L.E. BODELIER	
13.1	Introduction	331
13.2	Methodology in Rhizosphere Microbiology	334
13.3	Quantitative and Qualitative Aspects of Root Oxygen Release	335
13.4	Interactions Between Oxygen-Releasing Roots and Aerobic Microbial Processes involved in C- and N-Cycling	339
13.4.1	Heterotrophic Bacteria	339
13.4.2	Methane-Consuming Bacteria	341
13.4.3	Nitrifying Bacteria	344
13.5	Interactions Between Oxygen-Releasing Roots and Anaerobic Microbial Processes Involved in C- and N-Cycling	346
13.5.1	Denitrifying Bacteria	346
13.5.2	Iron- and Sulphate-Reducing Bacteria	348
13.5.3	Methanogenic Bacteria	350
13.5.4	Nitrogen-Fixing Bacteria	352
13.6	Summary and Prospects	353
	References	355
 14	 Root-Animal Interactions	 363
	J.B. WHITTAKER	
14.1	Introduction	363
14.2	The Organisms Involved	364
14.3	Indirect Effects of Aboveground Grazing on Roots	367
14.4	Direct Herbivory on Roots	370
14.5	Interactions Between Above- and Belowground Herbivory	374
14.6	Physiological Responses	376
14.7	Community Responses	378
14.8	Summary and Prospects	380
	References	381
 Subject Index		 387

Root Ecology

de Kroon, H.; Visser, E.J.W. (Eds.)

2003, XXI, 397 p. 153 illus., 4 illus. in color., Hardcover

ISBN: 978-3-540-00185-0