

Contents

1	Soil Factors Affecting Nutrient Bioavailability	1
	N.B. COMERFORD	
1.1	Introduction	1
1.2	Release of Nutrients from the Soil Solid Phase	2
1.3	Nutrient Movement Through the Soil Solution	5
1.4	Nutrient Uptake by the Root System	7
1.5	Modeling Nutrient Bioavailability	9
1.6	Summary	10
	References	11
2	Decomposition and Mineralization of Nutrients from Litter and Humus	15
	C.E. PRESCOTT	
2.1	Introduction	15
2.2	Decomposition	15
2.2.1	Early (Litter) Decomposition	16
2.2.1.1	Moisture	17
2.2.1.2	Temperature	17
2.2.1.3	Litter Quality	18
2.2.1.4	Nitrogen Availability	20
2.2.2	Completeness of Decomposition	21
2.2.3	Late-Stage Decomposition (Humus and Soil Organic Matter)	22
2.2.3.1	Moisture	22
2.2.3.2	Temperature	23
2.2.3.3	Humus Quality	24
2.2.3.4	Nitrogen Availability	24

2.2.3.5	Soil Texture	25
2.2.3.6	Labile Carbon	26
2.3	Nutrient Mineralization	28
2.4	Summary	31
References		32

3 **Integrated Root Responses to Variations in Nutrient Supply** 43

D. ROBINSON

3.1	Introduction	43
3.2	Spatial and Temporal Variations in Soil Nutrient Supplies .	44
3.3	Single Roots and Root Systems	47
3.4	Local and Systemic Response Systems	50
3.4.1	Local Responses	50
3.4.2	Systemic Responses	51
3.5	Emergent Integration	55
3.6	Summary	57
References		58

4 **Internal Regulation of Nutrient Uptake**

by Relative Growth Rate and Nutrient-Use Efficiency 63

V.P. GUTSCHICK, J.C. PUSHNIK

4.1	Introduction	63
4.2	Phenomenology of Uptake Rate Responding to Nutrient-Use Efficiency and Growth Rate	65
4.2.1	The Evolutionary and Ecological Perspective of Physiological Demand	65
4.2.2	A View from Physiology: Response of Growth Rate to Nutrient Availability, Cost, and Utility	66
4.2.3	Does a Simple Model Predict an Optimal Uptake Capacity and Root Allocation?	68
4.3	Toward a Model of Uptake Regulation in Response to Nutrient Utility	71
4.3.1	Predicted Response to an Intrinsic, Physiological or Developmental Limit on Relative Growth Rate	71
4.3.1.1	Do Internal N and Carbohydrate Pools Explain Responses of $V_{\max}$ to Photosynthetic N Utility and to Developmental Limitations on Relative Growth Rate?	73

4.3.2	Applying the Model: Differences from Simple Functional Balance	77
4.4	Additional Questions: Stress, Root Turnover, Low Set Points of Woody Plants	80
4.4.1	Role of Root Lifetime	80
4.4.2	Effects of Water Stress and Salinity	81
4.4.3	Why Is Uptake so Low in Some Species?	82
4.5	Conclusions	83
4.6	Summary	83
	Appendix: Definitions of Terms and Symbols	84
	References	86
5	Biological Nitrogen Fixation Associated with Angiosperms in Terrestrial Ecosystems	89
	J.I. SPRENT	
5.1	Introduction	89
5.2	Cyanobacteria and Their Symbioses	91
5.2.1	Free-Living Nitrogen-Fixing Cyanobacteria	91
5.2.2	Cyanobacterial Symbioses	92
5.2.3	Cycads	92
5.2.4	<i>Gunnera</i>	93
5.3	Non-nodulating Associations Between Angiosperms and Non-photosynthetic Nitrogen-Fixing Microorganisms	94
5.3.1	Loose Associations	94
5.3.2	Endophytic Associations	95
5.3.2.1	Kallar Grass	95
5.3.2.2	Rice	95
5.3.2.3	Sugarcane	96
5.4	Nodulated Plants: Symbioses with <i>Frankia</i> and Rhizobia	96
5.4.1	Actinorhizal Plants	98
5.4.2	<i>Parasponia</i>	100
5.4.3	Legumes	100
5.5	Ecological Role and Uses of Nodulated Plants	103
5.5.1	Actinorhizal Plants	103
5.5.2	Legumes	104
5.5.2.1	Nodulated and Non-nodulated Plants	104
5.5.2.2	Geographical Trends	104
5.5.2.3	Dry, Flooded and Saline Environments	105
5.5.2.4	Possible Chemical Constraints	106
5.5.2.5	Rhizobial Constraints	106

5.5.2.6	Problems with Nodulated Legumes	107
5.6	Mycorrhizas, Cluster (Proteoid) Roots and Other Nutrient Acquisition Systems	108
5.7	How Much Nitrogen Is Fixed Biologically?	109
5.8	What Does the Future Hold for Nitrogen-Fixing Plants?	109
5.9	Summary	110
	References	111
6	Homeostatic Processes for the Optimization of Nutrient Absorption: Physiology and Molecular Biology	117
	A.D.M. GLASS	
6.1	Introduction	117
6.2	Kinetic Constants for Ion Influx	120
6.2.1	Definitions	120
6.2.2	Methodology	120
6.2.3	Effects of Nutrient Status on Kinetic Constants	120
6.2.4	Natural Selection and Kinetic Constants	122
6.2.5	High-Affinity and Low-Affinity Transporters	123
6.3	From Black Box Kinetic Models of Regulation to Better Defined Mechanisms of Transport Regulation	125
6.3.1	Molecular Basis of Nutrient Homeostasis	125
6.3.1.1	Potassium	126
6.3.1.2	Phosphate	128
6.3.1.3	Sulfate	130
6.3.1.4	Nitrogen	131
6.4	Summary	139
	References	140
7	Root Architecture and Nutrient Acquisition	147
	J.P. LYNCH	
7.1	Introduction	147
7.1.1	Architectural Types	149
7.1.2	Classes of Nutrient Resources	152
7.2	Intrinsic and Extrinsic Roles of Root Architecture in Nutrient Acquisition	153
7.2.1	Intrinsic Roles of Root Architecture in Nutrient Acquisition	156
7.2.1.1	Efficiency of Vascular Networks	156

Contents		XIII
7.2.1.2	Dispersal of Root Foraging	157
7.2.1.3	Structure of Root Demographics	158
7.2.1.4	The Importance of Scale	160
7.2.2	Extrinsic Roles of Root Architecture in Nutrient Acquisition	161
7.2.2.1	Exploiting a Non-uniform Environment	161
7.2.2.2	Interaction with Soil Organisms	164
7.2.2.3	Competition Among Plants	166
7.3	Practical Applications	169
7.3.1	The Agroecology of Root Architecture – Improving Crop Nutrient Efficiency	169
7.3.2	Understanding and Managing Global Change	172
7.4	Future Prospects	173
7.5	Summary	176
References		177
8	The Efficiency of Nutrient Acquisition over the Life of a Root	185
	D.M. EISSENSTAT, A. VOLDER	
8.1	Introduction	185
8.2	Root Length and Absorptive Surface Area	186
8.2.1	Importance	186
8.2.2	Inconsistencies Between Root Length, Mycorrhizal Colonization and Observed Nutrient Uptake	187
8.2.3	Root Architecture and Variation Among Fibrous Roots in a Single Root System	188
8.2.4	Variation in Root Life Span in Different Environments and Among Species	189
8.3	Costs of Root Production and Maintenance over a Root's Lifetime	191
8.3.1	Biomass Costs of Producing Root Absorptive Surface Area .	191
8.3.1.1	Root:Shoot Biomass Partitioning	191
8.3.1.2	Specific Root Length	191
8.3.1.3	Root Hairs and Mycorrhizal Hyphae	192
8.3.2	Costs of Root Respiration	193
8.3.2.1	Construction Cost and Growth Respiration	193
8.3.2.2	Maintenance Respiration	194
8.3.2.3	Ion-Uptake Respiration	194
8.3.3	Cost of Mycorrhizal Colonization and Maintenance	195
8.3.4	Changes in C Costs as the Root Ages	195
8.3.5	Other Costs	197

8.4	Uptake of Mineral Nutrients over a Root's Lifetime	198
8.4.1	Initial Advantages to Root Growth	198
8.4.2	Importance of Mycorrhizal Colonization	198
8.4.3	Longevity of Root Tissues	200
8.4.3.1	Overview	200
8.4.3.2	Longevity of Root Hairs and Epidermis	200
8.4.3.3	Longevity of Cortex	202
8.4.3.4	Longevity of Xylem Vessels	203
8.4.4	Changes in Nutrient Uptake Capacity as the Root Ages	203
8.5	The Efficiency of Nutrient Acquisition over a Root's Lifetime	205
8.5.1	Efficiency Concepts and Model Simulations	205
8.5.2	Problems Associated with Efficiency	207
8.5.2.1	Efficiency Versus Effectiveness	207
8.5.2.2	Problems of Currency	208
8.6	Heterogeneous Soil	209
8.6.1	Overview	209
8.6.2	Effects of Water and Temperature	209
8.6.3	Effects of Nutrient-Rich Patches	210
8.7	Summary	212
	References	212
 9	 Action and Interaction in the Mycorrhizal Hyphosphere – a Reevaluation of the Role of Mycorrhizas in Nutrient Acquisition and Plant Ecology	 221
	R. FINLAY	
9.1	Introduction	221
9.2	Mycorrhizal Symbiosis and Its Quantitative Effects on Plant Nutrition	224
9.2.1	Mycorrhizal Symbiosis – an Overview	224
9.2.2	Mycorrhizal Mycelia as Physical Extensions of Root Systems	229
9.3	Qualitative Effects of Mycorrhizal Interactions with the Abiotic Environment	232
9.3.1	Uptake and Utilisation of Organic Nutrients	232
9.3.2	Weathering and Acquisition of Poorly Soluble Minerals	239
9.4	Biotic Interactions	241
9.4.1	Interactions with Bacteria	245
9.4.2	Interactions with Fungi	251
9.4.3	Interactions with Other Soil Organisms	253
9.5	Multiplicity of Function – Non-nutritional Roles	254
9.6	Implications for Nutrient Cycling and Plant Ecology	258

9.7	Practical Implications of Mycorrhizosphere Effects	259
9.8	Concluding Remarks	261
9.9	Summary	261
	References	262
10	Effects of Soil Temperature on Nutrient Uptake	277
	K.S. PREGITZER, J.S. KING	
10.1	Introduction	277
10.2	Dynamics of Soil Temperature	279
10.2.1	The Soil Energy Balance	279
10.2.2	Spatial and Temporal Variation in Soil Temperature	281
10.3	Soil Temperature Effects on Soil Physical and Chemical Properties	286
10.3.1	Soil Water	286
10.3.2	Nutrient Transport	287
10.3.3	Chemical Reactions	287
10.4	Soil Temperature Effects on Root Biology	288
10.4.1	Root Growth and Morphology	289
10.4.2	Root Physiology	293
10.5	Soil Temperature Effects on Soil Biology	295
10.5.1	Decomposition and Nutrient Mineralization	296
10.5.2	Soil Fauna	298
10.5.3	Symbiotic Relationships	299
10.6	Summary and Areas of Future Research	300
	References	301
11	Nutrient Acquisition of Terrestrial Plants in a Changing Climate	311
	D.G. BIELENBERG, H. BASSIRIRAD	
11.1.	Introduction	311
11.2.	Elevated Tropospheric Ozone or Elevated UV-B Radiation	312
11.2.1	Extent of the Problem and Relevance to Nutrient Uptake	312
11.2.2	Direct Effects on Nutrient Uptake	313
11.2.2.1	Changes in Root-to-shoot Ratios, Morphology and Architecture	313
11.2.2.2	Changes in Root Respiration and Carbohydrate Supply to the Roots	314

11.2.2.3	Changes in Root Uptake Kinetics	314
11.2.2.4	Changes in Foliar Uptake/Leaching	315
11.2.3	Indirect Effects on Nutrient Uptake	315
11.3	Elevated Atmospheric CO ₂ Concentration	317
11.3.1	Extent of the Problem and Relevance to Nutrient Uptake . .	317
11.3.2	Direct Effects of CO ₂ on Plant Nutrient Uptake	317
11.3.2.1	Changes in Root-to-Shoot Ratios	317
11.3.2.2	Changes in Root Morphology and Architecture	319
11.3.2.3	Changes in Root Uptake Kinetics	320
11.3.3	Indirect Effects of CO ₂ on Nutrient Availability at the Root Surface	322
11.4	Summary	322
References		323
12	From Molecular Biology to Biogeochemistry: Toward an Integrated View of Plant Nutrient Uptake	331
	H. BASSIRIRAD	
12.1	Introduction	332
12.2	Nutrient Bioavailability	332
12.3	Plant Nutrient Demand and Use Efficiency	334
12.4	Root System Traits That Regulate Nutrient Acquisition . . .	334
12.5	Global Change and Plant Nutrient Acquisition	336
12.6	Broader Issues and Directions for Future Research	337
References		339
Subject Index		341