

Contents

Preface xv

Introduction 1

1	Soil Ecosystems: Physical and Chemical Boundaries	5
1.1	Soil as an Ecosystem	11
1.1.1	Soil System Function	12
1.1.2	Soil Formation and the Microbial Community	15
1.1.3	Implications of Definition of the Soil Ecosystem	18
1.2	The Micro-ecosystem	19
1.2.1	Interaction of Individual Soil Components with the Biotic System	19
1.2.2	Aboveground and Belowground Communities and Soil Ecosystem Synergistic Development	31
1.3	The Macro-ecosystem	37
1.4	Concluding Comments	39
2	The Soil Ecosystem: Biological Participants	45
2.1	The Living Soil Component	45
2.1.1	Biological and Genetic Implications of Occurrence of Living Cells in Soil	46
2.1.2	Implications of Microbial Properties for Handling of Soil Samples	55
2.2	Measurement of Soil Microbial Biomass	56
2.2.1	Direct Counting Methods	58
2.2.2	ATP Measure of Soil Microbial Biomass	59
2.2.3	Soil Aerobic Respiration Measurements	60
2.2.4	Chloroform Fumigation (Extraction and Incubation) Technique	61
2.2.5	Limitations of Microbial Biomass Measurements	64
2.3	The Nature of Soil Inhabitants	65
2.4	Autecology and Soil Microbiology	66

2.4.1	Limitations to Autecological Research	67
2.4.2	Autecological Methods	67
2.4.3	PCR for Quantification of Soil Microbes	72
2.4.4	Expression of Population Density per Unit of Soil	78
2.4.5	Products of Soil Autecological Research	78
2.5	Principles and Products of Synecological Research	79
2.6	Interphase Between Study of Individual and Community Microbiology	80
2.7	Concluding Comments	81
3	Microbial Diversity of Soil Ecosystems	89
3.1	Classical Culture-Based Studies of Soil Microbial Diversity	90
3.1.1	Value of Culture-Based Studies of Soil Microbial Diversity	90
3.1.2	Limitations of Culture-Based Studies of Soil Microbial Diversity	90
3.1.3	The Challenge of Defining Bacterial Species	91
3.1.4	Alternatives to Bacterial Strain Isolation	92
3.2	Surrogate Measures of Soil Microbial Diversity	92
3.3	Diversity Surrogates: Physiological Profiling	93
3.3.1	Physiological Profiling of Isolates	93
3.3.2	Community-Level Physiological Profiling	94
3.3.3	Value of Community-Level Physiological Profiling	95
3.3.4	Limitations of Community Level Physiological Profiling	95
3.4	Diversity Surrogates: Phospholipid Fatty Acid Analysis	96
3.4.1	PLFA Analysis of Isolates	96
3.4.2	Community PLFA Analysis	97
3.4.3	Value of PLFA Analysis	98
3.4.4	Limitations of PFLA Analysis	98
3.5	Nucleic Acid-Based Analyses of Soil Microbial Diversity	98
3.5.1	Nucleic Acid Based Analysis of Isolates	99
3.5.2	Community Nucleic Acid Analysis	99
3.5.3	DNA Extraction	100
3.5.4	Analysis of Community DNA	101
3.6	PCR-Based Methods	101
3.6.1	Clone Library Sequencing	101
3.6.2	DNA-Based Fingerprinting Techniques	102
3.6.3	High-Throughput Amplicon Sequencing	103
3.6.4	Limitations of PCR-Based Methods	105
3.7	Metagenomics	105
3.7.1	Limitations of Metagenomics	106
3.8	Conclusions: Utility and Limitations of Diversity Analysis Procedures	107

4	Energy Transformations Supporting Growth and Survival of Soil Microbes	115
4.1	Microbial Growth Kinetics in Soil	116
4.2	Microbial Growth Phases: Laboratory-Observed Microbial Growth Compared to Soil Population Dynamics	120
4.3	Mathematical Representation of Soil Microbial Growth	126
4.4	Uncoupling Energy Production from Microbial Biomass Synthesis	130
4.5	Implications of Microbial Energy and Carbon Transformation Capacities for Soil Biological Processes	132
4.5.1	Energy Acquisition in Soil Ecosystems	132
4.5.2	Microbial Contribution to Soil Energy and Carbon Transformation	136
4.6	Concluding Comments	143
5	Process Control in Soil	149
5.1	Microbial Response to Abiotic Limitations: General Considerations	151
5.1.1	Definition of Limitations to Biological Activity	151
5.1.2	Elucidation of Limiting Factors in Soil	153
5.2	Impact of Individual Soil Properties on Microbial Activity	157
5.2.1	Availability of Nutrients	158
5.2.2	Soil Water	164
5.2.3	Aeration	172
5.2.4	Redox Potential	173
5.2.5	pH	175
5.2.6	Temperature	178
5.3	Microbial Adaptation to Abiotic Stress	180
5.4	Concluding Comments	181
6	Soil Enzymes: Basic Principles and Their Applications	185
6.1	A Philosophical Basis for the Study of Soil Enzymes	187
6.2	Basic Soil Enzyme Properties	192
6.3	Principles of Enzyme Assays	196
6.4	Enzyme Kinetics	202
6.5	Distribution of Enzymes in Soil Organic Components	206
6.6	Ecology of Extracellular Enzymes	210
6.7	Concluding Comments	212
7	Microbial Interactions and Community Development and Resilience	217
7.1	Common Concepts of Microbial Community Interaction	220
7.2	Classes of Biological Interactions	222

7.2.1	Neutralism	223
7.2.2	Positive Biological Interactions	223
7.2.3	Negative Biological Interactions	227
7.3	Trophic Interactions and Nutrient Cycling	235
7.3.1	Soil Flora and Fauna	235
7.3.2	Earthworms: Mediators of Multilevel Mutualism	238
7.4	Importance of Microbial Interactions to Overall Biological Community Development	239
7.5	Management of Soil Microbial Populations	241
7.6	Concluding Comments: Implications of Soil Microbial Interactions	242

8 The Rhizosphere/Mycorrhizosphere 251

8.1	The Rhizosphere	252
8.1.1	The Microbial Community	254
8.1.2	Sampling Rhizosphere Soil	256
8.1.3	Plant Contributions to the Rhizosphere Ecosystem	258
8.1.4	Benefits to Plants Resulting from Rhizosphere Populations	263
8.1.5	Plant Pathogens in the Rhizosphere	264
8.1.6	Manipulation of Rhizosphere Populations	265
8.2	Mycorrhizal Associations	268
8.2.1	Mycorrhizae in the Soil Community	271
8.2.2	Symbiont Benefits from Mycorrhizal Development	273
8.2.3	Environmental Considerations	275
8.3	The Mycorrhizosphere	276
8.4	Conclusion	278

9 Introduction to the Biogeochemical Cycles 287

9.1	Introduction to Conceptual and Mathematical Models of Biogeochemical Cycles	289
9.1.1	Development and Utility of Conceptual Models	290
9.1.2	Mathematical Modeling of Biogeochemical Cycles	295
9.2	Specific Models of Biogeochemical Cycles and Their Application	297
9.2.1	The Environmental Connection	300
9.2.2	Interconnectedness of Biogeochemical Cycle Processes	302
9.3	Biogeochemical Cycles as Sources of Plant Nutrients for Ecosystem Sustenance	306
9.4	General Processes and Participants in Biogeochemical Cycles	307
9.5	Measurement of Biogeochemical Processes: What Data Are Useful?	309

9.5.1	Assessment of Biological Activities Associated with Biogeochemical Cycling	309
9.5.2	Soil Sampling Aspects of Assessment of Biogeochemical Cycling Rates	310
9.5.3	Environmental Impact of Nutrient Cycles	311
9.5.4	Example of Complications in Assessing Soil Nutrient Cycling: Nitrogen Mineralization	312
9.6	Conclusions	315
10	The Carbon Cycle	321
10.1	Environmental Implications of the Soil Carbon Cycle	323
10.1.1	Soils as a Source or Sink for Carbon Dioxide and Methane	324
10.1.2	Diffusion of Soil Carbon Dioxide to the Atmosphere	325
10.1.3	Managing Soils to Augment Organic Matter Contents	327
10.1.4	Carbon Recycling in Soil Systems	328
10.2	Biochemical Aspects of the Soil Carbon Cycle	329
10.2.1	Individual Components of Soil Organic Carbon Pools	330
10.2.2	Analysis of Soil Organic Carbon Fractions	337
10.2.3	Structural versus Functional Analysis	339
10.2.4	Microbial Mediators of Soil Carbon Cycle Processes	342
10.3	Kinetics of Soil Carbon Transformations	344
10.4	Conclusions: Management of the Soil Carbon Cycle	348
11	The Nitrogen Cycle: Mineralization, Immobilization, and Nitrification	355
11.1	Nitrogen Mineralization	359
11.1.1	Soil Organic Nitrogen Resources	359
11.1.2	Assessment of Nitrogen Mineralization	361
11.2	Nitrogen Immobilization	362
11.2.1	Process Definition and Organisms Involved	362
11.2.2	Impact of Nitrogen Immobilization Processes on Plant Communities	362
11.2.3	Measurement of Soil Nitrogen Immobilization Rates	365
11.3	Quantitative Description of Nitrogen Mineralization Kinetics	366
11.4	Microbiology of Mineralization	370
11.5	Environmental Influences on Nitrogen Mineralization	370
11.6	Nitrification	372
11.6.1	Identity of Bacterial Species that Nitrify	373
11.6.2	Benefits to the Microorganism from Nitrification	374
11.6.3	Quantification of Nitrifiers in Soil Samples	374
11.6.4	Discrepancies between Population Enumeration Data and Field Nitrification Rates	376

11.6.5	Sources of Ammonium and Nitrite for Nitrifiers	377
11.6.6	Environmental Properties Limiting Nitrification	377
11.7	Concluding Observations: Control of the Internal Soil Nitrogen Cycle	381
12	Nitrogen Fixation: The Gateway to Soil Nitrogen Cycling	389
12.1	Biochemistry of Nitrogen Fixation	391
12.1.1	The Process	391
12.1.2	The Enzyme, Nitrogenase	394
12.1.3	Measurement of Biological Nitrogen Fixation in Culture and in the Field	396
12.2	General Properties of Soil Diazotrophs	401
12.2.1	Free-Living Diazotrophs	401
12.2.2	Examples of Function of Nonsymbiotic Diazotrophs in Soil Ecosystems	404
12.2.3	Diazotrophs in Rhizosphere Populations	404
12.2.4	Diazotrophs in Flooded Ecosystems	408
12.3	Conclusions	409
13	Biological Nitrogen Fixation	415
13.1	Rhizobium–Legume Symbioses	416
13.1.1	Grouping of Rhizobial Strains	416
13.1.2	Rhizobial Contributions to Nitrogen Fixation	418
13.1.3	Nodulation of Legumes	419
13.1.4	Plant Control of Nodule Formation	423
13.2	Manipulation of <i>Rhizobium</i> –Legume Symbioses for Ecosystem Management	424
13.3	Rhizobial Inoculation Procedures	426
13.3.1	Inocula Delivery Systems	426
13.3.2	Survival of Rhizobial Inocula	427
13.3.3	Biological Interactions in Legume Nodulation	432
13.4	Nodule Occupants: Indigenous vs Foreign	432
13.5	Actinorhizal Associations	434
13.6	Conclusions	436
14	Denitrification	447
14.1	Pathways for Biological Reduction of Soil Nitrate	448
14.2	Biochemical Properties of Denitrification	450
14.2.1	Carbon and Energy Sources for Denitrifiers	450
14.2.2	Induction of Synthesis of Nitrogen Oxide Reductases	451
14.3	Environmental Implications of Nitrous Oxide Formation	452
14.4	Microbiology of Denitrification	453

14.4.1	Assessment of Soil Denitrifier Populations	453
14.4.2	General Traits of Denitrifiers	454
14.4.3	Generic Identity of Denitrifiers	455
14.5	Quantification of Nitrogen Losses from an Ecosystem via Denitrification	456
14.5.1	Nitrogen Balance Studies	456
14.5.2	Use of Nitrogen Isotopes to Trace Soil Nitrogen Transformations	458
14.5.3	Soil Nitrogen Oxide Transformations	459
14.5.4	Acetylene Block Method for Assessing Denitrification Processes in Soil	460
14.6	Environmental Factors Controlling Denitrification Rates	462
14.6.1	Nature and Amount of Organic Matter	462
14.6.2	Nitrate Concentration	464
14.6.3	Aeration/Moisture	464
14.6.4	pH	465
14.6.5	Temperature	466
14.6.6	Interaction of Limitations to Denitrification in Soil Systems	467
14.7	Conclusions	467
15	Fundamentals of the Sulfur, Phosphorus, and Mineral Cycles	477
15.1	Sulfur in the Soil Ecosystem	477
15.2	Biogeochemical Cycling of Sulfur in Soil	479
15.3	Biological Sulfur Oxidation	482
15.3.1	Microbiology of Sulfur Oxidation	482
15.3.2	Environmental Conditions Affecting Sulfur Oxidation	486
15.4	Biological Sulfur Reduction	488
15.4.1	Anaerobic Biodegradation	490
15.4.2	Reducing Acidity of Acid Mine Drainage	490
15.4.3	Reduction of Complications of Metal Contamination in Soil	490
15.5	Mineralization and Assimilation of Sulfurous Substances	491
15.6	The Phosphorus Cycle	492
15.7	Microbially Catalyzed Soil Metal Cycling	494
15.7.1	Interactions of Soil Metals with Living Systems	495
15.7.2	Microbial Response to Elevated Metal Loading	497
15.7.3	Microbial Modifications of Metal Mobility in Soils	498
15.7.4	Managing Soils Contaminated with Toxic Metals	501
15.8	Conclusion	502
16	Soil Microbes: Optimizers of Soil System Sustainability and Reparation of Damaged Soils	511
16.1	Foundational Concepts of Bioremediation	514
16.1.1	Bioremediation Defined	514

16.1.2	Conceptual Unity of Bioremediation Science	515
16.1.3	Complexity of Remediation Questions	516
16.2	The Microbiology of Bioremediation	517
16.2.1	Microbes as Soil Remediators	518
16.2.2	Substrate–Decomposer Interactions	519
16.2.3	Microbial Inoculation for Bioremediation	528
16.3	Soil Properties Controlling Bioremediation	532
16.3.1	Physical and Chemical Delimiters of Biological Activities	532
16.3.2	Sequestration and Sorption Limitations to Bioavailability	536
16.4	Concluding Observations	538
	Concluding Challenge	545
	Index	549