



SOIL MICROBIOLOGY

Second Edition

Robert L. Tate III

Soil Microbiology

Second Edition

Robert L. Tate III

Rutgers University



John Wiley & Sons, Inc.

New York | Chichester | Weinheim | Brisbane | Singapore | Toronto

This book is printed on acid-free paper. ☉

Copyright © 2000 by John Wiley & Sons, Inc. All rights reserved.

Published simultaneously in Canada.

No part of this publication may be reproduced, stored in a retrieval system or transmitted in any form or by any means, electronic, mechanical, photocopying, recording, scanning or otherwise, except as permitted under Sections 107 or 108 of the 1976 United States Copyright Act, without either the prior written permission of the Publisher, or authorization through payment of the appropriate per-copy fee to the Copyright Clearance Center, 222 Rosewood Drive, Danvers, MA 01923, (978) 750-8400, fax (978) 750-4744. Requests to the Publisher for permission should be addressed to the Permissions Department, John Wiley & Sons, Inc., 605 Third Avenue, New York, NY 10158-0012, (212) 850-6011, fax (212) 850-6008, E-Mail: PERMREQ @ WILEY.COM.

The publication is designed to provide accurate and authoritative information in regard to the subject matter covered. It is sold with the understanding that the publisher is not engaged in rendering professional services. If professional advice or other expert assistance is required, the services of a competent professional person should be sought.

Library of Congress Cataloging-in-Publication Data:

Tate, Robert L., 1944-

Soil microbiology / Robert L. Tate. —2nd ed.

p. cm.

Includes bibliographical references.

ISBN 0-471-31791-8 (cloth : alk. paper)

1. Soil microbiology. I. Title.

QR111.T28 2000

579'.1757—dc21

99-21922

Printed in the United States of America.

10 9 8 7 6 5 4 3 2 1

Soil Microbiology

To
Ann, Robert, and Geoffrey

Preface

Slightly over four years ago, I was putting the finishing touches on the preface to the first edition of *Soil Microbiology*. As the final stages of this second edition of the treatise were completed and I gathered the thoughts for writing a second preface, questions of just why the rather long endeavor of writing another edition was necessary. Certainly, the basic tenets of the discipline are evolving, but not at a rapid rate. The objective of the first edition — “to provide the student with a strong basic knowledge of the biological, physical, and chemical properties of the soil and the microbes contained therein” — is unchanged. What has expanded significantly is our experience in using the concepts of soil microbiology to solve our expanding list of environmental problems. Thus, the most obvious differences between the two editions of this text is the inclusion of chapters on soil microbial diversity and bioremediation of soil systems. Although the “central dogma” underlying these topics is still evolving, opportunities now exist for including in a basic textbook an elucidation of the status of the topics and for highlighting areas of deficiency in our knowledge base.

When I first began contemplating the task of writing this edition, I asked many of my close associates what they felt was the greatest need of the text. Bioremediation and microbial diversity were frequently mentioned as possible topics. But one response stands out in my mind. An individual whose opinion I highly respect strongly stated that no “new words” should be added. Students were already faced with a “mountain of information” to master. I must admit that I too must agree, at least in part, with this observation. Students in my own classes commonly are overwhelmed by the vast amount of information before them. It is with this thought in mind that I went ahead and added more “words” to each of the chapters. My goal was to clarify the relationship of soil microbiology concepts to the general environmental matters with which students are experienced and to highlight new endeavors in the area of primary research. Since much of the foundation of soil microbiology derives from agriculturally based studies and the fact that our discipline remains a

primary support for efficient production of food and fiber, the understanding of the agricultural environment is still a major part of our soil microbiology foundation, but this foundation is now extended greatly into more general soil concerns, such as urban soil management and soil stewardship and reclamation practices.

Last, this edition attempts to maintain the flavor of the first edition. Students need more than just a presentation of the “facts.” Entries into the world of primary research literature are essential to provide a foundation for careers in our science. Thus, although complete review of the literature is not possible, an attempt was made to highlight a significant mass of current as well as historical research references. My apologies are offered to associates whose publications were overlooked, but such omissions are unavoidable under the circumstances of page limitations for a basic text and to meet the objective of not overwhelming students with masses of new information. Students are challenged to explore not only the summary of the principles provided in *Soil Microbiology* but also to delve into the rich variety of primary research that has been amassed supporting the principles of soil microbiology and pointing the way to future endeavors. It is only through such perhaps difficult but rewarding treks that students can truly master the challenges of the study of soil microbiology.

I take this opportunity to thank my colleagues and students who have provided the inspiration and conducted the research that has made this book possible. In particular, I also thank the current members of my soil microbiology research group, who have had to endure my deficiencies in providing true focus to their research endeavors as I put these words to paper. Their patience is gratefully acknowledged and highly appreciated. It is again my hope that this treatise will provide a basis for growth of the science of soil microbiology and an inspiration to the careers of young scientists.

Robert L. Tate III

New Brunswick, New Jersey
October 1999

Preface to the First Edition

In the past, soil microbiology has been identified as a second tier science produced by the merger of soil science and microbiology—two disciplines of somewhat recent birth compared to the longer-lived basic sciences of chemistry, physics, mathematics, and biology. Now, soil microbiology has reached sufficient maturity to provide the underpinning of such newly emerging disciplines as environmental science and related studies. The necessities arising from managing the long undervalued soil ecosystem have produced a myriad of complex problems that can be solved only with an application of the primary principles of soil microbiology. Complex questions emerging from the necessities of reclamation of polluted or contaminated soil as well as the requirement to properly manage less affected, perhaps pristine terrestrial ecosystems require an appreciation of the delicate balance between the soil microbial community and its environment. This habitat of the soil microbe not only includes the minerals and organic matter of the soil matrix but also encompasses levels of life occurring therein or indeed thereupon.

It is with this concept of the growing necessity to understand the diversity of life contained within a gram of soil as well as the intricacies of the linkages of these living entities with terrestrial life in general that has provided the impetus for production of this treatise on soil microbiology. It is hoped that the words contained herein will provide a clear understanding of the principles upon which the discipline of soil microbiology is built, as well as illuminate their applicability to current soil-related environmental problems.

A concerted effort was made in assembling the material for this text to avoid the myopic impression that soil microbiology and related disciplines have developed strictly to meet the needs of agricultural scientists. Indeed, the roots of soil microbiology have long been fed by the requirements to provide food and fiber to a growing society, but the principles of the science are essential for

guiding decisions of soil-related questions in all realms of our society. Hence, a conscious attempt has been made to illustrate the applicability of studies of the soil microbiology to the grander array of environmental science problems facing our society.

One further foundational assumption in writing *Soil Microbiology* is that the science of soil microbiology has grown to the point that it now is self-sustaining. That is, students of the science should be sufficiently versed in the basic sciences that their repetition within these pages would be redundant. Thus, inclusion of introductory chapters describing the basic tenets of soil science and microbiology would be as inappropriate in a soil microbiology text as would introductions to biology, chemistry, and physics. Students are expected to have a fundamental understanding of these foundational course materials before entering the realm of the soil microbe. Discussions of elementary chemical and biological principles in this text are presented only in the context of their applicability to the soil situation.

A book of this type cannot be prepared without the input of many friends and associates. I especially thank those unnamed colleagues and students who in their discussions with me have provided the seeds of inspiration that have matured into the concepts of our study. Last, the inputs of the many soil microbiologists who have conducted the experiments upon which the basic tenets of soil microbiology have been constructed must be gratefully acknowledged. It is the author's hope that assembly of this information in this treatise will provide the basis for extension of the introductory information contained herein far beyond our current images of our science.

Robert L. Tate III

New Brunswick, New Jersey
January 1994

Introduction

Members of the soil microbial community have been appreciated as interesting life forms. They have been exploited as producers of substances of great societal importance, such as a variety of antibiotics. This knowledge alone has been sufficient to produce the books occupying a multitude of library shelves. But such information alone is inadequate to provide solutions to the variety of microbially associated environmental problems facing society today. Environmental scientists and regulators as well as the lay public are faced with decisions regarding the proper stewardship of our soil resources as well as the management or reclamation of damaged systems. Solutions to these at times lifestyle-altering problems may be provided by considering soil to be a closed system with only external manifestations of the processes occurring therein deemed to be worthy of consideration. The most limited external implication could be the production of an aesthetically pleasing ecosystem. Such a viewpoint provides short-sighted, temporary solutions to long-term problems. Indeed, not only is an appreciation of the biological processes occurring in soil essential to achieve societal goals of caring for terrestrial systems, but true wisdom in decision-making is predicated on an understanding of how the individual soil biologically based processes combine to produce a vital, sustainable whole. The parts assembled into a viable soil system clearly produce a whole much more dynamic, much greater than can be predicted by their simple summation.

This thesis is underscored by the magnitude and multitude of anthropogenically affected soil sites currently demanding some form of reclamation management. For example, refuse from energy fuel or mineral recovery forms unsightly slag piles extending across the countryside. From within these piles, a yellow leachate with a pH of nearly 1 frequently flows. Nearly sterile soil and waters result from encounters with this deadly by-product of resource recovery. The questions become, "How best to prevent the production of

leaching of the substance commonly known as acid mine drainage? How to restore the affected soils and waters to functional, aesthetic ecosystems? How can the remains of the mining industry be managed to prevent further environmental degradation?"

Perhaps less dramatic but of similar concern is the problem of evaluating potential difficulties of genetically engineered microorganisms (gems). The answers seem simple. An organic chemical has reached a soil system at toxic concentrations, but no microorganisms capable of decomposing the toxicant exist therein. Yet such microbes can be created in the laboratory through commonly available genetic manipulation procedures. Concerns involve unanticipated ecosystem degradation from the introduction of laboratory-created, alien organisms into established soil communities. "Will the introduced microbe survive sufficiently long to achieve the objective of its utilization? Will the unique gene carried by this gem be transferred to indigenous organisms, thereby creating an individual with capacity to wreak havoc on an otherwise stable soil system?" These questions represent concerns to which soil microbiologists must respond. Resolution of the conflict requires a clear understanding of the behavior of alien microbes within a functioning soil ecosystem, as well as of the dynamics of gene transfer within soil populations.

These two initial examples relate to environmental problems whose impact involves the reclamation or management of a limited region of soil. Solutions to environmental problems affecting the totality of our terrestrial system also rely on expansion of our knowledge and databases relating to soil microbial processes. For example, soil is a natural source and sink of greenhouse gases, such as methane and carbon dioxide. Basically, soil organic matter (humus) resources are the source and sink for these carbon compounds. Furthermore, the quantity of humus retained within a particular soil is the product of the physical, chemical, and biological properties of the system as well as any associated anthropogenic intervention. Therefore, all soil systems are characterized by occurrence of an equilibrium level of soil organic matter. Anthropogenic intervention into the ecosystem can result in a shift in the quantity of carbon sequestered in the soil. This situation is nowhere more obvious than in soils developed for intensive agricultural production. Historically, the yield of carbon dioxide to the atmosphere due to reduction in the quantity of soil humus in these soils has been significant. Thus, a simplistic means of managing greenhouse gases that could be proposed is to alter the management of soil systems so that they become a sink rather than a source of atmospheric carbon dioxide. An appreciation of the potential benefits of this process can be derived from consideration of variation of soil humus levels resulting from the conversion of intensive cultivation practices into reduced till or no-till agricultural soil management. Unfortunately, the questions associated with assessing the role of soil in managing greenhouse gases are more complicated. Decisions related to greenhouse gas management and associated terrestrial effects are affected by, among other factors, the fact that soil temperatures are anticipated to increase due to global climate changes associated with the greenhouse

phenomenon. Now, an interaction of human soil management decisions, changes in the chemistry of plant inputs due alteration of plant biomass composition by the elevated atmospheric temperatures, and alteration of soil physical properties (e.g., temperature and moisture) acting together create soil microbial community dynamics that are not as easily forecasted as was possible with alteration of agricultural soil management. An expanded comprehension of soil microbial dynamics and the effect of total-ecosystem processes on soil biological processes is needed.

It is with these types of concerns in mind that this treatise is presented. The overall object of the study is to provide the student with the strong basic knowledge of the biological, physical, and chemical properties of soil and the microbes contained therein necessary to provide the basis for sound environmental management and stewardship decisions.

Contents

Preface	v
Preface to the First Edition	vii
Contents	ix
Introduction	xx

1

The Soil Ecosystem: Physical and Chemical Boundaries

1

- 1.1 The Soil Ecosystem 5**
 - 1.1.1 Soil Defined 6
 - 1.1.2 Designation of Soil Ecosystems 8
 - 1.1.3 Implications of Definition of the Soil Ecosystem 11
- 1.2 The Micro-Ecosystem 12**
 - 1.2.1 Interaction of Individual Soil Components with the Biotic System 13
 - 1.2.1.1 Clay and Ecosystem Function 14
 - 1.2.1.2 Humic Substances and Ecosystem Function 20
 - 1.2.2 Soil Aggregate Structure and Biological Systems 24
 - 1.2.2.1 Native Soil Aggregate Structure and Its Impact on Ecosystem Function 24
 - 1.2.2.2 Separation of Soil Particulates by Density Fractionation 29
- 1.3 The Macro-Ecosystem 30**

1.4	Concluding Comments	32
	References	33

2	The Soil Ecosystem: Biological Participants	37
----------	--------------------------------------------------------	-----------

2.1	The Living Soil Component	38
2.1.1	Biological and Genetic Implications of Occurrence of Living Cells in Soil	38
2.1.1.1	Gene Pool Potential	39
2.1.1.2	Cell Structure and Biochemical Stability in Soil	44
2.1.1.3	Resting Structures and Soil Respiration	44
2.1.1.4	Soil Mineral Transformation by Microbial Cells	45
2.1.1.5	Microbial Link to Aboveground Communities	46
2.1.2	Implications on Microbial Properties of Handling of Soil Samples	46
2.2	Measurement of Soil Microbial Biomass	47
2.3	The Nature of the Soil Inhabitants	57
2.4	Autecological Soil Microbiology	58
2.4.1	Viable Counts/Enrichment Cultures	59
2.4.2	Intrinsic Limitations of Viable Count Procedures	63
2.4.3	DNA Hybridization/PCR Procedures	64
2.4.4	Expression of Population Density per Unit of Soil	66
2.4.5	Products of Soil Autecological Research	66
2.5	Principles and Products of Synecological Research	68
2.6	Interphase between Study of the Individual and Community Microbiology	68
2.7	Concluding Comments	69
	References	70

3	Microbial Diversity of Soil Ecosystems	76
----------	-----------------------------------------------	-----------

3.1	Classical Studies of Soil Microbial Diversity: Numerical Taxonomy	77
3.2	Biochemical Measures of Soil Microbial Diversity	79
3.3	Metabolic Diversity of Soil Systems	80
3.4	Phospholipid Fatty Acid Analysis	86
3.5	Nucleic Acid-Based Analysis of Soil Microbial Diversity	87

3.6	Conclusions: Utility and Limitations of Diversity Analysis Procedures	89
	References	90

4 **Energy Transformations and Metabolic Activities of Soil Microbes** **95**

4.1	Microbial Growth Kinetics in Soil	96
4.1.1	Microbial Growth Phases: Laboratory-Observed Microbial Growth Compared to Soil Population Dynamics	98
4.1.2	Mathematical Representation of Soil Microbial Growth	104
4.1.3	Uncoupling Energy Production from Microbial Biomass Synthesis	108
4.2	Implications of Microbial Energy and Carbon Transformation Capacities on Soil Biological Processes	109
4.2.1	Energy Acquisition in Soil Ecosystems	110
4.2.2	Microbial Contributions to Soil Energy and Carbon Transformations	114
4.3	Concluding Comments	119
	References	121

5 **Process Control in Soil** **125**

5.1	Microbial Response to Abiotic Limitations: General Considerations	127
5.1.1	Definition of Limitations to Biological Activity	127
5.1.2	Elucidation of Limiting Factors in Soil	130
5.2	Impact of Individual Soil Properties on Microbial Activity	133
5.2.1	Availability of Nutrients	133
5.2.2	Moisture	139
5.2.3	Aeration	147
5.2.4	Redox Potential	148
5.2.5	pH	149
5.2.6	Temperature	152
5.3	Microbial Adaptation to Abiotic Stress	155
5.4	Concluding Comments	156
	References	156

6	Soil Enzymes as Indicators of Ecosystem Status	159
6.1	Philosophical Basis for the Study of Soil Enzymes	161
6.2	Basic Soil Enzyme Properties	164
6.3	Principles of Enzyme Assays	169
6.4	Enzyme Kinetics	175
6.5	Distribution of Enzymes in Soil Organic Components	180
6.6	Ecology of Extracellular Enzymes	183
6.7	Concluding Comments	185
	References	185
7	Microbial Interactions and Community Development and Resilience	189
7.1	Common Concepts of Microbial Community Interaction	192
7.2	Classes of Biological Interactions	194
	7.2.1 Neutralism	195
	7.2.2 Positive Biological Interactions	195
	7.2.3 Negative Biological Interactions	198
7.3	Trophic Interactions and Nutrient Cycling	206
	7.3.1 Soil Flora and Fauna	207
	7.3.2 Earthworms: Mediators of Multilevel Mutualism	209
7.4	Importance of Microbial Interactions to Overall Biological Community Development	210
7.5	Management of Soil Microbial Populations	212
7.6	Concluding Comments: Implications of Soil Microbial Interactions	213
	References	214
8	The Rhizosphere/Mycorrhizosphere	218
8.1	The Rhizosphere	219
	8.1.1 The Microbial Community	221
	8.1.2 Sampling Rhizosphere Soil	223
	8.1.3 Plant Contributions to the Rhizosphere Ecosystem	224
	8.1.4 Benefits to Plants Resulting from Rhizosphere Populations	229
	8.1.5 Plant Pathogens in the Rhizosphere	231
	8.1.6 Manipulation of Rhizosphere Populations	232
8.2	Mycorrhizal Associations	235

- 8.2.1 Mycorrhizae in the Soil Community 238
- 8.2.2 Symbiont Benefits from Mycorrhizal Development 239
- 8.2.3 Environmental Considerations 241
- 8.3 The Mycorrhizosphere 243**
- 8.4 Conclusions 244**
- References 244**

9**Introduction to the Biogeochemical Cycles 253**

- 9.1 Conceptual and Mathematical Models of Biogeochemical Cycles 255**
 - 9.1.1 Development and Utility of Conceptual Models 255
 - 9.1.2 Mathematical Modeling of Biogeochemical Cycles 259
- 9.2 Specific Conceptual Models of Biogeochemical Cycles and Their Application 262**
 - 9.2.1 The Environmental Connection 265
 - 9.2.2 Interconnectedness of Biogeochemical Cycle Processes 268
- 9.3 Biogeochemical Cycles as Sources of Plant Nutrients for Ecosystem Sustenance 271**
- 9.4 General Processes and Participants in Biogeochemical Cycles 272**
- 9.5 Measurement of Biogeochemical Processes: What Data Are Meaningful? 274**
 - 9.5.1 Assessment of Biological Activities Associated with Biogeochemical Cycling 274
 - 9.5.2 Soil Sampling Aspects of Assessment of Biogeochemical Cycling Rates 275
 - 9.5.3 Environmental Impact of Nutrient Cycles 276
 - 9.5.4 Examples of Complications in Assessing Soil Nutrient Cycling: Nitrogen Mineralization 277
- 9.6 Conclusions 280**
- References 280**

10**The Carbon Cycle 284**

- 10.1 Environmental Implications of the Soil Carbon Cycle 286**
 - 10.1.1 Soils as a Source or Sink for Carbon Dioxide 287