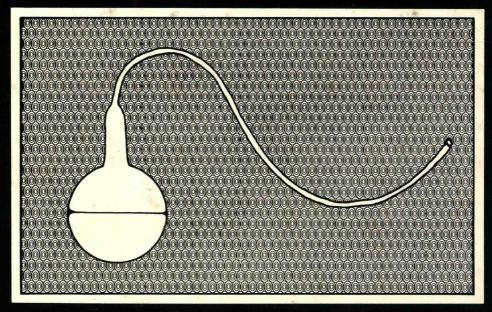
BACTERIA IN NATURE



Volume 1 Bacterial Activities in Perspective

Edited by

Edward R. Leadbetter

Jeanne S. Poindexter

BACTERIA IN NATURE

Volume 1
Bacterial Activities
in Perspective

Edited by

Edward R. Leadbetter

University of Connecticut Storrs, Connecticut

and

Jeanne S. Poindexter

The Public Health Research Institute of The City of New York, Inc. New York, New York

Library of Congress Cataloging in Publication Data

Main entry under title:

Bacteria in nature.

Includes bibliographies and index.

Contents: v. 1. Bacterial activities in perspective.

1. Bacteria – Ecology – Collected works. 2. Bacteria – Collected works. I. Leadbetter, Edward R. II.

Poindexter, Jeanne S. (Jeanne Stove)

QR100.B33 1985

589.9'05

85-3433

ISBN 0-306-41944-0 (v. 1)

© 1985 Plenum Press, New York A Division of Plenum Publishing Corporation 233 Spring Street, New York, N.Y. 10013

All rights reserved

No part of this book may be reproduced, stored in a retrieval system, or transmitted, in any form or by any means, electronic, mechanical, photocopying, microfilming, recording, or otherwise, without written permission from the Publisher

Printed in the United States of America

BACTERIA IN NATURE

Volume 1 Bacterial Activities in Perspective

BACTERIA IN NATURE

Editors

Edward R. Leadbetter University of Connecticut Storrs, Connecticut

Jeanne S. Poindexter
The Public Health Research Institute
of The City of New York, Inc.
New York, New York

Editorial Advisory Board

Albert Balows
Centers for Disease Control

L. E. Casida, Jr.

The Pennsylvania State University

Richard W. Castenholz
University of Oregon

Patricia H. Clarke University College, London

Martin Dworkin University of Minnesota

M. V. Ivanov USSR Academy of Science

Holger W. Jannasch
Woods Hole Oceanographic
Institution

David M. Karl University of Hawaii J. Gijs Kuenen

Delft University of Technology

Barbara B. Lippincott Northwestern University

R. G. E. Murray University of Western Ontario

Monica Riley State University of New York at Stony Brook

Moshe Shilo Hebrew University, Hadassah Medical School

Ralph S. Wolfe University of Illinois

Volume 1 Bacterial Activities in Perspective Volume 2 Methods for Bacterial Ecology

PREFACE TO THE TREATISE

The effects of bacteria on their environments were known and variously explained by human societies long before these microorganisms were recognized. Even after they had been detected microscopically, nearly two centuries elapsed before it was demonstrated that bacteria were causes, rather than effects, of fermentations, infectious diseases, and transformations of both organic and inorganic materials in soils, waters, and sediments. It was these demonstrations of the ecological roles of bacteria that gave birth to bacteriology as an experimental science. The applications of the understanding of ecological activities of bacteria have in no small part been responsible for this century's revolution in human health and longevity through changes in agricultural, medical, and sanitation practices.

However, the ecology of bacteria has only relatively recently emerged as a science in itself, having as its goal the elucidation of the interactions of bacteria and their habitats whether or not those activities appear immediately relevant to human affairs. In this ten-volume treatise, it is our intention to present this broadened view of bacterial existence, that the work may serve as a synthesis of current ideas and information that will be valuable both to basic scientists and to those directly engaged in applications of science to specific problems of human existence. Our hope is that the completed project will expose and explore the diversity of bacterial capabilities and culpabilities, limitations and sensitivities, and will imply the equally diverse ways in which they can be exploited. We hope, especially, that investigators trained in other disciplines—clinicians, oceanographers, molecular biologists, engineers—who may not expect that their disciplines are interrelated with bacterial ecology, will find this treatise both stimulating and valuable.

The introductory volume traces main points in the history of bacteriology that have led to the present state of bacterial ecology, to the awareness that bacteria constitute distinctive populations that separately and in concert affect the physiochemical conditions of the biosphere and interact, sometimes intimately, with other organisms. The second volume will review and evaluate the technical and philosophical tools presently available to the student of bacteria in nature. This volume is intended to provide evaluations of methods and not to serve as a procedural manual.

Although the initial stimulus to interest in bacteria arose from attempts to understand natural phenomena and to distinguish abiotic from biotic causes of these phenomena, most of the progress in managing and learning about bacteria has been accomplished in the laboratory, very largely through the study of pure cultures. While some devoted naturalists eschew the study of monotypic populations as artificialities, it would not be possible to understand the activities of a bacterial community in ignorance of the separate, respective potential activities of the members of the community. For this reason, two volumes will comprise information regarding structure, composition, genetics, physiology, and biochemistry of bacteria, obtained predominately from pure culture studies, that is essential to unraveling the interactions of bacteria with their environment and with each other. The goal of those volumes is not simply to review the information, but to demonstrate its importance to inferences based on studies of natural, polytypic populations.

The remaining six volumes in this series will explore bacterial habitats. Because a bacterial activity of any type—polymer solubilization, oxygen consumption, toxin production, or other—is not confined to one type of habitat, we anticipate that some groups of bacteria and some bacterial activities will be mentioned in more than one ecological context. However, since the emphasis throughout the series will be on interactions, the role of the habitat in influencing the extent and consequence of bacterial activities will vary with its own inherent stability, its resilience to the effects of bacteria, and its capacity for supporting and restricting those activities. An additional reason for organizing the treatise principally around habitats reflects the fact that human problems and advantages that arise from bacterial activities are most often met within the context of a particular kind of site. Similarly, the general ecological significance of a bacterial activity is proportional to the rate of activity allowed by a habitat, the geographical extent of the habitat, and the degree of dependence of other forms of life on the condition of the habitat affected by that activity. Accordingly, for all conceptual and practical purposes other than classification, the study of bacterial ecology is, we believe, most usefully presented by grouping the information into volumes that reflect the manner in which bacterial communities are gathered and interact in nature.

The treatise will conclude with a consideration of the frontiers and the relic habitats of the biosphere, those environments inhabited almost solely by bacteria. Modern biology recognizes bacteria as the pioneering populations—demonstrably so in the past and predictably so in the future—of this and possibly also of other worlds. It is the humble yet confident hope of the editors that the insights and experimental results of today's bacterial ecologists, compiled in these volumes, will contribute significantly to the continuing elucidation of the roles and potentials of our bacterial cohabitants—so long a major influence on this earth, yet only so recently appreciated.

This series was conceived partly as a result of our participation as instructors in the summer program in microbial ecology at the Marine Biological Laboratory, Woods Hole, Massachusetts. Our interests in bacterial ecology

antedate that participation by many years, having been earlier stimulated and guided by R. A. Slepecky and J. W. Foster (E.R.L.), by W. A. Konetzka and R. Y. Stanier (J.S.P.), and by one of the greatest appreciators of microorganisms, C. B. van Niel. To our colleagues—students and faculty—in the M.B.L. course, and to our several mentors, we dedicate this series.

The Editors

CONTRIBUTORS

- MARY MENNES ALLEN, Department of Biological Sciences, Wellesley College, Wellesley, Massachusetts 02181
- DAVID R. BENSON, Microbiology Section, University of Connecticut, Storrs, Connecticut 06268
- PATRICIA H. CLARKE, Department of Biochemistry, University College London, London WC1E 6BT, England
- HENRY L. EHRLICH, Department of Biology, Rensselaer Polytechnic Institute, Troy, New York 12181
- D. M. GRIFFIN, Department of Forestry, Australian National University, Canberra 2601, Australia
- GEORGE HEGEMAN, Microbiology Group, Biology Department, Indiana University, Bloomington, Indiana 47405
- ROBERT E. HUNGATE, Department of Bacteriology, University of California at Davis, Davis, California 95616
- NORBERT PFENNIG, Faculty of Biology, Konstanz University, D-7750 Konstanz, Federal Republic of Germany

PREFACE

Any branch of biology depends for its progress on the development of new concepts and to a lesser, but sometimes crucial, extent on the elimination of erroneous notions. Understanding the roles of bacteria required first the observation that such minute creatures existed, and subsequently the experimental demonstrations that their presence was necessary for the occurrence of particular phenomena.

In this first volume, the authors review the development of scientific understanding of the role of microbes as agents of diverse natural processes. Notably absent is a separate review of the history of microbes as agents of disease, a history available in many other publications. Regrettably absent is a review of the history of microbes as agents of inorganic transformations, a serious omission that resulted from the illness of the prospective author late in the preparation of this volume. The topic will of course be treated in later volumes, although not predominantly in a historical manner. Otherwise, the emphasis in this volume is on the history of understanding interrelationships between modes of bacterial existence and the inanimate environment. These relationships were established long before multicellular, differentiated organisms appeared as potential microbial habitats, and their recognition and elucidation contributed greatly to the widened appreciation of bacterial diversity and the importance of these simpler creatures to the physiochemical conditions of the biosphere.

As bacterial ecology matures as a microbiological discipline, an appreciation of the foundation constructed during the past two centuries is indispensable to its students, and so we offer this first volume to acknowledge the historical context in which current studies proceed. Some of the concepts that arose in the nineteenth century proved important to the development of several subdisciplines, and so are reviewed by more than one author; their recurrent mention serves to emphasize their central role in the development of our present understanding.

We especially thank the authors in this volume for giving time, energy, and consideration to topics which are not the immediate concern of their present research. None is a historian by trade, but all have responded to a call to review the background of today's view of bacterial activities in nature.

CONTENTS

CHAITER I	
The Scientific Study of Bacteria, 1780–1980	
Patricia H. Clarke	
Introduction	1
How Were the Activities of Bacteria Recognized?	3
Steps toward a Science of Bacteriology	3
Constancy of Form	5
Spontaneous Generation	5
The Process of Fermentation	8
Pasteur and Fermentation	8
Ferments and Enzymes	9
The Growth of Medical Bacteriology	10
Bacteria and Disease	10
Pure Cultures and Mixed Cultures	12
Public Health Aspects	14
Bacteria and the Natural Cycles	15
Isolates from Nature	15
Nitrifiers	16
Nitrogen Fixation	17
Autotrophic Sulfur Bacteria	17
Photosynthetic Bacteria	18
Chemical Transformations Carried Out by Bacteria	18
Oxidations	18
Anaerobic Fermentations	19
Bacterial Metabolism and the Unity of Biochemistry	20
Biochemical Variation	21
Genetic Variation	22
Levels of Understanding	23
From Nature to the Laboratory	23
What about Bacterial Species?	24
The Impact of Genetics	25

xiii

xiv	CONTENTS

Adaptation—Genotype or Phenotype? Molecular Biology Bacterial Growth Present and Future	27 29 29 32
References	33
Chapter 2	
Anaerobic Biotransformations of Organic Matter	
ROBERT E. HUNGATE	
Introduction	39
Abiotic Transformations	39
Synthesis	40
Evolution of Metabolism	41
The Advent of Dioxygen	42
Human Appreciation of Anaerobiosis	43
Pasteur's Great Contributions	44
Development of Biochemistry in Relation to	
Anaerobic Transformations	44
Hydration and Dehydrogenation	45
Types of Fermentation of Carbohydrates	45
Lactacidigenesis	46
Ethanolic Fermentation	46
Acetigenic Fermentation	47
Succinigenic and Propionigenic Fermentations	48
Butyrigenic Fermentation	50
Mixed Product Fermentations	50
Development of Anaerobic Methods	51
Ecological Considerations	52
The Liquid Enrichment Method	52
The Solid Medium Enrichment Method	53
Gradients in Anaerobiosis—the Redox Potential	53
Factors Influencing Redox Potential	54
Redox Potentials in the Organism	
Categories of Organismic Relationships to Dioxygen	56 57
Methanogenic Fermentations	
Modern Anaerobic Habitats: The Alimentary Tracts of Animals	58
The Competition Model	59
The Cooperation Model	60 61
The Combined Competition–Cooperation Model	62
Continuous Fermentation	63
The Rumen	71
Modern Nonalimentary Anaerobic Habitats	/ 1

•

CONTENTS	xu
----------	----

	Aquatic Habitats	71
	Soils and Sediments	72
	Anaerobic Digestors	74
	Digestion of Plant Cell Walls	74
	Transformations of Nitrogenous Materials	77
	Ultimate Events in Anaerobic Transformations	81
	Soluble Nutrients in Anaerobic Transformations	85
	Leakage of Metabolites from Anaerobic Digesters	00
	of Wall Materials	87
	Conclusion	88
	References	88
	Chapter 3	
	The Mineralization of Organic Materials under Aerobic Conditions	
	George Hegeman	
	Introduction	97
	History	97
	Chemistry	98
	Regulation	101
	The Bacteria	102
	Stages of Mineralization	103
	Pathway Structure	105
	Genetic Organization	106
	The Chromosome	
	Plasmids	
	Prospects and Trends in Research	107
	Pathways	107
*	Xenobiotic Compounds as Pollutants	107
	Mixed Cultures	108
	Conclusions	
	References	110
	Chapter 4	
	Stages in the Recognition of Bacteria Using Light as a Source of Energy	
	Norbert Pfenning	
	Introduction	113
	The Studies of Engelmann on the Responses of Green Algae	
	and of Purple Bacteria to Light	114
	Winogradsky's Work on the Sulfur Bacteria	116
	The second secon	

•

xvi CONTENTS

The Contribution of Molisch to the Knowledge	
of the Purple Bacteria	118
Progress in the Study of the Sulfur Bacteria	119
The Work of Buder with Purple Sulfur Bacteria	
Van Niel's Broadened Concept of Photosynthesis	
Oxygenic and Anoxygenic Photosynthesis: Solutions to	
Classical Problems	122
Structure of the Photosynthetic Apparatus in Purple and	
Green Bacteria	123
Purple Bacteria	
Green Bacteria	
Conclusion	
References	128
Chapter 5	
Oxygenic Photosynthesis in Prokaryotes	
MARY MENNES ALLEN	
T 1 2	100
Introduction	
From Blue-Green Algae to Cyanobacteria	133
History of the Relationship between Blue-Green Algae	105
and Bacteria	135
Modern Methods for Establishment of Affinities	100
among Organisms	
Recognition as Prokaryotae	137
Discovery of the Role of Photosynthetic Pigments and	197
Electron Carriers in Cyanobacteria	137
Accessory Pigments	137
Mechanisms of Energy Transfer	139
Existence of Two Photosystems	139
Other Components of Cyanobacterial Photosynthesis	140
Fractionation of Photosynthetic Function	141
Photosynthetic Mutants of Cyanobacteria	142
Path of Carbon in Photosynthesis	142
Photosynthetic Structures in Cyanobacteria	142
Thylakoids	143
Phycobilisomes	
Nutritional Adaptations in the Photosynthetic Apparatus	
Light Quality and Quantity	145
Temperature Effects	145
Other Nutritional Adaptations	
Facultative Anoxygenic Photosynthesis	147
Conclusions	
References	148

CONTENTS xvii

Chapter 6	
Consumption of Atmospheric Nitrogen	
DAVID R. BENSON	
Introduction	156 156
Plant Nitrogen Advances Prior to 1940 Methodological Problems Development of an Ecological Understanding Advent of Isotopic Techniques Discovery of New N ₂ -fixing Organisms Expansion of Ecological Understanding Development of a Biochemical Understanding Advent of the Acetylene Reduction Technique Further Advances in Ecological Understanding Current Perspectives and Future Prospects References	167 168 172 172 172 174 175 175
CHAPTER 7 The Position of Bacteria and Their Products in Food Webs HENRY L. EHRLICH	
Introduction Concepts Bacterial Interactions in Food Webs Primary Producers Decomposers Bacteria as Predators and Prey Bacteria as Mutualistic, Commensal, or Parasitic Symbionts Syntrophy Antibiosis Conclusion References	199 204 204 206 207 207 209 213 213
CHAPTER 8 A Comparison of the Roles of Bacteria and Fungi D. M. GRIFFIN Introduction	221
indoduction	441

xviii	· ·	CONTENTS
-------	-----	----------

Significance of Growth Habit	222
Unicellular and Filamentous Forms	222
Translocation	223
Growth Pattern of Mycelial Colonies	225
Complex Structures	227
Attachment and Penetration	228
Physiological Aspects	229
General	229
Maximal Activity Rates	230
Copiotrophs and Oligotrophs	230
Temperature	239
Hydrogen Ion Concentration	232
Water Stress	232
Genetics	238
Some Important Microbial Ecosystems	230
Soil	239
Lichens	249
Associations between Microbes and Higher Organisms	943
Conclusions	947
References	947
	447
ė.	
INDEX	957

THE SCIENTIFIC STUDY OF BACTERIA, 1780–1980

Patricia H. Clarke

INTRODUCTION

This chapter covers a period of approximately 200 years that begins around 1780. The concept of "the bacterium" changed and developed during this time, and strong and often conflicting views were held by the leading scientists of the day. Leeuwenhoek's (1677) animalcules (described in his famous letter of 1676) are now considered to have included bacteria, and although at the beginning of the period under review there were those who thought that small living organisms might cause disease and bring about fermentations, there was no firm scientific evidence for either of these activities. The methods of the natural scientists, particularly the botanists, were used to observe and describe the teeming life that could be seen with the help of the improved microscopes. From a time when all very small organisms, including worms, protozoa, microfungi, and bacteria were regarded as similar creatures to be observed and described, we can trace an increasing awareness of the special attributes of bacteria. It took many years to settle the two major controversies over whether bacteria arose by spontaneous generation and whether fermentation was carried out by living organisms. The supporters of the spontaneousgeneration origin of microorganisms had arguments of common sense to sustain them, together with weak experimental technique. Until good methods for sterilization were available, it was difficult to refute their claims, and until the heat resistance of bacterial spores had been recognized, it was difficult to ensure that sterilization methods were adequate. The most vociferous supporters of spontaneous generation were mainly biologists, and a few chemists, while the main opposition to the concept of the microbiological basis of fermentation came from the leading organic chemists. Berzelius, Liebig, and

Patricia H. Clarke • Department of Biochemistry, University College London, London WC1E 6BT, England.