

CURRENT PERSPECTIVES IN

# MICROBIAL ECOLOGY

Edited by

M.J. KLUG AND C.A. REDDY

CURRENT PERSPECTIVES IN  
**MICROBIAL  
ECOLOGY**

Proceedings of the Third International Symposium  
on Microbial Ecology  
Michigan State University  
7-12 August 1983



Edited by  
**M. J. KLUG & C. A. REDDY**

American Society for Microbiology  
Washington, D.C.  
1984

Copyright © 1984, American Society for Microbiology  
1913 I Street, N.W.  
Washington, DC 20006

**Library of Congress Cataloging in Publication Data**

International Symposium on Microbial Ecology (3rd :  
1983 : Michigan State University)  
Current perspectives in microbial ecology.

Includes bibliographies and indexes.

I. Microbial ecology—Congresses. I. Klug, M. J.  
II. Reddy, C. A. III. American Society for Microbiology.  
IV. Title.  
QR100.I57 1983 576'.15 84-489  
ISBN 0-914826-60-3

All Rights Reserved

Printed in the United States of America

## Preface

Microbial ecology is a young discipline which has recently gained prominence because of recognition of the important role that microbial processes play in all ecosystems and ultimately in maintaining the environment of our planet. In the past decade, microbial ecology has emerged into a discipline with a body of knowledge and an identity of its own. Yet microbial ecology has not and should never lose its cross-disciplinary connections with other fields of microbiology as well as those of oceanography, limnology, soil science, atmospheric chemistry, and plant and animal sciences. Since a major goal of microbial ecology is to understand microbial activity in natural habitats, knowledge of both the microorganisms and the habitat is essential. During the past decade this integration has been successfully achieved by the practitioners of microbial ecology. It is now time that there be a further integration among microbial ecologists studying different habitats, since common principles transcend the habitat being studied. To illustrate the latter, one rarely sees an interaction between those who study microbial processes in oceans and those studying microbial activities in soil, and neither of these groups frequently interact with those studying the microbiology of the gastrointestinal tract. However, all these groups have a common interest in the strategies and processes that the inhabiting microbes utilize irrespective of the habitat. Such multi-disciplinary exchange can also lead to new insights and to the transfer of methods to new fields, and hence can aid our progress in understanding microbial processes in natural habitats. It is this multi-disciplinary objective that served as a guide for planning the invited paper sessions at the Third International Symposium on Microbial Ecology.

A second objective of this meeting was to emphasize certain directions in which we felt microbial ecology would be moving in the future and the ways in which microbial ecology affects practical problems. For example, the benefits from a relationship between microbial ecology and modern genetics have just recently been recognized. The role of and mechanisms associated with genetic exchange in the environment, and the impact it has on evolution, survival of microorganisms, and ecosystem stability, are all basic questions for which little experimental evidence has been obtained. On the practical side, it is the microbial diversity in nature that yields the genes of concern to commercial interests. This diversity has not been explored in a

comprehensive manner, nor has it been studied with an understanding of the ecological principles responsible.

Microbial ecology has been and will continue to be useful in biotechnology and industrial microbiology. Understanding the behavior of microbial populations requires knowledge of the growth, competition, and physiology of these populations within natural microbial communities. These principles are central to an understanding of microbial function in natural habitats as well as useful to the management of these populations within an industrial fermentation vat. Further examples of the important roles microbes play in our environment include the production and consumption of gases in our atmosphere, which can have a long-term impact upon our climate and quality of atmosphere; the degradation of numerous xenobiotic pollutants; and the bioconversion of natural and synthetic polymers. Microbes in nature also transform, corrode, and enhance the recovery of metals and are becoming increasingly important in the biological control of plant and animal pests.

The future importance of microbial ecology, at least in the commercial world, was recently emphasized by Bernard Dixon in an editorial in *Biotechnology*, in which he states that "most of the winners, I predict, would be those biotechnology teams which have had a microbial ecologist on board" (1). The knowledge of the diverse capacities of microorganisms in nature, understanding of how to recover those organisms, and experience with the physiology and growth of the more unusual organisms are all of use to a team that includes microbial geneticists and process engineers.

Invited papers for the Third Symposium on Microbial Ecology were grouped into sections representing four themes of microbial ecology: microbial adaptations, microbial interactions, microorganisms in ecosystems, and microbial bioconversions. This volume contains papers which represent highlights of oral presentations by the invited speakers on a wide range of subjects within the scope of the four themes of the symposium. These papers present the current status and projected future research directions of selected topics within these areas and are not meant to be comprehensive reviews. Subjects were selected on the basis of their current and predicted future importance and intentionally include different scales of investigations ranging from molecular to ecosystem. We hope this demonstrates how both reduction-

istic and holistic approaches are utilized to unravel the complexities of cellular, population, and community interactions involved in processes within natural habitats. For example, information at the subcellular level (e.g., genetics, biochemistry) is necessary to understand many mechanisms and processes in nature. Information at the cellular and population level (e.g., growth, competition, and interaction with other organisms or with the environmental matrix) is important to understanding the success of a process or the composition of a community. Finally, information at the ecosystem level is important to understanding the impact of the process or of environmental stresses on our environment. Furthermore, it is this level which is the ultimate test of whether knowledge from the reductionist approach can reliably predict behavior at the ecosystem level.

Because of these various approaches and subject matter the format and style of the papers also vary, from those reporting original research results to those of a review nature. It is hoped that this combination provides a balance which will increase the usefulness of this volume and enhance multi-disciplinary communication, and thus lead to a better understanding of microbial ecology. The volume should be useful as a textbook for an advanced or topics course in Microbial Ecology, as well as a reference source to current literature in the multitude of presented topics.

The local organizing committee thanks the

National Science Foundation for a major financial contribution to the meeting and recognizes the additional contributions from the Agricultural Experiment Station, Departments of Crop and Soil Science, Microbiology, and Public Health, and The W. K. Kellogg Biological Station, all of Michigan State University. We also thank Unesco and UNEP for support of some participants from developing nations.

We are indebted to Clayton Wells of The Kellogg Conference Center Staff for his experienced assistance in organizing the meeting. We gratefully acknowledge the contributions of Alice Gillespie, Jean Marek, Carolyn Hammar-skjold, Charlotte Adams, and Ellie Tupper. Their diligent handling of correspondence, information retrieval, copy editing, and organization have allowed this volume to meet an early deadline.

#### *Local Organizing Committee*

John A. Breznak  
Frank B. Dazzo  
Michael J. Klug  
John L. Lockwood  
C. A. Reddy  
James M. Tiedje

East Lansing, December 1983

#### LITERATURE CITED

1. Dixon, B. 1983. Commentary. The need for microbial ecologists. *Biotechnology* 1:45.

# CURRENT PERSPECTIVES IN MICROBIAL ECOLOGY

## Contents

Preface.....	xi
<b>MICROBES AND ECOLOGICAL THEORY</b>	
Relevance of <i>r</i> - and <i>K</i> -Theory to the Ecology of Plant Pathogens. JOHN H. ANDREWS .	1
Microbial Diversity and Decomposer Niches. M. J. SWIFT .....	8
Some Potentials for the Use of Microorganisms in Ecological Theory. WILLIAM J. WIEBE .....	17
Geographical Ecology of Marine Bacteria: Physical and Biological Variability at the Mesoscale. HUGH W. DUCKLOW .....	22
<b>PHYSIOLOGICAL AND MORPHOLOGICAL ADAPTATIONS</b>	
Role of Prostheca Development in Oligotrophic Aquatic Bacteria. JEANNE S. POINDEXTER.....	33
Effect of Light-Nutrient Interactions on Buoyancy Regulation by Planktonic Cyanobacteria. ALLAN KONOPKA.....	41
Adaptation of Bacteria to External pH. ETANA PADAN.....	49
Effects of Iron on Bacterial Growth and Bioluminescence: Ecological Implications. MARGO G. HAYGOOD AND KENNETH H. NEALSON.....	56
<b>GENETIC ADAPTATION TO THE ENVIRONMENT</b>	
The Role of Plasmids in Microbial Ecology. JOHN E. BERINGER AND PENNY R. HIRSCH	63
Evolution of New Phenotypes. PATRICIA H. CLARKE .....	71
Adaptation by Acquisition of Novel Enzyme Activities in the Laboratory. BARRY G. HALL .....	79
Genetic Interactions in Microbial Communities. J. HOWARD SLATER .....	87
Genetic Adaptations Involving Heavy Metals. ANNE O. SUMMERS .....	94
Factors Affecting Conjugal Plasmid Transfer in Natural Bacterial Communities. ROLF FRETER .....	105
<b>MECHANISMS OF MICROBIAL ADHESION TO SURFACES</b>	
Direct Ultrastructural Examination of Adherent Bacterial Populations in Natural and Pathogenic Ecosystems. J. WILLIAM COSTERTON.....	115
Microbial Attachment to Nonbiological Surfaces. MADILYN FLETCHER AND S. McELDOWNY.....	124
Attachment of Nitrogen-Fixing Bacteria to Plant Roots. FRANK B. DAZZO .....	130
Mechanisms of the Attachment of Bacteria to Animal Cells. G. W. JONES.....	136
Mechanisms of Specific Bacterial Adhesion to Cyanobacterial Heterocysts. F. S. LUPTON AND K. C. MARSHALL .....	144
Effects of Interfaces on Survival Mechanisms of Copiotrophic Bacteria in Low-Nutrient Habitats. STAFFAN KJELLEBERG.....	151

*Continued on following page*

Continued from preceding page

## NEW AND UNUSUAL MICROORGANISMS AND NICHES

Stem-Nodulating Rhizobia. B. L. DREYFUS, D. ALAZARD, AND Y. R. DOMMERGUES .	161
Recent Progress in the Microbiology of Hydrothermal Vents. H. W. JANNASCH AND D. C. NELSON .....	170
Endolithic Microorganisms in Extreme Dry Environments: Analysis of a Lithobiontic Microbial Habitat. E. IMRE FRIEDMANN AND ROSELI OCAMPO-FRIEDMANN .....	177
Evidence for Microbial Growth in High-Pressure, High-Temperature Environments. JOHN A. BAROSS, JODY W. DEMING, AND ROBERT R. BECKER .....	186
Habitats of <i>Chloroflexus</i> and Related Organisms. RICHARD W. CASTENHOLZ .....	196

## INFECTIOUS PROCESSES IN PLANTS

Development of Vesicular-Arbuscular Mycorrhizae. GLYNN D. BOWEN .....	201
Molecular Basis for the Specificity of Plant Pathogenic Microorganisms for Their Hosts. R. N. STRANGE .....	208
Infection Process in the <i>Rhizobium</i> -Legume Symbiosis. BJØRN SOLHEIM .....	217
The Actinorhizal Infection Process: Review of Recent Research. ALISON M. BERRY...	222
Adherence and Host Recognition in <i>Agrobacterium</i> Infection. JAMES A. LIPPINCOTT, BARBARA B. LIPPINCOTT, AND JONATHAN J. SCOTT .....	230
Future Paths in Rhizosphere Studies .....	237

## GASTROINTESTINAL MICROECOLOGY

Physiological Basis for Interactions Among Rumen Bacteria: <i>Streptococcus bovis</i> and <i>Megasphaera elsdenii</i> as a Model. J. B. RUSSELL AND M. S. ALLEN .....	239
Adaptations of Gastrointestinal Bacteria in Response to Changes in Dietary Oxalate and Nitrate. M. J. ALLISON AND C. ADINARAYANA REDDY .....	248
Role of Mycophagy and Bacteriophagy in Invertebrate Nutrition. MICHAEL M. MARTIN AND JEROME J. KUKOR .....	257
Influence of Plasmids on the Colonization of the Intestine by Strains of <i>Escherichia coli</i> in Gnotobiotic and Conventional Animals. Y. DUVAL-IFLAH AND J. P. CHAPPUIS .....	264
Importance of Microbial Nitrogen Metabolism in the Ceca of Birds. ATLE MORTENSEN .....	273

## MICROBIAL COMPETITION

Competition Among Bacteria: an Overview. H. VELDKAMP, H. VAN GEMERDEN, W. HARDER, AND H. J. LAANBROEK .....	279
Growth and Interactions of Microorganisms in Spatially Heterogeneous Ecosystems. J. W. T. WIMPENNY, J. P. COOMBS, AND R. W. LOVITT .....	291
Evaluation of Competition in <i>Rhizobium</i> spp. NOËLLE AMARGER .....	300
Competition Among Chemolithotrophic Bacteria Under Aerobic and Anaerobic Conditions. J. G. KUENEN AND L. A. ROBERTSON .....	306
Freshwater Algal Ecology: Taxonomic Trade-Offs in the Temperature Dependence of Nutrient Competitive Abilities. DAVID TILMAN AND RICHARD L. KIESLING .....	314

## MICROBES AS PREDATORS OR PREY

Heterotrophic, Free-Living Protozoa: Neglected Microorganisms with an Important Task in Regulating Bacterial Populations. MARIANNE CLARHOLM .....	321
Fungal Development, Predacity, and Recognition of Prey in Nematode-Destroying Fungi. BIRGIT NORDBRING-HERTZ AND HANS-BÖRJE JANSSON .....	327
<i>Bdellovibrio</i> as a Predator. M. SHILO .....	334

Continued on following page



Continued from preceding page

Natural Bacteria as Food Resources for Zooplankton. KAREN G. PORTER .....	340
Simulation Model of a Food Web with Bacteria, Amoebae, and Nematodes in Soil. H. W. HUNT, D. C. COLEMAN, C. V. COLE, R. E. INGHAM, E. T. ELLIOTT, AND L. E. WOODS .....	346

### BIOLOGICAL CONTROL

Ecological Principles of Biocontrol of Soilborne Plant Pathogens: <i>Trichoderma</i> Model. YIGAL HENIS .....	353
Bacteria as Biocontrol Agents of Plant Disease. M. N. SCHROTH, J. E. LOPER, AND D. C. HILDEBRAND .....	362
Biocontrol of <i>Botrytis cinerea</i> on Grapevines by an Antagonistic Strain of <i>Trichoderma</i> <i>harzianum</i> . BERNADETTE DUBOS .....	370
Control of Gastrointestinal Pathogens by Normal Flora. GERALD W. TANNOCK .....	374
Can Pathogenic Microorganisms Be Established as Conventional Control Agents of Pests? DE-MING SU .....	383

### COMPARATIVE CARBON AND ENERGY FLOW IN ECOSYSTEMS

Role of Microbes in Global Carbon Cycling. J. E. HOBBIIE AND J. M. MELILLO .....	389
Carbon and Energy Flow in Terrestrial Ecosystems: Relevance to Microflora. O. W. HEAL AND P. INESON .....	394
Significance of Microorganisms in Carbon and Energy Flow in Marine Ecosystems. LAWRENCE R. POMEROY .....	405
Role of Heterotrophic Protozoa in Carbon and Energy Flow in Aquatic Ecosystems. BARRY F. SHERR AND EVELYN B. SHERR .....	412
Carbon and Energy Flow Through Microflora and Microfauna in the Soil Subsystem of Terrestrial Ecosystems. E. T. ELLIOTT, D. C. COLEMAN, R. E. INGHAM, AND J. A. TROFYMOW .....	424

### COMPARATIVE N AND S CYCLES

Oxygenic Photosynthesis, Anoxygenic Photosynthesis, and Sulfate Reduction in Cyano- bacterial Mats. YEHUDA COHEN .....	435
Interrelation of Carbon, Nitrogen, Sulfur, and Phosphorus Cycles During Decomposition Processes in Soil. JOHN W. B. STEWART .....	442
Seasonal Variation and Control of Oxygen, Nitrate, and Sulfate Respiration in Coastal Marine Sediments. JAN SPØRENSEN .....	447
Denitrification and Nitrification in Coastal and Estuarine Sediments. ISAO KOIKE, TAKASHI NISHIO, AND AKIHIKO HATTORI .....	454

### ATMOSPHERIC-BIOSPHERIC EXCHANGES

Capacity of Aerobic Microorganisms to Utilize and Grow on Atmospheric Trace Gases (H <sub>2</sub> , CO, CH <sub>4</sub> ). RALF CONRAD .....	461
Contribution of Biological Processes to the Global Budget of CH <sub>4</sub> in the Atmosphere. WOLFGANG SEILER .....	468
Sources and Sinks of Nitrous Oxide. WARREN KAPLAN .....	478

### ECOLOGICAL SIGNIFICANCE OF BIOMASS AND ACTIVITY MEASUREMENTS

Factors Affecting Bacterioplankton Density and Productivity in Salt Marsh Estuaries. RICHARD T. WRIGHT AND RICHARD B. COFFIN .....	485
Aquatic Bacteria: Measurements and Significance of Growth. ÅKE HAGSTRÖM .....	495

Continued on following page



*Continued from preceding page*

Diurnal Responses of Microbial Activity and Biomass in Aquatic Ecosystems. CHRISTIANE KRAMBECK .....	502
Field Interpretation of Microbial Biomass Activity Measurements. E. A. PAUL AND R. P. VORONEY .....	509
Microbial Biomass and Activity Measurements in Soil: Ecological Significance. P. NANNIPIERI .....	515

#### MICROBIAL RESPONSES TO ECOSYSTEM PERTURBATIONS

Influence of Clear-Cutting on Selected Microbial Processes in Forest Soils. JAMES R. GOSZ AND FREDRICK M. FISHER .....	523
Catastrophic Disturbances to Stream Ecosystems: Volcanism and Clear-Cut Logging. JAMES R. SEDELL AND CLIFFORD N. DAHM .....	531
Use of Microbial Diversity Measurements to Assess Environmental Stress. RONALD M. ATLAS .....	540
Effects of Oil on Bacterial Activity in Marine and Freshwater Sediments. JOHN H. BAKER AND ROBERT P. GRIFFITHS .....	546

#### METABOLISM OF NATURAL POLYMERS

Biofuels and Oxychemicals from Natural Polymers; a Perspective. DOUGLAS E. EVELEIGH .....	553
Physiology and Biochemistry of Lignin Degradation. C. A. REDDY .....	558
Factors Affecting Cellulase Activity in Terrestrial and Aquatic Ecosystems. A. E. LINKINS, J. M. MELILLO, AND R. L. SINSABAUGH .....	572
Microbial Degradation of Pectin in Plants and Aquatic Environments. BERNHARD SCHINK .....	580
Microbial Ecology of Cellulose and Hemicellulose Metabolism in Gastrointestinal Ecosystems. N. O. VAN GYLSWYK AND H. M. SCHWARTZ .....	588

#### BIOCONVERSION OF INORGANIC MATERIALS

Mechanisms of the Binding of Metallic Ions to Bacterial Walls and the Possible Impact on Microbial Ecology. T. J. BEVERIDGE .....	601
Biological Transformation and Accumulation of Uranium with Emphasis on <i>Thiobacillus ferrooxidans</i> . OLLI H. TUOVINEN AND ALAN A. DISPIRITO .....	608
Bacterial Transformations of Manganese in Wetland Environments. W. C. GHORSE ...	615
Anaerobic Corrosion of Iron and Steel: a Novel Mechanism. W. P. IVERSON AND G. J. OLSON .....	623

#### ECOLOGICAL STRATEGIES FOR THE FERMENTATION INDUSTRY

Recruitment of Novel Reactions: Examples and Strategies. I. JOHN HIGGINS, DAVID J. BEST, GRAEME MACKINNON, AND PHILIP J. WARNER .....	629
Pelletization of Anaerobic Sludge in Upflow Anaerobic Sludge Bed Reactors on Sucrose-Containing Substrates. L. W. HULSHOFF POL, J. DOLFING, K. VAN STRATEN, W. J. DE ZEEUW, AND G. LETTINGA .....	636
Relevance of Low-Nutrient Environments to Fermentation Process Design and Control. D. W. TEMPEST, O. M. NEIJSSSEL, AND J. J. TEIXEIRA DE MATTOS .....	643
Marine Microorganisms as a Source of Bioactive Substances. YOSHIRO OKAMI .....	651
Mixed-Culture Fermentations in Industrial Microbiology. IAN SALMON AND ALAN T. BULL .....	656

*Continued on following page*

*Continued from preceding page*

# BIODEGRADATION OF XENOBIOTICS

Experimental Evolution of Azo Dye-Degrading Bacteria. H. G. KULLA, R. KRIEG, T. ZIMMERMANN, AND T. LEISINGER .....	663
Biodegradation of Chlorophenolic Compounds in Wastes from Wood-Processing Industry. M. S. SALKINOJA-SALONEN, R. VALO, J. APAJALAHTI, R. HAKULINEN, LIISA SILAKOSKI, AND T. JAAKKOLA .....	668
Kinetic and Ecological Approaches for Predicting Biodegradation Rates of Xenobiotic Organic Chemicals in Natural Ecosystems. ROBERT J. LARSON.....	677
Biochemistry and Practical Implications of Organohalide Degradation. H.-J. KNACKMUSS .....	687
Genetics of Xenobiotic Degradation. RICHARD W. EATON AND KENNETH N. TIMMIS. ....	694
Author Index .....	705
Subject Index .....	706

# Microbes and Ecological Theory

## Relevance of *r*- and *K*-Theory to the Ecology of Plant Pathogens

JOHN H. ANDREWS

*Department of Plant Pathology, University of Wisconsin, Madison, Wisconsin 53706*

Identifying the selection pressures responsible for evolution of a group of interrelated characteristics such as an organism's size, fecundity, and generation time presents an important and fascinating ecological challenge. One pressure that might explain many life history differences is the density of a species with respect to its resource. This is the basis for the theory of *r*- and *K*-selection.

My intent in this chapter is to discuss the origin of the theory of *r*- and *K*-selection, its current status, and its relevance to microbial ecology, particularly to the ecology of plant pathogens. The terminology and concepts are drawn largely from macroecology, but this seems appropriate since each organism, whether a bird or a bacterium, has evolved coadapted traits which promote its survival.

### THE *r*- AND *K*-THEORY

It is intuitively logical that a species living near the carrying capacity (given as *K*-selected individuals) of its environment is subjected to a different form of selection pressure than one essentially in a rarefied habitat, exposed to flushes of abundant resources which provide for population expansion. The premium is on competitiveness in the former case, whereas genotypes with a high intrinsic rate of increase (*r*) are favored in the latter. These hypothetical situations are grounded in Dobzhansky's (5) observations that adaptation in the tropics is to a harsh biological environment (e.g., competition, parasitism), whereas in temperate or cold climates, characterized by fewer species, adaptation consists primarily in coping with the physical environment and securing food. He interpreted differences between tropical and temperate organisms as the outcome of different evolutionary patterns. Intricate interactions and density-dependent (DD) controls were viewed as the major factors influencing populations in the tropics, whereas in severe environments density-independent (DI) regulation selected for traits such as cold resistance or accelerated development. (DD controls cause proportionate changes in mortality or fecundity as population density

changes; normally, mortality increases and percent fecundity decreases with increasing population size. DI controls operate essentially independently of population density; i.e., the same proportion of organisms is affected at any density.)

MacArthur and Wilson (15, 16) focused and formalized Dobzhansky's abstract idea in their theoretical analysis of island biogeography. They emphasized that in uncrowded environments (*r*-selection), represented by initially uncolonized islands, individuals harvesting the most food, even if wastefully, will be the fittest. Evolution here favors productivity, i.e., high *r* values. However, in time as islands "saturate" with species and food becomes limiting (*K*-selection), genotypes which can at least replace themselves even with smaller families will be superior. Evolution here favors efficiency of converting food into offspring. Hence, colonizing or pioneering organisms will be subject to *r*-selection, but as they establish, the pressure will swing to *K*-selection. This trend will be influenced by changes in the local environment (16).

Given this elegant framework, one might pose several questions, among them: (i) Which environmental conditions favor *r*- or *K*-selection? (ii) How can an organism alter its life history or other factors to maximize *r* or *K*? (iii) Can the attributes of an organism be correlated with life in the anticipated environment (9)? Not surprisingly, the apparent predictive and explanatory power of the *r*-*K* concept has been used in many contexts and has provoked much controversy. For instance, Pianka (19) proposed an *r*-*K* continuum along which species could be placed on the basis of their suites of characteristics (Table 1), and Southwood (23) related position of insect pests along such a spectrum to implications for control tactics.

Current use of the theory has been criticized as confusing and misleading. Wilbur et al. (26) pointed out that although aspects of life history strategy can be correlated with certain environmental parameters, there may not be a cause-and-effect relationship. For example, although characters such as high fecundity and short

TABLE 1. Some life history traits predicted to be associated with *r*- or *K*-selection<sup>a</sup>

Criterion	<i>r</i> -selected species	<i>K</i> -selected species	Plant pathogens
Mortality	Often catastrophic; density-independent	More directed; density-dependent	Predominantly density-independent
Reproductive method	Asexual mitosis to biparental sexual	Predominantly biparental sexual	Predominantly asexual; sexual hermaphroditism common; biparental sexual occasionally
Phenotypic plasticity	Polymorphic to monomorphic	Monomorphic	Usually polymorphic
Structure of species	Monotypic to polytypic	Usually monotypic	Usually polytypic
Length of life	Short; usually less than 1 yr	Longer; usually more than 1 yr	Hours to years
Migratory tendency	High	Low	High
Utilization of resources	For productivity	For efficiency	Usually for productivity; may or may not destroy host
Population size	Variable; nonequilibrium; usually below carrying capacity; frequent recolonization necessary	Constant; equilibrium; at or near carrying capacity; no recolonization necessary	Generally variable; nonequilibrium; recolonization often necessary
Tolerance to niche overlap	Larger	Smaller	Larger

<sup>a</sup> Modified after Pianka (19) and Andrews and Rouse (2).

generation time in an unlimited environment will result in a high *r*, it is incorrect to reverse the logic and conclude that relatively nonlimiting environments are primarily responsible for evolution of organisms with such features (26). Furthermore, they argued that life history strategies cannot be fully explained as resulting from single selection pressures such as *r*- and *K*-selection.

Use of the theory has also been criticized as inexact and inappropriate. Parry (17) commented that use of the terms is now so broad that any life history dichotomy is attributed to *r*- or *K*-selection. His criticism needs to be reviewed briefly so that this chapter can be placed clearly in context.

Of the four meanings Parry discussed (Table 2), meanings III and IV are really predictions rather than explanations and can be dispensed with initially. Meaning III predicts where *r*- or *K*-selected organisms would live, i.e., in "ephemeral" or "permanent" habitats, respectively. Meaning IV suggests what they would be doing, i.e., allocating large (*r*) or small (*K*)

percentages of their resources to reproduction. Whatever else may detract from these latter two definitions as accurate descriptors (see 17), they imply merely a correlative and not necessarily a causative relationship (cf. 26). Hence, although *r*-selected species may occupy temporary habitats, life history features of these species may have arisen for reasons other than *r*-selection pressure (e.g., seasonality).

Meanings I and II are the more substantive and deal with the nature of *r*- and *K*-selection. Meaning I, stemming from MacArthur and Wilson (16), focuses on crowding. To the extent that this implies competitive pressure only, it is more restricted than meaning II, dealing with all DD and DI effects. Meaning II is acceptable, if it is understood that in nature *K* is set by the interplay of many factors and not by resources alone. Resources (primarily food) remain the center of attention in debates over *r*- and *K*-selection because the pioneering work which led to the formulation and early testing of the logistic model involved closed-system laboratory cultures of yeasts and protozoa. This emphasis

TABLE 2. Various meanings of *r*- and *K*-selection<sup>a</sup>

Meaning	Central aspect	Conditions under	
		<i>r</i> -selection	<i>K</i> -selection
I	Crowding	Uncrowded; productivity	Crowded; competitiveness
II	Density effects	Density-independent component	Density-dependent effects
III	Habitat	Relatively ephemeral	Relatively permanent
IV	Resource allocation	Large percent to reproduction	Small percent to reproduction

<sup>a</sup> Summarized from Parry (17).

continued in island biogeographic theory which implicitly or explicitly emphasized competition for food or space (e.g., 16, 18), although subsequent papers by Wilson and his colleagues (e.g., 21) discussed the role of predation and other factors in species extinction. However, MacArthur and Wilson's model did not address the factors that determine  $K$ , or fluctuations in  $K$  over time. Crowding implies the density at which adverse effects of individuals on one another become limiting, and not all such effects arise from competition (25). Other impacts include waste product accumulations, cannibalism, emigration, and increased parasitism and predation. In fact, to account for such metabolic alterations and social interactions, as well as for competition, modification of the logistic model has been suggested (22).

Provided that the broader implications of crowding are recognized, then in practice there is little difference between meaning I and meaning II, because DD controls will be more influential in crowded than uncrowded environments. Although the various sources of DD mortality (e.g., predation, metabolite accumulation) may well affect life history strategies differently, the common stimulus for this evolutionary response is crowding. Such an enlarged perspective also aligns current thinking on  $r$ - and  $K$ -theory more closely with Dobzhansky's (5) original observations. Clearly, he viewed competition as only one of many factors playing a role in complex tropical communities. The challenge in experimental design is, first, to assess the relative influence of DD versus DI mortality and, second, to identify the specific DD components involved.

In overview,  $r$ - and  $K$ -selection should be used with respect to a particular selection regime, rather than basing meanings on the individual traits predicted by the selection conditions. A consequence of arguing backwards from the traits to a definition is circular reasoning, and the theory reduces to a tautology.

### TESTS OF THE THEORY

In general, there are two ways to test life history theories: the comparative approach and the predictive approach (24). The former involves comparing representative species or genera under present conditions, which are assumed to be identical to those under which they evolved, and testing hypotheses against field or laboratory observations. This provides an interesting intellectual exercise, but as Stearns (24) pointed out, the logic is weaker than that used predictively. The method is also subject to many pitfalls (12, 24). For example, differences in the trait studied may be easier to interpret between closely related species than between those that

are distantly related. Despite their shortcomings, comparisons are often used in macroecology because many of the adaptations of interest lie beyond the realm of experimentation. In the predictive approach, selective differences between habitats are measured, and predictions are made about how life history differences of the species of interest might alter if the populations were interchanged or otherwise manipulated (24). If the traits do not change as anticipated, then either the experiment or the theory is flawed. Regardless of the approach taken, there are numerous ambiguities which complicate tests of  $r$ - and  $K$ -theory, and Stearns has outlined (24) a set of "reliability criteria" which could be used in the design or evaluation of experiments.

Andrews and Rouse (2) proposed that  $r$ - and  $K$ -theory is relevant to the analysis of plant pathogen life histories and used the comparative approach to rank representative pathogens along a continuum relative to each other. Two criteria were emphasized as determinants of strategy: first, the proportionate allocation of resources to maintenance, growth, and reproduction; and second, the nature of the parasitic association, particularly with respect to derivation of nutrients and impact on the host. A conceptual model was devised to describe the theoretical relationships between the population parameters biomass, or numbers, and life history strategies. A central idea was that  $r$ -selected organisms channel more resources to reproduction than  $K$ -strategists (see 7; criticized in 17). With respect to mode of nutrition, biotrophic parasites (which obtain nutrients from living host cells) were considered to be more  $K$ -selected than necrotrophic parasites and were viewed as inducing stress to host plants; by contrast, necrotrophic parasites (derivation of nutrients from killed cells), which cause "disturbance" by actively destroying plant biomass (2; cf. 10), were viewed as  $r$ -strategists. The reasoning for this distinction was that  $K$ -strategists clearly have an investment in maintaining the vigor of their hosts, with which they would tend toward coexistence. On the other hand,  $r$ -strategists can aggressively invade and destroy their hosts (the so-called "sweepstakes" strategy) and then adopt an expanding saprophytic phase (cf. insects, 23). Within the biotrophic category one might visualize a continuum ranging from parasites such as the apple scab pathogen ( $r$ -selected) to the mistletoes (e.g., *Phoradendron flavescens*), which are generally consistent with Pianka's (19) correlates for a  $K$ -strategist. In addition to being small and having a short generation time, the former channels much of its resources to asexual reproduction during the summer and can cause severe disturbance to the

host. However, the mistletoes appear to emphasize efficiency over productivity. As perennial, semiparasitic evergreens, they produce carbohydrate photosynthetically and rely upon their host for minerals and water. They rarely destroy biomass, but act as low-grade stressors. DD controls (e.g., competition for sunlight) likely play an important role in population regulation of mistletoes, whereas populations of apple scab are markedly affected by DI factors such as temperature and rainfall.

There is an aspect of "story-telling" to comparisons or analogies such as the above, and appealing stories can easily be concocted to fit the facts. Comparisons fall short as explanations because of the criticisms raised earlier—for one reason, they do not separate correlation from causation. (It is significant that Pianka [19] referred to the features of  $r$ - and  $K$ -selection as *correlates*.) Convincing tests of  $r$ - and  $K$ -theory can only be made by identifying key components of its broad nature and then posing specific, falsifiable hypotheses which have some predictive value. Plant pathogens are used as examples in the following experiments, but the same concepts apply to free-living microbes.

A direct test of  $r$ - and  $K$ -theory is to crowd populations and see what happens (Table 3). According to the central idea,  $K$ -selection involves DD regulation in environments where populations approach the carrying capacity; conversely,  $r$ -selection results when DI factors maintain populations below equilibrium. Thus, one would predict that various life history traits such as fecundity and competitiveness should be influenced differently in the two environments. Microbial systems generally are much more amenable to such experimental manipulations than are plants or animals, and most of Stearns' (24) other "reliability criteria" can also be satisfied with less difficulty. Thus, crowding or abiotic factors can be varied while holding other conditions constant, thereby avoiding the correlative-type approach and inferential evidence. The underlying premise of these tests is that there are two opposing types of selection which result in a trade-off; i.e., a  $K$ -strategist will be less fit under conditions of  $r$ -selection and vice versa. (Note that the terms  $K$ -strategist and  $r$ -strategist are relative descriptors and are appropriately used to compare one organism with another.)

Direct tests are feasible with plant pathogens (especially procaryotes, fungi, and nematodes) by adapting populations in vitro or in vivo to DD and DI controls and then testing how these adapted strains perform against each other and the parental types in the two environments. DD conditions could be achieved in vitro by allowing populations to reach and remain at the

TABLE 3. Some possible tests of the theory of  $r$ - and  $K$ -selection<sup>a</sup>.

Trait	Prediction under	
	DI controls	DD controls
Biomass allocation	Reproduction	Growth and maintenance
Ontogeny	Higher rate	Lower rate
Fecundity	Higher	Lower
Reserves	Lower	Higher
Nutrient responsiveness	Faster	Slower
"Competitiveness"	Lower	Higher

<sup>a</sup> Hypothesis: certain life history traits result from crowding. Experiment: subject populations to crowding; compare populations from, or introduce populations to, crowded and uncrowded environments.

carrying capacity over many generations in fed batch or continuous culture; for DI regulation, populations could be serially transferred or subjected to abiotic controls (e.g., heat or cold shock). This approach was used by Luckinbill (14), who grew pairwise combinations of  $r$ - and  $K$ -adapted strains and parental types of *Escherichia coli* in mixed culture. The proportion of competitively neutral auxotrophic and prototrophic markers for histidine provided an indication of whether adaptation to culture conditions had occurred. Experiments with plant pathogens that produce unambiguous results in vivo would be considerably more complicated to design, partly because the carrying capacity of plants for the organism of interest would need to be defined operationally and could be expected to be highly variable. Nevertheless, such tests are needed for a realistic appraisal of the theory, and some possibilities are outlined below.

Some of the life history traits that could be expected to vary under DD or DI controls are listed in Table 3. In theory these features are measurable; in practice they could be quantified more or less accurately depending on the trait, the species characteristics, and the assay system. For example, a measure of ontogeny could be time to sporulation, to symptom development, or to completion of life cycle. Reserves could be quantified by monitoring storage products (e.g., lipids, poly- $\beta$ -hydroxybutyrate) or calorific values (11). "Competitiveness" is a more subjective criterion and involves several possible features, among them tolerance of antibiotics, the production of secondary substances such as inhibitory materials, siderophores, or slime, the ability to store a wide variety of materials, the ability to utilize many carbon and energy sources concurrently, and the ability to efficiently convert limiting nutrients into biomass. A common problem, as elaborated on

elsewhere (1), seems to be the confusion of colonizing ability with competitiveness per se.

There are two corollaries to the direct test. The first is that populations isolated in nature from crowded and uncrowded environments should show traits consistent with predictions (Table 3). This has been the indirect, observational approach traditionally used in macroecology. The second corollary is that populations adapted to *r*- and *K*-selection in vitro, when reintroduced to nature, should become established best in the environments that present the corresponding selective pressure. An expectation might also be a shift in adaptive features over time; i.e., a newly colonizing species will be subjected to *r*-selection, but after establishment it should shift under *K*-selection pressure (see following comments on phenotypic and genotypic changes). This latter corollary is consistent with the biogeographic implications foreseen by MacArthur and Wilson (16). Both corollaries offer less rigorous tests of the theory than does the original proposition. The problem of correlation versus causation was noted earlier. Additionally, the corollaries are weakened by several assumptions, e.g., that *r*- and *K*-selection will be the factor determining survival of adapted populations reintroduced to nature. There is also some circular logic in that if experiments proceed according to expectations all is well, but if evidence is produced against the hypothesis one can always argue that the environments did not really present *r*- or *K*-selection pressure or, in any case, that there were too many uncontrolled variables.

If one elects to test the corollaries, a possible approach to the first would be to make inter- or intraspecific comparisons, including competitive tests, of plant pathogens based on the criteria described above, from a host species subjected to lax versus intense parasitism (e.g., early versus late in the growing season). Such comparisons should also be made on organisms from natural communities, where the artifacts of agroecosystems do not pose problems to interpretation of results. The expectations would be that parasites colonizing early have characteristics of *r*-strategists, whereas later, when DD controls such as competition for infection sites and resources intensify, the predominant species or biotypes are relatively *K*-selected. In addition to exhibiting life history traits typical of *r*- or *K*-strategists (Table 3), the early colonizers should outclass the later colonizers when tested in vitro under controlled DI conditions and vice versa (see 14). A complementary approach would be to compare characteristics of parasites, at any given time, from newly emerging roots or shoots and those attacking older portions.

The second corollary could be tested by adapting populations in vitro to DI or DD controls as described above (14) and releasing them alone and in combination to relatively "unsaturated" versus "saturated" environments. Similar studies with antagonists to the apple scab pathogen are in progress (J. H. Andrews and D. Cullen, unpublished data), but we have not extended this work yet to specifically test *r*- and *K*-concepts. If introduced populations are not sufficiently morphologically distinct (e.g., color mutants), they need to be marked (e.g., auxotrophy, antibiotic resistance) for recovery on test media. An example is to adapt in culture a physiologically marked color mutant of the scab organism to DI and DD controls. Severely infected ("saturated" environment) and slightly infected ("unsaturated" environment) apple trees in growth rooms and in an orchard could then be inoculated with these adapted strains alone and in combination. The introduced populations and their progeny could be monitored over time, distinguished from the wild type by color and from each other by nutritional requirements. The hypothesis would be that relative establishment of the *K*-selected strain is greater than the *r*-selected strain on severely infected leaves; the reverse would be expected on slightly infected leaves. Of course, the usual assumptions pertaining to marked populations, such as stability and competitive neutrality of the marker, apply and would have to be verified in advance.

#### IMPLICATIONS OF THE THEORY

The extent to which *r*- and *K*-selection is eventually found relevant to microbiology is secondary for the time being to the fact that microbial systems seem to have excellent potential for critical appraisals of the theory. These tests in themselves can provide for new perspectives and interpretations. If the evidence is supportive, there are numerous implications and predictions stemming from the theory. If the evidence overall is negative, then the obvious question would be: If crowding does not play a major role in shaping microbial strategies, what does? Either way, the investigator will be forced to identify the factors which control microbe populations.

If *r*-*K* theory is upheld for microbial communities, a major benefit would be the strengthening of bridges between microbial ecology and macroecology. An elegant body of ecological theory on life history tactics would be opened to microbiologists and plant pathologists. Conversely, ecologists would become better informed and appreciative of how microbes can be used to test ecological theory. Microbial systems should provide the means in large part to



quell a typical criticism, namely, that speculation flourishes in the absence of fact.

For populations shown to be *r*- or *K*-selected, the next step might be to identify the specific conditions that increase *r* or *K*. Is the ability to produce several spore crops from a given conidiophore going to increase *r* more than increasing conidiophore numbers by a given increment? What factors would promote either option? Would *K* be increased more by a tolerant than by a susceptible host? What influence has the presence of a diverse epiphytic microbial community on carrying capacity for a given pathogen and is interspecific competition a more significant DD control than intraspecific competition?

Luckinbill (14) has posed the question of the specific genetic mechanisms involved in *r*- or *K*-adaptations induced in culture. To move back a step further, one might start by asking whether the changes induced in vitro and in vivo are phenotypic or genotypic adaptations. The expectation would be for the former to occur initially, followed by quick deadaptation if selection were relaxed. If the *r*- or *K*-selection pressure were severe or imposed for a long time (typically hundreds of generations), genetic change should occur. How will the persistence of strains reintroduced to nature vary in the presence or absence of the corresponding selection pressure? The issue of the kind of change is very important because of the largely genetic origins of *r*- and *K*-theory in island biogeography and because the concept deals with the evolution of life history traits. Gadgil and Solbrig (7) proposed that the crucial evidence for *r*- and *K*-selection is whether an organism maintained a particular strategy (e.g., resource allocation) under any and all DD and DI mortality conditions.

The idea that microorganisms with distinct phases (biphasic or heteromorphic) may be evolving simultaneously as *r*-strategists under one set of environmental conditions and as *K*-strategists under another has been developed elsewhere (1), and there are analogies with other systems, especially seaweeds (13). Presumably, this phenomenon is one example of Dobzhansky's (5) adaptive polymorphism whereby a species consists of two or more types, each having high fitness in a particular environment. Bimodal *r*- and *K*-selection is one attractive explanation for the life history features of many parasites which use abundant host resources during the summer to reproduce exponentially, and then channel resources to vegetative growth and maintenance in a competitive environment during the winter. However, there are other explanations, such as the constraints imposed by seasonality. Definitive explanations cannot be made until experiments are designed to test

the various hypotheses.

From the perspective of a plant pathologist, one of the more important implications relates to prospective strategies for biological control. Recently, there have been much attention and debate about biological control of soil-borne and foliar plant pathogens by microbial antagonists (3, 4). The role of competition as a significant organizing factor in epiphytic communities has been questioned (4). This, in turn, throws into question whether sustained biocontrol is realistic and, if so, what the best tactics should be. Can *r*- and *K*-theory provide guidelines for addressing these problems? Is an *r*-selected antagonist which can rapidly colonize emerging plant tissue the preferred candidate, or should an organism with a lower *r*, but which is highly competitive, be chosen? Perhaps a mixed species community with one or more members of both groups is the preferred approach. It is too early to resolve these questions, but *r*- and *K*-theory does provide a stimulating framework as a point of departure for experiments.

Finally, *r*- and *K*-selection provides a possible interpretation for the various growth dynamics of nonparasitic as well as parasitic microbes. For instance, are life history traits such as antibiotic production or slime secretion triggered by DD controls related to crowding or by other factors? Analogies between *r*- and *K*-strategists and allochthonous (zymogenous) or autochthonous soil microbes, respectively, have been drawn (8, 20). The former group comprises transients or invaders, microorganisms which do not participate significantly in community activity. Microbes in the latter class are residents and at some point in their life cycle are involved in community metabolism. Some similarities with the *r*-*K* descriptors are readily apparent, but as with other analogies (2, 6), these are merely correlations. The causative mechanism for each set of traits remains to be established. The major challenge for the immediate future is the design of appropriate experiments to test whether specific parameters have actually been responsible for evolution of life history traits attributed to *r*- and *K*-selection.

This is a contribution from the College of Agricultural and Life Sciences, University of Wisconsin-Madison. Partial research support from the National Science Foundation, grant DEB-8110199, and from the United States Department of Agriculture, grant 81-CRCR-1-0707, during the period in which these ideas were formulated is gratefully acknowledged.

I thank numerous colleagues, in particular F. Berbee, D. Cullen, and two anonymous reviewers, for their comments on the manuscript.

#### LITERATURE CITED

1. Andrews, J. H. 1984. Life history strategies of plant parasites. *Adv. Plant Pathol.* 2:in press.

2. Andrews, J. H., and D. I. Rouse. 1982. Plant pathogens and the theory of r- and K-selection. *Am. Nat.* 120:283-296.
3. Blakeman, J. P., and N. J. Fokkema. 1982. Potential for biological control of plant diseases on the phylloplane. *Annu. Rev. Phytopathol.* 20:167-192.
4. Cullen, D., and J. H. Andrews. 1984. Epiphytic microbes as biological control agents. In T. Kosuge and E. W. Nester (ed.), *Plant-microbe interactions*, vol. 1, Molecular and genetic perspectives. Macmillan Publishing Co., Inc., New York.
5. Dobzhansky, T. 1950. Evolution in the tropics. *Am. Sci.* 38:209-221.
6. Esch, G. W., T. C. Hazen, and J. M. Aho. 1977. Parasitism and r- and K-selection, p. 9-62. In G. W. Esch (ed.), *Regulation of parasite populations*. Academic Press, Inc., New York.
7. Gadgil, M., and O. T. Solbrig. 1972. The concept of r- and K-selection: evidence from wild flowers and some theoretical considerations. *Am. Nat.* 106:14-31.
8. Gerson, U., and I. Chet. 1981. Are allochthonous and autochthonous soil microorganisms r- and K-selected? *Rev. Ecol. Biol. Sol.* 18:285-289.
9. Gould, S. J. 1977. *Ontogeny and phylogeny*. Harvard University Press, Cambridge, Mass.
10. Grime, J. P. 1979. *Plant strategies and vegetation processes*. John Wiley & Sons, Inc., New York.
11. Jennings, J. B., and P. Calow. 1975. The relationship between high fecundity and the evolution of entoparasitism. *Oecologia (Berlin)* 21:109-115.
12. Lack, D. 1968. *Ecological adaptations for breeding in birds*. Methuen, London.
13. Lubchenco, J., and J. Cubitt. 1980. Heteromorphic life histories of certain marine algae as adaptations to variations in herbivory. *Ecology* 61:676-687.
14. Luckinbill, L. S. 1978. r and K selection in experimental populations of *Escherichia coli*. *Science* 202:1201-1203.
15. MacArthur, R. H., and E. O. Wilson. 1963. An equilibrium theory of island zoogeography. *Evolution* 17:373-387.
16. MacArthur, R. H., and E. O. Wilson. 1967. *The theory of island biogeography*. Monographs in Population Biology, no. 1. Princeton University Press, Princeton, N.J.
17. Parry, G. D. 1981. The meanings of r- and K-selection. *Oecologia (Berlin)* 48:260-264.
18. Patrick, R. 1967. The effect of invasion rate, species pool, and size of area on the structure of the diatom community. *Proc. Natl. Acad. Sci. U.S.A.* 58:1335-1342.
19. Planka, E. R. 1970. On r- and K-selection. *Am. Nat.* 104:592-597.
20. Pugh, G. J. F. 1980. Strategies in fungal ecology. *Trans. Br. Mycol. Soc.* 75:1-14.
21. Simberloff, D. S., and E. O. Wilson. 1969. Experimental zoogeography of islands: the colonization of empty islands. *Ecology* 50:278-290.
22. Slobodkin, L. B. 1961. *Growth and regulation of animal populations*. Holt, Rinehart and Winston, New York.
23. Southwood, T. R. E. 1977. The relevance of population dynamic theory to pest status, p. 35-54. In J. M. Cherrett and G. R. Sagar (ed.), *Origins of pest, parasite, disease and weed problems*. Blackwell Scientific Publications, Oxford.
24. Stearns, S. C. 1977. The evolution of life history traits: a critique of the theory and a review of the data. *Annu. Rev. Ecol. Syst.* 8:145-171.
25. Whittaker, R. H. 1975. *Communities and ecosystems*, 2nd ed. Macmillan Publishing Co., Inc., New York.
26. Wilbur, H. M., D. W. Tinkle, and J. P. Collins. 1974. Environmental certainty, trophic level, and resource availability in life history evolution. *Am. Nat.* 108:805-817.