

教育部高等教育司推荐
国外优秀生命科学教学用书

Prescott's Principles of Microbiology

Prescott 微生物学原理

(影印版)

Mc
Graw
Hill

Joanne M. Willey
Linda M. Sherwood
Christopher J. Woolverton



高等教育出版社
Higher Education Press



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Joanne Willey

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Nobel Prizes Awarded for Research Related to Microbiology

Date	Scientist ^a	Research	Date	Scientist ^a	Research
1901	E. von Behring (GR)	Diphtheria antitoxin	1978	H. O. Smith (US)	Discovery of restriction enzymes
1902	R. Ross (GB)	Cause and transmission of malaria		D. Nathans (US)	and their application to the
1905	R. Koch (GR)	Tuberculosis research		W. Arber (SW)	problems of molecular genetics
1907	C. Laveran (F)	Role of protozoa in disease	1980	B. Benacerraf (US)	Discovery of the histocompatibility
1908	P. Ehrlich (GR)	Work on immunity		G. Snell (US)	antigens
	E. Metchnikoff (R)			J. Dausset (F)	
1913	C. Richet (F)	Work on anaphylaxis		P. Berg (US)	Development of recombinant
1919	J. Bordet (B)	Discoveries about immunity		W. Gilbert (US) &	DNA technology (Berg);
1928	C. Nicolle (F)	Work on typhus fever		F. Sanger (GB)	development of DNA
1930	K. Landsteiner (A)	Discovery of human blood groups			sequencing techniques
1939	G. Domagk (GR)	Antibacterial effect of prontosil			(Chemistry Prize)
1945	A. Fleming (GB)	Discovery of penicillin and its	1982	A. Klug (GB)	Development of crystallographic
	E. B. Chain (GB)	therapeutic value			electron microscopy and the
	H. W. Florey (AU)				elucidation of the structure of
1951	M. Theiler (SA)	Development of yellow fever			viruses and other nucleic-
		vaccine			acid-protein complexes
1952	S. A. Waksman (US)	Discovery of streptomycin	1984	C. Milstein (GB)	Development of the technique
1954	J. F. Enders (US)	Cultivation of poliovirus in tissue		G. J. F. Kohler (GR)	for formation of monoclonal
	T. H. Weller (US)	culture		N. K. Jerne (D)	antibodies (Milstein & Kohler);
	F. Robbins (US)				theoretical work in
1957	D. Bovet (I)	Discovery of the first antihistamine	1986	E. Ruska (GR)	immunology (Jerne)
1958	G. W. Beadle (US)	Microbial genetics			Development of the transmission
	E. L. Tatum (US)				electron microscope
	J. Lederberg (US)				(Physics Prize)
1959	S. Ochoa (US)	Discovery of enzymes catalyzing	1987	S. Tonegawa (J)	The genetic principle for
	A. Kornberg (US)	nucleic acid synthesis			generation of antibody
1960	F. M. Burnet (AU)	Discovery of acquired immune	1988	J. Deisenhofer, R. Huber	Crystallization and study of the
	P. B. Medawar (GB)	tolerance to tissue transplants		& H. Michel (GR)	photosynthetic reaction center
1962	F. H. C. Crick (GB)	Discoveries concerning the			from a bacterial membrane
	J. D. Watson (US)	structure of DNA		G. Elion (US)	Development of drugs for the
	M. Wilkins (GB)			G. Hitchings (US)	treatment of cancer, malaria,
1965	F. Jacob (F)	Discoveries about the regulation	1989	J. M. Bishop (US)	and viral infections
	A. Lwoff (F)	of genes		H. E. Varmus (US)	Discovery of oncogenes
	J. Monod (F)			S. Altman (US)	Discovery of catalytic RNA
1966	F. P. Rous (US)	Discovery of cancer viruses		T. R. Cech (US)	
1968	R. W. Holley (US)	Deciphering of the genetic code	1993	K. B. Mullis (US)	Invention of the polymerase chain
	H. G. Khorana (US)				reaction
	M. W. Nirenberg (US)			M. Smith (C)	Development of site-directed
1969	M. Delbrück (US)	Discoveries concerning viruses			mutagenesis
	A. D. Hershey (US)	and viral infection of cells		R. J. Roberts (US)	Discovery of split genes
	S. E. Luria (US)			P. A. Sharp (US)	
1972	G. Edelman (US)	Research on the structure of	1996	P. C. Doherty (AU)	Discovery of the mechanism by
	R. Porter (GB)	antibodies		R. M. Zinkernagel (SW)	which T lymphocytes
1975	H. Temin (US)	Discovery of RNA-dependent			recognize virus-infected cells
	D. Baltimore (US)	DNA synthesis by RNA	1997	S. Prusiner (US)	Discovery of prions
	R. Dulbecco (US)	tumor viruses; reproduction	2003	R. MacKinnon (US)	Structure of bacterial potassium
		of DNA tumor viruses			and chloride channel proteins
1976	B. Blumberg (US)	Mechanism for the origin and		P. Agre (US)	Discovery of aquaporins
	D. C. Gajdusek (US)	dissemination of hepatitis B	2005	B. Marshall (AU)	Discovery of the causative role
		virus; research on slow virus		R. Warren (AU)	of <i>Helicobacter pylori</i> in
1977	R. Yalow (US)	infections			gastric ulcers
		Development of the			
		radioimmunoassay technique			

^aThe Nobel laureates were citizens of the following countries: Australia (AU), Austria (A), Belgium (B), Canada (C), Denmark (D), France (F), Germany (GR), Great Britain (GB), Italy (I), Japan (J), Russia (R), South Africa (SA), Switzerland (SW), and the United States (US).

About the Authors

Joanne M. Willey is Professor of Biology at Hofstra University on Long Island, N.Y. Dr. Willey received her BA in biology from the University of Pennsylvania, where her interest in microbiology began with work on cyanobacterial growth in eutrophic streams. She earned her PhD in biological oceanography (specializing in marine microbiology) from the Massachusetts Institute of Technology–Woods Hole Oceanographic Institution Joint Program in 1987. She then went to Harvard University, where she spent four years as a postdoctoral fellow studying the filamentous soil bacterium *Streptomyces coelicolor*. Dr. Willey continues to actively investigate this fascinating microbe through funding provided by the National Institutes of Health and the National Science Foundation. She has coauthored a number of publications that focus on the complex developmental cycle of the streptomycetes. She is an active member of the American Society for Microbiology (ASM) and has served on the editorial board of the journal *Applied and Environmental Microbiology* since 2000. Dr. Willey regularly teaches microbiology to biology majors as well as allied health students. She also teaches courses in cell biology, marine microbiology, and laboratory techniques in molecular genetics. Dr. Willey lives on the north shore of Long Island with her husband and two sons. She is an avid runner and enjoys skiing, hiking, sailing, and reading. She can be reached at biojmw@hofstra.edu.



Linda M. Sherwood is a member of the Department of Microbiology at Montana State University. Her interest in microbiology was sparked by the last course she took to complete a BS degree in psychology at Western Illinois University. She went on to complete an MS degree in microbiology at the University of Alabama, where she studied *Pseudomonas acidovorans* physiology. She subsequently earned a PhD in genetics at Michigan State University, where she studied sporulation in *Saccharomyces cerevisiae*. Dr. Sherwood has always had a keen interest in teaching, and her psychology training has helped her to understand current models of cognition



and learning and their implications for teaching. Over the years, she has taught courses in general microbiology, genetics, biology, microbial genetics, and microbial physiology. She has served as the editor for ASM's *Focus on Microbiology Education* and has participated in and contributed to numerous ASM Conferences for Undergraduate Educators. She also has worked with K-12 teachers to develop a kit-based unit to introduce microbiology into the elementary school curriculum and has coauthored with Barbara Hudson a general microbiology laboratory manual, *Explorations in Microbiology: A Discovery Approach*, published by Prentice-Hall. Her nonacademic interests focus primarily on her family. She also enjoys reading, hiking, gardening, and traveling. She can be reached at lsherwood@montana.edu.

Christopher J. Woolverton is Professor of Biological Sciences and a member of the graduate faculty in Biological Sciences and the School of Biomedical Sciences at Kent State University in Kent, Ohio. Dr. Woolverton also serves as the director of the KSU Center for Public Health Preparedness, overseeing its BSL-3 Training Facility. He earned his BS from Wilkes College, Wilkes-Barre, Pa., and a MS and a PhD in medical microbiology from West Virginia University, College of Medicine. He spent two years as a postdoctoral fellow at the University of North Carolina at Chapel Hill, studying cellular immunology. Dr. Woolverton's research interests are focused on the detection and control of bacterial pathogens. Dr. Woolverton and his colleagues have developed the first liquid crystal biosensor for the immediate detection and identification of microorganisms and a natural polymer system for controlled antibiotic delivery. He publishes and frequently lectures on these two technologies. Dr. Woolverton has taught microbiology to science majors and allied health students, as well as graduate courses in immunology and microbial physiology. He is an active member of ASM, serving as the editor of ASM's *Microbiology Education*. He has participated in and contributed to numerous ASM Conferences for Undergraduate Educators, serving as cochair of the 2001 conference. Dr. Woolverton resides in Kent with his wife and three daughters. When not in the lab or classroom, he enjoys hiking, biking, tinkering with technology, and just spending time with his family. His email address is cwoolver@kent.edu.



Preface

Prescott's Principles of Microbiology continues in the tradition of *Prescott, Harley, and Klein's Microbiology* by covering the broad discipline of microbiology at a depth not found in any other textbook. In using the 7th edition of *PHK's Microbiology* as the foundation for the development of *Principles*, we identified two overarching goals. First, we sought to present material likely to be covered in a single semester microbiology course, with the knowledge that not all introductory microbiology courses cover the same topics. Therefore, each chapter in *Prescott's Principles of Microbiology* was revised from the 7th edition of *PHK's Microbiology* to provide a streamlined, briefer discussion of key concepts that include only the most relevant, up-to-date examples. Secondly, we strove to further extend the student-friendly approach used in the 7th edition by enhancing readability and adding tools designed to promote learning.

OUR STRENGTHS

Connecting with Students

We have retained the relatively simple and direct writing style used in *PHK's Microbiology*, but have added style elements designed to further engage students. For example, we frequently use the first person voice to describe important concepts—especially those that our students find most difficult. Each chapter is divided into numbered section headings and organized in an outline format—the same outline format that is presented in the end-of-chapter summaries. Key terminology is boldfaced and clearly defined. We have introduced a glossary of essential terms at the beginning of each chapter to serve as an easy reference for students, while retaining the full glossary in the back of the book. Our belief that concepts are just as important as facts, if not more, is also reflected in the questions for review and reflection that appear throughout each chapter. These questions are of two types: those that quiz student retention of key facts and vocabulary and those designed to foster critical thinking.

Instructive Artwork

To truly engage students, a textbook must do more than offer words and images that just adequately describe the topic at hand. We view the artwork of a text as a critical tool in enticing students to read the text. *Principles* features the art program introduced in the 7th edition of *PHK's Microbiology*. The three-dimensional renderings help students appreciate the beauty and elegance of the cell, while at the same time make the material more comprehensible. Of course we also believe that figures should be content-rich, not just pretty to look at. Therefore, the art program also includes pedagogical features such as concept maps (e.g., see figures 9.1 and 13.1) and annotation of key pathways and processes (e.g., see figures 10.8 and 12.12).

x

Unique Organization Around Key Themes

With the advent of genomics, proteomics, metabolomics and the increased reach of cell biology, the divisions among microbiology subdisciplines have become blurred. This is reflected in the emergence of fields like disease ecology and metagenomics. In addition, today's microbiologist must be acquainted with all members of the microbial world: viruses, bacteria, archaea, protists, and fungi. It follows that students new to microbiology are asked to assimilate vocabulary, facts, and most importantly, concepts, from a seemingly vast array of subjects. The challenge to the professor of microbiology is to effectively communicate essential concepts while conveying the ingenuity of microbes and excitement of this dynamic field.

Microbial Evolution and Ecology

Because microbial evolution and ecology are no longer subdisciplines to be ignored by those interested in microbial genetics, physiology, or pathogenesis, *Principles* strives to integrate these themes throughout the text. We begin in chapter 1 with a discussion of the universal tree of life and whenever possible, discuss diverse microbial species so that students can begin to appreciate the tremendous variation in the microbial world. In addition, *Principles* uses the topics of intercellular communication (chapters 6 and 13), biofilms (throughout the text, but specifically in chapters 6, 13, and 29), microbial evolution (chapter 17), and polymicrobial diseases (chapter 33) to emphasize that evolution must be linked to genetics, physiology to diversity, and ecology to pathogenesis.

Microbial Pathogenicity and Diversity

Unique to *Principles* is the inclusion of microbial pathogens into the diversity chapters (chapters 19–24). Thus when students read about the metabolic and genetic diversity of each bacterial, protist, and viral taxon, they are also presented with the important pathogens. In this way, the physiological adaptations that make a given organism successful can be immediately related to its role as a pathogen and pathogens can be readily compared to phylogenetically related nonpathogenic microbes.

In addition, *Principles* introduces viruses and other acellular agents in chapter 5, following the chapters of Prokaryotic and Eucaryotic Cell Structure and Function (chapters 3 and 4, respectively). By placing a similarly themed chapter on viruses here, professors can introduce all divisions of the microbial world to their students early in the term. For those professors who include more in-depth coverage of viruses, chapter 24 explores the molecular genetics of bacteriophages and other viruses as well as the pathogenicity of important animal and plant viruses. As in *PHK's Microbiology*, we use the classification schemes set forth in the second edition of *Bergey's Manual of Systematic Bacteriology*, the Baltimore System of virus classification (chapters 5 and 24), and the International Society of Protistologists' new classification scheme for eucaryotes (chapter 23).

Visual Tour

STUDENT RESOURCES

Laboratory Exercises in Microbiology

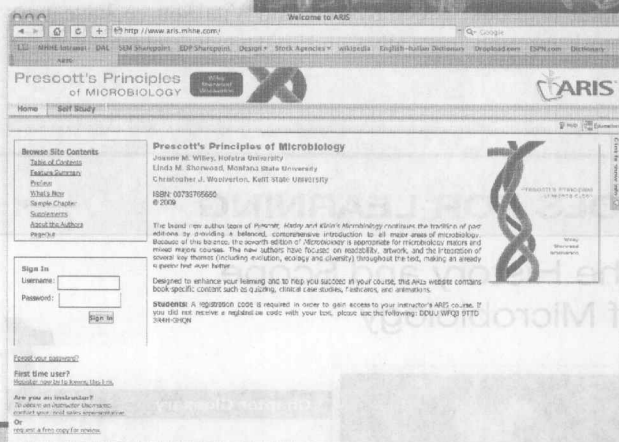
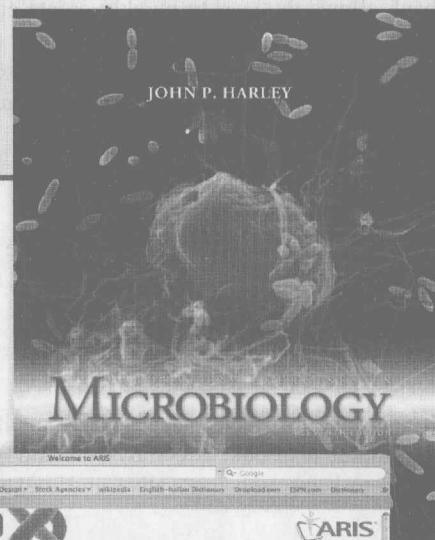
The seventh edition of *Laboratory Exercises in Microbiology* by John P. Harley has been prepared to accompany the text. Like the text, the laboratory manual provides a balanced introduction in each area of microbiology. The class-tested exercises are modular and short so that instructors can easily choose those exercises that fit their course.

ARIS™

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INSTRUCTOR RESOURCES

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TOOLS FOR LEARNING

The History and Scope of Microbiology



Louis Pasteur, one of the greatest scientists of the nineteenth century, maintained that "Science knows no country, because knowledge belongs to humanity, and is a torch which illuminates the world."

Archaea: The domain of life that contains prokaryotic cells with cell walls that lack peptidoglycan; they have unique lipids in their membranes and archaeal rRNA (among many differences).

Bacteria: The domain of life that contains prokaryotic cells with cell walls that contain the structural molecule peptidoglycan; they have bacterial rRNA.

Eucarya: The domain of life that features organisms made of cells that have a membrane-delimited nucleus and differ in many other ways from prokaryotic cells; includes protists, fungi, plants, and animals.

Fungi: A diverse group of microorganisms that range from unicellular (some yeasts) to multicellular molds and mushrooms.

Chapter Glossary

Koch's postulates: A set of rules for proving that a specific microorganism causes a particular disease.

microbiology: The study of organisms that are usually too small to be seen with the naked eye; special techniques are required to isolate and grow them.

microorganism: An organism that is too small to be seen clearly with the naked eye and lacks highly differentiated cells and distinct tissues.

prions: Infectious agents that cause spongiform encephalopathies such as scrapie in sheep; they are composed only of protein.

prokaryotic cells: Cells that lack a true, membrane-enclosed nucleus; Bacteria and Archaea are prokaryotic and have their genetic material located in a nucleoid.

protists: Mostly unicellular eukaryotic organisms that lack cellular differentiation into tissues; cell differentiation is limited to cells involved in sexual reproduction, alternate vegetative morphology, or resting states such as cysts; includes organisms often referred to as algae and protozoa.

spontaneous generation: An early belief, now discredited, that living organisms could develop from nonliving matter.

viroids: Infectious agents composed only of single-stranded, circular RNA; they cause numerous plant diseases.

viruses: Infectious agents having a simple acellular organization with a protein coat and a nucleic acid genome, lacking independent metabolism, and reproducing only within living host cells.

viroids: Infectious agents composed only of single-stranded RNA; they are unable to replicate without the aid of specific viruses that infect the host cell.

Dans les champs de l'observation, le hasard ne favorise que les esprits préparés.
(In the field of observation, chance favors only prepared minds.)

—Louis Pasteur

The importance of microorganisms cannot be overemphasized. In terms of sheer number and mass—microbes contain an estimated 50% of the biological carbon and 90% of the biological nitrogen on Earth—they greatly exceed every other group of organisms on the planet. Furthermore, they are found everywhere: from geothermal vents in the ocean depths to the coldest Arctic ice. They are major contributors to the functioning of the biosphere, being indispensable for the cycling of the elements essential for life. They also are

a source of nutrients at the base of all ecological food webs. Most important, certain microorganisms carry out photosynthesis, rivaling plants in their role of capturing carbon dioxide and releasing oxygen into the atmosphere. Those microbes that inhabit humans are also important, helping the body digest food and producing vitamins B₁₂ and K. In addition, society in general benefits from microorganisms. Indeed, modern biotechnology rests upon a microbiological foundation, as microbes are necessary for the production of bread, cheese,

Chapter Glossary

Each chapter begins with a glossary—a list of key terms discussed in the chapter. Each term is succinctly defined.

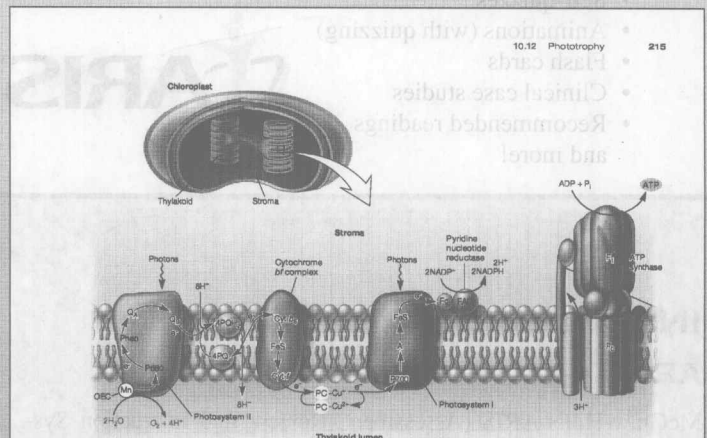


FIGURE 10.30 The Mechanism of Photosynthesis. An illustration of the chloroplast thylakoid membrane showing photosynthetic ETC function and noncyclic photophosphorylation. The chain is composed of three complexes: PS II, the cytochrome *b₆/f* complex, and PS I. Two diffusible electron carriers connect the three complexes. Plastoquinone (PQ) connects PS II with the cytochrome *b₆/f* complex, and plastocyanin (PC) connects the cytochrome *b₆/f* complex with PS I. The light-driven electron flow pumps protons across the thylakoid membrane and generates an electrochemical gradient, which can then be used to make ATP. Water is the source of electrons and the oxygen-evolving complex (OEC) produces oxygen.

Anoxygenic phototrophs have photosynthetic pigments called bacteriochlorophylls (figure 10.27). In some bacteria, these are located in membranous vesicles called chlorosomes. The absorption maxima of bacteriochlorophylls (Bchl) are at longer wavelengths than those of chlorophylls. Bacteriochlorophylls *a* and *b* have maxima in ether at 775 and 790 nm, respectively. In vivo maxima are about 830 to 890 nm (Bchl *a*) and 1,020 to 1,040 nm (Bchl *b*). This shift of absorption maxima into the infrared region better adapts these bacteria to their ecological niches.

>>> **Photosynthetic bacteria (section 19.3)**

Many differences found in anoxygenic phototrophs are because they have a single photosystem. Because of this, they are restricted to cyclic photophosphorylation and are unable to produce O₂ from H₂O. Indeed, almost all anoxygenic phototrophs are strict anaerobes. A tentative scheme for the photosynthetic ETC of a purple nonsulfur bacterium is given in figure 10.31. When the reaction-center bacteriochlorophyll (P870) is excited, it donates an electron to bacteriopheophytin. Electrons then flow to quinones and through an ETC back to

P870 while generating sufficient PMF to drive ATP synthesis by ATP synthase. Note that although both green and purple bacteria lack two photosystems, the purple bacteria have a photosynthetic apparatus similar to photosystem II of oxygenic phototrophs, whereas the green sulfur bacteria have a system similar to photosystem I.

>>> **Class Alphaproteobacteria: Purple non-sulfur bacteria (section 20.1)**

Anoxygenic phototrophs face a further problem because they also require reducing power (NAD(P)H or reduced ferredoxin) for CO₂ fixation and other biosynthetic processes. They are able to generate reducing power in at least three ways, depending on the bacterium. Some have hydrogenases that are used to produce NAD(P)H directly from the oxidation of hydrogen gas. This is possible because hydrogen gas has a more negative reduction potential than NAD⁺ (see table 9.1). Others, such as the photosynthetic purple bacteria, use reverse electron flow to generate NAD(P)H (figure 10.31). In this mechanism, electrons are drawn off the photosynthetic ETC and "pushed" to NAD(P)⁺ using PMF. Electrons from electron donors such as

Cross-Referenced Notes

In-text references with icons refer students to other parts of the book to review.

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This text is dedicated to our families for their patience and to our students for teaching us how to teach better.

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Figure 16.21 The Mode of Action of the *Bacillus thuringiensis* Toxin. (a) Release of the protoxin from the parasporal crystal and modification by protease in the midgut. (b) Insertion of the 68 kDa active toxin molecule into the membrane. (c) Aggregation and pore formation, showing a cross section of the pore. (d) Final hexagonal pore, which causes an influx of water and cations as well as a loss of ATP, resulting in cell imbalance and lysis.

- What is the TI plasmid and how is it modified for the genetic modification of plants?
- How is the Bt toxin produced and why is it so widely accepted?
- Can you think of other traits that might be useful, either to the farmer or the consumer, that could be introduced into plants?

16.12 MICROBES AS PRODUCTS

So far, we have discussed the use of microbial products to meet defined goals. However, microbial cells can be marketed as valuable products. Perhaps the most common example is the inoculation of legume seeds with rhizobia to ensure efficient nodulation and nitrogen fixation, as discussed in chapter 26. Here we introduce several other microbes and microbial structures that are of industrial or agricultural relevance.

Diatoms have aroused the interest of nanotechnologists. These photosynthetic protists produce intricate silica shells that differ according to species (figure 16.22). Nanotechnologists are interested in diatoms because they create precise structures at the micrometer scale. Three-dimensional structures in nanotechnology are currently built plane by plane, and meticulous care must be taken to etch each individual structure to its final, exact shape. Diatoms, on the other hand, build directly in three dimensions and do so while growing exponentially. There have been a number of ideas and approaches to harness these microbial “factories,” but one technique is especially fascinating. Diatom shells are incubated at 900°C in an atmosphere of magnesium for several hours. Amazingly, this results in an atom-for-atom substitution of

Learn More 607

Summary

25.1 Biogeochemical Cycling

- Microorganisms—functioning with plants, animals, and the environment—play important roles in nutrient cycling, which is also termed biogeochemical cycling. Assimilatory processes involve incorporation of nutrients into the organism's biomass during metabolism; dissimilatory processes, in comparison, involve the release of nutrients to the environment after metabolism.
- Biogeochemical cycling involves oxidation and reduction processes, and changes in the concentrations of gaseous cycle components, such as carbon, nitrogen, phosphorus, and sulfur, can result from microbial activity (figures 25.1–25.8).
- Major organic compounds used by microorganisms differ in structure, linkage, elemental composition, and susceptibility to degradation under oxic and anoxic conditions. Lignin is degraded only under oxic conditions, a fact that has important implications in terms of carbon retention in the biosphere.

25.2 Microbial Ecology and Its Methods: An Overview

- A variety of staining techniques are used to observe microbes in natural environments. Fluorescent *in situ* hybridization (FISH) labels specific microbes that possess a specific nucleotide sequence, usually a region of the SSU rRNA gene (figure 25.9).
- Although most microbes cannot be grown in pure culture, enrichment techniques are invaluable in isolating microorganisms.
- The analysis of rRNA from natural samples can be accomplished after amplification by PCR (to determine nucleotide sequence) or by DNA fingerprinting (figure 25.13).
- DNA reassociation is also used to evaluate the size and complexity of microbial communities. This technique considers the community as a collection of genomes.
- Microelectrodes can be used to determine physical and biological parameters such as pH, O_2 , and H_2S concentrations in microcosms (figure 25.14).
- Stable isotope analysis is based on the fact that organisms discriminate between heavy and light naturally occurring isotopes. It is often used to monitor nutrient flux through ecosystems.

Critical Thinking Questions

- Examine the carbon cycle shown in figure 25.1. What do you think are some major biogenic sources of CO_2 emission into the atmosphere? What are the major biogenic sinks of atmospheric CO_2 ?
- How might you show that a microorganism found in a particular extreme environment is actually growing there?

Learn More

Learn more by visiting the Prescott website at www.mhhe.com/prescottprinciples, where you will find a complete list of references.

Review and Reflection Questions Within Narrative

Review questions throughout each chapter assist students in mastering section concepts before moving on to other topics.

End-of-Chapter Material

- End-of-chapter summaries are organized by numbered headings and provide a snapshot of important chapter concepts.
- Critical Thinking Questions supplement the questions for review and reflection found throughout each chapter; they are designed to stimulate analytical problem-solving skills.

Microbial Diversity & Ecology

35.2 A Fungus with a Voracious Appetite

The basidiomycete *Phanerochaete chrysosporium* (the scientific name means "visible hair, golden spore") is a fungus with unusual degradative capabilities. This organism is termed a "white rot fungus" because of its ability to degrade lignin, a randomly linked, phenylpropane-based polymeric component of wood. The cellulosic portion of wood is attacked to a lesser extent, resulting in the characteristic white color of the degraded wood. This organism also degrades a truly amazing range of xenobiotic compounds (nonbiological foreign chemicals) using both intracellular and extracellular enzymes.

As examples, the fungus degrades benzene, toluene, ethylbenzene, and xylenes (the so-called BTEX compounds), chlorinated compounds such as 2,4,5-trichloroethylene (TCE), and trichlorophenols (figure 35.12). The latter are present as contaminants in wood preservatives and are used as pesticides. In addition, other chlorinated benzenes can be degraded with or without toluenes being present. Even the insecticide Dieldrin is degraded.

How does this microorganism carry out such feats? Apparently most xenobiotic degradation occurs after active growth, during secondary metabolic lignin degradation. Degradation of some compounds

involves important extracellular enzymes including lignin peroxidase, manganese-dependent peroxidase, and glyoxal oxidase. A critical enzyme is pyranose oxidase, which releases H_2O_2 for use by the manganese peroxidase enzyme. The H_2O_2 also is a precursor of the hydroxyl radical, which participates in wood degradation. The pyranose oxidase enzyme is located in the interseptal fungal cell wall, where it can function either as a pass or be released and penetrate into the wood substrate. It is a nonspecific enzymatic system that releases these oxidized lignins.

We can expect to continue hearing of many new uses for this organism. Potentially valuable applications being growth in bioreactors, where intracellular and extracellular enzymes are maintained in the bioreactor while liquid wastes flow through.



organism physical protection, as well as possibly supplying nutrients. This makes it possible for the microorganism to survive in spite of the intense competitive pressures that exist in the natural environment, including pressure from protozoan predators. Microhabitats may be either living or inert. Specialized living microhabitats include the surface of a seed, a root, or a leaf. Here, higher nutrient fluxes and rates of initial colonization by the added microorganisms protect against the fierce competitive conditions in the natural environment. For example, to ensure that the nitrogen-fixing microbe *Rhizobium* is in close association with the legume, seeds are coated with the microbe using an oil-organism mixture or the bacteria are placed in a band under the seed where the newly developing primary root will penetrate. <<< *Microorganisms in terrestrial environments: The Rhizobium* (section 26.2)

Recently it has been found that microorganisms can be added to natural communities together with protective inert microhab-

itats. As an example, if microbes are added to microporous glass, the survival of added microorganisms is markedly enhanced. Other microbes have been observed at their own microhabitats. Microorganisms in the overlying PCB-contaminated sand-clay soils have been found to create their own "clay hitches" by binding clay particles with exopolysaccharides. Thus the application of principles of microbial ecology can facilitate the successful management of microbial communities in nature.

1. What factors might limit the ability of microorganisms, after addition to a soil or water, to persist and carry out desired functions?
2. What types of microhabitats can be used with microorganisms when they are added to a complex environment?

Techniques and Applications

30.1 Detection and Removal of Endotoxins

Bacterial endotoxins plagued the pharmaceutical industry and medical device producers for years. For example, administration of drugs contaminated with endotoxins resulted in complications—even death—to patients. In addition, endotoxins can be problematic for individuals and firms working with cell cultures and genetic engineering. The result has been the development of sensitive tests and methods to identify and remove these endotoxins. The procedures must be very sensitive to trace amounts of endotoxins. Most firms have set a limit of 0.25 endotoxin units (E.U.), 0.025 ng/ml, or less as a release standard for their drugs, media, or products.

One of the most accurate tests for endotoxins is the *in vitro* Limulus amoebocyte lysate (LAL) assay. The assay is based on the observation that when an endotoxin contacts the clot protein from circulating amoebocytes of the horseshoe crab (*Limulus*), a gel-clot forms. The assay kits contain calcium, proclotting enzyme, and procoagulogen. The proclotting enzyme is activated by bacterial endotoxin (lipopolysaccharide) and calcium to form active clotting

enzyme (box figure). Active clotting enzyme then catalyzes the cleavage of procoagulogen into polypeptide subunits (coagulogen). The subunits join by disulfide bonds to form a gel-clot. Spectrophotometry is then used to measure the protein precipitated by the lysate. The LAL test is sensitive at the nanogram level but must be standardized against U.S. Food and Drug Administration Bureau of Biologics endotoxin reference standards. Results are reported in endotoxin units per milliliter and reference made to the particular reference standards used.

Removal of endotoxins presents more of a problem than their detection. Those present on glassware or medical devices can be inactivated if the equipment is heated at 250°C for 30 minutes. Soluble endotoxins range in size from 20 kDa to large aggregates with diameters up to 0.1 μm. Thus they cannot be removed by conventional filtration systems. Manufacturers have developed special filtration systems and filtration cartridges that retain these endotoxins and help alleviate contamination problems.

Historical Highlights

33.1 John Snow—The First Epidemiologist

Much of what we know today about the epidemiology of cholera is based on the classic studies conducted by the British physician John Snow between 1849 and 1854. During this period, a series of cholera outbreaks occurred in London, England, and Snow set out to find the source of the disease. Some years earlier when he was still a medical apprentice, Snow had been sent to help during an outbreak of cholera among coal miners. His observations convinced him that the disease was usually spread by unwashed hands and shared food, not by "bad" air or casual direct contact.

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In 1854 another cholera outbreak struck London. Part of the city's water supply came from two different suppliers: the Southwark and Vauxhall Company, and the Lambeth Company. Snow interviewed cholera patients and found that most of them purchased their drinking water from the Southwark and Vauxhall Company. He also discovered that this company obtained its water from the Thames River below locations where Londoners had discharged their sewage. In contrast, the Lambeth Company took its water from the Thames before the river reached the city. The death rate from cholera was over eightfold lower in households supplied with Lambeth Company water. Water contaminated by sewage was transmitting the disease. Finally, Snow concluded that the cause of the disease must be able to multiply in water. Thus he nearly recognized that cholera was caused by a microorganism, though Robert Koch did not discover the causative bacterium (*Vibrio cholerae*) until 1883.

To commemorate these achievements, the John Snow Pub now stands at the site of the old Broad Street pump. Those who complete the Epidemiologic Intelligence Program at the Centers for Disease Control and Prevention receive an emblem bearing a replica of a barrel of Whitley's Ale—the brew dispensed at the John Snow Pub.

Disease

31.1 Antibiotic Misuse and Drug Resistance

The sale of antimicrobial drugs is big business. In the United States, millions of pounds of antibiotics valued at billions of dollars are produced annually. As much as 70% of these antibiotics are added to livestock feed.

Because of the massive quantities of antibiotics being prepared and used, an increasing number of diseases are resisting treatment due to the spread of drug resistance. A good example is *Neisseria gonorrhoeae*, the causative agent of gonorrhea. Gonorrhea was first treated successfully with sulfonamides in 1936, but by 1942 most strains were resistant and physicians turned to penicillin. Within 16 years, a penicillin-resistant strain emerged in Asia. A penicillinase-producing gonococcus reached the United States in 1976 and is still spreading in this country. Thus penicillin is no longer used to treat gonorrhea.

In late 1968 an epidemic of dysentery caused by *Shigella* broke out in Guatemala and affected at least 112,000 persons; 12,500 deaths resulted. The strains responsible for this devastation carried an R plasmid conferring resistance to chloramphenicol, tetracycline, streptomycin, and sulfonamide. In 1972 a typhoid epidemic swept through Mexico producing 100,000 infections and 14,000 deaths. It was due to a *Salmonella* strain with the same multiple-drug-resistance pattern seen in the previous *Shigella* outbreak.

Haemophilus influenzae type b is responsible for many cases of childhood pneumonia and middle ear infections, as well as respiratory infections and meningitis. It is now becoming increasingly resistant to tetracyclines, ampicillin, and chloramphenicol. Similarly, the worldwide rate of penicillin-nonsusceptible (i.e., resistant) *Streptococcus pneumoniae* (PNSP) continues to increase. There is a direct correlation between the daily use of antibiotics (expressed as defined daily dose [DDD] per day) and the percent of PNSP isolates cultured (box figure). This dramatic correlation is alarming. More alarming is the continued indiscriminate use of antibiotics in light of these data.

In 1946 almost all strains of *Staphylococcus* were penicillin sensitive. Today most hospital strains are resistant to penicillin G, and some are now also resistant to methicillin and gentamicin and only can be treated with vancomycin. Strains of *Enterococcus* have become resistant to most antibiotics, including vancomycin, and a few cases of vancomycin-resistant *S. aureus* have been reported in the United States and Japan.

It is clear from these and other examples (e.g., *Mycobacterium tuberculosis*) that drug resistance is a serious public health problem. Much of the difficulty

Microbial Tidbits

21.1 Spores in Space

During the nineteenth-century argument over the question of the evolution of life, the panspermia hypothesis became popular. According to this hypothesis, life did not evolve from inorganic matter on Earth but arrived as viable bacterial spores that escaped from another planet. More recently the British astronomer Fred Hoyle has revived the hypothesis based on his study of the absorption of radiation by interstellar dust. Hoyle maintains that dust grains were initially viable bacterial cells that have been degraded and that the beginning of life on Earth was due to the arrival of bacterial spores that had survived their trip through space.

Even more recently Peter Weber and J. Mayo Greenberg from the University of Leiden in the Netherlands have studied the effect of very high vacuum, low temperature, and UV radiation on the survival of *Bacillus subtilis* spores. Their data suggest that spores within an interstellar molecular cloud might be able to survive between 4.5 to 45 million years. Molecular clouds move through space at speeds sufficient to transport spores between solar systems in this length of time. Although these results do not prove the panspermia hypothesis, they are consistent with the possibility that bacteria might be able to travel between planets capable of supporting life.

Special Interest Essays



Interesting essays on relevant topics are included in most chapters. Readings are organized into these topics: Historical Highlights, Techniques & Applications, Microbial Diversity & Ecology, Disease, and Microbial Tidbits.

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The History and Scope of Microbiology



Louis Pasteur, one of the greatest scientists of the nineteenth century, maintained that "Science knows no country, because knowledge belongs to humanity, and is a torch which illuminates the world."

Archaea The domain of life that contains procaryotic cells with cell walls that lack peptidoglycan; they have unique lipids in their membranes and archaeal rRNA (among many differences).

Bacteria The domain of life that contains procaryotic cells with cell walls that contain the structural molecule peptidoglycan; they have bacterial rRNA.

Eucarya The domain of life that features organisms made of cells that have a membrane-delimited nucleus and differ in many other ways from procaryotic cells; includes protists, fungi, plants, and animals.

fungi A diverse group of microorganisms that range from unicellular forms (yeasts) to multicellular molds and mushrooms.

Dans les champs de l'observation, le hasard ne favorise que les esprits préparés.
(In the field of observation, chance favors only prepared minds.)

—Louis Pasteur

The importance of microorganisms cannot be overemphasized. In terms of sheer number and mass—microbes contain an estimated 50% of the biological carbon and 90% of the biological nitrogen on Earth—they greatly exceed every other group of organisms on the planet. Furthermore, they are found everywhere: from geothermal vents in the ocean depths to the coldest Arctic ice. They are major contributors to the functioning of the biosphere, being indispensable for the cycling of the elements essential for life. They also are

Chapter Glossary

Koch's postulates A set of rules for proving that a specific microorganism causes a particular disease.

microbiology The study of organisms that are usually too small to be seen with the naked eye; special techniques are required to isolate and grow them.

microorganism An organism that is too small to be seen clearly with the naked eye and lacks highly differentiated cells and distinct tissues.

prions Infectious agents that cause spongiform encephalopathies such as scrapie in sheep; they are composed only of protein.

procaryotic cells Cells that lack a true, membrane-enclosed nucleus; *Bacteria* and *Archaea* are procaryotic and have their genetic material located in a nucleoid.

protists Mostly unicellular eucaryotic organisms that lack cellular differentiation into tissues; cell differentiation is limited to cells involved in sexual reproduction, alternate vegetative morphology, or resting states such as cysts; includes organisms often referred to as algae and protozoa.

spontaneous generation An early belief, now discredited, that living organisms could develop from nonliving matter.

viroids Infectious agents composed only of single-stranded, circular RNA; they cause numerous plant diseases.

viruses Infectious agents having a simple acellular organization with a protein coat and a nucleic acid genome, lacking independent metabolism, and reproducing only within living host cells.

virusoids Infectious agents composed only of single-stranded RNA; they are unable to replicate without the aid of specific viruses that coinfect the host cell.

a source of nutrients at the base of all ecological food webs. Most important, certain microorganisms carry out photosynthesis, rivaling plants in their role of capturing carbon dioxide and releasing oxygen into the atmosphere. Those microbes that inhabit humans are also important, helping the body digest food and producing vitamins B and K. In addition, society in general benefits from microorganisms. Indeed, modern biotechnology rests upon a microbiological foundation, as microbes are necessary for the production of bread, cheese,

beer, antibiotics, vaccines, vitamins, enzymes, and many other products. Their ability to produce biofuels such as ethanol is also being intensively explored. These alternative fuels are both renewable and can help decrease pollution associated with burning fossil fuels.

Although most microorganisms play beneficial or benign roles, some harm humans and have disrupted society over the millennia. Microbial diseases undoubtedly played a major role in historical events such as the decline of the Roman Empire and the conquest of the New World. In 1347, plague (Black Death), an arthropod-borne disease, struck Europe with brutal force, killing one-third of the population (about 25 million people) within four years. Over the next 80 years, the disease struck repeatedly, eventually wiping out 75% of the European population. The plague's effect was so great that some historians believe it changed European culture and prepared the way for the Renaissance. Today the struggle by microbiologists and others against killers such as AIDS and malaria continues.

In this chapter, we introduce the microbial world to provide a general idea of the organisms and agents that microbiologists study. We next discuss the scope and relevance of modern microbiology. Finally, we describe the historical development of the science of microbiology and its relationship to medicine and other areas of biology.

1.1 MEMBERS OF THE MICROBIAL WORLD

Microbiology often has been defined as the study of organisms and agents too small to be seen clearly by the unaided eye—that is, the study of **microorganisms**. Because objects less than about 1 millimeter in diameter cannot be seen clearly and must be examined with a microscope, microbiology is concerned primarily with organisms and agents this small and smaller. However, some microorganisms, particularly some eucaryotic microbes, are visible without microscopes. For example, bread molds and filamentous algae are studied by microbiologists yet are visible to the naked eye, as are the two bacteria *Thiomargarita* and *Epulopiscium*.

>> Microbial Diversity & Ecology 3.1: Monstrous Microbes

The difficulty in setting the boundaries of microbiology has led to the suggestion of other criteria for defining the field. For instance, an important characteristic of microorganisms, even those that are large and multicellular, is that they are relatively simple in their construction, lacking highly differentiated cells and distinct tissues. Another suggestion, made by Roger Stanier, is that the field also be defined in terms of its techniques. Microbiologists usually first isolate a specific microorganism from a population and then culture it. Thus microbiology employs techniques—such as sterilization and the use of culture media—that are necessary for successful isolation and growth of microorganisms.

Microorganisms are diverse, and their classification has always been a challenge for microbial taxonomists. Their early descriptions as either plants or animals were too simple. For instance, some microbes are motile like animals but also have cell walls and

are photosynthetic like plants. Such microbes cannot be placed easily into one kingdom or another. Another important factor in classifying microorganisms is that some are composed of procaryotic cells and others of eucaryotic cells. **Procaryotic cells** (Greek *pro*, before, and *karyon*, nut or kernel; organisms with a primordial nucleus) have a much simpler morphology than eucaryotic cells and lack a true membrane-delimited nucleus. In contrast, **eucaryotic cells** (Greek *eu*, true, and *karyon*, nut or kernel) have a membrane-enclosed nucleus; they are more complex morphologically and are usually larger than procaryotes. These observations eventually led to the development of a classification scheme that divided organisms into five kingdoms: the *Monera*, *Protista*, *Fungi*, *Animalia*, and *Plantae*. Microorganisms (except for viruses and other acellular infectious agents, which have their own classification system) were placed in the first three kingdoms.

In the last few decades, great progress has been made in three areas that profoundly affect microbial classification. First, much has been learned about the detailed structure of microbial cells from the use of electron microscopy. Second, microbiologists have determined the biochemical and physiological characteristics of many different microorganisms. Third, the sequences of nucleic acids and proteins from a wide variety of organisms have been compared. The comparison of ribosomal RNA (rRNA), begun by Carl Woese in the 1970s, was instrumental in demonstrating that there are two very different groups of procaryotic organisms: *Bacteria* and *Archaea*, which had been classified together as *Monera* in the five-kingdom system. Later studies based on rRNA comparisons showed that *Protista* is not a cohesive taxonomic unit and that it should be divided into three or more kingdoms. These studies and others have led many taxonomists to conclude that the five-kingdom system is too simple. A number of alternatives have been suggested, but currently most microbiologists believe that organisms should be divided among three domains: *Bacteria* (the true bacteria or eubacteria), *Archaea*,¹ and *Eucarya* (all eucaryotic organisms) (figure 1.1). We use this system throughout the text, and it is discussed in detail in chapter 17. However, a brief description of the three domains and of the microorganisms placed in them follows.

Bacteria² are procaryotes that are usually single-celled organisms. Most have cell walls that contain the structural molecule peptidoglycan. They are abundant in soil, water, and air, and are major inhabitants of our skin, mouth, and intestines. Some bacteria live in environments that have extreme temperatures, pH, or salinity. Although some bacteria cause disease, many more play beneficial roles such as cycling elements in the biosphere, breaking down dead plant and animal material, and producing vitamins. Cyanobacteria (once called blue-green algae) produce significant amounts of oxygen through the process of photosynthesis.

Archaea are procaryotes that are distinguished from *Bacteria* by many features, most notably their unique ribosomal RNA sequences. They lack peptidoglycan in their cell walls and have unique membrane lipids. Some have unusual metabolic

¹ Although this is discussed further in chapter 17, it should be noted here that several names have been used for the *Archaea*. The two most important are archaeobacteria and archaebacteria. In this text, we use only the name *Archaea*.

² In this text, the term bacteria (s., bacterium) is used to refer to procaryotes that belong to domain *Bacteria*, and the term archaea (s., archaean) is used to refer to procaryotes that belong to domain *Archaea*. In some publications, the term bacteria is used to refer to all procaryotes. That is not the case in this text.