Biology of Plants

SIXTH EDITION

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Preface

As a man tramps the woods to the lake
he knows he will find ponds and lilies,
blue heron and golden shiners,
shadows on the rocks,
and the glint of light on the wavelets,
just as they were in the summer of 1354,
as they will be in 2054 and beyond.
He can stand on a rock by the shore
and be in a past he could not have known,
in a future he will never see.
He can be a part of time that was
and time yet to come.

William Chapman White, *Adirondack Country*, 1954

Only a half-century ago, such was the perception that educated people enjoyed of the permanence of beloved natural settings, in this case, the Adirondack Mountains of northern New York State. Since it was written, we have learned of the extraordinary effects of human activity on climate and species, ponds and lilies included. In an astonishingly short period, climate changes could force plant species to migrate or to perish. Vastly increased human populations are altering nature as we have known it. Knowledge of the natural world, which depends ultimately on the botanical world, is all the more essential if we are to have any hope of a sustainable future.

It was with this in mind that we approached the writing of the sixth edition of *Biology of Plants*. If we are to be the proper stewards of this planet, we must know how and why it functions as it does. Throughout this new edition, therefore, we have strengthened the coverage of environmental issues, and we close the book with an essay on "A New Millennium: The Transition to Sustainability."

Major changes in our understanding of the botanical world and shifts in how we view its components have occurred since the last edition. Reactions to that edition, as well as previous editions, have been gratifying. However, as we scrutinized the existing chapters in light of the many advances that have been made in the plant biological sciences over the past eight years, it became obvious to us that this new edition would require a substantial level of revision. Extensive updating and rewriting has taken place, and virtually all of the chapters have been reorganized to provide an even more logical sequence. Indeed, this edition represents the most thorough revision that *Biology of Plants* has undergone. We believe it provides a solid and exciting botanical foundation for our entry into the twenty-first century.

Major reorganizational changes involved moving the chapter on The Molecular Composition of Plant Cells (now Chapter 2) before the chapter dealing with Introduction to the Plant Cell (now Chapter 3), which provides the chemical foundation for a more complete discussion of the structure and function of plant cells. A section on Secondary Metabolites has been added to Chapter 2 so that, early on in the book, students are made aware of the wide variety of familiar chemical products manufactured by plant cells. More emphasis on cellular functioning and cell-to-cell communication at the molecular level meant a new approach to the plasma membrane, particularly in Chapter 4 (Membrane Structure and Function), and new diagrams clarify chemiosmotic coupling and other features of Respiration (Chapter 6) and Photosynthesis (Chapter 7).

Consideration of cell division has been moved from the plant cell chapter to Section 3 (Genetics and Evolution) as Chapter 8 (The Reproduction of Cells), and the entire section has been expanded to provide a solid introduction to genetic engineering, population genetics, and speciation. Included are many advances based on the application of recombinant DNA techniques and procedures, which are discussed in detail.

The vast changes in taxonomic relationships, based on molecular sequencing, required a complete overhaul of the Diversity section. The introductory chapter to the Diversity section has been substantially enlarged to consider cladistic methods and molecular systematics, and with this edition we have incorporated the taxonomic scheme that recognizes the three domains of *Bacteria*, *Archaea*, and *Eukarya*. The new methods of genetic analysis have caused major shifts across organismal groups, with the most profound effects seen among the relationships of the protists.

New findings, especially those based on *Arabidopsis* research, have been integrated throughout. The most significant impact has been on portions of the Anatomy and Physiology chapters (Sections 5 and 6), where new discussions, micrographs, and diagrams have been added.

As with past revisions, we found explanations that would benefit from rewriting and artwork that could be improved by adding labels or clarifying captions. For this edition, we also added many new illustrations, especially in the early cellular, energetics, and genetics chapters. We were grateful to be able to adapt a number of well-conceived illustrations drawn by Shirley Baty for *Invitation to Biology*, Fifth Edition, by Helena Curtis and N. Sue Barnes, published by Worth Publishers.

After taking a hard look at the matter of accessibility, we added a number of pedagogical features to this edition. Each chapter now opens with an Overview that previews in general terms the content of the chapter. The Overview is followed by Checkpoints, a list of specific questions that help the student read with greater understanding. Within each chapter, subheadings have been reworded as full sentences, providing a series of guideposts through the material. Similar headings also appear in the end-of-chapter summary. Lists of key terms, with page references, allow students to test their vocabulary, and new end-of-chapter questions place the emphasis on critical thinking rather than memorization of facts. In all, the effect is a clearer, more cohesive presentation of the material in each chapter.

As always, we have appreciated the support and constructive recommendations made by teachers who used the last edition in their classes. We have also received substantial assistance from: Kay Robinson-Beers, who read the previous edition and made detailed recommendations regarding the incorporation of molecular biology; Wayne Becker, of the University of Wisconsin, who carefully read and reread the important and heavily revised chemistry, cell, energetics, and genetics chapters; Peter Crane, Vice President, Academic Affairs and Director of the Field Museum in Chicago, who scrutinized the Diversity chapters through several drafts, introduced a number of cladograms, and integrated important information concerning systematics and paleobotany; Linda Graham, of the University of Wisconsin, who helped significantly with the major revision of the protist and bryophyte chapters undertaken in this edition; Anthony Bleecker, also of the University of Wisconsin, who contributed enormously to the chapters on growth regulation and growth response; and Bob Evans, of Rutgers University, Camden, who skillfully wrote the Overviews, Checkpoints, and subheadings, in addition to reviewing every single chapter in various drafts of manuscript.

We also wish to express our sincere thanks to the following people, who provided critiques of chapters in the last edition or reviewed various drafts of revised manuscript:

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Again, we are most grateful to Rhonda Nass for her exquisite paintings that grace each section opener and for the beautifully drawn new artwork, as well as for the illustrations she created for previous editions that we have continued to use, most notably the superb life cycles. Added to this edition are expertly rendered electronic illustrations by Kandis Elliot, who performed with uncommon skill and good humor.

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As in the past, our work on the book took far more time and effort than we originally envisioned, and we wish to thank Mary Evert for her enthusiastic support and encouragement throughout the difficult and lengthy process, and Henry (Ike) Eichhorn for his patience and steady presence during the evenings and weekends that were devoted to work on the book.

Once again, we have relied on the capable people associated with Worth Publishers. Sally Anderson, our developmental editor, has worked with us on three editions now, and the association has been warm, supportive, and rewarding. We are enormously grateful for her many outstanding contributions at every stage of the process, from the early stages of planning the new edition through all of the manuscript stages to the finished book. Others who have made important contributions are most notably Deena Cloud, our dedicated project editor, as well as Sarah Segal, Bernadine Richey, George Touloumes, Michael Weinstein, Demetrios Zangos, Jennie Nichols, Lee Mahler, John Miller, and Yuna Lee. We extend our sincerest appreciation to Linda Strange, who was instrumental in improving the text and art throughout the copyediting and proofreading stages, and to Laura Evert for her skilled proofreading of galleys. We also wish to thank Susan Driscoll, President of Worth Publishers, for her enthusiasm and support from the beginning of her tenure until the present. And, with this edition, we have been grateful for the marketing efforts of the following people at W. H. Freeman: John Britch, Sara Tenney, Todd Elder, and Nicole Folchetti. The combined talents and hard work of an enormous number of people, only some of whom are mentioned here, have contributed in important and essential ways to the book you now hold in your hand, and we extend to them our sincerest appreciation.

Peter H. Raven
Ray F. Evert
Susan E. Eichhorn

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The *Raven PLUS+* CD-ROM is organized by text chapter and features: (a) Plants and People: Sixteen essays linked to a key concept in selected chapters focus on topics of general interest, including: "Cellulase: A Bright Future in Faded Jeans," "The World's Largest Organism," "The Coffee Connection," "Kudzu: Way Too Much of a Good Thing," "Sweetness and Light: The Making of Maple Syrup," and "Murder Preserved: Tales of the Bogmen." (b) Video and Animations: Approximately thirty minutes of newly created three-dimensional animation illustrating the life cycle of the moss and pine, as well as well-conceived animations of photosynthesis, are supplemented with original live-action footage. (c) Drill and Practice: Numerous study aids, including multiple-choice quizzes, chapter outlines, drag-and-drop interactive exercises, and flashcards. (d) Annotated Web links: A collection of selected Web sites that illustrate concepts from each chapter. (e) Ongoing updates: The student version of *Raven PLUS+*, like the Instructor's version, can be updated via the Web.

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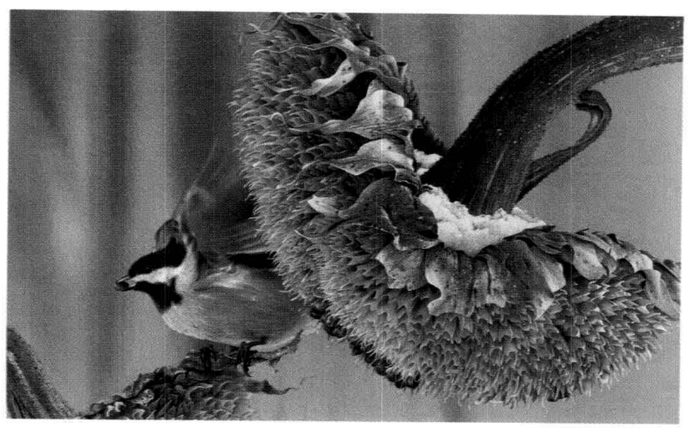
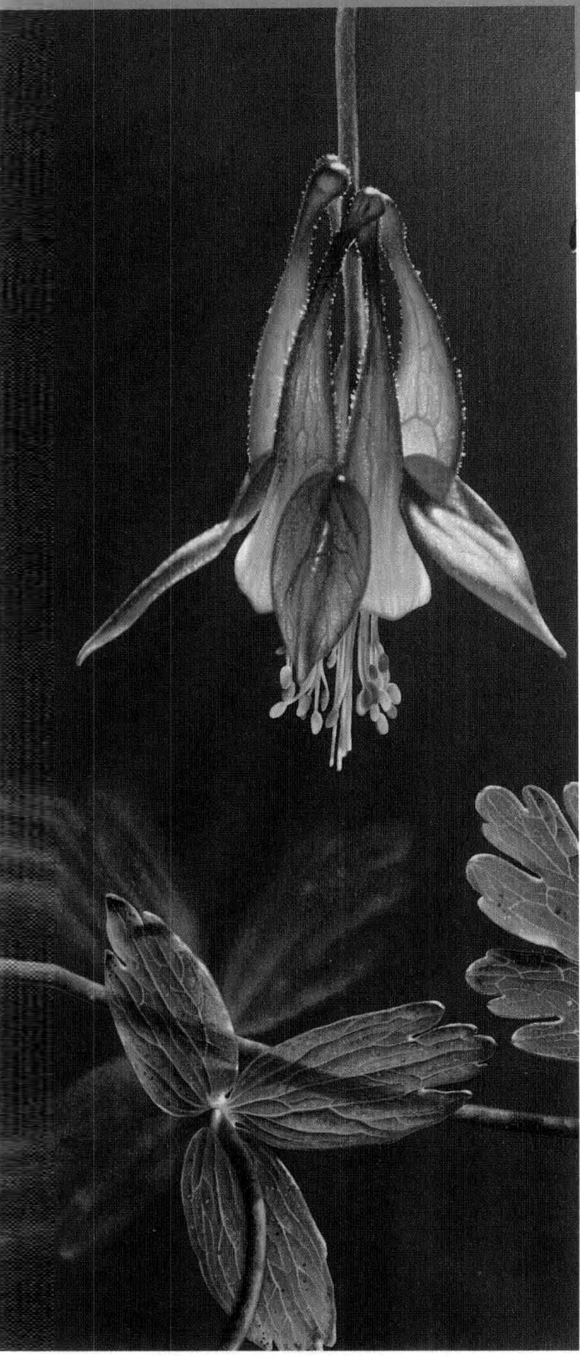
Contents in Brief

Contents





Chapter 1

Botany: An Introduction

OVERVIEW

When you begin your study of botany, you start on a journey that leads both to the future and to the past. To understand—and appreciate—the structure, function, and diversity of plants, it is first necessary to mentally travel back billions of years to a time soon after the Earth was formed and follow the hypothesized sequence of events that gave rise first to the chemical building blocks of life in the early oceans and then to cells—the smallest units of life itself. As you will see in this chapter, a key event occurred when some of these cells began to photosynthesize—that is, to use the sun's energy to manufacture their own food from simple building blocks present in the marine environment. Such photosynthetic cells changed the composition of the early atmosphere and influenced the evolution of plants and animals alike. Eventually, plants from the sea colonized the land, and many of the structures seen in present-day terrestrial plants—such as roots, stems, and leaves—can be considered evolutionary adaptations for surviving in this relatively dry environment.

Your study of botany leads to the future because it provides the background you will need to understand and perhaps solve the many challenges facing us in the years to come. Problems such as pollution, food shortages, global warming, and the destruction of the ozone layer, as well as such solutions as the development of new crops using genetic engineering, require a knowledge of plant biology.

CHECKPOINTS

By the time you finish reading this chapter, you should be able to answer the following questions:

1. What are the main factors thought to be responsible for the origin of life on Earth, and what evidence supports the hypothesis that life arose in the oceans?
2. What is the principal difference between a heterotroph and an autotroph, and what role did each play on the early Earth?
3. Why is the evolution of photosynthesis thought to be such an important event in the evolution of life in general?
4. What were some of the problems encountered by plants as they made the transition from the sea to the land, and what structures in terrestrial plants apparently solve those problems?
5. What are biomes, and what are the principal roles of plants in an ecosystem?

"What drives life is . . . a little current, kept up by the sunshine," wrote Nobel laureate Albert Szent-Györgyi. With this simple sentence, he summed up one of the greatest marvels of evolution—photosynthesis. During the photosynthetic process, radiant energy from the sun is captured and used to form the sugar on which all life, including our own, depends. Oxygen, also essential to our existence, is released as a by-product. The process begins when a particle of light strikes a molecule of the green pigment chlorophyll, boosting one of the electrons in the chlorophyll to a higher energy level. The "excited" electron, in turn, initiates a flow of electrons that ultimately converts the radiant energy from the sun to the chemical energy of sugar molecules. Sunlight striking a leaf of the columbine shown on the preceding pages, for example, is the first step in the process leading to production of the sugary nectar that will provide nourishment for the hummingbird.

Only a few types of organisms—plants, algae, and some bacteria—possess chlorophyll, which is essential for a living cell to carry out photosynthesis. Once light energy is trapped in chemical form, it becomes available as an energy source to all other organisms, including human beings. We are totally dependent upon photosynthesis, a process for which plants are exquisitely adapted.

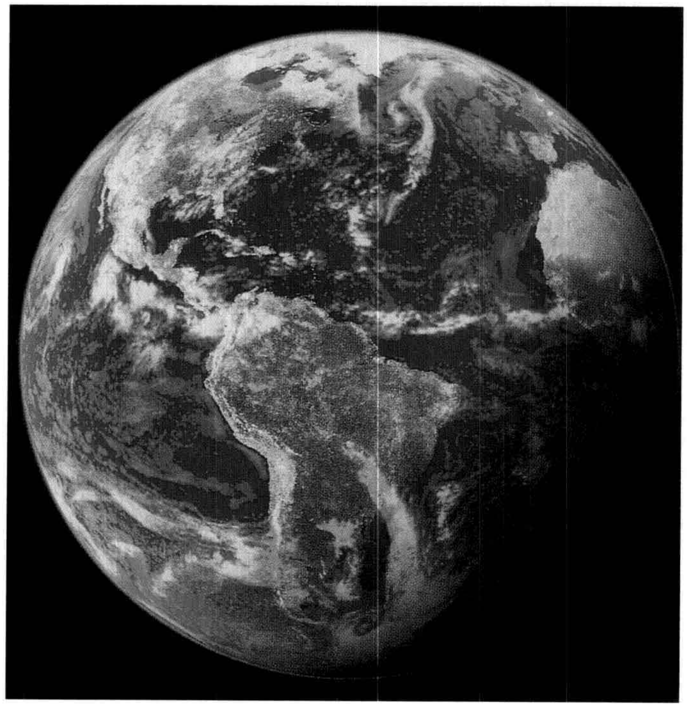
The word "botany" comes from the Greek *botanē*, meaning "plant," derived from the verb *boskein*, "to feed." Plants, however, enter our lives in innumerable ways other than as sources of food. They provide us with fiber for clothing; wood for furniture, shelter, and fuel; paper for books (such as the page you are reading at this moment); spices for flavor; drugs for medicines; and the oxygen we breathe. We are utterly dependent on plants. Plants also have enormous sensory appeal, and our lives are enhanced by the gardens, parks, and wilderness areas available to us. The study of plants has provided us with great insight into the nature of all life and will continue to do so in the years ahead. With modern technology, including continued development of molecular and computer techniques, we have just entered the most exciting period in the history of botany.

Evolution of Plants

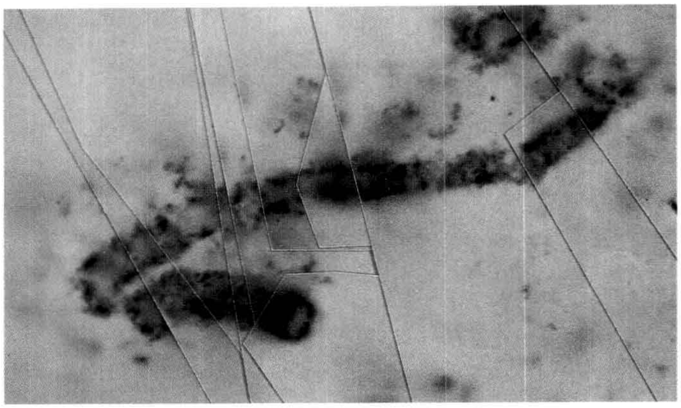
Life Originated Early in Earth's Geologic History

Like all other living organisms, plants have had a long history during which they have **evolved,** or changed, over time. The planet Earth itself—an accretion of dust and gases swirling in orbit around the star that is our sun—is some 4.5 billion years old (Figure 1–1). The earliest known fossils are found in rocks of Western Australia about 3.5 billion years old and consist of several kinds of small, relatively simple cells resembling bacteria (Figure 1–2). Evidence obtained by analysis of carbon particles embedded in the oldest rocks on Earth—from Akilia Island in southern West Greenland—indicate, however, that life already existed on Earth 3.85 billion years ago.

It is believed that Earth sustained a lethal meteor bombardment that ended 3.8 billion years ago, marking the end of Earth's earliest geologic period. Vast chunks of rubble slammed into the planet, helping to keep it hot. As the molten Earth began to cool, violent storms raged, accompanied by lightning and the release of electrical energy. Radioactive substances in the Earth emitted large quantities of energy, and widespread volcanism spewed molten rock and boiling water from beneath Earth's surface. Evidence of the presence of life on Earth as early as 3.85 billion years ago might mean that life was eliminated and reemerged, or that it originated elsewhere and reached Earth through space in the form of spores—resistant reproductive cells—or by some



1–1
Of the nine planets in our solar system, only one, as far as we know, has life on it. This planet, Earth, is visibly different from the others. From a distance, it appears blue and green, and it shines a little. The blue is water, the green is chlorophyll, and the shine is sunlight reflected off the layer of gases surrounding the planet's surface. Life, at least as we know it, depends on these visible features of Earth.



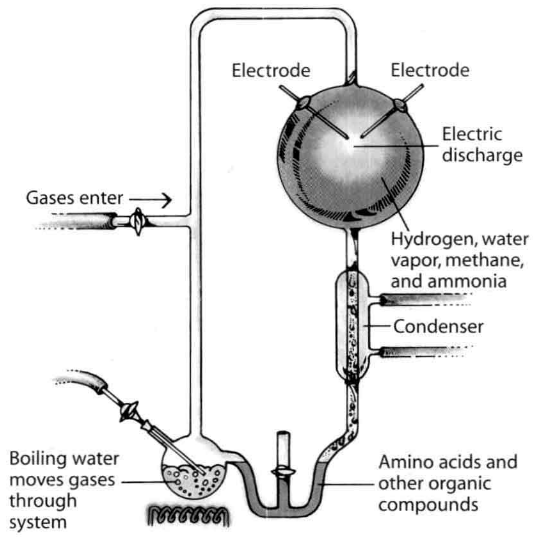
1–2
The earliest known fossils from ancient rocks in northwestern Western Australia, dated at 3.5 billion years of age. They are about a billion years younger than the Earth itself, but there are few suitable older rocks in which to look for earlier evidence of life. More complex organisms—those with eukaryotic cellular organization—did not evolve until about 1.5 billion years ago. For at least 2 billion years, therefore, prokaryotes were the only forms of life on Earth. These so-called "microfossils" have been magnified 260 times.

other means. Life may have formed on Mars, for example, whose early history apparently paralleled that of Earth. This possibility has been raised by the conclusion of NASA scientists that a Martian meteorite discovered in Antarctica in 1984 contains remains of bacteria-like life forms about 3.6 billion years old. In addition, evidence provided by the Galileo spacecraft in 1996 suggested that one of Jupiter's moons, Europa, might have liquid water beneath its frozen surface—raising the possibility of environments beyond Earth that could support life. We will continue to assume, however, that life on Earth originated on Earth.

The Chemical Building Blocks of Life Accumulated in the Early Oceans

In 1871, Charles Darwin speculated that life started in "a warm little pond," and this concept of the origin of life from some primordial soup has persisted. This view was first elaborated upon in the 1930s by the Russian scientist A. I. Oparin, who proposed that vast quantities of carbon- and hydrogen-containing compounds were formed in the early atmosphere from volcanic gases composed of methane, ammonia, water vapor, and hydrogen. Washed out of the atmosphere by driving rains, these compounds accumulated in the oceans where, with the driving forces of the energy of lightning and solar radiation, they gave rise to the first forms of life. Oparin's proposal seemed to have been borne out in 1953 with experiments carried out by Stanley L. Miller, then a graduate student working with Dr. Harold Urey at the University of Chicago. Using a similar gas mixture over an "ocean" of heated water and electric sparks to simulate lightning, Miller obtained a variety of complex organic molecules similar to those that form the fundamental building blocks of all life (Figure 1–3).

One problem with the Miller–Urey experiments is that the gas mixture included methane and ammonia, but these compounds may not have been present in Earth's first atmosphere. In the absence of an ozone layer, these gases would have been destroyed by ultraviolet radiation. The major atmospheric gases at the time probably were carbon dioxide and nitrogen emitted by volcanoes, in addition to water vapor. These three molecules contain the chemical elements carbon, oxygen, nitrogen, and hydrogen, which make up about 98 percent of the material found in living organisms today.



1–3
Stanley Miller, while a graduate student at the University of Chicago in the 1950s, used apparatus such as that shown here to simulate conditions he believed existed on the primitive Earth. Hydrogen, methane, and ammonia were circulated continuously between a lower "ocean," which was heated, and an upper "atmosphere," through which an electric discharge was transmitted. At the end of 24 hours, about half of the carbon originally present in the methane gas had been converted to amino acids and other organic molecules. This was the first test of Oparin's hypothesis.