



Biology of Plants

SIXTH EDITION

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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 chap-

ters 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 Bleeker, 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.

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

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Contents in Brief



<i>Chapter</i> 1	Botany: An Introduction	1
SECTION 1 <i>The Biology of the Plant Cell</i>		16
<i>Chapter</i> 2	The Molecular Composition of Plant Cells	17
<i>Chapter</i> 3	Introduction to the Plant Cell	40
<i>Chapter</i> 4	Membrane Structure and Function	73
SECTION 2 <i>Energetics</i>		92
<i>Chapter</i> 5	The Flow of Energy	93
<i>Chapter</i> 6	Respiration	108
<i>Chapter</i> 7	Photosynthesis, Light, and Life	126
SECTION 3 <i>Genetics and Evolution</i>		154
<i>Chapter</i> 8	The Reproduction of Cells	155
<i>Chapter</i> 9	Meiosis and Sexual Reproduction	169
<i>Chapter</i> 10	Genetics and Heredity	183
<i>Chapter</i> 11	Gene Expression	207
<i>Chapter</i> 12	The Process of Evolution	235
SECTION 4 <i>Diversity</i>		260
<i>Chapter</i> 13	Systematics: The Science of Biological Diversity	261

<i>Chapter</i> 14	Prokaryotes and Viruses	281	SECTION 6	<i>Physiology of Seed Plants</i>	672
<i>Chapter</i> 15	Fungi	306	<i>Chapter</i> 28	Regulating Growth and Development: The Plant Hormones	673
<i>Chapter</i> 16	<i>Protista</i> I: Euglenoids, Slime Molds, Cryptomonads, Red Algae, Dinoflagellates, and Haptophytes	347	<i>Chapter</i> 29	External Factors and Plant Growth	702
<i>Chapter</i> 17	<i>Protista</i> II: Heterokonts and Green Algae	370	<i>Chapter</i> 30	Plant Nutrition and Soils	726
<i>Chapter</i> 18	Bryophytes	400	<i>Chapter</i> 31	The Movement of Water and Solutes in Plants	750
<i>Chapter</i> 19	Seedless Vascular Plants	424	SECTION 7	<i>Ecology</i>	772
<i>Chapter</i> 20	Gymnosperms	466	<i>Chapter</i> 32	The Dynamics of Communities and Ecosystems	773
<i>Chapter</i> 21	Introduction to the Angiosperms	495	<i>Chapter</i> 33	Global Ecology	796
<i>Chapter</i> 22	Evolution of the Angiosperms	517	<i>Chapter</i> 34	The Human Prospect	823
SECTION 5	<i>The Angiosperm Plant Body: Structure and Development</i>	554	<i>Suggested Readings</i>		851
<i>Chapter</i> 23	Early Development of the Plant Body	555	<i>Appendix A:</i>	Fundamentals of Chemistry	863
<i>Chapter</i> 24	Cells and Tissues of the Plant Body	570	<i>Appendix B:</i>	The Hardy–Weinberg Equation	877
<i>Chapter</i> 25	The Root: Structure and Development	589	<i>Appendix C:</i>	Metric Table and Temperature Conversion Scale	879
<i>Chapter</i> 26	The Shoot: Primary Structure and Development	610	<i>Appendix D:</i>	Classification of Organisms	881
<i>Chapter</i> 27	Secondary Growth in Stems	647	<i>Glossary</i>		889
			<i>Illustration Credits</i>		915
			<i>Index</i>		920
			<i>Geologic Eras</i>		inside front cover

Contents

Chapter 1	Botany: An Introduction	1
	Evolution of Plants	2
	Evolution of Communities	9
	Appearance of Human Beings	11
	Summary	14

SECTION 1	The Biology of the Plant Cell	16
------------------	--------------------------------------	-----------



Chapter 2	The Molecular Composition of Plant Cells	17
	Organic Molecules	18
	Carbohydrates	18
	<i>Essay: Representations of Molecules</i>	19
	Lipids	22
	<i>Essay: Amino Acids and Nitrogen</i>	26
	Proteins	26
	Nucleic Acids	30
	Secondary Metabolites	32
	Summary	37

Chapter 3	Introduction to the Plant Cell	40
	Development of the Cell Theory	41
	Prokaryotic Cells and Eukaryotic Cells	41
	<i>Essay: Viewing the Cellular World</i>	42
	The Plant Cell: An Overview	45
	Plasma Membrane	46
	<i>Essay: Cytoplasmic Streaming in Giant Algal Cells</i>	47
	Nucleus	47

	Chloroplasts and Other Plastids	48
	Mitochondria	52
	Peroxisomes	53
	Vacuoles	54
	Oil Bodies	55
	Ribosomes	55
	Endoplasmic Reticulum	56
	Golgi Complex	57
	Cytoskeleton	58
	Flagella and Cilia	60
	Cell Wall	61
	<i>Essay: Cell Theory versus Organismal Theory</i>	65
	Plasmodesmata	66
	Summary	68

Chapter 4	Membrane Structure and Function	73
	Structure of Cellular Membranes	74
	Movement of Water and Solutes	76
	Cells and Diffusion	78
	<i>Essay: Imbibition</i>	80
	Osmosis and Living Organisms	80
	Transport of Solutes across Membranes	82
	<i>Essay: Patch-Clamp Recording in the Study of Ion Channels</i>	83
	Vesicle-Mediated Transport	85
	Cell-to-Cell Communication	86
	Summary	89

SECTION 2	Energetics	92
------------------	-------------------	-----------



Chapter 5	The Flow of Energy	93	Chapter 8	The Reproduction of Cells	155
	The Laws of Thermodynamics	95		Cell Division in Prokaryotes	156
	Oxidation-Reduction	98		Cell Division in Eukaryotes	156
	Enzymes	99		The Cell Cycle	157
	Cofactors in Enzyme Action	102		Interphase	158
	Metabolic Pathways	103		Cell Division in Plants	158
	Regulation of Enzyme Activity	103		<i>Essay: Immunofluorescence Microscopy</i>	159
	The Energy Factor: ATP Revisited	105		Cell Division and the Reproduction of the Organism	166
	Summary	106		Summary	166
Chapter 6	Respiration	108	Chapter 9	Meiosis and Sexual Reproduction	169
	An Overview of Glucose Oxidation	109		Haploid and Diploid	170
	Glycolysis	109		Meiosis, the Life Cycle, and Diploidy	171
	The Aerobic Pathway	113		The Process of Meiosis	172
	<i>Essay: Bioluminescence</i>	122		The Phases of Meiosis	173
	Other Substrates for Respiration	122		Asexual Reproduction: An Alternative Strategy	179
	Anaerobic Pathways	122		<i>Essay: Vegetative Reproduction: Some Ways and Means</i>	180
	The Strategy of Energy Metabolism	123		Advantages of Sexual Reproduction	180
	Summary	124		Summary	181
Chapter 7	Photosynthesis, Light, and Life	126	Chapter 10	Genetics and Heredity	183
	Photosynthesis: A Historical Perspective	127		The Concept of the Gene	184
	The Nature of Light	128		The Principle of Segregation	185
	<i>Essay: The Fitness of Light</i>	130		<i>Essay: Mendel and the Laws of Probability</i>	188
	The Role of Pigments	130		The Principle of Independent Assortment	188
	The Reactions of Photosynthesis	133		Discovery of the Chromosomal Basis of Mendel's Laws	189
	<i>Essay: Chemiosmotic Coupling in Chloroplasts and Mitochondria</i>	137		Linkage	190
	The Carbon-Fixation Reactions	139		Mutations	192
	<i>Essay: The Carbon Cycle</i>	150		Broadening the Concept of the Gene	194
	Summary	152		The Chemical Basis of Heredity	197
SECTION 3	Genetics and Evolution	154		The Chemistry of the Gene: DNA versus Protein	197
				The Structure of DNA	197
				DNA Replication	201
				The Problem of the Ends of Linear DNA	203
				The Energetics of DNA Replication	203
				DNA as a Carrier of Information	204
				Summary	204
			Chapter 11	Gene Expression	207
				From DNA to Protein: The Role of RNA	208
				The Genetic Code	209
				Protein Synthesis	210
				Regulating Gene Expression	214
				The Prokaryotic Chromosome	216
				The Eukaryotic Chromosome	218
				Regulation of Gene Expression in Eukaryotes	220
				The DNA of the Eukaryotic Chromosome	221
				Transcription and Processing of mRNA in Eukaryotes	223



Recombinant DNA Technology	224
<i>Essay: Arabidopsis thaliana: The Model Plant</i>	228
Summary	231
Chapter 12 The Process of Evolution	235
Darwin's Theory	237
The Concept of the Gene Pool	239
The Behavior of Genes in Populations: The Hardy-Weinberg Law	239
The Agents of Change	240
Preservation and Promotion of Variability	242
Responses to Selection	243
The Result of Natural Selection: Adaptation	245
The Origin of Species	248
How Does Speciation Occur?	249
<i>Essay: Adaptive Radiation in Hawaiian Tarweeds</i>	250
Maintaining Reproductive Isolation	256
The Origin of Major Groups of Organisms	256
Summary	258

SECTION 4 Diversity 260



Chapter 13 Systematics: The Science of Biological Diversity	261
Taxonomy and Hierarchical Classification	262
Classification and Phylogeny	264
<i>Essay: Convergent Evolution</i>	266
Methods of Classification	267
Molecular Systematics	268
The Major Groups of Organisms: <i>Bacteria, Archaea,</i> and <i>Eukarya</i>	271
Origin of the Eukaryotes	272
The Eukaryotic Kingdoms	275
Summary	279

Chapter 14 Prokaryotes and Viruses	281
Characteristics of the Prokaryotic Cell	282
Diversity of Form	284
Reproduction and Gene Exchange	285
Endospores	286
Metabolic Diversity	286
<i>Bacteria</i>	287
<i>Archaea</i>	294
Viruses	296
Viroids: Other Infectious Particles	302
The Origin of Viruses	303
Summary	303

Chapter 15 Fungi	306
The Importance of Fungi	307
Biology and Characteristics of Fungi	310
Evolution of the Fungi	312
Chytrids: Phylum <i>Chytridiomycota</i>	312
Phylum <i>Zygomycota</i>	313
<i>Essay: Phototropism in a Fungus</i>	315
Phylum <i>Ascomycota</i>	317
Phylum <i>Basidiomycota</i>	320
Yeasts	330
Deuteromycetes	332
<i>Essay: Predaceous Fungi</i>	333
Symbiotic Relationships of Fungi	334
<i>Essay: From Pathogen to Symbiont:</i> Fungal Endophytes	335
Summary	344

Chapter 16 Protista I: Euglenoids, Slime Molds, Cryptomonads, Red Algae, Dinoflagellates, and Haptophytes	347
Ecology of the Algae	348
Euglenoids: Phylum <i>Euglenophyta</i>	350
Plasmodial Slime Molds: Phylum <i>Myxomycota</i>	352
Cellular Slime Molds: Phylum <i>Dictyosteliomycota</i>	354
Cryptomonads: Phylum <i>Cryptophyta</i>	356
Red Algae: Phylum <i>Rhodophyta</i>	357
Dinoflagellates: Phylum <i>Dinophyta</i>	361
<i>Essay: Red Tides/Toxic Blooms</i>	364
Haptophytes: Phylum <i>Haptophyta</i>	366
Summary	368

Chapter 17 Protista II: Heterokonts and Green Algae	370
The Heterokonts	371
Oomycetes: Phylum <i>Oomycota</i>	371
Diatoms: Phylum <i>Bacillariophyta</i>	375
Chrysophytes: Phylum <i>Chrysophyta</i>	378

Brown Algae: Phylum <i>Phaeophyta</i>	379
<i>Essay: Algae and Human Affairs</i>	380
Green Algae: Phylum <i>Chlorophyta</i>	383
Summary	398
Chapter 18 Bryophytes	400
The Relationships of Bryophytes to Other Groups	401
Comparative Structure and Reproduction of Bryophytes	403
Liverworts: Phylum <i>Hepatophyta</i>	407
Hornworts: Phylum <i>Anthoceroophyta</i>	412
Mosses: Phylum <i>Bryophyta</i>	412
Summary	423
Chapter 19 Seedless Vascular Plants	424
Evolution of Vascular Plants	425
Organization of the Vascular Plant Body	425
Reproductive Systems	430
The Phyla of Seedless Vascular Plants	431
Phylum <i>Rhyniophyta</i>	432
Phylum <i>Zosterophyllophyta</i>	434
Phylum <i>Lycophyta</i>	435
Phylum <i>Trimerophytophyta</i>	443
Phylum <i>Psilotophyta</i>	443
Phylum <i>Sphenophyta</i>	445
Phylum <i>Pterophyta</i>	449
<i>Essay: Coal Age Plants</i>	456
Summary	463
Chapter 20 Gymnosperms	466
Evolution of the Seed	468
Progymnosperms	470
Extinct Gymnosperms	472
Living Gymnosperms	472
Phylum <i>Coniferophyta</i>	474
The Other Living Gymnosperm Phyla: <i>Cycadophyta</i> , <i>Ginkgophyta</i> , and <i>Gnetophyta</i>	486
<i>Essay: Wollemia nobilis: A Newly Discovered Living Fossil</i>	488
Summary	493
Chapter 21 Introduction to the Angiosperms	495
Diversity in the Phylum <i>Anthophyta</i>	496
The Flower	498
The Angiosperm Life Cycle	503
<i>Essay: Hay Fever</i>	508
Summary	514

Chapter 22 Evolution of the Angiosperms	517
Relationships of the Angiosperms	518
Origin and Diversification of the Angiosperms	519
Evolution of the Flower	524
<i>Essay: An Ambiguous Aquatic Plant</i>	526
Evolution of Fruits	543
Biochemical Coevolution	549
Summary	552

SECTION 5 *The Angiosperm Plant Body: Structure and Development* 554



Chapter 23 Early Development of the Plant Body	555
Formation of the Embryo	556
The Mature Embryo and Seed	562
<i>Essay: Wheat: Bread and Bran</i>	563
Requirements for Seed Germination	564
From Embryo to Adult Plant	566
Summary	568
Chapter 24 Cells and Tissues of the Plant Body	570
Apical Meristems and Their Derivatives	571
Growth, Morphogenesis, and Differentiation	571
Internal Organization of the Plant Body	572
Ground Tissues	573
Vascular Tissues	576
Dermal Tissues	583
Summary	588

Chapter 25 The Root: Structure and Development 589

Root Systems	590
Origin and Growth of Primary Tissues	591
Primary Structure	595
Effect of Secondary Growth on the Primary Body of the Root	600
Origin of Lateral Roots	603
Aerial Roots and Air Roots	603
<i>Essay: Getting to the Root of Organ Development</i>	604
Adaptations for Food Storage: Fleshy Roots	606
Summary	608

Chapter 26 The Shoot: Primary Structure and Development 610

Origin and Growth of the Primary Tissues of the Stem	611
Primary Structure of the Stem	614
<i>Essay: Plants, Air Pollution, and Acid Rain</i>	616
Relation between the Vascular Tissues of the Stem and the Leaf	622
Morphology of the Leaf	624
<i>Essay: Leaf Dimorphism in Aquatic Plants</i>	626
Structure of the Leaf	626
Grass Leaves	632
Development of the Leaf	632
Sun and Shade Leaves	636
Leaf Abscission	636
Transition between Vascular Systems of the Root and the Shoot	636
Development of the Flower	639
Stem and Leaf Modifications	641
Summary	644

Chapter 27 Secondary Growth in Stems 647

Annuals, Biennials, and Perennials	648
The Vascular Cambium	648
Effect of Secondary Growth on the Primary Body of the Stem	650
The Wood: Secondary Xylem	659
<i>Essay: The Truth about Knots</i>	668
Summary	670

SECTION 6 *Physiology of Seed Plants* 672



Chapter 28 Regulating Growth and Development: The Plant Hormones 673

Auxins	675
Cytokinins	679
Ethylene	682
Abscissic Acid	683
Gibberellins	684
The Molecular Basis of Hormone Action	687
Plant Biotechnology	693
<i>Essay: Totipotency</i>	695
Summary	700

Chapter 29 External Factors and Plant Growth 702

The Tropisms	703
Circadian Rhythms	706
Photoperiodism	709
Chemical Basis of Photoperiodism	711
Hormonal Control of Flowering	715
Genetic Control of Flowering	716
Dormancy	717
Cold and the Flowering Response	719
Nastic Movements	719
Generalized Effects of Mechanical Stimuli on Plant Growth and Development: Thigmomorphogenesis	721
Solar Tracking	722
Summary	723

Chapter 30 Plant Nutrition and Soils 726

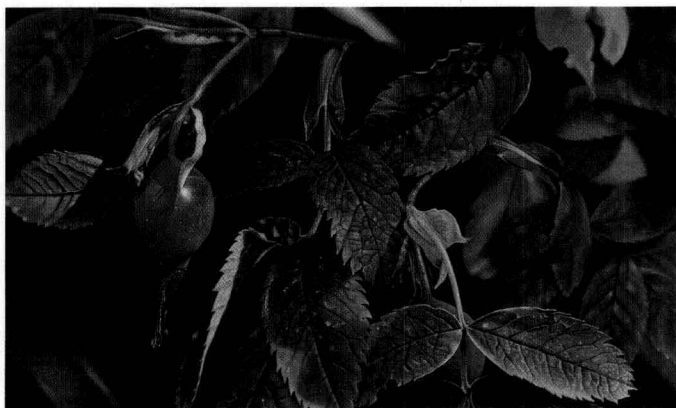
Essential Elements	727
Functions of Essential Elements	729
The Soil	731
<i>Essay: The Water Cycle</i>	734
Nutrient Cycles	735

Nitrogen and the Nitrogen Cycle 736
Essay: Carnivorous Plants 737
 Assimilation of Nitrogen 742
 The Phosphorus Cycle 742
 Human Impact on Nutrient Cycles and Effects of Pollution 743
Essay: Halophytes: A Future Resource? 744
 Soils and Agriculture 744
 Plant Nutrition Research 745
Essay: Compost 746
 Summary 747

Chapter 31 The Movement of Water and Solutes in Plants 750

Movement of Water and Inorganic Nutrients through the Plant Body 751
 Assimilate Transport: Movement of Substances through the Phloem 764
 Summary 769

SECTION 7 Ecology 772



Chapter 32 The Dynamics of Communities and Ecosystems 773

Interactions between Organisms 774
Essay: Competing for Light 778
Essay: Pesticides and Ecosystems 781
 Nutrient Cycling 782
 Trophic Levels 783
 Development of Communities and Ecosystems 786
Essay: The Great Yellowstone Fire 790
 Summary 793

Chapter 33 Global Ecology 796

Life on the Land 797
Essay: Alexander von Humboldt 802
 Rainforests 803
 Savannas and Deciduous Tropical Forests 805
 Deserts 807
Essay: How Does a Cactus Function? 809
 Grasslands 810
 Temperate Deciduous Forests 812
Essay: Jobs versus Owls 815
 Temperate Mixed and Coniferous Forests 815
 Mediterranean Scrub 816
 Taiga 818
 Arctic Tundra 819
 Summary 821

Chapter 34 The Human Prospect 823

The Agricultural Revolution 824
Essay: The Origin of Maize 829
 The Growth of Human Populations 835
 Agriculture in the Future 837
Essay: A New Millennium: The Transition to Sustainability 844
 Summary 847

Suggested Readings 851

Appendix A: Fundamentals of Chemistry 863
Appendix B: The Hardy–Weinberg Equation 877
Appendix C: Metric Table and Temperature Conversion Scale 879
Appendix D: Classification of Organisms 881

Glossary 889

Illustration Credits 915

Index 920

Geologic Eras inside front cover

Botany: An Introduction

OVERVIEW

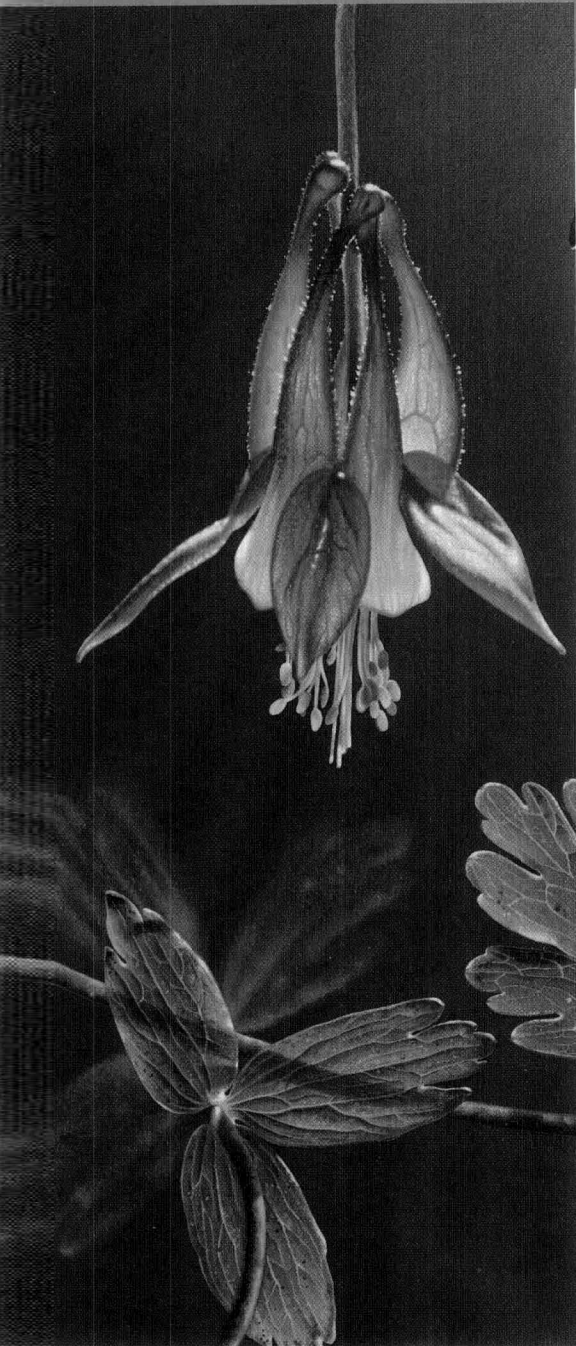
When you begin your study of botany, you start on a journey that leads both to the future and to the past. To understand—and appreciate—the structure, function, and diversity of plants, it is first necessary to mentally travel back billions of years to a time soon after the Earth was formed and follow 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.

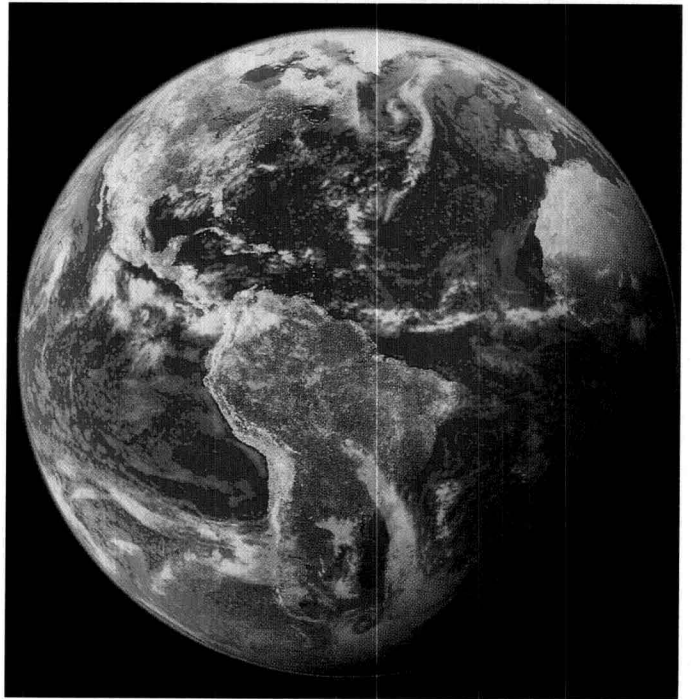
Evolution of Plants

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

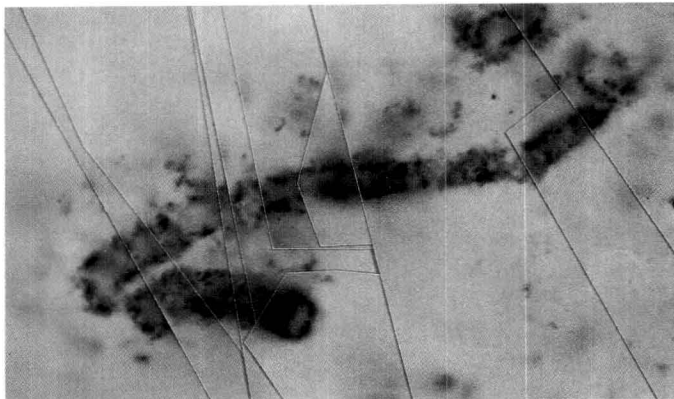
bacteria (Figure 1–2). Evidence obtained by analysis of carbon particles embedded in the oldest rocks on Earth—from Akilia Island in southern West Greenland—indicate, however, that life already existed on Earth 3.85 billion years ago.

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.

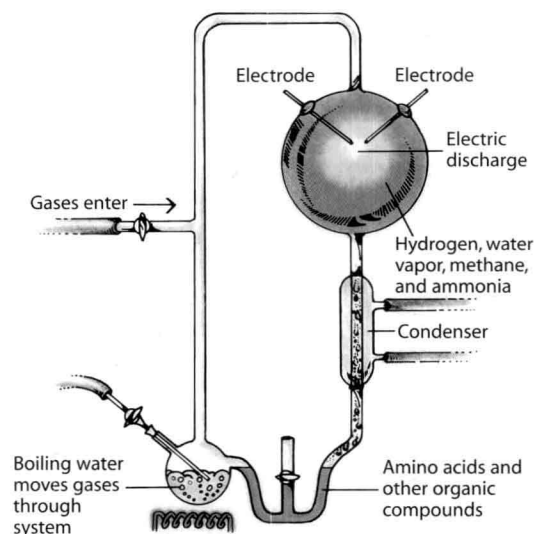
other means. Life may have formed on Mars, for example, whose early history apparently paralleled that of Earth. This possibility has been raised by the conclusion of NASA scientists that a Martian meteorite discovered in Antarctica in 1984 contains remains of bacteria-like life forms about 3.6 billion 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.