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Kenneth A. Mason

University of Iowa

Jonathan B. Losos

William H. Danforth Distinguished University Professor and Director, Living Earth Collaborative, Washington University

Tod Duncan

University of Colorado Denver

Contributor:

Charles J. Welsh

Duquesne University

Based on the work of

Peter H. Raven

President Emeritus, Missouri Botanical Garden; George Engelmann Professor of Botany Emeritus, Washington University

George B. Johnson

Professor Emeritus of Biology, Washington University

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Brief Contents

Committed to Excellence xi

Preparing Students for the Future xv

Part I The Molecular Basis of Life 1

1 The Science of Biology 1
2 The Nature of Molecules and the Properties of Water 18
3 The Chemical Building Blocks of Life 35

Part II Biology of the Cell 63

4 Cell Structure 63
5 Membranes 92
6 Energy and Metabolism 112
7 How Cells Harvest Energy 128
8 Photosynthesis 154
9 Cell Communication 176
10 How Cells Divide 194

Part III Genetic and Molecular Biology 217

11 Sexual Reproduction and Meiosis 217
12 Patterns of Inheritance 231
13 Chromosomes, Mapping, and the Meiosis–Inheritance Connection 250
14 DNA: The Genetic Material 268
15 Genes and How They Work 290
16 Control of Gene Expression 317
17 Biotechnology 340
18 Genomics 366
19 Cellular Mechanisms of Development 389

Part IV Evolution 416

20 Genes Within Populations 416
21 The Evidence for Evolution 443
22 The Origin of Species 463
23 Systematics, Phylogenies, and Comparative Biology 484
24 Genome Evolution 504

Part V Diversity of Life on Earth 523

25 The Origin and Diversity of Life 523
26 Viruses 537
27 Prokaryotes 557
28 Protists 584
29 Seedless Plants 608
30 Seed Plants 623
31 Fungi 641
32 Animal Diversity and the Evolution of Body Plans 664
33 Protostomes 687
34 Deuterostomes 720

Part VI Plant Form and Function 762

35 Plant Form 762
36 Transport in Plants 788
37 Plant Nutrition and Soils 807
38 Plant Defense Responses 825
39 Sensory Systems in Plants 838
40 Plant Reproduction 866

Part VII Animal Form and Function 900

41 The Animal Body and Principles of Regulation 900
42 The Nervous System 924
43 Sensory Systems 955
44 The Endocrine System 982
45 The Musculoskeletal System 1006
46 The Digestive System 1026
47 The Respiratory System 1047
48 The Circulatory System 1066
49 Osmotic Regulation and the Urinary System 1088
50 The Immune System 1106
51 The Reproductive System 1135
52 Animal Development 1157

Part VIII Ecology and Behavior 1188

53 Behavioral Biology 1188
54 Ecology of Individuals and Populations 1218
55 Community Ecology 1242
56 Dynamics of Ecosystems 1265
57 The Biosphere and Human Impacts 1289
58 Conservation Biology 1318

Appendix A

Glossary G-1

Index I-1

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About the Authors



©Kenneth Mason

Kenneth Mason maintains an association with the University of Iowa, Department of Biology after having served as a faculty member for eight years. His academic positions, as a teacher and researcher, include the faculty of the University of Kansas, where he designed and established the genetics lab, and taught and published on the genetics of pigmentation in amphibians. At Purdue University, he successfully developed and grew large introductory biology courses and collaborated with other faculty in an innovative biology, chemistry, and physics course supported by the National Science Foundation. At the University of Iowa, where his wife served as president of the university, he taught introductory biology and human genetics. His honor society memberships include Phi Sigma, Alpha Lambda Delta, and, by vote of Purdue pharmacy students, Phi Eta Sigma Freshman Honors Society.



©Jonathan Losos

Jonathan Losos is the William H. Danforth Distinguished University Professor in the Department of Biology at Washington University and Director of the Living Earth Collaborative, a partnership between the university, the Saint Louis Zoo and the Missouri Botanical Garden. Losos's research has focused on studying patterns of adaptive radiation and evolutionary diversification in lizards. He is a member of the National Academy of Sciences, a fellow of the American Academy of Arts and Science, and the recipient of several awards, including the Theodosius Dobzhanksy and David Starr Jordan Prizes, the Edward Osborne Wilson Naturalist Award, and the Daniel Giraud Elliot Medal, as well as receiving fellowships from the John Guggenheim and David and Lucile Packard Foundations. Losos has published more than 200 scientific articles and has written two books, *Lizards in an Evolutionary Tree: Ecology and Adaptive Radiation of Anoles* (University of California Press, 2009) and *Improbable Destinies: Fate, Chance, and the Future of Evolution* (Penguin-Random House, 2017).



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Tod Duncan is a Clinical Assistant Professor at the University of Colorado Denver. He currently teaches first semester general biology and coordinates first and second semester general biology laboratories. Previously, he taught general microbiology, virology, the biology of cancer, medical microbiology, and cell biology. A bachelor's degree in cell biology with an emphasis on plant molecular and cellular biology from the University of East Anglia in England led to doctoral studies in cell cycle control, and postdoctoral research on the molecular and biochemical mechanisms of DNA alkylation damage *in vitro* and in *Drosophila melanogaster*. Currently, he is interested in factors affecting retention and success of incoming first-year students in diverse demographics. He lives in Boulder, Colorado, with his two Great Danes, Eddie and Henry.

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Contents

Committed to Excellence xi

Preparing Students for the Future xv

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Part I The Molecular Basis of Life

1 The Science of Biology 1

1.1 The Science of Life 1
1.2 The Nature of Science 4
1.3 An Example of Scientific Inquiry: Darwin and Evolution 8
1.4 Core Concepts in Biology 12

2 The Nature of Molecules and the Properties of Water 18

2.1 The Nature of Atoms 19
2.2 Elements Found in Living Systems 23
2.3 The Nature of Chemical Bonds 24
2.4 Water: A Vital Compound 26
2.5 Properties of Water 29
2.6 Acids and Bases 30

3 The Chemical Building Blocks of Life 35

3.1 Carbon: The Framework of Biological Molecules 36
3.2 Carbohydrates: Energy Storage and Structural Molecules 40
3.3 Nucleic Acids: Information Molecules 43
3.4 Proteins: Molecules with Diverse Structures and Functions 46
3.5 Lipids: Hydrophobic Molecules 56

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Part II Biology of the Cell

4 Cell Structure 63

4.1 Cell Theory 63
4.2 Prokaryotic Cells 67
4.3 Eukaryotic Cells 69
4.4 The Endomembrane System 73
4.5 Mitochondria and Chloroplasts: Cellular Generators 77
4.6 The Cytoskeleton 79
4.7 Extracellular Structures and Cell Movement 83
4.8 Cell-to-Cell Interactions 86

5 Membranes 92

5.1 The Structure of Membranes 92
5.2 Phospholipids: The Membrane's Foundation 96
5.3 Proteins: Multifunctional Components 98
5.4 Passive Transport Across Membranes 100
5.5 Active Transport Across Membranes 103
5.6 Bulk Transport by Endocytosis and Exocytosis 106

6 Energy and Metabolism 112

6.1 The Flow of Energy in Living Systems 113
6.2 The Laws of Thermodynamics and Free Energy 114
6.3 ATP: The Energy Currency of Cells 117
6.4 Enzymes: Biological Catalysts 118
6.5 Metabolism: The Chemical Description of Cell Function 122

7 How Cells Harvest Energy 128

7.1 Overview of Respiration 129
7.2 Glycolysis: Splitting Glucose 133
7.3 The Oxidation of Pyruvate Produces Acetyl-CoA 136
7.4 The Citric Acid Cycle 137
7.5 The Electron Transport Chain and Chemiosmosis 140
7.6 Energy Yield of Aerobic Respiration 143
7.7 Regulation of Aerobic Respiration 144
7.8 Oxidation Without O_2 145
7.9 Catabolism of Proteins and Fats 147
7.10 Evolution of Metabolism 149

8 Photosynthesis 154

8.1 Overview of Photosynthesis 154
8.2 The Discovery of Photosynthetic Processes 156
8.3 Pigments 158
8.4 Photosystem Organization 161
8.5 The Light-Dependent Reactions 163
8.6 Carbon Fixation: The Calvin Cycle 167
8.7 Photorespiration 170

rav69618_FM_i-xxii.indd 5 12/11/18 7:24 PM

9 Cell Communication 176

9.1 Overview of Cell Communication 176
9.2 Receptor Types 179
9.3 Intracellular Receptors 181
9.4 Signal Transduction Through Receptor Kinases 182
9.5 Signal Transduction Through G Protein–Coupled Receptors 186

10 How Cells Divide 194

10.1 Bacterial Cell Division 195
10.2 Eukaryotic Chromosomes 197
10.3 Overview of the Eukaryotic Cell Cycle 200
10.4 Interphase: Preparation for Mitosis 201
10.5 M Phase: Chromosome Segregation and the Division of Cytoplasmic Contents 203
10.6 Control of the Cell Cycle 206
10.7 Genetics of Cancer 211

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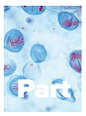

III Genetic and Molecular Biology

11 Sexual Reproduction and Meiosis 217

11.1 Sexual Reproduction Requires Meiosis 217
11.2 Features of Meiosis 219
11.3 The Process of Meiosis 220
11.4 Summing Up: Meiosis Versus Mitosis 225

12 Patterns of Inheritance 231

12.1 The Mystery of Heredity 231
12.2 Monohybrid Crosses: The Principle of Segregation 234
12.3 Dihybrid Crosses: The Principle of Independent Assortment 238
12.4 Probability: Predicting the Results of Crosses 240
12.5 The Testcross: Revealing Unknown Genotypes 241
12.6 Extensions to Mendel 242

13 Chromosomes, Mapping, and the Meiosis–Inheritance Connection 250

13.1 Sex Linkage and the Chromosomal Theory of Inheritance 251
13.2 Sex Chromosomes and Sex Determination 252
13.3 Exceptions to the Chromosomal Theory of Inheritance 255
13.4 Genetic Mapping 255
13.5 Human Genetic Disorders 260

14 DNA: The Genetic Material 268

14.1 The Nature of the Genetic Material 268
14.2 DNA Structure 271
14.3 Basic Characteristics of DNA Replication 275
14.4 Prokaryotic Replication 278
14.5 Eukaryotic Replication 283
14.6 DNA Repair 285

15 Genes and How They Work 290

15.1 The Nature of Genes 290
15.2 The Genetic Code 293
15.3 Prokaryotic Transcription 296
15.4 Eukaryotic Transcription 299
15.5 Eukaryotic pre-mRNA Splicing 301
15.6 The Structure of tRNA and Ribosomes 303
15.7 The Process of Translation 305
15.8 Summarizing Gene Expression 309
15.9 Mutation: Altered Genes 311

16 Control of Gene Expression 317

16.1 Control of Gene Expression 317
16.2 Regulatory Proteins 318
16.3 Prokaryotic Regulation 321
16.4 Eukaryotic Regulation 325
16.5 Chromatin Structure Affects Gene Expression 328
16.6 Eukaryotic Posttranscriptional Regulation 330
16.7 Protein Degradation 334

17 Biotechnology 340

17.1 Recombinant DNA 340
17.2 Amplifying DNA Using the Polymerase Chain Reaction 345
17.3 Creating, Correcting, and Analyzing Genetic Variation 348
17.4 Constructing and Using Transgenic Organisms 350
17.5 Environmental Applications 354
17.6 Medical Applications 356
17.7 Agricultural Applications 360

18 Genomics 366

18.1 Mapping Genomes 366
18.2 Sequencing Genomes 370
18.3 Genome Projects 373
18.4 Genome Annotation and Databases 374
18.5 Comparative and Functional Genomics 378
18.6 Applications of Genomics 383

19 Cellular Mechanisms of Development 389

19.1 The Process of Development 389
19.2 Cell Division 390

rav69618_FM_i-xxii.indd 6 12/11/18 7:25 PM

19.3 Cell Differentiation 392
19.4 Nuclear Reprogramming 397
19.5 Pattern Formation 400
19.6 Evolution of Pattern Formation 406
19.7 Morphogenesis 409

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IV Evolution

20 Genes Within Populations 416

20.1 Genetic Variation and Evolution 416
20.2 Changes in Allele Frequency 418
20.3 Five Agents of Evolutionary Change 420
20.4 Quantifying Natural Selection 425
20.5 Reproductive Strategies 426
20.6 Natural Selection's Role in Maintaining Variation 430
20.7 Selection Acting on Traits Affected by Multiple Genes 432
20.8 Experimental Studies of Natural Selection 434
20.9 Interactions Among Evolutionary Forces 436
20.10 The Limits of Selection 437

21 The Evidence for Evolution 443

21.1 The Beaks of Darwin's Finches: Evidence of Natural Selection 444
21.2 Peppered Moths and Industrial Melanism: More Evidence of Selection 446
21.3 Artificial Selection: Human-Initiated Change 448
21.4 Fossil Evidence of Evolution 450
21.5 Anatomical Evidence for Evolution 454
21.6 Convergent Evolution and the Biogeographical Record 456
21.7 Darwin's Critics 458

22 The Origin of Species 463

22.1 The Nature of Species and the Biological Species Concept 463
22.2 Natural Selection and Reproductive Isolation 468
22.3 The Role of Genetic Drift and Natural Selection in Speciation 469
22.4 The Geography of Speciation 471
22.5 Adaptive Radiation and Biological Diversity 473
22.6 The Pace of Evolution 478
22.7 Speciation and Extinction Through Time 479

23 Systematics, Phylogenies, and Comparative Biology 484

23.1 Systematics 484
23.2 Cladistics 486
23.3 Systematics and Classification 489
23.4 Phylogenetics and Comparative Biology 493
23.5 Phylogenetics and Disease Evolution 499

24 Genome Evolution 504

24.1 Comparative Genomics 504
24.2 Genome Size 508
24.3 Evolution Within Genomes 511
24.4 Gene Function and Expression Patterns 515
24.5 Applying Comparative Genomics 516

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V Diversity of Life on Earth

25 The Origin and Diversity of Life 523

25.1 Deep Time 525
25.2 Origins of Life 525
25.3 Evidence for Early Life 528
25.4 Earth's Changing System 530
25.5 Ever-Changing Life on Earth 531

26 Viruses 537

26.1 The Nature of Viruses 538
26.2 Viral Diversity 542
26.3 Bacteriophage: Bacterial Viruses 544
26.4 Viral Diseases of Humans 546
26.5 Prions and Viroids: Infectious Subviral Particles 552

27 Prokaryotes 557

27.1 Prokaryotic Diversity 558
27.2 Prokaryotic Cell Structure 562
27.3 Prokaryotic Genetics 567
27.4 The Metabolic Diversity of Prokaryotes 571
27.5 Microbial Ecology 573
27.6 Bacterial Diseases of Humans 575

28 Protists 584

28.1 Eukaryotic Origins and Endosymbiosis 584
28.2 Overview of Protists 587
28.3 Characteristics of the Excavata 589
28.4 Characteristics of the Chromalveolata 592
28.5 Characteristics of the Rhizaria 598
28.6 Characteristics of the Archaeplastida 599
28.7 Characteristics of the Amoebozoa 602
28.8 Characteristics of the Opisthokonta 603

rav69618_FM_i-xxii.indd 7 12/11/18 7:25 PM

29 Seedless Plants 608

29.1 Origin of Land Plants 608
29.2 Bryophytes Have a Dominant Gametophyte Generation 611
29.3 Tracheophytes Have a Dominant Sporophyte Generation 613
29.4 Lycophytes Diverged from the Main Lineage of Vascular Plants 616
29.5 Pterophytes Are the Ferns and Their Relatives 617

30 Seed Plants 623

30.1 The Evolution of Seed Plants 623
30.2 Gymnosperms: Plants with "Naked Seeds" 624
30.3 Angiosperms: The Flowering Plants 628
30.4 Seeds 634
30.5 Fruits 635

31 Fungi 641

31.1 Classification of Fungi 642
31.2 Fungal Forms, Nutrition, and Reproduction 643
31.3 Fungal Ecology 646
31.4 Fungal Parasites and Pathogens 650
31.5 Basidiomycota: The Club (Basidium) Fungi 652
31.6 Ascomycota: The Sac (Ascus) Fungi 654
31.7 Glomeromycota: Asexual Plant Symbionts 656
31.8 Zygomycota: Zygote-Producing Fungi 656
31.9 Chytridiomycota and Relatives: Fungi with Zoospores 658
31.10 Microsporidia: Unicellular Parasites 659

32 Animal Diversity and the Evolution of Body Plans 664

32.1 Some General Features of Animals 664
32.2 Evolution of the Animal Body Plan 666
32.3 Animal Phylogeny 670
32.4 Parazoa: Animals That Lack Specialized Tissues 674
32.5 Eumetazoa: Animals with True Tissues 677
32.6 The Bilateria 682

33 Protostomes 687

33.1 The Clades of Protostomes 688
33.2 Flatworms (Platyhelminthes) 689
33.3 Rotifers (Rotifera) 692
33.4 Mollusks (Mollusca) 693
33.5 Ribbon Worms (Nemertea) 699
33.6 Annelids (Annelida) 700
33.7 Bryozoans (Bryozoa) and Brachiopods (Brachiopoda) 703
33.8 Roundworms (Nematoda) 705
33.9 Arthropods (Arthropoda) 707

34 Deuterostomes 720

34.1 Echinoderms 721
34.2 Chordates 723
34.3 Nonvertebrate Chordates 725
34.4 Vertebrate Chordates 726
34.5 Fishes 728
34.6 Amphibians 733
34.7 Reptiles 737
34.8 Birds 742
34.9 Mammals 746
34.10 Evolution of the Primates 751

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VI Plant Form and Function

35 Plant Form 762

35.1 Organization of the Plant Body: An Overview 763
35.2 Plant Tissues 766
35.3 Roots: Anchoring and Absorption Structures 772
35.4 Stems: Support for Above-Ground Organs 776
35.5 Leaves: Photosynthetic Organs 781

36 Transport in Plants 788

36.1 Transport Mechanisms 789
36.2 Water and Mineral Absorption 792
36.3 Xylem Transport 795
36.4 Rate of Transpiration 797
36.5 Water-Stress Responses 799
36.6 Phloem Transport 801

37 Plant Nutrition and Soils 807

37.1 Soils: The Substrates on Which Plants Depend 807
37.2 Plant Nutrients 811
37.3 Special Nutritional Strategies 813
37.4 Carbon–Nitrogen Balance and Global Change 816
37.5 Phytoremediation 819

38 Plant Defense Responses 825

38.1 Physical Defenses 825
38.2 Chemical Defenses 827
38.3 Animals That Protect Plants 831
38.4 Systemic Responses to Invaders 832

39 Sensory Systems in Plants 838

39.1 Responses to Light 838
39.2 Responses to Gravity 843
39.3 Responses to Mechanical Stimuli 845

rav69618_FM_i-xxii.indd 8 12/11/18 7:25 PM

39.4 Responses to Water and Temperature 847
39.5 Hormones and Sensory Systems 849

40 Plant Reproduction 866

40.1 Reproductive Development 867
40.2 Making Flowers 869
40.3 Structure and Evolution of Flowers 874
40.4 Pollination and Fertilization 877
40.5 Embryo Development 882
40.6 Germination 888
40.7 Asexual Reproduction 891
40.8 Plant Life Spans 893

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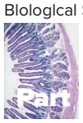

VII Animal Form and Function

41 The Animal Body and Principles of Regulation 900

41.1 Organization of Animal Bodies 901
41.2 Epithelial Tissue 902
41.3 Connective Tissue 905
41.4 Muscle Tissue 908
41.5 Nerve Tissue 909
41.6 Overview of Vertebrate Organ Systems 910
41.7 Homeostasis 913
41.8 Regulating Body Temperature 915

42 The Nervous System 924

42.1 Nervous System Organization 925
42.2 The Mechanism of Nerve Impulse Transmission 928
42.3 Synapses: Where Neurons Communicate with Other Cells 933
42.4 The Central Nervous System: Brain and Spinal Cord 939
42.5 The Peripheral Nervous System: Spinal and Cranial Nerves 946

43 Sensory Systems 955

43.1 Overview of Sensory Receptors 956
43.2 Thermoreceptors, Nociceptors, and Electromagnetic Receptors: Temperature, Pain, and Magnetic Fields 958
43.3 Mechanoreceptors I: Touch, Pressure, and Body Position 959
43.4 Mechanoreceptors II: Hearing, Vibration, and Balance 961
43.5 Chemoreceptors: Taste, Smell, and pH 967
43.6 Vision 969
43.7 Evolution and Development of Eyes 975

44 The Endocrine System 982

44.1 Regulation of Body Processes by Chemical Messengers 983
44.2 Overview of Hormone Action 988
44.3 The Pituitary and Hypothalamus: The Body's Control Centers 991
44.4 The Major Peripheral Endocrine Glands 996
44.5 Other Hormones and Their Effects 1000

45 The Musculoskeletal System 1006

45.1 Types of Skeletal Systems 1007
45.2 A Closer Look at Bone 1009
45.3 Joints 1012
45.4 Muscle Contraction 1013
45.5 Vertebrate Skeleton Evolution and Modes of Locomotion 1020

46 The Digestive System 1026

46.1 Types of Digestive Systems 1027
46.2 The Mouth and Teeth: Food Capture and Bulk Processing 1029
46.3 The Esophagus and the Stomach: The Early Stages of Digestion 1030
46.4 The Intestines: Breakdown, Absorption, and Elimination 1032
46.5 Accessory Organ Function 1035
46.6 Neural and Hormonal Regulation of the Digestive Tract 1037
46.7 Food Energy, Energy Expenditure, and Essential Nutrients 1038
46.8 Variations in Vertebrate Digestive Systems 1042

47 The Respiratory System 1047

47.1 Gas Exchange Across Respiratory Surfaces 1048
47.2 Gills, Cutaneous Respiration, and Tracheal Systems 1049
47.3 Lungs 1052
47.4 Structures, Mechanisms, and Control of Ventilation in Mammals 1055
47.5 Transport of Gases in Body Fluids 1059

48 The Circulatory System 1066

48.1 Invertebrate Circulatory Systems 1066
48.2 The Components of Vertebrate Blood 1068
48.3 Vertebrate Circulatory Systems 1071
48.4 Cardiac Cycle, Electrical Conduction, ECG, and Cardiac Output 1074
48.5 Blood Pressure and Blood Vessels 1078

49 Osmotic Regulation and the Urinary System 1088

49.1 Osmolarity and Osmotic Balance 1088
49.2 Nitrogenous Wastes: Ammonia, Urea, and Uric Acid 1090

rav69618_FM_i-xxii.indd 9 12/11/18 7:25 PM

49.3 Osmoregulatory Organs 1091
49.4 Evolution of the Vertebrate Kidney 1093
49.5 The Mammalian Kidney 1095
49.6 Hormonal Control of Osmoregulatory Functions 1100

50 The Immune System 1106

50.1 Innate Immunity 1106
50.2 Adaptive Immunity 1112
50.3 Cell-Mediated Immunity 1117
50.4 Humoral Immunity and Antibody Production 1119
50.5 Autoimmunity and Hypersensitivity 1125
50.6 Antibodies in Medical Treatment and Diagnosis 1127
50.7 Pathogens That Evade the Immune System 1130

51 The Reproductive System 1135

51.1 Animal Reproductive Strategies 1135
51.2 Vertebrate Fertilization and Development 1138
51.3 Structure and Function of the Human Male Reproductive System 1142
51.4 Structure and Function of the Human Female Reproductive System 1146
51.5 Contraception and Infertility Treatments 1150

52 Animal Development 1157

52.1 Fertilization 1158
52.2 Cleavage and the Blastula Stage 1162
52.3 Gastrulation 1164
52.4 Organogenesis 1168
52.5 Vertebrate Axis and Pattern Formation 1173
52.6 Human Development 1180

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VIII Ecology and Behavior

53 Behavioral Biology 1188

53.1 The Natural History of Behavior 1189
53.2 Nerve Cells, Neurotransmitters, Hormones, and Behavior 1190
53.3 Behavioral Genetics 1191
53.4 Learning 1193
53.5 The Development of Behavior 1194
53.6 Animal Cognition 1197
53.7 Orientation and Migratory Behavior 1198
53.8 Animal Communication 1200
53.9 Behavior and Evolution 1203
53.10 Behavioral Ecology 1204
53.11 Reproductive Strategies 1207
53.12 Altruism 1209
53.13 The Evolution of Group Living and Animal Societies 1213

54 Ecology of Individuals and Populations 1218

54.1 The Environmental Challenges 1218
54.2 Populations: Groups of a Single Species in One Place 1221
54.3 Population Demography and Dynamics 1224
54.4 Life History and the Cost of Reproduction 1227
54.5 Environmental Limits to Population Growth 1230
54.6 Factors That Regulate Populations 1232
54.7 Human Population Growth 1235

55 Community Ecology 1242

55.1 Biological Communities: Species Living Together 1243
55.2 The Ecological Niche Concept 1244
55.3 Predator–Prey Relationships 1249
55.4 The Many Types of Species Interactions 1253
55.5 Ecological Succession, Disturbance, and Species Richness 1259

56 Dynamics of Ecosystems 1265

56.1 Biogeochemical Cycles 1266
56.2 The Flow of Energy in Ecosystems 1272
56.3 Trophic-Level Interactions 1277
56.4 Biodiversity and Ecosystem Stability 1281
56.5 Island Biogeography 1284

57 The Biosphere and Human Impacts 1289

57.1 Ecosystem Effects of Sun, Wind, and Water 1289
57.2 Earth's Biomes 1294
57.3 Freshwater Habitats 1297
57.4 Marine Habitats 1300
57.5 Human Impacts on the Biosphere: Pollution and Resource Depletion 1304
57.6 Human Impacts on the Biosphere: Climate Change 1310

58 Conservation Biology 1318

58.1 Overview of the Biodiversity Crisis 1318
58.2 The Value of Biodiversity 1323
58.3 Factors Responsible for Extinction 1325
58.4 An Evolutionary Perspective on the Biodiversity Crisis 1336
58.5 Approaches for Preserving Endangered Species and Ecosystems 1339

Appendix A

Glossary G-1

Index I-1

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Committed to Excellence

With the new 12th edition, Raven and Johnson's *Biology* continues the momentum built over the last four editions. We continue to provide an unmatched comprehensive text fully integrated with a continually evolving, state-of-the-art digital environment. We have used this revision to recommit ourselves to our roots as the majors biology text that best integrates evolution throughout. We have added material emphasizing the relevance of evolution throughout the ecology section, not only in all four ecology chapters, but also in the chapters on behavior and conservation biology. In the animal form and function section we have done extensive revision to modernize, and to emphasize evolution in the context of physiology. Important contributions to this effort came from Dr. Charles Welsh (Duquesne University), who provided his knowledge and experience to this important section. We have also moved the examples and insights from the chapter devoted to the evolution of development to place them into the appropriate context throughout the book. This emphasizes the importance of evolution and development by continually providing examples rather than gathering them together in a single chapter.

We have also renewed our commitment to the ideas set forth in the Vision and Change report from the AAAS, which provides a framework for modern undergraduate biology education. This report will have been with us for a decade coincident with our 12th edition. One important idea articulated by Vision and Change was an emphasis on core concepts. One of the key differences between the way an expert organizes information in their brain compared to a novice is that the expert has a conceptual framework in place to incorporate new information. We have designed the new Connecting the Concepts feature to address this disparity. We emphasize core concepts in each chapter, then at the end of the chapter show how these can be used to build a conceptual framework, and encourage the student to begin building their own. At the end of each part of the book we expand this to show how core concepts are interrelated and how a much larger conceptual framework is constructed.

One unanticipated consequence of the Vision and Change movement was how publishers chasing new approaches would produce books so "feature-laden" as to be virtually unreadable by the average student. We have not abandoned the idea that narrative flow is important, even in a science textbook. While we include a variety of features to improve student learning, they are integrated into the text and not at the expense of the concise, accessible, and engaging writing style we are known for. We maintain the clear emphasis on evolution and scientific inquiry that have made this a leading textbook of choice for majors biology students.

Faculty want textbooks that emphasize student-centered approaches, and core concepts for the biological sciences. As a team, we continually strive to improve the text by integrating the latest cognitive and best practices research with methods that are known to positively affect learning. We emphasize scientific inquiry, including an increased quantitative emphasis in the Scientific Thinking figures. Our text continues to be a leader with an organization that emphasizes important biological concepts, while keeping the student engaged with learning outcomes that allow assessment of progress in understanding these concepts. An inquiry-based approach with robust, adaptive tools for discovery and assessment in both text and digital resources provides the intellectual challenge needed to promote student critical thinking and ensure academic success.

We continue to use our digital environment in the revision of *Biology*. A major strength of both text and digital resources is assessment across multiple levels of Bloom's taxonomy that develops critical-thinking and problem-solving skills in addition to comprehensive factual knowledge.

McGraw-Hill Education's Connect® platform offers a powerful suite of online tools that are linked to the text and includes new quantitative assessment tools. We now have available interactive exercises that use graphical data, controlled by the student, to engage them in actively exploring quantitative aspects of biology. Our adaptive learning system helps students learn faster, study efficiently, and retain more knowledge of key concepts.

The 12th edition continues to employ the aesthetically stunning art program that the Raven and Johnson *Biology* text is known for. Complex topics are represented clearly and succinctly, helping students to build the mental models needed to understanding biology.

We continue to incorporate student usage data and input, derived from thousands of our SmartBook® users. SmartBook "heat maps" provided a quick visual snapshot of chapter usage data and the relative difficulty students experienced in mastering the content. This "heat-mapping" technology is unique in the industry, and allows direct editing of difficult areas, or problem areas for students.

- If the data indicated that the subject was more difficult than other parts of the chapter, as evidenced by a high proportion of students responding incorrectly to the probes, we revised or reorganized the content to be as clear and illustrative as possible.
- In other cases, if one or more of the SmartBook probes for a section was not as clear as it might be or did not appropriately reflect the content, we edited the probe, rather than the text.

We're excited about the 12th edition of this quality textbook providing a learning path for a new generation of students. All of us have extensive experience teaching undergraduate biology, and we've used this knowledge as a guide in producing a text that is up to date, beautifully illustrated, and pedagogically sound for the student. We are also excited about the continually evolving digital environment that provides unique and engaging learning environment for modern students. We've worked hard to provide clear explicit learning outcomes, and more closely integrate the text with

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its media support materials to provide instructors with an excellent complement to their teaching.

Ken Mason, Jonathan Losos, Tod Duncan

Cutting Edge Science

Changes to the 12th Edition

Part I: The Molecular Basis of Life

Chapter 1—New section added that elaborates on the core concepts and prepares the student for the use of the Connecting the Concepts feature.

Chapter 2—Edited for clarity, especially regarding atomic structure and the periodic table.

Chapter 3—Edited for clarity especially regarding the structure of nucleotides, the role of ATP in cells, and secondary structure in proteins.

Part II: Biology of the Cell

Chapter 4—The section on the endomembrane system has been completely rewritten. This includes new material on lipid droplets. Material on adhesive junctions has been rewritten to give a more evolutionary perspective.

Chapter 5—New material on proteins that can alter membrane structure has been added. This provides information on how the different cellular membranes can have different structures. Figure on Na^+/K^+ pump was redone to address errors in mechanism. Material on diffusion and facilitated diffusion was rewritten.

Chapter 6—The material on free energy and chemical reactions was completely rewritten, including redoing the figures. These changes significantly improve clarity and accuracy. Material on the role of ATP in cells was rewritten for clarity. Discussions of energy throughout the chapter were rewritten to improve clarity and accuracy of chemical concepts.

Chapter 7—The nature and action of cofactors in redox reactions and the role of ATP in cells were improved.

Chapter 8—The nature and structure of photosystems was rewritten for clarity and accuracy.

Chapter 10—The section on chromosome structure was completely rewritten to reflect new data and views of this important topic. The material on cancer was expanded and updated, producing a new section "Genetics of Cancer." This contains significant new information and pulls together material on cancer from this chapter and others.

Part III: Genetic and Molecular Biology

The overall organization of this section remains the same. We have retained the split of transmission genetics into two chapters as it has proved successful for students.

Chapter 11—Edited for clarity and readability for the student, especially regarding the events of meiosis I.

Chapter 12—The material on extensions to Mendel was rewritten for clarity and accuracy.

Chapter 13—The material on analyzing and mapping genetic variation in humans was updated and rewritten. The section on human genetic disorders was completely rewritten to reflect new information, and to make more accessible for the student. A new figure on imprinting in mouse was added to clarify this important and difficult concept.

Chapter 14—The material on eukaryotic DNA replication was rewritten and updated. Particular emphasis was placed on the evolution of DNA replication. The section on DNA repair was rewritten and updated and information on mismatch repair was added.

Chapter 15—Content on process of transcription was rewritten to reflect new data on elongation machinery. New data on alternative splicing was included, along with information on the integration of RNA modification during transcription. The section on the nature of mutations was rewritten and includes latest data on human mutation rates.

Chapter 16—Overview of control of eukaryotic transcription was rewritten to reflect modern views. Continued updating of the material on chromatin structure and the control of gene expression. Material on control of gene expression at the level of transcription was updated.

Chapter 18—New section added on the 1000 Genomes project to illustrate how fast information on genetic diversity is accumulating. The material on the wheat genome was updated, which provides both new information and approaches to complex genomes.

Chapter 19—Added a new section on the evolution of pattern formation using new material and material from chapter 25. This consolidates material on this subject, and provides a clear vision for the student.

Part IV: Evolution

Chapter 20—The topic of sexual selection was moved into this chapter from the Behavioral Biology chapter. Some material on Lamarck was eliminated, natural selection was explicitly defined, information on snp variation in humans and other animals was added. New examples of pleiotropy were added, and new data on how the speed of racehorses has not changed through time were added along with a revised figure. A new section was added on the role of sensory exploitation as a mechanism for traits to evolve under sexual selection.

Chapter 21—A number of points were updated and an example of vestigial traits involving the toenails of manatees was added.

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Chapter 23—The figure on the evolution of feathers in dinosaurs was updated to incorporate new paleontological findings. Discussion of HIV evolution and other points were also revised in light of new science.

Chapter 24—Updated material on comparative genomics of vertebrates. New data on Neanderthal and Denisovan genomes have been added. Presentation of genes unique to humans has been updated and edited for clarity.

Note: *Evolution of Development* (chapter 25 in the 11th edition) was eliminated and material moved to other chapters, placing the topic of evolution of development into the appropriate context. This reflects the view that evolution and development are now so clearly intertwined with all of biology that setting off the material in a separate chapter no longer made sense.

Part V: Diversity of Life on Earth

Chapter 26—This chapter has been largely rewritten and now includes material on viral diversity, classification, metagenomics, and taxonomy. The latter part of the chapter now focuses on viruses of medical importance to promote student engagement and interest.

Chapter 27—This chapter has been largely rewritten. In addition to the traditional discussion of prokaryotic structure and function, and taxonomy, there is new emphasis placed on microbial ecology and medical microbiology with relevant examples.

Chapter 31—The chapter has been rewritten for clarity. The chapter has also been reordered to bring material most relevant to society to the front of the chapter. The reorganization includes expanding and moving the fungal ecology up earlier in the chapter, as well as expanding and moving the fungal parasites and pathogens up earlier in the chapter. The chapter now ends with the coverage of fungal classification.

Chapter 32—Aspects of taxonomy and natural history were updated in line with new findings.

Chapter 33—The presentation of taxonomic relationships was revised as a result of new findings based primarily on molecular phylogenetic studies, specifically with regards to Platyhelminthes, lophotrochozoans (formerly Spiralia) and a few others. New natural history information was included.

Chapter 34—The discussion of the evolutionary history of vertebrates was substantially revised, especially the sections on lobe-finned fishes/early tetrapods/early amniotes (emphasizing now those terms, rather than referring to all of the early diverging lineages as amphibians or reptiles). Also, the terminology about human evolution was revised to acknowledge the new meaning of "hominin" and "hominid." A new paragraph on *Homo naledi* was added to discuss recent discoveries.

Part VI: Plant Form and Function

There have been no major changes in the plant form and function chapters. There has been overall editing for readability and responding to recommendations by reviewers and users of the 11th edition.

Part VII: Animal Form and Function

Charles Welsh of Duquesne University, brought his expertise in animal anatomy and physiology as a Contributor to the Animal Form and Function Part in the 12th edition, placing greater emphasis on evolutionary aspects of animal biology.

Chapter 41—The discussion of the evolution of tissues in invertebrates and vertebrates was expanded, including the addition of a phylogeny and an image of cnidarian tissues.

Chapter 42—The graph of an action potential was revised and improved. Discussions and images of glial cells and cranial nerves were added.

Chapter 43—The chapter was revised and reorganized with regards to the general senses. The evolution of eyes material found in chapter 25 in the 11th edition was moved to this chapter with a revised phylogeny added. The illustration depicting the evolution of the inner ear has been revised to make it more clear, concise, and informative.

Chapter 44—Section 44.2 was formerly organized as action of lipophilic vs. hydrophilic hormones. This has now been reorganized to be a complete overview of how hormones work. This organization should improve clarity for students.

Chapter 45—The chapter was extensively revised. This included the addition of images for the human skeleton, ossification, osteoporosis, invertebrate muscle, comparative anatomy of flying vertebrates, and a new phylogeny that reveals the evolution of various vertebrate skeletal characters.

Chapter 46—The structure of the latter half this chapter was completely reorganized for better conceptual flow.

Chapter 47—The images for the bicarbonate buffering system and the mechanics of breathing have been revised. The discussion of lung volumes and capacities was expanded with the addition of an accompanying figure.

Chapter 48—The chapter was reorganized and extensively revised. Invertebrate circulatory systems is now the first section in the chapter. The sections on Cardiac Cycle, ECG, Electrical Conduction, and Cardiac Output have been reorganized and revised. The discussions of blood vessels and blood pressure are now in the same section. The phylogeny of the evolution of vertebrate hearts has been revised.

Chapter 50—Material on innate immunity was updated and rewritten for clarity. The coverage on effects of AIDS was also updated to reflect new information.

Chapter 51—A discussion of some select invertebrate reproductive strategies has been added, with accompanying images.

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Chapter 52—A section detailing the classic experiments regarding pattern formation in chick limb buds has been added. This includes a discussion of AER, ZPA, FGF, *Hox* genes, and Shh. The material on gene regulation from chapter 25 in the 11th edition has also been added.

Part VIII: Ecology and Behavior

Chapter 53—Stronger emphasis on phylogenetic and evolutionary perspectives was added throughout the chapter, including a new section on evolution and behavior.

Chapter 54—Human population trends and other timely data were updated to stay current. An evolutionary perspective on population adaptation was added to the beginning of the chapter.

Chapter 55—An evolutionary perspective was added in several places.

Chapter 56—New material on the impact of anthropogenic changes on nutrient cycling was added. An evolutionary perspective to discussion of the species-area relationship was incorporated.

Chapter 57—Evolution was discussed more thoroughly in the section on microclimate adaptation during adaptive radiation. All of the data on biosphere impacts of humans were updated to stay current.

Chapter 58—The chapter was substantially revised, including much new discussion of the relevance of evolution to conservation biology, including the role of natural selection, the importance of phylogenetic perspectives, and how speciation can lead to biodiversity hotspots.

A Note From the Authors

A revision of this scope relies on the talents and efforts of many people working behind the scenes and we have benefited greatly from their assistance.

Dr. Charles Welsh made significant contributions to the Animal Form and Function section. He updated them to provide a more modern perspective, and added new examples.

Beth Bulger was the copyeditor for this edition. She has labored many hours and always improves the clarity and consistency of the text. She has made significant contributions to the quality of the final product.

We were fortunate to work again with MPS to update the art program and improve the layout of the pages. Our close collaboration resulted in a text that is pedagogically effective as well as more beautiful than any other biology text on the market.

We have the continued support of an excellent team at McGraw-Hill Education. Andrew Urban, preceded by Justin Wyatt, the portfolio managers for *Biology* have been steady leaders during a time of change. Senior Product Developer Liz Sievers, provided support in so many ways it would be impossible to name them all. Kelly Hart, content project manager, and David Hash, designer, ensured our text was on time and elegantly designed. Kelly Brown, senior marketing manager, is always a sounding board for more than just marketing, and many more people behind the scenes have all contributed to the success of our text. This includes the digital team, whom we owe a great deal for their efforts to continue improving our Connect assessment tools.

Throughout this edition we have had the support of spouses and families, who have seen less of us than they might have liked because of the pressures of getting this revision completed. They have adapted to the many hours this book draws us away from them, and, even more than us, looked forward to its completion.

In the end, the people we owe the most are the generations of students who have used the many editions of this text. They have taught us at least as much as we have taught them, and their questions and suggestions continue to improve the text and supplementary materials.

Finally, we need to thank instructors from across the country who are continually sharing their knowledge and experience with us through market feedback and symposia. The feedback we received shaped this edition. All of these people took time to share their ideas and opinions to help us build a better edition of *Biology* for the next generation of introductory biology students, and they have our heartfelt thanks.

Reviewers for Biology, 12th edition

Carron Bryant *East Mississippi Community College*
Mickael J. Cariveau *University of Mount Olive*
Daniel Czerny *Reading Area Community College*
Frank J. Dirrigl, Jr. *University of Texas Rio Grande Valley*
Kathy McCann Evans *Reading Area Community College*
Eric Ford East *Mississippi Community College-Golden Triangle*
Mark Jonas *Purchase College, SUNY*
Kimberly Kushner *Pueblo Community College*
Mark Levenstein *University of Wisconsin, Platteville*
Cindy Malone *California State University Northridge*
David McClellan *University of Arkansas Fort Smith*
Shilpi Paul *SUNY College at Old Westbury*
Crima Pogge *City College of San Francisco*
Josephine Rodriguez *The University of Virginia's College at Wise*
Connie Rye *East Mississippi Community College*
Devinder Sandhu *USDA—Agricultural Research Service*
Ken Saville *Albion College*
Steven Shell *The University of Virginia's College at Wise*
Walter Smith *The University of Virginia's College at Wise*
Qiang Sun *University of Wisconsin, Stevens Point*
Christopher Vitek *University of Texas Rio Grande Valley*
D. Alexander Wait *Missouri State University*
Maureen Walter *Florida International University*
Darla Wise *Concord University*

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Preparing Students for the Future

Developing Critical Thinking with the Help of . . .

Scientific Thinking Figures

Key illustrations in every chapter highlight how the frontiers of knowledge are pushed forward by a combination of hypothesis and experimentation. These figures begin with a hypothesis, then show how it makes explicit predictions, tests these by experiment and finally demonstrates what conclusions can be drawn, and where this leads. Scientific Thinking figures provide a consistent framework to guide the student in the logic of scientific inquiry. Each illustration concludes with open-ended questions to promote scientific inquiry.

Data Analysis Questions

It's not enough that students learn concepts and memorize scientific facts, a biologist needs to analyze data and apply that knowledge. Data Analysis questions inserted throughout the text challenge students to analyze data and Interpret experimental results, which shows a deeper level of understanding.

Inquiry Questions

Questions that challenge students to think about and engage in what they are reading at a more sophisticated level.

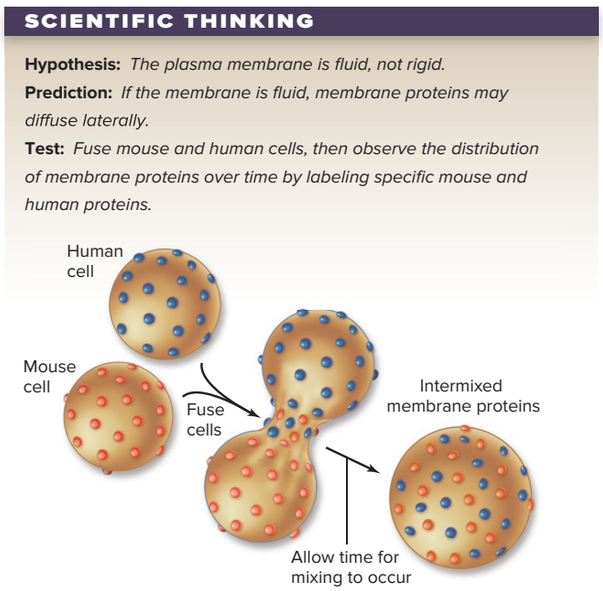

Figure 5.5 Test of membrane fluidity.

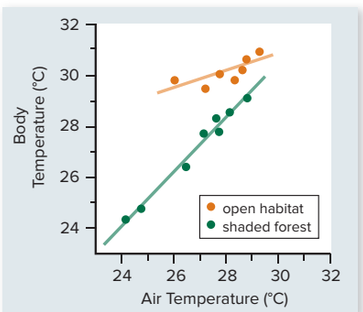



Figure 55.3 Behavioral adaptation. In open habitats, the Puerto Rican crested lizard, *Anolis cristatellus,* maintains a relatively constant temperature by seeking out and basking in patches of sunlight; as a result, it can maintain a relatively high temperature even when the air is cool. In contrast, in shaded forests, this behavior is not possible, and the lizard's body temperature conforms to that of its surroundings.

(inset) ©Melissa Losos

Inquiry question When given the opportunity, lizards regulate their body temperature to maintain a temperature optimal for physiological functioning. Would lizards in open habitats exhibit different escape behaviors from those of lizards in shaded forest?

Data analysis Can the slope of the line tell us something about the behavior of the lizard?

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Connecting the Concepts

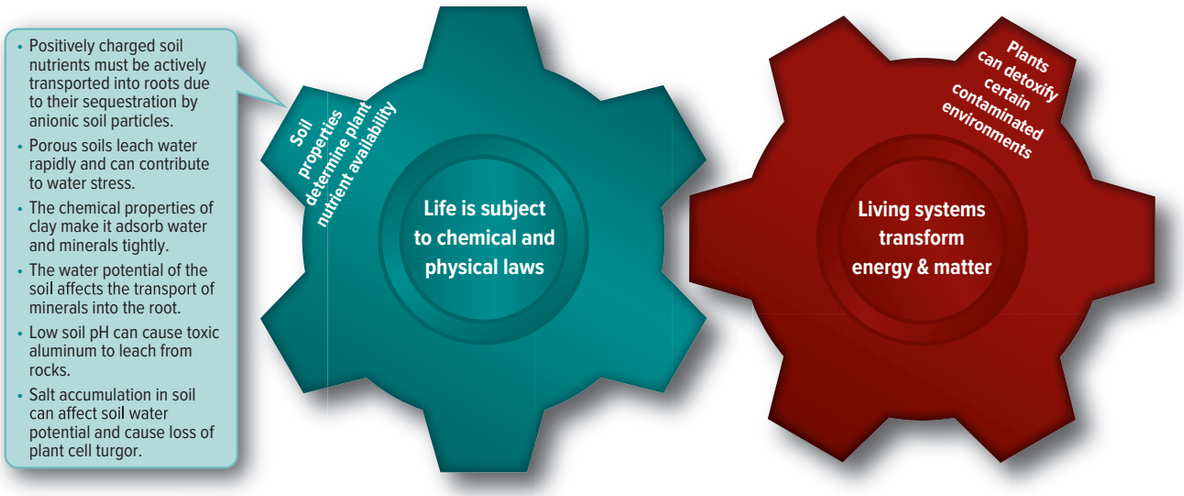
There are two new but related features in *Biology*, 12th edition that help students build a conceptual framework into which they can insert new knowledge. The Connecting the Concepts feature at the end of the chapters identifies core concepts that are related to material in the chapter. The conceptual framework begins with a core concept that is represented by a gear icon. Examples from the chapter that relate to the core concept are secondary concepts that are placed on the cogs. Each cog contains a list of observations from the chapter that connects the secondary concept to the core concept.

At the chapter level:

The Connecting the Concept shows the student a completed concept (core concept, secondary concept, list of observations). A second cog or gear is presented that lacks the list of observations. The student is challenged to identify examples from the chapter that demonstrate how the secondary concept is related to the core concept.

CONNECTING THE CONCEPTS

This feature is intended to give you practice in organizing information using core concepts. We use a metaphor of gears and cogs to represent a conceptual hierarchy with each core concept represented as a gear. Secondary concepts are the cogs, and tertiary concepts, which are particular examples from the chapter, are presented as a list of bulleted points. Using the completed conceptual unit as a guide, build from material in the chapter a list of tertiary concepts that support the open secondary concept.



At the Part level:

As valuable as that exercise is, the full understanding of a conceptual framework and how that helps students see the connections to core concepts is when the chapter-ending Connecting the Concepts are pulled together. This happens at the Part level, which themselves present a higher level to the conceptual framework. When these are built, students see how topics that appear unrelated fit into the conceptual framework of the core concepts. Once students begin to see these connections, the topics and information in biology make more sense.

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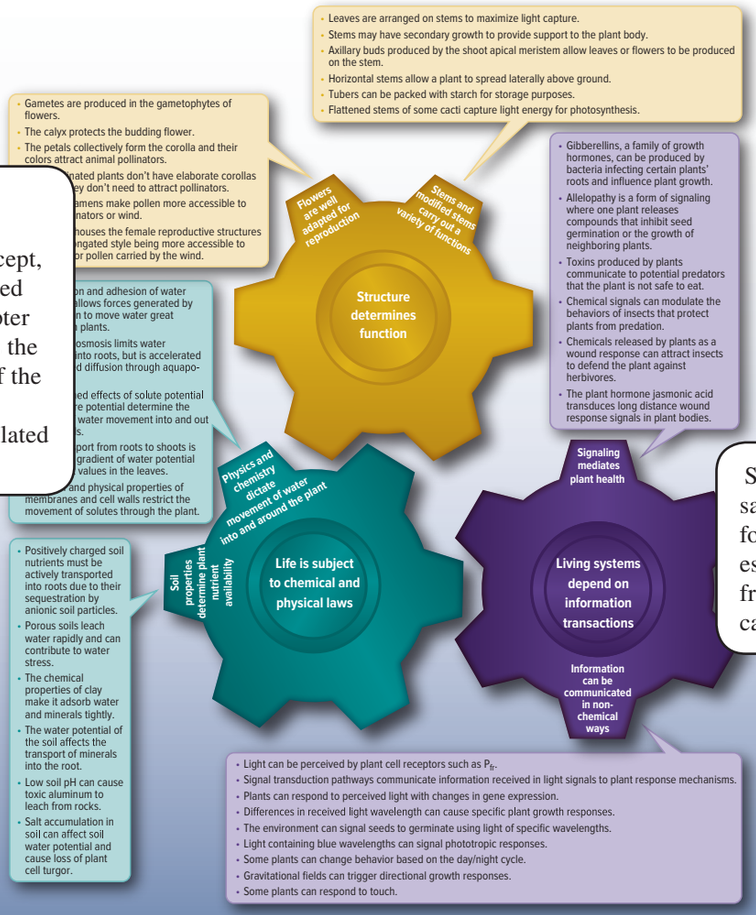
Connecting the Concepts Part VI Plant Form and Function

Vascular plants are comprised of roots and shoots, which in turn are made of three principal tissue types. Each of these tissues has distinct cell types that express the genes needed to produce the proteins necessary for their specialized functions. Plants move fluids using differences in solute concentration and pressure. Plant form is often an evolutionary compromise between competing needs such as maximizing the surface area of leaves for photosynthesis while minimizing water loss when exchanges gases. The reproductive structures of plants are organized into flowers that have evolved to facilitate the dissemination of genetic information.



Each Connecting the Concept unit (a Core concept, secondary concept, and bulleted list) is picked up from the end-of-chapter features. This reinforces the overarching hierarchy of the Core concepts, tying together seemingly unrelated material.

Students will see how the same Core concepts are found throughout the book, establishing the conceptual framework into which they can insert new knowledge.

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Strengthen Problem-Solving Skills with Connect®

Detailed Feedback in Connect®

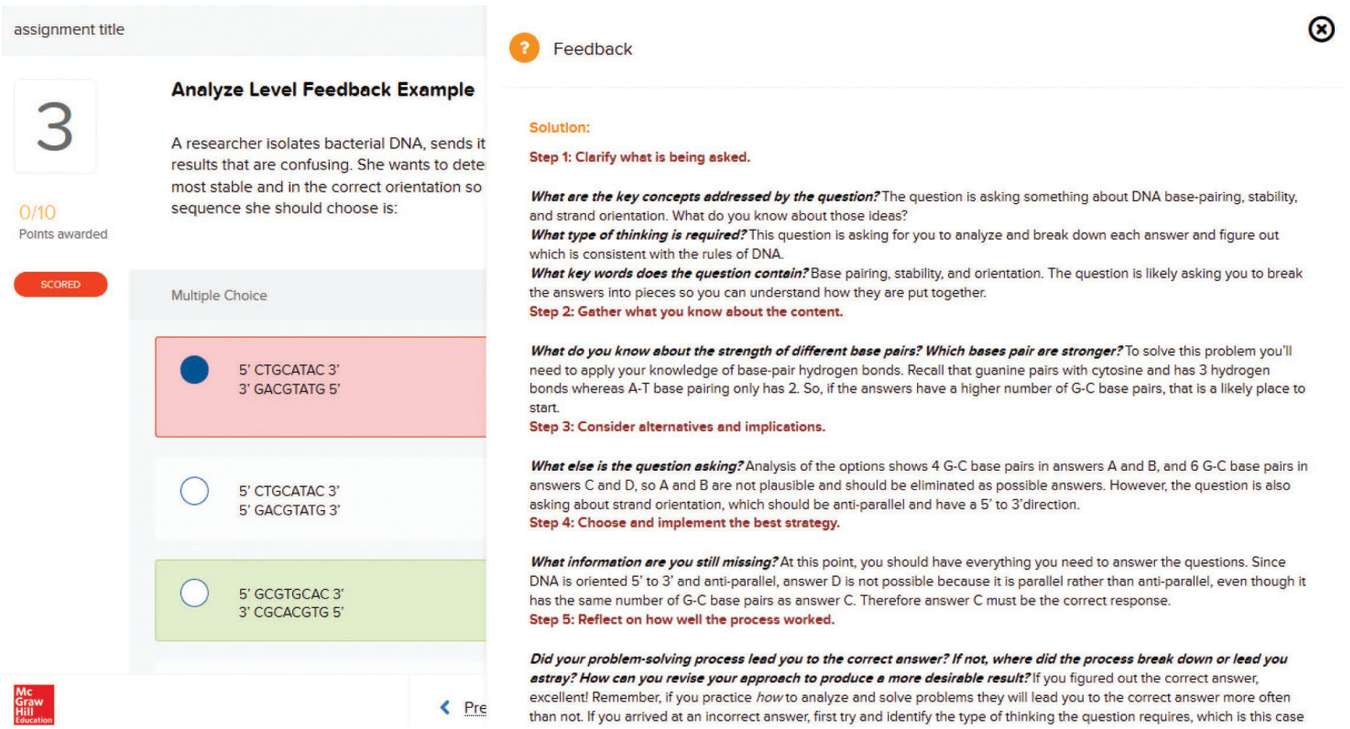
Learning is a process of iterative development, of making mistakes, reflecting, and adjusting over time. The question and test banks in Connect® for *Biology*, 12th edition, are more than direct assessments; they are self-contained learning experiences that systematically build student learning over time.

For many students, choosing the right answer is not necessarily based on applying content correctly; it is more a matter of increasing their statistical odds of guessing. A major fault with this approach is students don't learn how to process the questions correctly, mostly because they are repeating and reinforcing their mistakes rather than reflecting and learning from them. To help students develop problem-solving skills, all higher level Blooms questions in Connect are supported with hints, to help students focus on important information for answering the questions, and detailed feedback that walks students through the problem-solving process, using Socratic questions in a decision-tree-style framework to scaffold learning, where each step models and reinforces the learning process.

The feedback for each higher level Blooms question (Apply, Analyze, Evaluate) follows a similar process: Clarify Question, Gather Content, Choose Answer, Reflect on Process.

Unpacking the Concepts

We've taken problem solving a step further. In each chapter, three to five higher level Blooms questions in the question and test banks are broken out by the steps of the detailed feedback. Rather than leaving it up to the student to work through the detailed feedback, a second version of the question is presented in a stepwise format. Following the problem-solving steps, students need to answer questions about earlier steps, such as "What is the key concept addressed by the question?" before proceeding to answer the question. A professor can choose which version of the question to include in the assignment based on the problem-solving skills of the students.



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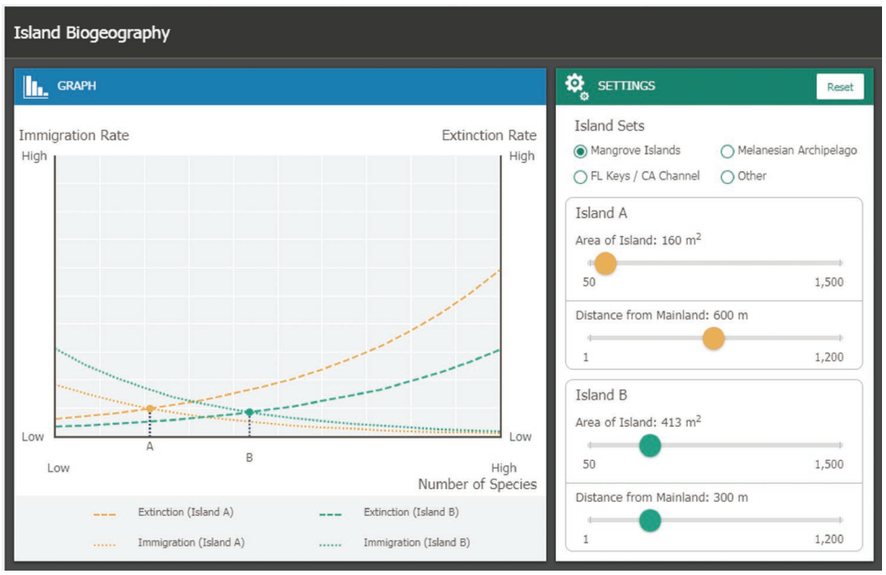
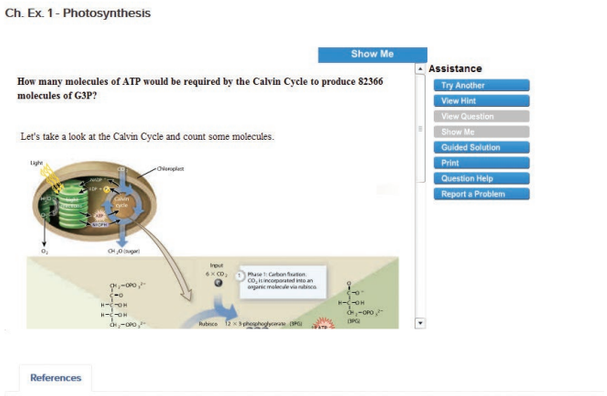
Graphing Interactives

To help students develop analytical skills, Connect® for *Biology*, 12th edition, is enhanced with interactive graphing questions. Students are presented with a scientific problem and the opportunity to manipulate variables, producing different results on a graph. A series of questions follows the graphing activity to assess if the student understands and is able to interpret the data and results.



Quantitative Question Bank

Many chapters also contain a **Quantitative Question Bank.** These are more challenging algorithmic questions, intended to help your students practice their quantitative reasoning skills. Hints and guided solution options step students through a problem.



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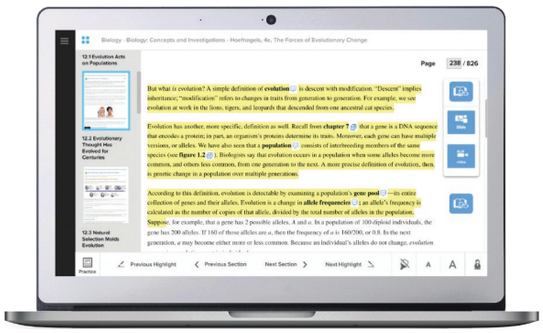

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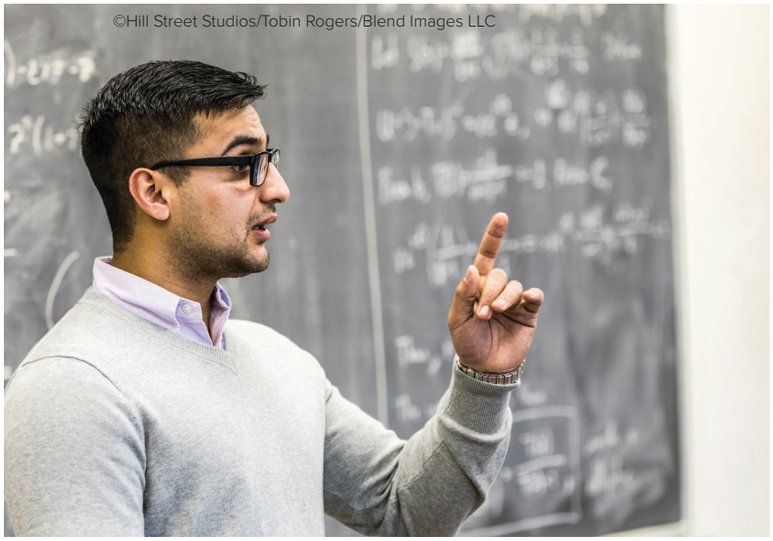

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- Jordan Cunningham,
Eastern Washington University

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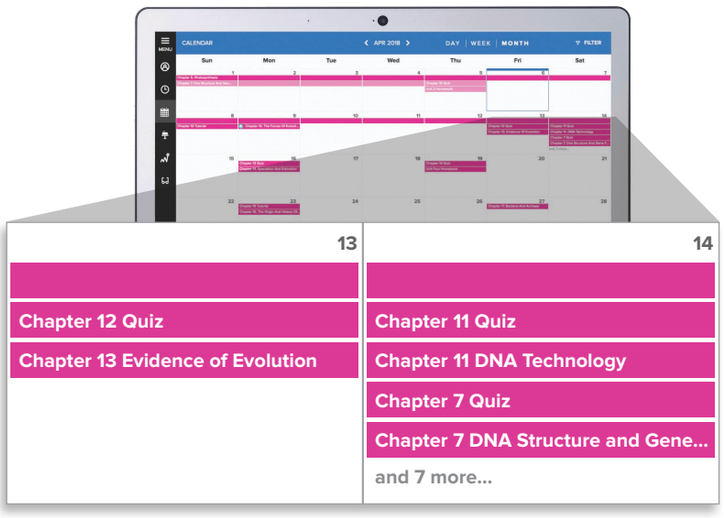

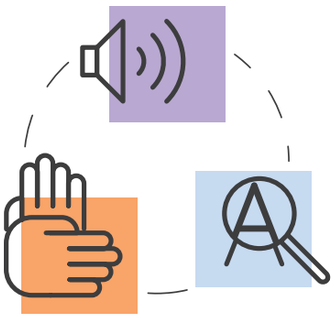

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CHAPTER 8

Photosynthesis



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Chapter Contents

8.1 Overview of Photosynthesis
8.2 The Discovery of Photosynthetic Processes
8.3 Pigments
8.4 Photosystem Organization
8.5 The Light-Dependent Reactions
8.6 Carbon Fixation: The Calvin Cycle
8.7 Photorespiration

Introduction

The rich diversity of life that covers our Earth would be impossible without photosynthesis. Almost every oxygen atom in the air we breathe was once part of a water molecule, liberated by photosynthesis. All the energy released by the burning of coal, firewood, gasoline, and natural gas, and by our bodies' burning of all the food we eat—directly or indirectly—has been captured from sunlight by photosynthesis. It is vitally important, then, that we understand photosynthesis. Research may enable us to improve crop yields and land use, important goals in an increasingly crowded world. In chapter 7, we described how cells extract chemical energy from food molecules and use that energy to power their activities. In this chapter, we examine photosynthesis, the process by which organisms such as the aptly named sunflowers in the picture capture energy from sunlight and use it to build food molecules that are rich in chemical energy.

8.1 Overview of Photosynthesis

Learning Outcomes

1. *Explain the reaction for photosynthesis.*
2. *Describe the structure of the chloroplast.*

Life is powered by sunshine. The energy used by most living cells comes ultimately from the Sun and is captured by plants, algae, and bacteria through the process of photosynthesis.

The diversity of life is only possible because our planet is awash in energy streaming Earthward from the Sun. Each day, the radiant energy that reaches Earth equals the power from about 1 million Hiroshima-sized atomic bombs. Photosynthesis captures about 1% of this huge supply of energy and uses it to provide the energy that drives all life.

Photosynthesis combines CO_2 and H_2O, producing glucose and O_2

Photosynthesis occurs in a wide variety of organisms, and it comes in different forms. These include a form of photosynthesis that does not produce oxygen (anoxygenic) and a form that does (oxygenic). Anoxygenic photosynthesis is found in four different bacterial groups: purple bacteria, green sulfur bacteria, green non-sulfur bacteria, and heliobacteria. Oxygenic photosynthesis is found in cyanobacteria, seven groups of algae, and essentially all land plants. These two types of photosynthesis share similarities in the types of pigments they use to trap light energy, but they differ in the arrangement and action of these pigments.

In the case of plants, photosynthesis takes place primarily in the leaves. Figure 8.1 illustrates how leaves are organized. As you learned in chapter 4, the cells of plant leaves contain organelles called chloroplasts, which are required for photosynthesis. No other structure in a plant cell is able to carry out photosynthesis.

Photosynthesis takes place in three stages:

1. capturing energy from sunlight;
2. using the energy to make ATP and to reduce the compound $NADP^+$, an electron carrier, to NADPH; and
3. using the ATP and NADPH to power the synthesis of organic molecules from CO_2 in the air.

The first two stages require light and are commonly called the **light-dependent reactions.**

The third stage, the formation of organic molecules from CO_2, is called **carbon fixation.** This process takes place via a cyclic series of reactions. As long as ATP and NADPH are available, the carbon fixation reactions can occur either in the presence or in the absence of light, and so these reactions are also called the **light-independent reactions** (figure 8.2).

The following simple equation summarizes the overall process of photosynthesis:

$$\underset{\textit{carbon dioxide}}{6CO_2} + \underset{\textit{water}}{12H_2O} + \text{light} \longrightarrow \underset{\textit{glucose}}{C_6H_{12}O_6} + \underset{\textit{water}}{6H_2O} + \underset{\textit{oxygen}}{6O_2}$$

You may notice that this equation is the reverse of the reaction for respiration. In respiration, glucose is oxidized to CO_2 using O_2 as an electron acceptor. In photosynthesis, CO_2 is reduced to glucose using electrons gained from the oxidation of water. The oxidation of H_2O and the reduction of CO_2 requires energy that is provided by light. Although this statement is an oversimplification, it provides a useful "global perspective."

In plants, photosynthesis takes place in chloroplasts

In chapter 7, you saw that a mitochondrion's complex structure of internal and external membranes is critical to its function. The same is true for the structure and function of the chloroplast, which can also synthesize ATP by a chemiosmotic mechanism.

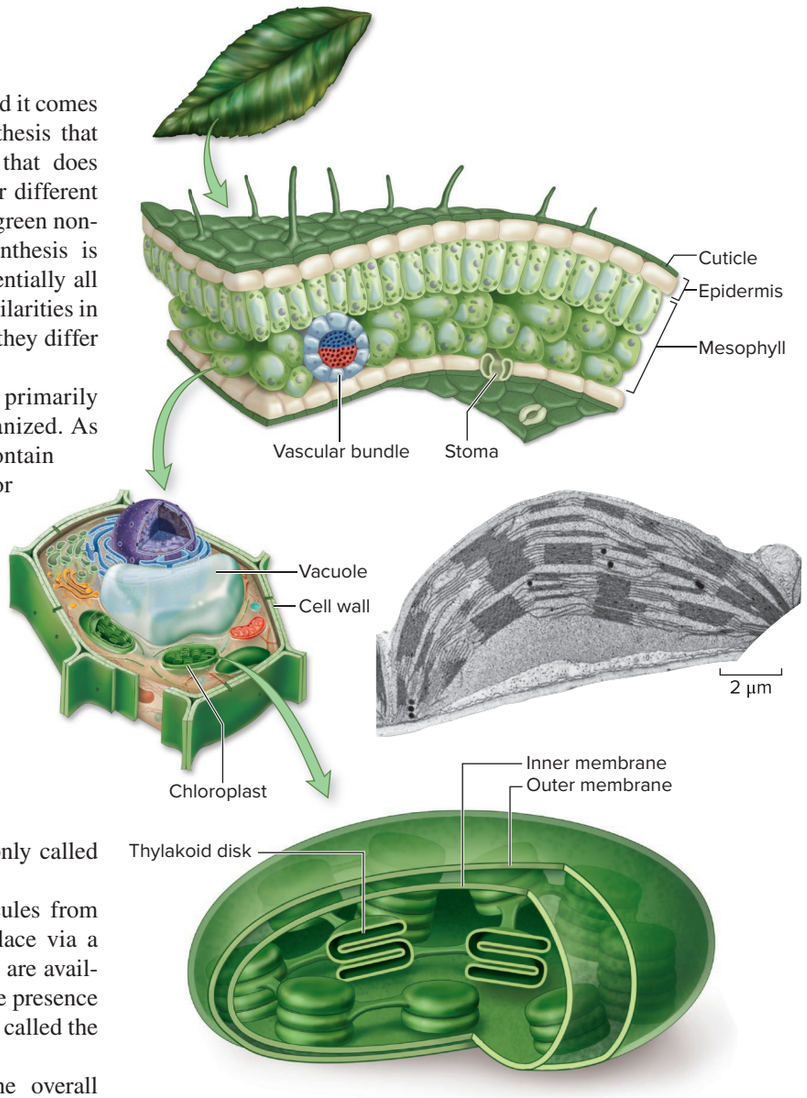

Figure 8.1 Journey into a leaf. A plant leaf possesses a thick layer of cells (the mesophyll) rich in chloroplasts. The inner membrane of the chloroplast is organized into flattened structures called thylakoid disks, which are stacked into columns called grana. The rest of the interior is filled with a semifluid substance called stroma.
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The internal membrane of chloroplasts, called the *thylakoid membrane,* is a continuous phospholipid bilayer organized into flattened sacs called thylakoid disks. These are stacked in columns called *grana* (singular, granum). This forms three compartments: the thylakoid membrane itself, and the spaces inside and outside this membrane. The thylakoid membrane contains the enzymatic machinery to make ATP, and **chlorophyll** and other photosynthetic pigments that capture light energy.

The compartment outside the thylakoid membrane system is called the **stroma,** and it is analogous to the matrix in mitochondria. The stroma is a semiliquid substance containing the enzymes necessary to incorporate CO_2 into organic compounds using energy from ATP coupled with reduction by NADPH.

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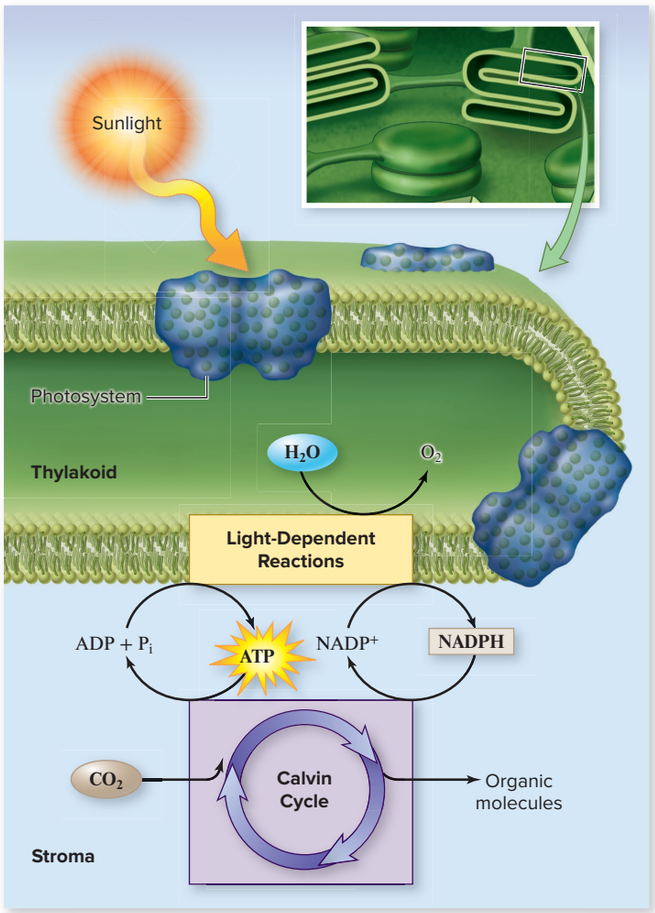

Figure 8.2 Overview of photosynthesis. Chlorophyll molecules are organized into photosystems. The light-dependent reactions begin when a chlorophyll molecule absorbs a photon of light. This light energy is used to generate ATP and NADPH. Electrons lost from chlorophyll are replaced by oxidizing water, producing O_2 as a by-product. The ATP and NADPH are used to reduce CO_2 via the Calvin cycle in the stroma, producing organic molecules.

In the thylakoid membrane, photosynthetic pigments are organized into **photosystems** that absorb light, which excites an electron that can be passed to an electron carrier. Each pigment molecule within the photosystem is capable of capturing photons, which are packets of energy. When light of a proper wavelength strikes a pigment molecule in the photosystem, the resulting excitation passes from one pigment molecule to another. This is similar to kinetic energy being transferred along a row of upright dominoes. If you push the first one over, it falls against the next, which falls against the next, and the next, until all of the dominoes have fallen over.

The energy arrives at a key chlorophyll molecule in contact with a membrane-bound protein that can accept an electron. The energy is transferred as an excited electron to that protein, which passes it on to a series of other membrane proteins that put the energy to work making ATP and NADPH. These compounds are then used to build organic molecules. The photosystem thus acts as a large antenna, gathering the light energy harvested by many individual pigment molecules.

Learning Outcomes Review 8.1

Photosynthesis consists of light-dependent reactions that require sunlight, and others that convert CO_2 into organic molecules. The overall reaction is essentially the reverse of respiration and produces O_2 as a by-product. The chloroplast's inner membrane, the thylakoid, is the site in which photosynthetic pigments are clustered, allowing passage of energy from one molecule to the next. The thylakoid membrane is organized into flattened sacs stacked in columns called grana.

- *How is the structure of the chloroplast similar to that of the mitochondria?*

8.2 The Discovery of Photosynthetic Processes

Learning Outcomes

1. *Describe experiments that support our understanding of photosynthesis.*
2. *Differentiate between the light-dependent and light-independent reactions.*

The story of how we learned about photosynthesis begins over 300 years ago, and it continues to this day. It starts with curiosity about how plants manage to grow, often increasing their organic mass considerably.

Plants do not increase mass from soil and water alone

From the time of the Greeks, plants were thought to obtain their food from the soil, literally sucking it up with their roots. A Belgian doctor, Jan Baptista van Helmont (1580–1644) thought of a simple way to test this idea.

He planted a small willow tree in a pot of soil, after first weighing the tree and the soil. The tree grew in the pot for several years, during which time van Helmont added only water. At the end of five years, the tree was much larger, its weight having increased by 74.4 kg. However, the soil in the pot weighed only 57 g less than it had five years earlier. With this experiment, van Helmont demonstrated that the substance of the plant was not produced only from the soil. He incorrectly concluded, however, that the water he had been adding mainly accounted for the plant's increased biomass.

A hundred years passed before the story became clearer. The key clue was provided by the English scientist Joseph Priestly (1733–1804). On the 17th of August, 1771, Priestly put a living

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sprig of mint into air in which a wax candle had burnt out. On the 27th of the same month, Priestly found that another candle could be burned in this same air. Somehow, the vegetation seemed to have restored the air. Priestly found that while a mouse could not breathe candle-exhausted air, air "restored" by vegetation was not "at all inconvenient to a mouse." The key clue was that *living vegetation adds something to the air.*

How does vegetation "restore" air? Twenty-five years later, the Dutch physician Jan Ingenhousz (1730–1799) solved the puzzle. He demonstrated that air was restored only in the presence of sunlight and only by a plant's green leaves, not by its roots. He proposed that the green parts of the plant carry out a process that uses sunlight to split carbon dioxide into carbon and oxygen. He suggested that the oxygen was released as O_2 gas into the air, while the carbon atom combined with water to form carbohydrates. Other research refined his conclusions, and by the end of the 19th century, the overall reaction for photosynthesis could be written as:

$$CO_2 + H_2O + \text{light energy} \longrightarrow (CH_2O) + O_2$$

It turns out, however, that there's more to it than that. When researchers began to examine the process in more detail in the 20th century, the role of light proved to be unexpectedly complex.

Photosynthesis includes both light-dependent and light-independent reactions

At the beginning of the 20th century, the English plant physiologist F. F. Blackman (1866–1947) came to the surprising conclusion that photosynthesis is in fact a multistage process, only one portion of which uses light directly.

Blackman measured the effects of different light intensities, CO_2 concentrations, and temperatures on photosynthesis. As long as light intensity was relatively low, he found photosynthesis could be accelerated by increasing the amount of light, but not by increasing the temperature or CO_2 concentration (figure 8.3). At high light intensities, however, an increase in temperature or CO_2 concentration greatly accelerated photosynthesis.

Blackman concluded that photosynthesis consists of an initial set of what he called "light" reactions, that are largely independent of temperature but depend on light, and a second set of "dark" reactions (more properly called light-independent reactions), that seemed to be independent of light but limited by CO_2.

Do not be confused by Blackman's labels—the so-called "dark" reactions occur in the light (in fact, they require the products of the light-dependent reactions); his use of the word *dark* simply indicates that light is not *directly* involved in those reactions.

Blackman found that increased temperature increased the rate of the light-independent reactions, but only up to about 35°C. Higher temperatures caused the rate to decrease rapidly. Because many plant enzymes begin to be denatured at 35°C, Blackman concluded that enzymes must carry out the light-independent reactions.

O_2 comes from water, not from CO_2

In the 1930s, C. B. van Niel (1897–1985), working at the Hopkins Marine Station at Stanford, discovered that purple sulfur bacteria do not release oxygen during photosynthesis; instead, they convert hydrogen sulfide (H_2S) into globules of pure elemental sulfur that accumulate inside them. The process van Niel observed was:

$$CO_2 + 2H_2S + \text{light energy} \longrightarrow (CH_2O) + H_2O + 2S$$

The striking parallel between this equation and Ingenhousz's equation led van Niel to propose that the generalized process of photosynthesis can be shown as:

$$CO_2 + 2H_2A + \text{light energy} \longrightarrow (CH_2O) + H_2O + 2A$$

In this equation, the substance H_2A serves as an electron donor. In photosynthesis performed by green plants, H_2A is water, whereas in purple sulfur bacteria, H_2A is hydrogen sulfide. The product, A, comes from the splitting of H_2A. Therefore, the O_2 produced during green plant photosynthesis results from splitting water, not carbon dioxide.

When isotopes came into common use in the early 1950s, van Niel's revolutionary proposal was tested. Investigators examined photosynthesis in green plants supplied with water containing heavy oxygen (^{18}O); they found that the ^{18}O label ended up in oxygen gas rather than in carbohydrate, just as van Niel had predicted:

$$CO_2 + 2H_2{}^{18}O + \text{light energy} \longrightarrow (CH_2O) + H_2O + {}^{18}O_2$$

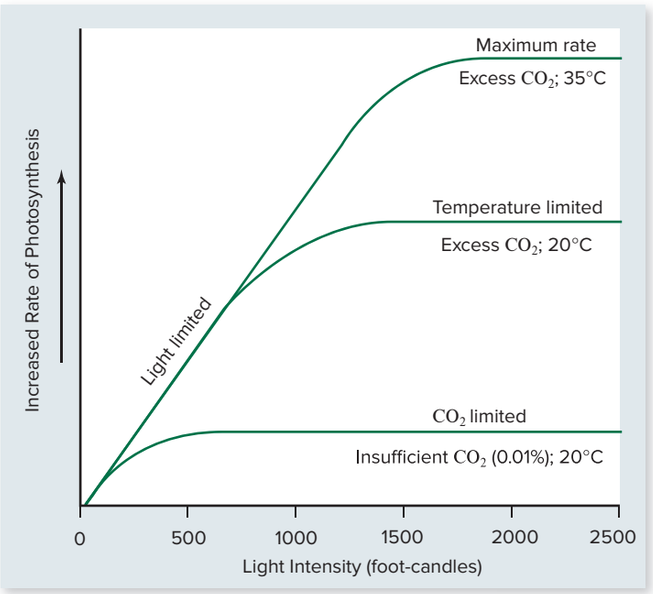

Figure 8.3 Discovery of the light-independent reactions. Blackman measured photosynthesis rates under differing light intensities, CO_2 concentrations, and temperatures. As this graph shows, light is the limiting factor at low light intensities, but temperature and CO_2 concentration are the limiting factors at higher light intensities. This implies the existence of reactions using CO_2 that involve enzymes.

Data analysis Blackman found that increasing light intensity above 2000 foot-candles did not lead to any further increase in the rate of photosynthesis. Can you suggest a hypothesis that would explain this?

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In algae and green plants, the carbohydrate typically produced by photosynthesis is glucose. The complete balanced equation for photosynthesis in these organisms thus becomes:

$$6CO_2 + 12H_2O + \text{light energy} \longrightarrow C_6H_{12}O_6 + 6H_2O + 6O_2$$

ATP and NADPH from light-dependent reactions reduce CO_2 to make sugars

In his pioneering work on the light-dependent reactions, van Niel proposed that the H^+ ions and electrons generated by the splitting of water were used to convert CO_2 into organic matter in a process he called *carbon fixation.* In the 1950s, Robin Hill (1899–1991) demonstrated that van Niel was right: Light energy could be harvested and used in a reduction reaction. Chloroplasts isolated from leaf cells were able to reduce a dye and release oxygen in response to light. Later experiments showed that the electrons released from water were transferred to $NADP^+$ and that illuminated chloroplasts deprived of CO_2 accumulate ATP. If CO_2 is introduced, neither ATP nor NADPH accumulate, and the CO_2 is assimilated into organic molecules.

These experiments are important for three reasons: First, they firmly demonstrate that photosynthesis in plants occurs within chloroplasts. Second, they show that the light-dependent reactions use light energy to reduce $NADP^+$ and to manufacture ATP. Third, they confirm that the ATP and NADPH from this early stage of photosynthesis are then used in the subsequent reactions to reduce carbon dioxide, forming simple sugars.

Learning Outcomes Review 8.2

Early experiments indicated that plants "restore" air to usable form—that is, produce oxygen—but only in the presence of sunlight. Further experiments showed that there are both light-dependent and independent reactions. The light-dependent reactions produce O_2 from H_2O, and generate ATP and NADPH. The light-independent reactions synthesize organic compounds through carbon fixation.

- ***Where does the carbon in your body come from?***

8.3 Pigments

Learning Outcomes

1. *Discuss how pigments are important to photosynthesis.*
2. *Relate the absorption spectrum of a pigment to its color.*

For plants to make use of the energy of sunlight, some biochemical structure must be present in chloroplasts and the thylakoids that can absorb this energy. Molecules that absorb light energy in the visible range are termed **pigments.** We are most familiar with them as dyes that impart a certain color to clothing or other materials. The color that we see is the color that is not absorbed—that is, it is reflected. To understand how plants use pigments to capture light energy, we must first review current knowledge about the nature of light.

Light is a form of energy

The wave nature of light produces an electromagnetic spectrum that differentiates light based on its wavelength (figure 8.4). We are most familiar with the visible range of this spectrum because we can actually see it, but visible light is only a small part of the entire spectrum. Visible light can be divided into its separate colors by the use of a prism, which separates light based on wavelength.

A particle of light, termed a **photon,** acts like a discrete bundle of energy. We use the wave concept of light to understand different colors of light and the particle nature of light to understand the energy transfers that occur during photosynthesis. Thus, we will refer both to wavelengths of light and to photons of light throughout the chapter.

The energy in photons

The energy content of a photon is inversely proportional to the wavelength of the light: Short-wavelength light contains photons of higher energy than long-wavelength light (figure 8.4). X-rays, which contain a great deal of energy, have very short wavelengths—much shorter than those of visible light.

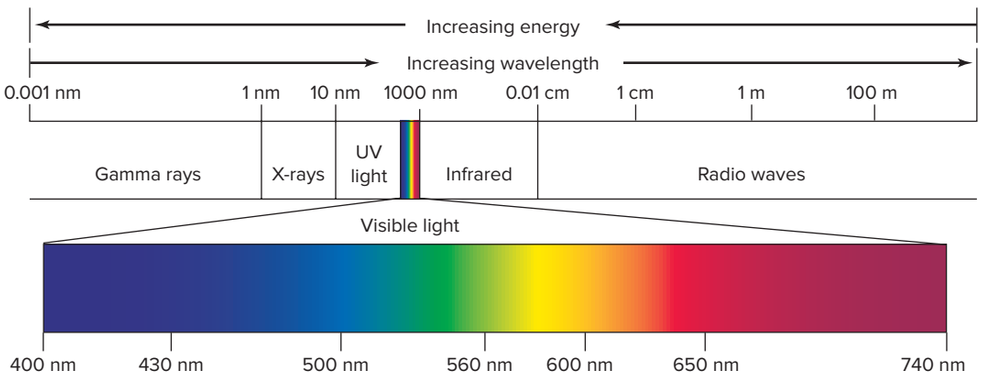

Figure 8.4 The electromagnetic spectrum. Light is a form of electromagnetic energy conveniently thought of as a wave. The shorter the wavelength of light, the greater its energy. Visible light represents only a small part of the electromagnetic spectrum between 400 and 740 nm.

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A beam of light is able to remove electrons from certain molecules, creating an electrical current. This phenomenon is called the **photoelectric effect,** and it occurs when photons transfer energy to electrons. The strength of the photoelectric effect depends on the wavelength of light—that is, short wavelengths are generally much more effective than long ones in producing the photoelectric effect because they have more energy.

In photosynthesis, chloroplasts are acting as photoelectric devices: They absorb sunlight and transfer the excited electrons to a carrier. As we unravel the details of this process, it will become clear how this process traps energy and uses it to synthesize organic compounds.

Each pigment has a characteristic absorption spectrum

When a photon strikes a molecule with sufficient energy, the molecule will absorb the photon, which will raise an electron to a higher energy level. Whether the photon's energy is absorbed depends on how much energy it carries (defined by its wavelength), and also on the chemical nature of the molecule it hits.

As described in chapter 2, electrons occupy discrete energy levels in their orbits around atomic nuclei. To boost an electron into a different energy level requires just the right amount of energy, just as reaching the next rung on a ladder requires you to raise your foot just the right distance. A specific atom, therefore, can absorb only certain photons of light—namely, those that correspond to the atom's available energy levels. As a result, each molecule has a characteristic **absorption spectrum,** the range and efficiency of photons it is capable of absorbing.

As mentioned earlier in this section, pigments are good absorbers of light in the visible range. Organisms have evolved a variety of different pigments, but only two general types are used in green plant photosynthesis: chlorophylls and carotenoids. In some organisms, other molecules also absorb light energy.

Chlorophyll absorption spectra

Chlorophylls absorb photons within narrow energy ranges. Two kinds of chlorophyll in plants, chlorophyll *a* and chlorophyll *b,* preferentially absorb violet-blue and red light (figure 8.5). Neither of these pigments absorbs photons with wavelengths between about 500 and 600 nm; light of these wavelengths is reflected. When these reflected photons are subsequently absorbed by the retinal pigment in our eyes, we perceive them as green.

Chlorophyll *a* is the main photosynthetic pigment in plants and cyanobacteria and is the only pigment that can act directly to convert light energy to chemical energy. **Chlorophyll *b,*** acting as an **accessory pigment,** or secondary light-absorbing pigment, complements and adds to the light absorption of chlorophyll *a.*

Chlorophyll *b* has an absorption spectrum shifted toward the green wavelengths. Therefore, chlorophyll *b* can absorb photons that chlorophyll *a* cannot, greatly increasing the proportion of the photons in sunlight that plants can harvest. In addition, a variety of different accessory pigments are found in plants, bacteria, and algae.

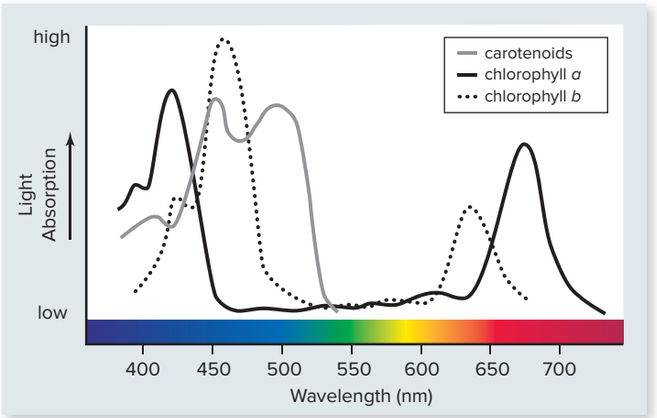

Figure 8.5 Absorption spectra for chlorophyll and carotenoids. The peaks represent wavelengths of light of sunlight absorbed by the two common forms of photosynthetic pigment, chlorophylls *a* and *b,* and the carotenoids. Chlorophylls absorb predominantly violet-blue and red light in two narrow bands of the spectrum and reflect green light in the middle of the spectrum. Carotenoids absorb mostly blue and green light and reflect orange and yellow light.

Structure of chlorophylls

Chlorophylls absorb photons by means of an excitation process analogous to the photoelectric effect. These pigments contain a complex ring structure, called a *porphyrin ring,* with alternating single and double bonds. At the center of the ring is a magnesium atom (figure 8.6).

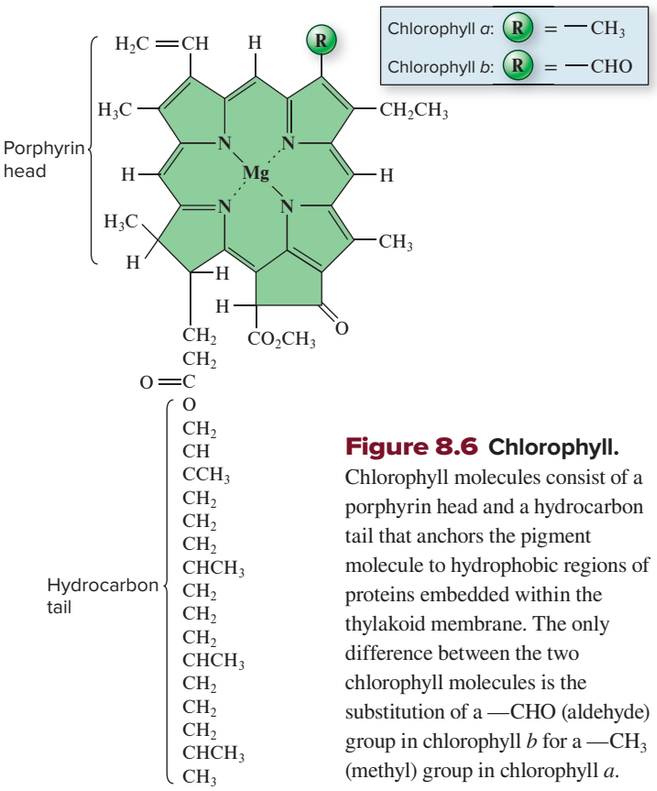

Figure 8.6 Chlorophyll. Chlorophyll molecules consist of a porphyrin head and a hydrocarbon tail that anchors the pigment molecule to hydrophobic regions of proteins embedded within the thylakoid membrane. The only difference between the two chlorophyll molecules is the substitution of a —CHO (aldehyde) group in chlorophyll *b* for a —CH_3 (methyl) group in chlorophyll *a.*

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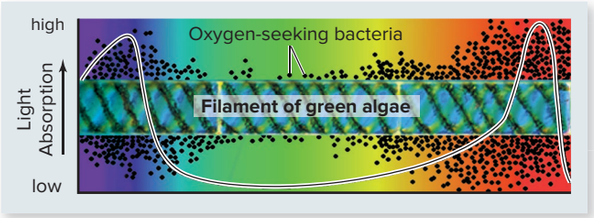
SCIENTIFIC THINKING

Hypothesis: *All wavelengths of light are equally effective in promoting photosynthesis.*

Prediction: *Illuminating plant cells with light broken into different wavelengths by a prism will produce the same amount of O_2 for all wavelengths.*

Test: *A filament of algae immobilized on a slide is illuminated by light that has passed through a prism. Motile bacteria that require O_2 for growth are added to the slide.*



Result: *The bacteria move to regions of high O_2, or regions of most active photosynthesis. This is in the purple/blue and red regions of the spectrum.*

Conclusion: *All wavelengths are not equally effective at promoting photosynthesis. The most effective constitute the action spectrum for photosynthesis.*

Further Experiments: *How does the action spectrum relate to the various absorption spectra in figure 8.5?*

Figure 8.7 Determination of an action spectrum for photosynthesis.

Photons excite electrons in the porphyrin ring, which are then channeled away through the alternating carbon single- and double-bond system. Electrons not associated with a single atom or bond are said to be delocalized. Different side groups attached to the outside of the ring alter the absorption properties of different types of chlorophyll (figure 8.6). The precise absorption spectrum is also influenced by the association of chlorophyll with different proteins.

The **action spectrum** of photosynthesis—that is, the relative effectiveness of different wavelengths of light in promoting photosynthesis—corresponds to the absorption spectrum for chlorophylls. This is demonstrated in the experiment in figure 8.7. All plants, algae, and cyanobacteria use chlorophyll *a* as their primary pigments.

It is reasonable to ask why these photosynthetic organisms do not use a pigment like retinal (the pigment in our eyes), which has a broad absorption spectrum that covers the range of 500 to 600 nm. The most likely hypothesis involves *photoefficiency.* Although retinal absorbs a broad range of wavelengths, it does so with relatively low efficiency. Chlorophyll, in contrast, absorbs in only two narrow bands, but does so with high efficiency. Therefore, plants and most other photosynthetic organisms achieve far higher overall energy capture rates with chlorophyll than with other pigments.

Carotenoids and other accessory pigments

Carotenoids consist of carbon rings linked to chains with alternating single and double bonds. They can absorb photons with a wide range of energies, although they are not always highly efficient in transferring this energy. Carotenoids assist in photosynthesis by capturing energy from light composed of wavelengths that are not efficiently absorbed by chlorophylls (figure 8.8; see also figure 8.5).

Carotenoids also perform a valuable role in scavenging free radicals. The oxidation–reduction reactions that occur in the chloroplast can generate destructive free radicals. Carotenoids can act as general-purpose antioxidants to lessen damage. Thus carotenoids have a protective role in addition to their role as light-absorbing molecules. This protective role is not surprising, because unlike the chlorophylls, carotenoids are found in many different kinds of organisms, including members of all three domains of life.

You may have heard that eating carrots, which contain β-carotene, can enhance vision. If you had a vitamin A deficiency, then this would be true as β-carotene is a precursor of vitamin A. The oxidation of vitamin A produces retinal, the pigment used in vertebrate vision.

Phycobiliproteins are accessory pigments found in cyanobacteria and some algae. These pigments contain a system of

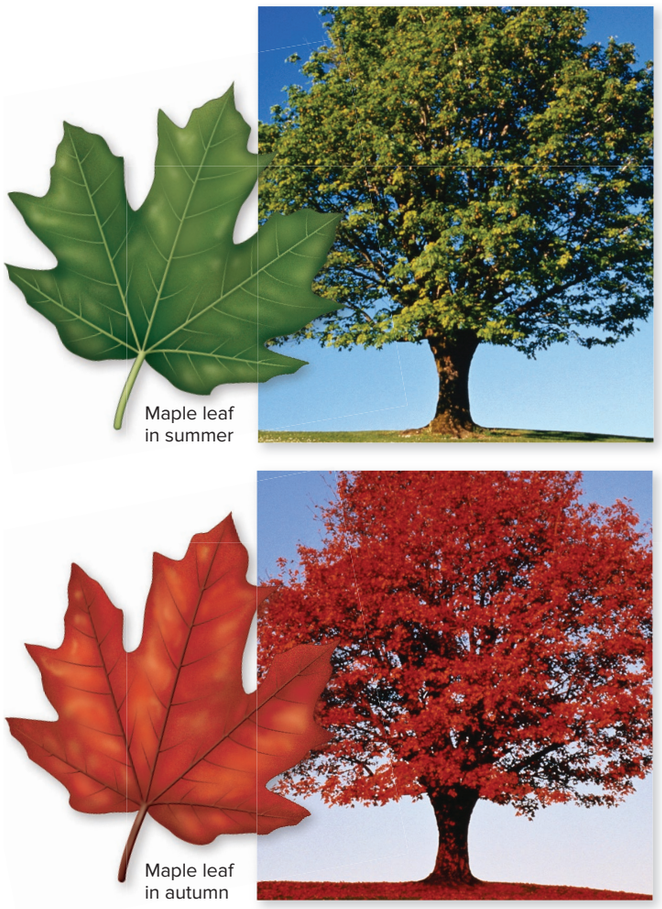


Figure 8.8 Fall colors are produced by carotenoids and other accessory pigments. During the spring and summer, chlorophyll in leaves masks the presence of carotenoids and other accessory pigments. When cool fall temperatures cause leaves to cease manufacturing chlorophyll, the chlorophyll is no longer present to reflect green light, and the leaves reflect the orange and yellow light that carotenoids and other pigments do not absorb. ©Rich Iwasaki/Stone/Getty Images

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alternating double bonds similar to those found in other pigments and molecules that transfer electrons. Phycobiliproteins can be organized to form another light-harvesting complex that can absorb green light, which is reflected by chlorophyll. These complexes are probably ecologically important to cyanobacteria, helping them to exist in low-light situations in oceans. In this habitat, green light remains because red and blue light has been absorbed by green algae closer to the surface.

Learning Outcomes Review 8.3

A pigment is a molecule that can absorb light energy; its absorption spectrum shows the wavelengths at which it absorbs energy most efficiently. A pigment's color results from the wavelengths it does not absorb, which we then see. The main photosynthetic pigment is chlorophyll, which exists in several forms with slightly different absorption spectra. Many photosynthetic organisms have accessory pigments with absorption spectra different from that of chlorophyll; these increase light capture.

- ***What is the difference between an action spectrum and an absorption spectrum?***

8.4 Photosystem Organization

Learning Outcomes

1. *Describe the nature of photosystems.*
2. *Contrast the function of reaction center and antenna chlorophyll molecules.*

One way to study the role that pigments play in photosynthesis is to measure the correlation between the output of photosynthesis and the intensity of illumination—that is, how much photosynthesis is produced by how much light. Experiments on plants show that the output of photosynthesis increases linearly at low light intensities, but eventually becomes saturated (no further increase) at high-intensity light. Saturation occurs because all of the light-absorbing capacity of the plant is in use.

Production of one O_2 molecule requires many chlorophyll molecules

Given the saturation observed with increasing light intensity, the next question is how many chlorophyll molecules have actually absorbed a photon. The question can be phrased this way: "Does saturation occur when all chlorophyll molecules have absorbed photons?" Finding an answer required being able to measure both photosynthetic output (on the basis of O_2 production) and the number of chlorophyll molecules present.

Using the unicellular algae *Chlorella,* investigators could obtain these values. Illuminating a *Chlorella* culture with pulses of light with increasing intensity should increase the yield of O_2 per pulse until the system becomes saturated. Then O_2 production can be compared with the number of chlorophyll molecules present in the culture.

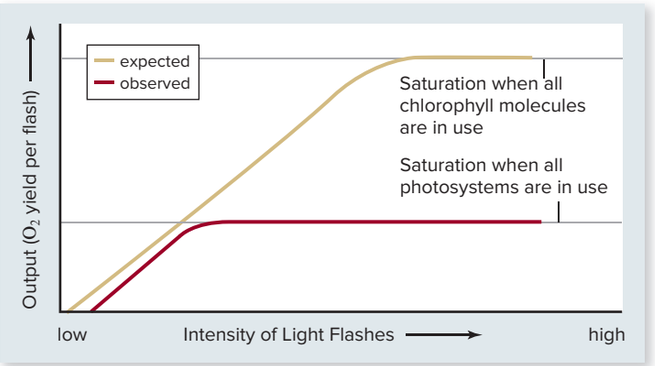

Figure 8.9 Saturation of photosynthesis. When photosynthetic saturation is achieved, further increases in intensity cause no increase in output. This saturation occurs far below the level expected for the number of individual chlorophyll molecules present. This led to the idea of organized photosystems, each containing many chlorophyll molecules. These photosystems saturate at a lower O_2 yield than that expected for the number of individual chlorophyll molecules.

Data analysis Draw the curves for photosystems that have a greater or lesser number of chlorophyll molecules than the curve shown.

The observed level of O_2 per chlorophyll molecule at saturation, however, turned out to be only one molecule of O_2 per 2500 chlorophyll molecules (figure 8.9). This result was very different from what was expected, and it led to the idea that light is absorbed not by independent pigment molecules, but rather by clusters of chlorophyll and accessory pigment molecules (photosystems). Light is absorbed by any one of hundreds of pigment molecules in a photosystem, and each pigment molecule transfers its excitation energy to a single molecule with a lower energy level than the others.

A generalized photosystem contains an antenna complex and a reaction center

In chloroplasts and all but one class of photosynthetic prokaryotes, light is captured by photosystems. Each photosystem is a network of chlorophyll *a* molecules, accessory pigments, and associated proteins held within a protein matrix on the surface of the photosynthetic membrane. Like a magnifying glass focusing light on a precise point, a photosystem channels the excitation energy gathered by any one of its pigment molecules to a specific molecule, the reaction center chlorophyll. This molecule then passes the energy out of the photosystem as excited electrons that are put to work driving the synthesis of ATP and organic molecules.

A photosystem thus consists of two closely linked components: (1) an *antenna complex* of hundreds of pigment molecules that gather photons and feed the captured light energy to the

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reaction center; and (2) a *reaction center* consisting of one or more chlorophyll *a* molecules in a matrix of protein, that passes excited electrons out of the photosystem.

The antenna complex

The **antenna complex** is also called a light-harvesting complex, which accurately describes its role. This light-harvesting complex captures photons from sunlight (figure 8.10) and channels them to the reaction center chlorophylls.

In chloroplasts, light-harvesting complexes consist of a web of chlorophyll molecules linked together and held tightly in the thylakoid membrane by a matrix of proteins. Varying amounts of carotenoid accessory pigments may also be present. The protein matrix holds individual pigment molecules in orientations that are optimal for energy transfer.

The excitation energy resulting from the absorption of a photon passes from one pigment molecule to an adjacent molecule on its way to the reaction center. After the transfer, the excited electron in each molecule returns to the low energy level it had before the photon was absorbed. Consequently, it is energy, not the excited electrons themselves, that passes from one pigment molecule to the next. The antenna complex funnels the energy from many electrons to the reaction center.

The reaction center

The **reaction center** is a transmembrane protein–pigment complex. The reaction center of purple photosynthetic bacteria is simpler than the one in chloroplasts but better understood. A pair of bacteriochlorophyll *a* molecules acts as a trap for photon energy, passing an excited electron to an acceptor precisely positioned as its neighbor. Note that here in the reaction center, the excited electron itself is transferred, and not just the energy, as was the case in the pigment–pigment transfers of the antenna complex. This difference allows the energy absorbed from photons to move away from the chlorophylls, and it is the key conversion of light into chemical energy.

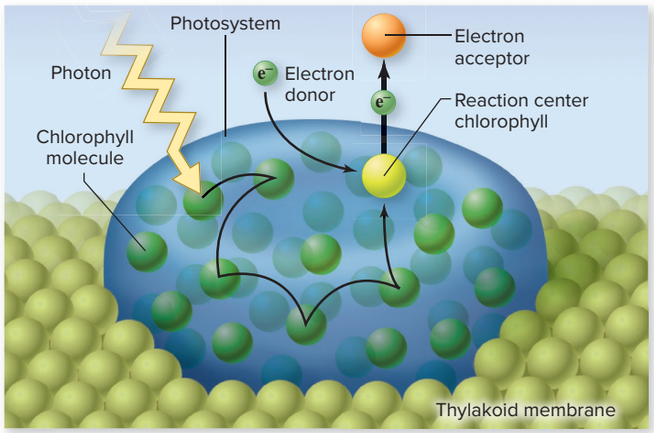

Figure 8.10 How the antenna complex works. When light of the proper wavelength strikes any pigment molecule within a photosystem, the light is absorbed by that pigment molecule. The excitation energy is then transferred from one molecule to another within the cluster of pigment molecules until it encounters the reaction center chlorophyll *a*. When excitation energy reaches the reaction center chlorophyll, electron transfer is initiated.

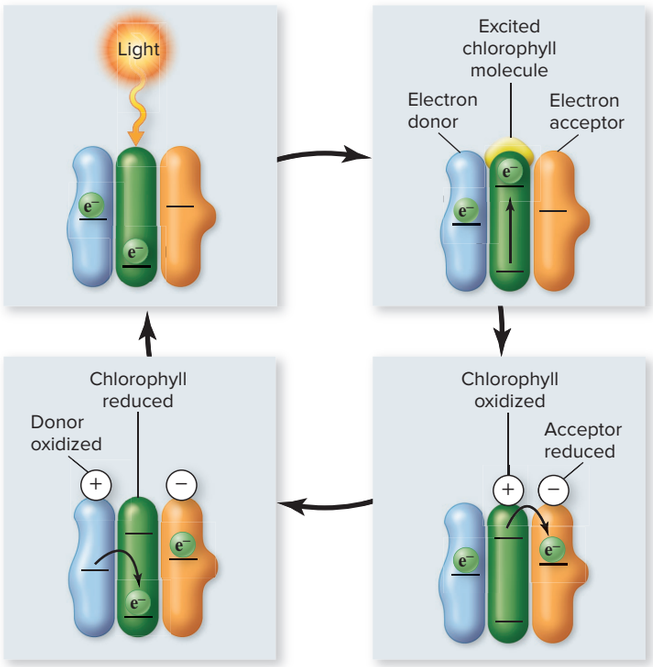

Figure 8.11 Converting light to chemical energy. When a chlorophyll in the reaction center absorbs a photon of light, an electron is excited to a higher energy level. This light-energized electron can be transferred to the primary electron acceptor, reducing it. The oxidized chlorophyll then fills its electron "hole" by oxidizing a donor molecule. The source of this donor varies with the photosystem, as discussed in the text.

Figure 8.11 shows the transfer of excited electrons from the reaction center to the primary electron acceptor. By energizing an electron of the reaction center chlorophyll, light creates a strong electron donor where none existed before. The chlorophyll transfers the energized electron to the primary acceptor (a molecule of quinone), reducing the quinone and converting it to a strong electron donor. A nearby weak electron donor then passes a low-energy electron to the chlorophyll, restoring it to its original condition. The quinone transfers its electrons to another acceptor, and the process is repeated.

In plant chloroplasts, water serves as this weak electron donor. When water is oxidized in this way, oxygen is released along with two protons (H^+).

Learning Outcomes Review 8.4

Chlorophylls and accessory pigments are organized into photosystems found in the thylakoid membrane. The photosystem can be subdivided into an antenna complex, which is involved in light harvesting, and a reaction center, where the photochemical reactions occur. In the reaction center, an excited electron is passed to an acceptor; this transfers energy away from the chlorophylls and is key to the conversion of light into chemical energy.

- ***Why were photosystems an unexpected finding?***

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8.5 The Light-Dependent Reactions

Learning Outcomes

1. *Compare the function of the two photosystems in green plants.*
2. *Explain how the light reactions generate ATP and NADPH.*

As you have seen, the light-dependent reactions of photosynthesis occur in membranes. In photosynthetic bacteria, the plasma membrane itself is the photosynthetic membrane. In many bacteria, the plasma membrane folds in on itself repeatedly to produce an increased surface area. In plants and algae, photosynthesis is carried out by chloroplasts, which are thought to be the evolutionary descendants of photosynthetic bacteria.

The internal thylakoid membrane is highly organized and contains the structures involved in the light-dependent reactions. For this reason, the reactions are also referred to as the thylakoid reactions. The thylakoid reactions take place in four stages:

1. **Primary photoevent.** A photon of light is captured by a pigment. This primary photoevent excites an electron within the pigment.
2. **Charge separation.** This excitation energy is transferred to the reaction center, which transfers an energetic electron to an acceptor molecule, initiating electron transport.
3. **Electron transport.** The excited electrons are shuttled along a series of electron carrier molecules embedded within the photosynthetic membrane. Several of them react by transporting protons across the membrane, generating a proton gradient. Eventually the electrons are used to reduce a final acceptor, NADPH.
4. **Chemiosmosis.** The protons that accumulate on one side of the membrane now flow back across the membrane through ATP synthase where chemiosmotic synthesis of ATP takes place, just as it does in aerobic respiration (see chapter 7).

These four processes make up the two stages of the light-dependent reactions mentioned at the beginning of this chapter. Steps 1 through 3 represent the stage of capturing energy from light; step 4 is the stage of producing ATP (and, as you'll see, NADPH). In the rest of this section we discuss the evolution of photosystems and the details of photosystem function in the light-dependent reactions.

Some bacteria use a single photosystem

Photosynthetic pigment arrays are thought to have evolved more than 2 BYA in bacteria similar to the purple and green bacteria alive today. In these bacteria, a single photosystem is used that generates ATP via electron transport. This process returns the electrons back to the reaction center. For this reason, it is called cyclic photophosphorylation. These systems do not produce oxygen and so are also anoxygenic.

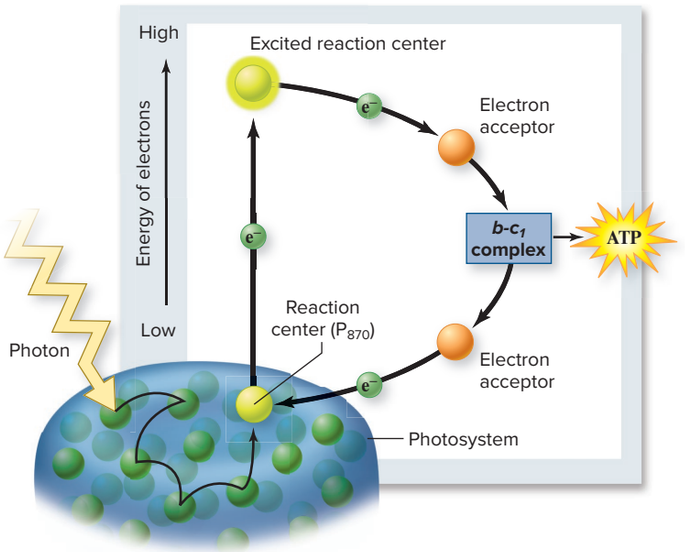

Figure 8.12 The path of an electron in purple nonsulfur bacteria. When a light-energized electron is ejected from the photosystem reaction center (P_{870}), it returns to the photosystem via a cyclic path that produces ATP but not NADPH.

In the purple nonsulfur bacteria, peak absorption occurs at a wavelength of 870 nm (near infrared, not visible to the human eye), and thus the reaction center pigment is called P_{870}. Absorption of a photon by chlorophyll P_{870} does not raise an electron to a high enough level to be passed to NADP, so they must generate reducing power in a different way.

When the P_{870} reaction center absorbs a photon, the excited electron is passed to an electron transport chain that passes the electrons back to the reaction center, generating a proton gradient for ATP synthesis (figure 8.12). The proteins in the purple bacterial photosystem appear to be homologous to the proteins in the modern photosystem II.

In the green sulfur bacteria, peak absorption occurs at a wavelength of 840 nm. Excited electrons from this photosystem can either be passed to NADPH, or returned to the chlorophyll by an electron transport chain similar to that in the purple bacteria. They then use electrons from hydrogen sulfide to replace those passed to NADPH. The proteins in the green sulfur bacterial photosystem appear to be homologous to the proteins in the modern photosystem I.

Neither of these systems generates sufficient oxidizing power to oxidize H_2O. They are both anoxygenic and anaerobic. The linked photosystems of cyanobacteria and plant chloroplasts generate the oxidizing power necessary to oxidize H_2O, allowing it to serve as a source of both electrons and protons. This production of O_2 by oxygenic photosynthesis literally changed the atmosphere of the world.

Chloroplasts have two connected photosystems

In contrast to the sulfur bacteria, plants have two linked photosystems. This overcomes the limitations of cyclic photophosphorylation by providing an alternative source of electrons from the oxidation of water. The oxidation of water also generates O_2, and

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thus is called oxygenic photosynthesis. The noncyclic transfer of electrons also produces NADPH, which can be used in the biosynthesis of carbohydrates.

One photosystem, called **photosystem I,** has an absorption peak of 700 nm, so its reaction center pigment is called P_{700}. This photosystem can pass electrons to NADPH similarly to the photosystem found in the sulfur bacteria discussed earlier in this section. The other photosystem, called **photosystem II,** has an absorption peak of 680 nm, so its reaction center pigment is called P_{680}. This photosystem can generate an oxidation potential high enough to oxidize water. Working together, the two photosystems carry out a noncyclic transfer of electrons that generate both ATP and NADPH.

The photosystems were named I and II in the order of their discovery, and not in the order in which they operate in the light-dependent reactions. In plants and algae, the two photosystems are specialized for different roles in the overall process of oxygenic photosynthesis. Photosystem I transfers electrons ultimately to $NADP^+$, producing NADPH. The electrons lost from photosystem I are replaced by electrons from photosystem II. Photosystem II with its high oxidation potential can oxidize water to replace the electrons transferred to photosystem I. Thus there is an overall flow of electrons from water to NADPH.

These two photosystems are connected by a complex of electron carriers called the **cytochrome b_6-f complex** (explained shortly). This complex can use the energy from the passage of electrons to move protons across the thylakoid membrane to generate the proton gradient used by an ATP synthase enzyme.

The two photosystems work together in noncyclic photophosphorylation

Evidence for the action of two photosystems came from experiments that measured the rate of photosynthesis using two light beams of different wavelengths: one red and the other far-red. Using both beams produced a rate greater than the sum of the rates using individual beams of these wavelengths (figure 8.13). This surprising result, called the *enhancement effect,* can be explained by a mechanism involving two photosystems acting in series (that is, one after the other); one photosystem absorbs preferentially in the red, the other in the far-red.

Plants use photosystems II and I in series, first one and then the other, to produce both ATP and NADPH. This two-stage process is called **noncyclic photophosphorylation** because the path of the electrons is not a circle—the electrons ejected from the photosystems do not return to them, but rather end up in NADPH. The photosystems are replenished with electrons obtained by splitting water.

The scheme shown in figure 8.14, called a *Z diagram,* illustrates the two electron-energizing steps, one catalyzed by each photosystem. The horizontal axis shows the progress of the light reactions and the relative positions of the complexes, and the vertical axis shows relative energy levels of electrons. The electrons originate from water, which holds onto its electrons very tightly (redox potential = +820 mV), and end up in NADPH, which holds its electrons much more loosely (redox potential = –320 mV).

Data analysis If "both lights on" showed a rate equal to the sum of both lights, what would you conclude?

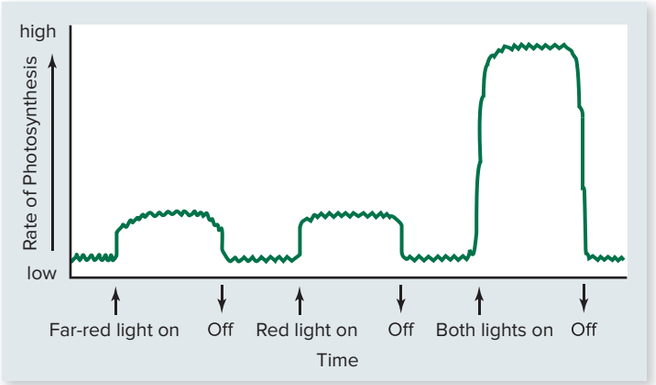

Figure 8.13 The enhancement effect. The rate of photosynthesis when red and far-red light are provided together is greater than the sum of the rates when each wavelength is provided individually. This result baffled researchers in the 1950s. Today, it provides key evidence that photosynthesis is carried out by two photochemical systems that act in series. One absorbs maximally in the far red, the other in the red portion of the spectrum.

Photosystem II acts first. High-energy electrons generated by photosystem II are used to synthesize ATP and are then passed to photosystem I to drive the production of NADPH. On average, for every pair of electrons obtained from a molecule of water, one molecule of NADPH and slightly more than one molecule of ATP are produced.

Photosystem II

The reaction center of photosystem II closely resembles the reaction center of purple bacteria. It consists of a core of 10 transmembrane protein subunits with electron transfer components and two P_{680} chlorophyll molecules arranged around this core. The light-harvesting antenna complex consists of molecules of chlorophyll *a* and accessory pigments bound to several protein chains. The reaction center of photosystem II differs from the reaction center of the purple bacteria in that it also contains four manganese atoms. These manganese atoms are essential for the oxidation of water.

Although the chemical details of the oxidation of water are not entirely clear, the outline is emerging. Four manganese atoms are bound in a cluster to reaction center proteins. Two water molecules are also bound to this cluster of manganese atoms. When the reaction center of photosystem II absorbs a photon, an electron in a P_{680} chlorophyll molecule is excited, which transfers this electron to an acceptor. The oxidized P_{680} then removes an electron from a manganese atom. The oxidized manganese atoms, with the aid of reaction center proteins, remove electrons from oxygen atoms in the two water molecules. This process requires the reaction center to absorb four photons to complete the oxidation of two water molecules, producing one O_2 in the process.

The role of the b_6-f complex

The primary electron acceptor for the light-energized electrons leaving photosystem II is a quinone molecule. The reduced quinone that results from accepting a pair of electrons (*plastoquinone*) is a strong electron donor; it passes the excited electron pair to a

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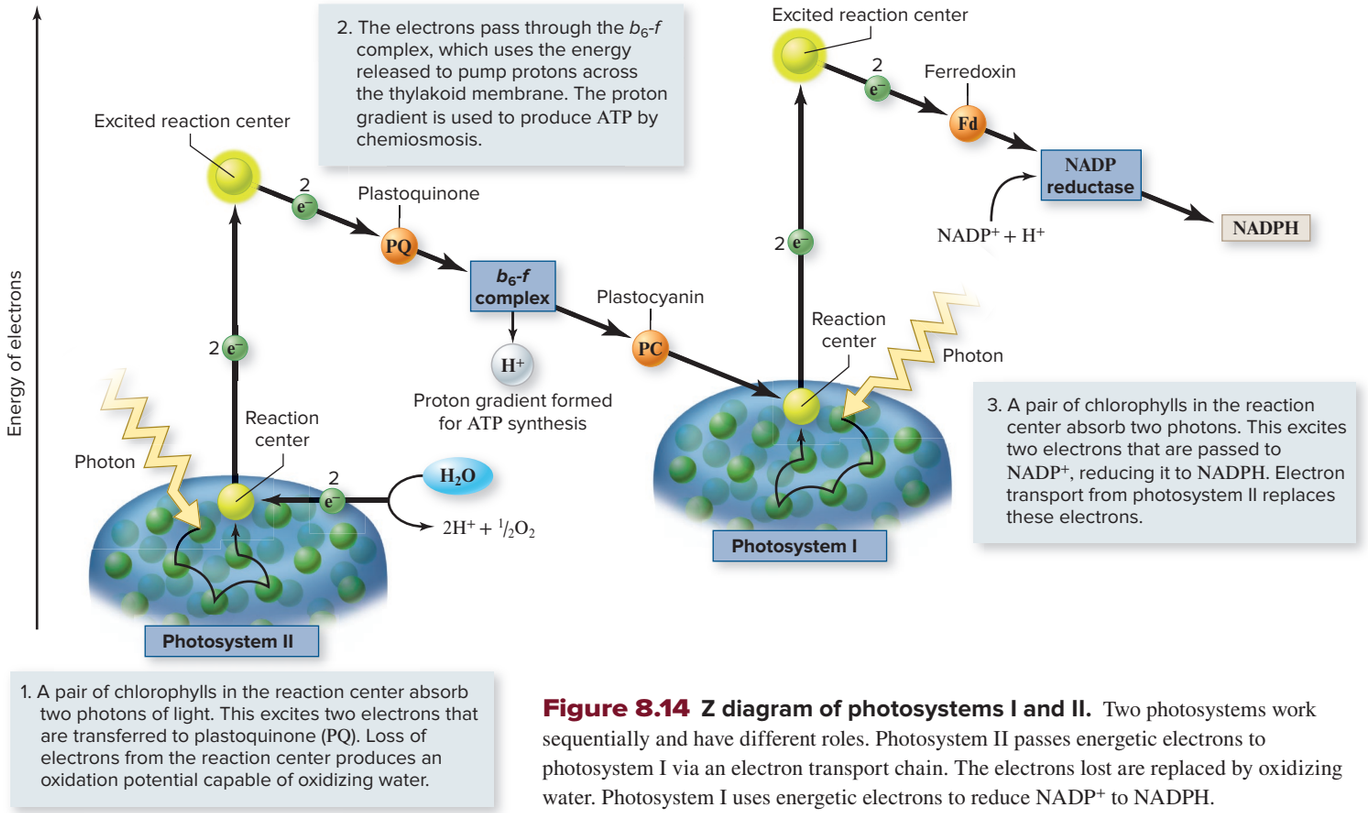

Figure 8.14 Z diagram of photosystems I and II. Two photosystems work sequentially and have different roles. Photosystem II passes energetic electrons to photosystem I via an electron transport chain. The electrons lost are replaced by oxidizing water. Photosystem I uses energetic electrons to reduce $NADP^+$ to NADPH.

proton pump called the ***b_6-f* complex** embedded within the thylakoid membrane (figure 8.15). This complex closely resembles the bc_1 complex in the respiratory electron transport chain of mitochondria, discussed in chapter 7.

Arrival of the energetic electron pair causes the b_6-f complex to pump a proton into the thylakoid space. A small, copper-containing protein called *plastocyanin* then carries the electron pair to photosystem I.

Photosystem I

The reaction center of photosystem I consists of a core transmembrane complex consisting of 12 to 14 protein subunits with two bound P_{700} chlorophyll molecules. Energy is fed to it by an antenna complex consisting of chlorophyll *a* and accessory pigment molecules.

Photosystem I accepts an electron from plastocyanin into the "hole" created by the exit of a light-energized electron. The absorption of a photon by photosystem I boosts the electron leaving the reaction center to a very high energy level. The electrons are passed to an iron–sulfur protein called *ferredoxin*. Unlike photosystem II and the bacterial photosystem, the plant photosystem I does not rely on quinones as electron acceptors.

Making NADPH

Photosystem I passes electrons to ferredoxin on the stromal side of the membrane (outside the thylakoid). The reduced ferredoxin carries an electron with very high potential. Two of them, from two molecules of reduced ferredoxin, are then donated to a molecule of $NADP^+$ to form NADPH. The reaction is catalyzed by the membrane-bound enzyme *NADP reductase.*

Because the reaction occurs on the stromal side of the membrane and involves the uptake of a proton in forming NADPH, it contributes further to the proton gradient established during photosynthetic electron transport. The function of the two photosystems is summarized in figure 8.15.

ATP is generated by chemiosmosis

Protons are pumped from the stroma into the thylakoid compartment by the b_6-f complex. The splitting of water also produces added protons that contribute to the gradient. The thylakoid membrane is impermeable to protons, so this creates an electrochemical gradient that can be used to synthesize ATP.

ATP synthase

The chloroplast has ATP synthase enzymes in the thylakoid membrane that form a channel, allowing protons to cross back out into the stroma. These channels protrude like knobs on the external surface of the thylakoid membrane. As protons pass out of the thylakoid through the ATP synthase channel, ADP is phosphorylated to ATP and released into the stroma (figure 8.15). The stroma contains the enzymes that catalyze the reactions of carbon fixation—the Calvin cycle reactions.

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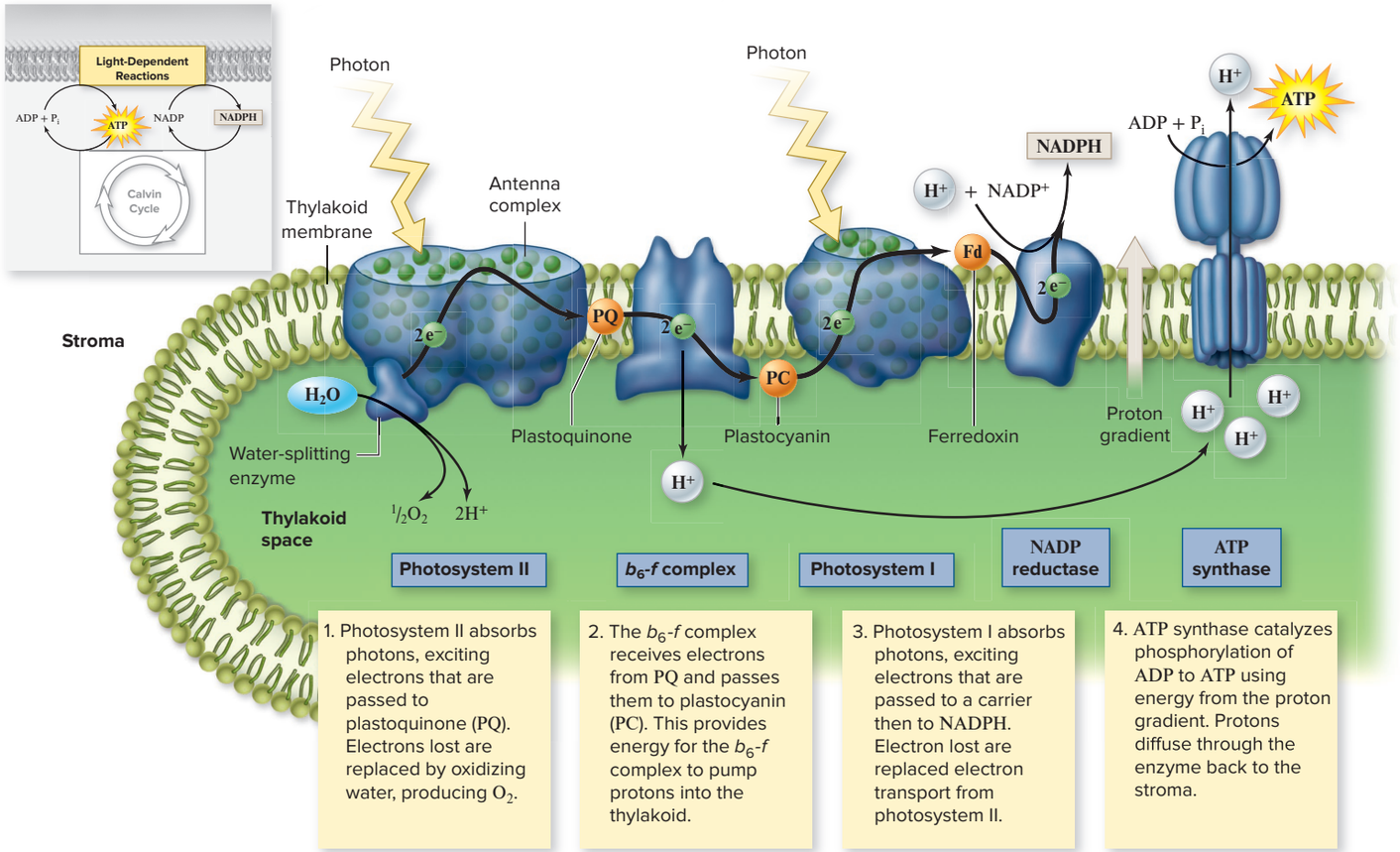


Figure 8.15 The photosynthetic electron transport system and ATP synthase. The two photosystems are arranged in the thylakoid membrane joined by an electron transport system that includes the b_6-f complex. These function together to create a proton gradient that is used by ATP synthase to synthesize ATP.

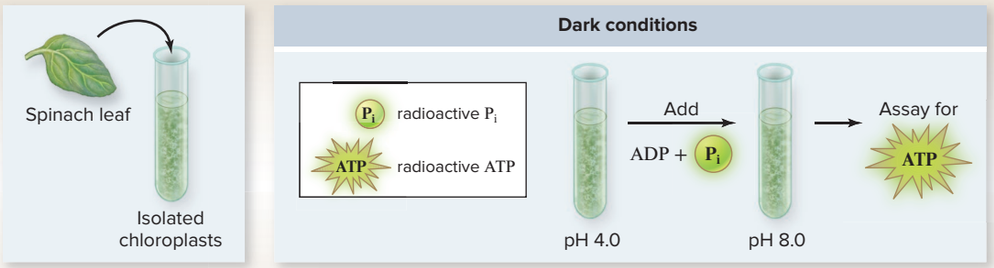
This mechanism is the same as that seen in the mitochondrial ATP synthase, and, in fact, the two enzymes are evolutionarily related. This similarity in generating a proton gradient by electron transport and ATP by chemiosmosis illustrates the similarities in structure and function in mitochondria and chloroplasts. Evidence for this chemiosmotic mechanism for photophosphorylation was actually discovered earlier (figure 8.16) and formed the background for experiments using the mitochondrial ATP synthase.

SCIENTIFIC THINKING

Hypothesis: *Photophosphorylation is coupled to electron transport by a proton gradient.*

Prediction: *If a proton gradient can be formed artificially, then isolated chloroplasts will phosphorylate ADP in the dark.*

Test: *Isolated chloroplasts are incubated in acid medium, then transferred in the dark to a basic medium to create an artificial proton gradient.*



Result: *Isolated chloroplasts can phosphorylate ADP in the dark as assayed by the incorporation of radioactive PO_4 into ATP.*

Conclusion: *The energy from electron transport in the chloroplast is coupled to the phosphorylation of ADP by a proton gradient.*

Further Experiments: *How would the use of agents that inhibit electron transport affect this outcome? How could such agents be used as a further test of the hypothesis?*

Figure 8.16 The Jagendorf acid bath experiment.

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The production of additional ATP

The passage of an electron pair from water to NADPH in noncyclic photophosphorylation generates one molecule of NADPH and slightly more than one molecule of ATP. But as you will learn in section 8.6, building organic molecules takes more energy than that—it takes 1.5 ATP molecules per NADPH molecule to fix carbon.

To produce the extra ATP, many plant species are capable of short-circuiting photosystem I, switching photosynthesis into a *cyclic photophosphorylation* mode, so that the light-excited electron leaving photosystem I is used to make ATP instead of NADPH. The energetic electrons are simply passed back to the b_6-f complex, rather than passing on to $NADP^+$. The b_6-f complex pumps protons into the thylakoid space, adding to the proton gradient that drives the chemiosmotic synthesis of ATP. The relative proportions of cyclic and noncyclic photophosphorylation in these plants determine the relative amounts of ATP and NADPH available for building organic molecules.

Thylakoid structure reveals components' locations

The four complexes responsible for the light-dependent reactions—namely photosystems I and II, cytochrome b_6-f, and ATP synthase—are not randomly arranged in the thylakoid. Researchers are beginning to image these complexes with the atomic force microscope, which can resolve nanometer scale structures, and a picture is emerging in which photosystem II is found primarily in the grana, whereas photosystem I and ATP synthase are found primarily in the connections between grana called stroma lamella. Photosystem I and ATP synthase may also be found in the edges of the grana that are not stacked. The cytochrome b_6-f complex is found in the borders between grana and stroma lamella. One possible model for the arrangement of the complexes is shown in figure 8.17.

The thylakoid itself is no longer thought of only as stacked disks. Some models of the thylakoid, based on electron microscopy and other imaging, depict the grana as folds of the interconnecting stroma lamella. This kind of arrangement is more similar to the folds seen in bacterial photosynthesis, and it would therefore allow for more flexibility in how the various complexes are arranged relative to one another.

Learning Outcomes Review 8.5

The chloroplast has two photosystems located in the thylakoid membrane that are connected by an electron transport chain. Photosystem I passes an electron to NADPH. This electron is replaced by one from photosystem II. Photosystem II can oxidize water to replace the electron it has lost. A proton gradient is built up in the thylakoid space, and this gradient is used to generate ATP as protons pass through the ATP synthase enzyme.

- ***If the thylakoid membrane were leaky to protons, would ATP still be produced? Would NADPH?***

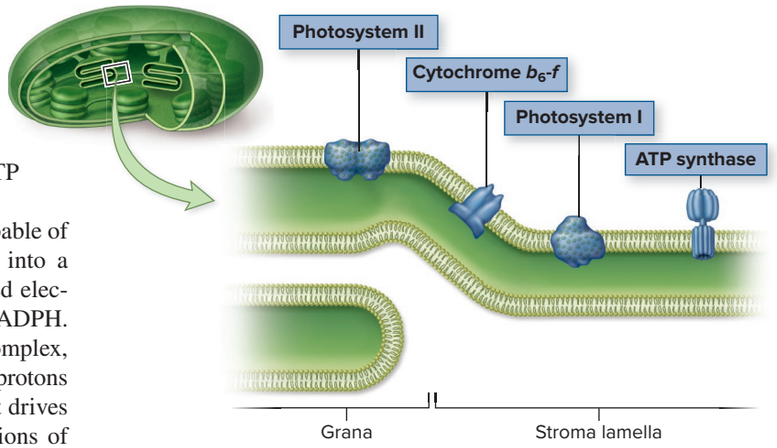

Figure 8.17 Model for the arrangement of complexes within the thylakoid. The arrangement of the two kinds of photosystems and the other complexes involved in photosynthesis is not random. Photosystem II is concentrated within grana, especially in stacked areas. Photosystem I and ATP synthase are concentrated in stroma lamella and the edges of grana. The cytochrome b_6-f complex is in the margins between grana and stroma lamella. This is one possible model for this arrangement.

8.6 Carbon Fixation: The Calvin Cycle

Learning Outcomes

1. ***Describe carbon fixation.***
2. ***Demonstrate how six CO_2 molecules can be used to make one glucose.***

Carbohydrates contain many C—H bonds and are highly reduced compared with CO_2. To build carbohydrates, cells use energy and a source of electrons produced by the light-dependent reactions of the thylakoids:

1. **Energy.** ATP (provided by cyclic and noncyclic photophosphorylation) drives the endergonic reactions.
2. **Reduction potential.** NADPH (provided by photosystem I) provides a source of protons and the energetic electrons needed to bind them to carbon atoms. Much of the light energy captured in photosynthesis ends up invested in the energy-rich C—H bonds of sugars.

Calvin cycle reactions convert inorganic carbon into organic molecules

Because early research showed temperature dependence, photosynthesis was predicted to involve enzyme-catalyzed reactions. These reactions form a cycle of enzyme-catalyzed steps much like the citric acid cycle of respiration. Unlike the citric acid cycle, however, carbon fixation is geared toward producing new compounds, so the nature of the cycles is quite different.

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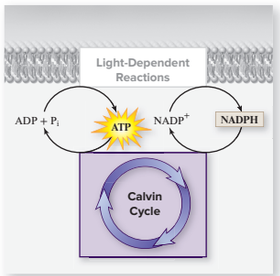
The cycle of reactions that allow carbon fixation is called the **Calvin cycle,** after its discoverer, Melvin Calvin (1911–1997). Because the first intermediate of the cycle, phosphoglycerate, contains three carbon atoms, this process is also called **C_3 photosynthesis.**

The key step in this process—the event that makes the reduction of CO_2 possible—is the attachment of CO_2 to a highly specialized organic molecule. Photosynthetic cells produce this molecule by reassembling the bonds of two intermediates in glycolysis—fructose 6-phosphate and glyceraldehyde 3-phosphate (G3P)—to form the energy-rich 5-carbon sugar **ribulose 1,5-bisphosphate (RuBP).**

CO_2 reacts with RuBP to form a transient 6-carbon intermediate that immediately splits into two molecules of the 3-carbon *3-phosphoglycerate (PGA).* This overall reaction is called the *carbon fixation reaction* because inorganic carbon (CO_2) has been incorporated into an organic form: the acid PGA. The enzyme that carries out this reaction, **ribulose bisphosphate carboxylase/oxygenase** (usually abbreviated **rubisco**) is a large, 16-subunit enzyme found in the chloroplast stroma.

Carbon is transferred through cycle intermediates, eventually producing glucose

We will consider how the Calvin cycle can produce one molecule of glucose, although this glucose is not produced directly by the cycle (figure 8.18). In a series of reactions, six molecules of CO_2 are bound to six RuBP by rubisco to produce 12 molecules of PGA (containing $12 \times 3 = 36$ carbon atoms in all, 6 from CO_2 and 30 from RuBP). The 36 carbon atoms then undergo a cycle of reactions that regenerates the six molecules of RuBP used in the initial step (containing $6 \times 5 = 30$ carbon atoms). This leaves two molecules of



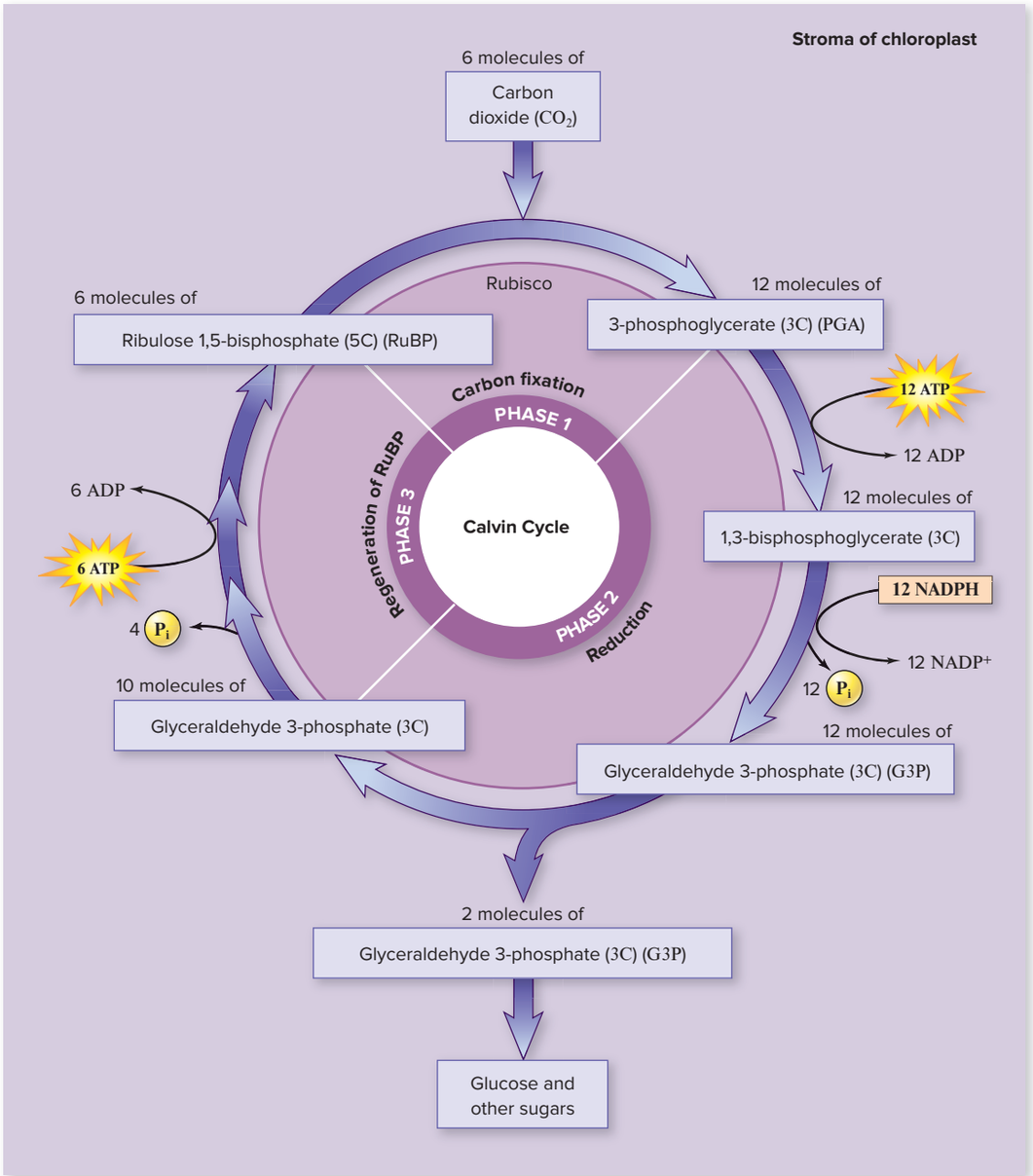


Figure 8.18 The Calvin cycle. The Calvin cycle accomplishes carbon fixation: converting inorganic carbon in the form of CO_2 into organic carbon in the form of carbohydrates. The cycle can be broken down into three phases: (1) carbon fixation, (2) reduction, and (3) regeneration of RuBP. For every six CO_2 molecules fixed by the cycle, a molecule of glucose can be synthesized from the products of the reduction reactions, G3P. The cycle uses the ATP and NADPH produced by the light reactions.

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glyceraldehyde 3-phosphate (G3P) (each with three carbon atoms) as the net gain. (You may recall G3P as also being the product of the first half of glycolysis, described in chapter 7.) These two molecules of G3P can then be used to make one molecule of glucose.

The net equation of the Calvin cycle is:

$$6CO_2 + 18\ ATP + 12\ NADPH + water \longrightarrow$$
$$2\ glyceraldehyde\ 3\text{-}phosphate + 16\ P_i + 18\ ADP + 12\ NADP^+$$

With six full turns of the cycle, six molecules of carbon dioxide enter, two molecules of G3P are produced, and six molecules of RuBP are regenerated. Thus six turns of the cycle produce two G3P that can be used to make a single glucose molecule. The six turns of the cycle also incorporated six CO_2 molecules, providing enough carbon to synthesize glucose, although the six carbon atoms do not all end up in this molecule of glucose.

Phases of the cycle

The Calvin cycle can be thought of as divided into three phases: (1) carbon fixation, (2) reduction, and (3) regeneration of RuBP. The carbon fixation reaction generates two molecules of the 3-carbon acid PGA; PGA is then reduced to G3P by reactions that are essentially a reverse of part of glycolysis; finally, the PGA is used to regenerate RuBP. Three turns around the cycle incorporate enough carbon to produce a new molecule of G3P, and six turns incorporate enough carbon to synthesize one glucose molecule.

We now know that light is required *indirectly* for different segments of the CO_2 reduction reactions. Five of the Calvin cycle enzymes—including rubisco—are light-activated—that is, they become functional or operate more efficiently in the presence of light. Light also promotes transport of required 3-carbon intermediates across chloroplast membranes. And finally, light promotes the influx of Mg^{2+} into the chloroplast stroma, which further activates the enzyme rubisco.

Output of the Calvin cycle

Glyceraldehyde 3-phosphate is a 3-carbon sugar, a key intermediate in glycolysis. Much of it is transported out of the chloroplast to the cytoplasm of the cell, where the reversal of several reactions in glycolysis allows it to be converted to fructose 6-phosphate and glucose 1-phosphate. These products can then be used to form sucrose, a major transport sugar in plants. (Sucrose, table sugar, is a disaccharide made of fructose and glucose.)

In times of intensive photosynthesis, G3P levels rise in the stroma of the chloroplast. As a consequence, some G3P in the chloroplast is converted to glucose 1-phosphate. This takes place in a set of reactions analogous to those occurring in the cytoplasm, by reversing several reactions similar to those of glycolysis. The glucose 1-phosphate is then combined into an insoluble polymer, forming long chains of starch stored as bulky starch grains in the cytoplasm. These starch grains represent stored glucose for later use.

The energy cycle

The energy-capturing metabolisms of the chloroplasts studied in this chapter and the mitochondria studied in chapter 7 are intimately related (figure 8.19). Photosynthesis uses the products of

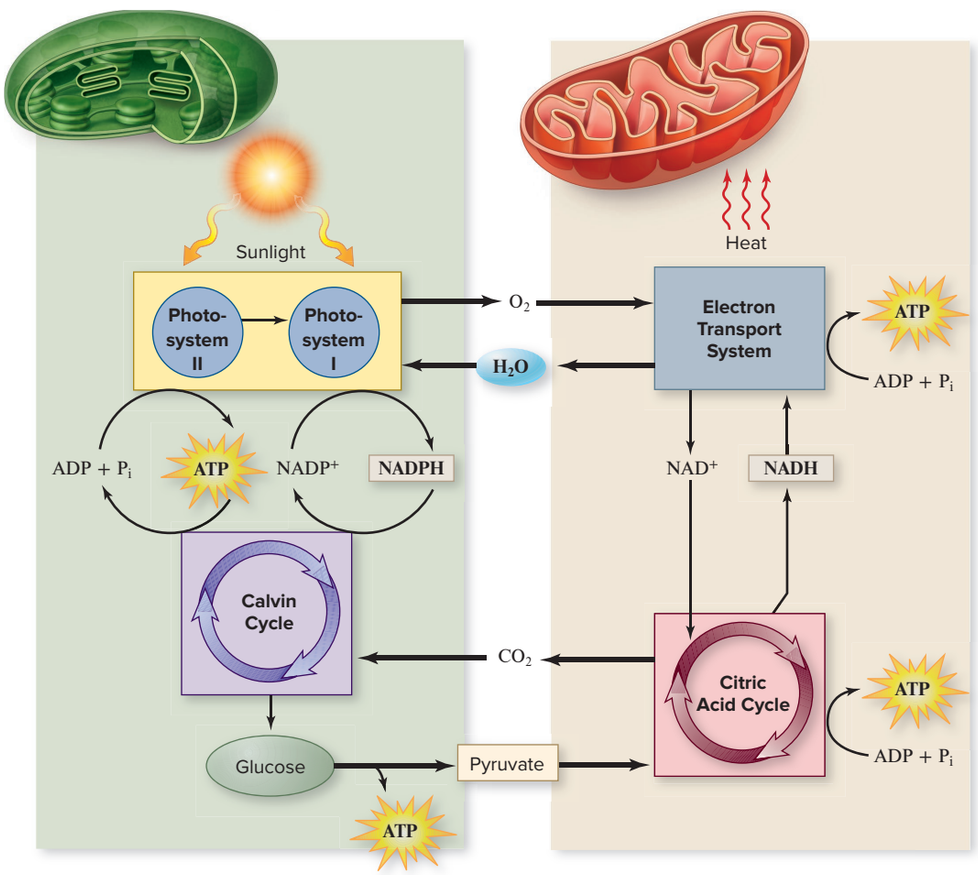

Figure 8.19 Chloroplasts and mitochondria: completing an energy cycle. Water and O_2 cycle between chloroplasts and mitochondria within a plant cell, as do glucose and CO_2. Cells with chloroplasts take in CO_2 and H_2O and produce glucose and O_2. Cells without chloroplasts, such as animal cells, take in glucose and O_2 and produce CO_2 and H_2O. This leads to global cycling of carbon through photosynthesis and respiration (see figure 56.1).

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respiration as starting substrates, and respiration uses the products of photosynthesis as starting substrates. The production of glucose from G3P even uses part of the ancient glycolytic pathway, run in reverse. Also, the principal proteins involved in electron transport and ATP production in plants are evolutionarily related to those in mitochondria.

Photosynthesis is but one aspect of plant biology, although it is an important one. In chapters 35 through 40, we examine plants in more detail. We have discussed photosynthesis as a part of cell biology because photosynthesis arose long before plants did, and because most organisms depend directly or indirectly on photosynthesis for the energy that powers their lives.

Learning Outcomes Review 8.6

Carbon fixation takes place in the stroma of the chloroplast, where inorganic CO_2 is incorporated into an organic molecule. The key intermediate is the 5-carbon sugar RuBP that combines with CO_2 in a reaction catalyzed by the enzyme rubisco. The cycle can be broken down into three stages: carbon fixation, reduction, and regeneration of RuBP. ATP and NADPH from the light reactions provide energy and electrons for the reduction reactions, which produce G3P. Glucose is synthesized when two molecules of G3P are combined.

- ***How does the Calvin cycle compare with glycolysis?***

8.7 Photorespiration

Learning Outcomes

1. *Distinguish between how rubisco acts to make RuBP and how it oxidizes RuBP.*
2. *Compare the function of carbon fixation in the C_3, C_4, and CAM pathways.*

Evolution does not necessarily result in optimum solutions. Rather, it favors workable solutions that can be derived from features that already exist. Photosynthesis is no exception. Rubisco, the enzyme that catalyzes the key carbon-fixing reaction of photosynthesis, provides a decidedly suboptimal solution. This enzyme has a second enzymatic activity that interferes with carbon fixation, namely that of *oxidizing* RuBP. In this process, called **photorespiration,** O_2 is incorporated into RuBP, which undergoes additional reactions that actually release CO_2. Hence, photorespiration releases CO_2, essentially undoing carbon fixation.

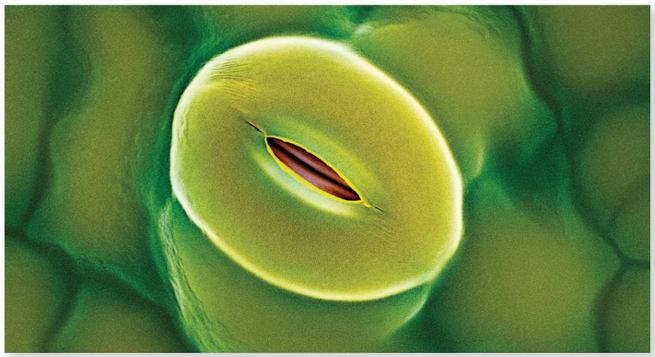
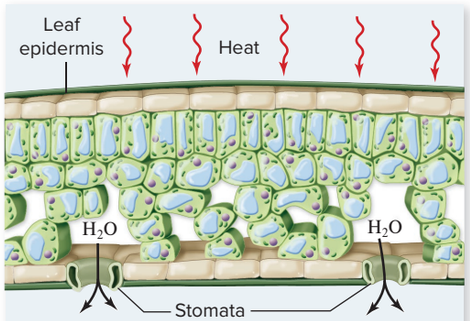


Figure 8.20 Stoma. A closed stoma in the leaf of a tobacco plant. Each stoma is formed from two guard cells whose shape changes with turgor pressure to open and close. Under dry conditions plants close their stomata to conserve water. ©Dr. Jeremy Burgess/Science Source

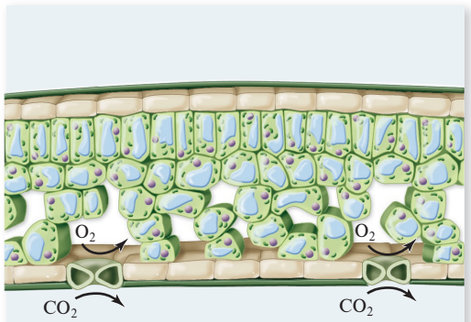
Photorespiration reduces the yield of photosynthesis

The carboxylation and oxidation of RuBP are catalyzed at the same active site on rubisco, and CO_2 and O_2 compete with each other at this site. Under normal conditions at 25°C, the rate of the carboxylation reaction is four times that of the oxidation reaction, meaning that 20% of photosynthetically fixed carbon is lost to photorespiration.

This loss rises substantially as temperature increases, because under hot, arid conditions, specialized openings in the leaf called *stomata* (singular, *stoma*) (figure 8.20) close to conserve water. This closing also cuts off the supply of CO_2 entering the leaf and does not allow O_2 to exit (figure 8.21). As a result, the low-CO_2 and high-O_2 conditions within the leaf favor photorespiration.



Under hot, arid conditions, leaves lose water by evaporation through openings in the leaves called stomata.



The stomata close to conserve water but as a result, O_2 builds up inside the leaves, and CO_2 cannot enter the leaves.

Figure 8.21 Conditions favoring photorespiration. In hot, arid environments, stomata close to conserve water, which also prevents CO_2 from entering and O_2 from exiting the leaf. The high-O_2/low-CO_2 conditions favor photorespiration.

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a. C_3 pathway



b. C_4 pathway

Figure 8.22 Comparison of C_3 and C_4 pathways of carbon fixation. ***a.*** The C_3 pathway uses the Calvin cycle to fix carbon. All reactions occur in mesophyll cells using CO_2 that diffuses in through stomata. ***b.*** The C_4 pathway incorporates CO_2 into a 4-carbon molecule of malate in mesophyll cells. This is transported to the bundle-sheath cells where it is converted back into CO_2 and pyruvate, creating a high level of CO_2. This allows efficient carbon fixation by the Calvin cycle. (a) ©Steven P. Lynch; (b) ©Joseph Nettis/National Audubon Society Collection/Science Source

Plants that fix carbon using only C_3 photosynthesis (the Calvin cycle) are called **C_3 plants** (figure 8.22*a*). Other plants add CO_2 to phosphoenolpyruvate (PEP) to form a 4-carbon molecule. This reaction is catalyzed by the enzyme PEP *carboxylase*. This enzyme has two advantages over rubisco: it has a much greater affinity for CO_2 than rubisco, and it does not have oxidase activity.

The 4-carbon compound produced by PEP carboxylase undergoes further modification, only to be eventually decarboxylated. The CO_2 released by this decarboxylation is then used by rubisco in the Calvin cycle. This allows CO_2 to be pumped directly to the site of rubisco, which increases the local concentration of CO_2 relative to O_2, minimizing photorespiration. The 4-carbon compound produced by PEP carboxylase allows CO_2 to be stored in an organic form, to then be released in a different cell, or at a different time, to keep the level of CO_2 high relative to O_2.

The reduction in the yield of carbohydrate as a result of photorespiration is not trivial. C_3 plants lose between 25% and 50% of their photosynthetically fixed carbon in this way. The rate depends largely on temperature. In tropical climates, especially those in which the temperature is often above 28°C, the problem is severe, and it has a major effect on tropical agriculture.

The two main groups of plants that initially capture CO_2 using PEP carboxylase differ in how they maintain high levels of CO_2 relative to O_2. In **C_4 plants** (figure 8.22*b*), the capture of CO_2 occurs in one cell and the decarboxylation occurs in an adjacent cell. This represents a spatial solution to the problem of photorespiration. The second group, **CAM plants,** perform both reactions in the same cell, but capture CO_2 using PEP carboxylase at night, then decarboxylate during the day. CAM stands for **crassulacean acid metabolism,** after the plant family Crassulaceae (the stonecrops, or hens-and-chicks), in which it was first discovered. This mechanism represents a temporal solution to the photorespiration problem.

C_4 plants have evolved to minimize photorespiration

The C_4 plants include corn, sugarcane, sorghum, and a number of other grasses. These plants initially fix carbon using PEP carboxylase in mesophyll cells. This reaction produces the organic acid oxaloacetate, which is converted to malate and transported to bundle-sheath

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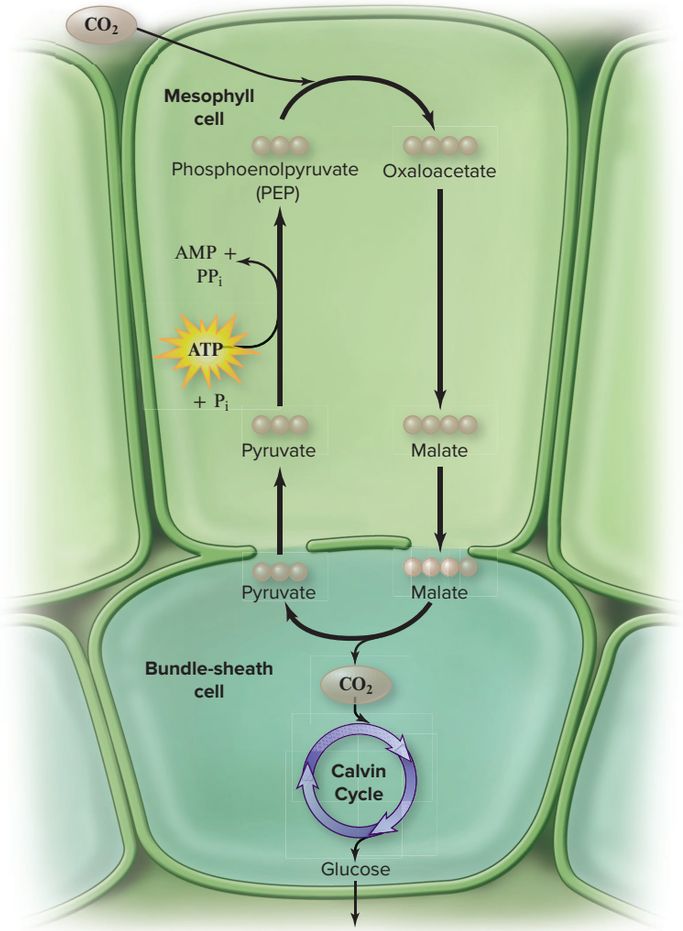

Figure 8.23 Carbon fixation in C_4 plants. This process is called the C_4 pathway because the first molecule formed, oxaloacetate, contains four carbons. The oxaloacetate is converted to malate, which moves into bundle-sheath cells where it is decarboxylated back to CO_2 and pyruvate. This produces a high level of CO_2 in the bundle-sheath cells that can be fixed by the usual C_3 Calvin cycle with little photorespiration. The pyruvate diffuses back into the mesophyll cells, where it is converted back to PEP to be used in another C_4 fixation reaction.

cells that surround the leaf veins. Within the bundle-sheath cells, malate is decarboxylated to produce pyruvate and CO_2 (figure 8.23). Because the bundle-sheath cells are impermeable to CO_2, the local level of CO_2 is high and carbon fixation by rubisco and the Calvin cycle is efficient. The pyruvate produced by decarboxylation is transported back to the mesophyll cells, where it is converted back to PEP, thereby completing the cycle.

The C_4 pathway, although it overcomes the problems of photorespiration, does have a cost. The conversion of pyruvate back to PEP requires breaking two high-energy bonds in ATP. Thus each CO_2 transported into the bundle-sheath cells cost the equivalent of two ATP. To produce a single glucose, this requires 12 additional ATP compared with the Calvin cycle alone. Despite this additional cost, C_4 photosynthesis is advantageous in hot, dry climates where photorespiration would remove more than half of the carbon fixed by the usual C_3 pathway alone.

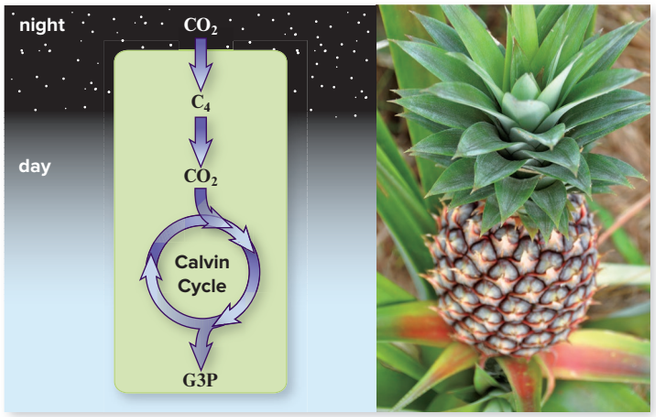

Figure 8.24 Carbon fixation in CAM plants. CAM plants also use both C_4 and C_3 pathways to fix carbon and minimize photorespiration. In CAM plants, the two pathways occur in the same cell but are separated in time: The C_4 pathway is utilized to fix carbon at night, then CO_2 is released from these accumulated stores during the day to drive the C_3 pathway. This achieves the same effect of minimizing photorespiration, while also minimizing loss of water by opening stomata at night when temperatures are lower. ©jessica solomatenko/Getty Images

The Crassulacean acid pathway splits photosynthesis into night and day

A second strategy to decrease photorespiration in hot regions has been adopted by the CAM plants. These include many succulent (water-storing) plants, such as cacti, pineapples, and some members of about two dozen other plant groups.

In these plants, the stomata open during the night and close during the day (figure 8.24). This pattern of stomatal opening and closing is the reverse of that in most plants. CAM plants initially fix CO_2 using PEP carboxylase to produce oxaloacetate. The oxaloacetate is often converted into other organic acids, depending on the particular CAM plant. These organic compounds accumulate during the night and are stored in the vacuole. Then during the day, when the stomata are closed, the organic acids are decarboxylated to yield high levels of CO_2. These high levels of CO_2 drive the Calvin cycle and minimize photorespiration.

Like C_4 plants, CAM plants use both C_3 and C_4 pathways. They differ in that they use both of these pathways in the same cell: the C_4 pathway at night and the C_3 pathway during the day. In C_4 plants the two pathways occur in different cells.

Learning Outcomes Review 8.7

Rubisco can also oxidize RuBP under conditions of high O_2 and low CO_2. In plants that use only C_3 metabolism (Calvin cycle), up to 20% of fixed carbon is lost to this photorespiration. Plants adapted to hot, dry environments are capable of storing CO_2 as a 4-carbon molecule and avoiding some of this loss; they are called C_4 plants. In CAM plants, CO_2 is fixed at night into a C_4 organic compound; in the daytime, this compound is used as a source of CO_2 for C_3 metabolism when stomata are closed to prevent water loss.

- *How do C_4 plants and CAM plants differ?*

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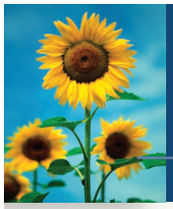

Chapter Review

8.1 Overview of Photosynthesis

Photosynthesis is the conversion of light energy into chemical energy (figure 8.2).

Photosynthesis combines CO_2 and H_2O, producing glucose and O_2.

Photosynthesis has three stages: absorbing light energy, using this energy to synthesize ATP and NADPH, and using the ATP and NADPH to convert CO_2 to organic molecules. The first two stages consist of light-dependent reactions, and the third stage of light-independent reactions.

In plants, photosynthesis takes place in chloroplasts.

Chloroplasts contain internal thylakoid membranes and a fluid matrix called stroma. The photosystems involved in energy capture are found in the thylakoid membranes, and enzymes for assembling organic molecules are in the stroma.

8.2 The Discovery of Photosynthetic Processes

Plants do not increase mass from soil and water alone.

Early investigations revealed that plants produce O_2 from carbon dioxide and water in the presence of light.

Photosynthesis includes both light-dependent and light-independent reactions.

The light-dependent reactions require light; the light-independent reactions occur in both daylight and darkness. The rate of photosynthesis depends on the amount of light, the CO_2 concentration, and temperature.

O_2 comes from water, not from CO_2.

The use of isotopes revealed the individual origins and fates of different molecules in photosynthetic reactions.

ATP and NADPH from light-dependent reactions reduce CO_2 to make sugars.

Carbon fixation requires ATP and NADPH, which are products of the light-dependent reactions. As long as these are available, CO_2 is reduced by enzymes in the stroma to form simple sugars.

8.3 Pigments

Light is a form of energy.

Light exists both as a wave and as a particle (photon). Light can remove electrons from some metals by the photoelectric effect, and in photosynthesis, chloroplasts act as photoelectric devices.

Each pigment has a characteristic absorption spectrum (figure 8.5).

Chlorophyll *a* is the only pigment that can convert light energy into chemical energy. Chlorophyll *b* is an accessory pigment that increases the harvest of photons for photosynthesis.

Carotenoids and other accessory pigments further increase a plant's ability to harvest photons.

8.4 Photosystem Organization (figure 8.10)

Production of one O_2 molecule requires many chlorophyll molecules.

Measurement of O_2 output led to the idea of photosystems—clusters of pigment molecules that channel energy to a reaction center.

A generalized photosystem contains an antenna complex and a reaction center.

A photosystem is a network of chlorophyll *a,* accessory pigments, and proteins embedded in the thylakoid membrane. Pigment molecules of the antenna complex harvest photons and feed light energy to the reaction center. The reaction center is composed of two chlorophyll *a* molecules in a protein matrix that pass an excited electron to an electron acceptor.

8.5 The Light-Dependent Reactions

The light reactions can be broken down into four processes: primary photoevent, charge separation, electron transport, and chemiosmosis.

Some bacteria use a single photosystem (figure 8.12).

An excited electron moves along a transport chain and eventually returns to the photosystem. This cyclic process is used to generate a proton gradient. In some bacteria, this can also produce NADPH.

Chloroplasts have two connected photosystems (figure 8.14).

Photosystem I transfers electrons to $NADP^+$, reducing it to NADPH. Photosystem II replaces electrons lost by photosystem I. Electrons lost from photosystem II are replaced by electrons from oxidation of water, which also produces O_2.

The two photosystems work together in noncyclic photophosphorylation (figure 8.14).

Photosystem II and photosystem I are linked by an electron transport chain; the b_6-*f* complex in this chain pumps protons into the thylakoid space.

ATP is generated by chemiosmosis.

ATP synthase is a channel enzyme; as protons flow through the channel down their gradient, ADP is phosphorylated producing ATP, similar to the mechanism in mitochondria. Plants can make additional ATP by cyclic photophosphorylation.

Thylakoid structure reveals components' locations.

Imaging studies suggest that photosystem II is primarily found in the grana, while photosystem I and ATP synthase are found in the stroma lamella.

8.6 Carbon Fixation: The Calvin Cycle (figure 8.18)

Calvin cycle reactions convert inorganic carbon into organic molecules.

The Calvin cycle, also known as C_3 photosynthesis, uses CO_2, ATP, and NADPH to build simple sugars.

Carbon is transferred through cycle intermediates, eventually producing glucose.

The Calvin cycle occurs in three stages: carbon fixation via the enzyme rubisco's action on RuBP and CO_2; reduction of the resulting 3-carbon PGA to G3P, generating ATP and NADPH; and regeneration of RuBP. Six turns of the cycle fix enough carbon to produce two excess G3Ps used to make one molecule of glucose.

8.7 Photorespiration

Photorespiration reduces the yield of photosynthesis.

Rubisco can catalyze the oxidation of RuBP, reversing carbon fixation. Dry, hot conditions tend to increase this reaction.

C_4 plants have evolved to minimize photorespiration.

C_4 plants fix carbon by adding CO_2 to a 3-carbon molecule, forming oxaloacetate. Carbon is fixed in one cell by the C_4 pathway, then CO_2 is released in another cell for the Calvin cycle (figure 8.23).

The Crassulacean acid pathway splits photosynthesis into night and day.

CAM plants use the C_4 pathway during the day when stomata are closed, and the Calvin cycle at night in the same cell (figure 8.24).

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Review Questions

UNDERSTAND

1. The *light-dependent* reactions of photosynthesis are responsible for the production of
   a. glucose.
   b. CO_2.
   c. ATP and NADPH.
   d. H_2O.
2. Which region of a chloroplast is associated with the capture of light energy?
   a. Thylakoid membrane
   b. Outer membrane
   c. Stroma
   d. Both a and c are correct.
3. The colors of light that are most effective for photosynthesis are
   a. red, blue, and violet.
   b. green, yellow, and orange.
   c. infrared and ultraviolet.
   d. All colors of light are equally effective.
4. During noncyclic photosynthesis, photosystem I functions to _____, and photosystem II functions to _____.
   a. synthesize ATP; produce O_2
   b. reduce $NADP^+$; oxidize H_2O
   c. reduce CO_2; oxidize NADPH
   d. restore an electron to its reaction center; gain an electron from water
5. How is a reaction center pigment in a photosystem different from a pigment in the antenna complex?
   a. The reaction center pigment is a chlorophyll molecule.
   b. The antenna complex pigment can only reflect light.
   c. The reaction center pigment loses an electron when it absorbs light energy.
   d. The antenna complex pigments are not attached to proteins.
6. The ATP and NADPH from the light reactions are used
   a. in glycolysis in roots.
   b. directly in most biochemical reactions in the cell.
   c. during the reactions of the Calvin cycle to produce glucose.
   d. to synthesize chlorophyll.
7. The carbon fixation reaction converts
   a. inorganic carbon into an organic acid.
   b. CO_2 into glucose.
   c. inactive rubisco into active rubisco.
   d. an organic acid into CO_2.
8. C_4 plants initially fix carbon by
   a. the same pathway as C_3 plants, but they modify this product.
   b. incorporating CO_2 into oxaloacetate, which is converted to malate.
   c. incorporating CO_2 into citrate via the citric acid cycle.
   d. incorporating CO_2 into glucose via reverse glycolysis.

APPLY

1. The overall flow of electrons in the light reactions is from
   a. antenna pigments to the reaction center.
   b. H_2O to CO_2.
   c. photosystem I to photosystem II.
   d. H_2O to NADPH.
2. If you could measure pH within a chloroplast, where would it be lowest?
   a. In the stroma
   b. In the lumen of the thylakoid
   c. In the cytoplasm immediately outside the chloroplast
   d. In the antenna complex
3. The excited electron from photosystem I
   a. can be returned to the reaction center to generate ATP by cyclic photophosphorylation.
   b. is replaced by oxidizing H_2O.
   c. is replaced by an electron from photosystem II.
   d. Both a and c are correct.
4. If the Calvin cycle runs through six turns
   a. all of the fixed carbon will end up in the same glucose molecule.
   b. 12 carbons will be fixed by the process.
   c. enough carbon will be fixed to make one glucose, but they will not all be in the same molecule.
   d. one glucose will be converted into six CO_2.
5. Which of the following are similarities between the structure and function of mitochondria and chloroplasts?
   a. They both create internal proton gradients by electron transport.
   b. They both generate CO_2 by oxidation reactions.
   c. They both have a double membrane system.
   d. Both a and c are correct.
6. Given that the C_4 pathway gets around the problems of photorespiration, why don't all plants use it?
   a. It is a more recent process, and many plants have not had time to evolve this pathway.
   b. It requires extra enzymes that many plants lack.
   c. It requires special transport tissues that many plants lack.
   d. It also has an energetic cost.
7. If the thylakoid membrane became leaky to ions, what would you predict to be the result on the light reactions?
   a. It would stop ATP production.
   b. It would stop NADPH production.
   c. It would stop the oxidation of H_2O.
   d. All of the choices are correct.
8. The overall process of photosynthesis
   a. results in the reduction of CO_2 and the oxidation of H_2O.
   b. results in the reduction of H_2O and the oxidation of CO_2.
   c. consumes O_2 and produces CO_2.
   d. produces O_2 from CO_2.

SYNTHESIZE

1. Compare and contrast the fixation of carbon in C_3, C_4, and CAM plants.
2. Diagram the relationship between the reactants and products of photosynthesis and respiration.
3. Do plant cells need mitochondria? Explain your answer.

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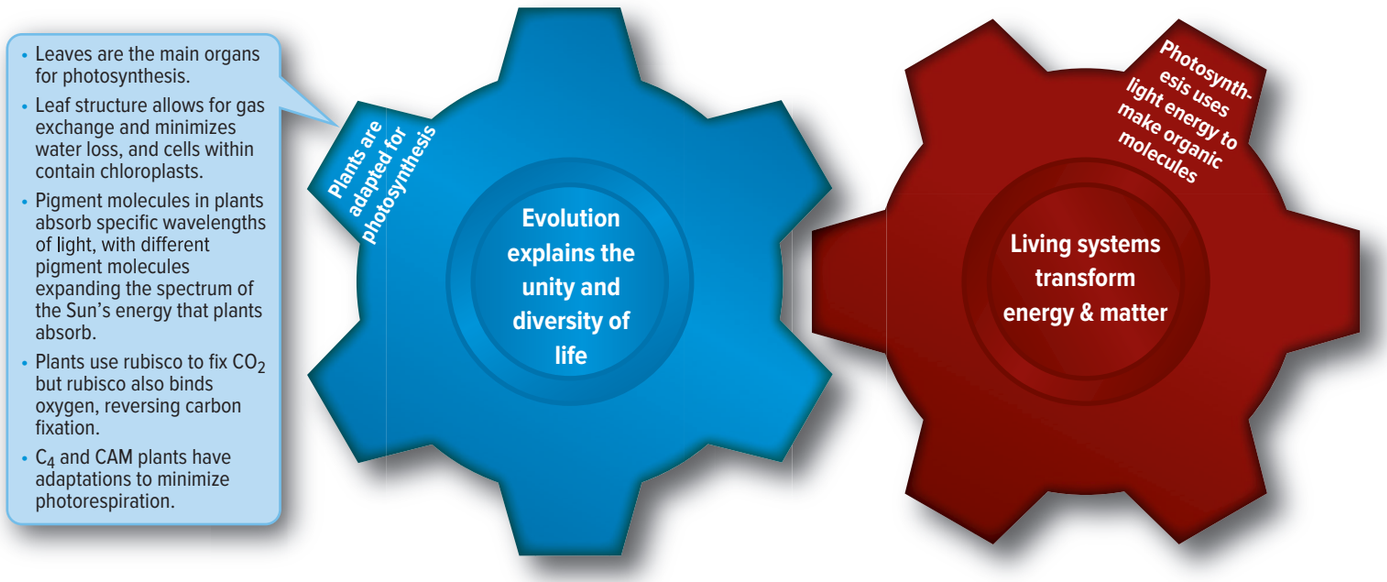
CONNECTING THE CONCEPTS

This feature is intended to give you practice in organizing information using core concepts. We use a metaphor of gears and cogs to represent a conceptual hierarchy with each core concept represented as a gear. Secondary concepts are the cogs, and tertiary concepts, which are particular examples from the chapter, are presented as a list of bulleted points. Using the completed conceptual unit of Evolution explains the unity and diversity of life as a guide, build a list of examples from the chapter that illustrate how the secondary concept "Photosynthesis uses light energy to make organic molecules" supports the core concept "Living systems transform energy & matter."



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