

19. Organization in Time	409
20. Patterns of Nutrition in Development	448
21. Dormancy, Senescence, and Death	466
22. Action of Hormones and Growth Substances	494

## SECTION V

**Physiology of Special Organisms**

23. Tree Physiology	519
24. Physiology of Marine Algae	529
25. Parasites and Disease	540
26. Symbiosis	552

## SECTION VI

**Physiology of Plant Distribution and Communities**

27. Physiology of Plants Under Stress	563
28. Physiological Factors in Plant Distribution	577
29. Plants and Man	594

Author Index	613
Index of Plant Names	619
General Index	625

---

# Detailed Contents

---

## SECTION I

**Introduction and Background**

## CHAPTER 1. Introduction 3

Plant Physiology	3
Plants and Animals	3
Characteristics of Plants and Plant Life That Lead to Specialized Physiology	4
Evolution	5
Applied Botany and Economics	6
Additional Reading	7

## CHAPTER 2. Chemical Background 8

Solutions	8
<i>Solutions of Gas</i>	9
<i>Concentrations</i>	9
Acids and Bases	11
Buffers	11
Colloids	12
Chemical Bonds	14
<i>Electrovalent or Ionic Bonds</i>	14
<i>Covalent Bonds</i>	15
<i>Hydrogen Bonds</i>	16
<i>Weak Forces</i>	16
Oxidation and Reduction	16
Some Organic Chemicals	17
Carbohydrates	23
<i>Stereoisomers</i>	23

<i>Lactones</i>	24
<i>Disaccharides and Polysaccharides</i>	27
<i>Sugar Alcohols, Uronic Acids, and Sugar Acids</i>	28
Amino Acids, Peptides, and Proteins	29
Nucleic Acids	36
Additional Reading	41

## CHAPTER 3. The Cell

42

The Cell Theory	42
The Cell and Its Parts	43
<i>Cell Wall</i>	43
<i>Membranes</i>	47
<i>Nucleus</i>	50
<i>Endoplasmic Reticulum</i>	50
<i>Golgi Apparatus and Dictyosomes</i>	54
<i>Ribosomes</i>	54
<i>Mitochondria</i>	55
<i>Plastids</i>	56
<i>Glyoxysomes and Peroxisomes</i>	58
<i>Other Subcellular Structures</i>	58
<i>The Vacuole</i>	58
Water and Cells	59
<i>Water Potential</i>	59
<i>Diffusion</i>	60
<i>Differentially Permeable Membranes</i>	60
<i>Osmosis</i>	60
<i>Osmotic Potential and Pressure Potential</i>	61
<i>Measuring <math>\psi_{\pi}</math></i>	62
<i>Water Potential in Cells</i>	64
<i>Movement of Water Between Cells</i>	65
<i>Imbibition</i>	66
<i>The Old Approach to Osmosis and Water Movement</i>	67
Growth of Cells	67
Additional Reading	69

## CHAPTER 4. Structure and Growth of Familiar Higher Plants

70

Germination	70
Roots	71
The Stem	77
Leaf Structure	80
Flowers and Fruit	81
Meristems: Patterns of Growth	84
Additional Reading	84

SECTION II  
Plant Metabolism

## CHAPTER 5. Energy Conversion

87

Synthesis of ATP	87
An Electron Transport Chain	89
Measuring Energy Changes	91
High Energy Compounds	93
Group Transfer Reactions	94
<i>The "Energy Charge" Concept</i>	95
Enzyme Action	97
Additional Reading	99

## CHAPTER 6. Respiration

100

Introduction	100
Glycolysis	100
<i>Reactions</i>	100
<i>Energy Balance</i>	102
Krebs Cycle	103
<i>Formation of Acetyl-Coenzyme A</i>	103
<i>Reactions of the Cycle</i>	104
<i>Energy Balance</i>	107
Pentose Shunt	107
<i>Reactions</i>	107
<i>Energy Balance</i>	109
Fermentation	110
Localization of Pathways	110
Links Between Respiration and Other Metabolic Systems	112
<i>Mobilization of Substrates</i>	112
<i>Glycolysis Intermediates</i>	114
<i>Shunt Intermediates</i>	115
<i>Krebs Cycle Intermediates</i>	115
<i>Anaplerotic Reactions</i>	115
Control of Respiration	117
<i>Pasteur Effect</i>	117
<i>Feedback and Allosteric Control</i>	117
<i>Cofactor Control</i>	119
<i>Side Reactions</i>	119
Other Respiratory Systems and Oxidases	119
<i>Phenol Oxidases</i>	119
<i>Ascorbic Acid Oxidase</i>	120
<i>Catalase and Peroxidase</i>	121
<i>Glycolic Acid Oxidase</i>	121
<i>Participation of Other Oxidases in Respiration</i>	121
Factors Affecting Respiration of Tissues	122
<i>Respiratory Quotient and Substrates of Respiration</i>	122

<i>Age and Tissue Type</i>	123
<i>Temperature</i>	126
<i>Oxygen</i>	127
<i>Carbon Dioxide</i>	128
<i>Salts</i>	129
<i>Wounding and Mechanical Stimulus</i>	129
The Study and Measurement of Respiration	130
<i>Measurement of Rates</i>	130
<i>Understanding Pathways</i>	132
<i>Enzymology</i>	134
Additional Reading	136

## CHAPTER 7. Photosynthesis

137

Introduction	137
Historical Background	139
Light Reactions	142
<i>Light</i>	142
<i>Pigments</i>	143
<i>Electron Transport</i>	148
<i>The Light Trap</i>	150
<i>Release of Oxygen</i>	151
<i>Alternative Mechanisms</i>	151
<i>Energy Balance</i>	152
The Dark Reactions	153
<i>Introduction</i>	153
<i>Radioactivity and Chromatography</i>	153
<i>The Calvin Cycle</i>	156
<i>Energy Balance of the Calvin Cycle</i>	160
<i>Photosynthesis of Other Compounds</i>	161
<i>Other Carbon Dioxide Fixations</i>	163
Photorespiration	166
Factors Affecting Photosynthesis	167
<i>Temperature</i>	167
<i>Oxygen</i>	168
<i>Carbon Dioxide</i>	169
<i>Light</i>	170
The Evolution of Photosynthesis	171
Additional Reading	172

## CHAPTER 8. Nitrogen Metabolism

173

Nitrogen Fixation	173
<i>Symbiotic Nitrogen Fixation</i>	173
<i>Nonsymbiotic Nitrogen Fixation</i>	174
<i>Mechanism of Nitrogen Fixation</i>	177
Nitrate Reduction	179
<i>Mechanism of Nitrate Reduction</i>	179

<i>Nitrate Reduction and Metabolism</i>	180
Absorption of Nitrogen by Plants	181
<i>Inorganic Nitrogen</i>	181
<i>Organic Nitrogen</i>	182
Amino Acids	183
<i>Amination</i>	183
<i>Transamination</i>	184
<i>Carbon Transformation</i>	185
<i>Some Metabolic Patterns</i>	188
Amides	190
<i>Synthesis</i>	190
<i>Metabolism</i>	192
<i>Behavior of Glutamine and Asparagine</i>	192
Proteins	195
<i>Types of Proteins</i>	195
<i>Protein Formation and Breakdown</i>	196
<i>Protein Turnover</i>	197
Peptides	197
Purines and Pyrimidines	198
Alkaloids	201
Additional Reading	206

## CHAPTER 9. Polymers and Large Molecules

207

Polysaccharides	207
<i>Starch</i>	207
<i>Inulin</i>	208
<i>Cellulose</i>	208
<i>Other Polysaccharides</i>	208
Lipids	209
Chlorophyll	212
Isoprenoids	212
Phenols and Aromatic Compounds	217
<i>Aromatic Amino Acids, Indoleacetic Acid</i>	217
<i>Simple Phenols and Lignin</i>	217
<i>Flavones and Anthocyanins</i>	219
Additional Reading	221

## SECTION III

### Soil, Water, and Air: The Nutrition of Plants

## CHAPTER 10. Soil and Mineral Nutrition

225

The Soil	225
<i>Soil Texture and Structure</i>	225
<i>Soil Water</i>	226
<i>Nutrients</i>	228

Mineral Nutrition	231
<i>Chemical Composition of Plants</i>	231
<i>Macro- and Micronutrients</i>	232
<i>Essential Nutrients</i>	234
<i>Culture Media</i>	234
Macronutrients	235
Calcium	235
Magnesium	237
Potassium	238
Nitrogen	238
Phosphorus	239
Sulfur	239
Micronutrients	240
Iron	241
Manganese	242
Boron	242
Copper	243
Zinc	243
Molybdenum	243
Chlorine	244
A Key to Nutrient Deficiency Symptoms	244
Beneficial and Toxic Elements	245
<i>Beneficial Elements</i>	245
<i>Replacement</i>	246
<i>Toxic Elements</i>	246
Trace Elements in Economic Plants	246
<i>Deficiency Diseases and Toxic Effects in Animals</i>	246
<i>Plants as Indicators</i>	247
Additional Reading	248

## CHAPTER 11. Uptake and Movement of Water

249

Water Movement	249
<i>The Problem of Water Loss</i>	249
<i>Entry of Water into Cells</i>	250
<i>Apparent Free Space</i>	250
Entry of Water into Roots	251
<i>Root Pressure</i>	251
<i>Apoplast and Symplast</i>	251
<i>Mechanism of Absorption</i>	251
Pathway of Water Through Tissues	253
The Ascent of Sap	255
<i>The Forces Required</i>	255
<i>Cohesion of Water</i>	256
<i>Vessel Size</i>	257
<i>Alternative Theories</i>	257
Flow of Water	258
Summary	260
Additional Reading	260

## CHAPTER 12. Uptake and Transfer of Solutes

261

Mechanisms for the Movement of Solutes	261
Diffusion	261
<i>Membrane and Solute Characteristics</i>	261
<i>Diffusion and Permeability</i>	262
<i>Accumulation by Diffusion</i>	263
Movement of Ions	263
<i>Special Problems</i>	263
<i>Antagonism</i>	263
<i>Electrochemical Potential</i>	264
<i>Donnan Equilibrium</i>	265
<i>Membrane Potential</i>	265
Active Transport	267
<i>Definition</i>	267
<i>Demonstration and Proof of Active Transport</i>	267
<i>Charge Balance</i>	269
Mechanisms of Active Transport	270
<i>Source of Energy</i>	270
<i>Possible Mechanisms</i>	270
<i>Importance</i>	272
Additional Reading	272

## CHAPTER 13. Translocation

273

The Problems of Translocation	273
Tissues of Translocation	274
<i>Xylem</i>	274
<i>Phloem</i>	274
Location of Solutes	274
<i>Ringing Experiments</i>	274
<i>Analysis of Tissues</i>	275
<i>Tracer Experiments</i>	276
<i>Summary</i>	280
Xylem Transport	280
Phloem Translocation	282
<i>Bulk Flow</i>	282
<i>Activated Diffusion</i>	284
<i>Cytoplasmic Streaming</i>	284
<i>Interface Diffusion</i>	286
<i>Electroosmosis</i>	286
<i>Summary</i>	286
Circulation	287
Additional Reading	290

## CHAPTER 14. Leaves and the Atmosphere

291

Leaves	291
Gas Exchange	294

Diffusion Through Pores	294
Carbon Dioxide Diffusion Through Stomata	295
Stomatal Movement	298
Factors Affecting Stomatal Action	299
Mechanism of Stomatal Action	301
Control of Stomata	302
Nonstomatal Gas Exchange	304
Photosynthesis	304
Environmental Factors	304
Plant Factors	307
Photorespiration	309
Rates and Efficiency of Photosynthesis	311
Water Loss	311
Guttation	311
Transpiration	312
Transpiration	312
Factors That Affect Transpiration	312
Control of Transpiration	314
Necessity of Transpiration	315
Measurement of Transpiration	315
Heat Exchange	316
Plants and the Weather	317
Additional Reading	318

## SECTION IV

**The Developing Plant—Plant Behavior**

## CHAPTER 15. Interpretation of Growth and Development 321

Introduction	321
Growth and Its Measurement	321
Parameters of Growth	321
Growth Versus Development	322
Kinetics of Growth	323
Measurement of Development	327
Kinds of Developmental Control	327
Genetic Controls	327
Organismal Controls	330
→ Auxins	330
→ Gibberellins	333
→ Cytokinins	333
→ Ethylene	333
→ Abscissic Acid	337
Hypothetical Growth Substances	337
Environmental Controls	337
Level of Action of Controls	338
The Genetic Level	338

Biochemical Level	340
Cellular Level	340
Organizational Level	343
Initiation of Events	346
Rhythmic Behavior	346
Additional Reading	347
General References for Section IV	348

## CHAPTER 16. Sexual Reproduction in Higher Plants 349

The Gametophyte Generation	349
Carpel and Egg	349
Anther and Pollen	349
Sex Determination	351
Pollination and Fertilization	352
Pollen Tube Growth	352
Fertilization	352
Embryo Development	353
Capacity to Grow	353
Embryo Growth	354
Embryo Growth in Vitro	355
Embryogenesis in Cell and Tissue Culture	356
Totipotency of Plant Cells	357
One-Way Streets in Development	357
Fruit and Seed Formation	360
Fruit Set	360
Fruit and Seed Development	360
Fruit Ripening	361
Germination	363
Conditions for Germination	364
Mobilization of Reserves	365
Seedling Nutrition	366
Additional Reading	367

## CHAPTER 17. Patterns of Growth 368

Seedling Growth	368
Photomorphogenesis	368
Initiation of Organs in Tissue Cultures	370
Root Growth	373
Terminal Meristem	373
Control of Root Growth	374
Differentiation of Tissues	375
Lateral Roots	376
Shoot Growth	376
Terminal Meristem	376
Stem Growth	377

- Leaf Primordia* 379
- Differentiation* 381
- Growth of Leaves 384
- Floral Development 386
- Additional Reading 389

## CHAPTER 18. Spatial Organization

390

- Direction of Growth 390
- Tropic Responses 390
  - Geotropism* 390
  - Perception of Gravity* 391
  - Mechanism of Response to Gravity* 393
  - Phototropism* 395
  - Phototropic Light Perception* 397
  - Thigmotropism* 398
  - Other Tropisms* 399
- Shape 399
  - Correlative Effects* 399
  - Other Factors* 400
  - Apical Dominance* 401
- Nastic Responses 402
  - Epinasty* 403
  - Thermonasty* 403
  - Nyctinasty* 403
  - Seismonasty* 405
  - Traps* 406
  - Rapid Leaf Movements* 407
  - Nutation* 408
- Additional Reading 408

## CHAPTER 19. Organization in Time

409

- Introduction 409
  - The Importance of Timing* 409
  - Ways to Measure Time* 410
- How Biological Clocks Might Work 410
  - Hourglass* 410
  - Oscillator* 410
  - Interactions* 411
  - Extrinsic Rhythms* 413
- Timing of Flowering 413
  - Photoperiodism and Vernalization* 413
  - The Discovery of Photoperiodism* 413
  - Night Interruptions and Dark Measurement* 417
  - Sites of Perception* 419
  - Phytochrome* 419
- The Mechanism of Phytochrome Action 423

- The Range of Reactions Mediated by Phytochrome* 423
- Some Attempted Explanations of Phytochrome Action* 424
- Active and Inactive Phytochrome* 424
- Some Recent Ideas* 425
- High Energy Reactions* 426
- The Relationship Between Flowering and Rapid Responses* 427
- Floral Induction 428
  - Induction and Floral Development* 428
  - Perception and Translocation of Floral Stimulus* 428
  - Inhibitors* 433
  - Growth Substances* 433
  - Anthesin* 435
  - Changes at the Shoot Apex* 436
  - Phytochrome as an Hourglass Timer* 437
- Rhythmic Processes 437
  - Circadian Rhythms* 437
  - Circadian Rhythms and Photoperiodism* 440
  - The Nature of the Oscillating Timer* 440
- Vernalization 441
  - Cold Induction* 441
  - Interactions with Other Factors* 443
  - Site of Perception of Cold Stimulus* 443
  - Vernalin and Gibberellins* 443
  - The Nature of the Vernalization Process* 444
- Summary: Flowering and Floral Induction 446
- Additional Reading 447

## CHAPTER 20. Patterns of Nutrition in Development

448

- Photosynthesis and Nutrition 448
- The Onset of Photosynthesis in Seedlings 449
- Patterns of Nutrition in the Mature Plant 450
  - Patterns of Assimilation* 450
  - Patterns of Export from Leaves* 452
  - Fruit Formation* 455
  - Wood Formation* 456
- Nutritional Traffic Control 457
  - Movement of Nutrients Toward Sinks* 457
  - Apical Dominance and Nutrition* 459
  - Hormonal Control of Translocation* 459
  - Hormone Control of Photosynthesis* 462
- Additional Reading 465

## CHAPTER 21. Dormancy, Senescence, and Death

466

- Dormancy 466
- Causes of Dormancy 467
  - Environmental Factors* 467

<i>Absciscic Acid</i>	467
<i>Interaction of ABA with Other Growth Substances</i>	469
Seed Dormancy	473
<i>Types of Seed Dormancy</i>	473
<i>Light Requirement</i>	474
<i>Temperature</i>	474
<i>Seed Coat Effects</i>	476
<i>Other Factors</i>	478
Dormancy of Vegetative Organs	478
<i>Day Length and Dormancy</i>	478
<i>Other Factors</i>	479
<i>Interacting Factors</i>	479
<i>Breaking Dormancy</i>	481
Senescence and Death	483
<i>Patterns of Aging and Death</i>	483
<i>Metabolic Aspects of Senescence</i>	483
<i>Nutritional Competition in Senescence</i>	486
<i>Effects of Growth Factors</i>	486
<i>Abscission</i>	488
Additional Reading	493

## CHAPTER 22. Action of Hormones and Growth Substances

494

Introduction	494
Auxins	494
<i>Synthesis, Movement, and Inactivation</i>	494
<i>IAA and Ethylene Formation</i>	497
<i>IAA Effects on Specific Enzymes</i>	497
<i>Auxins and Translocation</i>	497
<i>Cell Wall Effects</i>	498
<i>Effects on RNA and Protein Synthesis</i>	499
<i>Structure and Activity</i>	501
Gibberellins	502
<i>Synthesis and Distribution</i>	502
<i>Elongation</i>	504
<i>Flowering</i>	505
<i>Enzyme Synthesis</i>	505
<i>Mechanism of Action</i>	506
Cytokinins	506
<i>Distribution</i>	506
<i>Effects</i>	506
<i>Prevention of Senescence</i>	508
<i>Enzyme Formation</i>	509
<i>Cytokinins as Constituents of RNA</i>	509
<i>Cytokinin Action</i>	511
Absciscic Acid	512
<i>Absciscic Acid Effects</i>	512
<i>Absciscic Acid Action</i>	513

Ethylene	513
<i>Ethylene Effects</i>	513
<i>Mechanism of Action</i>	513
Other Substances That Influence Growth	514
Summary of Hormone Actions	515
Additional Reading	516

## SECTION V

### Physiology of Special Organisms

#### CHAPTER 23. Tree Physiology

519

Special Characteristics of Trees	519
Assimilation	519
Wood Formation	521
<i>Hormones</i>	521
<i>Photoperiod</i>	522
<i>Water</i>	522
<i>Temperature</i>	522
<i>Assimilation</i>	522
<i>Reaction Wood and Orientation Movement</i>	522
Form	525
<i>Crown Shape</i>	525
<i>Plagiotrophism</i>	525
Consequences of Perennial Growth	525
<i>Metabolism of Perennial Tissue</i>	525
<i>Dormancy</i>	526
<i>Nutrient Salvage Prior to Leaf Fall</i>	527
Communities of Trees	527
Additional Reading	528

#### CHAPTER 24. Physiology of Marine Algae

529

Introduction	529
Productivity of Marine Algae	529
Peculiarities of Algal Metabolism and Biochemistry	530
<i>Chemotaxonomy</i>	530
<i>Pigments</i>	531
<i>Small Molecules</i>	531
<i>Storage Compounds</i>	531
<i>Calcareous Algae</i>	533
Reactions to Environmental Factors	533
<i>Light</i>	533
<i>Temperature</i>	534
<i>Desiccation</i>	535
<i>pH</i>	535
<i>Salinity and Osmotic Potential</i>	535

- Wave Action* 536
- Some Physiological Mechanisms 536
  - Seasonal Growth* 536
  - Uptake of Solutes* 537
  - Antifouling* 538
  - Pheromones* 538
- Additional Reading 539

## CHAPTER 25. Parasites and Disease

540

- Introduction 540
- Infection 541
  - Organisms of Disease* 541
  - Resistance* 541
  - Immunity* 541
  - Stimulus to Infection* 542
  - Invasion* 542
  - Toxins* 542
- Physiological Responses to Parasitism 543
  - Respiration* 543
  - Photosynthesis* 544
  - Nitrogen Metabolism* 544
  - Translocation* 544
  - Growth Substances and Morphological Response* 545
  - Responses to Environment* 550
  - Injury* 550
- Host-Parasite Interaction 550
- Additional Reading 551

## CHAPTER 26. Symbiosis

552

- Types of Symbiosis 552
- Mycorrhiza 553
- Orchids 555
- Lichens 555
  - Lichen Associations* 555
  - Metabolic Interactions* 557
  - Water Relations* 559
  - Pigments* 559
- Additional Reading 559

## SECTION VI

### Physiology of Plant Distribution and Communities

## CHAPTER 27. Physiology of Plants Under Stress

563

- Introduction 563
- Effects of Stress 563
- Types of Stress 564

- Stress Resistance: Avoidance and Tolerance 565
- Measurement of Hardiness 565
- Drought 566
  - Drought Avoidance and Tolerance* 566
  - Consequences of Dehydration* 566
  - Mechanisms of Drought Tolerance* 567
- Heat 568
  - Limits of Heat Tolerance* 568
  - Mechanisms of Heat Tolerance* 568
- Low Temperature and Freezing 569
  - Chilling and Freezing* 569
  - Theories of Freezing Resistance* 570
  - Frost Hardening* 571
- Radiation 571
- Soil Conditions 572
- Altitude 572
- Pollution 573
- Additional Reading 576

## CHAPTER 28. Physiological Factors in Plant Distribution

577

- Introduction 577
- Physiological Factors in Ecology 577
- Factors Affecting Vegetation 579
  - Vegetation Types* 579
  - Historical Factors* 579
  - Geographical Factors* 580
  - Rainfall* 580
  - Relative Humidity* 581
  - Temperature* 581
  - Wind* 584
  - Periodicity and Season Length* 584
- Factors Affecting Flora 585
  - Climatic* 585
  - Physiographic* 587
  - Pollution* 589
  - Competition* 590
  - Succession* 591
- Physiological Mechanisms of Competition 592
- Additional Reading 593

## CHAPTER 29. Plants and Man

594

- Introduction 594
- Man's Impact on the Landscape 594
  - Levels of Interaction* 595
  - Modification of the Environment* 595
  - Modification in Agriculture* 597



<i>Environment Management</i>	598
Productivity and Agriculture	598
<i>Use of Growth Factors</i>	599
<i>Timing</i>	604
<i>Environmental Control</i>	604
<i>"The Sun's Work in a Cornfield"</i>	608
Adaptation and Development of Plants for Special Needs	610
Plants and Pollution	610
The Role of the Plant Physiologist	611
Additional Reading	612

Author Index	613
Index of Plant Names	619
General Index	625

---

# SECTION

# I

## Introduction and Background

---