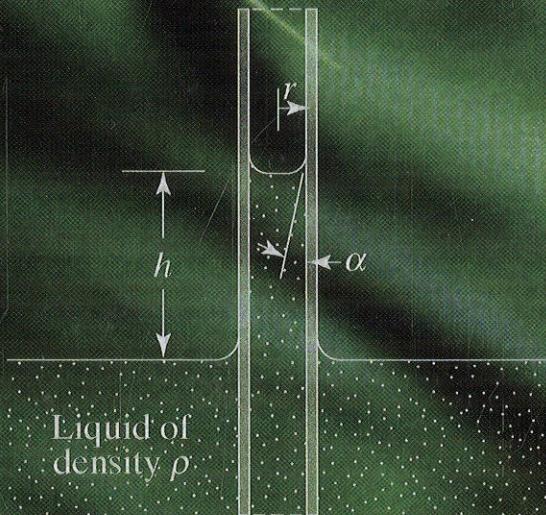
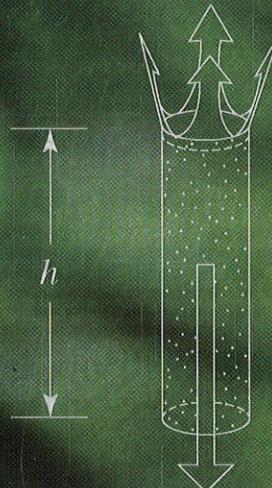


FOURTH EDITION

PHYSICOCHEMICAL  
AND ENVIRONMENTAL  
PLANT  
PHYSIOLOGY



Force/length ( $\sigma$ )  
due to surface tension  
(upward component =  $\sigma \cos \alpha$ )



Downward gravitational force  
( $\pi r^2 h \rho g$ )

PARK S. NOBEL



# Contents

<b>Preface</b>	xiii
<b>Symbols and Abbreviations</b>	xv
<b>1. Cells and Diffusion</b>	<b>3</b>
1.1. Cell Structure	3
1.1A. Generalized Plant Cell	3
1.1B. Leaf Anatomy	5
1.1C. Vascular Tissue	7
1.1D. Root Anatomy	9
1.2. Diffusion	11
1.2A. Fick's First Law	12
1.2B. Continuity Equation and Fick's Second Law	14
1.2C. Time–Distance Relation for Diffusion	16
1.2D. Diffusion in Air	19
1.3. Membrane Structure	21
1.3A. Membrane Models	21
1.3B. Organelle Membranes	23
1.4. Membrane Permeability	25
1.4A. Concentration Difference Across a Membrane	26
1.4B. Permeability Coefficient	28
1.4C. Diffusion and Cellular Concentration	29
1.5. Cell Walls	31
1.5A. Chemistry and Morphology	33
1.5B. Diffusion Across Cell Walls	34
1.5C. Stress–Strain Relations of Cell Walls	37
1.5D. Elastic Modulus, Viscoelasticity	39
1.6. Problems	40
1.7. References and Further Reading	42
<b>2. Water</b>	<b>45</b>
2.1. Physical Properties	46
2.1A. Hydrogen Bonding—Thermal Relations	47
2.1B. Surface Tension	49
2.1C. Capillary Rise	50
2.1D. Capillary Rise in the Xylem	53

2.1E. Tensile Strength, Viscosity	54
2.1F. Electrical Properties	55
2.2. Chemical Potential	56
2.2A. Free Energy and Chemical Potential	56
2.2B. Analysis of Chemical Potential	60
2.2C. Standard State	63
2.2D. Hydrostatic Pressure	64
2.2E. Water Activity and Osmotic Pressure	65
2.2F. Van't Hoff Relation	66
2.2G. Matric Pressure	69
2.2H. Water Potential	71
2.3. Central Vacuole and Chloroplasts	72
2.3A. Water Relations of the Central Vacuole	73
2.3B. Boyle–Van't Hoff Relation	74
2.3C. Osmotic Responses of Chloroplasts	76
2.4. Water Potential and Plant Cells	78
2.4A. Incipient Plasmolysis	78
2.4B. Höfler Diagram and Pressure–Volume Curve	81
2.4C. Chemical Potential and Water Potential of Water Vapor	84
2.4D. Plant–Air Interface	87
2.4E. Pressure in the Cell Wall Water	88
2.4F. Water Flux	91
2.4G. Cell Growth	93
2.4H. Kinetics of Volume Changes	95
2.5. Problems	96
2.6. References and Further Reading	98

### 3. Solutes 101

3.1. Chemical Potential of Ions	102
3.1A. Electrical Potential	103
3.1B. Electroneutrality and Membrane Capacitance	104
3.1C. Activity Coefficients of Ions	106
3.1D. Nernst Potential	108
3.1E. Example of $E_{N_K}$	110
3.2. Fluxes and Diffusion Potentials	112
3.2A. Flux and Mobility	113
3.2B. Diffusion Potential in a Solution	116
3.2C. Membrane Fluxes	119
3.2D. Membrane Diffusion Potential—Goldman Equation	122
3.2E. Application of Goldman Equation	125
3.2F. Donnan Potential	127
3.3. Characteristics of Crossing Membranes	129
3.3A. Electrogenicity	130
3.3B. Boltzmann Energy Distribution and $Q_{10}$ , a Temperature Coefficient	131
3.3C. Activation Energy and Arrhenius Plots	135
3.3D. Ussing–Teorell Equation	137
3.3E. Example of Active Transport	140

3.3F. Energy for Active Transport	142
3.3G. Speculation on Active Transport	143
3.4. Mechanisms for Crossing Membranes	144
3.4A. Carriers, Porters, Channels, and Pumps	145
3.4B. Michaelis–Menten Formalism	149
3.4C. Facilitated Diffusion	151
3.5. Principles of Irreversible Thermodynamics	153
3.5A. Fluxes, Forces, and Onsager Coefficients	154
3.5B. Water and Solute Flow	156
3.5C. Flux Densities, $L_p$ , and $\sigma$	158
3.5D. Values for Reflection Coefficients	161
3.6. Solute Movement Across Membranes	163
3.6A. Influence of Reflection Coefficients on Incipient Plasmolysis	165
3.6B. Extension of the Boyle–Van’t Hoff Relation	167
3.6C. Reflection Coefficients of Chloroplasts	169
3.6D. Solute Flux Density	169
3.7. Problems	170
3.8. References and Further Reading	173

## 4. Light 177

4.1. Wavelength and Energy	179
4.1A. Light Waves	179
4.1B. Energy of Light	182
4.1C. Illumination, Photon Flux Density, and Irradiance	185
4.1D. Sunlight	188
4.1E. Planck’s and Wien’s Formulae	190
4.2. Absorption of Light by Molecules	191
4.2A. Role of Electrons in Absorption Event	192
4.2B. Electron Spin and State Multiplicity	194
4.2C. Molecular Orbitals	195
4.2D. Photoisomerization	198
4.2E. Light Absorption by Chlorophyll	199
4.3. Deexcitation	201
4.3A. Fluorescence, Radiationless Transition, and Phosphorescence	202
4.3B. Competing Pathways for Deexcitation	203
4.3C. Lifetimes	206
4.3D. Quantum Yields	208
4.4. Absorption Spectra and Action Spectra	208
4.4A. Vibrational Sublevels	210
4.4B. The Franck–Condon Principle	211
4.4C. Absorption Bands, Absorption Coefficients, and Beer’s Law	214
4.4D. Application of Beer’s Law	216
4.4E. Conjugation	217
4.4F. Action Spectra	219
4.4G. Absorption and Action Spectra of Phytochrome	220

4.5. Problems	223
4.6. References and Further Reading	225

## **5. Photochemistry of Photosynthesis** **229**

5.1. Chlorophyll—Chemistry and Spectra	232
5.1A. Types and Structures	232
5.1B. Absorption and Fluorescence Emission Spectra	233
5.1C. Absorption in Vivo—Polarized Light	236
5.2. Other Photosynthetic Pigments	238
5.2A. Carotenoids	238
5.2B. Phycobilins	242
5.2C. General Comments	244
5.3. Excitation Transfers Among Photosynthetic Pigments	245
5.3A. Pigments and the Photochemical Reaction	246
5.3B. Resonance Transfer of Excitation	247
5.3C. Specific Transfers of Excitation	248
5.3D. Excitation Trapping	250
5.4. Groupings of Photosynthetic Pigments	253
5.4A. Photon Processing	253
5.4B. Excitation Processing	253
5.4C. Photosynthetic Action Spectra and Enhancement Effects	256
5.4D. Two Photosystems Plus Light-Harvesting Antennae	256
5.5. Electron Flow	260
5.5A. Electron Flow Model	260
5.5B. Components of the Electron Transfer Pathway	262
5.5C. Types of Electron Flow	268
5.5D. Assessing Photochemistry using Fluorescence	269
5.5E. Photophosphorylation	271
5.5F. Vectorial Aspects of Electron Flow	271
5.6. Problems	273
5.7. References and Further Reading	274

## **6. Bioenergetics** **277**

6.1. Gibbs Free Energy	278
6.1A. Chemical Reactions and Equilibrium Constants	280
6.1B. Interconversion of Chemical and Electrical Energy	283
6.1C. Redox Potentials	285
6.2. Biological Energy Currencies	286
6.2A. ATP—Structure and Reactions	287
6.2B. Gibbs Free Energy Change for ATP Formation	291
6.2C. NADP <sup>+</sup> –NADPH Redox Couple	293
6.3. Chloroplast Bioenergetics	295
6.3A. Redox Couples	295
6.3B. H <sup>+</sup> Chemical Potential Differences Caused by Electron Flow	299
6.3C. Evidence for Chemiosmotic Hypothesis	300
6.3D. Coupling of Flows	302

6.4.	Mitochondrial Bioenergetics	303
6.4A.	Electron Flow Components—Redox Potentials	304
6.4B.	Oxidative Phosphorylation	307
6.5.	Energy Flow in the Biosphere	310
6.5A.	Incident Light—Stefan–Boltzmann Law	311
6.5B.	Absorbed Light and Photosynthetic Efficiency	313
6.5C.	Food Chains and Material Cycles	314
6.6.	Problems	315
6.7.	References and Further Reading	317

## **7. Temperature and Energy Budgets**

7.1.	Energy Budget—Radiation	320
7.1A.	Solar Irradiation	322
7.1B.	Absorbed Infrared Irradiation	326
7.1C.	Emitted Infrared Radiation	327
7.1D.	Values for $a$ , $a_{IR}$ , and $e_{IR}$	328
7.1E.	Net Radiation	330
7.1F.	Examples for Radiation Terms	330
7.2.	Heat Conduction and Convection	333
7.2A.	Wind	334
7.2B.	Air Boundary Layers	336
7.2C.	Boundary Layers for Bluff Bodies	339
7.2D.	Heat Conduction/Convection Equations	340
7.2E.	Dimensionless Numbers	341
7.2F.	Examples of Heat Conduction/Convection	345
7.3.	Latent Heat—Transpiration	346
7.3A.	Heat Flux Density Accompanying Transpiration	346
7.3B.	Heat Flux Density for Dew or Frost Formation	347
7.3C.	Examples of Frost and Dew Formation	348
7.4.	Further Examples of Energy Budgets	350
7.4A.	Leaf Shape and Orientation	350
7.4B.	Shaded Leaves within Plant Communities	352
7.4C.	Heat Storage	352
7.4D.	Time Constants	354
7.5.	Soil	355
7.5A.	Thermal Properties	356
7.5B.	Soil Energy Balance	357
7.5C.	Variations in Soil Temperature	358
7.6.	Problems	360
7.7.	References and Further Reading	362

## **8. Leaves and Fluxes**

8.1.	Resistances and Conductances—Transpiration	366
8.1A.	Boundary Layer Adjacent to Leaf	368
8.1B.	Stomata	371
8.1C.	Stomatal Conductance and Resistance	373

8.1D. Cuticle	376
8.1E. Intercellular Air Spaces	376
8.1F. Fick's First Law and Conductances	377
8.2. Water Vapor Fluxes Accompanying Transpiration	380
8.2A. Conductance and Resistance Network	380
8.2B. Values of Conductances	383
8.2C. Effective Lengths and Resistance	384
8.2D. Water Vapor Concentrations, Mole Fractions and Partial Pressures for Leaves	385
8.2E. Examples of Water Vapor Levels in a Leaf	387
8.2F. Water Vapor Fluxes	389
8.2G. Control of Transpiration	390
8.3. CO <sub>2</sub> Conductances and Resistances	392
8.3A. Resistance and Conductance Network	392
8.3B. Mesophyll Area	394
8.3C. Resistance Formulation for Cell Components	397
8.3D. Partition Coefficient for CO <sub>2</sub>	398
8.3E. Cell Wall Resistance	399
8.3F. Plasma Membrane Resistance	400
8.3G. Cytosol Resistance	401
8.3H. Mesophyll Resistance	402
8.3I. Chloroplast Resistance	402
8.4. CO <sub>2</sub> Fluxes Accompanying Photosynthesis	403
8.4A. Photosynthesis	403
8.4B. Respiration and Photorespiration	406
8.4C. Comprehensive CO <sub>2</sub> Resistance Network	410
8.4D. Compensation Points	412
8.4E. Fluxes of CO <sub>2</sub>	416
8.4F. CO <sub>2</sub> Conductances	418
8.4G. Photosynthetic Rates	420
8.4H. Environmental Productivity Index	420
8.5. Water-Use Efficiency	422
8.5A. Values for WUE	423
8.5B. Elevational Effects on WUE	425
8.5C. Stomatal Control of WUE	426
8.5D. C <sub>3</sub> versus C <sub>4</sub> Plants	429
8.6. Problems	432
8.7. References and Further Reading	434

## 9. Plants and Fluxes 439

9.1. Gas Fluxes above Plant Canopy	440
9.1A. Wind Speed Profiles	441
9.1B. Flux Densities	442
9.1C. Eddy Diffusion Coefficients	443
9.1D. Resistance of Air above Canopy	445
9.1E. Transpiration and Photosynthesis	445
9.1F. Values for Fluxes and Concentrations	446
9.1G. Condensation	448
9.2. Gas Fluxes within Plant Communities	449
9.2A. Eddy Diffusion Coefficient and Resistance	449

9.2B. Water Vapor	451
9.2C. Attenuation of the Photosynthetic Photon Flux	453
9.2D. Values for Foliar Absorption Coefficient	454
9.2E. Light Compensation Point	455
9.2F. CO <sub>2</sub> Concentrations and Fluxes	456
9.2G. CO <sub>2</sub> at Night	458
9.3. Water Movement in Soil	459
9.3A. Soil Water Potential	460
9.3B. Darcy's Law	462
9.3C. Soil Hydraulic Conductivity Coefficient	463
9.3D. Fluxes for Cylindrical Symmetry	465
9.3E. Fluxes for Spherical Symmetry	467
9.4. Water Movement in the Xylem and the Phloem	469
9.4A. Root Tissues	469
9.4B. Xylem	470
9.4C. Poiseuille's Law	471
9.4D. Applications of Poiseuille's Law	472
9.4E. Phloem	476
9.4F. Phloem Contents and Speed of Movement	478
9.4G. Mechanism of Phloem Flow	479
9.4H. Values for Components of the Phloem Water Potential	480
9.5. Soil-Plant-Atmosphere Continuum	483
9.5A. Values for Water Potential Components	483
9.5B. Resistances and Areas	485
9.5C. Values for Resistances and Resistivities	487
9.5D. Root-Soil Air Gap and Hydraulic Conductances	490
9.5E. Capacitance and Time Constants	492
9.5F. Daily Changes	495
9.5G. Global Climate Change	497
9.6. Problems	500
9.7. References and Further Reading	503
<b>Solutions To Problems</b>	<b>507</b>
<b>Appendix I. Numerical Values of Constants and Coefficients</b>	<b>545</b>
<b>Appendix II. Conversion Factors and Definitions</b>	<b>553</b>
<b>Appendix III. Mathematical Relations</b>	<b>557</b>
III.A. Prefixes (for units of measure)	557
III.B. Areas and Volumes	557
III.C. Logarithms	557
III.D. Quadratic Equation	558
III.E. Trigonometric Functions	558
III.F. Differential Equations	558
<b>Appendix IV. Gibbs Free Energy and Chemical Potential</b>	<b>561</b>
IV.A. Entropy and Equilibrium	561
IV.B. Gibbs Free Energy	563
IV.C. Chemical Potential	565
IV.D. Pressure Dependence of $\mu_j$	565
IV.E. Concentration Dependence of $\mu_j$	568
<b>Index</b>	<b>571</b>