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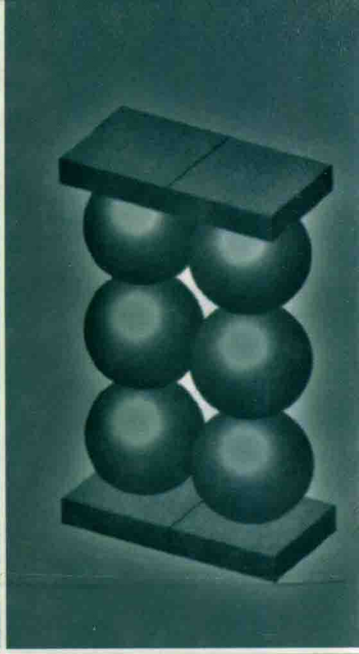
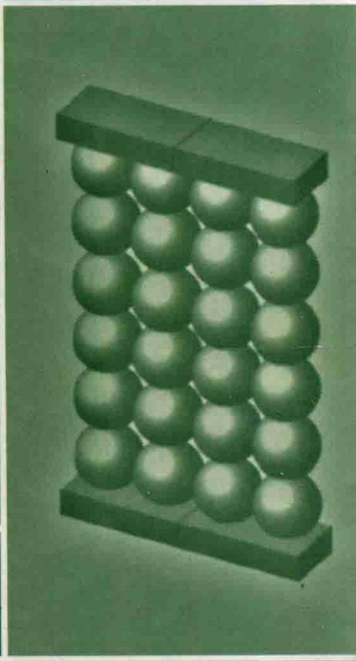


PHYSICOCHEMICAL AND ENVIRONMENTAL PLANT PHYSIOLOGY



PARK S. NOBEL

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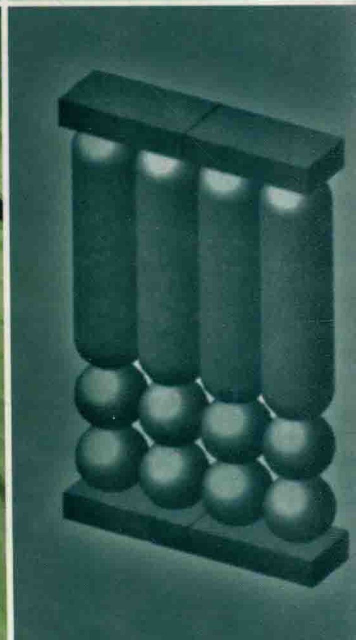

Physicochemical and Environmental
Plant Physiology

THIRD EDITION

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Preface

"Physiology," which is the study of the function of cells, organs, and organisms, derives from the Latin *physiologia*, which in turn comes from the Greek *physi-* or *physio-*, a prefix meaning natural, and *logos*, meaning reason or thought. Thus *physiology* suggests natural science and is now a branch of biology dealing with processes and activities that are characteristic of living things. "Physicochemical" relates to physical and chemical properties, and "Environmental" refers to topics such as solar irradiation and wind. "Plant" indicates the main focus of this book, but the approach, equations developed, and appendices apply equally well to animals and other organisms.

We will specifically consider water relations, solute transport, photosynthesis, transpiration, respiration, and environmental interactions. A physiologist endeavors to understand such topics in physical and chemical terms; accurate models can then be constructed and responses to the internal and the external environment can be predicted. Elementary chemistry, physics, and mathematics are used to develop concepts that are key to understanding biology—the intent is to provide a rigorous development, not a compendium of facts. References provide further details, although in some cases the enunciated principles carry the reader to the forefront of current research. Calculations are used to indicate the physiological consequences of the various equations, and problems at the end of chapters provide further such exercises. Solutions to all of the problems are provided, and the appendixes have a large list of values for constants and conversion factors at various temperatures.

Chapters 1 through 3 describe water relations and ion transport for plant cells. In Chapter 1, after discussing the concept of diffusion, we consider the physical barriers to diffusion imposed by cellular and organelle membranes. Another physical barrier associated with plant cells is the cell wall, which limits cell size. In the treatment of the movement of water through cells in response to specific forces presented in Chapter 2, we employ the thermodynamic argument of chemical potential gradients. Chapter 3 considers solute movement into and out of plant cells, leading to an explanation of electrical potential differences across membranes and establishing the formal criteria for distinguishing diffusion from active transport. Based on concepts from irreversible thermodynamics, an important parameter called the reflection coefficient is derived, which permits a precise evaluation of the influence of osmotic pressures on flow.

The next three chapters deal primarily with the interconversion of various forms of energy. In Chapter 4 we consider the properties of light and its absorption. After light is absorbed, its radiant energy usually is rapidly converted to heat. However, the arrangement of photosynthetic pigments and their special molecular structures allow some radiant energy from the sun to be converted by plants into chemical energy. In Chapter 5 we discuss the particular features of chlorophyll and the accessory pigments for photosynthesis that allow this energy conversion. Light energy absorbed by chloroplasts leads to the formation of ATP and NADPH. These compounds represent currencies for carrying chemical and electrical (redox potential) energy, respectively. How much energy they actually carry is discussed in Chapter 6.

In the last three chapters we consider the various forms in which energy and matter enter and leave a plant as it interacts with its environment. The physical quantities involved in an energy budget analysis are presented in Chapter 7 so that the relative importance of the various factors affecting the temperature of leaves or other plant parts can be quantitatively evaluated. The resistances (or their reciprocals, conductances) affecting the movement of both water vapor during transpiration and carbon dioxide during photosynthesis are discussed in detail for leaves in Chapter 8, paying particular attention to the individual parts of the pathway and to flux density equations. The movement of water from the soil through the plant to the atmosphere is discussed in Chapter 9. Because these and other topics depend on material introduced elsewhere in the book, the text is extensively cross-referenced.

This text is the third edition of *Physicochemical and Environmental Plant Physiology* (2nd ed., Academic Press, 1999; 1st ed., 1991), which evolved from *Biophysical Plant Physiology and Ecology* (Freeman, 1983), *Introduction to Biophysical Plant Physiology* (Freeman, 1974), and *Plant Cell Physiology: A Physicochemical Approach* (Freeman, 1970). The text has been updated based on the ever-increasing quality of plant research as well as comments of colleagues and especially students. The goal is to integrate the physical sciences, engineering, and mathematics to help understand biology, especially for plants.

Park S. Nobel
July 14, 2004

Symbols and Abbreviations

Where appropriate, typical units are indicated in parentheses.

Quantity	*Description*
a	absorptance or absorptivity (dimensionless)
a^{st}	mean area of stomata (m^2)
a_{IR}	absorptance or absorptivity in infrared region (dimensionless)
a_j	activity of species j (same as concentration)[a]
at	subscript indicating active transport
Å	angström (10^{-10} m)
A	electron acceptor
A	area (m^2)
A^j	area of component j (m^2)
A_λ	absorbance (also called "optical density") at wavelength λ (dimensionless)
ABA	abscisic acid
ADP	adenosine diphosphate
ATP	adenosine triphosphate
b	nonosmotic volume (m^3)
b	optical path length (m)
bl	superscript for boundary layer
c	centi (as a prefix), 10^{-2}
c	superscript for cuticle
c_d	drag coefficient (dimensionless)
c_j	concentration of species j (mol m^{-3})[b]
$\bar{c}_s$	a mean concentration of solute s
cal	calorie
chl	superscript for chloroplast
clm	superscript for chloroplast limiting membranes
cw	superscript for cell wall
cyt	superscript for cytosol
C	superscript for conduction
C	capacitance, electrical (F)
C^j	capacitance for water storage in component j (m^3 MPa^{-1})
C'	capacitance/unit area (F m^{-2})

Quantity	*Description*
Chl	chlorophyll
Cl	subscript for chloride ion
C_P	volumetric heat capacity (J m^{-3} $°C^{-1}$)
Cyt	cytochrome
d	deci (as a prefix), 10^{-1}
d	depth or distance (m)
d	diameter (m)
dyn	dyne
D	electron donor
D	dielectric constant (dimensionless)
D_j	diffusion coefficient of species j (m^2 s^{-1})
e	electron
e	superscript for water evaporation site
e_{IR}	emissivity or emittance in infrared region (dimensionless)
eV	electron volt
E	light energy (J)
E	kinetic energy (J)
E	electrical potential (mV)
E_j	redox potential of species j (mV)
E_j^{*H}	midpoint redox potential of species j referred to standard hydrogen electrode (mV)
E_M	electrical potential difference across a membrane (mV)
E_{Nj}	Nernst potential of species j (mV)
f	femto (as a prefix), 10^{-15}
F	farad
F	subscript for fluorescence
F	Faraday's constant (coulomb mol^{-1})
F	average cumulative leaf area/ground area (dimensionless)
FAD	flavin adenine dinucleotide (oxidized form)
$FADH_2$	reduced form of flavin adenine dinucleotide
FMN	flavin mononucleotide
g	gram
g_j	conductance of species j (mm s^{-1} with Δc_j and mmol m^{-2} s^{-1} with ΔN_j)
G	giga (as a prefix), 10^9
G	Gibbs free energy (J)
Gr	Grashof number (dimensionless)
G/n_j	Gibbs free energy/mole of some product or reactant j (J mol^{-1})
h	height (m)
h_c	heat convection coefficient (W m^{-2} $°C^{-1}$)
$h\nu$	a quantum of light energy
H	subscript for heat
i	superscript for inside
i	electrical current (ampere)
ias	superscript for intercellular air spaces
in	superscript for inward
in vitro	in a test tube, beaker, flask (literally, in glass)
in vivo	in a living organism (literally, in the living)

Quantity	*Description*
I	electrical current (ampere)
IR	infrared
j	subscript for species j
J	joule
J_j	flux density of species j (mol m^{-2} s^{-1})
J_j^{in}	inward flux density (influx) of species j (mol m^{-2} s^{-1})
J_j^{out}	outward flux density (efflux) of species j (mol m^{-2} s^{-1})
J_{V_j}	volume flux density species j (m^3 m^{-2} s^{-1}, i.e., m s^{-1})
J_V	total volume flux density (m s^{-1})
k	kilo (as a prefix), 10^3
k	foliar absorption coefficient (dimensionless)
k_j	first-order rate constant for the jth process (s^{-1})
K	temperature on Kelvin scale
K	subscript for potassium ion
K	equilibrium constant (concentration raised to some power)
K_h	hydraulic conductance per unit length (m^4 MPa^{-1} s^{-1})
K^j	thermal conductivity coefficient of region j (W m^{-1} °C^{-1})
K_j	partition coefficient of species j (dimensionless)
K_j	concentration for half-maximal uptake rate of species j (Michaelis constant) (mol m^{-3}, or M)
K_j	eddy diffusion coefficient of gaseous species j (m^2 s^{-1})
$K_{pH\ 7}$	equilibrium constant at pH 7
l	liter
l	superscript for lower
l	length (m), e.g., mean distance across leaf in wind direction
ln	natural or Napierian logarithm (to the base e, where e is 2.71828...)
log	common or Briggsian logarithm (to the base 10)
L^{soil}	soil hydraulic conductivity coefficient (m^2 Pa^{-1} s^{-1})
L_{jk}	Onsager or phenomenological coefficient (flux density per unit force)
L_P	hydraulic conductivity coefficient (in irreversible thermodynamics) (m Pa^{-1} s^{-1})
L_w	water conductivity coefficient (m Pa^{-1} s^{-1})
m	milli (as a prefix), 10^{-3}
m	meter
m	molal (mol per kg solvent)
m_j	mass per mole of species j (molar mass) (kg mol^{-1})
max	subscript for maximum
memb	superscript for membrane
mes	superscript for mesophyll
min	subscript for minimum
mol	mole, a mass equal to the molecular weight of the species in grams; contains Avogadro's number of molecules
M	mega (as a prefix), 10^6
M	molar (mol $liter^{-1}$)
M_j	amount of species j per unit area (mol m^{-2})
n	nano (as a prefix), 10^{-9}

Quantity	*Description*
n	number of stomata per unit area (m^{-2})
$n(E)$	number of moles with energy of E or greater
n_j	amount of species j (mol)
N	newton
Na	subscript for sodium ion
NAD^+	nicotinamide adenine dinucleotide (oxidized form)
NADH	reduced form of nicotinamide adenine dinucleotide
$NADP^+$	nicotinamide adnine dinucleotide phosphate (oxidized form)
NADPH	reduced form of nicotinamide dinucleotide phosphate
N_j	mole fraction of species j (dimensionless)
Nu	Nusselt number (dimensionless)
o	superscript for outside
0	subscript for initial value (at $t = 0$)
out	superscript for outside
p	pico (as a prefix), 10^{-12}
p	period (s)
pH	$-\log (a_{H^+})$
pm	superscript for plasma membrane
ps	superscript for photosynthesis
P	pigment
P	subscript for phosphorescence
P	hydrostatic pressure (MPa)
Pa	pascal
P_j	permeability coefficient of species j ($m\ s^{-1}$)
P_j	partial pressure of gaseous species j (kPa)
PPF	photosynthetic photon flux (400 to 700 nm)
PPFD	photosynthetic photon flux density (same as PPF)
q	number of electrons transferred per molecule (dimensionless)
Q	charge (coulomb)
Q_{10}	temperature coefficient (dimensionless)
r	radius (m)
r	reflectivity (dimensionless)
r + pr	superscript for respiration plus photorespiration
r_j	resistance for gaseous species j ($s\ m^{-1}$)
R	electrical resistance (ohm)
R	gas constant ($J\ mol^{-1}\ K^{-1}$)
R^j	resistance of component j across which water moves as a liquid ($MPa\ s\ m^{-3}$)
Re	Reynolds number (dimensionless)
RH	relative humidity (%)
s	subscript for solute
s	second
s_j	amount of species j (mol)
st	superscript for stoma(ta)
surf	superscript for surface
surr	superscript for surroundings
S	singlet
$S_{(\pi,\pi)}$	singlet ground state
$S_{(\pi,\pi^*)}$	singlet excited state in which a π electron has been promoted to a π^* orbital

Quantity	*Description*
S	magnitude of net spin (dimensionless)
S	total flux density of solar irradiation, i.e., global irradiation (W m^{-2})
t	time (s)
ta	superscript for turbulent air
T	superscript for transpiration
T	triplet
$T_{(\pi,\pi^*)}$	excited triplet state
T	temperature (K, °C)
u	superscript for upper
u_j	mobility of species j (velocity per unit force)
u_+	mobility of monovalent cation
u_-	mobility of monovalent anion
U	kinetic energy (J mol^{-1})
U_B	minimum kinetic energy to cross barrier (J mol^{-1})
UV	ultraviolet
υ	magnitude of velocity (m s^{-1})
υ	wind speed (m s^{-1})
υ^{wind}	wind speed (m s^{-1})
υ_j	magnitude of velocity of species j (m s^{-1})
υ_{CO_2}	rate of photosynthesis per unit volume (mol m^{-3} s^{-1})
vac	subscript for vaccum
V	volt
V	subscript for volume
V	volume (m^3)
$\bar{V}_j$	partial molal volume of species j (m^3 mol^{-1})
V_{max}	maximum rate of CO_2 fixation (mol m^{-3} s^{-1})
w	subscript for water
wv	subscript for water vapor
W	watt (J s^{-1})
x	distance (m)
z	altitude (m)
z_j	charge number of ionic species j (dimensionless)
α	contact angle (°)
γ_j	activity coefficient of species j (dimensionless, but see a_j)
$\gamma_\pm$	mean activity coefficient of cation–anion pair (dimensionless)
δ	delta, a small quantity of something, e.g., δ^- refers to a small fraction of an electronic charge
δ	distance (m)
δ^{bl}	thickness of air boundary layer (mm)
Δ	delta, the difference or change in the quantity that follows it
ε	volumetric elastic modulus (MPa)
ε_λ	absorption coefficient at wavelength λ (m^2 mol^{-1})
η	viscosity (N s m^{-2}, Pa s)
λ	wavelength of light (nm)
λ_{max}	wavelength position for the maximum absorption coefficient in an absorption band or for the maximum photon (or energy) emission in an emission spectrum
μ	micro (as a prefix), 10^{-6}
μ_j	chemical potential of species j (J mol^{-1})

Quantity	*Description*
ν	frequency of electromagnetic radiation (s^{-1}, hertz)
ν	kinematic viscosity (m^2 s^{-1})
π	ratio of circumference to diameter of a circle (3.14159...)
π	an electron orbital in a molecule or an electron in such an orbital
π^*	an excited or antibonding electron orbital in a molecule or an electron in such an orbital
Π	total osmotic pressure (MPa)
Π_j	osmotic pressure of species *j* (MPa)
Π_s	osmotic pressure due to solutes (MPa)
ρ	density (kg m^{-3})
ρ	resistivity, electrical (ohm m)
ρ^j	hydraulic resistivity of component *j* (MPa s m^{-2})
σ	surface tension (N m^{-1})
σ	reflection coefficient (dimensionless)
σ_j	reflection coefficient of species *j* (dimensionless)
σ_L	longitudinal stress (MPa)
σ_T	tangential stress (MPa)
τ	matric pressure (MPa)
τ	lifetime (s)
τ_j	lifetime for the *j*th deexcitation process (s)
ϕ_j	osmotic coefficient of species *j* (dimensionless)
Φ_i	quantum yield or efficiency for *i*th deexcitation pathway (dimensionless)
Ψ	water potential (MPa)
Ψ_Π	osmotic potential (MPa)
°C	degree Celsius
°	angular degree
*	superscript for a standard or reference state
*	superscript for a molecule in an excited electronic state
*	superscript for saturation of air with water vapor
∞	infinity

[a] The activity, a_j, is often considered to be dimensionless, in which case the activity coefficient, γ_j, has the units of reciprocal concentration ($a_j = \gamma_j c_j$; Eq. 2.5)

[b] We note that mol liter^{-1}, or molarity (M), is a concentration unit of widespread use, although it is not an SI unit.

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