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Physicochemical and Environmental Plant Physiology
(Fourth Edition)

植物生理学：物理化学与环境 (原著第四版)

Park S. Nobel



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(原著第四版)

Park S. Nobel

Department of Ecology and Evolutionary Biology

University of California, Los Angeles

Los Angeles, California

科学出版社

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导 读

Park S. Nobel 是美国加利福尼亚大学洛杉矶分校生态和进化生物学教授。Nobel 出生于 1938 年 11 月, 1965 年在加利福尼亚大学伯克利分校获博士学位, 此后曾在日本东京大学、英国伦敦大学从事博士后研究。1967 年, Nobel 博士在加利福尼亚大学洛杉矶分校担任分子生物学助理教授, 1971 年晋升为生物学副教授、1975 年晋升为教授。教授的主要课程有《生物学》、《物理化学生物学》、《植物生理生态》等。他担任过 *Plant Physiology*、*Plant Cell and Environment* 和 *Journal of Experimental Botany* 等刊物的编委或编辑。Nobel 教授的主要研究方向为植物生理生态学, 其研究成果甚丰, 在植物光合作用、水分生理、营养生理和环境生理等领域发表了 370 多篇学术论文、出版了 7 本著作, 包括《植物生理学: 物理化学与环境》。Nobel 教授至今仍在从事环境生理等方面的研究工作, 2008 年还有相关研究论文发表。

植物生理学是研究植物生命活动规律的科学, 这一学科有着悠久的历史, 其特点是重在对植物生长发育过程和代谢途径等的描述。而 Nobel 教授成功地把物理化学和数学的方法引入到植物生理学的研究中, 以描述和解释植物细胞、组织、器官和个体中的生理过程。概括起来, 这些过程主要集中在两个方面, 一是水、气和溶质的扩散过程, 二是各种形式能量的相互转换过程。Nobel 教授已经成为这一研究领域的开拓者之一, 在国际上有较高的学术声誉。《植物生理学: 物理化学与环境》一书继承了多本该领域专著的精华, 自 1991 年首次出版以来, 不断充实更新, 2009 年已经是第四版。

《植物生理学: 物理化学与环境》全书共九章。第一章是细胞和扩散。该章首先介绍了细胞结构和物质的扩散, 扩散是物质从高浓度向低浓度处移动的自发过程, 可以用扩散定律来描述。作者由此展开, 分别从介绍生物膜和细胞壁结构开始, 对跨生物膜和跨细胞壁的扩散作用进行了定量描述。该章的最后还定量分析了细胞壁胁迫-胁变关系, 并阐释了细胞壁的弹性在细胞伸长中的重要作用。第二章的内容是关于水分, 重点介绍了水的物理性质、化学势和植物细胞水势。化学势是判断一个物质能否自发运动的依据。根据化学势的概念, 作者详细分析了液泡和叶绿体中的水分关系、植物细胞中的水势变化、水分通量及细胞生长与水势的关系。第三章的内容是关于溶质, 作者首先分析了离子的化学势和扩散电位, 然后主要从能量角度上分析了离子跨膜运输的特性和机理。

第四章的主题是光, 分析了光波和能量的关系, 阐述了一般分子吸收光子后的变化, 包括电子自旋、分子轨道及异构化和激发态分子的去激发 (包括荧光、无辐射跃迁和磷光), 并且就吸收光谱与作用光谱进行分析。该章就叶绿素对光的吸收、光敏色素的吸收光谱与作用光谱也有阐述。第五章介绍了光合作用和光化学反应, 可以看作是第四章的延续与展开。该章内容包括叶绿素结构、吸收光谱和荧光, 其他光合色素的结构和吸收光谱, 光能吸收与光化学反应、激发能在色素分子间的传递, 光合色素的群体作用及电子传递与电子传递体等。第六章主要讨论了生物能。作者首先用吉布斯自由能来

衡量化学反应中的能量转移及化学能与电能的相互转换，然后分析了生物能的贮存形式——ATP 和 NADPH 的分子结构和能量变化。叶绿体和线粒体作为能量转换的两个重要细胞器，作者对其中发生的氧化还原反应、电子传递及偶联的磷酸化过程及能量转换等作了详细论述。

第七章内容是关于温度和能量平衡。植物叶片吸收的能量形式是太阳辐射和红外辐射，同时也以红外辐射的形式散失。叶片的能量还可以发生热传导和热对流，而叶片蒸腾作用也是叶片能量散失的重要形式，作者对这些过程都作了详细的论述。该章的最后，作者还讨论了土壤的热性质、能量平衡及温度变化。第八章内容是关于叶片的水、气流动。叶是植物进行光合作用和蒸腾作用的重要器官，与周围空气发生水、气（CO₂）交换。作者在分析叶表面的界面层、气孔结构的基础上，论述了气孔导度和水、气运动的阻力，并对蒸腾作用中的水分散失过程和光合作用中的 CO₂ 吸收过程作了详尽描述。该章的最后，作者讨论了植物的水分利用效率及影响因子。第九章是关于植物的水、气流动。内容包括植物冠层上的气体流动、植物群落内的气体流动、土壤中的水分运动、植物木质部和韧皮部中的水分运动等。该章还用较大篇幅讨论了土壤-植物-水连续体及水分运动的阻力。

与一般的植物生理学教材和著作不同之处是，该书使用了大量的物理化学概念和数学方程。因此，阅读该书需要有一定的物理化学相关基础知识，才能正确理解各种方程的意义。该书各章把所用到的主要方程列在章前，向读者提示这些方程的重要性。同时，在章后都附有思考题、参考文献和建议读者进一步阅读的文献。该书可以作为植物生理学科各领域教学和科研人员的参考书。

沈振国

2009 年 11 月 12 日

前 言

我们先从这本书的书名说起。“Physiology”（生理学）是研究细胞、器官和生物的功能的科学，来源于拉丁文 *physiologia*，后者来自希腊语的前缀 “*physi-*” 或 “*physis-*”（自然）和 “*logos*”（道理思想）。因此，生理学这个名字，从开始便意味着隶属于自然科学，现在则是专指生物学中研究生物特征——生命过程和活动的的一个分支。“Physicochemical”（物理化学）是有关物理和化学性质；“Environmental”（环境）是指日照和风等。尽管本书的主要内容集中在“植物”，但是所用方法、推导的公式和附录也同样适用于动物和其他生物。

本书重点讨论了植物的水分关系、溶质运输、光合作用、蒸腾作用、呼吸作用，以及与环境的相互作用。生理学者的研究任务旨在理解物理和化学方面的相关内容，从而构建出精确的模型、预测生物对内部和外部环境的反应。因此，应用基础化学、物理和数学可以发展一些概念，这些概念对我们研究生物学非常重要，其目的是提供一个严谨的发展过程而非简单的事实概要。虽然一些章节中阐述的原理已向读者呈现了植物生理学领域研究的前沿，但每章仍提供了扩展阅读的参考文献。书中使用各种计算用以表明各种方程的生理意义，并在每章后面提供了更进一步练习的题目。附录中有问题的答案，还包括各种温度下常数和转化因子数值的列表。

第 1~3 章讲述植物细胞水分关系和离子运输。第 1 章在讨论扩散的概念之后，我们分析了细胞膜和细胞器膜对扩散的物理屏障。另外一个物理屏障是限制植物细胞大小的细胞壁。第 2 章，在讨论水在特定力作用下进入细胞这一运动时，我们引入了热力学理论——化学势梯度。第 3 章描述溶质进出植物细胞的运动，引出跨膜电势梯度的概念以及区分扩散和主动运输的标准。基于不可逆热力学概念，我们导出了一个重要的参数——反射系数，可以精确评估渗透压对流动的影响。

接下来三章主要论述各种形式的能量互换。在第 4 章我们讨论了光的特性及其吸收。光被吸收后，其辐射能通常被快速转化为热。然而，光合色素的排列和它们特殊的分子结构使得一部分太阳的辐射能被植物转化成化学能。在第 5 章我们论述了叶绿素的特性和负责能量转化的其他光合色素。叶绿体吸收光能产生 ATP 和 NADPH。这些化合物分别传递化学能和电能（氧化还原势）。它们到底携带了多少能量？这个问题将在第 6 章论述。

最后三章，我们讨论了植物在与环境相互作用时物质和能量流入流出的各种形式。第 7 章提出了能量收支分析中的物理量，由此，我们就能定量评估影响叶片和植物其他部分温度的因子的相对重要性。第 8 章详细讨论了影响蒸腾作用中水蒸气运动和光合作用中二氧化碳运动的阻力（或者它们的互作物、导度）；其中，特别关注了路径中的个别部分以及通量密度公式。水分通过植物从土壤向大气的运动在第 9 章得到论述。该章与其他章节的内容相关，正文中有较多的交叉引用。

本书是《植物生理学：物理化学与环境》（Academic Press, 3rd ed., 2005; 2nd ed.,

1999; 1st ed., 1991) 的第四版, 第一版则是综合了以下几本书的内容发展而来, 包括: 《生物物理与植物生理学和生态学》(*Biophysical Plant Physiology and Ecology*, Freeman, 1983)、《生物物理的植物生理学导论》(*Introduction to Biophysical Plant Physiology*, Freeman, 1974) 和《植物细胞生理学: 物理化学的研究方法》(*Plant Cell Physiology: A Physicochemical Approach*, Freeman, 1970)。本书根据植物学研究的持续发展而不断更新, 并及时采纳同事和学生们的意见。目的是整合物理科学、工程学和数学以帮助加深对生物尤其是植物的理解。本书继承传统, 强调定量方法, 这也适应现在的研究形式、习惯及新的应用。

Park S. Nobel

2008. 10. 20

(高 璐 沈振国 译)

Preface

Let us begin with some comments on the title. “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 fourth edition of *Physicochemical and Environmental Plant Physiology* (Academic Press, 3rd ed., 2005; 2nd ed., 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 students. The goal is to integrate the physical sciences, engineering, and mathematics to help understand biology, especially for plants. *Physicochemical and Environmental Plant Physiology*, 4th ed., thus continues a tradition to emphasize a quantitative approach that is suitable for existing situations and habitats as well as new applications.

Park S. Nobel
October 20, 2008

Symbols and Abbreviations

Where appropriate, typical units are indicated in parentheses.

<i>Quantity</i>	<i>Description</i>
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
\AA	Angstrom (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

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- 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.

<i>Quantity</i>	<i>Description</i>
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 ($\text{m}^3 \text{MPa}^{-1}$)
C'	capacitance/unit area (F m^{-2})
Chl	chlorophyll
Cl	subscript for chloride ion
C_P	volumetric heat capacity ($\text{J m}^{-3} \text{ } ^\circ\text{C}^{-1}$)
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 ($\text{m}^2 \text{s}^{-1}$)
e	electron
e	superscript for water evaporation site
e	base of natural logarithm
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_{N_j}	Nernst potential of species j (mV)
f	femto (as a prefix), 10^{-15}
F	farad
F	subscript for fluorescence
F	Faraday's constant (C 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 $\text{mmol m}^{-2} \text{s}^{-1}$ with ΔN_j)

<i>Quantity</i>	<i>Description</i>
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 ($\text{W m}^{-2} \text{ } ^\circ\text{C}^{-1}$)
$h\nu$	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)
I	electrical current (ampere)
IR	infrared
j	subscript for species j
J	joule
J_i	flux density of species j ($\text{mol m}^{-2} \text{ s}^{-1}$)
J^{in}	inward flux density (influx) of species j ($\text{mol m}^{-2} \text{ s}^{-1}$)
J^{out}	outward flux density (efflux) of species j ($\text{mol m}^{-2} \text{ s}^{-1}$)
J_{V_j}	volume flux density of species j ($\text{m}^3 \text{ m}^{-2} \text{ s}^{-1}$, 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 j th 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 ($\text{m}^4 \text{ MPa}^{-1} \text{ s}^{-1}$)
K^j	thermal conductivity coefficient of region j ($\text{W m}^{-1} \text{ } ^\circ\text{C}^{-1}$)
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 ($\text{m}^2 \text{ s}^{-1}$)
$K_{\text{pH } 7}$	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)

<i>Quantity</i>	<i>Description</i>
L^{soil}	soil hydraulic conductivity coefficient ($\text{m}^2 \text{Pa}^{-1} \text{s}^{-1}$)
L_{jk}	Onsager or phenomenological coefficient (flux density per unit force)
L_P	hydraulic conductivity coefficient (in irreversible thermodynamics) ($\text{m Pa}^{-1} \text{s}^{-1}$)
L_w	water conductivity coefficient ($\text{m Pa}^{-1} \text{s}^{-1}$)
m	milli (as a prefix), 10^{-3}
m	meter
m	molal (mol/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}
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 adenine 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	$-\log(a_{\text{H}^+})$
pm	superscript for plasma membrane
ps	superscript for photosynthesis
P	pigment
P	subscript for phosphorescence
P	hydrostatic pressure (MPa)
Pa	pascal

<i>Quantity</i>	<i>Description</i>
P_j	permeability coefficient of species j (m s^{-1})
P_j	partial pressure of gaseous species j (kPa)
PPF	photosynthetic photon flux (400–700 nm)
PPFD	photosynthetic photon flux density (same as PPF)
q	number of electrons transferred per molecule (dimensionless)
Q	charge (C)
Q_{10}	temperature coefficient (dimensionless)
r	radius (m)
r	reflectivity (dimensionless)
$r + \text{pr}$	superscript for respiration plus photorespiration
r_j	resistance for gaseous species j (s m^{-1})
R	electrical resistance (Ω)
R	gas constant ($\text{J mol}^{-1} \text{K}^{-1}$)
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
S	magnitude of net spin (dimensionless)
S	total flux density of solar irradiation, i.e., global irradiation (W m^{-2})
t	time (s)
t^{cw}	cell wall thickness (m)
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})

<i>Quantity</i>	<i>Description</i>
U_B	minimum kinetic energy to cross barrier (J mol^{-1})
UV	ultraviolet
v	magnitude of velocity (m s^{-1})
v	wind speed (m s^{-1})
v^{wind}	wind speed (m s^{-1})
v_j	magnitude of velocity of species j (m s^{-1})
v_{CO_2}	rate of photosynthesis per unit volume ($\text{mol m}^{-3} \text{s}^{-1}$)
vac	subscript for vacuum
V	volt
V	subscript for volume
V	volume (m^3)
\bar{V}_j	partial molal volume of species j ($\text{m}^3 \text{mol}^{-1}$)
V_{max}	maximum rate of CO_2 fixation ($\text{mol m}^{-3} \text{s}^{-1}$)
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 ($^\circ$)
γ_j	activity coefficient of species j (dimensionless, but see a_j)
γ_{\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 ($\text{m}^2 \text{mol}^{-1}$)
ϵ_0	permittivity of a vacuum
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})
ν	frequency of electromagnetic radiation (s^{-1} , hertz)
ν	kinematic viscosity ($\text{m}^2 \text{s}^{-1}$)
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

<i>Quantity</i>	<i>Description</i>
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 ($\Omega \text{ m}$)
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)
$^\circ\text{C}$	degree Celsius
$^\circ$	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

目 录

前言	xiii
符号与缩略词	xv
1. 细胞与扩散	3
1.1. 细胞结构	3
1.1A. 一般植物细胞	3
1.1B. 叶解剖	5
1.1C. 维管组织	7
1.1D. 根解剖	9
1.2. 扩散	11
1.2A. Fick 第一定律	12
1.2B. 连续方程与 Fick 第二定律	14
1.2C. 扩散的时间-距离关系	16
1.2D. 空气扩散	19
1.3. 膜结构	21
1.3A. 膜模型	21
1.3B. 细胞器膜	23
1.4. 膜渗透	25
1.4A. 跨膜浓度差	26
1.4B. 渗透系数	28
1.4C. 扩散和细胞内浓度	29
1.5. 细胞壁	31
1.5A. 化学与形态学	33
1.5B. 跨细胞壁扩散	34
1.5C. 细胞壁胁迫-胁变关系	37
1.5D. 弹性模数、黏弹性	39
1.6. 问题	40
1.7. 参考文献和扩展阅读	42
2. 水	45
2.1. 物理特性	46
2.1A. 氢键-热力学关系	47
2.1B. 表面张力	49
2.1C. 毛细管上升	50