

Plant Physiological Ecology

Second Edition

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 Springer

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Foreword to Second Edition

In the decade that has passed since the first edition of this book, the global environment has changed rapidly. Even the most steadfast “deny-ers” have come to accept that atmospheric CO₂ enrichment and global warming pose serious challenges to life on Earth. Regrettably, this acceptance has been forced by calamitous events rather than by the long-standing, sober warnings of the scientific community.

There seems to be growing belief that “technology” will save us from the worst consequences of a warmer planet and its wayward weather. This hope, that may in the end prove to be no more than wishful thinking, relates principally to the built environment and human affairs. Alternative sources of energy, utilized with greater efficiency, are at the heart of such hopes; even alternative ways of producing food or obtaining water may be possible. For plants, however, there is no alternative but to utilize sunlight and fix carbon and to draw water from the soil. (Under a given range of environmental conditions, these processes are already remarkably efficient by industrial standards.) Can we “technologize” our way out of the problems that plants may encounter in capricious, stormier, hotter, drier, or more saline environments? Climate change will not alter the basic nature of the stresses that plants must endure, but it will result in their occurrence in places where formerly their impact was small, thus exposing species and vegetation types to more intense episodes of stress than they are able to handle. The timescale on which the climate is changing is too fast to wait for evolution to come up with solutions to the problems.

For a variety of reasons, the prospects for managing change seem better in agriculture than in forests or in wild plant communities. It is possible to intervene dramatically in the normal process of evolutionary change by genetic manipulation. Extensive screening of random mutations in a target species such as *Arabidopsis thaliana* can reveal genes that allow plants to survive rather simplified stress tests. This is but the first of many steps, but eventually these will have their impact, primarily on agricultural and industrial crops. There is a huge research effort in this area and much optimism about what can be achieved. Much of it is done with little reference to plant physiology or biochemistry and has a curiously empirical character. One can sense that there is impatience with plant physiology that has been too slow in defining stress tolerance, and a belief that if a gene can be found that confers tolerance, and it can be transferred to a species of interest, it is not of prime

importance to know exactly what it does to the workings of the plant. Such a strategy is more directed toward outcomes than understanding, even though the technology involved is sophisticated. Is there a place for physiological ecology in the new order of things? The answer is perhaps a philosophical one. Progress over the centuries has depended on the gradual evolution of our understanding of fundamental truths about the universe and our world. Scientific discovery has always relished its serendipitous side but had we been satisfied simply with the outcomes of trial and error we would not be where we are today.

It is legitimate to ask what factors set the limits on stress tolerance of a given species. To answer this one must know first how the plant “works”; in general, most of this knowledge is to hand but is based on a relatively few model species that are usually chosen because of the ease with which they can be handled in laboratory conditions or because they are economically important. As well as describing the basic physiology of plants the authors of this book set out to answer more difficult questions about the differences between species with respect to environmental variables. The authors would be the first to admit that comprehensive studies of comparative physiology and biochemistry are relatively few. Only in a few instances do we really understand how a species, or in agriculture, a genotype, pulls off the trick of surviving or flourishing in conditions where other plants fail.

Of course, the above has more than half an eye on feeding the increasing world population in the difficult times that lie ahead. This has to be every thinking person’s concern. There is, however, more to it than that. Large ecosystems interact with climate, the one affecting the other. It would be as rash, for example, to ignore the effects of climate change on forests as it would be to ignore its effects on crops.

There is more to the successful exploitation of a given environment than can be explained exclusively in terms of a plant’s physiology. An important thrust in this book is the interaction, often crucial, between plants and beneficial, pathogenic or predatory organisms that share that environment. Manipulation of these interactions is the perennial concern of agriculture either directly or unintentionally. Changes in temperature and seasonality alter established relations between organisms, sometimes catastrophically when, for example, a pathogen or predator expands its area of influence into plant and animal populations that have not been exposed to it previously. Understanding such interactions may not necessarily allow us to avoid the worst consequences of change but it may increase our preparedness and our chances of coming up with mitigating strategies.

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Foreword to First Edition

The individual is engaged in a struggle for existence (Darwin). That struggle may be of two kinds: The acquisition of the resources needed for establishment and growth from a sometimes hostile and meager environment and the struggle with competing neighbors of the same or different species. In some ways, we can define *physiology* and *ecology* in terms of these two kinds of struggles. Plant ecology, or plant sociology, is centered on the relationships and interactions of species within communities and the way in which populations of a species are adapted to a characteristic range of environments. Plant physiology is mostly concerned with the individual and its struggle with its environment. At the outset of this book, the authors give their definition of *ecophysiology*, arriving at the conclusion that it is a point of view about physiology. A point of view that is informed, perhaps, by knowledge of the real world outside the laboratory window. A world in which, shall we say, the light intensity is much greater than the 200–500 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$ used in too many environment chambers, and one in which a constant 20°C day and night is a great rarity. The standard conditions used in the laboratory are usually regarded as treatments. Of course, there is nothing wrong with this in principle; one always needs a baseline when making comparisons. The idea, however, that the laboratory control is the norm is false and can lead to misunderstanding and poor predictions of behavior.

The environment from which many plants must acquire resources is undergoing change and degradation, largely as a result of human activities and the relentless increase in population. This has thrown the spotlight onto the way in which these changes may feed back on human well-being. Politicians and the general public ask searching questions of biologists, agriculturalists, and foresters concerning the future of our food supplies, building materials, and recreational amenities. The questions take on the general form, “Can you predict how ‘X’ will change when environmental variables ‘Y’ and ‘Z’ change?” The recent experience of experimentation, done at high public expense, on CO₂ enrichment and global warming, is a sobering reminder that not enough is known about the underlying physiology and biochemistry of plant growth and metabolism to make the confident predictions that the customers want to hear. Even at the level of individual plants, there seems to be no clear prediction, beyond that the response depends on species and other ill-defined circumstances. On the broader scale, predictions about the response of

plant communities are even harder to make. In the public mind, at least, this is a failure. The only way forward is to increase our understanding of plant metabolism, of the mechanisms of resource capture, and the way in which the captured resources are allocated to growth or storage in the plant. To this extent, I can see no distinction between plant physiology and ecophysiology. There are large numbers of missing pieces of information about plant physiology—period. The approach of the new millennium, then, is a good time to recognize the need to study plant physiology anew, bringing to bear the impressive new tools made available by gene cloning and recombinant DNA technology. This book is to be welcomed if it will encourage ecologists to come to grips with the processes which determine the behavior of “X” and encourage biochemistry and physiology students to take a more realistic view of the environmental variables “Y” and “Z”.

The book starts, appropriately, with the capture of carbon from the atmosphere. Photosynthesis is obviously the basis of life on earth, and some of the most brilliant plant scientists have made it their life’s work. As a result, we know more about the molecular biophysics and biochemistry of photosynthesis than we do about any other plant process. The influence of virtually every environmental variable on the physiology of photosynthesis and its regulation has been studied. Photosynthesis, however, occurs in an environment over which the individual plant has little control. In broad terms, a plant must cope with the range of temperature, rainfall, light intensity, and CO₂ concentration to which its habitat is subjected. It cannot change these things. It must rely on its flexible physiological response to mitigate the effects of the environment. At a later stage in the book, the focus shifts below ground, where the plant has rather more control over its options for capturing resources. It may alter the environment around its roots in order to improve the nutrient supply. It may benefit from microbial assistance in mobilizing resources or enter into more formal contracts with soil fungi and nodule-forming bacteria to acquire nutrient resources that would otherwise be unavailable or beyond its reach. Toward its close, the book turns to such interactions between plants and microbes and to the chemical strategies that have evolved in plants that assist them in their struggles with one another and against browsing and grazing animals. The authors end, then, on a firmly ecological note, and introduce phenomena that most laboratory physiologists have never attempted to explore. These intriguing matters remind us, as if reminders were needed, of “how little we know, how much to discover” (Springer and Leigh).

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HANS LAMBERS
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Abbreviations

<i>a</i>	radius of a root (a_r) or root plus root hairs (a_e)
<i>A</i>	rate of CO ₂ assimilation; also total root surface
A_n	net rate of CO ₂ assimilation
A_f	foliage area
A_{max}	light-saturated rate of net CO ₂ assimilation at ambient C_a
A_s	sapwood area
ABA	abscisic acid
ADP	adenosine diphosphate
AM	arbuscular mycorrhiza
AMP	adenosine monophosphate
APAR	absorbed photosynthetically active radiation
ATP	adenosine triphosphate
<i>b</i>	individual plant biomass; buffer power of the soil
<i>B</i>	stand biomass
c_s	concentration of the solute
<i>C</i>	nutrient concentration in solution; also convective heat transfer
C_3	photosynthetic pathway in which the first product of CO ₂ fixation is a 3-carbon intermediate
C_4	photosynthetic pathway in which the first product of CO ₂ fixation is a 4-carbon intermediate
C_a	Atmospheric CO ₂ concentration
C_c	CO ₂ concentration in the chloroplast
C_i	Intercellular CO ₂ concentration
C_{li}	initial nutrient concentration
C_{min}	solution concentration at which uptake is zero
C:N	carbon:nitrogen ratio
CAM	crassulacean acid metabolism
CC	carbon concentration
CE	carbohydrate equivalent
chl	chlorophyll
CPF	carbon dioxide production value
<i>d</i>	plant density; also leaf dimension
<i>D</i>	diffusivity of soil water
D_e	diffusion coefficient of ion in soil
DHAP	dihydroxyacetone phosphate
DM	dry mass

DNA	deoxyribonucleic acid
e	water vapor pressure in the leaf (e_i ; or e_l in Sect. 2.5 of the Chapter 4A) or atmosphere (e_a); also emissivity of a surface
E	transpiration rate
f	tortuosity
F	rate of nutrient supply to the root surface; also chlorophyll fluorescence, minimal fluorescence (F_0), maximum (F_m), in a pulse of saturating light (F_m'), variable (F_v)
FAD(H ₂)	flavine adenine dinucleotide (reduced form)
FM	fresh mass
FR	far-red
g	diffusive conductance for CO ₂ (g_c) and water vapor (g_w); boundary layer conductance (g_a); mesophyll conductance (g_m); stomatal conductance (g_s); boundary layer conductance for heat transport (g_{ah})
GA	gibberellic acid
GE	glucose equivalent
GOGAT	glutamine 2-oxoglutarate aminotransferase
HCH	hydroxycyclohexenone
HIR	high-irradiance response
I	irradiance, above (I_o) or beneath (I) a canopy; irradiance absorbed; also nutrient inflow
I_{max}	maximum rate of nutrient inflow
IAA	indoleacetic acid
IR _s	short-wave infrared radiation
J	rate of photosynthetic electron flow
J_{max}	maximum rate of photosynthetic electron flow measured at saturating I and C_a
J_v	water flow
k	rate of root elongation; extinction coefficient for light
K	carrying capacity (e.g., K species)
k_{cat}	catalytic constant of an enzyme
K_i	inhibitor concentration giving half-maximum inhibition
K_m	substrate concentration at half V_{max} (or I_{max})
l	leaf area index
L	rooting density; also latent heat of evaporation; also length of xylem element
L_p	root hydraulic conductance
LAI	leaf area index
LAR	leaf area ratio
LFR	low-fluence response
LHC	light-harvesting complex
LMA	leaf mass per unit area
LMR	leaf mass ratio
LR	long-wave infrared radiation that is incident (LR _{in}), reflected (LR _r), emitted (LR _{em}), absorbed (SR _{abs}), or net incoming (LR _{net}); also leaf respiration on an area (LR _a) and mass (LR _m) basis
mRNA	messenger ribonucleic acid
miRNA	micro ribonucleic acid
M	energy dissipated by metabolic processes
ME	malic enzyme
MRT	mean residence time
N_w	mol fraction, that is, the number of moles of water divided by the total number of moles
NAD(P)	nicotinamide adenine dinucleotide(phosphate) (in its oxidized form)
NAD(P)H	nicotinamide adenine dinucleotide(phosphate) (in its reduced form)
NAR	net assimilation rate
NDVI	normalized difference vegetation index
NEP	net ecosystem production
NIR	near-infrared reflectance; net rate of ion uptake
NMR	nuclear magnetic resonance
NPP	net primary production
NPQ	nonphotochemical quenching
NUE	nitrogen-use efficiency, or nutrient-use efficiency

p	vapor pressure
p_o	vapor pressure of air above pure water
P	atmospheric pressure; also turgor pressure
P_{fr}	far-red-absorbing configuration of phytochrome
P_i	inorganic phosphate
P_r	red-absorbing configuration of phytochrome
PAR	photosynthetically active radiation
PC	phytochelatins
PEP	phospho <i>enol</i> pyruvate
PEPC	phospho <i>enol</i> pyruvate carboxylase
PEPCK	phospho <i>enol</i> pyruvate carboxykinase
pH	hydrogen ion activity; negative logarithm of the H^+ concentration
PGA	phosphoglycerate
pmf	proton-motive force
PNC	plant nitrogen concentration
PNUE	photosynthetic nitrogen-use efficiency
PQ	photosynthetic quotient; also plastoquinone
PR	pathogenesis-related protein
PS	photosystem
PV'	amount of product produced per gram of substrate
q_N	quenching of chlorophyll fluorescence due to non-photochemical processes
qP	photochemical quenching of chlorophyll fluorescence
Q	ubiquinone (in mitochondria), in reduced state (Q_r = ubiquinol) or total quantity (Q_t); also quinone (in chloroplast)
Q_{10}	temperature coefficient
Q_A	primary electron acceptor in photosynthesis
r	diffusive resistance, for CO_2 (r_c), for water vapor (r_w), boundary layer resistance (r_a), stomatal resistance (r_s), mesophyll resistance (r_m); also radial distance from the root axis; also respiration; also growth rate (in volume) in the Lockhart equation; also proportional root elongation; also intrinsic rate of population increase (e.g., r species)
r_i	spacing between roots
r_o	root diameter
R	red
R	radius of a xylem element; also universal gas constant
R_a	molar abundance ratio of $^{13}C/^{12}C$ in the atmosphere
R_d	dark respiration
R_{day}	dark respiration during photosynthesis
R_e	ecosystem respiration
R_p	whole-plant respiration; also molar abundance ratio of $^{13}C/^{12}C$ in plants
R_h	heterotrophic respiration
R^*	minimal resource level utilised by a species
RGR	relative growth rate
RH	relative humidity of the air
RMR	root mass ratio
RNA	ribonucleic acid
RQ	respiratory quotient
RR	rate of root respiration
RuBP	ribulose-1,5-bisphosphate
Rubisco	ribulose-1,5-bisphosphate carboxylase/oxygenase
RWC	relative water content
S	nutrient uptake by roots
$S_{c/o}$	specificity of carboxylation relative to oxygenation by Rubisco
SHAM	salicylhydroxamic acid
SLA	specific leaf area
SMR	stem mass ratio
SR	short-wave solar radiation that is incident (SR_{in}), reflected (SR_r), transmitted (SR_{tr}), absorbed (SR_{abs}), used in photosynthesis (SR_A), emitted in fluorescence (SR_{FL}), or net incoming (SR_{net}); also rate of stem respiration
SRL	specific root length

t^*	time constant
tRNA	transfer ribonucleic acid
T	temperature
T_L	leaf temperature
TCA	tricarboxylic acid
TR	total radiation that is absorbed (TR_{abs}) or net incoming (TR_{net})
u	wind speed
UV	ultraviolet
V	volume
V_c	rate of carboxylation
V_o	rate of oxygenation
V_{cmax}	maximum rate of carboxylation
V_w^o	molar volume of water
VIS	visible reflectance
VLFR	very low fluence response
V_{max}	substrate-saturated enzyme activity
VPD	vapor pressure deficit
w	mole fraction of water vapor in the leaf (w_i) or atmosphere (w_a)
WUE	water-use efficiency
Y	yield threshold (in the Lockhart equation)
γ	surface tension
Γ	CO ₂ -compensation point
Γ^*	CO ₂ -compensation point in the absence of dark respiration
δ	boundary layer thickness; also isotopic content
Δ	isotopic discrimination
ΔT	temperature difference
ϵ	elastic modulus; also emissivity
η	viscosity constant
θ	curvature of the irradiance response curve; also volumetric moisture content (mean value, θ' , or at the root surface, θ_a)
λ	energy required for transpiration
μ_w	chemical potential of water
μ_{w0}	chemical potential of pure water under standard conditions
σ	Stefan–Boltzman constant
ϕ	quantum yield (of photosynthesis); also yield coefficient (in the Lockhart equation); also leakage of CO ₂ from the bundle sheath to the mesophyll; also relative yield of de-excitation processes
Ψ	water potential
Ψ_{air}	water potential of the air
Ψ_m	matric potential
Ψ_p	pressure potential; hydrostatic pressure
Ψ_π	osmotic potential

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