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Physiological Plant Ecology

Second, Totally Revised Edition

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Translated by
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With 193 Figures

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Preface to the Second Edition

Since the first edition of this book appeared the field of plant physiology and ecology has advanced so far as to call for a complete revision of the material. To the extent that they could be accommodated in an introductory text, the requests and critical comments of users and reviewers of the original edition have been taken into account. The chapters have been rearranged; a survey of the effects of the physical environmental factors radiation and heat, and the plants' responses to them, is given in Chapter 2, whereas the chemical factors are treated in the chapters on metabolism and the turnover of matter. The ecophysiology of tropical plants and of plants growing in arid regions has been more strongly emphasized. The environmental influences affecting growth and development are mentioned occasionally, but are not discussed in such detail as those affecting metabolism, for as a rule the former are treated extensively in textbooks of plant physiology. References to ecosystems have been omitted to permit a sharper focus upon physiological relationships. I hope that the book will continue to be useful in this new form. It is not intended as – nor could it be – a comprehensive textbook of plant ecology; it is one of many possible ways of presenting what is known in the field.

Many readers of the first edition have asked for expansion of the reference list. The data and interpretations on which the text and many tables are based were drawn from thousands of original publications, so that it is impossible to document each item of information with the appropriate citation. To provide the reader with better access to the literature and a greater opportunity to advance from the general to the concrete, most of the tables and figures are accompanied by additional references to reviews as well as papers on special topics. The list has thus grown to comprise almost 800 references. Nevertheless, many publications of proved value could not be included; I beg the understanding of the authors.

While revising the text I have received the generous cooperation of many colleagues in providing advice and documentation. Dr. M. A. Biederman-Thorson again conscientiously translated the new sections, and Mr. R. Gapp prepared most of the new

illustrations. Dr. K. F. Springer and his coworkers responded to my wishes with helpful understanding. To all of them I extend my sincere thanks.

Innsbruck, April 1980 W. LARCHER

Preface to the First Edition

Ecology is the science of the relationship between living organisms and their environment. It is concerned with the web of interactions involved in the circulation of matter and the flow of energy that makes possible life on earth, and with the adaptations of organism to the conditions under which they survice. Given the multitude of diverse organisms, the plant ecologist focuses upon the plants, investigating the influence of environmental factors on the character of the vegetation and the behavior of the individual plant species.

Plant ecophysiology, a discipline within plant ecology, is concerned fundamentally with the physiology of plants as it is modified by fluctuating external influences. The aim of this book is to convey the conceptual framework upon which this discipline is based, to offer insights into the basic mechanisms and interactions within the system "plant and environment", and to present examples of current problems in this rapidly developing area. Among the topics discussed are the vital processes of plants, their metabolism and energy transformations as they are affected by environmental factors, and the ability of these organisms to adapt to such factors. It is assumed that the reader has a background in the fundamentals of plant physiology; the physiological bases of the phenomena of interest will be mentioned only to the extent necessary for an understanding of the ecological relationships.

Ecology is very much a modern field, but by no means a recent innovation. I have tried to portray this rich historical background in the choice of illustrations and tabular material; the results presented reflect the broadness of vision, the struggles and the successes of the pioneering experimental ecologists in the first half of this century, as well as the advances in knowledge made most recently. Moreover, the student of ecology must bear in mind the particular characteristics of different localities; I have tried to include a broad selection of examples illustrating the ecophysiological behavior of plants in the greatest possible variety of habitats.

My first thanks are due to Dr. K. F. Springer; his publication of this English edition has made the textbook accessible to a wider circle of readers. I am grateful to the publisher of the original German edition, Roland Ulmer, for his cooperation. In particular, I thank Dr. Marguerite Biederman-Thorson for her thoughtful and sympathetic translation into English of the German text.

Above all, however, I should like to express my thanks to the pioneers of experimental ecology – Arthur Pisek, Otto Stocker, Heinrich Walter, and the late Bruno Huber. They inspired my enthusiasm for this difficult, but so attractive, field, and allowed me to benefit from their experience.

Innsbruck, September 1975 W. LARCHER

Abbreviations, Symbols and Conversion Factors

A	Area
Acc	Acceptor molecule
ADP	Adenosine diphosphate
ATP	Adenosine triphosphate
B	Plant biomass (also called phytomass, the mass of a stand of plants)
ΔB	Change in biomass (positive for a growing stand)
bar	Unit of pressure (1 bar = 10^5 Pascal)
°C	Degree Celsius; relative measure of temperature
C	Concentration
C_a	Concentration of CO_2 and H_2O in the air outside a leaf
C_i	Concentration of CO_2 and H_2O in the intercellular system of a leaf
cal	Calorie, a unit of energy (1 cal = 4.1868 joule = $4.1868 \cdot 10^7$ erg)
CAM	Crassulacean acid metabolism
Chl	Chlorophyll
D	Molecular diffusion coefficient ($m^2 \cdot s^{-1}$)
d	Day as a unit of time
d	Diameter
DL_{50}	Drought lethality (degree of dryness causing 50% injury)
DM	Dry matter
dm^2	Unit of area; for leaves, it refers to one (projected) surface
dm_2^2	Unit of leaf area referring to the entire surface (upper and lower)
dyn	Measure of force (1 dyn = 10^{-5} N)
E	Amount of water transpired
E	Einstein; amount of light quanta (1 E = 1 mol photons)
E_p	Evaporative power of the air; potential evaporation
erg	Unit of energy or work (1 erg ≙ 1 dyn · cm)
F	Photosynthesis
F_g	Rate of gross photosynthesis (true photosynthesis)
F_n	Rate of net photosynthesis (apparent photosynthesis)
g	Gram; unit of mass
G	Grazing (loss of dry matter to consumers)
GAP	Glyceraldehyde-3-phosphate
h	Hour
ha	Hectare (1 ha = 10^4 m^2)
h	Planck's constant ($6.625 \cdot 10^{-34}$ J · s)
I	Irradiance; the radiation flux at a given level within a stand of plants or body of water
I_0	Maximum radiation flux; that incident upon a stand of plants or body of water
I_a	Long-wavelength radiation from the atmosphere

I_{abs}	Absorbed radiation
I_K	Compensation light intensity (at which $F = R$)
$\bar{I}_l$	Long-wavelength radiation balance
$\bar{I}_s$	Short-wavelength radiation balance
I_S	Light intensity at which photosynthesis is saturated
IAA	Auxin, indole acetic acid
IR	Infrared radiation (> 750 nm)
J	Joule; unit of energy ($1\ \mathrm{J} = 1\ \mathrm{N} \cdot \mathrm{m}$)
J	Flux, mass flow
K	Kelvin; unit of temperature
k	Coefficient, conversion factor
k_F	Photosynthetic efficiency coefficient
k_M	Recycling factor for mineral nutrients in a stand of plants
k_{PP}	Productivity coefficient
k_T	Reaction rate of biochemical processes at a given temperature
kcal	Kilocalorie ($1\ \mathrm{kcal} = 10^3\ \mathrm{cal}$)
kg	Kilogram; unit of mass
kJ	Kilojoule ($1\ \mathrm{kJ} = 10^3$ joule)
kLx	Kilolux ($1\ \mathrm{kLx} = 10^3$ lux)
kW	Kilowatt ($1\ \mathrm{kW} = 10^3$ watt)
l	Liter; unit of volume
L	Loss of organic dry matter as detritus
L_E	Water loss via evapotranspiration
L_I	Water loss via interception
L_O	Water loss via runoff and percolation
l	Wavelength (radiation)
λ	Latent heat of vaporization of water
LAI	Leaf-area index
LAR	Leaf area ratio
lx	Lux; photometric unit of light intensity
m	Meter; unit of length
M	Molar; measure for concentration
M_{abs}	Quantity of minerals absorbed
M_B	Mineral content of a stand of plants
M_G	Loss of minerals via grazing
M_i	Quantity of minerals incorporated
M_L	Loss of minerals as detritus
M_r	Minerals lost in inorganic form ("recretion")
mg	Milligram ($1\ \mathrm{mg} = 10^{-3}\ \mathrm{g}$)
min	Minute
ml	Milliliter ($1\ \mathrm{ml} = 10^{-3}\ \mathrm{l} = 1\ \mathrm{cm}^3$)
mm	Millimeter; measure of length ($1\ \mathrm{mm} = 10^{-3}\ \mathrm{m}$) and measure of precipitation (1 mm precipitation = 1 liter water $\cdot\ \mathrm{m}^{-2}$ of ground)
mol	Mole; measure of amount
μm	Micrometer ($1\ \mu\mathrm{m} = 10^{-6}\ \mathrm{m}$)
n	Number of particles
N	Newton; unit of force ($1\ \mathrm{N} = 1\ \mathrm{kg} \cdot \mathrm{m} \cdot \mathrm{s}^{-2}$)
NAD^+	Nicotinamide-adenine-dinucleotide, reduced form: $NADH + H^+$ (simplified notation $NADH_2$); reduction system
$NADP^+$	Nicotinamide-adenine-dinucleotide-phosphate, reduced form: $NADPH + H^+$ ($NADPH_2$); reduction system

NAR	Net assimilation rate (= unit leaf rate)
nm	Nanometer (1 nm = 10^{-9} m)
OAA	Oxalacetate
ω	Water use efficiency
P	Turgor pressure
P	Production of vegetation
P_g	Gross productivity
P_i	Inorganic phosphate
P_n	Net productivity
π	Osmotic pressure
Pa	Pascal; unit of pressure (1 Pa = 1 $N \cdot m^{-2}$ = 10^{-5} bar)
PEP	Phosphoenol pyruvate
PGA	3-phosphoglyceric acid
pH	Negative logarithm of the hydrogen ion concentration
PhAR	Photosynthetically active radiation (400–700 nm)
PP	Primary production (yield of a stand)
ppm	Parts per million
PPR	Primary production rate (yield of a stand per unit time)
PR	Production rate (yield of a plant per unit time)
Pr	Precipitation (total falling on a stand of plants)
Pr_n	Precipitation reaching the ground beneath a plant canopy
π^*	Potential osmotic pressure
Φ	Quantum yield [mol $O_2 \cdot$ Einstein^{-1}]
Ψ	Water potential
PWP	Permanent wilting percentage
Py	Pyruvate
Q	Energy flow
Q_E	Energy conversion associated with evaporation and condensation
Q_H	Energy conversion associated with convection
Q_I	Energy conversion associated with radiation from the sun and reradiation
Q_M	Energy conversion associated with metabolism
Q_P	Energy conversion in plant communities
Q_{Soil}	Energy conversion in the soil
Q_{10}	Temperature coefficient of biochemical and physiological process
r	Transport or diffusion resistance
r_s	Stomatal diffusion resistance
R	Gas constant (R = 8.3 $J \cdot K^{-1} \cdot mol^{-1}$)
R	Respiration
R_d	Dark respiration
R_l	Respiration in the light
RH	Relative humidity
RuBP	Ribulose-1,5-bisphosphate
RuP	Ribulose-5-phosphate
RWC	Relative water content
s	Second; unit of time
σ	Surface tension of water
SLA	Specific leaf area
t	Time (point in time or duration)
t	Ton (Metric; 1 t = 10^3 kg)
T	Temperature (all temperature data in °C)
τ	Matric pressure or potential
TCA	Tricarboxylic acids
TL_{50}	Temperature-stress lethality (the temperature at which 50% of plants are killed by heat or cold)
torr	Unit of pressure (1 torr = $1.33 \cdot 10^{-3}$ bar $\doteq$ a 1-mm column of Hg)

Tr	Transpiration
UV	Utraviolet radiation (< 400 nm)
W	Watt; unit of power ($1\ W = 1\ J \cdot s^{-1}$)
W	Weight
W_{abs}	Quantity of water absorbed
W_{act}	Actual water content (when sample is taken)
W_{av}	Available water
W_d	Dry weight
W_{FC}	Water content of soil at field capacity
W_{PWP}	Water content of soil at permanent wilting percentage
W_f	Fresh weight
W_s	Water content in saturated state
WSD	Water saturation deficit
yr	Year
z	Relative height or depth
$\doteq$	Approximately equal to
>	Larger than
<	Smaller than

Equivalents

Energy (work)

$1\ J = 1\ N \cdot m = 1\ kg \cdot m^2 \cdot s^{-2} = 1\ W \cdot s = 0.239\ cal = 10^7\ erg$
$1\ W \cdot h = 3.6\ kW \cdot s = 3.6\ kJ = 0.86\ kcal$
$1\ MJ = 0.278\ kWh$
$1\ cal = 4.1868\ J$
1 cal (thermochemical) = 4.184 J
$1\ kcal = 1.163\ W \cdot h$

Energy Consumption in the Evaporation of Water

Heat of vaporization at 0° C = $2.50\ kJ \cdot g^{-1}\ H_2O$ ($597\ cal \cdot g^{-1}\ H_2O$)
at 10° C = $2.48\ kJ \cdot g^{-1}$ ($592\ cal \cdot g^{-1}$)
at 20° C = $2.45\ kJ \cdot g^{-1}$ ($586\ cal \cdot g^{-1}$)
at 30° C = $2.43\ kJ \cdot g^{-1}$ ($580\ cal \cdot g^{-1}$)

Radiation

$1\ W \cdot m^{-2} = 1\ J \cdot m^{-2} \cdot s^{-1} = 1.43 \cdot 10^{-3}\ cal \cdot cm^{-2} \cdot min^{-1}$
$1\ cal \cdot cm^{-2} \cdot min^{-1} \doteq 6.98 \cdot 10^2\ W \cdot m^{-2} = 6.98 \cdot 10^{-5}\ erg \cdot cm^{-2} \cdot s^{-1}$
$1\ erg \cdot cm^{-2} \cdot s^{-1} \doteq 1.43 \cdot 10^{-6}\ cal \cdot cm^{-2}\ min^{-1} = 10^{-3}\ W \cdot m^{-2}$
1 klx $\doteq$ 4—10 $W \cdot m^{-2}$ (depending on light source)
$1\ W \cdot m^{-2}$ (PhAR) $\doteq$ 3—5 $\mu E \cdot m^{-2}$ = 30—50 $nE \cdot cm^{-2} \cdot s^{-1}$
$1\ E = 1.7 \cdot 10^5\ J$ (at $\lambda = 700$ nm) to $3 \cdot 10^5\ J$ (at $\lambda = 400$ nm)
1 fc (foot candle, obsolete) = 10.76 lux
1 ly (langley, obsolete) = $1\ cal \cdot cm^{-2}$

Pressure

1 MPa = 10^6 Pa = 10 bar
1 bar = 10^5 $N \cdot m^{-2}$ = 10^5 Pa = 100 $J \cdot kg^{-1}$ = 10^6 $erg \cdot cm^{-3}$
1 bar = 750 torr = 0.9869 atm
1 torr = $1.33 \cdot 10^{-3}$ bar ≐ 1-mm column of mercury
1 atm = 1.0132 bar = 760 torr

Phytomass

1 g $DM \cdot m^{-2}$ = 10^{-2} $t \cdot ha^{-1}$
1 g org. DM ≐ 0.45 g C ≐ 1.5 g CO_2
1 g C ≐ 2.2 g org. DM ≐ 3.4 g CO_2
1 g CO_2 ≐ 0.65 g org. DM ≐ 0.30 g C

Gas Exchange

1 g CO_2 turnover ≐ 0.73 g O_2 turnover (RQ : CO_2/O_2 = 1)
1 g O_2 turnover ≐ 1.38 g CO_2 turnover
$D_{CO_2} = 0.64\ D_{H_2O}$
$D_{H_2O} = 1.56\ D_{CO_2}$

Further aids to conversion can be found in the manuals of methods by Šestak et al. (1971), Slavík (1974), O'Connor and Woodford (1975), Rose (1979), and Savage (1979), as well as in volumes of physiological and biological tables.

Contents

1 The Environment of Plants

Plants have colonized nearly all regions of the earth, including the oceans and inland waters; on land they can be found even in such inhospitable places as deserts and fields of ice. Far back in geological time, when the first land plants were evolving, they encountered a world of water, air and stone. That is, their environment consisted of the hydrosphere, atmosphere and lithosphere. Later, as the cover of vegetation gradually closed, and with the assistance of microorganisms and animals, there developed the most important substrate of plants: the soil—the pedosphere.

1.1 The Hydrosphere

The hydrosphere comprises the *oceans* of the world, which cover an impressive 71% of the earth's surface, as well as the *inland waters* and the *groundwater*. Great differences exist in the chemical compositions of these bodies of water (Fig. 1.1). Sea water, rich in Na^+, Mg^{2+}, Cl^- and SO_4^{-2} and with an average salt content of 35 g $\cdot$ l^{-1}, differs fundamentally from fresh water, which usually contains more Ca^{2+} and HCO_3^-; but there are local differences as well, depending on the nature of the inflowing waters and the degree of mixing. Moreover, *currents* have an effect upon temperature gradients. Where there are no currents, the strong absorption of radiation in the upper levels of the water leads to a characteristic layering with respect to temperature and density; this has a marked influence upon nutrition, productivity and distribution of aquatic organisms.

1.2 The Atmosphere

The *air enveloping the earth* provides plants with carbon dioxide and oxygen. It also mediates the balance of water through the processes of rain, condensation and "evapotranspiration". Continual movement of the air ensures that its composition remains fairly constant—79% nitrogen (by volume), 21% oxygen and 0.03% carbon dioxide, water vapor and noble gases (Fig. 1.1). In addition the air contains gaseous, liquid and solid impurities; these are primarily sulfur dioxide, unstable nitrogen compounds, halogen compounds, dust, and soot.

The part of the atmosphere with which plants come into contact is the *troposphere*, the weather zone of the earth's envelope of air. The nature of this zone varies over short distances and is characterized in several ways: (1) by the *weather* (short-term events such

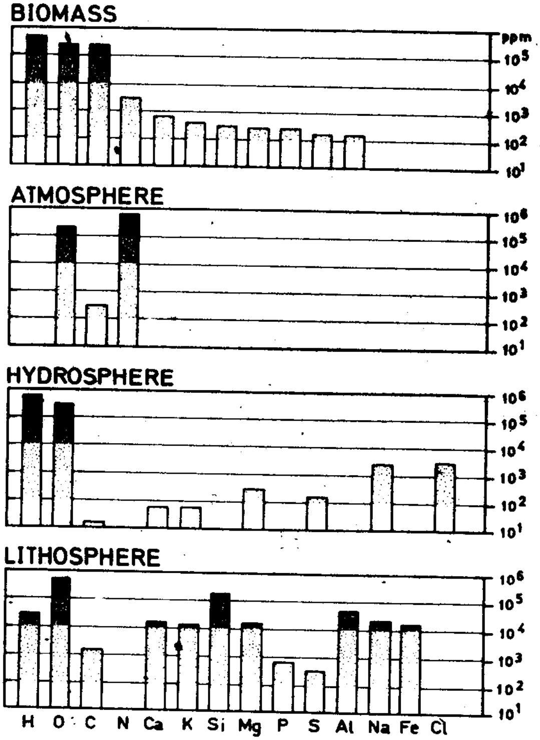

Fig. 1.1. Composition of the biomass, atmosphere, hydrosphere and lithosphere, in terms of the relative numbers of atoms (atoms per million atoms, not the proportion by weight) of the various chemical elements. The composition of living organisms is clearly distinct from that of the three components of their environment; they select from the available elements, according to their needs. The scale of the ordinate is logarithmic. For example, in the biomass H, O, C and N are present in the greatest proportions: $4.98 \cdot 10^5$ atoms per million (i.e., about 50% of all atoms) are hydrogen atoms; oxygen and carbon atoms each comprise $2.49 \cdot 10^5$ atoms per million (about 25%), and $2.7 \cdot 10^3$ (about 0.3%) are nitrogen atoms. After Deevey (1970)

as showers, thunderstorms, and gusts of wind), (2) by meteorological events of intermediate duration such as periods of rain or frost and (3) by the *climate* (the average state and ordinary long-term fluctuations in meteorological factors at a given place). Depending on the terrain and on the density, height and type of vegetation, individual climatic regions of different sizes are formed. Within the large-scale "*macroclimate*" measured by the network of meteorological stations, one may distinguish "*microclimates*" that prevail in specific places such as certain slopes or narrow valleys, the *bioclimate* in (for example) stands of vegetation, and an "interface" climate–in the layer of air near the ground and the surface of leaves. Thus the parts of plants above ground are exposed to variability, in space and time, with respect to radiation, temperature, humidity, precipitation, and air motion; any of these can from time to time represent a threat to the organism.

1.3 The Lithosphere and the Soil

The **earth's crust** is the inexhaustible reservoir of the variety of chemical elements of which organisms are composed (Fig. 1.1). The lithosphere exchanges matter with the hydrosphere, and also affects the composition of the atmosphere through volcanic ac-