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*This book is dedicated to my family
for their enduring patience.*

*Marian Penley Gates and our children,
Murray, Julie, Heather, and Marilyn*

Preface

The objective of this book is to make analytical methods available to students of ecology. The text deals with concepts of energy exchange, gas exchange, and chemical kinetics involving the interactions of plants and animals with their environments. The first four chapters are designed to show the applications of biophysical ecology in a preliminary, simplified manner. Chapters 5–10, treating the topics of radiation, convection, conduction, and evaporation, are concerned with the physical environment. The spectral properties of radiation and matter are thoroughly described, as well as the geometrical, instantaneous, daily, and annual amounts of both shortwave and longwave radiation. Later chapters give the more elaborate analytical methods necessary for the study of photosynthesis in plants and energy budgets in animals. The final chapter describes the temperature responses of plants and animals.

The discipline of biophysical ecology is rapidly growing, and some important topics and references are not included due to limitations of space, cost, and time. The methodology of some aspects of ecology is illustrated by the subject matter of this book. It is hoped that future students of the subject will carry it far beyond its present status. Ideas for advancing the subject matter of biophysical ecology exceed individual capacities for effort, and even today, many investigators in ecology are studying subjects for which they are inadequately prepared. The potential of modern science, in the minds and hands of skilled investigators, to advance our understanding of the interactions of organisms with their environment is enormous.

My students have contributed significantly to the development of this subject matter. They have helped to formulate many of the techniques and have constructively criticized much of the material. I am much in-

debted to Drs. George Bakken, John Tenhunen, and James Weber and to Peter Harley. My secretary, Meredy Gockel, typed and retyped chapter after chapter with infinite patience. All the early versions, done while I was Director of the Missouri Botanical Garden, were typed by Florence Guth. My administrative assistant, Mark Paddock, has suffered loyally through this arduous task and made it possible for me to devote the necessary time to it. I am deeply grateful to all who have helped. If the science of ecology advances from this effort, I will feel generously rewarded.

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Symbols

Roman Symbols

A	surface or cross-sectional area (m^2); subscripts 1, 2, 3, 4, 5 for surface area receiving particular streams of radiation) a constant in the respiration-temperature equation (dimensionless); activation energy of reacting molecules in chemical reactions.
A_i	increment of surface area exposed to a particular radiation source (m^2) (subscripts: a, atmospheric radiation; g, ground radiation; S, solar; s, skylight; rS, reflected solar; rs, reflected skylight).
A_g	animal surface area in contact with the ground (m^2).
A_p	projected area (m^2) (subscripts: c, cylinder; s, sphere).
A_r	effective emitting area for thermal radiation from an animal surface (m^2).
A_0, A_j	coefficients in Fourier series expression of environmental temperature ($^{\circ}\text{C}$).
a	radius of the earth (m); acceleration (m s^{-2}); absorptance (decimal fraction); altitude angle of the sun (degrees) (subscripts: s, for normal to a slope; c, for the axis of a cylinder).
a_i	absorptance of a surface to a particular source i of incident radiation (decimal fraction) (subscripts 1, 2, 3, 4, 5 for direct solar, skylight, reflected sunlight, atmospheric, and ground radiation, respectively).
${}_i a_j$	absorptance of the i th incremental element of animal surface

	to the j th source of radiation ($j = S, s, rS, rs$, and t for direct solar, skylight, reflected direct solar, reflected skylight, and thermal radiation).
a_{d1}, a_{u1}	absorptance of a downward- or upward-facing surface to direct sunlight (decimal fraction).
a_λ, a_λ	monochromatic absorption, coefficient decimal fraction.
$\mathcal{B}$	radiance ($\text{W m}^{-2} \text{sr}^{-1}$) (subscript o , in direction of a normal).
B	proportionality constant in chemical rate equation.
B_j	coefficients in Fourier series expression of environmental temperature ($^{\circ}\text{C}$).
BR	breathing rate (breaths min^{-1} or breaths s^{-1}).
C	quantity of heat exchange by convection (W m^{-2}); heat capacity, ($\text{J m}^{-2} ^{\circ}\text{C}^{-1}$); carbon dioxide concentration (mmole m^{-3}) (subscripts: a , in the air; c , chloroplasts; i , intercellular air space; w , sites of respiration).
$\bar{C}$	monthly average amount of sky covered by clouds (decimal fraction).
c	velocity of light (m s^{-1}).
c_b	specific heat of blood ($\text{J kg}^{-1} ^{\circ}\text{C}^{-1}$).
c_p	specific heat at constant pressure ($\text{J kg}^{-1} ^{\circ}\text{C}^{-1}$).
c_1	a constant in the light response of photosynthesis.
c_2	a constant in the temperature function for photosynthesis.
D	characteristic dimension (m).
$\mathcal{D}_i$	diffusion coefficient ($\text{m}^2 \text{s}^{-1}$).
${}_hD, {}_h\bar{D}$	average daily diffuse radiation incident on a horizontal surface ($\text{J m}^{-2} \text{day}^{-1}$).
D_h, D_c	fraction of total active time spent in the hot or cold microclimate parts, respectively, of a duty cycle when shuttling (s).
$d, \bar{d}$	instantaneous and average distance between earth and sun (m).
d	thickness of material (m) (subscript f for fat); diameter of a cylinder (m).
${}_h d, {}_h \bar{d}$	instantaneous and average hourly diffuse radiation incident on a horizontal surface at the ground (W m^{-2}) (subscript λ monochromatic intensity $\text{W m}^{-2} \text{nm}^{-1}$).
E	evaporation rate ($\text{kg m}^{-2} \text{s}^{-1}$) (subscripts b , by respiration; r , from skin or pelage); energy (J) elastic modulus (kg m^{-2}); apparent activation energy (J mole^{-1}); internal energy of a molecule (J mole^{-1}) (subscripts: e , electronic; v , vibrational; r , rotational); $\mathcal{E}$.
${}_ \lambda E$	flux density per unit of wavelength ($\text{W m}^{-2} \text{nm}^{-1}$).

${}_vE$	flux density per unit of wavenumber ($W\ m^{-2}\ cm^{-1}$).
ETL	eating time limit (min).
e	water vapor pressure ($N\ m^{-2}$, mbar) (subscripts: a, of the air, s, at saturation); Napierian logarithm base (dimensionless).
F	radiant flux (W); Helmholtz free energy ($J\ mole^{-1}$); view factor (decimal fraction); duration of oscillating temperature cycle (s).
f	force (N); fraction of saturation for air exhaled from the lungs (decimal fraction); a temperature function $f(T)$.
G	heat flow by conduction ($W\ m^{-2}$); Gibbs free energy ($J\ mole^{-1}$); storage term ($W\ m^{-2}$).
${}_hG$	total daily shortwave radiation incident on a horizontal surface ($J\ m^{-2}\ day^{-1}$).
${}_hG'$	total daily shortwave radiation incident on a horizontal surface on a cloudy day ($J\ m^{-2}\ day^{-1}$).
$G(T_K)$	temperature function for photosynthesis.
g	acceleration by gravity ($m\ s^{-2}$).
${}_hg, \overline{{}_hg}$	global and mean hourly global radiation incident on a horizontal surface at the ground ($J\ m^{-2}\ hr^{-1}$).
${}_sg$	global shortwave radiation incident on a slope ($W\ m^{-2}$).
H	convection coefficient ($W\ m^{-2}\ ^\circ C^{-1}$); enthalpy ($J\ mole^{-1}$); elevation of a site above mean sea level (m).
${}_h\bar{H}_0$	average hourly extraterrestrial direct solar radiation incident on a horizontal surface ($J\ m^{-2}\ hr^{-1}$).
h	height (m); length of a cylinder (m); relative humidity (decimal fraction); Planck's constant ($J\ s$); hour angle (rad).
h_c	convection coefficient ($W\ m^{-2}\ ^\circ C^{-1}$).
h_s	hour angle at sunrise or sunset, or half-day length (rad).
I	radiant intensity ($W\ m^{-2}$) (subscripts: o, along direction of a normal to the source surface; λ , monochromatic intensity); thermal insulation ($m^2\ ^\circ C\ W^{-1}$) (superscript a, apparent value); moment of inertia of a molecule ($kg\ m^2$).
i	angle of incidence (degrees).
J	upward flux of radiation in a leaf ($W\ m^{-2}$); proportionality constant in respiration relationship ($mmole\ m^{-2}\ s^{-1}$); rotational quantum number of a molecule.
J_j	flux density of molecular species j (water vapor, oxygen, or carbon dioxide) ($kg\ m^{-2}\ s^{-1}$).
K	thermal conductance ($W\ m^{-2}\ ^\circ C^{-1}$) (subscripts f, fur; s, skin; sf, skin and fur; o, overall heat conductance for an animal; c, surface boundary layer for convection); an affinity coef-

	efficient for carboxylation equal to the chloroplast concentration of CO_2 at which $P = P_M/2$ (mmole m^{-3}).
K_L	value of L at which $P_m(L) = P_{ML}/2$ (mmole m^{-3} , $\text{E m}^{-2} \text{ s}^{-1}$, or W m^{-2}).
K_{rl}	value of L such that $r_s = 2(\min r_s)$ ($\text{E m}^{-2} \text{ s}^{-1}$ or W m^{-2}).
K_O	an affinity coefficient for oxygenation equal to the oxygen concentration (vol/vol) which will double K or at which $W_p = W_M/2$ with $C_c = 0$.
k	thermal conductivity ($\text{W m}^{-2} \text{ }^\circ\text{C}^{-1}$) (subscript f, fat); Coulomb force constant, $8.99 \times 10^9 \text{ N m}^2 \text{ C}^{-2}$; von Karman constant (dimensionless); Napierian absorption coefficient (decimal fraction).
k_1, k_2	proportionality constants.
k_T	velocity constant for chemical reaction.
k_d	ratio of skylight to direct sunlight incident at the earth's surface (decimal fraction).
λk	monochromatic attenuation coefficient ($\text{m}^2 \text{ kg}^{-1}$); monochromatic "Napierian" absorption coefficient (m^{-1}) (subscripts: s, scattering; a, Mie scattering; r, Rayleigh scattering).
L	photosynthetically active radiant flux, between 400 and 700 nm ($\text{E m}^{-2} \text{ s}^{-1}$ or W m^{-2}).
L_H	a constant such that when $L = L_H$, $\exp [(-\ell n 2)(L/L_H)] = 1/2$ ($\text{E m}^{-2} \text{ s}^{-1}$).
ℓ	length of a cylinder (m); distance (m).
l_{cr}	critical length for buckling (m).
M	metabolic rate (W m^{-2}) (superscript *, dry metabolic heat production); molecular weight of a gas (kg mole^{-1}) (subscripts: a, dry air; w, water vapor); ratio of resistance R_2/R_4 .
$\bar{M}$	average number of days in a month with 1 in or more of snow cover.
m	mass (kg); atomic mass (kg or g); air mass (dimensionless).
m_w	molecular weight (kg mole).
N	number of stomates; number of elements in a leaf (number m^{-2}).
N_o	Avogadro's number (6.023×10^{23}).
N_r	molecular density (molecules m^{-3}).
NR	net radiation (W m^{-2}).
n	index of refraction (fractional number) (subscript λ , at a given wavelength); number of quanta; number of kilogram-moles of

a gas; number of absorbing and scattering elements in a leaf (number m^{-2}).

$[\text{O}_2]$	oxygen concentration (vol/vol).
P	photosynthesis rate ($\text{mmole m}^{-2} \text{ s}^{-1}$) (subscripts: M, at saturating CO_2 ; ML, at saturating light and saturating CO_2 ; MLT, at optimum temperature, saturating light, and saturating CO_2 1, between external air and intercellular air space; 2, intercellular air space and chloroplasts; 3, intercellular air space and respiration sites; 4, respiration and fixation sites; 5, at the chloroplasts); power (W) (subscript max, maximum for muscle contraction); pressure (N m^{-2}); slope of line giving dry metabolic heat production versus temperature ($\text{W m}^{-2} \text{ }^\circ\text{C}^{-1}$).
p	atmospheric pressure (N m^{-2} or mbar) (subscript 0, at sea level).
Q	rate of heat flow (W m^{-2}); irradiance (W m^{-2}) (subscripts: c, on a cylinder; s, on a sphere; h, on a horizontal flat plate; superscripts: u, upward facing; d, downward facing).
Q_a	amount of radiation absorbed (W m^{-2}); subscripts: c, by a cylinder; s, by a sphere; h, by a horizontal flat plate; superscripts: u, upward facing; d, downward facing).
${}_hQ_o$	daily amount of radiation incident on a horizontal surface just outside the earth's atmosphere ($\text{J m}^{-2} \text{ day}^{-1}$).
${}_h\bar{Q}_o$	monthly average extraterrestrial daily insolation incident on a horizontal surface ($\text{J m}^{-2} \text{ day}^{-1}$).
Q_r	thermal radiation emitted by an animal surface (W m^{-2}).
Q_{10}	factor by which the rate of activity (such as oxygen consumption) increases with each 10°C rise in temperature, (dimensionless number).
q	quantity of heat (J) (subscript c for local amount); specific humidity (dimensionless).
R	resistance to CO_2 diffusion (s m^{-1}) (subscripts: m, mesophyll; s, stomatal; min, minimum stomatal; 1, between external air and intercellular air space; 2, intercellular air space and chloroplasts; 3, intercellular air space and respiration sites; 4, respiration sites and chloroplasts); gas constant ($8.31 \text{ J mole}^{-1} \text{ }^\circ\text{K}^{-1}$); ratio of photosynthetic to transpiration rate (molecules of H_2O /molecules of CO_2).
R_λ	spectral emittance.
$\mathcal{R}$	radiant emittance (W m^{-2}) (subscripts: a, from atmosphere; g, from ground surface; i, a particular source; λ , monochromatic); linearized radiation coefficient $4\epsilon\sigma\bar{T}_r^3$ (W m^{-2}).

r	reflectance (decimal fraction) (subscripts: g, of ground or lower leaf surface; S, to direct sunlight; s, to skylight); diffusion resistance to water vapor (s m^{-1}) (subscripts: a, boundary layer; c, cuticular; i, intercellular; ℓ , leaf internal; m, mesophyll; s, stomatal); resistance to heat flow (s m^{-1}) (subscripts: h, ha, boundary layer; j, diffusion resistance to molecular species j; radius (m) (subscripts: b, of inside body wall of animal; r, of outer surface of animal).
r_d	ratio of average hourly diffuse to the average daily diffuse radiation received on a horizontal surface (decimal fraction).
S	amount of sunlight incident upon the earth's surface (W m^{-2}) (subscripts: c, on a cylinder; cv, on a vertical cylinder; ch, on a horizontal cylinder; h, on a horizontal surface; λ , monochromatic); entropy ($\text{J mole}^{-1} \text{ } ^\circ\text{C}^{-1}$); equivalent network resistances (s m^{-1}); (subscript λ , monochromatic).
$S_0, \bar{S}_0$	instantaneous and average amount of sunlight incident at a point just outside the earth's atmosphere (W m^{-2}) (subscript h, on a horizontal surface).
${}_{\text{ch}}^0S, {}_{\text{ch}}^{90}S$	irradiance of a horizontal cylinder with $\alpha - \alpha_c = 0^\circ$ and 90° , respectively (W m^{-2}).
s	intensity of scattered skylight (W m^{-2}); radius of a stomate (m); scattering coefficient (decimal fraction).
sd	saturation deficit (N m^{-2} or mbar).
T	temperature ($^\circ\text{C}$) (subscripts: a, air; b, body; c, animal casting or cold side of thermal barrier; e, operative environmental; g, ground surface; h, hot side of thermal barrier; K, leaf; ℓ , leaf; r, animal surface; S, sky; v, wall; v, vegetation; o, initial or of surroundings; ∞ , final); transmitted flux through leaf (W m^{-2}).
T_b	body temperature ($^\circ\text{C}$) (superscripts: c, lower setpoint; h, upper set point; superscripts: lc, lower equilibrium; lh, upper equilibrium); equivalent blackbody temperature ($^\circ\text{C}$).
T_c	critical body temperature ($^\circ\text{C}$) (subscripts: ℓ , lower; u, upper).
T_d	daily average transmittance of the atmosphere to diffuse radiation (decimal fraction).
$\bar{T}_d$	monthly average daily transmittance of the atmosphere to diffuse radiation (decimal fraction).
T_e	operative environmental temperature ($^\circ\text{C}$) (superscripts: a, apparent; lc, lower; lh, upper).

T_p	temperature at which the dry metabolic heat production has a linear increase with body temperature ($^{\circ}\text{C}$).
T_{Δ}	physiological offset temperature ($^{\circ}\text{C}$) (superscripts: a, apparent; lc, lower when shuttling; lh, upper when shuttling).
T_t	daily average transmittance of the atmosphere to total short-wave radiation (decimal fraction).
$\bar{T}_t$	monthly average daily transmittance of the atmosphere to total shortwave radiation (decimal fraction).
TV	tidal volume for breathing (m^3 or cm^3).
t	transmittance (decimal fraction); time (s).
U	internal energy content of a system (J mole^{-1}).
u	optical thickness (kg m^{-2}).
V	velocity (m s^{-1}); volume (m^3) (subscript w, partial molar); photopic efficiency (decimal fraction).
v	vibrational quantum number of a molecule.
W	leaf dimension perpendicular to wind (m); weight (kg); work (J); respiration rate ($\text{mmole m}^{-2} \text{s}^{-1}$) (subscripts: m, dark; p, light).
W_M	maximum rate of photorespiration at saturating oxygen concentration ($\text{mmole m}^{-2} \text{s}^{-1}$).
W_{ML}	value of W_M at zero light intensity and optimum temperature ($\text{mmole m}^{-2} \text{s}^{-1}$).
w	mixing ratio for air (dimensionless) (subscript s, at saturation).
X	heat in storage (W m^{-2}).
x	distance (m); thickness (m); ratio of length to radius for a cylinder (decimal fraction).
y	distance (m).
z	distance, or height above a surface (m); zenith angle (degrees).

Dimensionless Groups

Sc	Schmidt number
Sh	Sherwood number
Nu	Nusselt number
Re	Reynolds number
Pr	Prandtl number
Gr	Grashof number
Le	Lewis number

Greek Symbols

α	initial slope of photosynthesis versus light intensity curve (mmoles E^{-1}); angle (rad or degrees); azimuth angle of the sun (degrees).
α_c	azimuth of the axis of a cylinder (degrees).
α_s	azimuth angle of a normal to a slope (degrees).
β	slope angle, direction of normal from horizontal (degrees); coefficient of volumetric thermal expansion ($^{\circ}C^{-1}$); competitive inhibition factor (dimensionless); proportionality coefficient for Mie scattering; Bowen's ratio, $C/\lambda E$; psychrometer constant (m $^{\circ}C^{-1}$); parameter (exponent) for Mie scattering.
Δ	change of saturation vapor pressure with temperature (N m $^{-2}$ $^{\circ}C^{-1}$ or mbar $^{\circ}C^{-1}$).
Δe	concentration difference of water vapor (kg m $^{-3}$).
ΔH_1	activation energy for denaturation equilibrium of the photosynthetic reaction (J mole $^{-1}$).
$\Delta H^{\neq}$	activation energy for enzyme-catalyzed photosynthetic reaction (J mole $^{-1}$).
ΔS	entropy of the denaturation equilibrium (entropy units).
δ	declination of the sun (degrees); boundary-layer thickness (m).
ϵ	emissivity (decimal fraction) (subscript a, of atmosphere). angle (rad degree $^{-1}$); angle between axis of a cylinder and direction of the sun's rays; equivalent temperature ($^{\circ}C$).
λ	latent heat of vaporization (J kg $^{-1}$); wavelength of radiation (m, cm, μm , nm, $\text{\AA}$).
μ	viscosity coefficient (N s m $^{-2}$). chemical potential of water (J mole $^{-1}$).
ν	frequency of radiation (s $^{-1}$); kinematic viscosity coefficient (m 2 s $^{-1}$).
$\tilde{\nu}$	wavenumber of radiation (m $^{-1}$ or cm $^{-1}$).
π	osmotic pressure (bars or N m $^{-2}$).
ρ	density (kg m $^{-3}$) (subscripts: a, of dry air; j, of molecular species; o, of standard air; w, of water vapor); radius of a cylinder (m); reflectivity (decimal fraction).
${}_s\rho_a(T_a)$	water vapor density in the air at saturation as a function of air temperature T_a (kg m $^{-3}$).
${}_s\rho_{\ell}(T_{\ell})$	water vapor density in the leaf at saturation as a function of the leaf temperature T_{ℓ} (kg m $^{-3}$).

Σ	number of hours of sunshine.
σ	Stefan-Boltzmann constant, $5.673 \times 10^{-8} \text{ W m}^{-2} \text{ }^{\circ}\text{K}^{-4}$; compressive stress on a cylinder (N m^{-2}) (subscript max for maximum).
τ	transmittance (decimal fraction) (subscripts: d, to diffuse radiation; t, to total radiation); thermal time constant (s or hr) (superscript a, apparent).
$_{\lambda}\tau$	monochromatic transmittance (decimal fraction) (subscripts: a, Mie scattering; m, minor constituents; o, ozone; r, Rayleigh scattering).
τ_t	average hourly transmittance of the atmosphere to shortwave radiation (decimal fraction).
τ_c	length of time an animal can spend in a cold microclimate when shuttling (s).
τ_h	length of time an animal can spend in a warm microclimate when shuttling (s).
ϕ	latitude (degrees); angle between scattered and incident light directions (degrees); profile function.
Ψ	water potential (bars or N m^{-2}).
ω	angular velocity of the earth (rad day^{-1}); solid angle (sr).

Chemical Reaction Symbols

[A]	concentration of acception molecule for photosynthesis.
[A _o]	concentration of total carbohydrate pool.
[ACO ₂]	concentration of Calvin–Benson pathway intermediates or carboxylated acceptor.
[AO ₂]	concentration of oxygenation product of the photorespiration reaction.
[B]	concentration of intermediates formed in the regeneration of RuDP in photosynthesis.
[H]	concentration of reducing power (NADPH).
K	rate constants (subscripts 1, 2, 3, 4, and 5 for various reactions).
[O]	concentration of oxygen.
[X]	concentration of a regulating enzyme.
[π]	concentration of the carboxylation product.