

An Introduction to Environmental Biophysics

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Preface

The study of environmental biophysics probably began earlier in man's history than that of any other science. The study of organism–environment interaction provided a key to survival and progress. Systematic study of the science and recording of experimental results goes back many hundreds of years. Benjamin Franklin, the early American statesman, inventor, printer, and scientist studied conduction, evaporation, and radiation. One of his observations is as follows:

My desk on which I now write, and the lock of my desk, are both exposed to the same temperature of the air, and have therefore the same degree of heat or cold; yet if I lay my hand successively on the wood and on the metal, the latter feels much the coldest, not that it is really so, but being a better conductor, it more readily than the wood takes away and draws into itself the fire that was in my skin.¹

Franklin probably was not the first to discover this principle, and certainly was not the last. Modern researchers rediscover this principle frequently in their own work. It is sometimes surprising how slowly progress is made.

Progress in environmental biophysics, since the observations of Franklin and others, has been mainly in two areas: use of mathematical models to quantify rates of heat and mass transfer and use of the continuity equation that has led to energy budget analyses. In quantification of heat- and mass-transfer rates, environmental biophysicists have followed the lead of physics and engineering. There, theoretical and empir-

¹From a letter to John Linning, written April 14, 1757. The entire letter, along with other scientific writings by Franklin, can be found in Reference [1.2].

ical models have been derived that can be applied to many of the transport problems encountered by the design engineer. These same models were applied to transport processes between living organisms and their surroundings.

This book is written with two objectives in mind. The first is to describe the physical microenvironment in which living organisms reside. The second is to present a simplified discussion of heat- and mass-transfer models and apply them to exchange processes between organisms and their surroundings. One might consider this a sort of engineering approach to environmental biology, since the intent is to teach the student to calculate actual transfer rates, rather than just study the principles involved. Numerical examples are presented to illustrate many of the principles, and problems are given at the end of each chapter to help the student develop skill in using the equations. Working of problems should be considered as essential to gaining an understanding of modern environmental biophysics as it is to any course in physics or engineering. The last four chapters of the book attempt to apply physical principles to exchange processes of living organisms. The intent was to indicate approaches that either could be or have been used to solve particular problems. The presentation was not intended to be exhaustive, and in many cases, assumptions made will severely limit the applicability of the solutions. It is hoped that the reader will find these examples helpful but will use the principles presented in the first part of the book to develop his own approaches to problems, using assumptions that fit the particular problem of interest.

Literature citations have been given at the end of each chapter to indicate sources of additional material and possibilities for further reading. Again, the citations were not meant to be exhaustive.

Many people contributed substantially to this book. I first became interested in environmental biophysics while working as an undergraduate in the laboratory of the late Sterling Taylor. Walter Gardner has contributed substantially to my understanding of the subject through comments and discussion, and provided editorial assistance on early chapters of the book. Marcel Fuchs taught me about light penetration in plant canopies, provided much helpful discussion on other aspects of the book, and read and commented on the entire manuscript. James King read Chapters 7 and 8 and made useful criticisms which helped the presentation. He and his students in zoology have been most helpful in providing discussion and questions which led to much of the material presented in Chapter 7. Students in my Environmental Biophysics classes have offered

many helpful criticisms to make the presentation less ambiguous and, I hope, more understandable. Several authors and publishers gave permission to use figures, Karen Ricketts typed all versions of the manuscript, and my wife, Judy, edited the entire manuscript and offered the help and encouragement necessary to bring this project to completion. To all of these people, I am most grateful.

Pullman, 1977

G.S.C.

List of Symbols

A	area; amplitude of the diurnal temperature wave in soil
A_p	projected area on a plane perpendicular to the solar beam
A_h	projected area on a horizontal plane
a	absorptivity (subscripts: s , short wave; L , long wave); empirical coefficient; atmospheric attenuation coefficient
B_M	minimum metabolic rate for animals
b	empirical coefficient
C	fraction of sky covered by clouds; solution concentration
c	speed of light (3×10^8 m/s)
c_p	specific heat of air
c_s	specific heat of soil or other solid
c_b	body specific heat
D	diffusivity (subscripts: H , sensible heat; v , vapor; c , CO_2); damping depth
d	zero plane displacement; characteristic dimension; diameter of stomatal pore
E	water vapor flux density (subscripts: s , sweating; R , respiratory)
e	photon energy
F	mass flux density
$f(u)$	empirical wind function for Penman equation
G	soil heat flux density; conduction heat loss
$G(T)$	temperature function for photosynthesis
g	gravitational acceleration (9.8m/s^2)

H	flux density of sensible heat
h_r	relative humidity
h	crop canopy height; Planck's constant (6.62×10^{-34} J s)
i_B	spectral emittance of a blackbody
J_w	liquid water flux density
K	crop canopy attenuation coefficient; rate constant for CO_2 fixation
K	eddy transport coefficient (subscripts: M , momentum; H , sensible heat; v , water vapor)
K_L	rate constant for light reaction of photosynthesis
k	hydraulic conductivity; von Karman constant (0.4); thermal conductivity
L	leaf area index
L^*	sunlit leaf area index
L	long-wave flux density (subscripts: i , incoming; oe , outgoing emitted)
l	length or distance
M	molecular weight; heat flux density to animal surface from metabolism (subscript: B , basal metabolic rate)
m	body mass; airmass number
n	number of moles
P	photosynthetic rate; air permeability of clothing; atmospheric pressure
P_M	photosynthetic rate at CO_2 saturation
P_{MLT}	photosynthetic rate at CO_2 and light saturation and optimum temperature
PAR	photosynthetically active radiation (0.4–0.7 μm)
p	water vapor pressure
q	rate of heat storage
R_{abs}	absorbed long- and short-wave radiation
R	gas constant ($8.31 \text{ J K}^{-1} \text{ mol}^{-1}$); plant respiration rate
R_n	net radiant flux density
r_H	sensible heat transport resistance (additional subscripts: a , air boundary layer; c , clothing or animal coat; t , animal tissue; b , coat plus tissue)
r_v	vapor transport resistance (additional subscripts: a , air boundary layer; c , clothing or coat; s , surface, stomate, or skin)
r_c	CO_2 transport resistance (additional subscripts: a , air boundary layer; s , stomate; m , mesophyll cell wall)
r_r	radiative transfer resistance ($\rho_c p / 4\sigma T^3$)
r_e	parallel equivalent resistance of r_{Ha} and r_r

r	reflectivity
S	short-wave flux density (subscripts: i , incoming; t , total on horizontal surface; b , direct on horizontal surface; d , diffuse; p , direct perpendicular to beam)
S_{po}	solar constant (1.36 kW/m^2)
s	slope of the saturation vapor density curve; radius of cylinders or spheres for diffusion calculations
T	temperature (Kelvin or Celsius) (subscripts: a , ambient or air; b , body; w , wet bulb; d , dew point; o , ground or canopy surface temperature; e , equivalent blackbody temperature; ew , equivalent wet blackbody temperature)
t	time, transmissivity
t_o	time of solar noon
u	wind velocity in direction of mean wind; windspeed
u^*	friction velocity
u'	fluctuation of instantaneous wind about mean
u_c	windspeed in plant canopy
u_{ch}	windspeed at top of canopy
V	volume
v	lateral wind velocity
v'	fluctuation of lateral wind velocity
W	crop standing dry mass
w	vertical wind velocity
w'	fluctuation in vertical wind velocity
z	height above the soil surface
z_M, z_H, z_v	roughness parameters for momentum, heat, water vapor
α	surface albedo (short-wave reflectivity)
β	Bowen ratio
Γ	heat production per unit of oxygen consumed
γ	thermodynamic psychrometer constant ($\rho C_p / \lambda$)
γ^*	apparent psychrometer constant ($\gamma r_v / r_H$ or $\gamma r_v / r_e$)
δ	solar declination
ϵ	surface emissivity, dissipation rate for turbulent kinetic energy
ϵ_A	clear sky emissivity
ϵ_{AC}	cloudy sky emissivity
θ	zenith angle or angle from a surface normal
κ	thermal diffusivity of soil or other solids
λ	latent heat of vaporization; wavelength of light; latitude angle
ν	wavenumber or frequency of light; kinematic viscosity
ρ	air density

ρ_v, ρ_v'	water vapor density and saturation water vapor density (additional subscripts: <i>a</i> , ambient or air; <i>s</i> , evaporating surface; <i>w</i> , wet bulb)
ρ_s	soil or solid density
ρ_c	CO ₂ density (subscripts: <i>a</i> , air; <i>c</i> , chloroplast)
ρ_b	animal body density
ρ_o	oxygen density in air (subscripts: <i>e</i> , expired; <i>i</i> , inspired; <i>a</i> , ambient)
σ	Stephan-Boltzmann constant ($5.67 \times 10^{-8} \text{ W m}^{-2}\text{K}^{-4}$)
τ	shear stress or momentum flux density; period of oscillation; time constant
ϕ	solar elevation angle
ϕ_M, ϕ_H	adiabatic influence functions for momentum and heat
Φ	radiant flux density (subscript: <i>B</i> , blackbody)
Ψ	water potential (subscripts: <i>g</i> , gravitational; <i>o</i> , osmotic; <i>m</i> , matric; <i>p</i> , pressure)
ψ_M, ψ_H	adiabatic profile correction functions for momentum and heat
ω	frequency ($= 2\pi/\tau$, where τ is the period of oscillation)
ζ	atmospheric stability index (+ is stable, - is unstable, 0 is neutral)
Gr	Grashof number
Nu	Nusselt number
Pr	Prandtl number (ν/D_H)
Re	Reynolds number
Sc	Schmidt number (ν/D_j)
Sh	Sherwood number
log	base 10 logarithm
ln	base <i>e</i> logarithm
exp	exponential ($\exp x = e^x$, where $e = 2.7183 \dots$)

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1 Introduction

The effects of the physical environment on behavior and life are such an intimate part of our everyday experience that one may wonder at the need to study them. Heat, cold, wind, and humidity have long been common terms in our language. A few simple experiments, however, can easily convince us that our common expressions lack precision in explaining interactions with our environment, and in many cases we mislead ourselves or unnecessarily complicate the picture by not understanding the physical principles involved in environment-organism interactions.

One experiment can be tried the next time you step from a warm shower on a cold morning. By standing on the tile floor and then on the bath mat, try to estimate the relative temperature of each. Which is colder? Our senses tell us that the tile is colder, but if we were to make a measurement with a thermometer we would likely find them to be at the same temperature. What, then, did we sense? With little thought we will conclude that we sensed heat flux. Because of its higher thermal conductivity, the tile caused more rapid loss of heat from our feet than did the bath mat, and we registered that as a colder temperature. Careful consideration will indicate that essentially every interaction we have with our surroundings involves energy or mass exchange. Sight is possible because emitted or reflected photons from our surroundings enter the eye and cause photochemical reactions at the retina. Hearing results from the absorption of acoustic energy from our surroundings. Smell involves the flux of gasses and aerosols to the olfactory sensors. We could list numerous other sensations—such as sunburn, heat stress, cold stress—and each

involves the flux of something to or from the organism. We can express the steady-state exchange of most forms of matter and energy between organisms and their surroundings as

$$\text{Flux} = \frac{C_s - C_a}{r} \quad (1.1)$$

where C_s is the concentration at the organism exchange surface, C_a is the ambient concentration, and r is the exchange resistance. As we already noted, we sense fluxes but we generally interpret them in terms of ambient concentrations. Even if we maintained the concentration at the organism constant (generally not the case) our judgment about ambient concentration would always be tempered by the magnitude of the exchange resistance. The shower experiment illustrates this nicely. The bath mat resistance to heat transfer was higher than that of the tile, so we judged the bath mat temperature to be higher.

Microenvironments

Microenvironment is an intimate part of our everyday life, but we seldom stop to think of it. Our homes, our beds, our cars, the sheltered side of a building, the shade of a tree, an animal's burrow are all examples of microenvironments. The "weather" in these places cannot usually be described by measured and reported weather data. The air temperature may be 10°C and the wind 5 m/s, but a bug, sitting in an animal track sheltered from the wind and exposed to solar radiation may be at a comfortable 25°C.

It is the microenvironment that is important when considering organism energy exchange, but descriptions of microclimate are often complicated because the organism influences its microclimate and because microclimates are extremely variable over short distances. Specialized instruments are necessary to measure relevant environmental variables. Variables of concern may be temperature, atmospheric moisture, radiant energy flux density, wind, oxygen and CO₂ concentrations, temperature and thermal conductivity of the substrate (floor, ground, etc.), and possibly spectral distribution of radiation. Other microenvironmental variables may be measured for special studies.

We will first concern ourselves with a study of the environmental variables—namely, temperature, humidity, wind, and radiation. We will then discuss energy and mass exchange, the fundamental link between organisms and their surroundings. Next we will apply the principles of energy and mass exchange to a few selected problems in plant, animal, and human environmental biophysics. Finally, we consider some problems

in radiation, heat, and water vapor exchange for vegetated surfaces such as crops or forests.

Energy Exchange

The fundamental concept behind all of biophysical ecology is energy exchange. Energy may be exchanged as stored chemical energy, heat energy, or mechanical energy. Our attention will be focused primarily on the transport of heat energy.

Four modes of heat transfer are generally recognized. These are convection, conduction, radiative exchange, and latent heat transfer. These modes of energy transport are recognized in our common language when we talk of the "hot" sun (radiative exchange) or the "cold" floor tile (conduction), the "chilling" wind (convection), or the "stifling" humidity (reduced latent heat loss). An understanding of the principles behind each of these processes will provide the background we need to determine the physical suitability of a given environment for a particular organism.

The total heat content of a substance is proportional to the total random kinetic energy of its molecules. Heat can flow from one substance to another if the average kinetic energies of the molecules in the two substances are different. Temperature is a measure of the average random kinetic energy of the molecules in a substance. If two substances at different temperatures are in contact with each other, heat is transferred from the high-temperature substance to the low by conduction, a direct molecular interaction. If you touch a hot stove, your hand is heated by conduction.

Heat transport by a moving fluid is called convection. The heat is first transferred to the fluid by conduction, but the fluid motion carries the heat away. Most home heating systems rely on convection to heat the air and walls of the house.

Unlike convection and conduction, radiative exchange requires no intervening molecules to transfer heat from one surface to another. A surface radiates energy at a rate proportional to the fourth power of its absolute temperature. Both the sun and the earth emit radiation, but because the sun is at a higher temperature the emitted radiant flux density is much higher for the sun's surface than for the earth's surface. Much of the heat you receive from a campfire or a stove may be by radiation, and your comfort in a room is often more dependent on the amount of radiation you receive from the walls than on the air temperature.

To change from a liquid to a gaseous state at 20°C, water must absorb about 2450 joules per gram (the latent heat of vaporization), almost 600 times the energy required to raise the temperature of one gram of water by one degree. Evaporation

of water from an organism can therefore be a very effective mode of energy transfer. Almost everyone has had the experience of stepping out of a swimming pool on a hot day and feeling quite cold until the water dries from his skin.

Mass and Momentum Transport

Organisms in natural environments are subject to forces of wind or water on them, and rely on mass transport to exchange oxygen and carbon dioxide. The force of wind or water on an organism is a manifestation of the transport of momentum from the fluid to the organism. Transport of momentum, oxygen, and carbon dioxide in fluids follows principles similar to those developed for convective heat transfer. We can therefore learn just one set of principles and apply it to all three areas.

Applications

From the examples already given, it is quite obvious that environmental biophysics can be applied to a broad spectrum of problems. Fairly complete evaluations already exist for some problems, though much work remains to be done. Analysis of human comfort and survival in hot and cold climates requires a good understanding of the principles we will discuss. Preferred climates, survival, and food requirements of domestic and wild animals can also be considered. Plant adaptations in natural systems can be understood, and optimum plant types and growing conditions in agriculture and forestry can be selected through proper application of these principles. Even the successful architectural design of a building, which makes maximum use of solar heat and takes into account wind and other climatologic variables, requires an understanding of this subject.

Table 1.1 Examples of derived SI units and their symbols

Quantity	Name	Symbol	SI base units	Derived units
area	square meter	—	m^2	—
volume	cubic meter	—	m^3	—
velocity	meter per second	—	$m\ s^{-1}$	—
density	kilogram per cubic meter	—	$kg\ m^{-3}$	—
force	newton	N	$m\ kg\ s^{-2}$	—
pressure	pascal	Pa	$m^{-1}kg\ s^{-2}$	$N\ m^{-2}$
energy	joule	J	$m^2\ kg\ s^{-2}$	$N\ m$
power	watt	W	$m^2\ kg\ s^{-3}$	$J\ s^{-1}$
heat flux density	watt per square meter	—	$kg\ s^{-3}$	$W\ m^{-2}$
specific heat capacity	joule per kilogram kelvin	—	$m^2s^{-2}K^{-1}$	$J\ kg^{-1}K^{-1}$

Negative exponents are used to indicate units in the denominator