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BIOPHYSICAL ECOLOGY: AN INTRODUCTION TO ORGANISM RESPONSE TO ENVIRONMENT

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Biophysical Ecology: An Introduction to Organism Response to Environment

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Methodology

The direct effects of environmental factors on the physiology and behavior of individuals comprise the building blocks upon which ecology is based. In the reductionist view (Gates, 1980), all ecological interactions may be carried down to the level of the cell and individual through careful analysis of physical and chemical processes. This approach, involving the detailed analysis of the underlying processes in a natural system, is in practice limited by the complexity of biological systems. Interactions may be viewed at levels from the molecular, through tissue, organ, and individual, and beyond to population, community and ecosystem. The viewpoint of biophysical ecology is that general ecological perspectives may be obtained by considering the effects of environments on individuals and that knowledge of processes at this level is critical to understanding the structure of populations and communities. The known results from scientific fields as varied as chemical kinetics, fluid flow, thermodynamics, atmospheric physics, and soil mechanics are applied to structure a cohesive framework for analysing organism response to environmental factors. The great advantage of this framework is that it applies independent of the type of organism, animal or plant, terrestrial, aquatic or arboreal. The same physical principles underly all of nature. In practice of course, this advantage is ameliorated by the great range of environments which organisms inhabit, each providing their own unique challenges for organism survival.

Three alternative approaches to ecological investigation - descriptive, functional, and evolutionary - have been mentioned by Krebs (1978). Descriptive methodology is natural history in the sense of merely observing characteristics of organisms in the field without any explicit attempt to explain them. A functional approach attempts to determine the proximate causes of responses of organisms, for example through correlations between environments and species distributions. The evolutionary approach attempts to study the ultimate causes of organism response through the dynamics of the evolutionary process. It is only within the past few decades that the emphasis of ecological studies has shifted from the descriptive to the functional and evolutionary. For the study of

physiological adaptations, Calow and Townsend (1981) describe two methodologies which are intermediary between the above. The first of these *a posteriori*, takes as given that certain organism characters are observed to be correlated with particular environments, and then asks what it is about these characters which aid the individual in surviving and reproducing in its environment. For example, it may be observed that leaf sizes in hot desert conditions are generally much smaller than in more moist environments. Given this, one may attempt to explain it in terms of heat loading on the leaf as it affects leaf photosynthetic rate and water status. The second methodology, *a priori*, assumes a range of potential characteristics are accessible to the organism and asks which of these is the most appropriate for certain ecological circumstances. Thus, in the leaf example, the approach would be to assume that a range of leaf sizes are possible and then determine according to some criterion of fitness, which sizes would be most adaptive in dry *versus* moist habitats.

The *a posteriori* approach, consisting of a combination of the descriptive and functional views, inherently has the potential to view all characteristics of organisms as adaptive. By an adaptation is meant any character of an individual which gives that individual a selective advantage relative to individuals without that character. As has been pointed out by Maynard Smith (1978) and others however, there is no reason to believe that all traits are adaptive. Evolution may lag behind and be out of phase with a changing environment, and certain traits may be merely a side-effect of other traits which are adaptive. Care must therefore be taken in assigning adaptive significance to traits observed to be correlated with certain environments. Another difficulty surrounds the multiplicity of selective forces operating in any particular environment. It may be very difficult to separate out any one factor to use as a criterion for selection. For example, although one might expect the distribution of fat in vertebrates to be determined by the needs for thermoregulation, a critical analysis shows such factors as buoyancy, sexual and social signalling, and locomotory mechanics to be much more significant (Pond, 1978).

The proper choice of fitness criteria is also a difficulty in the *a priori* approach, which is an amalgam of the functional and evolutionary methods. However, evolutionary mechanisms at the level of population genetics are not considered, but rather it is assumed that phenotypic traits can be closely linked to fitness (in the genetic sense). Also the phenotypes which are optimal for the chosen selection criterion are assumed feasible in that they are on an evolutionary trajectory which could be reached by an ancestor population. These assumptions are all open to criticism (Lewontin, 1978), but when care is taken, this approach is often preferable to the *a posteriori* one (Calow and Townsend, 1981).

My procedure in what follows is to first give a brief review of the environmental factors most critical to organism behavior. I will then discuss several cases of applications of biophysical techniques to investigations of adaptation. Hopefully these will give some indication of the diversity of problems and the highly interdisciplinary efforts needed to understand them. The approach will be *a priori* as discussed above. I draw heavily from the books of Campbell (1977), Gates (1980), and Townsend and Calow (1981). It will be noted that I do not particularly emphasize the mathematics involved in these analyses. Often the analysis is either straight-forward calculus, or is beyond the tractability of analytic methods. Quite frequently in my view, it is the simplest models which give us the greatest insight, though the more complex ones may enable us to synthesize and analyze the effects of multiple interacting factors. However, as I emphasized in my first lecture, it is important not to lose sight of the biological goals of the research while joyfully tramping through the mathematical woods which surround them.

Environmental Factors

I. Radiation

Essentially all the energy utilized by life forms on this planet is derived from solar radiation. The energy incident upon the earth's upper atmosphere, the so-called solar constant, is approximately 1360 Watts meter^{-2}, although this is subject to variation. The energy actually incident upon the earth's surface may be determined from a very complicated combination of factors such as time of year, location, cloud cover, elevation, and time of day. Instantaneous values of global radiation (the sum of direct beam solar radiation and diffuse skylight) on a horizontal surface may vary from 50 to 1250 W m^{-2}, depending mainly upon sky conditions (Gates, 1980, page 127). Much of the loss of radiation is due to refraction and diffraction in the high atmosphere, reflection from clouds, and absorption by the atmosphere. Not only does this large variation in radiation affect the light conditions at a site, but temperature, windiness and moisture are also all

affected. Total global radiation at a fixed site is highly variable with a dynamic pattern due to cloud and atmospheric turbidity changes induced on top of diurnal patterns. These dynamic patterns can be quite significant determinants of organism behavior.

Global radiation has direct effects on primary productivity at a site. The efficiency of gross primary productivity, measured as the world average percent of incident radiation converted to biomass, is approximately 0.2 %. Considered on a net basis, when respiratory losses are subtracted, this is reduced to .09 %. The maximum potential gross primary productivity of a managed crop is estimated to be 8 %, while the average annual value for U.S. crops is about 1.7 %. The conversion efficiency of natural ecosystems varies from about 4.4% for a tropical forest, to .04% for a Nevada desert, all measured on a gross basis (Gates, 1980, page 135). As can be seen, a very small fraction of incident energy is actually productively captured by plants, partially due to the inefficiencies of the photosynthetic process, and in some systems the incomplete capture of utilizable energy.

For many biophysical questions, not only is the total radiation at a site important, but also its spectral composition. Although the spectrum of energy incident on the atmosphere is essentially that of a black body and follows Planck's law, the spectrum is markedly changed the absorption and scattering characteristics of the atmosphere, particularly in the infra-red. The minor gases of water vapor, CO_2, and ozone absorb strongly in the infra-red, and this is one reason why there is concern about the potential increases in atmospheric CO_2. Since oxygen and ozone concentrations control the amount of ultra-violet radiation below 290 nm wavelength, which reaches the lower atmosphere, the potential degradation effects of fluorocarbons from aerosol spray cans on these gases is also of concern.

The radiation spectrum at any given location on the earth's surface can change quite markedly through a day, particularly due to cloud cover and solar angle shifts. The spectrum also shifts with depth in a plant canopy since leaves transmit more in the green, from 500 to 580 nm, than in the red or blue, and have a very low absorptance in the near infra-red from 700 to 1500 nm. These properties of leaves are critical to their ability to photosynthesize and avoid overheating. Similarly, there are changes in radiation spectra with depth in bodies of water, with rapid absorption of infra-red and higher attenuation in the red than in the blue-green. This can be expected to have significant effects on the visual processes of fish. It is worth keeping in mind that other organisms may be quite sensitive to light qualities outside the range of human perception. For example, reflectance properties of some flowers in the ultraviolet play an important role in pollenation by insects (Silberglied, 1979), and the polarization of skylight may be significant during the migration of birds (Able, 1982).

II Temperature

The thermal regime of a habitat is of critical importance to the survival, reproduction, and types of organisms which live there. At any particular location, temperatures are affected by an immense collection of factors in part because most terrestrial objects emit a broad spectrum of infrared radiation, above 2.5 μm, and environmental temperatures are strongly coupled to thermal radiation from the surroundings. Because they have relatively low absorptances to shortwave radiation, below 2.5 μm, organism temperatures are mainly affected by longwave radiation. Relationships between organism temperatures and environmental ones can be quite complex, as is discussed later under heat loading. It is also true that although environmental temperatures are one of the easiest measurements to make, and enormous amounts of data have been taken, much of this is of relatively little ecological significance (Remmert, 1980, page 24). Organism temperatures may bear little relationship to the meteorological temperatures usually measured, even for poikilotherms. Behavioral actions, such as sunbathing by grasshoppers on cool mornings to raise body temperature and solar tracking by arctic flowers, are just two of the many thermoregulatory mechanisms available. Due to the great variability of environmental temperatures, it is quite difficult to establish relationships with species distributions.

Temperatures may affect organisms quite differently at different stages of their life cycles, with especially strong effects on development and reproduction. Such processes as seed germination, flowering times, and larval development rates are strongly coupled with temperature. Again, it often isn't clear what aspect of temperature is most critical - maximum, minimum, averages, or ranges. Which measurement is meaningful is often specific to a given process. This is complicated by the ability of organisms to adapt, both genetically at the population level, and physiologically for individuals, to temperature ranges. Thus, although most temperate-zone plants are very tolerant of midwinter cold, early frosts may damage them due to inadequate time to adapt physiologically (Weiser, 1970). Although much laboratory work has been done to determine the temperature tolerance limits of organisms, along with optimal temperature ranges for various physiological processes, applying these results to natural environments is complicated by the necessary transformation from environmental measurements to physiologically significant ones (Campbell, 1981).

III Moisture

Water is critical to life, not only because it is the major constituent of biomass and is necessary for most metabolic processes, but also due to its importance to evaporative cooling. Aquatic environments present unique osmotic challenges to fresh-water organisms which have a higher osmotic pressure than their environment and thus are faced with the problem of keeping water out, whereas ocean-dwelling organisms have the reverse problem of keeping water in. Many terrestrial organisms must maintain themselves internally at water-saturated conditions, while the moisture content of their environment is often quite low. It is thus expected that organisms will have developed quite complex mechanisms to buffer themselves from changes in external moisture. For example most benthic (deep-sea dwelling) organisms can only tolerate very small fluctuations in salinity of the surrounding water, whereas species in tidal zones and estuaries have developed active mechanisms to alter internal osmotic pressure in order to maintain a proper ionic balance. The stomata of leaves are critically important for the maintenance of internal water level in plants, and respond dynamically to a complex of factors including light, humidity, and CO_2 (Raschke, 1979).

As in the case of temperature, it is often quite difficult to obtain measurements of environmental moisture which are indeed physiologically significant in terms of water actually available to the individual. For terrestrial organisms, humidity, soil moisture (for plants), and drinking water (for animals) may all be important in setting tolerance limits for individuals. These moisture measurements must be tied together with the evaporative and transpirational needs of the organism for heat balance, and thus are highly dependant upon other environmental factors. Biophysically important measurements are usually made in terms of the water potential, or chemical potential, of water in various components of the system. See Nobel (1974) for an overview of water relations in plants, and Tracy (1975) for the application of a mass balance approach to water budgets of animals.

IV Nutrients

Organism nutritional requirements, in which I include utilization of gases such as O_2 and CO_2, vary qualitatively and quantitatively among taxa. For more on animal nutrition, see the lecture on foraging theory. Soil concentrations of nutrients which are critical to plant growth, such as nitrogen and potassium, tend to be extremely low, requiring active mechanisms within plant roots in order to obtain adequate supplies. Further complications arise due to the importance of microorganisms to nutrient supply, for example in legumes which have symbiotic relationships with nitrogen-fixing bacteria in their root systems. The difficulties involved in studying roots in *vivo* also contributes to the general lack of theoretical development on the subject of plant nutrition. Generally, experimental studies are unable to ascertain minimum and optimal nutrient concentrations necessary for growth, partially due to the great plasticity of growth response. Nutrient-stressed plants can change root-to-shoot ratios, photosynthesis, and root absorption capacity, and there are consistently different patterns of nutrient response in plants from different soil fertility growth regimes (Chapin, 1980). All these complications combine to make mineral nutrition one of the least developed areas of plant growth analysis, although there have been models both of root growth (Plant, 1982), and of nutrient transport after partitioning (Thornley, 1975). For an overview of mineral nutrition in plants, see Hewitt and Savage (1974).

In contrast contrast to the situation with soil nutrients, a great deal is known about the CO_2 and O_2 requirements of plants and animals. CO_2 is the building block of all organic matter, and critically affects photosynthesis. It's low concentration in the atmosphere, approximately 340 parts per million, limits the growth of plants, particularly crop plants under good growing conditions. I discuss it's relationship to photosynthesis later, and at this point just mention that its concentration in the atmosphere is increasing due to fossil fuel burning. The implications of this increase are complex and debatable, though most agronomists feel that it will lead to increased crop yields. For land organisms, the availability of O_2 for respiratory processes is generally non-limiting, however aquatic species have evolved adaptations to utilize the low levels of dissolved O_2 in water bodies. The production of O_2 in water by aquatic plants is critical to fish life. There can be complex interactions with nutrients and bacteria, leading to reduction in dissolved O_2 and the death of fish - the process of eutrophication.

In this situation, the fish production in a nutrient-poor lake may well be much higher than in a nutrient-rich lake. See Schmidt-Nielson (1975) for an overview of physiological oxygen requirements of animals.

V Other Factors

A variety of other environmental factors have important influences on organisms in particular environments. Wind plays a critical role in convective heat exchange and evaporative water loss, as is discussed later. This has implications for such characters as leaf shape, body size, and fur thickness. Wind is a major factor limiting trees at timberline (Tranquillini, 1979) and greatly affects the morphology of plants. See Nobel (1981) for a review of the ecological effects of wind. Similarly, water currents can affect the distribution of fish within streams, and are critical to the larval stages of many marine invertebrates. Fire, caused by lightning or spontaneous combustion, is a regular feature of many natural ecosystems. In a complex manner, it brings about regular changes in community structure and affects the nutrient availability at a site. Physiologically, some species of plants have developed adaptations to fire, including in some cases (e.g. *Pinus banksiana*, jack pine) the production of seeds which only germinate after a fire. See Rundel (1981) for an overview of fire as an ecological factor.

All of the above mentioned environmental factors may interact in ways that often make predictions of organism response quite difficult and process-specific. Some examples of interactions are given in the case studies below. In some cases, factors do indeed act independantly, at least over certain ranges of the variables. For example, many plant species distributional limits can be determined independently by soil conditions and climate. Generally, however, it is preferable to view an individual as an (often non-linear) integrator of the environmental influences upon it. Further difficulties arise due to the temporal and spatial variation of environmental factors, leading to possibilities for temporal acclimation to changing environments. Biophysical methods often provide the framework for analysis of response dynamics, but require enormous quantities of temporal data, which limits their utility. Thus, steady-state approaches are prevalent. It should also be kept in mind that biotic factors, such as local densities of individuals, along with their growth forms, play an important role in specifying organism response. For example, relative size structures of many plant parts depends greatly upon planting densities (Harper, 1977, Chp.7) In what follows however, I limit the discussion to cases of response to physical factors.

Case Studies

I. Heat Loading

One of the most useful of biophysical analyses is the study of the energy budgets of organisms. The basic physical principles underlying heat exchange are the same in plants and animals, and at steady-state may be expressed as (Gates, 1980, Page 20):

$$M + Q_a = R + C + \lambda E + G + X \qquad (1)$$

where M = metabolic rate
Q_a = radiation absorbed
R = radiation emitted
C = energy transmitted by convection
λE = energy exchanged by evaporation or condensation
G = energy exchanged by conduction
X = energy put into or obtained from storage.

All these are expressed as rates per unit time per unit surface area, with units of watts meter^{-2}. We may consider each of these components in turn, and then combine their effects. Note that this separation still averages the effects of each form of energy exchange over the whole organism, which introduces errors since there may be quite different interactions between the exchange factors on different parts of the organism. For example radiant absorption and convective cooling may be quite different for upper *versus* lower leaf surfaces, and using average values for each of these over the whole organism is incorrect. However, for purposes of investigating large-scale trends in comparative ecology, the approach is a good approximation (Bakken and Gates, 1975). The main variable will be organism surface temperature, T_s, which will be assumed uniform over the individual.

By the laws of radiation,

$$R = \epsilon \sigma (T_s + 273)^4 \qquad (2)$$

where σ = Stefan-Boltzman constant
ϵ = emissivity of the organism surface.

If the organism's environment is at a uniform temperature T_o, with the same emissivity as the organism, then the radiative energy exchange rate for an organism of surface area A is

$$\frac{1}{A}\frac{dE}{dt} = \epsilon \sigma \left\{ (T_s + 273)^4 - (T_o - 273)^4 \right] \qquad (3)$$

If T_s and T_o are close, we may approximate (3) by linearizing the right hand side to get

$$\frac{1}{A}\frac{dE}{dt} = K(T_s - T_o) \qquad (4)$$

where $K = 4\epsilon\sigma(T_o + 273)^3$. Equation (4) is often called Newton's law of cooling, though this has led to confusion in the literature as to whether convection and conduction should be included (Bakken and Gates 1974). It is probably best to omit the use of the term completely.

Convective heat exchange with the surrounding air or water in the case of a uniform environment of temperature T_a is

$$C = h_c (T_s - T_a) \qquad (5)$$

where h_c is the convection coefficient. The convection coefficient here is really an average over the organism surface, which may have a very complex boundary layer. The relationship between h_c and organism shape can be quite difficult to establish, but fairly accurate results are obtained by taking

$$h_c \propto D^m V^n$$

where D is a characteristic dimension of the organism in the direction of air flow, V is wind speed, and m and n are constants. Estimated values for leaves are $m \approx -.3$ and $n \approx .5$ (Gates, 1980, page 298), indicating the effects that increasing wind speed and decreasing leaf size have on reducing the boundary layer thickness (proportional to h_c^{-1}) around a leaf. Quite similar values are used for animal models, though the use of animal-shaped metal castings in wind tunnels has provided the best estimates of h_c (Bakken and Gates, 1975). For applications to leaves, the conduction term in (1) is ignored, while for animals it is proportional to the surface area in contact with the ground and the temperature difference between ground and organism surface. The proportionality coefficient (of conduction) will depend greatly upon the fur, feathers, and structure of the organism (Gates, 1980, pages 406-410). Estimates of the coefficient have been made for a variety of fur thicknesses (Skuldt et al., 1975).

The general form for evaporative heat loss is

$$\lambda E = \lambda(T_s)\, E(T_s, T_a, h, r)$$

where λ is the latent heat of vaporization, which is a function of organism surface temperature, and E is the rate of water loss per unit surface area, which depends on relative humidity h, and a resistance to water loss, r, along with the temperatures. For leaves, Gates (1980, page 27) suggests

$$E = \frac{d_\ell(T_s) - h\, d_a(T_a)}{r_\ell + r_a} \qquad (6)$$

where $d_\ell(\cdot)$ and $d_a(\cdot)$ are the saturation densities of water vapor in leaf intercellular air spaces and air, respectively, at the respective temperatures, r_ℓ is internal leaf resistance and r_a is boundary layer resistance. A similar form holds for water loss from animals, either by sweating or respiration, in which case there is no r_ℓ term if the animal skin is wet from sweat. In all cases the boundary layer resistance r_a is approximately proportional to $V^{-.5}$.

For a plant leaf, the above is sufficient to specify the thermal budget since metabolic rate and photosynthesis have no measurable effect on leaf temperatures. Thus in the simplest application of (1), we take $M = G = K = 0$, and can solve numerically for the steady-state temperature at any level Q_a of absorbed radiation, using (2), (3), and (6). Through this analysis, we can determine the effects of transpiration, radiation, leaf dimension, and wind speed on leaf temperatures. There is good evidence that leaves do indeed undergo thermal regulation, with a variety of strategies taken to adjust leaf energy exchange (Gates, 1980, pages 38-46). The relative advantages of smaller leaves in dryer, hotter environments may be explored with the above type of analysis. Since plant growth rates are correlated with photosynthesis, and photosynthetic rates depend upon leaf temperature, the above types of energy budget calculations are also useful in specifying potential plant growth rates under a variety of environmental conditions.

The application to animals is a bit more complex. The net heat production, $M - \lambda E$, is the net heat produced by metabolic processes less the heat lost through breathing and perspiration. This may be taken as

$$M - \lambda E = \frac{T_b - T_s}{I} \qquad (7)$$

where T_b is internal body temperature (not surface), and I is a measure of insolation, which depends upon fur, fat, and feather thicknesses. Since it is internal body temperature T_b that is critical to metabolic processes, one solves (7) for T_s and substitutes into (1) to obtain

$$M - \lambda E + Q_a - \epsilon\sigma\left(T_b + 273 - I(M - \lambda E)\right)^4 - k\left(\frac{V}{D}\right)^{.5}\left[T_b - T_a - I(M - \lambda E)\right] - G = 0 \qquad (8)$$

Values of Q_a are one of the most difficult to estimate, though an approach by breaking the animal's surface into increments with different absorptances and summing does give some estimates (Gates, 1980, pages 416-418). By considering each segment of the energy budget in turn, it is possible to derive from (8) information about how such factors as fur thickness and coloration, body size, wind speed, and fat content affect the range of body temperatures a poikilotherm may experience, and the range of environmental conditions over which a homeotherm may maintain a fixed temperature. These techniques have been applied to a variety of organisms including hummingbirds (Southwick and Gates, 1975), rabbits (Kluger, 1975), deer (Moen and Jacobsen, 1975), and amphibians (Tracy, 1975). The approach is also useful in making comparisons across taxonomic lines of organisms under similar ecological conditions. For example, in explaining the thermal conductance and basal metabolic rate differences between subterranean rodents and insectivores, and why for burrowing mammals, males tend to be larger than females (Nevo, 1979).

The entire approach to energy budgets is often viewed analogously to simple electrical circuits, where heat flows are analogous to current. For example, see figure 1 for the case of negligible conductance to the ground. Arrows represent thermal currents not directly related to temperature, the nodes represent parts of the body/environment system at which temperature measurements may be made, and resistors correspond to thermal conductances between nodes. A fully dynamic analysis may be performed rather than just the steady-states as done above (Bakken and Gates, 1975), to examine the effects of such behaviors as shuttling from one environment to another. In general of course, time dependent solutions require more data on both the environment and potential organism response to it. Many more complicated circuit analogs may be set up, for example to include conduction through the ground, and metabolic or respiratory rates which are body temperature dependent.

II. Photosynthesis

As the most basic process for energy transformation on this planet, photosynthesis has been intensely studied, with the result that there is a wealth of data, but as yet no complete understanding of it at any level. The environmental inputs to photosynthesis are light, CO_2, water potential in the soil, humidity, wind, temperature, and soil mineral status. Photosynthetic rates for leaves depend upon many plant characters including biochemical and photochemical capacities (there are at least three different major types of photosynthesis), the nature and density of stomata (pores in leaf surfaces through which gases diffuse), the ability of the plant to withstand water stress, the form and size of leaves, and the extent of the root system. Securing the appropriate conditions for photosynthesis presents distinct adaptive problems to plants. Only about 2% of incoming solar radiation can be utilized, requiring the dissipation of energy to avoid overheating. Since CO_2 levels in the atmosphere are very low, and CO_2 is absorbed through passive diffusion, for every molecule of CO_2 absorbed, 300 to 1000 molecules of H_2O are lost. This trade-off between CO_2 uptake and water loss due to the fact that they use the same diffusive pathway, is of major importance to questions of leaf form and size. Many attempts have been made to model various aspects of photosynthesis, but due to its great complexity, the models have limited scope. See Hesketh and Jones (1980) for the most complete compendium of models to date.

The great majority of photosynthetic models deal with the leaf level, and I here would like to give some indication of the most common approach. This uses an electrical circuit analog, as mentioned above for heat loading, only the fluxes are now fluxes of CO_2 rather than heat. The models compartmentalize a leaf and consider the resistances to flow of CO_2 between the compartments. An example is given in figure 2. This is a steady-state type of model which is analyzed using Kirchoff's law, meaning in this case mass balance at every junction in the circuit. The underlying physical principle is Fick's law of diffusion

$$J = D\frac{\partial \rho}{\partial x} \qquad (9)$$

where J is flux of CO_2, D is diffusivity of CO_2, ρ is CO_2 concentration, and x is distance into the leaf. A discrete analog of (9) is used:

$$J = \frac{\rho_1 - \rho_2}{r} \qquad (10)$$

where ρ_1 and ρ_2 are CO_2 concentrations at two points in the circuit, and $r = \Delta x / D$ is the resistance across a distance Δx of some medium (such as inter-cellular air space or cytoplasm). Note that D is temperature and pressure dependant and the Δx's aren't easily specified, but various techniques have been employed to estimate the resistances R_i for the diffusive pathways in a leaf (Gates, 1980, pages 328-329).

Analyzing the fluxes of CO_2 in figure 2 produces for example from (10)

$$P_1 = \frac{C_A - C_I}{R_1} \qquad (11)$$

and similar forms for P_2, P_3, and P_4. From mass balance,

$$P_2 = P_1 + P_3, \quad W = P_3 + P_4, \quad P_5 = P_2 + P_4 \qquad (12).$$

The flux P_5 must equal the rate of biochemical uptake of CO_2 at the chloroplast, which depends upon light, CO_2, and O_2 inputs. A Michaelis-Menton form is often used, such as

$$P_5 = \frac{P_M}{1 + \frac{K\beta}{C_c}}, \quad \beta = 1 + \frac{[O_2]}{K_o} \qquad (13)$$

where P_M is the CO_2 saturated rate of photosynthesis, K and K_o are constants, and $[O_2]$ is the O_2 concentration at the site of carbon fixation. The introduction of O_2 levels is needed because it inhibits the activity of the major enzyme of photosynthesis, ribulose 1-5 bisphosphate carboxylase. P_M in turn depends upon light level L, and a variety of forms have been utilized such as

$$P_M = \frac{\alpha L}{\left(1 + \frac{\alpha^2 L^2}{P_{ML}^2}\right)^{1/2}} \qquad (14)$$

where P_{ML} is photosynthetic rate at light and CO_2 saturation, and α is the maximum efficiency to light

$$\alpha = \lim_{L \to 0^+} \frac{dP_M}{dL}.$$

The measured quantities in the above are P_1, C_A, and L, while values of $R_1, \ldots, R_4$, W can be estimated. Using (11)-(14) and a bit of algebraic manipulation, it is possible to solve for the unknown fluxes $P_2, \ldots, P_4$, back substitute and arrive at

$$P_1 + W = \frac{P_M}{1 + \frac{K\beta}{C_A - P_1 S_1 - W S_2}} \qquad (15)$$

where S_1 and S_2 are functions of the R_i's. This gives a quadratic in P_1 which can be solved. The model can then be analyzed by varying the environmental inputs and making comparisons to observations to test its validity. Generally, this model gives qualitatively similar results to those observed in laboratory experiments. See Gates (1980, pages 514-522) for a complete analysis.

The above model is of course quite limited in applicability, for it is inherently steady-state, ignores the spatial structuring of leaves, and the biochemistry is handled in a very simplistic manner. Yet, this approach has been most useful for combining the many factors which affect photosynthesis, and has stimulated much research to more accurately specify the parameters and functional forms used in the model. Models have been formulated which emphasize the biochemical dynamics of photosynthesis (Milstein and Bremerman, 1979) along with the photochemical energy absorption involved (Crill, 1977). Relatively few attempts have been made to analyze photosynthetic dynamics at the leaf level. Parkhurst (1977) analyzes the steady-state behavior of a continuous model of internal leaf CO_2 uptake

$$\frac{\partial C}{\partial t} = \frac{\partial}{\partial x}\left(p_1 D \frac{\partial C}{\partial x}\right) + \frac{\partial}{\partial y}\left(D p_2 \frac{\partial C}{\partial y}\right) + \frac{\partial}{\partial z}\left(D p_3 \frac{\partial C}{\partial z}\right) - U \qquad (16)$$

for the purpose of investigating the effect of 3-dimensional structure on CO_2 uptake. Here C is CO_2 concentration, U is photosynthetic rate, p_i's are leaf porosities, and D is diffusivity. Gross (1981) analyzes the dynamic behavior of (16) to compare with data on photosynthetic responses to light changes and concludes that the dynamics of diffusion do not account for the observed dynamics. The dynamics of stomatal response to variations in CO_2, water, and light have been investigated by Cowan and Farquhar (1977), while Rand et al. (1981) have investigated the potential for Hopf bifurcations to occur in models of stomatal mechanics. At the leaf level, photosynthetic models for the dynamic response to external CO_2 changes (Kaitala et al., 1982) and environmental light variations (Gross, 1982) have been constructed, but as yet there are no models which combine these factors, or include others such as water availability in a dynamic manner.

III Leaf Size

It is possible to use the above results concerning heat loading and photosynthesis to analyze the question of what leaf sizes are expected to be most adaptive in a variety of environments. The central problem revolves around the fact that most of the radiant energy incident upon a leaf cannot be utilized by photosynthesis, so that much absorbed energy must be dissipated as heat through evaporation. Photosynthesis increases with leaf temperature over certain ranges, and leaf temperatures rise as leaf size increases, due to an increase in boundary layer thickness. Transpiration rates also increase with leaf size, but not in the same manner as photosynthesis. There are trade-offs involved in how high a leaf temperature can be supported by the root system's capacity to supply water, and also by the reduction in photosynthesis at high temperatures. Thus a number of studies have attempted to establish the relationship between leaf size and benefit to the plant, and I here review some of these.

Due to the trade-offs between carbon gain and water use, it is unclear what might be the proper criterion to use for determining optimal leaf sizes. Parkhurst and Loucks (1972) use for their criterion water use efficiency, meaning the ratio of photosynthesis to transpiration. For photosynthetic rate, they use a simpler resistance analog than investigated above, letting

$$P = \frac{C_A - C_c}{R_A + R_M + R_S} f(T_s)\, g(L) \qquad (17)$$

where R_A, R_M, and R_S are respectively air, mesophyll, and stomatal resistance and $f(\cdot)$ describes the temperature response of photosynthesis and $g(\cdot)$ the light response. Then using (6) for evaporation, and the simpler form of (1)

$$Q_a = \sigma \epsilon (T_s + 273)^4 + h_c (T_s - T_A) + \lambda E \qquad (18)$$

they choose leaf size so as to maximize water use efficiency, $P/\lambda E$, using a numerical technique. There are seven independent variables they investigate: convection coefficient h_c, air temperature T_A, relative humidity h, absorbed radiation Q_a, stomatal resistance R_s, mesophyll resistance R_M, and stomatal distribution. At first the dependence of photosynthesis and transpiration on leaf temperature is ignored, but these may be included later. This analysis produces, among others, the following predictions:

1. When radiation absorbed by the leaf is high, smaller leaf sizes have a higher water use efficiency.

2. When absorbed radiation and air temperature are low, smaller leaves should again prevail.
3. When absorbed radiation is low, but temperatures high, larger leaves should be favored.

These are generally born out by the available data, but it should be noted that the use of efficiency as an optimization criterion allows for the optimal leaf to be either infinitely large or infinitesimally small (Solbrig, 1981).

An alternative approach, taken by Givnish (1979), is to look at transpiration as having a photosynthetic "cost" in terms of maintaining root and shoot tissue to support a given level of transpiration. This view, similar to a cost-benefit analysis, uses net carbon assimilation as the optimization criterion, given by

$$N = (P - R - bE)\,A \qquad (19)$$

where N is net carbon gain, R, P, and E are daily rates per unit leaf area of nightly respiration, net photosynthesis, and transpiration respectively, and A is leaf area. The parameter b is a constant giving the metabolic costs of supplying a unit of transpirational water. Using a graphical approach, Givnish has investigated how the maximum value of N changes with leaf area depending upon solar radiation inputs and water supply. Qualitative predictions can be made such as

1. Small leaves are favored over large leaves in very sunny and very shady environments, though for different reasons.
2. In intermediate radiation regimes, transpiration is rather independent of leaf size, so leaf size is at the point where photosynthesis alone is maximized.

These types of results have been tested against observations of vine leaves (Givnish and Vermeij, 1976), with generally good agreement. This approach has advantages in that it is possible to include in it a whole variety of other factors which could affect optimal leaf size including leaf thickness, costs of support structures such as petioles, and the role of nutrients.

Although the above has gone a long way in resolving such questions as under what circumstances plants should be energy maximizers (e.g. maximize photosynthesis) or cost minimizers (e.g. minimize water use), the criteria used are still very crude. The approaches consider only steady-state environments, and introduction of dynamics would extremely complicate the picture. Although the models give good qualitative predictions of general trends, they are generally at a loss to explain the great variability in leaf shapes and sizes which may be observed at any single location. The whole question of plant interactions is basically unexplored in this context and it may well be, as suggested by Givnish (1979), that for these situations criteria of maximal carbon gain need to be replaced with those based upon evolutionarily stable strategies.

References

1. Able, K.P. (1982). Skylight polarization patterns at dusk influence migratory orientation in birds. Nature 299: 550-551.

2. Bakken, G.S. & D.M. Gates. (1974). Notes on "Heat loss from a Newtonian animal". J. theor. Biol. 45: 283-292.

3. ______________. (1975). Heat transfer analysis of animals: some implications for field ecology, physiology and evolution. Pages 255-290 in D. Gates & R. Schmerl (eds), ibid.

4. Calow, P. & C.R. Townsend. (1981). Energetics, ecology and evolution. Pages 3-19 in C.R. Townsend & P. Calow (eds). ibid.

5. Campbell, G.S. (1977). An introduction to environmental biophysics. Springer-Verlag, N.Y.

6. ______________. (1981). Fundamentals of radiation and temperature relations. Pages 11-40 in O.L. Lange et al. (eds.) ibid.

7. Chapin, F.S. III. (1980). The mineral nutrition of wild plants. Ann. Rev. Ecol. System. 11: 233-260.

8. Cowan, I.R. & G.D. Farquhar. (1977). Stomatal function in relation to leaf metabolism and environment. Symp. Soc. Exp. Biol. 31: 471-505.

9. Crill, P.A. (1977). The photosynthesis-light curve: a simple analog model. J. theor. Biol. 64: 503-516.

10. Gates, D.M. (1980). Biophysical ecology. Springer-Verlag, N.Y.

11. ______________ & R.B. Schmerl. (1975)(eds) Perspectives of biophysical ecology. Springer-Verlag, N.Y.

12. Givnish, T. (1979). On the adaptive significance of leaf form. Pages 375-407 in O.T. Solbrig, S. Jain, G.B. Johnson, & P.H. Raven (eds). Topics in Plant Population Biology. Columbia Univ. Press, N.Y.

13. ________ & G.J. Vermeij. (1976). Sizes and shapes of liane leaves. Amer. Nat. 110: 743-776.

14. Gross, L.J. (1981). On the dynamics of internal leaf carbon dioxide uptake. J. Math. Biol. 11: 181-191.

15. ________. (1982). Photosynthetic dynamics in varying light environments: a model and its application to whole leaf carbon gain. Ecology 63: 84-93.

16. Harper, J.L. (1977). Population biology of plants. Academic, London.

17. Hesketh, J.D. & J.W. Jones. (1980). Predicting photosynthesis for ecosystems models. CRC Press, Boca Raton, Fla.

18. Hewitt, E.J. & T.A. Smith. (1974). Plant mineral nutrition. English Univ. Press, London.

19. Kaitala, V., P. Hari, E. Vapaavuori, & R. Salminen. (1982). A dynamic model for photosynthesis. Ann. Bot. 50: 385-396.

20. Kluger, M.J. (1975). Energy balance in the resting and exercising rabbit. Pages 497-507 in D.M. Gates & R.B. Schmerl (eds). ibid.

21. Krebs, C.J. (1978). Ecology. Harper & Row, N.Y.

22. Lange, O.L., P.S. Nobel, C.B. Osmond, & H. Ziegler. (eds). (1981). Physiological Plant ecology I. Encyl. Pl. Physiol. Vol. 12 A, Springer-Verlag, Berlin.

23. Lewontin, R.C. (1978). Fitness, survival, and optimality. P. 3-21 in D.H. Horn, R. Mitchell, & G.R. Stairs (eds). Analysis of ecological systems. Ohio St. Univ. Press, Columbus, Oh.

24. Maynard Smith, J. (1978). Optimization theory in evolution. Ann. Rev. Ecol. System. 9: 31-56.

25. Milstein, J. & H.J. Bremermann. (1979). Parameter identification of the Calvin photosynthesis cycle. J. Math. Biol. 7: 99-116.

26. Moen, A.N. & N.K. Jacobsen. 1975. Thermal exchange, physiology, and behavior of white-tailed deer. Pages 509-524 in D.M. Gates & R.B. Schmerl (eds), ibid.

27. Nevo, E. (1979). Adaptive convergence and divergence of subterranean mammals. Ann. Rev. Ecol. System. 10: 269-308.

28. Nobel, P.S. (1974). Introduction to biophysical plant physiology. Freeman, San Francisco.

29. ________. (1981). Wind as an ecological factor. Pages 475-500 in O.L. Lange et al. (eds). ibid.

30. Parkhurst, D.F. (1977). A 3-dimensional model for CO_2 uptake by continuously distributed mesophyll in leaves. J. theor. Biol. 67: 471-488.

31. ________ & O.L. Loucks. (1972). Optimal leaf size in relation to environment. J. Ecol. 60: 505-37.

32. Plant, R.E. (1982). A continuum model for root growth. J. theor. Biol. 98: 45-59.

33. Pond, C.M. (1978). Morphological aspects and the ecological significance of fat distribution in wild vertebrates. Ann. Rev. Ecol. System 9: 519-570.

34. Rand, R.H., S.K. Upadhyaya, J.R. Cooke, & D.W. Storti. 1981. Hopf bifurcation in a stomatal oscillator. J. Math. Biol. 12: 1-11.

35. Raschke, K. (1979). Movements of stomata. Pages 383-441 in W. Haupt & M.E. Feinleib (eds). Physiology of movements. Encycl. Pl. Phys. Vol. 7, Springer-Verlag, Berlin.

36. Remmert, H. (1980). Ecology. Springer-Verlag, Berlin.

37. Rundel, P.W. (1981). Fire as an ecological factor. Pages 501-538 in O.L. Lange et. al. (eds). ibid.

38. Schmidt-Nielsen, K. (1975). Animal physiology. Adaptation and environment. Cambridge Univ. Press, Cambridge.

39. Silberglied, R.E. (1979). Communication in the ultra-violet. Ann Rev. Ecol. System. 10: 373-98.

40. Skuldt, D.J., W.A. Beckman, J.W. Mitchell, & W.P. Porter. (1975). Conduction and radiation in artificial fur. Pages 549–558 in D.M. Gates & R.B. Schmerl (eds). *ibid*.

41. Solbrig, O.T. (1981). Energy, information and plant evolution. Pages 274–299 in C.R. Townsend & P. Calow (eds). *ibid*.

42. Southwick, E.E. & D.M. Gates. (1975). Energetics of occupied hummingbird nests. Pages 417–442 in D.M. Gates & R.B. Schmerl (eds). *ibid*.

43. Thornley, J.H.M. (1976). Mathematical models in plant physiology. Academic Press, N.Y.

44. Townsend, C.R. & P. Calow. (1981). Physiological ecology: an evolutionary approach to resource use. Sinauer, Sunderland, Mass.

45. Tracy, C.R. (1975). Water and energy relations of terrestrial amphibians: insights from mechanistic modeling. Pages. 325–346 in D.M. Gates & R.B. Schmerl (eds). *ibid*.

46. Tranquillini, W. (1979). Physiological ecology of the alpine timberline. Springer Verlag, Berlin.

47. Weiser, C.J. (1970). Cold resistance and injury in woody plants. Science *169*: 1269–1278.

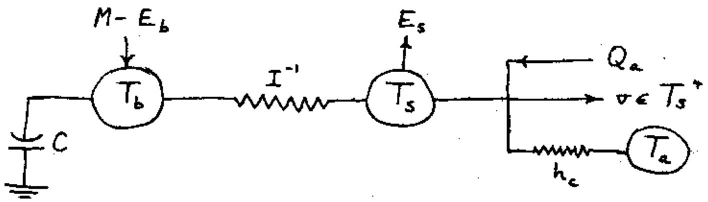

Figure 1: E_b is heat loss in respiratory evaporation, E_s is heat loss from surface evaporation, C is the heat capacity of the body of the animal, and all other variables are as given in the text. This represents an animal with negligible conduction to the ground. See text for further explanation. (Bakken and Gates, 1975).

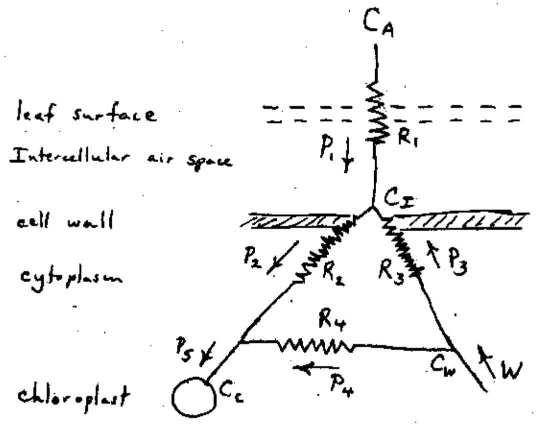

Figure 2: Resistors represent resistances, R_i, to diffusive flow between various leaf compartments, P_i's are CO_2 fluxes between compartments, C_i's are CO_2 concentrations (air, intercellular air space, chloroplast, and respiratory), and W is the flux of respiratory CO_2. See text for analysis. (Gates, 1980, page 496).