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**"Plant Physiological Ecology:  
A Theoretician's Perspective"**

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**These are preliminary lecture notes, intended only for distribution to participants.**

PERSPECTIVES  
IN  
*Ecological Theory*

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FROM INDIVIDUALS  
TO POPULATIONS

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I

*Chapter 1*

Plant Physiological Ecology:  
A Theoretician's Perspective

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The central issues of plant physiological ecology concern the effects of environment on individual plant growth, survival, and reproduction. In this regard, physiology is viewed as the mechanism through which the joint effects of heredity and environment are coupled to determine the growth form and reproductive success of an individual (Kramer 1948). My goal here is to provide a very brief review of the major questions that the field addresses, with emphasis on the use of theory; give a few examples of how theory has contributed new perspectives; point out some directions I feel are as yet relatively unexplored; and, finally, make some comments about coupling with other levels of organization. This is meant as a theoretical complement to the excellent review and set of recommendations for future research by Ehleringer et al. (1986). What I discuss is limited by my own biases, including a blatantly terrestrial one. A comprehensive review of the area accessible to a general audience is contained in the January 1987 issue of *BioScience*. The most exhaustive compilation of research in the area to date is the series of books edited by Lange et al. (1981, 1982, 1983). Relatively few mathematically oriented books have appeared, but those containing some relevant material include Thornley (1976), DeWit (1978), Rose and Charles-Edwards (1981), Charles-Edwards (1981), Jean (1984), and Gross and Miura (1986). On the biophysical end, the books by Gates (1980) and Nobel (1983) are standards. For a fine collection of papers that take an economic, cost-benefit approach to energy capture and utilization by plants, see Givnish (1986a).

Generally, I have found that two quite different viewpoints prevail in plant physiological studies. On the one hand, ecologists approach problems from an evolutionary perspective and consider physiology as a means to carry out adaptations necessitated by selective forces. Those with an agronomic approach, on the other hand, are more typically reductionist in that they are primarily concerned with the "how" of direct hormonal control of physiology and not with the ultimate questions of how that hormonal control arose. In fact, ecologists also typically view hormonal control as fixed, and then try to explore its ecological role. To a certain extent, these differing viewpoints have produced a schism in the field. Much of what is published under the rubric of plant physiology deals with specific details of biochemical control of physiology, and recent emphasis on the cellular and molecular levels has relegated whole-plant physiology to a back water, making it a retrospective rather than a predictive field (Kramer 1986). A great deal might be gained if ecologists recognized that their assumptions about the fixity of hormonal control are often overly restrictive and if physiologists took a more holistic view of plant functioning. In addition, ecophysiology has relatively recently become much more instrumentation oriented. The electronic revolution has made both field and lab measurements of certain physiological processes affordable even to those with minimal financial resources.

These trends have allowed us to learn a great deal about particular details of physiology, and they have produced a basic data set on physiological responses to a reasonably large fraction of the world's habitats. At the same time, however, the integration of our knowledge at the detailed biochemical level to investigate whole-plant phenomena is very inadequate. Modern physiology seems to have drifted far from practical applications to crop and forest population. This is not to say that the questions investigated are not of interest in their own right, nor that they will not eventually be important in addressing practical problems, but rather that currently most ecophysiologicals, agronomists, and foresters make minimal use of recent plant physiology research. These difficulties are very much tied to the current limitations of reductionist approaches at longer time and larger spatial scales.

## THE BASIC THEORETICAL APPROACHES

The central questions of ecophysiology concern (1) plant form; (2) response of metabolic processes—including photosynthesis, respiration, transpiration, and translocation—to environments within an individual's life span; (3) inferred population-level responses to environment over many generations; (4) partitioning of resources among plant parts and for defense from herbivores; and (5) interactions at other levels, including host-parasite relationships, ecosystem productivity and nutrient cycling analysis, and agricultural system analysis. These

questions are, of course, not independent of each other. It is, however, often possible to effect a separation by recognizing that some processes take place on significantly different time scales than others. Thus, questions of metabolic responses on a daily time scale, or acclimation responses over weeks, consider the genetic makeup of the population as fixed, separating the questions of ecotypic differentiation from those of short-time responses of physiology. The following sections will briefly review the theoretical approaches to these questions.

### *Plant Form*

The branched architecture of plants and the spiral patterns of phyllotaxis have long been topics of interest among botanists. A variety of mathematical theories have been proposed to both describe and provide a mechanistic basis for understanding phyllotaxis (Jean 1984). The theories are based on quite different physiological mechanisms, including those that maintain that primordia (1) grow until they are "pressured" by adjacent primordia (Adler 1977); (2) arise as a gap-filling process in regions of some minimal size (Adler 1975); and (3) produce a morphogen that acts as an inhibitor of new primordia, with reaction-diffusion equations describing the field of inhibition and predicting where new primordia will arise (Thornley 1976). Even the fairly elaborate mathematical models for these alternative physiological mechanisms do not produce testable hypotheses that would allow experiments to differentiate between them.

Much work has been done on the simulation of branching patterns to determine the general patterns one might expect under alternative design constraints (Bell, Roberts, and Smith 1979), including maximizing effective leaf area (Honda and Tomlinson 1982). Niklas (1986) has compared the conflicting requirements for light interception, biomechanical constraints of an upright form, hydraulic constraints for water supply, and reproductive display and maintenance. In addition to yielding fascinating comparisons to data on the evolution of architecture, these analyses show that there is no single "optimal" form: because of the non-linear relationships between the constraints, the form predicted for a particular habitat varies with environmental conditions. Even with linear main effects, the multiplicity of interactions and constraints can preclude a single optimal form and hence promote diversity (Horn 1981). Indeed, the diversity of plant form evident in any single habitat argues that either form is only weakly coupled to mild environmental differences, that the models do not accurately take into account the alternative selective pressures on plant form, or that the phenotypic optimization approach of these models is inappropriate due to their neglect of the historical nature of the evolutionary process. Nevertheless, these models, especially when coupled with biophysically realistic analyses of environmental effects on basic physiological processes, provide a template to check overall patterns of plant form among differing environments.

Many sophisticated mathematical models have been derived to analyze the response of basic plant metabolic processes to differing environmental conditions. These generally include simplifications of the known complexities of the biochemistry involved, and at some level even the most reductionist models are empirical. The vast majority of work has been done on static models that assume the plant is sitting in constant environmental conditions. In considering diurnal variations, the assumption is that the physiology instantaneously tracks the environment by moving among the associated steady states. This approach is reasonable only if the dynamics of physiological response operate much more rapidly than the environmental variations driving the response. In most natural conditions, I believe this assumption is not justified and the accuracy of calculations based on steady-state assumptions needs to be checked by reference to dynamic models that have been carefully validated. It would be useful to delineate the types of habitat in which the physiology can keep pace with environmental changes, making it possible to specify when dynamic models are necessary. Such work on light and photosynthesis is being carried out by Chazdon (1988) and Pearcy, Chazdon, and Kirschbaum (1987).

Dynamic responses may be investigated on physiological, acclimation, and evolutionary time scales (Gross 1986). The physiological time scale concerns variations in environmental components within a day, and I believe the theory can be developed in a straightforward manner once an adequate data base is established from lab and field measurements. In addition to allowing us to more accurately estimate ecologically important properties such as carbon gain in varying environments, such measurements should provide new insights into the basic physiology of the processes involved. The acclimation time scale concerns changes in physiology and anatomy that occur throughout the life span of the individual, including developmental changes, production of new branches and leaves, and the senescence of plant parts. This couples the dynamics of physiological changes (e.g., stomatal density and mesophyll thickness can change within a leaf because of light changes during development) to the demography of plant parts (e.g., the initiation of new leaves with a differing physiology) (Bazzaz 1984). On this time scale it may be useful to consider quasi-independent plant parts as individuals competing for resources, which premise forms the basis for much of the source-sink models developed to date. To be truly successful, however, we need more information on the mechanisms involved in the shedding of plant parts. Theoretical approaches on this time scale have been limited (but see Gross 1984 for an application to photosynthetic capacity, and the section below on allocation patterns). The evolutionary time scale concerns ecotypic differentiation of physiological traits and alternative physiological solutions to environmental constraints observed between taxa. Life-history theory is applied on this scale and

one cannot really divorce the population from the individual here (Bazzaz et al. 1987). To date, however, even the most complete life-cycle models used to analyze alternative life histories include very little physiological detail (Caswell 1986). Linking the population-level parameters of fecundity and mortality to measurable physiology remains a very open area.

Of all the metabolic processes in plants, photosynthesis has been the one most intensively modeled. The starting point is often some simplification of the biochemical pathways for carbon assimilation, coupled with assumptions about stomatal behavior, to consider the effects of light, temperature, carbon dioxide, and humidity on net photosynthetic rates. A compendium of models is given by Hesketh and Jones (1980). These models are inherently steady-state and are designed mainly to grapple with the problem of how to combine the effects of the many environmental variables that control uptake. They have been extensively used in many physiologically based crop growth models and as submodels in ecosystem simulations (Reynolds and Acock 1985).

Models that attend to more biochemical and photochemical details (Farquhar, von Caemmerer, and Berry 1980; Farquhar and von Caemmerer 1982) have been instrumental in focusing attention on the importance of the intercellular carbon dioxide concentration in coupling stomatal function with the biochemical photosynthetic pathways. The basic approach is to utilize detailed biochemical models to specify the functional relationship,

$$A = f(p_i), \quad (1.1)$$

between net carbon assimilation rate  $A$  per unit leaf area and the intercellular partial pressure of carbon dioxide,  $p_i$ . The function  $f(\cdot)$  contains a variety of parameters related to enzyme activation and sizes of various pools of metabolites, as well as environmental inputs such as light and partial pressure of oxygen. The result is a concave function of  $p_i$ , similar to a Michaelis-Menton curve, though with sharp transitions when alternative biochemical processes are limiting. This is then coupled to stomatal conductance, since by definition conductance  $g$  is such that

$$A = \frac{g(p_a - p_i)}{P} \quad (1.2)$$

where  $p_a$  is the partial pressure of carbon dioxide external to the leaf, and  $P$  is atmospheric pressure. Since, as a function of  $p_i$ , (1.1) is concave and (1.2) is linear with negative slope, upon setting (1.1) equal to (1.2) there is a unique solution for  $p_i$ . This solution, obtained numerically, gives the equilibrium  $p_i$  and  $A$  values for given leaf and environmental conditions. By pointing out the importance of the relationship (1.1), this modeling effort has led to changes in the way experimentalists carry out their observations. Together with advances in instrumentation over the last decade, particularly the availability of good mass flow meters, such

modeling has led many researchers to measure the relationship (1.1) rather than to measure assimilation as a function of light or of other environmental factors, which were the prevalent measurements taken prior to the Farquhar-von Caemmerer approach. This modeling was among the first to integrate appropriately a variety of physiological functions, and ecophysiologicals use it as a basis to couple detailed physiology with conditions in natural environments.

Another modeling approach that has had great influence on ecophysiology concerns the control of stomatal conductance (Cowan 1977, 1982). The goal is to determine how  $g$  in (1.2) behaves as a function of environmental variables as well as how it correlates with assimilation, since  $g$  is viewed as an externally determined variable in the Farquhar-von Caemmerer model. Here calculus of variations is applied to determine optimal patterns of stomatal opening. The objective is to minimize water loss, subject to the constraint that integrated carbon assimilation is maintained at some fixed level, presumably that which will assure adequate photosynthate production to meet plant needs for growth and reproduction. The mathematical form of the model involves the assumption that transpiration rate per unit leaf area,  $E$ , is an implicit function of  $A$ , and that each of these depend on time and location on the leaf. Then, if  $s$  is the space variable (one-dimensional here), the requirement is that

$$\int_0^T \int_0^S [E(A, s, t) - \lambda A] ds dt \quad (1.3)$$

be minimized, where  $\lambda$  is a Lagrange multiplier. The solution implies that

$$\left( \frac{\partial E}{\partial A} \right)_{s,t} = \lambda. \quad (1.4)$$

Here  $\lambda$  may be viewed as the benefit of carbon gain relative to the cost of water loss. Since both  $A$  and  $E$  may be measured, by varying environmental conditions (1.4) may be tested, though there are some difficulties related to constraints on stomatal control that are not taken into account in this simple framework (Cowan 1986). Alternative models for the trade-offs between carbon gain and water loss are closely related to this model (Givnish 1986b).

Considerably less theoretical work has been done on other physiological processes. Our most detailed knowledge is at the level of individual leaf function (Percy et al. 1987). Respiration remains an area in which lack of data and the confounding of dark and light respiration make theoretical developments quite difficult (Penning de Vries 1983). Maintenance respiration is normally assumed to be just proportional to biomass, with some temperature dependence, and the respiratory load of below-ground material as well as any associated mycorrhizae

is relatively unexplored. Patterns of fluid flow within a plant have been investigated with a variety of models (Rand 1983), though with rather little concern for the detailed operations of the associated conductive tissue. Elaborate biomechanical models of stomatal behavior (Delwiche and Cooke 1977; Sharpe and Wu 1978), often specifically constructed to mimic stomatal oscillations, have thus far led to rather little in the way of ecological insight, though they are mathematically interesting. Indeed, I believe a more feasible approach is to consider a "statistical mechanics" of stomata taking account of the coupling between stomata that can produce spatially structured patterns across a leaf surface (Rand and Ellenson 1986).

Biophysical models allow the coupling of the many physical processes which affect plant function, with particular emphasis being given to energy-balance models. These models can predict how alterations in wind, ambient temperature and radiation, and humidity affect heat loads on organisms of any given shape. They have been particularly useful in predicting trends in leaf size and shape across habitats (Parkhurst and Loucks 1972; Givnish 1979). They serve as the basis for understanding plant-atmosphere interactions (Grace 1983) and allow the coupling of detailed within-canopy radiation models (Norman 1980) with leaf distribution models to produce whole canopy assimilation estimates (Baldocchi and Hutchison 1986). Despite their utility, these approaches can provide only a fairly crude understanding of the biophysical limitations to growth in a particular habitat, which is inadequate to explain the great variability in leaf shape and size in many habitats. Although there are some fine and detailed models of simple canopies, they ignore much of the variation in both environment and leaf physiology within canopies, often by simply breaking the canopy into sunlit and nonsunlit fractions.

#### Allocation Patterns

Knowledge about plant allocation patterns is largely empirical, and relatively little is known about their control (Percy et al. 1987). Because a limited amount of available resources (photosynthate, water, and nutrients) must be apportioned between alternative demands, there are trade-offs, and two alternative approaches have been taken to analyze them. The first is a cost-benefit analysis that takes biomass or a limited nutrient as a currency to measure the allocation pattern. A key assumption is that increasing photosynthetic capacity will lead to increased growth, though there is surprisingly little data to support this. Growth is strongly correlated with total light interception capacity and is typically limited by environment, not physiology (Kramer 1986). The second approach is to construct mechanistic compartment models for whole plant growth that break a plant into roots, shoot, leaves, fruit, etc. Flows of nutrients between compartments are driven by sink and source strengths, and partitioning of new material is governed

by a goal-seeking assumption that is set a priori—for example, to maintain a fixed C:N ratio or fixed root:shoot ratio (Thornley and Johnson 1986). This structure is typically applied in physiologically based crop-growth models where the model predictions can be readily tested against data.

An alternative to compartment-type models is to assume the existence of underlying organizing principles of evolutionary origin that specify the growth form in any particular environment. The cost-benefit analysis here takes the form of an optimal control problem, first analyzed by Cohen (1971). The chosen optimization criterion is usually some measure of reproduction, and elaborations consider random season lengths, varying environments, herbivory, and several vegetative compartments (Roughgarden 1986). This approach, though capable of producing allocation patterns similar to those observed (i.e., bang-bang allocation of resources in annuals), is almost totally lacking in the physiological detail necessary to couple its parameters to measurable aspects of any particular species or group of species. Nevertheless, the models do produce reasonably accurate portrayals of the general balance that seems to exist in plant allocation, and they mimic the types of adjustments that are observed to occur when there are imbalances in the availability of different resources (Chapin et al. 1987). Detailed validation for particular taxa cannot be attempted until the models become more physiologically realistic, but the models *can* provide hypotheses about trends across taxa and environmental conditions. The approach suffers all the difficulties associated with optimization schemes, but see Givnish (1986a) for arguments as to why the adaptationist program has proven so useful here.

There are a host of open theoretical questions regarding allocation of resources for defense from herbivores. Models that relate plant quality to herbivore population dynamics are few (Edelstein-Keshet 1986) but represent a first step toward producing a physiologically based approach. Such an approach involves a partial differential equation for the change in plant quality through time, and represents only one of many potential ways to tie physiology to population-level models by using a relevant physiological variable to structure the population (Metz and Diekmann 1986). This approach still needs to be used with a control-type problem to produce, for example, a cost-benefit analysis related to plant apparency. Gulmon and Mooney (1986) have already proposed a starting framework for a theory of allocation to defense, particularly as it relates to resource availability. Remaining theoretical questions involve spatial and temporal patterns of allocation to defensive compounds and the multiple constraints that act on such allocations (Bazzaz et al. 1987).

#### *Systems and Future Directions*

Physiological models are combined to serve as the basis for complex systems models of both natural and managed ecosystems (Reynolds and Acock 1985).

Systems models are typically structured around particular crops or natural habitats, though there have been recent attempts to construct a generic model (Reynolds et al. 1986). These mechanistically based models have served to reveal areas in which our ignorance limits the model's usefulness, and they conveniently join the vast array of physiological processes operating in these systems. But they do have their limitations. They cannot compensate for our lack of expertise in certain areas, such as how to handle the interactions of multiple environmental stresses (Chapin et al. 1987). Systems models typically contain hundreds of parameters whose values we can only approximate from our knowledge of physiology, and we know little about them regarding variation between individuals or species. Even the most elaborate crop growth models are not yet as accurate in yield prediction as relatively simple regression models. On the other hand, the complex mechanistic models serve as the only means to track the dynamics of the components of ecosystems, and thereby determine appropriate control measures. Indeed, this is one of the current uses of detailed crop models, particularly with respect to irrigation, fertilization, and pesticide scheduling. Regression approaches lack this capability because they are strictly limited by the data set used in their construction.

At certain levels, it may simply be inappropriate to include the details of physiology. Forest-stand simulation models appear to reflect forest composition changes realistically over periods of centuries by tracking individual trees through their lifespan (Shugart 1984). Yet their physiological component is extremely naive, causing some physiologists to lambast the approach. This disagreement occurs in part because the time scales that are of interest to physiologists are much shorter than the centuries that this simulation approach is designed to work on. Of course, the lack of knowledge about physiology limits the types of questions for which the simulation approach is appropriate. It would be absurd, for example, to attempt to apply it in a rigorous way to predict effects of atmospheric carbon dioxide increases on forest successional patterns, since that would necessitate making a priori assumptions about how these atmospheric changes would differentially affect the component species of the system. Despite the lack of physiological detail in these individual-based models, the approach provides one of the few available means to investigate how altering physiological characteristics of component species will affect community-level processes (Huston and Smith 1987).

A further remark regarding the carbon dioxide question is relevant. One argument in support of continuing physiological studies about the direct effects of enhanced carbon dioxide emphasizes that the data are necessary to predict worldwide effects of the predicted increases. It may well be that this problem is impossible to solve. That is, no matter how much effort we exert to understand physiological responses to enhanced carbon dioxide, we cannot possibly answer the questions posed by policymakers because of the complexity of applying even

our limited knowledge at the population and community levels. In this case, although one can make an argument that the basic physiological questions are inherently interesting in their own right, completely different top-down methods may be much more appropriate to carry out a sort of risk analysis on the predictions demanded by politicians. A reductionist approach based on physiological details may be so incomplete that it is irrelevant, and it may even be counterproductive by taking attention and limited funding away from approaches more appropriate for the policy questions being posed.

Many areas of plant physiological ecology are still ripe for further theoretical development. Some of these were mentioned above. With relatively few exceptions (Hay 1986; Koehl 1986), many of the questions posed above have been unanswered for aquatic plants, for example. Another open area involves the application of the theory of evolutionarily stable strategies to partitioning among plant parts and to competition between individuals. A very crude example of this area is given in Riechert and Hammerstein (1983) in regard to rooting behaviors. There is also a need to develop a general theory of plant epidemiology. Though there has been a tremendous burst of activity in epidemiological modeling over the last decade, it has not been reflected in plant studies. Indeed, considering the severe economic and ecological effects of plant diseases, it is unfortunate that much of plant epidemiology is tied to specific agronomic situations. Although theories developed for animals do not apply directly to plants because of the importance of spatial effects and the display among populations of a continuum of resistance levels to any particular pathogen, models developed for macroparasites (Hassell and May, chapter 22) may be quite useful in plant situations. Coupling the physiological response to pathogen infection with the demographics of pathogens presents a fascinating and ultimately highly applicable area of theory. Gilligan (1985) has reviewed the state-of-the-art with regard to crop disease models, and a recent series of papers by van den Bosch, Zadoks, and Metz (1988a,b) covers spatial aspects of crop disease spread.

The general problems of scaling up, from our relatively good understanding of processes on a leaf-level, short-time scale to the whole canopy and plant, center around what can be reasonably ignored on the scales of the questions being posed. Indeed, the hope is that we need not consider much of the physiological detail when the focus is on population and community-level interactions. Determining how much physiology can be safely ignored in a particular problem is still debatable. One hope is that detailed physiological models will lead the way to more appropriate holistic descriptions of natural systems than are currently available. This uses reductionism to scale up rather than down by giving us clues as to how representative particular models at the population and community level are when used across different environmental circumstances. The idea is that physiologically based models not only specify the appropriate form for more empirical macrodescriptors of system behavior at larger scales, but also provide

means to test the robustness of these descriptors across different natural systems. The advances in our knowledge of molecular control of physiology and its genetic manipulation must be explored from an ecophysiological viewpoint before we can hope to ascertain community-level effects of the release of manipulated organisms. A physiological perspective is essential to let us know which manipulations will be successful agronomically as well as to allow us to evaluate what the long-term systems effects might be. In the hierarchy of natural systems, ecophysiology links cellular and biochemical phenomena to population and community-level processes, and this ability to consider the implications of vastly different scales adds to the exciting prospects in the field. Besides this coupling between scales, ecophysiology has its own interesting questions to address, independent of its utility to transfer information upscale to the population and community levels.

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## Chapter 2

# Individual Behavior and the Procurement of Essential Resources

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The relationship between behavior and the availability of resources is a central part of behavioral ecology. Accordingly, many questions asked by behavioral ecologists deal with either the procurement or allocation of resources. In the case of procurement, the resources in question may be food, mates, space, or refuges and the individual in question must decide how to acquire them. On the other hand, questions concerning sex ratio, life-history strategy, and helping behavior deal with the allocation of resources such as nutrients, energy, and time that are already at the disposal of the individual in question. In this paper, I discuss only the theory of resource procurement, though the basic philosophy and theoretical approach is similar for questions dealing with resource allocation and, in many cases, procurement and allocation must be considered simultaneously.

Many of the original practitioners of behavioral ecology were ecologists interested in behavioral mechanisms of population regulation and species interaction. More recently, the discipline has attracted the interest of other behaviorists, particularly ethologists and behavioral psychologists, interested more in behavior for its own sake. Practitioners of behavioral ecology can also be divided according to their theoretical approach. Most behavioral ecologists routinely use optimization models to guide their research and interpret their results. Other behavioral ecologists employ more descriptive or mechanistic models to summarize behavior and predict the consequences of behavior for higher-level phenomena such as spatial distribution, population dynamics, and species interactions (e.g., Hassell and May 1985; Pulliam 1987; Turchin 1986; and Kareiva 1987).

Those behavioral ecologists who make extensive use of optimization theory have commonly used static optimization procedures, including game theory, and in recent years have begun to employ dynamic programming, optimal control

