Commentary: What is Physiological Ecology?
A collection of commentaries by noted physiological ecologists (1982)
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Introduction

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The name "physiological ecology" clearly indicates that this discipline is a hybrid of physiology and ecology. But is physiological ecology simply another dimension of physiology or ecology alone, or is physiological ecology unique in some fundamental way from its parent disciplines (in the jargon of ecology, "are there any emergent properties to physiological ecology?")? These and other questions were asked of several biologists who were requested to submit short essays outlining their views. We hoped to use these essays to compile (a) definitions of physiological ecology, and (b) opinions on the relationship between physiological ecology and its parent disciplines. Not surprisingly, the opinions were eclectic. They varied all the way from the opinion that "there is (not) a lizard's eyelash of difference between 'physiological ecology,' 'environmental physiology,' 'ecophysiology,' or 'comparative physiology'" (Bennett), to a jesting comment that physiological ecologists and environmental physiologists can be identified on the basis of their wardrobe (Strain).

The lack of unanimity among the essays is perhaps the most striking result of this "experiment" with opinion. It suggests that physiological ecology has not yet "sorted out" as a discipline with distinct boundaries. Thus, while it is usually possible to distinguish the bulk of ecology from most of physiology, it is often more difficult to distinguish between physiological ecology and environmental physiology, although differences in emphasis appear to exist (Gates, Heinrich, Huey, Janzen, King, McClure, McNab, Miller and Strain). Further obscuring distinctions between these subdisciplines is the fact that other areas of science, such as behavioral ecology and ecological morphology, have developed intimate connections with physiological ecology. Indeed, the opinion was expressed more than once that physiological ecology would be poor science if it did not deal with behavioral and morphological aspects of the questions addressed (see Huey and King).

The lack of clear definition may not be troublesome to many, but as knowledge expands, there is a natural tendency to subdivide scientific disciplines and to define sharp boundaries of these new disciplines. This process can have the undesirable effect of isolating scientists into parochial "clubs," and it can have the beneficial effect of allowing scientists to throw off the shackles of "standard methods" and "acceptable questions" that practitioners of an established discipline might define. Sharp definition of the borders of any scientific discipline in its incipient stages of development can also stifle the interchange of ideas that fuels progress in science. On the other hand, scientists asking new kinds of questions often need to develop new ways of approaching a problem, without being obliged to conform to standards, from other disciplines, which may be inappropriate. Indeed, some essayists warn that simply borrowing methods from comparative physiology to examine questions in physiological ecology can yield misleading results (see Huey and McClure). Thus it appears that good scientific judgment may be a better guide to the pursuit of knowledge than those guidelines imposed by arbitrary doctrines associated with scientific disciplines.

Separate from the philosophical question of the relationship between physiological ecology and related areas of science are the practical necessities of our day-to-day lives as scientists which force us to engage in some classification of our colleagues. For example, we seek out colleagues with interests similar to our own with whom we may discuss ideas. We also need to identify scientists who can evaluate scientific reports submitted to our professional journals. Categorization of scientific material also is necessary to ensure that our journals publish material that is appropriate for the state purposes of the journal. For example, physiological ecology is seen to provide the mechanistic explanations of ecological processes at higher levels of integration (e.g., population growth, patterns of mortality, vulnerability to extinction, nutrient cycling, competitive exclusion, etc.; see essays by Bartholomew, Billings, Chabot, Gates, Heinrich, Huey, Janzen, King, McClure, McNab, Miller, Strain). But must a manuscript explicitly address questions at a higher level of integration than physiology to be acceptable material for publication in ESA journals? How do we simultaneously protect authors from reviewer prejudices and whimsical opinions not shared by all peers in a developing area of science, at the same time that we protect subscribers to journals from research reports that diverge a great deal from the stated mission of the journal?

A philosophical examination of the position, state of development, and importance of physiological ecology is an exercise that cannot be avoided, but it should be approached cautiously. While classification of a biological species does not affect either the previous or subsequent evolution of that taxon, classification of scientific disciplines can profoundly affect the field's course of future development. Thus, the membership of ESA should be challenged by these essays to participate in the processes that result in the evolution (and/or extinction) of scientific disciplines.

Definitions and Opinions

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Biology is a continuum, but for its study the establishment of subdivisions is an operational necessity. Unfortunately, nature is not organized on the basis of the fields of scientific specialization. Elaborate partitioning is apt to be biologically unrealistic and intellectually sterilizing. It probably does more harm than good to distinguish between environmental physiology, ecological physiology, and physiological ecology. Each deals with aspects of physiology that are relevant to ecology, and vice versa. If one defines ecology as the study of the relations between organisms and environment, ecologically relevant physiology covers an enormous area, including all those aspects of physiology that affect exchanges between organism and environment, or that affect the behavioral interactions between organisms.

Physiological ecologists attempt to identify and describe the biophysical and biochemical mechanisms that individual organisms use in coping with environmental factors, or that they employ in ecological interactions. Such findings establish a framework or mechanism that can also be used to analyze and interpret ecological interactions at population and higher levels of integration.

The methods of physiological ecology tend to make it more empirical than theoretical. Although the primary data of physiological ecology are physiological, these data are interpreted in the context of ecology. The intent of the physiological ecologist is more important than the methods he uses to gather his data. Ideally, he should be a technically competent physiologist and also a good naturalist and an able ecologist. If he has sufficient insight he can draw ecological inference from material derived from virtually any physiological discipline.

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I do not believe there is a lizard's eyelash of difference between "physiological ecology," "environmental physiology," "ecophysiology," or (these days) "comparative physiology." To me, these fields are synonymous: I have called my interests all these things and more. I think the distinctions among them are contrived and/or trivial. They all represent the same approach to organismal biology.

To my mind, physiological ecology involves functional studies that have three characteristics: (1) they are highly empirical, (2) they emphasize function under natural biotic and abiotic conditions, and (3) they consistently refer to performance within the context of an intact individual organism. The range of possible observations is thus exceptionally broad: virtually any aspect of mechanistic performance, from the biochemical level up, is appropriate and at times necessary. Sometimes our measurements will be indistinguishable from those of a systemic physiologist, a behaviorist, an histologist, or a population ecologist; our interpretive context is often different. This breadth and interpretation sometimes present problems for other biologists, and we may be told that a particular study is not "ecology" or not "behavior" or not "respiratory physiology." I regard this type of outlook as largely the problem of the observer. We cannot really expect everything we do to appeal to all our co-workers; one person's stunning insight is another's turned page. What we should do is to interpret our data in own context and make explicit the implications of our observations for as many different levels of biological organization as we find possible.

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Physiological ecology is not a science in isolation, but an integral part of ecology as a whole. It is not clearly distinct, if at all, from ecophysiology; both must deal with problems of organisms in field environments.

I view physiological ecology as playing at least two major roles in ecology. First, to understand how ecosystems operate in a changing biosphere, we must know how the plants, animals, and microorganisms in the ecosystem grow and reproduce. Whole ecosystems should be studied with regard to gains and losses of populations, soils, nutrients, energy, water and atmospheric components. But if one wants to know what makes an ecosystem tick, some further dissection is necessary. What are the roles of the physical components? How do the component organisms become established, metabolize, grow, and reproduce?

The second major role of physiological ecology is in helping to explain migrations and geographical distributions of taxa. Involved here is research on the physiological, morphological, and reproductive adaptations of local populations, ecotypes, and higher genetically based units in relation to the total environment and its components. Biospheric change can often be very fast. It is imperative that we know the potential environmental tolerance ranges of many plant and animal taxa as soon as possible. Without the observations and experimental results of physiological ecology, we will be hard pressed to predict or explain migrations, extinctions, and ecosystemic roles of important taxa, if, indeed, such predictions are possible at all.

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Physiological ecology is, as the name implies, a hybrid enterprise. This is its strength. Any attempt to construct a definition which distinguishes this from other approaches in ecology is likely to be self-defeating. The boundaries between most related disciplines are indistinct and should be left so. In the end, it is the biological phenomenon, itself, and its attendant hypotheses that justify the research effort and the spectrum of approaches used. There is little added virtue in identifying the question as lying within the realm of physiological ecology or any other discipline.

Physiological ecologists are usually interested in the mechanisms ("adaptations") by which organisms interact with their environment. These mechanism frequently include physiological processes, but may also involve anatomy, morphology, and behavior. For a physiological ecologist, these component processes achieve a necessary integration at the whole-organism level. In addition to questions of "how," the question of "why" specific traits are employed is often asked. This is the evolutionary aspect that involves placing adaptive mechanisms within more encompassing strategies. Increasingly, physiological ecology is providing insights into phenomena at the population (what controls reproductive output?), community (what traits determine competitive success?), and ecosystem (how do plants respond to herbivory? How do animal metabolic requirements affect feeding strategies?) levels. Increasingly, these other ecological disciplines are providing an added relevance for physiological ecology.

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To understand the response of organisms to their environments one needs to understand as thoroughly and rigorously as possible all pieces of the problem. The environment must be known correctly (radiation, temperature, nutrients, food, etc.). The organism must be known correctly (metabolic rate, respiration rate, photosynthetic rate, size, absorptance to radiation, insulation, etc.), including all the functional relationships (dependencies on temperature, light, carbon dioxide, nitrogen, etc.). Furthermore, the genotypic and phenotypic variations and dependencies of the various properties and functions must be understood. Clearly this involves understanding physics, meteorology, soils, physiology, genetics, anatomy, and even biochemistry. The use of such terms is unfortunate, because their use constrains one's thinking. What one desires is high-quality science irrespective of labels, whether it be physical or biological science.

Physiological ecology suggests that the goal is ecological, but the methodology will use physiological information. However, the ecology of an organism involves its interactions with the community of organisms in which t is immersed and includes competition, succession, and population dynamics. To understand physiology per se is not the goal, but only a means to an end, the end being the ecology of the organism. Environmental physiology has physiology as the goal, but uses environmental information to achieve that goal. The goal is the distinguishing factor here.

Most plant and animal responses to environmental conditions must ultimately be measured in the field, although laboratory measurements are often necessary as well. Organisms respond to a multitude of variables, and usually several variables are varying at any moment. Measurements must allow for this simultaneity of change. Plants and animals are in transient states very often. Many challenging physiological ecology questions relate to transient states of short duration: the effects of sunflecks on the productivity of understory vegetation, for example.

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An organism must respond to at least two different components of its environment. One component that elicits adaptive response concerns challenges from the physical world. The other major challenge that requires response originates from the biosphere.

In my opinion, the aim of physiological ecology is to determine physiological bases or limits that affect an organism's responses to its physical environment. The behavioral/physiological capacities ultimately determine niche-limits within the environment that the organism can occupy. For example, knowledge of the thermal tolerance and/or thermoregulatory capacity of insects of various sizes might allow one to make some predictions of weather conditions that exclude certain insects physically (diurnally, seasonally, or geographically), but favor others. Given a physiological explanation, sharpened by biophysical insights, for observed phenomena, one can then either examine potential responses that could act to circumvent an organism's physiological limits so as to broaden its niche, or the other type of environmental factors, such as low energy supplies and competitors, that might contract it.

The data, as such, with which physiological ecologists concern themselves may not be unique. The uniqueness concerns the interpretation of physiology and homeostatic mechanisms in terms of adaptation to the environment, and hence on evolution. The same data on thermoregulation, for example, might also be considered in the realm of comparative physiology, because they could be used to make general statements about body size and endothermy. The file one uses to categorize depends on one's broader frame of reference.

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Ecology is the study of interactions of organisms with each other and with the physical environment, whereas physiology is the exploration of underlying mechanistic processes that determine how organisms work. Physiological capacities strongly influence ecological interactions of organisms. Nevertheless, ecologists wishing to elucidate these influences should not unhesitatingly adopt the elegant experimental methods developed over many years by physiologists. Ecologists and physiologists ask complementary but different questions concerning physiology. Consequently, a study suitable for one field may not be suitable for the other.

Level of Analysis

Organismal performance reflects the integration of many component processes, each of which may respond differently to a given environmental variable. Thus organismal performance in nature, the primary focus of ecologists, is more reliably predicted from studies directed at whole organisms rather than from those directed at isolated tissues or biochemical reactions. In contrast, the mechanistic bases of performance, the focus of physiologists, can be determined only from lower level studies.

Control over Behavior and Morphology

Behavioral and morphological adjustments mediate an animal's physiological interactions and performance. Thus, performance in nature can be reliably predicted only from experiments permitting animals to use these adjustments. Lower level studies exclude such adjustments: this is appropriate for analyses of mechanisms, but not for prediction of organismal performance.

Acclimation

The recent history of an organism influences its capacity and performance. Most terrestrial organisms live in fluctuating environments that can have complex and often unpredictable effects on physiology. Thus, performance in nature is more reliably predicted from experiments in which animals have been exposed to natural acclimation regimes. In contrast, mechanistic, and especially comparative, studies in physiology may require exposure to constant acclimation regimes.

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Physiological ecology is the study of how physiological processes function with respect to environment, or are generated by interactions with the environment. The stress is on 'interactions' and they may be with anything from subcellular components to bogs. If a study in comparative physiology (e.g., interspecific variation in kidney blood processing rate) is focused on the processes that generate the variation (e.g., water and toxin content of the animals' foods) it is also a study in physiological ecology. It is a very human trait to concoct clubs (ecophysiology, environmental physiology, physiological ecology, etc.) and design the membership rules so as to benefit the members; the subdivsion of ecology into physiological, population, etc. is severely straining (and is generally detrimental through encouraging a narrowing of perspective), and certainly further subdivision can only have political or economic motives.

The important kinds of problems in physiological ecology are those that enlarge our conceptual and general framework of understanding, and those that fill in the interstices with specific examples, so that we can talk about both central tendency and variation in nature's solutions to the physiological challenges faced by organisms (e.g., what fraction of developing fruits bear chlorophyllous embryos in which habitats). Use and appropriateness of method and tools are specific to the question and organism rather than some imagined subdiscipline.

We study how organisms interact with their environments. It is appropriate to examine that interaction at all levels of organization (molecular, biochemical, cellular, physiological, morphological, individual, family, population, habitat, etc.). The 'importance' of physiological ecology is merely that it represents one of these levels.

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An essay of 250 words enforces a dogmatic approach, and the following observations about animal physiological ecology are therefore ex cathedra pronouncements shorn of redeeming weasel words. Organismal adjustments, broadly speaking, may be morphological, behavioral, or physiological, and can involve either genotypic responses (speciation) or phenotypic responses to proximate environmental factors in present time. Only the latter are in the realm of environmental physiology or physiological ecology. Environmental physiology typically focuses on physiological responses to abiotic factors, most commonly in the laboratory, without reference to natural environments or the life-styles of free-living organisms. The emphasis is on mechanisms of response or the limits of physiological plasticity (e.g., CNS control of thermal panting, renal or sweat-gland adjustments to water shortage or dehydration). The textbooks by Folk or Slonim (editor) entitled "Environmental Physiology" exemplify this perspective. In contrast, physiological ecology focuses not only on physiological adjustments by the phenotype, but also on the ways in which morphological and behavioral adjustments ameliorate or substitute for physiological limitations. The investigation of operational factors (biotic as well as abiotic) in natural microenvironments is an essential component of physiological ecology. To the extent that conspecifics and other species (through competition or predation) affect energy expenditure or access to nutrients, for instance, they may indirectly necessitate physiological adjustments, and thus constitute environmental factors within the scope of physiological ecology. At this interface, physiological ecology merges with behavioral ecology. As yet there are no textbooks on physiological ecology. Gates' "Biophysical Ecology" is the closest approximation. In short, the key concepts of physiological ecology that can guide editors who insist on distinguishing environmental physiology or comparative physiology from physiological ecology are: phenotypic physiological responses, natural microenvironmental variables, and morphological or behavioral substitutes for physiological capacities. Finally, readers should notice that I have not used the word "adaptation" even once.

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Physiological ecology is a branch of biological science in which the questions have their origins at the evolutionary or ecological level and their answers at the level of organismal or suborganismal physiology. This differs from comparative physiology in which the focus of questions is a specific organismal and sub-organismal process and a variety of organism "tools" are used to study the process. It also differs from environmental physiology in which the focus is on a specific (usually stressful) environmental factor such as altitude, cold, heat, and the organism's physiological responses to that factor.

The questions characteristically important concern basic issues of evolutionary and ecological biology, for example studies of the basis of ecotypic differentiation. The methods range from fairly descriptive correlation analyses to precise biochemical and physical measurements, sometimes in the context of designed experiments, sometimes not. The methods are usually not unique to physiological ecology except that, where possible, they are increasingly being adapted for use in the animal's natural environment. The most obvious example here is the method of measuring metabolic rate. Most studies employ the procedures for measuring oxygen consumption and carbon dioxide production in use in physiology laboratories, but we are having increasing success in measuring metabolic rate in the field using doubly labeled water. It is important that physiological ecologists differentiate between those questions answerable with standard physiological methods and those that require new methods, and that they expend the effort to develop appropriate and precise techniques.

The relationship of physiological ecology to population and community ecology on the one hand, and biochemistry and biophysics on the other, is that of a bridge between two otherwise isolated land masses. Physiological ecology can provide the ecological "so what?" at the population and community level to studies of variations in otherwise esoteric chemical and physical processes. It can also provide the predictability at the ecological level that comes from sound mechanistic foundations based on fundamental principles of chemistry and physics.

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Physiological ecology is an intellectual brew of elements taken from natural history, ecology, and evolution, and operationally tied to the experimental discipline of physiology. It differs from comparative and environmental physiology, not in subjects or techniques, but in goals: the former is principally concerned with the integrative view of ecology and evolution, the latter with reductionism. Physiology brings to ecology an analytic approach based in the physical sciences, although there is disagreement as to how far mathematics can be used to analyze the responses of organisms without unduly idealizing the problems. Ultimately, the principal concern of most physiological ecologists is the nature of, and the limits to, adaptation. As these limits are approached, physiological ecologists examine the means by which such limits are evaded, or how these limits are translated into a functional basis for the limits to climatic and geographic distribution. This field also has significance for other disciplines, such as population ecology (in that the reproduction of animals appears to depend on their rates of energy expenditure) or community ecology (where energy distribution and exchange in communities vary significantly with the trade-off between the size of individuals and the size of populations). Finally, the bedrock of physiological ecology is a thorough understanding of the natural history of the organisms being studied; not only does such knowledge influence the interpretation of our observations, but it can suggest which species should be studied to determine the rules by which evolution has produced the diversity of life on the planet Earth.

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Physiological ecology should include as its domain of interest the physiological attributes of species that allow them to live in and restrict them to their natural habitat or ecosystem. The dependent variable is the organism's place in nature. In comparative physiology or environmental physiology, the dependent variable or the focus of interest is on the internal and morphological adjustments of an organism or species to its habitat. While the focus of the disciplines differ in direction of emphasis, both may involve evolutionary interpretations and may utilize similar research techniques or measurements. Historically, physiological ecology in the United States has emphasized plant water and carbon balance measurements. As these aspects have become better known, and with the development of better techniques for synthesizing information on plant processes, the linkages of water and carbon balance to whole plant behavior, population attributes, and ecosystem functioning have been developed. These linkages are the current active areas of research; they provide a means to develop the significance of detailed physiological attributes in a fuller ecological setting, and to develop a general mechanistic basis for observations at the population and community level.

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To me there is no sharp distinction among plant physiology, environmental plant physiology, physiological plant ecology (or ecological plant physiology), and a biophysical plant ecology. In fact, I have taught courses with titles in all four areas and the material has overlapped considerably.

The objective of ecological plant physiology is to explain processes in plant ecology, such as plant performance, survival, and distribution, in physiological, biophysical, biochemical, and molecular terms. This means that we cannot only be preoccupied with events at the molecular levels, but must also broach broader questions. At one extreme, we find the physiologist preoccupied with states and processes within relatively small scales of space and time. These concerns lead to understanding of adaptation in terms of the way component processes are fitted together for optimal performance of the individual organism in a particular habitat. At the other extreme, we find the ecologist preoccupied with much larger scale states and processes, in which the survival of the individual organism is but one component of the performance of the larger system, the ecosystem. These two views lead to a concern with the physiology of performance within the environmental limits to survival on the one hand, and the biology of survival on the other.

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As the term implies, this is a discipline in which physiological techniques are used to study ecological problems. Ecology is the noun and physiology an adjective. Thus, ecology remains the primary objective. Environmental physiology, ecophysiology, or comparative physiology, on the other hand, imply that physiological questions are at the center of the scientific curiosity.

Physiological ecology is generally practiced at the organism level. Studying physiological responses of organisms allows the analysis of the integrated effects of environmental and biological interaction. Supraorganism taxonomic-, population-, or ecosystem-level questions can be addressed by monitoring certain physiological characteristics of representative organisms.

It is true that a physiological ecologist will frequently have to work at the suborganismal level. The stated objective of the experiment and the interpretation of results, however, will be both integrative and extrapolative. The ecologist will not stop at an explanation of the physiological mechanism examined but will go on to a discussion of how that mechanism affects the establishment and survi val of the organism or species.

In summary, all ecologists study organisms in relation to their environment. A physiological ecologist simply uses physiological techniques in that study. Somewhat in jest, I tell my students that physiological ecologists drive four-wheelers, wear desert boots, and use Scholander bombs, while environmental physiologists drive sedans, wear dress shoes, and use Waring Blenders. Both approaches are valid, of course. Neither is innately preferable to the other. In fact, a given investigator may be an ecologist in one study and a physiologist in another.

Plant Physiological Ecology Today

by H.A. Mooney, R.W. Pearcy, and J. Ehleringer (1987)

Recent advances are helping to determine the biochemistry and physiology behind plant performance under natural conditions

During the past few decades plant physiological ecology has expanded tremendously. This growth has come partly from substantial technological advances that now make it possible to quantify precisely, under natural conditions, the microenvironment of plants and plant tissues as well as their metabolic responses. In addition, accompanying theoretical developments have provided a conceptual framework for relating environmental factors to plant mass and energy exchanges. Such information has been incorporated into simulation and optimization models of both morphological characteristics (e.g., leaf color, size, angle) and physiological properties (e.g., photosynthesis, transpiration, stomatal conductance). Plant physiological ecology is thus becoming increasingly predictive and is providing management tools in a number of areas, including forestry and pollution control. It is also providing a new understanding of community function and evolutionary development.

To summarize past progress and set priorities for future research in this field, the National Science Foundation sponsored a symposium at Asilomar, California, in December 1985. We previously discussed these priorities (Ehleringer et al. 1986). Here, in a series of five articles broadly encompassing the field of plant physiological ecology, we review recent accomplishments. In this introduction we sketch some of the important events of the past two decades. Billings (1985) provides a comprehensive review of earlier influences.

In the mid to late 1950s, a number of developments that initiated the consolidation of modern plant physiological ecology were Monsi and Saeki's (1953) theoretical work on the light climate within plant communities; Gaastra's (1959) work on the transport resistances to the movement of gases in and out of leaves; and Gates' (1962) and Raschke's (1956) studies of leaf energy balance. These pioneering studies, each performed in a different nation, provided a quantitative framework for relating environmental influences to plant metabolism. Given the physical and physiological input, researchers could predict exchange rates of carbon dioxide, water, or energy between a plant and its environment. This energy-balance approach provided, for example, the means for predicting transpirational water loss of leaves. Scientists could answer such questions as: "If a leaf were a different size and shape, what would be its temperature and rate of water loss under given environmental conditions?"

These studies also laid the foundation for the plant growth models of the late 1960s (Brouwer and de Wit 1969). Developed initially for crops, and soon thereafter extended to natural communities (Miller and Tieszen 1972), these models integrated environmental conditions and plant metabolism to allow researchers to predict biomass accumulation rates under various scenarios including, for example, elevated CO2 concentrations. An important conceptual advance in growth modeling was the theory estimating biomass maintenance and conversion efficiencies from tissue analysis (Penning de Vries et al. 1974, Penning de Vries 1975). More recently, researchers have developed photosynthesis models based on the underlying biochemical reactions (Farquhar et al. 1980), and optimization theory models to explain stomatal behavior (Cowan and Farquhar 1977).

Stimulating and interacting with these theoretical advances was the development of instrumentation to measure accurately, under field conditions, plant microenvironment and metabolism. Probably most important was the availability in the 1950s of portable infrared gas analyzers for measuring photosynthesis (Bosian 1960) and pressure chambers for measuring plant water potential

(Scholander et al. 1964). Instrumentation and conceptual advances in microclimatology, stimulated by Geiger's (1957) masterful synthesis, were equally important.

Along with new tools and theories, the unique working philosophy that now characterizes research in this field developed during the 1960s and 1970s. This philosophy brought a vertical integration to the study of plant adaptive traits by leading investigators to seek the biochemical and physiological mechanisms underlying adaptive features and to demonstrate the relevance of these mechanisms to performance under natural conditions. This powerful approach is best illustrated by the studies of Björkman and coworkers (1972a) on sun and shade leaves and on C3 and C4 metabolism (Björkman et al. 1970).

An additional important dimension was the incorporation of a strong evolutionary approach, which stemmed in part from studies on species evolution (Clausen et al. 1940). These studies led to important comparisons of the physiological behavior of ecotypes, or closely related species, from contrasting environments. The increasingly popular tools of cost-analysis and optimization also have their basis in evolutionary theory.

The recent development of plant physiological ecology thus has multiple roots. The Germans have contributed almost continuously since Schimper (1898), particularly in analyzing the physiological basis for plant distribution (Lang 1957, Stocker 1935, Walter 1964). The English laid the foundations for examining soil-plant interrelationships in natural environments (Rorison 1969) and for rigorous microclimatic analysis (Monteith 1973). The Scandinavians pioneered studies of plants' carbon economy (Boysen-Jensen 1932) and ecotypic differentiation (Turesson 1922). The French have contributed heavily to the development of instrumentation (Eckardt 1966), and the Australians to our understanding of plant-water relations (Slatyer 1967), US scientists, following the early lead of the Carnegie Institution desert group (Billings 1980), examined adaptive traits in a variety of habitats, initially severe ones such as deserts and tundra.

Certain study sites and research programs have played particularly important roles. Austrian timberline studies of Tranquillini (1957); tundra studies of Billings and students (Billings 1973); and desert studies in Death Valley, California (Björkman et al. 1972b), and Avdat, Israel (Lange et al. 1969). These studies demonstrated that precise physiological and microenvironmental measurements could be made, even under adverse conditions, on plants growing in their natural environments. The results of these measurements in turn provided the basis for meaningful experiments in controlled-environment growth facilities.

As a result of these multiple approaches, several major but closely interrelated research focuses have emerged. Physiological ecologists have long studied how plants acquire carbon, water, and nutrients. Advances in the biochemistry of leaf CO2 exchange are now allowing detailed understanding of the metabolic limitations to photosynthesis and how these interact with environmental limitations (see Chapin et al., page 49, and Pearcy et al, page 21, this issue). At the same time, researchers are increasingly aware that the investments of acquired carbon and nutrients in new structure and the losses due to respiration and herbivores are also critical to plant performance in natural environments. In addition, plant architecture influences the capture of light aboveground (see Pearcy et al., page 21, this issue) and water and nutrients belowground (see Chapin et al., page 49, and Schulze et al., page 30, this issue). One new focus in physiological ecology concerns the interactions of multiple resource limitations and stresses. Although earlier research usually concentrated on single factors, field studies made it clear that plants are often subjected to multiple limitations and stresses and that studies of their interactions provide new insights. Chapin et al. (page 49, this issue) discuss these interactions and their consequences for efficient resource use and maximal plant performance. Studies of the relationship between water less and carbon gain have been stimulated by new techniques measuring carbon isotope ratios (see Schulze et al., page 30, this issue). These techniques promise novel approaches to understanding the nature and significance of efficient water use by plants in natural environments. Osmond et al. (page 38, this issue) consider the interaction of stresses, such as high light, temperature and drought, that often occur together. Studies of these interactions may reveal the underlying mechansims of stress damage and tolerance, as well as indicate how genetic manipulation could lead to improved crop or forest productivity.

Analysis of energetic costs has gained considerable momentum in plant physiological ecology in recent years. These studies focusing on various compounds and structures have made possible cost-benefit analyses of the production of any plant trait -- such as herbivore protection and leaf longevity (see Bazzaz et al., page 58, this issue). These approaches are particularly important because they focus on whole-plant performance and the trade-offs among various developmental or allocation patterns. Such information is crucial in, for example, analyzing the overall benefit of moving a single trait by genetic manipulation. It also provides important linkages between physiological ecology and ecosystem and evolutionary ecology.

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