

Plant Physiological Ecology Today

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

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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.

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Plant physiological ecology is providing a new understanding of community function and evolutionary development

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). Instrumen-

ration 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 C_3 and C_4 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 (Lange 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 yielded 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 CO_2 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 loss 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 mechanisms 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.

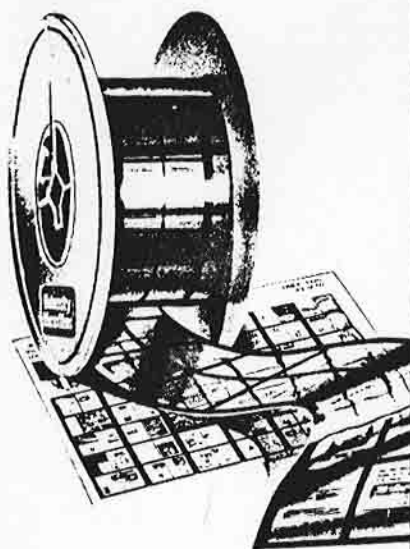
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