Plant Physiological Ecology

Field methods and instrumentation

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Contents

Introduction

Physiological plant ecology is primarily concerned with the function and performance of plants in their environment. Within this broad focus, attempts are made on one hand to understand the underlying physiological, biochemical and molecular attributes of plants with respect to performance under the constraints imposed by the environment. On the other hand physiological ecology is also concerned with a more synthetic view which attempts to understand the distribution and success of plants measured in terms of the factors that promote long-term survival and reproduction in the environment. These concerns are not mutually exclusive but rather represent a continuum of research approaches. Osmond *et al.* (1980) have elegantly pointed this out in a space–time scale showing that the concerns of physiological ecology range from biochemical and organelle-scale events with time constants of a second or minutes to succession and evolutionary-scale events involving communities and ecosystems and thousands, if not millions, of years. The focus of physiological ecology is typically at the single leaf or root system level extending up to the whole plant. The time scale is on the order of minutes to a year. The activities of individual physiological ecologists extend in one direction or the other, but few if any are directly concerned with the whole space–time scale. In their work, however, they must be cognizant both of the underlying mechanisms as well as the consequences to ecological and evolutionary processes.

IMPORTANCE OF FIELD METHODS TO PHYSIOLOGICAL ECOLOGY

Field research in physiological ecology is heavily dependent on appropriate methods and instrumentation. The writings of early plant geographers and ecologists, such as Schimper (1898), Warming (1896) and Clements (1907), were rich with hypotheses and speculations concerning the role of environment, physiology and morphology in the distributions of plants. Indeed as early as the 1880s attempts were made to measure physiological difference (transpiration) between populations at different elevations (Bonnier, 1890). The theory for water vapor and heat transfer from leaves, including the concept of stomatal resistance, was published in 1900 by Brown and Escombe and porometers capable of providing at least a relative measure of stomatal aperture were first used shortly thereafter (Darwin and Pertz, 1911). The Carnegie Institution of Washington's Desert Research Laboratory in Tucson from 1905 to 1927 was the first effort by plant physiologists and ecologists to conduct team research on the water relations of desert plants. Measurements by Stocker in the North African deserts and Indonesia (Stocker, 1928, 1935) and by Lundegardh (1922) in forest understories were pioneering attempts to understand the environmental controls on photosynthesis in the field.

While these early physiological ecologists were keen observers and often posed hypotheses still relevant today they were strongly limited by the methods and technologies available to them. Their measurements provided only rough approximations of the actual plant responses. The available laboratory equipment was either unsuited or much more difficult to operate under field than laboratory conditions. Laboratory physiologists distrusted the results and ecologists were largely not persuaded of its relevance. Consequently, it was not until the 1950s and 1960s that physiological ecology began its current resurgence. While the reasons for this are complicated, the development and application of more sophisticated instruments such as the infrared gas analyzer played a major role. In addition, the development of micrometeorology led to new methods of characterizing the plant environments. However, most of the instruments such as the infrared gas analyzer and recorders were primarily designed for industrial process control applications and required considerable ingenuity on the part of the physiological ecologist to adapt them for use in the field. There were no instruments manufactured specifically for ecophysiological applications. Physiological ecologists had to be intimately involved with developing instrumentation systems, and be familiar with techniques from many fields, including meteorology, physiology and soil science.

The last 15 years have brought about remarkable changes in the instrumentation available for physiological ecology. This has been in part driven by the electronics revolution that has allowed the development of highly sophisticated 'smart' instruments with microprocessors that control their performance and low-power circuits that allow operation on batteries in the field. In addition, the notebook and analog recorder have been largely replaced by data acquisition systems and solid-state memory, making at least the chore of collecting the numbers less demanding. However, at least as important is the increased demand for ecophysiological and environmental measurements. This has given rise to the development of commercially available instruments specifically designed for ecophysiological measurements and environmental monitoring in the field. For many research problems there is no longer a need for the physiological ecologists to design and assemble the instrumentation systems since commercially available systems function so well. Physiological ecologists have and will continue to play an important role in this development, and the strong cooperation between researchers and instrument companies that has developed in the past few years will lead to further progress.

The increased availability of instruments, however, is a two-edged sword. Physiological ecologists who assembled their gas exchange system were familiar with its limitations. Those who purchase instrumentation systems may not be. It is the responsibility of the investigator to become familiar with the system, its components and their limitations.

METHODOLOGICAL BOOKS FOR PHYSIOLOGICAL ECOLOGY

Since 1960 many important books covering instrumentation of use in physiological ecology have appeared. Environmental measurements were covered by Slatyer and McIlroy (1961), Tanner (1963), Platt and Griffiths (1964) and Fritschen and Gay (1979). Tanner's volume was available only in mimeographed form but was widely utilized because of the practical information it contained on constructing instruments, including such details as the properties of solders and paints. Similarly, Slatyer and McIlroy had only a limited printing but also had enormous impact because of the practical information it provided.

The first treatise covering methods of plant ecophysiology was *Methodology of Plant Ecophysiology. Proceedings of the Montpellier Symposium* edited by F.E. Eckhardt (1965). This volume contained probably the first detailed descriptions of the application of infrared gas analyzers in the field for measuring photosynthesis. *Plant Photosynthetic Production, Manual of Methods* by Sestak, Catsky and Jarvis followed in 1971 and served nearly as a bible for ecophysiologists measuring gas exchange of plants. Although it is clearly dated, the book still contains much valuable information. More recently, several books covering methods have appeared. *Instrumentation for Environmental Physiology* edited by Marshall and Woodward (1985) had the specific objective of covering developments in instrumentation since 1971. *Techniques in Bioproductivity and Photosynthesis* edited by Coombs, Hall, Long and Scurlock (1985) covers a wide array of techniques ranging from growth analysis to enzymology.

SCOPE OF THIS BOOK

This book is intended as a guide to the methodology appropriate for field measurements in physiological ecology, including both measurements of the environment and of the physiological and morphological responses of the plants. In some cases, for example stable isotope measurements (Chapter 13), the measurement is done in the laboratory but on samples collected under field conditions and with the primary objective of understanding the ecological behavior of plants in the field. Other chapters, especially those on soils (Chapter 5) and growth and allocation (Chapter 15), similarly cover analytical techniques on field samples. There has been an attempt to avoid an exhaustive review of all techniques but rather to concentrate on those that have proved most useful to the authors. These techniques provide the basis of evaluating the acquisition of resources (e.g. carbon, light, water, nutrients) and the use of these resources for plant growth. Methods for estimating some of the costs of allocation of resources to particular functions are also covered (Chapter 15). In addition, the methodological framework for extending from organ level (leaf, root) measurements to whole plants is provided in chapters on root systems (Chapter 16) and canopy structure (Chapter 14) and to ecosystem level processes (Chapter 13).

There are many techniques not included in this book that might rightly be an important component of a research program in physiological ecology. The focus is on performance of plants in the field and therefore instrumentation systems and facilities such as growth chambers and phytotrons are not covered. We have also not covered the various biochemically based techniques such as analysis of leaf anatomy, carboxylation enzyme activities, chlorophyll content, electron-transport activities, hormones, or for that matter, root enzyme activities involved in such processes as flooding tolerance. These techniques can clearly be applied to leaf samples collected in the field but are more commonly conducted on greenhouse or growth chamber plants. Methods for biochemical analysis of the photosynthetic apparatus are given in Hipkins and Baker (1986) and Coombs *et al.* (1985) and there are many sources for general information such as the series *Methods in Enzymology*. Problems of experimental design, statistics, etc. are also not covered for reasons of space.

We have also not covered the analytical framework necessary for much research in physiological ecology such as simulation models or cost–benefit analyses. Jones (1983) discusses the important role of models and their interrelationship with experiments in physiological ecology and Loomis *et al.* (1979) provides a discussion of modeling approaches. Biochemically based photosynthetic models such as the one of Farquhar and his colleagues (Farquhar *et al.*, 1980; Farquhar and von Caemmerer, 1982; Farquhar and Sharkey, 1982) have indeed played an important role in linking biochemical events to an understanding of whole-leaf gas exchange. More empirical models have similarly been useful in understanding, for example, limitations on annual carbon gain in specific habitats (e.g. Schulze *et al.*, 1976). Cost–benefit analyses also provide an important analytical framework for understanding plant function and adaptation. The reader is referred to Bloom *et al.* (1985), Givnish (1986) and Gutschick (1987) for thorough discussions of this approach.

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