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Key words: genetic modification (GM), plant breeding, recombinant DNA technologies, anti-GM, pro-GM, genetic engineering.

Meetings

Plant physiological ecology: linking the organism to scales above and below

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From its origins as a small subdiscipline of ecology, plant physiological ecology has become a dynamic, highly experimental field focusing on questions of both basic scientific importance and deep social concern. A comprehensive understanding of organismal function remains central, but physiological ecology now provides the underpinnings for the emerging field of ecosystem physiology (Mooney *et al.*, 2000) on the one hand and organismal adaptation on the other (Ackerly *et al.*, 2000). Moreover, physiological ecology is embracing advances in molecular biology, providing new insight into the adaptive significance of physiological and morphological traits, thus strengthening its connection to population genetics and evolutionary biology. A symposium at the 2000 meeting of the Ecological Society of America provided an opportunity for introspection and the expression of a new vision for the discipline. Here we report some emerging themes from this symposium.

Physiological ecology – the foundation

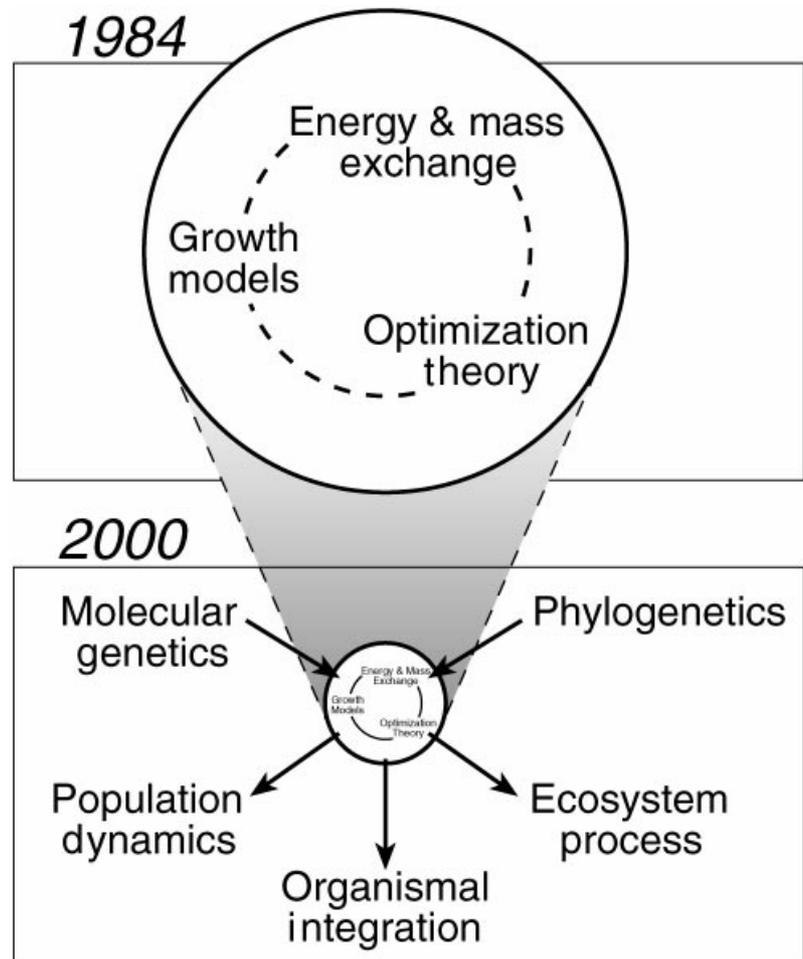
A solid foundation for physiological ecology took shape in 1987 with the publication of a seminal series of articles, leading with 'Plant physiological ecology today' (Mooney *et al.*, 1987). These articles defined the core of physiological

ecology and brought integration to its various avenues of inquiry. The study of physiological and morphological responses of plants to variation in the physical world, the 'adaptive value' of these responses, and their contribution to our understanding of the factors defining the distribution of individual species were the central themes of the discipline. Theories of resource optimization, matter and energy exchange, and mathematical growth modelling provided a conceptual framework (Fig. 1); evolutionary inferences were drawn largely from comparative measurements. Thirteen years later, new methodologies are bringing a renewed experimental approach to organismal research and entirely new avenues of inquiry have opened at the molecular and ecosystem scales.

Organismal biology and evolution

Fuelled by the arrival of the complete sequence of the *Arabidopsis* genome, momentum is building among physiological ecologists to employ molecular methods in their research (Purrlington & Bergelson, 1999). Documenting genetic variance and heritability are mainstays of the population approach to establishing the adaptive significance of traits, or at least their capacity to respond to selection (Geber & Dawson, 1997; Ackerly *et al.*, 2000). This approach is, at times, problematic because environmental variance for most physiological traits is large and measurements are time-consuming. Ecological genetic approaches have advanced our understanding of what leads to trait variation and how it evolves (Schmitt *et al.*, 1999). In addition, molecular transformation, either to introduce new genes or to silence existing ones, and the use of single-gene mutations (Baldwin & Schmelz, 1996; Arntz *et al.*, 2000) are powerful new tools for examining microevolutionary processes.

Fig. 1 In the early 1980s plant physiological ecology focused on organismal physiology and ecology; theories of energy and mass exchange, mathematical growth models and optimization theory were central to the discipline. In 2000, phylogenetic and molecular analyses are providing new tools for examining the adaptive significance of physiological and morphological traits and the bridges between physiological, population and community ecology are being strengthened. Because many of the processes within plant organs scale to the ecosystem level, physiological ecology is playing an important role in understanding biotic and environmental control of ecosystem fluxes.



Using molecular transformation, physiological ecologists can obtain a greater understanding of the fitness consequences of important ecophysiological traits such as variation in photosynthetic rates, biomass allocation, plant size and flowering time.

Genomics and other molecular approaches present tremendous opportunities for physiological ecologists to increase our understanding of organismal function and the evolution of physiological traits (Coleman *et al.*, 1995). Because of the focus on the organism and interactions with other organisms and the environment, physiological ecologists are well positioned to use molecular tools such as DNA microarray technology to advance our understanding of organismal function and evolutionary processes.

Traditionally, physiological ecologists have relied on comparative studies to document evolutionary convergence as a method to understand the adaptive value of traits, like leaf size and shape or the pattern of biomass allocation. A limitation of this approach has been the inability to isolate the potential influence of phylogeny. For example, have members of the genus *Pinus* evolved a low leaf area-to-stem area ratio (DeLucia *et al.*, 2000) as an adaptation to drought or is this feature a vestige from the shared evolutionary history of the

members of this genus? A new synthesis of physiological ecology and phylogenetics will help resolve this issue.

Recent attempts to unravel the evolution of physiological and morphological traits using a phylogenetic approach are very promising. A study of variation in leaf size in maples, for example, established a relationship between leaf, twig and fruit size (Ackerly & Donoghue, 1998). This observation raises the possibility that selection pressures operating on dispersal biology may confound our interpretation of the relationship between leaf properties and the environment. Framing ecophysiological questions in a phylogenetic context is helping physiological ecologists crack the nut of seemingly intractable questions such as the number of times that C_4 photosynthesis (Monson, 1996) or N fixation have evolved, or the adaptive value of water-use efficiency. This new union between physiological ecology and phylogenetics promises to uncover exciting new perspectives to organismal ecology and the evolution of physiological traits.

Physiological mechanisms and ecosystem processes

Changes to global biogeochemical cycles and worldwide

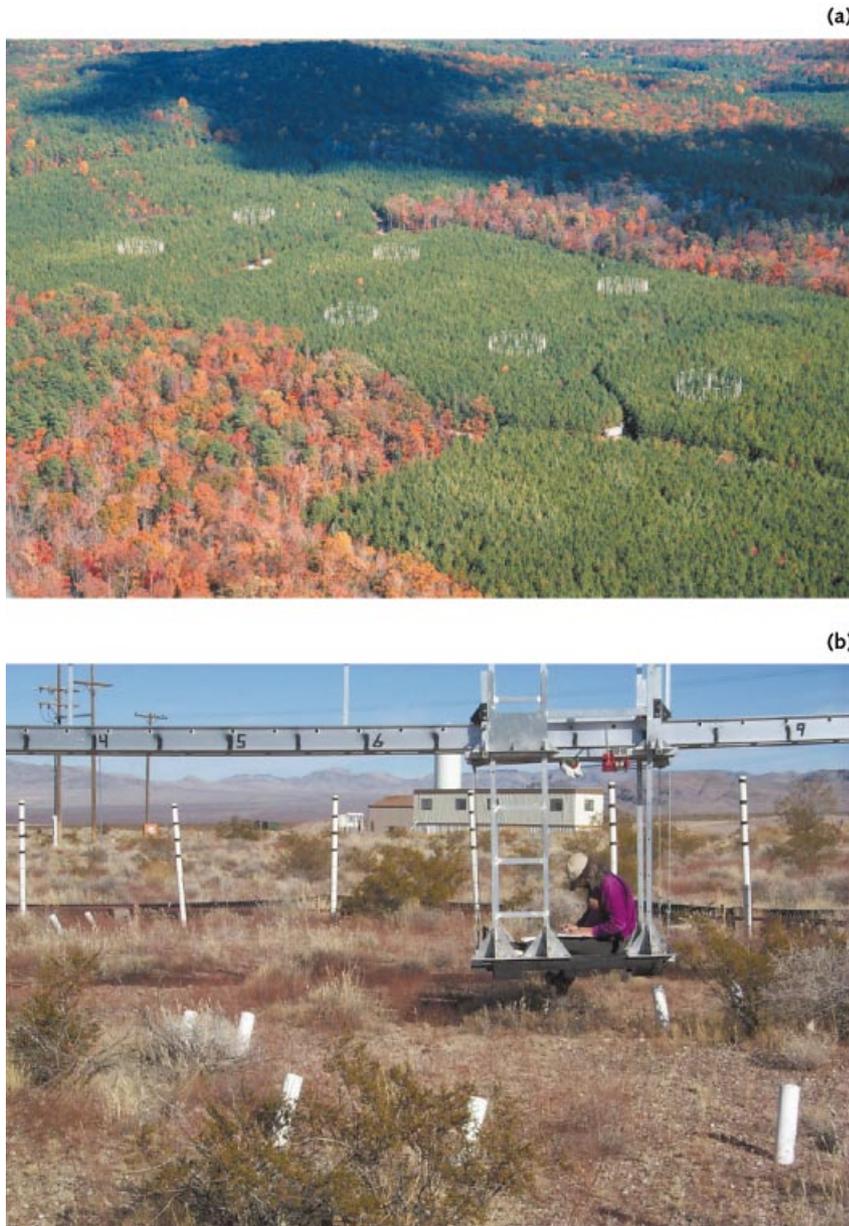


Fig. 2 Plant physiological ecologists measure fluxes of carbon, water, and nitrogen from the leaf to ecosystem scale in large manipulative experiments such as the North Carolina (a) and Nevada (b) free-air CO₂ enrichment (FACE) experiments. These experiments involve many investigators from several different Institutions. Large collaborative research projects provide another way to approach important questions such as how ecosystems will respond to rapid global change. In North Carolina, circular plots in a 17-yr-old loblolly pine forest are exposed to ambient or ambient plus 200 $\mu\text{l l}^{-1}$ CO₂, simulating the atmospheric composition expected in the year 2050 (DeLucia *et al.*, 1999). A similar experimental treatment is applied in Nevada to a Mohave Desert scrub community, dominated by *Larrea tridentata* and *Ambrosia dumosa* (Smith *et al.*, 2000). In the Nevada experiment, researchers are suspended above the plot to avoid trampling delicate desert crusts. The North Carolina and Nevada photographs are courtesy of Will Owens and Lynn K. Fenstermaker, respectively.

reductions of biological diversity have fostered intense interest in the processes regulating productivity and other aspects of ecosystem function (Eviner & Chapin, 1997; Chapin *et al.*, 2000). Many of these processes scale directly from leaf to canopy function. The carbon and water cycles, for example, are directly regulated by physiological processes operating at the scale of individual leaves, creating a direct feedback from leaf physiology to canopy fluxes to regional climate. Because many of the characteristics that determine the success of individuals in stressful environments are also the processes driving ecosystem-level fluxes, it has been argued that '[e]cophysiology is ... preadapted for large scale problems' (Field & Ehleringer, 1993). By providing the

conceptual and analytical bases for scaling physiological processes to the ecosystem level, physiological ecology is helping to accelerate our understanding of the responses of ecosystems to global change.

Physiological ecologists have shortened the traditional measurement cycle of ecosystem processes from an annual time step to seconds or below, and by doing so have revealed new understanding of mechanisms regulating carbon and water fluxes. Beginning in the 1960s, and coinciding with the rise of ecosystem ecology and the International Biosphere Program, ecologists estimated net primary production of different ecosystems by harvest methods. Though useful for comparing ecosystems under different climatic regimes, this approach

could not assess the effect of seasonal variation in climate on productivity. Instantaneous measurements of net ecosystem exchange with rapid-response gas analysers and advanced data management methods are extending these early studies by allowing, for the first time, an examination of fine-scale environmental control of ecosystem carbon fluxes (Goulden *et al.*, 1996). Such advances have also been driven by interactions with micrometeorologists and scientists in disciplines outside ecology.

From the inception of physiological ecology, conceptual advances and technological breakthroughs have come hand-in-hand. New molecular tools can help physiological ecologists better understand the genetic controls and environmental interactions that affect above- and below-ground plant functioning and their ecosystem links (Zhang & Forde, 1998; Jackson *et al.*, 1999). This progression is also readily apparent from carbon budget studies.

The earliest field infra-red gas analysis systems were housed in bulky 'portable' laboratories and making field measurements was a challenge. Today's miniaturized portable gas-exchange systems control the environment of the leaf precisely and reproducibly, permit rapid measurement and are readily carried to a mountain top or the depths of a tropical forest. Open-path analysers have revolutionized and dramatically reduced the cost of measuring ecosystem carbon fluxes. Rapid advances in our ability to measure and understand the factors regulating the distribution and fractionation of stable isotopes are helping to resolve previously intractable questions, like the proportion of soil CO₂ efflux from plant roots vs soil microbes (Norby & Jackson, 1999; Ehleringer *et al.*, 2000). The next generation of physiological ecologists will probably incorporate new and advancing technologies to help resolve longstanding ecological questions.

Physiological ecology in practice

Large, collaborative experiments are playing a more prominent role in physiological ecology than ever before (Fig. 2). Though single-investigator research remains strong, the solution to many global ecological questions also requires large-scale collective research efforts. The effect of elevated CO₂ or variation in species composition on the biogeochemical cycling of carbon and nitrogen, for example, is being addressed in expansive, highly collaborative experiments (DeLucia *et al.*, 1999; Smith *et al.*, 2000). And, policy-driven question about the capacity of ecosystems to store atmospheric carbon have spawned international research programs using coordinated methodologies and analytical tools (e.g. see www-eosdis.ornl.gov/FLUXNET/index.html). This new model for physiological ecology research is opening exciting opportunities for collaboration. Funding, however, has not kept pace with this new research model; the cultivation of new revenue sources will be essential for maintaining a healthy balance between creative single-investigator research and larger collaborative projects.

Summary

Molecular genetics and the broader evolutionary view made possible by phylogenetic analyses, particularly when combined with the next generation of growth models (Pearcy & Yang, 1996), is bringing a new focus to organismal biology. With these tools in hand, physiological ecology is well positioned for further advances in the future. Genome sequences and other new molecular tools can be used to improve the understanding of plant biochemistry and physiology, and physiological ecologists could build many productive collaborations with molecular biologists to examine single and multiple gene responses and their interactions with the environment. Working up from the organism, physiological ecology now provides the mechanistic understanding of ecosystem fluxes. It is likely that plant physiological ecology will continue to grow along this axis, incorporating new molecular and biochemical tools and extending the physiology of the organism to larger scales of the community (Bazzaz, 1996), the ecosystem and beyond (Fig. 1).

Acknowledgements

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Key words: plant physiological ecology, ecosystem physiology, organismal adaptation, ecosystem processes, global biogeochemical cycles.



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