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Book review

Review for Phytochemistry of Handbook of Functional Plant Ecology

edited by F.I. Pugnaire and F. Valladares 1999. Marcel Dekker, Inc., New York. ISBN: 0-8247-1950-6. 912 pages; \$250

As the majority of plant biologists (and the readership of Phytochemistry) are rapidly becoming *Arabidopsis* biologists, it is useful to be reminded of the remarkable phenotypic and ecological diversity of plants and that there are biologists who are trying to understand and organize this diversity in the context of plant function.

Functional plant ecology, as defined by the editors of this volume seeks to derive functional 'laws' about physiological processes that scale from the whole-plant level to the ecosystem with the ultimate goal of organizing a complete functional screen of the plant kingdom, a 'periodic table of functional traits' to be derived from comparative studies. The *Handbook of Functional Plant Ecology* falls short of this vision, but does an admirable job of outlining a research landscape which will likely grow in importance in the postgenomics era as plant biologists return to the longstanding question of understanding plant functional diversity, or, in other words, understanding why are there so many ways of being an evolutionarily successful plant.

The volume consists of 24 separately-authored chapters which are loosely organized into five sections that cover, in a bottom-up fashion, the domain of functional plant ecology, namely: (1) the role of structure and growth form in plant performance — seven chapters; (2) physiological ecology — three chapters; (3) habitats and plant distribution — six chapters; (4) populations and communities — six chapters; and (5) 'new' research methods — four chapters. While a few of the chapters are little more than sophomoric treatments, most are insightful, crisp reviews that capture the rancor and debate of their research area. Many of the chapters admirably meet the 'handbook' appellation and provide detailed appendices to the frequently turgid vocabulary and concepts of plant architecture and morphology (in the chapter by Valladares), relative growth rate analysis (in the chapter by Poorter and Garnier) canopy photosynthesis modeling (in the chapter by Beyschlag and Ryel) and plant defense theory (in the chapter by Zamora, Hodar and Gomez). As edited volumes go, the styles and content of the individual chapters are well integrated and provide introductions to the many sub-disciplines of plant functional ecology that are useful for both the uninitiated and seasoned researcher. Collectively, the chapters represent a pastiche of whole-plant functional ecology worthy of a place on every plant biologists' bookshelf.

The Handbook's breadth of coverage is both its principle strength and liability. The liability stems from a lack of consistent treatment by the authors of the individual chapters of two components that the editors define as central to the field, namely (a) the emphasis on whole-plant or higher-level processes, and (b) the role of comparative studies in defining the functional laws which the discipline seeks to uncover. These topics have been thoroughly debated in the context of 'scaling' processes in biological hierarchies and the use of phylogenetically independent contrasts in making across-taxa comparisons. Only the latter of the two receives the attention that it deserves in The Handbook. Indeed the editors' choice to end their volume with Westoby's artfully crafted chapter on the species sampling problem in comparative studies (a chapter which contains an appendix of FAQs), brilliantly underscores the importance of this issue.

The editors' emphasis on whole-plant and higherlevel processes represents a limitation to the development of the field in the post-genomics era. Only the chapter by Barnes et al. on ozone resistance (in the 'New Research Methods' section) includes references to the molecular biological literature, creating the impression that the advances in plant molecular biology have done little to understand the observed variation in plant performance. Many of the authors note that performance is an emergent property of the wholeplant which has been difficult to ascribe to cellular or physiological processes functioning at lower levels in biological hierarchy. For example, after extensive study, variation in RGR is best attributed to variation in net nitrogen uptake rate and specific leaf area, two other whole-plant traits. Similarly, the temporal variation in plant photosynthetic rates requires both an understanding of the control over RuBPCase activation as well as stomatal conductance, traits operating at the cell- and leaf-levels of organization. However, the apparent lack of advances may be more a reflection of the screens used by molecular biologists. It is likely that some genetic controls over whole-plant functional responses will be discovered in the near future and the expertise of whole-organismic biologists will be needed for their characterization. Advocating a focus on only whole-plant traits will only serve to widen the growing gap between molecular biologists and ecologists. Moreover, an understanding of the genetic controls over whole-plant performance will be necessary if functional ecologists wish to move beyond categorizing functional diversity to understanding its

A widely adopted scheme for organizing the functional diversity among plants is the Competition–Stress–Disturbance (CSR) concept first articulated by J.P. Grime and coworkers. This scheme serves as a common organizing principle for the many chapters that analyze functional convergence in extreme habitats (tropics, arid environments, arctic and Antarctic) as well as those examining responses to complex selective regimes (herbivory, pollution, competition and facilitation) and as such, is a defining paradigm for the field. The CSR concept is recast by Westoby in the final chapter into a scheme with parameters more readily quantified (leaf;height;seed) with the hope of

stimulating more comparative studies and thereby a deeper consideration of the consequences of selecting particular species for study. In addition, the CSR concept helps frame expectations for what we might learn about plant ecology from the *Arabidopsis* genome project.

In the CSR scheme, Arabidopsis thaliana is the quintessential 'ruderal' species. Its small stature and short life span has allowed it to become an ecological 'escape artist', avoiding many of the ecological selection pressures (herbivory, competition) that are so important for plants of larger stature and life span. It remains to be seen how many of its ancestors' ecologically important genes have been lost when Arabidopsis evolved its small, highly condensed genome, the trait that makes it such a wonderful model system for molecular biology. If it turns out that much has been lost, wholeorganismic plant biologists, such as those that have authored 'The Handbook' will need to identify other model systems that might reveal the molecular basis of the vast array of ecological sophistication that plants possess.

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