

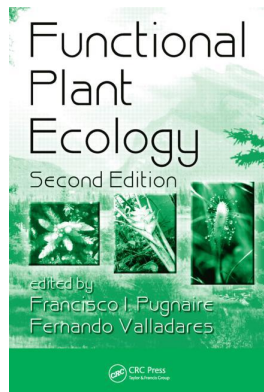
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## **Functiona Plant Ecology**

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## **Methods in Comparative Functional Ecology**

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# 1 Methods in Comparative Functional Ecology

*Carlos M. Duarte*

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## DEVELOPMENT OF FUNCTIONAL PLANT ECOLOGY

The quest to describe the diversity of extant plants and the identification of the basic mechanisms that allow them to occupy different environments have shifted scientists' attention from ancient Greece to the present. This interest was prompted by two fundamental aims: (1) a pressing need to understand the basic functions and growth requirements of plants because they provide direct and indirect services to human kind and (2) the widespread belief that the distribution of organisms was not random, for there was essential order in nature, and that there ought to be a fundamental link between differences in the functions of these organisms and their dominance in contrasting habitats. The notion that differences in plant functions are essential components of their fitness, accounting for their relative dominance in differential habitats, was, therefore, deeply rooted in the minds of early philosophers and, later on, naturalists. While animal functions were relatively easy to embrace from a simple parallel with our own basic functions, those of plants appeared more inaccessible to our ancestors, and the concepts of "plant" and "plant functions" have unfolded through the history of biology.

The examination of plant functions in modern science has largely followed a reductionistic path aimed at the explanation of plant functions in terms of the principles of physics and chemistry (Salisbury and Ross 1992). This reductionistic path is linked to the parallel transformation of traditional agricultural science into plant science and the technical developments needed to evolve from the examination of the coarser, integrative functions to those occurring at the molecular level. While this reductionistic path has led us toward a thorough catalog and understanding of plant functions, its limited usefulness to explain and predict the distribution of plants in nature has been a source of frustration. This is largely because of the multiple interactions that are expected to be involved in the responses of plants to a changing environment (Chapin et al. 1987). Yet, the need to achieve this predictive power has now transcended the academic arena to be a critical component of our ability to forecast the large-scale changes expected from on-going climatic change. For instance, increased CO<sub>2</sub> concentrations are expected to affect the water and nutrient requirements of plants, but resource availability is itself believed to be influenced by rising temperatures. Such feedback effects cannot be appropriately predicted from knowledge of the controls that individual factors

exert on specific functions. Moreover, the changes expected to occur from climate change are likely to derive mostly from changes in vegetation and dominant plant types rather than from altered physiological responses of extant plants to the new conditions (Betts et al. 1997).

Failure of plant physiology and plant science to provide reliable predictions of the response of vegetation to changes in their environment likely derives from the hierarchical nature of plants. The response of higher organizational levels is not predictable from the dynamics of those at smaller scales, although these set constraints on the larger-scale responses of hierarchical systems. Component functions do not exist in isolation, as the dominant molecular approaches in modern plant physiology investigate them. Rather, these individual functions are integrated within the plants, which can modulate the responses expected from particular functions, leading to synergism, whether amplifying the responses through multiplicative effects or maintaining homeostasis against external forcing.

Recognition of the limitations of modern physiology to provide the needed predictions at the ecological scale led to the advent of plant ecophysiology, which tried to produce more relevant knowledge by the introduction of larger plant components, such as plant organs (instead of cells or organelles), as the units of analysis. Plant ecophysiology represented, therefore, an effort toward approaching the relevant scale of organization, by examining the functions of plant organs. Most often, however, practitioners of the discipline laid somewhere between the molecular approaches dominant in plant physiology and the more integrative approaches championed by plant physiological ecology. Because of the strong roots in the tradition of plant physiology, the suite of plant functions addressed by plant ecophysiology still targeted basic functions (e.g., photosynthesis, respiration, etc.) that can be studied through chemical and physical laws (Salisbury and Ross 1992). As a consequence, plant ecophysiology failed to consider more integrative plant functions, such as plant growth, which do not have a single physiological basis, but which are possibly the most relevant function for the prediction of plant performance in nature (cf. Chapter 3).

The efforts of plant ecophysiology proved, therefore, to be insufficient to achieve the prediction of how plant function allows the prediction of plant distribution and changes in plant abundance in a changing environment. Realization that the knowledge required to effectively address this question would be best achieved through a more integrative approach led to the advent of a new approach, hereafter referred to as “Functional Plant Ecology,” which is emerging as a coherent research program (cf. Duarte et al. 1995). Functional plant ecology is centered on whole plants as the units of analysis, the responses of which to external forcing are examined in nature or under field conditions. Functional plant ecology, therefore, attempts to bypass the major uncertainties derived from the extrapolation of responses to nature (tested in isolated plant organs maintained under carefully controlled laboratory conditions) and to incorporate the integrated responses to multiple stresses displayed by plants onto the research program.

Although centered in whole plants, functional plant ecology encompasses lower and higher scales of organization, including studies at the organ or cellular level (e.g., Chapter 8), as well as the effect of changes in plant architecture or functions (e.g., Chapters 4 and 5), and the importance of life history traits (e.g., Chapters 15 and 16), interactions with neighbors (e.g., Chapters 17 and 18), and those with other components of the ecosystem (e.g., Chapter 19). In fact, this research program is also based on a much broader conception of plant functions than hitherto formulated. The plant functions that represent the core of present efforts in functional plant ecology are those by which plants influence ecosystem functions, particularly those that influence the services and products provided by ecosystems (Costanza et al. 1997). Hence, studies at lower levels of organization are conducted with the aim of being subsequently scaled up to the ecosystem level (e.g., Chapter 10).

Because of the emphasis on the prediction of the consequences of changes in vegetation structure and distribution for the ecosystem, functional plant ecology strives to encompass

the broadest possible range of functional responses encountered within the biosphere. Yet, the elucidation of the range of possible functional responses of plants is not possible with the use of model organisms that characterize most of plant (and animal) physiology. Functional plant ecology arises, therefore, as an essentially comparative science concerned with the elucidation of the range of variations in functional properties among plants and the search for patterns and functional laws accounting for this variation (Duarte et al. 1995). While practitioners of functional plant ecology share the emphasis on the comparative analysis of plant function, the approaches used to achieve these comparisons range broadly. These differences rely largely on the breadth of the comparison and the description of the subject organisms in the analysis. The implications of these choices have not, however, been subject of explicit discussions despite their considerable epistemological implications and their impact on the power of the approach.

## SCREENING, BROAD-SCALE COMPARISONS, AND THE DEVELOPMENT OF FUNCTIONAL LAWS

The success and the limitations of comparative functional plant ecology depend on the choices of approach made, involving the aims and scope of the comparison, as well as the methods to achieve them. The aims of the comparisons range widely, from the compilation of a “functional taxonomy” of particular sets of species or floras to efforts to uncover patterns of functional properties that may help formulate predictions or identify possible controlling factors. Many available floras incorporate considerable knowledge, albeit rarely quantitative, on the ecology of the species, particularly as to habitat requirements. An outstanding example is the Biological Flora of the British Isles (cf. *Journal of Ecology*), which incorporates some functional properties of the plants (e.g., Aksoy et al. 1998). The likely reason why “functional” floras are still few is the absence of standardized protocols to examine these properties while ensuring comparability of the results obtained. A step toward solving this bottleneck was provided by Hendry and Grime (1993), who described a series of protocols to obtain estimates of selected basic functional traits of plants in a comparable manner. Unfortunately, while exemplary, those protocols were specifically designed for use within the screening program of the British flora conducted by those investigators (Grime et al. 1988), rendering them of limited applicability in broader comparisons or comparisons of other vegetation types.

The screening approach may, if pursued further, generate an encyclopedic catalog of details on functional properties of different plants. Some ecologists may hold the hope that, once completed, such catalogs will reveal by themselves a fundamental order in the functional diversity of the plants investigated, conforming to a predictive sample similar to a “periodic table” of plant functional traits. While I do not dispute here that this goal may be eventually achieved, the resources required to produce such catalogs are likely to be overwhelming, since, by definition, such a screening procedure is of an exploratory nature, where the search for pattern is made a posteriori. Provided the number of elements to be screened and the potentially large number of traits to be tested, the cost-effectiveness of the approach is likely to prove suboptimal. A screening approach to functional plant ecology is, therefore, unlikely to improve our predictive power or to uncover basic patterns unless driven by specific hypotheses. Moreover, a hypothesis-driven search for pattern is likely to be most effective if based on a comparative approach, encompassing the broadest possible relevant range of plants. It is not necessary to test every single plant species to generate and test such general laws.

The comparisons attempted may differ greatly in scope, from comparisons of variability within species to broad-scale comparisons encompassing the broadest possible range of

phototrophic organisms, from the smallest unicells to trees (e.g., Agustí et al. 1994, Nielsen et al. 1996). Experience shows, however, that the patterns obtained at one level of analysis may differ greatly from those observed at a broader level (Duarte 1990), without necessarily involving a conflict (Reich 1993). The scope of the comparison depends on the question that is posed. However, whenever possible, progress in comparative functional plant ecology should evolve from the general to the particular, thereby evolving from comparisons at the broadest possible scales to comparisons within species or closely related species. In doing so, we shall first draw the overall patterns, which yield the functional laws that help identify the constraints of possible functional responses in organisms.

The simplest possible comparison involves only two subjects, which are commonly enunciated under the euphemism of “contrasting” plant types. Such simple comparisons between one or a few subject plants are very common in the literature. These simple comparisons are, however, deceiving, for they cannot possibly be conclusive as to the nature of the differences or similarities identified. The implicit suggestion in these contrasts is that the trait on which the contrast is based (e.g., stress resistance vs. stress tolerance) is the cause underlying any observed differences in functional traits. This is fallacious and at odds with the simplest principles of method in science. Hence, contrasts are unlikely to be an effective approach to uncover regular patterns in plant function, since the degrees of freedom involved are clearly insufficient to venture any strong inferences on the outcome of the comparison.

Broad-scale comparisons involving functional responses across widely different species are, therefore, the approach of choice when the description of general laws is sought. The formulation of the comparative analysis of plant functions at the broadest possible level has been strongly advocated (Duarte et al. 1995), on the grounds that it will be most likely to disclose the basic rules that govern functional differences among plants. Broad-scale comparisons are most effective when encompassing the most diverse range of plant types possible (e.g., Agustí et al. 1994, Niklas 1994). In addition, they are most powerful when the functional properties are examined in concert with quantification of plant traits believed to influence the functions examined, for comparisons based on qualitative or nominal plant traits cannot be readily falsified and remain, therefore, unreliable tools for prediction. Hence, the development of broad-scale comparisons requires that both the functional property examined and the plant traits, which account for the differences in functional properties among the plants, are to be tested and carefully selected.

Broad-scale comparisons must be driven by a sound hypothesis or questions. Yet, this approach is of a statistical nature, often involving allometric relationships (e.g., Niklas 1994), so that observation of robust patterns is no guaranty of underlying cause and effect relationships, which must be tested experimentally. Nevertheless, the functional laws developed through broad-scale comparative analysis may hold predictive power, irrespective of whether they represent direct cause–effect relationships. This use requires, however, that the independent, predictor variable be simpler than the functional trait examined, if the law is to have practical application. Examples of such functional laws are many (e.g., Niklas 1994, Agustí et al. 1994, Duarte et al. 1995, Enriquez et al. 1996, Nielsen et al. 1996) and have been generally derived from the compilation of literature data and the use of plant cultures in phytotrons or the use of the functional diversity found, for instance, in botanical gardens (e.g., Nielsen et al. 1998). This choice of subject organisms is appropriate whenever the emphasis is on the functional significance of intrinsic properties. However, the effect of environment conditions can hardly be approached in this manner, and functional ecologists must transport the research to the field, which is the ultimate framework of relevance for this research program.

The comparative approach is also a powerful tool to examine the effect of environmental conditions in situ. Gradient analysis, where functional responses are examined along a clearly defined environmental gradient, has proven a powerful approach to investigate the

relationship between plant function and environmental conditions (Vitousek and Matson 1990). Gradient analysis is particularly prone to spurious relationships where the relationship between the gradient property and the functional response reflects a functional relationship to a hidden factor covarying with that nominally defining the gradient. Inferences from gradient analysis are, therefore, also statistical in nature and have to be confirmed experimentally to elucidate the nature of underlying relationships.

Broad-scale comparisons often entail substantial uncertainty—typically in the order-of-magnitude range—in their predictions, which is a result of the breadth—typically four or more orders of magnitude—in the functions examined. This imprecision limits the applicability of these functional laws and renders their value greatest in the description of general, large-scale patterns, over which the effect of less-general functional regulatory factors, both intrinsic and extrinsic, is superimposed. Hence, multiple factors that constrain the functional responses of plants are nested in a descending rank of generality, whereby the total number of traits involved in the control is very large and only a few of them are general across a broad spectrum of plants.

The nested nature of the control of functional responses implies uncertainties when scaling functional laws, either toward lower or higher levels of organization (Duarte 1990). There is, therefore, no guaranty that the patterns observed at the broad-scale level will apply when focusing on particular functional types. Changes in the nature of the patterns when shifting across scales have prompted unnecessary disagreement in the past (Reich 1993). A thorough investigation of functional properties of plants should include, whenever possible, a nested research program, whereby the hypotheses on functional controls examined are first investigated at the broadest possible scale, to focus subsequently on particular subsets of species or functional groups, along environmental gradients.

The chapters in this volume provide a clear guide to functional ecology with examples, emphasizing the nested nature of the research program both within the chapters and in the manner in which they have been linked into different parts. The chapters also provide an overview of the entire suite of approaches available to address the goals of functional ecology, providing, therefore, a most useful tool box for prospective practitioners of the research program. The resulting set provides, therefore, a heuristic description of functional ecology, which should serve the dual role of providing a factual account of the achievements of functional ecology while endowing the reader with the tools to design research within this important research program.

## REFERENCES

- Agustí, S., S. Enríquez, H. Christensen, K. Sand-Jensen, and C.M. Duarte, 1994. Light harvesting among photosynthetic organisms. *Functional Ecology* 8: 273–279.
- Aksoy, A., J.M. Dixon, and W.H.G. Hale, 1998. *Capsella bursa-pastoris* (L.) Medikus (*Thlapsi bursa-pastoris* L., *Bursa bursa-pastoris* (L.). Shull, *Bursa pastoris* (L.) Weber). *Journal of Ecology* 86: 171–186.
- Betts, R.A., P.M. Cox, S.E. Lee, and F.I. Woodward, 1997. Contrasting physiological and structural vegetation feedbacks in climate change simulations. *Nature* 387: 796–799.
- Chapin III, F.S., A.J. Bloom, C.B. Field, and R.H. Waring, 1987. Plant responses to multiple environmental factors. *Bioscience* 37: 49–57.
- Costanza R., R. d'Arge, R. de Groo, S. Farber, M. Grasso, B. Hannon, K. Limburg, S. Naeem, R.V. O'Neill, J. Paruelo, R.G. Raskin, P. Sutton, and M. van der Belt, 1997. The value of the world's ecosystem services and natural capital. *Nature* 387: 253–260.
- Duarte, C.M., K. Sand-Jensen, S.L. Nielsen, S. Enríquez, and S. Agustí, 1995. Comparative functional plant ecology: Rationale and potentials. *Trends in Ecology and Evolution* 10: 418–421.

- Enríquez, S., S.L. Nielsen, C.M. Duarte, and K. Sand-Jensen, 1996. Broad-scale comparison of photosynthetic rates across phototrophic organisms. *Oecologia (Berlin)* 108: 197–206.
- Grime, G.P., J.G. Hodgson, and R. Hunt, 1988. *Comparative plant ecology*. Unwin Hyman, Boston, MA.
- Hendry, G.A.F. and J.P. Grime, 1993. *Methods in Comparative Plant Ecology. A Laboratory Manual*. Chapman and Hall, London.
- Nielsen, S.L., S. Enríquez, and C.M. Duarte, 1998. Control of PAR-saturated CO<sub>2</sub> exchange rate in some C<sub>3</sub> and CAM plants. *Biologia Plantarum* 40: 91–101.
- Nielsen, S.L., S. Enríquez, C.M. Duarte, and K. Sand-Jensen, 1996. Scaling of maximum growth rates across photosynthetic organisms. *Functional Ecology* 10: 167–175.
- Niklas, K.J., 1994. *Plant Allometry. The Scaling of Form and Process*. The University of Chicago Press, Chicago, IL.
- Salisbury, F.B. and C.W. Ross, 1992. *Plant Physiology*, 4th edn. Wadsworth, Belmont, CA.
- Vitousek, P.M. and P.A. Matson, 1990. Gradient analysis of ecosystems. In: J.J. Cole, G. Lovett, and S. Findlay, eds. *Comparative Ecology of Ecosystems: Patterns, Mechanisms, and Theories*. Springer-Verlag, NY, pp. 287–298.