

## Plants and Vegetation: Origins, Processes, Consequences

Author: Bond, William

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ide may produce a response that is not at all like the tree-line advance of the Holocene; greater tree densities may result, but the tree line may not advance it may even retreat—in oceanic areas. At this point, Crawford summarizes evidence that tree lines reflect not the negative carbon balance in trees but rather the point at which warmth becomes limiting to seasonal development.

Plants at the Margin *is a scientific synthesis of Crawford's life work, and thus covers a full range of marginal environments. The biological wisdom found in just the first few pages, and the concise way in which it is expounded, is remarkable.* 

I must disagree that the Arctic can be defined climatically as the region underlain by permafrost (p. 199), since much of the boreal zone, especially in Siberia, is also underlain by massive permafrost. Although the chapters on coastal environments and flooding emphasize the North Sea and the Arctic regions, they offer good summaries of physiological and other adaptations in general, including the need for large carbohydrate reserves in unpredictable, flooded, frozen, and other marginal areas. The chapter on marginal woody plants (tundra shrubs, birches, etc.) was of special biogeographic interest to me, as was the chapter on high altitudes, which presents examples from many parts of the world, including tropical mountains. The discussion of lapse rates as upwardly limiting in coastal areas, although interesting, left me wondering whether adiabatic and environmental lapse rates were sometimes being confused. The last major chapter weaves aspects of plant and vegetation ecology through accounts of mainly prehistoric human settlement in peripheral environments.

Among the strong points of *Plants at the Margin* are its many definitions and names for some lesser-known phenomena; its many physiological and other

scientific insights (e.g., the relatively limited value of short-term experiments and field studies); the enormous range and amount of information; and the many photographs, some stunning both in their beauty and in the marginality of the landscapes shown. Weaknesses are few. More information on the modeling basis for the maps of warming-induced range shifts would have been helpful. Some apparently inadvertent mistakes crept in (e.g., incorrect latitudes), some items needed an explanation, and a degree of repetition was present throughout the book. Sentences are sometimes long, but grammatical errors are relatively few, and in general the writing is careful and efficient. The format for literature cited is clumsy, with all its unnecessarily inverted names and extra commas. The many historical tidbits throughout the book contribute nicely to the text, but references for the various historical records cited would also have been useful.

The overall approach of Plants at the Margin is physiological and somewhat regional, although the strong focus on survival mechanisms ensures applicability far beyond the regional detail. Some background in plant anatomy and physiology would be useful for complete understanding of some mechanisms, but the book is a wonderful checklist of things to study up on. The book is also a good argument for the concept of plant functional types, recognizing the "overriding importance of plant form" but also that functional mechanisms do not always have form manifestations. This book should be read by all modelers, as well as by anyone interested in environmental limitation, biogeography, environmental anthropology, or biosphere responses to climate change.

## ELGENE O. BOX

Elgene O. Box (boxeo@uga.edu) is a professor in the Department of Geography and a member of the courtesy faculty in the Odum School of Ecology at the University of Georgia in Athens.

## **REAL-WORLD VEGETATION**

Plants and Vegetation: Origins, Processes, Consequences. Paul A. Keddy. Cambridge University Press, 2007. 706 pp., illus. \$84.00 (ISBN 9780521864800 cloth).

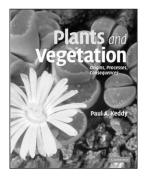
oo often, "general" textbooks on ecology give a worldview that is blind to the past, narrowly parochial in the present, and blinkered in coverage of useful theory. Paul A. Keddy opens Plants and Vegetation: Origins, Processes, Consequences, his new textbook on plant ecology, with a chapter on the ecology of the deep past. He follows this with a discourse on the diversity, functional and phylogenetic, of contemporary world vegetation, and, in the bulk of the book, presents a diversity of ideas to explain it all. Keddy is opinionated, but he owns up to it and warns the reader where he departs from mainstream views. He delights in older literature and has a scholar's respect for those who made key contributions to the development of the subject.

Keddy writes about the ecology of real plants and real vegetation (his emphases) as distinct from, say, modeled abstractions used in global climate models or distant images of satellites. He admonishes the reader to "get out in the field and identify plants." But which field and which plants? Too often, general ecology textbooks are written for students familiar with northern temperate forests and associated meadows and old fields. But ecological understanding developed in these systems can be misleading and irrelevant for other ecological arenas, such as some extensive ecosystems of the southern hemisphere, with which I am most familiar.

Keddy's research area, like that of many other authors of ecology texts, is the northern temperate zone, so I was expecting the worst. I was pleasantly surprised: His geographic reach is impressive and extensive. He has selected examples from vegetation around the

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world and makes a special point of including plants from extreme environments. He has also done justice to the range of ecological processes that are important in my backyard (fire, mammal herbivory, drought, nutrient stress) and not just those that typically fill the pages of textbooks (competition, stress, disturbance). This, then, is a book that will particularly appeal to field biologists. It will take them far from the familiar and introduce them to the vegetation of the world. The focus on "real" vegetation is a useful antidote to the "virtual" world of models, molecules, and satellite images that have become prominent in the last few years.



Keddy's overall philosophy in writing the book is to seek generality while respecting the details. As he notes, there are many subdivisions of ecology, and finding generality is challenging and may even be seen as threatening to the various schools within vegetation ecology. Part of seeking generality is to define the main objectives of the science and to elucidate the way to reach them. On this score, Plants and Vegetation has mixed success. One common objective is to determine what limits membership of a species or a growth form in a community or vegetation type. What ecological processes admit, or exclude, plants from a community, region, or continent? Keddy explores the answers in chapters on resources, stress, competition, disturbance, herbivory, mutualism, and time, all of which can influence which species, growth forms, and vegetation occur, and where. In several of the chapters Keddy explicitly considers the importance of these ecological processes in structuring plant communities, and how they change across large

and small scales. The discussion is interesting and insightful. But in some chapters, such as the one on mutualism, he loses the ecological thread and wanders into the territory of evolution, with discussions on the fitness benefits of various plant reproductive traits. But the currencies of ecology and evolution are different. A novel gene may sweep through a population without changing its size or distribution. I was looking for the ecological perspective, which would ask whether, say, loss of a pollinator would cause loss of a plant species or measurably change species composition within a plant community.

Keddy, an empiricist, strongly emphasizes experimental approaches to answering questions in plant ecology. This is a strength of the book but also a weakness, in my view. Most chapters begin with a definition of a relevant process, followed by descriptions of experimental studies, often ending in an excursion into mathematical models. Students reading Plants and Vegetation will gain a better feel for experiments, data and their interpretation, and experimental design. But as a means to reach the objectives of vegetation ecology, field experiments have limits. For example, to demonstrate forest trees' competitive exclusion by experiment would take several professional lifetimes. By default, experimentalists focus on recruitment stages because things happen faster there. Field experiments on plants are intrinsically local in nature, and tools for scaling up from the local to the landscape level are poorly developed in this book. Keddy repeatedly emphasizes the risks of correlative and comparative methods, and he is wary of models. Yet these are essential tools for extending the spatial and temporal domains of a field study-without them, the larger objectives can get lost in a forest of detail. The problem of how to move from local to global scales is one that ecologists must address, and one that experimentalists cannot ignore.

Keddy writes in a lively, entertaining manner. Here is an example from his discussion of ordination techniques: "A simple analogy may be the process of taking a complex three-dimensional object like a frog or a porcupine and reducing [it] to a two-dimensional array by driving a large truck over it" (p. 465). I particularly enjoyed the text boxes, which contain some of the book's gems. In the essay on Raunkiær, Keddy does honor to the man, but not so much for his invention of Raunkiærian growth forms as for his early use of null models to test how different floras depart from the "expected" growth-form spectra. The description of the difficulties of arriving at an expected spectrum and how Raunkiær dealt with them provides the reader with an entertaining and instructive introduction into null models, why we need them, and what problems may be encountered in constructing them.

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The book is attractively presented with eye-catching line drawings of plants and vegetation. Some of the graphs are not adequately labeled, however, and figure legends could be expanded to make interpretation easier. There are also some quirky tables listing plant communities from various parts of the world that seem too parochial for a general textbook.

*Plants and Vegetation* is intended for senior undergraduates, beginning postgraduates, and professional ecologists. I will be placing it on my list of recommended reading for senior students. Its encyclopedic coverage, spread over 600 pages, means that the reader will find some discussion of a very wide range of topics. If you find the text to be sometimes unconventional and idiosyncratic, Keddy would probably feel complimented.

## WILLIAM BOND

William Bond (William.Bond@ uct.ac.za) is the Harry Bolus Professor of Botany at the University of Cape Town, South Africa.