



## Plants at the Margin: Ecological Limits and Climate Change

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Those who are interested in geochemistry, and those who are looking to broaden their knowledge of the connections between chemical compounds and the diversity of life, will find *Echoes of Life* well worth reading. Readers will come away with an understanding of what those compounds mean in a given time and place. Although the science Gaines and her coauthors present is sometimes difficult, the book nicely blends chemical structures with the researchers behind the discoveries.

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### NOT JUST CARBON BALANCE

**Plants at the Margin: Ecological Limits and Climate Change.** R. M. M. Crawford. Cambridge University Press, 2008. 494 pp., illus. \$72.00 (ISBN 9780521623094 cloth).

**P**lant carbon balance is a key interest of many modelers and ecologists because of its supposed role in limiting distributions. *Plants at the Margin* shows that carbon balance is not the only limiting factor for plants, and in many cases, not even a significant one. For people like me who never had enough physiology but have nonetheless attempted to model plants and environmental limits, it is a great book.

R. M. M. Crawford, author of *Plants at the Margin* and an emeritus professor at the University of St. Andrews in Scotland, is a specialist in the physiology of

plants, especially those in northern and oceanic environments. He is perhaps best known for his work on root respiration and anoxia tolerance, and for his early insights into the physiological effects of climatic warming. *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.

The book comprises four sections: introductory chapters on the essence and biodiversity of marginal areas; two rigorous chapters on physiology and reproduction in marginal situations; six chapters treating particular marginal environments in more detail; and a final chapter called "Man at the Margins," plus a short conclusion.

Habitats are marginal when survival is threatened, so limitation mechanisms should be sought in demography, physiology, and genetics. Plant species are seen as having similar resource requirements and differing mainly in their tolerance to adverse factors. Thus a species' competitive success in good times, when resources are plentiful, matters less to its survival than its ability to utilize and exploit alternative resources in bad times. Crawford offers a good discussion of the significance of carbon balance to both plants and researchers, with recognition that it is the physiology of particular plant organs that may be critical.

In the second chapter, Crawford summarizes various measures of biodiversity, including genetic variation, and contends that variation between habitats (beta diversity) is more suitable for assessing biodiversity than is species richness. Several biodiversity hot spots, as well as dry lands and the Arctic, are described in some detail, with nice examples of remarkable species. This chapter in particular establishes some of the main themes found throughout the book: diversity includes genetic, morphological, and physiological aspects; marginal species often show surprising levels of diversity (which could provide biogenetic resources for restoration efforts); genetically diverse species in refugia may be especially vulnerable to

extinction once the stability of the refuge changes; and marginal areas are prone to disruption, and may be stressed even more by global warming.

The second section of the book focuses on resource acquisition and reproduction. An important theme here is that adaptation to one extreme situation is usually maladaptive to others, as illustrated by the opposing strategies a plant needs for the reducing and oxidizing conditions at root surfaces in dry as opposed to flooded situations. The harm to root systems caused by warm periods during winter is very well explained, and discussions on life-history strategies, resource allocation, and shade tolerance are clear and understandable. The treatment of tolerance mechanisms is strong, acknowledging that avoidance strategies, rather than tolerance, obviate the need for specializing adaptations that lead to dependence on particular conditions. Portions of this section describe how some plants find alternative sources of light, water, nutrients, and carbon dioxide, and the summary on mycorrhizae and their significance in nutrient-poor habitats is well done. The reproduction chapter illustrates obstacles in marginal environments at all stages of a plant's development, from flowering to final establishment. Genetic invasion and the high degree of hybridization in marginal areas are well explained, and the degree of invasibility is seen as a result more of resource fluctuations and disturbance than of diversity, productivity, or reproductive rates. Short sections follow on reproduction in particular environments, mast seeding, seed banks, and clonal growth, covering the advantages of asexual reproduction, dioecy, and longevity.

The six case studies go into more detail about the problems of tree lines, a warmer Arctic zone, coastal environments, flooding, woody plants at margins, and high-altitude environments. There is a good history of the tundra-taiga interface, including the idea that grazing by Pleistocene megafauna may have precluded tundra and created a subpolar steppe instead (cf. Zimov's "Pleistocene Park"). Current warming and higher atmospheric carbon diox-

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.

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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.

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## REAL-WORLD VEGETATION

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

Too 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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