Plants and Vegetation

Origins, Processes, Consequences

Plants make up 99.9 percent of the world's living matter, provide food and shelter, and control the Earth's climate. The study of plant ecology is therefore essential to understanding the biological functions and processes of the biosphere. This vibrant new introductory textbook integrates important classical themes with recent ideas, models, and data.

The book begins with the origin of plants and their role in creating the biosphere as the context for discussing plant functional types and evolutionary patterns. The coverage continues logically through the exploration of causation with chapters, amongst others, on resources, stress, competition, herbivory, and mutualism. The book concludes with a chapter on conservation, addressing the concern that as many as one-third of all plant species are at risk of extinction.

Each chapter is enriched with striking and unusual examples of plants (e.g., stone plants, carnivorous plants) and plant habitats (e.g., isolated tropical tepui, arctic cliffs). Paul Keddy's lively and thought-provoking style will appeal to students at all levels.

Paul Keddy is the first holder of the Schlieder Endowed Chair for Environmental Studies at Southeastern Louisiana University. His current research explores the environmental factors that control plant communities, and how these factors can be manipulated to maintain and restore biological diversity. Dr. Keddy has published more than a hundred scholarly papers on plant ecology, and is designated a Highly Cited Researcher in Ecology and Environment by the Institute for Scientific Information. He is the author of *Wetland Ecology: Principles and Applications* (winner of the Society of Wetland Scientists' Merit Award) and *Competition* (awarded the Lawson Medal by the Canadian Botanical Association and the Gleason Prize by the New York Botanical Garden). Dr. Keddy also co-edited *The World's Largest Wetlands: Ecology and Conservation* and *Ecological Assembly Rules: Perspectives, Advances, Retreats*.

Plants and Vegetation

Origins, Processes, Consequences

Paul A. Keddy

CAMBRIDGE
UNIVERSITY PRESS

CAMBRIDGE UNIVERSITY PRESS
Cambridge, New York, Melbourne, Madrid, Cape Town, Singapore, São Paulo

Cambridge University Press
The Edinburgh Building, Cambridge CB2 8RU, UK

Published in the United States of America by Cambridge University Press, New York

www.cambridge.org
Information on this title: www.cambridge.org/9780521864800

First published 2007

Printed in the United Kingdom at the University Press, Cambridge

A catalog record for this publication is available from the British Library

ISBN-13 978-0-521-86480-0 hardback

Epigraph

The mass of vegetation on the Earth very far exceeds that of animal organisms; for what is the volume of all the large living Cetacea and Pachydermata when compared with the thickly-crowded colossal trunks of trees, of from eight to twelve feet in diameter, which fill the vast forests covering the tropical region of South America, between the Orinoco, the Amazon, and the Rio da Madeira? And although the character of different portions of the earth depends on the combination of external phenomena, as the outlines of mountains – the physiognomy of plants and animals – the azure of the sky – the forms of the clouds – and the transparency of the atmosphere – it must still be admitted that the vegetable mantle with which the earth is decked constitutes the main feature of the picture.

von Humboldt, A. 1845.
Cosmos: *A Sketch of the Physical Description of the Universe*.
Volume 1. Translated by E. C. Otté. Foundations of Natural History.
Baltimore: Johns Hopkins University Press. 1997.
(Originally produced in five volumes:
1845, 1847, 1850–51, 1858, and 1862.) p. 343.

Contents

Chapter 3 Resources

Chapter 4 Stress

Chapter 7 Herbivory

Chapter 8 Positive interactions: mutualism, commensalism, and symbiosis

Chapter 12 | Conservation and management

Preface

For many years it has been apparent to me that there is a need for a good textbook in plant ecology. This book is aimed at middle to senior level undergraduates. I also hope that it will serve graduate students, fellow professors, and resource managers. Since many of the topics I include were new to me, I assume that they will be new to even relatively advanced readers.

In writing this book, I made two key assumptions regarding the experience of my audience and the availability of introductory biological information. I deliberately wrote for an audience who already had some exposure to both botany and ecology – an audience having had, perhaps, a first semester course in botany and another first semester course in general ecology, or a comprehensive introductory biology course. I assumed my readers would own, or at least would have access to, a basic introductory text in biology. I have *not* tried to repeat or rewrite such texts and have taken for granted that readers will have a working familiarity with topics in plant biology such as photosynthesis, transpiration, and meiosis. I have also *not* tried to repeat basic ecological concepts such as primary production, population growth, decomposition, and nutrient cycling, nor provide a broad illustrated summary of biomes. My impression is that such topics are not only well-covered in good biology texts, but are gradually filtering their way even into the elementary school system. I do, however, revisit many basic topics from photosynthesis to nutrient cycling when important aspects need more emphasis – for example, the way early plants changed the composition of the atmosphere, or how humans have altered the nitrogen cycle with the Haber process. Similarly, while I address the general processes that unify grasslands (e.g., competition, grazing, fire, drought), anyone seeking an elementary enumeration of grassland types or basic information about the geographic distribution of individual grassland types will have to go back to an introductory text. For such background, one might choose among an introductory text in botany, an introductory text in ecology, or the outstanding *Ecology of World Vegetation* (Archibold 1995). I also do not provide a glossary as this is a standard component of introductory texts. Rather than replicating existing textbooks, I have chosen to emphasize unifying topics such as:

1. How populations of plants are assembled into communities and ecosystems.
2. How plants affect their surroundings, and how they are affected by those surroundings, at scales ranging from millimeters (the rhizosphere) to kilometers (the atmosphere).

3. How plants interact with one another, and how they interact with other species, with examples ranging from fungi and worms to tortoises and elephants.
4. How plants and plant communities are dispersed along gradients of time and space. Since so much work these days emphasizes small-scale interactions, I have tried to balance this trend with a temporal scale that includes topics often overlooked in "modern" plant ecology and consequently poorly understood by my own students, such as trends in early plant evolution, consequences of catastrophes such as meteor impacts, and responses to continental glaciations. The spatial scale is equally large, and deliberately emphasizes natural sources of variation in plant communities such as gradients of topography, flooding, fire-frequency, soil fertility, and altitude.
5. How general models and actual applications both have great value in guiding research and classifying thought. I therefore tried to provide most topics with both a theoretical context (e.g., simple mathematical models), and an applied context (e.g., examples of these ideas being applied to manage real ecosystems). These sections tend to occur toward the end of chapters. On first reading you may, if you wish, skip the sections on theory, or skip the sections on applications, or both, and still receive a workable treatment of plant ecology. I, however, would strongly encourage you to read them, at least on the second time through, as these approaches (theoretical and applied) need not be mutually exclusive, and they enrich the rest of the text.

This is explicitly a book about **plant** ecology. It draws upon and respects the variety and complexity of real plants in real plant communities (Keddy 2005b). I have gone out of my way to add examples from parts of the Earth rarely highlighted – the Guyana highlands of South America, the deserts of South Africa, and islands such as the Galapagos and New Caledonia. I have also made a point of including unusual plants – carnivorous plants, arctic-alpine plants, epiphytic plants, parasitic plants, succulent plants, and plants that attract ant colonies. I have not hesitated to include many unfamiliar plant names. As a student, I found lectures on corn and beans, or on weeds and old fields, to be boring. I wanted to learn about the full diversity of the Earth's plant types, and what determined where they were found. Some reviewers have criticized the manuscript for having insufficient examples from North America, where many college texts are marketed. This was a conscious decision on my part. *All* college students whatever their country of origin need to know about noteworthy plants and plant communities found in the rest of the world.

After choosing the audience, and deciding that I would write about real plants in real habitats, the third decision was to include the occasional opinion. I assume that by buying a book by a certain

scholar (me, in this case), you wish to benefit from the experience of that scholar. It is traditional to take textbooks and rewrite them with countless referees until all traces of the writer's personality have vanished. This, indeed, was the advice given to my editor, Alan Crowden. It also was the process that another publisher tried to impose upon me. My reaction as a reader was – how boring! My reaction as a writer was – if the committee thinks they are so clever, let them write it themselves. If you want such a book go elsewhere. But before you do, be very clear on one point – all textbooks have enormous amounts of opinion in them. In most cases, that opinion is hidden – that is, the opinion is an *act of omission* – with bodies of work, ideas, and papers simply ignored. Students are unable to protect themselves from these kinds of hidden opinions (e.g., Wardle 1995, Keddy 2004, 2005a). In this book, there really are no more opinions than in any competing text – it is merely that my opinions are out in the open where you can see them; my opinions are acts of *commission*. I try to make it clear where my opinions may be particularly strong, but I am not embarrassed by them. Many papers and books in our field that pass for objective science are in fact laden with opinion, political agendas, and ignorance of history. Students using such books and papers have no way of knowing how much mere opinion they are absorbing. Here you do.

The examples I incorporate to illustrate the topics covered are drawn from work conducted over the last hundred years, including studies by long dead scholars and other scholars whom I know only from reading their work. I provide many suggestions for additional reading, including lists at the end of each chapter – I invite students to broaden their perspective and to seek out original sources. It is not a matter of who you know – it is a matter of who you have read. One referee thought that I cited too much old work – I am of the opinion that too much important old work is being ignored making students (and their professors) vulnerable to false claims of novelty. I would like nothing more than to stimulate a student to go to the library and read old and new work by other scholars. Trust no one, and certainly not me. Read it for yourself.

If there is one other philosophy that guides this book, it is the need to seek general relationships while respecting the details (Keddy 1987, 1994, 2005b). In any field there is a risk that one may become so fascinated by detail that one is unable to relate to any coherent set of principles for summarizing the detail, or for extending them to new situations. At the other extreme, there are monographs written by physicists or zoologists regarding computer models – treatises that are so far removed from botanical reality that they mislead students into thinking that superficial assumptions are a substitute for knowledge about plants. I have tried to ride the razor's edge (or perhaps the enormous valley) between the two – combining respect for the detail (e.g., Figures 4.31, 5.2, 7.11, 8.11) with respect for scientific generalities (e.g., Figures 3.5, 6.3, 7.23, 12.26).

One obstacle to the synthesis of general relationships in ecology is the development of myriad factions, each emphasizing a different view of the discipline. For example, there is a school of phytosociology, a school of plant demography, a school exploring the multivariate techniques of ordination and classification, a school focussed upon mineral nutrition, a school that uses molecular techniques to explore phylogenetic patterns, a school that emphasizes field experiments, and a school studying theoretical models. Superimposed upon this are the schools that organize themselves by habitat, such as wetland ecologists, foresters, desert ecologists, grassland ecologists, and agronomists. Given all these subdivisions of plant ecology, finding generality is challenging. Indeed, any attempt at unification seems to be interpreted as a threat to the importance of each school.

My scientific philosophy is rooted in the pragmatic tradition (e.g., James 1907, Keddy 2001, 2005b). I strove to find unifying principles that organize the mass of botanical data that exist today. Some principles may be well-established, others may be more speculative, and I hope that I have made this distinction clear. Further, I try to emphasize that the search for general principles and their strict testing provide both a unifying framework for the discipline and a means of scientific progress. Without a unifying framework, and without an emphasis upon the experimental testing of hypotheses, plant ecology will stagnate (perhaps wither is a better term). We will then lose the best minds to other *apparently* more exciting fields and be left with second-rate minds recycling second-rate ideas.

My objective is to write a text that provides a unified perspective of plant ecology, while including a variety of frames of reference and taking the best from each. No doubt experienced scholars will find inadequacies in their focal areas. I ask them to consider the scope of the discipline that I have covered. Further, anticipating such views, let me suggest that the balance provided is a strength of this book – I do not belong to any one school (I have worked in a range of them), I do not identify with a single habitat (although I confess to having written a book on wetland ecology), and I do not have a small circle of friends whom I intend to cultivate by citing their work to the exclusion of others. Indeed, chronic illness has tended to isolate me for the past 15 years, and from such isolation comes a certain distance and therefore perhaps, a clearer perspective. Hermits and monks have even been thought to obtain wisdom from such isolation.

Will instructors want to use this book in their courses? Or, as some referees suggested, is it too demanding for undergraduates? I am of the opinion that students come to university to learn topics in depth and breadth, and therefore we short-change them when we fail to challenge them sufficiently. If you believe your class to be insufficiently versed in topics such as photosynthesis, transpiration, meiosis or biomes, include these topics in your lectures and guide students through the chapters they find more difficult. Other instructors using this book may prefer to work through chapter by chapter, having

students read one chapter each week, and perhaps requiring extra reading for each chapter from the current literature and from papers prior to 1970. Students should be encouraged to visit the library in addition to using the internet to obtain literature. To assist with this process, I have included a set of recommended readings at the end of each chapter. I further suggest instructors add a personal perspective, drawing upon their own experiences in plant ecology. Encourage students to get out in the field and to identify local plants. Emphasize the importance of clear testing of conflicting hypotheses. Raise the topic of the enormous number of plants facing extinction. Remind students that this is a living discipline where bright young minds can make a difference.

My message to students is straightforward: get on with the development of plant ecology. Learn something about the history of your discipline. Learn to identify plants. Buy a good field guide and a magnifying glass. Travel to wild places. Learn about the areas you visit. Find a good ecologist to train you. Do not get involved in political games or one-upmanship. Show respect for those who have gone before by reading their work and thinking about their ideas. Enjoy yourselves. Contribute something to society.

Acknowledgements

I thank the many colleagues who contributed the original research that I have drawn upon for this book. Some of you I still know only from your writing, but that perhaps is the way it should be. I have greatly appreciated the many permissions to reproduce drawings and photographs, and authors' efforts to send originals and notify me of changes. Not every contributor is mentioned here, but the origins of each drawing and photo are clearly stated. Ian Keddy provided considerable assistance, manipulating files in multiple formats to create and adjust illustrations. In addition, line drawings by Howard Coneybeare appear courtesy of Friends of Algonquin Park, line drawings by Rochelle Lawson were borrowed from *Wetland Ecology: Principles and Conservation*, and Betsy Brigham contributed several new illustrations. Cheryl Cundell greatly assisted with compiling the first version of the manuscript. Jennifer Tynes helped with updating permissions. Over the years I have talked with many colleagues about this project, and may not always be aware of important ideas borrowed from them. Early input from Evan Weiher was most helpful. Sara Tenney and Alan Crowden provided solid editorial advice. Recent input from the following was much appreciated: Peter Bellingham, Walter Judd, Walter Larcher, Craig Loehle, Tiffany McFalls, Rick Miller, and Susan Wiser. The librarians at Southeastern Louisiana University provided steady support with many interlibrary loans. Throughout this lengthy process, Cathy Keddy provided encouragement and editorial services beyond compare.