

Plant Ecology

Origins, Processes, Consequences

Second Edition

Presenting a global and interdisciplinary approach to plant ecology, this much-awaited new edition of *Plants and Vegetation* integrates classical themes with the latest ideas, models and data. Keddy draws on extensive teaching experience to bring the field to life, guiding students through essential concepts with numerous real-world examples and full-colour illustrations throughout. The chapters begin by presenting the wider picture of the origin of plants and their impact on the Earth, before exploring the search for global patterns in plants and vegetation. Chapters on resources, stress, competition, herbivory and mutualism explore causation. After chapters on how pattern in vegetation is studied, the book concludes with a chapter on conservation that addresses the concern that one-third of all plant species are at risk of extinction. The scope of this edition is broadened further by a new chapter on population ecology, along with extensive examples including South African deserts, the Guyana Highlands of South America, Himalayan forests and arctic-alpine environments.

Paul A. Keddy has taught plant ecology for more than 30 years. He is often a conference keynote speaker, and delights in bringing science alive for his audience. Dr. Keddy's research explores environmental factors that control plant communities and their manipulation to maintain and restore biodiversity. His awards include a National Wetlands Award for Science Research, and the Lawson Medal and Gleason Prize for *Competition*, and his first edition of *Wetland Ecology* (Cambridge University Press, 2000) won the Society of Wetland Scientists' Merit Award. He has also advised organisations including World Wildlife Fund, Earthjustice and The Nature Conservancy.

Cover: The Socotra archipelago off the east coast of Africa has many endemic plants, including this dragon's blood tree (*Dracaena cinnabari*). You can read more about these trees in Section 9.4.3, and about the harm being caused by goat grazing in Box 13.2. The archipelago is a fragment of the former continent of Gondwana, which is discussed in Section 8.2.2. (Vladimir Melnik, Shutterstock).

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PAUL A. KEDDY



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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.

Alexander von Humboldt. 1845. *Cosmos: A Sketch of the Physical Description of the Universe*

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Preface

Welcome to the second edition!

When planning the first edition, I wanted to write the book that should have been there to instruct me when I was a young biologist, the book I wish I had to consult when I was 18. The chapters consist of 13 topics that should be included in every plant ecology course. That would be about two weeks per topic area in a one-semester course. Each chapter begins with some inescapable basics (about one-third of the chapter), some more in-depth reading for senior students (another third), and some advanced material that might be of use later in one's career (another third). I assume of course that you will buy this book and keep it as a lifetime companion, not just rent it for a few months.¹ You can, of course, rent or borrow if you wish but good books grow along with you. I have written this book with that in mind: some basic principles are so obvious we need to hear them first when we are young and then repeatedly as we age.

At the time the first edition went to press, I was seriously ill and leaving my position in Louisiana, as well as trying to finish a guide to nature in Louisiana, and coping with unusual levels of academic perfidy. Not to mention the aftermath of Hurricanes Katrina and Rita. Louisiana was meanwhile beginning her march of folly into the ocean, amidst chants of "Drill, baby, drill!" In a perfect world, I would have had a few more quiet months for reflection and editing and revision but, of course, if you wait for the perfect time to write the perfect book, it is possible that one will die long before that state of perfection is attained. I have since had five years in the deciduous forests – living in solitude longer than Thoreau, but not so long as St. Francis. This has allowed me to reflect further on the material in the book, to consider the suggestions and opinions of published reviews, and to correspond with students.

So, you ask, what about the new edition?

My first task has been some pruning. Most plants benefit from pruning, so long as it is carried out with precision. I have taken branches out of nearly every chapter. I like the form and architecture much better now. I hope the flow of ideas is clearer, and that the remaining figures more perfectly illuminate the text. Each chapter has, more

¹ Yes, I know good books are expensive. Particularly in hard cover. But they last a lifetime. I still have a hard cover of *Geographical Ecology* that I bought as an undergraduate. I do understand that money is in short supply for most students – I once lived in a basement apartment where I met many of the invertebrates, including scutigera, that I was learning about at university. My suggested solution for books? Let your relatives know. Many family members are desperate for a long-lasting and worthwhile Christmas or birthday gift. Instead of an ill-fitting sweater, or a piece of kitsch that will soon be forgotten, let them choose a book from your list, and write something personal in it. Long after they have passed on, you will still have a treasured reminder of them in your personal library.

clearly I hope, those three sections: (1) basics, (2) more in-depth reading and (3) advanced material. Given this structure, beginners should remember that if any chapter seems overwhelming, it is fine to stop part way through. Even a writer has to do this. There really are parts of the book that still challenge my understanding, and I was the one who wrote it! If you merely read the first third of every chapter you will have grasped the essentials.

Having marked thousands of exams and attended an excruciating number of seminars and oral exams, I can assure you that many people who claim to have had a plant ecology course have either been badly taught or fail to remember much at all. Or both. Hence you will find certain topics continue to be emphasized simply because I found that most students I met did not know them.

Although I wrote this book for a one-semester undergraduate plant ecology course, you could also use this book in a graduate course. In this case, having laid the foundations early in the chapter (perhaps as preparatory reading assignments) you could explore the examples and discussions later in the chapter. I have continued to include important people in ecology. You will meet people including Carolus Linnaeus, Alexander von Humboldt, Joseph Banks, Alfred Wallace, Charles Darwin, Wilhelm Hofmeister, Vladimir Vernadsky, Bernhard Frank, Armen Takhtajan, Christen Raunkiaer, Fritz Haber, Ronald Fisher and Robert Whittaker. No, these are not the people who are currently promoting themselves with trumpets and headlines, nor their sycophants, but people who were devoted to botany, often overcoming great hardship to advance our understanding of plants and plant ecology. (Well, except for Haber. His wife shot herself in shame; but even so, he is part of the story.) When we forget them, we lose a part of ourselves.

I also had my fellow professors and other scholars in mind. There is so much pressure to specialize into narrow sub-disciplines that it is easy to lose track of the big picture. This book provides such a big picture as a backdrop against which your own work can be viewed more clearly. It should also help you teach topics well beyond your own specialty. The chapters end with difficult problems that remain to be solved, and so, in a general way, provide trajectories of how other people are trying to solve problems in other sub-disciplines. I hope I have dealt with your own specialty adequately but, of course, no one can claim to be an expert in every field, however widely one reads. Still, someone has to make the leap to the big picture. I often advise younger scholars struggling with their own field that one of the best ways to find new approaches and insights is to read about other fields. In this sense, deserts really have taught me a great deal about wetlands.

I have also added new material, where it was important, but very selectively. I am not of the opinion that every piece of work rushed into print in 2012 is necessarily an improvement over excellent and classic work from 1972. I have added work, much as I would have added in my lectures, to update major themes, but not to obscure the past or stroke friends' egos. Good work will stand the test of time; we ignore it at our peril. This is doubly true now that the internet and hand-held devices fragment our attention spans and reduce pages of text to a few headlines. In the past, when I had to walk across campus to the library (sometimes through the snow) and pay to photocopy articles page by page, there was an incentive to read them, not just collect them. But even then

(ca. 1975) one easily slipped into the mistaken belief that if you had a copy you must have understood the content! Desks then easily accumulated piles of papers that had been copied but not read. Now that pdf files flow effortlessly over the internet, even right into my office in the forest, how easy it is to assume that the electronic acquisition of a paper, or (gasp) automatic download of a citation, is a substitute for having read and considered the contents. Increasingly, I suspect that many young scholars are citing work they have not even read. (Yes, my friends, it is far more obvious than you might suspect.) This is a dangerous route to error and ignorance. I assure you that every single article I cite in this book, I have read. Many of the books I even own. From time to time I take them down, dust them off, and re-read them. The effort is usually well rewarded.

I have also had the time to reconsider each figure. Some have been removed. I thought Lonesome George the Galapagos tortoise would have to leave, particularly as he has died, but Ole Hamman has helped me keep him in as a cheerful insert in Figure 13.8. Some figures have been revised for clarity (world floristic regions now appears in colour in Figure 2.12). A few more have been added, such as the world leaf economic spectrum (Figure 3.26). If you simply flip through the figures, you will see the improvements.

When Cambridge decided to print in full colour, I went through the entire book again. This time I was able to add in some beautiful and strange plants from around the world: the saguaro cactus, *Dendrobium* orchids, *Myrmecodia beccarii*, the ant house epiphyte, *Magnolia sinica*, the yareta, *Telopea speciosissima*, the dragon's blood tree, *Welwitschia mirabilis*. There are also more colour maps, including an accurate map of world grasslands (Figure 10.7) and the latest maps of global plant diversity (Figure 12.10). The images also range across time, from early paintings of newly discovered plants to a recent highly processed satellite image from the NASA Earth Observatory. For those of you who remain intimidated by the size of the book, may I suggest you begin by just flipping through the colour images and reading those captions? I think you will find they tell quite a story in their own right.

Three technical challenges remained.

First, there was explaining what we know about the origin of plants and their impact on the Earth. I do think it is one the most important biological stories. In my experience, it is not well taught in schools, and over the last five years, I have seen important topics such as evolution and global warming systematically undermined by people being paid to shill for ignorance. I still meet students who tell me, gravely, that evolution violates the second law of thermodynamics, when, as plants brilliantly illustrate, evolution is, in fact, a direct and necessary consequence of the second law of thermodynamics. The story of plant evolution must be told, but some think it should not start the book. I have tried to juggle sections here, keeping the story near the beginning, but introducing modern plants earlier, and moving energy flow to a sub-theme.

Second, in a related way, some reviewers thought the book covered too much basic work that students should already know. I don't disagree. Early land plants and coal swamps, and the oxygen revolution and major types of plants should indeed have been

taught. All I know is that I have repeatedly sat on graduate qualifying exams where students who assured us they had earned a BSc really did not know why coal was a fossil fuel, or what early land plants looked like, or what is meant by alternation of generations. We may expect that students should know such basics, but apparently they often do not.

The third issue was population ecology. Some reviewers wanted a chapter on the topic. My graduate research was in population ecology. But this experience taught me as much about its limitations as well as its strengths. In the first edition I tried to show you how populations fit into several different themes. That is, they are a tool for understanding plant communities, not an end in themselves. Still, many readers have told me that in a book on plant ecology, there should be a separate chapter on populations. I accepted this request, and have moved many population examples into a separate chapter. I also try to explain why one would study plant populations, the fundamental importance of exponential population growth to ecology and evolution, and how populations expand our understanding of processes and consequences altogether. I have also added some interesting stories about Brazil nuts and century plants.

I like this second edition better and I hope that you will agree. My aspiration in writing this book was to teach you about plants, to pass on wisdom from researchers who are now dead or retired (or both), to challenge young scientists to revisit certain problems, to share my enthusiasm for wild places, and to encourage a new generation of botanists and conservationists. I also wanted to prepare an accurate historical record of work, to counter-balance those who are deliberately distorting our field to benefit their own egos. As I worked on *Plant Ecology* I occasionally received fan mail for *Wetland Ecology*. One student recently emailed me from his hand-held device (as he studied for finals) that it had him laughing as he studied and that it was “such an enjoyable read that I hesitate to call it a text book.” Based on that email, I can add one more aspiration: may you enjoy a jolly good read.