Seedling Ecology and Evolution

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been introduced into the United States are estimated to have become invasive. They have caused widespread and hugely expensive damage, particularly to agriculture but also to power generation systems, waterways, and infrastructure generally. Yet reliable information about their effects is not just of interest to environmentalists, economists, and the public. Ecologists are well aware of the impacts that invasive species have on biodiversity: Many invaders have reduced native species' numbers and ranges by outcompeting them, by feeding on them, or by parasitizing them. Some invaders have caused extinctions of native species.

In assessing these impacts, economists attempt to consider both the costs of controlling the invasive species and the damages they cause to agriculture and the environment broadly. The authors of *Bioeconomics of Invasive Species* provide an in-depth perspective on numerous attempts to understand and manage the consequences of invasive species. They concentrate particularly on those that are a hazard to the environment or are costly in terms of the harm they cause and the price of control. The book provides valuable insights for combating the threat that nonindigenous species pose for the environmental and economic well-being of society.

The scientific issues involved in both these considerations are highly complex and difficult to understand and assess. Interestingly, more than 99 percent of all US crops, including corn, wheat, soybeans, and others, were introduced into the United States. But this fact does not diminish the serious ecological and economic problems associated with invasive species. The increasing movement of people and goods throughout the world makes it likely that invasive species will continue to be a serious problem.

The diversity of behaviors and activities of invasive species makes it more difficult to find solutions to control them. In addition, the effects of invasives on agriculture, fisheries, public health, and other aspects of the economy are widespread. Ecologists and economists have occasionally worked with one another to understand the complex issues that invasive species raise for each discipline independently and jointly. Each discipline has a distinctive perspective and is itself an obstacle to comprehension. When they attempt to merge their techniques and focus on one approach to the problem, the situation becomes highly complicated.

Ecologists tend to rely on the estimates of economic consequences of invasive species provided by managers and specialists in agriculture, fisheries, and energy production activities. Such estimates of costs and benefits may lack the sophistication of assessments provided by some economists. Yet ecologists sometimes question the approach typically employed by economists, which is based on the concept of measuring "willingness to pay."

Measuring willingness to pay can be a highly valuable measure for some problems, including some caused by invasive species. For example, the technique is sound when determining the public's willingness to pay for a specific program of mosquito control to limit the spread of West Nile disease, because the public can be made aware of the risks of the disease and of control measures. However, use of the willingness-to-pay approach in surveys of public attitudes to the use of pesticides generally can be misleading as a way of assessing their public health impacts. Few members of the public have adequate knowledge of the extent of pesticide use and the damage it causes to beneficial native organisms in forests, grasslands, lakes, rivers, and other ecosystems. In addition, the public often does not understand the effects pesticide use may have on human health. These limitations compromise the value of attempts to use the willingness-to-pay approach to assess many of the economic impacts of pesticide use.

In *Bioeconomics of Invasive Species,* the authors attempt to investigate and untangle the complexity of the ecology of many notable invasives and identify their economic interrelationships in various environmental situations. Two chapters examine approaches to modeling of the spread of invasives. The book's major strength may be its integrated analyses of fisheries and various other societal institutions that are adversely affected by invasive species. The authors warn against relying on oversimplified investigations.

In short, the book is valuable as a source of reliable information related to the management of invasive species ranging from plants to animals to microbes. Its messages are well worth studying for readers interested in biology, ecology, economics, geography, and related applied disciplines.

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SEEDLINGS FINALLY GET THEIR DUE

Seedling Ecology and Evolution. Mary Allessio Leck, V. Thomas Parker, and Robert L. Simpson, eds. Cambridge University Press, 2008. 536 pp., illus. $63.00 (ISBN 9780521694667 paper).

At some point, many plant demographers find themselves staring at a data set full of detailed information on seeds or juvenile and adult plants, but lacking any meaningful information on the seedling stage. Adult plants are usually easily located and either marked for field study or collected for lab study. Even seeds, mysterious little black boxes in their own right, can be collected and brought into the lab and made to jump through experimental hoops. But seedlings lack the attributes that make other life-history stages relatively easy to study; in many systems, seedlings are episodic and ephemeral, difficult to find, and tricky to identify. My personal experience indicates that studying them can cause permanent knee damage.

For these reasons, seedlings have been understudied by most subspecialties of plant science. This lack of information has been reflected in the absence of any comprehensive volume reviewing

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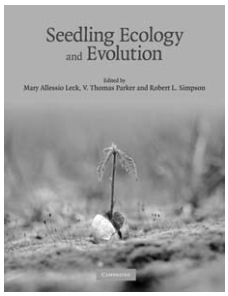
seedling research. Carol and Jerry Baskin's *Seeds* book, and Mary Allessio Leck's *Ecology of Soil Seed Banks* have compiled information on the seed stage, but the seedling stage has not, until now, been represented by its own book. This is true despite the fact that seedlings are arguably the most important stage of the plant's life history, from both an ecological and an evolutionary point of view. Unlike seeds, which are buffered from environmental vagaries by seed dormancy, and juvenile and adult plants, which have modularity, physiological adaptations, and belowground reserves, seedlings are virtually defenseless against hostile conditions. From an ecological point of view, seedling environmental tolerances are essential in determining the species composition of plant communities. From an evolutionary point of view, seedlings are subject to the highest mortality—and therefore potentially to the strongest selection—of any stage in a plant's life. Seedlings are wonderful subjects for study, if you can find them.

Seedling Ecology and Evolution was coedited by Mary Allessio Leck (Rider University), V. Thomas Parker (San Francisco State University), and Robert L. Simpson (University of Michigan). These three editors, known for their work on seed bank ecology, first worked together in the 1970s when all were on the faculty at Rider University. From their first studies of seed banks of tidal freshwater wetlands grew the idea for a symposium, and from that came their coedited volume *Ecology of Seed Banks* (1989, Academic Press). Simpson and Leck continued their work with a 10-year field study of seed and seedling dynamics in a tidal freshwater marsh, and their observations about the importance of the seedling stage in structuring populations led to this book. The editors identified and recruited expert contributors across many fields of plant science.

The content of this book is extremely diverse, and will be of use to specialists ranging from ecophysiologists to paleobotanists. As a plant scientist who looks at seedlings through a lens colored primarily by my interest in demography, I was especially interested in the chapters looking at the role of seedlings in the life history of plants. Angela Moles and Michelle Leishman address the question of how seedling survival and seed number together influence the total number of reproductive offspring produced by a plant during its lifetime, an essential question because so many studies look at only single-year seedling survival or seed output. In a subsequent chapter, Ove Eriksson and Johan Ehrlén examine the relative roles of different sources of seedling mortality in structuring communities (at least in the geographic areas where natural seedling death has been quantified). Because I have always studied seedlings in arid environments, I was surprised to learn that in studied systems, drought is the second most common cause of mortality, following herbivory.



Seedling Ecology and Evolution illuminates questions that remain unresolved and brings us up-to-date on current thinking. Taylor Feild looks into the evidence about the characteristics of the first angiosperm seedlings. This is a fascinating question whose answer has dramatically changed. Previously, paleobotanists believed that the earliest angiosperms were slow-growing trees, but in the 1960s the view shifted to favor weedy herbs; more recently, interpretations of molecular phylogenies have suggested that these herbs are small-seeded, yet they established in dark, disturbed sites. This result is surprising and stimulates further research because understory species are most often large-seeded.

Of particular interest for those of us who do applied work is the last section of the book on applications of our knowledge about seedling biology. Laura Hyatt looks at the role of seedling traits in promoting invasions. She starts by pointing out that many familiar litanies of invasive species' traits lack any generalizations about the seedling stage, and she addresses the question of whether this is due to (a) multiple, alternative strategies utilized by invasive seedlings, or (b) a lack of information on seedling traits of invaders. Likewise, Susan Galatowitsch asks how seedling requirements influence revegetation success. Most interesting to me was her discussion of how species selection for restoration influences outcomes—how the establishment characteristics of seeded species influence site dynamics over the long term.

I was surprised, even amazed, by some of the things I learned about seedlings. Thomas Horton and Marcel van der Heijdin state that 80 percent of species rely on mycorrhizal networks, into which seedlings are usually quickly incorporated after germination. In Jon Keeley and Phillip van Mantgem's chapter on seedling communities, I learned that closely related species can have different strategies in the same environment; for example, seedlings of *Acer saccharum* and *Acer rubrum* recruit into very different environments, with *A. saccharum* seedlings recruiting continuously and successfully in shady understories and *A. rubrum* seedlings waiting years in understory seedling banks until a canopy gap allows their continued growth. In Elizabeth Farnsworth's excellent overview of the role of phytohormones in seedlings, I learned how auxin and ethylene can work together to guide seedling roots to patches with higher nutrient availability.

After reading many of the chapters, I came away with a sense of how little we do know about seedlings. In many cases, the lack of a conclusive answer to the question addressed by a particular chapter is attributable to the difficulty of identifying generalizations in ecology. For example, Johannes Kollmann asks whether there are identifiable functional groups of seedlings. The likely answer to this question is that seedling traits are widely variable among species, different species have different traits in different systems, and overarching patterns

are hard to find. Other chapters reinforced my impression that we know much, much more about the seed than we do about the seedling stage. For example, Angela Moles and Michelle Leishman discuss the relationship between seed mass and number in depth, but their review indicates that the literature has much less to offer about the role of seedling traits in life histories.

The editors recognize and acknowledge the lack of identifiable generalities about seedlings in the summary chapter, stating that "there is no typical seedling." The diversity of definitions of the seedling stage's beginning (embryo enlargement? radicle protrusion? cotyledon emergence?) and end (end of dependence on seed reserves? loss of cotyledons? appearance of first true leaf?) illustrates this point. Various authors use different definitions, each quite likely the most appropriate one for a particular species or situation.

One of the most fascinating and valuable aspects of this book is the tour it gives us of the bizarre and idiosyncratic seedlings that most of us will never see. We are introduced to Australian perennial seedlings with contractile roots that pull the shoot below the soil surface, buoyant aquatic seedlings, the few-celled protocorms of orchids (with fabulous photographs by John O'Neill and Melissa McCormick), the pseudorhizomatous seedlings of *Amborella trichopoda,* and the 1.5-meter-long first leaf of *Lodoicea maldivica.* For those of us who study seedlings in one or two systems, it is fascinating to see these diverse and surprising facts of global seedling natural history gathered in one place. And, in reading the book, I had a growing sense that it is partly this great (and still largely unstudied) diversity that makes generalization about seedlings difficult.

Discussion of a few kinds of seedlings that went unremarked in *Seedling Ecology and Evolution* would have added even more interest to this volume: species that finish their lives as seedlings (i.e., plants that flower when still relying on stored seed reserves) and seedlings of true aquatic plants. A few chapters also strayed a bit too far off topic (particularly the one on embryo evolution in nonflowering plants). In fact, sometimes sections that were off topic (particularly those that seemed to be about seeds rather than seedlings) emphasized the point that relatively little is known about seedlings, and that much more is known about the other life-history stages. The book does an amazing job, however, of amassing and synthesizing, for the first time, our knowledge of the lives of seedlings, and it provides a great jumping-off point for future seedling research. I hope that it will stimulate further research and that it will be updated in the future as our knowledge of the most precarious stage of a plant's life history grows.

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