Seedling Ecology and Evolution

Seedlings are highly sensitive to their environment. After seeds, seedlings typically suffer the highest mortality rate of any life history stage. This book provides a thoughtful and comprehensive review by leading researchers of the interconnected topics that constitute seedling ecology and ecophysiology, focusing on how and why seedlings are successful. It considers the importance of seedlings in plant communities; environmental factors with special impact on seedlings; the morphological and physiological diversity of seedlings, including mycorrhizae; the relationship of the seedling with other life stages; seedling evolution; and seedlings in human-altered ecosystems, including deserts, tropical rainforests, and habitat-restoration projects. The diversity of seedlings is portrayed by specialized groups, such as orchids, bromeliads, and parasitic and carnivorous plants. This important text sets the stage for future research and is valuable to graduate students and researchers in plant ecology, botany, agriculture, and conservation.

The editors are well known for their work in soil seed-bank ecology. *Mary Allessio Leck*, Emeritus Professor of Biology, Rider University, has worked on seed ecology of tidal freshwater wetland species, and on wetland education for urban youth; *V. Thomas Parker*, Professor of Biology, San Francisco State University, on tidal wetland, chaparral, and mycorrhizal ecology, and *Arctostaphylos* evolution; and *Robert L. Simpson*, Professor of Biology and Environmental Science, University of Michigan – Dearborn, on freshwater wetland ecology and the natural history of Michigan.

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Foreword

The properties of seedlings are potentially important to all plant ecologists, whether they be interested chiefly in understanding seminatural indigenous vegetation, invasive plants, or the problems of restoration. In seminatural vegetation, seedling properties may determine the climatic regions occupied on a continental scale and the habitats occupied within a landscape, the ability of one species to coexist with another in a community, and the abundance of one species relative to another at a given time and place. The requirements of seedlings often determine the sites in which potentially invasive species can succeed and whether a given approach to restoration of seminatural vegetation is effective.

During the last 40 years, there has been a steady increase in the amount of research by ecologists on the properties of seedlings as opposed to those of mature plants. Great pioneers such as F. E. Clements and E. J. Salisbury appreciated the importance of studying seedlings, although papers on experimental studies on seedlings were uncommon before the 1960s. Several factors have driven the increase in work on seedlings. Here I emphasize seven.

First, there has been a desire to seek generalizations about seedlings. For example, how does relative growth rate vary with the mass of reserves in the seed, and how does it differ at a given seed-reserve mass between plants of different growth forms (such as tree vs. herb), or species from different kinds of habitat (where the vegetation shows high and low productivity, respectively)? For the mechanistically minded, the key questions become (1) how do seedlings of species with smaller seeds have higher relative growth rates, and (2) how do species of different functional types have different relative growth rates at a given seed-reserve mass? Of course, the answers to these questions have turned out to be related to our increased understanding of the ecophysiology of the vegetative organs of the adult plant, at least of the leaves – there still is much to learn regarding stems and roots.

Second, there has been a realization that differences among species with regard to the requirements of juveniles may play a significant role in making possible long-term coexistence of species in communities. Within a community, the conditions vary more at the scale of the juvenile than of the adult, and juveniles are generally less tolerant of adverse conditions. Here, we are concerned not only with the seedling as defined in a very narrow sense, but also with plants in their first few weeks, months, years, or decades of life – depending on the type of vegetation.

Third, it seemed at one time that a seed number–seedling survival trade-off had considerable potential in explaining the coexistence of species that differ appreciably in seed size but have very

similar requirements for regeneration. In this event, most researchers have concluded that the trade-off by itself is not enough to explain the coexistence of the full range of seed sizes, either where greater survival results from greater competitive ability or where it results from greater tolerance of hazards during establishment.

Fourth, there has been a greatly increased appreciation that seedlings, more often than not, are in symbiosis with a type of microorganism, most commonly with at least one arbuscular mycorrhizal fungus. Gradually, plant ecologists have come to realize that in one community, some plant species are more dependent on a symbiont than in others, and that symbionts of a given type can have inhibitory as well as stimulatory effects. There have been parallel advances in our knowledge of the seedlings of plants that are partially or wholly parasitic. There remains open the question of how much specialization exists in the relationship between plant species and their symbionts – a question that can now be tackled more satisfactorily as a result of the development of molecular techniques.

Fifth, the development of molecular biology has greatly increased the potential for advances in understanding the physiology of seedlings – particularly their tolerances of shade, drought, low nutrient supply, and excess salt. The same goes for our understanding of seedling development, including the part played by phytohormones.

Sixth, there has been a revolution in our thinking about the kinds of seeds of the most primitive angiosperms and the habitats in which they functioned. Also, there has been renewed attention to the earliest true seeds of gymnosperms and the analogous seed-like structures of certain tree lycophytes.

Seventh, in the last two decades, there has been a surge of interest in the long-standing problem of why some species are much more invasive than others and in the related issue of how to restore vegetation at degraded sites. Some of us feel that it is difficult to extract generalizations in these areas, and, in many cases, the key species are idiosyncratic in their requirements. Nevertheless, the great practical importance of the problems makes it imperative that they be tackled by some of the ablest ecologists. Every stage in a plant's life cycle must be considered, but, in many cases, the seedling stage will turn out to be of critical importance.

With this background, we may welcome a new book that covers the whole range of issues I have outlined. An especially attractive feature of the book is that a good many of the schools of thought that have dominated developments in thinking are represented among the authors and, more specifically, that many of the authors have been among those who have taken leading roles in plant ecology in the last two decades.

Studies on seedlings, despite real advances, are still at an immature stage, and there remain significant disagreements. I cannot accept all of the assertions in this book and, indeed, I have argued in print with some of the authors. However, for me, this does not detract

from the value of the book. I strongly recommend it to all those who seek thoughtful, up-to-date reviews of the wide range of interconnected topics that constitute seedling ecology and ecophysiology.

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June 2007

Preface

Interest in developing this multiauthored book grew from our work with seeds and seed-bank ecology. While seed production and seed-bank dynamics are critical stages, what happens to seedlings is also fundamental to explaining field observations of vegetation dynamics and recruitment. Although several recent books discuss seedlings, indicating their importance to plant regeneration (Fenner, 2000) and to seed ecology (Fenner & Thompson, 2005), only one, Swaine (1996), focuses on seedling ecology; it, however, deals exclusively with tropical forest seedlings and is now more than 10 years old. A fourth volume, Forget *et al*. (2005), is primarily about seed predation and dispersal. *Seedling Ecology and Evolution* will complement these works and provide a more all-encompassing discussion. Moreover, it bridges the life-cycle gap following seeds (e.g. Baskin & Baskin, 1998) and seed banks (e.g. Leck *et al*., 1989). Additional information about regeneration strategies may be found in Harper (1977), Grubb (1977, 1998), and Grime (2001).

We acknowledge the importance of understanding seedling biology in agriculture and horticulture; however, seedlings are well studied in these settings, whereas in natural systems, seedlings are less studied, and the literature is more diffuse. This book explores seedling adaptations and constraints to regeneration in natural and disturbed systems, where a better understanding of seedlings would stimulate study and development of theory regarding this dynamic and often neglected part of the plant life cycle.

After seeds, seedlings typically suffer the highest mortality rate of any life history stage and, therefore, are important in the selection and evolution of species. Seedlings appear to be a "bottleneck" in plant establishment because they are particularly sensitive to the vagaries of the environment. Our purpose is to explore their ecology and evolution and, in the process, bring a diverse literature together for the first time – examining the diverse morphologies and physiologies of seedlings; environmental factors that impact seedlings; driving factors in the evolution of seedlings, including phylogenetic and ecophysiological constraints; seedlings in plant community dynamics, especially how they relate to species and community sustainability; seedling strategies and syndromes, including seedling banks; and the impact of human-generated perturbations, such as invasive species, desertification, and habitat fragmentation and restoration. To accomplish this, contributors were invited to explore a range of topics that are gathered in the book as follows:

- Part I – Introduction. Chapter 1 provides a review of seedling structure, as well as an introduction to the seedling stage of the seed plant life cycle.
- Part II – Seedling diversity. Chapters 2–4 consider aspects of seedling natural history, strategies in stressful habitats where shade,

drought, inundation, and other stressors affect establishment, and strategies of highly specialized plants, including epiphytes, orchids, and parasites.

- Part III – Seedling morphology, evolution, and physiology. Chapters 5–9 examine seedling evolution in the context of embryo evolution and the rise of angiosperm ecological diversity, as well as seedling morphological and developmental changes, phytohormones, maintenance of carbon balance, and the role of symbioses in establishment and survival.
- Part IV – Life history implications. Chapters 10–13 examine the trade-offs of the seedling stage with other stages, and seedlings in population and community contexts, as well as functional groups among and within habitats.
- Part V – Applications. Chapters 14–17 examine seedlings as the advancing front for biological invasions, in deteriorating ecosystems (e.g. deserts), in systems in which they are used for system maintenance (forests), and for restoration.
- Part VI – Synthesis. Chapter 18 considers the multiple perspectives presented by the chapters of this book, presents overarching seedling strategies, and summarizes areas for future study.

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