

grassland/savanna ecosystems are closely linked with seasonally dry forests. The latter ecosystem is among the most endangered category of all, and our knowledge about it is fairly poor, which might explain why this ecosystem is scarcely mentioned at all in this book.

In the chapter on tropical rain forests the reader is informed that this ecosystem is home to nearly two-thirds of the plant species in the world and that plant-animal interactions have developed there to an extraordinary extent. Moreover, this chapter serves to introduce the reader into the many facets of biodiversity research. A fairly short account is given on the different levels of biodiversity and, moreover, several hypotheses concerning the question of why rain forests are so rich in species are discussed. According to the author tropical rain forests are characterized by a luxuriant abundance of epiphytes. However, this is certainly not true for most lowland rain forests where, typically; only relatively small numbers of vascular epiphytes are present. Moreover, in contrast to what the author says, the mistletoes are not epiphytes, but true parasites. Apart from several minor mistakes (e.g. the flowers of figs are not borne inside the developing fruit but are surrounded by the fleshy inflorescence axis) a more serious flaw is a map that shows the distribution of tropical rain forests. It is not indicated in the legend to the map that the present day rain forest distribution is depicted and not the potential distribution of this ecosystem. To the inexperienced reader it seems therefore as if the rain forests along the Brazilian Atlantic coast are nearly completely absent and only a short remark in the text explains that this absence is due to human impact.

In addition to the descriptions of particular tropical ecosystems the last chapters of the book provide an overview on mankind's impact on the use of natural resources. In particular the following issues are covered: population growth, urbanization, agriculture and fisheries, pollution, climate change and the concept of ecological sustainability.

This book is well written and only a few orthographic errors were found. The author provides the reader with many illustrative examples from tropical ecosystems and the geographical spectrum that is dealt with is fairly broad. This volume thus forms a good introduction into all major tropical ecosystems and will be of particular relevance for students, not only from tropical regions.

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Vuorisalo, T. O., Mutikainen, P. K. (eds.): Life History Evolution in Plants. 364 pp. Kluwer Academic Publishers, Dordrecht. Hardcover 1999, £ 91.00, US \$ 145.00. ISBN 0-792-35818-X; Softcover 2001, £ 31.00, US \$ 46.00. ISBN 1-402-00279-3.

All organisms have life histories – those features of an individual's biology that describe how it grows and reproduces. This brief definition is deliberately vague as these "features" are themselves more or less likely to be studied as aspects of life history, according to fashion and the whims and biases of researchers, a theme I shall return to at the end of this review. Timo Vuorisalo and Pia Mutikainen are to be congratulated on putting together a timely volume which presents a broad (though not exhaustive) sequence of subjects relating to life history evolution in plants, a topic that has generated much research interest in recent years. As the editors note in their introduction, animal ecologists were responsible for the original formulations of life history theory and a zoocentric perspective has dominated since then (even to the point of describing seed number per fruit as "clutch size"). At last, plant ecologists are stepping out from the shadow of their zoologist colleagues and proclaiming that plant life histories are dissimilar to those of animals; they share some features in common, it is true, but there are many, many differences.

One of the most fundamental differences is tackled in Chapter 1, in which Timo Vuorisalo and Pia Mutikainen deal with “Modularity and plant life histories”. Relatively few animals possess a modular morphology, whereas the large majority of plants grow by the iteration of new stem and leaf units. Modular growth has profound implications for plant life span, resource allocation and the autonomy of plant components, and therefore must influence life history evolution. For example, flower production of many plants increases linearly with vegetative biomass, as new modules monotonically manufacture reproductive structures. The chapter also serves as a good introduction to some of the themes developed later in the book, though there are occasions when a lack of detail misleads. For example, in the discussion of the source-sink hypothesis on page 15, it is stated that “typical sinks include developing seeds and fruit”. This is true for some resources but not all; as Edward Reekie discusses in Chapter 5, developing seeds and fruits are often photosynthetically active and “Photosynthesis by reproductive structures [can] account for a significant proportion of the total carbon allocated to flowers and fruits...”. This is a minor quibble though and the authors of the first chapter do a good job of introducing modularity and how it affects the evolution of life history components.

In Chapter 2, Johan Ehrlén deals with “Modelling and measuring plant life histories” and provides an excellent introduction to matrix modelling of plant demography. He argues cogently for the importance of considering all phases of a plant’s life cycle when relating fitness measures to life history traits. In Chapter 3, Juha Tuomi, Magnus Augner and Olof Leimar deal with “Fitness interactions among plants: optimal defence and evolutionary game theory”. Once again, it’s easy to pick up the odd contentious comment made in passing (is it true that “Most direct interactions [between plants] presumably are negative....”? There are many examples of direct facilitation between different species of

plants. Perhaps it’s a matter of how one defines “direct”) but that doesn’t detract from the review.

Chapter 4, by Susan Mazer and Gretchen LeBuhn, is entitled “Genetic variation in life-history traits: heritability estimates within and genetic differentiation among populations”. It begins with a general introduction to the topic, which leads into a very useful overview of the pitfalls and complications of assessing the heritability of life history traits. This, together with the section comparing different methods for detecting genetic differentiation, contains lots of good, common sense advice and this chapter would make a useful starting point for a postgraduate student interested in the topic. One of the most interesting aspects of this chapter is the comparative survey of the relative heritabilities of different kinds of life history traits. In summary, this shows that traits directly related to reproduction (e.g. seed traits, timing of flowering, etc.) have much higher heritabilities than traits indirectly affecting reproduction, such as plant survival and size. This comparison deserves to be looked at in more detail. There are a couple of examples of sloppy editing in the chapter. For example, in Table 4.1, Mann-Whitney U test results are presented in relation to mean values rather than median and, on pages 103 and 104, there are a couple of statistically nave comments about mean values being lower or higher “although not significantly so”. Otherwise this is a fine chapter; the appendix, summarising published studies of genetic differentiation in plant life history traits, is a particularly useful resource.

In Chapter 5, Edward Reekie provides a very valuable review of “Resource allocation, trade-offs, and reproductive effort in plants”, with case studies drawn from the author’s own work. His conceptual consideration of plant allocation to reproductive effort highlights the sheer difficulty of measuring allocation in a biologically meaningful way, and of getting different workers to agree on the best approach, particularly with regard to allocation currencies. Simply put, most studies of

reproductive allocation measure biomass, typically dry weight of vegetative versus reproductive structures. However, as Reekie and others have argued, "...biomass allocation is not a very good indicator of how some mineral nutrients are allocated....". On the other hand, Table 5.1 presents correlation coefficients between different allocation currencies for *Agropyron repens* and shows that, in this case, biomass allocation to flowers + fruits + reproductive support structures is very highly correlated with nitrogen ($r=0.93$) and phosphorous ($r=0.95$) allocation to reproduction. I therefore think that the author is too cautious when he states that "...although biomass allocation....may be used as an indicator of.... [reproductive effort]..... it is only an approximate measure....". In fact, with such high correlation coefficients, it appears to be an excellent measure! The reader is therefore left confused - how often is biomass allocation closely correlated with allocation of mineral nutrients? A comparative survey of published data would have helped to clarify this issue.

Chapter 6, by Vincent Eckhart and Jon Seger, deals with "Phenological and developmental costs of male sex function in hermaphroditic plants". In this absorbing chapter, the authors conceptually (though not mathematically) extend existing models of resource allocation by including a phenological component (relative timing of male and female function) and subsequent variation in the size of the resource pool as the gender balance changes. They emphasise that male function can be much more costly for a plant within a season than previously imagined because stamens do not photosynthesise (is this always true, and if so, why?) and, in protandrous species, future allocation to female function may therefore be restrained. The "Next steps" section made me want to rush out and collect some data – surely the mark of a thought provoking chapter!

Chapter 7 deals with "Evolution of plant dispersal" and the authors, Ove Eriksson and Katariina Kiviniemi, present a wide-ranging and interesting review which deals with vege-

tative as well as sexual diaspores. Their short history of dispersal studies provides a useful context to the next section, which gives an overview of the evolutionary arguments for the selective advantage of dispersal in time and space. They tabulate seven hypotheses which have been proposed and evaluate the arguments for and against each. The authors rightly point out that these hypotheses are not mutually exclusive and that there is some overlap. However, they do not, I feel, sufficiently stress that each of these evolutionary advantages to dispersal, and others besides, may have been more or less important in different plant lineages. There is no reason why, for example, the evolution of fleshy fruits in the Rosaceae should have occurred under the same selective regime as that in the Areaceae. Simple, "one size fits all" ecological and evolutionary explanations are rarely correct. Subsequent sections deal with trade-offs between dispersal and other seed traits and the question of "are vegetative diaspores different from seeds?" (the answer seems to be yes and no). I was pleased to see a section on the influence of phylogeny on seed dispersal traits as this is rather lacking in most of the other chapters (see also comments below).

"Senescence in plants" is dealt with by Bård Pedersen in Chapter 8. Prior to reading this review, I was dimly aware that plants sometimes underwent senescence, but did not appreciate the amount of published literature there was on the subject, and how difficult it is to make a judgement as to how common senescence is among plants. The evidence for true senescence in plants (analogous to animal senescence) is limited, but this may be because we do not have the tools to measure it properly. The discussion of a hypothesised senescence-inducing "death hormone" (pp. 250–251) is intriguing, though as the author stresses, purely speculative and with no supporting evidence. In fact, I can think of at least one piece of evidence against the hormone's existence: many *Agave* and other "monocarpic" species actually produce vegetative offsets

(basally or along the inflorescence) which are initially physiologically integrated with the flowering unit. These would surely be killed by the “death hormone”, if it exists, but they are not.

Chapter 9, on “Pathogens and plant life histories”, by Keith Clay and Wim van der Putten is perhaps the least successful chapter in this volume. The authors have accumulated and presented a huge range of material, but I found that it was dealt with rather descriptively and uncritically and with limited attempt at conceptual generalization, synthesis or hypothesis testing. There is surely enough published data available to begin this task. The discussions of the effects of pathogens on clonal versus sexual reproduction, annual versus perennial life histories and on the evolution of dispersal was useful, though the authors would have benefited from approaching these ideas from a phylogenetic perspective. It may well be true that annual grasses in North America are attacked by fewer pathogenic fungi than perennial grasses - but is this due to the different life cycles of these grasses, or because of the influence of their phylogenetic identity? There is also an odd statement on page 290 to the effect that, as flower-suppressing fungal pathogens increase the clonal growth rate of their hosts, the relationship can be considered to be mutualistic. Mutualism is usually defined by the effect of each partner on the fitness of the other, so by this definition the relationship cannot be mutualistic.

The final chapter, on the “Impact of herbivore tolerance and resistance on plant life histories” is by Kari Lehtilä. This chapter gives a summary of how plants may endure destruction of vegetative tissue and how this in turn can affect (or not, as the case may be) plant fitness. The chapter successfully combines a critical literature review with the exploration of published models of tolerance and resistance.

Overall, the ten chapters are well-balanced between the discursive and the mathematical. The chapters are generally short and therefore

very readable, enabling the reader to gain a taste of each topic prior to following up the primary literature. The glossary is also extremely useful.

Do I have any major criticisms of the book? Well, as I hinted at in the opening paragraph, the decision of what components are considered suitable for inclusion in books and chapters reviewing plant life histories is often arbitrary, and this volume is certainly not alone in containing very little about the evolution of plant-pollinator interactions. Obviously, I'm biased in my attitude to this (it's my own research area) but there exists a developing theoretical framework that seeks to explain why, say, a plant should evolve to become bird rather than bee pollinated, why reliance on one pollinator is probably a less stable strategy than using the services of several, and so forth. Surely these are aspects of a plant's life history, just as much as seed dispersal, resource allocation and sex expression?

The second deficiency in the book is that none of the authors deals with the use of modern cladistic phylogenetic techniques for exploring the evolution of life history traits. Many studies have been published which have mapped breeding systems, pollination systems, seed dispersal strategies and so forth onto species phylogenies, but the unwitting reader would not be aware of such work from this book. This is a much more fundamental omission than the previous one - comparative phylogenetics is a powerful tool.

Overall, however, I found this book to be a useful refresher course on aspects of plant life history evolution that I had not considered for a while, and an excellent introduction to some topics about which I knew little. I recommend this book to postgraduate students (in the more affordable paperback edition) and to established researchers. It's a useful resource to allocate to your personal or institutional library.

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