

Plant Reproductive Ecology

PATTERNS AND STRATEGIES

Edited by

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and

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*This book is dedicated to David Lloyd
in appreciation of his theoretical insights,
empirical investigations, and generosity of spirit.*

Preface

Our aim in editing this volume has been to produce a cohesive series of synthetic reviews of the field of plant reproductive ecology. These up-to-date accounts appraise past work and seek to highlight new and exciting research fronts. The book is intended for researchers in the discipline of plant reproductive ecology and those just entering the field. The first seven chapters present a critical discussion of important conceptual issues. The next five chapters cover particular biotic interactions shaping the evolution of plant reproductive strategies. The final three, taxonomically based chapters, review the reproductive ecology of the major non-angiosperm plant groups.

We are very grateful to the colleagues who kindly assisted by reviewing particular chapters. Peter Alpert and Robert Nakamura were especially helpful in this regard; in addition we are grateful to Robert Edyvean, Henry Ford, Tom Lee, David Mulcahy, and Jennifer Ramstetter. Authors of individual chapters make their own acknowledgments; we would simply add our appreciation of the spirit of cooperation and enthusiasm that has grown from this shared venture.

*South Hadley, Mass.
June 1987*

J. L. D.
L. L. D.

Foreword

George C. Williams recently wrote that “Historians may one day marvel at the tardiness of the realization that life history attributes are subject to natural selection, and evolve no less than teeth and chromosomes. . . . I attribute this tardiness to a persistent and widespread failure to make full use of the Mendelian formulation of natural selection. What is sometimes called modern Darwinism is a field in its infancy, at best.” Jon and Lesley Lovett Doust’s *Plant Reproductive Ecology: Patterns and Strategies*, with a dozen and a half first-rank authors, aims to place the study of the evolution of plant reproduction at least in toddlerhood. In the same way that two to three-year-old children challenge their parents (and themselves) with their blend of dependency and zeal for exploration, so does this field mix the old with what “might be the new.”

A fuller use of the “Mendelian formulation of natural selection” has made us keenly aware of new possibilities in plant reproduction. The *fact* that pollen and ovules contribute equal numbers of chromosomal genes to seeds leads immediately to the question of how male (pollen) reproductive success influences floral characters and many other aspects of plant reproduction. Historians may one day wonder why this broad question was not posed until the late 1970s. Although male fertility is hard to measure (compared to counting seeds) this does not explain the virtual absence of *speculation* on the importance of the male role in most plant biology texts, which often seem to imply that plants attract pollinators in order to set seed.

Further use of Williams’s “natural selection on life histories” question has led to even more subtle possibilities. Whereas many plant reproductive features (e.g., dioecy) have been viewed classically in a Panglossian fashion as regulators of inbreeding, now we are not so sure, and we ask how the features might have been molded by natural selection operating on differential opportunities for male and female reproduction. Whereas seed provisioning has been assumed to represent a strategy employed by the maternal plant to balance offspring size and number, we now realize that mother, father, and offspring have somewhat different interests in the reproductive allocations. The various reproductive tissues present in the ovary can be viewed as close relatives, able to influence each other’s reproduction and therefore subject to kin selection. As surprising as some of these suggestions might seem at first, the greatest surprise is how simply Darwinian they are; they follow almost automatically from the use of “the Mendelian formulation of natural selection.”

Of course *ecology* is also a key word. As they grow, plants compete for light, nutrients, space, time, and water. Fruits and seeds face the often conflicting demands of dispersal and predator escape. The authors of this book never forget that the plant’s

life history takes place on an ecological stage and that that history's tradeoffs and compromises are balanced in the face of particular ecological challenges. In addition, many *kinds* of plant reproduction are brought together in this book, crossing divisions of algae, bryophytes, ferns, and flowering plants. Discussion of such phyletic diversity is both unusual and fruitful.

The fifteen chapters are state-of-the-art statements that blend old and new ideas in a pot called skepticism, with a dash of the spice called enthusiasm. For many of the ideas, the data needed to test them are not yet in. But this is clearly an exciting time to be studying plant reproduction.

The authors of this book wish to dedicate it to Professor David G. Lloyd. David's work combines the best of the old and the new and spans the full range between muddy boots and the equations of population genetics. His work inspires us all.

Summit Park, Utah
May 1987

Eric L. Charnov

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Contents

Foreword ix
Eric L. Charnov

I Conceptual Issues in Plant Breeding Systems

1. Sociobiology of plants: an emerging synthesis 5
Jon Lovett Doust and Lesley Lovett Doust
2. Paternity in plants 30
Robert I. Bertin
3. Inclusive fitness, seed resources, and maternal care 60
David Haig and Mark Westoby
4. Monomorphic and dimorphic sexual strategies: a modular approach 80
Paul Alan Cox
5. The evolution, maintenance, and loss of self-incompatibility systems 98
Spencer C. H. Barrett
6. Sex determination in plants 125
Thomas R. Meagher
7. Gender diphasy ("sex choice") 139
Mark A. Schlessman

II Ecological Forces

8. Nectar production, flowering phenology, and strategies for pollination 157
Michael Zimmerman
9. Patterns of fruit and seed production 179
Thomas D. Lee
10. Plant morphology and reproduction 203
Donald M. Waller
11. The influence of competition on plant reproduction 228
Jacob Weiner
12. Herbivory and its impact on plant reproduction 246
Stephen D. Hendrix

III Reproductive Strategies of Non-Angiosperms

- 13. Reproductive strategies in algae **267**
R. E. DeWreede and T. Klinger
- 14. Reproductive ecology of bryophytes **285**
Brent D. Mishler
- 15. Reproductive strategies of pteridophytes **307**
Michael I. Cousens
- Subject Index **329**
- Organism Index **339**

PLANT REPRODUCTIVE ECOLOGY

I

Conceptual Issues in Plant Breeding Systems

1

Sociobiology of Plants: An Emerging Synthesis

JON LOVETT DOUST and LESLEY LOVETT DOUST

An exciting new synthesis is taking place within the literature of evolutionary biology. Botany, especially plant ecology, is being reexamined in light of theory derived from animal sociobiology. Greater communication between ecologists who study plants and those who study animals has led to some sharing and trading of concepts and contexts. Recently, for example, a number of workers have used the theory of sexual selection to explain intersexual differences in particular plant traits. These include floral traits that may attract pollinators in animal-pollinated plants and involve particular patterns of floral resource allocation.^{7,8,14,27,111,124} Others have shown how double fertilization in plants may have arisen through a process of kin selection.²⁷

With this interchange has come what Russell Baker has referred to as “young fogeyism,” a new pedantry that (in this case) resists the transfer of terms or ideas between the study of plants and animals. Some authors have reservations about applying concepts like “mate choice” and “parental care” to plants. Others argue that the identification of the *possibility* of mate choice in plants has in itself stimulated exciting research. However, although theories of animal behavior are valuable stimuli for good research in plant ecology, a direct one-to-one transfer is not always possible.^{91,125}

Plants show greater biological diversity and peculiarities than the best-studied animal systems. Theory and research appropriate to plants still need to be developed, and such development may better fit colonial animals than existing animal theory does. One reason for the difference between plants and animals is the nature of plant form. Plant sexuality is a diffuse and fundamentally quantitative phenomenon: Reproduction in plants may involve many parts of the individual through the formation of many separate flowers and fruits. An analogy can be drawn between the behavior of an animal and the form, or morphology, of a plant: Animals gain evolutionary advantage in large part by virtue of flexible behavioral responses to their environment; they are able to move about and escape circumstances that may be stressful or otherwise unfavorable. Plants, being sessile, enhance their evolutionary fitness mainly through modular architecture and a capacity for reiterative growth.¹²⁰ This characteristic allows for much acclimatization by way of variable or plastic patterns of growth and reproduction.

Research over the next few years should clarify the extent to which animal models, based on theories such as kin selection, parent-offspring conflict, and sexual selection, retain their force in the translation to plant systems. In this overview, we draw together ideas and evidence concerning sex allocation, sex habits and dimorphism,

sexual selection, paternity, female choice, and aspects of sexual incompatibility in plants; that is, what has been called "sociobotany."¹²⁵

SEX ALLOCATION

Organisms may acquire evolutionary fitness as either paternal or maternal parents. Some organisms (in particular plants, modular animals, and many invertebrates) may be maternal and/or paternal to varying degrees at the same time or at different times in their life cycles. An organism's *gender* (i.e., its relative maleness or femaleness) represents the proportion of its evolutionary fitness transmitted through sperm and eggs, respectively (e.g., Refs. 65, 78). Sex allocation theory addresses opportunities for gains in fitness that may be made via maternal routes and/or paternal routes.

Historically, academic interest in plant sex has been sporadic, but recently it has greatly increased. Charnov, in particular, has been instrumental in pointing out the value of viewing breeding systems as the result of natural selection acting upon separate male and female strategies.^{27,29} Charnov is concerned with sexual selection and the evolution of sex allocation, that is, the allocation of reproductive resources to male versus female function. He has lucidly reviewed the argument that patterns of parental resource allocation to different sex functions reflect the evolutionary fitness that may be gained by that sex function. (It should be noted that a number of confusions and resultant problems can arise due to imprecise uses of the concepts of evolutionary fitness, biological success or reproductive success, lifetime reproductive success, inclusive fitness, and various combinations of these. Some of these are described in Clutton-Brock.³⁵)

In most cases, it is the evolutionarily stable strategy (ESS sensu Maynard Smith⁸⁴) that Charnov considers. Selection "should favor a mutant gene which alters various life history parameters, if the percent gain in fitness through one sex function exceeds the percent loss through the other sex function" (Ref. 29, p. 17). Charnov points out that the ESS pattern of resource allocation to male and female function is often that which maximizes the product of the fitness that can be gained through male function, and the gain through female function. In organisms where there is complete separation between the sexes (dioecy), selection should favor those males and females that control their clutch size (number of eggs per reproductive session), the sex ratio of offspring, and the allocation of resources among offspring, such that this product is maximized.

Charnov presents the central theme of sex allocation as a series of questions. For species with separate sexes, what is the equilibrium sex ratio? For a sequential hermaphrodite, which sex should come first, and when should any sex change take place? For a simultaneous hermaphrodite what is the equilibrium pattern of allocation of resources to male and female function? What sorts of situations favor one sex habit over another? And under what kinds of selective regimes may sexual lability be favored? Answers to all of these questions for any species must, of course, take into account both biotic and abiotic selection pressures. Yet, as Charnov makes clear, the answers to all of these questions may assume the same general form.

Ronald Fisher⁴⁷ first pointed out explicitly that in a population the fitness to be

gained by males must be, on average, precisely equal to the fitness to be gained by females. The same identity must also hold for male and female function in hermaphrodites.³⁴ As regards the equilibrium sex ratio, Fisher concluded that, in the absence of any inbreeding, the sex ratio at conception should be adjusted by selection so that the total parental expenditure in raising male offspring should be the same as in raising female offspring. He indicated that where the cost of any one male equals the cost of one female, then natural selection favors production of a 1 : 1 sex ratio.

Fisher's concept of "parental expenditure," however, is difficult to assess biologically. He suggested energy and time as measures of expenditure, and later theoreticians have used either energy allocation or Fisher's undefined term. Energy investment *may* be an appropriate estimate of parental investment, but the evolutionary importance of such investment can be seen only if it is measured in terms of the limiting resource, which is likely to differ across species and environments and vary with season.

Unfortunately, Charnov does not develop the problem of the currency to be used in empirical studies of sex allocation. The adequacy of a carbon-based economy has recently been questioned in whole plant studies, where dry-matter distribution studies have become common. This is an important area needing further work. Goldman and Willson review many of the theoretical and methodological problems which hamper studies of sex allocation; in particular they review the problems of hermaphroditic plants.⁵⁴

Using a resource allocation model of sex function and outcrossing in hermaphrodites, Ross and Gregorius¹⁰² showed that sexual polymorphism could be maintained in a population by frequency-dependent selection if there is variation in the population in pollen and seed fertilities and/or in the extent of selfing. These allocation models (as well as that of Charnov²⁹) assume a trade-off takes place between seed and pollen production. However, recent work by Devlin,⁴³ for example, studying sex allocation in *Lobelia cardinalis*, found no negative correlation between seed and pollen production per flower, which the above model requires.

Models for sex allocation versus the selfing rate predict that allocation to male function should decrease with increasing rates of selfing.^{26,27,29,30} Charnov recently described sex allocation as a function of selfing rate in 31 strains of wild rice, *Oryza perennis*.³⁰ He showed that the male/female allocation ratio was linearly related to the selfing rate (just as was shown by Schoen¹⁰⁶ for *Gilia achilleifolia*). According to Charnov, such linearity indicates that the intermediate selfing rates would have to be maintained by frequency-dependent selection. Using the selfing-sex allocation model proposed by the Charlesworths,²⁶ Charnov suggested that selfed offspring were half as fit as outcrossed, and that this may be a consequence of frequency-dependent selection, which itself stabilizes the intermediate rates of selfing. Subsequently, Charnov³¹ concluded that the Charlesworths' model is flawed by the confounding of sex allocation with selection for/against selfing. He pointed out that their model considers the proportion of seeds which are selfed as being fixed, and allows selection to adjust the proportion of resources given to pollen versus seeds. Charnov argued that the Charlesworths' "fixed selfing rate" is, in effect, *not* fixed. Since in their model selection is able to alter the proportion of reproductive resources given to selfed progeny (by allocating more or less to seeds), the "fixed selfing rate" can be adjusted, as Charnov says, "through the back door by altering sex allocation." He suggests that in a model