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PLANT BREEDING SYSTEMS[1]

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It is remarkable that, although plant breeding systems have been an active area of research for over a century, no comprehensive treatment has been attempted since Darwin's two volumes on the subject. Prior to the 1960's, information on plant reproductive systems gradually accumulated as a by-product of work in early Mendelian genetics, experimental taxonomy, and crop improvement. During the past 25 years, however, the study of breeding systems has expanded and diversified so that today, studies in this area are central to many important contemporary issues in plant evolutionary biology. The broadening of interest in plant breeding systems has largely resulted from three developments in population biology: 1) the application of electrophoretic procedures for measuring mating-system parameters such as selfing rates, gene flow, and male fertility; 2) the development of theoretical models concerned with the evolution and maintenance of various breeding systems such as gynodioecy, heterostyly, and selfing; and 3) associated with the growth of evolutionary ecology, an increase in experimental field studies in which the breeding system is viewed not in isolation but within the context of demography, sexual selection, and life-history evolution. The recent emphasis on theory and experimentation and the move away from Darlingtonian group selectionist explanations to account for the evolution of breeding systems are attributable to the influence of population geneticists and several prominent animal ecologists. While many plant biologists have been reluctant to accept concepts borrowed from the animal literature (botanists, after all, are a conservative lot who value tradition), there is no doubt that the study of plant breeding systems can no longer proceed in a theoretical vacuum and that our thinking about the way plants mate has been dramatically influenced by the realization that most plants, although hermaphroditic, are unlikely to transmit genes equally via pollen and ovules.

These changing ideas and the sheer volume of work being conducted in plant reproductive biology make it a daunting task to write a broad synthesis of the subject, and yet this is what A. J. Richards has attempted to do in his recent book *Plant Breeding Systems*. Perhaps because of the pace of research in the field, many recent topics of inquiry in plant reproduction such as "mate choice," paternity analysis, gametophytic selection, optimal outcrossing, late-acting incompatibility systems, and the significance of inbreeding depression to mating-system evolution either are not mentioned or are scantily treated. Nevertheless, the book does cover an enormous literature and represents the first really comprehensive treatment of plant reproductive systems. Although the work was written primarily as a text rather than as a research monograph, Richards has not refrained from critically reviewing earlier studies, taking stands on controversial issues or speculating freely. While many previous works have been either encyclopedic (and thus uncritical) or idiosyncratic in nature, this volume provides a stimulating introduction to the field.

The book is composed of 12 chapters, a glossary of terms, and over 700 references. It is profusely illustrated, but, with the exception of the excellent photographs by M. C. F. Proctor, many are out of focus (e.g., 4.16, 4.26, 9.1, 9.5, and 11.8). The first three chapters are introductory in nature and deal with general aspects of sexual reproduction, elementary population genetics, alternation of generations, and the major reproductive characteristics of higher plant groups. The next two chapters are concerned primarily with pollination biology with discussions of floral evolution, pollination syndromes, foraging behavior, gene flow, seed dispersal, and the measurement of pollen transport and neighborhood sizes. These five chapters cover nearly 200 pages, provide a good review of plant reproductive biology, and develop the necessary systematic and ecological context in which to discuss the diversity of breeding systems displayed by flowering plants.

The next six chapters represent the main focus of the work, as Richards deals in turn with homomorphic self-incompatibility systems, heterostyly, dicliny, self-fertilization, vegetative reproduction, and agamospermy. Each chapter discusses the evolution, genetic basis, and adaptive significance of the breeding systems, as well as their influence(s) on the genetic structure of populations. Where appropriate, as with selfing and agamospermy, Richards also discusses the taxonomic difficulties that arise because of the complex patterns

[1] *Plant Breeding Systems*. A. J. Richards. Allen and Unwin, Winchester, MA. 1986. xiv + 529 pp. $75.00 cloth, $34.95 paperback.

of phenotypic variation that occur in groups with these types of reproductive systems. Richards is well qualified for this task, having spent 20 years struggling with dandelion taxonomy and the sceptics who question the value of such work. Judging by some of his comments, these experiences have left their scars: "I am struck by the lack of sympathy and understanding of agamospecies taxonomy displayed by authors who discuss the subject, but have not themselves worked on the taxonomy of such a group" (p. 449).

The chapter on agamospermy (Ch. 11) is of particular value, since the topic has been studiously avoided in earlier works, probably because of its complexity. The most intriguing and controversial of Richards' ideas on agamospermous groups concerns the mechanisms that generate genetic variation in supposedly obligate agamosperms. He suggests that, in dandelions, "the very high levels of chromosome breakage and refusion cycles (somatic recombination) which are apparently being observed . . . are a product of transposable genetic elements" (p. 443). Richards further suggests that "somatic recombination should greatly affect the phenotypic expression of a genotype, either morphologically or as isozyme bands" (p. 443) and that the resultant variation, along with that produced by meiotic recombination and chromosome loss and gain, could become subject to natural selection leading to what he calls "asexual speciation" (p. 444). These novel ideas on genetic variation in asexual dandelions are certainly worth investigating and could be profitably examined by molecular probes in a fashion similar to the work currently being undertaken on *Daphnia.*

A disappointing feature of Richards' book is the number of factual mistakes, errors of interpretation, and statements based on little hard evidence, which are apparent throughout the work. Some examples close to this reviewer's heart may serve to illustrate the point. In Chapter 10 on vegetative reproduction, we learn that *Eichhornia crassipes* exhibited explosive growth at the Kariba Dam and that its "flowers are tristylous and self-incompatible, so the introduced single clones set little if any seed" (p. 373). In fact, the weed problem at Kariba involved the aquatic fern *Salvinia molesta,* and, moreover, clones of *E. crassipes* are self-compatible and usually produce seed. Concerning the genetic control of tristyly and its evolution, Richards speculates that "the *M* linkage group is a duplicate of the *S* group and that tristylous plants have thus evolved from distylous systems. This is very probably the case in both *Oxalis* and *Lythrum,* both of which also have distylous species" (p. 245). While the idea that *S* and *M* are duplicate loci is interesting, the implication that the occurrence of both distyly and tristyly in the above genera is evidence for this is disingenuous. In both cases, careful study (e.g., Weller, 1976) has shown that distyly is derived from tristyly by loss of one of the style morphs. Other statements guaranteed to raise a few eyebrows include the following: "Most trees which are individually large . . . are wind pollinated" (p. 174); "Indeed, derived small-flowered inbreeders may be typical of dry areas, and Moore and Lewis (1965) described the origin of a small-flowered, autogamous segregate of *Clarkia xantiana, C. franciscana,* after a dry period extended the desert margin near San Francisco into the range of the former, thus favouring the inbred mutant" (p. 334); "Cleistogamous flowers are not uncommon, but chiefly occur in allogamous species, frequently after the 'conventional' allogamous flowers have failed to set seed" (p. 334); and "Linhart et al. (1979) demonstrated '*r*' and '*K*' selection within a Colorado population of *Pinus ponderosa.* Genetically slow-growing individuals showed greater sexual fertility ('*r*') than fast growing genets ('*K*')" (p. 395).

While a certain amount of speculation is valuable, since it provokes discussion and stimulates others into action, the frequent errors and misinformation in Richards' book are likely to detract from its overall significance. Part of this problem lies in using a textbook as a vehicle for publishing primary data and interpretation. Richards presents a considerable amount of his own unpublished research findings and those of his students, particularly in Chapters 7 and 11, and one wonders how much of this would survive the rigors of the reviewing process (see Figs. 7.13 and 11.11 and Table 11.5 for examples).

Richards also has a tendency to construct complex alternative hypotheses to account for phenomena for which simple explanations are available. An example of this involves his treatment of the evolution of homostyly in *Primula* populations. Long and short homostyles should arise by recombination with equal frequency, yet long homostyles seem to spread preferentially in populations. In a paper discussed but not cited by Richards, Charlesworth and Charlesworth (1979) solved this problem by showing that, because of the dominance relationships at the distyly locus, long homostyles have a segregation advantage in crosses with pins and thrums compared with short homostyles. Richards proposes two additional explanations (pp. 248–249): 1) short homostyles experience more inbreeding depression than long homostyles; and 2) the reproductive organs in short homostyle flowers are prone to immersion by rain that accumulates in the corolla tube, resulting in pollen germination; whereas in long homostyles the organs are at the top of the tube and are not affected by rain in this way. While in principle there is nothing obviously wrong with looking for additional explanations, no evidence is presented in support of the first theory, and the evidence used to support the second involves a complex and unconvincing argument that requires the presence or absence of a mysterious germination inhibitor. In some cases, Richards' critical, even combative approach to earlier studies is refreshing (since the reader is left in no doubt as to his views), but at times the criticisms seem misplaced. Two approaches central to modern developments, namely the formulation of theoretical models and the use of electrophoresis, are treated in a particularly suspicious and desultory fashion. For example, on models of the evolution of agamospermy, Richards states, "mathematical models that assess the success of agamospermy are hopelessly naive, and take account of too few factors. An examination of the real world suggests that agamospermy has proved to be a successful form of reproduction . . ." (p. 456); and on electrophoresis, "Unfortunately this method is both costly and time consuming. . . . However, populational work using isozymes is fashionable at present" (p. 389). On the use of electrophoresis in estimating outcrossing, Richards says that "such techniques are unfortunately untestable" (p. 343); "In particular, circularity can be involved when electrophoretic variation in progeny is

used to characterise a breeding system" (p. 434). While it is certainly true that gel electrophoresis has its limitations at present, it does provide the most accurate method for measuring many of the critical parameters of value in breeding-system studies.

Surprisingly, given the theme and size of the work, the whole area of mating-system estimation is given only a cursory mention, despite recent advances in the field. This is unfortunate, since inferences about the breeding patterns of plants based on pollinator behavior, floral morphology, controlled crosses, and emasculation techniques provide only indirect evidence and can often give misleading information. Difficulties of this type are evident in some of Richards' own studies of agamospermous dandelions in which he advocates emasculation as a way of "checking the breeding system" (p. 434) and as proof of obligate agamospermy (p. 439). Yet, in a confusing table with no legend, at the foot of p. 439, electrophoretic data from three heterozygous families of supposedly obligately agamospermous dandelions indicate segregation at a tyrosinase locus. The data surely cast doubt on the completely asexual nature of the plants, as well as on the emasculation technique as evidence of the occurrence of obligate agamospermy under field conditions.

What is the message in this work? Richards successfully demonstrates that, since the pattern of mating exhibited by a given population can vary in space and time as a result of local demographic and environmental conditions, the study of plant breeding systems requires a synthetic approach involving detailed field studies, as well as the traditional glasshouse and laboratory work. Richards' treatment of breeding-system evolution involves both orthodox views on the regulation of recombination and the more recent theories concerning sexual allocation. One has the feeling that the latter ideas were emerging as the book was being written and, as a result, they are not always well integrated with the remaining text (see, for examples, Chapters 7 and 8). This difficulty highlights a general problem faced by workers in the field. Future genetic models of breeding-system evolution are likely to become increasingly complex as additional factors involving ecological, demographic, and sex-allocation data are incorporated.

Finally, Richards' treatment of the evolution of plant breeding systems may be easily subject to misinterpretation regarding the level at which selection occurs. This is apparent when the "efficiency" of one breeding system is compared with another (p. 233) or the unusual chromosomal system of the *Rosa canina* complex is discussed: "If one was to 'play God' and design an ideal breeding system, evolutionarily, this would be it" (p. 426). While part of the problem may stem from an overly teleological use of prose, this reviewer had the uneasy feeling that rather more than the choice of words is involved. In his concluding remarks, Richards states that "mixed strategy mechanisms (of selfing and outcrossing) are revealed to be evolutionarily rather efficient, which may help to explain why so many species of plants possess them" (p. 462). Unfortunately, the book presents little solid evidence in support of this conclusion, which is disappointing, given the current debate (Lande and Schemske, 1985; Waller, 1986) concerning the evolutionary role of the mixed mating system.

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