CURRENT ISSUES IN PLANT REPRODUCTIVE ECOLOGY

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ABSTRACT

Plant reproductive ecology is largely concerned with the adaptive significance of the variation in traits associated with pollination, seed dispersal, and seedling establishment. Reproductive success in many flowering plants depends on ecological interactions with animal pollinators and seed dispersal agents. Plants exhibit diverse reproductive strategies involving a variety of different sexual systems as well as asexual reproduction. Traditional explanations for this diversity have focussed on the benefits of genetic variability and the harmful effects of inbreeding. Recent interest in ecological aspects of reproduction has led to a diversification of approaches, with models of sexual selection and optimal resource allocation currently receiving considerable attention.

BACKGROUND

Reproduction in flowering plants includes three sequential phases: flowering and pollination, fruiting and seed dispersal, and germination and seedling establishment. Variation in reproductive success results from variation in many ecological factors, including growing conditions, pollinator service, dispersal agents, and pest and disease pressures. Because of the direct contribution of reproductive output to fitness, considerable effort in plant reproductive ecology concerns the investigation of factors responsible for differences in reproductive performance among individuals and populations. Of particular importance is to determine how much variation results from genetic differences among individuals in reproductive traits and how much is the result of environmental modification.

Although the fundamental genetic and cytological features of gamete and zygote formation are similar in plants and animals, the ecology of reproduction differs in distinctive ways that have necessitated the development of specialized areas of enquiry within plant reproductive biology. The sessile habit of plants has led to the evolution of diverse mutualisms between plants and animals involving both the directed transfer of pollen among conspecifics and the dispersal of seeds to new environments.

During the 1950s and 1960s, much work was devoted to ecological aspects of pollination and seed dispersal (Percival, 1965; Faegri & van der Pijl, 1966; van der Pijl,

1969), and the diversity of reproductive systems was increasingly interpreted within an adaptive framework. With the development of evolutionary ecology in the 1970s and 1980s, description and *post hoc* explanation gave way to modelling, hypothesis testing, and experimental field studies as the primary research protocols. The introduction of experimental field studies in conjunction with theoretical advances has transformed plant reproductive ecology into a burgeoning field of enquiry that today encompasses many broader issues in contemporary evolutionary biology (Willson, 1983; Lovett Doust & Lovett Doust, 1988).

REPRODUCTIVE STRATEGIES

Plant species may employ sexual or asexual reproduction, or both. Two forms of asexual reproduction, vegetative reproduction and agamospermy, occur. Both result in offspring that are genetically identical to the parent and to each other. Genetic models of the evolution of sex (Michod & Levin, 1988) show that because a gene for asexual reproduction doubles its own transmission compared to a gene for sexual reproduction, asexuality should quickly spread to fixation in sexual populations, unless there is a benefit to producing genetically variable offspring. Thus asexuality should be less successful in biotically heterogeneous habitats replete with competitors, pathogens, and parasites. The geographical distribution of asexuality in plants provides some support for this hypothesis. However, many asexual species are polyploid, confounding interpretation of these data (Bierzychudek, 1985). Experimental work on the adaptive significance of sexual vs. asexual reproduction in plants is limited (Ellstrand & Antonovics, 1984), and most recent work has focussed on the demography of clonal populations and on determining the amounts of genetic diversity using electrophoretic techniques (Silander, 1985; Ellstrand & Roose, 1987).

Since most plants are hermaphroditic, offspring may be produced through self- or cross-fertilization. Phylogenetic evidence suggests that in many plant families the shift from outcrossing to selfing occurs repeatedly with ecological radiations into temporary or pioneer environments. This suggests that self-fertilization is adaptive under such circumstances (Jain, 1976). Selfed offspring of outcrossers may suffer, however, from inbreeding depression owing to the expression of deleterious recessive alleles or reduction in heterosis. A recent review (Charlesworth & Charlesworth, 1987) suggests that inbreeding depression is a major factor maintaining outcrossing in many plant groups. Although data from natural populations are limited (Schoen, 1983), the relationship between inbreeding depression and mating system variation is currently under investigation in several laboratories.

Darwin (1877) and most subsequent workers have emphasized the adaptive value of outcrossing in the evolution of plant sexual systems. Under this paradigm, floral mechanisms that separate male and female function in either space (e.g., herkogamy and monoecism) or time (dichogamy), as well as genetic polymorphisms involving different sexual types (e.g., dioecism, heterostyly, and self-incompatibility), are all thought to have evolved to restrict self-fertilization. This hypothesis does not explain, however, why so many different outcrossing mechanisms occur, nor why some sexual arrangements, such

as herkogamy or monoecy, occur in species that are self-incompatible, which alone would enforce outcrossing (Bawa & Beach, 1981; Lloyd & Webb, 1986).

MATING PATTERNS AND SEXUAL SELECTION

During the last decade, other explanations have been advanced to account for the diversity of plant sexual systems. One approach considers how sexual strategies may have evolved to optimize the allocation of resources between male and female function (Charnov, 1982). Another asks how selection might maximize the quantity and/or quality of partners with which an individual mates (Willson & Burley, 1983).

Sexual selection acts on reproductive traits when the success of one sex (usually female) is limited by resources, while that of the other (usually male) is limited by mating success. Thus heritable traits which help males accrue more than their share of matings are selected for. This can be mediated by competition among males for access to females (intrasexual selection) and/or by mate choice on the part of females (intersexual selection). Because plants are sessile and lack the obvious sensory capacities of many animals, the role of sexual selection in shaping plant reproductive traits has been controversial (Charlesworth et al., 1987). Nevertheless, several ecological observations support its import to the study of plant sexual systems.

Many outcrossing species mature fruit from a small fraction of flowers, even though all may be pollinated (Stephenson, 1981). This observation is consistent with female success being limited by resources and also suggests that fruit abortion might be a mechanism for postzygotic mate choice (Willson & Burley, 1983). Intrasexual selection should prolong and intensify competition for mates. Observations of flowering patterns in dioecious species support this since males almost always produce more flowers and bloom longer than females (Lloyd & Webb, 1977). Encouraged by these types of observations, a growing number of workers are experimentally testing sexual selection theory using plant species (Stephenson & Bertin, 1983).

Experimental studies have attempted to determine whether female reproductive success is limited by resources rather than pollen availability. Work on animal-pollinated plants has shown variation among species and populations in this regard (Bierzychudek, 1981; Barrett & Helenurm, 1987), but the experimental requirements for unambiguous tests of pollen limitation are complex since both pollen and resource limitation may operate simultaneously (Zimmerman & Pyke, 1988).

Perhaps the major challenge for ecologists studying sexual selection in plants is to determine the evolutionary significance of variation in male success in natural populations. Male success will depend on the production, delivery, and competitive interactions of pollen grains (Harder & Thompson, 1989). The heterogeneity of natural environments and high phenotypic plasticity in plants make it inevitable, however, that both male and female reproductive success will vary among individuals, with large plants both producing and siring most seeds. Accordingly, large environmental components to variance in male success may limit opportunities for selection to act on genetic variation for male traits. This may reduce evolutionary response to the extent that it is difficult to detect in natural populations.

RESOURCE ALLOCATION TO SEXUAL FUNCTION

Sex allocation theory has recently been used to investigate the equilibrium conditions under which individuals should be hermaphroditic rather than unisexual and how hermaphrodites should optimally allocate limited resources between male and female function (Charnov, 1982). Although average fitness gains through male and female function must be equal in hermaphroditic populations, the average investment to each sexual function may not. When both sexes obtain the same fitness for each level of investment, the optimal allocations are equal. Asymmetric fitness curves, on the other hand, favor uneven allocations.

Examining plant sexual systems using sex allocation theory poses several difficult problems. First, in what units should allocation be measured? Since resources are invested in a variety of structures and substances, some of which are shared (e.g., petals, nectar, pedicels), some common currency must be used, and decisions are required as to how much of each structure represents allocation to male or female function. Second, in order to measure fitness gains, intraspecific variation in allocation patterns or the creation of variation by experimental manipulation (e.g., trimming or embellishing floral displays, or adding or removing nectar) is required. Third, sex allocation models assume that populations are at evolutionary equilibrium and that optimal allocation is not empeded by genetic or developmental constraints. These difficulties may limit their role in some research programs to that of a tool for "selection thinking" (Charnov, 1982) rather than for building falsifiable hypotheses.

GENE FLOW

Gene flow determines the scale over which selection and genetic drift operate, and, in plants, requires gene dispersal (pollen and seed movement) and gene establishment (fertilization, seed maturation, germination, and survival to reproduction). Pollen movement is influenced by the density and distribution of plants, structural features of the surrounding habitat, and, in animal-pollinated species, by the behavioral responses of pollinators to floral rewards (Handel, 1983). Studies of pollen carry-over and the movement of genetic markers in synthetic populations indicate that pollinator observations alone underestimate pollen dispersal within populations (Levin, 1981). Early work on crop plants suggested that pollen flow between populations separated by as little as 500 m was rare (i.e., 1% of the seeds were interpopulation hybrids), but recent electrophoretic data from small natural populations of wild radish show levels of gene flow at least an order of magnitude higher (Ellstrand & Marshall, 1985). Measures of gene movement through seed dispersal indicate that most seeds are dispersed in close proximity to the maternal plant. However, the frequency and extent of long-distance seed movements are largely unknown.

The establishment of dispersing genes is influenced by the scale and nature of differentiation within and among populations. Recent studies using controlled field pollinations indicate that the fertility and/or offspring fitness of crosses increase(s) with interparent distance (Schemske & Pautler, 1984; Sobrevilla, 1988). This suggests that

although selection should favor increased pollen dispersal, most matings probably occur on a small scale resulting in local inbreeding. Some crossing data also suggest that beyond a point progeny may suffer lower fitness as a consequence of the disruption of locally adapted gene complexes (Waser & Price, 1983). As a whole, gene flow in plants appears to be limited and, while proximity-dependent fitness gradients may provide selection for increased gamete dispersal within populations, longer distance gene flow is unlikely to be important in maintaining the genetic cohesion of species on a geographical scale (Levin, 1981).

REPRODUCTIVE PHENOLOGY

Descriptive work on temporal patterns of reproduction in a wide range of plant communities has led to recent interest in the phenology of reproduction. Reproductive phenology is measured by the timing, duration, and synchrony of events· such as flowering, fruiting, and germination within and between seasons. Patterns are evident at several levels including the organ (e.g., flower or fruit), individual, population, species, and community. Attempts to explain differences in phenology among species have led to a variety of hypotheses concerned with evolutionary forces shaping species interactions and proximate factors controlling the timing of reproductive events.

The selective forces operating on flowering patterns at the community level have been discussed extensively. The proposition that divergence in the flowering times of species within a community results from interspecific competition for pollinator visits has been particularly controversial (Rathke & Lacey, 1985). Some experimental support for this type of interaction has been obtained for species pairs that share pollinators (Waser, 1978). In contrast, statistical analyses of flowering phenology at the community level have shown that flowering is usually either synchronized or random, but not dispersed (Rathke, 1983). The availability of animal dispersers and the competitive interactions between them may also influence the ripening times of fruit in plant communities (Rathke & Lacey, 1985). In temperate areas, most species with fleshy fruits ripen them during the period of autumn bird migration (Thompson & Willson, 1979), whereas in the aseasonal tropics, where dispersal agents are likely to be available throughout the year, fruiting tends to occur continuously. Although these patterns are suggestive, a problem of circularity occurs. Is the availability of pollinators or dispersers a cause or an effect of the specific flowering or fruiting patterns?

Experimental manipulation of flowering and fruiting times is one way of assessing the reproductive consequences of variation in phenology. Augspurger (1981) demonstrated that individuals of the neotropical shrub *Hybanthus prunifolius* suffered both lower seed set and higher seed predation when experimentally induced to flower out of synchrony with the rest of the population. The data were consistent with the hypothesis that reproductive synchrony within and between individuals of a species serves to satiate seed predators (Janzen, 1971). While manipulations of this type are valuable for population studies, they present practical difficulties for studies at the community level.

FUTURE DIRECTIONS

Natural history observations of plants and of the animals with which they interact will continue to provide challenging problems in the ecology and evolution of plant reproduction. Future research is likely to involve a greater integration of ecology and genetics as workers recognize that while natural selection acts on phenotypes, it is the genetic response to selection that determines evolutionary change. The application of phenotypic selection models (Schemske & Horvitz, 1989) in conjunction with quantitative genetic approaches (Mitchell-Olds & Rutledge, 1986) will enable a more realistic assessment of the relative roles of selection and drift to evolutionary change. Measuring genotype by environment interactions will be a critical aspect of estimating genetic and ecological parameters in plant populations since environmental conditions vary greatly in both space and time.

Electrophoretic techniques will continue to be a valuable tool for estimating outcrossing rates, paternity, and gene flow within and between populations (Brown, 1989). The major challenge will be to estimate male reproductive success (see above). Ideally, such studies should involve highly polymorphic markers in small populations so that deterministic paternity exclusion methods can be used (Ellstrand, 1984). However, this situation may occur rarely so that unless new molecular approaches using hypervariable markers can be applied to plant populations, measuring male components of fitness will continue to be a difficult problem.

Most work in reproductive ecology has concentrated on single life cycle stages in isolation from other facets of growth and reproduction (Primack, 1987). Future studies are likely to be more comprehensive since reproductive strategies involve a syndrome of correlated traits expressed at different stages of the life history. Selection does not act on isolated traits; rather it "evaluates" the total phenotype with response depending on the genetic variance and covariance of traits. Constraints imposed by morphology, physiology, and epigenetic background will limit the kinds of evolutionary changes that can occur to flowers, fruits, and seeds.

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