

# SPECIATION

## and Its Consequences

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# MATING SYSTEM EVOLUTION AND SPECIATION IN HETEROSTYLOUS PLANTS

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## INTRODUCTION

A rekindling of interest in the processes that result in reproductive isolation and speciation is evident in the recent evolutionary literature (White 1978; Barigozzi 1982; Carson and Templeton 1984; Barton and Charlesworth 1984; Brown 1985; Iwatsuki et al. 1986). Two major stimuli are largely responsible for renewed discussion of the mechanisms responsible for species formation. Electrophoretic surveys of enzyme polymorphisms have enabled comparative studies of the magnitude of genetic divergence among populations, races, and species. The results have highlighted our ignorance of the kinds and amount of genetic change that are required for species formation. Second, the controversy over the relative importance of punctuated versus gradual change during evolutionary diversification (e.g., Gould 1980; Charlesworth et al. 1982) has focused interest on the tempo of species formation and the role of founder events in fostering rapid speciation. In particular, the recent literature has addressed the question of whether reproductive isolation evolves slowly, as an incidental by-product of the adaptive divergence of gene pools, or whether new species are formed in rare events distinct from the normal processes of phyletic evolution.

A notable feature of much of the recent literature on the genetics and evolution of species formation is the paucity of information from plants. Where these are considered it is not uncommon that only diploid cross-

fertilizing groups are discussed (e.g., Carson 1985). Yet these features are hardly representative of the diversity of genetic and reproductive systems that occur, particularly in flowering plants and ferns. The limited coverage of plant data in controversies such as the significance of sympatric speciation, or the role of small, isolated populations in the speciation process, is unfortunate since information from plants may serve to temper the polarization of viewpoints that often accompanies any healthy debate. By broadening the discussion to include organisms with diverse ecological and genetic characteristics, a more realistic *biological* viewpoint of what is undoubtedly a varied and complex process is likely to prevail. For it seems that the specific details of the speciation process will, in large part, be governed by the biological peculiarities of the organisms themselves. Among flowering plants, for example, annual species usually develop strong postzygotic isolating mechanisms, whereas in many long-lived perennials these are absent (Grant 1981). With such divergent patterns within a single group of organisms, it may be a futile exercise to attempt a truly unified theory of speciation for plants and animals, although Carson (1985) has recently suggested this is possible and a worthwhile goal.

This review focuses on just one aspect of the speciation process in plants: the role of mating system evolution in promoting character divergence and reproductive isolation in herbaceous plants. The approach taken is largely empirical and involves a review of experimental work on contemporary plant populations using the tools of population and evolutionary genetics. Since the work I discuss largely concerns the evolution of heterostylous reproductive systems, I begin by briefly summarizing some salient features of plant genetic systems relevant to the main themes of the chapter.

### **Plant reproductive systems**

As originally recognized by Darwin (1876, 1877), flowering plants display a considerable diversity of reproductive systems. This variation has important implications for the modes of speciation that can occur (Baker 1959; Grant 1981). Although three modal reproductive classes are traditionally recognized (outbreeders, inbreeders, and apomicts), each of these groupings contains a variety of different mechanisms associated with pollination biology and sexual systems of individual taxa (see Richards 1986, for a recent review). A notable feature of many plant groups is the occurrence among closely related taxa of contrasting reproductive modes. This suggests that the evolution of floral syndromes, and their influence on mating patterns, is intimately associated with the development of reproductive isolation and speciation (Grant 1949; Baker 1961; Stebbins 1970).

One of the most prominent evolutionary pathways leading to species

formation in herbaceous plants involves the replacement of outcrossing by a mating system based on predominant self-pollination (Stebbins 1957; Jain 1976). Numerous biosystematic studies have documented this shift in mating system among related species in genera such as *Amsinckia* (Ray and Chisaki 1957), *Arenaria* (Wyatt 1984), *Armeria* (Baker 1966), *Clarkia* (Lewis 1973), *Gaura* (Raven and Gregory 1972), *Gilia* (Grant and Grant 1965), *Lasthenia* (Ornduff 1966), *Leavenworthia* (Lloyd 1965), *Limnanthes* (McNeill and Jain 1983), *Lycopersicon* (Rick et al. 1977), *Melochia* (Martin 1967), *Oxalis* (Ornduff 1972), *Plectritis* (Carey and Ganders 1986), *Petrorhagia* (Thomas and Murray 1981), and *Stephanomeria* (Gottlieb 1973). The evolution of self-fertilization favors establishment of chromosomal rearrangements and new homozygous genotypes and contributes toward the reproductive isolation of the selfing derivative.

A frequent observation in genera with related outcrossers and selfers is the tendency for selfing taxa to occur at the geographic margins of the range of their outcrossing progenitors or in ecologically marginal sites within the ancestral species range (Jain 1976; Lloyd 1980). This pattern is in accord with the view that self-fertilizing individuals are at a selective advantage at low density and has led to the suggestion that they are favored in pioneer environments or under conditions in which population bottlenecks frequently occur.

It is evident from the literature on the evolution of selfing that many workers envision that genetic processes occurring rapidly in small populations play a significant role in the development of reproductive isolation and speciation in herbaceous plants. This viewpoint is of relevance to broader issues associated with the significance of founder effect speciation. Both Templeton (1981) and McNeill and Jain (1983) have suggested that although the vast majority of founder events do not lead to rapid speciation via genetic transience, this mode of species formation may occur commonly in association with the evolution of selfing in plants. Unfortunately students of plant speciation have rarely examined the microevolutionary forces operating within populations in sufficient detail to provide evidence in support of this claim.

### Ployploidy

A second important feature of evolutionary diversification in plants is the frequent occurrence of ployploidy and its role as an isolating mechanism. Since current estimates suggest that 70–80% of angiosperm species are of ployploid origin (Goldblatt 1980; Lewis 1980), it could be argued that this form of sympatric speciation is among the commonest modes of speciation in flowering plants. This is sometimes neglected from debates concerned with the likely occurrence of sympatric speciation in nature. Unfor-

tunately, in spite of the widespread nature of polyploidy in flowering plants, we are still woefully ignorant of the population processes that lead to the origin and establishment of polyploid species. The wider adaptability and evolutionary success of many polyploids are believed to arise from extensive gene duplication and subsequent diversification, fixed heterozygosity, and the reduced effects of inbreeding depression (Roose and Gottlieb 1976; Stebbins 1980; Grant 1981; Levin 1983; Barrett and Shore 1989). Although heterosis may be involved in the success of many polyploids of hybrid origin, other changes that accompany polyploidization may also be involved. In particular, alterations in breeding system are frequently associated with changes in ploidal level so that among related taxa, diploids are often primarily outcrossing, whereas polyploids tend to be selfers (Grant 1981). The kind of polyploidy can also vary with breeding system. Selfing is commonly associated with allopolyploidy, whereas autopolyploidy is almost exclusively found in outcrossing species (Bingham 1980). These patterns indicate that to fully understand polyploid speciation in flowering plants all aspects of the evolution of their genetic systems, including both chromosomal and reproductive factors, need to be considered.

### Heterostyly

Beginning with Darwin's original work (Darwin 1877), heteromorphic incompatibility systems (distyly and tristyly) have provided a rich source of experimental material for researchers interested in the evolution of plant genetic systems (see Ganders 1979; Barrett 1988b). These outbreeding floral polymorphisms, which have evolved independently in 24 angiosperm families, are simply inherited and particularly susceptible to genetic modifications that influence the mating systems of populations. In almost every distylous or tristylous genus there are selfing homostylous taxa that have originated as a result of the breakdown of heterostyly. In most cases the evolution of homostyly is associated with dramatic reductions in flower size, acquisition of the self-pollinating habit, and the evolution of reproductive isolation. One consequence of the differences between closely related heterostylous-homostylous pairs is that the homostylous derivatives are usually given separate taxonomic status (Ornduff 1969).

In this chapter I review two studies of mating system evolution in heterostylous groups currently being conducted in our laboratory, and discuss their overall relevance to speciation theory. In the first I examine the relationship between polyploidy and breeding system diversification in the *Turnera ulmifolia* complex and evaluate several hypotheses to account for the evolution of selfing taxa from distylous members of the complex. The second study examines the breakdown of tristyly to homostyly in *Eichhor-*

*nia* and assesses the potential role of population bottlenecks in initiating mating system change. A common theme in studies of both groups is that relatively simple genetic alterations in floral traits can have profound effects on mating patterns and that these changes have important ecological and evolutionary consequences.

### POLYPLOID SPECIATION IN THE *TURNERA* *ULMIFOLIA* COMPLEX

*Turnera ulmifolia* L. (Turneraceae) is a polymorphic polyploid complex of herbaceous, perennial weeds native throughout much of the New World tropics and adventive in parts of Africa, India, and southeast Asia. Populations are conspicuous on roadsides and open waste ground but rarely colonize arable land (Barrett 1978a). The only monograph of the genus, by Urban (1883), recognized 12 intergrading taxonomic varieties within the *T. ulmifolia* complex. Later regional treatments have elevated some varieties to specific rank, whereas others are of dubious taxonomic status. In our studies we have followed Urban's treatment with the knowledge that most of the varieties we have studied are good biological species. Details of the morphological variation and crossability of selected varieties are presented in Shore and Barrett (1985a), and Arbo (1985) and Arbo and Fernández (1983) provide recent taxonomic treatments of some members of the complex.

#### Breeding systems and polyploidy

Surveys of the *T. ulmifolia* complex throughout much of its New World range have revealed an association between the breeding systems of populations and their chromosome numbers (Table 1). Diploid and tetraploid populations are uniformly distylous with strong self-incompatibility and a

TABLE 1. Relationships between ploidal level and breeding system in the *Turnera ulmifolia* complex.<sup>a</sup>

Ploidal level	Varieties	Populations	Compatibility	Stamen-style polymorphism
Diploid	3	15	SI	Distylous
Tetraploid	3	33	SI	Distylous
Hexaploid	3	25	SC	Homostylous

<sup>a</sup>SI, self-incompatible; SC, self-compatible;  $x = 5$ . After Barrett and Shore (1987).

1:1 ratio of the floral morphs, whereas hexaploid populations are homostylous and self-compatible. The three homostylous varieties that we have studied are differentiated for morphological traits and allozymes, occur at different margins of the geographical range of the species complex, and are intersterile. This indicates that distyly has broken down to homostyly on at least three separate occasions in the complex, each time in association with the hexaploid condition (Shore and Barrett 1985b). Cytological and isozyme studies indicate that although tetraploid varieties form quadrivalents and exhibit tetrasomic inheritance, hexaploids form bivalents and display considerable fixed heterozygosity at isozyme loci. These findings suggest that tetraploid populations are autopolyploids, whereas hexaploid populations may be allopolyploids, or at least the respective polyploids lie toward different ends of the auto-allopolyploid continuum (Barrett and Shore 1987).

Although it is unusual to find autopolyploidy and allopolyploidy within the same species complex, their association with outcrossing and selfing breeding systems in *T. ulmifolia* parallels a more general pattern found among other flowering plant groups. Stebbins (1980) has suggested that to be successful an autopolyploid is dependent on heterozygosity and that the biochemical and physiological advantages conferred by heteroallelism are important components of autopolyploid vigor. Evidently the polysomic condition cannot tolerate the homozygosity associated with self-pollination. It is significant that among the many polyploid crop cultivars there are no examples of successful polysomic polyploid species that are self-pollinated (Bingham 1980). In contrast, heterozygosity in allopolyploids results from gene multiplication rather than through allelic variation maintained by outcrossing. The simultaneous contribution of high biochemical diversity, as a result of fixed heterozygosity, and assured reproduction through selfing may be the key components of the genetic system responsible for the success of many allopolyploid weeds (Barrett and Shore 1989). In *T. ulmifolia* the three homostylous varieties occur at the geographic margins of the range, suggesting that the ability of homostyles to reproduce under conditions of low pollinator availability may have been important in their initial establishment and spread.

### Origin and evolution of homostyly

What factors account for the association between the breakdown of distyly to homostyly and the hexaploid condition in the *T. ulmifolia* complex? Formal genetic analysis of distyly and homostyly has demonstrated that distyly is governed by a single gene "locus" with L plants of genotypes *ss* and *ssss* and S plants of genotypes *Ss* and *Ssss* in diploids and tetraploids, respectively. Homostyly arises by a crossover in the supergene that controls the

polymorphism (Shore and Barrett 1985b). The shift from outcrossing to selfing is therefore a relatively simple genetic change that occurs in one mutational step as a result of recombination. There is no evidence that polyploidy per se promotes increased recombination in heterostylous plants as suggested by Dowrick (1956). In *T. ulmifolia* hexaploids, synthesized from triploids by the use of colchicine, remain distylous and self-incompatible. This indicates that at its inception hexaploidy does not stimulate homostyle formation, at least in the experimental material with which we have worked (Shore and Barrett 1986).

One explanation for the puzzling association between hexaploidy and homostyle formation in the *T. ulmifolia* complex concerns the hybrid origin of homostylous varieties. It is possible that the spread of recombinant homostyles is favored in allohexaploid populations because of reduced inbreeding depression in comparison with diploid and tetraploid populations. Several authors have modeled the spread of homostyles in distylous populations (Crosby 1949; Bodmer 1960; Charlesworth and Charlesworth 1979a) and it is clear that inbreeding depression is one of the most important factors restricting the spread of selfing phenotypes in outcrossing populations (Lloyd 1979; Lande and Schemske 1985). Although theoretical studies indicate that the magnitude of inbreeding depression resulting from deleterious recessive genes is reduced by population bottlenecks, a similar effect can also arise from polyploidy (Lande and Schemske 1985). This has been termed a "hybridity bottleneck" by Hedrick (1987), who suggests that genes that increase the rate of selfing are likely to increase in frequency in newly established allopolyploids as a result of their decreased genetic loads. Similar arguments may apply to *T. ulmifolia*, and it would be of interest to investigate the genetic load of populations with contrasting ploidal levels to examine whether inbreeding depression declines with increased ploidal level. Unfortunately, since homostyles in the complex are well-established species and may be of considerable age, an analysis of this type may not be particularly informative for inferring the past history of selection associated with the origin and establishment of homostyly.

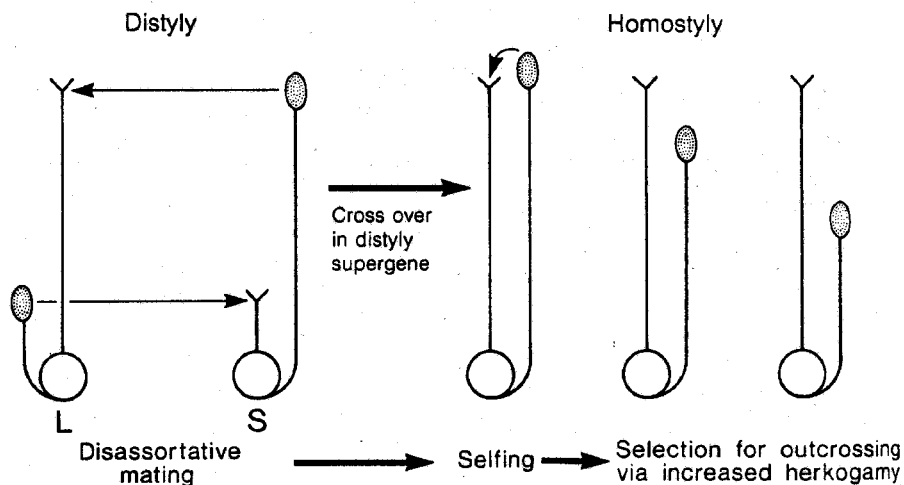
#### Mating system evolution in homostyles

The evolution of homostyly in *T. ulmifolia* has not resulted in the adoption of selfing as the principal reproductive mode (Figure 1). Although some populations in the complex are small-flowered and highly autogamous, others have large, showy flowers and well-developed herkogamy (spatial separation of anthers and stigmas) and are outcrossing. Experimental studies on the range of homostylous floral phenotypes in the *T. ulmifolia* complex suggest that outcrossing phenotypes are derived from selfing phenotypes (Barrett and Shore 1987). This mating system change is par-

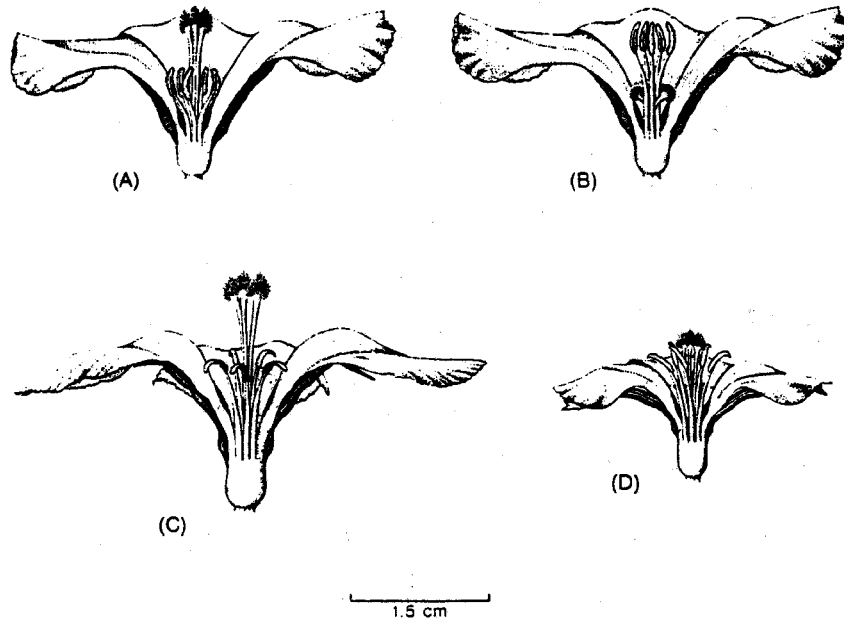


ticularly well illustrated in *T. ulmifolia* var. *angustifolia* in the Caribbean region. On small islands (e.g., Bahamas) small-flowered selfing phenotypes occur, whereas on the larger, more ecologically complex islands (e.g., Greater Antilles, Jamaica) large-flowered, outcrossing homostyles predominate (Figure 2). These patterns of floral variation suggest that frequent episodes of extinction and colonization favor selfing homostyles on small islands, whereas on larger islands selection pressures for outcrossing, associated with adaptive radiation, occur following the initial establishment of selfing colonists. The autochthonous development of outcrossing mechanisms in island plants is well known and has been reviewed by Baker (1967), Carlquist (1974), and Ehrendorfer (1979).

The reestablishment of outcrossing, following homostyle formation in *T. ulmifolia*, points to the evolutionary lability of the mating system and demonstrates its ability to respond to local selection pressures, if sufficient genetic variation for traits influencing mating behavior are maintained in populations. The allohexaploid status of homostyles must be important in this regard. What role processes such as intergenomic recombination, gene silencing, and regulatory divergence have played in releasing variation locked up within individuals as fixed heterozygosity is not known. It is notable that the spectacular adaptive radiation of *Bidens* species on the Hawaiian islands (Sun and Ganders 1988) also involves allohexaploid taxa. Interestingly, *Bidens* has also evolved alternative outcrossing systems (e.g., gynodioecism) following island colonization (Sun and Ganders 1986).



**FIGURE 1.** Model of the evolutionary relationships among distylous and homostylous forms within the *Turnera ulmifolia* complex.



**FIGURE 2.** Floral variation in the *Turnera ulmifolia* complex. (A, B) Long- and short-styled morphs of distylous var. *intermedia* (4x) showing the reciprocal arrangement of stamens and styles; (C) var. *angustifolia* (6x) large-flowered outcrossing homostyle from Jamaica; (D) var. *angustifolia* (6x) small-flowered selfing homostyle from the Bahamas.

#### POPULATION BOTTLENECKS AND MATING SYSTEM SHIFTS IN *EICHHORNIA*

As discussed earlier, the evolution of self-fertilization in flowering plants is frequently associated with colonization of geographically or ecologically marginal environments. In several of the studies cited, population bottlenecks arising through drought or founder events have been implicated in the establishment of self-fertilizing variants. Although the role of founder events in the speciation process remains a contentious issue in most animal groups (see Barton, this volume), they play an important role in mating system shifts in many herbaceous plant groups. Barton and Charlesworth (1984, p. 144) state "there are no grounds for expecting a strong association between change in mating system and founder events, except in self-compatible hermaphrodites." Many cases of the shift from outcrossing to selfing in plants involve this condition. Our own studies of self-compatible tristylous species of *Eichhornia* (Pontederiaceae) indicate that genetic and ecological processes operating in small populations can be of

major importance for initiating evolutionary changes in the mating system. The remainder of this chapter documents these changes, examines the selective forces responsible for the evolution of selfing, and discusses the genetic and developmental basis of changes in floral phenotype.

### Interspecific patterns

Of the eight species of *Eichhornia*, three possess large, showy, entomophilous flowers and are primarily tristylous, and the remaining five are small-flowered, largely monomorphic for floral traits, and predominantly self-pollinating. Two sources of evidence indicate that the major pathway of breeding system evolution in the genus involves the repeated breakdown of tristily to give rise to selfing, semihomostylous (with one set of stamens adjacent to the stigma) species (Barrett 1985a, 1988b). The first is the occurrence of semihomostylous variants in each of the three tristylous species, *E. azurea* (Barrett 1978b), *E. crassipes* (Barrett 1979), and *E. paniculata* (Barrett 1985b). This indicates that the microevolutionary forces responsible for the breakdown of tristily occur under the present ecological conditions in which *Eichhornia* species are found. The second line of evidence is the presence of residual genetic polymorphisms associated with the tristylous syndrome in several autogamous semihomostylous species (e.g., *E. diversifolia*, *E. heterosperma*, *E. paradoxa*). The occurrence of these floral polymorphisms indicates that the semihomostylous condition is derived from tristily, unless of course we are prepared to accept that tristily is in *statu nascendi* within each semihomostylous species. Given the complexity of the polymorphism and its extreme rarity in the angiosperms as a whole, this seems unlikely (Eckenwalder and Barrett 1986).

### Microevolutionary studies of the breakdown process

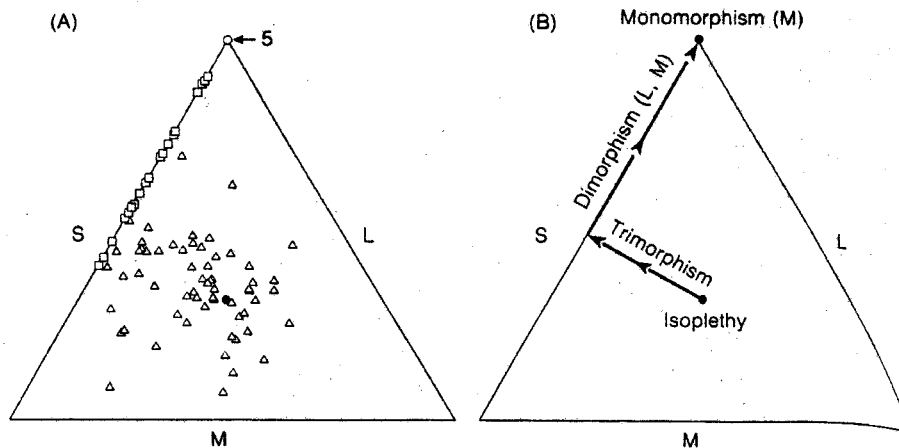
Our early studies on the evolutionary breakdown of tristily in *E. azurea* and *E. crassipes* were restricted because of their long-lived clonal nature, the absence of sexual reproduction in many populations, and the rarity of semihomostyle formation. These features hinder ecogenetic studies and reduce the likelihood of detecting microevolutionary changes in the mating system. More recently we have focused our attention on the remaining tristylous species, *E. paniculata*, since it possesses the full range of mating systems represented in the genus and is a short-lived perennial or annual that is easily crossed and cultured under glasshouse conditions.

*Eichhornia paniculata* is an emergent aquatic that grows in seasonal pools, ditches, marshes, and rice fields. The species is distributed primarily in northeast Brazil and the Caribbean islands of Cuba and Jamaica, with single isolated collections reported from west Brazil, Ecuador, and Nica-

ragua. Two aspects of *E. paniculata* ecology make it particularly susceptible to population size fluctuations. The species' major center of distribution, northeast Brazil, is an arid region with one of the most unpredictable rainfall regimes in the world (Nimer 1972). Variation in rainfall has a major influence on the availability of aquatic habitats inhabited by *E. paniculata* and fluctuations in population size and frequent local extinctions are an integral feature of the population biology of the species. In addition, *E. paniculata* produces large numbers of tiny seeds and, like many aquatic plants, the species is particularly prone to both short- and long-distance dispersal by water birds. The founding of isolated populations by long-distance bird dispersal probably accounts for the scattered distribution of the species in the New World tropics. Colonizing events of this type are frequently associated with population bottlenecks, and, in *E. paniculata*, these have a major disruptive effect on the maintenance of tristily.

Genetic studies of the inheritance of tristily in *Eichhornia* indicate that the polymorphism is under the control of two diallelic loci (*S*, *M*) with *S* epistatic to *M* (S. C. H. Barrett, unpublished data). With this inheritance pattern and legitimate mating between the floral morphs, an isoplethic equilibrium (1:1:1) is the only possible condition in large populations if the morphs are of equal fitness (Heuch 1979). This expectation provides a logical starting point for studies concerned with the maintenance and breakdown of heterostyly and surveys of style morph frequency in natural populations can provide valuable clues to the mechanisms responsible for anisoplethy (Charlesworth 1979; Barrett et al. 1983; Morgan and Barrett 1988). Our surveys of morph frequencies in populations of *E. paniculata* from northeast Brazil and Jamaica indicate major deviations from isoplethy (Barrett 1985a; Barrett et al. 1989). Of 84 populations sampled in northeast Brazil, 58 were trimorphic, 21 were dimorphic with only the L and M morphs represented, and 5 were monomorphic containing only the M morph. On the island of Jamaica a total of 26 populations were sampled, of which 19 were monomorphic with M plants only and 7 were dimorphic with L and M plants. The S morph is absent from Jamaica, presumably as a result of founder events (see below). Similar patterns of floral morph distribution are evident in *E. crassipes* where the S morph is restricted to lowland tropical South America and is absent from the remainder of the species' New and Old World ranges, whereas the M morph predominates in most areas (Barrett 1977; Barrett and Forno 1982).

By plotting the frequency of floral morphs in Brazilian populations of *E. paniculata* it is possible to discern several patterns in population structure that aid in formulating a model of the breakdown process (Figure 3). Large areas of the triangle in Figure 3A are not occupied by populations, and trimorphic populations tend to be concentrated on the left side of the triangle as a result of a reduced frequency of the S morph in many pop-



**FIGURE 3.** Morph frequencies in 84 populations of *Eichhornia paniculata* from northeast Brazil. (A) Small triangles are trimorphic populations, squares are dimorphic populations, and open circles are monomorphic populations. Isoplethy (filled circle) is equidistant from all axes and the distance of a point from each axis is proportional to the frequency of the morph in the population, e.g., points close to the S axis have a low frequency of the S morph. (B) Pathway from floral trimorphism through dimorphism to monomorphism associated with the breakdown of tristily to semihomostyly in *Eichhornia paniculata*.

ulations. Among the sample of dimorphic populations the L morph is usually underrepresented in comparison with a 1:1 expectation, with the M morph predominating in most populations. These patterns indicate that the breakdown of tristily to floral monomorphism is associated with two key stages: (1) loss of the S allele and hence the S morph from populations, and (2) loss of the *m* allele and thus the L morph. These stages are depicted in Figure 3B with arrows indicating the pathway of evolutionary change from floral trimorphism through dimorphism to monomorphism. The breakdown of tristily may not always follow the trajectory illustrated in Figure 3B, for a variety of reasons associated with founder events and local conditions. However, the available data indicate that the most frequent pathway of mating system change in *E. paniculata* involves the stages outlined above. This pathway and associated changes in floral phenotype and mating system are illustrated schematically in Figure 4 and discussed in detail below.

#### Evolution of dimorphism from trimorphism

What factors account for the loss of the S morph from populations of *E. paniculata* and its absence from Jamaica? The most likely explanation in-

volves stochastic influences on population size and the influence of founder events. Since *E. paniculata* is highly self-fertile, polymorphic populations can arise from selfing and segregation in genotypes heterozygous at the *S* and *M* loci. The *m* allele governing the L phenotype can be carried by all three style morphs, and the *M* allele, controlling the M phenotype, by the *S* and *M* morphs. In contrast, the dominant *S* allele is only carried by the *S* morph and separate introductions of this morph are therefore necessary for it to become established in populations. Presumably the *S* morph is absent from Jamaica because it was not involved in early dispersal events to the island. Computer simulation studies on the effects of random fluctuations in population size in tristylous systems verify that the *S* morph is most often lost from populations (Heuch 1980; Barrett et al. 1989).

Although similar processes on a neighborhood scale may contribute to the reduced frequency of the *S* morph in Brazilian populations of *E. paniculata*, selective factors also appear to play an important role. For tristily to function effectively, populations should provide sufficient pollen and nectar rewards to attract specialized long-tongued pollinators, usually bees in the genera *Ancyloscelis* and *Florilegus* (Barrett 1985b). Where long-tongued pollinators are absent, either because of local ecological conditions or demographic factors associated with small population size, the maternal fitness of the *S* morph may suffer disproportionately, in comparison with L and M morphs, because of its concealed female reproductive parts. This effect has been implicated as the cause of low seed set in *E. crassipes* (Barrett 1977), and comparisons of fruit set in floral morphs from

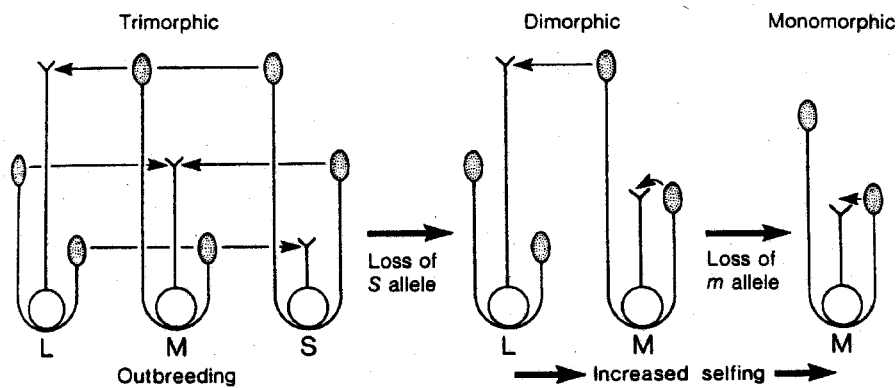
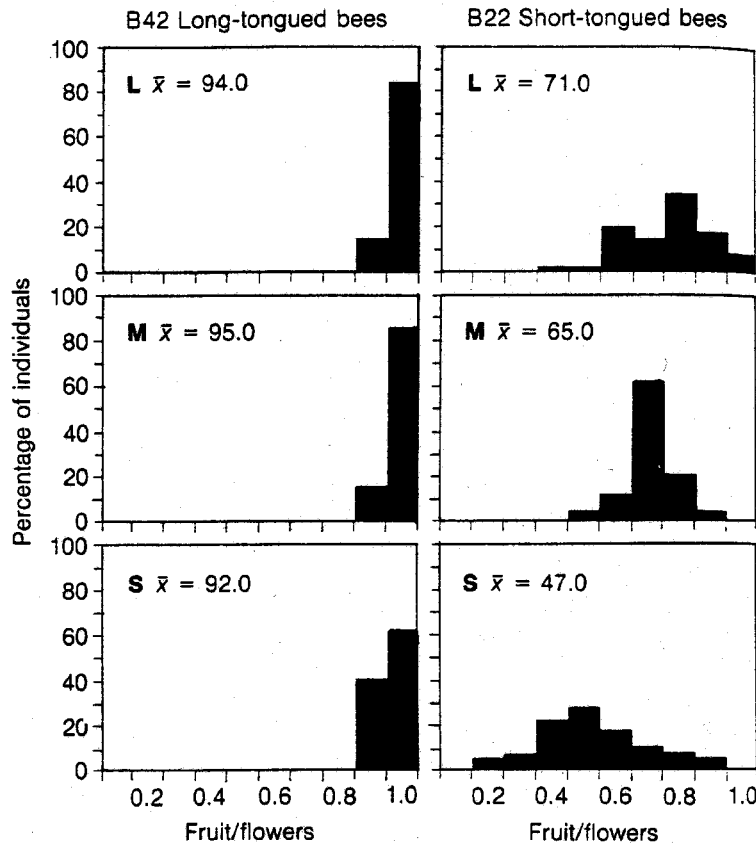


FIGURE 4. Model of the breakdown of tristily to semihomostyly in *Eichhornia paniculata*. Arrows indicate the predominant matings that occur within populations. Note the modification in short-stamen position of the M morph in dimorphic and monomorphic populations and the reduction in dimensions of floral organs in the monomorphic population.

populations of *E. paniculata*, with and without the services of long-tongued bees, have demonstrated the potential fitness penalties to the S morph associated with the absence of specialized pollinators (Figure 5). Simulation studies confirm that reductions in the female fertility of the S morph will result in its loss from trimorphic populations. The decline in frequency of the S morph occurs more rapidly when mating patterns change from disassortative to random mating. This effect is likely in small populations serviced by generalist pollinators (Barrett et al. 1989).

Several lines of evidence suggest that nontrimorphic populations are more capable of persisting in marginal environments. Censuses of popula-



**FIGURE 5.** Female fertility of the floral morphs of *Eichhornia paniculata* in populations from northeast Brazil serviced by contrasting pollinators. The distributions are of percentage fruit set of the L, M, and S morphs in two populations. B42 was visited by long-tongued specialist bees (*Florilegus* and *Ancyloscelis*) and B22 was visited by short-tongued generalist bees (*Trigona* and *Apis mellifera*).

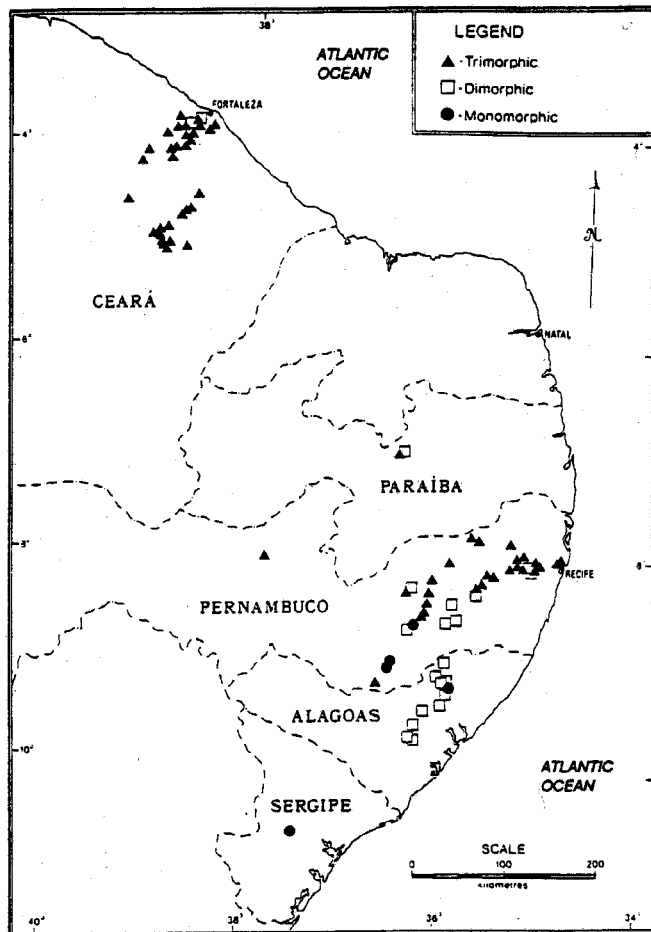


FIGURE 6. Geographical distribution of *Eichhornia paniculata* in northeast Brazil. Triangles are trimorphic populations, squares are dimorphic populations, and circles are monomorphic populations.

tion size in northeast Brazil indicate that although trimorphic populations range from large to small, nearly all monomorphic and dimorphic populations are composed of less than 100 individuals. In addition, whereas trimorphic populations are concentrated in two main areas of northeast Brazil, dimorphic and monomorphic populations are more commonly found at the southern margins of the region surveyed (Figure 6). The habitats occupied by many nontrimorphic populations are distinct from those in which trimorphic populations are found and, in addition, the density of plants in nontrimorphic populations is significantly lower than in

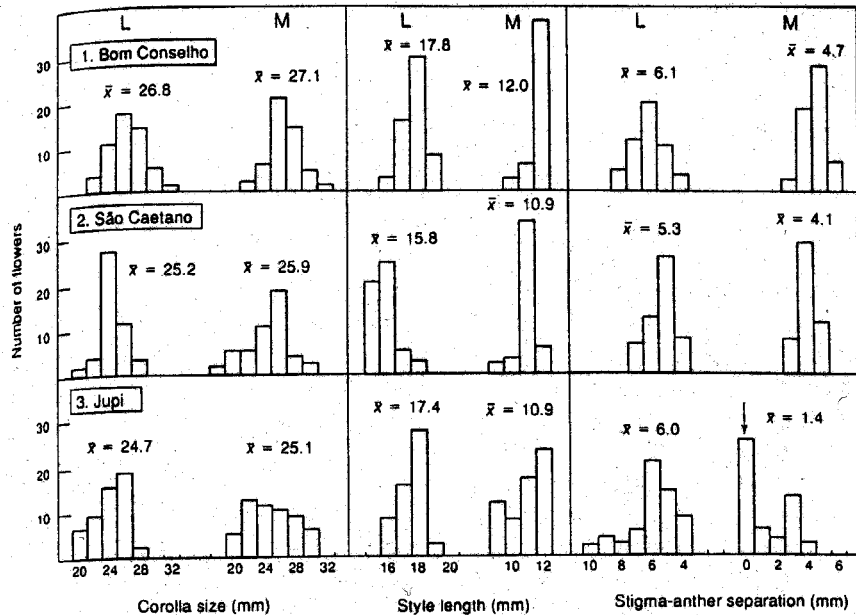


trimorphic populations (Barrett et al. 1989). The association between selfing and low-density conditions is a recurrent theme in the mating system literature and data from *E. paniculata* provide support for the hypothesis that reproductive assurance is an important selective force in the evolution of selfing.

Studies of floral biology and estimates of outcrossing rate in *E. paniculata* populations have demonstrated major differences between trimorphic and nontrimorphic populations in their mating systems (Barrett 1985a; Glover and Barrett 1986; Barrett et al. 1987). Virtually all monomorphic and dimorphic populations that have been examined are composed of selfing variants of the M morph. The variants possess modified short-level stamens in which one, or more rarely two or three, stamens are elongated into the mid-level position adjacent to the stigma of the mid style (Figure 4). Because of the close proximity of their stigmas and anthers, the variants are highly self-pollinating. Floral modifications that increase selfing rates occur most commonly in the M morph and are found only rarely in the L and S morphs. Although they are frequent in dimorphic populations and usually fixed in monomorphic populations, the variants are uncommon in trimorphic populations. Figure 7 provides measurements of several floral traits from the L and M morph in two trimorphic populations and a dimorphic population in which selfing variants appear to have recently originated. As can be seen, alterations in the short-stamen level of the M morph result in a marked reduction in stigma-anther separation in the dimorphic population. In spite of this change the average values of the remaining floral traits are largely unaffected, although an increased variance is evident, perhaps because of inbreeding effects (see below). The occurrence of dimorphic populations of *E. paniculata* with different frequencies of modified M plants provides a rare opportunity to investigate the initial stages of the evolution of selfing and, as we shall see, alterations in floral phenotype that promote self-pollination involve relatively minor genetic and developmental changes.

#### Evolution of monomorphism from dimorphism

Once selfing variants of the M morph have become established in dimorphic populations they are more likely than unmodified plants to found new populations because of their capacity to set seed in the absence of pollinators. The observation that all monomorphic populations in northeast Brazil and Jamaica are composed exclusively of selfing variants of the M morph provides strong evidence of the selective advantage of this morph during colonizing episodes. But what are the microevolutionary processes that operate *within* dimorphic populations? Can these populations retain an outcrossed mating system? Is a stable equilibrium of outcrossing and



**FIGURE 7.** Distributions of corolla size, style length, and stigma-anther separation (mm) in the long- and mid-styled morphs (L and M, respectively) from two trimorphic (Bom Conselho, São Caetano) and one dimorphic (Jupi) population of *Eichhornia paniculata* from northeast Brazil. The arrow indicates the breakdown of herkogamy in the M morph. Flowers in the O class are capable of autonomous self-pollination. Note the wider distributions of floral traits in the dimorphic population. This may result from reduced canalization associated with inbreeding (see text).

selfing morphs likely, or will the selfing variants spread to fixation, giving rise to additional monomorphic populations? Although we do not have all of the answers to these questions, several lines of evidence suggest that the maintenance of a dimorphic mixed mating system can occur only under rather restrictive conditions and that the spread and ultimate fixation of the M morph are more likely outcomes.

Once selfing variants of the M morph have become established in dimorphic populations they enjoy several important fitness advantages over the L and unmodified M morphs. The most obvious of these, reproductive assurance in the absence of pollinators, has already been considered in the context of colonization. However, even where pollinator service is available, modified M plants may also experience an asymmetrical mating advantage. This is because genes that promote self-fertilization bias their own transmission through the mating cycle and thus tend to be

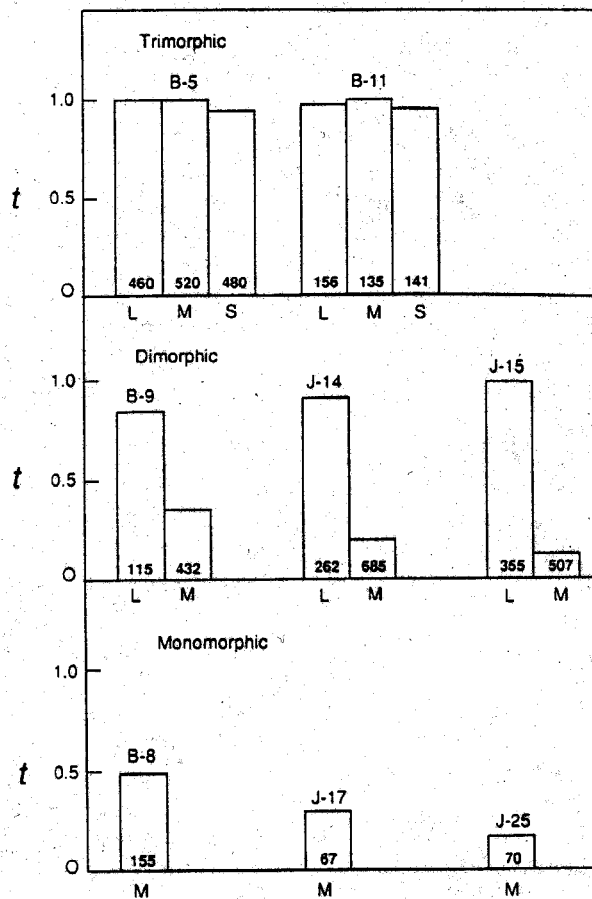
automatically selected (Fisher 1941). As illustrated in Figure 4, selfing variants are potentially capable of transmitting genes via pollen and ovules through selfing as well as through outcrossing. In contrast, the L morph suffers under this model, since it acts principally as a female in matings with the selfing variant because its pollen is incapable of effectively out-competing with the selfed pollen of the M variant.

Pollen discounting (Holsinger et al. 1984) and inbreeding depression (Lande and Schemske 1985) can potentially prevent the spread of selfing variants in outbreeding populations. However, these factors appear to be of minor significance in dimorphic populations of *E. paniculata*. Long-level anthers of selfing variants are unaffected by genetic changes in the position of "short-level" stamens and hence continue to contribute genes to the outcrossed pollen pool. Inbreeding depression in dimorphic populations appears to be mild enough that it presents no major obstacle to the spread of selfing variants (P. Toppings and S. C. H. Barrett, unpublished data). It is possible that the population bottlenecks that contribute to the loss of the S morph reduce genetic load sufficiently that if selfing variants do arise in populations they are almost always automatically selected unless, of course, they are lost by genetic drift when at low frequency.

#### Mating systems and floral morphology

Electrophoretic studies of the mating systems of floral morphs in populations of *E. paniculata* from northeast Brazil and Jamaica have demonstrated the important influence of floral morphology on outcrossing and selfing rates (Glover and Barrett 1986; B. C. Husband and S. C. H. Barrett, unpublished data). In trimorphic populations outcrossing rates are high, with no significant differences among the floral morphs. In dimorphic populations, however, the M morph experiences a high level of self-fertilization, whereas the L morph remains largely outcrossed (Figure 8). There are difficulties in estimating the outcrossing rates of monomorphic populations since they are often devoid of polymorphism at isozyme loci. In populations with some polymorphism high levels of self-fertilization have been observed, although it is likely that higher selfing rates occur in populations with no electrophoretic variation. Among 11 populations surveyed by Glover and Barrett (1987), outcrossing rates were significantly correlated with the number of polymorphic loci, alleles per locus, and observed heterozygosity of populations.

The floral phenotypes of selfing M variants in monomorphic populations usually differ from those that are present in dimorphic populations. Although only minor modifications in floral morphology are evident in most dimorphic populations (Figure 7), selfing phenotypes in monomorphic populations frequently display a suite of floral traits that normally distinguishes selfing species of *Eichhornia* from their outcrossing



**FIGURE 8.** Estimates of the outcrossing rate ( $t$ ) of floral morphs in trimorphic, dimorphic, and monomorphic populations of *Eichhornia paniculata* from northeast Brazil (B) and Jamaica (J). The number of progeny assayed per morph are indicated. Outcrossing rates were estimated using isozyme loci. Within trimorphic populations there were no significant differences between the outcrossing rate of floral morphs whereas in dimorphic populations the morphs differed significantly ( $p < 0.001$ ) in outcrossing rate.

progenitors. These include smaller, less showy flowers, fewer flowers per inflorescence, lower pollen-ovule ratios, lower fruit and seed abortion rates, and reduced allocation of resources to male function (Barrett 1985, 1988a; Morgan and Barrett 1989). Populations that possess these attributes have all three "short-level" stamens adjacent to the mid stigma and are usually referred to as semihomostyles (Ornduff 1972). In spite of the major differences in reproductive biology between tristylous and semihomo-

stylous flowers of *E. paniculata*, populations possessing these floral syndromes are fully interfertile. This indicates that not all changes in mating systems are necessarily accompanied by the evolution of reproductive isolation.

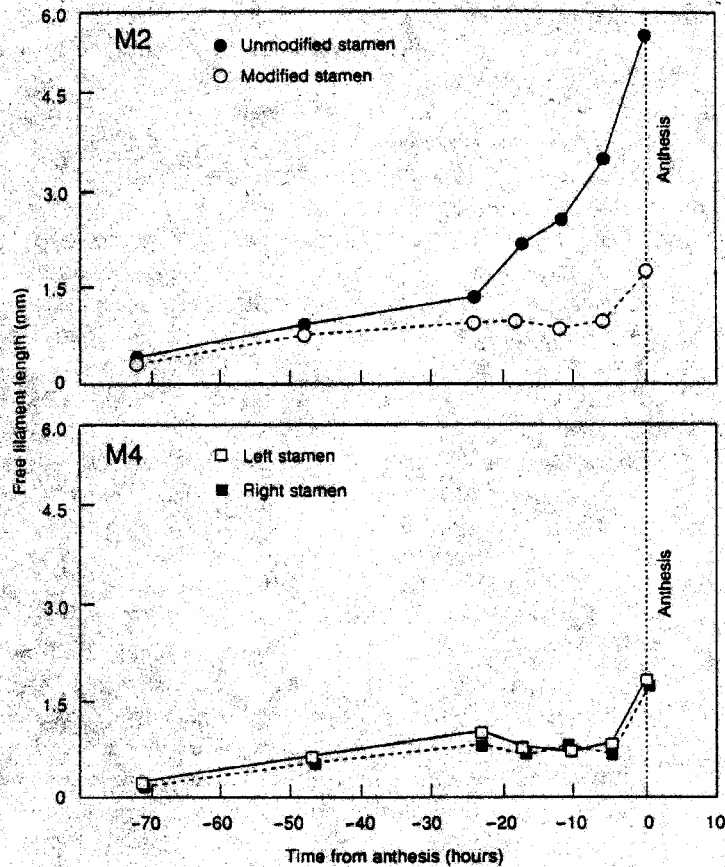
#### Genetic and developmental basis of floral modification

An important question in our studies of the evolution of self-fertilization in *E. paniculata* has concerned the processes responsible for the origin of variation in floral phenotype. What genetic and developmental mechanisms are involved and how does the variation initially arise in populations? Trimorphic populations usually exhibit a highly canalized floral phenotype with relatively minor phenotypic variation in stamen and style length (see Figure 7 for example). Constancy of floral traits is typical of many animal-pollinated species (Berg 1959) and is particularly likely in heterostylous species in which the precise positioning of reproductive parts is required to effect legitimate pollination between the floral morphs (Barrett and Glover 1985). A different pattern is encountered in nontrimorphic populations of *E. paniculata* that frequently display considerable developmental instability for a range of floral traits (Barrett 1985b; Seburn et al. 1989). Instability may arise from inbreeding, in normally outcrossing species, as a result of the exposure of deleterious recessive genes that affect developmental pathways (Lerner 1954). Genes of this type are more likely to be exposed in small inbred populations following population bottlenecks (Levin 1970).

Studies of the inheritance of stamen elongation in selfing variants of the M morph indicate recessive gene control (S. C. H. Barrett, unpublished data). This suggests that the association between developmental instability, the occurrence of floral modifications, and nontrimorphic population structure may result from biparental inbreeding in small populations. According to this hypothesis recessive genes with effects on floral morphology and mating systems are part of the segregational load of tristylous populations. The genes, however, are rarely exposed to selection because of the predominantly outcrossed mating system of populations. However, bottlenecks and subsequent inbreeding may expose mating system modifier genes to selection, and because of reduced genetic load and their effects on mating (previously discussed), the genes experience an automatic advantage. Since selfing variants of the M morph appear to have originated independently in different parts of the range of *E. paniculata*, it will be of particular interest to determine whether the same modifier genes are involved. Crosses between the variants and tests of allelism are currently underway to determine the genetic basis of mating system modification.

Simple genetic changes in floral morphology and reproductive physiology can often have important effects on the mating systems of plants

(Bachmann 1983; Hilu 1983; Gottlieb 1984). Frequently these changes are manifested relatively late in development and, as a result, they may have only minimal effects on other facets of floral phenotype when they first appear in populations. Developmental studies of the range of floral phenotypes in *E. paniculata* (Richards and Barrett 1985 and unpublished data) indicate that the most common phenotypic alteration that gives rise to selfing results from rapid changes in filament length that occur primarily in the 24 hours prior to anthesis (Figure 9). This modification involves only one stamen of the six that occur within an *E. paniculata* flower. The



**FIGURE 9.** Developmental changes in the free filament length of short-level anthers in two genotypes of the mid-styled morph of *Eichhornia paniculata*. Genotype M2 possesses modified stamens that cause autonomous self-pollination of mid-level stigmas. Genotype M4 is unmodified and incapable of autonomous self-pollination. Only one stamen within each flower of genotype M2 is modified; the stamen can be either the left or right stamen of the short-level.

remaining stamens are unaffected by its change in position. The single stamen produces sufficient pollen, released at the commencement of anthesis, to self-fertilize the hundred or so ovules within a flower. It seems likely that the expansion of filament length in modified stamens of *E. paniculata* is regulated by hormones, such as gibberellic acid. These have been implicated in the regulation of reproductive organ size and position in a range of other flowering plants (Greyson and Tepfer 1967; Pharis and King 1985).

Although inheritance studies of the modified genotype illustrated in Figure 9 are consistent with single recessive gene control, many additional genes with small effects are likely to govern the syndrome of floral traits that has accompanied the evolution of semihomostyly in *E. paniculata*. However, the important point is that the initial change in floral phenotype that precedes the evolution of the selfing syndrome in *E. paniculata* can be under simple genetic control.

## CONCLUSIONS

Our studies of mating system evolution in heterostylous plants indicate that changes in the reproductive behavior of flowering plants can often be rapid and result from relatively simple genetic and developmental modifications in floral plan. In the *Turnera ulmifolia* complex recombination in the distyly supergene, in association with polyploidy, leads to a quantum change in mating system with reproductive isolation arising in a single step. Unfortunately, the low frequency of recombination events in heterostylous plants (see Charlesworth and Charlesworth 1979b; Shore and Barrett 1985b) has prevented us from conducting population studies on the selection dynamics of homostyles in distylous populations of *T. ulmifolia*. However, our studies of homostyle evolution do provide empirical support for Charlesworth and Charlesworth's (1979a) theoretical model of the breakdown of distyly. They demonstrated that when the "allele" that determines short styles is dominant, as in *T. ulmifolia*, long homostyles (phenotypes with long styles and long-level stamens) are likely to spread to fixation with greater probability than other recombinant phenotypes. Each breakdown event in the *T. ulmifolia* complex has given rise to the long homostylous phenotype, notwithstanding the secondary evolutionary modifications in floral structure that have taken place in each taxon subsequent to its origin. It is remarkable that a simple genetic constraint, involving the dominance relationships at the distyly locus, can determine the particular pathway of floral evolution that is followed in heterostylous species.

In contrast to *T. ulmifolia*, the breakdown of heterostyly in *Eichhornia* involves several key steps with the mating system changing in stages from outcrossing to selfing. However, the initial modifications in floral morphol-

ogy of the M morph appear, in some cases at least, to be simply inherited and to originate quite frequently in local populations. Semihomostylous species of *Eichhornia* are largely composed of populations that possess modified M phenotypes and selfing variants in the remaining tristylous species usually possess this phenotype (Barrett 1988b). This suggests that in common with *T. ulmifolia*, genetic constraints associated with floral development may play an important role in guiding the specific reproductive modifications that can occur.

Although the acquisition of predominant self-fertilization does not necessarily result in speciation, the effective reproductive isolation that results is likely to enhance character divergence, particularly in floral traits, and the gradual build-up of postzygotic isolating mechanisms. In many genera of herbaceous plants outcrossing species have given rise to clusters of selfing microspecies, many of which are notoriously difficult to classify (Davis and Heywood 1963; Grant 1981). In *Eichhornia* two putative progenitor-derivative species pairs (*E. azurea* tristylous, *E. heterosperma* homostylous, and *E. paniculata* tristylous, *E. meyeri* homostylous) involve outcrossing and selfing taxa. The derived homostyles are almost indistinguishable from their putative outcrossing progenitors in vegetative traits and as a result have not been recognized as distinct from them by most taxonomists. However, the homostyles cannot be crossed with the outcrossing taxa, perhaps because floral traits associated with the selfing syndrome impair reproductive function.

In selfers, the reduced dimensions of reproductive structures, low pollen production, and small pollen size must restrict opportunities for mating with outcrossers irrespective of whether postzygotic isolating mechanisms occur. Supplementing these intrinsic barriers to mating that result from reproductive character divergence, ecological and geographical isolation may arise because of the ability of selfing variants to invade environments not occupied by their outcrossing ancestors. In both *Turnera* and *Eichhornia*, for example, selfing variants have colonized areas at the geographic margins of the range, presumably because of the capacity of single individuals to establish colonies following long-distance dispersal (Baker 1955). Once established, the geographic isolation of selfing populations, exposure to novel selection pressures, and genetic drift in small populations are all likely to enhance genetic changes in other aspects of plant phenotype, leading to the evolution of reproductive isolation.

With the exception of changes in genetic system associated with polyploidy and chromosomal rearrangements, the evolution of reproductive isolation in plants appears to evolve most commonly in allopatric populations as a result of the normal processes of adaptive divergence. A growing body of evidence from population studies of herbaceous plants does, however, suggest that mating system shifts in small populations may play a



more significant role in species formation than is generally recognized, by initiating processes that lead to reproductive isolation. Population sizes in many herbaceous plants are small, gene flow is often highly restricted, and local differentiation is widely observed (Levin 1978). These microevolutionary characteristics of plants, in association with the simple genetic basis of many morphological and physiological traits associated with the mating system, foster reproductive character divergence and speciation. Nowhere is this more evident than in association with the evolution of selfing from outcrossing in herbaceous flowering plants.

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