

MATING STRATEGIES IN MONOCOTYLEDONS

Spencer C.H. Barrett, Angela M. Baker and Linley K. Jesson

Department of Botany, University of Toronto, Toronto, Ontario M5S 3B2, Canada; email: Barrett@botany.utoronto.ca

Abstract

Mating strategies in monocotyledons resemble those found in dicotyledons despite their distinguishing floral traits. This similarity arises because the principal selective mechanisms (inbreeding depression, effective pollen dispersal, reproductive assurance, and the optimal allocation of resources to female and male function) governing mating and fertility are of general significance for all seed plants. Here we review selected mating strategies in animal-pollinated monocotyledons emphasizing fitness gain through both maternal and paternal function. The sexual polymorphisms: heterostyly, stigma-height dimorphism and enantiostyly are interpreted as floral designs that increase the proficiency of cross-pollination by reducing mating costs associated with geitonogamy. Sexual systems involving combinations of unisexual and/or hermaphrodite flowers are widespread among monocotyledons. The most common conditions are monoecy, andromonoecy, gynodioecy, and dioecy. Several examples of size-dependent gender modification in taxa with different sexual systems are reviewed. In animal-pollinated plants, large size is often associated with increased relative allocation to female function whereas in those that are wind-pollinated the reverse pattern is sometimes evident.

Key words: cross- and self-fertilization; floral design; stilar polymorphisms; pollen dispersal; geitonogamy; gender strategies, monocots

INTRODUCTION

Mating involves the mode of transmission of genes from one generation to the next through sexual reproduction. Patterns of mating in flowering plants are diverse and are the outcome of complex ecological interactions between environmental factors, pollen vectors and the specific floral traits of individual species (Brown *et al.* 1990; Barrett and Harder 1996; Holsinger 1996). Despite the striking evolutionary diversification of floral traits among angiosperm groups, this variation serves but one function, to optimise reproductive success for the range of environments a species is likely to encounter. Natural selection on patterns of mating and fertility is therefore the most powerful influence on floral evolution and can account for the diverse pollination and sexual systems that occur in flowering plants. Mating strategies are governed by several classes of floral adaptations. Floral design and display influence the

quantity and quality of pollen dispersed during the pollination process (Harder and Barrett 1996; Harder, this volume); self-incompatibility mechanisms screen pollen receipt rejecting particular male gametophytes, particularly those from self pollination (de Nettancourt 1997; Sage *et al.*, this volume); and the selective abortion of related offspring increases fitness and reduces maternal investment in inferior progeny (Willson and Burley 1983). Because of the hermaphroditic (cosexual) condition of most flowering plants, genetic transmission through pollen and ovules both contribute to overall fertility. However, while individuals usually vary in the fitness they gain through female and male reproductive pathways (Lloyd 1979a), gender equality must occur at the population level since all new offspring have but one maternal and paternal parent (Charnov 1982; Morgan and Schoen 1997).

Among flowering plants the monocotyledons are a monophyletic group of largely herbaceous families that represent approximately 22% of the 241,000 species of extant angiosperms. About half of all monocot species occur in the two large families Orchidaceae

and Poaceae. Distinctive features of monocotyledons include embryos with one cotyledon, parallel-veined leaves and trimerous flowers, although recent cladistic analyses suggest as many as 13 synapomorphies distinguish the group from the dicotyledons (Dahlgren *et al.* 1985; Donoghue and Doyle 1989; Herendeen and Crane 1995). Many unique and intricate pathways of floral evolution are evident within particular monocotyledonous families (Endress 1995); however, at a functional level there is no evidence that the distinguishing taxonomic features of the group have influenced mating strategies in ways fundamentally different from those of dicotyledons. All major sexual systems represented among dicotyledonous families (i.e. cosexuality, monoecy, dioecy, gynodioecy, self-incompatibility, heterostyly) occur in monocotyledons and the prominent pathways of mating-system evolution, such as the evolution of selfing from outcrossing (Stebbins 1974) and sexual dimorphism from cosexuality (Charlesworth and Charlesworth 1978), occur commonly among monocotyledons. The absence of unique sexual systems in monocotyledons is not at all surprising. The major selective forces that direct floral evolution and plant mating strategies – inbreeding depression, effective pollen dispersal, reproductive assurance, and the optimal allocation of resources to female and male function (Lloyd 1979b; Charnov 1982; Charlesworth and Charlesworth 1987; Uyenoyama *et al.* 1993; Harder and Barrett 1996, Holsinger 1996) – influence all seed plants. The adaptive basis of floral evolution in any monocotyledonous group therefore requires an understanding of these factors.

Here we review mating strategies among diverse animal-pollinated monocotyledons. Our goals are to illustrate some of the solutions that have evolved to secure reproductive success, emphasizing the importance of fitness gain through both maternal and paternal function. We begin by presenting the available data on selfing rates among monocotyledonous species and discuss some of the ecological and genetic factors responsible for this variation. We then introduce several polymorphic floral strategies involving contrasting patterns of sex-organ deployment and discuss their adaptive significance. Finally, we review the main gender strategies in monocotyledons and illustrate how both genetic and environmental factors interact to influence patterns of gender expression.

SELFING AND OUTCROSSING : GENERAL PATTERNS

The study of plant mating has been dominated by comparison of the average frequency of selfing and outcrossing of maternal parents among populations. Indeed until it was recognized that mating also involves fitness gain through male fertility (Gregorius *et al.* 1987) this comparison defined the 'mating system' for most plant populations. The selfing rate s and its complement, the outcrossing rate ($t = 1-s$) have profound biological significance because of their influence on progeny fitness, population genetic structure, and floral evolution (Uyenoyama *et al.* 1993; Barrett and Harder 1996). Over the past two decades, use of genetic markers, primarily allozymes, has enabled measurements to be made of the incidence of selfing in plant populations (Brown *et al.* 1990). Data on selfing rates can be used to examine overall trends among specific groups and to explore relations between life-history traits and mating patterns. A recent survey reported estimates for 217 species from 43 families of seed plants

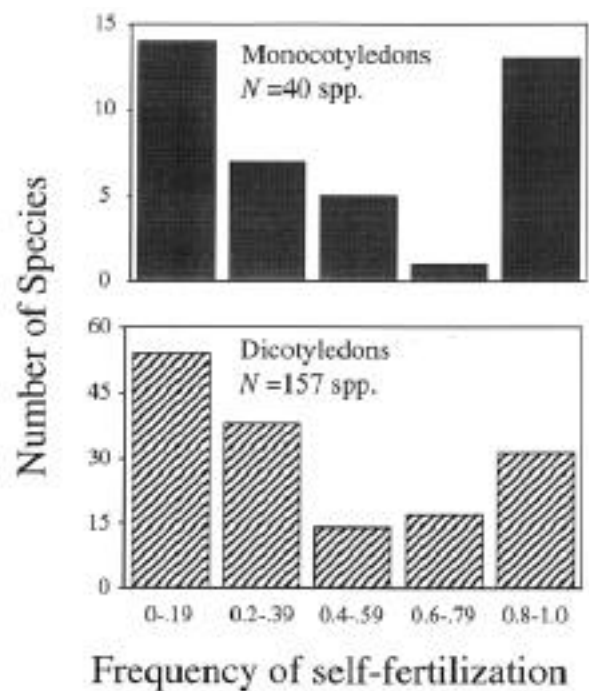


Fig. 1. Distribution of selfing rates among 40 species of monocotyledons and 157 species of dicotyledons estimated using genetic markers. Estimates were obtained from a literature survey. Monocotyledonous families represented were: Poaceae – 20 spp., Liliaceae – 6 spp., Amaryllidaceae – 5 spp., Pontederiaceae – 3 spp., Iridaceae – 2 spp., Agavaceae – 1 sp., Arecaceae – 1 sp., Posidoniaceae – 1 sp., Potamogetonaceae – 1 sp. The two distributions were not significantly different following a two-sample Kolmogorov-Smirnov test ($D = 0.172$, $P = 0.30$).

(Barrett *et al.* 1996a). Of these 27 were monocotyledons with the majority from grass species.

We have updated the survey by reviewing recent literature in an effort to include more monocotyledonous taxa. At the present time estimates are available for 40 species from nine monocotyledonous families. Estimates range from complete outcrossing to predominant selfing but the distribution is not significantly different to that for dicotyledons (Fig. 1). Although the sample is too limited to reveal any clear associations between the selfing rate and plant traits, the data resemble other published distributions in displaying a deficiency of taxa with intermediate (0.5–0.7) selfing rates (Schemske and Lande 1985; Barrett and Eckert 1990). This pattern is predicted by theoretical models of the joint evolution of inbreeding depression and the selfing rate (Lande and Schemske 1985). Clearly, more quantitative estimates of selfing rate are needed for monocotyledons, especially for families in which little is known about reproductive biology.

In the surveys discussed above, a single selfing rate was used to represent a particular species; where multiple estimates were reported, an average value was calculated. This raises the issue of whether mating patterns are relatively stable and where variation among populations exists what factors are involved. In species that are dioecious or self-incompatible there is unlikely to be significant variation in selfing rate among populations. However, opportunities for selfing can occur since many sexually dimorphic taxa exhibit sex inconstancy (see below), and self-incompat-

ibility is rarely absolute in expression (e.g. see Barrett and Anderson 1985). Nevertheless, it seems reasonable to expect less variation in selfing rate among populations for species with these systems than for those that are self-compatible. Several monocotyledonous species have been the subject of intensive investigations of mating patterns enabling these issues to be addressed.

Population surveys of self-incompatible *N. triandrus* (Barrett *et al.* 1997), *N. assoanus* (Baker *et al.* 1999a) and *N. papyraceus* (C. Hildago, J. Arroyo and S.C.H. Barrett, unpubl. data) revealed similar patterns. Selfing rates were generally low (0–20%) with relatively little variation among populations. In contrast, in two self-compatible species, *N. dubius* (Baker *et al.* 1999a) and *N. longispithus* (S.C.H. Barrett, W. Cole and C.M. Herrera, unpubl. data), selfing rates were significantly higher (20–40%) but, surprisingly, there was no significant variation among populations despite differences in ecology and population size. This result suggests that either cross and self pollen dispersal by pollinators was similar among populations, or that post-pollination mechanisms operate to buffer the mating system against variable pollen delivery by regulating the fertilization frequency of these pollen types. Studies of highly selfing species, such as *Hordeum spontaneum* (Brown *et al.* 1978), have also demonstrated little variation in mating patterns among populations although the small amount of outcrossing that occurs can have important fitness consequences owing to heterosis.

In contrast, studies of other self-compatible species have demonstrated striking variation among populations in the incidence of selfing. In the tristylous, annual aquatic *Eichhornia paniculata* (Pontederiaceae), the evolutionary breakdown of tristily involves the progressive loss of style morphs from populations and the spread of genes modifying stamen position thus resulting in increased levels of self-fertilization (Barrett *et al.* 1989). In a survey of 54 populations from N.E. Brazil and Jamaica selfing rates ranged from 0–99% with small-flowered, autogamous populations from Jamaica exhibiting the highest selfing rates. Increased selfing was significantly associated with the frequency of selfing variants within populations, small population size, and low plant density (Barrett *et al.* 1993) indicating that both genetic and environmental factors play a role in governing the evolution of the selfing rate. The striking variation in selfing rates among populations of the hydrophilous sea grass *Posidonia australis* (Posidoniaceae) reported by Waycott and Sampson (1997) is thought to be associated with environmental factors governing water currents (Waycott, this volume).

FLORAL DESIGN AND POLLEN DISPERSAL

Selfing and outcrossing rates measure the fraction of ovules that are self- or cross-fertilized and therefore consider mating only from a maternal perspective. We now consider the role that floral design plays in promoting more effective pollen dispersal among plants. This involves the concept of male outcrossing (Horovitz and Harding 1972), and requires knowledge of pollen fates (Harder, this volume) and the fitness dividends a plant experiences through enhanced male fertility. Many floral traits previously considered as anti-selfing mechanisms may function to promote fitness through enhanced pollen dispersal. This could explain their occurrence in species already protected from the

harmful effects of inbreeding by self-incompatibility or other post-pollination mechanisms that selectively favour outcross progeny (Lloyd and Webb 1986; Harder and Barrett 1996).

In animal-pollinated plants the spatial arrangement of female and male sex organs within flowers is of fundamental importance in governing pollen dispersal, mating patterns and fertility (reviewed in Barrett *et al.* 1998). Of particular interest are populations that are polymorphic for sex-organ position since they provide opportunities for investigating the reproductive consequences and functional significance of contrasting reproductive morphologies (Harder and Barrett 1993). The most prominent sex-organ polymorphisms involve the heterostylous conditions distily and tristily (see Fig. 1 in Barrett 1992a). These have been the subject of intensive genetic and evolutionary investigations since Darwin's pioneering studies over a century ago (Darwin 1877; Barrett 1992a). Experimental evidence indicates that these floral syndromes, and their associated self- and cross-incompatibility systems, function to promote more proficient pollen dispersal and reduce selfing and its harmful effects (reviewed in Lloyd and Webb 1992a, b). Heterostyly occurs in at least 28 flowering plant families, but only four genera in three families of monocotyledons contain heterostylous species. In Pontederiaceae, *Eichhornia* (3 spp.) and *Pontederia* (5 spp.) are tristylous but distily is absent from the family (Graham and Barrett 1995). In Iridaceae, *Nivenia* contains five distylous species but no tristylous species (Goldblatt and Bernhardt 1990). Finally, *Narcissus triandrus* of the Amaryllidaceae is tristylous but is the only heterostylous member of the family (Barrett *et al.* 1996b). The overall rarity of heterostyly in monocotyledons implies that there may be strong developmental constraints on its origin in this group. In some families this may be associated with reduced stamen number or pronounced zygomorphy, neither of which are associated with the polymorphism in dicotyledonous families.

Two other sexual polymorphisms that also involve stylar polymorphism are stigma-height dimorphism (see Fig. 13-1b in Barrett *et al.* 1996b) and enantiostyly (see Fig. 3c in Graham and Barrett 1995). Neither of these floral designs are well understood, particularly in comparison with heterostyly, and there has been confusion in the literature as to their nature and functional significance. To clarify the status of these polymorphisms we next provide a summary of our current research on them beginning with dimorphisms of stigma height.

Stigma-Height Dimorphism

Populations of some animal-pollinated plants exhibit dimorphism for stigma height with long- and short-styled morphs coexisting within populations. Unlike the distylous condition, anther levels in the two morphs are of similar height without the clear reciprocity of organ position that is the hallmark of the heterostylous syndrome. Stigma-height polymorphisms have been viewed as part of the variation encompassed by heterostyly (Richards 1997, and pers. comm.), or on theoretical grounds as transient stages in the build-up of these polymorphisms (Charlesworth and Charlesworth 1979; Lloyd and Webb 1992a, b). However, we believe that there are good grounds for recognising them as a sex-organ polymorphism that is distinct from heterostyly. As discussed below, in some groups they are not associated with the

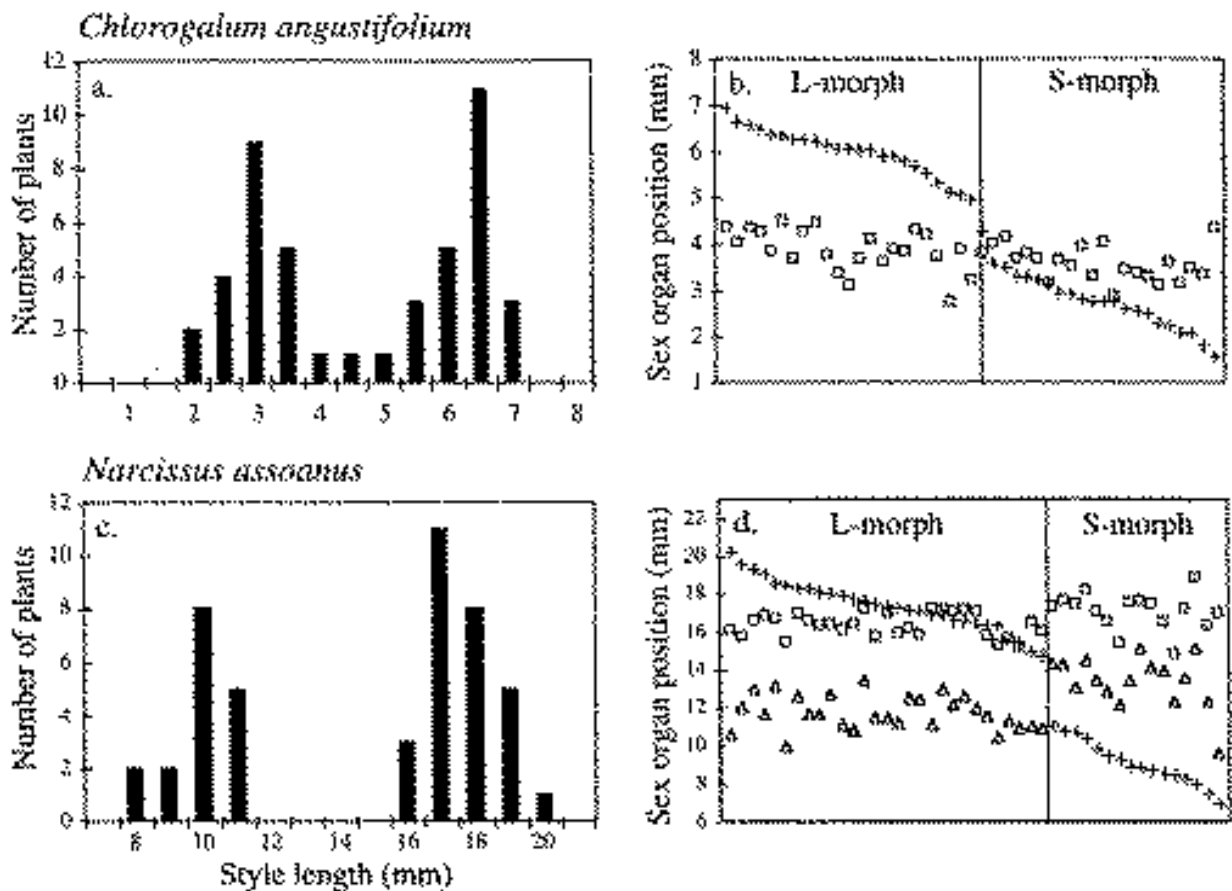


Fig. 2. Patterns of sex-organ variation in a natural population of (a, b) *Chlorogalum angustifolium* (Liliaceae) and (c, d) *Narcissus assoanus* (Amaryllidaceae). a, c: Distributions of style length. b, d: Stigma height (cross) and mean anther heights of flowers ranked by style length. L-morph and s-morph refer to long- and short-styled plants, respectively. In *N. assoanus* there are two anther levels, upper (squares) and lower (triangles). The *C. angustifolium* population was sampled from Palermo Road, Nr. Oroville, Butte Co., California and the *N. assoanus* population from St-Pierre-de-la-Fage, N.W. of Montpellier, S.W. France. Sex organ position was adjusted to account for the effect of flower length by ANCOVA.

evolution of distyly, while in others they represent stable features of clades and are clearly not evolutionarily transient states.

Examples of stigma-height dimorphism among monocotyledonous groups include *Chlorogalum* (Liliaceae) and *Narcissus* spp. (Amaryllidaceae). *Chlorogalum* (Fig. 2a, b) is composed of seven species of geophytes native to California, only *C. angustifolium* has been examined in detail (Jernstedt 1982; S.C.H. Barrett, unpubl. data). Other *Chlorogalum* spp. appear to be monomorphic for the long-styled condition and heterostyly is unknown in Liliaceae. Flowers of *C. angustifolium* are white, radially symmetric with a short tube. Anthesis commences at dusk and flowers are pollinated by moths. The single whorl of anthers is similarly positioned in the two style morphs. Inspection of floral measurements in Fig. 2a & b raises the issue of what constitutes evidence of a true stigma-height polymorphism. The population sample indicates a bimodal distribution of style length although inspection of individual values illustrates near continuous variation. While it would be possible to define the polymorphism simply by whether stigmas were above (long-styled) or below (short-styled) the anthers, we believe this is not permissible since evidence for genetic polymorphism should involve the occurrence of discrete rather than continuous patterns of trait variation.

Since samples of *C. angustifolium* flowers show a bimodal distribution of style length this species qualifies as possessing a true stigma-height dimorphism. The selective forces that maintain this polymorphism are as yet unknown but are likely associated with the pollination biology of the species.

Stigma-height dimorphisms are well established in the Mediterranean geophyte *Narcissus* occurring in at least a dozen species in three of the 10 sections of the genus (Barrett *et al.* 1996b). Data on patterns of variation in stigma and anther height for a representative species, *N. assoanus*, are illustrated in Fig. 2c & d. In contrast to *Chlorogalum*, the strongly tubular flowers of *Narcissus* possess two anther levels positioned at the top part of the floral tube. Major pollinators include long-tongued bees, sphingids and flies, depending on species. Studies of the inheritance of style-length in *N. tazetta* indicate the same genetic control found in most distylous species with the long- versus short-styled condition governed by a pair of alleles (*S*, *s*) at a single locus with short dominant to long (Dulberger 1964, and unpubl.). Geographical surveys of style-morph frequency in *N. papyraceus* from SW Spain (Barrett *et al.* 1996b) and *N. dubius* from SW France (Baker *et al.* 1999b) indicate that the long-styled morph predominates in most populations with some consisting entirely of this

morph. In *N. assoanus*, morph frequencies are often 'long'-biased in small populations but in very large populations from SW France they are always close to 1L:1S in frequency (Baker *et al.* 1999b). These patterns are quite different from distylous species and raise the question of what selective mechanisms cause the wide range of style-morph frequencies.

Unlike heterostylous plants, stilar polymorphism in *Narcissus* is associated with a self-incompatibility system that permits intramorph matings (Dulberger 1964; Barrett *et al.* 1997; Baker *et al.* 1999b). Any cross-pollination can produce seed, and style-length is uncoupled from mating type. This feature of the mating system of *Narcissus* is undoubtedly a factor associated with the wide range of morph frequencies found in natural populations and explains how monomorphic populations are able to persist. Since there is no evidence that female fertility or outcrossing rates of style morphs differ (Baker *et al.* 1999a), it seems reasonable to assume that morph ratios are governed by morph-specific differences in male fertility associated with the pollination biology of the morphs (Barrett *et al.* 1996b).

The presence of 1:1 morph ratios in large populations of *N. assoanus* indicates equivalent levels of disassortative mating since this is generally a requirement to maintain this particular equilibrium in distylous populations. This implies that despite the lack of reciprocity between lower-level anthers and stigmas of the short-styled morph, intermorph pollen transfer is roughly equivalent. However, since most *Narcissus* populations are 'long'-biased, it would appear that this symmetry in pollen dispersal occurs infrequently. Biased morph frequencies likely result because the long-styled morph has a greater share of total matings than the short-styled morph because of its superior male fertility. Studies of how pollinators influence pollen dispersal in populations of different morph structure would be valuable in testing this differential male fertility hypothesis.

Stigma-height dimorphism remains an enigmatic and difficult floral design to explain. It likely functions to promote more proficient pollen dispersal among plants in a manner similar to distyly. However, how this is achieved without well developed sex-organ reciprocity is unclear. Interestingly, no examples are known of species in which anthers are polymorphic in height but stigmas are of uniform length. This suggests that variants arising with altered stamen position are more strongly selected against than those with novel stigma heights. Variation in stigma height may have less influence on female fertility than any corresponding variation in anther height has on male fertility. If anther position is indeed under stronger stabilizing selection than stigma position we might expect it to show less phenotypic variation within plant populations. Comparative studies on patterns of variation in stigma and anther heights in animal-pollinated monocotyledonous flowers could profitably examine these ideas.

ENANTIOSTYLY

Enantiostyly is a form of floral asymmetry in which the style is deflected away from the main axis of the flower either to the left (left-styled) or the right (right-styled) side. It is often associated with other floral features including heteranthery, vibrational pollen collection by bees, a lack of nectaries, and bilaterally symmetric, horizontally oriented flowers. This association of traits suggests

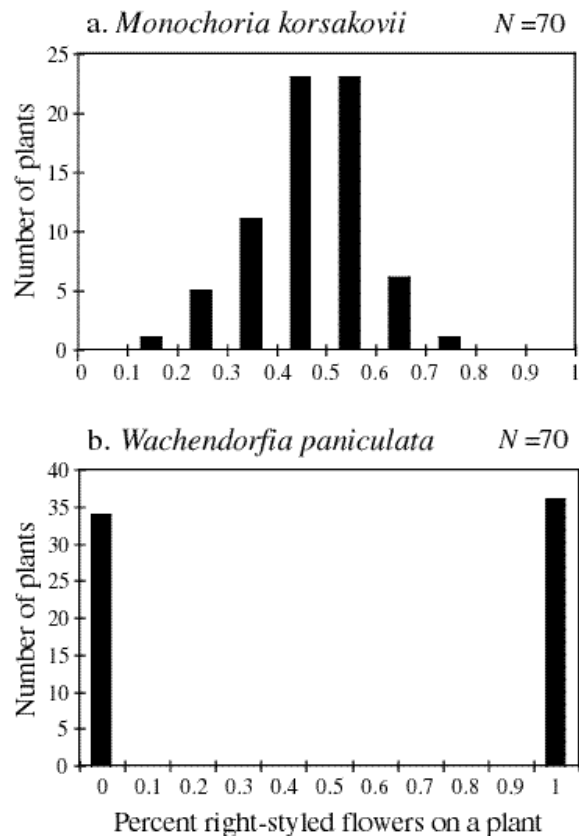


Fig. 3. The two forms of enantiostyly. a: monomorphic enantiostyly in *Monochoria korsakovii*. (Pontederiaceae). b: dimorphic enantiostyly in *Wachendorfia paniculata*. (Haemodoraceae). For each species the number of right-handed flowers were recorded for a sample of plants. Note the unimodal distribution of values for the monomorphic condition and the bimodal distribution for the dimorphic condition. *Monochoria korsakovii* plants were scored under uniform glasshouse conditions and grown from a large random bulk sample obtained from a single open-pollinated population from Japan. The sample of *W. paniculata* plants was from a natural population at Kleinmond, Cape Province, South Africa.

the presence of a pollination syndrome in which the position of the pollinator is important for reproductive success. Enantiostyly is widely distributed among angiosperm families including both dicotyledons and monocotyledons (see Graham and Barrett 1995 and references therein). The occurrence of enantiostyly among many unrelated families indicates that the polymorphism has had multiple origins and suggests that similar selection pressures associated with pollination account for its origin.

Interpretation of the adaptive significance of enantiostyly is complicated by the occurrence of two distinct forms. In by far the most common form, all plants within a population produce **both** left- and right-styled flowers. Less common is the situation where a true genetic polymorphism for style orientation exists and individual plants produce **either** left- or right-styled flowers. We refer to these two conditions as monomorphic and dimorphic enantiostyly, respectively, since in the former situation all plants in the population have the same floral phenotype, whereas in the latter two distinct phenotypes co-occur. These conditions have also been described as somatic (mixed) and genetic (fixed) enantiostyly, respectively. Fig. 3 illustrates the two enantiostylous

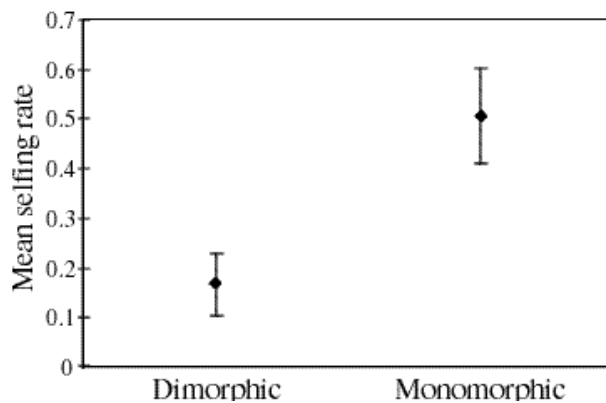


Fig. 4. Mean selfing rates and their standard errors of experimental arrays of *Monochoria korsakovii* exhibiting monomorphic versus dimorphic enantiomorphy. Three replicate arrays per treatment were run on different days. Plants originated from seed collected in a population from Japan and arrays were conducted in Etobicoke, S. Ontario. See text for further details. There was a significant difference in selfing rate between the two treatments ($t_4 = 2.93$, $P = 0.04$). Differences in sampling error associated with each estimate of s were accounted for by weighting the impact of each estimate in the t -test by the inverse of its squared standard error.

conditions in *Monochoria korsakovii* of Pontederiaceae (see also Wang *et al.* 1995) and *Wachendorfia paniculata* of Haemodora-ceae (see also Ornduff and Dulberger 1978), respectively.

Most workers have interpreted enantiostyly as a mechanical contrivance for promoting cross-fertilization and more specifically intermorph pollinations. For example, Wilson (1887) stated that insects visiting both morphs of *W. paniculata* would effect cross-fertilization by coming into contact with stigmas of one morph in the same location that they had picked up pollen from the opposite morph. If this occurs geitonogamous pollination would also be reduced because pollen picked up within a given inflorescence would be located on the opposite side of a pollinator's body to stigmas of that plant. The widespread occurrence of 1:1 morph ratios in natural populations of *W. paniculata* (Ornduff 1974; L.K. Jesson and S.C.H. Barrett, unpubl. data) supports the view that intermorph cross-pollination resulting in disassortative mating is an important component of the reproductive biology of dimorphic enantiostyly. This syndrome therefore shares features in common with both distyly and stigma-height dimorphism. However, the view that enantiostyly is a mechanism that actively promotes cross-pollination has been called into question for monomorphic enantiostyly. By having both flower types on the same plant, a pollinator could potentially visit successive flowers and cause geitonogamous self-pollination (Fenster 1995). This may cause inbreeding depression and losses in male fertility through pollen discounting (Lloyd 1992; Harder and Barrett 1995). What evidence exists that geitonogamy is indeed higher in monomorphic versus dimorphic enantiostyly and if so what is the function of monomorphic enantiostyly?

We addressed this problem by manipulating inflorescences of *M. korsakovii* and estimating the incidence of selfing in open-pollinated garden arrays using genetic markers. Plants were arranged in a grid and naturally foraging bumblebees (mostly *Bombus vagans* and *B. fervidus*) were allowed to visit plants (see Harder and Barrett 1995 for similar protocols). We contrasted two types

of arrays representing monomorphic versus dimorphic enantiostyly. To simulate the polymorphic condition we removed either left- or right-styled flowers from plants so that each plant produced only one flower type. The ratio of left- and right-styled plants in dimorphically enantiostylous arrays were kept equal. Inflorescence sizes were equalized in the two treatments by removing flowers at random from monomorphic arrays to control for the effects of inflorescence size on geitonogamy. Seeds from open-pollinated progenies were assayed at a polymorphic allozyme locus (*PGI-2*) and the average selfing rate of arrays estimated. The results we obtained (Fig. 4) were consistent with our predictions. Selfing rates were significantly lower in dimorphic arrays compared with monomorphic arrays. This undoubtedly results from differences between the arrays in levels of geitonogamy since there is no reason to expect intrafloral selfing rates to differ between the two enantiostylous conditions.

Our results appear to present a paradox. If monomorphic enantiostyly results in greater geitonogamy than dimorphic enantiostyly, why is the former condition much more common given the well-established mating costs associated with geitonogamy? Since geitonogamy is a non-adaptive outcome of adaptations for outcrossing and cannot be directly selected (Lloyd 1992) it seems highly unlikely that monomorphic enantiostyly functions to promote geitonogamy. Resolution of this paradox lies in recognising that monomorphic enantiostyly has evolved from a non-enantiostylous condition and, in the few cases where both enantiostylous conditions occur within a group, the monomorphic condition appears to be ancestral (L.K. Jesson and S.C.H. Barrett, unpubl.). With this in mind the critical question is therefore: do levels of geitonogamy differ between related non-enantiostylous and monomorphically enantiostylous species? A recent theoretical model suggests that monomorphic enantiostyly can indeed reduce levels of geitonogamy in comparison with the non-enantiostylous condition (L.K. Jesson and S.C.H. Barrett, unpubl.). This is because for a given inflorescence size the number of potential pollen transfers between flowers in somatic enantiostyly is reduced in comparison with non-enantiostyly where all flowers can potentially receive and donate pollen to one another. Empirical tests of this model are currently being conducted by comparing levels of geitonogamy in various taxa with enantiostylous and non-enantiostylous species. If geitonogamy is reduced in enantiostylous species it will support the view that these floral polymorphisms function to promote more proficient pollen dispersal by reducing geitonogamous pollen discounting.

We are aware of only a few cases of possible evolutionary transitions from monomorphic to dimorphic enantiostyly (e.g. *Heteranthera* of Pontederiaceae, L.K. Jesson and S.C.H. Barrett, unpubl.; and *Dilatris* and *Wachendorfia* of Haemodora-ceae, Ornduff 1974) despite the apparent functional benefits that this polymorphism possesses. What constraints might therefore limit the spread of dimorphic enantiostyly? It is possible that there is little heritable variation for the amount of style orientation within a plant and hence selection for entirely left- or right-styled morphs is difficult. Attempts to select for the direction of asymmetry in animal species have proven difficult (e.g. Maynard-Smith and Sondhi 1960) and the same principle may be at work here because of the absence of genes providing the appropriate

positional information (Coen and Meyerowitz 1991). For dimorphic enantiostyly to establish, genes would be required to distinguish both dorsal from ventral and left from right sides of the flower. There may be strong genetic and developmental constraints on assembling this genetic architecture, particularly in radially symmetric flowers where organs of the same whorl are unlikely to have the appropriate positional information. Another explanation of the rarity of transitions from monomorphic to dimorphic enantiostyly concerns the contrasting mating strategies of the two systems. In monomorphic populations all individuals are proficient at mating with all others, whereas in dimorphic populations only half of the individuals in a population are potential mates. If this difference affects overall fitness it could influence whether entirely dimorphic populations can establish.

SEXUAL SYSTEMS AND GENDER

The mating strategies discussed so far all involve plants with hermaphrodite flowers; we now examine populations in which unisexual flowers (dicliny) occur. Sexual systems involving different combinations of unisexual and/or hermaphrodite flowers are widespread among monocotyledonous families. The most common conditions are monoecy, andromonoecy, gynodioecy and dioecy. Many sexually dimorphic taxa have abiotic pollination systems or if biotically pollinated are visited by unspecialized bees and flies (an exception is the vertebrate-pollinated *Freycinetia* of the Pandanaceae: Cox 1982). Sexual dimorphism is well established in wind-pollinated Poaceae and Cyperaceae, among water-pollinated seagrasses and among animal-pollinated taxa with simple radially symmetric flowers in Liliaceae and allies.

The adaptive benefits of deploying female and male gametes in various structural and temporal combinations at the flower, inflorescence, plant, and population level are often difficult to determine. Theoretical models attempt to explain the evolution of contrasting gender strategies based on several key parameters of which outbreeding advantage, the optimal allocation of resources to female and male function and the genetic control of the sex types are most important (Charlesworth and Charlesworth 1978; Seger and Eckhart 1996; Geber *et al.* 1999). The most common evolutionary modification from the predominantly cosexual condition of angiosperms is the evolution of dioecy. Two major pathways to sexual dimorphism are generally recognized, via monoecy and gynodioecy (Bawa 1980; Charlesworth 1999). We next consider examples of these pathways and discuss how ecological factors play an important role in modifying gender patterns.

Gender variation and dioecy

Sagittaria (Alismataceae) is composed of approximately 20 mostly New World species of freshwater aquatics with simple, predominantly unisexual, white trimerous flowers visited by pollen-collecting bees and flies. Three basic sexual systems are represented in the genus. The vast majority of species are monoecious with andromonoecy and dioecy more restricted in distribution. A fourth sexual system 'subandrodioecy', with monoecious and male plants with limited female expression, has recently been reported in *S. lancifolia* (Muenchow 1998). The distribution of sexual systems in *Sagittaria* suggest that monoecy is the ancestral

condition in the genus and that dioecism is derived. Confirmation of this hypothesis awaits explicit phylogenetic analysis.

Ecological studies are providing clues about the selective forces maintaining the diverse gender strategies in *Sagittaria*. There is evidence for an association between sexual system, ecology and life history among *Sagittaria* spp. The only annual species in the genus, *S. guyanensis* and *S. calycina*, are andromonoecious. Flowers in basal whorls of the inflorescence are hermaphroditic producing a ring of functional stamens surrounding the carpellar dome; numerous male flowers occur in more terminal positions of the inflorescence. Since these species are colonizing weeds of rice fields it seems likely that bisexual flowers have been selected to provide some reproductive assurance. Among perennial species, bisexual flowers are less common but can be observed on male plants of dioecious species owing to sex inconstancy in this morph (see below).

Sagittaria latifolia is of particular interest since this species has both monoecious and dioecious populations (Wooten 1971). Our recent studies in S. Ontario, Canada, indicate that the two sexual systems differ in ecology and life-history (S.C.H. Barrett, unpubl.). Monoecious populations occur primarily in disturbed environments such as roadside ditches, shorelines and ephemeral ponds, whereas dioecious populations are restricted to large river systems and permanent marshes. Plants in dioecious populations tend to be larger in size and form more extensive clones than those in monoecious populations. Several hypotheses may help explain this pattern. Monoecious populations may be favoured in disturbed aquatic environments because the possession of both sex functions by individual plants provides reproductive assurance not available to unisexual plants from dioecious populations. This hypothesis assumes that selfing occurs in colonists via between-inflorescence geitonogamy since there is little overlap in sex function within inflorescences. Alternatively, monoecious populations may be prevented from invading the habitats of dioecious populations because these more stable and competitive environments demand large plant size and prolific clonal growth. Extensive clone size would increase opportunities for geitonogamous selfing since plants are self-compatible and have no apparent mechanisms to synchronize sex function among inflorescences of a clone. In these environments self progeny of monoecious colonists would unlikely succeed against outcrossed progeny of established dioecious clones due to inbreeding depression. Reciprocal transplant experiments and marker-gene studies of selfing rates are required to test these hypotheses.

The monoecious aquatic *Hydrocharis morsus-ranae* (Hydrocharitaceae) has simple, white, trimerous flowers similar to *Sagittaria* and is also pollinated by generalist insects. This species has an interesting reproductive strategy that may aid in reducing levels of geitonogamous selfing that can be a problem for monoecious species with extensive clonal growth. Clones continually fragment due to weak stolon connections and ramets are readily dispersed by water currents in a manner similar to the notorious aquatic weed *Eichhornia crassipes* (Pontederiaceae). This mechanism provides opportunities for the mixing of distinct genotypes thus increasing opportunities for outcrossing. Because floating ramets that become detached from clones are unisexual, workers have often misinterpreted the sexual system of this species and

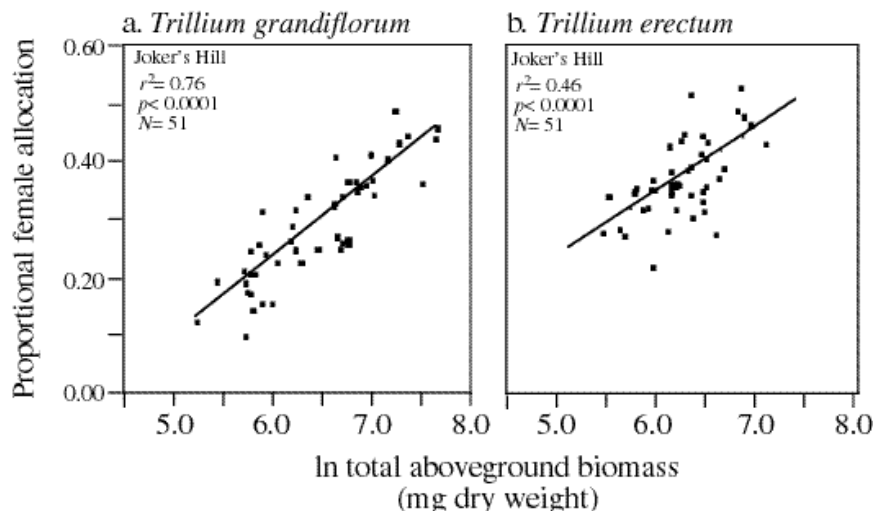


Fig. 5. Size-dependent gender modification in the simultaneous hermaphrodite *Trillium*. (Trilliaceae). Relation between sex allocation (pistil biomass/pistil biomass+anther biomass) and size (natural log of total above-ground biomass) in populations at Joker's Hill, S. Ontario. a: *Trillium grandiflorum*, and b: *T. erectum*. Lines are based on least-squares regression analysis. For further details see Wright and Barrett (1999).

reported it as dioecious rather than monoecious (e.g. Scribailo *et al.* 1984). Surveys of floral sex ratios in introduced populations of this species in S. Ontario have never detected unisexual populations (Scribailo and Poslusny 1984; S.C.H. Barrett, unpubl.). The absence of unisexual populations would be highly unlikely in a truly dioecious species with rampant clonal growth and highly dispersed floating ramets. Unisexual populations are widely reported in the introduced range of several other clonal dioecious aquatics such as *Elodea canadensis* (Sculthorpe 1967) and *Myriophyllum brasiliense* (Baker 1972). The consequences of clonal dispersal for mating patterns and genetic diversity in aquatic plants has rarely been considered.

While most shifts to dioecy probably occur from a monoecious ancestral state (Renner and Ricklefs 1995), another common transition to sexual dimorphism involves the gynodioecious pathway. Here females invade cosexual populations through the spread of male-sterility genes. Once females are established selection favours increased maleness in cosexual individuals through the spread of female-sterility genes. Subdioecious populations composed of three sex phenotypes with female, male and hermaphrodite sex function commonly occur as a transitional stage prior to the establishment of dioecy or form stable end points of this evolutionary pathway (Lloyd 1976; Charlesworth 1999).

Patterns of gender variation in the geophyte *Wurmbea* (Colchicaceae) indicate that sexual dimorphism has originated via the gynodioecious evolutionary pathway (Barrett 1992b). The African species of this genus are uniformly cosexual whereas in Australia dioecy is well established. In *W. dioica* a wide spectrum of gender strategies are evident from cosexual populations with hermaphrodite flowers, through gynodioecious and subdioecious populations to stable dioecy. As with *Sagittaria latifolia*, there is evidence that shifts in sexual system in *W. dioica* are associated with ecological factors. In this case arid conditions may play a role in promoting the evolution of sexual dimorphism (A.L. Case and S.C.H. Barrett, unpubl.). This might occur if cosexual plants are unable to maintain both sex functions in habitats in

which resources are limited, or if inbreeding depression is magnified under stress, favouring the spread of unisexuals. Associations between stress conditions and sexual dimorphism have been noted in several other taxa (reviewed in Geber *et al.* 1999).

Size-Dependent Gender Modification

Gender strategies of plants are determined by the relative contribution to fitness from maternal and paternal investment. An important observation is that as plants increase in size they often alter their gender in a predictable manner. Theoretical models based on sex allocation theory predict size-dependent gender modification under various ecological circumstances (Lloyd and Bawa 1984; Klinkhamer *et al.* 1997). Most models indicate that in animal-pollinated plants relative allocation to female versus male function should increase with size. A variety of factors may be involved including the differential reproductive costs of female versus male reproduction, local mate and resource competition, and reduced fitness returns owing to size-dependent geitonogamous pollination. Studies of several monocotyledonous taxa support this prediction; below we briefly review the empirical evidence.

The best known example of size-dependent gender modification in plants involves the woodland herb *Arisaema* (Araceae). Species in this genus exhibit sequential hermaphroditism (diphasy) in which small plants are male and large plants are usually female (Policansky 1981; Bierzychudek 1984; Lovett Doust and Cavers 1982). This sexual system has been misinterpreted as dioecy since in any one season plants are predominantly unisexual. Diphasy is very rare in flowering plants raising the question of whether size-dependent gender modification also occurs in cosexual species with simultaneous hermaphroditism. This issue is of general significance since this condition is the most common sexual system in angiosperms, including most monocotyledons.

Recent studies of the simultaneous hermaphrodites *Trillium erectum* and *T. grandiflorum* (Trilliaceae) have revealed strong evidence for size-dependent gender modification in these long-lived woodland herbs (Wright and Barrett 1999). In both species, there is a strong relation between size and gender; larger plants

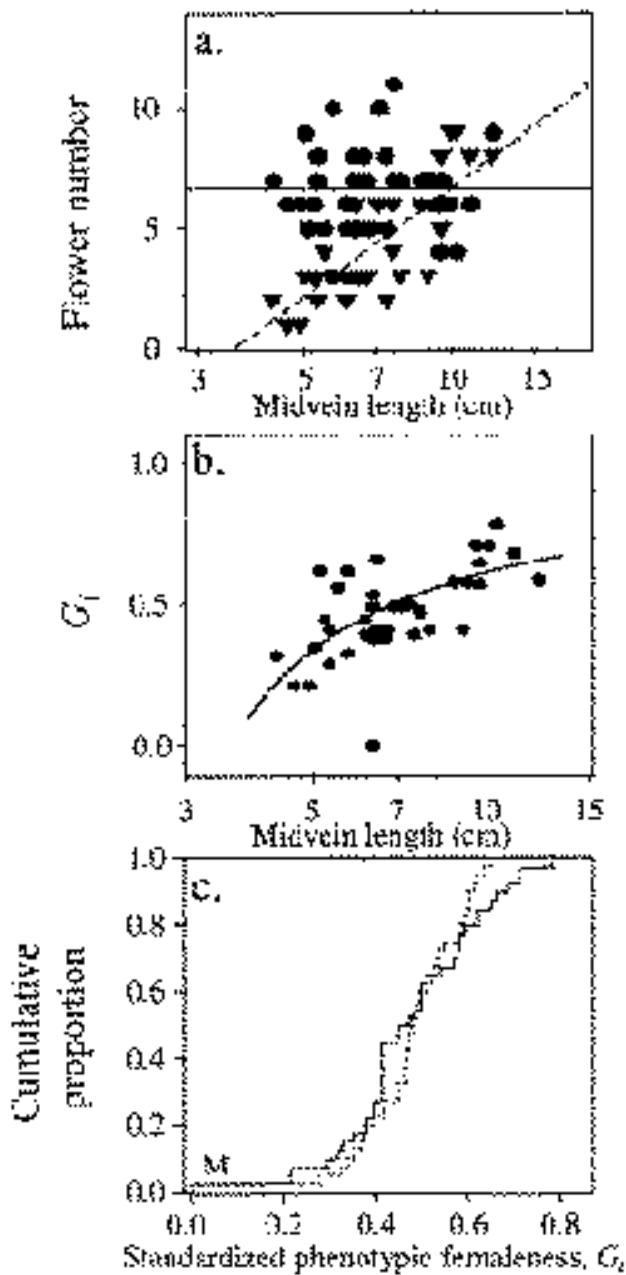


Fig. 6. Size-dependent gender modification in monoecious *Sagittaria latifolia* (Alismataceae). Data were collected from a sample of plants from a population at Carnarvon, S. Ontario. a: Observed production of female (triangles) and male (circles) flowers for cosexual plants of different sizes, with predicted flower numbers based on regression analysis indicated by dashed and solid lines, respectively. b: The observed (circles) and predicted (solid line) relations between standardized phenotypic femaleness G_f and leaf mid-vein length. Predicted values were based on the regression relations in a. See Lloyd and Bawa (1984) for details of the calculation of phenotypic gender. c: The observed (solid line) and predicted (dashed line) standardized phenotypic femaleness (G_f) of plants in the Carnarvon population. Predicted values were obtained from the regression relations of female and male flower production to leaf mid-vein length. There was no significant difference between the two cumulative frequency distributions following a two-sample Kolmogorov-Smirnov test ($D = 0.225$, $P > 0.05$). For further details see Sarkissian *et al.* 1999.

allocate proportionately more biomass to female reproduction (Fig. 5), and produce fewer pollen grains relative to ovules than smaller plants. Since *Trillium* plants can be aged it is possible to examine the relations between age, size and gender. Variation in gender is better explained by size than age, although age and size are correlated. While the relation between size and gender is similar between the two species, *T. erectum* allocates proportionately more to female reproduction independent of size (ANCOVA results in Wright and Barrett 1999; Fig. 5b). This finding is consistent with theoretical models and information on the mating systems of the two species. *Trillium grandiflorum* is predominantly outcrossed whereas *T. erectum* exhibits a mixed mating system (Broyles *et al.* 1997). Selfing is expected to select for greater relative investment in female function because of reduced levels of pollen competition between related plants and thus enhanced local mate competition (Charlesworth and Charlesworth 1981; Charnov 1982).

Size-dependent gender modification is also evident in monoecious populations of *Sagittaria latifolia* (Sarkissian *et al.* 1999). In four of six populations examined, leaf mid-vein length, a correlate of ramet size, was positively correlated with the number of female flowers on inflorescences but not with the number of male flowers (Fig. 6a). Large ramets displayed more female-biased floral sex ratios than smaller ramets. Plants below a certain size threshold were often phenotypically male. Presumably these plants when larger would be capable of producing female flowers (but see Muenchow 1998 for an alternative perspective). Using a model based on the relation between leaf size and floral sex ratio these authors were able for the first time to predict the phenotypic gender of plants in a natural population (Fig. 6b,c; see Sarkissian *et al.* 1999 for further details).

In wind-pollinated, monoecious Poaceae, there is evidence for the opposite pattern of size-dependent gender modification to that found in animal-pollinated species. Larger plants produce proportionately more male flowers than smaller plants (Bickel and Freeman 1993). This reversal of pattern with pollination mode may arise because of greater fitness returns through male function in taller plants because of more effective pollen dispersal. It would be interesting to examine floral sex ratios in the abiotically pollinated, monoecious sea grasses to determine whether size-dependent gender modification occurs and if so what pattern is evident.

Demographic studies of *Wurmbea dioica* in the Australian Capital Territory, Australia, have also demonstrated size-dependent effects on gender (Barrett *et al.* 1999). In groups such as *Wurmbea*, in which sexual dimorphism has evolved, male plants frequently exhibit sex inconstancy whereas female plants most often show canalized sex expression (reviewed in Geber *et al.* 1999). In *W. dioica*, sex inconstancy in males is, in part, governed by environmental factors. Large male plants frequently produce some hermaphrodite flowers at basal positions within inflorescences whereas female plants, irrespective of size, never do. Hence, in this species, polymorphism for size-dependent gender modification is evident. Differences in sex lability between females and males may have a functional basis. The production of ovules in

male plants is unlikely to reduce total fitness since this is largely achieved through male function. In contrast, the main reproductive pathway in female plants may be more vulnerable to interference from the opposite sex function since even small amounts of pollen produced in female plants could result in selfing and inbreeding depression (Charlesworth and Charlesworth 1978). According to this hypothesis sex inconstancy will be more strongly selected against in female than male plants, a pattern that appears to be in accord with empirical observations.

CONCLUSION

This brief review illustrates that among the monocotyledons a diverse array of mating strategies have evolved to promote reproductive success. Appreciation that reproductive success in flowering plants involves fitness gain through both pollen and ovules can lead to new insights into the evolution and function of floral traits. While considerable diversification in floral characters associated with pollination biology is evident among monocotyledonous families, it is clear from our studies that significant variation also occurs between related species, and at the intraspecific level. One of the major challenges in evolutionary biology is to link microevolutionary processes to macroevolutionary patterns and hence this floral variation at different levels in the genealogical hierarchy of the monocotyledons provides excellent opportunities to achieve this goal. Integrative studies on the phylogeny and ecology of reproductive traits in monocotyledonous taxa will not only inform reproductive biology but also systematics and evolutionary biology.

ACKNOWLEDGEMENTS

We thank Juan Arroyo, Andrea Case, Deborah Charlesworth, Bill Cole, Lawrence Harder, Carlos Herrera, Charo Hildago, Taline Sarkissian, John Thompson and Stephen Wright for valuable discussion and permission to cite unpublished manuscripts. Our work on mating strategies has been funded by a research grant from the Natural Sciences and Engineering Research Council of Canada to SCHB. Angela Baker and Linley Jesson were supported by student fellowships from N.S.E.R.C., the Ontario Government, and the Connaught Foundation of the University of Toronto.

REFERENCES

- Baker, A. M., Thompson, J. D., and Barrett, S. C. H. (1999a). Evolution and maintenance of stigma-height dimorphism in *Narcissus*: II. Fitness comparisons between style morphs. (submitted).
- Baker, A. M., Thompson, J. D., and Barrett, S. C. H. (1999b). Evolution and maintenance of stigma-height dimorphism in *Narcissus*: I. Floral variation and style-morph ratios. (submitted).
- Baker, H. G. (1972). Migration of weeds. In 'Taxonomy, Phytogeography and Evolution'. (Ed. D. H. Valentine.) pp. 327–347. (Academic Press: London)
- Barrett, S. C. H. (Ed.) (1992a). 'Evolution and Function of Heterostyly.' (Springer Verlag: Berlin).
- Barrett, S. C. H. (1992b). Gender variation in *Wurmbea dioica* (Liliaceae) and the evolution of dioecy. *Journal of Evolutionary Biology* **5**, 423–444.
- Barrett, S.C.H. (1985). Variation in expression of trimorphic incompatibility in *Pontederia cordata* L. (Pontederiaceae). *Theoretical and Applied Genetics* **70**, 355–362.
- Barrett, S. C. H., Case, A. L., and Peters, G. B. (1999). Gender modification and resource allocation in subdioecious *Wurmbea dioica* (Colchicaceae). *Journal of Ecology* **87**, 123–137.
- Barrett, S. C. H., Cole, W. W., Arroyo, J., Cruzan, M. B., and Lloyd, D. G. (1997). Sexual polymorphisms in *Narcissus triandrus* (Amaryllidaceae): Is this species heterostylous? *Heredity* **78**, 135–145.
- Barrett, S. C. H., Cole, W. W., and Harder, L. D. (1998). Experimental studies on the effects of floral design and display on plant mating. In 'Reproductive Biology in Systematics, Conservation and Economic Botany'. (Eds S. J. Owens and P. J. Rudall.) pp. 1–13. (Royal Botanic Gardens: Kew.)
- Barrett, S. C. H., and Eckert, C. (1990). Variation and evolution of mating systems in seed plants. In 'Biological Approaches and Evolutionary Trends in Plants'. (Ed. S. Kawano.) pp. 229–254. (Academic Press: Tokyo, Japan.)
- Barrett, S. C. H., and Harder, L. D. (1996). Ecology and evolution of plant mating. *Trends in Ecology and Evolution* **11**, 73–79.
- Barrett, S. C. H., Harder, L. D., and Worley, A. C. (1996a). The comparative biology of pollination and mating in flowering plants. *Philosophical Transactions of the Royal Society of London Series B* **351**, 1271–1280.
- Barrett, S. C. H., Kohn, J. R., and Cruzan, M. B. (1993). Experimental studies of mating-system evolution: The marriage of marker genes and floral biology. In 'Ecology and Evolution of Plant Reproduction: New Approaches'. (Ed. R. Wyatt.) pp. 192–230. (Chapman & Hall: London.)
- Barrett, S. C. H., Lloyd, D. G., and Arroyo, J. (1996b). Styler polymorphisms and the evolution of heterostyly in *Narcissus* (Amaryllidaceae). In 'Floral Biology: Studies on Floral Evolution in Animal-Pollinated Plants'. (Eds D. G. Lloyd and S. C. H. Barrett.) pp. 339–376. (Chapman & Hall: New York.)
- Barrett, S. C. H., Morgan, M. T., and Husband, B. C. (1989). The dissolution of a complex genetic polymorphism: The evolution of self-fertilization in tristylous *Eichhornia paniculata* (Pontederiaceae). *Evolution* **43**, 1398–1416.
- Bawa, K. S. (1980). Evolution of dioecy in flowering plants. *Annual Review of Ecology and Systematics* **11**, 15–39.
- Bickel, A. M., and Freeman, D. C. (1993). Effects of pollen vector and plant geometry on floral sex ratio in monoecious plants. *American Midland Naturalist* **130**, 239–247.
- Bierzuchudek, P. (1984). Determinants of gender in jack-in-the-pulpit: The influence of plant size and reproductive history. *Oecologia* **65**, 14–18.
- Brown, A. H. D., Burdon, J. J., and Jarosz, A. M. (1990). Isozyme analysis of plant mating systems. In 'Isozymes in Plant Biology'. (Eds D. E. Soltis and P. S. Soltis.) pp. 73–86. (Dioscorides Press: Portland, OR.)
- Brown, A. H. D., Zohary, D., and Nevo, E. (1978). Outcrossing rates and heterozygosity in natural populations of *Hordeum spontaneum* Koch in Israel. *Heredity* **41**, 49–62.
- Broyles, S. B., Sherman-Broyles, S. L., and Rogatl, P. (1997). Evidence for outcrossing in *Trillium erectum* and *Trillium grandiflorum* (Liliaceae). *Journal of Heredity* **88**, 325–329.
- Charlesworth, B., and Charlesworth, D. (1978). A model for the evolution of dioecy and gynodioecy. *American Naturalist* **112**, 975–997.
- Charlesworth, D. (1999). Theories on the evolution of dioecy. In 'The Evolution of Gender and Sexual Dimorphism in Flowering Plants'. (Eds M. A. Geber, T. E. Dawson and L. F. Delph.) pp. 33–60. (Springer-Verlag: Berlin.)

- Charlesworth, D., and Charlesworth, B. (1979). A model for the evolution of distyly. *American Naturalist* **114**, 467–498.
- Charlesworth, D., and Charlesworth, B. (1981). Allocation of resources to male and female functions in hermaphrodites. *Biological Journal of the Linnean Society* **15**, 57–74.
- Charlesworth, D., and Charlesworth, B. (1987). Inbreeding depression and its evolutionary consequences. *Annual Review of Ecology and Systematics* **18**, 237–268.
- Charnov, E. L. (1982). 'The Theory of Sex Allocation.' (Princeton University Press: Princeton, NJ.)
- Coen, E. S., and Meyerowitz, E. M. (1991). The war of the whorls: Genetic interactions controlling flower development. *Nature* **353**, 31–37.
- Cox, P. A. (1982). Vertebrate pollination and the maintenance of dioecism in *Freyinetia*. *American Naturalist* **120**, 65–80.
- Dahlgren, R. M. T., Clifford, H. T., and Yeo, P. F. (1985). 'The Families of the Monocotyledons: Structure, Evolution and Taxonomy.' (Springer-Verlag: Berlin.)
- Darwin, C. (1877). 'The Different Forms of Flowers on Plants of the Same Species.' (John Murray: London)
- de Nettancourt, D. (1997). Incompatibility in Angiosperms. *Sexual Plant Reproduction* **10**, 185–199.
- Donoghue, M. J., and Doyle, J. A. (1989). Phylogenetic analysis of angiosperms and the relationships of Hamamelidae. In 'Evolution, Systematics, and Fossil History of the Hamamelidae'. (Eds P. Crane and S. Blackmore.) pp. 17–45. (Clarendon Press: Oxford.)
- Dulberger, R. (1964). Flower dimorphism and self-incompatibility in *Narcissus tazetta* L. *Evolution* **18**, 361–363.
- Endress, P. K. (1995). Major evolutionary traits of monocot flowers. In 'Monocotyledons: Systematics and Evolution'. (Eds P. J. Rudall, P. J. Cribb, D. F. Cutler and C. J. Humphries.) pp. 43–79. (Royal Botanic Gardens: Kew.)
- Fenster, C. B. (1995). Mirror image flowers and their effect on the outcrossing rate in *Chamaecrista fasciculata* (Leguminosae). *American Journal of Botany* **82**, 46–50.
- Geber, M. A., Dawson, T. E., and Delph L. F. (Eds) (1999). 'The Evolution of Gender and Sexual Dimorphism in Flowering Plants.' (Springer-Verlag: Berlin.)
- Goldblatt, P., and Bernhardt, P. (1990). Pollination biology of *Nivenia* (Iridaceae) and the presence of heterostylous self-compatibility. *Israel Journal of Botany* **39**, 93–111.
- Graham, S. W., and Barrett, S. C. H. (1995). Phylogenetic systematics of Pontederiales: Implications for breeding-system evolution. In 'Monocotyledons: Systematics and Evolution'. (Eds P. J. Rudall, P. J. Cribb, D. F. Cutler and C. J. Humphries.) pp. 415–451. (Royal Botanic Gardens: Kew.)
- Gregorius, H. R., Ziehe, M., and Ross, M. D. (1987). Selection caused by self-fertilization. 1. Four measures of self-fertilization and their effects on fitness. *Theoretical Population Biology* **31**, 91–115.
- Harder, L. D. (this volume). Pollen dispersal and the floral diversity of monocotyledons.
- Harder, L. D., and Barrett, S. C. H. (1993). Pollen removal from tristylous *Pontederia cordata*: Effects of anther position and pollinator specialization. *Ecology* **74**, 1059–1072.
- Harder, L. D., and Barrett, S. C. H. (1995). Mating cost of large floral displays in hermaphrodite plants. *Nature* **373**, 512–515.
- Harder, L. D., and Barrett, S. C. H. (1996). Pollen dispersal and mating patterns in animal-pollinated plants. In 'Floral Biology: Studies on Floral Evolution in Animal-Pollinated Plants'. (Eds D. G. Lloyd and S. C. H. Barrett.) pp. 140–190. (Chapman & Hall: New York.)
- Herendeen, P. S., and Crane, P. K. (1995). The fossil history of the monocotyledons. In 'Monocotyledons: Systematics and Evolution'. (Eds P. J. Rudall, P. J. Cribb, D. F. Cutler and C. J. Humphries.) pp. 1–21. (Royal Botanic Gardens: Kew.)
- Holsinger, K. E. (1996). Pollination biology and the evolution of mating systems in flowering plants. In 'Evolutionary Biology'. (Eds M. K. Hecht, W. C. Steere and B. Wallace.) pp. 107–149. (Plenum Press: New York.)
- Horovitz, A., and Harding, J. (1972). The concept of male outcrossing in hermaphrodite higher plants. *Heredity* **29**, 223–236.
- Jernstedt, J. A. (1982). Floral variation in *Chlorogalum angustifolium* (Liliaceae). *Madroño* **29**, 87–94.
- Klinkhamer, P. G., de Jong, T. J., and Metz, H. (1997). Sex and size in cosexual plants. *Trends in Ecology and Evolution* **12**, 160–265.
- Lande, R., and Schemske, D. W. (1985). The evolution of self-fertilization and inbreeding depression in plants. I. Genetic models. *Evolution* **39**, 24–40.
- Lloyd, D. G. (1976). The transmission of genes via pollen and ovules in gynodioecious angiosperms. *Theoretical Population Biology* **9**, 199–216.
- Lloyd, D. G. (1979a). Parental strategies of angiosperms. *New Zealand Journal of Botany* **17**, 595–606.
- Lloyd, D. G. (1979b). Some reproductive factors affecting self-fertilization in angiosperms. *American Naturalist* **113**, 67–79.
- Lloyd, D. G. (1992). Self- and cross-fertilization in plants. II. The selection of self-fertilization. *International Journal of Plant Science* **153**, 370–380.
- Lloyd, D. G., and Bawa, K. S. (1984). Modifications of the gender of seed plants in varying conditions. *Evolutionary Biology* **17**, 255–388.
- Lloyd, D. G., and Webb, C. J. (1986). The avoidance of interference between the presentation of pollen and stigmas in angiosperms. I. Dichogamy. *New Zealand Journal of Botany* **24**, 135–162.
- Lloyd, D. G., and Webb, C. J. (1992a). The evolution of heterostyly. In 'Evolution and Function of Heterostyly'. (Ed. S. C. H. Barrett.) pp. 151–178. (Springer-Verlag: Berlin.)
- Lloyd, D. G., and Webb, C. J. (1992b). The selection of heterostyly. In 'Evolution and Function of Heterostyly'. (Ed. S. C. H. Barrett.) pp. 179–208. (Springer-Verlag: Berlin.)
- Lovett Doust, J., and Cavers, P. B. (1982). Sex and gender dynamics in jack-in-the-pulpit, *Arisaema triphyllum* (Araceae). *Ecology* **63**, 797–808.
- Maynard-Smith, J., and Sondhi, K. C. (1960). The genetics of a pattern. *Genetics* **45**, 1039–1049.
- Morgan, M. T., and Schoen, D. J. (1997). The role of theory in an emerging new plant reproductive biology. *Trends in Ecology and Evolution* **12**, 231–234.
- Muenchow, G. E. (1998). Subandrodioecy and male fitness in *Sagittaria lancifolia* subsp. *lancifolia* (Alismataceae). *American Journal of Botany* **85**, 513–520.
- Ornduff, R. (1974). Heterostyly in South African flowering plants: A conspectus. *Journal of South African Botany* **40**, 169–187.
- Ornduff, R., and Dulberger, R. (1978). Floral enantiomorphy and the reproductive system of *Wachendorfia paniculata* (Haemodoraceae). *New Phytologist* **80**, 427–434.
- Policansky, D. (1981). Sex choice and the size advantage model in jack-in-the-pulpit (*Arisaema triphyllum*). *Proceedings of the National Academy of Sciences, USA* **78**, 1306–1308.
- Renner, S. S., and Ricklefs, R. E. (1995). Dioecy and its correlates in flowering plants. *American Journal of Botany* **82**, 596–606.
- Richards, A. J. (1997). 'Plant Breeding Systems,' 2nd edn. (Chapman & Hall: London.)
- Sage, T. L., Pontieri, V., and Christopher, R. (this volume). Incompatibility and mate recognition in monocotyledons.
- Sarkissian, T. S., Barrett, S. C. H., and Harder, L. D. (1999). Gender variation in *Sagittaria latifolia* (Alismataceae): is size all that matters? (submitted).

- Schemske, D. W., and Lande, R. (1985). The evolution of self-fertilization and inbreeding depression in plants. II. Empirical observations. *Evolution* **39**, 41–52.
- Scribailo, R. W., Carey, K., and Poluszny, U. (1984). Isozyme variation and the reproductive biology of *Hydrocharis morsus-ranae* L. (Hydrocharitaceae). *Botanical Journal of the Linnean Society* **89**, 305–312.
- Scribailo, R. W., and Posluszny, U. (1984). The reproductive biology of *Hydrocharis morsus-ranae*. I. Floral biology. *Canadian Journal of Botany* **62**, 2779–2787.
- Sculthorpe, C. D. (1967). 'The Biology of Aquatic Vascular Plants.' (Edward Arnold: London)
- Seeger, J., and Eckhart, V. M. (1996). Evolution of sexual systems and sex allocation in plants when growth and reproduction overlap. *Proceedings of the Royal Society of London, Series B* **263**, 833–841.
- Stebbins, G. L. (1974). 'Flowering Plants: Evolution Above the Species Level.' (Belknap Press: Cambridge, MA.)
- Uyenoyama, M. K., Holsinger, K. E., and Waller, D. (1993). Ecological and genetic factors directing the evolution of self fertilization. *Oxford Surveys in Evolutionary Biology* **9**, 327–382.
- Wang, G., Miura, R., and Kusanagi, T. (1995). The enantiostyly and the pollination biology of *Monochoria korsakovii* (Pontederiaceae). *Acta Phytotaxa Geobotanica* **46**, 55–65.
- Waycott, M. (this volume). Mating systems and population genetics of marine angiosperms (seagrasses).
- Waycott, M., and Sampson, J. F. (1997). The mating system of a hydrophilous angiosperm *Posidonia australis* (Posidoniaceae). *American Journal of Botany* **84**, 621–625.
- Willson, M. F., and Burley, N. (1983). 'Mate Choice in Plants: Tactics, Mechanisms, and Consequences.' (Princeton University Press: Princeton NJ.)
- Wilson, J. (1887). On the dimorphism of flowers of *Wachendorfia paniculata*. *Transactions and Proceedings of the Botanical Society of Edinburgh* **17**, 73–77.
- Wooten, J. W. (1971). The monoecious and dioecious conditions in *Sagittaria latifolia* L. (Alismataceae). *Evolution* **25**, 549–553.
- Wright, S. I., and Barrett, S. C. H. (1998). Size-dependent gender modification in a hermaphroditic perennial herb. *Proceeding of the Royal Society of London, Series B* **266**, 225–232.