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Floral sex ratios and gynomonoecy in Aster (Asteraceae)

Robert I. Bertin
College of the Holy Cross, rbertin@holycross.edu

Maureen A. Kerwin
College of the Holy Cross

Floral sex ratios and gynomonoecy in *Aster* (Asteraceae)[1]

Robert I. Bertin[2,4] and Maureen A. Kerwin[2,3]

[2]Biology Department, Holy Cross College, Worcester, Massachusetts 01610; and
[3]Harvard University Herbaria, 22 Divinity Avenue, Cambridge, Massachusetts 02138

Gynomonoecy is the sexual system in which female and bisexual flowers occur on the same plant. This system has received little attention despite the considerable work on other plant sexual systems in the past few decades. Our study examines one hypothesized advantage of having two flower types on a plant, namely that this arrangement permits flexibility in allocation of resources to male and female reproductive functions. We examined 16 species of *Aster* (Asteraceae), a genus of gynomonoecious, perennial herbs. Plants in this genus produce heads consisting of a whorl of female flowers around a cluster of bisexual flowers. Among field-grown plants we found no evidence that plant size, date, position of heads, rainfall, or shade influenced the proportion of female flowers. A series of greenhouse experiments likewise revealed no large or consistent effects of light, nutrients, or position of heads on the proportion of ray flowers. While floral ratios proved very stable in the face of environmental and physiological variables, they exhibited significant variation among plants and among sibships in most species. We conclude that the presence of two flower types in gynomonoecious asters is not advantageous in permitting flexibility in allocation of resources to male and female functions. We believe that the advantage of the female flowers in aster heads lies either in reducing pollen–pistil interference or in attracting pollinators.

Key words: *Aster*; capitula; disk flowers; gynomonoecy; ray flowers; sex allocation; sexual systems.

Considerable attention has been devoted to the study of plant sexual systems over the past two decades, as evidenced by the reviews of Willson (1983), Richards (1986), and others. Little progress has been made, however, in understanding gynomonoecy, the sexual system in which female and bisexual flowers co-occur on individual plants. Several reviews have noted the lack even of basic data on patterns of variability in the relative frequency of the two flower types in gynomonoecious species (Willson, 1983; Bertin, 1989), information that is essential in evaluating the function of this sexual system.

Gynomonoecy was estimated by Yampolsky and Yampolsky (1922) to occur in ~2.8% of flowering plants, being especially abundant in the Asteraceae. Gynomonoecious members of this family typically have small flowers aggregated into dense heads, or capitula. Within a head, bisexual disk flowers are surrounded by female ray flowers, each of which bears a single petal. The entire head resembles a single large flower (Leppik, 1977).

One possible explanation for the occurrence of gynomonoecy is that the presence of the two flower types permits flexibility in allocation of resources to male and female reproductive functions in response to variation in environmental factors, or such internal factors as plant age, size, or physiological status. Such explanations have been given considerable attention for two other diclinous sexual systems, i.e. those in which flowers of two sexual types occur on the same plant: monoecy (male and female flowers) and andromonoecy (male and bisexual flowers) (Charnov and Bull, 1977; Willson, 1983). The same arguments have received only passing attention for gynomonoecious species (Willson, 1983).

If gynomonoecy is advantageous in permitting flexible resource allocation, variability in the ratios of flower types (hereafter floral ratios) might occur in several circumstances.

First, differences in floral ratios might occur in plants exposed to different environmental conditions, involving light, nutrients, or water. The common expectation is that the female function should be emphasized under conditions of greater resource availability (Lloyd, 1980; Lloyd and Yates, 1982; Lloyd and Bawa, 1984; Traveset, 1992, and references therein), and maleness under conditions of resource scarcity or environmental harshness (Ashman and Baker, 1992). Underlying these expectations is the presumption that female success is commonly limited by resources other than pollen, while male success is more often limited by access to ovules (Bateman, 1948; Janzen, 1977). Empirical studies have shown a greater emphasis on femaleness in high-light environments for monoecious orchids (Gregg, 1975, 1978), for woodland herbs (Cid-Benevento, 1987; Menges, 1990), and for the andromonoecious species *Aesculus pavia* (Bertin, 1982) and *Solanum carolinense* (Solomon, 1985), but not for the composites *Iva xanthifolia* (Freeman et al., 1981) and *Ambrosia artemisiifolia* (Traveset, 1992; Lundholm and Aarssen, 1994). The addition of various nutrients resulted in increased female sex expression in several andromonoecious or monoecious species (Randhawa and Singh, 1974; Primack and Lloyd, 1980; Solomon, 1989; Emms, 1993), but not in monoecious orchids (Gregg, 1978), nor in the monoecious sex-changer *Arisaema triphyllum* (perhaps due to inadequate enrichment; Bierzychudek, 1984), nor in the andromonoecious umbellifer *Smyrnium olusatrum* (Lovett-Doust and Harper, 1980). Low moisture conditions have been linked to a greater emphasis on the male function in various species (Freeman et al., 1981; Schlessman, 1982; Solomon, 1985; Stromberg and Patten, 1990), but not in monoecious *Ambrosia artemisi-*

ifolia (McKone and Tonkyn, 1986) nor andromonoecious *Passiflora incarnata* (May and Spears, 1988), nor hermaphroditic *Cynoglossum officinale* (Klinkhamer and de Jong, 1993). Female individuals of some dioecious species are also associated with more xeric environments than males (Freeman, Klikoff, and Harper, 1976).

A second expectation is that floral ratios might differ on plants of different sizes. Fitness gains accompanying an increase in plant size are expected to be greater for the female function than for the male function (Ghiselin, 1974; Charnov, 1982; Lloyd and Bawa, 1984; Bickel and Freeman, 1993; Emms, 1993; Klinkhamer and de Jong, 1993). Underlying this notion is the assumption that opportunities for increased male success become progressively more limited as nearby stigmas become saturated with pollen. Conversely, female success is likely to increase with the greater availability of resources on larger plants. Supporting data come from studies of various monoecious and andromonoecious plants (Gregg, 1978; Lovett-Doust and Cavers, 1982; Bierzychudek, 1984; Cid-Benevento, 1987; Delesalle, 1989). In contrast, studies of several other species, most but not all of which are wind-pollinated, reveal an increase in relative maleness in larger plants (Burd and Allen, 1988; Ackerly and Jasienski, 1990; Menges, 1990; Bickel and Freeman, 1993; Emms, 1993; Fox, 1993; Lundholm and Aarssen, 1994). This pattern might reflect the fact that the wind, unlike animal vectors, is unlikely to become saturated with pollen, leading to continued gains in male success with increasing plant size. Additionally, taller plants may be more successful as pollen donors than small plants because pollen dispersal from a greater height is more effective (Burd and Allen, 1988). In still other plants there is no relationship between plant size and maternal investment (Lloyd and Bawa, 1984).

A third pattern sometimes observed in diclinous species is for the relative frequencies of the flower types to differ on different parts of a plant. For example, pistil-bearing flowers (female or bisexual) are more common in the terminal inflorescences of *Leptospermum scoparium, Zigadenus paniculatus,* and *Quercus gambelii* than on lower inflorescences (Freeman et al., 1981; Emms, 1993). In contrast, species of *Solanum* may bear more male flowers distally and more bisexual flowers proximally (Solomon, 1985; Diggle, 1991). Such differences are often interpreted as reflecting different optimal positions for exporting pollen or for maturing fruit. Greater frequencies of female flowers at the base of inflorescences and near the inflorescence axis in *Aesculus pavia* may be related to a greater availability of photosynthate at these positions (Bertin, 1982).

Seasonal patterns in the relative allocation to male and female functions have also been observed. Many andromonoecious species, for example, produce relatively fewer male flowers later in the year (Lloyd, Webb, and Primack, 1980; Lovett-Doust, 1980; Primack and Lloyd, 1980; Webb, 1981; Coleman and Coleman, 1982; Emms, 1993). The reverse pattern has also been documented in other species (Schlessman, 1982; Willson and Ruppel, 1984; May and Spears, 1988).

Altogether, many theoretical and empirical studies have examined the factors influencing ratios of flower types in diclinous species, but rarely have these been gy-

nomonoecious species. To remedy this gap in our knowledge, we undertook the current study with several specific objectives. We sought first to quantify floral sex ratios in several species of *Aster,* and to determine how variation in floral ratios is distributed (within plants, among plants within populations, and among populations). We then investigated whether floral ratios vary significantly with position on plant, plant size, or date, and whether these ratios are affected by environmental factors such as light and nutrient availability. We also collected data on numbers of flowers per head, and present this information as a possible aid in understanding the effects of the various independent variables on the reproductive patterns in *Aster*.

MATERIALS AND METHODS

The plants—The genus *Aster* in the family Asteraceae includes nearly 200 species, mostly North American perennial herbs. Plants in this genus are insect-pollinated, bloom mostly in late summer and fall, and are found in various terrestrial habitats (Jones, 1978). They are gynomonoecious, with the heads exhibiting a combination of intrafloral and interfloral dichogamy (Knuth, 1908). Female (ray) flowers are functional before the bisexual (disk) flowers (interfloral protogyny). Disk flowers open in centripetal fashion over a period of several days. Within a disk flower, the pollen is presented first, followed by stigma receptivity (intrafloral protandry).

Field collections—Heads from 16 species of *Aster* were collected in 1992–1995 from Paxton, Massachusetts (latitude 42°18′N, longitude 71°56′W) and adjacent towns. The one exception was *A. dumosus,* collected from Jamestown, Rhode Island. Each collection involved selecting plants at regular intervals (1–2 m, depending on the population sampled) along a transect. We sampled 10–12 plants in most populations, but fewer in several small populations. In all collections, except those for analysis of the effects of head position within a plant, heads were collected arbitrarily from scattered positions on each plant. For samples used to evaluate position effects, we collected heads from three different branch positions: the terminal 5 cm of the main stem, the lowest branch, and that branch closest to the middle of the stem. For each branch position we obtained two samples, one of the most proximal heads, the other of the most distal heads. Heads were collected only if at least one disk flower was open and apparently sexually functional. We collected a constant number of heads from each plant used in a given analysis. This number was 3–5 in the different species except for plants examined repeatedly during the blooming season, wherein the number of functional heads was < 3 on some dates. The number of heads chosen for a particular species was dictated in part by the number of functional heads typically occurring on a plant at one time. We preserved heads in 70% ethanol and later counted the numbers of ray and disk flowers in each head under a dissecting microscope.

These collections were used to examine several different issues. (1) We examined variation in flower number per head and in proportion of ray flowers within and among plants in a single population in each of nine species. (2) We examined variation within and among plants and among sites in three species. The sites for a given species were separated by a minimum of 600 m, and a maximum of 12 km. (3) We examined variation over the course of the blooming season in six species. In these species, marked individuals were sampled at 5-d intervals. (4) We examined variation at different positions on a plant in field collections of two species. (5) We examined differences between small and large plants in four species. The number of flowering heads was used as an index of plant size in forming our small and large categories as follows: *A. divaricatus* ≤ 6 vs. ≥ 50, *A. ericoides* ≤ 13 vs. ≥ 100, *A. novae-angliae* ≤ 6 vs. ≥ 50, *A. umbellatus* ≤ 12 vs. ≥ 100 flowering

TABLE 1. Descriptions of greenhouse experiments.

Species	Number of sibships	Number of plants of each sibship in each treatment	Environmental variables[a]	Heads harvested by position	Number of heads harvested per plant
A. acuminatus	20	3	N	no	6
A. acuminatus	1	22	N	no	6
A. ericoides	7	2	L, N	no	10
A. ericoides	4	1	L	no	10
A. laevis	16	2	L, N	no	10
A. laevis	5	1	L	yes	25
A. lanceolatus	1	9	L	yes	25
A. linariifolius	6	1	L	no	5
A. pilosus	11	4	N	no	10
A. undulatus	14	1	L	yes	25

[a] N = nutrients, L = light.

heads. (6) We examined differences between sites having different light levels in three species. In one of these species (*A. laevis),* two populations were in open fields and one population was on the edge of woods. In *A. divaricatus,* three populations were under half-open canopies, and the other was under a closed canopy. In *A. umbellatus,* four populations were along the edge of woods, and the fifth was in an open field. Finally, (7) we sampled five populations distributed among five species in 1995, a very dry year, for comparison with samples from the same populations collected in either 1993 or 1994. Collections for a given species were made within 4 d of the same date in the two years.

Greenhouse experiments—We conducted greenhouse experiments using varied levels of light and/or nutrients in seven species. We collected seeds of *A. acuminatus, A. ericoides, A. laevis, A. lanceolatus, A. linariifolius, A. pilosus,* and *A. undulatus* in either Worcester or Paxton, Massachusetts in 1993, 1994, or 1996. Seeds were stratified in moist vermiculite in an unheated greenhouse over the winter. Emerging seedlings were transplanted individually to 8-cm pots containing the soilless mix Metromix 350. The plants were later transplanted to 20-cm pots containing the same medium. Plants were assigned to their experimental treatments in June.

A total of ten experiments was run, each using one of the above species. The experiments differed in whether light, nutrients, or both were included as treatments, in the number of plants and sibships employed and in the number of heads scored on each plant (Table 1). These differences were in part intentional, and in part reflected the availability of material and of greenhouse space, and the numbers of heads present on the plants at harvest time. Where light was manipulated, the two light levels were full-light intensity on the south side of the greenhouse, and low-light intensity resulting from use of 40% transmission shade cloth or 50% transmission through a slatted cover on the north side of the greenhouse. Where nutrients were manipulated, the high-nutrient treatment resulted from weekly fertilizations with a 50-ppm solution of Peters 20–20–20, while low nutrient plants received no fertilizer after being transplanted to the 20-cm pots in June. Heads were collected from five specific locations on the plants in several experiments to examine the effects of a head's position on a plant. These sampling locations were the base and tip of the lowest branch, the base and tip of the branch closest to the middle of the stem, and the tip of the plant. Heads from plants in other experiments were collected at scattered, arbitrary locations on the plant. We counted numbers of ray and disk flowers in each head under a dissecting microscope.

Data analysis—Although the collections for a particular comparison generally had equal numbers of plants and heads, insect damage of field-collected flowers sometimes necessitated dropping certain plants or heads from the data set. In these cases, data were randomly eliminated from the other samples in the comparison to maintain balanced sample sizes. The only exceptions were analyses of flowering on dif-

ferent dates, where sample sizes were dictated by the number of flowering heads available on marked plants on each sampling date.

All proportions were transformed by arcsine square root before further analysis. Mean proportions reported in this paper are back-transformed. Results described as significant achieved at least the 0.05 significance level.

Plant and population analyses were intended to reveal the levels at which variation occurred. These data were analyzed using model II ANOVA, with nesting in the latter case, followed by calculations of the percentage variation at each level (Sokal and Rohlf, 1995). Plant size was examined in a mixed-model nested ANOVA, with plant size as a fixed factor, and plant a random factor nested within size. Flowering date was examined for each population in a one-way model I ANOVA. The numbers of heads varied among sampling dates depending on the intensity of flowering, and no attempt was made to balance sample sizes. Additional analyses of variance were performed for individual plants, but these revealed no consistent patterns and are not discussed further.

Effects of head position in field-collected plants were analyzed with three-way mixed-model ANOVA. Plant was a random factor and the fixed factors were height of branch (tip, middle, and bottom) and position on branch (base or tip). Effects of different light levels in the field were examined with planned, orthogonal contrasts. A single planned comparison was made for each species, comparing plants in the single population with the unusual light level (light or dark) to those in all other populations combined.

Comparisons between years with different rainfall amounts were made for *A. divaricatus* using a mixed-model two-way ANOVA, with year as a fixed factor and plant as a random factor. In both *A. laevis* and *A. umbellatus,* two populations were sampled in each year. These data were analyzed in a two-way nested mixed-model ANOVA, with year and population as main effects and plant nested within population.

Results of the greenhouse experiments were analyzed with different models of ANOVA. Light and nutrients were treated as fixed effects, as was head position in those experiments where heads were collected from specific locations on each plant. If plants from multiple sibships were included in an analysis, sibship was a random factor crossed with the fixed effects. If multiple plants were included from each sibship, plant was a random factor nested within all the crossed treatments. In those experiments where significant interactions were present in the overall analysis, data were split up and examined by simpler analyses for each sibship separately.

RESULTS

The average number of flowers per head ranged from a low of 23 in *A. ericoides* to a high of 141 in one collection of *A. novae-angliae.* The proportion of these flowers that were female (ray flowers) ranged from 0.26 in one population of *A. umbellatus* to 0.61 in *A. dumosus* (Fig. 1).

Levels of variation—Of the three species in which plants were examined from several populations, significant variation in flower number per head occurred among populations in two species, and among plants within populations in all three species. Only 10–27% of variation was found within plants. In contrast, the added variance component among populations in the proportion of ray flowers was not significant for any species. Significant variation in this variable did exist among plants within populations in all species, and 38–44% of total variation occurred within plants (Table 2).

Of the nine species in which plants in a single population were sampled, most of the variation in total flower
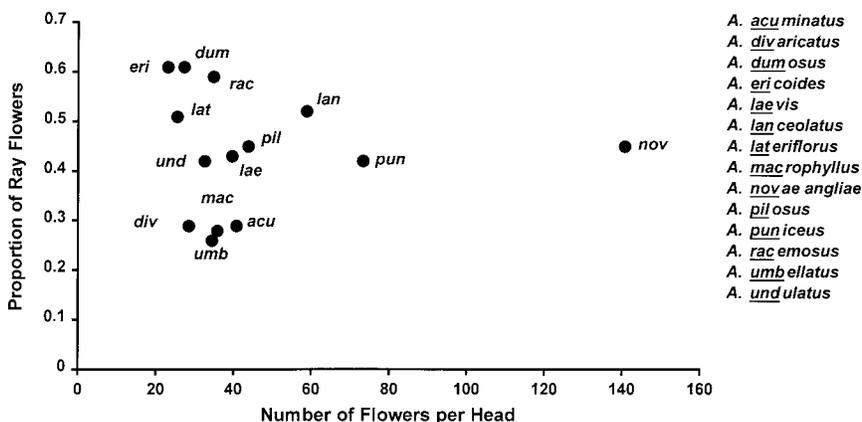
Fig. 1. Proportion of ray flowers and flower number per head in 14 aster species.

number was among plants (58–77%). The pattern was less consistent for the proportion of ray flowers, with 35–100% of variation occurring within plants (Table 3). However, the added variance component among plants was significant for seven of the nine species.

Light environment in the field—The proportion of ray flowers did not differ between shady and sunny populations for any of the three species (Table 4). For two of the species, however, the number of flowers per head differed in the different light environments. Specifically, in the most shaded population of *A. laevis*, plants had smaller heads than in the other two populations. In contrast, plants of *A. umbellatus* in the sunniest population had the fewest flowers per head (Table 4).

Plant size—In all four species examined, large plants bore more flowers per head than did small plants, in two cases significantly so (Table 5). Proportions of ray flowers were, however, unaffected by plant size in all species. In every analysis, there was a significant added variance component among plants.

Flowering date—Flowering date had a significant effect on the average number of flowers per head in three of the five species examined (Table 6). For the most part, heads produced early in the season contained more flowers than heads produced later in the season. The proportion of ray flowers was unaffected by sampling date in any species.

Position on plant—Neither the position of a head on its branch, nor the height of a branch on its stem had an effect on either the average number of flowers per head

or on the proportion of ray flowers (Table 7). There were, however, significant added variance components due to plant for both variables. For the proportion of ray flowers in *A. divaricatus* and for the number of flowers per head in *A. umbellatus,* there were significant interactions between the main effects. However, an inspection of means for each plant revealed no consistent patterns with regard to either branch height or position of heads on their branches.

Rainfall—Precipitation in Worcester during the period January-June 1995 was the lowest on record, totaling 37.2 cm. In contrast, the precipitation totals for the first six months of 1993 and 1994 were 47.1 and 58.7 cm, respectively (U.S. Department of Commerce 1993, 1994, 1995). In analyses of variance comparing plants in 1995 with plants in 1993 or 1994, no significant variation in either proportion of ray flowers or number of flowers per head could be attributed to year, although a significant added variance component was associated with plant in every species (Table 8). In *A. umbellatus,* a significant year $\times$ population interaction in the analysis of flower number per head necessitated separate one-way ANOVAs for the two populations. Year had a significant effect on the flower number in one of the two populations, and a significant added variance component was associated with plant in both populations.

Greenhouse experiments—The shading and nutrient enrichment of greenhouse plants often had conspicuous effects on plant stature, number of heads per plant, and general plant vigor. As an example of these differences, we recorded the numbers of heads per plant in *A. acuminatus* plants grown at high- and low-nutrient levels.

TABLE 2. Distribution of variation in total flower number and percentage of ray flowers among and within populations and within plants.

Species	No. of heads per plant	No. of plants per pop.	No. of pops.	Percentage of variation in flower number per head			Percentage of variation in proportion of ray flowers		
				Within plants	Among plants	Among pops.	Within plants	Among plants	Among pops.
A. divaricatus	3	10	5	26.7	70.7***	2.5	40.4	66.3***	−6.7
A. laevis	3	7	3	10.2	61.1***	28.7*	37.9	56.2***	5.9
A. umbellatus	5	10	5	21.2	38.6***	40.1***	43.5	49.5***	6.9

* $P < 0.05$; *** $P < 0.001$.

TABLE 3.   Distribution of variation in total flower number per head and proportion of ray flowers within and among plants in *Aster* spp.

| | | | Percentage of variation in | | | |
| | | | Flower number per head | | Proportion of ray flowers | |
Species	Number of heads per plant	Number of plants	Among plants	Within plants	Among plants	Within plants
A. acuminatus	4	11	61.8***	38.2	37.1**	62.9
A. dumosus	5	9	58.5***	41.5	55.6***	44.4
A. lanceolatus	5	10	70.3***	29.7	64.8***	35.2
A. lateriflorus	5	10	73.9***	26.1	35.4**	64.6
A. macrophyllus	3	8	78.7***	25.3	−1.9	101.9
A. novae-angliae	5	11	73.7***	26.3	49.7***	50.3
A. pilosus	5	12	77.3***	22.7	36.0***	64.0
A. racemosus	5	12	62.8***	37.2	18.9*	81.1
A. undulatus	5	10	71.7***	28.3	17.7	82.3

* P, 0.05; ** $P < 0.01$; *** $P < 0.001$.

Plants in the high-nutrient treatment bore an average of 88 heads, significantly more than the 38 heads on plants in the low-nutrient treatment ($T = 6.37$, $P < 0.001$). Thus the difference between the high- and low-resource treatments was large enough to produce conspicuous plant responses. These treatments often also affected the number of flowers per head, but had at most slight effects on the proportion of ray flowers (Tables 9, 10).

Specifically, flower number per head was significantly influenced by light levels in three of seven experiments, and by nutrient levels in two of five experiments (Table 9). In each experiment involving a significant difference, heads in the high resource treatment contained more flowers than heads in the low resource treatment (Fig. 2). The percentage difference between the two treatment means ranged from 4.4% for *A. acuminatus* (nutrients) to 38.0% for *A. linariifolius* (light). Several of the analyses revealed significant interaction terms involving sibship. An inspection of the means for each sibship reveals a strong tendency for more flowers in heads in the high-resource treatments. For all species and both resource types combined, 32 sibships exhibited more flowers per head in the high-resource treatments, and only 12 in the low-resource treatments (a significant departure from an even distribution, $X^2 = 9.09$, $P < 0.01$).

TABLE 4.   Effects of high- and low-light levels on flower number per head and proportion of ray flowers in three *Aster* spp. The *F* values are from planned orthogonal comparisons of plants in the population growing in the most different light environment (noted as D for darkest or L for lightest) to the plants in all other populations of the same species.

| | | Means | | *F* values (df) | |
Species	Popu-lation	Flower no.	Prop. ray	Flower no.	Prop. ray
A. divaricatus	L	27.1	0.28	0.19 (1, 36)	0.01 (1, 36)
	D	28.0	0.29		
	L	28.7	0.29		
	L	29.9	0.29		
A. laevis	D	41.3	0.44	4.99* (1, 18)	3.09 (1, 18)
	L	45.1	0.40		
	L	51.6	0.40		
A. umbellatus	L	26.9	0.30	33.19*** (1, 45)	1.58 (1, 45)
	D	32.0	0.32		
	D	33.0	0.33		
	D	35.3	0.30		
	D	36.5	0.30		

* $P < 0.05$; *** $P < 0.001$.

The proportion of ray flowers was significantly influenced by light level in only one of seven experiments, and by nutrients in two of five experiments (Table 10, Fig. 3). The differences between means were small in all cases. The proportion of ray flowers in the low-light treatment of *A. linariifolius* exceeded the number in the high-light treatment by 3.3%. The proportion of ray flowers was 1.3% higher in the high-nutrient treatment of *A. acuminatus* than in the low-nutrient treatment, whereas the proportion of ray flowers in the low-nutrient treatment of *A. ericoides* exceeded that in the high-nutrient treatment by 2.6%. Sibship means from those experiments with significant interaction terms likewise revealed no patterns. The mean proportion of ray flowers in the high-resource treatment exceeded that in the low-resource treatment in 19 sibships, while the reverse pattern held in 21 sibships.

DISCUSSION

The flexible allocation hypothesis—Perhaps the most common adaptive explanation of diclinous sexual systems is that the possession of two flower types permits flexibility in allocation of resources to male and female reproductive functions. However, our data provide virtually no evidence to support this contention for gynomonoecy in *Aster*.

A common pattern underlying both theoretical and empirical studies of sex allocation is that the female function is emphasized under conditions of greater resource availability (Ghiselin, 1974; Lloyd, 1980). In *Aster,* however, we observed none of the patterns that would be expected if this were true. Specifically, we did not find that larger plants, presumably with better access to resources, bore more female flowers than smaller plants. We also found no relationship between the proportion of ray flowers and position of the heads on the plant, either in the field or the greenhouse. There was no evidence, for example, that heads in better illuminated positions near the tip of the plant, nor in positions at the bases of branches (closer to stem-borne nutrients) had a greater proportion of female flowers. There were no seasonal trends in the proportions of ray flowers that were consistent with a resource-based model of sex expression, such as greater femaleness at the beginning of the blooming season. Finally, while the proportion of ray flowers differed significantly between plants grown at high and low light and nutrient levels in

TABLE 5. Effects of plant size on number of flowers and proportion of ray flowers in *Aster* spp.

Species	No. of heads per plant	No. of plants per sample	Number of flowers per capitulum				Proportion of ray flowers			
			Mean		Sig. of ANOVA		Mean		Sig. of ANOVA	
			Small	Large	Size	Plant	Small	Large	Size	Plant
A. divaricatus	3	9	26.8	29.2	ns	***	0.29	0.29	ns	***
A. ericoides	5	9	21.0	25.3	***	***	0.62	0.60	ns	***
A. novae-angliae	3	10	107.2	142.7	**	***	0.44	0.45	ns	***
A. umbellatus	5	10	34.4	37.8	ns	***	0.31	0.29	ns	***

** $P < 0.01$; *** $P < 0.001$; ns = nonsignificant.

a few species, these differences were small and inconsistent in direction.

In contrast to our results with floral ratios, variation in total flower number per head was often evident. Specifically, large plants bore significantly more flowers per head than small plants in two of four species. Flower number per head varied significantly with date in three of five species, and among different light environments in field populations of two of three species. Resource levels influenced flower number per head in four of the seven species examined. In each greenhouse experiment showing a significant effect of light or nutrients, plants grown at higher resource levels had more flowers per head.

One possible explanation for the lack of large or consistent effects of resource levels on the proportion of ray flowers is that the treatments were begun too late in the plant's development to produce an effect. We consider this explanation unlikely, however, because plants in the different resource treatments often differed conspicuously in other characteristics, such as stature, total number of heads, and number of flowers per head.

Despite the lack of effect of the various environmental and physiological variables on floral ratios, these ratios usually varied significantly among sibships and among plants, even when plants were grown in the relatively constant environment of the greenhouse. Significant variation among plants was found in field collections of 10 of 12 aster species examined for such variability, in all four species examined for effects of size, in both species examined for position effects, in all five species examined for effects of rainfall, and in all experiments in which plant was treated as a random variable in the greenhouse. Additionally, where sibship was treated as a random variable in greenhouse experiments, it accounted for a significant amount of the variation in proportion of ray flowers in five of eight experiments.

We believe that the substantial variation among plants

may have contributed to the few significant treatment effects on floral ratios that we found in this study. The significant effects of plant even in the relatively uniform environment of the greenhouse suggest the existence of considerable genetic variation in the proportion of ray flowers within aster populations. This high level of (presumably) genetic variation in floral ratios seems anomalous given the striking constancy of sex expression in the face of environmental variation.

Other examples of constancy of sex expression in response to varying environmental conditions have been reported in various taxa (Gregg, 1978; Lovett-Doust and Harper, 1980; Freeman et al., 1981; McKone and Tonkyn, 1986; May and Spears, 1988; Traveset, 1992). Several andromonoecious species of umbellifer exhibit a "remarkably constant" ratio of four male flowers to one bisexual flower (Lovett-Doust, 1980). In these species, however, there is a well-defined patterning of flower types in regard to both date and position on the plant. Such patterns were not observed in *Aster*. The stability of floral ratios found in *Aster* resembles that found by Lloyd (1972b) in monoecious species of *Cotula,* which are also members of the Asteraceae. Lloyd showed in several species that ratios of male to female flowers were similar in plants growing in a greenhouse and (under unspecified but different environmental conditions) in the field. Lloyd's study did not, however, examine the effects of particular environmental factors on floral ratios as in our study.

Maternal investment in Aster—Although species of *Aster* appear not to regulate their allocation to male and female function by varying the ratio of flower types, this does not preclude them from altering sex expression in other ways. These alternative pathways may include variation in the numbers of pollen grains per flower and in the extent of ovule abortion. Variation in ovule number

TABLE 6. Effects of flowering date on flower number and proportion of ray flowers in *Aster* spp.

Species	No. of plants	Flower no. per head		Proportion of ray flowers
		F values (df)		
A. laevis	7	2.26	(5, 64)	1.79 (5, 64)
A. macrophyllus	10	0.98	(6, 127)	0.76 (6, 127)
A. puniceus	10	14.54***	(6, 225)	1.52 (6, 225)
A. racemosus	9	4.57**	(5, 164)	1.05 (5, 164)
A. umbellatus	5	5.69***	(6, 99)	1.05 (6, 99)

** $P < 0.01$; *** $P < 0.001$.

TABLE 7. Position effects on flower number per head and proportion of ray flowers in two *Aster* spp. growing in the field.

Species	Plant *F* values		Height of branch *F* values		Position on branch *F* values	
	Flower no.	Prop. ray	Flower no.	Prop. ray	Flower no.	Prop. ray
A. divaricatus[a]	8.98**	43.18***	0.62	0.79	16.00	0.11
A. umbellatus[b]	6.42***	30.59***	0.33	0.19	0.49	0.78

** $P < 0.01$; *** $P < 0.001$.
[a] df = 2, 18 for plant; 2, 4 for height of branch; 1, 2 for position on branch.
[b] df = 5, 72 for plant; 2, 10 for height of branch; 1, 5 for position on branch.

TABLE 8. Effects of natural variation in rainfall on proportion of ray flowers and flower number per head in three *Aster* species.

Species	Dependent variable	Mean square[a]				
		Year	Population	Yr. × Pop.	Plant	Error
A. divaricatus	prop. ray flowers	0.0014	—	—	0.0148***	0.0026
A. laevis	prop. ray flowers	0.0224	0.0044	0.0106	0.0045***	0.0009
A. umbellatus	prop. ray flowers	0.0124	0.0186	0.0170	0.0062***	0.0010
A. divaricatus	flowers per head	147.27	—	—	36.76***	5.05
A. laevis	flowers per head	14.01	407.01	33.08	103.40***	7.72
A. umbellatus	flowers per head	890.42	1752.32	302.58**	49.41***	6.69

** $P < 0.01$; *** $P < 0.001$.

[a] df for *A. divaricatus* = 1, 40 (year); 18, 40 (plant); df for *A. laevis* = 1, 1 (year); 1, 36 (population and year × plant); 36, 80 (plant); df for *A. umbellatus* = 1, 1 (year); 1, 36 (population and year × plant); 36, 160 (plant).

is not part of the repertoire as every flower produces but a single ovule. Further work is needed to determine whether these mechanisms in fact operate in *Aster*.

Patterns in other gynomonoecious species—Gender variation in gynomonoecious species has received much less attention than, for example, gender variation in monoecious or andromonoecious species. The only references to floral ratios in gynomonoecious species that we have seen are the results of two unpublished studies cited by Lloyd and Bawa (1984). In one species (*Artemisia vulgaris*), the gender of different plants varied little, while in the second (*Gunnera insignis*) the percentage of female flowers varied from a low of 0 in one plant to 40.

Alternative explanations—Gynomonoecy could be advantageous in increasing the frequency of outcrossing, especially in combination with interfloral protogyny (Ornduff, 1966; Lloyd, 1972a, b; Burtt, 1977; Willson, 1983; Abbott and Schmitt, 1985). The lack of pollen production by female flowers probably increases the fraction of nonself pollen on their stigmas. Data for the self-compatible species *Senecio vulgaris* do in fact show a higher level of outcrossing for the ray flowers than for the bisexual disk flowers (Abbott and Schmitt, 1984). Additionally, the peripheral location of female flowers in gynomonoecious composites may promote outcrossing if pollinators visit the peripheral flowers in a head before moving to the center (Willson, 1983). However, most or all *Aster* species appear to be self-incompatible. All ten species of *Aster* examined by Jones (1978) were self-incompatible, as were three species (*A. cordifolius, A. divaricatus,* and *A. laevis*) examined in our laboratory. In a self-incompatible species, all florets are outcrossed whether they are female or bisexual, and therefore the issue of outcrossing is unimportant.

Another possible explanation of gynomonoecy is that female flowers are advantageous because they suffer from less pollen–pistil interference. That is, self-pollen may interfere in some way with the success of outcross pollen even though self-fertilization does not occur. We have sought the existence of pollen–pistil interference in three *Aster* species by comparing the success of cross pollinations with the success of cross pollinations following self pollinations, but with inconsistent results. One species showed evidence of interference, while two others did not.

A third possible explanation is related to insect predation. Burtt (1977) noted that a capitulum "offers a well stocked larder" to herbivorous insect larvae, and suggests that herbivory may have led to "the massive evolution of bitter chemicals" in the Asteraceae. If some herbivorous insects are attracted primarily by pollen, but also cause damage to the ovaries of these flowers, then maternal success will be greater in female flowers than in bisexual flowers, and a plant's maternal success will be enhanced if a fraction of its flowers are female. In our flower counts we observed that disk flowers were in fact much more likely to be damaged than were ray flowers. We cannot, however, rule out the possibility that the lower herbivory on ray flowers is related to their peripheral

TABLE 9. Results of analyses of variance examining effects of light, nutrients, and position of head on plant on the number of flowers per head in greenhouse experiments on seven species of *Aster*.

Species	Significance of effects					Significant interactions[a]
	Light	Nutrients	Position	Sibship	Plant	
A. acuminatus[b]	—	*	—	***	***	none
A. acuminatus	—	ns	—	—	***	—
A. ericoides	*	*	—	***	***	L × N
A. ericoides	ns	—	—	ns	—	L × S
A. laevis	***	ns	—	***	***	none
A. laevis	ns	—	ns	***	—	L × S
A. lanceolatus	ns	—	***	—	***	Po × Pl
A. linariifolius	**	—	—	*	—	none
A. pilosus	—	ns	—	***	***	N × S
A. undulatus	ns	—	*	***	—	L × Po × S, Po × S, L × S

[a] L = light; N = nutrients; S = sibship; Po = position on plant; Pl = plant.
[b] Each line summarizes a single experiment; some species were used in two experiments.
* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$; ns = nonsignificant.

TABLE 10. Results of analyses of variance examining effects of light, nutrients, and position of head on plants on the proportion of ray flowers in seven species of *Aster*.

	Significance of effects					Significant interactions
Species	Light	Nutrients	Position	Sibship	Plant	
A. acuminatus[b]	—	ns	—	***	***	none
A. acuminatus	—	*	—	—	***	—
A. ericoides	ns	**	—	ns	***	none
A. ericoides	ns	—	—	ns	—	L × S
A. laevis	ns	ns	—	**	***	none
A. laevis	ns	—	ns	***	—	none
A. lanceolatus	ns	—	ns	—	***	none
A. linariifolius	*	—	—	ns	—	L × S
A. pilosus	—	ns	—	***	***	N × S
A. undulatus	ns	—	ns	***	—	L × S × Po, L × S, S × Po

[a] L = light; S = sibship; N = nutrients; Po = position on plant.
[b] Each line summarizes a single experiment; some species were used in two experiments.
* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$; ns = nonsignificant.

position in the head or to their earlier anthesis, rather than to their lack of pollen.

A fourth possible explanation is that the presence of ray flowers has been favored because of their attractiveness to pollinators (Leppik, 1977). An aster head without its ray flowers certainly presents a smaller visual target to potential pollinators. It seems reasonable to assume that such heads would receive fewer pollinator visits, although this appears not to have been tested in *Aster*. In another composite, *Senecio vulgaris,* genotypes with rays have higher outcrossing rates than genotypes without rays, presumably because of higher insect visitation rates to the former (Marshall and Abbott, 1984). For this explanation to be correct, we must assume that the presence of a ray is evolutionarily and developmentally incompat-

ible with the presence of a functional androecium within a single flower. Consistent with this view is Ingram and Taylor's (1982) demonstration of an inverse developmental linkage between stamens and rays in another composite, *Senecio squalidus.* In the congener *S. vulgaris,* plants bear either radiate or nonradiate heads, the condition being determined by a single gene (Trow, 1912). Abbott and Schmitt (1985) consider the femaleness of ray flowers in self-incompatible composites as a developmental side effect of ray production, rather than adaptive in its own right. In a broader context it should be noted, however, that many species of composites (Liguliflorae)
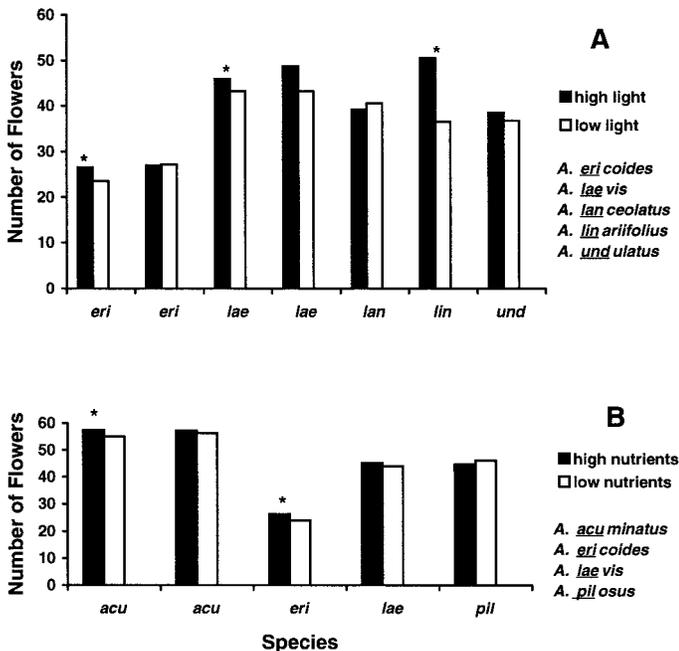

Fig. 2. Mean numbers of flowers per head in plants of five aster species raised at high- or low-light levels (A), and in plants of four aster species raised at high- or low-nutrient levels (B). * denotes significant effect of light level for a given species.
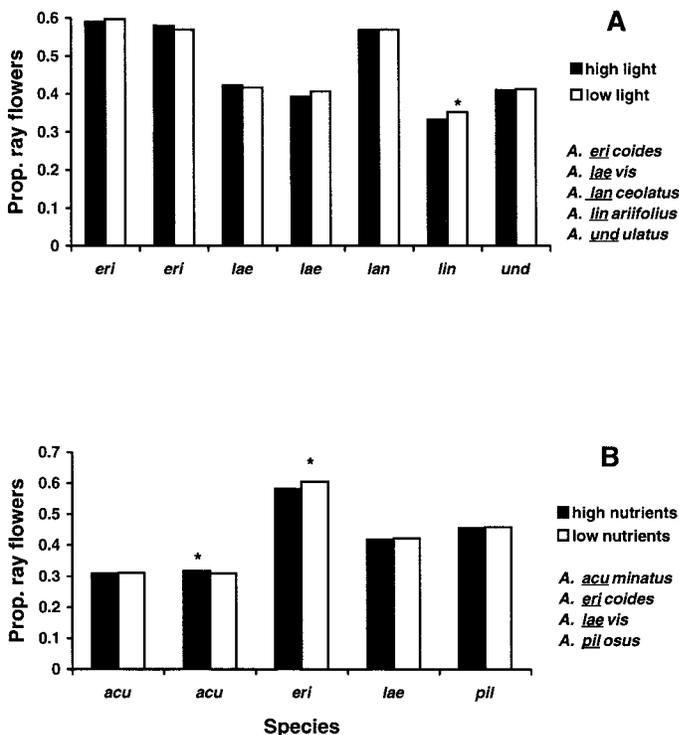

Fig. 3. Mean proportions of ray flowers in plants of five aster species raised at high- or low-light levels (A), and in plants of four aster species raised at high- or low-nutrient levels (B). * denotes significant effect of light level for a given species.

possess only bisexual flowers, each of which bears both an androecium and a ray. Other members of the family possess only bisexual disk flowers. Thus various arrangements are within the evolutionary scope of the family Asteraceae. Considering all the evidence, we believe that the attractiveness of ray flowers may have been the most important ecological factor favoring gynomonoecy in asters.

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