Sex Expression in a Natural Population of the Monoecious Annual, Ambrosia artemisiifolia (Asteraceae)

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ABSTRACT.—Sex allocation in the monoecious annual, *Ambrosia artemisiifolia* L., was investigated in an old field of southeastern Pennsylvania. I tested the hypothesis that floral sex ratio (male:female) changes with plant size (height and weight) and with light availability. The results do not agree with the traditional expectations of the resource limitation model of sex allocation, and support predictions of increasing maleness in plants that presumably grow under favorable conditions. The floral sex ratio was determined for each plant axis (primary, secondary and tertiary) and did not differ significantly among them. More female flowers on the primary axis resulted in a lower sex investment (male plus female flowers) in the secondary and tertiary axes, indicating that there might be a resource allocation constraint in plant architecture. The possible adaptiveness of the floral architectural arrangement in this wind-pollinated species is discussed.

INTRODUCTION

Gender or sex allocation in plants, in general, is determined by interactions between genotype and environment. Evolutionary theories based on relative costs and benefits of male and female reproductive structures predict that plants growing under favorable conditions should produce more female flowers, whereas plants growing in less favorable environments should increase maleness (*e.g.*, Charnov, 1982; Lloyd and Bawa, 1984; Freeman and Vitale, 1985; Lovett Doust *et al.*, 1987). Environmental parameters usually hypothesized as proximate causes of gender variation are temperature, soil moisture, light intensity, nutrients, photoperiod and plant density.

Because female reproduction is generally more costly than male reproduction (Charnov, 1982), plants growing in high-quality conditions are expected to maximize overall fitness by allocating a greater proportion of their limited resources to female function. However, wind-pollinated species, in particular, do not appear to follow that prediction, increasing relative maleness as patch quality improves (*e.g.*, Abul-Fatih *et al.*, 1979; Barker *et al.*, 1982; McKone and Tonkyn, 1986; Burd and Allen, 1988; Solomon, 1989; Ackerly and Jasieński, 1990). The advantages for larger wind-pollinated plants of having a relatively greater male investment are that pollen can be carried longer distances (and thus has a greater access to mates) and that local mating competition among sib pollen is lowered (Burd and Allen, 1988). Nevertheless, changes in floral sex ratio might not be adaptive. In those species in which male and female flowers are distributed differently on the plant in relation to branching pattern, which may vary with environmental conditions, changes in sex ratio might result from alterations in the architectural arrangement of inflorescences (*e.g.*, Smith, 1981; McKone and Tonkyn, 1986; Solomon, 1989; Ackerly and Jasieński, 1990). Regardless of the adaptive significance of these changes, they can affect the reproductive success of an individual (Solomon, 1989). It is thus important to study the relationship between plant architecture and floral sex ratio, and how modifications of the former affect the latter.

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In the present study, I examined a monoecious, wind-pollinated annual, *Ambrosia artemisiifolia* L. (Asteraceae). Monoecious species are particularly interesting because they have the opportunity for continuous fine tuning of allocation to male and female function (Lloyd and Bawa, 1984). I tested the hypotheses that floral sex ratio (male : female) in a natural population changed with both plant size (height and weight) and light availability. Data on the relationship between sex allocation and plant size in this species seem to be inconsistent. Gebben (1965) reported that plants at low densities were larger and had more female flowers than those at high density, whereas McKone and Tonkyn (1986) and Ackerly and Jasieński (1990) found that plant height was positively correlated with maleness. In a closely related species, *Ambrosia trifida*, taller and heavier plants grown at low density were relatively more male than shorter and lighter plants grown at high density (Abul-Fatih *et al.*, 1979). In the greenhouse, soil moisture and levels of herbivory do not affect gender in *A. artemisiifolia* (McKone and Tonkyn, 1986). Nutrient levels affect (at least in greenhouse conditions) the variability in gender among plants of this species through their effect on plant density and competition (Ackerly and Jasieński, 1990).

Based on the conventional expectations, I predicted that plants growing in the sun would be taller and heavier and would have a lower floral sex ratio (male : female; FSR hereafter) than plants growing under shady conditions. I further examined the absolute number of male and female flowers and the FSR on the primary, secondary and tertiary axes to test for correlations among them.

METHODS

Ambrosia artemisiifolia, common ragweed, is a herbaceous annual plant native to North America (Bazzaz, 1970). It is a monoecious species producing male flowers in terminal racemes and female flowers in the leaf axes, singly or in small groups. Male heads usually contain 10–30 staminate flowers while female heads consist of a single pistillate flower (Payne, 1963). It is wind-pollinated and produces a large number of one-seeded fruits in autumn (Bazzaz, 1970).

I arbitrarily selected 45 adult plants from three contiguous sites in a field located on the Pink Hill serpentine barren in the Tyler Arboretum (about 25 km W of Philadelphia, Pennsylvania): 15 growing in sun, 15 in shade and 15 which received sun only in the morning (site termed intermediate). Ragweed density was ca. 1–2 indiv./m² in all three sites. The plants were uprooted manually. The severed root tips left in the ground represented a minute fraction of the total weight of the root system. In the laboratory, I measured the aboveground height of each individual, and dried the plants (including roots) to constant weight in an oven at 50 C for 48 h. The total number of branches, regardless of length, was recorded for each plant.

The floral sex ratio (male : female) on primary, secondary and tertiary axes, and the total number of male and female flowers on each plant were recorded. Biomass allocated to sexual parts was estimated by weighing 25–30 flowers of each sex from each of five plants taken randomly from each of the three sites.

All statistical analyses were done using SAS (1987). A two-way ANOVA tested for differences in biomass allocated to each sex in the three sites (site was considered a fixed effect). Plant height and weight, the total number of flowers produced, and the proportion of total plant biomass invested in flowers (male + female) were compared among sites in separate one-way ANOVAs. An ANCOVA was used to test for differences in the FSR among sites controlling for plant height and weight (after determining that there was homogeneity of slopes). The FSR were compared among the three plant axes in another one-way ANOVA. The logarithmic and the angular transformations were used to normalize and equalize the variances of ratios and proportions, respectively. Correlation analyses (both

Table 1.—Mean and standard errors of the plant variables compared among sites. F and P values of the ANOVAs and ANCOVA (*) are given. n = 15 plants from each site

Variable	Site			F	P
	Sun	Interm.	Shade		
Plant height (cm)	64.97 ± 2.30	49.11 ± 3.35	45.46 ± 3.08	12.40	0.0001
Plant dry weight (g)	1.28 ± 0.18	0.93 ± 0.14	0.78 ± 0.11	3.02	0.06
Total no. flowers	378 ± 52	252 ± 43	226 ± 32	3.57	0.04
Prop. biomass invested in sex	0.31 ± 0.03	0.26 ± 0.03	0.26 ± 0.03	1.32	0.28
FSR	4.56 ± 0.65	3.88 ± 0.49	3.96 ± 0.87	1.05	0.36

Pearson and Spearman) were performed to determine whether FSR varies with height and weight of the plant regardless of site, and whether FSR at the three axes are related among them.

RESULTS

Plants growing in the sun were significantly taller, slightly heavier and produced more flowers than plants in the other two sites (Table 1). However, the proportion of the total biomass invested into flowers (male + female) did not vary among sites (Table 1) and was on average about 28%. For all three sites, the average weight of female flowers (2.22 ± 0.21 mg) was significantly higher than that of male flowers (0.59 ± 0.07 mg).

The differences in FSR among sites were not significant; that is, plants living under sunny conditions had the same number of male flowers relative to female flowers as those living in the shade, independently of plant size.

In all sites, taller and heavier plants branched more and produced more flowers (Table 2). FSR appeared to be associated with plant height, i.e., taller plants tended to have a higher number of male flowers relative to female flowers. The tallest plant had a FSR ca. six times greater than the smallest. However, there were no significant correlations between FSR and either plant weight or number of branches per plant (Table 2). The total number of branches was more correlated with weight than with height, i.e., plants with more branches were heavier but not necessarily taller than those with less branches.

The FSR did not differ significantly among axes ($F_{2,103}$ = 1.42, P > 0.05), the average being 9.42 ± 13.65 (SD) n = 34, 4.50 ± 5.86 n = 43, and 3.19 ± 2.79 n = 31, for primary, secondary and tertiary, respectively. Within a plant, there was no significant correlation among the FSR in the different axes. Significant negative correlations appeared only between number of female flowers on primary axes and number of male flowers and female flowers on secondary and tertiary ones (Table 3), i.e., as the number of female flowers on primary axes increased, the allocation to reproduction on secondary and tertiary axes decreased. The number of primary female flowers was also negatively correlated with plant weight (r =

Table 2.—Pearson correlation coefficients among plant traits. TNF = total number of flowers, FSR = floral sex ratio, * = P < 0.05, ** = P < 0.01, *** = P < 0.001

	Height	TNF	No. branches	FSR
Weight	0.56***	0.92***	0.83***	0.16
Height	—	0.58**	0.41**	0.30*
TNF	—	—	0.91***	0.17
No. branches	—	—	—	0.05

TABLE 3.—Spearman correlation coefficients between numbers of male and female flowers and sex ratios in the different plant axes. Plants with no secondary or tertiary axes are not included in the analysis. NOPF = number of primary females, NOPM = number of primary males, and so on. S = secondary, T = tertiary, SRP = sex ratio in the primary axis, and so on. * = P < 0.05, ** = P < 0.01, *** = P < 0.001

	NOPM	NOSF	NOSM	NOTF	NOTM	SRP	SRS	SRT
NOPF	−0.13	−0.33*	−0.46**	−0.30	−0.16	−0.86***	−0.23	−0.15
NOPM	—	0.05	0.39*	−0.03	−0.15	0.75***	0.38*	−0.02
NOSF	—	—	0.58***	0.26	−0.08	0.27	−0.30	−0.11
NOSM	—	—	—	0.31	−0.01	0.42*	0.49***	0.22
NOTF	—	—	—	—	0.82***	0.29	0.08	0.12
NOTM	—	—	—	—	—	−0.38	−0.03	0.59*
SRP	—	—	—	—	—	—	0.23	−0.07
SRS	—	—	—	—	—	—	—	0.25

−0.47, P < 0.01) and with plant height (r = −0.39, P = 0.01); taller and heavier plants produced fewer female flowers on the primary axes.

DISCUSSION

Some studies (*e.g.,* Freeman *et al.,* 1981; Lloyd and Bawa, 1984; Solomon, 1985; McKone and Tonkyn, 1986; Lovett Doust *et al.,* 1987; Solomon, 1989) have shown that proportional allocation of resources to male as opposed to female reproductive function in plants varies from site to site and is a function of environmental quality. Patch quality differentially affects the success of male and female reproductive functions, probably because of the greater cost associated with seed and fruit production as opposed to pollen production. Based on this, a large plant growing in a favorable environment with sufficient available resources would be expected (1) to produce more female flowers or (2) to allocate the same amount of energy in producing more (cheaper) male flowers, than a smaller plant living in less favorable conditions. The phenotypic outcome probably varies among plant species, depending upon other factors (biotic and abiotic) that may affect sexual expression.

In *Ambrosia artemisiifolia,* light availability did not affect the proportional allocation to male function relative to female function. This result disagreed with the prediction that plants growing in the sun would have a lower floral sex ratio than those living in the shade. Changes in floral sex ratio due to different light conditions have been reported for other monoecious, wind-pollinated plants such as *Croton suberosus* (Euphorbiaceae); this species has a significantly higher FSR in sunny conditions than in shady or intermediate ones (Domínguez and Bullock, 1989).

Relative maleness and plant height were positively correlated, a result reported also by McKone and Tonkyn (1986) and by Ackerly and Jasieński (1990). Further, plant weight was not associated with sex ratio, consistent with the field studies of McKone and Tonkyn (1986); however, greenhouse studies (McKone and Tonkyn, 1986; Ackerly and Jasieński, 1990) showed a positive correlation between these two parameters. The cause of this inconsistency is not clear. For other wind-pollinated species in which the correlation between plant size and floral sex ratio has been examined, the results vary. Some studies find a positive correlation (*e.g.,* Abul-Fatih *et al.,* 1979; Willson and Ruppel, 1984; McKone and Tonkyn, 1986; Burd and Allen, 1988; Solomon, 1989; Ackerly and Jasieński, 1990) whereas others find a negative correlation (*e.g.,* Hibbs and Fischer, 1979; Smith, 1981; Lloyd and Bawa, 1984; Primack and McCall, 1986; Garnock-Jones, 1986).

Assuming that changes in sex ratio are adaptive, organisms should alter their sex allocation as they grow to favor the sex with the greatest fitness gain (Ghiselin, 1969). For wind-pollinated species such as *Ambrosia artemisiifolia*, once a plant has reached a given size, it might be more advantageous to produce more male than female flowers as plant size increases. The advantage would rely, as Burd and Allen (1988) point out, on the increased pollen flight distance and on the reduced local mating competition among sib pollen. Such a pollination advantage has probably been important in the evolution of plant architecture in species like *A. artemisiifolia* where male flowers are mostly in terminal racemes and at the uppermost inflorescences. Another advantage of such an architectural arrangement might be a decrease in herbivory and seed predation, in the case that seeds were more protected from insects in the lower portions of the axes of the plant. Indeed, Abul-Fatih *et al.* (1979) reported a greater percentage of seed damage in tall "apparent" individuals of *A. trifida* than in short ones. However, Raynal and Bazzaz (1975) found the opposite in *A. artemisiifolia*. There is also evidence that mechanical removal of flowers or leaves in some species can affect the sex of flowers developing later (Hendrix and Trapp, 1981; Whitham and Mopper, 1985; Spears and May, 1988). There are no data on this for *A. artemisiifolia*.

Alternatively, assuming that the architectural arrangement of flower sexes is not adaptive, changes in floral sex ratio could be caused by (1) *resource allocation constraints*. Having produced more female flowers in the innermost inflorescences, the plant would have less energy to allocate in the periphery; the present study actually shows that the higher the number of female flowers on the primary axis the lower the number of males and females on the secondary and tertiary ones. The flower arrangement could also result from (2) *physiological constraints* caused by hormones. Terminal buds in general have higher levels of auxins than lateral buds, and these auxins favor maleness (Heslop-Harrison, 1972; Friedlander *et al.*, 1977). Other hormones such as gibberellins and cytokinins, are also involved in sex expression (Chailakhyan, 1979). Modification of the FSR could further result from changes in the branching pattern of the plant caused, for instance, by fluctuations in the environmental conditions. In the case of *Ambrosia artemisiifolia*, even though sexes are distributed differently on the plant, FSR does not vary with the number of branches and it is not significantly different between the three plant axes. Therefore, it seems unlikely that the branching pattern has an important effect on sex expression in this species.

In short, sex expression in *Ambrosia artemisiifolia* was not significantly affected by the degree of insolation in the different sites. Floral sex ratio appeared to be more influenced by plant size, in particular by plant height. An increase in sex ratio with plant height may be adaptive through a more efficient pollination or through a lowered insect seed predation. Changes in sex ratio, however, may just be the result of different kinds of constraints in plant architecture. Further investigation will, it is hoped, allow us to determine the adaptiveness of the architectural floral arrangement in this and other similar species.

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