

## Aspects of the determination of the number of flowers and sex allocation in *Acanthospermum hispidum* DC. (Heliantheae: Compositae)

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**ABSTRACT** – Aspects of the determination of the number of flowers and sex allocation in *Acanthospermum hispidum* DC. (Heliantheae: Compositae). Data on the variation in the number of flowers and sex allocation for a monoecious plant, *Acanthospermum hispidum*, were obtained in 4 areas in the region of Campinas, SE Brazil. Differences in sex allocation were observed among the areas sampled. The results indicate that the floral sex ratio tends to 1.0 when the population density of *A. hispidum* is low, the advantages obtained by the association with the culture are small, the system of cultivation is irregular and the culture são characteristics are unfavorable. When the inverse occurs, the floral sex ratio tends to show a higher number of female than male flowers.

**RESUMO** – (Aspectos da determinação do número de flores e alocação sexual em *Acanthospermum hispidum* DC. (Heliantheae: Compositae). Foram obtidos dados sobre a variação no número de flores e alocação sexual em uma planta monóica, *Acanthospermum hispidum*, em 4 áreas na região de Campinas, SE Brasil. Foram observadas diferenças na alocação sexual entre as áreas amostradas. Os resultados indicam que a razão sexual floral tende a 1,0 quando a densidade populacional de *A. hispidum* é baixa, as vantagens obtidas pela associação com a cultura são pequenas, o sistema de cultivo é irregular e as características da cultura são desfavoráveis. Quando o inverso ocorre, a razão sexual floral tende a mostrar um número maior de flores femininas que masculinas.

**Key words** – sex allocation, *Acanthospermum hispidum*.

### Introduction

Several studies have looked at the factors and mechanisms that control the sex allocation in plants (Fisher 1958, Godley 1964, Maynard Smith 1971, Kaplan 1972, Putwain & Harper 1972, Eshel 1975, Opler & Bawa 1978, Charnov 1982). Many of them have shown a correlation between sex allocation and several aspects of breeding systems in flowering plants (Queller 1984), so that an increase in the degree of self-fertilization implies a reduction of the allocation for male reproductive function (Hamilton 1967, Gibbs et al. 1975, Cruden 1977, Schoen 1982). Some authors have drawn attention to the relative advantages of self- and cross-fertilization in relation to differences both in growth habits and habitats (Solbrig 1976, Lloyd 1980). The data obtained suggest that sex allocation must be variable in different environments. In fact, the sex allocation control seems to be influenced by environmental uncertainty and by the biotic interactions of the community (Cruden 1976, Levin 1978, Crawford & Balfour 1983), and may show variation between populations (Mulcahy 1967, Harris 1968, Freeman et al. 1976) and temporal variation within populations (Bawa 1977).

The study of intra-specific variation has evidenced the existence of high levels of variation both within and between populations of many plant species (Burdon 1980). The characters chosen for quantifying variation in such studies have been extremely diverse. Many plant species show variation in the number of flowers as a response to environmental cues. However, most of the data published about sex allocation in plants has been obtained either for dioecious plants, or for comparisons between species with different breeding systems (Lemen 1980). Little is known about the variation in the number of flowers and sex allocation for monoecious plants and between populations of a single species.

In this paper, we present data on the variation in the number of flowers and floral sex ratios for a monoecious plant, *Acanthospermum hispidum*, a very common weed that occurs in pasture and cultivated areas in Brazil. We also propose some hypothesis to explain the patterns observed.

### Material and methods

*Acanthospermum hispidum* is an annual herb which is widely distributed throughout Brazil. Its life cycle lasts about 120 days, and in São Paulo State it commonly flowers from February to April and fruits from March to May (Leitão Filho et al. 1972). The capitula are isolated, with male flowers located at the center, and female ones at the margin of the flower heads (Kissman 1978). The flowers are mainly wind-pollinated and seem to have high levels of self-pollination, since self-compatibility has already been shown to occur

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in this species (Santos 1983). The seeds have the ability to remain dormant and viable while buried and they may form a dense seed bank. Germination is rapid when seeds emerge to the soil surface after a disturbance (Santos 1983).

The samples were taken in 1982, from four cultivated areas in the region of Campinas (22°53'S, 47°04'W), State of São Paulo, SE Brazil. Two of the sample areas (A and D) are located at the Centro Experimental do Instituto Agrônômico de Campinas and the other two areas (B and C) are located at Fazenda Santa Genebra. In area A, the population of *A. hispidum* occurred at the edge of an area planted with soybean. The plants were frequently damaged by workers and by the machinery used to prepare the soil for cultivation. Furthermore, as the plants were located at the edge of the culture, the influences they suffered from soil fertilization, soil turnover and other cultivating treatments were relatively small. In this area, the utilization of the surroundings of the main culture for subsistence agriculture was observed. Here, the variety of weeds was greater and the density of adult individuals of *A. hispidum* lower than in the other areas. Area C was cultivated with cotton in 1980 and with maize in 1981 and 1982. Here, the density of *A. hispidum* was higher than in the other areas studied. In areas B and D, the populations of *A. hispidum* occurred in cotton plantations.

In each area we took two capitula from each of 25 plants. The number of male, female and total flowers per capitulum was recorded and the floral sex ratio obtained, as the ratio of male to female flowers per capitulum. In other studies, the ratio of pollen to ovule has been considered as the most appropriate measure to describe sex allocation in monoecious plants. Alterations in pollen/ovule ratio may be brought about by allocation changes in the number of pollen grains per anther, the number of anthers per flower, and/or the number of functionally male flowers (Willson 1979). We considered the floral sex ratio as the best indicator of variations in sex allocation between populations of *A. hispidum*, in view of the inflorescence and floral characteristics of this species.

## Results

The frequency distribution of the number of male and female flowers, as well as the total number of flowers per capitulum in each study area are shown in figures 1 and 2, respectively.

The mean number of flowers and floral sex ratio per capitulum for each area are presented in table 1. The differences in the mean numbers among the four areas were significant, except for the number of female flowers between areas A and B and for the floral sex ratio between areas B and D. Furthermore, within areas, the variation observed in the number of female flowers is smaller than the variation of the number of male flowers ( $F=1.9290$ ;  $p<0.001$ ).

## Discussion

The variation in the number of flowers and floral sex ratio showed by *Acanthospermum hispidum* seems to be a response to different environmental cues. All characters showed the same pattern in each area: whenever the number of male flowers per capitulum is greater, both the number of female flowers per capitulum and floral sex ratio are also greater (table 1). However, the variation in the number of female flowers is smaller than in the number of male flowers (figure 1), suggesting a greater commitment of the plant with the former character, probably due to its importance in the control of seed number.

The variation observed in the floral sex ratio in *A. hispidum* (table 1) suggests some hypothesis to explain the differences among the four areas. First, we must consider that an increase in the floral sex ratio is correlated with an increase in the chance of cross-fertilization and consequently an increase in genetic variability. Then we may expect balancing mechanisms which increase the chance of outcrossing in areas where the genetic variability may not be maintained by other means. This hypothesis can be applied to explain the greater floral sex ratio in area A. In this area the effect of cultivation practice is low, since the population is at the edge of the planted area, where the frequency and intensity of soil overturning is smaller than in the center of the culture. This may reduce the chance of increasing genetic variability and increase the chance of loading some genetic combinations within the population due to the poor recruitment of seeds emerging from the seed bank (which includes seeds produced in several years). This hypothesis can be tested by experimentally sowing seeds in fields with different levels of perturbation and following the effects of perturbation regimes on the floral sex ratio. Moreover, the seeds of plants at the edge of the cultivated area have a lower probability of parallel dispersion together with the seeds of the culture (in the harvest period) than the ones inside the cultivated area. An increase in the number of male flowers can increase the probability of pollen reaching the stigma of a female flower, therefore increasing the chance of outcrossing and then the chance of maintaining the genetic variability under these circumstances.

Some studies have shown that the proportion of male to female plants increases with the

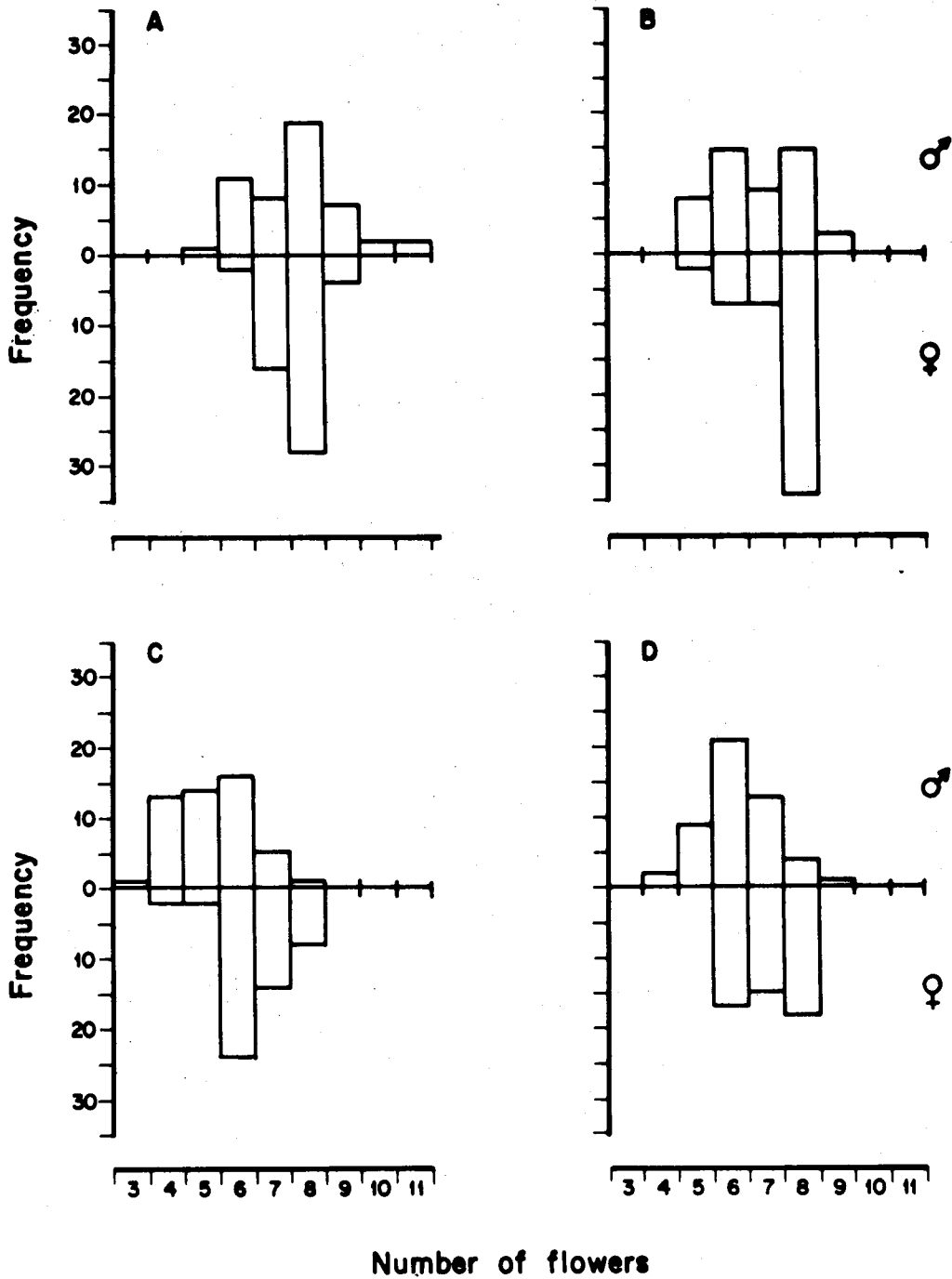


Figure 1. Frequency distribution of the number of male and female flowers per capitulum in each study area.

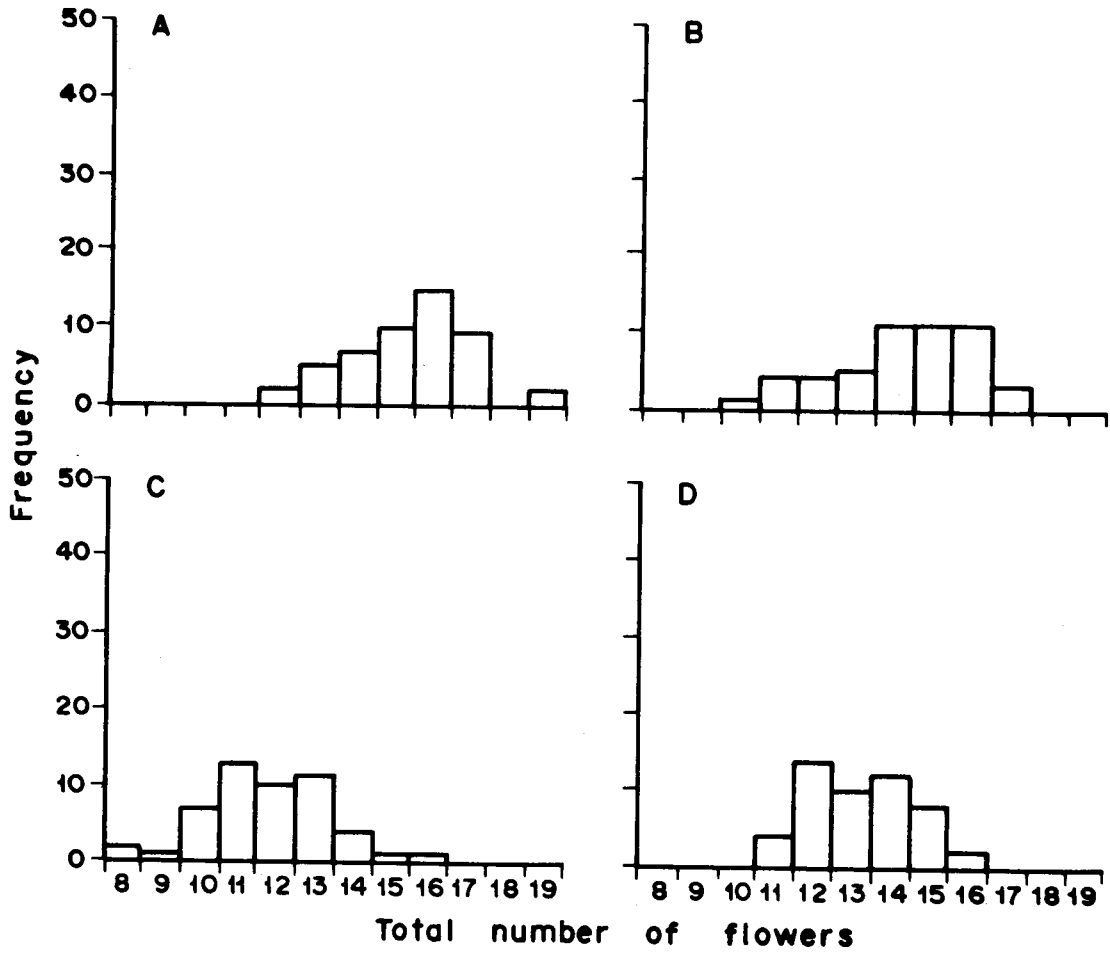


Figure 2. Frequency distribution of the total number of flowers per capitulum in each study area.

Table 1. Mean values ( $\pm 1$  S.D.) of the number of flowers and floral sex ratios for the study areas. For each variable, values followed by different superscripts are significantly different at  $p=0.05$  (Student-Newman-Keuls test).  $n=50$ ; \*\*\*  $p<0.001$ .

Number of flowers	F-values	AREAS			
		A	B	C	D
Male	36.68***	7.68 $\pm$ 1.35 <sup>a</sup>	6.80 $\pm$ 1.21 <sup>b</sup>	5.28 $\pm$ 1.09 <sup>c</sup>	6.22 $\pm$ 1.04 <sup>d</sup>
Female	19.55***	7.68 $\pm$ 0.68 <sup>a</sup>	7.46 $\pm$ 0.89 <sup>a</sup>	6.48 $\pm$ 0.95 <sup>b</sup>	7.02 $\pm$ 0.84 <sup>c</sup>
Total	46.59***	15.36 $\pm$ 1.57 <sup>a</sup>	14.26 $\pm$ 1.76 <sup>b</sup>	11.76 $\pm$ 1.64 <sup>c</sup>	13.24 $\pm$ 1.35 <sup>d</sup>
Sex ratio	8.54***	1.01 $\pm$ 0.19 <sup>a</sup>	0.92 $\pm$ 0.16 <sup>b</sup>	0.83 $\pm$ 0.18 <sup>c</sup>	0.90 $\pm$ 0.18 <sup>b</sup>

harshness and uncertainty of the habitat (Harris 1968, Freeman et al. 1976). This pattern may be observed in the proportion of male to female flowers in the monoecious *A. hispidum*, if we consider area A as being the most adverse and spatially uncertain to seeds due to its spatial heterogeneity.

Other hypothesis proposes that when the population density is low, and consequently the distances among individuals are greater, there may be selection for increasing the number of male flowers, thus enhancing the chances of outcrossing. According to Crawford & Balfour (1983), a slightly lower proportion of females may be expected where the efficiency of pollen dispersal is low. In wind-pollinated plants, the pollen flow follows a leptokurtic pattern with a rapid decrease in the probability of pollen reaching an area as a function of its distance from the source plant (Levin & Kerster 1974, Antonovics 1976). We would therefore expect that the floral sex ratio shows an inverse relation to population density of *A. hispidum*. This seems to be the case for areas A and C, that showed the highest and lowest floral sex ratios (table 1), and lowest and greatest population densities for adult individuals (Santos 1983), respectively.

Finally, the variation in floral sex ratio could be due to different biotic pressures in the areas. This hypothesis may explain the observed similarity in sex allocation between areas B and D (cotton culture), although there are differences in the number of flowers (table 1). Competitive interactions seem to be an important factor in area A, where there is a high density of weeds and the soybean culture has a dense leaf cover. Here, competition seems to provoke an additional benefit for an increase in the chance of outcrossing. However, in the maize-cultivated area (C) we observed the lowest floral sex ratio (table 1) despite the rapid growth and the high densities of the maize culture. Probably the high population

densities of *A. hispidum* (Santos 1983) and the advantages obtained by the association with the maize culture (high dispersal rates and intense soil overturning) may have a greater influence in the determination of the sex allocation. This indicates that different factors may act in the determination of the patterns observed in different areas.

The results indicate that the floral sex ratio tends to 1.0 when 1 – the population density of *A. hispidum* is low, 2 – the advantages obtained by the association with the culture are small, 3 – the system of cultivation is irregular, and 4 – the culture characteristics are unfavorable. When the inverse occurs, the floral sex ratio tends to show an excess of female flowers. The sex allocation seems to be adjusted according to a balance among the levels of importance of these factors in each area.

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