Variation in sexual expression in relation to plant height and local density in the andromonoecious shrub *Caesalpinia gilliesii* (Fabaceae)

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Abstract Based on the hypothesis that both plant size and local conspecific density influence allocation to female/male functions, we explored the relationship between plant height, local conspecific density, sexual expression, and fruit production in the andromonoecious shrub *Caesalpinia gilliesii*. We quantified the total number of perfect and staminate flowers, the pollen received and fruits produced per plant in two populations, and estimated phenotypic gender and fruit set. Local density failed to explain phenotypic gender, nevertheless, plant height and fruit set increased with local density in one population where, in addition, the slopes for the size-dependent sex allocation curve were steeper. As observed for other plant species, this suggests that between population differences in resource availability is the main underlying factor for the observed population differences in the size-dependent allocation pattern to flowers and fruits. On the other hand, the number of staminate and perfect flowers per plant increased with plant height and the fastest increase of staminate flowers resulted in a male-biased size-dependent sex allocation strategy in both populations. Since pollination intensity was not correlated with plant height in any population, the observed allocation strategy cannot be attributed to differences in pollen availability between different sized individuals, but to differences in plant size. Finally, because fruit set and total fruit number increased with plant height in one population, the obtained results provide further evidence that animal-pollinated, andromonoecious species may exhibit a male-biased size-dependent sex allocation strategy, which may favor female fecundity.

Keywords Fitness · Local density · Phenotypic gender · Plant height · Size-dependent sex allocation

Introduction

Variability in plant size can explain sexual phenotypic expression in species with different pollination vectors and reproductive systems (e.g., Bickel and Freeman 1993; Klinkhamer et al. 1997; Sarkissian et al. 2001; Dorken and Barrett 2003). In this regard, there is growing empirical and theoretical evidence that allocation to female function (i.e., ovules and seeds) generally increases with plant size in animal-pollinated species (Klinkhamer et al. 1997; Sarkissian et al. 2001; de Jong and Klinkhamer 2005; but see Emms 1993; Ishii 2004).

Plant size, however, usually covaries with conspecific density (Weiner 1988; Silvertown and Lovett Doust 1993), and it has been suggested that both plant size and local density may influence sexual expression (Weiner 1988). Nevertheless, while the relationship between plant size and sexual expression has been

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extensively explored, the influence of plant density on sexual expression is much less known. In a careful revision of lability in sexual expression, Korpelainen (1998) highlighted the importance of population density in the variation of sexual expression in different plant taxa, including Bryophyta, and pointed out that femaleness is likely in environments favorable for plant growth and reproduction. Considering that the same environmental factors that influence seedling establishment and mortality, and therefore adult density may also influence the resources available for flower and fruit production, differences in local density may reflect resource availability for the reproductive function (Kunin 1992; Roll et al. 1997; Bosch and Waser 2001). Thus, higher local plant density as well as larger plant size may reflect better local environments for flower and fruit production and possibly for allocation to the female function. Accordingly, femaleness can be expected to increase with plant size and density. Competition for resources, however, may prevail at higher densities (Silvertown and Lovett Doust 1993) reducing the availability of resources and in such cases, maleness could also be expected to increase with increasing density (Weiner 1988). In agreement with the former assumption, femaleness tends to increase with conspecific density in populations of a polygamous willow (Faliński 1998) and in cosexual plants of an androdioecious herb (Pannell 1997). Although examples are scarce, they reveal that sex expression may be under the influence of conspecific density. Furthermore, whereas conspecific density could be considered an extrinsic estimate of the local resource availability, plant size has been related to the individual resource status (Herrera 1991; Sarkissian et al. 2001; Griffin and Barrett 2002) and therefore, intraspecific differences in sex allocation may respond to variability in both plant size and local conspecific density.

Not all sexual systems, however, are equally susceptible to resource availability. Andromonoecy (i.e., the production of staminate and perfect flowers in the same plant) is a sexual system characterized by a strong resource dependence (Lloyd 1980a; Bertin 1982). Accordingly, resource-depleting factors, such as shading or water stress (Solomon 1985), florivory (Krupnick and Weis 1998), and fruiting success of earlier flowers (Diggle 1994; Gibbs et al. 1999) can alter the production of perfect and staminate flowers. More recently, it has been suggested that female

fitness of andromonoecious plants is limited by resources rather than by pollen availability (Liao et al. 2006). According to Liao and Zhang (2008), if resources limit fitness, larger plants of andromonoecious species should benefit from increasing maleness with plant size (Liao and Zhang 2008). Nevertheless, allocation to male function may either decrease (e.g., Schlessman and Graceffa 2002) or increase (e.g., Emms 1993; Liao and Zhang 2008) with plant size in andromonoecious species. In addition, species with other sexual systems showed intraspecific variation in the relationship between plant size and sex allocation (e.g., Sarkissian et al. 2001; Dorken and Barrett 2003; Guitián et al. 2004; Méndez and Karlsson 2004; Cao and Kudo 2008), but whether differences in the size-dependent sex (SDS) allocation strategy between species are part of intraspecific variation remains largely unexplored. Due to the close relationship of plant size and conspecific density with resource availability, and with the latter and sex allocation in andromonoecious species, we expect that both factors contribute to explain intraspecific variability in sexual expression and SDS allocation in andromonoecious species.

Here, we analyzed the influence of plant size and local conspecific density on the sexual expression of the andromonoecious shrub *Caesalpinia gilliesii* (Fabaceae), by examining the linear relationship between plant height, local conspecific density, and two measures of sexual expression (perfect and staminate flower number and phenotypic gender) in two populations. Intraspecific variation of this sexual system in *Caesalpinia* spp. was studied in a few species, mainly at the inflorescence level (e.g., Gibbs et al. 1999; Jausoro and Galetto 2001; Calviño and Carrizo García 2005). As in other andromonoecious species, basal fruits of *C. calycina* inflorescences influence the production of apical staminate flowers (Gibbs et al. 1999). In *C. gilliesii*, however, the size of the inflorescence rather than the presence of basal fruits would account for differential sexual expression (Jausoro and Galetto 2001; Calviño and Carrizo García 2005). Furthermore, the fact that plant height may covary with local conspecific density in this species (Calviño 2006) makes it suitable for the study of the influence of both plant height and local density on the sexual allocation strategy. The aim of this study was to address the following questions: (1) Does plant height correlate with local conspecific

density in *Caesalpinia gilliesii*? (2) Does plant height and and/or local conspecific density correlate with perfect or staminate flower number and relative sex allocation (i.e., phenotypic gender) in this species? (3) Does the relationship between plant height and sexual expression of individuals differ between populations? And, (4) do pollination and fruit production relates to plant size as in other andromonoecious species?

Materials and methods

Study species

Caesalpinia gilliesii (Fabaceae) is a native andromonoecious shrub that grows in arid and semi-arid regions of Argentina (Ulibarri 1997). While it flowers from September to December, the flowering period of plants within a population spans up to 60 days (Jausoro and Galetto 2001). *C. gilliesii* does not set fruits by spontaneous self-pollination (Cocucci et al. 1992). Fruit set per plant is usually low in this species (3–12%) and plants may be severely pollen-limited (Calviño 2006). Pollen limitations, measured as the percent of ovules that fail to produce seeds, vary in different populations and years from 21 to ∼90% (Calviño 2006). In addition, controlled pollination experiments indicate that this species is self-incompatible (Jausoro and Galetto 2001), but can set fruits by geitonogamous pollination (Calviño 2006). Pollinators are long-tongued nocturnal hawkmoths (Cocucci et al. 1992; Moré et al. 2006). Diurnal bees and bumblebees usually visit the flowers, but rarely contact the stigma; therefore, they cannot be considered pollinators (Calviño 2006).

Variation in sexual expression

Study populations of *C. gilliesii* were located on the eastern slope of Sierras Chicas hills, Córdoba province, Argentina. The vegetation in the region corresponds to Bosque Serrano woodlands (Luti et al. 1979) within the Chaco phytogeographical province (Cabrera 1994). *C. gilliesii* grows sparsely beneath the canopy of dominant trees, such as *Lithraea molleoides* and *Prosopis* spp., or forms pure patches in canopy gaps.

In order to analyze the relationship between plant height, local density, and sexual expression at the plant level, 25 shrubs were marked in San Nicolás (SN) and La Quebrada (LQ) populations in 2003. During that reproductive season, pollen limitation reached intermediate values in both populations, and ∼40% of the open perfect flowers failed to produce fruits compared with hand-cross pollinated flowers (Calviño et al. unpublished data).

The studied populations differed in both plant height and local conspecific density of *C. gilliesii*, with SN showing lower plant height and higher conspecific density than LQ (results not shown). The number of conspecific neighbors within a 3-m radius was counted for each focal plant, with local density expressed as the number of neighbors per square meter. Because plant height is highly and positively correlated with total flower production per plant ($R^2 = 0.44$, $t = 3.21$, $P = 0.03$), it was used as a measure of plant size. The total number of perfect and staminate flowers was recorded every 4 days on each focal plant, and was used as absolute measure of sexual expression. The phenotypic gender index (G_i) of relative sexual expression developed by Lloyd (1980b) was obtained as:

$$G_i = g_i/(g_i + a_iE)$$
$$E = (\sum g_i/n)/(\sum a_i/n),$$

where g_i represents total ovule number, a_i stands for total anther number per plant, and E corresponds to an equivalence factor obtained as the ratio of population averages of g_i and a_i (Lloyd 1980b). This standardized index varies between 0 and 1 for complete male and female plants, respectively.

A sample of 10 mature fruits per plant was used to estimate average number of ovules by counting the scar of attachment each ovule leaves on the fruit wall. Total ovule number per plant was estimated as the average number of ovule scars per fruit per plant multiplied by the total number of perfect flowers. Total ovule and pollen production per plant depends on number of flowers with ovules or pollen, regardless of the number of ovules or pollen per flower (Calviño 2006); therefore, flower number is a good estimate of female/male gametophyte production. Total number of anthers was obtained as anther number per flower (10) multiplied by the total number of flowers. At the end of the flowering

period, the number of mature fruits produced by each plant was recorded, and fruit set per plant was obtained as the ratio of total fruits to total perfect flowers. In addition, pollen load deposition was recorded in the field (20–25 stigmas per plant) using a $\times 20$ magnifying glass, and pollination intensity was expressed as the ratio of mean number of pollen grains on the stigma to mean ovule number per ovary (Kearns and Inouye 1993).

Statistical analysis

In order to test the dependence of sexual expression on plant size or local conspecific density, the number of perfect and staminate flowers produced, phenotypic gender, pollination intensity, fruit set, and total fruit number per plant were regressed against individual plant height and local conspecific density. Analyses of covariance with one interaction term (plant height * population) were used to test for slope differences between SN and LQ populations in that season. Fruit set between populations and the fruit set-plant height/local density relationship were compared with a generalized linear model using the glm command of R package (family = binomial, link = logit). Total number of staminate flowers was ln-transformed to achieve normality. Similarly, pollination intensity was

log$_{10}$-transformed, but in all cases, back-transformed values are shown. ANCOVAS were performed with SPSS 10.0.

Results

Unfortunately, five plants should be discarded for the analysis because flowering shoots were damaged; thus, sample size was reduced to 45 shrubs. Within populations, plant height increased with local density in SN, but not in LQ (Fig. 1; $R^2 = 0.21$, $b = 3.31 \pm 1.40$, $t = 2.36$ $P = 0.028$ for SN). Regression slopes between staminate flower number, perfect flower number, phenotypic gender, and local density did not differ from zero in any population. Only fruit set per plant in SN showed that a positive relationship with local density ($R^2 = 0.17$, $b = 0.85 \pm 0.40$, $t = 2.28$ $P = 0.033$). On the other hand, the number of staminate and perfect flowers increased with plant height in the two populations, staminate flowers increasing more rapidly than perfect flowers (Fig. 2a, b; Table 1). This resulted in an increased maleness (i.e., lower phenotypic gender) with greater plant height in both populations (Fig. 2c; Table 1). In general, the size-dependent relationships tended to be steeper in SN than in LQ, the relationship between

Fig. 1 Relationship between plant height and local conspecific density in two populations of *Caesalpinia gilliesii* studied in 2003. *Empty circles* = San Nicolás, *solid circles* = La Quebrada
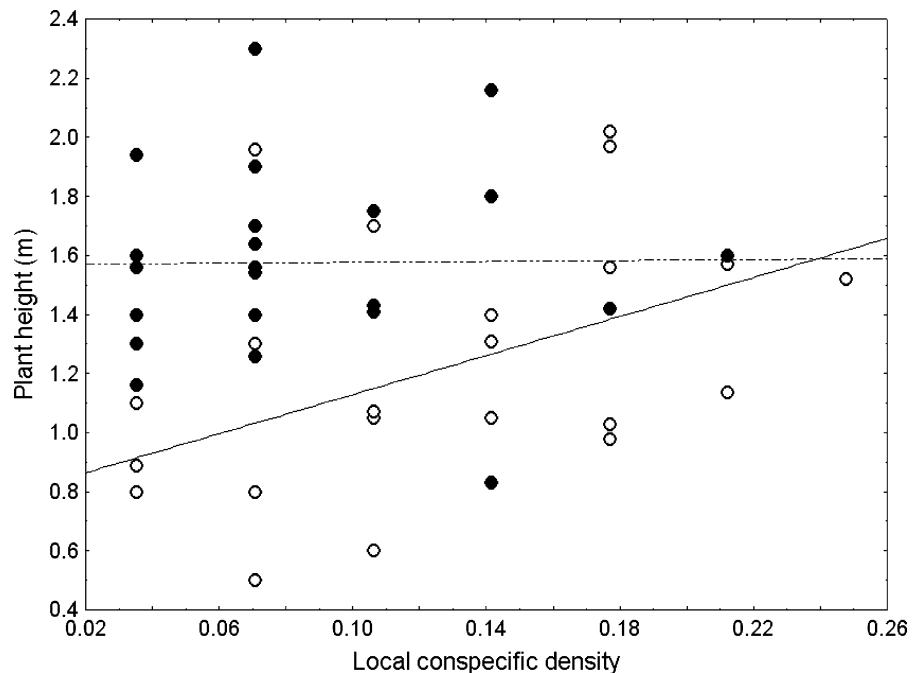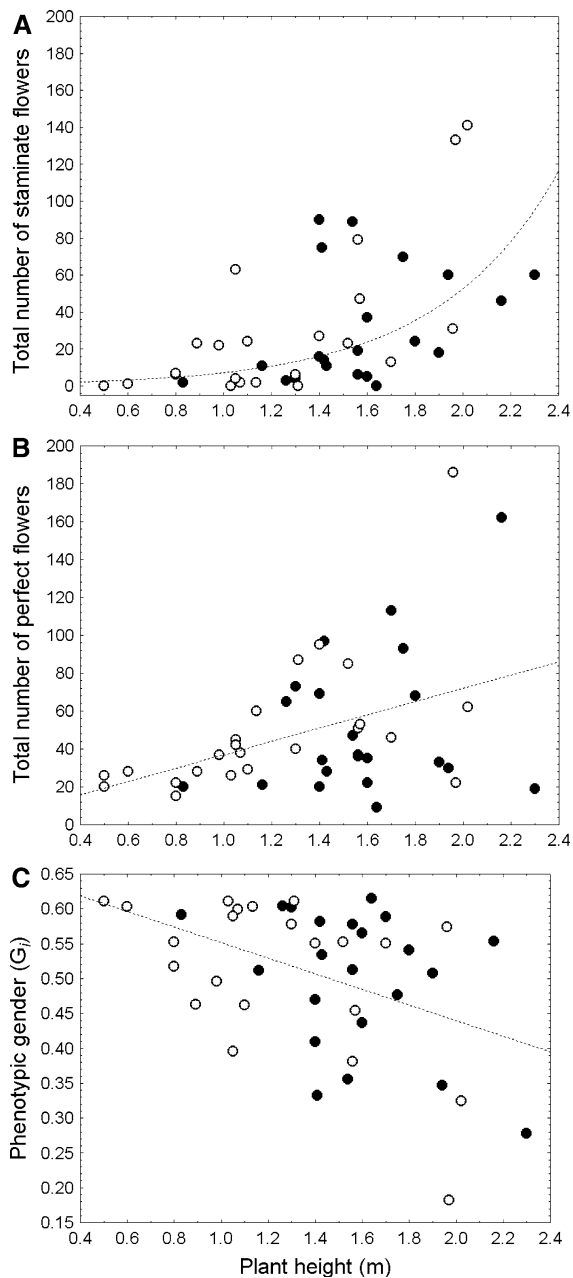
Fig. 2 Relationship between total staminate flowers (**a**), total perfect flowers (**b**), and phenotypic gender (**c**) with plant height in two populations of *Caesalpinia gilliesii*. Exponential fit for total staminate flowers–plant height relationship was considered significant at $P < 0.05$. *Empty circles* = San Nicolás, *solid circles* = La Quebrada. Slope differences between populations were not significant (Table 1). Removing plants with more than 130 staminate flowers from the analysis did not modify the observed trends

total flower number and plant height being significantly different between the two populations (Table 1). Pollination intensity was lower in LQ than in SN (0.20 ± 0.41 and 0.59 ± 0.31 pollen grains per ovule, respectively), and was not correlated with plant height in either population (Table 2). For shrubs in SN, however, fruit set and total fruit number per plant increased with plant height, whereas for shrubs in LQ the slopes did not differ from zero (Table 2; Fig. 3).

Discussion

We explored the relationship between plant height, local conspecific density, and sexual expression of an andromonoecious shrub in two populations, considering that plant size and local density may reflect differences in resources available for the reproductive function. Plant height influenced both absolute and relative sex allocation measures in *C. gilliesii*. The observed relationship between flower number (perfect and staminate) and phenotypic gender with plant height in *C. gilliesii* indicates a male-biased size-dependent sex allocation pattern, whereas no relationship with local density was observed at flowering.

A male-biased sex allocation strategy with increasing plant size was interpreted as favorable for pollen dispersal in wind-pollinated plants (e.g., Bickel and Freeman 1993; Klinkhamer et al. 1997). More recently, a male-biased SDS allocation pattern was also observed in an animal-pollinated species in which pollen dispersal would be favored in taller plants by increasing pollinator visits (Ishii 2004). While, we have no data on pollen dispersal in *C. gilliesii* by hawkmoths, it is unlikely that the observed plant height differences would significantly increase pollen dispersal. Using the presence of scales of hawkmoths' wings as an indicator of pollinator visits, we found no evidence that plant height could favor visits and hence pollen dispersal in *C. gilliesii* (Calviño 2006).

Alternatively, an increase in male allocation with plant size can be the result of decelerating female fitness curves (de Jong and Klinkhamer 1994). When increased seed production leads to competition among related seedlings, female fitness gain curve may level

Table 1 Regression slopes ± standard errors for the relationship between plant height and different parameters of sexual expression in two populations of *Caesalpinia gilliesii*

Sexual expression measures	San Nicolás	La Quebrada	
Staminate flower number	**2.50 ± 0.56** (0.48)	**1.72 ± 0.75** (0.21)	$F = 0.682$ $P = 0.414$
Perfect flower number	**47.26 ± 14.75** (0.31)	31.26 ± 21.09 (0.10)	$F = 0.324$ $P = 0.572$
Total flower number	**324.9 ± 42.34** (0.74)	94.90 ± 49.00 (0.16)	$F = 11.769$ $P = 0.001$
Phenotypic gender	**−0.13 ± 0.04** (0.30)	−0.11 ± 0.06 (0.14)	$F = 0.053$ $P = 0.820$

Slopes in bold were significantly different from zero at $P < 0.05$, the others were marginally significant at $P \leq 0.065$. R^2 values are between brackets. F values test for difference in slope between San Nicolás and La Quebrada populations in the ANCOVA. $N = 45$ shrubs

Table 2 Regression slopes ± standard errors for the relationship between pollination intensity, fruit set and total fruit number per plant with plant height in two populations of *Caesalpinia gilliesii*

	San Nicolás	La Quebrada	
Pollination intensity	−0.87 ± 0.048 (0.10)	0.15 ± 0.070 (0.27)	$F = 6.089$ $P = 0.018$
Fruit set	**0.13 ± 0.05** (0.22)	0.004 ± 0.041 (0.01)	$z = -2.684$ $P = 0.007$
Total fruit number	**40.32 ± 11.01** (0.39)	8.57 ± 5.99 (0.10)	$F = 11.34$ $P = 0.002$

Slopes in bold were significantly different from zero at $P < 0.05$. R^2 values are between brackets. F and z values test for differences in slope between San Nicolás and La Quebrada populations in the ANCOVA and generalized linear model, respectively. $N = 45$ shrubs
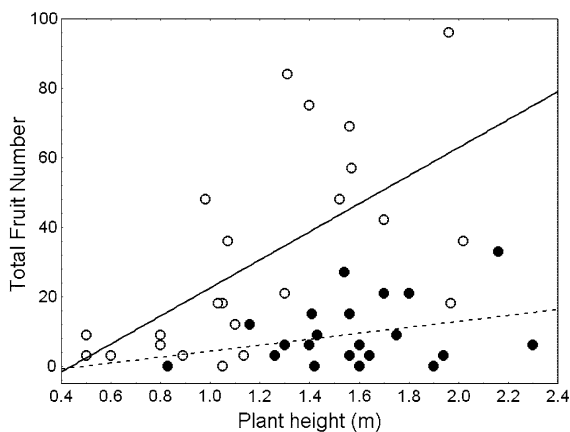
Fig. 3 Relationship between total fruit number and plant height in two populations of *Caesalpinia gilliesii*. *Empty circles* = San Nicolás, *solid circles* = La Quebrada

off, and saturate more quickly than male fitness curve (de Jong and Klinkhamer 1994). Since dispersal distances in *C. gilliesii* are rather short (Jausoro and Galetto 2001), related seedlings may compete for establishment, reducing female fitness returns of the mother plant (de Jong and Klinkhamer 2005). The occurrence of a male-biased SDS allocation strategy, however, requires that geitonogamy levels be independent of plant size (Klinkhamer and de Jong 1997),

and pollinators of *C. gilliesii* usually visit all the flowers of one inflorescence (Cocucci et al. 1992; Moré et al. 2006), promoting geitonogamous pollination. Nevertheless, geitonogamy may level off female fitness when pollinators are abundant (de Jong and Klinkhamer 1994), and because *C. gilliessi* is usually pollen-limited in the studied populations, it is rather unlikely that geitonogamy predominates to reduce female fitness. In addition, stigma receptivity usually starts after anther dehiscence and lasts more than the duration of pollen viability (Calviño 2006), which makes geitonogamy less likely. According to the available evidence, the male-biased SDS allocation strategy observed in *C. gilliesii* may have evolved to avoid local resource competition of related seedlings, but further studies are necessary to discard definitely the influence of geitonogamous pollination on the observed pattern of sex allocation.

Our results in *C. gilliesii* agree with several works in that SDS allocation patterns vary intraspecifically (e.g., Sarkissian et al. 2001; Dorken and Barrett 2003; Guitián et al. 2004; Méndez and Karlsson 2004; Cao and Kudo 2008). For the two populations studied, absolute allocation to female and male function (perfect and total flower number) increased with plant height in SN and LQ. In SN, however,

regression slopes tend to be steeper. Steeper slopes for the SDS relationship are likely in favorable environments (Méndez and Karlsson 2004 and references therein) and may decrease in environments with lower light availability (e.g., Cao and Kudo 2008) or disappear under low nutrient levels (e.g., Liu et al. 2008). A decrease in the slope between vegetative and reproductive allocation is also expected for woody perennial plants due to the biomechanical costs imposed by the increase in size (Weiner 1988); in agreement with this, plants in SN were, on average, shorter than in LQ and may exhibit lower size costs.

In addition, the positive slope for the plant height-local density relationship observed in SN can be interpreted as better quality microsites in SN than in LQ (e.g., Kunin 1992), and hence steeper slopes for the SDS relationship may reflect better environmental quality in SN than in LQ. Furthermore, since pollination intensity was size-independent, but both fruit set and total fruit number increased with plant height in SN, fruiting may have also benefited from higher resource availability in that population. Fruit set, however, also increased with local density in SN, and further research should then be aimed at disentangling the relative influence of plant size from that of local density on *C. gilliesii* fruit production.

Furthermore, absolute allocation to female function increased with plant height in *C. gilliesii*, whereas the relative SDS-allocation strategy observed was male-biased. In the andromonoecious *Veratrum nigrum*, Liao and Zhang (2008) also found a relative male-biased SDS allocation strategy and, similarly to our findings in *C. gilliesii*, increased perfect flower number with plant height. This apparent discrepancy may rely on the observation that relative and absolute measures yield different results, if larger plants divert disproportionately more resources to reproduction than smaller plants (Sarkissian et al. 2001). As Sarkissian et al. (2001) have pointed out, when total reproductive effort changes with plant size, absolute (e.g., flower number), and relative (e.g., phenotypic gender) measures of sex allocation will reflect different gamete contributions. Staminate flowers showed a rapid exponential increase with plant height in *C. gilliesii*, suggesting that taller plants would invest more resources in reproduction than shorter plants. Similarly, and despite only linear relationships were examined, the increase of staminate flowers of

V. nigrum with plant height is faster than that of perfect flowers (Liao and Zhang 2008). These findings suggest that an increase in reproductive investment in larger andromonoecious plants may be achieved by producing more staminate, less costly flowers.

A male-biased sex allocation pattern has, however, particular implications for andromonoecious species. First, maleness and fruit production increased with plant height in one population, but if shorter *C. gilliesii* plants were more pollen-limited than taller plants, fruit set might also increase with plant height and the observed trends would reflect a size-dependent pollination pattern. Nevertheless, pollination intensity did not correlate with plant size in any population; therefore, the assumption that smaller plants would be more pollen-limited than larger plants seems unlikely. Therefore, irrespective of the pollination level or the fruit set/plant height relationship, taller plants of *C. gilliesii* were male-biased in both populations. This agrees with previous studies in this species in which fruit set failed to explain the proportion of perfect flowers at the inflorescence level (Jausoro and Galetto 2001). Smaller inflorescences of *C. gilliiesii* are, however, male-biased (Calviño and Carrizo García 2005) and due to the inverse relationship between inflorescence size and plant height observed in this species (Calviño 2006), the results obtained suggest an architectural adjustment of sex allocation strategy. Changes in both plant height and inflorescence size may interact to produce the SDS-allocation strategy observed in *C. gilliesii*. Furthermore, given that inflorescence size may decrease at higher densities (e.g., Mustajärvi et al. 2001), density may influence sex allocation not only by differences in resource availability as expected here, but also by means of a non-resource mechanism, in which the aggregation of neighbors triggers an architectural response and, in turn, affect sex allocation.

Second, female fitness in andromonoecious species would be favored by an increase in staminate flower production when the optimum female allocation was achieved, and fruit set is not pollen-limited (Liao and Zhang 2008). An increase in staminate flowers may enhance fitness by increasing siring success, as in *S. carolinense* (Elle and Meagher 2000), and/or allowing selective fruit abortion, as suggested by Bertin (1982). Our results in *C. gilliesii* indicate that maleness may favor fruiting success, as well as in other andromonoecious species. For

instance, studies on other andromonoecious species have also shown that the production of staminate flowers may favor female fecundity (e.g., Vallejo-Marín and Rausher 2007; Liao and Zhang 2008). However, as Burd and Callahan (2000) have pointed out, when pollen limits fruit set, as is the case of *C. gilliesii*, extra flowers (non-fruiting perfect and staminate) should act attracting pollinators to increase female rather than male fitness. Accordingly, we expect that the male-biased size-dependent pattern observed in *C. gilliesii* at flowering would benefit fitness by attracting pollinators and improving selectivity by embryo abortion, which is a matter of future research.

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