



Cumulative individual seed production in the polycarpic *Caesalpinia gilliesii* (Fabaceae): effects of temporal variability in floral display, plant density and pollination

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ABSTRACT

In polycarpic species, floral display size and density of conspecific neighbours are time variable as well as their effects on pollination and fecundity. Here, we address how individual pollinator-dependent seed production responds to changes in floral display size and the density of flowering conspecific neighbours. Using path analysis, we disentangle the partial effects of floral display size, the density of flowering neighbours and pollination intensity on the total seed output of the partially self-compatible shrub *Caesalpinia gilliesii* during three consecutive reproductive seasons. We also modelled the effects of temporal variability in floral offer and pollination intensity (as the coefficient of variation) on cumulative seed production over the study period. Floral display size had either positive or negative effects on pollination intensity in different reproductive seasons, but conspecific density had no significant effect within each season. However, cumulative seed production increased under lower temporal variability in conspecific density. Our results suggest that, because of the dynamic nature of floral offer in a polycarpic species, the temporal changes in floral display size and density may counteract each other reducing the risk of successive pollination failures and increasing seed production over time.

Keywords: conspecific density, floral offer, path analysis, pollination variability, size-dependent fecundity.

INTRODUCTION

The abundance and distribution of the floral resource in plant populations are dynamic factors that vary in time and space, and have diverse consequences with respect to plant fecundity. The final effect that pollination has on fecundity depends on the variability of floral display size, the abundance of conspecific neighbours and the availability of soil nutrients, among other factors, but also on species attributes such as the

compatibility system (e.g., Vaughton 1991, Aizen 1997, Harder & Johnson 2005, Ågren *et al.* 2008). Variability in the local abundance of flowering conspecifics can influence the effect that floral display size has on pollinators' behaviour (Ohashi & Yahara 2002, Makino *et al.* 2007). For instance, floral display size may favour pollination under low but not under high conspecific density (e.g., Grindeland *et al.* 2005). Moreover, individual plants in denser patches of conspecifics can either decrease or increase their seed production due to

stronger resource competition (e.g., Stoll & Pratt 2001), better resource availability (e.g., Bosch & Waser 2001) or effects mediated by mutualistic and antagonistic plant-animal interactions (e.g., Stein *et al.* 2013). In addition, floral display size can increase attractiveness to pollinators, visitation rates and pollen deposition (e.g., Mitchell 1994, Cariveau *et al.* 2004), but also geitonogamous pollination through within-plant pollinator movement (Klinkhamer & de Jong 1993). Consequently, fecundity can increase substantially with floral display size in a self-compatible species (e.g., Mustajärvi *et al.* 2001, Jacquemyn & Brys 2010), but not in a self-incompatible or highly outcrossed species (e.g., Kato & Hiura 1999).

The size of the floral display and the density of conspecific flowering neighbours usually change yearly in polycarpic plants with different life forms (e.g., Copland & Whelan 1989, Kato & Hiura 1999, Somanathan *et al.* 2004, Jacquemyn & Brys 2010) and consequently the degree of pollen/resource limitation may change accordingly (Copland & Whelan 1989, Ivey *et al.* 2003). This temporal variability in the floral offer at the population level may have diverse consequences on pollination and fecundity of the individuals. On the one hand, for species which strongly depend on pollinators for seed production, temporal variability in floral display size, conspecific density, or in both together would increase pollination variability, thus reducing the chances of leaving descendants for individuals. For instance, if increases in floral display size and the density of flowering neighbours were positively correlated over time, plants would become increasingly attractive to pollinators over time. Enhanced pollinator attraction could trigger either an increase or a decrease in pollination and fecundity, depending on the prevalence of facilitative versus competitive interactions between the flowering plants and their pollinators (Rathcke 1984). However, if temporal variability in floral display size offsets the temporal variability in density (e.g., temporal increases in floral display and density are uncoupled in time), the potential for attracting pollinators could remain similar and therefore would not affect the probability of setting seeds over time. On the other hand, when a plant's seed production is mainly resource limited rather than pollen limited (e.g.,

Vaughton 1991), temporal variability in pollination can be less important for seed production than the resources available to mature seeds (Copland & Whelan 1989, Andrieu *et al.* 2007). Differences in floral display size and conspecific density reveal differences in the resources available for seed production (e.g., Kunin 1992, Andrieu *et al.* 2007, Stein *et al.* 2013). Therefore, as individuals are subjected to successive temporal changes in floral display size or in the density of conspecifics, they may experience changes in resource availability (Ågren *et al.* 2008), and in fecundity.

Several studies have analysed the relationship between annual seed production and its temporal variability (reviewed by Koenig *et al.* 2003), or between temporal variability in pollination and variability in seed production (Price *et al.* 2005), but up to now less attention has been given to disentangling the factors (e.g., floral display or density) potentially influencing temporal variability in pollination and annual seed production by polycarpic individuals. Furthermore, studies which attempt to disentangle the effects of floral display size and density on pollination and fecundity either focus on monocarpic perennials (e.g., Mitchell 1994, Colas *et al.* 2001) or only test for effects during one reproductive event (e.g., Ohashi & Yahara 2002, Cariveau *et al.* 2004). Therefore, the effect that the temporal variability of floral display and density may have on pollination and fecundity in a polycarpic species remains poorly understood.

While studying the partially self-compatible, hawkmoth-pollinated shrub *Caesalpinia gilliesii*, it was observed that fruit production can increase with both plant height (a proxy of floral display size) and local density of flowering conspecifics (Calviño & Galetto 2010). Fruiting seems to be resource rather than pollen limited because plant height and conspecific density were not correlated with pollen deposition (Calviño & Galetto 2010). However, given that pollination intensity may vary considerably between years and that fruiting success depends on pollinator activity (Calviño 2006), the relative importance of pollen deposition to seed production may be temporally variable in this species, and this may also be the case for the relative influence that floral display and conspecific density have on

pollination and fecundity. In fact, the same individual could experience a considerable change in floral display and local conspecific density over the course of a few years (Calviño 2006) thus offering a suitable system for studying the effects of temporal variability in floral offer on pollination and fecundity.

Using path analysis we examined how flower display size and the density of flowering conspecifics affect pollination and seed production by individual plants during three successive reproductive seasons in a population of the shrub *Caesalpinia gilliesii*. We also modelled the effects of temporal variability in floral display, density and pollination on the cumulative seed production of the same individuals over the three seasons. We used a cumulative measure of seed production instead of average seed production in order to obtain a clearer picture of net reproductive output. Our aim was to address the following questions: (i) How do floral display size and the density of conspecifics are related (or not) with pollination and total seed number in individuals of *C. gilliesii* during different reproductive seasons? (ii) Does temporal variability in floral display size or in the density of conspecifics influence temporal variability in pollination? and if so (iii) How does cumulative seed production depend on temporal variability in floral display size, conspecific density and pollination?

MATERIAL & METHODS

Study species and site—*Caesalpinia gilliesii* (Fabaceae) is a native shrub (up to 2.5 m height) that grows in the arid and semiarid regions of central Argentina. At the study site *C. gilliesii* grows sparsely beneath the canopy of dominant trees, or forms pure patches in canopy gaps. It flowers from September to December and the flowering period within a population lasts up to 60 days (Jausoro & Galetto 2001). In this andromonoecious shrub, the relative size-dependent sex-allocation pattern is similar between populations and within a population in different years (Calviño 2006, Calviño & Galetto 2010). Although the species displays inflorescences (Fig 1 A) with perfect and staminate flowers simultaneously, both flower types produce similar amounts of nectar (Fig 1 B) with a similar sugar composition (Jausoro & Galetto 2000) and thus

differential attractiveness to pollinators for perfect and staminate flowers is unlikely. *C. gilliesii* strictly depends on sphingid moths to set fruits (Figs. 1 C-D), and it is pollinated by at least seven species of nocturnal long-tongued hawkmoths that usually visit all the flowers of one inflorescence (Cocucci *et al.* 1992, Calviño 2006). Though it shares pollinators with other simultaneously flowering species, *C. gilliesii* does not have heterospecific pollen deposition owing to a specialized mechanism of pollen transfer (Calviño 2006, Moré *et al.* 2006). At the study site, *C. gilliesii* is able to set fruits by hand-cross and geitonogamous pollination, but not by self-pollination (Calviño 2006).

The study population (31°27'22" S; 64°25'22" W) was located on the eastern slope of Sierras Chicas Hills, Cordoba province, Argentina. The vegetation is Bosque Serrano woodlands located within the Chaco phytogeographical province (Cabrera 1994), and with patches of trees (*Lithraea molleoides*, *Prosopis* spp. and *Aspidosperma quebracho-blanco*) and shrubs (mainly *Acacia caven*) intermingled with open clear-cut areas. In the study area, most of the species flower between September and March, the months of the summer rainfall, when precipitation may surpass 700 mm year⁻¹. The climate is warm temperate to subtropical, with mean annual temperatures of 19 °C.

Floral display size—We marked a total of 25 focal plants along a 300 m transect crossing patches of both dense and sparse vegetation. On each focal plant we counted all (staminate and perfect) open flowers every four days over the entire the flowering period during 2000, 2002 and 2003. A late frost killed all bud inflorescences in the spring of 2001 and plants did not flower again at the study site that season. Some plants were damaged between 2000 and 2002 and were replaced by other plants to maintain the minimum of 25 shrubs per year.

Density of flowering conspecifics—During each reproductive season, we counted the number of conspecific flowering neighbours in a circumference with a 3 m radius around each focal plant; flowering conspecific density was expressed as the number of conspecific flowering neighbours per square meter. The radius length used represents the usual foraging distance

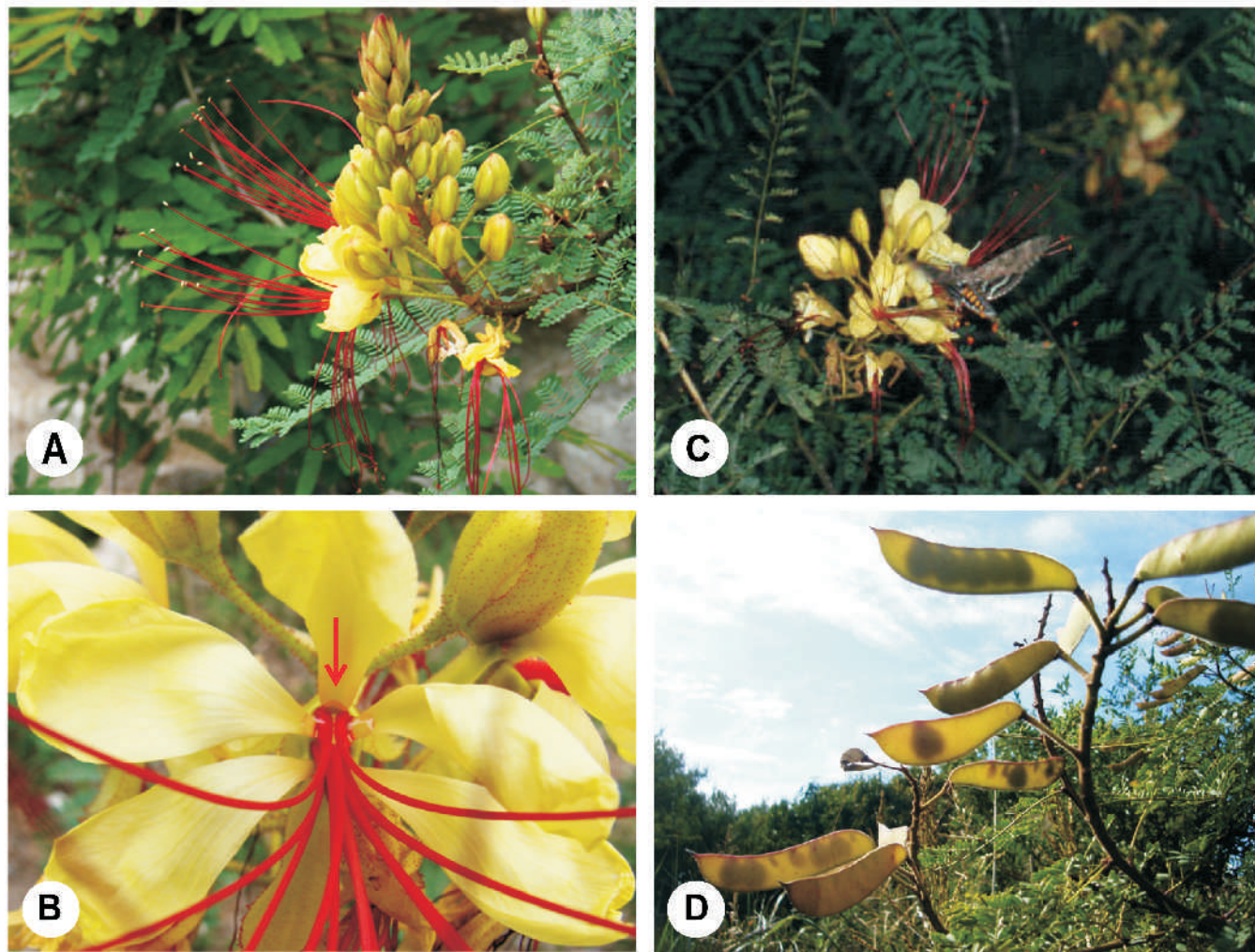


Fig. 1— *Caesalpinia gilliesii*. A. Inflorescence showing flowers at the beginning of the anthesis. B. An open flower showing a nectar droplet indicated by the arrow. C. *Manduca diffusa*. D. Developing fruits.

of *C. gilliesii*'s pollinators (Calviño 2006). Local densities around focal plants of flowering and all conspecifics (flowering and non-flowering plants) were positively correlated in this and other populations of *C. gilliesii* (Calviño 2006) so we used the density of flowering conspecifics because it is a better indicator of attractiveness to pollinators.

Pollination—At flower senescence, we counted the number of pollen grains deposited on the stigmas of perfect flowers on each focal plant in the field using a 20 \times magnifying glass (20-25 stigmas per plant/season; $N=1470$ stigmas in total). We calculated pollination intensity on a per plant basis as the ratio of the average

stigmatic pollen load over the average number of ovules per style/plant (Kearns & Inouye 1993). Mean ovule number per style is 7.7 ± 0.4 for the population studied (Calviño & Carrizo García 2005).

Seed production—We collected all mature fruits produced by each focal plant and counted the total number of viable (non-aborted) seeds per fruit each season ($N=849$ fruits and $N=2636$ viable seeds from 25 focal plants sampled each year over three years). Aborted seeds can be easily distinguished from viable ones by their smaller size, thinner coats and brownish colour. The total number of viable seeds produced per plant was used as a measure of fecundity. Cumulative

seed production per plant was obtained as the sum of the total number of seeds produced by each of those focal plants that remained across the three years (N=16).

Temporal variability in floral display size, density and pollination—Following Herrera (1998), we calculated the coefficient of temporal variation (CV_i , hereafter) for floral display, the density of flowering conspecifics and pollination intensity over the three study years for each of the focal plants which remained undamaged throughout the study period (N=16). CV_i was calculated as the standard deviation above the mean *100.

Statistical analysis—We hypothesized the effect of floral display size and conspecific density on plant pollination intensity and total seed production within each reproductive season using a path diagram (Model A, Fig. 2). We assumed that both floral display size and density were correlated with each other and might influence total seed number indirectly through the pollination pathway or directly by the availability of resources (i.e. the variance in total seed number that is independent of the pollination intensity path). We used Multigroup Structural Equation Modeling (MSEM) to

test the fit of the model for the three reproductive seasons simultaneously (2000, 2002 and 2003), considering each season as a group and using the 25 focal plants studied in each reproductive season. MSEM analysis tests the fit of the model for two or more data sets simultaneously (i.e. sets from reproductive seasons), assuming that the observation units (i.e. plants) are not subject to the same conditions in each group (Shipley 2000). This method was used instead of testing three independent models for each reproductive season because most of the plants employed were the same; i.e., the reproductive response in one reproductive season was not completely independent of that of the previous or following seasons. We analysed two alternative models to our basic Model A, to test the effect of only one factor (floral display size in Model B and conspecific density in Model C) on pollination intensity and total seed number. We tested the goodness-of-fit of the models with a statistic that approximates a chi-square distribution. The chi-square goodness-of-fit statistic tests the null hypothesis that the covariance matrix implied by the model does not differ from that observed (Shipley 2000). Because the alternative models are nested in Model A, they can be also compared through a chi-square test against Model A

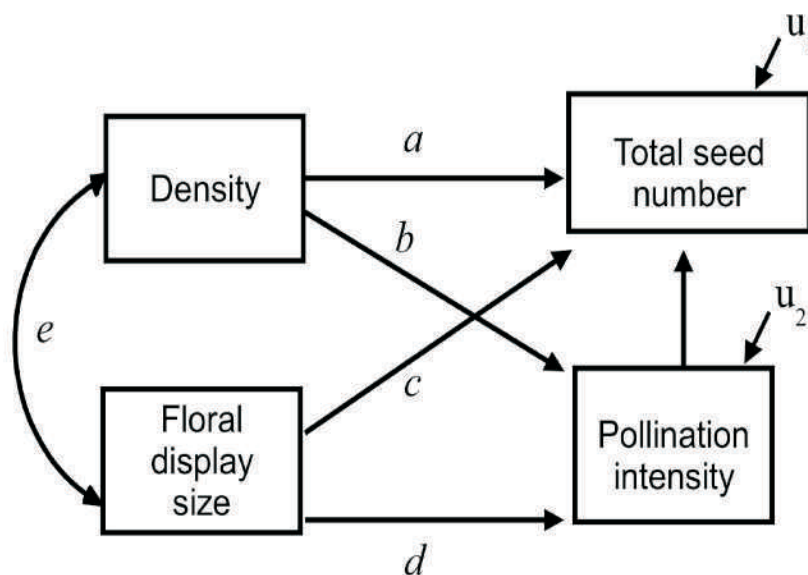


Fig. 2— Basic model (Model A) for the hypothesized effects of floral display size and the density of conspecifics on pollination intensity and total seed number in *Caesalpinia gilliesii* plants. Floral display size and density can influence total seed number either directly (a , c , respectively) or indirectly by affecting pollination intensity (b , d). U_1 and U_2 represent unmeasured factors.

Table 1— Goodness of fit for the three path models analysed, and nested comparisons with respect to the basic model shown in Fig. 2 (Model A). AIC= Akaike Information Criterion, TLI= Tucker-Lewis index

Model	Goodness of fit measures					Nested comparisons with Model A		
	χ^2	<i>df</i>	<i>P</i>	AIC	TLI	χ^2	<i>df</i>	<i>P</i>
A	0.63	2	0.73	80.63	1.54
B	7.12	8	0.52	75.12	1.09	6.49	6	0.37
C	44.71	8	0.00	112.71	-2.66	44.07	6	0.00

(Shipley 2000). Given that well fitting models usually yield consistent results on different indices (Tabachnick & Fidell 1996), we also used the Akaike Information Criterion (AIC) and the Tucker-Lewis index (TLI) to contrast the fit of the data to the proposed models. TLI compares the chi-square values of each model with the one that assumes complete independence taking into account the degrees of freedom of the model (Tabachnick & Fidell 1996). TLI values close to 1 indicate a very good fit while a higher AIC value indicates a poorer fit. The path coefficients and the MSEM analyses were estimated using the maximum likelihood method included in the AMOS 4.0 package (SmallWaters Corporation 1999). The multivariate normality assumption for the model was also examined with the same package. The variance inflation factor (VIF) among the variables was explored using the collinearity diagnosis of SPSS (SPSS 10.0; SmallWaters Corporation 1999). VIF values were lower than 2 in all cases, so a collinearity effect was discarded (Zuur *et al.* 2010).

To test the effects of temporal variability in plant size, density and pollination intensity on the cumulative seed number of focal plants we used the same basic model given in Figure 2, but with the CV_i values of each predictor variable on a separate path model. The resulting path model allowed us to postulate how both the direct and indirect effects of variability in the floral resource may have influenced cumulative seed production directly or through variability in pollination. The model also summarizes the results obtained for the effects of floral display size and density on pollination and total seed production in different reproductive seasons.

Owing to the small sample size (i.e. only 16 of the original focal plants were used throughout the study

period) we obtained the path coefficients and did not test for model fit. The validity of this procedure to test potential causal relationship is theoretically justified (e.g., Sterck & Bongers 2001, Vazquez & Simberloff 2004, Price *et al.* 2005)

RESULTS

Effects of floral display size and conspecific density on pollination and seed production—Model A, which included the simultaneous effects of floral display size and density on total seed production per plant, fitted the data (Model A; Table 1), as did the more restricted Model B, which was not significantly different from Model A (Table 1). Assuming Model A to be correct, Model B is a more parsimonious solution that also had the best fit according the AIC and TLI values (Table 1). Model B offers a more accurate representation of the dynamics of these variables than Model A does, owing to its parsimony (e.g., Mitchell 1992). Density had no significant effects on pollination or seed number for any year. However, in 2003 floral display size and density were positively correlated: individuals with more flowers occurred in denser patches (Fig. 3). Pollination intensity had a positive, significant effect on total seed production in 2000 and 2002 and a positive, marginally significant effect in 2003 (Fig. 3). In addition, pollination intensity first increased with floral display size in 2000 and then decreased with floral display in 2002 and 2003 (Fig. 3). Concurrently, the direct effect of floral display size on seed number showed the opposite pattern, changing from negative in 2000 to positive in 2002-2003 (Fig. 3). The total effects of floral display size resulting from the sum of the direct and indirect effects in the path model were always positive, and increased abruptly from 2000 to 2002 (standardized total effects: 0.016, 0.837, 0.799 for each season, respectively).

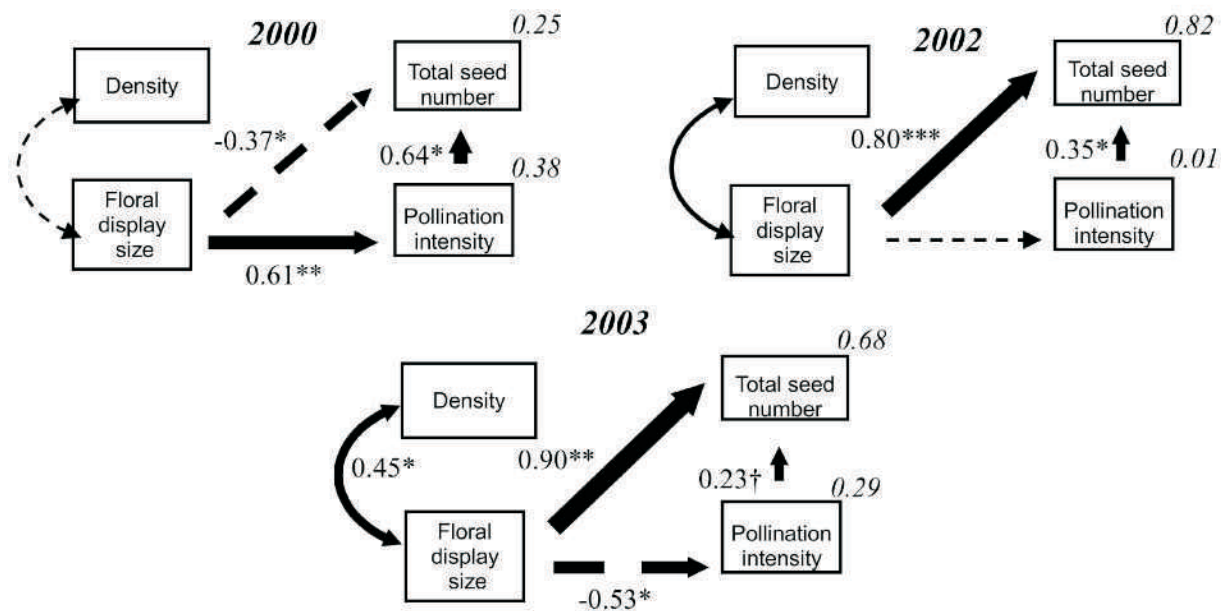


Fig. 3—Resolved path diagrams for the most parsimonious Multigroup Model (Model B) obtained for the hypothesized effects of floral display size and the density of conspecifics on pollination intensity and total seed number in *Caesalpinia gilliesii* plants during three reproductive seasons. Solid lines indicate positive effects and dashed lines, negative effects. Line thickness is proportional to the value of the standardized path coefficient beside each arrow. Only significant path coefficients are shown. Variance explained (R^2) is in italics. $^\dagger P=0.07$, $*P<0.05$, $**P<0.01$, $***P<0.001$

Temporal variability in floral display size, conspecific density and pollination and their effects on cumulative seed production—Floral display size per plant was highly variable among years, ranging from ~100 to more than 350 flowers on the same plant, with a similar proportion of perfect flowers across seasons (results not shown). This temporal increase in the floral display was also variable between plants, ranging from +9% to +245%. However, for the same period, the floral display of six of the focal plants decreased to a lesser degree (range: -16% to -100%).

Focal plants with no flowering neighbours within a 3 m radius were only recorded during the first season (2000). The density of flowering conspecifics increased for most of the focal plants from 2000 to 2003, mainly because juveniles became reproductive. On average, 2 ± 1.5 juveniles started flowering from 2000 to 2003 within the 3 m radius around each focal plant. The conspecific density of two focal plants increased from 0.04 to 0.21 flowering plants.m⁻²; i.e., density increases ca. 400%. However, for most plants density increases between a range of 25 to 200%.

Changes in pollination intensity were more pronounced than those in floral display or conspecific density, with most plants showing a substantial increase in average stigmatic pollen load. The highest pollen load increase was from an average of 0.4 ± 1.4 in 2000 to 8.7 ± 12.8 pollen grains per style/plant in 2003; a 20-fold increase over the study period. For most plants, however, increases in pollen load ranged from a three- to a six-fold increase. Regarding pollination intensity (i.e. the number of pollen grains on a per ovule basis), on average 60% of the ovules of an individual would be developed seeds in 2003 compared with the 2% in 2000.

The temporal CV_i per plant ranged from 6% to 65% for floral display size, and from 0% to 87% for density of flowering conspecifics. These CV_i were lower than those calculated for pollination intensity which ranged from 70% to 164% among focal plants. Cumulative seed production over the three reproductive events ranged from a minimum of ten to a maximum of 460 seeds per plant.

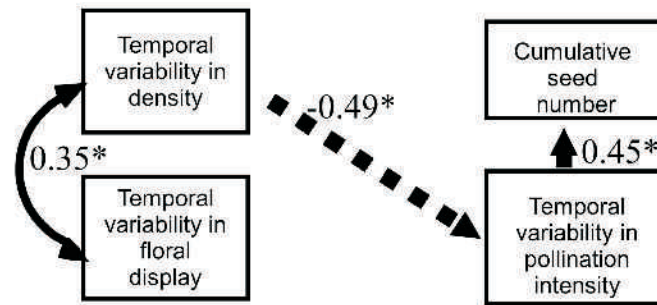


Fig 4— Resolved path diagram for the hypothesized effects of temporal variability in floral display size, the density of conspecifics and pollination intensity on cumulative seed number in *Caesalpinia gilliesii* plants over three reproductive seasons. Solid lines indicate positive effects and dashed lines, negative effects. Line thickness is proportional to the value of the standardized path coefficient beside each arrow. Only significant path coefficients are shown. * $P < 0.05$.

Temporal variability in floral display size and density were positively and significantly correlated, but only temporal variability in density had a significant, negative effect on pollination variability which, in turn, had a positive effect on cumulative seed production (Fig. 4). Accordingly, focal plants with temporally less variable densities (i.e., lower CV_i in the density of flowering conspecifics) experienced greater temporal variability in pollination, but also reached a higher cumulative seed production than individuals with more variable densities (i.e., higher CV_i in the density of flowering conspecifics). Temporal variability in floral display had also a direct, negative effect on cumulative seed production, however this effect was not significant, and the effect of temporal variability in floral display on temporal variability in pollination was not significant either.

DISCUSSION

Seasonal effects of the floral offer—Floral display size has been shown to be crucial for attracting pollinators and seed production in different polycarpic species (e.g., Klinkhamer & de Jong 1993; Gómez & Zamora 2000; Ehrlén 2002), with this effect modulated by local conspecific density (Ohashi & Yahara 2001; 2002). Here, we found for *Caesalpinia gilliesii* that the magnitude and direction of the effects that floral display size and conspecific density had on pollination and total plant seed production were significant and variable with time. Given that pollination increased with floral display

size in one of the reproductive season (2000) but decreased later (2003), the change in the effect of floral display size on pollination can be interpreted as a switch in the pollinators' foraging strategy as the density of conspecifics increases in the same plant population over different reproductive seasons. Although the density of conspecifics had no a general significant effect on either pollination or seed production, our results suggest that pollinators (long-tongued hawk moths) mainly foraged within plants of *C. gilliesii* with large floral displays where the density of conspecifics was low (in 2000) and foraged in plants with rather smaller floral displays when more flowering neighbours were available (in 2003). Similar behaviour has been observed in bumblebees which exhibit a stronger preference for highly flowered plants at lower densities (Ohashi & Yahara 2001; but see Grindeland *et al.* 2005). *Manduca sexta*, one of the main pollinators of *C. gilliesii* (Moré *et al.* 2006), responds positively to greater floral density (Raguso & Willis 2002). Furthermore, spatial and temporal changes in floral offer can modify the scale of pollinators' response (Thomson 1981). Floral display size of *C. gilliesii* plants was positively correlated with density in one of the reproductive seasons (2003); this combination at the individual and population levels may facilitate pollinators to increasingly perceive clusters of flowers belonging to neighbouring individuals as a unit (e.g., Murawski 1987). If this is true, the aggregation of flowering individuals of the population as a whole rather than the local flowering density of conspecific plants

may have triggered the seasonal changes in the behaviour of *C. gilliesii*'s pollinators and, consequently, produced different effects on pollination according variations in floral display size.

As found in previous studies that used path analysis (e.g., Mitchell 1994, Cariveau *et al.* 2004), the direct and indirect (i.e. through the pollination path) effects of floral display size on total seed number of *C. gilliesii* were different. Consequently, and depending on the relative magnitude of direct vs. indirect effects in *C. gilliesii*, the effect of floral display on total seed number was positive in two (2002 and 2003) of the three (in 2000 the total effect in the path model was zero because indirect and direct effects of plant size cancelled each other out) sampled reproductive seasons. Variable effects of floral display size on fecundity are expected under environments in which pollen limitation varies. It has been found that in the absence of pollen limitation, seed production is positively correlated with plant size, and fecundity is mainly resource limited (e.g., Griffin & Barrett 2002, Andrieu *et al.* 2007). Conversely, where pollen limitation is strong, individuals of different sizes should exhibit similar fecundities because resource limitation is expected to be negligible under these conditions (Griffin & Barrett 2002). In agreement with this, and considering that floral display size is a measure of plant size in *C. gilliesii*, floral display size had no effect on total seed number for the reproductive season with lowest pollination intensity (2000), but did have a positive effect on seed number the following seasons when pollination intensity increased (2002 and 2003). Since natural levels of pollination intensity and pollen limitation are closely related in *C. gilliesii* (Calviño 2006), the species appears to be mainly pollen limited in years with low pollination intensity but resource limited in years with higher pollination intensity (e.g., 2000 vs. 2003), a trend found for different polycarpic species (e.g., Copland & Whelan 1989, Baker *et al.* 2000, Griffin & Barrett 2002, Ivey *et al.* 2003).

Temporal variability in the floral offer and cumulative seed production—Analysing how temporal variability in floral display size, density of conspecific neighbours and pollination intensity affects the seed production of individual plants is particularly

relevant in polycarpic plants, given that it allows us to understand the relative contribution of different individuals to the population's reproductive dynamics. As stated in Herrera's review (1998), population variability in seed production is an individual-based phenomenon. Therefore, to understand the underlying mechanisms responsible for such variability it is necessary to identify the roles of individuals in generating such patterns (Herrera 1998). For instance, individuals of the polycarpic species *Silene virginica* that flowered for three consecutive years contributed less to the population's seed pool with their cumulative seed production than individuals that only flowered two years (Dudash & Fenster 1997). Contrasting results were obtained for the herbaceous *Paeonia officinalis* where larger individuals that flower every year made the greatest seed contribution (Andrieu *et al.* 2007). In our study, however, those focal *C. gilliesii* plants that flowered during all three consecutive reproductive seasons, temporal variability in floral display size did not affect temporal variability in pollination or cumulative seed production per individual. Interestingly, we found that a factor extrinsic to the plant, such as temporal variability in the density of flowering conspecifics, influenced the individuals' contribution to the seed pool by means of its negative effect on pollination variability. This unexpected result may reflect how temporal variability in the density of conspecifics affected pollination variability and plant fecundity. For those plants whose flowering conspecific density was more variable over time, competition by pollinators may have increased, thus reducing pollen deposition and seed production. Increasing competition for pollinators over time is likely in the study population because first, the number of flowering neighbours around the focal plants of *C. gilliesii* tended to increase in successive years and second, larger floral displays progressively occur in denser patches, increasing the available floral offer surrounding each focal plant. For competition to have a negative effect on a plant's fecundity, nevertheless, a reduction in pollination is necessary (Caruso 1999). However, the temporal increase in pollination and seed production registered for *C. gilliesii* do not support a negative effect of competition on pollinators/pollination. On the contrary,

it suggests that temporal variability in plant density may relax competitive behavior and enhance pollination and fecundity over time. These results suggest that when the floral conspecific neighbourhood remains stable from year to year, temporal changes in the abundance and composition of pollinator assemblage of *C. gilliesii* (caused by differences in foraging behaviour, variability in the abundance of co-flowering hawkmoth-pollinated species, larval/adult depredation, etc.) have a more obvious impact on the pollination service provided to individuals than when their floral neighbourhood varies between reproductive seasons. If animal pollinators visiting dense and sparse patches do differ as well as do their foraging strategies (Esseberg 2013), such patterns may help to explain the results obtained for *C. gilliesii* but further studies are needed to confirm these ideas.

In summary, the annual seed production by individual plants of *C. gilliesii* seem to depend more on floral display size than on the density of flowering conspecifics. An increase in cumulative seed production, however, varied with temporal variability in local conspecific density, rather than on variability in floral display size. The relevance of these findings for the local survival of *C. gilliesii* populations will depend on the relative impact that cumulative seed production has on population growth rates. Contrary to common expectation, it has been shown that fruit and seed production can have an important influence on the population growth rates of long-lived polycarpic species (e.g., Jacquemyn *et al.* 2010; but see García *et al.* 2008). Furthermore, increasing the number of flowers per plant may also increase population growth rates through fruiting success (Ehrlén 2002), whereas temporal (i.e. inter-annual) switches in the flowering/non-flowering stage can reduce population growth rates (Jacquemyn *et al.* 2010). Therefore, the effects of both temporal variability in floral display and the density of flowering conspecifics on pollination and fecundity of *C. gilliesii* could then influence the population growth rate of this polycarpic species.

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