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What is left after sex in fragmented habitats? Assessing the quantity and quality of progeny in the endemic tree *Prosopis caldenia* (Fabaceae)

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ABSTRACT

Prosopis caldenia (caldén) is a commercially valuable tree endemic to Central Argentina, a region that holds one of the highest estimates of deforestation rates worldwide. Caldén woodlands within Córdoba province currently remain as a highly fragmented mosaic with a single continuous area of forest left. Here, we assess reproduction, seed predation, and progeny performance of trees growing in continuous forest, small forest fragments and isolation. By assessing both mutualistic and antagonistic interactions we aim to determine net fragmentation effects on the quantity and quality of the surviving progeny. Contrary to expectations, the probability of setting fruits and seeds as well as the levels of seed predation were similar among trees growing across the three contrasting landscape conditions. However, trees growing in isolation produced significantly larger numbers of flowers than trees growing in continuous forest. Thus, the absolute quantity of progeny left for potential recruitment was higher in isolated trees, despite their lower pollination efficiency. However, progeny generated in continuous forest significantly outperformed the progeny from forest fragments and isolated trees, which also suffered higher levels of mortality. Finally, the cumulative performance across all measured life stages was also significantly greater in continuous forest. Therefore, it is within the last continuous forest tract that progeny produced may successfully grow and survive in natural conditions. Assurance of long-term persistence of remaining caldén populations should involve the incorporation of propagules from the continuous forest together with effective restoration efforts to enable gene flow via pollen and seeds among populations through forest corridors.

1. Introduction

Land use changes imposed by human activities represent the main driving forces behind current biodiversity loss around the globe (Sala et al., 2000). Particularly in developing countries, the rapid and widespread expansion of agricultural frontiers over the past decades has drastically reduced the original area of native forests (Skole and Tucker, 1993; Dinerstein et al., 1995; Lambin and Meyfroidt, 2011). This is evidenced in several regions of South America and Asia, with some of the highest estimates of deforestation rates worldwide, as reported for Central Argentina (Dinerstein et al., 1995; Zak et al., 2004, 2008). While there are no clear perspectives of reversing or ending this process, conservation biology research must be oriented to assessing the immediate, mid, and long-term consequences of habitat loss in the viability and persistence of plant populations, which represent the sources of potential habitat regeneration for the future.

Landscape changes driven by habitat fragmentation can alter mutualistic interactions involved in sexual reproduction and seed dispersal, and hence potentially affect the reproductive success and genetic connectivity of remnant populations; key aspects for long-term plant population persistence (Sork et al., 1999; Young and Clarke, 2000; Hobbs and Yates, 2003; Aguilar et al., 2006, 2008, 2009; Sork and Smouse, 2006; Eckert et al., 2009). The amount of progeny produced in a reproductive event by plant individuals growing in fragmented habitats is an important demographic parameter, as it defines the maximum population recruitment potential for the next generation (Wilcock and Neiland, 2002). However, another important feature that determines the recruitment of populations is the genetic and biological quality of those progeny (Cascante et al., 2002; Mathiasen et al., 2007; Gonzalez-Varo et al., 2010; Ashworth and Martí, 2011).

The quality of progeny can be mainly determined by maternal effects and the levels of outcrossing (or selfing) in a given reproductive event (e.g., Dudash, 1990; Charlesworth and Willis, 2009). In this regard, it has been recently observed that outcrossing rates in fragmented populations are, on average, significantly lower, while the overall mean inbreeding coefficient of progeny

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is significantly higher in comparison to populations in continuous habitats (Aguilar et al., 2008; Eckert et al., 2009). Such results suggest changes in mating patterns of fragmented plant populations towards selfing and/or mating among relatives, increasing inbreeding and the likelihood of inbreeding depression. Rather limited research, showing divergent results, has been conducted to evaluate plant progeny performance in fragmented habitats; i.e., the *quality* aspect of reproductive success (e.g., Kery et al., 2000; Cascante et al., 2002; Fuchs et al., 2003; Kolb, 2005; Krauss et al., 2007; Yates et al., 2007; Mathiasen et al., 2007; Gonzalez-Varo et al., 2010; Ashworth and Martí, 2011).

Furthermore, seed predation is an important selective pressure that determines the amount and characteristics of surviving progeny for population recruitment (Crawley, 2000). Although habitat fragmentation is expected to reduce seed predation by decreasing the abundance of predators, the limited research on this antagonistic interaction shows inconsistent response patterns (Cascante et al., 2002; Chacoff et al., 2004; Ward and Johnson, 2005; Burgos et al., 2008). Particularly in the Fabaceae family, and for the genus *Prosopis*, seed predation by bruchids (Coleoptera) is probably one of the main selective forces in determining progeny survival (Center and Johnson, 1974; Janzen, 1980). Due to this tight antagonistic relationship, any alteration in bruchid abundance due to habitat fragmentation should have large effects on plant demography (Wright and Duber, 2001; Chacoff et al., 2004).

Many studies have reported negative habitat fragmentation effects on the abundance and/or richness of different animal taxa involved in both mutualistic and antagonistic interactions with plants (e.g., Didham et al., 1996; Winfree et al., 2009; Aguilar et al., 2009). Therefore, the balance in fragmentation effects on both types of interactions will determine the net effects on the quantity and quality of the surviving progeny. For example, decreased pollination and seed output in fragmented habitats maybe offset by similar decreases in seed predation. Whether such compensation occurs or not, and whether surviving progeny generated in fragmented habitats are less vigorous than progeny from continuous forests has been scantly assessed (but see Cascante et al., 2002).

Here we evaluate the effects of habitat fragmentation on reproduction, seed predation, and progeny performance of *Prosopis caldenia*, a self-incompatible, endemic tree of Central Argentina. We hypothesize that individuals growing in fragmented and isolated conditions produce less quantity and quality of progeny as a result of decreased pollination and higher incidence of endogamous crosses among parental plants. However, we also hypothesize that seed predation is lower in fragmented forests and isolated trees. Therefore, the final proportion of viable, non-predated seeds should be similar in continuous and fragmented conditions; but the progeny from trees in continuous forest should outperform the progeny from trees growing in fragmented forests or in isolation.

2. Methods

2.1. Studied system and species

The Caldén Floristic District is a temperate semiarid, thorny deciduous region dominated by the endemic tree Caldén (*P. caldenia* Burkart, Fabaceae), and constitutes together with the Ñandubay and Algarrobo Districts, the southernmost forest formation from the Dry Chaco, known as the Espinal phytogeographical region (Cabrera, 1976). Originally, these were semi-open or open woodlands dominated by *P. caldenia* and accompanied by *Prosopis flexuosa* DC, *Celtis ehrenbergiana* (Klotzch) Liemb., and *Geoffroea decorticans* Gill. ex. H. et A. Burkart. Today, *P. caldenia* woodlands (known as the *Caldenales*) present a patchy distribution across semiarid western-central Argentina as a result of intense deforestation, agriculture, and fire throughout the area over the past several decades (Zak et al., 2008; Bogino and Villalba, 2008). While the area of original woodlands decreased in size, the relicts of adjacent grasslands that had not been occupied by crops experienced woody encroachment by caldén; a process favored by sheep and cattle grazing (Distel et al., 1996; Dussart et al., 1998). *P. caldenia* represents an important economic resource; for more than a century its wood has been largely used for fuel, carpentry, and floors (Bogino and Villalba, 2008).

Within the Province of Córdoba in particular, a century ago the *Caldenales* constituted nearly 20% of its southeastern territory (ca. 3 million Ha). However, the continuing expansion of agricultural practices during the past decades, which has been facilitated by economic trends (higher prices of agricultural products, particularly soybean), technological improvements (direct sowing), and social factors related to changes in land tenancy, have resulted in a drastic reduction of its original distribution (Collado et al., 2002; Pengue, 2004; Zak et al., 2008). Today, the *Caldenales* in Córdoba remain as a highly fragmented mosaic where small forest patches alternate with cultivated lands or abandoned fields, distributed in an area of no more than 50,000 Ha, representing only 0.3% of the provincial territory (Zak et al., 2004).

P. caldenia is a hermaphroditic tree that reaches heights up to 12 m with a short trunk and basal branches forming a parabolic crown up to 15 m in diameter. It can only reproduce sexually via seeds. Flowering takes place in November–January and fruit shedding occurs in March–April. Fruits are indehiscent, formed by a yellowish and purple exocarp, a spongy and nutritious mesocarp that contrary to other *Prosopis* species is bitter and astringent, and a hard endocarp. At maturity, seeds have a hard coat that delays germination, remaining inside the cavity of the endocarp until its degradation. Fruits of *P. caldenia* are palatable to wildlife and domestic livestock; the latter have been observed to consume them in large quantities (Peinetti et al., 1992). Accordingly, scarification of seeds significantly increases germination (Peinetti et al., 1993).

2.2. Sampling design

The study was conducted in an area of c.a. 300 km^2 where the last remaining of *Caldenales* concentrate within the southeastern provincial limit of Cordoba, right next to the borders of San Luis and La Pampa provinces (Fig. 1). We selected nine sites containing trees growing in three contrasting landscape conditions: continuous forest, forest fragments, and isolated tree individuals. Three sites were located within the last tract of continuous forest in Córdoba (~5000 Ha, Estancia Realicó) and were spatially separated amongst them by at least 1000 m. Three sites were located within small forest fragments (0.76–2.29 Ha) embedded in agricultural matrices (see details in Table 1). Within each site, we marked 10–12 adult individuals of similar height and diameter at breast height (DBH: 40–50 cm). Finally, we marked 25 isolated *P. caldenia* individuals growing in three different sites (8–9 per site), within matrices or along agricultural and dirt road verges. Overall, we sampled a total of 88 adult tree individuals across the three contrasting landscape conditions.

2.3. Reproduction

In November 2008 we counted and marked the number of inflorescences on a 50 cm section length of three different branches in each maternal tree throughout the landscape conditions. Also, we bagged two extra branches per tree with bridal net to prevent animal pollination and check for wind pollination. We simultaneously collected five inflorescences from each maternal tree to count the number of flowers per inflorescence and also the number of ovules

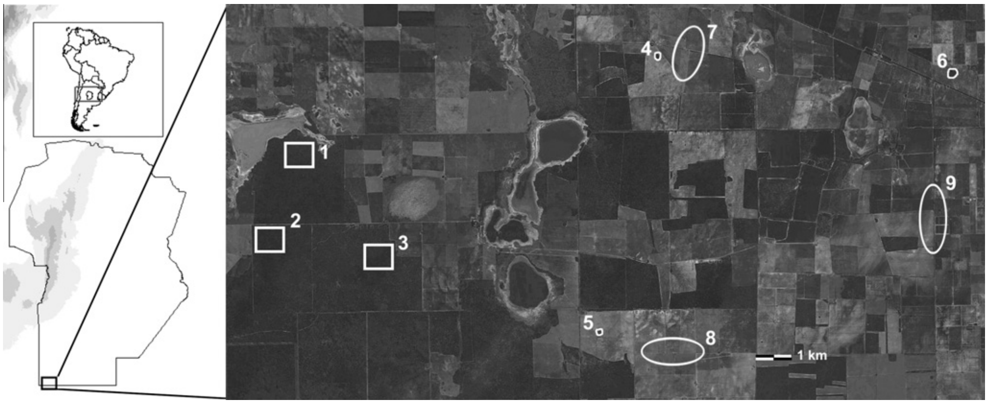

Fig. 1. Map of the studied area, where the last relicts of caldenales remain within the province of Cordoba. Denoted in white lines (boxes, fragment boundaries, and ovals) are the nine studied populations located in continuous forest, forest fragments, and isolation, respectively. See details of each site in Table 1.

Table 1
Characteristics of the nine studied *P. caldenia* populations growing in three contrasting landscape conditions. NA: not applicable.

Landscape condition	Area (Ha)	Mean (±SD) conspecific density around focal maternal trees (individuals per 100 m^2)	Distance to nearest large population (m)
Continuous forest			
Site 1	~5000	10.44 ± 3.04	NA
Site 2	~5000	9.70 ± 2.69	NA
Site 3	~5000	11.33 ± 2.23	NA
Forest fragments			
Site 4	1.04	5.90 ± 2.93	304
Site 5	0.76	7.11 ± 3.06	572
Site 6	2.29	4.88 ± 2.62	608
Isolated individuals			
Site 7	NA	2.77 ± 1.98	1520
Site 8	NA	4.11 ± 2.73	835
Site 9	NA	2.33 ± 1.63	1136

per flower to obtain an average value per maternal tree. In early April 2009 we counted all fruits produced on each marked branch. Fruit-set was calculated as: number of mature fruits/mean number of flowers marked (i.e., number of inflorescences × mean number of hermaphrodite flowers per inflorescence). We also counted the number of seeds per fruit and calculated seed-set as: number of seeds per fruit/mean number of ovules per flower.

2.4. Seed predation

To assess the degree of seed predation across landscape conditions we collected ten fruits per maternal tree from different branches. Fruits were stored in a refrigerator at 4 °C until processing, to avoid bruchid reinfection. From each fruit we recorded the total number of: (1) healthy seeds, (2) predated seeds, (3) aborted seeds, and (4) bruchid larvae. With these variables we calculated the proportion of predated and aborted seeds per pod. To determine the taxonomical identity of bruchid beetles, another group of five fruits per tree was enclosed in wired bags of 1 mm mesh under natural conditions until adults emerged. All healthy viable seeds (non-predated and non-aborted) in each fruit were individually weighted in a Mettler Toledo PB153 balance (accuracy 2 mg). We calculated mean seed mass per maternal tree from all healthy seeds of each pod.

2.5. Progeny performance

To assess progeny performance, we randomly selected two healthy seeds from each of three fruits per tree, completing a total of 528 seeds. Performance was measured as seed germination, seedling growth and survival in a greenhouse. In August 2009, seeds were individually weighted, scarified with sandpaper, and placed on filter paper in Petri dishes, which were carefully tabulated by the origin of each seed. Seeds were moistened with distilled water, placed in a germination chamber at 25 °C and 12 h of photoperiod, and monitored daily. We quantified germination time and proportion of germinated seeds. Germinated seeds were then sowed in tubular nylon pots (tabulated by site, maternal tree, and fruit) of 6 cm diameter and 20 cm depth filled with a mixture of 40% sand and 60% of blended natural soil from the entire sampling area, which were used for all seedling. Pots were grouped in trays (40–50 per tray) that were randomly interchanged around the greenhouse every 2 weeks. Pots were automatically watered once a week. During the first 3 weeks after sowing, we monitored each seedling on a daily basis to determine the number of days until complete opening of cotyledons (cotyledon emergence time) and until emergence of the first true leaf (true leaf emergence time). We measured seedling height with a digital caliper every 30 days throughout 5 months (i.e., 150 days after sowing). Measurements were taken from the cotyledon scars to the base of the newest leaf growing in the apical meristem. We calculated a relative growth rate in height (RGR_H; Hunt, 1990; Simonetti et al., 2007) per seedling as: ($LnH_2 - LnH_1/T_2 - T_1$), where LnH_1 and LnH_2 are the natural logarithm of seedling height measured every 30 days across 5 months (i.e., $T_2 - T_1 = 30$). In January 2010, all surviving seedlings were collected and dried at 60 °C for 72 h in a drying chamber. Aerial and subterranean dry biomass of each seedling was weighted separately. We quantified the proportion of seedling survival at the end of the experiment. Finally, we estimated the multiplicative performance across all measured life stages: reproductive success, seed survival, germination, seedling survival and seedling growth after 150 days. For each maternal tree, we calculated cumulative performance by multiplying performance across life stages (Michaels et al., 2008):% ovules turning into seeds (i.e., seed-set),% healthy seeds,% seed germination,% seedling survival, and total dry biomass of progeny at the end of the experiment.

2.6. Statistical analyses

Analyses were performed using R environment (R development Core Team, 2009). We used linear mixed effects model (*lme* function from the *nlme* package, Pinheiro et al., 2009) for quantitative response variables (germination time, cotyledon and first true leaf emergence time, seedling height, and dry biomass) and generalized linear mixed effect models (*lmer* function from the *lme4* package, Bates and Maechler, 2009), for binomial-distributed (e.g., proportions such as fruit- and seed-set, seed predation, and survival) or Poisson-distributed variables (number of flowers and inflorescences, number of ovules per flower and seeds per fruit). We used landscape condition as the fixed main effect with three levels (continuous forest, forest fragments, and isolated individuals), site as a random effect ($N = 9$) nested within landscape condition and maternal tree ($N = 88$) as a random effect nested within site and landscape condition. We analyzed fragmentation effects on seed mass and found no significant effects. Thus, we included seed mass as a covariate in the model for all progeny performance variables (from germination to seedling biomass). Significance of fixed effect was assessed with *F*-tests in linear mixed models and with Wald-*Z* in generalized linear mixed models. We fitted the most complete model first, which included all effects (fixed and random), the covariate and their interactions, and then we simplified it by removing non-significant interactions and random-effects terms until we were left with a minimal adequate model. Each random effect was tested by comparing two nested models (i.e., analysis of deviance), one with- and one without the random effect using a χ^2 test. Model parameters were estimated with restricted maximum likelihood methods and Laplace approximation for *lme* and *lmer* functions, respectively.

3. Results

3.1. Reproduction

Overall, fruit-set in *P. caldenia* was extremely low: the ratio of flowers to fruits was only 0.02%, indicating that, on average, it took a tree around 4000 flowers (with an average of 80% of hermaphrodite flowers within a tree; pers. obs.) to produce a single fruit. No fruits were produced by wind pollination, indicating a complete dependence on animals for successful pollination. Although we did not formally assess pollinator visitation, main floral visitors to *P. caldenia* were honeybees (*Apis mellifera*) and native bees (mainly Apidae and Halictidae). We found no significant differences in natural fruit-set of trees across landscape conditions (Table 2). However, trees growing in isolation produced significantly larger absolute numbers of inflorescences than trees growing in continuous forest, while the number of flowers per inflorescence remained similar across conditions (Table 2). Given equal probabilities of setting fruits across conditions, larger production of inflorescences in isolated trees imply they yield larger number of pods. Such total yield increase per individual would be around 1.2 and 1.5 times larger in forest fragments and isolated trees, respectively, compared to the production in continuous forest (Table 2). Maternal and site effects (random factors) significantly explained part of the variation (33% and 17%, respectively) in the levels of flower production and fruit-set as revealed by analyses of deviance ($\chi^2 > 14.3$, $P < 0.001$). Ovule number per flower, as well as the total number of seeds produced per fruit, were comparable among all sampled trees; hence, seed-set was also similar across all landscape conditions (Table 2). Likewise, the proportion of aborted seeds per fruit was not affected by landscape condition (Table 3). Neither maternal tree nor site had an effect on ovule number, seed-set or seed abortion ($\chi^2 < 1.33 \times 10^{-10}$, $P > 0.99$).

3.2. Seed predation

The proportion of predated seeds was not significantly different across landscape conditions (Table 3). Maternal tree, but not site, explained much of the variation in seed predation, with nearly 45% of the model variance attributable to variations among maternal trees within the same site. Similarly, the average number of larvae found within pods was not significantly different across landscape conditions (Table 3). Bruchid predation ranged from 16% to 33% of seeds within a pod, and all predated seeds were completely non-viable (pers. obs.). The bruchid species *Rhipibruchus picturatus* (Bruchidae, Coleptera; Fahraeus, 1839) was the only seed predator found throughout landscape conditions. This is the first published report of a species-specific seed predator for *P. caldenia.*

The proportion of remaining healthy seeds per pod was also similar across different landscape conditions (Table 3), and no significant variation was explained by maternal tree or site ($\chi^2 < 2.20 \times 10^{-5}$, $P > 0.744$). On average, non-predated, non-aborted seeds represented nearly 50% of the seeds within a pod.

3.3. Progeny performance

Seed mass was not significantly different across landscape condition ($F_{[2;\ 264]} = 0.546$, $P = 0.699$), thus we incorporated seed mass as a covariate within the model of progeny performance analyses. After manual scarification, seed germination was overall high; c.a. 90% of the seeds germinated successfully (Table 3). Germination time was not different across landscape conditions ($F_{[2;\ 264]} = 0.58$, $P = 0.332$), sites or maternal trees ($\chi^2 < 3.12 \times 10^{-4}$, $P > 0.554$); seeds germinated within 24–36 h after sowed in Petri dishes. The proportion of germinated seeds was only marginally significantly lower in fruits from isolated maternal trees (Table 3), and seed mass did not influence germination success ($Z = -0.558$, $P = 0.577$). Maternal tree identity explained 36% of the variation in seed germination ($\chi^2 = 8.33$, $P = 0.001$) whereas site explained none ($\chi^2 = 2.20 \times 10^{-6}$, $P = 0.866$). Cotyledon emergence time did not significantly differ among conditions (Table 3), and neither seed mass affected this parameter ($F_{[2;\ 264]} = 1.78$, $P = 0.183$). Test of deviance showed that maternal tree and site explained 46% and 13% of model variance, respectively ($\chi^2 > 26.6$, $P < 0.001$). In contrast, first true leaf emergence time was significantly different throughout landscape conditions (Table 3). Seedlings from maternal trees growing in continuous forest and forest fragments took significantly less time to develop the first true leaf compared to seedlings from isolated trees (Table 3). Seed mass did not influence this parameter ($F_{[1;\ 264]} = 0.409$, $P = 0.523$), and only maternal tree identity significantly explained 26% of model variance ($\chi^2 = 17.3$, $P = 0.0003$).

Table 2

Reproductive parameters in populations of *P. caldenia* growing in three contrasting landscape conditions. Values are means ± SD. Different letters in bold indicate statistical significant differences in parameter value among landscape conditions.

	Continuous forest	Forest fragments	Isolated individuals	Statistical tests
Number of inflorescences per 50 cm of branch	55.91 ± 28.09 **a**	69.32 ± 25.13 **ab**	83.80 ± 26.16 **b**	$Z = 4.842$; $P < 0.001$
Number of flowers per inflorescence	138.08 ± 27.24	144.19 ± 25.08	141.2 ± 21.84	$Z < -0.233$; $P > 0.784$
Fruit-set × 10^{-04}	2.5 ± 4.2	1.8 ± 3.3	2.1 ± 3.6	$Z < -0.154$; $P > 0.878$
Number of seeds per pod	24.65 ± 6.72	27.14 ± 5.59	27.55 ± 5.63	$Z < 1.721$; $P > 0.086$
Ovules per flower	36.23 ± 4.09	36.77 ± 3.85	38.07 ± 3.34	$Z < 0.165$; $P > 0.129$
Seed-set	0.680 ± 0.184	0.738 ± 0.151	0.723 ± 0.147	$Z < 0.780$; $P > 0.435$

Table 3
Proportion of seed predation, abortion, and germination, early progeny performance parameters, seedling survival, and cumulative performance of *P. caldenia* seedlings originated from maternal trees growing in three contrasting landscape conditions. Values are means ± SD. Different letters in bold indicate statistical significant differences in parameter value among landscape conditions.

	Continuous forest	Forest fragments	Isolated individuals	Statistical tests
Seed predation	0.218 ± 0.236	0.237 ± 0.284	0.191 ± 0.228	$Z < 0.740$; $P > 0.459$
Number of bruchid larvae	1.92 ± 2.20	1.75 ± 1.54	1.10 ± 1.15	$Z < 0.339$; $P > 0.734$
Seed abortion	0.227 ± 0.235	0.196 ± 0.179	0.190 ± 0.171	$Z < -0.453$; $P > 0.376$
Healthy seeds	0.475 ± 0.226	0.479 ± 0.269	0.530 ± 0.234	$Z < 0.564$; $P > 0.573$
Seed germination	0.917 ± 0.208	0.893 ± 0.258	0.801 ± 0.296	$Z = -1.782$; $P = 0.074$
Cotyledon emergence time (days)	7.33 ± 1.72	6.77 ± 1.16	7.35 ± 1.04	$F_{[2;\ 264]} = 0.11$; $P = 0.932$
First true leaf emergence time (days)	10.22 ± 1.13 **a**	11.76 ± 2.46 **a**	14.48 ± 1.88 **b**	$F_{[2;\ 264]} = 4.39$; $P = 0.023$
Seedling survival	0.834 ± 0.243 **a**	0.747 ± 0.314 **ab**	0.630 ± 0.304 **b**	$Z = -2.465$; $P = 0.013$
Cumulative performance	0.241 ± 0.106 **a**	0.117 ± 0.08 **b**	0.103 ± 0.05 **b**	$Z = 3.\ 24$; $P = 0.007$
Cumulative performance corrected by inflorescences	0.241 ± 0.106 **a**	0.153 ± 0.09 **b**	0.154 ± 0.08 **b**	$Z = 2.121$; $P = 0.031$

Landscape condition had a strong effect on subsequent seedling growth. Seedlings from maternal trees growing in continuous forest had significantly greater height than seedlings from forest fragments and isolated trees (Fig. 2). Such differences became statistically significant only after 60 days of growth in the greenhouse, and continued consistently throughout all measuring dates until day 150 (Fig. 2). From day 90 on, seedlings from isolated trees showed on average similar height as those from forest fragments (Fig. 2). Neither maternal trees nor sites explained any of the variation in total growth rate at different measuring dates ($\chi^2 < 1.27 \times 10^{-4}$, $P > 0.743$). The relative growth rate in height (RGR_H) was also significantly higher in seedlings from continuous forest throughout the entire growth period (Fig. 3). RGR_H decreased with time in all seedlings, indicating a common growth rate pattern regardless of their condition. Site and maternal identity did not explain any variation in RGR_H ($\chi^2 < 0.02$; $P > 0.662$). The larger absolute growth in seedlings from continuous forest was also found in final seedling biomass. Total dry biomass (aerial and subterranean) was almost twofold larger in seedlings generated from trees growing in continuous forest (Fig. 4; $F_{[2;\ 195]} = 16.72$, $P < 0.001$). None of the random factors explained any of the variance in biomass ($\chi^2 < 1.06 \times 10^{-5}$, $P > 0.885$). Seed mass did not significantly affect any of these later-stage progeny performance parameters ($F_{[1;\ 221-195]} < 0.622$, $P > 0.341$). Seedling survival was also significantly different across landscape conditions. Progeny from isolated maternal trees were significantly less likely to survive to the end of the experiment than progeny generated in continuous forest (Table 3). Seed mass did not affect survival ($Z = -1.440$, $P = 0.149$). Neither site nor maternal tree explained any of the variation in seedling survival ($\chi^2 < 1.47 \times 10^{-9}$, $P > 0.921$). Although all seedlings were subjected to identical

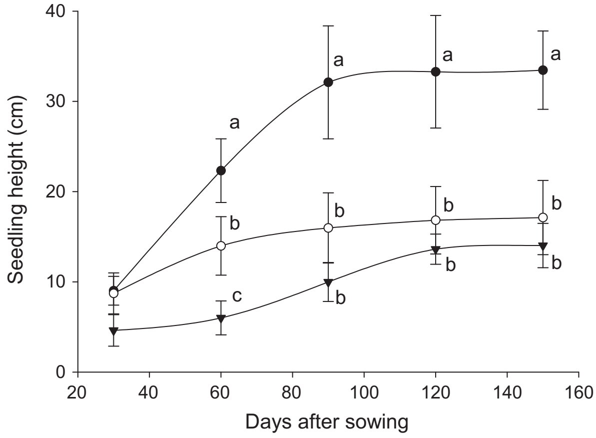

Fig. 2. Height of *P. caldenia* seedlings growing in controlled greenhouse conditions for 5 months. Values are the mean ± SD. Different symbols indicate the landscape condition of parental trees: filled circles: continuous forest, white circles: fragmented forests, filled triangles: isolated condition. Different letters indicate statistical significant ($p < 0.05$) differences between seedling heights at five measuring dates.

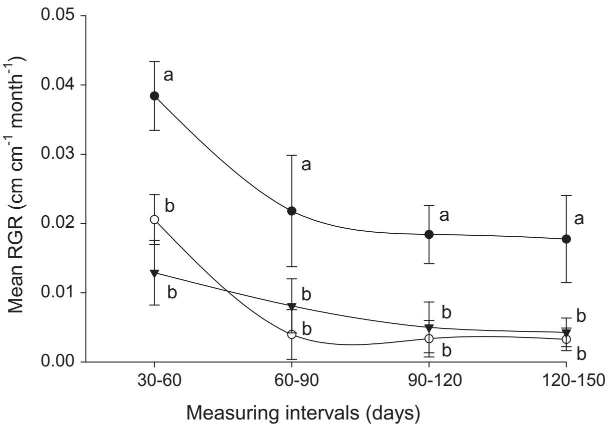

Fig. 3. Relative growth rate in height of *P. caldenia* seedlings growing in controlled greenhouse conditions for 5 months. Values are the mean ± SD. Different symbols indicate the landscape condition of parental trees: filled circles: continuous forest, white circles: fragmented forests, filled triangles: isolated condition. Different letters indicate statistical significant ($p < 0.05$) differences between RGR in height at 4 measuring intervals.

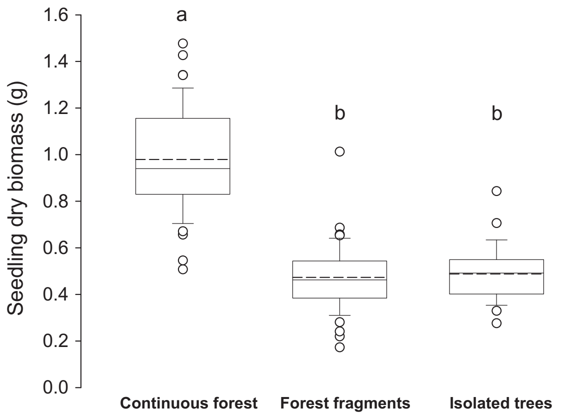

Fig. 4. Total dry biomass after a 5-month growth period of *P. caldenia* seedlings originated from parental trees growing in three contrasting landscape conditions. Boxes delimit 25th and 75th percentiles, the solid and dashed lines within the box are the median and mean, respectively. Whiskers indicate the 90th and 10th percentiles while circles represent outlying points. Different letters indicate statistical significant differences at $p < 0.05$.

controlled environmental conditions, nearly 40% of seedlings from isolated trees died before day 150.

Finally, the cumulative performance of progeny per maternal tree was significantly different among landscape conditions (Table 3), with higher overall performance across different early life-stage components (from reproduction to seedling growth) in seedlings from continuous forest. None of the random factors explained any part of the variation in cumulative performance ($\chi^2 < 3.55 \times 10^{-7}$; $P > 0.619$). Because isolated trees produced more inflorescences and thus produce more progeny in absolute terms, we corrected the cumulative performance by the yield increase observed in inflorescence number (multiplying each cumulative performance parameter by 1.2 and 1.5 for trees in fragmented and isolated conditions, respectively) and re-analyzed it. After this correction, seedlings from continuous forest still showed significantly larger cumulative performance (Table 3), without significant effects of random factors ($\chi^2 < 2.10 \times 10^{-5}$; $P > 0.103$).

4. Discussion

The simultaneous evaluation of mutualist and antagonist interactions may give us a closer look of how fragmentation is eventually affecting local plant population persistence (e.g., García and Chacoff, 2007; Herrerias-Diego et al., 2008; Kolb, 2008; Aguilar et al., 2009; Herrera et al., 2011; Magrach et al., 2011). Here, we expected that negative fragmentation effects on plant-pollinator and plant-seed predator interactions would compensate the net quantity of progeny left across landscape conditions. However, similar probability of leaving viable, non-predated seeds in continuous and fragmented conditions was not due to compensatory effects but to the absence of fragmentation effects on both animal interaction partners. However, the quality of progeny produced in continuous forest was significantly higher. Below, we discuss possible causes for the response patterns found.

4.1. Reproduction

In contrast to the generalized findings of depleted sexual reproduction in self-incompatible species growing in fragmented habitats (Aguilar et al., 2006), we found no fragmentation effects on fruit- and seed-set of this animal-pollinated, self-incompatible tree. Although isolated trees produced significantly more flowers, they set a similar proportion of fruits as trees from continuous forest, so that a larger number of their flowers were not effectively pollinated. In contrast, trees in continuous forest had similar probability of setting fruits yet producing less number of flowers, indicating greater pollination efficiency. Nevertheless, the significant larger numbers of inflorescence produced by isolated trees imply an absolute larger number of progeny left per maternal tree in this condition. Higher investment in floral resources may result from increased light availability of isolated trees that grow in open areas without conspecific or heterospecific neighbor trees overlapping their crowns (Mulkey et al., 1996; Cunningham, 1997; Fuchs et al., 2003; Herrerías-Diego et al., 2006), and/or due to increased soil nutrients resulting from low-intensity fertilization practices around the agricultural fields were they grow (Winter et al., 2008; Tsaliki and Diekmann, 2010). Such higher floral display in *P. caldenia* may helped to attract pollinators in such isolated conditions, especially of *Apis mellifera*, which was frequently observed pollinating isolated trees (pers. obs.). Beekeeping activity is common within the studied area, particularly around the agricultural farms, where many forest fragments and isolated trees remain. While the flying capability of *A. mellifera* may potentially allow pollination connectivity among isolated individuals and other populations, its particular behavior of concentrating foraging on one or a few nearby individuals of large floral display may minimize such possibility (Aizen and Feinsinger, 1994; Steffan-Dewenter et al., 2001; Aguilar, 2005). Low population density and large floral displays typically increase visitation duration per individual, reducing outcrossing and increasing geitonogamy, particularly affecting reproductive output of self-incompatible species (e.g., Murawski and Hamrick, 1992; Aldrich and Hamrick, 1998; Cascante et al., 2002).

4.2. Seed predation

Seed predation by bruchid beetles in *Prosopis* species represents probably the strongest antagonistic interaction affecting the quantity and quality of the surviving progeny after a reproductive event (Center and Johnson, 1974; Kingsolver et al., 1977; Janzen, 1980; Wright and Duber, 2001). Fragmentation research on seed predation by insects shows disparate results, reporting either decreased seed predation (Bigger, 1999; Cunningham, 2000; Steffan-Dewenter et al., 2001; Cascante et al., 2002; Chacoff et al., 2004; Johnson et al., 2004; Herrerías-Diego et al., 2006) or no changes in predation levels in fragmented habitats (Cunningham, 2000; Ward and Johnson, 2005; Diekötter et al., 2007; Burgos et al., 2008). Here, the variability of seed predation levels and relative bruchid larvae abundance was mainly driven by maternal identity. Trees growing within the same site had very different infestation levels, and this pattern occurs across different landscape conditions. Bruchid beetles persistence in small forest fragments and isolated trees may be due to their tight evolutionary relationship with *Prosopis* species and their capability to remain nearby adult trees throughout their lifecycle. Bruchids can spend winter seasons either in seeds (as pupae or adult) within shed pods or in litter on the ground, emerging in time for oviposition on new green pods (Lerner and Peinetti, 1996; and references therein).

4.3. Progeny performance

Habitat fragmentation did not affect any of the early progeny performance parameters (seed mass, seed germination and cotyledon emergence time). However, variation in all of these parameters was significantly explained, to different degrees, by the identity of the mother, which was included as a random factor in the models. The contribution of the maternal parent to the phenotype of its offspring (i.e., maternal effects) are expected to particularly influence early-stage growth parameters via genetic and endosperm characteristics in the seed (Roach and Wulff, 1987; Stephenson, 1992). Maternal effects result from complex interactions involving maternal genetic properties and of the environment where maternal plants grow (e.g., Roach and Wulff, 1987; Stephenson, 1992). While observational studies are not able to distinguish between the genetic or environmental origin of maternal effects, the lack of significant site-effects in the variation of any of the early progeny performance parameters suggest that different genetic characteristics of maternal trees may have played a more prevalent role than environmental ones.

In contrast, habitat fragmentation had strong negative effects in the growth and survival of seedlings from forest fragments and isolated trees. Interestingly, none of these later-seedling-growth parameters was significantly influenced by maternal or site effects, suggesting that contrasting landscape conditions, where parental trees reside, are likely to be responsible for such marked response patterns. Accordingly, the cumulative performance was also significantly greater in continuous forest, even after correcting for the number of inflorescences originally produced. Previous research has found evidence of significant changes in mating patterns of animal-pollinated trees and shrubs in fragmented populations, where outcrossing rates tend to decrease and inbreeding coefficients of progeny generated in forest fragments or isolated conditions significantly increase (reviewed in Aguilar et al., 2008; Eckert et al., 2009; Angeloni et al., 2011). Although we did not evaluate genetic parameters here, some particular characteristics of the species and the land-use history of the area may support the idea that decreased progeny performance is the result of inbreeding depression due to increased matings among genetically related trees.

Cattle introduction in the late 19th century has played an important role in dispersing caldén seeds by increasing its establishment and population densities, and even expanding its original boundaries to grasslands in the past (Peláez et al., 1992; Dussart et al., 1998). Cattle and other ungulated mammals are known to promote clumped or correlated seed dispersal patterns due to their social foraging and deposition behaviors (Karubian and Duraes, 2009). Most of our selected adult trees are likely to have been established by cattle dispersal events in the past, as their estimated age would be less than 100 years-old based on their DBH (cf. Boggino and Villalba, 2008). Moreover, individuals of *P. caldenia* are highly variable in their fruiting patterns, so that a few individuals may concentrate the resources in any given reproductive episode. Finally, seeds within a pod are always full-sibs since pollen deposition occurs through polyads. Such characteristics of the species and the presence of cattle as main dispersal vector may have resulted in the distribution of genetically related individuals over relatively short distances (e.g., Schnabel et al., 1998; Gonzales et al., 2010). In isolated conditions and small forest fragments, such pronounced spatial genetic structure implies that most of the individuals left within the mating neighborhood would present high levels of relatedness, creating a strong founder effect. In continuous forest, however, such spatially structured genetic mosaics would be spread throughout its uninterrupted area, holding a larger number of genotypes and non-related mates. Thus, in fragmented conditions most exogamous crosses would concentrate among close relatives, leading to increased biparental inbreeding, which may result in the expression of inbreeding depression, reducing progeny fitness and survival (Schnabel et al., 1998; Gonzales et al., 2010; Angeloni et al., 2011). Trees in continuous forest may offset such family spatial structure if pollinators forage on a larger number of individuals and make fewer visits per individual, as is often the case in large continuous populations (e.g., Mustajarvi et al., 2001; Grindeland et al., 2005).

Alternatively, lower population sizes in fragmented conditions can also affect self-incompatibility mechanisms (Quesada et al., 2004; Busch and Schoen, 2008; Willi, 2009). Changes from a strict self-incompatibility system to a mixed mating system may arise due to pleiotropic effects of modifying genes (Good-Avila and Stephenson, 2003), polyploidy or gene duplication (de Nettancourt, 2001), or temporal plasticity in the expression of self-incompatibility (Vogler et al., 1998). Such alterations may allow isolated trees to set autogamous seeds but may not prevent the expression of inbreeding depression, especially in predominantly outcrossing species (Charlesworth and Willis, 2009; Angeloni et al., 2011).

4.4. Conclusions and conservation implications

Long-lived trees are thought to be resilient to immediate fragmentation effects as they have many reproductive opportunities throughout their lifetime (Wilcock and Neiland, 2002). However, longevity does not necessarily guarantee their long-term local persistence should their mating patterns are mainly biased towards endogamy, decreasing the performance and survival of their progeny. Research conducted in La Pampa province has shown that seed germination, seedling establishment and survival of *P. caldenia* in the field are overall low and limited by water availability, grazing, and grass competition (Peláez et al., 1992; Distel et al., 1996). Also, the species does not form persistent soil seed bank (Lerner and Peinetti, 1996), so only after endozoocorious dispersal has taken place, chances of recruitment of caldén seedlings may occur in years where rainfall is above normal (Peláez et al., 1992). Considering such particular conditions, the chances of establishment of potentially inbred progeny in the field are almost null.

Central Argentina holds one of the highest estimates of deforestation rates worldwide (Zak et al., 2004, 2008). The caldenales within Córdoba currently remain as a highly fragmented mosaic with a single continuous area of forest left. Our results indicate that it is only within this last continuous forest tract that reproductive adult trees produce higher quality of progeny that may successfully grow and survive in natural conditions. Accordingly, active conservation management of remaining populations should involve the incorporation of propagules from the continuous forest, which represent the main local source of high quality progeny. While such strategy may help to genetically enrich remnant populations in the long term, it will not assure genetic connectivity. More ambitiously, effective restoration efforts should be undertaken to enable physical connectivity among populations through forest corridors. Plantations along dirt roads around the area and along verges limiting land properties could act as stepping-stones to gene flow via pollen and seeds. This type of restoration efforts in the landscape imply no changes in current land-use practices assuring long-term persistence of Caldén woodlands in the studied area.

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