

Extremely reduced sexual reproduction in the clonal cactus *Echinopsis thelegona*

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Abstract Sexual and asexual reproduction may occur simultaneously in some plant species. Under certain environmental conditions asexual reproduction is predominant, which generates ecological consequences on sexual fecundity. In this context, we studied the reproductive ecology of the creeping clonal cactus *Echinopsis thelegona* in La Bodega (Salta, Argentina), where low fruit and seed production was preliminarily observed. Specifically, we studied the flower availability, fruit and seed production, reproductive system, floral visitors and effects of neighbor ramets on reproductive success. The number of available flowers per day was low, and fruit production was low or null as well. *Echinopsis thelegona* is self-incompatible. Although its flowers have sphingophilous traits, we did not find evidence of moths visiting them. Only native and exotic bees visited the flowers of this species, though with a low number of visits. Therefore, nocturnal visitors were not registered as pollinators of *E. thelegona*, perhaps because of their low local abundances. On the other hand, bees behaved as inefficient pollinators of *E. thelegona* due to their foraging behavior, which moves pollen within individuals. A pollen-addition experiment revealed that there is no fruit production at short distances among ramets. Therefore, the combination of self-incompatibility, low flower production and low local abundance of pollinators could account for the low fruit production observed in this species. This finding suggests that populations of *E. thelegona* persist by clonality and that they tend toward the loss of sexuality.

Keywords Cactaceae · Clonal cacti · *Echinopsis* · Moth pollination · Trichocereae · Pollen limitation

Introduction

In many flowering plant species, sexual and asexual reproduction occur simultaneously, and these two reproductive modes interact. Sexual reproduction provides advantages because it allows new genetic recombination and facilitates colonization of new environments. On the other hand, asexual reproduction (or clonal reproduction) allows the long-term persistence of successful genotypes and sometimes allows the colonization of new sites through asexual specialized propagules (Abrahamson 1980). This mode of reproduction tends to predominate in environments that are unfavorable for sexual recruitment and has ecological consequences on fecundity, especially in self-incompatible plants (Eriksson 1993; Vallejo-Marín et al. 2010) because of its effect on pollen dispersal and mating availability (Charpentier 2002).

Cacti are conspicuous elements of arid and semiarid environments in the Western Hemisphere (Ortega-Baes and Godínez-Alvarez 2006; Ortega-Baes et al. 2010c). Processes associated with early establishment are considered critical in the cactus lifecycle. Seedling emergence and survival are episodic processes strongly affected by factors such as water availability in the soil, characteristics of the substrate and the presence of nurse plants (Godínez-Alvarez et al. 2003). Although seeds are produced annually, only a few seedlings emerge and few or none of them survive for more than a year (Godínez-Alvarez et al. 2003). Like other arid zone species, some cacti exhibit clonal reproduction (e.g., *Opuntia* species; Mandujano et al. 2010), which generates advantages (e.g., local persistence)

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over infrequent sexual recruitment. The relative importance of sexual and clonal reproduction for a particular species of cactus may vary spatially and temporally, affecting population dynamics (Mandujano et al. 1998). Despite its advantages, clonality can be disadvantageous in self-incompatible species due to a reduction in mate availability (Honnay and Jacquemyn 2008), affecting early sexual recruitment. Current studies show that in clonal cactus there is a significant reduction of female fecundity because pollen dispersal occurs among neighboring ramets located at short distances (Clark-Tapia and Molina-Freaner 2004; Clark-Tapia et al. 2006; Mandujano et al. 2010; Carrillo-Angeles et al. 2011). Particularly, Clark-Tapia and Molina-Freaner (2004) and Clark-Tapia et al. (2006), studying the creeping clonal cactus *Stenocereus eruca* of the Sonoran Desert suggested that the rare sexual recruitment of this species could be, at least in part, a consequence of its clonality. In this species, the floral traits correspond with moth pollination; however, bees were the most frequent visitors during the study period. Due to bees behavior, much of the pollen produced by self-incompatible clonal species is wasted when it is dispersed among neighboring ramets, so the chances of producing fruits are greater as the distance between the donor and the receptor increases (Clark-Tapia and Molina-Freaner 2004; Clark-Tapia et al. 2006). A similar finding was recently registered by Carrillo-Angeles et al. (2011) in the clonal cactus *Ferocactus robustus*.

In this context, we studied the reproductive ecology of *Echinopsis thelegona* (F.A.C. Weber) Friedrich & G.D. Rowley (Cactaceae), a creeping clonal cactus endemic to northwestern Argentina. This cactus species presents nocturnal flowers with extended floral cycles that could be pollinated by moths at night and by bees during the day, as it has been registered for other *Echinopsis* species in northwestern Argentina (Ortega-Baes et al. 2011). Preliminary field observations indicated that *E. thelegona* has low fruit production. This fact would be a consequence of its clonality if the species were self-incompatible, since local populations would consist of very few genets, thus reducing mate availability as it has been suggested for other clonal cactus species (Clark-Tapia and Molina-Freaner 2004; Clark-Tapia et al. 2006; Mandujano et al. 2010; Carrillo-Angeles et al. 2011). In this scenario, if the pollinators either moved within a foraging patch or moved among short distances, they would be ineffective in depositing cross-pollen, negatively affecting fruit and seed production (Carrillo-Angeles et al. 2011). Specifically, we have analyzed if low fruit production in *E. thelegona* was due to failure in pollination and we have explored if this could be related to clonality. To do so: (1) we registered temporal variation of flowers, fruit and seed production; (2) we evaluated whether *E. thelegona* depends on pollinators

to produce fruits; (3) we studied the floral visitors and their effectiveness as pollinators; and (4) we explored the influence of clonality on fecundity to analyze if fruit and seed production depends on distances among ramets.

Materials and methods

Study area

The study was conducted in La Bodega (25°17'31.72"S, 65°16'25.13"W) in Salta province (Argentina). The climate of the study site is subtropical, with a mean annual temperature of 18.4 °C (Bianchi 1996). The mean annual rainfall at the site is 416 mm (Bianchi and Yañez 1992). The vegetation corresponds to the Dry Chaco ecoregion (Olson and Dinerstein 2002). The cactus flora in the study area includes several species of genera *Cereus*, *Cleisto-cactus*, *Echinopsis*, *Gymnocalycium*, *Harrisia*, *Opuntia* and *Parodia*.

Natural history of the species

Echinopsis thelegona (F.A.C. Weber) Friedrich & G.D. Rowley is a columnar cactus with long, dark green stems (2 m long, 7–8 cm diameter) that creeps along the ground with ascending tips (Hunt 2006; Fig. 1a). Its flowers are funnel-form, with a well-defined floral tube and an internal width of 0.42 ± 0.11 cm (Fig. 1b, c). The tepals are white, and the floral tube has reddish hairs and bristles. The floral length is 18.25 ± 1.15 cm, while the floral diameter is 14.21 ± 1.11 cm. The flowers present a nectarial chamber, which is located 16.32 ± 0.98 cm from the upper extreme of the corolla. On average, there are 455.43 ± 48.15 stamens per flower, and the longest stamens have an average length of 12.92 ± 0.64 cm. The average length of style-stigma is 13.3 ± 1.25 cm. The stigma presents numerous lobules and has an average width of 2.2 ± 0.45 cm. The ovary is inferior and contains an average of $4,718 \pm 277.5$ ovules. The fruits are fleshy, globose and yellowish with a diameter of 5.78 ± 0.4 cm. The flowers start opening by 2100 hours and are completely opened at 2300 hours. By 0900 hours, they begin to close and are totally closed at 1100 hours. The seeds are positively photoblastic and non-dormant (Ortega-Baes et al. 2010a, b). *Echinopsis thelegona* shows geographic rarity, with a distribution limited to northwestern Argentina (Salta, Jujuy and Tucumán provinces; Ortega-Baes unpublished data; Hunt 2006).

Flower availability and fruit production

During three consecutive reproductive periods (November 2008–January 2009, November 2009–January 2010 and



Fig. 1 Individuals of the clonal cactus *Echinopsis thelegona* (a). The flowers are funnel-shaped (b). They are white and with nocturnal anthesis (c)

November 2010–January 2011; hereafter written as 2008, 2009 and 2010, respectively), the number of flowers available in a 1 km × 100 m transect was registered. In each reproductive period, sampling was carried out on ten non-consecutive days. All the flowers registered were marked and monitored until fruit development, determining the reproductive success (fruit set). All available fruits were taken to the laboratory to determine the seed number per fruit and the seed viability (germinated seed proportion). To determine the seed viability, five replicates of 25 seeds were sown on agar (1 %) in Petri dishes and were incubated at 25 °C with an 8 h-light/16 h-dark photoperiod for 30 days.

Reproductive system

In November 2008, we carried out an experiment to determine the reproductive system of *E. thelegona*. Fifteen bagged buds, chosen randomly, were used in each of the following treatments: (1) natural pollination, flowers were not manipulated; (2) automatic self-pollination, flowers were excluded with voile bags without manipulation; (3) hand self-pollination, flowers were hand-pollinated using pollen from the same flower and pollen from other flowers of the same ramet and then excluded with voile bags; and (4) hand cross-pollination, emasculated flowers were hand-pollinated with pollen from three flowers from individuals

of another population that is located 45 km away (25°37'26.25"S, 65°36'21.13"W) and then excluded with voile bags. In November 2007, we checked pollen viability of the studied population fertilizing each of every ten flowers of another population (located at 45 km), with ten different flowers of the studied population. This evaluation resulted in a fruit set of 0.7; therefore, we considered that the studied population produced viable pollen. The response variables were fruit set and seed set. Fruit set was estimated as fruit–flower ratio, while seed set was estimated as seed number–ovules ratio. For the latter, fruits were dissected and the number of seeds and unfertilized ovules were counted. Thus, number of ovules per flower was estimated as the number of seeds plus the number of unfertilized ovules.

Floral visitors

To determine the floral visitors, three flowers were observed on three non-consecutive days, at night and during the day as well (in 2008, 2009 and 2010). Night observations (performed with a soft artificial light) took place from 2200 to 0200 hours, while daytime observations took place from 0800 to 1000 hours (flower closing time). All observations were conducted every 2 h, for a period of 15 min each. Because no visits were registered at night, we

captured moths using a UV light trap that was opened from 2200 to 0100 hours on three non-consecutive nights in 2008, 2009 and 2010. Pollen samples were taken with agar from the moths bodies and analyzed in the laboratory. In addition, moth visits to flowers were also evaluated by determining the proportion of stigmas with moth scales. Five stigmas were collected before dawn on three consecutive nights during 2008, 2009 and 2010. Sample size was low because of the low flower availability (see “Results” section). Bees that visited the flowers were identified using a bee reference collection from the study area (LABIBO, Universidad Nacional de Salta). Bees were registered as visitors only if they entered the flowers and touched the stigma and/or the anthers.

Effectiveness of nocturnal and diurnal visitors

The effectiveness of nocturnal and diurnal visitors was evaluated through an experiment carried out during 2009 and 2010. The treatments were as follows: (1) natural pollination, in which the emasculated flowers were not manipulated; (2) nocturnal natural pollination, in which the emasculated flowers were available only to nocturnal pollinators from 2000 to 0500 hours and excluded from diurnal pollinators using voile bags; and (3) diurnal natural pollination, in which the emasculated flowers were available only to diurnal pollinators from 0700 hours until flower closing and excluded from nocturnal pollinators using voile bags. For this experiment, 30 flowers were selected, and ten flowers were assigned to each treatment. Response variables were fruit set and seed set.

Distance among ramets and fruit set

We carried out an experiment with pollen supplementation to evaluate the effect of the distance among ramets (floral shoots) on sexual reproduction. This experiment was conducted during the 2010 reproductive period. We used pollen from five flowers to fertilize flowers (five for each distance) located at five different distances (1, 50, 100, 250 and 500 m) within the studied population. A small number of flowers were used due to their low availability in the population. All flowers were excluded with voile bags to avoid interference by flower visitors. The response variables were the fruit set, seed set, number of seeds per fruit, and seed germination proportion (Clark-Tapia et al. 2006). Seed germination was evaluated as indicated above.

Statistical analysis

ANOVA was used to compare the mean number of flowers among reproductive periods (using the transformation \sqrt{x}). In addition, ANOVA was used to compare the number of

visits among bee species (using the transformation \sqrt{x}), considering the year factor as a block. Statistical analyses were conducted using the statistical software InfoStat (2009).

Results

Flower availability and fruit production

The number of available flowers varied between 0.3 ± 0.31 flowers per day/ha (2008) and 0.18 ± 0.18 flowers per day/ha (2009); however, no significant differences were registered among the years ($F = 0.24$, $df = 27$, $p = 0.7904$; Table 1). Fruits were produced only in 2008 and 2009 (one per year), with a very low fruit set (0.033 and 0.056, respectively). The seed sets were 0.628 and 0.501, respectively. The germination proportion was always above 0.9 (Table 1).

Reproductive system

Only the hand cross-pollination treatment produced fruits (fruit set 0.73). In this treatment, the seed set was 0.6 ± 0.031 , whereas the mean seed number was $2,389 \pm 22.81$.

Floral visitors

We did not register moths visiting flowers of *E. thelegona*. In the light trap, three species of Sphingidae (*Erinnyis ello*, *Manduca sexta* and *M. florestan*), two species of Noctuidae (*Condica sutor* and *Achaea ablunaris*) and 23 species of small moths (unidentified species) were registered, but none of them had pollen on their bodies. In all years, the average number of registered individuals in light trap for Sphingidae and Noctuidae moths was very low (Table 2). None of the stigmas presented moth scales.

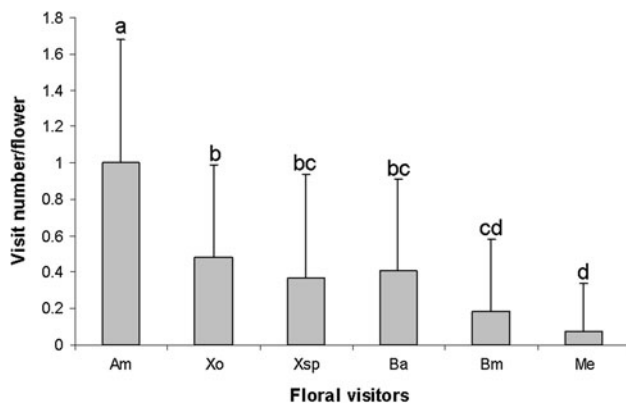
Table 1 Flower availability/day/ha (mean \pm SD), flower number, fruit number, fruit set, seed set, seed number and seed germination (germination proportion; mean \pm SD) of *Echinopsis thelegona*

	2008–2009	2009–2010	2010–2011
Flower availability	0.3 ± 0.31	0.18 ± 0.18	0.23 ± 0.23
Flower number	30	18	23
Fruit number	1	1	0
Fruit set	0.033	0.056	–
Seed set	0.628	0.50	–
Seed number	2,512	1,998	–
Seed germination	0.9 ± 0.05	0.93 ± 0.03	–

The number of flowers and fruits indicates the total recorded in each reproductive period

Table 2 Moth species captured in the UV light traps (mean \pm SD per year) at the study site (La Bodega, Salta, Argentina)

	2008–2009	2009–2010	2010–2011
Sphingidae			
<i>Erinnyis ello</i>	0	0.33 \pm 0.58	0
<i>Manduca florestan</i>	0.33 \pm 0.58	0	0
<i>M. sexta</i>	0	0.33 \pm 0.58	0.33 \pm 0.58
Noctuidae			
<i>Achaea ablunaris</i>	0.33 \pm 0.58	0	0.33 \pm 0.58
<i>Condica sutor</i>	0	0	0.33 \pm 0.58
Small moths	2 \pm 1	2.67 \pm 1.15	3 \pm 2

**Fig. 2** Number of visits (mean \pm SD) of diurnal animals to *Echinopsis thelegona* flowers at La Bodega (Salta, Argentina). Am *Apis mellifera*, Xo *Xylocopa ordinaria*, Xsp *Xylocopa* sp., Ba *Bombus atratus*, Bm *Bombus morio*, Me unidentified species of Megachilidae. Different letters indicate significant differences ($p < 0.05$)

Diurnal visitors included *Apis mellifera*, *Bombus atratus*, *B. morio*, *Xylocopa ordinaria*, *Xylocopa* sp., and one unidentified species from the family Megachilidae. No significant differences in the number of bee visits to flowers of *E. thelegona* were registered among the years, although there were differences among bee species ($F = 10.70$, $df = 154$, $p < 0.0001$). *Apis mellifera* presented the highest number of visits, while *B. morio* and Megachilidae species presented the lowest number of visits, according to the Fisher LSD test (Fig. 2).

Effectiveness of nocturnal and diurnal visitors

We did not register fruits in any treatments of the experiment on the effectiveness of nocturnal and diurnal visitors.

Distance among ramets and fruit set

Fruits were only produced in the 50 and 500 m treatments, with a low fruit set (0.2; 1 fruit in each treatment). In these treatments, the seed sets were 0.55 (50 m) and 0.64

(500 m), whereas the seed numbers were 2,021 and 2,401, respectively. The seed germination proportions were 0.89 ± 0.038 (50 m) and 0.88 ± 0.065 (500 m).

Discussion

Echinopsis thelegona presented a very low flower production, the lowest registered for columnar cacti (Fleming et al. 1996; Petit and Pors 1996; Sahley 1996), including creeping columnar cacti (Clark-Tapia and Molina-Freaner 2004) and other species of the same genus (e.g., *E. atacamensis*, *E. leucantha*, *E. schickendantzii*, *E. terscheckii*; Ortega-Baes, unpublished data). In the same way, a very low or null fruit production was registered, confirming our original observation. In clonal species, low fecundity is associated with a reduced production of reproductive structures that can be explained by a trade-off between sexual and asexual reproduction, in favor of the latter. Increased investment in clonal growth can lead to functional antagonism between the reproductive activities of clones, with the loss of or low sexual reproduction (Eckert 2002; Vallejo-Marín et al. 2010). This characteristic decreases the genetic diversity and alters the demographic behavior of the population along the geographic range of clonal species (Dorken and Eckert 2001; Eckert 2002; Billingham et al. 2003; Gross and Caddy 2006; Beatty et al. 2008). In these species, establishment through clonal reproduction would be advantageous, allowing long-term persistence.

According to our results, *E. thelegona* is a self-incompatible species; therefore, it depends on pollinators for fruit and seed production. This trait is common among columnar cacti (Pimienta-Barrios and del Castillo 2002), especially those of the genus *Echinopsis* (Ortega-Baes et al. 2011; Alonso-Pedano and Ortega-Baes 2012; Ortega-Baes, unpublished data). This characteristic explains, to some extent, the low fruit production registered in our study. In clonal species, much of the pollen that moves in the population is self-pollen. The movement of self-pollen reduces fecundity in self-incompatible species because the stigma becomes saturated with geitonogamous pollen (Charpentier 2002; Vallejo-Marín et al. 2010). However, this effect is expected in systems where the availability of pollinators is not a limiting factor, which does not correspond with the pollination system that we have studied. The *E. thelegona* pollination system exhibits pollinator limitation as well as pollen limitation, the latter caused by a low flower production.

Although the flowers of *E. thelegona* have sphingophilous traits, we have not found evidence of moths visiting them. The lack of moth visits could be due to their low local abundance, which was evidenced by the low number

of individuals registered in the light traps. We collected a great diversity of small moths, but none of them was registered visiting the flowers of *E. thelegona* nor did they present pollen in their bodies; thus, we assume that these moths do not behave as pollinators. Sphingidae and Noctuidae moths have been indicated as effective pollinators of species of the genus *Echinopsis* (Walter 2010; Ortega-Baes et al. 2011; Alonso-Pedano and Ortega-Baes 2012); however, this finding was not confirmed by the present study.

As the flowers remain open for a few hours the following morning, they are available for diurnal visitors, such as bees. We have registered six bee species visiting the flowers of *E. thelegona*, including the exotic bee *Apis mellifera*, although the number of visits was lower than for other species of the *Echinopsis* genus in northwestern Argentina (e.g., *E. terscheckii*, Ortega-Baes et al. 2011). Because bees move among neighboring flowers that may belong to the same clone, much of the pollen deposited on the stigmas would be self-pollen (Clark-Tapia and Molina-Freaner 2004; Vallejo-Marín et al. 2010). The results of the pollen supplementation experiment using pollen donors of different distances within the studied population support this idea. However, these results should be cautiously taken due to the low number of flowers used in our experiment. In addition, some bees, like *A. mellifera*, may behave as pollen thieves because they do not touch the stigmas during their visits (Ortega-Baes et al. 2011). So, nocturnal visitors were not registered as pollinators of *E. thelegona* (during the study), maybe because of their low local abundances; whereas bees behaved as inefficient pollinators due to their foraging behavior (Clark-Tapia and Molina-Freaner 2004).

Our results suggest antagonism between sexual and asexual reproduction associated with the self-incompatibility in *E. thelegona*, with consequences for pollen dispersal and mating. In clonal species, flowers have a greater likelihood of receiving self-pollen rather than cross-pollen. This self-pollination affects negatively male and female mating costs (and therefore impacts overall plant fitness), with significant implications for the evolution of mating systems (e.g., total loss of sexual reproduction; Eckert 2002; Vallejo-Marín et al. 2010). In addition, we have registered low flower production and pollinator limitations. Therefore, self-incompatibility, low flower production, low local abundance of pollinators and clonality in combination could account for the low fruit production observed in the populations of *E. thelegona*. This finding suggests that populations of this cactus species persist mainly by clonality and that they are tending to the loss of sexuality (Honday and Bossuyt 2005). Future studies should evaluate the last hypothesis along the geographical distribution of this species, and the generality of the ideas presented here should be tested in other clonal cactus species that are distributed in Argentina.

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