



Short communication

Floral morphometry, anthesis, and pollination success of *Mammillaria pectinifera* (Cactaceae), a rare and threatened endemic species of Central Mexico



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ABSTRACT

Reproductive biology in the highly diverse Cactaceae family is described in only few species. Given that a large number of species are rare, threatened, or endangered, and the entire family is included in Appendix II of CITES, the limited knowledge about their reproductive biology is of major concern. *Mammillaria pectinifera* is an endangered, small, globose cactus endemic to the Tehuacán-Cuicatlán region in Central Mexico. We aimed to characterize some basic aspects of its reproductive biology in three populations. We described flower morphology and anthesis, identified floral visitors, and evaluated the occurrence of spontaneous self-fertilization and the success of open pollination. Diurnal anthesis in flowers lasted about 4 h/day and almost all flowers lasted only one day after opening. The analyses of variance revealed differences in flower morphology among populations. Herkogamy was positive and significantly different among populations. Field experiments revealed that open-pollinated flowers were highly successful in setting fruits and seeds. These results corroborate those reported in other *Mammillaria* species. Autonomous self-pollination was negligible and ineffective. Bees of the genus *Ceratina* were dominant among the captured flower visitors, and estimations of their maximum foraging distance indicated successful outcrossing in plants. This study indicates almost complete dependency of *M. pectinifera* on pollinators for fruits and seeds production. Our results serve as a basis for future research on reproductive biology of *M. pectinifera* and other rare and endangered cacti.

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1. Introduction

In Cactaceae, a notable and very diverse family of nearly 2000 species native to the Americas, a high number of species are considered rare, threatened, or endangered as a result of habitat destruction and international trade. The entire family is included in Appendix II of the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES) (UNEP-WCMC, 2013)

and requires urgent evaluation of population status. Consequently, the lack of information about their reproductive biology in their natural habitat is of major concern (Mandujano et al., 2010). The few available studies reveal that a large proportion of cacti species have hermaphroditic (Mandujano et al., 2010) and xenogamous flowers (Guerrero et al., 2012) pollinated by numerous species of birds, mammals, and insects (Guerrero et al., 2012). However, the scarce studies on reproductive biology are not equally distributed across taxa (Nassar and Ramírez, 2004), and cacti genera, including *Mammillaria* need to be studied (but see Bowers, 2002; Flores-Martínez et al., 2013).

This study focuses on the rare and endangered small globose

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cactus, *Mammillaria pectinifera* F.A.C. Weber, endemic to the Tehuacán-Cuicatlán region in Central México (Bravo-Hollis and Sánchez-Mejorada, 1991). This species is considered threatened under the Mexican law (NOM-059-ECOL-2001) and it is already included in Appendix I of the CITES (Valverde et al., 2009). *M. pectinifera* is an extremely rare species with a narrow geographic range, high habitat specificity, and small population size (Zavala-Hurtado and Valverde, 2003). Previous studies have examined important aspects of its biology and ecology (e.g., Valverde and Zavala-Hurtado, 2006; Valverde et al., 2009), but studies on reproductive biology are lacking.

This study aimed to characterize some basic aspects of the reproductive system of *M. pectinifera*, identify floral visitors in three populations, and through field experiments address two basic ecological questions. 1) Does spontaneous self-fertilization occur without the intervention of pollinators? 2) How does the fruit and seed production of open-pollinated flowers of *M. pectinifera* compare to those reported in other small globose cacti? Given the available data for the *Mammillaria* genus, we hypothesized very low or no success rate of self-fertilization without the assistance of pollinators and that the reproductive output of the open-pollination treatment would be relatively high and similar to those recorded for other small globose species.

2. Methods

2.1. Study area

The study was carried out in the Tehuacán-Cuicatlán Biosphere Reserve (TCBR) (17°20' to 18°53' N and 96°55' to 97°44' W; 500–2400 m a.s.l.) in Central Mexico. The climate is mainly semi-arid with summer rainfall. Annual precipitation ranges from 400 to 500 mm and temperature from 18 to 26 °C, and the vegetation is dominated by xerophytic scrub. The northern portion of the TCBR is the known area of distribution of *M. pectinifera*. We studied three populations: El Riego, Texcala, and Frontera (1905–1950 m a.s.l.) with population densities of 65.1, 132.2, and 23.0 individuals/100 m², respectively (Valverde et al., 2009). Distances between populations ranged from 4.84 to 29.18 km (Valverde et al., 2009). Further details on vegetation and environmental characteristics of the three populations have been reported elsewhere (Valverde et al., 2009).

2.2. Anthesis and flower morphology

To describe the time and events occurring during anthesis, we monitored flowers (*n*) at 90-min intervals in each population (El Riego: *n* = 15 from 13 plants, Texcala: *n* = 9 from nine plants, and Frontera: *n* = 7 from five plants). Flower opening and closure were determined by measuring the corolla aperture (the distance between the opposite petal tips; Valiente-Banuet et al., 2004). To infer flower receptivity, we monitored anther dehiscence and stigma turgidity (see Molina-Freaner et al., 2004; Valiente-Banuet et al., 2004). We also described changes in the stigma position and diameter of the anther area (area occupied by anthers) during anthesis. Measurements were made using a digital calliper (CD-S6, Mitutoyo Corp., Kawasaki, Japan). Ambient temperature was recorded 30 cm aboveground using a pocket weather tracker (Kestrel 4000, Niels-Kellerman Co., Boothwyn, PA, USA). Flower and temperature measurements were made during two consecutive days at El Riego (18 and 19 January, 2006) and one day at Texcala and Frontera (18 and 27 January, 2006, respectively).

To determine nectar production, five flowers in each population were excluded from pollinators with nylon mesh netting. Nectar was sampled with 10 µL capillary tubes (Sigma, St. Louis, MO, USA)

at 90-min intervals from opening until closure of the flowers.

Variation in flower morphology was assessed by morphological measurements (Table 1) on a sample of fully opened flowers collected in each population and preserved in 75% ethanol (El Riego *n* = 17, Texcala *n* = 14, and Frontera *n* = 7; one flower per plant). The differences among populations were analysed with one-way analysis of variance with population included as a fixed factor. All morphological variables were log₁₀-transformed to ensure normality. Analyses were carried out using JMP v. 3.2.5 (SAS Institute, Cary, NC, USA).

2.3. Field experiments

Fruit and seed production by autonomous self-pollination and by open pollination were determined in field experiments. Different number of flowers and individuals were assigned to each of the following two treatments (Table 2): 1) flower buds were bagged with nylon mesh netting preventing exposure to pollinators during anthesis, and 2) flowers were tagged and exposed to pollinators during anthesis. The flower exclusion experiments were carried out in January of 2006 (El Riego and Texcala) and 2007 (Frontera) and mature fruits were collected in late April. Seeds were counted and compared with the average number of ovules to estimate seed set.

2.4. Floral visitors

In order to identify flower visitors, 4–6 flowers in each population were observed over two consecutive days for 30 min at 1-h intervals from 1000 to 1600 (i.e. the time of flower opening and closure) on the 19 and 20 January 2006. Voucher specimens were captured directly from the flowers and preserved in 75% ethanol for

Table 1

Morphometric description of *Mammillaria pectinifera* floral traits in three populations at the Tehuacán-Cuicatlán Biosphere Reserve, Mexico. Different letters indicate significant differences (*P* < 0.05) among populations. The values are means (SE).

Floral traits	El Riego	Texcala	Frontera	P
Perianth diameter ⁽¹⁾	7.043 (0.34) ^a	12.92 (0.4) ^b	4.85 (0.52) ^a	<0.0001
Corolla aperture ⁽¹⁾	3.55 (0.32)	2.60 (0.16)	3.22 (0.69)	ns
Flower basal diameter ⁽¹⁾	3.28 (0.09) ^b	2.72 (0.13) ^a	2.81 (0.30) ^a	0.013
Flower height ⁽¹⁾	12.01 (0.82)	11.48 (0.35)	10.74 (1.64)	ns
Nectar chamber diameter ⁽¹⁾	1.38 (0.05) ^b	1.20 (0.09) ^b	1.03 (0.05) ^a	0.0038
Nectar chamber height ⁽¹⁾	1.37 (0.06)	1.31 (0.06)	1.17 (0.10)	ns
Ovary ecuatorial diameter ⁽¹⁾	1.42 (0.07) ^b	1.17 (0.12) ^b	0.76 (0.08) ^a	<0.0001
Ovary polar diameter ⁽¹⁾	1.25 (0.07) ^b	1.08 (0.05) ^b	0.73 (0.04) ^a	<0.0001
Style length ⁽¹⁾	10.9 (0.52)	10.65 (0.40)	8.98 (1.44)	ns
Stigma lobes length ⁽¹⁾	1.18 (0.08)	0.97 (0.07)	0.94 (0.10)	ns
Stigma lobes ⁽²⁾	4.93 (0.29)	4.29 (0.23)	4.00 (0.28)	ns
Basal stamens length ⁽¹⁾	3.87 (0.24)	4.54 (0.28)	3.51 (0.41)	ns
Middle stamens length ⁽¹⁾	4.5 (0.27)	5.35 (0.30)	5.25 (0.47)	ns
Distal stamens length ⁽¹⁾	7.026 (0.32) ^b	5.91 (0.17) ^a	5.37 (1.09) ^a	0.015
Stamens ⁽²⁾	111.8 (6.68) ^b	86.57 (4.19) ^a	97.5 (9.13) ^b	0.018
Ovules/ovary ⁽²⁾	22.9 (1.85) ^a	28.9 (2.96) ^b	19.2 (2.97) ^a	0.0093
Stigma–anthers distance ⁽¹⁾	0.46 (0.06) ^a	0.80 (0.09) ^b	0.23 (0.07) ^a	<0.0001

⁽¹⁾Measurement in mm; ⁽²⁾Counts.

Table 2

Fruit set, number of seeds/fruit and seed set (proportion of ovules forming seeds, given that a fruit matured) in autonomous self-pollination and open-pollination treatments in three populations of *Mammillaria pectinifera* at the Tehuacán-Cuicatlán Biosphere Reserve, Mexico.

	El Riego	Texcala	Frontera
<i>Natural autonomous self-pollination</i>			
Number of plants	20	20	20
Number of flowers	20	20	27
Number of fruits	0	0	1
Fruit set	0	0	0.04
Mean number of seeds/fruits (SE)	0	0	4 (0.0)
Seed set (SE)	—	—	0.21 (0.0)
<i>Open-pollination</i>			
Number of plants	27	10	16
Number of flowers	46	13	30
Number of fruits	28	11	27
Fruit set	0.61	0.85	0.90
Mean number of seeds/fruits (SE)	17.61 (2.19)	29.18 (2.61)	19.11 (2.23)
Seed set (SE)	0.80 (0.10)	0.97 (0.09)	0.99 (0.09)

later identification.

3. Results and discussion

In the three populations, all dissected flowers were hermaphroditic, homogamous (anther dehiscence and stigma turgidity occur simultaneously), and showed diurnal anthesis (about 4 h/day), which is analogous to other species of the genus (e.g. Bowers, 2002; Giovanetti et al., 2007; Flores-Martínez et al., 2013). Flowers started opening at 1030–1130 reaching the maximum corolla aperture, stigma turgidity, and diameter of anther area between 1200 and 1400, at the time of the highest ambient temperature (19.6 and 22.3 °C at El Riego, 31 °C at Texcala, and 25 °C at Frontera). After 1400, corolla aperture decreased and flowers closed at 1500–1600. At the beginning and the end of anthesis, anthers and stigma lobes were bent towards the centre of the flower, whereas after midday, the stigma lobes reached their maximum extension and anthers occupied the total internal area of the floral tube. Similarly to most cacti species (Mandujano et al., 2010), flowers lasted only one day after opening. However, some flowers opened the second day at El Riego (attaining up to 8 h of anthesis), suggesting that a single anthesis event did not always result in successful pollination, as Bowers (2002) reported for *Mammillaria grahamii*. It has been proposed that an increment in floral longevity would enhance the number of ovules pollinated under a low-availability-of-pollinators scenario (Flores-Martínez et al., 2013).

Flowers arose from the axils of lateral tubercles on the stem. They were bell-shaped with naked perianth, and inner segments were pale pinkish to white with a light to deep pink midrib. The stamens, generally pinkish to purplish, emerged from the bottom of the flower tube, and the central style was light to deep pink, ending in a greenish stigma with four to five lobes. The anthers were yellowish to greenish. Different colour displays were found in the same population. The observed colour patterns are consistent with those described elsewhere (Bravo-Hollis and Sánchez-Mejorada, 1991). In the three populations, flowers were present from December to late March.

We failed to detect nectar production during anthesis. It could have been very low or absent as has been reported for *Mammillaria huitzilopochtli* (Flores-Martínez et al., 2013); hence, pollen is probably the main award to insect visitors (mainly bees) in *M. pectinifera*. In fact, pollen as a reward is one of the suites of floral traits associated with bee pollination (Wyatt, 1983).

The analyses of flower morphology revealed significant differences among populations. Flowers from Frontera populations were

the smallest whilst having the highest number of ovules/flower (Table 1). Based on 95% confidence intervals (Nassar and Ramírez, 2004), herkogamy was positive and significantly different from zero in the three populations, with stigma above anthers in all flowers sampled. Herkogamy was greater in Texcala than in El Riego and Frontera populations (Table 1). These floral characteristics further affect the reproductive traits of the populations (Nassar and Ramírez, 2004). Herkogamy, a plant trait that prevents selfing and promotes outcrossing, favouring pollen transfer among conspecifics (Geber and Moeller, 2006) is common in Cactaceae (Mandujano et al., 2010). Selfing is related to small flowers since herkogamy covaries positively with flower size (Elle, 2004). Thus, in Frontera populations (Table 2), where the single autonomous self-pollination event was detected, anthers were closest to the receptive surface of the stigma and corolla width was the smallest.

Most cacti have xenogamous flowers (Guerrero et al., 2012) although some autogamy has been found. For example, fruits and seeds produced by non-manipulated self-pollination have been detected in other cacti including *Ferocactus cylindraceus*, *F. wislizeni* (McIntosh, 2002), *Melocactus curvispinus* (Nassar and Ramírez, 2004), and *M. andinus* (Nassar et al., 2007). Herein, fruits were not produced after the autonomous self-pollination in El Riego and Texcala populations (Table 2). However, in Frontera population, only one out of 27 excluded flowers produced a fruit containing only four seeds (Table 2). This finding is remarkable since the unique published evidence related to reproductive biology of *M. pectinifera* cited self-incompatibility after artificial self-pollination under greenhouse conditions (Ross, 1981). Our field experiments revealed a possibility for fruit and seed set resulting from selfing in the absence of pollinators at least in one population of *M. pectinifera*. Rare and endangered species often occur in small populations where pollinators are more likely to be absent or ineffective (Neel, 2002). The uncommonness of autonomous self-pollination and its low seed set in *M. pectinifera* were very similar to those reported for *M. huitzilopochtli* (Flores-Martínez et al., 2013).

Fruit and seed set in open-pollination experiments were consistently high in all populations (≥ 0.61 and ≥ 0.80 , respectively, Table 2). These values are high in respect to those reported for columnar cacti (e.g., Molina-Freaner et al., 2004; Valiente-Banuet et al., 2004) but not outstanding relative to *M. huitzilopochtli* (Flores-Martínez et al., 2013) and *M. grahamii* (and other small cacti, Bowers, 2002). Although there is no proof that such high fruit and seed set observed in our field experiments were due to outcross rather than self-pollination, the exceptional fruit and seed set from open-pollinated flowers indicated high efficiency of the pollination and fertilization system of *M. pectinifera*.

Table 3

Insect visitors captured on flowers of *Mammillaria pectinifera* in three populations at the Tehuacán-Cuicatlán Biosphere Reserve, Central Mexico. ER = El Riego, T = Texcala, and F = Frontera; n = number of captured individuals. All captures occurred between 1100 and 1400 h.

Order	Family	Species	Population (n)
<i>Hymenoptera</i>			
	Apidae	<i>Ceratina</i> sp. 1	ER (2), T (2), F (5)
		<i>Ceratina</i> sp. 2	T (2), F (3)
	Andrenidae	<i>Perdita</i> sp.	ER (2), T (3)
	Halictidae	<i>Sphecodosoma</i> sp.	F (3)
		<i>Lassioglossum</i> sp.	T (2)
	Megachilidae	<i>Ashmeadiella</i> sp.	F (1)
		<i>Dianthidium</i> sp.	T (1)
	Vespidae	<i>Stenodynerus</i> sp.	T (1)
		<i>Diptera</i>	
		Bombyliidae	<i>Ogcodocera</i> sp.
Syrphidae		<i>Eristalis</i> sp.	ER (1)

The insects-visitors captured on flowers of *M. pectinifera* were predominantly bees, mainly from the genus *Ceratina* (Table 3). All collections occurred between 1100 and 1400, during the maximum corolla aperture, stigma turgidity, and anther area. Although we did not test their effectiveness as pollinators, other studies report on their potential role as pollinators of *Mammillaria* (Giovanetti et al., 2007). Assuming that these bees are pollinators, we estimated the maximum foraging distances for two *Ceratina* species from our sample of captured individuals (Table 3). Based on equations that correlate body size (measured as intertegular span) to maximum foraging distance using the homing method (Greenleaf et al., 2007), the average maximum homing distance estimations were 57.05 ± 9.28 m and 79.98 ± 18.01 m for *Ceratina* sp. 1 and sp. 2, respectively. If the mean population density in the studied populations is 73.43 ± 31.8 individuals/100 m², both bee species are probably able to transfer pollen among individual plants and promote outcrossing within populations.

4. Conclusions

Our study showed that flowers of *M. pectinifera* have diurnal anthesis in all populations. The size, colour, shape, and diurnal habit of the flowers, together with the observations of insect visitors (primarily bees), suggest that flowers are bee-pollinated. Analyses of flower morphology revealed significant differences among populations in nine out of 17 traits. Field experiments showed that open-pollinated flowers of *M. pectinifera* were highly efficient in fruit and seed set and that the species is almost completely dependent on insect pollinators to produce fruits. Finally, the results of the present study serve as a basis for future research on reproductive biology of *M. pectinifera* and other rare and endangered cacti.

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