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THE ADAPTIVE VALUE OF CUED SEED DISPERSAL IN DESERT PLANTS: SEED RETENTION AND RELEASE IN *MAMMILLARIA PECTINIFERA* (CACTACEAE), A SMALL GLOBOSE CACTUS¹

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Serotiny, or delayed seed dispersal, is common in fluctuating environments because it hedges the risks of establishment. *Mammillaria pectinifera* (Cactaceae) facultatively expels fruits in the year they are produced or retains them to disperse the seed over several years. We tested whether *M. pectinifera* increased fruit expulsion as a response to increased rainfall. While no fruit expulsion was observed in 1997, a dry year, in the wetter 1998 around 20% of all fruits formed were expelled from the maternal plant. A greenhouse experiment showed that high moisture results in the plants expelling all their fruits. Because in 1998 establishment was five times higher than in 1997, this response seems to be highly adaptive: Active fruit expulsion and consequent seed release increases the probability of establishment during pulses of high precipitation.

Key words: bet-hedging; Cactaceae; environmental triggers; *Mammillaria*; Mexico; serotiny; Tehuacán Valley.

Serotiny or delayed dispersal—the retention of mature seeds within the maternal plant for more than one year—is a syndrome of adaptive significance in randomly fluctuating environments such as dry, fire-prone scrubs and forests (e.g., Lamont et al., 1991; Lamont and Enright, 2000; Midgley, 2000), and arid ecosystems (Ellner and Schmid, 1981; Kamenetsky and Gutterman, 1994; Van Oudtshoorn and Van Rooyen, 1999). Serotiny can be adaptively advantageous through (1) early establishment within the germination season (Went, 1949; Beatley, 1974), (2) protection of seeds against granivores (Reichman, 1979; Van Oudtshoorn and Van Rooyen, 1999; Albert, 2005), (3) bet-hedging risks by spreading seed dispersal in time (Cohen, 1966, 1968; Venable and Lawlor, 1980), and (4) retaining seeds in a favorable microhabitat (Gutterman, 1994, 1995).

A special case of serotiny is found in many small globose cacti (Anderson, 2001; Rodríguez-Ortega et al., 2006). Bravo-Hollis and Sánchez-Mejorada (1991) described at least 25 species (belonging to the genera *Mammillaria*, *Coryphantha*, *Dolichothele*, *Neobesseyia*, *Echinocactus*, *Aztekium*, *Lophophora*, *Obregonia*, *Ariocarpus*, and *Pelecypora*, all in the subtribe Cactaeae within the tribe Cactoideae) that show some degree of fruit retention. The flowers grow from meristems deep in woolly apices or in the folds between stem tubercles and tend to sprout in coetaneous whorls near the top of the plant. The resulting fruits may be retained for up to six years.

Working with three species of *Mammillaria*, Rodríguez-Ortega et al. (2006) showed that one species growing in drier and more variable environments retained more seeds (ca. 25%) than other species that grow under milder and more constant

conditions (only ca. 5% retained). They concluded that serotiny in *Mammillaria* may be an adaptive trait that confers some advantage in harsh and unpredictable arid environments.

However, fruit retention varies not only between individuals but also over time within a single plant. In this study we assessed whether a serotinous cactus can facultatively regulate the fraction of seeds that are retained. We worked with *Mammillaria pectinifera* F.A.C. Weber (Cactaceae), a rare and threatened plant that has two modes of seed release: (1) Whole fruits may be released with their complete seed content immediately after maturation, while (2) other fruits are retained, and they gradually release seeds through an apical aperture as they age (Fig. 1). The ability of the plant to follow one or the other path may have adaptive value in response to climatic variability because the probability of establishment during wet pulses may increase (Noy-Meir, 1973; Gutterman, 1995).

This hypothesis is especially important because germination and establishment constitute the most vulnerable stages in the life cycle of cacti (e.g., Steenberg and Lowe, 1983; Valiente-Banuet and Ezcurra, 1991) and establishment of desert plants occurs mostly during pulses of high precipitation (Evenari et al., 1971; Lacey, 1980; Holmgren et al., 2001; Bowers et al., 2004; Venable, 2007). Thus, while gradual seed release in serotinous cacti may be a bet-hedging strategy that spreads the risks of establishment, the sudden release of a large proportion of seeds may be of even greater advantage if the plants can in some reliable way synchronize the release with an environmentally favorable period (Cohen, 1966, 1968; Venable and Lawlor, 1980). The driving question of our research was: Can serotinous plants adaptively regulate fruit and seed release according to environmental conditions? And, if they can, will this increase the probability of successful establishment?

To answer these questions, we studied the role of seed retention and dispersal in *M. pectinifera* in the field during two contrasting years and also under different experimental conditions. Through this study, we tested two hypotheses. If the probability of establishment is raised during wet pulses, we predict that fruit expulsion should increase in wet years. Further, we predict that, in fully optimal circumstances (only to

¹ Manuscript received 1 May 2008; revision accepted 21 October 2008.

The authors thank S. Arizaga, E. Castillo, and the people at Texcala, Puebla, for their help. This paper is part of the graduate research of E.M.P., supported by a CONACYT scholarship. The research was also funded by CONABIO project R-166, and the Instituto de Ecología-UNAM provided logistic support.

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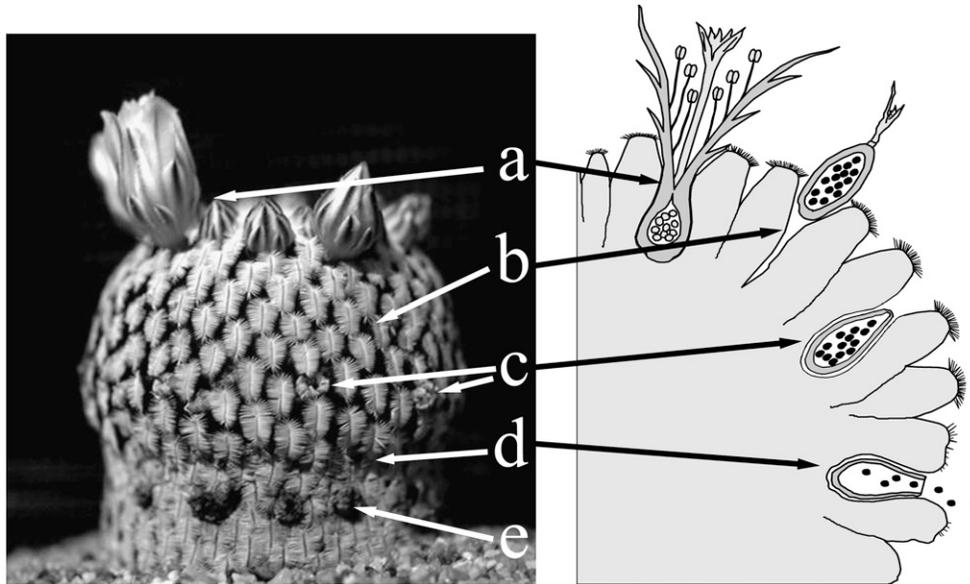


Fig. 1. Photograph of *Mammillaria pectinifera* with five whorls of fruits of different ages showing the possible fates of floral buds. (a) Flowers; (b) expelled fruit from the most recent whorl (only the gap between areoles is seen in the photo); (c) retained fruits from the previous whorl (over two years of age); (d) third whorl of fruits, three or more years of age, with eroded tips and most of the seeds dispersed; (e) the dry remains of a whorl of old empty fruits, clearly seen at the base of the photo but not drawn in the diagram. In this species, expelled fruits always belong to the most recent cohort.

be realized under field conditions in extraordinary occasions), the expulsion of fruits should be the dominant mode of seed dispersal.

MATERIALS AND METHODS

Description of the species and study site—*Mammillaria pectinifera* is a globose, hemicryptophytic cactus, 3–4 cm in diameter. The pectinate areoles possess white appressed spines that cover and shade the plant. The flowers open in circular crowns around the apex. The fruit is a whitish berry that may be completely expelled or may remain inserted inside the stem of the plant, gradually releasing seeds for 7–8 years (Boke, 1960; Bravo-Hollis and Sánchez-Mejorada, 1991) (Fig. 1). The species is endemic to the Tehuacán Valley, a small semiarid area in the southeast of the State of Puebla, Mexico (Bravo-Hollis and Sánchez-Mejorada, 1991), and is confined to deep alkaline soils with relatively high surface stoniness and high water retention capacity, receiving ca. 400 mm of annual precipitation (Zavala-Hurtado and Valverde, 2003). Our field study was done near the town of Texcala, in a dense stand of *M. pectinifera*. As a result of its restricted distribution, specialized habitat, habitat destruction (Martorell and Peters, 2005), looting, and illegal trade, the species has been included in the Appendix I of the Convention on International Trade in Endangered Species (CITES, 2007), and in the Mexican Government's endangered species list (SEMARNAT, 2002).

Rainfall data—Rainfall data for the study period (June 1997–May 1999) were collected with rainfall gauges in the field. The long-term series used for comparison was obtained from the public databases of Mexico's Weather Service (Servicio Meteorológico Nacional, México, D.F.).

Seed release from embedded fruits and viability—Twenty plants were collected near the study site, and the seeds that were retained inside 615 fruits of known age were extracted and counted. Age was easily estimated because annual rings of fruits are readily distinguishable in the stem (see Fig. 1). Curves were fitted through a log-linear regression minimizing a χ^2 error function (Crawley, 1993) to predict the number of seeds that remain in the fruits at different ages. The seeds extracted from the fruits were placed in Petri dishes with agar gel and incubated at 25°C and a 12-h photoperiod to estimate viability loss in the embedded seeds as the fruits age. Germination was counted after 30 d (no further germination was observed after this time).

Fruit expulsion and seedling establishment in the field—The area under study was delimited by a 238-m² polygon. Eighty-one adult individuals of different sizes were randomly selected and marked. The number of fruits produced and number of fruits expelled were recorded every month for two years, from June 1997 (at the beginning of the summer monsoon season) to May 1999 (at the end of the spring drought). Seedlings were carefully searched for and marked on November of both years (once the monsoon season had ended, when seedlings are more easily found) in 55 randomly chosen 1-m² quadrats. They were monitored monthly until May (the onset of the following monsoon season), and the number of survivors was then extrapolated to the whole study area (238 m²).

Experiment on fruit expulsion—To assess whether fruit expulsion occurs as a response to increased precipitation, we transplanted 30 adult individuals of *M. pectinifera* with recently formed fruits to a greenhouse and randomly assigned them to an experimental watering treatment (2 plants/treatment) ranging from 0 to 30 mm of watering three times a week for 21 wk. The proportion of fruits expelled by each plant was fitted against total simulated precipitation using logistic regression with a χ^2 error function. All curve-fitting procedures were done using the GLIM 4.0 statistical package (Francis et al., 1993).

RESULTS

Rainfall data—The first year of our study (June 1997–May 1998) coincided with an unusually dry period for the region, in synchrony with the 1997 El Niño anomaly (Caso et al., 2007). The second year (June 1998–May 1999) corresponded with a relatively wet period, in synchrony with La Niña conditions. Precipitation during the first year (267 mm) was ca. 40% lower than the 36-yr average for the region (424 mm), while during the second year, rainfall (817 mm) almost doubled the mean (Fig. 2).

Seed release from embedded fruits and viability—The number of seeds remaining inside the fruits decreased as the non-expelled fruits aged within the plant ($\chi^2 = 26.85$ for the two-parameter loglinear model, $df = 1$, $p < 0.0001$). On average, 42.6% of the seeds are retained in each fruit during the first year. Seeds rarely occurred in retained fruits greater than 4 yr of

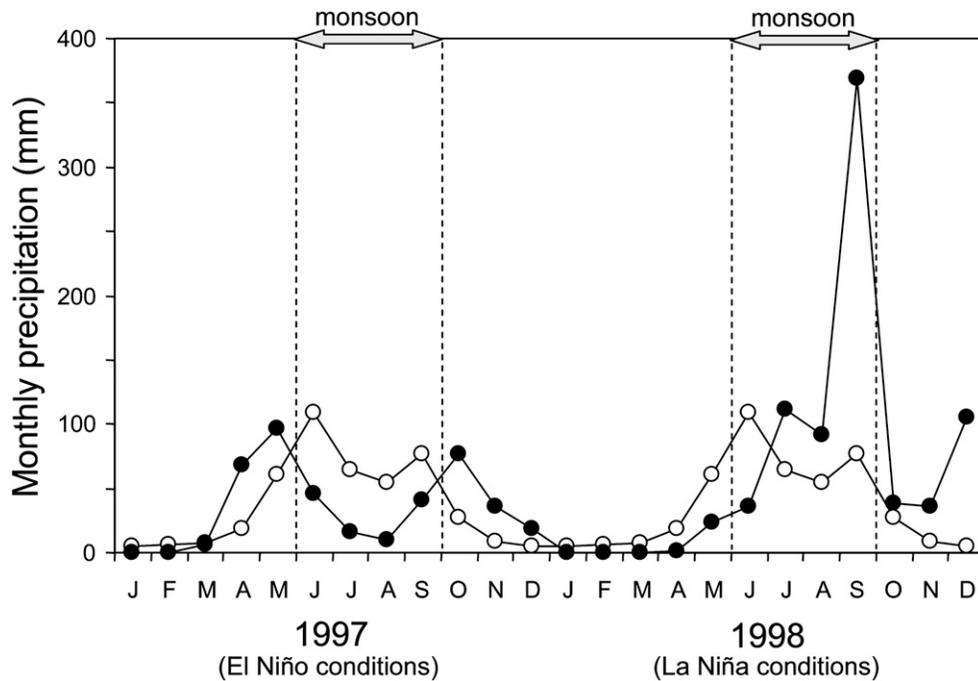


Fig. 2. Precipitation in the study area in the Tehuacán Valley, Mexico, during 1997–1998. Black circles show the measured monthly precipitation and open symbols the 40-yr average. The monsoon season (June–September) is shown for both years. Note the low monsoon precipitation in 1997 under strong El Niño conditions, followed by intense monsoonal downpours in the late summer of 1998, when La Niña conditions prevailed in the Pacific coast of Mexico.

age (Fig. 3). On average, 46% of the seeds germinated regardless of their age ($\chi^2 = 0.7$, $df = 1$, $p > 0.4$); i.e., seeds did not lose viability as they aged inside the maternal plant.

Fruit expulsion and seedling establishment in the field—An average of 6.1 fruits per plant was produced every year. No significant differences in fruit production were observed between years, but the fraction of fruits expelled did differ ($\chi^2 = 115$, $df = 1$, $p < 0.0001$). During the dry 1997, no fruits were

expelled from the plant stems, and all seeds released into the environment came from embedded fruits. In contrast, 21.5% of all new fruits were expelled in 1998, in synchrony with the onset of the intense monsoon rains that fell during this year. Assuming that fruit production remains roughly the same over time and that fruit expulsion in the two dry years preceding 1997 was negligible, we estimated the total number of seeds that were likely shed in 1997 (when no fruits were expelled) and in 1998 (when 21.5% of all new fruits were expelled). The high moisture of the second year was reflected in the greater number of seedlings and the higher establishment success observed in 1998, five times greater than in 1997 (Table 1).

Experiment on fruit expulsion—Under greenhouse conditions, watering significantly increased the expulsion probability of fruits ($F = 78.77$, $P < 0.0001$, $df = 1$, Fig. 4). When the simulated annual precipitation exceeded 1000 mm, almost all fruits were expelled from the plants.

DISCUSSION

As hypothesized by Rodríguez-Ortega et al (2006), the retention of fruits containing seed and the protracted viability of seed suggest that adult plants of *M. pectinifera* are acting as a seed bank that regulates dispersal over time. While whole-fruit release is triggered by a form of predictive cueing during favorable seasons, fruit retention followed by gradual seed release may act as a bet-hedging strategy in a taxonomic group with extraordinarily high seedling mortality (Godínez-Álvarez et al., 2003).

Compared to other mammillarias (Rodríguez-Ortega et al., 2006), *M. pectinifera* retains a very large proportion (~43%) of

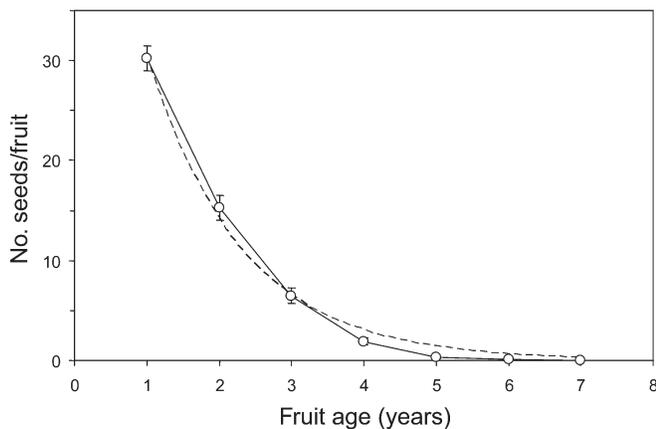


Fig. 3. Number of seeds in fruits of different ages inserted between the areoles of the mother plants of *Mammillaria pectinifera*. Confidence intervals correspond to ± 1 SE. The broken line shows the fit of the two-parameter log-linear model ($s = 30.5 \times e^{-0.77t}$), for a constant retention rate of 46% per year ($e^{-0.77} = 0.464$; see the results section, “Seed release from embedded fruits” for significance of the fit).

TABLE 1. Seed production and seedling establishment by *Mammillaria pectinifera* for the two study years within the 238-m² study plot. Establishment success (the probability of establishment of a dispersed seed) was estimated as the ratio of seedlings that germinated each year and survived the following dry season divided by the total number of seeds released in that year.

Reproductive variable	1997–1998	1998–1999
Seeds from embedded fruits	35 508	32 259
Seeds from extruded fruits	0	7 634
Total seed production (<i>a</i>)	35 508	39 893
Seedlings (<i>b</i>)	17	95
Establishment success (<i>b/a</i>) (%)	0.47	2.38

its seeds in nonexpelled fruits during the first year after they mature. However, if the 21% fruit expulsion rate observed during the wetter 1998 period is taken into account, the fraction of seeds from recent fruits being released in a good year may increase substantially. Precipitation acts as the environmental cue triggering fruit expulsion. From the adaptive point of view, it seems to be a reliable signal because the probability of germinating and establishing was five times higher in the rainy year of 1998 than in the dry 1997. Our greenhouse experiment showed that when moisture conditions are optimal, the plants may risk their full fruit production.

We conclude that *M. pectinifera* has two well-defined seed dispersal mechanisms: (1) passive dispersal of seeds retained in the stem and (2) active expulsion of new fruits formed during the previous reproductive season. The way in which these two processes operate seems to depend on the amount and timing of precipitation (Evenari et al., 1971; Noy-Meir, 1973). Under normal conditions, fruit retention prevails because whole-fruit expulsion requires precipitation well above the local average. These anomalies are linked to rare variations in climatic conditions and the ability to take advantage of them gives the plants a significant increase in seedling establishment.

Cohen (1968) showed that a strategy in which only a fraction of seeds germinate and the rest remain dormant maxi-

mizes fitness in environments where the probability of successful establishment is low and randomly variable. Because soil seed banks in cacti are very reduced (Rojas-Aréchiga and Batis, 2001), fruit retention may effectively take the place of delayed germination in other plants (Venable and Lawlor, 1980). In years with high moisture availability, fruit expulsion allows plants to adaptively increase the fraction of seeds released for immediate germination. Thus, while the gradual release of seeds seems to provide an effective risk-hedging strategy during normally harsh years, an added capacity for the active expulsion of fruits during anomalous high-moisture pulses seems to provide an important opportunity for successful establishment.

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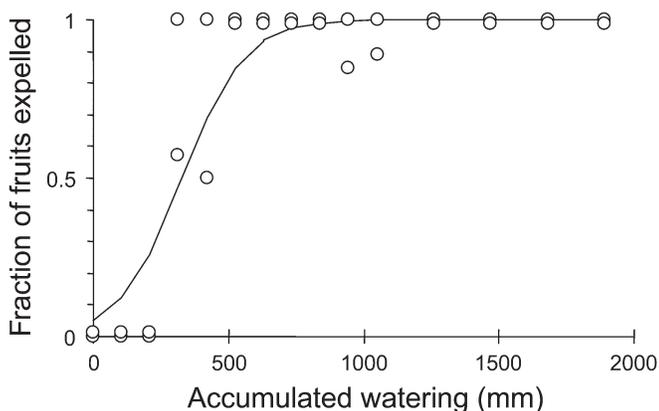


Fig. 4. Fraction of fruits of *Mammillaria pectinifera* expelled as a function of increased watering under greenhouse conditions, and logistical regression describing the threshold phenomenon ($R^2 = 0.74$; $P < 0.0001$). Simulated precipitation ≥ 600 mm during a period equivalent to that of the monsoon at the study site (21 wk or ~ 5 mo) is predicted to release practically all fruits embedded in the plant. Because evaporative demand in the greenhouse is lower than in the field, however, this threshold is expected to be higher under field conditions.

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