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Seed Age Germination Responses and Seedling Survival of an Endangered Cactus That Inhabits Cliffs

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ABSTRACT: Seed dormancy and seed longevity partially determine the crucial stages of germination and establishment of seedlings for rare Cactaceae in arid environments. We studied the effect of seed age and seed dormancy on germination and seedling establishment of an endangered species of cactus (*Mammillaria huitzilopochtli*) from Oaxaca, Mexico, in controlled and natural conditions. Germination experiments were conducted in greenhouse conditions and seedling survival was assessed in controlled and natural areas. We found that *M. huitzilopochtli* has non-dormant seeds and that germination occurred during the first seven days after sowing for seeds less than one year old ($\bar{x} = 90\%$). Germination decreased with time, which indicated that this species might be able to form a transient seed bank (maximum one year old). Scarification treatments in *M. huitzilopochtli* did not interact with seed age response and did not enhance germination percentages, asserting that seeds are nondormant. When compared with other species of the same genus inhabiting the same region, we conclude that dormancy in cacti is probably more related to environmental heterogeneity than to phylogenetic constraints. Similar to the majority of cacti species, seedlings of *M. huitzilopochtli* only established in shade conditions. The seeds and seedling traits of this endangered species must be taken into account for conservation programs. Because few seeds were produced yearly, no seeds could be stored at room conditions for long time periods (> 2 yr) and seedling survival was low (mean = 13.75%).

Index terms: nurse plant, seed bank, seed dormancy, seed longevity, seedling establishment

INTRODUCTION

Germination and establishment are crucial processes in the life cycle of a plant in arid and semiarid environments. Seeds in these environmentally unpredictable areas should be strongly selected to germinate at the most favorable time for seedling establishment (Mandujano et al. 1997; Jurado et al. 2000; Csontos and Tamás 2003); therefore, seeds available for potential germination and recruitment, under selection, should develop attributes (for ex., seed dormancy and longevity) that promote seed bank formation (Harper 1959; Montiel and Montaña 2003; Jurado and Flores 2005). Dormancy occurs when seeds do not germinate due to unfavorable environmental conditions or to some property of the seed (Crocker 1916; Harper 1959; Baskin and Baskin 1998). On the other hand, seed longevity is the ability of a seed to retain its viability for a period of time under particular environmental conditions (Fenner 1985; Vázquez-Yanes and Orozco-Segovia 1993). Thus, soil seed banks are either transient (upon seed dormancy) or persistent (upon seed longevity) (Thompson and Grime 1979). In addition, dormancy types combined with timing of seed release and germination have been proposed as adaptations for various disturbance regimes (Grime 1981).

Seed longevity and seed dormancy are probably the most important factors con-

trolling seed germination and seed bank formation (Vleeshouwers et al. 1995; Baskin and Baskin 1998; Bowers 2000; Rojas-Aréchiga and Batis 2001; Flores et al. 2005; Mandujano et al. 2005). These two factors are especially relevant for species that live in heterogeneous (spatially and temporally) environments, because conditions that promote germination and enable seedling establishment are rarely found (Nobel 1984; Franco and Nobel 1989). In desert environments, seeds often respond to specific combinations of light, temperature, and soil moisture that are more favorable to their establishment; however, these conditions may not occur every year. Therefore, the characteristics that could lead to a viable seed bank are an important long-term attribute for plant success in deserts (Mandujano et al. 1997; Rojas-Aréchiga and Vázquez-Yanes 2000; De la Barrera and Nobel 2003).

In addition to seed longevity and dormancy, establishment of seedlings is another crucial phase in the life cycle of many plants inhabiting arid environments (Flores and Jurado 2003). In deserts, cacti seedlings (even those species with high germination rates) rarely establish successfully due to the unpredictable environmental conditions of high temperatures and low soil water content (Nobel 1984; Franco and Nobel 1989; Valiente-Banuet and Ezcurra 1991; Mandujano et al. 1998, 2001). The environmental problems imposed on seedling

establishment have been partially avoided by many species by the facilitation found in nurse-protégé relationships (Shreve 1951; Fenner and Thompson 2005). This interaction leads to germination events that are preferentially found under the canopy of trees and shrubs because of their ability to modify the micro-environmental conditions (Shreve 1951; Rodríguez-Ortega and Ezcurra 2000). A number of studies have demonstrated that under the canopies of nurse plants, levels of humidity and protection against direct solar radiation are more favorable for seedling establishment (Turner et al. 1966; Steenbergh and Lowe 1969; McAuliffe 1984; Franco and Nobel 1989; Valiente-Banuet and Ezcurra 1991; Flores-Martínez et al. 1994; Nolasco et al. 1997; Mandujano et al. 1998, 2001).

Species of the Cactaceae are typically found in the arid environments of North and South America. Unfortunately, this Family accounts for a large number of species, which are naturally rare and prone to extinction. Even though the behavior of seeds is one of the main elements affecting population dynamics (Mandujano et al. 2005; Ramírez-Padilla and Valverde 2005), it is rarely taken into account in the conservation and management of endangered cacti species. In addition, few studies have addressed germination behavior where the spatial and temporal environmental heterogeneity are considered (Trejo-Hernández and Garza-Castillo 1993; Bowers 2000; Rojas-Aréchiga and Batis 2001; Flores-Martínez and Manzanero 2003; Flores et al. 2005).

The purpose of this study was to determine the germination potential of seeds of a rare endemic cactus, *Mammillaria huitzilopochtli* D.R. Hunt, over time and to determine the factors that would favor establishment in controlled and natural conditions. We specifically addressed the following questions: (1) Can the seeds of this species persist viable for a period of time, which could allow the generation of a seed bank? (2) Which conditions promote seed germination? and (3) Does seedling establishment rely on nurse protégé relationships?

METHODS

Studied species

Mammillaria huitzilopochtli Serie *Super-textae* is a globose cactus that inhabits cliff faces. In this habitat, gravity prevents soil accumulation, and humidity is limited to run-offs, which usually remain for short periods of time and dry rapidly. The species has been classified as threatened by the Mexican environmental agency, due to their limited distribution and because there are only seven populations of *M. huitzilopochtli* established on 1058 ha, with an average density of 1718 ind/ha (Peters and Martorell 2000). In addition, over-collection of plants has been detected for this species (Hernández and Godínez 1994; Arias et al. 1997; SEMARNAT 2002). *M. huitzilopochtli* is found in the Tehuacan-Cuicatlan Biosphere Reserve that covers portions of the states of Puebla and Oaxaca, Mexico. This region shows a high floristic diversity (Dávila et al. 1993) and is a center of endemism and diversity of cacti (Villaseñor et al. 1990; Arias 2000). The area is semiarid with an annual mean temperature of 21 °C and an average annual rainfall of 400 mm (Dávila et al. 1993). The habitat of *M. huitzilopochtli* (within the Cuicatlan municipality, Oaxaca, 17°48' N, 96° 58' W) has a mean annual rainfall of 553 mm – most of which falls between May and October – with mean annual temperatures of 25.5 °C (García 1981).

Individual plants of *M. huitzilopochtli* have been found under different micro-environmental conditions (Flores-Martínez and Manzanero 2005); in some populations, individuals can be found either in bare areas or under the canopies of nurse plants such as: *Opuntia* spp., *Bursera morelensis*, *Plumeria rubra*, *Cercidium praecox*, *Acacia cochliacantha*, *A. farne-siana*, *Amphypteringium adstringens*, and *Cnidoscylus multilobus* (Flores-Martínez and Manzanero 2005).

Germination experiments

Mature fruits were collected annually from 1998 to 2001 from 25 plants of *M. huitzilopochtli* (the endangered status precludes the

collection of large amounts of seeds, and seed collection was also largely dependent on the number of available reproductive plants). Seeds were separated by dissection, washed with distilled water to remove pulp residues, dried at room temperature (18-28 °C), and stored in paper bags until the onset of the experiment. Germination tests for seeds of differing ages were performed in August 2001, using Petri dishes with sterile filter paper, saturated with distilled water, kept at room temperature (18-28 °C) and in natural daylight conditions in a greenhouse at the Cassiano Conzatti Botanical Garden of CIIDIR-IPN Oaxaca. *Mammillaria huitzilopochtli* seeds were 3, 15, 27, and 39 months old (<1, 1, 2 and > 3 years old, respectively), treatments were replicated three times, and each experimental unit had 50 seeds. Before sowing, seeds were disinfected by immersion in 10% sodium hypochlorite solution for 5 min. When the radicle appeared, germination was considered successful; and final germination percentages were determined when no germination was observed for more than 7 days.

Additionally, eight treatments were used for *M. huitzilopochtli* seeds of different ages in order to determine the presence of attributes related to seed dormancy. Seeds used for this analysis were < 1 year old (4 months) and one year old seeds (16 months). The treatments were: (1) mechanical scarification with fine sandpaper, (2) mechanical scarification plus immersion in 1% or (3) 10% hydrochloric acid (HCl) for 10 min, (4) immersion for 10 minutes in HCl solutions of 1% or (5) 10%, (6) soaked in water for 2 days, (7) soaked in water for 4 days, (8) soaked in water for 6 days, and (9) a control with no treatment. Seed germination was recorded daily (radicle protrusion) during 30 days or until no germination was observed for more than 7 days. Three replicates of 20 seeds per treatment were used in these experiments. Differences in germination percentages (arcsine transformed) between treatments were analyzed using ANOVAs and Tukey HSD tests for multiple comparisons (Sokal and Rohlf 1981; SAS Institute 1995).

Seedling survival

Experiment under controlled conditions

Mammillaria huitzilopochtli seedling survival experiments were carried out in the Cassiano Conzatti Botanical Garden of CIIDIR-IPN, Oaxaca. In June 2001, in order to obtain seedlings, seeds were sown in soil brought from the original sites and germinated under greenhouse conditions. These seedlings were kept in the greenhouse for 45 days and were then transplanted to a nursery at the Botanical Garden. Two treatments of 20 seedlings each with four replicates were used to assess the effect of nurse plants on survival. Experimental treatments followed a factorial experimental design, with two levels of exposure: (1) bare areas (direct solar radiation) and (2) under the protection of a nurse plant commonly found in the natural habitat (*Bursera morelensis* and *Opuntia* sp.) established at the Botanical Garden. The experiment started in August 2001 and total-surviving seedlings were recorded every 15 days for 3 months. Transplanted seedlings were subjected to prevailing environmental conditions. For all treatments, log-linear models were fitted to survivorship data, considering time as a continuous variable. Two models were fitted to the data, one considering a constant mortality rate (d), $N_t = \exp(a - dt)$ where $a = \ln N_0$ (number of seedlings at the beginning of the experiment) and N_t the number of seedlings surviving at time t . This model describes a type II survivorship curve. The second model relaxed the assumption of constant mortality through time, $N_t = \exp(a - dt + ct^2)$ where $d =$ initial mortality rate, $a = \ln N_0$, $c =$ parameter that indicates the shape of the curve and N_t the number of seedlings surviving to time t . The parameter c was a measure of the intensity with which the mortality rates vary in time. If $c < 0$, the initial mortality tends to increase with time and the model describes a type I survivorship curve. If $c > 0$, the initial mortality tends to decrease with time and the model describes a type III curve. If c does not differ significantly from zero, then the mortality rate tends to be constant in time (Valiente-Banuet and Ezcurra 1991).

Experiment under field conditions

Previous experiments in natural conditions demonstrated no seedling survival under direct solar radiation, so we only used seedlings under nurse canopies in the field. Seedling survival was assessed in field conditions under the canopy of common nurse plants found in the natural habitat, *Cercidium praecox* and *Opuntia* sp. In order to determine survival functions, four replicates containing 20 seedlings each were transplanted under the canopy of these two species. The experiment was conducted in September 2002, and the number of surviving seedlings was recorded monthly for 8 months. Log-linear models were fitted to survivorship data in order to determine survival functions as explained above.

RESULTS

Seed germination

Seed germination for this species occurred during the first 7 days after the experiment started in seeds <1 year old and germination was consistently lower as seed age increased. The results of age treatments for *M. huitzilopochtli* showed that there were significant differences among treatments ($F_{3,8} = 130.6$, $P < 0.0001$). These

differences separated the data into three groups: (1) seeds < 1 year old, (2) 1 and 2 year old seeds, and (3) seeds > 3 years old. The maximum germination percentage was obtained using < 1 year old seeds ($\bar{x} = 90\%$, S.E. = 9.6%), followed by the 1 and 2 year old group ($\bar{x} = 55\%$, S.E. = 8.4% and 46%, S.E. = 2.2%). The lowest percentage was obtained for > 3 year old seeds ($\bar{x} = 9.7\%$, S.E. = 1.5%; Figure 1).

Seed dormancy attributes

The results of pregerminative treatments of *M. huitzilopochtli* showed that there were significant differences between each age ($F_{1,36} = 243.05$, $P < 0.0001$), but there were no differences between germination pretreatments ($F_{8,36} = 1.57$, $P = 0.167$) and the interaction between age and treatment ($F_{8,36} = 0.7984$, $P = 0.6078$). Mechanical scarification, the immersion in acid solution, and soaking in running water treatments did not increase germination in seeds of *M. huitzilopochtli* for all ages.

Establishment experiments

The establishment experiment showed differences in seedling survival between direct solar radiation (bare areas) treatments and under the canopy of shrubs established in the Botanical Garden of CIIDIR-IPN

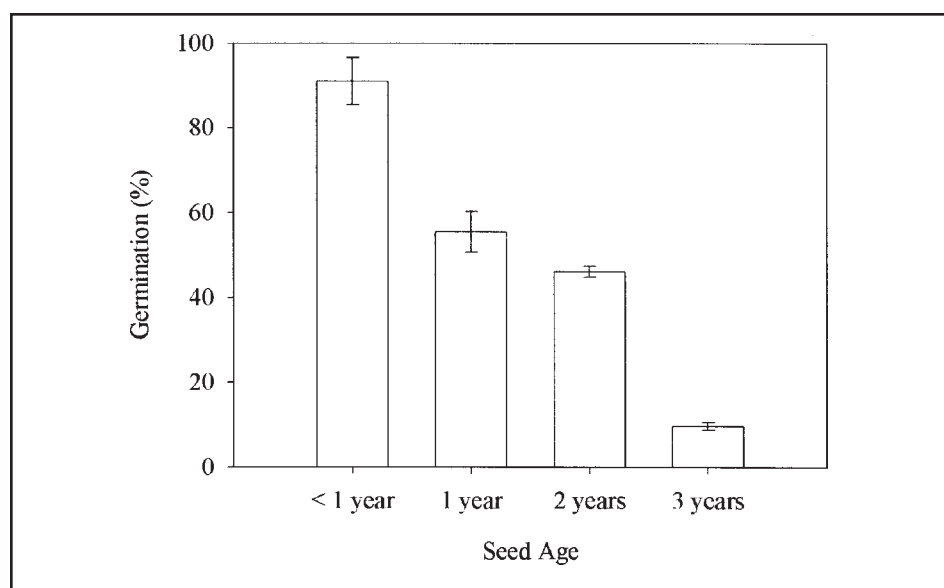


Figure 1. Mean \pm SE germination of seeds of *Mammillaria huitzilopochtli*. Seeds were 3 months old (<1 year), 15 and 27 months (pooled, 2 years) and 39 months old (3 years).

Oaxaca (nurse plant treatments). Only seedlings in the shaded treatments survived until the end of the experiment (after three months). Mean seedling mortality was 82% in direct solar radiation treatments after 15 days, 96% after 28 days, and all seedlings were dead after 45 days. The mean mortality of seedlings under the canopy of nurse plants was 5% after 15 days and 6% after 30 and 42 days. A strong storm in day 43 killed many seedlings; so, the mean mortality increased to 46% after 45 days, 56% after 60 days, 59% after 75 days, and 60% after 90 days (Figure 2A). When the survivorship functions of the shaded treatments were fitted ($a = 4.648$; $d = -0.102$; $c = 0.0000427$), the calculated N_0 was very similar to the real N_0 (20.88 vs. 20 seedlings). The quadratic coefficient was positive, indicating a type III survivorship curve in which the initial mortality is high and tended to decrease with time. When we adjusted means of the open space treatments ($a = 1.042$; $d = -0.027$; $c = 0.00085$), the calculated N_0 was very different from that observed N_0 (2.836 vs. 20 seedlings); however, a better fit was found when we adjusted a log normal curve with constant mortality (i.e., $a = 3.1$; $d = -0.119$; calculated N_0 was very similar to observed N_0 22.19 vs. 20 seedlings). Mean seedling survival under the canopy of nurse plants after eight months was 13.75% (Figure 2B). The results of the shaded treatments adjusted to a lognormal equation ($a = 1.9428$; $d = -0.2229$; $c = 0.0622$). The quadratic coefficient was positive which indicated a type III survivorship curve.

DISCUSSION

Seeds of *M. huitzilopochtli* are non-dormant according to Jurado and Flores (2005) who classified seeds as dormant when more than 80% of the viable fresh seeds do not germinate without a germinative pretreatment and to Baskin and Baskin (1998) who described a non-dormancy state when seeds are prevented from germination by external constraints, such as a lack of moisture or light requirements. Rojas-Aréchiga and Vázquez-Yanes (2000) reported two types of dormancy in cacti: innate and enforced. Following Harper (1959), the seeds of *M.*

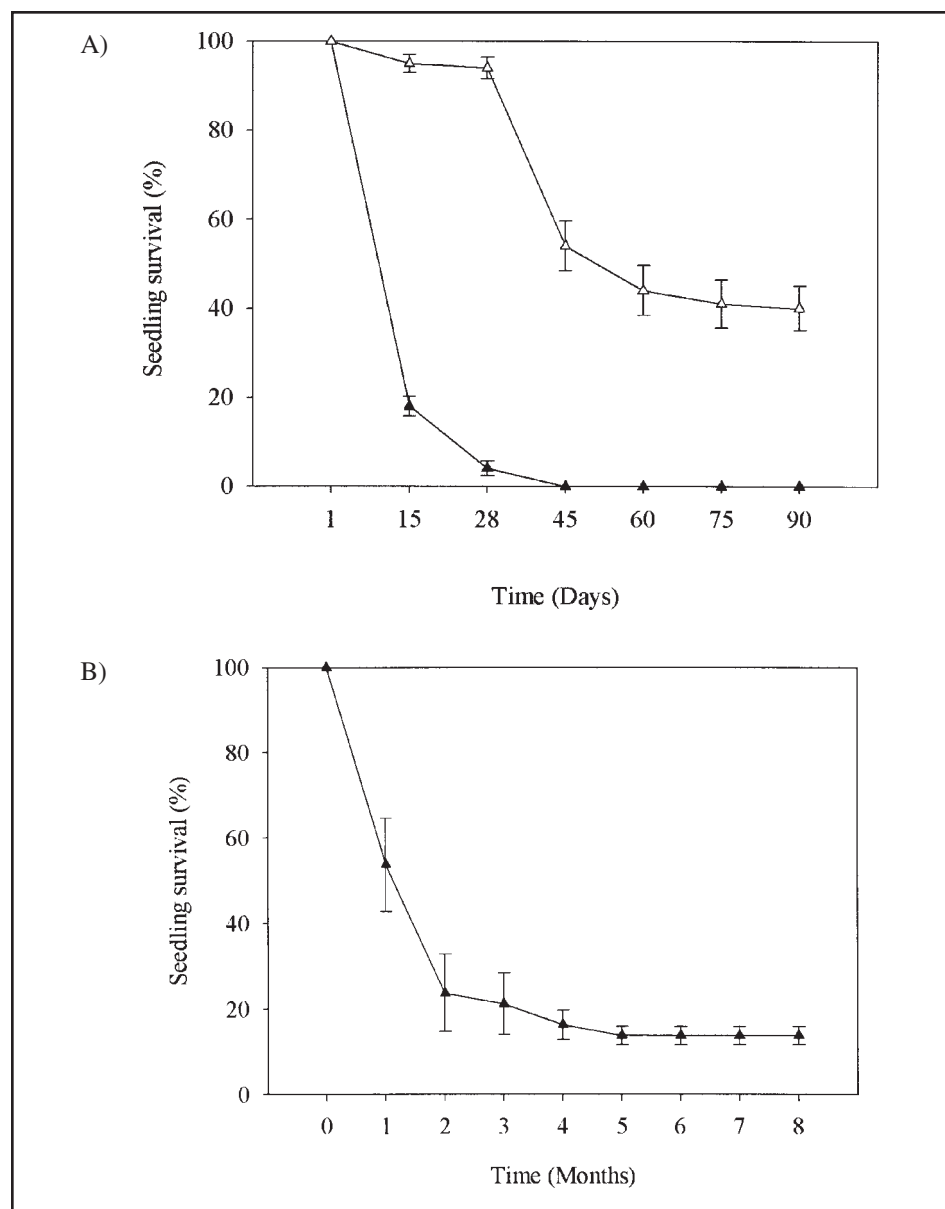


Figure 2. A) Survival curves of *Mammillaria huitzilopochtli* seedlings under controlled conditions at the Botanical Garden, Oaxaca, Mexico. Solid triangles = bare areas and open triangles = under nurse plants. B) Survival curve of seedlings in the field experiment under nurse plants in Cuicatlan, Oaxaca, Mexico.

huitzilopochtli show enforced dormancy (= quiescence; Vegis 1964). Seeds of this species germinated rapidly within the first week after sowing, only requiring contact with moist substrates. This response is similar to *Mammillaria haageana*, *M. carnea*, *M. mystax*, and *M. supertexta*, which do not present a physiological or morphological dormancy mechanism (Benítez-Rodríguez et al. 2004). *Mammillaria supertexta* is closely related to *M. huitzilopochtli*; they belong to the same taxonomic Series and both inhabit cliff

faces in the region. However, some species of *Mammillaria* do need a maturation period after shedding (afterripening), such as *M. zeilmanniana* that is within the Serie *Stylothelae* and inhabit more arid regions in the states of Guanajuato, San Luis Potosí, and Querétaro, Mexico (Anderson 2001; Rojas-Aréchiga and Batis 2001; Guzmán et al. 2003), which could indicate the presence of physiological dormancy, suggesting that dormancy is strongly influenced by environmental conditions. Unfortunately, these two factors have been ignored in

seed traits or germination studies within the cactus family. Additionally, we found that none of the germination pretreatments used had a positive effect on germination (independently of seed age). These results strongly contrast with other studies with *Mammillaria* species in which acid treatments increased germination percentages (*M. kraehenbuehlii*; Flores-Martínez et al. 2002 and *M. haageana*; Genis and Manzanero 2002), but are consistent with results found for other cacti (Nolasco et al. 1996; Mandujano et al. 1997, 2005; Godínez-Alvarez and Valiente-Banuet 1998; Ruedas et al. 2000). Acid treatments have been biologically related to dispersal mechanisms, whereby birds or mammals disperse the species that require germination pretreatments. For *M. huitzilopochtli*, dispersal is mainly by water runoff or being carried out by small lizards (A. Flores-Martínez, pers. observation).

Final germination percentages are consistently lower as seed age increases for the studied species. The decrease in germination with an increase in seed age has been reported for other Cactaceae: *Brasilicactus* spp., *Cephalocereus senilis*, *Cleistocactus strausii*, *Echinocereus reichenbachii*, *Echinopsis tegeleriana*, *Escobaria tuberculosa*, *Ferocactus acanthodes*, *Melocactus peruvianus*, *Notocactus scopa*, *Pseudobolivia kermesina*, and *Samaipaticereus corroanus* (Rojas-Aréchiga and Vázquez-Yanes 2000; Flores et al. 2005). In contrast, seed germination tended to increase with age in *Opuntia* spp. (Mandujano et al. 1997, 2005), *Ferocactus wislizenii* (Bowers 2000), *Notocactus submammulosus* (Shimomura et al. 2000), *Stenocereus stellatus* (Rojas-Aréchiga et al. 2001), *S. queretaroensis* (De la Barrera and Nobel 2003), *Turbinicarpus lophophoroides*, and *T. pseudopectinatus* (Flores et al. 2005). Interestingly, seed germination of one-year-old seeds does not differ from fresh seeds in *Mammillaria magnimamma* (Ruedas et al. 2000), *M. supertexta*, *M. mystax*, *M. carnea*, and *M. haageana* (Rojas-Aréchiga, unpubl. data), while seed germination of *M. heyderi*, a species from the arid Chihuahuan desert, increased with seed age (Trejo-Hernández and Garza-Castillo 1993). The contrasting evidence also supports the idea that dormancy in the Cactaceae may be more

associated to environmental heterogeneity than constrained by phylogeny (Jurado and Flores 2005).

Our results suggest that the seeds of *M. huitzilopochtli* could retain viability with germination percentages of nearly 50% for at least two years. This implies that most of the seeds of the species do not have induced dormancy (*sensu*, Harper 1959) or secondary dormancy (Crocker 1916); however, the species possess seeds that are able to form a short term persistent seed bank as defined by Thompson et al. (1997). Higher germination percentages in fresh seeds also suggest a mechanism that can overcome conditions imposed by the cliffs they inhabit, which are characterized by short and irregular periods of water in fissures. Most of *M. huitzilopochtli* plants were located in rock cracks in very steep slopes. Long-term seed survival after dispersion is unlikely because high water flow from steep slopes causes loss of seeds, seedlings, and even adult plants; therefore, seeds have a higher probability of being washed away from safe sites. The fast germination response to humid conditions is highly suggestive that this is the only environmental cue that triggers germination. In such conditions, seeds germinate as soon as they are dispersed during the first rainy seasons. Precipitation in the Tehuacan region is high in comparison to other semiarid regions (mean annual rainfall 553 mm) and occurs between May and October, with a low coefficient of variation among years (García 1981). This evidence suggests that the seeds of these species do not require surviving in the soil (or in the rock) for a period longer than a year, as precipitation is relatively predictable.

According to the seedling establishment results, shade is the necessary condition for the establishment of seedlings of *M. huitzilopochtli*, because it reduces daytime and summer high temperatures, lowering soil temperatures (Turner et al. 1966; Franco and Nobel 1989; Valiente-Banuet and Ezcurra 1991; Flores-Martínez et al. 1994; Mandujano et al. 2001). However, *M. huitzilopochtli* individuals can be found either without nurse shrub protection (bare areas) or with an association to other plant species. Martorell and Patiño (2006) have

also reported the absence of nurse plants in *M. crucigera*, a species also occurring in the same region. *Mammillaria crucigera*, as well as *M. huitzilopochtli*, is established on steep cliffs, and the shade provided by this particular topography provides adequate shade conditions for establishment (38.2 % reduction in solar radiation compared with flat surfaces).

CONCLUSIONS

In this study, we were able to assess that *M. huitzilopochtli* seeds can generate a transient seed bank, seeds do not require germination pretreatments, and seedling survival is associated with either nurse plants or conditions that decrease the severity of environmental conditions. An ongoing demographic study would help to understand the relevance of seed age and the role of short term seed banks in the life history of these threatened *Mammillaria*, which can add to the information needed to adequately manage these rare cacti.

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LITERATURE CITED

- Anderson, E.F. 2001. The Cactus Family. Timber Press, Portland, Ore.
- Arias, M.S. 2000. The Cactaceae in the valley of Tehuacán-Cuicatlán, México. *Cactus & Co.* 4:20-25.
- Arias, S., S. Gama, and U. Guzmán. 1997. Flora del Valle de Tehuacán-Cuicatlán. Fascículo 14. Cactaceae A.L. Juss. Instituto de Biología, Universidad Nacional Autónoma de México, México D.F.
- Baskin, C., and J.M. Baskin. 1998. Seeds: Ecology, Biogeography, and Evolution of Dormancy and Germination. Academic Press, San Diego, Calif.
- Benítez-Rodríguez, J.L., A. Orozco-Segovia, and M. Rojas-Aréchiga. 2004. Light effect on seed germination on four *Mammillaria* species from Tehuacán-Cuicatlán Valley, Central México. *The Southwestern Naturalist* 49:11-17.
- Bowers, J.E. 2000. Does *Ferocactus wislizenii* (Cactaceae) have a between-year seed bank? *Journal of Arid Environments* 45:197-205.
- Crocker, W. 1916. Mechanism of dormancy in seeds. *American Journal of Botany* 3:99-120.
- Csontos, P., and J. Tamás. 2003. Comparisons of soil seed bank classification systems. *Seed Science Research* 13:101-111.
- Dávila, A.P., J.L. Villaseñor, R. Medina, A. Ramírez, A. Salinas, K.J. Sánchez, and P. Tenorio. 1993. Listados florísticos de México X. Flora del Valle de Tehuacán-Cuicatlán. Instituto de Biología, Universidad Nacional Autónoma de México, México D.F.
- De la Barrera, E., and P.S. Nobel. 2003. Physiological ecology of seed germination of the columnar cactus *Stenocereus queretaroensis*. *Journal of Arid Environments* 53:297-306.
- Fenner, M. 1985. *Seed Ecology*. Chapman and Hall, London.
- Fenner, M., and K. Thompson. 2005. *The Ecology of Seeds*. Cambridge University Press, Cambridge, U.K.
- Flores, J.A., and E. Jurado. 2003. Are nurse-protégé interactions more common among plants from arid environments? *Journal of Vegetation Science* 14:911-916.
- Flores, J., A. Arredondo, and E. Jurado. 2005. Comparative seed germination in species of *Turbincarpus*: an endangered cacti genus. *Natural Areas Journal* 25:183-187.
- Flores-Martínez, A., E. Ezcurra, and S. Sánchez-Colón. 1994. Effect of *Neobuxbaumia tetetzo* on growth and fecundity of its nurse plant *Mimosa luisana*. *Journal of Ecology* 82:325-330.
- Flores-Martínez, A., and G.I. Manzanero. 2003. Germinación comparativa de especies del género *Mammillaria* endémicas de Oaxaca, México. *Cactáceas y Suculentas Mexicanas* 48:36-51.
- Flores-Martínez, A., and G.I. Manzanero. 2005. Método de evaluación de riesgo de extinción de *Mammillaria huitzilopochtli* D.R. Hunt. *Cactáceas y Suculentas Mexicanas* 50:15-26.
- Flores-Martínez, A., G.I. Manzanero, G.C. Martínez H., and G.S. Pacheco V. 2002. Aspectos sobre la ecología y reproducción de *Mammillaria kraehenbuehlii* (Kraenz) Krainz en la Mixteca de Oaxaca, México. *Cactáceas y Suculentas Mexicanas* 47:57-68.
- Franco, A.C., and P.S. Nobel. 1989. Effect of nurse plants on the microhabitat and growth of cacti. *Journal of Ecology* 77:870-886.
- García, E. 1981. Modificaciones al sistema de clasificación climática de Köppen (para adaptarlo a las condiciones de la República Mexicana). Universidad Nacional Autónoma de México, México D.F.
- Genis, V.M.F., and G.I. Manzanero. 2002. Estudio sobre germinación y crecimiento de plántulas en *Mammillaria haageana* y *Melocactus ruestii*. Bachelor thesis, Benemérita Universidad Autónoma de Puebla, Puebla, México.
- Godínez-Alvarez, H., and A. Valiente-Banuet. 1998. Germination and early seedling growth of Tehuacán Valley cacti species: the role of soils and seed ingestion by dispersers on seedling growth. *Journal of Arid Environments* 39:21-31.
- Grime, J.P. 1981. The role of seed dormancy in vegetation dynamics. *Annals of Applied Biology* 98:555-558.
- Guzmán, U., S. Arias, and P. Dávila. 2003. Catálogo de cactáceas mexicanas. CONABIO, UNAM, México.
- Harper, J.L. 1959. The ecological significance of dormancy and its importance in weed control. Pp. 415-420 in *Proceedings IVth International Congress of Crop Protection*, Hamburg, Germany.
- Hernández, H., and H. Godínez. 1994. Contribución al conocimiento de las cactáceas mexicanas amenazadas. *Acta Botánica Mexicana* 26:33-52.
- Jurado, E., O. Aguirre, J. Flores, J. Navar, H. Villalón, and D. Wester. 2000. Germination in tamaulipan thornscrub of north-eastern Mexico. *Journal of Arid Environments* 46:413-424.
- Jurado, E., and J. Flores. 2005. Is seed dormancy under environmental control or bound to plant traits? *Journal of Vegetation Science* 16:559-564.
- Mandujano, M.C., J. Golubov, and C. Montaña. 1997. Dormancy and endozoochorous dispersal of *Opuntia rastrera* seeds in the southern Chihuahuan Desert. *Journal of Arid Environments* 36:259-266.
- Mandujano, M.C., C. Montaña, M. Franco, J. Golubov, and A. Flores-Martínez. 2001. Integration of demographic annual variability in a clonal desert cactus. *Ecology* 82:344-359.
- Mandujano, M.C., C. Montaña, I. Méndez, and J. Golubov. 1998. The relative contributions of sexual reproduction and propagation in *Opuntia rastrera* from two habitats in the Chihuahuan Desert. *Journal of Ecology* 86:911-921.
- Mandujano, M.C., C. Montaña, and M. Rojas-Aréchiga. 2005. Breaking seed dormancy in *Opuntia rastrera* from the Chihuahuan desert. *Journal of Arid Environments* 62:15-21.
- Martorell, C., and P. Patiño. 2006. Globose cacti (*Mammillaria*) living on cliffs avoid high temperatures in a hot dryland of Southern Mexico. *Journal of Arid Environments* 67:541-552.
- McAuliffe, J.R. 1984. Sahuaro-nurse tree association in the Sonoran Desert: competitive effects of sahuaros. *Oecologia* 64:319-321.
- Montiel, S., and C. Montaña. 2003. Seed bank dynamics of the desert cactus *Opuntia ras-*

- trera* in two habitats from the Chihuahuan Desert. *Plant Ecology* 166:241-248.
- Nobel, P.S. 1984. Extreme temperatures and thermal tolerances for seedling of desert succulents. *Oecologia* 62:310-317.
- Nolasco, H., F. Vega-Villasante, and A. Diaz-Rondero. 1997. Seed germination of *Stenocereus thurberi* (Cactaceae) under different solar irradiation levels. *Journal of Arid Environments* 36:123-132.
- Nolasco, H., F. Vega-Villasante, H.L. Romero-Schmidt, and A. Diaz-Rondero. 1996. The effects of salinity, acidity, light and temperature on the germination of seed of cardón (*Pachycereus pringlei* (S. Wats.) Britton and Rose, Cactaceae). *Journal of Arid Environments* 33:87-94.
- Peters, E., and C. Martorell. 2000. Conocimiento y conservación de las mamilarias endémicas del Valle de Tehuacán-Cuicatlán. R166. CONABIO, Instituto de Ecología, UNAM, México.
- Ramírez-Padilla, C.A., and T. Valverde. 2005. Germination responses of three congeneric cactus species (*Neobuxbaumia*) with differing degrees of rarity. *Journal of Arid Environments* 61:333-343.
- Rodríguez-Ortega C.E., and E. Ezcurra. 2000. Distribución espacial en el hábitat de *Mammillaria pectinifera* y *M. carnea* en el Valle de Zapotitlán, Salinas, Puebla. *Cactáceas y Suculentas Mexicanas* 45:4-14.
- Rojas-Aréchiga, M., and A. Batis. 2001. Las semillas de cactáceas.... ¿forman bancos en el suelo? *Cactáceas y Suculentas Mexicanas* 46:76-82.
- Rojas-Aréchiga, M., A. Casas, and C. Vázquez-Yanes. 2001. Seed germination of wild and cultivated *Stenocereus stellatus* (Cactaceae) from the Tehuacán-Cuicatlán Valley, Central México. *Journal of Arid Environments* 49:279-287.
- Rojas-Aréchiga, M., and C. Vázquez-Yanes. 2000. Cactus seed germination: a review. *Journal of Arid Environments* 44:85-104.
- Ruedas, M., T. Valverde, and A.D. Castillo. 2000. Respuesta germinativa y crecimiento de plántulas de *Mammillaria magnimamma* (Cactaceae) bajo diferentes condiciones ambientales. *Boletín de la Sociedad Botánica de México* 66:22-35.
- SAS Institute. 1995. JMP Statistics and Graphics Guide. SAS Institute, Cary, N.C.
- SEMARNAT. 2002. Norma Oficial Mexicana NOM-059-ECOL-2001. Diario Oficial de la Federación. 2a. sección. 06 marzo 2002.
- Shimomura, T., T. Kondo, and S. Fukai. 2000. Breaking seed dormancy of *Notocactus submammulosus* var. *pampeanus* (Cactaceae) by Benzyl Adenine and Hydrogen Peroxide. *Japan Journal of Agricultural Education* 31:21-27.
- Shreve, F. 1951. Vegetation of the Sonoran Desert. Carnegie Institute of Washington Publication 591:1-192.
- Sokal, R.R., and J.H. Rohlf. 1981. *Biometry*, 2nd ed. W.H. Freeman, San Francisco, Calif.
- Steenbergh, W.F., and C.W. Lowe. 1969. Critical factors during the first years of life of the saguaro (*Cereus giganteus*) at Saguaro National Monument, Arizona. *Ecology* 50:825-834.
- Thompson, K., J.P. Bakker, and R.M. Bekker. 1997. *The Soil Seed Banks of North West Europe: Methodology, Density and Longevity*. Cambridge University Press, Cambridge, U.K.
- Thompson, K., and J.G. Grime. 1979. Seasonal variation in the seed banks of herbaceous species in ten contrasting habitats. *Journal of Ecology* 67:97-100.
- Trejo-Hernández, L., and M.R. Garza-Castillo. 1993. Efecto del tiempo de almacenamiento en la germinación de semillas de *Mammillaria heyderi* Muchl. en cuatro sustratos. *Biotam* 5:19-24.
- Turner, R.M., S.M. Alcorn, G. Olin, and J.O. Boutin. 1966. The influence of shade, soil and water on saguaro seedling establishment. *Botanical Gazette* 12:95-102.
- Valiente-Banuet, A., and E. Ezcurra. 1991. Shade as a cause of the association between the cactus *Neobuxbaumia tetetzo* and the nurse plant *Mimosa luisana* in the Tehuacan Valley, Mexico. *Journal of Ecology* 79:961-971.
- Vázquez-Yanes C., and A. Orozco-Segovia. 1993. Patterns of seed longevity and germination in the tropical rainforest. *Annual Review of Ecology and Systematics* 24:69-87.
- Vegis, A. 1964. Dormancy in higher plants. *Annual Review of Plant Physiology* 15:185-224.
- Villaseñor J.L., P. Dávila, and F. Chiang. 1990. Fitogeografía del Valle de Tehuacán-Cuicatlán. *Boletín de la Sociedad Botánica de México* 50:135-149.
- Vleeshouwers, L.M., H.J. Bouwmeester, and C.M. Karssen. 1995. Redefining seed dormancy: an attempt to integrate physiology and ecology. *Journal of Ecology* 83:1031-1037.