

Effect of light on germination of seeds of *Cactaceae* from the Chihuahuan Desert, Mexico

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Abstract

In the Chihuahuan Desert, there are many cacti species considered to be at risk due to illegal extraction, land-use change and overgrazing. To reduce their illegal extraction, *ex situ* plant propagation has been suggested. However, the literature regarding seed germination biology of these species is scarce. We investigated the effect of light on germination percentages and germination rate (t_{50}) in seeds of 28 cactus species from the Chihuahuan Desert. Seeds were incubated at a 14-h daily photoperiod (light) and in continuous darkness at 25°C for 30 d, after which seeds failing to germinate in darkness were transferred to light for 30 d. Only 11 of the species had non-dormant seeds, germinating $\geq 70\%$ in the light; thus an evaluation of the effect of light versus darkness on germination was confined to them. All species were positively photoblastic, and all of them had seeds weighing < 1 mg. Ten species did not germinate in darkness, and one species had only 7% germination. From these 11 species, 8 did not germinate to a significantly higher percentage when the same set of seeds was transferred from dark to light, suggesting that darkness had triggered secondary dormancy (skotodormancy). To our knowledge, these results are the first to show that darkness triggers secondary dormancy in cacti. Implications of having a light requirement for germination and having small seeds to accumulate a persistent soil seed bank are discussed. These results contribute to understanding the germination biology of cactus species at risk, and could enhance the propagation of large

numbers of cultivated individuals outside their habitats, promoting *ex situ* conservation.

Keywords: *Cactaceae*, photoblastic seeds, seed dormancy, skotodormancy

Introduction

Mexico is the country with the highest number of cactus species and endemic cactus species (Ortega-Baes and Godínez-Álvarez, 2006). Many of these species are classified as rare, vulnerable or endangered, due to illegal extraction, land-use change and overgrazing (Hernández and Godínez, 1994; Hernández and Bárcenas, 1995, 1996; Gómez-Hinostrosa and Hernández, 2000). *Ex situ* plant propagation has been suggested as a means to reduce illegal extraction of cacti (Hernández and Bárcenas, 1995; Rojas-Aréchiga and Vázquez-Yanes, 2000; Boyle and Anderson, 2002; Robbins, 2003). However, in spite of the importance of seed germination biology in the reproduction of cacti, pioneer studies on cactus seed germination did not start until the 1960s (Rojas-Aréchiga and Vázquez-Yanes, 2000; Godínez-Álvarez *et al.*, 2003).

Light is one of the most important environmental signals in response to which seed germination is regulated (Gutterman, 1993; Rojas-Aréchiga *et al.*, 1997; Rojas-Aréchiga and Vázquez-Yanes, 2000). In arid and semi-arid environments, sandy soils can modify the photon fluxes and light quality [red (R):far-red (FR)] underground, according to the colour and size of the sand grains and soil moisture (Tester and Morris, 1987; Gutterman, 1994); thus, light can be relevant for triggering germination of desert plant seeds. In American deserts, plants of the *Cactaceae* family are very common (Ortega-Baes and Godínez-Álvarez, 2006). The effect of light on the induction of seed germination has been studied for

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several cactus species. Exposure to light promotes germination of 57 cactus species and has no influence on 9 species. Seeds of many cacti cannot germinate in constant darkness, and it might be expected that seeds of such species would readily germinate if placed under adequate light conditions. However, Romero-Schmidt *et al.* (1992) found that seeds of *Ferocactus peninsulæ* showed higher germination in light than when their seeds were transferred from dark to light, although the authors did not explore whether the lower germination was due to damage to seeds, or if darkness induced seed dormancy. For 13 species in 9 plant families, a secondary type of dormancy, which prevents germination even after the presence of light, has been reported (Taylorson and Hendricks, 1973; Duke *et al.*, 1977, Georgiou and Thanos, 1983; Hsiao and Huang, 1988; Thanos and Georgiou, 1988; Small and Guttermann, 1992; Amritphale *et al.*, 1993; Steadman, 2004). This type of dormancy is known as skotodormancy and involves a reduction in light sensitivity for light-requiring seeds (Bewley and Black, 1994; Baskin and Baskin, 1998). In our study,

we determined the light requirements for seeds of 28 at-risk cacti (Table 1), with the aim to better understand their germination biology.

Materials and methods

Study site

This study was carried out at the San Luis Experimental Field Station of INIFAP in San Luis Potosí, S.L.P., Mexico. We collected seeds of at least 10 individuals from each species. All studied species were from the highly diverse Chihuahuan Desert (Hernández and Bárcenas, 1995; Hernández and Gómez-Hinostrosa, 2002). Seeds were collected from mature fruits when available during 2003 and stored in paper-bags at room temperature. For three species (*Mammillaria crinita*, *M. orcuttii* and *Ariocarpus fissuratus* subsp. *hintonii*), seeds from 2003 were not viable, so older seeds that we collected in 2002 were used. Thus, for the species studied, the time from seed

Table 1. Conservation status (based on the *Norma Oficial Mexicana NOM-059-ECOL-2001*; Semarnat, 2002), seed mass and germination rate (t_{50}) of 28 cactus species. Nomenclature follows that of Guzmán *et al.* (2003). E, endangered; T, threatened; U, under special protection

Species	Conservation status	Seed mass \pm SD (mg)	t_{50} (d)
<i>Ariocarpus fissuratus</i> subsp. <i>bravoanus</i> (H.M. Hern. & E.F. Anderson)	E	0.092 \pm 0.004	10.0
<i>Ariocarpus fissuratus</i> subsp. <i>hintonii</i> (Stuppy & N.P. Taylor)	E	0.091 \pm 0.007	11.4
<i>Ariocarpus kotschoubeyanus</i> (Lem.) K. Schum.	U	0.077 \pm 0.012	11.4
<i>Ariocarpus retusus</i> subsp. <i>retusus</i> (Scheidw.)	U	0.089 \pm 0.015	8.8
<i>Ariocarpus retusus</i> subsp. <i>trigonus</i> (F.A.C. Weber)	A	0.141 \pm 0.013	11.0
<i>Epithelantha micromeris</i> (Engelm.) F.A.C. Weber ex Britton & Rose	U	0.062 \pm 0.006	11.6
<i>Mammillaria aureilanata</i> Backeb.	U	0.110 \pm 0.009	12.0
<i>Mammillaria bocasana</i> Poselg.	U	0.016 \pm 0.005	12.0
<i>Mammillaria crinita</i> D.C.	U	0.023 \pm 0.005	12.0
<i>Mammillaria longimamma</i> D.C.	T	0.200 \pm 0.014	15.4
<i>Mammillaria orcuttii</i> Roed.	U	0.036 \pm 0.005	20.0
<i>Mammillaria plumosa</i> F.A.C. Weber	T	0.029 \pm 0.002	12.4
<i>Mammilloidya candida</i> (Scheidw.) Buxb.	T	0.059 \pm 0.007	7.4
<i>Obregonia denegrii</i> Fric.	T	0.057 \pm 0.008	10.0
<i>Pelecypora strobiliformis</i> (Werderm.)	T	0.038 \pm 0.009	7.4
<i>Thelocactus conothelos</i> subsp. <i>flavus</i> (Mosco & Zanovello)	U	0.250 \pm 0.046	9.4
<i>Turbincarpus alonsoi</i> Glass & S. Arias	**	0.027 \pm 0.004	8.0
<i>Turbincarpus gielsdorfianus</i> (Werderm.)	E	0.046 \pm 0.009	11.6
<i>Turbincarpus jauernigii</i> (Gerhart Frank)	E	0.052 \pm 0.014	10.6
<i>Turbincarpus laui</i> Glass & R.A. Foster	U	0.080 \pm 0.009	12.2
<i>Turbincarpus lophophoroides</i> (Werderm.)	U	0.090 \pm 0.016	9.5
<i>Turbincarpus pseudopectinatus</i> Backeb.	U	0.074 \pm 0.011	8.0
<i>Turbincarpus schmidickeanus</i> subsp. <i>flaviflorus</i> (Gerhart Frank & A.B. Lau)	T	0.035 \pm 0.006	7.8
<i>Turbincarpus schmidickeanus</i> subsp. <i>frailensis</i>	**	0.028 \pm 0.005	6.4
<i>Turbincarpus schmidickeanus</i> subsp. <i>klinkerianus</i> Backeb. & H. Jacobsen	U	0.071 \pm 0.004	5.0
<i>Turbincarpus schmidickeanus</i> subsp. <i>macrochele</i> (Werderm.)	T	0.062 \pm 0.008	5.0
<i>Turbincarpus schmidickeanus</i> subsp. <i>rubriflorus</i> (Gerhart Frank)	**	0.051 \pm 0.008	7.6
<i>Turbincarpus schmidickeanus</i> subsp. <i>schwarzii</i> (Shurly)	T	0.055 \pm 0.006	6.4

** These species are not listed in the *Norma Oficial Mexicana NOM-059-ECOL-2001*, since there have been no studies of their populations.

collection until commencement of germination trials varied from 1 to 21 months (see Table 2).

We determined germination percentages and rates under two conditions: a 14-h daily photoperiod (hereafter 'light') and continuous darkness at 25°C. This temperature was used following Nobel (1988). Seeds were placed in Petri dishes containing sterilized sand for 30 d. Sand was chosen as a substrate, since preliminary tests showed that sand retained moisture longer than filter paper. There were five replicates per treatment, with 20 seeds in each. For incubation in darkness, Petri dishes were wrapped in aluminium foil (Baskin and Baskin, 1998). All dishes were placed in a germination chamber (Seedburo Equipment Company, Chicago, Illinois, USA). To reduce temperature fluctuations, fluorescent lamps and air ventilation were used. A green safe light (Baskin and Baskin, 1998) was used to examine the dark-incubated seeds. At the end of the 30-d incubation period, seeds that did not germinate in darkness were transferred to light for 30 d. The light and dark treatments simulate seeds on the soil surface and buried in the soil, respectively, and moving seeds from dark to light

simulates seeds that are brought to the surface by soil-disturbing agents, such as rodents.

Seeds were watered daily with distilled water, and germination (radicle protrusion) was checked daily. From these observations we determined final germination percentages (Jurado and Westoby, 1992; Flores and Briones, 2001) and rates of germination, as time (d) required for half of the seed sample to germinate (t_{50}) (Grime *et al.*, 1981; Jurado and Westoby, 1992; Flores and Briones, 2001). At the end of the incubation periods, viability of ungerminated seeds was checked by cutting open each seed, to see if an embryo was present and looked healthy.

Statistical analysis

To explore potential differences in germinability among treatments, a two-way ANOVA was used, with taxa and light as main factors. All data were arc-sine transformed prior to analysis of variance (Sokal and Rohlf, 1994). For all species, differences among treatments were explored through orthogonal

Table 2. Seed germination of cacti at 25°C after an initial light treatment (30 d), darkness (30 d) or after an initial 30 d dark incubation followed by transfer to the light (30 d), and time from seed harvest. For each species, significant differences ($P < 0.0001$) between treatments are indicated by different lower-case letters. Species with an asterisk are skotodormant

Species	Light	Dark	Light after dark	Time from seed harvest (months)
<i>Turbincarpus schmiedickeanus</i> subsp. <i>macrochele</i> *	98.00 a	7.00 b	11.80 b	6
<i>Mammillaria crinita</i>	97.00 a	0.00 b	94.00 a	14
<i>Ariocarpus retusus</i> subsp. <i>trigonus</i> *	94.00 a	0.00 b	57.00 c	8
<i>Turbincarpus schmiedickeanus</i> subsp. <i>flaviflorus</i> *	86.00 a	0.00 b	6.00 b	9
<i>Turbincarpus schmiedickeanus</i> subsp. <i>schwarzii</i> *	84.00 a	0.00 b	38.00 c	5
<i>Mammillaria bocasana</i> *	83.00 a	0.00 b	41.00 c	3
<i>Turbincarpus schmiedickeanus</i> subsp. <i>klinkerianus</i> *	80.00 a	0.00 b	8.00 b	3
<i>Mammillaria longinamma</i> *	75.00 a	0.00 b	35.00 c	1
<i>Pelecypora strobiliformis</i>	74.00 a	0.00 b	84.00 a	1
<i>Thelocactus conothelos</i> subsp. <i>flavus</i>	74.00 a	0.00 b	78.00 a	4
<i>Turbincarpus schmiedickeanus</i> subsp. <i>frailensis</i> *	74.00 a	0.00 b	1.00 b	7
<i>Turbincarpus schmiedickeanus</i> subsp. <i>rubriflorus</i>	69.00	0.00	0.00	9
<i>Mammillaria orcuttii</i>	68.00	0.00	34.00	18
<i>Turbincarpus gielsdorfianus</i>	68.00	0.00	2.00	3
<i>Ariocarpus fissuratus</i> subsp. <i>bravoanus</i>	66.00	0.00	45.00	7
<i>Ariocarpus kotschoubeyanus</i>	56.00	1.00	1.00	9
<i>Ariocarpus retusus</i> subsp. <i>retusus</i>	53.00	0.00	10.00	10
<i>Mammillaria plumosa</i>	51.00	0.00	1.00	7
<i>Turbincarpus laui</i>	48.00	0.00	3.00	8
<i>Mammilloidya candida</i>	46.00	0.00	21.00	5
<i>Mammillaria aureilanata</i>	42.00	0.00	6.00	3
<i>Obregonia denegrii</i>	41.00	0.00	4.00	5
<i>Turbincarpus alonsoi</i>	41.00	0.00	25.00	6
<i>Turbincarpus jauernigii</i>	37.00	0.00	0.00	10
<i>Ariocarpus fissuratus</i> subsp. <i>hintonii</i>	36.00	5.00	31.00	21
<i>Epithelantha micromeris</i>	33.00	0.00	4.00	4
<i>Turbincarpus lophophoroides</i>	8.00	0.00	1.00	1
<i>Turbincarpus pseudopectinatus</i>	5.00	5.00	5.40	8

contrasts. In addition, germination rate (t_{50}) was analysed for treatments exhibiting seed germination, and correlation analysis was performed to test for an association between time since collection and germination percentages.

Results

We tested viability by dissection and found that ungerminated seeds were viable. Thus, although all species had at least a small percentage of ungerminated (and therefore presumably dormant) seeds, we adopted $\geq 70\%$ germination after initial light exposure as a criterion for lack of dormancy. We confined our formal analysis of the effect of light on germination to the 11 species that (according to this criterion) lacked dormancy, although our results suggested that germination seemed to require light in almost all species. Data from all 28 species are presented in the tables.

A small set of seeds from species that failed to germinate in the light after dark treatment were cut open to determine the presence of healthy embryos, and all were considered viable. Time since seed collection and germination percentages were not correlated ($R^2 = -0.0018$, $P = 0.99$).

Seed germination was significantly affected by light ($F = 170.99$; $P < 0.0001$), species ($F = 104.17$; $P < 0.0001$), and by the light \times species interaction ($F = 16.23$; $P < 0.0001$). All species were positively photoblastic, and all of them had seed weights < 1 mg. Ten non-dormant species (i.e. those germinating $> 70\%$ after an initial light treatment) did not germinate at all in darkness, while one species germinated only to 7% (Table 2). Eight of these non-dormant species showed higher germination in light than when their seeds were transferred from dark to light, and three species had similar germination in both treatments (Table 2).

Since there was little or no germination for the dark treatment, t_{50} was estimated only for seeds exposed to light. We found significant differences among all 28 species (Table 1; $F = 25.2874$; $P < 0.0001$). *Turbiniarpus schmiedickeanus* subsp. *macrochele* and *T. schmiedickeanus* subsp. *klinkerianus* had the fastest t_{50} (5 d) and *Mammillaria orcuttii* had the slowest (20.0 d).

Discussion

From the 28 species studied, 11 had non-dormant ($> 70\%$ germination in the light) seeds. These 11 species were positively photoblastic, and all of them had small seeds (< 1 mg). These results support the suggestion that cacti that need light as a trigger for germination have small seeds (Maiti *et al.*, 2003). A light requirement for germination is important, because positive photoblastism is one of the

morphological and physiological characteristics that could favour formation of a soil seed bank (Bowers, 2000; Rojas-Aréchiga and Batis, 2001). In addition, small seed size has been associated with a light requirement for germination (Grime *et al.*, 1981; Pons, 1991a, 2000; Milberg *et al.*, 2000; Maiti *et al.*, 2003), as well as with persistent seed banks (Thompson *et al.*, 1993, 2001; Hodkinson *et al.*, 1998). Thus, it is possible that species of the *Cactaceae* having a light requirement for germination, and having small seeds, also have the ability to accumulate a persistent soil seed bank, as suggested by Rojas-Aréchiga and Batis (2001), and reported for species of other families by Baskin and Baskin (1989) and Pons (1991b). However, there are few studies investigating the existence of soil seed banks in cacti (but see De Viana, 1999; Bowers, 2000; Montiel and Montaña, 2003).

Some of our 11 species with non-dormant seeds were also found to be non-dormant in other studies, e.g. *M. longimamma* (Zimmer, 1998) and *Turbiniarpus* spp. (Flores *et al.*, 2005). Results for dormant seeds, found here, were also similar to those for other studies, e.g. Haslinger (1999) for *T. lophophoroides*, Reyes-Santiago *et al.* (2000) for *Mammilloidya candida*, and Flores *et al.* (2005) for *T. jauernigii*, *T. lophophoroides* and *T. pseudopectinatus*.

In arid and semiarid environments, Gutterman (1993, 1994) suggested that there are fast-germinating seeds that germinate during the first rain event, and slow-germinating seeds that need a long period of wetting and light before they can germinate. We found differences in germination rate (t_{50}) among species; the subspecies of *Turbiniarpus schmiedickeanus* had the fastest germination rate and *M. orcuttii* had the slowest one. It is probable that species with the slowest seed germination have hard and thick testas, as well as low numbers of starch grains, as suggested by Maiti *et al.* (1994, 2003). Gutterman (1994) suggested that, as it is very rare for the soil surface to remain wet for long in desert areas, massive germination of the slowest species takes place only once in several years.

Seventeen species had germination lower than 70% in the light. These species had some form of dormancy, since their seeds were viable at the end of the experiments. Dormancy in cacti can be broken by acid treatments (Potter *et al.*, 1984; Romero-Schmidt *et al.*, 1992; De la Rosa-Ibarra and García, 1994; Nolasco *et al.*, 1996; Dehgan and Pérez, 2005), by the passage of seeds through digestive systems of vertebrates (Cortés-Figueira *et al.*, 1994; Pedroni and Sánchez, 1997), by washing or imbibing the seeds for certain periods of time before sowing (Pilcher, 1970; Potter *et al.*, 1984; Sánchez-Venegas, 1997), by mechanical scarification that simulates the natural abrasion of the soil when the seeds are transported by water runoff (Moreno *et al.*, 1992; Sánchez-Venegas, 1997), by stratification periods (Baskin and Baskin, 1989), by cold temperatures

(Zimmer, 1972) or by after-ripening (Zimmer, 1967, 1980; Mandujano *et al.*, 1997, 2005; Rojas-Aréchiga *et al.*, 2001; De la Barrera and Nobel, 2003; Flores *et al.*, 2005). All these treatments are consistent with physiological dormancy, which is listed by Baskin and Baskin (1998) as the main type of dormancy in the *Cactaceae*.

From the 11 species with 70% germination or higher in the light, only three species showed higher germination in light after an initial dark incubation than in darkness, consistent with results for several cacti from Romero-Schmidt *et al.* (1992) and Maiti *et al.* (1994). However, the other eight species showed higher germination in an initial light treatment than when their seeds were transferred from dark to light. Baskin and Baskin (1998) suggested that light-requiring seeds of some species may enter dormancy during imbibition in darkness for extended periods of time (skotodormancy). Thus, it is possible that the dark treatment triggered loss of photosensitivity (secondary dormancy) in seeds of these cacti. This is the first report of skotodormancy in cacti.

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