

Effect of light on seed germination and seedling shape of succulent species from Mexico

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Abstract

Aims

Light requirements for cactus seed germination have been considered to be associated with their adult plant height and seed mass, but this has not been thoroughly studied for other succulent species. In order to understand seed photosensitivity from desert species belonging to Asparagaceae (subfamily Agavoideae) and Cactaceae, we performed a germination experiment with and without light for 12 species and 2 varieties from 1 species from the Southern Chihuahuan Desert. We also determined if adult growth is totally determined by seedling 'growth form' in cacti.

Methods

We performed a germination experiment using light and darkness for 13 species from Southern Chihuahuan Desert: 10 rosette species (Asparagaceae), as well as 1 globose, 1 columnar and 2 varieties from 1 depressed-globose species (Cactaceae). The response variables were seed germination percentage and relative light germination (RLG). In addition, in order to determine if adult-globose cacti could have cylindrical seedlings, we calculated the shape index (height/width ratio) for *Coryphanta clavata* and *Mammillaria compressa*.

Important Findings

All species were considered neutral photoblastic. Eleven species had similar seed germination in both light and dark

conditions, and three taxa (*M. compressa* and the two varieties of *Ferocactus latispinus*) showed higher germination with light than without it. *Agave salmiana*, *M. compressa* and the two varieties of *F. latispinus* had higher RLG than the other species. Seed mass was an important factor because with higher seed mass there was lower dependence to light. These findings support the hypothesis that small seed mass and light requirements have coevolved as an adaptation to ensure germination. One adult-globose cactus species, *M. compressa*, and one adult-columnar species, *C. clavata*, had small seeds and neutral fotoblasticism. Seedlings from these two species exposed to light were cylindrical and those under darkness conditions were columnar. Perhaps seeds from this species are able to germinate in the dark because they produce columnar seedlings with the ability to emerge from greater soil depths where sunlight cannot penetrate.

Keywords: Asparagaceae, Cactaceae, Chihuahuan Desert, photoblasticism, seed germination, succulent plants

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INTRODUCTION

Plants can be classified in terms of their responses to light for germination as follows: (i) those that require light to germinate, (ii) those that require darkness to germinate and (iii) those that have a large percentage of seeds neutral to light. These groups have been named positive photoblastic, negative photoblastic and neutral photoblastic by Baskin and

Baskin (2014). Although understanding specific light requirements for germination of many species can be more complex, with species responding to small variations in the light spectra, associated with season or shaded habitat triggering or inhibiting germination (Fenner and Thompson 2005), the three groups presented by Baskin and Baskin (2014) are an important first approach. The knowledge of light effects on germination is relevant in propagation of wild species for

restoration purposes (Khurana and Singh 2001) but also to better understand germination ecology (Baskin and Baskin 2014). Small seeded plants that form soil seed banks for instance, are expected to germinate only in the presence of light, as a mechanism to avoid germinating too deep in the soil where they would deplete seed nutrients before reaching light for photosynthesis (Pons 2000). Although the penetration of light through soil is greatly affected by factors such as soil moisture content and particle size and colour, it generally appears that physiologically and ecologically significant amounts of light rarely penetrate >4–5 mm through the soil (Tester and Morris 1987).

Germination responses of light are likely to vary between habitats, for instance in shaded environments such as forests, the presence of strong light can be associated with a canopy gap that increases probabilities of establishing seedlings (Khurana and Singh 2001), whereas in arid lands with little plant overlap, light may not be relevant for germination. Jurado and Westoby (1992) for instance, found high germination percentage for 105 Australian Desert plants without providing light. In environments where seeds are likely to burry in the soil or to grow better under the shade of other plants (nurse–protégé interactions, Flores and Jurado 2003), light can be an important key to determine safer conditions for germination. The influence of light on germination has also been associated with plant growth form (seeds from columnar cacti being neutral photoblastic, and the barrel-shaped and globose being positive photoblastic; Rojas-Aréchiga et al. 1997); perennality (light promotes the germination of annual species; de Villiers et al. 2002); plant size (seeds from shorter plants have a stronger light requirement for germination than those from taller plants; Flores et al. 2011); and seed size (seeds requiring light are small; Flores et al. 2006, 2011). Positive photoblastism is also considered to be associated with phylogeny (Fenner and Thompson 2005; Flores et al. 2011) and with temperature

variation during seed development (Rojas-Aréchiga et al. 1997).

In North American deserts, Asparagaceae and Cactaceae are two very common plant families (Nobel 2010). Several authors have suggested that cacti that require light for germination have small seeds (Flores et al. 2006, 2011). This light requirement is probably a physiological trait that could induce the formation of a seed bank in the soil (Bowers 2000; Thompson et al. 2001). In contrast, cactus seeds that do not require light to germinate tend to be large (Flores et al. 2011). Thus, it is possible that seedlings from the tallest species have the ability to emerge from greater soil depths (in the dark) since their seeds have more resources.

Cacti growth form as adults does not always match the shape of seedlings. For instance, some species that have globose seedlings are columnar at the adult stage (Sosa-Pivatto et al. 2014). Perhaps columnar seedlings would be better competitors for light, but globose seedlings would be more resistant to temperature variations due to their lower surface/volume ratio.

Light requirements for seed germination of Asparagaceae species have been poorly studied. *Agave* and *Yucca* are the main rosette genera of the Asparagaceae in North American Deserts (Irish and Irish 2000). Seven *Agave* spp. and three *Yucca* spp. are neutral photoblastic (Jiménez-Aguilar and Flores 2010, and references therein), but *A. americana* is positive photoblastic (Pritchard and Miller 1995). In order to understand seed photosensitivity from desert species belonging to Asparagaceae and Cactaceae, we performed a germination experiment with and without light for 12 species and 2 varieties from 1 species from the Southern Chihuahuan Desert (Tables 1 and 2).

MATERIALS AND METHODS

Study site and species

The study was carried out at the Ecology Lab of IPICYT in San Luis Potosí, S.L.P., México. We collected seeds from at least

Table 1: list of species, their family, growth form and seed mass ($n = 40$)

Species	Family	Growth form	Seed mass (mg)
<i>Agave americana</i> L.	Asparagaceae	Rosette	11.54±0.25
<i>Agave angustifolia</i> Haw.	Asparagaceae	Rosette	9.81±0.55
<i>Agave asperrima</i> Jacobi	Asparagaceae	Rosette	5.68±0.24
<i>Agave gentryi</i> Ullrich	Asparagaceae	Rosette	7.31±0.23
<i>Agave lechuguilla</i> Torr.	Asparagaceae	Rosette	8.10±1.03
<i>Agave salmiana</i> Otto ex Salm	Asparagaceae	Rosette	6.01±0.14
<i>Yucca carnerosana</i> (Trel.) McKelvey	Asparagaceae	Rosette	77.08±2.23
<i>Yucca filifera</i> Chab.	Asparagaceae	Rosette	69.75±2.33
<i>Yucca potosina</i> Rzed.	Asparagaceae	Rosette	103.89±2.25
<i>Yucca queretaroensis</i> Piña	Asparagaceae	Rosette	140.52±4.29
<i>Coryphanta clavata</i> (Scheidw.) Backeb.	Cactaceae	Columnar	1.51±1.01
<i>Ferocactus latispinus</i> (Haw.) (yellow spines)	Cactaceae	Depressed globose	1.59±0.14
<i>Ferocactus latispinus</i> (Haw.) (red spines)	Cactaceae	Depressed globose	0.39±0.01
<i>Mammillaria compressa</i> DC.	Cactaceae	Globose	0.39±0.01

Table 2: date and locality of collection of the studied species

Species	Date of collection	Locality of collection
<i>Agave americana</i>	December, 2012	San Luis Potosí
<i>Agave angustifolia</i>	July, 2012	San Luis Potosí
<i>Agave asperrima</i>	December, 2010	Tamaulipas
<i>Agave gentryi</i>	November, 2012	Tamaulipas
<i>Agave lechuquilla</i>	December, 2011	San Luis Potosí
<i>Agave salmiana</i>	August, 2011	San Luis Potosí
<i>Yucca carnerosana</i>	September, 2013	San Luis Potosí
<i>Yucca filifera</i>	December, 2012	San Luis Potosí
<i>Yucca potosina</i>	August, 2013	San Luis Potosí
<i>Yucca queretaroensis</i>	August, 2013	Querétaro
<i>Coryphanta clavata</i>	July, 2013	San Luis Potosí
<i>Ferocactus latispinus</i> (yellow)	July, 2013	San Luis Potosí
<i>Ferocactus latispinus</i> (red)	July, 2013	San Luis Potosí
<i>Mammillaria compressa</i>	July, 2013	San Luis Potosí

10 individuals for each species. Seeds were collected from mature fruits and stored in paper-bags for ca. 8 months at room temperature before the germination experiment. Seeds from *Yucca queretaroensis* were obtained from 'Jardín Botánico Cadereyta' in Cadereyta, Qro, México. Most of the studied species (Table 1) are from the highly diverse Chihuahuan Desert (Hernández and Gómez-Hinostrosa 2002) and one species (*Y. queretaroensis*) is from the Queretano-Hidalguense Desert (Magallán-Hernández *et al.* 2014), the southern portion of the Chihuahuan Desert (Hernández and Godínez 1994). This species is specially protected in the framework of the environmental laws and regulations of México (Semarnat 2010).

Germination experiment

We evaluated seed germination under two conditions: a 12-h daily photoperiod (hereafter 'light') and one in continuous darkness (hereafter 'dark') in a germination chamber for 30 days. The chamber was set at 25°C following Nobel (1988) as the most suitable temperature for agaves and cacti. To reduce temperature fluctuations, fluorescent lamps and air ventilation were used. Seeds were placed in Petri dishes containing agar. There were five replicate dishes per treatment, with 20 seeds in each replicate. For incubation in dark conditions, Petri dishes were wrapped in double aluminium foil, as suggested by Baskin and Baskin (2014). Germination (radicle protrusion) was monitored daily for 'light' seeds and at the end of the 30-day incubation period for seeds in the dark. At the end of the incubation period, viability of un-germinated seeds was checked by cutting open each seed, to see if an embryo was present and looked healthy.

From the observed number of germinated seeds we evaluated final germination percentage (Flores and Briones 2001; Flores *et al.* 2005), and relative light germination (RLG) (Milberg *et al.* 2000) according to the formula $RLG = Gl/(Gd + Gl)$; where Gl = the germination percentage in light, and

Gd = the germination percentage in darkness. RLG represents a range of values varying from 0 (germination only in the dark) to 1 (germination only with light), and it is relatively unaffected by dormancy (Milberg *et al.* 2000). This is important as many desert species have dormant seeds (Jurado and Flores 2005; Flores *et al.* 2008, 2011; Delgado-Sánchez *et al.* 2013).

At the end of the experiment, un-germinated seeds were found viable under dissection. Thus, although all species had at least a small percentage of un-germinated (and therefore presumably dormant) seeds, we adopted 70% germination after initial light exposure as a criterion for lack of dormancy, following Flores *et al.* (2006).

Shape index

In order to determine if adult-globose cacti could have cylindrical seedlings, or *vice versa*, we measured seedling height and width from *Coryphanta clavata* and *Mammillaria compressa*, with a digital caliper. With these data we calculated a shape index (height/width ratio), with a value of 1 indicating spherical seedlings—typical of globose cactus—and values higher than 1 indicating cylindrical seedlings, typical of columnar cacti (Sosa-Pivatto *et al.* 2014). We evaluated 44 individuals for *C. clavata* and 18 for *M. compressa* in both light and dark treatments.

Statistical analyses

A two-way ANOVA was conducted on the germination percentage using light (2 levels) and species (14 levels) as factors. Before the analysis was done, the percentage data were normalized using a square root arc-sine transformation (Sokal and Rohlf 1994). For each species, differences among treatments were explored using Tukey multiple comparison tests. We performed one-way ANOVA for RLG, with species as the main factor. Differences among species were explored using Tukey multiple comparison tests. Correlation analysis was performed to test for an association between log seed mass and RLG. In addition, *t*-tests were performed to evaluate the shape index of *C. clavata* and *M. compressa*.

RESULTS

Seed germination (%)

There was a significant effect of species ($F = 161.92$; $P < 0.0001$) and light ($F = 39.63$; $P < 0.0001$) treatments, and the interaction of both factors was significant ($F = 7.771$; $P < 0.0001$). Seven species had at least 71% germination in light conditions, so they were not considered dormant; five species and the two varieties of *Ferocactus latispinus* were considered dormant (Table 3).

All species were considered neutral photoblastic. For these, we found two response patterns: (i) 11 species having similar seed germination in both light and dark conditions and (ii) two species (*M. compressa* and the two varieties of *F. latispinus*) showing higher germination in light than in dark conditions.

Table 3: seed germination of 13 species from the Chihuahuan Desert at 25°C under light and darkness treatments

Species	Light	Darkness
	Seed germination (%)	
<i>Agave americana</i>	82 ± 2.5 ^a	73 ± 3.4 ^a
<i>Agave angustifolia</i>	29 ± 5.8 ^a	19 ± 4.8 ^a
<i>Agave asperima</i>	9 ± 1 ^a	6 ± 1.2 ^a
<i>Agave gentryi</i>	93 ± 2.5 ^a	82 ± 1.2 ^a
<i>Agave lechuguilla</i>	99 ± 1 ^a	98 ± 1.2 ^a
<i>Agave salmiana</i>	25 ± 4.2 ^a	8 ± 2 ^a
<i>Yucca carnerosana</i>	91 ± 1.9 ^a	94 ± 2.9 ^a
<i>Yucca filifera</i>	95 ± 3.2 ^a	99 ± 1 ^a
<i>Yucca potosina</i>	71 ± 8.1 ^a	80 ± 4.5 ^a
<i>Yucca queretaroensis</i>	37 ± 2 ^a	42 ± 3 ^a
<i>Coryphanta clavata</i>	100 ± 0 ^a	100 ± 0 ^a
<i>Ferocactus latispinus</i> (yellow)	36 ± 5.8 ^a	14 ± 6 ^b
<i>Ferocactus latispinus</i> (red)	64 ± 9.1 ^a	21 ± 2.9 ^b
<i>Mammillaria compressa</i>	51 ± 2.9 ^a	19 ± 1.8 ^b

Average final germination percentages (based on five replicates) for each species are shown. For each species, significant differences ($P < 0.001$) between treatments are indicated by different lowercase letters. All species had seeds germinating in both light and dark conditions and are therefore considered neutral photoblastic.

Relative light germination

Species differed in terms of RLG ($F = 6.74$; $P < 0.0001$; Table 4). *Agave salmiana*, *M. compressa* and the two varieties of *F. latispinus* had higher RLG than the other species. Four species showed intermediate RLG (RLG 0.53 – 0.63), and six species had low RLG (around 0.5). Log seed mass and RLG were negatively correlated ($R = -0.80$, $P < 0.05$; Fig. 1).

Shape index

Coryphanta clavata seedlings exposed to light had a lower shape index (1.97 ± 0.08) than those grown in darkness (6.04 ± 0.30 ; $P < 0.0001$). Similarly, *M. compressa* seedlings exposed to light had a lower shape index (1.47 ± 0.07) than those grown in darkness (3.78 ± 0.48 ; $P < 0.0001$).

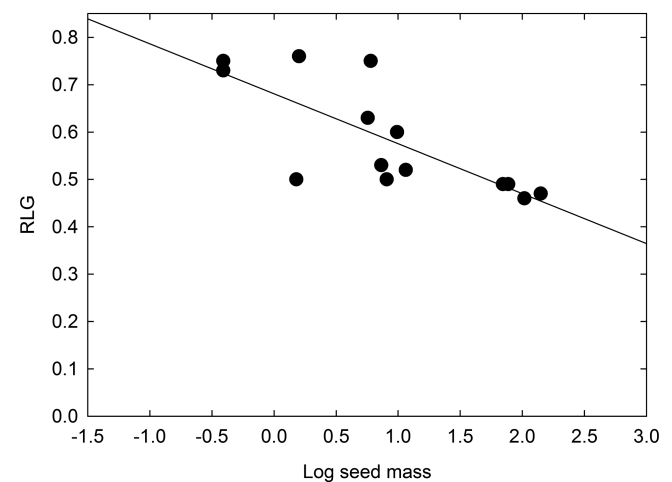
DISCUSSION

Five species (*Agave angustifolia*, *Agave asperima*, *A. salmiana*, *Y. queretaroensis* and *M. compressa*) and the two varieties of *F. latispinus* had germination <70% in light conditions. These species had some form of dormancy, since their ungerminated seeds were viable at the end of the experiments. Physiological dormancy is listed by Baskin and Baskin (2014) as the main type of dormancy in the Asparagaceae and the Cactaceae families. This is the first germination study for the specially protected *Y. queretaroensis*, these results may help propagation of large numbers of cultivated individuals outside their habitats, promoting *ex situ* conservation.

Table 4: RLG of 13 species from the Chihuahuan Desert at 25°C after light and darkness treatments

Species	RLG
<i>Agave americana</i>	0.52 ± 0.01 ^{a,b}
<i>Agave angustifolia</i>	0.60 ± 0.07 ^{a,b}
<i>Agave asperima</i>	0.63 ± 0.11 ^{a,b}
<i>Agave gentryi</i>	0.53 ± 0.01 ^{a,b}
<i>Agave lechuguilla</i>	0.50 ± 0 ^{b,c}
<i>Agave salmiana</i>	0.75 ± 0.05 ^a
<i>Yucca carnerosana</i>	0.49 ± 0.01 ^{b,c}
<i>Yucca filifera</i>	0.49 ± 0.01 ^{b,c}
<i>Yucca potosina</i>	0.46 ± 0.02 ^{b,c}
<i>Yucca queretaroensis</i>	0.47 ± 0.03 ^{b,c}
<i>Coryphanta clavata</i>	0.50 ± 0 ^{b,c}
<i>Ferocactus latispinus</i> (yellow)	0.76 ± 0.08 ^a
<i>Ferocactus latispinus</i> (red)	0.75 ± 0.03 ^a
<i>Mammillaria compressa</i>	0.73 ± 0.02 ^a

Average RLG (based on five replicates) for each species are shown. Significant differences ($P < 0.0001$) among species are indicated by different lowercase letters.

**Figure 1:** effect of seed mass on RLG ($R = -0.80$, $P < 0.05$) of 13 species from the Chihuahuan Desert.

Seeds can use light to detect if they are close to the soil surface, this is especially important in the case of small-seeded species, because small seeds have limited resources and these seedlings could not emerge successfully if they germinate too deep in the soil (Fenner and Thompson 2005; Pons 2000). It has been suggested that light response and seed mass coevolved as an adaptation to ensure germination of small-seeded species only when they are close enough to the soil surface as to be able to emerge (Milberg et al. 2000).

In our experiment, we found one adult-globose cactus species, *M. compressa*, and one adult-columnar species, *C. clavata*, to have small seeds and neutral fotoblasticism. However, analysing data from all species we found that with higher seed

mass there was a lower dependence to light for germination. Thus, our findings support the hypothesis that small seed mass and light requirements are coevolved as an adaptation to ensure germination (Milberg *et al.* 2000). Our results support findings that cacti seed requiring light are small (Flores *et al.* 2006, 2011; Maiti *et al.* 2003; Ortega-Baes *et al.* 2010), but they are not in agreement with Rojas-Aréchiga *et al.* (2013) findings of no evidence of a relationship between seed size and photoblastic response for cacti.

We found neutral photoblastism for cacti, this is in contrast to other studies that found positive photoblastism (See Flores *et al.* 2011 and references therein). Our results did not support the hypothesis that response to light is associated with common ancestors (Fenner and Thompson 2005) or the hypothesis that tall life-forms are neutral photoblastic and short life-forms are positive photoblastic (Rojas-Aréchiga *et al.* 1997), as we found short globose cacti to be neutral photoblastic.

Vázquez-Sánchez *et al.* (2012) recognized four adult growth-forms occurring in the tribe Cactaceae from the Cactaceae: (i) Globose, if stem has approximately the same length as its diameter; (ii) Globose-depressed, if stem diameter is higher than the length and the vertical axis is compressed; (iii) Cylindrical, if stem is <2 times higher in length than in diameter; (iv) Columnar, if stem growth is 2–5 times higher in length than in diameter. However, adult growth is not totally determined by seedling ‘growth-form’ in cacti. For instance, Sosa-Pivatto *et al.* (2014) found that some Argentinian cacti species that had globose seedlings were columnar at the adult stage, but all globose species had globose seedlings. In contrast, for the globose species *M. compressa* we found columnar seedlings (shape index 3.78) under darkness, and cylindrical seedlings (shape index 1.47) under light conditions. For the columnar cactus *C. clavata*, we found also columnar seedlings (shape index 6.04) under darkness, and cylindrical seedlings (shape index 1.97) under light conditions. Perhaps seeds from these species germinate in the dark because they produce columnar seedlings with the ability to emerge from greater soil depths and to reach the surface even if their seeds are small.

Positive photoblastism is one of the physiological characteristics that could favour the formation of seed bank in the soil (Bowers 2000). Perhaps neutral photoblastic species do not have the ability to form soil seed banks, because they can germinate in the dark. However, there are other environmental factors like temperature and available moisture that can enforce dormancy and thus help in creating seed banks for these species (Jurado and Flores 2005).

Following the seed germination percentage analyses, all species were neutral photoblastic, even if there were statistical differences between species. However, following the RLG analyses, the two varieties of *F. latispinus* and *M. compressa*, as well as *A. salmiana*, showed higher light dependence to germinate; the other 10 species (all of them from the Asparagaceae family) had low light dependence to germinate.

In conclusion, all succulent species, including adult-globose species, were neutral photoblastic but seed mass was an important factor because with higher seed mass there was a lower dependence to light. The adult-columnar species *C. clavata* and the adult-globose *M. compressa* were columnar at the seedling stage under darkness and cylindrical under light conditions. Thus, seeds from these species can germinate in the dark because they produce columnar seedlings with the ability to emerge from greater soil depths where there is no sunlight penetration. This is the first time that a globose cactus having small seeds is found to have columnar or cylindrical shape at the seedling stage.

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REFERENCES

- Baskin CC, Baskin JM (2014) *Seeds: Ecology, Biogeography, and Evolution of Dormancy and Germination*, 2nd edn. San Diego, CA: Academic Press.
- Bowers J (2000) Does *Ferocactus wislizeni* (Cactaceae) have a between-year seed bank? *J Arid Environ* **45**:197–205.
- de Villiers AJ, van Rooyen MW, Theron GK (2002) Germination strategies of Strandveld Succulent Karoo plant species for revegetation purposes: I. Temperature and light requirements. *Seed Sci Technol* **30**:17–33.
- Delgado-Sánchez P, Jiménez-Bremont JF, de la Luz Guerrero-González M, *et al.* (2013) Effect of fungi and light on seed germination of three *Opuntia* species from semiarid lands of central Mexico. *J Plant Res* **126**:643–9.
- Fenner M, Thompson K (2005) *The Ecology of Seeds*. Cambridge, UK: Cambridge University Press.
- Flores J, Arredondo A, Jurado E (2005) Comparative seed germination in species of *Turbinicarpus*: an endangered cacti genus. *Nat Area J* **25**:183–7.
- Flores J, Briones O (2001) Plant life-form and germination in a Mexican inter-tropical desert: effects of soil water potential and temperature. *J Arid Environ* **47**:485–97.
- Flores J, Jurado E (2003) Are nurse-protégé interactions more common among plants from arid environments? *J Veg Sci* **14**:911–6.
- Flores J, Jurado E, Arredondo A (2006) Effect of light on germination of seeds of Cactaceae from the Chihuahuan Desert, México. *Seed Sci Res* **16**:149–55.
- Flores J, Jurado E, Chapa-Vargas L, *et al.* (2011) Seeds photoblastism and its relationship with some plant traits in 136 cacti species. *Environ Exp Bot* **71**:79–88.

- Flores J, Jurado E, Jiménez-Bremont JF (2008) Breaking seed dormancy in specially protected *Turbinicarpus lophophoroides* and *Turbinicarpus pseudopectinatus* (Cactaceae). *Plant Spec Biol* **23**:43–6.
- Hernández HM, Godínez H (1994) Contribución al conocimiento de las cactáceas mexicanas amenazadas. *Acta Bot Mex* **26**:33–52.
- Hernández HM, Gómez-Hinostrosa C (2002) An integrated approach to the conservation of cacti in Mexico. In Maunder M, Clubbe C, Hankamer C, et al. (eds). *Plant Conservation in the Tropics*. Kew, UK: Royal Botanic Garden, 350–7.
- Irish G, Irish MF (2000) *Agaves, Yuccas, and Related Plants: A Gardener's Guide*. Portland, OR: Timber Press, Inc.
- Jiménez-Aguilar A, Flores J (2010) Effect of light on seed germination of succulent species from the southern Chihuahuan Desert: comparing germinability and relative light germination. *J Prof Assoc Cactus Dev* **12**:12–9.
- Jurado E, Flores J (2005) Is seed dormancy under environmental control or bound to plant traits? *J Veg Sci* **16**:559–64.
- Jurado E, Westoby M (1992) Germination biology of selected Central Australian plants. *Aust J Ecol* **17**:341–8.
- Khurana E, Singh JS (2001) Ecology of tree seed and seedlings: implications for tropical forest conservation and restoration. *Curr Sci* **80**:748–57.
- Magallán-Hernández F, Maruri-Aguilar B, Sánchez-Martínez E, et al. (2014) Consideraciones taxonómicas de *Yucca queretaroensis* Piña (Agavaceae), una especie endémica del semidesierto queretano-hidalguense. *Acta Bot Mex* **108**:51–66.
- Maiti RK, Singh VP, Baquie A, et al. (2003) *Cactus: Biology Propagation and Conservation*. Hisar, India: The Gaurav Society of Agricultural Research Information Centre.
- Milberg P, Andersson L, Thompson K (2000) Large-seeded species are less dependent on light for germination than small-seeded ones. *Seed Sci Res* **10**:99–104.
- Nobel PS (1988) *Environmental Biology of Agaves and Cacti*. Cambridge, UK: Cambridge University Press.
- Nobel PS (2010) *Desert Wisdom/Agaves and Cacti: CO₂, Water, Climate Change*. New York, NY: iUniverse, Inc.
- Ortega-Baes P, Aparicio-González M, Galíndez G, et al. (2010) Are cactus growth forms related to germination responses to light? A test using Echinopsis species. *Acta Oecologica* **36**:339–42.
- Pons TL (2000) Seed responses to light. In Fenner M (ed). *Seeds: The Ecology of Regeneration in Plant Communities*, 2nd edn. Wallingford, UK: CABI Publishing, 237–60.
- Pritchard HW, Miller AP (1995) The effects of constant temperatures, light and seed quality on the germination characteristics of *Agave americana*. *Bol Soc Bot Mex* **57**:11–14.
- Rojas-Aréchiga M, Mandujano MC, Golubov JK (2013) Seed size and photoblastism in species belonging to tribe Cacteeae (Cactaceae). *J Plant Res* **126**:373–86.
- Rojas-Aréchiga M, Orozco-Segovia A, Vázquez-Yanes C (1997) Effect of light on germination of seven species of cacti from the Zapotitlan Valley in Puebla, México. *J Arid Environ* **36**:571–8.
- Semarnat (2010) *Norma Oficial Mexicana NOM-059-ECOL-2010 Protección Ambiental—Especies nativas de México de flora y fauna silvestres—Categorías de riesgo y especificaciones para su inclusión, exclusión o cambio—Lista de especies en riesgo*. México City: Secretaría de Medio Ambiente y Recursos Naturales. Diario Oficial de la Federación.
- Sokal RR, Rohlf FJ (1994) *Biometry: The Principles and Practice of Statistics in Biological Research*. New York, NY: W.H. Freeman.
- Sosa-Pivatto M, Funes G, Ferreras AE, et al. (2014) Seed mass, germination and seedling traits for some central Argentinian cacti. *Seed Sci Res* **24**:71–7.
- Tester M, Morris C (1987) The penetration of light through soil. *Plant Cell Environ* **10**:281–6.
- Thompson K, Jalili A, Hodgson JG, et al. (2001) Seed size, shape and persistence in the soil in an Iranian flora. *Seed Sci Res* **11**:345–55.
- Vázquez-Sánchez M, Terrazas T, Arias S (2012) El hábito y la forma de crecimiento en la tribu Cacteeae (Cactaceae, Cactoideae). *Bot Sci* **90**:97–108.