The following article appeared in *Journal of the Professional Association for Cactus Development 12 (2010): 12-19;* and may be found at http://www.jpacd.org/

Effect of light on seed germination of succulent species from the southern Chihuahuan Desert: comparing germinability and relative light germination

Angélica Jiménez–Aguilar and Joel Flores*

División de Ciencias Ambientales, Instituto Potosino de Investigación Científica y Tecnológica,
Camino a la Presa de San José 2055, Apartado Postal 3–74, Tangamanga, CP 78210,
San Luis Potosí, San Luis Potosí, México

* Corresponding author: e–mail, joel@ipicyt.edu.mx

Received18th May, 2009; accepted 15th January, 2010

Abstract

Light requirements for cactus seed germination have been considered to be associated with their life–form, but this has not been thoroughly studied for other succulent species. In this study, we performed a light and darkness experiment in 11 species: seven rosette species (*Agavaceae*) and two columnar, one barriliform, and one globose species (*Cactaceae*) from the Southern Chihuahuan Desert. The response variables were seed germination percentage or germinability and relative light germination (RLG). Following germinability analyses, only the barriliform cacti *E. platyacanthus* was positive photoblastic. All other species were neutral photoblastic, although we found three response patterns: species having similar seed germination in light and darkness conditions, species showing higher seed germination in darkness than in light, and species showing higher germination in light than in darkness. However, following the relative light germination (RLG) analyses, two columnar species had higher RLG than the other species, seven species showed intermediate RLG (RLG 0.49–0.67), and two species had low RLG, which indicates that they germinated best in darkness. Our results do not support the suggestion that columnar cacti are neutral photoblastic and that globose cacti are positive photoblastic. We suggest that RLG is a better expression of the species' light requirement than seed germination percentage.

Key words: Agavaceae, Cactaceae, Chihuahuan Desert, photoblasticism, seed germination, succulent plants.

Introduction

In arid and semiarid environments, sandy soils can modify the photon fluxes and light quality [red (R):far–red (FR)] underground, according to the color and size of the sand grains and soil moisture (Tester and Morris, 1987; Gutterman, 1994); thus, light may trigger germination of desert plant seeds (Gutterman, 1993; Rojas–Aréchiga *et al.*, 1997; Flores *et al.*, 2006). It is possible that both light quantity and quality are signals that a seed can use to determine changes in soil depth or in plant cover, like species from other environments (Vázquez–Yañes and Orozco–Segovia, 1993).

There are three possible germination responses to light, following Baskin and Baskin (1998): i) species having an absolute light requirement (positive photoblasticism), ii) species germinating similar in both light and in darkness (neutral fotoblasticism), if the seeds germinate in higher % in light there are more light requiring seeds within that sample, but still can be classified as neutral photoblastic because certain considerable percentage germinated under darkness, and viceversa, and iii) species having absolute darkness requirement (negative photoblasticism).

For cacti species, which are very common in desert American environments, Rojas–Aréchiga *et al.* (1997) suggest that light requirements for seed germination can be associated with their life–form, since they found that columnar cacti *Cephalocereus chrysacanthus* (*Pilosocereus chrysacanthus*), *Neobuxbaumia tetetzo* and *Pachycereus hollianus* (*Lemaireocereus hollianus*) are neutral photoblastic, and the barriliforms *Ferocactus flavovirens*, *Ferocactus recurvus* and *Ferocactus robustus* are positive photoblastic. Both columnar and barriliform cacti are taller than globose cacti. Thus, it is possible that seedlings from the tallest life–forms (including rosette) have the ability to emerge from greater soil depths (in the dark) since their seeds have more resources.

Several results support the hypothesis that columnar cacti are neutral photoblastic (Nolasco *et al.*, 1996; Zimmer, 1998; Yang, 1999; Ramírez–Padilla and Valverde, 2005), and that both barriliform (Del Castillo, 1986; Romero–Schmidt *et al.*, 1992; Maiti *et al.*, 1994; Bowers, 2000) and globose cacti (Zimmer 1969a,1969b; Maiti *et al.*, 1994; Ruedas *et al.*, 2000, Benítez–Rodríguez *et al.*, 2004; Flores *et al.*, 2006; Rojas–Aréchiga *et al.*, 2008) are positive photoblastic. However, there are several columnar cacti exhibiting positive photoblasticism (Martínez–Holguín, 1983; Rojas–Aréchiga *et al.*; 2001, De la Barrera and Nobel, 2004).

Light requirements for seed germination of other succulent life–forms (e.g. rosette, shrub, herbaceous), have been poorly studied. *Agave* and *Yucca* (Agavaceae) are the main rosette genera in North American Deserts (Irish and Irish, 2000). *Agave lechuguilla* (Freeman, 1973), *A. parry* (Freeman, 1975), *A. macroacantha* (Arizaga and Ezcurra, 2002), *A. stricta* and *A. salmiana* (Maiti *et al.*, 2005) are neutral photoblastic, but *A. americana* is positive photoblastic (Pritchard and Miller, 1995). We found no research done on light effect on germination of *Yucca* spp. or other rosette species (*i.e. Crassulaceae* and *Euphorbiaceae* species). For succulent rosettes from *Agavaceae*, a germinative pattern in response to light has not been found, however the number of species studied is smaller than for *Cactaceae*. At least 94 cacti species have been studied (see Flores *et al.*, 2006 for a review) as well as six *Agavaceae* species (Freeman, 1973, 1975; Pritchard and Miller, 1995; Arizaga and Ezcurra, 2002; Maiti *et al.*, 2005).

In order to gain knowledge on the seed photosensitivity from desert species belonging to several succulent life–forms, we performed a light and darkness experiment in *Agavaceae* (seven rosette species) and *Cactaceae* (two columnar, one barriliform, and one globose species) from Southern Chihuahuan Desert. In order to better understand the expression of species' light requirement, two response variables were tested: germinability and relative light germination (RLG). RLG represents a range of values varying from 0 (germination only in darkness) to 1 (germination only in light), and it is relatively unaffected by dormancy level (Milberg *et al.*, 2000). This is very important since in the Chihuahuan Desert many species of cacti have dormant seeds (Flores *et al.*, 2005, 2006, 2008; Ochoa–Alfaro *et al.*, 2008).

Materials and methods

Study site

This study was carried out at the Ecology Lab of IPICYT in San Luis Potosí, S.L.P., México. We collected seeds of at least 10 individuals from each species. All studied species (Table 1) were from the highly diverse Chihuahuan Desert (Hernández and Gómez–Hinostrosa, 2002). Seeds were collected from mature fruits and stored in paper–bags at room temperature.

Table 1. List of species and their life–form and family.

Species	**Life form**	**Family**
Agave filifera Salm.	Rosette	*Agavaceae*
Agave lechuguilla Torr.	Rosette	*Agavaceae*
Agave salmiana Otto ex Salm	Rosette	*Agavaceae*
Agave striata Zucc.	Rosette	*Agavaceae*
Coryphanta delicata L.Bremer	Globose	*Cactaceae*
Echinocactus platyacanthus Link & Otto	Barriliform	*Cactaceae*
Myrtillocactus geometrizans (Mart. ex Pfeiff.) Console	Columnar	*Cactaceae*
Stenocereus queretaroensis (F.A.C.Weber) Buxb.	Columnar	*Cactaceae*
Yucca carnerosana (Trel.) McKelvey	Rosette	*Agavaceae*
Yucca elata (Engelm.)	Rosette	*Agavaceae*
Yucca filifera Chab.	Rosette	*Agavaceae*

We evaluated seed germination 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 filter paper for 30 days. There were five replicates per treatment, with 20 seeds in each replicate. For incubation in darkness, Petri dishes were wrapped in double aluminium foil (Baskin and Baskin, 1998). All dishes were placed in a germination chamber. To reduce temperature fluctuations, fluorescent lamps and air ventilation were used. A green safe light was used to examine the dark–incubated seeds (Baskin and Baskin, 1998; Schütz *et al.*, 2002). Seeds were watered daily with distilled water, and germination (radicle protrusion) was monitored daily. From these observations we determined final germination percentages or germinability (Flores and Briones, 2001; Flores *et al.*, 2005) and relative light germination (RLG) (Milberg *et al.*, 2000). The RLG = Gl / (Gd + Gl); where Gl = the germination percentage in light, and Gd = the germination percentage in darkness.

Statistical analysis

A two–way anova was conducted on the germination percentage using light (two levels) and species (11 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 test. We performed one way ANOVA for RLG, with species as the main factor. Differences among species were explored using Tukey multiple comparison test.

Results

Germinability or seed germination (%)

There was a significant effect of species (DF=10; F=29.27; p<0.0001) and light (DF=1; F=86.71; p<0.0001) treatments, as well as the interaction of both factors (DF=21; F=29.48; p<0.0001). All species had at least 63% germination in light, so they were not considered dormant (Table 2).

Only one species, the barriliform cacti *E. platyacanthus* was positive photoblastic, with nil seed germination in darkness. All other species were considered neutral photoblastic. For these we found three response patterns: i) species having similar seed germination in both light and darkness conditions, like the globose *C. delicata*, and the rosette species *A. filifera*, *A. striata*,*Y. carnerosana* and *Y. filifera* ii) species showing higher seed germination in darkness than in light, like *A.*

lechuguilla and *A. salmiana*, and iii) species showing higher germination in light than in darkness, like the columnar cacti *M. geometrizans* and *S. queretaroensis*), and the rosette *Yucca elata*.

Table 2. Seed germination of 11 species from the Chihuahuan Desert at 25°C after light and darkness treatments. Average final germination percentages or germinability (based on five replicates) for each species are shown. For each species, significant differences (p<0.001) between treatments are indicated by different lower–case letters.

Species	**Light**	**Darkness**	**Photoblastism**
	Germinability (%)		
Agave filifera	63 ± 16.4 a	64 ± 9.6 a	Neutral
Agave lechuguilla	65 ± 3.5 a	80 ± 17.0 b	Neutral
Agave salmiana	70 ± 23.2 a	94 ± 5.5 b	Neutral
Agave striata	96 ± 4.2 a	98 ± 4.5 a	Neutral
Coryphanta delicata	98 ± 4.5 a	97 ± 4.5 a	Neutral
Echinocactus platyacanthus	90 ± 7.9 a	0 b	Positive
Myrtillocactus geometrizans	81 ± 9.6 a	9 ± 14.7 b	Neutral
Stenocereus queretaroensis	88 ± 5.7 a	59 ± 29.5 b	Neutral
Yucca carnerosana	81 ± 9.6 a	79 ± 6.5 a	Neutral
Yucca elata	63 ± 22.8 a	29 ± 9.6 b	Neutral
Yucca filifera	88 ± 5.7 a	72 ± 19.2 a	Neutral

Relative Light Germination (RLG)

Species differed in terms of RLG (DF=10; F=22.3; p<0.0001; Table 3). Two columnar species had higher RLG than the other species. Seven species showed intermediate RLG (RLG 0.49–0.67), and two species had low RLG, which indicates that they had higher germination in darkness (*Agave lechuguilla*, RLG = 0.45; *Agave salmiana*, RLG = 0.42).

Table 3. Relative Light Germination (RLG) of 11 species from the Chihuahuan Desert at 25°C after light and darkness treatments. Average RLG (based on five replicates) for each species are shown. Significant differences (pP<0.0001) among species are indicated by different lower–case letters.

Species	**RLG**	**Category**
Agave filifera	0.49 ± 0.06 b	Intermediate
Agave lechuguilla	0.45 ± 0.06 c	Low
Agave salmiana	0.42 ± 0.09 c	Low
Agave striata	0.49 ± 0.02 b	Intermediate
Coryphanta delicata	0.50 ± 0.02 b	Intermediate
Echinocactus platyacanthus	1.00 ± 0.00 a	High
Myrtillocactus geometrizans	0.91 ± 0.13 a	High
Stenocereus queretaroensis	0.62 ± 0.14 b	Intermediate
Yucca carnerosana	0.51 ± 0.01 b	Intermediate
Yucca elata	0.67 ± 0.06 b	Intermediate
Yucca filifera	0.56 ± 0.07 b	Intermediate

Discussion

Following the seed germination analyses only one species was positive photoblastic (the barriliform *E. platyacanthus*), and seven rosette, one globose and two columnar species were neutral photoblastic. However, following the RLG analyses, *E. platyacanthus* and the columnar *S. queretaroensis* showed higher light dependence to germinate; five rosette, one columnar and one globose species had intermediate light dependence to germinate, and two rosette species had the lower light dependence. Thus, we suggest that RLG is a better expression of the species' light requirement than the seed germination percentage.

Our results do not support the suggestion that all columnar cacti are neutral photoblastic and that globose cacti are positive photoblastic (Rojas–Aréchiga *et al.*, 1997). In fact, *Coryphanta delicata* is the second globose species found to be neutral photoblastic with similar seed germination in both light and darkness conditions, after *Mammillaria kraehenbuehlii* (Flores–Martínez *et al.*, 2002).

There are several other globose species considered as neutral photoblastic, although showing higher germination in light than in darkness, *i.e. Coryphanta gladispina* (*C. delaetiana*), *Mammillaria potosiana* (*Coryphanta potosiana*), and *Mammillaria longimamma* (Zimmer, 1969b); *Mammillaria huitzilopochtli* (Flores–Martínez *et al.*, 2002); *Mammillaria magnimamma* (Ruedas *et al.* 2000) and *Turbinicarpus schmiedickeanus* ssp. *macrochele* (Flores *et al.*, 2006). In addition, *Euphorbia nicaeensis* (herbaceous succulent) is also neutral photoblastic (Narbona *et al.*, 2006); this species is similar in height to globose cacti. Thus, there seems to be no support for the hypothesis that tall life–forms are neutral photoblastic and small life–forms are positive photoblastic.

All rosette species were also neutral photoblastic. These results are similar to those found for *Agave lechuguilla* (Freeman, 1973), *Agave parry* (Freeman, 1975), *A. macroacantha* (Arizaga and Ezcurra, 2002), *A. salmiana* and *A. stricta* (Maiti *et al.*, 2005). However, we found three response patterns to light conditions: four rosette species had similar seed germination in both light and darkness conditions, two species had higher seed germination in darkness than in light, and one species showed higher germination in light than in darkness.

In this study germination was checked under green safe light. Because this light may trigger germination (Baskin and Baskin 1988) in some species, it is possible that green safe light triggered darkness germination in some of the studied species that probably are highly sensitive to light.

Light requirement for germination is important, because positive photoblastism is one of the physiological characteristics that could favour formation of a soil seed bank (Bowers, 2000; Rojas–Aréchiga and Batis, 2001). Thus, it is probable that neutral photoblastic species don´t have the ability to form soil seed banks, since they can germinate in the dark. However, there are other environmental factors (*i.e.* droughts and frosts) that can enforce dormancy and thus help in creating seed banks for these species (Jurado and Flores, 2005).

More studies are needed before understanding the implications of photoblastism in seeds from succulent species. These results contribute to understanding the germination biology of cactus and agave species, and could enhance the propagation of large numbers of cultivated individuals outside their habitats, promoting *ex situ* conservation.

Acknowledgements

We wish to thank Carlos Sandoval for seed collection. The results of this paper were obtained from experiments made during the Conservation Biology course of postgraduate studies by Angélica Jiménez–Aguilar. Financial support was obtained from SEMARNAT (S–3406).

References

Arizaga, S. and E. Ezcurra. 2002. Propagation mechanisms in *Agave macroacantha* (Agavaceae), a tropical arid–land succulente rosette. American Journal of Botany 89: 632–641.

Baskin, C.C. and J.M. Baskin. 1998. Seeds: Ecology, Biogeography, and Evolution of Dormancy and Germination. San Diego, Academic Press.

Bowers, J. 2000. Does *Ferocactus wislizeni* (Cactaceae) have a between–year seed bank? Journal of Arid Environments 45: 197–205.

De la Barrera, E. and P.S. Nobel. 2003. Physiological ecology of seed germination for the columnar cactus *Stenocereus queretaroensis*. Journal of Arid Environments 53: 297–306.

Del Castillo, R. 1986. Semillas, germinación y establecimiento de *Ferocactus histrix*. Cactáceas y Suculentas Mexicanas 31: 5–11.

Flores, J. and O. Briones. 2001. Plant life–form and germination in a Mexican inter–tropical desert: effects of soil water potential and temperature. Journal of Arid Environments 47: 485–497.

Flores, J., A. Arredondo and E. Jurado. 2005. Comparative seed germination in species of *Turbinicarpus*: An endangered cacti genus. Natural Areas Journal 25: 183–187.

Flores, J., E. Jurado and A. Arredondo. 2006. Effect of light on germination of seeds of Cactaceae from the Chihuahuan Desert, México. Seed Science Research 16: 149–155.

Flores, J., E. Jurado and J.F. Jiménez–Bremont. 2008. Breaking seed dormancy in specially protected *Turbinicarpus lophophoroides* and *Turbinicarpus pseudopectinatus* (Cactaceae). Seed Science Research 16: 149–155.

Flores–Martínez, A., G.I. Manzanero–Medina, G.C. Martínez–Hernández and G.S. Pacheco–Vásquez. 2002. Aspectos sobre la ecología y reproducción de *Mammillaria kraehenbuehlii* (Krainz) Krainz en la Mixteca de Oaxaca, México. Cactáceas y Suculentas Mexicanas 47: 57–68.

Freeman, C.E. 1973. Some germination responses of lechuguilla (*Agave lechuguilla* Torr.). Southwestern Naturalist 18: 125–134.

Freeman, C.E. 1975. Germination responses of a New Mexico population of Parry agave (*Agave parryi* Englem. var. *parryi*.). Southwestern Naturalist 20: 69–74.

Gutterman, Y. 1993. Seed Germination in Desert Plants (Adaptations of Desert Organisms). Berlin, Springer–Verlag.

Gutterman, Y. 1994. Strategies of seed dispersal and germination in plants inhabiting deserts. Botanical Review 60: 373–425.

Hernández, H.M. and C. Gómez–Hinostrosa. 2002. An integrated approach to the conservation of cacti in Mexico. pp. 350–357. *In*: Maunder, M., C. Clubbe, C. Hankamer and M. Groves (Eds.) Plant Conservation in the Tropics. Kew, Royal Botanic Garden.

Irish, G. and M.F. Irish. 2000. Agaves, Yuccas, and Related Plants: A Gardener's Guide. Timber Press, Inc.

Jurado, E. and J. Flores. 2005. Is seed dormancy under environmental control or bound to plant traits? Journal of Vegetation Science 16: 559–564.

Maiti, R.K., J.L. Hernández–Piñero and M. Valdés–Marroquín. 1994. Seed ultrastructure and germination of some species of Cactaceae. Phyton – International Journal of Experimental Botany 55: 97–105.

Maiti, R.K., P. Wesche–Ebeling, E. Sánchez–Arreola and O.E. Ramírez–Bravo. 2005. Effect of different lights on germination and seedling growth of *Agave* species. Crop Research 30: 90–95.

Martínez–Holguín, E. 1983. Germinación de semillas de *Stenocereus griseus* (Haw) Buxbaum (Pitayo de mayo). Cactáceas y Suculentas Mexicanas, 28: 51–57.

Milberg, P., L. Andersson and K. Thompson. 2000. Large–seeded species are less dependent on light for germination than small–seeded ones. Seed Science Research 10: 99–104.

Narbona, E., P.L. Ortiz and M. Arista. 2006. Germination variability and the effect of various pre–treatment on germination in the perennial spurge *Euphorbia nicaeensis* All. Flora 201: 633–641

Nobel, P.S. 1988 Environmental Biology of Agaves and Cacti. Cambridge, Cambridge University Press.

Nolasco, H., F. Vega–Villasante, H.L. Romero–Schmidt and A. Díaz–Rondero. 1996. The effects of salinity, acidity, light and temperature on the germination of seeds of cardón (*Pachycereus pringlei* (S. Wats.) Britton & Rose, Cactaceae). Journal of Arid Environments 33: 87–94.

Ochoa–Alfaro, A.E., C.O. Silva–Ortega, A. Becerra–Flora, J. Flores–Rivas and J.F. Jiménez–Bremont. 2008. Effect of salt stress, proline, and polyamines on seed germination of *Opuntia streptacantha*. Journal of the Professional Association for Cactus Development 10: 56–70.

Pritchard, H.W. and A.P. Miller. 1995. The effects of constant temperatures, light and seed quality on the germination characteristics of *Agave americana*. Boletín de la Sociedad Botánica de México 57: 11–14.

Ramírez–Padilla, C.A. and T. Valverde. 2005. Germination responses of three co–generic cactus species (*Neobuxbaumia*) with differing degrees of rarity. Journal of Arid Environments 61: 333–343.

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. Orozco–Segovia and C. Vázquez–Yanes. 1997. Effect of light on germination of seven species of cacti from the Zapotitlán Valley in Puebla, México. Journal of Arid Environments 36: 571–578.

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., J. Golubov, O. Romero and M.C. Mandujano. 2008. Efecto de la luz y la temperatura en la germinación de dos especies de cactáceas en CITES I. Cactáceas y Suculentas Mexicanas 53: 51–57.

Romero–Schmidt, H.L., F. Vega–Villasante, H. Nolasco and C. Montaño. 1992. The effect of darkness, freezing, acidity and salinity on seed germination of *Ferocactus peninsulae* (Cactaceae). Journal of Arid Environments 23: 389–395.

Ruedas, M., T. Valverde and S. Castillo–Agüero. 2000. Respuesta germinativa y crecimiento de plántulas de *Mammillaria magnimamma* (Cactaceae) bajo diferentes condiciones ambientales. Boletín de la Sociedad Botánica de México 66: 25–35.

Schütz, W., P. Milberg and B.B. Lamont. 2002. Seed dormancy, after–ripening and light requirements of four annual Asteraceae in Southwestern Australia. Annals of Botany 90: 707–714.

Sokal, R.R. and F.J. Rohlf. 1994. Biometry: The Principles and Practice of Statistics in Biological Research. New York, W.H. Freeman.

Tester, M. and C. Morris. 1987. The penetration of light through soil. Plant, Cell and Environment 10: 281–286.

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.

Yang, X–Y., H.W. Pritchard and H. Nolasco. 2003. Effects of temperature in seed germination in six species of Mexican Cactaceae. pp. 575–588. *In*: Smith, R.D., J.B. Dickie, S.H. Linington, H.W. Pritchard and R.J. Probert (Eds.). Seed Conservation: Turning Science Into Practice. Kew: Royal Botanic Gardens, Kew.

Zimmer, K. 1969a. Über die keimung von kakteensamen (III). Die bedeutung des lichtes. Kakteen und Andere Sukkulenten 20: 144–147.

Zimmer, K. 1969b. Über die keimung von kakteensamen (Schluβ). Bedeutung des lichts und zusammenfassung. Kakteen und Andere Sukkulenten 20: 178–180.

Zimmer, K. 1998. Zur keimung von kakteensaatgut. Schumannia 2: 75–84.